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Article *in* Arthropod Systematics and Phylogeny · June 2010

Rolf Beutel
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Arthropod Systematics & Phylogeny
68 (2) 239–287

The morphology and evolution of the adult head of Adephaga (Insecta: Coleoptera)[1]

Carina Dressler[1] & Rolf Georg Beutel[2]

[1] Museum für Tierkunde, Senckenberg Naturhistorische Sammlungen Dresden,
Königsbrücker Landstraße 159, 01109 Dresden, Germany
[carina.dressler@senckenberg.de]

[2] Institut für Spezielle Zoologie und Evolutionsbiologie, FSU Jena,
Erbertstraße 1, 07745 Jena, Germany
[rolf.beutel@uni-jena.de]

Received 15.iii.2009, accepted 31.v.2010.

> Abstract

The adult head of representatives of different adephagan families – aquatic, semiaquatic and terrestrial – were examined and compared. External and internal structures were described and documented in detail for the genera *Trachypachus* (Trachypachidae), *Haliplus* (Haliplidae), *Amphizoa* (Amphizoidae) and the recently discovered *Aspidytes* (Aspidytidae). A list of characters of potential phylogenetic relevance was compiled and the data matrix combined with the large data set of thoracic and abdominal features for different life stages. The cladistic analysis of this comprehensive data matrix of 138 characters for 16 taxa covering all adephagan families led to one most parsimonious tree. The monophyly of the Geadephaga (Trachypachidae + Carabidae) is strongly supported. The Gyrinidae are the sistergroup of all remaining adephagan beetles. The Meruidae are sister to the Dytiscoidea and both together form the sistergroup of the Haliplidae. The sistergroup relationship of Aspidytidae and Amphizoidae is confirmed. The placement of Meruidae is impeded by the lack of larval characters. It may change when information on structural features of immature stages becomes available.

The Trachypachidae, a small relict family with its greatest diversity and distribution in the early Mesozoic, probably come close to the last common ancestor of the Adephaga in the structural features of the adult head. They share structural similarities with the aquatic Dytiscoidea and the terrestrial Carabidae. It is hypothesized that the common ancestor of Adephaga had a relatively unspecialised head morphology and was a predator, possibly with a preference for a riparian habitat. Adaptations for an aquatic environment evolved at least two times and possibly even three times independently. Within these lineages a great diversity of different life styles developed such as the highly specialised surface gliding Gyrinidae, the hygropetric Aspidytidae, the strongly miniaturised Meruidae or the algophagous Haliplidae.

> Key words

Adephaga, Trachypachidae, Haliplidae, Aspidytidae, Amphizoidae, adephagan ground plan, cladistic analysis, head morphology, Geadephaga, Hydradephaga.

1. Introduction

The order Coleoptera is composed of the very small suborders Archostemata (ca. 30 spp.) and Myxophaga (ca. 100 spp.), the extremely diverse Polyphaga (ca. 330.000 spp.), and the Adephaga (ca. 30.000), the latter are mainly characterized by predacious habits as adults and larvae. The discussion of the phylogeny and evolution of adephagan beetles has been greatly stimulated by the recent discovery of two new

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[1] This study is dedicated to the late Prof. Dr. Robert E. Roughly, whose untimely death came as a great loss to the community of adephagan workers.

hygropetric families, Aspidytidae (Ribera et al. 2002a; Balke et al. 2003, 2005) and Meruidae (Spangler & Steiner 2005; Beutel et al. 2006; Balke et al. 2008). The position of these relict families with only 2 and 1 species, respectively, is not unambiguously resolved (Balke et al. 2003, 2008). Likewise, the placement of the terrestrial relict family Trachypachidae (6 species in 2 genera), which has long been recognised as a key taxon (e.g., Bell 1983; Roughley 1981; Beutel 1993), is still controversial. Trachypachidae share apomorphic characters with two large lineages, the aquatic Dytiscoidea (e.g., subcubital setal binding patch, fused metacoxae), and the terrestrial Carabidae (e.g., protibial antenna-cleaning organ) (e.g., Beutel 1993; Beutel et al. 2006). A sistergroup relationship with the entire Hydradephaga was suggested by Roughley (1981) and a sistergroup relationship with Dytiscoidea by Bell (1983) and Beutel (1993, 1997). However, in more recent years a clade Geadephaga comprising Trachypachidae and Caraboidea has gained strong support in several studies, e.g., Beutel & Haas (1996) and Shull et al. (2001). Apparently the placement of the small family is important for the reconstruction of the adephagan groundplan and crucial for the interpretation of evolutionary changes between aquatic and terrestrial habitats.

The present study was focussed on head structures of adults, a complex character system which has been proven as phylogenetically informative in studies on other groups of insects (e.g., Beutel & Vilhelmsen 2007; Beutel & Baum 2008). Numerous publications on the larval head anatomy of adephagans are available (e.g., Arndt 1993; Arndt & Beutel 1994; Beutel 1991, 1992a, 1993; Alarie et al. 2004), but very few detailed treatments of adult head structures have been published. The only studies covering both external features and internal soft parts are those of Korschelt (1923, 1924) on *Dytiscus*, Honomichl (1975) on *Gyrinus*, Beutel (1986a, 1989a) on *Hygrobia* and *Spanglerogyrus*, respectively, and Belkaceme (1991) on *Noterus*. No detailed data are available for the Aspidytidae and Meruidae, and surprisingly also not for the phylogenetically critical families Trachypachidae, Haliplidae, and Amphizoidae. Consequently, the primary purpose of this study was to provide detailed descriptions of external and internal head structures of representatives of these families. The obtained characters of the head were included in a comprehensive data matrix from Beutel et al. (2006) and analysed cladistically, and an evolutionary scenario for adult head structures was developed.

2. Material and methods

2.1. List of examined taxa

Archostemata, **Cupedidae**: *Priacma serrata* LeConte, 1861.

Adephaga, **Gyrinidae**: *Gyrinus* (s.str.) *substriatus* Stephens, 1828. **Haliplidae**: Indet. sp. of *Haliplus* (subgenus *Liaphlus*) Latreille, 1802. **Amphizoidae**: *Amphizoa lecontei* Matthews, 1872. **Hygrobiidae**: *Hygrobia tarda* Herbst, 1779. **Dytiscidae**: *Dytiscus lapponicus* Gyllenhal, 1808. Indet. sp. of *Agabus* Leach, 1817. **Aspidytidae**: *Aspidytes niobe* Ribera et al., 2002. **Trachypachidae**: *Trachypachus holmbergi* Mannerheim, 1853. **Carabidae**: *Carabus linnei* Panzer, 1813. *Carabus silvestris* Panzer, 1793. *Carabus coriaceus* Linné, 1758. Indet. sp. of *Pterostichus* Bonelli, 1810.

To evaluate the variability of the chosen characters within highly diverse taxa such as Dytiscidae or Carabidae, further representatives of these groups were examined (indet. sp. of *Nebria*, *Elaphrus*, *Loricera*, *Notiophilus*, *Brachinus*, *Bembidion* and *Trechus*), and *Systolosoma breve* Solier, 1849 as a second trachypachid species. The variability of the observed character states is minimal or absent as in Trachypachidae. The additional specimens were not included in the analysis.

2.2. Morphological techniques

The specimens were stored in ethanol (70%). The external morphology was studied under a binocular microscope (Leica MZ 125) and documented with line drawings. For the detailed morphological description of particular adephagan families, the heads of *Trachypachus*, *Aspidytes*, *Amphizoa* and *Haliplus* were critical point dried and scanning electron micrographs were made with an FEI Philips XL 30 ESEM with Scandium software. Furthermore the mouthparts of all representatives were removed and compared under a binocular microscope and for specific details examined with the SEM. To minimize backscatter, improve backround contrast and enable scanning each specimen in different viewing angles a special specimen holder was used (Pohl 2010).

For studying the internal structures specimens of all listed taxa were dissected and drawn in successive stages. Detailed features of the musculature and endoskeleton were studied with serial cross-sections. The heads of *Trachypachus* and *Haliplus* were embedded in Araldite, cut at 1.5 µm with a Microm microtome (HM 360), and stained with toluidine blue and pyronin G (red). For *Aspidytes* a microtome series in Historesin cut at 3 µm and stained with methylene blue and acid fuchsine was already available. For comparative analysis and documentation, selected sections were photographed on a Zeiss Axioplan microscope with AnalySIS® imaging software.

The line drawings were digitised and all images were edited and arranged for publication with Adobe®Photoshop® CS2 and/or Adobe®Illustrator® CS2.

The terminology of the musculature refers to von Kéler's (1963) nomenclature. The homologisation of the M. tentoriopraementalis inferior (M.29a,b), M. praementopalpalis externus (M.34) and Mm. compressores epipharyngis (Mm.III) follows Belkaceme (1991).

The characters examined comprise the skeletomuscular system, the cranial parts of the digestive tract, the brain and other elements of the nervous system, and glands.

2.3. Cladistic analysis

The observed features of external and internal morphology were coded as defined, comparable character states. To complete and evaluate the matrix of characters of the head, data were taken from literature for the following taxa: *Priacma serrata* LeConte (Hörnschemeyer et al. 2002), *Helophorus* spp. (Anton & Beutel 2004), *Catops* sp. (E. Anton, pers. comm.), *Gyrinus substriatus* Stephens (Honomichl 1975), *Spanglerogyrus albiventris* Folkerts (Beutel 1989a, b), *Meru phyllisae* Spangler & Steiner (Spangler & Steiner 2005; Beutel et al. 2006), *Noterus laevis* Sturm (Belkaceme 1991), *Hygrobia tarda* Herbst (Beutel 1986).

The data set of 58 head characters of Adephaga was combined with the comprehensive data set in Beutel et al. (2006). The data matrix (16 taxa, 138 characters – Tab. 1) was generated in Winclada (Nixon 1999) and analysed with NONA (Goloboff 1995) (Ratchet search/Island Hopper, 1000 replicates, all characters equally weighted) and PAUP 4.0b10 (Swofford 2001) (branch and bound search [computed via stepwise, minimal trees only, addition sequence furthest]). Bremer support values were calculated with AutoDecay 5.0 (Eriksson 2003). The bootstrap analysis was run with 1000 replicates.

3. List of abbreviations

abt	abductor tendon
adt	adductor tendon
agur	apodeme of gular ridge
ahy	anterior hypopharynx
ai	apical incisor (md)
anc	circumantennal ridge with process
app	sclerotised appendage of ephl
apocr	dorsal apodeme of postoccipital ridge
ata	anterior tentorial arm
atp	anterior tentorial pit
bs	basistipes
ca	cardo
cap	cardo process
ce	compound eye
cer	cerebrum
cerl	anterior cerebral lobe
cgur	process of gular ridge
cirl	circular line
cl	clypeus
clfs	clypeofrontal suture
cn	connective
coa	corpus allatum
coc	corpus cardiacum
cor	circumocular ridge
ct	central tentorial body
cue	cutting edge (md)
dta	dorsal tentorial arm
eph	epipharynx
ephc	epipharyngeal cusp
ephl	epipharyngeal lobe
epr	epistomal ridge
f	frons
F	function of the muscle
fh	ventral fringe of hairs (md)
ga	galea
ge	gena
gf	frontal ganglion
gu	gula
gua	gular apodeme
gur	gular ridge
gus	gular suture
ha	hypostoma
hag	hypostomal groove
has	hypostomal suture
hy	hypopharynx
hyl	hypopharyngeal lobes
I	insertion of the muscle
irf	insertion ridge of fh (md)
lb	labium
lc	lacinia
lp	labial palp
lr	labrum
lrb	median bar of labrum
lrr	transverse labral ridge
lt	laminatentorium
ltl	median lamella of laminatentorium
md	mandible
mdp	mandibular pore
mea	mesal trapezoid area (md)
mec	mesal cusp (md)
met	mesal tooth (md)
mf	microtrichia field (lr)

mo	mouth opening
mp	maxillary palp
ms	mediostipes
mt	mentum
mtr	mental ridge
n.ant	nervus antennalis
n.md	nervus mandibularis
n.rec	nervus recurrens
O	origin of the muscle
opl	optic lobe
pcm	pharyngeal circular musculature
pe	pedicellus
pf	palpifer (mx)
pg	palpiger (lb)
pgur	postgular ridge
php	postpharynx
phy	posterior hypopharynx
plm	pharyngeal longitudinal muscles
pmdj	primary mandibular joint
pmt	prementum
pocr	postoccipital ridge
por	postocular ridge
pph	prepharynx
pta	posterior tentorial arm
ptp	posterior tentorial pit
sai	subapical incisor (md)
sc	scapus
se	sensilla (sensory processes)
sf	apical sensory field (mp, lp)
smdj	secondary mandibular joint
smt	submentum
soe	suboesophageal ganglion
sor	supraocular ridge
st	stipes
su-cb	suspensorial cross-bar
su-da	dorsal suspensorial arm
su-va	ventral suspensorial arm
tb	tentorial bridge
tcn	tritocerebral connective
tcr	tritocerebral commissure
tm	torma
V-r	V-shaped ridge on ventral side of labrum

4. Results

4.1. Head morphology of *Trachypachus holmbergi*

4.1.1. External head capsule

Figs. 1, 5

The head is prognathous and almost as broad as long (about 1 mm). Its colouration is dark brown to black without a metallic sheen. The surface is almost glabrous without granulation, specific sculpture or pubescence. The compound eyes are laterally protruding. The clypeus is almost three times as long as the labrum. The clypeofrontal suture is a continuous furrow and forms an obtuse angle medially. The distinct anterior tentorial pits lie within the clypeofrontal suture close to its lateral margins. The globular protuberances articulating with the secondary mandibular joints are located at the posterolateral edges of the clypeus (Fig. 5A). A long seta originates close to the lateral clypeal margin. Longitudinal strengthening ridges, the supraocular ridges, extend from the clypeus along the dorsal margins of the compound eyes and reach their posterior border. Frontal and coronal sutures are absent. A low circular ridge on the caudal third of the head almost reaches the gular sutures ventrally (Fig. 5F). Up to this ridge the head is retracted into the thorax.

In lateral view the head appears distinctly wedge-shaped with a widened, almost globular posterior part. On the ventral side a transverse constriction is recognisable between submentum and gula, which are placed at a distinct angle to each other. The fusion line is marked by a pair of conspicuous posterior tentorial pits. The gula is narrow in relation to the width of the entire head. The median gular apodeme is recognisable externally in the anterior part of the gula. The gular sutures are anteriorly continuous with the hypostomal sutures which reach the hypostomal grooves. The fairly extensive hypostomata are not fully covered by the maxillary bases and form an acute angle with the genae. The maxillae are inserted in the hypostomal grooves. The caudal occipital foramen is surrounded by a wide postoccipital ridge except for the ventral gular part. The postgular ridge is formed by the hind margin of the gula.

4.1.2. Internal skeletal structures

Figs. 2, 3, 5

A distinct internal transverse epistomal ridge corresponds to the external clypeofrontal suture. The longitudinal gular ridges – externally marked by the gular sutures – are thin high internal walls with a strengthened dorsal edge. They are posteriorly continuous with the postoccipital ridge. The anterior edges are fused with the posterior tentorial arms arising from the posterior tentorial pits. At their cranial third the gular ridges are connected by the tentorial bridge – a thin, sclerotised, slightly arched bar with a short anteriorly directed median process. The gular ridges slope conspicuously in the caudal third before reaching the postoccipital ridge. At their lowest part a pair of slender, medially projecting apodemes serves as insertion area of M. profurcatentorialis (M.58). The mid-gular apodeme is a strongly developed, triangular, median process on the cranial third of the gula. Labial muscles originate on its lateral faces and the cranial edge.

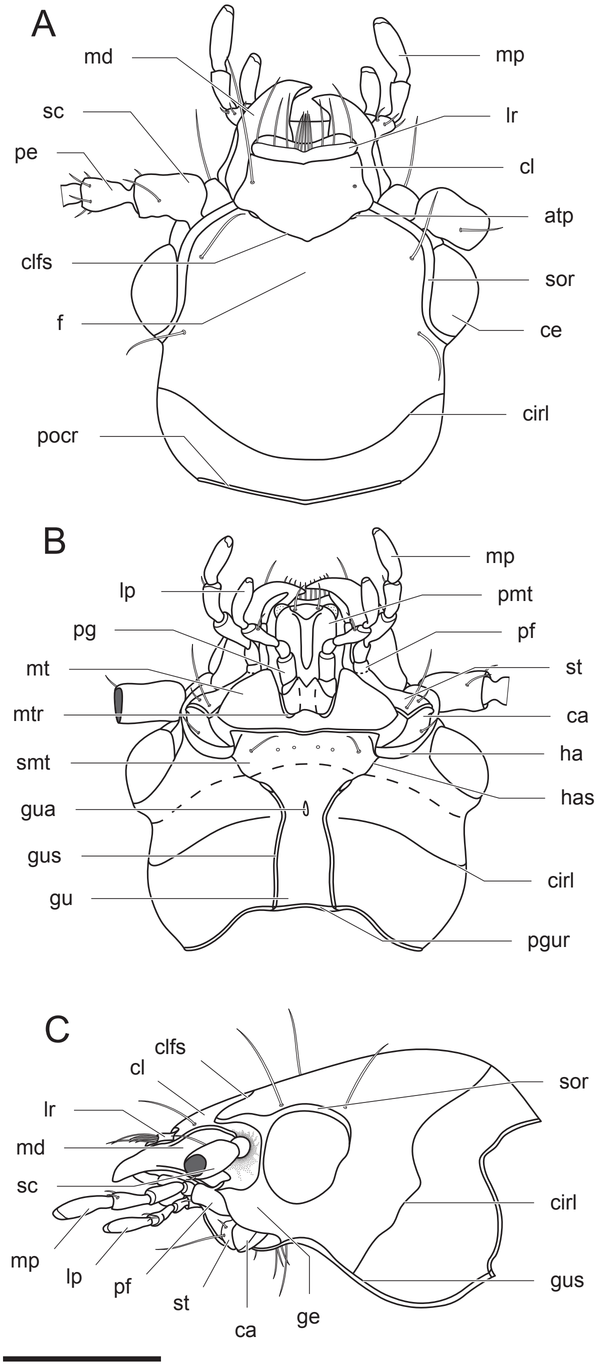


Fig. 1. *Trachypachus holmbergi*, head, habitus. **A**: Dorsal view. **B**: Ventral view. **C**: Lateral view. Abbreviations: atp = anterior tentorial pit, ca = cardo, ce = compound eye, cirl = circular line, cl = clypeus, clfs = clypeofrontal suture, f = frons, ge = gena, gu = gula, gua = gular apodeme, gus = gular suture, ha = hypostoma, has = hypostomal suture, lp = labial palp, lr = labrum, md = mandible, mp = maxillary palp, mt = mentum, mtr = mental ridge, pe = pedicellus, pf = palpifer, pg = palpiger, pmt = prementum, pocr = postoccipital ridge, ptp = posterior tentorial pit, sc = scapus, smt = submentum, sor = supraocular ridge, st = stipes. (Scale bar: 500 μm)

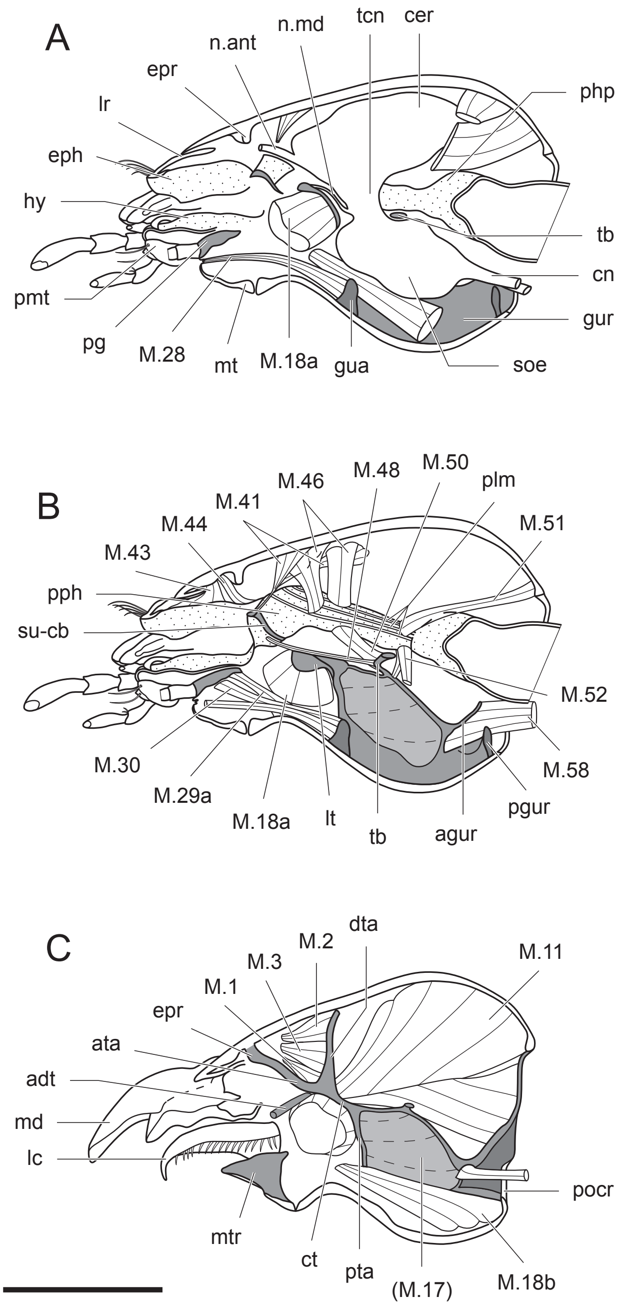


Fig. 2. *Trachypachus holmbergi*, head, sagittal sections. **A**–**C**: Sagittal view in successive stages of dissection. Endoskeletal elements grey, semimembranous parts punctured, translucent structures marked by dashed lines. Abbreviations: adt = adductor tendon, agur = apodeme of gular ridge, ata = anterior tentorial arm, cer = cerebrum, cn = connective, ct = central tentorial body, dta = dorsal tentorial arm, eph = epipharynx, epr = epistomal ridge, gua = gular apodeme, gur = gular ridge, hy = hypopharynx, lc = lacinia, lr = labrum, lt = laminatentorium, md = mandible, mt = mentum, mtr = mental ridge, n.ant = nervus antennalis, n.md = nervus mandibularis, pg = palpiger, pgur = postgular ridge, php = postpharynx, plm = pharyngeal longitudinal musculature, pmt = prementum, pocr = postoccipital ridge, pph = prepharynx, pta = posterior tentorial arm, smt = submentum, soe = suboesophageal ganglion, su-cb = suspensorial cross-bar, tb = tentorial bridge, tcn = tritocerebral connective. (Scale bar: 500 μm)

The tentorium is well developed. The anterior arms arise from the epistomal ridge. The dorsal arms are attached to the dorsal head capsule by fibrillae (Fig. 5E). The central body of the tentorium connects the anterior, dorsal and posterior arm (incl. gular ridge). The laminatentoria, a pair of medially projecting, nearly horizontal plate-like processes, arise from the central body. The plates almost meet medially but are not fused (Fig. 5D). They provide a wide area of origin for the large stipital retractor. Further endoskeletal structures are the circumantennal ridges and the circumocular ridges, enclosing the antennal bases and the compound eyes, respectively (Fig. 5B). The internal ridges of the mentum will be described in section 4.1.7. (Labium) and the suspensorium in section 4.1.8. (Hypopharynx).

4.1.3. Antennae

Figs. 1, 4B,C, 5B

Skeletal features. The antennae are inserted laterally in a wide groove between the eyes and mandibles. The articulation area of the antenna is enclosed by a circumantennal ridge with an inconspicuous anteroventral process, which corresponds to a small furrow on the scapus.

The antenna is 11-segmented and filiform. The scapus is bipartite and the largest antennomere. The proximal articulatory part is globular and separated from the distal cylindrical part by a deep constriction. The longitudinal axes of both parts form a distinct angle. Because of this acentric attachment of the globular part its anterior base appears distinctly prominent (Fig. 4C). All the following antennomeres are centrically attached to each other and widening distally. The pedicellus is about half the size of the scapus and shorter than the flagellomeres. The apical segment is slightly longer than the preceding ones.

The antennomeres are not pubescent. An apical circle of setae is present on all antennomeres except the scapus. A second, basal circle is present on the third and following flagellomeres. In addition several single setae are scattered on the scapus and the apical segment. The tip of the apical antennomere bears a sensory field of fine, very short sensilla.

Musculature (Figs. 2C, 3A,B, 5B–D)**. *M. tentorioscapalis anterior* (*M.1*):** (O) entire length of the anterior tentorial arm, fan-shaped (broad at the origin and converging towards the insertion); (I) anteroventrally on the condyle of the scapus; (F) depressor and rotator of the antenna. — ***M. tentorioscapalis posterior* (*M.2*):** (O) dorsal tentorial arm, reaching the head capsule dorsally, fan-shaped; (I) posterodorsally on the condyle of the scapus; (F) elevator, retractor, and rotator of the antenna. — ***M. tentorioscapalis lateralis/medialis* (*M.3/4*):** (O) dorsal tentorial arm, between M.2 and the central tentorial body, fan-shaped; (I) medioventrally on the inner basal margin of the scapus; (F) depressor of the antenna, together with M.1. The muscle is the largest of the antennal muscles. An unambiguous homologisation is not possible. V. KÉLER's (1963) nomenclature refers to an orthognathous head with antennae inserting anteriorly between the compound eyes. — ***M. scapopedicellaris lateralis* (*M.5*):** (O) dorsal wall of the scapus, distad the constriction, broad at the origin; (I) dorsally on the base of the pedicellus, (F) extensor and elevator of the flagellum. — ***M. scapopedicellaris medialis* (*M.6*):** (O) ventral wall of the scapus, distad of the constriction, broad at the origin; (I) ventrobasal margin and anterior wall of the pedicellus; (F) flexor and depressor of the flagellum, antagonistic to M.5. The muscle is bipartite and twice as large as the dorsal M.5.

4.1.4. Labrum

Figs. 1, 2, 4E,F

Skeletal features. The labrum is movably connected to the clypeus. Its surface is divided into an anterior and a slightly elevated and longer posterior part by a distinct transverse ridge. A row of setae inserts on this ridge; the inner setae are shorter and more densely arranged. The anterior labral edge appears bilobed due to a shallow median emargination.

The anterior labral margin is folded inwards and forms a triangular plate projecting into the membranous epipharynx. It is posteriorly enclosed by a V-shaped ridge converging into a broad median bar (Fig. 4F). The ventral side of this bar is covered with minute microtrichiae. Tormae are present at the caudolateral labral angles. They are firmly connected to the dorsal suspensorial arms (see section 4.1.8. [Epipharynx]). Thus the epipharynx is supported by the median bar and the tormae and the following suspensorial arms.

Musculature. Extrinsic (***M. labroepipharyngalis*, *M.7***; ***M. frontolabralis*, *M.8***) and intrinsic (***M. frontoepipharyngalis*, *M.9***) labral muscles are absent.

4.1.5. Mandibles

Figs. 1, 3, 4K–N, 5A, 6

Skeletal features. The mandibles are distinctly protruding beyond the anterior and lateral labral margin. The length/width ratio is 1.6. The dorsal and ventral sides are flattened. The lateral side is concave at the base with pronounced rims enclosing the concavity dorsally, ventrally, and posteriorly.

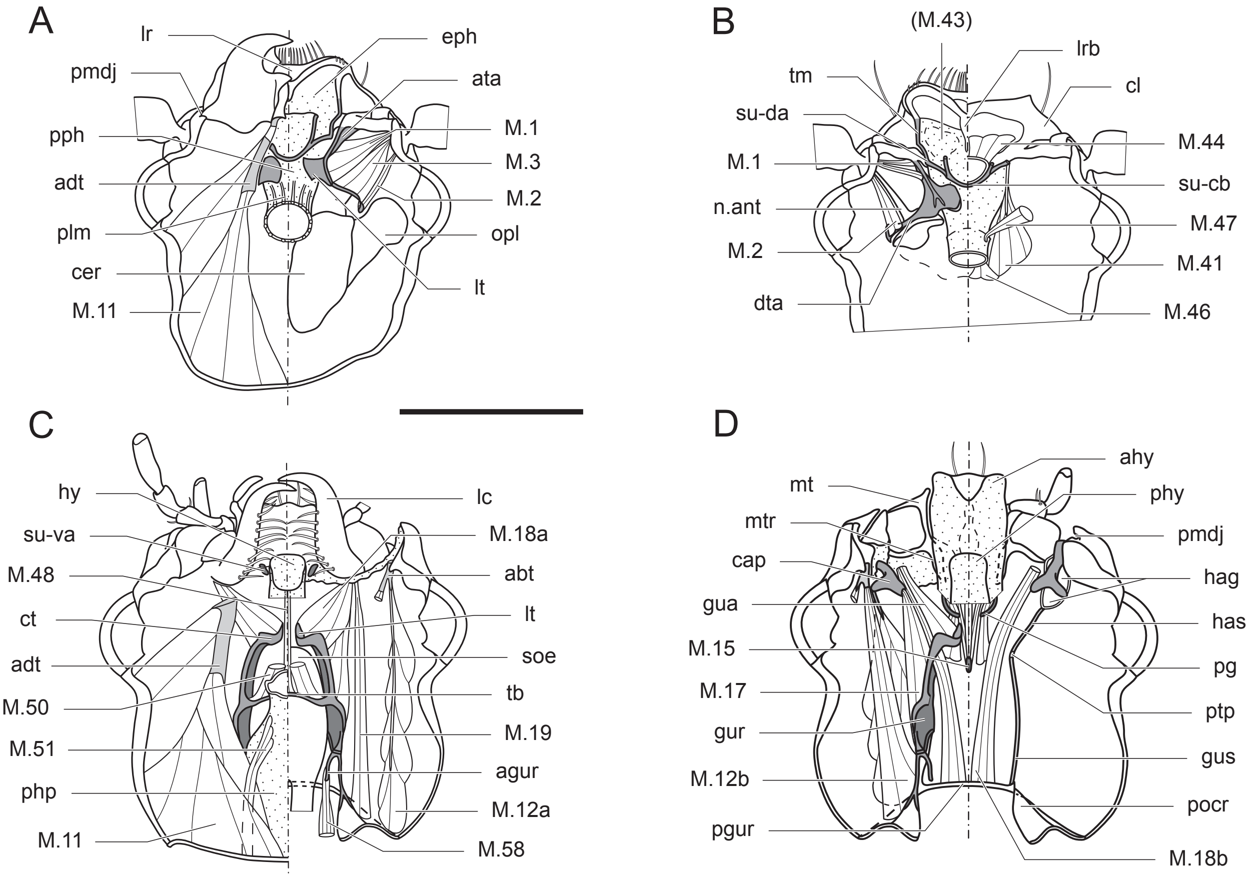


Fig. 3. *Trachypachus holmbergi*, head, horizontal sections. **A–B**: Ventral view of dorsal half in successive stages of dissection. **C–D**: Dorsal view of ventral half in successive stages of dissection. Endoskeletal elements grey, semimembranous parts punctured, translucent structures marked by dashed lines. Abbreviations: abt = abductor tendon, adt = adductor tendon, agur = apodeme of gular ridge, ahy = anterior hypopharynx, ata = anterior tentorial arm, cap = cardo process, cer = cerebrum, cl = clypeus, ct = central tentorial body, dta = dorsal tentorial arm, eph = epipharynx, gua = gular apodeme, gur = gular ridge, gus = gular suture, hag = hypostomal groove, has = hypostomal suture, hy = hypopharynx, lc = lacinia, lr = labrum, lrb = median bar of labrum, lt = laminatentorium, mt = mentum, mtr = mental ridge, n.ant = nervus antennalis, opl = optic lobe, pg = palpiger, pgur = postgular ridge, php = postpharynx, phy = posterior hypopharynx, plm = pharyngeal longitudinal musculature, pmdj = primary mandibular joint, pocr = postoccipital ridge, pph = prepharynx, ptp = posterior tentorial pit; soe = suboesophageal ganglion, su-cb = suspensorial cross-bar, su-da = dorsal suspensorial arm, su-va = ventral suspensorial arm, tb = tentorial bridge, tm = torma. (Scale bar: 500 µm)

The well developed apical incisor is acute and slightly bent downwards, whereas the subapical tooth is markedly smaller and blunt. In mesal view the distal cutting edge between them is shaped like a reversed J. A third, mesal tooth on the inner margin is separated from the subapical incisor by a deep emargination. A mola is absent. The mesal side of the mandible between the mesal tooth and the basal margin is broadened, forming a nearly trapezoid, concave area (Fig. 6D,E). On the ventral side a fringe of hairs is inserted along a minute ridge parallel to the inner margin (Fig. 6G–K).

