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The adult head of *Axymyia furcata* (Insecta: Diptera: Axymyiidae)

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Abstract

The external and internal cephalic morphology of males and females of *Axymyia furcata* is described and illustrated in detail. The documented features are compared with those of potentially related groups. *Axymyia* displays a number of apomorphic features of the adult head, like the subdivision of the compound eyes, the absence of several mucles (M. clypeolabralis, M. stipitopalpalis externus, M. palpopalpalis maxillae primus, Mm. palpopalpalis maxillae primus and secundus), the absence of both maxillary endites, and the loss of the salivary pump musculature (M. hypopharyngosalivarialis). Another apomorphic character is the origin of M. tentorioscapalis anterior on the head capsule. Some features are plesiomorphic and probably belong to the groundplan of Diptera: the orthognathous head, three ocelli, 5-segmented maxillary palps, 2-segmented labial palps transformed into medially fused labella, one premental retractor, a dense vestiture of microtrichia on all exposed parts of the head except the labrum, and the presence of an epipharyngeal food channel. The systematic position of Axymyiidae is discussed. Our findings do not provide support for the phylogenetic position of Axymyiidae.

Key words

Axymyiidae, Diptera, morphology, head, phylogeny, position.

1. Introduction

Axymyiidae are a poorly known group among the nematoceran lineages of Diptera. The family contains only eight described species, which are widely distributed throughout the Holarctic Region (Wihlm & Courtney 2011; Sinclair 2013). They are placed in three extant genera, *Axymyia* McAtee, *Mesaxymyia* Mamayev and *Protaxymyia* Mamayev & Krivosheina (Mamayev 1968). Additionally three fossil species are known from the Jurassic (Zhang 2010).

The larvae live in small, lotic habitats, including seeps, springs and streams (Wihlm & Courtney 2011). The diets of larvae and adults are unknown (Wihlm 2009). Very little is known about the biology of the family. Adults are considered as short-lived based on the greatly reduced mouthparts (Wood 1981). After Wihlm & Courtney (2011) they have a life span of 2 – 7 days. The size of the adults (5 – 8 mm wing length) and pupae is highly variable within species, but the mechanism of this polymorphism is still unclear (Wihlm & Courtney 2011).

Axymyia furcata was first described by McAtee (1921) and placed in Bibionidae. Shannon (1921) established a subfamily Axymyiinae and placed it in Anisopodidae, a concept which was later adopted by Alexander (1942). In other contributions other species of *Axymyia* were placed in Pachyneuridae or Bibionidae, respectively (Duda 1930; Ishida 1953). Mamayev & Krivosheina (1966) pointed out that the peculiar larval features suggest a more isolated lineage and consequently proposed a separate family Axymyiidae.

The phylogenetic relationships of Axymyiidae to the other nematoceran families is apparently one of the most persistent problems in "lower" dipteran systematics. Rohdendorf (1974) (informal non-Hennigian interpretation of morphological characters) placed Axymyiidae in Tipulomorpha as a part of Perissommatidae. Mamayev & Krivosheina (1966) (morphological characters of the larvae) and Wood & Borkent (1989) (morphological characters) proposed a status as a separate infraorder Axymyiomorpha. Hennig (1973) (based on morphological characters) suggested a placement in Bibionomorpha. This was also supported by Oosterbroek & Courtney (1995) (morphological characters, mainly of larvae and pupae), who placed the family as sistergroup of the remaining Bibionomorpha. And Michelsen (1996) suggested a closer relationship of Axymyiomorpha (containing only Axymyiidae) with Bibionomorpha and Psychodomorpha (Neodiptera) (morphological characters of the prothorax and neck). Analyses of a molecular data set (Bertone et al. 2008) yielded a placement of Axymyiidae as sistergroup of Nymphomyiidae, and both groups together were placed as close relatives of Culicomorpha. However, it was pointed out by the authors that this is likely an artefact caused by long-branch attraction. Finally, in agreement with Hennig (1973) and based on a comprehensive data set Wiegmann et al. (2011) (combined analysis of 14 nuclear genes, complete mitochondrial genomes and morphological characters) suggested a placement within Bibionomorpha.

The situation is complicated by a number of hypotheses concerning the composition of Bibionomorpha: only Bibionidae, Pachyneuridae, Mycetophilidae, Sciaridae and Cecidomyiidae were included by Wood & Borkent (1989) and Blaschke-Berthold (1994). Oosterbroek & Courtney (1995) added Axymyiidae as the sister group of a clade comprising these five families. Analyses of 28SrDNA suggested an expanded concept including also Anisopodidae and Scatopsidae (Friedrich & Tautz 1997). Interestingly analyses of combined nuclear ribosomal (28S) and protein coding genes (CAD, PGD and TPI) supported the inclusion of Canthyloscelidae (Bertone et al. 2008) but the exclusion of Axymyiidae. The most comprehensive data set to date, assembled by Wiegmann et al. (2011; see above), again supported the inclusion of Axymyiidae in Bibionomorpha. The family was placed as the 3rd branch following Anisopodidae and a clade comprising Scatopsidae and Canthyloscelidae. However, only few superficial morphological data for Axymyiidae were available for these analyses.

Morphological treatments of an axymyiid fly were provided by Michelsen (1996) and Wihlm et al. (2012). Michelsen (1996) described the prothorax and neck region. Whilm et al. (2012) documented the external morphology of all life stages of *Axymyia furcata*, with the main focus on the larvae. Internal morphological features of all life stages remained largely or completely unknown including the head of adults. Consequently the main aim of our study is to provide detailed data on this tagma. The phylogenetic implications we suggest here have to be considered as preliminary. The comprehensive analysis of Wiegmann et al. (2011) provides a solid phylogenetic framework for the discussion. A formal analysis of the characters treated here is presently not feasible due to a serious lack of detailed anatomical data for a number of relevant nematoceran taxa (see Discussion).

2. Materials and methods

2.1. Material examined

Axymyiidae (Diptera): *Axymyia furcata* McAtee, 1921 (95% Ethanol; North Carolina, USA), 2 females, 2 males.

Bibionidae (Diptera): *Bibio marci* Linnaeus, 1758 (70% Ethanol, Jena, Germany).

Anisopodidae (Diptera): *Sylvicola fenestralis* Scopoli, 1763 (70% Ethanol, Jena, Germany).

2.2. Methods

Drawings were made using a stereo microscope MZ 125 (Leica). Figures were processed with Adobe Photoshop® and Adobe Illustrator®. For scanning electron microscopy the specimens were dehydrated with ethanol (95% – 100%) and acetone, critical point dried (EmiTech K500 Critical Point Dryer; Ashford, Kent, UK), glued on a fine pin and sputter coated. Images were taken with a Philips XL 30 ESEM using a specimen holder after Pohl (2010).

