



## The tantulocarid genus *Arcticotantulus* removed from Basipodellidae into Deoterthridae (Crustacea: Maxillopoda) after the description of a new species from Greenland, with first live photographs and an overview of the class

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### Abstract

A new species of Tantulocarida was found off the coast of Disko Island, West Greenland. The new species, *Arcticotantulus kristenseni* **sp. nov.**, is exclusively found on an as yet undescribed species of *Bradya* Boeck, 1873 (Copepoda, Harpacticoida) caught at depths of 200 m off the coast in muddy sediments. A total of 44 individuals were found, and 38 were examined by use of LM and SEM; these represented different stages of the life cycle: tantulus larvae, developing males, parthenogenetic females, and what may be only the third record of a developing sexual female. *Arcticotantulus kristenseni* is tentatively placed in Deoterthridae based on the mode of formation of the male trunk sac, the pattern of ornamentation on the tergites and cephalic shield, and the number of setae on the thoracopods and caudal rami. It is suggested that the genus *Arcticotantulus* Kornev, Tchesunov & Rybnikov, 2004 is removed from Basipodellidae and placed in Deoterthridae instead, in accordance with the mode of trunk sac development in males and the absence in the latter family of a cephalic rostrum. Various internal anatomical features were examined, including the tubular structures inside the head of the tantulus larvae. The first live photographs of any species of Tantulocarida are presented. This is also the first report on Tantulocarida from West Greenland.

**Key words:** Deoterthridae, parasite, ectoparasitic crustacean, Harpacticoida, parthenogenetic, *Bradya*, sexual female tantulocarid

### Introduction

The Tantulocarida are tiny marine ectoparasitic crustaceans that have been found exclusively on other small or minute crustaceans. The Tantulocarida were established as a new class of Crustacea by Boxshall & Lincoln (1983) but the roots of their taxonomic history go back to the beginning of the 20th century, when the French naturalist Bonnier (1903) and the Danish carcinologist Hansen (1913) described some minute crustaceans parasitic on cumaceans and tanaidaceans, respectively (Huys 1991). Other reports on tantulocaridans prior to their establishment as a separate taxon include those of Greve (1965), Becker (1975), and Bradford & Hewitt (1980).

The peculiar life cycle of the Tantulocarida was elucidated by Boxshall & Lincoln (1987) and Huys *et al.* (1993b) by combining information from several species. According to Huys *et al.* (1993b), there is an infecting tantulus larva that passes through a short benthic phase before infecting a suitable epibenthic host. In their short epibenthic phase the larvae are regarded as temporary meiobenthos (Huys 1991). After attachment, three different developmental pathways apparently exist for an individual tantulus larva. It can develop into a

sexual male, a sexual female, or into a parthenogenetic female that produces numerous tantulus larvae. Hence, the life-cycle of the Tantulocarida is now understood to be composed of two cycles: a sexual cycle and a parthenogenetic cycle. The exact relation between these cycles is not yet understood (Huys *et al.* 1993b). It is also unclear whether the offspring of the sexual cycle are also tantulus larvae, a gap in knowledge highlighted by a preliminary recent report on previously unknown benthic, non-feeding, nauplius-like tantulocarid stages by Martinez Arbizu (2005).

In the Arctic, tantulocaridans are known to parasitize harpacticoid copepods (Huys *et al.* 1997; Kornev *et al.* 2004) and Tanaidacea (Hansen 1913). Worldwide, the range of hosts is wide, with different species of Tantulocarida being found on copepods, ostracods, isopods, cumaceans, amphipods, and tanaidaceans (Huys 1991; Boxshall & Vader, 1993). New genera and species are continuously being discovered. Other reports from northern areas include those of Huys and Boxshall (1988) and Huys *et al.* (1992a), but sampling in coral reefs, shallow subtidal localities, anchialine lava pools (Boxshall & Huys 1989), and hydrothermal vents (Huys & Conroy-Dalton 1997) has shown that tantulocaridans are not only found in cold-water habitats, such as the deep sea or at high latitudes, as was thought in 1983 when the class was established by Boxshall and Lincoln. Tantulocarid diversity has apparently been greatly underestimated, and species have surely been overlooked due to the minute size of the animals.

The intrinsic taxonomy of the Tantulocarida is largely based on the tantulus larvae, the stage most commonly described for the different species. The pore pattern on the cephalon, thoracopod morphology and urosome ornamentation (thorax segment 7 plus abdomen) have also been used to describe different species. Cephalic appendages such as first and second antennae and mouthparts are absent among tantulocaridans in most stages of their life cycle (first antennae present in sexual females; see Huys *et al.* 1993b). In general, our understanding of these tiny crustaceans has been complicated by their size (80 to 200  $\mu\text{m}$ ) and by the fact that not all stages are known for all species (e.g., Huys 1991). Today, the Tantulocarida comprise five families, 22 genera, and 30 species, excluding one species *incertae sedis* and the new species described in this paper (see Table 1).

Suggestions as to the systematic position of the Tantulocarida prior to their establishment as a separate crustacean class included placements close to epicaridean isopods (Bonnier 1903; Greve 1965), copepods (Hansen 1913), or cirripedes (Bradford & Hewitt 1980). Recently, the Tantulocarida have been treated as closely related to the Thecostraca (Facetotecta, Ascothoracida, and Cirripedia) based on similarities in the tagmosis between tantulus larvae and the various cypridiform thecostracan larvae and, for crustaceans, the unusual position of the female gonopores on thoracic segment 1 (see Huys *et al.* 1993b; Ohtsuka & Boxshall 1998; Walossek & Müller 1998). Furthermore, Huys (1991) reinterpreted the thorax of the Tantulocarida as being composed of seven somites (in contrast to six) which is another feature shared not only with the Thecostraca but also with copepods.

Tantulocaridans for this study were collected in August, 2001, at Disko Island off Western Greenland and again in July, 2002, during a summer course at Disko Island, and are the first ever to be reported from this region. The collected specimens resemble a recently described species found in the White Sea, *Arcticotantulus pertzovi* Kornev, Tchesunev, and Rybnikov, 2004 (*q.v.*), but this study indicates that sufficient difference from the latter warrants the description as a new species in the same genus. Based on the present description of *Arcticotantulus kristenseni* **sp. nov.**, we furthermore move *Arcticotantulus* from Basipodellidae, to which it was assigned by Kornev *et al.* (2004), to Deoterthridae (see Table 2). The photos presented in this paper are the first published of live tantulocaridans.

## Methods

Samples were taken off the rocky coast of West Greenland near Qeqertarsuaq (Disko) in two shrimp fishing grounds, the relatively undisturbed Iqpik (Disko Bay) and the heavily fished Kuanit (Disko Fjord), both sites being situated near the shore and in relatively shallow water (100–200 m; Fig. 1). A triangular dredge was

TABLE 1. List of known species of Tantulocarida

| Family                           | Species                              | Host family (order)  | Reference                          | Family characters and notes  |   |
|----------------------------------|--------------------------------------|--|------------------------------------|--|---|
| Basipodellidae                   | <i>Basipodella atlantica</i>         | Tisbidae (Harpacticoida)                                   | Boxshall & Lincoln 1983            | Rostrum present. Cephalic shield with 1 pair of pores anteriorly and 2 pairs posteriorly. Subdorsal pores absent.  |   |
|                                  | <i>Basipodella harpacticola</i>      | Cletodidae (Harpacticoida)                                 | Becker 1975                        | First protopod with 2 setae on exopod and 2 setae on endopod. Second to fifth protopods with 3-4 setae on exopod and 2 setae on endopod. Urosome multisegmented.   |   |
|                                  | <i>Hyperantantulus siphonicola</i>   | Asterocheridae (Siphonostomatoida)                         | Ohtsuka & Boxshall 1998            | Trunk sac with male forming behind sixth tergite, with additional swelling between cephalon and first tergite.   |   |
|                                  | <i>Nipponotantulus heteroxenus</i>   | Pseudocyclopiidae (Calanoida)                              | Huys et al. 1994                   |  |   |
|                                  | <i>Polynapodella ambrosei</i>        | Cerviniidae, Harpacticoida (Copepoda)                      | Huys et al. 1997                   |  |   |
|                                  | <i>Rimilitantulus hirsutus</i>       | Argesidae (Harpacticoida)                                  | Huys & Conroy-Dalton 1997          |  |   |
|                                  | <i>Stygotantulus stocki</i>          | Tisbidae, Canuellidae (Harpacticoida)                      | Boxshall & Huys 1989               |  |   |
|                                  | Deoterthridae                        | <i>Amphitantulus harpiniarcheres</i>                       | Phoxocephalidae (Amphipoda)        | Boxshall & Vader 1993  | Rostrum absent. Cephalic shield with 4 pair of pores anteriorly and 6 pairs posteriorly. 1 pair of subdorsal pores.   |
|                                  |                                      | <i>Aphotocentor spix</i>                                   | Unknown (free in sediment)         | Huys 1991  | First protopod with 2-3 setae on exopod and 0-1 setae on endopod. Second to fifth protopods with 2-5 setae on exopod and 2 setae on endopod. Urosome two-segmented. |
|                                  |                                      | <i>Arcticotantulus kristenseni</i>                         | Ectinosomatidae (Harpacticoida)    | This study   | Trunk sac with male forming behind sixth tergite. Only sexual female found by Huys et al. (1993) within <i>I. misophricola</i> .                                    |
| <i>Arcticotantulus pertzovi</i>  |                                      | Ectinosomatidae (Harpacticoida)                            | Kornev, Tchesunov & Rybnikov 2004  |  |   |
| <i>Boreotantulus kunzi</i>       |                                      | Cylindropsyllidae (Harpacticoida)                          | Huys & Boxshall 1988               |  |   |
| <i>Campyloxiphos dineti</i>      |                                      | Zosimidae (Harpacticoida)                                  | Huys 1990a                         |  |   |
| <i>Coralliotantulus coomansi</i> |                                      | Longipediidae (Harpacticoida)                              | Huys 1990b                         |  |   |
| <i>Cumoniscus kruppi</i>         |                                      | Leuconidae (Cumacea)                                       | Bonnier 1903; Huys et al. 1993a    |  |   |
| <i>Deoterthron dentatum</i>      |                                      | Cypridinidae (Myodocopida)                                 | Bradford & Hewitt 1980             |  |   |
| <i>Deoterthron lincolni</i>      |                                      | Diosaccidae, (Miracidae)                                   | Boxshall 1988; Huys 1990           |  |   |
| Microdajidae                     | <i>Dicrorichura trincta</i>          | Unknown (free in sediment)                                 | Huys 1989                          |  |   |
|                                  | <i>Itoitantulus misophricola</i>     | Misophridae (Misophrionida)                                | Huys et al. 1992b                  |  |   |
|                                  | <i>Tantulicus hoeft</i>              | Unknown  | Huys et al. 1992a                  |  |   |
|                                  | <i>Microdajus aporosus</i>           | Nototanaididae (Tanaidacea)                                | Grygier & Sieg 1988                | All limbs strongly reduced, with very few setae on exo- and endopods. No endites on thoracopods. Trunk sac with male forming behind sixth tergite. Urosome two-segmented.  |   |
|                                  | <i>Microdajus gaelicus</i>           | Typhlotanaidae (Tanaidacea)                                | Boxshall & Lincoln 1987            |  |   |
|                                  | <i>Microdajus langi</i>              | Leptognathidae, Anarthruridae, Typhlotanaidae (Tanaidacea) | Greve 1965                         |  |   |
|                                  | <i>Microdajus pectinatus</i>         | Typhlotanaidae (Tanaidacea)                                | Boxshall et al. 1989               |  |   |
|                                  | <i>Xenodytus scotophilus</i>         | Unknown (free in sediment)                                 | Huys 1991                          |  |   |
|                                  | <i>Onceroxenus birdi</i>             | Agathotanaididae (Tanaidacea)                              | Boxshall & Lincoln 1987            | Rostrum minimal and incorporated into cephalic shield. Cephalic shield with 3 sets of 2 pairs of pores dorsally. No subdorsal pores. First protopod with 2 setae on exopod and 0 setae on 1-segmented endopod. Second to fifth protopods with 4 setae on exopod and 2 setae on endopod. Urosome three-segmented. |   |
|                                  | <i>Onceroxenus curtus</i>            | Leptognathidae (Tanaidacea)                                | Boxshall & Lincoln 1987            |  |   |
| Doryphallophoridae               | <i>Doryphallophora asellotitcola</i> | Haplomiscidae (Isopoda)                                    | Boxshall & Lincoln 1983            | Rostrum distinct. Cephalic shield with 8 pairs of pores, of which 1 pair slit-shaped. No subdorsal-pores. First protopod with 4 setae on exopod and 0-1 setae on endopod.  |   |
|                                  | <i>Doryphallophora harrisoni</i>     | Macrostylidae (Isopoda)                                    | Boxshall & Lincoln 1987; Huys 1990 | Second to fifth protopods with 4 setae on exopod and 2 setae on endopod. Urosome two-segmented. Trunk sac with male forming behind sixth tergite, with additional swelling between fifth and sixth tergites. All known species with tantulus larvae >100 µm long.  |   |
|                                  | <i>Doryphallophora megacephala</i>   | Haplomiscidae (Isopoda)                                    | Lincoln & Boxshall 1983            |  |   |
|                                  | <i>Paradoryphallopora inusitata</i>  | Haplomiscidae (Isopoda)                                    | Ohtsuka & Boxshall, 1998           |  |   |
| <i>Incertae sedis</i>            | <i>Tantulocarida</i> sp. indet       | Leptognathidae (Tanaidacea)                                | Hansen 1913 in Huys 1991           |  |   |

hauled behind the research vessel *Porsild*. The dredge was dragged up the slope over a muddy bottom, at a speed of one or two knots (2–4 km/hr). Eight hauls were made in August, 2001 in the Iqpiq ground. Seven hauls were made in July, 2002: Two each in the Iqpiq ground on July 5 and 12, two in the Kuanit ground on July 17, and one in the Iqpiq ground on July 19 (Table 3). Some mud samples with living material were kept cold (<4°C) and analysed over the following days, but most specimens of interest were sorted and fixed in buffered formalin or alcohol immediately upon retrieval on board the vessel. Tantulocaridans were only found at Iqpiq. Immediate fixation on board turned out to be necessary because it was usually not possible to find tantulocarid specimens in the samples in the laboratory after approximately 24 hours. However, a few samples with live material provided the first opportunity for examining and obtaining pictures of live tantulocaridans. Some preserved samples were stained with Rose Bengal in order to facilitate sorting.

