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Revision of *Trigonostomum* Schmidt, 1852 (Platyhelminthes, Typhloplanoida, Trigonostomidae) with the description of seven new species

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A morphological and taxonomic account of the genus *Trigonostomum* is provided. All known species are discussed and briefly re-described where necessary. Seven new species are described: ***T. franki*** from Curaçao, Florida (USA), the East African Coast and New Caledonia, ***T. nataschae*** from the French sub-Antarctic island Kerguelen, ***T. spinigerum*** from New Caledonia and ***T. watsoni*** from the Australian East Coast and New Caledonia. ***T. tori*** and ***T. galapagoensis***, both formerly enclosed in *T. setigerum*, are considered new species, while ***T. australis*** also belongs to the same species group. *Proxenetes denhartogi* is transferred to *Trigonostomum*. Based on a comparison of old and new material, *T. marki* is synonymized with *T. penicillatum*, while *T. prytherchi* and *T. divae* are regarded as junior synonyms of *T. lilliei*; *T. intermedium* and *T. quadrifolium* are considered synonyms of *T. coronatum*. Three species are considered *species inquirendae*: *T. brunchorsti*, *T. piriforme* and *Marinellia lingulifera*. Similarities and differences of the 17 valid species are discussed and summarized in an identification key. © 2004 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2004, **141**, 271–296.

ADDITIONAL KEYWORDS: identification key – morphology – phylogenetic nomenclature – taxonomy – Trigonostominae.

INTRODUCTION

The genus *Trigonostomum* was introduced by Schmidt (1852) for a single species, *T. setigerum*. Thirty years later, Graff (1882) changed the name to *Hyporhynchus* and added a new species, *H. coronatus*. He also brought three previously described species – *Kylosphaera armata* Jensen, 1878, *Orcus venenosus* Uljanin, 1870 and *Vortex penicillatus* Schmidt, 1857 – into the genus and considered *Spiroclytus nisus* Schmidt, 1857 and *S. euryalus* Schmidt, 1857 to be synonyms of *Hyporhynchus setigerus*. The number of species grew rapidly in the late 19th and early 20th centuries (Uljanin, 1870; Pereyaslawzewa, 1893; Attems, 1897; Graff, 1905, 1911a, b, 1913) most of them described as belonging to *Hyporhynchus*, although Graff (1905) changed *Hyporhynchus venenosus* (Uljanin, 1870) into *Hyporcus venenosus*. Eventually, Meixner (1924b) re-introduced the first name *Trigonostomum* Schmidt, 1852, and also considered *Woodsholia lilliei* Graff, 1911, to be a species of *Trigonostomum*.

When changing the name to *Hyporhynchus* in 1882, Graff placed the genus within the subfamily Pseudorhynchina of the family Proboscida Carus, 1863. All members of this ‘family’ were characterized by the presence of a ‘proboscis’, a muscular frontal organ for capturing prey. In 1905, Graff changed the name Proboscida to Kalyptorhynchia, enclosing four families: Trigonostomidae, Schizorhynchidae, Polycystididae and Gyratricidae. However, in a detailed study of the proboscis of several Kalyptorhynchia, Meixner (1924b, 1926) showed that the ‘proboscis’ of *Trigonostomum* is by no means the same structure as that found in the other Kalyptorhynchia. He therefore transferred the Trigonostomidae from the Kalyptorhynchia to the Euliporhynchia Graff, 1905, which also included the families Proxenetidae Graff 1908, Byrsophlebidae Graff, 1905 and Typhloplanidae

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Luther, 1904. Two decades later, Luther (1948) grouped the Proxenetidae within the Trigonostomidae. Den Hartog (1964) split this taxon again, this time into Promesostomidae and Trigonostomidae, based on the structure of the female genital system: the Trigonostomidae are characterized by female gonads connected with the genital atrium by two ducts. Within the Trigonostomidae Den Hartog (1964) recognized two taxa, Trigonostominae and Paramesostominae, while a third, Mariplanellinae, was added by Ax & Heller (1970). The Trigonostominae comprises 11 genera, the phylogenetic relationships of which were described by Ax (1971), who considered *Marinellia lingulifera* Riedl, 1954 to be the sister taxon of *Trigonostomum*.

Due to the detailed studies by Graff (1913) and Meixner (1924b), the general anatomy of *Trigonostomum* is well known. The anatomy of a number of other representatives of the family, in particular that of the genital system, has been thoroughly described by Luther (1943). In the morphological section we summarize the essentials of the anatomy of representatives of *Trigonostomum*.

Not all described species are easy to recognize, often due to inaccurate descriptions and poor figures, especially in the older literature. The main purpose of this revision is to elucidate the species' identities and synonyms. A neotype is designated for each of the following species – *T. armatum*, *T. breitfussi*, *T. coronatum*, *T. lilliei*, *T. mirabile*, *T. penicillatum*, *T. setigerum* and *T. venenosum* – as a name-bearing type was never designated for any of them. Data for these species can be found in the taxonomy section, and all conditions for considering the designation of a neotype are fulfilled (ICZN, 1999: Art. 75). One new combination (*T. denhartogi*) and seven new species are added, three of them resulting from the analysis of the polymorphic '*T. setigerum*'. Since their anatomy is uniform, the descriptions of the separate species focus on the hard parts of the copulatory organ and the bursal appendage, with additional remarks where needed. A separate section provides a comparison of the species and the taxonomic conclusions resulting from this analysis, and includes an identification key, replacing the differential diagnoses.

Some preliminary indications of relationships within *Trigonostomum* are mentioned, but we refrain from discussing in depth possible phylogenetic relationships both within the taxon and with other taxa within the Trigonostomidae. A cladistic analysis of the Typhloplanoida, based on morphological and molecular characters, is currently in progress. Consequently, each diagnosis given now should not be seen as a phylogenetic definition (De Queiroz & Gauthier, 1990, 1992, 1994). However, as, in our view, species are fundamentally different from higher taxa because they cannot be monophyletic in a Hennigian sense (see Nixon & Wheeler, 1990), we propose for every species an alternative to the Linnean binomen, which can be used within the framework of phylogenetic nomenclature. This alternative species name consists of a praenomen and epithet, connected with a hyphen, and is unchangeable (see Cantino *et al.*, 1999; Artois, 2001). In the taxonomy section, the species are listed in alphabetical order.

MATERIAL AND METHODS

The zoological collection of Limburgs Universitair Centrum (LUC), Diepenbeek, Belgium, contains very rich material of both new and known *Trigonostomum* species from many parts of the world, collected by the authors (Australia, New Caledonia, Curaçao, Florida, East Africa, Zanzibar, French Mediterranean coast, Greece, Sardinia, Sweden, Kerguelen, and the Weddell Sea) and by some earlier collaborators of the Diepenbeek group: Corsica (Dr P. Martens), Kenya (Dr P. Jouk and Mr G. De Clerck). Material from the Swedish Museum of Natural History (SMNH) and of the Smithsonian Institution (SI-NMNH) was also at our disposal. Of the following species no material is available: *T. brunchorsti* Graff, 1905, *T. intermedium* (Attems, 1897) Graff, 1913, *T. marki* Graff, 1911, *T. piriforme* (Pereyaslawzewa, 1893) Graff, 1905 and *Marinellia lingulifera* Riedl, 1954.

Animals were extracted from sediment or from algae using the $MgCl_2$ decantation method (see Schockaert, 1996), studied while live and mounted in lactophenol. If sufficient specimens were available, some were fixed in hot Bouin's solution, embedded in paraffin and serially sectioned. The 4 μm-thick sections were stained with Heidenhain's iron haematoxylin using eosin as a counterstain. Camera lucida drawings of the hard parts were made with Nomarski phase contrast microscopy on a Reichert Polyvar microscope. Drawings without a scale are freehand. Measurements of the (inner) stylet and the bursal appendage are taken along the axis, unless indicated otherwise in the text. The length of the whole copulatory organ is given as a top–bottom measurement; it is not measured for species where the organ is coiled as the spires can spread, causing a great degree of variability in such a measurement. The positions of the gonopore and organs are expressed in percentages of the total body length (distance from the anterior tip of the body).

All material (including type material), except that from Australia and that belonging to other institutions, is deposited in LUC. The type material of the Australian species (*T. australis* and *T. watsoni* spp. nov.) is deposited in the collection of the Queensland Museum, Brisbane, Australia.

GENERAL MORPHOLOGY

Mature *Trigonostomum* species are 0.5–1.5 mm long, mostly uncoloured with a whitish-yellowish hue. Some individuals of species of the *T. setigerum* species group have a spot of black reticulated epidermal pigment (reflecting white under incident light; Fig. 8I) and a mid-dorsal pigment stripe of a subepidermal brown pigment (Fig. 8B, G); other individuals may have a spot on the head (Fig. 8A). There is always one pair of eyes, but sometimes each eye is divided into two parts, giving the impression that there are two pairs of eyes (Fig. 8A–B, I). At the rostral tip two bundles of rhabdites are present, the glands (Fig. 1: rg) which are found in front and next to the pharynx. Rostrally there is also a tuft of sensory bristles (Fig. 1: ac). The epidermis is cellular, completely ciliated, and contains many rhabdites.

Trigonostomum species have a 'proboscis', which is an antero-ventral integumental invagination with a highly developed system of retractors and dilators, described by Meixner (1924b). In the live animal it is triangular (Fig. 1: i) and not always clearly visible in a mounted specimen. Retractors (Fig. 2: rr) insert on the dorsal and lateral body wall, causing the invagination. The opening of the invagination can be enlarged by several dilators, inserting on the ventral body wall in front of it (Fig. 2: dil1) and near the mouth (Fig. 2: dil2), probably with the help of integument retractors (Fig. 2: ir), with the origin on the ventro-caudal side of the opening and insertion on the dorsal body wall. The 'proboscis' can be evaginated by contraction of the strong circular muscles of the body wall in the frontal part of the animal, causing a local rise in the internal body pressure. A bundle of eosinophilic glands enters near the opening (Fig. 2: ig). The epithelium of the invagination appears to be glandular and contains a few small nuclei. In *Marinellia lingulifera*, there seems to be a delimited muscle mass behind the invagination (Riedl, 1954).

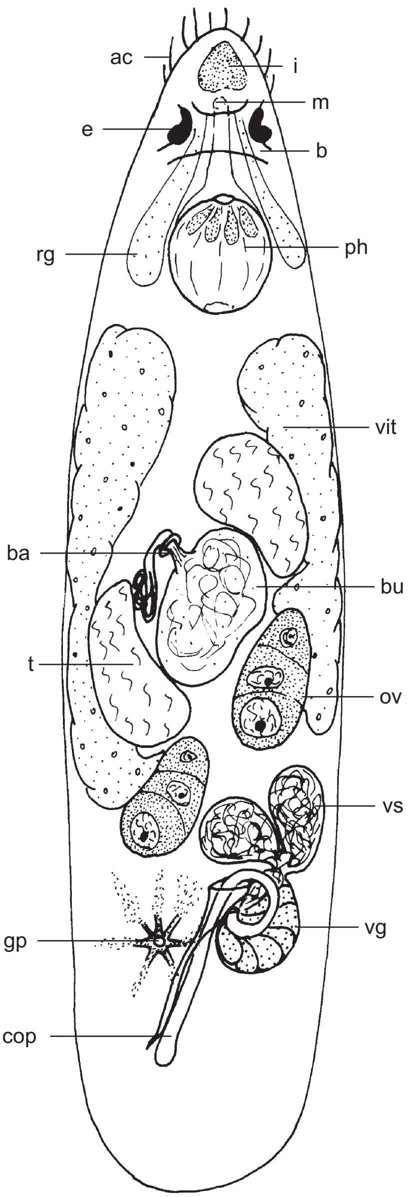

Figure 1. Habitus of live animal (*Trigonostomum venenosum*). *Abbreviations*: ac, apical tuft of cilia; b, brain; ba, bursal appendage; bu, bursa; cop, copulatory organ; e, eye; gp, common genital pore; i, antero-ventral invagination; m, mouth; ov, ovary; ph, pharynx; rg, rostral rhabdite glands; t, testis; vg, prostate vesicle; vit, vitellary; vs, seminal vesicle.

