



Dalytyphloplanida (Platyhelminthes: Rhabdoceola) from Andalusia, Spain, with the description of four new species

NIELS VAN STEENKISTE¹, BART TESSENS, KATHLEEN KRZMARIC & TOM ARTOIS

Hasselt University, Centre for Environmental Sciences, Research Group Zoology: Biodiversity and Toxicology, Universitaire Campus Gebouw D, B-3590 Diepenbeek, Belgium

¹Corresponding author. E-mail: niels.vansteenkiste@uhasselt.be

Abstract

Nineteen taxa of Dalytyphloplanida Willems *et al.*, 2006 collected from southwestern Andalusia are discussed. Although most taxa were found in freshwater, three are marine, one occurred in brackish water and *Protoplanella simplex* Reisinger, 1924 was even collected in a dry, limnoterrestrial habitat. Four taxa are new to science. *Castrada purgatorialis* n. sp., *Castrada paradisea* n. sp. and *Strongylostoma devleeschouweri* n. sp., all belong to the Typhloplanidae Graff, 1905. The first two species differ from other species of *Castrada* Schmidt, 1861 by the presence of a large accessory bursa and the morphology of the copulatory atrium. *C. purgatorialis* n. sp. has zoochlorellae while these are lacking in *C. paradisea* n. sp. *Strongylostoma devleeschouweri* n. sp. is unique because of its coalescing testes and because of the presence of a sphincter around the stalk of the seminal receptacle. *Gieysztoria iberica* n. sp. belongs to the Dalyelliidae Graff, 1905 and is characterized by the extreme length of the girdle of the stylet. Except for five taxa, all specimens were collected within the boundaries of the Doñana National Park. Most of the taxa could easily be identified to species level except for one taxon of Kytorrhynchidae Rieger, 1974 and one species of *Phaenocora* Ehrenberg, 1836. Four species are new for the Iberian Peninsula. Three of these, *Trigonostomum penicillatum* (Schmidt, 1857) Micoletzky, 1910, *Promesostoma maculosum* Ax, 1956 and *Gieysztoria macrovariata* (Weise, 1942) Ruebush & Hayes, 1939, were already known from other European localities, whereas *Parapharyngiella involucrum* Willems *et al.*, 2005, a marine species, has previously only been found in Zanzibar, Tanzania.

Key words: turbellaria, Dalytyphloplanida, Palearctic, taxonomy, new species

Introduction

Rhabdoceola is one of the most species-rich groups of free-living flatworms. In freshwater about 50% of the free-living flatworms belong to this group (Schockaert *et al.* 2008). As opposed to Northern and Central Europe, most regions of Southern Europe have been undersampled. Although some work has been done on the rhabdoceol fauna of Spain, there is no information on many parts of this vast peninsula. Previous research mainly focussed on the region around Valencia (Gieysztor 1931), Extremadura (Noreña *et al.* 1999) and the central areas of Spain such as Castilla y León, Castilla-La Mancha and Madrid (Gamo 1987a, 1987b; Farías *et al.* 1995; Gamo & Noreña-Janssen 1998), as well as brackish habitats of the coastal areas of Atlantic Spain including Galicia, Principado de Asturias, Cantabria and País Vasco (Noreña *et al.* 2007). For continental Portugal, Andorra and Gibraltar, no records exist up to date.

Recent molecular research split the Rhabdoceola into two monophyletic sister-clades, the Kalyptorrhynchia Graff, 1905 and the Dalytyphloplanida Willems *et al.*, 2006. The latter clade consists of the “Dalyellioida” and “Typhloplanoida s.s.” of the old phylogenetic system of Ehlers (1985) (see Willems *et al.* 2006). In total, 103 species (43 genera) of rhabdoceols have been reported from the Iberian Peninsula (Noreña 1997–2008, web reference [1]; Noreña *et al.* 2007). Ninety two of these taxa belong to the Dalytyphloplanida.

In this contribution, an overview is given of the dalytyphloplanid fauna found during a four-week sampling campaign in southwestern Andalusia. Eighteen taxa are discussed, four of which are new to science. The sampling

mainly concentrated on freshwater fauna. Three taxa are marine, one occurred in brackish water and one species was even collected in a very dry, limnoterrestrial habitat. All known taxa could be identified to species level except for one taxon of Kytorrhynchidae Rieger, 1974 and one species of *Phaenocora* Ehrenberg, 1836.

Material and methods

The material was collected during a sampling campaign in March–April 2008 in Andalusia, southern Spain. Except for five taxa, all specimens were sampled within the boundaries of the Doñana National Park by Bart Tessens and Niels Van Steenkiste. Additional sampling localities include several intertidal rocky outcrops south of the National Park and some temporal cattle ponds and a dry mossy brook north of the Park.

Marine animals were extracted from the sediment and algae using the $MgCl_2$ decantation method, whereas freshwater animals were collected by the oxygen depletion method (see Schockaert 1996). The limnoterrestrial specimens of *Protoplanella simplex* Reisinger, 1924 were extracted using the Baermann pan method (see Townshend 1963). All specimens were studied and drawn alive. Of most species one or more specimens were whole-mounted with lactophenol. Specimens intended for sectioning were fixed in hot (50°C) Bouin's solution, embedded in paraffin, serially sectioned (4 µm sections), and stained with Heidenhain's iron haematoxylin, using erythrosin as counterstain. The positions 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).

Holotypes are deposited in the collections of the Museo Nacional de Ciencias Naturales, Madrid, Spain (MNCN). All other material, including paratypes, are deposited in the collections of the research group Zoology: Biodiversity and Toxicology of the Hasselt University, Belgium (HU).

Abbreviations used in the figures

ac: atrium copulatorium; b: bursa; ba: accessory bursa; bap: bursal appendage; bc: copulatory bursa; bca: bursal canal; bg: basophilic glands; bs: blind sac; bt: buccal tube; bv: vesicle with basophilic secretion; cga: common genital atrium; co: copulatory organ; de: ejaculatory duct; e: egg; ey: eye; fb: female bursa; fd: female duct; fg: female glands; gg: prostate glands; gp: gonopore; *j*: stylet tube; *k*: stylet protrusion; *l*: stylet mantle; ma: male atrium; np: nephridiopore; od: oviduct; ov: ovary; ovv: ovovitellarium; p: proboscis; pc: prepharyngeal cavity; ph: pharynx; rg: rhabdite glands; rs: seminal receptacle; seg: subepidermal glands; sph: sphincter; spt: spermatophore; st: stylet; t: testis; u: uterus; vd: vitelloduct; vdf: vas deferens; vi: vitellaria; vs: seminal vesicle; *x*: dorsal protrusion of blind sac; *y*: longer spines of blind sac.

Taxonomic account

Dalytyphloplanida Willems *et al.*, 2006

Trigonostomidae Graff, 1905

Parapharyngiella involucrum Willems *et al.*, 2005

(Figs. 1A–1D)

New locality. Doñana National Park, Provincia de Huelva, Spain (36°52'40"N, 6°22'03"W). Salinas de San Rafael: small algae in shallow, brackish pools of abandoned salt pans (25/03/2008).

Known distribution. Western Indian Ocean (Tanzania: Zanzibar) (Willems *et al.* 2005).

Material. Observations on a live animal that was subsequently whole-mounted. Type material from *Proxenetes mackfirae* Karling, 1978 (SMNH, no. 42498) and *Parapharyngiella involucrum* Willems *et al.*, 2005 (HU, nos. 281–283) for comparison.

Remarks. The animal is about 0.4–0.5 mm long. The pharynx is at 50–60% of the body length. The two testes lie anterolaterally from the pharynx. The genital system is situated in the caudal body half.

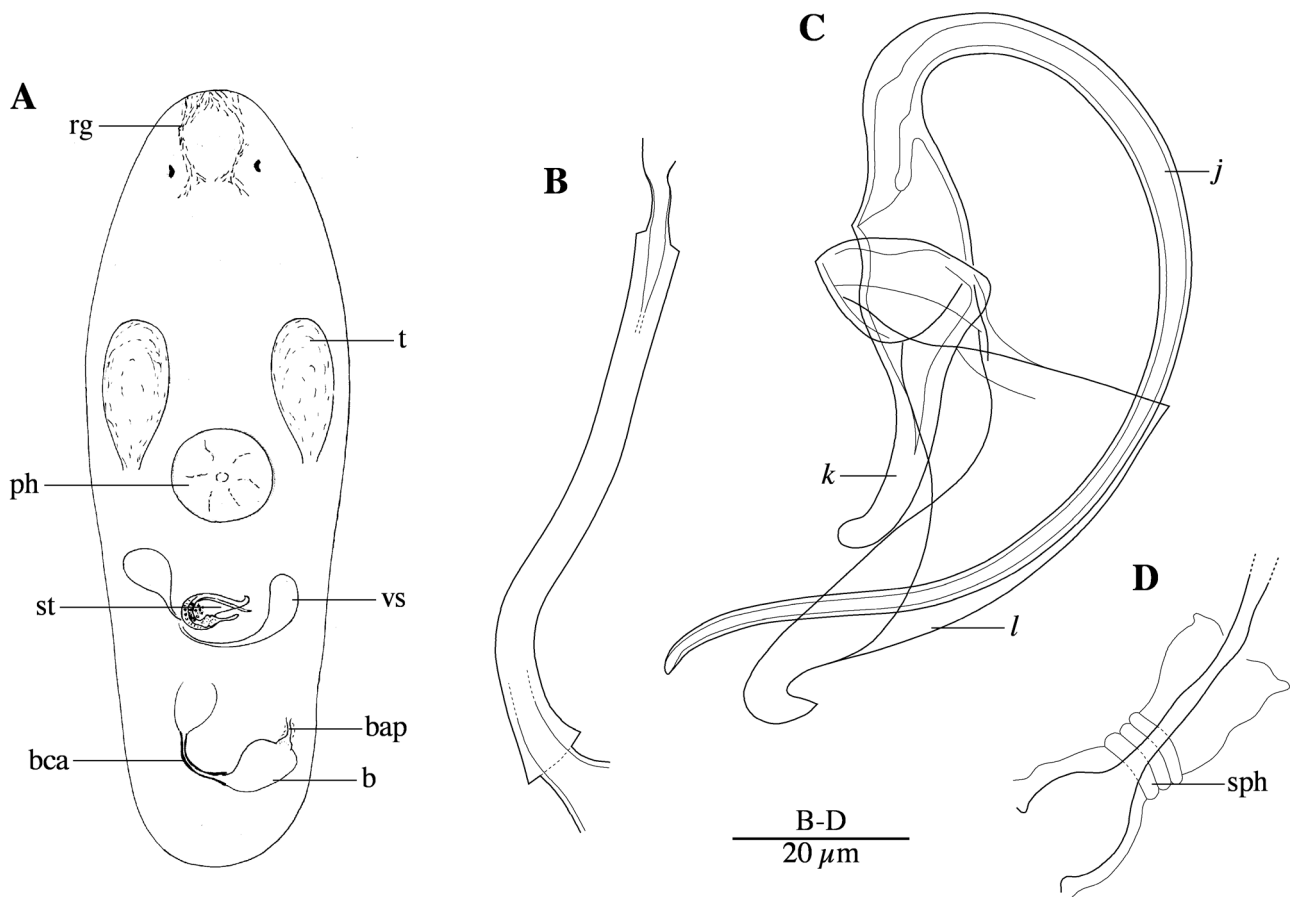


FIGURE 1. *Parapharyngiella involucrum* Willems *et al.*, 2005 (A) Habitus from a live animal. (B) Bursal canal. (C) Stylet. (D) Bursal appendage.

The stylet (Fig. 1C) is almost identical to that of the specimens from Zanzibar. It measures about 30 μm at its widest and is 60 μm long. It consists of a semicircular tube with a funnel-shaped base and a curved distal point (*j*); a curved, slender protrusion with a bluntly-rounded distal end (*k*); a mantle with a straight proximal rim and a distal hook encompassing the distal half of the semicircular tube (*l*).

The bursal canal (Fig. 1B) (bursal stalk in Willems *et al.* 2005) is sclerotized and about 52 μm long. It seems to connect the male or common genital atrium with the bursa. When entering the bursa it broadens to become slightly funnel-shaped. The bursal appendage (Fig. 1D) is not clearly visible in the whole mount. It is about 30 μm long and seems to consist of a pyriform to club-shaped proximal part, 10 μm long originating on the bursa, and a slender distal tube of 20 μm . Both parts appear to be separated by a sphincter. The tubular part seems provided with a very thick tissue, of which the exact origin could not be determined. It could not be seen whether it connects the bursa to the female duct as described by Willems *et al.* (2005) or not.

Discussion. When considering the different structures of the genital system visible in the live specimen and the whole mount, the Spanish specimen agrees with those from Zanzibar. *Parapharyngiella involucrum* is a monotypic taxon within the Trigonostomidae Graff, 1905. The stylet, although slightly smaller and with a less slender distal hook than in the animals from Zanzibar ($\pm 50 \mu\text{m}$ long), is almost identical to that of the Zanzibar specimens (see Willems *et al.* 2005). Both populations have a sclerotized bursal canal between the male or common genital atrium and the bursa, and a slender tubiform bursal appendage with a club-shaped base. In the Tanzanian specimens the latter tube connects the bursa with a sperm-containing vesicle on the female duct, but this could not be seen in the animal from Spain.

One difference concerns the position of the pharynx and the genital organs. While all reproductive structures of the East African specimens are located just behind the pharynx (which is situated in the first body half), male and female organs of the Andalusian specimen occupy a large fraction of the caudal body half behind the centrally-located pharynx. Despite this difference and awaiting the availability of new material, we prefer to preliminarily assign the specimen from Spain to *P. involucrum*.

