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Catching prey with the antennae – The larval head of *Corethrella appendiculata* (Diptera: Corethrellidae)

Maria Förster, Rolf G. Beutel, Katharina Schneeberg*

Entomology Group, Institut für Spezielle Zoologie und Evolutionsbiologie, Friedrich-Schiller-Universität Jena, Erbertstraße 1, 07743 Jena, Germany

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ABSTRACT

The larval cephalic morphology of *Corethrella appendiculata* Grabham, 1906 is described and documented in detail. The observed features are compared to conditions found in Chaoboridae, Culicidae, and other culicomorph families. The function of antennae, mouthparts and associated muscles is interpreted based on the morphological results. The prey catching mechanism is compared to what occurs in other predaceous larvae of Culicomorpha. The cephalic larval morphology is discussed with respect to homology and possible phylogenetic implications. The horizontal frontoclypeal antennal grooves and the lateral rows of strongly developed bristles are likely larval autapomorphies of Corethrellidae. The presence of raptorial antennae is a highly unusual apomorphy shared with Chaoboridae. The systematic position of Corethrellidae remains ambiguous.

1. Introduction

Corethrellidae or frog-biting-midges are a small and not very well known group of Culicomorpha (Wood and Borkent, 1989). It comprises only the genus *Corethrella* Conquillett, 1902 with 106 extant species, with the oldest fossils described from Lower Cretaceous deposits (Szadziewski, 1995; Borkent, 2014; Amaral and Pinho, 2015). Most species occur in tropical and subtropical regions, but they are also extending into Japan, southern Sakhalin, southern Canada and parts of New Zealand (Borkent, 1993, 2008; Giłka and Szadziewski, 2009; Baranov et al., 2016).

Larvae of Corethrellidae occur in small standing water bodies or phytotelmata, water held by plants (Borkent, 1993, 2008, 2012; McKeever and French, 1991). The postembryonic development comprises four larval instars. The abdominal siphon bears small barbs anchoring the larvae to the substrate (Borkent, 2008). The larvae only ascend to the surface to renew their air supply (Borkent, 2008). They are specialized ambush predators, slowly turning towards their prey similar to predaceous culicid larvae, and then grasping it with extremely rapid movements of the antennae and mouthparts (Borkent, 2008). Lounibos et al. (2008) described "surplus" – or "wasteful killing". The larvae kill some prey, which is not consumed as food (Lounibos et al., 2008), a habit also described for larvae of the culicid genus *Toxorhynchites* Theobald, which partly occur in the same water body (Corbet, 1985; Russo, 1986; Lounibos et al., 2008). A possible advantage is the decimation of potential predators of pupae. The behavior can be observed from the 3rd instar and the intensity increases in the fourth (Lounibos et al., 2008).

Adults of both sexes (0.6–2.5 mm) feed on blood and the females need the blood meal to develop eggs (McKeever, 1977). Suitable hosts are found using the acoustic signal of male frogs (McKeever and French, 1991). Chemical cues play a role when the females are close to the host (Borkent, 2008).

Recognition of Corethrellidae as a separate family was first suggested by Wood and Borkent (1989). Autapomorphies separating the group from Chaoboridae are larval antennae held in a cephalic pouch at rest and the presence of a lateral row of bristles on the head capsule (Wood and Borkent, 1989). This concept is also supported by molecular data (Pawlowski et al., 1996; Miller et al., 1997; Bertone et al., 2008; Wiegmann et al., 2011). Potential sistergroups of Corethrellidae are Chaoboridae (Pawlowski et al., 1996; Wiegmann et al., 2011) or a clade Chaoboridae + Culicidae (Wood and Borkent, 1989; Oosterbroek and Courtney, 1995; Miller et al., 1997; Sæther, 2000; Bertone et al., 2008; Borkent, 2008, 2012).

Even though larval characters may be crucial for solving the ambiguities of the systematic placement of Corethrellidae,

* Corresponding author.
E-mail address: katharina.schneeberg@gmx.de (K. Schneeberg).

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anatomical data were not available yet. External skeletal features of the larvae were described by Grabham (1906), Lane (1953), Belkin and McDonald (1955), Cook (1981), Borkent and McKeever (1990), and Borkent (2012), and the chaetotaxy by McKeever and French (1991) and Borkent (2008). Internal structures such as muscles or tentorial elements were not included in these studies. Consequently the primary aim of the present contribution is a detailed description of the larval cephalic anatomy of *Corethrella appendiculata* Grabham, 1906. External and internal structures including soft parts are documented in detail. Characters are compared to conditions found in larvae of species of some other groups of Culicomorpha and interpreted phylogenetically. Special emphasis is on characters related to prey capture in *Corethrella* and some other predaceous larvae of Culicomorpha.

2. Material and methods

2.1. Examined taxa

Corethrellidae: *C. appendiculata*, 3rd larval stage (in culture, Florida Medical Entomology Laboratory, University of Florida) — Chaoboridae: *Chaoborus chrystallinus* (pet shop, Jena, Germany). — All larvae were killed and stored in 70% ethanol.