Three-dimensional reconstructions were carried out using Imaris® 6.2.1 (Bitplane AG, Zürich, Suisse) and Maya 2012 (Autodesk) software based on the µCT-image stack. For the synchrotron radiation based micro-computed tomography the specimens were dehydrated with ethanol (95% – 100%) and acetone, critical point dried (EmiTech K850 Critical Point Dryer; Ashford, Kent, UK) and mounted with superglue on a metal rod. The scans were performed at Beamline BW2 on the German Electron Syncrotron Facility (DESY, Hamburg) using a low energy beam (8 kV) and absorptions contrast (see Friedrich et al. 2010).

2.3. Terminology

The regions and sclerites of the head are named following the nomenclature of DuPorte (1946). Muscles are named following the nomenclature of v. Kéler (1963).

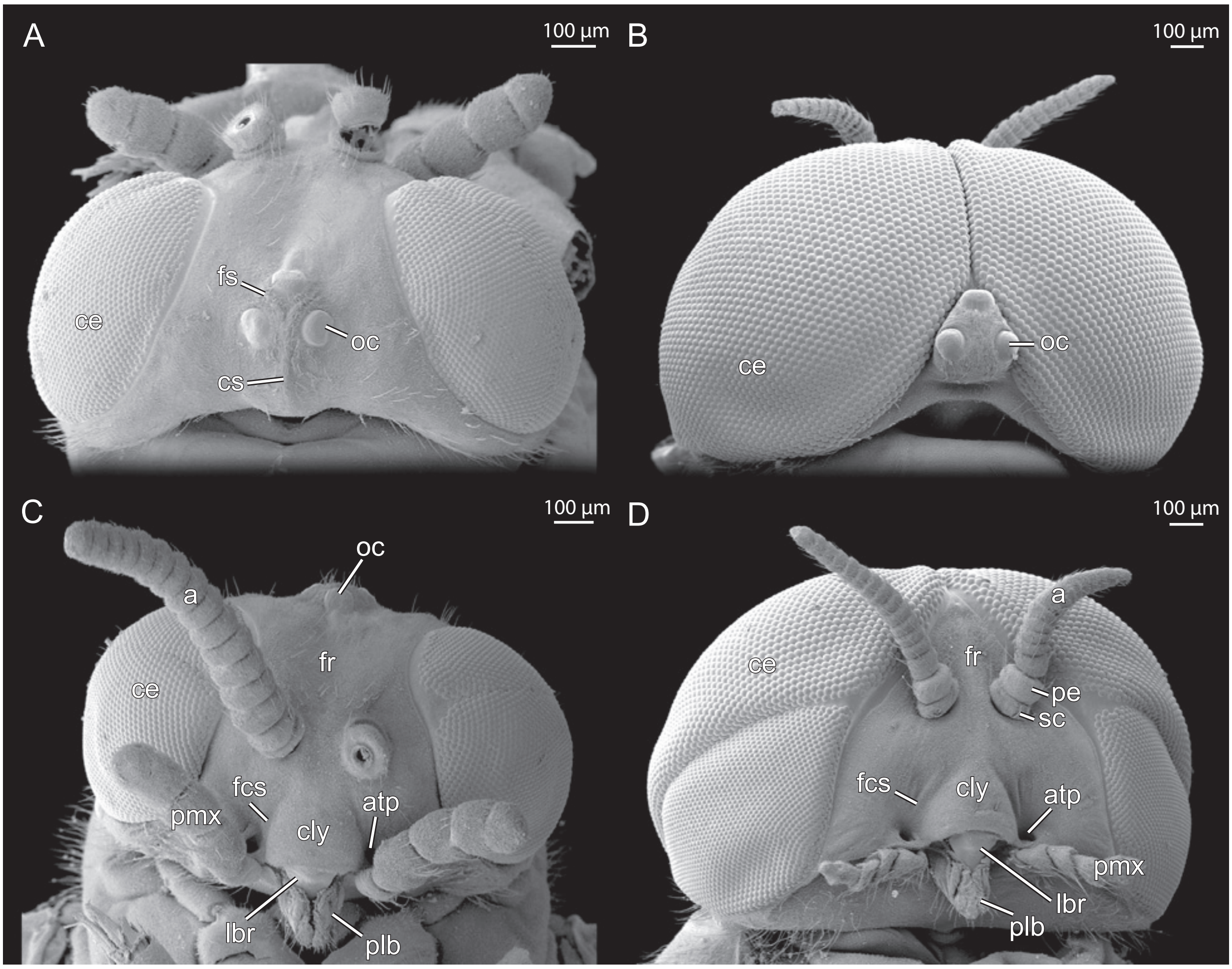

Fig. 1. *Axymyia furcata*, female and male, entire head, SEM images. **A**: Female, dorsal. **B**: Male, dorsal. **C**: Female, frontal. **D**: Male, frontal. Abbreviations: a – antenna, atp – anterior tentorial pits, ce – compound eyes, cly – clypeus, cs – coronal suture, fcs – frontoclypeal suture, fr – frons, fs – frontal suture, lbr – labrum, oc – ocelli, pe – pedicellus, plb – labellum, pmx – maxillary palp, sc – scapus.

3. Results

3.1. Head capsule

The orthognathous head is kidney-shaped in dorsal view and nearly oval in frontal view (Fig. 1). It is sclerotized and densely covered with microtrichia. The posterodorsal, lateroventral and posteroventral margins are covered with numerous bristles. A row of setae is present on the frons of the females, below the frontal ocellus and above the antennae (Fig. 1A). Their arrangement approximately agrees with the three sides of a triangle (pointing upward), with a horizontal row and two rows with an oblique longitudinal orientation. In males, the triangular area between the antennal insertions and the area of fusion of the compound eyes is densely covered with setae.

The frons extends between the compound eyes and completely separates them medially in females, whereas in males a part of the frons is reduced in size by expansion of the compound eyes (ce, Fig. 1B). It is approximately triangular and distinctly reduced in size in males. The frons is laterally separated from the clypeus by a faintly developed, oblique lateral part of the frontoclypeal ridge (= epistomal suture [Schiemenz 1957]), which is interrupted medially (see below); the area of origin of M. clypeobuccalis (M 44) also defines the clypeal area. The triangular clypeus lies below the antenna (cly, Fig. 1C,D). It is distinctly convex, not subdivided into an anteclypeus and a postclypeus, and covered by a very dense vestiture of microtrichia. The labrum is separated from it by an inwardly directed membranous fold (lbr, Figs. 1C,D, 4). A pair of forked, antler-like setae is present on the central region of the clypeus of males (Fig. 2B).

