MOUTHPARTS OF THE PONTO-CASPIAN INVADER *DIKEROGAMMARUS VILLOSUS* (AMPHIPODA: PONTOGAMMARIDAE)

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A B S T R A C T

The pontogammarid amphipod *Dikerogammarus villosus*, originally a Ponto-Caspian faunal element, has, in the recent 15-20 years, successfully invaded various aquatic systems in Europe including Lake Constance. In these rivers and lakes it had and still has severe ecological impact on native macro-invertebrates, often eliminating the native and earlier established gammaridean species. In order to test the hypothesis that the mode of food acquisition of *D. villosus* is of significance for this phenomenon, we focused on the mouthparts of *D. villosus*, i.e., mandibles, the two pairs of maxillae and the maxillipeds using SEM. Contrary to expectations, provoked by field and laboratory observations, the results of this study show that the mouthparts of *D. villosus* are not highly specialized just for carnivory and predation. Indeed, the stout mandibles, with their well-developed incisors enable to kill even prey with robust integument, but other modes of feeding are possible. On the maxillulae, maxillae, and maxillipeds we found setae that can be used, together with the gnathopods and the antennae, for filtering suspended algae and other small particles from the respiration current. The same structures are involved in collecting detritus. In contrast, *D. villosus* does not possess any specific tools for scraping periphyton from the substrate. Feeding on macrophytes may be possibly but not very effective because the surfaces of the molars are not well suited for grinding such plant material. It is shown that *D. villosus* is neither a shredder, as traditionally predicated for most gammarideans, nor is it a specialized carnivore, as predation experiments proposed, but rather unspecialized. Its ability to be carnivorous and to use a wide spectrum of other food may be an important reason for the success of this invader, being an advantage compared to mainly herbivorous gammarideans, which have been eliminated in many places by *D. villosus*.

KEY WORDS: Amphipoda, feeding, functional morphology, *Dikerogammarus*

INTRODUCTION

The Ponto-Caspian amphipod *Dikerogammarus villosus* Sowinsky, 1894 (Gammaridea: Pontogammaridae; Fig. 1), originally distributed in the rivers leading into the Black Sea and Caspian Sea, is apparently a very successful invader of aquatic ecosystems in Europe and expected to invade North America (Dick and Platvoet, 2001). In 1989, the species was recorded for the first time in the Austrian part of the river Danube and three years later in Germany near Straubing and Regensburg (Nesemann et al., 1995). The opening of the Main-Danube Canal enabled *D. villosus* to colonize the rivers Main and Rhine, in which the species was recorded for the first time in 1994 (Bij de Vaate and Klink, 1995). Subsequently, *D. villosus* spread westward into the French and German rivers Moselle (1996), Saône (1997), Rhône (1998), Meuse (1998), Seine (2000), Loire and eastward by using the Mittelland Canal joining the rivers Rhine, Weser (1998), Elbe (1999) and Oder (2000) (Grabow et al., 1998; Devin et al., 2001; Müller et al., 2001; Bij de Vaate et al., 2002; cf. particularly Nehring, 2003, and Bollache et al., 2004, for overviews of the history of invasion). In 2002, *D. villosus* was observed for the first time in Lake Constance Germany (Mürle et al., 2004; Rey et al., 2005) and Lake Geneva (2002), Lake Bienne (2005), Lake Zurich (2006), Switzerland (Bollache, 2004; Lods-Crozet, 2006; Reymond, 2006 and citations therein), and it was found, at a high population density, in 2003 in Lake Garda, Italy (Casellato et al., 2006) (Fig. 2). Another, new route has been followed by this species from the east into Europe but until now has reached only Poland (central corridor sensu Grabowski et al., 2007), so not having mixed with or affected any of the western populations so far.

Field surveys and laboratory experiments indicate that the ecological impact of *Dikerogammarus villosus* on native macro-invertebrates can be severe. This invasive species spreads fast, occurs at high population densities, suppresses and even eliminates other native or longer established gammaridean species (Dick and Platvoet, 2000; Kley and Maier 2003; Kinzler and Maier, 2003; Kley and Maier, 2005; MacNeil and Platvoet, 2005). In the river Rhine, *D. villosus* and the caprellid amphipod *Corophium curvispinum* G. O. Sars, 1895, another invader from the Ponto-Caspian region, represent 80-90% of its macro-invertebrate community in number and in biomass (Van Riel et al., 2006). In addition, it could be demonstrated that *D. villosus* preys very effectively on numerous macro-invertebrates, attacking even animals larger than itself (Dick et al., 2002; Krisp and Maier, 2005; Van Riel et al., 2006).

Previous work on *Dikerogammarus villosus* investigated its success as an invasive species, focusing on ecology, reproduction and behavior. It could, for example, be shown that *D. villosus* is euryoecious having a wide temperature and salinity tolerance (Bruijs et al., 2001). Therefore the authors suggested that *D. villosus* might be able to sustain longer periods in ballast water tanks and subsequently be dispersed over large distances. *D. villosus* is able to colonize
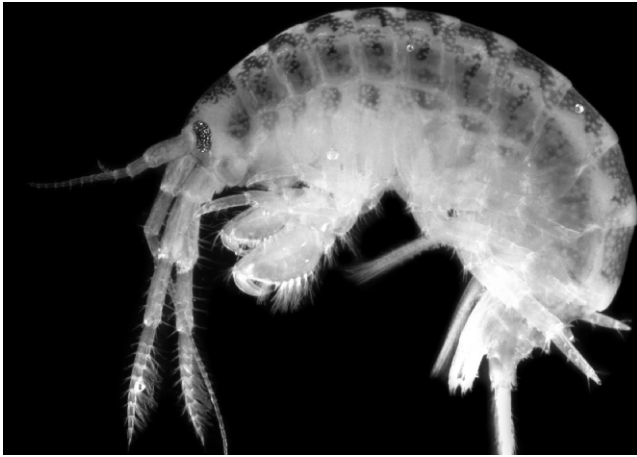
Fig. 1.   Photograph of an adult male of *Dikerogammarus villosus*.

a wide range of substratum types except sand. There is a spatial segregation of different size classes of individuals with smallest individuals in particular found on roots and macrophytes and the largest individuals in cobble. Spatial overlap of different generations is, therefore, reduced and intraspecific competition, including cannibalism, is limited (Devin et al., 2003). *D. villosus* is able to coexist with other gammarideans in river sections with high habitat complexity (Kley and Maier, 2005). Investigations of live history traits evidenced a reproductive period of *D. villosus* lasting for more than 10 months, a female biased sex-ratio, exceptional

growth rates, early sexual maturity and one of the highest fecundities of Western European gammarideans with up to 194 eggs per clutch (Ciolpan, 1987; Devin et al., 2004; Kley and Maier, 2003, 2006; Pöckl, 2007).

In laboratory experiments, native and other earlier established or more recently invaded gammarid species such as *Gammarus roeseli* Gervais, 1835, *G. pulex* (Linnaeus, 1758), *G. duebeni* Liljeborg, 1852, *G. fossarum* Koch in Panzer, 1835, *G. tigrinus* Sexton, 1939, and *Echinogammarus ischnus* Stebbing, 1899 suffered from severe intraguild predation (= predation among potential competitors; Polis et al., 1989) in mixed populations, regardless of whether alternative food, such as chironomids, was available or not (Dick and Platvoet, 2000; Dick et al., 1999; Dick et al., 2002; Kinzler and Maier, 2003; MacNeil and Platvoet, 2005). Investigations of stable isotope values indicate that *D. villosus* has a higher predatory level in comparison to the other amphipod species in the Rhine food web (Van Riel et al., 2006).

The results of the investigations mentioned above imply that *D. villosus* is more specialized in predation and carnivorous feeding than its relatives. Corresponding modifications of the mouthparts to these modes of food acquisition should, therefore, be expected. Little is known, however, about details of the mouthpart morphology of this invasive species and no SEM-study has been published yet, except for some pictures of the second antennae and gnathopods in Platvoet et al. (2006).

