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Revision of the endoparasitic copepod genus *Ismaila* Bergh, 1867, with description of eight new species

(Copepoda, Poecilostomatoida, Splanchnotrophidae)

Ulrike Haumayr & Michael Schrödl

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The genus *Ismaila* Bergh, 1867 was a poorly known group of endoparasitic copepods associated with shell-less opisthobranchiate hosts. Descriptions were limited to the gross body shape or, where given, details did not agree regarding the number and identity of cephalic and body appendages. The present study gives a complete revison of the known species of the genus *Ismaila*, including the description of eight new species (*I. obtusa*, spec. nov., *I. jenseniana*, spec. nov., *I. androphila*, spec. nov., *I. aliena*, spec. nov., *I. damnosa*, spec. nov., *I. robusta*, spec. nov., *I. socialis*, spec. nov., *I. magellanica*, spec. nov.). The parasites' morphology is described in detail based on SEM examinations. All *Ismaila* species studied possess 5 pairs of highly complex cephalic appendages which are two pairs of antennae, one pair of sickle-shaped, hairy mandibles, and 2 pairs of special-shaped maxillae, all of which showing surprisingly little intraspecific and interspecific variation. Differences between the congeners are mainly related to body proportions (stocky *vs.* delicate body), shape and proportions of thoracopods and dorsal body processes, and to the shape of the egg-sacs. All *Ismaila* species appear to be host-specific, showing special biological adaptations to the host species such as different site preferences and sex ratios. While most species do not obviously damage their hosts, *I. damnosa*, spec. nov. usually sterilize their hosts, the aeolidoidean nudibranch *Flabellina* sp. 1.

The homology of *Ismaila* body structures, such as cephalic, thoracic and abdominal segments and appendages, is discussed showing that the aberrant morphology of *Ismaila* can be plausibly related to a general copepod bauplan. A set of potential autapomorphies, e.g. the presence of an unique unpair dorsal process, strongly suggests the monophyly of the genus *Ismaila*.

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Introduction

Copepods of the Poecilostomatoida Thorell, 1859, which are characterized by a sickle-shaped mandible, generally parasitize a variety of marine fishes and invertebrates. The Splanchnotrophidae are highly specialized and aberrantly shaped parasites of shelless opisthobranchs (see review by Jensen 1987). Most recently, the family has been critically revised and reorganized by Huys (2001). A new family Micrallectidae Huys, 2001 was established to comprise the genus *Micrallecto* Stock, 1971 and its junior synonym *Nannallecto* Stock, 1973, ectoparasites of pteropod Gymnosomata which previously were discussed to belong to the Splanchnotrophidae (Ho 1981, Belcik 1981, Jensen 1987). Of the four endoparasitic genera traditionally placed into the Splanchnotrophidae, Huys (2001) transferred *Briarella* Bergh,

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1876, and, with some reservations, *Chondrocarpus* Basset-Smith, 1903, to the Philoblennidae, formerly only known as ectoparasites of prosobranch gastropods in the Far East. The genus *Splanchnotrophus* Hancock & Norman, 1863 was divided into *Splanchnotrophus* s.s. and *Lomanoticola* Scott & Scott, 1895. In addition, two new monotypic genera, *Arthurius* Huys, 2001, and *Ceratosomicola* Huys, 2001, were established with *S. elysiae* Jensen, 1990 and *S. sacculatus* O'Donoghue, 1924 as the type species, respectively. The placement of the genus *Ismaila* Bergh, 1867 within the Splanchnotrophidae was confirmed by Huys (2001). Based on the re-examination of the antennae and mouthparts of *I. belciki* Ho, 1987, Huys (2001) also briefly discussed the mandibular morphology within the Splanchnotrophidae and presented an hypothesis on the evolution and historical distribution of *Ismaila*.

However, morphological knowledge of most *Splanchnotrophus* (s.l.) and *Ismaila* species is still limited to the gross body shape from few female specimens examined. In particular, taxonomically important structures such as antennae, mouthparts or leg structures are either unknown or may differ considerably even between congeners (e.g. Belcik 1981 *vs.* Ho 1981). Dwarf males have been rarely studied at all. Hence, the taxonomy of *Splanchnotrophus* (s.l.) and *Ismaila* still can be considered as being tentative with a strong need of revision on the basis of detailed structural data. Since segment limits are hardly recognizable in splanchnotrophids, it is also difficult to draw conclusions on the homology of certain body appendages and body portions with corresponding structures of a general copepod or crustacean bauplan.

Within the genus *Ismaila*, only three species were described. *Ismaila monstrosa* Bergh, 1867, the type species, seemed to have an extremely wide geographical distribution and low host specifity. The original description was based on a single specimen (Bergh 1867) found at St. Thomas, Virgin Islands, Caribbean Sea in the aeolid nudibranch host *Phidiana lynceus* Bergh, 1967. Jensen (1987) mentioned a further specimen of *I. monstrosa* which was found at the same locality and in the same host species in 1897. Two parasites from the Chilean Pacific coast found in two different hosts, *Archidoris incerta* Bergh, 1898 (Nudibranchia: Doridoidea) and *Aeolidia papillosa serotina* Bergh, 1873 (Nudibranchia: "Aeolidioidea"), were also assigned to *I. monstrosa* by Bergh (1898), who, however, mentioned slight differences to the Caribbean specimens. Belcik (1981) described further specimens of *Ismaila monstrosa* from the Californian *Janolus fuscus* O'Donoghue, 1924 (Nudibranchia: Arminoidea), which Ho (1987a) considered to be a distinct species, *Ismaila belciki* Ho, 1987. Finally, Jensen (1987) assigned a few parasites found at St. Thomas, Virgin Islands in *Ercolania funerea* Costa, 1867 (Sacoglossa) to *I. monstrosa*.

In a very detailed light-microscopical study, Ho (1981) described the third species, *Ismaila occulta* Ho, 1981 from the Californian nudibranch *Dendronotus iris* Cooper, and was the first to add ontogenetic data from larval stages (Ho 1987b).

More recently, endoparasitic *Ismaila* species have been reported from a variety of Chilean opisthobranchs (Millen et. al. 1994, Schrödl 1996, 1997, 2002). These findings induced the present study, which 1) describes the parasite morphology in detail using SEM, 2) discusses the homology of *Ismaila* body structures, 3) gives a complete revison of the known species of the genus *Ismaila* Bergh, 1867, including the description of eight new species.

Material and Methods

From 1991 to 1995, 42 species of nudibranch and sacoglossan Opisthobranchia have been collected along the Chilean coast (Millen et al. 1994, Schrödl 1996, 1997). Eight of these species were infected with endoparasites of the genus *Ismaila* (see Schrödl, 2002). Parasites of five nudibranch species, *Okenia luna* Millen et al., 1994; *Thecacera darwini* Pruvot-Fol, 1950; *Flabellina* sp. 1; *Phidiana lottini* (Lesson, 1831); *Aeolidia papillosa serotina* Bergh, 1873, and the sacoglossan *Elysia patagonica* Muniaín & Ortea, 1997 have been examined in this study. In addition, with the courtesy and support of Dr. Francis Belcik, Dr. Charles Coleman, Dr. Frank Ferrari and Dr. Kathe Jensen, it was possible to re-examine specimens of *I. occulta*, *I. belciki* and *I. monstrosa*. The type of *I. monstrosa* and Chilean material assigned to *I. monstrosa* by Bergh (1898) have also been examined. For the first time, specimens of the genus *Ismaila* have been studied with the aid of SEM. This kind of examination is suitable to identify and document even very fine structures and, thus, to critically challenge bibliographic light-microscopical data.

Class Copepoda H. M. Edwards, 1840
Order Poecilostomatoida Thorell, 1859
Family Splanchnotrophidae Norman & Scott, 1906

Genus *Ismaila* Bergh, 1867

Diagnosis (see Figs 1,2; for details see description of *I. androphila*, spec. nov., and *I. aliena*, spec. nov.: Figs 17,18).

Female

Body elongate, and either delicate or stout. Cephalothorax distinctly set off from trunk, consisting of five head-segments and the first thoracic seg-

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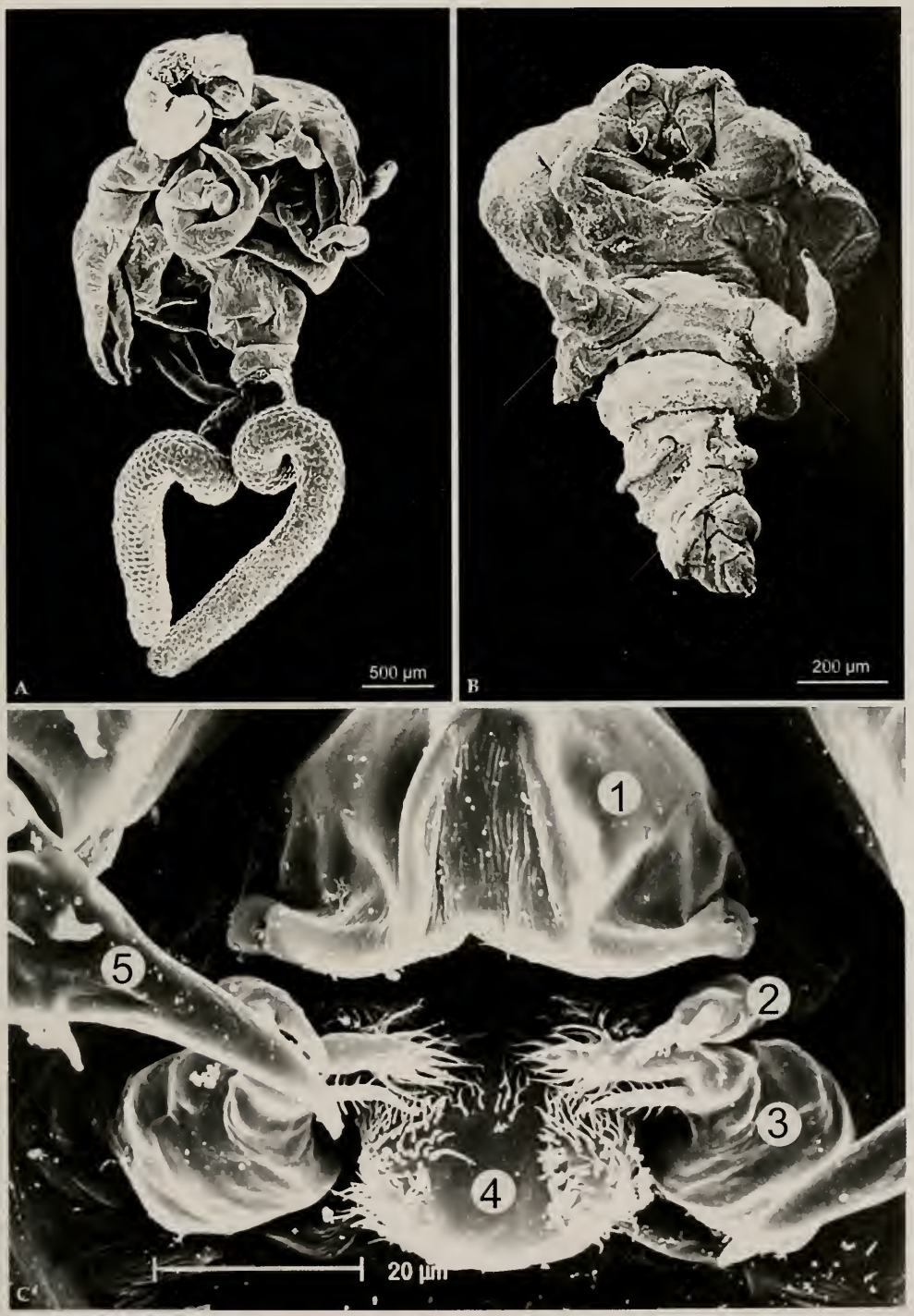

Fig. 1. Morphology of *Ismaila* spp. by SEM (specimens critical point dried, gold coated). **A.** ♀ *Ismaila androphila*, spec. nov., ventral view. **B.** ♂ *Ismaila aliena*, spec. nov., ventral view. **C.** Detail of mouthparts (*Ismaila aliena*, spec. nov.). Note the triangular labrum (**1**), biramous, setigerous maxillules (**2**) and maxilles (**3**), the tongue-shaped labium (4), and the tips of the large, sickle-like second antennae (**5**).

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Fig. 2. Nudibranch hosts of *Ismaila* spp. **A.** *Okenia luna* (lateral and ventral view), with parasite egg-sacs (arrows) protruding under the notal rim. **B.** *Thecacera darwini* (lateral view), with parasite egg-sacs protruding behind the gill circle (arrows). **C.** *Flabellina* sp. 1 (lateral view) with parasite egg-sacs between cerata (arrow).

ment, no external segmentation detectable. Head with two ventral protrusions framing the mouthparts. Thorax with remaining five segments (no superficial segmentation). Abdomen with three externally detectable segments.

Cephalothorax contains five pairs of head-extremities: antennule (Figs 1C, 17A): unbranched and 2-segmented, distal limb with terminal hairs. Antenna (Figs 1C, 17B): unbranched and 3-segmented, distal segment formed as large hook. Labrum (Fig. 1C): triangular and scalloped. Mandible (Figs 1C, 17C): biramous, with one atrophied ramus and a second long, sickle-shaped and pointed ramus (or, as interpreted by Huys (2001), "gnathobase bearing one stylet-like and several short teeth"). Maxillule (Figs 1C, 17D): inwards-bent lobes, terminal part biramous; rami equally short, with short hairs (= "two setae" according to Huys (2001). Maxilla (Figs 1C, 17E): 3-segmented, second limb bears 1) an additional limb with long elongate outgrows, and 2) two pointed, hairy processes (= "unarmed syncoxa with allobasis drawn into multipinnate endite with 2 accessory elements" cf. Huys, 2001). Labium (Fig. 1C): hairy, with paragnath lobes. First thoracopod (= maxilliped): absent.

Thorax, ventral: second thoracopod (Fig. 18A):

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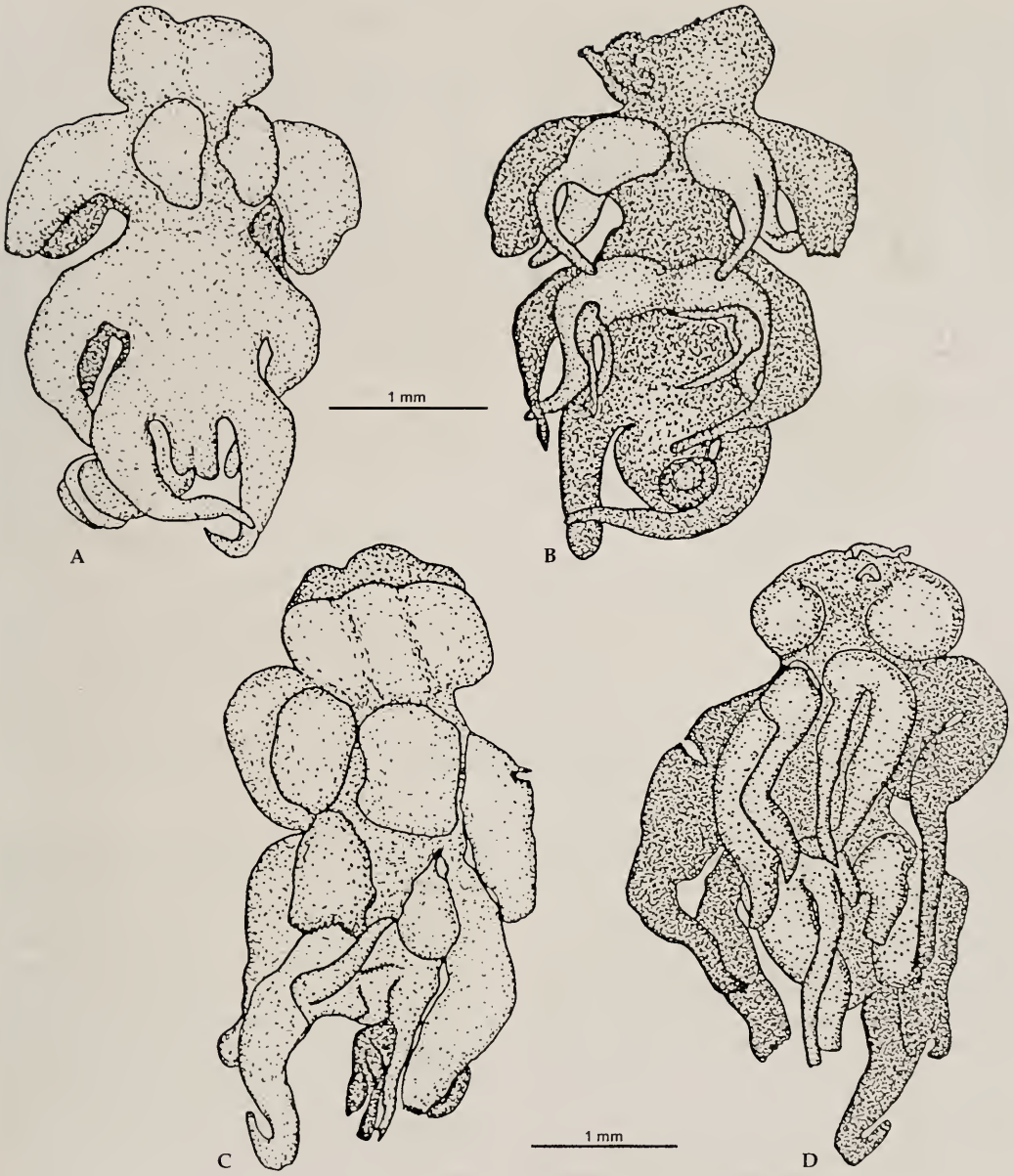

Fig. 3. *Ismaila monstrosa* Bergh, ♀. **A.** Holotype (specimen collected in 1867), dorsal view. **B.** Holotype, ventral view. **C.** Specimen collected in 1897, dorsal view. **D.** Specimen collected in 1897, ventral view.

biramous; exopodit either conical or flattened, with a rounded tip, endopodit conical with a terminal claw. Third thoracopod (Fig. 18B): 3-branched; exopodit either conical or flattened, with a rounded tip, endopodit conical with a terminal claw, endopodit bears one basal process. Second and third thoracopods long, extending considerably beyond the body laterally (see also Jensen 1987). Fourth thoracopod (Fig. 18C): rudimentary, uniramous. Fifth thoracopod (Fig. 18D): two very small, rudimentary and pointed processes, arise either together from one common base or are separate but close to each other. Between fourth and fifth pair of thoracopods: sclerotized ring. Sixth thoracopod: absent.

