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Functional mouthpart morphology of the squat lobster *Munida sarsi*, with comparison to other anomurans

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Abstract The mouthparts of *Munida sarsi* Huus, 1935, including the labrum and paragnaths, are described using LM and SEM, with special attention to the setal composition and its function. We also used high-resolution macrovideo equipment to record the feeding processes and monitor setae in action. This combination of morphological and preliminary behavioral data enabled us to arrive at a more comprehensive understanding of the functional morphology. *M. sarsi* was found to be an opportunist and capable of handling and eating most kinds of animal tissue. The species can also be a selective deposit feeder, sorting the sediment by quality and not by size. This sorting is performed by the setae on the medial rim of the bases of maxilla 1, maxilla 2 and maxilliped 1. Many of the other mouthpart functions ranging from food detection to ingestion are mapped with comparison to what has been found for other anomurans. Grooming was shown to be a significant function of many mouthparts, especially the endopod of maxilliped 3. In general the mouthparts closest to the mouth have the least complex movements and functional scheme, with the mandibles being able to perform only one movement, i.e. cutting or crunching food objects. Some functions are attributed to the paragnath, the endopod of maxilla 2 and the epipod of maxilliped 1.

Introduction

The genus *Munida* currently contains well over 150 species (MacPherson 1994; Baba in preparation); the majority live in waters below 200 m. Most are tropical,

but five species can be found in the North East Atlantic: *M. rugosa*, *M. sarsi*, *M. intermedia*, *M. tenuimana* and *M. microphthalma* (Hartnoll et al. 1992). The most abundant is *M. sarsi*, which occurs from the North Cape in Norway and Greenland to the Bay of Biscay in the south, at depths between 200 and 800 m (Rice and De Saint Laurent 1986). Ecologically it is an important species, which in some habitats is found in densities of up to 20 m⁻² (A. Freiwald unpublished results).

One reason for the success may be the capability to utilize many different food resources, as the depths they inhabit are sparse in high-quality organic material. The range of organic material a crustacean is able to utilize largely depends on the handling capability of the mouthparts. Cephalization provides the decapods with a total of six pairs of mouth appendages (plus paragnaths and labrum); this implies that they have a tremendous potential for specialization in food handling. Knowledge on how the mouth apparatus works and what types of specialization have taken place are therefore important clues in understanding the success of the Decapoda.

Many earlier studies have dealt with functional mouthpart morphology of decapods (Gemmell 1979; Kunze and Anderson 1979; Suthers and Anderson 1981; Schembri 1982a, b; Felgenhauer and Abele 1983; Suthers 1984; Skilleter and Anderson 1986; Manjulatha and Babu 1991; Lavalli and Factor 1992; Heeren and Mitchell 1997; Nickell et al. 1998; Stamhuis et al. 1998). These studies clearly show that one of the main keys to understanding a crustacean mouth apparatus is the setal composition of the appendages, but also that mere morphological descriptions will in many cases not provide all the answers. Some earlier studies (Felgenhauer and Abele 1983; Schembri 1982a) combined morphological and behavioral data but very few (Stamhuis et al. 1998) have used macrovideo recordings of live animals to document the usage of various structures. No studies of this kind exist on *Munida*.

The main purpose of the present study is to give a detailed morphological description of the mouthparts of *Munida sarsi* and combine this information with

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behavioral data from high-resolution video recordings to provide a functional interpretation of both gross structures and setal composition.

Materials and methods

LM and SEM

Munida sarsi fixed in 2% formalin was obtained from The BIO-FAR 1 project (Stn 070, 61°24'69N; 08°43'97E, Nørrevang et al. 1994) at the Faeroe Islands. Adult males and females were used with carapace lengths between 17 and 28 mm. The mouthparts were cleaned by ultrasound and manually with a beaverhair brush. A standard dissection microscope was used for the drawings. SEM preparation followed Felgenhauer (1987), except for not using osmium, which did not improve the results significantly. The scanning electron micrographs were taken on a Jeol 840 microscope and were stored electronically using the program SEMafore. They were processed and manipulated in Corel Draw 8.0.

Setal system

The characterization of the setal system (Fig. 1) and the terminology used in the present study are modifications of the systems proposed by Jacques (1989), Watling (1989) and Lavalli and Factor (1992). Although it has been stressed that setae should be classified by homologies only, we have considered their grouping from a functional point of view, since we could not definitely decide which structures are homologous and which are not. Thomas (1970) claimed that all setae have an apical pore, but we found this to be the rare case and have given pore setae their own category. The other seta categories (serrate, cuspidate, plumose, etc.) can possibly be applied to all decapods, but the subdivisions we use (Table 1) might be useful only for *Munida* and closely related genera.

Video recordings

Munida sarsi was caught with a Snell dredge at Faeroe Bank (61°24'46N; 08°44'08E) at depths between 330 and 345 m in 7 °C water. We obtained 70 specimens with carapace lengths between 7 and 28 mm, which we kept alive at the Kaldbak Laboratory in a 1000 liter tank. They were video filmed in 50-liter tanks at 10°C with three different kinds of sediment: mud/gravel from the area of catch (many foraminiferans), mud from shallow water (very rich in organic material) and shell gravel (low in organic material). Furthermore the specimens were fed different kinds of animals from the samples plus animal and algal tissue from shallow waters. Three specimens had their right branchiostegite removed to allow recordings of the movements of the scaphognathite and the epipods of maxilliped 1 and maxilliped 3 inside the gill chamber. The recordings were made from outside the tank by a Y/C ccd camera with a Micronikkor 105 mm lens and recorded on super VHS (50 fields s⁻¹). Light was obtained from a 120 W spotlight. By comparison with the behavior of *M. sarsi* recorded in situ, it was documented that the animals in the tanks behaved naturally.

Results

Orientation of the mouthparts

The mouthparts (Fig. 2), defined as structures which contact food objects while eating, are the labrum (Lb), mandible (Md), paragnath (Pg), maxilla 1 and 2 (Mx1 and Mx2) and maxilliped 1, 2 and 3 (Mxp1 to Mxp3).

The unpaired labrum is located anterior to the mouth. The mandible, maxilla 1 and 2 and maxilliped 1 are paired and located in dorso-ventral layers ventral to the mouth (Fig. 2A, B). The coxae of these appendages are bent dorsally, towards the mouth. The paragnaths, not seen on Fig. 2, are situated between the mandible and maxilla 1. The pediform maxillipeds 2 and 3 are found ventral and lateral to the other mouthparts (Fig. 2B). With the mandibles as an exception, the left and right sides of mouthparts are identical; therefore illustrations are generally only of the right side.

Labrum

The labrum (upper lip) is situated just anterior to the mouth and is weakly sclerotized. It consists of three lobes forming two furrows on the ventral side (Fig. 3A), and the middle lobe narrows towards the mouth giving the labrum a slightly triangular shape. On the posteriormost part, the furrows have micro-setae pointing towards the mouth (Fig. 3B).

Paragnaths

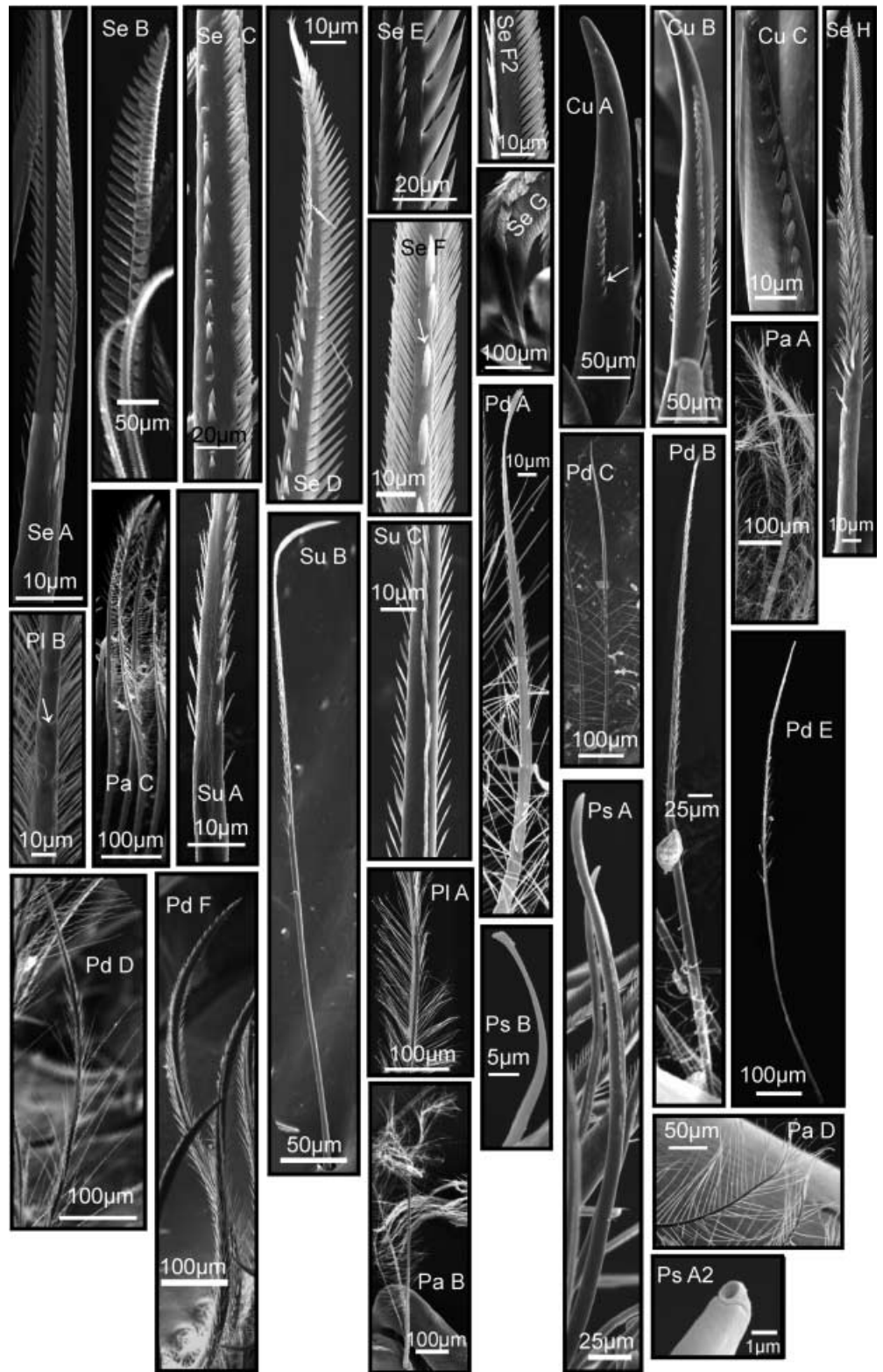
Like the labrum the tongue-shaped paragnaths (lower lip) are weakly sclerotized (Fig. 4A). Similar to other decapods the paragnaths of *Munida sarsi* are situated laterally to the mouth and lie between the incisor processes of the mandible and the bases of maxilla 1. There is a field of micro-setae on the ventral side of the paragnaths with the micro-setae pointing medially (Fig. 4A, B) and a pore field on the antero-lateral edge (Fig. 4C).

