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Tantulocarida (Crustacea) from the Southern Ocean deep sea, and the description of three new species of *Tantulacus* Huys, Andersen & Kristensen, 1992

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Abstract During the expedition ANT XIX/3 meiofauna samples were collected from the German research vessel *Polarstern* near the Shackleton Fracture Zone. During sorting of the samples 86 tantulus larvae were found. Extensive examination of the larvae revealed a high diversity of tantulocaridans in the Southern Ocean deep sea (33 species). A remarkable proportion of these were new species of *Tantulacus* Huys, Andersen & Kristensen, 1992. The present paper reports the discovery of three new Antarctic tantulocarids which are referred to *Tantulacus*. The affiliation of *T. longispinosus* n. sp., *T. karolae* n. sp. and *T. dieteri* n. sp. to *Tantulacus* is straightforward: all representatives of the Tantulocarida are characterised by the presence of 1-2 slender setae on the endopod of the second to fifth thoracopods, but in none of the hitherto described genera, other than *Tantulacus*, are these elements modified. *Tantulacus hoegi* Huys, Andersen & Kristensen, 1992 and the three new species share the possession of a distal rigid spine on the endopod of the second to fifth thoracopods as a synapomorphy and thus can be readily distinguished from other tantulocaridans. This is the first record of free-living sediment-inhabiting tantulus larvae from this area, although this probably reflects the degree of undersampling.

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Introduction

Tantulocaridans are highly specialised ectoparasitic crustaceans that exclusively use other marine crustaceans as hosts. They can be found on the integument of copepods (Harpacticoida, Calanoida, Cyclopoida, Siphonostomatoida, Misophrioida) (Becker, 1975; Huys et al., 1992b, 1994; Huys & Conroy-Dalton, 1997; Ohtsuka & Boxshall, 1998; Kornev et al., 2004), peracaridans (Tanaidacea, Isopoda, Amphipoda, Cumacea) (Bonnier, 1903; Greve, 1965; Grygier & Sieg, 1988; Boxshall & Vader, 1993; Ohtsuka & Boxshall, 1998) and ostracods (Myodocopida) (Bradford & Hewitt, 1980). Tantulocaridans were not recognised as a discrete group of parasites within the Crustacea until 1983 (Boxshall & Lincoln, 1983). Currently they are assigned to the Maxillopoda and regarded as most closely related to the Thecostraca based on the unusual position of the female gonopore on the first thoracic somite and the presence of a median penis in the male, corresponding to a fused seventh pair of thoracopods (Boxshall & Lincoln, 1987; Huys et al., 1993).

The infective life-cycle stage, the tantulus larva, has also been found living free in marine sediments (Huys, 1989, 1991; Huys et al., 1992a). The location and infection of a suitable host takes place during this presumably short benthic phase. After attachment by means of an oral disc, the larva penetrates the host cuticle using an internal cephalic stylet which can be protruded out through the central opening of the disc. Once attached, the individual tantulus larva apparently develops into either a sexual male, a sexual female or into a sac-like parthenogenetic female. A hypothesis of the life-cycle of the Tantulocarida has been proposed by Boxshall & Lincoln (1987) and complemented by Huys et al. (1993). It is obvious that there are two separate reproduction strategies: a parthenogenetic and a sexual strategy. However, the relationship between these cycles is not known. It is assumed that the tantulus larva is the offspring of the sexual stage, but sexual reproduction, as well as the development from larva to adult in sexual females, has never been observed. Despite their worldwide distribution and abundance in well-sampled areas, only three findings of the relatively large (up to 500 µm length) sexual females have hitherto been recorded (Huys et al., 1993; Ohtsuka & Boxshall, 1998; Knudsen et al., 2009). It is not known what happens with the sexual female after its release from the larval trunk sac. Recent findings of nauplius-like tantulocarid stages (Martínez Arbizu, personal observation) raise the question of whether the offspring of the sexual stages is actually the tantulus larva.

Currently the Tantulocarida comprise 33 described species and 23 genera which are assigned to 5 families, excluding the new species described in this paper and some considered *incertae sedis*. Due to their minute size tantulocaridans were often overlooked in the past and most findings represent single specimens. Since new species are continuously being discovered, it is assumed that the present number of described tantulocaridans greatly underestimates their actual diversity.

Tantulocaridans described here were collected during the 2002 ANDEEP I cruise to the Drake Passage, Shackleton Fracture Zone, Weddell Sea Basin and South Shetland Slope. During sorting of the meiofauna samples, 86 tantulus larvae were found. They were regularly present in the samples, even at abyssal depths (Gutzmann et al., 2004). This is remarkable, because most species have previously been found accidentally during microscopic inspection of host crustaceans and not living free in sediments. The present paper reports the discovery of three new Antarctic tantulocarids which are referred to *Tantulacus* Huys, Andersen & Kristensen, 1992. The new species are described and compared with the type-species, *T. hoegi* Huys, Andersen & Kristensen, 1992. This is the first record of sediment-inhabiting tantulus larvae from this area.

Materials and methods

During the expedition ANDEEP I (ANT XIX/3) meiofauna samples were collected from the German research vessel *Polarstern* near the Shackleton Fracture Zone. Samples were taken between 30 January and 23 February, 2002 using a multicorer equipped with 62 mm diameter tubes. The multicorer was used at seven locations with 2–3 replicate drops per station, covering a depth range from 5,194 m (station PS61/099) to 2,274 m (station PS61/105) (Table 1).

Table 1 List of data on samples taken during expedition ANT XIX/3 by the RV "*Polarstern*" in 2002, showing date, coordinates, depth and gear (MUC: Multicorer, GKG: Box Corer)

Station	Date	Coordinates		Depth (m)	Gear
042-05	28.01.2002	59°40.39′S	57°35.74′W	3,695	MUC
042-07	28.01.2002	59°39.49′S	57°34.51′W	3,650	MUC
043-04	03.02.2002	60°27.05′S	56°04.77′W	3,958	MUC
043-06	03.02.2002	60°27.00′S	56°04.24′W	3,954	MUC
046-04	30.01.2002	60°38.12′S	53°57.67′W	2,893	MUC
046-06	30.01.2002	60°38.64′S	53°57.27′W	2,893	MUC
099-05	30.01.2002	61°07.09′S	59°16.50′W	5,190	MUC
099-07	30.01.2002	61°07.06′S	59°15.53′W	5,194	MUC
105-02	14.02.2002	61°24.14′S	58°51.15′W	2,289	MUC
105-04	14.02.2002	61°23.81′S	58°50.24′W	2,274	MUC
105-06	14.02.2002	61°23.73′S	58°50.26′W	2,274	MUC
114-05	18.02.2002	61°43.52′S	60°44.13′W	2,917	MUC
114-07	18.02.2002	61°43.48′S	60°43.50′W	2,900	MUC
114-09	19.02.2002	61°43.58′S	60°43.22′W	2,875	MUC
129-04	23.02.2002	59°52.40′S	59°57.88′W	3,598	GKG
129-05	23.02.2002	59°52.39′S	59°57.78′W	3,797	MUC
129-07	23.02.2002	59°52.30′S	59°57.63′W	3,614	MUC

In addition, two tantulocarids were collected with the 0.25 m^2-box corer at station PS61/129-04. For meiofaunal analysis, the top 10 cm sediments of each core (together with the supernatant water) was fixed with buffered formalin at a final concentration of about 4% on board of the R/V *Polarstern.* Sorting of organisms took place at the DZMB (German Centre for Marine Biodiversity Research), Senckenberg Research Institute and recovered a total of 86 tantuli. Information on the meiofaunal community structure was analysed by Gutzmann et al. (2004). Specimens were sorted to species level and given either Linnean names or preliminary names consisting of family name plus numeral (e.g. Deoterthridae sp. 1, Deoterthridae sp. 2, etc.). Drawings were made under a Leica DMR microscope with differential interference contrast optics and oil immersion at magnifications of up to 1,600 times. The specimens were not dissected due to their small size, but judicious manipulation of the coverslip allowed careful examination of the detailed morphology of the thoracopods and the cephalon. The type-material is deposited in the Forschungsinstitut und Naturmuseum Senckenberg (Frankfurt, Germany).

Family Deoterthridae Boxshall & Lincoln, 1987

Genus *Tantulacus* Huys, Andersen & Kristensen, 1992

Amended diagnosis

Body of tantulus larva comprising cephalon with dorsal shield, thorax with 6 pedigerous somites and 1 limbless seventh thoracic somite, and 1 abdominal somite. First thoracic tergite largely concealed beneath posterior margin of dorsal cephalic shield. Cephalic shield more or less triangular with 6–14 pairs of integumental pores; D_{II} pores present or absent. Cephalic stylet curved in lateral aspect; apex of stylet with minute spinous processes. Thoracopods 1–5 with protopodal endite and well-developed rami. First thoracopod with 2–4 setae on exopod and 1 seta on endopod; exopod of thoracopods 2–5 with 4 or 5 setae. Endopod with 1 seta (leg 1) or 1 seta plus a rigid, acutely curved spine (legs 2–5). Thoracopod 6 without distinct rami but with 2 setae apically; coupling spines present or absent. Abdomen with transverse lamellae around somite; caudal rami each bearing 2 long and 1 short setae. Host unknown.

Tantulacus longispinosus n. sp.

Type-host: Unknown.
Type-locality: West of Shackleton Fracture Zone, Southern Ocean, station 129-05 (59°52.39′S, 59°57.78′W; depth 3,797 m).
Type-material: Holotype tantulus larva, coll. no. SMF 36935, 23 February, 2002; 2 paratype tantulus larvae, coll. no. SMF 36936, West of Shackleton Fracture Zone, station 129-05 (59°52.39′S, 59°57.78′W; depth 3,797 m) (same locality information as for holotype), 23 February, 2002; 1 paratype tantulus larva, coll. no. SMF 36937, South Shetland Trench, Southern Ocean, station 99-05 (61°7.09′S, 59°16.50′W; depth 5190 m), 30 January, 2002.
Etymology: The specific name *longispinosus* refers to the extremely long endopodal spine on the second to fifth thoracopods.

