

The adult head morphology of *Dascillus* (L.) (Dascilloidea: Dascillidae) and *Glaresis* Erichson (Scarabaeoidea: Glaresidae) and its phylogenetic implications

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> Abstract

External and internal structures of the adult head of *Glaresis* sp. and *Dascillus cervinus* are described in detail and compared with conditions found in other polyphagan representatives such as *Rhipicera* sp. and members of Staphyliniformia and Elateroidea. The structures examined do not support a clade Scarabaeoidea + Dascilloidea. No potential synapomorphic features of the head could be identified. In *Dascillus* a very unusual configuration of mouthparts is described for the first time, notably the inframandibular antepipharynx. This complex apomorphic feature was also found in members of different groups of Elateroidea s.l., but not in other potentially related lineages. This suggests a possible monophylum 'Elateroidea s.l. incl. Dascilloidea'. Additional new arguments for such clade are: characteristic scale-like setae on the galea and ligula; a ventrally expanded and bipartite foramen occipitale; a sclerotized tub-shaped prepharyngeal suspensorium; an epipharyngeal surface uniformly covered with microtrichia; similarly shaped mandibles with a concave ventral surface. Characteristics of *Dascillus* are the presence of a *M. verticopharyngalis* (plesiomorphic), the presence of two muscles of the posterior hypopharyngeal suspensorium, and bifurcate galeomeres II and ligular lobes. New arguments for a clade 'Staphyliniformia incl. Scarabaeoidea' are presented. The most important are the following: presence of a 'craniobasimaxillary' muscle; articulation of antennal club segments strongly excentric on outer margin of segments; distal club segment with characteristic sensory pouch; scapus with long bristle- or peg-like setae; ligula separated into a pair of oval shaped and anteriorly setiferous sclerites. Possible autapomorphies of Scarabaeoidea are the following: anterior part of clypeus projecting and covering the labrum; anterior clypeal margin concave and with a transverse row of trichia on its frontal or ventral surface; gula large, rectangular and strongly bulged; inner mandibular edge deeply interrupted by semimembranous lobe. Additionally, a revised terminology of head musculature is newly introduced for Coleoptera.

> Key words

Head, adults, mouth parts, musculature, Dascillidae, Glaresidae, Elateroidea, Scarabaeoidea, Staphyliniformia.

1. Introduction

With approximately 320.000 described species Polyphaga comprise ca 90% of the total number of the megadiverse Coleoptera (BEUTEL & LESCHEN 2005a). They do not only greatly surpass the other beetle suborders (Archostemata: ca 40 spp.; Myxophaga ca 100; Adephaga: ca 30.000), but also all other insect orders (e.g. GRIMALDI & ENGEL 2005). The Polyphaga are well-founded as a monophylum (e.g. presternal cervical sclerites; internalized prothoracic trochantinopleura; BEUTEL & LESCHEN 2005a) but the phylogeny within the group, especially the basal splitting events and the relationships between the 'series' (Staphyliniformia, Bostrichiformia, Cucujiformia, Elateriformia, Scarabaeiformia; sensu BEUTEL & LESCHEN 2005a) is a matter of longstanding dis-

pute and without reasonably supported hypotheses so far (BEUTEL & LESCHEN 2005a; LAWRENCE et al. 2011). Furthermore, beside the established series there are some taxa with an unknown or controversially discussed position within the suborder, which are apparently crucial for a better understanding of the higher level phylogeny of Polyphaga. Examples are the Scirtoidea and Derodontidae (e.g. FRIEDRICH & BEUTEL 2006; GE et al. 2007), and also Scarabaeoidea and Dascilloidea, which are in the focus of the present study.

Dascillidae, with the subfamilies Dascillinae and Karamiinae, is a rather small family comprising about 80 described species in 15 genera (its exact definition is still in flux; for detailed information see LAWRENCE

2005). It is mainly distributed on the northern hemisphere. Members of Karumiinae occur in (semi-)arid regions of all continents except Europe and Australia. In Central Europe only one dascillid species occurs, *Dascillus cervinus* (L.). Little is known on the feeding habits of dascillid adults. They are assumed to be floricolous (CROWSON 1960) or termitophilous (Karumiinae; LAWRENCE 2005). Adults of *Dascillus cervinus* can be found in (sub)montanous regions, near moist or aquatic habitats, where they stay in the lower vegetation. Dascillid larvae develop in soil. Larvae of Dascillinae feed on subterranean parts of plants, whereas larvae of Karumiinae are probably generally inquilines of termites (LAWRENCE 2005). Together with Rhipiceridae s.str. (ca 100 species in seven genera; LAWRENCE 2005) Dascillidae were combined in a superfamily Dascilloidea by different authors (CROWSON 1971; LAWRENCE 1988; LAWRENCE et al. 1995). Most hypotheses are proposing a close relationship of Dascilloidea either to Elateriformia or to Scarabaeoidea (see below).

Glaresidae was chosen for this study as it was addressed as the most ancestral extant scarabaeoid taxon (SCHOLTZ et al. 1994). *Glaresis* is the only genus of the family. It was treated as a member of Trogidae until SCHOLTZ (1986) omitted *Glaresis* from Trogidae and erected a separate family Glaresidae (SCHOLTZ et al. 1987). Approximately 50 species are described in the genus. It has a worldwide distribution with the exception of Australia. The beetles are small (2.5–6 mm) and brownish in coloration. Very little information is available on the biology and feeding habits and the larvae are still unknown. Most species occur in sandy areas in semi-arid regions (SCHOLTZ et al. 1994; SCHOLTZ & GREBENNIKOV 2005). A sister-group relationship between Glaresidae and all remaining subgroups of Scarabaeoidea was proposed for the first time by SCHOLTZ et al. (1994). This placement implies that *Glaresis* is highly important for the reconstruction of the groundplan of the superfamily, and also for the investigation of the phylogenetic affinities of Scarabaeoidea within Polyphaga. Despite the widely recognized phylogenetic importance of *Glaresis*, the available morphological information is scarce (SCHOLTZ et al. 1994; NEL & SCHOLTZ 1990). External features were not described in detail so far, and internal structures are largely unknown.

As pointed out above, the placement and taxonomic status of Dascilloidea and also Scarabaeoidea (or Scarabaeiformia) has been an object of dispute since some decades (for a detailed historical overview see LAWRENCE & NEWTON 1995; LAWRENCE 2005; and BEUTEL & LESCHEN 2005a,b). Initially placed within an elateriform clade (= Dascilliformia sensu CROWSON 1955), Dascilloidea were shifted by CROWSON (1960) to a series Scarabaeiformia, together with the Scarabaeoidea. This assumed relationship is mainly based on larval characters (e.g. grub-like habitus, cribriform spiracles, separate lacinia and galea, complex epi- and hypopharynx; LAWRENCE & BRITTON 1991) but also on some

characters of adults such as the exocone ommatidium structure (BROWNE & SCHOLTZ 1999), similar male genitalia (D'HOTMAN & SCHOLTZ 1990) and pore plate sensilla on the antennae (CROWSON 1995; MEINECKE 1975). LAWRENCE & NEWTON (1982) and GREBENNIKOV & SCHOLTZ (2003) interpreted the similarities of scarabaeoid and dascilloid larvae as habitat dependent convergencies, and suggested possible relationships of Dascilloidea with Eucinetoida (LAWRENCE & NEWTON 1982) or dryopoid subgroups (Eulichadidae; GREBENNIKOV & SCHOLTZ 2003). Current cladistic analyses also refute a dascilloid–scarabaeoid relationship, suggesting phylogenetic affinities of Dascilloidea with Buprestidae (LAWRENCE et al. 1995) and a placement of Scarabaeoidea within Staphyliniformia (= Haplogastra sensu KOLBE 1908) (e.g. HANSEN 1997; KORTE et al. 2004; CATERINO et al. 2005) or near staphyliniform subgroups (Hydrophiloidea s.l. + Scarabaeoidea; e.g. BEUTEL & LESCHEN 2005c). Molecular studies on Elateriformia based on rRNA and mitochondrial gene sequences (BOCAKOVA et al. 2007) showed possible affinities of Dascilloidea to Buprestoidea and different byrrhoid subgroups. Although primarily dealing with staphyliniform phylogeny, the cladistic analysis carried out by CATERINO et al. (2005) (including 85 representatives of all major clades of Coleoptera [except Cucujiformia]; based on molecular [18S rDNA] and morphological [119 chars.] data) placed the Dascillidae within Elateriformia, close to Elateroidea s.l. In a recent study based on a cladistic evaluation of a very large morphological data set (LAWRENCE et al. 2011 [Beetle Tree of Life project]) Dascillidae again were placed as sistergroup of Scarabaeoidea.

Considering the ongoing controversies regarding the systematic placement of Dascilloidea, it is surprising that the present knowledge of the morphology is very incomplete, especially of internal structures. This and the general lack of detailed anatomical data for most polyphagan groups induced us to carry out this study, which may contribute to a better understanding of polyphagan evolution in the future. The morphology of the adult head was chosen because the head is the most complex tagma of the insect body and contains a lot of phylogenetic information (e.g. BEUTEL et al. 2003; ANTON & BEUTEL 2004). The characters outlined are discussed with respect to their possible phylogenetic implications. A cladistic character evaluation is not presented in this primarily morphological study. However, the information given here will also provide data for a comprehensive cladistic analysis planned in the near future.

2. Material and methods

2.1. List of taxa examined

Scarabaeoidea, Glaresidae: indet. sp. of *Glaresis* Erichson, 1848 (SEM micrographs = 'SEM', cross sections = 'CS').

Dascilloidea, Dascillidae: *Dascillus cervinus* (Linnaeus, 1758) (SEM, CS).

For comparison representatives of all major clades of non-cucujiform Polyphaga were examined, with a special focus on scarabaeoid, staphyliniform and elateriform taxa:

Scarabaeoidea, Passalidae: *Passalus* Fabricius, 1792 spp., SEM; **Lucanidae:** *Platycerus caraboides* (Linnaeus, 1758), SEM; *Sinodendron cylindricum* (Linnaeus, 1758), SEM; **Trogidae:** *Trox* Fabricius, 1775 spp., SEM; *Polynoncus* Burmeister, 1847 sp., SEM, CS; **Geotrupidae:** *Trypocopriss vernalis* (Linnaeus, 1758), SEM; *Typhaeus typhoeus* (Linnaeus, 1758), SEM; **Scarabaeidae:** *Aegialia (Psammoporus) sabuleti* (Panzer, 1797), SEM; *Aphodius* Illiger, 1798 spp., SEM; *Oxyomus sylvestris* (Scopoli, 1763), SEM, CS; *Onthophagus* Latreille, 1802 spp., SEM; *Melolontha melolontha* (Linnaeus, 1758); *Amphimallon solstitiale* (Linnaeus, 1758); *Serica brunnea* (Linnaeus, 1758), SEM; *Phyllopertha horticola* (Linnaeus, 1758), SEM; *Oxyomus sylvestris* (Scopoli, 1763), SEM; *Valgus hemipterus* (Linnaeus, 1758), SEM; *Oryctes nasicornis* (Linnaeus, 1758), SEM.

Hydrophiloidea s.l., Sphaeritidae: *Sphaerites glabratus* (Fabricius, 1792), CS.

Dascilloidea, Rhipiceridae: indet. sp. of *Rhipicera* Latreille, 1817, 1 ex.

Elateroidea s.l. (= Elateroidea sensu LAWRENCE & NEWTON 1995), **Elateridae:** *Agrypnus murinus* (Linnaeus, 1758), SEM; *Athous subfuscus* (Müller, 1767), SEM; *Dalopius marginatus* (Linnaeus, 1758), SEM; **Throscidae:** *Trixagus dermestoides* (Linnaeus, 1767), SEM; **Eucnemidae:** *Hylis foveicollis* (Thomson, 1874); **Omalisidae:** *Omalisus fontisbellaquaei* Fourcroy, 1785; **Lycidae:** *Dictyoptera aurora* (Herbst, 1874); *Lygistopterus sanguineus* (Linnaeus, 1758), SEM; *Platycis minutus* (Fabricius, 1787), SEM; **Drilidae:** *Drilus concolor* Ahrens, 1812, SEM; **Lampyridae:** *Lamprohiza splendidula* (Linnaeus, 1767), SEM; **Cantharidae:** *Cantharis obscura* Linnaeus, 1758, SEM; *Rhagonycha fulva* (Scopoli, 1763), SEM; *Malthodes* Kiesenwetter, 1852 sp.

Byrrhoidea (incl. **Dryopoidea**) (= Byrrhoidea sensu LAWRENCE & NEWTON 1995), **Byrrhidae:** *Byrrhus pilula* (Linnaeus, 1758), SEM; *Simplocaria semistriata* (Fabricius, 1794), SEM; *Lamprobyrrhulus nitidus* (Schaller, 1783), CS; **Ptilodactylidae:** *Ptilodactyla* Illiger, 1807 sp., SEM; **Dryopidae:** *Dryops auriculatus* (Geoffroy, 1785), SEM; **Elmidae:** *Elmis aenea* (Müller, 1806), SEM; **Heteroceridae:** *Heterocerus fenestratus* (Thunberg, 1784), SEM.

Scirtoidea, Eucinetidae: *Eucinetus* Germar, 1818 sp.; **Clambidae:** *Clambus nigriclavus* Stephens, 1835, SEM; *Calyptomerus dubius* Marsham, 1802; **Scirtidae:** *Cyphon coarctatus* Paykull, 1799, SEM, CS; *Elodes pseudominuta* Klausnitzer, 1971.

Buprestoidea, Buprestidae: *Anthaxia nitidula* (Linnaeus, 1758), SEM; *Trachys minutus* (Linnaeus, 1758).

The material listed in ANTON & BEUTEL (2004) was also used for this contribution.

All examined specimens were fixed in ethanol or FAE (formaldehyde-ethanol-acetic acid – 3:6:1). From specimens of all listed species (except for *Rhipicera* sp.) mouthparts and antennae were dissected from the head capsule and usually processed as slide preparations (not in the case of very large species). For embedding Berlese medium or Euparal was used. For SEM micro-

graphs heads or mouthparts of selected specimens were cleaned with ultrasonic sound and phosphatic acid. SEM micrographs were made with a FEI (Philips) XL 30 ESEM TMP. As embedding medium for microtome sectioning Araldit or Histoiresin was used. The sections were stained with Azan (Araldit) or methylene blue and acid fuchsine (Histoiresin). Drawings were made with a camera lucida.

2.2. Terminologies and classification

The muscular terminology is based on v. KÉLER (1963). WIPFLER et al. (2011) introduced a revised terminology of head musculature for Dicondylia with the advantage to be more complete and more flexible in naming novel muscles compared with that of v. KÉLER (1963). As the present study is the one introducing the terminology of WIPFLER et al. (2011) for adults of Holometabola and for Coleoptera in particular both terminologies will be used with respect to the traditional system of v. KÉLER (1963) (see Table 1).

The taxonomic classification generally follows BEUTEL & LESCHEN (2005a), with few exceptions: Scarabaeoidea is used synonymous with Scarabaeiformia sensu BEUTEL & LESCHEN (2005a) to avoid confusion with Scarabaeiformia sensu CROWSON (1960) (= Scarabaeoidea + Dascilloidea); subgroups of Hydrophiloidea s.str. are treated in the sense of HANSEN (1991) (e.g. Helophoridae instead of Helophorinae).

The morphological directions used herein to describe relative positions of structures of the head capsule and especially of the mouthparts (i.e. dorsal, ventral, anterior, posterior) always are applied to a strictly prognathous condition of the head. For example, the exposed surface of the labrum is considered the dorsal surface, the distal margin of the mental sclerite equates the anterior margin and the apex of the mandibles is considered positioned anterior with respect to the mandibular base.

3. Morphology

3.1. *Glaresis* sp.

3.1.1. Head capsule

3.1.1.1. External structures (Figs. 1–3, 16–26). Head prognathous, slightly inclined in resting position, and retracted into prothorax; anterior prothoracic margin reaches posterior margin of compound eyes, covering



occipital area, gula and posterior genae. Head capsule wider than long in dorsal view (~1 mm width, ~0.8 mm length); lateral outline markedly interrupted between clypeus and frons (Figs. 1, 3, 16–19; see below); wedge-shaped in lateral view; maximum height at occipital region (~0.6 mm), narrowing towards mouthparts. Coloration of cuticle orange to brownish, slightly transparent; distinctly sclerotized; average thickness of cuticle ca 25 µm, with the endo- and exocuticle about equally strong. Surface dull and rough on most parts of head capsule; dorsal side irregularly set with tubercles and stout, laterally serrate and apically frayed setae, especially on posterior part of clypeus and anterior part of frons (e.g. Figs. 1, 16, 19, 22); anterior clypeus with rather smooth surface; posterior head region with large and shallow punctures with irregular distribution (Figs. 1, 3, 16); surface structure of occipital and genal region scale-like (Figs. 18, 25); gena posterior with irregularly arranged large setiferous punctures (Fig. 25); surface of postocular area smooth, with a row of ventrally directed long hairs (Figs. 3, 18, 25); gula smooth, shiny, without pubescence (Figs. 17, 25).

Clypeal region broad and elongate, not distinctly separated from frons; border between both areas marked by conspicuous lateral incision and large and deep epistomal grooves (Figs. 1, 16); clypeal surface slightly curved in transverse and longitudinal direction; anterior and lateral clypeal areas strongly projecting, covering labrum and antennal insertion; lateral margin longer than lateral margin of frons anterior to eyes; anterior margin with broad concave emargination and distinct transverse ridge on dorsal side (Fig. 20); deep sockets bearing long hair-like setae and shorter, upward curved setae with several minute distal processes present anterior to transverse ridge (Figs. 20, 21); ventral side of projecting anterior part of clypeus with transverse irregular row of thin setae (Figs. 34, 35; 'trs'); anteromedian clypeal edge sharp; anterolateral edge broadly rounded. Deep and fairly wide incision separating lateral margin of clypeus and frons allows dorsally directed antennal movements. Surface of frons slightly convex in transverse and longitudinal direction. Triangular epicanthus formed by anterior edge of clypeofrontal incision and anterolateral frontal margin separates anterior region of compound eyes into upper and lower portion (Figs. 3,

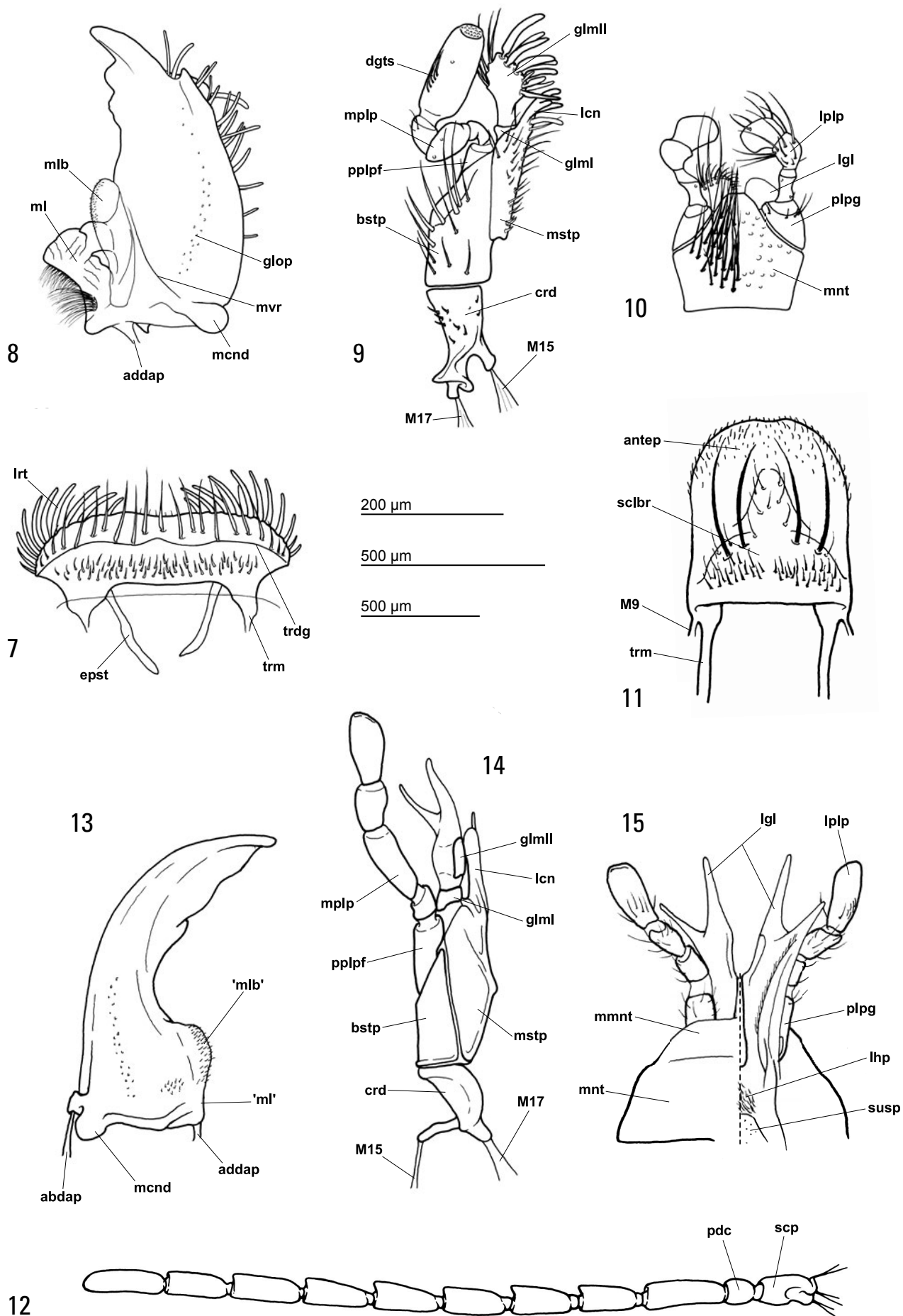
18, 19). Main part of frontal region elevated and shield-like, above level of compound eyes (Figs. 3, 18); lateral and posterior borders of elevated region delimited by sharp ridge; narrow area between lateral frontal ridge and compound eyes and posterior frontal ridge and occiput, respectively, pubescent (Figs. 3, 18, 24); lateral frontal ridge and epicanthus set with row of spine-like setae (Figs. 1, 19); posterior frons with moderately distinct internal median ridge (endocarina), which is extended posteriorly as a caudally directed projection serving as attachment area for cervical musculature (Fig. 2; 'pM55'). A well developed transverse postocular ridge connects posterodorsal corners of eyes (Figs. 1, 3, 18, 24; 'por'). Dorsal occipital area of head capsule short (Figs. 1, 3, 16, 24; 'occ').

Antennal furrow distinctly developed on ventral side of head capsule, receiving scapus and pedicellus in resting position (Figs. 2, 17, 26); reaching posterior region of compound eye; mesally delimited by high ridge; laterally bordered by ventral part of eye. Gula large, trapezoid, distinctly convex, bulging (Figs. 2, 3, 17, 25); with rounded, posteriorly diverging lateral margins; posterolateral edges rounded; concave hind margin bordering foramen occipitale ventrally. Anterior gular margin straight, connected with submentum.

Superposition compound eyes well developed, spherical (Figs. 17, 18); ventral region strongly convex, with ventral margin lying below ventromedian surface of head (Fig. 3); projecting ventral part of eyes forming lateral border of ventral antennal furrow (Figs. 17, 26); anterior part strongly incised by frontal epicanthus (see above); posterior ocular margin concave; enclosed triangular postocular area nearly perpendicular to longitudinal axis of head (Figs. 18, 25); ommatidia eucone; crystalline cone and clear zone of ommatidia well developed; cornea lacking screening pigment; facet diameter ~20 µm, ommatidia length ~130 µm, with dorsal ommatidia slightly shorter than ventral ones (Fig. 172; see also CAVENEY 1986; CAVENEY & SCHOLTZ 1993).