The primary and secondary mandibular joints at the laterobasal corners are connected by the protruding basal rim (Fig. 6L,M). The axis through them is nearly vertical, resulting in almost horizontal movements of the mandibles. The ventral primary joint is a globular condyle of the mandible articulating with a shallow socket on the hypostoma. A round, flat bulge immediately above the condyle is the insertion point of the abductor tendon (M.12). The dorsal secondary joint is a triangular, concave socket on the mandible articulating with a protuberance of the clypeus.

Numerous sensilla inserted in deep, round pores are scattered on the distal dorsal and lateral surfaces (Fig. 6C). Laterally a large elliptic pore (diameter 4 µm × 28 µm) is present. Viewed with SEM the pore appears bipartite with a less deep and smaller anterior part and an extremely deep and larger posterior part (Fig. 6N). Apparently the latter completely penetrates the mandibular wall. In *Systolosoma* this pore is associated with a long curved seta. It is likely that the socket of the setae in *Trachypachus* is combined with a glandular duct associated with glandular tissue posterad the mandibular base within the head capsule.

The mandibles are nearly symmetrical, but differ in some details. The left mandible is slightly longer than the right, which appears more compact. The distal cutting edge of the right mandible is shorter and concave (Fig. 6A,B), and its subapical incisor fits with a minute notch of the straight and longer cutting edge of the left mandible (Fig. 6G). The mesal mandibular regions also differ slightly in their proportions.

Musculature (see also Fig. 5B–F)**. *M. craniomandibularis internus* (*M.11*):** (O) lateral, dorsolateral and dorsal wall of the head capsule, reaches the postoccipital ridge, extremely extensive area of origin; (I) mesal mandibular base with a strongly developed, sclerotised adductor tendon; (F) adductor of the mandible. The muscle is the most complex and voluminous muscle of the head. Its bundles converge strongly towards the adductor tendon. — ***M. craniomandibularis externus* (*M.12a,b*):** (O) subcomponent ***a***: narrow, elongate area on the lateroventral wall of the head capsule; subcomponent ***b***: postoccipital ridge, posterad of M.15; (I) flat bulge on the lateral mandibular base with a sclerotised abductor tendon; (F) abductor of the mandible. The muscle is irregularly bipartite on its origin with a clearly separated lateral and a mesal part. The subcomponents converge towards the single adductor tendon. — ***M. hypopharyngomandibularis* (*M.13*):** absent.

4.1.6. Maxillae

Figs. 1, 3C,D, 4G,H, 5

Skeletal features. The maxillae are inserted in the hypostomal grooves below the mandibles. The elongate cardo is at a right angle to the body axis. A single seta originates on its lateral side. A bifurcated internal process with a mesal and lateral branch is present on the dorsal side of the cardo. The stipes is posteriorly connected to the cardo and divided into a lateral basistipes and a ventral mediostipes. Two setae originate close to the stipito-cardinal border. The basistipes is convex and triangular. The mediostipes forms an acute angle posteriorly and is anteriorly continuous with the lacinia without a visible suture. The lacinia is sclerotised and hook-shaped. A dorsal and a ventral row of strong bristles originate along the mesal edge. The bipartite, palp-like galea is movably connected to the mediostipes and is adjacent to the ventral side of the lacinia.

The palpifer is connected to the basistipes. It forms a distal socket which bears the palp; the dorsal side is enlarged as a nearly rhomboid plate between the lacinia and the basistipes. The palp is 4-segmented and half as long as the head from the anterior labral margin to the dorsal postoccipital ridge. Palpomere 1 is conspicuously shortened, palpomeres 2 and 3 are twice as long as wide, and palpomere 4 is elongated. The first three segments bear a single seta distally. An extensive, undivided sensory field is present on the apex of the distal palpomere.

Musculature. *M. craniocardinalis externus* (*M.15*): (O) posteroventral area of the head capsule, laterad of the gular ridges, between M.17 and M.12, fan-shaped; (I) lateral branch of the internal cardinal process, with a short sclerotised tendon; (F) extensor of the cardo (inserts laterad of the cardinal articulation pivot). — ***M. craniocardinalis internus* (*M.16*):** absent. — ***M. tentoriocardinalis* (*M.17*):** (O) lateral face of the gular ridge, strongly fan-shaped; (I) mesal branch of the internal cardinal process; (F) flexor of the cardo, adductor of the maxilla, antagonistic to M.15 (muscle inserts mesad of the articulation pivot). — ***M. tentoriostipitalis* (*M.18a,b*):** (O) subcomponent ***a***: anterior face of the laminatentorium; subcomponent ***b***: posteriormost gular region and postgular ridge; (I) ventral membrane between the cardo and the stipital base; (F) stipital adductor and retractor, with vertical component (subcomponent ***a***). The muscle is bipartite with a short, stout, almost vertical subcomponent ***a*** and a thinner, longer and almost horizontal subcomponent ***b***. — ***M. craniolacinialis* (*M.19*):** (O) ventral postoccipital ridge, laterad of the gular ridge; (I) membranous fold at the base of the lacinia, with a slender tendon; (F) adductor and retractor of the lacinia. The muscle shows a characteristic position. It lies above the cardinal process between the mesal and lateral branch of the cardo process. — ***M. stipitolacinialis* (*M.20*):** (O) basal margin of the dorsal plate of the palpifer, mesad of M.22; (I) lateral margin of the mediostipes; (F) adductor of the lacinia and the galea. The homologisation is problematic as v. Kéler (1963) defined this muscle originating on the stipital wall next to the maxillary palp and inserting on the lacinia base. But due to the fact that the palpifer actually bears the palp, and the lacinia and mediostipes are fused the resulting movement corresponds to the function described by v. Kéler. — ***M. stipitogalealis* (*M.21*):** (O) basal wall of the basistipes; (I) ventral basal margin of the galea; (F) movements of the galea. — ***M. stipitopalpalis externus* (*M.22*):** (O) base of the dorsal plate of the palpifer, fan-shaped; (I) lateral base of palpomere 1; (F) abductor of the palp. This homology assessment with v. Kéler (1963) is based on the function whereas the origin is different from that assigned to the muscle in his description. — ***M. stipitopalpalis internus* (*M.23*):** absent. — ***M. palpopalpalis tertius* (*M.26*):** (O) lateral wall of palpomere 2; (I) mesal margin of palpomere 3; (F) flexor of palpomere 3. — ***M. palpopalpalis quartus* (*M.27*):** (O) lateral wall of palpomere 3; (I) mesal margin of palpomere 4; (F) flexor of palpomere 4.

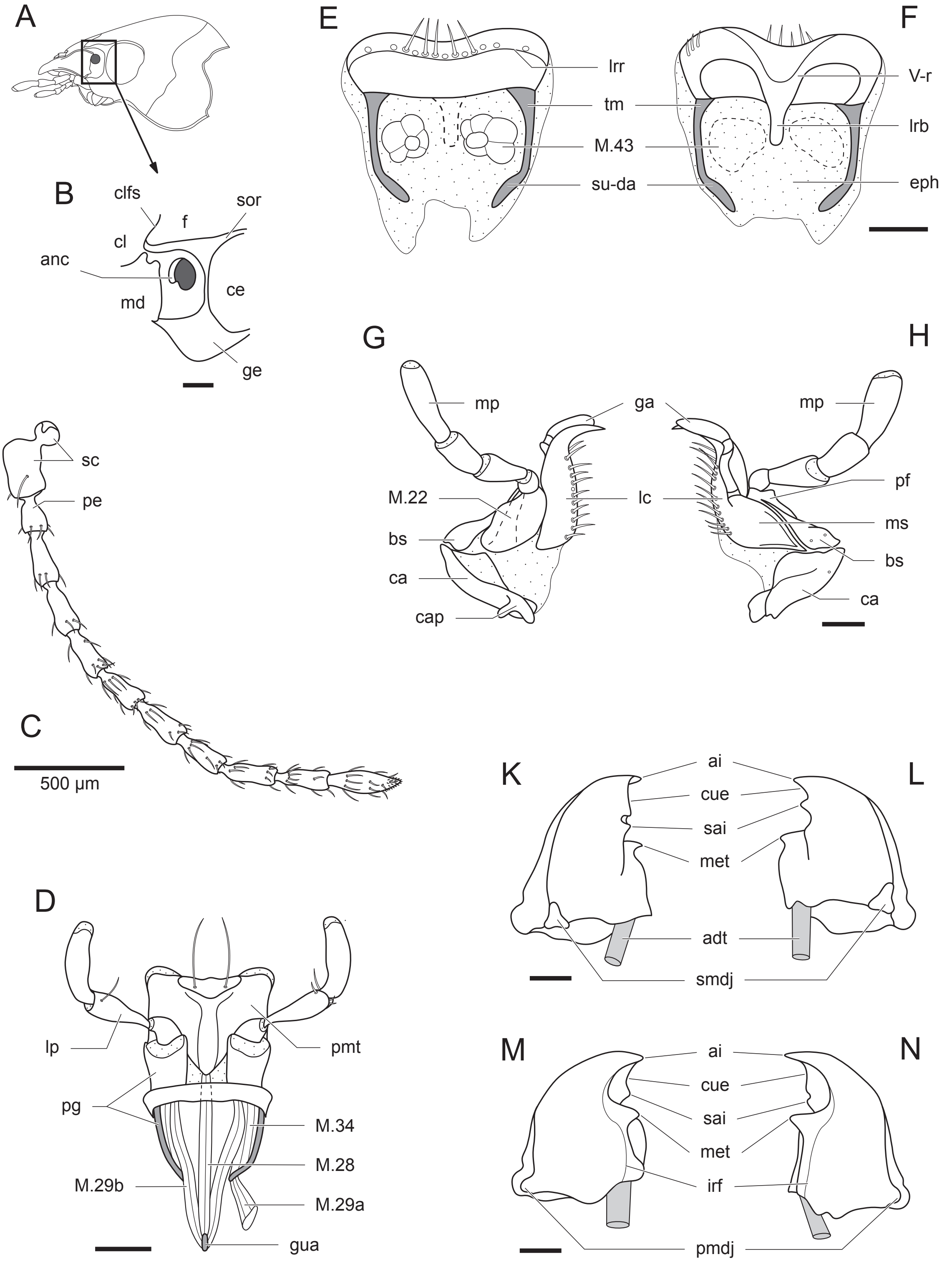


Fig. 4. *Trachypachus holmbergi*, head appendages. **A**: Head, lateral view. **B**: Antennal insertion. **C**: Antenna. **D**: Labium ventral view. **E**: Labrum, dorsal view. **F**: Labrum, ventral view. **G**: Maxilla, dorsal view. **H**: Maxilla, ventral view. **K**: Left mandible, dorsal view. **L**: Right mandible, dorsal view. **M**: Right mandible, ventral view. **N**: Left mandible, ventral view. Endoskeletal elements grey, semimembranous areas punctured, translucent structures marked by dashed lines. Abbreviations: adt = adductor tendon, ai = apical incisor, anc = circumantennal ridge with process, bs = basistipes, ca = cardo, cap = cardo process, ce = compound eye, cl = clypeus, clfs = clypeofrontal suture, cue = cutting edge, eph = epipharynx, f = frons, irf = insertion ridge of ventral fringe of hairs, ga = galea, ge = gena, gua = gular apodeme, lc = lacinia, lp = labial palp, lrb = median bar of labrum, lrr = transverse labral ridge, md = mandible, met = mesal tooth, mp = maxillary palp, ms = mediostipes, pe = pedicellus, pf = palpifer, pg = palpiger, pmdj = primary mandibular joint, pmt = prementum, sai = subapical incisor, sc = scapus, smdj = secondary mandibular joint, sor = supraocular ridge, su-da = dorsal suspensorial arm, tm = torma, V-r = V-shaped ridge of ventral labrum. (Scale bars, except in A and C: 100 µm)

4.1.7. Labium

Figs. 1B, 2, 3, 4D, 5

Skeletal features. The submentum is firmly connected to the head capsule and posteriorly completely fused with the gula. The anterior margin is connected to the mentum. A transverse row of six setae is present parallel to the anterior margin. The submentum and mentum are more than twice as wide as the gula. Two large lateral lobes of the mentum enclose a deep emargination with two paramedian cusps. The internal mental ridges (Fig. 5B) are recognisable externally. The upper posterior corners of the triangular ridges are firmly connected to the ventral suspensorial arms. The surface of the mentum bears no setae. The prementum is connected to the anterior mental margin and is inserted in its median emargination. A pair of setae arises from the anterior margin, which is folded inwards and forms a triangular sclerite extending onto the surface of the hypopharynx. The ventral wall of the prementum forms a blunt longitudinal keel (Fig. 5A). The palpigera are attached to the prementum and subdivided into an external cylindrical part and an internal arcuate process. The palps fit into the groove between the premental median keel and the mental lateral lobes. They are 3-segmented and distinctly shorter than the maxillary palp. Palpomere 1 is markedly shortened. Palpomere 2 bears mesally two small setae and palpomere 3 a large terminal undivided sensory field.

Musculature. ***M. submentopraementalis* (*M.28*):** (O) basal anterior margin of the gular apodeme; (I) medially on the connecting membrane between mentum and prementum, with a short sclerotised tendon; (F) retractor and depressor of the prementum. The components of M.28 are attached to the prementum at a single point of insertion but cross-sections of the posterior part show that it is a paired muscle. — ***M. tentoriopraementalis inferior* (*M.29a,b*):** (O) subcomponent ***a***: ventral head capsule at the submento-mental border, in front of the gular apodeme; subcomponent ***b***: lateral faces of the gular apodeme; (I) subcomponent ***a***: apically on the internal process of the palpiger; subcomponent ***b***: ventrally on the base of the cylindrical part of the palpiger; (F) retractor of the labial palp, adductor (subcomponent ***a***). The muscle is bipartite with a short, almost vertical subcomponent ***a*** and an almost horizontal and widened subcomponent ***b***. Part ***a*** is located laterally of part ***b***. — ***M. tentoriopraementalis superior* (*M.30*):** (O) anterior margin of gular apodeme, dorsally of M.28; (I) medially on the membranous fold between the anterior and posterior hypopharynx, with a thin tendon; (F) retractor of the anterior hypopharynx and of the prementum. M.30 is a paired muscle (as cross-sections show) but it is inserted on the hypopharynx at a single point. — ***M. praementopalpalis externus* (*M.34*):** (O) inner margin of the internal process of the palpiger, fan-shaped, opposite to M.29a; (I) ventral base of palpomere 1; (F) movements of the labial palp.

4.1.8. Epipharynx and hypopharynx

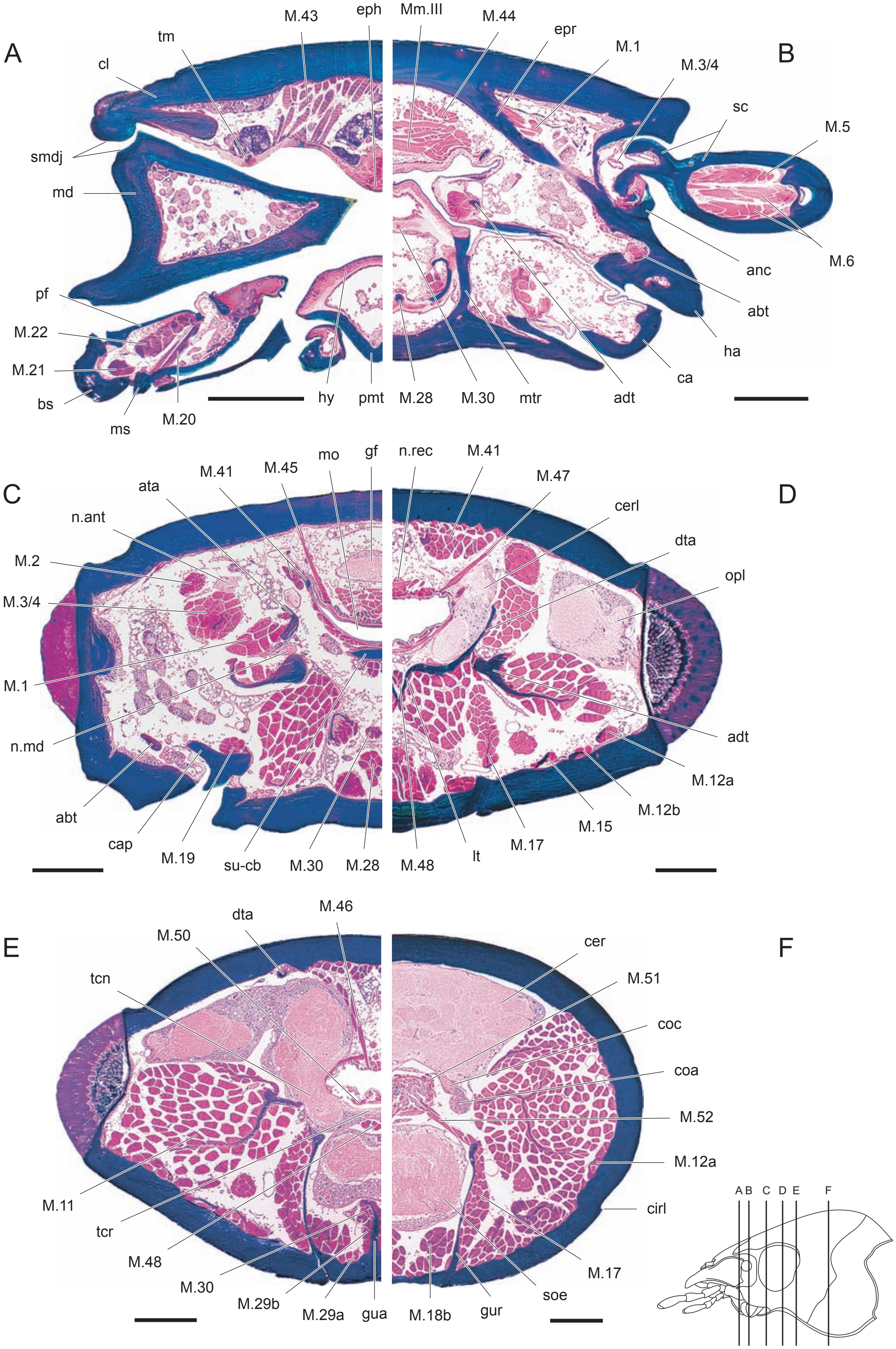
Figs. 2, 3, 4D–F, 5

General features. The anterior epipharynx is internally subdivided by a median labral bar that is posteriorly continuous with a median bulge (Fig. 5A). Epipharyngeal lobes are not developed and sensory appendages are also lacking. The surface is smooth except for the area below the bar, which is covered with microtrichia.

The hypopharynx is subdivided into an anterior and a posterior part. The anterior hypopharynx is retractile into the posterior hypopharynx and covers the prementum dorsally. A pair of membranous lobes overlaps the anterior margin of the prementum and encloses the median triangular premental sclerite (Fig. 3D). The hypopharyngeal surface is entirely smooth. The preoral cavity between the dorsal epipharyngeal bulge and the convex posterior hypopharynx is distinctly narrowed and appears x-shaped in cross-section (Fig. 5B). The anatomical mouth opening is ventrally strengthened by a transverse sclerite, the suspensorial cross-bar. It is anteriorly connected to a pair of dorsal and ventral arms. The dorsal suspensorial arms are continuous with the tormae (see section 4.1.4.) and support the epipharynx laterally. The ventral suspensorial arms similarly strengthen the lateral edges of the hypopharynx (see section 4.1.7.). They are firmly connected to the mental ridges.

Musculature. ***M. frontohypopharyngalis* (*M.41*):** (O) frons, laterally of M.46, strongly broadened at the

Fig. 5. *Trachypachus holmbergi*, head, cross-sections. Lateral view of the head on the left side with the section planes marked. **A–F**: Cross-sections in anterior-posterior sequence. Abbreviations: abt = abductor tendon, adt = adductor tendon, anc = circumantennal ridge with process, ata = anterior tentorial arm, bs = basistipes, ca = cardo, cap = cardo process, cer = cerebrum, cerl = anterior cerebral lobe, cirl = circular line, cl = clypeus, coa = corpus allatum, coc = corpus cardiacum, dta = dorsal tentorial arm, eph = epipharynx, epr = epistomal ridge, gf = frontal ganglion, gua = gular apodeme, gur = gular ridge, ha = hypostoma, hy = hypopharynx, lt = laminatentorium, md = mandible, mo = mouth opening, ms = mediostipes, mtr = mental ridge, n.ant = nervus antennalis, n.md = nervus mandibularis, n.rec = nervus recurrens, opl = optic lobe, pf = palpifer, pmt = prementum, sc = scapus, smdj = secondary mandibular joint, soe = suboesophageal ganglion, su-cb = suspensorial cross-bar, tcn = tritocerebral connective, tcr = tritocerebral commissure, tm = torma. (Scale bars: 100 μm)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origin, (I) apicolaterally on the suspensorial cross-bar, with a slender sclerotised tendon; (F) elevator of the suspensorium, contraction of the anatomical mouth. — ***M. tentoriohypopharyngalis*** (***M.42***)**:** absent. — ***M. clypeopalatalis*** (***M.43***)**:** (O) paramedially on the clypeus; (I) dorsal wall of the preoral cavity, between the tormae and the median epipharyngeal bulge, widened at the insertion area; (F) dilator of the preoral cavity. — ***Mm. compressores epipharyngis*** (***Mm. III***)**:** (Fig. 5B) Numerous transverse muscle bundles connect the upper edges of the posterior epipharynx. Between these bundles fibres of M. clypeobuccalis (M.44) insert on the dorsal wall of the preoral cavity. The muscle functions as depressor of the posterior epipharyngeal wall, antagonistic to M. clypeopalatalis (M.43). — ***M. clypeobuccalis*** (***M.44***)**:** (O) paramedially on the posterior clypeus, between M.43 and the epistomal ridge; (I) posteriormost epipharynx, immediately anterad of the mouth opening, between the muscle fibres of Mm.III; (F) dilator of the posterior preoral cavity.

4.1.9. Pharynx

Figs. 2, 3, 5

General features. The anatomical mouth opening is defined by the insertion of M. frontopharyngalis anterior (M.45) and the frontal ganglion which separates this muscle from the epipharyngeal muscles. Further structures associated with the mouth opening are the dorsal transverse Mm. compressores epipharyngis (Mm.III) and the suspensorial cross-bar (see section 4.1.8.) (Fig. 5B,C).

The anterior precerebral pharynx lies in the upper region of the head. The posterior postcerebral pharynx declines slightly towards the foramen occipitale. The pharyngeal wall is equipped with ring muscles and longitudinal muscles (Fig. 5C,D). The lumen of the anterior pharynx is oval in cross-section, whereas the lumen of the posterior pharynx is strongly narrowed by folds. The folds provide space for the strongly developed longitudinal muscles and the edges serve as attachment areas for dilators.

Musculature. ***M. frontobuccalis anterior*** (***M.45***)**:** (Fig. 5C) (O) paramedially on the anterior frons, mesally of M.41; (I) paramedially on the dorsal wall of the precerebral pharynx, immediately posterad of the frontal ganglion; (F) dilator of the precerebral pharynx. — ***M. frontobuccalis posterior*** (***M.46***)**:** (Fig. 5E) (O) posterior frons, mesally of M.41; (I) paramedially on the dorsal wall of the posterior precerebral pharynx, opposite to M.50; (F) dilator of the precerebral pharynx; together with M.50. — ***M. frontobuccalis lateralis*** (***M.47***)**:** (Fig. 5D) (O) middle region of the frons, laterally of M.41; (I) lateral wall of the anterior pharynx, close to M.45 and the frontal ganglion; (F) dilator of the precerebral pharynx. The muscle was often considered as absent in adephagan beetles. Lateral muscles attached to the anterior pharynx are usually addressed as subcomponents of M.45 or M.46 (e.g., Honomichl 1975; Beutel 1986a; Belkaceme 1991). The homologisation suggested here is based on the lateral insertion area and the position close to the frontal ganglion. Moreover the muscle is separated from M.45 and M.46 by the area of origin of M.41. — ***M. tentoriobuccalis anterior*** (***M.48***)**:** (Fig. 5C–E) (O) median process of the tentorial bridge; (I) medially on the hypopharynx, immediately in front of the suspensorial cross-bar; (F) retractor and depressor of the hypopharynx, dilator of the preoral cavity. The muscle always stretches posteriorly between the tritocerebral commissure and the suboesophageal ganglion (Fig. 5E) and anteriorly between the mesal margins of the laminatentoria (Fig. 5D). It was often misinterpreted as M. tentoriohypopharyngalis (M.42) due to its insertion and function. The homologisation presented here follows v. Kéler (1963) referring to its position relative to the tritocerebral commissure. Thus the insertion of the muscle has shifted anteriorly from the anterior pharynx to the hypopharynx and the function has changed from a dilator of the precerebral pharynx to a retractor of the hypopharynx. — ***M. tentoriobuccalis posterior*** (***M.50***)**:** (O) anterior margin of the tentorial bridge, laterally of M.48; (I) ventral wall of the precerebral pharynx, opposite to M.46; (F) dilator of the precerebral pharynx, together with M.46. The muscle always lies between the tritocerebral commissure and the pharynx (Fig. 5E). — ***M. verticopharyngalis*** (***M.51***)**:** (O) posterior head capsule, reaches the postoccipital ridge, between larger bundles of M.11; (I) dorsolaterally on the postcerebral pharynx, ventrally of the central part of the cerebrum, opposite to M.52; (F) dilator of the postcerebral pharynx, together with M.52. — ***M. tentoriopharyngalis*** (***M.52***)**:** (O) dorsal margin of the gular ridge, immediately posteriorly of the tentorial bridge; (I) ventrolaterally on the postcerebral pharynx, above the suboesophageal ganglion, opposite to M.51; (F) dilator of postcerebral pharynx; together with M.51.

4.1.10. Nervous system

Cerebrum and suboesophageal ganglion (Figs. 2A, 3A,C, 5D–F)**.** The cerebrum is large in relation to the head size. Two anterior lobes comprise the anteriormost part of the protocerebrum and the deuto- and tritocerebrum. They are adjacent to the inner faces of the dorsal tentorial arms and reach the laminatentoria. Posterior protocerebral lobes nearly reach the occipital

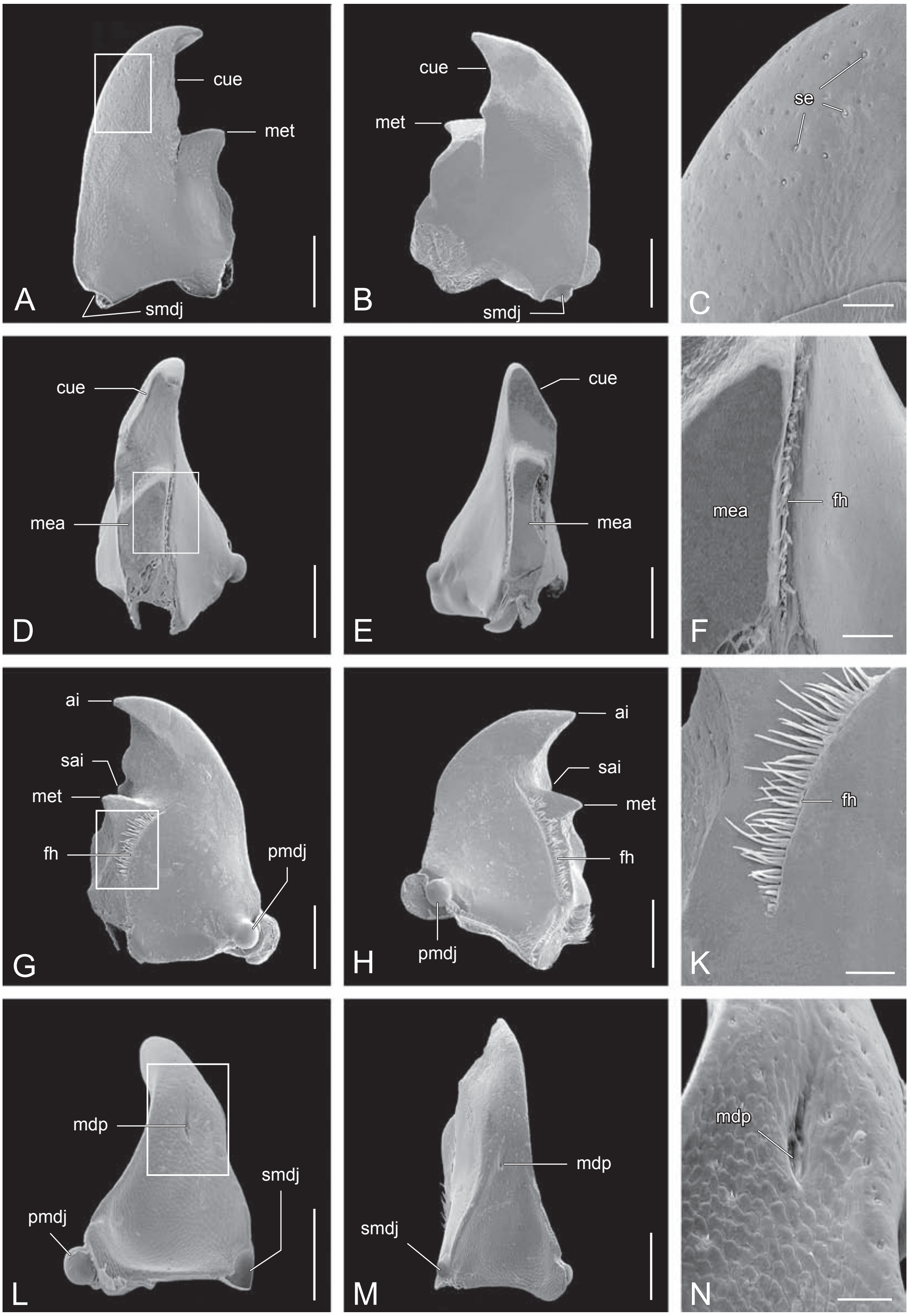


Fig. 6. *Trachypachus holmbergi*, mandible, SEM micrographs. **1st column**: Left mandible. **2nd column**: Right mandible. **3rd column**: Detail magnifications of the framed sectors. **1st line**: Dorsal view. **C**: Sensory grooves. **2nd line**: Median view. **F**: Mesal area. **3rd line**: Ventral view. **K**: Ventral fringe of hairs. **4th line**: Lateral view. **N**: Lateral pore. Abbreviations: ai = apical incisor, cue = cutting edge, fh = ventral fringe of hairs, mdp = mandibular pore, mea = mesal trapezoid area, met = mesal tooth, pmdj = primary mandibular joint, sai = subapical incisor, se = sensilla, smdj = secondary mandibular joint. (Scale bars: 100 µm, except detail magnification in third column: 20 µm)

foramen. The central body of the protocerebrum fills out the entire width of the dorsal head capsule. The circumoesophageal tritocerebral connectives are connected by the tritocerebral commissure posterad of the laminatentoria. The suboesophageal ganglion reaches the anterior margin of the gular ridges anteriorly. Posteriorly it splits into paired connectives leading to the prothoracic ganglia.

