



## Research paper

## Germ-line cells do not form syncytial cysts in the ovaries of the basal clitellate annelid *Capilloventer australis*



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## ABSTRACT

Capilloventridae are regarded as the putative sister taxon to all other Clitellata. To shed more light on their internal anatomy, we studied the ovary organization and the course of oogenesis in *Capilloventer australis*. We found that the ovary organization differs substantially from that known in all other clitellate annelids. In contrast to other clitellate annelids, the germ cells in *C. australis* ovaries develop individually and do not form syncytial cysts. Neither intercellular bridges nor central cytoplasmic mass (cytophore) – structures that are characteristic of gametogenesis in other Clitellata – were found. The paired ovaries of *C. australis* are located in segment XIII and form chains that are composed of linearly arranged growing germ cells that are covered by a thin envelope of somatic cells. The progression of germ cell development can be observed along the long ovary axis. The ovary tip is occupied by oogonia and below it, previtellogenic and early vitellogenic oocytes occur. Large, vitellogenic oocytes, which are filled with yolk, detach from the ovary and fill the segment lumen. Vitellogenic oocytes are not enveloped by somatic cells. With the exception of the lack of germ-line cyst formation, oogenesis is similar to that found in other Clitellata. It is not clear whether the lack of germ-line cysts is a basal condition for Clitellata that is retained in *C. australis* or, by contrast, did clitellate annelids inherit a female germ-line cysts from their ancestors and their lack in *C. australis* is a derived condition?

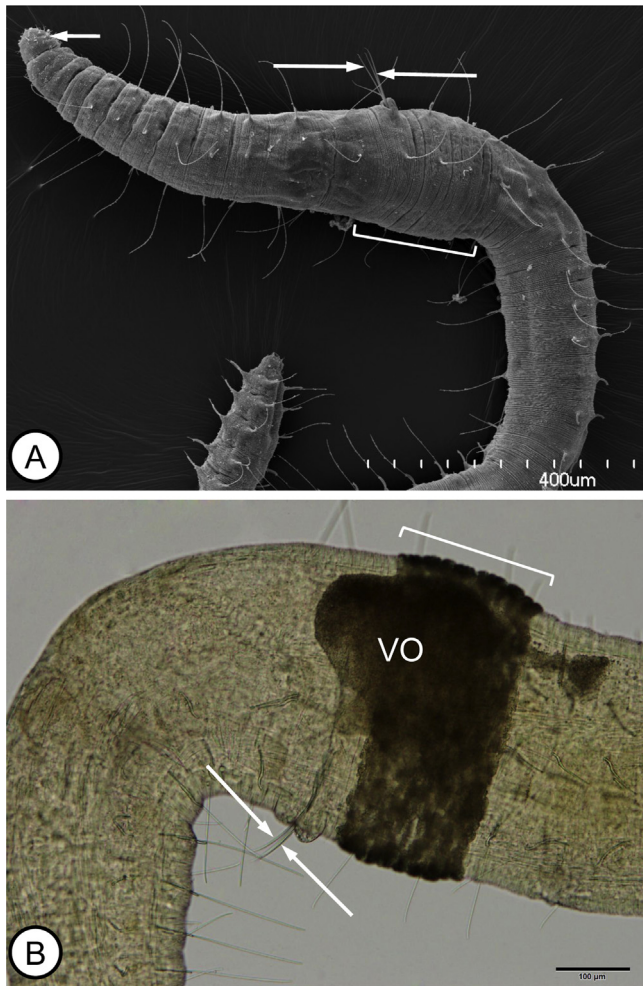
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### 1. Introduction

In 1984 Harman and Loden examined nine specimens of a tiny unknown annelid from the Bay of Rio de Janeiro, collected in 1975. Due to the unusual morphology of these specimens (see below), a new family, Capilloventridae, which had a single species *Capilloventer atlanticus*, was established within the Oligochaeta (Harman and Loden, 1984). Later, Erséus (1993) reviewed the family and described two new species – one from the Weddell Sea (*Capilloventer antarcticus*) and one from the estuary of the Hawkesbury River in New South Wales, Australia (*Capilloventer australis*). Finally, Pinder and Brinkhurst (1997) described two additional *Capilloventer* species from Australian rivers and demonstrated that both the marine and freshwater species belong to this family. Morphological analysis showed that *Capilloventer*, apart from the characters

typical for Oligochaeta (e.g., a clitellum, hermaphroditism with gonads restricted to a few segments and a muscular eversible pad formed by dorsal wall of the pharynx), bears some primitive characters namely the presence of hair as well as bifid chaetae in all somatic bundles located dorsally and ventrally (Fig. 1A and B; Harman and Loden, 1984; Erséus, 1993; Pinder and Brinkhurst, 1997). This latter character is unusual for clitellate annelids and it was suggested that it is reminiscent of an arrangement that is known from polychaetous annelids (Erséus, 1993). Based on these morphological characters, it was suggested that capilloventrids are basal Oligochaeta with possible, but unresolved, relationships with Enchytraeidae, Popappidae and Randiellidae (Harman and Loden, 1984; Erséus, 1993; Pinder and Brinkhurst, 1997). The ultrastructural analysis of *C. australis* spermiogenesis and sperm structure also suggested that capilloventrids are basal Oligochaeta (Ferraguti et al., 1996). In 2004 Erséus and Källersjö (2004) presented the 18S rDNA phylogeny of Clitellata and showed that Capilloventridae is the sister-group to all other clitellates of those included in the study. Later, molecular analysis suggested that *C. australis* is a

