The head morphology of *Micromalthus debilis* (Coleoptera: Micromalthidae) – an archostematan beetle with an unusual morphology and a unique life cycle

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Abstract. Cephalic features of *Micromalthus debilis* were examined and described in detail for the first time. The head displays several seemingly plesiomorphic features compared to other extant species of Archostemata, especially representatives of Cupedidae and Ommatidae. Cephalic protuberances characteristic for species of these two families are missing and antennal grooves are also absent. The surface of the head capsule is largely smooth, without the characteristic tubercles found in stemgroup beetles and ommatid and cupedid species. Cuticular scales, probably ancestral for Archostemata and possibly for Coleoptera, are also completely absent. The arrangement of three mandibular teeth in a vertical row and an immobilized labrum are derived features shared with Ommatidae. The maxillary endite lobes are absent, as in the very small *Crowsoniella relicta* (Crowsoniellidae). Like in all other examined archostematan species, mandibular molae and prosthecae are missing. The simplified maxillae apparently play no role in the food uptake but rather function as accessory "ventral antennae". Derived features include the partly reduced maxillary musculature and lack of extrinsic labial muscles. Apomorphies of the digestive tract include the sclerotized median protuberances of the anterior epipharynx and hypopharynx, and the presence of a vertical anterior pharyngeal loop and a subcerebral postpharyngeal pouch. The tentorium is strongly reduced. Consequently, all antennal muscles originate from the head capsule. A very unusual and possibly plesiomorphic feature is the presence of a short salivary tube and two associated muscles. This is a unique condition in Coleoptera as far as known at present. Structural features suggest that *Micromalthus* probably feeds on wood infested with fungi. A robust phylogenetic evaluation of anatomical features is presently not possible due to the lack of data for *Crowsoniella* (Crowsoniellidae) and *Sikhotealinia zhiltzovae* (Jurodidae). Moreover, phylogenetic and evolutionary interpretations are impeded by possible effects of vestigialization of adults possibly resulting from endosymbionts (e.g. *Wolbachia*, Rickettsiales)

Key words. *Micromalthus*, Micromalthidae, Archostemata, head, morphology.

1. Introduction

Micromalthus debilis LeConte, 1878 is the only extant species of Micromalthidae, one of the four or five families of the small beetle suborder Archostemata (e.g. Beutel et al. 2008; Hörnschemeyer 2016). This relict group, which has retained many ancestral features (e.g. Lawrence 1999; Beutel et al. 2008; Friedrich et al. 2009), comprises only approximately 40 extant species, and only one of them occurs in Europe, the miniaturized and strongly flattened *Crowsoniella relicta* Pace (Crowsoniellidae) (Pace 1975; Crowson 1975).

Micromalthus debilis is also miniaturized, highly modified structurally (e.g. Barlet 1996; Hörnschemeyer 2016), and has the most complicated life cycle of all beetles, including vivipary, hypermetamorphosis, different kinds of parthenogenesis, and paedogenetic larvae (Philips & Young 2001; Pollock & Normark 2002; Perotti et al. 2016). The "ghost-sex life" was treated in a recent study by Perotti et al. (2016), who pointed out effects of endosymbionts likely resulting in a vestigialization of adults. Like other species of Archostemata, *M. debilis* is considered rare and is only sporadically collected (e.g. Crowson 1962; Philips & Young 2001). Adults of *Micromalthus* were recently described from Eocene amber from France (Kirejtshuk et al. 2010), and larval speci-

mens were found in Eocene Baltic amber, in Oligocene amber from Mexico and in Early Cretaceous Lebanese amber (e.g. LAWRENCE & NEWTON 1995; HÖRNSCHEMEYER 2010). The original area of distribution of *M. debilis* is the eastern part of North America, but today, resulting from transportation with timber, there are records from many parts of the world, including for instance Austria, Hong Kong, Hawaii, and South Africa (HÖRNSCHEMEYER 2016).

Like in some other groups of Coleoptera (e.g. Adephaga, Staphyliniformia, Myxophaga, Cupedidae; BEUTEL 1993, 1999; BEUTEL & MOLENDA 1997; BEUTEL et al. 1998; YAVORSKAYA et al. 2016), larval head structures of *Micromalthus* are described in detail (BEUTEL & HÖRNSCHEMEYER 2002). However, despite of the exceptionally interesting biology and apparent phylogenetic importance, the morphology of the head and other body regions of adults is not well known. The external cephalic structures were treated briefly in a chapter of the Handbook of Zoology (HÖRNSCHEMEYER 2016) and features of the head were discussed in phylogenetic studies focused on Archostemata (BEUTEL et al. 2008; HÖRNSCHEMEYER 2009). However, a detailed description and documentation was still lacking. Even though only two adult specimens of *M. debilis* were available for this study, and both of them were not optimally preserved for histological investigations, it appeared worthwhile to increase the knowledge of the cephalic morphology of this apparent key taxon. The observed features of the head and its appendages are compared to conditions found in other archostematan taxa, and discussed with respect to their functional, phylogenetic and evolutionary implications.

2. Material and methods

Material. *Micromalthidae*: *Micromalthus debilis* LeConte, 1878 (fixed and preserved in 70% ethanol; adults and larvae from laboratory colony, M.A. PEROTTI, Bangor, UK) — *Ommatidae*: *Tetraphalerus bruchi* Heller, 1913 (fixed in FAE [formaldehyde, ethanol, acetic acid] and preserved in 70% ethanol; Argentina, Provincia de Mendoza, collected by Dra. Adriana Marvaldi) — *Cupedidae*: *Priacma serrata* LeConte, 1861 (fixed and preserved in 70% ethanol; Montana, USA, collected by one of the authors [T.H.]).

Anatomy. One specimen of *Micromalthus debilis* was embedded in araldite CY 212® (Agar ScientiWc, Stansted/Essex, England) and sectioned with a microtome HM 360 (Microm, Walldorf, Germany) equipped with a diamond knife. The sections were stained with toluidine blue and pyronin G (Waldeck GmbH and Co.KG/Division Chroma, Münster, Germany). The other specimen used for confocal laser scanning microscopy (CLSM) was dehydrated with ethanol (20–100%) and acetone. BABB (mixture of benzyl alcohol and benzyl benzoate 1:2) was used as a clearing solution, according to a standard BABB protocol. The head was mounted in small droplets of BABB between two cover slips and scanned with a Zeiss LSM 510 in two channels – red 633 nm and green 488 nm and from both (ventral and dorsal) sides. Series

of digital slices were produced providing information on all internal structures including muscles. They were imported in Amira and used for 3D reconstruction.

All cephalic structures were manually outlined and surfaces of each were created separately. The raw surfaces were converted and scaled with Transform2 64-bit software (freeware, Heiko Stark, FSU Jena, Germany; URL: http://starkrats.de). Afterwards, Autodesk MAYA 2016 (Alias Wavefront, Toronto/Ontario, Canada) was used for smoothing and coloring the 3D models.

Scanning electron microscopy (SEM). Specimens for SEM investigation were dehydrated with ethanol, dried at the critical point and sputter-coated with gold (Balzers SCD050) and studied and imaged with a LEO 438 VP scanning electron microscope.