3.1.1.2. Internal skeletal structures (Figs. 135, 137). Gular ridges well developed and long; dorsally continuous with anteriorly narrowing and converging posterior tentorial arms. Posterior part of tentorium flat and tent-like; tentorial bridge solid, short and straight; rod-like

← **Figs. 1–6.** Head capsule, antennae and pubescence/setation partly removed. **1–3:** *Glaresis* sp. (upper scale); **1:** dorsal view, muscle insertions on dorsal head capsule in grey; **2:** ventral view, antennal sensory pouch and distinct setose area on distal antennomere in grey; **3:** lateral view. **4–6:** *Dascillus cervinus* (lower scale); **4:** dorsal view, muscle insertions on dorsal head capsule in grey; **5:** ventral view; **6:** lateral view, tentorium in grey. acIp – anteclypeus, ant – antenna, antc – antennal club, antcm – compressor muscle of antennal heart, antep – inframandibular antepipharynx, antf – antennifer, antsa – distinct setose area on distal antennomere, antsp – antennal sensory pouch, ata – anterior tentorial arm, bstp – basistipes, ce – compound eye, clp – clypeus, clpr – dorsal clypeal ridge, crd – cardo, dta – dorsal tentorial arm, epc – ocular epicanthus, epstg – epistomal groove, focc – foramen occipitale, frn – frons, gl – gula, glmII – galeomere II, iant – antennal socket, idta – attachment area of dorsal tentorial arm, inc – clypeofrontal incision, lbplp – labial palp, lbr – labrum, lgl – ligula, lt – laminatentorium, M4–55/Mx₄ – musculature, mnd – mandible, mnt – mentum, mstp – mediostipes, mx – maxilla, mxplp – maxillary palp, occ – occiput, occprc – processus separating dorsal and ventral part of foramen occipitale, pclp – postclypeus, pdc – pedicellus, pfocc – posterior part of foramen occipitale, pplpf – pseudopalpifer, pM55 – intracranial process, insertion of M55, poca – postocular area, por – postocular ridge, pta – posterior tentorial arm, scp – scapus, smnt – submentum, stp – stipes, tb – tentorial bridge, vantf – ventral antennal furrow, vfocc – ventral part of foramen occipitale.



longitudinal arms originating on anterodorsal posterior arms; longitudinal arms distally fused with each other, forming small laminatentorium; short and flattened anterior tentorial arms arise from head capsule within epistomal grooves (Fig. 135; 'ata'); posterior and anterior arms only connected by thin connective tissue.

3.1.2. Appendages

3.1.2.1. Labrum (Figs. 7, 20, 21, 34, 35, 135). Well developed, short, ca 3 times as broad as long; almost completely covered by clypeus, scarcely visible from above. Anterior corners rounded; anterior edge nearly straight, with very shallow concavity; posterior corners forming acute angle interacting with ventral clypeal carinae, thus forming an arresting mechanism (Figs. 34, 35; 'vcr'). Posterior internal sclerotized part of labrum distinctly narrowed, ca 3/4 as wide as exposed anterior part. Posterior margin with reduced sclerotized tormae of triangular shape, serving as attachment site for M9 (Fig. 7; 'trm'); pair of slightly sclerotized, posteriorly converging paramedian struts mediad of tormae (Figs. 7, 139E; 'epst') support longitudinal epipharyngeal process (see below). Dorsal surface of exposed part of labrum subdivided by sharp transverse ridge (Fig. 7; 'trdg') into anterior and posterior region; posterior part relatively smooth, regularly and densely set with short hairs. Anterior part rugulose with very long and strong bristle-like hairs (Fig. 21). Row of very long and thick bristles present on anterolateral edge (Figs. 7, 34, 35); middle region of anterior edge ventrally set with few short and thin bristles (Fig. 35).

3.1.2.2. Antennae (Figs. 2, 3, 17, 27–33, 175). 10-segmented, short compared to head length, with asymmetrical club. Surface of scapus and club segments scale-like; pedicellus and flagellum glabrous. Scapus elongated (Figs. 27, 28); its condyle tube-like and thickened; proximal part of scapus widening distally; curved to fit into ventral antennal furrow, adapted to contour of compound eyes; scapo-pedicellar condyle subapical; apex of scapus knee-shaped. Pedicellus mesally slightly convex (Fig. 29); lateral edge proximally extended, forming hook-shaped process. Very long and thick setae on outer side

of distal scapus and pedicellus form cleaning or protection device for compound eyes; surface of scapus and pedicellus also with vestiture of short and thin setae.

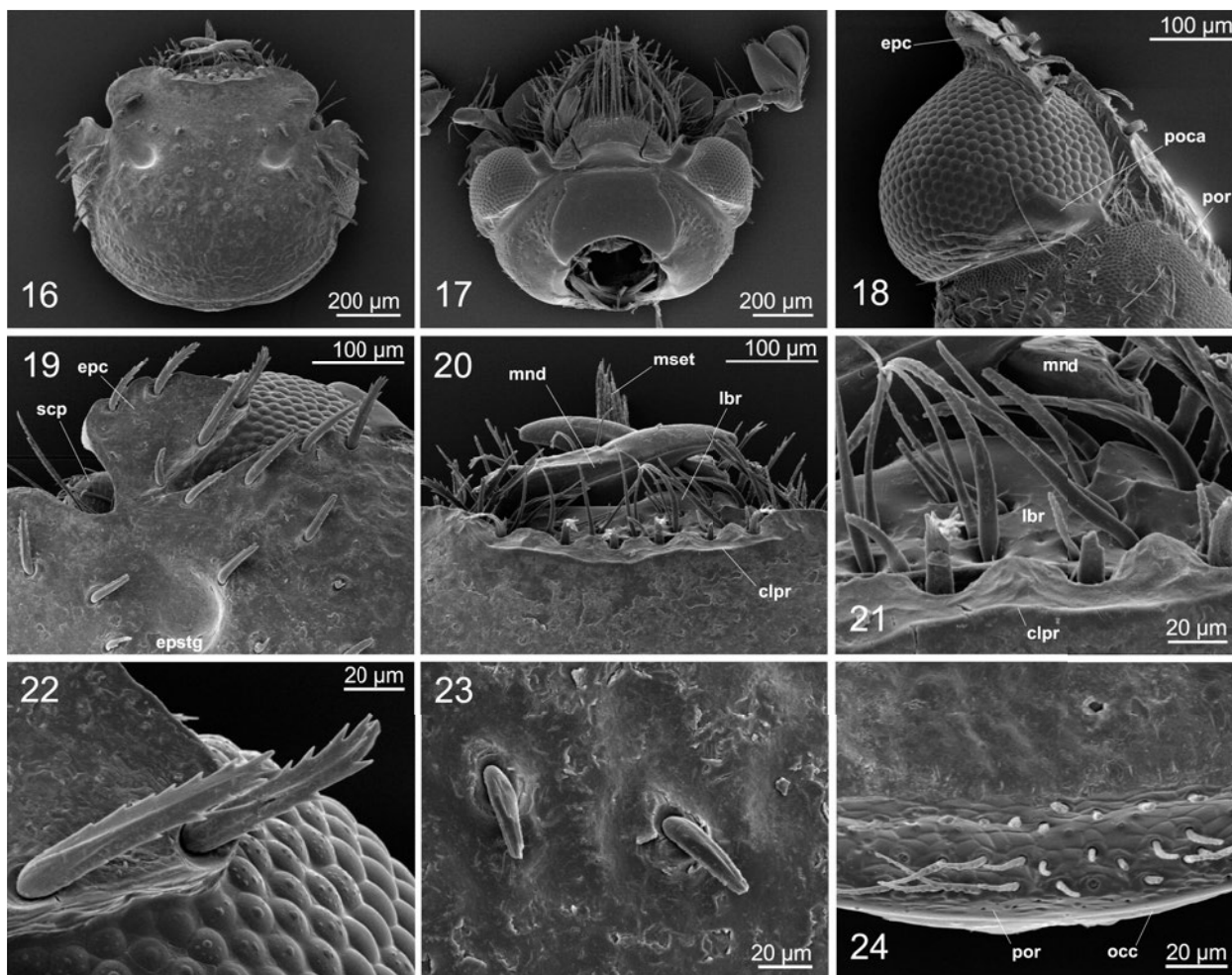
Antennomeres III–VII very small and short (Figs. 17, 29), broader than long, widening distally, cup-shaped; segments without short pubescence or longer setae; a distinct cupuliform segment absent.

Antennal club large, 3-segmented, strongly asymmetric (Fig. 27); articulation near outer margin of club segments (Figs. 30–33); antennomeres VIII and IX flat, ovoid, similar in size and shape (Figs. 30, 31); antennomere X slightly smaller than preceding segments (Fig. 32). Edge of club segments densely set with bristle-like setae; proximal surface scale-like, without pubescence; distal surface of segments VIII and IX densely set with peg-like olfactory sensilla (Figs. 30, 33, 175); third club segment sparsely covered with setae distally, apart from long and narrow area with dense setation parallel to segmental edge (Figs. 2, 27, 175; 'antsa'); pore of long tube-shaped sensory pouch originates on apical part of this setiferous area (Figs. 2, 175; 'antsp'); pouch densely filled with longitudinally directed hair-like sensilla of unknown function.

3.1.2.3. Mandibles (Figs. 1–3, 8, 37–43, 139). Mandibles about two times as long as broad; triangular and distinctly asymmetric. Lateral part relatively wide proximally, narrowing distally; with long and thick serrate hairs (Figs. 37, 38); lateral margin shallowly rounded, with small process on ventral side of left mandible (Fig. 38). Dorsolateral edge of both mandibles forming a high ridge fitting with lateral and anterolateral labral margin in resting position (Figs. 20, 37). Dorsal and ventral surface of mandibles even to slightly concave; surface structure glabrous to scale-like; distinct, curved ridge on ventral face extending from mandibular condyle to mesal mandibular edge (Figs. 8, 38; 'mvr'), possibly mechanically interacting with maxillae (Fig. 139B–C).

Apex of mandible large, pointed, ca 1/2 of total mandibular length; mesal edge with two blunt proximal teeth and long cutting edge; semimembranous mesal mandibular lobe well developed, placed in broad concavity of mesal edge, extending over ca 1/5 of mesal mandibular margin (Figs. 8, 37, 40–43, 139); interacting with hypopharyngeal lobes (Fig. 139; see below); continuing ventrally along ventral side of molae (Fig. 8). Asymmetric molae very large, extending over ca 1/3 of mesal

← **Figs. 7–15.** Mouthparts. **7–10:** *Glaresis* sp. (upper scale); **7:** labrum, dorsal view; **8:** left mandible, ventral view; **9:** right maxilla, ventral view; **10:** labium, ventral view, setation of mentum and ligula on left side and of palpus on right side removed. **11–15:** *Dascillus cervinus* (median scale and lower scale for antenna respectively); **11:** labrum with antepipharynx, dorsal view; **12:** antenna, setation/pubescence removed; **13:** right mandible, ventral view; **14:** right maxilla, ventral view, setation/pubescence removed; **15:** labium, ventral view on the left, dorsal view on the right. abdap – apodeme of mandible abductor (M12), addap – apodeme of mandibular adductor (M11), antep – antepipharynx, bstp – basistipes, crd – cardo, dgts – digitiform sensilla, epst – epipharyngeal struts, glml/II – galeomere I/II, glop – glandular pores, lcn – lacinia, lgl – ligula, lhp – longitudinal hypopharyngeal process, lplp – labial palpomere, lrt – transverse labral row of teeth, M9/15/17 – musculature, mcnd – mandibular condyle, ml – mandibular mola, mlb – semimembranous median mandibular lobe, mmnt – semimembranous anterior part of mentum, mnt – mentum, mplp – maxillary palpomere, mstp – mediostipes, mvr – ventral mandibular ridge, pdc – pedicellus, pplpf – pseudopalpifer, plpg – palpiger, sclbr – sclerotized part of labrum, scp – scapus, susp – suspensorium, trdg – transverse labral ridge, trm – tormae.



Figs. 16–24. *Glaresis* sp., SEM, head capsule. **16:** dorsal view; **17:** ventral view; **18:** lateral view of posterior part; **19:** clypeofrontal incision, epicanthus and epistomal groove, right side, dorsal view; **20:** anterior part of clypeus, showing transverse clypeal ridge, mandibles, dorsal view; **21:** setation on anterior clypeal margin and labrum, detail from Fig. 20; **22:** setation on margin of posterior epicanthus; **23:** setation on vertex; **24:** occiput, dorsal view. clpr – dorsal clypeal ridge, epc – ocular epicanthus, epstg – epistomal groove, lbr – labrum, mnd – mandible, mset – setae of mentum, occ – occiput, poca – postocular area, por – postocular ridge, scp – scapus.

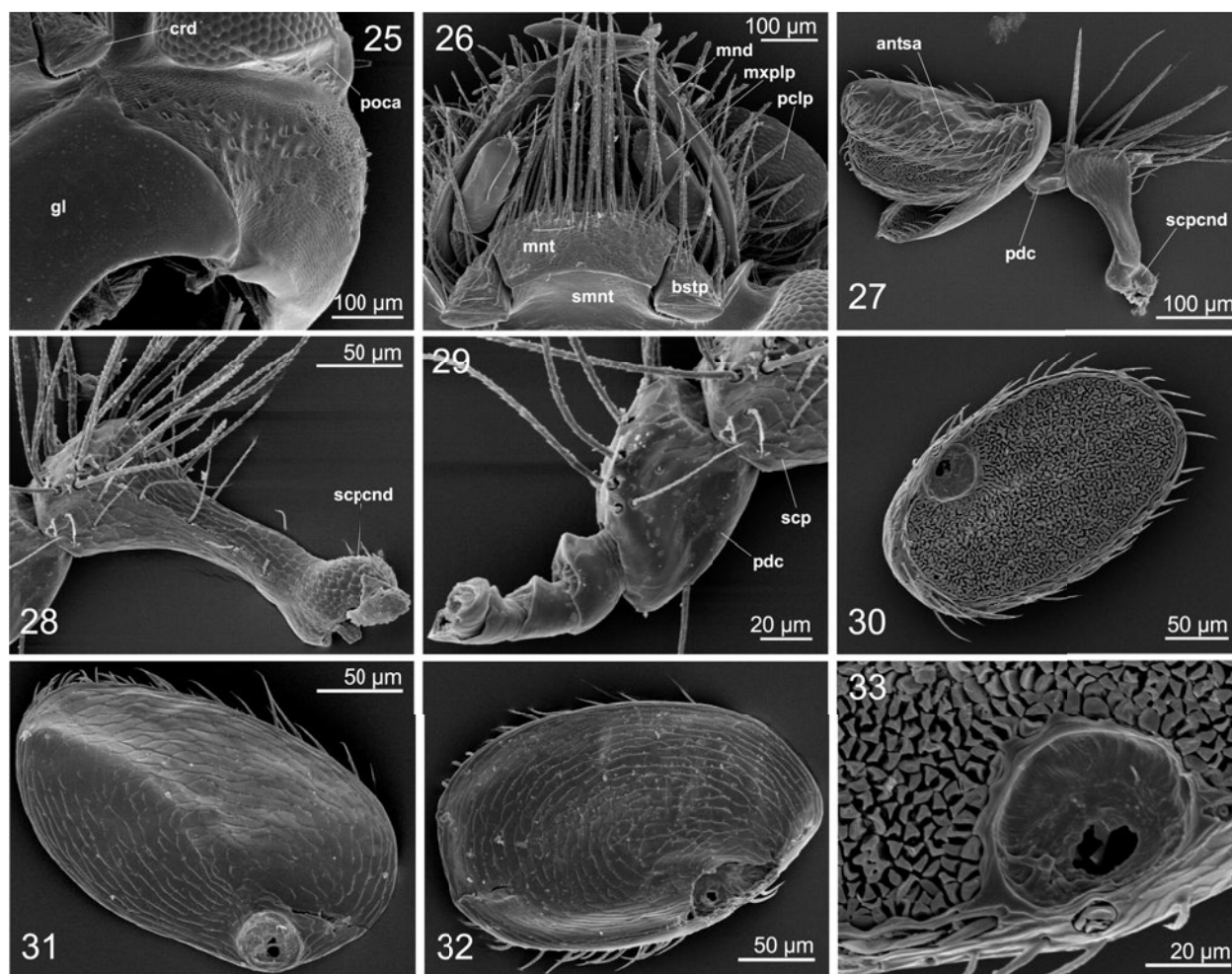
mandibular edge (Figs. 8, 42, 43); left mola broadly concave, with two strong teeth anteriorly; right mola slightly convex, with anterior tooth fitting between two teeth of left mola; dorsal surface of right mola and posterior surface of left mola densely set with microtrichia; ventral surface of both molae with long setae, covered by semimembranous lobe (Fig. 41; ‘vps’).

Dorsal (secondary) acetabular joint of mandible positioned on exterior angle of mandibular base (Fig. 37); bordered by high, rounded ridge; obliquely directed posterolaterad; forming hemispherical concavity. Ventral (primary) condyle of mandible also positioned on exterior angle of mandibular base (Figs. 8, 38); hemispherical; obliquely directed posterolaterad; proximally smoothly continuous with ventral mandibular ridge (see above).

3.1.2.4. Maxillae (Figs. 9, 44–52, 139). Cardo relatively large, with well developed processes for insertion of *M. craniocardinalis* (M15) and *M. tentoriocardinalis* (M17) (Fig. 9), respectively. Basistipes large, trapezoid

in ventral view, with projecting anteromesal angle; surface set with long setae. Mediostipes narrow, elongate, parallel-sided, not distinctly separated from lacinia. Lacinia narrow and slender; sclerotized mesal edge set with trichia; distal part strongly sclerotized, hook-shaped; several strong thorn-like setae present subapically (Fig. 46). Galea two-segmented; galeomere I very small and short, scarcely visible; galeomere II large, axe-shaped, distally broadened, projecting beyond anterior margin of lacinia; apical edge set with few long setae and several spine-like setae arranged in a row (Figs. 47, 48).

Based on plausible arguments, especially of musculature, a ‘true palpifer’ obviously does not exist in Coleoptera, instead the palpifer-like structure is represented by a transformed anatomical palpomere I, thus forming a ‘pseudopalpifer’ (see also sections 3.1.6.4. and 4.5.). In *Glaresis* the pseudopalpifer is well developed, inserted dorsolaterally on the basistipes, not visible in ventral view (Fig. 45); deep longitudinal furrow on dorsal maxillary body enclosed by lacinia and pseudopalpifer; thus max-



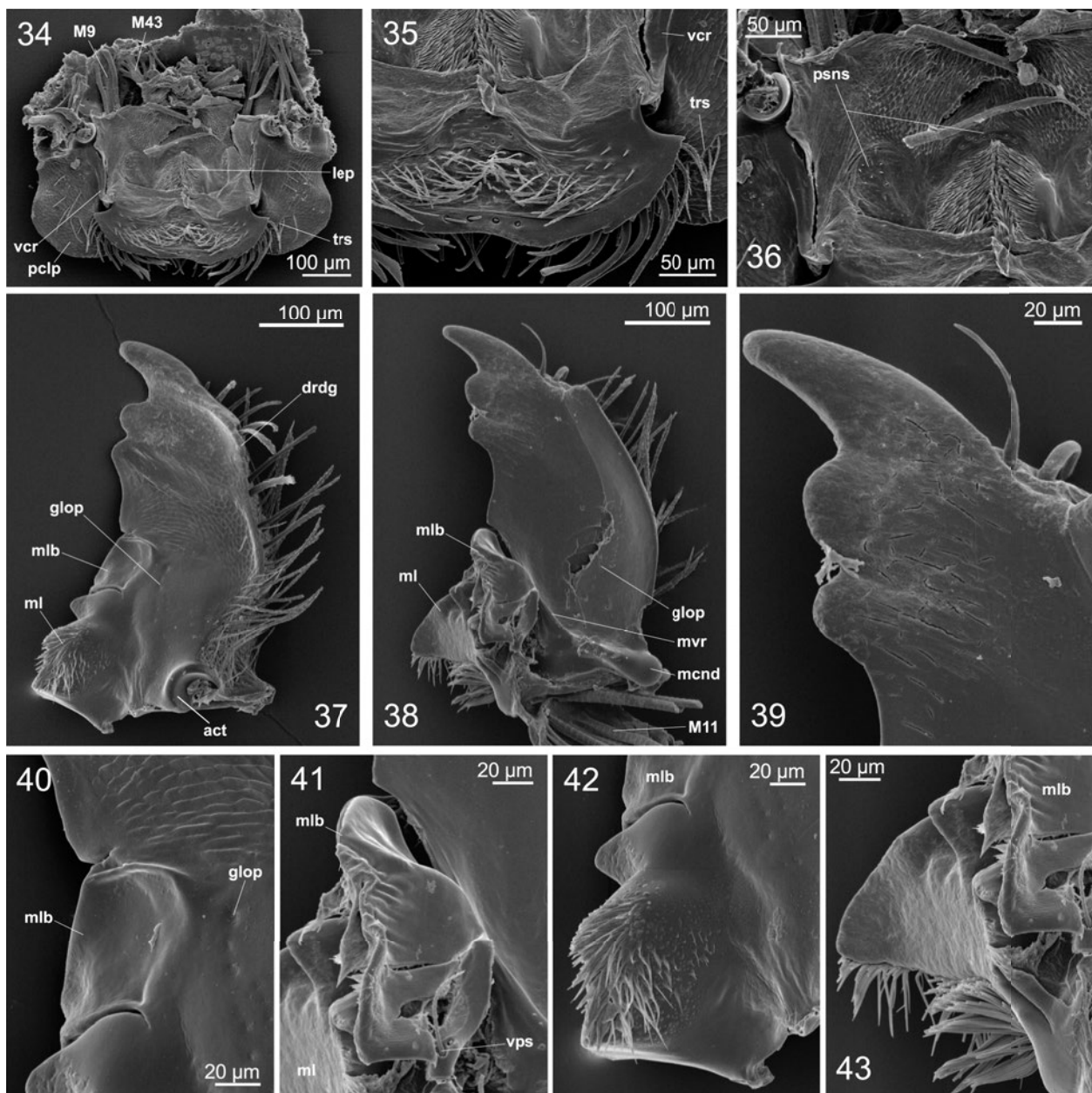
Figs. 25–33. *Glaresis* sp., SEM, head capsule and antenna; **25:** gula and posterior gena, left side; **26:** mouth parts, ventral view; **27:** right antenna; **28:** left scapus; **29:** left pedicellus and proximal flagellomeres; **30:** first club segment, distal view; **31:** second club segment, proximal view; **32:** distal club segment, proximal view; **33:** detail from Fig. 30, articulation area and olfactory sensilla. antsa – distinct setose area on distal antennomere, crd – cardo, gl – gula, mnd – mandible, mxplp – maxillary palp, pclp – anterolateral projecting part of clypeus, pdc – pedicellus, poca – postocular area, scp – scapus, scpcnd – basal condyle of scapus.

illa appearing U-shaped in cross section (Fig. 139B). Functional palpomere I (see above) small, bent outwards; palpomere II ca 2 times as long and wide as palpomere I, ovoid to cup-shaped. Palpomere III small, only slightly longer and broader than first palpomere, slightly bent inwards. Palpomere IV cylinder-shaped, as long as preceding segments together, ca 2 times as broad as palpomere II; apex with semimembranous sensory area densely set with conical peg-like sensilla; conspicuous field of numerous digitiform sensilla present on dorsolateral side of proximal half of palpomere IV (Figs. 51, 52).

3.1.2.5. Labium (Figs. 10, 53–58, 139). Well developed submentum laterally bordered by maxillae (Figs. 2, 17); anterior margin slightly convex. Mentum moderately sized, plate-like, pentagonal in outline; surface strongly convex (Figs. 3, 135), densely set with very long, anteriorly directed bristles (Figs. 2, 3, 26); lateral margins of posterior part anteriorly diverging, forming acute angle about at midlength of mentum; anterior part with strong-

ly converging concave lateral margins; palpiger inserted in this concavity (Fig. 10); anterior mental margin blunt, slightly concave, lateral sides of mentum folded up dorsad (visible in cross sections, Fig. 139); upper posterior edge of fold firmly connected with lower anterior edge of hypopharyngeal sclerite (Fig. 139C shows position shortly behind this connection).

Relatively small ligular part firmly connected with mentum and hypopharynx, forming a compact labiohypopharyngeal complex (Fig. 53); anterior half of dorsal side densely set with long bristles; anterior edge with anteromesally directed spines; ligula forming pair of distinct lobe-like semimembranous sclerites; both posteriorly connected by small strut-like median premental sclerite bearing insertion of retractor muscle (Figs. 135, 137; ‘M42’, see below). Palpiger large, ventrally not covered by mentum. Labial palp 3-segmented (Figs. 10, 57). Palpomere I small, widened proximally and apically, slightly bent laterally. Palpomere II cup-shaped, laterally bulging; lateral region and median part of distal



Figs. 34–43. *Glaresis* sp., SEM, labrum and mandibles; **34:** labrum, epipharynx, anterior clypeus, ventral view; **35:** anterior part of epipharynx; **36:** posterior part of epipharynx; **37:** right mandible, dorsal view; **38:** left mandible, ventral view, surface slightly damaged; **39:** apex of left mandible; **40:** semimembranous median mandibular lobe of right mandible; **41:** semimembranous median mandibular lobe of left mandible; **42:** right mola; **43:** left mola. act – acetabulum, drdg – dorsal outer ridge, glop – gland opening, lep – longitudinal epipharyngeal process, M9/11/43 – musculature, mcnd – mandibular condyle, ml – mola, mlb – semimembranous median mandibular lobe, mvr – mandibular ventral ridge, pcip – anterolateral projecting part of clypeus, psns – patch of sensilla, trs – transverse row of setae on ventral clypeus, vcr – ventral clypeal carina, vps – ventral patch of setae.

margin set with long hairs. Palpomere III short, knob-shaped; lateral edge convex; long bristles present laterally and apically; palpomere III with distinctly enlarged semimembranous apical area, densely covered with numerous conical peg-like sensilla (Figs. 57, 58).

