Adult head structures of Deuterophlebiidae (Insecta), a highly derived “ancestral” dipteran lineage

Katharina Schneeberg
Gregory W. Courtney
Rolf G Beutel

Available at: https://works.bepress.com/gregory_courtney/21/
1. Introduction

Deuterophlebiidae are a highly specialised dipteran group comprising only 14 species (Courtney, 1994a; Wagner et al., 2008). The larvae are aquatic and always associated with cool, running water. The adults live only a few hours (Courtney, 1991a; Wagner et al., 2008).

A close relationship between Deuterophlebiidae and Blephariceridae was suggested by Hennig (1973), Wood and Borkent (1989), Courtney (1990b, 1991b) and Oosterbroek and Courtney (1995). Hennig (1973) placed the Deuterophlebiidae and Blephariceridae in the Psychodemorpha. Cutten and Kevan (1970) pointed out that Deuterophlebiidae and Nymphomyiidae may form a monophyletic group. Wood and Borkent (1989) suggested a clade Blephariceromorpha comprising Deuterophlebiidae, Blephariceridae and Nymphomyiidae, and the monophyly of the lineage was also supported by Courtney (1990b, 1991b) and Oosterbroek and Courtney (1995). In contrast to this concept, analyses of 28S rRNA and protein-coding (CAD, PGD, TPI) genes sequence data suggest that Deuterophlebiidae form the sister group of all remaining lineages of Diptera (Bertone et al., 2008). A basal placement was also suggested for Nymphomyiidae (Rohdendorf, 1974; Hackman and Väisänen, 1982; Bertone et al., 2008 [analyses of reduced data set]), Culicomorpha + Psychopteromorpha (Oosterbroek and Courtney, 1995; Yeates and Wiegmann, 1999, 2005; Yeates et al., 2007) and Tipulomorpha (or Tipulidae s.l.) (Hennig, 1973; Wood and Borkent, 1989; Beutel and Corb, 2001; Blagoderov et al., 2007).

The larval morphology of Deuterophlebiidae was treated in detail in Courtney (1990a,b) but morphological data on adults were quite limited. Courtney (1990a) described external features of the adult head, but a study on the internal head anatomy including musculature, endoskeleton, digestive tract and nervous system was not available so far. Consequently, the primary aim of this study was to document the head morphology of this potentially basal dipteran taxon in detail. In addition to Deuterophlebia Edwards, 1922, we examined external and internal head structures of potentially related groups, notably Nymphomyiidae and Blephariceridae. To create a solid framework for a discussion of morphological features we compiled an extensive list with potentially relevant phylogenetic characters. Based on these data...
we discuss whether the highly specialised features have evolved as autapomorphies of Deuterophlebiidae in correlation with a specialised life style, or at least some of them indicate a common ancestry with Nymphomyiidae, Blephariceridae or other groups. We also evaluate whether some of the head features we identified support a clade Blephariceromorpha or alternatively the concept of Deuterophlebiidae as “the most ancestral” lineage of Diptera. A formal phylogenetic evaluation of the presented characters was not performed, as phylogenetic conclusions based on only one character system are questionable. However, our data will serve as a starting point for future comprehensive phylogenetic evaluations including characters of other body parts and life stages, as well as molecular data.

2. Materials and methods

2.1. Material examined

Diptera, Deuterophlebiidae: Deuterophlebia coloradensis Pennak, 1945 (both sexes) (USA, Colorado, Boulder Co.; 95% Ethanol, SEM (scanning electron microscopy), microtome sections [ms], micro-computer tomography [μCT]).

Nymphomyiidae: Nymphomyia dolichopeza Courtney, 1994 (undetermined sex) (USA, NC, Macon Co.; 95% Ethanol, SEM, ms) Blephariceridae: Edwardsina gracilis Edwards, 1929 (male) (Chile, Las Lagos, Parque Nacional Puyehue; 95% Ethanol, SEM, ms).

Tipulidae: Tipula paludosa Meigen, 1930 (both sexes) (Germany, vicinity of Jena; 70% Ethanol, FAE [=formaldehyde–ethanol–acetic acid], SEM, confocal laser scanning microscopy [CLSM], ms). Limoniidae: Limonia sp. (female) (Germany, vicinity of Jena; FAE, SEM, ms).

Trichocera: Trichocera saltator Harris, 1776 (both sexes) (Germany, Jena; FAE, SEM, ms).

Tanyderidae: Mischoderus sp. (male) (New Zealand, New Zealand Arthropod Collection; 70% Ethanol, μCT).

Culicidae: Culex pipiens Linnaeus, 1758 (female) (Germany, Orlamünde; 70% Ethanol, SEM, CLSM, ms), Anopheles maculipennis Meigen, 1818 (female) (Germany, Orlamünde; 70% Ethanol, SEM, ms).

2.2. Methods

Drawings were made using a stereo microscope MZ 125 (Leica). Figures were processed with Adobe Photoshop®. Adobe Illustrator® and Image J 1.410 (freeware: http://rsb.info.nih.gov/ij). Specimens were embedded in Araldit CY 212® (Agar Scientific, Stansted, Essex, England) for sectioning. Longitudinal sections (1 μm) and cross section (1 μm) series were carried out with an HME 360 (Microm, Walldorf, Germany) microtome. The sections were stained with Toluidine blue and Pyronin G (Waldeck GmbH & Co. KG/Division Chroma, Münster, Germany), documented with a PixeLINK PL-A622C digital camera and examined with a light microscope Leica DME. The alignment of the image stack was calculated by AutoAligner® 6 (Bitplane AG, Zürich, Suisse) software. Three-dimensional reconstructions were carried out using Imaris® 6.2.1 (Bitplane AG, Zürich, Suisse) and MAYA® 7.0 (Alias Wavefront, Toronto/Ontario, Canada) software based on the μCT-image stack. For the synchrotron radiation based micro-computed tomography the specimens were dehydrated with ethanol (70%–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 Synchrotron Facility (DESY, Hamburg) using a low photon energy beam (8 kV) and absorption contrast (see Friedrich et al., 2008). For scanning electron microscopy specimens were dehydrated with ethanol (70%–100%) and acetone, critical point dried, glued on a fine pin and sputter coated. Images were taken with an FEI (Philips) XL 30 ESEM on a specimen holder after Pohl (in press). One specimen was examined with a confocal scanning microscope LSM 510 (Zeiss, Göttingen, Germany). As insect cuticle, musculature and nervous system are autofluorescent, treatment with antibodies was not necessary (see Klaus et al., 2003).

Muscles are named following the nomenclature of Kéler (1963).

3. Results

The head structures are described in detail for the male, whereas the treatment of the female is focussed on sexually dimorphic features.

3.1. Head capsule

The head is held in an unusual position on the ventral side of the thorax (Fig. 1). Its ventral part is closely adjacent to the forelegs. The head capsule is sclerotised and all parts except the ventral side are densely covered with microtrichia. More widely spaced longer setae are present on the clypeal region. The head is broader than long in frontal view, flattened in lateral view and ventromedially concave. The nearly rounded compound eyes are placed on the ventral head lateral region. On their mesal side they are delimited by a circumcular ridge. The antennae insert on the frontal side, dorsally between the compound eyes. The articulation fossae are widely separated. A deep furrow is present below the antennal bases (Fig. 1A). The anterior tentorial grooves are distinctly recognisable between the compound eyes (atg, Fig. 1A). Ocelli are absent.

