

Function and Functional Groupings of the Complex Mouth Apparatus of the Squat Lobsters *Munida sarsi* Huus and *M. tenuimana* G.O. Sars (Crustacea: Decapoda)

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Abstract. Like all other decapods, the anomuran squat lobsters *Munida sarsi* and *M. tenuimana* have a mouth apparatus composed of six pairs of mouthparts plus labrum and paragnaths (upper and lower lips). To study the functional significance of this complexity, we examined the mouthparts with scanning electron microscopy and also observed their function directly, under laboratory conditions, using macro-video equipment. No differences were found between the two species. The movement patterns of the mouthparts are described in detail and illustrated as serial drawings. Proceeding from maxillipeds 3 towards the mandibles, the movement pattern gets increasingly stereotypical, with the mandibles performing but a single movement in a medio-lateral plane. From morphology, the mouthparts are subdivided into 20 parts, but from the functional analyses the 20 parts form 8 functional groups: 1, *transporting mouthparts* (maxilliped 2 endopod and maxilliped 3 endopod); 2, *transporting-aligning mouthparts* (maxilliped 1 basis); 3, *sorting-aligning mouthparts* (maxilla 1 basis and maxilla 2 basis); 4, *current-generating mouthparts* (flagella of maxilliped 2 and maxilliped 3 exopods); 5, *cutting-crushing mouthparts* (incisor and molar processes, labium, and mandibular palp); 6, *ingesting mouthparts* (maxilla 1 coxa, maxilla 2 coxa, and maxilliped 1 coxa); 7, *respiratory mouth-*

parts (scaphognathite, maxilliped 1 epipod, and maxilliped 2 and maxilliped 3 exopods); and 8, *dorso-ventral mouthparts* (maxilla 1 endopod, maxilla 2 endopod, maxilliped 1 endopod, and maxilliped 1 exopod). These groupings apply mostly to the processes of food handling and have little significance with respect to grooming. When comparing our results to the literature on other decapods, we found much resemblance to conditions in other anomurans.

Introduction

One of the most interesting features among crustaceans is their very complex mouth apparatus. The basic limb-pattern for Eucrustacea (the condition in the stem species to all recent Crustacea) was a labrum, paired paragnaths, and two pairs of mouthparts (mandibles and maxillae 1), followed by a large number of more-or-less similar limbs (Walossek, 1998). Extant members of the Cephalocarida retain this system, but almost all other recent species have at least three pairs of mouthparts, *i.e.*, mandibles (Md), maxillae 1 (Mx1), and maxillae 2 (Mx2). Further specialization of the mouth apparatus is a very significant event in most crustacean lineages and often involves the specialization of thoracic limbs for food manipulation. This is especially so in the Decapoda, which has the first three pairs of thoracic appendages, the maxillipeds (Mxp1-3), specialized into feeding appendages. In many of these decapods, the feeding apparatus is even more advanced since one or more of the pairs of pereopods, especially if chelate, take part in food manipulation. This complexity has without doubt played an important role in the success of the Decapoda, since it enables the members of the order to feed on such a great diversity of food objects (Schembri, 1982c; Cartes, 1993).

Received 2 February 2000; accepted 12 January 2001.

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Abbreviations: Lb, labrum; Inc, incisor process; Mp, molar process; Mdp, mandibular palp; Mx1 cox, maxilla 1 coxa; Mx1 bas, maxilla 1 basis; Mx1 endo, maxilla 1 endopod; Mx2 cox, maxilla 2 coxa; Mx2 bas, maxilla 2 basis; Mx2 endo, maxilla 2 endopod; Scapho, scaphognathite; Mxp1 cox, maxilliped 1 coxa; Mxp1 bas, maxilliped 1 basis; Mxp1 endo, maxilliped 1 endopod; Mxp1 exo, maxilliped 1 exopod; Mxp1 epi, maxilliped 1 epipod; Mxp2 endo, maxilliped 2 endopod; Mxp2 exo, maxilliped 2 exopod; Mxp3 endo, maxilliped 3 endopod; Mxp3 exo, maxilliped 3 exopod.

Unfortunately, we have but little understanding of the functional significance of this very complex feeding apparatus found in decapods, which on each side consists of at least 20 parts, each with their separate functions. Earlier functional studies of the decapod mouth apparatus have resulted in a division into inner mouthparts (Md, Mx1, Mx2, and Mxp1) and outer mouthparts (Mxp2 and Mxp3) (Nicol, 1932; Kunze and Anderson, 1979; Schembri, 1982a). This division is based on morphology, but is often used in ways that indicate similar functions within the groupings. Many of the studies have concentrated mostly on Mxp3, the largest of the mouthparts, but again many of the functional interpretations are based on morphology alone (*e.g.*, Greenwood, 1972; Farmer, 1974; Suthers and Anderson, 1981; Suthers, 1984; Lavalli and Factor, 1992). Grooming of the anterior part of the body using Mxp3 is well documented, and functional similarities are found throughout the Decapoda (Bauer, 1981, 1989). We know much less about the functions of Mx1, Mx2, and Mxp1. The small size and fast movements of these appendages impede any detailed observation, and in many decapods they are also hidden behind the larger Mxp2 and Mxp3. Recording mouthpart movements with macro-video equipment overcomes the first two problems (Stamhuis *et al.*, 1998); studying anomurans solves the last, since most are bottom dwellers with a rather open mouth apparatus, and pagurids in particular have received a lot of attention. At the gross level, anomurans have quite similar mouthparts, and the similarity with respect to Md, Mx1, Mx2, and Mxp1 is particularly striking (Pike, 1947; Roberts, 1968; Kunze and Anderson, 1979; Schembri, 1982a). The Anomura is accordingly an especially suitable taxon for studying mouthpart function, both from an experimental point of view and because it offers a chance to evaluate to what extent similar morphology implies similar function.

In a scanning electron microscopy (SEM) study of the morphology of mouthparts in the anomuran species *Munida sarsi*, we offered some provisional interpretations of their function (Garm and Høeg, 2000). In the present study we present detailed video-based evidence of mouthpart functions in this species and in *M. tenuimana*, with particular attention to the roles of Mx1, Mx2, and Mxp1.

Materials and Methods

Video-recordings

Seventy specimens of *Munida sarsi* with carapace lengths between 7 mm and 28 mm were caught with a Sneli dredge at the Faeroe Bank (08°44'08" E, 61°24'46" N) at depths between 330 and 345 m in water with a temperature of 7°C. Six specimens of *M. tenuimana* were caught with a triangular dredge northeast of the Faeroe Bank (09°28'95" E, 61°25'52" N) at depths between 690 and 715 m in water with a temperature of 4°C. Both species were caught in

August 1998. The animals were kept alive at the Kaldbak Laboratory in 1000-l tanks with running natural seawater, keeping the temperature at 10°C. The animals were fed with other animals from the catch areas, but also with animal and algal tissue from shallow waters.

Video-recording took place in 50-l tanks under the same conditions with four kinds of sediment: two kinds of mud-gravel from the areas of the catches (many foraminiferans at 330-345 m); mud from shallow water (very rich in organic material); and shell-gravel (low in organic material). The recordings were made from outside the tank by a color (Y/C) CCD camera with a Micronikkor 105-mm lens, which enabled us to record structures 5 µm wide. Recordings were made on super VHS, and light was obtained from a 120-W spotlight. Comparison of our videos with *in situ* recordings of *M. sarsi* made by a submersible shows that *M. sarsi* behaved naturally in the tanks. To trace the movement patterns of the mouthparts, we analyzed video sequences on computer using the MS DOS version of Sigmascan. Representative shots of the mouthpart movements were grabbed with a time resolution of 0.02 s (50 fields/s) and imported into Corel PhotoPaint 8.0, with a resolution of 786×564 pixels (Fig. 1). We outlined the involved mouthparts and used the outlines for serial drawings. These drawings therefore accurately reflect the positions of mouthparts in the video sequences. For the analyses of the respiratory movements, the right branchiostegite of four individuals was dissected to get a clear view of the structures involved. All four animals behaved normally afterwards, although they only survived for a further 3-4 days.

Light and scanning electron microscopy

Specimens of *Munida sarsi* and *M. tenuimana* that had been fixed in 2% formalin were obtained from The BIOFAR I project at the Faeroe Islands (Station 070, 61°24'69" N, 08°43'97" E and Station 314, 60°51'8X" N, 10°14'0X" E, Norrevang *et al.*, 1994). Adult males and females with a carapace length between 17 mm and 28 mm were used. The mouthparts were cleaned by ultrasound and manually with a beaverhair brush. A standard dissection microscope was used for the drawings (Fig. 2). SEM preparation followed Felgenhauer (1987), except that osmium was not used. The photographs were taken on a JEOL 840 scanning electron microscope and were stored electronically using the JEOL program SemAfore 3.0. They were processed and manipulated in CorelDraw 8.0.

Abbreviations of mouthpart subdivisions

Labrum (Lb), mandibular incisor (Inc) and molar process (Mp), mandibular palp (Mdp), maxilla 1 coxa (Mx1 cox), maxilla 1 basis (Mx1 bas), maxilla 1 endopod (Mx1 endo), maxilla 2 coxa (Mx2 cox), maxilla 2 basis (Mx2 bas), maxilla 2 endopod (Mx2 endo), scaphognathite (Scapho).

