

Head morphology of the smallest beetles (Coleoptera: Ptiliidae) and the evolution of sporophagy within Staphyliniformia)

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Abstract

Ptiliidae include the smallest known beetles. External and internal head structures of species with different body sizes and feeding preferences were examined and described in detail. Saprophagous and sporophagous species are compared. The observed features are evaluated with respect to their phylogenetic and functional significance, and their correlation with extreme size reduction. A putative autapomorphy of Staphyliniformia is an unusual extrinsic maxillary muscle, which among ptiliids is only present in the saprophagous species. Synapomorphies of Ptiliidae and their sister group Hydraenidae are a lateral mandibular process forming a unique locking device with a lateral groove of the labrum, and mandibles divided into a main body and a mesal molar part, both connected by a membrane. Extreme body size reduction is a presumptive autapomorphy of Ptiliidae that probably resulted in the following derived features: the loss of cephalic sutures and ridges, a simplified tentorium, and a brain modified in shape and very large in relation to the head size. The ptiliid species with saprophagous and sporophagous feeding habits show only subtle differences in their cephalic structures, notably in details of the epipharynx and galeae and in the configuration of maxillary muscles. Two alternative scenarios are suggested for the evolution of feeding habits, based on the morphological results and presently available information on phylogenetic relationships. One option is to assign saprophagy to the groundplan of the family, with two switches to sporophagy; first in the basal *Nossidium* and then a second time in the extremely small *Nanosellini*, which are characterized by feeding habits that we address as microsporophagy. An alternative scenario is that feeding on spores is ancestral for Ptiliidae, with reversals to saprophagy in several branches of the family, and a specialization on very small spores in the strongly miniaturized nanoselline species. A well-founded species level phylogeny of Ptiliidae with a dense taxon sampling will help to clarify this issue.

Key words

Staphylinidea, Ptiliidae, sporophagy, head morphology, phylogeny.

1. Introduction

Mycophagy, i.e. feeding on fungal mycelia or spores, was considered as the ancestral feeding type of Coleoptera (LAWRENCE 1989). Alternatively, it was suggested by NEWTON (1984) that this feeding type has evolved independently at least 18 times within the staphylinoid families Ptiliidae, Leiodidae and Staphylinidae. Sporophagy in Staphylinoid-

dea is a mode of feeding that is particularly well suited for investigating the evolution of function and form of insect mouthparts (BETZ et al. 2003). Sporophagous habits in this case means feeding on fungal spores, in contrast to consumption of other fungal materials (e.g. mycelia) or saprophagous habits, i.e. feeding on decaying material.

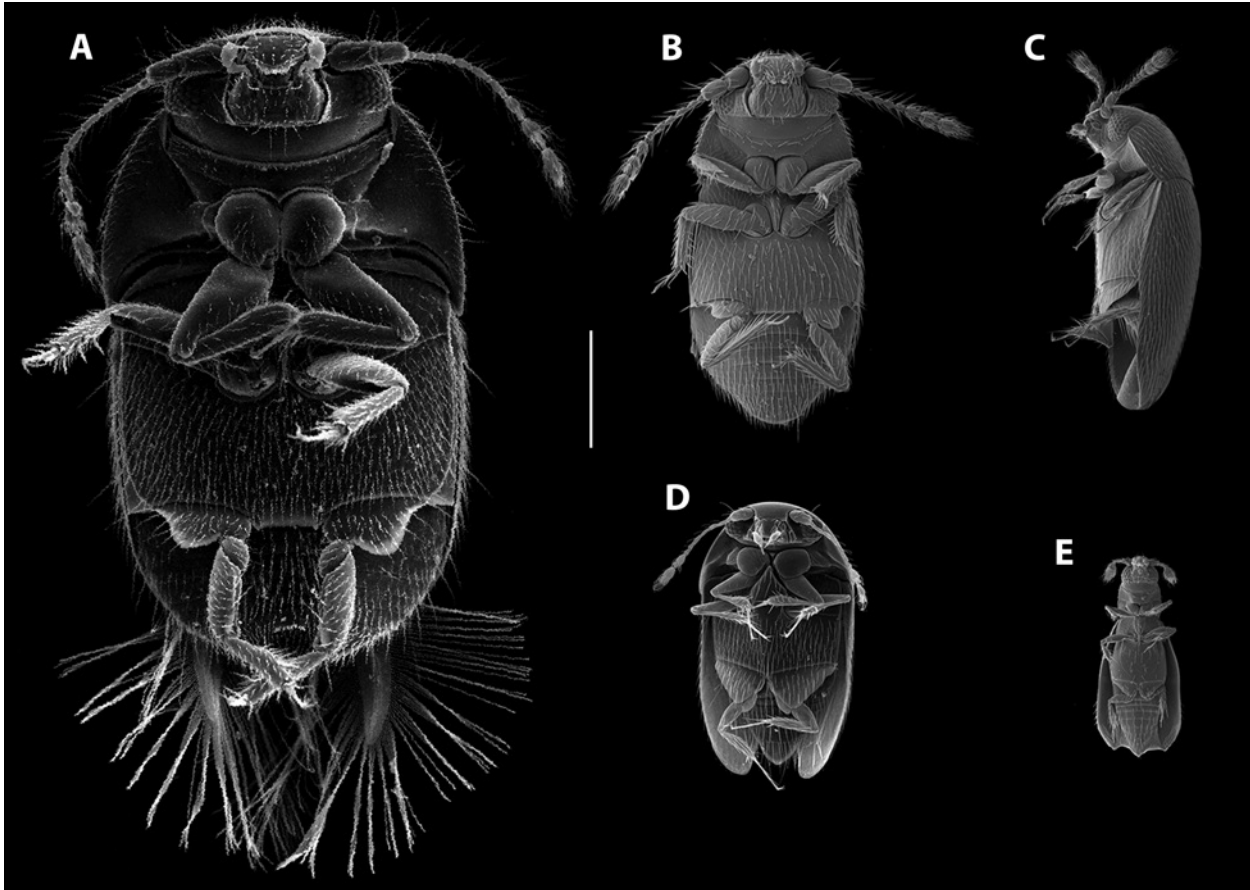


Fig. 1. SEM micrographs, ventral view. **A:** *Acrotrichis grandicollis*; **B:** *Nephanes titan*; **C:** *Porophilla mystacea*; **D:** *Mikado* sp.; **E:** *Scydosella musawasensis*. — Scale bar 0.2 mm.

Mycophagous beetles can vary strongly in body size. Relatively large species have been investigated already, either with a focus on functional morphology (BETZ 2004; BETZ et al. 2003; WEIDE et al. 2010) or on ecomorphology and evolution (LAWRENCE & NEWTON 1982; LESCHEN 1993). However, detailed data on the morphology and biology of very small mycophagous staphylinoids are very scarce. Associations with fungi have also played an important role in the evolution of very small cucujiform beetles, for instance in Corylophidae which were already investigated in detail (POLILOV & BEUTEL 2010; YAVORSKAYA et al. 2014; YAVORSKAYA & POLILOV 2016; POLILOV 2016a). Considering the very distant relationship to Ptiliidae and other staphylinoid groups, this family is well suited for a comparative analysis of phenomena related to sporophagy.

Ptiliidae (featherwing beetles), a family of Staphylinoida closely related to the aquatic Hydraenidae and the terrestrial Leiodidae and Agyrtidae (BEUTEL & LESCHEN 2005; MCKENNA et al. 2015), includes extremely small species. The minimum body length is 0.325 mm, less than half the size of an amoeba. The group consists of approximately 80 genera and over 600 species (HALL 2016). Very little specific information is available about their feeding preferences. Most ptiliids are considered to be microphagous (LAWRENCE 1989), feeding on spores and hyphae of fungi (i.e. a part of the family is sporophagous), but also on decaying plant parts and similar organic substrates.

Two strictly sporophagous groups are also part of the family – *Nossidium* (and presumably closely related genera; KILIAN & BURAKOWSKI 2000) and the extremely small Nanosellini (DYBAS 1976; HALL 1999). Almost all known species of the latter group inhabit basidiomycete fungi, particularly Polyporaceae and Steccherinaceae (DYBAS 1961; HALL 1999). Their body size varies from 0.3 to 0.9 mm, fitting with the very small spore size of the fungi they inhabit ($3\text{--}9\ \mu\text{m} \times 1\text{--}4.5\ \mu\text{m}$). There is also very limited detailed information on the structure of the mouthparts of Ptiliidae (BETZ et al. 2003; WEIDE & BETZ 2009; POLILOV & BEUTEL 2009; POLILOV 2016a) and almost no information on the head musculature. Presently available studies show quite complicated structures, only minimal muscle reductions and many features found in larger relatives with similar feeding types.

Considering the scarcity of anatomical data, the primary aim of this study is to document the head morphology of several representatives of Ptiliidae with different feeding preferences (saprophagy and sporophagy), with a main focus on mouthpart structure and musculature. The morphological results are compared with conditions found in larger relatives with similar feeding types. The phylogenetic and functional interpretations are discussed with respect to their implications for the evolution of sporophagy in Ptiliidae and other groups of Coleoptera.

2. Material and methods

2.1. List of Ptiliidae adults examined

Acrotrichinae. Acrotrichini: *Acrotrichis sericans* Heer, 1841 (Russia, Moscow Oblast (M.O.), 2010, leg. Polilov; Germany, Jena, 2015–2016, leg. Yavorskaya); *Acrotrichis grandicollis* Mannerheim, 1844 (Russia, Far East, 2005, leg. Polilov); Nephaniini: *Nephanes titan* Newman, 1834 (Russia, M.O., 2015, 2016; leg. Polilov).

Ptiliinae. Ptenidiini: *Nossidium pilosellum* Marsham, 1802 (Russia, Krimski zap., 1956, leg. Tihonravov); *Ptenidium pusillum* Gyllenhal, 1808 (Russia, M.O., 2008, leg. Polilov); Nanosellini: *Porophilla mystacea*, Polilov 2008 (Russia, Far East, 2006, leg. Polilov); *Mikado* sp. (Vietnam, 2007, leg. Polilov), *Nanosella russica* Polilov, 2008 (Russia, Far East, 2007, leg. Polilov); *Scydosella musawasensis* Hall, 1999 (Columbia, 2015, leg. Polilov).

2.2. Anatomy

Microtome sectioning, scanning electron microscopy (SEM), confocal laser microscopy (CLSM) and light microscopy were used. Several specimens of *Acrotrichis sericans*, *Ptenidium pusillum*, *Mikado* sp. and *Nanosella russica* were fixed in FAE, embedded in araldite and cut at 1 mm using a Leica RM2255 microtome equipped with a diamond knife. The sections were stained with toluidine blue and pyronin G. Pictures were taken of every section using a Motic BA410 light microscope and Zeiss Axioplan. The images were aligned using Amira 6 software (Visage Imaging, Berlin, Germany) and used for 3D reconstruction.

All other examined specimens except for *Nossidium* were fixed with 70% ethanol. For CLSM heads of *Porophilla*, *Mikado*, *Nephanes* and *Scydosella* were 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 heads were mounted in small droplets of BABB between two coverslips 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 structures were manually outlined and surfaces of each head structure were created separately for them. 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.

SEM (Philips XL 30 ESEM) was used to document surface structures of all examined species. Specimens were dehydrated in alcohol with increasing concentration (70-80-90-96-100%) and 100% acetone (two changes),

sputter-coated with gold (EmitechK500) and mounted on the tip of a fine needle and fixed on a rotatable specimen holder (POHL 2010). Several heads of *Acrotrichis*, *Ptenidium*, and *Mikado* were dissected and the mouthparts examined. The single available specimen of *Nossidium pilosellum* was dried and glued onto a paper triangle. It was removed using warm distilled water and KOH solution, transferred to 70% ethanol, then dehydrated and prepared for SEM.