The coronal-, frontal-, frontoctypeal-, subgenal- and occipital-sutures are missing, and also the median frontal apodeme. The head regions can only be vaguely identified by their position and the muscle insertion areas. The genal regions lie frontally between the compound eyes and reach the clypeus. The insertion area of M. clypeobuccalis (M. 43) and the anterior tentorial grooves can be considered as landmarks identifying the clypeal region. The frontal area can be identified by the insertion area of M. fronto-buccalis posterior (M. 46) (46, Fig. 4D). The ventral closure of the head is completely sclerotised and corresponds with the postgenal regions. They are fused mediadly thus forming a postgenal or hypostomal bridge. Laterally on the ventral side, lateral the “smooth” region, the distinct posterior tentorial grooves are present (ptg, Fig. 2A). The mouth opening lies also on the ventral side of the head (mo, Fig. 2A). Movable mouthparts are completely missing. Posterad the mouth opening there is a second small opening, probably representing opening of the vestigial salivary duct (sd, Fig. 2A). A field with five sensilla is present anterior to the mouth opening.

The head capsule of the female is less sclerotised and less flattened in lateral view but otherwise very similar.

3.2. Tentorium

The tentorium is represented by a simple hollow rod connecting the ventral and dorsal side of the head capsule (tnt, Fig. 4B). The internal surface of the tentorium is covered with short microtrichia like most parts of the external head capsule.

3.3. Labrum

Absent or completely fused with the head capsule.

Musculature: absent.
3.4. Antenna

The antenna is composed of 6 segments, the scape, pedicel and 4 flagellomeres. They insert frontally between the compound eyes. All antennomeres are densely covered with short microtrichia (Fig. 2B).

The scape is cylindrical and about three times as long as the small, globular pedicel (sc, pe, Fig. 1A). Flagellomere 1 is about \(\frac{1}{4}\) longer than the scape, but narrower. The diameter of the following antennomeres is similar to flagellomere 1, but they differ in their length. Flagellomeres 2 and 3 are about \(\frac{1}{2}\) as long as flagellomere 1. The last segment is greatly enlarged, distinctly longer than the entire body and narrows from its base to the conical apex.

Widely spaced sensilla are regularly distributed between the microtrichia of all antennal segments. A tuft of about eight sensilla is on the ventral side of the proximal part of flagellomere 1. Two additional sensilla are inserted distally. Several sensilla sunk in mesal grooves are present lateral of the sensilla tuft. Tufts of eight sensilla are also present on the middle region of flagellomeres 2 and 3, and five countersunk sensilla on the lateral side of both segments (Fig. 2B). The extremely elongated flagellomere 4 bears two rows of hook-shaped sensilla on the mesal side. Their size decreases from the base to the apex of the segment.

The antenna of the female is distinctly shorter. The apical segment is not elongated.

**Musculature:** (1, 2, 5, 6, Fig. 4A, B, D) M. 1: M. tentorioscapalis anterior: a muscle with multiple areas of origin; O (origin) = genal region, laterally of the tentorial base (1), dorsal side of the tentorium (2), on the clypeal region mesally of the first two bundles (3), dorsolaterally of the third bundle (4); I (insertion) = ventromedial margin of the scapus; F (function) = depressor of the antenna. M. 2: M. tentorioscapalis posterior: a very broad and flat muscle on the dorsal side of the head; O = vertex; I = dorsal margin of the scapus; F = levator, antagonist of M. tentorioscapalis anterior. M. 3:

3.5. Mandible
Absent.
Musculature: Absent.

3.6. Maxilla
Absent.
Musculature: Absent.

3.7. Labium
Absent.
Musculature: Absent.

3.8. Epi- and hypo-pharynx
The anterior epipharynx is completely reduced. The posterior epipharynx is largely membranous and devoid of microtrichia. The hypopharynx forms the U-shaped floor of the cibarium (cib, Fig. 5). Posteriorly the cibarium is continuous with the pharynx. At the anatomical mouth opening the hypopharynx forms two dorsolateral apophyses.

Musculature: (43, Figs. 3, 4A, D, 5) M. 41: M. frontohyopha-

3.9. Pharynx
The position of anatomical mouth opening is marked externally by the antennal insertions. The precerebral part of the pharynx is U-shaped in cross section, with the upper edges forming dorsolateral extensions. The following part of the pharynx between the brain and the suboesophageal complex and also the postcerebral part of the pharynx are Y-shaped in cross section, with distinct drawn out edges (ph, Fig. 4C). The spaces between these extensions are the attachment areas of the muscles forming the postpharyngeal pumping apparatus (S1, S2, Figs. 3, 4C, 5). In the postoccipital region the pharynx is continuous with the oesophagus.

Musculature: (46, 51, 52, 68, Figs. 3, 4A, C, D, 5) M. 45: M. fron-
tudinalis stomodaei: absent.

3.10. Salivarium
The salivary duct opens ventrally of the mouth opening on the ventral side of the head (sd, Fig. 2A). It is only a short vestigial duct, without a connection to salivary glands or any other structure.

Musculature: Absent.

3.11. Nervous system
The brain and suboesophageal complex are very large in relation to the size of the head capsule (Figs. 3 and 4). Both units form a compact complex around the posterior pharynx (Fig. 4C). It lies within the posterior half of the head capsule and occupies a large proportion of the lumen. Proto-, deuto- and trito-cerebrum are completely fused, without externally recognisable borders. A trito-
cerebral commissure is not recognisable as a separate structure. The optic lobes are very large (Fig. 4). They comprise about one third of the brain volume. The thin antennal nerves (Nn. anten-
nales) arise at the frontal region on the head. The frontal ganglion lies above the palatum and thick frontal connectives connect it with the brain (fg, Fig. 3). The N. frontale, N. connectivus and N. recures

3.12. Tracheal system
Four pairs of tracheae enter the head, two of them in the dorsal region and the two others laterally. The dorsolateral and the lateral pairs split into many thin tracheae, which mainly supply the brain with oxygen. The branches arising from the dorsomedian pair mainly supplies the musculature of the antennae.

3.13. Fat body
A larger assemblage of fat body tissue is posterior to the brain.
3.14. Phylogenetically relevant characters

(see Table 1, 2)

1. Frontal apodeme (fap): (0) present; (1) absent
A frontal apodeme between the antennal bases is absent in Deuterophlebia and also missing in Nymphomyia Tokunaga, 1932 (Tokunaga, 1935), Tipula Latreille, 1802 (Tipulidae) (Schneeberg and Beutel, in press), Bibio Geoffroy, 1762 (Bibionidae) (Skanda, 2008), Eristalis Latreille, 1804 (Syrphidae) (Schiemenz, 1957), Hemipenthes Loew, 1861, Bombylius Linnaeus, 1758 (Bombyliidae) (Szucsich and Krenn, 2000), Ctenocephalus Curtis, 1826 (Siphonaptera) (Wenk, 1953), and also in members of all groups of Mecoptera with the notable exception of Nannochoristidae (Heddergott, 1938; Hepburn, 1969; Beutel and Baum, 2008: Fig. 5 [fap]). A small apodeme-like structure is present in Tri- chocera Meigen, 1803 (Trichoceridae) dorsally between the antennal bases (Schneeberg and Beutel, in press). It is distinctly developed in Edwardsina Alexander, 1920, Limonia Meigen, 1803 (Limoniidae), Mischoderus Handlirsch, 1909 (Tanyderidae) (Schneeberg and Beutel, in press), in representatives of Culicidae (Schiemenz, 1957; Christophers, 1960; Owen, 1985; Harbach and Kitching, 1998), and in Wilhelmia Enderlein, 1921 (Simuliidae) (Wenk, 1962).