The stylet is also very similar to that of *Proxenetes mackfirae* from Bermuda (see Karling 1978). Although the stylet of this taxon is somewhat larger (70–100 µm), it also consists of a semicircular tube and a slender hooked mantel, a feature unique within *Proxenetes* Jensen, 1878. Obvious differences distinguish *P. mackfirae* from *Parapharyngiella involucrium*. Compared with the protrusion of the stylet of *P. involucrium* (*k* in Fig. 1C), the protrusion of *P. mackfirae* is longer, more pointed and connected with a cup-shaped membrane with its distal border cut out in a right angle. This membrane is lacking in *P. involucrium*. Minor differences are to be found in a longer bursal canal (± 80 µm) in *P. mackfirae* and the bursal appendage that seems to lack a thickened wall in the species from Bermuda. Although the construction of the stylet and the presence of a tubular bursal canal (internal vagina in Karling 1978) and a funnel-shaped, double-barrelled bursal appendage as described above, seem clear indications of its kinship with *Parapharyngiella*, we refrain from transferring *P. mackfirae* to this taxon because the female system of this species has not been described.

***Trigonostomum penicillatum* (Schmidt, 1857) Micoletzky, 1910**

(Figs. 2A–2B)

syn. *Vortex penicillatus* Schmidt, 1857

syn. *Hyporhynchus penicillatus* Diesing, 1862

syn. *Trigonostomum intermedium* nomen nudum Graff, 1910

syn. *Trigonostomum marki* Graff, 1911

New locality. Rota, Provincia de Cádiz, Spain (36°38'09"N, 6°23'50"W). Los Corrales: small algae in intertidal pools on a rocky cape (11/04/2008).

Known distribution. Northeast Atlantic: European Atlantic coast; Mediterranean Sea; Northwest Atlantic: North American Atlantic coast (see Willems *et al.* 2004 for a complete overview).

Material. Observations on a live animal. One whole mount.

Remarks. The studied specimen undoubtedly belongs to the taxon *Trigonostomum* Schmidt, 1852 when considering the construction of the stylet and the bursal appendage. It can easily be recognized as *Trigonostomum penicillatum* (Schmidt, 1857) Micoletzky, 1910 because the stylet is proximally bent over 90° (Fig. 2A) and the bursal appendage has a proximal barrel-like casing and a number of tubules, diverging distally (Fig. 2B) (for a review and identification key of all species of *Trigonostomum*, see Willems *et al.* 2004). The stylet from the Spanish specimen measures 53 µm (measured axially), while the bursal appendage has a length of 72 µm. Compared to the size-ranges given by Willems *et al.* (2004) (stylet: 44–53 µm; bursal appendage: 60–70 µm), the stylet and bursal appendage from the Spanish specimen are among the largest found in this species.

Promesostomidae Den Hartog, 1964

***Promesostoma maculosum* Ax, 1956**

(Fig. 2C)

New locality. Rota, Provincia de Cádiz, Spain (36°38'09"N, 6°23'50"W). Los Corrales: thin layer of very coarse sand in intertidal pools on a rocky cape (11/04/2008).

Known distribution. Northeast Atlantic: European Atlantic coast (Ax 1956; Ehlers & Sopott-Ehlers 1989); Bosphorus and Sea of Marmara (Ax 1959); Mediterranean: Corsica and Sardinia (Willems 2005 and pers. comm. from Wim Willems).

Material. Several individuals studied alive. Five whole mounts.

Remarks. Animals are between 0.8–2 mm (\bar{x} = 1.2 mm; *n* = 4) long. This species can easily be distinguished from other species of *Promesostoma* Graff, 1882 because the stylet is curled over 360° in the middle (Fig. 2C). The stylet of the Spanish specimens is between 364–396 µm long (\bar{x} = 383 µm; *n* = 5), which is longer than in specimens from other known localities (± 250 µm in the specimens from the French Atlantic coast, Ax 1956; ± 290 µm in the specimens from Corsica, Willems 2005; no measurements given for the specimens from the Eastern Mediter-

ranean, Ax 1959). Its new intermediate location in southern Spain suggests this animal is probably widespread throughout the Mediterranean and Atlantic coast of southwestern Europe.

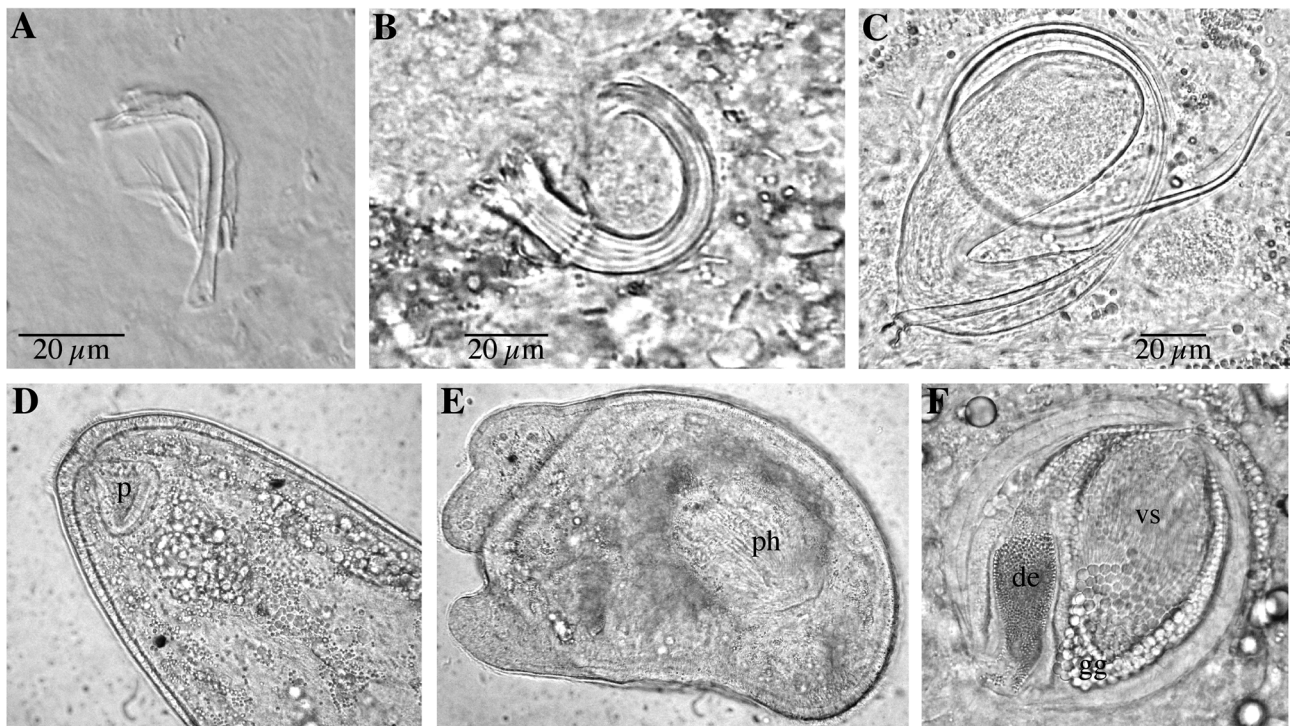


FIGURE 2. *Trigonostomum penicillatum* (Schmidt, 1857) Micoletzky, 1910 (A) Stylet from the whole mount. (B) Bursal appendage from a live animal. *Promesostoma maculosum* Ax, 1956 (C) Stylet and copulatory organ from a live animal. *Kytorrhynchidarum* sp. (D) Head region. *Phaenocora* sp.? Ehrenberg, 1836 (E) Live animal. *Strongylostoma elongatum* Hofsten, 1907 (F) Copulatory organ from a live animal.

Kytorhynchidae Rieger, 1974

Kytorrhynchidarum sp.

(Fig. 2D)

Locality. Rota, Provincia de Cádiz, Spain (36°38'09"N, 6°23'50"W). Los Corrales: thin layer of very coarse sand in intertidal pools on a rocky cape (11/04/2008).

Material. Observations on a live animal and one serially-sectioned specimen of poor quality, probably a young animal.

Remarks. The animal has two lateral eyes and the typical proboscis-like anterior invagination diagnostic for Kytorhynchidae Rieger, 1974 (Fig. 2D). Behind the eyes, two oblong structures, probably the testes, stretch caudally. The pharynx is situated in the caudal body half.

Because neither the observations on the live animal, nor the serially-sectioned specimen revealed much about its internal structures, it is impossible to identify these specimens.

Kytorhynchidae is a peculiar and rare taxon, traditionally placed in the non-kalyptorhynch rhabdocoels. Kytorhynchidae have only been recorded from the Atlantic and Pacific coast of North America (North Carolina: Rieger 1974; California: pers. comm. from Karling in Rieger 1974), the Caribbean Sea (Florida Keys: Rieger 1974), Bermuda (Rieger 1974), the Galapagos Islands (Ehlers & Ehlers 1981), the Hawaiian Islands (own unpublished data), the Skagerrak (record from Karling in Rieger 1974), the North Sea (Sylt: pers. comm. from Ehlers in Schockaert & Martens 1985; Belgian Continental Shelf: own unpublished records), Sardinia (pers. comm. from Christopher Laumer, Ernest Schockaert and Wim Willems) and Somalia (Schockaert & Martens 1985), making the record from Spain the fifth locality in Europe. However, as for the specimens from Andalusia, none of the other animals found along the European or African coasts yielded a positive identification.

Typhloplanidae Graff, 1905

Protoplanellinae Reisinger, 1924

Protoplanella simplex Reisinger, 1924

(Fig. 3)

New locality. La Puebla del Rio, Provincia de Sevilla, Spain (37°13'39"N, 6°10'52"W). Area recreativa Pozo de los Conejos along road A3114 from La Puebla del Rio to Aznalcazar: mosses on bank of dried up temporal brook in open coniferous forest (21/03/2008).

Other localities in Spain. Central areas (Sierra de Guadarrama and river Tajo basin; see Gamo & Noreña-Janssen 1998).

Known distribution. Palearctic: Northern Europe (Finland) (Luther 1963) and Central Europe (Austria: Eastern Alps) (Reisinger 1924, 1954; An der Lan & Franz 1954; An der Lan 1963).

Material. One drawing of a live animal and two serially-sectioned specimens.

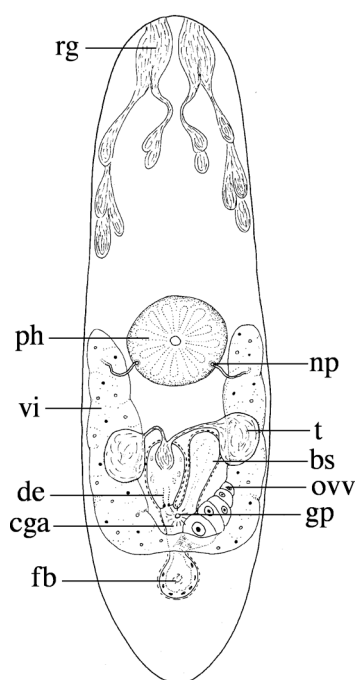


FIGURE 3. *Protoplanella simplex* Reisinger, 1924. Habitus based on observations on live animals and serial sections.

Remarks. As is also the case for other representatives of Protoplanellinae Reisinger, 1924, *Protoplanella simplex* Reisinger, 1924 is difficult to identify (for a recent discussion on Protoplanellinae, see Van Steenkiste *et al.* 2010). Not many accounts of this species are known from the literature (Reisinger 1924, 1954; An der Lan & Franz 1954; Luther 1963; Gamo & Noreña-Janssen 1998). Therefore a more detailed description and discussion is provided here.

At 0.4 mm long (measured on the serial sections), the animals from Andalusia are relatively small when compared to other populations (0.8–0.9 mm for Central and Northern European populations; see Reisinger 1924 and Luther 1963). The ciliated epidermis is cellular and its apical end is darkly stained.

The first third of the body is filled with two bundles of massive rhabdite glands, almost entirely encompassing the brain. The rhabdites are oblong, but seem to be variable in shape. The proximal parts of the gland cells are clearly visible as basophilic cells containing packages of rhabdites. Only adenal rhabdites are present.

The mouth is situated at about 50–55%. The pharynx rosulatus is typical of Typhloplanidae and has a central position. Two separate nephridiopores open on the ventral body surface slightly caudally to the mouth. The gonopore lies at 70%.

The paired, globular testes lie laterally behind the pharynx, ventrally to the vitellaria. Between the testes, an oviform copulatory organ provided with circular muscles is present. Proximally it contains a great amount of sperm, while distally the faint contours of a muscular ejaculatory duct were visible. The copulatory organ enters the common genital atrium dorsally. Rostral to the copulatory organ, the common genital atrium enlarges significantly. This sack-like protrusion (bs in Fig. 3) is provided with well-developed, circular muscles, as is the common genital atrium.

The female system is relatively simple. Paired vitellaria stretch dorsolaterally at both sides up to the frontal part of the pharynx. At the caudal end of the left vitellarium is an ovary, which is partly embedded in this vitellarium, thus forming an ovovitellarium. The oviduct merges with a spherical female bursa with a relatively thick epithelium. The female bursa contains remnants of (disintegrated) sperm. Both the epithelium of the oviduct and the proximal part of the female bursa contain a large number of cell nuclei. The female duct (ductus communis in Reisinger 1924) is surrounded by circular muscles and enters the common genital atrium caudally. Eosinophilic glands surround the oviduct, but their exact entry position could not be determined. An uterus is absent.

Discussion. The specimens from Spain can be placed in the taxon *Protoplanella* Reisinger, 1924, because they have all diagnostic features of this taxon: adenal rhabdites in the rod tracks, a typical pharynx rosulatus, a muscular ejaculatory duct and the presence of an ovovitellarium. At present *Protoplanella* contains two species: *P. simplex* and *P. macrorhabdiphora* An der Lan, 1955. However, as stated by An der Lan (1955), the position of *P. macrorhabdiphora* is highly questionable since the construction of the genital system was not clear. Therefore *P. simplex* remains the only certain representative of *Protoplanella*.