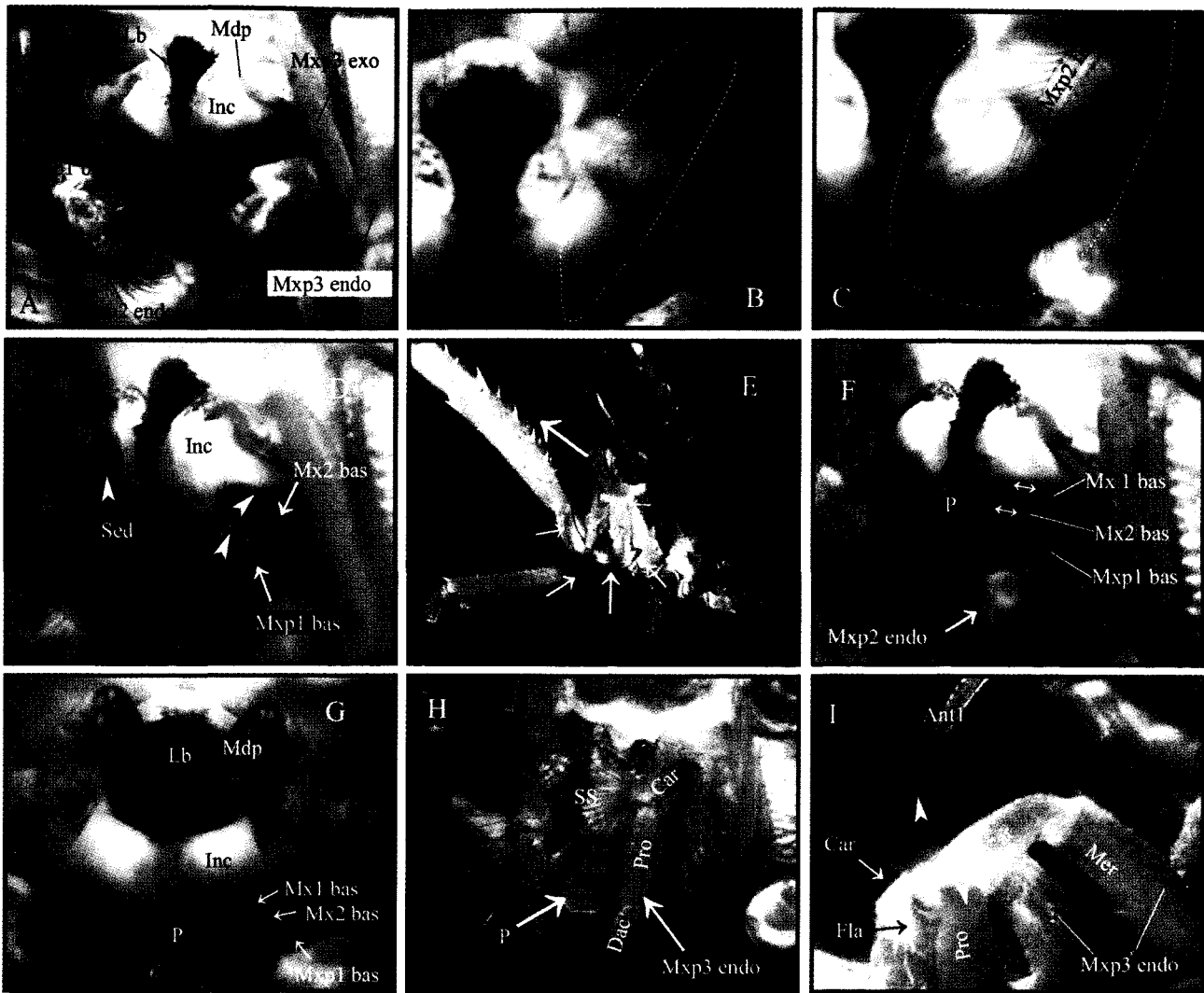


Figure 1. Frame-grabbed video images of *Munida sarsi*. (A) Overview of buccal area in resting position. (B) Flagellum of Mxp2 exopod in resting position. Dotted line outlines flagellum. (C) Flagellum from B spread out when moving antero-dorsally. Dotted line outlines flagellum. (D) Sediment sorting by Mx2 basis and Mxp1 basis. (E) *M. sarsi* on muddy sediment. Arrows indicate flagella currents. Size of arrows indicate strength of current measured as relative velocity of suspended particles. (F) Holding a small prey item with Mx1 basis and Mx2 basis. (G) Biting by incisor processes. Mandibular palps and Lb are raised and incisor processes overlap with left on dorsal side. (H) Mxp3 endopods hold large prey; setal screen prevents prey items from escaping anteriorly. (I) Flagellum of Ant1 is groomed by setae distally on carpus of Mxp3 endopod. Arrowheads indicate direction of movements. Ant1 = antenna 1, Bas = basis, Car = carpus, Dac = dactylus, Endo = endopod, Exo = exopod, Fla = flagellum, Inc = incisor process, Lb = labrum, Mer = merus, Mdp = mandibular palp, Mx1 = maxilla 1, Mx2 = maxilla 2, Mxp1 = maxilliped 1, Mxp2 = maxilliped 2, Mxp3 = maxilliped 3, P = prey item, Pro = propodus, Sed = sediment, SS = setal screen.

maxilliped 1 coxa (Mxp1 cox), maxilliped 1 basis (Mxp1 bas), maxilliped 1 endopod (Mxp1 endo), maxilliped 1 exopod (Mxp1 exo), maxilliped 1 epipod (Mxp1 epi), maxilliped 2 endopod (Mxp2 endo), maxilliped 2 exopod (Mxp2 exo), maxilliped 3 endopod (Mxp3 endo), maxilliped 3 exopod (Mxp3 exo).

Results

Munida sarsi and *M. tenuimana* have very similar mouthparts, which differ only in details of setation (unpubl. re-

sults). Similarly, from the video-recordings we found no differences in feeding behavior between the two species, and the results presented below therefore apply to both species referred to hereafter as *Munida*.

The mouthparts have a wide variety of functions, including food manipulation, ingestion, water current generation, and grooming (Table 1), and the patterns of movement are often complex. When the endopods of Mxp2 and Mxp3 handle large prey items, the movements and structures

involved largely depend on the size and shape of the prey. This changes with every situation, though some generalizations can still be made. Other movement patterns are much more stereotypical, especially those performed by Md,

Mx1, Mx2, and Mxp1 when handling small prey items, and we will principally focus on these latter functions. Duration or frequency for the stereotypical movements are listed in Table 1 and illustrated in Figures 3 to 13.

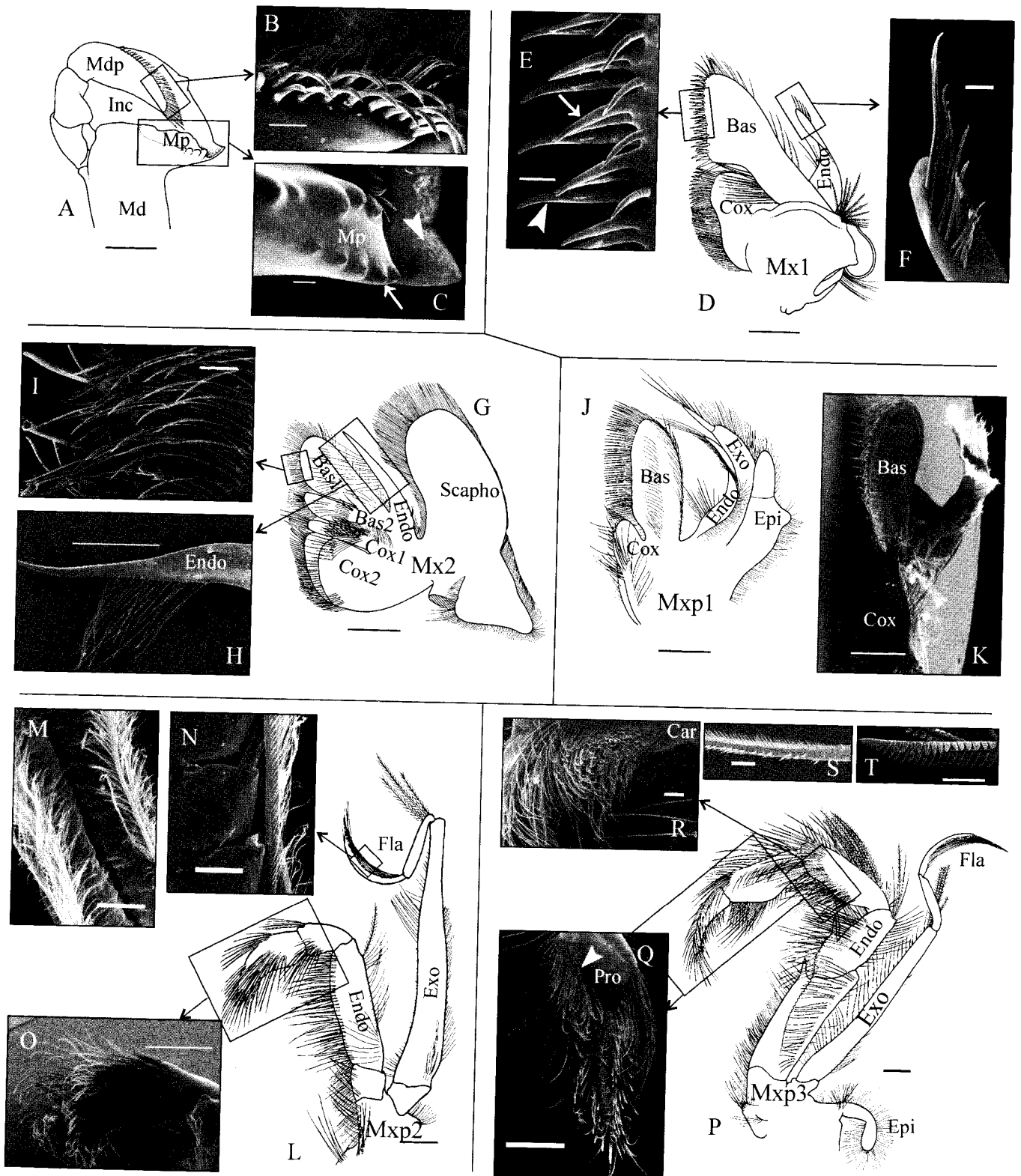


Table 1

Behavioral processes and the structures involved

| Behavioral process | Structures involved ¹ | Duration (s) ² | Frequency (Hz) ² |
|---|---|---------------------------|-----------------------------|
| 1. Current generation | Mxp2 fla, Mxp3 fla | | 15.2 ± 1.6 |
| 2. Prey gathering | Mxp3 endo, P1 | Variable | |
| 3. Sediment gathering | Mxp3 endo, P1-P4 | Variable | |
| 4. Transfer sediment to inner mouthparts | Mxp2 endo, Mxp3 endo | Variable | |
| 5. Sediment sorting/Particle rejection ³ | Mx1 bas, Mx2 bas, Mxp1 bas | | 3.26 ± 0.28 |
| 6. Rejection of large prey | Mxp2 endo, Mxp3 endo | Variable | |
| 7. Rotating particle (transverse plan) ³ | Mx1 bas, Mx2 bas (Mxp1 bas ⁴) | | 3.21 ± 0.08 |
| 8. Rotating particle (medial plan) ³ | Mx1 bas, Mx2 bas (Mxp1 bas ⁴) | | 3.18 ± 0.27 |
| 9. Put prey between mandibles | Mxp1 bas, Mxp2 endo ⁵ | Variable | |
| 10. Biting soft prey | Inc, Mx1 bas | 1.20 ± 0.15 | |
| 11. Biting calcified prey | Inc, Mx1 bas | Variable | |
| 12. Crushing very calcified prey | Mp | Variable | |
| 13. Transfer prey to mouth | Lb, Mdp | Variable | |
| 14. Ingestion ⁶ | Mx1 cox, Mx2 cox, Mxp1 cox | Not observed | |
| 15. Grooming of Ant1 | Mxp3 endo (car) | 1.77 ± 0.48 | |
| 16. Grooming of Ant2 | Mxp3 endo (pro) | 2.28 ± 0.34 | |
| 17. Respiration ⁷ | Mx2 scapho | | 2.6 ± 0.1 |

¹ Bas = basis, Car = carpus, Cox = coxa, Endo = endopod, Fla = flagellum, Inc = incisor process, Lb = labrum, Mdp = mandibular palp, Mp = molar process, Mx1 = maxilla 1, Mx2 = maxilla 2, Mxp1 = maxilliped 1, Mxp2 = maxilliped 2, Mxp3 = maxilliped 3, P1-4 = pereopod 1-4, Pro = propodus, Scapho = scaphognathite.