Nerves (Figs. 2A, 3A, 5C,D)**.** The optic neuropils originate on the anterior cerebral lobes, close to the nervi antennalis and the nervi frontalis, which belong to the deutocerebrum and tritocerebrum, respectively. The nervi mandibulares originate on the tritocerebral connectives close to the tritocerebral commissure and lie above the laminatentoria. The nervi maxillares and nervi labiales arise anteriorly on the suboesophageal ganglion.

Frontal ganglion and neuroendocrine glands (Fig. 5)**.** The frontal ganglion is of rhombic shape and lies above the anteriormost region of the pharynx close to the anatomical mouth opening (Fig. 5C). Two pairs of nerves and two single nerves originate from the ganglion's body. The nervus procurrens arises anteromedially. A pair of anterolateral nerves innervates the epipharyngeal glands in the median bulge and around the tormae. The nervi frontales connecting the ganglion to the tritocerebrum arise laterally. The nervus recurrens originates posteromedially. It is connected to the ganglion ventriculare posterad of the tentorial bridge and sends out fine nerves to the corpora cardiaca and corpora allata (Fig. 5F). These neuroendocrine glands are laterally adjacent to the posterior pharynx.

4.2. Head morphology of *Haliplus* sp.

4.2.1. External head capsule

Figs. 7, 11, 12

The head is prognathous and slightly broader than long. The large kidney-shaped compound eyes are largely integrated into the contour of the head capsule but protrude to some extend anteriorly. The colouration is light brown. The surface displays an irregular pattern of distinct pores with sensilla. The diameter of the pores, their distribution and the shape of the sensilla varies on different head regions. The central area of the dorsal head capsule is glabrous without any pores, sensilla or setae (Fig. 12E). The retracted posteriormost part of the head, a broad collar around the postoccipital ridge, is also smooth. Generally the pores increase in diameter from anterior to posterior and in density around the compound eyes, and towards the anterior margin of the head and the posterior collar. The ventral head capsule is largely devoid of pores.

The clypeal region is short. Its pores bear broadened and flattened, short setae. The clypeofrontal suture is interrupted and the clypeus confluent with the frontal region. The clypeal musculature is shifted posteriorly (see section 4.2.8. [Hypopharynx]). The protuberances of the secondary mandibular joint are present at the posterolateral angles of the clypeus. The dorsally shifted antennal insertions are concealed by the frons. The anterior tentorial pits are not visible externally.

The frontal and coronal sutures are absent. Two postocular ridges parallel to the posterior margins of the compound eyes are present on the lateral side of the head. The anterior ridge is curved and continuous with the circumocular ridge ventrally and dorsally. The longer posterior ridge is almost straight laterally. It reaches the ventrolateral head capsule, where it is bent anteriorly towards the cardo. A further, short, longitudinal ridge extends from the hypostoma posteriorly (Fig. 12K).

The gula is broad and fused with the submentum anteriorly. The posterior tentorial pits are concealed by a pair of small submental lobes. The few pores on the gular surface bear small, hook-shaped sensilla. The hypostoma, which is entirely concealed by the maxillary base, forms an acute angle with the gena with a strengthened edge. The deep socket of the primary mandibular joint is present anterolaterally on the hypostoma (Fig. 11A).

On the posteriormost gula the internal gular apodeme is recognisable. The postoccipital ridge is widened laterally, where it is connected to the gular ridges. A pair of small apodemes is present dorsally. The thoracic M. praephragmapostoccipitalis medialis (M.55) originates on these apodemes.

4.2.2. Internal skeletal structures

Figs. 8, 9, 11

The epistomal ridge is largely absent, but a short internal ridge connects the well developed circumantennal ridges with the posterior clypeal angles. The dorsal margins of the gular ridges are strengthened and their anterior margins are fused with the posterior tentorial arms. Their bases are anteriorly continuous with the hypostomal ridges. The gular ridges are posteriorly fused with the postoccipital ridge. Above the middle gular region the tentorial bridge connects the gular ridges. The bridge is distinctly curved anteriorly and bears a median process. Immediately behind the bridge a pair of small apodemes arises on the mesal sides of the gular ridges. Two muscles originate on their front or back sides, respectively. The median gular apodeme is small and triangular, and placed on the posterior gula close to the postgular ridge.

The central element of the well developed tentorium connects the dorsal and anterior arm to the posterior arm which is fused with the gular ridge. The

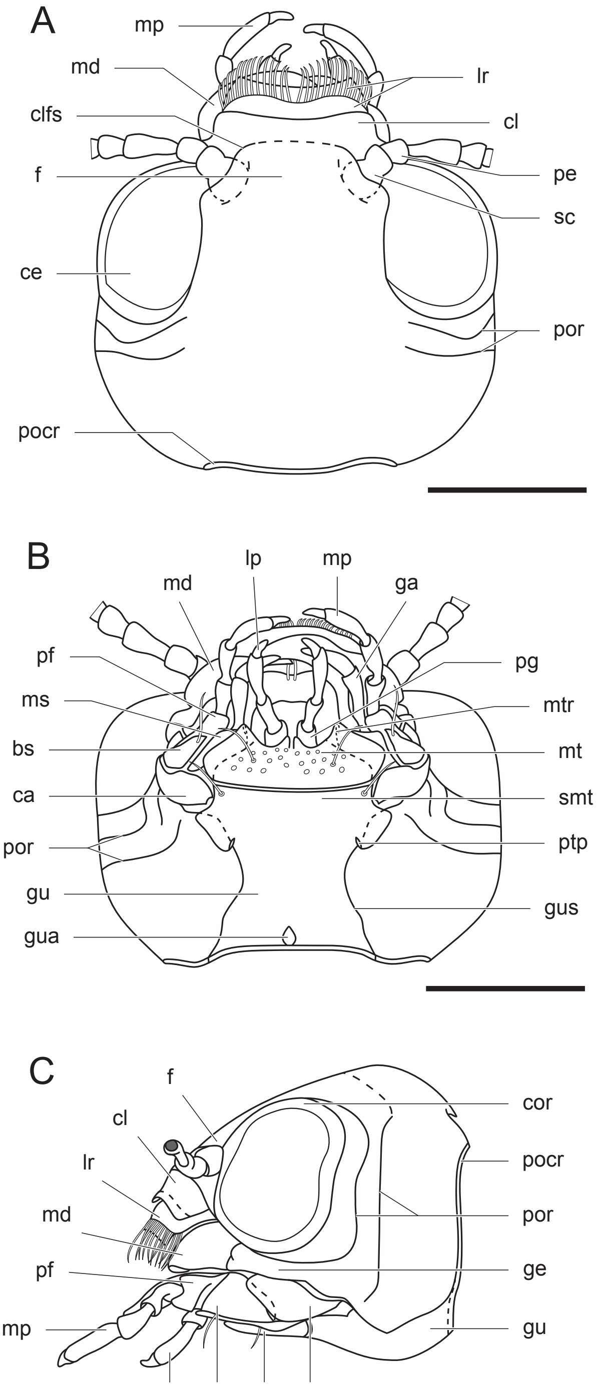


Fig. 7. *Haliplus* sp., head, habitus. **A**: Dorsal view. **B**: Ventral view. **C**: Lateral view. Abbreviations: bs = basistipes, ca = cardo, ce = compound eye, cl = clypeus, clfs = clypeofrontal suture, cor = circumocular ridge, f = frons, ga = galea, ge = gena, gu = gula, gua = gular apodeme, gus = gular suture, lp = labial palp, lr = labrum, md = mandible, mp = maxillar palp, ms = mediostipes, mt = mentum, mtr = mental ridge, pe = pedicellus, pf = palpifer, pg = palpiger, pocr = postoccipital ridge, por = postocular ridge, ptp = posterior tentorial pit, sc = scapus, smt = submentum. (Scale bar: 500 μm)

anterior arm arises from the circumantennal ridge. The dorsal arm is shortened and does not reach the head capsule (Fig. 11D). The laminatentorium originates mesally on the central tentorial body. The laminatentoria are medially fused, forming a pair of adjacent vertical plates (Fig. 11D,E). The voluminous stipital retractor (M. tentoriostipitalis, M.18a) originates on the lateral faces of these plates, whereas the hypopharynx-retractor (M. tentoriobuccalis anterior, M.48) passes through the median space between them (Fig. 11E).

The internal ridges of the mentum are described in section 4.2.7. (Labium) and the suspensorium in section 4.2.8. (Hypopharynx).

4.2.3. Antennae

Figs. 7A,C, 10B,C, 12F

Skeletal features. The filiform, 11-segmented antenna is inserted dorsolaterally above the anterior margin of the compound eye. The insertion area is distinctly separated from the mandibular base. The surface is glabrous except for one seta on the distal scapus (Fig. 12F). Several sensory pores with paddle-shaped sensilla are scattered over the surface of the scapus and pedicellus (Fig. 12F). The bipartite scapus is the widest antennomere. The proximal part is globular and articulates with the head capsule, whereas the distal part is almost cylindrical but strongly shortened. The parts are separated by a deep constriction. A small, anterior process on the antennal circular ridge articulates with a basal emargination on the scapus. The pedicellus is distinctly smaller than the scapus with a proximal globular articulatory part and a cylindrical, but shortened distal part. The first flagellomere is as long as the scapus but more slender. The remaining flagellomeres are similar to the pedicellus in length and barrel-shaped.

Musculature (Figs. 8B, 9A,B, 11B)**.** ***M. tentorioscapalis anterior*** **(*M.1*):** (O) mesal face of the anterior tentorial arm; (I) anteroventrally on the condyle of the scapus; (F) depressor and rotator of the antenna. — ***M. tentorioscapalis posterior*** **(*M.2*):** (O) entire dorsal tentorial arm, fan-shaped; (I) posterodorsally on the condyle; (F) elevator, retractor and rotator of the antenna. — ***M. tentorioscapalis lateralis/medialis*** **(*M.3/4*):** (O) lateral face of the anterior tentorial arm, fan-shaped; (I) medioventrally on the inner basal margin of the condyle; (F) depressor of the antenna, together with M.1 (homology see section 4.1.3.). — ***M. scapopedicellaris lateralis*** **(*M.5*):** (O) dorsal wall of the scapus, proximad of the constriction; (I) dorsally on the base of the pedicellus; (F) extensor and elevator of the flagellum. — ***M. scapopedicellaris medialis*** **(*M.6*):** (O) ventral wall of the scapus, close to the constriction; (I) ventrobasal margin of the pedicellus; (F) flexor and depressor of the flagellum, antagonist of M.5.

4.2.4. Labrum
Figs. 7, 9B, 10E,F, 12B,C

Skeletal features. The short labrum is inclined downwards. Its anterior edge is broadly concave. A superficial, transverse ridge separates an anterior part from the longer and wider posterior part. A row of strong setae is inserted along this ridge (Figs. 10E, 12B). The finer lateral setae are arranged in two rows.

The anterior margin is folded inwards and forms an extensive sclerite on the ventral side (Fig. 10F). Some short and thick setae are inserted ventrally, close to the anterior edge (Fig. 12C). A broad, heart-shaped, dense field of long microtrichia is integrated into the ventral sclerite (Fig. 12C). An internal median bar is present between the anterior half of the labrum. The posterolateral angles form a pair of tormae, which are connected to the dorsal suspensorial arms (see section 4.2.8. [Hypopharynx]) by strong ligament-like structures.

Musculature. Absent.

4.2.5. Mandibles
Figs. 7, 9A, 10K–N, 11, 12A,D

Skeletal features. The mandibles are slightly protruding laterally but not beyond the anterior labral margin. They are longer than wide with a length/width ratio of 1.6. The ventral side is flat whereas the dorsal side is moderately convex. The surface is smooth except for the lateral side, which is covered with pores with styliform sensilla (Fig. 12A). The distal part of the mandibles is conspicuously darker than the remaining regions. The apical tooth is slightly bent downwards. The distal cutting edge between the subapical and the apical incisor is formed like a reversed letter J. A smaller tooth is present in the middle region of the inner margin. The ventral edge between the mesal and the apical tooth is deeply emarginated. On the ventral side a dense brush of microtrichia is inserted on a distinct ridge parallel to the mesal margin. The fringe reaches the emargination distally. The long microtrichia overtop the mesal edge. A mola is absent.

The lateral margin is convex and rounded. The abductor tendon is attached to a bulge on the lateral base which is anteriorly delimited by a constriction. The small condyle of the primary mandibular joint is located submarginally on the ventrobasal margin of the mandible. The dorsobasal margin is emarginated close to the lateral bulge thus forming a concavity, the socket of the secondary joint. The rim surrounding the emargination is strengthened. The axis through both joints is almost vertical.

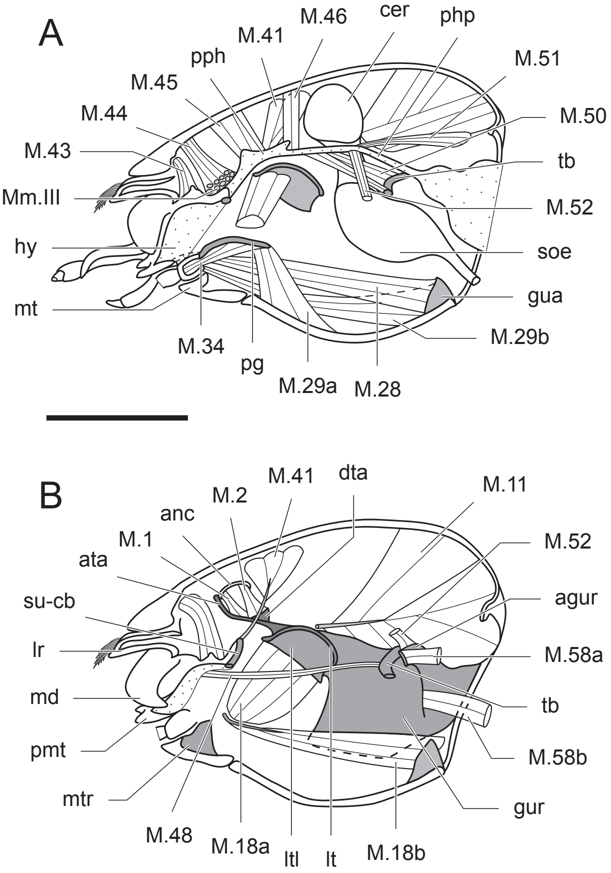


Fig. 8. *Haliplus* sp., head, sagittal sections. **A–B**: Sagittal view in successive stages of dissection. Endoskeletal elements grey, semimembranous parts punctured, translucent structures marked by dashed lines. Abbreviations: agur = apodeme of gular ridge, anc = circumantennal ridge, ata = anterior tentorial arm, cer = cerebrum, dta = dorsal tentorial arm, gua = gular apodeme, gur = gular ridge, hy = hypopharynx, lr = labrum, lt = laminatentorium, ltl = median lamella of laminatentorium, md = mandible, mt = mentum, mtr = mental ridge, pg = palpiger, php = postpharynx, pmt = prementum, pph = prepharynx, soe = suboesophageal ganglion, su-cb = suspensorial cross-bar, tb = tentorial bridge. (Scale bar: 500 μm)

The left and the right mandible are moderately asymmetric, with the left mandible appearing less compact. Its distal cutting edge is longer and straight, whereas the cutting edge of the right mandible is emarginated close to the subapical incisor. The right mesal tooth is reduced to a rounded shallow bump. The mesal margin of the left mandible is concave, whereas it is slightly convex on the right.

Musculature (see also Figs. 8B, 9C)**.** ***M. craniomandibularis internus* (*M.11*):** (O) dorsal and lateral wall of the postocular head capsule, reaches the postoccipital ridge posteriorly; (I) mesal mandibular base with a strongly developed, sclerotised adductor tendon; (F) adductor of the mandible. The areas of origin of this most voluminous head muscle meet dorsomedially. — ***M. craniomandibularis externus* (*M.12*):** (O) narrow,

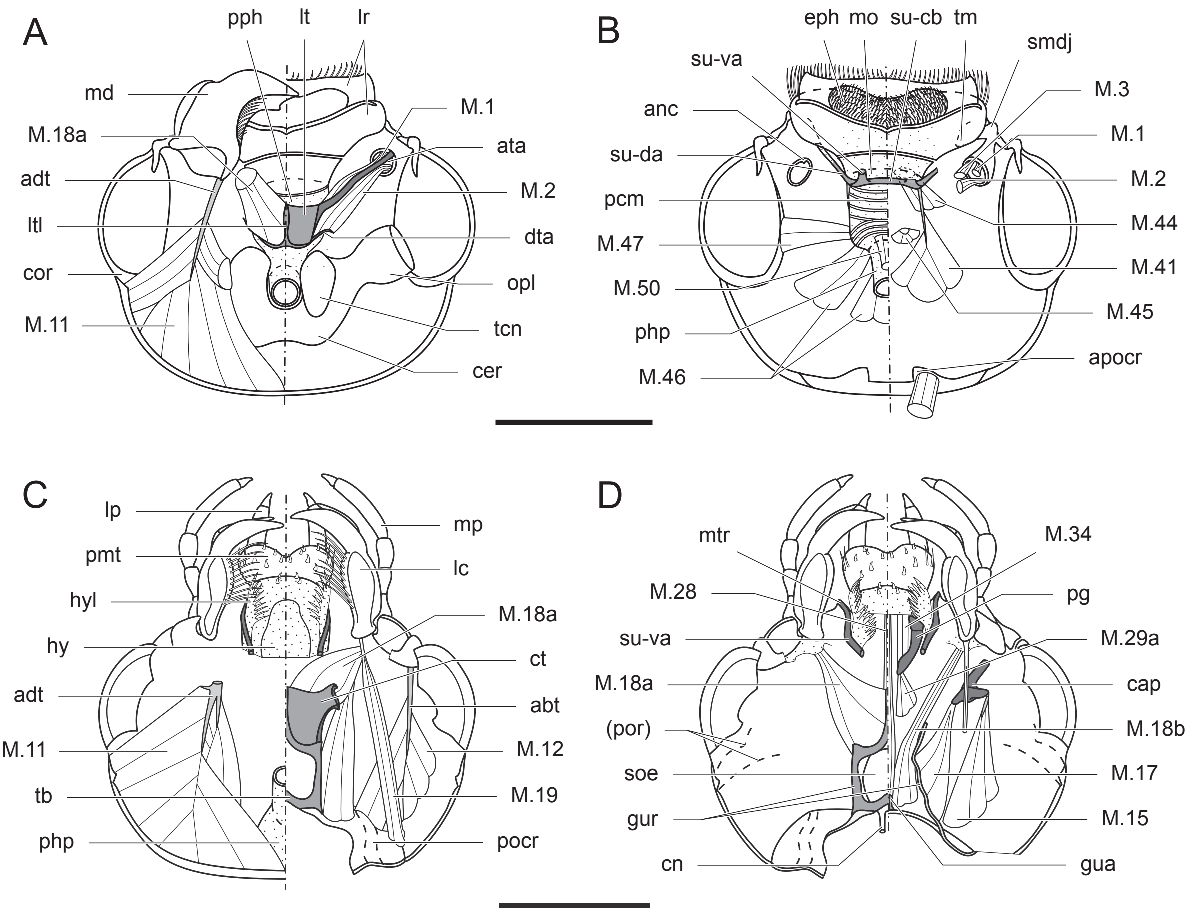


Fig. 9. *Haliplus* sp., head, horizontal sections. **A–B**: Ventral view of dorsal half in successive stages of dissection. **C–D**: Dorsal view of ventral half in successive stages of dissection. Endoskeletal elements grey, semimembranous parts punctured, translucent structures marked by dashed lines. Abbreviations: abt = abductor tendon, adt = adductor tendon, anc = circumantennal ridge, apocr = dorsal apodeme of postoccipital ridge, ata = anterior tentorial arm, cap = cardo process, cer = cerebrum, cn = connective, cor = circumocular ridge, ct = central tentorial body, dta = dorsal tentorial arm, eph = epipharynx, gua = gular apodeme, gur = gular ridge, hy = hypopharynx, hyl = hypopharyngeal lobe, lc = lacinia, lp = labial palp, lr = labrum, lt = laminatentorium, ltl = median lamella of laminatentorium, md = mandible, mo = mouth opening, mp = maxillary palp, mtr = mental ridge, opl = optic lobe, pcm = pharyngeal circular musculature, pg = palpiger, php = postpharynx, pmt = prementum, pocr = postoccipital ridge, por = postocular ridge, pph = prepharynx, smdj = secondary mandibular joint, soe = suboesophageal ganglion, su-cb = suspensorial cross-bar, su-da = dorsal suspensorial arm, su-va = ventral suspensorial arm, tb = tentorial bridge, tcn = tritocerebral connective, tm = torma. (Scale bars: 500 μm)

elongated area on the ventrolateral wall of the head capsule, reaches the postoccipital ridge, fan-shaped; (I) flat bulge on the lateral mandibular base with a sclerotised abductor tendon; (F) abductor of the mandible. — ***M. hypopharyngomandibularis* (*M.13*):** absent.

4.2.6. Maxillae

Figs. 7, 9C,D, 10G,H, 11, 12G

Skeletal features. The maxillae are inserted in the deep hypostomal grooves. The elongate cardo bears an internal bifurcate process on the dorsal side, with a longer, slender lateral branch and a shorter mesal one. The concave anterior cardinal margin is connected to the convex basal margin of the basistipes. The lateral basistipes and the ventral mediostipes are movably connected. The lateral margin of the mediostipes is rim-like and prominent (Fig. 12G). Its mesal margin is rigidly fused to the lacinia. On the ventral side of the hook-shaped lacinia a distinct furrow is formed by a pair of prominent rims (Fig. 12G). The bipartite, palp-like galea, which is connected to the anterior margin of the mediostipes, fits in this furrow. On the dorsal side of the lacinia a central, less sclerotised area is recognisable (Fig. 10G). A row of strong setae is inserted above the mesal margin and a few setae below it. The palpifer is composed of a palp-socket with an enlarged dorsal plate. The socket is formed as a box with rim-like and prominent lateral longitudinal edges. The palp is inserted in a deep emargination of the anterior margin on lateral side. The maxillary palp is 4-segmented and distinctly protruding beyond the lacinia. Palpomere 1 is almost twice as long as wide. Palpomere 2 is somewhat longer and cylindrical. Palpomere 3 is strongly enlarged and at least four times longer than wide, whereas the apical palpomere is greatly shortened. It is cone-shaped, hardly longer than wide, with an undivided sensory field at the tip. The pores which are densely scattered over the basistipes and scarcely on the cardo, palpifer and the palp bear paddle-shaped sensilla.

Musculature (see also Fig. 8)**. *M. craniocardinalis externus* (*M.15*):** (O) posteroventral area of the head capsule, between M.12 and M.17, fan-shaped; (I) lateral branch of the internal cardinal process, with a short tendon; (F) abductor of the maxilla. — ***M. craniocardinalis internus* (*M.16*):** absent. — ***M. tentoriocardinalis* (*M.17*):** (O) lateral face of the gular ridge, reaches the postoccipital ridge, fan-shaped; (I) mesal branch of the internal cardinal process; (F) adductor of the maxilla, antagonist of M.15. — ***M. tentoriostipitalis* (*M.18a,b*):** (O) subcomponent ***a***: ventral face of the laminatentorium and lateral face of the middle lamella, strongly broadened at the origin; subcomponent ***b***: posterior gular region and postgular ridge; (I) membrane close to the mediostipes, both subcomponents are fused anteriorly, subcomponent ***a*** dinstinctly steeper than ***b***; (F) adductor and retractor of the stipes, with vertical component (subcomponent ***a***). — ***M. craniolacinialis* (*M.19*):** (O) posterior wall of the head capsule and ventrolateral postoccipital ridge, laterad of M.12; (I) base of the lacinia, with long thin tendon; (F) adductor and retractor of the lacinia. The slender muscle is intercrossing with M.12 posteriorly and its anterior tendon lies between the two branches of the internal process of the cardo. — ***M. stipitolacinialis* (*M.20*):** (Fig. 11C) (O) mesal margin of the dorsal plate of the palpifer, mesad of M.22; (I) lateral margin of the mediostipes; (F) adductor of the lacinia and the galea (homology see section 4.1.6.). — ***M. stipitogalealis* (*M.21*):** (Fig. 11C) (O) basal wall of the basistipes; (I) basal margin of the galea; (F) movements of the galea. — ***M. stipitopalpalis externus* (*M.22*):** (Figs. 10G, 11A,C) (O) – base of the palpifer's dorsal plate, fan-shaped; (I) lateral base of palpomere 1; (F) abductor of the palp. — ***M. stipitopalpalis internus* (*M.23*):** absent. — ***M. palpopalpalis tertius* (*M.26*):** (O) lateral wall of palpomere 2; (I) mesal base of palpomere 3; (F) flexor of palpomere 3. — ***M. palpopalpalis quartus* (*M.27*):** (O) lateral wall of the distal part of palpomere 3; (I) mesal base of palpomere 4; (F) flexor of palpomere 4.

4.2.7. Labium

Figs. 7B, 8, 9C,D, 10D, 11

Skeletal features. The submentum is distinctly wider than the gula and fused to it without a recognisable suture. Two pairs of long setae are inserted at the anterior angles. A pair of lateral submental lobes reaches the hypostomal grooves anteriorly and covers the posterior tentorial pits. The lateral lobes of the anteriorly attached mentum enclose a broad median emargination with two paramedian cusps. The lobes are narrowing anteriorly forming rounded tips. The surface of the lobes is smooth without any setae or pores, whereas the central mentum is covered with pores with styliform sensilla. A pair of long setae is inserted close to the lateral lobes. The longitudinal triangular internal mental ridges (Fig. 11B) are visible externally and originate at the rounded tip of the lateral lobes. The upper posterior angles of the mental ridges are continuous with the ventral suspensorial arms.

The small prementum fits into the median emargination of the mentum. Between the palpal bases the prementum forms a blunt ventral keel. A row of deep setiferous pores is arranged along the anterior edge and a pair of long setae inserts paramedially. The anterior margin of the prementum is broadly folded inwards and forms a bilobed sclerite on the dorsal side (Fig. 9D), which is posteriorly connected to the membranous hypopharynx. The dorsal sclerite is covered with irregularly arranged short bristles.

The palpiger consists of an anterior external cylindrical part and a posterior internal process. The internal process is longer than the cylindrical part and its posterior end is curved inwards. The 3-segmented palps are distinctly shorter than the maxillary palps. Palpomere 2 is enlarged, whereas palpomere 3 is shortened, similar to palpomeres 3 and 4 of the maxillary palp. The surface of the palps is glabrous.

Musculature. *M. submentopraementalis* (*M.28*): (O) anterior margin of the gular apodeme; (I) medially on the ventral margin of the prementum; (F) retractor and depressor of the prementum. — ***M. tentoriopraementalis inferior* (*M.29a,b*):** (O) subcomponent ***a***: ventral wall of the head capsule at the submento-mental border, fan-shaped; subcomponent ***b***: basal region of the lateral faces of the gular apodeme, close to M.28; (I) subcomponent ***a***: posterior margin of the process of the palpiger; subcomponent ***b***: ventral base of the cylindrical part of the palpiger with a slender tendon; subcomponent ***a*** is steeper than ***b***; (F) retractor and adductor (subcomponent ***a***) of the palp. — ***M. tentoriopraementalis superior* (*M.30*):** (O) apical region of the lateral faces of the gular apodeme; (I) medially on the connection between dorsal prementum and hypopharynx; (F) retractor of the prementum. The muscle is bipartite at its origin. The bundles are very close to each other and fused anteriorly. — ***M. praementopalpalis externus* (*M.34*):** (O) inner margin of the process of the palpiger, opposite to M.29a; (I) ventral base of palpomere 1; (F) movements of the labial palp.

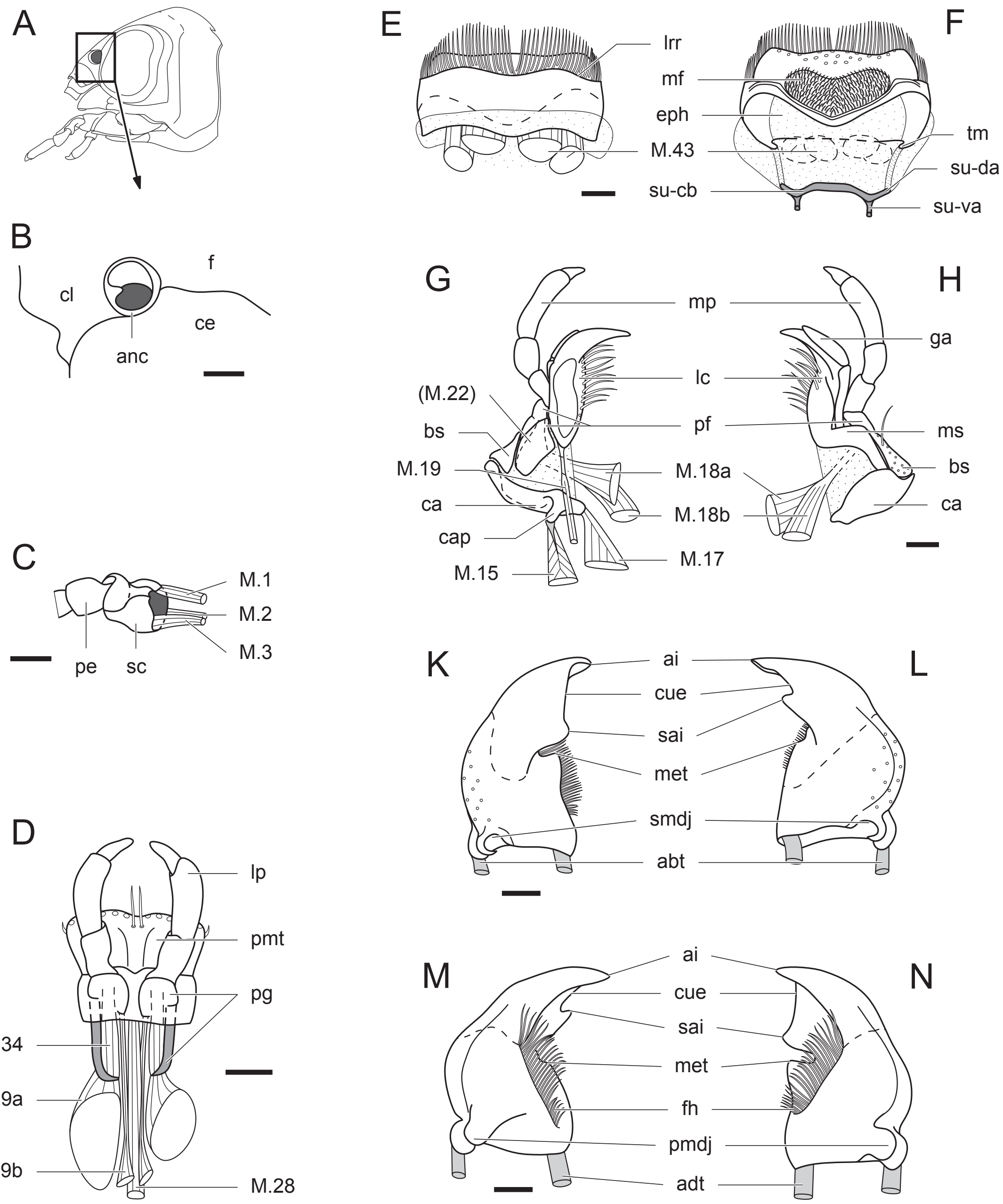


Fig. 10. *Haliplus* sp., head appendages. **A**: Head, lateral view. **B**: Antennal insertion. **C**: Antenna, basal segments. **D**: Labrum, dorsal view. **E**: Labrum, ventral view. **F**: Maxilla, dorsal view. **G**: Maxilla, ventral view. **H**: Left mandible, dorsal view. **K**: Right mandible, dorsal view. **L**: Right mandible, ventral view. **M**: Left mandible, ventral view. **N**: Labium ventral view. Endoskeletal elements grey, semimembranous areas punctured, translucent structures marked by dashed lines. Abbreviations: abt = abductor tendon, adt = adductor tendon, ai = apical incisor, anc = circumantennal ridge with process, bs = basistipes, ca = cardo, cap = cardo process, ce = compound eye, cl = clypeus, cue = cutting edge, eph = epipharynx, f = frons, fh = ventral fringe of hairs, ga = galea, lc = lacinia, lp = labial palp, lrr = transverse labral ridge, met = mesal tooth, mf = microtrichia field, mp = maxillary palp, ms = mediostipes, pe = pedicellus, pf = palpifer, pg = palpiger, pmdj = primary mandibular joint, pmt = prementum, sai = subapical incisor, sc = scapus, smdj = secondary mandibular joint, su-cb = suspensorial cross-bar, su-da = dorsal suspensorial arm, su-va = ventral suspensorial arm, tm = torma. (Scale bars, except A: 100 μm)

4.2.8. Epipharynx and hypopharynx

Figs. 8, 9, 10E,F, 11A

General features. The preoral cavity is strongly narrowed due to the conspicuously convex hypopharyx. The membranous epipharynx is glabrous and short due to the extensive ventral sclerite of the labrum.