Terminology. The muscular terminology is based on V. KÉLER (1963)

3. Results

3.1. General features

Micromalthus debilis is a small and comparatively weakly sclerotized species, varying in length between 1.5 and 2.5 mm (HÖRNSCHEMEYER 2016). The body surface is largely smooth, with a sparse vestiture of fine setae but lacking cuticular tubercles or scales. The elytra are shortened and lack window punctures. The abdomen comprises six or seven visible segments (HÖRNSCHEMEYER 2016).

3.2. Head capsule
(Figs. 1–3)

The head is prognathous, compact, only moderately flattened dorsoventrally, and slightly retracted into the prothorax (Figs. 1A,B). It is 0.38 mm long from the anterior clypeolabral margin to the hind margin of the head capsule, 0.51 mm broad at the ocular region, and 0.4 mm at the temporal region shortly behind the compound eyes (measurements based on a single male specimen examined with SEM). The cuticle of the head capsule is largely smooth; it lacks tubercles and scales but the surface of the posterior genal region posterior to the compound eyes is wrinkled, and indistinct scale-like surface structures with slightly serrated edges are present on the clypeolabral region. The head capsule lacks dorsal protuberances and antennal grooves are absent; it is nearly parallel-sided, with very slightly rounded posterolateral edges that slightly converge towards the large foramen occipitale. A vestiture of medium length setae (ca. 30 μm) is present, with a higher density on the clypeal area (Fig. 2A) and below the compound eyes. The compound eyes are large and strongly protruding laterally, with ca. 160 ommatidia with distinctly convex cuticular lenses; the ommatidia are not separated by chitin-
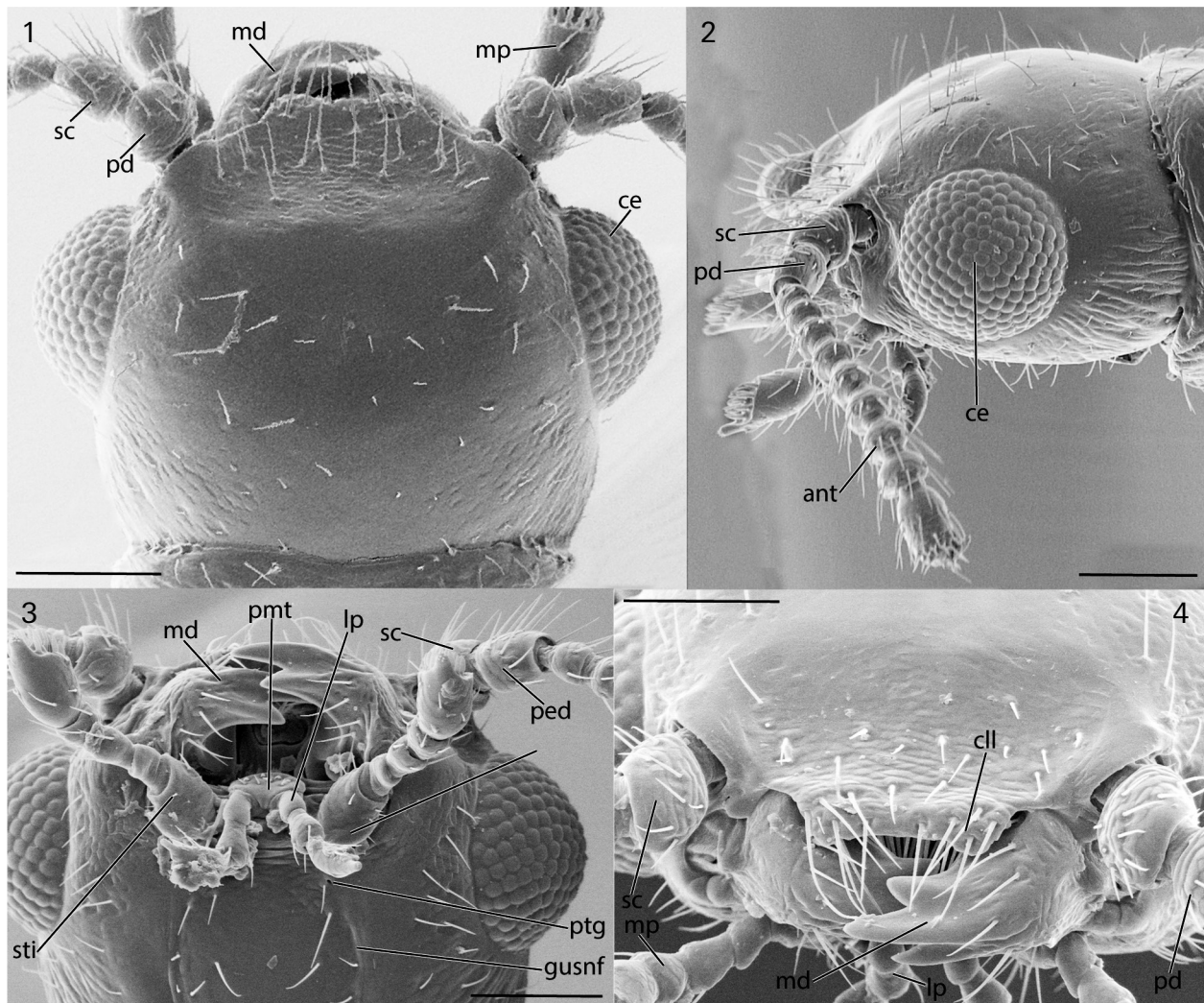
Fig. 1. Head of *Micromalthus debilis*, SEM micrographs. **A**: dorsal view; **B**: lateral view; **C**: ventral view; **D**: frontal view. — ***Abbreviations***: ant – antenna, ca – cardo, ce – compound eye, cll – clypeolabral region, gusuf – gula-submental furrow, lp – labial palp, md – mandible, mp – maxillary palp, pd – pedicellus, pmt – prementum, ppm1/4 – palpomere 1/4, ptg? – posterior tentorial groove (?), sc – scapus. Scale bar 100 μm. See also DOI 10.5281/zenodo.897754.

ous bridges and ocular setae are also lacking. Ocelli are absent. Dorsal ecdysial sutures and the transverse frontoclypeal strengthening ridge are lacking. External furrows enclosing the gula and posterior submentum on the ventral side of the head are very distinct (Fig. 1C); they are distinctly curved outwards and the enclosed gula-submental sclerite is widest at a level slightly posterior to the posterior ocular margin. The anterior and posterior tentorial grooves could not be identified with certainty (see Fig. 1C); a narrow furrow mesad the antennal base (visible on one side on Figs. 1D and 2A) does not correspond with an internal invagination and is very likely not a vestige of an anterior groove.

3.3. Cephalic endoskeleton
(Figs. 3, 4)

The tentorium is strongly reduced. A pair of rudimentary, short posterior arms arise from the gula-submental furrows below the tritocerebral commissure; it is connected by a vestigial ligamentous tentorial bridge. Dorsal arms,

anterior arms and laminatentoria are lacking. The circumocular ridges are strongly developed, with a relatively narrow passage for the optic lobes. Other internal cephalic ridges are absent including those enclosing the gula.

3.4. Labrum
(Figs. 1, 2A, 3B)

The labrum is completely fused with the clypeus. The anterior edge of the clypeofrons is slightly concave, without specific structural modifications; the lateral clypeolabral edges are slightly converging and the anterolateral corners are rounded. Ten long setae are inserted on the anterior clypeolabral surface.

