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Elongated mouthparts of nectar-feeding Meloidae (Coleoptera)

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Abstract Coleoptera of at least three taxa in the Nemognathini (Meloidae) possess mouthparts that are specialized for nectar feeding from flowers with a deep corolla. Parts of the maxillae are modified to form an elongate proboscis-like organ. In *Leptopalpus* species, the four-segmented maxillary palps form the proboscis, whereas in *Nemognatha* and *Gnathium* species, the elongated galeae enable nectar feeding. With the use of scanning electron microscopy and micro computerized tomography, the present study clearly demonstrated that neither of the two kinds of proboscides possesses a median food canal. The filiform galeae of *Nemognatha* and *Gnathium* species are densely covered with long bristles; in *Gnathium* species the tip bears conspicuous sensilla. Nectar uptake is probably accomplished by capillarity along the bristles of the proboscis and is enhanced by the cibarial and pharyngeal musculature. The investigation of *Leptopalpus* species revealed a muscular valve-like structure in the head that probably closes the pharynx and could be part of a sucking pump in conjunction with the compressor and dilator muscles of the cibarium and prepharynx. In addition to nectar feeding by means of the maxillae, these Coleoptera feed on pollen using their mandibles. Morphological and anatomical results yield new insights into the functional aspects of proboscides in nectar-feeding Meloidae that probably evolved at least two times convergently, that is, by elongation of the maxillary palps or the galeae.

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Introduction

The mutualistic associations between insects and flowers are essential for the global existence of present-day terrestrial ecosystems, since they ensure the reproductive success of many angiosperm plants and provide insects with valuable food and other resources. Adult insects of numerous taxa possess a great variety of mouthpart adaptations to take up floral rewards, such as the coilable proboscis of Lepidoptera, the variously composed proboscides of Hymenoptera or the specialized mouthparts of some pollen-feeding Coleoptera (Krenn et al. 2005; Karolyi et al. 2009). Paleontological records indicate that the evolution of entomophilous pollination started in the Cretaceous or even earlier (Labandeira 1997; Ren et al. 2009). Flower-visiting Coleoptera were among the earliest pollinating insects. However, it is unlikely that Coleoptera were the first pollinators of angiosperms although cantharophilous plants must have evolved by the mid–late Cretaceous (Bernhardt 2000). Most anthophilous Coleoptera species possess biting-chewing mouthparts (Leschen et al. 2010) to consume pollen and floral tissue (Bernhardt 2000; Johnson and Nicolson 2001; Krenn et al. 2005). Many flower-visiting Coleoptera are generalized plant tissue feeders, which devastate rather than pollinate flowers. Despite the long history of flower–beetle interaction, morphological or behavioral adaptations to floral rewards are usually less conspicuous than in other flower-visiting insects, which evolved, for example, long sucking proboscis-like mouthparts (Iablokoff-Khnzorian 1968; Krenn et al. 2005). Even specialized flower-visiting Coleoptera, which consume pollen, nectar, or starchy food bodies (Goldblatt et al. 1998; Bernhardt 2000; Johnson and Nicolson 2001), have prognathous mouthparts that are only slightly modified for this purpose. Some Scarabaeidae, for example, sweep pollen into the mouth using the maxillary tips, which are densely covered with setae, and mop up nectar at the same time (Johnson and Nicolson 2001). When Coleoptera additionally feed on nectar, they do so from exposed surfaces and shallow flowers (Barth 1991), since in most species, elongated mouthparts are lacking. Within Coleoptera, proboscis-like mouthparts for nectar uptake are found only in species of Meloidae, that is, *Leptopalpus*, *Nemognatha, Gnathium* and *Zonitis* species (Handschin 1929; Schremmer 1961; Kaszab 1963; Pinto 2009), Ripiphoridae, that is, *Macrosiagon* species (Williams 1938; Lawrence et al. 2010), and Cantharidae, that is, *Chauliognathus* species (Hentz 1830; Campau 1940; Rausher and Fowler 1979).

The Meloidae contain more than 2,500 species worldwide (Bologna and Pinto 2001). Except for some taxa in which the adults do not feed, the adults of the meloid subgroups, Eleticinae, Meloinae, Tetraonycinae, and Nemognathinae, are phytophagous and possess prognathous mouthparts of the biting-chewing type (Pinto and Bologna 1999). In the Nemognathini species of *Leptopalpus*, *Nemognatha*, *Gnathium*, *Zonitodema*, *Zonitolytta* and *Zonitis* possess elongated mouthparts that are modified (Bologna et al. 2010) to take up nectar from deep flowers with concealed nectaries (Barth 1991) as the main food source (Handschin 1929; Schremmer 1961; Kaszab 1963; Matthes 1991). Astonishingly, different parts of the maxillae compose the proboscis in Meloidae. It is either formed by the elongated four-segmented maxillary palps (*Leptopalpus*: Handschin 1929) or by the elongated galeae (*Zonitis*, *Nemognatha* and *Gnathium*: Schremmer 1961; Pinto 2009). In the latter two taxa, the galeae vary in length from short and brush-like organs to filiform structures that are longer than the body (Schremmer 1961; Kaszab 1963; Pinto and Bologna 1999; Pinto 2009). The presence of concave mesal margins, which would form a true food tube between the loosely connected galeae, was suggested for some North American *Nemognatha* species (Schremmer 1961; Matthes 1991).

Although the elongation of mouthparts in Meloidae has been known since the study of Handschin (1929), and despite the fact that they are depicted in entomological text books as an example of amazing adaptations in Coleoptera (i.e., Chaudonneret 1990; Beutel 2003; Klausnitzer 2005), detailed studies of proboscis morphology in nectar-feeding meloid species are lacking. This might be due to the fact that these coleopteran species have a short flight period and their occurrence is often extremely localized (Handschin 1929). This in turn aggravates the availability of fresh material for morphological studies although species of *Nemognatha* are distributed worldwide except Australia, Oceania, and the cold high latitudes of the New World (Pinto and Bologna 1999). *Leptopalpus* species are distributed in the Mediterranean region of Europe and northern Africa (Schremmer 1961), while *Gnathium* species are limited to the western and southern United States and northern Mexico (Pinto 2009).

The aim of the present study is to compare the proboscis-like mouthparts in nectar-feeding meloid species and to evaluate to what extent the proboscides of different taxa among the Nemognathini are different in their fundamental compositions. We expect to find structures that lock the parts of the proboscis together into a functional unit as well as specialized structures for adhesion, uptake, and transport of nectar into the mouth and alimentary tract as they are present in most specialized nectar-feeding insects that are adapted to feed from concealed nectaries (Krenn et al. 2005). The comparison of nectar-feeding mouthparts in the various species of Meloidae should help to understand functional aspects of nectar sucking mouthparts in Coleoptera and should give evidence to reconstruct the putative convergent evolution of mouthpart adaptations to nectar feeding in this special case of anthophilous Coleoptera.

Materials and methods

Representatives of *Leptopalpus rostratus* (Fabricius, 1792) (three individuals stored in 70 % ethanol; collected near Galapagar, central Spain), *Nemognatha chrysomelina* (Fabricius, 1775) (two stored in 70 % ethanol; collected near Marmaris, southwest Turkey and two dried; collected on Rhodes, Greece), and *Gnathium nitidum* Horn, 1870 (two stored in 70 % ethanol; collected near Christmas Valley, Oregon, USA) (Meloidae, Nemognathinae) were investigated. Photos of species were taken with a Nikon D5100 digital camera.