Our work within an EU-funded programme on invader species of Lake Constance, southwestern Germany, aims to
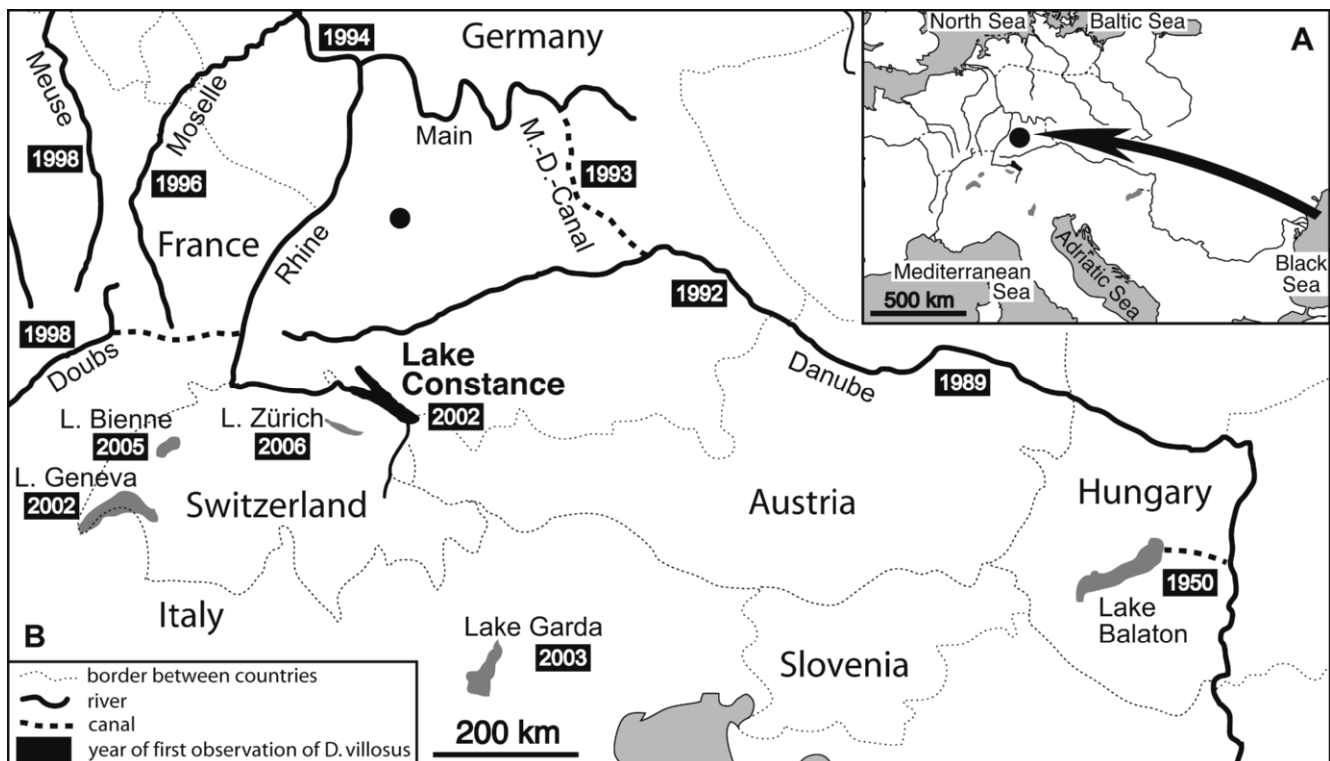

Fig. 2.   A, Map of Europe with waterways which are supposedly relevant for the expansion of the invasive gammaridean *Dikerogammarus villosus* into central Europe; B, Migration history of D. villosus in the Danube region (see text) (M.-D.-canal = Main-Danube Canal).

close this gap by focusing on the detailed description of the mouthpart morphology of *D. villosus* using scanning electron microscopy (SEM), with some notes also on associated structures such as the antennae, the labrum and the paragnaths. This is taken to discuss the feeding habits of this invasive species as being of significance for its success over various native gammarideans. Our investigations shall be expanded, in the future, in two ways, laboratory experiments (done by a collaborating working group) and comparative investigations of the feeding apparatus including *Gammarus roeseli*. This includes more work on the morphology and function of the antennae in more detail and the posterior pereiopods, the latter being of significance for substrate choice, another candidate for distinction between the invader and the displaced gammarideans.

MATERIAL AND METHODS

Specimens of *Dikerogammarus villosus* were collected between 2005 and 2006 from the shore of the river Danube near Regensburg and Deggendorf, the Main-Danube Canal near Hilpoltstein and from the littoral of Lake Constance near Langenargen and Constance (Konstanz). For life observations, some specimens were kept in a container of $65 \times 90 \times 15$ cm in water from the Danube near Ulm at a nearly constant temperature of 18°C (Aquarium chiller: Aqua Medic Titan 150). Species was identified following the taxonomic key of Eggers and Martens (2001).

For SEM studies approximately 30 adult males (lengths: 14-18 mm) – known to be more aggressive than females (Kinzler and Maier, 2003) – were fixed and stored in 7% formaldehyde or in 70% ethanol. According to Felgenhauer (1987) the specimens were, later on, rinsed in distilled water containing the detergent Tween 80 and sonicated for 20 seconds in a Merck Eurolab ultrasonic cleaner to remove debris from the cuticle. We selected the four post-antennal appendages, the so-called mouthparts, for our studies because they appeared particularly promising for the identification of the feeding habit. After dissection with the aid of a binocular, the mouthparts (mandibles, the 2 pairs of maxillae and maxillipeds) were prepared for SEM work in a standard way (ethanol series, critical-point drying, sputter-coating using a gold-palladium mixture). SEM work was done with a Zeiss DSM 962 Scanning Electron Microscope. Images were obtained as much as possible in a standardized way, i.e., from medial, anterior and posterior. This takes into consideration the fact that details such as bristles, setae and spines are positioned in different manner mainly along the inner sides of the appendages and also facilitates identification of asymmetry. The digital images obtained from the SEM were trimmed in Adobe Photoshop™. Drawings were made using the graphics software Adobe Illustrator™. Most of the terminology applied follows that in use for amphipods, respectively gammarideans. Only in a few cases we adjusted the terminology to a more general crustacean terminology for better comparability (Walossek, 1993). For example, the maxillulary proximal part, termed protopod in amphipod terminology, is split into a coxa and basipod, both drawn out into antero-posteriorly flattened endites, as in the ground pattern of Malacostraca (Walossek and Müller, 1998).

RESULTS

In natural position, all mouthparts are mostly hidden underneath the two pairs of large anterior pereiopods, the so-called gnathopods (Fig. 3). Likewise, the maxillipeds overlay most of the more anterior mouthparts, which become partly visible when the maxillipeds swing laterally and if progressively dissecting off the limbs from the posterior to the anterior until the mandibles are freed. All mouthparts are anteriorly held in a way that the posterior surfaces of the appendages are exposed, i.e., facing the ventral side. Another feature readily visible is the asymmetry of right and left appendages. The appendages are described here in anterior-posterior order, as reconstructed in Figure 4. The problem of describing the three posterior mouthparts is that the standard crustacean limb terminology
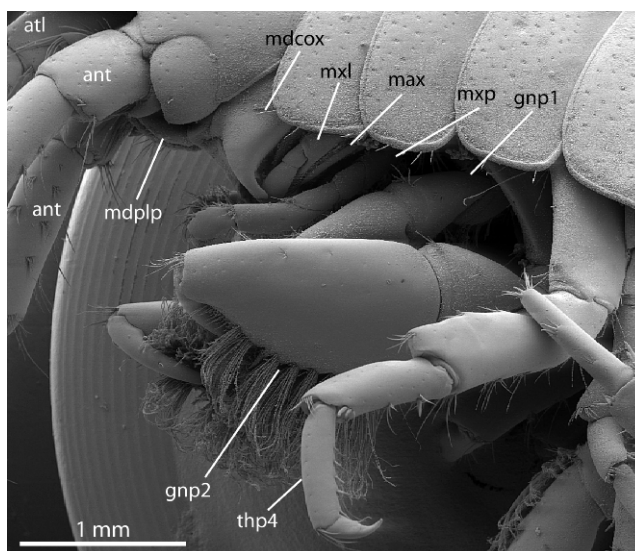

Fig. 3. SEM image of the anterior body region of *Dikerogammarus villosus* in lateral view. Gnathopods (2nd and 3rd thoracopods) covering the mouthparts in front of them. Abbreviations: ant, antenna; atl, antennula; gnp1, gnathopod 1 (= peraeopod 1 = thoracopod 2); gnp2, gnathopod 2 (= peraeopod 2 = thoracopod 3); max, maxilla; mdcox, mandibular coxa; mdplp, mandibular palp; mxl, maxillula; mxp, maxilliped (= thoracopod 1); thp4, thoracopod 4.

cannot easily be adopted for these appendages. Even more, all limbs have their own special terms in different taxa. Since these terms seem not quite consistent and do not help further from a comparative point of view, we try to adopt an as neutral terminology as possible in the description below (Walossek, 1993; Richter et al., 2002).

