“Typhloplanoida” (Platyhelminthes: Rhabdocoela) from the Indian Ocean, with the description of six new taxa

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Abstract

Seven typhloplanoids from the Indian Ocean are discussed; six of them are new to science. We place four of the new species within the Trigonostomidae. *Gandalfia bilunata* gen. nov. sp. nov. is characterized by a tubiform stylet and two semilunar structures in the afferent duct. *Mahurubia clava* gen. nov. sp. nov. has a gutter-shaped stylet and a club-shaped mouthpiece on the bursa. *Parapharyngiella involucrum* gen. nov. sp. nov. is characterized by a stylet in the form of a question mark and a bursal mouthpiece with a club-shaped and a barrel-shaped part. *Poseidoplanella halleti* gen. nov. sp. nov. is characterized by an unpaired ovary, a funnel-shaped stylet connected with a plate, and a small, tubular bursal mouthpiece. Furthermore, new data are given on *Ceratopera axi*. The two other new species belong to the Typhloplanidae. *Aegira annabellae* gen. nov. sp. nov., a marine species, is characterized by a box-shaped stylet and a long, pseudocuticularized ejaculatory duct. *Castrada trispina* sp., a freshwater species, has a copulatory bursa with three spines. *Mahurubia clava* gen. nov. sp. nov. and *Parapharyngiella involucrum* gen. nov. sp. nov. occur at Zanzibar, Tanzania. The other five species have been found on Kerguelen.

Keywords: Biodiversity, taxonomy, Trigonostomidae, “Turbellaria”, Typhloplanidae

Introduction

The marine turbellarian fauna of the Southern Hemisphere in general and of the Indian Ocean in particular is little known. This is especially true for the so-called microturbellaria, and the “Typhloplanoida” is no exception. There are only some scattered reports on marine typhloplanoids in the Indian Ocean, from Somalia (Schockaert and Martens 1985), Kenya (De Clerck and Schockaert 1995), the Seychelles (De Clerck and Schockaert 1995), and La Réunion (Artois et al. 2000). Recently, five *Trigonostomum* Schmidt, 1852 species, three of them new to science, were reported from Kerguelen,
Zanzibar and Kenya, (Willems et al. 2004a). This brings the total number of known “Typhloplanoida” for the Indian Ocean to 14 species. In this contribution five new marine taxa (three from Kerguelen and two from Zanzibar) and one new freshwater species (from Kerguelen) are described. In addition, new data on Ceratopera axi (Riedl, 1954) Den Hartog, 1964 from Kerguelen are given.

In addition to the traditional Linnean binomen, for each species we also propose an alternative form of species name, which could be used in a system of phylogenetic nomenclature (De Queiroz and Gauthier 1990, 1992, 1994). This converted name (for each species) is chosen according to the system proposed by Artois (2001) and can be found directly below the Linnaean name.

Material and methods

The material was collected during two sampling expeditions. The specimens from Kerguelen were collected by Ernest Schockaert during an expedition to La Réunion, Crozet and Kerguelen in November and December 1992. Material from Zanzibar was collected by Huguette Sas, Tom Artois and Ernest Schockaert during a stay in August 1995.

The marine animals were extracted from sediment and algae using the MgCl$_2$ decantation method (see Schockaert 1996), whereas the freshwater Castrada species was collected by the oxygen depletion method (see Schockaert 1996); a moss sample was inundated, causing animals to move to the water surface. A few individuals of each species were studied alive and whole-mounted with lactophenol. The remaining specimens were fixed in marine Bouin’s solution, embedded in paraffin, serially sectioned (4 μm sections), and stained with Heidenhain’s iron haematoxylin, using eosin as a counterstain.

Camera lucida drawings of hard parts were made with Nomarski phase contrast microscopy. Drawings without a scale bar are freehand. Measurements of hard parts are taken axially, unless indicated otherwise. The position of the gonopore and organs, and the measurements of the pharynx, are expressed in percentages of the total body length (distance from the anterior tip of the body).

The type material of the newly described species is deposited in the zoological collection of the Limburgs Universitair Centrum (LUC), Diepenbeek, Belgium.

To enable us to compare the Ceratopera axi (Riedl, 1954) Den Hartog, 1964 specimens from Kerguelen with those of other populations, we borrowed voucher specimens from California and the Falklands from the collections of the Swedish Museum of Natural History in Stockholm (SMNH). Two whole mounts from Australia are also present in the collections of the LUC (Diepenbeek, Belgium).

The following abbreviations are used in the figures: ac, atrium copulatorium; ad, afferent duct; av, additional vesicle; bc, bursa copulatrix; bg, basophilic glands; bh, bursal hook; bs, bursal stalk; bu, bursa; cg, caudal glands; cga, common genital atrium; cil, cilia; de, ejaculatory duct; ds, seminal duct; e, eye; ecm, external circular muscle; elm, external longitudinal muscle; fa, female atrium; fd, female duct (= efferent duct); fg, female glands; gg, prostate glands; gp, common genital pore; gw, “Greifwulst”; icm, internal circular muscle; ilm, internal longitudinal muscle; lm, longitudinal muscle; m, mouth; ma, male atrium; mp, mouthpiece; mt, “mantle”; od, oviduct; ov, ovary; pc, prepharyngeal cavity; pg, pharynx glands; ph, pharynx; pl, pharynx lumen; rg, rostral glands; rm, radial muscle; rs, seminal receptacle; s, stylet; so, stylet opening; t, testis; ut, uterus; v, vas
deferens; vd, vitelloduct; vg, prostate vesicle; vit, vitellarium; vs, seminal vesicle; x, y, z, features described in respective text.

