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ANATOMICAL DESCRIPTION AND BIOLOGY OF THE SPLANCHNOTROPHID *Splanchnotrophus gracilis* HANCOCK & NORMAN, 1863 FOUND PARASITIZING THE DORIDACEAN NUDIBRANCH *Trapania tartanella* IHERING, 1886 AT THE RÍA DE FERROL (GALICIA, NW IBERIAN PENINSULA)

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Key words: *Splanchnotrophus gracilis*, *Trapania tartanella*, SEM, anatomical description, infection rate, parasitic load, host damage.

ABSTRACT

The genus *Splanchnotrophus* (Copepoda, Poecilostomatoida, Splanchnotrophidae) is a small group of endoparasites infesting certain shell-less marine opisthobranchs. The present study is focused on the type species *Splanchnotrophus gracilis* Hancock & Norman, 1863 and its relationship with its host, the doridacean nudibranch *Trapania tartanella* Ihering, 1886. This nudibranch presents large populations at the Ría de Ferrol, frequently found on the porifera *Desmacidon fructicosum* with a large part of specimens parasitized. The parasite female is exteriorly visible due to the presence of ovigerous sacs. In most of the nudibranchs the parasite can be directly observed through the almost transparent integument of the host. The females, much larger than the males and with a highly modified anatomy, take up the posterior body cavity of *T. tartanella*, clutching the gonad and digestive gland with their long body appendages. Males move freely within the interior of the host's body, although they preferably position themselves near the female and along the reproductive system of the nudibranch. Generally, at least a single female of *S. gracilis* appears per nudibranch specimen. In the case of males, they appear in a number varying from 1 to 4.

The collection of specimens was carried out by means of autonomous diving. In the present work a description of the species *Splanchnotrophus gracilis* using Scanning Electronic Microscopy (SEM) and light microscopy is presented. New data on the biology of this species is given. High infection rates (94%) and parasitic loads (up to 43 parasites per host) were found. No clear damage has been found in the infected viscera of *T. tartanella* or during the reproductive process, as normal copulations and spawns were observed in lab conditions. However, data suggest that a higher mortality exists in those specimens presenting a higher parasite load.

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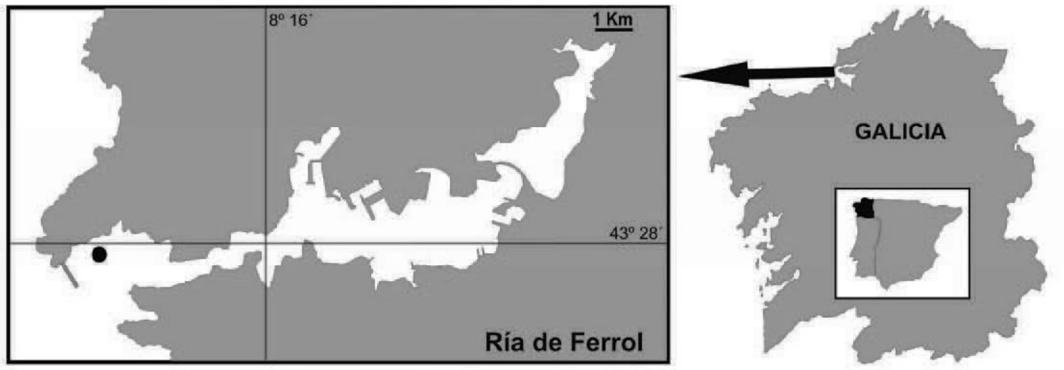

Figure 1:
Ría de Ferrol map, showing the sampling area (black circle).

INTRODUCTION

The family Splanchnotrophidae (Copepoda, Poecilostomatoidea) is a poorly known group of highly modified endoparasites on marine opisthobranchs. 23 species belonging to five genera are currently known: *Splanchnotrophus* Hancock & Norman, 1863, *Lomanoticola* Scott & Scott, 1895, *Ismaila* Bergh, 1867, *Ceratosomicola* Huys, 2001, and *Arthurius* Huys, 2001 (Salmen, 2010).