Thorax, dorsal: three pairs of long uniramous,

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Fig. 4. *Ismaila monstrosa* Bergh, cephalic appendages of female collected in 1897. **A.** Antennule (left). **B.** Antenna (right). **C.** Mandible (right). **D.** Maxillule (right). **E.** Maxilla (left).

conical or flattened processes. One single medial dorsal process between third pair of dorsal processes (Fig. 16B). An additional pair of dorsolateral processes (Fig. 6) may be present inserting between second dorsal processes and second thoracopods.

Abdomen: first segment, externally visible: bears genital openings, mature specimens usually with a pair of straight, curved or coiled egg sacs (e.g. Fig. 16).

Third, externally visible segment: pair of caudal rami with basal hairs.

Male (dwarf)

Body pear-shaped with, depending on maturity, strongly enlarged cephalothorax (head plus first and second, strongly swollen thoracic segments). Thorax with four segments (no external segmentation detectable). Abdomen with three externally detectable segments (Fig. 1B).

Cephalothorax: indistinctly set off from trunk. Cephalic extremities as in female. First thoracopod: absent. Second thoracopod (Fig. 18E): uniramous (exopodit reduced), long, conical, with terminal claw.

Thorax, ventral: third thoracopod (Fig. 18F): biramous (exopodit reduced); endopodit long, with terminal claw; with shorter inner process with blunt tip. Fourth thoracopod (Fig. 18G): rudimentary, unbranched. Fifth thoracopod (Fig. 18H): very small, rudimentary processes, arising either together from a common base or being separate. Sclerotized ring (Fig. 18I) located between fourth and fifth pairs of thoracopods. Sixth thoracopod (Fig. 18I): three setae on elongated genital lobes (see Ho 1981).

Thorax, dorsal: without processes.

Abdomen: first segment with genital openings. Pair of caudal rami with basal hairs (Fig. 18I).

Type species: *Ismaila monstrosa* Bergh, 1867: 97-130, Tab. III+IV.

Ismaila monstrosa Bergh, 1867
Figs 3, 4

Ismaila monstrosa Bergh, 1867: 97-130, Tab. III +VI; Hecht 1895: 625, 630 (*partim*); Belcik 1981: 16-25 (*partim*); Ho 1981: 130-136 (*partim*); Ho 1987a: 67-83 (*partim*); Ho 1987b: 109-111 (*partim*); Jensen 1987: 75-84 (*partim*); Jensen 1990:291-296 (*partim*).

Types. Holotype: ♀, Zoological Museum Copenhagen (ZMUC), collected at St.Thomas, Virgin Islands, Carib-

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bean Sea, in 1867. Host: *Phidiana lynceus* Bergh, 1867. Examined under stereomicroscope.

Additional material: 1♀, collected at St.Thomas, Virgin Islands, Caribbean Sea, in 1897. Host: *Phidiana lynceus* Bergh, 1867. Examined by SEM.

Description of holotype (♀) (Figs 3A,B)

Elongate and delicate body, measuring 3.2 mm in length. Head severely damaged, antennule and antenna present. Two pairs of thoracopods (2nd and 3rd) macroscopically detectable. Second thoracopod: exopodits and endopodits conical, equal in length, exopodit thicker than endopodit. Third thoracopod: exopodit longer and thicker than endopodit. Endopodit and its inner process equally long and thick.

First pair of dorsal processes damaged on both sides. Second and third pair each 1 mm long. Single medio-dorsal process damaged, giving it a bifid appearance.

Description *I. monstrosa* det. Bergh, 1897 (♀) (Figs 3C,D, 4)

Hind body damaged. Body size approx. 4 mm. Cephalic appendages (Fig. 4) as described in the genus diagnosis. Exopodit of second thoracopod thicker and slightly longer than endopodit. Third thoracopods damaged, exopodit thicker than endopodit.

First and second pair of dorsal appendages still *in situ*, remaining part of trunk damaged.

Remarks. The original description of *Ismaila monstrosa* Bergh, 1867 refers exclusively to the female holotype from 1867, since the second specimen was collected 30 years later in 1897. Bergh (1867) mentioned the single medio-dorsal process of *I. monstrosa* as being branched, respectively paired. Re-examining both individuals, from 1867 and 1897, Jensen (1987) showed Bergh's description to be erroneous since the medio-dorsal process of the holotype was damaged and that of the specimen from 1897 is unbranched. Both specimen were also re-examined in this study and each definitely have an unpaired and unbranched medio-dorsal process.

Both individuals agree regarding gross body shape and proportions. The exopodit and endopodit of the second thoracopod have about the same length in both specimens. The inner process of the endopodit of the 3rd thoracopod is as long as the endopodit. This feature is distinctive to all other congeners in which the inner process is shorter than the endopodit (see Tab. 1), except for *I. jenseniana*, spec. nov. The latter species, however, has an additional pair of dorso-lateral processes and, thus, is clearly distinct from *I. monstrosa*.

In absence of morphological differences it is concluded that both individuals from St. Thomas, Virgin Islands, and from the same host species *(Phidiana lynceus)*, belong to *I. monstrosa*. All other specimens formerly assigned to *I. monstrosa* by Bergh (1898), Belcik (1981) and Jensen (1987) clearly differ morphologically (see Tab. 1) and, thus, are regarded to be distinct species. *Ismaila monstrosa* occurs in tropical Caribbean waters parasitizing an aeolid nudibranch host, while *I. jenseniana*, spec. nov. was found at the same locality (St. Thomas) but in a sacoglossan host. All other *Ismaila* species occur in temperate waters, i.e. the southern and northern East-Pacific.

Ismaila obtusa, spec. nov.
Fig. 5

Ismaila monstrosa Bergh, 1867: Bergh 1898: 506, Tab.. 29; Monod & Dollfus 1934: (*partim*); Belcik 1981: 23 (*partim*); Jensen 1987: 76 (*partim*).

Types. Holotype: ♀, Zoologisches Museum Berlin (ZMB), No. 13512, Chile. Host: nudibranch, probably *Anisodoris fontaini* (D'Orbigny, 1837) (see below).

Etymology. Specific name comes from the latin *obtusus* (= stocky) and refers to the stocky body shape with large and broad dorsal processes and exopodits of thoracopods.

Description (♀) (Figs 5A,B)

Body size at least 11 mm, hindmost parts of thorax and abdomen damaged. General body shape stocky. Cephalic appendages lacking, since cephalothorax damaged in this region.

Exopodit of second thoracopod thick and distally flattened. Endopodit shorter, conical and much thinner. Exopodit of third thoracopod thicker than that of second thoracopod, distally flattened. Endopodit shorter and much thinner than exopodit. Inner process of endopodit thinner and shorter than endopodit (ratios see Tab. 1).

Dorsal processes voluminous, relatively short, with very blunt tips. First two pairs distally flattened, third pair conical. Single medio-dorsal process shorter, thinner, conical.

Remarks. Bergh (1898) mentioned two parasite specimens which he assigned to *I. monstrosa* from two different nudibranch hosts, the doridoidean *Archidoris incerta* (junior synonym of the common *Anisodoris fontaini* D'Orbigny, 1837; see Schrödl 2000) and the aeolidoidean *Aeolidia papillosa serotina* Bergh, 1873. According to Bergh (1898), both parasite specimens were collected at the same locality, Tumbes, Chile, and during the same time period. However, the specimen from the ZMB examined in this study

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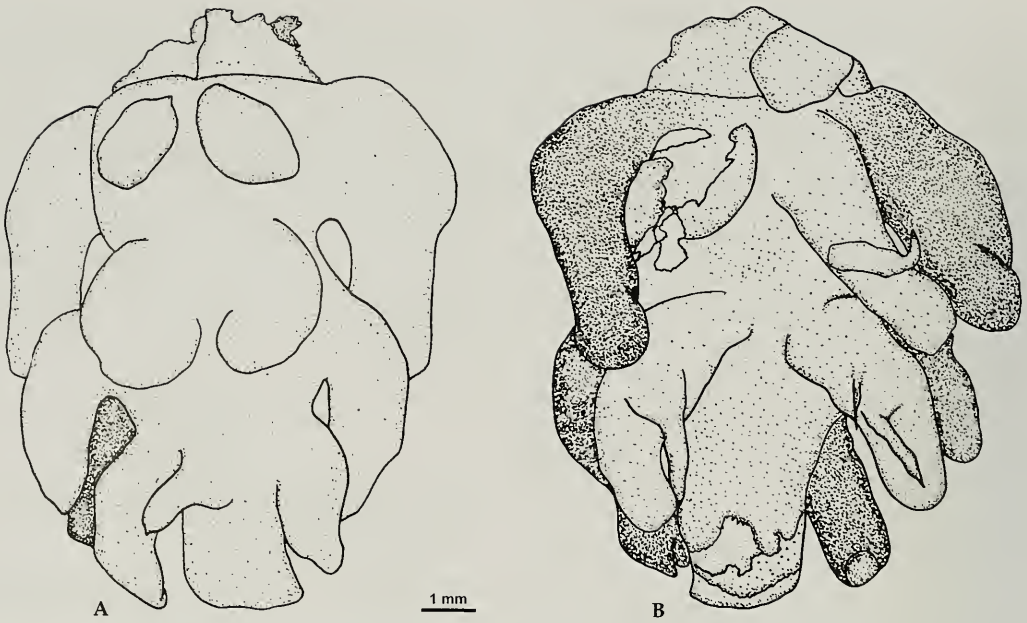

Fig. 5. *Ismaila obtusa,* spec. nov. **A.** Dorsal view. **B.** Ventral view.

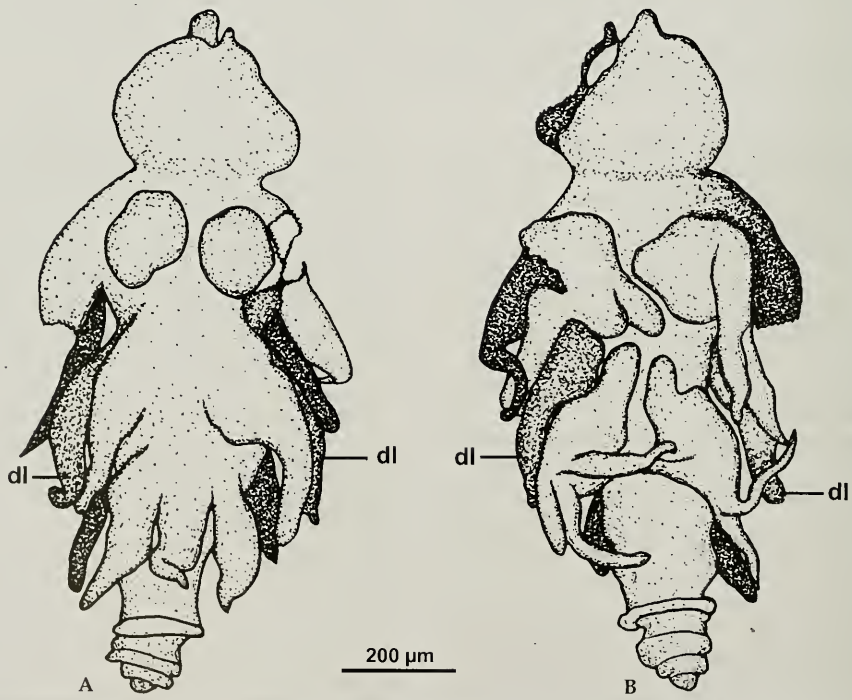

Fig. 6. *Ismaila jenseniana, spec.* nov. Note the additional, dorsolateral pair of processes (dl). **A.** Dorsal view. **B.** Ventral view.

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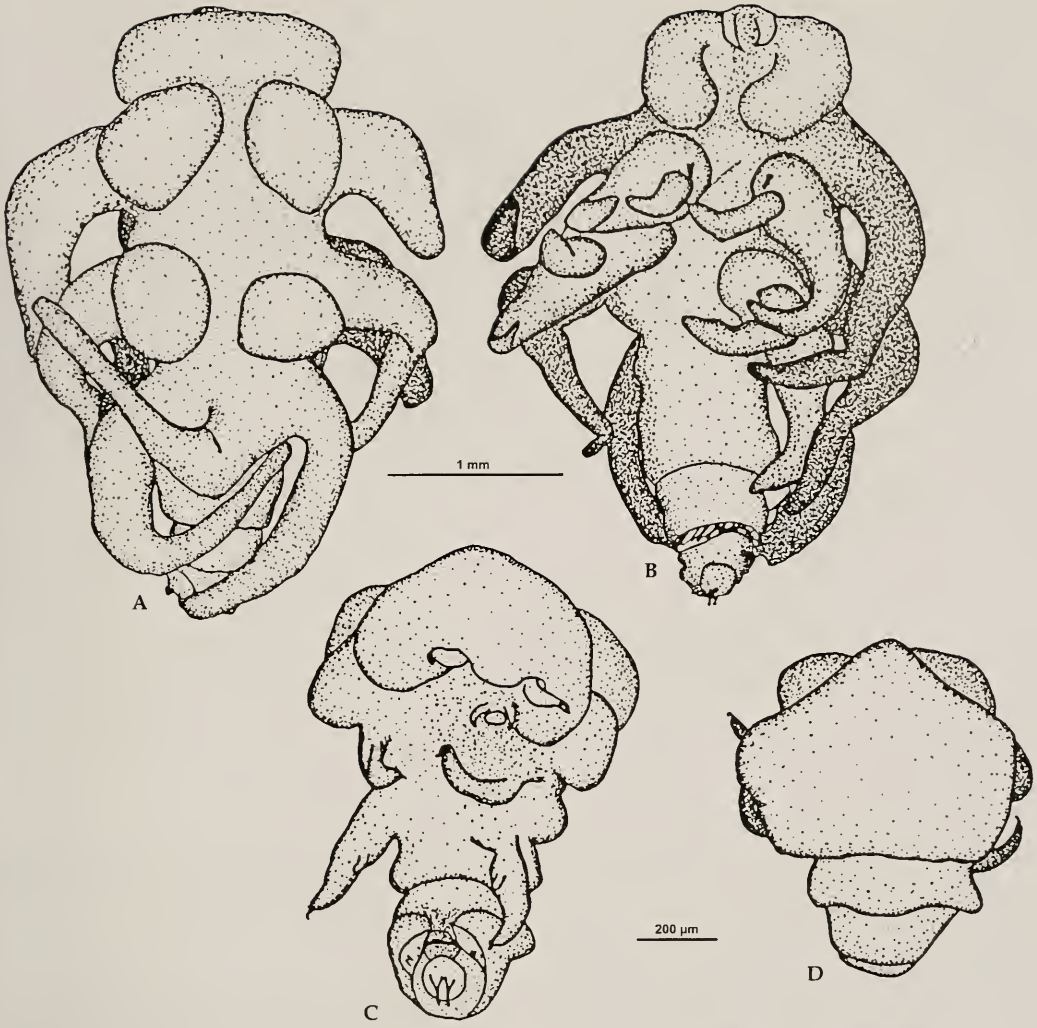

Fig. 7. *Ismaila occulta* Ho. **A.** ♀, dorsal view. **B.** ♀, ventral view. **C.** ♂, ventral view. **D.** ♂, dorsal view.

was labelled with '*I. monstrosa*, Puerto Montt', and no host was mentioned. This specimen (Fig. 5) resembles the parasite from *A. incerta* which was sketched by Bergh (1898: pl. 29, fig. 26) as having very thick exopodits. According to Bergh (1898), the parasite specimen from *A. papillosa serotina* also looks like that from *A. incerta*. However, there is no original illustration nor any museum material remaining, thus, this statement cannot be verified. Parasites found in *A. papillosa serotina* and described in this study (Figs 25B,C) are clearly distinct from *I. obtusa* since they have a grazile body shape.

In spite of considerable morphological differences, Bergh (1898) assigned the parasite of *A. incerta* to *I. monstrosa* and did not differentiate it from the parasite found in *A. papillosa serotina*. It thus seems that Bergh generally assigned all splanchnotrophids to *I. monstrosa* as far as they were distinguishable from *Splanchnotrophus*. With our present knowledge we can conclude that *A. incerta* is the host of the parasite specimen from the ZMB described above and that the museum label was probably wrong.

The specimen from the ZMB differs significantly from the holotype of *I. monstrosa*, as well as from all other congeners, due to its stocky body with voluminous and unique, distally flattened dorsal processes and exopodits. Thus it is described as *I. obtusa*, spec. nov.