The hypopharynx forms a distinct dorsal bulge. A pair of membranous, comb-shaped lobes is inserted at the base of the prementum and laterally adjacent to the hypopharynx (Fig. 9D). It is possible that these structures represent modified paraglossae.

The suspensorium consists of a transverse cross-bar and a pair of ventral and dorsal arms. The dorsal arms are rigidly connected to the cross-bar and attached to the labral tormae by a membrane. The ventral suspensorial arms are weakly sclerotised and connected to the mental ridges.

Musculature. ***M. frontohypopharyngalis*** **(*M.41*):** (O) frons, between M.45, M.46 and M.47, fan-shaped; (I) apicolaterally on the suspensorial cross-bar, with a slender sclerotised tendon, intercrossing with M.45 and M.47; (F) elevator of the suspensorium, contraction of the anatomical mouth. — ***M. tentoriohypopharyngalis*** **(*M.42*):** absent. — ***M. clypeopalatalis*** **(*M.43*):** (O) paramedially on the anteriormost frons; (I) paramedially on the dorsal wall of the preoral cavity, close to the labral margin; (F) dilator of the preoral cavity. Due to the shortened clypeus the origin is shifted posteriorly to the frontal region. — ***Mm. compressores epipharyngis*** **(*Mm.III*):** (Fig. 11A) Numerous layers of transverse muscle bundles connect the upper edges of the posterior wall of the preoral cavity. Contraction of the bundles results in a depression of the posterior epipharynx, antagonistic to M.43. The fibres of M.44 insert between the transverse muscles. — ***M. clypeobuccalis*** **(*M.44*):** (Fig. 11A) (O) paramedially on the anterior frons, between M.43 and the frontal ganglion; (I) posteriormost epipharynx, between the fibres of Mm.III; (F) dilator of the posterior preoral cavity. The homologisation of this muscle is ambiguous due to its closeness to M.43 and the posterior shift of its area of origin. As it was defined by v. Kéler (1963) the muscle inserts immediately anterad of the frontal ganglion. The insertion between the muscle fibres of Mm.III is not described by v. Kéler but present in all examined taxa of Adephaga (in this study).

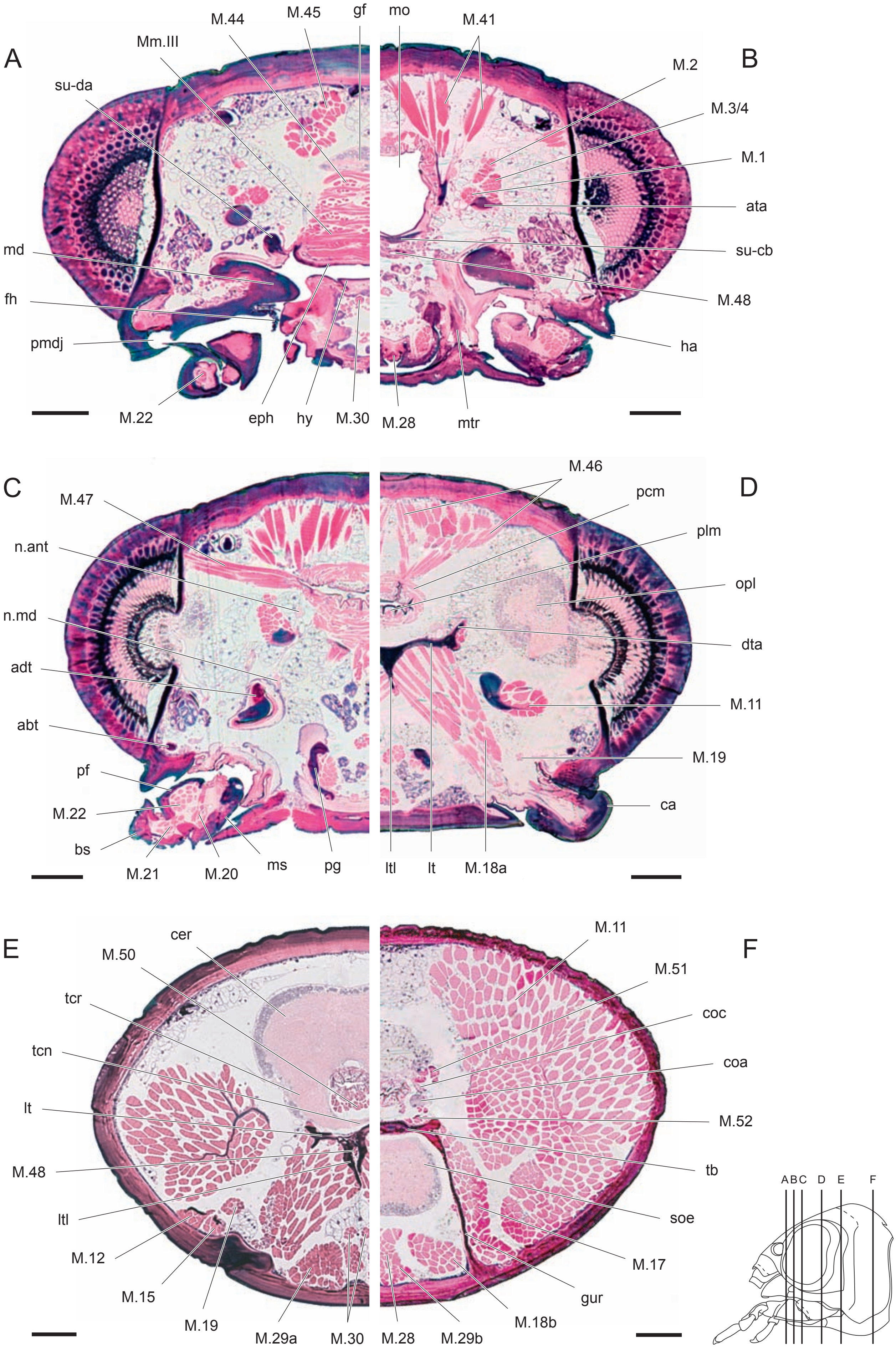
4.2.9. Pharynx

Figs. 8, 9, 11

General features. The anatomical mouth is marked by the frontal ganglion dorsally and the suspensorial cross-bar ventrally (Fig. 11A,B). The anterior part of the precerebral pharynx ascends and the posterior part lies in the upper head region. The postcerebral pharynx gradually slopes towards the foramen occipitale. The precerebral pharynx is equipped with transverse or ring muscles and a longitudinal muscle layer (Fig. 11D). The ventral transverse muscles between the suspensorial cross-bar and the laminatentorium are multilayered and large, corresponding to the dorsal Mm.III. The pharyngeal lumen is narrowed by folds, thus providing space for the longitudinal muscle bundles of the precerebral pharynx. The extent of the pharyngeal musculature and the lumen of the pharynx decrease from anterior to posterior. The anterior part of the oesophagus is devoid of ring musculature. The lumen is not narrowed by folds.

Musculature. ***M. frontobuccalis anterior*** **(*M.45*):** (O) paramedially on the frons, posteriorly of M.44; (I) dorsolateral folds of the precerebral pharynx, immediately posteriorly of the frontal ganglion; (F) dilator of the precerebral pharynx. — ***M. frontobuccalis posterior*** **(*M.46*):** (Fig. 11D) (O) posterior frons, anterad the cerebrum, several bundles laterad and posterad M.41; (I) dorsolateral folds (lateral bundles) and dorsal folds (posterior bundles) of the posterior precerebral pharynx; (F) dilator of the posterior precerebral pharynx. — ***M. frontobuccalis lateralis*** **(*M.47*):** (O) dorsolaterally on the middle frons, reaches the circumocular ridge, laterad of M.41 and anterad of M.46; (I) lateral folds of the precerebral pharynx, intercrossing with M.41; (F) dilator of the precerebral pharynx. — ***M. tentoriobuccalis anterior*** **(*M.48*):** (O) median process of the tentorial bridge; (I) medially on the hypopharynx immediately anterad of the suspensorial cross-bar; (F) retractor and depressor of the hypopharynx, dilator of the preoral cavity. M.48 is always separated from the following M.50 by the tritocerebral commissure. A specific feature in *Haliplus* is its passage through the gap between the ventral parts of the vertical plates of the laminatentorium (Fig. 11E) (homology see section 4.1.9.). — ***M. tentoriobuccalis posterior*** **(*M.50*):** (O) anterior margin of the tentorial bridge, laterad M.48; (I) ventral wall of the middle pharynx, opposite to the anterior part of the cerebrum; (F) dilator of the middle region of the pharynx. The muscle is separated from M.48 by the laminatentorium and the tritocerebral commissure. — ***M. verticopharyngalis*** **(*M.51*):** (O) posterior head capsule and dorsal postoccipital ridge, adjacent to M.11; (I) dorsally on the postcerebral pharynx, immediately behind the cerebrum, opposite

Fig. 11. *Haliplus* sp., head, cross-sections. Lateral view of the head on the left side with the section planes marked. **A–F**: Cross-sections in anterior-posterior sequence. Abbreviations: abt = abductor tendon, adt = adductor tendon, ata = anterior tentorial arm, bs = basistipes, ca = cardo, cer = cerebrum, coa = corpus allatum, coc = corpus cardiacum, dta = dorsal tentorial arm, eph = epipharynx, fh = ventral fringe of hairs, gf = frontal ganglion, gur = gular ridge, ha = hypostoma, hy = hypopharynx, lt = laminatentorium, ltl = median lamella of laminatentorium, md = mandible, mo = mouth opening, ms = mediostipes, mtr = mental ridge, n.ant = nervus antennalis, n.md = nervus mandibularis, opl = optic lobe, pcm = pharyngeal circular musculature, pf = palpifer, pg = palpiger, plm = pharyngeal longitudinal musculature, pmdj = primary mandibular joint, soe = suboesophageal ganglion, su-cb = suspensorial cross-bar, su-da = dorsal suspensorial arm, tb = tentorial bridge, tcn = tritocerebral connective, tcr = tritocerebral commissure. (Scale bars: 100 μm)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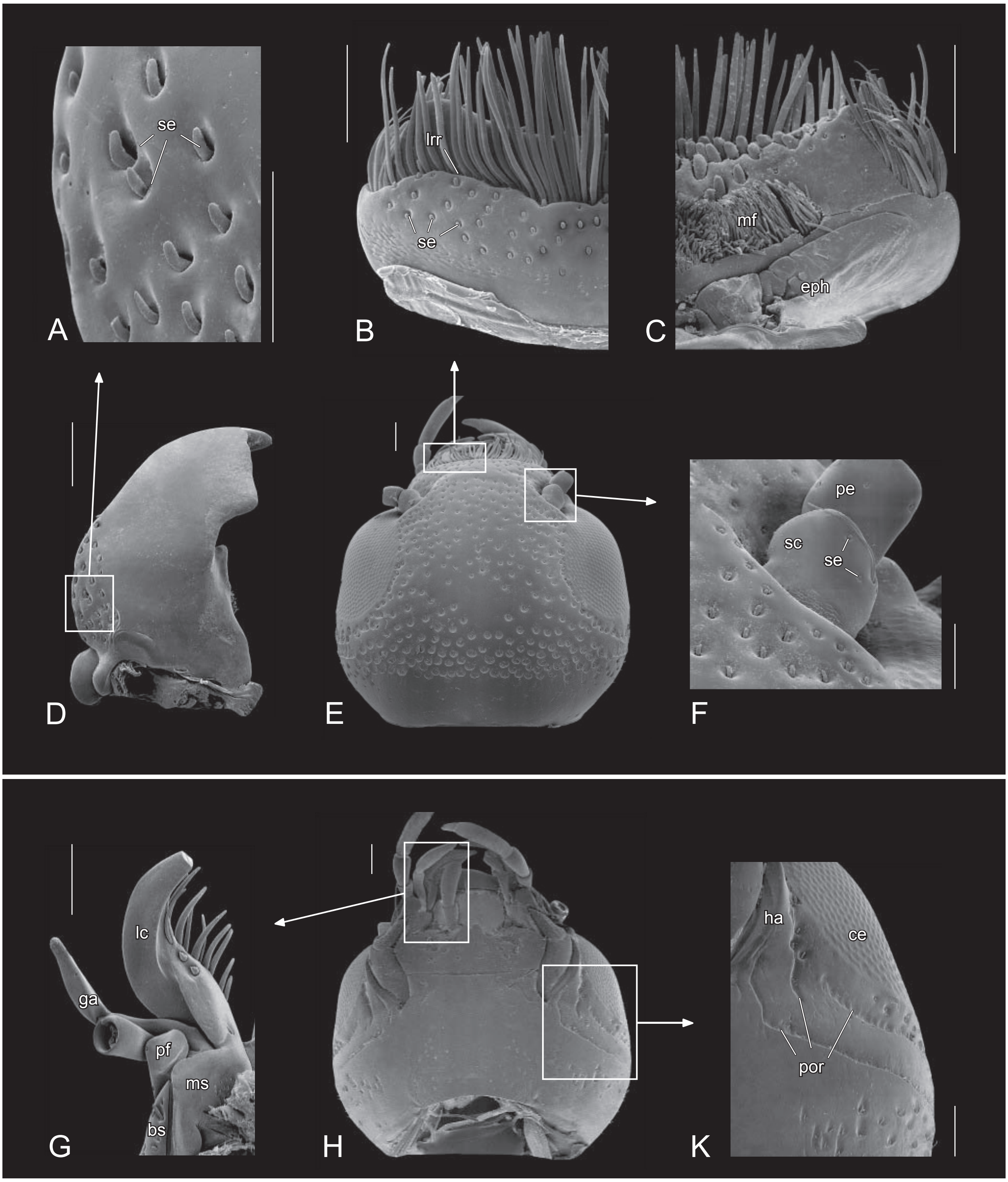

Fig. 12. *Haliplus* sp., head, SEM micrographs. **A**–**F** (except C): Dorsal view. **C**,**G**–**K**: Ventral view. **A**: Detail magnification of D, sensilla. **B**–**C**: Labrum. **D**: Left mandible. **E**,**H**: Head. **F**: Detail magnification of E, antennal basis. **G**: Maxilla. **K**: Detail magnification of H, postocular ridges. Abbreviations: bs = basistipes, ce = compound eye, eph = epipharynx, ga = galea, ha = hypostoma, lc = lacinia, lrr = transverse labral ridge, mf = microtrichia field, ms = mediostipes, pe = pedicellus, pf = palpifer, por = postocular ridge, sc = scapus, se = sensilla. (Scale bars: 100 µm, except A,F: 50 µm)

to M.52; (F) dilator of the anterior postcerebral pharynx, together with M.52. — ***M. tentoriopharyngalis* (*M.52*):** (O) anterior face of the mesal apodeme of the gular ridge, adjacent to M.48; (I) ventrally on the postcerebral pharynx, opposite to M.51; (F) dilator of the anterior postcerebral pharynx, together with M.51.

4.2.10. Nervous system

Figs. 8A, 9A,D, 11

The cerebrum occupies about one fourth of the length of the head capsule. The suboesophageal ganglion is somewhat longer. Anterior or posterior lobes of the protocerebrum are absent. The optic neuropils originate laterally from the protocerebrum near its anterior margin.

The frontal ganglion lies above Mm.III and between M.44 and M.45. It is approximately triangular. The nervus recurrens connects it to the ganglion ventriculare, which lies above the postcerebral pharynx.

The corpora cardiaca and allata are almost globular. They are located posterad the cerebrum and enclose the postcerebral pharynx. They are connected to the ventricular ganglion.

4.3. Head morphology of *Aspidytes niobe*

4.3.1. External head capsule
Fig. 13

The head is prognathous, broadly oval. The colouration is dark brown. Numerous fine pores are spread over the nearly glabrous surface. The kidney-shaped compound eyes are completely integrated in the contour of the head capsule. The clypeus is longer than the labrum and the clypeofrontal suture is broadly interrupted medially. The condyles of the secondary mandibular joint are present at the posterior angles on the ventral side. Several short setae are inserted on the lateral clypeal margins. The anterior tentorial pits are not visible externally. The frontal or coronal sutures are absent.

The broad gula is fused with the submentum anteriorly. A pair of inconspicuous posterior tentorial pits indicates the border between both sclerites. The hypostomata are almost fully covered by the maxillary bases and form an acute angle with the genae. The postoccipital ridge forms a pair of paramedian dorsal apodemes which serve as area of origin of a thoracic muscle (Fig. 14B). The gula forms a narrow postgular ridge.

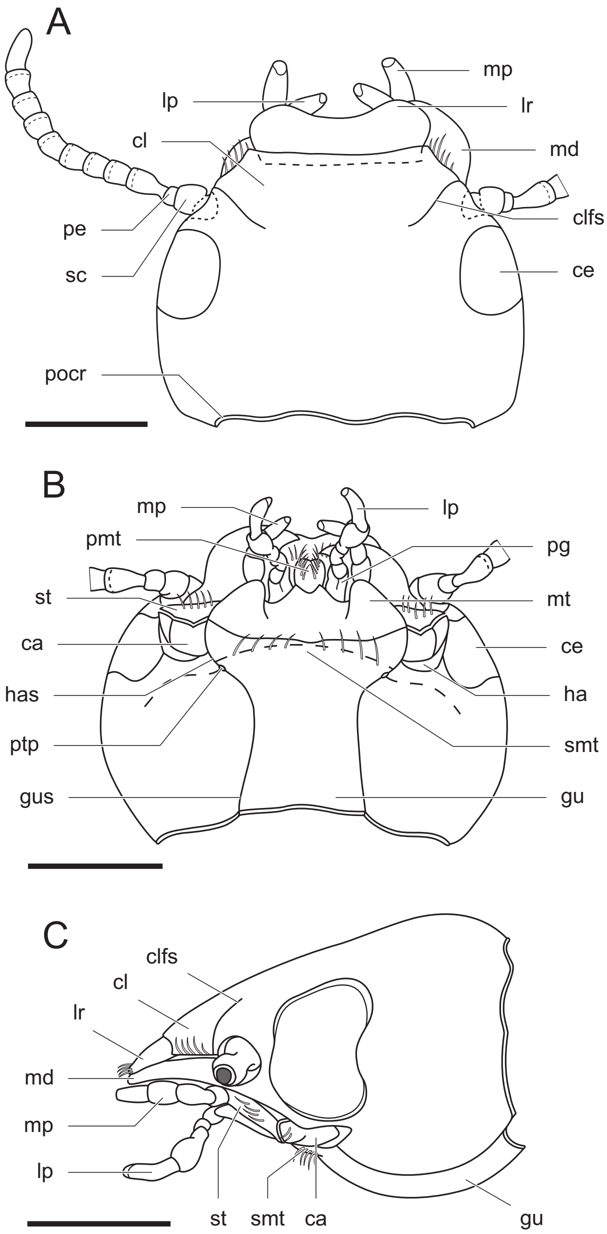

Fig. 13. *Aspidytes niobe*, head, habitus. **A**: Dorsal view. **B**: Ventral view. **C**: Lateral view. Abbreviations: ca = cardo, ce = compound eye, cl = clypeus, clfs = clypeofrontal suture, gu = gula, gus = gular suture, ha = hypostoma, has = hypostomal suture, lp = labial palp, lr = labrum, md = mandible, mp = maxillary palp, mt = mentum, pe = pedicellus, pg = palpiger, pmt = prementum, pocr = postoccipital ridge, ptp = posterior tentorial pit, sc = scapus, smt = submentum, st = stipes. (Scale bar: 500 μm)

4.3.2. Internal skeletal structures
Figs. 14, 15

The lateral remnants of the clypeofrontal suture (Fig. 13A) correspond internally with short, low ridges, which are connected to the circumantennal ridges. The gular ridges are high with strengthened dorsal edges. Their anterior margins are fused with the posterior tentorial arms which are continuous with the hypostomal ridges. The tentorial bridge connects the gular ridges at their mid-length. The bridge is distinctly curved anteriorly and bears a median process. A pair of mesally projecting apodemes arises from the gular ridges posteriorly of the bridge. A mid-gular apodeme is not present. The anterior and posterior parts of the well developed tentorium are connected by a central tentorial body. The anterior arms arise from the antennal ridges (Fig. 16B). The distinctly broader dorsal arms reach the dorsal head capsule but are not firmly connected to it. Plate-like laminatentoria arise from the mesal side of the central element. They are not fused medially.

Further endoskeletal structures are the mental ridges and the suspensorium (see sections 4.3.7. [Labium] and 4.3.8. [Hypopharynx]).

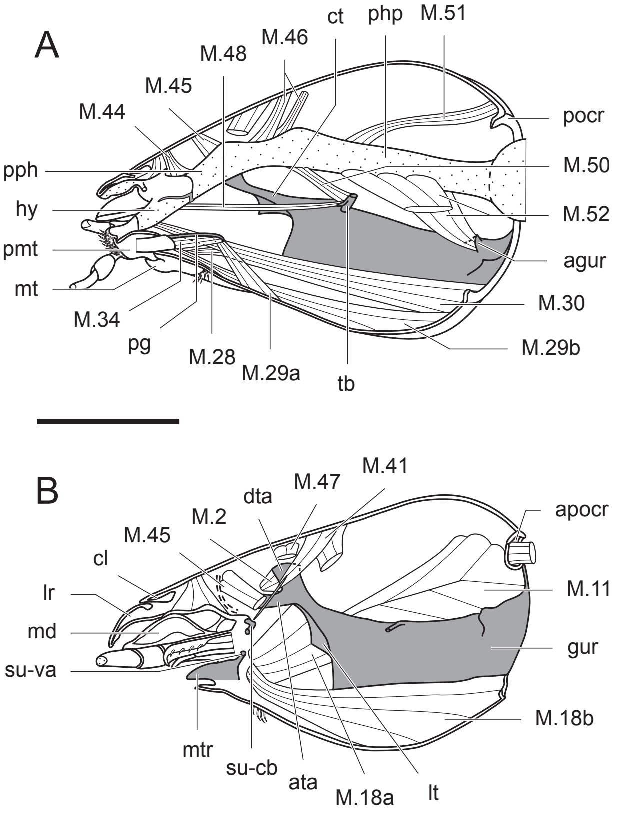

Fig. 14. *Aspidytes niobe*, head, sagittal sections. **A**–**B**: Sagittal view in successive stages of dissection. Endoskeletal elements grey, semimembranous parts punctured, translucent structures marked by dashed lines. Abbreviations: agur = apodeme of gular ridge, apocr = dorsal apodeme of postoccipital ridge, ata = anterior tentorial arm, cl = clypeus, ct = central tentorial body, dta = dorsal tentorial arm, gur = gular ridge, hy = hypopharynx, lr = labrum, lt = laminatentorium, md = mandible, mt = mentum, mtr = mental ridge, pg = palpiger, php = postpharynx, pmt = prementum, pocr = postoccipital ridge, pph = prepharynx, su-cb = suspensorial cross-bar, su-va = ventral suspensorial arm, tb = tentorial bridge. (Scale bar: 500 µm)

4.3.3. Antennae

Figs. 13A,C 16B,C

Skeletal features. The antennae are inserted laterally between the compound eyes and the mandibles in deep grooves. In dorsal view the insertion areas are concealed by the lateral margins of the frons.

The 11-segmented antennae are filiform and completely glabrous. The antennomeres are scarcely longer than wide except for the scapus, the first and the last flagellomere, which are almost twice as long as their diameter (Fig. 13A). The scapus is bipartite with a proximal spherical articulatory part and a distal strongly shortened cylindrical part, separated by a constriction (Fig. 16C; see also Ribera et al. 2002a: fig. 1C). The proximal part is acentrically attached to the distal part, i.e. their longitudinal axes form a distinct angle. A groove on the spherical part articulates with an anteroventral process on the circumantennal ridge (Fig. 16B,C). The small pedicellus is partly enclosed by the distal part of the scapus. The flagellomeres II–VIII are partly enclosed by the preceding ones. Therefore the antennal flexibility is restricted.

Musculature (Figs. 14B, 15A,B, 16C)**. *M. tentorioscapalis anterior* (*M.1*):** (O) anterior tentorial arm and basal dorsal tentorial arm; (I) anteroventrally on the condyle of the scapus; (F) depressor and rotator of the antenna. — ***M. tentorioscapalis posterior* (*M.2*):** (O) dorsal tentorial arm, reaching the head capsule dorsally, fan-shaped; (I) posterodorsally on the condyle of the scapus; (F) elevator, retractor and rotator of the antenna. — ***M. tentorioscapalis lateralis/medialis* (*M.3/4*):** (O) dorsal tentorial arm, between M.1 and M.2, fan-shaped; (I) medioventrally on the inner basal margin of the scapus; (F) depressor of the antenna, together with M.1. The homologisation is ambiguous. Von Kéler's (1963) nomenclature refers to an orthognathous head with antennae inserting anteriorly between the compound eyes. — ***M. scapopedicellaris lateralis* (*M.5*):** (O) dorsal wall of distal part of the scapus; (I) dorsally on the base of the pedicellus; (F) elevator and extensor of the flagellum. — ***M. scapopedicellaris medialis* (*M.6*):** (O) ventral wall of the distal part of the scapus; (I) ventrally on the base of the pedicellus; (F) depressor and flexor of the flagellum, antagonistic to M.5.

4.3.4. Labrum

Figs. 13, 15, 16E,F

Skeletal features. The glabrous surface is covered with fine pores similar to that on the head capsule. Two thin setae insert on the ventral side close to the anterior edge. It forms a broad median emargination and thus a pair of lateral lobes. The anterior margin is folded inwards and continuous with a triangular plate-like structure on the ventral side which is covered with microtrichia. Laterad of it an additional row of short spines is arranged arch-like. Tormae are present at the posterior angles of the ventral labrum. They are membranously connected to the dorsal suspensorial arms (see section 4.3.8. [Epipharynx]).

Musculature. Absent.

4.3.5. Mandibles

Figs. 13, 15A,C, 16K–N, 17

Skeletal features. The mandibles are not protruding beyond the labral margin anteriorly and only slightly laterally. They are somewhat longer than wide, with a length/width ratio of 1.25. The ventral side is flat,

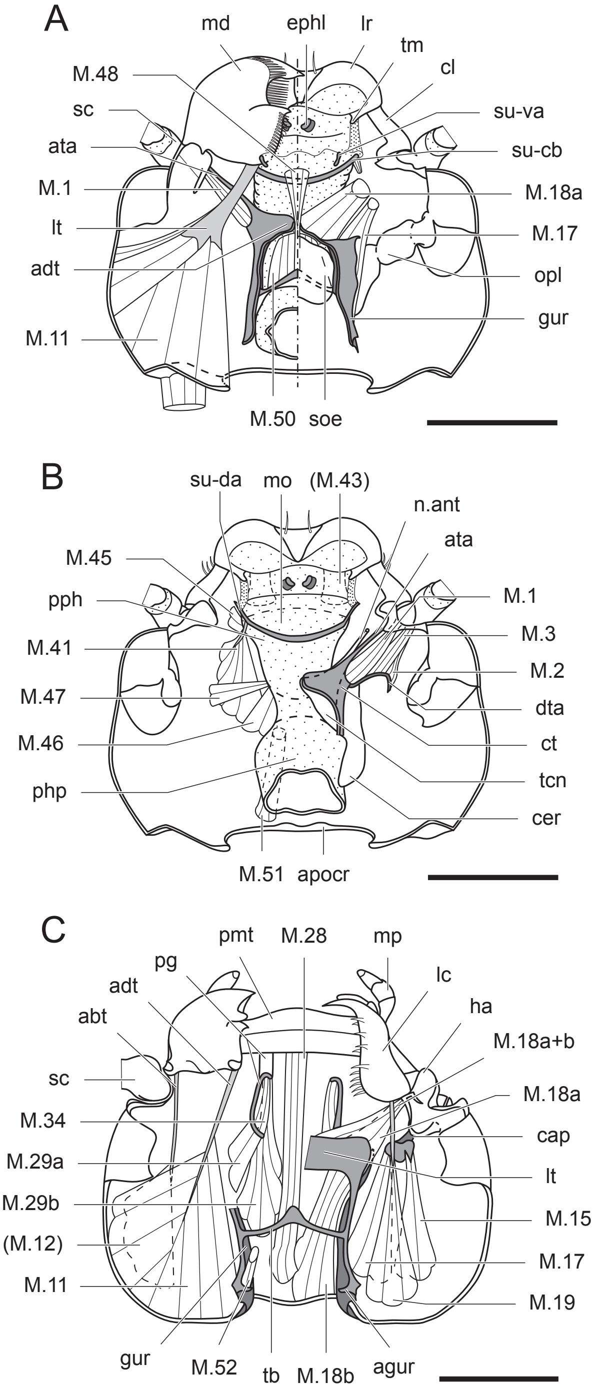

Fig. 15. *Aspidytes niobe*, head, horizontal sections. **A**–**B**: Ventral view of dorsal half in successive stages of dissection. **C**: Dorsal view of ventral half. Endoskeletal elements grey, semimembranous parts punctured, translucent structures marked by dashed lines. Abbreviations: abt = abductor tendon, adt = adductor tendon, agur = apodeme of gular ridge, apocr = dorsal apodeme of postoccipital ridge, ata = anterior tentorial arm, cer = cerebrum, cl = clypeus, cap = cardo process, ct = central tentorial body, dta = dorsal tentorial arm, ephl = epipharyngeal lobe, gur = gular ridge, ha = hypostoma, lc = lacinia, lr = labrum, lt = laminatentorium, md = mandible, mo = mouth opening, mp = maxillary palp, n.ant = nervus antennalis, opl = optic lobe, pg = palpiger, php = postpharynx, pmt = prementum, pph = prepharynx, sc = scapus, soe = suboesophageal ganglion, su-cb = suspensorial cross-bar, su-da = dorsal suspensorial arm, su-va = ventral suspensorial arm, tb = tentorial bridge, tcn = tritocerebral connective, tm = torma. (Scale bars: 500 µm)

whereas the dorsal side is convex. The exposed parts of the dorsal surface are covered with sensilla inserted in small grooves (Fig. 17A,C). The subapical incisor is blunt; the apical incisor is more acute and slightly bent downwards. So the dorsal cutting edge between these teeth is formed like a reversed letter J. The mesal tooth is small and closely located to the subapical incisor. The ventral edge between the apical and the mesal tooth is deeply emarginated. A mola is absent. Three fringes of microtrichia (Figs. 16M,N, 17B,D,E) are present on the ventral side; one along the mesal edge, reaching the apical tooth, the second immediately inserted on the mesal margin, and a third, very short one behind the apical incisor. The hairs of the first fringe are longer than that of the second one, but do not overtop the mesal edge.