² Average ± standard deviation.

³ The movements are circular, and the frequency is for one round of movements.

⁴ Mxp1 bas are not directly involved, see text for details.

⁵ Mxp2 endo are used only for large prey items.

⁶ See Garm and Høeg (2000).

⁷ When not handling any prey. When handling prey, the frequency is higher, see 6, 8, 9.

Resting position and current generation

Figure 1A shows the position of the mouthparts when they are not handling food. Lb and mandibular palps are in ventro-posterior positions, and Md, Mx2, and Mxp1 are opened to only about one-third of their maximum. Mxp2 and Mxp3 are held laterally, with their endopods bent into a U-shape and the flagella on their exopods (Mxp2 exo and

Mxp3 exo) beating almost continuously in a dorso-ventral plane. This high-frequency beating generates a unidirectional current around the anterior end of the animal; the current proceeds from the sediment up through the mouthparts (Fig. 1E). During beating, the right Mxp2 flagellum is synchronized with the left Mxp3 flagellum and *vice versa*. The high frequency is correlated with the special morphol-

Figure 2. Morphology of the mouthparts. B, F, H, N, Q from *Munida tenuimana*, rest from *M. sarsi*. (A) Left Md seen postero-medially. (B) Setae on mandibular palp bending ventrally. (C) Mp with tubercles (arrow). Note large posterior tooth on incisor process (arrowhead). (D) Dorsal view of right Mx1. (E) Closeup of spines (arrow) and robust setae (arrowhead) on medial edge of Mx1 basis. (F) Cluster of setae on tip of Mx1 endopod. (G) Dorsal view of right Mx2. Scapho inserts asymmetrically on rest of Mx2. (H) Dorsal view of dissected Mx2 endopod. Long slender setae project medially. (I) Medial edge of Mx2 basis1 composed of rather fragile setae. (J) Dorsal view of right Mxp1. Note close contact between endopod and exopod. (K) Medial view of Mxp1. Mxp1 basis is curved blade shaped. (L) Medial view of Mxp2. Fla is in resting position. (M) Dorsal view of Mxp2 fla cuticle in resting position. (N) Medial view of Mxp2 fla cuticle in resting position. (O) Posterior view of shovel-shaped distal end of Mxp2 endopod. (P) Medial view of Mxp3. Fla is in upper most position. (Q) Posterior view of shovel-shaped distal end of Mxp3 endopod. Arrowhead indicate setal cluster on Pro used for grooming antenna 2. (R) Setal cluster on Car used for grooming antenna 1. (S) Weakly serrate seta from cluster used for grooming antenna 1. (T) Strongly serrate setae from cluster used for grooming antenna 2. Scalebars: A, D, H, G, J, K, L, O, P, Q = 1 mm; B, C, E, F, I, M, T = 100 µm; N = 50 µm; R = 200 µm; S = 20 µm. Bas = basis, Car = carpus, Cox = coxa, Endo = endopod, Epi = epipod, Exo = exopod, Fla = flagellum, Inc = incisor process, Md = mandible, Mdp = mandibular palp, Mp = molar process, Mx1 = maxilla 1, Mx2 = maxilla 2, Mxp1 = maxilliped 1, Mxp2 = maxilliped 2, Mxp3 = maxilliped 3, Pro = propodus, Scapho = scaphognathite.

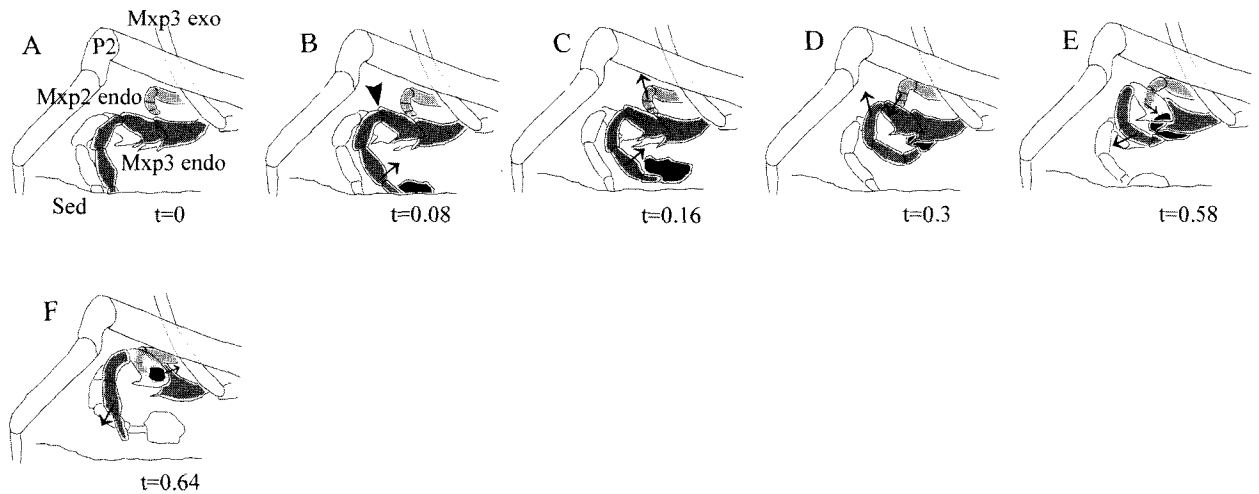


Figure 3. Sediment gathering by the endopods of Mxp3 (Mxp3 endo, dark gray), seen antero-laterally. (A) Both dactyli of Mxp3 endopod are in the sediment (Sed). (B-D) Left Mxp3 endopod moves dorso-posteriorly, lifting up a lump of Sed sticking to the setae, and endopod of left maxilliped 2 (Mxp2 endo, light gray) moves dorso-anteriorly to get in front of the lump. Arrowhead in B indicates flexible merus-carpus joint. (E) Left Mxp2 endopod moves posteriorly, combing through setae of Mxp3 endopod, picking up Sed with distal segments. (F) Mxp2 endopod moves further posteriorly, transferring Sed to Mxp1 bas (see Fig. 4). Note that now right Mxp3 endopod has picked up a lump of Sed. Mxp3 exo = exopod of maxilliped 3, P2 = pereopod 2, t = time in seconds (specific for series of pictures, not generalized).

ogy of the flagellar cuticle (Fig. 2M, N). When the flagellum is moving dorso-anteriorly, the water pressure causes the folded and flexible cuticle on the dorsal side of the flagellum to unfold. This raises the plumose setae into a fan, and this movement thus becomes the power stroke (Fig. 1C). During the ventro-posteriorly directed recovery stroke, the flagellar cuticle folds again, causing the setal fan to close (Fig. 1B). The flagellar current serves to reject small particles and gives the animal an opportunity to detect the composition of the sediment, since water is pumped up from close to the sediment and past the setae on the mouthparts (for details, see Garm and Høeg, 2000).

Food gathering

Most larger food particles are picked up by the long chelipeds and passed to the Mxp3 endopods, both of which extend to grasp the food between their dactyli and propodi. In some cases, the dactyli of the Mxp3 endopods can also pick up food objects directly from the sediment.

Sediment is gathered either with the dactyli of pereopods 2-4 (P2-4), the chelipeds (P1), or the dactyli of the Mxp3 endopods. In the first two cases, the sediment is passed on to the dactyli of the Mxp3 endopods as they comb through the setae that hold the sediment on the cheliped or P2-4.

When the Mxp3 endopods collect sediment, they start by pressing the dactylus and sometimes also the propodus into it (Fig. 3A). Thereafter the distal end of the endopod bends postero-dorso-medially (towards the mouth) and shovels up a lump of sediment (Fig. 3B-D). The great flexibility of the

endopod, especially in the merus-carpus joint (Fig. 3B, arrowhead; Fig. 4), greatly facilitates this process. The efficacy of the Mxp3 endopods in handling sediment is improved by a rim of strong, serrate setae along the distal end (Fig. 2P, Q); this enlarges the shovel, and the setae serve as hooks. The Mxp3 endopods usually pick up sediment from the area right under the flagella. The two Mxp3 endopods may move synchronously when gathering sediment, but they are normally used one at a time, as seen in Figure 3.

Handling large prey items

With respect to larger food items, the animals were not at all choosy and ate all kinds of animal tissue presented to them, even sponges (Porifera) and gorgonians (Gorgonacea). Such large food objects are grasped by the endopods of Mxp2 and Mxp3 (Fig. 1H) and pushed directly towards the mandibles. The Mxp3 endopods are bent into a U-shape and hold the prey between the meri and the propodi. The dactyli are held under the prey if it is not too large. The bases of Mx1 and Mx2 are fairly inactive and mostly press against the prey, while possibly making fine adjustments of the food item for the mandibles. When the mandibles cut into a large food item, the bases of Mxp1 often scrape very actively along the object in circles, as shown in Figure 5. If the prey is soft, such as a lump of fish meat, the movements of the Mxp1 bases tend to squeeze it so it will fit more easily between the incisor processes of the mandibles (Inc). On a few occasions, the animals were also observed attempting to