Description (Figs. 1–4)

Tantulus larva

Body (Figs. 1a,b, 2, 3a–e, 4a,b) comprising cephalon covered by dorsal cephalic shield, thorax of 6 pedigerous somites and single limbless somite, and undivided abdomen. First thoracic tergite largely concealed beneath posterior margin of dorsal shield. Total body length of specimen, measured from tip of cephalon to posterior margin of caudal rami, *c.*130 µm. Cephalic shield *c.*1.2 times long as wide (55 × 45 µm). Posterior margin of cephalon more or less straight in dorsal view. Cephalic appendages and rostrum absent. Cephalon, rounded anteriorly, tapering towards ventral oral attachment disc. Oral disc (Fig. 1b) *c.*13 µm in diameter, with 2 filament-like structures implanted laterally on either side of disc. Ornamentation of cephalic shield consisting of 3 anterior and 3 posterior pairs of pores with 2 pairs being sensillate (D_{II}, D_{III}); surface lamellae absent. Ventral surface of cephalon with 1 pair of pores medially (V_{IV}). Cephalic pore formula as follows: $A_{II–IV}$, $D_{I–III}$, L_{IV}, V_{IV} (after Boxshall & Vader, 1993). Cephalic stylet (Figs. 1a,b, 2) slender and curved apically in lateral aspect. Total length approx. 25 µm. Stylet medially positioned in cephalon, with distal part protruding through central pore of oral attachment disc. Stylet tip with several minute spinous processes. Stylet protractors in form of

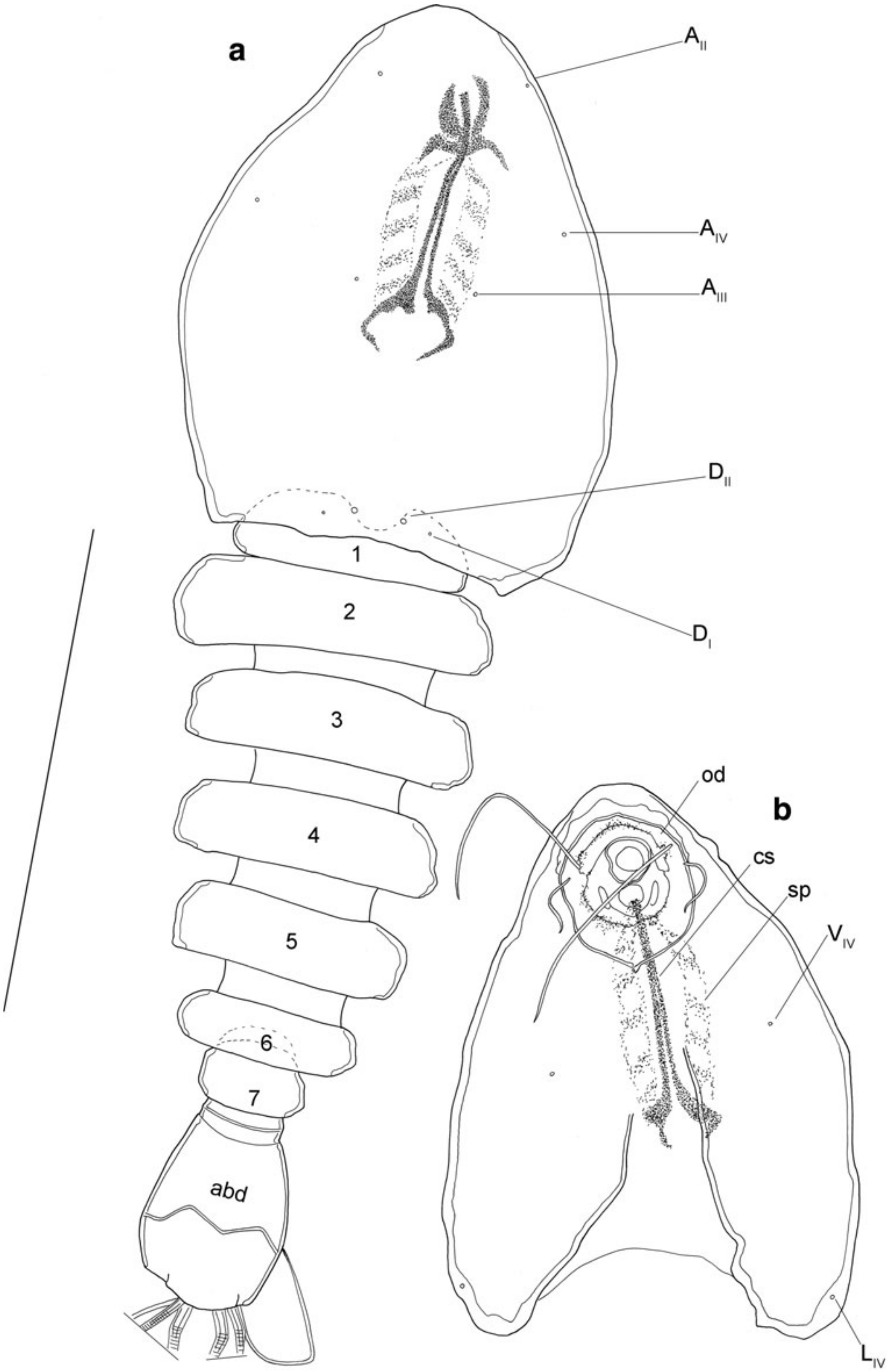

Fig. 1 *Tantulacus longispinosus* n. sp., tantulus larva, holotype; a. Habitus, dorsal view with pores labelled, external morphology; b. Cephalon in ventral view with pores labelled. *Abbreviations*: abd, abdomen; cs, cephalic stylet; od, oral disc; sp, stylet protractors; t1–t7, thoracic somites 1–7 . *Scale-bar*: 50 μm

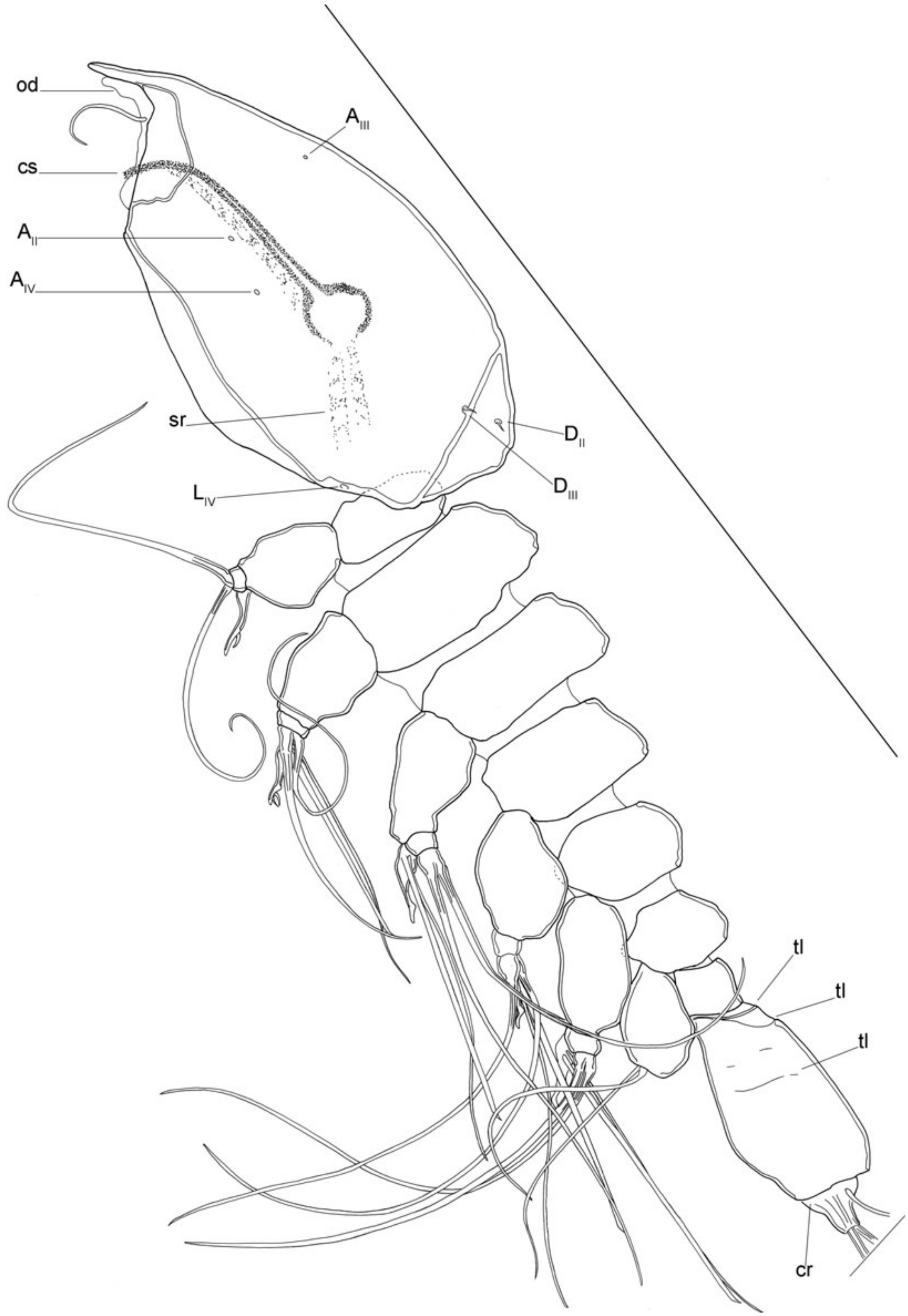

Fig. 2 *Tantulacus longispinosus* n. sp., tantulus larva, holotype; habitus, lateral view with pores labelled. *Abbreviations*: cr, caudal rami; cs, cephalic stylet; od, oral disc; sr, stylet retractors; tl, transverse lamella. *Scale-bar*: 100 µm

