Mouthpart morphology of *Synurella ambulans* (F. Müller, 1846)

(Amphipoda, Crangonyctidae)

Gerd Mayer, Andreas Maas & Dieter Waloszek

The morphology of the mouthparts and other structures involved in food acquisition of *Synurella ambulans* (F. Müller, 1846) was studied using scanning electron microscopy. Based on the obtained morphological data, conclusions are drawn regarding the food spectrum of *S. ambulans*. This species does not possess specific structures on its mouthparts for sieving or filtering fine particulate organic matter out of the respiration current. Likewise the mouthparts do not appear to be suited for removing periphyton from substrates and the little structured surfaces of the molar processes of the mandibles suggest that they are not suited for grinding fresh and hard plant material. On the contrary, the mouthparts of *S. ambulans* exhibit structures apparently suitable for collecting, manipulating, biting and grinding dead plant material, detritus and carrion of small animals. This spectrum of food fits to the strong affinity of *S. ambulans* to the groundwater system and a semi-subterraneous life in the interstitial of waters influenced by groundwater.

Gerd Mayer, Andreas Maas & Dieter Waloszek, Workgroup Biosystematic Documentation, University of Ulm, Helmholtzstr. 20, 89081 Ulm, Germany; e-mail: gerd.mayer@uni-ulm.de

Introduction

Synurella ambulans (Fig. 1) is a small freshwater amphipod with a maximum body length of 7.0 mm for females and 5.3 mm for males (Konopacka & Blazewicz-Paszkowycz 2000, Mürle et. al. 2003). This species was first described by Müller (1846) as *Gammarus ambulans*; as locus typicus a ditch covered with *Lemna* and *Hydrocharis* near Greifswald, Germany was mentioned. Stebbing (1906) assigned the species to the genus *Synurella* Wrzesniowski, 1877, but some scientists consider the genus *Synurella* as a synonym of *Stygobromus* Cope, 1872. Therefore, in literature the species is sometimes named *Stygobromus ambulans* (F. Müller, 1846) (e.g. Barnard & Barnard 1983, Lowry 2014). Sidorov & Palatov (2012) discussed the taxonomy of *S. ambulans* and gave a detailed description of characters relevant for taxonomy.

Occurrence of *S. ambulans* ranges from Poland, Latvia, Estonia, Russia, Czech Republic, and Slovakia to Austria, Hungary, northern Italy, Romania, Bulgaria, the area of former Yugoslavia, Albania and Turkey (Borutzky 1927, Karaman 1931a, Karaman 1931b, Dobreanu & Manolache 1933, Jazdzewski & Konopacka 1993, Konopacka & Sobocinska 1992, Musko 1992, Heckes et al. 1996, Konopacka & Blazewicz-Paszkowycz 2000). The border of the continuous area of distribution of *S. ambulans* in the southwest is the Vienna Basin in Austria and the Podan Plain in Italy, where the species also inhabits Lake Garda (Casellato et al. 2006); and in the northwest the border is Northern Germany (Nesemann 1993). Surprisingly the first records for Lithuania and Estonia are from 2005 and 2008 respectively (Arbaciauskas 2008, Tempelman et al. 2010). As a reason for the late detection in this region, these authors suspect that specimens of *S. ambulans* might have been confused with juveniles of other gammaridean species, because of their small size.

In Germany *S. ambulans* was originally distributed only in the north-east, in Mecklenburg-West

Pomerania, but in 1994 it was found in southern Germany in a pond near Lake Starnberg, Bavaria (Müller 1846, Heckes et al. 1996, Zettler 1998). Heckes et al. (1996) assumed that individuals of *S. ambulans* were unintentionally transported into the lake with recreational crafts or together with stocking fish and migrated from the lake via the groundwater into the pond. Possibly *S. ambulans* hitherto has been overlooked in Lake Starnberg. Mürle et al. (2003) supposed a similar spreading mechanism for another isolated population in a reservoir of the river Aare in Switzerland. Another isolated population of *S. ambulans* westward from the original area of distribution was recorded in Belgium (Boets et al. 2010). Here individuals of *S. ambulans* were found in samples taken in 2003 from a stream, which is connected to fishponds. Boets et al. (2010) term *S. ambulans* as a "new Ponto-Caspian invader", although this species always occurs only in local populations with low densities. Furthermore, because of its small size it is unlikely that *S. ambulans* is a serious competitor for native gammarideans.

At first sight, the habitats of *S. ambulans* seem to be very diverse: small water bodies in floodplains, oxbow lakes, peat-ditches, pools, swamps, sections of brooks and rivers with low flow velocity, lakes, caves and wells are mentioned in literature (e. g. Jarocki & Krzysik 1925, Zettler 1998, Arbaciauskas 2008). However, one requirement for the occurrence of *S. ambulans* is the contact of the water body to groundwater. This is also an explanation for the occurrence of *S. ambulans* in temporary pools as well as in wells.

Digging in gravel of a dried-out brook bed Heckes et al. (1996) found juveniles of *S. ambulans* in groundwater. Also Sket (1999) mentioned that *S. ambulans* is able to penetrate into groundwater, and Borutzky (1927) described this species as a typical representative of inhabitants of groundwater discharges. According to Karaman (1931b) all members of the genus *Synurella* are cold water animals, which avoid summer-warm waters and therefore cannot be found in pools and brooks in summer, because they retreat into the groundwater.

