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Cirrifera genitoductus sp.n. (Platyhelminthes, Proseriata, Coelogynoporidae) from the Belgian coast, with observations on its ultrastructure and its significance for the taxonomy of the Coelogynoporidae

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ABSTRACT. *Cirrifera genitoductus* sp.n. (Platyhelminthes, Proseriata, Coelogynoporidae) is described from sandy beaches at the Belgian and Northern French coasts. The species is characterised by a cirrus with small spines, all of the same size, a prostate vesicle far behind the copulatory bulb, a long genito-intestinal duct and a pair of large gland complexes behind the genital pore. An identification key for the *Cirrifera*-species is given as are some data on the ultrastructure. A brief discussion on the character distribution within the Coelogynoporidae shows that the discovery of a species of *Cirrifera* with a genito-intestinal duct makes the demarcation of the genera even more blurred than it already is.

KEY WORDS: Platyhelminthes, Proseriata, Coelogynoporidae, *Cirrifera genitoductus,* ultrastructure, taxonomy.

INTRODUCTION

The family Coelogynoporidae was erected by Bresslau (1933) to include two proseriate species described by Steinböck in 1924, *Coelogynopora gynocotyla* and *C. bresslaui*, in which there is a communication between the female system and the gut; hence the name of the genus. More than 20 species have been added to the genus since and several genera have been added to the family: *Vannuccia* Marcus, 1948, *Carenscoilia* Sopott, 1972, *Cirrifera* Sopott, 1972, *Invenusta* Sopott-Ehlers, 1976, *Ezona* Tajika, 1980, *Macroatrium* Riser, 1981, *Pseudovannucia* Faubel & Rohde, 1998 and *Stilivannucia* Faubel & Rohde, 1998. However, the more species become known, the greater the variation within each genus appears and the "boundaries" between the "genera" become more confused. The "mosaic-like" distribution of the genito-intestinal connection and some other characters within the Coelogynoporidae are discussed at the end of this contribution. An identification key for the *Cirrifera* species is given as well.

Thus far, one of the diagnostic characters for the taxon *Cirrifera* was the absence of a bursal organ and of a genito-intestinal connection. Now a species, *C. genitoductus* n.sp., is found that shows all other characters of the representatives of the taxon *Cirrifera*, but has a genito-intestinal duct. The species is described in detail, including a number of electron microscopic observations, adding some data to what was known of the ultrastructure of *Cirrifera aculeata* Ax, 1951 from the work of Martens & Schockaert (1985).

MATERIALS AND METHODS

Specimens were collected from sandy beaches using the $MgCl_2$-decantation method (see Martens, 1984), studied alive and mounted with lactophenol, one of those designated holotype. Specimens for transmission electron microscopy were fixed with 2% glutaraldehyde in 0.1M phosphate buffer and post-fixed in 1% OsO_4 in the same buffer at 4°C for 1h, dehydrated in a graded acetone series and embedded in araldyte using propylene oxide. Specimens were sectioned serially in alternating 1µm and ultrathin sections. Ultrathin sections were treated with aqueous solutions of 2% uranyl acetate and 1.2% lead citrate; 1µm sections were stained with toluidine blue (for further details: see Martens & Schockaert, 1985).

The holotype is deposited in the collections of the Swedish Museum of Natural History (Holotype Nr. 6339); all other material is deposited in the collection of the Research Group "Biodiversity, Phylogeny and Population Studies" of the Centre for Evironmental Sciences, Hasselt University, Diepenbeek, Belgium.

RESULTS

Family Coelogynoporidae Bresslau, 1933

Genus *Cirrifera* Sopott, 1972

Cirrifera genitoductus n. sp.

Localities

Mariakerke (Belgium): March, June and August 1983 (type locality); medium fine sand with fine shell debris in the mid-littoral. Heist (Belgium): October and November 1984 and in January and March 1984; fine sand, rich in silt in the mid-littoral. Wimereux (France): medium fine sand of the mid-littoral with abundant *Arenicola marina*: May 2006.

Etymology

The name refers to the presence of a genito-intestinal duct.

Description

Living adult animals (Fig. 1) are up to 16mm long and about 0.6mm wide. Like most coelogynoporids they have the tendency to curl up the posterior part of their body. The slender anterior tip is provided with two to three tufts of sensory hairs on either side. Anterior to the encapsulated brain there is a statocyst with four statocytes. The pharynx, directed ventrally, is about at 2/3 of the body. The intestine extends to a point close to the brain and has a solid pre-cerebral diverticulum reaching almost to the front end.