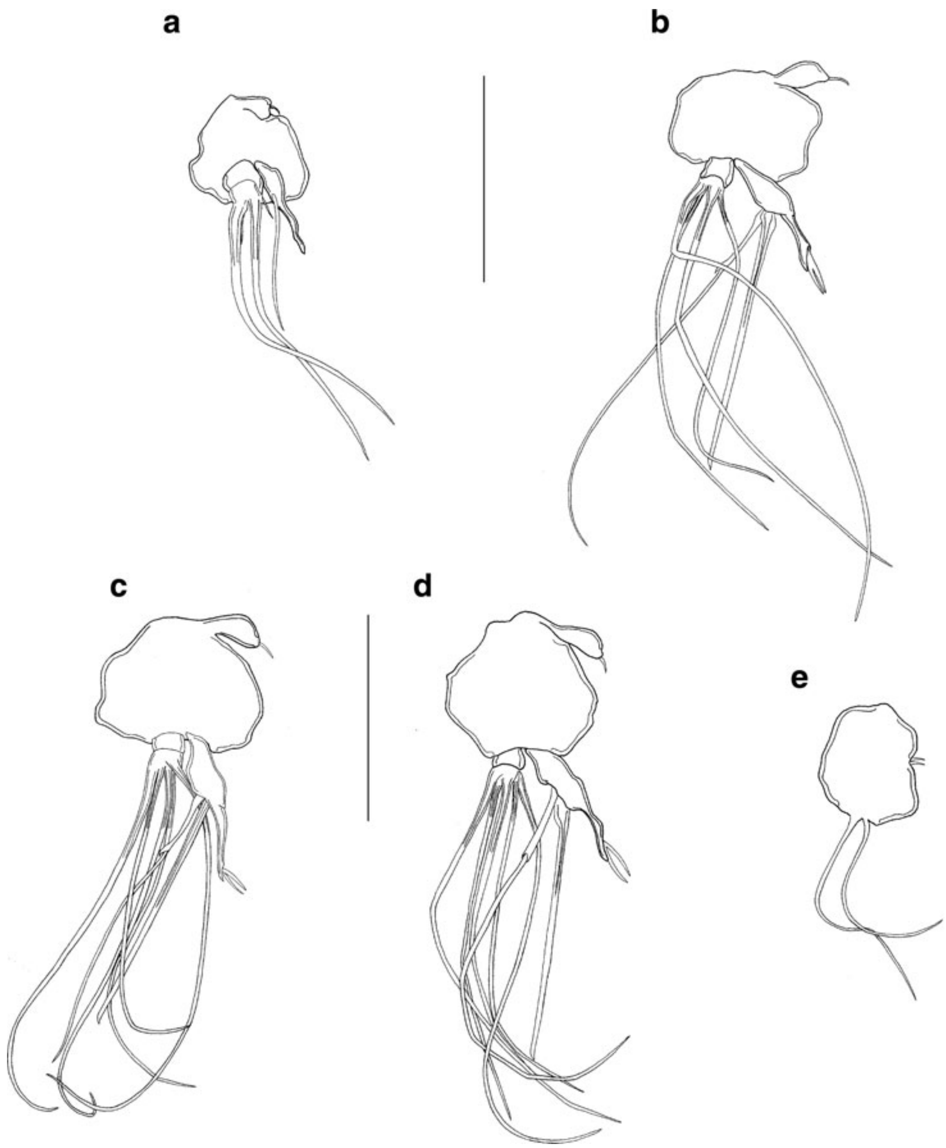

Fig. 3 Thoracopods of *Tantulacus longispinosus* n. sp., tantulus larva, holotype; a. Thoracopod 1; b. Thoracopod 3; c. Thoracopod 4; d. Thoracopod 5; e. Thoracopod 6. *Scale-bar*: 20 µm

broad strands originating anteriorly and inserting posteriorly at lateral barbs of stylet. Retractor muscles extending from posterior margin of cephalon to stylet base, apparently also linked with stylet barbs.

Seven free thoracic somites with smooth integument. Thoracic somites 1–6 each bearing pair of swimming legs with well-developed rami (Fig. 3a–e). Protopods of legs 1–5 (Fig. 3a–d) broad, with defined proximal part bearing medial endite armed with 1 small seta. Exopod of thoracopods 1–5 clearly 2-segmented. Proximal segment unarmed and wider than long; distal segment with 2 long and 2 very short setae (leg 1) (Fig. 3a), 4 long slender setae (leg 1–2) (Fig. 3b) or 5 long slender (leg 3–4) (Fig. 3c,d) setae. Endopod of thoracopod 1 (Fig. 3a) represented by elongate segment bearing single slender seta at inner lateral margin and spatulate process armed apically with 2 coupling spines. Endopod of thoracopods 2–5 (Fig. 3b–d) similar in structure, bearing 1 long slender seta with proximal process and 1 rigid, apically curved spine originating midway along lateral margin of ramus. Endopodal apex transformed into subdistal

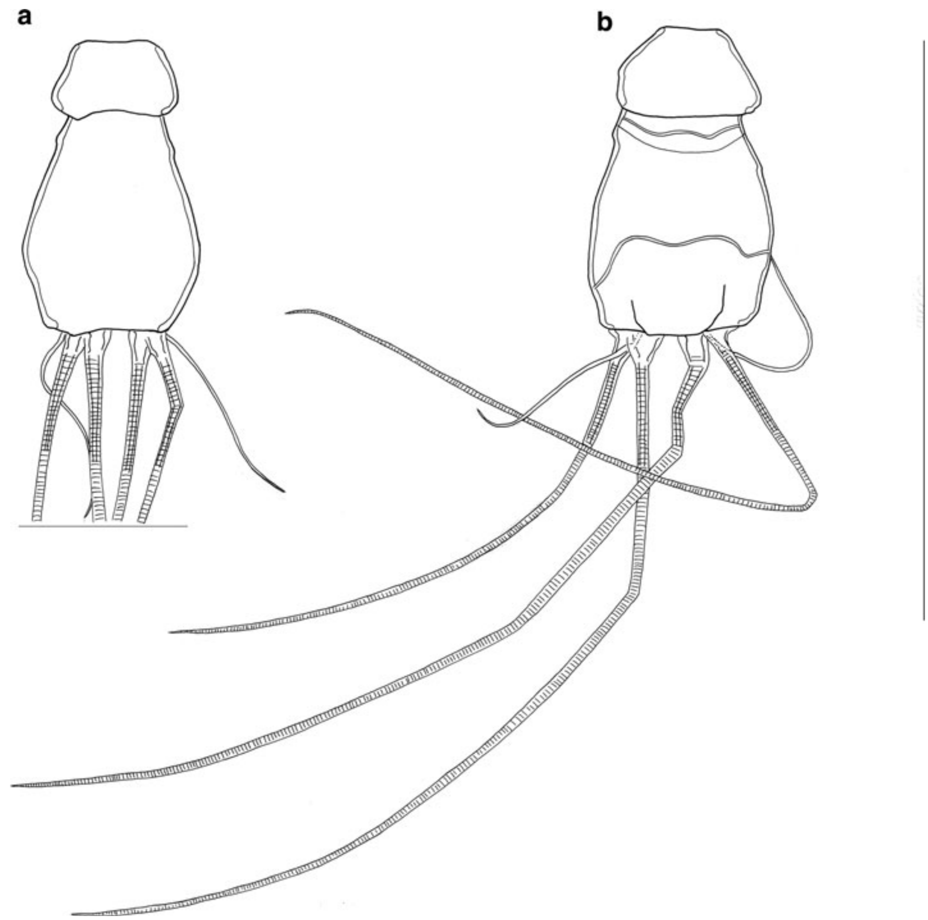

Fig. 4 *Tantulacus longispinosus* n. sp., tantulus larva, holotype; a. Urosome, ventral view; b. Urosome, dorsal view. *Scale-bar*: 50 µm

spatulate element and distal gripping apparatus consisting of spinous process. Thoracopod 6 (Fig. 3e) with unsegmented protopod bearing 2 coupling spines located midway along inner margin and 1 unsegmented ramus with 2 medium-length slender setae terminally.

Urosome (Fig. 4a,b) comprising small unornamented seventh thoracic somite and large abdominal somite. Abdomen about 1.27 times longer than wide (19 × 15 µm), ornamented dorsally with 3 transverse surface lamellae (Fig. 4b). Postero-dorsal margin of abdomen with medial protrusion. Ventral surface (Fig. 4a) without ornamentation. Caudal rami small, each furnished with 3 setae (2 large terminal and 1 small subterminal). Caudal setae not modified.

Adult male and female. Unknown

***Tantulacus karolae* n. sp.**

Type-host: Unknown.
Type-locality: West of Shackleton Fracture Zone, Southern Ocean, station 129-07 (59°52.30′S, 59°57.63′W; depth 3,614 m).
Type-material: Holotype tantulus larva, coll. no. SMF 36938, 23 February 2002.
Etymology: The specific name *karolae* is given in dedication to the senior author's mother, Karola Mohrbeck.

Description (Figs. 5–8)

Tantulus larva
Body (Figs. 5, 6) comprising cephalon covered by dorsal shield, 7-segmented thorax with thoracopods on somites 1–6, and 1-segmented abdomen. Total body

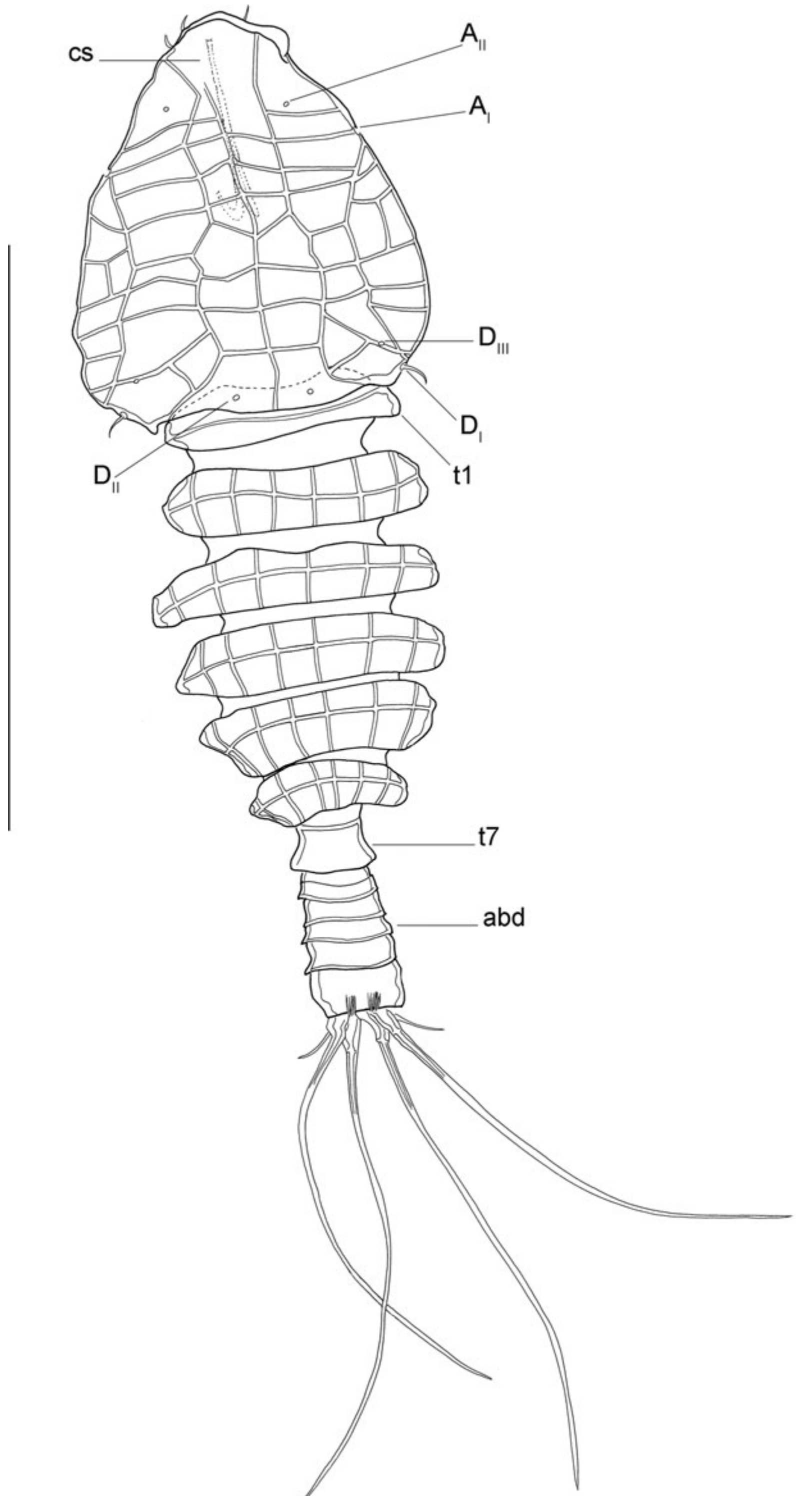

Fig. 5 *Tantulacus karolae* n. sp., tantulus larva, holotype; habitus, dorsal view with pores labelled. *Abbreviations*: abd, abdomen; cs, cephalic stylet; t1, t7, thoracic somites 1 and 7. *Scale-bar*: 50 μm