Musculature: Musculus (= M.) labroepipharyngalis (7), probably absent (but see below); M. frontoepipharyngalis (8), absent; M. frontoepipharyngalis (9), absent. The homology of a non-skeletal structure in the clypeolabral region could not be clarified with the available CLSM images and the microtome section series.
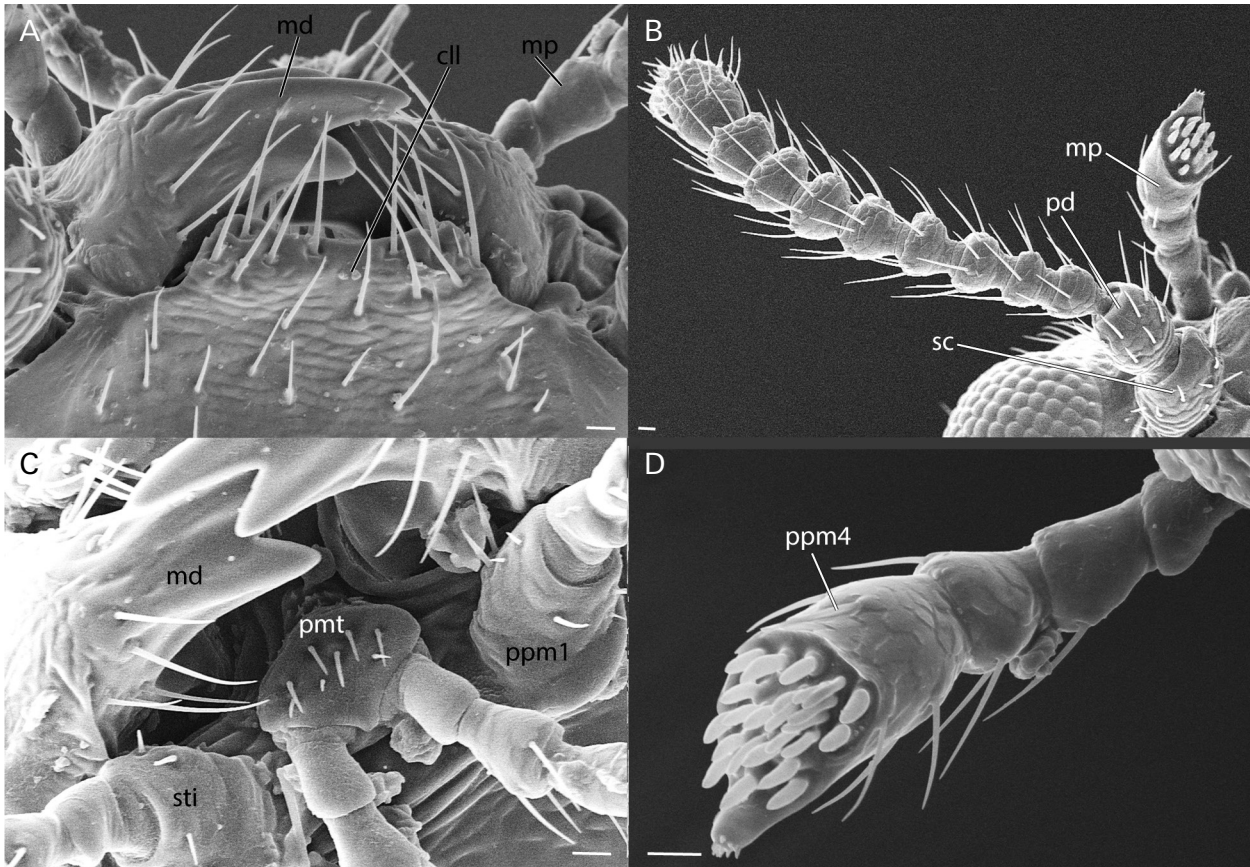
Fig. 2. Head structures of *Micromalthus debilis*, SEM micrographs. **A**: clypeolabral region and mandibles, dorsal view; **B**: antenna; **C**: mouthparts, frontal view; **D**: maxillary palpus. — **Abbreviations**: ce – compound eye, cll – clypeolabrum, lp – labial palpus, md – mandible, mp – maxillary palp, pd – pedicellus, pmt – prementum, ppm1/4 – palpomere 1/4, sc – scapus, sti – stipes. Scale bar 10 µm. See also DOI 10.5281/zenodo.897754.

3.5. Antennae
(Figs. 2B, 3A)

The moniliform, 11-segmented antennae are inserted anterolaterally on the head capsule. The antennal foramen is dorsally covered by a shallow, rounded anterolateral frontal projection. The scapus is large compared to flagellomeres 1–8 but is about as long as the pedicellus and the apical flagellomere; a deep constriction divides it into a proximal articulatory piece and an enlarged, rounded, cup-shaped distal part. Like the other antennomeres it bears a moderately dense vestiture of medium length setae (ca. 25 µm). A fine antennal pubescence is lacking; the surface of the scapus is largely smooth on the distal part but a scale-like surface structure is recognizable on the proximal area of the cup-shaped portion; scale-like surface modifications are also present on the other antennomeres, most distinct on the distal 2/3 of the apical one. The barrel-shaped pedicellus is slightly longer but narrower than the distal part of the scapus; it bears two circular rows of setae. Flagellomeres 1–8 are cup-shaped and each bears a loose whorl of setae on the widened distal part with the scale-like surface modifications; the apex of flagellomere 9 is about twice as long as the preceding ones, almost cylindrical, slightly widening distally, and rounded apically; its medium length setae are

less regularly arranged than on the other segments and stiff shorter setae are concentrated on the apical region.
Musculature (Figs. 3A, 4A,B): strongly developed, M. tentorioscapalis anterior (1), M. tentorioscapalis posterior (2), M. tentorioscapalis medialis (4), O: all three from the central region of the dorsal wall of the head capsule (Fig. 3A), I: anteriorly, dorsally and posteriorly on the base of the scapus; M. scapopedicellaris lateralis/medialis (5/6), three bundles, O: two dorsally and one on the anterior wall of the scapus, I: dorsally and posteroventrally on the base of the pedicellus.