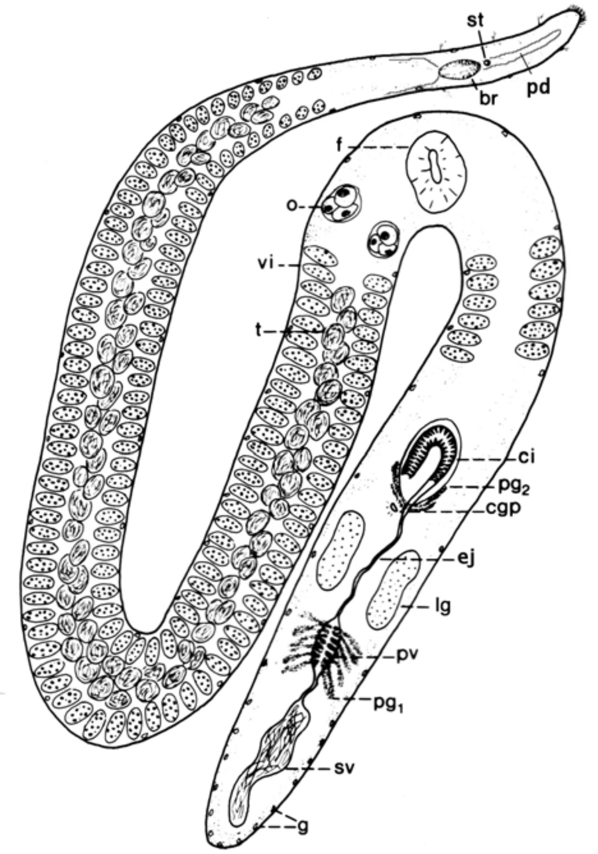

Fig. 1. – *Cirrifera genitoductus* n. sp.. Drawing of the living animal.

The epidermis (Fig. 2A,B) is 2.3 to 2.8µm thick and consists of irregularly-shaped cells with intra-epithelial lobate nuclei. The cilia are 6-8µm at the ventral side and 4-5µm at the dorsal side. Between the cilia are microvilli, about 0.05µm wide and 0.9µm long. The cilia have a long anteriorly-directed rootlet, almost parallel to the cell surface and a short rootlet perpendicular to it. The rostral rootlets converge into an extension of the anterior cell wall. A layer of ultrarhabdites can be observed just under the free cell surface. Various kinds of glands open through the epidermis among which are large glands, about 5µm in diameter with large electron-lucent granules up to 2µm in diameter. In the living animal, these glands are very apparent and might be confused with paracnids, which are absent in this species. Monociliary sensory collar receptors like those described e.g. by Ehlers & Ehlers (1977) were seen (but also receptors with two, three and four cilia) as were adhesive duo-gland organs.

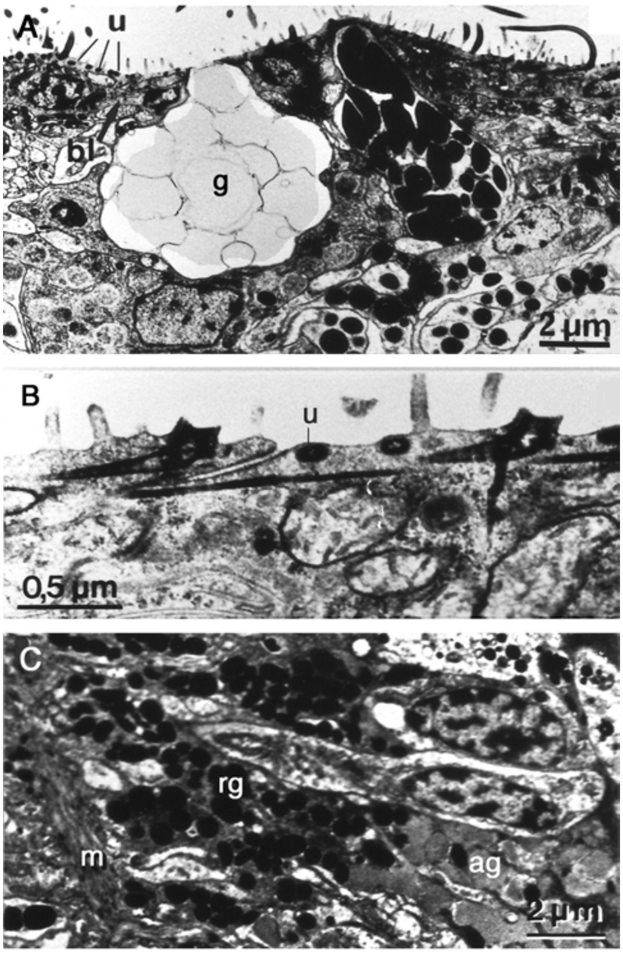

Fig. 2. – *Cirrifera genitoductus* n. sp.. Electronmicrographs of epithelial elements. A: Part of the epidermis showing some glands, among which the large hyaline glands, characteristic for species of *Cirrifera*. B: Longitudinal section through the epidermis, showing the ciliary rootlets and the ultrarhabdites. C: Section through the lateral glands.

The common genital pore without an obvious sphincter is about mid-way between pharynx and caudal end. The common genital atrium is almost completely filled with the protruding copulatory organ and is lined with a very low epithelium (Fig. 3A).