In contrast, Spandl (1923) mentioned that specimens of *S. ambulans* can easily be kept in aquaria and that they are able to withstand high temperatures. Moreover, *S. ambulans* is also able to tolerate low oxygen concentrations, which is a requirement for living in groundwater (Konopacka & Blazewicz-Paszkowycz 2000). According to habitat descriptions *S. ambulans* seems to have a clear preference for waters with muddy sediments covered with dead plant material and ample submerse and riparian vegetation (Jarocki & Krzysik 1925, Borutzky 1927, Heckes et al. 1996).

In our earlier works we described the morphol-ogy of mouthparts and other structures involved in food acquisition of several native and invasive gammaridean amphipods occurring in German inland waters (Mayer et al. 2008, 2009, 2012a,b). With the present work on *S. ambulans* we continue this series with the aim to understand the fact that this species is able to increase its area of distribution in Europe, despite its relative small size and growing competition from an increasing number of non-native amphipod species. We lay the focus of our study on structures, which are known to be involved in the acquisition of food in amphipods. These structures are the antennulae, antennae, the true mouthparts with mandibles, maxillulae and maxillae, the maxillipeds, the two pairs of gnathopods, and also the third pair of uropods (e. g. Schellenberg 1942, Schram 1986, Schmitz 1992, Platvoet et al. 2009).

Material and methods

Specimens of *Synurella ambulans* (F. Müller, 1846) were kindly provided by the Leibniz-Institut für Ostseeforschung Warnemünde. They had been sampled from Kreutzsee near Hartwigsdorf, Mecklenburg-Western Pomerania, Germany in May 2008. All samples were stored in 70 % ethanol.

For the photograph (Fig. 1) 30 frames were taken with a Canon MP-E 65 mm lens mounted on a Canon 450D digital camera. These frames were trimmed using Adobe® Lightroom® and fused to an image stack with the free software CombineZP. Preparation of mouthparts was done with the aid of watchmaker forceps and a Leica MZ12 stereomicroscope. For removing debris from the cuticle, the samples were treated for five minutes with a solution of Corega® Tabs®, a denture cleaning agent, and afterwards sonicated for 30 seconds. After rinsing with demineralised water the samples were dehydrated in an alcohol series and critical-point dried. Sputter-coated with a mixture of gold and palladium, the samples were investigated and documented with a Zeiss DSM 962 scanning electron microscope (SEM). Digital images from the SEM were trimmed with Adobe® Photoshop® and arranged to plates using Adobe® Illustrator®. Samples are stored at the University of Ulm, Workgroup Biosystematic Documentation.

Results

The main part of the antennula (Fig. 2) consists of a three-jointed peduncle and a flagellum with 13 annuli, which are slender and cylindrical. The two-joint accessory flagellum is very thin and shorter than the first annulus of the flagellum. The setation of the antennula is sparse; each annulus is armed with a pair of short simple setae on its median and lateral face.
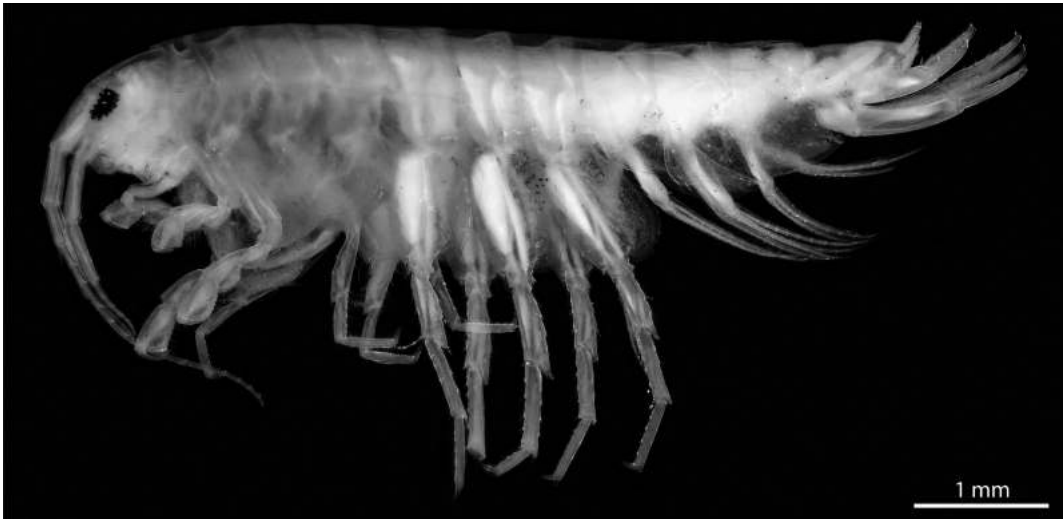
The flagellum of the short antenna (Fig. 2) con-