Historically, little attention has been paid to this parasitic group. The first works date back to the 19th century (Hancock & Norman 1863; Bergh 1868, 1898; Hetch 1893, 1895) and they are brief descriptions with sketchy habitus drawings. In the 20th century some works (Delamare-Deboutteville, 1950; Belcik, 1981) were focused on this group, but they followed some confused data of the precedent authors and they paid little attention on cephalic appendages (except: Laubier, 1964) and their tiny structures. Schrödl (1997, 2002) published solid new data on splanchnotrophid parasitism in Chilean opisthobranchs from the genus *Ismaila*. But it was not until the review of the family done by Huys (2001) when the "taxonomic myopia" surrounding this group was solved, thanks to the detailed light microscopy descriptions and drawings. Huys gathers all those endoparasites on marine opisthobranchs, except for those belonging to the genus *Briarella* (Salmen *et al.*, 2010), in the family Splanchnotrophidae, which now comprises five genera: *Splanchnotrophus*, *Lomanoticola* (splitted from the latter), *Ismaila*, *Arthurius* and *Ceratosomicola*. Shortly after Haumayr & Schrödl (2003) introduced the Scanning Electronic Microscopy (SEM) as a new and suitable tool to study tiny structures in great detail, giving new light on the study of these parasites. Very recently, Salmen *et al.* (2008a, b) used this technique successfully when they described new species belonging to the genera *Ceratosomicola* and *Arthurius*.

Like other poecilostomatoids, splanchnotrophids have a sickle-shaped mandible. There are also some common characteristics shared by all species belonging to the family Splanchnotrophidae: 3-segmented antenna, 2- segmented maxilla, second and third biramous thoracopods and one pair of caudal rami (Huys, 2001).

Splanchnotrophids show a remarkable sexual dimorphism concerning body size and shape (Huys, 2001; Haumayr & Schrödl, 2003): females are much bigger than males, with a highly modified body and having 3-6 pairs of lateral processes with three possible functions (Salmen *et al.*, 2008a): the first consists in wrapping the inner host organs, the second in holding the ovotestis branches (white strings of newly formed eggs shining through the tissue can be easily observed) and finally, the third

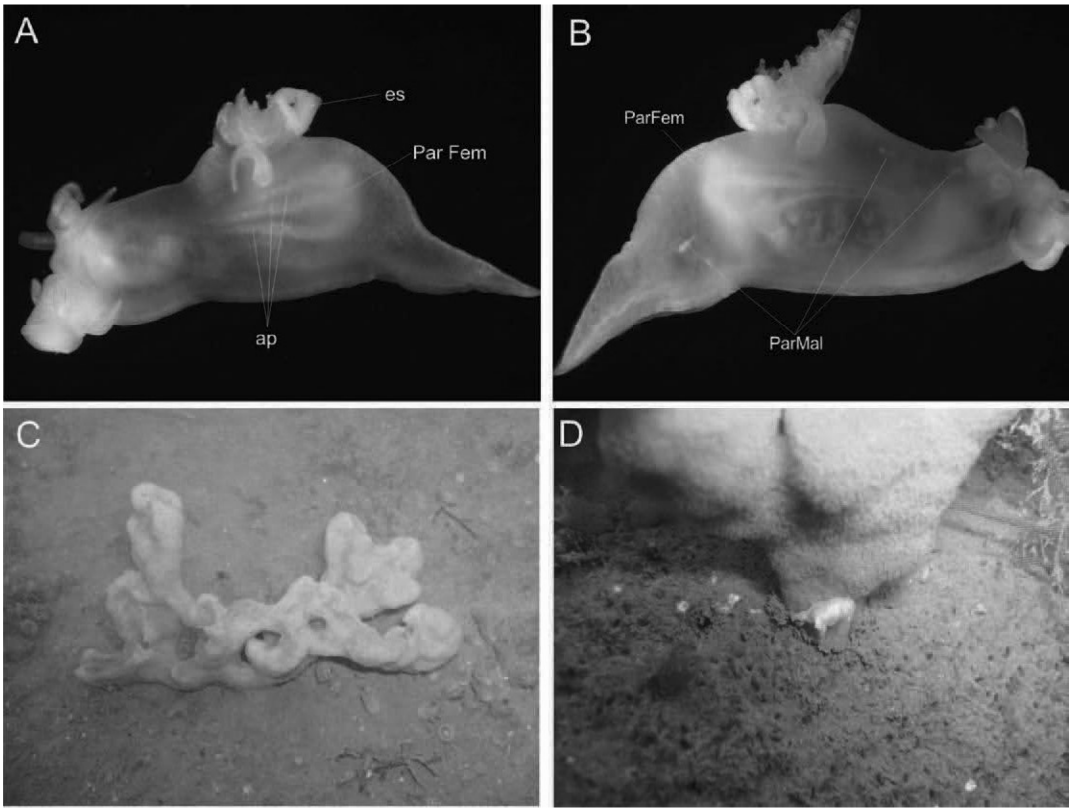

Figure 2:
A. T. tartanella *parasitized by a* S. gracilis *female. B.* T. tartanella *parasitized by a* S. gracilis *female and several males. C, D.* Desmacidon fructicosum*. ap: lateral appendages; es: egg sacs. ParFem: parasite female; ParMal: parasite male.*

