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Marine Biology Research

Publication details, including instructions for authors and subscription information:

<http://www.informaworld.com/smpp/title~content=t713735885>

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First published on: 18 November 2009

To cite this Article Alberico, Natalia A. and Roccatagliata, Daniel(2010) '*Homoeoscelis meridionalis* sp. nov. (Copepoda, Nicothoidae) parasitic on two cumaceans from southern South America with comments on its biology, and partial redescription of *H. frigida* Hansen, 1923', *Marine Biology Research*, 6: 1, 66 – 77, First published on: 18 November 2009 (iFirst)

To link to this Article: DOI: 10.1080/17451000902810777

URL: <http://dx.doi.org/10.1080/17451000902810777>

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ORIGINAL ARTICLE

***Homoeoscelis meridionalis* sp. nov. (Copepoda, Nicothoidae) parasitic on two cumaceans from southern South America with comments on its biology, and partial redescription of *H. frigida* Hansen, 1923**

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Abstract

The adult female and male, and the copepodite stage of the nicothoid copepod *Homoeoscelis meridionalis* sp. nov. are described. This parasite infests the branchial chambers of two closely related cumaceans from southern South America: *Diastylis planifrons* and *D. fabrizioi*. The maxilliped of the adult female of *Homoeoscelis minuta* is reillustrated, and the copepodite stage of *H. frigida* is briefly redescriptioned on the basis of their respective type materials. Of the 1768 specimens of *Diastylis fabrizioi* examined, 2.6% were found to be infested by *Homoeoscelis meridionalis* sp. nov. The copepod prevalence differs significantly between the female and male of *D. fabrizioi* (4.2 vs. 0.7%), and it was much higher in older instars of *D. fabrizioi* (adults and subadults) than in younger ones (juveniles and manca) (7.1 vs. 0.3%).

Key words: *Copepoda*, *Cumacea*, *Homoeoscelis meridionalis* sp. nov., *H. frigida*, *H. minuta*, *parasitic*, *South-West Atlantic*

Introduction

The family Nicothoidae contains 20 genera and more than 120 species of small, highly modified copepods, all of them parasitic on other crustaceans (Boxshall & Halsey 2004).

Up to now, six species of the genus *Homoeoscelis* are known to infest the branchial chambers of cumaceans; namely, *H. sedentaria* (Bonnier, 1896), *H. minuta* Hansen, 1897, *H. mediterranea* Hansen, 1897, *H. frigida* Hansen, 1923, *H. longipes* Hansen, 1923 and *H. elongata* Boxshall and Defaye, 1995. All of these infested cumaceans have been reported from the Northern Hemisphere (see Boxshall & Defaye 1995). An additional new species of this genus from Japan, found in the branchial chambers of *Iphinoe sagamiensis* Gamô, 1958, is under description (S. Ohtsuka & G.A. Boxshall, personal communication).

In a recent survey of the cumaceans from southern South America, over 1700 specimens of *Diastylis*

fabrizioi Alberico and Roccatagliata, 2008 and a few specimens of *Diastylis planifrons* Calman, 1912 were examined. Of these, 46 specimens of the former species and 3 of the latter harboured nicothoid copepods in their branchial chambers (Alberico & Roccatagliata, 2008). Based on this material, the adult female and male and the copepodite stage of *Homoeoscelis meridionalis* sp. nov. are described, and preliminary data on the biology of this cumacean–copepod association are reported.

In his figure 1h, Hansen (1897) presented a tiny drawing of the anterior part of an adult female of *Homoeoscelis minuta*, in which the maxillipeds are depicted. Since this appendage is very useful for the identification of the nicothoid copepods, it is herein reillustrated based on a female from the type series. In addition, the copepodite stage of *H. frigida* Hansen, 1923 is briefly redescriptioned also on the basis of type material.

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Published in collaboration with the University of Bergen and the Institute of Marine Research, Norway, and the Marine Biological Laboratory, University of Copenhagen, Denmark

Material and methods

The parasites and their ovisacs are usually visible through the hosts' partially translucent cuticle. In addition, in many infested cumaceans the parasitized branchial chamber is swollen (see Figure 1A). The parasites and their ovisacs were carefully removed from the branchial chambers of the hosts using sharpened tungsten needles under a dissecting microscope.

Some copepod specimens were cleared in lactic acid, and then mounted in polyvinyl-lacto-glycerol (PVLG) for examination. We observed, however, that this medium continues shrinking, thus flattening the specimens excessively. The remaining cope-

pods were not mounted but kept in microvials with 70% ethanol.

Illustrations were made with the aid of a drawing tube attached to a Carl Zeiss Axioskop compound microscope. A few copepodites, adult females and males were prepared for scanning electron microscopy (SEM), i.e. they were dehydrated through a graded series of ethanol, critical point dried and examined under a Philips XL30 TMP microscope. Prior to dehydration, the adult females and males (but not the copepodites) were cleaned with 0.5% non-ionic detergent Triton X100 and ultrasonicated.

Total length was taken from the anterior margin of the head to the end of the body (caudal rami excluded). For the setae and ornamentations we

