



The larval abdomen of the enigmatic Nannochoristidae (Mecoptera, Insecta)

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ABSTRACT

External and internal structures of the larval abdomen of *Nannochorista* are described in detail, with emphasis on the posterior segments. The results are compared with conditions found in other groups of Antliophora, especially the mecopteran subgroups Boreidae and Pistillifera. Like the entire postcephalic body, the larval abdomen of *Nannochorista* is extremely slender and nearly cylindrical. The anterior segments are largely unmodified. The surface is smooth and lacks any protuberances or prolegs. The term “cloaca” for the posterior membranous pouch of *Nannochorista* sp. is morphologically unjustified. A list of muscles of segments IX and X is presented. The abdominal musculature was partly homologized following Snodgrass. The muscles of segment X are highly modified. They move the membranous pouch, the anal papillae, and the terminal lobes. The presence of these structures is likely an adaptation to the specific aquatic life style of nannochoristid larvae. The anal papillae are possibly homologous to the 4-lobed terminal attachment apparatus of larvae of *Caurinus* (Boreidae) and Pistillifera (Panorpidae, Bittacidae, Choristidae) but this is uncertain. The specific condition in both groups, i.e. two retractile papillae with tracheae and Malpighian tubules in Nannochoristidae, and a 4-lobed exposed attachment device in Pistillifera + Boreidae (groundplan) are very likely autapomorphic for both groups, respectively. A slender abdomen with smooth surface is very likely plesiomorphic within Antliophora and Mecoptera. This condition is found in Trichoptera (partim), Nannochoristidae, Siphonaptera, and many basal groups of Diptera. An eruciform or scarabaeiform body shape with a soft, largely unsclerotised cuticle is probably a synapomorphy of Boreidae and Pistillifera. The presence of ventral protuberances resembling prolegs on the anterior segments is an autapomorphy of the latter group. The homology of paired or unpaired terminal appendages of segment X is uncertain. However, the specific condition of paired and 3-segmented appendages with hooks in Nannochoristidae is almost certainly autapomorphic for this family. The protracted opening of the hind gut on the membranous pouch is another potential autapomorphy of Nannochoristidae. Aquatic habits of larvae, also very likely an apomorphic condition, have likely evolved several times independently in Antliophora.

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1. Introduction

Nannochoristidae (Tillyard, 1917) or Nannomecoptera (Hinton, 1958) is one of the most disputed holometabolan taxa with respect to its systematic position. The small relict group is restricted to the southern hemisphere and comprises only one extant genus and eight described species (Penny, 1975; Kristensen, 1989). The fossil record reaches back to the early Jurassic (Grimaldi and Engel, 2005).

The biology of the immature stages is relatively well known. The extremely slender larvae are predacious and aquatic. Until pupation they stay in the substrate in shallow regions of streams. They mainly feed on larvae of Chironomidae (Pilgrim, 1972). The

prepupae leave the water and pupation takes place close to the edge of the river in moist soil substrate or below bark of tree logs in the riparian zone, which may be partly immersed (Pilgrim, 1972).

In recent phylogenetic studies different placements of Nannochoristidae within Antliophora were suggested (see e.g., Friedrich and Beutel, 2010). According to Willmann (2005) they are a basal group of Mecoptera, outside of the monophyletic mecopteran subgroup Pistillifera, but a separate order Nannomecoptera was suggested earlier by Hinton (1981). A sistergroup relationship with Diptera was suggested by Wood and Borkent (1989) and Beutel and Baum (2008). In a study based on molecular data, Whiting (2002) placed Nannochoristidae as sistergroup of a clade Boreidae + Siphonaptera. A basal placement within Mecoptera, as sister taxon of all other mecopteran families, was again confirmed in a study based on a comprehensive morphological data set (Beutel et al., 2010) and a clade Mecoptera incl. Nannochoristidae was also supported by analyses of six single copy nuclear genes (Wiegmann et al., 2009).

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The adult morphology of Nannochoristidae is very well known (Evans, 1942; Imms, 1944; Richards, 1965; Richards and Richards, 1969; Hepburn, 1969a, b; Mickoleit, 1975, 1976, 1978, 2008; Willmann, 1981, 1989; Kristensen, 1989; Simiczjiew, 2002; Beutel and Baum, 2008; Friedrich and Beutel, 2010; Hünefeld and Beutel, in press). External larval structures were described by Williams (1968), Melzer et al. (1994), Pilgrim (1972) and Kluge (2003). Beutel et al. (2009) provided a comprehensive description of the external and internal morphology of the larval head. However, postcephalic internal structures were almost completely unknown so far (see Pilgrim, 1972). Considering the apparent key position of Nannochoristidae, a better knowledge of the larval anatomy appeared highly desirable. This induced us to carry out this study on the larval abdomen, with emphasis of the highly differentiated posterior segments. The results are compared with conditions found in other groups of Mecoptera and larvae of basal dipteran lineages and Siphonaptera. The character interpretation is based on a formal phylogenetic analysis using a modified, comprehensive morphological data matrix from Beutel et al. (2010).