Behind the copulatory bulb there are two lateral masses of densely packed glands, very obvious in the living animal, even under the stereomicroscope (lg in Fig. 1). These glands discharge through the ventral epidermis and the gland cells contain round granules with low electron density (0.8µm in diameter) or very dense ovoid granules (0.2 to 1µm in diameter) (Fig. 2C).

The male genital organs consist of a row of up to 80 testis follicles, more or less in pairs, from some distance behind the brain to some distance in front of the pharynx. The follicle size increases from about 15µm in diameter anteriorly to about 50µm caudally (Fig. 1). The vasa deferentia fuse behind the copulatory organ and continue as a single seminal duct, which enters a large seminal vesicle at its anterior end (Fig. 3B, E). The long ejaculatory duct from the seminal vesicle to the copulatory organ enlarges to a prostate vesicle close after it has left the seminal vesicle. A second set of prostate glands enter the ejaculatory duct just before it enters the copulatory organ. The copulatory organ proper is a cirrus enclosed in a cirrus bulb (the duplex type of KARLING, 1956) (Fig. 3A,D). The ejaculatory duct enters the cirrus bulb at its caudal end, the cirrus bends over almost 180° and enters the atrium at its anterior side. Some protractor and dilatator muscles cross the bulb. The cirrus is about 130µm long, armed with up to 200 spines. These spines are symmetrically arranged in the cirrus, are 6µm long proximally and 8-9µm distally, with a basis 3-5µm wide. Cirrus and the bulb in which it is enclosed are surrounded by two muscle layers.

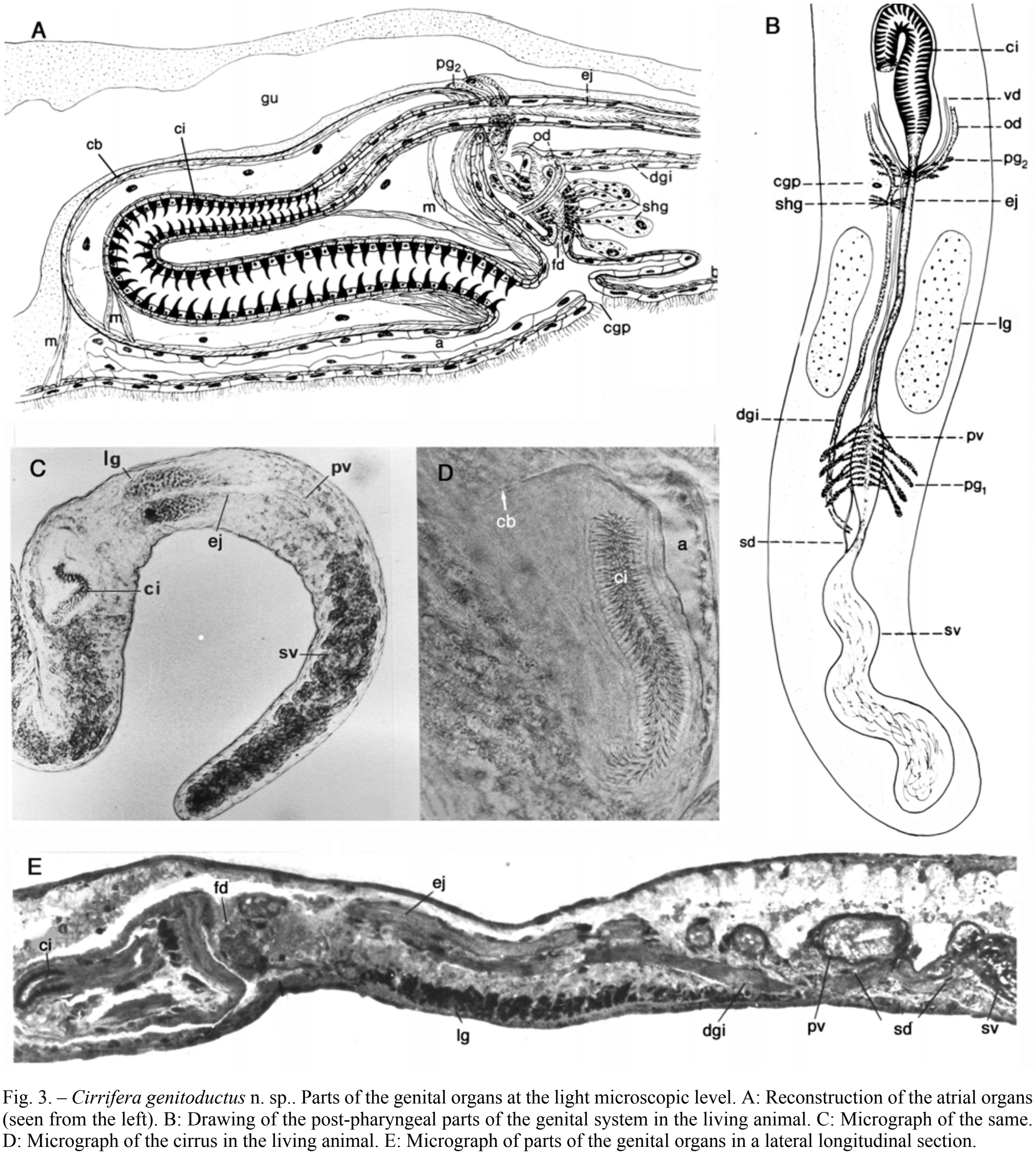

Fig. 3. – *Cirrifera genitoductus* n. sp.. Parts of the genital organs at the light microscopic level. A: Reconstruction of the atrial organs (seen from the left). B: Drawing of the post-pharyngeal parts of the genital system in the living animal. C: Micrograph of the same. D: Micrograph of the cirrus in the living animal. E: Micrograph of parts of the genital organs in a lateral longitudinal section.