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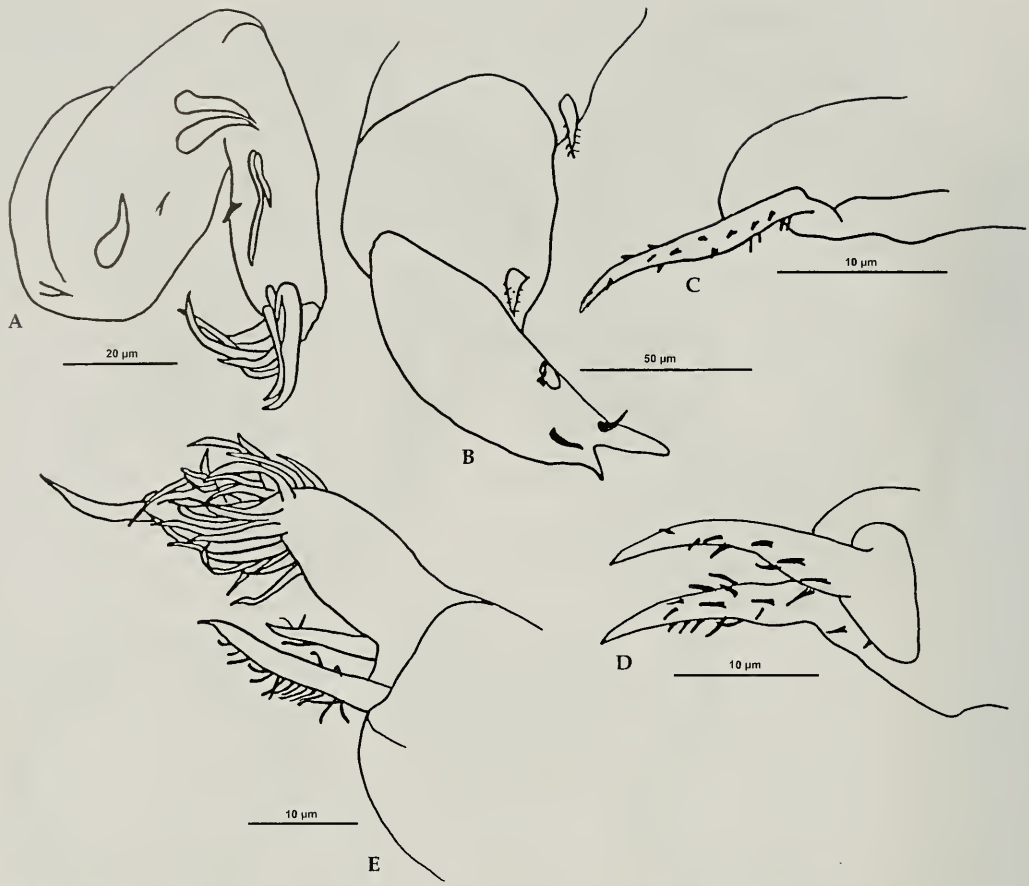

Fig. 8. *Ismaila occulta* Ho, cephalic appendages. **A.** Antennule (left). **B.** Antenna (right). **C.** Mandible (left). **D.** Maxillule (left). **E.** Maxilla (left).

Ismaila jenseniana, spec. nov.
Fig. 6

Ismaila monstrosa Bergh, 1867: Jensen 1987: 75-84 (*partim*); Schrödl 1997: 45 (*partim*).

Types. Holotype: ♀, ZMUC, collected at St. Thomas, Virgin Islands, from *Ercolania funerea* Costa, 1867, 28 April 1987.

Etymology. Named in honor of Dr. Kathe Jensen.

Description (Figs 6A,B)

Delicate body measuring 1.2 mm in length. Cephalic appendages were lost due to damage of the head.

Exopodit of second thoracopod longer and thicker than endopodit. Exopodit of third thoracopod shorter than endopodit (artifact?). Endopodit about the same length as inner process, both equally thick.

First pair of dorsal processes damaged. Processes of second pair measuring 0.4 mm, those of third pair 0.3 mm in length, just like the medio-dorsal process. One additional pair of unbranched processes is situated laterally between first and second pair of dorsal processes and second and third thoracopods. They are called "dorso-lateral processes" in the following.

Remarks. This specimen from St.Thomas which was described by Jensen (1987) as *I. monstrosa*, at first glance resembles the holotype of *I. monstrosa* by Bergh (1867), despite of the fact that both specimens were found parasitizing two rather different host groups (sacoglossan *vs.* nudibranch hosts). Body proportions are just slightly different, and, in contrast to all other congeners, these specimens have 3rd thoracopods with equally long endopods and the endopods' inner processes (see Tab. 1). The fundamental difference of *I. monstrosa* det. Jensen, 1987, however, is the unique additional pair of dorso-

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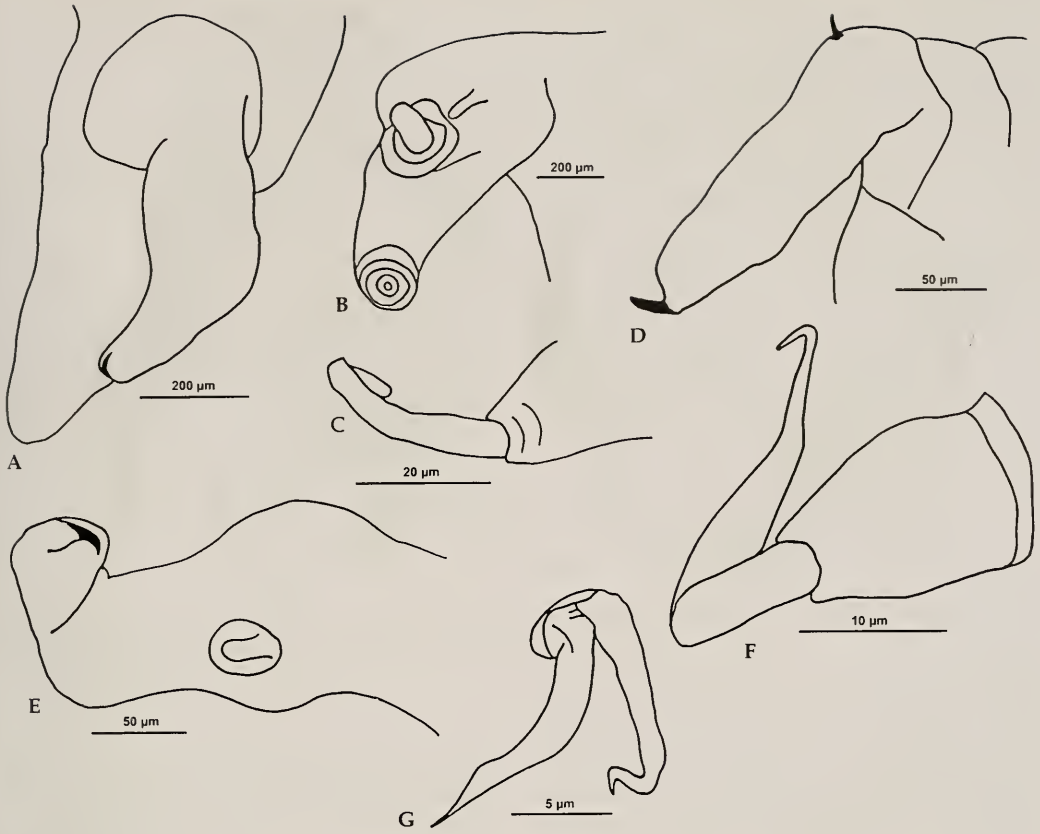

Fig. 9. *Ismaila occulta* Ho, legs. **A.** 2nd thoracopod (♀, right). **B.** 3rd thoracopod (♀, right). **C.** 4th thoracopod (♀, right). **D.** 2nd thoracopod (♂, left). **E.** 3rd thoracopod (♂, left). **F.** 4th thoracopod (♂, left). **G.** 5th thoracopod (♂, right).

lateral processes which is absent in *I. monstrosa* and in any other species of the genus *Ismaila* (Tab. 1). Therefore, the parasites from the sacoglossan *Ercolania funerea* described by Jensen (1987) are considered to be a new species, *Ismaila jenseniana*, spec. nov.

Ismaila occulta Ho, 1981
Figs 7-9

Ismaila occulta Ho, 1981: 130-136; Ho 1987: 67-83; Jensen 1987: 75-83.

Types. Allotype: ♂, National Museum of Natural History Washington (USNM), No. 184045; collected at Alamitos Bay, California. Host: the nudibranch *Dendronotus iris* Cooper, 1863. – Paratypes (3♀♀, 3♂♂): USNM No. 184046; collected together with the allotype. 1♀ (3.4 mm) and 1♂ (1.1 mm) paratype examined by SEM.

Description (♀) (Figs 7A,B, 8, 9A-C)

Delicate body, measuring up to 3 mm in length. Cephalic appendages resemble Ho's (1981) original description and are similar to cephalic appendages of other congeners which could be examined in detail by SEM (see *I. androphila*, spec. nov. and genus diagnosis).

Exopodit of second thoracopod thicker and longer than endopodit. Exopodit of third thoracopod longer and thicker than endopodit. Inner process of endopodit rudimentary and very small. Two pointed processes of fifth thoracopod arise from a common base.

Three pairs of dorsal processes, medio-dorsal process between third pair; all processes conical with tip almost pointed.

Description (♂) (Figs 7C,D; 9D-G)

Body size up to 1.1 mm. Cephalic appendages as in females and as in all congeners examined in detail.

Third thoracopod with a, compared to endopodit, very small and reduced inner process. Both processes of fifth toracopod arise from a common base.

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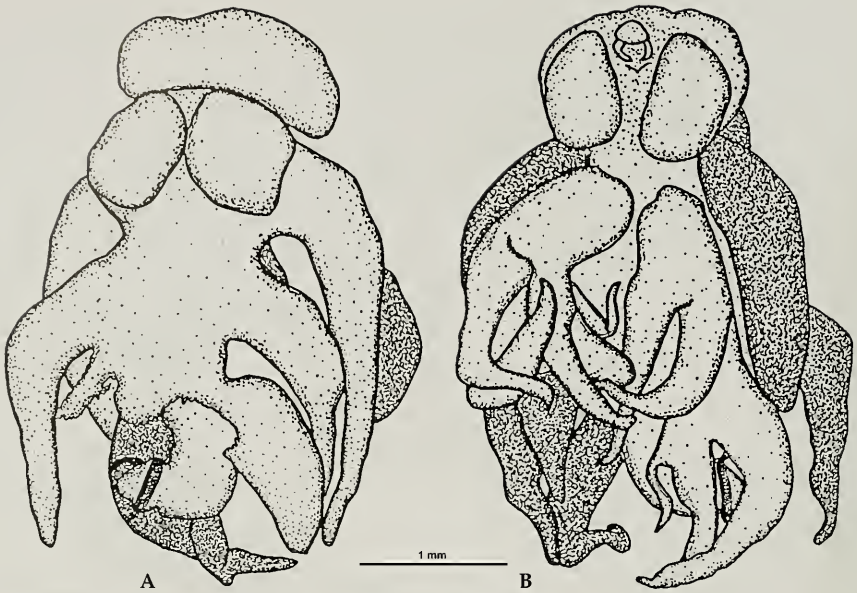

Fig. 10. *Ismaila belciki* Ho, ♀ (damaged postero-dorsally). **A.** Dorsal view. **B.** Ventral view.

Remarks. The results of our re-examination using SEM correspond to a great extent with the light-microscopical original data presented by Ho (1981). The mandibles seem to be longer than illustrated by Ho (1981: fig 1I). The shape of the (second) maxilla differs from the original description in that the finger-shaped third segment does not bear stiff spinules but numerous long hairs. Thus, the maxilla of *I. occulta* closely resembles that of other congeners.

The number and morphology of thoracopods agrees with the original description of *I. occulta*. Interestingly, the fifth pair of thoracopods in *I. occulta* consists of two small, pointed processes arising from a common base (Fig. 9G), while in all other *Ismaila* species which could be studied in detail the two processes arise separately. Due to this feature, with present knowledge, it is possible to distinguish *I. occulta* from *I. aliena*, spec. nov. (Fig. 18D,H), *I. damnosa*, spec. nov. (Fig. 21G) and *I. belciki* (Fig. 12F).

Ismaila occulta can be easily distinguished from *I. belciki* Ho, 1987 and from all other species of the genus *Ismaila*: the inner process of the endopodit of the third thoracopod is just an atrophied, rudimentary appendage in female *I. occulta*. The same is true for the endopodit of the third thoracopod of male *I. occulta*. In all other congeners these processes are much longer (Tab. 1).

Ismaila belciki Ho, 1987
Figs 10-12

Ismaila monstrosa Bergh, 1867: Belcik 1981: 16-25 (*partim*); Jensen 1987: 75-84 (*partim*).
Ismaila belciki Ho, 1987: 109-111; Huys 2001: 118-123.

Material studied. 6♀♀, 5♂♂, partly damaged (3♀♀, 3♂♂: ZSM No. 20010026); collected at Fossil Point, Empire, Oregon, 20 June 1963 (preserved 23 June 1963). 3♀♀, 1♂, partly damaged (2♀♀, 1♂: ZSM No. 20010027); collected at Charleston, Small Boat Basin, Oregon, 24 July 1963. Host: all specimens were from the nudibranch *Janolus fuscus* O'Donoghue, 1924. 3♀♀, 3♂♂ examined by SEM.

Description (♀) (Figs 10, 11, 12A,B)

Delicate body measuring 1.8-4.4 mm. None of the specimens had egg sacs.

Cephalic appendages like in other *Ismaila* species (see *I. androphila*, spec. nov. and genus diagnosis).

Endopodit of second thoracopod almost as long as exopodit. Exopodit of third thoracopod slightly longer and thicker than endopodit. Inner process of endopodit thinner but almost as long as endopodit. Further thoracopods not visible, because this region is covered by host tissue in all specimens examined.

Thorax dorsally with three pairs of processes and one single medio-dorsal process. All processes are conical, unbranched and relatively thin compared to body.

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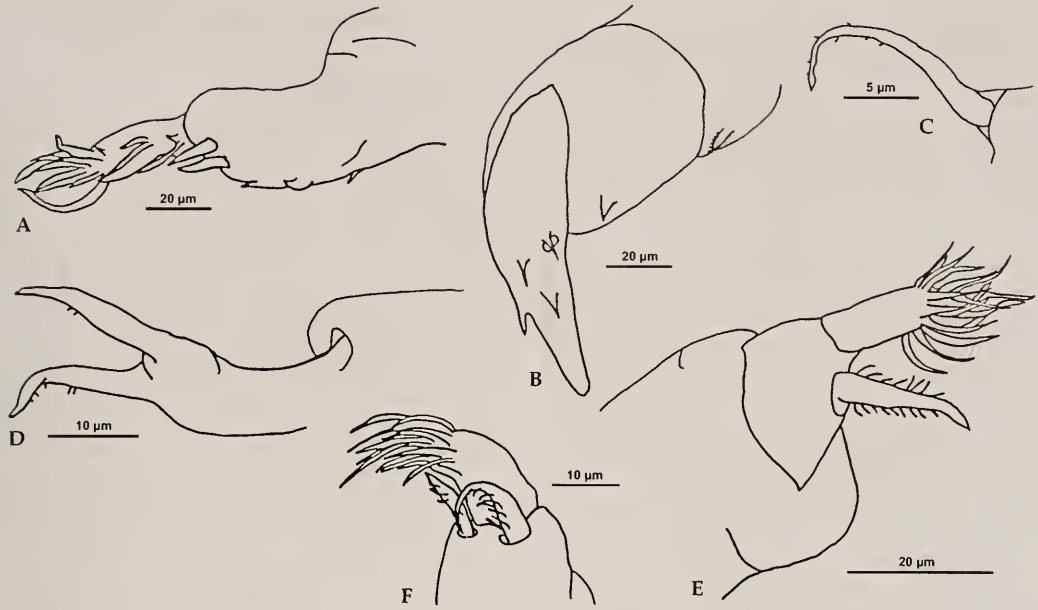

Fig. 11. *Ismaila belciki* Ho, cephalic appendages (♀). **A.** Antennule (right). **B.** Antenna (right). **C.** Mandible (right). **D.** Maxillule (left). **E.** Maxilla (right). **F.** Tip of Maxilla, inner side.

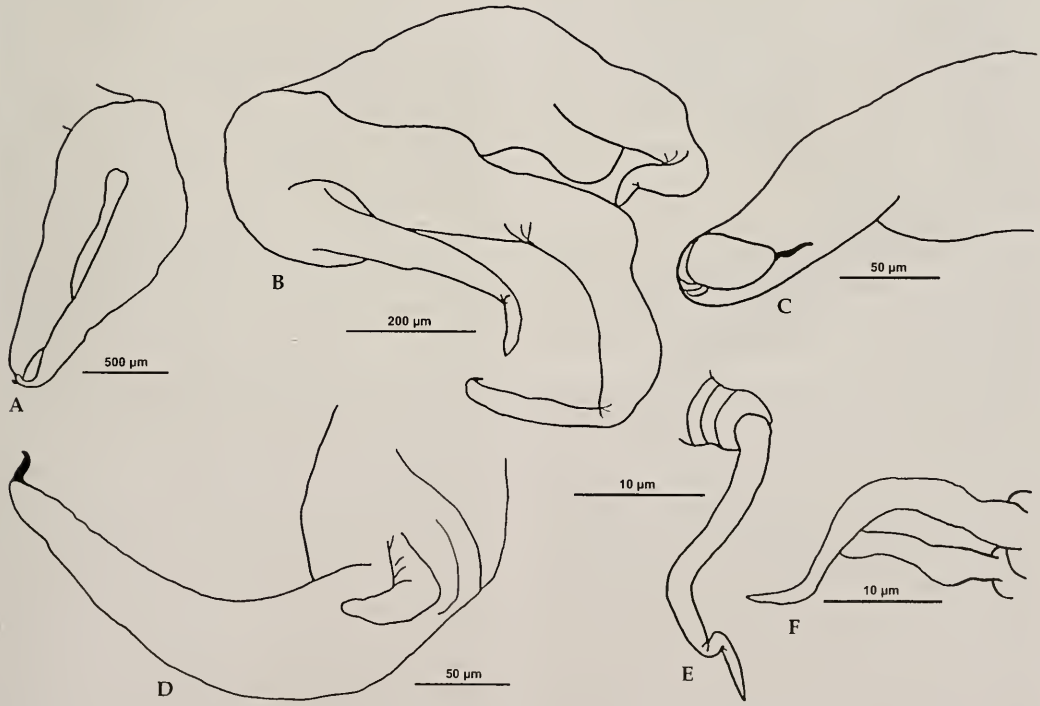

Fig. 12. *Ismaila belciki* Ho, legs. **A.** 2nd thoracopod (♀, right). **B.** 3rd thoracopod (♀, left). **C.** 2nd thoracopod (♂, right). **D.** 3rd thoracopod (♂, right). **E.** 4th thoracopod (♂, right). **F.** 5th thoracopod (♂, right).