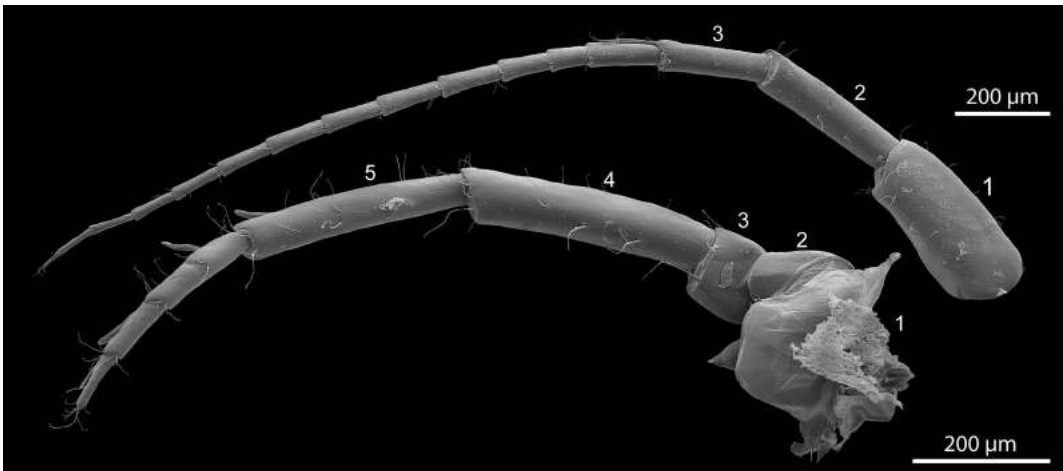**Fig. 1.** Photograph of *Synurella ambulans* (adult female, stored in ethanol).

Fig. 2. SEM images of right antennula in median view (top) and left antenna in lateral view (bottom) of *S. ambulans*. Abbreviations: **1–5**, portions of peduncle.

sists of only four to five annuli and is, as a whole, about as long as the fifth joint of the peduncle. Its sparse setation consists of short simple setae. In males, the annuli of the flagellum and the distal portion of the peduncle bear so-called calceoli, special sound and vibration receptors found in amphipods.

Compared with the mandibular coxa, the three-segmented palp of the mandibles (Fig. 3) is large. The basipod is a short tubular element, while the first portion of the endopod is medio-laterally flattened with a straight anterior margin and a protruding posterior margin bearing some long simple setae.

The distal portion of the palp is plump and bears a row of about 15 serrated setae on the distal third of its posterior margin (Fig. 3A). The relatively small mandibular coxa is slender in medio-lateral aspect and proximo-distally elongated, being only about as long and wide as the second portion of the palp. Its gnathal edge is small and occupies about one third of the coxal body (Fig. 3A).

The molar process of the left mandible (Fig. 3B,D,F) is a conical protrusion, which is arranged perpendicularly to the line between the proximal pivot of the mandible and its incisor process. The

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small surfaces of left and right molar processes are built by partly fused columnar cuticular elements and there is no rasp-like structure (Fig. 3F,G). The gnathobasic seta is very long (Fig. 3A) and extends into the oesophagus. The surface of the right molar process is tilted toward the incisor process (Fig. 3A).

The incisor process of the left mandible is stout, broad and composed of five teeth (Fig. 3B,D). The lacinia mobilis of the left mandible is nearly as long as the neighbouring incisor process and is likewise five-toothed (Fig. 3D). Its articular condyle, a rounded process reaching into the cavity of the neighbouring incisor process, is remarkably well developed and broad (Fig. 3B). The setal row of the left mandible consists of a tuft of pappose setae near the molar process and two rows of setae near the lacinia mobilis. The posterior row consists of four pappose setae, whereas the setae of the anterior row are stiletto-shaped, with short setulae only on the distal third of the shafts on the side facing the molar process. The bases of these setae are broadened medio-laterally and flattened proximo-distally (Fig. 3B,D).

The incisor process of the right mandible is stout and four-toothed (Fig. 3C,E). The right lacinia mobilis is distally deeply cleaved and, therefore, exhibits two distal margins, which are orientated perpendicular to the gnathal edge. Each of the two edges bears two lateral thorns and some small cusps in-between (Fig. 3E). The articular condyle of the right lacinia mobilis is well developed (Fig. 3C). The setal row of the right mandible consists of two rows of setae (Fig. 3C,E). The bases of the three stout setae of the anterior row are broadened medio-laterally and flattened proximo-distally. The distal halves of these three setae bear short setulae on the side facing the molar process. The posterior row consists of three pappose setae with band-shaped setulae (Fig. 3C).

The distal margin of the paragnaths, a pair of lobe-like elevations of the sternum of the mandibular segment, is broadly notched (Fig. 5F). In the area of the notch the paragnaths are densely adorned with hair-like cuticular outgrowths.

The coxal endite (= inner plate) of the maxillulae is rhomboid, small, and the median margin is sparsely set with six to eight in situ medio-distally oriented pappose setae (Fig. 4A,B). The basipodal endite (= outer plate) bears seven firm spine-like cuspidate setae in two rows. These setae are equipped with up to five pointed, medio-distally oriented and thorn-like setulae (Fig. 4C). The endopod of the maxillula (also called palp) is two-segmented. Its distal part has a blunt distal margin, which on the right as well as on the left maxillula is armed with a row of stout simple setae (Fig. 4A). An exopod is missing.