3.1.3. Digestive tract

3.1.3.1. Epipharynx (Figs. 34–36). Semimembranous epipharynx extended over entire length of ventral surface

of labrum; anterior part densely set with trichia; trichia on central region longer and mesally directed; anteromesally oriented on lateral part. Well developed longitudinal epipharyngeal process (Figs. 36, 139D–E; ‘lep’) present, which is densely set with mesally directed layers of microtrichia. Surface of epipharynx laterad and immediately posterior to longitudinal epipharyngeal process glabrous, with three patches of sensilla, one laterally on both sides of the process and one posteriorly at midline (Fig. 36, ‘psns’). Surface of epipharynx posterior to epipharyngeal process evenly covered with microtrichia (Fig. 36).

3.1.3.2. Hypopharynx (Figs. 53–56, 135, 139). Well developed, forming a structural unit with anterior labium. Salivarium completely absent. Hypopharynx transversely subdivided into two parts. Posterior part with strongly sclerotized lateral walls; posteriorly, below level of mandibular molae, sclerotizations continuous with each other (Fig. 135; ‘hppbr’, ‘hypopharyngeal bridge’); two thin and long sclerotized struts emerging from sides of this bridge, connecting hypopharynx with anatomical mouth angles and serving as insertion point for frontohypopharyngeal musculature (M41, see below) (Fig. 135; ‘sspscl’, suspensorial sclerites). Posterior hypopharynx appearing hourglass-shaped in cross sections (Figs. 139A,B); anteroventrally firmly connected with mentum (see above). Dorsal surface of posterior part with well developed longitudinal hypopharyngeal process formed by dense layers of microtrichia (Figs. 56, 139A; ‘lhp’); shape triangular in cross sections, corresponding with semimembranous lobe on ventral side of mandibular molae. Anterior part of hypopharynx composed of large and strongly folded semimembranous lobes corresponding with lobe-like median mandibular brush (Figs. 139C–E); rostrad evenly continuous with prementum.

3.1.3.3. Pharynx and oesophagus (Fig. 135). A closed prepharyngeal tube is absent. Pharynx in its whole length strongly folded, with narrow lumen; pharyngeal wall incl. musculature (M68/69) very thin; oesophagus not distinctly separated from pharynx.

3.1.4. Cerebrum and suboesophageal ganglion

Brain (Fig. 135) small in relation to head size; placed in the posterodorsal head region but not reaching foramen occipitale; enclosed by posterior frons dorsally, by mandibular muscles (M11/12) laterally and lateroventrally, by the pharynx ventrally, and by the posterior precerebral pharyngeal dilator anteriorly (M46). Frontal ganglion normally developed; frontal connectives rather thin. Circumoesophageal connectives rather short and stout, a well developed tritocerebral commissure situated directly anterodorsally to them. Suboesophageal ganglion also relatively small, filling space between posterior gula, posterior tentorial arms and tentorial bridge.

3.1.5. Glands

3.1.5.1. Mouthpart associated glands (Fig. 139). Shallowly invaginated multicellular glands, more or less semicircular in cross section, are present in the mandibles, maxillae and labium. Mandibular glands attached to dorsal and ventral mandibular walls, each forming a longitudinal stripe-like patch; ventral glands with thin and long cuticular opening pores with a more diffuse distribution (Figs. 8, 38; ‘glop’); dorsal pores wide and shallow, with a linear arrangement (Fig. 37). Maxillary

gland small, uniporous, opening on lacinia (Fig. 139D). Labial gland positioned inside lateral folds of mentum (Fig. 139E), opening dorsally on anterior edges of folds (Fig. 53). Tubular glands absent.

3.1.5.2. Endocrine glands. Corpora cardiaca and corpora allata placed ventrally and posteriorly to cerebrum between mandibular adductor (M11), pharynx and posterior tentorium or suboesophageal ganglion respectively. Corpora cardiaca relatively long and thin; connected with cerebrum by long nervi corporis cardiaci (I & II) which are fused with each other just before leaving the brain. Corpora cardiaca ventrally broadly connected with corpora allata. Corpora allata compact, of ovoid shape.

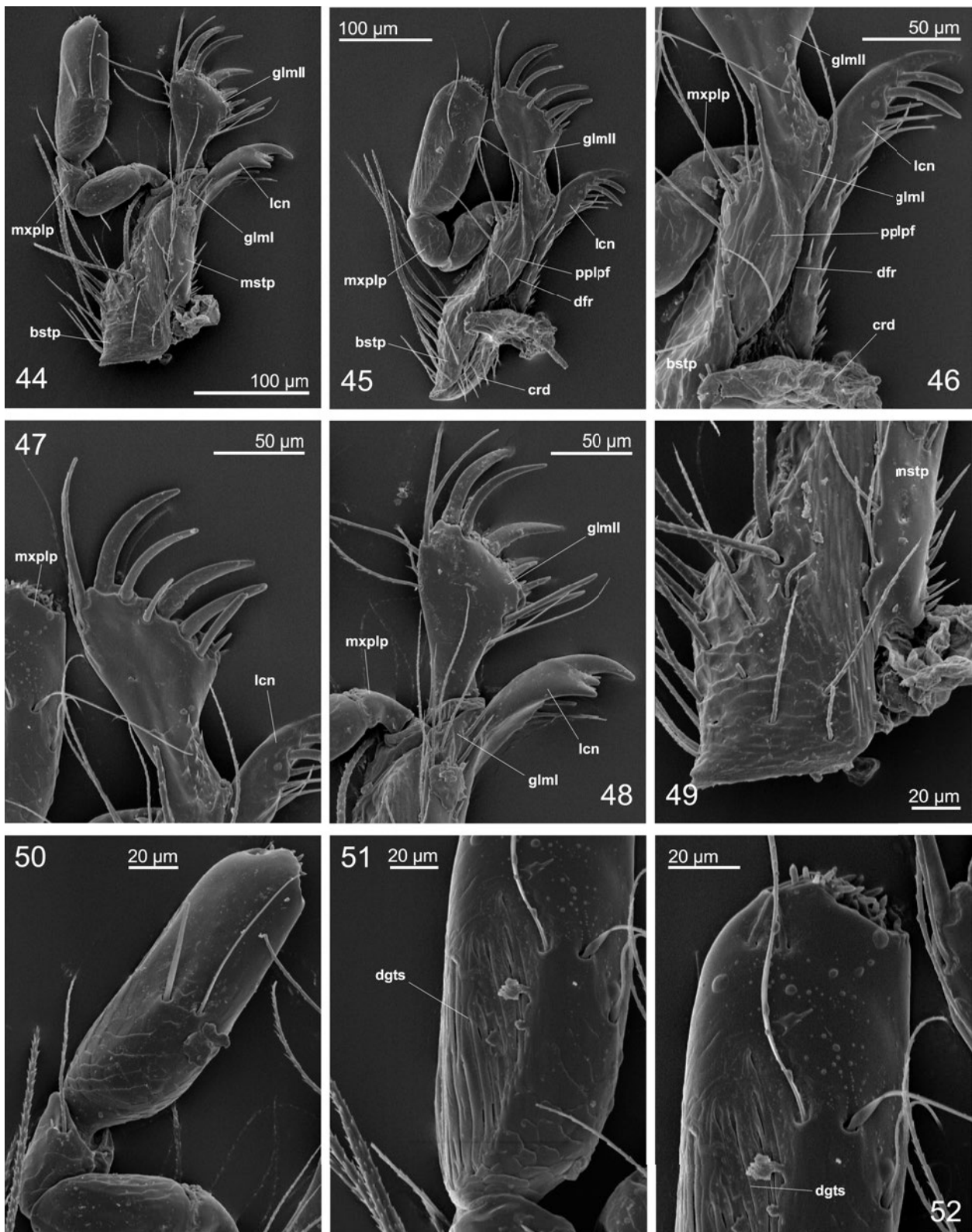
3.1.6. Musculature

3.1.6.1. Antennae. M1 – M. tentorioscapalis anterior (‘0an1’ after WIPFLER et al. 2011; see Table 1), Origin (= ‘O’): ventrally on anterior tentorial arm, ventral of origin of M2, Insertion (= ‘I’): medially on base of scapus; M2 – M. tentorioscapalis posterior (0an2), antagonist of M1, O: ventrally on anterior tentorial arm, dorsad of M1, I: laterally on scapal base; M4 – M. tentorioscapalis medialis (0an4) (Figs. 1, 135), very long muscle, antagonist of M1 and M2, O: broadly on posterior frons in front of cerebrum, laterad of origin of M9, I: with long tendon ventrally on scapal base; M5/M6 – Mm. scapopedicellares lateralis/medialis (0an6/0an7), O: internal wall of distal quarter of scapus, very small and short (sensory nerve bundle very strongly developed), I: basal pedicellar condyle.

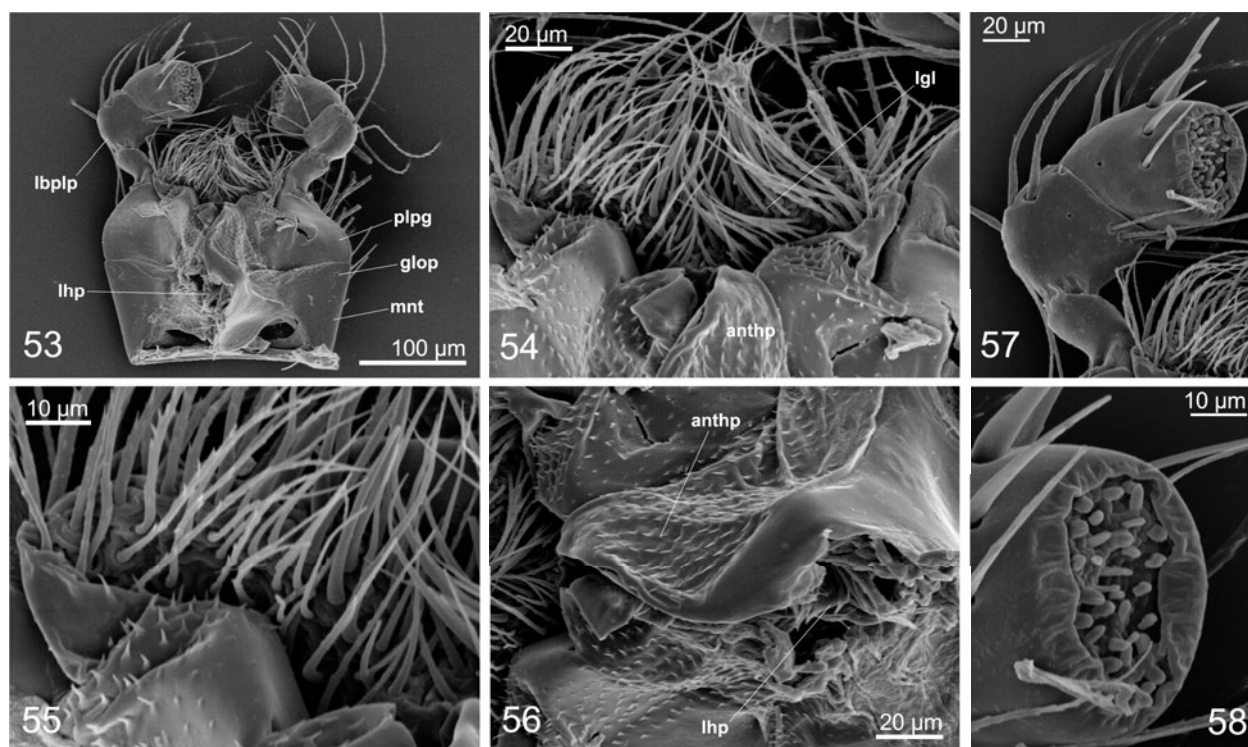
A compressor muscle of the antennal heart (M. frontofrontalis, 0ah6; WIPFLER et al. 2011) (see also PASS 1980; PASS 2000) is present but very weakly developed (Fig. 1; ‘antcm’). It is thin, flat and extending in a drapery-like manner between epistomal groove, mesal part of anterior tentorial arm and lateral frontal margin near base of epicanthus.

3.1.6.2. Labrum. M7 – M. labroepipharyngalis (0lb5) (Fig. 135), levator of epipharynx, bundles closely adjacent, diverging towards insertion area, posteriorly directed, O: broadly on posterodorsal wall of labrum, I: lateral wall of anterior epipharyngeal process; M9 – M. frontoepipharyngalis (0lb2) (Figs. 1, 34, 135), retractor or depressor of labrum, O: posterior frons in front of cerebrum, between M41 and M4, I: with long tendon on labral tormae.

3.1.6.3. Mandibles. M11 – M. craniomandibularis internus (0md1) (Figs. 1, 135), adductor, O: dorsolateral head capsule between compound eyes and occiput (M11 pars verticalis) and ventrolateral posterior head capsule between internal occipital carina and inner wall of antennal furrow (M11 pars genalis), bordered by cerebrum



Figs. 44–52. *Glaresis* sp., SEM, maxilla; **44:** right maxilla, ventral view; **45:** left maxilla, dorsal view; **46:** maxillary body with dorsal longitudinal furrow, dorsal view; **47:** galeomere II, dorsal view; **48:** galea and lacinia, ventral view; **49:** basistipes; **50:** maxillary palp; **51:** field of digitiform sensilla on distal maxillary palpomere; **52:** apex of distal maxillary palpomere. bstp – basistipes, crd – cardo, dfr – dorsal furrow of maxilla, dgts – digitiform sensilla, glml/II – galeomere I/II, lcn – lacinia, mstp – mediostipes, mxplp – maxillary palp, pplpf – pseudopalpifer.



Figs. 53–58. *Glaresis* sp., SEM, labium and hypopharynx; **53:** dorsal view; **54:** ligula; **55:** left ligular lobe; **56:** hypopharynx; **57:** labial palp; **58:** apex of distal labial palpomere; anthp – anterior part of hypopharynx, glop – glandular pores, lbplp – labial palp, lgl – ligular lobe, lhp – longitudinal hypopharyngeal process & posterior part of hypopharynx, mnt – mentum, plpg – palpiger.

dorsally and by antennal nerve anteriorly, I: with strong plate-like adductor tendon on mandibular process posterior of molar; M12 – *M. craniomandibularis externus* (0md3), abductor of mandible, O: posterolateral head capsule between pars genalis and pars verticalis of M11, bordered by cerebrum dorsally and by optic nerve anteriorly, laterally bordered by inner wall ('oculata', circumocular ridge) of compound eyes, I: on lateral mandibular base by means of a long and thin tendon.

3.1.6.4. Maxillae. M15 – *M. craniocardinalis externus* (0mx1) (Figs. 9, 137), promotor of the maxilla, long and round in cross section, O: ventrolaterally on posterior head capsule, between M11 pars genalis and gular carinae, I: with long tendon on laterally directed process of cardo; M17 – *M. tentoriocardinalis* (0mx3) (Figs. 9, 137), promotor of the maxilla, relatively large, posteriorly flattened, O: entire lateral surface of posterior tentorial arms, I: median process of cardo; M18 – *M. tentoriostipitalis* (0mx4) (Figs. 135, 137), adductor of stipes, O: mesal and anterior surface of posterior tentorial arms and ventral laminatentorium, mesad of M17, laterad of suboesophageal ganglion, I: with short tendon, broadly on stipital base; M19 – *M. craniolacinialis* (0mx2): absent; M20 – *M. stipitolacinialis* (0mx6) (Figs. 137, 139), adductor of lacinia, extending diagonally along invaginated semimembranous dorsal part of maxillary body, O: lateral base of basistipes, I: base of lacinia; M21 – *M. stipitogalealis* (0mx7) (Figs. 137, 139), extending longi-

tudinally along basistipes, O: base of basistipes, mediad of origin of M20, I: ventral wall of galea; M23 – *M. stipitopalpalis internus* (0mx10) (Figs. 137, 139), extending through maxillary body oblique in anterolaterad direction, crossing the course of M20 ventrally, O: base of mediostipes, mesad of M21, I: distal half of the dorsal median edge of pseudopalpifer (this muscle, as well as the following ones, was misinterpreted by many authors [e.g. ANTON & BEUTEL 2004, 'Mx3'; DRESSLER & BEUTEL 2010, 'M20'] due to the interpretation of the pseudopalpifer as 'true palpifer'; for a more detailed discussion of this issue, see section 4.5.); M24 – *M. palpopalpalis maxillae primus* (0mx12) (Figs. 137, 139), extending longitudinally through pseudopalpifer, O: base of pseudopalpifer, dorsad of insertion of M20, I: base of functional palpomere I; M26/M27 – *Mm. palpopalpalis tertius/quartus* (0mx14/0mx15), O: lateral wall of (functional) palpomere II or III, respectively, I: basal margin of (functional) palpomere III or IV, respectively.

3.1.6.5. Labium. M28 – *M. submentopraementalis* (0la8) (Figs. 135, 137, 139), seemingly unpaired retractor of prementum, O: medially on nearly entire length of mentum, I: ventrally on base of ligular lobes; M29 – *M. tentoriopraementalis inferior* (0la5) (Figs. 135, 137, 139), paired muscle, O: paramedially on anterior submentum, I: posterior surface of mesally directed process of posterolateral wall of palpiger (this process also bears the areas of origin of muscles of the ligula and palpus: M31/

33/34, see below); M30 – *M. tentoriopraementalis superior*: absent (see below); M33 – *M. praementopalpalis internus* (0la13) (Figs. 137, 139), O: anterior surface of mesally directed process of posterior lateral wall of palpiger, ventrad and mediad of origin of 34, I: inner basal margin of palpomere I; M34 – *M. praementopalpalis externus* (0la14) (Figs. 137, 139), ca 2 times as large as M33, consists of two bundles, O: anteriorly on palpiger process, dorsal and ventral subunit separated by a sclerotized bar connecting the palpiger process with lateral wall of labium (Figs. 139D,E), I: lateral margin of palpomere I; M35/36 – *Mm. palpopalpales primus/secundus* (0la16/0la17): not identified, possibly absent.

3.1.6.6. Hypopharynx. M41 – *M. frontohypopharyngalis* (0hy1) ('retractor anguli oris'; SNODGRASS 1935) (Figs. 1, 135), levator of hypopharynx and mouth angles, moderately large, O: frons, posterolaterad of M43, mesad of M9, both muscle bundles not adjacent in midline, separated relatively far from another, I: short strong tendon attached on angles of anatomical mouth and connected with hypopharynx via long and thin suspensorial sclerites (see above); M42 – *M. tentorihypopharyngalis* (0hy3 – *M. craniohypopharyngealis*) (Figs. 135, 137, 139), seemingly unpaired, O: medially on submentum, posterad of M29, I: posteriorly on a long rod-like sclerite situated between level of anterior longitudinal hypopharyngeal process and anteromedian border of ligula (in literature on Coleoptera this muscle regularly has been described as M30 [*M. tentoriopraementalis superior*], e.g. ANTON & BEUTEL 2004, DRESSLER & BEUTEL 2010, MEDVEDEV 1960, etc.; however, after v. KÉLER 1963 and WIPFLER et al. 2011 M30 inserts between paraglossae and labial palps, which is not the case here, as Coleoptera lack paraglossae at the one hand and on the other the debatable muscle is inserting median between the border of prementum and hypopharynx instead, thus lets suggest a homologization with M42 or 0hy3, respectively).

3.1.6.7. Digestive tract. M43/44 – *Mm. clypeopalatalis/clypeobuccalis* (0ci1/0bu1) (Figs. 1, 34, 135), several bundles, short anteriorly, increasing in length posteriorly, converging towards points of insertion, O: entire length of clypeus, mesad of M9, I: paramedially on dorsal wall of posterior epipharynx (cibarium); M45 – *M. frontobuccalis anterior* (0bu2) (Figs. 1, 135), long and thin, O: anterior frons, directly posterad of M44, slightly shifted mesally, posteriorly directed, I: dorsally on anterior pharynx, posterior to insertion of M41, laterad of ganglion frontale; M46 – *M. frontobuccalis posterior* (0bu3) (Figs. 1, 135), two or three thin bundles, converging towards insertion, O: frons, between origin of M41 and M9 and behind origin of M41, I: dorsolateral folds of pharynx, anterior to cerebrum; M48 – *M. tentoriobuccalis anterior* (0bu5) (Figs. 135, 137), unpaired muscle, moving between tritocerebral commissure and suboesophageal ganglion, O: anteromedially on tentorial

bridge, I: medially on ventral pharynx, in level of insertion of M41; M50 – *M. tentoriobuccalis posterior* (0bu6) (Figs. 135, 137), O: dorsal surface of tentorial bridge, laterad of M48, I: ventrolaterally on pharynx; M52 – *M. tentoriopharyngalis* (0ph2) (Figs. 135, 137), pair of small muscles, O: dorsal surface of posterior tentorial arms, posterior to origin of M50, extending caudad, I: ventrolaterally on pharynx, near foramen occipitale; M67 – *M. transversalis buccae* (0hy9) (Fig. 135), several transverse cibarial muscle bundles; M68 – *M. anularis stomodaei* (0st1), pharyngeal ring musculature, posterior to insertion of M41; M69 – *M. longitudinalis stomodaei* (0st2), layer of longitudinal muscles, covered by M68.

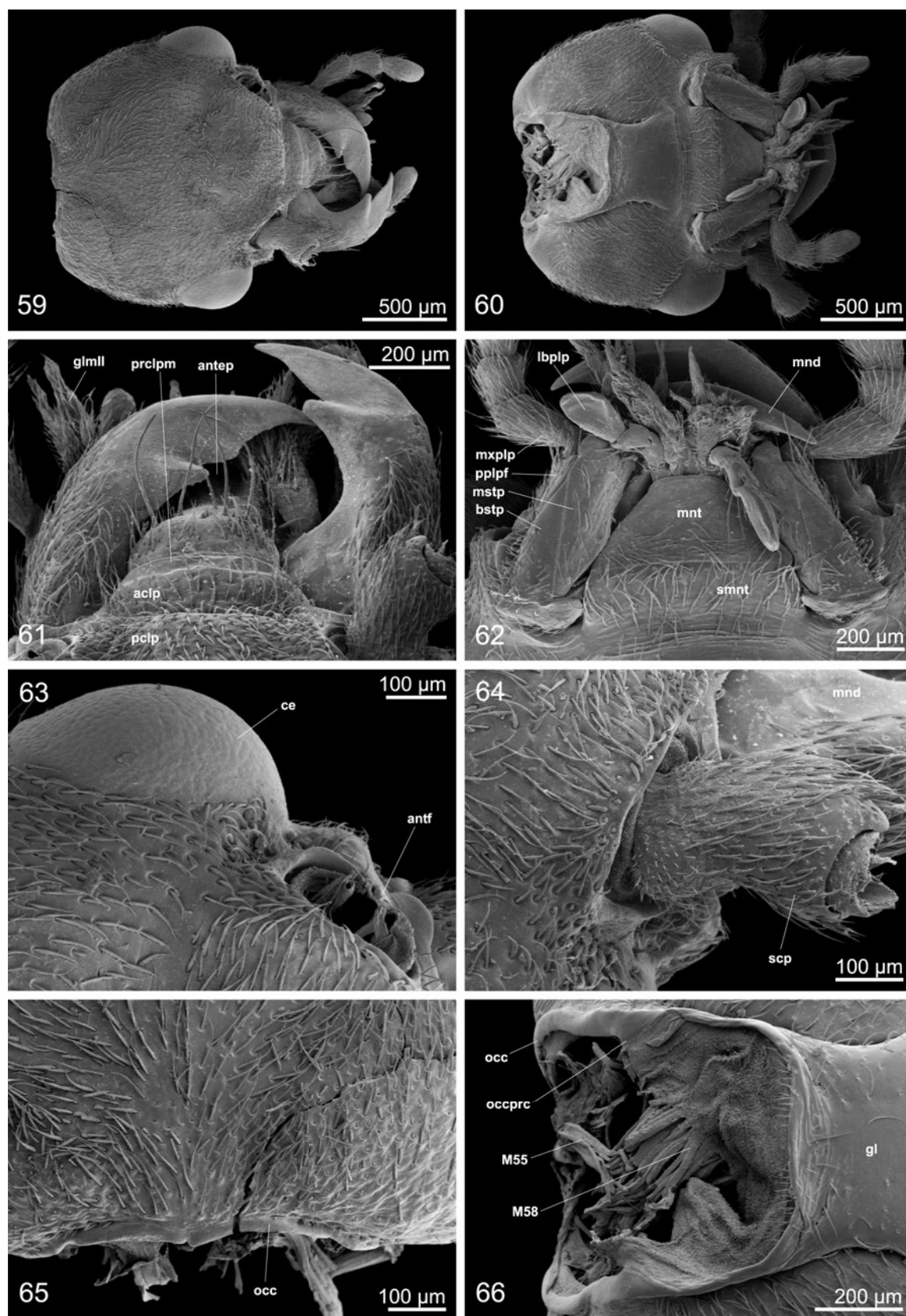
3.1.6.8. Head capsule. M55 – *M. praephragmapostoccipitalis* (Idlm1 – *M. prophragma-occipitalis* sensu FRIEDRICH & BEUTEL 2008a), O: prothorax; I: dorsally, on median endocarina forming a projection protruding out of foramen occipitale (Figs. 1, 2; 'pM55'); M58 – *M. profurcatentorialis* (IvIm3 – *M. profurcata-tentorialis* sensu FRIEDRICH & BEUTEL 2008a), O: prothorax, I: caudal surface of posterior tentorial arms, below origin of M52 (Fig. 137).