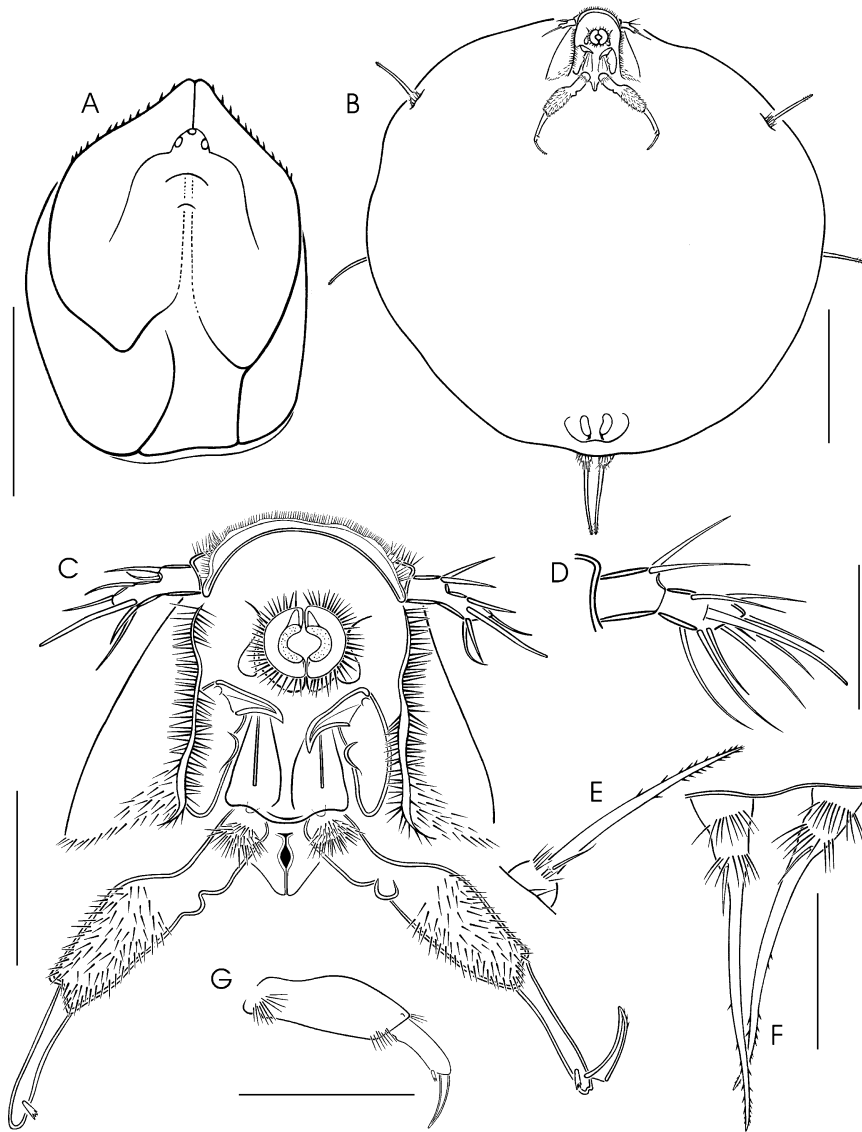


Figure 1. *Diastylis fabrizioi* Alberico and Roccatagliata, 2008; **A**, carapace of juvenile ♂ in dorsal view, left branchial chamber conspicuously inflated. **B–F**, *Homoeoscelis meridionalis* sp. nov., adult ♀. **B**, habitus in ventral view (holotype MACN-Pa. 476/1). **C**, head, claw of right maxilliped missing. **D**, first antenna in ventral view. **E**, first leg (**C–E**, paratype MACN-Pa. 476/5a). **F**, caudal rami (paratype MACN-Pa. 476/5b). *Homoeoscelis minuta* Hansen, 1897, adult ♀. **G**, maxilliped (syntype ZMUC-CRU-9241). Scale bars: 1 mm (**A**), 0.2 mm (**B**), 0.05 mm (**C**, **E–G**), 0.025 mm (**D**). Figures **E** and **F** share scale.

followed the terminology proposed by Huys and Boxshall (1991).

The number of ovisacs found inside the branchial chamber of each cumacean was recorded. The shape of ovisacs is affected by pressure of other sacs or of the expanding female, therefore, for the diameter assessment only rounded (not flattened) ovisacs were measured. The stages within the ovisac were arbitrarily categorized into developing embryos and partially to fully developed copepodites. The former are round, yellow, and lack appendages, whereas the latter are pyriform, whitish, and have rudimentary appendages (with a few vestigial setae) or fully developed ones.

The position of the parasite (on left or right branchial chamber) was recorded. The gill condition (damaged or normal) was not obtained immediately after removing the parasite from the host, but from the re-examination of the gills some months later.

All the specimens of *Homoeoscelis meridionalis* sp. nov. were deposited in the parasitology collection of the Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia' (MACN). They are either preserved in vials with 70% ethanol, mounted on slides or, as was the case of those specimens used for SEM photographs, stuck on aluminium stubs.

The following type materials were examined: *Homoeoscelis minuta* Hansen, 1897. Infesting the branchial chamber of *Diastylis lucifera* Krøyer, 1841. – Hellebæk, Denmark. 1885, coll. Dr. Joh. Petersen: 1 parasitized cumacean; 1887, coll. H. J. Hansen: 2 parasitized cumaceans. – Expeditions of 'Hauch', coll. Dr. Joh. Petersen. Sta. 25, 110 fathoms: 1 parasitized cumacean. Sta. 368, 13 fathoms: 1 parasitized cumacean. Sta. 370, 15 fathoms: 1 parasitized cumacean. Sta. 383: 1 parasitized cumacean. – A shell vial labelled '*Hom. minuta* H. J. H., Dania, parasiter med Æg' [*Hom. minuta* H. J. Hansen, Denmark, parasites with eggs]: 23 parasitized *D. lucifera* (syntypes ZMUC-CRU-9241; we removed 1 adult ♀, 1 ♂ and 5 ovisacs from the branchial chamber of one of these cumaceans, and we kept this host and its parasites in a separate vial inside the jar containing the remaining 22 infested cumaceans). – A shell vial labelled '*Hom. minuta* H. J. H., Dania, parasiter uden Æg' [*Hom. minuta* H. J. Hansen, Denmark, parasites without eggs]: 18 *D. lucifera* (only 3 parasitized) (syntypes ZMUC-CRU-7285). – A shell vial, without catalogue number, labelled '*Diast. lucifera* Kr. Snylterne udtagne' [*Diast. lucifera* Kr. parasites removed] containing 13 cumaceans was also included among the material sent to us by the ZMUC. – An empty shell vial, without catalogue number, labelled '*Homoeoscelis minuta* H. J. H. på *Diastylis lucifera*,

Danmark, typer' [*Homoeoscelis minuta* H. J. Hansen on *Diastylis lucifera*, Denmark, type]. – Three microscope slides labelled: '1 Han og 10 Æggesække' [1 ♂ and 10 ovisacs], '9 Hanner, den ene hængende på Gjælleapparatet' [9 ♂♂, one of them attached to the host gills], 'Larver af en Æggesæk' [larvae from one ovisac]. The latter is badly damaged, the larvae (copepodites) are unnoticeable, and the mounting media is dry and dark.

Homoeoscelis frigida Hansen, 1923. Infesting the branchial chamber of *Diastylis polaris* Sars, 1871. – Danish Ingolf Expedition 1895–1896, South of Jan Mayen Is. (Arctic Ocean). Sta. 113, 69°31'N, 07°06'W, 1309 fathoms: 1 ♀, 3 ovisacs (syntypes ZMUC-CRU-6462), 1 dissected cumacean (syntypes ZMUC-CRU-6463). Sta. 117, 69°13'N, 08°23'W, 1003 fathoms: 1 ♀, 3 ovisacs, and 1 dissected cumacean (syntypes ZMUC-CRU-9239; we removed three copepodites from one of the ovisacs and we kept them in a separate vial together with the remaining material).

Homoeoscelis longipes Hansen, 1923. Infesting the branchial chamber of *Leptostylis villosa* Sars, 1869. – Thor Expedition, Sta. 171 2/VII 1904, West of South Iceland, 63°46'N, 22°56'W, 150 m, coll. Dr. J. Schmidt: 2 cumaceans with the carapaces partially dislodged and without parasites (syntypes ZMUC-CRU-7124).

Taxonomy

Homoeoscelis Hansen, 1897

Homoeoscelis meridionalis sp. nov.

