

Mechanical Functions of Setae From the Mouth Apparatus of Seven Species of Decapod Crustaceans

Anders Garm*

Department of Zoomorphology, Zoological Institute, University of Copenhagen, 2100 Copenhagen Ø, Denmark

ABSTRACT The mouthpart setae of seven species of decapods were examined with macro-video recordings and scanning electron microscopy. The general mechanical (nonsensory) functions of the different mouthparts are described and an account of their setation is given. This offers the possibility to determine the mechanical functions of the different types of setae. Pappose setae do not participate in food handling but in general make setal barriers. Plumose setae likewise do not contact food objects but assist in current generation. Papposerrate setae are rare but they were seen to assist in pushing food particles into the mouth. Serrulate setae are very common and mainly participate in gentle food handling and grooming. Serrate setae are used for more rough food manipulation and grooming. The roughest shredding, tearing, and manipulation of prey items are handled by the cuspidate setae. Simple setae seem to be divided into two populations with very different functions. On the maxillipeds of *Panulirus argus* they are used for shredding, tearing, and holding the food objects, but on the basis of maxilla 2 of three other species they appear to have very little mechanical influence and only when handling small prey items. The functional scheme seems to be consistent within the Decapoda. *J. Morphol.* 260:85–100, 2004.

© 2004 Wiley-Liss, Inc.

KEY WORDS: Crustacea; Decapoda; mouthparts; setal types; mechanical functions; sensory functions

Crustaceans have hair-like outgrowths in their exoskeleton on all body parts. These outgrowths, the setae, have a variety of different functions, which fall in two major groups: sensory and mechanical. The setae are a very important part of crustacean sensory systems and the sensory functions have received a fair amount of attention, especially when it comes to the aesthetascs, which are olfactory setae situated on antenna 1 of most crustaceans (Guse, 1980; Gleeson et al., 1996; Hallberg et al., 1997; Derby et al., 1997; Derby, 2000). Crustacean setae have been found to be chemosensory (both olfactory and gustatory), mechanosensory (both tactile and vibration sensitive), osmosensory, or a combination of two or more of these modalities, but the data more or less exclusively stem from studies on decapods (Tazaki, 1975; Hatt and Bauer, 1980; Altner et al., 1983; Laverack, 1987; Derby, 1989; Voigt and Atema, 1992; Derby et al., 2001; Garm et al., 2003).

Most setae also have many and just as important mechanical functions during behaviors such as locomotion, digging, grooming, and feeding and this mainly involves the setae on the appendages. There are indications that the mechanical functions are largely correlated with the size, shape, and location of the setae and with the ultrastructure of the cuticle. It has for example been found in numerous cases that setae on appendages used for swimming are almost always feather-like setae (plumose setae) (e.g., Kohlhage and Yager, 1994). These setae have long lateral outgrowths along the entire length of the setal shaft, which provides a large surface and thereby a large drag. Other appendages, such as the mouthparts, participate in more diverse behaviors and they have a much more complex setation. This complexity concerns both the arrangement of the setae and their morphology. The mechanical functions are therefore harder to detect but morphological studies supported by behavioral observations have mapped some of them (Fryer, 1977; Schembri, 1982a; Stamhuis et al., 1998; Garm and Høeg, 2001). The morphological diversity has led to several studies of decapod mouthparts suggesting more than 20 setal subtypes (Lavalli and Factor, 1992; Garm and Høeg, 2000; Coelho et al., 2000), but often there is little or no consideration given as to whether these extremely detailed separations based on morphology have any functional implications or not. The functions of a single mouthpart seta can be manifold, in that most are bimodal sensory structures containing both mechano- and chemoreceptor cells. On top of that they are normally involved in one or more behaviors where they serve mechanical functions (Garm et al., 2003).

Supplementary material for this article is available via the internet at <http://www.interscience.wiley.com/jpages/1526-954X/suppmat>

Contract grant sponsor: Ph.D. program at Copenhagen University.

*Correspondence to: Department of Zoomorphology, Zoological Institute, University of Copenhagen, Universitetsparken 15, 2100 Copenhagen Ø, Denmark. E-mail: algarm@zi.ku.dk

DOI: 10.1002/jmor.10213

The major determining factor for the external morphology is not known but it is the goal of this study to map the mechanical functions of the mouthpart setae of seven species of decapod crustaceans and to test the hypothesis that these functions are correlated with the external morphology. This is done by macrovideo-recording eating animals combined with scanning electron microscopy.

MATERIALS AND METHODS

The seven species studied were: *Penaeus monodon* Fabricius 1798, *Palaemon adspersus* Rathke 1837, *Stenopus hispidus* Olivier 1811, *Cherax quadricarinatus* von Martens 1868, *Panulirus argus* Latreille 1804, *Pagurus bernhardus* (L.), and *Carcinus maenas* (L.). They were chosen to cover a wide phylogenetic range within the Decapoda.

Six *Penaeus monodon* were obtained from the Australian Institute of Marine Science (AIMS), Townsville, Australia. They were young adults of both sexes with a carapace length between 4–5.5 cm. *Palaemon adspersus* was caught in Øresund, north of Copenhagen, Denmark. The specimens used were all large adults. Six *Stenopus hispidus* (three pairs of medium-sized adults) were supplied by the public aquarium, Danmarks Akvarium. Ten young adults of *Cherax quadricarinatus* were used and they were likewise obtained from Danmarks Akvarium. Seven *Panulirus argus* were obtained from the Bermuda Biological Station Research. They were of both sexes and had carapace lengths between 10–15 cm. *Pagurus bernhardus* and *Carcinus maenas* were caught in Øresund north of Copenhagen.

All the animals were kept in the facilities of Danmarks Akvarium, Copenhagen, Denmark. Single individuals of *Penaeus monodon* and pairs of *Stenopus hispidus* were kept in 50-L tanks with running seawater at 22–24°C and the seven specimens of *Panulirus argus* were kept in a 200-L tank with the same water conditions. Several individuals of *Palaemon adspersus*, *Pagurus bernhardus*, and *Carcinus maenas* were kept together in 200-L tanks with running seawater at 12°C and *Cherax quadricarinatus* were kept in a 500-L tank with running freshwater at 15°C. In the maintenance tanks the animals were fed squid, mussel, or krill.

Light Microscopy

A specimen of *Pagurus bernhardus* was fixed in 70% ethanol and dissected through the midline to reveal the arrangement of the feeding apparatus. For the line drawing in Figure 1 a standard dissection microscope equipped with camera lucida was used.

Scanning Electron Microscopy

Both sides of the mouth apparatus from one or two specimens of each species were prepared for SEM. The specimens were anesthetized in a freezer and dissected in sea- or freshwater according to the species and the individual mouthparts were cleaned with a beaver-hair brush and fixed in 2% formalin in either sea- or freshwater. After at least 3 days of fixation they were dehydrated in a series of ethanol, transferred to 100% acetone, and critical-point dried. After drying they were sputter-coated with gold and the specimens were viewed with a JEOL 840 standard microscope or a JEOL JSM 6335F field emission microscope and the pictures were taken digitally using the programs SEMafore 3.0 or PC-SEM and manipulated in CorelDraw 10.0.

Video Recordings

Except for *Penaeus monodon* and *Panulirus argus*, the animals were fastened during recordings. A knot was glued to their car-

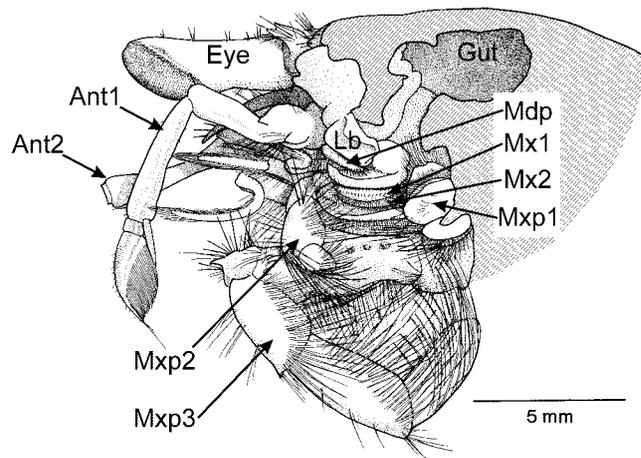


Fig. 1. Overview of the mouthpart arrangement of decapods exemplified by the mouth apparatus of *Pagurus bernhardus*. Animal is sectioned along the midline and striated area indicates dissected tissue. Positions of mouthparts resemble nonfeeding living animal. Most of the setae on mouthparts seen in the drawing are directly involved in food handling. Ant1, antenna 1; Ant2, antenna 2; Lb, labrum; Mdp, mandibular palp; Mx1, maxilla 1; Mx2, maxilla 2; Mxp1, maxilliped 1; Mxp2, maxilliped 2; Mxp3, maxilliped 3.

apace with cyano-acrylate and an iron bar was screwed into the knot. The iron bar could be manipulated in all three dimensions, ensuring the right angle during recordings, which took place in a 25-L tank. After attachment, the animals acclimated for 15 min. The specimens of *P. monodon* and *P. argus* were too forceful to be attached in this way and these animals moved freely in a 50-L tank during recordings. For the recordings, all animals were fed pieces of squid, pieces of fish filet, krill, live artemia, dead artemia, chopped blue mussel, whole blue mussel, blue mussel shell with little tissue, algal tissue, muddy sediment, and gravel with a thin layer of biofilm. Before recordings, warm-water animals were starved for 24 h and cold-water animals for 3 days.

Recordings were done from the outside with a 3CCD color camera (Sony DXC-950P) equipped with a macrolens (MicroNikor 105 mm) and stored on either DV or S-VHS videotapes. Light was supplied by a standard 120W bulb. Recordings were also obtained from *Panulirus argus* using an endoscope (Olympus Trueview II Telescope) mounted on a S-VHS camera (Olympus OTV-SC). This technique was only used on *P. argus*, as it was the only species large enough to eat without being disturbed by the endoscope. Prior to recordings the endoscope was smeared in mussel juice to allow entrance into the animals mouth apparatus.

Video sequences and series of still pictures were stored on a PC via a framegrabber card (DVRaptor, Canopus) with a time-resolution of 0.02 sec (50 fields/sec). The actions of single setae or clusters of setae were followed in the series and representative pictures were selected for the figures.

RESULTS

Types of Setae

Seven types of setae can be distinguished from the manner in which the substructures are combined: pappose, plumose, serrulate, serrate, papposerrate, simple, and cuspidate setae. The types are only briefly described here and are dealt with in more detail in a parallel article. The terminology in general follows Lavalli and Factor (1992) except for the

papposerrate setae, which they refer to as plumodenticulate.

Pappose setae. The shaft of pappose setae is often very long and slender and they never display a pore. They have long, well-defined setules scattered randomly along the total length of the shaft. The setules are clearly articulated with the shaft and have serrate edges, with most teeth situated distally.

Plumose setae. Plumose setae have long setules along the entire shaft arranged in two strict rows on opposite sites of the seta, giving them a feather-like appearance. Plumose setae are the only setae that have a supracuticular articulation with the general cuticle and this makes them extremely flexible

Serrulate setae. Serrulate setae are slim, have a naked proximal part, but have small setules (<15 μm long) distal to the annulus. The setules can be arranged in rows, normally three, or occur randomly along the shaft. They point towards the tip of the seta with an angle of less than 45° .