consists in extending the body surface in order to facilitate the breathing as the gas exchange is improved. Males are dwarf, with the typical ciclopoid body shape and do not show any lateral process. But this sexual dimorphism is not seen concerning the cephalic appendages, which have the same or nearly the same structure in both sexes (Huys, 2001; Haumayr & Schrödl, 2003; Salmen *et al.*, 2008a, b).

The females are situated inside their hosts with the lateral processes embracing the inner organs (usually gonads or kidney) and the males are normally situated close to the females or lying freely in the body cavity of the host (Huys, 2001; Salmen 2005). Except for some of the species belonging to the genus *Ismaila* (Schrödl, 1997, 2002; Haumayr & Schrödl, 2003) the members of the Splanchnotrophidae do not cause a visible damage on their host, except those related with the space competition with the inner structures of the host.

The genus *Splanchnotrophus* was established by Hancock & Norman in 1863. Until the review of the family by Huys (2001), *Lomanoticola* was believed to belong to *Splanchnotrophus*, but this author gives it genus category, so the old *Splanchnotrophus* genus is divided in *Splanchnotrophus* s.s and *Lomanoticola*. *Splanchnotrophus* currently possesses 4 species distributed in the Mediterranean Sea and in the European Atlantic: *S.gracilis*, *S. angulatus*, *S. willemi* and *S. dellachiajei*.