Mandible

The highly calcified mandible (Fig. 5) consists of three parts: the incisor process, the molar process and the mandibular palp (Fig. 5A). Seen from the medial side the incisor process is concave and has a sharpened edge. On the right mandible the edge possesses three teeth, one posterior, one in the middle and one anterior, but the left incisor has somewhat larger anterior and middle teeth and nearly lacks the posterior tooth (Fig. 5B, C). The flattened molar process is situated dorsal and posterior to the incisor and is framed by seven to ten tubercles (Fig. 5B, C). Together the molar and the incisor processes form a furrow that accommodates the mandibular palp (Fig. 5D).

The U-shaped mandibular palp attaches on the dorsal side of the mandible and projects ventrally into the furrow between the incisor and the molar from the anterior. It consists of three segments, the two proximal are cylindrical and the distalmost is laterally flattened and pointed. The ventral rim of the distal segment carries three rows of stout, serrate setae bending towards the apical end of the segment (Fig. 5E).

Fig. 1 *Munida sarsi*. Seta types: *Se A* serrate A, mid-section; *Se B* serrate B, distal half; *Se C* serrate C, mid-section; *Se D* serrate D, distal 1/3; *Se E* serrate E; *Se F* serrate F, arrow indicates setule; *Se F2* *Se F* rotated 90°; *Se G* serrate G, distal 1/3; *Se H* serrate H; *Cu A* cuspidate A, arrow indicates denticle; *Cu B* cuspidate B; distal 2/3; *Cu C* cuspidate C, distal half; *Pl A* plumose A; *Pl B* plumose B, arrow indicates joint; *Su A* setulate A, mid-section; *Su B* setulate B; *Su C* setulate C, mid-section; *Pd A* plumodenticulate A; *Pd B* plumodenticulate B; *Pd C* plumodenticulate C; *Pd D* plumodenticulate D, distal 1/3; *Pd E* plumodenticulate E; *Pd F* plumodenticulate F; *Pa A* pappose A, distal 3/4; *Pa B* pappose B; *Pa C* pappose C; *Pa D* pappose D, distal half; *Ps A* pore setae A; *Ps A2* pore setae A, close up of pore; *Ps B* pore setae B, distal half



Maxilla 1

Maxilla 1 (Fig. 6) is composed of a well developed protopod (coxa and basis) and a very reduced endopod.

The coxa and basis are dorso-ventrally flattened, and the endopod is finger-shaped (Fig. 6A, B).

The coxa is strongly curved towards the mouth, and the medial edge has long plumodenticulate setae on the

Table 1 *Mumida sarsi*. Descriptions of seta categories (most types illustrated in Fig. 1)

Seta category	Description
Simple	Seta without any pores, annuli or outgrowths
Si A	(not illustrated) Long slender seta without any pores, annuli or outgrowths
Serrate	With two well defined rows of denticles (smooth-pointed outgrowths not articulated with shaft) all the way to the tip, normally the proximal half of shaft is naked. Denticles point towards distal end of seta. There is an annulus proximal to the denticles. It may have setules (slim and serrated outgrowths articulated with shaft)
Se A	Short denticles, 5–7 μm , and no setules
Se B	Like Se A, but denticles are much more robust and 50 μm long
Se C	Large and robust seta with denticles around 10 μm . Two additional less distinct rows of denticles on middle part
Se E	Like Se C, but denticles larger, around 30 μm long
Se F	With two additional rows of denticles as distinct as the primary ones. On distal 1/3 a few setules between the two additional rows of around the same size as the denticles (Fig. 1 Se F, arrow)
Se G	Dense and small denticles, 3–5 μm , two rows of setules on distal half. Seta strongly curved with denticles on concave side
Se H	Dense field of setules opposite to the denticles. Tip without setules. Denticles and setules around 10 μm long
Cuspidate	Stout setae without outgrowths on the tip and on proximal 1/3–1/2. One or two rows of denticles midway, and an annulus proximal to the denticles
Cu A	Very robust. Two rows of approx. 10 denticles midway on each side (Fig. 1 Cu A, arrow)
Cu B	Two rows of denticles on distal half, but distalmost 1/6 is naked. The middle 1/3 has some setules
Cu C	Small curving seta with one row of small denticles, 3–5 μm , on convex side
Plumose	Two well-defined rows of long (up to 100 μm) setules (lacking articulation) along the total length of the seta. The angle between the rows is approx. 180°
Pl A	Supracuticular articulation. On proximal half the setules sit in furrows. Tip of the setules hook-shaped
Pl B	Like Pl A, but has more dense setules and a segmented shaft
Setulate	Short (normally less than 10 μm) setules on distal half, size decreasing towards the tip. There is an annulus at the most proximal setules
Su A	Setules in two more or less well defined rows
Su B	Like Su A, but longer and thinner
Su C	Very long (> 1 mm) and slender seta with three well defined rows of setules
Plumodenticulate	Long setules (up to 100 μm) on proximal part, denticles in two rows and short setules on distal part. The distal setules sit on the side opposite of the denticles
Pd A	Denticles and small setules on distal 1/5. The large setules on proximal 4/5 dense and randomly spaced
Pd B	Denticles and dense setules on distal half. A few randomly placed setules on proximal half
Pd C	Like Pd B, but proximal setules arranged in two rows on opposite sides of setal shaft
Pd D	Like Pd A but proximal setules longer and less dense
Pd E	Like Pd A but proximal half lacks setules
Pd F	Shaft is S-shaped. Denticles but no setules on distal 1/5. Setules on proximal 4/5 very dense and relatively small, 50–60 μm
Pappose	Long setules (up to 100 μm) along total length of the seta, often randomly spaced
Pa A	Dense and randomly spaced setules, with a tendency towards two rows on proximal 2/3. The most proximal setules are very thin
Pa B	Very long seta, more than 2 mm. Setules in two rows on proximal half, and dense randomly spaced setules on distal half
Pa C	Relatively short setules, 50–70 μm , in two rows separated by 120°. Additional setules on distal 1/5. Setules get smaller towards the tip
Pa D	Like Pa C but, smaller and with longer setules
Pore seta	With annulus and apical pore. Two to four rows of setules on the distal half, the setules can be very small
Ps A	Four rows of small setules on distal 1/3. Distalmost 30 μm naked. The tip bends so the pore opens laterally. Pore 1 μm wide
Ps B	Small curved seta with very small, less than 1 μm , protrusions on distal half. Tip is wide and like in Ps A the pore opens laterally
Ps C	(not illustrated) Long slender seta. Distal 20 μm like Ps B, but the proximal part resemble Se H

posterior part which also curve into the mouth (Figs. 2A, 6C). The anterior part of the medial rim carries more stout setae, some cuspidate. The dorsal surface lacks setae, while the ventral surface has some scattered serrate setae.

The basis is situated ventral to the paragnaths and is curved to fit the form of the mandibular incisor process. The medial edge (Fig. 6E) has two rows of spines (no sign of articulation even at high magnification) flanked by two outer rows of robust cuspidate setae. Along the

ventral side a row of serrate setae point towards the medial rim (Fig. 6F). Plumodenticulate and setulate setae occupy the space between the coxa and the basis. The cuticle on the dorsal surface of the basis has some pores resembling the paragnathal pores (Fig. 4C).

The endopod projects from the lateral rim of the basis, and the distal end lies on the lateral side of the incisor process of the mandible. Apically it carries a small cluster (5 to 10) of serrate setae pointing medially (Fig. 6D).