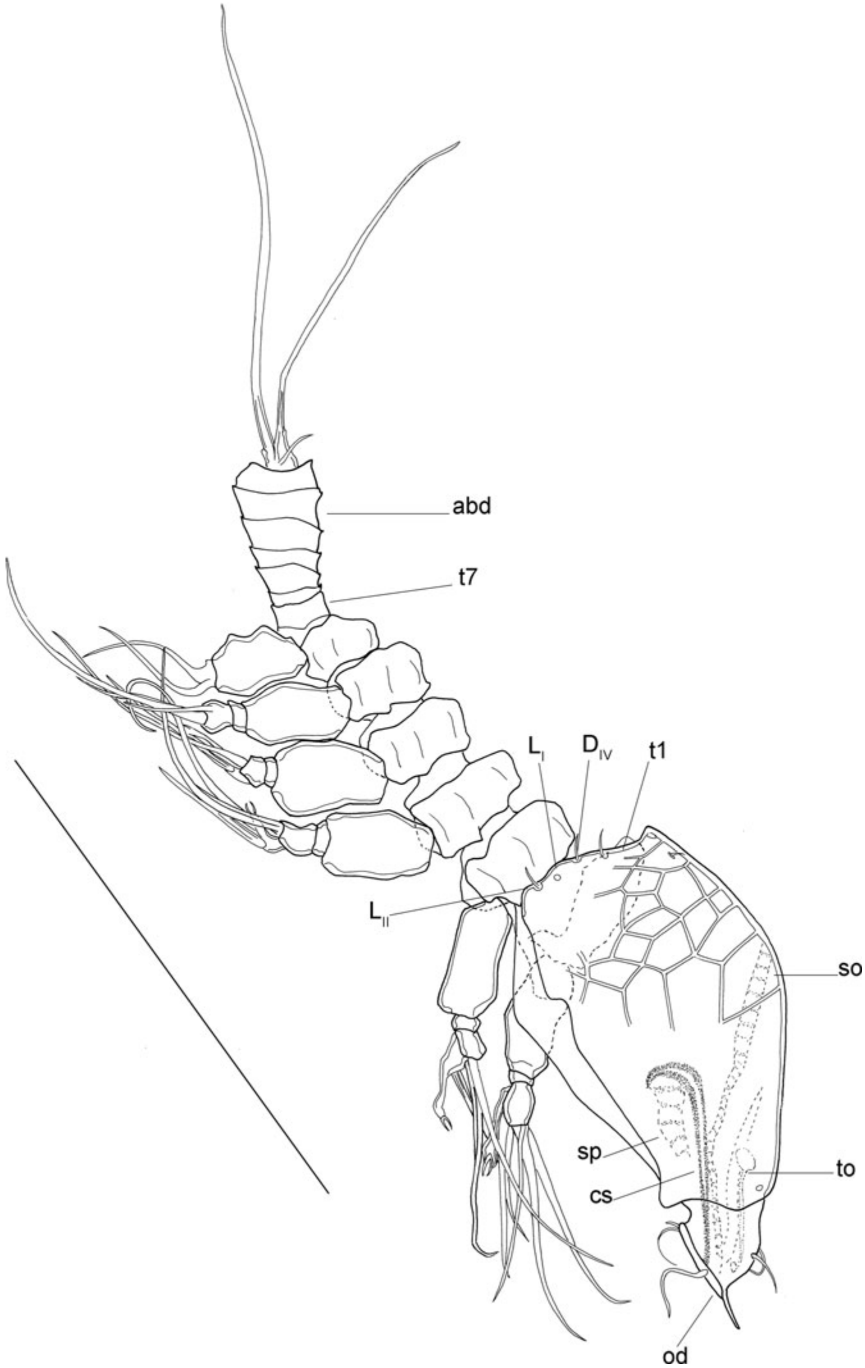

Fig. 6 *Tantulacus karolae* n. sp., tantulus larva, holotype; habitus, lateral view with pores labelled. *Abbreviations*: abd, abdomen; cs, cephalic stylet; od, oral disc; so, striated organ; sp, stylet protractors; t7, thoracic somite 7; to, tubular organ. *Scale-bar*: 50 µm

length of specimen *c*.90 µm, measured from tip of cephalon to posterior margin of caudal rami. Cephalic shield about as long as wide (33 × 35 µm); posterior margin convex in dorsal view. Cephalic appendages and rostrum lacking, but anterior margin of cephalon with lobe-like extension bearing 2 tiny filaments laterally. Cephalon triangular, tapering anteriorly towards ventral oral attachment disc. Oral disc

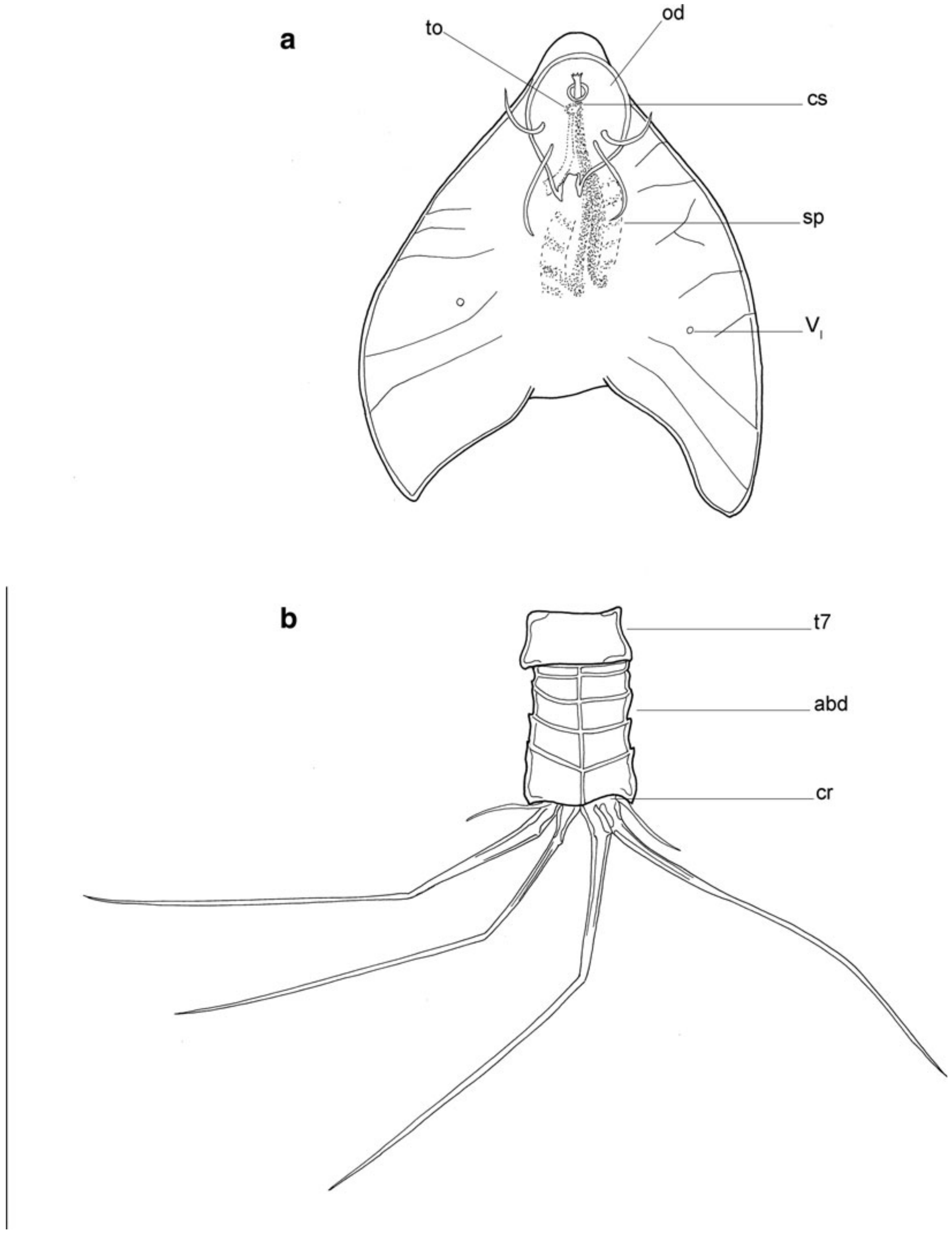

Fig. 7 *Tantulacus karolae* n. sp., tantulus larva, holotype; a. Cephalon, ventral view with pores labelled; b. Urosome, ventral view. *Abbreviations*: abd, abdomen; cs, cephalic stylet; od, oral disc; sp, stylet protractors; t7, thoracic somite 7; to, tubular organ. *Scale-bar*: 50 µm

(Fig. 7a) small, *c*.7 µm in diameter. No microvilli apparent, but 2 filament-like structures on either side of oral disc. Disc positioned far anteriorly, so visible in lateral aspect. Slender cephalic stylet (Figs. 6, 7a) medially positioned in cephalon; distal part protruding through central pore of oral disc. Length approx.

