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A new species of Tantulocarida (Crustacea) parasitic on a deep-water cumacean host from the southwestern Atlantic, with a review of tantulocaridan host utilization, distribution, and diversity

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ABSTRACT

Tantulocaridans (Class Tantulocarida) are primarily known to parasitize copepods, tanaidaceans, and isopods while only single species have been recorded from amphipod, ostracod, and cumacean hosts. Examination of a collection of deep-water peracarids from the Campos Basin off northeastern Brazil resulted in the discovery of a tantulus larva attached to a juvenile *Styloptocuma angustatum* (Jones, 1984) (Cumacea, Nannastacidae), representing a new species and only the fifth record for this host group. The new species is provisionally assigned to the genus *Aphotocentor* Huys, 1991 (Cumoniscidae) based on the proximally dilated terminal caudal ramus setae, the conspicuous polygonal surface ornamentation on the thoracic somites, the spinous processes around the posterior border of the abdomen, the dorsal abdominal surface pattern consisting of four continuous transverse lamellae, and the spinular ornamentation on the protopods of legs 2–6. The tantulus of *A. kolbasovi* **sp. nov.** is characterized by its large body size (175 μm), disproportionally long cephalic shield, the presence of paired papillae on the midventral surface of the cephalon, and the unique swimming leg setal formula, displaying the highest number of setation elements ever reported for leg 1. Except for the asymmetrically arranged median pores, the new species exhibits the full complement of cephalic pores, including the anterior pore A_V. Current classification, known stages, tantulus body length, and distribution of all valid tantulocaridan species are presented. Literature records of Tantulocarida, including host group/species and depth, as well as those based exclusively on tantulus stages from the temporary meiobenthos or unidentified stages from the meroplankton are summarized. The authenticity of recently reported tantulus larvae on the lysianassid amphipod *Lepidepecreella debroyeri* Schiaparelli, Alvaro, Kilgallen, Scinto & Lörz, 2015 from Terra Nova Bay (Ross Sea, Antarctica) is scrutinized. Tumour-like anomalies on the exoskeleton of planktonic copepods in the central Red Sea and around hydrothermal vent fluids off Taiwan have erroneously been attributed to tantulocaridan infections.

Key Words: Campos Basin, Cumoniscidae, false records, new species, *Styloptocuma angustatum*, taxonomy

SPECIAL ISSUE: CRUSTACEAN SYMBIOSES

INTRODUCTION

Tantulocaridans, together with epicaridean isopods, rhizocephalan barnacles, and nicothoid copepods, are marine parasitic crustaceans that exclusively utilize other crustaceans as hosts (Huys *et al.*, 2014). They can be regarded as non-conformists among Crustacea, deviating from the typical ontogenetic sequence, moulting cycle, and basic body plan. Unlike other crustaceans there is as yet no published substantiated evidence for moulting between the successive stages of their dual life cycle. Unpublished observations suggest that some tantuli develop inside an as yet undescribed naupliar instar but this has yet to be confirmed (see Martínez Arbizu, 2005). Attempts to homologize their highly specialized feeding apparatus with that of other crustaceans, including the cuticular stylet of the rhizocephalan kentrogon stage, proved largely futile (e.g., Høeg *et al.*, 2009; Ewers-Saucedo *et al.*, 2019; Petrunina *et al.*, 2019) and recent molecularly based analyses have remained inconclusive about their precise relationships with or within the Thecostraca (Petrunina *et al.*, 2014; Khodami *et al.*, 2017). All described tantulocaridan larvae lack antennules (a basic crustacean attribute), which only become expressed either as unsegmented appendages (female) or aesthetasc clusters (male) in the adults of the sexual cycle. Tantulocaridans have also repeatedly been dubbed as the smallest crustaceans known so far but this is not strictly true because the claim of extreme miniaturization has traditionally not been based on the adults but on the size of the tantulus larvae. Although some copepod nauplii are markedly inferior in size compared to these developmental stages (e.g., Rao, 1967; Dahms, 1990), the tantuli of most species, however, hold the position of pre-eminence of being the smallest segmented larvae known in Crustacea. The tantulus of *Serratotantulus chertoprudae* Savchenko & Kolbasov, 2009, parasitic on a canthocamptid harpacticoid host from the southern Indian Ocean, is currently the smallest one reported (76 µm!). Clearly, the evolution of such extreme miniaturized forms involves the breaking of constraints governed by traditional scaling laws (Minelli & Fusco, 2019). Adults of certain copepods can also be extremely small, such as members of the planktonic Oncaeidae (Cyclopoida) (170 µm; Shmeleva, 1979) or interstitial Paramesochridae (Harpacticoida) (217 µm; Wells, 1967), and it is conceivable that their early copepodids may approach this lower size limit for crustacean postnaupliar stages.

