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## The glandular canals present in some chaetognath species are coelomoducts: Phylogenetical implication

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### Abstract

The chaetognaths live in various marine habitats, mostly in plankton. Some species are provided with glandular canals, described herein; they are true coelomoducts. Their nature was already suspected but, curiously, this information was overlooked. Knowledge of this fact would have prevented numerous incorrect positioning of the phylum in the tree of life.

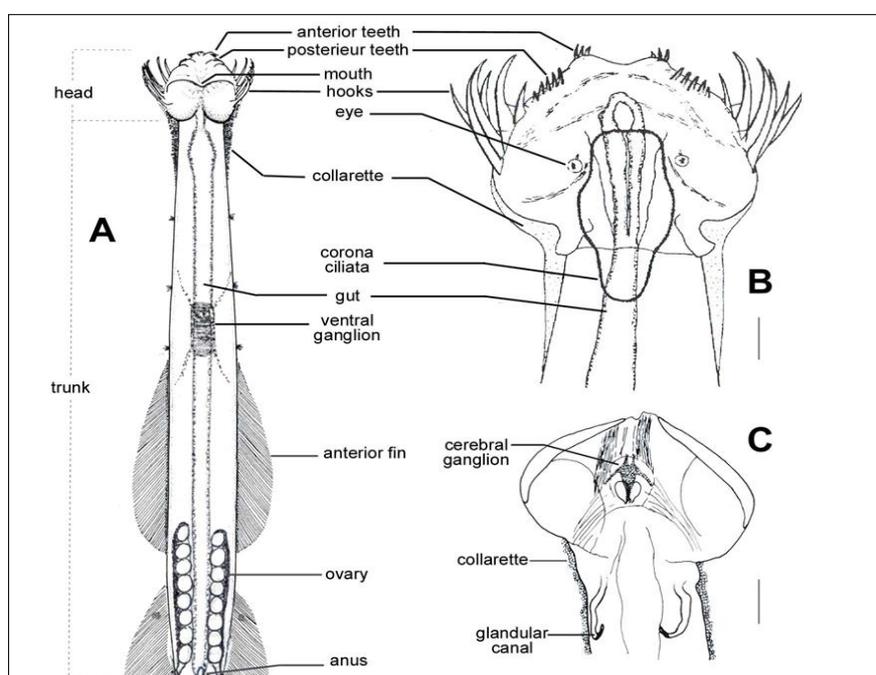
**Keywords:** chaetognatha, coelomoducts, phylogeny

### 1. Introduction

The small marine phylum Chaetognatha comprises actually about 130 to 140 species living in various habitats, mostly in the open sea and on or near the bottom. Planktonic chaetognaths (length 2-120mm) are the most numerous and have a key role in pelagic food webs. For a long time, they were considered as strictly carnivores but different aspects of their feeding biology have led to consider that they feed primarily on dissolved and fine particulate matter, not on prey [1]. They are very ancient animals whose presence is attested in the Lower Cambrian rocks (ca 525 million years) from South China [2]. Their bodyplan is strikingly conserved since then [3].

#### 1.1 Main features of the phylum

The body is transparent to semi-opaque, sometimes with pigmented areas. It consists of three regions: the head, the trunk and the tail (Fig. 1). The head is rounded and slightly flattened. It bears on each side one set of grasping spines or hooks and one or two rows of teeth. These formations surround the mouth that opens ventrally. A hook-sack or hood keeps the hooks.

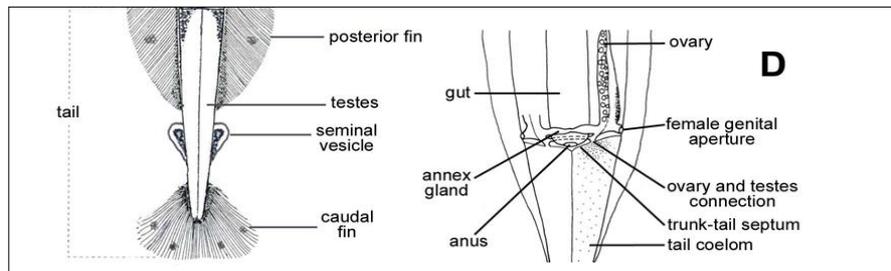


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**Fig 1:** Main diagnostic characters of chaetognaths in ventral (A) and dorsal (B, C) views. A: *Sagitta* sp.; B: *Sagitta lucida*; C: *Heterokrohnia furnestinae* showing the glandular canals embedded in the collarette (epidermis); D: diagram of genitals (ventral side) of *Heterokrohnia*. Scale bars: B, 400 $\mu$ m; C, 1mm.