Protoplanella strongly resembles another monotypic taxon within the Protoplanellinae, i.e. *Olisthanellinella* Reisinger, 1924 (*O. rotundula* Reisinger, 1924), but the latter taxon has a separate ovary and vitellaria. Luther (1963) also refers to the position of the testes as being a valuable field character in discerning *Protoplanella* from *Olisthanellinella*, although this is not mentioned by Reisinger (1924). In the taxon *Protoplanella* the testes are situated behind the pharynx, while the testes of *O. rotundula* lie next to or in front of the pharynx.

Despite their small size, the Spanish specimens can be placed within *Protoplanella simplex* because they share all diagnostic characters. In addition, Reisinger (1924) describes the female bursa as a seminal receptacle. We prefer to describe it as a female bursa because it is relatively thick-walled and contains disintegrated sperm. Many older authors denote the female duct in Typhloplanidae as a ductus communis (e.g. Graff 1882; Sekera 1912; Dorner 1902; Findenegg 1930; Luther 1963). In more recent taxonomic accounts on Typhloplanidae, the terms ductus communis (e.g. Gamo & Schwank 1987; Müller & Faubel 1993; Noreña *et al.* 1999), female common duct (e.g. Kolasa & Schwartz 1988), female duct (e.g. Artois *et al.* 2004; Willems *et al.* 2005) and female canal (e.g. Noreña-Janssen 1995) are used to describe the distal part of the female genital system, while Noreña and Faubel (1992) consider the female duct as the collective name for the germarium (ovary), oviduct, seminal receptacle and distal ductus communis in their review on the Mesostominae. We prefer to use the term female duct to avoid confusion with other ducts in the genital system and to stress its presence in the female system.

Finally we would like to remark that the specimens were sampled in spring when the area regularly receives rainfall. During summer (June to September), this area is prone to long periods of drought, suggesting this species might be anhydrobiotic (see Van Steenkiste *et al.* 2010).

Phaenocorinae Wahl, 1910

Phaenocora sp.? Ehrenberg, 1836

(Fig. 2E)

Locality. Doñana National Park, Provincia de Huelva, Spain (36°54'50"N, 6°17'48"W). La Montaña del Rio: green algae in shallow brackish pool (06/04/2008).

Material. Two drawings of live animals. One whole mount and three serially-sectioned specimens, two of poor quality and one juvenile.

Remarks. The frontal position of the barrel-shaped, obliquely forward-slanting pharynx, the crenulate posterior end of the body and the separate openings of the protonephridia indicate that this species probably belongs to the taxon *Phaenocora* Ehrenberg, 1836 (Phaenocorinae Wahl, 1910). Since the genital system could not be observed, a definite identification was impossible.

Mesostominae Ehrenberg, 1836

Mesostoma lingua (Abildgaard, 1789) Graff, 1882

syn. *Planaria lingua* Abildgaard, 1789
syn. *Planaria ehrenbergii* Focke, 1836
syn. *Mesostomum lingua* Schmidt, 1848
syn. *Turbella cyathus* Diesing, 1862
syn. *Turbella lingua* Diesing, 1862
syn. *Mesostoma cyathus* Schmidt, 1858
syn. *Mesostoma chromobactrum* Braun, 1885
syn. *Mesostoma cyanthus* Dörner, 1902
syn. *Mesostoma sigmoideum* Plotnikow, 1905

New locality in Spain. Doñana National Park, Provincia de Huelva, Spain (36°57'28"N, 6°26'59"W). Laguna del Sopeton near Casa del Puntal: large open pond with many filiform algae and zooplankton (mainly *Daphnia* sp.) (25/03/2008).

Other localities in Spain. Central areas (Sierra de Guadarrama and river Tajo basin, see Gamo & Noreña-Janssen 1998); Alburquerque (Provincia de Badajoz, Extremadura) and Cáceres (Provincia de Cáceres, Extremadura) (Noreña *et al.* 1999); Pla, Valencia (Provincia de Valencia, Comunidad Valenciana) and Almenara (Provincia de Castellón, Comunidad Valenciana) (Gieysztor 1931).

New localities outside Spain. Palearctic: Département du Var, Provence-Alpes-Côte d'Azur, France. Dry mud from a temporal pond provided by Dr. Alain Thiéry (09/2007) and hatched at Hasselt University (Belgium) (10/2007).

Nearctic: Cootes Paradise, Hamilton, Ontario, Canada (43°16'01"N, 79°55'54"W). Submersed and floating aquatic vegetation in a ditch adjacent to Spencer Creek (14/05/2009).

Known distribution. Widespread throughout the Palearctic: many localities in Europe, Western Russia, Siberia, Central Asia, Western Tibet and Japan (see Luther 1963 and Heitkamp & Schrade-Mock 1978 for localities and references), Western Europe (UK: West Midlands and North Wales; the Netherlands: Friesland) (Young 1970, 1972a, 1973), Central Europe (Germany: Thuringia, Lake Constance, Franconia, South Lower Saxony; Austria: Burgenland) (Kraus 1965; Pörner 1966; Rixen 1968; Bauchhenss 1971; Heitkamp 1981, 1982, 1988), Eastern Europe (Romania: Wallachian Plain, littoral freshwater lakes of the Black Sea, Danube Delta) (Mack-Fira 1968, 1970b), Western Russia (Yaroslavl Oblast, Urals, Northern Dvina River and upper Volga River) (Birstein 1991; Rogozin 1996; Korgina 1999, 2002; Kotikova 2001), Siberia and the Russian Far East (Rogozin 1996), North Africa (Algeria) (Gauthier 1929; Schrade 1974); Nearctic: Greenland (Steinböck 1932); Afrotropic: many localities in East Africa (Kenya, Tanzania and Uganda) (see Beauchamp 1953; Young 1976; Young & Young 1976); Neotropic: Argentina (Noreña-Janssen 1995).

Material. Many live animals and serially-sectioned specimens from the new locality in Spain. Studies on live animals from France and several sectioned specimens from Canada.

Remarks. Adult specimens were highly variable in length (most between 2 and 5 mm) and were milky white to pink. Body shape is bluntly rounded anteriorly and somewhat bluntly pointed posteriorly. Eggs were present on both sides of the body. Internal organization as described by several authors (e.g. Luther 1963; Noreña-Janssen & Faubel 1992).

Mesostoma lingua (Abildgaard, 1789) Graff, 1882 was captured with a small plankton net pulled through algae and vegetation, and was very abundant (more than 50 individuals in three throws). It seems to be a widespread species (Palearctic, Nearctic, Neotropic, Afrotropic), although records from the Oriental, Australasian, Pacific and Antarctic regions are presently lacking (see Noreña-Janssen & Faubel 1992; Noreña-Janssen 1995).

Rhynchomesostominae Bresslau, 1933

Rhynchomesostoma rostratum (Müller, 1774) Luther, 1904

syn. *Fasciola rostrata* Müller, 1774
syn. *Planaria rostrata* Abildgaard, 1789

syn. *Planaria velox* Dalyell, 1814
syn. *Derostoma rostratum* Dugès, 1830
syn. *Mesostoma rostratum* Ehrenberg, 1836
syn. *Dalyellia velox* Johnston, 1846
syn. *Mesostomum rostratum* Schmidt, 1848
syn. *Mesostomum wandae* Schmidt, 1858
syn. *Turbella rostrata* Diesing, 1862
syn. *Turbella wandae* Diesing, 1862
syn. *Mesostomum variabile* Weismann, 1864
syn. *Mesostomum montanum* Graff, 1875

New locality in Spain. Doñana National Park, Provincia de Huelva, Spain (36°58'50"N, 6°29'11"W). Laguna Dulce: swamp vegetation on the northern edge of the lake (19/03/2008).

Other localities in Spain. Central areas (Sierra de Guadarrama and river Tajo basin, see Gamo & Noreña-Janssen 1998); Alcalá de Henares (Provincia de Madrid, Comunidad de Madrid) (Gamo 1987a); Beleña and Algora (Provincia de Guadalajara, Castilla-La Mancha), Cantalejo (Provincia de Segovia, Castilla y León) and Naval-uenga (Provincia de Avila, Castilla y León) (Fariás *et al.* 1995); Alburquerque (Provincia de Badajoz, Extremadura) and Cáceres (Provincia de Cáceres, Extremadura) (Noreña *et al.* 1999).

New localities outside Spain. Palearctic: Hamme, East Flanders, Belgium (51°06'29"N, 04°10'14"E). Bunt: organic material and aquatic vegetation from a shallow pool in a tidal freshwater marsh of the Scheldt (29/04/2009).

Zonhoven, Limburg, Belgium (50°58'16"N, 05°20'13"E). Platweyers: aquatic vegetation and leaf litter in a shallow marsh (06/05/2009).

Kalmthout, Antwerp, Belgium (51°22'49"N, 04°26'12"E). Kalmthoutse Heide: grasses and floating vegetation in a shallow part of the moorland pool "Putse Moer" (25/05/2009).

Sölktaier Nature Park, Schladminger Tauern, Niedere Tauern, Styria, Austria (47°17'42"N, 13°52'31"E, alt. 1222 m). Schwarzensee near Kleinsölk: aquatic vegetation and sedges in a pool filling a small depression in the coniferous forests north of the Schwarzensee (27/06/2009).

Bavarian Forest National Park, Bavaria, Germany (48°57'56"N, 13°35'16"E, alt. 1150 m). Border crossing with the Czech Republic near Finsterau: aquatic vegetation in *Sphagnum* bog along a mountain stream (02/07/2009).

Longskär, Raseborg, Uusimaa, Finland (59°49'09"N, 23°15'36"E). Plants and moss from freshwater lake (07/08/2008).

Oriental: Bicholim, Goa, India (15°34'33"N, 73°56'32"E). Mayem Lake: rich submersed aquatic vegetation in an eastern inlet of the lake (01/12/2008).

Nearctic: Wheeler National Wildlife Refuge, Decatur, Alabama, USA (34°33'17"N, 86°57'17"W). Crabtree Slough: impoundment with submerged aquatic vegetation (*Myriophyllum spicatum*) along the Tennessee River (23/05/2009).

Known distribution. Widespread throughout the Palearctic: many localities in Europe, Western Russia, Central Asia, Siberia, the Russian Far East, Japan (see Luther 1963 for localities and references), Western Europe (UK: South East England, West Midlands and North Wales) (Young 1970, 1973), Central Europe (Germany: Thuringia, Franconia, South Lower Saxony; Austria: Burgenland) (Kraus 1965; Pörner 1966; Kaiser 1967; Bauchhenss 1971; Heitkamp 1981, 1982), Eastern Europe (Romania: floodplain of the Danube, Wallachian Plain; Poland: Greater Poland Province) (Mack-Fira 1968; Kolasa 1974), Western Russia (Yaroslavl Oblast, Urals, upper Volga River) (Birstein 1991; Rogozin 1996; Kotikova 2001; Korgina 2002), the Caucasus (Georgia: Tbilisi) (Graff 1913), Siberia and the Russian Far East (Rogozin 1996); Nearctic: Greenland and the USA (New York, Virginia, Idaho, Mississippi basin, Wisconsin) (see Luther 1963 and Watermolen 2005 for localities and references); Afrotropic: East Africa (Kenya: Central Province) (Young 1976; Young & Young 1976); Oriental: Taiwan (Okugawa 1953) and Sri Lanka? (this record is questioned by Graff 1913).

Material. Observations on one live animal from the new locality in Spain. Studies on several live specimens from the other new localities and two whole mounts from Belgium.

***Castrada purgatorialis* n. sp.**

(Figs. 4A–4B)

Locality. Doñana National Park, Provincia de Huelva, Spain (37°04'23"N, 6°22'28"W). Laguna de la FAO: permanent water body with submersed vegetation (05/04/2008) (type locality).

Material. Observations on several live animals. Two whole mounts, both designated as paratypes (HU, nos. 394–395) and one serially-sectioned specimen, designated as the holotype (MNCN, no. 4.01/53).

Etymology. The species epithet refers to its morphological resemblance to *C. infernalis* Papi, 1951. Purgatorio (Italian; Lat.: *Purgatorium*) and Inferno (Italian; Lat.: *Infernum*) are two of the three canticas of Dante's Divine Comedy.

Description. Animals are about 1.2–1.3 mm long, lanceolate with a more bluntly-rounded front end and without eyes. Rostrally, rhabdite glands containing small, elongated rhabdites are present. Zoochlorellae dispersed throughout the whole body give the animal a bright green colour. A maximum of seven brown eggs were observed inside the specimens.

The cellular epidermis is about 5 µm thick with 4 µm-long cilia. Dermal rhabdites have not been observed.

The pharynx rosulatus contains eosinophilic and basophilic glands and is situated in the first body half between 25–40% (ph in Fig. 4A). Similarly to other species of *Castrada* Schmidt, 1861, the prepharyngeal cavity is separated from the buccal tube by a sphincter (see Luther 1946, 1963; Papi 1959). This buccal tube (bt in Fig. 4B) is lined with a ciliated and nucleated epithelium not differing from the body epithelium. Proximally, it receives the protonephridial ducts to form the excretory cup. A second sphincter around the mouth surrounds the buccal tube distally.

The paired, globular testes are rather small and lie in front of the pharynx, ventral to the vitellaria. Vasa deferentia and extracapsular seminal vesicles have not been observed in live specimens, nor in the serial sections. The construction of the male genital system is characteristic for the taxon *Castrada*: atrium copulatorium receiving a copulatory bursa, the copulatory bulb and a blind sac with spines. The copulatory bulb is oviform and apparently surrounded by two spiral muscle layers. In live specimens two types of prostate glands could be seen entering the copulatory bulb proximally, completely filling it with two different coarse-grained secretions. These could not be retrieved in the serial sections. Distally, the copulatory bulb contains the sclerotized and funnel-shaped ejaculatory duct, which opens into a small, muscular male genital atrium. A strong sphincter surrounds the distal part of the ejaculatory duct. Dorsal to the copulatory bulb, a relatively large, dual blind sac surrounded by circular muscles and provided with numerous spines, enters the atrium copulatorium. Although slightly variable, most spines are of equal size except for two regions with conspicuously larger spines. In a dorsal protrusion of the sac (*x* in Fig. 4B), a group of very long spines, measuring ± 18 µm up to 22 µm maximum, contrasts with the other spines of the blind sac. The average length of the small spines is about 3–4 µm. In the other part of the blind sac, closer to the copulatory bulb, another group of longer spines with a maximum length of 12 µm is present (*y* in Fig. 4B). All have a broad base and many of the small spines have a bent tip. Ventral to the copulatory bulb, the atrium copulatorium receives the copulatory bursa. A bursal stalk is absent. The proximal two thirds of the low bursal epithelium bears small spines (± 1.5 µm) becoming slightly larger in the most proximal part (± 2 µm), but still clearly smaller than those of the blind sac. The whole copulatory bursa is provided with a well-developed circular muscle layer. The atrium copulatorium is relatively large and has a low epithelium without nuclei. On its caudal wall, where the blind sac enters, a field of tiny sclerotized spines (size less than 1 µm) appears to be present. The atrium copulatorium has strong circular muscles and is separated from the common genital atrium by a large sphincter. The entire male genital system consisting of the spined blind sac, the copulatory bulb and the copulatory bursa, is surrounded by a muscular septum.