Serrate setae. Serrate setae have a naked proximal half but distal to the annulus they have two rows of denticles with $120\text{--}180^\circ$ between them. The denticles are arranged parallel to the long axis of the seta and point towards the tip of the seta. The distal half may also have setules on the opposite side of the denticles and there can be from a few to a few hundred.

Papposerrate setae. Like pappose and plumose setae, papposerrate setae are long and slender. On their proximal half to two-thirds they have long, randomly arranged setules, like pappose setae, but on the distal part they have two rows of denticles, like serrate setae. In the area with the denticles there may be additional small setules on the opposite side of the denticles.

Simple setae. Simple setae are long and slender and, as the name implies, they completely lack outgrowths on the setal shaft. They have a pointed tip, which may or may not have a terminal pore

Cuspidate setae. Cuspidate setae are very robust, with a L/W ratio below 8 when width is measured at the base of the seta. They have a broad base and taper gradually towards the somewhat rounded tip. They may or may not have a subterminal pore and in most cases they have no outgrowths. The distal one-third is always naked.

In the following, the mechanical functions of the different mouthparts are described. It is not done in great detail because it is the comparison of the overall functions of the mouthparts correlated with the setation that is the focus of this article. The setal composition of the mouthparts of the seven species is summarized in Table 1.

Labrum

The labrum lies anterior to the mouth and is large and fleshy in all the species (Fig. 1). The labrum of

Cherax quadricarinatus is the only one carrying setae. They are papposerrate, sit on the ventral and posterior surface, and point posteriorly towards the mouth (Fig. 2A). The other species have setules or small denticles on the labrum. The labrum is held in a lowered position at rest or when food objects are placed between the mandibles (Fig. 2B), but during a bite it moves anteriorly to make room for the mandibles (Fig. 2C). After the bite has been performed it moves posteriorly again, pushing the bitten off piece towards the mouth.

Mandible

The mandibles of all seven species are divided into a molar and an incisor process and a mandibular palp (Fig. 3A–C). Normally the mandible only has setae on the mandibular palp, but in the case of *Cherax quadricarinatus* papposerrate setae are found on the ventrolateral side of the incisor process where they contact the paragnath. These setae do not contact the prey items but fill the space between the mandible and the paragnath.

The mandibular palp has three segments and is attached laterally on the mandible (Fig. 3A–C). In the case of *Stenopus hispidus*, *Cherax quadricarinatus*, *Carcinus maenas*, and *Pagurus bernhardus* it is U-shaped and lies in a groove between the molar and incisor processes (Fig. 3A). It moves dorsoventrally and assists the labrum in pushing pieces of food into the mouth after biting or crunching (Fig. 3D,E). The distalmost segment has a dense population of stout serrate or serrulate setae, ensuring a firm grip on the food. The proximal segments do not contact the food and have many fewer setae, which are mostly pappose, serrulate, or serrate. These setae do not have any detectable mechanical functions.

The mandibular palp of *Panulirus argus* is almost straight and it is situated in front of the mandible (Fig. 3F). It only makes small independent movements and in general follows the movements of the incisor process. The distal segment has simple setae pointing ventrally, which have prey contact during feeding (Fig. 3F). They do not manipulate the prey items but may function as a “roof,” preventing food from escaping anterodorsally.

Palaemon adspersus has a rudimentary mandibular palp with a few serrulate setae on the distal segment (Fig. 3B). It was not seen to move independently, nor did it have prey contact, but when the mandibles close it sweeps the lateral side of the labrum.

The mandibular palp of *Penaeus monodon* is flattened and very large and especially the rim is packed with pappose setae (Fig. 3C). It projects anteriorly and lies as a roof over the feeding area (Fig. 3G) but ventral to the scaphognathite, which sweeps the basal part. It occasionally makes ventral flicking movements but does not have prey contact.

TABLE 1. Summary of setation on the mouthparts of seven species of decapods

Species	Labrum	Mdp seg1	Mdp seg2	Mdp seg3	Mx1 bas med	Mx1 bas dor	Mx1 bas ven	Mx1 cox	Mx1 endo	Paragnath
<i>P. monodon</i>	<i>Setules</i>	na	Pa, Se	Pa	Cu	—	Su	Cu, Su	Pa, Ps, Su	Setules
<i>S. hispidus</i>	Steules	—	Se	Se, Su	Su, Cu	—	—	Su, Pa	Pa	Setules
<i>P. adspersus</i>	Setules	—	Su	Su	Su, Cu	—	?	Su, Se, Cu	<i>Si</i>	Setules
<i>C. quadriqarinatus</i>	Ps, Su	Pa	Pa	Su	Cu, Su	Su	Su	Su, Pd, Se	Se, Su	Ps
<i>P. argus</i>	Denticles	<i>Si</i>	<i>Si, Pa</i>	Si	Cu	—	—	Cu	Su, Se	Denticles
<i>C. maenas</i>	Denticles	?	Pa, Su	Se, Su, Pa, Ps	Cu, Se	—	?	Cu	Pa, Su	Setules
<i>P. bernhardus</i>	—	—	—	Su	Cu, Su	—	?	Su, Pa, Cu	<i>Si</i>	Setules
Species	Mx2 bas med	Mx2 bas dor	Mx2 bas ven	Mx2 cox med	Mx2 cox dor	Mx2 cox ven	Mx2 endo	Scapho	Mxp1 Bas med	Mxp1 bas dor
<i>P. monodon</i>	Su, Se	—	—	Se, Su	—	—	Cu	Pl	Su, Se	<i>Ps</i>
<i>S. hispidus</i>	Su	Su	Su	Su	Pa, Ps	?	Pa	Pl	Su, Se	Su
<i>P. adspersus</i>	Su, Se	—	—	na	na	na	<i>Pa, Su</i>	Pl	Su, Se	—
<i>C. quadriqarinatus</i>	Si, Su	—	<i>Su</i>	Se, Su	<i>Pa</i>	Su	Pa	Pl, Su	Se, Su, Si	Su
<i>P. argus</i>	Su	—	—	Se	—	—	Pa, Su	Pl, Su	Si, Se	Pa, Su
<i>C. maenas</i>	Si, Su	—	—	Su	—	—	Su	Pl	Si, Se, Su	—
<i>P. bernhardus</i>	Si, Se, Su	—	<i>Pd</i>	Se, Su	—	<i>Pd</i>	Su	Pl	Su, Se, Si	Su
Species	Mxp1 bas ven	Mxp1 cox	Mxp1 endo	Mxp1 exo	Mxp1 exo fla	Mxp2 Isc-mer	Mxp2 car	Mxp2 pro	Mxp2 dac	
<i>P. monodon</i>	?	Su	Pa, Pd, Su	Ps, Su, Se, Cu	—	Se	Se	Se	Se, Cu, Su	
<i>S. hispidus</i>	Su	Su	Pl, Su	—	Pl	Se	Se	Se	Se	
<i>P. adspersus</i>	Su	Su, Pa	<i>Su</i>	Pl	Pl	<i>Su</i>	Su	Su, Cu	Se, Cu	
<i>C. quadriqarinatus</i>	Pa, Ps, Su	Pa, Ps	Pa, Ps	Pl	Pl	Se, Su?	Se	Se, Cu	Se, Cu	
<i>P. argus</i>	?	Su, Se, Pa, Si	Pa, Se, Su	Pa, Cu	Pl	<i>Si</i>	Si	Si, Cu	Cu, Si	
<i>C. maenas</i>	—	Su	Pa, Su	Pa, Su	Pl	Su, Se	Su, Se	Se, Cu, Su	Cu	
<i>P. bernhardus</i>	—	Su, Pa	Pl	Pl, Su	Pl	Se	<i>Se</i>	Se	Se, Cu	
Species	Mxp2 exo	Mxp2 exo fla	Mxp3 Isc	Mxp3 mer	Mxp3 car	Mxp3 pro	Mxp3 dac	Mxp3 exo	Mxp3 exo fla	
<i>P. monodon</i>	—	Pl	Se	Pa, Se	Se, Pa, Ps	Se	Se, Pa	—	Pl	
<i>S. hispidus</i>	—	Pl	Se	Se	Se	Se	Se	—	Pl	
<i>P. adspersus</i>	—	Pl	Se, Su	—	Se, Su	—	Se, Cu	—	Pl	
<i>C. quadriqarinatus</i>	Pa, Ps, Se	Pl	Se, Su?	Se	Se, Su	Se	Se	Pa, Ps	Pl	
<i>P. argus</i>	<i>Pa, Su</i>	Pl	Si, Se?	Si, Se?	Se, Si	Si, Se	Si, Cu	Pl	Pl	
<i>C. maenas</i>	Pa, Su, Se	Pl	Su	Su, Se, Pa	Se, Pa, Su	Se	Se, Pa	Pa	Pl	
<i>P. bernhardus</i>	Su	Pl	Se?	Se?	Se	Se	Se	<i>Pa, su</i>	Pl	

bas, basis; car, carpus; cox, coxa; Cu, cuspidate setae; dac, dactylus; dor, dorsal side; endo, endopod; exo, exopod; fla, flagellum; isc, ischium; Mdp, mandibular palp; mer, merus; Mx1, maxilla 1; Mx2, maxilla 2; Mxp1, maxilliped 1; Mxp2, maxilliped 2; Mxp3, maxilliped 3; na, not applicable; Pa, pappose setae; Pl, plumose setae; pro, propodus; Ps, papposerrate setae; Se, serrate setae; seg, segment; Si, simple setae; Su, serrulate setae; ven, ventral side; ?, data not available; **Bold, abundant**; normal, moderate; *italic, few*.