Fig. 2 *Munida sarsi*. Orientation of the mouthparts. **A** Left side of *M. sarsi* sectioned through the medial plane. The position of the mouthparts compares to the resting position in living animals. **B** Relative position of the mouthparts in the transverse plane indicated by arrowheads in **A** (anterior view) (*Lb* labrum; *Md* mandible; *Mp* mandibular palp; *Mx1* maxilla 1; *Mx2* maxilla 2; *Mxp1* maxilliped 1; *Mxp2* maxilliped 2; *Mxp3* maxilliped 3)

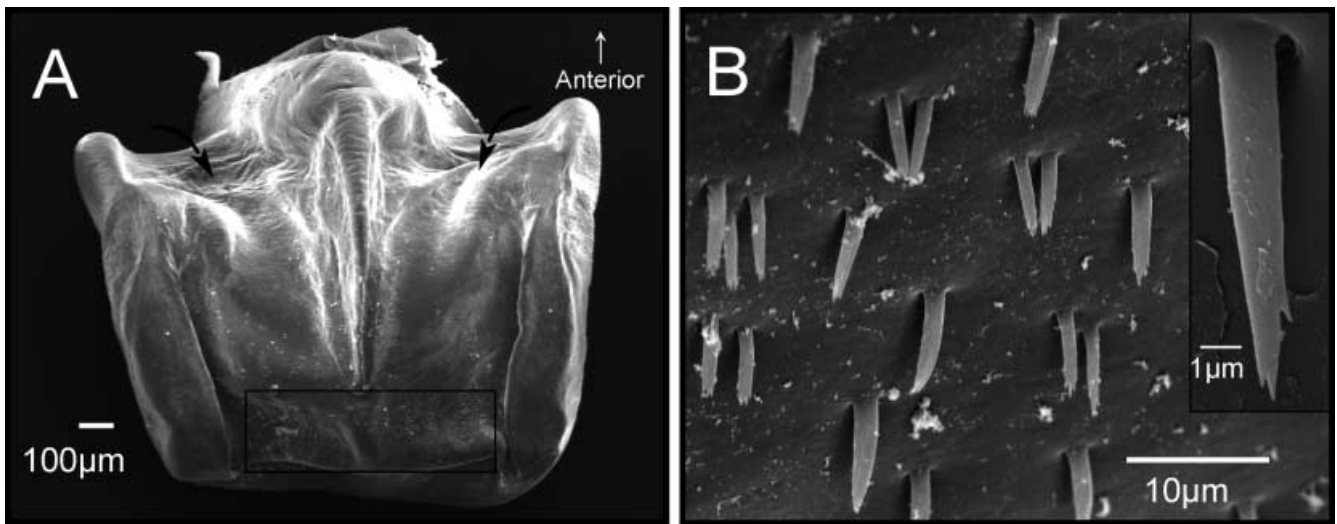
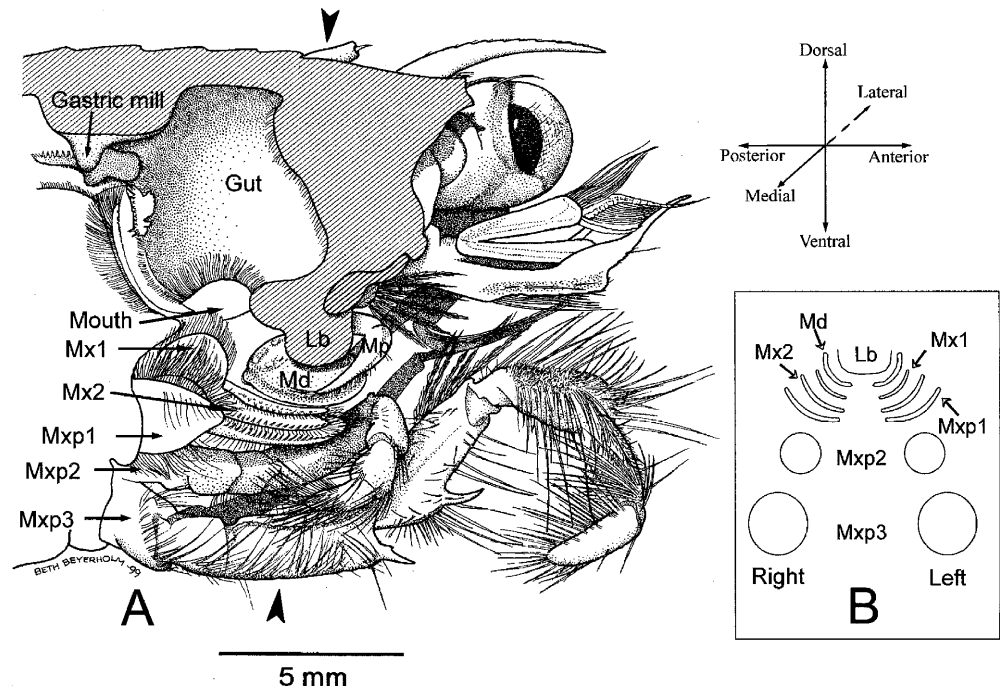


Fig. 3 *Munida sarsi*. Labrum. **A** Ventral view, note the two furrows. Arrows show how the mandibular palps move through the furrows. Frame indicates area with micro-setae. **B** Micro-setae from framed area in **A** pointing towards the mouth. *Inset*: close up of micro-seta, note the articulation with the labrum indicating a seta and not a spine

Maxilla 2

Like *Mx1*, maxilla 2 has a well developed coxa and basis and a reduced endopod, but also a large scaphognathite (Fig. 7A). The limb is dorso-laterally flattened and lies just ventral to *Mx1*.

The coxa bears two endites, labeled coxa 1 and 2. Coxa 2 is about three times as large as coxa 1. The medial edge of both parts is densely covered with setae which extend the bending of the coxa towards the mouth

(Fig. 7F). This is especially true for a row of curved pappose setae on the dorsal surface of coxa 2, covering parts of the medial edge and forming a setal screen (Fig. 7D). Posteriorly on coxa 2 there are some long pappose setae.

The basis also bears two endites; basis 1 is about twice as large as basis 2. The medial rim has a complex setation (Fig. 7C). The dorsal surface has few setae and some pores appearing similar to those of the paragnaths (Fig. 4C). The ventral side has a row of serrate setae pointing towards the medial margin. As in *Mx1*, the space between the coxa and the basis is filled with plumodenticulate and setulate setae. The unsegmented and lancet-shaped endopod (Fig. 7B, E) articulates proximally onto the basis; the distal end lies in the articulation between the mandibular palp and the incisor

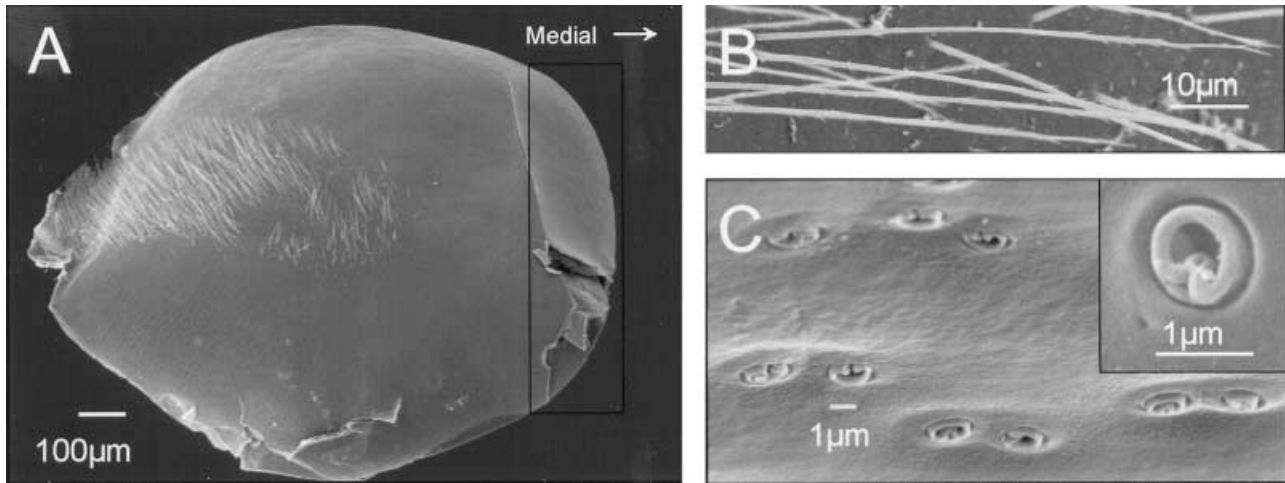
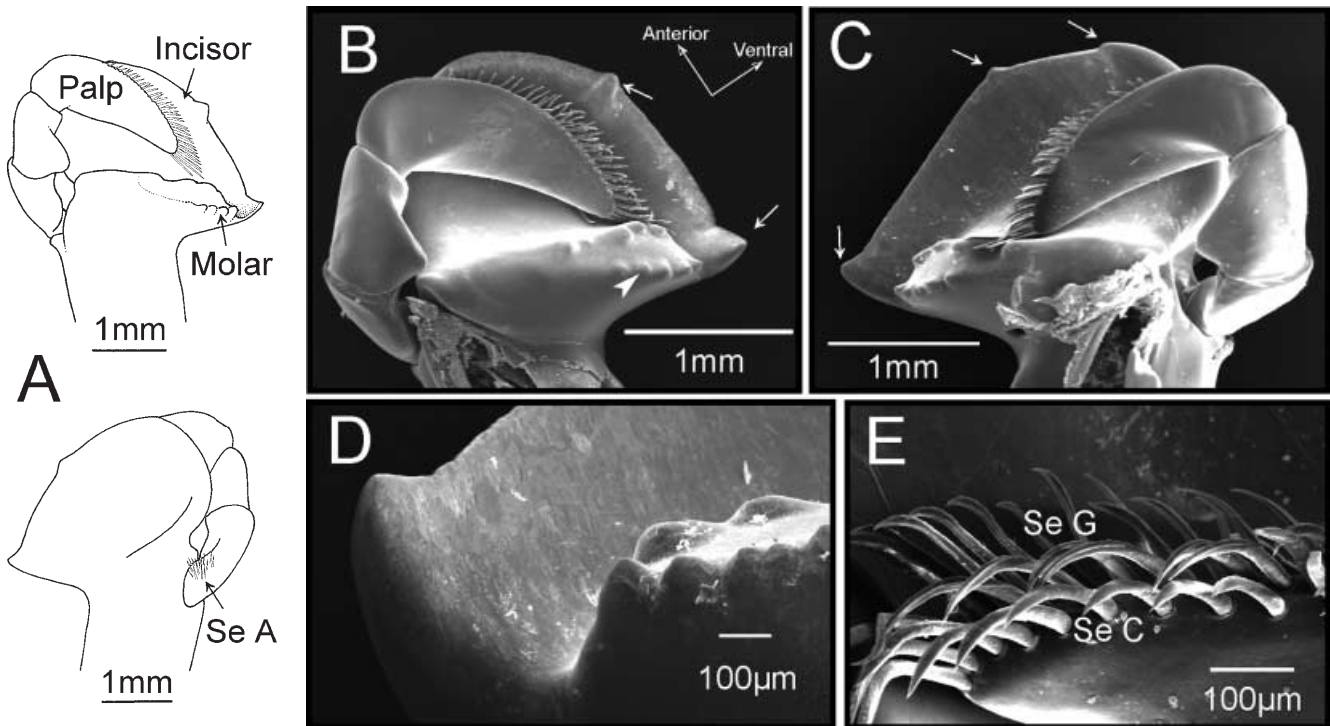


Fig. 4 *Munida sarsi*. Paragnath. **A** Ventral view of the right paragnath, frame indicates the pore field. **B** Micro-setae from the paragnaths. **C** Close up of the dense pore field. *Inset*: pore, note the fold in the cuticle rim

process. It is also in close contact with the endopod of Mx1. Midway along the edge, the endopod has approximately 20 very long setulate setae pointing towards the medial rim of basis 2 on the dorsal side (Fig. 7E).