**Taxonomic account**

Systematic relationships within the “Typhloplanoida” s.s. (see Ehlers 1985) have never been assessed from a cladistical point of view. Pending a cladistical analysis of the “Typhloplanoida” by the first author, we will, for the time being, use the system proposed by Den Hartog (1964) and refined by Ax and Heller (1970). In this system the “Typhloplanoida” are divided into eight families, all of them further subdivided into several subfamilies. None of these taxa has yet been assessed for its monophyletic status. We would like to stress that the discussions in this paper must be seen as provisional, and are only intended to compare the new species with strongly similar species (as a differential diagnosis) and are not intended as primary homology assessments (*sensu* Patterson 1982).

**TRIGONOSTOMIDAE** Graff, 1905 *sensu* Den Hartog, 1964

**PARAMESOSTOMINAE** Luther, 1948

*Gandalfia bilunata* gen. nov. sp. nov.

\textit{gandalfia-bilunata} sp. nov.

(Figure 1)

**Diagnosis**

*Gandalfia* gen. nov. Paramesostominae with the pharynx situated in the middle of the body, with a ciliated collar in the distal part of the lumen. Unpaired testis and seminal vesicle. Distal part of the seminal vesicle and the proximal part of the prostate vesicle enclosed within the same muscle layer. With a straight, single-walled stylet. Ovaries paired. Glands enter the female duct about half way. Muscular afferent duct, widened near the common genital atrium, with basophilic glands and two sclerotized semilunar structures. Type species: *Gandalfia bilunata*.

*Gandalfia bilunata* sp. nov. Provisionally with the same diagnosis as the genus. Stylet $\pm 240 \mu$m long.

**Locality**

Kerguelen, Port Couvreux: between Ceramium-like red algae and thread-like green algae, mid-eulittoral, 0.4 m deep at high tide (25 November 1992) (type locality).

**Material**

Four specimens studied alive, and mounted, one of them designated holotype (LUC no. 266), the others paratypes (LUC nos 267–269). Five serially sectioned specimens (paratypes; LUC nos 270–274).

**Etymology**

The genus name/praenomen refers to the wizard Gandalf from the books by J. R. R. Tolkien; gender: feminine. The species epithet refers to the two semilunar structures in the bursa; *bis* (Latin): twice, *luna* (Latin): moon.
Description

Transparent, yellowish white animals, 1–1.6 mm long (measured on whole mounts), with two eyes. The cellular epidermis is about 4–5 μm thick, with cilia 2 μm long. It contains large, rod-shaped, slightly bent rhabdites, which are as long as the epithelium is high. Large eosinophilic rhabdite glands (Figure 1B: rg) converge to two long rhabdite strands towards the rostral tip of the body. The caudal glands are well developed (Figure 1A: cg), mainly eosinophilic, with a few basophilic ones.

The pharynx (Figure 1D) is situated at ±40%. The epithelium on the distal rim of the pharynx is provided with short, densely packed cilia (Figure 1D: cil1). The epithelium of the lumen is very low, with several nuclei and very high cilia in the distal part (Figure 1D: cil2). This part forms a so-called “Greifwulst” (prehensile girdle; Figure 1D: gw) with a sphincter of five thick fibres and a few weak radial muscles, running from the proximal end of the ciliation to the medial part of the rim of the pharynx bulb. There are 16 internal
longitudinal muscles. The pharynx bulb is filled with large glands, one type with a basophilic and two different types with eosinophilic secretion. The basophilic glands and the most proximal, eosinophilic glands enter the pharyngeal lumen at the level of the distal sphincter, whereas the other eosinophilic glands open near the distal rim.

The common genital pore is at 80–85%. The common genital atrium is lined with a high, cellular epithelium with cilia. It is surrounded by longitudinal muscles only.

There is only one small testis (see Figure 1B), dorsally next to the prostate bulb. The vas deferens is very short, leading to the seminal vesicle (Figure 1A, B: vs). This vesicle is lined with a low, nucleated epithelium, and surrounded by spirally running muscles. These muscles are very thick distally and also surround the proximal part of the prostate vesicle. The prostate vesicle, as seen in live animals (Figure 1B: vg), is divided into proximal and distal halves, each with a different secretion. In the sectioned material, on the other hand, the prostate vesicle is completely empty, while filled gland necks can be seen in the stylet (fixation artifact?). Where the glands, which have an extracapsular nucleated part (Figure 1A: gg), enter the prostate stylet, a number of nuclei are present (not drawn in Figure 1A). The fragile, single-walled, tubiform stylet (Figure 1C) is broken in every one of the whole mounted specimens, and is 212–250 μm long (mean = 237 μm; n = 3). The proximal opening is 30–38 μm wide (mean = 35 μm; n = 3). From this opening the stylet narrows, and at about one-quarter of its length it continues as a straight tube, 17–23 μm in diameter (mean = 19 μm; n = 3). The opening is situated at the blunt end (Figure 1C: so). A weak muscle (Figure 1A: lm) extends from the male atrium to the ventral body wall.

There are two large, elongated ovaries, lying ventrally just behind the pharynx. The paired vitellaria extend dorsally at both sides of the body, from behind the eyes towards the level of the gonopore. In the sectioned specimens both vitellaria anastomose with each other, which was not observed in live animals. The two short oviducts join each other to form the female (= efferent) duct (Figure 1A: fd). The vitelloducts enter the oviducts just before this junction. The female duct is surrounded by longitudinal muscles and lined with a high, nucleated epithelium. About half way, a large bundle of basophilic glands (Figure 1A: fg) enters the female duct. A second duct, the afferent duct (Figure 1A: ad), connects the common genital atrium with the junction of both oviducts. It is lined over its whole length with basement membrane only (pseudocuticula) and is surrounded by circular muscles, except for the part near the ovaries where it has a very thin wall. The muscular part is surrounded by parenchymatic tissue (myoblasts?), containing a large number of nuclei. Near the common genital atrium, the afferent duct is slightly widened and surrounded by very thick circular muscles. The basement membrane is very thick, forming two semilunar structures (Figure 1A, B: x), especially obvious in live animals. A large bundle of basophilic glands (Figure 1A: bg) opens into the distal part of the afferent duct, at the transition to the common genital atrium. A uterus is lacking.