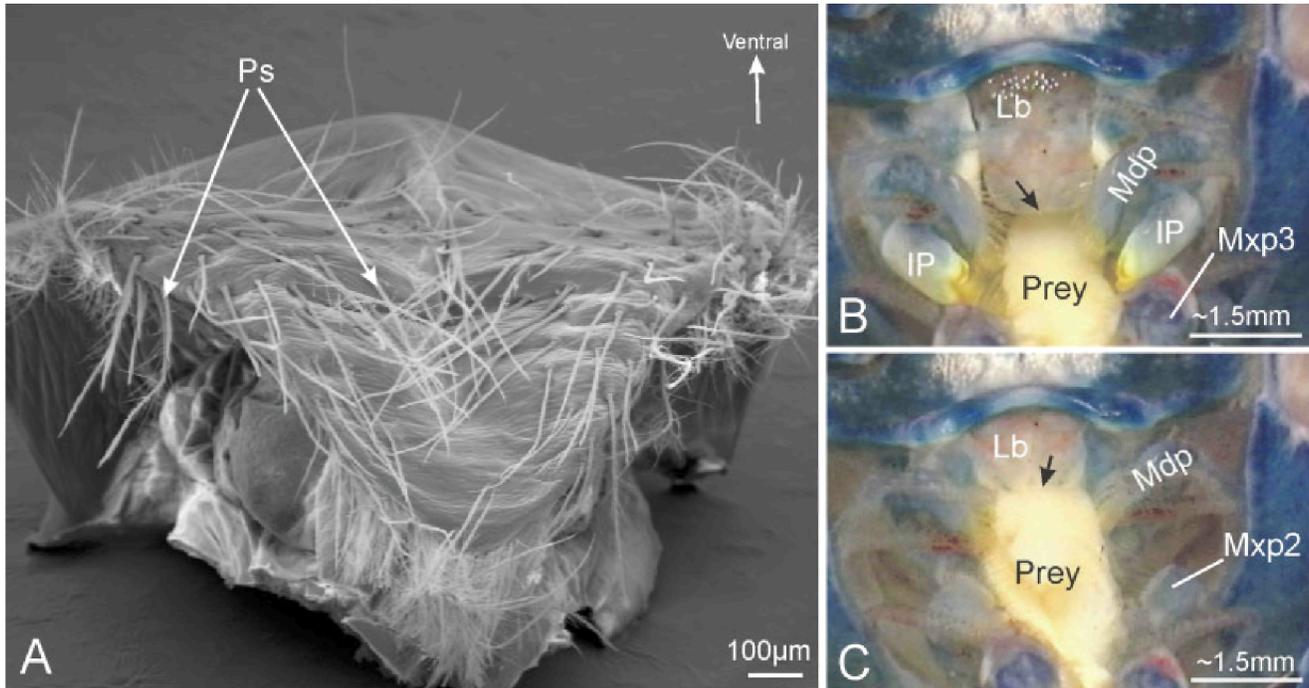


Fig. 2. The labrum. **A:** The labrum of *Cherax quadricarinatus* seen from the direction of the mouth opening (posteriorly). Most of the setae are papposerrate. SEM. **B:** Video still picture showing the labrum (Lb) of *C. quadricarinatus* in a lowered position when a prey item is being placed between the mandibles. Arrow indicates the ventroposterior edge of the labrum. **C:** Video still picture showing the labrum of *C. quadricarinatus* in a raised position when a prey item is bitten by the mandibles. Arrow indicates the ventroposterior edge of the labrum. Note that the mandibular palps follow the movements of the labrum. IP, incisor process of mandible; Lb, labrum; Mdp, mandibular palp; Mxp2, maxilliped 2; Mxp3, maxilliped 3; Ps, papposerrate setae.

Paragnaths

Of the seven species, *Cherax quadricarinatus* is the only one with setae on the paragnath (=labium). It has a row of serrulate setae on the ventral side, which contacts the dorsal side of the basis of maxilla 1. The only species where the paragnaths are clearly seen in the footage is *Penaeus monodon* (Fig. 4D), and here they made small movements in the lateromedial plane.

Maxilla 1

Maxilla 1 is very similar for all seven species in shape, setation, and function. It has a basis, a coxa, and an endopod (Fig. 4A). The coxa points into the mouth (Fig. 1) and has all its setae near the medial edge. They are mostly cuspidate and serrulate setae. Behavioral data from the coxa were only obtained from *Panulirus argus* via the endoscope, since the coxa of maxilla 1 is hidden behind the coxae of the other mouthparts. Here, cuspidate setae push the prey items into the esophagus (Fig. 4C).

The basis of maxilla 1 is situated just ventral to the incisor process of the mandible (Fig. 1), only separated by the paragnaths, and it is very active during feeding. The setae on the medial edge of the basis are very robust and in most species two or more rows of cuspidate setae are present (Fig. 4B).

In the case of *Pagurus bernhardus* the setae are extremely robust and have lost their articulation with the general cuticle. Besides cuspidate setae, there are normally dorsal and ventral rows of serrulate setae. The dorsal row projects dorsomedially (Fig. 4B) and contacts the ventral side of the basis of the paragnath. The basis of maxilla 1 moves in the lateromedial plane and assists in pushing the prey item between the mandibles (Fig. 4D) and in holding the prey in front of the mandibles during a bite. It also helps in reorienting small items such as gravel (Fig. 5E) and in sediment sorting. In the latter case, large quantities of sediment are passed onto the bases of the maxillae, which probe the sediment particles and push the unwanted particles anteriorly, where they are expelled (see Garm and Høeg, 2001, for detailed description).

The endopod of maxilla 1 projects lateroanteriorly and lies against the lateral side of the mandible, in close contact with the base of the mandibular palp. It was only visible in the video sequences of *Cherax quadricarinatus* and *Pagurus bernhardus*, and was not seen to move independently but made small rubbing movements against the base of the mandibular palp when the whole limb was moving (Fig. 4E). In *Panulirus argus* it does not contact the mandibular palp but lies on the ventrolateral side of the incisor process of the mandible.

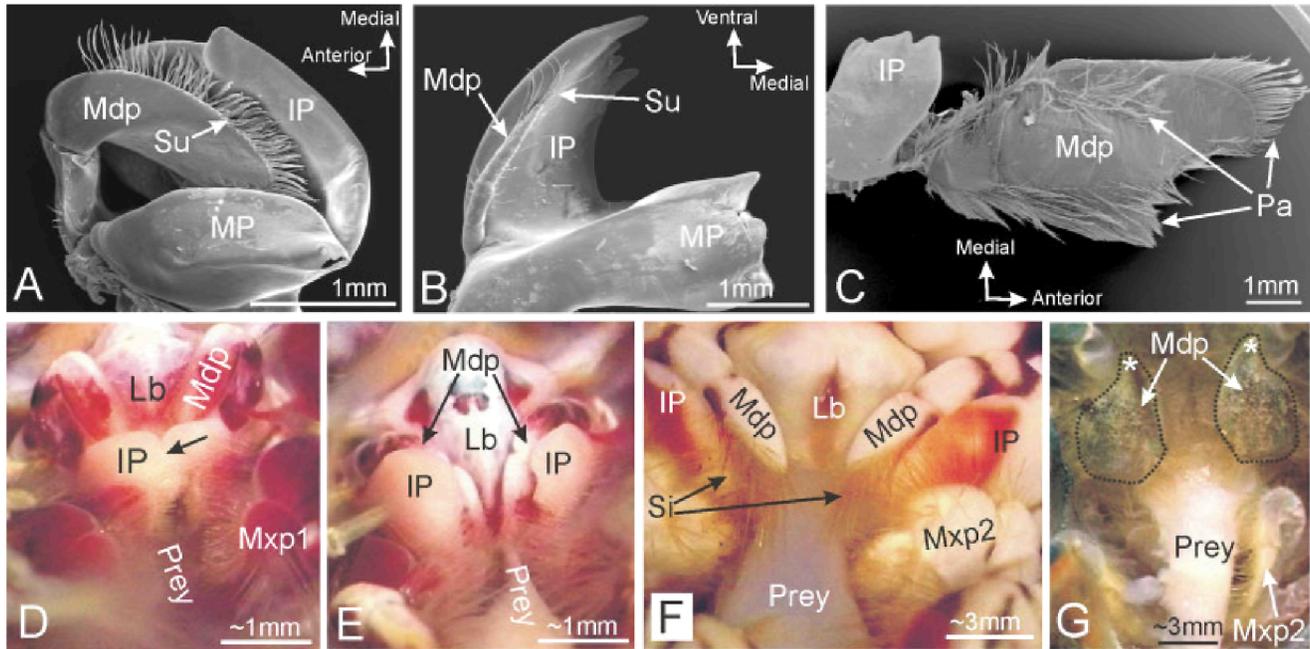


Fig. 3. The mandible. **A–C**: SEM. **D–G**: Video still pictures. Scale bars are estimates. **A**: Left mandible of *Pagurus bernhardus* seen dorsomedially. The mandibular palp fits between the molar and incisor processes and has dense serrulate setae on the distal segment. **B**: Left mandible of *Palaemon adspersus* seen anteriorly. The reduced mandibular palp has only a few serrulate setae. **C**: Left mandible of *Penaeus monodon* seen ventrally. The mandibular palp is very large, flattened, and has pappose setae along the rim. **D**: Mandibular palps (Mdp) of *P. bernhardus* are raised during a bite. Arrows indicate overlapping incisor processes. Compare with **E**. **E**: Mandibular palps of *P. bernhardus* are lowered after a bite; compare with **D**. **F**: Mandibular palps of *Panulirus argus* are placed in front of the incisor processes with their long simple setae pointing ventrally, where they contact the prey items. **G**: Mandibular palps of *P. monodon* lie as a roof above the feeding area and do not normally contact the prey items. Broken lines outline the mandibular palps and asterisks indicate the distal tip. IP, incisor process; Lb, labrum; Mdp, mandibular palp; MP, molar process; Mxp1, maxilliped 1; Mxp2, maxilliped 2; Pa, pappose setae; Si, simple setae; Su, serrulate setae.

Maxilla 2

Maxilla 2 is in all seven cases comprised of a coxa, a basis, an endopod, and a scaphognathite (gill bailer) (Fig. 5A,B). It is placed between maxilla 1 and maxilliped 1 (Fig. 1) and the major part of the limb is therefore restricted to movements in the lateromedial plane, which makes the scaphognathite functions to ventilate the gill chamber, and since it cannot move independently the whole maxilla 2 moves more or less constantly. The entire rim of the scaphognathite has dense plumose setae that enlarge the surface and make a tight seal with the walls of the gill chamber.

The coxa of maxilla 2 differs among the seven species. In *Stenopus hispidus*, *Cherax quadricarinatus*, *Carcinus maenas*, and *Pagurus bernhardus* the coxa has two well-developed endites that have dense setation on the medial edge pointing into the mouth (Figs. 1, 5A). The setae are serrate and serrulate setae. In *Penaeus monodon* and *Panulirus argus*, two reduced endites are present (Fig. 5B) and on *Palaemon adspersus* the endites are missing (see Garm et al., 2003). In the two former cases the medial edge has few serrulate setae. The coxa of

maxilla 2 was not visible on the videos but it is situated very similar to the coxa of maxilla 1 (Fig. 1).

In all seven species the basis of maxilla 2 has two well-developed endites, which have very dense setation on the medial rim (Fig. 5A–C). In *Penaeus monodon*, *Palaemon adspersus*, *Stenopus hispidus*, and *Panulirus argus* the vast majority of these setae are serrulate, with a prominent terminal pore, and their setules are small and scale-like. In *Cherax quadricarinatus*, *Carcinus maenas*, and *Pagurus bernhardus* most are simple setae but also exhibit a terminal pore (Fig. 5C). In all the species these setae probe the prey 1–5 times/sec (Fig. 5D), and were never seen to hold or shred any prey items. When small prey items such as sediment particles are handled, the basis of maxilla 2 takes part in reorientation and rejection (Fig. 5E). These serrulate or simple setae are in most species flanked by a dorsal and a ventral row of more robust serrulate or serrate setae. The dorsal row contacts maxilla 1 and the ventral row contacts maxilliped 1.