Fig. 5 *Munida sarsi*. Mandible. **A** Left mandible (*top* dorso-medial view; *bottom* ventro-lateral view). **B** Left mandible. Arrows indicate medial and posterior teeth, the anterior is missing, note the tubercles on the molar process (*arrowhead*). **C** Right mandible, note small anterior tooth (*uppermost arrow*). **D** Furrow between molar and incisor processes. **E** Setal composition on distalmost segment of mandibular palp. Serrate setae bend towards the distal end of segment (*Se serrate setae*, see Table 1)



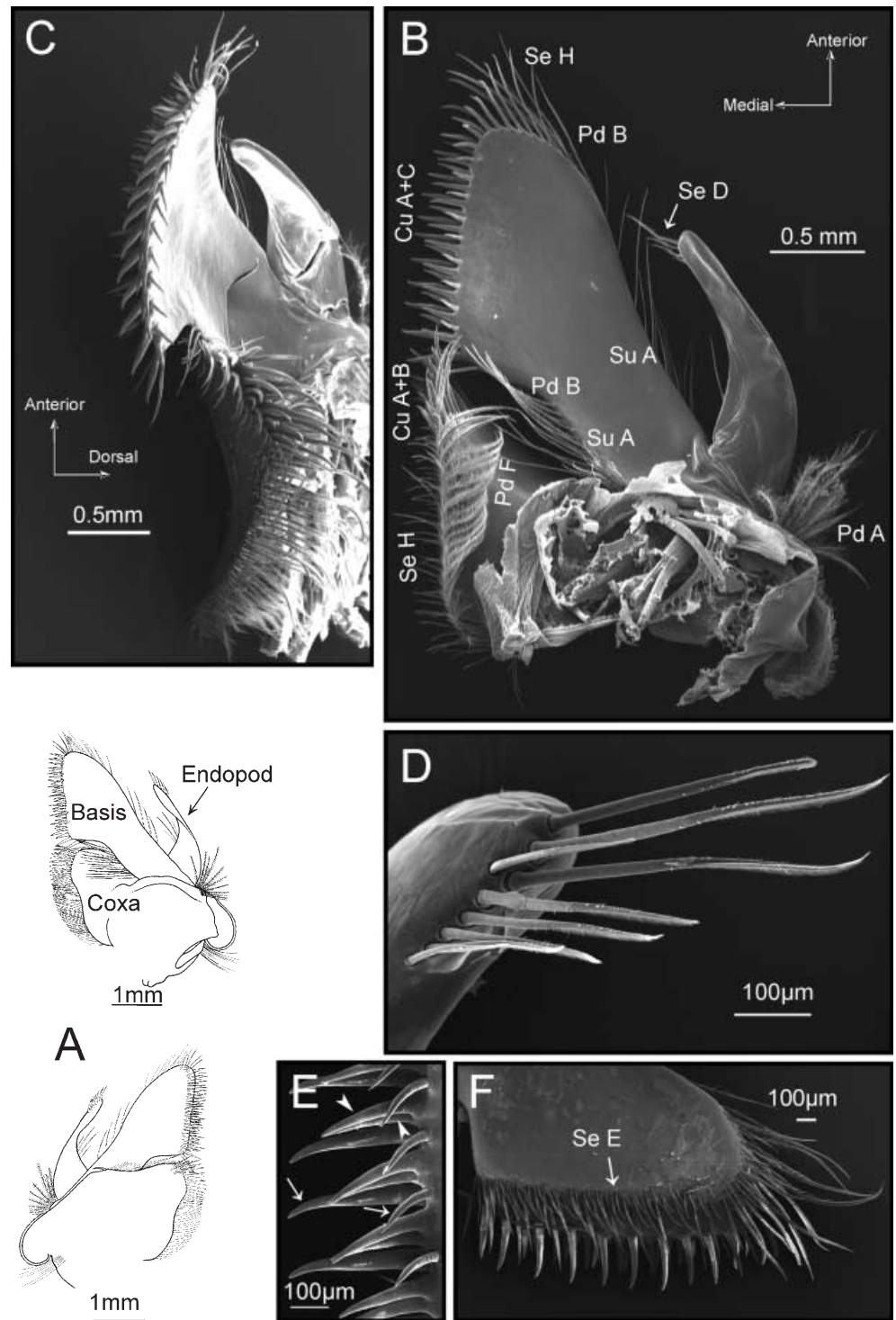
The very thin and flexible scaphognathite (Fig. 7A, B) is about the same size as the rest of the limb. It attaches laterally to the coxa and lies within the gill chamber above the two anteriormost gills. Densely packed plumose setae along the edge of the scaphognathite enlarge the surface.

Maxilliped 1

Maxilliped 1 consists of a large coxa, a large basis, reduced endo- and exopods and an epipod (Fig. 8A, B). The limb is situated ventral to Mx2 and, except for the coxa which is rather thick (Fig. 8E, F), the limb is dorso-ventrally flattened.

The coxa is triangular with a broad medial rim (Fig. 8F) along the dorsal edge of which a row of long

Fig. 6 *Munida sarsi*. Maxilla 1. **A** Right Mx1 (*top* dorsal view; *bottom* ventral view) **B** Dorsal view of right Mx1 with setal composition. **C** Medial view of right Mx1 with the coxa bending dorsally. **D** Distal tip of endopod with well defined cluster of Se D setae. **E** Dorsal view of medial rim of basis (*arrows* cuspidate setae; *arrowheads* spines). **F** Ventral view of the basis with a row of serrate setae (*arrow*) parallel to the medial rim (*Cu* cuspidate; *Pd* plumodenticulate; *Se* serrate; *Su* setulate setae, see Table 1)



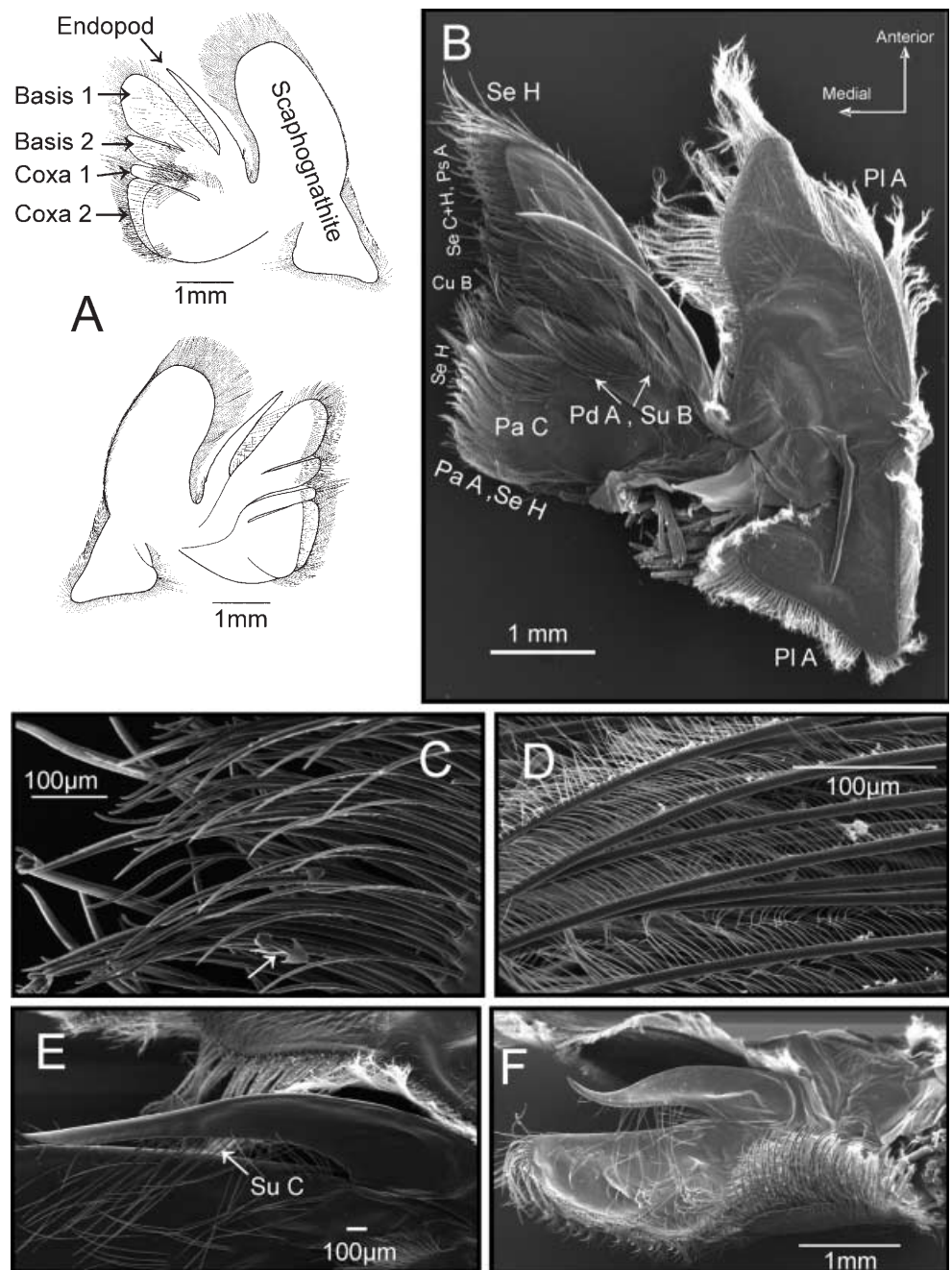
pappose setae curves towards the mouth. Robust cuspidate setae occur anteriorly next to the medial rim of the basis. Both the dorsal and the ventral surfaces have setae pointing medially.