In order to understand the feeding process more thoroughly, living beetles were observed. *Acrotrichis*, *Nephanes* and *Ptenidium* were collected and held in petri-dishes (method similar to the one described by JAŁOZYŃSKI 2015). Their behavior and mouthparts movements were documented using a digital microscope Keyence VHX-2000.

The heads of *Acrotrichis sericans* and *Porophilla mystacea* are described in detail, but in the case of other ptiliids under consideration only features that distinguish them from these two species.

2.3. Terminology

The terminology used for the musculature is based on v. KÉLER (1963) but muscle designations of the new system of WIPFLER et al. (2011) are given in brackets.

3. Morphological results

3.1. Acrotrichinae

Acrotrichis sericans

Body length 0.7–0.9 mm.

External features of head capsule. Head inclined, subprognathous, broad (ca. 0.25 mm wide) and laterally rounded, not flattened (Figs. 1A, 2C). Coloration of cuticle dark brown. Setae yellowish with slight silvery shine. Cuticle with fairly rough surface structure dorsally and regular scale-like reticulation on ventral side. Sutures absent. Clypeus and gula not separated by ridges from rest of head capsule. Entire dorsal surface with dense vestiture of setae with increasing length towards anterior margin of head capsule. Maximum length of setae 0.035 mm. Compound eyes large and round, only slightly protruding, consisting of ~ 55–60 large ommatidia with slightly convex lenses. Ocelli absent. Posterior and anterior tentorial grooves not recognizable externally.

Tentorium with widely separated nearly parallel anterior and posterior arms, the latter connected by a thin tentorial bridge slightly curved in the middle region. Posterior arms broad and flattened, with large surface for muscle attachment, shorter than anterior and dorsal arms. Elongated anterior arms fairly thin, round in cross-section, mesally connected with apical part of posterior arms,

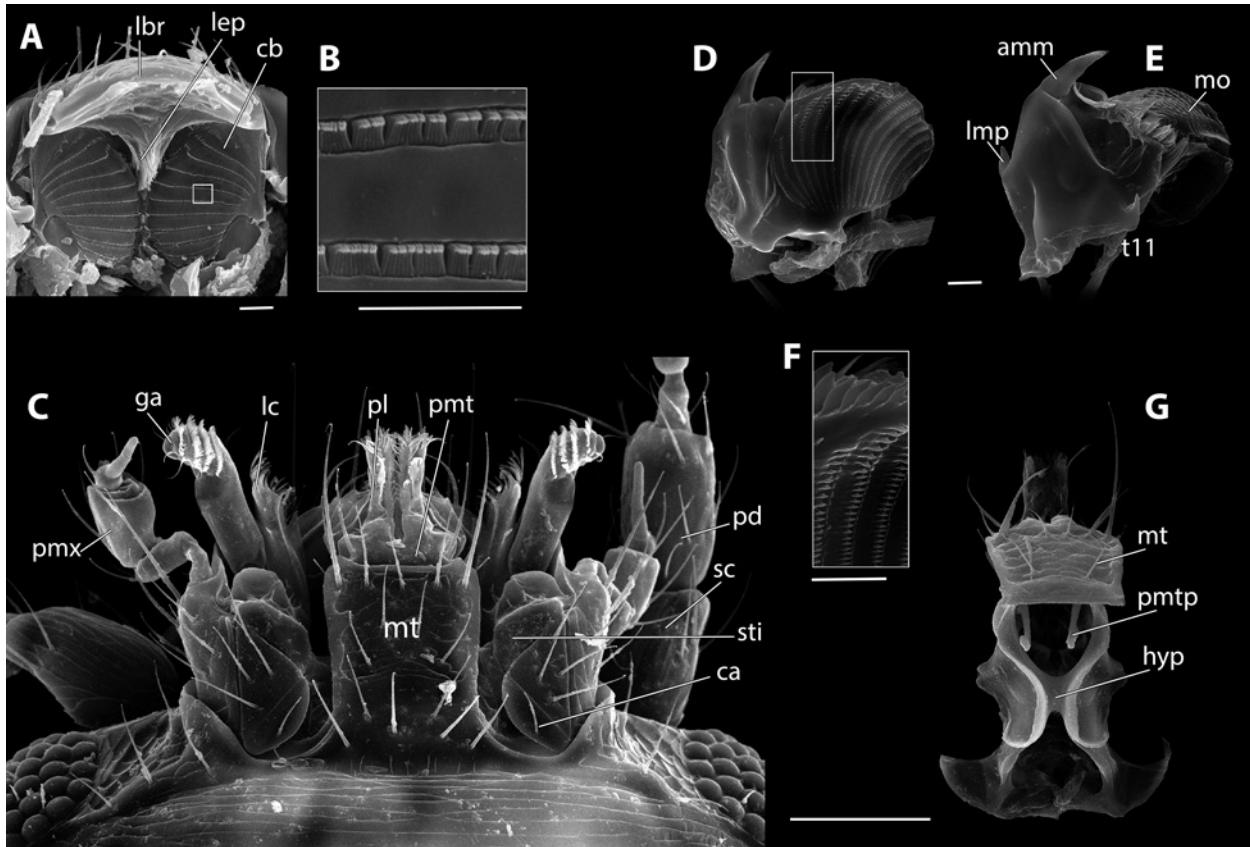


Fig. 2. *Acrotrichis sericans*, mouthparts, SEM micrographs. **A:** cibarial roof and epipharynx, ventral view; **B:** fragment of the cibarial roof; **C:** mouthparts, ventral view; **D:** mandible, dorsal view; **E:** mandible, ventral view; **F:** fragment of mola, dorsal view; **G:** labium and hypopharynx, ventral view. — **Abbreviations:** amm – anterior mandibular margin, ca – cardo; cb – cibarial roof, gal – galea, hyp – hypopharynx, lbr – labrum, lc – lacinia, lep – longitudinal epipharyngeal process, lmp – lateral mandibular peg, mo – mola, mt – mentum, pd – pedicellus, pl – palpus labialis, pmt – prementum, pmtp – premental process, pmx – palpus maxillaris, sc – scapus, sti – stipes, t11 – tendon of *M. craniomandibularis internus*. — Scale bar: A, B, D–F: 10 μm ; C, G: 50 μm .

slightly curved laterad towards anterior end. Dorsal arms of similar shape, originating on middle part of anterior arms, dorsally attached to head capsule (Fig. 3C).

Labrum approximately rectangular, movably attached to head capsule by internal membranous fold, apical edge rounded, exposing distal part of epipharynx. Pair of large grooves (sockets) fitting with lateral mandibular pegs (described below) present near lateral labral base. Covered with ca. 24 setae, two of which (on dorsal edge) are twice as long as the others. Surface structure fairly smooth. **Musculature** (Fig. 3B): M7 – *M. labroepipharyngalis* (0lb5 of WIPFLER et al. 2011), two pairs of short parallel bundles, Origin (O): posterior margin of dorsal wall of labrum, Insertion (I): paramedially on epipharynx; M9 – *M. frontoepipharyngalis* (0lb2), well-developed, O: posterior frons, I: with tendon on tormae, near posterior corners of labrum.

Antennae 11-segmented, widening towards apex with a 2-segmented club. Slightly less pigmented than head capsule. Scapus and pedicellus large and cylindrical, much larger than proximal flagellomeres (Fig. 2C). Scapus with broad ventral notch on apical margin, pedicellus with small anterior notch on apical margin. Flagellomere 1 short and ovoid; flagellomeres 2–6 cylindrical; flagellomere 7 distinctly widened, 10 and 11 wider and longer

than all other flagellomeres. All antennomeres with long, thin setae, the apical two each with several bundles of shorter and thicker digitiform sensilla. **Musculature** (Fig. 3C,D): M1 – *M. tentorioscapalis anterior*, O: proximal part of anterior arms and ventral surface of posterior arms, I: ventrally on base of scapus with a long tendon, M2 – *M. tentorioscapalis posterior*, two bundles merging on a common tendon, O: proximolateral surface of posterior tentorial arms, I: very close to M1; M4 – *M. tentorioscapalis medialis* (0an4), antagonist of M1 and M2, O: distal half of lateral surface of dorsal tentorial arms, I: posterodorsal scapal base.

Mandibles distinctly retracted, symmetrical, short and broad, almost completely concealed by labrum (Fig. 2D,E). Molae large, flattened, enclosing longitudinal epipharyngeal process (LEP); connected with mandibular body by membranous zone, not firmly fused with it; dorsal molar surface parallel to cibarial roof, with parallel transverse rows of posteriorly directed microtrichia, corresponding with very similar structures of the epipharyngeal surface (Fig. 2F). Anterior mandibular margin slightly elongated. Prostheca present, ventro-mesally oriented. Distinct peg at lateral margin (lateral process) present as part of labral locking device (Fig. 2E). Mesal molar surface differentiated into several areas with