3.6. Mandibles
(Figs. 1A,D, 2A,C, 3A, 4A,B)

The robust, almost evenly curved mandibles are articulated in a typical dicondylic manner, with a strongly developed ventral condyle forming the mandibular part of the primary joint. The surface is largely smooth but the proximolateral area is wrinkled; this sculptured surface reaches the ventral condyle posteriorly. Approximately 10 medium length setae are inserted dorsally, laterally and ventrally. The mandibular bases are relatively broad (ca. 60 µm) but widely separated and completely lacking molae (Fig. 4A); a retinaculum or moveable appendages (prosthecae) are also missing. The curved distal part is
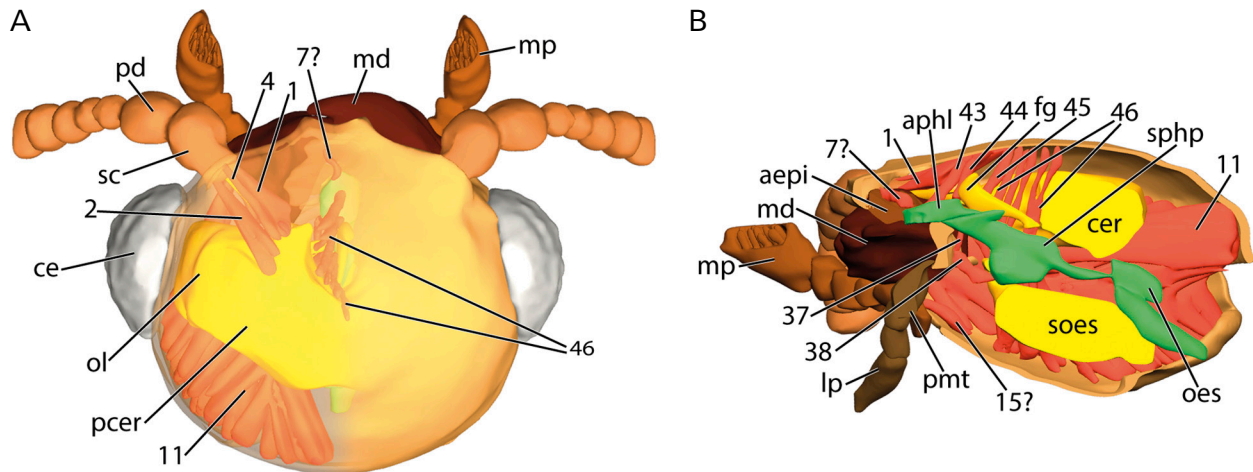
Fig. 3. Head of *Micromalthus debilis*, three-dimensional reconstructions. **A**: dorsal view, cuticle on left side transparent, antenna reconstructed without distal segments; **B**: sagittal section, muscles, digestive tract and nervous system. — ***Abbreviations***: 1, 2, 4 – Mm. tentorioscapales anterior, posterior, medialis, 7? – M. labroepipharyngalis(?), 15? – M. craniocardinalis(?), 37 – M. hypopharyngosalivarialis, 38 – M. prementosalivarialis anterior, 45 – M. frontopharyngalis anterior, 46 – M. frontopharyngalis posterior, aepi – anterior epipharynx, aphl – anterior pharyngeal loop, ce – compound eye, cer – cerebrum, fg – frontal ganglion, lp – labial palp, md – mandible, mp – maxillary palp, oes – oesophagus, ol – optic lobe, pcer – protocerebrum, pd – pedicellus, pmt – prementum, sc – scapus, soes – suboesophageal ganglion, sphp – subcerebral pharyngeal pouch.

concave on its inner side, which results in a spoon-like condition; three strongly developed and acuminate distal teeth are vertically arranged (Fig. 2C); the middle tooth is longer than the others.

Musculature (Figs. 3A, 4C,D): M. craniomandibularis internus (11), largest muscle of the head, filling out about $1/3^{rd}$ of the cephalic lumen, composed of numerous thin bundles, O: extensive parts of the posterior head capsule, I: extensive, approximately horizontal adductor tendon; M. craniomandibularis externus (12), much smaller than M. 11, less than ten bundles, O: ventrolaterally on posterior head capsule, I: abductor tendon; M. tentoriomandibularis (13), distinctly developed, O: head capsule, close to the antennal insertion area, I: dorsomesally on the basal part of the mandible.

3.7. Maxillae
(Figs. 1, 2C, 3B)

The distinctly simplified maxillae are inserted in very shallow maxillary fossa below the ventral mandibular bases and laterad the mentum. The large cardo is only indistinctly separated from the stipes mesally. The stipes is simple, almost tubular and undivided, with few short setae inserted on its surface. The galea and lacinia are missing (Fig. 2C). The palpus is composed of four distinctly developed palpomeres (Fig. 2D). A palpifer is absent. The short palpomere 1 is distally extended and lacks setae. Palpomeres 2 and 3 are slightly larger but of similar shape. One medium length seta is mesally inserted on palpomere 2 and three setae are present on palpomere 3. The apical palpomere is distinctly enlarged, distally widening, with a distinct ventrolateral protuberance with extremely short apical sensilla and a slightly concave apical field with ca. 20 peg-shaped, hyalinous sensilla (ca. 12 μm) (Fig. 2D); the proximal surface shows a very

indistinct scale-like pattern. Three setae are inserted mesally on the apical segment, one dorsally and one laterally.

Musculature (Fig. 4): Only two extrinsic muscles are present; they likely function as extensor and levator of the maxilla; the homology assessment is difficult as the maxillary base is strongly simplified; the origin and function tentatively suggests that the muscle with originating on the wall of the head capsule is M. craniocardinalis, O: ventrolaterally on the posterior head capsule, at the level of the posterior ocular margin, I: dorsally on the maxillary base with a tendon. The second extrinsic muscle is either M. tentoriocardinalis (17) or M. tentoriostipitalis (18), O: vestigial posterior tentorial arm, I: laterally on the maxillary base; M. stipitopalpalis externus/internus (22/23), a single bundle, O: ventrally on maxillary base, I: base of proximal palpomere. Intrinsic palp muscles are present but the exact arrangement could not be reconstructed with the material at hand.

3.8. Labium
(Figs. 1C, 2C, 4A,B)

The submentum is not present as a separate unit but completely integrated in the large and laterally distinctly delimited gula-submental plate (Fig. 1C). The mentum is a small element between the maxillary bases and the prementum, but distinctly separated from the anterior submental border by a very distinct transverse suture. The small prementum bears the three-segmented palpi (Fig. 1C) on distinct palpigers; a sclerotized, roughly triangular structure resembling a ligula is present above the insertion areas of the palps; it is nearly vertically oriented, with paired ventrolateral emarginations and a slightly convex upper edge; it bears eight short setae on its surface. Palpomeres 1 and 2 are moderately widening

distally; palpomere 2 is slightly longer than the proximal one and bears three or four setae on its apical region. The terminal palpomere 3 is spindle-shaped, slightly curved, and slightly longer than the intermediate segment; it bears two setae on its dorsal side and a very small sensillum is present on its slender, apically rounded distal part; a second subapical projection also bears a similar sensillum.

Musculature (Figs. 3B, 4): extrinsic muscles and muscles of labial endite lobes are absent. M. praementopalpalis externus (34), distinctly developed, O: lateral wall of prementum, I: laterally on the base of the proximal palpomere. Intrinsic labial palp muscles are probably present but could not be identified with certainty.

3.9. Epipharynx and anterior stomodaeum (= cibarium)
(Figs. 3A,B, 4A,B)

The anteriormost part of the ventral wall of the clypeolabrum is slightly convex, glabrous and sclerotized. A strongly sclerotized but rather shallow median elevation with several setae and an irregular surface is present in the middle region. It is followed by a reverse V-shaped median rim with sclerotized wall. The posteriormost epipharyngeal section below the anteriormost pharynx is flat and semimembranous. The entire epipharyngeal region is devoid of microtrichia and a longitudinal epipharyngeal process (ANTON & BEUTEL 2004, 2006: lep) is not developed. A closed prepharyngeal tube is missing.

Musculature (Fig. 3B): M. clypeopalatalis (43), a V-shaped pair of medially converging bundles, O: clypeolabral region, between areas of origin of extrinsic antennal muscles, I: medially on the rim of the middle epipharyngeal region. Transverse epipharyngeal muscles are completely lacking.