The coxal endite (= inner plate) of the maxillae (Fig. 4D) is covered with a dense fluff of thin, band-shaped cuticular outgrowths on its median margin and on the median half of its anterior surface. In addition, the median margin of the coxal endite bears a few pappose setae, and another row of setae starts on the distal part of the median margin curving onto the anterior surface of the coxal endite. These setae are equipped with long thin setulae, which are arranged in two opposing rows on the proximal half of each seta, whereas on the distal half the setulae are randomly arranged around the shaft of the seta. The spatulate basipod (= outer plate) bears only a few serrate setae on its distal margin.

The endopods of the maxillipeds (Fig. 4E,G) are elongated carrying claw-like dactyli distally (Fig. 4H). The endite of the maxilliped's ischium is distally pointed. Its median and distal margins are sparsely set with simple setae, there are no cuspidate setae (Fig. 4F). The median margins of carpus and propodus are armed with long serrate setae. A large area of the antero-median surface of the propodus is covered with densely set, very fine, short serrate cuticular outgrowths (Fig. 4H).

The propodi of the first gnathopods (Fig. 5A) are remarkably big and flat. Their setation is sparse and there are only short simple setae along the median margin. Merus and carpus are armed with a row of distally oriented serrate setae.

The propodus of the second gnathopods (Fig. 5B) are likewise big and flat. Its setation is sparse, bearing only a few simple setae along its median margin. The carpus of the second gnathopods is armed with a group of short, medio-distally oriented serrate setae. All uropods are styliform (Fig. 5C–E). Their cuspidate setae are thorn-like and there are no plumose or pappose setae. The third uropods are uniramous and shorter than the telson, covering the anus flap-like (Fig. 5D).

Discussion

As described in detail in our previous work, a relation between mouthpart morphology, mode of feeding and preferred food is shown for several feeding-specialists among amphipods. In these species details of the structures involved in feeding are modified, enabling effective use of a certain food resource. Such morphological specializations are described for amphipods feeding on carrion, sponges, holothurians, detritus, periphyton and macrophytes (e.g. Agrawal 1965, Dahl 1979, McGrouther 1983, Sainte-Marie 1984, Coleman 1991, Mayer et al. 2008). Trying to assume the feeding capabilities of *Synurella ambulans*, we can also use our investigations of the feeding system of currently 16 different gammaridean species as a backbone here.
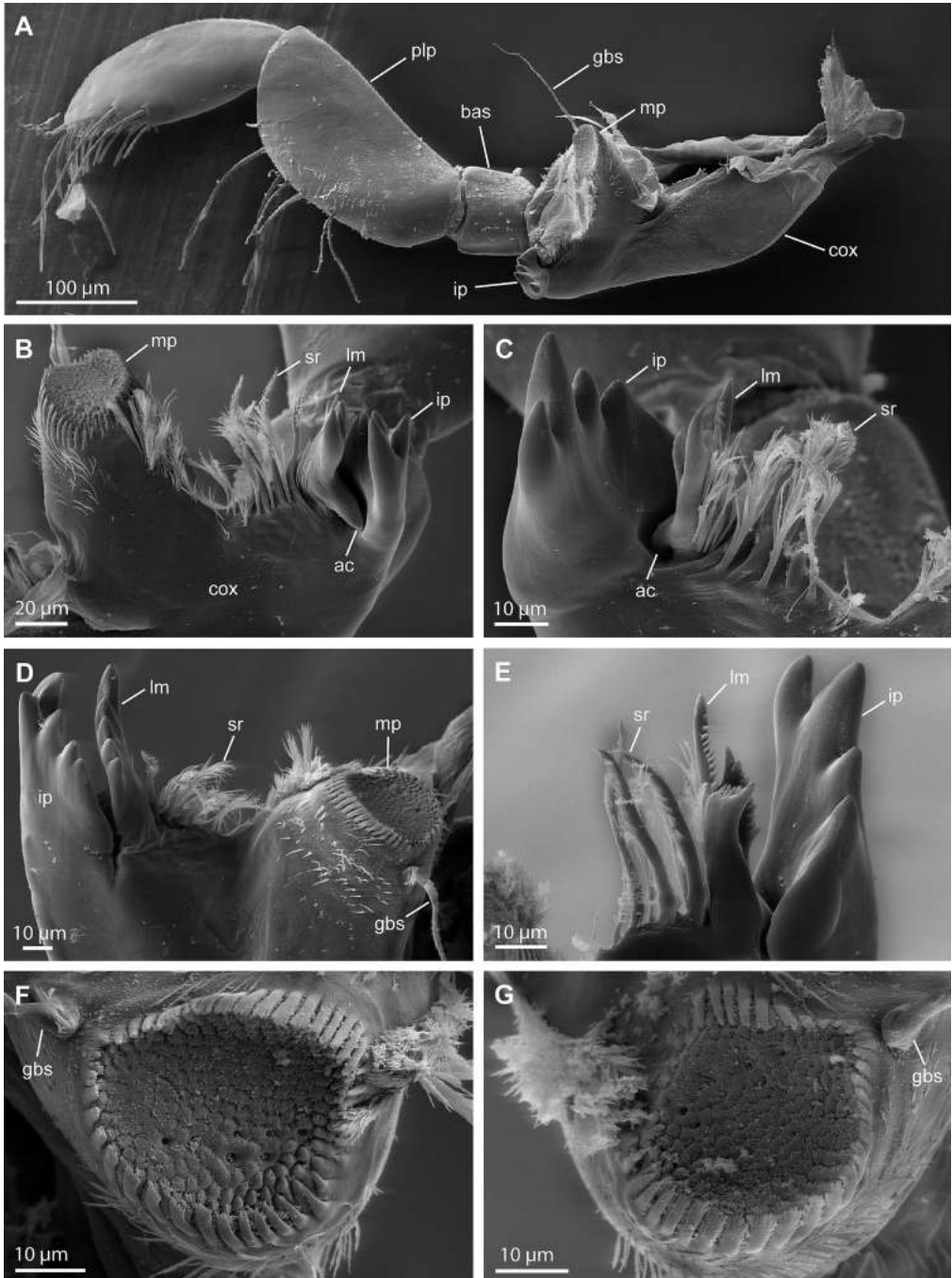
Fig. 3. SEM images of mandibles of *S. ambulans*. **A.** median view of right mandible; **B.** coxa of left mandible in posterior view; **C.** incisor process lacinia mobilis and setal row of right mandible in posterior view; **D.** gnathal edge of left mandible in anterior view; **E.** incisor process, lacinia mobilis and setal row of right mandible in anterior view; **F.** surface of left molar process; **G.** surface of right molar process. Abbreviations: **ac**, articular condyle; **bas**, basipod; **cox**, coxa; **ip**, incisor process; **lm**, lacinia mobilis; **gbs**, gnathobasic seta; **mp**, molar process; **plp**, mandibular palp; **sr**, setal row.