(Figures 1–6)

Material examined

Inside the branchial chamber of *Diastylis fabrizioi*. – R/V *Aldebarán*. Sta. 9906-23, 34°08'01"S, 53°34'04"W, 19 m, 11 Dec 1999: 1 ♀, 1 ♂ (host: subadult ♀); 1 ♀, 1 ♂, 2 ovisacs (host: subadult ♀); 1 ♀, 1 ♂, 4 ovisacs (host: juvenile ♀) [paratypes MACN-Pa. 476/2]. Sta. 2002-05 R2, 34°10'S, 53°00'W, 33 m, ? Dec 2002: 1 ♀ (host: subadult ♀) [holotype MACN-Pa. 476/1]; 1 ♂ (host: adult ♀); 1 ♀, 11 ovisacs (host: adult ♀); 1 ♀, 1 ♂, 6 ovisacs (host: adult ♀); 1 ♀, 8 ovisacs (host: adult ♀); 1 ♀, 1 ♂ (host: adult ♀); 1 ♀, 1 ♂ (host: adult ♀); 1 ♀, 1 ♂, 8 ovisacs (host: adult ♀); 1 ♀, 1 ♂, 12 ovisacs (host: adult ♀); 1 ♀, 1 ♂, 10 ovisacs (host: adult ♀); 1 ♂, 14 ovisacs (host: subadult ♀); 1 ♀, 4 ovisacs (host: subadult ♀); 1 ♀, 1 ♂, 12 ovisacs (host: subadult ♀); 1 ♀, 1 ♂, 10 ovisacs (host: subadult ♀); 1 ♀, 1 ♂, 12 ovisacs (host: subadult ♀); 1 ♀, 1 ♂ (host: juvenile ♂); 1 ♀, 1 ♂ (host: juvenile ♂); 1 ♀ (host: juvenile ♂ shown in Figure 1A; female parasite not detached from the branchial chamber, male parasite missing?)

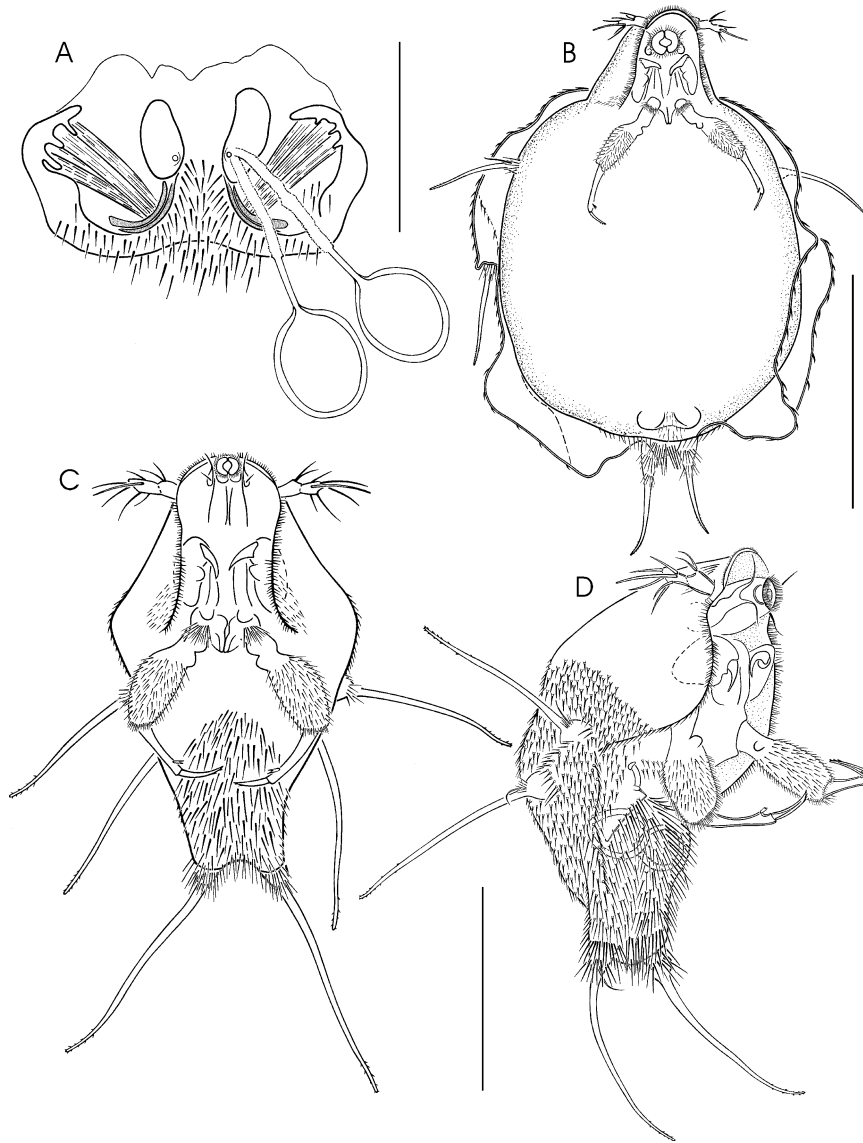


Figure 2. *Homoeoscelis meridionalis* sp. nov. **A**, genital area of adult ♀ (paratype MACN-Pa. 476/4a). **B**, habitus in ventral view of immature ♀, cuticle detached from body showing scale-like spinules on their margins (paratype MACN-Pa. 476/5c). **C**, **D**, adult ♂. **C**, habitus in ventral view (paratype MACN-Pa. 476/5c). **D**, habitus in ventro-lateral view (paratype MACN-Pa. 476/5a). Scale bars: 0.05 mm (**A**), 0.2 mm (**B**), 0.1 mm (**C**, **D**). Figures **C** and **D** share scale.

[paratype MACN-Pa. 476/3]. Sta. 9901-25, 34°48'07"S, 54°21'09"W, 25 m, 27 Jan 1999: 1 ♀, 1 ♂, 10 ovisacs (host: adult ♀); 1 ♀, 1 ♂, 8 ovisacs (host: adult ♀); 1 ♀, 2 ♂ (host: adult ♀); 1 ♀, 1 ♂ (host: adult ♀); 1 ♀ (host: adult ♀); 1 ♀, 1 ♂, 12 ovisacs (host: subadult ♀); 1 ♀, 1 ovisac (host: subadult ♀); 1 ♀, 1 ♂, 8 ovisacs (host: subadult ♀); 1 ♀, 1 ♂, 14 ovisacs (host: subadult ♀); 1 ♀, 1 ♂, 10 ovisacs (host: subadult ♀); 1 ♀, 1 ♂, 6 ovisacs (host: subadult ♀); 1 ♀, 1 ♂, 8 ovisacs (host: subadult ♀); 1 ♀, 1 ♂, 10 ovisacs (host: subadult ♀); 1 ♀, 1 ♂, 8 ovisacs (host: subadult ♀); 1 ♀, 1 ♂, 12 ovisacs (host: subadult ♀); 1 ♀, 1 ♂, 2 ovisacs (host: subadult ♀); 1 ♀, 1 ♂, 8 ovisacs (host: subadult ♂); 1 ♀, 1 ♂, 6

ovisacs (host: subadult ♂) [paratypes MACN-Pa. 476/4]. Sta. 2002-05 R1, 35°11'S, 54°16'W, 30 m, 13 Dec 2002: 1 ♀, 1 ♂, 4 ovisacs (host: adult ♀); 1 ♀, 1 ♂, 4 ovisacs (host: adult ♀); 1 ♀, 1 ♂, 12 ovisacs (host: adult ♀); 1 ♀, 1 ♂, 4 ovisacs (host: adult ♀); 1 ♀, 1 ♂, 12 ovisacs (host: subadult ♀); 1 ♀, 1 ♂, 12 ovisacs (host: subadult ♀); 1 ♀, 1 ♂, 16 ovisacs (host: subadult ♀); 1 ♀, 1 ♂, 1 ovisac (host: subadult ♀) [paratypes MACN-Pa. 476/5]. – Puerto Quequén, Sta. 11, 38°50'32"S, 58°41'15"W, 58.7 m, 15 Dec 2005: 1 ♀, 1 ♂, 9 ovisacs (host: subadult ♀) [paratypes MACN-Pa. 476/6].