The single ovary lies caudal from the male genital system. The oviduct protrudes distally to form the seminal receptacle. This seminal receptacle consists of a number of large, nucleated cells. Neither a lumen nor sperm were observed. Before the oviduct and the seminal receptacle enter the female duct, the vitelloduct joins the female system. The vitellaria stretch dorsolaterally at both sides beyond the pharynx. The female duct is lined with a high, nucleated epithelium and provided with circular muscles. Ventrally, it receives eosinophilic female glands. The female duct enters the common genital atrium caudally. The latter has a high, nucleated epithelium with cilia, very similar to the body epithelium, and is also surrounded by a circular muscle layer.

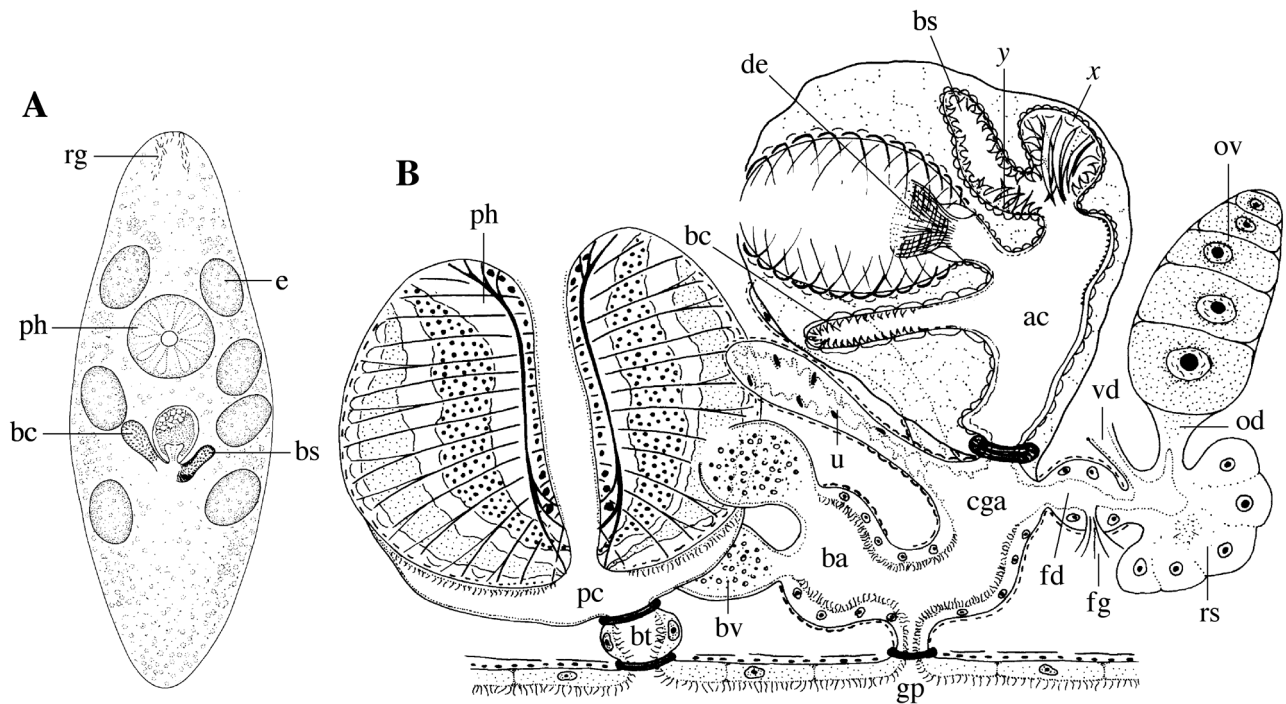


FIGURE 4. *Castrada purgatorialis* n. sp. (A) Habitus from a live animal. (B) Reconstruction of the atrial organs from the left hand side.

The same ciliated epithelium and muscle layer continue in a large accessory bursa, which enters the common genital atrium from the rostral side. Proximally this bursa receives two large vesicles filled with a basophilic, granular secretion of which the origin and function remain unknown. Paired uteri with a rather high, degenerated epithelium enter the common genital atrium just rostrally from the atrium copulatorium. Up to seven eggs have been observed in the animal.

Diagnosis. Species of *Castrada* with zoochlorellae, a spined copulatory bursa, an atrium copulatorium with a large blind sac armed with small spines (3–4 μm) and two fields of large slender spines (± 12 and $20 \mu\text{m}$ respectively). Ejaculatory duct a simple, sclerotized funnel. Large accessory bursa with two vesicles filled with glandular secretion.

Discussion. See the discussion following the remarks on *C. infernalis* Papi, 1951.

Castrada paradisea n. sp.

(Figs. 5A–5B)

Locality. Doñana National Park, Provincia de Huelva, Spain (37°04'23"N, 6°22'28"W). Laguna de la FAO: permanent water body with submersed vegetation (05/04/2008) (type locality).

Material. Observations on several live animals. Four serially-sectioned specimens, one of which designated holotype (MNCN, no. 4.01/54), and eight whole mounts, five of which designated paratype (HU, nos. 396–399; 422).

Etymology. The species name refers to the third cantica of Dante's Divine Comedy: Paradiso (Italian; Lat.: *Paradisum*).

Description. Animals have an average length of 0.8 mm and are lanceolate with bluntly-rounded frontal and caudal ends. Eyes are lacking. All specimens are a dull white colour and most have faint red spots. Zoochlorellae are absent. Adenal rhabdite glands with small, elongated rhabdites fill the body anterior to the pharynx. Basophilic glands, not observed in live animals, but conspicuously present in the serial sections, are interspaced between the rhabdite glands. In one specimen, two brown eggs were observed caudo-laterally to the pharynx.

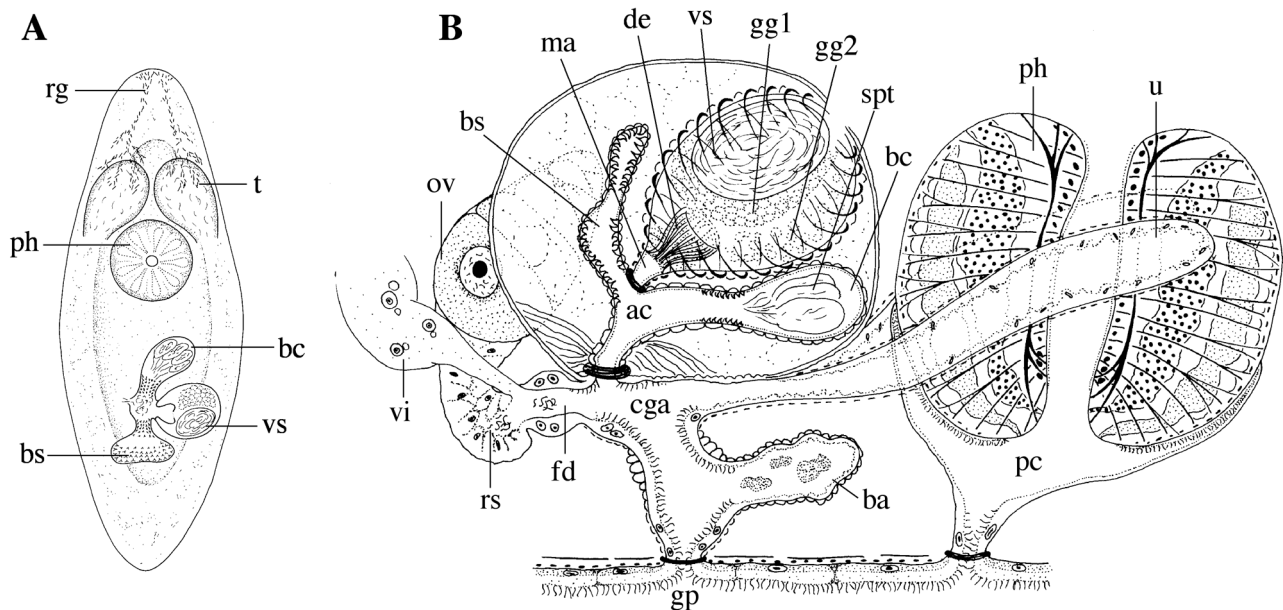


FIGURE 5. *Castrada paradisea* n. sp. (A) Habitus from a live animal. (B) Reconstruction of the atrial organs from the right hand side.

The ciliated epidermis is cellular and is 5–6 μm thick. Cilia are about 6 μm long. As in many other species of *Castrada*, the epidermal cells consist of a basal, more darkly-stained part containing the nuclei, and an apical more weakly-coloured part (e.g. Luther 1946; Willems *et al.* 2005). Dermal rhabdites have not been observed.

The pharynx rosulatus is identical with that of most other species of *Castrada* (see Luther 1904, 1963). Nephridiopores are combined with the buccal tube.

The paired, globular to club-shaped testes lie anterior to the pharynx. The overall organization of the male genital system is similar to that of *Castrada purgatorialis* n. sp. The copulatory bulb is oviform, contains two types of coarse-grained prostate secretion and is provided with two spirally-running muscle layers. The sclerotized, funnel-shaped ejaculatory duct apparently lacks a distal sphincter and enters a narrow male atrium, which enters the atrium copulatorium through a weak sphincter. The large blind sac and the caudal wall of the atrium copulatorium are armed with numerous, relatively small spines of equal size (around 4–5 μm). A small, central part without spines divides the blind sac into a distal and a proximal part. The copulatory bursa only bears spines on its relatively wide, distal part, while the proximal part is filled with several bean-shaped spermatophores. The atrium copulatorium, blind sac and copulatory bursa are all lined with a low, anucleated epithelium and surrounded by well-developed circular muscles. A muscular septum surrounds all male organs (copulatory organ, atrium copulatorium with blind sac and copulatory bursa). The atrium copulatorium enters the common genital atrium through a large sphincter. The common genital atrium is lined with a high, nucleated and ciliated epithelium.

The female system is similar to that of *C. purgatorialis* n. sp. However, the distinction between oviduct and the cellular seminal receptacle is less clear in *C. paradisea* n. sp. Whether female glands are present or not, is not fully clear in the sections.

In contrast with the conspicuous accessory bursa of *C. purgatorialis* n. sp., the accessory bursa of this species is a relatively simple but large, rostral protrusion of the common genital atrium. Its epithelium is low, anucleated and has no cilia. The paired uteri stretch laterally on both sides of the pharynx.

Diagnosis. Species of *Castrada* without zoochlorellae, with a copulatory bursa with spined stalk, containing spermatophores, and an atrium copulatorium with a large blind sac armed with uniform small spines (4–5 μm). Ejaculatory duct a simple, sclerotized funnel. Large accessory bursa a simple protrusion of the common genital atrium.

Discussion. See the discussion following the remarks on *C. infernalis* Papi, 1951.

Castrada infernalis Papi, 1951

New locality. Doñana National Park, Provincia de Huelva, Spain (36°49'27"N, 6°21'40"W). Llanos del Taraje near Ecomuseo Robledo de la Plancha: muddy temporal pond with *Ranunculus aquatilis* and sedges (25/03/2008).

Other localities in Spain. Central areas (Sierra de Guadarrama and river Tajo basin, see Gamo & Noreña-Janssen 1998); Congostrina (Provincia de Guadalajara, Castilla-La Mancha) (Gamo 1987b), Beleña lagoons (Provincia de Guadalajara, Castilla-La Mancha) (Gamo & Schwank 1987), Albuquerque (Provincia de Badajoz, Extremadura) and Cáceres (Provincia de Cáceres, Extremadura) (Noreña *et al.* 1999).

Known distribution. Palearctic: Southern Europe (Italy) (Papi 1951, 1954).

Material. Observations on a live animal.

Remarks. The animal is transparent and colourless. Rostrally, the typical darkly-stained pigment spots are visible in transmitted light. The pharynx is situated between 40 and 50%.

The male system consists of an atrium copulatorium receiving the oviform copulatory bulb, a large blind sac with small proximal spines and large, slender distal spines, and a copulatory bursa without bursal stalk and armed with small spines. The ejaculatory duct is a thick-walled funnel, proximally curled inwards. Of the female system, only the ovary could be observed, flanking the male system at one side.

Although an accessory bursa has not been observed, all other features, including the lack of zoochlorellae, the pigmented spots in the front, the organization of the male system and the armature of the blind sac in particular, are diagnostic for *C. infernalis* Papi, 1951. Papi (1954) also describes the subspecies *C. infernalis breviorispina* Papi, 1954, from the same region in Italy as *C. infernalis*. It only differs from *C. infernalis* by shorter spines in the blind sac of the atrium copulatorium, smaller spines in the copulatory bursa, a double sphincter separating the atrium copulatorium and the common genital atrium, and less pigment in the front end of the body. This subspecies has also been found in central Spain (see Gamo 1987b). Since the spines of the specimen from Andalusia have not been measured and the sphincter around the atrium copulatorium has not been observed, its infraspecific taxonomic position could not be established.