The endopod of maxilla 2 is small and is in all species situated in close contact with the endopod of maxilla 1. This means that except for *Panulirus argus* it also has contact with the base of the mandibular palp. The edge normally has serrulate or

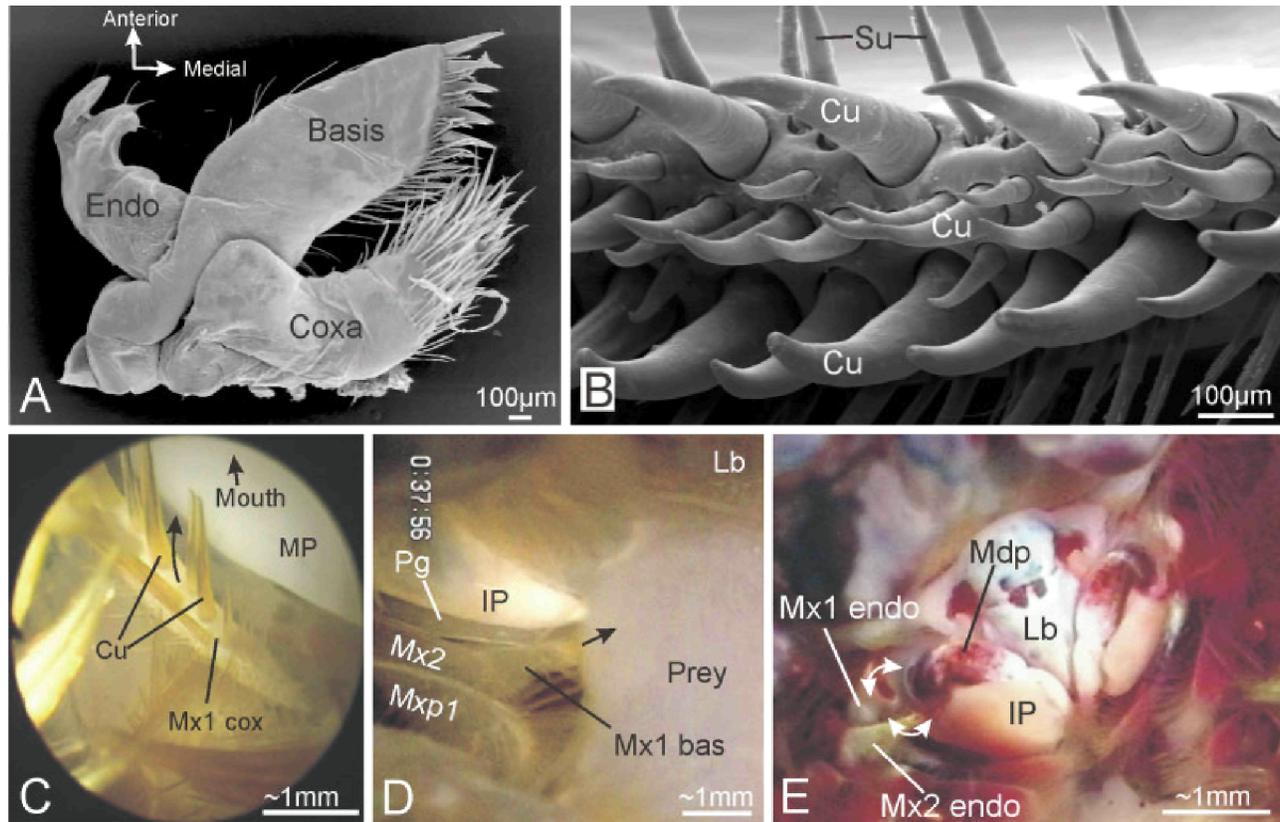


Fig. 4. Maxilla 1. **A–B:** SEM. **C–E:** Video still pictures. Scale bars are estimates. **A:** Right maxilla 1 of *Palaemon adspersus* seen ventrally. **B:** Medial rim of the basis of maxilla 1 of *Penaeus monodon* armed with robust cuspidate setae. **C:** Left coxa of *Panulirus argus* seen anteromedially through an endoscope. The robust cuspidate setae (Cu) push food particles towards the mouth. Arrow indicates direction of movements. **D:** Right side of mouth apparatus of *P. monodon* seen anteriorly. The basis of maxilla 1 pushes prey items between the mandibles. Arrow indicates direction of movement. **E:** Mouth apparatus of *Pagurus bernhardus* seen anteriorly. Endopods of maxilla 1 and 2 are situated close together and rub the basis of the mandibular palp. Arrows indicate movements. Cu, cuspidate setae; Endo, endopod; IP, incisor process; Lb, labrum; Mdp, mandibular palp; MP, molar process; Mx1 bas, basis of maxilla 1; Mx1 cox, coxa of maxilla 1; Mx1 endo, endopod of maxilla 1; Mx2, maxilla 2; Mx2 endo, endopod of maxilla 2; Mxp1, maxilliped 1; Pg, paragnath.

pappose setae but in *Penaeus monodon* only cuspidate setae are found in this area. The endopod of maxilla 2 was seen in the videos of *Cherax quadricarinatus* and *Pagurus bernhardus*, and moves as described for the endopod of maxilla 1 (Fig. 4E).

Maxilliped 1

Maxilliped 1 has a broad coxa, a blade-shaped basis, an elongate endopod, an exopod, and one or two epipods (missing in *Pagurus bernhardus*) (Fig. 6A). The medial rim of the coxa is packed with setae and in most cases they are rather robust serrulate setae, but pappose setae are also common (Fig. 6B). Due to its position, the coxa of maxilliped 1 was only seen in a few sequences of *Panulirus argus* and only when using the endoscope. Here the setae were not seen to have prey contact.

The basis has most of its setae on the medial rim, but rows of setae are also found on both the dorsal and ventral side (Fig. 6A,D). The setae on the medial

rim of *Penaeus monodon*, *Palaemon adspersus*, *Stenopus hispidus*, *Cherax quadricarinatus*, and *Pagurus bernhardus* are mostly serrulate (Fig. 6C), but for *Panulirus argus* and *Carcinus maenas* simple setae make up the major part. In all seven species most of these setae have a prominent terminal pore. All seven species have one or two rows of serrate setae, which are the longest and most robust setae on the basis of maxilliped 1 (Fig. 6C).

The basis of maxilliped 1 is very active during feeding and appears to have many different mechanical functions. When a prey is held by the mandibles and maxilliped 2 or 3 the basis of maxilliped 1 makes outward circular movements and the setae on the medial rim “squeeze” the prey and possibly tear off small pieces and make it fit more readily between the mandibles (Fig. 6G–N). The same circular movements, but in the opposite direction, are used to pick up small prey items from maxilliped 2 and pass them on to the maxillae. Afterwards, when the small prey items are handled by the maxillae, the circular

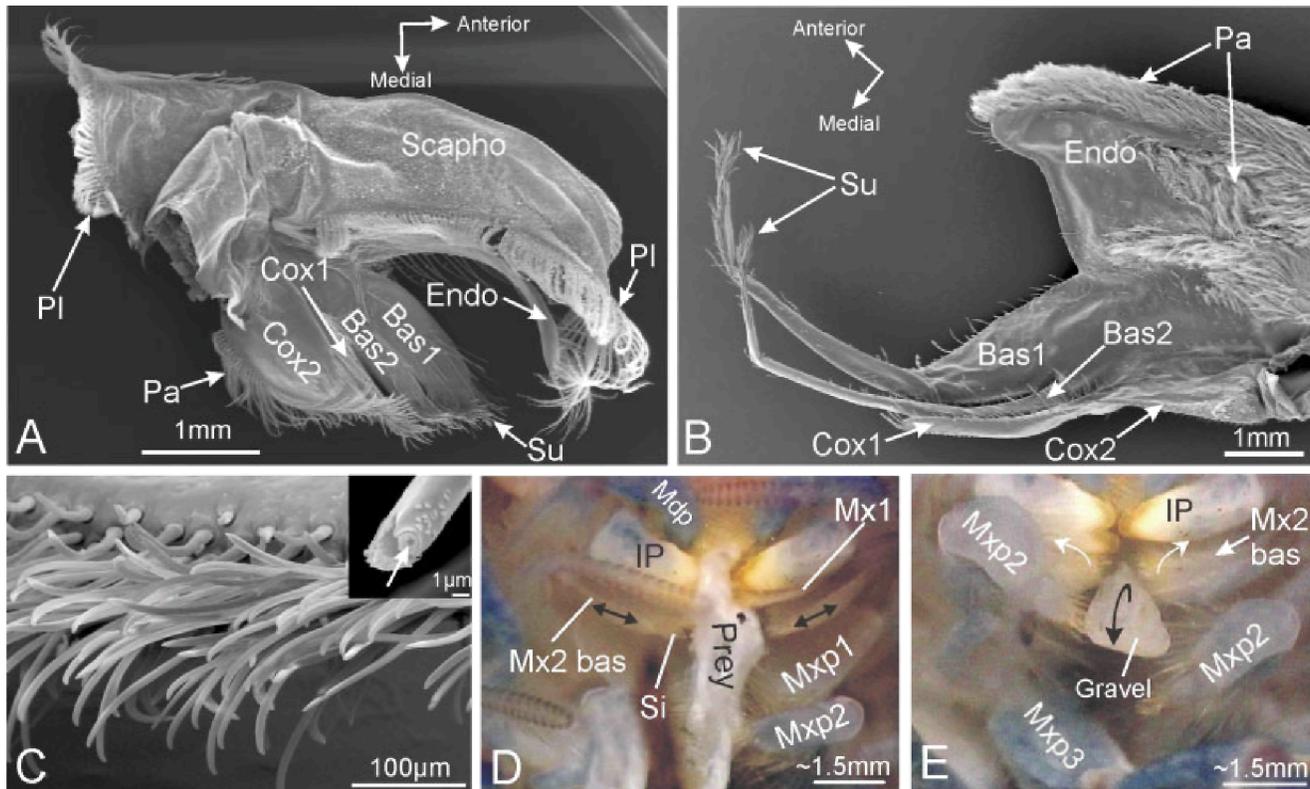


Fig. 5. Maxilla 2. **A–C**: SEM. **D–E**: Video still pictures. Scale bars are estimates. **A**: Left maxilla 2 of *Stenopus hispidus* seen dorsally. Both coxa and basis are divided in two and all four parts are well developed. Compare with **B**. **B**: Right maxilla 2 of *Panulirus argus* seen dorsally. Scaphognathite is removed. Both coxa and basis are divided in two parts but especially the coxal endites are much reduced. Compare with **A**. **C**: Simple setae from the medial rim of the basis of maxilla 2 of *Cherax quadricarinatus*. Insert = closeup of tip of simple seta. Arrow indicates terminal pore. **D**: Prey is held by the mandibles and maxilliped 2 of *C. quadricarinatus* and the setae on the basis of maxilla 2 probe the prey item by lateromedial movements. Arrows indicate direction of movements. **E**: A piece of gravel is examined by the mouthparts of *C. quadricarinatus*. It is reoriented by anterolateral movements of maxilla 2. Arrow indicates direction of movements. Bas1, basis part 1; Bas2, basis part 2; Cox1, coxa part 1; Cox2, coxa part 2; Endo, endopod; IP, incisor process; Mdp, mandibular palp; Mx1, maxilla 1; Mx2 bas, basis of maxilla 2; Mxp1, maxilliped 1; Mxp2, maxilliped 2; Mxp3, maxilliped 3; Pa, pappose setae; Pl, plumose setae; Scapho, scaphognathite; Si, simple setae; Su, serrulate setae.

movements ensure that the particles are not lost anteroventrally. When larger prey items are eaten the basis of maxilliped 1 helps guide the prey between the mandibles by lateromedial movements (Fig. 6E).