Labrum

The labrum (Fig. 5A-D) is a dome-like extension above the mouth opening, adorned with hair-like setae marginally. In life, the labrum is flanked by the mandibular coxa and the proximal part of its palp in its resting position (Fig. 5B).

Mandibles

The mandible (Fig. 5B-I) comprises a prominent proximal portion, the coxa, and a distal portion, the palp consisting of three tube-like articles. The coxal body is cylinder-like and is drawn out medially into a proximo-distally extending protrusion, being different in the left and right mandible. This protrusion is divided into a distal incisor process (= pars incisiva) and a proximal molar process (= pars molaris) (Fig. 5E). Adjacent to the incisor the movable lacinia mobilis inserts. A row of setae is located between lacinia mobilis and the molar. These setae, some are feathered and some are stiletto-like, point medio-dorsally in situ. The right incisor consists of four teeth and fits into the gap between the five-toothed left incisor and the left lacinia mobilis (Fig. 5G-H). The left lacinia mobilis is four-toothed and more robust than that of the right side. The right lacinia mobilis is distally notched and shows two rows of irregularly arranged teeth (Fig. 5E). The molars have an ellipsoidal, slightly excavated surface, the longer axis being vertical with respect to the proximo-distal extension of the coxal protrusion. The molar surface is only little structured
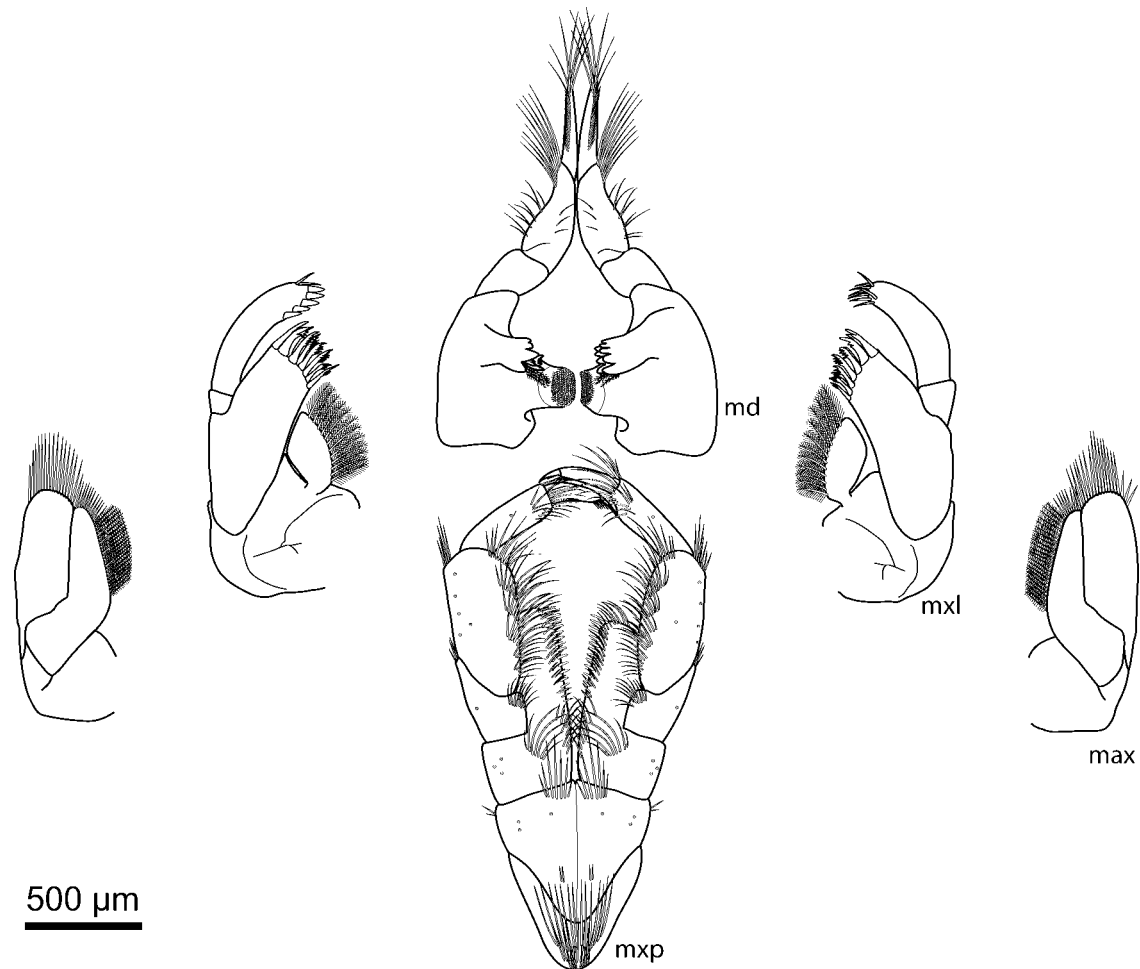
Fig. 4.   Illustration of the mouthparts of *Dikerogammarus villosus* in topological order, but separated from each other. Posterior view of right (left series) and left limbs (right series). Abbreviations: see Fig. 3.

in the form of a carpet of densely spaced, distally rounded, pillar-shaped setae. On some specimens, the surfaces were partly entirely smooth (Fig. 5E). The anterior side of the molar - the side of the mandible facing the labrum – bears a single gnathobasic seta pointing antero-medially into the esophagus in life (Fig. 5D-F). Its length corresponds well with the width of the molar process. The mandibular palps are three-divided (a plesiomorphy retained from the ground pattern of malacostracans; e.g., Olesen and Walossek, 2000) (Fig. 5I). The proximal portion of the palp, most likely the basipod, is the shortest article, while the second article is the largest. The distal article carries at its posterior straight edge a row of densely and regularly arranged short, double-spaced, sawed setae. In the resting position the mandibular palps are anteriorly oriented between the second antennae (Fig. 5B).

Paragnaths

The paragnaths (Fig. 8F-G) are a pair of lobe-like, medially fused extensions of the sternum of the mandibular segment (cf. Walossek, 1993; Waloszek, 2003; Wolff and Scholtz, 2006). In shape, they are symmetrical and distally rounded with a deep medial cut. On the posterior aspect they carry a proximo-laterally pointing lappet on each side. The paragnaths conceal in life the mandibular molar processes and limit the mouth area in the back. The setation of the anterior surface is sparse, there are hair-like setae only on the medial and lateral margin. The posterior surface is densely covered with hair-like setae on the medial area.