TRIGONOSTOMINAE Luther, 1948

_Ceratopera axi_ (Riedl, 1954) Den Hartog, 1964

_ceratopera-axi_ (Riedl, 1954) Den Hartog, 1964

_Proxenetes axi_ Riedl, 1954.

_Ceratopera bifida_ Ehlers and Ax, 1974.

Localities

_New locality._ Port Couvreux (Kerguelen): between filiform green algae, mid-eulittoral, 0.4 m deep at high tide (25 November 1992).
Other locality in the Indian Ocean. La Réunion (Artois et al. 2000).

*Known distribution.* Gulf of Naples and Sicily (Riedl 1954); Galapagos (Ehlers and Ax 1974); Falkland Islands and California (Karling 1986); Weddell Sea (Artois et al. 2000); Eastern Australia (Willems et al. 2004b).

*Material*
Observations on live specimens and one whole mount. Whole mounts from Falklands and California (collections of SMNH) and Australia (collections of LUC).

*Remarks*
The stylet of the specimen from Kerguelen measures 121\(\mu m\) (88\(\mu m\) if measured as in Ehlers and Ax 1974). The bursal appendage (or mouthpiece) is 117\(\mu m\) long. These measurements correspond with those on the specimen from the Weddell Sea (Artois et al. 2000), they are slightly larger than those of the specimen from La Réunion (Artois et al. 2000) and much larger than those of the Australian (Willems et al. 2004b) and the Galapagos specimens (Ehlers and Ax 1974). The last-mentioned population was formerly described as a different species, *C. bifida* Ehlers and Ax, 1974. According to Karling (1986), Artois et al. (2000) and Willems et al. (2004b), *C. bifida* Ehlers and Ax, 1974 is considered a junior synonym of *C. axi* (Riedl, 1954) Den Hartog, 1964.

As the variation in stylet size within *C. axi* is rather large, it would not be surprising that this “morphological plasticity” in fact hides a complex of cryptic species, as is the case for *Gyratrix hermaphroditus* Ehrenberg, 1831 (see Curini-Galletti and Puccinelli 1989, 1990, 1994, 1998; Artois et al. 2000; Artois and Schockaert 2001) or the “*setigerum* species complex” within the taxon *Trigonostomum* (see Willems et al. 2004a). However, since the only known difference between the different populations of *C. axi* is this size variation of the stylet, it is at the moment highly arbitrary to split this complex into different formal species. Such an action should be backed up by a much more thorough morphological (and molecular) study of the species, which is clearly not within the scope of this study.

*Mahurubia clava* gen. nov. sp. nov.

*mahurubia-clava* sp. nov.

(Figure 2)

*Diagnosis*

*Mahurubia* gen. nov. Trigonostominae with the pharynx in the middle of the body. Testes and seminal vesicles paired, far behind the pharynx. Prostate stylet consisting of two parts, one of which is gutter-shaped and receives the prostate secretion, the other one a folded plate-like structure, which carries several spines distally. Additional vesicle (with sperm) at the proximal part of the female (efferent) duct. Afferent system consisting of tortuous duct and large, thick-walled bursa. Mouthpiece of bursa club-shaped. Type species: *Mahurubia clava*.

*Mahurubia clava* sp. nov. Provisionally with the same diagnosis as the genus. Stylet 87\(\mu m\) long.
Locality

Zanzibar, Mahurubi Palace Ruins: open beach with fine sand in front of the mangroves, at low tide (5 August 1995) (type locality); same locality: sandflat with crab holes (17 August 1995).

Material

Three individuals studied alive and mounted: one designated holotype (LUC no. 275), another one paratype (LUC no. 276). Three serially sectioned animals (paratypes; LUC no. 277–279).

Figure 2. *Mahurubia clava* gen. nov. sp. nov. (A) General organization (from a live specimen); (B) habitus of a live animal; (C) stylet (from the holotype); (D) reconstruction of the atrial organs from the right side.
**Etymology**

The genus name/praeonomen refers to the type locality, Mahurubi (Zanzibar, Tanzania); gender: feminine. The species epithet refers to the shape of the mouthpiece; *clava* (Latin): club.

**Description**

The animals are \(0.6–0.9\) mm long (measured on whole mounts), with two eyes. The cellular epidermis is about \(2\) \(\mu\)m thick, with cilia \(1.5\) \(\mu\)m long. Large rhabdites occur throughout the epidermis, but are slightly more concentrated at the rostral and caudal ends. Rostrally there are two long strands of rhabdite glands (Figure 2B: rg). Caudal glands are also well developed.

The pharynx is situated at about 40%. There are basophilic and eosinophilic pharyngeal glands. The nucleated epithelium of the pharyngeal lumen is low. There are 24 internal longitudinal and 24 radial muscles in horizontal sections.

The common genital pore lies at \(90\%\). The common genital atrium is rather wide, lined with a high, nucleated epithelium, and surrounded by longitudinal muscles only. It extends rostrally to form the female atrium and communicates dorsally with the male atrium.

Paired testes are situated far behind the pharynx, just in front of the ovaries (Figure 2A, B). Seminal vesicles are paired, lined with low, nucleated epithelium and surrounded by spiral muscles. Both vesicles narrow and subsequently fuse to form the seminal duct (Figure 2D: ds), just before entering the prostate vesicle. The seminal duct continues through the prostate vesicle as a very narrow duct and widens just before entering the stylet. The prostate vesicle (Figure 2A: vg) is very large and elongated. It is surrounded by inner circular and outer longitudinal muscles. Two kinds of prostate glands are present: eosinophilic ones (Figure 2D: gg2) with extracapsular nucleated parts, and basophilic glands, which are completely intracapsular (Figure 2D: gg1). The very complex stylet (Figure 2C) is \(81–90\) \(\mu\)m long (mean=\(87\) \(\mu\)m; \(n=3\)) and consists of two parts: a bent, gutter-shaped one (maybe a closed tube) and a folded plate-like part at the concave side, which is attached to the gutter-shaped part over most of its length. Sperm is probably discharged in between these two parts, while the gutter-shaped one receives the prostate secretion. The male genital atrium is lined with a membranous epithelium and surrounded by inner circular and outer longitudinal muscles. Distally, the circular layer ends where the male atrium enters the common genital atrium. A short, but strong bundle of longitudinal muscle fibres (Figure 2D: lm) connects the proximal part of the male atrium with the common genital atrium.