Discussion of *Castrada*. Based on the position of the nephridiopores, Nasonov (1926) has split the taxon *Castrada* into *Castrada* and *Castradella* (Nasonov, 1926) Luther, 1963, whereas Luther (1963) lumped them back together as subgenera of the genus *Castrada*. Awaiting a thorough cladistical analysis, we adopt Luther's (1963) classification.

The position of the taxon *Castrada* and the closely related taxa *Mesocastrada* Volz, 1898, *Tetracelis* Ehrenberg, 1831, *Papiella* Mack-Fira, 1970a and *Rhynchomesostoma* Luther, 1904, has been controversial (for a discussion see Papi 1959; Mack-Fira 1970a; and more recently Willems *et al.* 2005 and Noreña *et al.* 2008). Formerly placed within the Typhloplaninae (*Castrada*, *Castradella*, *Mesocastrada*), Olisthanellinae Luther, 1904 (*Papiella*) and even the Protoplanellinae (*Castradella*), these taxa are now considered representatives of the Rhynchomesostominae Bresslau, 1933 because of the construction of the genital system, and in particular the presence of an atrium copulatorium (Papi 1959; Mack-Fira 1970a). The position of *Tetracelis* remains unclear. Most authors (including Luther 1963; Tyler *et al.* 2006–2010, web reference [2]; Noreña *et al.* 2008) put *Tetracelis* within the Typhloplaninae, but Papi (1959) and Mack-Fira (1970a) conjecture a close relationship with the above-mentioned taxa because of the presence of an atrium copulatorium.

With nephridiopores opening in the buccal tube, *C. purgatorialis* n. sp. and *C. paradisea* n. sp. clearly belong to the nominal subtaxon *Castrada*. Main differences between these two new species include the armature of the atrium copulatorium and its blind sac, the appearance of the ejaculatory duct and the presence of spermatophores in the copulatory bursa. Few species of *Castrada* have the combination of an accessory bursa and one spiny blind sac in the atrium copulatorium. Only *C. infernalis* and *C. viridis* Volz, 1898 share these characters. *C. viridis* differs from *C. purgatorialis* n. sp. in the fact that it has uniform, small spines in the blind sac and a less-developed accessory bursa, and from *C. paradisea* n. sp. by the presence of zoochlorellae in *C. viridis*.

C. purgatorialis n. sp. strongly resembles *C. infernalis* (and its subspecies *C. infernalis* subsp. *breviorispina* Papi, 1954), because of the combination of large and small spines in the blind sac of the atrium copulatorium, and the presence of a well-developed accessory bursa. It differs from *C. infernalis* by lacking the dark, pigmented spots in the front end of the body typical for this latter species. Moreover, *C. purgatorialis* has zoochlorellae and bursal vesicles, which are absent in *C. infernalis*. The two species also have a different granular secretion of the accessory bursa (eosinophilic in *C. infernalis*, while basophilic in *C. purgatorialis* n. sp.; see Papi 1951, 1954).

Other species within the subtaxon *Castrada* having large spines or teeth in the atrium copulatorium all lack an accessory bursa (*C. chloreia* Braun, 1885, *C. cristispina* Papi, 1951, *C. multispina* Noreña *et al.*, 2008, *C. neocomensis* Volz, 1898, *C. sphagnetorum* Luther, 1904 and *C. trispina* Willems *et al.*, 2005). *C. quadridentata* Hofsten, 1907 could also be included in this list, but it is not clear whether this species belongs to *Castrada* or *Castradella*. Moreover, whether this species has an accessory bursa or not, is not known (Hofsten 1907; Luther 1963). The seminal receptacle of *C. purgatorialis* n. sp., consisting of large nucleated cells, strongly resembles that of *C. montana* Papi, 1959 (see Papi 1959). However, the latter species differs in many other features including the lack of zoochlorellae and the general organization of the genital system (e.g. sphincter partitioning the common genital atrium, atrium copulatorium with two small blind sacs provided with small “allineated pseudocuticular bodies”, no accessory bursa; see Papi 1959).

A number of mostly poorly described taxa of *Castrada* share some common features of the male genital system with *C. paradisea* n. sp. (one blind sac, uniform spines and a simple ejaculatory duct). *C. spinulosa* Hofsten, 1907 is similar to *C. paradisea* n. sp., but has a stalked seminal receptacle in the female system. *C. horrida* Schmidt, 1861 is also poorly known, but lacks spermatophores and an accessory bursa. *C. subsalsa* Luther, 1946 is only known from brackish habitats and also lacks an accessory bursa and has no spines in the copulatory bursa.

As many species of *Castrada* lack a detailed description, identification and morphological comparison of specimens is often difficult. Many species may possibly consist of species complexes or could be lumped in one large species pool. A thorough molecular analysis would probably help to unravel the complex evolutionary history of this taxon, and help species delimitation and identification.

Typhloplaninae Luther, 1904

Strongylostoma elongatum Hofsten, 1907
(Fig. 2F)

New localities in Spain. Doñana National Park, Provincia de Huelva, Spain (36°49'27"N, 6°21'40"W). Llanos del Taraje near Ecomuseo Robledo de la Plancha: muddy temporal pond with *Ranunculus aquatilis* and sedges (25/03/2008).

Doñana National Park, Provincia de Huelva, Spain (37°04'23"N, 6°22'28"W). Laguna de la FAO: permanent water body with submersed vegetation (05/04/2008).

Other localities in Spain. Central areas (Sierra de Guadarrama and river Tajo basin, see Gamo & Noreña-Janssen 1998).

New locality outside Spain. Palearctic: Mol, Antwerp, Belgium (51°13'06"N, 05°10'49"E). Buitengoor: aquatic vegetation from a marsh in an open area (20/08/2008).

Known distribution. Widespread throughout the Palearctic: many localities in Europe, Western Russia, Siberia (see Luther 1963 for localities and references), Western Europe (UK: North Wales) (Young 1972b, 1973), Central Europe (Germany: South Lower Saxony) (Heitkamp 1982), Eastern Europe (Romania: floodplain of the Danube, littoral freshwater lakes of the Black Sea) (Mack-Fira 1968; 1970b), Western Russia (Urals, Northern Dvina River and upper Volga River) (Rogozin 1996; Korgina 1999, 2002) and the Middle East (Israel) (Noreña *et al.* 2008); Nearctic: Greenland (Steinböck 1932), USA (New York, Wisconsin) (Kolasa *et al.* 1987; Watermolen 2005), Canada (Ontario) (Gregory *et al.* 2000).

Material. Studies on several live animals from the new localities in Spain of which three were whole mounted. Observations on one live specimen from Belgium.

Remarks. *Strongylostoma elongatum* can easily be recognized from the other representatives of the taxon *Strongylostoma* Ørsted, 1844 by the construction of the copulatory organ. Spines are only present in the distal part of the ejaculatory duct, while other species have spines over the entire length of the ejaculatory duct (*S. cirratum* Beklemischew, 1922, *S. dicorymbum* Marcus, 1946 and *S. radiatum* Müller, 1774) or completely lack spines (*S. simplex* Meixner, 1915). In all live animals, the copulatory organ and the muscular copulatory bursa were clearly visible. However, the spines of the ejaculatory duct disappear when mounted with lactophenol. Although for *S. gonocephalum* (Silliman, 1884) Graff, 1911 and *S. coecum* (Sekera, 1906) Sekera, 1912 a detailed description of the copulatory organ is lacking, they can be easily distinguished from *S. elongatum* by the lack of eyes in *S. coecum*

and the presence of “Grübchenflecken” (deepened oval spots beside and behind the eyes) and reticulated vitellaria in *S. gonocephalum* (see Graff 1913), features the specimens from Spain do not show. For a more detailed discussion on the taxon *Strongylostoma*, see the discussion of *S. devleeschouweri* **n. sp.**

***Strongylostoma devleeschouweri* n. sp.**

(Figs. 6A–6B)

Localities. Doñana National Park, Provincia de Huelva, Spain (36°58'48.80"N, 6°28'55.60"W). Laguna de Santa Olalla: submersed parts of sedges along the western shore of the lake (19/03/2008) (type locality).

Doñana National Park, Provincia de Huelva, Spain (36°49'27"N, 6°21'40"W). Llanos del Taraje near Ecomuseo Robledo de la Plancha: muddy temporal pond with *Ranunculus aquatilis* and sedges (25/03/2008).

Doñana National Park, Provincia de Huelva, Spain (37°04'23"N, 6°22'28"W). Laguna de la FAO: permanent water body with submersed vegetation (05/04/2008).

Material. Observations on several live animals. Eleven serially-sectioned specimens, one of which designated holotype (MNCN, no. 4.01/55) and four designated paratype (HU, nos. 423–426). Six whole mounts.

Etymology. Species name in honour of Prof. Dr. Steven De Vleeschouwer, neurosurgeon at UZ Leuven, as a token of gratitude by the senior author (TA).

Description. The animals are 0.6–0.8 mm long measured in the serial sections. Brown, semilunar eyes are present at about 10%. The body shape is bluntly rounded anteriorly and more pointed posteriorly. The habitus is highly variable. Animals from Laguna de Santa Olalla are characterized by a conspicuous colouration. In general these specimens are relatively transparent, but the region coalescing with the position of the intestine has a red colouration. A very striking feature is the dense pattern of green spots, present throughout the entire animal. In contrast, the animals from Llanos del Taraje and Laguna de la FAO lack this green colouration.

The ciliated epidermis is syncytial, relatively thick ($\pm 15 \mu\text{m}$) and packed with small vacuoles. Nuclei are present in the basal part of the epidermis. The cilia measure about 7 μm . Tiny round dermal rhabdites lie on the apical side of the epidermis. Circular and longitudinal muscle layers are present under the basal membrane.

In the rostral part of the body, large rhabdite glands, originating just in front of the pharynx, form rod tracts between the eyes. They seem to secrete two different types of adenal rhabdites: small, darkly staining oblong rhabdites and larger eosinophilic rhabdites with a variable shape. In the specimens from Laguna de Santa Olalla subepidermal, darkly staining glands are also present dispersed over the entire body (seg in Fig. 6B). They secrete a basophilic granular secretion through the epidermis and are especially concentrated around the gonopore. These glands are absent in the specimens from Llanos del Taraje and Laguna de la FAO. Possibly they cause the green spots present in the animals from Laguna de Santa Olalla.

The mouth and pharynx are situated at about 30%. The organization and structure of the pharynx is identical with that of the other species of *Strongylostoma* Ørsted, 1844 (see e.g. Meixner 1915; Luther 1963). The nephridiopores are combined with the mouth.

Except for the position and structure of the testes, the internal organization strongly resembles that of *Strongylostoma simplex* Meixner, 1915.

The paired testes are visible as two broad lateral bands that run from the front of the pharynx to the caudal body end. In nearly all specimens, both testes coalesce caudally, forming one large U-shaped mass. At about 60%, the vasa deferentia emerge from both testes to run anteriorly. Just behind the pharynx they broaden to form two large extracapsular seminal vesicles, lined with a membranous epithelium and filled with sperm. When entering the copulatory organ, both seminal vesicles narrow and join to form an intracapsular seminal vesicle.

The rest of the genital system strongly resembles that of *Strongylostoma simplex simplex* Meixner, 1915 (see Meixner 1915 for a detailed description). The copulatory organ consists of a large copulatory bulb, containing an intracapsular seminal vesicle, a sclerotized ejaculatory duct and two types of prostate glands. The intracapsular seminal vesicle is surrounded by granular, eosinophilic prostate glands, originating extracapsularly (gg2 in Fig. 6B). The ejaculatory duct has smooth, sclerotized walls and is filled with a granular, basophilic secretion of prostate glands (gg1 in Fig. 6B) and surrounded by plasmatic tissue containing nuclei in its proximal part. The distal part of the ejaculatory duct (described as “male genital duct” by Meixner 1915) penetrates the bulbus wall and empties into the common genital atrium through its dorsal wall. The copulatory bulb is surrounded by well-developed, spirally-running muscles.

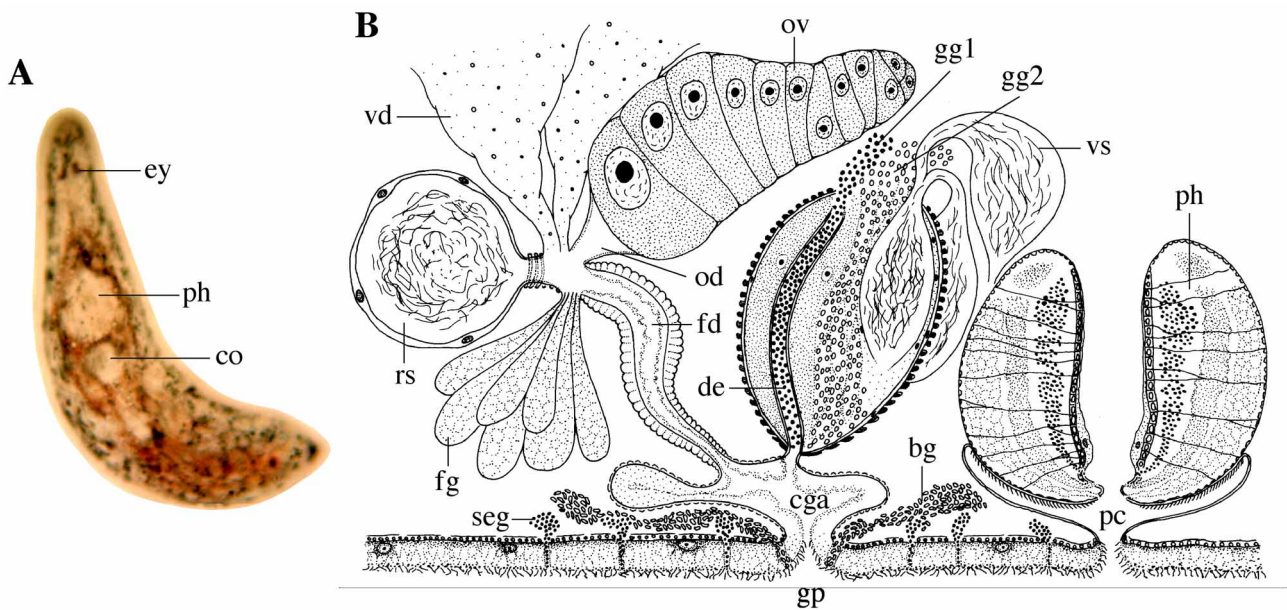


FIGURE 6. *Strongylostoma devleeschouweri* n. sp. (A) Live animal from Laguna de Santa Olalla with the conspicuous green-spotted colouration. (B) Reconstruction of the atrial organs from the right hand side based on specimens from Laguna de Santa Olalla.