An additional muscle ('Mx₄') not listed by v. KÉLER (1963) originates on tentorial bridge, laterad of M50, and inserts on occipital projection of median endocarina between insertion area of both bundles of M55 (Figs. 1, 135, 137). Mx₄ is extremely fine and long and processes along lateral sides of pharynx and dorsal aorta and closely adjacent to corpora cardiaca and allata, respectively. Obviously the muscle is homologous with *M. tentoriofrontalis anterior* (0te2) described by WIPFLER et al. (2011) (see discussion).

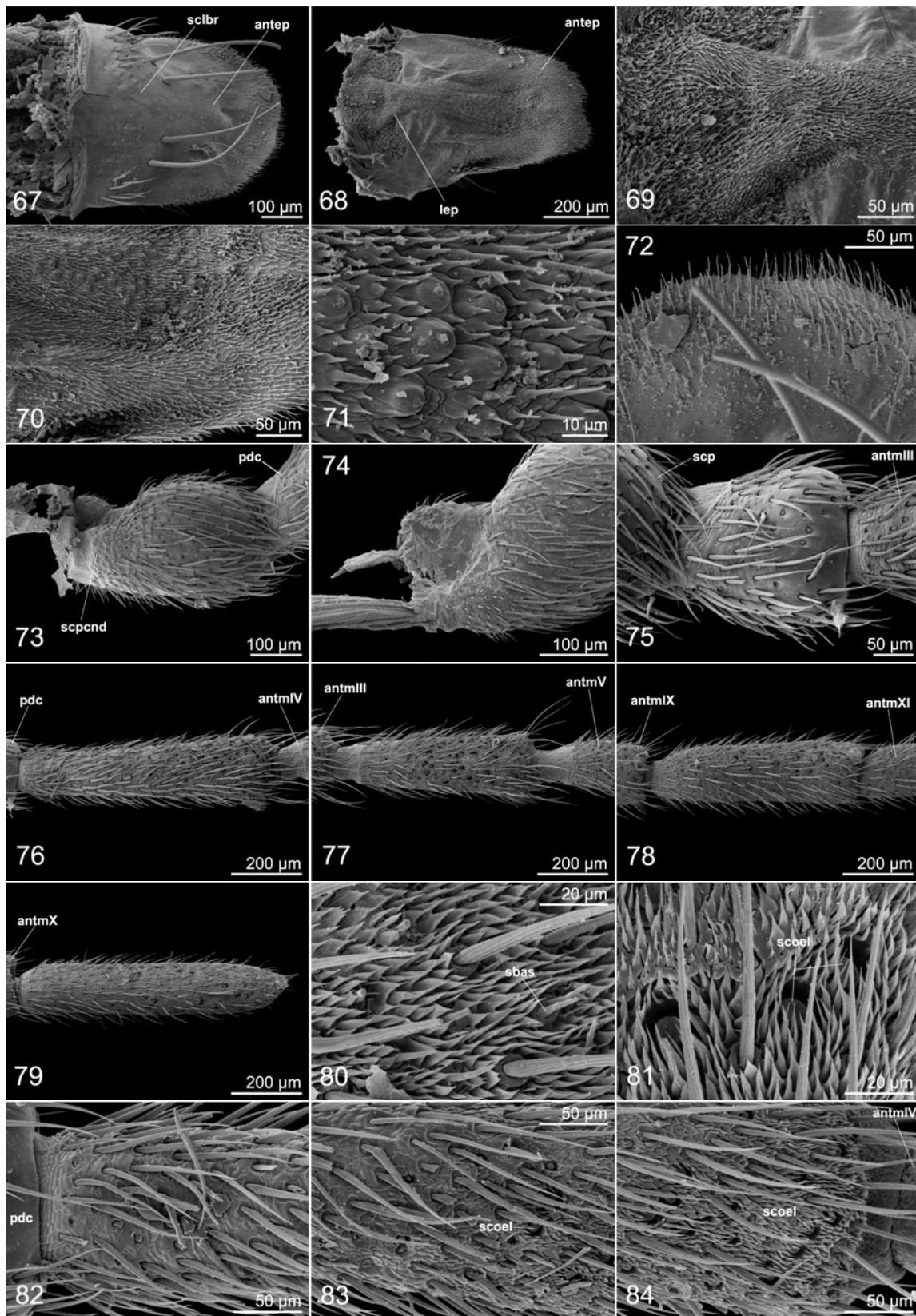
3.2. *Dascillus cervinus*

3.2.1. Head capsule

3.2.1.1. External structures (Figs. 4–6, 59–66). Head prognathous, slightly inclined in resting position. Approximately as long as wide in dorsal view; head length of examined specimens ~1.5–1.8 mm; width ~1.7–2.1 mm including compound eyes and ~1.5–1.9 mm without them; dorsal and ventral surface subparallel in lateral view except for clypeal region (see below); height ~0.85–1 mm. Cuticle smooth, rather weakly sclerotized; average thickness ca 30 µm, with the endo- and exocuticle about equally strong. Coloration grey or brown to black. Surface of head capsule except for gula and lateral occipital region regularly covered with short, recumbent pubescence (Figs. 59, 60, 63–65). External head capsule without recognizable sutures or demarcation lines; limits of clypeus, frons, vertex and occiput only defined by muscle origins. Clypeus divided in ante- and postclypeus by transverse line (Figs. 4, 6, 61; 'aclp',



Figs. 59–66. *Dascillus cervinus*, SEM, head capsule (antennae partly removed); **59:** dorsal view; **60:** ventral view; **61:** clypeal region, mouthparts, dorsal view; **62:** mouthparts, ventral view; **63:** left compound eye and antennal insertion, dorsal view; **64:** right antennal insertion and scapus, dorsal view; **65:** occipital area, dorsal view; **66:** occipital area, ventral view. acip – anteclypeus, antep – inframandibular antepipharynx, antif – antennifer, bstp – basistipes, ce – compound eye, gl – gula, glmlI – galeomere II, lbplp – labial palp, M55/58 – musculature, mnd – mandible, mnt – mentum, mstp – mediostipes, mxplp – maxillary palp, occ – occiput, occprc – processus separating dorsal and ventral part of foramen occipitale, pclp – postclypeus, pplpf – pseudopalpifer, prclpm – preclypeal membrane, scp – scapus, smnt – submentum.



Figs. 67–84. *Dascillus cervinus*, SEM, labrum and antenna. 67–72: Labrum and epipharynx; 67: dorsal view; 68: ventral view; 69: longitudinal epipharyngeal process; 70: epipharynx, surface structure, ventral view; 71: field of epipharyngeal sensilla, detail from Fig. 70; 72: distal part of semimembranous antepipharynx, dorsal view. 73–84: Antenna; 73: scapus; 74: scapal condyle; 75: pedicellus; 76: antennomere III; 77: antennomere IV; 78: antennomere X; 79: antennomere XI; 80: setation, sensilla and surface structure of antennomere X; 81: same as in Fig. 80, showing another part of antennomere X; 82: proximal part of antennomere III; 83: median part of antennomere III; 84: distal part of antennomere III. antep – antepipharynx, antmIII–XI – antennomeres, lep – longitudinal epipharyngeal process, pdc – pedicellus, sbas – sensillum basiconicum, sclbr – sclerotized part of labrum, scoel – sensilla coeloconica, scp – scapus, scpcnd – scapal condyle.

‘pclp’); postclypeus strongly declining anteriorly, thus level of anteclypeus very distinctly below level of remaining dorsal surface of head capsule; anteclypeus strip-like, ca four times as wide as long, with its anterior edge very slightly convex; labrum attached to it by externally exposed membrane (Fig. 61); anteclypeal region between mandibular articulation and antennal sockets strongly constricted and glabrous, indicating origin of anterior tentorial arms. Head capsule on frontopostclypeal region with shallow but distinct median bulge between compound eyes and antennal sockets, bearing the origin of clypeal and frontal muscles (Figs. 4, 59, 136); clypeal musculature (M43/44) originating on anterior half of bulge (Figs. 4, 136); origin of frontal muscles (M41/45/46; M9) restricted to posterior half (Figs. 4, 136). Area posterior to antennal sockets and between anterior part of compound eyes identified as frontal region by attachment of compressor muscle of antennal heart (Fig. 4) (see PASS 1980, 2000). Muscle of vertex (M51) originating on posteriormost fourth of head capsule (Figs. 4, 136); vertex not separated from other head regions, probably reaching from posterior part of compound eyes to postoccipital region. Dorsal wall of head capsule posterior to compound eyes ca half as long as entire head; sides slightly rounded and somewhat converging posteriorly. Occipital region not defined. Postoccipital ridge glabrous, narrow, bordering dorsal and lateral sides of foramen occipitale, ventrally continuous with gular ridges (Figs. 5, 66; see below). Dorsal postocciput medially extended as a tongue-shaped process, which is bent rostrad internally and serves as attachment area for flexor muscle of head capsule (M55) (Figs. 5, 136; ‘pM55’). Posterior genal region extensive, evenly rounded, not separated from other head regions; surface structure and pubescence like on dorsal head region; anterior genal region slightly concave, forming a slender strip between anteroventral compound eyes and articulation points of maxillae and mandibles; anteriorly continuous with anteclypeus. Ventral antennal furrow absent. Foramen occipitale large, incompletely divided into dorsal and ventral part by a pair of mesally directed processes (Figs. 5, 66; ‘occprc’) at transition area of gular ridges and postoccipital ridge; dorsal part of foramen vertically extending over entire height of head capsule, ca one third as wide as posterior head capsule; ventral part of foramen oriented more horizontally, laterally bordered by gular ridges, strongly extended anteriorly, thus resulting in a deep posterior emargination of the gula; space within this emargination completely covered by ventral cervical membrane (Fig. 66). Lower part of foramen serving for passage of connectives between suboesophageal and prothoracic ganglia and the ventral flexor muscle of head (M58) (Fig. 136). Gula deeply emarginated posteriorly (see above) but well developed, approximately rectangular, slightly broader than long; surface distinctly convex (Fig. 60), almost completely glabrous; anterior edge nearly straight; lateral margins concave. Gular ridges externally visible as deep fur-

rows; in anterior half forming lateral border of gula, in posterior half enclosing lower part of occipital foramen (see above). Compound eyes well developed, distinctly protruding, positioned laterally on head capsule (Figs. 59, 60, 63); outline oval in lateral view, more shallowly rounded posteriorly than anteriorly (Fig. 6); ventral margin bluntly angulated; angles forming lateral border of transverse submental depression (see below); ommatidia of exocone type (Fig. 173); diameter of ommatida ~13 µm; length ~90 µm; length of exocone ~55 µm (see also CAVENEY 1986). Antennal sockets positioned dorsally on head capsule, anteromesally adjacent with compound eyes; margin of sockets slightly raised; opening oblique, with anterolaterally and dorsally orientation (Figs. 4, 6, 59, 64); anterolateral edge with prominent antennifer, serving as pivot for scapus (Figs. 4, 6; ‘antf’).

3.2.1.2. Internal skeletal structures (Figs. 6, 136, 138).

Gular ridges well developed (see above), long, reaching from ventral third of foramen occipitale to submentum; anterior part bordering gula (see above) is dorsally continuous with posterior tentorial arms. Posterior arms narrowing and converging dorsad, connected with each other by a horizontal broad and plate-like tentorial bridge. Rod-like longitudinal arms connected with anterior corners of tentorial bridge, subparallel and horizontal, relatively close to each other; anteriorly continuous with anteriorly directed finger-shaped processes forming a nearly or completely fused laminatentorium, with the processes of either side placed above each other (Fig. 138; ‘lt’). Anterior and dorsal tentorial arms formed by division of longitudinal arms; area between them forming extensive dorsolaterally extending attachment area for antennal muscles. Distal part of dorsal arms narrowed, thin, strut-like; connected with head capsule by strong ligament; attachment areas visible on external surface as small pits between posterior antennal sockets and frontoclypeal bulge (Fig. 4; ‘idta’). Anterior arms narrowing towards origin; anterior pits not visible as groove or concavity; area of origin between compound eyes and mandibular articulation, separating anteclypeus and anterior genae.

3.2.2. Appendages

3.2.2.1. Labrum (Figs. 11, 61, 67, 68, 72, 136, 140).

Well developed, movably connected to head capsule by distinct preclypeal membrane (Fig. 61; ‘prelpm’). Resting position of anterior part of labrum (‘antepipharynx’; obviously an epipharyngeal element, see below and 3.2.3.1. for more detailed description) below mandibles (Figs. 61, 136); dorsally bordered by intersecting mandibles; adjacent to dorsal surface of maxillae and prementum, respectively. Shape of entire labrum approximately rectangular, ca 1.4 times as long as broad, subdivided into semimembranous anterior epipharyngeal part (see 3.2.3.1.) and sclerotized posterior true labral region. Posterior re-



gion triangular, laterally and anteriorly enclosed by antepipharyngeal part; dorsal surface smooth, glabrous, with large patch of longer setae on each side (Figs. 11, 67); anterior edge bordering with antepipharynx with transverse row of very long setae projecting above mandibles (Figs. 61, 136). Tormae well developed as long, rod-like structures, attached to hind corners of labrum (Fig. 11); connected with suspensorial sclerite of hypopharynx (see below) by a long ligament on the level of the mouth angles, and thus indirectly also with *M. frontohypopharyngalis* (M41).

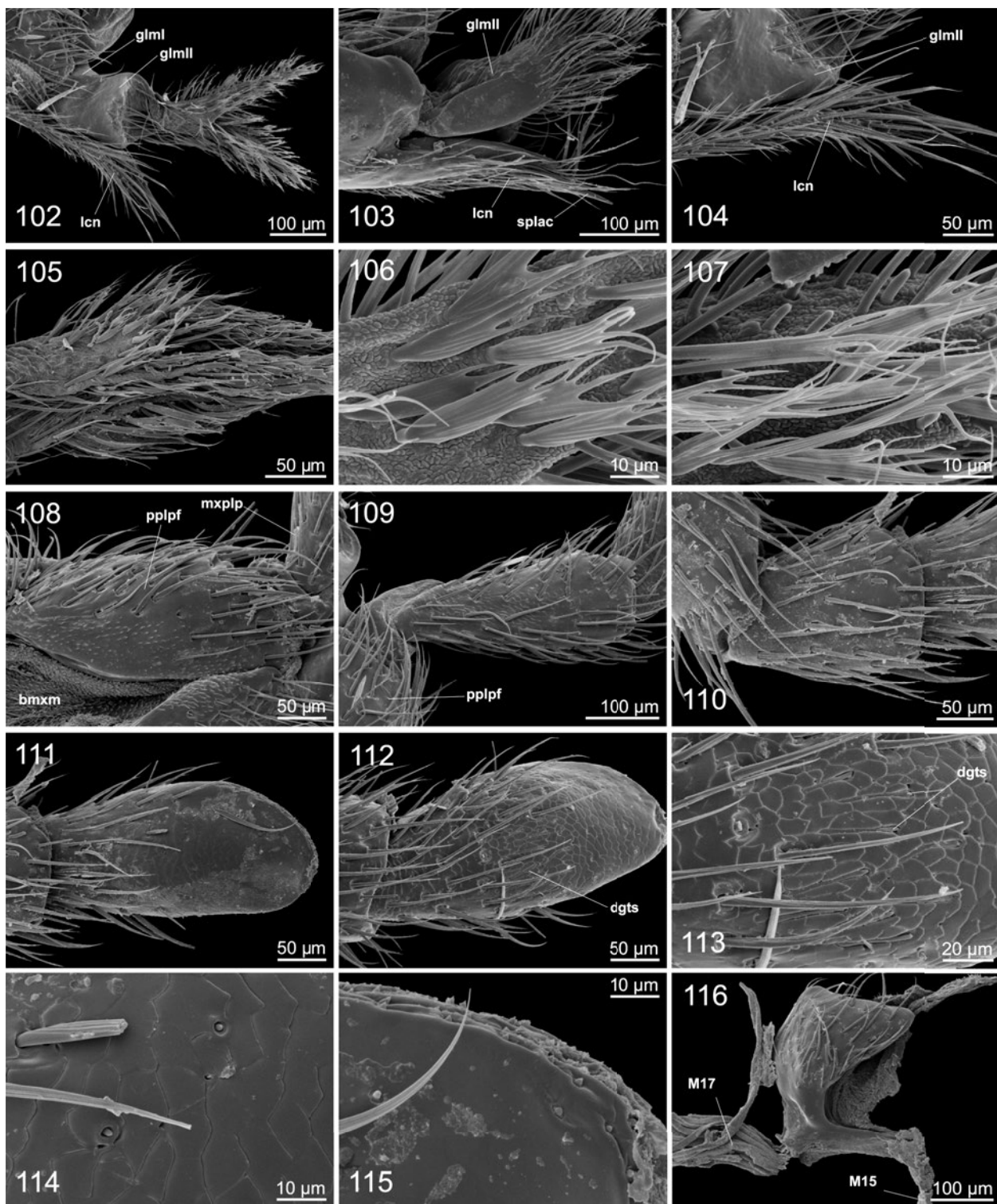
3.2.2.2. Antennae (Figs. 12, 73–84). 11-segmented, nearly filiform, very slightly serrate. Surface of scapus and pedicellus glabrous; flagellomeres with furrows on proximal parts (antennomeres III and IV) (Fig. 82), remaining surface densely covered with scale-like surface modifications (Figs. 80, 81, 84). All antennomeres densely and regularly set with long setae. Scapus relatively short, shorter than flagellomeres; without condyle slightly longer than broad, thickened (Fig. 73). Condyle only slightly distinct from scapus, with concave gap on anterior margin fitting with antennifer and forming antennal joint (Fig. 74). Remaining parts of scapal condyle rather flexible connected with antennal socket by well developed membranous area (Fig. 64). Setation on condyle short and spine-like. Pedicellus representing shortest antennal segment, slightly longer than wide, its sides diverging distally (Fig. 75); inserted apically on scapus. All flagellar segments of very similar shape and armature, with the exception of antennomere III, which represents a transition state between scapus/pedicellus and flagellum with respect to surface structure (see above) and sensillar equipment (see below) (Fig. 76). Flagellomeres elongated, each nearly four times as long as wide, with subparallel sides; proximal articulation area constricted and without setae or scales (Figs. 77, 78); distal articulation area not exactly concentric on distal surface, thus resulting in an asymmetrical shape and a slightly serrate appearance of the flagellum; aside from dense and long setation, surface densely set with conspicuous sensilla coeloconica and more scattered sensilla basiconica (Figs. 80, 81, 84). Distal antennomere of similar shape as preceding segments but slightly longer; ca five times as long as broad; apex rounded (Fig. 79).

3.2.2.3. Mandibles (Figs. 13, 59, 61, 85–88, 93–95, 136, 140). Mandibles well developed, elongated, ca 2

times as long as broad, nearly symmetrical; projecting far beyond anterior margin of head capsule; intersecting in resting position. Lateral edge shallowly rounded on proximal 2/3 of mandibular length, forming approximately a quarter-circle in distal third. Lateral surface relatively wide proximally, narrowing distally; ventrally delimited from ventral mandibular surface by an edge; dorsally continuous with dorsal mandibular surface without recognizable border. Lateral mandibular surface densely set with moderately long setae; rest of mandibular surface smooth, without setation. Dorsal and ventral surface of mandibular corpus without distinct ridges; ventral surface with a longitudinally arranged series of glandular pores and a spot of microtrichia laterad of molar part (Figs. 94, 95); proximal ventral surface of mandibular corpus with some rows of transverse folds (Figs. 94, 95); dorsal surface of mandibular corpus small, occupying not more than half length of mandible. Apical part very large, about half as long as entire mandible; bent inwards; apex directed oblique to perpendicular to longitudinal body axis; ventral surface of apical part with concavity fitting with and covering antepipharynx (Figs. 85, 87). Distinct retinaculum present near mid-length of incisory edge, followed by sharp incision. Molar parts of mandibles small, not distinctly set off from mandibular corpus, symmetric, without grinding surface; the two molar parts broadly separated from each other by longitudinal epipharyngeal process and hypopharynx (Fig. 140B); mesally directed surfaces as well as adjacent dorsal area densely set with microtrichia. Mesal mandibular edge with small, ventrally directed semi-membranous lobe, occupying ca one sixth of mandibular length, densely set with microtrichia (Fig. 94). Acetabular joint on external edge of mandibular base laterally directed, forming hemispherical concavity (Fig. 93). Ventral condyle also placed on external angle of mandibular base; slightly elongated, distally hemispherical; with oblique orientation, posterolaterally and ventrally directed (Fig. 95).

3.2.2.4. Maxillae (Figs. 14, 62, 96–116, 140). Largely exposed, mediostipes and lacinia not covered by postlabium (Fig. 62). Connected with the head capsule by the cardo, and with the other mouthparts by a large basimaxillary membrane with a surface densely covered with microtrichia (Fig. 101). Almost entire maxillary surface densely set with long setae. Cardo well developed and of complex shape (Fig. 116); broadly and mo-

← **Figs. 85–101.** SEM, mandibles and maxillae. **85–88:** *Dascillus cervinus*; **85:** right mandible, ventral view; **86:** left mandible, dorsal view; **87:** left mandible, ventral view; **88:** right mandible, dorsal view. **89–90:** *Drilus concolor*; **89:** right mandible, ventral view; **90:** left mandible, dorsal view. **91–92:** *Cantharis obscura*; **91:** left mandible, ventral view; **92:** right mandible, dorsal view. **93–101:** *Dascillus cervinus*; **93:** basal part of left mola with acetabulum and molar region; **94:** left mandible, molar region and semimembranous median lobe; **95:** mandibular condyle of right mandible; **96:** left maxilla, ventral view, maxillary palp removed; **97:** right maxilla, dorsal view; **98:** right maxilla, dorsolateral view; **99:** maxillary corpus of left maxilla, ventral view; **100:** proximal part of left maxilla, dorsal view; **101:** surface structure of basimaxillary membrane. act – acetabulum, bmxm – basimaxillary membrane, bstp – basistipes, crd – cardo, glmII – galeomere II, glop – gland opening, lcn – lacinia, M15–18 – musculature, mcnd – mandibular condyle, 'ml' – molar region, mlb – semimembranous median mandibular lobe, mstp – mediostipes, mxplp – maxillary palp, pplpf – pseudopalpifer, rtn – retinaculum.