The frontal sutures and the coronal suture are completely absent in males. Landmarks for the upper part of the frons are the origin of M. frontobuccalis posterior (M. 46) and the frontal ocellus (see v. Kéler 1963: pp. 615, 732). The genae alongside the lower hemispheres of the compound eyes and the lower parts of the frons and clypeus form the ventrolateral and ventromedian marginal parts of the head capsule. Its ventral posterior margins are formed by the postgenae, which are adjacent below

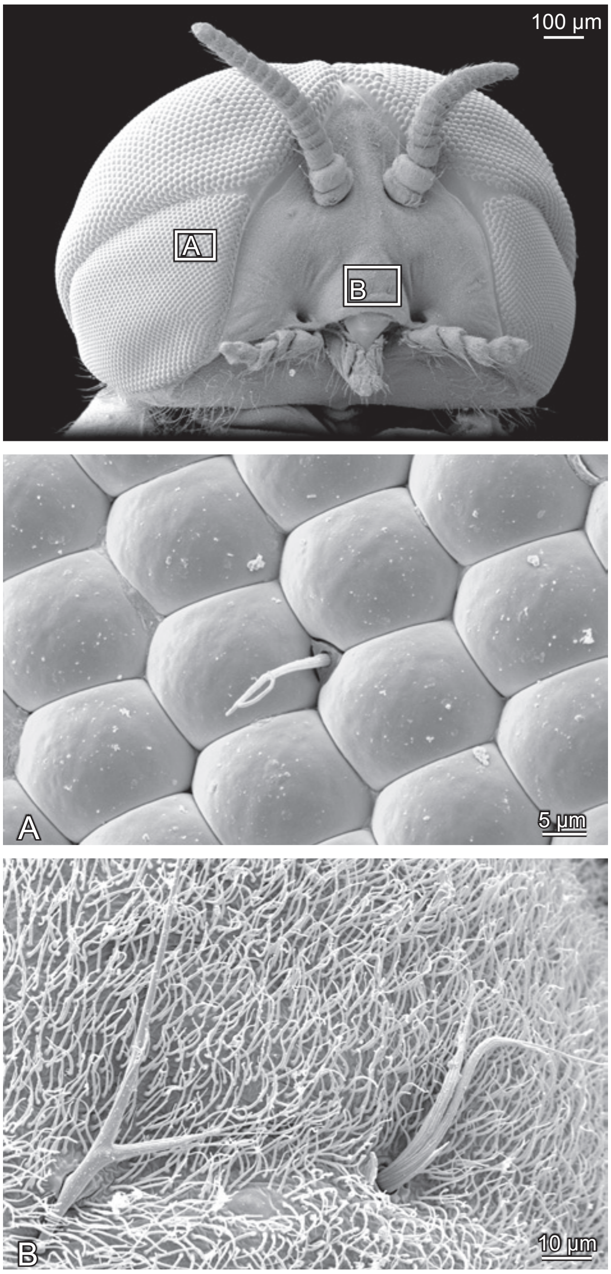

Fig. 2. *Axymyia furcata*, male, SEM images. **A**: Higher magnification of compound eyes. **B**: Higher magnification of setae of the clypeus.

the compound eyes and fused medially, thus forming a postgenal or hypostomal bridge.

The vertex is separated from the occipital region by the transverse epicranial ridge. Its lateral parts extend along the circumocular suture reaching approximately the horizontal division of the eyes. In males the eyes are fused medially and the vertex lies directly above the dorsal area (Fig. 1B). It is prominent, cupola-shaped, and approximately triangular. Its entire surface is covered with setae. In females the vertex lies directly above the frons and is less convex (Fig. 1A). The Y-shaped line representing the parts of the frontal and coronal sutures around their junction in females (absent in males, see above) is flanked by setae on all sides. The median ocellus is located on the upper part of the frons and the lateral ocelli are located on the vertex. The lateral ocelli of males are approximately round and smaller than the oval median ocellus (oc, Fig. 1B). All three ocelli are oval and of equal size in females (oc, Fig. 1A). The postoccipital region is almost vertical posterad the vertex. The postocciput is a narrow bulge enclosing the foramen occipitale. It is separated from the occipital region by a faintly impressed postoccipital furrow. The foramen occipitale has the shape of a medially open 8, with the upper part almost 4 times as large as the ventral portion.

Cuticular strengthening ridges are distinctly developed. This includes the well-developed circumocular ridge, several internal folds laterad the clypeus and above the anterior tentorial pits, and a large, smooth extension above the posteroventral margin of the compound eyes. A frontal apodeme located between the antennal bases in many Diptera (and also Nannochoristidae) is lacking. A subgenal ridge and a prefrontal suture or ridge are also missing.

The compound eyes are sexually dimorphic. The outline of the dichoptic eyes of the females, which cover almost 1/3 of the surface of the head, is nearly circular (ce, Fig. 1A,C). The holoptic eyes of the males are oval and cover approximately 3/4 of the head surface (ce, Fig. 1B,D). The compound eyes are subdivided into a dorsal and a ventral part in both sexes by a flat horizontal chitinous stripe, which bears several terminally curved setae (Fig. 1C,D). The ventral part of females is slightly concave mesally and about twice as large as the dorsal portion. The dorsal hemisphere of males is about 2.5 times as large as the ventral one and concave posteroventrally.

3.2. Tentorium

The anterior tentorial pits at the lateral ends of the frontoclypeal strengthening ridge are oval in outline and funnel-shaped (atp, Figs. 1C,D, 7A). The fissure-shaped posterior pits lie on the posterior side of the head beside the ventrolateral margins of the foramen occipitale (ptp, Fig. 7B). Anterior and posterior arms form a nearly straight, hollow tube-like structure on each side. The dorsal arms are absent. The posterior arms bear small thorn-shaped processes, they are directed mesally and are fused ventrally with the head capsule.

3.3. Antenna

The moniliform antennae insert on the frontal part of the head, approximately at the level of the division of the compound eyes (a, Fig. 1C,D). The distance between the antennal bases is approximately equal to their distance to the margin of the compound eyes. The antennae of

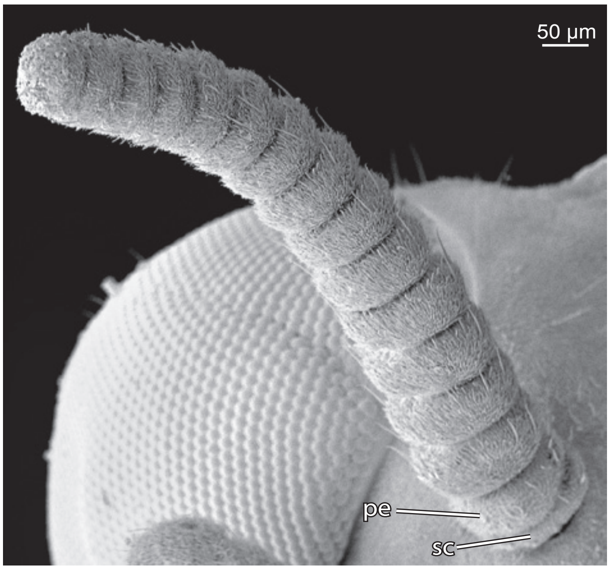

Fig. 3. *Axymyia furcata*, female, antenna, SEM image. Abbreviations: pe – pedicellus, sc – scapus.