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Description (♂) (Figs 12C-F)

Body size 1.5-2.0 mm. Cephalic appendages resemble those of females as well as those of congeners.

Second to fourth and sixth thoracopods as usual (see genus diagnosis). Fifth thoracopod consisting of two very small, pointed processes arising separately.

Remarks. Belcik (1981) described one pair of antennules, antennae, mandibles and maxilles in his material. Additionally, a labrum and a labium with lateral appendages were mentioned. Small sclerotized structures underneath the labium were interpreted as being remainders of maxillipeds. Regarding antennulae and antennae, the results of our re-examination of *I. belciki* confirm the original description. The sickle-like mandibles seem to be longer than illustrated by Belcik (1981: Figs 9, 10); in addition, the SEM-examination showed tiny hairs, which were not detected by light microscopical examination, on the mandibles. Overlooked by Belcik (1981), *I. belciki* possesses maxillules (Fig. 11D) which resemble in structure those of other congeners. As also seen by Huys (2001), the maxilles of *I. belciki* bear a second hind process, and thus closely resemble the maxilles of *I. occulta*. In contrast to the original description by Belcik (1981), no traces of maxillipeds have been detected in *I. belciki*, nor in any other *Ismaila* species. Ho (1981) assumed that there are no maxillipeds in adult *I. occulta*, while in larval stages (copepodit II) he found small knobs, which represent the maxillipeds; these knobs already disappeared in the copepodit III (Ho, 1987b).

Due to tissue covering the relevant regions, the small thoracopods of female *I. belciki* could not be examined by SEM. Since male *I. belciki* agree with congeners regarding the number and structure of thoracopods (see genus diagnosis), this can also be assumed for females.

Ismaila belciki is distinguishable from other *Ismaila* species with delicate body shape due to body proportions (Tab. 1). The inner process of the endopodit of the third thoracopod is slightly shorter than the endopodit, while in *I. monstrosa* and *I. jenseniana*, spec. nov. they have the same length. In *I. androphila, spec.* nov, *I. magellanica*, spec. nov., and *I. socialis*, spec. nov. the inner process reaches just half the length of the endopodit and the exopodit is obviously thicker than the endopodit. In *I. belciki* they have about the same diameter. In *I. occulta* the inner process of the endopodit of the third thoracopod is only a rudimentary, tiny appendage. The dorsal processes of *I. aliena*, spec. nov. are as long as the body, while they measure about half of the body size in *I. belciki*.

Ismaila androphila, spec. nov.

Figs 1A, 2A, 13-15

Ismaila sp. Schrödl, 1996: 31.

Types. Holotype: ♀, ZSM No. 20010011. – Allotype: ZSM No. 20010012. – Paratypes: 5♂♂ (ZSM 20010013), 5♀♀ (ZSM 20010014), 5♂♂, 6♀♀ on SEM-mounts (ZSM 20010015). All collected by M. Schrödl, Bahia de Coliumo (36°32'S, 72°57'W), Chile, 25 January 1994. Hosts: 50 *Okenia luna* Millen, Schrödl, Vargas & Indacochea, 1994.

Additional material. 38♀♀, 109♂♂, collected together with the types from 50 *Okenia luna*. 14♂♂ and 9♀♀ examined by SEM.

Etymology. The species name refers to the several males associated with a single female parasite per host.

Description (♀) (Figs 2A, 13B,C, 14, 15A-C)

Delicate body measuring 1.9-4.2 mm in length.

First segment of antennule (Fig. 14A) with three short hairs on ventral side; distal portion bears two long hairs. Base of second segment bearing two or three thin hairs ventrally, one shorter than the other(s); distal edge with usually seven long, thin hairs. First and second segments of antenna (Fig. 14B) with a stubby inner seta each. Third segment hook-shaped, bearing three setae on ventral side, of which one covers a small hole, possibly the opening of an antennal gland. Mandible (Fig. 14C) runs crosswise under the labrum, often covered by the latter. Base of mandible thick and oval, extending to a sickle-shaped ramus sparsely covered with fine, short hairs. Maxillule (Fig. 14D) curved inwards, distal third biramous, each ramus with hairs on the edge. First segment of maxilla (Fig. 14E) trapezoidal. Second segment smaller, bearing third segment and an additional process. Third segment carries approximately 15 long, terminal hairs. The process of the second segment is thin, with a pointed tip, and has short hairs on one side. It is not evident from any of the individuals examined by SEM if a second process behind the first one (as present in *I. occulta* and *I. belciki*) is present or absent.

Labium tongue-shaped and hairy. Distally, hairs are limited to the lateral portions of the labium. From the base of the labium arises a pair of paragnath, hairy lobes laterally. In the centre of the labium there is a triangular area with hairs. On both sides, between the central hairy area and the hairy paragnath lobes, there is a passage without hairs (see also Fig. 1C).

First thoracopod (maxillipeds) absent. Second thoracopod (Fig. 15A) branched into exo- and endopodit with about same lengths. Exopodit conical with a rounded tip, endopodid thinner, its tip bearing a claw. Exopodit and endopodit of third thoracopod having same length, but endopodit thinner

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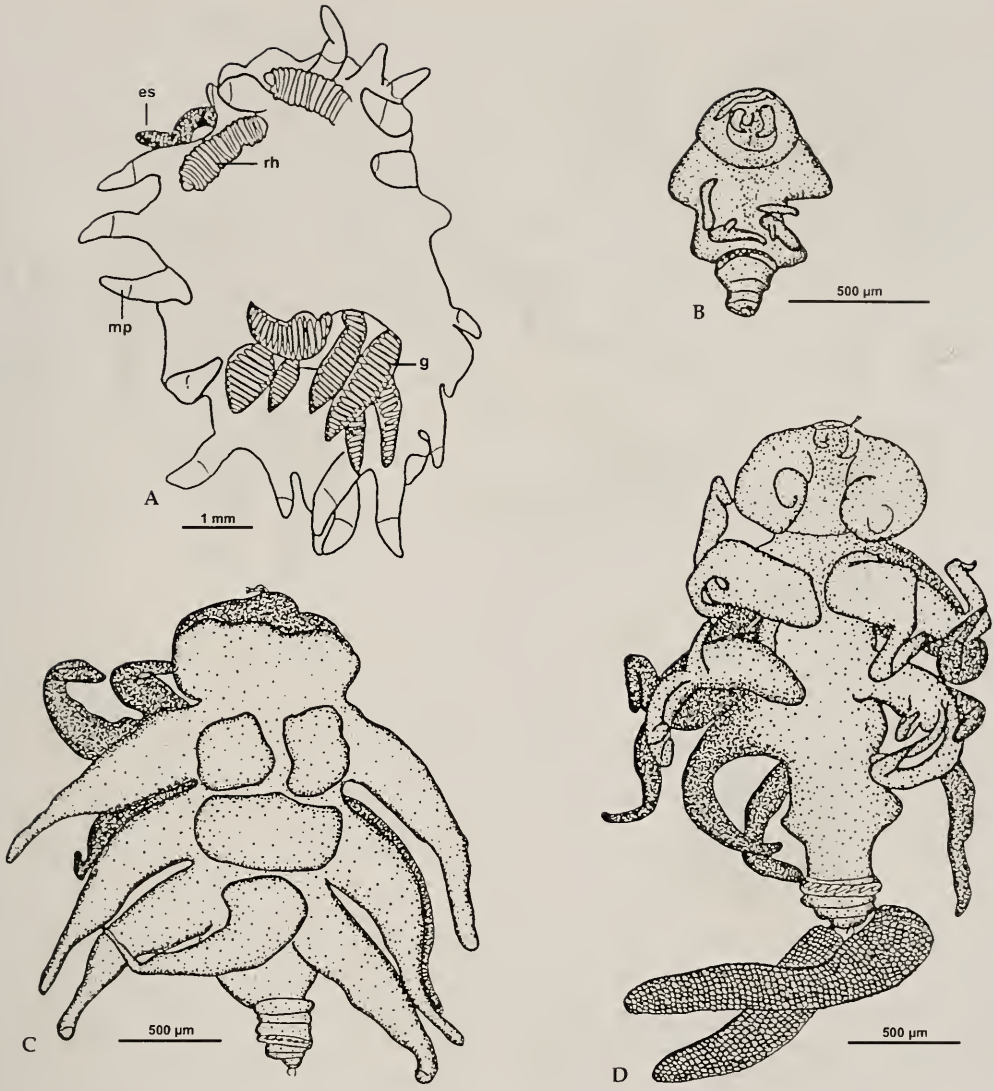

Fig. 13. *Ismaila androphila*, spec. nov. **A.** Nudibranch host specimen (*Okenia luna*) with egg-sacs protruding laterally under the mantle rim. **B.** ♀ parasite, ventral view. **C.** ♀ parasite, dorsal view. **D.** ♂ parasite, ventral view.

than the exopodit and bearing a basal, small and thin process (Fig. 15B). Protopodit of fourth thoracopod (Fig. 15C) round in cross-section, bearing a rather thin and pointed second limb. The fourth thoracopod is very small compared to second and third thoracopods. Posterior to the fourth thoracopod the body narrows and carries a sclerotized ring. No fifth thoracopods are visible because the area around the sclerotized ring is covered with host tissue or contracted. Behind the ring the body narrows further, sixth thoracopods are absent.

First visible segment of abdomen bears elongate and straight egg sacs.

Thorax with three pairs of dorsal processes. In adult females these processes are shorter than whole body, reaching about 60 % of total body length. One single process is situated medio-dorsally between the third pair of dorsal processes.

Description (♂) (Figs 13D, 15D-F)

Body length 0.6-1.6 mm, width of cephalothorax 0.3-1.5 mm.

Cephalic appendages are identical with those of the ♀.

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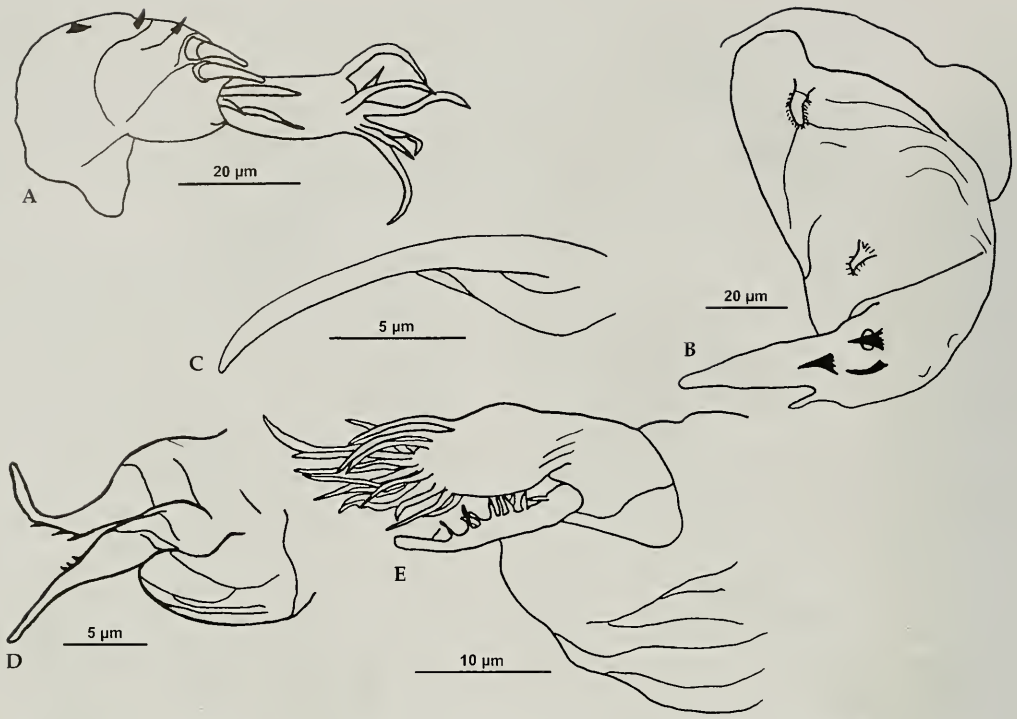

Fig. 14. *Ismaila androphila*, spec. nov., cephalic appendages (♀). **A.** Antennule (right). **B.** Antenna (left). **C.** Mandible (left). **D.** Maxillule (left). **E.** Maxilla (left).

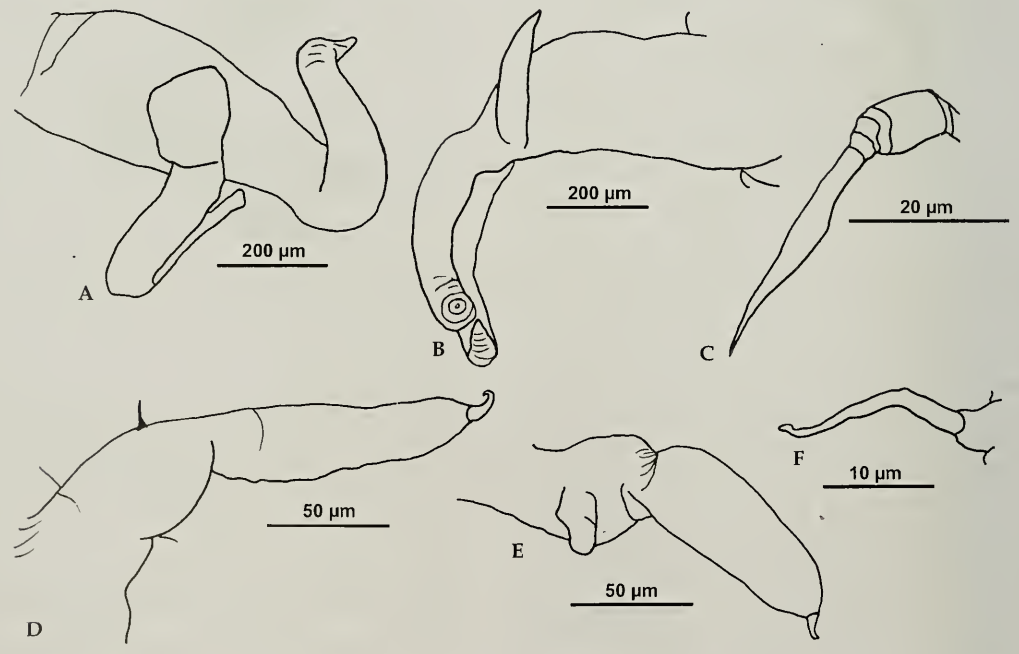

Fig. 15. *Ismaila androphila*, spec. nov., legs. **A.** 2nd thoracopod (♀, left). **B.** 3rd thoracopod (♀, right). **C.** 4th thoracopod (♀, right). **D.** 2nd thoracopod (♂, left). **E.** 3rd thoracopod (♂, right). **F.** 4th thoracopod (♂, right).

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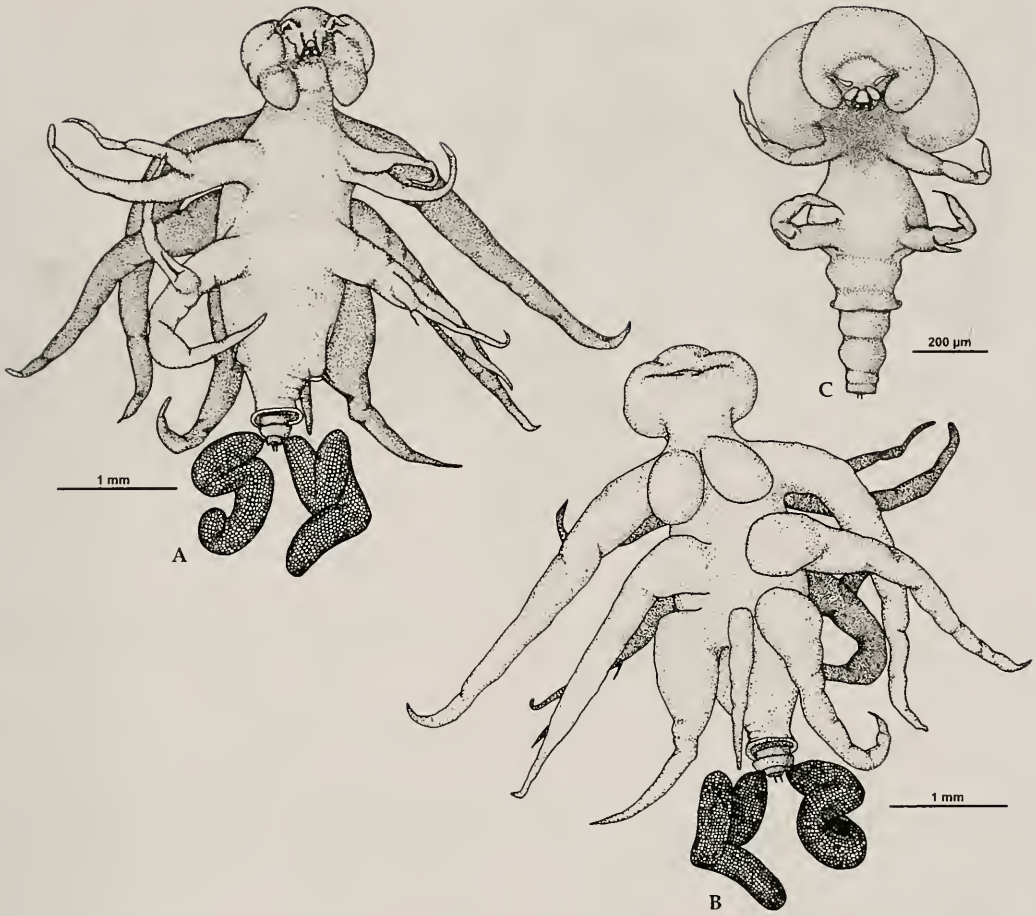

Fig. 16. *Ismaila aliena*, spec. nov. **A.** ♀ parasite, ventral view. **B.** ♀ parasite, dorsal view. **C.** ♂ parasite, ventral view.