The basis is knife-blade-shaped and the medial margin has a complex setation, which consists of several rows (Fig. 8C). On both the ventral and the dorsal surface a row of setulate setae runs along the total length

of the basis. These setae point toward the medial margin. Between the row on the dorsal side and the medial edge there are many pores in the cuticle (resembling the paragnathal pores Fig. 4C). The space between the coxa and the basis has a few plumodenticulate setae.

The finger-shaped endopod projects anteriorly and bends dorso-medially which places it behind the endopods of Mx1 and Mx2. The dorso-lateral rim carries

Fig. 7 *Munida sarsi*. Maxilla 2. **A** Right Mx2 (*top* dorsal view; *bottom* ventral view). **B** Dorsal view of right Mx2, note the large scaphognathite and its dense setal rim. **C** Setal composition of medial rim of basis, arrow indicates a sponge spicule. **D** Setal screen on dorsal side of coxa made of Pa C setae. **E** Endopod with very long setulate setae (*Su C*) midway along edge. **F** Medial view of Mx2. The coxa along with its setae bend dorsally (*Pa* pappose; *Pd* plumodenticulate; *Pl* plumose; *Ps* pore setae; *Se* serrate; *Su* setulate setae, see Table 1)



plumose and plumodenticulate setae. The flattened exopod sits lateral to the endopod, projecting anteromedially, which places the distal end in the exhalant current from the gill chamber. The distal end has a pseudoflagellum (Fig. 8D) which articulates with the proximal part but has no musculature (verified by LM), and all traces of segmentation are lost. Proximal to the pseudoflagellum the exopod has pappose setae, which become plumose more proximally (Fig. 8B).

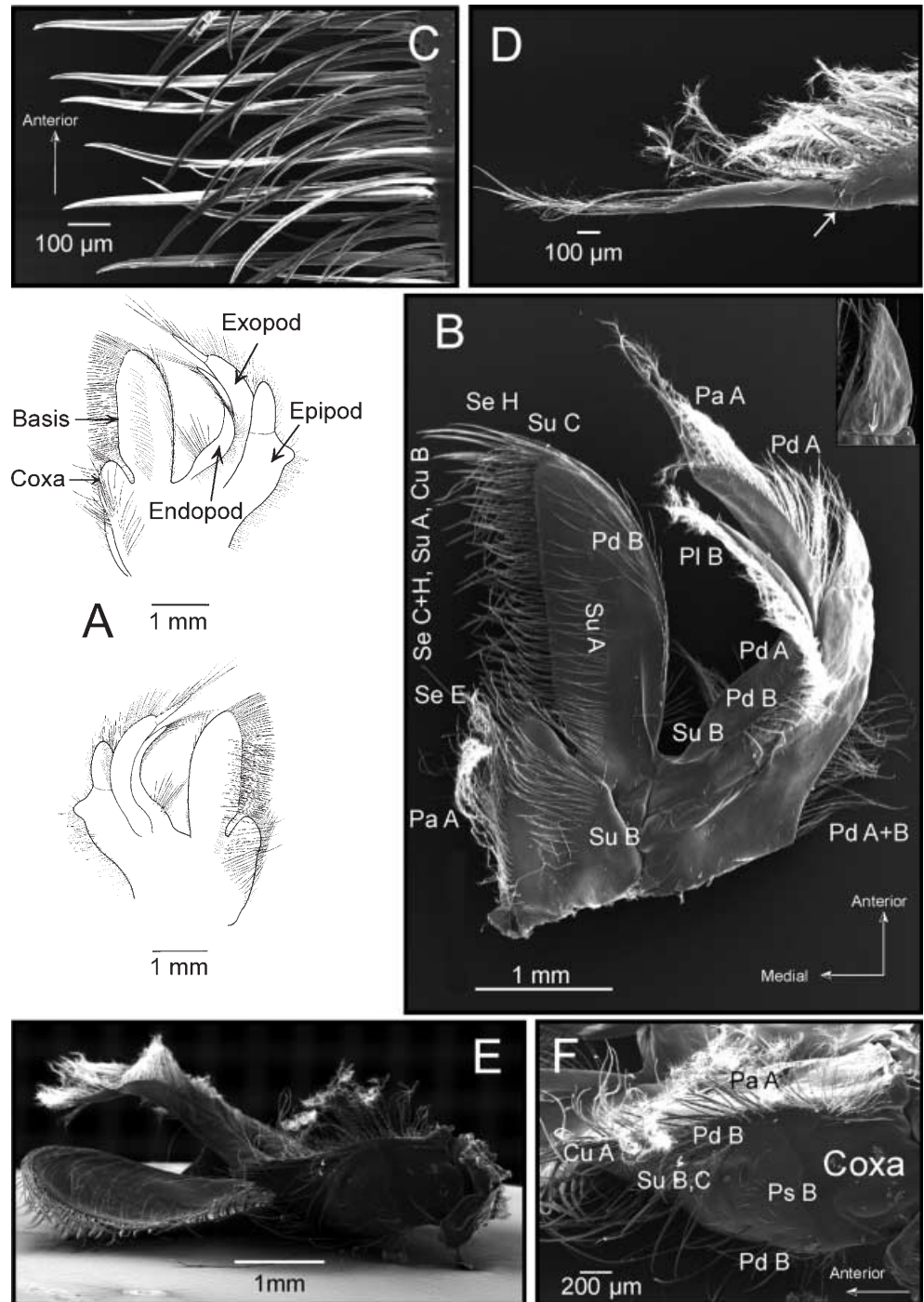
The epipod is broad, very thin and flexible. It is the lateralmost part of Mxp1, lying in the anterior part of the gill chamber ventral and anterior to the scaphog-

nathite. The edge carries a few plumodenticulate setae. The distal tip articulates with the rest of the epipod (Fig. 8B, insert), but like the pseudoflagellum it lacks musculature.

Maxilliped 2

Maxilliped 2 is situated ventral and lateral to Mxp1. It somewhat resembles a normal pereopod having a five-segmented endopod composed of ischium, merus, carpus, propodus and dactylus, but it also sports a long and

Fig. 8 *Munida sarsi*. Maxilliped 1. **A** Right Mxp1 (*top* dorsal view; *bottom* ventral view). **B** Dorsal view of right Mxp1. *Inset*: distal tip of epipod with joint (*arrow*). **C** Setae on medial rim of basis, the dorsalmost bend posteriorly. **D** Pseudoflagellum on tip of exopod, arrow indicates joint. **E** Medial view, note very broad medial rim of coxa. **F** Medial view of coxa. The anterior part has robust setae and the dorsal edge has long pappose setae (*Pa* pappose; *Pd* plumodenticulate; *Pl* plumose; *Ps* pore setae; *Se* serrate; *Su* setulate setae, see Table 1)