Figs. 102–116. *Dascillus cervinus*, SEM, maxillae; **102:** galea and lacinia, ventral view; **103:** galea and lacinia, dorsal view; **104:** lacinia, ventral view; **105:** distal galea; **106:** scale-like setae and sensilla basiconica; **107:** scale-like setae and sensilla basiconica; **108:** pseudopalpifer, dorsal view; **109:** first and second maxillary palpomeres; **110:** third maxillary palpomere; **111:** fourth maxillary palpomere, ventral view; **112:** fourth maxillary palpomere, dorsal view; **113:** field of digitiform sensilla on fourth maxillary palpomere; **114:** surface structure, setae and sensilla on ventral side of fourth maxillary palpomere; **115:** distal edge of fourth maxillary palpomere, ventral view; **116:** cardio of left maxilla. dgts – digitiform sensilla, glml/II – galeomere I/II, lcn – lacinia, M15/17 – musculature, mxplp – maxillary palp, pplpf – pseudopalpifer, splac – distal spine of lacinia.

vably connected to basistipes; flexed with respect to maxillary body (Fig. 100); exposed part triangular; internal part with two strong processes serving as muscle

attachment areas; knob-shaped mesal process serves as insertion area for tentoriocardinal muscle (M17); lateral process strongly elongated, rod-shaped, serving as inser-

tion area of craniocardinal muscle (M15) (Figs. 14, 100). Basistipes elongated, triangular, distally glabrous. Mediotipes large and of trapezoid shape; separated from basistipes by a ridge; anterolateral corner adjacent to pseudopalpifer. Lacinia moderately sclerotized, long and slender; proximal half fused with mediotipes, distal half free; apex sharply rounded, with a long spine which often is absent (Figs. 102–104; ‘splac’); mesal edge with long and irregularly arranged setae. Galea two-segmented, largely unsclerotized (Figs. 14, 102); galeomere I represented by small, glabrous, ring-like sclerite closely attached to distal mediotipital edge; galeomere II elongated, projecting beyond lacinia; glabrous basal half cylinder-shaped; distal half semimembranous, deeply bifurcated, densely set with long setae; setae broad, scale-like, with multiple thread-like apices (Figs. 105–107); mesal branch additionally with diffusely arranged sensilla basiconica (Fig. 107); lateral branch only with few sensilla placodea on its base. Pseudopalpifer (see also sections 3.1.2.4. and 4.5.) large, placed on dorsal side of maxilla, dorsad of basistipes, mediad adjacent to lacinia (Figs. 97, 98, 108). Palp 4-segmented, inserting apically on pseudopalpifer (Figs. 108–115); first (functional) palpomere small, ring-shaped, about as broad as long, with distal surface oblique and laterally directed; palpomere II elongated, distally widening, ca 2.5 times as long as broad; palpomere III shorter but somewhat broader than II, also widening distally, ca 1.5 times longer than broad; apical palpomere thin, axe-shaped, asymmetrical; inner outline rounded convexely, outer outline nearly straight; apical area oblique, mesally oriented, set with peg-shaped sensilla (Fig. 115); part of surface of palpomere IV scale-like, especially on dorsal side; glabrous in distal half, with few sensilla coeloconica (Fig. 114); dorsal side additionally with 8–10 digitiform sensilla (length $\sim 30 \pm 5 \mu\text{m}$) arranged in a more or less regular row near midline of lateral half of palpomere (Fig. 113).

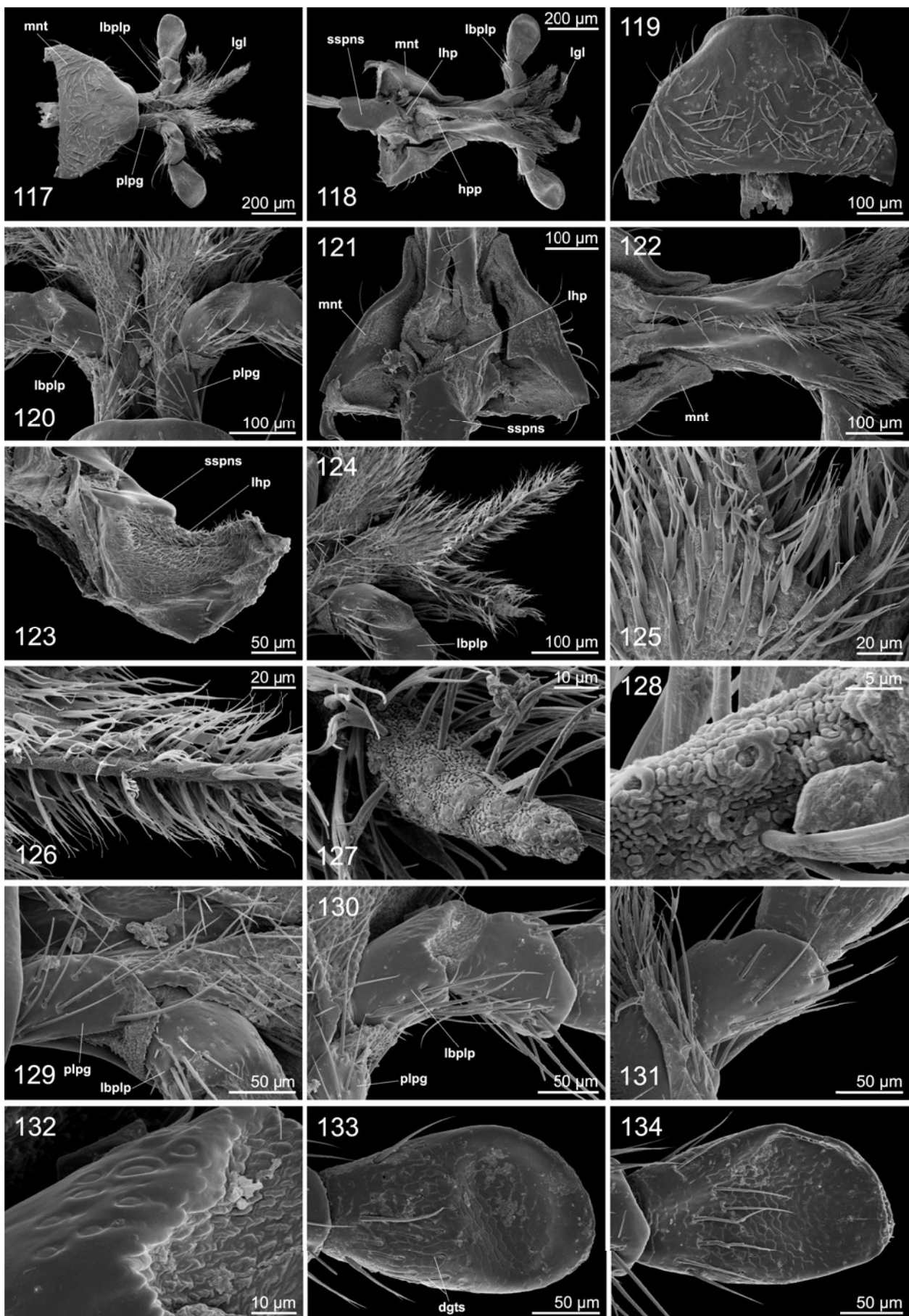
3.2.2.5. Labium (Figs. 15, 62, 117–134, 140). Submentum broad, rectangular, ca 2.5 times as broad as long; posteriorly with transverse depression (Fig. 62); anteriorly separated from mentum by a distinct suture; laterally bordered by maxillary grooves. Mentum plate-like, trapezoid, nearly 2 times as broad as long; lateral sides evenly converging anteriorly; anterior edge nearly straight, half as long as posterior edge (Fig. 117). Prementum loosely connected to mentum by internal membrane. Ligula divided medially, semimembranous; elongated, largely exposed; each ligular lobe deeply bifurcated (Figs. 117, 118, 124); with forked and scale-like setae and irregularly set with sensilla coeloconica (Figs. 125–128). Dorsal premental surface with pair of glabrous semimembranous lobes, their inner edges set with long microtrichia, posteriorly continuous with hypopharynx (Fig. 118). Internal dorsomedian and ventromedian premental strut-like sclerites serve as attachment device for musculature (M42 and M28 respectively) (Fig. 136).

Palpiger well developed, exposed, with sparse setation, placed at premental base; lateral wall posteriorly slightly bent inwards, forming small internal apodeme serving as attachment area for tentoriopremental (M29) and prementopalpal (M34) muscles (Fig. 138). Palp 3-segmented, apically inserting on palpiger; palpomeres I and II small, approximately as long as broad; lateral sides with setae; palpomere II with additional setae on inner side of proximal part; mesal side of palpomere I with some sensilla placodea (Fig. 132); apical palpomere larger than preceding segments together, thin, axe-shaped, more than 2 times as long as broad; apical edge oblique, mesally oriented, with peg-shaped sensilla (Fig. 134); surface structure of palpomere III scale-like; proximal area with some setae and with few sensilla coeloconica; dorsal side additionally with about ten digitiform sensilla (length $\sim 25 \mu\text{m}$), which are diffusely arranged near lateral base of palpomere (Fig. 133).

3.2.3. Digestive tract

3.2.3.1. Epipharynx (Figs. 11, 61, 68–71, 136). Semimembranous, extensive, strongly prolonged anteriorly; anterior part (= ‘antepipharynx’) surpassing anterior border of sclerotized labrum, placed between ventral surface of mandibles and dorsal surface of ventral mouthparts (see above) (Figs. 61, 136); dorsal antepipharyngeal surface laterally and distally with narrow stripes sparsely set with microtrichia; posteriorly smooth and glabrous, with a patch of few longer setae on each side. Ventral surface of epipharynx completely covered with anteriorly directed microtrichia (Fig. 70); length and density of microtrichia slightly varying from posterior to anterior (longer, less dense) and from midline to lateral regions (less dense), respectively; central region of ventral epipharyngeal surface with oval field with scarce vestiture of microtrichia and some papilla-shaped sensilla (Figs. 70, 71). Longitudinal epipharyngeal process present but not very distinct (Figs. 68, 69; ‘lep’); densely set with long microtrichia; anteriorly triangular in cross sections; posteriorly broad and flat; broadly facing hypopharynx and posterodorsal prementum; laterally enclosed by molar part of mandibles.

3.2.3.2. Hypopharynx (Figs. 15, 118, 121–123, 136, 138, 140). Inconspicuous, largely semimembranous, not distinctly separated from dorsal prementum (Fig. 121). Anteriorly folded, continuous with glabrous lobes of dorsal prementum without recognizable border (see above); surface covered with microtrichia; posterior hypopharyngeal process very short, triangular, densely covered with microtrichia; posteriorly bordered by glabrous hypopharyngo-suspensorial sclerite (Figs. 121, 123); internal hypopharyngeal sclerite weakly developed, present only in posteriormost part of hypopharynx, forming a compact sclerite with the prepharyngeal suspensorium (Figs. 136, 140A,B); posterior part tube-shaped, with



pair of strongly developed posterodorsally directed processes serving as attachment area for M41 (retractor of the mouth angle); anterior part of suspensorial sclerite more even and plate-like; at midlength with pair of ventrally directed strut-like internal processes serving as muscle attachment areas (Mx_1/Mx_2 , see below) (Figs. 136, 140A); anterior edge of hypopharyngo-suspensorial-sclerite rounded, bordering longitudinal hypopharyngeal process (Fig. 123). Hypopharynx over its entire length adjacent to longitudinal epipharyngeal process.

3.2.3.3. Prepharynx, pharynx and oesophagus (Fig. 136). Broad and long prepharyngeal tube formed by fusion of posterior part of epipharynx (cibarium) and posterior hypopharynx (hypopharyngo-suspensorial-sclerite); transverse musculature (M67) strongly developed. Pharynx roughly circular in cross section, with normally sized lumen.

3.2.4. Cerebrum and suboesophageal ganglion

Cerebrum (Fig. 136) of normal size, located shortly behind level of compound eyes; posteriorly bordered by M51, dorsally by vertex, ventrally by M11 pars verticalis and pharynx, and anteriorly by M46, dorsal tentorial arm and antennal musculature. Frontal connectives and tritocerebral commissure strongly developed, positioned in same transversal plane. Suboesophageal ganglion filling entire space between gula, posterior tentorial arms and tentorial bridge. Frontal ganglion well developed, placed above anatomical mouth between M44 and the paired bundles of M45.

3.2.5. Glands

3.2.5.1. Mouthpart associated glands. Small, shallowly invaginated multicellular glands more or less evenly distributed within mandibles, maxillae, labium and hypopharynx. Mandibular glands arranged as a longitudinal band on inner surface of ventral mandibular corpus (Figs. 94, 95). Tubular glands not observed.

3.2.5.2. Endocrine glands. Due to the insufficient preservation of the endocrine glands reliable statements on these structures are not possible at this point.

3.2.6. Musculature

3.2.6.1. Antennae. M1 – M. tentorioscapalis anterior ('0an1' after WIPFLER et al. 2011; see Table 1), O: ventrally on proximal third and on entire anterior side of anterior tentorial arm, I: ventrally on base of scapus; M2 – M. tentorioscapalis posterior (0an2), antagonist of M1, O: proximolateral surface of dorsal tentorial arms, dorsad of origin of M1, ventrad of origin of M4, I: anteriorly on scapal base; M4 – M. tentorioscapalis medialis (0an4), antagonist to M1 and M2, O: distal 2/3 of lateral surface of dorsal tentorial arms, I: posterodorsal scapal base; M5/M6 – Mm. scapopedicellares lateralis/medialis (0an6/0an7), O: proximally on dorsal and ventral wall of scapus, I: basal pedicellar condyle.

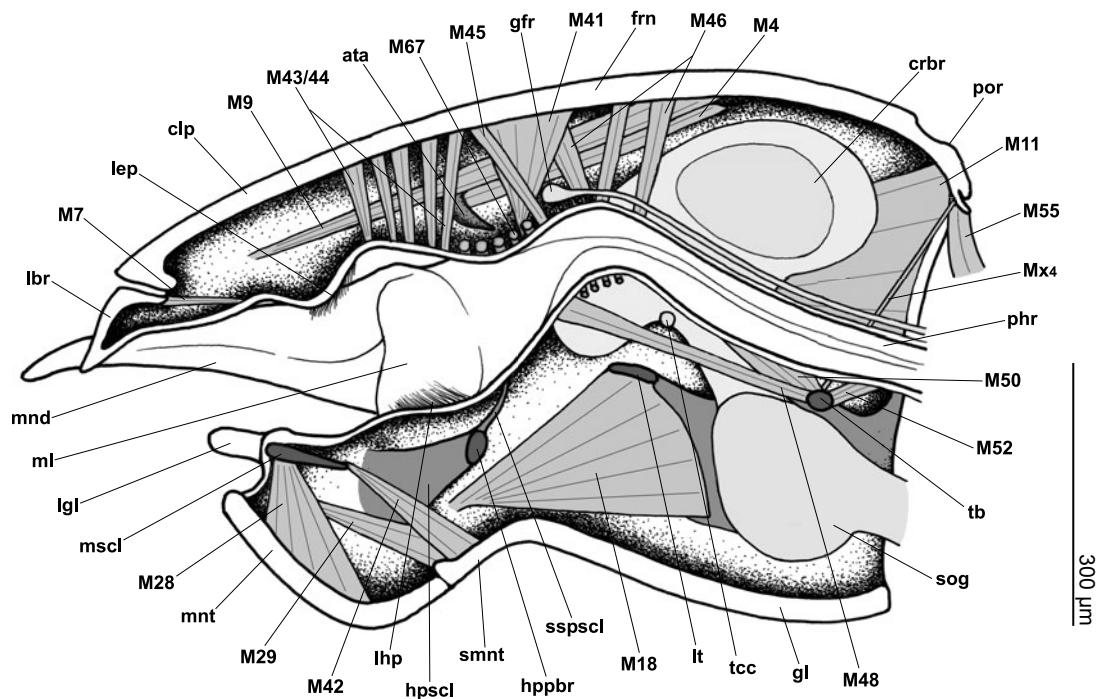
A well developed slender and elongated compressor muscle of the antennal heart (M. frontofrontalis, 0ah6; WIPFLER et al. 2011) (see also PASS 1980, 2000) is present immediately behind the antennal socket (Fig. 4; 'antcm'). Both ends insert on the frons, the mesal one immediately laterad of the origin of the frontoepipharyngeal (M9) and frontohypopharyngeal (M41) muscles, the lateral one near the anterodorsal border of the compound eye.

3.2.6.2. Labrum. M7 – M. labroepipharyngalis (0lb5) (Fig. 136), epipharyngeal levator, very strong developed, filling entire space between labrum and epipharynx, O: posterior part of dorsal wall of labrum, I: paramedially on epipharynx and longitudinal epipharyngeal process; M9 – M. frontoepipharyngalis (0lb2) (Figs. 4, 11, 136), retractor, O: frons, anterad of origin of M41, mesad of antennal heart and antennal musculature, laterad of M45, I: tormae, near posterior corners of labrum.

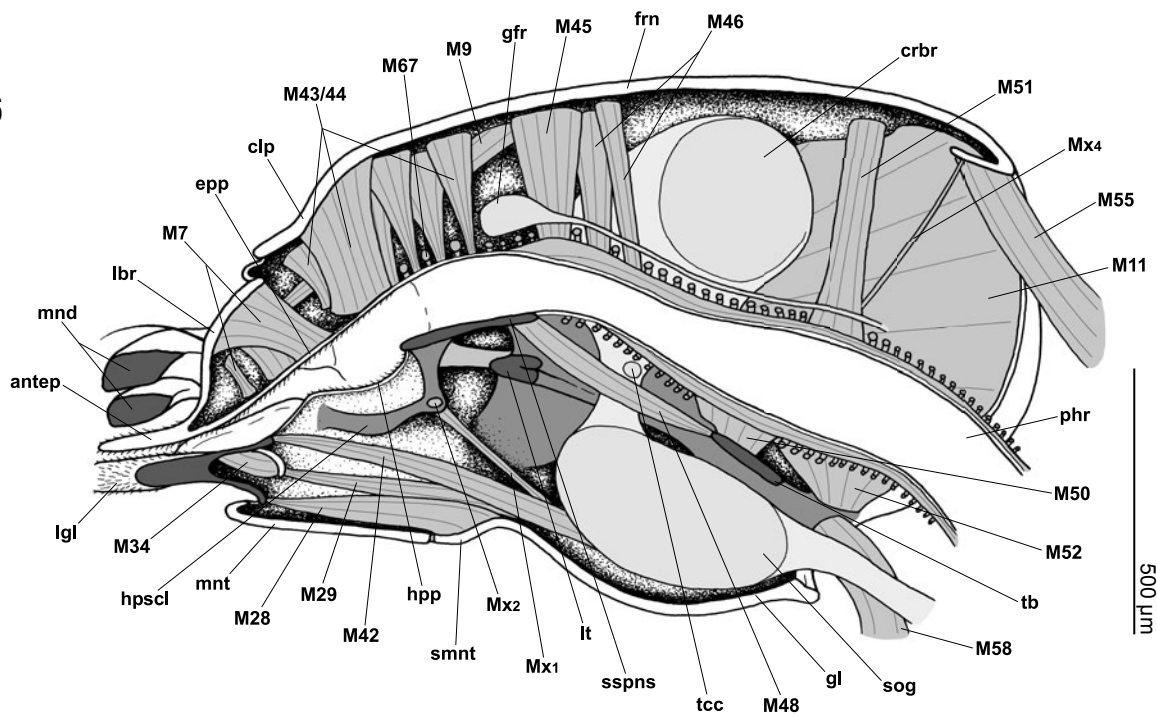
3.2.6.3. Mandibles. M11 – M. craniomandibularis internus (0md1) (Figs. 4, 136), adductor, largest muscle in the head, O: dorsolateral head capsule between compound eyes and occiput, dorsally not adjacent medially (M11 pars verticalis), ventrolateral posterior head capsule, enclosed by occipital ridge and gular ridges (M11 pars genalis), I: with strong plate-like adductor tendon on mesal mandibular base; M12 – M. craniomandibularis externus (0md3) (Fig. 138), abductor, laterad of M11, adjacent to ventral ocular ridge and anterior genae, O: narrow lateral region between compound eyes and occiput, completely enclosed by M11, I: lateral mandibular base by means of a long and thin tendon.

← **Figs. 117–134.** *Dascillus cervinus*, SEM, labium and hypopharynx; **117:** labium, ventral view; **118:** labium and hypopharynx, dorsal view; **119:** mentum, ventral view; **120:** prementum, palpiger and proximal labial palp, ventral view; **121:** mentum and hypopharynx, dorsal view; **122:** distal hypopharynx, proximal prementum, dorsal view; **123:** hypopharynx, lateral view; **124:** left ligular lobe, ventral view; **125:** scale-like setae on ligular lobe; **126:** scale-like setae on furca of ligular lobe; **127:** apex of furca of ligular lobe; **128:** surface structure of furca of ligular lobe; **129:** left palpiger and first labial palpomere, ventral view; **130:** first and second labial palpomeres, ventral view; **131:** second labial palpomere, dorsal view; **132:** surface of distal part of first labial palpomere with sensilla placodea and articulation area to second palpomere; **133:** third labial palpomere, dorsal view; **134:** third labial palpomere, ventral view. dgts – digitiform sensilla, hpp – hypopharynx, lbplp – labial palp, lgl – ligular lobe, lhp – longitudinal hypopharyngeal process, mnt – mentum, plpg – palpiger, ssps – suspensorium.

135



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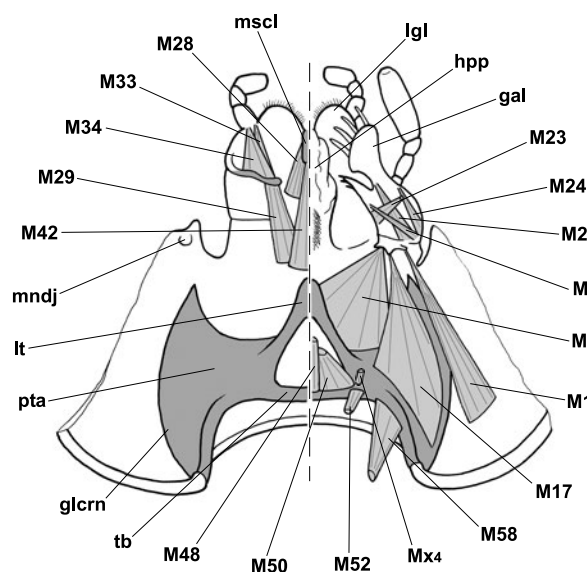


Figs. 135–136. Head, sagittal section (nervous system in lighter grey, musculature in mid grey, internal sclerotized parts in dark grey); **135:** *Glaresis* sp.; **136:** *Dascillus cervinus*. antep – inframandibular antepipharynx, ata – anterior tentorial arm, clp – clypeus, crbr – cerebrum, epp – epipharynx, gfr – frontal ganglion, frn – frons, gl – gula, hpp – hypopharynx, hppbr – hypopharyngeal bridge, hpscl – hypopharyngeal sclerite, lbr – labrum, lep – longitudinal epipharyngeal process, lgl – ligula, lhp – longitudinal hypopharyngeal process, lt – lamina tentorium, M4–67/Mx_{1–4} – musculature, ml – mola, mnd – mandible, mnt – mentum, mscl – median sclerite of prementum, phr – pharynx, por – postocular ridge, smnt – submentum, sog – suboesophageal ganglion, sspsc – suspensorial sclerite, sspns – prepharyngeal suspensorium, tb – tentorial bridge, tcc – tritocerebral commissure.

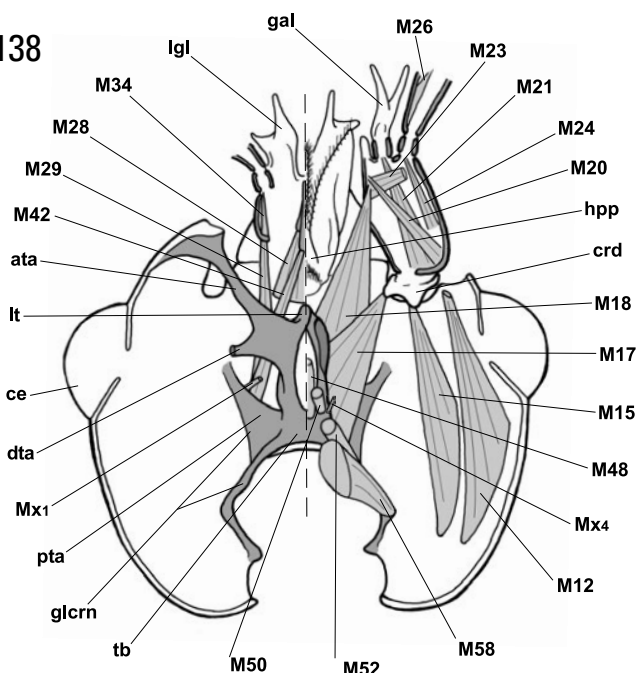
3.2.6.4. Maxillae. M15 – M. craniocardinalis externus (0mx1) (Figs. 14, 100, 116, 138, 140), promotor, O: long and thin area from lateroventral occiput to lateroventral genae posterior of compound eyes, completely

enclosed by M11 (pars genalis), I: with long tendon on lateral process of cardinal base; M17 – M. tentoriocardinalis (0mx3) (Figs. 14, 100, 116, 138), promotor, O: laterally on posterior tentorial arm from level of tentorial

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Figs. 137–138. Ventral head capsule, horizontal section, dorsal view, showing endoskeleton (dark grey) and musculature (light grey); labial musculature depicted on left side of each figure, right side showing musculature of maxilla and digestive tract. **137:** *Glareis* sp.; **138:** *Dascillus cervinus*. ata – anterior tentorial arm, ce – compound eye, crd – cardo, dta – dorsal tentorial arm, gal – galea, glcrn – gular carina, hpp – hypopharynx, lgl – ligula, lt – laminatentorium, M12–58/Mx_{1–4} – musculature, mndj – joint of mandibular condyle with head capsule, mscl – median sclerite of prementum, pta – posterior tentorial arm, tb – tentorial bridge.