The common genital atrium is relatively large and lined with a high, nucleated epithelium. Caudally a sack-like protrusion, variable in size, is present, resembling a sort of atrial bursa. It is, however, not separated from the rest of the common genital atrium, not by a sphincter nor by a different constitution or musculature of its wall, and therefore it cannot be considered as a true atrial bursa. In the specimens from Laguna de Santa Olalla, coarse-grained, basophilic glands (bg in Fig. 6B) empty into the gonopore, which is situated at around 50%.

Dorsocaudally the common genital atrium receives the female duct (described as “common duct” by Meixner 1915). This female duct is a relatively long, broad tube lined with the same epithelium as the common genital atrium and provided with strongly-developed circular muscles. Proximally it receives the oviduct, the vitelloducts, the seminal receptacle and the eosinophilic secretion of the female glands. The single ovary is relatively large in the animals from Laguna de Santa Olalla and smaller in the animals from the other localities. In live animals it was observed on the right side of the body, next to the centrally-located copulatory organ. The oviduct is broad and lined with a thin epithelium. The large, spherical seminal receptacle is filled with sperm and has a relatively high, nucleated epithelium. A short stalk, surrounded by a strong sphincter of several circular muscles, connects the seminal receptacle with the female duct.

Diagnosis. Species of *Strongylostoma* Ørsted, 1844 with very large, elongated testes, mostly coalescing at the rear end. Ejaculatory duct smooth, without spines. Seminal receptacle with strongly-developed sphincter around the stalk. Common genital atrium without division into upper and lower parts and having a large caudal protrusion. Subepidermal glands and green spots in one of the three populations.

Discussion. This species clearly belongs to the taxon *Strongylostoma*. According to different authors (e.g. Luther 1904, 1963; Graff 1913), *Strongylostoma* is characterized within the Typhloplanidae by the following features: nephridiopores combined with the mouth, absence of a copulatory atrium and presence of a seminal receptacle with a muscular stalk. However, *S. simplex simplex* (see further) lacks the muscular stalk of the seminal receptacle and complies therefore with the diagnosis of *Typhloplanella* Sekera, 1912. It is nevertheless placed in *Strongylostoma* because of the presence of dermal rhabdites, a feature lacking in *Typhloplanella* (see Meixner 1915).

Several species within *Strongylostoma* are uncertain (“species dubiae”: *S. gonocephalum*, *S. coecum*, *S. lanceolatum* Sekera, 1912, *S. levandovskii* Nasonov, 1924, *S. rocaseum* Higley, 1918; see Marcus 1946). The well-described species of *Strongylostoma* (*S. cirratum*, *S. dicorymbum*, *S. elongatum*, *S. radiatum*, *S. simplex*) can be distinguished from each other by a number of conspicuous features: overall body form, construction and position of

the testes and vitellaria, partition of the common genital atrium into an upper part receiving the male and female genital system and a lower part emptying into the gonopore, presence or absence of a copulatory bursa and construction of the copulatory organ (armature of the ejaculatory duct, prostate glands). *S. devleeschouweri* n. sp. is easily distinguished from the above-mentioned species (except for *S. simplex*), by the lack of spines in the ejaculatory duct. Moreover, it differs from *S. dicorymbum*, *S. elongatum* and *S. radiatum* by lacking a typical copulatory bursa. All these species also have a bipartite common genital atrium, while *S. cirratum* even possesses a bipartite seminal receptacle.

The construction of the ejaculatory duct is often one of the most important diagnostic characters. In most species, this sclerotized duct is completely or partly lined with spines (see Discussion of *S. elongatum*). In *S. radiatum*, it has a twofold construction with the longer part evacuating the prostate secretion and the minor “diverticulum” receiving sperm from the seminal vesicle (see Luther 1904). Other species (*S. dicorymbum*, *S. elongatum*) have a similar construction, but as opposed to Luther (1904, 1963), Marcus (1946) prefers to consider the smaller “diverticulum” as an ejaculatory duct and the larger part as a ductus granulorum. For *S. cirratum*, *S. simplex* and the new species from Andalusia, it is not clear from the descriptions or the observations on the serial sections where sperm enters the ejaculatory duct (see Meixner 1915; Luther 1963).

Considering all these diagnostic features, *S. devleeschouweri* n. sp. mostly resembles *S. simplex simplex*, which is considered a subtaxon of *S. simplex* together with *S. simplex lapponicum* Papi in Luther, 1963. The latter differs from *S. s. simplex* by the division of its common genital atrium into two parts. This feature is present in most other species of *Strongylostoma*, but is lacking in both *S. s. simplex* and in *S. devleeschouweri* n. sp. (see Luther 1963). Other similarities of *S. devleeschouweri* n. sp. with *S. s. simplex* are: body length, the smooth-walled ejaculatory duct and the absence of a copulatory bursa. However, *S. devleeschouweri* n. sp. differs from *S. s. simplex* by having a conspicuous green-spotted colouration, at least in the specimens from Laguna de Santa Olalla, the presence of granular eosinophilic prostate glands filling the copulatory bulb, the caudal protrusion of the common genital atrium and a strongly-developed sphincter surrounding the stalk of the seminal receptacle. Moreover, the specimens from Spain lack the different types of glands present in the frontal part of *S. simplex simplex* as described by Meixner (1915). Probably the most conspicuous difference with all known representatives of *Strongylostoma* is the construction of the testes. Although the position and volume varies in the different species, none of them has testes coalescing caudally. Because of the above-mentioned differences, the specimens from Spain are described as a new species.

In spite of the fact that there are some minor differences between the specimens from Laguna de Santa Olalla and those from Llanos del Taraje and Laguna de la FAO (see the description above), their internal organization is virtually identical. Therefore they are provisionally placed in the same species until additional morphological and/or molecular data prove otherwise.

Olisthanellinae Luther, 1904

***Olisthanella truncula* (Schmidt, 1858) Voigt, 1892**

(Figs. 7A–7C)

syn. *Mesostomum trunculum* Schmidt, 1858

syn. *Turbella truncula* Diesing, 1862

syn. *Mesostomum banaticum* Graff, 1875

syn. *Mesostoma nassonoffii* Graff, 1882

syn. *Mesostoma splendidum* Graff, 1882

syn. *Mesostoma truncatum* Graff, 1882

syn. *Olisthanella nassonoffii* Graff, 1882

syn. *Olisthanella splendida* Graff, 1882

syn. *Mesostomum truncatum* Voigt, 1892

syn. *Mesostomum trunculum* Voigt, 1892

New localities in Spain. Doñana National Park, Provincia de Huelva, Spain (36°58'48.80"N, 6°28'55.60"W). Laguna de Santa Olalla: submersed parts of sedges along the western shore of the lake (19/03/2008).

Doñana National Park, Provincia de Huelva, Spain (36°58'50"N, 6°29'11"W). Laguna Dulce: floating algae and submersed vegetation on the border of the marsh and open water and swamp vegetation on the northern edge of the lake (06/04/2008; 19/03/2008).

Other localities in Spain. Central areas (Sierra de Guadarrama and river Tajo basin, see Gamo & Noreña-Janssen 1998); Beleña (Provincia de Guadalajara, Castilla-La Mancha) (Gamo 1987a; Gamo & Schwank 1987); Alburquerque (Provincia de Badajoz, Extremadura) (Noreña *et al.* 1999).

New locality outside Spain. Nearctic: Cootes Paradise, Hamilton, Ontario, Canada (43°16'03"N, 79°55'13"W). Submersed aquatic vegetation in southern inlet of the impoundment (17/05/2009).

Known distribution. Widespread throughout the Palearctic: many localities in Europe, Western Russia, Siberia and Japan (see Luther 1963 for localities and references), Western Europe (the Netherlands: Friesland) (Young 1972a), Central Europe (Germany: Thuringia, Lake Constance, Franconia, Oberhessen, South Lower Saxony, Elbe estuary; Austria: Burgenland) (Kraus 1965; Pörner 1966; Kaiser 1967; Rixen 1968; Bauchhenss 1971; Schwank 1981; Heitkamp 1981, 1982; Müller & Faubel 1993), Western Russia (Urals, upper Volga River) (Rogozin 1996; Korgina 2002) and Siberia (Rogozin 1996); Nearctic: Canada (Ontario) (Gregory *et al.* 2000); Afrotropic: East Africa (Kenya: Rift Valley Province) (Young 1976; Young & Young 1976); Neotropic: eastern Amazon floodplain (Peru) (Noreña *et al.* 2006).

Material. Observations on several live animals from Spain and Canada. Eight serially-sectioned specimens and eight whole mounts from the new localities in Spain.

Description and remarks. Habitus and internal organization indicate these specimens belong to *Olisthanella truncula* (Schmidt, 1858) Voigt, 1892, a widespread and relatively common freshwater species of Olisthanellinae Luther, 1904, a monogeneric taxon of Typhloplanidae characterized by separate nephridiopores and testes dorsal to the vitellaria (for a recent discussion on this taxon see Van Steenkiste *et al.* 2010).

Although this species has been described and discussed by numerous authors (e.g. Schmidt 1858; Graff 1882, 1913; Dorner 1902; Sekera 1912; Nasonov 1917; Findenegg 1930; Luther 1963), an overall reconstruction of the genital system is lacking. Therefore, we give a reconstruction of the genital system as observed in the specimens from Andalusia (see Fig. 7C).

The animals are between 1.1–1.5 mm and have vivid red-pigmented areas dispersed throughout the body, accentuating the internal organs. Two dark red eyes are present at about 5%. Although the conspicuous marbled red colouration, typical for the specimens from Spain, is not always mentioned in other accounts of this species (e.g. Schmidt 1858; Findenegg 1930; Luther 1963), it seems to be described in most accounts as a yellow to reddish brown perivisceral “Flüssigkeit” (e.g. Graff 1882, 1913). Specimens of *Olisthanella truncula* have been described as many different species (see list of synonyms), which were later lumped together into one species.

The two testes lie dorsally to the vitellaria and fill a large part of the body in front of the pharynx. Vasa deferentia leave from each testis, merging when entering the copulatory bulb. The latter is filled with prostatic secretion from extracapsular prostatic glands, and contains a large intracapsular seminal vesicle in its proximal part. In its distal part the simple, sclerotized ejaculatory duct is present. This ejaculatory duct is relatively long, surrounded by a plasmatic tissue and evacuates the prostatic secretion (see Luther 1904 and Sekera 1912 for a detailed description of the ejaculatory duct). The exact position where the seminal vesicle merges with the ejaculatory duct could not be observed in the serial sections. The copulatory organ enters the common genital atrium through a sphincter. The common genital atrium is lined with a high cellular epithelium and surrounded by circular muscles. A protrusion of the common genital atrium ventrally from the copulatory organ is often denoted as an uterus (see e.g. Luther 1963) although its function is not fully clear.

The female duct enters the common genital atrium through a well-developed sphincter and is lined with a ciliated epithelium and provided with circular muscles. Proximally it receives the eosinophilic female glands, the oovitelloduct and the enormous female bursa. The ovary stretches rostrally on the left hand side of the body. The oviduct is broad and receives the vitelloducts to form an oovitelloduct. The vitellaria stretch dorsolaterally at both sides, and are situated ventrally from the testes. A sphincter separates the female bursa from the female duct. The female bursa is large and consists of several large vacuoles filled with sperm. These vacuoles are interconnected (seemingly tube-like in some live animals). Although this organ has a glandular wall and probably has some kind of a resorbing function, most authors describe it as a seminal receptacle (Luther 1963) or a bursa seminalis (Graff 1882). We prefer to describe it as a female bursa by reason of its glandular appearance and position in the female genital system. A similar construction of the female bursa is also mentioned by several authors (e.g. Nasonov 1917)

and is, combined with the other diagnostic characters of *Olisthanella*, a relatively easy feature to recognize this species. A copulatory bursa, described in most accounts of this species, was not observed in the specimens from Spain.