One head of *L. rostratus* and one of *N. chrysomelina*, both stored in 70 % ethanol, were dissected in ethanol using a stereo microscope (Nikon SMZ 10). The mouthparts were mounted in Polyvinyllactophenol on glass slides. To examine ingested pollen grains, guts of *L. rostratus, N. chrysomelina*, and *G. nitidum* were removed and prepared under a stereo microscope. The fore-, mid-, and hindgut were separately mounted in Polyvinyllactophenol on glass slides for analysis using an Olympus CX41compound light microscope.

The head musculature was examined by using serial semi-thin section technique. The heads of all three species were dehydrated in an ethanol series (70–100 %) and embedded in Agar Low viscosity Resin and polymerized at 60 °C. Serial semi-thin sections with a thickness of 1 µm were made using a Leica EM UC6 microtome with diamond knife (Blumer et al. 2002) and stained with 1:9

Richardson's blue for 30 s on a heating plate at 60 °C (Richardson et al. 1960). The head of each species was cut in parasagittal sections up to the sagittal plane. One galea of *G. nitidum* was cut in cross-section. The second segment of the maxillary palp of *L. rostratus* was cut in cross-section in the mid region. Photos were taken with an Olympus CX41 microscope equipped with an Olympus E330 digital camera. Line drawings were made with CorelDRAW X3® on the base of photographs of mounted mouthparts and semi-thin sections. All line drawings and photos were edited with Adobe®Photoshop® CS4.

Scanning electron microscopy (SEM)

One head of each of the following species was used for SEM: *L. rostratus, N. chrysomelina*, and *G. nitidum.* Dissected mouthparts were dehydrated with ethanol (70–100 %), submerged in Hexamethyldisilazan for 15 min, and subsequently air dried overnight. The heads or mouthparts were glued on stubs using doubled-sided carbon-containing adhesive tape and sputter-coated with gold (20–90 nm, using Agar sputtercoater B7340 for 240 s). Images were taken at the Core Facility of Cell Imaging and Ultrastructure Research (University of Vienna, Austria) using a Philips XL 20 SEM.

Micro computerized tomography (Micro CT)

One head of each species was rinsed with 70 % ethanol and transferred to 100 % ethanol for 1 h on a sample rotator. Subsequently, the ethanol was replaced by 1 % iodine solution and the heads were stained overnight and returned to 100 % ethanol again. Galeae of *G. nitidum* and the maxillary palps of *L. rostratus* were removed to be scanned separately. All objects were fixed in specially prepared Eppendorf tubes filled with 100 % ethanol (Metscher 2009a, b). Scans were taken overnight with an Xradia MicroXCT system at the Department of Theoretical Biology (University of Vienna, Austria). Objects were scanned in cross-section with different resolutions (pixel size*:* *L. rostratus* 4.5990 µm, *G. nitidum* 3.0570 µm, *N. chrysomelina* 5.0443 µm), each scan consisting of staples of 495 to 714 images. The recombination of the single cross-sections (tomography data) into 3D models of the objects was done with the ImageJ® software.

Results

External morphology of head and mouthparts

The heads of *Leptopalpus rostratus* (Fig. 1a, b), *Nemognatha chrysomelina* (Fig. 2a, b), and *Gnathium nitidum* (Fig. 3a, b) are prognathous, and their mouthparts are similar in gross morphology. The most conspicuous differences concern the maxillae as the main organ for nectar uptake.

Labrum

The labrum (Figs. 1c, 2c, 3c, 4c) closes the preoral cavity dorsally and is fused to the clypeus. The sutura clypeolabralis separates labrum and clypeus. The labrum is approximately square in *L. rostratus* (Fig. 1c) and oval in *N. chrysomelina* (Fig. 2c); in both specimens, it extends distally nearly to the apex of the mandibles. However, in *G. nitidum* (Fig. 3a, c), the labrum is round in shape and extends to the middle of the mandible.

A distinct epipharynx (sensu Snodgrass 1928, 1935) is located medially on the ventral surface of the labrum and nearly extends to the posterior edge of the clypeus. Laterally to the epipharynx is a pair of sclerotized apodemes (tormae), which originate from the proximal border of the labrum (Figs. 1c, 4c). In *L. rostratus*, the epipharynx possesses two paired rows of fine setae. In *N. chrysomelina*, the epipharynx is slender, possesses two rows of fine setae, and nearly reaches the proximal edge of the clypeus. In *G. nitidum*, the epipharynx is relatively broad and shallow on the ventral surface. The bristles are directed toward its median groove.

Mandibles

The mandibles (Figs. 1d, 2d, 3d, 4d) are symmetrical. Each mandible consists of an incisor part, a prostheca, a molar plate, and a postmola. The sclerotized incisor part is curved toward the sagittal plane. The soft prostheca extends between the molar plate and the incisor part. This lobe-like structure bears two different types of bristles at its free margins. The distal half bears rows of dense bristles with a bulb-like basis (Fig. 1f) forming a comb-like structure. The proximal edges (Figs. 1e, 2d) are covered with small rod-like bristles of different length. The postmola, also a setose lobe, originates at the proximal margin of the mola and extends into the prepharynx (sensu Kelér 1963).

In *Leptopalpus rostratus* (Fig. 1d), the incisor part is shovel-like with an acute apex (which is broken in Fig. 1d). The grinding surface of the molar plate is covered with small teeth that are posteriorly directed (Fig. 1e). The length of the bristles at the distal half of the prostheca (Fig. 1d) varies from 30 to 100 µm (Fig. 1f). The small rod-like bristles at the proximal edges are from 5 to 15 µm long.

In *Nemognatha chrysomelina* (Fig. 2d), the incisor part is moderately shovel-like with an acute apex that is strongly curved toward the body axis. The prostheca, the distal part of which is comb-like, is relatively strong and