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**Fig. 1.** (A) The general morphology of *Capilloventer australis* in dorsal view. The prostomium (short arrow) and the first three segments lack chaetae. The remaining segments have four rows of dorsal and ventral chaetal bundles (usually three rows are visible). Bundles of modified genital chaetae (penial chaetae) in segment XII are clearly visible (arrows). The clitellar region (segments XII–XIV) is denoted by bracket. Scanning electron microscopy. (B) A fragment of *C. australis* body with a clearly visible clitellum (denoted by bracket). The vitellogenic oocyte (VO) is clearly visible through the body wall. Note also the penial chaetae (arrows). Stereomicroscope.

sister to Dinophilidae (but with no jackknife support) and that these two taxa are sister groups to the remaining clitellates (Rousset et al., 2007). A combined analysis using 18S rDNA and morphology also supported the position of Capilloventridae as the sister taxon to all other Clitellata (Marrota et al., 2008). Finally, more recently, Martinez-Ansemil et al. (2012), who also used 18S rDNA sequences, and maximum likelihood and Bayesian analyses, once again showed that *C. australis* is a sister to the all remaining Clitellata.

Although it is accepted that Capilloventridae are the sister group to the rest of Clitellata, we still have sparse data about their biology, ecology, morphology and internal anatomy. To shed more light on the internal anatomy of capilloventrids, we analyzed the ovary organization and the course of oogenesis in *C. australis* at the ultrastructural level. We found that in the species studied, in contrast to all other clitellates that have been studied to date, the female germ-line cells do not form syncytial cysts. It seems that each female germ-line cell has a potential to become an oocyte (i.e., the oogenesis is panoistic). It is not yet clear whether the panoistic mode of oogenesis found in *C. australis* is a plesiomorphy that is shared with

other, polychaetous annelids, or an autapomorphy of capilloventrids.

## 2. Materials and methods

*C. australis* Erséus (1993) was sampled in December 2014 in Archeron River (37.3526 S, 145.7064 E) in Victoria, Australia.

*C. australis* was collected from a coarse substratum using a triangular hand net (30 cm base with a 0.2 mm mesh). In the laboratory, mature worms with clitellum were picked from the substratum under a stereomicroscope. The specimens were determined using the Pinder key (2013). Thirty to forty specimens were studied during the presented analyses.

### 2.1. Light and electron microscopy

Whole specimens were initially fixed with 2.5% glutaraldehyde in a 0.05 M cacodylate buffer (pH 7.4) for several days. After washing in a 0.1 M phosphate buffer (pH 7.4), the material was postfixed for 2 h in 1% OsO<sub>4</sub> in a phosphate buffer, dehydrated in a graded series of ethanol replaced by acetone and then embedded in an Epoxy Embedding Medium Kit (Sigma, St. Louis, MO). Semithin sections (0.8 μm thick) were stained with methylene blue and examined under an Olympus BX60 microscope equipped with an XC50 digital camera (Olympus) and cellSens Standard software (Olympus). Serial ultra-thin sections (70 nm) were cut on a Leica Ultracut UCT ultramicrotome. After contrasting with uranyl acetate (15 min.) and lead citrate (20 min.), the sections were examined using a Hitachi H500 electron microscope at 75 kV.

Additionally, some specimens were used for scanning electron microscopy studies. Whole specimens were fixed with 2.5% glutaraldehyde in a 0.05 M cacodylate buffer (pH 7.4) for several days. Later, the samples were dehydrated in ethanol as well as an acetone series, critical point dried in liquid CO<sub>2</sub> and coated with gold using a JEOLJFC 1100 E sputter coater. The specimens were viewed under a HITACHI S-4700 microscope (Scanning Microscopy Laboratory of Biological and Geological Sciences, Jagiellonian University in Kraków) at 20 kV. Two of the specimens studied in SEM were donated to the Zoological Museum of Jagiellonian University; number MZUJ 2012.01922 as documentary material.

## 3. Results

### 3.1. Gross morphology

The paired ovaries are located bilaterally in segment XIII. Each ovary has the form of a chain that is composed of individual linearly arranged growing germ cells that are covered by a thin envelope made up of somatic cells (Fig. 2A). The narrow (proximal) end of each ovary is connected to the intersegmental septum between the XII and XIII segments via a short thin ligament that is formed by elongated somatic cells (Fig. 2A). The developmental progression of germ cells can be observed along the long ovary axis (Fig. 2A). The ovary tip is occupied by small germ cells that are regarded as oogonia, and both previtellogenic and early vitellogenic oocytes can be seen below them (Fig. 2A). The biggest late vitellogenic oocytes are not arranged linearly, they are irregular in shape and appear to occupy the free spaces in the segment cavity (Fig. 2A and B). The late vitellogenic oocytes are easily visible through the body wall (Fig. 1B). Serial sectioning revealed that on average twelve germ cells (from oogonia to early vitellogenic oocytes) develop in an ovary ( $n=2$ ) at the same time. Additionally, about four large vitellogenic oocytes were usually found in the segment cavity. The somatic cells form the ligament and the thin envelope that surrounds growing germ cells (Fig. 2A). The somatic cells that form

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