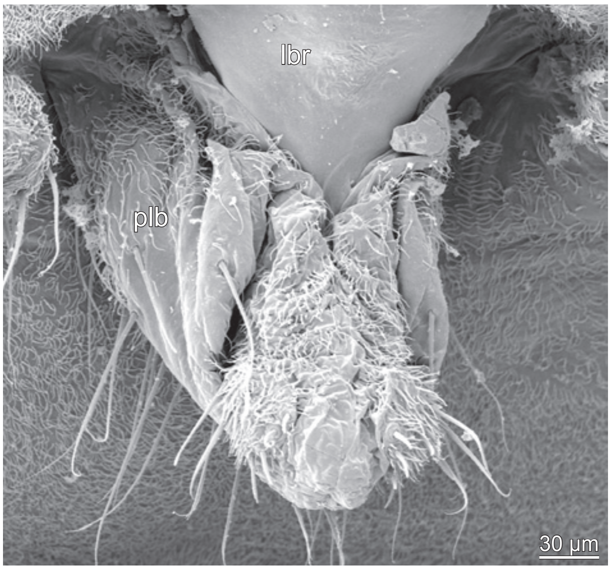

Fig. 4. *Axymyia furcata*, male, mouthparts, SEM image. Abbreviations: lbr – labrum, plb – labellum.

females are longer and thicker than those of the males. The 14 flagellomeres are rounded. All antennomeres are covered by a dense vestiture of microtrichia (Fig. 3). The scapus bears four longer setae medioventrally, three arranged in a line at the basal margin of the segment and the fourth placed above them. Additional lateroventral setae are present in males. The pedicellus is about twice as long as the scapus in both sexes. In males both basal antennomeres are longer and wider than the flagellomeres, and the basal flagellomere is approximately twice as long as the others. All flagellomeres bear a distal whorl of longer setae and a dense vestiture of sensilla trichodea. In females the whorl is placed at the distal margin on the pedicellus. In males the setae are not arranged in a regular row, but in alternating positions.

Musculature: (1, Fig. 5) M. 1: M. tentorioscapalis anterior: long and slender muscle; O (origin) – genae, laterally on the level of the most dorsal point of the frontoclypeal ridge; I (insertion) – anteroventral margin of the scapus; F (function) – depressor of the antenna. M. 2: M. tentorioscapalis posterior: long, slender muscle; O – genae, posterad M. tentorioscapalis anterior; I – posteriorly on the basal margin of the scapus; F – levator, antagonist of M. tentorioscapalis anterior. M. 3: M. tentorioscapalis lateralis: absent. M. 4: M. tentorioscapalis medialis: absent. Mm. 5/6: Mm. scapopedicellaris lateralis/medialis: not recognisable in the µCT data set.

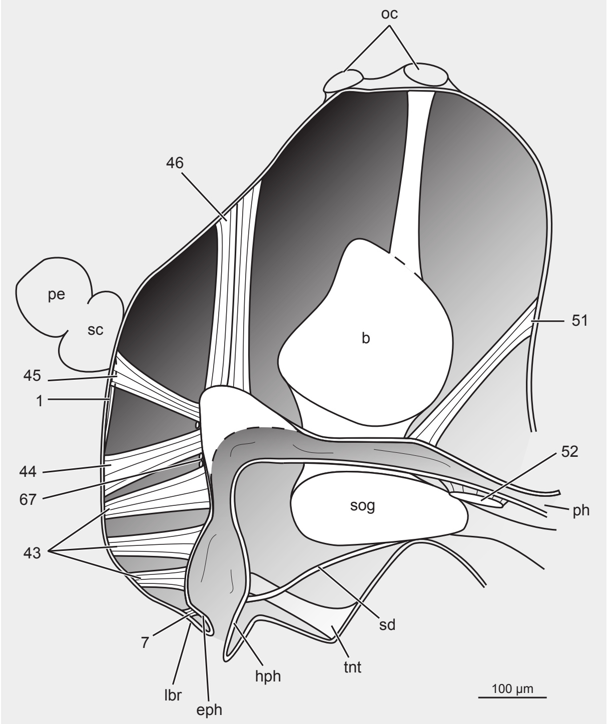

Fig. 5. *Axymyia furcata*, male, sagittal section of head. Abbreviations: b – brain, eph – epipharynx, hph – hypopharynx, lbr – labrum, oc – ocelli, pe – pedicellus, ph – pharynx, sc – scapus, sd – salivary duct, sog – sobesophageal ganglion, tnt – tentorium, 1 – M. tentorioscapalis anterior, 7 – M. labroepipharyngalis, 43 – M. clypeopalatalis, 44 – M. clypeobuccalis, 45 – M. frontobuccalis anterior, 46 – M. frontobuccalis posterior, 51 – M. verticopharyngalis, 52 – M. tentoriopharyngalis, 67 – M. transversalis buccae.

3.4. Labrum

The small triangular labrum is largely exposed (lbr, Fig. 4). Its relatively broad basal margin is connected with the clypeus by an inwardly directed membranous fold. The surface is smooth and glabrous. The pointed apex is embedded in the median fold between the labella. A paired bulge is present at the upper margin in males.

Musculature: (7, Figs. 5, 7A) M. 7: M. labroepipharyngalis: small paired muscle, diverging towards the in-

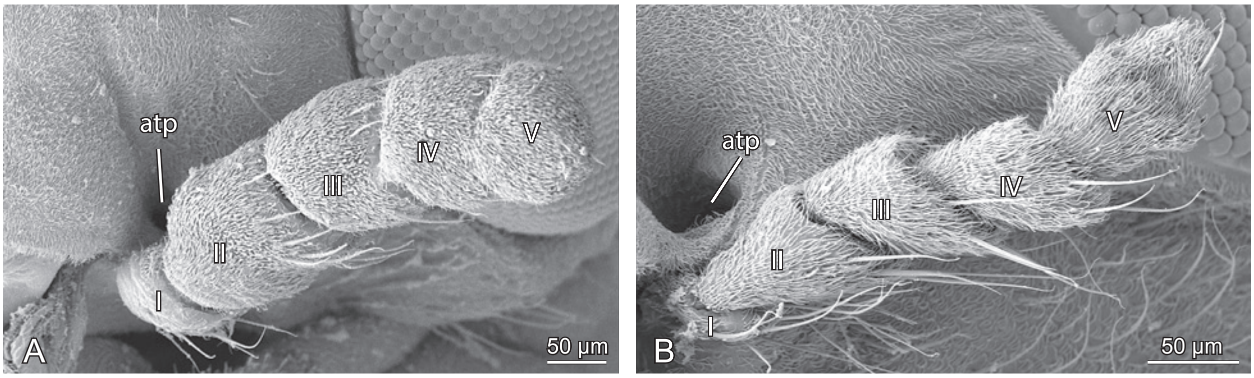

Fig. 6. *Axymyia furcata*, maxillary palp, SEM images. **A**: Female. **B**: Male. Abbreviations: atp – anterior tentorial pits; I–V – number of palpomeres.

sertion; O – dorsal labral wall; I – anteromesally on the epipharynx; F – levator of the anterior epipharynx. M. 8: M. clypeolabralis (by Schiemenz 1957): not recognisable in the µCT-data set, apparently absent.