The endopod of maxilliped 1 is small and inconspicuous in all species except *Penaeus monodon* and *Carcinus maenas* (Fig. 6A). It projects dorsolaterally, which places it lateral to the endopods of maxilla 2. Most of the setae found here are long and fragile pappose, plumose, papposerrate, or serrulate setae. The endopod of *Pagurus bernhardus* followed the movements of the rest of the limb and did not have prey contact, but touched the endopod of maxilla 2 at times.

In *Penaeus monodon* the endopod of maxilliped 1 is long, consists of three segments, and projects anterodorsally, which places the distal part in the exhalant current dorsal to the mandibular palp. It has some pappose, papposerrate, and serrulate setae and makes small flicking movements, which make the distal setae scrape the dorsal side of the man-

dibular palp. In *Carcinus maenas* the endopod of maxilliped 1 is large and broad and, together with the shaft of the exopod of maxilliped 1, it forms a tube that directs the respiratory currents.

The exopod of maxilliped 1 has two parts: a shaft and a flagellum (Fig. 6A) (in *Penaeus monodon* the flagellum is missing). The shaft is broad and flattened and may have plumose, pappose, papposerrate, or serrulate setae but the flagellum always has dense plumose setae along the edge. The exopod does not contact food items but the shaft is situated in the opening to the gill chamber (Fig. 6F), where it is swept by the distal part of the scaphognathite. It can make small independent movements and the flagellum generates an anteriorly directed current by repeated beating (5–15 Hz), similar to the flagella on the exopods of the other maxillipeds (see Fig. 7H–M).

The epipod(s) lie(s) in the anterior part of the gill chamber beneath the distal part of the scaphognathite. In four of the species they have no setae, but in *Penaeus monodon*, *Panulirus argus*, and *Carcinus*

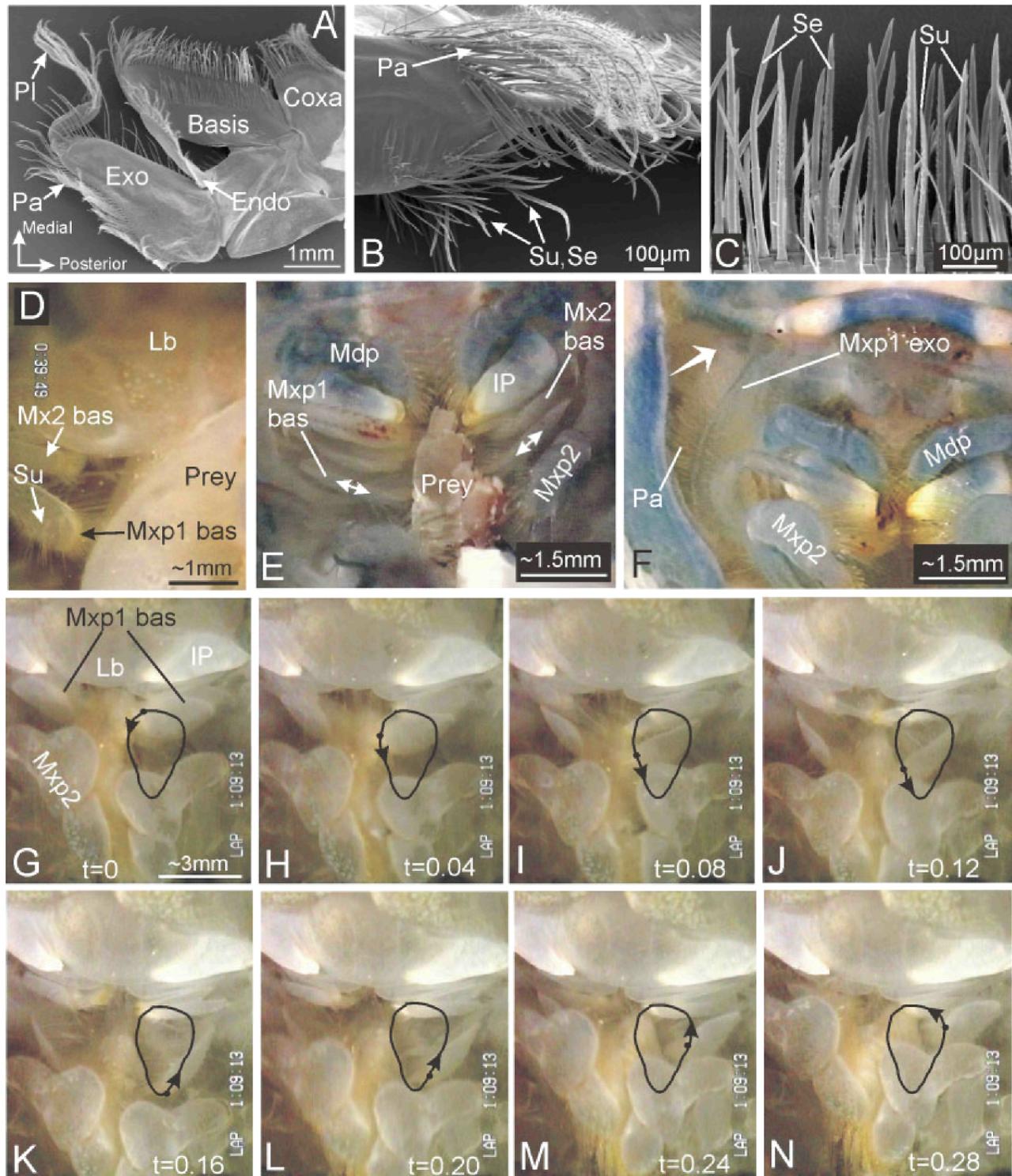


Fig. 6. Maxilliped 1. **A–C:** SEM. **D–N:** Video still pictures. Scale bars are estimates. **A:** Left maxilliped 1 of *Pagurus bernhardus* seen dorsally. Note the broad shaft of the exopod. **B:** Medial view of coxa of maxilliped 1 of *P. bernhardus*. The dorsal side has long pappose setae. **C:** Serrate and serrulate setae on the medial edge of maxilliped 1 of *Cherax quadricarinatus*. **D:** Basis of maxilliped 1 of *Penaeus monodon* in contact with prey item. A row of serrulate setae (Su) on the ventral side projects ventrally and has no prey contact. **E:** Prey is held by maxilliped 2 of *C. quadricarinatus* and is probed by lateromedial movements of maxilliped 1. Arrows indicate direction of movements. **F:** The exopod of maxilliped 1 of *C. quadricarinatus* with long pappose (Pa) setae is situated in the exhalent current from the gill chamber (arrow). **G–N:** Prey is held by maxilliped 2 of *P. monodon* and the basis of maxilliped 1 makes circular movements, squeezing the prey to fit between the mandibles. The black line indicates the trace of the movement and the dot indicates where maxilliped 1 is in the circle at the given picture. Endo, endopod; Exo, exopod; IP, incisor process; Lb, labrum; Mdp, mandibular palp; Mx2 bas, basis of maxilla 2; Mxp1 bas, basis of maxilliped 1; Mxp1 exo, exopod of maxilliped 1; Mxp2, maxilliped 2; Pa, pappose setae; Pl, plumose setae; Se, serrate setae; Su, serrulate setae; t, time in seconds.

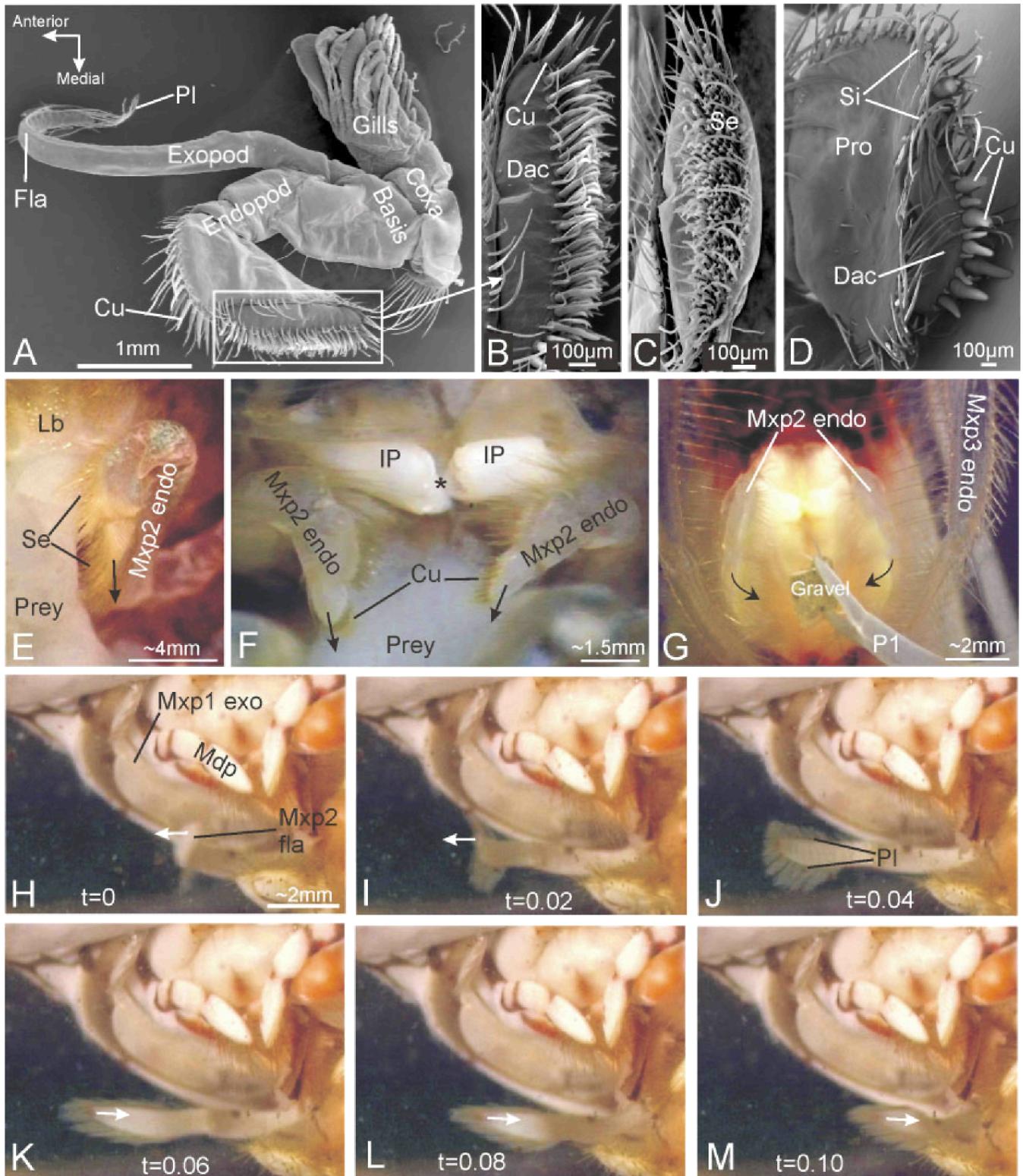


Fig. 7. Maxilliped 2. **A–D**: SEM. **E–M**: Video still pictures. Scale bars are estimates. **A**: Dorsal view of right maxilliped 2 of *Palaemon adspersus*. **B**: Close up of dactylus from framed area in **A**. **C**: Medial view of the dactylus of maxilliped 2 of *Palaemon adspersus*. Most setae are serrate. **D**: Medial view of the dactylus of maxilliped 2 of *Panulirus argus*. The dactylus has cuspidate setae; the propodus has long simple setae. **E**: Prey is held by the mandibles of *Penaeus monodon* and serrate setae on the distal segments of maxilliped 2 shred the prey as it moves ventrally. Arrow indicates direction of movement. **F**: Prey is held by mandibles of *Carcinus maenas* (asterisk indicates overlapping mandibles) and the endopod of maxilliped 2 helps in tearing the prey with cuspidate setae as it moves ventrally. Arrows indicate direction of movements. **G**: A periopod (P1) of *Stenopus hispidus* hands over food objects directly to the endopods of maxilliped 2. Arrows indicate movements. The endopods of maxilliped 3 are held laterally and do not contact the food object. **H–M**: Beating of the exopod flagellum of maxilliped 2 of *P. argus*. **H–J** is the power stroke, **K–M** is the recovery stroke. Note the behavior of the plumose setae (PI). Cu, cuspidate setae; Dac, dactylus; Fla, flagellum; IP, incisor process; Lb, labrum; Mdp, mandibular palp; Mxp1 exo, exopod of maxilliped 1; Mxp2 endo, endopod of maxilliped 2; Mxp2 fla, flagellum of exopod of maxilliped 2; Mxp3 endo, endopod of maxilliped 3; PI, plumose setae; Pro, propodus; Se, serrate setae; t, time in seconds.

maenas there are serrulate setae on the ventral side. They were never seen on any of the videos.