2. Frontoclypeal-/epistomal suture (fcs): (0) present as a strengthening ridge; (1) present as a joint; (2) absent
Both regions are fused in Deuterophlebia (Fig. 1A), Edwardsina, Nymphomyia (Tokunaga, 1935), Simulium Latreille, 1902 (Wenk, 1962, Fig. 1) and Ctenocephalus (Wenk, 1953). The suture is present in Limonia, Tri chocera (Schneeberg and Beutel, in press), Bibio (Skanda, 2008), Eristalis (Schiemenz, 1957), Bombylius (Szucsich and Krenn, 2000), Tabanus Linnaeus, 1758 (Bonhag, 1951), Mischoderus (Schneeberg and Beutel, in press) and Prot oplasa Oosten Sacken, 1859 (Williams, 1933). It is distinctly developed in T. pululoida (Schneeberg and Beutel, in press), whereas it appears to be absent in Tipula reesi Alexander, 1939 (Rees and Ferris, 1939) and Tipula sp. (Bitsch et al., 1973).
suture is also present in members of Mecoptera (Heddergott, 1938; Hebourn, 1969; Beutel and Baum, 2008; Beutel et al., 2008). A joint between the clypeus and frons in adults of Culicidae (e.g. Schiemenz, 1957; Christophers, 1960; Hennig, 1973) is a potential autapomorphy of the family. The increased mobility of the clypeus in relation to the anterior frontal margin is likely correlated with the formation of a fulcrum (see character 13).

3. Clypeus (cly): (0) subdivided into ante- and postclypeus; (1) undivided

A transverse suture separating an anterior anteclypeus from the posterior postclypeus is present in the groundplan of Diptera according to Crampton (1942). However, the division is absent in Deuterophlebia, Edwardsina and Nymphomyia (Courtney, 1994b), and is also almost generally missing in other groups (e.g. Williams, 1933; Tokunaga, 1935; Bonhag, 1951; Hoyt, 1952; Schiemenz, 1957; Wenk, 1962; Szucsich and Krenn, 2000; Skanda, 2008; Schneeberg and Beutel, in press). A transverse clypeal furrow is present in adults of Culicidae (e.g. Culex Linnaeus, 1758, Culiseta Felt, 1904; Aedes Meigen, 1818; Schiemenz, 1957; Christophers, 1960; Owen, 1985), and also in Nannochorista Tillyard, 1917 (Beutel and Baum, 2008) and Caurinus Russel, 1979 (Beutel et al., 2008). It is absent in other groups of Mecoptera (Heddergott, 1938; Hebourn, 1969) and also in Siphonaptera (Wenk, 1953) and some other groups of endopterygote insects (Beutel and Baum, 2008).

4. Insertion of antennae (ais): (0) frontally, not adjacent medially; (1) frontally, adjacent in midline; (2) laterally, widely separated

The antennae insert on the dorsal side of the head and are widely separated in Deuterophlebia (Fig. 1A) and Bibio (Skanda, 2008, Fig. 2A). They are also widely separated in Caurinus (Beutel et al., 2008) and Ctenocephalus (Wenk, 1953). The antenna insertions lie frontally between the compound eyes in Edwardsina, Nymphomyia (Tokunaga, 1935), Tipula, Limonia, Mischoderus (Schneeberg and Beutel, in press), Protoplase (Williams, 1933), in representatives of Culicidae (Schiemenz, 1957; Christophers, 1960; Owen, 1985; Harbach and Kitching, 1998), Simuliidae (Wenk, 1962), Tabanidae (Bonhag, 1951), Bombyliidae (Peterson, 1916), and also in Nannochorista (Beutel and Baum, 2008) and Panorpa Linnaeus, 1758 (Heddergott, 1938). This is also the case in Trichocera (Schneeberg and Beutel, in press) and Eristalis (Schiemenz, 1957, Fig. 31), where they are medially adjacent.

5. Terminal segment of the antenna (lae): (0) not elongated; (1) elongated

The last antennal segment is extremely elongated in males of Deuterophlebia and also elongated in Nymphomyia (Courtney, 1994b, Figs. 16, 26, 29). In Deuterophlebia only the terminal segment is elongate, whereas the enlarged element in Nymphomyia is probably formed by several fused flagellomeres. Nevertheless, a distinct increase in size of the true terminal segment has apparently taken place but the last part might be the elongated last flagellomere (see Courtney, 1994b, Fig. 79). The segment is not elongated in members of most other groups of Diptera (Williams, 1933; Bonhag, 1951; Schiemenz, 1957; Christophers, 1960; Wenk, 1962; Skanda, 2008; Schneeberg and Beutel, in press), and this condition is also unknown in Mecoptera (Beutel et al., 2008; Beutel and Baum, 2008).

6. Ocelli (oce): (0) present; (1) vestigial or absent

Ocelli are absent in adults of Deuterophlebia (Courtney, 1990a, 1991a), Tipula, Limonia, Culex, Anopheles Meigen, 1816 Mischoderus (Schneeberg and Beutel, in press), Culiseta (Schiemenz, 1957; Owen, 1985), Wilhemia (Wenk, 1962), Protoplase (Williams, 1933), Caurinus (Beutel et al., 2008), and also in Ctenocephalus (Wenk, 1953). Three ocelli are present on the vertex in Edwardsina, Trichocera (Schneeberg and Beutel, in press), Bibio (Skanda, 2008), Eristalis (Schiemenz, 1957), Exoprosopa Marcqart, 1840 (Peterson, 1916), Nannochorista (Beutel and Baum, 2008) and Panorpa (Heddergott, 1938). Christophers (1960) described a pair of degenerated ocelli on the frons of Aedes. A pair is present posterolaterad of the large compound

---

**Table 1**

Data matrix. Presumptive groundplan features of Diptera are coded as 0, regardless whether they are plesiomorphic or apomorphic compared to the corresponding character states in the other antiophoran taxa.
eyes of *Nymphomyia* (Tokunaga, 1935; Courtney, 1994b). Bonhag (1951) described three rudimentary ocelli on the vertex of *Tabanus*.

7. Coronal-/epicranial-suture (cos): (0) present; (1) absent
A coronal suture is absent in *Deuterophlebia*, *Edwardsina*, *Tipula*, *Limonia*, *Trichocera*, *Mischoderus* (*Schneeberg and Beutel, in press*), *Protoplala* (Williams, 1933), *Bibio* (Skanda, 2008), *Wilhelmina* (Wenk, 1962), *Tabanus* (Bonhag, 1951), *Eristalis* (Schiemenz, 1957), *Caurinus* (Beutel et al., 2008) and many other representatives of Mecoptera (Hepburn, 1969). It is present in *Culex* (Schneeberg and Beutel, in press), *Culiseta* (Schiemenz, 1957; Owen, 1985, Fig. 1), *Aedes* (Christophers, 1960, Fig. 53/1), *Nymphomyia* (Tokunaga, 1935), and in *Nannochorista* (Beutel and Baum, 2008). The presence is apparently a plesiomorphic condition preserved in *Nymphomyiidae* and *Culicidae*.