3.5. Mandible

Absent in both sexes.

3.6. Maxilla

The basal parts of the maxillae are fused with the head capsule. Externally only the moniliform palps are visible (pmx, Figs. 1C,D, 6). They insert below the anterior tentorial pits. The palps of the males are short and slender (Fig. 6B). Those of the females are longer and thicker (Fig. 6A). The 5 palpomeres are almost globular. The basal one bears a scattered vestiture of microtrichia in males and females. A denser ventral field of microtrichia is present on palpomere 1 of females. Several curved setae are present lateroventrally in both sexes. Palpomeres 2–5 bear a dense vestiture of microtrichia and sensilla on their entire surface. A sensorial pit, which is present in some dipteran groups, is absent in *Axymyia*. A distal row of setae is present on palpomeres 2–4. It is restricted to the ventral half in males but encloses the entire segment in females. Palpomere 5 bears setae on its apex. A circular concavity is present in males on this segment.

Musculature: absent.

3.7. Labium

The labium is not distinctly delimited externally. The prementum forms a part of the ventral closure of the head capsule and is partly fused with the head capsule. The postmentum is completely reduced or is a part of the ventral closure of the head. Glossae and paraglossae are absent. The labial palps are transformed into labella fused medially for most of their length (plb, Figs. 1C,D, 4). Their unsclerotized cuticle is folded, especially in the distal region. Pseudotracheae with internal strengthening ridges are missing. Basally and terminally numerous bristles are present, especially on the ventral surface. A small circle with dark setae is present on the apices of the labella.

Musculature: M. 28: M. submentopraementalis: absent. M. 29: M. tentoriopraementalis inferior: the only premental retractor. O – mesoventral part of the tentorium; I – hind margin of the prementum; F – retractor of the prementum. M. 30: M. tentoriopraementalis superior: absent or completely merged with M. tentoriopraementalis inferior. M. 31: M. praemento-paraglossalis: absent. M. 32: M. praementoglossalis: absent. M. 33: M. praementopalpalis internus: absent. M. 34: M. praementopalpalis externus: apparently absent. M. 35: M. palpopalpalis labii primus: a slender, paired muscle of the labellum; O – laterobasally on the labellum (palpomere 1) I – lateral basal margin of palpomere 2; F – extensor of the labellum. M. 36: M. palpopalpalis labii secundus: absent.

3.8. Epi- and hypopharynx

The epipharynx forms the internal wall of the labrum and the roof of the preoral cavity (cibarium) (eph, Fig. 5). It is smooth and unsclerotized. The lateral walls of the epipharynx are lightly bent inwards and form a flat epipharyngeal food channel. The sclerotized hypopharynx is U-shaped in cross section (U dorsally open). Its anterior wall forms the floor of the preoral cavity. The distal hypopharynx is also U-shaped, but it becomes flatter in the posterior region of the preoral cavity. The lumen between the hypo- and epipharynx is rather narrow close to the anatomical mouth opening.

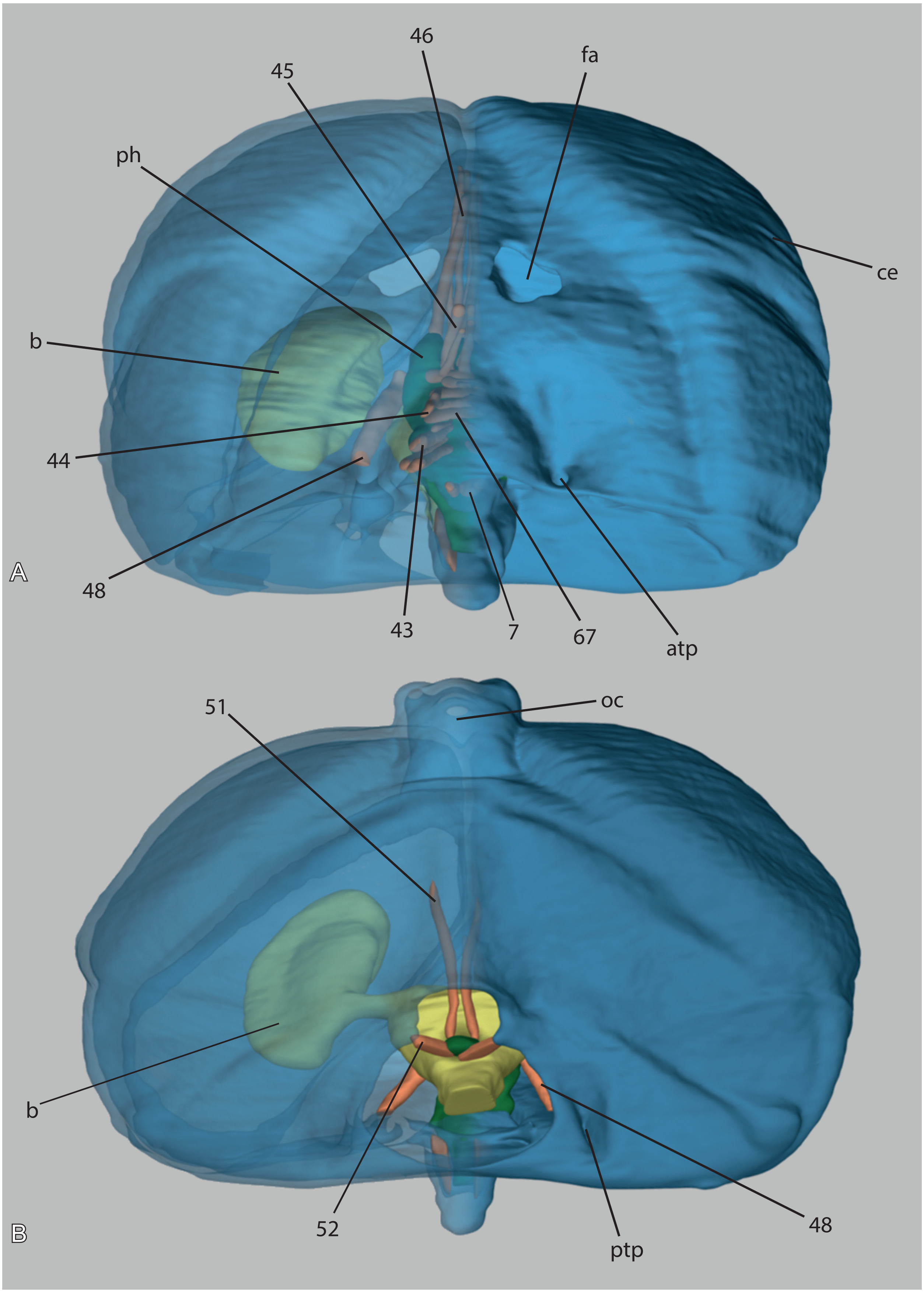

Fig. 7. *Axymyia furcata*, male, 3d-reconstruction of head. **A**: Frontal view. **B**: Caudal view. Abbreviations: atp – anterior tentorial pits, b – brain, ce – compound eye, fa – foramen antennale, oc – ocelli, ph – pharynx, ptp – posterior tentorial pits, 7 – M. labroepipharyngalis, 43 – M. clypeopalatalis, 44 – M. clypeobuccalis, 45 – M. frontobuccalis anterior, 46 – M. frontobuccalis posterior, 48 – M. tentoriobuccalis anterior, 51 – M. verticopharyngalis, 52 – M. tentoriopharyngalis, 67 – M. transversalis buccae.