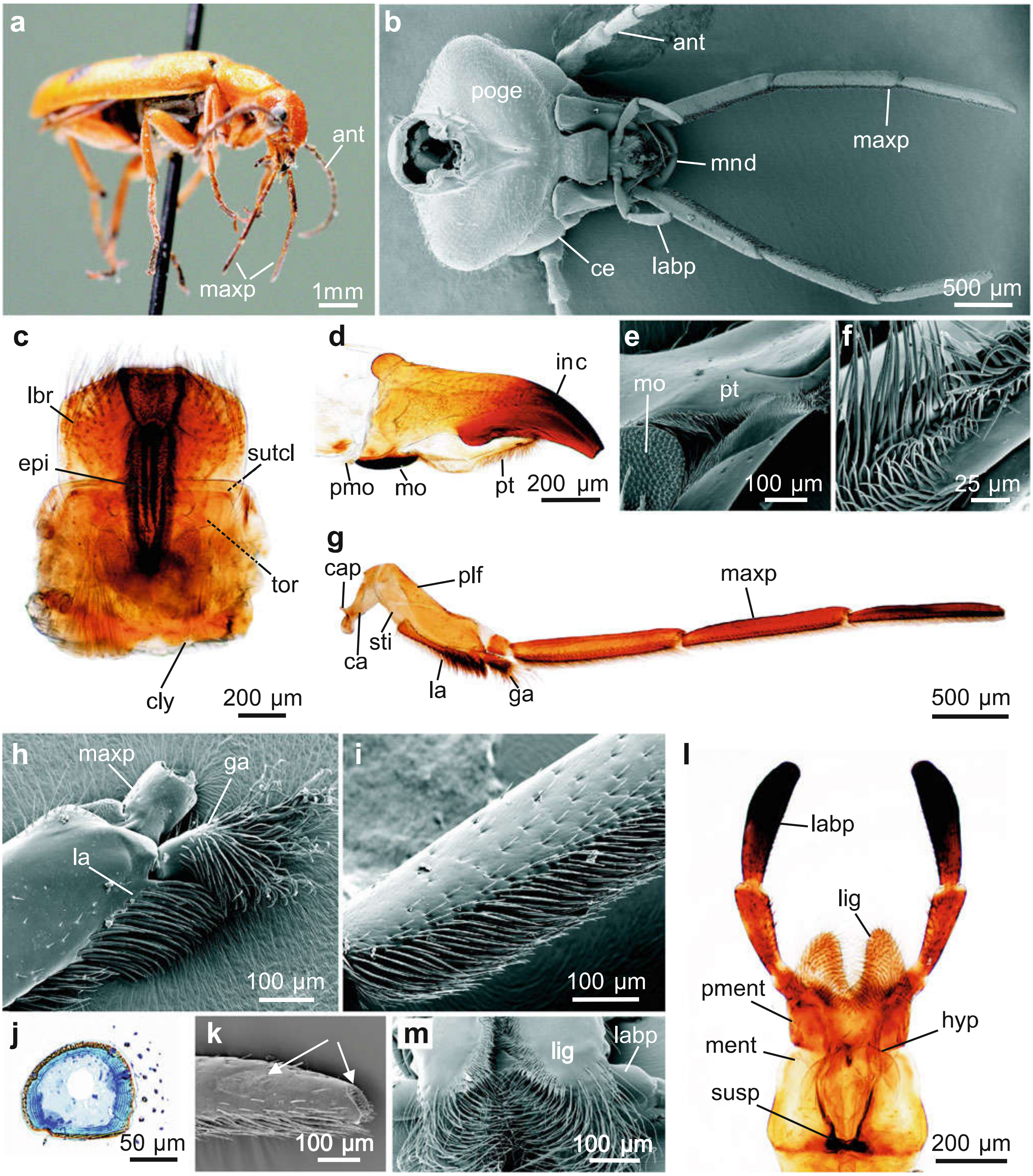

Fig. 1 *Leptopalpus rostratus*; **a** habitus of a dried specimen; **b** ventral view of the head; **c** ventral surface of the labrum and part of the clypeus; **d** right mandible in ventral view (apex broken off); **e** proximal part of the prostheca of the mandible; **f** distal part of the prostheca; **g** right maxilla in ventral view; **h** part of the right maxilla in ventral view; **i** part of the second palp segment with median bristle row in ventral view; **j** semi-thin cross-section of the second palp segment; **k** tip of the distal maxillary palp segment in ventral view, showing the two sensilla regions (*arrows*); **l** dorsal surface of the labium; **m** ligula and v-shaped rows of bristles and microtrichia in dorsal view. **a** stereo microscopy; **b**, **e**–**f**, **h**–**i**, **k** and **m** scanning electron microscopy; **c**–**d**, **g**, **j** and **l** compound light microscopy. *Dashed lines*: only visible by transparency. *ant* antenna, ca cardo, *cap* cardo apodeme, *ce* compound eye, *cly* clypeus, *epi* epipharynx, *ga* galea, *hyp* hypopharynx, *inc* incisor part of the mandible, *la* lacinia, *labp* labial palp, *lbr* labrum, *lig* ligula, *maxp* maxillary palp, *ment* mentum, *mnd* mandible, *mo* molar plate, *plf* palpifer, *pment* prementum, *pmo* postmola, *poge* postgena, *pt* prostheca, *sti* stipes, *susp* suspensorium, *sutcl* sutura clypeolabralis, *tor* torma