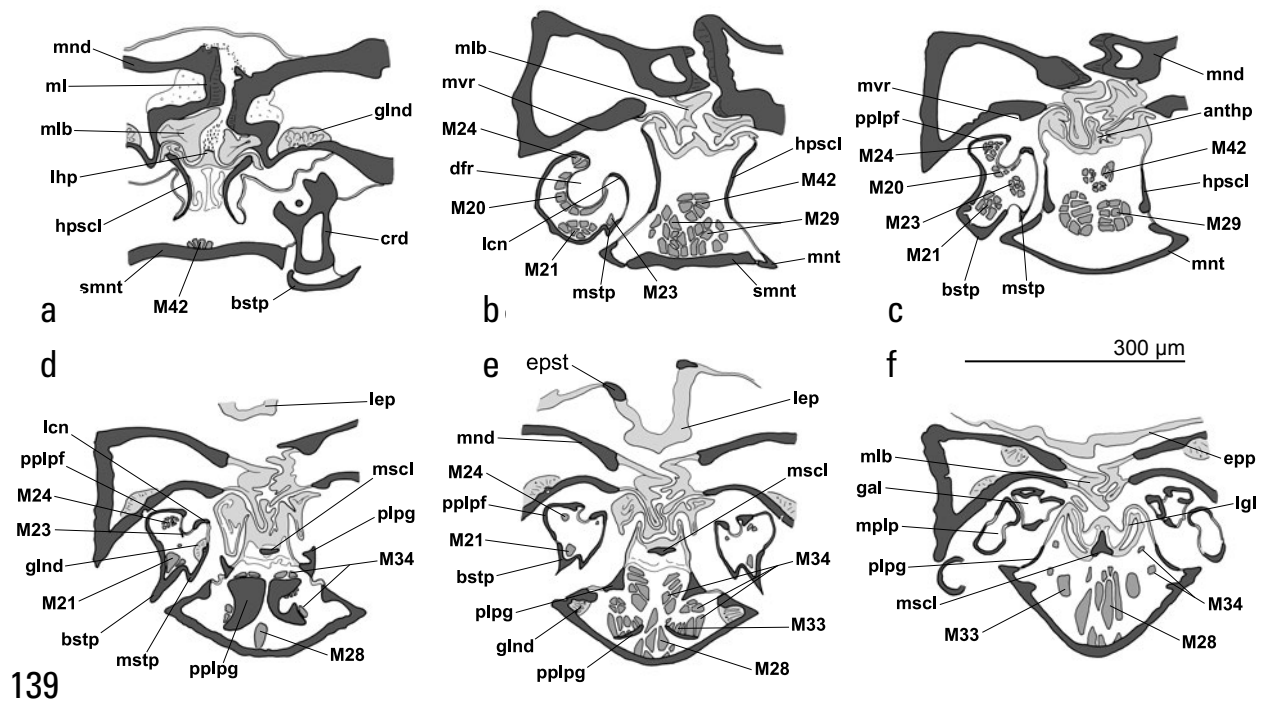
bridge to ventrolateral surface of anterior tentorial arms, I: without tendon on mesal process of cardo; M18 – M. tentoriostipitalis (0mx4) (Figs. 138, 140), stipital adductor, O: ventrally on anterior tentorial arms, anterad of M17, I: without tendon in middle of mesal mediostipital edge; M19 – M. craniolacinalis (0mx2): absent; M20 – M. stipitolacinalis (0mx6) (Figs. 138, 140), adductor of lacinia, relatively thin, extending diagonally through maxillary body along dorsal maxillary border, O: lateral basistipital base, I: base of lacinia; M21 – M. stipitogalealis (0mx7) (Figs. 138, 140), extending along basistipes in longitudinal direction, O: broadly on basistipital base, mediad of insertion of M20, I: ventral wall of galea; M23 – M. stipitopalpalis internus (0mx10) (Figs. 138, 140) (see also section 3.1.6.4.), extending diagonally, in anteriolaterad direction through maxillary body, crossing course of M20 ventrally, O: broadly on base of mediostipes, I: distal half of dorsomesal edge of pseudopalpifer; M24 – M. palpopalpalis maxillae primus (0mx12) (Figs. 138, 140), extending through entire pseudopalpifer in longitudinal direction, O: base of pseudopalpifer, I: base of (functional) palpomere I; M26/M27 – Mm. palpopalpalis tertius/quartus (0mx14/0mx15) (Figs. 138, 140), O: inner wall of (functional) palpomeres II/III, respectively, I: base of (functional) palpomeres III/IV, respectively.

3.2.6.5. Labium. M28 – M. submentopraementalis (0la8) (Figs. 136, 138, 140), unpaired retractor, O: anterior sur-

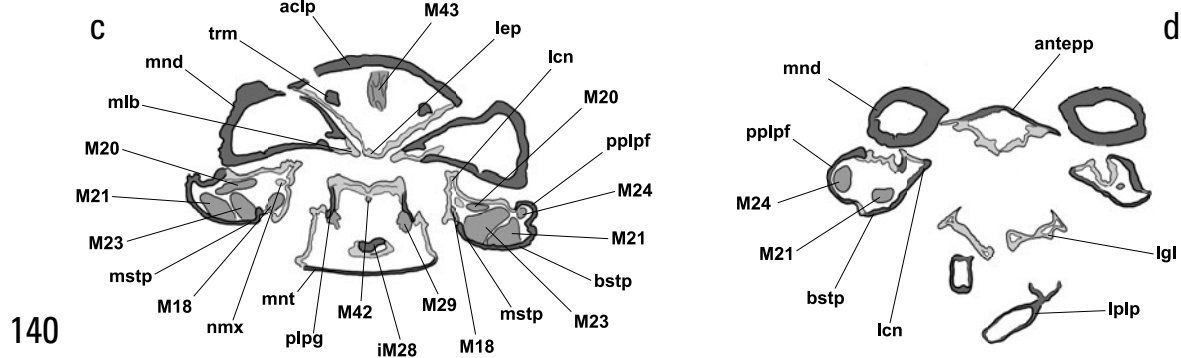
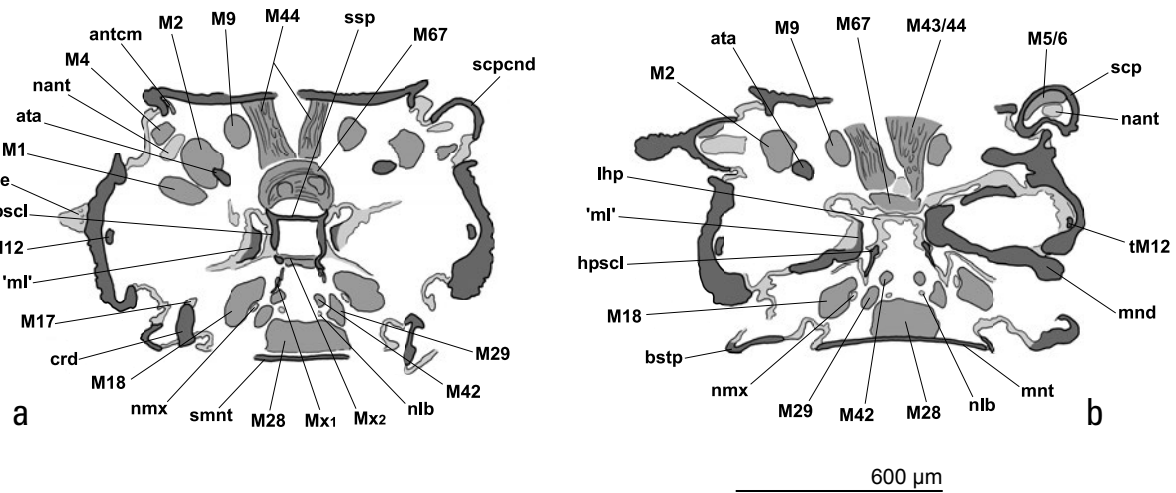
face of submentum, I: ventromedian premental strut; M29 – M. tentoriopraementalis inferior (0la5) (Figs. 136, 138, 140), retractor, O: mesally on anterior edge of gular ridges, ventrad of M17 and M18, I: posterolateral base of palpiger; M33 – M. praementopalpalis internus (0la13): absent; M34 – M. praementopalpalis externus (0la14) (Figs. 136, 138), abductor of palp, O: lateral wall of proximal palpiger, immediately anterad of insertion of M29; I: laterobasal margin of palpomere I; M35/36 – Mm. palpopalpalis primus/secundus (0la16/0la17): absent.

3.2.6.6. Hypopharynx. M41 – M. frontohypopharyngalis (0hy1) (Fig. 4), levator of hypopharynx and mouth angles ('retractor anguli oris'; SNODGRASS 1935) and retractor of labrum via elongated tormae, relatively small, O: frons, laterad of M45 and anterior bundle of M46, posterad of origin of M9, I: with short tendon on posterodorsal process of suspensorium; M42 – M. tentoriohypopharyngalis (0hy3 – M. craniohypopharyngealis) (Figs. 136, 138, 140), retractor, O: together with M29, I: on dorsomedian premental strut, opposite to insertion of M28 (see also section 3.1.6.6.).

Two additional hypopharyngeal muscles of uncertain homology are present, Mx₁ – paired, very small, (Figs. 136, 138, 140A), O: inner basal corner of anterior gular ridges, ventrad of origin of M29/42, extending dorsally, laterad of Mm29/42, I: ventral edge of ventrally directed struts of suspensorial-hypopharyngeal sclerite, probably functioning as hypopharyngeal retractor; Mx₂ (Figs.

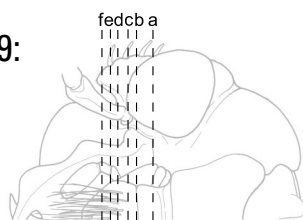


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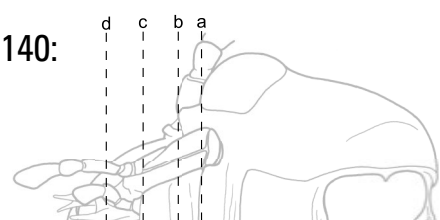


140

139:



140:



136, 140A) – very small transverse muscle, connecting both struts, inserting immediately anterad of the insertion of Mx_1 , possibly stabilizing the hypopharynx. This muscle possibly is homologous with $Ohy10$ (*M. loroloralis*) of WIPFLER et al. (2011).

3.2.6.7. Digestive tract. $M43/44$ – *Mm. clypeopalatalis/clypeobuccalis* ($Oci1/Obu1$) (Figs. 4, 136), complex of several more or less distinctly separated pairs of strong bundles, O: (para)medially on ante- and postclypeus, mesad of $M9$, anterior bundles medially adjacent, posterior ones separated, I: paramedially on dorsal wall of cibarium (anterior pair) to dorsal prepharyngeal wall ('bucca'; posterior pair); $M45$ – *M. frontobuccalis anterior* ($Obu2$) (Figs. 4, 136), very strongly developed, O: anterior frons, anteromesad of $M41$, mesad of $M9$, I: dorsally on anterior pharynx, immediately behind anatomical mouth opening; $M46$ – *M. frontobuccalis posterior* ($Obu3$) (Figs. 4, 136), two pairs of closely adjacent bundles, O: frons, posterolaterad of $M45$, I: dorsolateral corners of precerebral pharynx; $M48$ – *M. tentoriobuccalis anterior* ($Obu5$ or $Ohy5$) (Figs. 136, 138), retractor of hypopharyngeal suspensorium, unpaired, stretching between tritocerebral commissure and suboesophageal ganglion, O: dorsomesally on anterior margin of tentorial bridge, I: posterior border of sclerotized suspensorium, opposite to insertion of $M41$; $M50$ – *M. tentoriobuccalis posterior* ($Obu6$) (Figs. 136, 138), several pairs of short but thick bundles, O: dorsal surface of tentorial bridge, laterad and distad of the origin of $M48$, I: ventrolaterally on pharynx; $M51$ – *M. verticopharyngalis* ($Oph1$) (Figs. 4, 136), one pair of long and well developed muscles, antagonist to $M52$, O: posterior vertex, behind cerebrum, between dorsal components of $M11$, I: paramedially on dorsal wall of postcerebral pharynx; $M52$ – *M. tentoriopharyngalis* ($Oph2$) (Figs. 136, 138), paired, several strongly developed bundles, O: mesally on posterior gular ridges, I: laterally on posterior pharynx; $M67$ – *M. transversalis buccae* ($Ohy9$) (Fig. 136), strongly developed bundles; $M68$ – *M. anularis stomodaei* ($Ost1$) (Fig. 136), relatively thin layer; $M69$ – *M. longitudinalis stomodaei* ($Ost2$) (Fig. 136), layer of longitudinal muscles on dorsal side of pharynx, anteriorly very strongly developed, less distinct posteriorly.

3.2.6.8. Head capsule. $M55$ – *M. praephragmapostoccipitalis* ($Idlm1$ – *M. prophragma-occipitalis* sensu FRIED-

RICH & BEUTEL 2008a) (Figs. 4, 136), paired, O: prothorax; I: ventrally on large tongue-like internal process of dorsal postoccipital ridge, both bundles separated by a sagittal carina; $M58$ – *M. profurcatentorialis* ($IvIm3$ – *M. profurca-tentorialis* sensu FRIEDRICH & BEUTEL 2008a) (Figs. 136, 138), O: prothorax, I: posterior corners of gula, on mesal surface of gular ridges, ventrad of origin of $M52$.

An additional muscle ' Mx_4 ', conforming with that already described for *Glareis*, occurs also in *Dascillus*. Due to insufficient quality of the cross section series the muscular origin could not be identified without ambiguity, but is most likely on tentorial bridge, laterad of $M50$ (Fig. 138). Like in *Glareis*, the muscle is long and very thin; it processes along sides of pharynx, dorsal aorta and adjacent to endocrine glands and inserts on the internal process of the dorsal occipital ridge between insertion area of both parts of $M55$ (Figs. 4, 136) (see discussion).

4. Discussion

4.1. Possible relationships between Scarabaeoidea and Dascilloidea

Characters of the adult head examined during this study do not support a sistergroup relationship between Dascillidae (or Dascilloidea) and Scarabaeoidea, as it was suggested earlier by CROWSON (1960) and others (e.g. LAWRENCE & BRITTON 1991), and recently by LAWRENCE et al. (2011). Not a single potential synapomorphy shared only by these two groups could be identified, in contrast to numerous morphological differences, which will be outlined in the following sections. A bulging gula is a presumably derived condition occurring in both groups. However, the gula of *Dascillus* is only slightly convex (Fig. 60) and it is nearly even in *Rhipicera*. The very distinct convexity of the gula is presumably an autapomorphy of Scarabaeoidea (Fig. 17; see below). The absence of *M. craniolacinalis* ($M19$) in *Dascillus* and *Glareis* is certainly the result of parallel evo-

← **Figs. 139–140.** Head, cross sections through mouthpart region; sclerotized parts in darker grey, musculature in mid grey, nervous tissue, connective tissue and semimembranous parts in lighter grey; pictograms on the bottom (left for *Glareis* sp., right for *D. cervinus*) showing planes of section. **139:** *Glareis* sp.; **140:** *Dascillus cervinus*. acp – anteclypeus, antcm – compressor muscle of antennal heart, antep – inframandibular antepipharynx, anthp – anterior part of hypopharynx, ata – anterior tentorial arm, bstp – basistipes, ce – compound eye, crd – cardo, dfr – dorsal furrow of maxillary corpus, epp – epipharynx, epst – epipharyngeal struts, gal – galea, gland – gland, hpscl – hypopharyngeal sclerite, iM28 – insertion point of $M28$, lcn – lacinia, lep – longitudinal epipharyngeal process, lgl – ligula, lhp – longitudinal hypopharyngeal process, lplp – labial palp, $M1-67/Mx_{1/2}$ – musculature, ml – mola, mlb – semimembranous median mandibular lobe, mnd – mandible, mnt – mentum, mlp – maxillary palp, mscl – median sclerite of prementum, mstp – mediostipes, mvr – ventral mandibular ridge, nant – antennal nerve, nlb – labial nerve, nm – maxillary nerve, pplpf – pseudopalpifer, plpg – palpiger, pplpg – posterior process of palpiger, scp – scapus, scpcnd – basal condyle of scapus, smnt – submentum, ssp – prepharyngeal suspensorium, tM12 – tendon of mandibular abductor muscle, trm – torma.

Table 1. Musculature of the head of *Glaresis* sp. and *Dascillus cervinus*, homologized using the terminology of v. KÉLER (1963) and WIPFLER et al. (2011) (and FRIEDRICH & BEUTEL 2008a). ‘+’ – muscle present, ‘–’ – muscle absent, ‘/’ – muscle not treated by the author, ‘?’ – muscle of unclear homology, * see FRIEDRICH & BEUTEL (2008a).

Name of muscle	v. KÉLER (1963)	WIPFLER et al. (2011)	<i>Glaresis</i>	<i>Dascillus</i>
Antenna				
M. tentorioscapalis anterior	M1	0an1	+	+
M. tentorioscapalis posterior	M2	0an2	+	+
M. tentorioscapalis medialis	M4	0an4	+	+
Mm. scapopedicellares lateralis/medialis	M5/M6	0an6/0an7	+	+
Antennal heart				
M. frontofrontalis	/	0ah6	+	+
Labrum				
M. labroepipharyngalis	M7	0lb5 (M. labroepipharyngealis)	+	+
M. frontoepipharyngalis	M9	0lb2	+	+
Mandible				
M. craniomandibularis internus	M11	0md1	+	+
M. craniomandibularis externus	M12	0md3 (M. craniomand. ext. posterior)	+	+
Maxilla				
M. craniocardinalis externus	M15	0mx1 (M. craniocardinalis)	+	+
M. tentoriocardinalis	M17	0mx3	+	+
M. tentoriostipitalis	M18	0mx4 (M. tentoriostipitalis anterior)	+	+
M. craniolacinalis	M19	0mx2	–	–
Mx: M. craniobasimaxillaris n.n.	/	0mx16 n.n.	–	–
M. stipitolacinalis	M20	0mx6	+	+
M. stipitogalealis	M21	0mx7	+	+
M. stipitopalpalis internus	M23	0mx10	+	+
M. palpopalpalis maxillae primus	M24	0mx12	+	+
Mm. palpopalpalis maxillae tertius/quartus	M26/27	0mx14/0mx15	+	+
Labium				
M. submentopraementalis	M28	0la8	+	+
M. tentoriopraementalis inferior	M29	0la5 (M. tentoriopraementalis)	+	+
M. praementopalpalis internus	M33	0la13	+	–
M. praementopalpalis externus	M34	0la14	+	+
Mm. palpopalpalis primus/secundus	M35/36	0la16/0la17 (Mm. pp. labii prim./sec.)	–(?)	–
Hypopharynx				
M. frontohypopharyngalis	M41	0hy1 (M. frontooralis)	+	+
M. tentorihypopharyngalis	M42	0hy3 (M. craniohypopharyngealis)	+	+
Mx ₁ : M. submentosuspensorialis n.n.	/	0hy14 n.n.	–	+
Mx ₂ : M. loroloralis?	/	0hy10?	–	+
Digestive tract				
M. clypeopalatalis	M43	0ci1	+	+
M. clypeobuccalis	M44	0bu1	+	+
M. frontobuccalis anterior	M45	0bu2	+	+
M. frontobuccalis posterior	M46	0bu3	+	+
M. tentoriobuccalis anterior	M48	0bu5	+	+ (0hy5?)
M. tentoriobuccalis posterior	M50	0bu6	+	+
M. verticopharyngalis	M51	0ph1 (M. verticopharyngealis)	–	+
M. tentoriopharyngalis	M52	0ph2 (M. tentoriopharyngealis)	+	+
M. transversalis buccae	M67	0hy9 (M. oralis transversalis)	+	+
M. annularis stomodaei	M68	0st1 (M. annularis stomodaei)	+	+
M. longitudinalis stomodaei	M69	0st2	+	+
Head capsule				
Mx ₄ : M. tentoriofrontalis anterior	/	0te2	+	+
M. praephragmapostoccipitalis	M55	0lml1 (M. prophragma-occipitalis)*	+	+
M. profurcatentorialis	M58	0lvm3 (M. profurca-tentorialis)*	+	+

lution, as this muscle is well developed in different scarabaeoid taxa (e.g. *Trypocopriss*, *Aphodius*; pers. obs.; see below).

A tentoriofrontal muscle (Mx_4) observed in *Dascillus* and *Glaresis* has not been described previously for any member of Coleoptera. A muscle with a comparable position was known only from non-endopterygote dicondylid insects (e.g. *Zygentoma*: WOO 1950; Embioptera: RÄHLE 1970; Dictyoptera, Grylloblattodea, Mantophasmatodea: WIPFLER et al. 2011, FRIEDEMANN et al. 2011, 'Ote2' – *M. tentoriofrontalis* anterior). It can be assumed that the extremely thin muscle was overlooked and that its occurrence is rather common within Dicondylia and thus also within (adult) Coleoptera (B. Wipfler, pers. comm.). The function of the tentoriofrontal muscle is probably to keep the pharynx and the dorsal aorta in their median position and to fix the position of the neurohemal organs (corpora cardiaca & c. allata).

The few characters of the adult head previously used as arguments for a sistergroup relationship between Dascilloidea and Scarabaeoidea need critical re-evaluation. A possible synapomorphy suggested by BROWNE & SCHOLTZ (1999) is the similar exocone structure of the ommatidia, based on a study of CAVENEY (1986). However, exocone ommatidia are also usually present in Byrrhoidea (incl. Dryopoidea) (not in Dryopidae and Lutrochidae) and Elateroidea s.l. (not in Eucnemidae), and also occur in Nosodendridae and Bostrichoidea (CAVENEY 1986). In Scarabaeoidea, the group with the highest variability in this character system, exocone ommatidia are only known in Passalidae and some representatives of Trogidae, Pleocomidae and Bolboceratidae. Acone and duocone ommatidia occur in few groups (Diphylostomatidae; Lucanidae, Trogidae, Pleocomidae partim) but eucone ommatidia are present in the majority of scarabaeoid lineages (incl. *Glaresis*; Fig. 172). This was considered as a groundplan feature of this superfamily by CAVENEY & SCHOLTZ (1993) and of the entire Polyphaga (CAVENEY 1986). The widespread distribution of exocone ommatidia suggests that it may have evolved several times independently, such as for instance in *Omorgus* within Trogidae (CAVENEY & SCHOLTZ 1993).