3.10. Hypopharynx
(Fig. 4A,B)

The anterior hypopharyngeal region is fused with the prelabium and not visible as a protruding structure. A distinct, strongly sclerotized protuberance with a rough, irregular surface is present on the dorsal surface of the middle region of the hypopharynx, opposite to the sclerotized epipharyngeal elevation.

Musculature (Figs. 3, 4): M. frontohypopharyngalis (41), two vertical and slender bundles, O: central area of frontal region, anterad of M. 44, I: laterally on the anatomical mouth.

3.11. Salivarium
(Fig. 4A,B)

A salivarium as a cavity between the prelabium and hypopharynx is not developed. A short unpaired salivary duct is present in the prelabio-hypopharyngeal region.

Musculature (Figs. 3B, 4A,B): Two well developed muscles arise from the lateral prelabio-hypopharyngeal wall and insert at the opening of the salivary duct. M. hypopharyngosalivarialis (37), O: dorsolaterally on the anterior hypopharynx; M. prementosalivarialis anterior (38), O: laterally on anterior prepharynx, I: together with M. 37. A ring muscle layer of the salivary duct is missing.

3.12. Posterior stomodaeum (= pharynx and oesophagus)
(Figs. 3B, 4B–D)

The anteriormost pharyngeal section forms a vertical loop before connecting with the open preoral cavity. The precerebral region is moderately wide; indistinct dorsolateral and ventro-lateral folds serve as attachment areas of dilators. The postcerebral pharynx is narrow. A second vertical loop of the stomodaeum is formed at the pharyngeal-oesophageal border (Fig. 3B). A voluminous dorsal oesophageal pouch appears very closely connected with the posteriormost part of the protocerebrum (histological sections: Fig. 4C); its walls are smooth, whereas the posteriorly directed main tract of the oesophagus is strongly folded; it is very thin-walled and completely lacks a layer or circular or longitudinal muscles.

Musculature (Figs. 3B, 4B–D): M. clypeobuccalis (44), a V-shaped pair of bundles immediately anterior to the frontal ganglion, converging towards its insertion; O: posterior clypeofrontal region, I: anterior to anatomical mouth, medially on rim of posterior epipharynx, between insertions of M. 41; M. frontobuccalis anterior (45), one slender vertical bundle, O: posterad of M. 44 and frontal ganglion, I: laterally on indistinct fold of anterior precerebral pharynx; M. frontobuccalis posterior (46), five thin bundles, O: posterad of M. 45, I: successively on dorso-lateral folds of posterior precerebral pharynx; M. tentoriobuccalis posterior (50), several very thin bundles, O: ventral wall of head capsule, along the gula-submental furrows, I: ventrolaterally on pharynx, below tritocerebral commissure. M. tentoriopharyngalis (52), a series of very thin bundles, O: posterior part of the ventral head capsule, along the gula-submental furrows, I: ventrolateral postpharyngeal folds. A thin layer of circularly arranged muscle fibres is present around the pharynx.

3.13. Brain, suboesophageal complex and frontal ganglion
(Figs. 3A,B, 4B,C)

The brain is moderately sized in relation to the head and completely located within the cephalic lumen. The protocerebrum is slightly flattened; the optic lobes are well-developed. Strongly developed antennal nerves originate from the deutocerebrum. A thin but distinctly separate tritocerebral commissure is present. The moderately sized suboesophageal ganglion is located above the gula-submental sclerite; its posterior face reaches the cervical region; the adjacent first connectives are completely
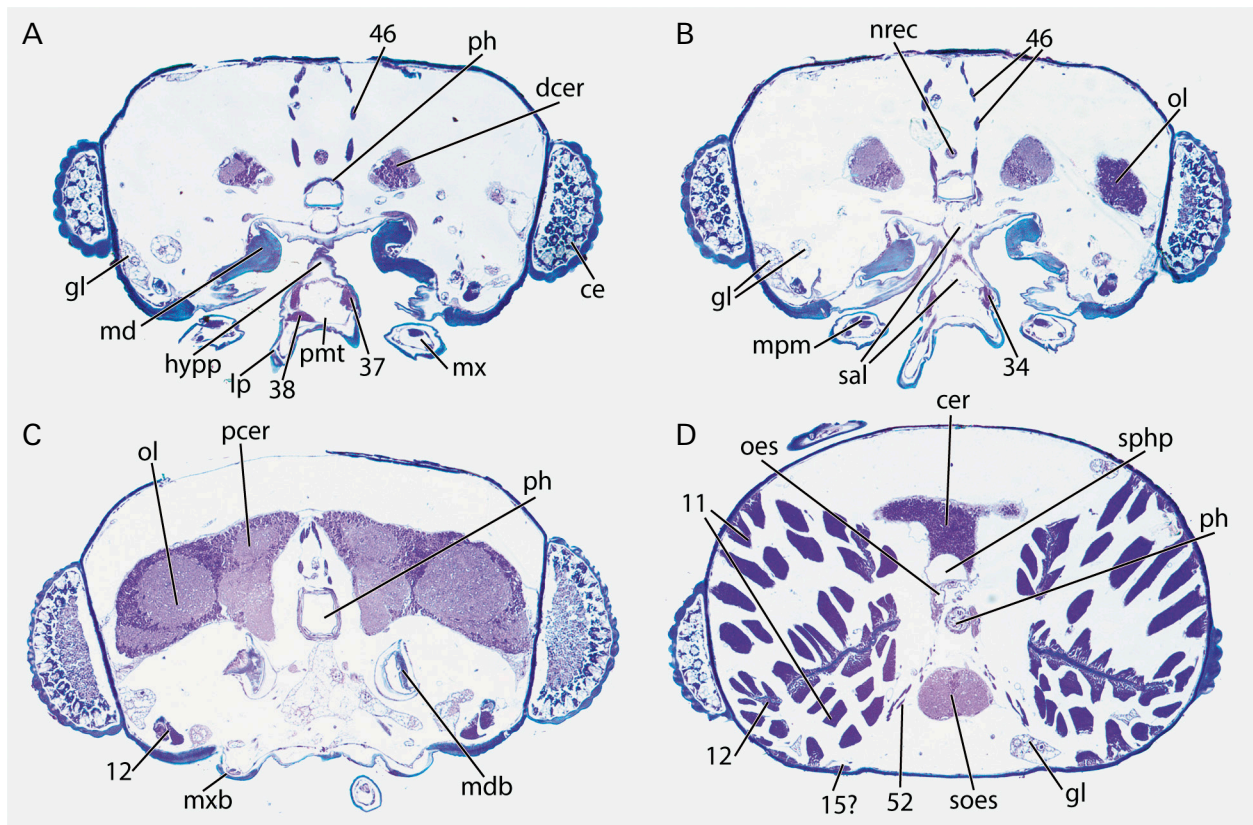
Fig. 4. Head of *Micromalthus debilis*, histological sections. **A**: clypeolabral region, epi- and hypopharyngeal protuberances and salivary duct; **B**: anterior clypeofrontal region, salivary duct, anterior pharynx and posteriormost epipharynx; **C**: anterior protocerebral region with optic lobes; **D**: occipital region, subcerebral pouch. — ***Abbreviations***: 11 – M. craniomandibularis internus, 12 – M. craniomandibularis externus, 15? – M. craniocardinalis (?), 34 – M. prementopalpalis, 37 – M. hypopharyngosalivarialis, 38 – M. prementosalivarialis anterior, 46 – M. frontopharyngalis posterior, 52 – M. tentoripharyngalis posterior, ce – compound eye, cer – cerebrum, dcer – deutocerebrum, gl – gland, hypp – hypopharyngeal protuberance, lp – labial palp, md – mandible, mpm – maxillary palp muscles, mx – maxilla, mxb – maxillary base, nrec – nervus recurrens, oes – oesophagus, ol – optic lobe, pcer – protocerebrum, ph – pharynx, pmt – prementum, sal – salivary duct, soes – suboesophageal ganglion, sphp – subcerebral pharyngeal pouch.

fused with each other and appear reverse drop-shaped in cross section. The frontal ganglion above the anatomical mouth opening is moderately sized.