2. Material and techniques

2.1. List of taxa examined (preserved in 70% ethanol unless otherwise noted)

Mecoptera, Nannomecoptera (= Nannochoristidae), *Nannochorista* sp. Tillyard, 1917; Turoa Stream, vicinity of Little River, Hukahuka, New Zealand; 03.01.2006; leg. A. Staniczek.

2.2. Histology

For histological sectioning an abdomen of a larva of *Nannochorista* sp. was embedded in Araldit CY 212 (Agar Scientific, Stansted/Essex, England). Sections of 1 µm thickness were made using a Microtom HM 360 (Microm, Walldorf, Germany). They were stained with Toluidine blue and Pyronin G (Waldeck GmbH and Co. KG/Division Chroma, Münster, Germany) and photographs were taken with an Axioplan (Carl Zeiss AG, Oberkochen, Germany) and AnalySIS software (Soft Imaging Systems, Münster, Germany).

2.3. Scanning electron microscopy (SEM)

Specimens were cleaned using ethanol (50%–10%), distilled water with detergent, and ultrasonic sound (Bandelin Eletronik, Berlin, Germany). After that, the specimen was retransferred in ethanol (70%–100%) and from 100% ethanol to acetone (100%). Finally it was dried at the critical point (EmiTech K850 Critical Point Dryer), sputter coated (EmiTech K500 Sputter Coater [both Quorum Technologies Ltd., Ashford, England]) and mounted on a special specimen holder (Pohl, 2010). SEM images were taken with an ESEM XL30 (Philips, Amsterdam, The Netherlands) and the software Scandium FIVE (Olympus, Münster, Germany). Figure plates with SEM images were processed with Adobe Photoshop and Illustrator CS2 (Adobe, San Jose, USA).

2.4. 3D-reconstruction

The image stacks of the sections of *Nannochorista* sp. were aligned and processed using AMIRA 5.3 (Visage Imaging GmbH, Berlin, Germany). The final reconstruction was carried out with MAYA 2011 (Autodesk, San Rafael, USA). Figure plates were made using Adobe Photoshop and Illustrator CS2.

2.5. Confocal laser scanning microscopy

The abdomen of one larva of *Nannochorista* sp. was cut parasagittally and images of the abdominal musculature were taken with a confocal laser scanning microscope Zeiss LSM 510 (Carl Zeiss AG, Oberkochen, Germany) with a 10× Plan-apochromat-objective. The Excitation-wavelength was 488 nm (see Klaus et al., 2003).

2.6. Phylogenetic analysis

For a reliable character interpretation an extensive morphological data set of Beutel et al. (2010) was analysed with two additional characters included (see Appendix 1) and several terminal taxa (e.g., Tenthredinidae, Coleoptera, Strepsiptera) excluded (see Appendix 2: data matrix, 367 characters, 278 characters informative). The analysis (informative characters only) was carried out with NONA version 1.5 (Goloboff, 1995) (ratchet, 1000 replicates) and TNT (Goloboff et al., 2003) (algorithm: traditional Search; starting trees: Wagner trees, 100 replicates; swapping algorithm: tree bisection reconnection) TNT (Goloboff et al., 2003) (algorithm Traditional Search Technology). All characters were unweighted and unordered.

2.7. Terminology

The musculature was partly classified following Snodgrass (1935). A serial homology assessment was not possible in some cases.

3. Morphological results

3.1. Abdominal segments I-IX

The 10-segmented abdomen is very elongated, slender and round in cross section. Like most other parts of the larva it is almost completely unpigmented, with the exception of the terminal hooks. The cuticle is thin, smooth and largely glabrous. The anterior segments are about 2 mm long. The length decreases towards the abdominal apex. The terminal segment X is approximately 1 mm long.

The segments I-IX are largely unmodified and very similar in size and shape. They completely lack prolegs or other appendages. Clearly defined sclerites are not present. Several scattered setae are inserted laterally. On the dorsal side of segment IX two setae are inserted on a line perpendicular to the longitudinal body axis, both approximately 100 µm below the dorsal midline.

The musculature of segments I–VIII consists of two pairs of external dorsal muscles (dem, del), one pair of internal dorsal muscles, two pairs of external ventral muscles (vem, vel), and two pairs of internal ventral (vim, vil) muscles. All muscles except the dorsal external medial and the ventral internal lateral muscle consist of numerous fibre-bundles.

One pair of oblique dorso-ventral muscles connects the ventrolateral segmental border of each segment with the dorso-lateral wall of the anterior third of the same segment. No lateral muscles were identified.

3.2. Abdominal segment X

The terminal segment differs distinctly from the preceding ones. A pair of ovoid fields of microtrichia is present on the anterior third (mtf; Fig. 1B). The microtrichia (mt; Fig. 2E) are arranged in approximately 60 circular groups of ca. 15 microtrichia in each of them. Close to the caudal end of the segment on the dorsal side a pair of setae is inserted approximately 60 µm below the dorsal midline. Approximately 50 µm below these setae two additional paired setae are inserted. A third pair is present approximately 50 µm anterior to the second pair. Approximately 50 µm below the third pair and

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