The paired, ovoid ovaries are situated on both sides of the prostate vesicle. They form the most caudal part of the elongated ovovitellaria (Figure 2B: ov+vit), which extend from just behind the eyes to the prostate vesicle. There is a large variation in size of the ovaries between different individuals, possibly due to differences in developmental stage. The female duct (=efferent duct; Figure 2D: fd) enters the female atrium (Figure 2D: fa) anteriorly. The common genital atrium, the female atrium and the female duct are all lined with a high, nucleated epithelium and surrounded by longitudinal muscles. Distally from the junction of the oviducts a large bundle of eosinophilic glands (Figure 2D: fg) opens into the female duct, which is guarded by a sphincter. Proximally from the junction, the female duct ends in a small sperm-containing vesicle (Figure 2D: av), lined with a low, nucleated epithelium and filled with motile sperm in the living animal. This additional vesicle can be
closed by a weak sphincter. At the transition between the female duct and the vesicle a tortuous duct (=part of the afferent duct) connects a large bursa (Figure 2D: bu) with the ovaries. Where the duct leaves the bursa, a sclerotized, club-shaped mouthpiece (Figure 2D: mp; not visible on whole mounts) is present. The bursa proper is thick-walled, surrounded by strong spirally running, almost longitudinal muscles, and enters the female atrium dorsally, just above the female duct. A uterus is lacking.

**Parapharyngiella involucrum** gen. nov. sp. nov.

*parapharyngiella-involucrum* sp. nov.

(Figure 3)

**Diagnosis**

*Parapharyngiella* gen. nov. Trigonostominae with the pharynx situated in the first body half. Paired testes in front of the pharynx. Paired ovovitellaria with the ovaries and atrial organs situated just caudally to the pharynx. Prostate stylet a curved tube, distally surrounded by the mantle. Additional vesicle (with sperm) at the proximal part of the female (efferent) duct. Afferent system consisting of curling duct and large, thin-walled bursa (with sclerotized bursal stalk). Mouthpiece of bursa consisting of a club-shaped part surrounded by a barrel-shaped part. Type species: *Parapharyngiella involucrum*.

*Parapharyngiella involucrum* sp. nov. Provisionally with the same diagnosis as the genus. Stylet 48 μm long.

**Locality**

Zanzibar, Mahurubi Palace Ruins: beach with detritus-rich sand, churned up by crabs, at low tide (5 August 1995) (type locality).

**Material**

Four specimens studied alive and whole mounted, one of them designated holotype (LUC no. 280), the others paratypes (LUC nos 281–283). One serially sectioned specimen (paratype; LUC no. 284).

**Etymology**

The genus name/praenomen refers to the position of the genital system, just behind the pharynx; *para* (Greek): close to; gender: feminine. The species epithet refers to the partially sclerotized wall of the bursal stalk, giving it the appearance of a kind of envelope; *involucrum* (Latin): envelope.

**Description**

The animals are ±1 mm long (measured on whole mounts), with two eyes. The cellular epidermis is about 3 μm thick with cilia of 3–4 μm long. Numerous minute rhabdites occur throughout the epidermis. Close behind the eyes, some basophilic glands (Figure 3A: rg) are present and produce rod-shaped adenal rhabdites, which are ±6 μm long. The gland necks are organized in two long tracts, fusing at the level of the eyes and opening terminally at the rostral body end.
Figure 3. Parapharyngiella involucrum gen. nov. sp. nov. (A) Habitus of a live animal; (B) general organization (from a live specimen); (C) stylet (from the holotype); (D) horizontal reconstruction of the atrial organs.
The pharynx is situated at about 30%. It has 24 internal longitudinal muscles. The more detailed structure could not be determined, but does not seem to differ from that of most other trigonostomids.

The paired testes are rather small and globular and lie just in front of the pharynx (Figure 3A). The dorsally situated, paired ovovitellaria extend from the level of the testes to the caudal body-end, with the ovaries just behind the pharynx. Also all other reproductive structures are located immediately behind the pharynx (see Figure 3A, B). The common genital pore is situated at ±40%. The common genital atrium is surrounded by inner circular and outer longitudinal muscles, and lined with a nucleated and frayed epithelium (pseudociliation).

The paired seminal vesicles are lined with a low, nucleated epithelium and surrounded by circular muscles. Just before entering the prostate vesicle (Figure 3B: vg), both seminal vesicles join to form the seminal duct (Figure 3D: ds). It runs axially through this prostate vesicle, but is only clearly visible in the proximal part. Both prostate vesicle and male atrium are surrounded by circular muscles. There are two types of prostate glands: eosinophilic glands situated dorsally (Figure 3D: gg2) and basophilic ones ventrally (Figure 3D: gg1). Extracapsular parts of the glands were seen only on live material (Figure 3B: gg). The complex stylet (Figure 3C) is 44–55 μm long (mean = 48 μm; n = 4) and consists of a very narrow, thick-walled tube, giving it the shape of a question mark when viewed laterally. The distal part (about 60%) is surrounded by a large plate ("mantle" of Ax 1971). Distally, this plate (Figure 3C: mt) ends in a broad hook.