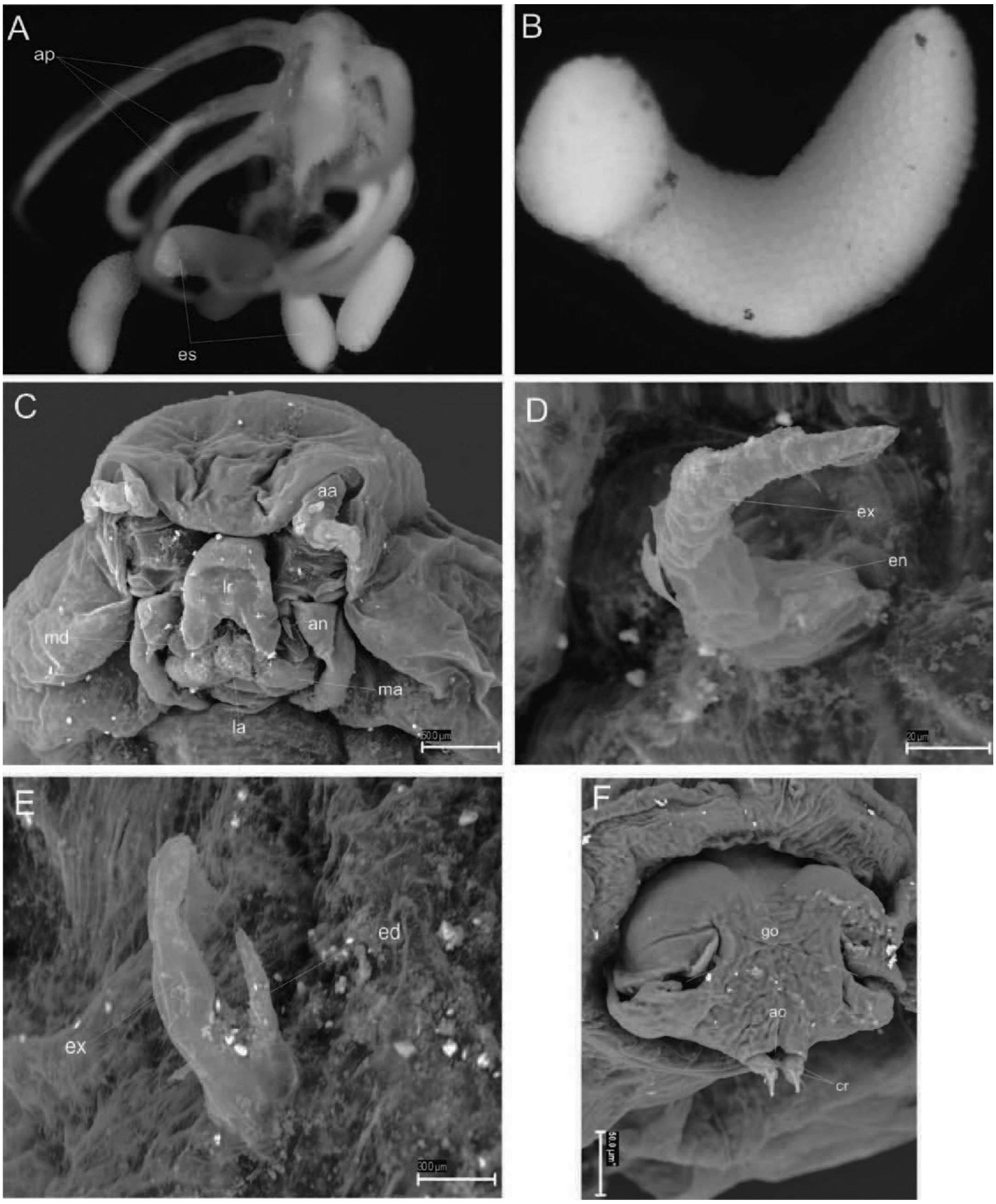

Figure 3:

S. gracilis *female. A. Habitus (light microscopy). B. Egg sac (light microscopy). C. Cephalic appendages (SEM). D. Second thoracopod (SEM). E. Third thoracopod (SEM). F. Abdomen, bearing caudal rami, genital openings and anal slit (SEM).*

aa: antenna; an: antennule; ao: anal opening; ap: lateral appendages; cr: caudal rami; ed: endopodit; es: egg sacs; ex: exopodit; go: genital opening; la: labium; lr: labrum; ma: maxilla; md: mandible.

The present work shows the results obtained during a research project carried out by the Estación de BIoloxía Mariña da Graña (EBMG) focused on the species *Splanchnotrophus gracilis*. High infection rates were discovered for the doridacean host *Trapania tartanella* at the Ría de Ferrol (Galicia, NW Península Ibérica). An anatomical description using SEM is given, as well as infection rates, parasitic loads and other biological aspects. All these data are critically compared and discussed taking into account previous works (Schrödl, 1997, 2002; Huys, 2001; Haumayr & Schrödl, 2003; Salmen *et al.* 2008a, b, 2010).

MATERIAL AND METHODS

Collecting

Infected nudibranchs were collected by scuba diving during the two last years in the sampling area, situated next to the location known as Fornelos, at the Ría de Ferrol (coordinates 43º 28' 02,16" N, 008º 14' 47,70" W) (Fig.1). Three samplings were made in these years. *T. tartanella* were found feeding upon the porifera *Desmacidon fructicosum* (Fig. 2 C, D), usually at 15 to 20 m depth. Then the specimens were observed in the laboratory under a binocular microscope searching for the parasites, and some photos were taken with a camera coupled in a binocular microscope. Most specimens were anaesthetized in a 7% $MgCl_2$ solution and then fixed in 70% ethanol, absolute ethanol (for further molecular analysis), Bouin solution or in 4% formalin seawater (for histological studies).

Some specimens were kept alive in aquariums with *D. fructicosum* and their behaviour was observed. Others were left in a Petri dish in starvation, with two water changes per day.

More specimens studied were taken from the Opisthobranch collection of Victoriano Urgorri, where they were preserved to date in 70% ethanol. He sampled by scuba diving several times in the years 1992 and 1996 in the same location as those made between 2009 and 2010.

Dissections

Those *T. tartanella* that were kept alive were vivisected after one hour in a 7% $MgCl_2$ solution with the aim of obtaining living parasite specimens and an observation *in vivo*. The extraction process took place under a binocular microscope. Photos and videos of the living parasites were taken. Afterwards *S. gracilis* specimens were fixed in 70% ethanol.

The dissection of the previously fixed *T. tartanella* specimens was like the vivisection process, but photos were not taken. The position, number and developmental stadium of the parasites on the host were recorded, as the inner organs of *T. tartanella* were observed in searching for any present potential damage.

SEM

Cleaning process was made with an ultrasonic device during 3 minutes in water with organic detergent.

Due to the shrinking problems observed following the acetone dehydration method previously used (Haumayr & Schrödl, 2003; and Salmen *et al.* 2008a, b) a new methodology based on a lyofilization (freeze-drying) process was developed: after an immersion of 10 minutes in liquid nitrogen, the specimens were lyofilized for at least 12 minutes.