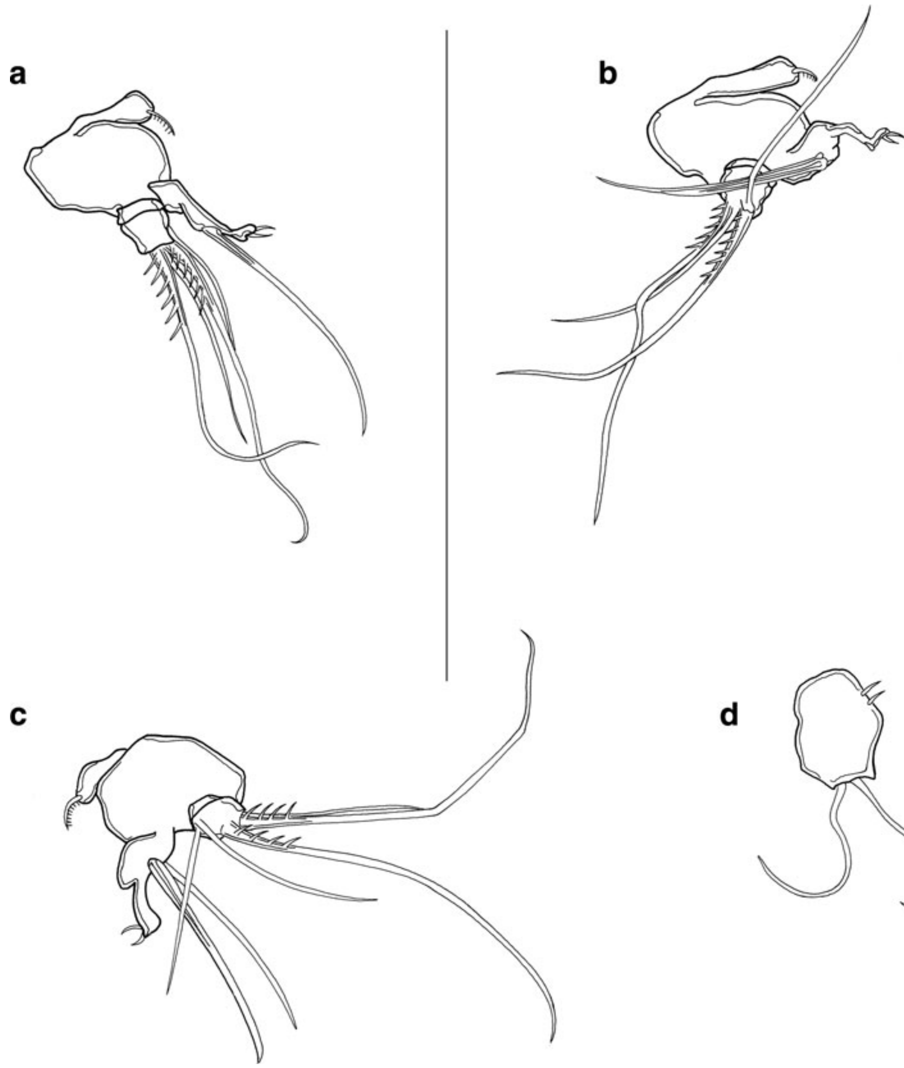

Fig. 8 Thoracopods *Tantulacus karolae* n. sp., tantulus larva, holotype; a. Thoracopod 1; b. Thoracopod 2; c. Thoracopod 3; d. Thoracopod 6. *Scale-bar*: 50 µm

24 µm in lateral view; stylet strongly curved at base and tapering towards apex; tip with several minute spinous processes. Stylet protractors in form of broad strands originating anteriorly and inserting posteriorly at lateral barbs of stylet; retractors not visible. Two muscles (termed striated organ in earlier accounts) running from middle of cephalon to dorsal apex of stylet. Anterior and dorsal to striated organ and cephalic stylet is funnel-shaped organ/proboscis with discoid apex. Considerable ornamentation present around entire cephalon (Figs. 5, 6). Pore pattern of cephalic shield consisting of 9 pairs of pores: $A_{I–II}$, $D_{I–IV}$, $L_{I–II}$, V_I (after Boxshall & Vader, 1993), 2 simple pairs anteriorly and 6 posteriorly with 4 sensillate pairs (L_{II}, D_I, D_{III}, D_{IV}). Ventral surface of cephalon with 1 pair of pores medially (V_I) (Fig. 7a). Integument of shield ornamented dorsally with 5 distinct epicuticular lamellae connected by numerous small transverse ones (Fig. 5). Free thoracic somites each with distinct tergite; that of first somite dorsal and lateral largely concealed beneath posterior rim of cephalic shield. Tergites with conspicuous surface ornamentation; those of somites 1–6 with several longitudinal surface lamellae and 1 transverse lamella. Thoracic somites 1–6 each bearing pair of swimming legs with well-developed rami (Fig. 6).

Thoracopod 1 (Fig. 8a) with subrectangular protopodal segment bearing large medial endite armed with 1 pinnate seta and well-developed rami. Endopod of thoracopod 1 represented by elongate segment bearing single apical slender seta and spatulate process armed with 2 coupling spines along inner lateral margin. Exopod 2-segmented; proximal segment much wider than long, unarmed; distal segment nearly wide as long, bearing 2 long strong setae, ornamented with rows of short pinnules and 2 medium-length slender setae.

Thoracopods 2–5 (Fig. 8b,c) with indistinctly 2-segmented protopod bearing bulbous medial endite; armature of endite under light microscope visible as 1 ornamented seta. Endopod 1-segmented and well developed; 1 long slender seta and 1 rigid, apically curved spine originate midway along lateral margin of ramus. Endopodal apex transformed into subdistal spatulate element and distal gripping apparatus consisting of spinous process. Exopod 2-segmented; proximal segment without armature and much wider than long. Distal segment bearing 2 long strong setae and 2 medium-length slender setae (leg 2) (Fig. 8b) or 2 long strong setae and 3 medium-length slender setae (legs 3–5) (Fig. 8c). All strong exopodal setae ornamented with rows of short pinnules. Thoracopod 6 (Fig. 8d) uniramous, comprising single protopodal segment with 2 coupling spines located midway along inner margin, and 2 similiar medium-length distally curved setae.

Urosome (Figs. 6, 7b) comprising small unornamented seventh thoracic somite (first urosome segment), lacking tergite, and large unsegmented abdominal somite (second urosome segment). Abdomen *c*.1.8 times longer than wide (13 × 7 μm). Surface ornamented with epicuticular lamellae arranged in regular pattern consisting mainly of 5 transverse lamellae surrounding entire abdominal somite and 1 longitudinal lamella ventrally. Third to fifth lamellae in posterior part of abdomen furnished dorsally with 6 minute spinous processes. Ventral lamellae smooth. Posterior margin of abdomen with 2 tiny denticles dorsally (Fig. 6) and 4 denticles ventrally (Fig. 7b). Caudal rami (Fig. 7b) each furnished apically with 2 similar slender setae, plus shorter lateral seta. Caudal setae not modified.

Adult male and female. Unknown

Tantulacus dieteri **n. sp.**

Type-host: Unknown.
Type-locality: Off Elephant Island, Southern Ocean, station 046-06 (60°38.64′S, 53°57.27′W; depth 2,893 m).
Type-material: Holotype tantulus larva, coll. no. SMF 36939, 30 January, 2002.
Etymology: The specific name *dieteri* is given in dedication to the senior author's father, Dieter Mohrbeck.

Description (Figs. 9–11)

Tantulus larva
Body (Figs. 9a, 10) consisting of cephalon covered by dorsal shield, 6 pedigerous somites and 2-segmented limbless urosome; body length *c*.85 μm, measured from tip of cephalon to posterior margin of caudal rami. Rostrum absent. Cephalon *c*.1.2 times longer than wide (30 × 25 μm). Surface of cephalic shield ornamented with 1 mid-dorsal longitudinal lamella and 1 pair of dorsolateral lamellae extending from anterior margin of cephalon to tergite 6. Ventral surface (Fig. 9b) concave, lacking lamellae. Oral disc *c*.12 μm in diameter, anteroventrally positioned with 1 seta and 1 filament on either side of disc. Cephalic stylet (Figs. 9b, 10) *c*.25 μm long, positioned medially in cephalon, with distal part protruding through central pore of oral attachment disc. Stylet tapering towards apex; base with well-developed lateral barbs and tip furnished with several minute spinous processes. Broad retractor strands (Fig. 10) originating at posterodorsal margin, extending to base of stylet and inserting at lateral barbs. Stylet protractors originating anteriorly and ending at lateral barbs of stylet; broad muscular striated organ running from middle of cephalon to dorsal apex of stylet and apparently associated with stylet. Anterior and dorsal to striated organ and cephalic stylet, funnel-shaped organ/proboscis with discoid apex discernable. Cephalon bearing 14 pairs of pores: A_{I-III},D_{II},D_V,L_{I-V},-V_{I-IV} (Figs. 9a,b, 10); anterior zone with 5 pairs, 2 pairs being sensillate and 2 ventral; posterior zone with 9 pairs, 2 pairs being sensillate and 2 ventral.

Thoracic somites 1–6 each provided with well-developed tergite and pair of thoracopods. First tergite largely concealed beneath posterior rim of