Maxillulae

The maxillulae (Fig. 6) insert immediately behind the paragnaths and are, with all parts, anteriorly arched like a spoon surface to fit around the paragnaths and mandibular bodies. They are made up of a proximal part being subdivided into a coxa and basipod and a distal so-called palp being the two-part endopod (Fig. 6A) (note that in the mandibles "palp" comprises basipod plus endopod!). The coxa is drawn out into a blade-like endite (= "inner plate", coxal endite) medially, which stems from a narrow socket. The inner edge of the blade is armed with a vertical row of medio-distally directed long, feathered setae, which form a close-set mesh apparatus. Apart from this, the entire surface of the endite is adorned with numerous more sparsely distributed, fine setae (Fig. 6B, D). The coxa is slightly excavated distally to give rise to the basipod. The basipod is longer than wide and
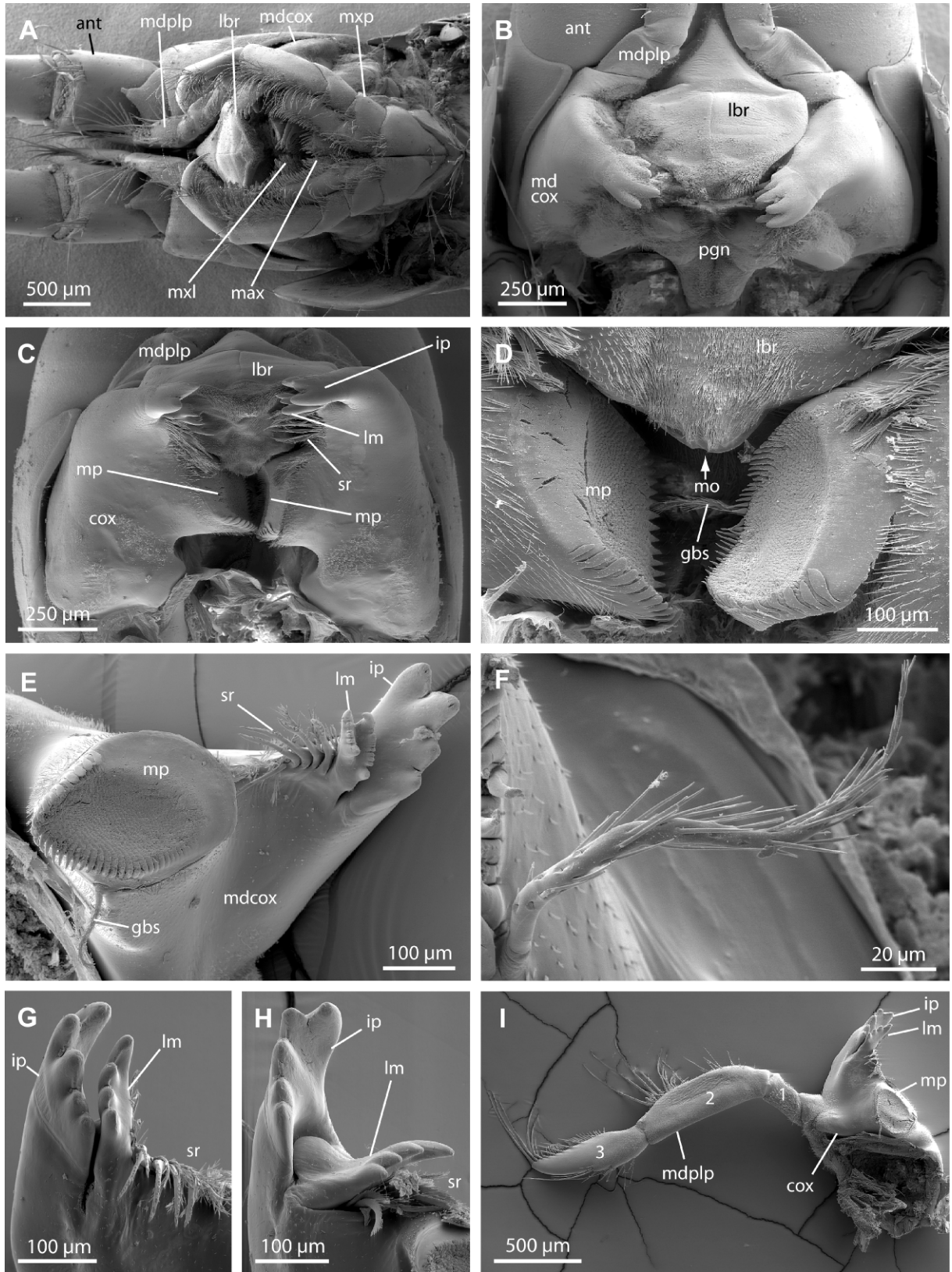
Fig. 5. SEM images of the mandibles. A, ventral view of head region (Thoracopod 2 and 3 removed); B, mouth area with mandibles and paragnaths (maxillipeds, maxillulae and maxillae removed); C, mouth area with mandibles (maxillipeds, maxillulae, maxillae and paragnaths removed); D, molars of mandibles in situ; E, coxa of right mandible in medial view; F, gnathobasic seta of left molar in medial view; G and H, Incisor and lacinia mobilis of left mandible; I: left mandible in medial view. Abbreviations other than in previous figures: cox, coxa; gbs, gnathobasic seta; ip, incisor process; lbr, labrum; lm, lacinia mobilis; 1, 2, 3, parts of mandibular palp (1 = basipod; 2 + 3 = endopod); mo, mouth; mp, molar process; pgn, paragnaths; sr, setal row.
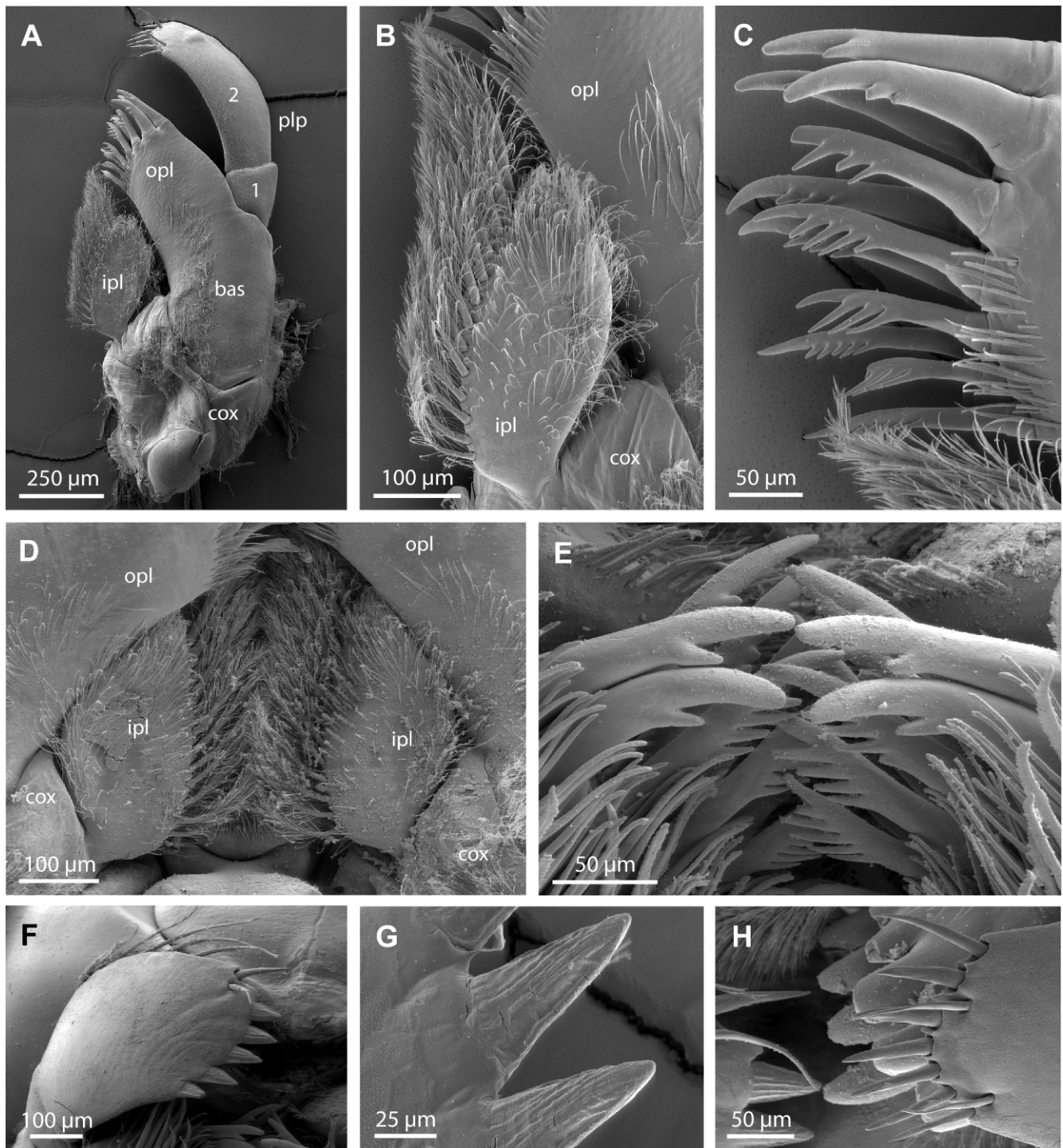
Fig. 6. SEM images of the maxillulae. A, left, shown from the posterior; B, left, endite of the coxa; C, left, distal setation of the basipodal endite; D, endites of the coxae in situ in ventral view; E, distal setation of basipodal endites in situ in ventral view; F, right palp in situ; G, distal setation of right palp; H, left palp and its distal setation in situ. Abbreviations other than in previous figures: bas, basipod; ipl, "inner plate" (= coxal endite; see text for discussion of this term); opl, "outer plate" (= basipodal endite; see text for discussion of this term); plp, palp (= two-segmented endopod).

turns in antero-median direction into an elongate flattened endite (= "outer plate", basipodal endite) (not constricted basally as the coxal endite). The vertically oriented median edge bears a row of 10-12 stout spines that continue in the direction of the endite. These spines bear up to six finger-shaped secondary spines mediodistally like a coarse comb.