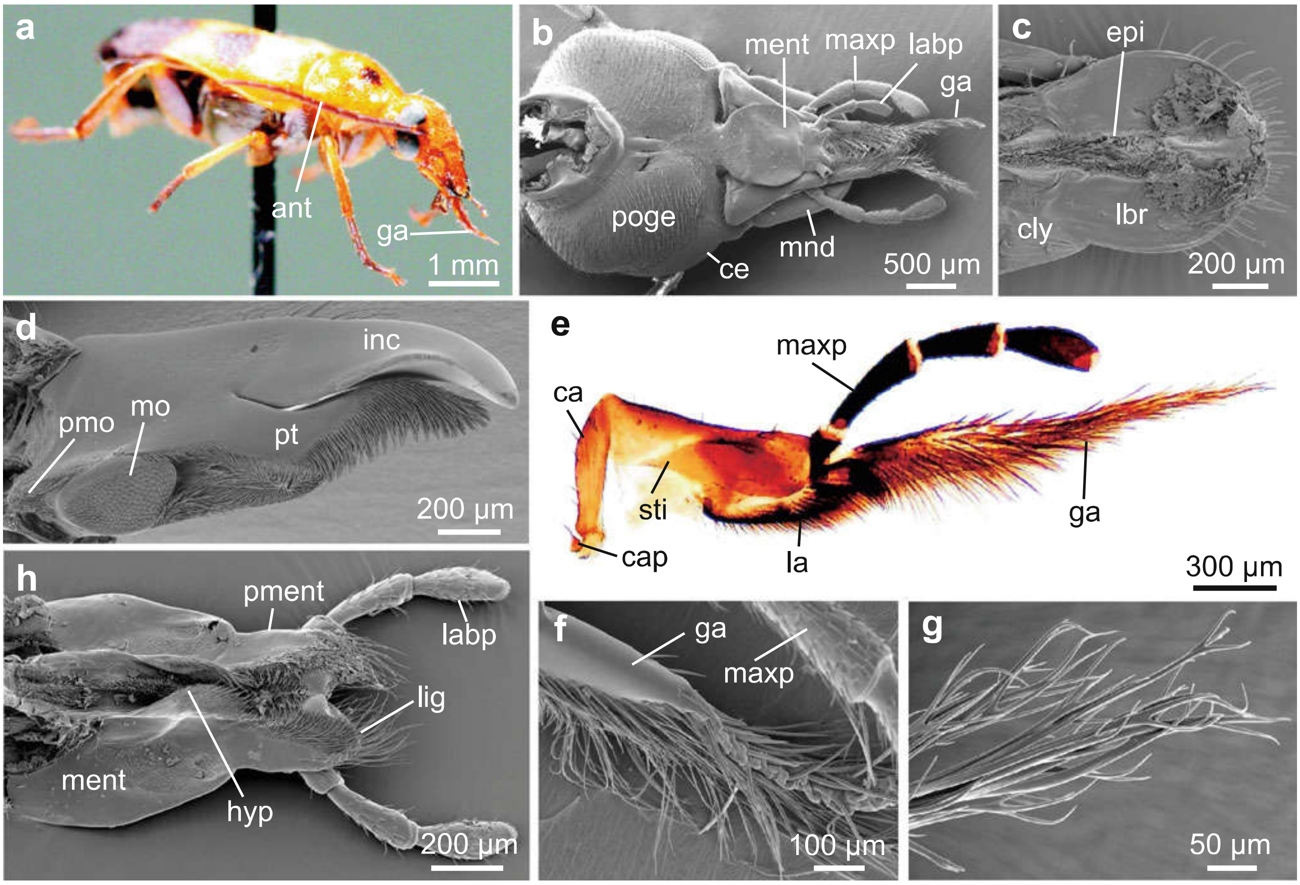

Fig. 2 *Nemognatha chrysomelina*; **a** habitus of a dried specimen; **b** ventral view of the head; **c** ventral surface of the labrum; **d** right mandible in ventral view; **e** right maxilla in ventro-mesal view; **f** surface structures of the right galea in the proximal region in ventral view; **g** branched bristles at the galea tip; **h** dorsal surface of the labium. **a** stereo microscopy; **b–d** and **f–h** scanning electron microscopy; **e** compound light microscopy. *ant* antenna, ca cardo, *cap* cardo apodeme, *ce* compound eye, *cly* clypeus, *epi* epipharynx, *ga* galea, *hyp* hypopharynx, *inc* incisor part of mandible, *la* lacinia, *labp* labial palp, *lbr* labrum, *lig* ligula, *maxp* maxillary palp, *ment* mentum, *mnd* mandible, *mo* molar plate, *pment* prementum, *pmo* postmola, *poge* postgena, *pt* prostheca, *sti* stipes

reaches the tip of the mandible. In *Gnathium nitidum* (Figs. 3a, d), the mandibles are as long as the head capsule and possess a slender and prolate incisor part with a moderately acute tip, which is smoothly curved to the body axis. The soft prostheca extends from the molar plate to half of the mandible length. The postmola is relatively small and originates behind the molar plate.

Maxillae

Each maxilla (Figs. 1g, 2e, 3e, 4e) consists of cardo, stipes, lacinia, galea, and palpifer with a four-segmented maxillary palp. Major differences are found in the length of the galea and the maxillary palp. In all species, two sensory fields are located in the distal region of the 4th free segment of the maxillary palp, one in a pit at the apical end, and the other ventrally in the distal region (Fig. 1k). The stipes is divided into a mediostipes that is fused with the lacinia and a basistipes adjoining to the palpifer.

In *Leptopalpus rostratus* (Figs. 1a, g), the maxillary palps are nearly as long as half the body and are the main organs for nectar uptake. The three distal segments of the maxillary palp are greatly elongated, each measuring approximately 1.3 mm. These segments possess a median row of distally directed, unbranched, and smooth curved bristles (Fig. 1i). All bristles have the same length with an average of about 130 µm, except those of the distal ends of the 2nd and 3rd free segment, which measure double length. The distal bristles of the 4th free segment are shorter; they extend to the rods of the sensory field at the apical end (Fig. 1k). All three segments are more or less round in cross-section (Fig. 1j). The 1st free palpal segment is clearly shorter than the remaining segments and is nearly as long as the galea, measuring about 100 µm. This segment is glabrous except for a single long and thin seta on the ventral side that points distally (Fig. 1h). The bulb-shaped galea (Fig. 1h) possesses long and corkscrew-like bristles in the distal region that form a brush-like structure