The pharynx (Fig. 1: ph; Fig. 2) is of the so-called 'bulbosus'-type and is situated in the first half of the body, highly inclined forwards and almost parallel to the ventral body wall. In section it is more or less barrel-shaped. The mouth is close to the anterior invagination, but never combined with it, though this impression may be given in highly contracted animals (Graff, 1911b; Meixner, 1924b). The pharynx cavity is tubiform and muscular at its distal end (with inner circular and outer longitudinal muscles), and lined with a low, anucleated epithelium with short cilia. The pharynx lumen has a low epithelium with only a few nuclei. The distal rim of the pharynx is devoid of cilia. The internal musculature of the pharynx bulb consists of 13 very thick outer circular muscle fibres (in *T. franki* and *T. setigerum*) and a continuous layer at the proximal and distal ends (Fig. 2: ecm), while circular (Fig. 2: icm) and longitudinal (Fig. 2: ilm) muscles around the lumen are much weaker. In the longitudinal sense, there are 11 radial muscles (of which the first is stronger than the other ten) and a fan-like group at the proximal end (Fig. 2: rm). In cross-section, there are 24 such radial muscles, insert-

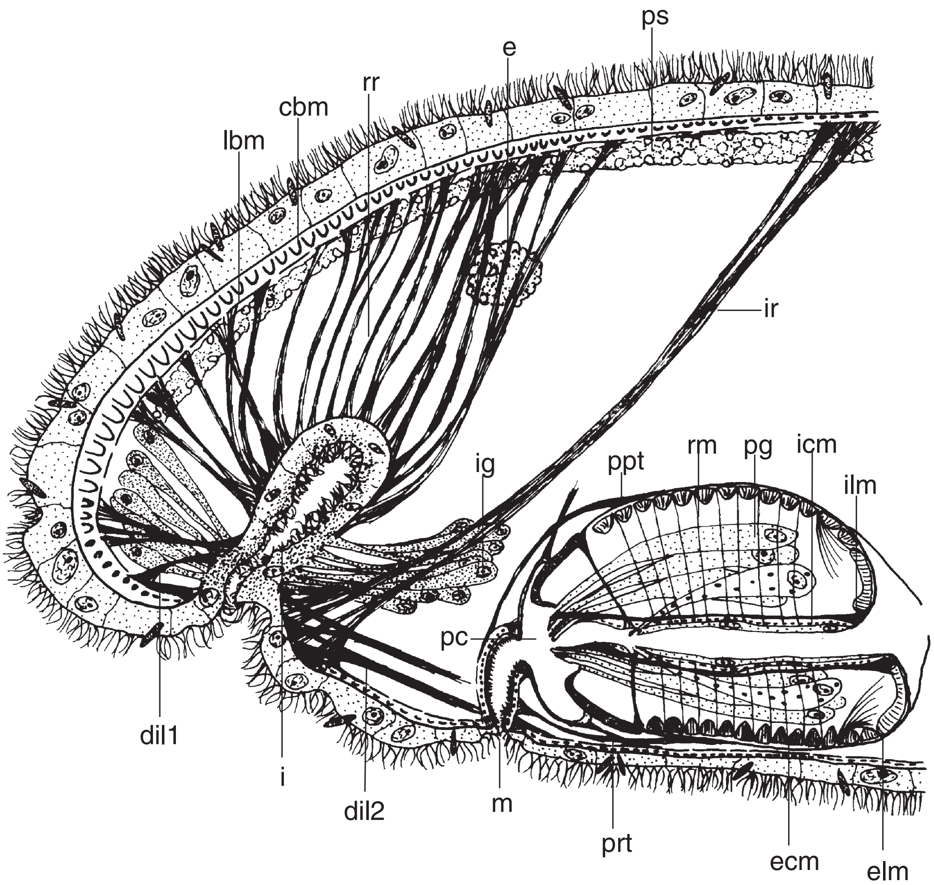

Figure 2. Reconstruction on sagittal sections of the rostral body end from the left hand side (***T. franki* sp. nov.**). *Abbreviations:* cbm, circular body muscles; dil1–2, dilators of opening of antero-ventral invagination; e, eye; ecm, external circular pharyngeal muscles; elm, external longitudinal pharyngeal muscles; i, antero-ventral invagination; icm, internal circular pharyngeal muscles; ig, invagination glands; ilm, internal longitudinal pharyngeal muscles; ir, integument retractors; lbm, longitudinal body muscles; m, mouth; pc, prepharyngeal cavity; pg, pharynx glands; ppt, pharynx protractors; prt, pharynx retractors; ps, pigment stripe; rm, radial pharyngeal muscles; rr, retractors of antero-ventral invagination.

ing on the pharynx lumen between 24 longitudinal muscles. Fine-grained eosinophilic glands enter the pharyngeal lumen at its distal end and coarse-grained basophilic ones more proximally. There are 16 of each.

The gonads are paired. The testes are positioned mid-body, just behind the pharynx. Ovaries and vitellaria are not separated, forming a pair of so-called 'ovovitellaria'. The vitellarian parts extend at both sides of the body from the level of the pharynx, and the ovaries are positioned slightly in front of the gonopore, situated at about 80%. The common genital atrium (Fig. 3: cga) is lined with a high, nucleated epithelium and surrounded by outer longitudinal and inner circular muscles, forming a sphincter at the porus.

The seminal vesicles (Fig. 3: vs) are paired, lined with a low epithelium without nuclei, and surrounded by spirally running muscles. Both vesicles narrow and join to form the short seminal duct (Fig. 3: sd), which enters the prostate vesicle (Fig. 3: vg) and runs axially through it, surrounded by mainly eosinophilic and some basophilic prostate glands, all parts of which are inside the vesicle. In some live individuals extracapsular parts of these glands can be seen. Relatively strong circular muscles surround the prostate vesicle. The male atrium, where the hard parts of the copulatory organ lie, is surrounded by an inner circular and an outer longitudinal muscle sheath, and enters the common genital atrium dorsally.

The copulatory organ proper consists of a stylet, surrounded by a second, very thin-walled stylet, called the 'mantle' by Ax (1971). The organ can thus be considered as double-walled with an inner 'stylet' (Fig. 4: s) and an outer 'mantle' (Fig. 4: mt), as shown in the theoretical diagram in Figure 4A.

In the species of the first group (see comparison of species, below) the mantle is attached to one side of

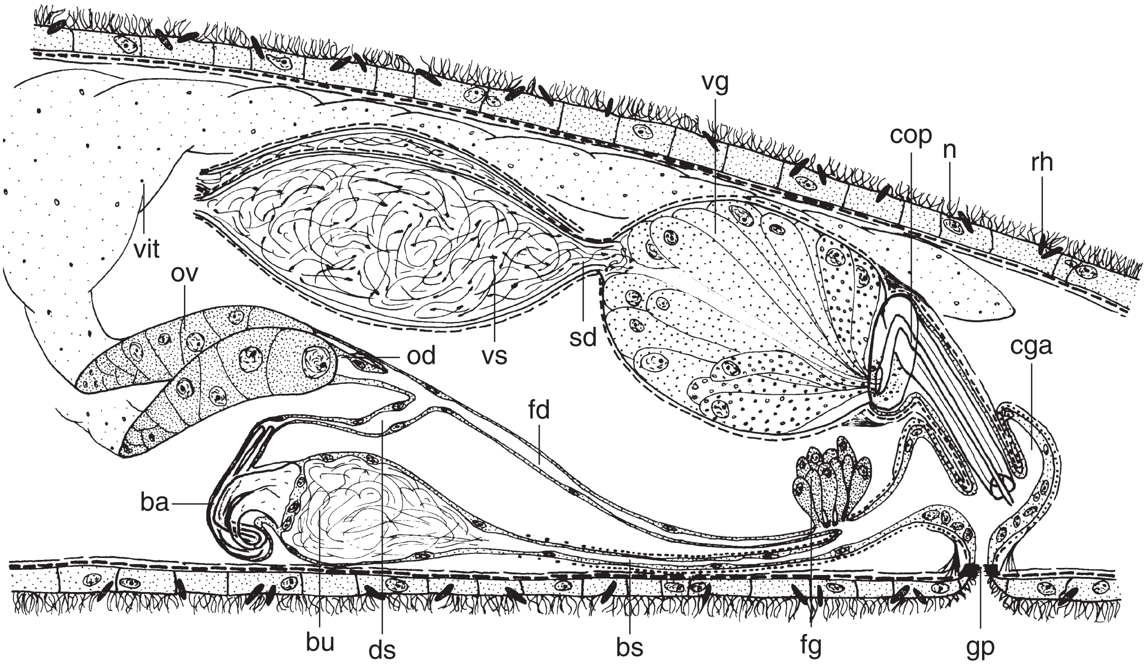

Figure 3. Reconstruction on sagittal sections of the genital system from the left hand side (***T. franki* sp. nov.**). *Abbreviations*: ba, bursal appendage; bs, bursal stalk; bu, bursa; cga, common genital atrium; cop, copulatory organ; ds, spermatic duct; fd, female duct; fg, female glands; gp, common genital pore; n, nucleus; od, oviduct; ov, ovary; rh, rhabdite; sd, seminal duct; vg, prostate vesicle; vit, vitellary; vs, seminal vesicle.

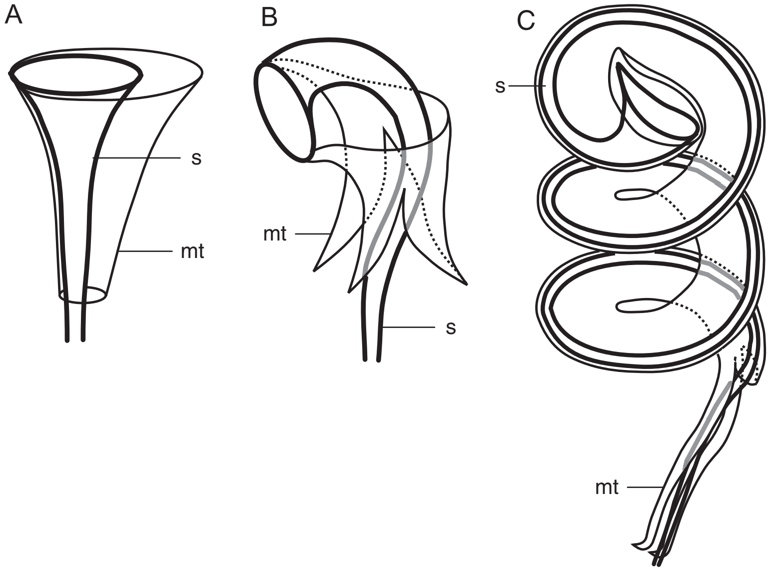

Figure 4. Schematic representation of the copulatory organ. A, theoretical diagram of a double-walled copulatory organ. B, diagram of the copulatory organ of the representatives of group 1. C, diagram of the stylet of the representatives of group 2. *Abbreviations*: mt, mantle; s, stylet.

the proximal rim of the stylet and distally divided into spiny plates (Fig. 4B). The stylet is a narrow tube, proximally curved over 90–270°, with a relatively thick wall and a broad proximal opening. In the species of the second group, the mantle follows the coils of the stylet over almost its entire length, forming two spiny plates at the very end (Fig. 4C). In sectioned material of *T. setigerum*, the way the mantle surrounds the stylet can be clearly seen. In *T. denhartogi* and in *T. spinigerum* the copulatory organ is far more complicated than in the other species, and the structure of the mantle is not yet well understood.

According to Meixner (1924b), the prostate secretion is discharged in the mantle, while sperm is released in the stylet. Observations on sectioned material of *T. franki*, *T. armatum* and *T. setigerum* revealed that both sperm and secretion are released through the (inner) stylet.

The ovaries are connected to the genital atrium by an efferent duct and an afferent system (see Luther, 1943). The oviducts are very short and lined with a nucleated epithelium. They join at the 'fecundatorium' (Luther's terminology) from where the (efferent) female duct (Fig. 3: fd) runs towards the atrium. This duct is long and narrow, lined with a low, nucleated epithelium and muscles are lacking. It enters the common genital atrium anteriorly, ventrally of the male system and dorsally of the afferent system. Eosinophilic glands (Fig. 3: fg) open into the female duct near the atrium. The afferent system consists of a bursal stalk (Fig. 3: bs), the bursa (Fig. 3: bu) and the sclerotic appendage (Fig. 3: ba) that leads into the spermatic duct (or insemination duct; Fig. 3: ds). This duct ends near the ovaries in the 'fecundatorium'. The bursal stalk is long and narrow (although short in *T. penicillatum* according to Meixner, 1924b). The whole afferent system is lined with a low nucleated epithelium. Only the bursal stalk is surrounded by (circular) muscles. There is no uterus.

Meixner (1924b) recognized two types of bursal appendage: (1) the *setigerum* type consists of two more or less coiled narrow tubes, attached to a ring- or funnel-like part at the bursa wall; (2) the *penicillatum* type consists of a bundle of many closely adhering tubules, which protrude into the bursa for some distance, where they may be held together by a casing. There are further variations, discussed below.

All *Trigonostomum* species are marine and are found all over the world, in areas ranging from tropical to polar. Most have been found in the intertidal zone, mainly on algae or seagrasses. Some species also occur in sand. Only two species, *T. messoplanoides* Artois, Vermin and Schockaert, 2000 and *T. nataschae* sp. nov., have not so far been found on algae (see further), while *T. messoplanoides* and *T. setigerum* are the only species collected at greater depths: 499–515 m and 137–150 m respectively (Westblad, 1952; Artois *et al.*, 2000).

COMPARISON OF THE SPECIES

The main differences between the species of *Trigonostomum* are to be found in the construction of the hard parts of the copulatory organ, the bursal appendage and, to a lesser extent, in the pigmentation.

As mentioned above and diagrammatically represented in Figure 4B, C, the copulatory organ consists of a proximally curved stylet surrounded by a thin-walled mantle, divided into spiniform plates. In the first group of species, the proximal rim of the mantle does not follow the curvature of the stylet, and thus only surrounds the distal (straight) part of the stylet (Fig. 4B). In two of these species (group 1A, *T. messoplanoides* and *T. venenosum*, see Fig. 6) the stylet is long and narrow and makes a proximal turn of 270°, while the mantle forms a narrow ring and bears one long, slender spine (spoon-like in *T. venenosum*). This kind of organ resembles that of species of the genus *Messoplana* Den Hartog, 1966.

The bursal appendage of *T. messoplanoides* and *T. venenosum* consists of two tubes attached to the bursa by a more or less conspicuous ring, and may be fused proximally in some individuals of *T. venenosum* (Fig. $6A_4$). In the construction of both the copulatory organ and the bursal appendage, these species demonstrate plesiomorphy, as found in several other taxa of the Trigonostominae (see Ax, 1971).

In the other species of this first group (group 1B; see Fig. 7), the stylet is relatively wider (and shorter) and makes a turn of about 90° in *T. coronatum*, *T. penicillatum* and *T. watsoni* to about 180° in the other species (*T. breitfussi*, *T. lilliei*, *T. mirabile* and *T. nataschae*). The mantle is divided into three pointed plates in the first three species, into two plates in *T. mirabile* and *T. nataschae*, and forms only one plate in *T. breitfussi* and *T. lilliei*. Some other, more subtle differences are seen: the plate is rather blunt in *T. breitfussi* and shorter than the stylet, which has a crested proximal rim, while in *T. lilliei* the plate ends in a little hook and is as long as the stylet, which in this case lacks the crested rim. In *T. nataschae*, the two plates are blunt and shorter than the stylet, while they are pointed in *T. mirabile* and at least as long as the stylet. In both these species the stylet has a wide spoon-like terminal opening, but in *T. nataschae* it has a proximal crested rim, not present in *T. mirabile*. Differences between the copulatory organs of *T. coronatum* and *T. penicillatum* are difficult to discern, while the plates in *T. watsoni* are very thin and easily folded. Moreover, in this last species, the stylet is inconspicuous and often impossible to find in some individuals. However, the bursal appendage in these three species is very different, as is the overall size of the copulatory organ, thus enabling clear distinction between the species.