A further previously proposed argument for a close scarabaeoid-dascilloid relationship is the shared presence of antennal sensilla of the type “‘series K porenplatten mit Sockel’ of MEINECKE (1975)”, suggested by CROWSON (1995). The implied homologization must be viewed critically for several reasons. MEINECKE (1975) used the cuticular fine structure to characterize types of sensilla, whereas CROWSON's homology assumption was only based on the similar shape (CROWSON 1995: figs. 1–4). Sensilla of similar shape also occur in other taxa such as for instance in Hydrophiloidea (OLIVA 1992). Furthermore, the type of sensilla referred to by CROWSON (1995) occurs only in some scarabaeoid subgroups (Scarabaeidae part., Geotrupidae; MEINECKE 1975) and may not belong to the groundplan of the superfamily

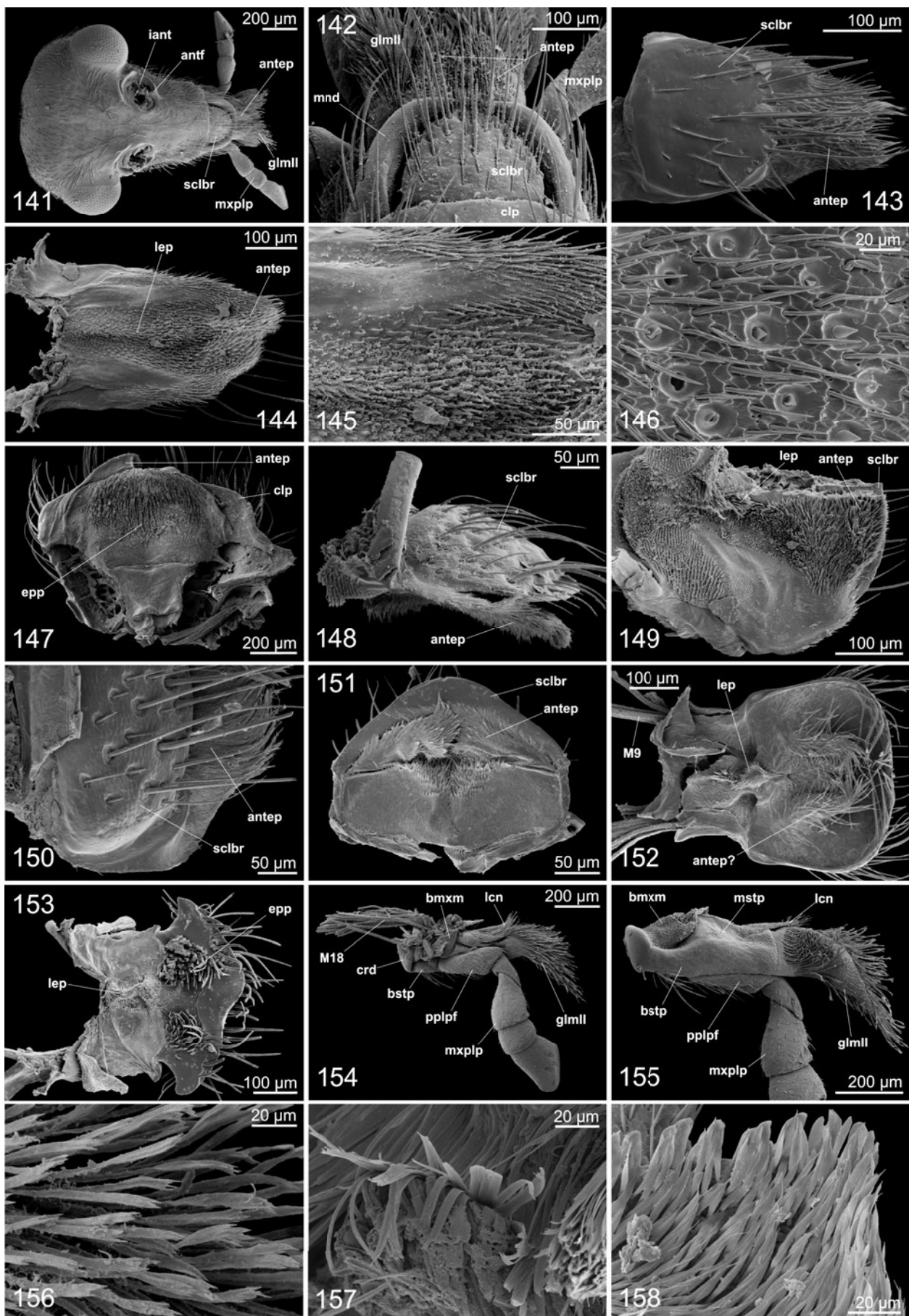
(absent in: Lucanidae, MEINECKE 1975; Passalidae, SLIFER & SEKHON 1964; pers. obs.). In the presumably basal Glaresidae (SCHOLTZ et al. 1994) the antennal sensilla are strongly modified, but in a manner distinctly different from other scarabaeoids and also from Dascillidae. They are free-standing, prolonged, peg- or prism-shaped in *Glaresis* (Figs. 30, 33) and flattened cone-like and sunk into cuticle in *Dascillus* (Figs. 81, 84) and in the mentioned scarabaeoid subgroups, respectively. Last, but not least, the sensilla in question are evenly distributed over nearly the entire surface of almost all antennomeres in *Dascillus* (Figs. 77, 78), whereas in the concerning scarabaeoid groups they are restricted to the antennal club segments and usually concentrated on specific regions of them.

Finally, BROWNE & SCHOLTZ (1999) and SCHOLTZ & GREBENNIKOV (2005) refer to NEL & SCHOLTZ (1990) and characters of the mouthparts treated in that study, without mentioning any specific features. NEL & SCHOLTZ (1990) is a descriptive work as explicitly mentioned therein in the abstract and introduction. Despite the amount of valuable data presented in this work, phylogenetic interpretations or specific arguments based on mouthparts (or other body regions) for a close relationship between Scarabaeoidea and Dascilloidea are missing.

4.2. Alternative hypotheses for a systematic placement of Dascilloidea

As pointed out above, numerous taxa were considered as possible relatives of Dascilloidea, more recently Eucinetoidae (sensu CROWSON 1960) (LAWRENCE & NEWTON 1982), Buprestoidea (LAWRENCE et al. 1995, based on morphological characters of adults and larvae), dryopoid lineages (Eulichadidae; GREBENNIKOV & SCHOLTZ 2003, based on larval morphology), byrrhoid groups (sensu LAWRENCE & NEWTON 1995) (BOCAKOVA et al. 2007, nuclear and mitochondrial rRNA and COI sequences) and Elateroidea s.l. (CATERINO et al. 2005, 18S rDNA and morphological characters). Characters investigated during this study strongly suggest a placement of Dascilloidea within the series Elateriformia, and more precisely within Elateroidea s.l., possibly close to Lycidae or Drilidae.

A unique and complex feature hitherto not described is the inframandibular antepipharynx. Because of its position below the mandibles and its close proximity to the ligula, the largest part of the mandibles is disconnected from the preoral cavity (Figs. 4, 59, 61, 136, 140D). This feature is not only present in Dascillidae and *Rhipicera* (pers. obs. E. Anton), but was also found in all examined members of Elateroidea s.l. with only slight variations (Figs. 141–145, 147–151, 174) (this mouthpart configuration is also depicted in a recent study of KA-



ZANTSEV 2003 on Lycidae, figs. 89 & 105, but without paying further attention to it). The antepipharynx found in the families Drilidae, Omalisidae and Lycidae (Figs. 141–145, 174) is strongly developed and similar to the condition found in *Dascillus*, with the exception that the sclerotized labrum of examined Lycidae forms an additional more or less strongly anterodorsally projecting ridge. An antepipharynx is also present in Cantharidae and Lampyridae, differing from *Dascillus* in the complete reduction of the dorsal labral sclerite, or its complete fusion with the clypeus, respectively (Fig. 147). The antepipharynx is also shorter and located within the concave ventral surface of the apical mandibular part. In the examined members of Elateroidea s.str. (Elateridae: Figs. 148–150; Throscidae: Fig. 151; Eucnemidae) the antepipharynx is also rather weakly developed compared to *Dascillus*, probably due to the shortened mandibles and the more compact arrangement of the mouth parts. Nevertheless, it is also lobe-like in Elateroidea s.str., adjacent to the labium and more or less distinctly positioned below the mandibular apices within a concave ventral mandibular surface. Outside of Elateroidea s.l., a comparable configuration was only found in *Ptilodactyla* (Fig. 152). The epipharynx is also lobe-like, forming a ventrally directed process close to the labium, but with the sclerotized labrum well developed and strongly projecting over the dorsal surfaces of the mandibles. Furthermore, in *Ptilodactyla* the micropubescence of the epipharynx is more distinct, leaving out a glabrous median area, and not evenly covered with microtrichia as in Dascilloidea and Elateroidea (see below). An epipharynx with more or less distinctly developed lobe-like extensions can be observed in few other taxa (for example in *Hydraena*; e.g. JÄCH et al. 2000: figs. 75, 122, 279; pers. obs.) but in all these cases the labrum and epipharynx are clearly placed completely on the dorsal side of the mandibles.

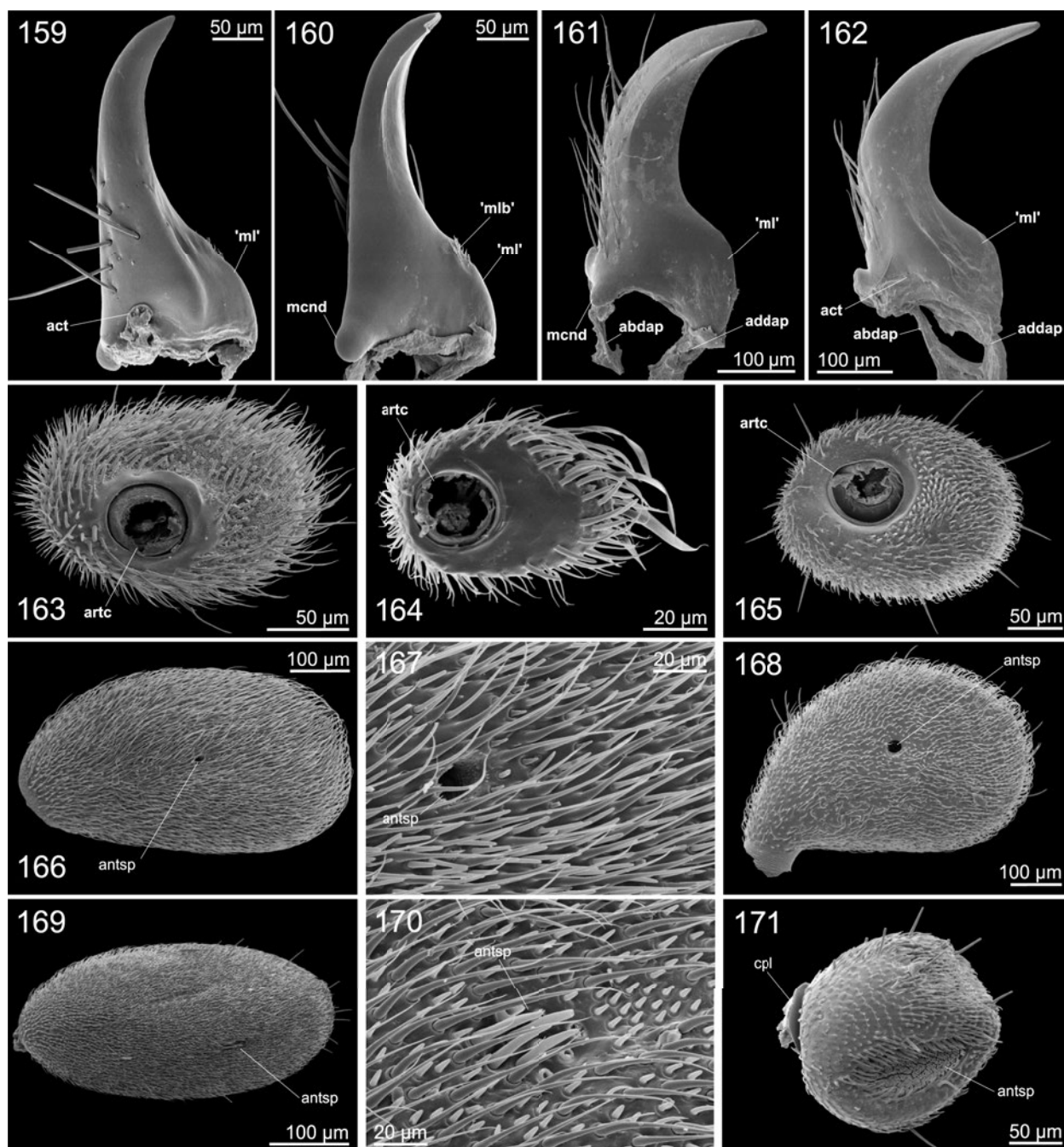
A functional implication of the (inframandibular) antepipharynx is probably that only liquid food can be ingested due to the extra-preoral position of the mandibles and the narrow space between the epipharynx and the labiohypopharyngeal complex. This interpretation is also supported by the even and dense (micro)pubescence of the epipharynx, ligula and galea/lacinia, providing a capillary mechanism and preventing intrusion of larger food particles. The predominantly predacious members

of Cantharoidea are apparently feeding on preorally liquefied food, even though, in contrast to Carabidae, detailed descriptions of the food uptake are scarce (e.g. COHEN 1995; TRAUGOTT 2003) and mainly dealing with the larval stages. A piercing-sucking mandible described for adults of *Dictyoptera* in the already mentioned work of KAZANTSEV (2003) cannot be confirmed. As observed by KAZANTSEV (2003), the mandible of *Dictyoptera* is hollow (like the typical hexapod mandible), but in contrast to the figure in KAZANTSEV (2003; fig. 166) it lacks an apical opening.

Additional structures functionally connected with the antepipharynx occurring in *Dascillus* and in subgroups of Elateroidea s.l. are a homogeneously micropubescent surface of the epipharynx, a semimembranous and lobe-like galeomere II, and characteristically modified setae on galeomere II. In the polyphagan groundplan the epipharynx is likely subdivided in several more or less distinct sections bearing microtrichia, papillae or pores (e.g. DRESSLER & BEUTEL 2010; ANTON & BEUTEL 2004). In *Dascillus* and all examined elateroids the epipharyngeal surface is not differentiated (Lycidae: Figs. 144, 145; Cantharidae: Fig. 147; Elateridae: Fig. 149; Throscidae: Fig. 151). In addition to the micropubescence, at most few scattered papillae are present. The galeomere II appears to be generally semimembranous and lobe-like in elateroids (e.g. Lycidae: Figs. 154, 155) but the bifurcation is only found in *Dascillus* (not in *Rhipicera*; pers. obs. E. Anton). A dense scale- or leaf-like flexible pubescence of the galeomere II as it is described for *Dascillus* occurs also in Lycidae (Fig. 156) and Cantharidae (Fig. 157), and in *Ptilodactyla* (Fig. 158). In most other elateroids the pubescence is also dense (except for *Drilus*) but composed of unmodified microtrichia.

A conspicuous structural affinity of Dascilloidea and Cantharoidea is the specific shape of the mandibles (*Dascillus*: Figs. 85–88; *Drilus*: Figs. 89–90; *Cantharis*: Figs. 91–92; Lycidae: Figs. 159–162). They are elongate with a long and pointed apex. The molar and the membranous mesal part are strongly or completely reduced; the ventral mandibular surface is concave (for accommodating the antepipharynx) and laterally bordered by a ridge, at least in its distal part. The dorsal surface is usually more or less convex (concave in *Rhipicera*, pers. obs. E. Anton) and continuous with the lateral side with-

← **Figs. 141–158.** Various parts of head, SEM. **141–146:** *Lygistopterus sanguineus*; **141:** head capsule, dorsal view; **142:** mandibles and labrum with inframandibular antepipharynx, dorsal view; **143:** labrum and antepipharynx, dorsal view; **144:** ant-/epipharynx, ventral view; **145:** surface structure of epipharynx, ventral view; **146:** surface structure of antennal flagellomere with trichiae and antennal sensilla. **147:** *Cantharis obscura*, epipharynx and clypeal part of head capsule, ventral view. **148–149:** *Dalopius marginatus*, labrum and antepipharynx; **148:** right side, lateral view; **149:** ventral view, right half cut off. **150:** *Athous subfuscus*, right half of labrum and antepipharynx, dorsal view. **151:** *Trixagus dermestoides*, labrum/epipharynx, ventral view. **152:** *Ptilodactyla* sp., labrum/epipharynx, ventral view. **153:** *Trox scaber*, labrum/epipharynx, ventral view. **154–156:** *Lygistopterus sanguineus*, maxilla; **154:** dorsal view; **155:** ventral view; **156:** scale-like setae on distal galeomere. **157:** *Rhagonycha fulva*, scale-like setae on distal galeomere. **158:** *Ptilodactyla* sp., scale-like setae on ligula. antep – inframandibular antepipharynx, antf – antennifer, bmxm – basimaxillary membrane, bstp – basistipes, clp – clypeus, crd – cardo, epp – epipharynx, glmII – galeomere II, iant – antennal socket, lcn – lacinia, lep – longitudinal epipharyngeal process, M9/18 – musculature, mnd – mandible, mstp – mediostipes, mxplp – maxillary palp, pplpf – pseudopalpifer, sclbr – sclerotized part of labrum.



Figs. 159–171. Various parts of head, SEM. **159–160:** *Lygistopterus sanguineus*; **159:** left mandible, dorsal view; **160:** right mandible, ventral view. **161–162:** *Platycis minutus*; **161:** right mandible, ventral view; **162:** left mandible, dorsal view. **163–171:** Antennal club segments; **163:** *Hydrobius fuscipes*, second club segment, view on distal surface; **164:** *Helophorus obscurus*, second club segment, view on distal surface; **165:** *Sphaeridium lunatum*, second club segment, view on distal surface; **166, 167:** *Polynoncus* sp., distal club segment, view on distal surface (166) and detail from Fig. 166 showing opening of sensilla pouch (167); **168:** *Platycerus caraboides*, distal club segment, view on lateral surface; **169:** *Typhaeus typhoeus*, distal club segment, view on distal surface; **170:** *Trypocopris vernalis*, distal club segment, detail on distal surface showing sensory groove; **171:** *Hypocaccus rugifrons*, club, viewed from aside, showing large sensory pits. abdap – apodeme of mandibular abductor (M12), act – acetabulum, addap – apodeme of mandibular adductor (M11), antsp – antennal sensory pouch ('Taschenöffnung'), artc – articulation area to distal club segment, cpl – cupuliform segment, mcnd – mandibular condyle, 'ml' – molar region, 'mlb' – semimembranous median region on mandible.

out an edge. In distinct contrast to that, the scarabaeoid mandible is dorsally concave and a dorsolateral edge is present (see below). Apart from moderate variations in size and shape (e.g. relatively broad in Dascilloidea), the mandibles of Dascilloidea and Cantharoidea differ only

in the presence or absence and size of the preapical retinaculum. It is reduced in most examined cantharoid taxa, but it is larger in *Drilus* and *Malthinus* (pers. obs. E. Anton) than in *Dascillus*. In Elateroidea s.str. the shape of the mandibles is quite variable, but in general it

is short and broad, with the apical part shortened. Molae and the membranous mesal part are either strongly developed or more or less strongly reduced. Specific structural affinities with the mandible of *Dascillus* are missing, and this applies also to other non-cantharoid elateriform taxa.

The mesal parts of the maxillae, especially the mediostipes and lacinia, are not or only slightly overlapped by the mentum and thus largely exposed in *Dascillus* (Fig. 62), *Rhipicera*, and also in most examined cantharoids. In Elateroidea s.str. and Byrrhoidea and also in examined scirtoids (*Eucinetus*, *Cyphon*, *Clambus*) the maxillary parts in question are exposed to varying degrees, whereas they are completely concealed by the mentum in Scarabaeoidea. The anterior part of the mentum is semimembranous in Dascilloidea, Elateroidea s.l. (except for *Trixagus*: mentum completely sclerotized), Byrrhoidea (incl. Dryopoidea), Buprestidae and also Scirtoidea. We consider this feature as a potential autapomorphy of Elateriformia. Nevertheless, an anteriorly semimembranous mentum can also be found in leioidids and Nicrophorinae (ANTON & BEUTEL 2004). Additionally, cantharoids are characterized by a tendency to reduce the size and sclerotization of the entire mentum, whereas it is plate-like and well sclerotized in Scarabaeoidea and Staphylinoidea (with some exceptions: Leioididae; ANTON & BEUTEL 2004).

A sclerotized tub-shaped suspensorium which forms the dorsal side of the posterior hypopharynx is an unusual feature in Polyphaga. It was found in *Dascillus* (Figs. 121, 123, 136) and Elateridae (*Agrypnus*), and also in Lycidae (*Lygistopterus*), where it is strongly elongated. This apparently derived feature needs further study in more taxa.

In most polyphagan groups the outline of the foramen occipitale is oval to rectangular and undivided, whereas a partial transverse division is recognizable in *Dascillus* (Figs. 5, 66). The ventral part of the foramen is functionally related with the inclined subprognathous posture of the head, as it gives passage to the commissures leaving the suboesophageal ganglion and the ventral neck musculature (M58 – M. profurcatentorialis) (Fig. 136). A similarly subdivided foramen occipitale and an emarginated and shortened gula are also present in *Rhipicera*, Lycidae, Cantharidae and Lampyridae (pers. obs. E. Anton).

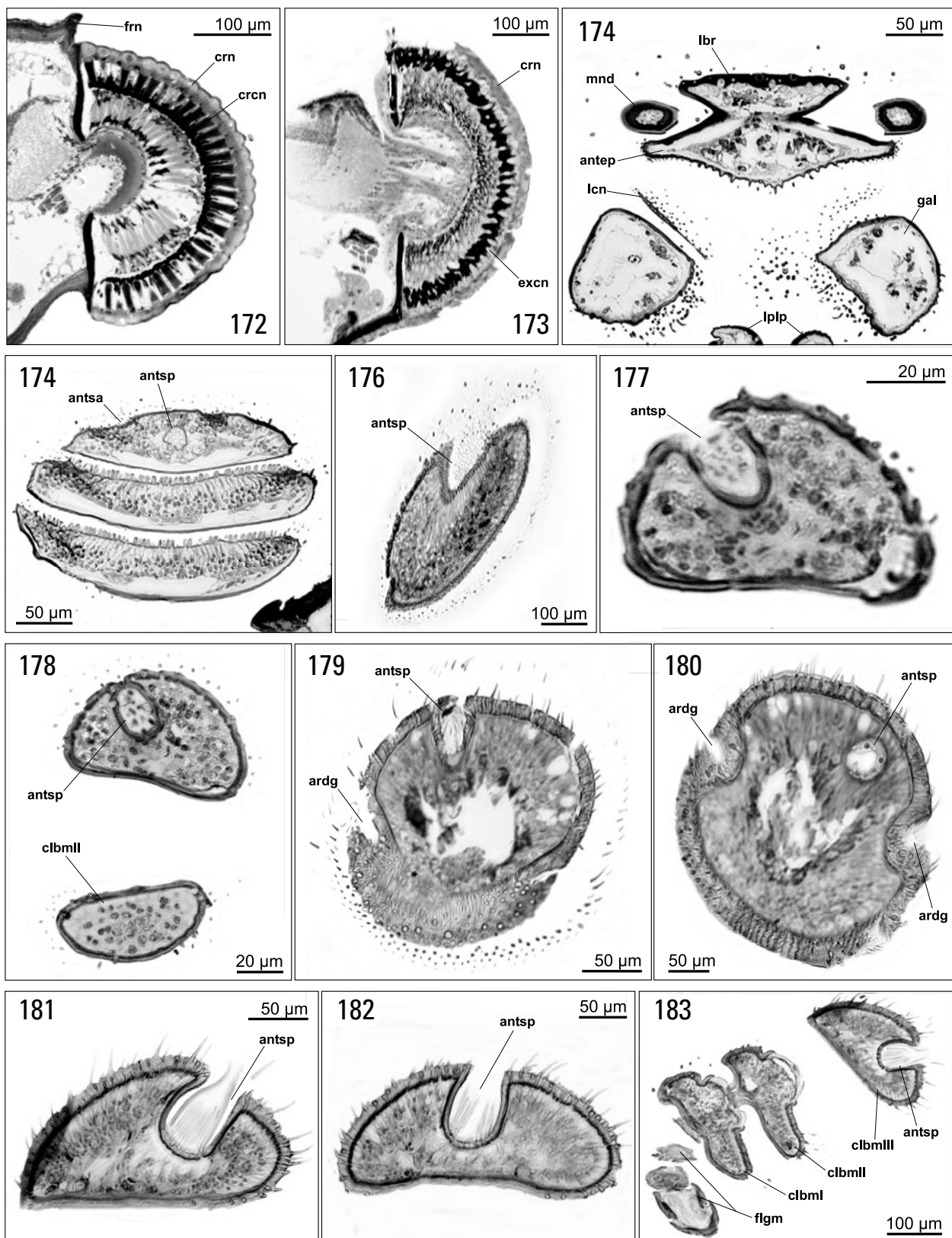
A further character linking Dascilloidea and Elateroidea s.l. is the specific location of the insertion of the antennae. In most of the presumably basal polyphagan taxa (e.g. Staphyliniformia, Scarabaeoidea) as well as in adephagans the antennae insert laterally on the head capsule in front of the compound eye, with the insertion often concealed by a lateral clypeal projection. In *Dascillus* the large antennal foramen is shifted dorsally (Figs. 4, 6, 59, 63, 64), and as a consequence the clypeus becomes raised and strongly arched in the sagittal plane (Fig. 136). In *Rhipicera* this feature is even more distinct and very similar to the condition found in many

prognathous elaterids, which are characterized by a strongly raised and partly edged clypeus. Generally, in Elateroidea s.l. a tendency can be observed to move the antennal insertion from a lateral to a more frontal or dorsal position. This is very distinct in Cantharidae, with a dorsal insertion area and a flat clypeus without edges or sutures. In Eucnemidae the insertion area is also shifted to the morphological dorsal side (secondarily orthognathous head), but in contrast to cantharids with clearly visible sutures running from the lateral sides of the head capsule mesad around the base of the antennae. This suggests its primarily lateral origin (a similar condition is also found in *Dryops*). In the examined Lycidae (Fig. 141), Omalidae, Lampyridae and Drilidae the clypeus is bulged and the antennal insertion is directed anteriorly and/or dorsally, comparable to the dascillid or (with a more strongly raised and edged clypeus; *Platycis*) elaterid conditions. A clypeus divided by a transverse suture in a distinct ante- and postclypeus as it occurs in *Dascillus* is also present in *Ptilodactyla*, where the antennal insertion is directed frontally and thus resembles the elaterid condition.