The ovoid ovaries are situated dorsal to the prostate vesicle. The short oviducts are lined with a low, nucleated epithelium and join to form the female duct (= efferent duct; Figure 3D: fd), which enters the atrium dorsally. The female duct is surrounded by a strong sphincter at its proximal end, where a large bundle of eosinophilic glands (Figure 3D: fg) surrounds and enters the female duct. Proximally the female duct ends in a small, globular sperm-containing vesicle (Figure 3D: av), the entrance of which is guarded by a sphincter. The afferent system consists of a large bursa (Figure 3D: bu) and a sclerotized duct, which connects the bursa with the sperm-containing vesicle on the female duct. Where it leaves the bursa, this duct widens and contains a large mouthpiece (Figure 3D: mp; not visible on whole mounts), which is a complex sclerotized structure, consisting of an inner club-like part, surrounded by a barrel-shaped part. The latter part is probably the thickened wall of the surrounding duct. The bursa has a thin and extremely folded wall, is filled with sperm and eosinophilic secretion, and is connected to the genital atrium by a narrow duct (bursal stalk; Figure 3D: bs), which is lined with a thick sclerotized basement membrane. In about its middle, the bursal stalk widens and the basement membrane is clearly thicker on one side, giving it the appearance of a kind of envelope. A uterus is lacking.

**MARIPLANELLINAE** Ax and Heller, 1970

*Poseidoplanella halleti* gen. nov. sp. nov.

*poseidoplanella-halleti* gen. nov. sp. nov.

(Figure 4)

**Diagnosis**

*Poseidoplanella* gen. nov. Mariplanellinae with complex stylet, consisting of tubiform and plate-like parts. Unpaired seminal vesicle. Extracapsular prostate glands. Afferent system
consisting of dome-shaped bursa, muscular duct, seminal receptacle and sclerotized mouthpiece. Type species: *Poseidoplanella halleti*.

*Poseidoplanella halleti* sp. nov. Provisionally with the same diagnosis as the genus. Stylet 61–67 µm long, consisting of a tube connected to a triangular plate that carries a spur.

**Locality**

Kerguelen, Port Couvreux: small bay, on thread-like green algae, mid-eulittoral, 0.4 m deep at high tide (25 November 1992) (type locality).
Material

Several individuals studied alive. Five whole mounts, one of them designated holotype (LUC no. 285), the others paratypes (LUC nos. 286–289). Two serially sectioned specimens (paratypes; LUC nos. 290–291).

Etymology

The genus name/praenomen refers to Poseidon, the Greek god of the sea. The suffix -planella ("little flat animal") is used in analogy with Mariplanella and Lonchoplanella, the genus names of the two other species in the subfamily (see Discussion); gender: feminine. The species is dedicated to Mr Peter Hallet, a friend of the first author.

Description

The colourless to pale yellow animals are 0.7–1.0 mm long (measured on whole mounts) and have two eyes with lenses. The cellular epidermis is about 3 μm thick (only slightly thicker at the rostral and caudal body end) with cilia ± 2 μm long. Cilia are almost completely lacking at the dorsal side. The rod-shaped rhabdites are ± 3 μm long and occur exclusively in the dorsal body epithelium. Two small, eosinophilic rhabdite glands (Figure 4A: rg) are present between the eyes in the rostral part of the body. Caudal eosinophilic and basophilic glands are very well developed (Figure 4D: cg).

The small, globular pharynx (Figure 4A, D: ph) is situated in the first body half at ± 25%. The distal rim carries short cilia (Figure 4D: cil). The prepharyngeal cavity (Figure 4D: pc) is lined with a low, anucleated epithelium and surrounded by longitudinal muscles. The pharynx lumen is lined with a low, anucleated epithelium without cilia. The exact number of inner longitudinal and radial muscles could not be determined. Distally the inner circular muscles form a thick sphincter within the so-called "Greifwulst" (prehensile gridle; Figure 4D: gw), which lacks cilia. The pharynx is filled with probably only one type of basophilic gland.

The genital pore is situated at ± 60% (Figure 4A, B, D: gp) and can be closed by a sphincter. The common genital atrium is very small, lined with a high, nucleated epithelium and surrounded by longitudinal muscles. It communicates with the male atrium rostrally, with the female duct caudally and with the bursa dorsally.

The paired, elongated testes lie caudally of the pharynx, ventrally of the vitellaria. The unpaired seminal vesicle is large and globular and lies just caudally of the pharynx. It is lined with a low, nucleated epithelium and surrounded by weak circular muscles. A short ejaculatory duct (Figure 4D: de) leads into the small barrel-shaped prostate vesicle (Figure 4D: vg), which contains the gland necks of the elongated, extracapsular prostate glands, and is surrounded by circular muscles. The stylet consists of a narrow tube (44–54 μm long; mean = 49 μm; n = 5) attached to a plate-like structure (54–58 μm long; mean = 56 μm; n = 5) that has a proximal rectangular part and a distal elongated triangular part. The stylet is attached to the plate at the transition of both parts, from where also a slender spur departs (40–47 μm long; mean = 43 μm; n = 5). The whole structure, plate plus stylet, measures 61–67 μm (mean = 65 μm; n = 5). Both sperm and prostate secretion are discharged through the tubiform part of the stylet. The male atrium is rather long, lined with a high, anucleated epithelium, and proximally surrounded by very strong spirally running muscles. In the distal part of the male atrium the muscles become weaker and circular.
The single ovary is situated caudally. The paired vitellaria lie dorsally and extend from the pharynx to the caudal body end. The vitellocytes join and, subsequently enter the female duct from behind and ventrally (Figure 4D: vd). The female or efferent duct (Figure 4D: fd) is lined with a high, nucleated epithelium (the lumen is very narrow) and surrounded by weak longitudinal muscles. Distally to the vitellocytes, basophilic glands enter the female duct from the dorsal side (Figure 4D: fg). In the proximal part of the female duct the lumen becomes wider, and close to the ovary it is swollen and filled with sperm. The afferent system begins with a dome-shaped bursa at the dorsal side of the common genital atrium. This bursa is lined with the same high, nucleated epithelium as the atrium. The bursa is connected to a globular sperm-containing vesicle or receptaculum seminis (terminology of Ax and Heller 1970 and Ehlers 1974) through a very narrow, muscular duct. The vesicle is embedded in a stromatic tissue with cavities filled with sperm in various stages of digestion, and is connected to the oviduct by a short, sclerotized duct or mouthpiece, not seen, however, in the living animal (Figure 4D: mp; terminology of Ax and Heller 1970 and Ehlers 1974). A uterus is lacking.