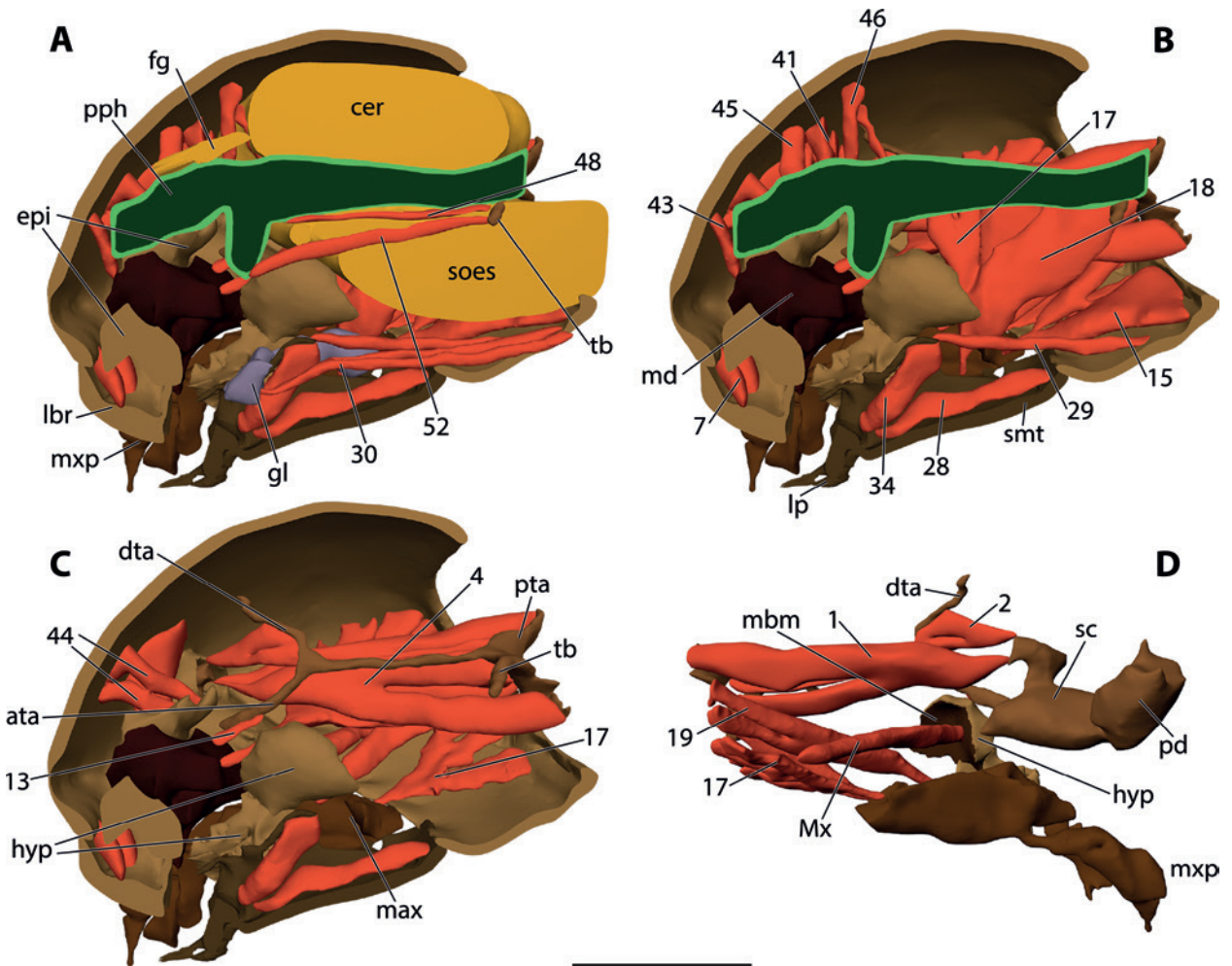


Fig. 3. *Acrotrichis sericans*, 3D reconstruction. **A–C:** sagittal sections; **D:** antennal and maxillary muscles, lateral view. — **Abbreviations:** ata – anterior tentorial arm, cer – cerebrum, dta – dorsal tentorial arm, epi – epipharynx, fg – frontal ganglion, gl – gland, hyp – hypopharynx, lbr – labrum, max – maxilla, mbm basal membrane of maxilla, mxp – maxillary palp, pd – pedicellus, pph – prepharynx, sc – scapus, smt – submentum, soes – suboesophageal ganglion, tb – tentorial bridge. Musculature: Mx – M. craniobasimaxillaris, 1 – M. tentorioscapalis anterior, 2 – M. tentorioscapalis posterior, 4 – M. tentorioscapalis medialis, 7 – M. labroepipharyngalis, 15 – M. craniocardinalis, 17 – M. tentoriocardinalis, 18 – M. tentoriostipitalis, 19 – M. craniolacinalis, 28 – M. submentopraementalis, 29 – M. tentoriopraementalis inferior, 30 – M. tentoriopraementalis superior, 34 – M. parentopalpalis externus, 41 – M. hypopharyngealis, 43 – M. clypeopalatalis, 44 – M. clypeobuccalis, 45 – M. frontobuccalis anterior, 46 – M. frontobuccalis posterior, 48 – M. tentoriobuccalis anterior, 52 – M. tentoriopharyngalis. — Scale bar 0.2 mm.

different surface properties: small smooth central area surrounded by several rows of prominent grinding cones and rows of trichomes (Fig. 2E). **Musculature:** M11 – M. craniomandibularis internus (0md1), largest head muscle, O: dorsolateral and lateral areas of posterior head capsule, I: adductor tendon; M12 – M. craniomandibularis externus (0md2), moderately large, O: lateral areas of posterior head capsule, I: lateral mandibular base; M13 – M. tentoriomandibularis (0md3), very thin, accompanied by a very indistinctly visible nerve, O: anterior tentorial arm, I: dorsally on base of mandible (Fig. 3C).

Maxillae composed of cardo, stipes, galea, lacinia and 4-segmented palp (Fig. 2C). Cardo and stipes triangular, distinctly separated from each other, with one long seta (10 µm) each. Maxillary palp 4-segmented; palpomere 3 much thicker than other segments, oval, with three long setae and several folds on apical margin; palpomere 4 long and slender. Galea moderately long and slender.

Distal part slightly bent outwards, with 4 parallel rows of curved microtrichia and several longer setae inserted on apical region. Lacinia much shorter and thinner; apical part with several bundles of setae of different length and a row of short teeth on lateral margin. **Musculature** (Fig. 3B–D): M15 – M. craniocardinalis (0mx1), O: ventromedially on posterior margin of head capsule, I: ventrolaterally on cardinal base; M17 – M. tentoriocardinalis (0mx3), composed of two subcomponents; M17a, O: posterior and anterior tentorial arm (two bundles), I: ventral surface of cardo; M17b, three bundles fused together into one tendon, O: posteroventral part of head capsule, I: ventral surface of cardo near M17a; M18 – M. tentoriostipitalis (0mx4): large, consists of two bundles that fuse into one tendon, O: anterior tentorial arm (2/3 of its length) very close to M17, I: ventral surface of stipes; M19 – M. craniolacinalis (0mx2), O: posterolateral part of head capsule, I: base of lacinia; Mx – M. craniobasi-

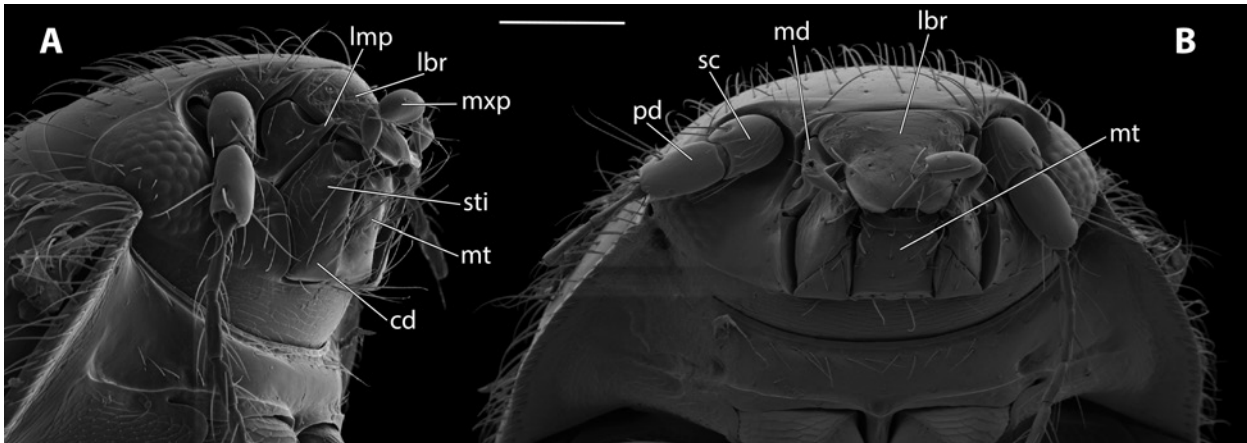


Fig. 4. *Nossidium pilosellum*, head, SEM micrographs. **A:** lateral view; **B:** ventral view. — **Abbreviations:** cd – cardo, lbr – labrum, lmp – lateral mandibular peg, md – mandible, mt – mentum, mx – maxilla, pd – pedicellus, sc – scapus. — Scale bar 0.2 mm.

maxillaris (ANTON & BEUTEL 2012): O: laterally on the genal region of the head capsule; I: membrane linked to maxillary base (Fig. 3D).

Labium. Mentum large, sclerotized, rectangular, posterior edge fused with anterior edge of the submental region of the head capsule; apical margin straight, with row of five long setae (Fig. 2C). Ten additional short setae scattered on surface of mentum. Prementum smaller and semimembranous, with asymmetrical angular anterolateral process. Two-segmented thin palps inserted on premental processes separated by narrow median gap (Fig. 2C); distal segment with row of short setae on inner side. Lateral walls of prementum transformed into pair of thin cylindrical processes to which M29 is inserted and which also serve as origin for M34 (Fig. 2G). **Musculature** (Fig. 3A,B): M28 – M. submentopraementalis (0la8), premental retractor, O: anterior surface of submentum, I: medially on posteroventral premental edge; M29 – M. tentoriopraementalis inferior (0la5), retractor, O: ventral part of posterior head capsule, I: posterior process of prementum; M30 – M. tentoriopraementalis superior (0la6), two long thin bundles fuse into one short tendon, O: ventral part of posterior head capsule near M29, I: posterior margin of prementum, on border with hypopharynx; M34 – M. praementopalpalis externus (0la14), O: ventral side of posterior process of prementum, I: basal margin of palpomere I.

Epipharynx. Anterior part, i.e. ventral labral wall, semimembranous, with sparse short microtrichia. Intermediate epipharyngeal part with well-developed longitudinal epipharyngeal process (LEP) formed by dense groups of microtrichia along midline (Fig. 2A). Posterior part connected with hypopharynx at attachment area of M. frontohypopharyngalis, posteriorly reaching anatomical mouth. Cibarial roof (cr) with 9 parallel transverse rows of posteriorly directed microtrichia that match with similar rows on dorsal mola surface. Several rows of longer trichia present between two sides of cibarial roof (Fig. 2B). **Musculature:** M43 – M. clypeopalatalis (0ci1); O: frontoclypeal region, I: posterior medial region of epipharynx; M44 – M. clypeobuccalis, two closely adjacent

thick bundles, O: frontoclypeal region I: posterolateral region of epipharynx (Fig. 3B,C).

Hypopharynx fused with anterior labium. Anterior part sclerotized, V-shaped in cross-section, continuous with short dorsal premental wall (Fig. 3C). Posterior hypopharynx laterally connected with posterior epipharyngeal part (see epipharynx), thus forming prepharyngeal tube, adjacent with ventral edge of anatomical mouth. **Musculature** (Fig. 3B): M41 – M. hypopharyngalis (0hy1), O: frons, I: laterally on epipharynx and M43, with short thin tendon. M42 – M. tentoriohypopharyngalis (0hy3), absent. Transverse hypopharyngeal muscle absent.

Pharynx almost circular in cross-section, with decreasing diameter towards its posterior end (Fig. 3A). Pharyngeal wall quite thin. Oesophagus separated from pharynx by thin transverse fold. **Musculature** (Fig. 3B): M45 – M. frontobuccalis anterior (0bu2), one bundle; M46 – M. frontobuccalis posterior (0bu3), three thin bundles, O: anterior part of frontal region, I: dorsolaterally on pharynx, directly posterior to frontal ganglion; M48 – M. tentoriobuccalis anterior (0bu5), unpaired muscle between tritocerebral commissure and suboesophageal ganglion, O: anteriomedially on tentorial bridge, I: medially on ventral pharynx; M51 – M. verticopharyngalis absent; M52 – M. tentoriopharyngalis (0ph2), O: tentorial bridge, I: ventral pharyngeal wall; M68 – M. anularis stomodaei (0st1), present; M69 – M. longitudinalis stomodaei (0st2) absent.

Pair of relatively large **glands** associated with labium, adjacent to each other over most of their length; open on dorsolateral corners of posterior hypopharynx; secretions released into preoral cavity (Fig. 3A).

3.2. Ptiliinae: Ptenidiini

Nossidium pilosellum

Body length 1.1–1.2 mm; head 0.37 mm wide.