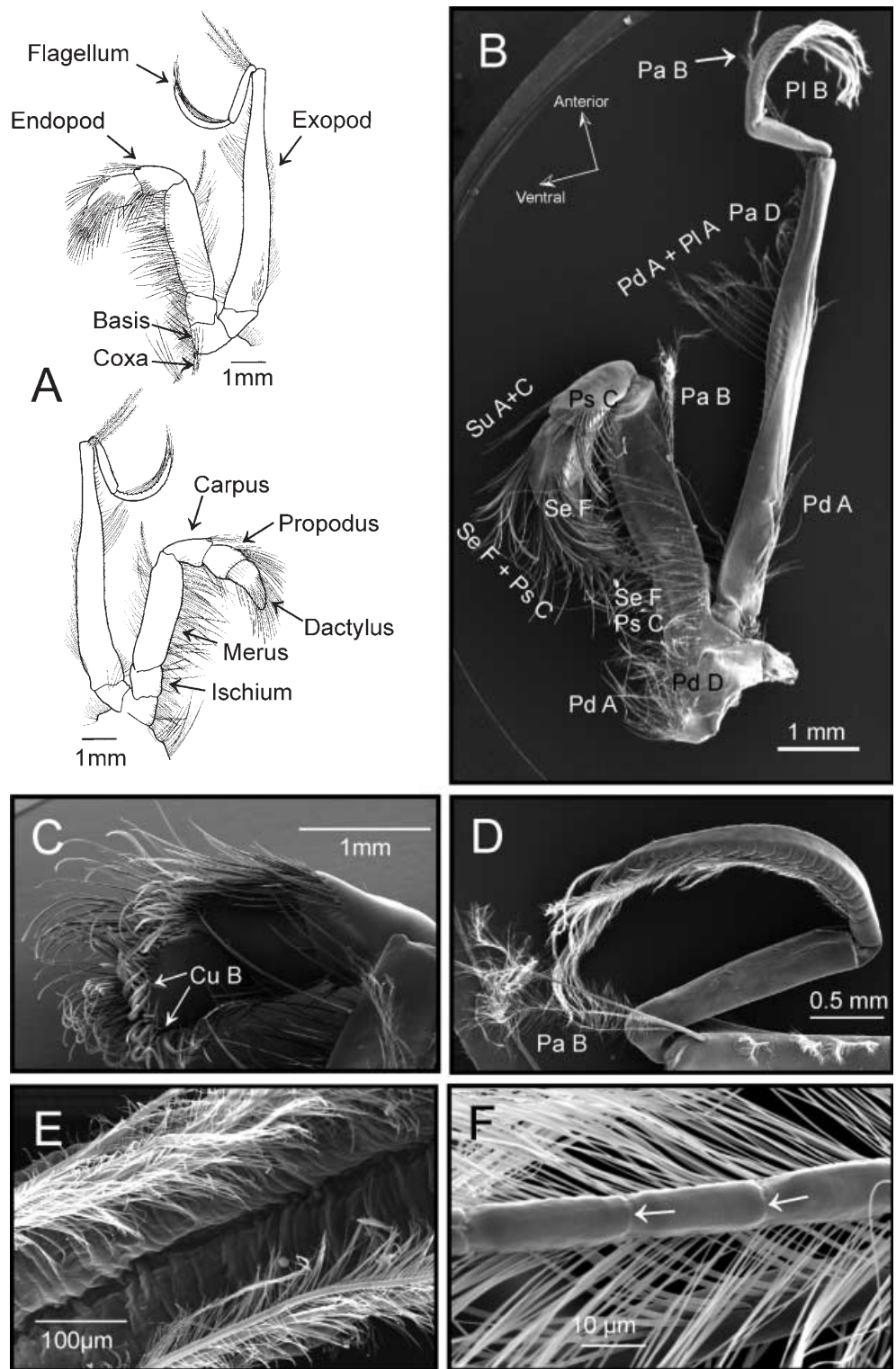


slender exopod (Fig. 9A, B). The coxa and basis are built like a normal thoracic protopod and carry long plumodenticulate setae.

The endopod is generally covered with robust setae, especially on the three distalmost segments (Fig. 9C). The dactylus has serrate and cuspidate setae distally and densely packed serrate setae on the medial and lateral rims. The propodus has a cluster of serrate setae distally on the medial side, and they intermingle with the setae on the dactylus. The carpus also has a cluster of serrate

setae distally on the medial side, reaching the cluster on the propodus. All these setae tend to bend dorsally. In general no setae attach to the posterior side of the distalmost segments where pores are found in the cuticle. The merus is relatively long (1/3 of the total length) and has a very flexible joint with the carpus, which enables the distal segments to bend posteriorly and medially, reaching the bases of Mxp1. Distally on the dorsal edge of the merus there is a cluster of long pappose setae, and on the ventral edge long serrate setae protrude medially.

Fig. 9 *Munida sarsi*. Maxilliped 2. **A** Right Mxp2 (*top* medial view; *bottom* lateral view). **B** Medial view of Mxp2 with setal composition. **C** Posterior view of carpus, propodus and dactylus, distalmost setae are very robust (Cu B). **D** Lateral view of flagellum. As in resting position, the Pl B setae are aligned with the distal segment. **E** Dorsal view of flagellum with heavily folded cuticle. **F** Close up of Pl B setae on flagellum, arrows indicate joints in setal shaft (Cu cuspidate; Pa pappose; Pd plumodenticulate; Pl plumose; Se serrate; Su setulate setae)



The long slim exopod attaches dorsally to the basis and points dorso-anteriorly. It terminates in a large two-segmented and sickle-shaped flagellum (Fig. 9D); the distalmost segment has a folded and flexible cuticle (Fig. 9E). When the flagellum moves upwards, the water pressure stretches the cuticle with the result that the

plumose setae (Fig. 9F) move to a perpendicular position, greatly enlarging the surface. A small cluster of very long pappose setae (Pa B) is situated close to the joint of the flagellum. Along the proximal part of the exopod there are long pappose, plumose and plumo-denticulate setae.

Maxilliped 3

Maxilliped 3 is situated ventral and lateral to Mxp2. It is the largest mouthpart and, like Mxp2, it is structured like a pereopod, with a small protopod and a large five-segmented endopod, but it also possesses a long exopod and, unlike Mxp2, an epipod (Fig. 10A, B).

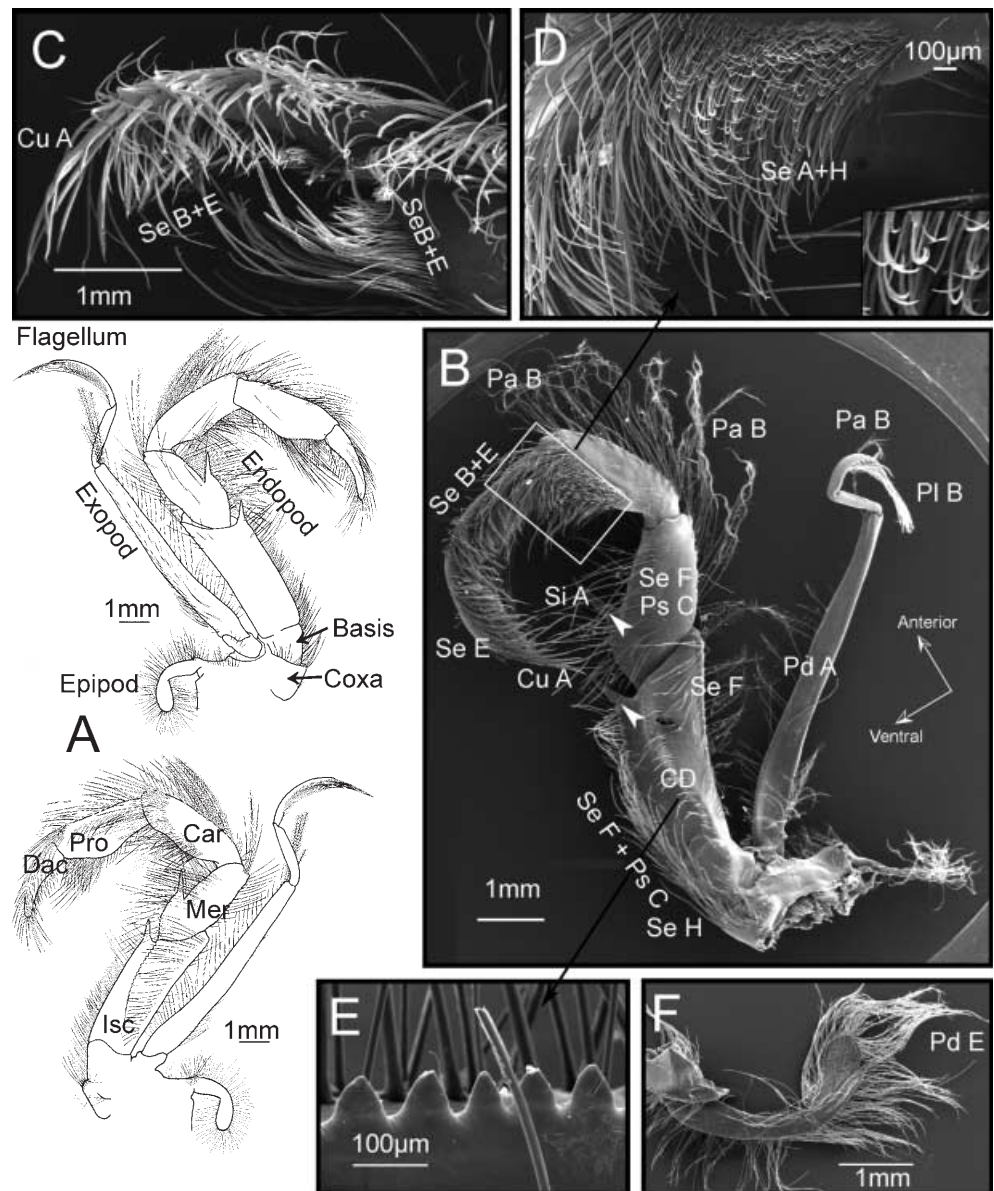
The endopod has very stout setae especially on the medial and lateral edges of the two distalmost segments (Fig. 10C). The dactylus has strong cuspidate setae on the distal tip and stout serrate setae (Se B) along the medial and lateral edges. On the edges bordering the naked posterior side, the propodus has clusters of robust serrate setae. A dense cluster of setae with hooked tips specialized for grooming occurs distally on the medial rim of the carpus (Fig. 10D). A large spine

is situated ventrally both on the merus and on the ischium (Fig. 10B, arrowheads). In addition the ischium has a row of 18 to 22 cuticular teeth, the crista dentata, along the total length of the medial side (Fig. 10E). The joint between the merus and the carpus is the most flexible.

The exopod resembles that of Mxp2 in both shape and size. It attaches dorsally to the basis pointing upwards and forwards, which places the flagellum a little lateral and ventral to the flagellum of Mxp2. The setal composition differs somewhat since the exopod of Mxp3 has fewer setae (Figs. 9B, 10B).

The epipod is small and flattened (Fig. 10A, F). It sits dorso-laterally on the coxa and points posteriorly, which places it under the first two pairs of gills. Along the margin of the epipod there are plumodenticulate setae which extend between the gill filaments.

Fig. 10 *Munida sarsi*. Maxilliped 3. **A** Right Mxp3 (*top* lateral view; *bottom* medial view). **B** Medial view of Mxp3 with setal composition, note large spines on the merus (*Mer*) and ischium (*Isc*) (*arrowheads*). **C** Posterior view of shovel-shaped propodus (*Pro*) and dactylus (*Dac*) with very stout setae. **D** Dense setal cluster on medial side of the carpus (*Car*) used for grooming antenna 1. Some setae with hooked tips (close up in inset). **E** Ventral view of crista dentata (*CD*). **F** Dorsal view of epipod. The long plumodenticulate setae lie between gill filaments (*Cu* cuspidate; *Pa* pappose; *Pd* plumodenticulate; *Pl* plumose; *Se* serrate; *Si* simple)



Movement patterns

From preliminary analyses of the video sequences we gleaned some behavioral data, which facilitate the understanding of the morphology.