The bursal appendage in a number of species of group 1B is clearly of Meixner's *penicillatum* type. It consists of many closely adhering parallel tubules, which protrude into the bursa for some distance, where they may be held together by a casing resembling a little barrel, connected to the bursa wall by a ring. This kind of appendage is found in *T. breitfussi, T. mirabile* and in *T. penicillatum*, where the tubules diverge at the very end, giving the appendage a brush-like appearance, but probably also in *T. mirabile* (see fig. 27 in Pereyaslawzewa, 1893). This brush-like appearance may be an artefact caused by squeezing the animals, especially when the tubules are long, as is the case in these two species.

In *T. nataschae* very narrow tubules protrude into the bursa beyond the proximal 'barrel' that has a rather thick wall. Just outside the bursa the tubules are still visible, but more distally they are very faint and separated into two coiled bundles, giving the impression that the bursal appendage ends in two broad tubes. The bursal appendage of *T. lilliei* has a highly coiled single part that ends in six tubules; the proximal 'barrel' seems to be missing, but there is a proximal ring at the inside of the bursa wall, beyond which the tubules protrude into the bursa (see also fig. 18 in Marcus, 1948 of *T. divae* = *T. lilliei*). The appendage of *T. coronatum*, on the other hand, has a proximal part that looks like a clover-leaf, and one, sometimes two (perhaps three: see fig. 23 in Attems, 1897) broad terminal 'tubes' with a fine striation. In *T. watsoni* the bursal appendage starts at the bursa with a broad funnel that splits into two highly coiled broad tubes, also with a fine striation, suggesting that they may consist of subtubules.

Though the bursal appendage of the species in this group exhibits variation (which needs further investigation), it clearly deviates in structure from that of all other members of the taxon *Trigonostomum* and even of all other taxa of the Trigonostominae. Perhaps this is a synapomorphy.

In a second group of species (group 2; see Fig. 10), the proximal mantle rim closely adheres to the proximal rim of the stylet, envelopes the stylet over its entire length, and diverges at the very end into two spiny plates with a terminal hook (see Fig. 4C). The narrow stylet is spirally coiled (except in *T. franki*, but see below) and the mantle follows the coils of the stylet. The stylet is at the periphery of the spire, while the mantle forms a double plate towards the centre, where it can be slightly thickened (wrongly called *Sekretrorh* by Graff, 1913) and shows radial wrinkles. At the very end, where the two plates are situated, there may be a straighter part of the stylet. The hooks of the plates are invariably directed towards the convex side of the curve. This combination of characters, especially the fact that the mantle entirely envelopes the stylet, is unique within the Trigonostominae and is without any doubt a synapomorphy for this group of species. On the other hand, the *setigerum* type of appendage (Fig. 8C) has the same construction as that of the majority of the other Trigonostominae, consisting of two tubules attached by a ring to the bursa, with both tubes coiled over 360°.

All animals with two, three or more spires in the copulatory organ have been considered representatives of *T. setigerum*, even those members of the Eastern Pacific population with five whole spires. According to Karling (1986), the number of spires depends on growth (and may thus vary in one and the same individual according to age), muscle contraction and degree of compression, while studied. We have collected data on all individuals of species/populations with a coiled stylet, including material available from many different localities and from the literature. The results are presented diagrammatically in Figure 5 and in Table 1.

The first three stylets represented are those of *T. franki* (Fig. 5A), *T. armatum* (Fig. 5B) and *T. setigerum* (Fig. 5C); individuals with the fourth type of stylet (Fig. 5D) have been collected on the East Australian coast. The stylet of the Galapagos population (Figs 5E, 9E) is from the micrograph in Ehlers &

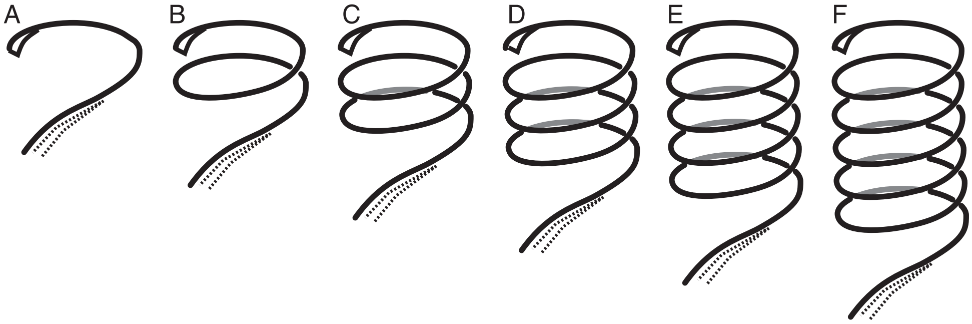

Figure 5. Schematic representation of the copulatory organ of the representatives of group 2, showing the different number of spires (dashed lines indicate the location of the mantle plates). A, ***T. franki* sp. nov.** ($^1/_2$ spire). B, T. armatum. ($1^1/_2$ spires). C, T. setigerum. ($2^1/_2$ spires). D, ***T. australis* sp. nov.** ($3^1/_2$ spires). E, ***T. galapagoensis* sp. nov.** ($4^1/_2$ spires). F, ***T. tori* sp. nov.** ($5^1/_2$ spires).

Table 1. Morphological differences between different populations of ***Trigonostomum franki* sp. nov.**, *T. armatum*, *T. setigerum*, ***T. australis* sp. nov.**, ***T. galapagoensis* sp. nov.** and ***T. tori* sp. nov.** (species group 2). *Abbreviations:* SL, stylet length (in µm); BAL, bursal appendage length (in µm); BAT, bursal appendage tubules; MSM, minimum no. of specimens measured; NM, not measurable; ? not known

Species	Distribution	Pigmentation	Coils	SL	BAL	BAT	MSM
T. franki	Caribbean, Florida	longitudinal stripe	1/2	86–101	84–100	normal	8
	East Africa	longitudinal stripe	1/2	90–101	120	normal	1
	New Caledonia	longitudinal stripe	1/2	95–111	62–166	normal constricted	4
T. armatum	northern Atlantic	none	1	158–196	NM	?	2
	southern Atlantic	rostral spot	1	434	149	normal	1
	Caribbean	rostral spot	1	274–378	100–108	normal	9
	eastern Australia	none	1	183	NM	?	1
	New Caledonia	none	1	386	127	normal	1
T. setigerum	western Mediterranean	rostral spot	2	413–492	87–113	normal	4
	eastern Mediterranean	none longitudinal stripe rostral spot	2	284–462	64–113	normal	21
	southern Atlantic	rostral spot	2	482	141	constricted	1
	East Africa	none	2	403	93	normal	1
	English Channel	rostral spot	2	477	NM	?	1
	Bermuda	none	2	434	NM	constricted	1
T. australis	eastern Australia	longitudinal stripe	3	414–445	34	normal	3
T. galapagoensis	Galapagos	rostral spot	4	?	?	?	0
T. tori	California	none	5	683–853	80–106	normal	3

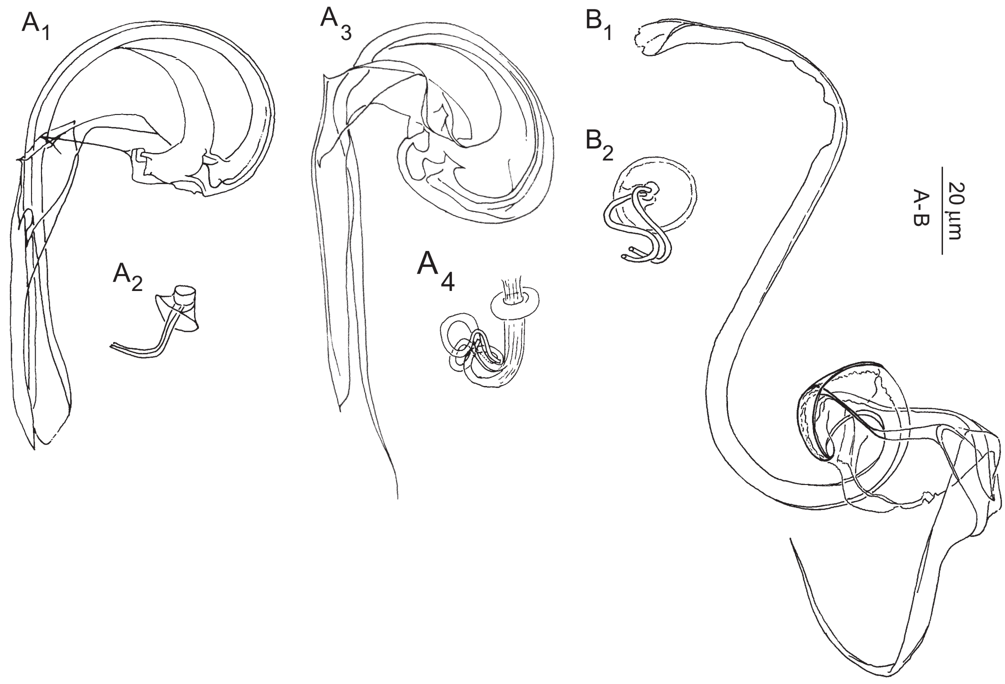

Figure 6. Copulatory organs and bursal appendages of the representatives of group 1A. A, *T. venenosum*: A$_{1,3}$ copulatory organ; A$_{2,4}$ bursal appendage. (A$_{1,2}$ specimen from Norway, neotype; A$_{3,4}$ specimen from Sardinia). B, *T. messoplanoides*: B$_1$ copulatory organ; B$_2$ bursal appendage. (from the holotype; after Artois *et al.*, 2000).

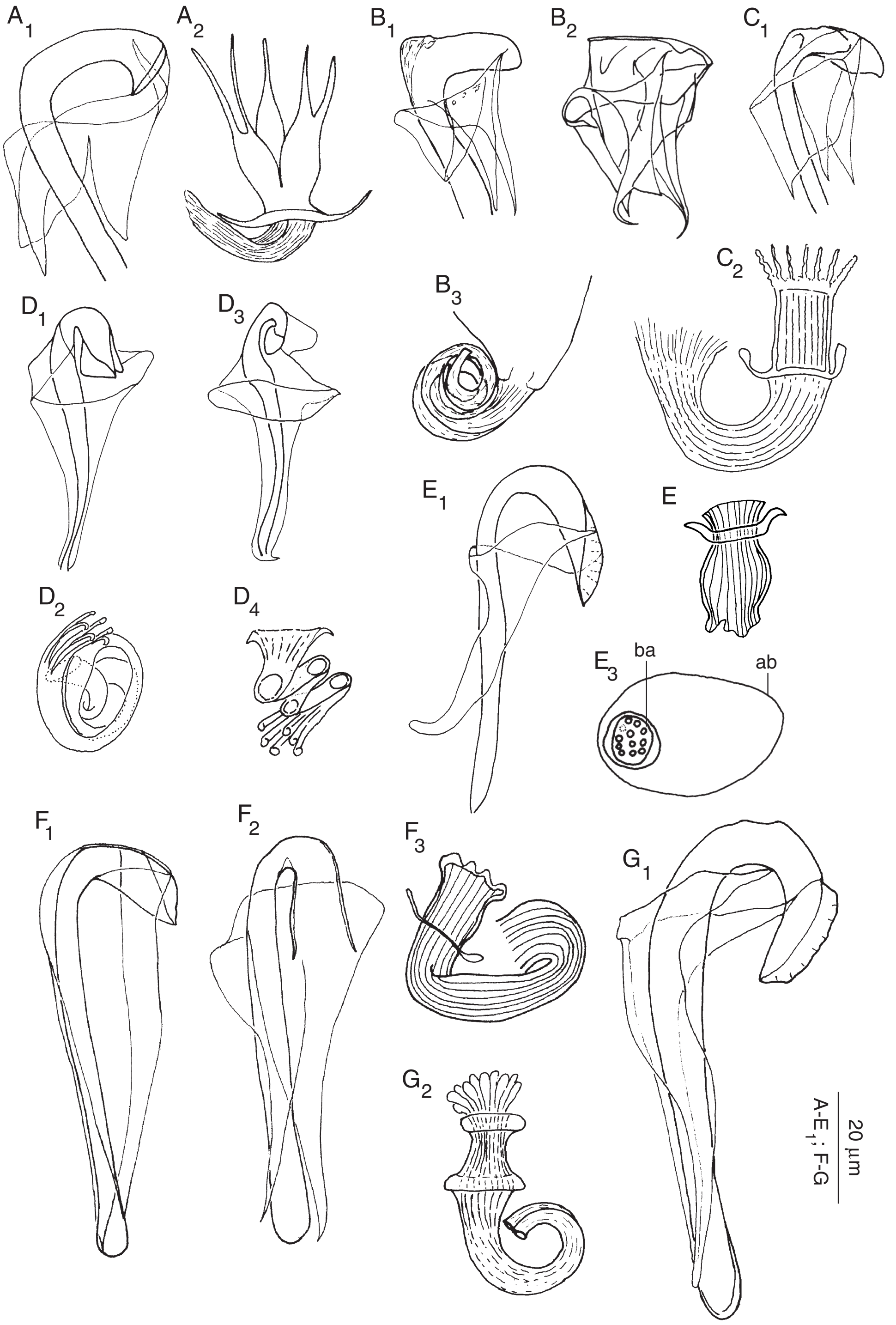

Figure 7. Copulatory organs and bursal appendages of the representatives of group 1B, A, *T. coronatum*: A_1 copulatory organ; A_2 bursal appendage. (from the neotype). B, ***T. watsoni* sp. nov.** $B_{1,2}$ copulatory organ; B_3 bursal appendage (B_1 from the holotype; $B_{2,3}$ from the paratype). C, *T. penicillatum*: C_1 copulatory organ; C_2 bursal appendage (from the neotype). D, *T. lilliei*: $D_{1,3}$ copulatory organ; $D_{2,4}$ bursal appendage. [$D_{1,2}$ specimen from Australia; $D_{3,4}$ specimen from the USA (neotype = holotype of *T. prytherchi*)]. E, *T. breitfussi*: E_1 copulatory organ; E_2 bursal appendage; E_3 section through the bursa and the bursal appendage (different specimens from Sweden; $E_{2,3}$ freehand drawings). F, *T. mirabile*: $F_{1,2}$ copulatory organ; F_3 bursal appendage ($F_{1,3}$ from the neotype; F_2 from another specimen from the Black Sea). G, ***T. nataschae* sp. nov.** G_1 Copulatory organ; G_2 Bursal appendage (from the holotype).