Inside the branchial chamber of *Diastylis planifrons* Calman, 1912. – R/V *Puerto Deseado*. GEF Patagonia II, EG 64, 43°40'S, 59°48'W, 108 m, 29 Mar 2006:

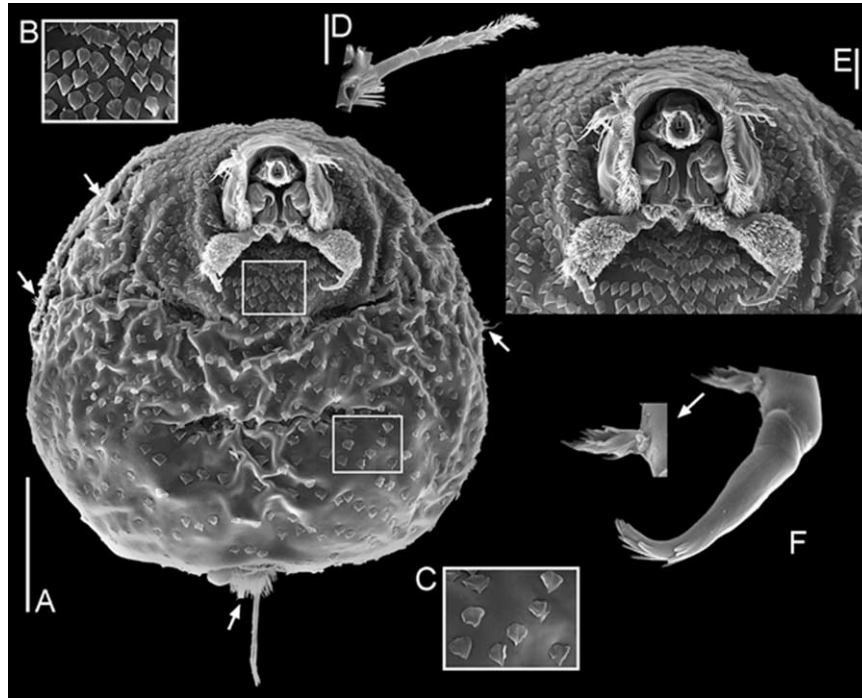


Figure 3. SEM of *Homoeoscelis meridionalis* sp. nov. A-F, adult ♀ (paratype MACN-Pa. 476/4b). A, habitus in ventral view, arrows point to the insertion areas of the missing legs and the basal part of right caudal ramus. B, C, details of the body surface enclosed by frames in the preceding figure. D, left first leg. E, head. F, detail of maxilliped showing the subapical tooth and the claw with small finger-like processes. Scale bars: 100 μm (A), 10 μm (D), 20 μm (E).

1 ♀, 1 ♂, 8 ovisacs (host: subadult ♀) [paratypes MACN-Pa. 476/7]. – Cape San Pio, Beagle Channel, 55°03'S, 66°37'W, 70–80 m, 27 Jan 2003: 1 ♀, 2 ovisacs (host: subadult ♀); 1 ♀, 1 ♂, 8 ovisacs (host: juvenile ♂) [paratypes MACN-Pa. 476/8].

Diagnosis

Homoeoscelis meridionalis sp. nov. Adult female and male: maxilliped, first article barely to densely setulose all over its distal half, second article elongate. Adult male: first article of maxilliped extending beyond second pair of legs, both pairs of legs and the caudal rami extremely long. Copepodite stage: distal article of second maxilla with a girdle or rosette of spinules distally.

Description of the adult female (based on holotype MACN-Pa. 476/1 and paratypes MACN-Pa. 476/4a, 476/5a and 476/5b, all four mounted on microscope slides; and on paratype MACN-Pa. 476/4b stuck on an aluminium stub for SEM photographs).

Total length 0.35–0.90 mm (mean = 0.49, $n = 27$).

Body (Figures 1B, 2B, 3A–C) globular, slightly flattened dorso-ventrally; covered with many scale-like spinules, more abundant on anterior part of trunk. Under compound microscope 'scales' detectable as 'curved projections' on body margins, or not visible at all, even after staining specimens and observing under high magnification.

Head (Figures 1C, 3E) distinctly defined from trunk and set on ventral surface at short distance from anterior margin (in young females clearly projecting from frontal margin of body, cf. Figures 1B and 2B). Frontal margin with minute setules, lateral margins with stouter and larger setules.

First antenna (Figure 1D) with 2 indistinctly separated articles. First article slightly shorter than second, with 2 simple setae on anterior margin. Second article with 1 subterminal aesthetasc and 11 simple setae (only those visible in ventral view drawn).

Second antenna absent.

First maxilla (Figures 1C, 3E) with 2 branches, 1 directed anteriorly and 1 medially (the latter omitted in Figure 1C).

Second maxilla (Figures 1C, 3E) with 2 articles: basal article robust, with rounded sclerotized process on inner surface; distal article curved, ending in single point.

Maxilliped (Figures 1C; 3E, F) with 2 articles and 1 claw. First article robust, longer than second and claw combined, with bunch of setules proximally and dense mat of setules extending over distal half (other specimens with fewer setules on distal half). Second article narrow, 6 to 8 times longer than wide (measured at half length along article), with a subapical tooth with multiple points (see detail