**TABLE 2.** Family characters of Basipodellidae and Deoterthridae compared to *Arcticotantulus*.

|  | Basipodellidae  | Deoterthridae  | Arcticotantulus   |
|--|---|--|---|
| Number of cephalic pore pairs  | 3   | Usually 10 <sup>a</sup>                                  | 4   |
| Anterior pore pairs  | 1   | 4 (or varying) <sup>b</sup>                              | 1–2   |
| Posterior pore pairs   | 2   | 6 (or varying) <sup>c</sup>                              | 2–3   |
| Subdorsal pore pairs   | Absent  | 1 (or more)  | 1   |
| No. of setae on exopod of first protopod                               | 2   | 2–3  | 2   |
| No. of setae on endopod of first protopod                              | 2   | 0–1  | 0   |
| No. of setae on exopod of 3 <sup>rd</sup> to 5 <sup>th</sup> protopods | 3–4   | 2–5  | 3–4   |
| Rostrum  | Present   | Absent   | Absent  |
| Urosome  | Multi-segmented   | Two-segmented  | Two-segmented <sup>d</sup>  |
| Swelling between cephalon and first tergite in developing male         | Remarkably larger than those between the other tergites | Remarkably smaller than those between the other tergites | Remarkably smaller than those between the other tergites <sup>e</sup> |

<sup>a</sup>) Usually 10, but fewer or more are not uncommon.

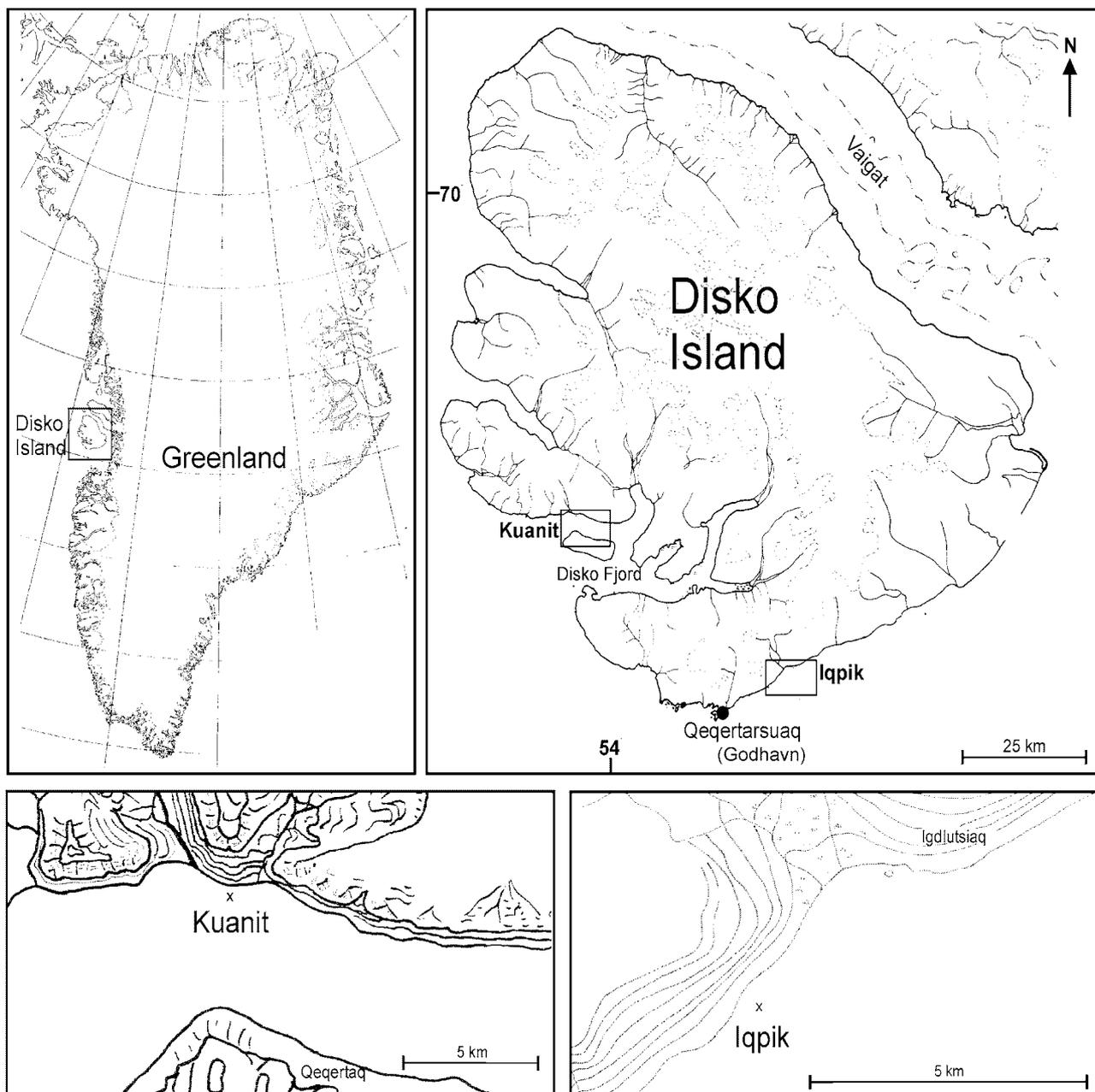
<sup>b</sup>) Both *Cumoniscus kruppi* (Huys *et al.* 1993a) and *Itoitantulus misophricola* (Huys *et al.* 1993b) have 5 pore pairs anteriorly.

<sup>c</sup>) *Boreotantulus kunzi* (Huys & Boxshall 1988) has 5 pairs of pores posteriorly and *Tantulacus hoegi* (Huys *et al.* 1992a) has 7 pairs of pores posteriorly.

<sup>d</sup>) The description of *Arcticotantulus* mentions an unsegmented abdomen. As the urosome consists of the abdomen and the preceding seventh limbless thoracic somite, *A. pertzovi* actually has a two-segmented urosome and an unsegmented abdomen.

<sup>e</sup>) The developing male of *Arcticotantulus pertzovi* depicted by Kornev *et al.* (2004: figs. 1B, 4A), does not appear to have a particularly large swelling between the cephalon and the first tergite. The swelling is, on the contrary, quite inconspicuous.

Drawings of selected specimens were made by SWK and MK with a camera lucida and by filling in details that could only be seen by scanning electron microscopy (SEM). Light microscopy (LM) using an Olympus microscope equipped with Nomarski objectives was carried out at the Arctic Station, Qeqertarsuaq, Disko, Greenland. Scanning Electron Microscopy (SEM) using a JEOL JSM-6335F was carried out at the Zoological Museum, University of Copenhagen. SEM techniques involved dehydration in acetone, critical-point drying, and subsequent coating with an alloy of palladium and platinum.



**FIGURE 1.** Localities where mud samples were collected, Iqpik and Kuanit. x marks the sampling stations. *Arcticotantulus kristenseni* **sp. nov.** were only found at the fishing ground at Iqpik.

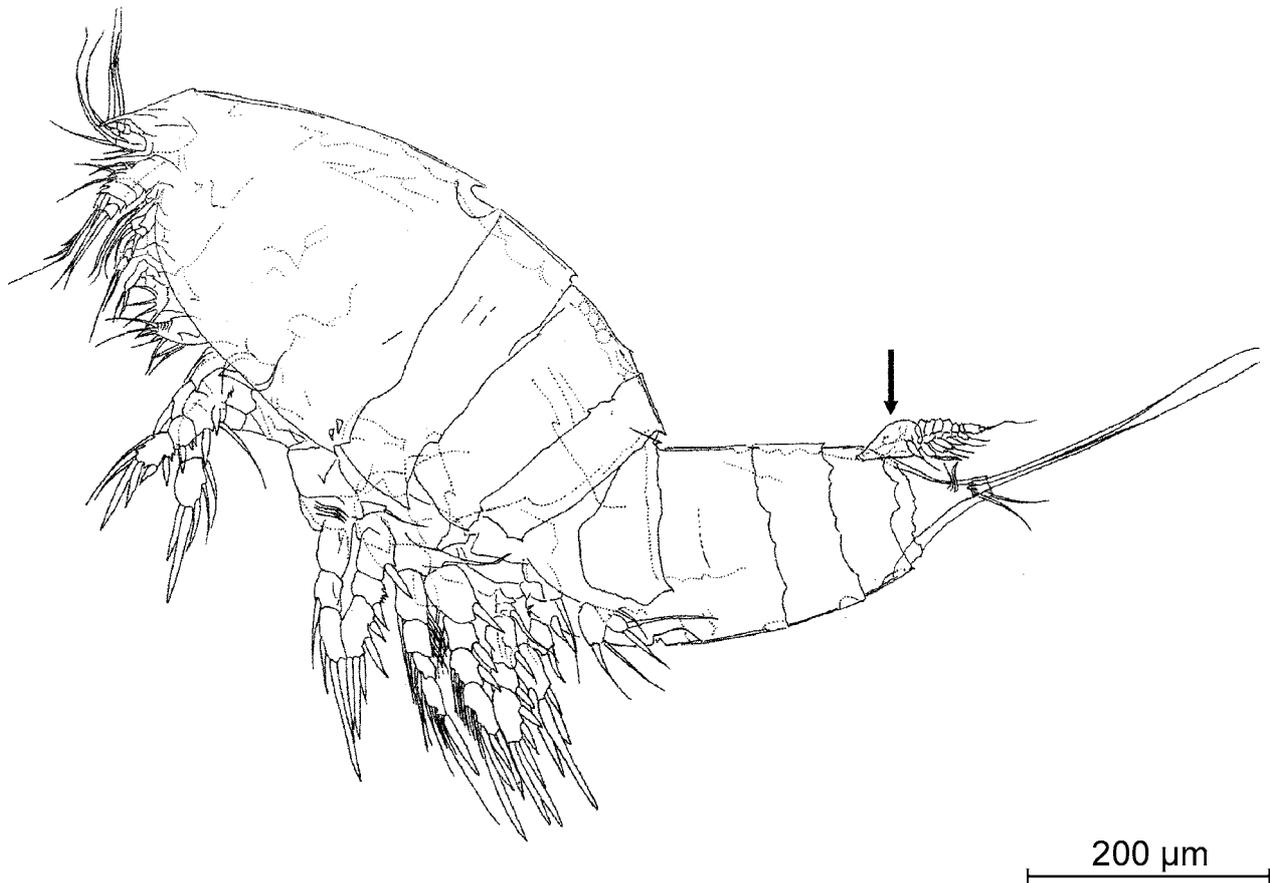
The type material is deposited in the Zoological Museum, University of Copenhagen (ZMUC), Denmark. Despite a request, we failed to obtain the type material of *Arcticotantulus pertzovi* from the P.P. Shirshov Institute of Oceanology, Moscow, for comparative purposes; the comparison is, therefore, based solely on published information.

All examined specimens of *Arcticotantulus kristenseni* **sp. nov.** were found as ectoparasites on harpacticoid copepods (*Bradya* sp.) (Figs. 2, 8, 9, 17D). In total, 44 tantulocaridans were found. Out of these, we identified six tantulus larvae, 20 males developing within the abdominal trunk sac of tantulus larvae, nine parthenogenetic females, and three that appeared to be sexual females in an early stage of development (Fig. 16A, 16B and 17C). Six specimens were not examined morphologically, but sent to Dr. Rony Huys for molecular analysis at the Natural History Museum in London.

Both of the two fishing grounds surveyed in the present study provided a variety of meiofauna, but

tantulocaridans were only found in the Iqqik ground. Apart from tantulocaridans, this ground was inhabited by Polychaeta, Kinorhyncha, Nematoda, Tanaidacea, and had a very rich harpacticoid fauna. The Kuanit ground produced Polychaeta, larvae of Bivalvia and Ophiuroida, Kinorhyncha, Nematoda, and Tanaidacea, but had fewer harpacticoid species (and specimens). The sediment at the Iqqik ground consisted of brown mud and fine organic particles, whereas that at the Kuanit ground consisted of sand and black mud.

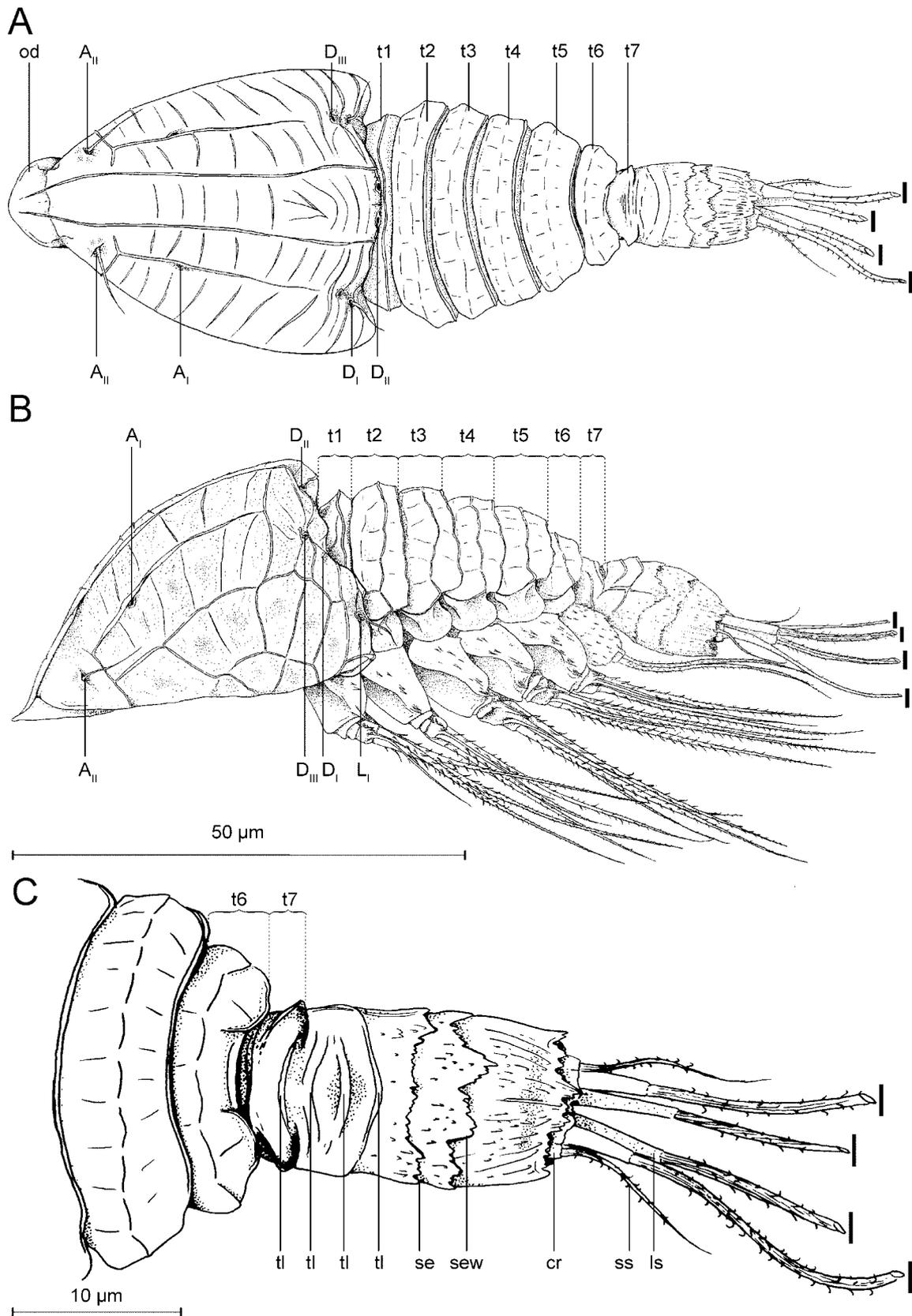
In total, 1181 copepods from the fishing ground at Iqqik were examined. The infection rate of the copepods in the samples varied from 1.5% to 6.2% (Table 3).