Maxilliped 2

Maxilliped 2 has a coxa and a basis, which carries a five-segmented endopod and an exopod (Fig. 7A). All species except *Pagurus bernhardus* also have one or two epipods, often functioning as gills. The five segments of the endopod are the fused ischium and merus, the carpus, the propodus, and the dactylus. The ischium-merus segment is long and slender but the carpus or the propodus bends, giving the endopod a U-shape (Fig. 7A). The medial side of the endopod has dense setation, especially on the dactylus, with its serrate setae, cuspidate setae, or both (Fig. 7B–D). On the four proximal segments there are mostly serrate and serrulate setae, but in *Panulirus argus* there are simple setae. On the propodus of *Palaemon adspersus*, *Cherax quadricarinatus*, *P. argus*, and *Carcinus maenas* additional cuspidate setae point medially (Fig. 7A).

The endopod is very active during feeding where it receives food items from the periopods (Fig. 7G) or from maxilliped 3. Small food items are passed on to maxilliped 1 and the maxillae and afterwards the endopods are often held together in a medial position, preventing prey from being lost anteroventrally. When larger prey items are eaten, it helps to push the prey between the mandibles and pulls it out again after a bite has been performed. It also helps in shredding and macerating large prey during biting. Then the mandibles hold the prey and the distal part of the endopod of maxilliped 2 is forced into the prey and pushes ventroanteriorly (Fig. 7E,F). This behavior is often correlated with the actions of the endopod of maxilliped 3 (see below). In all cases with direct prey manipulation, almost all of the prey contact is mediated through the setae on the dactylus and propodus.

The shaft of the exopod of maxilliped 2 is longer than the exopod of maxilliped 1 but not as broad (Figs. 6A, 7A). It carries the same types of setae but they are not as dense. In *Penaeus monodon*, *Stenopus hispidus*, and *Palaemon adspersus* setae are absent from the shaft (Fig. 7A). The exopod of maxilliped 2 always has a flagellum, which is more or less identical with the flagellum of maxilliped 1 and it also creates a dorsoanteriorly directed current by repeated beating (2–15 Hz). The arrangement of the plumose setae ensures that the beating has a power and a recovery stroke (Fig. 7H–N). In *P. monodon* the beating is of a rather low frequency, about 2 Hz, and a power stroke and a recovery stroke are not assured by the plumose setae but by reorienting the entire exopod. The exopod of maxilliped 2 never contacts prey items.

The epipod lies in the gill chamber and was never seen in the videos. In *Penaeus monodon*, *Cherax*

quadricarinatus, *Panulirus argus*, and *Carcinus maenas* it carries serrulate setae.

Maxilliped 3

Maxilliped 3 is the outermost and largest of the mouthparts (Fig. 1). Like maxilliped 2 it consists of a small coxa and basis, a large five-segmented endopod, a long exopod, and an epipod (missing in *Pagurus bernhardus*) (Fig. 8A). In *Palaemon adspersus* the segments of the endopod are fused and only three segments are visible. The distalmost segments of the endopod have dense serrate setae except in *Panulirus argus* where they are simple setae (Fig. 8B,D). The highest density is found in a cluster of serrate setae on the distal part of the carpus (Fig. 8C). Some of the serrate setae on the dactylus and sometimes also on the propodus are very robust and in *P. adspersus* and *P. argus* a few cuspidate setae are found on the distal part of the dactylus (Fig. 8B). In *P. adspersus*, *Penaeus monodon*, *Cherax quadricarinatus*, and *P. bernhardus* the serrate setae are of two subtypes. Serrate setae 1 have large denticles but no terminal pore. Serrate setae 2 have small denticles but a prominent terminal pore and are in general longer and more slender than serrate setae 1. On the endopod of maxilliped 3 of *Stenopus hispidus* only serrate setae 2 are present, except for a cluster of serrate setae 1 on the propodus.

The endopod of maxilliped 3 is very flexible and in general serves three major functions. It picks up prey items either directly from the substratum or from one of the periopods. It is normally the dactylus and sometimes also the propodus that contact the prey, but if it is a large prey the entire endopod may hold it. The food is passed on to the endopod of maxilliped 2 or directly to the mandibles. In *Carcinus maenas* the endopod is flattened (Fig. 8F) and restricted in its movements and always receives the prey items from the chelipeds.

The endopod of maxilliped 3 is especially important when larger food items are shredded. The food is then held by the mandibles and the endopods move dorsolaterally and grasp the food with the ischium and sometimes also with the merus. They then move anteroventrally and thereby shred the food objects (Fig. 8E). Many setae contact the food in this way but for most species a good grasp is mainly ensured by large cuticular projections on the ischium and sometimes also on the merus (*Panulirus argus*), the crista dentata. The endopod of maxilliped 3 of *Stenopus hispidus* has no crista dentata and does not participate in food manipulation, during which it is held in a lateral position (Fig. 7G). As a special case, the endopod of maxilliped 3 of *Pagurus bernhardus* can make circular movements and thereby filter zooplankton from the water (Fig. 8G,H).

The endopod of maxilliped 3 also serves grooming purposes and especially antenna 1 is frequently

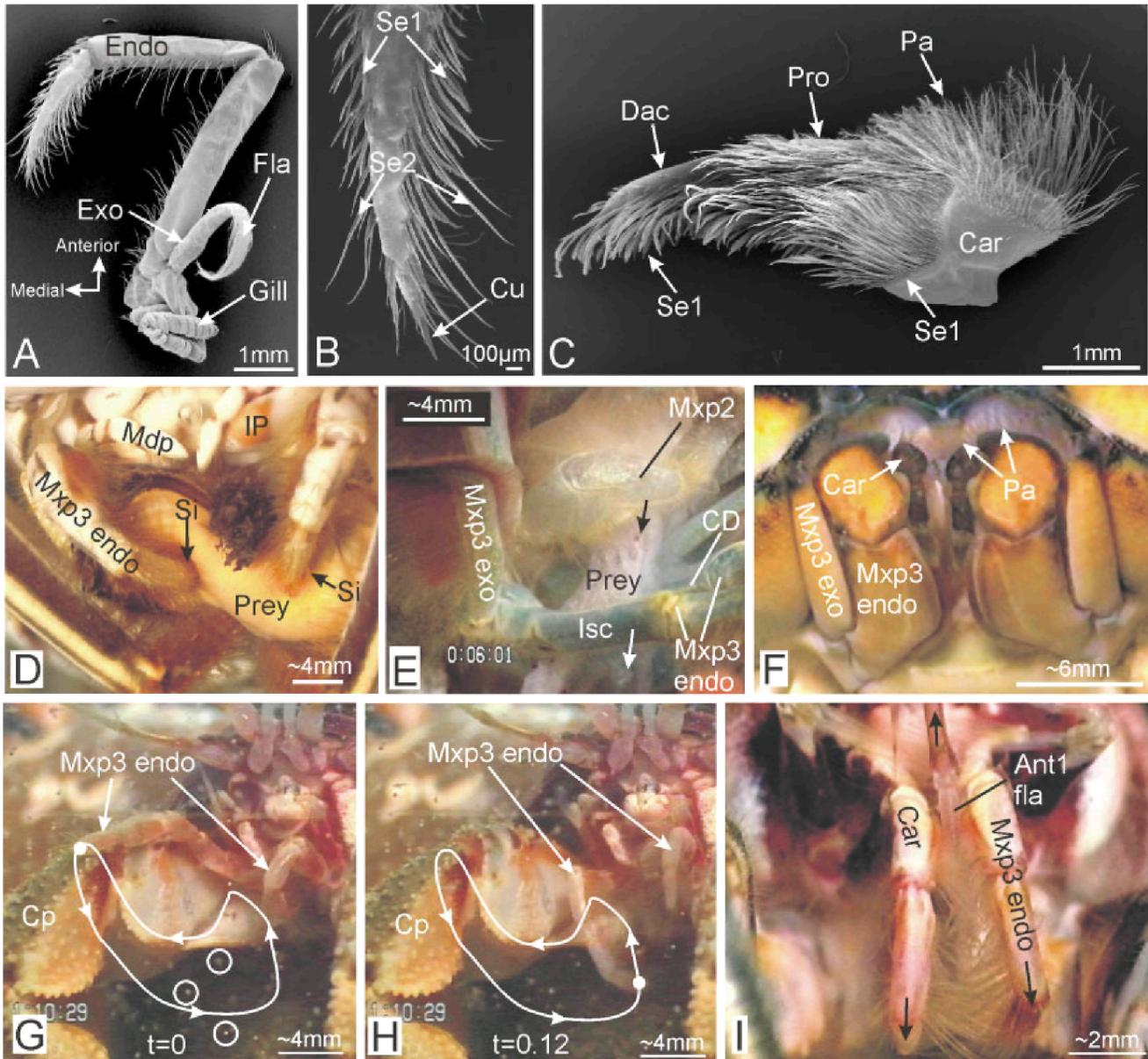


Fig. 8. Maxilliped 3. **A-C**: SEM. **D-I**: Video still pictures. Scale bars are estimates. **A**: Lateral view of maxilliped 3 of *Palaemon adspersus*. Most setae are situated on the distal-most segment. **B**: Closeup of the dactylus of maxilliped 3 of *P. adspersus*. Two types of serrate setae are found in this area (see text for details). **C**: Distal three segments of the endopod of maxilliped 3 of *Carcinus maenas*. These segments have a very dense and diverse setation. **D**: Endopods of maxilliped 3 of *Panulirus argus* are holding a prey item during a bite. Note that the simple setae (Si) on the dactylus are forced into the prey. **E**: A prey item is held by the mandibles of *Penaeus monodon* and is torn by the endopods of maxilliped 2 and 3. Maxilliped 3 holds the prey with the crista dentata on the ischium. Arrows indicate direction of movements. **F**: Closed mouth apparatus of *C. maenas*. A tight seal is made by pappose setae on the carpus and merus of maxilliped 3. **G-H**: *Pagurus bernhardus* filter *Artemia salina* (circles) from the water using serrate setae on the endopod of maxilliped 3. White line indicates circular movements performed by the endopod; dots indicate location in the circle. **I**: Grooming of antenna 1 in *P. bernhardus* is performed by serrate setae on the carpus of the endopod of maxilliped 3. Arrows indicate direction of the movements. Ant1 fla, flagellum of antenna 1; Car, carpus; CD, crista dentata; Cp, cheliped; Cu, cuspidate seta; Dac, dactylus; Endo, endopod; Exo, exopod; IP, incisor process of mandible; Isc, ischium; Lb, labrum; Mdp, mandibular palp; Mxp2, maxilliped 2; Mxp3 endo, endopod of maxilliped 3; Mxp3 exo, exopod of maxilliped 3; Pa, pappose setae; Pro, propodus; Se1, serrate setae type 1; Se2, serrate setae type 2; Si, simple setae; t, time in seconds.

groomed. This is handled by the cluster of serrate setae on the carpus mentioned earlier. Other serrate setae on the propodus groom antenna 2 except in *Panulirus argus*, where grooming of antenna 2 was

never observed. The setae on the dactylus also perform general grooming of the head region.

