

Ultrastructure of Oocytes and Female Copulatory Organs of Acoela

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Abstract—The ultrastructure of oocytes in four Acoela species representing different families (*Archaphanostoma agile*, *Otocelis rubropunctata*, *Symsagittifera japonica*, and *Amphiscolops* sp.) and of female copulatory organs (bursae) in *S. japonica* and *Amphiscolops* sp. is described for the first time. The sister relationship between the families Sagittiferidae and Convolutidae is confirmed by the similarity of their reproductive apparatus structure. It is suggested the ultrastructure of oocytes and specific features of oogenesis can be used in the phylogenetics of Acoela.

Keywords: Acoela, reproductive system, oocytes, ultrastructure, taxonomy, phylogeny

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INTRODUCTION

Peculiar features of the reproductive system are widely used in modern taxonomy and phylogeny of the animal kingdom (Reunov and Malakhov, 1993; Drozdov and Ivankov, 2000). For example, the taxonomy of the phylum Plathelminthes is currently based mostly on these characters (Ivanov and Mamkaev 1973; Raikova, 1991; Ehlers, 1985; Hendelberg, 1986). Electron microscopy studies of the reproductive system of flatworms are especially topical, considering the exceptional diversity that these worms display in the structure of gametes and copulatory apparatus and the relatively simple organization of their other organ systems.

Acoela, a group of invertebrates of somewhat unclear taxonomic placement, are of special interest in the comparative anatomy aspect. Some zoologists consider Acoela the most primitive representatives of Bilateria (Ivanov and Mamkaev, 1973), while others consider this group a product of secondary simplification (Livanov, 1955; Malakhov, 2009). The molecular phylogenetic data are also rather contradictory: Acoela are either considered a sister group to all other Bilateria (Baguna et al., 2008) or surprisingly placed in the superphylum Deuterostomia (Philippe et al., 2011). Thus, neither morphologists nor molecular biologists have a consensus on the taxonomic position of this group within the animal kingdom.

The structure of the reproductive system of acoel turbellarians is distinguished by high diversity and displays a combination of characters extremely archaic on the one hand and specialized on the other hand. All Acoela, like all other turbellarians, are hermaphroditic and have internal fertilization. The most primitive species have diffuse (asacular) gonads; i.e., gonads that

have no walls of their own and consist of spermatozoa and oocytes scattered in the parenchyma (Ivanov and Mamkaev, 1973; Gremigni and Falleni, 1998). Distinct true gonads (as organs) do not form in Acoela. However, this primitive state of gonads is compensated by the rich diversity of female and male copulatory organs, the specific structural features of which are used as important diagnostic and taxonomic characters (Mamkaev, 1967; Westblad, 1948; Dörjes, 1968; Petrov et al., 2004, 2006; Petrov, 2007, 2007a; Achatz et al., 2010). In the most primitive acoel turbellarians, female copulatory organs and even a female copulatory opening are often absent, although the male copulatory apparatus is invariably present (Mamkaev, 1967; Ivanov and Mamkaev, 1973). In advanced acoel turbellarians, the female copulatory apparatus is represented by one or several bursae (sperm sacs), usually opening onto the surface through an epithelized canal (vagina). Most authors believe that the bursae serve as seminal receptacles for storing semen after mating prior to delivering it to the egg for fertilization (Mamkaev, 1967; Westblad, 1948). In many Acoela species, seminal bursae form appendages in the form of rigid sclerotized tubes (bursa mouthpieces), serving to conduct sperms to oocytes for fertilization (Petrov et al., 2006; Petrov, 2007, 2007a).

The oocytes of Acoela represent the entolecital type of yolk position, typical of all archoophorous turbellarians. Maturing oocytes in Acoela and the closely related Nemertodermatida are surrounded by accessory cells, the function of which remains somewhat unclear. They are supposedly responsible for yolk synthesis or participation in eggshell formation (Rieger et al., 1991; Raikova et al., 1995). Fertilized eggs (zygotes) in Acoela, as in the other flatworms, are