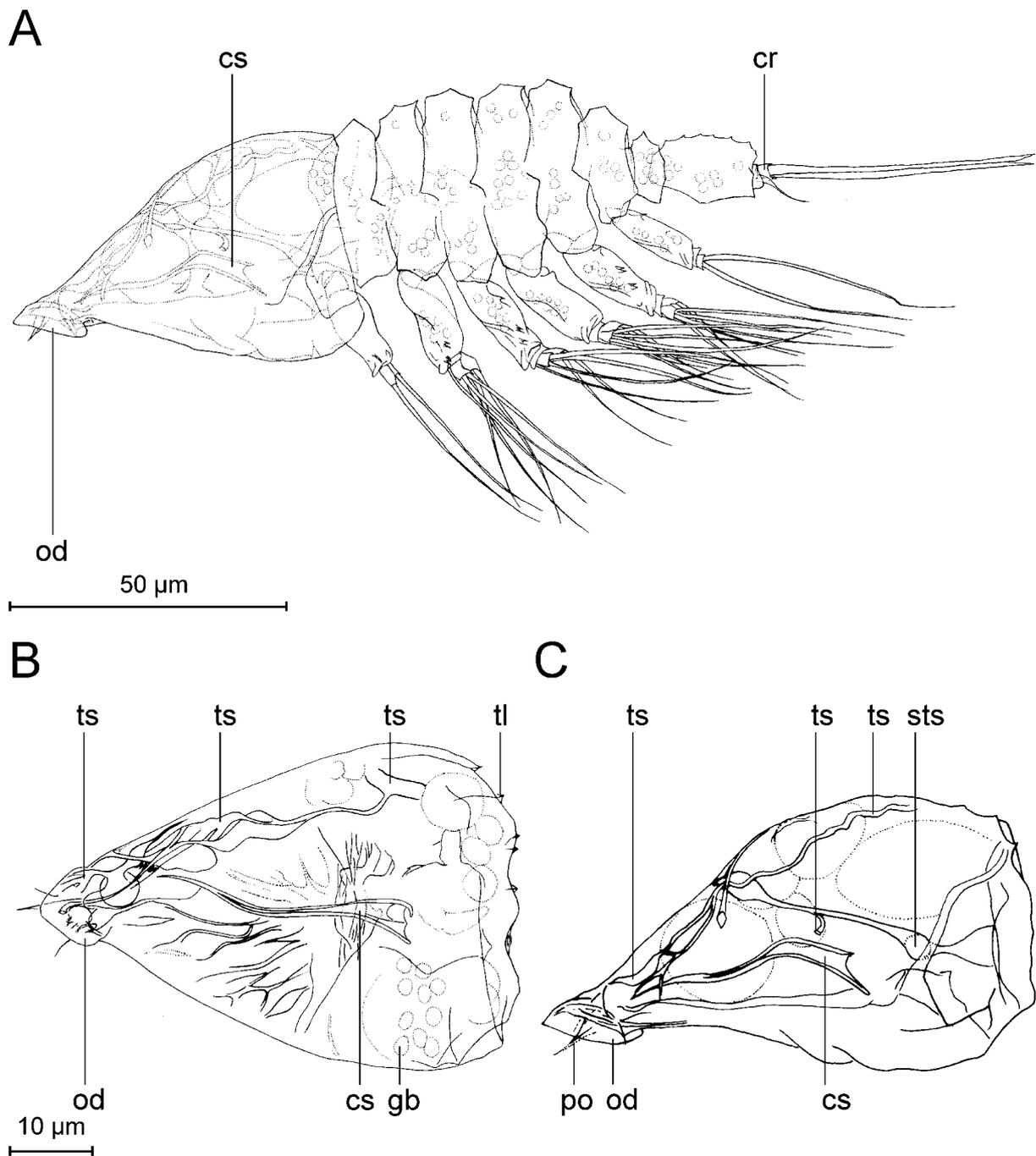
**FIGURE 2.** Harpacticoid copepod with a tantulus larva (ZMUC CRU4884) of *Arcticotantulus kristenseni* **sp. nov.** attached to the posterior abdominal somite. This attachment site is typical, but attachment can occur everywhere on the host. Arrow points at larval head.

**TABLE 3.** Sampling localities of *Arcticotantulus kristenseni* **sp. nov.** with catch depth and with prevalence and mean intensity of copepod hosts infected with tantulocaridans (counting all examined copepods). Mean intensity is determined from the total number of parasites on all infected copepod hosts.

| Station and date of sampling | Iqqik, 16th August 2001 | Iqqik, 5th July 2002    | Iqqik, 12th July 2002   | Kuanit, 17th July 2002  | Iqqik, 19th July 2002   |
|------------------------------|-------------------------|-------------------------|-------------------------|-------------------------|-------------------------|
| Copepods examined            | not recorded            | 330                     | 754                     | 72                      | 97                      |
| Tantulocaridans found        | 10                      | 5                       | 25                      | 0                       | 6                       |
| Prevalance (%)               | -                       | 1.5                     | 3.3                     | -                       | 6.2                     |
| Mean intensity               | -                       | 1.3                     | 1.3                     | -                       | 1.0                     |
| Depth (m)                    | 198                     | 195–214                 | 166–170                 | 105–130                 | 198–220                 |
| Location                     | 69°17.2'N,<br>53°14.4'W | 69°17.3'N,<br>53°13.1'W | 69°18.0'N,<br>53°11.5'W | 69°33.3'N,<br>54°15.0'W | 69°17.3'N,<br>53°13.2'W |



**FIGURE 3.** Tantulocaris larva of *Arcticotantulus kristenseni* sp. nov., external morphology (drawn from ZMUC CRU4882 and ZMUC CRU4889). A. Dorsal view. B. Lateral view. C. Urosome and urosomal setation, dorsal view. Abbreviations: caudal rami (cr), 'w-shaped' serrated edge (sew), serrated edges (se), long setae (ls), oral disc (od), short setae (ss), thoracic somites 1 to 7 (t1-t7), transverse lamellae (tl). See text for pore nomenclature. Setae on caudal rami are not shown at full length, but are cut off as indicated by the small bars.



**FIGURE 4.** Tantulid larva of *Arcticotantulus kristenseni* sp. nov., internal morphology (drawn from ZMUC CRU4882 and ZMUC CRU4887). A. Lateral view. B. Cephalon, internal structures, dorsal view. C. Cephalon of A, enlarged, internal structures, lateral view. Abbreviations: caudal rami (cr), cephalic stylet (cs), globular bodies (gb), protruding organ (po), oral disc (od), swellings on tubular structures (sts), transverse lamellae (tl), tubular structures (ts).

## Systematics

### Family Deoterthridae Boxshall & Lincoln, 1987

**Genus *Arcticotantulus* Kornev, Tchesunov & Rybnikov, 2004.** We propose below that the genus *Arcticotantulus* is transferred from Basipodellidae to Deoterthridae.

**Type species.** *Arcticotantulus pertzovi* Kornev, Tchesunov & Rybnikov, 2004 from the White Sea.

**Species.** *Arcticotantulus kristenseni* sp. nov.

**Material examined.** Holotype: ZMUC CRU4889, tantulus larva attached dorsally to the first abdominal somite of a copepodid IV stage of an unidentified harpacticoid copepod (*Bradya* sp.) mounted on a stub for SEM; collected at Iqqik fishing ground, Disko Bay, Greenland (69°17.2'N, 53°14.4'W), depth 198 m, by R. M. Kristensen, 16 August 2001.

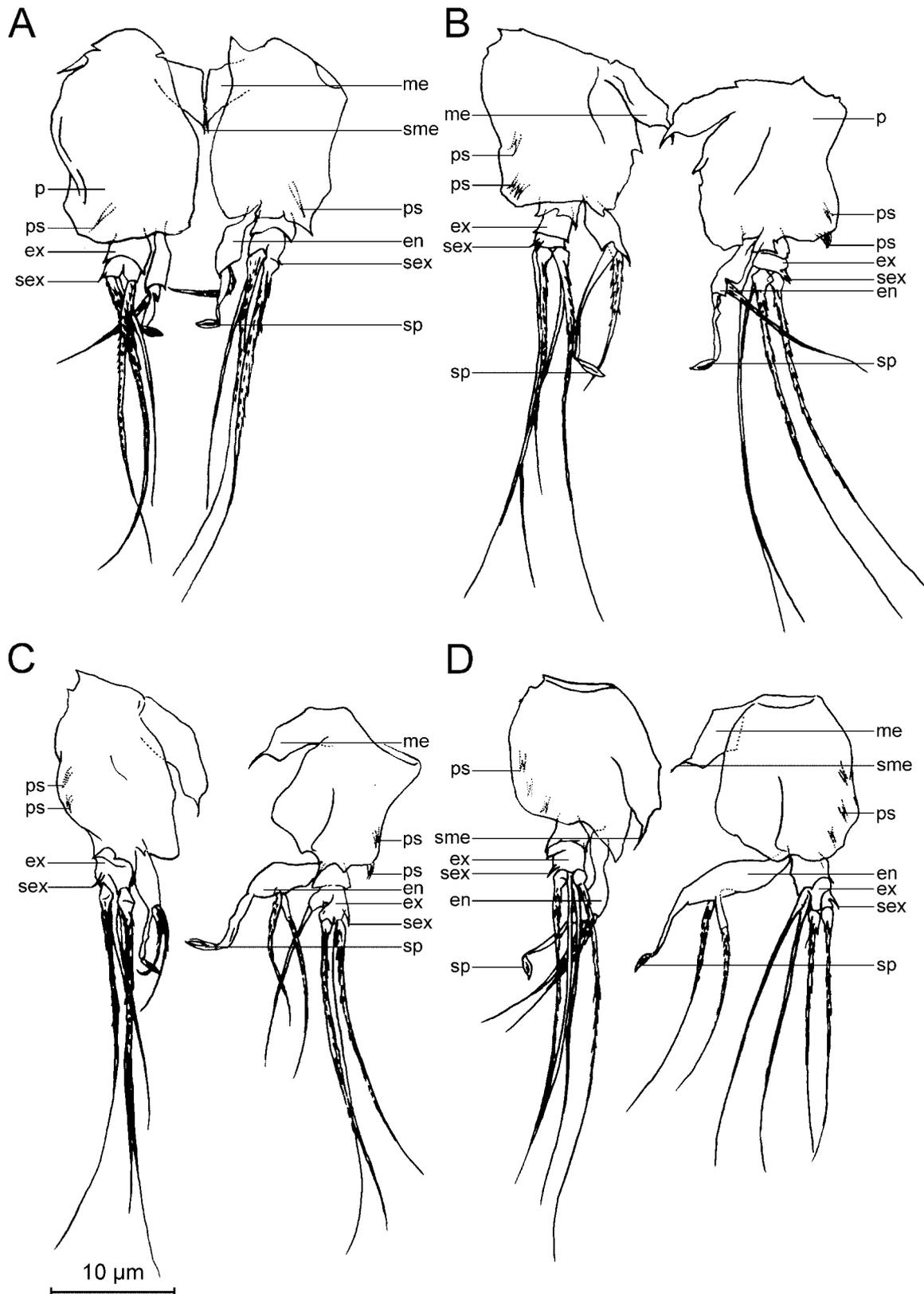
Paratypes: (n = 4) ZMUC CRU4890, mounted on a stub for SEM, same locality information as for holotype. ZMUC CRU4891 (n = 18) mounted on a stub for SEM; collected at Iqqik fishing field, Disko Bay, Greenland (69°18.0'N, 53°11.5'W), depth 166–170 m, by S. W. Knudsen, M. Kirkegaard, and R. M. Kristensen, 12 July 2002. ZMUC CRU4872–4888 (n = 15) as whole mounts in 100% glycogen solution for light microscopy; collected at Iqqik fishing ground, Disko Bay, Greenland (69°18.0'N, 53°11.5'W), depth 166–170 m, by S. W. Knudsen, M. Kirkegaard, and R. M. Kristensen, 12 July 2002.

**Diagnosis.** Tantulus larva comprising cephalon, thorax of six pedigerous somites and one limbless somite, and an undivided abdomen. First thoracic tergite largely concealed beneath posterior margin of dorsal cephalic shield. Cephalic shield triangular; ornamentation consisting of two anterior and four posterior pairs of pores, three pairs of which have an emergent sensillum; surface lamellae present. Cephalic stylet slightly curved in lateral aspect. Thoracopods 1 to 5 each with unsegmented protopod bearing a well developed medial endite. Exopod of thoracopods 1 to 5 two-segmented with 3 (leg 1) or 4 setae (legs 2–5). Of these, the two on the outer margin share a common base, and the one (or two) on the inward side has a second base – if two setae are present on the inward side, they also share a common base. Endopod indistinctly subdivided (terminal part as rigid spine bearing a spatulate process) with 1 seta (legs 1 and 2) or 2 setae (legs 3–5). The endopod setae originate medially from the first segment of the endopod. Thoracopod 6 with unsegmented protopod and one unsegmented ramus. Abdomen twice as long as wide with superficial ornamentation. Caudal rami small, each with three setae (two large and one small). Host is an undescribed species of the genus *Bradya* (Ectinosomatidae) (Copepoda: Harpacticoida).