With regard to these, the antennae of *Synurella ambulans* are relatively short with an only four- to five-articulated flagellum and their setation is generally sparse (Fig. 2). In some other species, such as *Dikerogammarus villosus* Sowinsky, 1894, long antennae with densely set long setae, can act as a sieve retaining fine-particulate organic matter (Mayer et al. 2008, Platvoet et al. 2009). Therefore, sieving small suspended food particles out of the respiration current seems not to be possible in *S. ambulans*. The function of both the antennulae and antennae during food acquisition appears rather restricted to gathering coarse detritus. In addition, with their calceoli, the antennae again seem to be mainly mechanosensitive organs, which can help to detect living prey.

A significant tool appears to be the mandible. Its coxal body is big in proportion to its gnathal edge (Fig. 3A). Accordingly, there is a large area for attachment of the mandibular musculature so that the mandibles seem to be able to bite firmly. This assumption is supported by the shape of the incisor processes and the left lacinia mobilis. The incisor processes are short, stout and broad, which also applies to the left lacinia mobilis (Fig. 3C–E). Remarkable is the very well developed broad articular condyle on the left lacinia mobilis and the broad cavity in the adjacent incisor process (Fig. 3B). Therefore, it seems that the left lacinia mobilis is well stabilized in its position parallel to the incisor process by the articular condyle during biting, when the right incisor process slides into the gap between the left lacinia mobilis and the left incisor process so that these three mandibular structures act as double-edged scissors with one blade on the right mandible and two blades on the left mandible, as described for *Dikerogammarus haemobaphes* Eichwald, 1841 (Mayer et al. 2013). However, in consequence of the small size of the individuals of *S. ambulans* and their mandibles, the range of application of this tool is limited.

The setae of the setal rows between the incisor processes and the molar processes of amphipods feeding on animal tissue are reduced in number and size compared to amphipods with other modes of feeding like feeding on suspended organic matter, periphyton or macrophytes (Dahl 1979, Coleman 1990). In *S. ambulans* the setal rows essentially consist of only a few pappose and stiletto-shaped setae (Fig. 3B–E). Bigger food particles can be pushed towards the molar processes by means of the stiletto-shaped setae. There are only a few pappose setae, which is why the setal rows seem not to be adapted for handling fine-particulate food. The surfaces of the molar processes are relatively small and little structured without rasp-like edges (Fig. 3F,G).

Such rasp-like surfaces of the molars are described for amphipods feeding on fresh plant material (McGrouther 1983). Therefore, the molar processes of *S. ambulans* do not seem to be suited for grinding hard plant material, but rather for squeezing soft food. All components of the mandibular gnathal edge are very similar to those in *Crangonyx pseudogracilis* Bousfield, 1958 (Mayer 2012b) and resemble those amphipods specialized in feeding on carrion (Watling 1993, Mekahnikova 2010).

The distal notch of the paragnaths is remarkably broad (Fig. 5F). This indicates that mainly bigger food items are guided towards the mandibles.

Again as compared to other gammarideans investigated, the coxal endites of the maxillulae are relatively small and their median margins are armed with only few pappose setae and there are gaps between these setae (Fig. 4B). Therefore, the maxillulae do not form an effective sieve, as e.g. in *Gammarus lacustris* Sars, 1863 (Mayer et al. 2012). This appears to hold also for the coxal endites of the maxillae in which the setation on the median margin is comparably sparse (Fig. 4D). These less effective maxillulary and maxillary sieves are another indicator to assume that fine-particulate organic matter plays only a subordinate role in the nutrition of *S. ambulans*. Furthermore, the thorn-like cuspidate setae on the basipodal endites of the maxillulae are neither comb-shaped nor chisel-shaped (Fig. 4C). Such comb-shaped setae are described e.g. for *Gammarus fossarum* Koch, 1836 and *Echinogammarus berilloni* (Catta, 1878) and chisel-shaped setae for *G. roeselii* Gervais, 1835. Both types of setae are interpreted as tools for removing periphyton from substrates (Mayer et al. 2009, 2012a). Therefore, the maxillulae of *S. ambulans* appear not to be suited for removing periphyton from substrates, but only for handling bigger food items, supporting the interpretation given above.