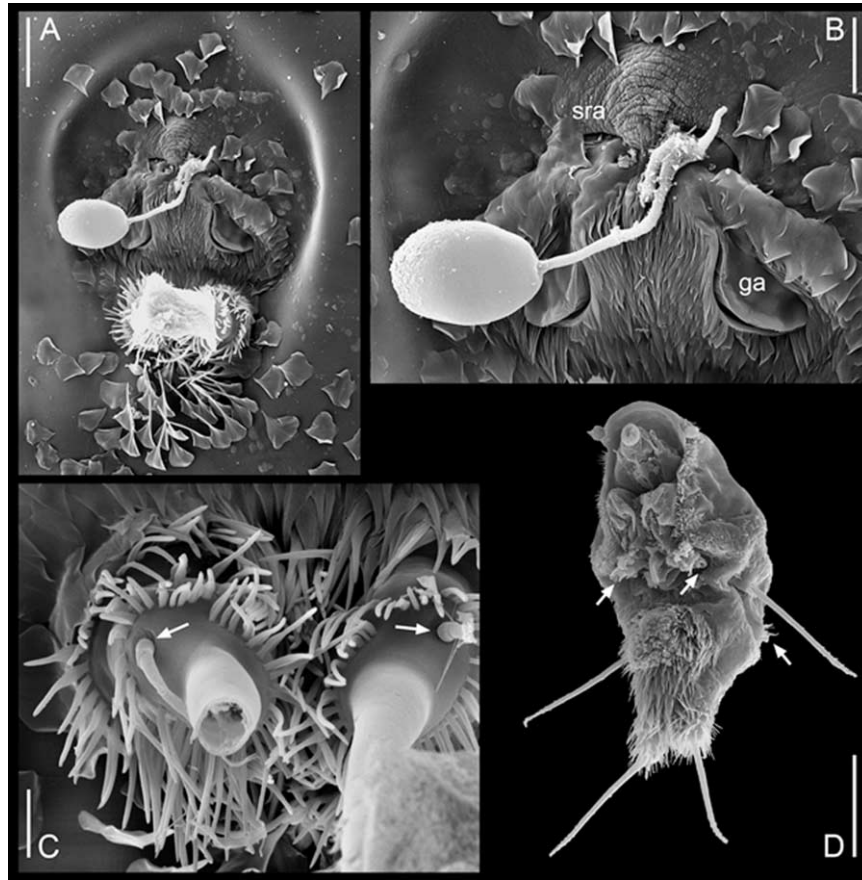


Figure 4. SEM of *Homoeoscelis meridionalis* sp. nov. **A–C**, adult ♀ (paratype MACN-Pa. 476/4b). **A**, genital area, spermatophore and caudal rami (right ramus broken, left ramus is hidden by a particle of dirt). **B**, detail of genital and seminal receptacle apertures (**ga** and **sra**, respectively). **C**, basal part of caudal rami with 2 whorls of setules, arrows point to the seta encircled by the distal whorl. **D**, habitus in ventral view of an adult ♂ (paratype MACN-Pa. 476/4b), arrows point to the insertion areas of missing maxillipeds and leg. Scale bars: 20 µm (**A**), 10 µm (**B**), 5 µm (**C**), 50 µm (**D**).

Figure 3F). Claw, distal end with small finger-like processes.

Anterior pair of legs ventrolateral, posterior pair somewhat shifted to dorsal surface (Figures 1B, 3A). Legs (Figures 1E, 3D) comprising thick, short basal part tapering to long pinnate stylet; basal part with 1 whorl of setules encircling a simple seta. Caudal rami (Figures 1F, 4C) slightly larger than legs, basal part with 2 whorls of setules, most distal whorl encircling a simple seta.

Genital area (Figures 2A; 4A, B) wider than long, consisting of single chitinous arc extending on both sides of and behind genital apertures. Surface covered with dense mat of flat spiniform setules, which are longer towards posterior margin (this arrangement is visible under SEM, only a few flat spiniform setules are detectable under compound microscope, cf. Figures 2A and 4B). With 2 spermatophores attached by long slender stalks to left seminal receptacle aperture (other adult females examined have either 2 spermatophores attached

respectively to left and right apertures, only 1 spermatophore attached to left or right aperture, or none).

Description of the adult male (based on paratypes MACN-Pa. 476/5a and 476/5c, both mounted on microscope slides; and on paratype MACN-Pa. 476/4b stuck on an aluminium stub for SEM photographs).

As female except for:

Total length 0.162–0.256 mm (mean = 0.19 mm, $n = 29$).

Body rhomboid (Figures 2C, D; 4D). Distal end of first article of maxilliped reaching basal part of second leg. Legs longer than body depth. Ventral surface of trunk covered over distal third with dense array of flat spiniform setules. Paired spermatophores (see Figure 2D) located just below level of second legs. Frontal and lateral margins of head, and appendages as in adult female.

Description of the copepodite stage. Based on unhatched specimens removed from one ovisac and

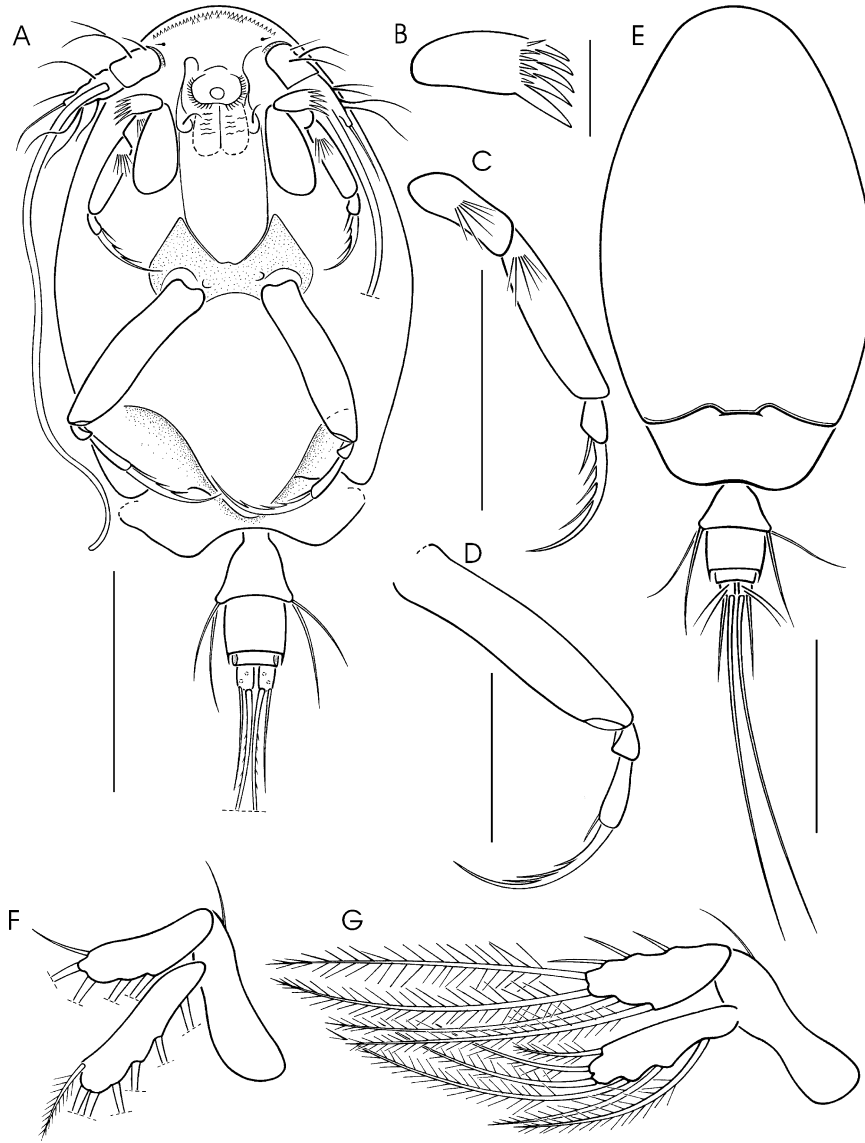


Figure 5. *Homoeoscelis meridionalis* sp. nov. **A–G**, copepodite stage (paratype MACN-Pa. 476/5d). **A**, habitus in ventral view (legs omitted). **B**, detail of distal article of second maxilla, having a girdle of spinules distally. **C**, second antenna. **D**, maxilliped. **E**, habitus in dorsal view. **F**, first leg, only basal part of long setulose setae drawn. **G**, second leg. Scale bars: 0.05 mm (**A**, **E**), 0.025 mm (**C**, **D**, **F**, **G**), 0.006 mm (**B**). Figures **F** and **G** share scale.

mounted on microscope slides (paratypes MACN-Pa. 476/5d, under this number there are also many specimens kept in 70% ethanol) and on unhatched specimens removed from another ovisac that were stuck on aluminium stubs for SEM photographs (paratypes MACN-Pa. 476/5e).