Before SEM microscopy, samples were coated with gold. Afterwards they were observed under electronic microscopy and photos were taken.

Light microscopy: For males, the results obtained with SEM were completed with light microscopy observations.

Terminology: The terminology used here is adopted from Huys (2001), Haumayr & Schrödl (2003), and Salmen et al. (2008a, b). Terms as cephalothorax (five head segments fused with the first thoracic segment), thorax and abdomen describe the body segmentation. It is also assumed that splanchnotrophids lack first thoracopods (Ho, 1987).

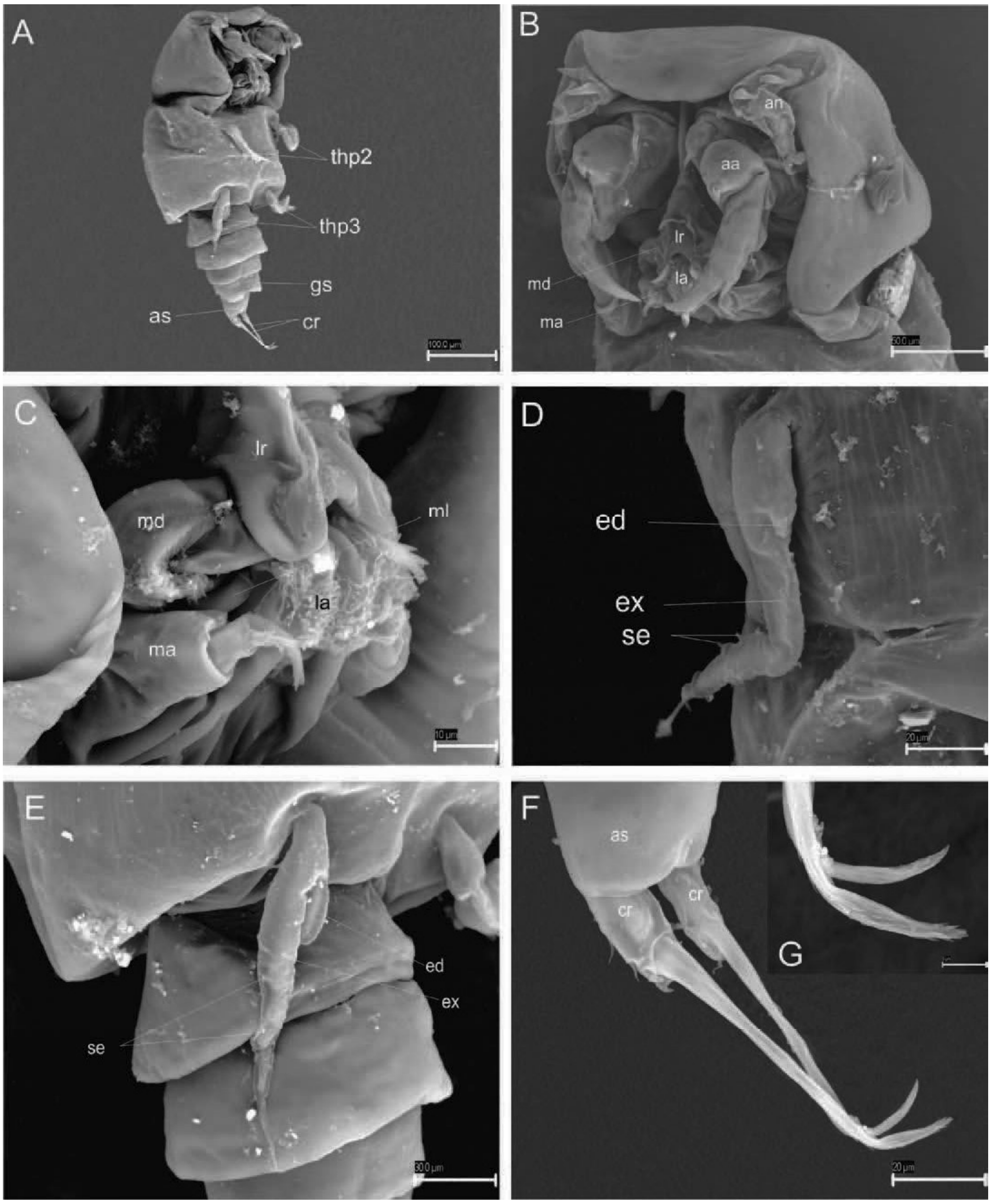

Figure 1:
S. gracilis *male. A. Habitus (SEM). B. Cephalic appendages (SEM). C. Mouthparts detail. D. Second thoracopod (SEM). E. Third thoracopod (SEM). F. Anal somite and caudal rami (SEM). F. Long caudal rami seda detail, showing the spines (SEM).*
aa: antenna; an: antennule; as: anal somite; cr: caudal rami; ed: endopodit; ex: exopodit; gs: genital somite; la: labium; lr: labrum; ma: maxilla; md: mandible; ml: maxillule; se: seda; thp 2, 3: thoracopods 2,3.