The distal end of the spine is slightly set off from the comb and medially curved (Fig. 6C, E). In the most anterior position of the maxillulae, the spine apparatus can reach the posterior edge of the labrum.

The well-developed endopod inserts medio-distally on the basipod. It consists of a short tube-like proximal portion

(laterally slightly longer than medially) and the spatulate distal portion. The distal portion curves slightly medially and overhangs the basipodal endite. The endopod is well movable in medio-lateral direction. The two endopods may contact each other above the mouth opening, hiding the mandibular incisivi, but they can be abducted laterally as wide as the incisors of the mandibles are exposed. The spatulate distal portions of the endopods of left and right maxillula show a conspicuous asymmetry: That of the right maxillula bears a row of five very robust, triangularly flattened teeth; that of the left maxillula shows at the same place a row of seven cylindrical and robust setae (Fig. 6F-H). Basipodal enditic spines of the opposing sides and those of the endopod may interlock.

Maxillae

The maxillae (Fig. 7) insert behind the maxillulae and are similarly modeled to fit the maxillulary curvature in that the anterior side is concave and the posterior side, which appears smoother and slightly better sclerotised, is convex. The maxillae appear to be slightly smaller than the maxillulae, also in their medio-distal extension. The slightly excavated sclerotic area between the limb insertions is difficult to interpret because it seems more or less combined with the limb base, thus making it difficult to distinguish between sternite and coxa (Fig. 7A). Yet it is clearly separate from the maxillulary sternite. The major body of the limb appears weakly subdivided into a small coxal element – best seen posteriorly as a sclerotised plate – and a sub-rectangular basipod which is weakly set off from a medio-distally pointing elongated part, the so-called "inner plate", which is roughly elongated triangular with a rounded distal end (Fig. 7C, D). The coxa, if being the small proximal element, does not bear an enditic extension, as in other Malacostraca, and may even be fused with the limb of the other side medially. The inner surface of the basipod and inner plate are adorned with numerous setae, while the basipod is smooth laterally. Its latero-distal rim bears another leaf-shaped outgrowth, the so-called "outer plate". The outer plate is slightly longer than the inner plate and its shape is almost rectangular. The plate is slightly inwardly bent, so overlapping the inner plate distally from behind. Anteriorly the inner plate bears two major rows of medio-distally pointing plumose setae, one inserting on the median edge of the plate, and one running from the inner edge distally and laterally (Fig. 7F-H). Thus, both rows diverge slightly towards the distal end of the plate. The anterior row of setae ends clearly before the tip. The outer plate bears a double row of setae on its stoutly rounded distal edge. The posterior row consists of long, robust setae, which are flattened on one side on their distal third and armed with fine triangular lobes (Fig. 7B, E). The anterior row consists of slightly shorter setae without specializations. The outer plate partly covers the inner plate, which is shorter and narrower than the outer plate. The inner margins of the plates are oriented straight distally, with the setae of the limbs approaching each other medially and closing the mouth chamber posteriorly. In resting position, both maxillae are held anteriorly so that the setal armature is, likewise, anteriorly oriented.

Maxillipeds

The maxillipeds (= first thoracopods) (Fig. 8A-8E) are almost twice as long as the maxillae and cover the mouth area including the labrum completely. Even with laterally abducted maxilliped palps, the maxillae remain covered apart from the distal setae of the outer plates. From the maxillulae only the distal setation of the basipod and endopod are exposed (Fig. 5A). Again, the entire anterior side of the limbs is concave, likewise is the posterior side convex (Fig. 8A, C). The morphology of the maxillipeds deviates from that of the maxillulae and maxillae, e.g., in having a large, segmented ramus (palp). To fit standard terminology, authors have traditionally named the most proximal part of the limbs coxa, the first endite-bearing element basipod and the subsequent endite-bearing portion the proximal endopodal podomere, which has received the special name ischium. Accordingly, the whole endopod has five podomeres. In anterior view the "coxal" portion is, however, just an ample joint membrane, while in posterior view this part forms a slightly more sclerotized V-shaped structure with a set of three rows of 9-12 fine but long setae proximo-medially. From these, a sharp keel runs latero-distally and merges into the border of the membrane between this sclerotic part and the basipod. The basipod is triangular in posterior aspect but almost square in anterior view, being extended into a plate-shaped endite there. The concave anterior side of the endite is setose, with a straight inner margin and round distal and lateral margins. The concave posterior side of the basipod bears 2-3 small setae in a depression proximally and a horizontal row of 7 setae distally. The basipodal endite is seen only anteriorly but disguised by the next limb portion posteriorly. The length of the endite is about the same as the basipod itself.