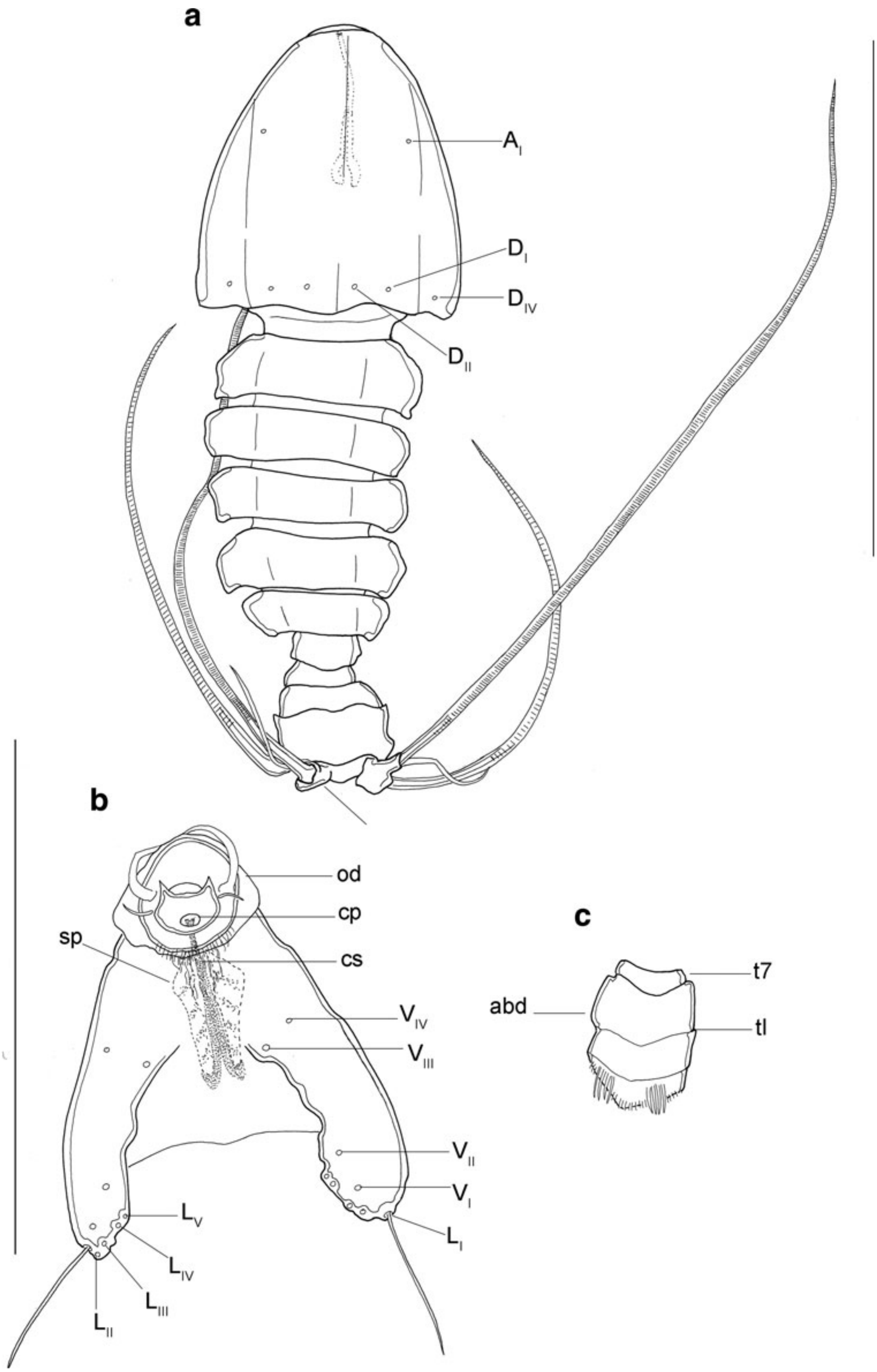

Fig. 9 *Tantulacus dieteri* n. sp., tantulus larva, holotype; a. Habitus, dorsal view with pores labelled, external morphology; b. Cephalon, ventral view with pores labelled; c. Urosome, ventral view. *Abbreviations*: abd, abdomen; cp, central pore; cs, cephalic stylet; od, oral disc; sp, stylet protractors; t7, thoracic somite 7; tl, transverse lamella. *Scale-bar*: 50 µm

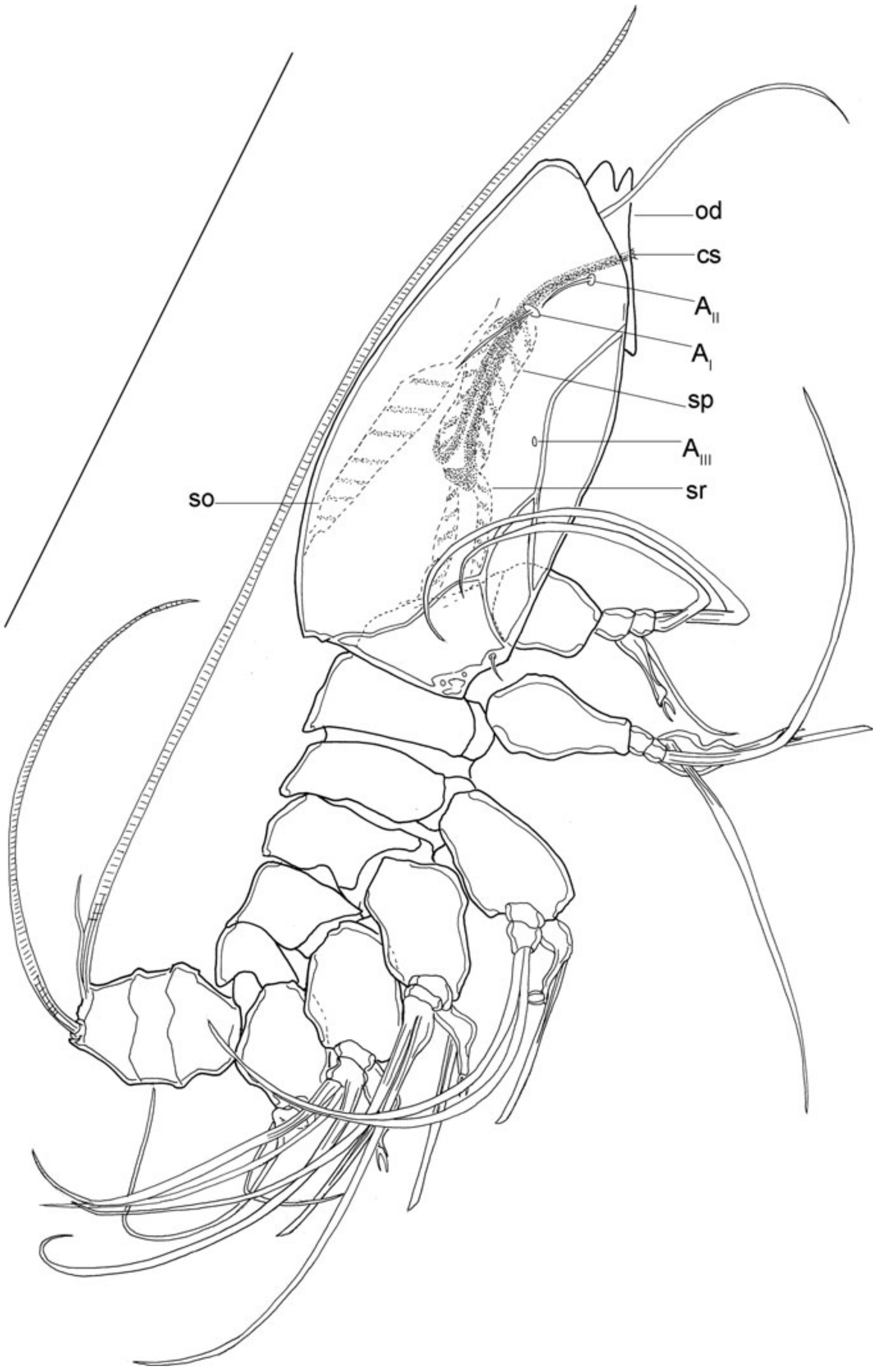

Fig. 10 *Tantulacus dieteri* n. sp., tantulus larva, holotype; habitus, lateral view with pores labelled. *Abbreviations*: cs, cephalic stylet; od, oral disc; so, striated organ; sp, stylet protractors; sr, stylet retractors. *Scale-bar*: 50 µm

cephalon (Figs. 9a, 10). Protopod of first thoracopod (Fig. 11a) bearing endite with minute spine and well-developed endo- and exopod. Endopod represented by digitiform segment, with proximal half swollen midway and distal half slightly bifid apically, ending in spatulate process armed with coupling spines terminally. Outer margin with seta. Exopod 2-segmented; distal segment with 2 long, stout setae

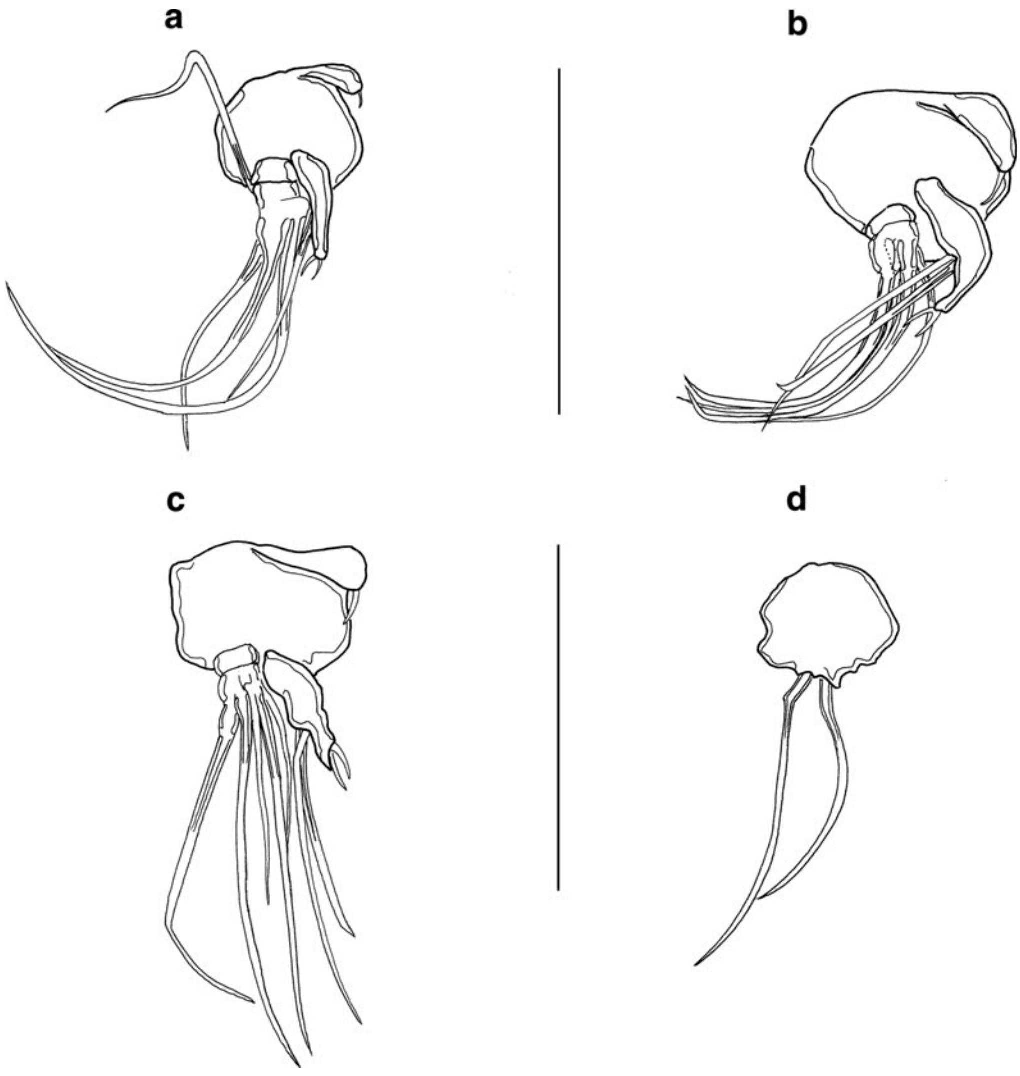

Fig. 11 Thoracopods of *Tantulacus dieteri* n. sp., tantulus larva, holotype; a. Thoracopod 1; b. Thoracopod 2; c. Thoracopod 3; d. Thoracopod 6. *Scale-bar*: 20 µm

and 2 short, slender setae. Thoracopod 2 (Fig. 11b) with larger protopodal segment than first thoracopod; endite armed with minute spine apically. Endopod 1-segmented, elongate with 1 seta plus 1 slender, rigid spine of equal length; endopodal apex transformed into gripping apparatus comprising movable, subdistal spatulate element and distal spinous process. Exopod 2-segmented; proximal segment without armature; distal segment with 2 long, strong setae and 2 smaller, slender setae. Protopodal segment of thoracopods 3–5 (Fig. 11c) similar to second thoracopod. Endopod unisegmented, elongate with 1 outer seta and 1 rigid spine midway; terminal process flattened, bearing movable spatulate process. Exopod 2-segmented; proximal segment unarmed; distal segment with 3 long, strong setae and 2 fine, shorter setae terminally. Thoracopod 6 (Fig. 11d) uniramous, comprising single protopodal segment, lacking both endite and coupling spines, bearing 2 similar setae terminally. Inner seta recurved basally.