RESULTS

Description:

Class Copepoda H.M. Edwards, 1840
Order Poecilostomatoida Thorell, 1859
Family Splanchnotrophidae Norman & Scott, 1906
Genus *Splanchnotrophus* Hancock & Norman, 1863
Splanchnotrophus gracilis Hancock & Norman, 1863
Material examined: 14 females and 20 males collected from August 2009 to September 2010. Station: Fornelos (Ría de Ferrol, Galicia, NW Iberian Peninsula).

Female: (Fig. 3A)

Compact body, measuring from 0.7 mm to 1 mm in length.

Segmentation:

The cephalothorax comprises the five cephalic segments (each of them with a pair of cephalic appendages) and first thoracic segment. Thorax with second and third segments enlarged. They bear three pairs of long (1.5-2 mm) lateral processes ending in a thin tip.

Fourth thoracic somite with one pair of lateral outgrowths. It is not clear if there is a fifth thoracic segment, as it can be retracted and segments edges are difficult to see. Abdomen short, one segmented, bearing caudal rami and the anal and genital openings.

Cephalic appendages (Fig. 3C):

Antennule 2-segmented, first segment with two strong spines, while second shows two constrictions that divides it in proximal, medial and distal part: proximal with two spines and one seta, medial with two short and one long seda; and distal with at least ten setae, three short and the other ones longer. Antenna 3-segmented, two first segments with a strong spine on the distal edge where they fit with the next segment; third segment with four spines, one long and three short, one with a hole on its basis. Labrum bilobate, larger than the labrum.of the male. Mandible with thick and strong base, it recurves on a sickle-shaped blade with 3-4 teeth. Maxillule is fused with mandible base; it shows a little seta in the apex. It is usually covered by the mandible and hard to detect. Maxilla 2-segmented, first longer and thicker, holds the second one, which is shorter and ends apically with two strong setae. Labium shows a great amount of hair. Cephalic appendages can be retracted when the animal is disturbed.

First thoracopod absent. Second thoracopod (Fig. 3D) is biramous, exopodit much longer, with three spines; endopodit much shorter than exopodit. Third thoracopod (Fig. 3E) as the second one. Fourth thoracopod not detected.

Abdomen (Fig. 3F) showing genital openings laterally disposed and bearing a pair of bilobate, kidney shaped egg sacs (Fig. 3E). Caudal rami (Fig. 3F) short, with six small setae all around it and one long seta at the apex. Anal slit between the caudal rami.

Male (Fig. 4A):

Body ciclopiform, elongate and measuring from 0.40 mm to 0.70 mm in length.

Segmentation:

Cephalothorax comprises five cephalic segments and first, second and third thoracic (second and third longer than first). Thorax comprises the last three thoracic segments (from fourth to sixth), with the same size. Abdomen 2-segmented: the first segment is the genital somite and the second is the anal somite (both with similar size). Genital somite bears two genital lobes (each one with three seda decreasing in size). Anal somite presents the caudal rami with the anal opening between them.

Table 1:
Infection rates in each sampling and total infection rate for all samplings.

Sampling date	Collected	infected	Infection rate
02/08/92	22	19	86.3 %
21/08/92	3	2	66.6%
23/08/92	3	2	66.6%
01/08/96	4	2	50%
05/08/96	3	3	100
05/08/09	85	81	98.4%
24/05/10	18	18	100%
20/09/10	6	6	100%
TOTAL	144	133	92.3%

Cephalic appendages (Fig.4B, C): Like in the female, but no hole on the third segment of the antenna; male labrum smaller in proportion to other cephalic appendages than in the female.