The mandibular joints are subapically located, i.e. medially shifted from the lateral angles. The abductor tendon is attached to a conspicuous bulge on the laterobasal angle. The ventral primary joint is more anteriorly positioned compared to the dorsal secondary joint, which results in a slightly inclined axis of movement. The mandibular condyle of the primary joint is small (Fig. 17B). The socket of the secondary joint is formed by a deep emargination with a strengthened mesal edge (Fig. 17A).

The left and the right mandible are nearly symmetric but differ in some details. The dorsal cutting edge of the left mandible is longer and straight whereas the right cutting edge is emarginated close to the subapical incisor. The right subapical tooth is more prominent and rounded. The asymmetry of the distal parts ensures a close fit of both mandibles in the flexed position.

Musculature (see also Fig. 14B)**.** ***M. craniomandibularis internus* (*M.11*):** (O) lateral and dorsolateral wall of the head capsule, reaches the postoccipital ridge, extremely broadened at the orgin; (I) mesal mandibular base, strongly converging towards the sclerotised tendon; (F) adductor of the mandible. — ***M. craniomandibularis externus* (*M.12*):** (O) narrow, elongate area on the ventrolateral wall of the head capsule, fan-shaped; (I) flat bulge on the lateral mandibular base, strongly converging towards the sclerotised tendon; (F) abductor of the mandible. — ***M. hypopharyngomandibularis* (*M.13*):** absent.

4.3.6. Maxillae
Figs. 13, 15C, 16G,H

Skeletal features. The maxillae are largely concealed by the lateral mental lobes. They are inserted in the deep hypostomal grooves. The cardo articulates with the head capsule at the base of this groove.

The elongate cardo is arranged in a transverse position. The dorsal side of the cardo bears an internal bifurcate process with a shorter mesal branch and a longer lateral one. The anterolateral margin is connected to the basistipes. Several short setae are inserted on the lateral side of the cardo and the basistipes. Basi- and mediostipes are completely separated from each other. The ventral mediostipes bears the galea and is continuous with the mesal lacinia. The galea is bipartite, palp-like and laterally adjacent to the lacinia. The lacinia is hook-shaped. Its base is widened and equipped with a field of microtrichia. A row of bristles is inserted along its mesal margin. An oval semimembranous field is present on the mesal base of the dorsal side. The anterior part of this area is densely set with fine microtrichia (Fig. 16G). The basistipes is anteriorly attached to the palpifer. The distal socket of the palpifer bears the maxillary palp; the elongated dorsal side forms a plate between the lacinia and the basistipes (Fig. 16G). The 4-segmented palp protrudes to some extent beyond the lacinia. All palpomeres are basally enclosed by the preceding ones and short, but distad slightly increasing in length. Palpomere 1 is only half the size of the other ones. Palpomere 2 is cup-shaped with a slender base and a widened apex. An undivided sensory field is present at the tip of palpomere 4. The palp is entirely glabrous.

Musculature (see also Figs. 14B, 15A)**. *M. craniocardinalis externus* (*M.15*):** (O) posteroventral area of the head capsule, between M.12 and M.17; (I) lateral branch of the internal cardinal process with a short slender tendon; (F) abductor of the maxilla. — ***M. craniocardinalis internus* (*M.16*):** absent. — ***M. tentoriocardinalis* (*M.17*):** (O) lateral face of the gular ridge, fan-shaped; (I) mesal branch of the internal cardinal process; (F) adductor of the maxilla, antagonistic to M.15. — ***M. tentoriostipitalis* (*M.18a,b*):** (O) subcomponent ***a***: anterior face of the laminatentorium; subcomponent ***b***: posterior gular region and postgular ridge, laterad of M.30, both parts strongly broadened at the origin; (I) membrane at the stipital base, tendons of both subcomponents fused, subcomponent ***a*** is distinctly steeper than subcomponent ***b***; (F) adductor and retractor of the stipes, with vertical component (subcomponent ***a***). — ***M. craniolacinialis* (*M.19*):** (O) posteroventral wall of the head capsule, posterad of M.15 and M.17; (I) base of the lacinia, with a long slender tendon, above the cardo process between the two branches; (F) adductor and retractor of the lacinia. — ***M. stipitolacinialis* (*M.20*):** (O) basal margin of the dorsal plate of the palpifer, mesad of M.22; (I) lateral margin of the mediostipes; (F) adductor of the lacinia and the galea (homology see section 4.1.6.). — ***M. stipitogalealis* (*M.21*):** (O) basal wall of the basistipes; (I) basal ventral margin of the galea; (F) movements of the galea. — ***M. stipitopalpalis externus* (*M.22*):** (O) base of the dorsal plate of the palpifer, fan-shaped; (I) lateral base of palpomere 1; (F) abductor of the palp. — ***M. stipitopalpalis internus* (*M.23*):** absent. — ***M. palpopalpalis tertius* (*M.26*):** (O) lateral base of palpomere 2; (I) mesal base of palpomere 3; (F) flexor of palpomere 3. — ***M. palpopalpalis quartus* (*M.27*):** (O) lateral base of palpomere 3; (I) mesal base of palpomere 4; (F) flexor of palpomere 4.

4.3.7. Labium
Figs. 13B, 14, 15C, 16D

Skeletal features. The submentum is very short and completely fused with the gula; only marked by the posterior tentorial pits. A transverse row of setae is arranged in a broad arch. The submentum is anteriorly connected to the mentum. The glabrous mentum forms a pair of anteriorly narrowing, lateral lobes. The median emargination between the lobes bears a pair of short paramedian cusps. The externally visible mental ridges originate internally along the mesal margin of the lateral lobes. The posterior angles of the triangular walls (Fig. 14B) are connected to the ventral suspensorial arms by a membrane. The prementum is inserted between the mental lobes. The widely inwards folded anterior margin forms an extended sclerite on the dorsal side which is connected to the hypopharynx. On the ventral side two converging rows of fine, long setae margin a median longitudinal blunt keel between the palpigers (Fig. 16D). The latter are composed of an external cylindrical part and an arcuate internal process. Palpomere 1 of the 3-segmented palp is short (similar to the maxillary palp), whereas palpomere 2 is distinctly enlarged with a nearly globular distal part. Palpomere 3 is of similar length but more slender. An undivided sensory field is present on its apex. The glabrous palp is due to the enlarged palpomere 2 slightly longer than the maxillary palp.

Musculature. *M. submentopraementalis* (*M.28*): (O) medially on posterior gula, mesally of M.18b; (I) medially on ventral margin of the prementum; (F) retractor and depressor of the prementum. The bundles of the paired muscle are closely adjacent at the origin and not distinguishable at the insertion area. — ***M. tentoriopraementalis inferior* (*M.29a,b*):** (O) subcomponent ***a***: ventral wall of the head capsule at the submento-mental border; subcomponent ***b***: middle region of the gula, mesad of subcomponent ***a***, both parts fan-shaped; (I) subcomponent ***a***: apically on the process of the palpiger; subcomponent ***b***: ventral base of the cylindrical part of the palpiger, subcomponent ***a*** is distinctly steeper than subcomponent ***b***; (F) retractor and adductor (subcomponent ***a***) of the

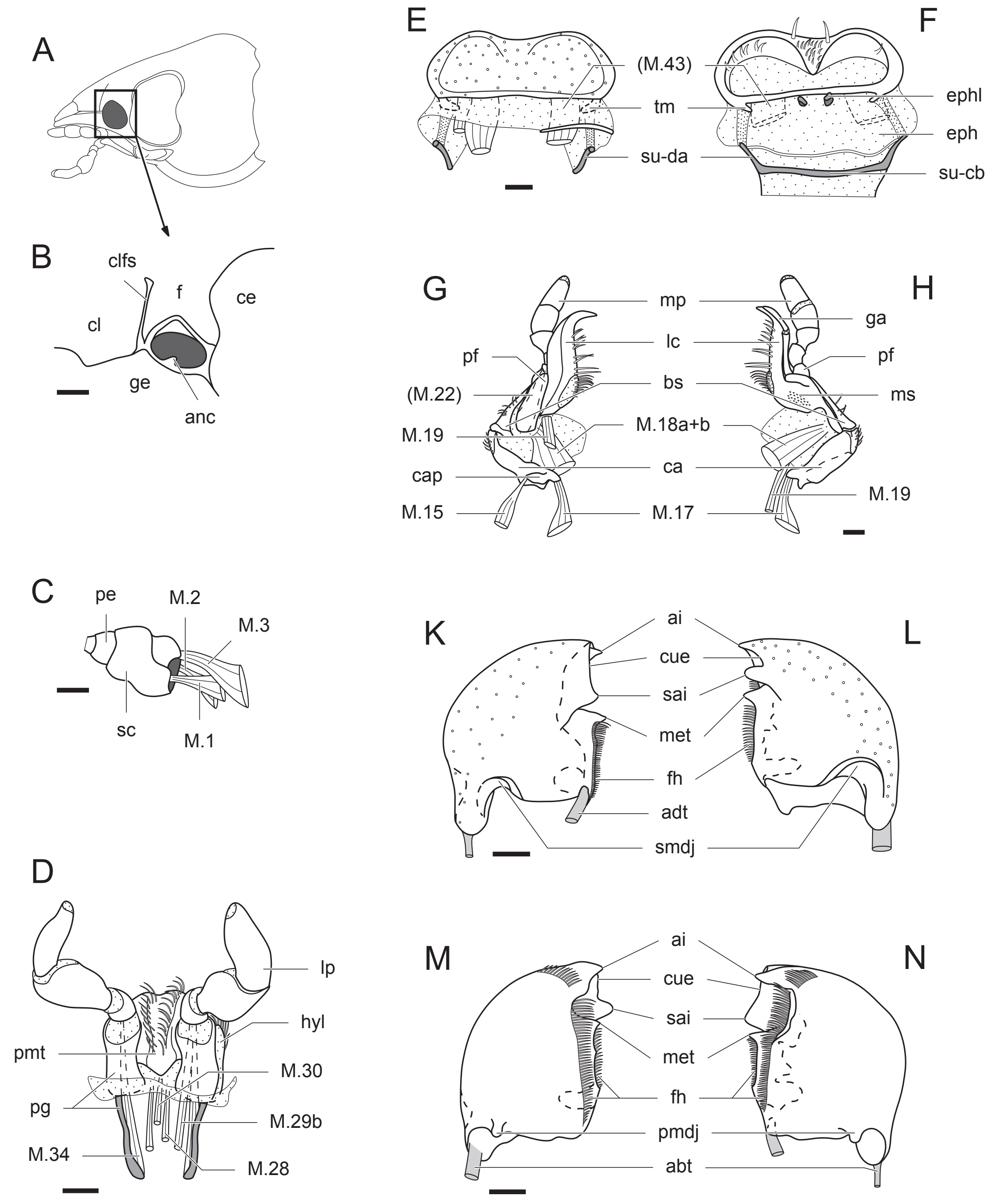

Fig. 16. *Aspidytes niobe*, head appendages. **A**: Head, lateral view. **B**: Antennal insertion. **C**: Antenna, basal segments. **D**: Labium ventral view. **E**: Labrum, dorsal view. **F**: Labrum, ventral view. **G**: Maxilla, dorsal view. **H**: Maxilla, ventral view. **K**: Left mandible, dorsal view. **L**: Right mandible, dorsal view. **M**: Right mandible, ventral view. **N**: Left mandible, ventral view. Endoskeletal elements grey, semimembranous parts punctured, translucent structures marked by dashed lines. Abbreviations: abt = abductor tendon, adt = adductor tendon, ai = apical incisor, anc = circumantennal ridge with process, bs = basistipes, ca = cardo, cap = cardo process, ce = compound eye, cl = clypeus, clfs = clypeofrontal suture, cue = cutting edge, eph = epipharynx, ephl = epipharyngeal lobe, f = frons, fh = ventral fringe of hairs, ga = galea, ge = gena, hyl = hypopharyngeal lobes, lc = lacinia, lp = labial palp, met = mesal tooth, mp = maxillary palp, ms = mediostipes, pe = pedicellus, pf = palpifer, pg = palpiger, pmdj = primary mandibular joint, pmt = prementum, sai = subapical incisor, sc = scapus, smdj = secondary mandibular joint, su-cb = suspensorial cross-bar, su-da = dorsal suspensorial arm, tm = torma. (Scale bars, except A: 100 µm)

palp (see section 4.1.7.). — ***M. tentoriopraementalis superior* (*M.30*):** (O) medially on posteriormost gula, posterad of M.28, mesad of M.18b; (I) medially on the dorsal margin of the prementum; (F) retractor of the prementum. The bundles of this paired muscle are closely adjacent. — ***M. praementopalpalis externus* (*M.34*):** (O) inner margin of the process of the palpiger, opposite to M.29a, fan-shaped; (I) ventral base of palpomere 1; (F) movements of the labial palp.

4.3.8. Epipharynx and hypopharynx
Figs. 14, 15, 16E,F

General features. The epipharynx is slightly concave and glabrous with a pair of kidney-shaped and sclerotised sensory epipharyngeal lobes.

The surface of the hypopharynx is glabrous and flat but ascending towards the anatomical mouth and thus narrowing the preoral cavitiy posteriorly. The cibarium appears oval in cross-section even close to the mouth opening.

The suspensorium consists of a transverse cross-bar below the anatomical mouth and a pair of dorsal and ventral suspensorial arms. The dorsal arms are connected to the tormae by distinct membranous strands. The ventral arms are connected to the mental ridges by a membrane.

Musculature. ***M. frontohypopharyngalis* (*M.41*):** (O) frons, between M.45, M.46 and M.47, strongly fan-shaped; (I) apicolaterally on the suspensorial cross-bar, with a slender sclerotised tendon, intercrossing with the bundles of M.45 and M.47; (F) elevation of the suspensorium, contraction of the mouth opening. — ***M. tentoriohypopharyngalis* (*M.42*):** absent. — ***M. clypeopalatalis* (*M.43*):** (O) paramedially on the clypeus; (I) anterior epipharynx, broad area between tormae and epipharyngeal lobes; (F) dilator of the preoral cavity. — ***Mm. compressores epipharyngis* (*Mm. III*):** Numerous dorsal transverse muscle bundles connect the upper edges of the posterior epipharynx. The fibres of M. clypeobuccalis (M.44) insert between the transverse bundles. The muscle functions as a depressor of the posterior epipharyngeal wall, antagonistic to M. clypeopalatalis (M.43). — ***M. clypeobuccalis* (*M.44*):** (O) paramedially on the clypeus, posteriorly of M.43; (I) posteriormost epipharynx, immediately anteriorly of the frontal ganglion, between the muscle fibres of Mm.III; (F) dilator of the posterior preoral cavity. Due to the rudimentary epistomal ridge the clypeal origin cannot be assessed unambiguously. The homologisation is based on the position closely anteriorly of the frontal ganglion (v. Kéler 1963) and the characteristically insertion between the muscle bundles of the Mm.III.

4.3.9. Pharynx
Figs. 14, 15

General features. The anatomical mouth opening is marked by the suspensorial cross-bar ventrally and by the frontal ganglion and the insertion of M. frontobuccalis anterior (M.45) dorsally. The pharynx is subdivided into an anterior precerebral and a posterior postcerebral part. It has a wide and approximately round lumen throughout its length and is located in the dorsal head region. The postcerebral pharynx is continuous with the voluminous oesophagus. The ring musculature of the pharynx is well developed, whereas the intermediate section between the parts of the brain is only equipped with ventral and dorsal transverse muscle fibres. A single layer of thin longitudinal muscle fibres underlies the ring musculature.

Musculature. ***M. frontobuccalis anterior* (*M.45*):** (O) paramedially on the anterior frons, between M.44 and M.41; (I) paramedially on the dorsal wall of the precerebral pharynx, posterad of Mm.III and frontal ganglion; (F) dilator of the precerebral pharynx. — ***M. frontobuccalis posterior* (*M.46*):** (O) posterior frons, posterad of M.41; (I) paramedially on the dorsal wall of the posterior precerebral pharynx, anterad of the cerebrum, opposite to M.50; (F) dilator of the precerebral pharynx, together with M.50. — ***M. frontobuccalis lateralis* (*M.47*):** (O) middle frons, laterad of M.41; (I) dorsolaterally on the wall of the anterior pharynx, intercrossing with M.41; (F) dilator of the precerebral pharynx (homology see section 4.1.9.). — ***M. tentoriobuccalis anterior* (*M.48*):** (O) median process of the tentorial bridge; (I) medially on the hypopharynx, immediately anterad of the suspensorial cross-bar; (F) retractor and depressor of the hypopharynx, dilator of the preoral cavity (homology see section 4.1.9.). — ***M. tentoriobuccalis posterior* (*M.50*):** (O) anterior margin of the tentorial bridge, laterally of M.48; (I) ventral wall of the precerebral pharynx, opposite to M.46; (F) dilator of the precerebral pharynx, together with M.46. The muscle is separated from M.48 by the tritocerebral commissure. — ***M. verticopharyngalis* (*M.51*):** (O) posteriormost dorsal wall of the head capsule, reaches the postoccipital ridge; (I) dorsal wall of the postcerebral pharynx, opposite to M.52; (F) dilator of the postcerebral pharynx, together with M.52. — ***M. tentoriopharyngalis* (*M.52*):** (O) anterior face of the mesal apodeme of the gular ridge; (I) ventral wall of the postcerebral pharynx, dorsad of the suboesophageal ganglion, opposite to M.51, insertion area longitudinally widened; (F) dilator of the postcerebral pharynx, together with M.51.

4.3.10. Cerebrum and suboesophageal ganglion
Figs. 15A,B

The optic neuropils originate on a pair of anterior protocerebral lobes adjacent to the dorsal tentorial arms. Posterior cerebral lobes are absent. The central part of the cerebrum extends over approximately half the length of the head. The circumoesophageal connectives and the tritocerebral commissures arise from the tritocerebrum of the unpaired cerebrum. The suboesophageal ganglion is of comparable length to

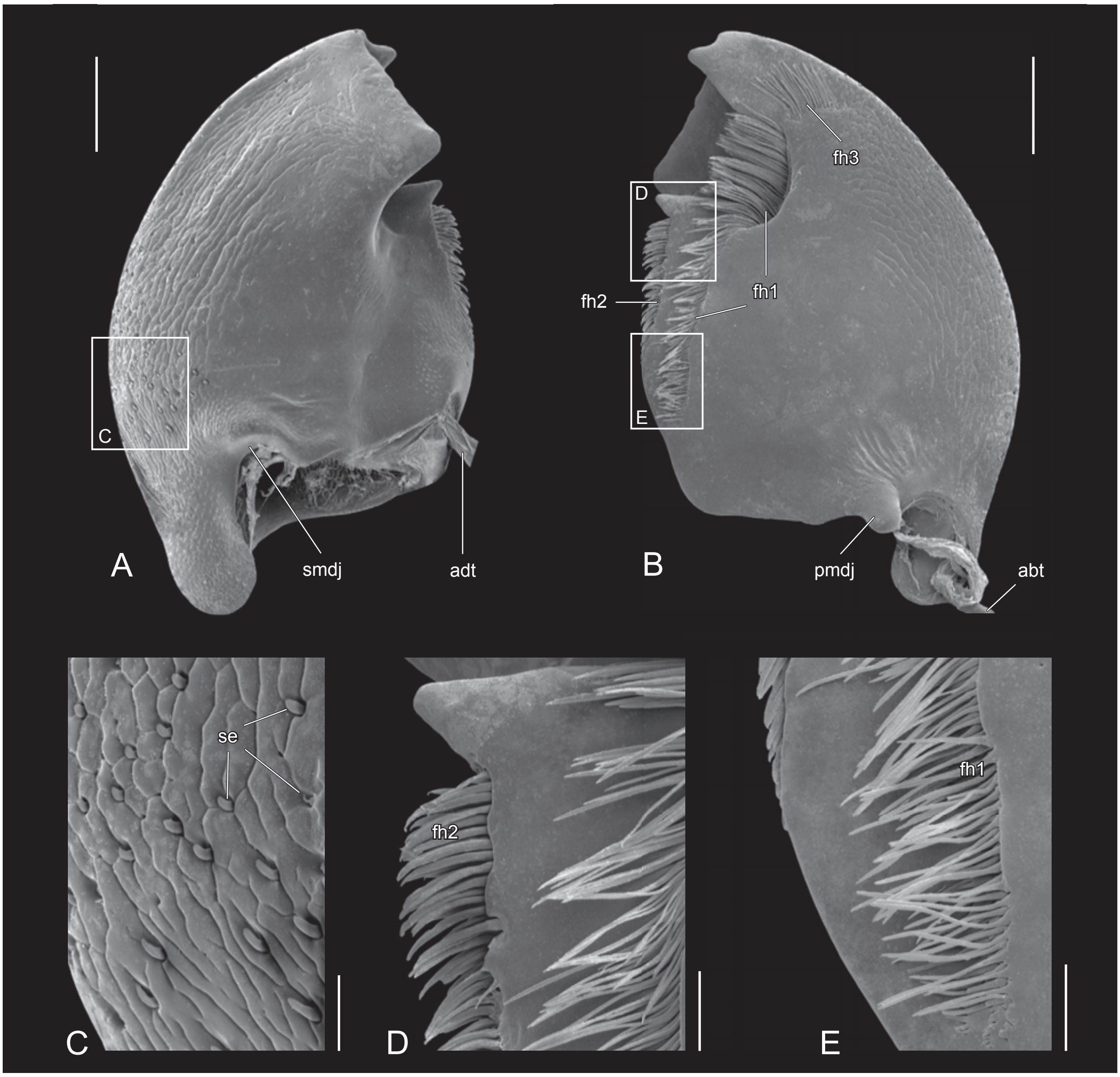

Fig. 17. *Aspidytes niobe*, mandible, SEM micrographs. **A**: Left mandible, dorsal view. **B**: Left mandible ventral view. **C–E**: Detail magnifications of the framed sectors in A and B. **C**: Sensilla. **D**: Part of the second fringe of hairs. **E**: Part of the first fringe of hairs. Abbreviations: abt = abductor tendon, adt = adductor tendon, fh1–3 = fringes of microtrichia (numeration described in section 4.3.5. [Mandibles]), pmdj = primary mandibular joint, se = sensilla, smdj = secondary mandibular joint. (Scale bars: A–B 100 µm, C–E: 20 µm)

the central part of the cerebrum and reaches the cardinal processes anteriorly. It is posteriorly continuous with the connectives to the prothorax.

4.4. Head morphology of *Amphizoa lecontei*

4.4.1. External head capsule

Figs. 18, 21

The prognathous head is somewhat longer than broad. The relatively small compound eyes are moderately protruding. The colour of the head capsule is dark-brown. The surface (except for the gula) and also the exposed parts of the head appendages are densely covered with small pores bearing sensory styliform processes (Fig. 21B,G,K). Tiny setae originate among these grooves, especially close to sclerite margins, around the eyes, and near the postoccipital ridge. Longer setae are absent. The clypeus is almost twice as long as the labrum. The rounded protuberances articulating with the secondary mandibular joints are located at the ventroposterior angles. The clypeofrontal suture is a complete transverse furrow and medially arcuate. The anterior tentorial pits are located in the lateral parts of the suture, close to the antennal ridge.

A frontal or coronal suture is absent. The broad supraocular ridges extend from the clypeofrontal suture to the posterior end of the compound eyes.

The ventral hypostomata are lobe-like extended and form an acute angle with the lateral genae. The edge between them is strengthened (Fig. 18C). The broad gula is fused with the submentum and the mentum (see section 4.4.7. [Labium]). The submento-gular border is not visible except for the conspicuous posterior tentorial pits. The median internal gular apodeme is visible on the anterior gula. The postoccipital ridge and postgular ridge are well developed. A pair of dorsal paramedian apodemes and a pair of lateral extensions serve as areas of origin for cervical muscles.

4.4.2. Internal skeletal structures

Figs. 19, 20

The circumantennal ridge forms a prominent external socket. The epistomal ridge corresponding with the clypeofrontal suture is low. A short lateral ridge connects the epistomal ridge and the antennal ring is the origin of the anterior tentorial arm. The arm is approximately triangular due to its widened base and the strongly narrowed posterior part (Fig. 19C). The constantly broad, dorsal tentorial arm reaches the head capsule but is not rigidly fused to it. The anterior and dorsal arms are connected to a central tentorial element which is continuous with the gular ridge posteriorly. The plate-like apodemes of the central elements, the laminatentoria, are not fused medially. The laminatentorial plate is composed of an anterior horizontal wall and a posterior almost vertical wall (Fig. 19A). The entire ventral and anterior face serves as area of origin of the large stipes-retractor (M.18a). The posterior tentorial arms are completely fused to the anterior margins of the gular ridges. The anterior bases are connected to the low hypostomal ridges which correspond to the hypostomal sutures. The gular ridges are high and their dorsal margins are bent outwards. They are continuous with the postoccipital ridge posteriorly. A pair of short mesal processes is present above the submento-gular border but obviously no muscle originates on it (Fig. 19A). A further pair of apodemes arises above the posterior gula close to the postoccipital ridge. The anterior and posterior faces serve as attachment areas for muscles. The tentorial bridge originates far posteriorly on the gular ridges closely to the apodemes. The bridge is deeply arched anterad and its median, almost straight part reaches the mid-gular region. The gular apodeme arises medially on the anterior gula. It is a vertical triangular plate and its lateral faces are the area of origin of labial muscles.

The mental ridges and the suspensorium are described in sections 4.4.7. (Labium) and 4.4.8. (Hypopharynx).

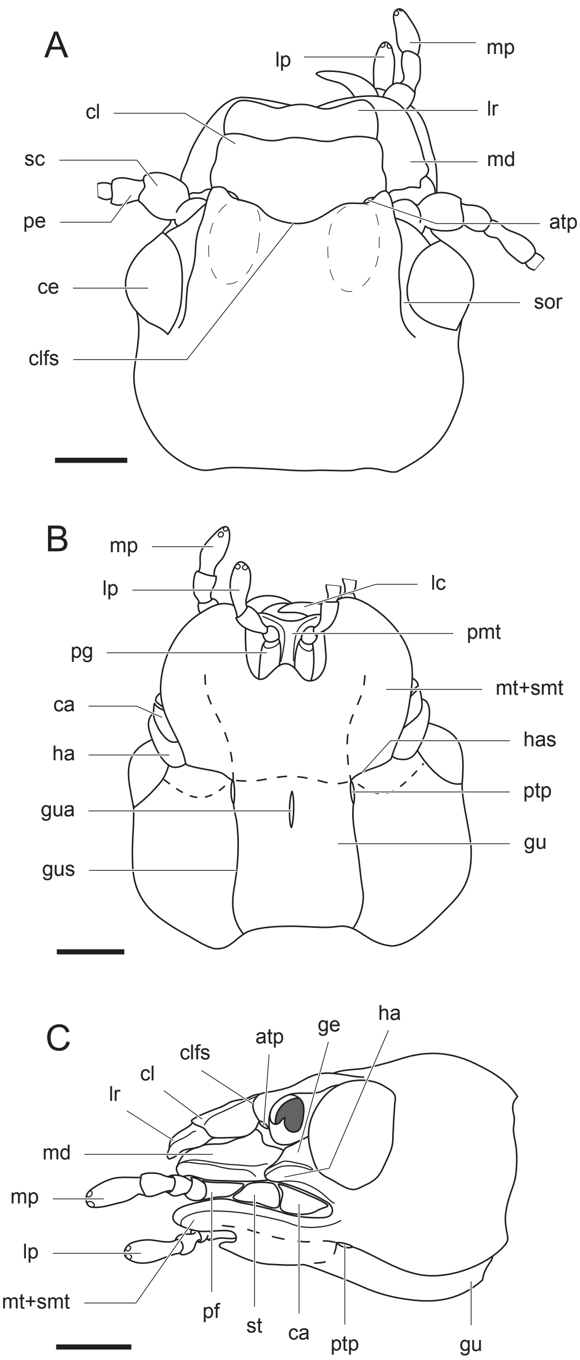

Fig. 18. *Amphizoa lecontei*, head, habitus. **A**: Dorsal view. **B**: Ventral view. **C**: Lateral view. Abbreviations: atp = anterior tentorial pit, ca = cardo, ce = compound eye, cl = clypeus, clfs = clypeofrontal suture, ge = gena, gu = gula, gua = gular apodeme, gus = gular suture, ha = hypostoma, has = hypostomal suture, lc = lacinia, lp = labial palp, lr = labrum, md = mandible, mp = maxillary palp, mt+smt = fused mental-submental sclerite, pe = pedicellus, pf = palpifer, pg = palpiger, pmt = prementum, ptp = posterior tentorial pit, sc = scapus, sor = supraocular ridge, st = stipes. (Scale bar: 500 μm)

4.4.3. Antennae

Figs. 18A, 20B,C, 21B

Skeletal features. The antennae are inserted laterally between the secondary mandibular joint and the compound eye. The articulation socket – the circumantennal ridge – is protruding. The 11-segmented, filiform antenna is glabrous but covered with pores containing sensory processes like those on the head capsule (Fig. 21B). The scapus is bipartite. A notch of the basal margin of the globular basal part articulates with an anteroventral process on the circumantennal ridge (Fig. 20B,C). The distal part of the scapus is barrel-shaped and about 1.5 times as long as wide. The two scapal subunits are separated by a deep constriction and their longitudinal axes form an obtuse angle. Due to this acentric attachment the anterobasal portion of the distal part appears distinctly prominent (Figs. 20C, 21B). The pedicellus is also barrel-shaped but only about half the size of the distal scapus. The flagellomeres are nearly cylindrical but slightly narrowing basally. They are as wide as the pedicellus but conspicuously longer.