Urosome (Fig. 9c) consisting of limbless seventh thoracic somite and unsegmented abdomen. Total length of urosome approx. 15 µm. Abdomen with 2 transverse epicuticular lamellae. Posterior margin smooth dorsally, with fine spinous processes ventrally consisting of 4 filaments. Caudal rami (Figs. 9c, 10) each with 1 relatively long seta (*c*.50 µm long), 1 mid-length seta and 1 short seta.

Adult male and female. Unknown

Worldwide geographical and bathymetric distribution

Most tantulocaridans have been collected in the Atlantic and Pacific Oceans (e.g. Huys, 1990a; Huys et al., 1992a, b; Ohtsuka & Boxshall, 1998), but there are also some records from the Mediterranean (Bonnier, 1903; Huys, 1989, 1991), the North Sea (Greve, 1965; Huys & Boxshall, 1988; Boxshall & Vader, 1993) and the White Sea (Kornev et al. 2004; Kolbasov et al., 2008; Kolbasov & Savchenko, 2010), and a few from the Southern and Indian Oceans (Grygier & Sieg, 1988; Savchenko & Kolbasov, 2009). This indicates a worldwide distribution of the group. As most records of tantulocaridans were from high-latitude waters (e.g. Greve, 1965; Bradford & Hewitt, 1980; Boxshall & Lincoln, 1987; Grygier & Sieg, 1988; Huys & Boxshall, 1988; Boxshall et al., 1989; Huys et al., 1997) or from deep waters at lower latitudes (Bonnier, 1903; Becker, 1975; Huys, 1990a), it seems that they prefer cold water habitats, but this might also reflect gaps in sampling coverage. However, tantulocaridans also have been reported from an anchialine pool (Canary Islands) (Boxshall & Huys, 1989), coral sands (Great Barrier Reef) (Huys, 1990b) and a hydrothermal vent field (Galapagos Rift) (Huys & Conroy-Dalton, 1997). These findings indicate that tantulocaridans are adapted to tropical conditions as well.

Bathymetric species distribution of hitherto known tantulocaridans, including the three species described above, ranges from zero (anchialine pool) (Boxshall & Huys, 1989) to over 5,000 m (Southern and Atlantic Oceans) (Becker, 1975; Mohrbeck, personal observation), with a clear preference for deep sea habitats. As summarised in Fig. 12, most tantulocarid species (66.67%) have been collected at depths below 200 m (bathyal zone) (e.g. *Microdajus aporosus* Grygier & Sieg, 1988, *Doryphallophora megacephala* Boxshall & Lincoln, 1983, *Dicrotrichura tricincta*, Huys, 1989, *Aphotocentor styx*, Huys, 1991) and even below 2,000 m (abyssal zone) (e.g. *Microdajus gaelicus* Boxshall & Lincoln, 1987, *Basipodella harpacticola* Becker, 1975, *Doryphallophora aselloticola* Boxshall & Lincoln, 1987, *Campyloxiphos dineti* Huys, 1990, *Rimitantulus hirsutus* Huys & Conroy-Dalton, 1997, *Serratotantulus chertoprudae* Savchenko & Kolbasov, 2009), whereas only 30.77% inhabit littoral and sublittoral areas (e.g. *Coralliotantulus coomansi* Huys, 1990, *Xenalytus scotophilus* Huys, 1991, *Amphitantulus harpiniacheres* Boxshall & Vader, 1993, *Hypertantulus siphonicola* Ohtsuka &

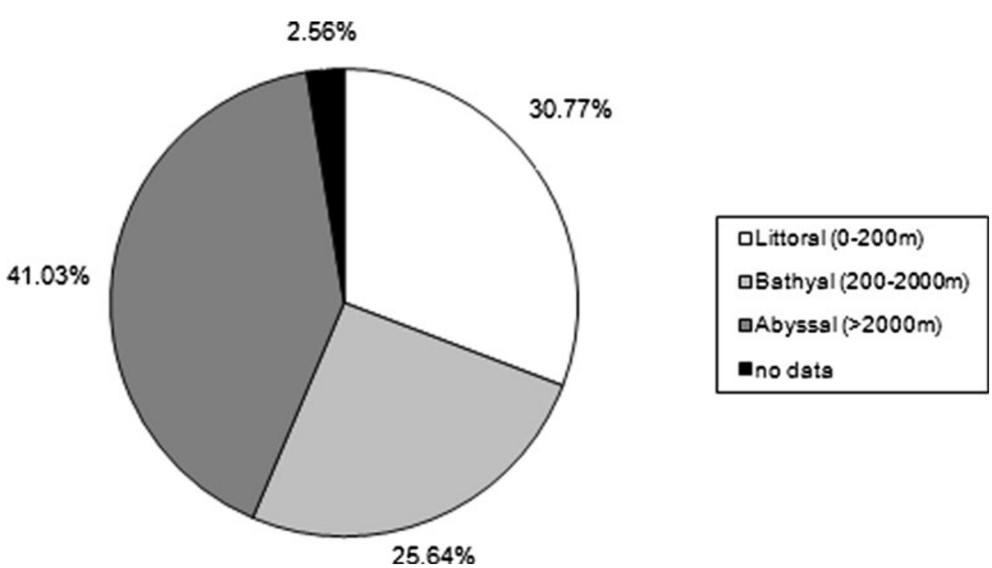

Fig. 12 Depth distribution (in % of species) of known Tantulocarida

Boxshall, 1998). One record (2.56% of all species) does not include data on the bathymetric distribution.

Tantulocarida collected near the Shackleton Fracture Zone are summarised in Table 2. Extensive study of larvae revealed a high diversity of tantulocaridans in the Southern Ocean and revealed a total of 33 species. Tantuli have been found at almost all (15 of 16) deep-sea stations sampled with the multicorer during the ANDEEP I cruise. Two tantulocaridans were collected with the 0.25 m^2-box corer at station 129-04. Five specimens could not be identified due to damage. Four of five tantulocaridan families (Basipodellidae Boxshall & Lincoln, 1983, Deoterthridae, Doryphallophoridae Huys, 1991 and Microdajidae Boxshall & Lincoln, 1987) and nine tantulocarid genera (*Amphitantulus* Boxshall & Vader, 1993, *Dicrotrichura* Huys, 1989, *Doryphallophora* Huys, 1990, *Hypertantulus* Ohtsuka & Boxshall, 1998, *Itoitantulus* Huys, Ohtsuka, Boxshall & Itô, 1992, *Microdajus* Greve, 1965, *Paradoryphallophora* Ohtsuka & Boxshall, 1998, *Tantulacus* and *Xenalytus* Huys, 1990) were recorded in the sampling area. Three species could not be assigned to any known genus and are therefore named 'Basipodellidae sp.1' and 'Deoterthridae sp.1' to 'Deoterthridae sp.2'. Thirty species (91%) are "new" to science and 32 species are new for the Southern Ocean. The number of species recorded is highest in *Tantulacus* (14 species) (Table 2). This is the first record of this group in the Antarctic deep sea, but this probably reflects the degree of undersampling in this area. The highest number of eight species was found at station 114–09 off King George Island, the lowest number, with only one species, was found at station 042–05 in the Ona Basin, station 046-06 off Elephant Island and station 129-04 west of the Shackleton Fracture Zone (Fig. 13).

Discussion

Tantulacus was erected by Huys, Andersen & Kristensen (1992) for a single species, *T. hoegi*. It was assigned to the family Deoterthridae on account of its larval characters, including the uni-segmented abdomen, the cephalic pore pattern and the absence of a rostrum (Huys et al., 1992a). Although the generic diagnosis given by Huys et al. (1992a) is relatively clear, the Deoterthridae has not been demonstrated to be monophyletic and the phylogenetic value of its diagnostic features is debatable. Because of confusion in defining the terms 'abdomen' and 'urosome' and varied interpretations of surface ornamentation of the abdominal somite, there are ongoing difficulties in assigning tantulocaridans to a family. The taxonomy of tantulocaridans is largely based on larval characteristics, such as body tagmosis and thoracopod morphology (Huys, 1991). To elucidate the phylogenetic relationships within the Tantulocarida it is necessary to investigate the morphology and diagnostic characters of the adult males as well. The morphology of the male abdomen and the structure of the median penis seem to be suitable characteristics for distinguishing tantulocaridans.

The affiliation of the three species described above, *Tantulacus longispinosus* n. sp., *T. karolae* n. sp. and *T. dieteri* n. sp., to *Tantulacus* is straightforward. All representatives of the Tantulocarida are characterised by the presence of one or two slender setae on the endopod of the second to fifth thoracopods, but in none of the known genera, except for *Tantulacus,* are these elements modified. *T. hoegi*, *T. karolae*, *T. dieteri* and *T. longispinosus* share the presence of a distal rigid spine on the endopod of the second to fifth thoracopods as a synapomorphy and can thus be readily distinguished from other tantulocarids. The endopodal spine is therefore considered as autapomorphic for *Tantulacus* and justifies its status as a monophylum. A major difference is observable in the shape and length of the endopodal spine. Whereas it is short and very robust in *T. hoegi,* in the new species it is slender and much longer. In particular, *T. longispinosus* differs from the other species, because of its extremely long endopodal spine.