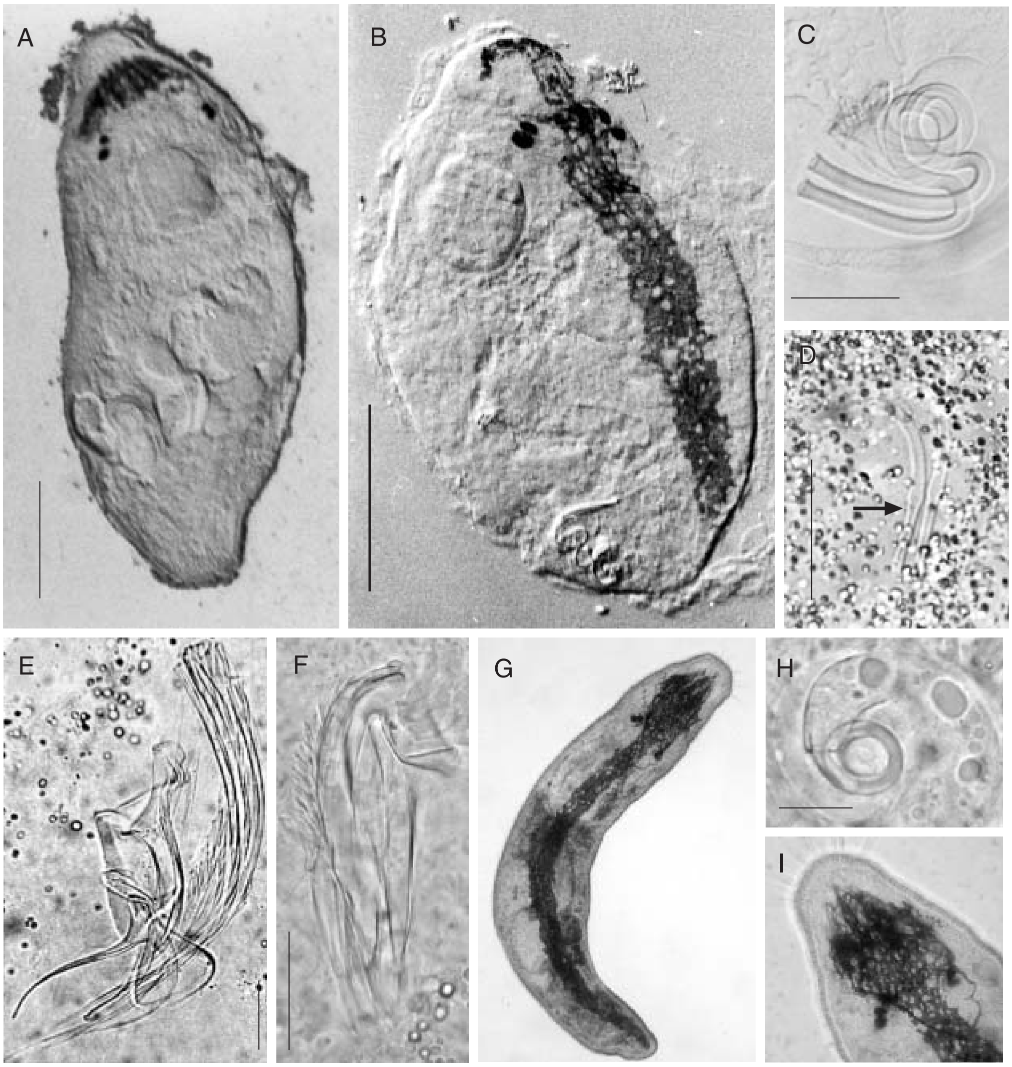

Figure 8. A, rostral spot in *T. armatum* (whole mounted specimen from Curaçao). B, dorsal stripe in *T. setigerum* (whole mounted specimen from Greece). C, bursal appendage of ***T. tori* sp. nov.** (from the paratype). D, constricted distal tubes of bursal appendage (arrow indicates constriction) in *T. setigerum* (specimen from Bermuda). E, copulatory organ of *T. denhartogi* **comb. nov.** (specimen from New Caledonia). F, copulatory organ of ***T. spinigerum* sp. nov.** (from the holotype). G, habitus of ***T. franki* sp. nov.** (live specimen from New Caledonia). H, bursal appendage of ***T. spinigerum* sp. nov.** (from the holotype). I, head region of ***T. franki* sp. nov.** showing both epidermal and subepidermal pigment (live specimen from New Caledonia). Scale bars: A, B = 200 μm. C–F = 20 μm. H = 10 μm.

Ax (1974), while the last type of stylet (Fig. 5F) is found in the population from California, as described by Karling (1986).

In *T. franki*, the stylet makes a turn of about 180° (although it shows all other characteristics of the stylet of this group of species) with an additional, more or less straightened part where the two spines of the mantle are (dashed lines in Fig. 5). This stylet thus has a half spire. In *T. armatum* there is one complete spire over 360° and an additional part ($1^1/_2$ spires), in *T. setigerum* $2^1/_2$ spires (see Figs 5C, 9C, $10C_1$), and so on. Muscle contraction and a degree of squeezing the animal causes the spires to stay close to each other or go apart (in some of our whole mounts of individuals of the Greek population, the spires had virtually disappeared). The number of coils in the spiral is constant in all studied populations, though one may count a different number of coils, depending on the side from which the stylet is viewed. In *T. setigerum*, for instance, with $2^1/_2$ spires, one counts three spires when looking at the stylet from the side where the stylet begins (including the 'half' spire), and only two when

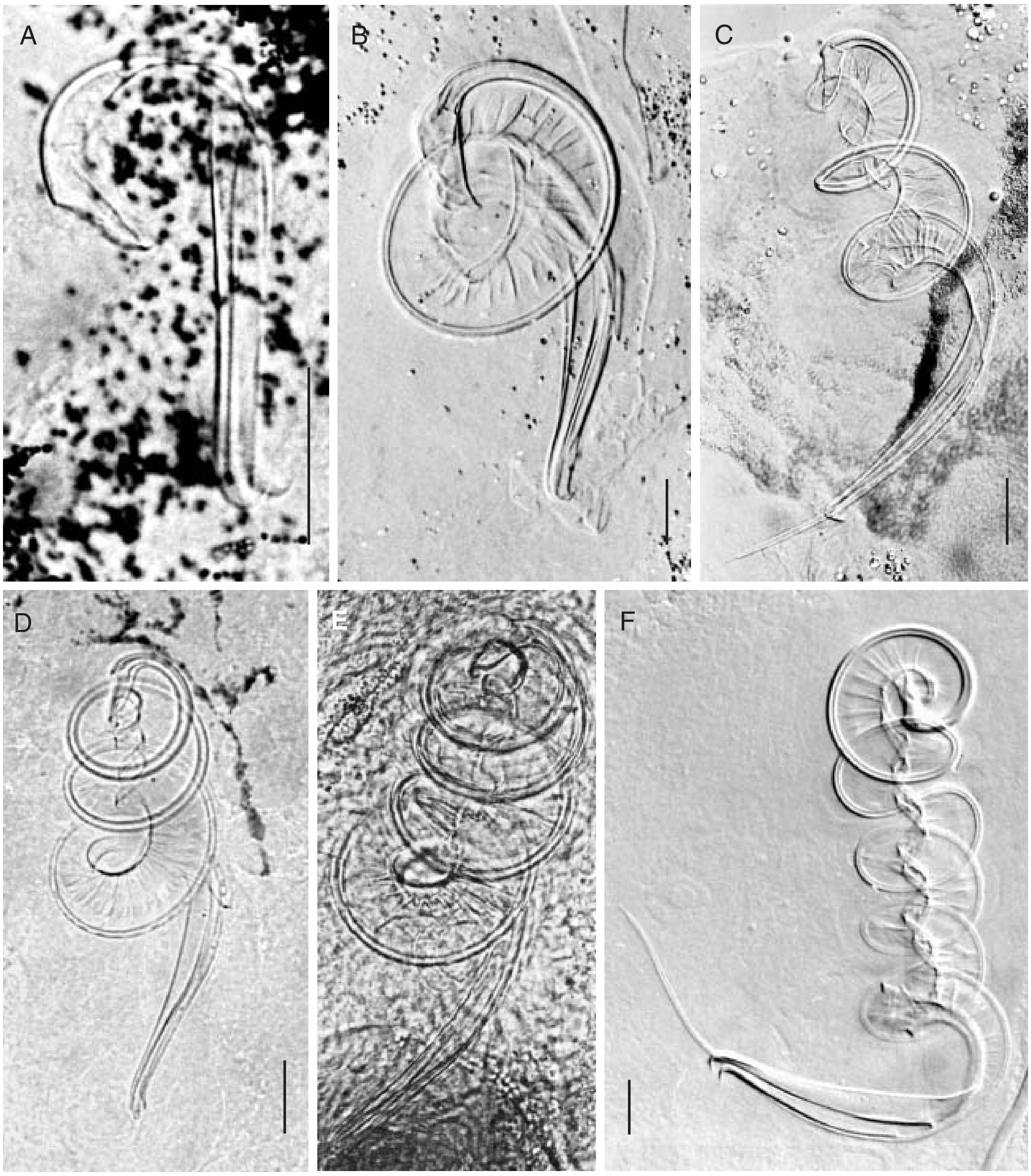

Figure 9. Copulatory organ of the representatives of group 2. A, ***T. franki* sp. nov.** (specimen from Curaçao) B, *T. armatum* (specimen from Curaçao). C, *T. setigerum* (from the neotype). D, ***T. australis* sp. nov.** (from the holotype). E, ***T. galapagoensis* sp. nov.** (from the holotype; after Ehlers and Ax, 1974: fig. 13C). F, ***T. tori* sp. nov.** (from the holotype). Scale bars: A–D, F = 20 µm.

looking from the opposite side. The spires turn clockwise (seen from the proximal end of the stylet) in all individuals; in those with a very long stylet (e.g. the Californian populations and some individuals in the Greek population), one of the spires may swing in the other direction, as often happens in spirals made of flexible material.

We believe that these stylets indicate that we are dealing with individuals from different species. Hence we give species status to the populations from Australia, the Galapagos and California, respectively, as *T. australis* sp. nov., *T. galapagoensis* sp. nov. (though no material is available, except the micrograph in Ehlers & Ax, 1974), and *T. tori* sp. nov., described as *T. setigerum* by Tor Karling in 1986. There may be some minor differences in some populations: Karling (1986) pointed to the constriction at the end of the tubes of the bursal appendage in the populations of *T. setigerum* in Bermuda, the Falkland Islands, South Georgia and in the English Channel (Fig. 8D; Table 1;

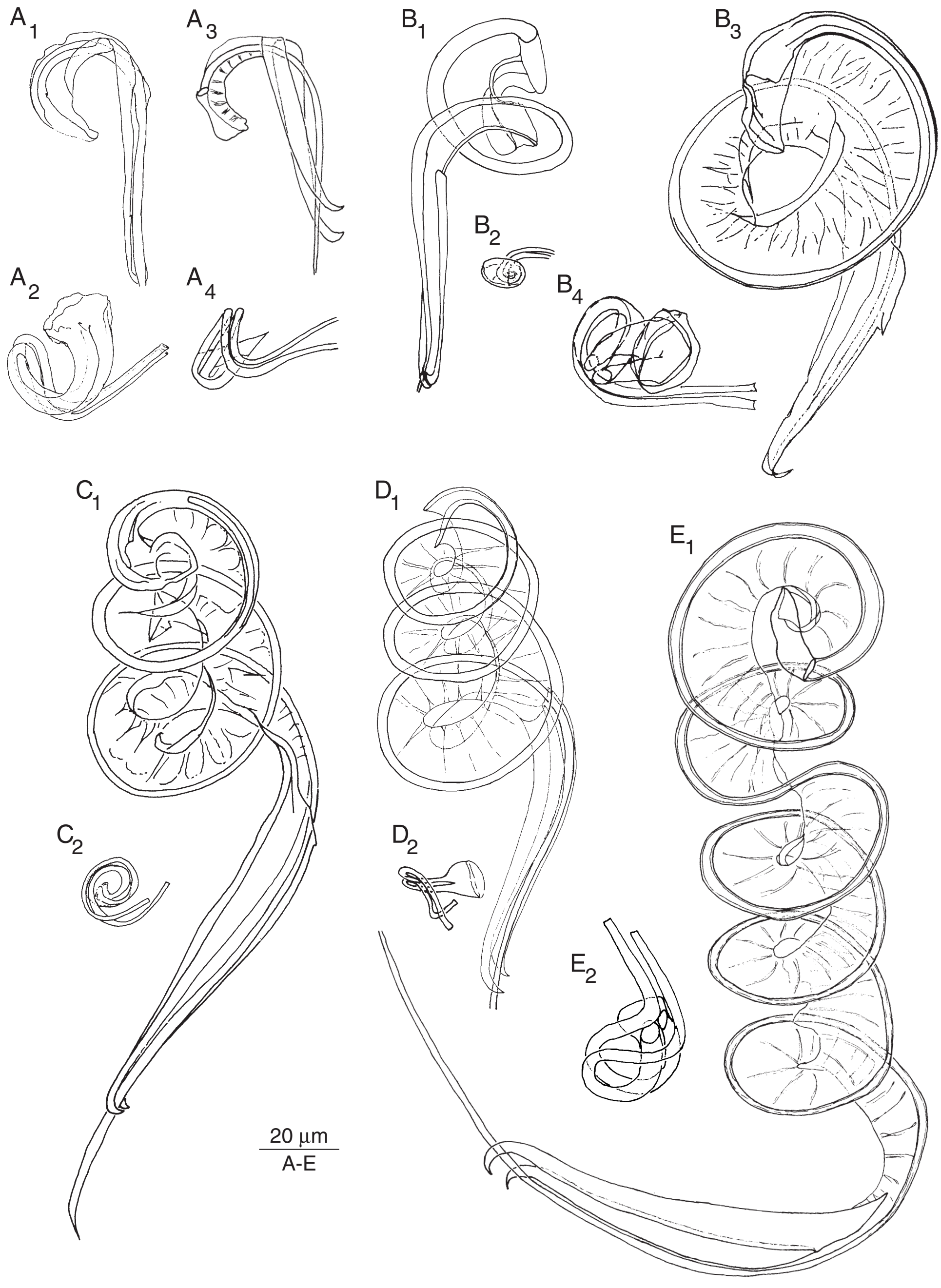

Figure 10. Copulatory organs and bursal appendages of the representatives of group 2. A, ***T. franki* sp. nov.** $A_{1,3}$ copulatory organ; $A_{2,4}$ bursal appendage ($A_{1,2}$ from the holotype; $A_{3,4}$ from a specimen from Kenya). B, ***T. armatum* sp. nov.** $B_{1,3}$ copulatory organ; $B_{2,4}$ bursal appendage ($B_{1,2}$ specimen from France; $B_{3,4}$ specimen from Curaçao). C, *T. setigerum*: C_1 copulatory organ; C_2 bursal appendage (specimen from Kenya). D, ***T. australis* sp. nov.** D_1 copulatory organ; D_2 bursal appendage (from the holotype). E, ***T. tori* sp. nov.** E_1 copulatory organ; E_2 bursal appendage (from the holotype).