Resting position/food detection

When the mouthparts are not handling any food objects the labrum and the mandibular palps remain in posterior positions. The mandibles, Mx1 and Mxp1 are opened slightly to approximately 1/3 of their maximum span. Mx2 perform synchronized latero-medial movements with a frequency of 2 to 3 Hz which make the scaphognathites undulate in the gill chamber creating the respiratory currents. The flexibility of the scaphognathite and the enlargement of its surface by the marginal plumose setae (Pl A) make it an efficient unidirectional pump. The endopods of Mxp2 and Mxp3 hold the positions seen in Fig. 2. The flagella on their exopods beat dorso-ventrally with a frequency of 13 to 17 Hz. For other anomurans it has been suggested that the current created hereby assists in respiration and the rejection of unwanted particles (Nicol 1932) or only in rejection (Kunze and Anderson 1979). In *Munida sarsi* the flagella pump up water from the sediment as described for the hermit crab *Pagurus rubricatus* by Schembri (1982b). The water passes through clusters of setae on the mouthparts, especially clusters of large pappose setae (Pa B) on Mxp2 and Mxp3.

The flexible cuticle of the flagella ensures that they are extended during the upward stroke only, creating a unidirectional current from the sediment upwards. The fast movements result in high pressure on the plumose (Pl B) setae, and therefore the joints in the setal shaft (Fig. 9F) probably serve to prevent them from breaking. Furthermore the flagella of the Mxp2 and Mxp3 exopods beat out of phase, which creates a steady flow.

Food gathering

Food gathering resembles the behavior described for *Pagurus rubricatus*. Large food objects, such as lumps of fish meat, are normally picked up by the long chelipeds and handed over to the endopods of Mxp3. Both endopods of Mxp3 stretch out as they grasp the food between their dactyli and propodi. In some cases the objects are picked up directly from the sediment by the dactyli of the endopods of Mxp3.

Muddy sediment (gravel is ignored) is gathered either with the dactyli of pereopods 2 to 4, the chelipeds or with the dactyli of the endopods of Mxp3. In the first two cases the sediment is passed on to the endopods of Mxp3 as the dactyli comb through the setae holding the sediment on the cheliped or pereopod. The distal end is

shovel shaped and makes Mxp3 suitable for digging up mud (Fig. 10C). This is optimized by the dense rim of Cu A and Se B + E setae on the propodus and dactylus, the large denticles of which function as hooks. These robust setae also enable the endopods of Mxp3 to collect mud picked up by the pereopods and to grasp and hold large objects handed over by the cheliped. The great flexibility of the endopods of Mxp3, especially in the merus–carpus joint, is important in the process of transferring food towards the mouth.

Food handling/sorting

From the endopods of Mxp3 the potential food is passed on to the 1/3 distalmost segments of the endopods of Mxp2 depending on the size or amount. The serrate setae (Se A + F) on the distal segments of the endopods of Mxp2 are not quite as robust as those on the Mxp3 endopods (Se B + E, Cu A), this enables Se A and Se F to pass between the setae of the Mxp3 endopods and collect potential food items. As found for the endopods of Mxp3, the very flexible merus–carpus joint of the Mxp2 endopods and their shovel-shaped distal segments (Fig. 9C) make them suitable for passing food to the bases of Mxp1. While Mxp2 and Mxp3 make these movements, Mx1, Mx2 and Mxp1 are fully opened. When Mxp2 are bent posteriorly, the more flexible Mxp1 perform dorso-ventral movements collecting items with the setae on their medial edges. Afterwards the endopods of Mxp2 and Mxp3 tend to be held more medially, where they form a setal screen and, with long Si A and Se F setae on the merus and ischium, prevent particles from being lost ventrally. Laterally the screen consists of the Mxp2 and Mxp3 exopods with their long Pd A and Pl A setae.

When sediment or other small particles reach Mx1, Mx2 and Mxp1 they are handled by the setae on the medial edges of their bases. They possess seven different seta types (Cu A + B + C, Se C + H, Su A and Ps A) in complex arrangements (Figs. 6E, 7C, 8C). The cuspidate setae are responsible for moving the particles (especially those on the bases of Mx1). The dorso-ventrally flattened form of these appendages makes it possible for the animal to have more movable structures just in front of the mouth. This is ideal for handling rather small objects, which are in general turned around until they are oriented correctly for the mandibles. The bases beat out of phase into the object and ensure that it is held tight at all times. Some particles are retained and put between the mandibles by the bases of Mxp1 and processed further (see below); others are pushed dorso-anteriorly into the strong flagellar current and thereby rejected.

Very large food objects such as lumps of fish or sea urchin spines are held by the endopods of Mxp2 and Mxp3 and pushed directly towards the mandibles. Here Mx1 actively presses against the object, possibly making fine adjustments in orientation. The bases of Mxp1 are

also active and tend to make dorso-ventral movements along the food object, squeezing it to fit between the mandibles. This is done by the long and stout Cu B setae. Large objects not to be eaten are not rejected by the flagellar current but simply dropped.

Cutting/crunching

Cutting is a very stereotyped and coordinated action, and the functions of the structures involved are fairly easy to interpret. The mandibles of *Munida sarsi* work in much the same way as earlier described for other anomurans (Nicol 1932; Kunze and Anderson 1979; Schembri 1982b). When a food object is passed to the mandibles, they move laterally, and the labrum and mandibular palps move to a dorso-anterior position making room for the item. Not too calcified objects are normally placed between the posterior and medial teeth of the incisor processes and held tightly by the spines on the bases of Mx1 (Fig. 6E). The mandibles move medially until the incisor processes overlap about 1/5, always with the left incisor on the dorsal side, and this eventually cuts off a piece of the object. The larger teeth on the left incisor are important since this incisor, along with the spines and very robust Cu A setae on the bases of Mx1, prevents the objects from slipping while cutting. The teeth on the right incisor are not as important since they lie between the left incisor and the bases of Mx1 during cutting.

Highly calcified objects are placed between the molar processes and crushed by the movements described above. The flattened structure of the molar processes with their rims of tubercles (Fig. 5B, C) ensures that even very smooth objects such as mollusk shells will not slip away.

Following a cut, the mandibles move apart and the labrum moves posteriorly along with the mandibular palps. The U-shape of the palps enables them to move the distal segment through the "tubes" created by the labrum, the incisor processes and the molar processes. This movement along with the movement of the labrum pushes the cut-off food item towards the mouth opening. *Munida sarsi* are able to direct this push in a finely tuned way. When the molar processes have crushed a calcified object, the pieces are not pushed towards the mouth opening immediately afterwards, rather they are pushed outside, ventral to the mandibles, where they are sorted by the bases of Mx1, Mx2 and Mxp1 and the calcified parts are rejected. The rest is ingested. The curved setae (Se C + G) on the distal palp segment and the spinelike micro-setae (Fig. 3B) on the posterior edge of the labrum come into contact with the food items, operating as hooks which ensure a good grip on the prey. If a piece of alga with attached polychaetes is cut off by the incisors, the algal part is pushed out ventrally and rejected, while the polychaetes are pushed towards the mouth and ingested.

Ingestion

When food particles are pushed towards the mouth they must also be pushed dorsally into the mouth proper to be ingested. We could not observe this part of the feeding process since the mouth is totally covered by the protopods of the maxillipeds. According to their location (Fig. 2A) and shape, the ingestion is due to the action of the coxae of at least Mx1 and Mx2, but possibly also the coxa of Mxp1. The curved form of the coxae and their setae ensure the direction of the push. The dense rows of Pa C and Pd F setae (Figs. 6B, 7D) form an efficient setal screen, preventing the animal from dropping any of the particles. The presence of robust setae (Cu A + B) indicates that the coxae may macerate the food one last time before ingestion.

Grooming

As for other galatheids most grooming is done by the modified fifth pereopod, but these appendages cannot reach the anterior part of the cephalic region, which therefore must be groomed in other ways. Especially the antennae are groomed frequently, and the endopods of Mxp3 are active in this process. Clusters of setae on the carpi (Fig. 10D) and propodi grasp antenna 1 and antenna 2, respectively. The serrate setae (some with hooked tips) found in these clusters are perfect for scraping dirt off the antennae and their setae. The setae on the carpi used for grooming antenna 1 are less robust (Se A + H) than those on the propodi (Se B + E) used for grooming antenna 2. The dactyli of the Mxp3 endopods groom the pereopods and especially the chelipeds. This process can be hard to separate from sediment gathering since everything groomed off by the endopods of Mxp3 is passed to the other mouthparts and sorted as described above.

The bases of Mx1, Mx2 and Mxp1 groom each other with rows of Se E and Su A setae placed on the dorsal and ventral surfaces (e.g. Fig. 6F). When the limbs move in a latero-medial plane these setae scrape the surface of the neighboring limb and remove attached particles. Since the setae along with their denticles and short setules point medially, the particles will be moved in this direction. The mandibles lack setae on the incisor processes, and therefore the dorsal part of Mx1 is groomed by the micro-setae of the paragnaths. The paragnaths also ensure that nothing is lost in the space between the incisor and Mx1. They were seen in a few of the video sequences and never seemed to move. The two anterior-most gills are groomed by the epipod of Mxp3 on the ventral side. The dorsal side is groomed by the epipod of Mxp1 but also by the scaphognathite. This additional function of the scaphognathite has also been noted for other decapods (Bauer 1981).

The functions of the very reduced endopods and of the exopods of Mx1, Mx2 and Mxp1 remain unclear.