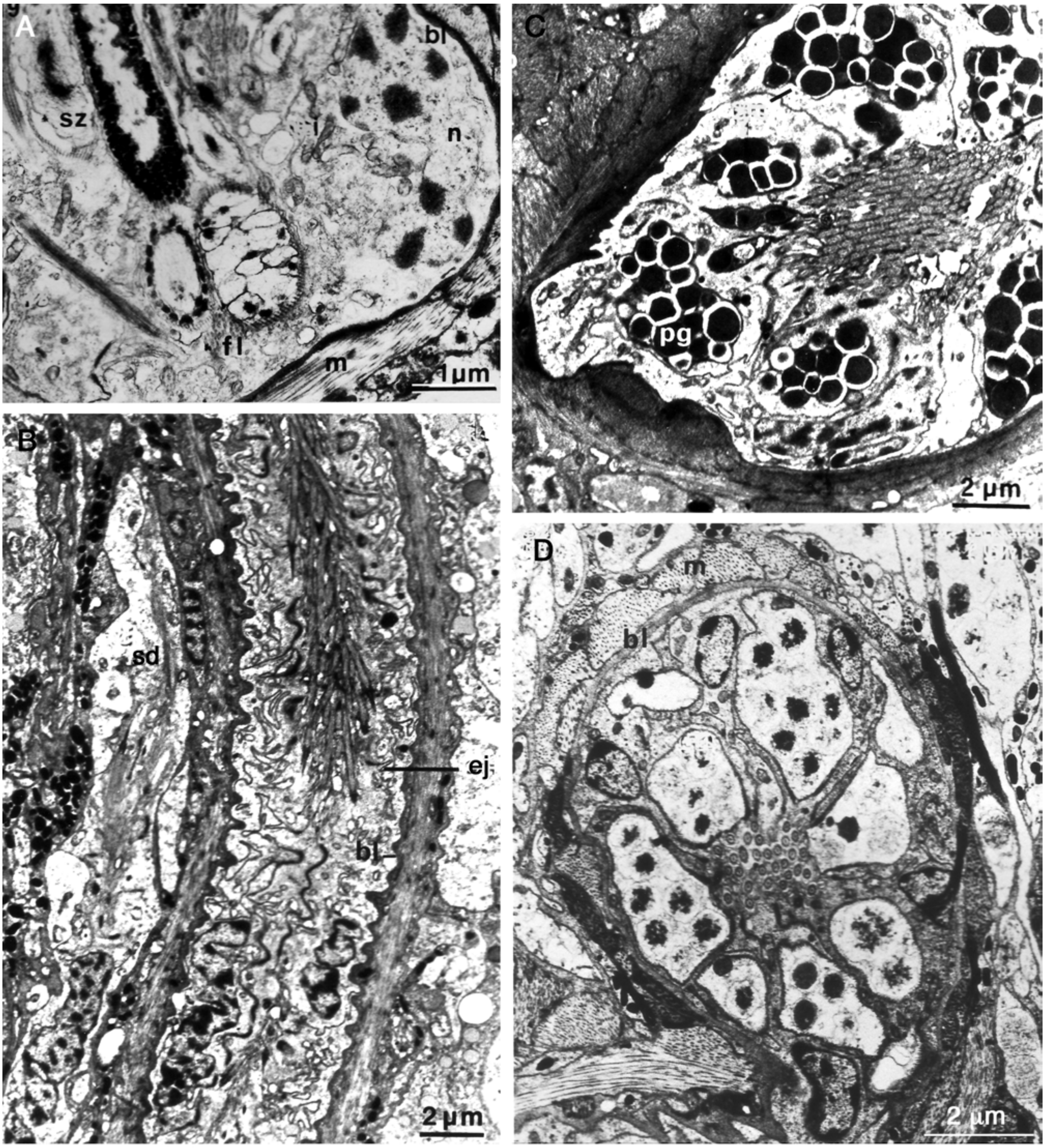

Fig. 4. – *Cirrifera genitoductus* n. sp.. Electronmicrographs of parts of the male genital system. A: The wall of the seminal vesicle, showing a spematozoon embedded in the epithelium. B: Longitudinal section though the ejaculatory duct. Note the convoluted plasmalemma of the epithelial cells, the thick basement membrane and the thick muscle layer. At the left is a section through the seminal duct with its very thin basement membrane. C: Section through the prostate vesicle, showing the glands with granules with a "halo". Note the thick muscle wall. D: Section through the prostate glands at the entrance to the copulatory organ, showing the granules with a flocculent core.

