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Ovaries and phylogeny of dermapterans once more: Ovarian characters support paraphyly of Spongiphoridae

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ABSTRACT

The Dermaptera is an insect order with ca. 2200 described species classified in 11 families. Interestingly, recent morphological and molecular data suggest that at least three dermapteran families (Diplatyidae, Pygidicranidae and Spongiphoridae) are paraphyletic. Here we present results of histological analyses of ovaries and ovarioles in two representatives of Spongiphoridae: *Chaetospania borneensis* and *Irdex chapmani*. We show that both the ovaries and ovarioles of studied species are morphologically disparate. The ovaries of *C. borneensis* consist of shortened ovarioles attached to elongated lateral oviducts and are apparently similar to the ovaries of the Eudermaptera. In contrast, *I. chapmani* share all the important ovarian characters with more basal taxa, i.e. Anisolabididae and Labiduridae. These findings lend additional support to the paraphyly of Spongiphoridae.

1. Introduction

The Dermaptera (earwigs) comprise ca. 2200 described extant species, usually classified in 11 families. Karschiellidae, Pygidicranidae and Diplatyidae reveal plesiomorphic state in many characters. These families are assembled together and referred to as basal or "lower" dermapterans, although relationships between them and the remaining earwigs are still controversial. Apachyidae, Labiduridae, Anisolabididae, Spongiphoridae, Forficulidae and Chelisochidae form a more derived clade, the higher Dermaptera. The latter three families (Spongiphoridae, Forficulidae and Chelisochidae) constitute the most derived dermapteran group, termed the Eudermaptera. In addition to typical free living earwigs classified in 9 aforementioned groups, the Dermaptera comprise also two highly modified, epizoic families: Hemimeridae and Arixeniidae. Traditionally, these groups have been placed into separate suborders, however recent results demonstrate that they should be nested in the Eudermaptera (Jarvis et al., 2005; Tworzydlo et al., 2013; Kocarek et al., 2013).

Insect ovaries consist of elongated units, termed the ovarioles (see Büning, 1994; Bilinski, 1998 for further details). As a rule, individual ovariole comprises four easily recognizable elements: a terminal filament, germarium, vitellarium and an ovariole pedicel connecting the ovariole to the lateral oviduct. Two basic categories of insect ovarioles are traditionally distinguished, the panoistic and meroistic (Büning, 1994). In the panoistic ovarioles, all the germline cells develop into the oocytes (egg cells). The ovarian follicles consist therefore of an oocyte and a surrounding monolayer of somatic cells, termed the follicular epithelium. In the meroistic ovarioles, some of the germline cells differentiate into oocytes, while others become specialized nurse cells. These cells synthesize and subsequently transport macromolecules and organelles to the growing oocyte (for a review see Büning, 1994; Matova and Cooley, 2001; Tworzydlo and Kisiel, 2010). Two subtypes of meroistic ovarioles are usually recognized: polytrophic and telotrophic (see Büning, 1994 for detailed description of ovariole types). In the polytrophic ovarioles, the germaria contain clones of sibling germline cells that arise as a result of mitotic divisions of a founder cell, the cystoblast. Within each cyst only one cell becomes an oocyte, while other differentiate into nurse cells. Classical and more recent studies have unambiguously shown that the ovaries of all dermapterans are merositic-polytrophic, and that ovarian follicles in this group of insects are composed of two germline cells only: an oocyte and a polyploid nurse cell (Zinsmeister and Zinsmeister, 1976; Yamauchi and Yoshitake, 1982; Büning, 1994; Tworzydlo and Bilinski, 2008; Tworzydlo and Kisiel, 2011; Tworzydlo et al., 2009, 2010a,