The maximum number of five setae found on the exopod of the second to fifth thoracopods is a plesiomorphic character retained only in *Deoterthron* Bradford & Hewitt, 1980*, Aphotocentor* Huys, 1991 and *Amphitantulus* (Bradford & Hewitt, 1980; Huys, 1989, 1991; Boxshall & Vader, 1993). *Tantulacus* holds an intermediate position because of the ancestral number of five exopodal setae on thoracopods 4 and 5 (*T. hoegi* and *T. longispinosus*) and thoracopods 3 to 5 (*T. karolae* and *T. dieteri*). In addition to the exopodal setation of thoracopod 3, *T. karolae* and *T. dieteri* also differ in the number of exopodal setae of the first thoracopod, bearing four long setae. In contrast, *T. longispinosus* and the type-species, *T. hoegi,* bear only two, plus two very short,

Table 2 List of Tantulocarida collected at the Drake Passage, Shackleton Fracture Zone, during expedition ANT XIX/3 by the RV "*Polarstern*" in 2002

No.	Species	042-05	042-07	043-04	043-06	046-04	046-06	099-05	099-07	105-02	114-05	114-07	114-09	129-04	129-05	129-07	n/S
1	*Amphitantulus* sp.1		1						1								2
2	*Dicrotrichura* sp.1				12							2					14
3	*Dicrotrichura* sp.2					1											1
4	*Dicrotrichura* sp.3				1												1
5	*Doryphallophora megacephala*								1								1
6	*Doryphallophora* sp.1		1														1
7	*Doryphallophora* sp.2									1							1
8	*Hypertantulus* sp.1				1												1
9	*Hypertantulus* sp.2							1									1
10	*Hypertantulus* sp.3										1	1					2
11	*Itoitantulus* sp.1				1												1
12	*Itoitantulus* sp.2												1				1
13	*Microdajus aporosus*	2		2		1					1				1		7
14	*Microdajus* sp.1								1								1
15	*Paradoryphallophora* sp.1														1		1
16	*Tantulacus dieteri* n. sp.						1										1
17	*Tantulacus karolae* n. sp.															1	1
18	*Tantulacus longispinosus* n. sp.							1							3		4
19	*Tantulacus* sp.1				1						1	2	2				6
20	*Tantulacus* sp.2		1						1								2
21	*Tantulacus* sp.3								3								3
22	*Tantulacus* sp.4														1		1
23	*Tantulacus* sp.5										3	1	1				5
24	*Tantulacus* sp.6											2					2
25	*Tantulacus* sp.7										1		1				2
26	*Tantulacus* sp.8		1														1
27	*Tantulacus* sp.9														1		1
28	*Tantulacus* sp.10		1	1		1							1	1	1		6
29	*Tantulacus* sp.11							1									1
30	*Xenalytus scotophilus*				1					1			1		1	1	5
31	Basipodellidae sp.1		1					1									2
32	Deoterthridae sp.1												1				1
33	Deoterthridae sp.2												1				1
	n/station	2	6	3	17	3	1	4	7	2	7	8	9	1	9	2	81
	S/station	1	6	2	6	3	1	4	5	2	5	5	8	1	7	2	

Abbreviations: n/S, number of individuals per species; n/station, number of individuals per station; S/station; number of species per station

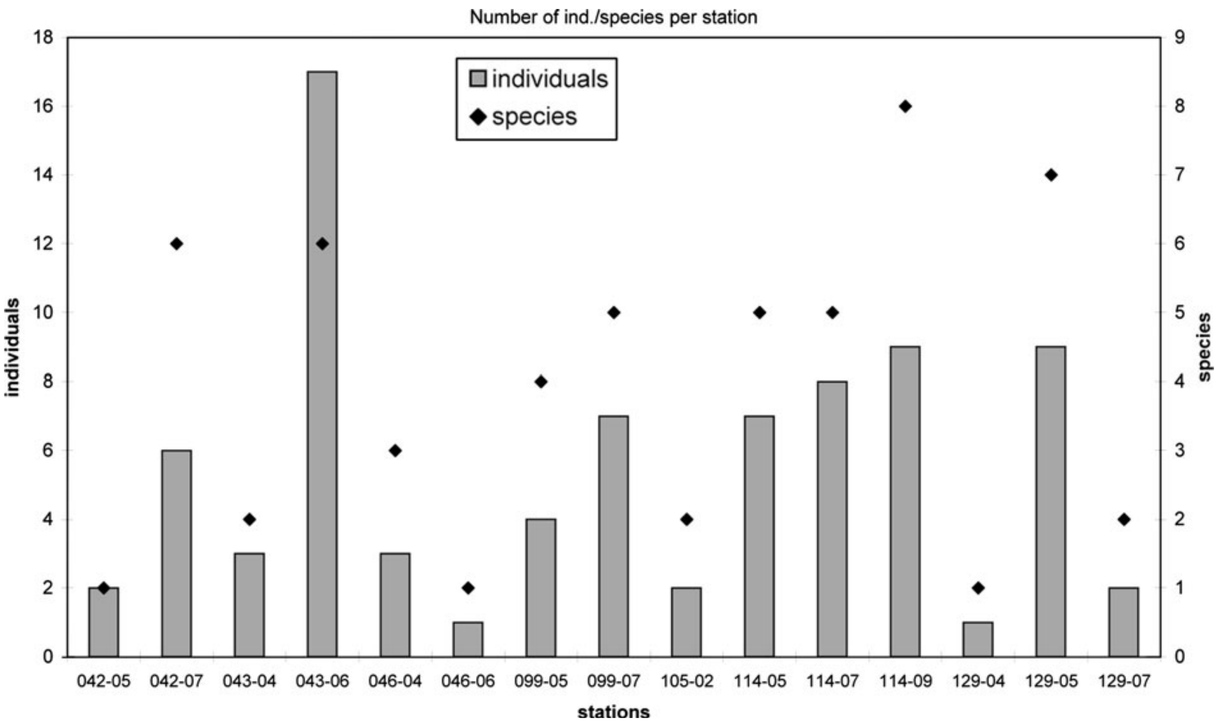

Fig. 13 Number of individuals/species per station sampled during ANT XIX/3

rudimentary setae. Moreover, there are variations in the protopodal structure: in *T. hoegi* the protopods are almost rectangular and ornamented with numerous minute spinous processes, whereas in *T. longispinosus*, *T. karolae* and *T. dieteri* the protopodal elements are more or less oval in shape and have little (*T. karolae*) or no ornamentation (*T. longispinosus* and *T. dieteri*).

The new species also differ in size, body ornamentation, morphology of the urosome and stylet structure. *T. karolae* and *T. dieteri* exhibit a total body length of about 80 µm. *T. longispinosus* resembles *T. hoegi* in size, with a body length of 130–150 µm. Exclusively in *T. hoegi*, the posterolateral angles of the cephalic shield are backwardly produced into spinous thin-walled extensions. Another major difference is represented by surface ornamentation especially in *T. karolae*, where epicuticular lamellae are an important aspect of its body ornamentation. The cephalic shield bears a great amount of ornamentation, consisting of several longitudinal lamellae connected by numerous transverse lamellae. Tergites 1–6 also exhibit several longitudinal and one transverse lamella extending over the dorsal mid-line. *T. longispinosus* has no cephalic or thoracic surface lamellae, whereas the ornamentation pattern of *T. hoegi* and *T. dieteri* is similiar. The cephalic shield of *T. hoegi* and *T.dieteri* bears several longitudinal surface lamellae dorsally, whereas transverse lamellae, clearly visible in *T. karolae,* are absent. *T. karolae* can also be distinguished from its congeners by the morphology of the abdominal somite, which is rectangular in shape and bears five transverse lamellae running around the somite. In *T. longispinosus*, *T. dieteri* and *T. hoegi,* the abdominal somite is more or less oval in shape and tapers towards the caudal rami. Ornamentation consisting of two transverse surface lamellae surrounding the whole somite is present in *T. hoegi* and *T. dieteri*, whereas *T. longispinosus* bears three transverse lamellae in the dorsal aspect only. In addition, there are differences in the posterior margin of the abdomen: in *T. karolae* the posterior margin bears two tiny spinous processes dorsally and four in the ventral aspect. In *T. hoegi* and *T. dieteri* there are paired combs consisting of several minute filaments at the ventral margin, whereas in *T. longispinosus* there is just a smooth protrusion on the dorsal side of the abdominal somite. The caudal setae are simple and similar in all congeners, but there are considerable differences in the length of the apical setae, particularly in *T. longispinosus*. The cephalic stylet is strongly curved towards its apex in all four congeners. According to the original description, lateral barbs are not apparent in the type-species, but a re-examination of *T. hoegi* revealed that the stylet base is provided with well-developed barbs in all representatives of this genus. The stylet tip is furnished with minute spinous processes and similar in all congeners. Further differences are displayed in the morphology and structure of the oral disc. For instance, *T. hoegi* and *T. dieteri* bear numerous microvilli at the posterior margin of the disc. Filaments originating from the lateral margin of the disc are much longer in the new species. Other differences between the congeners are observed in the pore pattern of the cephalic shield: *T. longispinosus* bears six, *T. karolae* nine, *T. dieteri* 14 and *T. hoegi* 11 pairs of pores. All species share the presence of the subdorsal D_{II} pores.

The new species undoubtedly belong to *Tantulacus*, displaying the only apomorphy of the genus, the modification of the inner seta into a spine on the endopod of legs 2–5. Moreover, the species resemble *T. hoegi* in having the ancestral number of five setae on exopods 4 and 5 and only a single seta on the endopod of the first thoracopod. There are now four species in *Tantulacus*, *T. hoegi*, *T. longispinosus* n. sp., *T. karolae* n. sp. and *T. dieteri* n. sp. The four species can be distinguished by means of the key presented below.

This is the first record of the genus *Tantulacus* in Antarctic sediments. First examination of material sampled during the DIVA 2 cruise on RV "Meteor" indicates that more species of this genus may be expected from the South Atlantic Ocean (Mohrbeck, personal observation).

Key to the species of *Tantulacus*

1 Thoracopod 1 with 2 setae plus 2 rudimentary setules on exopod; thoracopods 4–5 with 5 setae on exopod.. **2**

– Thoracopod 1 with 4 slender setae on exopod; thoracopods 3–5 with 5 setae on exopod. **3**

2 Endopodal spine of thoracopods 2–5 long and slender; cephalic shield without surface lamellae.................................*T. longispinosus*

– Endopodal spine of thoracopods 2–5 short and robust; cephalic shield with longitudinal surface lamellae; posterolateral angles of shield posteriorly produced into spinous extensions.… *T. hoegi*

3 Cephalic shield with longitudinal surface lamellae; abdominal somite more or less oval in shape, bearing 2 transverse lamellae............*T. dieteri*

– Cephalic shield with great amount of ornamentation consisting of several longitudinal lamellae connected by numerous transverse ones; abdominal somite rectangular in shape, bearing 5 transverse lamellae. ....*T. karolae*

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