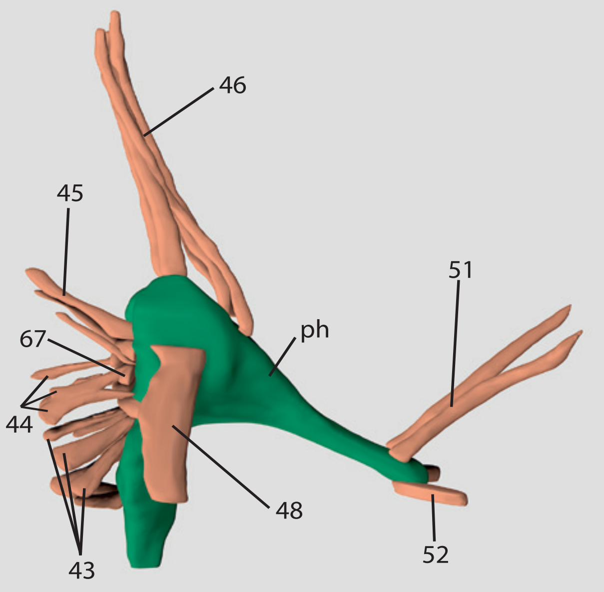

Fig. 8. *Axymyia furcata*, male, 3d-reconstruction, part of digestive tract in head. Orientation: ← anterior, ↓ ventral. Abbreviations: ph – pharynx, 43 – M. clypeopalatalis, 44 – M. clypeobuccalis, 45 – M. frontobuccalis anterior, 46 – M. frontobuccalis posterior, 48 – M. tentoriobuccalis anterior, 51 – M. verticopharyngalis, 52 – M. tentoriopharyngalis, 67 – M. transversalis buccae.

Musculature: (43, 44, 48, Figs. 5, 7, 8) M. 41: M. frontohypopharyngalis: absent. M. 42: M. tentoriohypopharyngalis: absent. M. 43: M. clypeopalatalis: strongly developed, composed of several bundles arranged in a longitudinal row; O – clypeus; I – on the roof of the cibarium (palatum); F – cibarial dilator. M. 44: M. clypeobuccalis: strongly developed, oblique, directed posteriorly; O – clypeus, immediately posterad of M. clypeopalatalis; I – dorsal wall of the palatum, immediately beside anatomical mouth; F – dilator of the posterior cibarium and mouth opening.

3.9. Pharynx

The lateral walls of the pharynx are sclerotized. The broad precerebral pharynx has a wide lumen and appears U-shaped in cross section (U dorsally open). The anterior pharynx is enhanced bag-shaped dorsally (ph, Fig. 5). Laterodorsally, approximately at the level of the antennal bases, two massive apodemes are developed. These are the insertion points of the precerebral dilators, which form the precerebral pumping apparatus, together with M. tentoriobuccalis anterior (M. 48). After the foramen oesophageale of the massive complex formed by the brain and the suboesophageal ganglion, the lumen of the pharynx becomes narrow and it appears elliptic in cross section and continuous with the oesophagus. The dilators of the postcerebral pumping chamber insert at the edges of the foramen occipitale (51, 52, Figs. 5, 7B).

Musculature: (45, 46, 51, 52, 67, Figs. 5, 7, 8) M. 45: M. frontobuccalis anterior: O – frons, medially on the level of the lower margin of the antennal insertion areas; I – dorsally on the roof of the anterior pharynx, posterad the ganglion frontale; F – dilator of the anterior pharynx. M. 46: M. frontobuccalis posterior: strongly developed, long muscle; O – posterior frontal region; I – roof of the anterior pharynx, immediately before the brain; F – widens the lumen of the precerebral pharynx. M. 48: M. tentoriobuccalis anterior: strongly developed; O – dorsally on the anterior tentorial arms; I – laterally on the anterior pharynx (dorsolateral apophyses); F – dilator of the precerebral pharynx. M. 49: M. tentoriobuccalis lateralis: absent. M. 50: M. tentoriobuccalis posterior. M. 51: M. verticopharyngalis: long, slender muscle; O – dorsally on the postoccipital region, at the edge of the foramen occipitale; I – dorsal wall of the postcerebral pharynx, immediately posterad the brain. M. 52: M. tentoriopharyngalis: short muscle; O – on the lateral margin of the foramen occipitale; I – ventrolateral wall of the posterior pharynx; F – dilator of the posterior pharynx, together with M. verticopharyngalis. M. 67: M. transversalis buccae: five muscle bands extending over the dorsal wall of the anterior pharynx. The anteriormost band lies immediately posterad of anatomical mouth. M. 68: M. anularis stomodaei: Not recognisable in the µCT data set. M. 69: M. longitudinalis stomodaei: absent.

3.10. Salivary duct and glands

The salivary duct opens posteriory on the hypopharynx, approximately at the level of the labral apex (sd, Fig. 5). It extends posteriorly below the suboesophageal ganglion and enters the thorax. It appears almost circular in cross section close to its anterior opening but its remaining part is transversely oval in cross section and narrowing posteriorly. The salivary duct is only sclerotized at its opening. The salivary glands lie in the prothorax.

Musculature: M. 37: M. hypopharyngosalivarialis: apparently absent. Mm. 38/39: Mm. praementosalivarialis anterior/posterior: absent. M. 40: M. anularis salivarii is not visible in the µCT-data set, but it cannot be excluded that the muscle is present.

3.11. Nervous system

The compact complex formed by the brain and suboesophageal ganglion lies in the medioventral area of the head and occupies a large proportion of the lumen (b, Fig. 7). The optic lobes are kidney-shaped and less strongly developed in the females. Each lobe is connected with the central part of the protocerebrum by a short, thick optic nerve. The protocerebrum is separated by a shallow furrow from the deutocerebrum. The three ocelli are connected with the protocerebrum by a single ocellar ganglion and three ocellar nerves (Fig. 5). The deutocerebrum contains the hemispherical antennal lobes where the antennal nerve originates. It is round in cross section. The tritocerebrum is represented by the tritocerebral lobes below the antennal lobes. A tritocerebral commissure is not recognisable as a separate structure, brain and suboesophageal ganglion are largely fused and form a compact structure around the pharynx (b, sog, Fig. 5). The foramen oesophageale between the brain and the suboesophageal ganglion is elliptical. The frontal ganglion is connected with the tritocerebrum by the frontal connectives below the antennal lobes. The nervus frontale is present, whereas the unpaired nervus connectivus is absent.