Thorax ventral: tip of the second thoracopod (Fig. 15D) armed with a claw. Protopodit of third thoracopod (Fig. 15E) with two branches; a long, thick and pointed exopodit with a claw, and a much shorter and thinner endopodit with a blunt tip. Fourth thoracopod resembling that of the female. Behind the fourth thoracopod there is a sclerotized ring. Males are fixed on hind body of females within a ring of (host?) tissue around the sclerotized ring. It was not visible if there is a fifth thoracopod or not because this area was strongly contracted in all individuals examined. Sixth thoracic segment (segmentation indistinct, see discussion) is dorso-laterally drawn into a pair of elongate genital lobes. Three apical setae on each of these lobes probably represent thoracopod six. Two of the setae are close to each other, the third is slightly higher and situated more laterally. The area between the genital lobes is deepened.

Genital pores presumably are situated laterally on the first abdominal segment but covered by the genital lobes. The third visible segment of the abdomen bears, as in females, two caudal rami each with two or three hairs on the base.

Males lack any dorsal processes, but there are sac-shaped lateral protrusions on the cephalothorax. One is above the second thoracopod and a smaller one above the third thoracopod. Both protrusions are distinctly set off from each other.

Remarks. Millen et al. (1994) and Schrödl (1996) already observed parasites of the genus *Ismaila* in *Okenia luna* (see Fig. 2A). Not only these endoparasites are confirmed as belonging to *Ismaila androphila*, spec. nov. but, obviously, also the cuticular giant "penis" of *O. luna* described by Muñoz et al. (1996: fig. 2B) can be recognized as a somewhat abstracted female *Ismaila* clearly showing three pairs of dorsal

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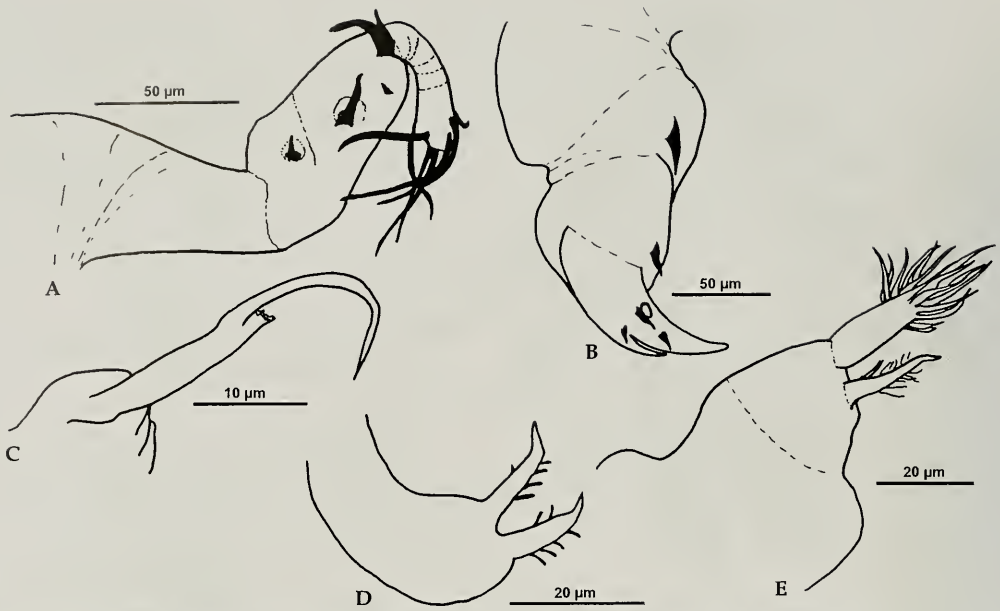

Fig. 17. *Ismaila aliena*, spec. nov., cephalic appendages (♀). **A.** Antennule (left). **B.** Antenna (right). **C.** Mandible (right). **D.** Maxillule (right). **E.** Maxilla (right).

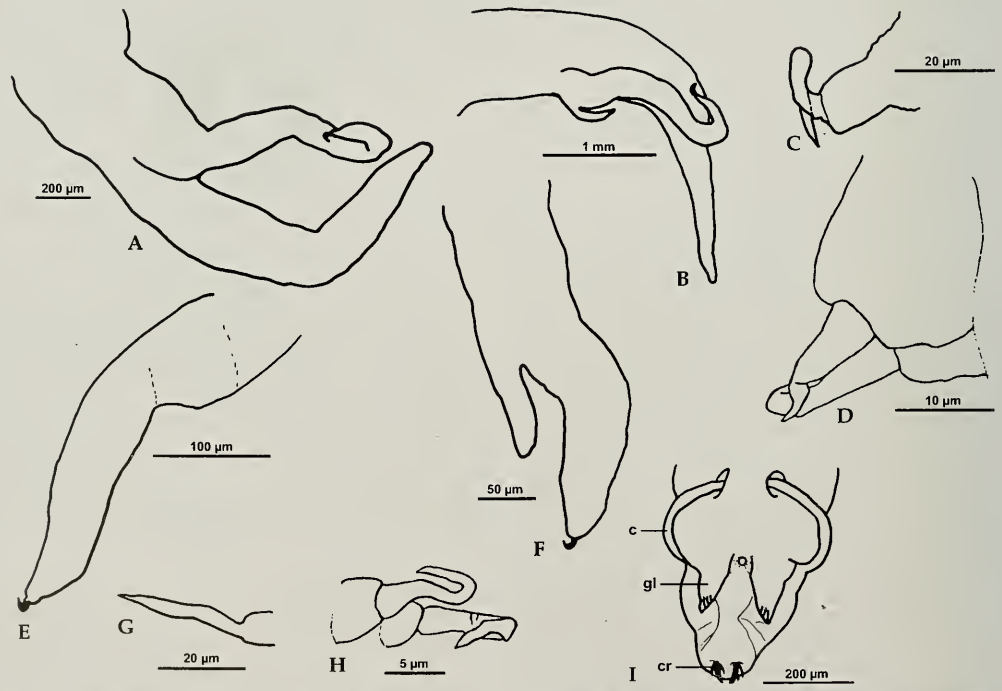

Fig. 18. *Ismaila aliena*, spec. nov., legs. **A.** 2nd thoracopod (♀, left). **B.** 3rd thoracopod (♀, left). **C.** 4th thoracopod (♀, right). **D.** 5th thoracopod (♀, right). **E.** 2nd thoracopod (♂le, left). **F.** 3rd thoracopod (♂, right). **G.** 4th thoracopod (♂, left). **H.** 5th thoracopod (♂, right). **I.** Posterior body portion. Note the cuticular ring (**c**), genital lobes (**gl**) with 3 setae (= 6th thoracopod) each, and caudal rami (**cr**).

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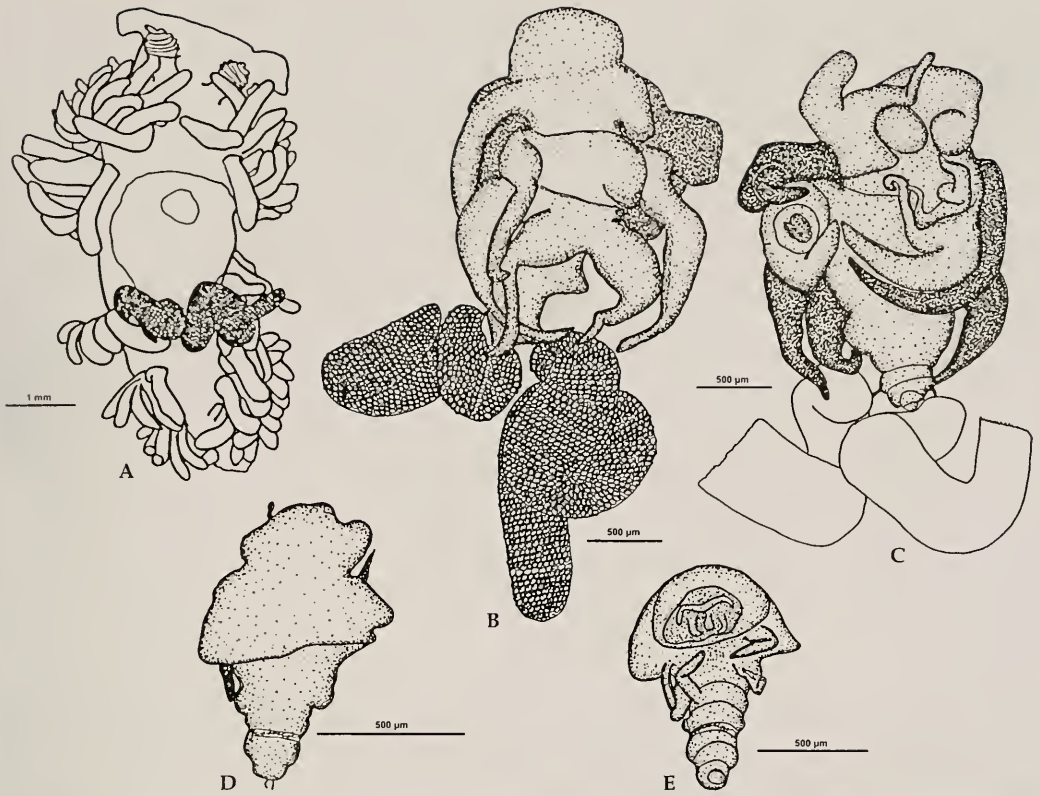

Fig. 19. *Ismaila damnosa*, spec. nov. **A.** Nudibranch host specimen (*Flabellina* sp. 1) with egg-sacs protruding dorsally, posterior to the pericardium. **B.** ♀ parasite, dorsal view. **C.** ♀ parasite, ventral view. **D.** ♂ parasite, dorsal view. **E.** ♂ parasite, ventral view.

processes and a single median process.

All individuals examined in this study possess very little morphological variation even regarding details like the number and position of hairs, claws and setae (see Tab. 1), therefore they all are regarded to belong to the same species. *Ismaila androphila*, spec. nov. is distinguishable from the otherwise similar *Ismaila magellanica*, spec. nov. and *I. socialis*, spec. nov. due to slight but consistent morphological differences regarding proportions of the 3rd thoracopod, i.e. the endopod being much thinner than the exopod, while being equally thick in *I. magellanica*, spec. nov. and *I. socialis*, spec. nov. (see Tab. 1).

Biological information. The infection rate of *O. luna* with *I. androphila*, spec. nov. was 100 % of the extensive material studied herein; this is the highest infection rate of an opisthobranch population with splanchnotrophids ever documented. In each host there was just a single female parasite together with one to seven males. At least one male was always associated with its hind body to the hind body of the female. The hosts were never obviously damaged by the parasites. In 98 % of the 50 examined hosts the female was lying crosswise in the anterior body cavity of the host, with egg-sacs protruding from the anterior left body portion of the host, mostly from the lateral body wall just below the mantle rim (Figs 2A, 13A).

Ismaila aliena, spec. nov.
Figs 1B,C, 2B, 16-18

Types. Holotype: ♀, ZSM 20010001, Bahía de Coliumo, Chile, 27 February 1995. – Allotype: ZSM 20010002, 8 April 1992. – Paratypes: 11♂♂ (ZSM 20010003), 6 April 1992; 5♂♂ (ZSM 20010004), 22 April 1992; 1♀ (ZSM 20010005), 6 April 1992; 10♀♀, 1 associated ♂ (ZSM 20010006), 8 April 1992; 5♀♀ (ZSM 20010007), 22 April 1992; 14♀♀, 6 juvenile ♀♀, 63♂♂ on 11 SEM-mounts (ZSM 20010000), April 1992. All types collected by M. Schrödl, Javier Sanchez and Claudio Pérez, Bahía de Coliumo, Chile. Host: *Thecacera darwini* Pruvot-Fol, 1950.

Additional material. 30♀ and 249♂parasites, collected by M. Schrödl, Javier Sanchez and Claudio Pérez, Bahía

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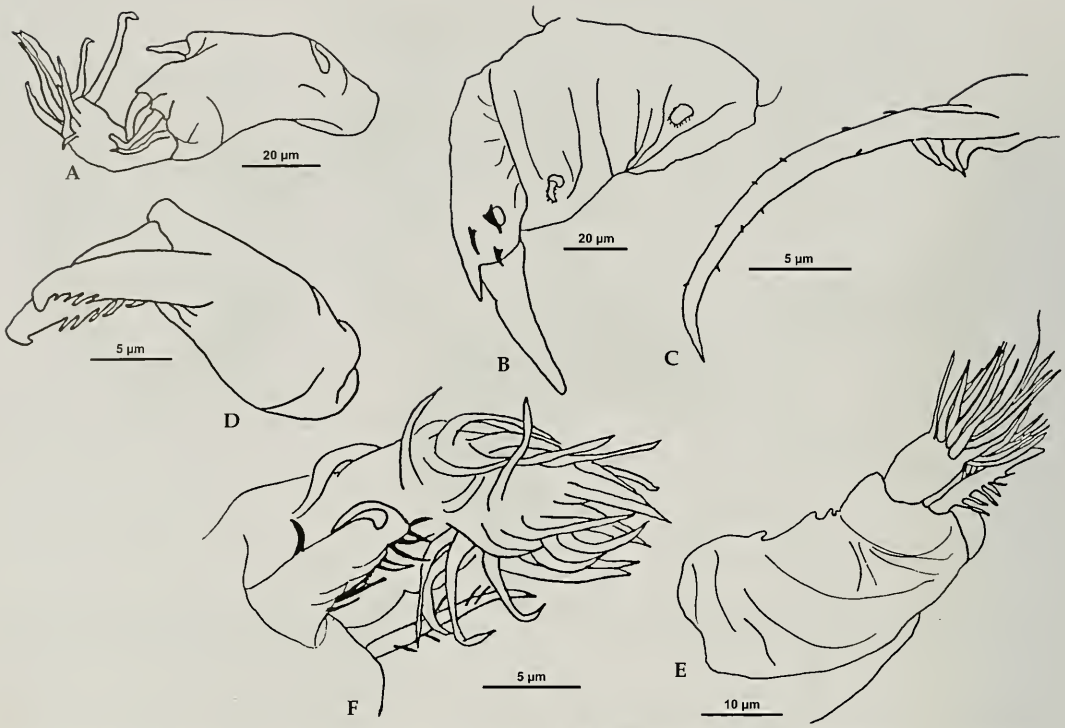

Fig. 20. *Ismaila damnosa*, spec. nov., cephalic appendages (♀). **A.** Antennule (left). **B.** Antenna (right). **C.** Mandible (left). **D.** Maxillule (left). **E.** Maxilla (right). **F.** Tip of maxilla.

de Coliumo, Chile between 31 March 1992 and 27 February 1995. 22♀♀ and 76♂♂ examined by SEM.

Etymology. The specific name is derived from the first finding of splanchnotrophids in *T. darwini*: while being observed under the binocular microscope, a male parasite protruded through the body wall of its host at the tip of one peribranchial process. This immediately recalled the first outbreak of an alien in the famous movie.

Description (♀) (Figs 16A,B, 17, 18A-D)

Delicate body, 1.2-6.9 mm body length. Body shape, cephalic and thoracic appendages as in *I. androphila* (see also genus diagnosis). The following description refers only to characters varying between different *Ismaila* species. Second thoracopod: exopodit longer and thicker than endopodit. Exopodits conical and rounded. Third thoracopod: exopodit longer and thicker than endopodit. Endopodit with small process. Fifth thoracopod: two rudimentary small, pointed processes arise separately but very close to each other.

First visible abdominal segment bears coiled, white to pink egg sacs forming one whorl.

Thorax with three pairs of unbranched dorsal processes, in adult females they are as long as the whole body. The dorso-median, unpaired process is relatively short and does not project behind the rear of the abdomen.

Description (♂) (Figs 1B,C, 16C, 18E-I)

Body length 0.7-3.1 mm. Width of cephalothorax 0.2-1.8 mm. For details regarding body shape, cephalic and body appendages see *I. androphila*, spec. nov. and genus diagnosis. Fifth thoracopod visible in some specimens, shape as in females.

Remarks. Splanchnotrophid parasites in *T. darwini* (see Fig. 1B) were already mentioned by Schrödl (1996), but not further identified. They clearly belong to the genus *Ismaila* (see Jensen 1987; genus diagnosis, this paper). All parasites from *T. darwini* examined in the present study are conspecific; they show little variation regarding number and position of hairs and setae, and proportions and shape of processes.

The most distinctive feature of female *I. aliena*, spec. nov. are the dorsal processes. They are at least as long as (or longer than) the total body, and thus much longer than in any other congener (Tab. 1). Male *I. aliena*, spec. nov. can reach considerable sizes being up to 2 times longer than males of any other congener known so far.