The distal margin of the palp of the right as well as the left maxillula is armed with a row of stout simple setae (Fig. 4A). There are no cuspidate setae on the palp of the right maxillula as is the case in all members of the Gammaroidea Latreille, 1802 investigated in previous works (e.g. Mayer et. al. 2009, 2012a,b). The functional meaning of this difference remains unclear.

The endites of the maxillipedal ischia lack cuspidate setae on their median edges (Fig. 4F). Also in this respect, *S. ambulans* does not seem to be able to remove periphyton from substrates with these mouthparts. The endopods of the maxillipeds (Fig. 4E,G) are very long and the claw-like dactyli can touch each other like a pair of tweezers. The maxillipeds accordingly are well suited for grasping and manipulating bigger food particles. The large area
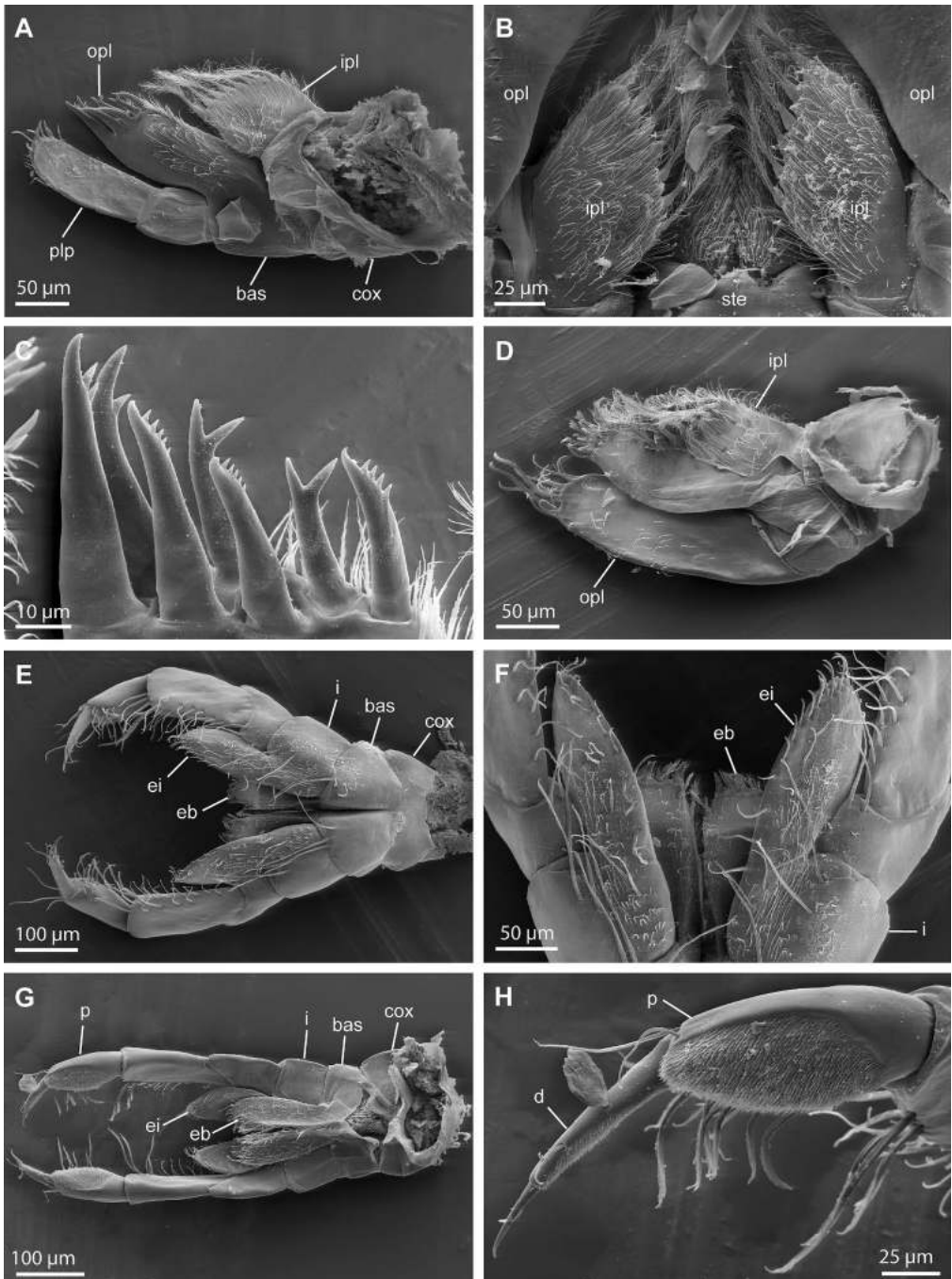
Fig. 4. SEM images of maxillulae, maxillae and maxillipeds of *S. ambulans*. **A.** left maxillula in anterior view; **B.** coxal endites of maxillulae in situ in posterior view; **C.** distal setation of basipodal endite of right maxillula in posterior view; **D.** left maxilla in anterior view; **E.** maxillipeds in posterior view; **F.** endites of maxillipeds in posterior view; **G.** maxillipeds in anterior view; **H.** propodus and dactylus with distal seta of right maxilliped in antero-median view. Abbreviations: **bas**, basipod; **cox**, coxa; **d**, dactylus; **eb**, endite of basipod; **ei**, endite of ischium; **i**, ischium; **ipl**, inner plate (= coxal endite); **opl**, outer plate (= basipodal endite); **p**, propodus; **ste**, sternum.

covered with densely set serrate cuticular outgrowths on the antero-median surface of the two opposing propodi (Fig. 4H) is possibly a specialization for holding bigger particles.