8. Postgenal bridge (pgb): (0) present; (1) absent
A postgenal bridge is present in *Deuterophlebia* (Courtney, 1990a), *Nymphomyia* (Tokunaga, 1935; Courtney, 1994b), and also in *Tipula* (Schneeberg and Beutel, in press), *Limmaphila* Marcquart, 1834 (Hoyt, 1952), *Aedes* (Christophers, 1960), *Bibio* (Skanda, 2008), *Tabanus* (Bonhag, 1951), *Eristalis* (Schiemenz, 1957), *Exoprosopa* (Peterson, 1916), *Rhagio Fabrícius*, 1775 (Hoyt, 1952), *Cenecocephalus* (Wenk, 1953), and in representatives of Mecoptera (e.g. Heddergott, 1938; Beutel et al., 2008) (with the possible exception of *Nannochorista*, *Beutel and Baum, 2008*). The ventral closure of the head capsule is largely membranous in *Limonia*, but a narrow postgenal bridge is present anterior to the foramen occipitale (*Schneeberg and Beutel, in press*). The bridge is absent in *Edwardsina*, *Erioptera* Meigen, 1803, *Dictanomyia* Stephens, 1829 (Hoyt, 1952), *Trichocera*, *Mischoderus* (*Schneeberg and Beutel, in press*), *Protoplala* (Williams, 1933), *Culiseta* (Schiemenz, 1957, Fig. 4 [gu]; Owen, 1985), *Pychoptera* Meigen, 1803, *Mycetophila* Meigen, 1818, *Mycomya* Rondani, 1856 (Hoyt, 1952), *Wilhelmina* (Wenk, 1962) and *Symphoromyia* Frauenfeld, 1867 (Hoyt, 1952). The head is largely membranous on its ventral side in adults of these taxa.

9. Tentorium (tnt): (0) present; (1) absent
The tentorium is present as a more or less straight tube-like rod in *Deuterophlebia* (tnt, Fig. 4B), *Edwardsina* and many other groups of Diptera (e.g. Thompson, 1905; Peterson, 1916; Williams, 1933, Fig. 3; Hoyt, 1952; Schiemenz, 1957; Christophers, 1960; Wenk, 1962; Owen, 1985; Skanda, 2008). A similar condition is found in representatives of Mecoptera (Heddergott, 1938; Hepburn, 1969; Beutel and Baum, 2008; Beutel et al., 2008) and *Siphonaptera* (*Wenk, 1953*). The tentorium is completely absent in *Nymphomyia* (Tokunaga, 1935) and *Tipula* (Schneeberg and Beutel, in press).

10. Dorsal tentorial arm (dta): (0) present or present as a thin thread-like structure; (1) short vestigial structure; (2) absent
The dorsal arm is completely missing in *Deuterophlebia* and *Edwardsina* (Courtney, 1991a), and is also absent in *Limonia* (Schneeberg and Beutel, in press), *Culex* (Thompson, 1905), *Aedes* (Christophers, 1960), *Bibio* (Skanda, 2008) and *Cenecocephalus* (Wenk, 1953). It is present as a short vestige in *Culiseta* (Schiemenz, 1957, Fig. 5 [d.Ta]; Owen, 1985, Fig. 4), *Eristalis* (Schiemenz, 1957, Figs. 38, 39), *Exoprosopa* (Peterson, 1916) and *Nannochorista* (Beutel and Baum, 2008, Fig. 2d [dta]). *Wenk* (1962) described a tentorial ridge for *Wilhelmina*, extending dorsad towards the antennal foramen (*Wenk*, 1962, Fig. 2). A typical, well-developed dorsal arm is apparently almost always absent in *Antiphora* (Heddergott, 1938; Hepburn, 1969; Beutel and Baum, 2008), but a thin, sclerotised structure is present and connected to the head capsule in *Caurinus* (Beutel et al., 2008, Fig. 5C, D). It is noteworthy that dorsal arms are also present in *Tabanus* (Bonhag, 1951, Fig. 5). However, considering the position of *Tabanidae*, it appears likely that the presence is due to reversal in this case.
Table 2
Insect taxa mentioned in the text (classification mostly after Oosterbroek and Courtney, 1995).

<table>
<thead>
<tr>
<th>Genus</th>
<th>Family</th>
<th>Suborder</th>
<th>Order</th>
</tr>
</thead>
<tbody>
<tr>
<td>Deuterophlebia</td>
<td>Deuterophlebiidae</td>
<td>Blephariceromorpha</td>
<td>Diptera</td>
</tr>
<tr>
<td>Nymphomyia</td>
<td>Nymphomyiidae</td>
<td>Blephariceromorpha</td>
<td>Diptera</td>
</tr>
<tr>
<td>Edwardina</td>
<td>Blephariceridae</td>
<td>Blephariceromorpha</td>
<td>Diptera</td>
</tr>
<tr>
<td>Culex</td>
<td>Cucicidae</td>
<td>Cucicormorpha</td>
<td>Diptera</td>
</tr>
<tr>
<td>Culiceta</td>
<td>Cucicidae</td>
<td>Cucicormorpha</td>
<td>Diptera</td>
</tr>
<tr>
<td>Aedes</td>
<td>Cucicidae</td>
<td>Cucicormorpha</td>
<td>Diptera</td>
</tr>
<tr>
<td>Anopheles</td>
<td>Cucicidae</td>
<td>Cucicormorpha</td>
<td>Diptera</td>
</tr>
<tr>
<td>Wilhelmina</td>
<td>Simulidae</td>
<td>Cucicormorpha</td>
<td>Diptera</td>
</tr>
<tr>
<td>Simulium</td>
<td>Simulidae</td>
<td>Cucicormorpha</td>
<td>Diptera</td>
</tr>
<tr>
<td>Ptychoptera</td>
<td>Ptychopterae</td>
<td>Ptychopteromorpha</td>
<td>Diptera</td>
</tr>
<tr>
<td>Mischoderus</td>
<td>Tanyderidae</td>
<td>Ptychopteromorpha</td>
<td>Diptera</td>
</tr>
<tr>
<td>Protoplasa</td>
<td>Tanyderidae</td>
<td>Ptychopteromorpha</td>
<td>Diptera</td>
</tr>
<tr>
<td>Tipula</td>
<td>Tipulidae</td>
<td>Tipulomorpha</td>
<td>Diptera</td>
</tr>
<tr>
<td>Limonia</td>
<td>Limoniidae</td>
<td>Tipulomorpha</td>
<td>Diptera</td>
</tr>
<tr>
<td>Linnophila</td>
<td>Limoniidae</td>
<td>Tipulomorpha</td>
<td>Diptera</td>
</tr>
<tr>
<td>Erioptera</td>
<td>Limoniidae</td>
<td>Tipulomorpha</td>
<td>Diptera</td>
</tr>
<tr>
<td>Dictranomyia</td>
<td>Limoniidae</td>
<td>Tipulomorpha</td>
<td>Diptera</td>
</tr>
<tr>
<td>Trichocera</td>
<td>Trichoceridae</td>
<td>Tipulomorpha</td>
<td>Diptera</td>
</tr>
<tr>
<td>Bibio</td>
<td>Bibionidae</td>
<td>Bibionomorpha</td>
<td>Diptera</td>
</tr>
<tr>
<td>Mycetophila</td>
<td>Mycetophilidae</td>
<td>Bibionomorpha</td>
<td>Diptera</td>
</tr>
<tr>
<td>Myconymia</td>
<td>Mycetophilidae</td>
<td>Bibionomorpha</td>
<td>Diptera</td>
</tr>
<tr>
<td>Tabanus</td>
<td>Tabanidae</td>
<td>Tabanomorpha</td>
<td>Diptera</td>
</tr>
<tr>
<td>Rhagionidae</td>
<td>Tabanomorpha</td>
<td>Tabanomorpha</td>
<td>Diptera</td>
</tr>
<tr>
<td>Symphoromyia</td>
<td>Rhagionidae</td>
<td>Tabanomorpha</td>
<td>Diptera</td>
</tr>
<tr>
<td>Eristalis</td>
<td>Syrphidae</td>
<td>Muscoromorpha</td>
<td>Diptera</td>
</tr>
<tr>
<td>Hemipenthes</td>
<td>Bombyliidae</td>
<td>Asilomorpha</td>
<td>Diptera</td>
</tr>
<tr>
<td>Bombylius</td>
<td>Bombyliidae</td>
<td>Asilomorpha</td>
<td>Diptera</td>
</tr>
<tr>
<td>Exoprosopa</td>
<td>Bombyliidae</td>
<td>Asilomorpha</td>
<td>Diptera</td>
</tr>
<tr>
<td>Nannochorista</td>
<td>Nannochoristidae</td>
<td>Mecoptera</td>
<td>Mecoptera</td>
</tr>
<tr>
<td>Caurinus</td>
<td>Boreidae</td>
<td>Mecoptera</td>
<td>Mecoptera</td>
</tr>
<tr>
<td>Panorpa</td>
<td>Panoropidae</td>
<td>Mecoptera</td>
<td>Mecoptera</td>
</tr>
<tr>
<td>Ctenocephalus</td>
<td>Siphonaptera</td>
<td>Siphonaptera</td>
<td>Siphonapte</td>
</tr>
<tr>
<td>Osmylus</td>
<td></td>
<td></td>
<td>Neuroptera</td>
</tr>
</tbody>
</table>