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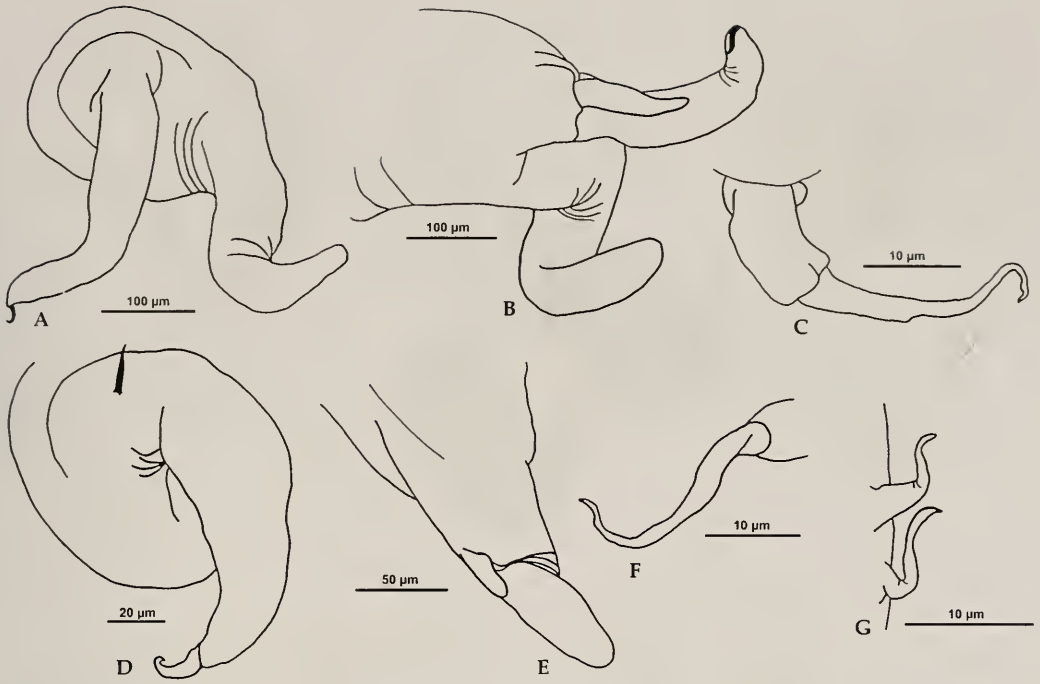

Fig. 21. *Ismaila damnosa*, spec. nov., legs. **A.** 2nd thoracopod (♀, left). **B.** 3rd thoracopod (♀, left). **C.** 4th thoracopod (♀, left). **D.** 2nd thoracopod (♂, left). **E.** 3rd thoracopod (♂, left). **F.** 4th thoracopod (♂, left). **G.** 5th thoracopod (♂, left).

Biological notes. 84.6 % of 52 (unselectively) collected *T. darwini* (31 March–22 April 1992, Bahía de Coliumo) were infected with *I. aliena*, spec. nov. 15 hosts had more than one female parasite. In every host one mature female was situated laterally left in the body cavity, with egg-sacs protruding posterior to the gills (Fig. 1B). While hosts infected with a single female parasite show no obvious damage, those infected with more than a single female tend to have swollen bodies and appear disturbed. Internally, no obvious organ damages caused by immobile mature females (beside penetrating the body wall with the abdomen) have been detected. However, the numerous males migrating freely in the body cavity of their hosts may produce obvious canals damaging the connective tissue.

Ismaila damnosa, spec. nov.
Figs 1C, 19-21

Ismaila sp. Schrödl, 1996: 37; 1997: 45-47.

Types. Holotype: ♀, ZSM 20010016. – Allotype: ZSM 20010017. – Paratypes: 5♀♀ (ZSM 20010018); 5♂♂ (ZSM 20010019); 15♂♂, 9♀♀, 3 juvenile ♀♀ on 4 SEM-mounts (ZSM 20010020). All types collected by M. Schrödl, Bahía de Coliumo, 22 January 1994. Host: *Flabellina* sp. 1 (see Schrödl 1996).

Additional material. 22♂♂, 13♀♀, collected by M. Schrödl, Bahía de Coliumo, 22 January and 31 March 1994. Host: *Flabellina* sp. 1 (see Schrödl 1996). 14♀ and 24♂ parasites studied by SEM.

Etymology. The specific name of *I. damnosa*, spec. nov. refers to the destructive effect of these parasites to their hosts.

Description (♀) (Figs 19B,C, 20, 21A-C)

Body length 0.9-3.4 mm. Body stocky. Dorsal appendages and exopodits of thoracopods voluminous. Cephalothorax not set off from trunk as distinctively as in congeners with delicate body shape.

Second thoracopod with voluminous exopodit. Endopodit as long as exopodit or slightly longer. Third thoracopod with thick exopodit; endopodit as long as or longer than exopodit.

First visible abdominal segment bears coiled egg sacs forming one whorl.

All dorsal processes (three pairs and one median process) voluminous and conical.

Description (♂) (Figs 19D,E, 21D-G)

Body length 0.7-1.6 mm. Cephalic and body appendages see *I. androphila*, spec. nov. and genus diagnosis.

Fifth thoracopod detectable, consisting of two processes with separate origins.

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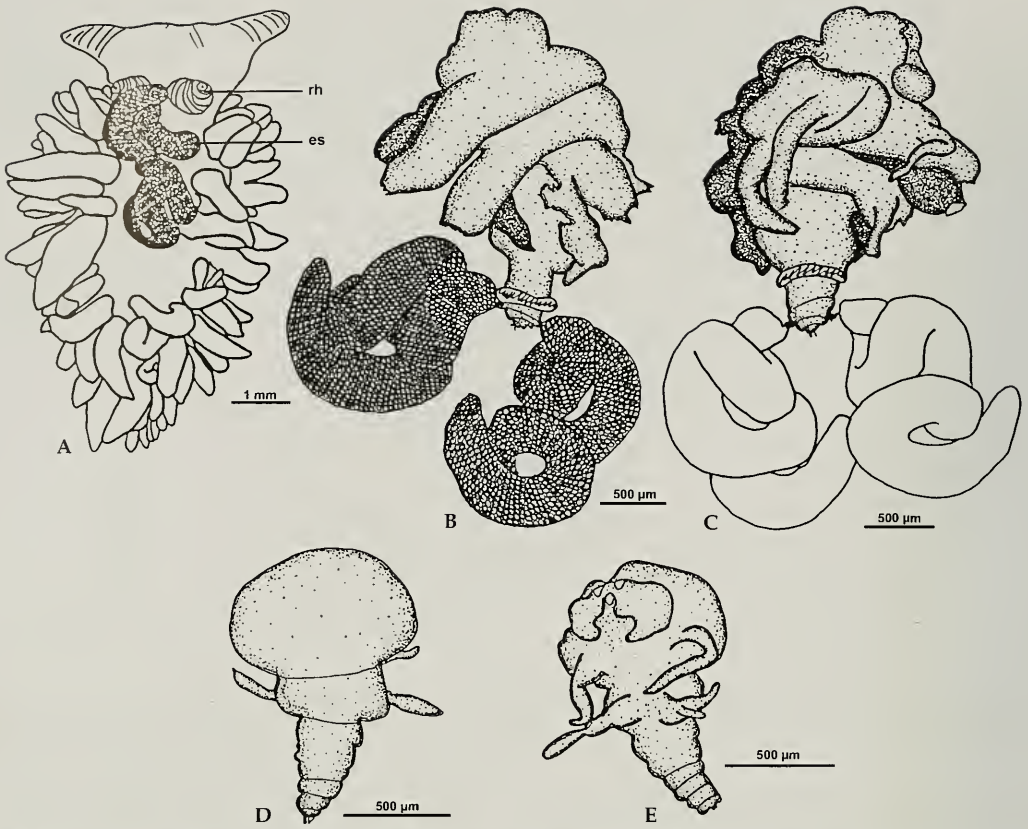

Fig. 22. *Ismaila robusta*, spec. nov. **A.** Nudibranch host specimen *(Phidiana lottini)* with egg-sacs protruding mediodorsally posterior to the rhinophores. **B.** ♀ parasite, dorsal view (dorsal processes damaged). **C.** ♀ parasite, ventral view. **D.** ♂ parasite, dorsal view. **E.** ♂ parasite, ventral view.

Remarks. Splanchnotrophids were already mentioned from *Flabellina* sp. 1 (Schrödl 1996) and their harmful influences on their hosts were shown by Schrödl (1997). The present study proves the parasites of *Flabellina* sp. 1 as belonging to the genus *Ismaila* (see Jensen 1987; genus diagnosis). All specimens examined are conspecific since there is very little morphological variation. *Ismaila damnosa*, spec. nov. shows a conspicuous, stocky and voluminous shape which is distinctive to all congeners with delicate body shape (Tab. 1). Also the proportions of dorsal processes and of thoracopod expodits are different to those of delicate species. Only two further *Ismaila* species have a stocky shape, *I. robusta*, spec. nov. and *I. obtusa*, spec. nov. *Ismaila damnosa*, spec. nov. has a less stocky body and longer dorsal processes in relation to the body length than *I. robusta*, spec. nov. With its flat dorsal processes and exopodits *I. obtusa*, spec. nov. clearly differs from any other *Ismaila* species.

Biological notes. The infection rate of the 33 *Flabellina* sp. 1 examined was 66.6 %. Five of the hosts were infected with more than one (up to five) female parasites. Gonadal tissue of several hosts was heavily damaged or almost absent, while gonads of non-infected *Flabellina* sp. 1 of comparable sizes were normally developed. Strict host specifity of *I. damnosa*, spec. nov. is assumed, since a second, syntopic and common species of *Flabellina* (*Flabellina* sp. 2, see Schrödl 1996) was not at all parasitized.

Ismaila robusta, spec. nov.
Figs 22-24

Types. Holotype: ♀, ZSM 20010021 (on SEM-mount), collected 7 March 1994. – Allotype: ZSM 20010021 (on SEM-mount), collected together with holotype. – Paratypes: 2♂♂, (ZSM 20010021, on SEM mount), collected together with holotype. 4♂♂, 1♀ (ZSM 20010022, on SEM-mount), collected 7 March 1994; 1♂, 1♀ (ZSM 20010023, on SEM-

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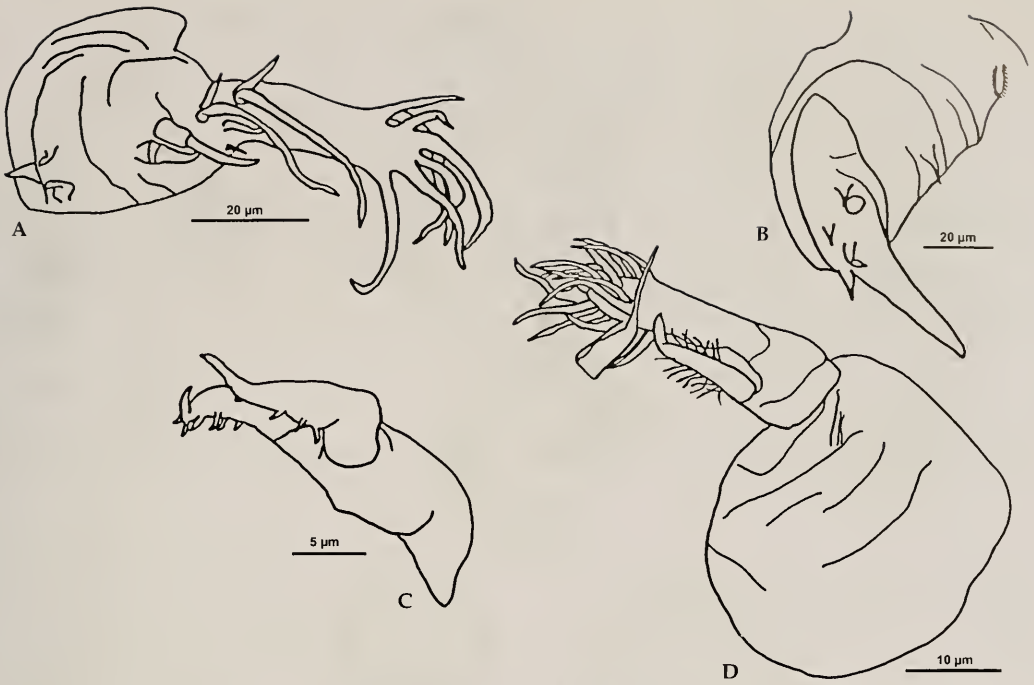

Fig. 23. *Ismaila robusta*, spec. nov., cephalic appendages (♀). **A.** Antennule (left). **B.** Antenna (right). **C.** Maxillule. **D.** Maxilla.

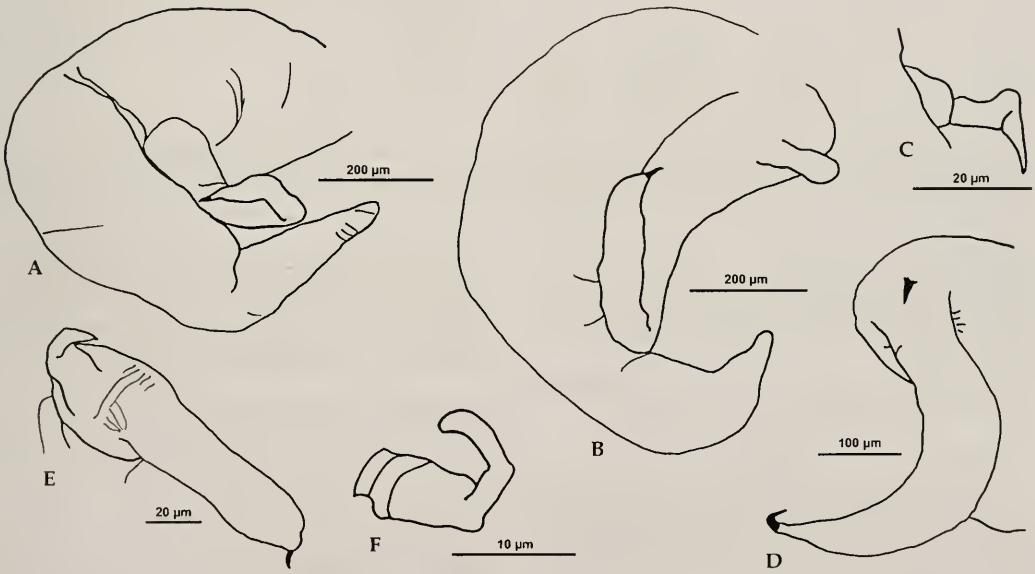

Fig. 24. *Ismaila robusta*, spec. nov., legs. **A.** 2nd thoracopod (♀, right). **B.** 3rd thoracopod (♀, right). **C.** 4th thoracopod (♀, left). **D.** 2nd thoracopod (♂, right). **E.** 3rd thoracopod (♂, right). **F.** 4th thoracopod (♂, left).

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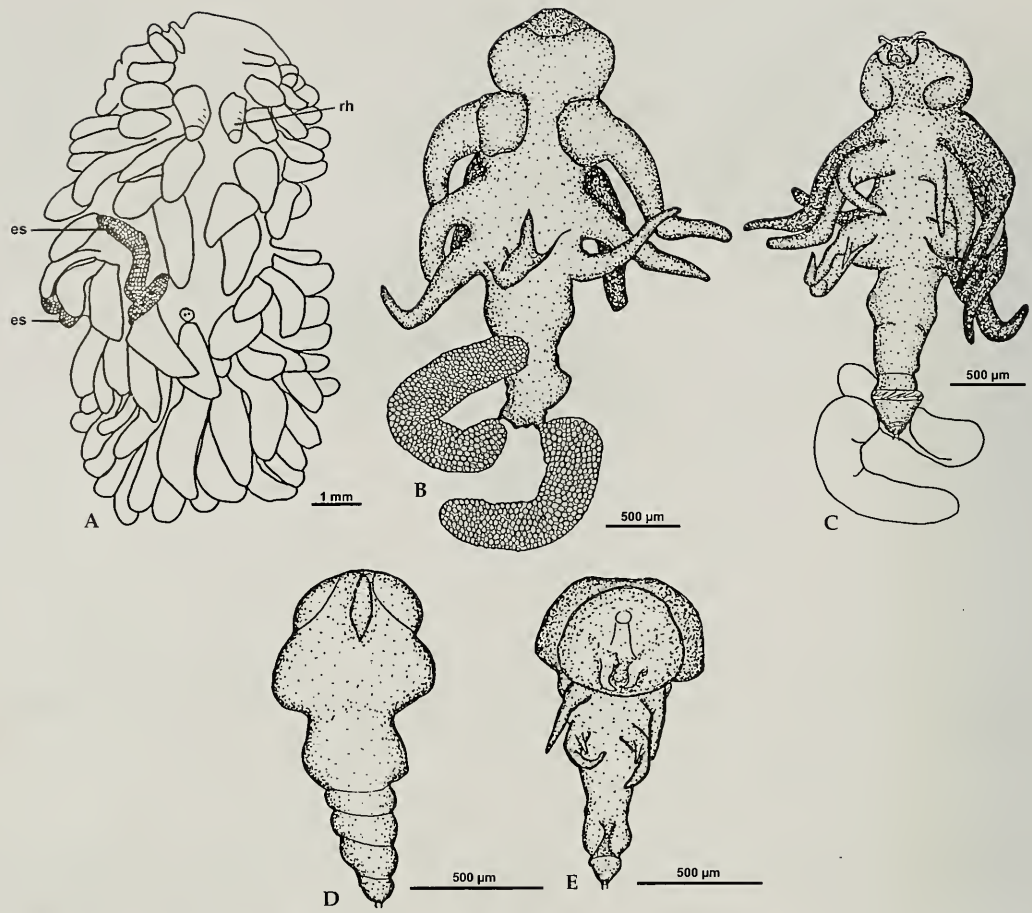

Fig. 25. *Ismaila socialis*, spec. nov. **A.** Nudibranch host specimen *(Aeolidia papillosa serotina)* with 2 pairs of egg-sacs (es) protruding latero-dorsally. **B.** ♀ parasite, dorsal view (medio-dorsal process damaged). **C.** ♀ parasite, ventral view. **D.** ♂ parasite, dorsal view. **E.** ♂ parasite, ventral view.

mount), collected 11 May 1996. All types collected by M. Schrödl, J. Sanchez and C. Pérez, Bahía de Coliumo, Chile. Host: the aeolidoidean nudibranch *Phidiana lottini* (Lesson, 1831).

Etymology. The specific name refers to the robust body form of the female parasites.

Description (♀) (Figs 22B,C, 23, 24A-C)

Very stocky body, measuring 1.9-2.4 mm. Cephalothorax not distinctly set off from trunk, body processes voluminous. Cephalic appendages as in other species of *Ismaila* (see *I. androphila*, spec. nov. and genus diagnosis).