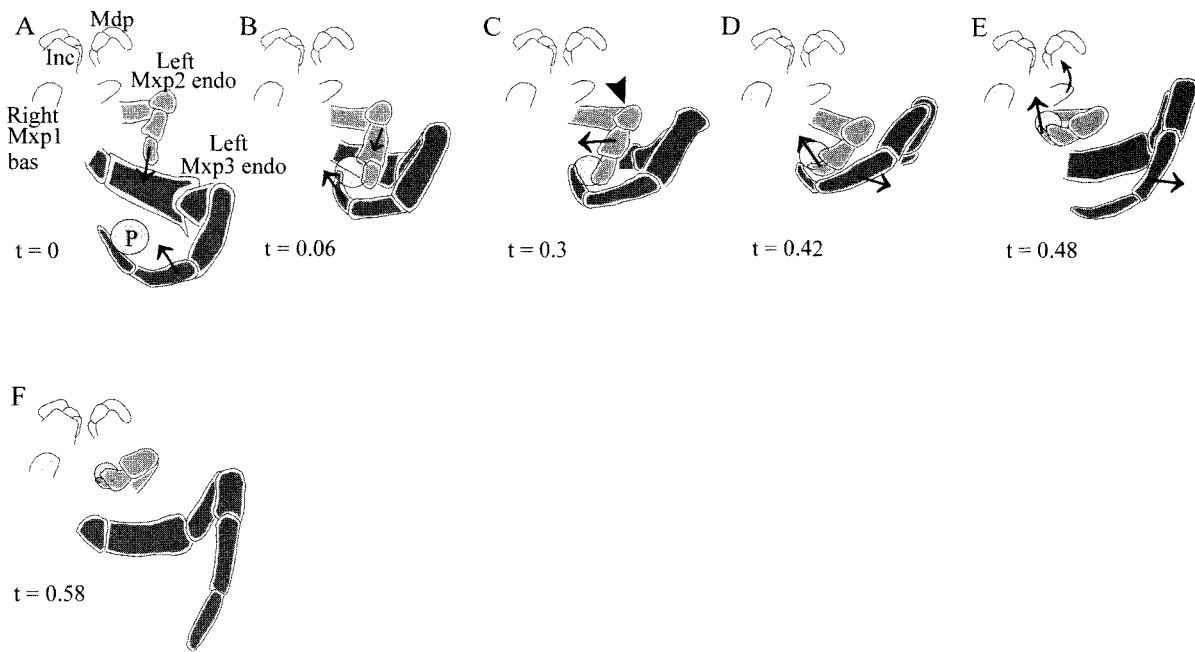


Figure 4. Transfer of particles (P) from endopod of maxilliped 3 (Mxp3 endo, dark gray) to the basis of maxilliped 1 (Mxp1 bas, light gray) seen ventro-anteriorly. Corresponds to D-F in Fig. 3. (A, B) Left Mxp3 endopod bends postero-medially. Endopod of left maxilliped 2 (Mxp2 endo, middle gray) moves ventrally towards Mxp3 endopod. (C, D) Mxp2 endopod moves posteriorly, with the setae on dactylus combing through the setae on the distal part of Mxp3 endopod. Arrowhead in C indicates flexible merus-carpus joint. (E, F) Mxp3 endopod moves antero-laterally; Mxp2 endopod moves posteriorly, with the distal part reaching the inner mouthparts. Left Mxp1 basis moves laterally to be able to collect P from Mxp2 endopod (see Fig. 5). Inc = incisor, Mdp = mandibular palp, t = time in seconds (specific for series of pictures, not generalized).

use the crista dentata on the ischium of Mxp3 endopods in a crablike manner. This would involve holding the prey between the incisor processes while both Mxp3 endopods move dorso-anteriorly, grasping the prey with the crista dentata while in the dorsal position, then lowering the Mxp3 endopods and thereby tearing the prey. However, this behavior was never observed to be successful in *Munida*, because the crista dentata never got hold of the prey items. Large objects are not rejected by the flagellar current, but are simply dropped or removed by Mxp2 endopods.

Handling small prey items

When carrying a small food item, the Mxp3 endopods bend postero-medially to meet the endopod of maxilliped 2 (Mxp2 endo) (Figs. 3, 4), which passes sediment and particles further towards the mouth, that is, to the bases of Mxp1.

When the Mxp3 endopod approaches the mouth, the collateral Mxp2 endopod moves first dorso-anteriorly to get in front of the food item held distally on the Mxp3 endopod (Fig. 3C) and thereafter ventro-posteriorly to shovel up the item (Figs. 3D-F, 4A-D). Holding the food with its distal end, the Mxp2 endopod bends further towards the mouth and reaches the area of the bases of Mxp1. Meanwhile the

collateral Mxp1 basis moves aside to make room for the food, and the Mxp3 endopod extends again (Fig. 4E, F). Most of the flexure of the Mxp2 endopod takes place in the merus-carpus joint (Fig. 4C, arrowhead), and the distal segments also form a shovel that enables them to carry the food (Fig. 2L, O). The serrate setae found distally on the Mxp2 endopod are less robust than those on the Mxp3 endopod, and therefore they can pass between the latter to collect the potential food. Like the Mxp3 endopods, the endopods of Mxp2 can be used at the same time—when one is moving anteriorly the other is moving posteriorly—but this is not the normal pattern.

The Mxp1 bases collect the particles from the Mxp2 endopod by making circular movements as shown in Figure 5, but in the opposite direction. Moving the curved and blade-shaped bases (Fig. 2J, K) medially when they reach the Mxp2 endopod and laterally when they meet the Mx2 bases ensures the direction of particle transport. Mx2 moves medially and grasps the prey.

Sediment sorting and particle rejection

Almost all collected particles eventually reach the Mx2 and Mx1 bases, which are the mouthparts responsible for rejecting or retaining food items. Figure 6 shows how the

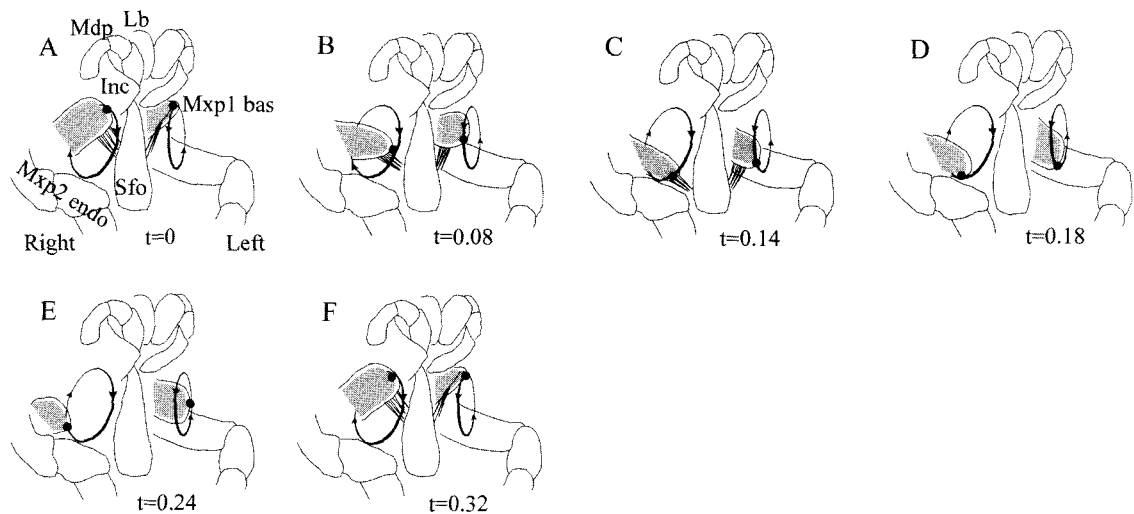


Figure 5. Movements of the bases of maxilliped 1 (Mxp1 bas, gray) seen antero-laterally. To simplify drawings, maxilla 1 and maxilla 2 are left out and setae are shown only when in contact with prey. The appendages make circular movements in an angle to plane of view indicated by ellipse; thin part of ellipse is towards the animal. Black dots indicate the positions of the limbs in the movement. This movement can shred small and soft food objects (Sfo) held by mandibles or move particles away from mandibles. Movement can be reversed, which will move particles from endopod of maxilliped 2 (Mxp2 endo) towards basis of Mx2. Inc = incisor process, Lb = labrum, Mdp = mandibular palp, t = time in seconds (specific for series of pictures, not generalized).

Mx1 and Mx2 bases move in circles parallel to the mandibular incisor (Inc) when sorting sediment. The direction of movement is dorso-anteriorly when they are in the medial position and ventro-posteriorly when they are in the lateral position. Thus, from the animal's point of view, the distal tips of the right-side appendages rotate clockwise, while those on the left side rotate counterclockwise. This ensures that the cuspidate setae on their medial edges hit the particles from the ventro-posterior and push them in a dorso-anterior direction. The Mx1 bases and the Mx2 bases move out of phase, ensuring that one of these appendage pairs remains in contact with the particle most of the time. The circular movements continue until the particle enters the flagellar current and is rejected anteriorly (Figs. 1D, 6), or until the animal decides to retain the particle. The Mx1 bases are responsible for most of the particle movement. The medial rims of the Mx1 bases have much more robust cuspidate setae than the Mx2 bases (Fig. 2E, I), and this allows them to press harder against the particles, obtaining a more firm hold. Within a specific pair (Mx1 bases or Mx2 bases), left and right sides are synchronized so they are in the medial position at the same time. The Mxp1 bases move as described under "Handling small prey items," providing more particles, pushing them towards the Mx2 bases, and ensuring that nothing is lost ventro-anteriorly (Fig. 6). During the sorting process, the Mxp2 endopods are held medially where they form a setal screen which also prevents particles from escaping ventro-anteriorly. When the animal

is handling large prey, the Mxp3 endopods provide a similar setal screen (Fig. 1H).

Particle rotation

When the animal finds a small particle worth eating, the Mx1 and Mx2 bases stop making circular movements and begin moving to and fro in the medio-lateral plane while keeping the particle in front of the incisor process (Fig. 1F). Again, the Mx1 and Mx2 bases move out of phase. If the particle is not orientated correctly for the Md, it will subsequently be rotated by the Mx1 and Mx2 bases (Figs. 7, 8).

During rotation of a particle in the transverse plane, the Mx2 and Mx1 bases again move out of phase and make circular movements parallel to the incisor process (Fig. 7). Unlike the situation during sediment sorting, all four mouthparts concerned (*i.e.*, both left- and right-side Mx2 bases and Mx1 bases) move either clockwise or counterclockwise. To turn a particle clockwise (as seen from the animal's point of view), the left-side Mx1 and Mx2 bases move dorso-anteriorly when in their medial position and ventro-posteriorly when in their lateral position, thereby pushing the left side of the particle dorso-anteriorly. In the medial position, the bases of the right-side Mx1 and Mx2 move in the opposite direction as the left-side bases; thus they push the right side of the particle ventro-posteriorly, and it is rotated in the transverse plane. The animal rotates the particle counterclockwise by reversing these movements.