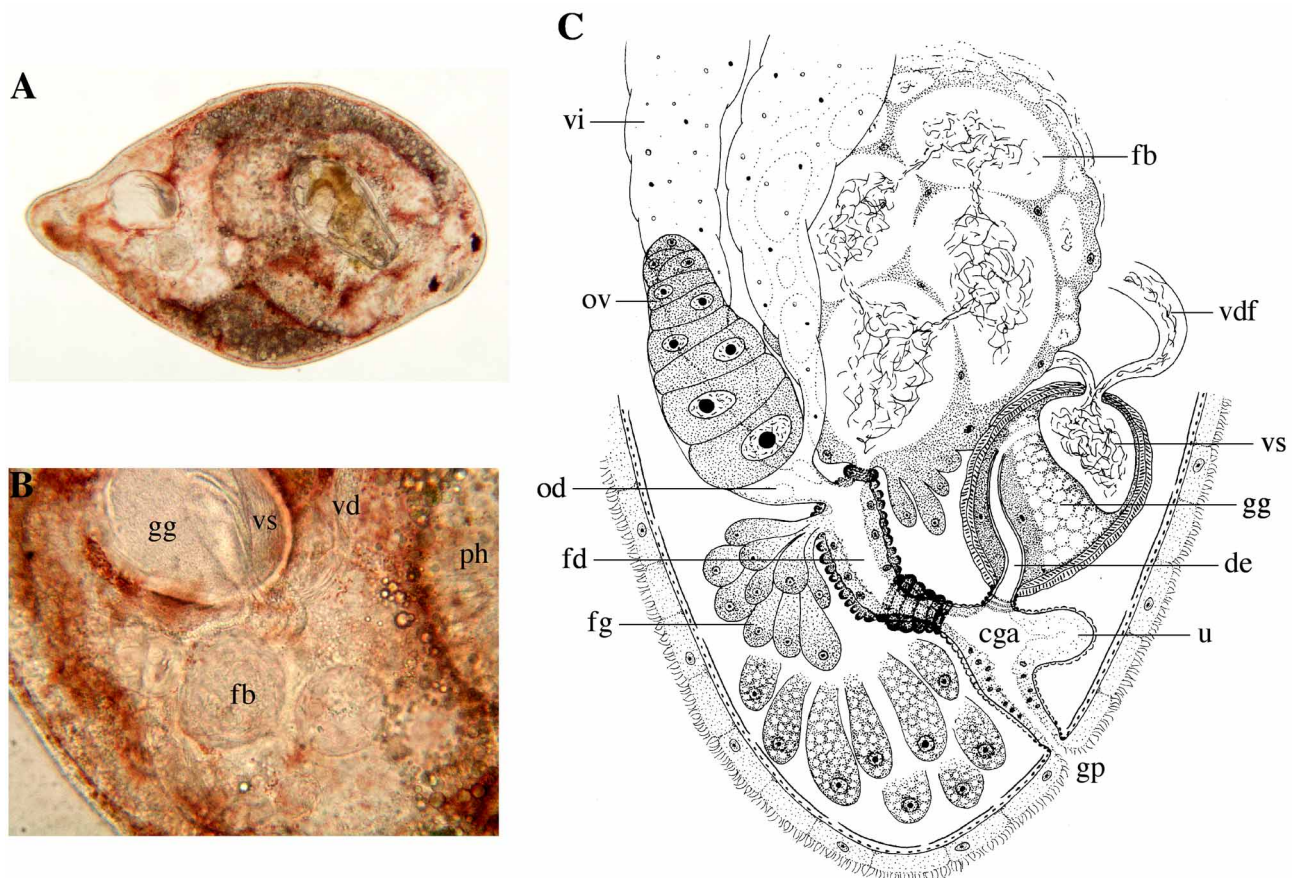


FIGURE 7. *Olisthanella truncula* (Schmidt, 1858) Voigt, 1892 (A) Live animal. (B) Atrial organs. (C) Reconstruction of the atrial organs from the right hand side.

Dalyelliidae Graff, 1908

Microdalyellia armigera (Schmidt, 1861) Gieysztor, 1938a (Fig. 8A)

syn. *Vortex armiger* Schmidt, 1861
 syn. *Dalyellia armiger* Graff, 1904–1908
 syn. *Dalyellia armigera* Hofsten, 1912
 syn. *Dalyellia armygera* Valkanov, 1926
 syn. *Microdalyellia armiger* Gieysztor, 1938a

New locality in Spain. Doñana National Park, Provincia de Huelva, Spain (36°58'50"N, 6°29'11"W). Laguna Dulce: swamp vegetation on the northern edge and floating algae and submersed vegetation on the border of the marsh and open water (19/03/2008; 06/04/2008).

Other localities in Spain. Central areas (Sierra de Guadarrama and river Tajo basin, see Gamo & Noreña-Janssen 1998); Corpa (Provincia de Madrid, Comunidad de Madrid), Fuentenovilla and Cogolludo (Provincia de Guadalajara, Castilla-La Mancha) (Gamo 1987a, 1987b).

New localities outside Spain. Palearctic: Stekene, East Flanders, Belgium (51°14'26"N, 04°05'26"E; 51°14'25"N, 04°05'29"E; 51°14'32"N, 04°05'03"E). Stropers: aquatic vegetation in ditches and temporal ponds along the forest edge (13/07/2008).

Genk, Limburg, Belgium (50°55'30"N, 05°23'39"E; 50°57'21"N, 05°27'41"E). De Maten: submersed aquatic vegetation (grasses and *Mentha aquatica*) from a pond and the Stiemerbeek (17/07/2008).

Kampenhout, Flemish Brabant, Belgium (50°55'40"N, 04°31'19"E). Hellebos: submersed grasses from a ditch (09/03/2009).

Opoeteren, Limburg, Belgium. Area of the Bosbeek: floating vegetation from a puddle with lots of pine needles and leaf litter (18/05/2009).

Seckauer Tauern, Nedere Tauern, Styria, Austria (47°20'39"N, 14°53'14"E, alt. 1315 m; 47°20'39"N, 14°53'22"E, alt. 1330 m). Valley north of Krautbath: aquatic vegetation in a small, shallow pond along the side of a track fed by a mountain stream; aquatic vegetation in marshy areas on the end of the track (23/06/2009).

Söltkäler Nature Park, Schladminger Tauern, Nedere Tauern, Styria, Austria (47°17'17"N, 13°52'01"E, alt. 1218 m). Schwarzensee near Kleinsölk: aquatic vegetation and mosses in a *Sphagnum* bog fed by a mountain stream southwest of the Schwarzensee (27/06/2009).

Gleinalpe, Lavanttal Alps, Styria, Austria (47°13'50"N, 14°58'57"E, alt. 1464 m). Glein Rachau: aquatic vegetation in mountain stream (29/06/2009).

Sumava National Park, South Bohemian Region, Czech Republic (48°58'13"N, 13°35'19"E, alt. 1216 m). Bogs and coniferous forests around Bučina: aquatic vegetation in forested *Sphagnum* bog (02/07/2009).

Palatinate Forest Nature Park, Rhineland-Palatinate, Germany (49°17'20"N, 07°49'14"E, alt. 536 m). Forests east of Leimen: moss and organic material in forest spring (04/08/2009).

Longskär, Raseborg, Uusimaa, Finland (59°49'09"N, 23°15'36"E). Submersed grasses in freshwater lake (07/08/2008).

Pojo, Raseborg, Uusimaa, Finland (60°05'30"N, 23°31'46"E). Mosses along small canal close to water edge (10/08/2008).

Known distribution. Widespread throughout the Palearctic: many localities in Europe, Western Russia, the Caucasus, Siberia and Japan (see Luther 1955 for localities and references), Western Europe (UK: East Midlands, East of England, West Midlands and North Wales) (Young 1970, 1973), Central Europe (Germany: Schleswig-Holstein, Black Forest, Lake Constance, Thuringia, Franconia, Oberhessen, South Lower Saxony, Elbe estuary; Austria: Burgenland) (Rixen 1961, 1965, 1968; Kraus 1965; Pörner 1966; Bauchhenss 1971; Schwank 1976, 1981, 1985; Heitkamp 1982; Müller & Faubel 1993), Eastern Europe (Romania: freshwater sources of littoral lakes of the Black Sea, Bucegi Mountains, Retezat Mountains, Wallachian Plain; Poland: Greater Poland Province) (Mack-Fira 1970b; Kolasa 1974), Western Russia (Northern Dvina River and upper Volga River) (Korgina 1999, 2002) and the Middle East (Israel) (Noreña *et al.* 2008); Nearctic: localities in the USA uncertain according to Ruebush (1937).

Material. Studies on live animals from Spain of which two were whole mounted. Observations on live animals from the other new localities and several whole mounts (14 from Belgium, 7 from Austria, 2 from the Czech Republic, 1 from Germany, 1 from Finland).

Remarks. Animals from Andalusia are translucent, with a reddish colour frontally. Habitus and internal organization as described by Luther (1955). The characteristic stylet is about 165 µm long. The left distal axis consists of one spine in the whole mounts, but two spines were observed in a live specimen. The right distal axis bears eight spines, the most proximal one being the largest. The length range of the stylet of other palearctic populations usually varies between 82–125 µm (see Luther 1955; Rixen 1961; Bauchhenss 1971). Only the specimens from the Elbe estuary (Müller & Faubel 1993) and *Microdalyellia armigera* var. *vinculosa* (Szydal, 1933) Gieysztor, 1938a from Franconia (Germany) (Bauchhenss 1971) and the Western and Eastern Carpathians (Szydal 1933; Gieysztor & Szydal 1939; Luther 1955), have considerably larger stylets (between 125–220 µm). As stated by Luther (1955) and other authors (see e.g. Bauchhenss 1971; Müller & Faubel 1993), the number of spines on the right distal axis (even within the same population) can range between three and nine. Also on the left distal axis, more than one spine can be present (up to four in Bauchhenss 1971). Its variable stylet morphology and widespread occurrence and abundance in many different types of freshwater habitats suggest a complex evolutionary history.

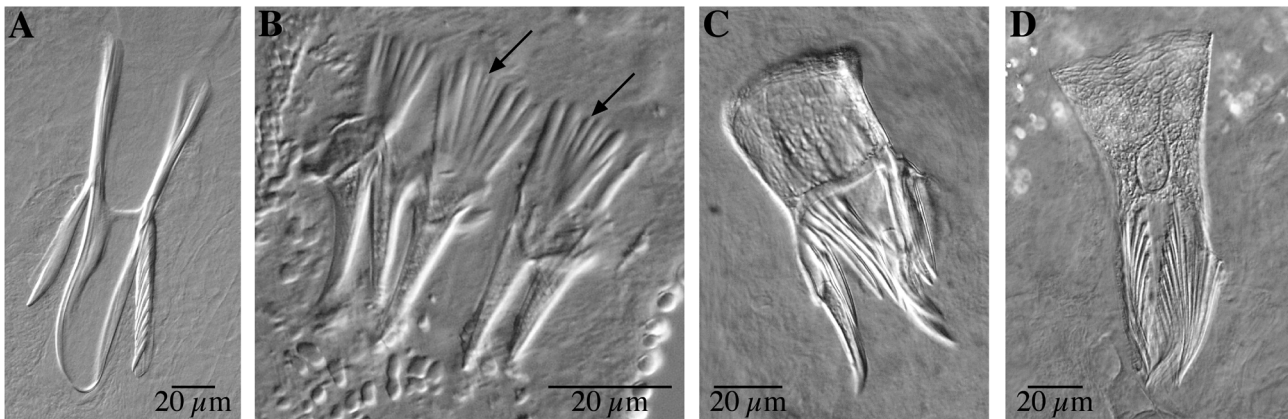


FIGURE 8. *Microdalyellia armigera* (Schmidt, 1861) Gieysztor, 1938a (A) Stylet. *Gieysztoria cuspidata* (Schmidt, 1861) Ruebush & Hayes, 1939 (B) Stylet (arrows indicate digitiform protuberances). *Gieysztoria macrovariata* (Weise, 1942) Ruebush & Hayes, 1939 (C) Stylet. *Gieysztoria beltrani* (Gieysztor, 1931) Ruebush & Hayes, 1939 (D) Stylet.

***Gieysztoria cuspidata* (Schmidt, 1861) Ruebush & Hayes, 1939**
(Fig. 8B)

syn. *Vortex cuspidatus* Schmidt, 1861

syn. *Vortex sexdentatus* Graff, 1882

syn. *Dalyellia cuspidata* Hofsten, 1907

syn. *Microdalyellia cuspidata* Gieysztor, 1938b

New locality in Spain. La Puebla del Rio, Provincia de Sevilla, Spain (37°11'42.84"N, 6°11'24.53"W). Reserva Natural Concertada Dehesa de Abajo: temporal cattle pond with vegetation and *Triops* sp. 500m west from Dehesa de Abajo (21/03/2008).

Other localities in Spain. Central areas (Sierra de Guadarrama and river Tajo basin, see Gamo & Noreña-Janssen 1998); La Albufera (Provincia de Valencia, Comunidad Valenciana) (Gieysztor 1931).

New localities outside Spain. Palearctic: Genk, Limburg, Belgium (50°57'29"N, 05°27'41"E). De Maten: floating and submersed aquatic vegetation in the Stiemerbeek (17/07/2008).

Lommel, Limburg, Belgium (51°14'42"N, 05°17'29"E; 51°14'53"N, 05°17'24"E; 51°14'44"N, 05°17'22"E). Lommelse Sahara: aquatic vegetation in a pond (23/07/2008).

Bernissart, Hainaut, Belgium (50°27'46"N, 03°40'52"E). Marais d'Harchies-Hensies-Pommeroeul: floating and submersed aquatic vegetation from the marsh between both bird hides (09/06/2009).

Favaskär, Raseborg, Uusimaa, Finland (59°50'01"N, 23°15'48"E). Organic material and mosses from small rock pool (07/08/2008).

Nearctic: Cootes Paradise, Hamilton, Ontario, Canada (43°16'08"N, 79°54'31"W). Aquatic vegetation in a small, temporal pond close to the Ravine Trail (04/05/2009).

Known distribution. Widespread throughout the Palearctic: many localities in Europe, Western Russia, Central Asia, Siberia, the Russian Far East (see Luther 1955 for localities and references); Central Europe (Germany: Schleswig-Holstein, Thuringia, Franconia, Oberhessen and South Lower Saxony; Austria: Burgenland) (Rixen 1961; Kraus 1965; Pörner 1966; [Bauchhenss 1971](#); [Schwank 1981](#); [Heitkamp 1982](#)), Eastern Europe (Romania: floodplain of the Danube, littoral freshwater lakes of the Black Sea, Danube Delta) ([Mack-Fira 1968](#), [1970b](#)), Western Russia (Urals, Northern Dvina River; upper Volga River; Yaroslavl Oblast) ([Rogozin 1996](#); [Korgina 1999](#), [2002](#); [Kotikova 2001](#)), Siberia and the Russian Far East ([Rogozin 1996](#)), the Middle East (Israel) ([Noreña et al. 2008](#)); Nearctic: Greenland ([Steinböck 1932](#)); Afrotropic: West Africa (Nigeria: Zaria) ([Mead & Kolasa 1984](#)).

Material. Observations on a live animal and one whole mount from the new locality in Spain. Studies of live specimens from the other new localities and four whole mounts from Belgium.