At the ultrastructural level, the male system is very similar to that in *Cirrifera aculeata* (see MARTENS & SCHOCKAERT, 1985). The two vasa deferentia, about 3µm in diameter, are lined with a ciliated epithelium as is the seminal duct. The circumference of the vasa deferentia consists of only two cells in any given cross-section, and of four cells in the seminal duct. The epithelium of the seminal vesicle is flattened with very few cilia. The basement lamina is very thin all along (0.15µm) with some dispersed muscles underneath, slightly thicker and more numerous around the seminal vesicle. As in *C. aculeata*, spermatozoa are seen deeply embedded in the epithelial cells of the seminal vesicle (Fig. 4A). In the ejaculatory duct (Fig. 4B), which is 6-7µm wide, the basement lamina is almost twice as thick (0.25µm) and there is a strong muscle layer with spirally- but mainly longitudinally-running muscles. The epithelial cells have lobate nuclei and highly convoluted walls and are densely ciliated. The glands that enter the prostate vesicle (pg1) are filled with homogeneous electron-dense granules of 0.50-0.85µm in diameter with a "halo" (perhaps an artefact) (Fig. 4C). The prostate vesicle is surrounded by several muscle layers. The second set of prostate glands (pg2) produce membrane-bound granules, about 0.75µm in diameter, with a flocculent electron-dense centre and a fine granular, much less electron-dense peripheral material (Fig. 4D). Where the ejaculatory duct becomes cirrus, the cilia disappear and the epithelium cells have 1µm long microvilli. More distally, as in *C. aculeata*, each cell contains a spine that protrudes from the cell (Fig. 5A,B). The protruding part of a spine (*in Fig. 5B) has an homogeneous, very electron-dense outer layer, about 80nm thick, and a less dark core. Within the cell, this core is surrounded by electron-dense flocculent material (black arrows in Fig. 5B). Some microtubules can be seen around the base of the spine and some more at the periphery of the cell (white arrows in Fig. 5B). The cell nuclei are horseshoe shaped and the distal cytoplasm contains numerous small electron-dense membrane-bound granules. Underneath the spine the cell is attached to a thick basement membrane with numerous “hemidesmosomes” (Fig. 5A).