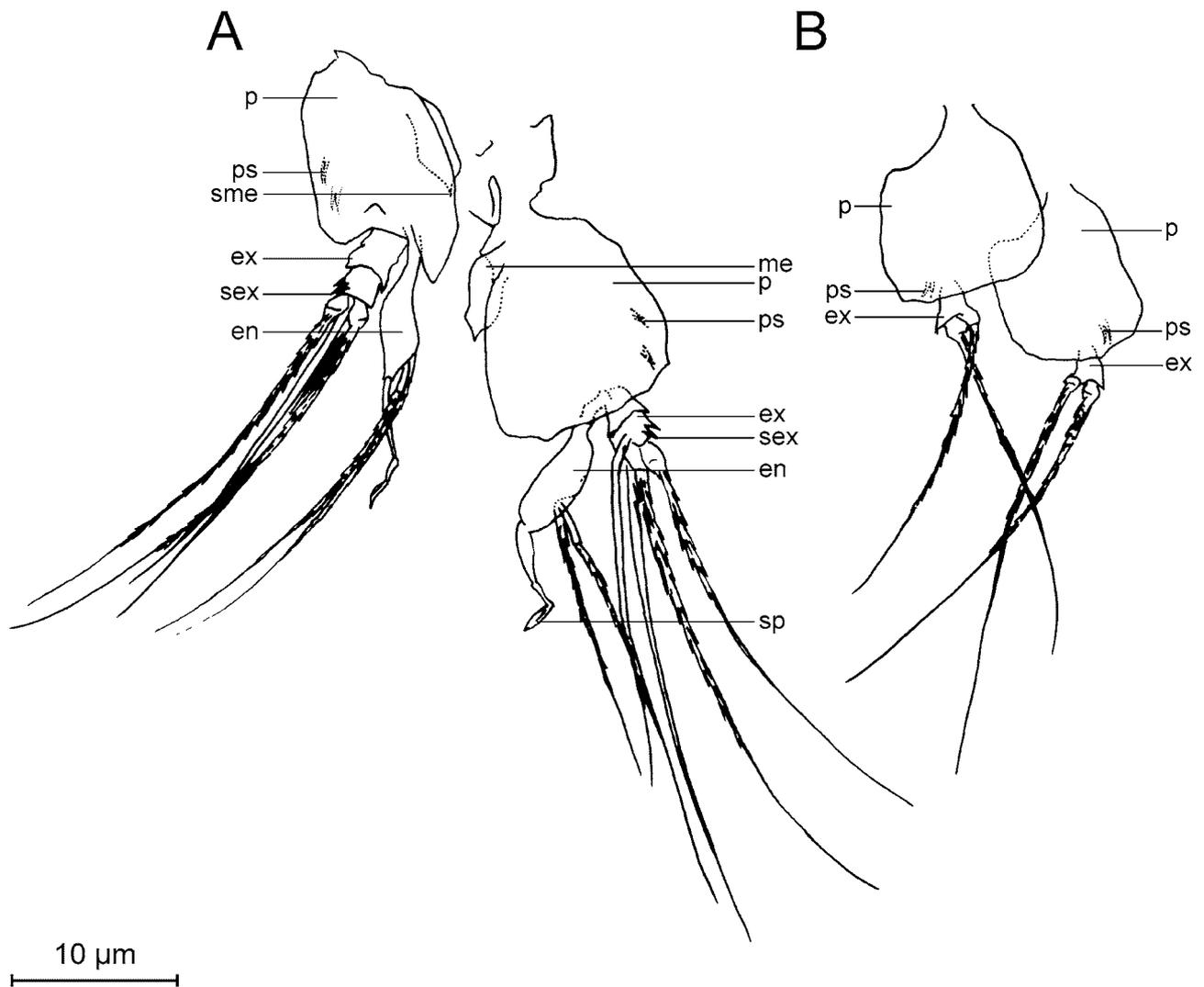
**Description.** *Tantulus larva*: The body consists of a prosome and a urosome (Figs 3, 10) (terminology after Boxshall & Vader 1993): Fig. 10B, D clarifies the relation between the prosome/urosome and the thorax/abdomen. The prosome consists of a cephalon and the six anterior pedigerous thoracic somites (Fig. 3A, t1–t6). The urosome is two-segmented, consisting of the seventh, limbless, thoracic somite (Fig. 3A, t7) and a free, rather long abdominal somite. Total body length varies from 147 µm to 192 µm, measured from the anterior margin of the cephalic shield to the posterior end of the caudal rami. The cephalic shield is 1.3 to 1.5 times longer than wide, varying in length from 43 µm to 48 µm, and in width from 29 µm to 37 µm. The cephalic shield tapers off towards the anteriorly located oral disc and is ornamented with longitudinal lamellae approximately 1 µm high. A rostrum is absent. The cephalon bears six pairs of pores in total (based on SEM) (Figs 3, 12). The cephalic pore pairs follow the formula: A<sub>I-II</sub>, D<sub>I-III</sub>, L<sub>I</sub>, and no median or ventral pores were observed. Two pairs are located anterior on the cephalon (Figs 3A, 12D) (A<sub>I-II</sub>); of them, A<sub>II</sub> has an emergent sensillum. Three pairs are located dorsally, more or less close to the posterior margin (Figs 3A, 12) (D<sub>I-III</sub>); of them, D<sub>I</sub> has an emergent sensillum. Finally, one pair is located subdorsally at the posterior margin of the cephalon (Figs 3A, 12) (L<sub>I</sub>), with an emergent sensillum. The oral disc (Figs 3A, 3B) is approximately 10–12 µm in diameter. A protruding organ (Fig. 4C, po) stretches from the oral disc into the host, but is barely visible.

Internal structures in the head were only weakly discernible in light microscopy. The cephalic stylet (Fig. 4A, cs) is slightly curved, with a hollow base. Tubular structures (ts) are spread throughout the inside of the head with no apparent symmetry (Fig. 4). No surface openings connecting to the tubular structures were discernable. Globular bodies (gb) seem to be randomly distributed near the posterior rim of the head (Fig. 4B).

Six thoracopods are present (Figs 5, 6, 13, 14). Thoracopods 1–5 consists of an unsegmented protopod with small, superficial spines or small ‘hairs’, a median endite with one spine, an exopod, and an endopod.



**FIGURE 5.** Thoracopods 1 to 4 of tantulus larva of *Arcticotantulus kristenseni* **sp. nov.**, right and left, seen from anterior (drawn from ZMUC CRU4887). A. Thoracopods 1. B. Thoracopods 2. C. Thoracopods 3. D. Thoracopods 4. E. Thoracopods 5. F. Thoracopods 6. Abbreviations: endopod (en), exopod (ex), medial endite (me), protopod (pro), spine on protopod (ps), spines on medial endite (sme), spine on exopod (sex), spatulate process (sp). The denticles on the setae, the spines on the exopods, and the spines on the protopods were not seen in the light microscope, but only observed on pictures obtained by SEM.



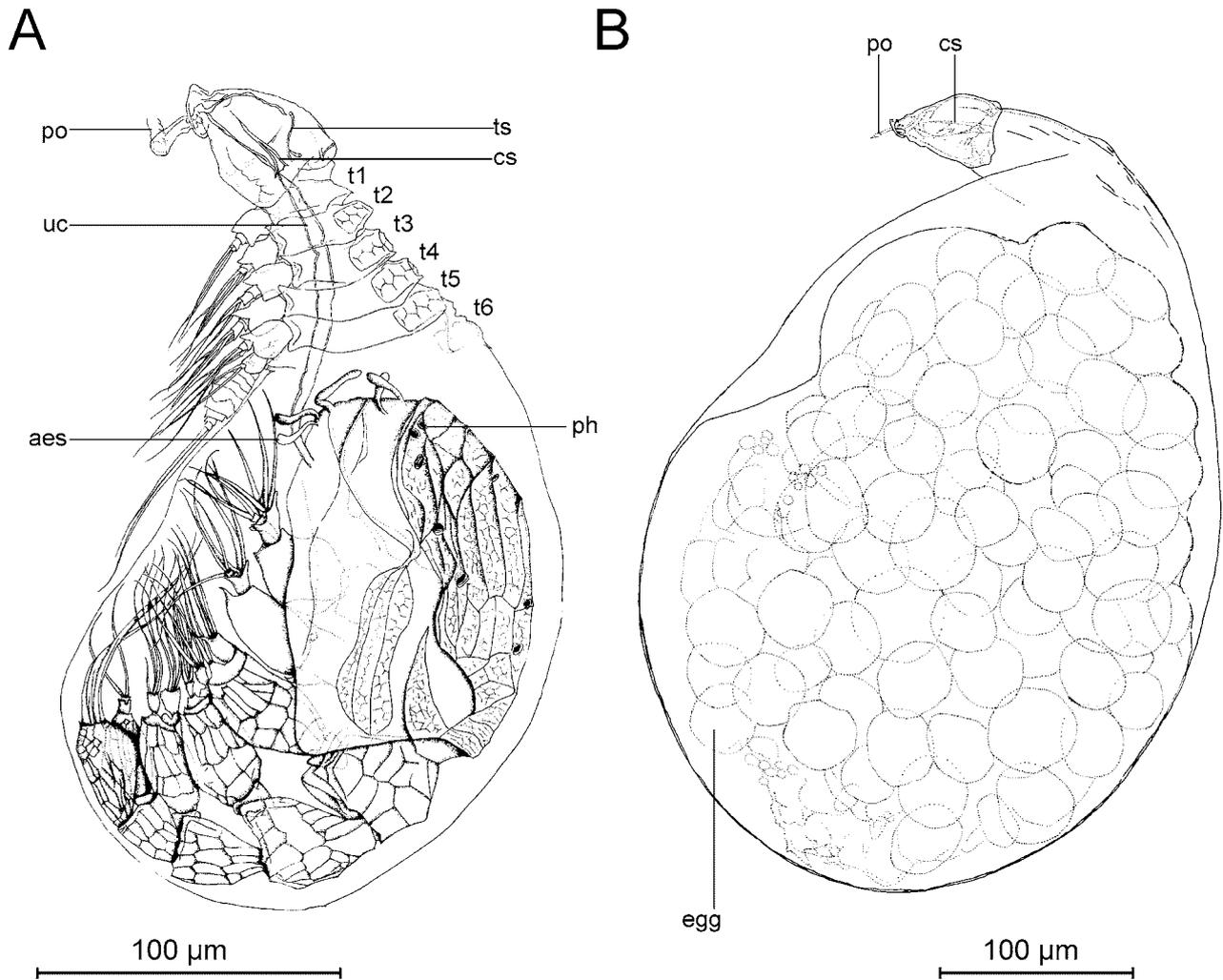
**FIGURE 6.** Thoracopods 5 and 6 of tantulus larva of *Arcticotantulus kristenseni* sp. nov., right and left side, seen from anterior (drawn from ZMUC CRU4887). A. Thoracopods 5. B. Thoracopods 6. Abbreviations: endopod (en), exopod (ex), medial endite (me), protopod (pro), spine on protopod (ps), spine on exopod (sex), spine on medial endite (sme), spatulate process (sp). The denticles on the setae, the spines on the exopods, and the spines on the protopods were not seen in the light microscope, but only observed on pictures obtained by SEM.

Thoracopod 1 (Figs 5A, 13C) has an endopod, which is indistinctly divided into two segments, and a two-segmented exopod. The exopod bears two long setae and one small, all with denticles (based on SEM). The endopod bears one seta with denticles and a long, slender process with a spatulate tip.

Thoracopod 2 (Figs 5B, 13C, 14A–C) has a two-segmented exopod that bears two small spines, two large setae with denticles, and two small, slender setae (these appear naked in LM but show small denticles in SEM). The endopod (Fig. 5B) is similar to that on thoracopod 1.

Thoracopods 3–4 (Fig. 5C and 5D) have a two-segmented exopod and an unsegmented endopod that is produced into a long, slender process. The exopod bears a small spine on the distal segment (Fig. 5C, 5D), two setae with long denticles, and two thin setae that appear naked in LM. The proximal portion of the endopod is thick relative to the long, slender distal portion, which bears two setae and has a spatulate process distally (Fig. 5C, 5D).

Thoracopod 5 (Fig. 6A) has a two-segmented exopod that bears two small spines (Fig. 6A, sex), two setae with denticles, and two thin setae that appear naked in LM. The endopod is similar to those on thoracopods 3 and 4.

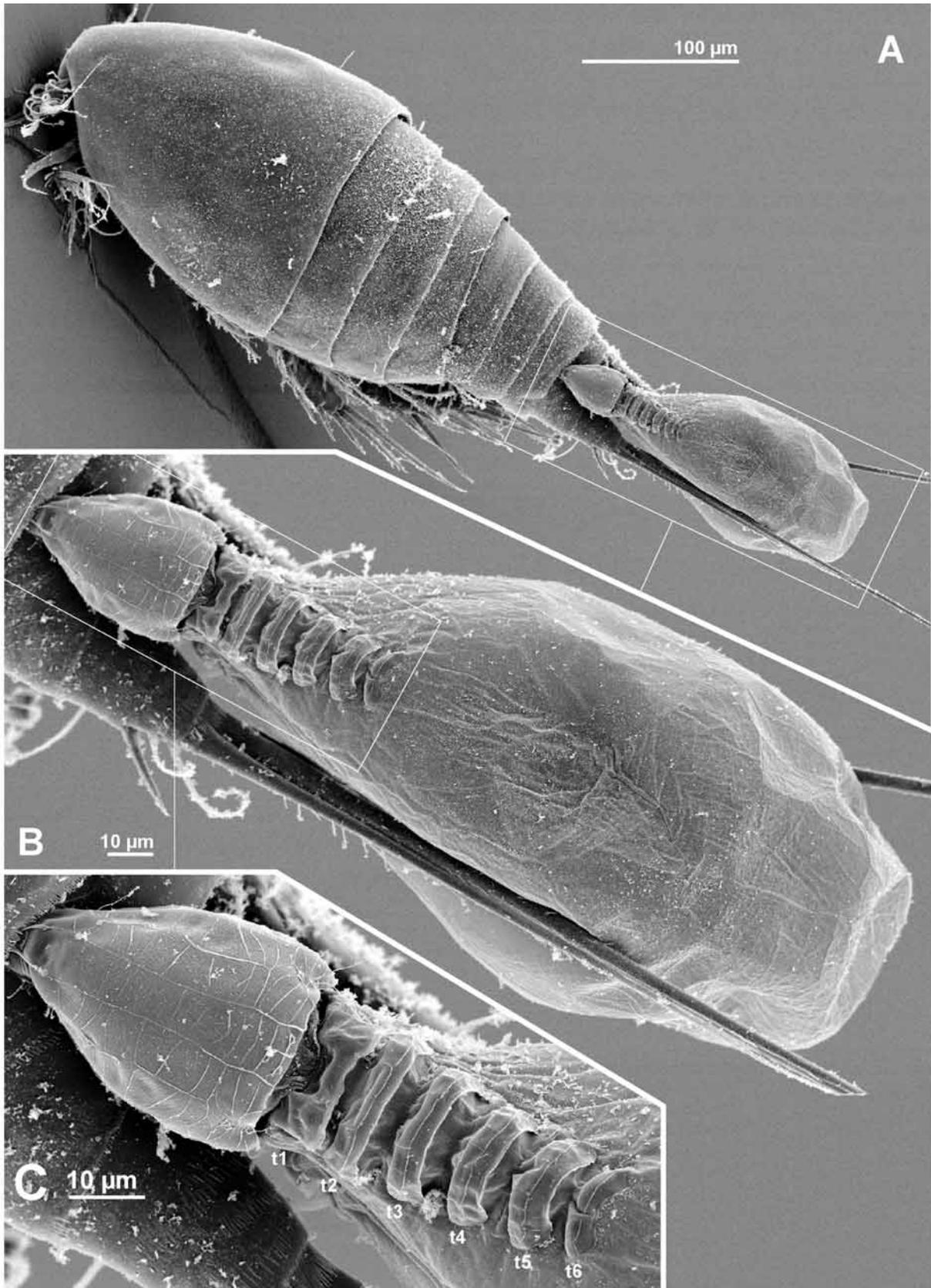


**FIGURE 7.** Adults of *Arcticotantulus kristenseni* sp. nov. A. Male developing inside the trunk sac of a tantulus larva, lateral view (drawn from ZMUC CRU4877). B. Parthenogenetic female with eggs, lateral view (drawn from ZMUC CRU4872). Abbreviations: aesthestascs (aes), cephalic stylet (cs), eggs (egg), pores in head shield (ph), protruding organ (po), tubular structures (ts), umbilical cord-like organ (uc).