Prosoma length 0.117–0.122 mm (mean = 0.119 mm, $n = 9$).

Prosoma oval (Figures 5A, E; 6A), approximately 5 times longer than urosoma, composing cephalothorax and 1 free pedigerous somite. Frontal margin with two rows of small teeth (see Figure 6D). Distance between maxillae and maxillipeds approximately half as long as basal article of latter. Postmaxillipedal

pouch equilateral triangular shaped, rounded posterior apex almost reaching distal end of prosoma. Urosoma 3-segmented. First urosomite subtriangular with 1 dorsal and 1 ventral seta at each postero-lateral angle, dorsal seta only slightly longer than ventral one and barely surpassing caudal rami. Second urosomite quadrangular. Third urosomite short. Each caudal ramus with 2 short setae on dorsal surface and 2 unequal setae distally; innermost almost as long as cephalothorax, with few hardly visible setules.

First antenna (Figures 5A, 6A) consisting of 2 large subequal articles, both with simple setae. Second article having a conspicuous aesthetasc at 1/3 length reaching end of prosoma.

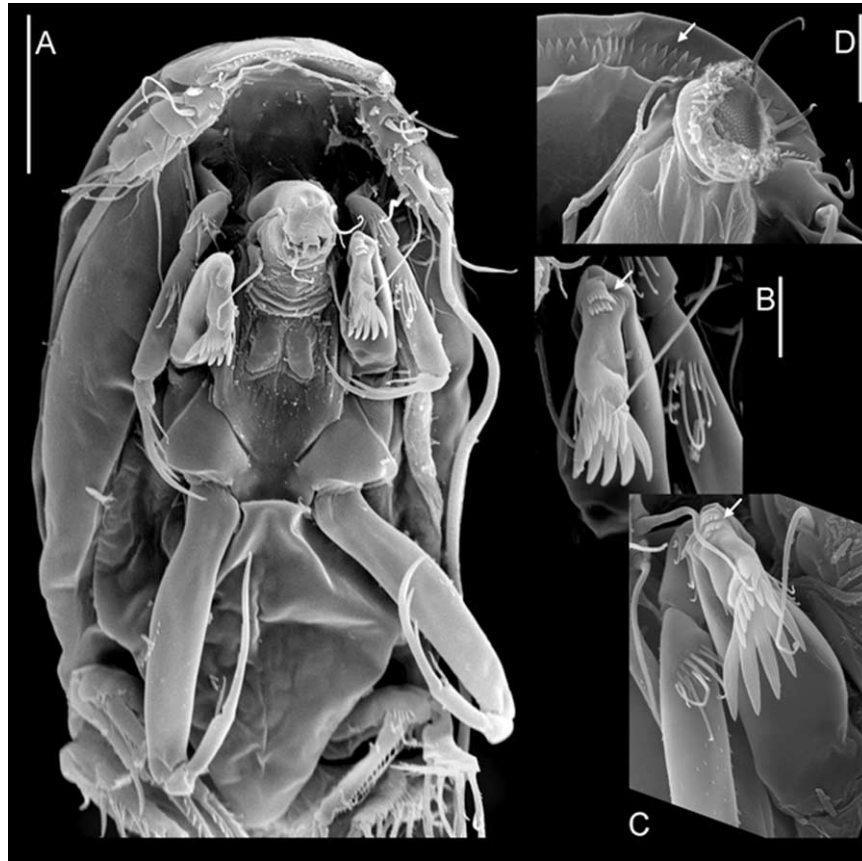


Figure 6. SEM of *Homoeoscelis meridionalis* sp. nov. **A–D**, copepodite stage (paratypes MACN-Pa. 476/5e). **A**, prosoma in ventral view. **B**, left second maxilla from the same specimen, arrow points to the basal rows of small spinules. **C**, right second maxilla from a second specimen, arrow points to the basal rows of spinules. **D**, oral cone and frontal margin from a third specimen, arrow points to the rows of small teeth. Scale bars: 20 μm (**A**), 5 μm (**B–D**). Figures **B** and **C** share scale.

Second antenna (Figures 5A, C; 6A) with 3 articles and 1 claw. First article approximately half as long as second and third together, with a group of setules halfway along article. Second article as long as third and claw together, with a group of setules basally. Third article with 1 simple seta distally. Claw with 2–3 slender teeth on inner margin.

First maxilla (Figures 5A; 6A) with 2 branches, anterior branch much longer than basal one.

Second maxilla (Figures 5A, B; 6B, C) situated closer to first maxilla than to maxilliped, perpendicular to ventral surface of body. With 2 articles, basal article stout, unarmed; distal article approximately 1/3 as long as basal one, having a few small spinules arranged in two rows basally (visible under SEM only, see Figures 6B, C), and a girdle or rosette of spinules (5 of them clearly larger than the rest) distally. Note: to facilitate examination the specimen examined under compound microscope was gently pressed between the slide and the cover glass, thus the distal article of the maxilla is rotated outwards (Figure 5A) and the girdle of spinules appears as a double row of spinules (Figure 5B).

Maxilliped (Figures 5A, D; 6A) with 3 articles and 1 claw. First article robust, naked, slightly longer than second, third and claw together. Third article with 1 simple seta distally. Claw distinctly longer than second and third articles together, with 2–3 slender teeth on inner margin.

Leg 1 (Figure 5F). Protopod with simple seta near distal end; endopod of 1 article, with 7 setulose setae (6 long ones extending from inner margin to distal end, 1 short subterminal on outer margin); exopod of 1 article, with 4 long setulose setae extending from inner margin to distal end, and 1 short simple seta on outer margin.

Leg 2 (Figure 5G) differing from leg 1 in setal formula only; i.e. endopod with 5 long and 1 short setulose setae; exopod with 4 setulose setae extending from inner margin to distal end, and 3 short simple setae on outer margin.

Description of the ovisac

Diameter 0.197–0.427 mm (mean = 0.312 mm, $n = 209$). Infested cumaceans carried from 0 to 16 ovisacs.