Karling, 1978: fig. 28; Karling, 1986: figs 40, 48). In one specimen of *T. franki* from New Caledonia the tubes are also slightly constricted.

On the other hand, considering the distribution of these species, some doubts may arise. *T. franki* and *T. armatum* have been found together on Curaçao, *T. australis* and *T. armatum* occur sympatrically on the Australian East coast, while *T. armatum* and *T. setigerum* can be found together in both North Atlantic (Westblad's material from Plymouth; Gamble, 1893; Southern, 1912, 1936; Graff, 1913) and South Atlantic populations (Westblad's material from South Georgia, all considered *T. setigerum* by Karling, 1986). *T. setigerum* is the only species that has, so far, been found in the Mediterranean Sea, while those species with more than $2^{1}/_{2}$ spires are confined to the Pacific (the further east, the more spires). We began to wonder whether these are all populations of a single 'species complex' similar to that of the kalyptorhynch *Gyratrix hermaphroditus* Ehrenberg, 1831 (Curini-Galletti & Puccinelli, 1989, 1990, 1994, 1998, Artois *et al.*, 2000; Artois & Schockaert, 2001), albeit of a highly polymorphic species. Are we dealing with a cline in the Indo-Pacific? We prefer, with the data now available, to consider these populations as different species, until proven otherwise.

It is also in this group that a variation in pigmentation occurs (see Table 1): a mid-dorsal stripe (Fig. 8B, G), a rostral spot (Fig. 8A) or no pigmentation. Graff (1905) considered that, based on pigmentation, there were three subspecies of *T. setigerum*. However, Southern (1912) rejected this finding; we follow the latter view as these three pigmented forms are known to occur sympatrically (see Table 1 and remarks on *T. setigerum*).

Finally, two more species, *T. denhartogi* and *T. spinigerum*, deserve comment regarding the construction of the copulatory organ and the bursal appendage. With the material now available of *T. denhartogi* a first analysis of the copulatory organ can be given (Fig. 11A$_3$). The stylet is rather broad with a wide proximal funnel to which the proximal rim of the mantel is attached. On the concave side of the stylet the mantle forms 4–5 plates or spines, while on the convex side it bears a bundle of numerous fine folds or rods, one of which is very long and flagelliform. The bursal appendage has a straight initial part, thickened at one side, and two extremely long, highly coiled distal tubes. Both characters are clear autapomorphies for the species, and have no equivalent within the Trigonostominae. With only one individual available, the precise structure of the copulatory

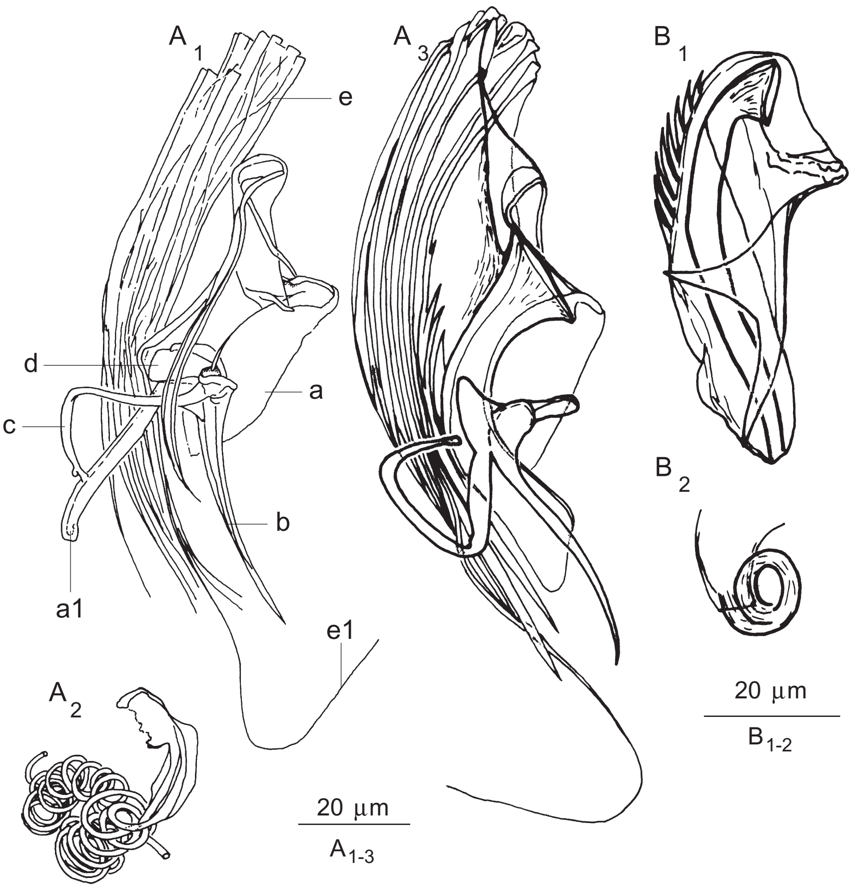

Figure 11. A, *T. denhartogi* **comb. nov.** A$_{1,3}$ copulatory organ; A$_2$ bursal appendage (A$_{1,2}$ specimen from Curaçao; A$_3$ specimen from New Caledonia). B, ***T. spinigerum* sp. nov.** B$_1$ copulatory organ; B$_2$ bursal appendage (from the holotype). *Abbreviations:* a–e, explained in text.

organ of *T. spinigerum* (Fig. 11B$_1$) cannot yet be well understood. The mantle seems to have its rim proximal to the beginning of the stylet, and envelopes the latter completely. On the convex side and in the proximal half, the mantle bears 8–10 spines (or folds?); on the concave side and in the distal half, the mantle forms plates and spines similar to those in species of group 1B (e.g. *T. coronatum* or *T. watsoni*). The bursal appendage on the other hand is very similar to that of *T. watsoni*, constituting a proximal funnel with two broad tubes coiled over more than 360°.

To conclude, within *Trigonostomum* two common types of copulatory organ occur: (1) a proximally curved stylet surrounded by the mantle in its distal part, the latter divided into spiny plates; (2) a coiled stylet completely surrounded by a mantle that ends in two spiny plates. The first condition is plesiomorphic, the second synapomorphic. The mantle exhibits a much more complicated structure in *T. denhartogi* and *T. spinigerum*. Three types of bursal appendage occur: (1) two tubes attached to the bursa with a ring or funnel; (2) a funnel with two highly coiled tubes; (3) many tubules held together in one way or another. The first condition is plesiomorphic, the second a possible autapomorphy, and the third synapomorphic, though variations may occur. The differences discussed here, together with some other characters, are reflected in the following key.

IDENTIFICATION KEY

1\. Copulatory organ 106–121 μm long and very complex, consisting of a gutter-shaped plate, enveloping a bundle of rods, of which one has a long thread-like distal tip; stylet funnel-shaped, ± 65 μm long; bursal appendage with initial straight part (22–44 μm long) and two heavily coiled distal tubes. (Figs 8E, 11A) .... *T. denhartogi* **comb. nov.**
– Copulatory organ ± 60 μm long; stylet bent over 90°, surrounded by the mantle that has 8–10 small spines at the convex side and with broad distal plates and spines distally (Fig. 11B$_4$); bursal appendage with two broad, highly coiled tubes (Figs 8F, H, 11B) .... ***T. spinigerum* sp. nov.**
– Copulatory organ otherwise 2
2\. Proximal part of the stylet curved over 90–270° and surrounded by the mantle only in its distal part. (Figs 4B, 6, 7) 3
– Copulatory organ spirally coiled over 360° or more (except in *T. franki*, where it is coiled over 180°); stylet surrounded over its whole length by the mantle, latter mostly wrinkled and split distally into two narrow, spiny plates with a terminal hook; bursal appendage consisting of two tubes (coiled over 270–360°), with a straight distal part; animals with dorsal stripe or rostral spot or without pigmentation (Figs 4C, 5, 8A, B, G, I, 9, 10) 7
3\. Stylet long and narrow with a proximal turn of 270°; mantle forming a narrow ring and carrying a long and slender spine; bursal appendage with two tubes, proximally with a ring (Fig. 6) 4
– Stylet broad, proximally curved over 90° or 180°; mantle split into one, two or three plates (Fig. 7) 5
4\. Copulatory organ consisting of a ±225 μm long slender stylet; mantle with flagelliform spine (± 75 μm); bursal appendage ± 22 μm long (Fig. 6B) .... *T. messoplanoides*
– Copulatory organ 74–130 μm long; stylet 117–194 μm long; mantle with a straight spine of 70–78 μm; bursal appendage ± 54 μm long (Fig. 6A) .... *T. venenosum*
5\. Stylet bent over 90°, mantle split into three pointed plates:
* Copulatory organ 30–45 μm long; stylet 44–53 μm long; bursal appendage 60–70 μm long, with a proximal barrel-like casing and ± 12 tubules, diverging distally (Fig. 7C) .... *T. penicillatum*
* Copulatory organ 28–36 μm long; stylet 29–41 μm; bursal appendage 62–78μm long, consisting of a short funnel-shaped proximal part and two coiled (>360°) tubes, all with a faint striation (Fig. 7B) .... ***T. watsoni* sp. nov.**
* Copulatory organ ± 44 μm long; stylet ± 70 μm long; bursal appendage ± 78 μm long, with a proximal part, shaped like a clover leaf, and one to three distal bent tubes with a fine striation (Fig. 7A) .... *T. coronatum*
– Stylet bent over 180°; mantle with one or two plates 6
6\. Mantle split into two plates, stylet with spoon-like terminal opening (Fig. 7F$_{1,2}$, G$_1$) (note that the copulatory organ of *T. franki* may easily be confused with this type):
* Plates of the mantle blunt and shorter than the stylet; copulatory organ ± 78 μm long; stylet ± 104 long, proximally with a crest; bursal appendage ± 65 μm long, curved proximally over 270°, with proximal barrel-like part and a bundle of very narrow, faint tubules, which form two bundles distally (Fig. 7G) .... ***T. nataschae* sp. nov.**

* Plates of the mantle pointed and at least as long as the stylet; copulatory organ slender, 72–74 µm long; stylet 83–84 µm long; bursal appendage ±66 µm long, with a proximal barrel-like part and ±10 distal tubules (Fig. 7F) .... *T. mirabile*

– Mantle with only one plate (see Fig. $7D_{1,\ 3}$, E_1):

* Plate of the mantle as long as the stylet and ending in a little hook; copulatory organ 42–46 µm long; stylet 40–57 µm long; bursal appendage 95–98 µm long consisting of a coiled tube, which distally splits into five to six tubules (Fig. 7D) .... *T. lilliei*

* Plate of the mantle blunt and shorter than the stylet; copulatory organ ± 62 µm long; stylet ± 64 µm long, proximally with a crest; bursal appendage 20–24 µm long with proximal barrel-like part and ±10 distal tubules (Fig. 7E) .... *T. breitfussi*

7. Copulatory organ 86–111 µm long, proximally bent over 180° and continuing in a straighter part, where the two spiny plates are; bursal appendage 62–166 µm long, coiled over 270°; animals mostly with dorsal pigment stripe (Figs 5A, 9A, 10A) .... ***T. franki* sp. nov.**

– Copulatory organ with 1–5 complete spire(s) of 360°, continuing in a straighter section, where the two spiny plates are situated (Fig. 5B–F):

* Copulatory organ with one spire, 158–434 µm long; bursal appendage 50–149 µm long, coiled over 270° (Figs 5B, 9B, 10B) .... *T. armatum*

* Copulatory organ with two spires, 284–498 µm long; bursal appendage 64–161 µm long, coiled over 360° (Figs 5C, 9C, 10C) .... *T. setigerum*

* Copulatory organ with three spires, 414–445 µm long; bursal appendage ± 34 µm long, coiled over 270° (Figs 5D, 9D, 10D) .... ***T. australis* sp. nov.**

* Copulatory organ with four spires (Figs 5E, 9E) .... ***T. galapagoensis* sp. nov.**

* Copulatory organ with five spires, 683–853 µm long; bursal appendage 80–106 µm long, coiled over 270° (Figs 5F, 9F, 10E) .... ***T. tori* sp. nov.**

TAXONOMY

TRIGONOSTOMUM SCHMIDT, 1852

Trigonostomum Schmidt, 1852: 500; Graff, 1905: 73, 113; 1908: 2542; 1913: 302–303; Meixner, 1924b: 91–92, 96, 103; Luther, 1948: 36, 38; Den Hartog, 1964: 373, t. 1; Ax, 1971: 146–150, fig. 1.

Vortex Schmidt, 1857: 352, 356.

Spiroclytus Schmidt, 1857: 352, 356; Claparède, 1863: 15.

Orcus Uljanin, 1870: 19.

Kylosphaera Jensen, 1878: 16, 36, 44–45.