Rotating a particle in the medial plane (Fig. 8) is always

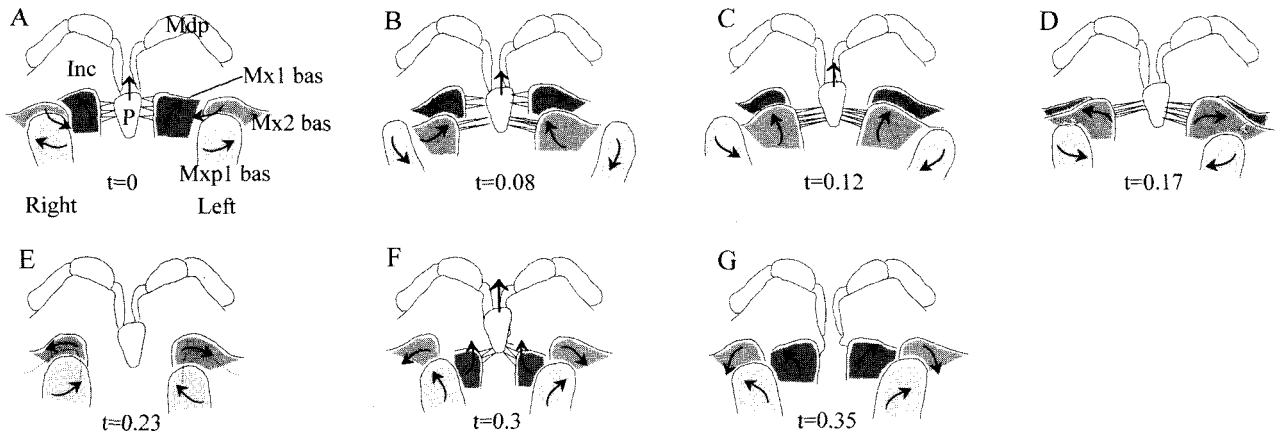


Figure 6. Rejection of unwanted particle (P) by bases of maxilla 1 (Mx1 bas, dark gray), maxilla 2 (Mx2 bas, middle gray), and maxilliped 1 (Mxp1 bas, light gray) seen ventro-anteriorly; setae are shown only when in contact with P. Arrows indicate direction of movements. (A) Mx1 basis in contact with P pushing dorso-anteriorly. (B, C) Mx2 basis gets in contact with P and pushes it dorso-anteriorly. Mx1 basis moves laterally and releases P. (D, E) Mx2 basis releases P. (F) P is pushed above mouthparts by Mx1 basis and enters the flagellar current. (G) P is rejected. During the rejection, Mxp1 basis is not in contact with P, but makes postero-anterior circles (see Fig. 5), probably ensuring that P is not lost anteriorly. Inc = incisor process, Mdp = mandibular palp, t = time in seconds (specific for series of pictures, not generalized).

done in one direction, with the part of the particle closest to the animal moving dorso-anteriorly and the part away from the animal moving ventro-posteriorly, that is, clockwise when seen from the animal's right side. The mouthparts of the left and right sides move in synchrony, as when rotating

particles in the transverse plane, but the distal tips of the Mx2 bases and the Mx1 bases now circle in opposite directions. The Mx1 bases move dorso-anteriorly when they are in the medial position and ventro-posteriorly when in the lateral position. They thereby hit the particle from a ventro-

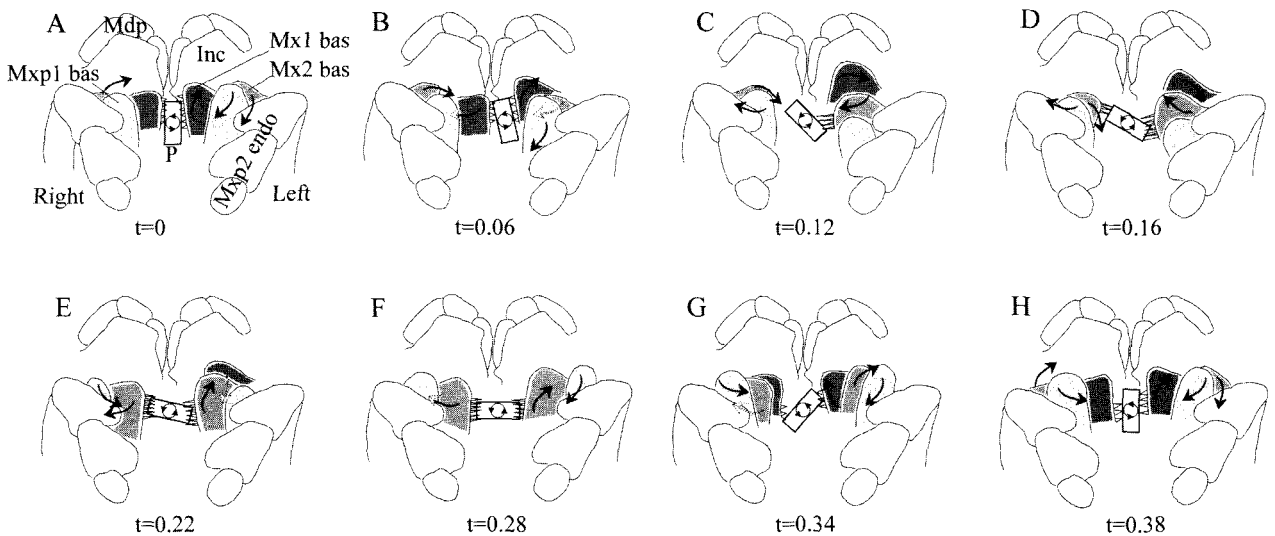


Figure 7. Rotation of a small particle (P) in a transverse plan by bases of maxilla 1 (Mx1 bas, dark gray) and maxilla 2 (Mx2 bas, middle gray). The view is ventro-anteriorly and setae are only shown when in contact with P. (A, B) P is held by Mx1 basis. Left Mx1 basis moves dorso-anteriorly; right Mx1 basis moves a little laterally. This starts the rotation. (C) Mx1 basis releases P; Mx2 basis gets in contact with P. (D-F) Mx2 basis in contact with P. Left moves dorso-anteriorly and right ventro-posteriorly, which rotates P further. (G) P is hit by left Mx1 basis from ventro-posterior and laterally by right Mx1. (H) Back in start position. During rotation the bases of maxilliped 1 (Mxp1 bas, light gray) are not in contact but tend to make antero-posteriorly circles (see Fig. 5), probably ensuring P is not lost anteriorly. Inc = incisor process, Mdp = mandibular palp, Mxp2 endo = endopod of maxilliped 2, t = time in seconds (specific for series of pictures, not generalized).

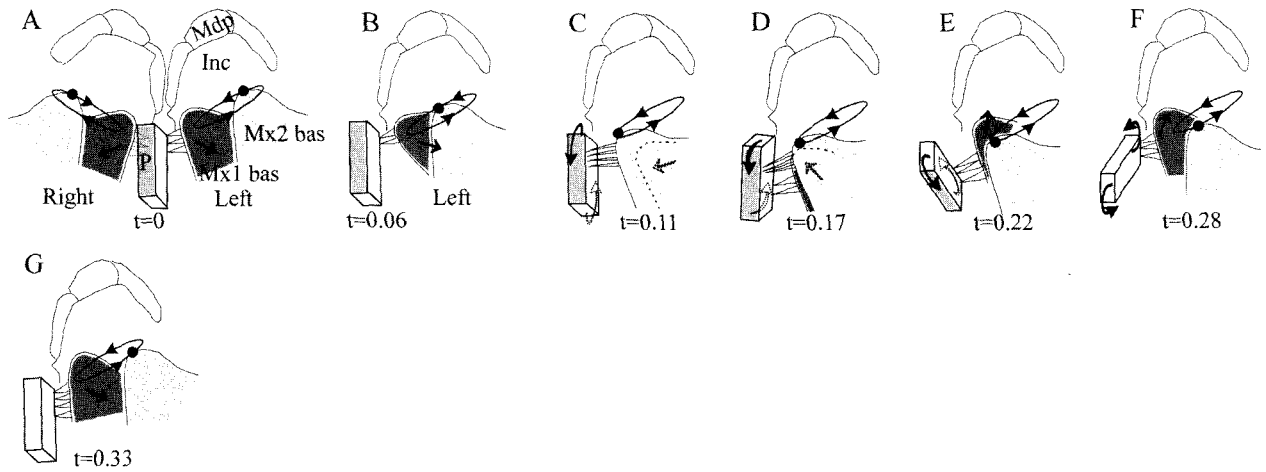


Figure 8. Rotation of a small particle (P) in a medial plan by the bases of maxilla 1 and maxilla 2 (Mx1 bas, dark gray and Mx2 bas, light gray). View is ventro-anterior. Only left side is shown in B-G, and setae are shown only when in contact with P. Right and left side move in synchrony and in phase. Arrows indicate direction of movements. Dotted line indicates hidden structure. Mx2 basis makes circular movements; black dots indicate the positions of the appendages in the circle. (A, B) Mx1 basis releases P. (C) Mx2 basis hits anterior edge of P from dorso-anterior, pushing it ventro-posteriorly. (D-F) Mx1 basis hits posterior edge of P from ventro-posterior, pushing it dorso-anteriorly. Mx2 basis releases P. (G) Mx2 basis moves laterally and up; Mx1 basis releases P. Process is ready to start again. Inc = incisor process, Mdp = mandibular palp, t = time in seconds (specific for series of pictures, not generalized).

posterior direction and push it dorso-anteriorly. When circling in the opposite direction, the Mx2 bases hit the particle from a dorso-anterior direction and push it ventro-posteriorly. This causes the particle to be rotated around a point between the bases of Mx1 and Mx2.

In both cases, the Mx1 bases are responsible for most of the rotation, and the animal has serrate and cuspidate setae in contact with the particle at all times. The Mxp1 bases tend to make circular movements that push the particle toward the Mx2 basis. Both during sediment sorting and when rotating a small particle, the Mx1, Mx2, and Mxp1 bases normally circle with the same frequency. The normal order of contact with the particle is Mx1 basis, Mx2 basis, Mxp1 basis, Mx1 basis, and so forth in a repeated way, as seen in Figure 6. However, the Mxp1 bases occasionally perform more complex movement patterns independent of the positions of the Mx1 and Mx2 bases, as indicated in Figure 7.