3.12. Tracheal system

A pair of dorsal tracheae enter the head. Several lateral tracheae originate from them and supply the brain, muscles and foregut with oxygene.

4. Discussion

The status as a separate family Axymyiidae was well established in more recent studies (Mamayev & Krivosheina 1966; Oosterbroek & Courtney 1995; Wiegmann et al. 2011). Whereas this is widely accepted, the precise position of the group remains largely obscure (see below).

We identified an entire series of apomorphic cephalic characters. The complete subdivision of the compound eyes into a dorsal and ventral part in both sexes is apparently an autapomorphy in Axymyiidae. The dorsal portion is larger than the ventral one in males, and also the ommatidia are larger in the dorsal hemisphere. The compound eyes are undivided in all potentially related dipteran groups (e.g. Schneeberg & Beutel 2011).

The absence (or extreme size reduction) of M. clypeolabralis is another potential autapomorphy of the family. Its presence is likely a derived groundplan apomorphy of Diptera (Schneeberg & Beutel 2011). The muscle is probably homologous to M. frontolabralis in other insects (see M. 8 in v. Kelér 1963). M. clypeolabralis is also missing in adults of Deuterophlebiidae (Schneeberg et al. 2011) and Nymphomyiidae (Tokunaga 1935). As the labrum is completely reduced in both groups and a close relationship with Axymyiidae is not supported by other features (and molecular data, e.g., Wiegmann et al. 2011), we assume that the loss of the muscle occurred independently.

Another complex of potential autapomorphies of Axymyiidae is related to the greatly reduced condition of the maxillae. This includes the complete absence of the endite lobes and the reduction of M. stipitopalpalis externus and M. palpopalpalis primus and secundus. However, the great reduction of the maxillae is possibly a feature shared Axymyiidae, without the newly described *Plesioaxymyia vespertina* (Sinclair 2013), whereas they have well-developed mouthparts. Both maxillary endites are also missing in *Tipula* (Tipulidae) (Schneeberg & Beutel 2011), *Erioptera* (Limoniidae), *Mycetophila* (Mycetophilidae), *Fucellia* (Anthomyiidae) (Hoyt 1952) and *Mayetiola* (Cecidomyiidae) (Schneeberg et al. 2013). The loss apparently occurred independently in different lineages of lower Diptera, as the absence does not correlate with recently suggested phylogenetic patterns (e.g., tree topology in Wiegmann et al. 2011). This also applies to the missing M. stipitopalpalis externus, which is also absent in *Coboldia* (Scatopsidae), *Aedes* (Culicidae) and all examined members of Brachycera (Bonhag 1951; Schiemenz 1957; Christophers 1960; Szucsich & Krenn 2000; Schneeberg et al. 2013). The loss of M. palpopalpalis maxillae primus and secundus is widespread among nematoceran Diptera. Both muscles are absent in *Axymyia*, *Coboldia*, *Spathobdella* (Sciaridae) (Schneeberg et al. 2013) and the brachyceran groups Bombyliidae (Szucsich & Krenn 2000) and Syrphidae (Schiemenz 1957). M. palpopalpalis maxillae secundus is absent in *Sylvicola* (Anisopodidae), *Wilhelmia* (Simuliidae) (Wenk 1962), *Edwardsina* (Blephariceridae) (Schneeberg et al. 2011) and all representatives of Tipulomorpha examined (Schneeberg & Beutel 2011), and also in *Tabanus* (Tabanidae) (Bonhag 1951). Apparently Bibionomorpha are characterized by a strong tendency to reduce the maxillary palp musculature (correlated with the reduction of the maxillary palpomere), but the muscles are present in the groundplan as they are preserved in *Bibio* (Bibionidae) and *Mayetiola* (Schneeberg et al. 2013). To which extent this is correlated with a simplification of the palp is unclear. *Bibio* and *Sylvicola* have 5-segmented well developed maxillary palps, whereas they are 3-segmented in *Mayetiola* and *Spathobdella*, and only one palpomere is present in *Coboldia.*

Another potential autapomorphy of the head is the absence of the salivary pump musculature (M. hypopharyngosalivarialis). M. hypopharyngosalivarialis is present in the groundplan of Diptera and preserved in most taxa examined. However, it is missing in *Axymyia*, *Deuterophlebia* (Deuterophlebiidae) (Schneeberg et al. 2011) and *Limonia* (Limoniidae) (Schneeberg & Beutel 2011). Again, parallel loss is very likely. The muscle is present in other members of Tipulomorpha (Schneeberg & Beutel 2011) and apparently in the groundplan of this lineage. An extremely reduced cephalic musculature characterizes adults of Deuterophlebiidae (Schneeberg et al. 2011: 8 pairs of cephalic muscles versus more than 40 in adults of Neuropterida), which have a very short life span and are not feeding (Courtney 1991). They were suggested as the sistergroup of all the remaining Diptera by Wiegmann et al. (2011), which implies that different structures which occur in most dipteran lineages have been reduced independently in *Deuterophlebia*.

Another apparent apomorphy is the origin of M. tentorioscapalis anterior (M. 1) on the head capsule. This condition does also occur in *Mayetiola* (Schneeberg et al. 2013), *Limonia*, *Tipula* (Schneeberg & Beutel 2011) and *Nymphomyia* (Nymphomyiidae) (Tokunaga 1935). In the case of the last two genera this is obviously linked with the complete reduction of the tentorium. Aside from this, there is a general tendency in Diptera to shift the origin of the antennal muscles from the tentorium to the head capsule without a recognizable phylogenetic pattern. The second antennal muscle M. tentorioscapalis posterior also originates on the head in *Axymyia*, *Culicoides* (Ceratopogonidae) (Gad 1951), *Edwardsina*, *Deuterophlebia* (Schneeberg et al. 2011), *Tipula* (Schneeberg & Beutel 2011), and *Nymphomyia* (Tokunaga 1935). M. tentorioscapalis medialis also originates on the head capsule in several dipteran groups (*Trichocera*, *Bibio*, *Spathobdella*, *Mayetiola*, *Sylvicola*, *Tabanus*, *Tipula*, *Nymphomyia*; Tokunaga 1935; Bonhag 1951; Schneeberg & Beutel 2011; Schneeberg et al. 2013). This muscle is completely missing in *Axymyia*, but also in many other dipteran groups such as Deuterophlebiidae (Schneeberg et al. 2011), Simuliidae (Wenk 1962), and Culicidae (Thompson 1905; Schiemenz 1957; Christophers 1960; Owen 1985).