Antenna 10-segmented, with 2-segmented club. Labrum trapezoidal. Grooves of labral locking mechanism

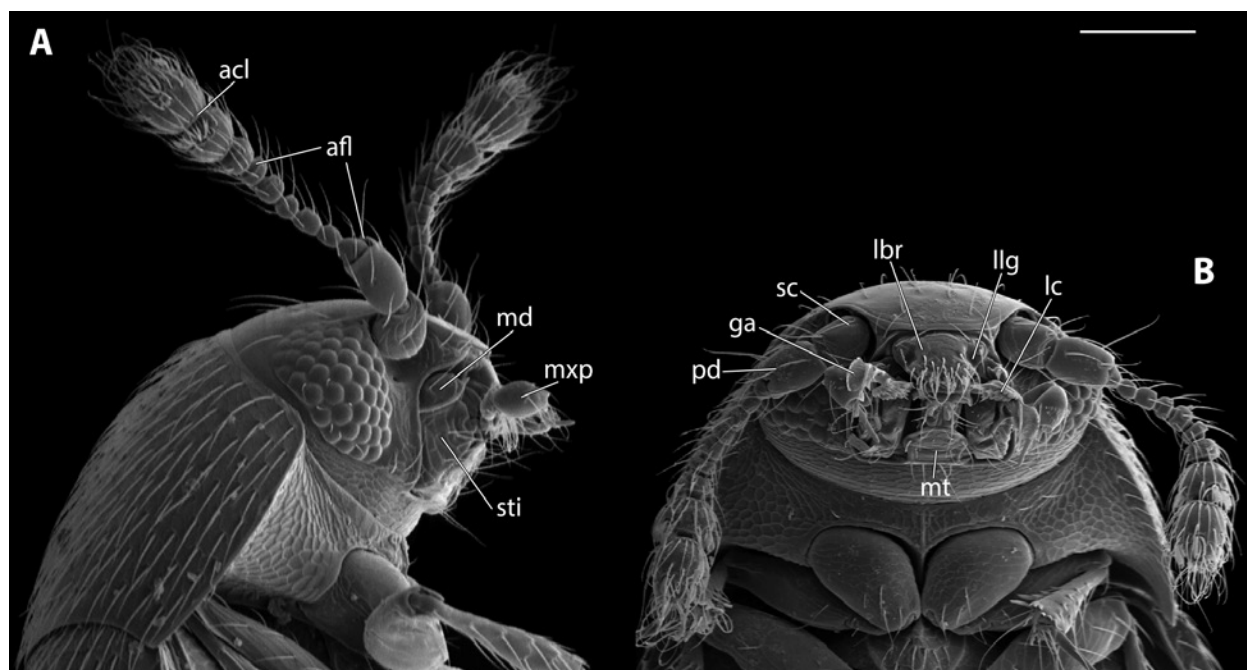


Fig. 5. *Porophilla mystacea*, head, SEM micrographs. **A:** lateral view; **B:** ventral view. — **Abbreviations:** acl – antennal club, afl – antennal flagellum, ga – galea, lbr – labrum, lc – lacinia, llg – lateral labral groove, lp – labial palp, md – mandible, mt – mentum, pd – pedicellus, sc – scapus, sti – stipes. — Scale bar 25 μ m.

quite indistinct, but lateral mandibular pegs long and pointed. Stipes also with small pointed process on distal margin. Mentum large, sclerotized, rectangular, posterior edge fused with anterior edge of submental region (Fig. 4).

3.3. Ptiliinae: Nanosellini

Porophilla mystacea

Body length 0.55–0.6 mm (Fig. 1C).

External features of head capsule. Head inclined, subprognathous, broad (maximum width 0.13 mm) and laterally rounded, not flattened (Fig. 5). Coloration light brown with darker regions along edges of head capsule. Cuticle with regular scale-like reticulation on ventral side. Sutures absent. Clypeus and gula not separated by ridges from rest of head capsule (Fig. 5A). Frontal region sparsely covered with erect setae of medium length (0.02–0.05 mm). Compound eyes large and round, only slightly protruding, consisting of ~ 45 ommatidia with strongly convex lenses (Fig. 5B). Ocelli absent. Posterior and anterior tentorial grooves not recognizable externally.

Tentorium distinctly simplified, lacking dorsal arms and laminatentoria, with widely separated, nearly parallel posterior and anterior arms (Fig. 5B). Tentorial bridge connects widely separated posterior arms, curved in middle region. Posterior arms strongly developed but short, broad and flattened, with large surface for muscle attachment. Elongated anterior arms distinct but fairly thin, round in cross-section, connected to apical part of pos-

terior arm, slightly curved laterad towards anterior end.

Labrum of trapezoidal shape, moveably attached to head capsule by internal membranous fold (Figs. 5B, 6D). Pair of large grooves (sockets) fitting with lateral mandibular pegs (described below) present near lateral labral base (Fig. 5B). Three setae inserted in posterior corner, one directly above grooves on distinct tubercle; several dense rows of setae present on central and anterior region. Surface structure similar to that of ventral side of head capsule. **Musculature:** M7 – M. labroepipharyngalis (0lb5), O: posterior margin of dorsal wall of labrum, I: paramedially on epipharynx (Figs. 6A, 7B); M9 – M. frontoepipharyngalis (0lb2), retractor of labrum, O: posterior frons, I: with short tendon on tormae, near posterior corners of labrum (Fig. 6D, 7A).

Antennae 11-segmented, with 2-segmented club (Fig. 5A). Scapus and pedicellus large and cylindrical, much larger than proximal flagellomeres; pedicellus with small notch anteriorly on apical margin. Flagellomere 1 short and conical, narrowing distally, 2 ovoid; flagellomeres 3–10 pedunculate, with visible narrowed basal part; 3 cylindrical, with straight distal edge; flagellomeres 4–7 short, cup-shaped, 7 distinctly widened apically. All antennomeres with long thin setae, apical two with several bundles of shorter and thicker digitiform sensilla. **Musculature** (Figs. 6C, 7B–F): M. tentorioscapalis, 3 adjacent bundles with same insertion site on ventral scapal margin. O: anterior and posterior tentorial arms.

Mandibles distinctly retracted, slightly asymmetrical, short and compact (Fig. 6B–D). Molae large, with several teeth, slightly extended dorsad, enclosing longitudinal epipharyngeal process (LEP) between them; connected with mandibular body by membranous zone, not firmly

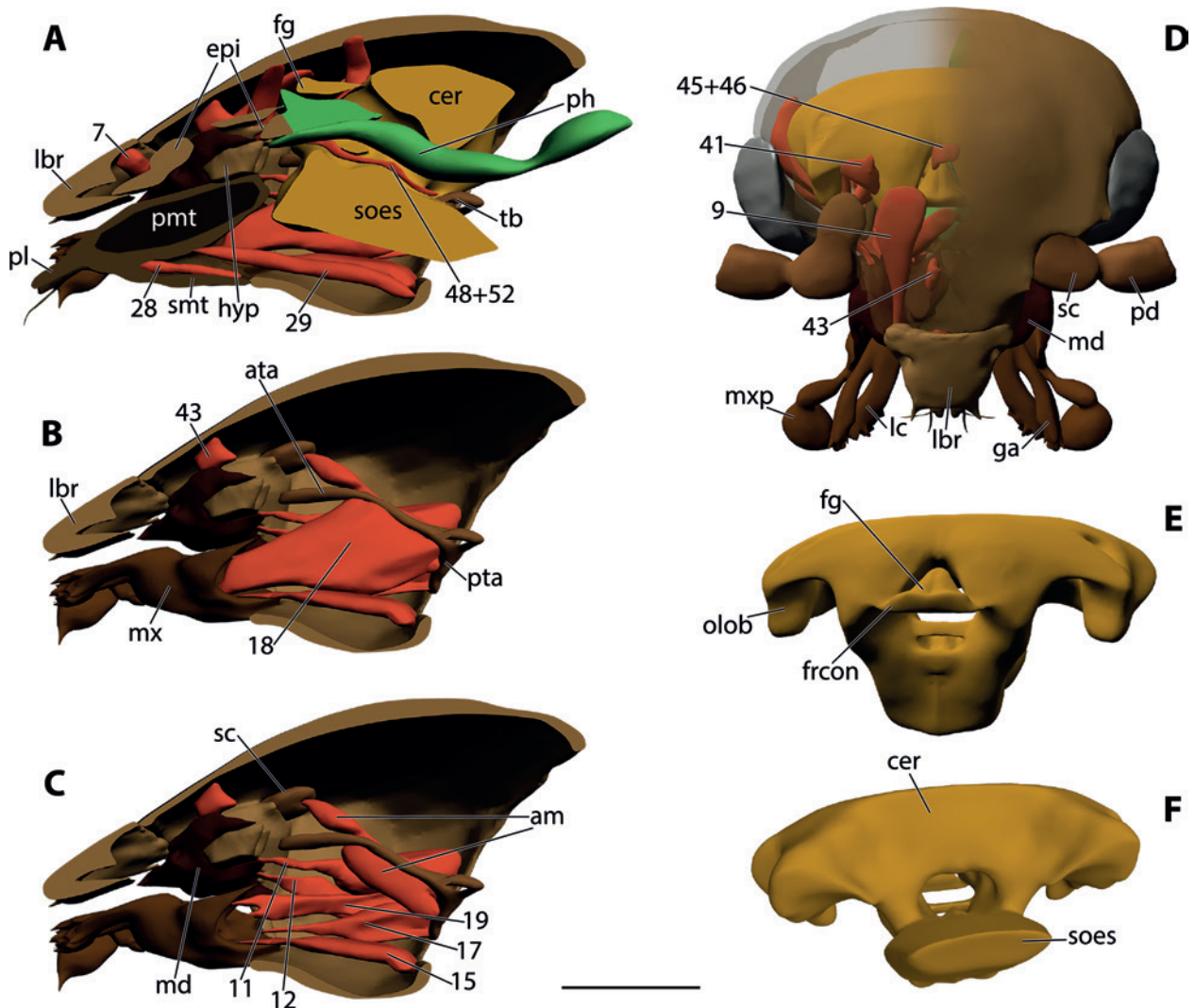


Fig. 6. *Porophilla mystacea*, 3D reconstruction. **A–C**: sagittal sections, **D**: frontal view, **E,F**: brain and suboesophageal ganglion, **E**: anterior view, **F**: posterior view. — **Abbreviations**: ata – anterior tentorial arm, cer – cerebrum, epi – epipharynx, fg – frontal ganglion, frcon – frontal connective, ga – galea, hyp – hypopharynx, lbr – labrum, lc – lacinia, md – mandible, mx – maxilla, olob – optic lobe, pd – pedicellus, pmt – prementum, pta – posterior tentorial arm, sc – scapus, smt – submentum, soes – suboesophageal ganglion. Musculature: am – antennal muscle M. tentorioscapalis, 7 – M. labroepipharyngalis, 9 – M. frontoepipharyngalis, 11 – M. craniomandibularis internus, 12 – M. craniomandibularis externus, 15 – M. craniocardinalis, 17 – M. tentoriocardinalis, 18 – M. tentoriostipitalis, 19 – M. craniolacinalis, 28 – M. submentopraementalis, 29 – M. tentoriopraementalis inferior, 41 – M. hypopharyngealis, 43 – M. clypeopalatalis, 45+46 – M. frontobuccalis anterior and M. frontobuccalis posterior, 48+52 – M. tentoriobuccalis anterior and M. tentoriopharyngalis. — Scale bar 50 μ m.

fused with it; insertion slightly different on left and right mandible; dorsal molar surface parallel to cibarial roof (Fig. 7B,C). Anterior mandibular margin slightly elongated and curved, without any prominent apical teeth. Distinct peg present at lateral margin (lateral process), pointing towards labral surface, closing preoral cavity tightly when interlocked with posterolateral labral grooves. Condyle of ventral mandibular joint large, bulb-shaped; dorsal joint with mandibular groove (Figs. 6D, 7C). **Musculature** (Figs. 6C, 7C,D): M11 – M. craniomandibularis internus (Omd1), largest head muscle, O: dorsolateral and lateral areas of posterior head capsule, I: adductor tendon; M12 – M. craniomandibularis externus (Omd2): moderately large, O: lateral areas of posterior head capsule, I: abductor tendon; M13 – M. tentoriomandibularis (Omd3) not recognizable.