The proximal endopodal podomere (ischium) stems from the straight laterodistal margin of the basipod. It is rectangular in anterior and posterior aspect, straight anteriorly and only slightly convex posteriorly. The anterior side is smooth, while the posterior side bears an obliquely disto-laterally running row of 7 setae (those in the center being the longest). As with the basipod, the so-called ischium is medially drawn out into a plate-like endite. In anterior aspect it is proximally covered by the basipodal endite but in posterior view this endite is completely free. The entire inner margins of the opposing maxillipeds are straight but gape slightly towards the distal end in the region of the ischial endite because of the movability of the ischium in medio-lateral plane (closure and opening). The inner margin of the endite is adorned with rather short setae, which become longer around the rounded distal margin and continue, but being much finer, laterally. More of these fine setae occur on the outer lateral area of the anterior surface of the endite. On the posterior side, the inner area bears a widely spaced group of setae similar to those of the rows or sets on this side. With a small gap they continue as rather short but distally a little longer setae onto the surface of the endite. This armature of two and more distally three vertical rows of setae is rather special in that the setae, nested in deep depressions, are slightly flattened, so spatulate. It seems that the setae of median and more posterior rows stand at an angle against each other (Fig. 8D).
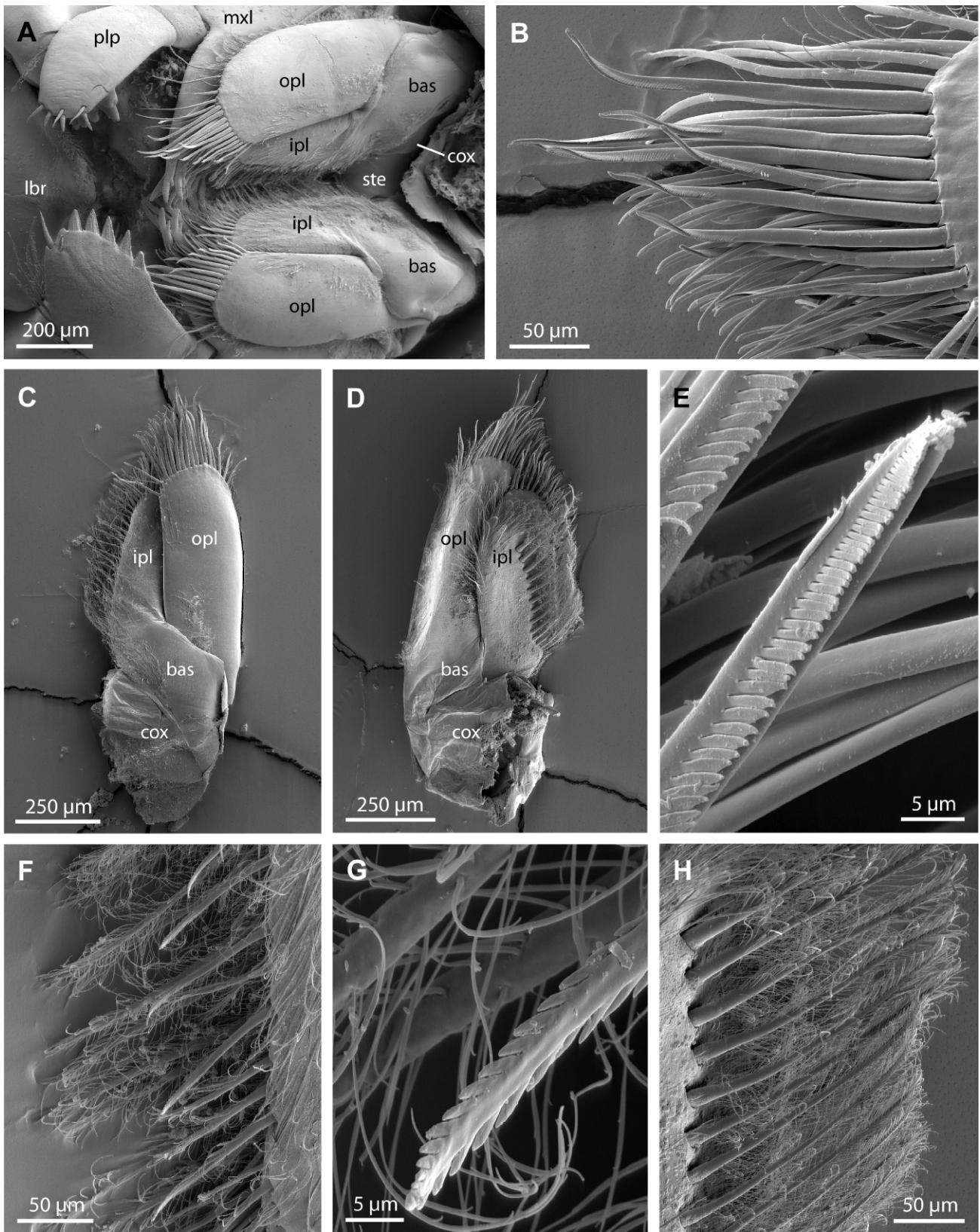
Fig. 7.   SEM images of the maxillae. A, in situ, in ventral view (maxillipeds removed); B, distal setation of left shown from posterior; C, left seen from posterior; D, left seen from anterior; E, distal setation; F, medio-marginal setation seen from posterior; G, detail from F; H, medio-marginal setation seen from anterior. Abbreviations other than in previous figures: ste, sternite.
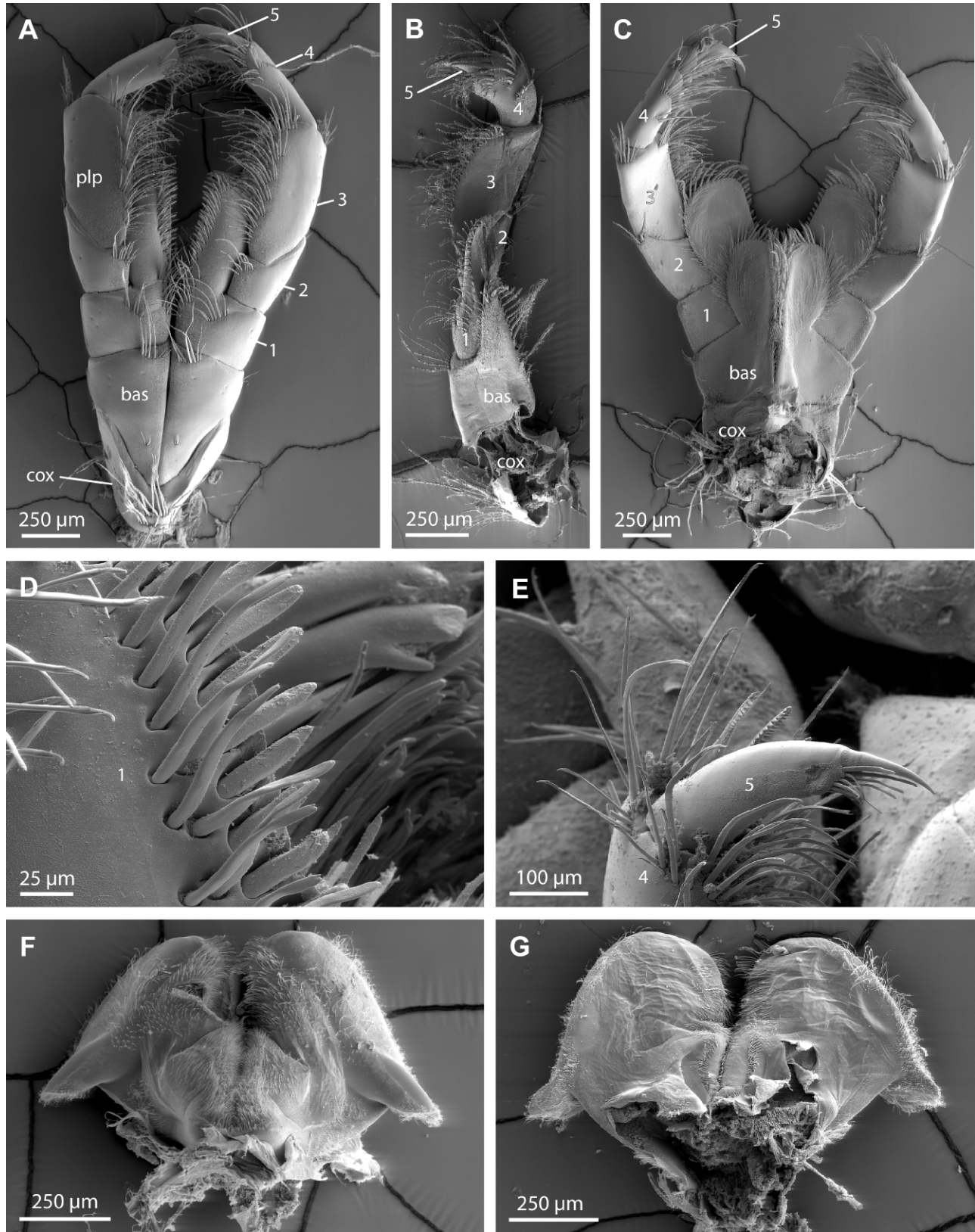
Fig. 8. SEM images of the maxillipeds and paragnaths. A, maxillipeds seen from posterior; B, separated right maxilliped in medial view; C, maxillipeds seen from anterior; D, medio-marginal setation on the endite of right ischium in situ seen from ventral; E, distal part of right palp in situ seen from ventral in situ; F, paragnaths shown from posterior; G, paragnaths shown from anterior. Abbreviations as in previous figures. Numbers refer to endopodal podomeres: 1, ischium; 2, merus; 3, carpus; 4, propodus; 5, dactylus.

All distal enditic setae curve medially. The coxae of the opposing maxillipeds are fused medially, and it seems that also the basipods of left and right limbs have a small median connection (Fig. 8B).

The merus (endopodal podomere 2) rests on the straight distal edge of the ischium. Pivots on either side document ability of slight inward-outward movements. The slightly concave anterior side is smooth, while the slightly convex posterior side bears a group of obliquely inwardly pointing setae medio-distally. Its distal margin is straight medially but inclines laterally to an outer, slightly bulged point on which a tuft of setae is located. This joint pre-forms the movability of the next endopodal podomere, the carpus, to a median rotatability, but blocks the outward movement.

The carpus is elongate/sub-rectangular and almost twice as long as the merus. Also the concave anterior surface of this podomere is smooth, while the medial rim and the inner area of the posterior side are adorned with groups and/or rows of medially oriented setae, which become progressive longer towards distally. The rows slightly slant down medially. The distal margin of the carpus is bluntly rounded. Since the insertion area and the subsequent propodus (endopod podomere 4) is about one third as long as the margin, this leaves slightly sloping areas on the inner and outer side. One row of densely spaced setae surrounds the medio-distal edge of the carpus, while a group or row of setae is located on the outer distal edge. There are two pivots at the joint between carpus and propodus. While the outer membrane is very small, it is wider medially, which facilitates an inward flexure of the entire distal part of the endopod – the major joint of this distal part of the maxilliped (for grasping items etc.).

The propodus (endopodal podomere 4) is about as long as the carpus and rod-shaped, so being oval in diameter. Its armature is very special in having no setae along the inner and outer edges, but 3 half-crescentic rows of setae anteriorly, that arise from sharp furrows, which are slanting medioproximally. The posterior side has a group of setae postero-distally and a row of setae mediodistally. Around the joint toward the dactylus podomere (endopodal podomere 5) sits a row of setae, most of them being simple or distally flattened setae, a few also sawed. The dactylus is also rod-shaped but less wide than the propodus and tapers distally to continue with a slight constriction into the terminal, slightly medially curved and claw-like spine. Disto-medially on a sloping area a set of flattened and simple setae is located. The longest do not reach to the tip of the terminal spine (Fig. 8E).