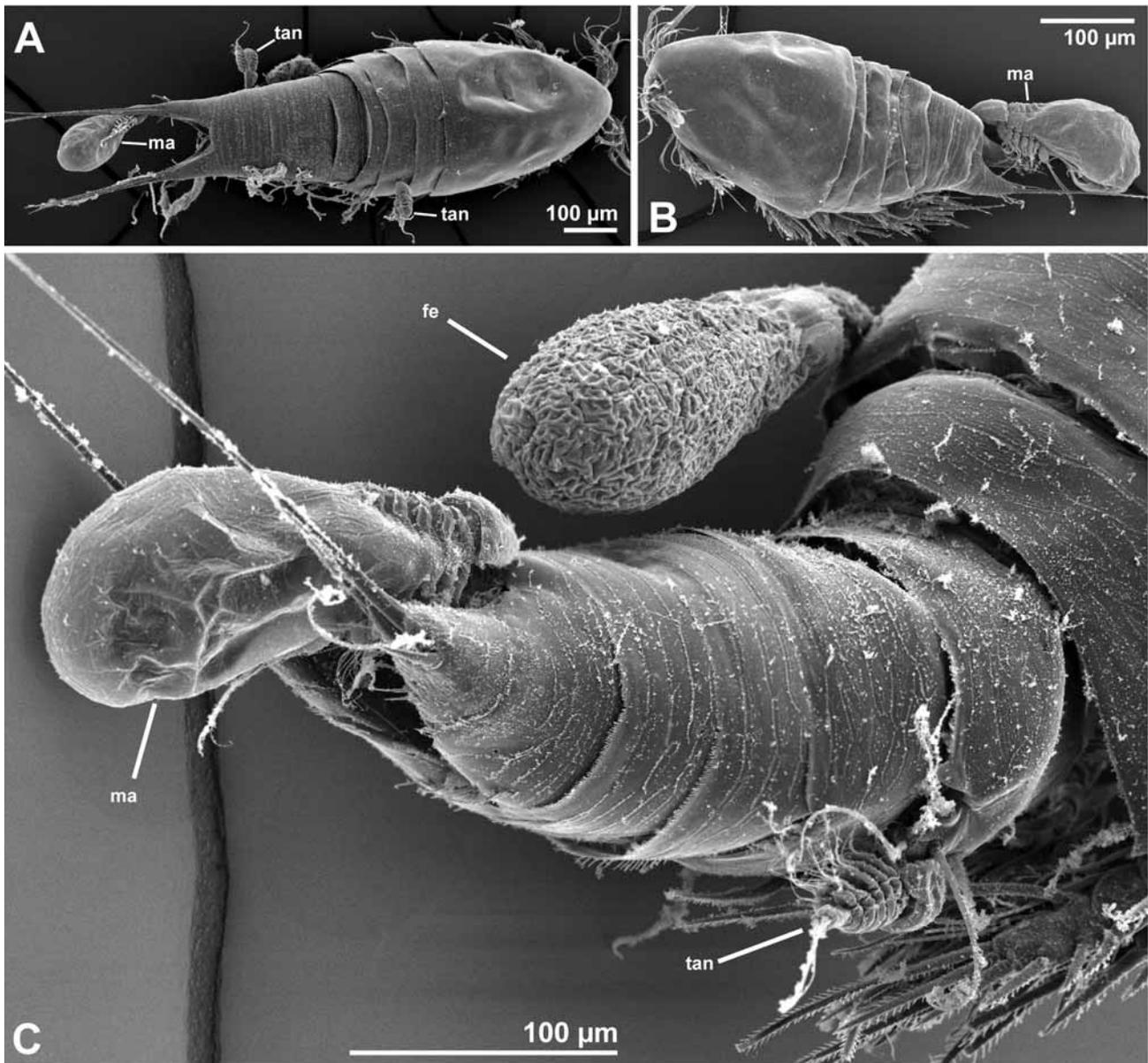
Thoracopod 6 (Fig. 6B) consists of a protopod with small spines but no median endite. The protopod has a one-segmented exopod with setae that have denticles. We did not detect any coupling spines on the median endites of the protopods but cannot exclude that they are present.

The first tergite is largely concealed beneath the posterior rim of the cephalon (Fig. 3, 10). The tergites on the first to sixth thoracic somites each have a distinct transverse lamella and are further subdivided into characteristic polygonal patterns (Figs 3, 10). The seventh thoracic somite (urosome segment 1) is short – about twice as wide as long (Figs 3C, 10D). The unsegmented abdomen (urosome segment 2) is relatively long – about twice its width – with sides that are parallel anteriorly but converge slightly posteriorly. Dorsally the abdomen is superficially divided into a segment-like pattern: the anterior part bears about three rows of curved, transverse lamellae, while the posterior part bears three transversely orientated and denticle-serrated lamellae, the middle one of which has a characteristic ‘w-shaped’ pattern (Fig. 10D, arrow). The posterior lamella partly covers a pair of small caudal rami, each with two large and one small setae all bearing denticles (Figs 3, 10B).

*Male:* In spite of several attempts, we were unable to free a male successfully from the sac of the tantulus larvae. A complete description of the male depends on the setation of the limbs, and we have been unable to

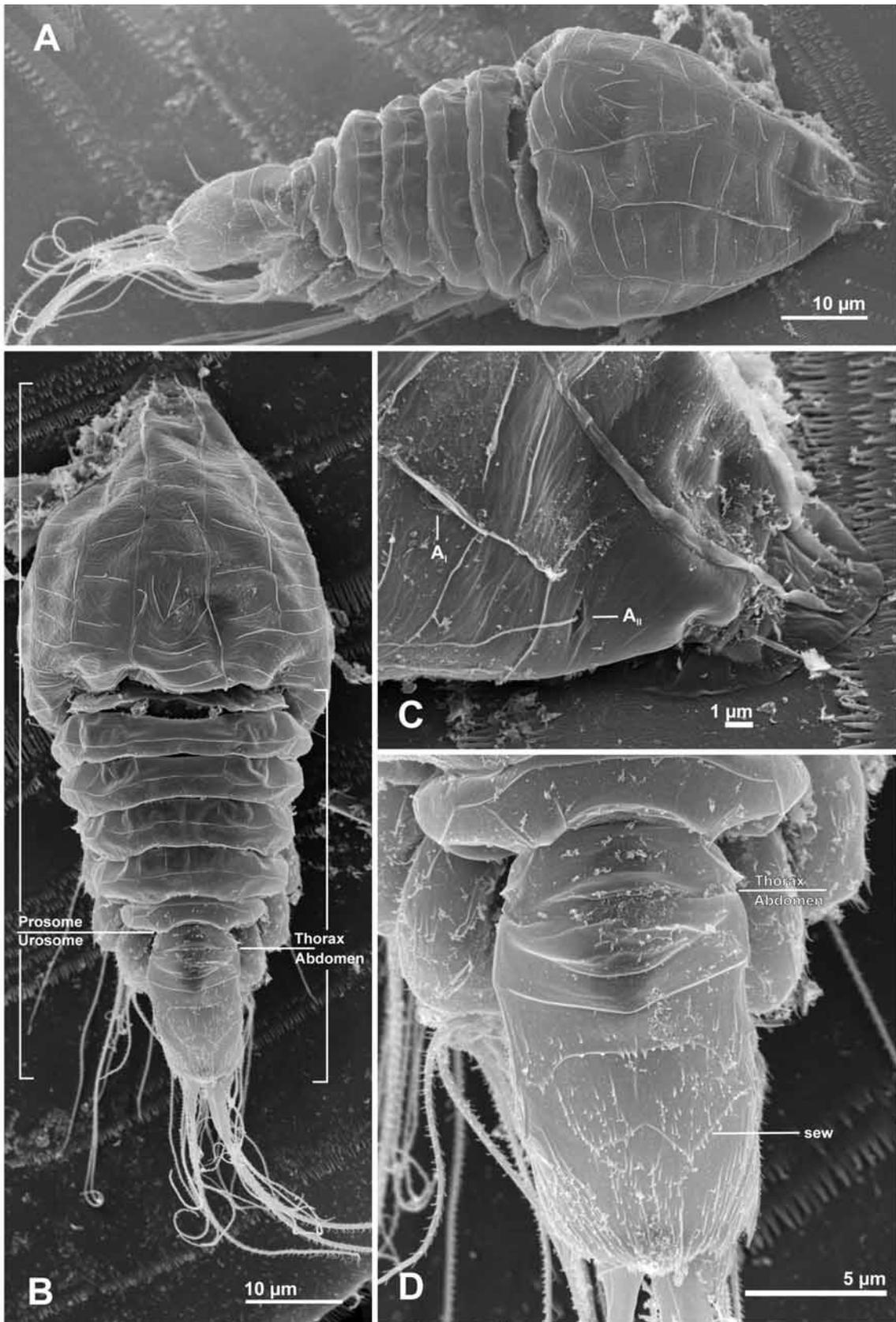


**FIGURE 8.** Harpacticoid host with attached developing male of *Arcticotantulus kristenseni* **sp. nov.** within trunk sac of tantulus larva (SEM) (ZMUC CRU4891). A. Dorsal view of host and developing tantulocarid male. B. Dorsal view of developing male, enlargement of A. C. Cephalon and thoracic tergites, enlargement of B. Abbreviations: thoracic somites 1 to 6 (t1-t6)

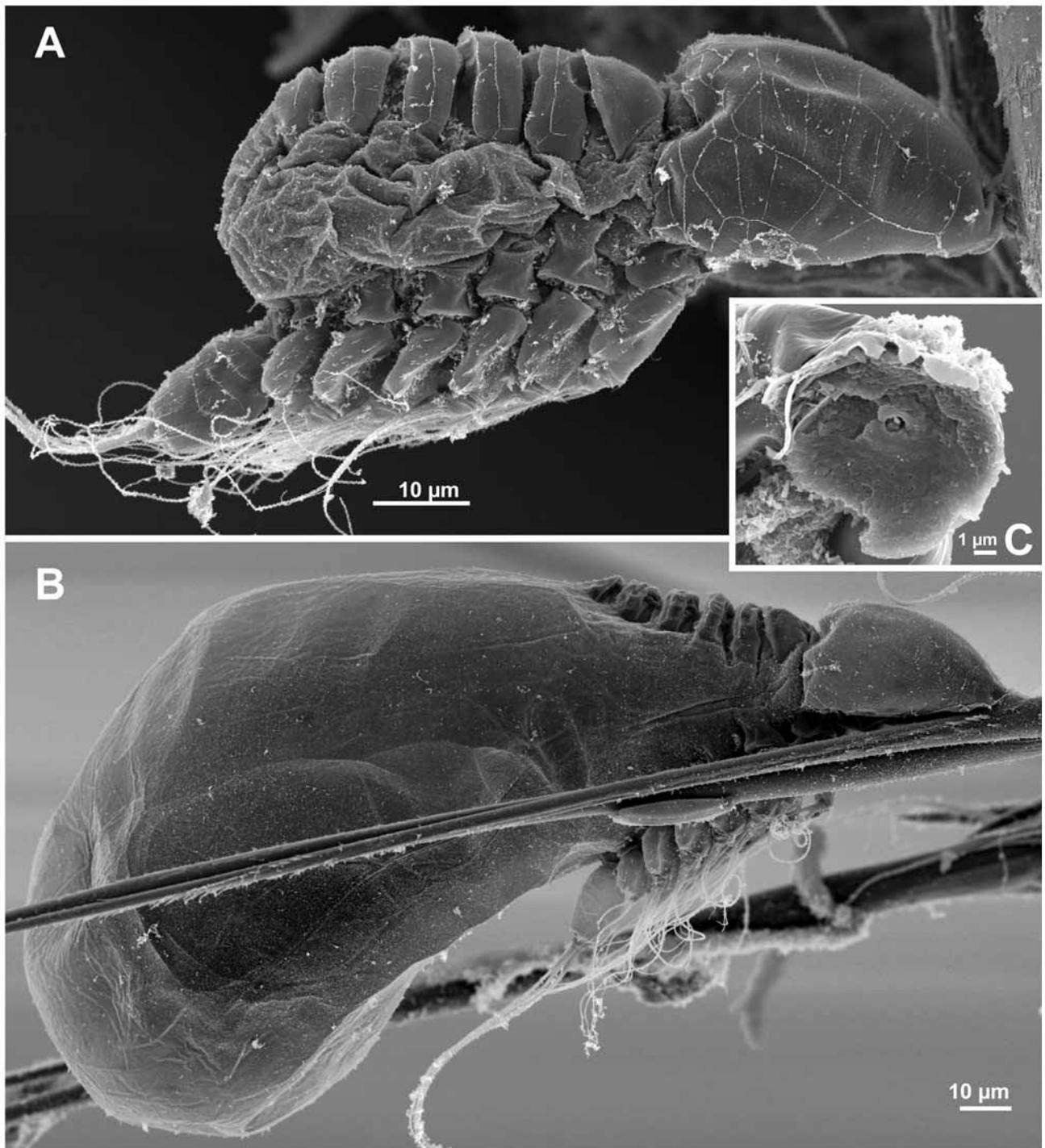


**FIGURE 9.** *Arcticotantulus kristenseni* sp. nov. in different stages of development attached to harpacticoid copepod hosts (SEM) (ZMUC CRU4891). A. Three tantulocaridans on one host: one developing male (ma) and two late tantulus larvae (tan). B. One tantulocarid attached to a copepod host: one developing male (ma). C. Three tantulocaridans on one host: a parthenogenetic female (fe), a developing male (ma), and a tantulus larva (tan).

discern these features with certainty in light microscopy alone. Instead, only a few remarks will be made to supplement the figures presented. The description is based on developing males not yet released from the surrounding tantulus trunk sac (Figs 7A, 8, 9, 11B, 14, 17). The trunk sac is developed behind the sixth tergite of the attached larva and there is no additional swelling between the cephalic shield and the first tergite (Figs 7A, 8, 11A). The developing male inside the trunk sac (Fig. 7A) has six pairs of thoracopods with setae and a fine, honeycomb-like ornamentation on the head shield as well as on the six tergites and the urosome. On the head shield of the developing male large pores are visible in LM, but apparently no internal structures are connected to them at this stage of development. A long umbilical cord-like organ (term from Boxshall 1988) is visible through the trunk sac, connecting the male with the head of the attached larvae. No penis could be discerned in light microscopy but it could have been overlooked, since it is usually found behind the sixth pair of thoracopods (see Boxshall & Huys 1989; Huys *et al.* 1992b; Boxshall *et al.* 1989). Three pairs of aesthetascs are present on the head of the male (Fig. 7A).