Maxillae composed of cardo, stipes, galea, lacinia and 4-segmented palp (Fig. 5). Cardo and stipes triangular, distinctly separated from each other, each with one long seta (10 μ m). Palpifer not distinct, maxillary palp 4-segmented; palpomere 3 much thicker than other segments, oval, with stout apical sensilla and several long setae; lateral surface with several sparse rows of microtrichia; palpomere 4 long and slender. Galeae moderately long, slender, fimbriate, with 3 parallel rows of short, curved microtrichia inserted on apical region. Basistipes and mediostipes fused; lacinia separated from stipes by thin fold, barely reaching base of apical part of galea; distal part of lacinia with several rows of teeth and short setae. **Musculature** (Figs. 6B,C, 7D–F): M15 – M. craniocardinalis (Omx1), O: ventromedially on posterior margin of head capsule, I: ventrolaterally on cardinal base; M17 –

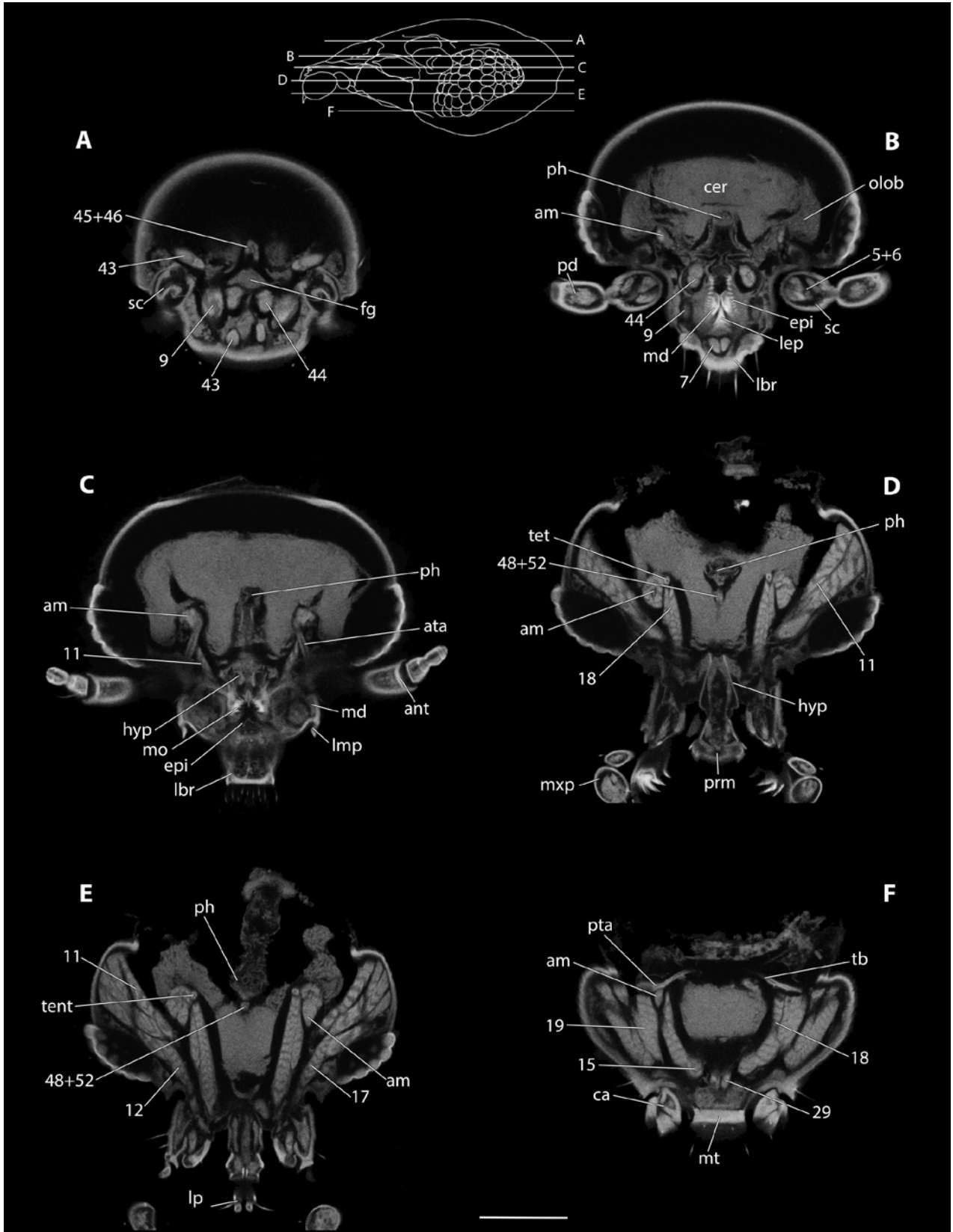


Fig. 7. *Porophilla mystacea*, CLSM digital sections of different planes of the head. — **Abbreviations:** ata – anterior tentorial arm, ca – cardo, cer – cerebrum, epi – epipharynx, fg – frontal ganglion, hyp – hypopharynx, lbr – labrum, lep – longitudinal epipharyngeal process, Imp – lateral mandibular peg, md – mandible, mo – mola, mt – mentum, mxp – maxillary palp, pd – pedicellus, ph – pharynx, prm – prementum, pta – posterior tentorial arm, sc – scapus, tb – tentorial bridge. Musculature: am – antennal muscle M. tentorioscapalis, 7 – M. labroepipharyngalis, 9 – M. frontoepipharyngalis, 11 – M. craniomandibularis internus, 12 – M. craniomandibularis externus, 15 – M. craniocardinalis, 17 – M. tentoriocardinalis, 18 – M. tentoriostipitalis, 19 – M. craniolacinalis, 29 – M. tentoriopraementalis inferior, 43 – M. clypeopalatalis, 44 – M. clypeobuccalis, 45+46 – M. frontobuccalis anterior and M. frontobuccalis posterior, 48+52 – M. tentoriobuccalis anterior and M. tentoriopharyngalis. — Scale bar 50 μ m.

M. tentoriocardinalis (0mx3), O: posterior tentorial arm, I: ventral surface of cardo; M18 – *M. tentoriostipitalis* (0mx4): very large, O: anterior tentorial arm (2/3 of its length) and ventral surface of posterior arm very close to M17, I: ventral surface of stipes; M19 – *M. craniolacinalis* (0mx2), O: posterolateral part of head capsule, I: base of lacinia, with a short tendon; Mx: absent.

Labium composed of submental region, mentum and prementum; submentum not recognizable as separate element, posteriorly fused with gular area and laterally with genal region (Fig. 6A). Mentum large, sclerotized, movably connected with anterior submental edge; apical margin rounded with two lateral pairs of setae (Fig. 5B). Prementum small and semimembranous, with asymmetrical angular lateral process at anterior edge. Palps inserted on premental processes, separated by narrow median gap; relatively small, cylindrical, indistinctly subdivided into two palpomeres; distal segment with two long and thick setae inserted on basal part. **Musculature** (Figs. 6A, 7F): M28 – *M. submentopraementalis* (0la8), paired premental retractor, O: posterolateral corners of submentum, I: medially on posteroventral premental edge; M29 – absent; M30 – *M. tentoriopraementalis superior* (0la6), O: ventral part of posterior head capsule, I: on posterior margin of prementum.

Epipharynx divided into anterior part equivalent with ventral labral wall, intermediate section with longitudinal process (LEP), and posterior part connected with posterior hypopharynx and reaching anatomical mouth posteriorly (Fig. 6A,D, 7B,C). Anterior part largely semimembranous, devoid of recognizable surface structures; lateral sclerotized strengthening rods anteriorly continuous with spike-like processes of anterolateral labral margin. Intermediate epipharyngeal part with well-developed longitudinal epipharyngeal process (LEP) formed by dense groups of microtrichia along midline (Fig. 7B). Complex posteriormost epipharyngeal part connected with intermediate region by lateral rod-like sclerotizations; firmly connected with hypopharynx at attachment area of *M. frontohypopharyngalis*; in dorsal view with large anteriorly rounded lateral projections and small, triangular process in deep anteromedian incision; large paired deep concavities form insertion site of *M. clypeobuccalis* (Fig. 7B); small posterolateral projection present above attachment site of *M. frontohypopharyngalis*; posteromedian cone-like extension seemingly with narrow connection to anteriormost dorsal wall of pharynx, below anterior part of frontal ganglion (Fig. 6D). **Musculature** (Fig. 6B,D): M43 – *M. clypeopalatalis* (0ci1), O: frontoclypeal region, I: posterior medial region of epipharynx; M44 – *M. clypeobuccalis*, consists of two closely adjacent bundles (not reconstructed separately), O: frontoclypeal region I: posterolateral region of epipharynx.

Hypopharynx fused with anterior labium and forming complicated three-dimensional structure with posterior epipharynx (Figs. 6C, 7C,D). Anterior part sclerotized, V-shaped in cross-section, continuous with short dorsal premental wall. Posterior hypopharynx laterally connected with posterior epipharyngeal part (see epipharynx),

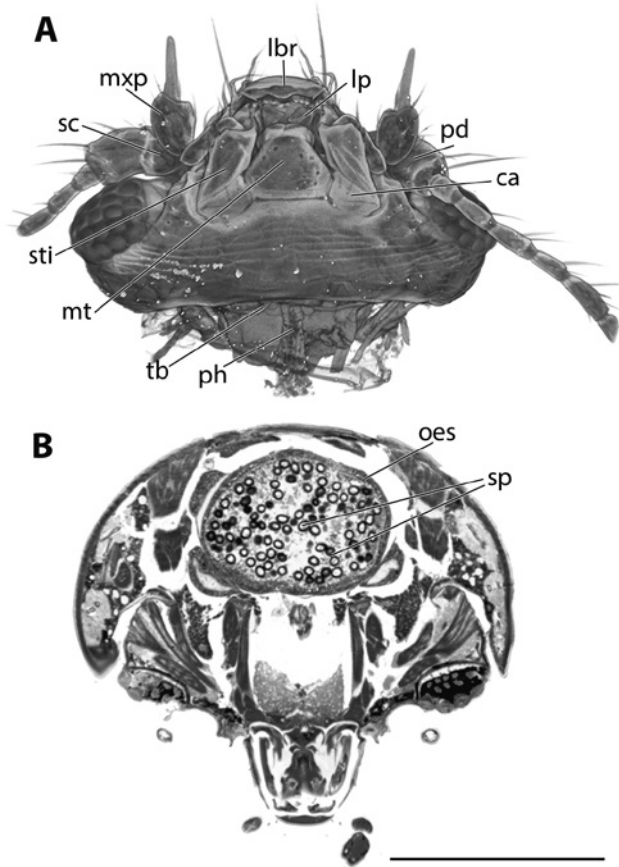


Fig. 8. *Mikado* sp., head. **A:** volume rendering based on CLSM data; **B:** LM micrograph of a transverse histological section through the head and pronotum. — **Abbreviations:** ca – cardo, lbr – labrum, lp – labial palp, mxp – maxillary palp, oes – oesophagus, pd – pedicellus, ph – pharynx, sc – scapus, sp – fungal spores, sti – stipes, tb – tentorial bridge. — Scale bar 0.1 mm.

reaching ventral edge of anatomical mouth. **Musculature:** M41 – *M. hypopharyngalis* (0hy1), O: frons, I: laterally on epipharynx and M43, with short tendon; M42 – *M. tentoriohypopharyngalis* (0hy3), absent. Transverse hypopharyngeal muscle absent.