Antennae and Gnathopods

These appendages support the mouthparts but are, though apparently important in the capture process (Platvoet, personal communication), only briefly mentioned here because we concentrated on the mouthpart morphology in our SEM study. The antennae consist of a two-divided proximal part (protopod) and distal part made of two long tubular endopod podomeres and a set of 14-15 tubular to annular segments that become progressively smaller in diameter (= "flagellum"). Setae occur, like a brush, along the entire inner (posteriorly oriented) side, those of the distal annuli are longer and simple, facing the mouthparts when the antennae are bent ventrally and posteriorly (Fig. 9C). The first and second gnathopods (= second and third thoracopods) (Fig. 9B) are much larger than the mouthpart limbs. They consist of a coxa bearing a plate on its lateral side (coxopleura), an elongate basipod and a 5-segmented endopod of very differently shaped podomeres. The distal two form a prominent subchela. Due to specific joints the gnathopods turn anteriorly behind the ischium, so that the robust propodus portions lie ventrally of the mouthparts, parallel to the body axis, in the resting position. Particularly the propodi bear long, medially directed simple setae arranged in tufts (like a brush).

DISCUSSION

Formerly, freshwater gammarideans have been regarded as representatives of the functional feeding group (FFG) of shredders which feed on autochthonous and allochthonous detritus, fallen leaves and particulate organic matter (Bärlocher and Kendrick, 1973; Cummins and Klug, 1979; Gayte and Fontvieille, 1997; Haeckel et al., 1973). More recent investigations have shown, however, that gammarideans can prey on conspecific animals and on a variety of live and dead macro-invertebrates (Hunte and Myers, 1984; Dick et al., 1990, 1993; Dick, 1995; Krisp and Maier, 2005). This cannibalistic and predatory feeding together with scavenging and more herbivorous feeding suggests that gammarideans are omnivorous (see review by MacNeil et al., 1997).

Specializations of the Mouthparts in Other Amphipods

A relation between the modes of feeding, preferred food and mouthpart morphology is shown for several feeding-specialists among the amphipods. Specialists, feeding on animal prey show modifications of the mandible for cutting out pieces of tissue. For example, the incisors of the acanthonotozomatid gammaridean *Echiniphimedia hodgsoni* Walker, 1906, feeding on sponges, are broadened and regularly toothed. The right lacinia mobilis is also broadened and arranged parallel to the right incisor as a supplementary cutting edge. While biting, the left incisor moves into the gap between the right incisor and right lacinia mobilis. The setae of the mouthparts of theses specialists are generally reduced in number and size or reduced into strong spiniform setae (Coleman, 1989a; see also Coleman, 1989b for another acanthonotozomatid *Gnathiphimedia mandibularis* Barnard, 1930). A similar adaptation of the mandible shows the stilipedid gammaridean *Bathypanoploea schellenbergi* Holman and Watling, 1983 as adaptation to cope with the leathery body wall of the holothuran prey. Here the left lacinia mobilis and the incisors are broadened. The molars are reduced and non-triturative (special term in amphipod morphology for grinding; Coleman, 1990). Comparable modifications are described for the stegocephalid gammaridean *Parandania boecki* Stebbing, 1888 (Moore and Rainbow, 1989). Some carrion-feeding lysianassids, e.g., *Orchomene chevreuxi* Stebbing, 1906, and the acanthonotozomatid *Maxilliphimedia longipes* Walker, 1906 show striking resemblance to these modifications (Dahl, 1979; Sainte-Marie, 1984). To summarize, incisors and the lacinia mobilis of amphipods specialized in feeding on animal tissue are broadened to sharp cutting edges,
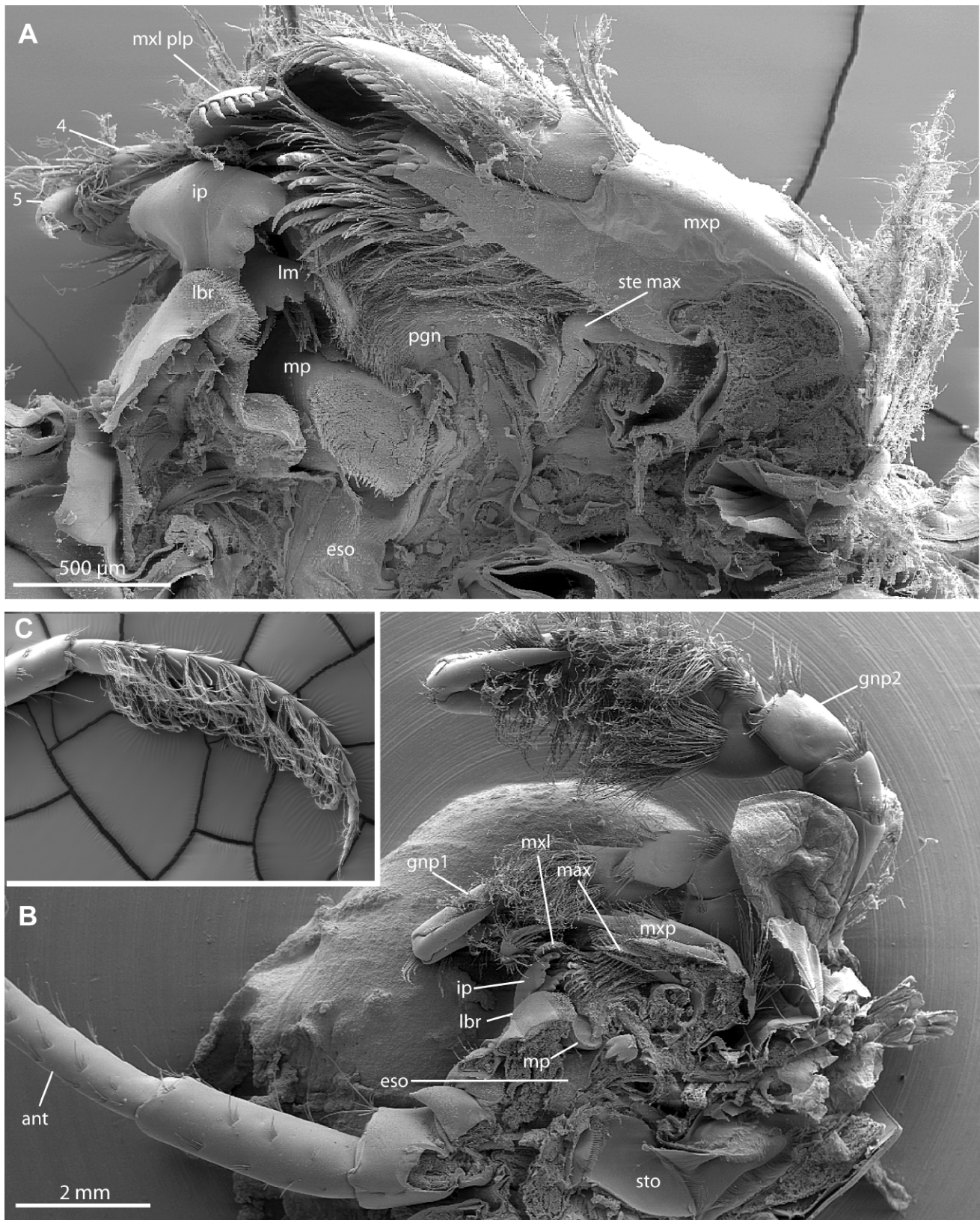
Fig. 9. SEM of the cephalothorax cut sagittally, view on left side. Images flipped horizontally to get the anterior left. A, orientation of the mouthparts in situ; B, Orientation of gnathopods in situ; C, Distal part of left antenna. Abbreviations other than in previous figures: eso, esophagus; sto, stomach.

molars are non-triturative, and setae are reduced in number and size.

The detritus-feeding iphimediid gammaridean *Anchiphimedia dorsalis* Barnard, 1930 has long and closely arranged setae on the medial and apical margins of the maxillipeds, maxillulae and maxillae for brushing food from sand grains or other structures and preventing it from being washed away. The molars are rudimentary (Coleman, 1991). The molars of the sand-burrowing and detritus feeding haustoriid gammaridean *Haustorius arenarius* Slabber, 1769 show a file-like surface, built by densely arranged fine and stiff setae. Palps and endites of maxillulae and maxillipeds are adorned with long simple setae. In the middle line between the maxillae, interlocking simple setae form a dense sieve (Dennell, 1933).