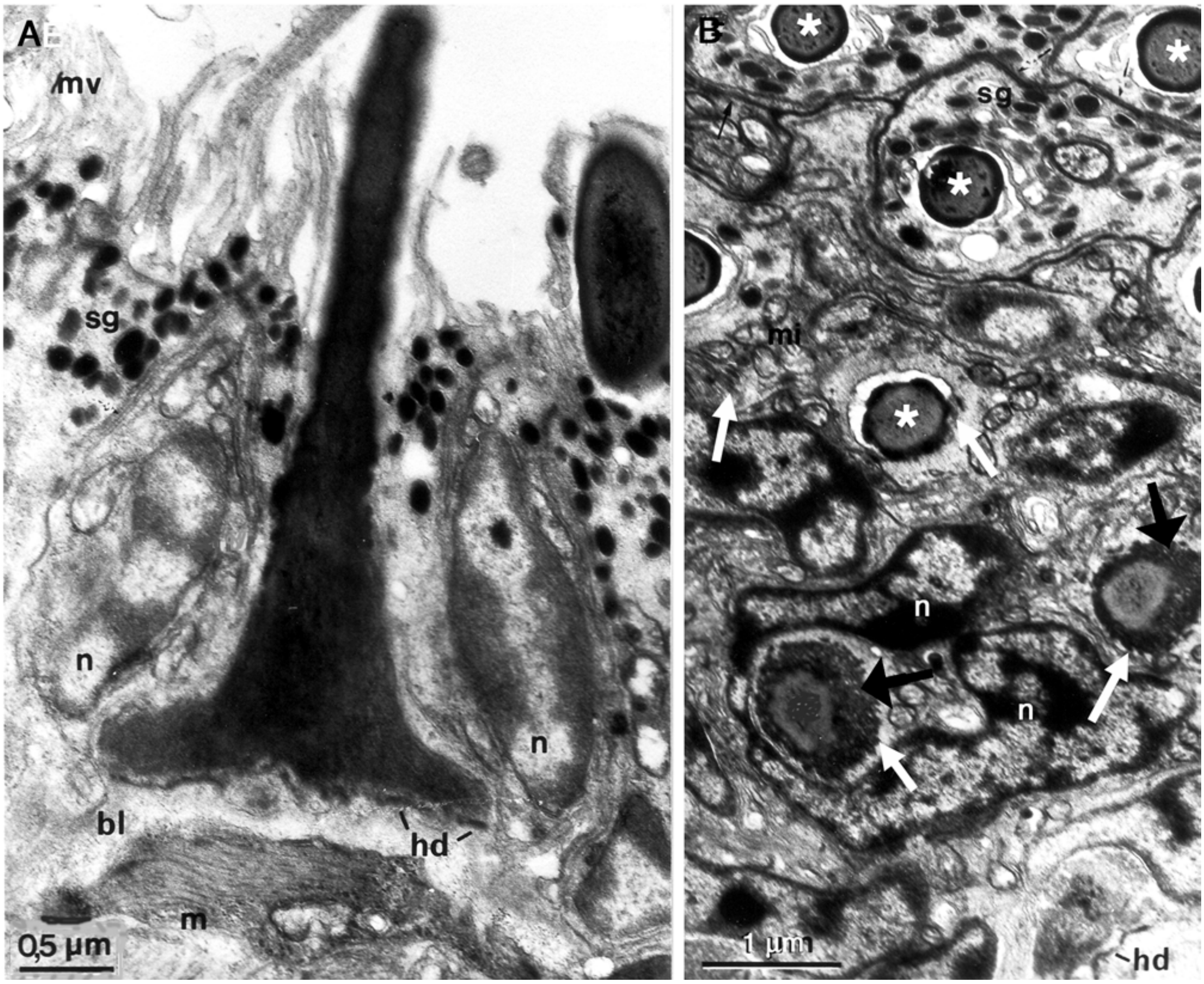

Fig. 5. – *Cirrifera genitoductus* n. sp.. Electronmicrographs of the cirrus spines. A: Longitudinal section through a spine in the cirrus. Note the “hemidesmosomes” with which the forming cell is attached to the thick basement membrane and the electron-dense granules at the apex of the cell. B: Cross sections at different levels of spines and forming cells in a tangential section through the cirrus wall. The black arrows point to the flocculent material at the base of the spines, the white arrows point to the microtubules and the * indicate the parts of the spines protruding from the forming cell. Note the horseshoe-shaped nucleus in A and in B.

The female system consists of a pair of globular ovaries in front of the pharynx and two rows of follicular vitellaria from just in front of the first testis follicle to about midway between pharynx and copulatory organ (Fig. 1). The two ovovitelloducts join just behind the copulatory organ to form a short common female duct, which receives the cement glands before it enters the atrium through its caudal wall (Fig. 3A). Just below the opening of the female duct is a short diverticulum of the atrium. From the junction of the oviducts a long genito-intestinal duct runs backwards and opens in the intestine behind the prostate vesicle and in front of the seminal vesicle (Fig. 3A,B).

The oviducts are two convoluting canals running next to the vasa deferentia. In the prepharyngeal region they are about 6μm wide, 10μm near their confluence. In any given cross section through an oviduct, its circumference is composed of only two cells, while that of the common duct is composed of four (and microvilli between the cilia), all with a very thin basement lamina and a weak muscle layer. Spermatozoa are frequently seen in the oviducts. The genito-intestinal duct is 9-12μm wide and has an epithelium similar to that of the common female duct, with four cells in cross-section, with microvilli, a very thin basement membrane and some weak muscles. All ducts in the female system have cilia.

DISCUSSION

The general anatomy of *C. genitoductus* n.sp. is like that of the majority of the representatives of the Coelogynoporidae: very long animals which may curl up, encapsulated brain, statocyst with four statocytes, numerous testes and vitellaria follicles, paired ovaries in front of the pharynx. The copulatory organ is clearly of the same construction as the members of the taxon *Cirrifera*: a long cirrus with many short spines, enclosed in a cirrus bulb and the seminal vesicle behind the copulatory organ. The ovovitelloducts enter a short common duct, which enters the atrium from behind. There is no bursa. Species of the taxa *Vannuccia* and *Stilivannuccia* also have a cirrus with many small spines enclosed in a bulb, but here the seminal vesicle(s) are in front of the cirrus. Moreover, there is a bursa in *Stilivannuccia*. *Macroatrium setosum* Riser, 1981 also has a cirrus and a posterior seminal vesicle, and it also has a bursa. The description of the latter species is, however, very elementary. *C. genitoductus* n.sp. deviates from all other *Cirrifera* species in that it has a long genito-intestinal duct. Main differences between the *Cirrifera* species can be derived from the identification key below:

Within several genera there are some species with a connection between the female system and the gut, while some other representatives of those genera lack such a connection. For example, in many species of *Coelogynopora* a bursa opens in the female duct, while in other species a duct running backwards from the common female duct opens in the gut: this is the so called genito-intestinal duct. This duct may be short or very long, ciliated or not and often a resorbing (bursal) tissue develops where the duct enters the intestine as in *Coelogynopora bresslaui* and *C. biarmata*, the two first coelogynoporid species described by Steinböck (1924). Such a genito-intestinal duct is also present in *Invenusta paracnida* Karling, 1966, in the species of *Ezona*, in *Vannuccia tripapillosa* and in *V. rotundouncinata* Ax & Sopott-Ehlers, 1979, while there is a bursa in *V. campana* Ehlers & Ehlers, 1980. In all previously-described species of *Cirrifera* and in the taxon *Carenscoilia* and in *Invenusta aestus* Sopott-Ehlers, 1976 the female system is very simple: both ovovitelloducts join each other behind the copulatory organ to form a short female duct, which opens in the atrium, and there are no bursal organs whatsoever. Now, in *Cirrifera genitoductus* sp.n., we have the first known example of a species of *Cirrifera* with a genito-intestinal duct.