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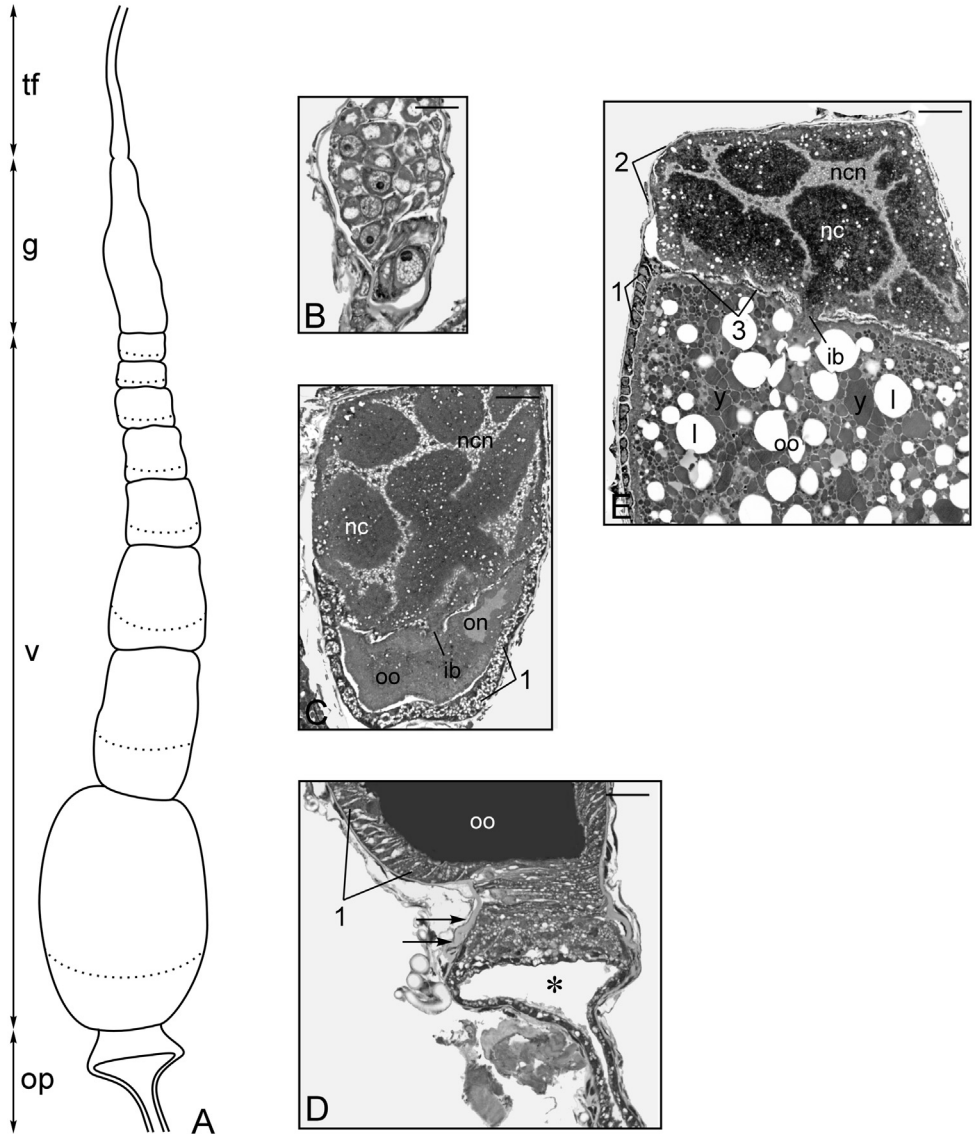

Fig. 1. Ovaries and ovarioles of *Irdex chapmani*. (A) Schematic diagram of an ovariole. Note elongated germarium and several ovarian follicles in a vitellarium; dotted lines show boundaries between oocytes and associated nurse cells. Reconstructed from 70 serial sections. (B and C) Ovariole of a young female. (B) Fragment of a germarium; note smaller and larger germline cells. (C) Previtellogenic ovarian follicle. (D) Ovariole stalk (arrows) attached to a lateral oviduct (asterisk). (E) Ovariole of an old female; fragment of a vitellogenic ovarian follicle. Note 3 subpopulations of follicular cells: cuboidal cells surrounding the oocyte (1); stretched cells covering nurse cell (2) and cells separating nurse cell from the oocyte (3). g, germarium; ib, intercellular bridge; l, lipid droplet; nc, nurse cell; ncn, nurse cell nucleus; on, oocyte nucleus; oo, oocyte; op, ovariole pedicel, v, vitellarium; tf, terminal filament; y, yolk sphere. Formalin, methylene blue. Scale bars, 100 μm.

2010b, 2013). Despite this fundamental similarities, the gross morphology of the ovaries/ovarioles as well as the processes leading to the formation of ovarian follicles are clearly different in basal versus derived taxa (see Tworzydlo et al., 2010a for further details).

Recent morphological as well as molecular studies strongly suggest that the phylogeny of the Dermaptera is not fully congruent with a current dermapteran classification. The cladistic analyses of morphological data sets have shown that certain dermapteran families are not monophyletic and/or supported only by single (sometimes not convincing) characters (Haas, 1995; Haas and Kukalová-Peck, 2001). This notion is in line with more recent molecular evidence (Colgan et al., 2003; Jarvis et al., 2005; Kocarek et al., 2013). All accumulated data clearly point out that additional work is needed to discover how many distinct lineages have been incorrectly placed within problematic families, e.g. Pygidicranidae, Diplatyidae, Labiduridae and Spongiphoridae. This task is of special importance in case of a large, species-rich family Spongiphoridae. The monophyly of this family is not supported by reliable morphological characters or molecular evidence. The latter data suggest, moreover, that the Spongophoridae consist of three, not closely related lineages (Jarvis et al., 2005), and that only one of them should be nested within the Eudermaptera, as a sister group to Chelisochidae + Forficulidae (+Hemimeridae + Arixeniidae, if we accept modern hypotheses) clade (Jarvis et al., 2005; Kocarek et al., 2013). Two other "spongiphorid" lineages are apparently not related to the Eudermaptera and have been placed next to Anisolabididae. It should be added here that the morphology and histology of ovaries of "spongiphorid" species have not been studied in detail and are practically unknown. In this context we have decided to investigate gross anatomy and histology of ovaries and ovarioles in two representatives of Spongiphoridae: *Chaetospania borneensis* (Dubrony, 1879) and *Irdex chapmani* Brindle, 1980. All the specimens used in