Dorsal appendages and exopodits of thoracopods inflated. Second thoracopod with voluminous exopodit, endopodit slightly shorter and much thinner. Third thoracopod with slightly less voluminous exopodit and endopodit, both with about the same length. Fifth thoracopod not visible due to contraction.

First visible abdominal segment with pair of coiled egg sacs, forming double whorls.

Description (♂) (Figs 22D,E, 24D-F)

Body length 1.9-2.4 mm. Cephalic appendages, thoracopods and other body processes as described for *I. aliena*, spec. nov. (see also genus diagnosis). Fifth thoracopod not visible.

Remarks. All parasites found in *Phidiana lottini* belong to the genus *Ismaila* (see Jensen 1987; genus diagnosis in this paper). Females have almost no morphological variation. *Ismaila robusta*, spec. nov. differs from *I. damnosa, spec.* nov. due to its even more voluminous shape, more inflated dorsal processes, due to 2nd thoracopods with exopodits being

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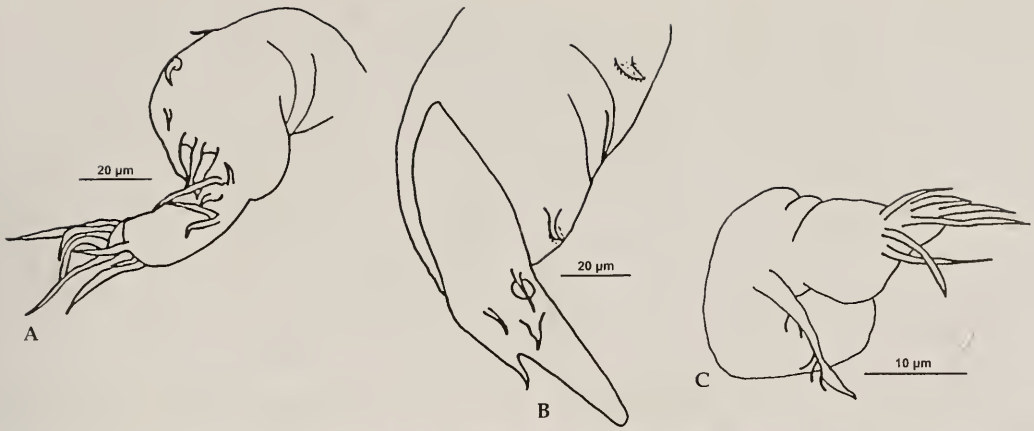

Fig. 26. *Ismaila socialis*, spec. nov., cephalic appendages (♀). **A.** Antennule (right). **B.** Antenna (right). **C.** Maxilla (right).

slightly longer than endopodits (*vs.* having the same length), and due to egg sacs coiled to a double whorl (*vs.* single whorl) (see Tab. 1). The third known congener with stout body shape, *I. obtusa*, spec. nov., differs due to its uniquely flattened dorsal processes and exopodits.

Biological information. Of more than 200 *P. lottini* examined, just three were infected by single ♀ parasites with 1-4♂♂ associated to their abdomens. Egg sacs protruded dorsally between the hosts's cerata (Fig. 22 A).

Ismaila socialis, spec. nov.
Figs 25-27

Types. Holotype: ♀, ZSM 20010008. – Allotype: ZSM 20010009. Paratypes: 5♀♀ (ZSM 20010010, on SEM-mounts). All types collected by S. Millen, S. Gigglinger, J. Sanchez, C. Pérez, Bahía de Coliumo, 17 December 1994, from a single *Aeolidia papillosa serotina* Bergh, 1873 (Fig. 25A). 5♀♀ examined by SEM, 5♂♂ were lost during critical point drying.

Etymology. The specific name refers to six ♀ and six ♂ parasites within a single host.

Description (♀) (Figs 25B,C, 26, 27)

Delicate body, measuring 2.6-3.6 mm. Antennules, antennes and maxilles as in other congeners (see *I. androphila*, spec. nov.; genus diagnosis). Mandibles and maxillules were not visible in the specimens studied since they were covered with host tissue.

Second and 3rd thoracopods with endopodits being shorter and thinner than exopodits. Third thoracopod with small process of endopodit, measuring about one third of the endopodit. Fifth thoracopod not visible.

First abdominal segment with pair of sausage-shaped and relatively short egg sacs.

Description (♂) (Figs 25D,E)

Body length 1.0-1.6 mm.

Remarks. There is almost no morphological variation among the female parasites from *A. papillosa serotina*. *Ismaila socialis*, spec. nov. has to be compared with other Chilean congeners with delicate body shape (see Tab. 1): *Ismaila aliena*, spec. nov. has much longer dorsal processes relative to the body length than *I. socialis*, spec. nov. In *I. androphila*, spec. nov. the exopodit and endopodit of the 2nd thoracopod have the same length, while in *I. socialis*, spec. nov. the endopodit is shorter than the exopodit. *Ismaila magellanica*, spec. nov. morphologically is very similar to *I. socialis*, spec. nov.. However, *Ismaila magellanica*, spec. nov. infects a sacoglossan host in the Magellan Strait area, while *I. socialis*, spec. nov. was found in *A. papillosa serotina* in central Chile.

Ismaila magellanica, spec. nov.
Figs 28-30

Types. Holotype: ♀, ZSM 20010024 (on SEM-mount). – Allotype: ZSM 20010024, on SEM-mount). – Paratypes: 2♀♀ (ZSM 20010024, on SEM-mount); 1♀, 2♂♂ (ZSM 20010025, on SEM-mount). All types collected by S. Millen, Fuerte Bulnes (53°39'S, 70°56'W), Magellan Strait, 5 January 1995. Host: *Elysia patagonica* Muniaín & Ortea, 1997 (Figs 28A,B).

Additional material. 3♀♀, collected together with the types, all together from 4 host specimens. All parasite specimens examined by SEM.

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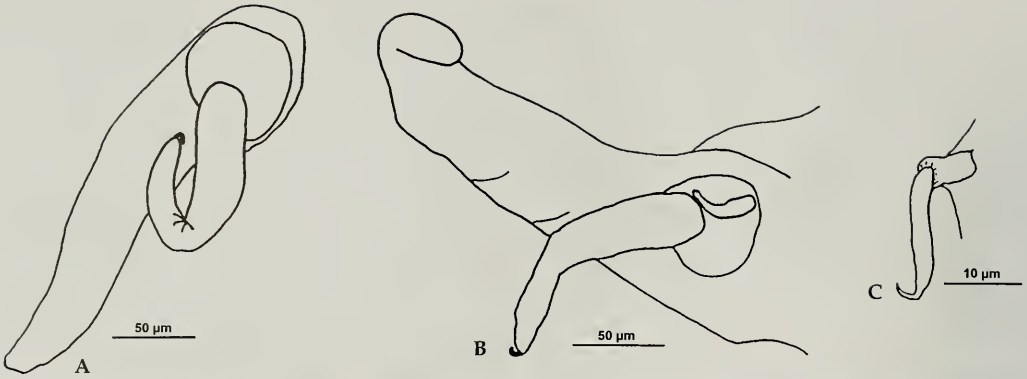

Fig. 27. *Ismaila socialis*, spec. nov., legs (♀). **A.** 2nd thoracopod (right). **B.** 3rd thoracopod (left). **C.** 4th thoracopod (right).

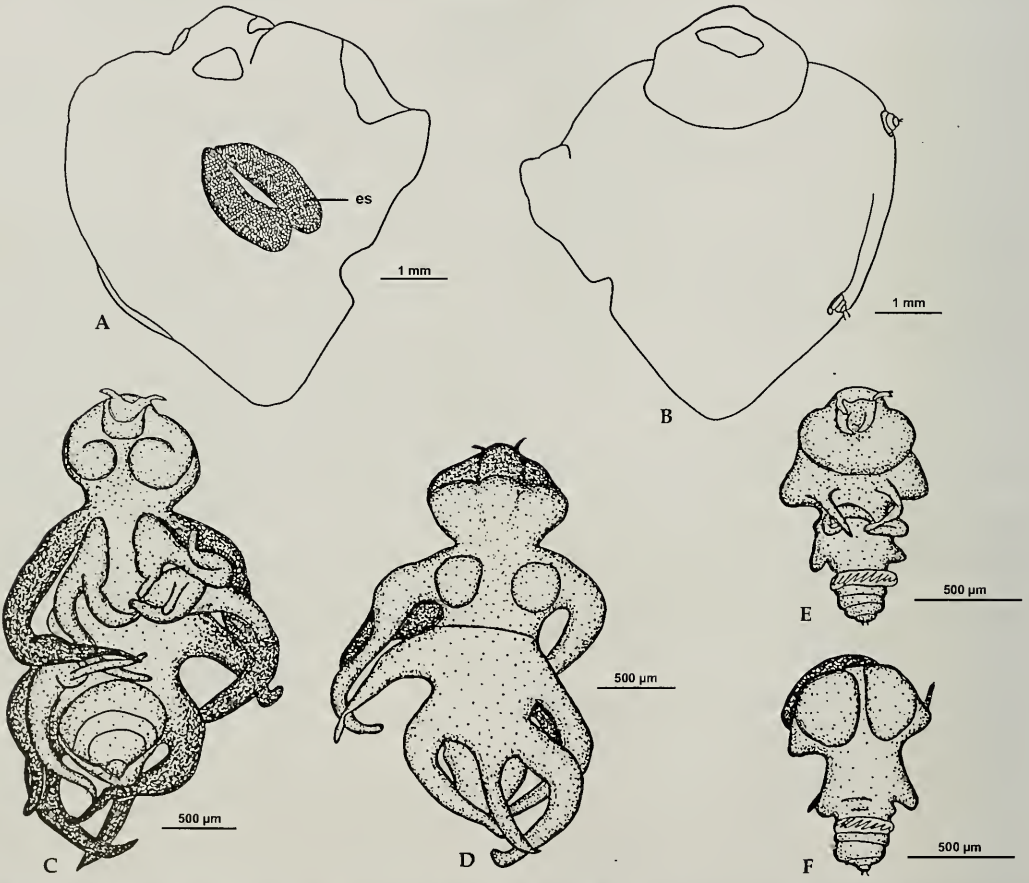

Fig. 28. *Ismaila magellanica*, spec. nov. **A.** Sacoglossan host specimen *(Elysia patagonica)* with egg-sacs protruding dorsally. **B.** Host with abdomina of parasites protruding the body laterally, ventral view. **C.** ♀ parasite, ventral view. **D.** ♀ parasite, dorsal view. **E.** ♂ parasite, ventral view. **F.** ♂ parasite, dorsal view.

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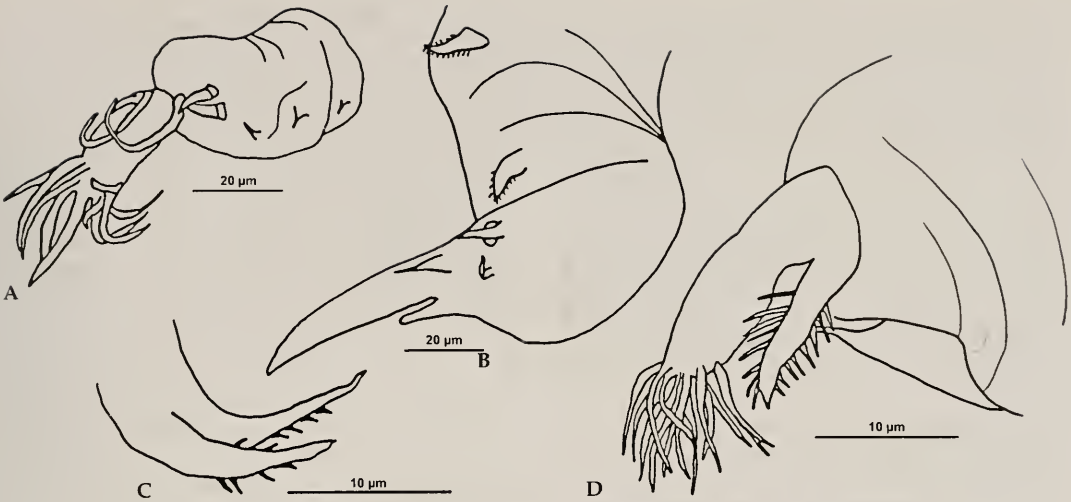

Fig. 29. *Ismaila magellanica*, spec. nov., cephalic appendages (♀). **A.** Antennule (right). **B.** Antenna (left). **C.** Maxillule (right). **D.** Maxilla (left).

Etymology. The specific name refers to the Magellan Strait, the type locality.

Description (♀) (Figs 28C,D, 29, 30A,B)

Delicate body measuring 1.1-2.5 mm. Cephalic appendages as in other congeners (see *I. androphila*, spec. nov. and genus diagnosis).

Exopodit and endopodit of second thoracopod with almost equal length, but endopodit thinner. Fifth thoracopod not visible.

First abdominal segment with pair of short, straight and relatively thick egg sacs.

Description (♂) (Figs 28E,F, 30C-E)

Body length 0.8-1.1 mm. Fifth thoracopod not visible.

Remarks. The endoparasitic copepods of *E. patagonica* belong to the genus *Ismaila* (see Jensen 1987; genus diagnosis in this paper), there is hardly any morphological variability detectable. *Ismaila magellanica*, spec. nov. comes closest to *Ismaila socialis*, spec. nov. (see Tab. 1), but due to different hosts and considerable geographical distance (and hydrographical differences; see Brattström & Johanssen 1983) of the collecting localities they are considered to be different species.

Biological notes. There are only few records of endoparasitic copepods in Sacoglossa. *Ismaila jenseniana*, spec. nov. was reported to parasitize *Ercolania funerea* (see Jensen 1987), Monod & Dollfus (1934) described a member of *Splanchnotrophus* from *Elysia ornata* Pease, and Jensen (1990) found *Arthurius elysiae* (Jensen, 1990) in *Elysia australis* (Quoy & Gaimard, 1832). All host species appear to be just sporadically infected. No parasites were mentioned from Argentinian *Elysia patagonica* by Muniaín & Ortea (1997). In contrast, the population of *Elysia patagonica* from the Magellan Strait showed a high infection rate (90 %; see Schrödl 2002) with *Ismaila magellanica*, spec. nov. Two of the four host specimens examined had single female parasites, one host had two and one had even three female parasites, thus also the infestation of Chilean *E. patagonica* may be much higher than previously known from any sacoglossan hosts.

Discussion

Cephalic appendages. There was little and contradictory information on the morphology of cephalic appendages of Splanchnotrophidae. According to Gotto (1993), there are first and second antennae, sickle-shaped mandibles and second maxilles. However, this referred to data on only one genus, *Splanchnotrophus* Hancock & Norman, 1863, of which only two species had been studied in more detail (see Laubier 1964), with contradictory results on number and identity of cephalic appendages. Most recently, Huys (2001) made an end to that long lasting debate showing *S. gracilis* Hancock & Norman, 1863, the type species, and *S. angulatus* Hecht, 1893, to possess a pair of 2-segmented antennules, 3-segmented antennae, one bilobate labrum, a pair of blade-like mandibles with denticulate tips, a pair of maxillules with an apical seta, and a pair of 2-segmented maxillae. Maxillipeds are definitely absent in adults.

Descriptions of head appendages of *Ismaila* spe-

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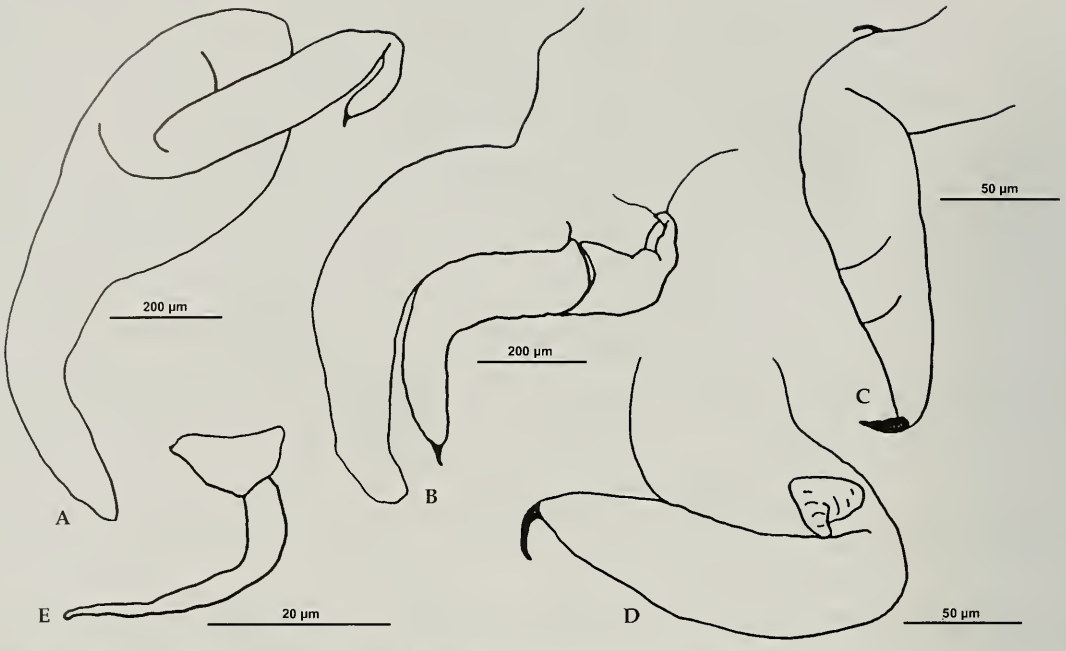

Fig. 30. *Ismaila magellanica*, spec. nov., legs. **A.** 2nd thoracopod (♀, right). **B.** 3rd thoracopod (♀, left). **C.** 2nd thoracopod (♂, right). **D.** 3rd thoracopod (♂, right). **E.** 4th thoracopod (♂, right).

cies also were highly contradictory: *Ismaila monstrosa* was mentioned to have two pairs of antennae, a labrum, and one pair of mandibles and maxillae by Bergh (1867). The cephalic appendages of *I. belciki* and *I. occulta* were described in detail (Belcik 1981, Ho 1981) but show significant differences concerning the number (4 *vs.* 5) and morphology of head appendages. Thus, one major aim of this study was to find out, with aid of the SEM, which kind of cephalic appendages are present in the different species of *Ismaila*, whether their structure is really that different, and to evaluate their taxonomic value.