Discussion of the new Trigonostomidae species

The four new species described above are members of the taxon Trigonostomidae Graff, 1905 (sensu Den Hartog, 1964), and belong to the subtaxa Paramesostominae Luther, 1948, Trigonostominae Luther, 1948, and Mariplanellinae Ax and Heller, 1970.

In the Trigonostomidae, the ovaries are connected to the atrium by two ducts: an efferent duct (“abführend” in Luther 1948), through which the fertilized egg descends to the atrium, and an afferent system (“zuführend” in Luther 1948) through which the alien sperm (presumably) reach the ovaries after copulation. This feature has always been considered diagnostic for the Trigonostomidae (see Den Hartog 1964; Ax and Heller 1970; Ax 1971). However, Karling et al. (1972) expressed some doubts about the homology of this double connection in all trigonostomids, and indeed such a double connection can also be found in, for example, some Polycystididae Graff, 1905 (see Artois and Schockaert forthcoming) and in some Solenopharyngidae Graff, 1882 (e.g. Proceropharynx litoralis Ehlers, 1972 and Adenopharynx mitrabursalis Ehlers, 1972; see Ehlers 1972). Moreover, the construction of the whole female system may be quite different in the various Trigonostomidae species. A thorough discussion on the matter is, however, beyond the scope of this contribution. We have used the terminology of previous authors to indicate different parts of the afferent system, without implying any homology. Comparison of each new species with known species is made within the present taxonomic system, pointing only to the most conspicuous differences (as a differential diagnosis).

Gandalfia bilunata sp. nov. exhibits all characters of the Paramesostominae enumerated by Karling et al. (1972, p 261), and shows the highest resemblance with Astrotorhynchus bifidus (McIntosh, 1874) Graff, 1905. Astrotorhynchus bifidus has a retractable “proboscis”, a uterus and spiral ridges on the stylet (see Luther 1950), whereas G. bilunata has none of these characters. Furthermore, in G. bilunata there is only one testis (two in A. bifidus; Luther 1950) and the basement membrane of the atrial bursa is thickened to form two semilunar structures, obvious in live animals, but absent in A. bifidus.

Mahurubia clava sp. nov. and Parapharyngiella involucrum sp. nov. must be considered members of the Trigonostominae (for diagnosis, see Den Hartog 1964 and Ax 1971). They have paired ovovitellaria, paired seminal vesicles, the copulatory organ is clearly of the trigonostominae construction, and the afferent female duct ends in a sclerotized
mouthpiece (except in *Petaliella spiracauda* Ehlers, 1974). Contrary to the situation in all other Trigonostominae, this mouthpiece is club-shaped in the two African species, and lies within a duct, which ends in an additional sperm-containing vesicle close to the ovaries. Such a vesicle is absent in all other known species. Moreover, the copulatory organ in each of the two new species is clearly different from those of all other Trigonostominae, allowing easy recognition.

The Mariplanellinae have a single ovary, separated from the (paired) vitellaria (see Ax and Heller 1970), and *Poseidoplanella halleti* sp. nov. must therefore be considered a representative of this taxon. So far, the taxon Mariplanellinae encompassed two species, *Mariplanella frisia* Ax and Heller, 1970 and *Lonchoplanella axi* Ehlers, 1974. Both these species have the pharynx in the second half of the body and the genital organs in the caudal body part (see Ax and Heller 1970; Ehlers 1974). *Poseidoplanella halleti* has the pharynx at 25%, and the genital organs in the middle of the body, and it has a single seminal vesicle, while the other two species have only one. The hard parts of the copulatory organ are clearly different in the three species.

**TYPHLOPLANIDAE** Graff, 1905

**RHYNCHOMESOSTOMINAE** Bresslau, 1933

*Castrada trispina* sp. nov.

*castrada-trispina* sp. nov.

(Figure 5)

**Diagnosis**

*Castrada* species with three spines in the copulatory bursa, two of them of the same shape and size (40 and 46 µm long), the third one of a different shape and larger (88 µm long). Ejaculatory duct a simple, bent, pseudocuticularized tube.

**Locality**

Kerguelen, Baie de la Table; on mosses in a freshwater torrent near a cascade on the beach (4 December 1992) (type locality).

**Material**

Several individuals studied alive. One whole mount, designated holotype (LUC no. 300). Four serially sectioned specimens on seven slides (paratypes; LUC nos 301A-C–304A-B).

**Etymology**

The species epithet refers to the presence of three spiny thorns in the copulatory bursa; *spina* (Latin): thorn.

**Description**

Small and slender animals, colourless and without eyes. Small rhabdite glands (Figure 5: rg) with slender, elongated rhabdites present in the rostral region, which is very agile in live individuals. The syncytial epidermis is about 4 µm thick ventrally, dorsally thinner (2–3 µm), with cilia ±5 µm long. These cilia are much shorter and less densely distributed
Dorsally. Dermal rhabditis could not be discerned. In sections, the epidermis shows a basal, strongly stained part in which the nuclei lie, and an outer, weakly coloured part, as in a number of *Castrada* species (Luther 1946, p 48).