2.2. Histology

One specimen was embedded in Araldit CY 212 (Agar Scientific, Stansted/Itsex, England) and sectioned with a Microtom HM 360 (Microm, Waldorf, Germany) with a diamond knife (Elementsix) (1 μm). The cross sections were stained with toluidine blue and pyronin G (Waldeck GmbH & Co. KG/Division Chroma, Münster, Germany) and photos were taken with an Axioplan (Carl Zeiss AG, Oberkochen, Germany) using a PixeLINK digital camera and AnalySIS software (Soft Imaging Systems, Münster, Germany) at a magnification of 100×. Images were processed with Adobe Photoshop® CS5 (Adobe Systems Incorporated, USA).

2.3. Scanning electron microscopy (SEM)

Specimens were dehydrated in an ascending series of ethanol (80%, 90%, 96%, 3× in 100%, each step 30 min) and acetone, dried at the critical point, mounted on a rotatable specimen holder (Pohl, 2010) and sputter-coated with gold (Sputter Coater, Sample preparation division, Quorum Technologies Ltd., Ashford, England). Images were taken with an ESEM XL30 (Philips, Amsterdam, Netherlands) and software Scandium FIVE (Olympus, Münster, Germany). Images were processed with Adobe Photoshop® CS5 and Adobe Illustrator® CS2.

2.4. 3D-reconstruction

The digitalized sections were aligned with TrakEM2 (Cardona, 2006; Schweiz) in Fiji Is Just ImageJ (Freeware http://fiji.sc/Fiji). AMIRA 5.4 (Visage Imaging GmbH, Berlin, Germany) was used for the reconstruction and MAYA 2011 (Autodesk, München, Germany) for processing of surfaces. Figure plates were produced using Adobe Photoshop® CS5 and Adobe Illustrator® CS2.

2.5. Drawings

Drawings were carried out using Adobe Photoshop® CS5 and Adobe Illustrator® CS2 based on 3D-models.

2.6. Nomenclature

The homology of the sclerites is consistent with the nomenclature used in Schneeberg and Beutel (2014). The muscle names of v. Kéler (1963) were used even though the homology remained uncertain in some cases.

3. Results

3.1. Habitus

The 3rd instar larvae are ca. 4 mm long. The postcephalic body is weakly sclerotized and largely unpigmented. The head is prognathous and distinctly separated from the legless thorax, which is distinctly enlarged and composed of three largely fused segments (Fig. 1). A lateral tuft of long setae inserted on the metathoracic region is continuous with a lateral row of setae on the abdominal segments. The abdomen is composed of ten (I–X) segments, with segments I–VII differing scarcely externally. Segment VIII, which is slightly shorter than the anterior ones, bears a thick siphon with barbs (Borkent, 2008), likely a modified segment IX. Segment X is narrower than all other abdominal segments and bears a tuft of long setae on its dorsal and ventral side. One row of serrate hooks and four anal lobes are present on its ventral side.

3.2. Head capsule

The head capsule is relatively weakly sclerotized and appears trapezoid in dorsal view (Fig. 2A). It narrows towards its anterior margin, with slightly rounded lateral edges. The posterior region is characterized by a pronounced, evenly rounded, temporal region. It is strongly narrowed at the foramen occipitale. The head capsule is nearly round in cross section anteriorly, oval in the middle region, and almost circular anterior to the cervical region. The cuticle is covered by scale-like structures, some of which display serrate edges, especially in the posterolateral area. An anteriorly directed oblique row of long setae is inserted on the rounded temporal region (Fig. 3B), which also bears small denticles. Fissure-shaped posterior tentorial grooves are visible on the lateral occipital region, between a row of setae and the lateral edge of the foramen occipitale, enclosed in a flat, almost circular oval concavity (Figs. 2A, 3B: ptg). Frontal sutures are present (Figs. 2A, 3A,B: fs), indistinct anteriorly, almost parallel in the middle region, and meeting each other immediately anterior to the dorsal edge of the foramen occipitale. The enclosed frons appears roughly U-shaped, slightly narrowing posteriorly (Figs. 2A, 3A,B: fr). The coronal suture and an endocarina are missing. The anteriormost part of the frons bears six setae. Those close to the median line are much shorter than the other two pairs. The anterior frontal margin is steeply inclined, thus forming a sharp anterior edge (Fig. 5A). A narrow and deep median incision separates conspicuous paired, pointed projections. Anterior edge of head capsule between these processes and the lateral margin is slightly convex. The unsclerotized clypeal region lies below the overhang formed by the anterior frontal margin. The anterior genal region is characterized by a conspicuous nearly triangular process. A single stemma is present in the middle region of the gena, between the frontal suture and a lateral row of strong setae. It lacks a distinctly developed convex lens (Figs. 2A, 3B: s). The antennal insertion lies below the median clypeal incision (Figs. 2A, 3A,B, 4A,B, 5A,B, 6A,B: a), above the semimembranous clypeal region (Figs. 2A, 3A,B, 7B: lbr). The antennal bases are only separated by a very narrow median cleft. A frontoclypeal strengthening ridge is not recognizable. A postoccipital ridge is recognizable dorsally and laterally at the hind margin of the head capsule (Figs. 2A,B, 3B: pocl). A narrow postgenal bridge is present.

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