The structure and function of the exopod and epipod of maxilliped 3 are almost identical to that de-

TABLE 2. Summary of the mechanical functions of the seven types of seta

Type of seta	Pappose	Plumose	Serrate	Serrulate
Mechanical functions	Setal barriers, current direction, filtering*	Surface extension of water pumps, setal barriers	Rough prey handling (collecting and holding prey and shredding soft prey), rough grooming, filtering	Gentle prey handling (reorientation and relocation of small prey items), gentle grooming
Type of seta	Papposerrate	Cuspidate	Simple	
Mechanical functions	Setal barriers, gentle prey handling	Very rough prey handling (holding, shredding, and tearing large prey items), restrict mouthpart movement, filtering*	Rough and gentle prey handling.	

*Taken from the literature, see text for reference.

scribed for maxilliped 2. The epipod of *Penaeus monodon* was seen in the videos and it moved between the gills when the rest of the limb was moved.

DISCUSSION

I have described the functions of the mouthparts of seven species of decapods and correlated it with their setation (Table 1). There are in general many similarities among the seven species both in functions and in setation. The high resolution of the macrovideo recordings and the detailed SEM surveys combine to allow an integration of form and function of the setae. One important factor was the unique ability to follow the actions of single setae over time. In the following the mechanical functions are discussed at the level of the seven setal types. The results are summarized in Table 2.

Pappose Setae

The pappose setae are never situated in the areas that directly take part in food handling. They are almost always found laterally on the mouthparts and are especially numerous on the exopods and endopods of the maxillae and maxilliped 1. They serve as setal barriers, preventing food particles from escaping the feeding area and in directing currents. They function as setal barriers on the shaft of the exopods of maxilliped 2 and 3, which forms the sides of the anterior part of the feeding area. This function is also present on the mandibular palp of *Penaeus monodon*, which in this species forms the roof of the feeding area. Current direction occurs on the shaft of the exopod of maxilliped 1, where pappose setae create walls that direct the respiratory current dorsoanteriorly. On the mandibular palp of *P. monodon* they likewise ensure that the respiratory current does not interfere with feeding. These functions are in good concordance with their structure, since the seta itself and the long setules are fragile and will not stand much applied force. The

slender shaft along with the dense setules acting at low Reynolds numbers make them flexible and efficient barriers

In some of the few existing behavioral accounts the functions of pappose setae are similar to what is described here (Garm and Høeg, 2000, 2001), but decapods specialized in filter feeding (thalassinideans and porcellainids crabs) have pappose setae on maxillipeds 2 and 3, which are used for filtering (Nicol, 1932; Stamhuis et al., 1998; Coelho and Rodrigues, 2001).

Plumose Setae

Like the pappose setae, plumose setae are only found on the lateral parts of the mouth appendages and were never seen to be in direct contact with food particles. They were exclusively found on the exopods of the maxillipeds and on the scaphognathite. Both the flagella of the exopods and the scaphognathite are water pumps, and here the main function of the plumose setae is to make very flexible surface extensions. The way they are hinged on the flagella also creates a power and a recovery stroke (Fig 7H–M). On the scaphognathite they additionally create a tight seal to the walls of the gill chamber. They are always arranged close together, and with their dense setules presumably functioning at low Reynolds numbers they are well suited for the described functions. On the shaft of the exopods of the maxilliped they probably serve as setal barriers along with the pappose setae.

This arrangement and function of plumose setae is in concordance with other reports from decapod mouthparts (Nicol, 1932; Thomas, 1970; Farmer, 1974; Kunze and Anderson, 1979; Schembri, 1982a,b; Suthers, 1984; Lavalli and Factor, 1995; Garm and Høeg, 2001). Plumose setae like-wise serve as flexible surface extensions during swimming in many crustaceans (e.g., see Kohlhaage and Yager, 1994).

Serrate Setae

Serrate setae are common in all of the seven species and are normally found on the areas of the mouthpart directly involved in rough prey handling. They in general collect, hold, and shred larger prey items and their robust denticles on the distal part and their lack of long fragile setules make them well suited for these purposes. Earlier studies combining scanning electron microscopy with some behavioral observations support that this is the most common function of serrate setae (Farmer, 1974; Kunze and Anderson, 1979; Schembri, 1982a; Lavalli and Factor, 1992; Garm and Høeg, 2001). The mechanical functions are somewhat differentiated. Serrate setae on maxilliped 1 have smaller denticles and often a terminal pore, and they perform less rough food manipulation. In special cases the robust serrate setae can even be used as a filter to catch zooplankton as demonstrated by *Pagurus bernhardus*, which is also reported in an earlier study (Gerlach et al., 1976). Similar behavior has been described for larvae of the American lobster, *Homarus americanus* (Lavalli and Factor, 1995).

Another very common mechanical function of serrate setae is grooming of the head region, and the antennae especially are groomed frequently. Specialized clusters on the propodus and carpus of the endopod of maxilliped 3 are used in this behavior. Here the denticles make the setae very efficient in scraping of debris and their size can be correlated with the robustness of the structure they groom (Garm and Høeg, 2001). Grooming by serrate setae is well documented in the literature (Bauer, 1989; Pohle, 1989; Fleisher et al., 1992). This suggests that when the serrate setae are found laterally on the mouthparts, such as the endopods of the maxillae, they may function in grooming the neighboring limbs.

Serrulate Setae

Serrulate setae are very common on both the medial and lateral part of most of the mouth appendages. It follows that their functions must be diverse and it seems like they follow the location of the seta. When situated on the medial edges of the mouthparts, which is predominately seen on the mandibular palp and the bases of maxilla 2 and maxilliped 1, they have direct prey contact and perform gentle manipulation. Serrulate setae on maxilla 2 and maxilliped 1 participate in reorientation and relocation of small food objects and on the mandibular palp they push pieces of food towards the mouth. On maxilla 2 they additionally probe all food objects repeatedly (2–5 Hz), probably to accomplish gustatory functions (Garm et al., 2003), and here they have distinct terminal pores.

These functions correlate with their external characteristics. The small and often scale-like set-

ules on the distal part probably do not stand rough handling, but give the seta a good grip on small particles. This, and their slender build, indicates that they do not apply much force on the prey items. Other studies on decapods focusing on mouthpart behavior find functions similar to what is described here (Kunze and Anderson, 1979; Schembri, 1982a; Lavalli and Factor, 1995; Garm and Høeg, 2001). When found elsewhere than the medial edges they mainly function in grooming of either the gills or the neighboring appendages. All the setae on the epipods of the maxillipeds are serrulate and, even though they were only observed on *Penaeus monodon*, there can be little doubt that they groom the gill filaments they lie between. The scale-like setules of serrulate setae found here are well suited for the gentle grooming needed to clean the gills, as opposed to the rough grooming performed by the serrate setae. This function is well documented for other crustaceans (Bauer, 1998, 1999; Batang and Suzuki, 1998). On the dorsal and ventral side of the maxillae and maxilliped 1 they contact the neighboring appendages, which they groom. This arrangement also serves to fill the space between these mouthparts, ensuring that nothing is lost laterally from the mouth field.

Papposerrate Setae

Papposerrate setae are rare and are normally situated in areas where they have no prey contact. The only place where they were observed on the videos was on the labrum of *Cherax quadricarinatus*. Here they function in gentle food manipulation, pushing pieces of prey down in front of the mouth opening. This fits well with their distal part having denticles, ensuring a good grip on the particles. The long setules proximally suggest that papposerrate setae additionally serve as a barrier, preventing even very small particles from escaping between the setae.

Few reports on the usage of papposerrate setae are available but Thomas (1970) describes such setae from the labrum and paragnaths of the crayfish *Austropotamobius pallipes* (plumodenticulate setae in his terminology), and his limited behavioral observations suggest that they are also involved in gentle prey manipulation in this species.

Cuspidate Setae

The cuspidate setae found on the mouthparts of the seven species are very uniform in their arrangement and mechanical functions. They are almost exclusively situated on the parts of the mouth apparatus doing very rough food handling such as shredding and tearing prey items and holding the prey during a bite. The former is true for the dactylus and propodus of maxilliped 2 and the dactylus of maxilliped 3 and the latter is true for the basis of maxilla 1. Their broad base, reduced articulation, and gen-

eral lack of outgrowths are very well matched with these functions. For *Penaeus monodon*, cuspidate setae are additionally found on the endopods of maxilla 2 and maxilliped 1. These were not observed on the videos but from their arrangement I suggest that here they serve to restrict and control the movements of these endopods.

The functions of cuspidate setae found in earlier studies are similar to what I have described here (Farmer, 1974; Kunze and Anderson, 1979; Lavalli and Factor, 1995; Garm and Høeg, 2001), but in the case of *Pagurus rubricatus* it was found that cuspidate setae on the medial rim of maxilla 1 can act as a filter (Schembri, 1982a). This is a surprising function of cuspidate setae, which stresses that one should be careful to extract the functions of setae from their morphology alone. It is also tempting to suggest that these setae have mere mechanical functions or at least reduced sensory functions, but they can at least have mechanosensory functions (Vedel, 1985).

Simple Setae

The results show that the simple setae are a functionally diverse group, and their mechanical functions are more closely connected to the location in the mouth apparatus than to their external morphology. On most of the mouthparts of *Panulirus argus* they perform rough prey handling, impeding the presence of breakable outgrowths. In this aspect they resemble cuspidate setae, but their more slender shaft makes them much more flexible, which is probably important for providing a good grip on prey items with variable shape and size. On the mandibular palp they also contact the prey items, but they were never seen to actually manipulate the prey. Their lack of outgrowths might therefore indicate that they are mainly sensory structures with reduced mechanical functions. The case with the aesthetascs on antenna 1, which are specialized unimodal chemosensory simple setae with no apparent mechanical function, stresses this possibility.