Prepharynx present as short closed tube, formed by posterior epi- and hypopharynx; anteriorly continuous with preoral cavity between anterior epipharynx, paired mouthparts and anterior labium.

Pharynx almost circular in cross-section anteriorly but flattened towards foramen occipitale, with longitudinal folds for muscle attachment (Fig. 6A). Pharyngeal wall thin. Oesophagus separated from pharynx by thin transverse fold. **Musculature** (Fig. 6D): M45 – *M. frontobuccalis anterior* (0bu2) (and probably M46 – *M. frontobuccalis posterior* (0bu3), several thin closely adjacent bundles (not reconstructed separately), O: anterior part of frontal region, I: dorsolaterally on pharynx, directly posterior to frontal ganglion; M51 – *M. verticopharyngalis* absent; M52 – *M. tentoriopharyngalis* (0ph2), O: tentorial bridge, I: ventral pharyngeal wall; M68 – *M. annularis stomodaei* (0st1), present; M69 – *M. longitudinalis stomodaei* (0st2) absent.

Cephalic central nervous system and stomatogastric nervous system mainly composed of brain, suboesopha-

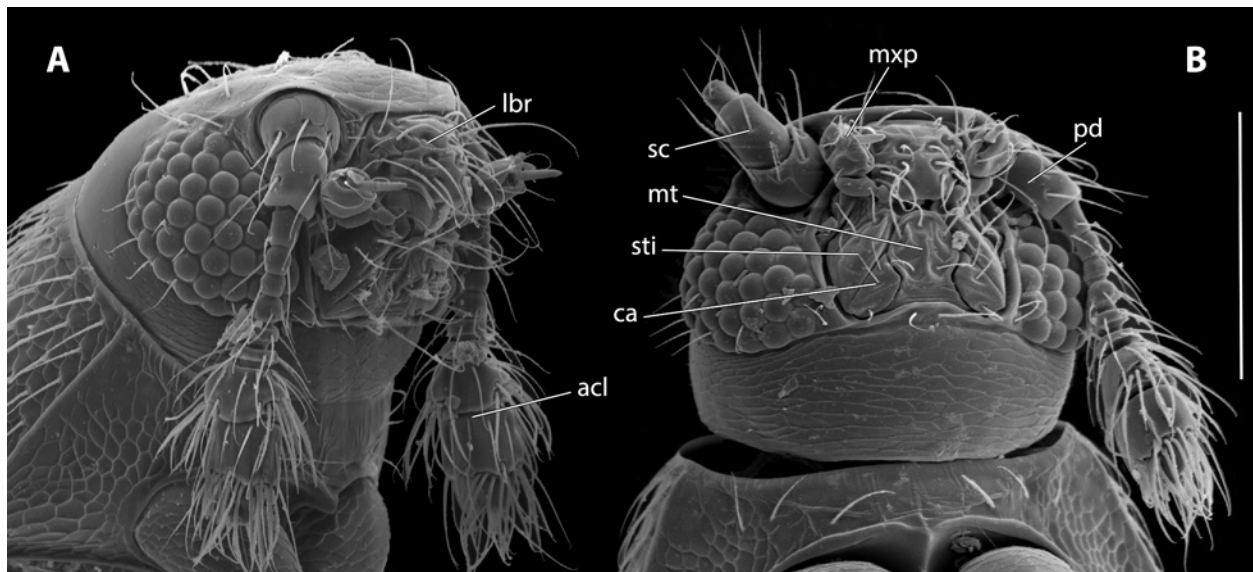


Fig. 9. *Nanosella russica*, head, SEM micrographs. **A:** lateral view; **B:** ventral view. — **Abbreviations:** acl – antennal club, ca – cardo, lbr – labrum, mt – mentum, mxp – maxillary palp, pd – pedicellus, sc – scapus, sti – stipes. — Scale bar 50 μ m.

geal ganglion and frontal ganglion (Fig. 6E,F). Brain large in relation to head size, located in posterior part of head and anterior prothorax; protocerebrum with large central body, corpora pedunculata, distinctly recognizable protocerebral bridge and well-developed optic lobes. Suboesophageal ganglion in posterior part of head almost fused with prothoracic ganglion (Fig. 6F). Frontal ganglion unusually large in relation to other parts, placed above anteriormost pharynx.

Cephalic glands not identified, probably missing.

The cephalic morphology and set of muscles of species of *Mikado*, *Nanosella* and *Scydosella* are similar to the conditions observed in *Porophilla*, but with the following distinguishing features:

Mikado sp.

Body length 0.4–0.45 mm, head width 0.16–0.17 mm (Figs. 1D, 8A).

All three antennal muscles (*M. tentorioscapalis*) present and well separated from each other.

Nanosella russica

Body length 0.4 mm, head width 0.09–0.1 mm. Head more compact, compound eyes larger, and more convex, with ~ 30 ommatidia (Figs. 9, 10A).

Antennae 10-segmented. Antennal musculature (Fig. 10D): three thin separate extrinsic muscles. M1 – *M. tentorioscapalis anterior* (0an1), O: ventrally on anterior tentorial arm (base and 2/3 of the length), I: medially on base of scapus; M2 – *M. tentorioscapalis posterior* (0an2), short and compact, O: anterior arm, dorsad and apicad of M1, I: dorso-laterally on scapal base; M4 – *M. tentorioscapalis medialis* (0an4), largest antennal muscle, antagonist of M1 and M2, O: ventral side of posterior

tentorial arms, I: with long tendon ventrally on scapal base.

Maxillary musculature (Fig. 10B,C): M15, M18 and M19 similar to *Porophilla*. M17 with shifted origin, O: postero-lateral wall of head capsule, I: ventral surface of cardo. Labial palps very short and with indistinct segmentation. M43 absent.

Scydosella musawasensis

Body length 0.32–0.35 mm, head width ~ 0.06 mm (Fig. 1E).

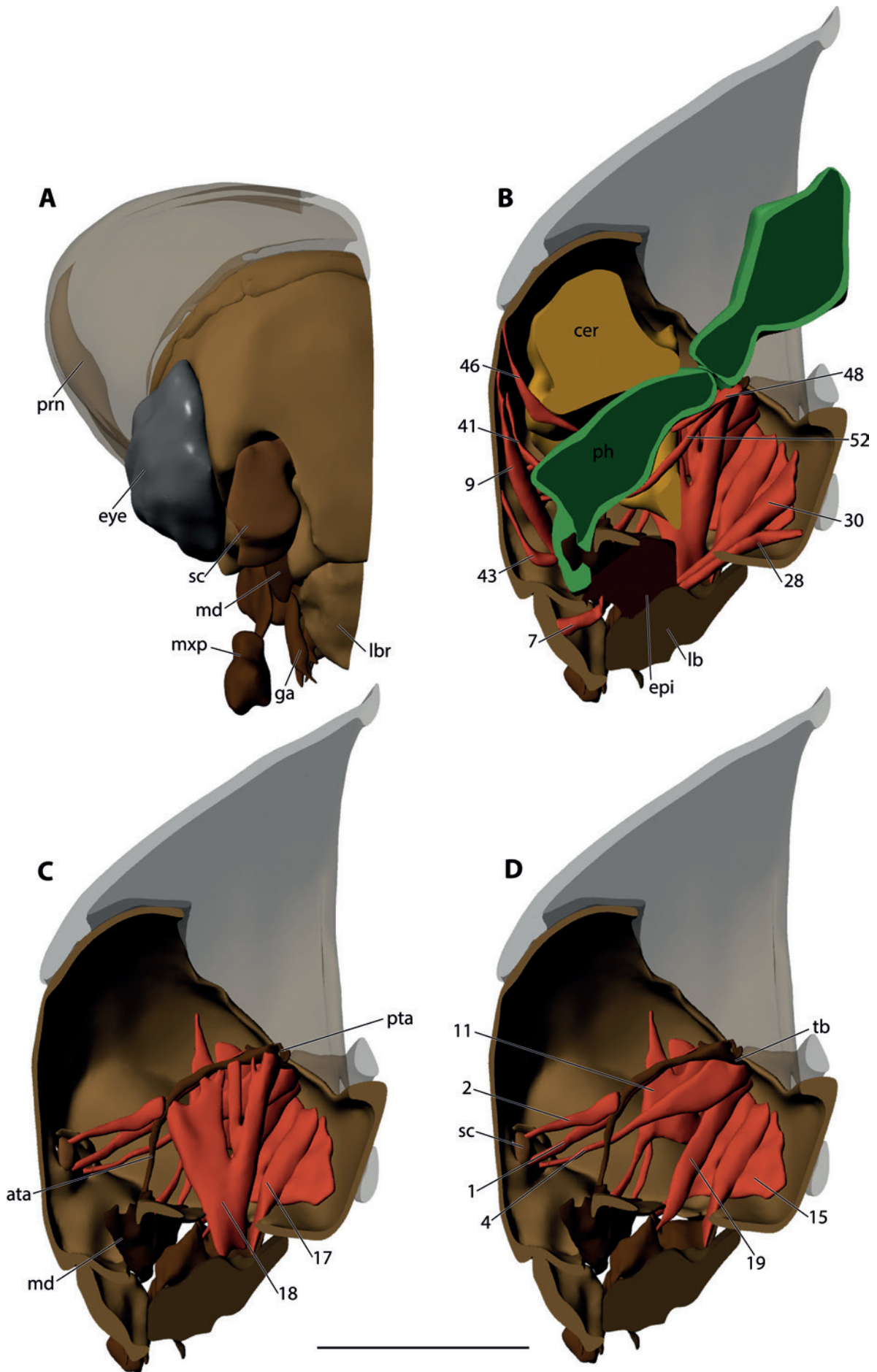
Compound eyes large, with 25–27 convex ommatidia (Fig. 11). Antenna 10-segmented. *M. tentorioscapalis*: only one bundle, like in *Porophilla mystacea*. Mentum distinctly separated from submental region of head capsule; labial palps scarcely recognizable. Muscle set: see Table 1.

4. Discussion

4.1. Phylogenetic interpretations

The cephalic morphology of Ptiliidae is affected by three different but interrelated phenomena, the phylogenetic background, i.e. the sistergroup relationship with Hydraenidae within large clades Staphylinoidea and Staphyliniformia, functional constraints linked with the specific feeding habits, and finally different degrees of miniaturization, with some species belonging to the smallest known beetles and free-living insects.