11. Shape of the anterior tentorial arm (ata): (0) thick, approximately round in cross section, hollow; (1) partly hollow; (2) massive
The tentorium of Deuterophlebia, Edwardina, Mischoderus, Trichocera (Schneeberg and Beutel, in press), Bibio (Skanda, 2008), Wilhelmina (Wenk, 1962) and Nannochorista (Beutel and Baum, 2008) is a thick, hollow tube, and this is also the case in Culicidae (Thompson, 1905; Schiemenz, 1957; Christophers, 1960; Owen, 1985), where the lumen is wider anteriorly. A recognisable lumen is not present in Eristalis (Schiemenz, 1957), Exoprosopa (Peterson, 1916) and Caurinus (Beutel et al., 2008). The lumen of the anterior part of the tentorium is narrow in Limonia. It widens at the level of the brain and the posterior hollow part is approximately round in cross section (Schneeberg and Beutel, in press). The anterior tentorial arms of Ctenocephalus are missing (Wenk, 1953).

12. Labrum (lbr): (0) present; (1) absent
With the exception of Deuterophlebia (Courtney, 1990a, 1991a) and Nymphomyia (Tokunaga, 1935), the labrum is present in all members of Diptera (e.g. Thompson, 1905; Williams, 1933; Bonhag, 1951; Hoyt, 1952; Schiemenz, 1957; Wenk, 1962; Christophers, 1960; McAlpine, 1981; Owen, 1985; Courtney, 1991a; Skanda, 2008; Schneeberg and Beutel, in press), Mecoptera (Heddergott, 1938; Hepburn, 1969; Beutel and Baum, 2008; Beutel et al., 2008) and Siphonaptera (Wenk, 1953) examined.

13. Fulcrum (flc): (0) absent; (1) present
A fulcrum with lateral fulcal plates, which join the external clypeal wall distally, is absent in Deuterophlebia, Edwardina, and Nymphomyia (Tokunaga, 1935), and is also missing in Tipula, Limonia, Trichocera (Schneeberg and Beutel, in press), Bibio (Skanda, 2008), Wilhelmina (Wenk, 1962), Tabanus (Bonhag, 1951), Nannochorista (Beutel and Baum, 2008), Caurinus (Beutel et al., 2008), Panorpa (Heddergott, 1938) and Ctenocephalus (Wenk, 1953). It is generally present in adults of Culicidae (Schiemenz, 1957; Christophers, 1960; Owen, 1985), and does also occur in Syrphidae (Schiemenz, 1957), Tanyderidae (Williams, 1933; Protoplasa) and Bombyliidae (Szusch and Krenn, 2000; Hemipenthes, Bombylius).

14. Origin of M. tentorioscapalis anterior (M. 1): (0) tentorium; (1) head capsule
In Deuterophlebia the muscle has multiple origins, three on the head capsule and one on the dorsal side of the tentorium (1, Fig. 4D). It originates on the prefrontal region of the head capsule in Tipula, Limonia (Schneeberg and Beutel, in press) and Nymphomyia (Tokunaga, 1935). The muscle originates on the clypeus in Ctenocephalus (Wenk, 1953), and on the tentorium in Edwardina, Trichocera (Schneeberg and Beutel, in press), Bibio (Skanda, 2008), Wilhelmina (Wenk, 1962), Tabanus (Bonhag, 1951), Eristalis (Schiemenz, 1957), and also in representatives of Culicidae (Thompson, 1905; Schiemenz, 1957; Christophers, 1960; Owen, 1985), Bombyliidae (Szusch and Krenn, 2000) and Mecoptera (Heddergott, 1938; Beutel and Baum, 2008; Beutel et al., 2008).

15. Origin of M. tentorioscapalis posterior (M. 2): (0) tentorium; (1) head capsule
M. 2 originates on the genal region of the head capsule in Tipula, between the clypeus and the margin of the compound eye (Schneeberg and Beutel, in press). It also originates on the head capsule in Deuterophlebia (2, Fig. 4D), Edwardina, Nymphomyia (Tokunaga, 1935), Hemipenthes (Szusch and Krenn, 2000) and Ctenocephalus (Wenk, 1953). It is difficult to distinguish between M. 2 and M. 4 in Limonia. Both muscles lie very closely together and have a nearly identical point of insertion on the scapus and closely adjacent areas of origin on the tentorium. In Trichocera the origin lies dorsally on the anterior tentorial arm (Schneeberg and Beutel, in press) and this is also the case in Aedes (Christophers, 1960) and Wilhelmina (Wenk, 1962). In Culiseta (Schiemenz, 1957; Owen, 1985) it originates laterally on the anterior tentorium and it arises on the dorsal arm in Tabanus (Bonhag, 1951). The muscle also originates on the tentorium in Bibio (Skanda, 2008) like in all adults of Mecoptera examined (e.g. Heddergott, 1938; Beutel et al., 2008; Beutel and Baum, 2008). The area of origin lies on the circumocular ridge in Eristalis (Schiemenz, 1957) and a similar M. orbitoscapalis is also present in Bombylius (Szusch and Krenn, 2000). Schiemenz (1957) interpreted this muscle as M. tentorioscapalis posterior (M. 2). However, it cannot be excluded that it is in fact M. tentorioscapalis medialis (M. 4).