Hyporhynchus Graff, 1882: 336.

Hyporcus Graff, 1905: 73, 1910; 1908: 2542; 1913: 299.

Woodshollia n.n. Graff, 1910: 947.

Woodsholia Graff, 1911a: 198; 1911b: 61; 1913: 312.

Woodsholia Graff, 1911b: 65.

Diagnosis: Trigonostominae with anterior integumental invagination, connected with the body wall by several muscles. Pharynx situated anteriorly, strongly inclined forwards, with 11 radial muscles lengthwise and 24 in cross section. Paired testes at 50%, caudal to the pharynx.

Type species: Trigonostomum setigerum Schmidt, 1852

TRIGONOSTOMUM ARMATUM (JENSEN, 1878) GAMBLE, 1900

(FIGS 5B, 8A, 9B, 10B; TABLE 1)

Alternative species name: trigonostomum-armatum

Kylosphaera armata Jensen, 1878: 7, 12, 14, 17, 45–47, t. 3, figs 14–22.

Hyporhynchus armatus Graff, 1882: 337; Gamble, 1893: 466–467; Attems, 1897: 228, t. 2, fig. 26.

Trigonostomum armatum Gamble, 1900: 813; Southern, 1912: 3, 9; Graff, 1913: 305–307, fig. 265; Southern, 1915: 34; Meixner, 1924b: 89, 94, 96, 99–100, 102; 1925: 256; Steinböck, 1931: 13, 23; Southern, 1936: 45, 57; Steinböck, 1938: 13, 22; Ax, 1952: 90–91, fig. 1; Westblad, 1954: 9.

Known distribution: Norway (Jensen, 1878; Graff, 1882; Westblad, 1954), English Channel (Gamble, 1893), North Sea (Attems, 1897; Meixner, 1924b, 1925), Ireland (Gamble, 1893, 1900; Southern, 1912, 1915, 1936), Faeroe Islands (Steinböck, 1931), Iceland (Steinböck, 1938), Baltic Sea (Ax, 1952).

New localities: Norway, Bergen, Karlsög, on algae, 9 July 1953, Westblad (coll. SMNH). Norway, Trondheim, Munkholmen, in sand, 45–50 m deep, 22 July 1955. Westblad (coll. SMNH). Norway, Leröy-Buröy, in fine-grained sand, 5–7 m deep, 1 August 1968, Karling (coll. SMNH; type locality).

United Kingdom, Plymouth, Salcombe, Saltstone, on algae, 11 July 1949, Westblad (coll. SMNH). Sweden, Gullmaren, Gåsövik, sheltered bay on brown algae, 19 August 2001. France, Wimereux, Langue du Chien, on algae, 20 October 1999. Curaçao (Dutch Antilles), Playa Canoa, on green algae, 10 December 1998. Curaçao (Dutch Antilles), Dam di Cabicuchi, 'Spaanse water', on *Turbinaria*-like algae, 14 and 30 December 1998 and 5 January 1999. Australia, New South Wales, Arrawarra, south of the marine station, on *Sargassum* sp., 1 November 1997. New Caledonia, Nouméa, Nouville, on algae in a lagoon, 10 August 2003. South Georgia, Cumberland Bay, May Creek, on seaweed, 9 May 1902 (coll. SMNH).

Material examined: Several individuals studied alive. Neotype (SMNH, no. 46427) from Norway. Whole mounts from France (1), Australia (1), New Caledonia (1), Curaçao (10) and South Georgia (SMNH, no. 46448). Serially sectioned specimens from Sweden (3), Curaçao (1), Norway (SMNH, no. 46425–6) and Plymouth (SMNH, nos. 46419–20).

Diagnosis: Trigonostomum species with coiled copulatory organ, with one whole spire. Stylet 158–434 μm long, enveloped by the mantle over its entire length. Mantle distally split into two spiny plates with terminal hook. Bursal appendage 50–149 μm long, with two tubules, proximally curved over 270° and with straight distal part.

***TRIGONOSTOMUM AUSTRALIS* SP. NOV.**
(FIGS 5D, 9D, 10D; TABLE 1)

Alternative species name: trigonostomum-australis sp. nov.

Holotype: Whole mount, Australia, Queensland, North Stradbroke Island, Point Lookout, algae in tidepool, 12 August 1996.

Other material: Observations on live material. Two whole mounts from Australia, New South Wales, Arrawarra, on *Sargassum* sp., 28 August 1996 and 1 November 1997.

Etymology: Reflects the species' occurrence in the southern hemisphere.

Diagnosis: Trigonostomum species with coiled copulatory organ, with three whole spires. Stylet 414–445 μm long, enveloped by the mantle over its entire length. Mantle distally split into two spiny plates with terminal hook. Bursal appendage 34 μm long, proximally curved over 270° and with straight distal section.

TRIGONOSTOMUM BREITFUSSI (GRAFF, 1905) MEIXNER 1924
(FIG. 7E)

Alternative species name: trigonostomum-breitfussi.

Hyporcus breitfussi Graff, 1905: 112, t. 3, figs 12–16; 1913: 301–302, figs 261, 262.

Hyporhynchus breitfussi Meixner, 1925: 256.

Trigonostomum breitfussi Meixner, 1924b: 89, 91–94, 96–99, 105, figs 3, 4; Steinböck, 1932: 309; Ax, 1952: 91–92, fig. 2; Westblad, 1954: 9; Armonies & Hellwig-Armonies, 1987: 104, table 5; Joffe & Kotikova, 1989: 70–72, 74–77, 79–82, figs 2, 3, 6 and 7.

Known distribution: Barents Sea (Graff, 1905), Baltic Sea (Ax, 1952), Greenland (Steinböck, 1932), North Sea (Meixner, 1924b, 1925; Ax, 1952; Armonies & Hellwig-Armonies, 1987), Norway (Westblad, 1954).

New locality: Sweden, Gullmaren, Kristineberg, 23, 26 and 27 July 1932, Westblad (coll. SMNH; type locality). Sweden, Gullmaren, on algae, 6 August 1945, Westblad (coll. SMNH). Sweden, Gullmaren, Harpo Bedar, on red algae, 20 m deep, 7 August 2001.

Material examined: Observations on live material from Sweden. Neotype (SMNH, no. 47461). Two whole mounts (SMNH, nos. 47462–3) and two serially sectioned specimens (SMNH, nos. 47469–70) from Sweden.

Diagnosis: Trigonostomum species with copulatory organ ± 62 μm long. Stylet ± 64 μm long, proximally bent over, 180° and with a crest. Mantle with one blunt plate (shorter than the stylet), surrounds only the distal part of the stylet. Bursal appendage 20–24 μm long, proximally with a barrel-like casing and nine or ten distal tubes.

Remarks: The observation of Ax (1952) that there is only one plate-like structure instead of two (Graff, 1905), surrounding the tubiform stylet, can be confirmed. This plate has a spine-like projection at its distal end, which lies close to the stylet but is displaced in highly squeezed animals (Fig. 7E_1). The bursal appendage is short (Graff, 1913 24 μm; Ax, 1952: 20–21 μm), barrel-shaped and consists of nine, maybe ten, short tubes (Fig. 7E_3).

TRIGONOSTOMUM CORONATUM (GRAFF, 1882) GRAFF, 1913
(FIG. 7A)

Alternative species name: trigonostomum-coronatum

Hyporhynchus coronatus Graff, 1882: 340, t. 9, fig. 21.

Hyporhynchus intermedius Attems, 1897: 228, t. 2, figs 22, 23.

Trigonostomum intermedium Graff, 1913: 308, fig. 267; Meixner, 1924b: 96, 98; Southern, 1936: 45, 57.

Trigonostomum coronatum Graff, 1913: 307–308, fig. 266; Meixner, 1924b: 96; Steinböck, 1933: 29.

Trigonostomum quadrifolium Riedl, 1954: 220–223, figs 28, 29.

Known distribution: Madeira (Graff, 1882), Irish Sea (Southern, 1936), North Sea (Attems, 1897), Mediterranean Sea (Steinböck, 1933; Riedl, 1954).

New locality: France, Banyuls, Ile Gros, on algae left of the jetty, 23 June 2000 (type locality).

Material examined: One specimen studied alive and mounted (neotype, LUC no. 228).

Diagnosis: Trigonostomum species with copulatory organ of ± 44 µm. Stylet ± 70 µm long, proximally bent over 90 °. Mantle split into three pointed plates, surrounding only the distal part of the stylet. Bursal appendage 78 µm long, with proximal crown-like part and one terminal bent, striated tube.

Remarks: According to Graff (1882, 1913) the copulatory organ of *T. coronatum* consists of an inner and an outer tube. The inner tube is proximally bent and twice as long as the outer one, which forms a broad mantle around the distal part of the inner tube. These observations can more or less be confirmed on the specimen from Banyuls, although it was squashed and the copulatory organ was rather damaged. The bursal appendage consists of a crown-like proximal part, enveloped by the bursa, and a tubular distal part. The bursal appendage of the Banyuls specimen consists of a plate proximally carrying a crown-like part, which is enveloped by the bursa, probably consisting of four plates, which are proximally split. Distally, the bursal appendage forms two bent tubes. These tubes show an inconspicuous striation, giving the impression that they consist of a number of smaller tubules.

Based on this resemblance, the Banyuls specimen is placed within *T. coronatum*. However, two other species have the same structure of the bursal appendage – *T. intermedium* Attems, 1897 and *T. quadrifolium* Riedl, 1954 – although little is known of the structure of their copulatory organs. In *T. quadrifolium* the appendage carries only one tube (Riedl, 1954), whereas the tube is apparently split into three tubules in *T. intermedium* (Attems, 1897; Graff, 1913), of which no material was available. These species also differ in the number of plates forming the crown of the appendage: four in *T. quadrifolium* (Riedl, 1954) and five in *T. intermedium* (Attems, 1897: fig. 22; Graff, 1913) and *T. coronatum* (Graff, 1882). Based on the descriptions of *T. intermedium* and *T. quadrifolium* and our experience that the mentioned differences are often difficult to assess, we synonymise both species with *T. coronatum*.

TRIGONOSTOMUM DENHARTOGI (KARLING, 1978) **COMB. NOV.**

(FIGS 8E, 11A)

Alternative species name: trigonostomum-denhartogi
Proxenetes denhartogi Karling, 1978: 233, figs 35, 36.

Known distribution: Bermuda (Karling, 1978).

New localities: Kenya, Mombasa area, McKenzie Point, in shallow pool on seagrass, 30 September 1991. Curaçao (Dutch Antilles), Dam di Cabicuchi ('Spaanse water'), on *Turbinaria*-like algae from exposed rocks, 14 December 1998. Curaçao (Dutch Antilles) 'Spaanse water', mixed sample of algae, 30 December 1998. New Caledonia, Nouméa, Nouville, on algae in a lagoon south of the asylum, 3 August 2003. New Caledonia, Nouméa, Anse Vata, on algae (*Ulva* sp. and *Enteromorpha* sp.) from a little estuary, 22 August 2003.

Material examined: Holotype (SMNH, no. 2965). Live material and five whole mounts, one from each new locality.

Diagnosis: Trigonostomum species with very complex copulatory organ, 106–121 µm long. Mantle with numerous folds, rods and spines, one of which has a thread-like distal part. Stylet 61–66 µm long. Bursal appendage with a straight initial part, 22–44 µm long, and two heavily coiled tubes.

Remarks and additional data: Karling (1978) described this species from Bermuda based on one whole mounted specimen, but without observations of live animals. On the holotype, the anterior invagination ('proboscis') is not visible and Karling therefore did not observe this important feature. Based on the structure of the copulatory organ he reluctantly placed the species within *Proxenetes* Jensen, 1878. He explicitly mentioned, however, that the bursal appendage was very unlike that of any other species of *Proxenetes*, where the bursal appendage consists of a split tube, surrounded by a ring. Observations on live material clearly show that this species indeed belongs to *Trigonostomum*, as it has the typical anterior invagination.

The specimens from Curaçao and New Caledonia are ± 0.8 mm long. The copulatory organ is of exactly the same structure as in the specimen from Bermuda (Karling, 1978), consisting of an outer plate-like structure (Fig. $11A_1$: a) that forms a broad gutter enclosing several long rods (Fig. $11A_1$: e). One of these rods has a long distal thread-like point (Fig. $11A_1$: e1). A second, triangular, plate-like part (Fig. $11A_1$: d) surrounds the rods and carries three distal hooks (Fig. 11A$_1$: a1, b and c). The length of the copulatory organ (excluding the thread-like tip) is 107–111 µm (Curaçao) and 109–121 µm (New Caledonia), which is almost identical to that of the holotype (115 µm: Karling, 1978). The exact number of rods could not be determined. The tubular stylet is only clearly visible in the New Caledonian specimens (Figs 8E, 11A$_3$). It is 61–66 µm long ($n = 2$) and rather broad, with a wide proximal funnel to which the mantle is attached. The bursal appendage of the specimens from Curaçao and New Caledonia clearly consists of two heavily coiled tubes and a proximal basal piece. This proximal part is 31 µm and 44 µm in the two specimens from Curaçao, 28 µm and 36 µm in the specimens from New Caledonia, and 22 µm in the specimen from Bermuda (Karling, 1978). Karling (1978) could not determine the exact number of coiled tubes in the Bermuda individuals.

***TRIGONOSTOMUM* FRANKI SP. NOV.**
(FIGS 2, 3, 5A, 8G, I, 9A, 10A; TABLE 1)

Alternative species name: trigonostomum-franki sp. nov.

Holotype: Whole mount, Curaçao (Dutch Antilles), Dam di Cabicuchi ('Spaanse water'), on *Turbinaria*-like algae from exposed rocks at the side of 'Caracasbaai', 14 December 1998 (LUC no. 225).

Paratype: Whole mount, same data as for the holotype (LUC no. 226).