Musculature (Figs. 19C, 20C)**. *M. tentorioscapalis anterior* (*M.1*):** (O) anterior tentorial arm, reaching the origin of the dorsal arm, fan-shaped; (I) anteroventrally on the condyle of the scapus; (F) depressor and rotator of the antenna. — ***M. tentorioscapalis posterior* (*M.2*):** (O) dorsal tentorial arm, reaching the dorsal head capsule; (I) posterodorsally on the condyle of the scapus; (F) elevator, retractor and rotator of the antenna. — ***M. tentorioscapalis lateralis/ medialis* (*M.3/4*):** (O) entire dorsal tentorial arm and posterior part of the anterior arm, ventrally adjacent to M.1, fan-shaped; (I) medioventrally on the inner basal margin of the scapus; (F) depressor of the antenna, together with M.1. — The ***M. scapopedicellaris lateralis* (*M.5*)** and ***M. scapopedicellaris medialis* (*M.6*)** are present but cannot be described in detail due to the lack of microtome section series.

4.4.4. Labrum

Figs. 18, 19A,C, 20E,F, 21C

Skeletal features. The labrum is about half as long as the clypeus. The anterior half of the dorsal surface is densely covered with pores similar to those of the head capsule (Fig. 21C). The anterior margin is broadly bent inwards thus forming a semicircular plate on the ventral side. This area is densely covered with microtrichia (Fig. 21C). The anterior edge forms a shallow median bulge and a pair of lateral lobes. Some minute setae originate on the median region along the edge.

A pair of tormae arises laterally from the posterior margin (Fig. 20E). The tormae are connected to the dorsal suspensorial arms by ligamental strands.

Musculature. Absent.

4.4.5. Mandibles

Figs. 18, 19, 20K–N, 21G–K

Skeletal features. The mandibles do not protrude beyond the anterior labral margin but are distinctly protruding laterally beyond the clypeal margin. The length/width ratio is about 0.8, i.e. the mandibles are broader than long. The dorsal side is convex whereas the ventral side is flat. The lateral and the anterior margin form a right angle, thus the mandibular shape appears square. The exposed parts of the surface are covered with pores bearing styliform or hooked processes. True setae are absent.

Both incisors are placed apically and thus the distal cutting edge between them is almost vertical. The dorsal incisor is more rounded and the ventral more acute. The cutting edge is distinctly bent on the left and notched on the right side. The third, mesal tooth is large and prominent on the right but small on the left mandible. The mesal edge between the tooth and the base forms another small cusp on the left mandible whereas it is convex on the right one. A mola is absent. Two fringes of microtrichia are present on the ventral side (Fig. 21H). The first close to the mesal margin reaches the ventral incisor anteriorly; the hairs do not overtop the margin. The second fringe behind the incisor is very short.

The abductor tendon is attached to a rounded bulge at the posterolateral angle of the mandible. The mandibular joints are located subapically. The axis of rotation is not vertical but inclined. The ventral primary joint is a hemispherical condyle. The dorsal secondary joint is a deep basal emargination mesad of the bulge surrounded by a crescent-shaped concave socket.

The left and the right mandible are asymmetrical in some details, e.g., the formation of the dorsal cutting edge, the mesal tooth or the mesal margin (see above).

Musculature. *M. craniomandibularis internus* (*M.11*): (O) lateral and dorsal wall of the head capsule, reaches the postoccipital ridge, strongly fan-shaped; (I) mesal mandibular base with a strong, sclerotised tendon, strongly converging towards the tendon; (F) adductor of the mandible. — ***M. craniomandibularis externus* (*M.12*):** (O) ventrolateral wall of the head capsule, reaches the postoccipital ridge; (I) round bulge on the lateral mandibular base with a thin, sclerotised tendon; (F) abductor of the mandible. — ***M. hypopharyngomandibularis* (*M.13*):** absent.

4.4.6. Maxillae

Figs. 18, 19D, 20G,H, 21L–N

Skeletal features. The maxillae are inserted in the hypostomal grooves and largely covered by the mento-

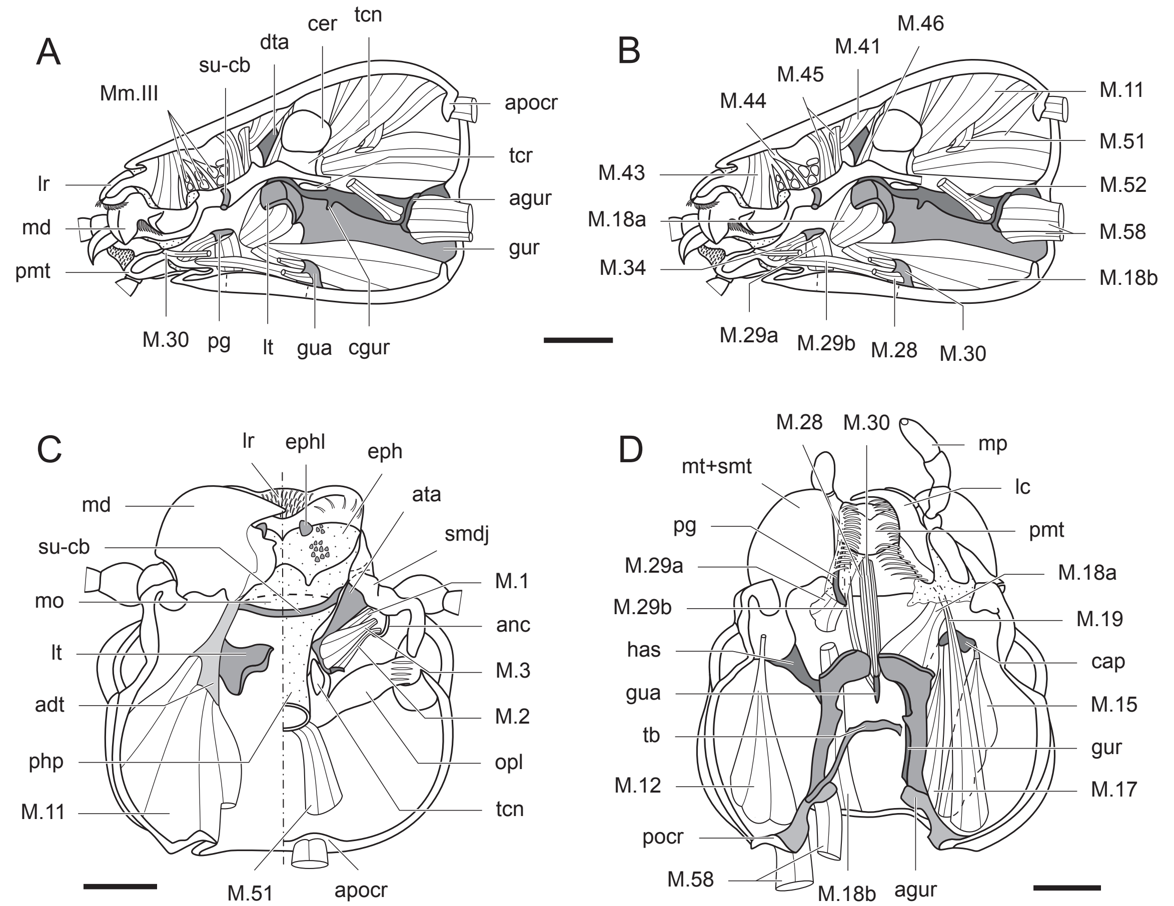

Fig. 19. *Amphizoa lecontei*, head, sagittal and horizontal sections. **A** = **B**: Sagittal view. **C**: Ventral view of dorsal half. **D**: Dorsal view of ventral half. Endoskeletal elements grey, semimembranous parts punctured, translucent structures marked by dashed lines. Abbreviations: adt = adductor tendon, agur = apodeme of gular ridge, anc = circumantennal ridge, apocr = dorsal apodeme of postoccipital ridge, ata = anterior tentorial arm, cap = cardo process, cer = cerebrum, cgur = process of gular ridge, dta = dorsal tentorial arm, eph = epipharynx, gua = gular apodeme, gur = gular ridge, has = hypostomal suture, lc = lacinia, lr = labrum, lt = laminatentorium, md = mandible, mo = mouth opening, mp = maxillary palp, mt+smt = fused mental-submental sclerite, opl = optic lobe, pg = palpiger, php = postpharynx, pmt = prementum, pocr = postoccipital ridge, smdj = secondary mandibular joint, su-cb = suspensorial cross-bar, tb = tentorial bridge, tcn = tritocerebral connective, tcr = tritocerebral commissure. (Scale bars: 500 µm)

submental sclerite. The exposed surfaces are covered with pores similar to those of the head capsule. The cardo comprises an elongate transverse external part and an internal bifurcate process on the dorsal side. The cardo and the anteriorly attached basistipes form a right angle. The elongate lateral basistipes bears a pair of setae and is completely separated from the ventral mediostipes. The latter is narrowed posteriorly and its anterior region is continuous with the mesal lacinia. The lacinial base is widened and forms a mesal elongate bulge whereas the distal part is hook-shaped. A row of irregularly arranged setae is inserted on both sides of the mesal edge of the hook. Close to the margin of the basal bulge a dense fringe of hairs is present on the dorsal side whereas the ventral face is scattered with single setae (Fig. 21L). The moveable galea is placed between the lacinia and the maxillary palp and distally sickle-shaped. The lateral and ventral side of the palp-bearing palpifer is somewhat longer than wide, whereas the dorsal side forms a distinctly elongated, approximately oval plate. The maxillary palp is 4-segmented. Palpomere 1 is small and curved; palpomere 2 and 3 are somewhat calyx-shaped and about 1.5 × the size of the first one. The apical segment is elongated (about three times as long as wide) with two small round sensory fields at the tip (Fig. 21N). No setae are inserted on galea, palpifer and the palp.

Musculature (see also Fig. 19B)**. *M. craniocardinalis externus* (*M.15*):** (O) ventral wall of the head capsule, between M.12 and M.17, longitudinally wide area of origin; (I) lateral branch of the internal cardinal process, strongly narrowing towards the short, sclerotised tendon; (F) extensor of the maxilla. — ***M. craniocardinalis internus* (*M.16*):** absent. — ***M. tentoriocardinalis* (*M.17*):** (O) lateral face of the gular ridge, reaches the postoccipital ridge, fan-shaped; (I) mesal branch of the internal cardinal process, strongly narrowing towards the insertion; (F) flexor of the maxilla, antagonistic to M.15. — ***M. tentoriostipitalis***

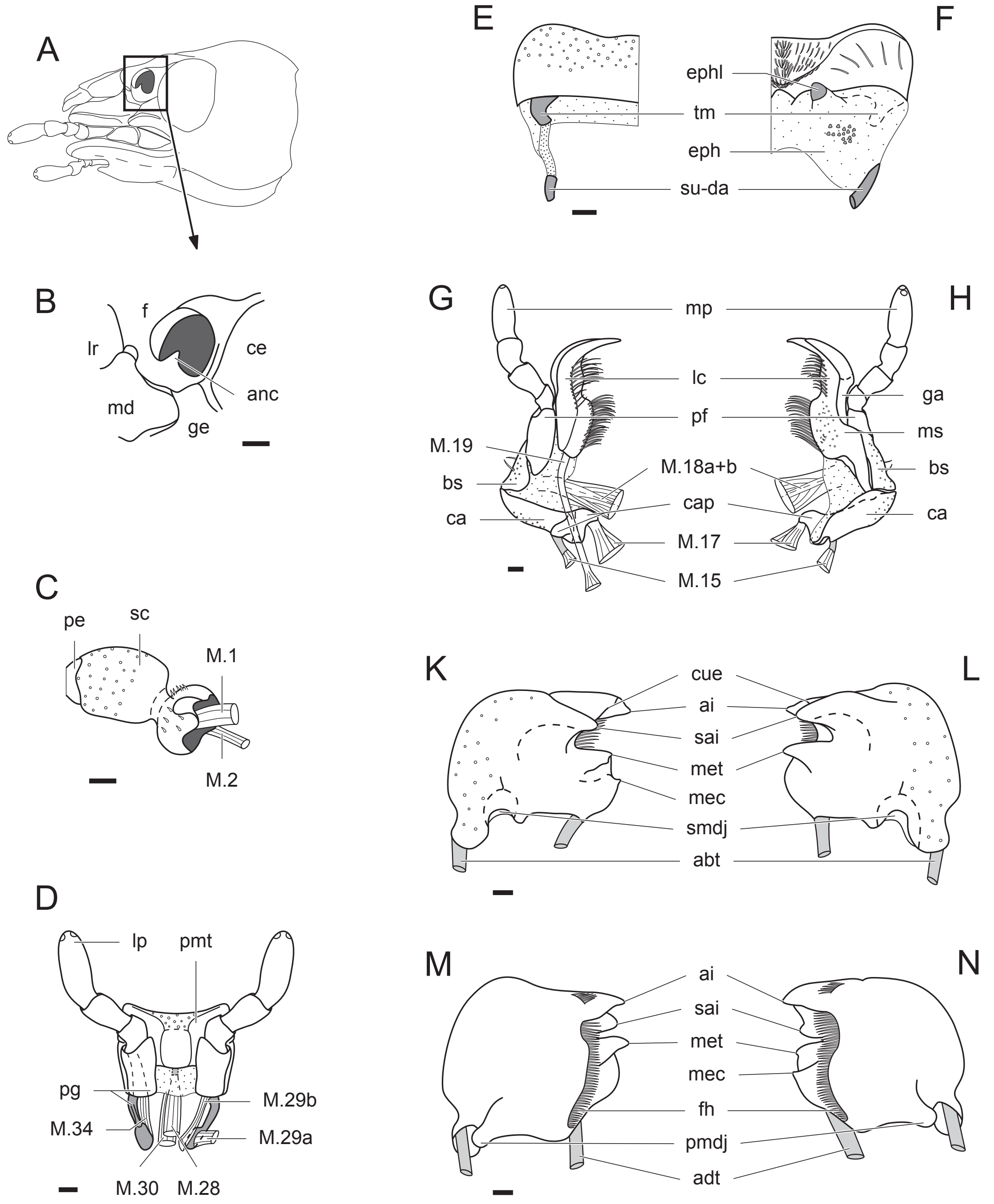

Fig. 20. *Amphizoa lecontei*, head appendages. **A**: Head, lateral view. **B**: Antennal insertion. **C**: Antenna, basal segments. **D**: Labrum, dorsal view. **E**: Labrum, ventral view. **F**: Maxilla, dorsal view. **G**: Maxilla, ventral view. **H**: Left mandible, dorsal view. **K**: Right mandible, dorsal view. **L**: Right mandible, ventral view. **M**: Left mandible, ventral view. **N**: Labium, ventral view. Endoskeletal elements grey, semimembranous areas punctured, translucent structures marked by dashed lines. Abbreviations: abt = abductor tendon, adt = adductor tendon, ai = apical incisor, anc = circumantennal ridge with process, bs = basistipes, ca = cardo, cap = cardo process, ce = compound eye, cl = clypeus, cue = cutting edge, eph = epipharynx, ephl = epipharyngeal lobe, f = frons, fh = ventral fringe of hairs, ga = galea, ge = gena, lc = lacinia, lp = labial palp, md = mandible, mec = mesal cusp, met = mesal tooth, mp = maxillary palp, ms = mediostipes, pe = pedicellus, pf = palpifer, pg = palpiger, pmdj = primary mandibular joint, pmt = prementum, sai = subapical incisor, sc = scapus, smdj = secondary mandibular joint, su-da = dorsal suspensorial arm, tm = torma. (Scale bars, except A: 100 μm)

(***M.18a,b***)**:** (O) subcomponent ***a***: ventral and anterior face of the laminatentorium; subcomponent ***b***: posteriormost gular region and postgular ridge; (I) membrane between the cardo and the stipital base; (F) adductor and retractor of the stipes, with vertical component (subcomponent ***a***). — ***M. craniolacinialis*** (***M.19***)**:** (O) posteroventral wall of the head capsule, reaches the postoccipital ridge, posterad of M.15; (I) dorsal base of the lacinia, with a long and slender tendon (lying above the cardinal process between the mesal and lateral branch); (F) adductor and retractor of the lacinia. — The intrinsic maxillary muscles (***M. stipitolacinialis***, ***M.20***; ***M. stipitogalealis***, ***M.21***; ***M. stipitopalpalis externus***, ***M.22***; ***M. palpopalpalis tertius***, ***M.26***; ***M.***

palpopalpalis quartus*, *M.27) cannot be identified and described without cross-section series.

4.4.7. Labium
Figs. 18, 19, 20D

Skeletal features. The mentum and submentum are completely fused to an extensive postlabial sclerite. It covers the remaining mouth parts almost completely in ventral view. The postlabial sclerite is about twice as broad as the gula and posteriorly fused to it. The surface is covered with sensory pores which are completely absent on the gular region. The submental region is posterolaterally limited by the hypostomal sutures. The mental part forms two large lateral lobes and one rounded median cusp in a broad emargination. The internal mental ridges arising from the mesal margins of the lobes are low. Their upper hind angles are continuous with the ventral arms of the suspensorium (see section 4.4.8. [Hypopharynx]). The prementum is inserted in the mental emargination. The ventral side forms a median blunt keel which is anteriorly covered with pores. The premental anterior margin is continuous with a triangular sclerite on the dorsal side which is covered with short microtrichiae. The palpigers fit in the concavities between the keel and the lateral mental lobes. The external cylindrical part of each palpiger is two times longer than wide and bears the 3-segmented labial palp. The posterior internal process is paddle-shaped with a curved shaft. The widened paddle-part is area of origin of two labial muscles. Similar to the maxillary palp the labial palpomere 1 is shortened and palpomere 3 is elongated and bears two small round sensory fields apically. True setae are absent on the entire labium.

Musculature. ***M. submentopraementalis* (*M.28*):** (O) basal anterior margin of the gular apodeme, (I) medially on the ventral margin of the prementum, with a short sclerotised tendon; (F) retractor and depressor of the prementum. — ***M. tentoriopraementalis inferior* (*M.29a,b*):** (O) subcomponent ***a***: middle region of the postlabial sclerite; subcomponent ***b***: lateral faces of the gular apodeme; (I) subcomponent ***a***: lateral face of the paddle-shaped internal process of the palpiger; subcomponent ***b***: ventral base of the cylindrical part of the palpiger; (F) retractor of labial palp, adductor (subcomponent ***a***), possibly elevator. — ***M. tentoriopraementalis superior* (*M.30*):** (O) anterior margin of gular apodeme, dorsally of M.28; (I) medially on a hypopharyngeal fold close to the dorsal premental margin, with a thin tendon; (F) retractor of the anterior hypopharynx and of the prementum. — ***M. praementopalpalis externus* (*M.34*):** (O) mesal face of the paddle of the internal process of the palpiger, opposite to M.29a; (I) ventral base of palpomere 1; (F) movements of the labial palp.

4.4.8. Epipharynx and hypopharynx
Figs. 19, 20E,F, 21C–F

General features. The epipharynx is distinctly convex, whereas the hypopharynx is almost flat and abruptly rising posteriorly. Epipharyngeal lobes are present close to the labral margin with large sclerotised appendages bearing styliform sensory processes (Fig. 21E). The surface of the lobes is densely covered with minute microtrichiae (Fig. 21E). Posterad of it a group of small sclerotised cusps is present (Fig. 21F).

The hypopharynx is attached to the dorsal margin of the prementum. A pair of membranous, flattened, comb-shaped lobes originates at the ventral base of the prementum and lies laterally adjacent to the hypopharynx and prementum. They possibly represent derivatives of the paraglossae (Fig. 19D). Epipharynx and hypopharynx are entirely lacking true setae.

The suspensorium is well developed. The transverse cross-bar supports the anatomical mouth opening ventrally (Fig. 19A,C). A pair of dorsal suspensorial arms is connected to the labral tormae by ligamental strands (Fig. 20E). The ventral suspensorial arms are firmly attached to the internal mental ridges. The suspensorial arms originate at the lateral ends of the cross-bar.

Musculature. ***M. frontohypopharyngalis* (*M.41*):** (O) frons, between M.45 and M.46, fan-shaped; (I) laterally on the suspensorial cross-bar, with a slender sclerotised tendon, intercrossing with M.45; (F) elevator of the suspensorium, contraction of the mouth opening. — ***M. tentoriohypopharyngalis* (*M.42*):** absent. — ***M. clypeopalatalis* (*M.43*):** (O) paramedially on the clypeus; (I) anterior epipharynx, broad area of insertion; (F) dilator of the preoral cavity. — ***Mm. compressores epipharyngis* (*Mm.III*):** Numerous transverse muscle bundles connect the dorsolateral edges of the posterior epipharynx. The fibres of M. clypeobuccalis (M.44) insert between them. In antagonism to M.43 contraction of the transverse muscles results in a compression of preoral cavity and the mouth opening. — ***M. clypeobuccalis* (*M.44*):** (O) paramedially on the clypeus, posteriorly of M.43; (I) posteriormost epipharynx, close to the mouth opening, between the muscle fibres of Mm.III; (F) dilator of the posterior preoral cavity.

4.4.9. Pharynx
Fig. 19

General features. The ventral suspensorial cross-bar and the dorsal frontal ganglion mark the anatomical mouth opening. Furthermore the muscles M.44 and M.45 insert immediately anterad and posterad of the mouth. The precerebral pharynx is gradually

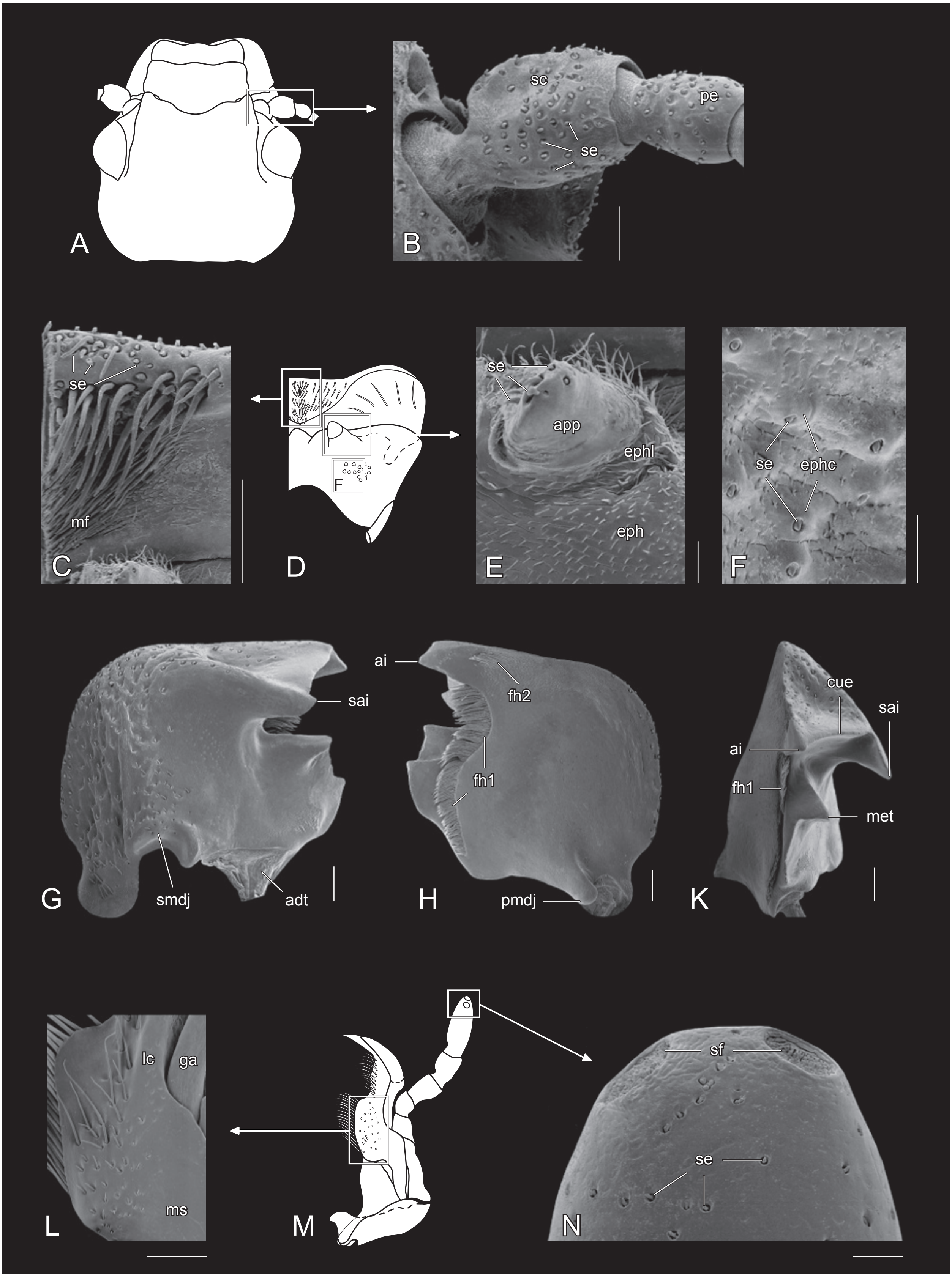

Fig. 21. *Amphizoa lecontei*, head, SEM micrographs. **A**: Head scheme, dorsal view. **B**: Detail magnification of the head, antennal basis. **D**: Labral scheme, ventral view. **C**,**E**,**F**: Detail magnifications of labrum. **C**: Microtrichia field. **E**: Epipharyngeal lobe. **F**: Epipharyngeal sclerotised cusps. Abbreviations: adt = adductor tendon, ai = apical incisor, app = sclerotised appendage of epipharyngeal lobe, cue = cutting edge, eph = epipharynx, ephc = epipharyngeal sclerotised cusp, ephl = epipharyngeal lobe, fh1/2 = ventral fringes of hairs (numeration described in section 4.4.5. [Mandible]), ga = galea, lc = lacinia, met = mesal tooth, mf = microtrichia field, ms = mediostipes, pe = pedicellus, pmdj = primary mandibular joint, sai = subapical incisor, sc = scapus, se = sensilla, sf = apical sensory field, smdj = secondary mandibular joint. (Scale bars: 100 µm, except E,F,N: 20 µm)

ascending to the dorsal half of the head capsule and has a distinctly wider lumen than the postcerebral pharynx which lies approximately in the mid level of the head capsule. Ring and longitudinal musculature of the pharynx are well developed.

Musculature. ***M. frontobuccalis anterior*** **(*M.45*):** (O) paramedially on the anterior frons, anteriorly of M.41; (I) paramedially on the dorsal wall of the anterior precerebral pharynx, posteriorly of Mm.III; (F) dilator of the precerebral pharynx. — ***M. frontobuccalis posterior*** **(*M.46*):** (O) posterior frons, posteriorly and laterally of M.41; (I) paramedially on the dorsal and dorsolateral wall of the posterior precerebral pharynx, anteriorly of the cerebrum, opposite to M.50; (F) dilator of the posterior precerebral pharynx, together with M.50. This muscle is likely represented by two closely adjacent bundles on either side. It cannot be fully excluded that the lateral portion is a separate muscle, e.g., M. frontobuccalis lateralis (M.47). The interpretation of both bundles as a bipartite M.46 is based on their adjacent position and the identical function. — ***M. frontobuccalis lateralis*** **(*M.47*):** probably absent (see above). — ***M. tentoriobuccalis anterior*** **(*M.48*):** (O) medially on the tentorial bridge; (I) medially on the hypopharynx, immediately anterad of the suspensorial cross-bar; (F) retractor and depressor of the hypopharynx, dilator of the preoral cavity (homology see section 4.1.9.). — ***M. tentoriobuccalis posterior*** **(*M.50*):** (O) anterior margin of the tentorial bridge, laterad of M.48; (I) ventral wall of the precerebral pharynx, opposite to M.46; (F) dilator of the posterior precerebral pharynx, together with M.46. The muscle is separated from M.48 by the tritocerebral commissure. — ***M. verticopharyngalis*** **(*M.51*):** (O) posterior dorsal wall of the head capsule, between fibres of M.11; (I) dorsal wall of the postcerebral pharynx, opposite to M.52; (F) dilator of the postcerebral pharynx, together with M.52. — ***M. tentoriopharyngalis*** **(*M.52*):** (O) anterior face of the posterior apodeme of the gular ridge; (I) ventral wall of the postcerebral pharynx, dorsally of the suboesophageal ganglion, opposite to M.51; (F) dilator of the postcerebral pharynx, together with M.51.

4.4.10. Cerebrum and suboesophageal ganglion

Figs. 19A,C

A pair of elongate optic neuropils originates on the cerebrum. Distinct anterior or posterior protocerebral lobes are absent. The length of the cerebrum is approximately quarter of the length of the head capsule. The circumoesophageal connectives and the equally broad tritocerebral commissures arise from the tritocerebrum. The suboesophageal ganglion is distinctly longer than the cerebrum. It is posteriorly continuous with the connectives to the prothorax.

4.5. List of characters and data matrix

The use of the terms Geadephaga and Hydradephaga does not imply the monophyletic origin of the aquatic and terrestrial families, respectively. Presumably plesiomorphic states are coded as 0 in most cases. However, this convention is irrelevant when a cladistic approach is used (a posteriori polarity determination).

4.5.1. Adults

Head capsule

1 Posterior part of the head delimited by a transverse ventral furrow: (0) present (Fig. 1C); **(1)** absent (Fig. 7C). — More or less globular posterior part of head capsule separated from anterior part by ventral transverse furrow in *Priacma*, Geadephaga, *Meru*, *Hygrobia* (Beutel 1986a; Beutel et al. 2006) and the examined Polyphaga. The posterior part forms a ball-and-socket joint with the thorax.

2 Compound eyes protruding beyond the lateral contour of head: (0) present (Figs. 1A, 18A); **(1)** absent, lateral contour equally rounded (Figs. 7A, 13A). — Lateral contour of head usually evenly rounded in Hydradephaga (Beutel 1989a, 1997; Belkaceme 1991). Eyes protruding in Geadephaga, *Meru*, *Amphizoa*, *Hygrobia* (Beutel 1986a, 1997; Beutel et al. 2006) and the outgroup taxa.

3 Division of compound eyes: (0) absent; **(1)** present, divided by a chitinous bridge. — Completely divided into upper and lower portion by a chitinous bridge in Gyrinidae. Bridge narrow in *Spanglerogyrus* but very broad in Gyrininae (Hatch 1927; Folkerts 1979; Honomichl 1975; Beutel 1989a).

4 Supraocular ridge: (0) absent; **(1)** present (Figs. 1, 18). — Usually present in Geadephaga and also in *Amphizoa* and *Meru* (Beutel et al. 2006). Internally connected to circumocular ridge.

5 Supraocular setae: (0) absent, **(1)** present (Fig. 1). — One or two long setae present in Trachypachidae, Carabidae and *Helophorus*. Absent in Hydradephaga.

6 Postocular ridge: (0) absent; **(1)** present only laterally (Figs. 7, 12K); **(2)** present circular around entire head capsule. — Thin lateral ridges close to the posterior margin of the compound eyes present in Haliplidae: single ridge in *Peltodytes* and *Brychius* and two ridges in *Haliplus* (Beutel & Ruhnau 1990). Postocular ridges surrounding the entire head capsule occur in Polyphaga (e.g., *Helophorus*, *Catops*).

7 Circular ridge of posterior head region: (0) absent; **(1)** present (Figs. 1, 5F). — Up to the circular ridge, present in the posterior third of the head region of Carabidae, *Trachypachus*, *Meru* and *Priacma*, the head is retracted into the thorax.