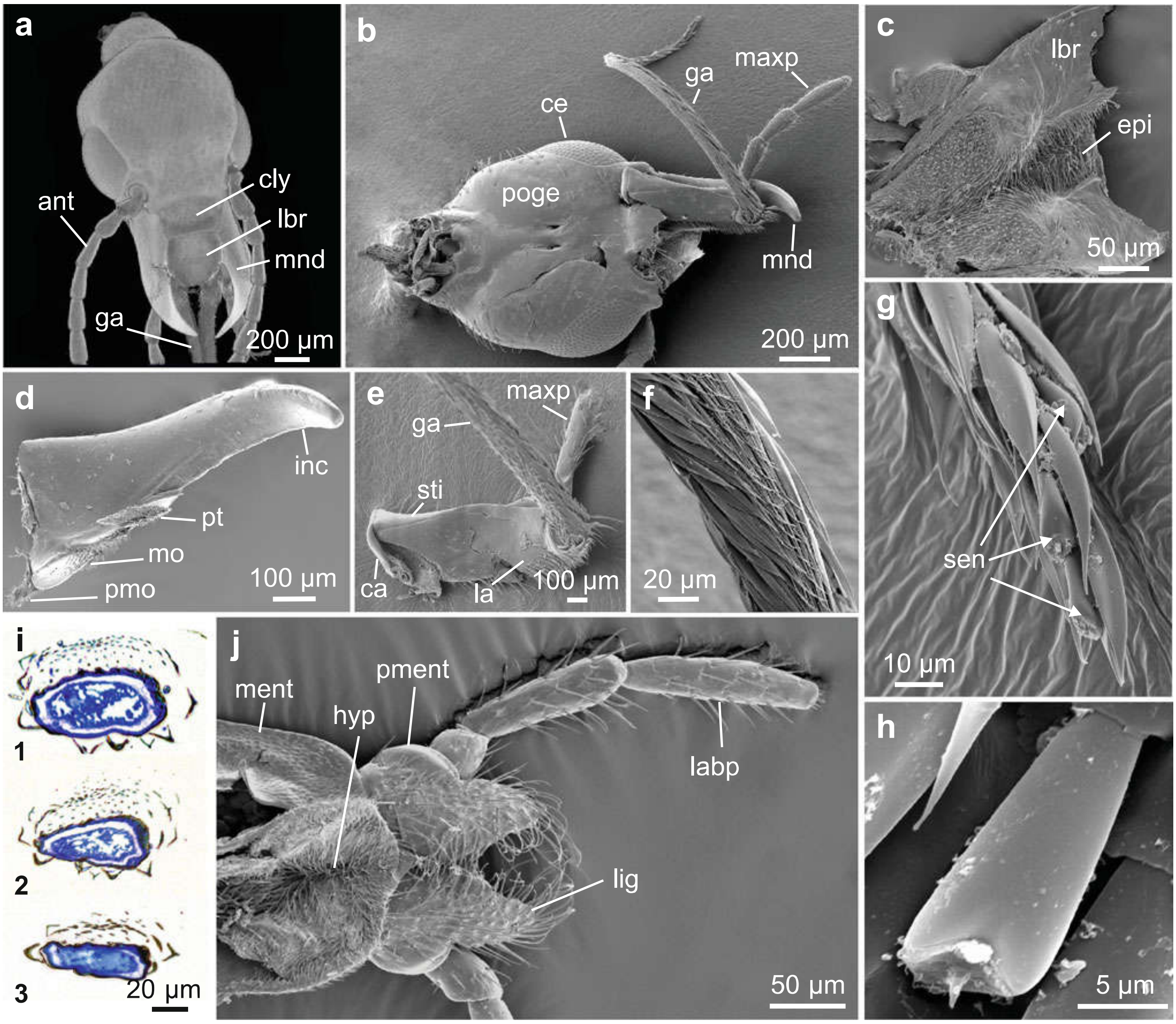

Fig. 3 *Gnathium nitidum*; **a** dorsal view of the head; **b** ventral view of the head; **c** ventral surface of the labrum (distal end broken off); **d** right mandible in ventro-mesal view; **e** right maxilla in ventro-mesal view (distal part of the maxillary palp missing); **f** mesal view of the galea in the mid region; **g** tip region of the galea with sensilla (*arrows*); **h** club-like sensillum of the galea; **j** dorsal surface of the labium and hypopharynx. **i** semi-thin cross-sections of the galea in the proximal region (*1*), in the middle (*2*) and in the tip region (*3*). **a** reconstruction of micro CT images; **b**–**h** and **j** scanning electron microscopy; **i** compound light microscopy. *ant* antenna, ca cardo, *ce* compound eye, *cly* clypeus, *epi* epipharynx, *ga* galea, *hyp* hypopharynx, *inc* incisor part, *la* lacinia, *labp* labial palp, *lbr* labrum, *lig* ligula, *maxp* maxillary palp, *ment* mentum, *mnd* mandible, *mo* molar plate, *pment* prementum, *pmo* postmola, *poge* postgena, *pt* prostheca, *sen* sensillum, *sti* stipes

positioned next to the first segment of the maxillary palp. The bristles of the basal region are shorter and less twisted and resemble those of the lacinia. On the mesal side, the distal half of the lacinia is densely covered with thick and smooth bristles that curve backward. Its proximal half is less densely covered with thin and short bristles.

In *Nemognatha chrysomelina* (Fig. 2e), the galea is conspicuously elongated measuring about 1.5 mm and is nearly as long as the head capsule. The basal region of the galea is only medially equipped with long and straight bristles (Fig. 2f), while the rest of the galea surface is completely covered with long and straight bristles. All bristles are smooth with acute tips, except for the distal ones that are branched up to five times and form a slender brush-like tongue (Fig. 2g). The lacinia is densely covered with smooth backward curving bristles, which form a comb-like structure. These bristles measure about half the length of the proximal galea bristles. The bristles of the proximal part are less dense, thinner, and shorter than the distal bristles.

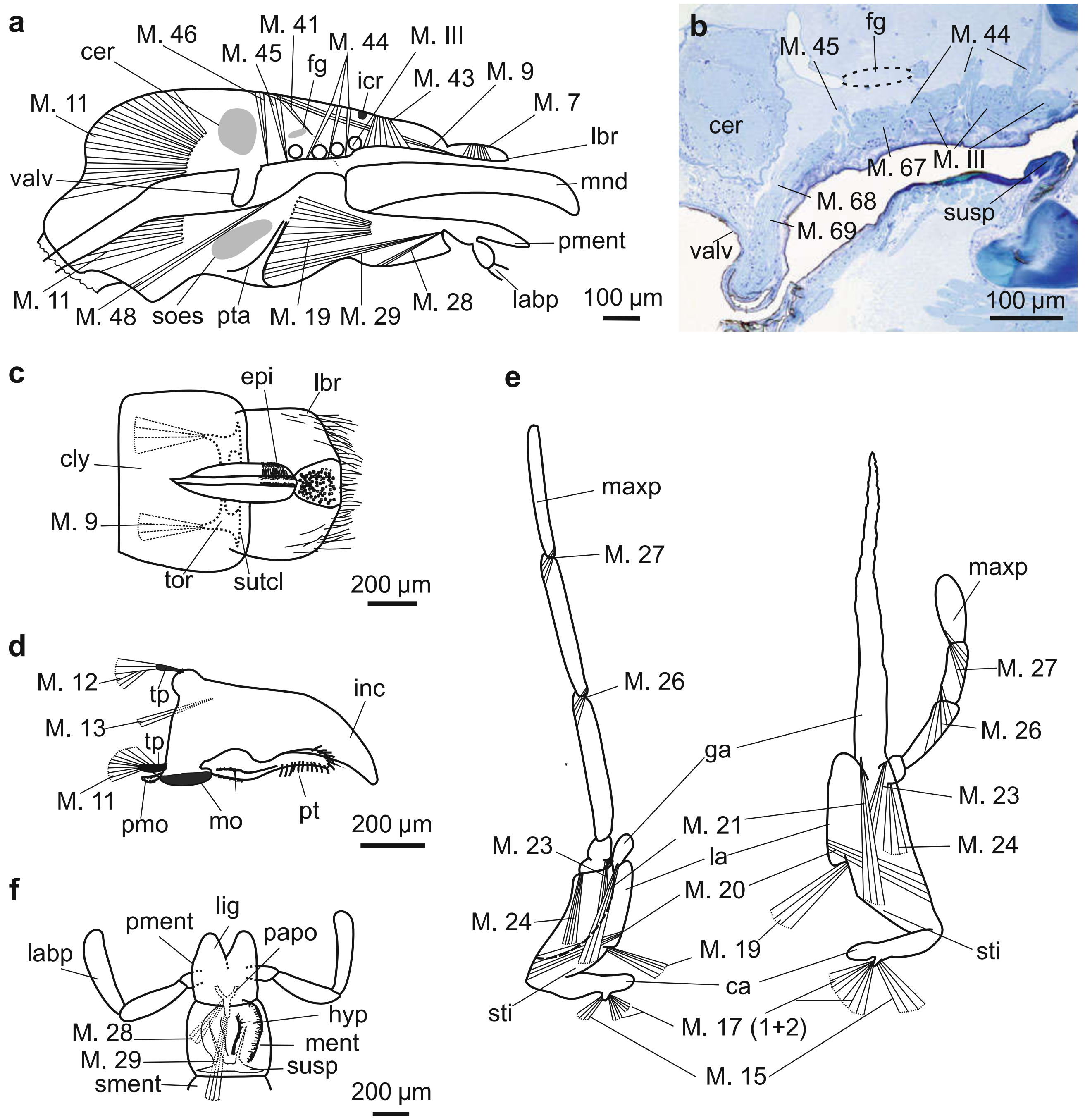

Fig. 4 Mouthparts and head musculature of Nemognathinae; nomenclature of muscles refers to Table 1; **a** head of *Leptopalpus rostratus* in sagittal view; note the muscular valve; **b** particular parasagittal semi-thin section of the head of *L. rostratus* showing the pharyngeal region with the valve in detail (position of the frontal ganglion is indicated by the *gray oval*); **c** ventral surface of the labrum and clypeus of *L. rostratus*; **d** right mandible of *L. rostratus* in ventral view; **e** right maxilla of *Leptopalpus* (*left side*) and left maxillae of *Nemognatha* and *Gnathium* (*right side*) both in ventral view. **f** dorsal surface of the labium of *L. rostratus*. **a** and **c**–**f** schematic drawings based on semi-thin sections and micro CT reconstruction; **b** compound light microscopy. *Dashed lines*: only visible by transparency or in another section plane. ca cardo, *cer* cerebrum, *cly* clypeus, *epi* epipharynx, *fg* frontal ganglion, *ga* galea, *hyp* hypopharynx, *icr* intraclypeal ridge, *inc* incisor part of the mandible, *la* lacinia, *labp* labial palp, *lbr* labrum, *lig* ligula, *maxp* maxillary palp, *ment* mentum, *mnd* mandible, *mo* molar plate, *papo* premental apodeme, *pment* prementum, *pmo* postmola, *pt* prostheca, *pta* posterior tentorial arm, *sment* submentum, *soes* subesophageal ganglion, *sti* stipes, *susp* suspensorium, *sutcl* sutura clypeolabralis, *tor* torma, *tp* tendon plate, *valv* valve; *M.* muscle according to the terminology of Kelér (1963)