3.14. Glands
(Figs. 3, 4)

Glands are present in the hypopharyngeal and postmaxillary region, and also in the posterodorsal area of the head; the posterior part of the hypopharyngeal gland is divided into an upper and a lower part by the vestigial tentorial bridge. Large and branched lobes of glandular tissue are present in the prothorax. The hypopharyngeal glands open with a short duct (see 3.11. Salivarium) on the prelabio-hypopharyngeal surface; the openings of the other glands (and connections between them) could not be identified with the available material.

3.15. Circulatory system
(Fig. 4D)

The cephalic aorta enters the posterior head capsule, accompanied by two narrow tracheal branches; it is keyhole-shaped in cross section and obliterates in the occipital region before it reaches the brain.

3.16. Characters of the adult head

1. Tubercles: **(0)** absent or very indistinct; **(1)** present. — Tubercles are absent in *Micromalthus debilis* (Figs. 1, 2), in the miniaturized *Crowsoniella relicta*, and in *Sikhotealinia zhiltovae* Lafer, 1996 (Lafer 1996), as it is usually the case in non-archostematan beetles. They are present in Cupedidae and Ommatidae, and also in stem-group Coleoptera (Ponomarenko 1969; Beutel et al. 2008; Hörnschemeyer 2009).

2. Scale-like setae: **(0)** absent; **(1)** present. — Absent in *Micromalthus* (Figs. 1, 2), *Crowsoniella* (Pace 1975) and *Sikhotealinia*, and also in non-archostematan beetles. Present in Cupedidae, Ommatidae, and stem-group Coleoptera (Ponomarenko 1969; Beutel et al. 2008; Hörnschemeyer 2009). The scale-like surface modifications occurring on some head regions of *Micromalthus* are possibly vestiges of distinct scales occurring in other archostematan groups.

3. Ocelli: **(0)** three; **(1)** absent. — Absent in *Micromalthus* (Fig. 1A), like in species of Cupedidae, Ommatidae and *Crowsoniella* (Beutel et. al. 2008). The presence of three true ocelli in *Sikhotealinia*

(LAFER 1996) is unconfirmed. Paired ocelli or a single ocellus occur in very few groups of Polyphaga (LESCHEN & BEUTEL 2004).

4. Constricted neck region of head capsule and postocular extensions: **(0)** absent or indistinct; **(1)** present. — The head of *Micromalthus* lacks a constricted cephalic neck region and postocular extensions (Fig. 1A,C), as they are present in the other groups of Archostemata (incl. *Sikhotealinia*) (BEUTEL et al. 2008; HÖRNSCHEMEYER 2009).

5. Dorsal cephalic protuberances: **(0)** absent; **(1)** present. — Paired dorsal protuberances of the head are characteristic for Cupedidae and Ommatidae. They also occur in *Crowsoniella* and *Sikhotealinia* (PACE 1975; LAFER 1996; BEUTEL et. al. 2008) but are completely absent in *Micromalthus* (Fig. 1A).

6. Cephalic antennal groove: **(0)** absent; **(1)** below compound eye; **(2)** above compound eye. — Completely missing in *Micromalthus* (Fig. 1A–C), and also absent in *Omma* Newman and Cupedidae (BEUTEL et al. 2008). Grooves are present below the compound eyes in *Tetraphalerus* Waterhouse, and above it in *Crowsoniella* and *Sikhotealinia* (BEUTEL et al. 2008; HÖRNSCHEMEYER 2009).

7. Gular sutures: **(0)** complete, reaching hind margin of head capsule; **(1)** incomplete, not reaching hind margin of head capsule; **(2)** absent. — Distinct and reaching hind margin of head in *Micromalthus* (Fig. 1C) and Cupedidae. Not reaching hind margin in *Omma* and obliterated in *Tetraphalerus* (BEUTEL et al. 2008; HÖRNSCHEMEYER 2009).

8. Tentorial bridge: **(0)** present, sclerotized; **(1)** ligamentous; **(2)** absent. — Only present as transverse ligamentous structure in *Micromalthus*. The bridge is present and sclerotized in *Tetraphalerus* but missing in Cupedidae (BEUTEL et al. 2008; HÖRNSCHEMEYER 2009). The condition in *Omma*, *Crowsoniella* and *Sikhotealinia* is unknown.

9. Anterior tentorial arms: **(0)** well developed; **(1)** distinctly reduced or absent, detached from posterior tentorium. — Absent in *Micromalthus* (Fig. 4A,B). Distinctly or completely reduced in *Tetraphalerus* and in other adults of Archostemata examined (HÖRNSCHEMEYER et al. 2002; BEUTEL et al. 2008).

10. Frontoclypeal strengthening ridge: **(0)** present; **(1)** absent. — Absent in *Micromalthus* (Fig. 1A,D) and other extant Archostemata with the exception of *Sikhotealinia* (LAFER 1996: fig. 137.1).

11. Labrum: **(0)** free, connected with clypeus by membrane; **(1)** indistinctly separated from clypeus, largely or completely immobilised; **(2)** fused with head capsule. — Fused with clypeus in *Micromalthus* (Figs. 1A,D, 2A), *Crowsoniella* and *Omma* (LAWRENCE 1999; BEUTEL et al. 2008; HÖRNSCHEMEYER 2009). Free in Cupedidae and *Sikhotealinia* (LAFER 1996). Not fused with head capsule but immobilised in *Tetraphalerus* (BEUTEL et al. 2008).

12. M. frontoepipharyngalis (M. 9): **(0)** present; **(1)** absent. — Absent in *Micromalthus* (Figs. 3, 4A,B), *Tetraphalerus* and *Priacma* (HÖRNSCHEMEYER et al. 2002). Also missing in many other beetles (e.g., DRESSLER & BEUTEL 2010; ANTUNES-CARVALHO et al. 2017). Present as a very thin bundle in *Ascioplaga* (HÖRNSCHEMEYER et al. 2006).

13. Antennal length: **(0)** not or scarcely reaching hind margin of head; **(1)** reaching middle region of prothorax; **(1)** reaching middle region of body. — Short in *Micromalthus* (Fig. 2B) and *Crowsoniella*, reaching the middle region of the prothorax in Ommatidae (e.g. LAWRENCE 1999) and *Sikhotealinia* (LAFER 1996), and strongly elongated in Cupedidae (e.g. HÖRNSCHEMEYER 2009).