First thoracopod absent. Second thoracopod (Fig.4D) biramous, with a little seta on protopodit. Exopodit longer and thicker, with five or six little spines in the distal portion; apex ending in a blister where a long and curved process starts. Endopodit small and thin, with a little spine on the distal portion. Third thoracopod (Fig.4E) biramous, without any seta on the protopodit. Exopodit longer and thicker, very similar to that of the second thoracopod, but with the blister more reduced and a shorter process. Endopodit shorter than exopodit, but longer and thicker than that of the second thoracopod, without distal spine. Fourth thoracopod very short and thin, with a small constriction on the medial portion. Fifth and sixth thoracopod: absent.

Caudal rami (Fig. 4F, G): Robust, they are located on the second abdominal segment (anal somite); with six or seven small setae, except for the one which is very long and presents its last third part pinnate.(Fig. 4G).

Biology

Infection rates: They are shown in table 1 and they are divided in samples, showing sampling date, individuals collected and individuals infected. Finally, the total infection rate on all the samplings is given.

Table 1 only shows the results obtained during the most favourable months to find the host of the parasite (from May to September) as no individuals of *T. tartanella* were found at the sampling locality during winter samplings (from October to April).

Position in the host: Females show a typical position inside the host, with their lateral processes wrapping the gonad, from the posterior cavity of the nudibranch to the most anterior part, where the tips of the processes are ravelled with the tubular portions of the reproductive apparatus of the host (Fig. 2A). They pierce the body of the nudibranch with their urosoma at the level of the anal papilla, among the gills and show a pair of white and kidney-shaped egg sacs. The anterior part of the female is located towards the ventral portion of the host with the mouthparts close to the gonad but not in contact with it.

During dissections two exceptions to this positioning general rule were found. In one case three females were inside the host: one showing the "most frequent" position but the urosome was not protruding the intertegument; another one was located between the first one and the gonad of the host, and seemed to be in a juvenile stadium; and the third one was ovigerous and embraced the gonad ventrally with the lateral processes, the urosome protruded the intertegument at the left medial part of the host and the mouthparts were close to the right part of the gonad. The other case is very similar, but there were four females: three were in the same position as the anterior case, except for the female that was located between the "most frequent" one and the gonad, which was more developed and "inverted"; the fourth one was lying in the posterior cavity and seemed to be juvenile.

Regarding the males, they show more plasticity when positioning themselves inside the host and referring to their number per host, but they can be usually found lying freely in the posterior cavity of the nudibranch, close to the female (Fig. 2B). Other positions frequently observed are the reproductive apparatus, the ventral side of the gonad, the interior of the prebranchial tentacles and pericardium. It was observed in two cases that mature males were situated embedded between the first and second lateral processes of the female. Their ventral side was situated towards the gonad of the host and fixed to it.

Parasitic load

This measure is defined as the number of parasites per host. At least one female was always found in the infected nudibranch hosts. Males were not always found (in 45 cases of the total nudibranchs dissected), and they usually appear in a number between 1 and 4. In some cases (those corresponding to the sampling of May) more parasite specimens, which could be males or copepodits, were found in high number, despite being very difficult to differentiate between the two due to the great likeness between these stages. In table 2 minimum and maximum parasitic loads found in the different samplings are shown. No distinction between females, males or copepodit stages was made.

Intraspecific variability

Females: Structures with taxonomic value, as cephalic appendages or thoracopods did not show any variability between the specimens studied, but some variability was found in other structures:

Lateral appendages: in those cases where the lateral appendages were found ravelled with the genital apparatus of the host, they ended tapering to a soft hooked tip; in other cases their length was not enough to rise the genital apparatus of the host, and the tips of the appendages were blunter.

Lateral outgrowths: some females showed a bulky pair of lateral outgrowth, while in other cases the shape was more flattened.

Males: The only intraspecific variability found between males was the length of the pinnated portion of the long seta of the caudal rami.

Host damage

No evident damage was found in the inner organs of the host, except for one case where the gonad was reduced. Parasitized and non parasitized *T. tartanella* show gonads of the same size. Normal nudibranch copulations and spawns were observed. But some indirect damage was found in starvation conditions: those *T. tartanella* with a higher parasitic load died before those with only a couple of parasites.

Table 2:
Maximum and minimum parasitic loads (parasites per host) in each sampling. No distinction between females, males or copepodit stages was made.

Sampling data	Minimum parasitic load	Maximum parasitic load
02/08/92	1	14
21/08/92	1	3
23/08/92	1	4
01/08/96	1	2
05/08/96	1	4
05/08/09	1	5
24/05/10	1	43
20/09/10	Not dissected	Not dissected

A strange phenomenon was also observed in starvation conditions: in four *T. tartanella*, after more than 21 days in the Petri dish, the parasite females broke with their dorsal side the intertegument of the host and went out freely in the water; the nudibranchs died in a time lapse between the next 1-5 hours.