One possible function of the endopod of Mx2 could be to groom the joint between the mandible and the mandibular palp, as the distal part rubs it constantly.

Discussion

Munida sarsi is an opportunist utilizing a wide spectrum of food types; in our experiments they ate almost all kinds of animal tissue, just as found for many hermit crabs (Schembri 1982c; Volvenko 1994, 1995) and for *Munida tenuimana* (Cartes 1993). In decapods, food is normally detected by the antennae, especially by the flicking flagellum of antenna 1 (Herrnkind 1983). *M. sarsi* also has another way of detecting food. The tank observations revealed that they possess sensory structures on the dactyli of pereopods 2 to 4, which “dance” on the bottom when they are near the food object. When no larger items were nearby, the animals started sorting the muddy sediment in search of food. Algal material was rejected and foraminiferans, which make up a large portion of the sediment at the collection area and could be a rich food resource, were, surprisingly, also ignored. Our preliminary video observations have shown that some mouthparts perform very stereotyped movements during feeding and grooming, while others are capable of a wider range of tasks. In general the mouthparts closest to the mouth have the least complex movements, with the mandibles being able to perform only one task even when handling different types of food objects.

Understanding the functional morphology of the mouthparts and their setation largely depends on understanding the correlation between seta type and function. We find some correlation, but it still remains questionable whether or not there is a connection between function (especially sensory) and seta type defined by external morphology.

Setae can have three different functions: mechanofactory, mechanosensory or chemosensory, but a single seta can easily combine all three functions (Derby 1982; Watling 1989). In *Munida sarsi* we found 30 different seta types (including variants) on the mouthparts alone, and we consider it likely that each seta type has a rather specific function. This massive diversity (Fig. 1) impedes functional interpretations, since almost any action of the mouthparts involves several seta types and almost every seta type is involved in several actions. The mechanofactory functions of the setae are the easiest to map because they can be seen on the video sequences, and the results are equivalent to earlier findings (Farmer 1974; Factor 1978; Derby 1982; Felgenhauer and Abele 1983; Lavalli and Factor 1992; Nickell et al. 1998).

Cuspidate setae such as Cu A from the bases of Mx1 (Fig. 6E) and endopods of Mxp3 (Fig. 10C) are in general used to hold and grind prey items, with their robust and naked tips ensuring that they are not damaged during the handling of prey. Serrate setae often serve in

grooming; their pointed denticles scrape off fouling material, and, since the denticles point distally, the particles are pushed away from the structures instead of being trapped. The composition of the structure to be groomed probably determines the size of the denticles, as seen in the case of the antennae: the delicate aesthetasces on the flagella of antenna 1 are groomed by serrate setae with small denticles (Se A + H, Fig. 10D), whereas the flagella of antenna 2 are groomed by very robust serrate setae (Se B + E). In addition to the denticles, many serrate setae possess setules which may also assist in grooming. The most delicate grooming might be performed by the slender setulate setae like Su B on the dorsal surface of the coxa of Mxp1 (Fig. 8B). Serrate setae are also often involved in the collection and transfer of food objects since their denticles ensure a good grip. Plumose setae either serve as filters, as setal screens or to enlarge surfaces. For *Munida sarsi* the two latter functions seem to apply to the plumose setae, which assist in the pumping of water (Pl A on the scaphognathite, Fig. 7B; and Pl B on the flagella of Mxp2 and Mxp3, Figs. 9B, 10B) and form setal screens preventing food objects from being lost (Pl A on exopod of Mxp2, Fig. 9B). Plumodenticulate and pappose setae have much the same mechanofactory functions as plumose setae. In *M. sarsi* Pd A + B form setal screens in the space between the coxa and base of Mx2 and Mx1, respectively (Fig. 6B); Pd A makes the finest screen, which is also seen on the exopods of Mxp2 and Mxp3 (Figs. 9B, 10B). Pd F on the coxae of Mx1 (Fig. 6B) have combined mechanofactory functions. The robust distal part provides the ability to push food into the mouth and the proximal setules catch small food particles.

With respect to the sensory function little can be added with hard evidence, but according to studies by Schmidt and Gnatzy (1984) and Crouau (1989) almost all setae have a sensory function. Serrate setae have been found to be chemoreceptive in *Homarus gammarus* (Shelton and Laverack 1970) and *Homarus americanus* (Derby 1982) and are in general thought to be contact chemosensory (Watling personal communication). This correlates well with our observations of *Munida sarsi*; we suggest that the mandibular palps have a sensory function (probably chemosensory) since they can distinguish between algal and animal tissue. All setae on this limb are serrate. The sensory structures could be cuticular, but we found no indication of this. It is also clear that the distal end of the endopod of Mxp3 has a sensory function during food collection, and almost all the setae found here are also serrate. Furthermore, we suggest a chemosensory function for pore setae due to their apical pore and slender build, and Ps A setae on the medial margin of Mx2 are probably the main actors in deciding whether or not to retain particles during sediment sorting. Setae with long setules (plumose, pappose and plumodenticulate) are often correlated with mechanoreception (Watling 1989), and this could be the case for the clusters of Pa B. Situated in the current produced by flagella, they may detect the presence of particles in that current. The Pa B setae could

also function as a filter and strain particles from the currents in a way similar to that suggested for *Pagurus bernhardus* by Gerlach et al. (1976).

The many pores on the dorsal surfaces of Mx1, Mx2 and Mxp1 and on the ventro-medial edge of the paragnaths (Fig. 4C) might also be chemoreceptors. But they are more likely tegumental glands since the size and shape corresponds with earlier descriptions of pores from such glands (Talbot and Demers 1993). There are many suggestions for the functions of these glands (Alexander 1989), mucus secretion is one of them, and mucus could be important for ingestion.

The organization and gross morphology of the mouthparts of *Munida sarsi* greatly resemble descriptions from earlier and less detailed studies on *Galathea* and *Munida* [*G. squamifera*, *G. stringosa*, *G. dispersa*, *Munida rundeleitii* (= *Munida rugosa*): Nicol 1932; *G. squamifera*, *G. nexa* and *G. intermedia*: Pike 1947; *M. rugosa*: Zainal 1990]. The sparse information on the setation given by these authors is also comparable to that for *M. sarsi*. They found very robust setae or spines on the medial edge of the bases of Mx1, strong or stout setae on the distal segments of the Mxp2 endopods and Mxp3 endopods, a cluster of setae distally on the carpi of Mxp3 endopods used for grooming, and plumose setae on the flagella of the Mxp2 and Mxp3 exopods. Similarity is also found in the functions of the mouthparts. For the three species of *Galathea* and for *Munida rugosa*, Nicol (1932) gave some details on food gathering, sediment sorting and maceration of large particles, and her results resembled our findings for *M. sarsi*. She was unable to detect the mechanism of sediment sorting, but due to the similar mouthpart morphology it seems very likely to be the same mechanism we describe for *M. sarsi*. Very stereotyped movements, such as the cutting of food objects, were shown to proceed in much the same way, however, she did not detect any asymmetry in the mandibles. Mandibular asymmetry has been found in Paguridea (Roberts 1968), *Brachyura* (Schembri 1982a; Skilleter and Anderson 1986), *Palinura* (Suthers and Anderson 1981) and *Astacidea* (Farmer 1974). None of these authors correlated it with function.

The organization and morphology of the mouthparts in Paguridea (hermit crabs) also resembles those in *Munida sarsi* (*Pagurus bernhardus*: Orton 1927; Gerlach et al. 1976; *Clibanarius taeniatus*, *C. virescens*, *Paguristes squamosus* and *Dardanus setifer*: Kunze and Anderson 1979; *Pagurus rubricatus*: Schembri 1982b; *Xylopagurus*: Lamaitre 1995). The greatest differences involve the endopods of Mx1, Mx2 and Mxp1, the exopod of Mxp1, and the total lack of epipod on Mxp1 in pagurids. These structures are not directly involved in food processing, but one of the differences found for the exopods of Mxp1 is significant. In hermit crabs they still have a functional flagellum taking part in producing the currents around the buccal area. Crushing by the molar processes is not described for any of the hermit crabs, and, from the morphological descriptions, it seems as though they are not suited for this purpose since they

lack tubercles. In the case of *Pagurus traversi* (Schembri 1982c) and *P. rubricatus* (Schembri 1982b) crushing is done by the chelipeds, and there is a tendency towards hermit crabs using their chelipeds more for maceration than seen in the case of *M. sarsi*. The long, slender and rather weak chelipeds of *M. sarsi* are mostly used in food gathering and aggressive behavior (Berril 1970; authors' observations).

The study of *Pagurus rubricatus* by Schembri (1982b) also provides detailed information on the setation of the mouthparts. He applies 19 seta types, and their overall arrangement and function are similar to *Munida sarsi*, especially with relation to the setal screens around the buccal area. The medial edges on the bases of Mx1 and Mx2 from *P. rubricatus* have setation similar to that of *M. sarsi*, but the setae are used differently. Schembri (1982b) describes specialized simple setae on the bases of Mx2 (his Fig. 12b) used for scrubbing sand grains. They seem identical to the Ps A setae in our study, for which we suggest a chemosensory but no mechanoeffector function due to their delicate structure. He also claims that the cuspidate setae on the bases of Mx1 have a filtering function. In the process of sediment sorting *P. rubricatus* use the bases of Mx2 to force the sediment through the setae on the medial edges of Mx1 which thereby withhold the largest particles for subsequent rejection.

Although the mouthparts of *Munida sarsi* show great morphological similarities to those of pagurids they have a somewhat more limited repertoire of feeding strategies. We therefore conclude that close similarity in mouthpart morphology, even on the SEM level, does not necessarily entail a similarity in the functional spectra. Distinct behavioral differences in food choice and manipulation may have evolved – without accompanying morphological changes – as a result of habitat-specific factors.

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