14. Shape of antennae: **(0)** filiform; **(1)** moniliform; **(2)** with cup-shaped flagellomeres and one-segmented distal club. — Moniliform in *Micromalthus* (Fig. 2B). With cup-shaped flagellomeres and one-segmented distal club in *Crowsoniella* (PACE 1975: fig. 6).

15. Location of antennal insertion on head capsule: **(0)** laterally; **(1)** dorsally. — Laterally in *Micromalthus* (Fig. 1B), Ommatidae, and *Crowsoniella*. On dorsal side of head capsule in Cupedidae excl. *Priacma* (HÖRNSCHEMEYER et al. 2002, 2006) and in *Sikhotealinia* (LAFER 1996).

16. Ventro-mesal margin of sculptured mandibular surface: **(0)** not reaching position of mandibular condyle; **(1)** reaching mandibular condyle. — The sculptured lateral surface of the mandibles of *Micromalthus* and Ommatidae reaches the posterior ventral condyle (BEUTEL et al. 2008; HÖRNSCHEMEYER 2009).

17. Cutting edge of mandible: **(0)** horizontal, **(1)** three vertically arranged teeth. — Three apical teeth are arranged in a vertical row in *Micromalthus* (Fig. 2C) and Ommatidae (BEUTEL et al. 2008; HÖRNSCHEMEYER 2009). The cutting edge is horizontal in Cupedidae and *Sikhotealinia* like in most other beetles (HÖRNSCHEMEYER et al. 2002; BEUTEL et al. 2008; LAWRENCE et al. 2011). Mandible apparently vestigial in *Crowsoniella* (PACE 1975) but insufficiently documented.

18. Galea: **(0)** present; **(2)** absent. — Completely reduced in *Micromalthus* (Fig. 2C). Apparently also missing in *C. relicta* (PACE 1975: fig. 6) but insufficiently documented.

19. Lacinia: **(0)** present; **(1)** absent. — Absent in *Micromalthus* (Fig. 2C; HÖRNSCHEMEYER 2005) and also in *Crowsoniella* according to PACE (1975).

20. Number of extrinsic maxillary muscles: **(0)** four; **(1)** two. — Four extrinsic muscles are almost generally present in adult beetles, two originating on the head capsule and two on the tentorium (HÖRNSCHEMEYER et al. 2002, 2006; BEUTEL et al. 2008; DRESSLER & BEUTEL 2010; ANTUNES-CARVALHO 2017). Only two bundles are recognizable in *Micromalthus* (Fig. 4C), one originating on the head capsule and one on the vestigial tentorium.

21. Digitiform sensilla on apical maxillary palpomere:

(0) absent, **(1)** present. — Missing in *Micromalthus* (Fig. 2D) and other archostematan beetles (e.g. Hörnschemeyer 2009). Countersunk digitiform sensilla of the apical palpomere occur in the other extant lineages of Coleoptera (Honomichl 1980).

22. Pit containing sensilla of dorsolateral field of apical maxillary palpomere: **(0)** absent; **(1)** present. — The sensilla of the dorsolateral field are exposed in *Micromalthus* (Fig. 2D) but placed in a deep pit in Ommatidae (Hörnschemeyer et al. 2002, 2006; Beutel et al. 2008; Hörnschemeyer 2009).

23. Basal cavity of prementum: **(0)** absent, **(1)** present. — Absent in *Micromalthus* (Fig. 1C), *Crowsoniella* (Pace 1975: fig. 6) and *Sikhotealinia* (Lafer 1996: fig. 2). The deep pit and a corresponding strongly developed apodeme for attachment of the median premental retractor are present in *Tetraphalerus, Omma* and Cupedidae (Beutel et al. 2008).

24. Lid-like ventral premental plate: **(0)** absent, **(1)** present. — A large lid-like premental plate is absent in *Micromalthus* (Fig. 1C; Beutel et al. 2008; Hörnschemeyer 2009). The presence is characteristic for Cupedidae and Ommatidae (Beutel et al. 2008). It is also present in *Crowsoniella*, with a fairly short transverse part and a median spoon-shaped process (Pace 1975: fig. 6).

25. Anterior appendages of prementum: **(0)** present; **(1)** absent. — Absent in *Micromalthus* (Fig. 2C) and also in *Crowsoniella* (Pace 1975: fig. 6; Beutel et al. 2008). Subdivided into many digitiform appendages in *Cupes, Ascioplaga, Distocupes* and *Tenomerga* (Hörnschemeyer 2009), presumably for the uptake of liquid food like nectar.

26. Mentum: **(0)** distinctly developed; **(1)** vestigial or absent. — Absent in *Micromalthus* (Fig. 1C) and most other representatives of Archostemata (Hörnschemeyer et al. 2002; Beutel et al. 2008). A short transverse sclerotized element is present in *Tetraphalerus* (Beutel et al. 2008) and *Crowsoniella* (Pace 1976: fig. 6).

27. Sclerotized protuberance of hypopharynx and corresponding sclerotized elevation of hypopharynx: **(0)** present; **(1)** absent. — Both structures are present in *Micromalthus* (Fig. 4A) and apparently involved in triturating food. Not described in other groups of beetles.

28. Closed prepharyngeal tube: **(0)** present; **(1)** absent. — Absent in *M. debilis* like in other archostematan species examined (Hörnschemeyer et al. 2002, 2006; Beutel et al. 2008). Usually present in other groups of beetles (Anton & Beutel 2004; Anton et al. 2016; Antunes-Carvalho et al. 2017; Dressler & Beutel 2010).

29. Arrangement of cibarial dilators: **(0)** parallel; **(1)** V-shaped. — The V-shaped arrangement of M. clyeopalatalis (43) and M. clypeobuccalis (44) in *Micromalthus* is an unusual condition in Coleoptera (Anton & Beutel 2004, 2006; Anton et al. 2016; Antunes-Carvalho et al. 2017; Hörnschemeyer et al. 2002, 2006; Beutel et al. 2008; Dressler & Beutel 2010).

30. Transverse epipharyngeal muscles: **(0)** present; **(1)** absent. — Absent in *M. debilis* (Figs. 3B, 4A) but almost generally present in other groups of beetles (Anton & Beutel 2004, 2006; Anton et al. 2016; Antunes-Carvalho et al. 2017; Hörnschemeyer et al. 2002, 2006; Beutel et al. 2008; Dressler & Beutel 2010).

31. Vertical loop of anterior pharynx: **(0)** absent; **(1)** present. — So far only described for *Micromalthus* (Fig. 3B).

32. Subcerebral oesophageal pouch: **(0)** absent; **(1)** present. — So far only described for *Micromalthus* (Figs. 3B, 4D).

33. Muscularis of oesophagus: **(0)** present; **(1)** absent. — Almost generally present but missing in *Micromalthus*. The cuticle of the oesophagus of *M. debilis* is very thin and strongly folded (Fig. 4D: oes).

34. Salivary duct: **(0)** present; **(1)** absent. — Present in *Micromalthus* (Fig. 4B). Not observed in any other group of beetles (e.g. Anton & Beutel 2004, 2006; Beutel et al. 2008; Dressler et al. 2010; Anton et al. 2016; Antunes-Carvalho et al. 2017).