Remarks. The sclerotized parts of the copulatory organ consist of five large spines of similar size with a length of 28–33 µm, which are not interconnected by a common base ("Aequales" group of the *Gieysztoria*-type in Luther

1955, see also Discussion of *G. iberica* n. sp.). Bundles of digitiform protuberances originating from each spine are clearly visible in the whole mount (arrows in Fig. 8B). The spines with fibres combined measure around 48 µm. This type of stylet is only known from two species: *Gieysztoria cuspidata* (Schmidt, 1861) Ruebush & Hayes, 1939, a well-known ubiquitous species of various freshwater habitats in large parts of the (Western) Palearctic (see Luther 1955) and *Gieysztoria isoldeae* Artois *et al.*, 2004, a species found in ephemeral rock pools in Botswana (see Artois *et al.* 2004). However, the spines of *G. isoldeae* only amount to four and are much longer (120–160 µm) and more slender. One or possibly two spines of the specimens from Andalusia seem to be more curved than the others, a feature which has also been mentioned for other populations by Luther (1955). The length of the spines of specimens from other localities seems to be highly variable but ranges mostly between 16–29 µm (see e.g. Beklemischew 1921; Gieysztor 1926, 1931; Bauchhenss 1971; Noreña *et al.* 2008), making the spines of the specimen from Dehesa de Abajo among the largest found in this species [except for one specimen reported by Gieysztor (1931) from eastern Spain with spines up to 40 µm in length].

***Gieysztoria macrovariata* (Weise, 1942) Ruebush & Hayes, 1939**
(Fig. 8C)

syn. *Dalyellia rubra* var. *macrovariata* Weise, 1942

New locality. Doñana National Park, Provincia de Huelva, Spain (36°58'50"N, 6°29'11"W). Laguna Dulce: swamp vegetation on the northern edge of the lake (06/04/2008).

Known distribution. Palearctic: Central Europe (Germany) and Southern Europe (Italy) (see Luther 1955 for localities and references), Western Europe (the Netherlands: South Holland) (Van Der Land 1965), Eastern Europe (Romania: littoral freshwater lakes of the Black Sea) (Mack-Fira 1970b), East China (Wuhu city, Anhui Province) (Wang & Deng 2006).

Material. Observations on a live animal and one whole mount.

Remarks. The animal is about 1 mm long and has vitellaria with fingerlike papillae. The 100 µm-long stylet consists of a 45 µm-long girdle bearing 9 spines, which differ in length. The girdle consists of a fibrous network and is strengthened by a distal ring, on which the spines originate. Although the folding of the stylet did not allow us to determine the precise order of all spines, it is clear that the outer spines are larger and protrude more from the girdle than the inner ones. At least three of the outer spines have a relatively long and broad funnel-shaped base, whereas the other spines have a shorter, more slender base.

***Gieysztoria beltrani* (Gieysztor, 1931) Ruebush & Hayes, 1939**
(Fig. 8D)

syn. *Dalyellia beltrani* Gieysztor, 1931

syn. *Microdalyellia beltrani* Ruebush & Hayes, 1939

New localities in Spain. Doñana National Park, Provincia de Huelva, Spain (36°49'27"N, 6°21'40"W). Llanos del Taraje near Ecomuseo Robledo de la Plancha: muddy temporal pond with *Ranunculus aquatilis* and sedges (25/03/2008).

Doñana National Park, Provincia de Huelva, Spain (37°04'23"N, 6°22'28"W). Laguna de la FAO: permanent water body with submersed vegetation (05/04/2008).

Doñana National Park, Provincia de Huelva, Spain (36°58'50"N, 6°29'11"W). Laguna Dulce: swamp vegetation on the northern edge and floating algae and submersed vegetation on the border of the marsh and open water (06/04/2008).

Doñana National Park, Provincia de Huelva, Spain (36°59'26.53"N, 6°26'32.16"W). Marsh with *Ranunculus aquatilis*, *Calla palustris* and sedges near El Palacio (06/04/2008).

Other localities in Spain. Central areas (Sierra de Guadarrama and river Tajo basin, see Gamo & Noreña-Janssen 1998); Navaescurial (Provincia de Avila, Castilla y León) (Gamo & Mayor 1987), La Albufera and el Jardín botánico de Valencia (Provincia de Valencia, Comunidad Valenciana) (Gieysztor 1931).

New locality outside Spain. Département du Var, Provence-Alpes-Côte d'Azur, France. Dry mud from a temporal pond provided by Dr. Alain Thiéry (09/2007) and hatched at Hasselt University (Belgium) (10/2007)

Material. Observations on live animals and several whole mounts from Andalusia. Studies on live specimens and three whole mounts from France.

Remarks. The animals from Andalusia are between 0.9 and 1.1 mm. The stylet is 119–134 μm long and consists of two parts of equal length: a proximal girdle with a fenestra and a distal part with spines (“Fenestratae” subgroup, “Inaequales” group of the *Gieysztoria*-type in Luther 1955, see also Discussion of *G. iberica* n. sp.), which corresponds completely with the stylet from *Gieysztoria beltrani* (Gieysztor, 1931) Ruebush & Hayes, 1939, as described by Gieysztor (1931) and Luther (1955).

This species has only been found in some localities in eastern and central Spain (Gieysztor 1931; Gamo & Mayor 1987; Gamo & Noreña-Janssen 1998). The animals from eastern Spain measured 0.9–1.4 mm, while the French animals attained a length of 1–1.3 mm. The stylet length of the specimens from Andalusia also falls within the range of other observations from this species (southern France: 125–139 μm ; eastern Spain: 100–125 μm ; central Spain: 130 μm) (see Gieysztor 1931; Gamo & Mayor 1987; own observations). Since records from other parts of Europe are lacking, *G. beltrani* seems to be preliminarily confined to permanent and temporal freshwater bodies of the Western Mediterranean region.

***Gieysztoria iberica* n. sp.**

(Figs. 9A–9C)

Localities. Doñana National Park, Provincia de Huelva, Spain (37°03'00"N, 6°16'42"W). Veta de Rivera: creek full of vegetation with a high diversity of macrobenthos (18/03/2008) (type locality).

Doñana National Park, Provincia de Huelva, Spain (36°54'50"N, 6°17'48"W). La Montaña del Rio: green algae in shallow brackish pool (29/03/2008; 06/04/2008).

Material. Observations on several live animals. Three whole mounts, one of which designated holotype (MNCN, no. 4.01/56), the other two paratype (HU, nos. 427–428). Two serially-sectioned specimens of rather poor quality.

Etymology. The species epithet refers to Iberia (Gr.: Ἰβηρία), a toponym used by the Ancient Greeks to designate the Iberian Peninsula (Lat.: *Paeninsula Iberica*), currently occupied by Spain and Portugal.

Description. Animals measure ± 0.7 mm and have a reddish-brown colour (parenchymatous). Two eyes are present. The pharynx doliiformis is about 1/3–1/4 of the body length long. As far as could be observed in the serial sections, the internal organization of the genital system seems to be similar to that of other species of *Gieysztoria* (see Luther 1955).

Two testes were observed in the live animals and are situated in the caudal body half. The ovary lies on the right side. The vitellaria are smooth without protrusions (papillae) and distally merge near the ovary.

The relatively elongated, pyriform prostate vesicle is 200–260 μm long ($\bar{x} = 225$ μm ; $n = 3$), when measured on the whole mounts, and surrounded by well-developed circular muscles. The copulatory organ is situated on the left side of the body. Distally it ends in a straight stylet, which is 95–108 μm long ($\bar{x} = 102$ μm ; $n = 3$). The exceptionally long, half open girdle has a length of 76–87 μm ($\bar{x} = 82$ μm ; $n = 3$) and consists of a branching network of lengthwise-orientated fibres. Proximally, the bundle of fibres fans out with straight or curved tips. Distally the stylet bears a half open ring of 14–16 spines. The distal parts of the outer lateral spines bend more inwards than those of the inner spines. The outer spines (± 10 μm long) are also shorter than the inner ones (17–20 μm long). The proximal parts of the spines are firmly fixed on the curved girdle rim. The ratio girdle/entire stylet is ± 0.8 .

A muscular bursa is situated between the male and female system and ends in the common genital atrium. Both circular and longitudinal muscles surround the bursa. The female duct was not clearly visible in the serial sections, but conspicuous glandular tissue and a sperm-filled seminal receptacle indicate its presence near the ovary. Vitellaria do not have digitiform protuberances. The uterus often contains a single egg.

Diagnosis. Species of *Gieysztoria* with a stylet consisting of a 76–87 μm -long girdle composed of a branching network of lengthwise-orientated fibres and a distal half open ring of 14–16 spines. Outer spines shorter and bending more inwards. Ratio girdle/entire stylet ± 0.8 .

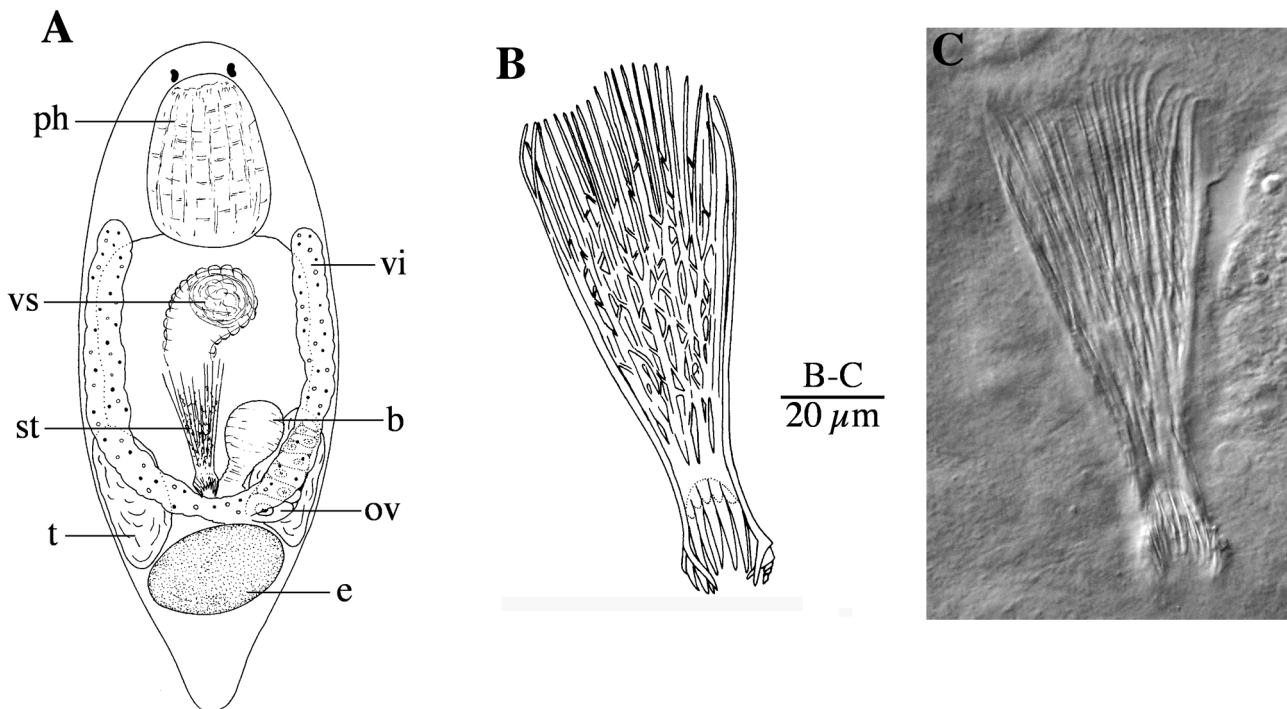


FIGURE 9. *Gieysztoria iberica* n. sp. (A) Habitus from a live animal. (B–C) Stylet from the holotype.

Discussion. *Gieysztoria* Ruebush and Hayes, 1939 is a cosmopolitan and species-rich taxon. Based on stylet morphology, Luther (1955) split the genus into the “Aequales”, having stylets with equal spines, and the “Inaequales”, having stylets with spines of different shapes and sizes. The latter group is subdivided in the “Fenestratae” (F) (with round to oval openings in the girdle), the “Radiata” (R) (stylet radially symmetric without openings in the girdle) and the “Aberrantes” (A) (irregular construction of the stylet). A recent phylogenetic analysis based on morphological characters of a number of taxa belonging to both “Aequales” and “Inaequales” (see Brusa *et al.* 2003), confirms the monophyly of the genus, but also shows that the “Aequales” are interspersed among the “Inaequales”, suggesting these groups do not reflect phylogenetic relationships. A thorough cladistical analysis of the Dalyelliidae Graff, 1908 and the taxon *Gieysztoria* in particular should further clarify the position of its representatives.

When following Luther’s classification, *Gieysztoria iberica* n. sp. can be placed in the “Inaequales”, subgroup “Radiata”, because of the difference in size and shape between the outer and inner spines of the stylet and the lack of an opening in the girdle. It is, however, the relative length of the girdle that makes this taxon unique within *Gieysztoria*. Only nine taxa of *Gieysztoria* have a girdle, which is at least as long as the length of the spines. Four belong to the “Aequales”: *G. japonica* (Okugawa, 1930) Ruebush & Hayes, 1939, *G. knipovici* (Beklemischew, 1953) Luther, 1955, *G. taurica* (Nasonov, 1923) Ruebush & Hayes, 1939 and *G. rubra* subsp. *caucasica* (Nasonov, 1919) Ruebush & Hayes, 1939; five are “Inaequales”: *G. faubeli* Artois *et al.*, 2004 (R), *G. beltrani* (Gieysztor, 1931) Ruebush & Hayes, 1939 (F), *G. pavimentata* (Beklemischew, 1926) Ruebush & Hayes, 1939 (F), *G. sasa* Damborenea *et al.*, 2005 (A) and *G. virgulifera* (Plotnikow, 1906) Ruebush & Hayes, 1939 (F). However, none of them has a girdle of this impressive size, clearly distinguishing *G. iberica* n. sp. from all other taxa within *Gieysztoria*.

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