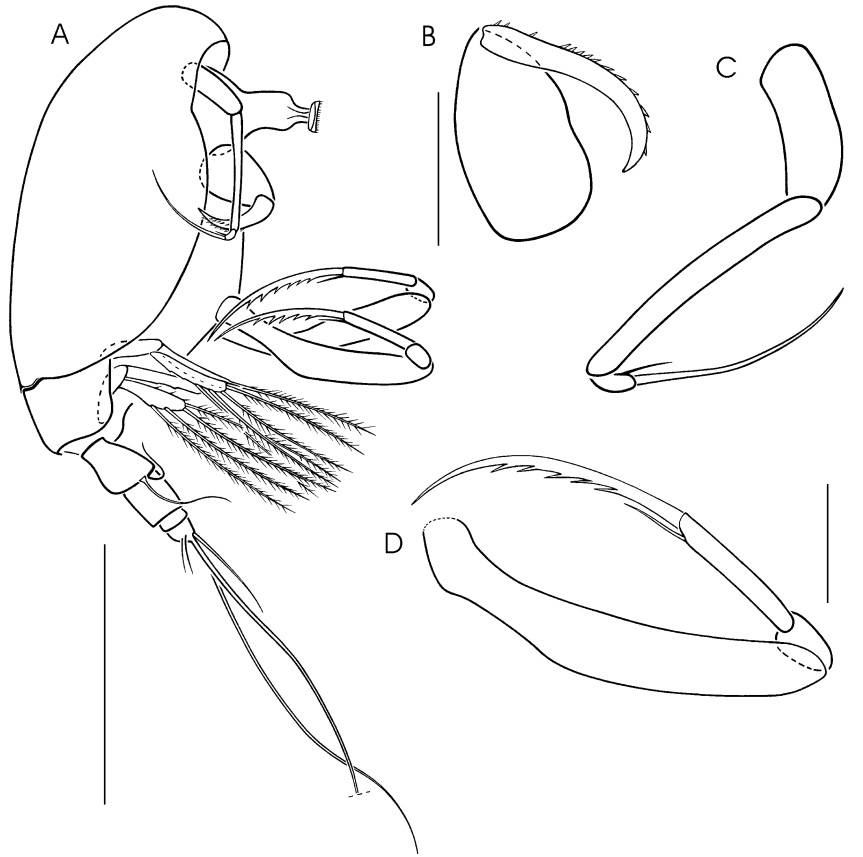


Figure 7. *Homoeoscelis frigida* Hansen, 1923. **A–D**, copepodite stage (syntypes ZMUC-CRU-9239). **A**, habitus in lateral view, first antenna and first maxilla omitted. **B**, second maxilla. **C**, second antenna. **D**, maxilliped. Scale bars: 0.1 mm (**A**), 0.025 mm (**B–D**).

Etymology

The specific epithet refers to the Southern Hemisphere, as *Homoeoscelis meridionalis* is the first species of this genus recorded from this hemisphere.

Homoeoscelis frigida Hansen, 1923 (Figure 7)

Material examined: see ‘Material and methods’ section.

Brief redescription of the copepodite stage (based on 3 unhatched copepodites removed from one ovisac, syntypes ZMUC-CRU-9239).

Prosoma length 0.178–0.188 mm (mean = 0.182 mm, $n = 3$).

Prosoma (Figure 7A) approximately 4 times longer than urosoma. Oral cone distinctly produced. Distance between maxillae and maxillipeds distinctly shorter than basal article of latter. Urosoma and caudal rami as in *Homoeoscelis meridionalis* sp. nov.

First antenna, aesthetasc reaching end of prosoma.

Second antenna (Figures 7A, C), similar to *H. meridionalis* sp. nov. but second article slender and without setules, and claw unarmed.

Maxilla (Figures 7A, B). Basal article stout. Distal article as long as basal one, claw-like, with small teeth on outer margin.

Maxilliped (Figures 7A, D) unusually large, almost as long as prosoma, distinctly projecting from body in lateral view. Similar to *H. meridionalis* sp. nov. but first article slightly shorter than second, third and claw together; third article thinner; claw with 5–6 short teeth on inner margin.

Legs as in *H. meridionalis*.

Parasite–host relationship

Despite the limited number of infested cumaceans collected, some general comments can be made on this host–parasite association. These brief remarks apply for *Diastylis fabrizioi* specimens only.

Of the 1768 specimens examined, 2.6% were found to be infested by *Homoeoscelis meridionalis* sp. nov. Of the 46 parasitized cumaceans gathered, 17 were adult females (with fully developed oostegites), 23 subadult

Table I. Prevalence of *Homoeoscelis meridionalis* sp. nov. on *Diastylis fabrizioi* by instars.

	Number of parasitized hosts	Number of non-parasitized hosts	Prevalence (%)
Adult ♀	17	176	8.8
Subadult ♀	23	211	9.8
Juvenile ♀	1	538	0.2
Adult ♂	0	56	0
Subadult ♂	2	109	1.8
Juvenile ♂	3	546	0.5
Juvenile (undifferentiated)	0	15	0
Manca	0	71	0
Total	46	1722	2.6

females, 2 subadult males, and 4 juveniles. Neither infested adult males nor infested mancas were recorded (see Table I). The prevalence of copepods differs significantly between female and male cumaceans (4.2 vs. 0.7%; $\chi^2 = 19.2$, $p < 0.001$). In addition, the prevalence of the parasite is much higher in later instars of the host (adults and subadults) than in earlier ones (juveniles and mancas) (7.1 vs. 0.3%; $\chi^2 = 70.1$, $p < 0.001$).

Thirty-eight cumaceans harboured a female accompanied by a male (in one case by two males) inside their branchial chambers, seven cumaceans had only a female parasite (males may have been overlooked among dissected remains), and one cumacean housed only a single male parasite. The female parasites occur nearly equally in the right and left branchial chambers (23 vs. 22), and no double infestations were observed. Thus, there appears to be no preference of the parasite for one or the other branchial chamber of the host.

Of the 45 cumaceans harboring female parasites, 36 also carried ovisacs in their branchial chambers. All the individuals in one ovisac are at the same developmental stage, but those in different ovisacs may be in different stages. Among the 36 cumaceans harboring ovisacs, 25 had both categories of ovisacs (with developing embryos and with partially to fully developed copepodites), 10 had only ovisacs with developing embryos, and 1 had only ovisacs with partially to fully developed copepodites. The maximum number of ovisacs recorded by a single female was 16. The most frequent size of ovisac was 0.3 mm, and the mean number of eggs for this size class was 49.2 ($n = 10$, $s = 8.1$). Therefore, we can roughly estimate that a female can produce about 800 eggs, or perhaps more, since this is just an instantaneous measurement (only those eggs that the female had inside its marsupium at the time it was collected were counted).

Among the infested cumaceans, 10 out of 17 adult females (58.8%) contained eggs or mancas inside their marsupia, while among non-infested cumaceans,

131 out of 159 adult females (82.4%) carried eggs or mancas. These figures suggest a detrimental effect of the parasite on the reproduction of the host ($\chi^2 = 5.276$, $p = 0.02$). However, the small sample studied prevents any firm conclusion.