DISCUSSION

Anatomical description:

The species is identified as *Splanchnotrophus gracilis* Hancock & Norman, 1863 due to the following facts:

The males found in the present work show a high resemblance with that redescribed by Huys (2001) concerning body shape, segmentation, cephalic appendages and thoracopods.

Salmen made a detailed description of this species in her thesis of 2005 using SEM, which coincides with the results of this work. Body shape and size, segmentation, cephalic appendages and thoracopods fine structure, positioning inside the host and parasite number per host are mostly the same as described here. The slight differences found (parasitic load, male caudal rami) could be explained thanks to the high numbers of specimens collected and studied in the present work.

The nudibranch host, *Trapania tartanella*, coincides with those that Salmen (2005) describes for the first time holding this parasite species. In addition, the sampling point belongs to the biogeographical distribution described by Schrödl (2002) for the genus *Splanchnotrophus* (Eastern North-Atlantic).

The male of this species is very similar to that of *S. angulatus*, but they can be distinguished thanks to the presence in *S. gracilis* of three setae in their genital segment and to the concave shape of the edges of this segment (Huys, 2001).

Biology

The total infection rate (92.3%) is very high and shows one of the biggest infection prevalence on one specific opisthobranch species. Other high infection rates found were those described by Schrödl in the Chilean nudibranch species *Thecacera darwini* (89-100%) and *Okenia luna* (70%), and the sacoglossan *Elysia patagonica* (89%) (Schrödl, 2002).

Nothing can be said about the seasonal infection rate variation, due to the fact that all *T. tartanella* recollections were made in the time lapse between the months of May and September, those months when the water increases its temperature and there seem to be the most favourable conditions for the growth of the nudibranch host populations. This idea is supported by the fact that during the collecting divings in the winter (from October to April) not a single *T. tartanella* specimen was found. To add more complications, few data exists concerning the host biology, except for that focused on its feeding behaviour (McDonald & Nybakken, 1996). What is stated below strongly suggests that further studies on the seasonal abundance of the splanchnotrophids first require solid knowledge on its opisthobranch host biology.

Positions found inside the host match those described by Huys (2001) and Salmen (2005), and some new ones for the males are given. An interesting condition is shown in the two cases where the adult male was in contact with the female and embedded between its first and second lateral appendages. One hypothesis to explain this positioning could be some kind of precopulatory behaviour, but more data are required to support it.

Regarding parasitic load, results show a clear seasonal variation, with the maximum load in May (43). During this period, the parasite load comprises both adult males and females and copepodit stages. In August, the number of parasites per host is stable (except in the 02/08/92 sampling) and all the specimens were adult parasites. According to the preceding data it could be suggested that during the period of April-May the infection processes are at their highest levels. This hypothesis is supported by the fact that four other *T. tartanella* showed high parasitic loads during the same sampling (39, 33, 26 and 23 parasites); and this surprising parasitic load is coincident with the biggest annual growth in the population of *T. tartanella*. Anyway, it is necessary to find more infected host specimens during the non recorded months (April, June and July) to follow the progress of the parasitic load. The nudibranch species with the highest parasitic load found so far was one specimen of the giant *Dendronotus iris* recorded by Ho (1981) with 425 *Ismaila occulta* individuals.

Although some intraspecific variability was found (lateral appendages and outgrowths of the female and caudal rami of the male) the studies are limited to a few individuals of the total. The variability found on the lateral outgrowths coincides with that expected by Huys (2001) for the genus *Splanchnotrophus*: it might show intraspecific variability concerning the prosomal region and lateral outgrowths.

Concerning host damage, the results set out here match in two ways with those set out in the 1997 paper of Schrödl. First, nudibranchs with higher parasitic loads seem to show a higher mortality under starvation conditions; and second, in two cases the nudibranch host was killed due to the wounds caused by the female when it exits the host. This phenomenon was observed for the first time by Schrödl (1997) in the nudibranch *Flabellina sp.* 1 parasitized by *Ismaila damnosa*. But the gonad reduction and reproductive cessation noted by Schrödl (1997) were not observed in the present study, due to the normal copulas and spawns observed. This suggests that *S. gracilis* may probably be better adapted than the Chilean *Ismaila* species to its nudibranch host.

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