Cutting-crushing

Having orientated the particle correctly for maceration, the animal puts it between the mandibles (Fig. 9). At first, the mandibular incisors (Inc) move laterally while the labrum (Lb) and mandibular palps (Mdp) retract dorso-anteriorly to make room for the item (Fig. 9B). Subsequently, the Mxp1 bases (and possibly also the Mx1 and Mx2 bases) push the particle between the incisor processes, which move medially until they overlap about one-fifth, always with the right incisor process on the anterior side (Fig. 9C, D). A large posterior tooth on the left incisor process assures a good grip on the item (Fig. 2C,

arrowhead). Meanwhile the food particle is held tight by the robust spines and cuspidate setae on the medial rim of the Mx1 bases (Fig. 2E). If the particle is slim, the incisor process will not move laterally first, but will move medially directly from resting position, thereby performing the cut. After the cut, the incisor processes move laterally and the mandibular palps and Lb move ventro-posteriorly (Fig. 9E, F), pushing the cut-off piece of food towards the mouth, an action facilitated by serrate setae on the mandibular palps (Fig. 2B) and setule-like outgrowths on Lb. The rest of the particle is pushed ventro-anteriorly to be further processed by the Mx1 and Mx2 bases. The ingestion is handled by the coxae of Mx1 and Mx2 and perhaps Mxp1. This is not seen on the videos but extrapolated from the organization of the mouth apparatus. The three pairs of coxae are situated just ventral to the mouth and, along with their setae, they curve into the mouth opening (for details, see Garm and Høeg, 2000).

Prey too hard to cut with the incisor process, such as calciferous polychaete tubes, are instead crushed by the molar processes of the mandibles (Mp). The flattened shape and their rim of tubercles ensure that even very smooth objects such as mollusc shells will not easily slip away (Fig. 2C). The movements are identical to the cutting action (Fig. 9), except that the prey is placed between the molar processes posteriorly to the incisor processes and the process lasts longer.

Grooming the antennae

Grooming of both antenna 1 (Ant1) and antenna 2 (Ant2) is performed by the Mxp3 endopods, but by two different

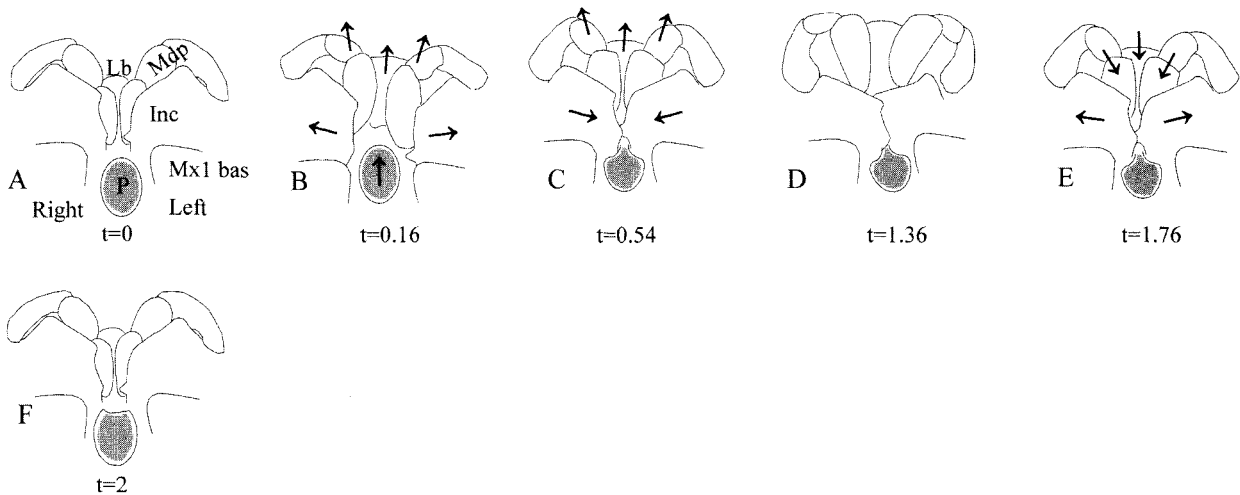


Figure 9. Cutting by mandibles seen ventro-anteriorly. (A) Resting position. Incisor processes (Inc) are a little opened; labrum (Lb) and mandibular palps (Mdp) are lowered. Prey (P) is held by bases of maxilla 1 (Mx1 bas). (B) Incisor processes move laterally; Lb and mandibular palps move anteriorly to make room for P. (C) Cut starts. Incisor processes move medially; Lb and mandibular palps move further anteriorly. (D) Incisor processes with maximum overlap, always left on dorsal side. Lb and mandibular palps in anteriormost position. (E) Cut ends. Incisor processes move laterally; Lb and mandibular palps move posteriorly and push the cut-off piece towards mouth. (F) Cut has ended; limbs back in resting position. During the cut, Mx1 are held medially to hold P. If P is small, stage B is skipped. t = time in seconds (specific for series of pictures, not generalized).

clusters of setae (Figs. 2P-R, 10, 11). The antennae are always groomed one at a time, and Ant1 are groomed much more frequently than Ant2. Grooming of an Ant1 starts with the appendage in question bending ventrally and both Mxp3

endopods moving dorsally (Fig. 10A). In the next step, Mxp3 endopods move medially and catch the peduncle of Ant1 with serrate setae on the carpi (Fig. 2R). With a loose grip, they move ventrally until they reach the flagellum of

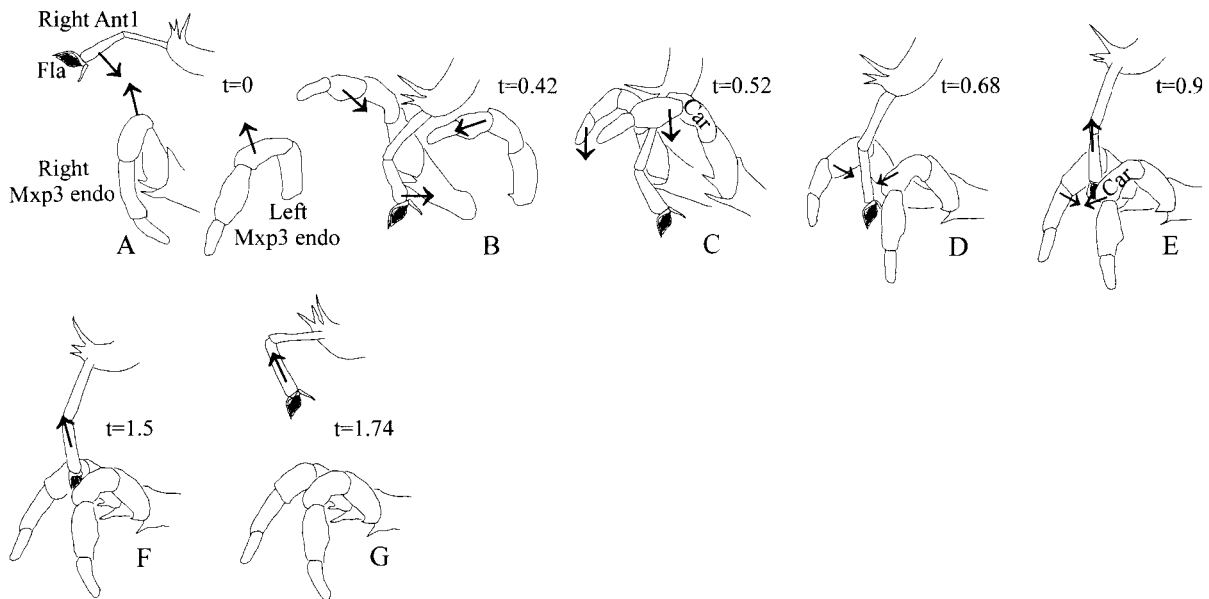


Figure 10. Grooming of antenna 1 (Ant 1) by endopods of maxilliped 3 (Mxp3 endo), seen antero-laterally. (A) Mxp3 endopods reach up while Ant1 bends down. (B) Mxp3 endopods move ventro-medially and Ant1 bends posteriorly. (C) Ant1 is caught by long setae distally on carpus (Car), which move along shaft of Ant1. (D) When the flagellum (Fla) is reached, Mxp3 endopods move further medially. (E-G) Mxp3 squeeze tight around Fla and aesthetascs are pulled through setae on Car. t = time in seconds (specific for series of pictures, not generalized).

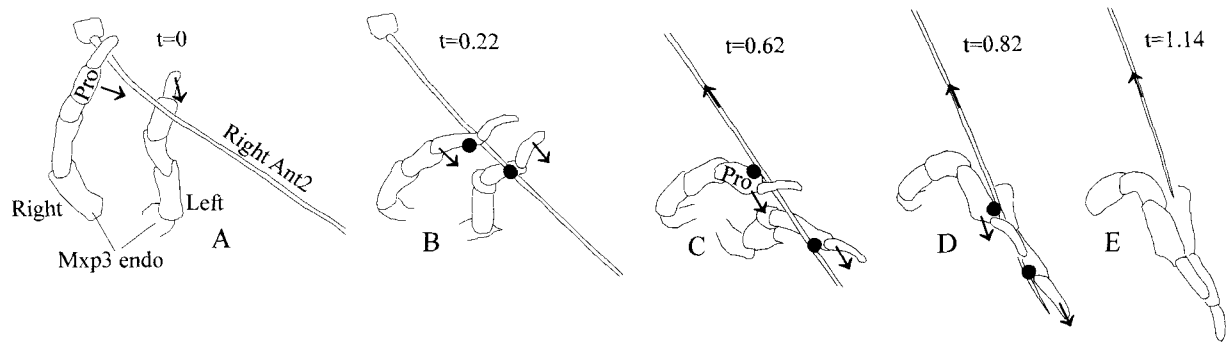


Figure 11. Grooming of right antenna 2 (Ant2) by endopod of maxilliped 3 (Mxp3 endo) seen ventro-anteriorly. The antenna is caught on right side and released on left. Arrows indicate direction of movements. Black dots indicate contact between Ant2 and propodus (Pro). (A) Mxp3 endopod has moved dorsally and right Ant2 has bent ventrally. Mxp3 endopod moves medially and catches Ant2 with long setae on distal part of Pro. (B) Mxp3 endopod moves downwards and Pro setae run along Ant2, grooming it. (C-E) Mxp3 endopod moves further down and Ant2 pulls itself up through setae distally on Pro. t = time in seconds (specific for series of pictures, not generalized).

Ant1 (Fig. 10B-D). Now the Mxp3 endopods move further medially, squeezing the Ant1 flagellum tightly between the carpi, and the flagellum is pulled through the serrate setae as the Ant1 moves dorsally (Figs. 11, 10E-G). Occasionally, the Mxp3 endopods move farther dorsally in the beginning of the process, reaching the eye situated just dorsal to Ant1. The eye is then groomed by setae on the dactyli and the propodi. The same setal clusters on the carpi also groom the Mxp2 and Mxp3 flagella, and the movements of the Mxp3 endopods are much the same.