Table 1 Musculature of heads and mouthparts of *Leptopalpus rostratus*, *Nemognatha chrysomelina*, and *Gnathium nitidum* with origins, insertions, and probable functions

Muscle	*Leptopalpus rostratus*	*Nemognatha chrysomelina*	*Gnathium nitidum*	Origin	Insertion	Function
Labrum						
M. labroepipharyngalis (M. 7)	+	+	+	Dorsal labral wall	Ventral labral wall	Epipharynx elevator
M. frontoepipharyngalis (M. 9)	++	++	++	Frons	Proximal end of torma	Depressor of labrum, moves epipharynx
Mandible						
M. craniomandibularis internus (M. 11)	+++	+++	+++	Posteriorly on head capsule	Tendon plate laterally to postmola	Adductor of mandible
M. craniomandibularis externus (M. 12)	+++	+++	+++	Postero-laterally on head capsule	Tendon plate near to mandibular condyle	Abductor of mandible
M. tentoriomandibularis (M. 13)	+	+	+	Anterior tenorial arm	Ventral lateral wall of mandible	Adductor of mandible?
Maxilla						
M. craniocardinalis externus (M. 15)	++	++	++	Lateroventrally on head capsule	Laterally on the cardo apodeme	Adductor of cardo
M. tentoriocardinalis (1 + 2) (M. 17)	++	++	++	Posterior tentorial arm	Medially on the cardo apodeme	
M. craniolacinialis (M. 19)	++	++	++	Posterior tentorial arm	Laterally on lacinia basis	Adductor of lacinia
M. stipitolacinialis (M. 20)	++	++	++	Ventrolaterally on stipes basis	Laterally on lacinia basis	Adductor of lacinia
M. stipitogalealis (M. 21)	+	+	+	Ventromedially on stipes wall	Laterally on galea basis	Abductor of galea
M. stipitopalpalis internus (M. 23)	+	+	+	Ventral stipital wall	Mesal basis of 1st free palpal segment	Adductor of palpus maxillaris
M. palpopalpalis maxillae primus (M. 24)	+	+	+	Basal at the palpifer	Lateral basis of 1st free palpal segment	Abductor of palpus maxillaris
M. palpopalpalis tertius (M. 26)	+	+	+	Dorsally on 2nd free palpal segment	Basis of 3rd free palpal segment	Flexor 3rd segment
M. palpopalpalis quartus (M. 27)	+	+	+	Dorsally on 3rd free palpal segment	Basis of 4th free palpal segment	Flexor 4th segment
Labium/Hypopharynx						
M. submentoprementalis (M. 28)	+	+++	++	Submentum	Transition mentum/prementum	Retractor of prementum
M. tentorioprementalis inferior (M. 29)	++	++	++	Proximal tentorial arm	Transition mentum/prementum	Adductor of prementum
M. frontohypopharyngalis (M. 41)	++	++	++	Frons median of M. 9	Hypopcharyngeal suspensorium	Hypopharynx elevator
Cibarium/Pharynx						
M. clypeopalatalis (M. 43)	+++	+	++	Clypeus, distal to the intraclypeal ridge	Dorsal cibarial wall	Dilator of cibarium
M. clypeobuccalis (M. 44)	++	++	++	Clypeus, proxilmal to the intraclypeal ridge	Dorsal cibarial wall	Dilator of cibarium
M. frontobuccalis anterior (M. 45)	++	++	++	Frons, distal of M. 46	Dorsal pharyngeal wall	Precerebral pharyngeal dilator

Table 1 continued

Muscle	*Leptopalpus rostratus*	*Nemognatha chrysomelina*	*Gnathium nitidum*	Origin	Insertion	Function
M. frontobuccalis posterior (M. 46)	++	++	++	Frons, proximal of M. 45	Dorsal pharyngeal wall	Precerebral pharyngeal dilator
M. tentoriobuccalis anterior (M. 48)	+	+	+	Ventral head capsule	Ventral pharyngeal wall	Precerebral ventral dilator of cibarium
M. compressores epipharyngis (M. III)	+++	+	++	Semicircular, dorsally passing over the cibarium		Compressor of the pharynx
M. transversalis buccae (M. 67)	+++	+	++	Semicircular, dorsally passing over the prepharynx		Compressor of the cibarium
M. anularis stomodaei (M. 68)	++	+	+	Circular musculature of the pharynx		Peristaltic movements of the pharynx
M. longitudinalis stomodaei (M. 69)	+	+	+	Longitudinal musculature of the pharynx		Peristaltic movements of the pharynx

The symbol (+) indicates presence of a slender muscle, (++) moderately developed muscle, (+++) well-developed muscle. Nomenclature and numeration of muscles follow Kéler (1963) and Honomichl (1975) for M. III; muscle M. 13 has been renamed in accordance with Beutel (1989)

In *Gnathium nitidum* (Figs. 3b, e), the galea is greatly elongated, filiform and forms the most conspicuous part of the maxilla. It is longer than the rest of the head and measures about 1.8 mm in length. The whole surface of the galea is densely covered with two types of long and distally oriented bristles (Fig. 3f). The median bristles are thin and smoothly flattened. The rest of the surface is covered with overlapping bristles possessing an acute tip and a keeled abaxial side. These thick bristles are as long as the thin median ones over the whole galea length. The length of both bristle types decreases from about 85 µm at the galea base, to 75 µm in the middle region and 50 µm in the tip region. In the tip region (Fig. 3g), the bristles are less dense. In addition, the tip region is equipped with several club-like sensilla (length about 20 µm), which point distally (Fig. 3h). The galeal surface is oval in cross-section in the proximal region, whereas it continuously flattens to a nearly rectangular cross-section in the distal region (Fig. 3i). The galeae do not possess a concave inner surface. Their mesal surfaces are covered by the thin and smoothly flattened bristles over the whole length. The lacinia forms a comb-like structure near the base of the galea; it is equipped with a median row of dense bristles in the distal region.

Labium

The labium (Figs. 1l, 2h, 3j, 4f) consists of the submentum, the mentum and the prementum with glossae, paraglossae, and the three-segmented labial palps. The submentum is fused to the head capsule. Glossae and paraglossae are fused to form a ligula, which is bifid to varying degrees. Each labial palp bears two regions of sensilla on the clubbed distal segment, similar to the maxillary palps. The hypopharynx extends medially over the mentum. Ventrally at the proximal edge of the prementum, a median apodeme arises, which projects into the mentum and on which the labial musculature (Table 1; Fig. 4f) inserts. The dorsal arms of the suspensorium reinforce the hypopharynx.