Against the head, except during feeding. There are two dorsal eyes, lacking in some deep-living species. The trunk is separated from the head by a transverse septum and begins as a narrow neck. It contains the gut and the paired ovaries. The anus and female gonads open just before the trunk-tail septum. Chaetognaths are hermaphrodite. The tail contains the testes and bears postero-laterally a pair of external seminal vesicles. In *Archeterokrohnia* and *Heterokrohnia*, the ovaries are connected ventrally by an annex gland and are in relation with the tail through the trunk-tail septum [4-6]. In some species, the epidermis is more or less thickened, and constitutes an alveolar tissue named collarette which occupies at least the neck area; sometimes, it even embeds the whole body. The body wall is made of four longitudinal muscles. The nervous system is mostly intraepidermal. An original particularity is the presence of a large ventral ganglion, easily visible on the anterior part of the trunk, under the epidermis. A dorsal corona ciliata, made of two parallel rows of cells, begins at the level of the eyes and may extend to the anterior trunk. A few genera, among which two are considered to be the most "primitive" of the phylum, exhibit a pair of so-called "glandular canals" embedded in the collarette tissue, opening posteriorly on the dorso-lateral sides of the neck (Fig. 1C), that are in fact typical coelomoducts. All these species are provided with transverse muscles.

The glandular canals have been firstly reported in *Eukrohnia* by Ritter-Zahony [7] as two elongated canals running dorso-laterally on the head and consisting of glandular cells, explaining the name he adopted for them. He did not observe them in *Heterokrohnia mirabilis*, a species and genus that he also described in the same paper, because the collarette tissue into which they run had been stripped off during sampling. Later, Hyman [8] said that in these two genera the glandular canals converge to a large glandular reservoir at the tip of the head. Tokioka [9] reported these canals on the neck region when he described the monotypic genus *Bathyspadella edentata* and said that they "... seem to terminate anteriorly into the cephalic coelom..." and that they opened posteriorly on the dorso-lateral side of the neck. In his remarkable and complete review of the phylum, Shinn [10] said that there was no information about the ultrastructure or function of these epidermal "glandular canals" and that explains why he put their name in inverted commas. In a review of the chaetognaths of the South Atlantic, Casanova [11] gave a rapid description of the phylum and wrote that, if Tokioka's [9] observations were correct, these canals would be excretory coelomoducts owing to the presence of cilia in the lumen of the canals (see below).

Indeed, many years ago, Casanova and Duvert (unpublished data) have done ultrastructural studies of the glandular canals

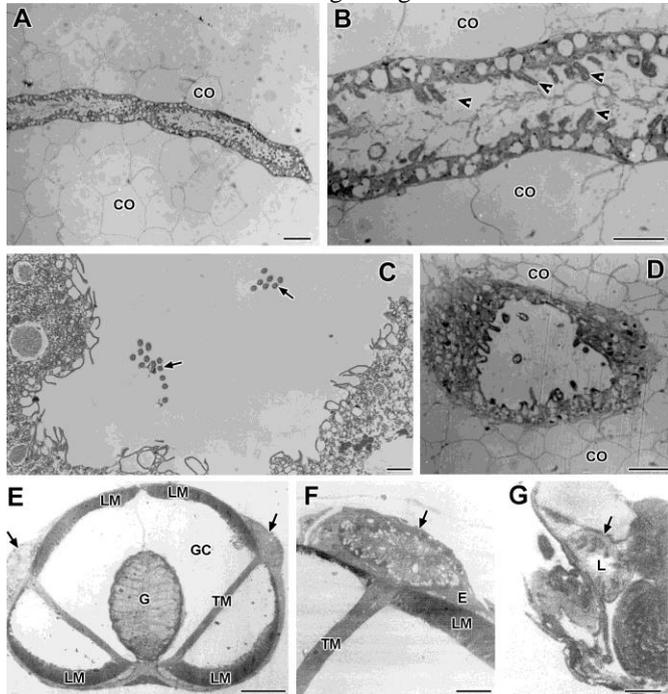
of the specimen of *Archeterokrohnia rubra* caught off California [12] because it was the first one having kept its collarette after sampling, and of one specimen of *Heterokrohnia furnestinae* described in the North-East Atlantic [13]. Although they knew that these animals were not preserved for such studies, they thought that it would be useful to have a first glance at their histology in view to get an idea of their nature. They also examined a few specimens of *Eukrohnia hamata*, but the aspect of the glandular canals was so different from those of the former that they decided to wait for correctly preserved specimens before publishing these observations. This opportunity never arose and it seems now useful to expose these old findings, saying that they are preliminary and need to be taken up again in the future. They are useful for a correct positioning of the phylum in the tree of life.