8 Labro-clypeal connection: (0) movable by a membrane; **(1)** firm. — Immovably connected to clypeus in *Carabus*.

9 Orientation of labrum: (0) nearly horizontal, parallel to clypeal surface (Fig. 1C); **(1)** nearly vertical, distinctly inclined relative to clypeal surface (Fig. 7C). — Almost vertical in Gyrinidae and in *Haliplus*, *Noterus*, *Dytiscus* and *Meru*.

10 Long clypeal setae: (0) absent; **(1)** (at least) one pair of longer setae close to the lateral margin of clypeus (Fig. 1A). — Clypeus pubescent in *Priacma*, *Catops* and *Helophorus*; with scattered short setae in *Spanglerogyrus* and *Amphizoa*; glabrous in *Gyrinus*, *Haliplus* and the remaining Dytiscoidea. A pair of long setae originates on the lateral parts of the clypeus in *Trachypachus* and Carabidae.

11 Clypeofrontal suture: (0) absent; **(1)** complete (Fig. 1A); **(2)** medially interrupted (Figs. 7A, 12E, 13A). — Absent in *Noterus* and *Priacma*. Medially interrupted in *Haliplus*, *Aspidytes* and *Agabus*.

12 Shape of clypeofrontal suture: (0) with obtuse angles laterally; **(1)** convex, evenly curved (Figs. 1A, 18A); **(2)** straight or slightly concave. — With obtuse lateral angles enclosing the anterior tentorial grooves in Carabidae. Distinctly convex and and evenly curved in *Spanglerogyrus*, *Amphizoa*, *Hygrobia* and *Trachypachus*. Suture straight or slightly concave in *Gyrinus*, *Meru*, *Dytiscus* and *Catops*.

13 Position of anterior tentorial pits: (0) ventrad of antennal insertion; **(1)** within clypeofrontal suture, internally attached to epistomal ridge (Figs. 1A, 2C); **(2)** dorsally close to antennal insertion, on antennal ring or on lateral ridge connected to epistomal ridge (Figs. 8B, 9A, 15A, 19C). — External pits correspond internally to the origin of the anterior tentorial arms. Originating from epistomal ridge in Carabidae and *Trachypachus*. Laterally shifted in Hydradephaga (except for *Agabus*), originating from antennal ring or from a lateral ridge connected to epistomal ridge (Gyrinidae).

14 Connection between anterior tentorial arms and posterior tentorium: (0) present, central tentorial body (Figs. 2C, 14A); **(1)** absent. — Absent in Gyrininae (Beutel 1989a) and *Priacma* (Hörnschemeyer et al. 2002).

15 Dorsal tentorial arms well developed: (0) present; **(1)** arms greatly reduced, i.e. membranous, represented by short buds or absent. — Reduced in *Priacma* (unsclerotised) (Hörnschemeyer et al. 2002), Gyrinidae (Honomichl 1975; Beutel 1989a), Dytiscidae and *Meru*.

16 Laminatentoria: (0) absent (Figs. 2B, 3A, 5D); **(1)** present. — Laminatentoria are absent in *Priacma* and *Gyrinus*.

17 Median fusion of laminatentoria: (0) absent; **(1)** present (Figs. 8B, 9A, 11D). — Fused in *Spanglerogyrus*, *Haliplus*, *Meru*, *Carabus*, *Pterostichus* and *Helophorus*.

18 Tentorial bridge: (0) present (Figs. 2B, 3C, 11F); **(1)** absent. — Absent in Gyrininae (Beutel 1989a) and *Priacma* (Hörnschemeyer et al. 2002).

19 Shape of gular ridges: (0) low, without reinforced dorsal margin; **(1)** high, with reinforced dorsal margin. — High, with reinforced dorsal margin in Adephaga. Ridges low in *Priacma*.

20 Sloping of posterior gular ridges: (0) absent; **(1)** present (Fig. 2B,C). — Gular ridges abruptly sloping posterad of tentorial bridge in *Hygrobia*, *Trachypachus* and Carabidae. Unknown for *Meru*.

21 Apodemal plate of gular ridges (attachment area of M. profurcatentorialis, M.58): (0) absent; **(1)** present, distinctly separated from foramen occipitale (Fig. 8B); **(2)** present, close to foramen occipitale (Figs. 2B, 3C, 14A, 15C, 19A,D). — Absent in *Dytiscus*, *Meru*, *Carabus* and *Priacma*. Close to foramen occipitale and postoccipital ridge in Gyrinidae, *Hygrobia*, *Aspidytes*, *Amphizoa*, *Trachypachus* and *Pterostichus*. Close to tentorial bridge in *Haliplus*, *Noterus*, *Agabus* and *Helophorus*.

22 Gular apodeme: (0) absent; **(1)** present. — Absent in *Hygrobia*, *Dytiscus*, *Agabus*, *Aspidytes*, *Meru* and in the outgroup taxa. Varying within *Carabus*.

23 Position of gular apodeme: (0) close to submento-gular border (Figs. 1B, 2A, 18B); **(1)** close to transverse postgular ridge and foramen occipitale (Figs. 7B, 8A). — Shifted posteriorly close to foramen occipitale in *Spanglerogyrus* and *Haliplus*.

Antennae

24 Antennal pubescence of appressed setae: (0) vestiture of longer setae present on all antennomeres; **(1)** vestiture of short setae present from antennomere 4 or 5 onward; **(2)** vestiture of short setae present only on distal antennomeres; **(3)** absent. — Antennae covered with longer setae in *Priacma* and *Catops*. Dense vestiture of very short setae present on antennomeres 4–11 or 5–11 in Carabidae and only on distal antennomeres in *Helophorus*. Absent in all aquatic and semiaquatic Adephaga.

25 Long erect setae on antennae: (0) absent or few irregularly distributed setae (Fig. 13A); **(1)** apical whorl on postscapal antennomeres (Fig. 4C); **(2)** setae concentrated on lateral margin of pedicellus. — Antennal vestiture completely absent in Dytiscidae, Haliplidae (e.g., Beutel & Ruhnau 1990), *Hygrobia* (Beutel 1986a), *Amphizoa*, *Aspidytes* and *Meru*. Few isolated setae present on apical part of flagellomeres in *Noterus*. Pedicellus densely set with long setae along outer margin in Gyrinidae (e.g., Beutel 1989a). Longer hairs apart from regular pubescence absent in *Priacma* and *Helophorus*. Apical whorls present in *Catops* and Geadephaga. Additional subapical whorls present in Trachypachidae.

26 Shape of distal part of scapus: (0) distal part cylindrical (Fig. 4C); **(1)** distal part longitudinally compressed, barrel-shaped (Fig. 16C); **(2)** distal part curved; **(3)** distal part calyx-shaped (see Honomichl 1975: figs. 3, 4); **(4)** separate distal part absent. — Cylindrical and at least twice as long as wide in *Hygrobia*, *Agabus*, *Trachypachus*, Carabidae, *Priacma* and *Catops*. Barrel-shaped, scarcely longer than wide in *Haliplus*, *Noterus*, *Amphizoa* and *Aspidytes*. Extremely modified, calyx-shaped in Gyrinidae (e.g., Honomichl 1975; Beutel 1989a). Curved in *Dytiscus* and *Helophorus*. Distal part absent in *Meru*, entire scapus short and forming a compact spheric unit.

27 Attachement of the distal scapal part to the basal condyle: (0) concentrically attached (Fig. 10C); **(1)** not concentrically attached (Fig. 4C). — Not concentrical in *Amphizoa*, *Dytiscus*, *Aspidytes* and *Trachypachus*.

28 Length ratio of scapus, pedicellus and antennomere 3: (0) scapus > pedicellus < antennomere 3 (Figs. 4C, 7A, 13A); **(1)** scapus > pedicellus ≅ antennomere 3; **(2)** scapus = pedicellus = antennomere 3. — Pedicellus forming a small and cuff-like connection between scapus and antennomere 3 in *Haliplus*, *Amphizoa*, *Dytiscus*, *Aspidytes*, *Trachypachus*, *Pterostichus*, *Priacma* and *Catops*. Scapus distinctly larger than pedicellus and antennomere 3 in *Hygrobia*, *Carabus* and *Helophorus*. Three basal antennomeres of approximately equal length in *Noterus* and *Agabus*.

Mouthparts

29 Vestiture of dorsal surface of labrum: (0) densely set with setae; **(1)** glabrous or only few short setae. — Densely pubescent in *Priacma* (Hörnschemeyer et al. 2002) and polyphagan groups *Catops* and *Helophorus* (Anton & Beutel 2004).

30 Arrangement of long setae at anterior labral margin: (0) along entire anterior margin (Fig. 12B); **(1)** limited to anteromedian concavity. — Concentrated in median concavity in Hygrobiidae and Dytiscidae, and less distinctly in *Noterus*.

31 Additional rows of setae along anterior labral margin: (0) absent; **(1)** present. — Two additional rows are present in Gyrininae (Honomichl 1975; Beutel 1989a).

32 Transverse edge of labrum: (0) absent; **(1)** present (Figs. 4E, 12B). — Transverse rigde-like edge on dorsal surface of labrum present in *Haliplus* and *Trachypachus*. Anterior row of setae inserted along this edge.

33 Epipharyngeal sensorial lobes: (0) absent; **(1)** present (Figs. 15A, 19C, 21E). — Present in *Noterus*, *Amphizoa*, *Hygrobia*, Dytiscidae and *Aspidytes* (e.g., Beutel 1986a; Belkaceme 1991; Beutel et al. 2006).

34 Sclerotisation of epipharyngeal lobes: (0) absent; **(1)** distinctly sclerotised (Figs. 16F, 20F). — Sclerotised in *Amphizoa*, Dytiscidae and *Aspidytes* (Beutel et al. 2006).

35 Mandibles protruding beyond labral margin: (0) present (Fig. 1A); **(1)** absent (Figs. 7A, 13A). — Largely covered by the more or less vertical labrum in the aquatic groups (incl. *Meru* and *Aspidytes*) with the exception of *Hygrobia*. Distinctly protruding in Geadephaga (excl. Rhysodidae) and in the outgroup taxa (*Priacma*, *Catops*, *Helophorus*; e.g., Anton & Beutel 2004).

36 Length/width ratio of mandibles: (0) twice as long as wide (factor ≥ 1.9); **(1)** longer than wide (factor ≥ 1.3 – 1.8) (Figs. 6, 10K – N); **(2)** about as long as wide (factor ≤ 1,2) (Figs. 16K – N, 20K – N). [The length is measured from the straight basal margin to the anterior margin of the apical part of the mandible, the width measured at the base.] — Approximately twice as long as wide in many Carabidae and *Priacma*. Ratio in most taxa under consideration between 1,3 and 1,8. Compact and short in Gyrinidae, *Amphizoa*, *Agabus* and *Aspidytes*, and also in *Catops*.

37 Mola: (0) absent; **(1)** present. — Always absent in Adephaga and also in adults of Archostemata.

38 Dorsolateral area of mandibles with fine pores: (0) absent; **(1)** present (Figs. 12D, 17A, 21G). — Lateral part pubescent in *Priacma*. Dorsolateral part densely covered with fine pores in *Haliplus*, *Amphizoa*, *Hygrobia* and *Aspidytes*. Surface thus distinctly differs from glabrous mesal part.

39 Longitudinal fringe of hairs parallel to mesal egde of mandibles: (0) absent; **(1)** present, hairs short, not reaching mesal edge (Figs. 6, 17, 21H); **(2)** present, hairs longer, at least reaching mesal edge (Fig. 10M,N); **(3)** present, very dense, inserted below and above mesal edge. — Absent in Gyrinidae (Beutel 1989a), *Hygrobia*, *Meru* and *Priacma*. Hairs short in *Amphizoa*, *Aspidytes*, *Trachypachus* and *Pterostichus*. Dense fringe of distinctly longer hairs present in *Haliplus*, *Noterus*, Dytiscidae and the examined polyphagan taxa. Very dense and inserted above and below the edge in *Carabus*. A second row of short hairs on the mesal edge is present in *Aspidytes*.

40 Shape and orientation of distal cutting edge of mandible: (0) straight, parallel to longitudinal axis of mandible; **(1)** J-shaped, apically curved (Figs. 6D,E, 10K, 17A); **(2)** straight, nearly perpendicular to longitudinal axis of mandible (Fig. 21K). — Cutting edge between distal teeth long and parallel to mandibular axis in Carabidae and all examined polyphagan taxa. Apically curved and J-shaped in *Haliplus*, *Noterus*, *Hygrobia*, *Aspidytes*, *Meru* and *Trachypachus*. Nearly vertical in all other hydradephagan taxa.

41 Shape of lateral side of mandible: (0) basal margin widened lateral side convex; **(1)** basal margin widened, lateral side concave (Fig. 6L,M); **(2)** basal margin not widened, lateral side convex (Figs. 12D, 17A); **(3)** basal margin not widened, distal part widened and convex (Fig. 21G). — Basally widened and externally convex in *Priacma* and *Catops*. Laterobasally concave in *Trachypachus*, Carabidae and *Helophorus*. Concavity usually bordered by distinct ridges. Basally not widened and laterally convex in *Haliplus*, *Noterus*, *Hygrobia*, Dytiscidae and *Aspidytes*. Distal part of external surface broadened in Gyrinidae and *Amphizoa*. Unknown for *Meru*.

42 Position of mandibular joints: (0) lateral corners of basal margin (Fig. 6L); **(1)** mesally of the lateral corners, on ventral and dorsal basal margin (Fig. 17A,B). — Placed further mesally in all aquatic groups of Adephaga except for *Haliplus*. Not identified for *Meru*.

43 Shape of secondary mandibular joint: (0) distinctly developed concave socket at basal dorsal corner of the lateral margin (Fig. 6L); **(1)** emargination on dorsal basal margin (Fig. 17A). — Distinct lateral process with approximately triangular socket for reception of a condyle of the head capsule present in Trachypachidae and Carabidae. Not protruding but triangular socket at basal margin in *Priacma*. Simple emargination on dorsal side in all aquatic Adephaga and examined Polyphaga.

44 Shape of distigalea: (0) distal part with brush; **(1)** palp-like, without distal brush (Figs. 4H, 12G); **(2)** distal part bilobed, without a brush; **(3)** sickle-shaped, without a brush (Fig. 20H). — Galea with distal brush in *Priacma*. Usually 2-segmented and palp-like in Adephaga. Distal part bilobed in *Hygrobia*. One-segmented and sickle-shaped in most Gyrininae (absent in Enhydrini and Orectochilini; Beutel 1989a) and *Amphizoa*. Character states do not overlap with each other.

45 Shape and proportion of maxillary palpomere 1: (0) cylindrical, at least twice as long as wide (Fig. 10G,H); **(1)** strongly shortened, about as wide as long (Fig. 4G,H). — Cylindrical and moderately long in *Haliplus*, *Dytiscus* and *Priacma*. Strongly shortened in all other taxa under consideration.

46 Shape and size of maxillary palpomere 4: (0) of similar length or slightly shorter than palpomere 3 and not subulate (Fig. 4G,H); **(1)** narrow and subulate (Fig. 10G,H). — Small, distinctly narrow and subulate in *Gehringia* and Haliplidae excl. *Peltodytes* (Beutel & Ruhnau 1990).

47 Apical sensorial fields on maxillary palpomere 4: (0) one large apical field (Fig. 4G,H); **(1)** two smaller apical fields (Fig. 21N). — Two small round fields present in *Agabus*, *Noterus*, *Amphizoa* and *Hygrobia*. Only separated by a narrow chitinous bar in *Dytiscus*. One larger field in all other groups.

48 Mental sclerite: (0) present; **(1)** absent. — Mentum reduced to an internal membrane between prementum and submentum in *Priacma* (Hörnschemeyer et al. 2002).

49 Anterior mental margin with median emargination and lateral lobes: (0) absent; **(1)** present (Fig. 1B). — With lateral lobes and median emargination in all adults of Adephaga.

50 Processes of median emargination of mentum: (0) absent; **(1)** one median process (Fig. 18B); **(2)** two paramedian processes (Figs. 1B, 7B, 13B). — Two small processes in *Haliplus*, *Noterus*, *Aspidytes*, *Trachypachus* and *Pterostichus*. Varying between species of *Carabus*. Absent in Gyrinidae, *Hygrobia* and Dytiscidae.

51 Submento-mental suture: (0) present (Fig. 1B); **(1)** absent (Fig. 18B); **(2)** internalised. — Absent in *Spanglerogyrus* and *Amphizoa*. Internalised due to the inward folded mentum in *Priacma* (Hörnschemeyer et al. 2002).

52 Lateral appendages of the complex formed by the anterior labium and anterior hypopharynx: (0) absent (Fig. 3D); **(1)** flattened lobes with at least two rows of setae or trichomes on their dorsal surface (see Beutel 1989a: fig. 13); **(2)** semimembranous comb-shaped lobes without setae (Figs. 9D, 16D, 19D); **(3)** fringes of hairs inserted on lobe with sclerotised base (see Anton & Beutel 2004: figs. 40, 43). — The appendages merge continuously with the hypopharynx towards the functional mouth opening. They fit closely with the lateral premental margin and merge with it to different degrees. The hairs are dorsally oriented. The base of the lobe is sclerotised in *Helophorus*. The appendages are missing in Trachypachidae, Carabidae and *Priacma*. Unknown for *Meru*.

53 Thorns (thickened, stiff setae) or strong setae on labial palpomere 2: (0) absent; **(1)** present. Present in Carabidae.

54 Apical sensorial fields on labial palpomere 3: (0) one large field (Fig. 4D); **(1)** two smaller fields (Fig. 20D). — Character state distribution as in character 47. Not identified for *Meru*.

Musculature

55 Origin of M. submentopraementalis (M.28): (0) submentum; **(1)** gular apodeme (Figs. 2A, 4D); **(2)** posteriormost gula (Fig. 15C). — On the gular apodeme in Gyrinidae, *Haliplus*, *Noterus*, *Amphizoa*, *Trachypachus* and many Carabidae. On the hind margin of the submentum in outgroup taxa and on the hind margin of the gula in *Hygrobia*, Dytiscidae and *Aspidytes*. Variable within the genus *Carabus*. Not examined in *Meru*.

56 Division of M. tentoriopraementalis inferior (M.29): (0) one bundle; **(1)** bipartite (Figs. 4D, 5E). — Only one bundle in Gyrinidae, *Priacma* and *Helophorus*. Bipartite in all other groups of Adephaga.

57 Origin of M. tentoriohypopharyngalis (M.48): (0) medially from tentorial bridge (Figs. 2B, 15A); **(1)** ventral side of anterior pharynx; **(2)** laminatentorium; **(3)** posterior tentorial arms. — Originates on tentorial bridge in most groups of Adephaga, but on the ventral side of the anterior pharynx in Gyrininae (Honomichl 1975) and on the laminatentorium in *Spanglerogyrus*. Originates from the posterior tentorial arms in *Priacma* (Hörnschemeyer et al. 2002).

58 M. tentoriobuccalis anterior (M.50): (0) absent; **(1)** present (Fig. 2B). — Absent in Gyrinidae, *Hygrobia*, *Dytiscus* and *Priacma*.

Thorax, legs and wings[1]

59 Pronotoelytral angle: (0) distinct; **(1)** indistinct; **(2)** absent.

60 Shape of prosternal process: (0) short and narrow; **(1)** longer and broader, converging towards apex; **(2)** long, apically broad and laterally rounded; **(3)** long, strongly broadened and apically truncate; **(4)** apex reduced, laterally fused with hypomeral process.

61 External posterior procoxal bridge: (0) absent; **(1)** present.

62 Internal posterior procoxal bridge: (0) absent; **(1)** present.

63 Prothoracic proprioreceptive organ: (0) absent; **(1)** present.

64 Prothoracic defensive gland: (0) absent; **(1)** present.

65 Ventral procoxal joint: (0) absent; **(1)** with distinct coxal condyle; **(2)** strongly shortened.

66 Profemoral antenna cleaning device: (0) absent; **(1)** present.

67 Protibial antenna cleaning device: (0) absent; **(1)** present.

68 External protibial spur: (0) not modified as burrowing spur; **(1)** modified as strong, curved burrowing spur.

69 Shape of mesoventrite (terminology: see Baehr 1975; Beutel 1986a; Belkaceme 1991)**: (0)** flat and extensive, without hexagonal groove and anterolateral grooves; **(1)** short, with hexagonal groove and anterolateral grooves for reception of the procoxae; **(2)** with rounded, horizontal anterior part and steeply ascending posterior part.

70 Contact between metanepisternum and mesocoxal cavity: (0) absent; **(1)** present (complex type) (Bell 1967).

71 Orientation of metepimeron: (0) elongate or triangular, not at right angle to longitudinal body axis; **(1)** parallel-sided, approximately at right angle to longitudinal body axis (Beutel 1992b).

72 Elytral apex: (0) not truncate; **(1)** truncate.

73 Shape of mesocoxae: (0) triangular; **(1)** rounded.

74 Proximal mesotarsomeres of males: (0) not distinctly elongated and broadened; **(1)** elongated and broadened.

75 Swimming hairs on middle legs: (0) absent; **(1)** sparse fringe of very thin and fine hairs; **(2)** dense fringe of longer hairs; **(3)** lamellae; **(4)** fimbriate hairs.

76 Transverse ridge of metaventrite: (0) complete; **(1)** partly reduced; **(2)** absent.

77 Contact between pro- and metasternal process: (0) absent; **(1)** present.

78 Origin of metafurca: (0) katepisternum; **(1)** intercoxal septum.

79 Subcubital setal binding patch: (0) absent; **(1)** present, round; **(2)** elongate.

80 Position of RP$_{3+4}$ (M$_4$ sensu Ward 1979): **(0)** anterior to the middle of the oblongum cell; **(1)** at or posterior to the middle of the oblongum cell.

81 Width of metacoxa: (0) distinctly broader than metaventrite; **(1)** not distinctly broader than metaventrite.

82 Mesal walls of metacoxa: (0) free; **(1)** connected, contact area small; **(2)** connected along ventral edge; **(3)** connected, contact area extensive, intercoxal septum.

83 Anterior margin of the metacoxa: (0) almost straight or slightly rounded anterolaterally; **(1)** with distinct angle; **(2)** rounded, strongly extended anteriorly; **(3)** oblique, strongly extended anteriorly, lateral part of metaventrite strongly reduced.

84 Metacoxal plates: (0) absent; **(1)** moderately sized; **(2)** mesal part of coxa prominent, but duplicature largely or completely reduced; **(3)** large.

85 Lateral margin of metacoxal plates: (0) reaching anterior margin of coxa at lateral edge; **(1)** slightly diverging anteriorly; **(2)** converging anteriorly, attaining anterior coxal margin; **(3)** very indistinct anteriorly.

86 Swimming hairs of metatibiae: (0) absent; **(1)** present, sparse fringe; **(2)** present, dense fringe; **(3)** lamellae; **(4)** fimbriate.

87 Mm. furcacoxales anteriores: (0) present; **(1)** absent.

88 Mm. furcacoxales posteriores: (0) present; **(1)** absent.

89 M. nototrochanteralis: (0) present; **(1)** absent.

Abdomen

90 Abdominal sternites III and IV: (0) clearly separated; **(1)** largely or completely fused.

91 Position of gonocoxosterna VIII: (0) not exposed; **(1)** exposed, sternite-like.

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[1] For explanation of all following characters and for references see Beutel et al. (2006).

92 Subdivision of gonocoxa: **(0)** absent; **(1)** present.
93 Laterotergite: **(0)** vertical orientation; **(1)** rod-like, cranial orientation; **(2)** rod-like, caudal orientation.
94 Torsion of aedeagus: **(0)** absent; **(1)** present.
95 Symmetry of parameres: **(0)** symmetric or only slightly asymmetric; **(1)** strongly asymmetric, left paramere shortened, triangular or "conchoid".
96 Pygidial defensive glands: **(0)** absent; **(1)** present.

4.5.2. Larvae

97 Orientation of head: **(0)** subprognathous; **(1)** prognathous; **(2)** hyperprognathous.
98 Labrum: **(0)** free; **(1)** fused.
99 Nasal teeth: **(0)** absent; **(1)** present.
100 Sensorial setae or pegs of anterior clypeolabral margin of 3rd instar larvae: **(0)** 6 or less; **(1)** 24 or more arranged in a transverse row.
101 Frontal suture: **(0)** straight or evenly curved; **(1)** with indistinct indentation; **(2)** sinuate.
102 Position of posterior tentorial grooves: **(0)** at foramen occipitale; **(1)** central region of ventral wall of head capsule; **(2)** posterior head region, at anterior margin of short gula or adjacent to foramen occipitale.
103 Caudal tentorial arm: **(0)** absent; **(1)** very short; **(2)** elongate and slender (Beutel 1993).
104 Shape of tentorial bridge: **(0)** straight; **(1)** U-shaped, posteriorly directed; **(2)** V-shaped, anteriorly directed.
105 Orientation of antennae: **(0)** anteriorly; **(1)** anterolaterally.
106 Sensorial appendage: **(0)** present, distinctly convex; **(1)** absent; **(2)** present as a flattened sensorial field.
107 Three long apical antennal setae: **(0)** present; **(1)** absent.
108 Mola: **(0)** present; **(1)** absent.
109 Retinaculum: **(0)** present; **(1)** vestigial or absent.
110 Mesal mandibular edge in mature larvae: **(0)** without distinct cutting edge; **(1)** one cutting edge; **(2)** two cutting edges delimiting a mesal groove; **(3)** mandibular sucking channel.
111 Adductor tendon [of mandible]: **(0)** undivided; **(1)** divided into an upper and lower portion.
112 Maxillary articulation: **(0)** retracted in deep maxillary group with exposed articulatory membrane; **(1)** slightly retracted, distinct oblique maxillary groove present; **(2)** slightly retracted, maxillary groove largely reduced, mesal maxillary base distinctly posterior to submento-mental border; **(3)** maxilla articulates at anterior margin of ventral wall of head capsule.
113 Intramaxillary moveability: **(0)** fully retained; **(1)** absent.
114 Width of cardo: **(0)** as broad as stipital base; **(1)** distinctly narrower than stipital base.
115 Subdivision of cardo into lateral and mesal sclerite: **(0)** absent; **(1)** present.
116 Lacinia: **(0)** present; **(1)** absent.
117 Shape of lacinia: **(0)** large, hook-shaped, broadly fused with stipes; **(1)** hook-shaped, articulated; **(2)** small, peg-like.
118 Shape of galea: **(0)** rounded and densely set with hairs; **(1)** slender, apically fimbriate; **(2)** palp-like, hairs largely or completely absent.
119 Stipitopalpal muscles: **(0)** two; **(1)** one.
120 Origin of M. craniolacinialis: **(0)** laterally on head capsule; **(1)** ventrally on head capsule between M. craniocardinalis and Mm. tentoriocardinalis and tentoriostipitalis (= M. craniostipitalis medialis sensu Beutel 1993).
121 Insertion of M. craniolacinialis: **(0)** base of lacinia; **(1)** dorsal side of stipes.
122 Prementum: **(0)** undivided; **(1)** with distinct anteromedian incision; **(2)** completely divided longitudinally.
123 Ligula: **(0)** distinctly developed as a median ligular node (Thompson 1979); **(1)** indistinct; **(2)** absent.
124 Prehypopharyngeal filter apparatus formed by long hairs: **(0)** absent; **(1)** present.
125 M. tentoriopharyngalis posterior (M.52): **(0)** moderately sized or absent; **(1)** very strong, several bundles.
126 M. verticopharyngalis (M.51): **(0)** present; **(1)** absent.
127 Position of cerebrum: **(0)** posterior part of head; **(1)** anterior part of head.
128 Trochanteral annulus: **(0)** absent; **(1)** present.
129 Primary setae FE7–FE10: **(0)** absent; **(1)** present.
130 Additional pore on tibia: **(0)** absent; **(1)** present.
131 Segment IX: **(0)** well developed; **(1)** small but distinct; **(2)** vestigial or absent.
132 Segment X: **(0)** present; **(1)** absent.
133 Spiracle VIII: **(0)** normally developed; **(1)** enlarged, terminal; **(2)** reduced; **(3)** small, shifted to dorsal side of segment VIII.
134 Large terminal tracheal trunks: **(0)** absent; **(1)** present.
135 Collar-like semimembranous connections between sclerites: **(0)** absent; **(1)** present.
136 Urogomphi: **(0)** absent; **(1)** present, articulated; **(2)** present, fixed.

Tab 1. Morphological data matrix of 16 taxa and 138 characters. Indications: A = polymorphism, states 0 and 1; B = polymorphism, states 1 and 2; - = character not applicable, ? = character state unknown.