16. Origin of M. tentorioscapalis medialis (M. 4): (0) tentorium; (1) frontal region of head capsule; (2) genal region of head capsule; (3) on the vertex
M. tentorioscapalis medialis originates on the genal region in Tipula (Schneeberg and Beutel, in press) and Nymphomyia (Tokunaga, 1935), and on the frons in Trichocera, Bibio, Tabanus and Nannochorista (Bonhag, 1951; Skanda, 2008; Beutel and Baum, 2008; Schneeberg and Beutel, in press). It originates on the vertex in Panorpa (Heddergott, 1938), and on the clypeus in Ctenocephalus (Wenk, 1953). The muscle is absent in representatives of Culicidae (Thompson, 1905; Schiemenz, 1957; Christophers, 1960; Owen, 1985) and Simuliidae (Wenk, 1962).
It originates on the anterior tentorium in Hemipenthes (Szcusch and Krenn, 2000) and Caurinus (Beutel et al., 2008). As pointed out above, the homology of the muscle is not entirely clear in Limonia, Eristalis and Bombylius (see character 15).

17. Mandible (mdb): (0) present; (1) absent
The mandibles are absent in males and females in Deuterophlebia (Courtney, 1990a, 1991a), Nymphomyia (Tokunaga, 1935; Courtney, 1994b), Tipula, Limonia, Trichocera (Schneeberg and Beutel, in press), Bibio (Skanda, 2008), Protoplasa (Williams, 1933), Eristalis (Schiemenz, 1957), in representatives of Bombyliidae (Szcusch and Krenn, 2000), and also in Ctenocephalus (Wenk, 1953). They are only developed in females of Edwardsina and Symphoromyia (Rhationidae) (Hoyt, 1952), whereas they are always present in adults of Culicidae (Schiemenz, 1957; Christophers, 1960; Owen, 1985), Simulidae (Wenk, 1962), Tabanidae (Bonhag, 1951) and Mecoptera (e.g. Heddergott, 1938; Hepburn, 1969; Beutel and Baum, 2008; Beutel et al., 2008).

18. Maxilla (max): (0) present; (1) absent
The maxilla is absent in Deuterophlebia (Courtney, 1990a, 1991a), Nymphomyia (Tokunaga, 1935; Courtney, 1994b) and also missing in some chironomids (Neumann, 1976). It is present in all other members of Diptera (e.g. Thompson, 1905; Williams, 1933; Bonhag, 1951; Hoyt, 1952; Schiemenz, 1957; Christophers, 1960; Wenk, 1962; Owen, 1985; Skanda, 2008; Schneeberg and Beutel, in press), Mecoptera (Heddergott, 1938; Hepburn, 1969; Beutel and Baum, 2008; Beutel et al., 2008) and Siphonaptera (Wenk, 1953).

19. Labium (lbm): (0) present; (1) absent
In all dipterans (e.g. Thompson, 1905; Williams, 1933; Bonhag, 1951; Hoyt, 1952; Schiemenz, 1957; Christophers, 1960; Wenk, 1962; Owen, 1985; Skanda, 2008; Schneeberg and Beutel, in press), Mecoptera (Heddergott, 1938; Hepburn, 1969; Beutel and Baum, 2008; Beutel et al., 2008) and siphonapterans (Wenk, 1953), with the exception of Deuterophlebia (Courtney, 1990a, 1991a), Nymphomyia (Tokunaga, 1935; Courtney, 1994b) and some Chironomidae (Neumann, 1976), a labium is present.

20. M. frontohypopharyngalis (M. 41): (0) present; (1) absent
The muscle is absent in Deuterophlebia, Edwardsina, Nymphomyia (Tokunaga, 1935), Limonia, Trichocera (Schneeberg and Beutel, in press), Bibio (Skanda, 2008), Wilhelmitina (Wenk, 1962), and in representatives of Bombyliidae (Szcusch and Krenn, 2000). A small bipartite muscle is present in Tipula. It extends from the lateral clypeal wall to the lateral wall of the hypopharynx (Schneeberg and Beutel, in press). The homology with M. frontohypopharyngalis is questionable. A muscle connecting the postfrontal ridge and the dorsal fulcral apophyses is present in representatives of Culicidae (Thompson, 1905; Schiemenz, 1957; Owen, 1985) and in Eristalis (Schiemenz, 1957). It is likely that it mainly stabilises the cibarium and it is probably homologous with M. frontohypopharyngalis. However, Schiemenz (1957) assumed its homology with M. frontobuccalis lateralis (M. 47) (Culiseta and Eristalis) and a similar muscle is present in Aedes. It originates on the median frontal ridge and is inserted on the lateral horn of the cibarium (Christophers, 1960, Fig. 67/1 [21]). A muscle, which connects the clypeofrontal ridge and the anterior surface of the pharynx, is present in Tabanus (Bonhag, 1951, Fig. 10 [22]), but the homology with M. 41 is also questionable. M. frontohypopharyngalis is present in Ctenocephalus (Wenk, 1953), Nannochorista and Caurinus, but absent in other mectoperans (Heddergott, 1938; Hepburn, 1969; Beutel and Baum, 2008; Beutel et al., 2008).

21. Size of M. clypeopatalalis (M. 43): (0) long series of bundles; (1) bipartite, strongly developed; (2) not enlarged
The muscle is not enlarged in Deuterophlebia (43, Figs. 3, 5). M. clypeopatalalis is a long series of bundles in Edwardsina and also in Tipula, Limonia, Trichocera, Mischoderus (Schneeberg and Beutel, in press), Bibio (Skanda, 2008), Tabanus (Bonhag, 1951), Eristalis (Schiemenz, 1957), Hemipenthes, Bombylius (Szcusch and Krenn, 2000), and most members of Culicidae (Thompson, 1905; Schiemenz, 1957; Owen, 1985). A similar condition is found in Panorpa (Heddergott, 1938) and Ctenocephalus (Wenk, 1953). Christophers (1960) described a bipartite muscle for Aedes, and a similar condition is present in Wilhelmitina (Wenk, 1962) and Nannochorista (Beutel and Baum, 2008). It is composed of three subcomponents in Caurinus and is not enlarged (Beutel et al., 2008). Tokunaga (1935) described a large muscle with three subcomponents for Nymphomyia (Tokunaga, 1935, Figs. 1, 7).

22. Mm. frontobuccalis anterior/posterior (Mm. 45/46): (0) both present; (1) one muscle; (2) absent
M. frontobuccalis posterior (M. 46) is the only dorsal precerebral dilator in Deuterophlebia (46, Figs. 3, 5). Tipula, Limonia (Schneeberg and Beutel, in press) and representatives of Bombyliidae (Szcusch and Krenn, 2000). Both precerebral dorsal dilators are present in Edwardsina, Trichocera (Schneeberg and Beutel, in press) and Mischoderus, in representatives of Culicidae (Thompson, 1905; Schiemenz, 1957; Christophers, 1960; Wenk, 1962; Owen, 1985), and in Tabanus (Bonhag, 1951), Caurinus (Beutel et al., 2008) and Ctenocephalus (Wenk, 1953). M. frontobuccalis anterior is present in Bibio according to Skanda (2008). Both muscles are absent in Eristalis (Schiemenz, 1957), Nannochorista (Beutel and Baum, 2008) and Panorpa (Heddergott, 1938). A series of bundles is present between the frontal ganglion and the brain in Nymphomyia (Tokunaga, 1935). It probably comprises both muscles.