A potential synapomorphic feature of Staphyliniformia + Scarabaeoidea (or Staphyliniformia incl. Scarabaeoidea) (see MCKENNA et al. 2015) is a characteristi-



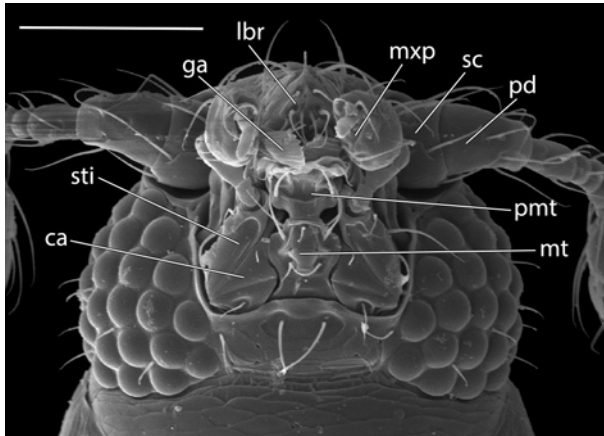


Fig. 11. *Scydosella musawasensis*, head, ventral view, SEM micrographs. — **Abbreviations:** ca – cardo, ga – galea, lbr – labrum, mt – mentum, mxp – maxillary palp, pd – pedicellus, sc – scapus, sti – stipes. — Scale bar 25 μ m.

cally modified hypopharynx, which appears hourglass-shaped in cross section. Another apomorphic feature of this lineage is the presence of an unusual extrinsic maxillary muscle, originating laterally on the head capsule and inserted on an internal membranous region proximad the mesal maxillary base (e.g. ANTON & BEUTEL 2004: Mx2; ANTON & BEUTEL 2012: M. craniobasimaxillaris). The former character is present in all examined species of Ptiliidae, whereas the latter is missing in some of them. Aside from these two derived features, Staphylinoidea are mainly characterized by plesiomorphic conditions of the adult head, with a character combination likely coming close to the groundplan of the entire Polyphaga (and arguably Coleoptera). Clubbed antennae have apparently evolved several or many times independently, as for instance in the primarily aquatic Hydraenidae, where they function as accessory breathing organs like in the non-related Hydrophiloidea (e.g. JÄCH et al. 2016; ARCHANGELSKY et al. 2016). A very unusual feature shared by Ptiliidae and their sistergroup Hydraenidae is the subdivision of the mandible, with a membranous connecting zone between the mandibular main body and the mesal molar part, apparently a synapomorphic condition. Another synapomorphy is a lateral process of the mandible, which is part of a unique mandibular-labral locking device (e.g. JÄCH et al. 2000; BEUTEL & LESCHEN 2005). Other common features of the mandibles of both families are the well-developed grinding mola and the prostheca, probably ancestral conditions retained from the groundplan of Polyphaga. Whether the weakly developed mandibular apex is a synapomorphy of the two families (BETZ et al. 2004; BEUTEL & LESCHEN 2005) is debatable. A fea-

ture of the maxilla shared by the two groups is the fimbriate galea with regularly arranged rows of curved microtrichia (BEUTEL & LESCHEN 2005). This condition has probably evolved independently in Hydrophiloidea (e.g. BEUTEL 1994) and some groups of Staphylinidae (BETZ et al. 2003), but it cannot be excluded that it is ancestral for Staphyliniformia, linked to primarily microphagous feeding habits.

Even though all species of Hydraenidae are small or very small (size range 0.8–3.3 mm; JÄCH et al. 2016), it is likely that an even stronger degree of miniaturization (size range 0.3–1.5 mm; HALL 2016) is an autapomorphy of Ptiliidae. Miniaturization can cause distinct modifications and rearrangements of organ systems (POLILOV 2015, 2016a). The very high degree of size reduction apparently had a considerable impact on the general morphology and also on cephalic structures. Ecdysial sutures and strengthening ridges are completely lacking. Whereas the former are generally missing in beetles, the absence of the latter is apparently linked with the extremely small size of the head, which makes mechanical reinforcement by internal ridges superfluous. The loss or partial reduction of the clypeofrontal suture is quite common in Coleoptera (e.g. LAWRENCE et al. 2011), whereas the absence of the ridge separating the gula from the head capsule and the lack of lateral delimitation of the postlabium are very unusual features. Correlation of the reduced cephalic sutures and ridges with miniaturization is indicated by the occurrence of the same derived condition in non-related groups with very small species (0.8–1.1 mm). This applies to Corylophidae (POLILOV & BEUTEL 2010; YAVORSKAYA & POLILOV 2016) and Clambidae (ANTON et al. 2016), but also to groups of Hymenoptera such as Mymaridae (POLILOV 2016b) or Trichogrammatidae (POLILOV 2016c, 2017), and also to other groups of insects with very small species (POLILOV 2016a).

An autapomorphy of Ptiliidae, which is possibly related with miniaturization, is the simplified structure of the tentorium, with thin and nearly parallel posterior and anterior arms and missing laminatentoria. Dorsal arms, as well as the laminatentorium, are present in the groundplan of the family (WEIDE et al. 2014) but missing in Nanosellini, the smallest representatives of the group (0.3–0.7 mm). In *Acrotrochis*, *Nephanes* and *Ptenidium* (0.6–1.1 mm) they are present but much shorter and slightly thinner than the anterior arms. A similar tendency was described for larvae and adults of Corylophidae, where the tentorium is more simplified in smaller representatives, and is completely absent in *Orthoperus* (0.8 mm) (pers. obs. M. Yavorskaya). Dorsal arms are

← **Fig. 10.** *Nanosella russica*, head, 3D reconstruction. **A:** frontal view, **B–D:** sagittal sections. — **Abbreviations:** ata – anterior tentorial arm, cer – cerebrum, epi – epipharynx, ga – galea, lb – labium, lbr – labrum, md – mandible, mxp – maxillary palp, ph – pharynx, pta – posterior tentorial arm, sc – scapus, tb – tentorial bridge. Musculature: 1 – M. tentorioscapalis anterior, 2 – M. tentorioscapalis posterior, 4 – M. tentorioscapalis medialis, 7 – M. labroepipharyngalis, 9 – M. frontoepipharyngalis, 15 – M. craniocardinalis, 17 – M. tentoriocardinalis, 18 – M. tentoriostipitalis, 19 – M. craniolacinalis, 28 – M. submentopraementalis, 30 – M. tentoriopraementalis superior, 41 – M. hypopharyngealis, 43 – M. clypeopalatalis, 46 – M. frontobuccalis posterior, 48 – M. tentoriobuccalis anterior, 52 – M. tentoriopharyngalis. — Scale bar 50 μ m.

Table 1. Musculature of saprophagous and sporophagous Ptiliidae, some other Staphyliniformia and Elateriformia (Clambidae) with similar feeding habits (partly based on ANTUNES-CARVALHO et al. 2016; BEUTEL & HAAS 1998, 2000; BETZ et al. 2003; POLILOV & BEUTEL 2009; WEIDE & BETZ 2009; WEIDE et al. 2010). The numbering of head muscles generally follows v. KELER (1963) (for Mx see text and ANTON & BEUTEL 2004). — **Abbreviations:** + – muscle present, – – muscle absent, ? – unknown condition, the number of bundles is given in some cases (instead of +).

Family	Genus	No. of muscle																											
		1	2	4	7	9	11	12	15	17	18	19	28	29	30	41	42	43	44	45	46	48	50	51	52	67	68	69	Mx
Ptiliidae	sporo	<i>Scydosella</i>	1	?	?	+	+	+	+	+	–?	?	+?	+?	+	+?	+	–	+	+	?	?	+?	–	–	+?	+	+	–
		<i>Mikado</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	–	–	+	+	3	+	–	–	+	+	+	–
		<i>Nanosella</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	–	–	+	+	?	+	–	–	+	+	+	–
		<i>Porophilla</i>	1	–	–	+	+	+	+	+	+	+	+	+	+	+	+	–	+	+	+	?	1	–	–	+	+	+	–
	sapro	<i>Acrotichis</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	–	+	2	+	+	+	–	–	+	+	+	+	+
		<i>Ptenidium</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	–	+	+	+	+	+	–	–	+	+	+	+	+
		<i>Nephanes</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	–	+	–	+	+	+	+	+	–	–	+	+	+	+
Leiodidae	<i>Catops</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	–	+	+	+	+	+	
Hydraenidae	<i>Ochthebius</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	?	–	–	+	?	?	?	–	
Hydrophilidae	<i>Helophorus</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	–	+	–	+	+	–	+	+	+	+	+	+	+	
Staphylinidae	<i>Aleochara</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	?	+	+	+	+	–	+	?	?	?	?	?	–	
	<i>Autalia</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	?	+	+	+	+	–	+	?	?	?	?	?	–	
	<i>Oligota</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	?	+	+	+	+	–	+	?	?	?	?	?	–	
	<i>Oxypoda</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	?	+	+	+	+	–	+	?	?	?	?	?	–	
	<i>Eumicrota</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	?	+	+	+	+	–	+	?	?	?	?	?	–	
	<i>Gyrophaena</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	?	+	+	+	+	–	+	?	?	?	?	?	–	
	<i>Homalota</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	?	+	+	+	+	–	+	?	?	?	?	?	–	
Clambidae	<i>Clambus</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	–	+	–	+	+	+	–	+	–	+	+	+	+	–	

also absent in adults of miniaturized Hymenoptera (POLILOV 2016b,c, 2017).

The configuration of the antenna of Ptiliidae is certainly autapomorphic, with large cylindrical scapus and pedicellus, and a flagellum which appears very slender in comparison. The plesiomorphic number of 11 antennomeres is preserved in the groundplan, but only 10 are present in Nanosellini, and a minimal number of 8 is reached in some Cephaloplectinae (SEEVERS & DYBAS 1943). Reduced numbers of antennomeres and palpomeres have been described for many minute insects (POLILOV 2016a) including Coleoptera, for instance in Hydroscaphidae (LAWRENCE et al. 2011), Corylophidae (POLILOV & BEUTEL 2010; YAVORSKAYA & POLILOV 2016) and in Clambidae (ANTON et al. 2016). However, reduced numbers can also occur in comparatively large beetles as for instance in Hydrophilidae (ARCHANGELSKY et al. 2016), and the full number is present in the very small Sphaeriusidae (LAWRENCE et al. 2011).

4.2. Effects of miniaturization

A general tendency towards simplification of major skeletal elements can be observed in very small beetles, where structural complexes like the head are simplified and compact but still maintain their functionality. This applies only to a lesser degree to the muscular system. Miniaturization apparently does not affect the general configura-

tion of the muscle set of the mouthparts in Ptiliidae, even though it can lead to reductions of subunits and fibers in single muscles. Even in the smallest known non-parasitic insect *Scydosella musawasensis*, the set of cephalic muscles does not show a distinct degree of reduction (Table 1). This suggests that minor differences to larger species may be due to the food preferences of extremely small ptiliids, rather than to effects of body size reduction. However, analyses of muscle variation between members of the family with different feeding habits also revealed a surprisingly homogenous picture. The set of muscles of saprophagous species is almost identical to the one in the spore-feeding Nanosellini (Table 1). Only the number of bundles of some of the head muscles can vary: only a single extrinsic antennal muscle is present in *Porophilla*, whereas the normal set of three muscles is present in *Mikado* and *Acrotichis*. The anterior prepharyngeal dilator M. clypeopalatalis (M43) is missing in *Mikado* and *Nanosella*, but is present in larger species, and also in the extremely small *Scydosella*. The number of bundles of M. frontopharyngalis posterior (M46) is also variable within the family. The variation of the unusual extrinsic maxillary muscle Mx is discussed below.