Other material: Observations on live material. Two whole mounts and one serially sectioned specimen from Curaçao (Dutch Antilles), 'Spaanse water', mixed sample of algae containing mainly *Caulerpa* sp. and *Halimedia gantia*, 30 December 1998. One whole mount from Florida (USA), Fort Pierce, in fine detritus-rich sand between rocks, 16 November 1994. Three whole mounts – Kenya, Mombasa area, McKenzie Point – on algae and seagrasses, 4 and 15 June 1987 and 27 September and 1 October 1991. One whole mount from Tanzania, Zanzibar, Pete, on seagrasses, 16 August 1995. Three whole mounts, New Caledonia, Nouméa, Nouville, on algae in a lagoon south of the asylum, 3 and 10 August 2003. One whole mount, New Caledonia, Nouméa, Baie des Citrons, on algae in a lagoon, 8 August 2003. Live observations from New Caledonia, Nouméa, Nouville, on algae covered with shells and sand on a reef in the western part of the Kuendu Bay, 16 August 2003.

Etymology: Dedicated to Mr Frank Van Belleghem, who helped to collect the material on Curaçao.

Diagnosis: Trigonostomum species with moderately coiled copulatory organ, with $^1/_2$ spire. Stylet 86–111 µm long, enveloped by the mantle over its entire length. Mantle distally split into two spiny plates with terminal hook. Bursal appendage 61–166 µm long, with two tubules, proximally curved over 270° and with straight distal part.

***TRIGONOSTOMUM GALAPAGOENESIS* SP. NOV.**
(FIGS 5E, 9E; TABLE 1)

Alternative species name: trigonostomum-galapagoensis sp. nov.

Trigonostomum setigerum Ehlers & Ax, 1974: 664–666, 668, fig. 13A–C.

Holotype: One micrograph (fig. 13C in Ehlers & Ax, 1974), Galapagos (Ecuador), Santa Cruz, Bahía Academy (Ehlers & Ax, 1974).

Etymology: The islands where the type material was found.

Diagnosis: Trigonostomum species with coiled copulatory organ, four whole spires. Stylet enveloped by the mantle over its entire length. Mantle distally split into two spiny plates with terminal hook. Bursal appendage coiled, with two tubules.

Remarks: Pigment spot rostrally, between the eyes (see Ehlers & Ax, 1974: fig. 13A). The length of both hard parts, copulatory organ and bursal appendage, could not be measured, because this species is only known from a micrograph of a live individual (Ehlers & Ax, 1974: fig. 13), without a scale bar.

TRIGONOSTOMUM LILLIEI (GRAFF, 1911A) MEIXNER 1924B
(FIG. 7D)

Alternative species name: trigonostomum-lilliei
Woodsholia lilliei Graff, 1911b: 61–65, fig. 3, t. IV, figs 29–43; 1913: 312–314, figs 277–279; Meixner, 1924b: 91, 92.
Trigonostomum prytherchi Kepner, Ferguson & Stirewalt, 1941: 243–252, figs 1–3, pl. 3.
Trigonostomum divae Marcus, 1948: 121–125, 189, t. III, figs 13–18.
Trigonostomum lilliei Meixner, 1924b: 92, 94, 96, 99, 102.

Known distribution: North American Atlantic coast (Graff, 1911b, 1913; Kepner *et al.*, 1941), Brazil (Marcus, 1948).

New locality: Australia, New South Wales, Arrawarra, rocky tidepool at low tide, on brown algae, 29 August 1996; south of the marine station, mideulittoral, on *Sargassum* sp., 1 November 1997.

Material examined: Observations on two live specimens, two whole mounts (all from Australia), the holotype of *T. prytherchi*, which is designated neotype (whole mount; SI-NMNH, Cat. no. 20593; Kepner *et al.*, 1941) and Marcus' (1948) material of *T. divae* (sections and whole mounts; SMNH, nos. 42204–8).

Diagnosis: Trigonostomum species with copulatory organ 42–46 µm long. Stylet 40–57 µm long, proximally bent over, 180°. Mantle with one hooked plate (as long as the stylet) surrounds only the distal part of the stylet. Bursal appendage 95–98 µm long, heavily coiled, consisting of one tube, which is distally split into five or six finer tubes.

Remarks and additional data: The stylet of the examined specimens is 40–57 µm long (57 µm in the holotype of *T. prytherchi*; 40–43 µm in Marcus' material of *T. divae*, $n = 2$; 44–46 µm in the Australian specimens, $n = 2$). The bursal appendage is a 95–98 µm long ($n = 2$). The bursal appendage could not accurately be measured in the second Australian specimen, or in Marcus' material.

According to the description, including figures, of Kepner *et al.* (1941), it seems that they observed not one but three bursal appendages (including two smaller nonfunctioning appendages). These observations could be due to a misinterpretation of the serially sectioned material, because a thorough examination of the type material revealed only one bursal appendage.

According to Marcus' (1948) drawings and description, the difference between *T. divae* and *T. lilliei* is the presence of only five tubes in the bursal appendage instead of six, a feature, which is often very difficult to assess. The overall construction of the bursal appendage of *T. divae* (i.e. the number and extent of coils) is identical to that of the Australian specimens. The bursal appendage of *T. prytherchi* is also identical in structure. The difference between *T. prytherchi* and *T. lilliei* would also be the ending of the prepharyngeal cavity in the 'proboscis' cavity as observed by Graff (1911b: fig. 31). According to Meixner (1924b) this feature is the result of the degree of contraction, and he therefore rejected the taxon *Woodsholia*. Because of these doubtful differences between these 'species' and the overall similarity in the structure of both the copulatory organ and the bursal appendage, we synonymise *T. prytherchi* and *T. divae*, with *T. lilliei*.

TRIGONOSTOMUM MESSOPLANOIDES ARTOIS *ET AL.,* 2000
(FIG. 6B)

Alternative species name: trigonostomum-messoplanoides

Trigonostomum messoplanoides Artois *et al.*, 2000: 104–105, fig. 1.

Known distribution: Weddell Sea, Antarctica (Artois *et al.*, 2000).

Material examined: Holotype (LUC, no. 207).

Diagnosis: Trigonostomum species with stylet 225 µm long, proximally bent over 270°. Mantle with stylet 75 µm long, flagelliform spine surrounding only the distal part of the stylet. Bursal appendage 22 µm long, with a proximal ring and two distal tubes.

Remarks: The copulatory organ of *T. messoplanoides* resembles that of some species of *Messoplana* (Artois *et al.*, 2000), for instance *M. elegans* (Luther, 1948) Den Hartog, 1966, *M. helgolandica* Ax, 1971, *M. pacifica* Karling, 1986 and *M. rugata* Ehlers, 1974. However, the presence of a ventral invagination clearly confirms that it is a species of *Trigonostomum*.

TRIGONOSTOMUM MIRABILE (PEREYASLAWZEWA, 1893) GRAFF, 1913
(FIG. 7F)

Alternative species name: trigonostomum-mirabile

Hyporhynchus mirabilis Pereyaslawzewa, 1893: 267, t. 4, fig. 27.

Trigonostomum mirabile Graff, 1913 : 310–311, fig. 273; Meixner, 1924b: 96, 98; Ax, 1959: 98–99, figs 80, 81; Mack-Fira, 1968: 179–180, figs 2–4; 1974: 249, 265, 273, 281, 284.

Proxenetes lictor Beklemischev, 1927: 190–191, 203–204, t. I, figs 8, 9.

Known distribution: Black Sea (Pereyaslawzewa, 1893; Beklemischev, 1927; Ax, 1959; Mack-Fira, 1968, 1974); Sea of Marmara (Ax, 1959).

New locality: Romania, Black Sea, Agigea, on *Ceramium* sp., 26 September 1968, Mack-Fira (coll. SMNH; type locality).

Material examined: Two individuals from Agigea (mounted on the same slide: SMNH, no. 47474). One of them designated neotype.

Diagnosis: Trigonostomum species with copulatory organ 72–74 µm long. Stylet 83–84 µm long, proximally bent over, 180°. Mantle with two pointed plates (as long as the stylet) surrounds only the distal part of the stylet. Bursal appendage 66 µm long, proximally with a barrel-like casing and ± ten distal tubules.

Remarks: The synonymization of *Proxenetes lictor* with *T. mirabile* was made by Ax (1959), but it was already recognized by Beklemischev in a personal note on the offprints of his article (see Ax, 1959).

***TRIGONOSTOMUM NATASCHAE* SP. NOV.**
(FIG. 7G)

Alternative species name: trigonostomum-nataschae sp. nov.

Holotype: Whole mount, Kerguelen (France, subantarctic territory), Port Raymond, tidepool with fine sand and silt, mixed with shells, 23 November 1992 (LUC no. 227).

Other material: Observations on live material from Kerguelen.

Etymology: Dedicated to Mrs Natascha Steffanie, technical assistant at LUC, Diepenbeek (Belgium).

Diagnosis: Trigonostomum species with copulatory organ ± 78 μm long. Stylet ± 104 μm long, proximally bent over, 180° and with a crest. Mantle with two blunt plates (shorter than the stylet) surrounds only the distal part of the stylet. Bursal appendage ± 65 μm long, with proximal barrel-like part and very narrow tubules, forming two curved bundles of tubules distally.

TRIGONOSTOMUM PENICILLATUM (SCHMIDT, 1857) MICOLETZKY, 1910
(FIG. 7C)

Alternative species name: trigonostomum-penicillatum

Vortex penicillatus Schmidt, 1857: 352, t. 1, fig. 3.

Hyporhynchus penicillatus Diesing, 1862: 227; Graff, 1882 : 341, t. 9, figs 15–20; Gamble, 1893: 467; Fuhrmann, 1898: 459; Gamble, 1900: 813; Meixner, 1925: 256; 1926: 577.

Trigonostomum intermedium n.n. Graff 1910: 4.

Trigonostomum penicillatum Micoletzky, 1910: 174; Graff, 1913 : 308–309, figs 268–270; Southern, 1912: 3, 9; 1915: 34; Meixner, 1924a: 202–203; 1924b: 89, 92, 94, 96, 98, 99, 105; Southern, 1936: 45, 58; Westblad, 1954: 8; Den Hartog, 1964: 378; Ax, 1971: 216–217, fig. 45.

Trigonostomum marki Graff, 1911b: 60, t.4, figs 44, 45; 1913: 309–310, fig. 271; Meixner, 1924b: 96, 99.

Known distribution: North American Atlantic coast (Graff, 1911b), French Atlantic coast (Ax, 1971), English Channel (Gamble, 1893), North Sea (Graff, 1913; Meixner, 1924b), Ireland (Southern, 1912, 1936), Norway (Westblad, 1954), Mediterranean Sea (Schmidt, 1857; Graff, 1913; Meixner, 1925, 1926) and Adriatic Sea (Meixner, 1925, 1926).

New localities: Great Britain, Plymouth, 5 July 1949, Westblad (coll. SMNH). France, Corsica, Ocellutia, large sandflat with coarse sand, 10–12 m deep, 19 October 1982 and 18 September 1983. Italy, Sardinia, Porticciolo, on algae at ± 10 m deep, 14 August 1994 (type locality). France, Banyuls, Ile Gros, on green algae near the jetty behind the station, 20, 22 and 23 June 2000. Yugoslavia, Adriatic Sea, Dubrovnik, 24 June 1952, Westblad (coll. SMNH). Bulgaria, Varna (Black Sea), on algae, 21 December 1953, Valkanov (coll. SMNH).

Material examined: Observations on live material from Corsica, Sardinia and Banyuls. Neotype (LUC no. 229) from Sardinia. One whole mount from Bulgaria (SMNH, no. 47485) and serially sectioned specimens from Great Britain (SMNH, nos. 47480–3) and Yugoslavia (SMNH, nos. 47484). Seven whole mounts from Banyuls and three from Corsica.

Diagnosis: Trigonostomum species with copulatory organ 30–45 μm long. Stylet 44–53 μm long, proximally bent over 90°. Mantle with three spiny plates, surrounds only the distal part of the stylet. Bursal appendage 60–70 μm long, with a barrel-like casing and ± 12 distal tubules.

Remarks: According to Meixner (1924b), the bursal appendage of *T. penicillatum* partially consists of ± 26 fine rods. However, our observations on serially sectioned material of *T. penicillatum* (SMNH) revealed only 12 fine, slightly bent rods in the bursal appendage of a specimen from Plymouth, though more in the individuals in the whole mounts.

In 1897, *T. intermedium* was described by Attems, but the same name was used by Graff as a *nomen nudum* in 1910 for a species he later (Graff, 1911b) described as *T. marki*. The structure of the bursal appendage of *T. marki* is identical to that of *T. penicillatum* (Graff, 1911b, 1913). According to Graff (1913) the species differ in the structure of the copulatory organ. In *T. penicillatum* the organ has a stylet, enclosed by a mantle, which carries three plates; the same structure is described and drawn by Graff (1911b: 61, table 4, figs 44, 45; 1913: 309, fig. 271) for *T. marki*. *T. marki* is therefore synonymized with *T. penicillatum*.

TRIGONOSTOMUM SETIGERUM SCHMIDT, 1852
(FIGS 5C, 8B, D, 9C, 10C; TABLE 1)

Alternative species name: trigonostomum-setigerum

Trigonostomum setigerum Schmidt, 1852: 500, t. 47, fig. 13; Diesing, 1862: 229; Graff, 1905: 113–114, t. 3, figs 17–21; Micoletzky, 1910: 173; Southern, 1912: 3, 9; Graff, 1913: 303–305, figs 263, 264; Southern, 1915: 34; Meixner, 1924a: 202–203; 1924b: 89, 90, 92, 93–94, 96, 99–101, 102, figs 1, 2, 5; 1925: 256; 1926: 577; Steinböck, 1933: 10–11; Southern, 1936: 45, 57; Meixner, 1938: 25, 114, fig. 23; Westblad, 1952: 30–31; Ax, 1959: 97; Riedl, 1959: 319–322, fig. 6; Den Hartog, 1964: 375; Karling, 1978: 231, figs 27, 28; 1986: 209–210, figs 39, 40, 47,48; Ax & Armonies, 1990: 100.

Trigonostomum setigerum setigerum Graff, 1905: 113, t. 3, figs 19–21; 1913: 305.

Trigonostomum setigerum album Graff, 1905: 114, t.3, figs 17, 18; 1913: 305.

Trigonostomum setigerum lunulatum Graff, 1905: 114; 1913: 305.