23. M. tentoriobuccalis anterior (M. 48): (0) present; (1) absent
The muscle is absent in Deuterophlebia, Nymphomyia (Tokunaga, 1935), Eristalis (Schiemenz, 1957), Nannochorista (Beutel and Baum, 2008), Panorpa (Heddergott, 1938), Caurinus (Beutel et al., 2008) and Ctenocephalus (Wenk, 1953). Szcusch and Krenn (2000) described a protractor of the fulcrum in Hemipenthes and Bombylius, which is possibly homologous with M. 48 (mge). A muscle that extends from the ventrolateral wall of the anterior pharynx, below the frontal ganglion, to the circumcucal ridge is present in Edwardsina. This muscle is probably homologous with M. tentoriobuccalis anterior. M. 48 is present in Tipula, Limonia, Trichocera (Schneeberg and Beutel, in press), Bibio (Skanda, 2008), Wilhelmitina (Wenk, 1962), Tabanus (Bonhag, 1951), and in representatives of Culicidae (Thompson, 1905; Schiemenz, 1957; Christophers, 1960; Wenk, 1962; Owen, 1985).

24. Postcerebral pharyngeal pump (Mm. 51/52): (0) present; (1) absent
A strongly developed postcerebral pharyngeal pump is present in Deuterophlebia (51, 52, Fig. 4C). Edwardsina, Nymphomyia (Tokunaga, 1935) and also in Tipula, Limonia, Trichocera (Schneeberg and Beutel, in press), Bibio (Skanda, 2008), Wilhelmitina (Wenk, 1962), Mischoderus, Tabanus (Bonhag, 1951), and generally occurs in Culicidae (Thompson, 1905; Schiemenz, 1957; Christophers, 1960; Owen, 1985). It is also present in Nannochorista (Beutel and Baum, 2008), Panorpa (Heddergott, 1938)
and Siphonaptera (Wenk, 1953), but is missing in Eristalis (Schiemenz, 1957) and representatives of Bombyliidae (Szcuch and Krenn, 2000). A bipartite M. verticopharyngalis and a moderately developed M. tentoriopharyngalis posterior are present in Caurinus (Beutel et al., 2008). The presence is a potential synapomorphy of Diptera, Nannochoristidae and Siphonaptera. The postcerebral pharyngeal pump is functionally replaced by the labro-epipharyngeal pump in Cyclorrhapha (Gouin, 1949).

25. M. anularis stomodaei (M. 68): (0) enclosing the lateral and ventral wall of the posterior pharynx; (1) comprising a ring muscle Complete ring muscles are restricted to the oesophagus in Deuterophlebia (M. 68, Fig. 3) and Edwardsina, and also in Tipula, Trichocera (Schneeberg and Beutel, in press) and Nannochorista (Beutel and Baum, 2008). The bundles enclose only the ventral and lateral walls of the posterior pharynx and of the anterior pharynx in Edwardsina. Postpharyngeal ring muscles are present in Limonia (Schneeberg and Beutel, in press), Aedes (Christophers, 1960), Wilhelmia (Wenk, 1962), Tabanus (Bonhag, 1951), Nymphomyia (Tokunaga, 1935) and Panorpedia (Heddergott, 1938).

26. M. hypopharyngosalivarialis (M. 37): (0) present; (1) absent A salivary pump is absent in Deuterophlebia and Limonia (Schneeberg and Beutel, in press). M. hypopharyngosalivarialis is present in Edwardsina, Tipula, Trichocera (Schneeberg and Beutel, in press), Bibio (Skanda, 2008) and Mischoedera. It connects the ventral wall of hypopharynx with the dorsal wall of the salivary duct. An extrinsic dilator is also present in adults of Culicidae (Thompson, 1905; Schiemenz, 1957; Christophers, 1960; Owen, 1985), Simuliidae (Wenk, 1962), Tabanidae (Bonhag, 1951), Syrphidae (Schiemenz, 1957), Bombyliidae (Szcuch and Krenn, 2000), and Nannochorista (Beutel and Baum, 2008). M. hypopharyngosalivarialis is bipartite in Nymphomyia. It originates on the ventral membrane of the basipharynx and inserts on the salivarium (Tokunaga, 1935, Fig. 1). A typical M. hypopharyngosalivarialis is absent in Mecoptera (excluding Nannochoristidae, e.g. Beutel and Baum, 2008), but a strong intrinsic muscle of the wall of the salivary duct (Heddergott, 1938; Beutel et al., 2008) may be a derivative of this muscle.

4. Discussion

Deuterophlebiidae are an extremely specialised group of Diptera (e.g., Kennedy, 1958; Courtney, 1991b). The monophyly of the family is well supported by features of the larvae, pupae and characters of the postcepalic body of adults (see Courtney, 1991a, chs. 46–57), and also by characters of the adult head described here. A conspicuous potential autapomorphy is the widely separated insertion of the antennae on the dorsal side of the head (Fig. 1A). This condition, which is very unusual for Diptera, is found in some Bibionidae (Hoyt, 1952; Skanda, 2008), but is absent in other groups of Bibionomorpha such as Sarcidinae and Mycetophiliidae (Peterson, 1916), and also in Asymyiidae (Wihlm, 2009, Figs. 3.43, 3.44). An anterior extrinsic antennal muscle (M. 1) with multiple origins (1, Fig. 4D) and the loss of M. hypopharyngosalivarialis (M. 37) are further potential autapomorphies of Deuterophlebiidae. M. hypopharyngosalivarialis (M. 37) is also missing in Limonia (Schneeberg and Beutel, in press), but considering the presence in other members of Tipulidae this is certainly due to parallel evolution. Adults of Deuterophlebiidae display an exceptional degree of muscle reduction in the head. They possess only eight muscles (excluding intrinsic muscles of the fore gut), five of which belong to the antenna. Eleven head muscles are present in adults of Nymphomyiidae (Tokunaga, 1935), which are also characterised greatly reduced head structures (see below), 19 in Nannochoriistidae (Nannomectoptera) (Beutel and Baum, 2008), and 40 in Osmymus Lateirell, 1802 (Neuroptera) (Beutel et al., in press), a number that may come close to the holometabolon groundplan.

Despite the high degree of specialisation and numerous derived features, a basal position of Deuterophlebiidae within Diptera was suggested by Bertone et al. (2008) based on analyses of multiple nuclear genes. This hypothesis is not supported by characters of the adult head. There is not a single retained plesiomorphic feature in Deuterophlebiidae with a corresponding apomorphic condition in the other dipteran lineages.

Interestingly, the results of our study suggest close phylogenetic affinities of Deuterophlebiidae with Nymphomyiidae, another family considered as a candidate for the most basal lineage of Diptera (Rohdendorf, 1974; Hackman and Väisänen, 1982; Bertone et al., 2008 [analyses of reduced data set]). Like Deuterophlebiidae, Nymphomyiidae are a highly specialised group of Diptera. The adults are also very small (<2 mm) and the larvae live in a similar type of habitat (Courtney, 1991a, 1994b). Nymphomyiids are doublyless a monophyletic group (see Courtney, 1991a, chs. 14–32), with autapomorphies such as the loss of the unpaired ocellus, the shift of the paired lateral ocelli posterior to the compound eyes (Tokunaga, 1935; Courtney, 1994b), the complete reduction of the tentorium (parallel loss in Tipulidiae; Schneeberg and Beutel, in press), and the correlated shift of the origin of all extrinsic antennal muscles to the head capsule.