The branchial cavities of 45 infested cumaceans were carefully examined for any damage caused by the parasites. The opposite uninfested chamber served for comparison. In 38% of the cases damage was apparent; i.e. the gills of the infested chamber were flattened and laterally displaced. In 58% of the cases it was not possible to decide which chamber housed the parasites, and in 4% of the cases the gills of the uninfested chamber were more damaged than those of the parasitized chamber.

Discussion

The females of the genus *Homoeoscelis* are much alike. However, *H. meridionalis* sp. nov. has a distinctive maxilliped: the first article is barely to densely setulose all over its distal half, and the second one elongate (see Figures 1C, 3E). We redrew the maxilliped of *Homoeoscelis minuta* Hansen, 1897 based on a female from the type series (ZMUC-CRU-9241, see Figure 1G) and we examined the syntypes of *H. frigida* Hansen, 1923 (ZMUC-CRU-6462 and -9239). In both species the first article of the maxilliped has on its distal half only a terminal row of setules, and the second article is short and stout. This agrees with the illustrations formerly presented by Hansen, 1897 (figure 1h) and 1923 (figure 1c). The maxilliped of *H. mediterranea* appears to be similar to those of *H. minuta* and *H. frigida* (see Hansen 1897, figure 1d). Regarding *H. sedentaria* (Bonnier, 1896) its inadequate description prevents us from arriving at any definite conclusion.

The males have been described for five of the seven species belonging to this genus, i.e. *Homoeoscelis minuta*, *H. mediterranea*, *H. sedentaria*, *H. longipes* and *H. meridionalis* sp. nov. The male of

H. meridionalis sp. nov. can be readily distinguished from those of the other four species by having (1) the basal article of maxillipeds extending beyond the second pair of legs, and (2) both pair of legs and the caudal rami extremely long (the latter is at least half as long as body length). From the type series of *H. minuta* we examined nine males mounted on a microscope slide labelled '9 Hanner, den ene hængende på Gjælleapparatet'. As shown by Hansen in his figures 1i, 1k, these males have short legs and caudal rami, and the basal article of the maxillipeds just reaches the first pair of legs. Hansen (1923) briefly described *H. longipes* based on a female and a male, both badly damaged. No illustrations were added, and only two specimens of *Leptostylis villosa* Sars, 1869, with their carapaces dislodged, were found inside the vial ZMUC-CRU-7124. Since one of these cumaceans is a subadult male (with developing pleopods), this seems to be the host from which Hansen collected the male and female parasites he described. The type material of *H. longipes* is apparently lost.

The copepodite has been described for four of the seven species included in this genus, i.e. *Homoeoscelis minuta*, *H. mediterranea*, *H. frigida*, and *H. meridionalis* sp. nov. The copepodite of *H. meridionalis* clearly stands apart from the other three copepodites known up to date for this genus by having a peculiar second maxilla with a rosette of spinules on the distal article (see Figures 6B, C). The syntypes of *H. frigida* were reexamined and we confirmed that this species has, as reported by Hansen (1923), extremely long maxillipeds (see Figures 7A, D). For *H. minuta* we checked a microscope slide labelled 'Larver af en Æggesæk', but unfortunately this slide is badly damaged and no copepodite, or copepodid remains, were detected. We also removed five ovisacs from one non-dissected specimen of *Diastylis lucifera* from the type series (ZMUC-CRU-9241), but none of them contained copepodites.

Female parasites and ovisacs are readily distinguishable when a light beam passes through the partially translucent cuticle of a preserved host. In addition, the host carapaces are usually swollen on the side containing the parasites. The greatest prevalence of parasite infestation was found among subadult and adult females, representing 87% of all infested cumaceans recovered. No newly established copepodites were obtained, but because of their small size they may have been overlooked. In contrast, we found many copepodites still within the membranes of the ovisacs. Based on this incomplete information it is not possible to reconstruct the life history of *H. meridionalis* sp. nov. However, it can be stated that the adult copepods

preferentially parasitize the largest hosts (subadult and adult cumaceans), whose branchial chambers are spacious enough to accommodate a large number of ovisacs (up to 16 herein reported).

Bowman and Kornicker (1967) proposed that it may be advantageous for those nicothoids that inhabit the brood chambers of ostracods and the marsupia of peracarids to lay their eggs in groups rather than singly. The individual eggs of these copepods are very small and vulnerable to being removed by the host's cleaning appendages or flushed by the circulating current of water. An analogous explanation appears to be valid for the nicothoids that infest the branchial chambers of cumaceans. In these hosts, the large epipodite of the first maxilliped rocks up and down creating a respiratory current, and the individual copepod eggs could also be washed out.

The epipodite of the first maxilliped divides the branchial chamber of cumaceans into an upper and a lower part. The female of *H. meridionalis* sp. nov. and their ovisacs fill most of the upper part of the branchial chamber of *Diastylis fabrizioi*, and may flatten and dislodge the gill lamellae situated on the dorsal surface of the epipodite. Whether the infested cumaceans can ventilate normally is not known, but it is quite likely that the female parasite and its ovisacs hamper the pumping action of the maxillipedal epipodite, obstructing the movement of water needed by the cumacean for respiration.

Nicothoid copepods infesting the marsupium (or brood chamber) may suppress egg production of their hosts (see Hansen 1897; Bowman & Kornicker, 1967; Hamond 1973; Sheader 1977; Just 1978; Daly & Damkaer 1986; Ohtsuka et al. 2007).

Regarding the nicothoid copepods inhabiting the branchial chamber of cumaceans, Hansen (1897) suggested that castration may take place in the specimens of *Diastylis lucifera* infested by *Homoeoscelis minuta*. He reported the following figures for this host-parasite relationship: 182 non-infested adult females carrying eggs or mancas, 74 non-infested adult females with empty marsupia, 13 infested adult females carrying mancas (none with eggs), and 31 infested adult females with empty marsupia. Statistical analysis of these data revealed that the number of infested females of *D. lucifera* without eggs or mancas in their marsupia is much higher than expected ($\chi^2 = 28.49$, $p < 0.001$). Therefore, we can conclude that the reproductive fitness of *D. lucifera* is most probably reduced by this parasite.

Concerning the association between *Homoeoscelis meridionalis* and *Diastylis fabrizioi* the egg production of parasitized and non-parasitized hosts shows to be significantly different at 5% but not at 1% level.

Thus, no definitive conclusions can be drawn until larger samples are examined.

Acknowledgements

The authors are grateful to Mr Fabrizio Scarabino for providing most of the specimens studied in this paper. Special thanks are given to Dr Jørgen Olesen for the loan of the syntypes of *Homoeoscelis minuta*, *H. frigida* and *H. longipes*, and for translating from Danish into English the handwritten labels that accompany this type material. We also thank Dr Martín Torres Jordá for the statistical analysis, Dr Peter Rehm and Dr Christopher Boyko for their help with the literature, and Mr Fabián Tricárico for the scanning electron micrographs. Dr Geoffrey Boxshall provided very helpful remarks on an earlier version of this manuscript. This research was partially supported by the Agencia Nacional de Promoción Científica y Tecnológica (PICT 02-11180), the University of Buenos Aires (Grant X162), and the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET, Argentina).

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Editorial responsibility: Egil Karlsbakk