Ant2 is also groomed by the Mxp3 endopods, but with setal clusters on the propodi instead of on the carpi (Figs. 2Q, T; 11). One of the Ant2 bends ventrally, and both Mxp3 endopods move dorsally and grasp the long flagellum of Ant2 between setal clusters distally on the propodi (Fig. 11A). When in contact with the flagellum, the Mxp3 endopods move ventro-anteriorly and Ant2 moves dorsally, pulling itself through the robust serrate setae (Fig. 11B-E). Ant2 grooming is an asymmetrical process: the appendage is grasped on the side of the animal where it is attached and subsequently released on the other side. Due to the twist of the movement, the two Mxp3 endopods move apart during the process and groom two different sites of Ant2 at a given time (Fig. 11C, D). This means that Mxp3 endopods cannot squeeze the Ant2 flagellum as tightly as when grooming the Ant1 flagellum.

The setal clusters grooming Ant1 and Ant2 are situated differently on the Mxp3 endopod and are composed of different types of serrate setae (Fig. 2S, T). Those grooming Ant2 are more stout and have much more robust denticles.

One curious observation concerned a specimen of *M. sarsi* that had lost both Mxp3 during sampling. It neither ate nor groomed Ant1, but it did groom Ant2 with the chelae.

Respiration

Beating of the scaphognathites (Scapho), also called gill bailers, produces the respiratory currents. The Scapho are situated laterally on Mx2 (Fig. 2G), which places them in the anterior part of the gill chambers. When an Mx2 basis executes medio-lateral movements, its Scapho moves ventro-dorsally (Fig. 12). The movements of the Scapho are comparable to swimming with flippers. Because it inserts on the Mx2 coxa with the less flexible posteriormost part, the flexible anterior part moves with a delay when compared to the posterior part. When the posterior part starts moving dorsally, the anterior part initially remains at rest, but after a while it follows until the entire Scapho reaches its dorsalmost position (Fig. 12A-E). During the ventral stroke, the movement is again initiated by the posterior part, followed, with some delay, by the anterior part (Fig. 12F-I). The delayed movements of the anterior part ensure that the respiratory current is unidirectional, with water entering the posterior part of the gill chamber and exiting anteriorly. We never observed the reversal of the respiratory current that Bauer (1981) described for other decapods.

When moving ventrally, the anterior part of the Scapho sweeps across the epipod of Mxp1 and the exopods of Mxp2 and Mxp3, and these structures help direct the exhalant current (Fig. 12G-I). The posterior part sweeps the two anteriormost pairs of gills.

Dorsoventral mouthparts

Four structures of the mouth apparatus have not yet been dealt with, since their activities are not clear. These structures, which constitute the dorso-lateral part of the mouth apparatus, are the endopods of Mx1, Mx2, and Mxp1, and the exopod of Mxp1. When the Mx1 and Mx2 bases move

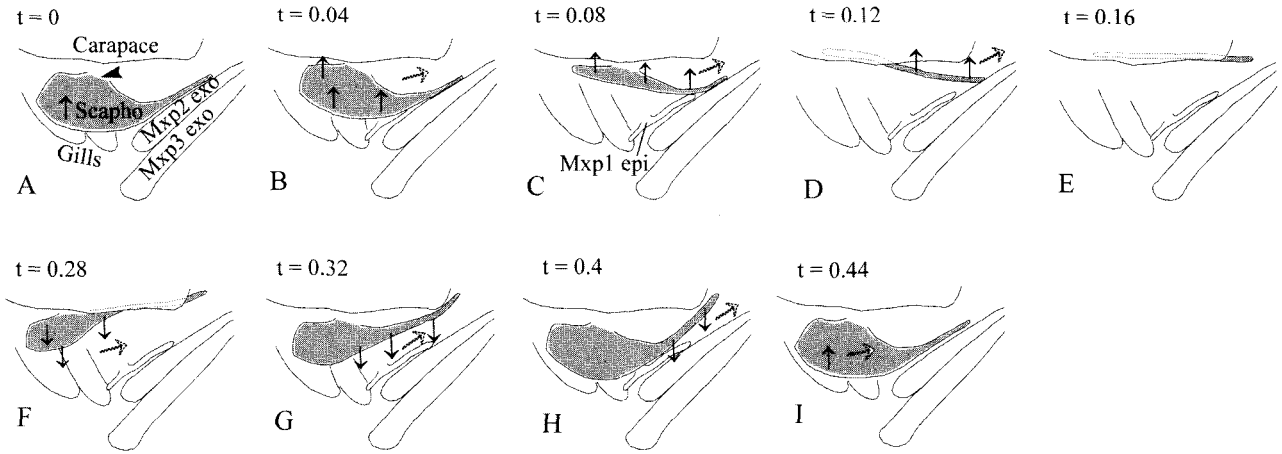


Figure 12. Respiratory movements of right scaphognathite (Scapho, gray) seen laterally; branchiostegite is removed. Arrows indicate moving part and direction of movement. Dotted arrows indicate respiratory current. Junction between Scapho and rest of maxilla 2 (arrowhead in A) is situated posteriorly on Scapho, which make posterior part follow movements of Mx2, dragging anterior part behind. Delayed movement of anterior part ensures that respiratory current is directed anteriorly. Note that Scapho sweeps across epipod of maxilliped 1 (Mxp1 epi). Mxp2 exo = exopod of maxilliped 2, Mxp3 exo = exopod of maxilliped 3, t = time in seconds (specific for series of pictures, not generalized).

in the medio-lateral plane, the endopods of Mx1 and Mx2 perform small semicircular movements (Fig. 13). This causes the distal tip of the Mx2 endopod to rub against the medial part of the base of the mandibular palp and the Mx1 endopod to sweep across a small part of the dorsal side of the Mx2 endopod. Both Mx1 and Mx2 endopods have a well-defined cluster of setae (Fig. 2F, H). The long serrulate setae of the Mx2 endopod lie in the space between the

incisor process and the Mx1 basis and are in contact with the incisor process. The smaller serrate setae of the Mx1 endopod seem not to contact anything. The flagellum of the exopod of Mxp1 lies in the exhalant current and moves very little, even when the rest of the Mxp1 is actively processing food. Water from the flagellar current also passes the flagellum of the Mxp1 exopod. The Mxp1 endopod lies very close and dorso-ventral to the Mxp1 exopod (Fig. 2J, K), and is therefore also placed in the currents, but in Fig. 13 the Mxp1 exopod obscures it from view.

Discussion

Functional grouping of mouthparts

The six pairs of mouthparts (Md, Mx1, Mx2, and Mxp1-3) and the labrum are very different in both morphology (Fig. 2) and function (Figs. 3-13, Table 1). To some degree, their pronounced differences in size and shape correlate with function, since the large and pediform Mxp2 and Mxp3 handle large prey items, whereas the smaller and flattened Mx1, Mx2, and Mxp1 enable the animal to accurately manipulate even very small food objects. The dorso-ventrally flattened form of these small mouthparts enables several independently moving structures to operate close together, a prerequisite to accurate manipulation of small food. The freedom of movement decreases in the mouthparts that are nearer to the mouth and arranged very close together, and this explains why the Lb, Mx1, Mx2, and Md perform rather stereotypical movements in a two-dimen-

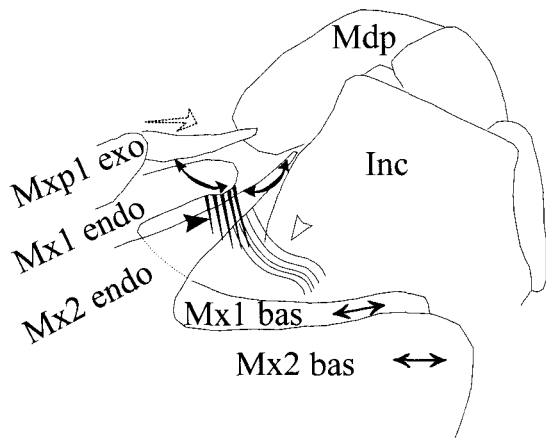


Figure 13. Placement and movements of dorso-ventral mouthparts (endopods of right maxilla 1 and maxilla 2 [Mx1 endo and Mx2 endo] and exopod of right maxilliped 1 [Mxp1 exo]), seen latero-anteriorly. Arrows indicate direction of movements. Dotted arrow indicates respiratory current. Open arrowhead indicates Mx2 setae lying in the space between Mx1 basis and incisor process (Inc) (see also Fig. 2H); black arrowhead indicates Mx1 setae (see also Fig. 2F). When Mx2 basis make medio-laterally movements, tip of Mx2 endopod rubs against base of the mandibular palp (Mdp). Setae on Mx1 endopod are apparently not in any contact. Flagellum of Mxp1 exopod is situated in respiratory current.

sional plane. The maxillipeds have much more space in which to operate, and the Mxp2 and Mxp3 endopods can move in all directions anterior to the animal due to their flexible joints. They can therefore manipulate a great variety of food items.

Although morphology and organization could support the division of the mouth apparatus into inner and outer mouthparts, this is a much too simplified view when it comes to functions of the mouthparts. As mentioned earlier, each side of the mouth apparatus can be divided into at least 20 separate parts, but these parts seldom work independently; rather they operate in functional groups. The Mxp2 and Mxp3 endopods have fairly similar functions and often work jointly, at least when processing potential food objects. The Mx1 and Mx2 bases form another group with very high correlation of movements and functions when processing food particles. Both of these two groups relate to the Mxp1 bases, which do not clearly belong to a single functional group, but can work closely together with either the Mxp2 and Mxp3 endopods or with the Mx1 and Mx2 bases (Fig. 4 and Fig. 7, respectively). Therefore, the Mxp1 bases constitute a group of their own. The flagella of the Mxp2 and Mxp3 exopods form a well-defined functional group having exactly the same function, and they almost always work together. The labium, the incisor processes, the molar processes, and the mandibular palps form another functional group, where the elements rarely move independently. The functional group composed of the coxae of Mx1, Mx2, and Mxp1 cannot be seen in the videos, but their role in ingestion can be interpreted from their position and morphology (for details, see Garm and Høeg, 2000). The scaphognathite, the Mxp1 epipod, and the Mxp2-3 exopods form a functional group because they cooperate in creating and directing the respiratory currents. The Mx1, Mx2, and Mxp1 endopods and the Mxp1 exopod seem to form the last functional group. This follows solely from their position, since their functions are but poorly understood. The distal tip of the Mx2 endopod might groom the base of the mandibular palp, and the setae might groom the ventrolateral side of the incisor process. Situated in the respiratory current, sensory setae on the Mxp1 endopod and exopod could allow them to be used to sense the need for gill grooming. The Mxp1 endopod in the brachyuran crab *Ebalia tuberosa* forms an exhalant canal, as do the Mxp1 endopod and exopod in the hermit crab *Pagurus rubricatus* (Schembri, 1982a, b), but this is unlikely to be the case in *Munida* because those structures are so slender. We never observed any contact between the setal cluster on the distal tip of the Mx1 endopod and any other object or mouthpart, and this could imply that these may be remote chemosensory setae.