Adults of Deuterophlebiidae and Nymphomyiidae display an entire array of shared derived features of the adult head. In both groups and differing from nearly all other groups of Diptera (e.g., Hennig, 1973), the labrum is completely reduced. The maxillae, which are usually modified but distinctly developed, are also completely absent. The same applies to the labium, which usually plays a vital role in the food uptake. The loss of these structures (also missing in some chironomids with short-lived adults; Neumann, 1976) is associated with a dramatic degree of muscle reduction in both groups (see above). All labral, labial, mandibular and maxillary muscles are absent. Another potential synapomorphy is the loss of the anterior ventral dilator of the pharynx (M. 48). This muscle is also missing in Eristalis and in members of Bombyliidae (and some other groups), but is certainly present in the groundplan of Diptera (e.g., Heddergott, 1938; Wenk, 1953; Schiemenz, 1957; Szcuch and Krenn, 2000; Beutel and Baum, 2008; Beutel et al., 2008). Another feature supporting a clade Deuterophlebiidae + Nymphomyiidae is the elongation of the ultimate segment of the antenna of males. However, as pointed out above, the conditions in both groups differ distinctly. The antenna of male deuterophlebiids is extremely long (ca. 9.5 mm, body length ca. 2 mm; Pennak, 1951: Fig. 1), with an extremely elongated ultimate flagellomere (see Courtney, 1994a: char. 11), whereas the female antenna is distinctly shorter and lacking an elongated apical segment. In nymphomyiids only the apical element is elongated in males and females, but the antenna as a whole is short (Courtney, 1994b).

Some other affinities concerning the morphology and life history were pointed out by Courtney (1991a). In both families females shed their wings after or during oviposition, the femur and tibia are subdivided by a membranous zone, all abdominal spiracles are vestigial, and the spermatheca is absent (see Courtney, 1991a: chs. 29–32). These similarities were interpreted as convergences, related to an independent evolution of a short-lived adult stage (Courtney, 1991a).

In contrast to the potential sister group relationship between Nymphomyiidae and Deuterophlebiidae discussed here, Hennig (1973), Wood and Borkent (1989), Courtney (1990b, 1991a), and
Oosterbroek and Courtney (1995) proposed a clade Blephariceroida, with Deuterophlebiidae as sister group of Blephariceridae. Thirteen synapomorphies for these two groups were suggested by Courtney (1991a). None of them was a feature of the adult head, and in this study we found only one character supporting Blephariceroida, the origin of M. tentorioscapalis posterior (M. 2) on the vertex (Deuterophlebiidae and Edwardsina). The monophyly of Blephariceroida would imply that an elongated apical flagellomere, a unique suite of reductional features of the adult head, larval features such as abdominal prolegs (in later instars) and multi-toothed apical mandibular combs (also present in some Blephariceridae; Oosterbroek and Courtney, 1995), miniatureisation, and very specific life habits have evolved independently in Deuterophlebiidae and Nymphomyiidae.

A clade Blephariceromorpha comprising Deuterophlebiidae, Nymphomyiidae and Blephariceridae (e.g., Courtney, 1991a; Oosterbroek and Courtney, 1995; Yeates and Wiegmann, 1999) is suggested by the specific habitat preference and associated features. The immature stages of all three families are aquatic and display features likely associated with life in cool, fast-flowing mountain streams, such as the presence of abdominal prolegs (only in first-instar larvae of Blephariceridae; Oosterbroek and Courtney, 1995). Blephariceromorpha is not well supported by features of the adult head. The missing frontoclypeal suture is a potential synapomorphy of the three families, but the frontoclypeal suture is also missing in members of Simuliidae (Wenk, 1962), and also in Crenocephalus (Wenk, 1953). The absence of the clypeolabral suture in Blephariceromorpha is a questionable argument, as the labrum is entirely reduced in deuterophlebiids and nymphomyiids, and the suture is also absent in Siphonopera (e.g., Wenk, 1953) and most groups of Mecoptera (Heddergott, 1938; Hepburn, 1969). Another potential autopomorph of Blephariceromorpha is the origin of M. tentorioscapalis posterior (M. 2) on the head capsule. However, the muscle originates on the vertex in Deuterophlebiidae and Edwardsina (see above) and in Nymphomyia on the genal region (Tokunaga, 1935), as is also the case in Tipula (Schneeberg and Beutel, in press). The origin of the muscle has apparently shifted several times. It lies on the frons in Hemipenthes (Szucsich and Krenn, 2000) and on the circumciliary ridge in Eristalis (Schiemenz, 1957: Fig. 41 [M. orb.-sc.]).

The crucial question of the sister group of the remaining Diptera remains unanswered. Features of the adult head do not support a basal position of either Nymphomyiidae or Deuterophlebiidae (or both), and characters suggesting other “ancestral candidates” such as Culicomorpha (Oosterbroek and Courtney, 1995; Yeates and Wiegmann, 1999, 2005; Yeates et al., 2007) or Tipulomorpha (Hennig, 1973; Wood and Borkent, 1989; Beutel and Gorb, 2001; Blagoderov et al., 2007) where not found. Likewise, the systematic affinities of Deuterophlebiidae must still be considered as uncertain. A placement in a clade Blephariceromorpha as sister group of Blephariceridae (e.g., Oosterbroek and Courtney, 1995) would imply that a considerable number of unusual morphological features and a very similar aquatic life style have evolved independently in Deuterophlebiidae and Nymphomyiidae. It is evident that analyses of a comprehensive data set for a representative sample of Diptera are required to solve these questions. Molecular data acquired in the Flytree project (NSF, see Bertone et al., 2008) may provide insights into the relationships of some taxa. Unfortunately, morphological data are still missing for many potential key taxa such as Tanyderidae, Psychopteridae, and Axymyiidae. The documentation and evaluation of morphological data for adults and immature stages, and analyses of extensive combined data sets will likely lead to a solid reconstruction of basal dipteran relationships in the near future.

Acknowledgements

The authors are very grateful to Prof. Dr. Douglas A. Craig (University of Alberta) and Dr. P. Oosterbroek (Universiteit van Amsterdam) for the gift of valuable material, and to Dr. Richard A. B. Leschen (New Zealand Arthropod Collection) for arranging the loan of specimens of Mischoderus. We also thank Dr. Felix Beckmann (DESY, Hamburg) for technical support. Comments and suggestions made by two anonymous reviewers have helped to greatly improve the manuscript. This is also gratefully acknowledged.

The study was funded mainly by the Deutsche Forschungsgemeinschaft (BE 1789/6–1). Additional support to Gregory W. Courtney came from the National Science Foundation Assembling the Tree of Life Project (EF-0334948; ATOL: Building the Dipteran Tree: Cooperative Research in Phylogenetics and Bioinformatics of True Flies (Insecta: Diptera)).

References


Beutel, R.G., Zimmermann, D., Krauß, M., Randolf, S., Wippff, B. Head morphology of Osmius fulvicephalus (Osmiidae, Neuroptera) and its phylogenetic implications. Organisms, Diversity and Evolution, in press.