The molars of *Hyperia galba* Montagu, 1812 (Hyperiidea: Hyperiidae) are triturative, covered by a regular pattern of densely arranged stout cusps. This amphipod infests large scyphozoan medusae and lives as a food parasite feeding on plankton captured by its host (Dittrich, 1992). *Paracalliope australis* Haswell, 1880 (Gammaridea: Paracalliopiidae), an amphipod feeding on periphyton shows modification for scraping off algae from the surface of the substratum: The basipodal endites of the maxillulae bear stout tooth-like spines on their apical margin. The coxal endites possess a row of plumose setae along their distal and medial edges for preventing loosened food from being washed away. The molar surfaces are triturative, built by densely arranged columnar teeth (McGrouther, 1983).

Hyale rupicola Haswell, 1879 (Gammaridea: Hyalidae) is adapted to feeding on macrophytes. The coxal endites of its maxillulae are small with only two pappose setae. The basipodal endites terminate in stout apical spine teeth. The mandibular palp is absent and the left incisor is lying anteriorly to the right incisor. The left lacinia mobilis is heavily toothed and the molars are clearly triturative, with rasp-like surfaces (McGrouther, 1983). Agrawal (1965) described the mouthparts of *Gammarus pulex*, a gammarid feeding on decaying leaf material and fresh *Nitella* (Charales) (Willoughby, 1983). Its molars are triturative, with rasp-like surfaces. The basipodal endites of the maxillulae are provided distally with a row of six robust knob-like setae, which are produced distally into small tooth-like projections.

Functional Morphology of Feeding in
Dikerogammarus villosus

Dikerogammarus villosus cannot be assigned to one of these groups of feeding specialists mentioned above. According to the morphology of its mouthparts, several modes of feeding are supposable for *D. villosus*:

For feeding on macrophytes, biting off pieces of plant material, a robust cutting tool and the ability for crushing the morsels prior to ingestion is needed. The incisors of the mandibles of *D. villosus* seem to be robust and sharp enough to cut off pieces of macrophytes or leaf material. But the molars appear to be non-triturative because both molar surfaces are concave and are only slightly structured. Two concave surfaces, which can be moved against each other, appear little suited for grinding. Rasp-like structures like those found in amphipods specialized to feed on macro-

phytes as mentioned above, are missing. *D. villosus* has not yet been observed feeding on leaf material under laboratory conditions, even when there was no alternative food available (MacNeil and Platvoet, 2005), while new information may point to such possibilities (Kley, personal communication). This seeming discrepancy requires more detailed investigations.

For scraping, abrading or grazing of algae and fungi from substratum or decaying leaves, the mouthparts must be adapted to solve a further functional problem: the periphyton must be removed from the substratum. Such a scraping tool can be found amongst various Crustacea, e.g., in the isopod *Ligia italica* Fabricius, 1798. The incisors of this isopod, feeding on epilithic algae are elongated and gouge-like, with a sharp un-toothed ridge (Arens, 1994). *D. villosus* does not possess any specific tools for scraping. The stout incisors with their toothed and equally rounded edges appear little suited for scraping. As mentioned above, flattened tooth-like spines on the apical margin of the basipodal endite of the maxillula can also be used as a scraping tool. In *D. villosus* these spines do not show such modifications. Yet, not having special tools may not exclude such mode of feeding, since it has been observed (Platvoet, personal communication).

The mechanism of producing a respiration current in gammarideans and the use of this current for filter feeding in pontogammarids has been described by Ponyi (1956, 1961) and Dahl (1977). The cephalothorax and anterior segments are curving slightly ventrally, the pleon being more distinctly arched, with the posterior part generally directed somewhat anteriorly. The fast and regular beating of the pleopods produces a posterior directed water flow. A part of this current is circulating on the ventral side of the animal. The setae on the flagella of the ventro-laterally bent antennae are pointing against this current and function as a particle-collecting device. The same can be observed for the setae of the gnathopods. According to Ponyi (1956) the maxillipeds are also involved in filtration. They swing into a ventrally pointing position and so they are held into the water current. Due to the long and medially directed setae on their palps, a filter function of the maxillipeds is likely, as well as catching of bigger particles with their claw-like dactyli. The antennae are cleaned with the propodus and dactylus of the first gnathopods or with the palps of the maxillipeds or with the maxillulae. The food gained thereby, is transported to the mouth and ingested. Ponyi (1956, 1961) distinguished between "filter feeding" amphipods such as *D. villosus* and "chewing" forms like *Gammarus roeseli*.

For cleaning the antennae, the maxillipeds of *D. villosus* seem to be well suited. Their palps encompass one antenna. When the antenna is pulled back, the particles adhering on the setae of its distal part are wiped off by the short and stout setae on the medial margin of the endites. It is also possible that the medially pointing spines on the basipodal endites of the maxillulae comb out the setae of the antennae and gnathopods. The closely arranged setae on the medial margin of the coxal endites of the maxillulae and of the maxillae are suited for keeping the food particles from being washed away and for concentrating the food prior to ingestion. Platvoet et al. (2006) showed that *D. villosus* is

also able to filter out and ingest suspended micro-algae in this way. The ingested algae were found undamaged in the foregut, but more and more algae fragments were found in the midgut and hindgut. Thus, triturating of this kind of food by means of the mandibles does not occur. As mentioned above, the mandibles are of little importance for food processing in amphipods specialized on detritus.

Scavenging, the grasping of non-living material, as dead organisms or pieces of detritus, is a further mode of food acquisition observed in *D. villosus*. Food particles are collected by means of the antennae and grasped with the gnathopods. Larger food items are hold with the Gnathopods and reduced to small pieces by means of the mandible's incisors.

Filter feeding and detritus feeding may be important even for carnivores, when temporarily there is no prey available. This applies especially for juveniles.

As shown in laboratory experiments, predation, the feeding on captured prey, is an important part of food acquisition in *D. villosus*. Indeed, the gnathopods are well suited for holding prey, while the robust mandibles crack firm structures such as the cuticle of crustaceans and aquatic insects. The concave molars seem not to be suited for mincing tissue. It is probable that prey, e.g., chironomids, or parts of it, is clamped with the molars and hold between the molars and the gnathopods. Food, oriented in this way, can be cut easily by the incisors. Special adaptations of the incisors for cutting animal tissue, as mentioned above for specialized carnivorous species, are not found in *D. villosus*. Another argument against adaptation to predation, is the large number of long setae, e.g., on the antennae and gnathopods. Long setae on the integument are increasing the flow resistance and may be negative when hunting living prey. Again, the versatile setation of the mouthparts is not in line with an amphipod, specialized on animal tissue, as shown by the comparison with the species described above. The mouthparts of *D. villosus* show striking similarity to those of *Gammarus wilkitzkii* Birula, 1897, living permanently associated with Arctic sea ice. This species feeds, like *D. villosus*, on detritus, living and dead animals and algae. Macrophytes are not available in its habitat (Arndt, 2002; Arndt et al., 2005; Poltermann, 2001; Werner et al., 2002).

CONCLUSIONS

Our SEM studies of the mouthparts of *Dikerogammarus villosus* and comparisons with gammarideans being adapted more or less to a single type of feeding mode suggest that *D. villosus* is not highly specialized just for predation, hence it is not an exclusively carnivorous species, as previous experiments on predation proposed. As indicated by the more generalized morphology of its mouthparts and structures involved in food acquisition such as antennae and gnathopods *D. villosus*, besides being a predator, is able to use a wide variety of food. Indeed, this species is able to collect detritus and dead bodies of small animals, to filtrate out and digest suspended organic particles and algae, and is also able to prey on a wide spectrum of macrozoobenthos. This is a significant advantage over food specialists, which depend on specifically suitable matter. It is also important for the success of an invader to sustain after decrease of easily

accessible, energy-rich prey. Furthermore it is shown that *D. villosus* cannot be assigned to the functional feeding group "shredder", because macrophytes and decaying leaves are almost the only food source, which is not used by *D. villosus*. Van der Velde et al. (2000) describe the qualities of successful crustacean invaders: short life span and generation time, rapid growth with early sexual maturity, high fecundity, female able to colonize alone, euryoecious, gregarious behavior, ability to repopulate depopulated habitats, larger than most relatives and suspension feeding and/or omnivorous. *D. villosus* seems to represent an excellent example of this model.

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