The globular pharynx is situated mid-body. The detailed structure does not deviate from that of other *Castradella* and *Castrada* species (Luther 1946, 1963; Papi 1959). The prepharyngeal cavity consists of two parts. Proximally it is wide and lined with a low, anucleated epithelium, whereas it narrows distally, forming a short tube. This tubular part can be closed by two sphincters, one proximally near the transition to the larger cavity, the second one at the mouth. The tubular part is lined with a high, nucleated epithelium,

Figure 5. *Castrada trispina* sp. nov. (A) General organization (from a live specimen); (B) bursal hooks; (C) reconstruction of the atrial organs from the right side.
covered with cilia. This epithelium strongly resembles the body epithelium. In all Castrada species, a very similar tubular part of the prepharyngeal cavity is present, into which the protonephridial ducts open, and that therefore is called the excretion cup (Luther 1946; Papi 1959). However, in live individuals of Castrada trispina sp. nov. the protonephridia clearly did not open into the mouth, albeit that the exact place of opening could not be determined.

The paired testes are situated left and right of the pharynx, ventrally to the vitellaria. The male genital system contains two major parts: the copulatory bulb and the copulatory bursa, both in close association with each other and surrounded by the same muscle layer. The vasa deferentia are narrow and enter the seminal vesicle together. This copulatory bulb is surrounded by very strong circular muscles and contains the seminal vesicle and the basophilic prostate glands, with no extracapsular parts. Seminal vesicle and glands open into the cup-shaped proximal part of the pseudocuticularized ejaculatory duct (Figure 5C: de), which becomes a narrow tube distally. The ejaculatory duct enters the proximal part of the common genital atrium (atrium copulatorium in Papi 1959) and can protrude into it. Here, the copulatory bulb can be closed by a sphincter. The atrium copulatorium also receives the copulatory bursa (Figure 5C: bc), which is a narrow, muscular sac, ventral to the copulatory bulb. A bursal stalk is absent. The bursa itself is lined with a high, nucleated epithelium, surrounded by strong circular muscles, and contains three hooks (Figure 5C: bh). Two of them are more or less sickle-shaped (Figure 5B: B1, B2) and lie near the opening of the bursa into the atrium copulatorium, keeping the opening wide. They are 40 and 46 μm long and their edges carry a row of knobs, reminiscent of a cobblestone pattern when viewed from above (as in Figure 5B: B2). The third spine (Figure 5B: B3) is somewhat larger (88 μm long), funnel-shaped and distally bent. The rounded proximal rim carries some small, thin spines. A thick-walled V-shaped structure probably represents the rim of the opening of the funnel. The exact position of this spine in the copulatory bursa could not be determined in sections. This hook is quite similar in outline to that drawn by Luther (1946, Figure 69) in the copulatory bursa of Castrada annebergensis Luther, 1946 and there called “spermatophore”.

The unpaired ovary is situated in the caudal part of the body. The vitellaria extend from the rostral to the caudal body end. The female duct enters the common genital atrium at the caudal side. It is rather narrow, lined with a high, nucleated epithelium and surrounded by longitudinal muscles, except for a weak sphincter near the atrium. Proximally it receives the vitelloduct and the oviduct, which is widened, has almost no lumen but contains a small amount of sperm. The paired uteri (Figure 5C: ut) enter the common genital atrium from the rostral side.

Discussion

This species clearly belongs to the Rhynchomesostominae, as it shows all diagnostic features of this taxon, as outlined by Papi (1959). Within the Rhynchomesostominae, Rhynchomesostoma Luther, 1904 is characterized by an anterior invagination of the epidermis and Mesocastrada Volz, 1898 by the presence of an accessory glandular organ connected to the common genital atrium (Papi 1959; Luther 1963). The lack of these features is typical of the taxon Castrada Schmidt, 1861, in which our species thus can easily be placed. In the past, the taxonomy of Castrada has been much debated (see for instance Luther (1948, p 117–118) and Papi (1959, p 45–47)). Originally all species were placed within the genus Castrada. Later on Nassonov (1926) erected the genus Castradella, based
on the opening of the protonephria on the body surface (in the mouth in *Castrada*), whereas Luther (1963) placed both taxa as subgenera into the taxon *Castrada*. As the taxonomic value of this diagnostic feature (location of protonephridia opening) is questionable and the division of the taxon *Castrada* into two genera is largely subjective, we prefer following the view of Luther (1963) in order to prevent establishing an unnecessary surplus of names.

Very few species within the taxon *Castrada* have large hooks in the male genital system: *C. baldii* Steinböck, 1949, *C. cristatisspina* Papi, 1951, *C. gladiata* (Schwank, 1980), *C. granea* Braun, 1885, *C. neocomensis* Volz, 1898, *C. quadridentata* Hofsten, 1907, and *C. trispina*. The new species resembles *C. cristafisspina* most because only in these two species are the hooks all situated in the copulatory bursa, whereas in the other species at least some of the hooks are situated in the atrium copulatorium and/or in a sac-like bulge of this atrium. However, in *C. cristatisspina* there are many more hooks, although an exact number is not given (Papi, 1951). Furthermore, *C. cristatisspina* has zoochlorellae and a blind sac on the atrium copulatorium, absent in *C. trispina*, and the detailed structure of the bursal hooks is different.

**INCERTAE SEDIS**

*Aegira annabellae* gen. nov. sp. nov.

*aegira-annabellae* sp. nov.

(Figure 6)

**Diagnosis**

*Aegira* gen. nov. Typhloplanidae with prostate vesicle surrounded by two spirally running muscle layers. Unpaired, intracapsular seminal vesicle. Pseudocuticularized ejaculatory duct. Prostate glands and ejaculatory duct open into a simple, thin-walled stylet. Simple female genital system with short female duct, proximally split into oviduct and bursa. Vitellaria connected with oviduct through single vitelloduct. Female glands and uterus absent. Type species: *Aegira annabellae*.

*Aegira annabellae* gen. nov. sp. nov. Provisionally with the same diagnosis as the genus. Box-shaped stylet 25–32 μm long, 14–19 μm wide with distal hook.