As mentioned above the shift of the antennal muscles to the head capsule is often correlated with a partial or complete reduction of the tentorium. In the dipteran groundplan a typical corpotentorium (establishing a left-right connection) is missing whereas anterior, posterior and dorsal arms are well developed (after Peterson 1916; Hennig 1973). This condition is described for Simuliidae (Peterson 1916; Wenk 1962) and the brachyceran Tabanidae (Bonhag 1951). In *Wilhelmia* all antennal muscles originate on the tentorium (Wenk 1962), whereas M. tentorioscapalis medialis is shifted to the head capsule in *Tabanus* (Bonhag 1951). Short vestigial dorsal arms occur in several groups (*Mischoderus* [Tanyderidae], *Culiseta* [Culicidae], *Chironomus* [Chironomidae], *Eristalis* [Syrphidae], *Exoprosopa* [Bombyliidae]; Peterson 1916; Schiemenz 1957; Owen 1985). In *Mischoderus* and *Eristalis* all antennal muscles still originate on the tentorium, whereas in *Culiseta* M. tentorioscapalis medialis is absent, like in all other members of Culicidae (Schiemenz 1957; Schneeberg & Beutel 2011). In most dipteran groups the dorsal arms are completely missing and the tentorium consists of a simple, more or less straight, wide and hollow tube on each side (e.g. *Axymyia*, Deuterophlebiidae, Trichoceridae, Bibionidae, Culicidae [with the exception of *Culiseta*]: Schiemenz 1957; Schneeberg & Beutel 2011; Schneeberg et al. 2011). Tentorial structures are completely missing in Tipulidae and Nymphomyiidae and all preserved extrinsic antennal muscles consequently arise from the head capsule (see above; e.g., Schneeberg & Beutel 2011; Schneeberg et al. 2011).

Aside from the apomorphic features treated above, the head of *Axymyia* displays many plesiomorphic character states. As it can be assumed for the groundplan of Diptera the head is orthognathous. The presence of three ocelli on the vertex, 5-segmented maxillary palps, 2-segmented labial palps modified as labella, and only one premental retractor (see also Schneeberg & Beutel 2011) are apparently also ancestral features.

All exposed parts of the head (except the labrum) are covered with short microtrichia in *Axymyia*. This is also the case in all other dipterans examined, including the two presumably basal families Deuterophlebiidae and Nymphomyiidae (Tokunaga 1935; Schneeberg et al. 2011) (also in e.g. *Spathobdella*, *Mayetiola*, *Coboldia*, *Tipula*, *Limonia*, *Trichocera*, *Culex* [Culicidae], *Aedes*, *Edwardsina*: Schneeberg & Beutel 2011; Schneeberg et al. 2013).

The epipharyngeal food channel is apparently also a groundplan condition as this structural modification is generally found in dipterans and also in *Nannochorista* and Siphonaptera (e.g. Vogel 1921; Bonhag 1951; Gad 1951; Wenk 1953; Schiemenz 1957; Snodgrass 1959; Wenk 1962; Sutcliffe 1985; Szucsich & Krenn 2000; Beutel & Baum 2008; Schneeberg & Beutel 2011).

Only few derived characters tentatively indicate systematic affinities between Axymyiidae and other nematoceran groups, notably with families of Bibionomorpha. A placement of Axymyiidae within this infraorder is presently best supported (Wiegmann et al. 2011). However, there are still controversies on the composition of Bibionomorpha, especially with regard to the inclusion of Axymyiidae (see above).

The interpretation of cephalic features, especially a comparison with other groups assigned to Bibionomorpha, is impeded by a serious lack of detailed data. Information on adult internal head structures is only available for *Bibio*, *Mayetiola*, *Spathobdella*, *Coboldia*, *Sylvicola* and *Axymyia*. Derived cephalic characters shared by *Axymyia* and other bibionomorph taxa are the loss of M. craniolacinialis and the loss of the concavity on the dorsal surface of the anterior labium. M. craniolacinialis is clearly present in the groundplan of Diptera, but was also reduced in several groups not belonging to Bibionomorpha, such as for instance *Mischoderus*, *Edwardsina* (Schneeberg et al. 2011) and Tipuloidea (*Pedicia*, *Limonia*, *Tipula*: Schneeberg & Beutel 2011). The concavity on the dorsal surface of the labium is preserved in Scatopsidae, which suggests that the absence may be an apomorphy of a bibionomorph subgroup which includes Axymyiidae but not Scatopsidae. This would be in agreement with the concepts of Bibionomorpha of Oosterbroek & Courtney (1995) and Wiegmann et al. (2011). The concavity is also absent in adults of *Tipula* (Schneeberg & Beutel 2011) but present in other members of Tipulomorpha.

Apomorphic features occuring in bibionomorph groups but not in *Axymyia* are the presence of only one precerebral pharyngeal dilator and the origin of M. tentorioscapalis medialis on the head capsule. The homology of the single precerebral dilator of Scatopsidae, Bibionidae, Sciaridae, Cecidomyiidae and examined members of Tipuloidea remains uncertain, whereas it is very likely M. frontobuccalis posterior in the case of *Deuterophlebia* (Schneeberg et al. 2011). The origin of M. tentorioscapalis medialis on the frontal region of the head would be conform with an expanded concept of Bibionomorpha also including Anisopodidae (Hennig 1973; Friedrich & Tautz 1997; Bertone et al. 2008; Wiegmann et al. 2011), but an origin on the frons is also described for Trichoceridae and Tabanidae (Bonhag 1951; Schneeberg & Beutel 2011). M. tentorioscapalis medialis is completely missing in *Axymyia* and it originates on the tentorium in Scatopsidae.

Bertone et al. (2008) suggested a sistergroup relationship between Axymyiidae and Nymphomyiidae and between these two groups and the infraorder Culicomorpha. Nymphomyiidae is also a small and highly specialized group comprising only seven described species (Courtney 1994). This concept is in contrast with all previously suggested placements of Nymphomyiidae, for instance as the sistergroup of the remaining Diptera (Hackman & Väisänen 1982; Bertone et al. 2008 [reduced data set]), as the second branch in the dipteran tree after Deuterophlebiidae (Wiegmann et al. 2011), as a member of Blephariceromorpha (Wood & Borkent 1989; Courtney 1990, 1991; Oosterbroek & Courtney 1995), or as the sistergroup of Deuterophlebiidae (Cutten & Kevan 1970; Schneeberg et al. 2011, 2012).

The phylogenetic affinities between Axymyiidae and Nymphomyiidae are very likely an artifact of long branch attraction as discussed in Bertone et al. (2008, p. 683), even though two derived cephalic features of adults are shared by the two groups (Schneeberg et al. 2012), the fusion of the frons and clypeus at least near the midline and the loss of the mandibles incl. their musculature (Togunaka 1935). But both features are reductions and common in the nematoceran dipteran lineages (see discussion in Schneeberg et al. 2013).

It is apparent that most cephalic features of Axymyiidae are either plesiomorphic or autapomorphies of the family. This evidently impedes the systematic placement of the group. Convincing cephalic synapomorphies with other groups are apparently lacking. Taking everything into consideration, especially the comprehensive study of Wiegmann et al. (2011), a placement in Bibionomorpha appears most likely at present. However, despite of strong efforts and an impressive progress in recent years, a sufficiently robust reconstruction of nematoceran relationships including the placement of Axymyiidae has not been achieved yet.

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