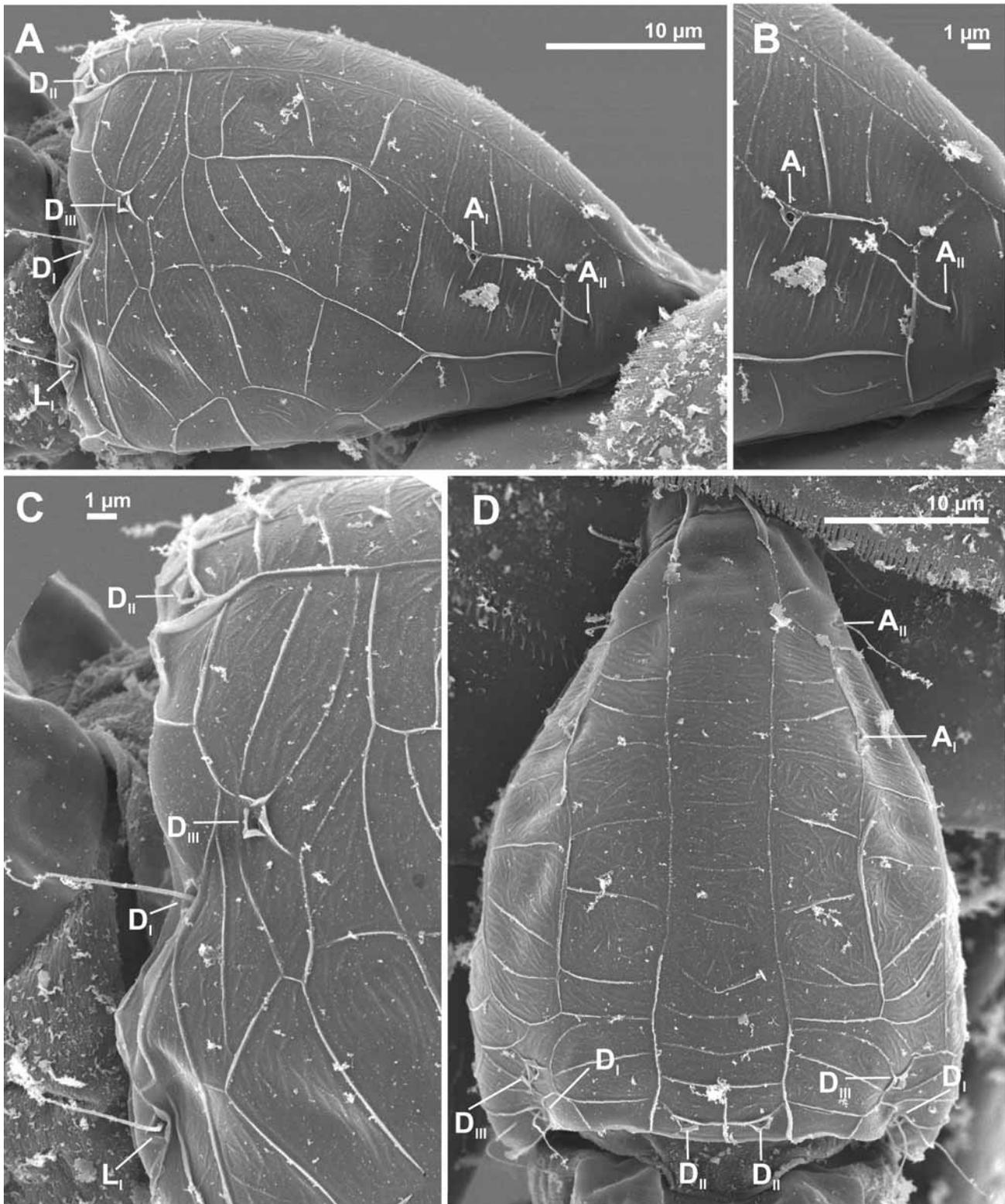
**FIGURE 10.** Tantulocaris larva of *Arcticotantulus kristenseni* sp. nov. (SEM), all photos of holotype (ZMUC CRU4889). A. Dorso-lateral view. B. Dorsal view, showing demarcations between prosome and urosome, and between thorax and abdomen. C. Close-up of anterior cephalic pores and oral disc, pore A<sub>I</sub> without emergent sensillum, pore A<sub>II</sub> with emergent sensillum. D. Dorsal view of urosome, showing demarcation between thorax and abdomen, With arrow pointing at characteristic 'w-shaped' serrated edge in cuticle of abdomen (sew).



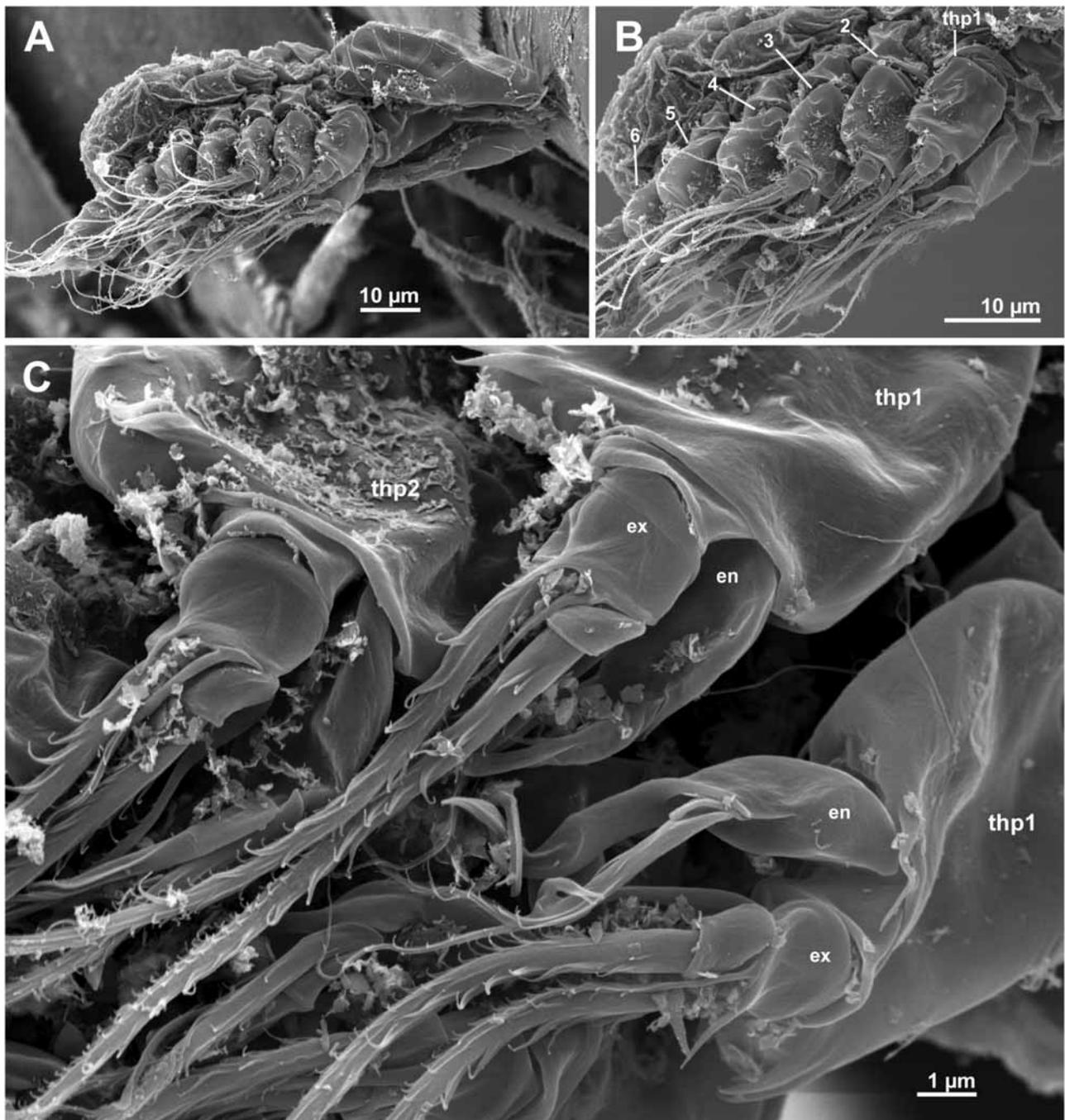
**FIGURE 11.** *Arcticotantulus kristenseni* **sp. nov.** at different stages of development (SEM) (ZMUC CRU4891). A. Early tantulus that has begun to develop a male inside. B. Developing male. C. Oral disc of detached parthenogenetic female, ventral view.

*Parthenogenetic female:* The larval thoracic somites and urosome are sloughed early in development when the trunk sac is as yet still smaller than the cephalon (Fig. 16A). The two least developed females found measured 67 µm and 82 µm in length, respectively (Fig. 16A, 16B). The trunk sac grows (Fig. 16) until the complete length of the female is about 405 µm (Figs 7B, 17A, 17B). The egg sac inside the trunk sac measured 345 µm in length. No gonopore or abscission scar of the larval trunk was discernible but it may have been overlooked. No long, slender neck was seen on any specimen, similar to the one reported from females of some other species (Boxshall 1991; Boxshall & Vader 1993; Grygier & Sieg 1988). Three

undeveloped females (Fig. 16) had what could be the beginning of a rootlet system penetrating the cuticle of the host through the oral disc (Fig. 16D, arrow).

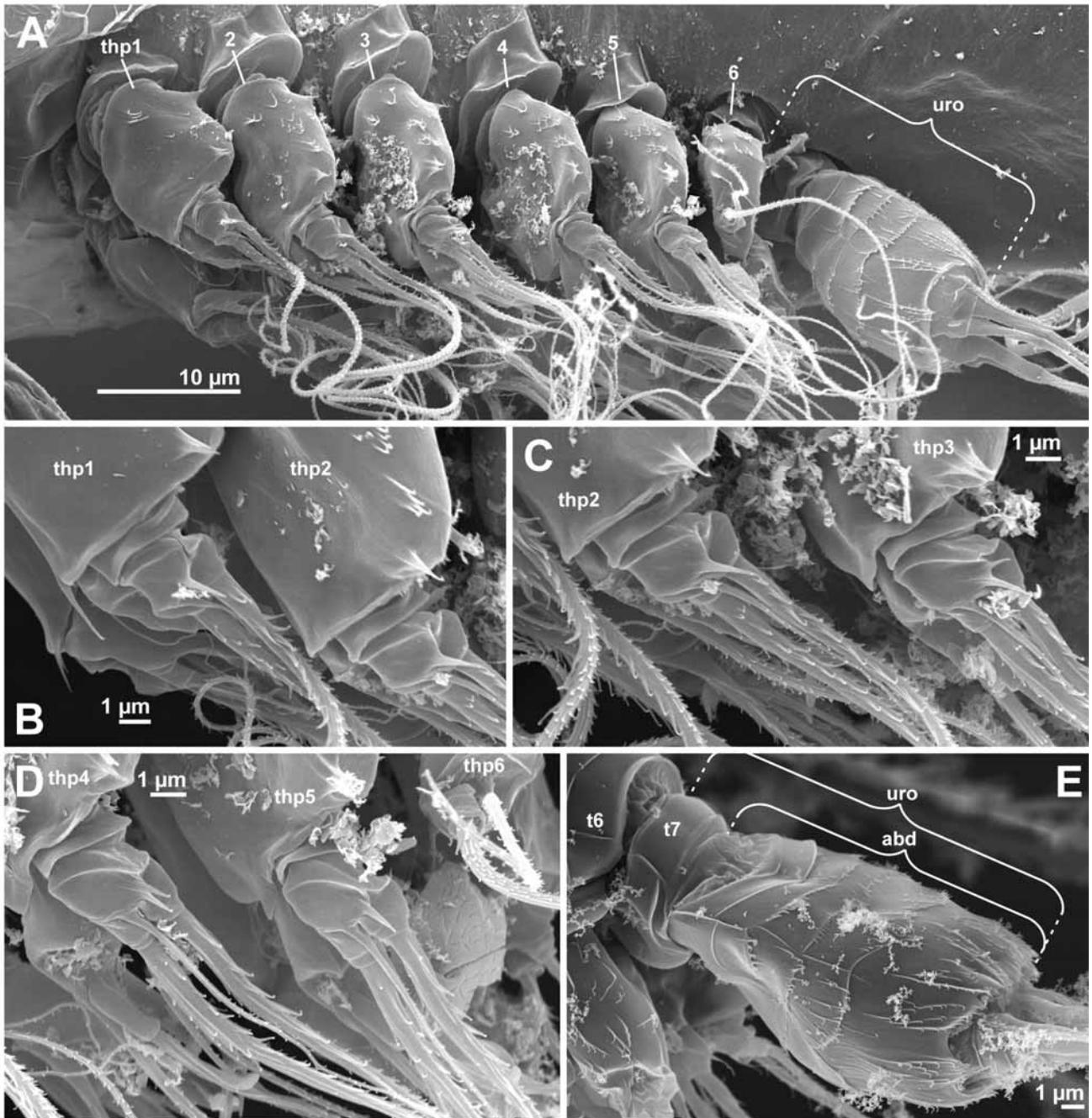


**FIGURE 12.** Cephalon of tantulus larva of *Arcticotantulus kristenseni* sp. nov. with well-developed male inside (SEM), all photos of same specimen (ZMUC CRU4891). Pores on cephalon: A<sub>I-II</sub>, D<sub>I-III</sub>, L<sub>I</sub>. A. Lateral view. B. Close-up of anterior pores: A<sub>I-II</sub>. C. Close-up of posterior pores: D<sub>I-III</sub>, L<sub>I</sub>. D. Dorsal view.