In *Leptopalpus rostratus* (Fig. 1l), the mentum is as long as wide and the ligula form two large lobes. The notch between the lobes extends to the base of the labial palps, at mid-length of the prementum. Both lobes are covered with long and individual setae forming a brush-like structure. Two rows of dense and short microtrichia on these lobes are arranged in a v-shape (Fig. 1m) and extend to the hypopharynx that consists of two large lobes covered with small setae at the distal edges. The dorsal arms of the suspensorium are connected by a superficial sclerotized bridge at the proximal edge of the mentum.

In *Nemognatha chrysomelina* (Fig. 2h), the mentum is rounded. The joint to the prementum is as wide as one half of the mentum. The groove between the two lobes of the ligula fails to reach the base of the labial palps. The lobes are covered with long and individual bristles. Two rows of dense microtrichia form a v-shape and lead to the strongly developed hypopharynx that extends to the proximal end of the mentum. A row of microtrichia is located in the median axis of the labium. These microtrichia face posteriorly in the proximal half of the groove and anteriorly in the distal half, which is largely covered by the hypopharyngeal lobes. The dorsal arms of the suspensorium are not connected by a sclerotized bridge.

In *Gnathium nitidum* (Fig. 3j), the mentum is twice as long as wide and has a rectangular shape. It is jointed to the prementum, which is as broad as the mentum but measures only half its length. The groove between the two lobes of the ligula reaches the base of the labial palps. Both lobes possess long and individual bristles that are curved in a ventro-mesal direction. The hypopharynx consists of two large lobes, the mesal surfaces of which are densely covered with microtrichia.

Pollen grains on mouthparts and in gut content

Pollen grains of various species of Asteraceae were found between the bristles of the ligula and galea in *Leptopalpus rostratus* and *Nemognatha chrysomelina* and in the guts of all three species. Inside the alimentary tract, pollen grains were evenly spread over fore-, mid-, and hindgut. The majority of pollen grains were intact, but some of them were empty.

Musculature of head and mouthparts (Table 1; Fig. 4)

The presence and course of the muscles of the head and mouthparts show no conspicuous differences among *Leptopalpus rostratus*, *Nemognatha chrysomelina*, and *Gnathium nitidum*. The origins and insertions of the single muscles are, in principle, similar for all three species (Table 1). This also applies to the musculature of the maxillae despite the differences in the length of the various maxillary parts. One special feature was found in the head of *L. rostratus*, a muscular lobe-like evagination of the dorsal wall of the foregut at its passage between cerebrum and subesophageal ganglion (Fig. 4a, b). This structure is absent in *G. nitidum* and *N. chrysomelina*. Noticeable differences among the investigated species were found in the compressor muscles of the cibarium and the pharynx. In *L. rostratus*, the three bundles of the semicircular *Musculus compressores epipharyngis* (M. III), which pass dorsally over the cibarium are relatively massive. They are less developed in *G. nitidum* and relatively slender in *N. chrysomelina*. The same applies to the posteriormost bundle *Musculus transversalis buccae* (M. 67) lying directly under the frontal ganglion and passing dorsally over the prepharynx. The probable functions of the muscles that are responsible for the mouthpart movements are mentioned in Table 1.

Discussion

Morphological comparison of the mouthparts

The proboscis-like mouthparts of representatives of nectar-feeding taxa of Meloidae were compared for the first time in detail. In *Leptopalpus*, the maxillary palps are greatly elongated, while in *Nemognatha* and *Gnathium*, the galeae are increased in length and representing the major organ of nectar uptake. The present study clearly shows that neither the maxillary palps nor the galeae of the examined species are tightly connected, neither of them possesses concave mesal margins and neither type of proboscis forms a closed tube, thus nectar cannot be taken up by a pressure gradient as is the case in the proboscides of other specialized nectar sucking insects.

The maxillary palps of *Leptopalpus rostratus* are round in cross-section, and the median bristles are directed medio-distally, not only medially (Handschin 1929) or caudally (Kaszab 1963). Moreover, the bristles do not form a mesal groove (Handschin 1929; Kaszab 1963), but they form a mesal path along which the nectar may ascend by capillarity. Likewise, the elongated galeae of both *Nemognatha chrysomelina* and *Gnathium nitidum* are filiform and more or less round in cross-section and never exhibit a median groove. In general, the bristles of the galeae in nectar-feeding Meloidae were described as long on short galeae and short on very long galeae (Kaszab 1963); however, the long galeae of *G. nitidum* are densely covered with relatively long and flat bristles. The present study discovered bottle-shaped sensilla near the galeal tips of *G. nitidum*. Their external shape is similar to the sensilla styloconica, which occur near the proboscis tip in myoglossatan Lepidoptera (Krenn and Kristensen 2000; Krenn 2010).

The palpifer of the investigated specimens is very likely to be homologous to that of other meloids. Since a stipital muscle (M. 23, see below) has been found to insert on the palpifer in *Mylabris pustulata* (Thunberg, 1821) (Saxena 1953), *Lytta vesicatoria* (Linnaeus, 1758) (Schneider 1981) and in *Epicauta segmenta* (Say, 1824) (Berríos-Ortiz 1986), the palpifer of meloids is likely to be homologous with the first palpal segment of other insects, which became fused to the stipes (Honomichl 1975).

The galeae of *Nemognatha chrysomelina* are covered with two types of bristles. The basal ones are straight and the distal ones are branched to enlarge the surface area and to improve their function as a brush-like tongue during nectar feeding. Nectar transport to the mouth is probably achieved by capillary forces of the bristles of the epipharynx and labium. The present study clearly shows the presence of a strongly developed hypopharynx, which is ventrally fused with the labium in all three species. The dorsal arms of the suspensorium, which support the hypopharynx, are separated in *Nemognatha*, similar to non-nectar-feeding Meloidae (Schneider 1981), but they are connected by a superficial sclerotized plate in *Leptopalpus*. In *Gnathium nitidum*, it remains unclear if these dorsal arms are connected.

The shape of the mandibles in all studied species is characteristic for pollen-feeding Coleoptera from various taxa (Fuchs 1974). Contrary to statements by Fuchs (1974), the biting capacity is not reduced since the sclerotized incisor part is curved and has an acute tip.

The musculature of the head and mouthparts are similar in all three taxa regarding their presence and course. The condition corresponds largely to the muscles found in the non-nectar-feeding meloid species *Lytta vesicatoria* (Schneider 1981). A lobe-like evagination of the dorsal wall of the foregut was found only in *L. rostratus*; it may be used to close the precerebral part of the alimentary canal proximally, separating it from the postcerebral part. This may enable the cibarium to effect changes in pressure and thus may function as a sucking pump.