The setation of both pairs of gnathopods (Fig. 5A,B) is sparse as compared to that of other gammarideans, e.g., *D. villosus*, in which these setae build brush-like structures (Mayer et al. 2008). These few setae appear neither suited for removing periphyton from the substrate, nor to collect fine-particulate detritus or to build an effective sieve in front of the mouth opening to prevent small particles from being washed away. Again, the large and flat propodi of the gnathopods appear well suited for handling bigger food items.

The extremely short styliform third uropods (Fig. 5C–E) bear, comparably to the first and second uropods, only thorn-like cuspidate setae and cover the anus like flaps. There is no evidence that these structures are involved in food acquisition in *S. ambulans*, as is the case in other gammarideans such as *G. lacustris* and *D. villosus*, in which the median and lateral margins of the third uropods are densely set with plumose setae, building a fan-like net, suited for sieving particles out of the respiration current (Platvoet et al. 2009, Mayer et al. 2012b).

In all, the mouthparts and other structures involved in feeding seem to enable *S. ambulans* to reduce food items to small pieces and to ingest soft particulate organic material like detritus, carrion and dead plant material. Likewise, feeding on smaller living members of the macrozoobenthos community seems to be possible. On the contrary, fine-particulate organic matter, fresh plant material and periphyton seems not to be part of the food spectrum of *S. ambulans*. An overview of morphology and function of the structures involved in food acquisition in *S. ambulans* is given in Table 1.

In the literature there is only little information provided on the nutrition of *S. ambulans*. Conclusions can be drawn from the nature of the habitats, in which individuals of this species can be found. All habitats described in literature share some common characteristics: the contact to groundwater, the fine-particulate and muddy substrate, the ample submerse and riparian vegetation, and the presence of dead plant material (e. g. Jarocki & Krzysik 1925, Borutzky 1927, Heckes et al. 1996). Spandl (1923)

Table 1. Morphology and function of the structures involved in food acquisition in *S. ambulans*.

| structure	quality	function
antennulae	slender; setation short and sparse	tactile organ
antennae	setation short and sparse; with calceoli	collecting detritus; mechanosensitive organ; detection of living prey
mandibles, incisor processes and laciniae mobiles	incisor processes and left lacinia mobilis broad an stout; articular condyle broad	biting
mandibles, setal rows	only few pappose and stiletto-shaped setae	transport of mainly bigger particles towards the molar processes
mandibles, molar processes	surfaces small and little structured	squashing soft particles; squeezing and concentrating food prior to ingestion
maxillulae, setation of coxal endites	sparse, only 6–8 pappose setae	sieve with low efficiency
maxillulae, setation of basipodal endites	thorn-like cuspidate setae; no comb- or chisel-like setae	handling of bigger food particles
maxillae, setation of coxal endite	sparse, only 6 setae, which are plumose proximally and pappose distally	sieve with low efficiency
maxillipeds, endopods	claw-like dactyli; area with densely set short cuticular structures on propodi	grasping, manipulating, and holding bigger food particles
maxillipeds, endite of ischium, setation of median margin	setation sparse, without cuspidate setae	handling of bigger food particles
2nd gnathopods, setation of carpus and propodus	setation sparse, with few short simple setae on median margin of propodus	handling of bigger food particles
3rd uropods, setation	all uropods styliform, only cuspidate setae	–
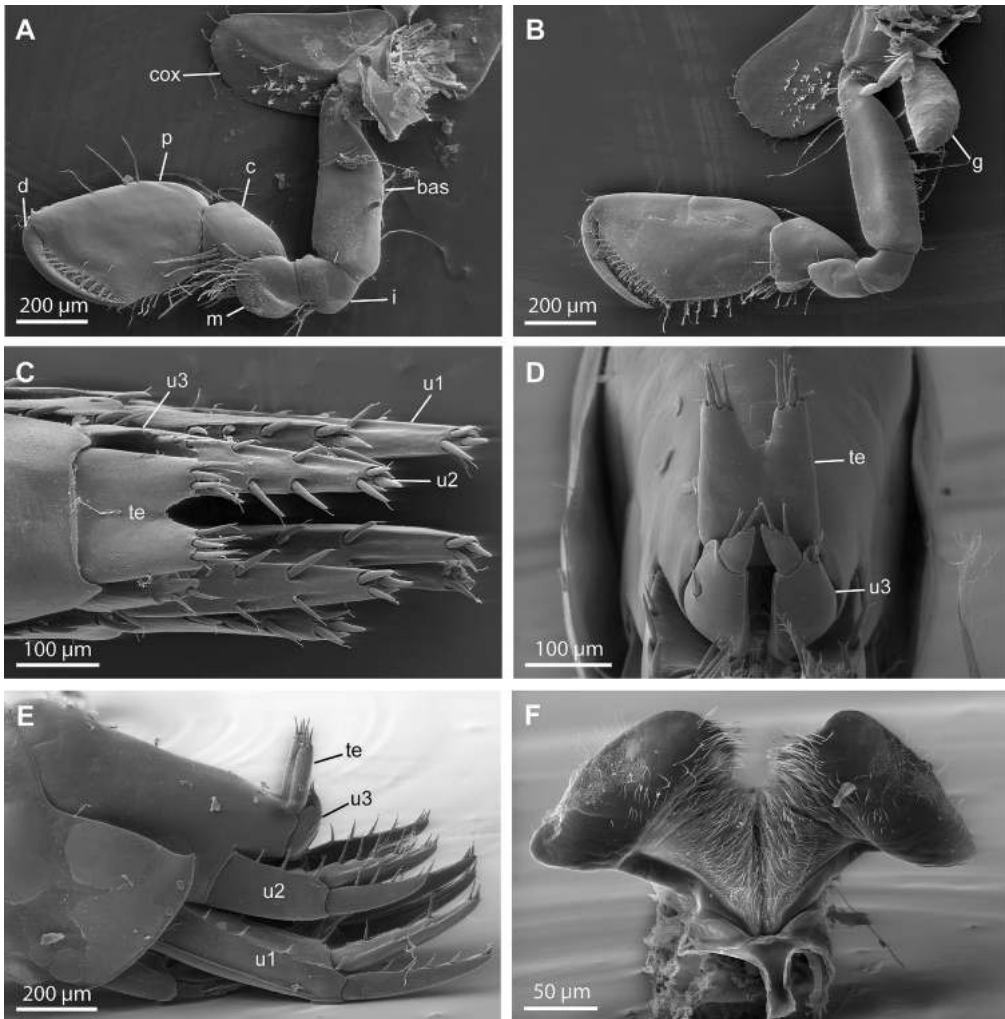
Fig. 5. SEM images of gnathopods, uropods and paragnaths of *S. ambulans*. **A.** right first gnathopod in anterior view; **B.** right second gnathopod in anterior view; **C.** uropods and telson in situ in dorsal view; **D.** telson and third pair of uropods in situ in posterior view; **E.** left lateral view of urosome with uropods and telson in situ; **F.** paragnaths in posterior view. Abbreviations: **bas**, basipod; **c**, carpus; **cox**, coxa; **d**, dactylus; **i**, ischium; **g**, gill; **m**, merus; **p**, propodus; **te**, telson; **u1–u3**, uropods 1–3.