All *Ismaila* specimens examined herein have antennules and antennae. Also the presence of sickle-shaped mandibles could be confirmed. Under the SEM, the mandibles show a broad base and a long, elongate blade with fine hairs (Fig. 8C) which had not yet been reported for any *Ismaila* species. In accordance with Ho (1981), all *Ismaila* species are shown to possess two pairs of maxillae. Maxillules similar in shape to those of other congeners are definitely present in *Ismaila belciki*, obviously they had been overlooked by Belcik (1981). The second segment of the maxillae bears three hairy processes in *I. occulta* (see Ho 1981), *I. belciki*, and, possibly, also in other congeners, but the third process was difficult to detect by SEM examination due to its posterior position (see Fig. 8E). In contrast to Belcik (1981) who mentioned maxillipeds from *I. belciki*, no traces of maxillipeds could be found in any adult *Ismaila* specimens examined. Thus, there is no variation regarding the number of cephalic appendages between the different *Ismaila* species. Also the shape of cephalic appendages of all species examined is similar even regarding details. Slight differences concerning the number of hairs or thorns of cephalic appendages, especially of the terminal hairs of antennules and maxilles, indicate that these may not be suitable features for taxonomic distinction: hairs may easily been torn off or may be hidden depending on the angle of view. The SEM results suggest that all *Ismaila* species have complex, special shaped antennae and mouthparts which differ clearly from those of other splanchnotrophids (see Huys 2001), and thus appear to be diagnostic for *Ismaila*. Future cladistic analyses may also confirm such special structures as autapomorphies for *Ismaila* as assumed by Huys (2001).

Our results on head appendages of *Ismaila* agree well with the general assumption that heads of copepods consist of five segments, each bearing one pair of extremities, i.e. two pairs of antennae, mandibles and two pairs of maxilles (e.g. McLaughlin 1980). Additionally, there is a labrum and a so-called labium with paragnath lobes also present in *Ismaila*.

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Body segmentation and appendages. Several attempts have been made to homologize splanchnotrophid body portions, segments, legs and body outgrows, i.e. by Ho (1981), Jensen (1987), and Huys (2001) who, regarding *Ismaila*, largely followed Ho's interpretation. The following interpretation is derived from results on different *Ismaila* species studied herein. In both sexes, the five head segments of *Ismaila* are characterized by the presence of one pair of extremities each. In females one thoracic segment is aggregated to the head (Jensen 1987). It lacks extremities in adult specimens, but one pair of maxillipeds was shown to be present in the copepodit II of *I. occulta* by Ho (1987b). In female *Ismaila*, the second thoracic segment bears a pair of large, biramous (second) thoracopods, the third thoracic segment has triramous (third) thoracopods ("legs 1 and 2" by Ho 1981). The first pair of dorsal appendages is situated slightly anterior to the second thoracopods and is supposed to belong to the second segment. The second pair of dorsal appendages lies in between the second and third thoracopods, and the third pair of dorsal appendages, together with the medio-dorsal process, is situated posterior to the third thoracopods. In contrast to Ho (1981) who assumed that the third pair of dorsal appendages belongs to the fourth thoracic segment, we think both the second and third dorsal appendages may more likely belong to a long third thoracic segment since Ho (1987b) showed copepodits IV to possess a long third but a short fourth thoracic segment. According to our interpretation it is the fourth thoracic segment that bears a vestigial, unbranched, 2-segmented process, the fourth thoracopod ("leg 3" by Ho 1981). The anterior portion of the fifth thoracic segment forms a strong cuticular ring, posteriorly it bears a vestigial (fifth) thoracopod, a small process tipped with two setae in *I. occulta* ("leg 5" by Ho 1981) or two separate setae in other congeners. We have not found further thoracopods, thus the sixth thoracopods appear to be completely reduced in female Ismaila. Ho (1981) interpreted small elements inserting in the area of egg-sac attachment of female I. occulta as being an additional "leg 6". However, no such structures have been detected in the present study. If present, such structures may also be abdominal outgrows rather than thoracopods.

In male *Ismaila* two laterally swollen thoracic segments are aggregated to the head (see Jensen 1987). In adult males the first thoracic segment lacks legs (i.e. maxillipeds), the second thoracic segment bears a pair of large uniramous (second) thoracopods. The third thoracic segment is distinctly set off from the cephalothorax; it bears a pair of large biramous (third) thoracopods. The thoracopods of the fourth and fifth segments resemble those of the females. In contrast to the females, the sixth thoracic segment of males bears a pair of (sixth) thoracopods which are modified into plate-like, triangular lobes with three distal setae which, as usual in in gymnoplean copepods, may serve as copulatory organs. The gonopores open at the following, first abdominal segment.

Although the abdomen of *I. occulta* was interpreted to be 1-segmented by Ho (1981), at least three segments may be distinguished in all *Ismaila* species examined. The first abdominal segment bears the genital openings in both sexes. The second visible segment does not bear any outgrows. The posterior segment is characterized by a pair of caudal rami.

Revision of the genus. Previously, the genus *Ismaila* was represented by three species. The type species is *Ismaila monstrosa* Bergh, 1867 with only four female museum specimens available for re-examination. Two of them, *I. obtusa, spec.* nov. (formerly *I. monstrosa* det. Bergh, 1898) and *I. jenseniana*, spec. nov. (formerly *I. monstrosa* det. Jensen, 1987), are shown herein to significantly differ from the holotype of *I. monstrosa* described by Bergh (1867). This confirms Monod & Dollfus' (1934) and Belcik's (1981) doubts that the Chilean specimen illustrated by Bergh (1898) belong to *I. monstrosa*.

Californian specimens originally assigned to *I. monstrosa* by Belcik (1981) already were shown to be distinct from *I. monstrosa* and another Californian species, *Ismaila occulta* Ho, 1981, by Ho (1987a) and described as *I. belciki* Ho, 1987. The main distinguishing criteria were related to the cephalic appendages and the thoracopods, i.e. the proportions of exopodits relative to endopodits of the 3rd thoracopods of females. Since Jensen (1987) showed the bilobed dorso-median process of *I. monstrosa* to be an artifact, this feature could no longer be used as a distinguishing feature to other congeners (see Ho 1981, Belcik 1981).

In the framework of this study specimens of the three currently known *Ismaila* species were re-examined critically. In addition, parasites of six different Chilean host species were described. All parasites out of one host species (if there were more than one parasite specimen to examine) are highly similar to each other and, thus, are certainly conspecific. On the other hand, except for *I. socialis*, spec. nov. and *I. magellanica*, spec. nov., they are distinguishable morphologically from the parasites of the other host species (Tab. 1).

Other than expected from the literature (see Ho 1981, Belcik 1981), all species of *Ismaila* show nearly identical cephalic appendages. Those of *I. jenseniana*, spec. nov. and *I. obtusa*, spec. nov. could not be examined because the head region was damaged in

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Tab. 1. Comparision of 11 known *Ismaila* species (literature data in quotation marks)

	I. monstrosa Bergh, 1867	*I. obtusa*, spec. nov.	*I. jenseniana*, spec. nov.	*I. occulta* Ho, 1981	*I. belciki* Ho, 1987
Host	*Phidiana lynceus* (Nudibranchia: Aeolidoidea)	*Anisodoris fontaini* (Nudibranchia: Doridoidea)	*Ercolania funerea* (Sacoglossa)	*Dendronotus iris* (Nudibranchia: Dendronotoidea)	*Janolus fuscus* (Nudibranchia: "Arminoidea")
Locality	St. Thomas, Virgin Islands, Caribbean Sea	Tumbes, central Chile	St. Thomas, Virgin Islands, Caribbean Sea	Alamitos Bay, California	Oregon
No. of females examined in detail herein	2	1	1	6	3
Body length of females (mm) (without egg-sacs)	3.2-4	>11	1.2	up to 3	1.8-4.4
Body shape (females)	delicate	very stocky, unique flattened dorsal processes	delicate, additional pair of dorso-lateral processes	delicate	delicate
Shape of egg-sacs	coiled (one whorl)	?	"elongate, straight"	"rather short, straight"	"short, straight"
Ratio length of first dorsal process/body length	damaged	0.4	0.3	0.2-0.3	0.5-0.6
2nd thoracopods females: relative length of exo-/endopodit	exo = endo	exo > endo	exo > endo	exo ≥ endo	exo = endo
2nd thoracopods: relative diameter of exo-/endopodit	exo > endo	exo ≫ endo	exo > endo	exo > endo	exo = endo
3rd thoracopods females: relative length of exo-/endopodit	exo > endo	exo > endo	?	exo > endo	exo (>) endo
3rd thoracopods females: relative diameter of exo-/endopodit	exo > endo	exo ≫ endo	?	exo > endo	exo (>) endo
3rd thoracopods females: ratio inner process/endopodit	1	0.3	1	0.1	0.8
No. of males examined	0	0	0	6	6
Body length males (mm)	?	?	?	up to 1.1	1.5-2.0
3rd thoracopods males: ratio inner process/endopodit	?	?	0.7	0.05	0.4
Setae of 5th thoracopod females	?	?	?	common base	separate

both specimens. Differences between the species refer to general body shape, number, proportions and structure of body appendages and the shape of egg sacs.

As in *Splanchnotrophus*, which was subdivided into subgenera *Lomanoticola* (stocky body shape) and *Splanchnotrophus* (delicate body shape) by Delamare Deboutteville (1950), the *Ismaila* species can be easily divided according to their stocky *vs.* delicate body shape (Tab. 1). *Ismaila robusta*, spec. nov., *I. damnosa*, spec. nov. and *I. obtusa*, spec. nov. have a conspicuous robust and stocky body. Within this group, species are distinguishable from another by the length and diameter of dorsal processes and proportions of exopodits to endopodits of the females' 2nd thoracopods (Tab. 1). *Ismaila obtusa*, spec.

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I. androphila, spec. nov.	*I. aliena*, spec. nov.	*I. damnosa*, spec. nov.	*I. robusta*, spec. nov.	*I. socialis*, spec. nov.	*I. magellanica*, spec. nov.
Okenia luna (Nudibranchia: Doridoidea)	*Thecacera darwini* (Nudibranchia: Doridoidea)	*Flabellina* sp. 1 (Nudibranchia: Aeolidoidea)	*Phidiana lottini* (Nudibranchia: Aeolidoidea)	*Aeolidia papillosa serotina* (Nudibranchia: Aeolidoidea)	*Elysia patagonica* (Sacoglossa)
Bahía de Coliumo, central Chile	Bahía de Coliumo, central Chile	Bahía de Coliumo, central Chile	Bahía de Coliumo, central Chile	Bahía de Coliumo, central Chile	Magellan Strait
15	15	15	4	4	7
1.9-4.2	1.2-6.9	0.9-3.4	1.9-2.4	2.6-3.6	1.1-2.5
delicate	delicate, very long dorsal processes	stocky	very stocky	delicate	delicate
elongate, straight	coiled (one whorl)	coiled (one whorl)	coiled (two whorls)	elongate, banana-like	short, straight
0.4-0.7	0.7-1.0	0.4-0.7	0.3-0.4	0.3-0.4	0.4-0.6
exo = endo	exo = endo	exo = endo	exo ≥ endo	exo > endo	exo > endo
exo > endo	exo > endo	exo > endo	exo ≫ endo	exo > endo	exo > endo
exo = endo	exo > endo	exo ≤ endo	exo = endo	exo > endo	exo > endo
exo > endo	exo > endo	exo = endo	exo > endo	exo > endo	exo > endo
0.5	0.2	0.4	0.2	0.3	0.3
10	10	10	7	4	4
0.6-1.6	0.7-3.1	0.7-1.6	1.0-1.2	1.0-1.6	0.8-1.1
0.3	0.5	0.3	0.3	?	0.2
?	separate	separate	?	?	?

nov. with its unique, large and flattened dorsal processes and exopodits is clearly distinct to the delicate shaped *I. monstrosa* (as it was identified by Bergh 1898) and to any other species of *Ismaila*.

All other *Ismaila* species show the delicate body type. The single known female of *I. jenseniana*, spec. nov. has an unique additional pair of dorsolateral processes and, thus, is clearly distinct from all congeners. With exceptional long dorsal processes, *I. aliena*, spec. nov. is easily distinguishable from any other *Ismaila* species (see Tab. 1). In contrast to all other delicate species, females of *I. aliena*, spec. nov. have coiled egg sacs. Both individuals of *I. monstrosa* have third thoracopods with equally long endopodits and inner processes, while in all other *Ismaila* species (except for *I. jenseniana*, spec.

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nov.) endopodits are longer than the inner processes (Tab. 1). *Ismaila occulta* and *I. belciki* are distinguishable from each other and from all remaining gracile species of *Ismaila* by the short *vs.* long inner process of the endopodit of the third thoracopod (Ho 1987b; Tab. 1). *Ismaila occulta* additionally may be well characterized with 5th thoracopods consisting of two setae arising from a common base while other congeners in which 5th thoracopods could be examined have setae arising separately. *Ismaila androphila*, spec. nov. differs slightly but consistently regarding the proportions of the rami of the 3rd thoracopod from the otherwise similar *Ismaila magellanica*, spec. nov. and *I. socialis*, spec. nov. (Tab. 1). The latter two species closely resemble each other regarding the shape of egg sacs, dorsal processes and proportions of endopodits and exopodits. However, *I. socialis*, spec. nov. parasitizes an aeolidoidean nudibranch and is so far only known from central Chile, while *Ismaila magellanica*, spec. nov. infects the sacoglossan *Elysia patagonica* which occurs in the Magellan Strait area. Thus, as a result of this study, 11 different species of the genus *Ismaila* are regarded to be valid, showing more or less distinctive morphological features (Tab. 1). The general body shape including the structure of antennae, mouthparts, legs, and body outgrows is consistent within the different *Ismaila* species showing surprisingly little variability. This is in clear contrast to *Splanchnotrophus* where the prosomal region and its lateral outgrows may show substantial intraspecific variability (Huys 2001).

An alternative hypothesis would be to regard at least some delicate Chilean *Ismaila* specimens as belonging to one single species; on one hand implying certain intraspecific varibility, and on the other hand quite rigid adaptations to certain host species causing slight but consistent morphological differences. However, biological data argue against this one-species-hypothesis. The parasites of *Thecacera darwini* and *Okenia luna*, two Chilean phanerobranch doridoidean nudibranchs, are highly specific regarding their position in the host (this study). Also the number of females in each host differs, in *Okenia luna* there was always just one single female parasite together with several males, while in *Thecacera darwini* (and other hosts) there may be more than one female. While the populations of *O. luna* and *T. darwini* in the Bahía de Coliumo were highly infected with *Ismaila*, another syntopic and common Chilean phanerobranch nudibranch, *Holoplcamus papposus* Odhner, 1926 was not infected at all. Another, morphologically well-characterized *Ismaila* species, *I. damnosa*, spec. nov., also infects just a single host species (*Flabellina* sp. 1) while other syntopic aeolids and even a very common and externally similar congener, *Flabellina* sp. 2, were not infected at all. In conclusion, it seems that the species of *Ismaila* are highly host specific.

Host specifity may be quite common in certain copepod groups. For example, Ho (1994) found a strong trend towards host specifity for the *Chondracanthidae* (parasites of marine fishes). Humes (1974) considered *Anthessius dolabellae* Humes & Ho, 1965, *Doridicola audens* Humes, 1959 and *Metaxymolgus commodus* Humes, 1964, three exoparasitic copepods which are associated with Opisthobranchia, as host specific. Over a geographical distance from Madagascar to New Caledonia, they occur in the same host species. However, in the future, it will be interesting to use molecular techniques to test such taxonomic hypotheses which until now are solely based on quite ambiguous morphological or biological data.

With the results of this study it is now possible to give a detailed diagnosis of the genus *Ismaila* and to identify all known members (Tab. 1). Attempts to define the genus had already been made by Belcik (1981), Jensen (1987), and Huys (2001). Belcik considered the maxilla of *I. belciki* as being characteristic for the genus. The present study shows a special type of mandible, maxillule and maxilla to be present in all *Ismaila* species and to be different in structure from such mouthparts of other splanchnotrophids studied by Huys (2001). These features, together with the sexual dimorphism of the 2nd and 3rd thoracopods ("legs 1 and 2", see Huys 2001) are certainly diagnostic for *Ismaila* and may also be autapomorphies. Jensen's (1987) observation that the females of *Ismaila*, in contrast to other genera of the Splanchnotrophidae, have always long and slender (anterior) thoracopods extending beyond the body laterally, could be verified in this study. A single medio-dorsal process is present in all *Ismaila* species which appears to be an unique autapomorphy of the group. Due to the absence of a comprehensive phylogenetic analysis it is still problematic to judge on the significance of characters and polarity of character states. However, all these potential autapomorphies coincide with each other clearly suggesting that the genus *Ismaila* is monophyletic. Three pairs of large dorsal processes, which are not homologous to thoracopods but formed *de novo* (Laubier 1966 *fide* Huys 2001), are common to *Ismaila*, *Splanchnotrophus*, *Lomanoticola*, and *Ceratosomicola*) and may indicate a common ancestry. The genus *Arthurius* is morphologically aberrant and, according to Huys (2001), shows a mix of highly derived and plesiomorphic characters which additionally differ between both sexes. However, as long as there is no sound hypothesis on the phylogeny of Splanchnotrophidae, either on their systematic position, it is difficult to draw reliable evolutionary conclusions.

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