At least for *Munida*, our groupings seem to have more

explanatory power than the conventional and superficial separation into inner and outer mouthparts. We suggest the following terms based on the observed functions:

1. *transporting mouthparts* for Mxp2 endopod and Mxp3 endopod;
2. *transporting-aligning mouthpart* for Mxp1 basis;
3. *sorting-aligning mouthparts* for Mx1 basis and Mx2 basis;
4. *current-generating mouthparts* for flagella of Mxp2 and Mxp3 exopods;
5. *cutting-crushing mouthparts* for incisor and molar processes, mandibular palp, and labrum;
6. *ingesting mouthparts* for Mx1 coxa, Mx2 coxa, and Mxp1 coxa;
7. *respiratory mouthparts* for scaphognathite, Mxp1 epipod, and Mxp2 and Mxp3 exopods;
8. *dorso-lateral mouthparts (with uncertain functions)* for Mx1 endopod, Mx2 endopod, Mxp1 endopod, and Mxp1 exopod.

These groupings are not entirely strict, as illustrated by the grooming behavior, in which each mouthpart (except Inc and Mp) partakes in grooming adjacent structures. The Mx2 bases can also move independently of the Mx1 bases, as evidenced by the respiratory movements, when the animal is not handling any food. Moreover, there is a slight division of functions between Mx1 and Mx2 when handling food items. The robust spines and serrate setae arming the Mx1 bases indicate their main function to be mechano-effector, whereas the several types of more delicate setae on the Mx2 basis suggest a mechanosensory function, a chemosensory function, or a combination of the two. If true, this gives the Mx2 bases a key role in sensing the quality of the potential food particles.

Comparison with other decapods

For most decapod taxa there is a lack of behavioral data, but a few earlier studies do describe some functional morphology accompanied by movement patterns (Anomura: Nicol, 1932; Roberts, 1968; Kunze and Anderson, 1979; Schembri, 1982a; Zainal, 1990. Thalassinidea: Stambuis *et al.*, 1998. Palinura: Suthers and Anderson, 1981. Brachyura: Schembri, 1982b. Astacidea: Barker and Gibson, 1977; Lavalli and Factor, 1995. Caridea: Moore *et al.*, 1993. Penaeidea: Hunt *et al.*, 1992).

Most of these data concern anomurans, and it seems as if morphology and organization of the mouth apparatus are very similar for pagurids and most galatheids. One of the more detailed observations on mouthpart function comes from Schembri's (1982a) study on the shallow-water hermit crab *Pagurus rubricatus*, which grooms the anterior body (antennae, eyes, and mouthparts), gathers sediment and other prey items, and processes potential food by the Mxp2

and Mxp3 endopods in a way similar to that reported here for *Munida*. The resemblance is especially pronounced in the handling and maceration of large, soft prey items. The cutting–crunching process of the mandible and associated structures proceeds in much the same way, although *P. rubricatus* seems to hold the prey with the mandibular palp and the labium. The palp and labium were also observed to push the food directly into the mouth, but we find this unlikely, because their movements must be perpendicular to the mouth opening (Schembri, 1982a, fig. 8). From his figure 8 it seems more likely that these structures deliver the food to the coxae of Mx1, Mx2, and Mxp1, which control ingestion. We agree with Schembri (1982a) in grouping together the Mxp2 and Mxp3 exopods, and the functions are identical: creating currents around the buccal field. The pattern is a little dissimilar, since in *P. rubricatus* a flagellum on the Mxp1 exopod also contributes to the currents around the buccal field, and the flagella beat on one side at a time producing an asymmetrical flow, which shifts when the animal changes the side of beating. Schembri (1982a) also observed that the flagellar currents merely place the particles in the respiratory flow, which thereafter causes the rejection of unwanted particles. This is clearly not the case for *Munida*, since the flagellar currents are much stronger than the respiratory ones.

Schembri (1982a) made some very interesting observations on the function of the bases of Mx1 and Mx2. *P. rubricatus* sorts the sediment in a different way from what we observed for *Munida*. The Mx2 bases seemed to be the most active, collecting the sediment from the Mxp2 endopods (Mxp1 bases are not involved) and pressing it through cuspidate setae on the medial edge of the Mx1 bases, which then serve as a passive filter. We emphasize this because it could indicate that very similar structures (even at the setation level) can have different movement patterns and thereby serve very different functions. One should notice that Schembri (1982a) did not use video-recordings, without which 3–4 Hz movements (observed for *Munida*) can be difficult to follow. Similar movement patterns for Mx1 and Mx2 are not mentioned in other studies on pagurids (Roberts, 1968; Kunze and Anderson, 1979).

In general, hermit crabs possess additional feeding mechanisms that we did not observe in *Munida*. These mechanisms are antennular filter feeding (Kunze and Anderson, 1979; Schembri, 1982c; Manjulatha and Babu, 1991), suspension feeding (Gerlach *et al.*, 1976; Schembri, 1982c), and gravel scrubbing (Orton, 1927; Roberts, 1968; Greenwood, 1972; Schembri, 1982a, c). The latter is the most significant and involves picking up pieces of gravel with the chelipeds and handing it over to the mouthparts, where the biofilm is scrubbed off. In *P. rubricatus*, the Mxp2 and Mxp3 endopods hold and turn the gravel, while the Mx2 and Mxp1 bases scrub it off

with “vigorous” movements. Compared to *Munida*, where the chelae are primarily used in aggressive behavior (Berril, 1970; pers. obs.), pagurids generally seem to make more extensive use of their chelae and cristae dentatae to macerate food items.

Nicol (1932) studied feeding in five species of galatheids (*Galathea dispersa*, *G. squamifera*, *G. strigosa*, *Munida rondelietii* (= *rugosa*), and *Porcellana longicornis*). Her description of the gross morphology of the mouthparts closely resembles what we found for *Munida sarsi* and *M. tenuimana*. The functions she ascribed to the Mxp2 endopods, Mxp3 endopods, and mandibles are also very similar to those reported here. The Mxp3 endopods of *Porcellana longicornis* are somewhat different than those of other galatheids, since they have long plumose setae used to entrap particles in suspension. The general function, however, is the same—to collect prey and transfer it toward the mouth. Our observations also agree with those of Zainal (1990), who reports on both morphology and function of the mouthparts of *Munida rugosa*, but with limited detail.

Outside the Anomura, the most detailed data comes from mud shrimps, Thalassinidea. Stamhuis *et al.* (1998) give video-based information on most of the mouthpart functions of the thalassinid *Callinassa subterranea* during sediment sorting. The animal lives as a selective deposit feeder in mud burrows; due to this specialized way of living, the mouthparts of *C. subterranea* and especially their setation are somewhat different from that described for *Munida*. Still, Mxp3 endopod is used for collecting and transporting the food items, whereas the Mxp2 endopod is used for sorting the sediment by size. The sediment is not further sorted, and the bases of Mxp1 and Mx2 are merely used for transporting the particles towards the mouth. However, these appendages move with the same frequency as we report for *Munida*, 3–4 Hz. Very unlike *Munida*, *C. subterranea* does not use its Mx1 during deposit feeding and uses Md only to open or close the mouth (Stamhuis *et al.*, 1998). The movements of the maxillipeds of *C. subterranea* are also much more stereotypical than what we find for *Munida*. It has to be kept in mind that Stamhuis *et al.* analyzed only one type of feeding (deposit feeding), which of course will reduce the functional scheme of the mouthparts. There is morphological evidence (*e.g.*, well-developed mandibles, spines on maxilla 1, and crista dentata) that *C. subterranea* possesses other feeding strategies; it is most likely also carnivorous (Stamhuis *et al.*, 1998).

Hunt *et al.* (1992) studied the role of “the anterior mouthparts” (Md, Mx1, Mx2, Mxp1, Lb, and paragnaths) in the penaeid prawn *Penaeus merguensis*. Much of the morphology is similar to *Munida*, but the mandibular palp is different and does not take part in feeding. When eating large prey items, Md, paragnaths, Mx2, and Mxp1 move laterally and Lb moves anteriorly to make room, while Mx1 basa put

the prey between the incisor processes for cutting (Hunt *et al.*, 1992). Afterwards the Lb alone pushes the prey towards Mx1 coxae for ingesting. When feeding on small particles, *P. merguensis* does not sort the sediment as *Munida* does, but filters them out of the water column by using pappose setae on Mxp1 and on the bases of Mx1 and Mx2 (Hunt *et al.*, 1992). The currents around the buccal area from which the particles are filtered are created by the respiratory beating of Mx2, since *P. merguensis* lacks flagella on the maxillipeds.

What these comparisons show is that within hermit crabs and squat lobsters there are great similarities in mouthpart morphology, even at the setation level. Despite some differences, the functions reported for other squat lobsters and for hermit crabs are more or less comparable to our findings for *Munida*. Therefore, there is reason to believe that the functional groupings we suggest could apply to other anomurans; it goes without saying that more data are needed from other species before any final conclusions can be drawn. The additional feeding strategies described for some hermit crabs (*i.e.*, Schembri, 1982c) indicate that more functional groups must be added. It would be of major interest to gain information from the Lithodidae and Porcellanidae, the two other groups of anomurans that have either a different size range than the Galatheidae and Paguridae (most lithodid crabs are very large) or a different way of eating (porcellanid crabs are filter-feeders). Very little information is available for decapod taxa other than the Anomura. Not surprisingly, the two comparable studies (Hunt *et al.*, 1992; Stamhuis *et al.*, 1998) show a great diversity of mouthpart morphology and function within the Decapoda, and the functional groupings suggested here do not seem appropriate for all taxa.

Acknowledgments

We thank the Coast Guard of the Faeroe Islands for the use of their ship *Tjaldur*. We also thank Grethe Bruntse for assistance with the field work and the Kaldbak Laboratory for generously allowing us to use their facilities. We are grateful for the material and data supplied by the BIOFAR I collection and by Dr. André Freiwald, Bremen. We appreciate the financial support given by The Hede Nielsen Family Foundation and The Danish Society of Natural History (to AG). JTH also gratefully acknowledges grant nos. 94-01636 and 96-01405 from the Danish Natural Science Research Council and nos. 970381/40-1228 and 950260/40-1190 from The Carlsberg Foundation. We thank Nikolai Konow for never-ceasing interest in our study and Dr. G. Walker for some constructive comments.

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