## 2. Results

***Archeterokrohnia rubra*:** The glandular canals are thin, almost straight and long [12]. They are embedded in the collarette tissue and extend from the level of the base of the hooks to about the anterior third of the trunk where they open dorso-laterally. Semi-thin longitudinal sections in the neck area show that its wall is formed by a single layer of cells, considerably smaller than those of the collarette (Fig. 2A, B). They contain a large vacuole occupying the greater part of the cell volume. Most of them have an extension in the lumen of the canal that may be as long as the height of the cell. All the extensions have the same orientation, seeming to indicate a flow of liquid circulating in the canal (Fig. 2B). Ultrastructural sections show that their inner side exhibits villousities and a tuft of about a dozen cilia that beat in the lumen of the canal (Fig. 2C). There are also vacuoles containing grey coloured secretions at different stages of filling. The nuclei of the cells are situated near the outer side of the canal. Smaller cells (myoepithelial cells?) are sometimes visible under the epithelium, against the large collarette cells.

***Heterokrohnia furnestinae*:** A report of the aspect of the glandular canals has been done when the species has been described [13]. They are short, roughly U-shaped, begin in the posterior part of the head, run into the collarette and open dorsally in the anterior part of the trunk, just after the neck area (Fig. 1D). In one of the 18 specimens observed, the canals are larger (diameter = 0.2 mm) and when stained by methylene blue, the large nuclei of the cells (gland cells?) constituting the canal wall are seen. The few exploitable semi-thin sections are those at their beginning. They show that they apparently open into the anterior end of the trunk coeloms,

recognizable like this by the fact that they contain the transverse muscles. They run slightly towards the tip of the head, inserted between the body wall and the collarette. Then they rapidly change their direction and go backwards inside the collarette (Fig. 2D). Ultrastructural sections are bad and cannot be well interpreted, but a few cilia are visible in the area of the opening of the canal into the trunk coelom, both in the coelom itself and in the beginning of the canal lumen.



**Fig 2:** Glandular canals (coelomoducts) of *Archeterokrohnia rubra* (A-C), *Heterokrohnia furnestinae* (D) and *Eukrohnia hamata* (E-G, arrows). A and B: semi-thin longitudinal sections at different magnifications; C: ultrastructural aspect of the cells constituting the canal showing tufts of cilia (arrows); D: semi-thin transversal section. Note in B the same orientation of cell extensions in the canal lumen (arrowheads) suggesting the discharge of wastes; E-G, semi-thin transversal sections (neck area). E and F: outside the body, the glandular canals have a spongy aspect without a lumen; C: inside the body, the glandular canal is typical, *i.e.*, a ring of cells with a central lumen. CO: collarette; E: epidermis, G: gut, GC: general cavity, L: lumen, LM: longitudinal muscles, TM: transverse muscles. Scale bars: A, 50µm; B, 25µm; C, 1µm; D, 25µm; E, 200µm; F, 50µm; G, 100µm.

***Eukrohnia hamata*:** The glandular canals are short. They have been observed in semi-thin sections (Fig. 2E-G). They are well visible in the head where they begin as a mass of cells situated against the internal wall of the coelom that may be considered as the trunk coelom by comparison with *Archeterokrohnia* and *Heterokrohnia*. Then these cells begin to be arranged in order to constitute a semicircle before becoming a well marked canal, *i.e.*, as a ring of a dozen cells delimiting a well apparent lumen (Fig. 2G). The canal is situated against the basement membrane, between a lateral plate and a muscular mass. Then it crosses the basement membrane to run externally, tightly applied against the basement membrane, under the epidermis, just at the level of the dorso-lateral insertion of the transverse muscles on the body wall (Fig. 2E, F). The aspect of the canal cells change when the canal is outside the basement membrane. They enlarge so that the lumen of the canal becomes hardly visible and they contain numerous vacuoles which give, at first sight, a spongy aspect to the whole canal.