**FIGURE 13.** Thoracopods of tantulus of *Arcticotantulus kristenseni* sp. nov. with male inside in early state of development (SEM), all photos of same specimen (ZMUC CRU4891). A. Ventro-lateral view. B. Close-up of thoracopods in A. C. Thoracopods 1 and 2 (enlargement of B). Abbreviations: endopod (en), exopod (ex), thoracopods 1 to 6 (thp 1–6).

*Sexual female:* One fully developed individual with the larval trunk sloughed – which is the external characteristic of a female – was observed (Fig. 17C). Since the trunk sac of this individual did not contain developing eggs, but a large mass of apparently undifferentiated tissue, we interpret it as being a sexual female in the early course of its development. The contents of the trunk sac displayed approximately the same shape as the developing sexual females reported by Huys *et al.* (1993b) and Ohtsuka and Boxshall (1998). Posteriorly, the presumptive abdomen is partly separated from the remaining body (Fig. 17C, arrow). Two other individuals had a similar trunk sac with undifferentiated tissue inside (Fig. 16A and 16B), and resembled the potential sexual female (Fig. 17C). No further observations were made on this specimen.

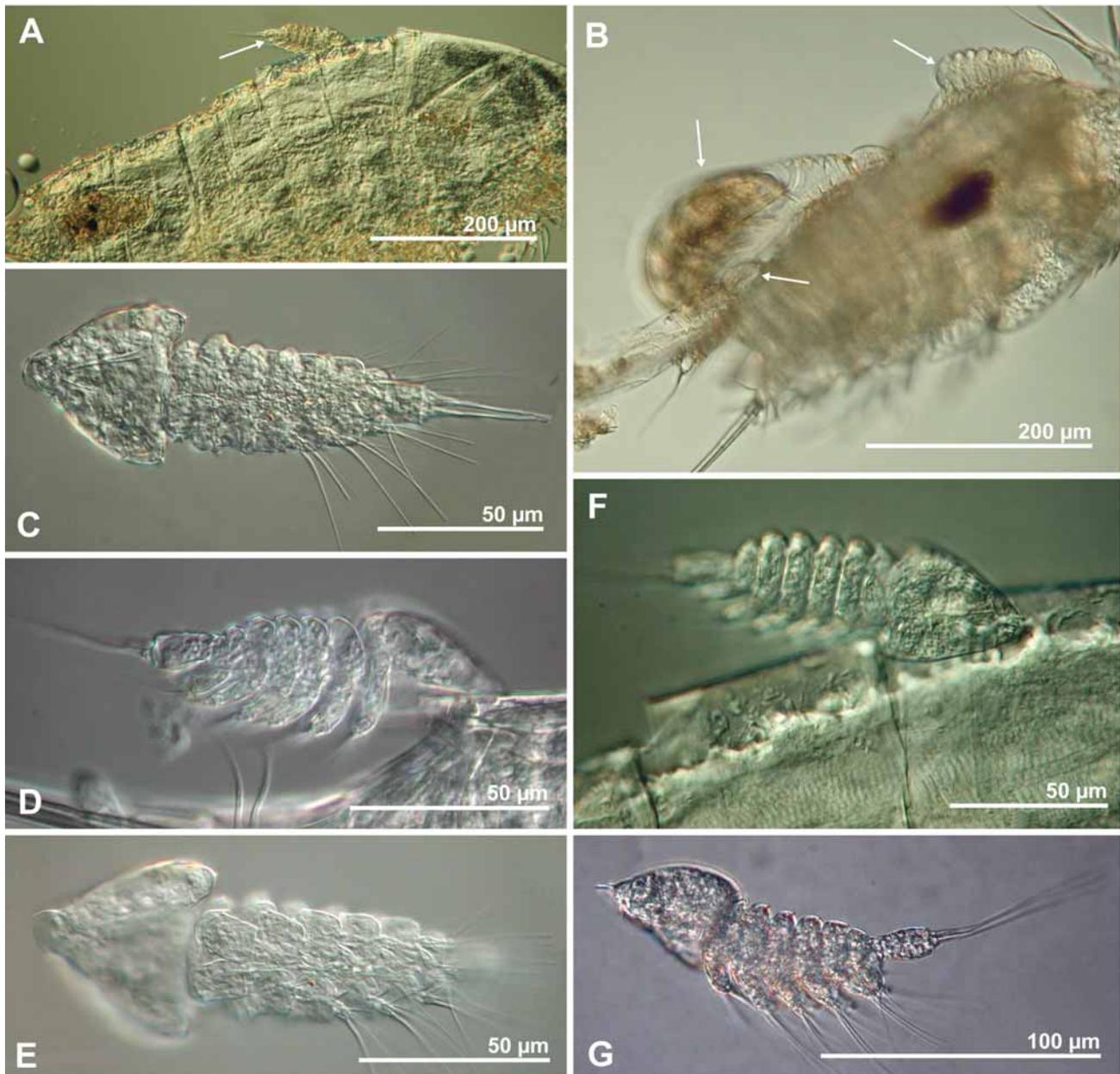


**FIGURE 14.** Thoracopods and urosome of *Arcticotantulus kristenseni* sp. nov. (SEM), tantulus with developing male inside. All photos are of same specimen (ZMUC CRU4891). A. Thoracopods 1 to 6 (left side) and urosome. B. Thoracopods 1 and 2 (left side). C. Thoracopods 2 and 3 (left side). D. Thoracopods 4 to 6 (left side). E. Urosome (and abdomen). Abbreviations: abdomen (abd), thoracopods 1 to 6 (thp1–6), thorax somite 7 (t7), urosome (uro).

**Etymology.** The species is named after Prof. Reinhardt Møbjerg Kristensen (Zoological Museum, Copenhagen), in honour of his work on marine invertebrates in Greenland. He was the first to catch the species described herein.

**Discussion.** The Tantulocarida are at present divided into five families, the Basipodellidae (with 8 species), Deoterthridae (with 11 species), Microdajidae (with 5 species), Onceroxenidae (with 2 species), and Doryphallophoridae (with 3 species). With this new species (*Arcticotantulus kristenseni* sp. nov.) included and with *A. pertzovi* assigned to the Deoterthridae, the family Basipodellidae contains 7 species, and the Deoterthridae, 13 species (Table 1). The present description of *A. kristenseni* sp. nov. from the coastal waters

of West Greenland broadens the geographical distribution of the Tantulocarida but is not the first discovery of this group in Greenland. *Polynyapodella ambrosei* Huys, Mølbjerg, and Kristensen, 1997 (q.v.) has previously been described from Northeast Greenland. Of all described tantulocaridans *A. kristenseni* **sp. nov.** is most similar to *A. pertzovi* and is therefore described as a second species in the same genus.



**FIGURE 15.** Live tantulus larvae and some developing males of *Arcticotantulus kristenseni* **sp. nov.** (LM). Animals in A, B, D, F were alive when the pictures were taken. A. Tantulus larva attached dorsally to harpacticoid host (arrow) (ZMUC CRU4882). B. Three tantulocaridans at different stages of development attached to harpacticoid host (arrows); the most developed tantulus has a male inside (ZMUC CRU4885). C. Detached tantulus larva, ventral view (ZMUC CRU4887). D. Attached tantulus larva, lateral view (ZMUC CRU4884). E. Detached tantulus larva, ventral view (same specimen as in C). F. Attached tantulus larva (close-up of specimen in A). G. Lateral view of detached tantulus larva (ZMUC CRU4887).

**Similarities between *A. kristenseni* and *A. pertzovi*.** Both species of *Arcticotantulus* are found on a harpacticoid copepod species of the genus *Bradya* [not *Pseudobradya* Sars, 1911 as mentioned for *A. pertzovi* by Kornev *et al.* (2004) (Huys, pers. com. 2006)]. The two species are found in different Arctic regions far from each other (White Sea and off the coast of West Greenland) and are considered separate. A comparison

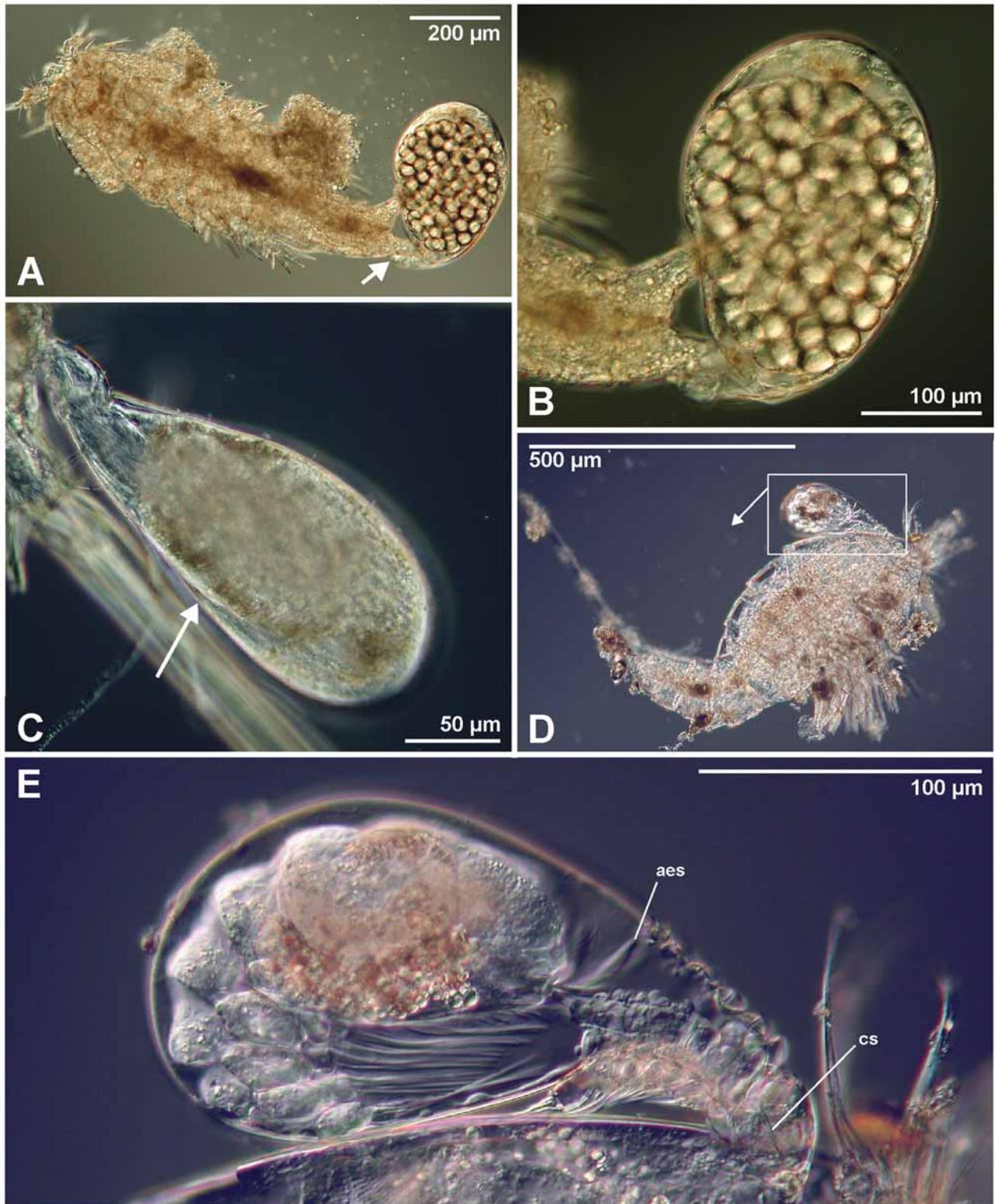
between *A. kristenseni* **sp. nov.** and the published information about *A. pertzovi* reveals several similarities (Table 4) that justify their placement in the same genus. Both *A. kristenseni* and *A. pertzovi* possess a limited number of pore pairs, and both species have the  $D_I$ - and  $L_I$ -pore pairs. In both *A. kristenseni* and *A. pertzovi* the cephalic lamellae are arranged longitudinally. Each of the exopods on the first to fifth thoracopods of both species is divided into two segments. Each of the endopods on the third to fifth thoracopods has two setae attached. The sixth thoracopods are similar in both species. A ‘w-shaped’ ornamentation and some minor denticles are present on the abdomen of both species.



**FIGURE 16.** Live females (most likely parthenogenetic) of *Arcticotantulus kristenseni* **sp. nov.** in early stages of development attached to harpacticoid host (LM). A. Very early female (ZMUC CRU4875). B. Later female (ZMUC CRU4883). C. Even later female (ZMUC CRU4875). D. Close-up of anterior part of cephalon in B showing protruding organ (arrow).

**Differences between *Arcticotantulus kristenseni* and other Arctic and North Atlantic Tantulocarida.**

Among other Arctic species of the Tantulocarida, *A. kristenseni* is clearly different from *Polynapodella ambrosei* with respect to the two-segmented urosome (superficially multisegmented in *P. ambrosei*) and in having fewer pore pairs on the cephalon (as concerns the A-, D-, and L-pore pairs). On the cephalon of *A. kristenseni* the  $A_I$ - and  $A_{II}$ -, the  $D_I$ -,  $D_{II}$ -, and  $D_{III}$ -, and the  $L_I$ -pore pairs are present, but on the cephalon of *A. pertzovi*, only the  $A_{III}$ -, the  $D_I$ - and the  $L_I$ -pore pairs. Furthermore, *A. pertzovi* also has a  $D_{IV}$ -pore pair (see Table 4). Another difference concerns the lamellae on the cephalon of the tantulus larvae. In addition to the longitudinal lamellae on the cephalon in both *A. kristenseni* and *A. pertzovi*, *A. kristenseni* has some lamellae arranged in polygons. The setation of the thoracopods in the two species is also different. In *A. kristenseni*, the protopods of the first and second thoracopods are unsegmented (two-segmented in *A. pertzovi*), the endopods



**FIGURE 17.** Developmental stages of *Arcticotantulus kristenseni* sp. nov. (LM). A. Parthenogenetic female (arrow points at head of female) attached to host (ZMUC CRU4872). B. Parthenogenetic female with embryos inside (enlargement of A). C. Living female in late stage of development, probably a sexual female (see Discussion), with developing abdomen (arrow) (ZMUC CRU4873). D. Live male in late stage of development (LM) attached to cephalon of harpacticoid host (ZMUC CRU4877). E. Close-up of D. Abbreviations: cephalic stylet in larval head (cs), male antennular aesthetascs (aes).