1 –	Seminal vesicles paired	2
–	Seminal vesicle unpaired	5
2. –	Prostate vesicle intracapsular (i.e. inside the copulatory bulb); spines of different sizes and shapes in the cirrus.	3
–	Prostate vesicle extracapsular, all spines have the same shape	4
3. –	Cirrus 120-130μm long, armed with spines 9-20μm long and with one large proximal spine, about 25μm long, with bifurcated base	*C. aculeata* (Ax, 1951)
–	Cirrus 80-100μm long, armed with three different types of spines: proximally about 20 curved spines each 4-9μm long, distally 60-70 spines, each 10-15μm long, and 2 or 3 lateral pairs of straight and axe-shaped spines in between, each 19-40μm long	*C. sopottehlersae* Noldt & Jouk, 1988
4. –	Cirrus 120-130μm long, spines of 7-12μm, lacking on the posterior wall in the distal part of the cirrus	*C. cirrifera* Sopott, 1972
–	Cirrus about 200μm long, uniformly armed with spines of 12-16μm	*C. xanthoderma* Riser, 1981
5. –	No prostate vesicle: prostate glands open in seminal duct close to copulatory bulb, but without a muscle coat. Cirrus mushroom-shaped, uniformly armed with spines of 8-13μm	*C. boletiformae* Sopott, 1972
–	An extra-capsular prostate vesicle between the seminal vesicle and the cirrus	
6 –	Ejaculatory duct short, prostate vesicle close behind copulatory bulb. Cirrus 100μm long, spines 5-10μm but lacking spines on the anterior wall in the distal part of the cirrus	*C. dumosa* Sopott, 1972
–	Ejaculatory duct very long, prostate vesicle close to the seminal vesicle. Cirrus 130μm long, uniformly armed with spines 6-9μm long. With a genito-intestinal duct and a pair of large glands behind the genital pore	*C. genitoductus* sp. n.

Several other characters, of which we give some examples hereafter, also have such a "mosaic-like" distribution in the representatives of the Coelogynoporidae.

The copulatory organ may be a simple cirrus enclosed in a bulb with many small spines of similar size and shape, as in most species of the taxa *Cirrifera*, *Vannuccia* and *Stilivannuccia*. However, spines and needles of dissimilar size and shape occur in the copulatory organ of *C. sopottehlersae*. In most members of the taxon *Coelogynopora*, the cirrus (and/or atrium) bears long needles, either all similar or dissimilar, either attached to each other or not, while some species have a central stylet-like element surrounded by needles, the needles being free or attached to the stylet. The latter situation is also found in the taxon *Carenscoilia*. By contrast, a totally unarmed copulatory organ either cirrus or penis papilla occurs in some other species such as *Coelogynopora gynocotyla*, *Vannuccia tripapillosa* Tajika, 1977 and in the taxon *Invenusta*. In several species "accessory" stylets, either attached to a glandular reservoir or not, occur next to the copulatory organ proper, as in *Coelogynopora axi* Sopott, 1972, *C. hangoensis* Karling, 1953 and several other species of *Coelogynopora*, but also in the species of *Ezona* and of *Stilivannuccia*. The seminal vesicles may be paired or unpaired, and lie behind the copulatory organ in all coelogynoporids with the exception of in the species of *Vannuccia* and of *Stilivannuccia*. The vasa deferentia may fuse to a single seminal duct or remain separated until entering the seminal vesicle(s) from behind, in the middle or at its frontal side. The prostate glands may be within the copulatory bulb or enter the ejaculatory duct before it enters the copulatory bulb, and they may or may not be surrounded by a muscle sheath. A very long ejaculatory duct as in *Cirrifera genitoductus* (with extra-capsular prostate glands) is exceptional; it is also quite long in *Cirrifera aculeata*, but here the prostate vesicle is inside the copulatory bulb.

These examples of the variations within the Coelogynoporidae may suffice to demonstrate that making any statements about phylogenetic relations between the members of this taxon is premature. Including the taxa *Calviria* Martens & Curini-Galletti, 1993 and *Asilomaria* Karling, 1966 in the Coelogynoporidaae as proposed by Currini-Galletti (2001), based on molecular data, makes the picture even more confused. An attempt to perform a parsimony analysis, using the character states of about 30 characters, resulted in an unresolved bush (own data). Moreover, a sound comparison is difficult because many species have not been adequately described. An additional problem is that the degree of sexual maturity may cause differences that are easily overlooked or misinterpreted. Individuals of *Cirrifera genitoductus* sp.n. that we collected in March 1983 had only a short genito-intestinal duct, while it had grown to full length in the individuals collected later in the year. Sopott (1972) and Ax & Sopott-Ehlers (1979) also mention that the bursal organs develop later than the male organs.