observed *S. ambulans* in an aquarium feeding on tubificids and algae. According to Jarocki & Krzysik (1925) *S. ambulans* is often accompanied by water organisms, which feed on plant matter.

More detailed information on the nutrition of *S. ambulans* were provided by Thiem (1941): Animals living in an aquarium mainly fed on plants, whereas only in some cases carcasses of bugs or dead copepods were gnawed away. Thiem sometimes also observed coprophagy in starving animals. Very young individuals mainly fed on detritus; older juveniles and adults mainly fed on dead leaves of

reeds and willow gnawing away the parenchyma and rejecting the vascular tissue. Faeces of the animals consisted mainly of remains of plants and detritus. Furthermore, Thiem (1941) observed individuals holding parts of leaves between the propodi of the gnathopods in reach of the mandibles, and also individuals holding small particles with the aid of the propodi of the maxillipeds.

The results of this study on the morphology of mouthparts and other structures involved in food acquisition are in accordance with findings reported in literature. Detritus and dead plant material are

important food resources for *S. ambulans* as the morphology of the antennulae, antennae, maxillipeds, and gnathopods indicate. If available, carrion as well as living organisms of the macrozoobenthos can be ingested, cut into pieces with the aid of the incisor processes and the left lacinia mobilis. On the other hand, fresh plant material cannot be eaten, because there are no structures on the surfaces of the molar processes of the mandibles for grinding such hard material. Again, sieving and filtering fine-particulate matter as well as removing periphyton from substrates does not play a major role in nutrition of *S. ambulans*, because the necessary setation on the inner plates of the maxillulae and maxillae, as well as on the antennae, gnathopods and uropods is missing. The latter would hinder the animals during locomotion in the pore systems of groundwater, whereas for example styliform uropods are an advantage in such a habitat.

The structures of *S. ambulans* involved in food acquisition are very similar to those in *Crangonyx pseudogracilis*, which is similar in size. This originally North American species, which was recorded in central Europe for the first time in 1979, is now still expanding its area of distribution (Pinkster et al. 1980, Mayer et al. 2012b). Like *S. ambulans*, *C. pseudogracilis* occurs in habitats with connection to groundwater and is likewise morphologically adapted to live in the interstitial and for feeding on organic matter available in such habitat. These adaptations might enable the two species to avoid direct competition for food and shelter with larger native and invasive gammaridean species.

Direct observations of the action of the mouthparts of amphipods are difficult if not impossible, because these structures are anteriorly directed and therefore covering each other in living animals. SEM-studies of the morphology of the mouthparts and other structures involved in food acquisition provide valuable evidence on possible capabilities of these structures during feeding.

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