Miniaturization can lead to distinct changes in the nervous system of insects. Detailed investigation of the brain was not a goal of this work, but data are available for the ptiliid genera *Acrotichis* and *Nanosella* (MAKAROVA & POLILOV 2016a). Typical tendencies observed in the majority of micro-insects (MAKAROVA & POLILOV

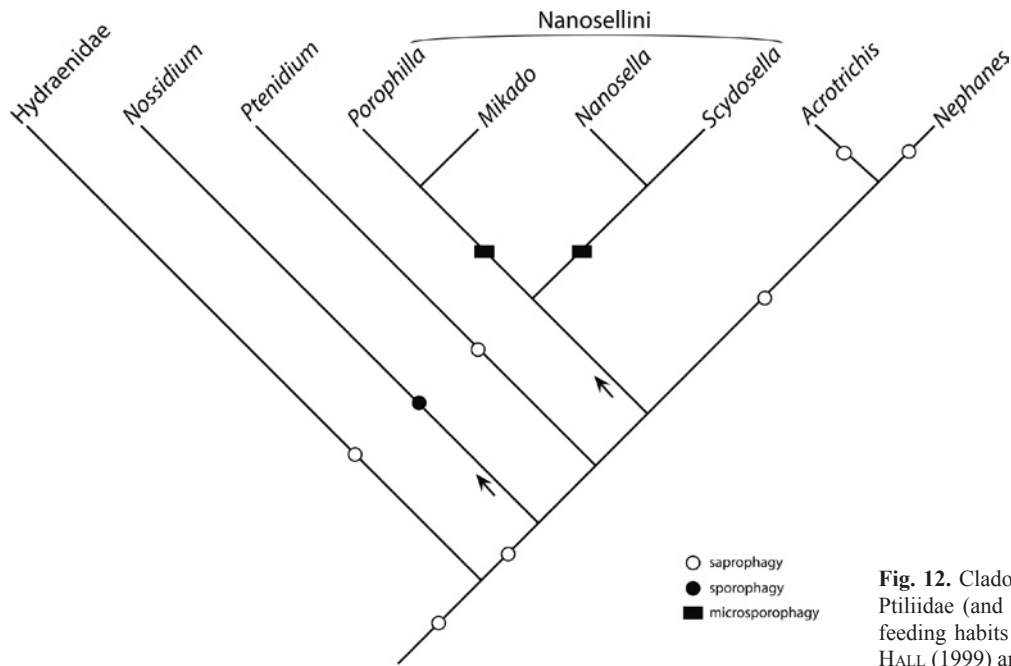


Fig. 12. Cladogram with selected taxa of Ptiliidae (and Hydraenidae as outgroup); feeding habits mapped on tree. Based on HALL (1999) and McKENNA et al. (2015).

2016a,b; POLILOV & MAKAROVA 2017) are also apparent in the examined Ptiliidae: macroscopic deformation of the brain, increase in size relative to the head capsule, partial shift into the prothorax, brain asymmetry, and fusion of the suboesophageal complex with the prothoracic ganglion.

4.3. Characters related to food uptake and shifts of feeding habits

The feeding apparatus of saprophagous, algophagous or sporophagous members of Myxophaga and Polyphaga is very complex (e.g., ANTON & BEUTEL 2004, 2006; ANTON et al. 2016; ANTUNES-CARVALHO et al. 2016) compared to that of predaceous Adepaga (e.g. DRESSLER & BEUTEL 2010; BEUTEL et al. 2017) or members of the “ancestral” Archostemata with largely unknown feeding habits (HÖRNSCHEMEYER & STAPF 2001; BEUTEL et al. 2008). It comprises epi- and hypopharyngeal longitudinal bulges set with microtrichiae, complicated mandibles with molae and brushes, and in some cases fimbriate galeae (see above). A noteworthy phenomenon observed in Ptiliidae is that the complexity of this apparatus is even increased, at least in some members of the family. Although sporophagy occurs in many species of Staphylinodea (BETZ et al. 2003), extremely small body size as it is typical for Ptiliidae apparently requires specific adaptations. In some cases, this apparently results in an increase in complexity rather than in simplification. The epipharynx, for instance, is more complicated than in examined species of related groups, such as Hydraenidae (JÄCH et al. 2000), Leiodidae (ANTUNES-CARVALHO et al. 2016), Staphylinidae (BETZ et al. 2003), or Hydrophilodea (ANTON & BEUTEL 2004). It is divided into an anterior part corresponding with the ventral labral wall, an intermediate section

with the longitudinal process (LEP), and a posterior part connected with the posterior hypopharynx and adjacent with the anatomical mouth. An additional feature in this context was observed in all examined ptiliid species, the composition of M44 of two thick bundles inserted in deep concavities of the epipharyngeal wall. The prementum bears slightly asymmetrical angular lateral processes at its anterior edge, separated by a narrow median gap. Another feature apparently unique to ptiliid beetles is the structure of the maxillary palp: palpomere 3 is much thicker and longer than the proximal two and often set with several rows of short microtrichia on its lateral surface, palpomere 4 is long, slender, and conical. It is likely that the palp with its specific modifications is involved in the process of collecting food particles.

Sporophagous feeding habits were assigned to the entire family Ptiliidae by some authors (BETZ et al. 2003). However, this specialization is in fact restricted to species of *Nossidium* (and presumably some closely related genera) and Nanosellini. All other representatives of the family should be considered as saprophagous.

Observations of living beetles (*Nephanes*, *Acrottrichis*) provided information about feeding preferences and feeding mechanisms of saprophagous ptiliid species. The beetles consumed rotten plant materials and mold, and collected droplets of condensed liquid on the walls of the petri-dish in which they were held. They also consumed liquid yeast solution and droplets containing mold spores. During the feeding process, regardless of the consistency of the substrate, the maxillary palp and galea are the main or even exclusive tools used for grasping and collecting food particles. The mandibles are concealed and apparently not involved in gathering food. Their main function is to push the food particles gathered by the galeae into the space between the molae with their elongate apical part. The substrate is processed between

the wide molar surfaces and presumably also between the molae and epipharyngeal lobes. The structures involved in these processes are very similar in the sporophagous Nanosellini. A rather surprising observation was that all spores in the oesophagus and anterior midgut appear intact (Fig. 8B). This suggests that they are not perforated and not noticeably deformed or broken by the activity of the molae. The function of these prominent structures is probably the transport of the substrate towards the prepharynx and anatomical mouth, and possibly cleaning of the distal maxillary elements and of the spores. Whether the minute molar surface structures leave very fine traces on the spore surface, which may facilitate infiltration of digestive enzymes, is presently unknown. In any case, a solid functional interpretation of the concerted activity of all involved complex and extremely small structural elements is a great challenge.

The sporophagous *Nossidium* likely belongs to the first branch separating from the remaining Ptiliidae (HALL 1999; MCKENNA et al. 2015) (Fig. 12). Although its species are strongly associated with *Polyporus squamosus* (spores $13 \times 4.5 \mu\text{m}$), they were also found on other Polyporaceae fungi and once on the agaric *Russula integra* (KILIAN & BURAKOWSKI 2000; NEWTON 1984). Due to lack of well-fixed material only external structures of *Nossidium pilosellum* could be examined. All its head features are similar to those of the other representatives of the family, including the lack of sutures and ridges, the presence of the lateral mandibular peg, and the labro-mandibular interlocking mechanism. Although *Nossidium* is sporophagous, its body size is much larger (1–1.1 mm) than in all known Nanosellini, and also the size of the spores it is feeding on. Despite the sporophagy of *Nossidium*, it is conceivable that this feeding type does not belong to the groundplan of Ptiliidae. It is found neither in the majority of this family, nor in its sister group Hydraenidae or, more generally, in closely related outgroup taxa (e.g. BEUTEL & LESCHEN 2005; MCKENNA et al. 2015). Most species of Agyrtae feed on dung, rotten fungi and similar decaying substances, and saprophagous feeding habits are also common in Leiodidae and Hydraenidae. This suggests that saprophagy is ancestral for Ptiliidae, and that feeding on spores evolved once in *Nossidium* (and probably some related genera), and independently in the distinctly smaller Nanosellini. Sporophagy as a groundplan feature of Ptiliidae cannot be completely excluded presently. However, it would imply that several ptiliid branches evolved saprophagy secondarily, which would be less parsimonious than the alternative.

The following features, previously described for spore-feeding Staphylinoida (summarized by BETZ 2003 for the first time), are present in all studied Ptiliidae and are also characteristic for some saprophagous beetles (e.g. ANTON & BEUTEL 2004; ANTON et al. 2016):

- cibarial roof with rows of parallel microtrichia
- galea with brushes and rows of long microtrichia, the main instrument for gathering spore masses and other food particles
- mandibles with well-developed molae

- epipharynx, prementum and hypopharynx with medial longitudinal bristle-troughs bordered by hairs or spines, involved in concentrating and directing the food stream in the median line (this and the previous feature are arguably groundplan characters of Coleoptera [BEUTEL et al. 2001; ANTON & BEUTEL 2004; ANTON et al. 2016; ANTUNES-CARVALHO et al. 2016] but a robust interpretation requires a robust inter-subordinal phylogenetic pattern, which is presently not available [e.g. MCKENNA et al. 2015]).

Our comparison of ptiliid species with saprophagous or sporophagous feeding habits surprisingly yielded only subtle differences in the involved cephalic structures. The galeae of saprophagous species usually bear 4 rows of longer setae and additional teeth on their apical end. In sporophagous species the setae are shorter and not arranged in rows in all cases. In *Scydosella* the apical part of the galea is flat and bears several parallel rows of short teeth, which are apparently better suited for gathering dry particles, whereas longer setae are used to filter and grasp moist clumps of mold, spores and rotting plant materials out of the half-liquid substrate.

An unusual maxillary muscle (Mx) consisting of one long bundle has been described earlier for some scarabaeoid representatives and for different staphyliniform beetles (ANTON & BEUTEL 2004, 2012; M. craniobasimaxillaris; BEUTEL et al. 2001, 2003; JÄCH et al. 2000; WEIDE & BETZ 2009). It was also found in all examined saprophagous Ptiliidae (Table 1). It originates laterally on the genal region and inserts on a membranous fold between the maxillary basis and the lateral hypopharyngeal wall. The precise function is unclear. Due to lack of suitable material the presence or absence in *Nossidium* could not be verified. However, our investigation revealed that it is probably generally absent in sporophagous Nanosellini.

Nanosellini is the ptiliid subgroup with extremely small species, most of them inhabiting basidiomycete fungi, particularly Polyporaceae and Steccherinaceae (DYBAS 1961; HALL 1999). Some of them can also inhabit Meripilaceae (Polyporales), Hymenochaetales (Schizoporaceae and Hymenochaetaceae) and Ascomycetes (Valsaceae) (POLILOV 2008). Their only source of food are fungal spores, with a size (diameter 2–6 μm) apparently compatible with the size of the mouthparts (approx. head width 50–130 μm). It is evident that their feeding mechanism differs distinctly from what is found in larger sporophagous staphylinids, where the mouthparts are at least hundred times larger than the spores. Therefore, it is appropriate to call their type of feeding microsporophagy. Although nanosellines preserve all main features of the feeding apparatus commonly found in larger spore-feeding staphylinoids (and also saprophagous ptiliids and saprophagous beetles of other families), they have evolved some new features to adjust to this modified feeding mode. The mandibles are more compact than those of larger ptiliid species, with a smaller molar surface more tightly attached to the main mandibular body. The un-

sual basal maxillary muscle Mx, which is usually present in staphyliniform beetles including saprophagous ptiliids, is missing. The extremely complicated epipharyngeal-hypopharyngeal structures could be also part of the adjustment to more specialized feeding habits.

Our study suggests that switches between saprophagy and more specialized sporophagous habits require only minimal modifications of the mouthparts and other involved cephalic structures, compared for instance with a change to predacious habits (e.g. DRESSLER & BEUTEL 2010). This makes switches between these feeding types relatively easy in Staphyliniformia and other groups of beetles. The most parsimonious explanation for the evolution of feeding habits in Staphylinioidea (based on phylogenetic patterns in MCKENNA et al. 2015) is to assume saprophagy for the groundplan of the superfamily and also Ptiliidae, and one secondary switch to sporophagy in *Nossidium* and related genera, and then another switch to microsporophagy in Nanosellini, in this case linked with extremely small size and life inside the fruiting bodies of basidiomycete fungi. In a possible alternative scenario feeding on spores would be ancestral for Ptiliidae, with reversal to saprophagy in several branches of the family. A solid phylogeny for the family will help to clarify this issue.

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