35. Glands associated with mouthparts: **(0)** absent; **(1)** present. — Present in *M. debilis* (Figs. 3B, 4) and also in representatives of Myxophaga, Polyphaga, Ommatidae and Cupedidae (Anton & Beutel 2004, 2006; Anton et al. 2016; Antunes-Carvalho et al. 2017; Hörnschemeyer et al. 2002, 2006; Beutel et al. 2008). Cephalic glands associated with mouthparts are usually absent in Adephaga (e.g. Dressler & Beutel 2010; Beutel et al. 2017) but present in *Haliplus* (R. Beutel pers. obs.).

36. Voluminous prothoracic glands: **(0)** absent; **(1)** present. — Strongly developed in *M. debilis*. Not described in other archostematan beetles (Baehr 1975; Beutel et al. 2008; Friedrich et al. 2009) and non-archostematan beetles (e.g. Beutel & Komarek 2006; Ge et al. 2007).

5. Discussion

The body organization of *Micromalthus* is likely affected by miniaturization. This may apply to the weak sclerotization and the fused prothoracic sclerites (e.g. Barlet 1996; Lawrence et al. 2011). However, modifications, especially structural simplifications, may be also due to the sporadic appearance and vestigialization of adults, especially males (Pollack & Normark 2002; Perotti et al. 2016). The head shows some apomorphies, which are arguably linked with reduced size. Cephalic ridges are missing except for extensive circumocular ridges. The tentorium, which is also partly reduced in other archostematan species (e.g. Hörnschemeyer et al. 2002,

2006; Beutel et al. 2008), is only preserved as vestigial posterior arms and a ligamentous bridge in *Micromalthus*. *Micromalthus* differs in many features from conditions observed in other archostematan groups, especially Cupedidae and Ommatidae. These two families are likely closest to the groundplan of the suborder and also show the greatest structural similarity with stem group beetles (Ponomarenko 1969; Beutel 1997; Beutel et al. 2008; Friedrich et al. 2009). This includes the lack of cuticular tubercles or scales, the absence of dorsal protuberances, and the absence of a narrowed cranial neck region. These structural features probably evolved in the stem group of beetles (Ponomarenko 1969; Beutel 1997; Beutel et al. 2008). This and the subordinate position of *Micromalthus* within Archostemata, either as sistergroup of Cupedidae (Beutel & Hörnschemeyer 2002) or of Ommatidae (Hörnschemeyer 2009), implies secondary loss, even though the absence is consistent with the condition found in most other groups of Coleoptera (e.g. Anton & Beutel 2004; Dressler & Beutel 2010; Anton et al. 2016; Antunes-Carvalho et al. 2017).

Micromalthus debilis is characterized by numerous autapomorphic features. It is arguably one of the most aberrant species of the entire order, especially in its life cycle, but also in some morphological traits. The distinctly moniliform antennae are probably autapomorphic, even though a similar condition occurs in *Omma* (partim) and *Sikhotealinia*. What is highly modified in *Micromalthus* is the feeding apparatus including the mouthparts. The maxillae lack endite lobes completely, as it is probably also the case in the very small *Crowsoniella*. The extrinsic maxillary musculature is distinctly simplified, largely restricting the maxillae to vertical movements. It is likely that they function like accessory ventral antennae, as is the case in larvae of Adephaga or Hydrophiloidea (e.g. Beutel 1993, 1999). The maxillary structural configuration clearly shows that they are not involved in the food uptake (Fig. 2C). The same applies to the prementum, which in contrast to other beetles lacks extrinsic retractors (Figs. 3B, 4). The complete lack of a mandibular mola (Fig. 2C) is a feature shared with other archostematan groups, with Adephaga (Dressler & Beutel 2010), and with some groups of Polyphaga (Lawrence et al. 2011). This shows that grinding of food is not achieved by the mandibular bases. The shovel-like distal mandibular region of *Micromalthus* (Fig. 2C) and Ommatidae is equipped with three vertically arranged teeth. It is apparently suitable for scraping off wood particles and moving them towards the functional mouth opening, but not for intensive mechanical processing. The structural configuration of the sclerotized epi- and hypopharyngeal protuberances (Fig. 4B) and preoral dilators (Mm. 43, 44) indicate that trituration of food takes place in this area. Food pulp is probably diluted with glandular secretions and then sucked back in the pharynx by coordinated contraction of the series of dorsal and ventral dilators (Mm. 45, 46, 50, 52) (Fig. 3B). The two vertical loops of the anterior stomodaeum are a very unusual condition

not known from other beetles. It is conceivable that the subcerebral pouch (Figs. 3B, 4D) functions as a fermenting chamber, but more material should be examined to verify that this condition is not an artifact. The presence of cephalic glands (Figs. 3B, 4) is a feature shared with other non-adephagan beetles. The presence of large and branched glands in the prothorax and the presence of a well-defined salivary duct with salivary duct muscles (Fig. 4B) are very unusual features of *Micromalthus* and arguably plesiomorphic and groundplan features of Coleoptera. These structures are missing all other beetles as far as known at present.

The reasons for the far-reaching modifications of the feeding apparatus remain unclear, as the feeding habits of adults are largely unknown (Hörnschemeyer 2016). A minor or obsolete role of food uptake linked with the vestigialization of adults can probably be ruled out. The entire configuration of the feeding apparatus is only partly simplified and rather increased in complexity as far as the pharynx is concerned. As the larvae develop in wood (e.g. Beutel & Hörnschemeyer 2002) and considering the shape of the mandibles, it is plausible to assume that feeding of wood infested with fungi plays a major role.

The phylogenetic affinities of *M. debilis* remain ambiguous presently. Due to scarcity of material, analyses of molecular data with a sufficient archostematan taxon sampling have not been carried out yet (see e.g. McKenna et al. 2015). However, the subordinate inclusion of Micromalthidae in Archostemata is largely undisputed (e.g. Forbes 1926; Böving & Craighead 1931; Beutel & Hörnschemeyer 2002; Beutel et al. 2008; Hörnschemeyer 2009), even though the adults of the family lack characteristic features of the suborder, like for instance a lid-like enlarged prementum and a constricted neck region (see above). A close relationship between *Micromalthus* and Ommatidae is tentatively supported by features of the adult head. Supposedly derived conditions shared by the two taxa are mandibular teeth arranged in a vertical row and the immobilization of the labrum. Additional features of the male genitalia were pointed out by Hörnschemeyer (2009). A clade *Micromalthus* + Ommatidae is in conflict with larval features, which suggest a sistergroup relationship between *Micromalthus* and Cupedidae, for instance reduced stemmata, shortened antennae, a quadrangular mola with a distinct margin, asperities on segment IX, and a sclerotized projection of tergum X. The reconstruction of the phylogeny of Archostemata is obviously impeded by fragmentary morphological information. The adult anatomy and larvae of *Crowsoniella* (only type series known) and *Sikhotealinia* (only female holotype known) are completely unknown. The larvae of *Tetraphalerus* are also unknown and detailed information on internal structures of adults of *Omma* is not available. Another factor impeding phylogenetic and evolutionary interpretations is the difficulty to assessing effects of vestigialization of adults, which may have resulted from the association with endosymbiotic *Wolbachia* (Perotti et al. 2016).

6. Acknowledgements

7. References

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