Our observations on the ultrastructure of *C. genitoductus* reveal a high degree of similarity with that of *C. aculeata*, in particular the ultrastructure of the cirrus spines. They consist of an intracellular floccular substance formed at the base of the cell, and its periphery is "smoothed" where it protrudes from the cell. Though we have no data on spine formation in sub-adults we can assume that the spines are formed in a "synchronous" way, indicated by the presence of microtubules and the forming cell that is attached to a thick basement membrane by halve-desmosomes immediately underneath the spine matrix (see Bruggeman 1984; 1985 and in particular the discussions in his contributions of 1986 and 1988). Contrary to Bruggeman's observations, the forming cell does not degenerate and remains active with the formation of the electron-dense granules found at the apical side of the cell (also in *C. aculeata*: fig. 12 of Martens & Schockaert, 1985). The significance of these granules remains unclear, but they are most probably not related to the formation of the spine.

In *C. aculeata*, two kinds of secretory granules have been observed in the glands of the prostate vesicle, as is the case in most flatworms. In *C. genitoductus* it looks as if the two glands are separated: one type in the prostate vesicle and the other type entering the ejaculatory duct near the copulatory bulb.

Basically, the ultrastructure of the epidermis is that of many free living Platyhelminthes (see Rieger et. al., 1991 and the references therein). The feature of horizontal ciliary rootlets converging in a wedge of the anterior wall of the epidermis cells is now found in yet another proseriate species (own unpublished data); this remarkable situation might be an apomorphy for the Proseriata. The fine structures of the adhesive organs are similar to those of *Nematoplana coelogynoporoides* Meixner, 1938 (Sopott-Ehlers, 1979) and the receptors are like those of other Proseriata Lithophora (see Sopott-Ehlers, 1984). The large packages of glands at both sides behind the copulatory organ are, to the best of our knowledge, unique within the Proseriata. They consist of two kinds of glands, glands with large granules of low electron-density and glands with small electron-dense granules. They have an adhesive function (as observed in the living animal) and are reminiscent of the duo-gland adhesive glands (Tyler, 1976). Unfortunately, we have no data on the relations of the glands with the epidermis.

Many (all?) coelogynoporids have large glandular elements in the body wall that may look similar in the living animal, but are very different under the electron microscope. The so-called "paracnids" have been studied by Sopott-Ehlers (1981) in *Coelogynopora axi* and in *Carenscoilia bidentata* (1985). The ultrastructure of the "paracnids" in these two species is very different and Sopott-Ehlers (1985) claims to have unpublished data on the "paracnids" of the two *Invenusta* species, and that those are again very different. The large glands with hyaline content, seen in *Cirrifera genitoductus* may be confused with paracnids in the living animal. To the best of our knowledge such large hyaline glands do not occur in other coelogynoporid species, and paracnids do not occur in the taxon *Cirrifera*. These glands were described by Sopott in 1972 as "gelblichen (langlich) ovalen Hautdrusen", and were included in the genus diagnosis.

The diagnosis of the genus *Cirrifera* may be refined as follows:

Coelogynoporidae with intraepithelial nuclei and large hyaline glands in the epidermis. Male copulatory organ is a cirrus with many small spines, enclosed in a cirrus bulb. Seminal vesicle(s) caudal to the copulatory organ, paired or unpaired. Prostate vesicle outside or within the cirrus bulb. Paired germovitelloducts join behind the copulatory organ and open in the common genital atrium through its caudal wall. There is no bursa but a genito-intestinal duct may be present.

Diagnosis of *Cirrifera genitoductus* n. sp.:

Cirrifera species with very long ejaculatory duct, prostate vesicle close to the seminal vesicle and additional prostate glands close to the copulatory bulb. Cirrus 130µm long, uniformly armed with spines 6-9µm long. With a long genito-intestinal duct and a pair of large glands behind the genital pore.

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ABBREVIATIONS USED IN THE FIGURES

a	genital atrium
ag	adhesive gland
bl	basement membrane
br	brain
cgp	common genital pore
ci	cirrus
cb	cirrus bulb
dgi	genito-intestinal duct
ej	ejaculatory duct
f	pharynx
fd	common female duct
fl	flagella of spermatozoon
g	hyaline glands
gu	gut lumen
hd	hemidesmosomes
lg	lateral gland complex
m	muscles
mi	mitochondrion
mv	microvilli
n	nucleus
o	ovary
od	oviduct
pd	pre-cerebral gut
pg	prostate glands
pv	prostate vesicle
rg	releasing gland
sd	seminal duct
sg	secretory granules
shg	"shell glands" or “cement glands”
st	statocyst
sv	seminal vesicle
sz	spermatozoon
t	testis
u	ultrarhabdite
vi	vitellaria
vd	vas deferens

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