Reduced mechanical functions could also explain the presence of simple setae on the medial rim of the basis of maxilla 2 of *Cherax quadricarinatus*, *Carcinus maenas*, and *Pagurus bernhardus*. On *P. bernhardus* and *C. quadricarinatus* they do have some mechanical functions when small particles are being handled, but they were not observed to apply great force, as indicated by large movements of the food objects. On *C. maenas*, which does not engage in eating small particles, the simple setae did not have any detectable mechanical functions. As suggested for serrulate setae of *Palaemon adspersus* situated in the same area as these simple setae, their most important function in all three species is probably gustatory (Garm et al., 2003).

Setal Morphology and Function

It is to a large extent possible to predict mechanical functions of mouthpart setae of decapod crustaceans from their external morphology when this is resolved to the scanning electron microscopy level. There are indications, though, that the best resolution is achieved when the location is also taken into consideration. This is especially true for the serrate, serrulate, and simple setae.

It is not surprising that the outgrowths especially are closely connected to the mechanical functions, but it has also been suggested that they should be innervated and therefore directly correlated with the sensory functions of the setae (Reaka, 1975). This suggestion has so far not been supported by any ultrastructural study on setae, but the outgrowths and other external features can be involved indirectly in the sensory properties of a seta. This is evident for mechanosensory plumose and pappose setae on the carapace and tail fan of several decapods which rely on waterborne vibrations as stimuli (Mellon, 1963; Wiese, 1976; Heinisch and Wiese, 1987; Douglass and Wilkens, 1998). They have no apparent mechanical functions and the long setules probably serve solely to catch vibrations.

On the mouthparts examined here both the serrate and the serrulate setae seem to be separated into two subgroups, depending on whether or not they have a prominent terminal pore. Serrate and serrulate setae with such a pore are only found on the areas of the mouth apparatus directly involved in food manipulation and likely indicates gustatory functions. For the serrate setae this is often combined with a longer and more slender shaft and smaller denticles and more gentle food handling. It is therefore possible that some overall sensory function can be deduced from the external morphology of the setae, but much more data are needed before any kind of conclusion can be drawn.

ACKNOWLEDGMENTS

I thank Dr. Jens Høeg, University of Copenhagen, for constructive comments on the manuscript, and Danmarks Akvarium for nursing the animals. The animals were kindly supplied by Danmarks Akvarium, Hank Trapido-Rosenthal at the Bermuda Biological Station of Research, and the Australian Institute of Marine Science (AIMS).

LITERATURE CITED

- Altner I, Hatt H, Altner H. 1983. Structural properties of bimodal chemo- and mechanosensitive setae on the pereopod chelae of the crayfish, *Austropotamobius torrentium*. *Cell Tiss Res* 228: 357–374.
- Batang ZB, Suzuki H. 1998. Gill-cleaning mechanisms of the mud lobster *Thalassinia anomala* (Decapoda: Thalassinidea: Thalassinidae). *J Crustacean Biol* 19:671–683.
- Bauer RT. 1989. Decapod crustacean grooming: functional morphology, adaptive value, and phylogenetic significance. In: Fel-

- genhauer B, Watling L, Thistle A, editors. Functional morphology of feeding and grooming in Crustacea. Rotterdam: A.A. Balkema. p 49–74.
- Bauer RT. 1998. Gill cleaning mechanisms of the crayfish, *Procambarus clarkii* (Astacidea: Camberidae): experimental testing of setobranch function. *Invertebr Biol* 117:129–143.
- Bauer RT. 1999. Gill-cleaning mechanisms of a dendrobranchiate shrimp, *Rimapenaeus similis* (Decapoda, Penaeidae): description and experimental testing of function. *J Morphol* 242:125–139.
- Coelho VR, Rodrigues SA. 2001. Trophic behavior and functional morphology of the feeding appendages of the laomediid shrimp *Axiannya australis* (Crustacea: Decapoda: Thalassinidea). *J Mar Biol Assoc UK* 81:441–454.
- Coelho VR, Williams AB, Rodrigues SA. 2000. Trophic strategies and functional morphology of feeding appendages, with emphasis on setae of *Upogebia omissa* and *Pomatogebia operculata* (Decapoda: Thalassinidea: Upogebiidae). *Zool J Linn Soc* 130:567–602.
- Derby CD. 1989. Physiology of sensory neurons in morphologically identified cuticular sensilla of crustaceans. In: Felgenhauer B, Watling L, Thistle A, editors. Functional morphology of feeding and grooming in Crustacea. Rotterdam: A.A. Balkema. p 27–48.
- Derby CD. 2000. Learning from spiny lobsters about chemosensory coding of mixtures. *Physiol Behav* 69:203–209.
- Derby CD, Cate HS, Gentilcore LR. 1997. Perireception in olfaction: molecular mass sieving by aesthetasc sensillar cuticle determines odorant access to receptor sites in the Caribbean spiny lobster *Panulirus argus*. *J Exp Biol* 200:2073–2081.
- Derby CD, Steullet P, Horner AJ, Cate HS. 2001. The sensory basis of feeding behavior in the Caribbean spiny lobster, *Panulirus argus*. *Mar Fresh Res* 52:1339–1350.
- Douglass JK, Wilkens LA. 1998. Directinal selectivities of near-field filiform hair mechanoreceptors on the crayfish tailfan (Crustacea: Decapoda). *J Comp Physiol A* 183:23–34.
- Farmer AS. 1974. The functional morphology of the mouthparts and pereopods of *Nephrops norvegicus* (L.) (Decapoda: Nephropidae). *J Nat Hist* 8:121–142.
- Fleisher J, Grell M, Hoeg JT, Olesen J. 1992. Morphology of grooming limbs in species of *Petroliustes* and *Pachycheles* (Crustacea: Decapoda: Anomura: Porcellanidae) a scanning electron microscopy study. *Mar Biol* 113:425–435.
- Fryer G. 1977. Studies on the functional morphology and ecology of the atyid prawns of Dominica. *Philos Trans R Soc Lond B* 277:57–129.
- Garm A, Høeg JT. 2000. Functional mouthpart morphology of the squat lobster *Munida sarsi*, with comparison to other anomurans. *Mar Biol* 137:123–138.
- Garm A, Høeg JT. 2001. Function and functional groupings of the complex mouth apparatus of the squat lobsters *Munida sarsi* Huus and *M. tenuimana* G.O. Sars (Crustacea: Decapoda). *Biol Bull* 200:281–297.
- Garm A, Hallberg E, Høeg JT. 2003. The role of maxilla 2 and its setae during feeding in the shrimp *Palaemon adspersus* (Crustacea: Decapoda). *Biol Bull* 204:126–137.
- Gerlach SA, Ekstrøm DK, Eckardt PB. 1976. Filter feeding in the hermit crab, *Pagurus bernhardus*. *Oecologia* 24:257–264.
- Gleeson RA, McDowell LM, Aldrich HC. 1996. Structure of the aesthetasc (olfactory) sensilla of the blue crab, *Callinectes sapidus*: transformations as a function of salinity. *Cell Tiss Res* 284:279–288.
- Guse GW. 1980. Development of antennal sensilla during moulting in *Neomysis integer* (Leach) (Crustacea, Mysidacea). *Protoplasma* 105:53–67.
- Hallberg E, Johansson KUI, Wallén R. 1997. Olfactory sensilla in crustaceans: morphology, sexual dimorphism, and distribution patterns. *Int J Insect Morphol Embryol* 26:173–180.
- Hatt H, Bauer U. 1980. Single unit analysis of mechano- and chemosensitive neurons in the crayfish claw. *Neurosci Lett* 17:203–207.
- Heinisch P, Wiese K. 1987. Sensitivity to movement and vibration of water in the North Sea shrimp *Crangon crangon* (L.). *J Crustacean Biol* 7:401–413.
- Kohlhage K, Yager J. 1994. An analysis of swimming in remipede crustaceans. *Philos Trans R Soc Lond B Biol Ser* 346:213–221.
- Kunze J, Anderson D. 1979. Functional morphology of the mouthparts and gastric mill in the hermit crabs *Clibanarius taenitua* (Milne Edwards), *Clibanarius virescens* (Krauss), *Paguristes squamousus* McCulloch and *Dardanus setifer* (Milne-Edwards) (Anomura: Paguridea). *Aust J Mar Fresh Res* 30:683–722.
- Lavalli KL, Factor JR. 1992. Functional morphology of the mouthparts of juvenile lobsters, *Homarus americanus* (Decapoda: Nephropidae), and comparison with the larval stages. *J Crustacean Biol* 12:467–510.
- Lavalli K, Factor J. 1995. The feeding appendages. In: Factor J, editor. *Biology of the lobster*. New York: Academic Press. p 349–393.
- Laverack MS. 1987. The nervous system of the Crustacea, with special reference to the organisation of the sensory system. In: Ali MA, editor. *Nervous system of the invertebrates*. Berlin: Springer. p 1–30.
- Mellon D Jr. 1963. Electrical responses from dually innervated tactile receptors on the thorax of the crayfish. *J Exp Biol* 40:137–148.
- Nicol EAT. 1932. The feeding habits of the Galatheidea. *J Mar Biol Assoc UK* 18:87–106.
- Pohle G. 1989. Gill and embryo grooming in lithodid crabs: comparative functional morphology based on *Lithodes maja*. In: Felgenhauer B, Watling L, Thistle AB, editors. Functional morphology of feeding and grooming in Crustacea. Rotterdam: A.A. Balkema. p 75–94.
- Reaka ML. 1975. Molting in stomatopod crustaceans. 1. Stages of the molt cycle, setagenesis, and morphology. *J Morphol* 146:55–80.
- Schembri PJ. 1982a. Functional morphology of the mouthparts and associated structures of *Pagurus rubricatus* (Crustacea: Decapoda: Anomura) with special reference to feeding and grooming. *Zoomorphology* 101:17–38.
- Schembri PJ. 1982b. The functional morphology of the feeding and grooming appendages of *Ebalia tuberosa* (Pennant) (Crustacea: Decapoda: Leucosiidae). *J Nat Hist* 16:467–480.
- Stamhuis EJ, Dauwe B, Videler JJ. 1998. How to bite the dust: morphology, motion pattern and function of the feeding appendages of the deposit-feeding thalassinid shrimp *Callinassa subterranea*. *Mar Biol* 132:43–58.
- Suthers I. 1984. Functional morphology of the mouthparts and gastric mill in *Penaeus plebejus* Hess (Decapoda: Penaeidea). *Aust J Mar Fresh Res* 35:785–792.
- Tazaki K. 1975. Sensory units respond to osmotic stimuli in the antennae of the spiny lobster *Panulirus japonicus*. *Comp Biochem Physiol* 51A:647–653.
- Thomas WJ. 1970. The setae of *Austropotamobius pallipes* (Crustacea: Astacidae). *J Zool Lond* 160:91–142.
- Vedel JP. 1985. Cuticular mechanoreception in the antennal flagellum of the rock lobster *Panulirus vulgaris*. *Comp Biochem Physiol* 80A:151–158.
- Voigt R, Atema J. 1992. Tuning of chemoreceptor cells of the second antenna of American lobster (*Homarus americanus*) with a comparison of four of its other chemoreceptive organs. *J Comp Physiol A* 171:673–683.
- Wiese K. 1976. Mechanoreceptors for near-field water displacement in crayfish. *J Neurophysiol* 39:816–833.