**TABLE 4.** Comparison between *Arcticotantulus pertzovi* and *A. kristenseni* **sp. nov.**, emphasizing features of the tantulus larvae.

| Character  |                             | <i>Arcticotantulus kristenseni</i>                  | <i>Arcticotantulus pertzovi</i>  |
|--|-----------------------------|---|----------------------------------|
| Total body length  |                             | 147–192 µm  | 140 µm                           |
| Size of oral disc  |                             | 10–12 µm in diameter                                | 7 µm in diameter                 |
| Length of cephalic stylet                                      |                             | Approx. 60 µm                                       | 30 µm                            |
| Cephalic pores   | Anterior pores              | A <sub>I</sub> , A <sub>II</sub>                    | A <sub>III</sub>                 |
|  | Dorsal pores                | D <sub>I</sub> , D <sub>II</sub> , D <sub>III</sub> | D <sub>I</sub> , D <sub>IV</sub> |
|  | Lateral pores               | L <sub>I</sub>                                      | L <sub>I</sub>                   |
| Swelling between cephalon and first tergite in developing male |                             | Not parted significantly                            | Not parted significantly         |
| Cephalic rostrum   |                             | Absent  | Absent                           |
| Cephalic lamellae ornamentation                                |                             | Longitudinal and polygonal                          | Longitudinal                     |
| Thoracopod 1   | No. of segments of protopod | 1   | 2                                |
|  | No. of endopod setae        | 1   | 0                                |
|  | No. of exopod setae         | 4   | 2                                |
|  | No. of segments of exopod   | 2   | 2                                |
|  | No. of segments of endopod  | 2   | 1                                |
| Thoracopod 2   | No. of segments of protopod | 1   | 2                                |
|  | No. of endopod setae        | 1   | 0                                |
|  | No. of exopod setae         | 4   | 2                                |
|  | No. of segments of exopod   | 2   | 2                                |
|  | No. of segments of endopod  | 2   | 1                                |
| Thoracopod 3   | No. of segments of protopod | 1   | 2                                |
|  | No. of endopod setae        | 2   | 2                                |
|  | No. of exopod setae         | 4   | 3                                |
|  | No. of segments of exopod   | 2   | 2                                |
|  | No. of segments of endopod  | 2   | 1                                |
| Thoracopod 4   | No. of segments of protopod | 1   | 2                                |
|  | No. of endopod setae        | 2   | 2                                |
|  | No. of exopod setae         | 4   | 3                                |
|  | No. of segments of exopod   | 2   | 2                                |
|  | No. of segments of endopod  | 2   | 1                                |
| Thoracopod 5   | No. of segments of protopod | 1   | 2                                |
|  | No. of endopod setae        | 2   | 2                                |
|  | No. of exopod setae         | 4   | 3                                |
|  | No. of segments of exopod   | 2   | 2                                |
|  | No. of segments of endopod  | 2   | 1                                |
| Thoracopod 6   | No. of segments of protopod | 1   | 1                                |
|  | No. of endopod setae        | No endopod  | No endopod                       |

to be continued.

**TABLE 4.** (continued)

| Character                           | <i>Arcticotantulus kristenseni</i> | <i>Arcticotantulus pertzovi</i>                    |
|-------------------------------------|------------------------------------|--|
| No. of exopod setae                 | 2                                  | 2  |
| No. of segments of exopod           | 1                                  | 1  |
| No. of segments of endopod          | No endopod                         | No endopod   |
| Abdomen                             |                                    |  |
| No. of transverse lamellae          | 4                                  | 6  |
| No. of caudal setae per caudal rami | 2                                  | 3  |
| Seta on caudal rami                 | Segmented                          | Unsegmented  |
| Ornamentation                       | 'w-shaped'                         | 'w-shaped'   |
| Denticles on setae(?)               | Present                            | Present  |
| No. of segments in urosome          | 2                                  | 2  |
| Host                                | Harpacticoid, <i>Bradya</i> sp.    | Harpacticoid, <i>Pseudobradya</i> sp. <sup>a</sup> |
| Catch depth                         | 166–220 m                          | 90 m   |
| Catch locality                      | Western Greenland                  | White Sea  |

<sup>a</sup>) Kornev *et al.* (2004) identified the host species as *Pseudobradya* sp. This may be incorrect as the host more resembles a *Bradya* sp. (Huys pers. com)

carry one seta (absent in *A. pertzovi*), the exopods carry four setae (two in *A. pertzovi*), and the endopod is divided indistinctly into two segments (unsegmented in *A. pertzovi*). Furthermore, in *A. kristenseni*, the protopods of the third to fifth thoracopods are undivided (two-segmented in *A. pertzovi*), the exopods carry four setae (three in *A. pertzovi*) and the endopods are divided into two segments (unsegmented in *A. pertzovi*) (Table 4).

**Relationship of the genus *Arcticotantulus* and comments on the description of *Arcticotantulus pertzovi*.** *Arcticotantulus* was assigned to the Basipodellidae by Kornev *et al.* (2004), but based on the information on *A. kristenseni* provided in this paper and the previously published information on *A. pertzovi*, and by using the family characteristics provided by Huys (1990a), we argue that the genus is better assigned to the Deoterthridae (Table 2). The classification of the Tantulocarida has mostly been based on external characteristics of the tantulus larvae, such as pore patterns of the cephalon, segmentation of the urosome, and setation of the thoracopods. In the following these characteristics are listed and discussed.

**Cephalon of *Arcticotantulus*.** The single pair of subdorsal cephalic pores found on *Arcticotantulus* is similar to the single pair (or more) of subdorsal cephalic pores found in Deoterthridae (Huys 1990a). The tantulus of *A. kristenseni* has a very characteristic pore pattern on the cephalon, a pattern which to our knowledge, is not found in any other tantulocaridans. There is a total of six pairs: four pairs close to the posterior margin of the cephalon and two additional pairs anteriorly (Figs 3A, 3B, 10C, 12). One of the anterior pore pairs and two of the posterior pore pairs has an emergent sensillum, consistently found in the same position in all examined specimens. The total number of pore pairs in *Arcticotantulus* deviates from the ten pairs usually found in the Deoterthridae, with only six pairs in *A. kristenseni* and only five pairs in *A. pertzovi* (Kornev *et al.* 2004), but since this number is known to vary within the Deoterthridae, we do not see the low count of pore pairs hindering a placement within this family (see Table 2). The absence of a cephalic rostrum favours the placement of *Arcticotantulus* within the Deoterthridae (see Table 2) (Huys 1990a).

**Thoracopod setation in *Arcticotantulus*.** Usually there is only one seta on the endopod of the first thoracopod in Deoterthridae, or setation is absent there (Table 2) (Huys, 1990a). This is consistent with the single seta found on the endopod of this limb in *A. kristenseni* and with the lack of setae seen in *A. pertzovi*. In contrast, Basipodellidae are characterised as carrying two setae on the endopod of the first thoracopod. Most

aspects of the setation of the trunk limbs in *Arcticotantulus* fit some of the existing families as they are defined by Huys (1990a), but the setation of one limb in *Arcticotantulus* is a notable exception. In addition to an elongate process with a spatula-shaped tip, the endopod of thoracopod 2 has only one seta, which is contrary to the situation in the Deoterthridae, Onceroxenidae, Basipodellidae, and Doryphallophoridae, in all of which two setae are present (Huys 1990a). In *Microdajus langi* Greve, 1965 (Microdajidae), two setae appear to be present as well, but without free rami (Boxshall & Lincoln 1987) it is difficult to infer where these setae inserted originally. This makes it difficult to compare *Arcticotantulus* with *Microdajus langi* Greve, 1965. The endopod of thoracopods 3–5 in *Arcticotantulus* has two setae, as is the case for all families: Microdajidae being a possible exception. The exopods of the thoracopods in *Arcticotantulus* have a well-developed setation that falls within the range of variation of the Deoterthridae (Huys, 1990a), but this differs only slightly from that of the Doryphallophoridae, the Onceroxenidae, and the Basipodellidae. Thus, the setation of thoracopods 3–5 is not usable for identifying the correct family (Table 2).

**Abdomen and urosome of *Arcticotantulus*.** Because of confusion in defining the terms ‘abdomen’ and ‘urosome’ in the Tantulocarida, there have continuously been difficulties assigning species to different families. When Huys (1990a) characterized the different families he regarded the abdomen as comprising the seventh, limbless, thoracic somite together with the part of the tantulus larvae posterior to it. In contrast, Boxshall and Vader (1993) used the term ‘urosome’ for this region (similar to Huys’ (1990a) use of ‘abdomen’), and restricted the term ‘abdomen’ only to more posterior parts of the tantulus larvae. As Boxshall and Vader’s terminology (1993) has been the most commonly used in descriptions after 1993, we have decided to apply it in the descriptions herein. Difficulties arise when tantulocaridans are assigned to families only based on the characteristics mentioned by Huys (1990a). Using the terminology applied by Boxshall and Vader (1993), Basipodellidae are characterized as having a multi-segmented urosome and Deoterthridae as having a two-segmented urosome. *Arcticotantulus* has an unsegmented abdomen and a seventh limbless thoracic somite. This implies that the urosome is two-segmented, and that *Arcticotantulus* therefore should be assigned to Deoterthridae. The abdomen (second segment of the urosome) of *Arcticotantulus kristenseni* resembles the abdomen of *Deoterthron dentatum* Bradford and Hewitt, 1980 and *Deoterthron lincolni* (Boxshall, 1988), two other species of Deoterthridae (see Huys 1990a), in having (1) a pair of semi-circular lamellae anteriorly, (2) being most narrow posteriorly, and (3) by being partly covered by cuticular hairs in the posterior half. The abdomen of *Doryphallophora harrisoni* (Boxshall and Lincoln, 1987), which is a species of the family Doryphallophoridae, resembles that of *A. kristenseni* to a lesser extent in being relatively unornamented with cuticular hairs only (Boxshall & Lincoln, 1987). In most other species of the Tantulocarida the abdomen of the tantulus larvae is more heavily ornamented, and often superficially subdivided into several ‘segments’. This is not the case in *Arcticotantulus*, which has an unsegmented abdomen (and a two-segmented urosome) with little ornamentation apart from a ‘w-shaped’ ridge in the cuticle (Fig. 10, Kornev *et al.* 2004: figs. 1A, 3B). One other potentially taxonomically important structure is the honeycomb-like ornamentation on the thoracic tergites, which hitherto have been only known from *Aphotocentor styx* Huys, 1991 (q.v.) and *Campyloxiphos dineti* Huys, 1990a (q.v.). Both of these are assigned to the Deoterthridae. This ornamentation is only conspicuous on *Arcticotantulus kristenseni* and not on *A. pertzovi*.

**The developing male of *Arcticotantulus*.** Huys (1990a) suggested that the three different types of thoracic swelling during male development are taxonomically significant at the family level. In *Arcticotantulus kristenseni* there is only one expansion zone of the tantulus trunk sac during male development - behind the sixth tergite. This is similar to that shown for *Microdajus* (Microdajidae), *Onceroxenus* (Onceroxenidae), and *Deoterthron* (Deoterthridae), while the trunk sac expansion in *Doryphallophora* and the Basipodellidae takes place between other tergites (Huys 1990a). Similarly, *A. pertzovi* (Kornev *et al.* 2004: fig. 1B) only has an expansion zone behind the sixth tergite (see Huys 1990a: fig. 7). The expansion zone in *Arcticotantulus* can thus be compared with the expansion zone observed in Microdajidae, Onceroxenidae, and Deoterthridae. According to Kornev *et al.* (2004), the developing male of *A. pertzovi* has its first tergite widely parted from the cephalon (Kornev *et al.* 2004: fig. 1B) as in

Basipodellidae; however, as far as we can tell, this partition is not nearly as large as would be expected for Basipodellidae (see Huys 1990a). On the contrary, the partition of the first tergite from the cephalon seen in *A. pertzovi* resembles the partition seen in Deoterthridae (see Huys 1990a).

**The host species of *Arcticotantulus*.** *Bradya* sp. (Huys pers. com) appears to be hosting all the specimens of *A. kristenseni* and the same harpacticoid genus appears to be infected by *A. pertzovi*. The host species of *A. pertzovi* was originally reported as *Pseudobradya* sp. (Kornev *et al.* 2004) but this may be incorrect as the host resembles *Bradya* sp. (Huys pers. com).

**Taxonomic conclusions.** In summary, it is not a straightforward matter to assign *Arcticotantulus kristenseni* to any existing family of the Tantulocarida. Since most characters are shared with species of Deoterthridae (see above), we assign this new species to this family, and also assign it to the genus *Arcticotantulus* in light of various similarities with *A. pertzovi*. We are aware that the pore pattern on the cephalon and the presence of only one seta on the endopod of thoracopod 2 do not fit the characteristics of the Deoterthridae as defined by Huys (1990a).

**Internal structures of *Arcticotantulus kristenseni* sp. nov.** The tubular structures inside the head of the tantulus larvae apparently do not connect with any superficial openings. Conversely, although, the developing male has superficial openings on the head shield, it does not have any clearly visible internal connecting structures (Fig. 7A). The existence of such connections can probably only be verified by transmission electron microscopy (TEM). The so-called tubular structures within the head could be a misinterpretation of glandular structures, but to confirm this TEM would be required as well. Glandular structures associated with the stylet have previously been recognized by Boxshall and Huys (1989), Huys (1991), and Huys *et al.* (1994). The purpose of these glandular or tubular structures remains uncertain. It is presumed that muscles associated with the cephalic stylet degenerate after it has served its purpose by piercing the host when the tantulocaridan attaches itself (Boxshall 1991). This could explain the asymmetrical placement of the stylet in the head. The purpose of the umbilical cord-like structure reported in this work and previous papers connecting the male's head with the head of the attached larvae is uncertain, but Boxshall and Lincoln (1987) suggested that it provides the male inside with nourishment extracted from the host. This work documents the presence of a tube-like structure crossing the cuticle of the host (Fig. 16D) of an undeveloped female. Huys (1991) suggested that a branching network of cells spreads out from the tantulocaridan and inside the host.

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