Character #	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
	0	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**3**	**3**	**3**	**3**	**3**	**3**	**3**	**3**	**3**	**3**	**4**	**4**	**4**	**4**	**4**	**4**	**4**
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**
Priacma	0	0	0	0	0	0	1	0	0	0	0	–	0	1	1	0	–	1	0	–	0	0	–	0	0	0	0	0	0	–	0	0	0	–	0	0	0	0	0	–	0	0	0	0	0	0
Helophorus	0	0	0	0	1	2	0	0	0	0	1	0	2	0	0	1	1	0	1	0	1	0	–	2	0	2	0	1	0	–	0	0	0	–	0	1	1	0	2	0	1	0	1	0	1	0
Catops	0	0	0	0	0	2	0	0	0	0	1	2	2	0	0	1	?	0	1	?	?	0	–	0	1	0	0	0	0	–	0	0	0	–	0	2	1	0	2	0	0	0	1	0	1	0
Gyrinus	1	1	1	0	0	0	0	0	1	0	1	2	2	1	1	0	–	1	1	0	2	1	0	3	2	3	0	–	1	0	1	0	0	–	1	2	0	0	0	2	3	1	1	3	1	0
Spanglerogyrus	1	1	1	0	0	0	0	0	1	0	1	1	2	0	1	1	1	0	1	0	2	1	1	3	2	3	0	–	1	0	0	0	0	–	1	2	0	0	0	2	3	1	?	1	1	0
Haliplus	1	1	0	0	0	1	0	0	1	0	2	–	2	0	0	1	1	0	1	0	1	1	1	3	0	1	0	0	1	0	0	1	0	–	1	1	0	1	2	1	2	0	1	1	0	1
Noterus	1	1	0	0	0	0	0	0	1	0	0	–	2	0	0	1	0	0	1	0	1	1	0	3	0	1	0	2	1	1	0	0	1	0	1	1	0	0	2	1	2	1	1	1	1	0
Amphizoa	1	0	0	1	0	0	0	0	0	0	1	1	2	0	0	1	0	0	1	0	2	1	0	3	0	1	1	0	1	?	0	0	1	1	1	2	0	1	1	2	3	1	1	3	1	0
Hygrobia	0	0	0	0	0	0	0	0	0	0	1	1	2	0	0	1	0	0	1	1	2	0	–	3	0	0	0	1	1	1	0	0	1	0	0	1	0	1	0	1	2	1	1	2	1	0
Dytiscus	1	A	0	0	0	0	0	0	1	0	1	2	2	0	1	1	0	0	1	0	0	0	–	3	0	2	1	0	1	1	0	0	1	1	1	1	0	0	2	2	2	1	1	1	0	0
Agabus	1	1	0	0	0	0	0	0	0	0	2	–	1	0	1	1	0	0	1	0	1	0	–	3	0	0	0	2	1	1	0	0	1	1	1	2	0	0	2	2	2	1	1	1	1	0
Aspidytes	1	1	0	0	0	0	0	0	0	0	2	–	2	0	0	1	0	0	1	0	2	0	–	3	0	1	1	0	1	?	0	0	1	1	1	2	0	1	1	1	2	1	1	1	1	0
Meru	0	0	0	1	0	0	1	0	1	0	1	2	2	0	1	1	1	0	1	?	0	0	–	3	0	4	–	–	1	–	0	0	0	–	1	1	0	0	0	1	?	?	?	1	1	0
Trachypachus	0	0	0	1	1	0	1	0	0	1	1	1	1	0	0	1	0	0	1	1	2	1	0	3	1	0	1	0	1	0	0	1	0	–	0	1	0	0	1	1	1	0	0	1	1	0
Carabus	0	0	0	1	1	0	1	1	–	1	1	0	1	0	0	1	1	0	1	1	0	A	0	1	1	0	0	1	1	0	0	0	0	–	0	0	0	0	3	0	1	0	0	1	1	0
Pterostichus	0	0	0	1	1	0	1	0	0	1	1	0	1	0	0	1	1	0	1	1	2	1	0	1	1	0	0	0	1	0	0	0	0	–	0	0	0	0	1	0	1	0	0	1	1	0

Character #	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
	4	**4**	**4**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**6**	**6**	**6**	**6**	**6**	**6**	**6**	**6**	**6**	**6**	**7**	**7**	**7**	**7**	**7**	**7**	**7**	**7**	**7**	**7**	**8**	**8**	**8**	**8**	**8**	**8**	**8**	**8**	**8**	**8**	**9**	**9**	**9**
	7	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**
Priacma	0	1	–	–	2	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	–	0	0	0	0	0	0	?
Helophorus	0	0	0	–	0	3	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	–	0	0	0	0	–	0	0	0	0	0	0	?
Catops	0	0	0	–	0	?	0	0	0	?	?	?	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	–	1	0	0	0	–	0	0	0	?	0	0	1
Gyrinus	0	0	1	0	0	1	0	0	1	0	1	0	2	0	0	1	1	0	0	0	0	–	0	0	0	1	0	0	3	2	0	0	0	0	0	2	3	0	–	3	1	0	0	0	1	0
Spanglerogyrus	?	0	1	0	1	1	0	?	1	0	2	0	2	0	0	1	1	0	1	0	0	0	0	0	0	1	0	0	4	0	0	0	0	0	0	2	0	0	–	2	0	0	1	0	1	0
Haliplus	0	0	1	2	0	2	0	0	1	1	0	1	1	3	0	1	0	0	1	0	0	0	1	0	0	0	1	0	1	0	1	0	0	0	0	0	0	3	0	1	0	0	1	0	0	0
Noterus	1	0	1	2	0	2	0	1	1	1	0	1	2	2	0	1	0	?	1	1	0	1	1	0	0	0	1	1	2	2	1	1	2	0	0	3	1	1	2	1	1	1	1	1	0	0
Amphizoa	1	0	1	1	1	2	0	1	1	1	0	1	0	2	0	1	0	0	1	0	0	0	1	1	0	0	1	0	1	1	0	1	2	0	0	3	0	1	1	1	1	1	1	0	0	0
Hygrobia	1	0	1	0	0	0	0	1	2	1	0	0	1	1	0	1	0	1	1	0	0	1	1	0	0	0	1	1	2	1	1	1	0	0	0	3	0	2	1	1	1	1	1	0	0	0
Dytiscus	1	0	1	0	0	2	0	1	2	1	0	0	2	1	0	1	0	1	2	0	0	0	1	1	0	0	1	0	2	2	1	1	2	0	0	3	2	2	3	1	1	1	1	0	0	0
Agabus	1	0	1	0	0	2	0	1	2	1	0	1	2	1	0	1	0	1	2	0	0	0	1	1	0	0	1	0	2	2	1	1	2	0	0	3	2	2	3	1	1	1	1	0	0	0
Aspidytes	0	0	1	2	0	2	0	0	2	1	0	1	2	2	0	1	0	0	1	1	0	0	1	1	0	0	1	0	0	1	0	1	2	0	0	3	0	1	1	0	1	1	1	0	0	0
Meru	0	0	1	1	0	?	0	0	?	1	0	1	1	2	0	1	0	0	?	0	0	0	1	–	–	0	1	0	0	2	1	1	0	–	0	3	–	2	–	0	1	0	1	1	0	0
Trachypachus	0	0	1	2	0	0	0	0	1	1	0	1	0	2	0	1	0	0	1	0	1	0	1	0	0	0	1	0	0	1	0	0	1	0	0	1	0	1	0	0	0	0	1	0	0	0
Carabus	0	0	1	B	0	0	1	0	B	1	0	1	0	1	0	0	0	0	1	0	1	0	1	0	1	0	1	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	1	0	0	1
Pterostichus	0	0	1	2	0	0	1	0	1	1	0	1	0	4	1	0	0	0	1	0	1	0	2	0	1	0	1	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	1	0	0	1

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	9	**9**	**9**	**9**	**9**	**9**	**9**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**3**	**3**	**3**	**3**	**3**	**3**	**3**	**3**	**3**
	3	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**
Priacma	?	0	0	0	1	0	0	–	–	0	0	–	0	0	0	0	1	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	1	0	0	?	?	0	0	0	0	0	0	0	0
Helophorus	?	0	0	0	1	1	1	0	0	3	0	–	1	0	0	1	0	0	0	1	1	0	1	1	–	1	1	1	1	0	2	0	0	1	0	0	?	?	0	0	0	0	0	1	1	?
Catops	?	0	0	0	0	0	0	–	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	2	0	0	0	0	?	0	0	1	0	0	?	?	0	0	0	0	0	1	0	1
Gyrinus	1	1	0	1	1	1	1	0	0	3	0	–	0	1	0	1	0	3	0	1	0	0	0	0	1	1	0	0	0	2	–	0	0	1	0	0	0	0	0	0	?	0	0	0	0	0
Spanglerogyrus	1	1	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Haliplus	1	1	1	1	1	1	0	0	0	1	0	0	0	0	0	1	0	3	0	2	1	0	0	0	2	0	1	1	1	0	2	0	1	1	0	0	0	0	0	0	?	0	0	0	0	1
Noterus	1	1	1	1	1	1	0	0	2	1	1	2	0	1	0	1	0	2	0	3	1	1	0	1	–	1	1	1	1	1	2	0	1	1	0	0	0	0	2	1	1	1	1	1	0	1
Amphizoa	2	1	0	1	1	1	0	1	0	2	2	0	0	0	0	1	0	2	1	3	1	1	0	1	–	1	1	1	1	0	2	0	1	0	0	0	1	1	2	1	1	1	0	1	1	?
Hygrobia	2	1	0	1	1	1	0	1	0	2	2	–	0	0	0	1	1	1	1	3	1	–	–	1	–	–	1	1	1	0	2	0	1	0	1	1	1	0	2	1	2	0	0	1	1	?
Dytiscus	2	1	0	1	1	1	0	1	0	2	2	0	0	0	0	1	1	3	1	3	1	1	0	1	–	1	1	1	1	0	2	0	1	0	1	1	1	0	2	1	1	1	0	1	1	1
Agabus	2	1	0	1	1	1	0	1	0	2	2	0	0	0	0	1	1	3	1	3	1	1	0	1	–	1	1	1	1	0	2	0	1	0	1	1	1	0	2	1	1	1	0	1	1	1
Aspidytes	2	1	0	1	1	1	1	0	1	1	2	0	0	0	0	1	0	2	1	3	1	1	0	1	–	1	1	1	1	0	2	0	1	0	0	0	1	1	1	1	3	1	1	1	1	?
Meru	–	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	–	?
Trachypachus	0	1	0	1	1	1	1	0	0	3	1	1	0	2	1	1	0	2	0	3	1	0	0	1	–	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	1	?
Carabus	0	1	0	1	1	1	1	0	2	3	0	1	1	0	1	1	0	1	0	3	1	0	1	0	2	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	2	1	1
Pterostichus	0	1	1	1	1	1	0	0	2	3	0	1	1	0	1	1	0	1	0	3	1	0	1	0	2	1	1	1	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	2	1	1

4.5.3. Pupae

137 Urogomphi: **(0)** present; **(1)** absent.

4.5.4. Eggs

138 Chorion: **(0)** distinctly developed, ribbed or honey-combed; **(1)** surface with granules; **(2)** very thin.

5. Results of the cladistic analysis

The cladistic analysis run with NONA (Ratchet search/ Island Hopper; 1000 replications) led to a single most parsimonious tree (TL 351 steps, CI 0.58, RI 0.65; Fig. 22). The analysis carried out with PAUP (branch and bound search) produced the same single tree.

The nodes within Adephaga are supported by the following unambigous apomorphies. The underlined numbers are possibly homoplastic changes.

Adephaga: 22.1 (gular apodeme present), 29.1 (labral surface glabrous or with only few short setae), 44.1 (galea 2-segmented and palp-like), 49.1 (mentum with lateral lobes and median emargination), 55.1 (origin of M. submentopraementalis on gular apodeme), 94.1 (torsion of aedeagus present), 96.1 (pygidial defensive glands present).

Adephaga excl. Gyrinidae: 56.1 (M. tentoriopraementalis inferior [M.29] bipartite), 60.2 (prosternal process long, apically broad and laterally rounded), 69.1 (mesoventrite short, with hexagonal groove and anterolateral grooves), 73.1 (mesocoxae rounded), 84.1 (metacoxal plates moderately sized), 112.3 (maxilla articulates at anterior margin of ventral wall of larval head capsule).

Gyrinidae: 3.1 (compound eyes divided), 15.1 (connection between dorsal tentorial arms and posterior tentorium absent), 25.2 (antennal setae concentrated on lateral margin of pedicellus), 26.3 (distal part of scapus calyx-shaped), 39.0 (longitudinal fringe of hairs on mandibles absent), 41.3 (basal mandibular margin not widened laterally, distal part widened), 42.1 (mandibular joints shifted mesally), 52.1 (hypopharyngeal appendages as flattened lobes with dorsal rows of hairs), 59.2 (pronotoelytral angle absent), 63.1 (prothoracic proprioreceptive organ present), 72.1 (elytral apex truncate), 82.2 (mesal walls of metacoxa connected along ventral edge), 91.1 (position of gonocoxosterna VIII exposed, sternite-like).

Geadephaga (= Trachypachidae + Carabidae): 4.1 (supraocular ridge present), 5.1 (supraocular setae present), 7.1 (circular ridge of posterior head present), 10.1 (long setae close to lateral margin of clypeus), 13.1 (anterior tentorial pits within clypeofrontal suture, internally attached to epistomal ridge), 20.1 (gular ridge sloping posterad of tentorial bridge), 25.1 (apical whorl of longer setae on postscapal antennomeres), 39.1 (mandibular fringe of short hairs present, not reaching mesal edge), 43.0 (secondary mandibular joint as concave socket on laterobasal mandibular margin), 67.1 (protibial antenna cleaning device present), 93.0 (vertical orientation of laterotergite), 104.1 (tentorial bridge U-shaped, posteriorly directed in larvae), 107.1 (three long apical antennal setae present in larvae), 136.2 (urogomphi present, fixed in larvae), 137.1 (urogomphi absent in pupae).

Trachypachidae: 17.0 (median fusion of laminatentoria absent), 27.1 (scapal condyle not concentrically attached to distal part), 32.1 (transverse edge of labrum present), 76.1 (transverse ridge of metaventrite partly reduced), 79.1 (subcubital setal binding patch present), 82.1 (mesal walls of metacoxa connected, contact area small), 103.1 (caudal tentorial arm very short in larvae), 106.2 (sensorial appendage present as a flattened sensorial field in larvae), 116.1 (lacinia absent in larvae).

Carabidae: 24.1 (antennal vestiture present from antennomere 4 or 5), 36.0 (mandible twice as long as wide, length/width ratio ≥1.9), 53.1 (short thorns on labial palpomere 2 present), 62.0 (internal posterior procoxal bridge absent), 71.1 (metepimeron parallel-sided, at right angle to longitudinal body axis), 80.1 (RP_{3+4} at or posterior to the middle of the oblongum cell), 81.1 (metacoxa not distinctly broader than metaventrite), 92.1 (subdivision of gongocoxa present), 101.2 (frontal suture sinuate in larvae), 105.1 (anterolateral orientation of antennae in larvae), 115.1 (subdivision of cardo into lateral and mesal sclerite present in larvae), 124.1 (prehypopharyngeal filter apparatus formed by long hairs present in larvae).

Haliplidae + Dytiscoidea (incl. Meruidae and Aspidytidae): 26.1 (distal scapal part compressed), 41.2 (basal mandibular margin not widened laterally, lateral side convex), 52.2 (hypopharyngeal appendages as semimembranous lobes with a fringe of hairs), 59.1 (pronotoelytral angle indistinct), 77.1 (contact between pro- and metasternal process present), 95.1 (parameres strongly asymmetric), 99.0 (nasal teeth absent in larvae), 102.1 (posterior tentorial grooves in central region of ventral wall of larval head capsule), 125.1 (M.52 very strong, several bundles in larvae).

Haliplidae: 6.1 (postocular ridge present laterally), 11.2 (clypeofrontal suture medially interrupted), 23.1 (gular apodeme close to postgular ridge), 32.1 (transverse edge on labral surface present), 38.2 (mandibular surface mesally smooth, dorsolaterally covered with fine pores), 45.0 (first maxillary palpomere cylindrical, twice as long as wide), 46.1 (maxillary palpomere

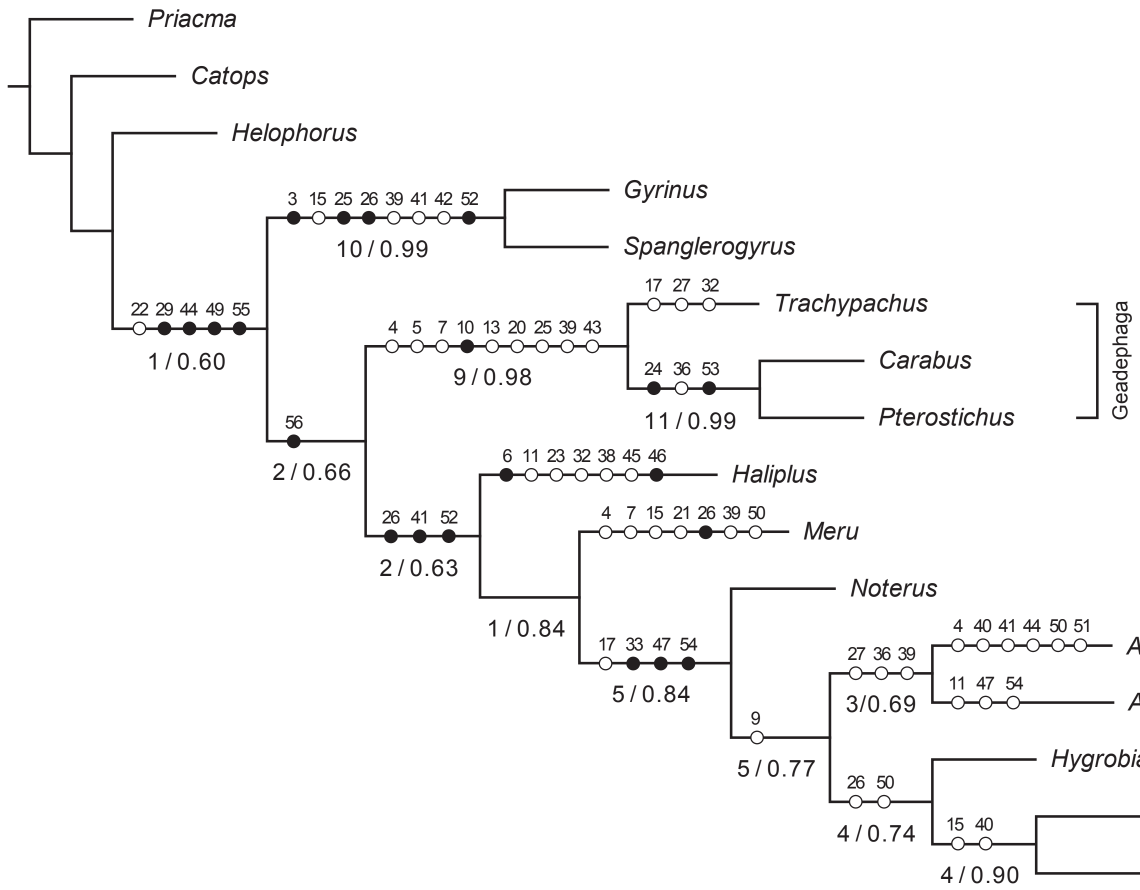

Fig. 22. Phylogeny of Adephaga. Single most parsimonious tree (351 steps, CI 0.58, RI 0.65) obtained in a cladistic analysis of 138 characters for 16 taxa (Ratchet search/1000 repl.). Unambiguous apomorphic characters of the head for selected monophyla (see also section 5.) are mapped on the branches (not for outgroup taxa and not for some of the terminals): filled circles represent non-homoplastic apomorphies, unfilled circles represent homoplastic changes. Support values are shown beneath the branches: Bremer support values on the left, bootstrap values on the right (only ingroup).

4 narrow and subulate), 60.3 (prosternal process long, strongly broadened and apically truncate), 75.1 (middle legs with sparse fringe of fine swimming hairs), 84.3 (metacoxal plates large), 112.2 (maxillary articulation slightly retracted, maxillary groove largely reduced, mesal base posterior to smt-mt border in larvae), 118.0 (galea rounded and densely set with hairs in larvae).

Dytiscoidea (incl. Meruidae): 76.2 (transverse ridge of metaventrite absent), 78.1 (origin of metafurca on intercoxal septum), 82.3 (mesal walls of metacoxa connected, contact area extensive, intercoxal septum), 87.1 (Mm. furcacoxales anteriores absent).

Meruidae: 4.1 (supraocular ridge present), 7.1 (circular ridge of posterior head present), 15.1 (connection between dorsal tentorial arms and posterior tentorium absent), 21.0 (apodemal plate of gular ridges absent), 26.4 (separate distal scapal part absent), 39.0 (longitudinal fringe of hairs on mandibles absent), 50.1 (one median process on mental emargination), 84.2 (mesal part of metacoxa prominent, but duplicature reduced).

Dytiscoidea excl. Meruidae: 17.0 (median fusion of laminatentoria absent), 33.1 (epipharyngeal sensorial lobes present), 47.1 (maxillary palpomere 4 with two small sensorial fields apically), 54.1 (labial palpomere 3 with two small sensorial fields apically), 59.2 (pronotoelytral angle absent), 79.2 (Subcubital setal binding patch elongate), 88.1 (Mm. furcacoxales posteriores absent).

Dytiscoidea excl. Meruidae and Noteridae: 9.0 (labrum nearly horizontally orientated, parallel to clypeus), 93.2 (laterotergite rod-like, caudal orientation), 95.0 (parameres symmetric or only slightly asymmetric), 111.1 (adductor tendon divided in larvae), 126.0 (M.51 present in larvae), 129.1 (primary setae FE7–FE10 present in larvae), 137.1 (urogomphi absent in pupae).

Amphizoidae + Aspidytidae: 27.1 (scapal condyle not concentrically attached to distal part), 36.2 (mandible about as long as wide, length/width ratio ≤ 1.2), 39.1 (mandibular fringe of short hairs present, not reaching mesal edge), 77.0 (contact between pro- and metasternal process absent), 130.1 (additional pore on tibia present in larvae).

Amphizoidae: 4.1 (supraocular ridge present), 40.2 (distal cutting edge of mandible straight, nearly vertical), 41.3 (basal mandibular margin not widened laterally, distal part widened), 44.3 (galea 1-segmented, sickle-shaped), 50.1 (one median process on mental emargination), 51.1 (submentomental suture absent), 59.0 (pronotoelytral angle distinct)

Aspidytidae: 11.2 (clypeofrontal suture medially interrupted), 47.0 (maxillary palpomere 4 with one large sensorial field apically), 54.0 (labial palpomere 3 with one large sensorial field apically), 66.1 (profemoral antenna cleaning device present), 86.0 (swimming hairs of metatibiae absent), 99.1 (nasal teeth present in larvae), 101.1 (frontal suture with indistinct indentation in larvae), 131.1 (segment IX small but distinct in larvae), 133.3 (spiracle VIII small, shifted to dorsal side in larvae), 135.1 (collar-like semimembranous connections between sclerites present in larvae).

Hygrobiidae + Dytiscidae: 26.0 (distal scapal part cylindrical), 50.0 (median process on mental emargination absent), 60.1 (prosternal process longer and broader, converging towards apex), 64.1 (prothoracic defensive gland present), 84.2 (mesal part of metacoxa prominent, but duplicature reduced), 109.1 (retinaculum vestigial or absent in larvae), 127.1 (position of cerebrum in the anterior part of larval head), 128.1 (trochanteral annulus present).

Dytiscidae: 15.1 (connection between dorsal tentorial arms and posterior tentorium absent), 40.2 (distal cutting edge of mandible straight, nearly vertical), 65.2 (ventral procoxal joint strongly shortened), 83.2 (anterior metacoxal margin rounded, strongly extended anteriorly), 85.3 (lateral margin of metacoxal plates very indistinct anteriorly).

6. Discussion

The results of our cladistic analysis support a clade Geadephaga comprising the terrestrial Trachypachidae and Carabidae (Kavanaugh 1986; Beutel & Haas 1996; Shull et al. 2001; Ribera et al. 2002b; Maddison et al. 2009), whereas the "Hydradephaga" (all aquatic and semiaquatic families) turned out as non-monophyletic, as already suggested in earlier morphology-based studies (e.g., Beutel & Roughley 1988; Beutel 1993). The obtained branching pattern implies that an aquatic lifestyle has evolved at least two times independently within Adephaga (see also Lawrence & Newton 1982; Evans 1985; Kavanaugh 1986; Beutel & Roughley 1988; Beutel & Haas 1996). This is in contrast to several older contributions (e.g., Burmeister 1976; Roughley 1981) and also recent molecular analyses, which support the monophyletic origin of Hydradephaga and a singular adaptive transition to aquatic lifestyle within Adephaga (Shull et al. 2001; Ribera et. al. 2002b; Hunt et al. 2007). All three molecular studies were based on analyses of a single gene, 18S rDNA, the last one of them (Hunt et al. 2007) with a very extensive polyphagan taxon sampling. In a study evaluating nuclear protein-coding genes (Wild & Maddison 2008) hydradephagan monophyly was not supported in three of four test analyses of the total data (only Bayesian posterior probabilities using nucleotides; Wild & Maddison 2008: fig. 2), and in only some of the single gene analyses. Apparently it is difficult to resolve the 'deep nodes' within Adephaga with molecular data. However, it has to be pointed out here that the basal branches of the adephagan tree we obtained are also not strongly supported statistically (see Fig. 22).

Synapomorphies of Trachypachidae and Carabidae are the supraocular ridge, supraocular setae, a circular ridge on the posterior head region, the position of the anterior tentorial pits, two long setae on the clypeus, the shape of the gular ridges, apical whorls of setae on the postscapal antennomeres, and the specific shape of the secondary mandibular joint. Except for the clypeal and specifically arranged antennal setae all other apomorphic conditions have evolved independently in one of the other adephagan families. The more elongate shape of the head in terrestrial Adephaga is probably plesiomorphic compared to the condition found in the more advanced aquatic lineages.

In our study, the highly specialised Gyrinidae were placed as the sister taxon of the remaining suborder, as already suggested by Beutel & Roughley (1988) and Beutel & Haas (1996). The monophyly of Adephaga excl. Gyrinidae is supported by several features of larvae and the thorax and abdomen of adults (see, e.g., Beutel 1997). However, there is only one potential apomorphy of the adult head, and the bootstrap value is rather low (0.66). A bifurcate M. tentoriopraementalis and the reduction of the hypopharynx were suggested as synapomorphic head features of Geadephaga, Haliplidae and Dytiscoidea by Beutel & Roughley (1988). The latter feature cannot be upheld, as hypopharyngeal structures comparable to those of *Spanglerogyrus* (Beutel 1989a) do also occur in Geadephaga, Haliplidae, and Dytiscoidea (see below).

The recently described Meruidae were placed as the sistergroup of Dytiscoidea in our analyses and the Haliplidae as the sistergroup of this taxon. Possible synapomorphies of Haliplidae and Dytiscoidea are the presence and specific shape of lateral appendages of the hypopharynx, and a distinctly shortened head capsule. The latter condition has obviously evolved several times independently in correlation with the aquatic life style (e.g., Gyrinidae). It is not present in the dytiscoid groups Amphizoidae and Hygrobiidae, and we assume that it does not belong to the groundplan of the lineage. The placement of Haliplidae as closest relative of Dytiscoidea would imply a position of Meruidae as sistergroup of all other aquatic lineages except for Gyrinidae. This appears unlikely as a sistergroup relationship with Noteridae was supported in an earlier morphological study (Beutel et al. 2006) and also in a recent molecular study using several mitochondrial and nuclear genes (Balke et al. 2008). Modified adult head structures of Meruidae may have resulted from adaptations to an unusual hygropetric habitat (see Spangler & Steiner 2005) and miniaturisation. Aside from this, the description of meruid larvae is not available yet (A. Short, pers. comm.). It is conceivable that our analysis was negatively affected by secondarily modified head structures of Meruidae and a lack of larval data.

The relict family Trachypachidae with 6 extant species had its greatest distribution and diversity in the early Mesozoic, before the remarkable diversification of Carabidae started (Ponomarenko 1977). Structural features found in *Trachypachus* and its sister genus *Systolosoma* are arguably closest to the ground plan of the suborder, as specialisations of Carabidae on the one hand (e.g., antennal vestiture of fine hairs, elongation of mandibles) and the aquatic groups on the other (e.g., shortened streamlined head capsule) are missing. To corroborate this, however, potential non-adephagan outgroup taxa are not really helpful, as all of them show different modifications of head structures, mainly correlated with specific feeding habits (e.g., algophagy in Myxophaga, saprophagy in Hydrophiloidea). The head structures of adults of Archostemata, arguably the sistergroup of the remaining three extant suborders (e.g., Beutel et al. 2007; Friedrich et al. 2009), are extremely derived as pointed out in Beutel et al. (2007). In any case, it appears plausible to assume that the last common ancestor of Adephaga was a predaceous beetle, lacking specialised head features that evolved in Gyrinidae, Haliplidae, and in the dytiscoid families, and possibly a preference for riparian habitats (e.g., Beutel 1997). Whether an aquatic or terrestrial origin of Adephaga is more parsimonious depends on the sistergroup of Adephaga and its ancestral life style. These issues, however, are presently still open to debate (e.g., Beutel et al. 2007; Caterino et al. 2002; Friedrich et al. 2009; Hunt et al. 2009; Wild & Maddison 2008; see above). Considering the strikingly different adaptations in larvae and adults of Gyrinidae and the other hydradephagan groups, two independent invasions of the aquatic environment appear plausible at least.

Evolutionary tendencies in Carabidae are elongation of the head capsule and the mouthparts (especially mandibles), a proximal extension of the dense antennal pubescence, and an elongation and proximal shift of the protibial antenna cleaning organ. Adaptations for aquatic and semiaquatic life styles such as reductions of the surface vestiture, a shortened and rounded head, eyes integrated in the contours of the head capsule, and largely concealed mouthparts evolved at least two times independently, namely in Gyrinidae and the remaining aquatic Adephaga, or possibly three times, in Gyrinidae, Haliplidae and Dytiscoidea (see above). Due to the great diversity of microhabitats (e.g., Gyrinidae on the water surface, Haliplidae among algae, Aspidytidae and Meruidae on rocks with a thin water film) considerably different adaptations have evolved in different aquatic or semiaquatic lineages. The highest degree of specialisation is doubtlessly reached in Gyrinidae, with subdivided compound eyes, an extremely modified antenna, one or three regular rows of long labral setae, and other unusual features (see, e.g., Honomichl 1975; Beutel 1989a,b). Mouthparts of Haliplidae are apparently adapted to their main diet of algae, but to a much lesser degree than those of the larvae (Seeger 1971; Beutel 1986b). Whether the comparatively elongate head of *Meru* is a plesiomorphy within the dytiscoid (or hydradephagan) complex is presently uncertain. Autapomorphic conditions are the extremely developed accessory tentorial bridge (formed by fusion of the laminatentoria) and the raspberry compound eyes, with comparatively few conspicuous corneal lenses. The latter condition is very likely a result of miniaturisation as a similar condition is found in the very small *Gehringia olympiaca* Darlington (Lindroth 1961) and other very small insects. Features of the antenna, notably the presence of sensorial fields on specific antennomeres, suggest noterid affinities of Meruidae (see Spangler & Steiner 2005; Beutel et al. 2006). A detailed investigation of *Phreatodytes*, which is very likely the sistergroup of the remaining Noteridae, would be highly desirable.

Aspidytidae and Amphizoidae were placed as sistergroups as suggested based on molecular data (Ribera et al. 2002b; Balke et al. 2003, 2005, 2008). Nevertheless, the adult head structures differ very distinctly in both groups. Interestingly the hygropetric *Aspidytes* has a streamlined head characteristic of the advanced aquatic groups, whereas the head of the fully aquatic *Amphizoa* is likely plesiomorphic in its general shape. This is possibly correlated with the specific habits of the beetles, which do not actively swim but mainly crawl among branches and leaf litter stuck in small creeks or rivers (R. Beutel, pers. obs.). Amphizoidae are characterised by a fused mentum and submentum, an undivided galea, and a specific cuticular surface structure as autapomorphies. A fairly elongate and non-streamlined head is also preserved in Hygrobiidae (*Hygrobia*), even though the beetles are excellent swimmers. Autapomorphies of this group such as the bifurcate apical galeomere, the rounded and deeply excavated hypopharynx, and the extremely strongly developed pharyngeal dilators are apparently correlated with the exclusive diet of tubificid worms (Beutel 1986a). The evolution of adult noterid head structures is discussed in detail in Belkaceme (1991). A fully streamlined head has apparently evolved independently from Dytiscidae. This is clearly suggested by the sistergroup relationship between Noteridae and the remaining Dytiscoidea (e.g., Beutel et al. 2006). Apomorphic conditions occuring within Noteridae are mainly modifications of antennomeres as outlined in Belkaceme (1991).

As already pointed out further detailed morphological data of adults and larvae of *Meru* (and *Phreatodytes*) may lead to a reliable clarification of the phylogenetic affinities. Even though supported by morphological and molecular data in Balke et al. (2005, 2008) and in the present study, the monophyly of Aspidytidae + Amphizoidae is not yet sufficiently supported. Furthermore, more representatives of the highly diverse ground beetles have to be examined and included in analyses in order to evaluate some features shared by Trachypachidae and subgroups of Carabidae. In contrast to morphology-based studies (e.g., Beutel et al. 2006) Trachypachidae was placed as a subordinate taxon within Carabidae in recent molecular analyses (Ribera et al. 2002b; Hunt et al. 2007).

7. Acknowledgements

We are grateful to Eric Anton (FSU Jena), Dr. Michael Balke (Zoologische Staatssammlung München), Dr. Ignacio Ribera (Museu de Zoologia, Barcelona), †Prof. Dr. Robert E. Roughley (University of Manitoba) and Dr. Andrew Short (University of Kansas) for providing valuable material. Our particular thanks go to PD Dr. Hans Pohl (FSU Jena) for kindly allowing us to use his extremely useful specimen holder for scanning electron microscopy. We are also indebted to Dr. Frank Friedrich (Biozentrum Grindel Hamburg) for the Bremer support calculation. Sincere thanks are due to the two anonymous reviewers for their helpful advices.

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