Spiroclytus nisus Schmidt, 1857: 356, 365, t. 3, fig. 8; Diesing, 1862: 225.

Spiroclytus euryalus Schmidt, 1857: 356, 365, t. 3, fig. 8.

Spiroclytus setigerus Claparède, 1863: 15.

Vortex ornatus Uljanin, 1870:, 18, t. 4, fig. 15.

Hyporhynchus setigerus Graff, 1882: 338–339, t. 9, figs 6–14, t. 11, fig. 27; Pereyaslawzewa, 1893: 267, t.4, fig. 29, t. 10, figs 60a–e, 63d; Fuhrmann, 1898: 459; Sekera, 1901: 81; Sabussow, 1905: 488.

Known distribution: Mediterranean Sea (Schmidt, 1852, , 1857; Graff, 1905; Sabussow, 1905; Micoletzky, 1910; Meixner, 1925; Steinböck, 1933; Riedl, 1959), Adriatic Sea (Meixner, 1925, 1926), Black Sea (Uljanin, 1870; Pereyaslawzewa, 1893; Graff, 1905; Ax, 1959), Sea of Marmara (Ax, 1959), northern Atlantic Ocean (Fuhrmann, 1898; Graff, 1905; Southern, 1912, 1915, 1936; Karling, 1978), North Sea (Meixner, 1924b), southern Atlantic Ocean (Westblad, 1952).

New localities: France, Corsica, Port de la station Stareso, on algae, 10 April, 9 May and 19 October 1982; Punta Reveletta, on algae, 11 May and 22 October 1982. France, Banyuls, Ile Gros, on green algae near the jetty behind the station, 20–23 June 2000. Greece, Perea, east side of the beach, coarse-grained detritus-rich sand mixed with shell gravel; on green and red algae, 22 July 2002; on green algae and seagrasses, ± 2 m deep, 31 July 2002. Greece, Nea Michaniona, flat exposed beach, on *Enteromorpha* sp. and seagrasses, 22 July 2002. Greece, Aghias Triada, flat beach, on green algae and seagrasses ± 2.5 m deep, 22 July 2002 and 6 August 2002 (type locality). Greece, Nea Fokea (Kassandra Peninsula), heavily exposed beach, on algae, 28 July 2002. United Kingdom, Plymouth, Wembury, tidepool, 21 July 1949, Westblad (coll. SMNH). Kenya, Tiwi, on algae, 6 October 1991.

Material examined: Several specimens studied alive. Neotype (LUC no. 230) from Greece. Whole mounts from Banyuls (2), Bermuda (SMNH, no. 46460), Corsica (5), Falkland (SMNH, nos. 46429, 46430, 46440), Greece (26), Kenya (1), Plymouth (SMNH, no. 46452) and South Georgia (SMNH, no. 46448). Serially sectioned specimens from Falkland (SMNH, nos. 46431–9, 46441–4), Plymouth (SMNH, nos. 46449–51), South Georgia (SMNH, nos. 46445–7) and Greece.

Diagnosis: Trigonostomum species with coiled copulatory organ, with two whole spires. Stylet 284–498 μm long, enveloped by the mantle over its entire length. Mantle distally split into two spiny plates with terminal hook. Bursal appendage 64–161 μm long, with two tubules, proximally curved over 360°.

Remarks: Graff (1905, 1913) recognized three subspecies, based on the pattern of pigmentation: *T. setigerum setigerum* (with dorsal stripe), *T. setigerum lunulatum* (with a rostral spot between the eyes) and *T. setigerum album* (without pigmentation). The validity of these subspecies was questioned by Southern (1912). Observations on a large number of live animals from one population in Greece showed that the three subspecies occurred sympatrically and that the difference between these three is not always clear. For example, specimens with a rostral spot (*T. s. lunulatum* of Graff, 1905) showed a large variation in size of the spot, making the difference with *T. s. album* very small. There is also variation in the length and width of the dorsal stripe: some individuals have a short dorsal stripe, which is broader between the eyes, while in other specimens the dorsal stripe is long and very broad over its whole length, giving it a network-like appearance. Based on the occurrence of all forms in one population (Greece, Thessaloniki), the lack of other distinctive features and the large variation of the three 'forms', the three subspecies are synonymized with *T. setigerum*.

TRIGONOSTOMUM SPINIGERUM SP. NOV.
(FIGS 8F, H, 11B)

Alternative species name: trigonostomum-spinigerum sp. nov.

Holotype: Whole mount, New Caledonia, Nouméa, Nouville, on algae in a lagoon south of the asylum, 3 August 2003 (LUC no. 231).

Etymology: Refers to the spines on the mantle surrounding the stylet; *spinigerum* (L.) = prickly, spiny, thorny.

Diagnosis: Trigonostomum species with copulatory organ 61 μm long. Stylet 57 μm long, proximally bent over almost 90°. Mantle surrounds the whole stylet and carries 8–10 small spines on the convex side. Bursal appendage ± 35 μm long, proximally funnel-shaped with two heavily coiled distal tubes, very faintly striated.

Remarks: The bursal appendage is measured (and drawn) on the whole mount, in which it appeared extremely thin-walled. Therefore, the length (35 μm) has to be interpreted as the minimum length. Furthermore, only one distal tube could be observed (two in the live individual), probably because both tubes are situated exactly above each other in the mounted specimen.

TRIGONOSTOMUM TORI **SP. NOV.**

(FIGS 5F, 9F, 10E; TABLE 1)

Alternative species name: trigonostomum-tori sp. nov.
Trigonostomum setigerum Karling, 1986: 209–210, figs 45, 46.

Holotype: One whole mount, USA, California, Pacific Grove (SMNH, no. 46459; Karling, 1986).

Paratypes: Two whole mounts (SMNH, nos. 46457–8; Karling, 1986).

Etymology: Dedicated to Prof. Dr Tor G. Karling, who collected the material.

Diagnosis: Trigonostomum species with coiled copulatory organ, with five whole spires. Stylet 683–853 μm long, enveloped by the mantle over its entire length. Mantle distally split into two spiny plates with terminal hook. Bursal appendage 80–106 μm long, with two tubules, proximally curved over 270° and with straight distal part.

TRIGONOSTOMUM VENENOSUM (ULJANIN, 1870) MEIXNER, 1924B

(FIGS 1, 6A)

Alternative species name: trigonostomum-venenosum
Orcus venenosus Uljanin, 1870: 19, t. 2, fig. 5.
Hyporhynchus venenosus Graff, 1875: 419; 1882: 341; Pereyaslawzewa, 1893: 265, 266, t. 4, fig. 28; Attems, 1897: 227, t. 2, figs 24, 25.
Hyporcus venenosus Graff, 1905: 110, t. 3, figs 9–11; Southern, 1912: 3, 8–9; Graff, 1913: 299–301, fig. 260; Southern, 1915: 34; Meixner, 1924b: 91, 92; Southern, 1936: 45, 57; Meixner, 1926: 577.
Trigonostomum venenosum Meixner, 1924b: 89, 92, 94, 96, 99, 102; 1925: 256; Steinböck, 1931: 12, 23; 1938: 12–13, 22; Ax, 1959: 98, figs 78, 79; Mack-Fira & Cristea-Nastasesco, 1971: 225, 227, figs 5, 6; Mack-Fira, 1974: 249, 265, 273, 281–282, 284.

Known distribution: Iceland (Steinböck, 1938), Ireland (Southern, 1912, 1936), Faeroe Islands (Steinböck, 1931), North Sea (Attems, 1897; Meixner, 1924b, 1925), Mediterranean Sea (Graff, 1882; Meixner, 1926), Adriatic Sea (Meixner, 1926), Black Sea (Uljanin, 1870; Pereyaslawzewa, 1893; Graff, 1905; Ax, 1959; Mack-Fira & Cristea-Nastasesco, 1971; Mack-Fira, 1974).

New localities: Sweden, Gullmarsfjord, Gåsövik, among algae, August 1945, Westblad (coll. SMNH). Norway, Bergen, Bay south of Tyssöy, stones, gravel, algae and fine shell-sand, 5–8 m depth, 29 July 1968, Karling (coll. SMNH). Norway, Bergen, sound between Leröy and Buröy; sand and mud, 5 m depth; 1 August 1968, Karling (coll. SMNH). France, Corsica, Port de la station Stareso, on algae, 6–4 m deep, 9 May 1982 and 12 March 1983, Martens; Bay of Calvi, 11 April 1984 and 26 March 1985. Italy, Sardinia, Porticello, about 0.2–1.5 m deep, on *Vaucheria*-like algae on rocks, 14 August 1994. France, Banyuls, Ile Gros, on green algae near the jetty behind the station, 22–23 June 2000. Kerguelen, Port Couvreux, bay at the right, green algae, 25 November 1992.

Material examined: Several specimens studied alive. Neotype (SMNH, no. 47499). Whole mounts from Sardinia (2), Corsica (4), Banyuls (3), Kerguelen (6), Norway (SMNH, nos. 47496–8) and Romania (SMNH, no. 47500–1). Two serially sectioned specimens (SMNH, nos. 47493–4) from Sweden.

Diagnosis: Trigonostomum species with copulatory organ 74–130 μm long. Stylet 117–194 μm long, proximally bent over 270°. Mantle with one pointed plate, surrounds only the distal part of the stylet. Bursal appendage ± 54 μm long, with a proximal ring and two distal tubes.

Remarks and additional data: The length of the stylet shows large variation between the populations of Banyuls (117–124 μm; $n = 2$), Sardinia (148–156 μm; $n = 2$), Corsica (165–179 μm; $n = 2$) and Kerguelen (157–194 μm; $n = 3$). The stylet resembles that of some species of *Messoplana* (e.g. *M. elegans* Luther, 1948; *M. helgolandica* Ax, 1971; *M. pacifica* Karling, 1986; *M. rugata* Ehlers, 1974).

TRIGONOSTOMUM WATSONI **SP. NOV.**

(FIG. 7B)

Alternative species name: trigonostomum-watsoni sp. nov.

Holotype: Whole mount, Australia, New South Wales, Arrawarra, on *Pavonina*-like algae in shallow tidepool between rocks near beach, 27 August 1996.

Paratype: One whole mount.

Other material: Observations on live material. Six whole mounts and six serially-sectioned specimens, Australia, New South Wales, Lennox Head, on beach with coarse sand and on algae in tide pool, 27 October and 1 November 1997. One whole mount, Australia, New South Wales, Arrawarra, on *Sargassum* sp. in permanent pool, 27 August 1996. One whole mount, Australia, New South Wales, Arrawarra, Mullaway headland, on algae in deep rock pools, 24 July 2003.

Two whole mounts, New Caledonia, Nouméa, Magenta, permanent pool near mangroves, on large algae covered with epiphytes, 22 August 2003.

Etymology: Dedicated to Dr Nikki Watson, Armidale, Australia, who assisted with the collection of material at Arrawarra.

Diagnosis: Trigonostomum species with copulatory organ 28–36 µm long. Stylet 29–41 µm long, proximally bent over 90°. Mantle with three spine-like plates surrounds only the distal part of the stylet. Bursal appendage 62–78 µm long, with two coiled (more than 360°) striated tubes.

SPECIES INQUIRENDAE

TRIGONOSTOMUM BRUNCHORSTI GRAFF, 1905

Trigonostomum brunchorsti Graff, 1905: 115–116, t. III, figs 24, 25; 1913: 311, figs 274, 275; Meixner, 1924b: 96, 98; Steinböck, 1932: 309.

Distribution: Norway (Graff, 1905), Greenland (Steinböck, 1932).

According to Graff's (1905, 1913) description, the overall morphology of the copulatory organ resembles that of *T. penicillatum*. The two plate-like structures differ somewhat in shape, ending both proximally as well as distally in a hook-like structure (see Graff, 1905: taf. 3, fig. 24). The bursal appendage is described as resembling that of *T. venenosum*. The position of the pharynx in the middle of the body is exceptional for a member of *Trigonostomum* and new material is needed to confirm the validity and/or the taxonomy of this species.

TRIGONOSTOMUM PIRIFORME (PEREYASLAWZEWA, 1893) GRAFF, 1905

Hyporhynchus piriformis Pereyaslawzewa, 1893: 266, t. 4, fig. 30.

Trigonostomum piriforme Graff, 1905: 115, t. III, figs 22,23; 1913: 310, fig. 272; Meixner, 1924b: 96, 99.

Distribution: Black Sea (Pereyaslawzewa, 1893; Graff, 1905)

According to Graff's (1905) drawings and description, the copulatory organ consists of three parallel plate-like structures, but without a central stylet. The bursal appendage is described as being identical with that of *T. penicillatum*. This species could be identical with *T. penicillatum*, but observations on new material are needed.

MARINELLIA LINGULIFERA RIEDL, 1954

Marinellia lingulifera Riedl, 1954: 223–231, figs 30–32.

Distribution: Mediterranean Sea (Riedl, 1954).

This species was considered by Riedl (1954) to be a close relative of *Trigonostomum*, mainly based on the presence of an antero-ventral invagination forming a kind of 'proboscis'. Other features in which *M. lingulifera* resembles *Trigonostomum* species are the pharynx, which is strongly inclined forwards and shows very strong external muscles and weak radial ones (Riedl, 1954: 227), the double connection in the female system (Riedl, 1954: fig. 31), the presence of a bursa (Riedl, 1954: fig. 31: rs) with a long and narrow bursal stalk, paired ovovitellaria and a bursal appendage that consists of two coiled tubes, fused at their base (Riedl, 1954: 225). Three other features of *M. lingulifera* are not found in any *Trigonostomum* species: the presence of a muscular tongue in front of the pharynx (Riedl, 1954: 227–228, fig. 31: z), a muscular septum connecting the invagination with the pharynx (Riedl, 1954: fig. 31: ms), and an unpaired seminal vesicle (Riedl, 1954: 226). Ax (1971) considered *M. lingulifera* to be the sister group of *Trigonostomum*, based only on the presence of the antero-ventral invagination. There is, however, no material of this species available and some of the observations, such as the unpaired seminal vesicle, the detailed structure of the copulatory organ and the invagination certainly need confirmation. In addition, the copulatory organ and the bursal appendage are insufficiently described and not even figured in the original description.

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