### 3. Discussion

As said above, the feeble number of individuals observed must be taken into account and one must have reservations about these first results. It seems that the aspect of the glandular canals differs according to the genera. Indeed, at least for two of them, *Archeterokrohnia* and *Heterokrohnia*, they perfectly correspond to Brusca & Brusca's [14] definition of coelomoducts, *i.e.*, "... tubular connections arising from the coelomic lining and extending to the outside via special pores in the body wall." The longest are those of *A. rubra*. They are made of the same tissue lining a part of the wall of the trunk coelomic cavity. The numerous cilia observed in the lumen seems to indicate that they have an active role in evacuation of waste fluids from the body. Those of *Heterokrohnia*, when described, are shorter. Staining by methylene blue shows large nuclei in *H. furnestinae* [13] and *H. wishnerae* [15]. Since in the former species the size of the canals and nuclei is larger in one specimen, one can wonder if these cells have perhaps also a secretory function, justifying thus the name of glandular canals given by Ritter-Zahony [7].

It appears that the chaetognaths are oligomeric animals with three pairs of coelomic cavities in each part of the body, head, trunk and tail. The coelomoducts of the tail coeloms are represented in all the species by the male ciliated gonoducts. Resorption of the fluids from the lumen of the sperm ducts observed during filling of the seminal vesicles would be due to the concentration of sperm into them [10]. This may also be interpreted as the other role of these ducts, *i.e.*, the evacuation of waste. There is a second pair of coelomoducts corresponding to the trunk coelomic cavities at least in four genera of the primitive order Phragmophora. In *Archeterokrohnia* where they are the longest, they seem to have only a waste role as indicated by the numerous tufts of cilia bating in the lumen of the coelomoducts. In *Heterokrohnia*, the variations of the size of the coelomoducts according to the individuals observed and the large size of their wall cell nuclei seem to indicate a double role, evacuation of waste together with a glandular function. In *Eukrohnia*, where they are the smallest, their function is desired since the wall cells occupy almost all the volume of the external part of the coelomoducts making thus their lumen very reduced. There is no information on their structure in the monospecific genus *Bathyspadella* (only one specimen known) where they are short [9]. The short size and location of the coelomoducts on the neck region of *B. edentata* perhaps explain why Tokioka suggested that they might open into the cephalic coelom.

How can the evolution of the trunk coelomoducts leading to their disappearance in the majority of the extant species be explained? The importance of the paired trunk coelomic cavities remains almost the same in all the chaetognaths, although the volume of the coelomic fluid varies, depending on the importance of the volume of the gut, rounded, or flattened, or provided with more or less large vacuolated cells. When these cells are hypertrophied as in certain *Sagitta*, the coelomic cavities are almost obliterated, while they are swollen when the cells are devoid of vacuoles in others [16, 17]. Nevertheless, in both cases, the coelomoducts do not exist indicating that the reduction of the volume of the coelomic fluid cannot be involved in their disappearance. Change in feeding is perhaps a conceivable explanation. Indeed, it has been recently shown by different converging approaches that chaetognaths feed preferentially on dissolved and fine

particulate organic matter than on prey <sup>[1]</sup> and at least for *Eukrohnia hamata* on planktonic snow <sup>[18]</sup>. Primitively, chaetognaths were beyond all doubt carnivores as attested by their circumoral grasping spines and teeth. They were present in the Early Cambrian biota and looked like the present forms <sup>[3]</sup>. Barthélémy *et al.* <sup>[19]</sup> have given an evolutionary history of the phylum combining paralog genes analyses and paleontological data. It appears that chaetognaths were among the first predators and yet well represented until the later Carboniferous as previously shown in sediments <sup>[3]</sup>. After this period, they are absent in fossils, indicating a drastic diminution of their number. Now, they are among the most abundant organisms in zooplankton. Carton <sup>[20]</sup> explained this gap by a major change in the foodweb by competition with increased new predators. This successful reappearance might be the consequence of a shift in their feeding mode, from carnivory to osmotrophy <sup>[1]</sup>. They would have in a way rediscovered the most important feeding style characterizing the first animals during the Proterozoic, just before the Cambrian <sup>[21]</sup>, among which lived their ancestors. As wastes are probably reduced when food mainly consists of dissolved organic matter, this might explain that a typical excretory apparatus was no longer necessary. Indeed, it has been demonstrated with diverse molecules that the paracellular routes are connected to the sea water <sup>[22]</sup>, so that the existence of a *milieu intérieur* has been questioned <sup>[23]</sup>.

The presence of coelomoducts allows the reduction of the number of phyla that have been postulated possibly allied to the chaetognaths (see, *e.g.*, Ghirardelli <sup>[24]</sup> and also recent molecular phylogenies). It is the case for all the phyla devoid of an excretory system, for those provided with protonephridia (flam cells and solenocytes), for those also having particular excretory cells such as the renette cells (Nematoda).

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