Likewise, the maxillary musculature is similar to that of non-nectar-feeding Meloidae. The maxillary *musculus stipitopalpalis internus* (M. 23) inserts at the inner median basis of the 1st free palpal segment in all three taxa and may function as a flexor of the palp. Although in other meloids, such as *Lytta vesicatoria*, *Epicauta segmenta*, and *Mylabris pustulatus*, this muscle barely reaches the distal border of the palpifer (Saxena 1953; Schneider 1981; Berríos-Ortiz 1986), it was previously regarded as a flexor of the maxillary palp by Saxena (1953). Four semicircular muscles extend dorsally over the cibarium and prepharynx. This differs from the condition in *L. vesicatoria*, where only three of these compressor muscles are present (Schneider 1981). The larger number and obvious larger size of these muscles in Nemognathinae are probable adaptations for nectar feeding, especially in *Leptopalpus* and *Gnathium.*

Feeding mechanisms

Leptopalpus rostratus was observed to feed from inflorescences of *Centaurea* species (Asteraceae) by inserting the mouthparts into the florets (Handschin 1929). The assumption that nectar ascends to the mouth between the median bristles of the loosely connected maxillary palps, galeae, and laciniae by capillarity is plausible. However, our study indicates that nectar uptake is supported by a sucking pump-like organ in the head. The contraction of the massive dilator and compressor muscles of the cibarium and prepharynx might accelerate nectar ingestion from the preoral cavity and force nectar uptake into the esophagus.

Handschin (1929) assumed that pollen is transported to the mouth by alternate movements of the maxillary palps and that pollen grains are manipulated by the mandibles. The morphology of the mouthparts, however, argues against a selective pollen uptake with the maxillary palps. Furthermore, the pollen of Asteraceae is presented above the surface of the florets, while the nectaries are located at the bottom of the corolla tube (Bresinsky et al. 2008). Thus, it can be assumed that the maxillary palps are inserted into the corolla tube to imbibe nectar and that pollen uptake occurs from above mainly with the mandibles. It can also be hypothesized that, similar to what observed when the *Nemoptera sinuata* Olivier, 1811 (Neuroptera: Nemopteridae) feed on Asteraceae (Krenn et al. 2008), nectar feeding and pollen feeding do not take place at the same time. In *Leptopalpus rostratus*, probably the galeae and the lobes of the ligula are the main organs for harvesting pollen in addition to their role in nectar uptake. The brush-shaped galeae resemble the galeae in pollen-feeding Scarabaeidae (Johnson and Nicolson 2001). Karolyi et al. (2009) observed that the mouthparts of *Cetonia aurata* (Linnaeus, 1761) (Coleoptera: Scarabaeidae) are covered with liquid and therefore pollen is probably removed by dabbing the anthers with the wet brush of the galeae rather than by a sweeping motion assumed previously. The assumption that nectar improves adhesion of pollen in *L. rostratus* seems obvious since nectar is present in the diet. Furthermore, special setae, such as spoon- and trumpet-shaped bristles found in *Malachius bipustulatus* (Linnaeus, 1758) (Coleoptera: Malachiidae) or apically broadened and sculptured bristles (Fuchs 1974; Schicha 1967), are lacking. Similar to other Coleoptera, pollen is presumably conveyed over the robust lacinia comb between the mandibles where the soft and also comb-like prostheca transports the pollen to the molar plate of the mandibles in conjunction with back-and-forth movements of the epi- and hypopharynx (Schremmer 1961).

The assumption that pollen is solely mechanically crushed with the mandibles is unlikely in Nemognathinae since the majority of pollen grains in the gut were intact and some of them were empty. In the studied species, possibly a combination of mechanical and enzymatic techniques is used to open pollen grains (Johnson and Nicolson 2001), provided that pollen is taken up actively.

Nemognatha chrysomelina was described to feed on nectar and pollen of thistle flowers (Schremmer 1961). The present study supports the assumption that nectar ascends between the bristles of the galea to the basal mouthparts by capillarity and is transported further by suction from the preoral cavity. The presence of branched bristles on the galeal tips suggests that they function like a brush-like tongue that increases the adherence of nectar. Although no mouthpart movements are known to occur during nectar feeding, it is unlikely that the galeae remain motionless when taking up nectar. Nectar feeding in *Nemognatha* species with short galeae may be akin to feeding behavior of Scarabaeidae (Johnson and Nicolson 2001) and different from that of *Nemognatha* and *Gnathium* species with long galeae. Pollen grains were lodged between the bristles of the galea in *N. chrysomelina*, which indicates that the brush-like galeae serve for both nectar feeding and pollen feeding. Since the majority of the pollen grains in the gut were intact but empty, it seems evident that both *L. rostratus* and *N. chrysomelina* utilize pollen in the same way.

Gnathium nitidum was observed under laboratory conditions walking over the inflorescences of *Chrysothamnus* species (Asteraceae) and probing individual florets for a second or two before they bury their heads in a floret for about 5 min (Pinto 2009). The fact that they probe florets supports the assumption that the sensilla on the galeal tips are used to mechanically detect the corolla opening and to locate the nectar reservoir inside using chemical cues, as already hypothesized for the similarly shaped and positioned sensilla of myoglossatan Lepidoptera (Krenn 2010). It is most likely that nectar ascends along the galeae by capillarity between the bristles. In *G. nitidum*, the galeal surface is densely covered with flat bristles forming a cavity around each galea surface. The massive semicircular compressor muscles of the cibarium and prepharynx may accelerate the nectar uptake from the preoral cavity into the pharynx.

The main diet of *G. nitidum* is most likely nectar; however, individuals have also been observed to bite the stigma and anthers (Pinto 2009). Pollen ingestion was interpreted to be a consequence of cleaning behavior of galeae, legs, and antennae to which pollen grains adhere (Pinto 2009).

Evolutionary aspects

Elongated mouthparts evolved convergently on numerous occasions in flower-visiting holometabolan insects. Although the adaptations of the mouthparts in nectarvorous Coleoptera are not as conspicuous as in Diptera and Lepidoptera (Iablokoff-Khnzorian 1968), those in Meloidae are nonetheless significant. Within the Meloidae, elongations of the different maxillary parts are present in representatives that all belong to the Nemognathini (Bologna and Pinto 2001). Phylogenetic studies on the systematics of Meloidae based on morphological characters (Bologna and Pinto 2001) and molecular analyses (Bologna et al. 2008) strongly support the monophyly of the Nemognathinae. Nevertheless, the Nemognathini includes a heterogeneous assemblage of taxa without clarified relationships (Bologna et al. 2010). The results of the present study support the hypothesis that proboscides evolved twice independently within the Nemognathini. While the proboscis of *Leptopalpus* is composed of the maxillary palps, in *Gnathium* and *Nemognatha* the galeae are elongated. A great variety of galeal lengths were found ranging from very short to a length that exceeds the body in the representatives of *Gnathium* and *Nemognatha* (Kaszab 1963; Pinto 2009). We found remarkable differences in the bristle shape and their arrangement on the galeae between *G. nitidum* and *N. chrysomelina,* as well as a conspicuous type of sensilla on the galea in *G. nitidum*. That may be an indication that the galeal elongation in *Gnathium* species evolved independently from long galeae in *Nemognatha* species. The small taxon sampling cannot preclude overlap in the assumed intrageneric homogeneity. Nevertheless, MacSwain (1956) gives evidence of a closer relationship between *Gnathium* and *Zonitis* than between *Gnathium* and *Nemognatha* what could support the contention of convergence. The lack of prolonged galeae in many *Zonitis* species (Enns 1956) would also support the independent galeal elongation in the species-rich taxon *Nemognatha*.

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