Regarding the already discussed antennal sensilla of *Dascillus* (see above), a superficially similar antennal vestiture occurs at least in *Lygistopterus* (Lycidae; Fig. 146). The sensilla are sunk below the cuticular surface and surrounded by a glabrous ring-like area. However, in contrast to the dascillid sensilla (Fig. 81), they are not flattened but tapering distally. Similar sensilla could not be detected in the other examined elateroid (and non-elateroid) taxa so far and need further investigation.

Considering the series of adult characters linking Dascilloidea with Elateroidea s.l., it is surprising that no larval characters support this hypothesis (e.g. LAWRENCE et al. 2011). GREBENNIKOV & SCHOLTZ (2003) intensively dealt with the larval (and pupal) morphology of Dascillidae and clearly refused a monophylum Dascilloidea + Scarabaeoidea (after CROWSON 1960), interpreting the similarities in both groups as habitat dependent convergencies. They discussed Eulichadidae as possible closest relatives of dascilloids. However, presently no well supported hypothesis dealing with larval characters is available. To complicate matters, larvae of Rhipiceridae are extremely modified due to their ectoparasitic mode of life. The presently known larval features do not support a close relationship of this family with Dascillidae (GREBENNIKOV & SCHOLTZ 2003).

Some internal features of *Dascillus* should not go unnoticed, even though they cannot be applied to a wider range of taxa due to a lack of detailed anatomical data. M. verticopharyngalis (M51; Fig. 136) as it is found in *Dascillus* is also present in Adephaga (e.g. BEUTEL 1986; DRESSLER & BEUTEL 2010) and also occurs in some members of Archostemata (*Ascioplaga*; HÖRNSCHEMEYER et al. 2006). It has not been described for members of Polyphaga so far (e.g. ANTON & BEUTEL 2004; BEUTEL et al. 2003; EVANS 1961) (but a very fine muscle extending from vertex to dorsolateral walls of



Figs. 172–183. Light microscopic photographs from cross-section series. **172:** *Glaresis* sp., compound eye, on level of its maximum diameter; **173:** *Dascillus cervinus*, compound eye, on level of its maximum diameter; **174:** *Lygistoapterus sanguineus*, section through distal mouthparts, showing inframandibular position of antepipharynx; **175:** *Glaresis* sp., section through antennal club, showing sensory pouch on distal antennomere; **176:** *Aphodius* sp., distal club segment; **177–178:** *Oxyomus silvestris*, distal club segment, showing antennal sensory pouch on two different section planes; **179–180:** *Sphaerites glabratus*, club, on two different section planes; **181–183:** *Polynoncus* sp., distal club segment on different section planes (181, 182) and section through club and distal flagellum (183). antep – inframandibular antepipharynx, antsa – distinct setose ridge on distal antennomere, antsp – antennal sensory pouch ('Taschenöffnung'), ardg – ridge demarcating segment border of fused club segments, clbmI/II/III – club segments I–III, crcn – crystalline cone, crn – cornea, excn – exocone, flgm – flagellomeres, frn – frons, gal – galea, lbr – labrum, lcn – lacinia, lplp – labial palpus, mnd – mandible.

pharynx could be observed in cross section series of *Lamprobyrrhulus*; pers. obs. E. Anton). The presence of M51 in Dascillidae (or Dascilloidea?: character state unknown in *Rhipicera*) is either due to reversal or a plesiomorphic feature. The latter option would imply that the muscle was reduced many times in Polyphaga. More data are required to resolve this issue. The presence of the small muscles Mx_1 and Mx_2 (Figs. 136, 138, 140A) is an unusual feature of Dascillidae or probably Dascilloidea (state unknown in *Rhipicera*). Both muscles are not described for any other group of Coleoptera and probably autapomorphic. It is possible that a well developed muscle observed in *Lygistopterus* and *Cantharis* originating on the posterior tentorial arms and inserting on the posterior hypopharyngeal suspensorium is homologous with Mx_1 of *Dascillus*. In Byrrhidae (*Lamprobyrrhulus*; pers. obs.) such a muscle is absent.

Surprisingly, despite the overall similarity of adult head structures of *Rhipicera* and *Dascillus*, not a single autapomorphic character state of Dascilloidea could be identified. A detailed anatomical study of members of Rhipiceridae (and other groups) is clearly required to assess some hitherto unconfirmed features such as for instance the presence (or absence) of M51 and Mx_2 .

4.3. Alternative hypotheses for scarabaeoid relationships

In contrast to the previously discussed phylogenetic affinities with Dascilloidea, Scarabaeoidea are either placed as sistergroup of the entire Staphyliniformia in recent concepts, or as the sistergroup of Staphyliniformia-Hydrophiloidea (see below and BEUTEL & LESCHEN 2005b). One of the first authors combining Staphyliniformia and Scarabaeoidea was KOLBE (1908) ('Haplogastra'), based on features of the abdominal sterna (see also SCHOLTZ & GREBENNIKOV 2005). This concept was recently supported by characters of the hind wing (BROWNE 1993; SCHOLTZ et al. 1994; KUKALOVÁ-PECK & LAWRENCE 1993), morphological characters of adults and larvae (HANSEN 1997; BEUTEL & LESCHEN 2005c), by molecular studies (18S & 28S rDNA; KORTE et al. 2004) and by analyses of combined data sets (CATERINO et al. 2005).

The present study offers additional evidence for a staphyliniform-scarabaeoid clade. An antennal club with asymmetrically widened club segments (Figs. 27, 30–32, 166, 168, 169, 183) is well-established as scarabaeoid autapomorphy (e.g. BROWNE & SCHOLTZ 1999). In Hydrophiloidea s.str. the club segments are also asymmetric with respect to their articulation (Figs. 163–165), as the sockets are placed close to the outer border of the distal surface of the antennomeres. The main difference is that the scarabaeoid antennomeres are strongly widened (at least 2 times as long as broad),

whereas they are only slightly longer than broad in hydrophiloids. The excentric articulation is obscured in histeroids and some Sphaeridiinae (*Megasternum*, *Cercyon*; pers. obs.) due to a more or less complete fusion of the club segments (Fig. 171). However, this is certainly a secondarily derived condition. Within Staphylinoida excentric articulations have evolved only rarely such as for instance in Hydraenidae (partim., e.g. *Hydraena*; JÄCH et al. 2000: figs. 123, 182, 277 etc.) and in Nicrophorinae.

In *Glaresis* a deep sensory pouch occurs on the third club segment, i.e. on the terminal antennomere (Figs. 2, 175). It opens on the distal surface of the antennomere and is filled with hair-shaped sensilla. This pouch, referred to as 'Taschenöffnung' in MEINECKE (1975), seems to exist in many members of Scarabaeoidea (e.g. *Dorcus*; MEINECKE 1975: fig. 1b). During this study the presence was also confirmed for *Platycerus* (Fig. 168), Trogidae (*Trox*, *Polynoncus*: Figs. 166, 167, 181–183) and Scarabaeidae (*Aegialia*; *Oxyomus*: Figs. 177, 178; *Aphodius*: Fig. 176). The pouch is also present in the examined members of Geotrupidae (*Trypocopris*, *Typhaeus*: Figs. 169, 170) but more shallow and groove-like. Interestingly, a 'Taschenöffnung' also occurs on the compact antennal club of histeroids (*Sphaerites*: Figs. 179, 180) (Sphaeritidae & Synteliidae: "... antennomere 11 with a pair of internal vesicles", NEWTON 2005), and sometimes it is strongly enlarged (*Hypocaccus*: Fig. 171) ("... sensilla basiconica occasionally arranged into plaques [fig. 10.4.2 C]; four large distinct ventral plaques constitute Reichardt's organ [some Saprininae].", KOVARIK & CATERINO 2005). The sensory pouch is not present in Hydrophiloidea s.str., which is possibly due to the aquatic lifestyle and the function of the antenna as an accessory breathing organ. It is conceivable that this organ belongs to the groundplan of Hydrophiloidea (s.l.). It seems to be almost generally absent in staphylinoids. However, invaginations on the penultimate antennomere with obviously sensory function have been described for members of Leiodidae (incl. Leptinidae) ('vésicule olfactive', CORBIÈRE-TICHANÈ 1974; 'Hamann's Organ', ACCORDI & SBORDONI 1978; PECK 1977).

Another apomorphy found in some scarabaeoid species (Geotrupidae: *Trypocopris*; Scarabaeidae: *Oxyomus*, *Aphodius*; pers. obs.) is the presence of an unusual maxillary muscle, which was not classified by v. KÉLER (1963) and which is apparently homologous with a very similar muscle described as 'Mx' in different studies on staphyliniform beetles (Hydraenidae: JÄCH et al. 2000, BEUTEL et al. 2003 [M19]; Hydrophilidae: BEUTEL et al. 2001 [M19a], ANTON & BEUTEL 2004 [Mx²]; Agyrtidae, Staphylinidae: WEIDE & BETZ 2009; *Hydrochus*, *Sphaerites*, *Proteinus*: pers. obs. E. Anton). 'Mx', which has not been found in any non-staphyliniform beetles so far, originates laterally on the genal region and inserts on a semimembranous fold between the proximal maxilla, the other mouthparts, and the anatomical mouth opening. Consequently it will be referred to as 'M. craniobasimax-

illaris' in the following. In the scarabaeoid groups with this muscle the insertion point is a patch-like sclerite located within the basimaxillary membrane, described as 'maxacorial sclerite' (NEL & SCHOLTZ 1990: fig. 3c1). After these authors the maxacorial sclerite occurs only in Scarabaeinae and Geotrupidae, which in fact is in agreement with the occurrence of *M. craniobasimaxillaris* verified in the present study. It is conceivable that the presence of this unusual muscle is a groundplan autapomorphy of Staphyliniformia including Scarabaeoidea, with secondary loss in *Glaresis* and other subgroups (e.g. *Cetonia*, BÜRGIS 1981) of the superfamily.

M. craniobasimaxillaris is possibly functionally linked with the specifically shaped hypopharynx in Staphyliniformia, which was already listed as a potential autapomorphy of Staphyliniformia incl. Scarabaeoidea in BEUTEL & LESCHEN (2005c). Due to a strong constriction between the maxillary bases the hypopharynx is hourglass-shaped in cross sections in most members of these groups (not in Scydmaenidae, Silphidae, Leiodidae part., Staphylinidae part., BEUTEL & LESCHEN 2005c; pers. obs. E. Anton: *Oxyomus*), whereas it is broad and not constricted in all non-'haplogastran' groups as far as known at present (BEUTEL & LESCHEN 2005c) (with the exception of *Lygistopterus*; pers. obs. E. Anton).

In Glaresidae (Figs. 7, 34), Trogidae (Fig. 153), Scarabaeidae, Hydrophiloidea s.str. and many members of Staphylinioidea (*Nargus*, *Thanatophilus*, *Limnebius*; pers. obs.) the sclerotized labrum is at least 2.5 times as broad as long. In Lucanidae, Passalidae and Geotrupidae as in most other polyphagans examined it is at most 2 times as broad as long. The dorsal surface of the labrum is divided into a smooth posterior and a rugulose and setose anterior part by a distinct transverse ridge in *Glaresis* (Fig. 7) and *Aegialia*, a condition which was also described for Helophoridae and Hydrochidae (ANTON & BEUTEL 2004). A bipartite labral surface without a distinct transverse ridge occurs also in other members of Hydrophiloidea (*Georissus*, *Epimetopus*, *Anacaena*) and in Trogidae (pers. obs. E. Anton).

The combined length of the scapus and pedicellus exceeds one third of the entire antennal length in the examined Scarabaeoidea (Figs. 27, 28), Hydrophiloidea s.l. and Hydraenidae. It is shorter than one third in all other examined taxa (with exception of *Dryops*; pers. obs. E. Anton), regardless of the presence of an antennal club. The setae on the scapus are very long, thick, stiff and bristle- or peg-like in Scarabaeoidea (Figs. 3, 27, 28) and Histeroidea (with few exceptions: *Platycerus*, *Paromalus*, *Plegaderus*). A secondary reduction of this setation in Hydrophiloidea s.str. appears plausible considering the aquatic habits and the changed antennal function.

The antennal club is three-segmented and usually preceded by a cupuliform segment VIII in Scarabaeoidea and Hydrophiloidea s.l. (a cupuliform segment is absent in Lucanidae, *Paromalus*, *Plegaderus*), but the two

groups differ in the shape of the cupula (distinct from the preceding flagellomeres in hydrophiloids; flagellomeres increasingly cupuliform towards antennal club in scarabaeoids; pers. obs.).

In *Glaresis* the ligular lobes are paired, strongly sclerotized and setose anteriorly (Fig. 10). The same condition was suggested as an autapomorphy of Hydrophiloidea s.str. in ANTON & BEUTEL (2004) and BEUTEL & LESCHEN (2005c).

4.4. Autapomorphies of Scarabaeoidea and Glaresidae

Some potential new autapomorphies of Scarabaeoidea are listed in the following. As already mentioned in BEUTEL & LESCHEN (2005c) an anteriorly (and laterally) projecting clypeus more or less completely covering the labrum (Figs. 2, 34) is a very characteristic autapomorphy. The anterior edge of the clypeal projection is concave in most groups (straight in Trogidae and *Sinodendron*). It has a ventral gliding surface facilitating labral movements (weakly developed or absent in *Sinodendron* and Melolonthinae) and a distinctly developed frontally directed surface (absent in *Glaresis* and Aphodiinae) equipped with a transverse row of setae (shifted to the ventral side in *Glaresis* [Fig. 34; 'trs'] and Aphodiinae).

An autapomorphic feature generally present in Scarabaeoidea is the glabrous, rectangular, and strongly convex gula (Fig. 17). In the resting position of the head, it is completely lowered into the anterior prothoracic foramen. Apparently the functional background is an arresting mechanism for the head capsule, reducing the degrees of freedom at the base of the head.

A tentorium with the anterior and posterior parts connected by a thin fibre or completely separated (Figs. 135, 137) is probably generally present in scarabaeoid beetles (NEL & SCHOLTZ 1990), with the notable exception of *Passalus* (STICKNEY 1923).

In most scarabaeoid taxa with a well developed labrum, it is deeply lodged in a cup-like concavity of the dorsal mandibular surface (Passalidae, Geotrupidae, *Oryctes*) or is bordered by high lateral ridges of the dorsal mandibular surface (*Glaresis*, Trogidae; Figs. 20, 37; 'drdg').

The proximal outer edge of the pedicellus is projecting in most scarabaeoids (Fig. 29), a feature which is probably also autapomorphic for the group.

In *Glaresis* the sclerotized inner mandibular edge is interrupted by a concavity (Figs. 37, 40) containing the semimembranous median lobe. Such a concavity is also present in Trogidae, Ochodaeidae, Geotrupidae, Hybosoridae and Scarabaeidae (NEL & SCHOLTZ 1990; pers. obs.), and therefore possibly a groundplan feature of Scarabaeoidea. A similar condition observed in Byrrhidae has very likely evolved independently.

In almost all examined scarabaeoids the mentum bears long and stiff anteriorly directed bristles (Figs. 3, 10, 26). They are absent in *Passalus*, *Platycerus* and *Amphimallon*, which possess a smooth or inconspicuously pubescent mentum. The bristles are absent also in all non-scarabaeoid polyphagans.

The following features are potential autapomorphies of Glaresidae:

1. A deep incision between the lateral parts of clypeus and frons allowing dorsal movements of the antennae (Figs. 1, 16, 19). A similar condition has probably independently evolved in few other scarabaeoid taxa (e.g. Cetoniinae). An incision between the clypeus and frons is also present in Clambidae.
2. A transverse ridge posterior to the anterior clypeal margin (Figs. 1, 20, 21; 'clpr').
3. Olfactory sensilla on the distal surface of the first two club segments (IX and X) peg-like (Figs. 30, 33). Based on SEM micrographs these sensilla appear different from other modified sensilla found in scarabaeids (e.g. MEINECKE 1975; Melolonthinae, ROMERO-LÓPEZ et al. 2004; Rutelinae, LEAL & Mochizuki 1993; Passalidae, SLIFER & SEKHON 1964; pers. obs.).
4. Maxillary body dorsally with deep longitudinal furrow bordered by lacinia and pseudopalpifer (Figs. 45, 46, 139B). At most a small and shallow inconspicuous furrow occurs in some groups of Staphyliniformia (e.g. ANTON & BEUTEL 2004: figs. 35, 49, 50; BEUTEL et al. 2001: fig. 15; BEUTEL et al. 2003: figs. 4d–f).
5. Mentum strongly convex (Figs. 3, 135). A similar condition is present in *Oryctes*. The mentum is moderately convex in Trogidae and Geotrupidae.

Glaresidae are considered as the sistergroup of the remaining Scarabaeoidea by some authors (SCHOLTZ et al. 1994; BROWNE & SCHOLTZ 1999; SCHOLTZ & GREBENNIKOV 2005). This is not supported by the results of the present study. In fact, some apparently derived characters are shared by *Glaresis* and Trogidae. This is conform with the earlier placement of *Glaresis* within Trogidae, and a recent molecular study by SMITH et al. (2006) in which Glaresidae and Trogidae were placed as sistergroups. Morphological affinities concern modifications of the frons, the labrum and the labial musculature:

1. The main part of the frons is elevated above the level of the compound eyes and separated from them by a sharp ridge in both groups (Figs. 18, 19).
2. The lateral frontal margin next to the compound eyes (incl. the ocular epicanthus) is set with a row of conspicuous hair-like sensilla (Figs. 16, 18, 19).
3. The posterior corners of the labrum are acute in both taxa (Fig. 153; NEL & SCHOLTZ 1990). In *Glaresis* they form an arresting mechanism together with a sclerotized carina on the ventral surface of clypeus (Figs. 34, 35).

4. *M. submentopraementalis* (M28) originates on the mentum in *Glaresis* (Figs. 135, 139D–F) and apparently also in *Polynoncus*. Further study of this feature in more scarabaeoid taxa is required.

4.5. Homology of intrinsic maxillary muscles

The intrinsic maxillary musculature of *Dascillus* and *Glaresis* is very unusual from the traditional point of view. Two muscles are present which cannot be homologized using the systems of v. KÉLER (1963) or WIPFLER et al. (2011): one is extending from base of the mediostipes to the dorsal wall of the palpifer (in a traditional sense), the other moves from base of the palpifer to base of the first palpomere. An examination of further taxa (e.g. *Trypocopriss*, *Aphodius*, *Hydrochus*, *Sphaerites*, *Lamprobyrrhulus*, *Lygistorphus*, *Agrypnus*, *Cyphon*; pers. obs.) and of relevant studies suggest that these muscles belong to the groundplan of Coleoptera and that they have either been overlooked in small species (e.g. EVANS 1961; BEUTEL et al. 2003; ANTON & BEUTEL 2006) or misinterpreted due to their unusual position (e.g. ANTON & BEUTEL 2004: 'Mx3', 'M22'; DRESSLER & BEUTEL 2010: 'M20', 'M22' in figs. 5A, 11C). In Neuropterida, which are likely the closest relatives of Coleoptera (see BEUTEL 2005; WIEGMANN et al. 2009), the maxillary musculature is apparently of the orthopteroid type in the sense of v. KÉLER (1963) (*Raphidia*, *Sialis*, *Chauliodes*, *Corydalus*: ACHTELIG 1967, Abb. 18; *Osmylus*: BEUTEL et al. 2010).

An intriguing and plausible hypothesis explaining this muscular setting in Coleoptera was given by MEDVEDEV (1960) (Tenebrionidae) and SCHNEIDER (1981) (*Lytta*), assuming that the 'palpifer' is in fact the first palpomere of the maxillary palp ('pseudopalpifer'). This hypothesis is supported by several arguments: SNODGRASS (1935) pointed out, for insects in general, that the stipitopalpal muscles never originate within the palpifer; the maxillary palp of most neuropterids is 5-segmented (instead of 4-segmented as in Coleoptera [following the traditional view]) and a palpifer is absent; the first palpal segment of neuropterids does not form a complete ring-shaped element but rather a simple clasp-shaped structure (ACHTELIG 1967). Accepting this 'pseudopalpifer'-hypothesis leads to a straightforward interpretation of the intramaxillary musculature, which is followed in this study (see sections 3.x.6.4.; Table 1): the muscle extending from the base of mediostipes to the 'palpifer' is homologous with M23 (*M. stipitopalpalis internus*; '0mx10' sensu WIPFLER et al. 2011) and the muscle extending within the (pseudo-)palpifer and inserting on the (functional) palpomere I is homologous with the first palpopalpal muscle (M24 – *M. palpopalpalis maxillae primus*; 0mx12). According to this interpretation the first functional maxillary palpomere is in fact palpomere II

(etc.), and the subsequent palpopalpal musculature (M26/27 – Mm. tertius/quartus; 0mx14/0mx15) originates on (functional) palpomeres II and III, respectively. This interpretation was already implicitly used in BEUTEL (1986, 1989) ('Hydradephaga'), but without considering the specific constitution of the pseudopalpifer. BÜRGIS (1981) (*Cetonia*) suggested that the function of the muscle connecting the stipes and the (pseudo-)palpifer is to increase the hemolymph pressure inside the maxillary corpus enabling the maxillary palp (and galea) to move back to its resting position. An antagonist of the single stipitopalpal (and -galeal) muscle is always absent.

4.6. Conclusions and outlook

The present study demonstrates that morphological investigations can still contribute to a clarification of phylogenetic problems and reveal character complexes which are important for the understanding of the evolution of the group under consideration. Generally, new phylogenetic concepts should be based on comprehensive cladistic analyses. As already pointed out above, this was not possible in the case of the present study as sufficiently detailed anatomical data are rare and scattered (e.g. ANTON & BEUTEL 2004; BEUTEL et al. 2003; JÄCH et al. 2000; WEIDE & BETZ 2009; WEIDE et al. 2010). This underlines the necessity of acquiring more detailed anatomical information for the megadiverse Polyphaga, which are presently not well understood with respect to the systematic relationships of the major lineages (see above). Even without a formal character evaluation, the results presented here, especially the new character complex of the antepipharynx, is likely an important step towards a solution of the "Dascilloidea-problem". The suggested elateroid affinities need further confirmation. However, considering the complexity of potential apomorphies and a recent molecular study (BOČAKOVA et al. 2007), they appear more likely to us than the result of a recent analysis of a very comprehensive morphological data set (LAWRENCE et al. 2011). The study of LAWRENCE et al. (2011) is characterized by a very extensive taxon sampling and a very large number of characters of larvae and adults, most of them external and relatively easy to observe. Whereas the documentation of data is an extremely valuable contribution, the strategy of analysis, and the restriction to more or less easily accessible characters, can be seen more critically. It is likely that the attempt to cover the entire Coleoptera and the use of many characters with a relatively fast rate of evolution may have led to some problematic results, among them the placement of Dascilloidea. Aside from molecular approaches, the next steps in clarifying high level coleopteran relationships could be to assess more detailed anatomical data at an accelerated speed using new morphological technologies (BEUTEL & FRIEDRICH

2008; FRIEDRICH & BEUTEL 2008b; BEUTEL et al. 2009, 2010), to combine these data with characters assessed by LAWRENCE et al. (2011), to break down the group in manageable monophyletic units, and finally to put the lineages together using a supertree approach (e.g. BEUTEL et al. 2008). Separate and combined analyses of molecular and well documented morphological data sets will probably lead to a deeper understanding of the evolution of the most successful order of Hexapoda in the near future.

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