**Locality**

Kerguelen, Port Couvreux: small bay, on Ceramium-like red algae, mid-eulittoral, 0.4 m deep at high tide (25 November 1992) (type locality).

**Material**

Several individuals studied alive. Seven whole mounts, one of them designated holotype (LUC no. 292), three others paratypes (LUC nos 293–295), two of them on the same slide as the holotype. The three remaining whole mounts are of poor quality. Four serially sectioned specimens (paratypes; LUC nos 296–299).

**Etymology**

The genus name/praenomen refers to the Viking god of the sea, Aegir; gender: feminine. The species epithet is dedicated to Miss Annabel Schreurs, the first author’s partner.
Description

The colourless to pale yellowish animals are 0.4–0.8 mm long (measured on whole mounts) and have two eyes with lenses. In the free-swimming animal, the anterior end is slightly
narrowed behind the eyes, giving it the appearance of a spatula. Between the eyes a small protrusion of the intestine is present (Figure 6A: y). Rhabdite glands are absent. The cellular epidermis is about 2 μm thick (only slightly thicker at the rostral and caudal body ends) with cilia ± 3 μm long. The cilia are more densely distributed on the ventral side of the body. The rod-shaped rhabdites are ± 5 μm long and occur exclusively in the dorsal body epithelium. The intestine of almost all studied individuals is filled with diatoms.

The pharynx (Figure 6A: ph) is situated in the hind part of the first body half, at ± 45%. The prepharyngeal cavity is lined with a very low, anucleated epithelium and surrounded by longitudinal muscles. The distal rim of the pharynx is void of cilia. The epithelium of the lumen is very low and anucleated. There are about 20 internal circular muscles, which are very strong. There are 16 internal longitudinal and 16 radial muscles. The outer circular muscles are rather weak. Basophilic glands are present, whereas eosinophilic ones could not be discerned. The exact location where the glands open into the lumen could not be determined due to the state of the sections. Furthermore, in all studied sections a large, circular cavity is present in the pharynx bulb, in between the glands.

The genital pore is situated at ± 55% and can be closed by a strong sphincter. The common genital atrium is small, lined with an anucleated epithelium and surrounded by outer longitudinal and inner circular muscles. It receives the male atrium from above and the female duct from behind.

The paired testes lie in the anterior body part and extend from just behind the eyes to the pharynx, in front of the vitellaria. The vasa deferentia are swollen (Figure 6B, E: v), filled with sperm and lined with a low, nucleated epithelium. They are rather long and winding and run separately into the copulatory bulb, in which they join, thus forming a single, intracapsular seminal vesicle (Figure 6B, E: vs). The seminal vesicle tapers towards the ejaculatory duct, which is thick-walled and sclerotized. The copulatory bulb is surrounded by two thick, spirally running muscle layers and fixed to the body wall by strong muscles (Figure 6E: lm): one to the dorsal and one to the ventral side of the animal. Besides the seminal vesicle, the bulb also contains coarse-grained, eosinophilic prostate glands (Figure 6E: gg) in its distal part. The prostate secretion enters the stylet, along with the ejaculatory duct. The stylet (Figure 6C, D) is a very simple, thin-walled and cup-shaped box, which can show some wrinkles distally (Figure 6C). It is 25–32 μm long (mean=28 μm; n=4), 14–19 μm wide (mean=16; n=4) and distally carries a slender, bent spine, 10–11 μm long (n=2). The stylet lies in an asymmetrical widening of the male atrium, which is lined with a thin, sclerotized epithelium and surrounded by an inner circular and an outer longitudinal muscle layer. These are the continuations of the muscle layers surrounding the copulatory bulb. Distally of the stylet, the male atrium narrows and forms a duct, which is lined with a low, anucleated epithelium and surrounded by outer longitudinal and inner circular muscles.

The single ovary is situated in the caudal body half. The vitellaria extend from the pharynx to the caudal region and lie at the same dorsoventral level as the testes. The ovary is connected to the female duct by a funnel-shaped oviduct (Figure 6E: od), lined with a low anucleated epithelium and filled with sperm. Proximally, the oviduct receives the broad vitelloduct. Distally, the oviduct narrows and opens into the broad female duct (Figure 6E: fd), which is lined with a low, anucleated epithelium and surrounded by inner circular and outer longitudinal muscles. The female duct is constricted by a sphincter proximally from the oviduct, where it forms a globular, sperm-filled vesicle, which is lined with a low, nucleated epithelium. This vesicle opens into a very large bursa, filled with a number of large inclusions, and a few cavities filled with sperm. In between the female duct and the
bursa, the epithelium becomes sclerotized, in some sections giving the appearance of a sort of mouthpiece (Figure 6E: z). A uterus is lacking.

Discussion

A striking feature of Aegira annabellae is the presence of only one ovary. This feature is found in the Mariplanellinae (a subtaxon of the Trigonostomidae) and the Typhloplanidae. As explained above, all Trigonostomidae are characterized by the presence of an afferent duct in the female system (see also Den Hartog 1964; Ax and Heller 1970; Ax 1971), absent in Aegira annabellae. Most members of the Typhloplanidae are freshwater species, whereas A. annabellae is marine. However, some marine representatives of the Typhloplanidae are known, and as the presence of a single ovary is diagnostic of the Typhloplanidae, A. annabellae can be placed within this taxon. The placement of A. annabellae within one of the eight subtaxa is rather difficult. The division of the Typhloplanidae into these subtaxa is based on the position of the excretory pore and the testes relative to the vitellaria (see Luther 1963). Both features are very difficult to assess in our material. As it is a marine species, the protonephridia are not very well developed or even absent. Furthermore, the testes are situated in front of the vitellaria and more or less lie at the same level (dorsoventrally). In addition, the combination of a pseudocuticularized ejaculatory duct and a stylet is unique within the Typhloplanidae. Therefore, A. annabellae is placed within the Typhloplanidae as a taxon incertae sedis.

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