Prior to their recognition as a separate subclass of Crustacea (Boxshall & Lincoln, 1983), tantulocaridans were variously, but erroneously, classified as enigmatic members of epicaridean isopods (Bonnier, 1903; Greve, 1965), copepods (Hansen, 1913; Becker, 1975), and thecostracans (Bradford & Hewitt, 1980). Since then the group has seen the addition of numerous taxa, currently totalling 38 species in 23 genera and five families (Table 1). Most early species descriptions were based on tantulus larvae that had accidentally been discovered during routine examinations of their crustacean hosts. The second discovery phase was initiated by Huys (1989, 1991) who discovered free-living infective stages in sediment samples and considered them a component of the temporary meiofauna. Increased sampling efforts in deep sea environments during the last two decades (e.g., Ahnert & Schriever, 2001; George & Schminke, 2002; Gutzmann *et al.*, 2004; Hoste *et al.*, 2007; Mahatma, 2009; Kalogeropoulou *et al.*, 2010; Mohrbeck *et al.*, 2010; Büntzow, 2011; Veit-Köhler *et al.*, 2011; Guidi-Guilvard & Dallot, 2014; Martínez Arbizu & Petrunina, 2017; Pape *et al.*, 2017; Kersten *et al.*, 2019; Richter & George, 2019; Schmidt *et al.*, 2019) have not only unveiled an unprecedented diversity of free-living tantulus larvae but also their cosmopolitan distribution in all oceans, ranging from the Arctic (Huys *et al.*, 1997; Martínez Arbizu, 1997; Martínez Arbizu *et al.*, 1998; Kornev *et al.*, 2004; Hoste *et al.*, 2007; Kolbasov & Savchenko, 2010) to Antarctica (Grygier & Sieg, 1988, 1989; Herman & Dahms, 1992; Mohrbeck *et al.*, 2010; Veit-Köhler *et al.*, 2011; Rose *et al.*, 2015), including seamounts, abyssal plains, and hadal trenches (Table 2).

Crustaceans utilized by tantulocaridans primarily include copepods, tanaidaceans, and isopods, while single species have been reported from amphipod, ostracod and cumacean hosts (Table 2). A single specimen of a juvenile cumacean bearing a tantulocaridan on its right uropod was found whilst examining a collection of peracarids from the Campos Basin off northeastern Brazil. This specimen, a tantulus larva, is described as a new species of Cumoniscidae and represents the fifth record for this host group (Bonnier, 1903; Huys *et al.*, 1993a; O'Reilly, 2006; Cortes & Bolaño, 2017).

MATERIAL AND METHODS

The habitus and swimming legs were drawn from the whole holotype temporarily mounted in lactophenol under a supported coverslip that was subsequently sealed with transparent nail varnish. All drawings were prepared using a *camera lucida* on a Leica DMR (Leica Microsystems, Wetzlar, Germany) differential-interference contrast microscope. Body length was measured along the dorsal curvature in lateral aspect, from the anterior margin of the cephalon to the posterior margin of the caudal rami. The pore pattern nomenclature follows Boxshall & Vader (1993). Scale bars in Figures 1–3 are indicated in µm. The holotype was deposited in the collections of The Natural History Museum, London.

SYSTEMATICS

Class Tantulocarida Boxshall & Lincoln, 1983
Family Cumoniscidae Nierstrasz & Brender à Brandis, 1923
Genus *Aphotocentor* Huys, 1991
***Aphotocentor kolbasovi* sp. nov.**
(Figs. 1–3)

Type material: Holotype tantulus collected by dredging by the late Paulo S. Young on 14 December 2002; attached to the peduncle of the right uropod of a deep-water cumacean host (Fig. 1A). Mounted on a slide and deposited under registration NHMUK 2020.5350.

Type locality: Brazil, Campos Basin, 22°02′50.811″ S, 39°52′24.100″ W; 1,050 m depth; collected from the upper 2 cm of the muddy sediment.

Host: The cumacean host (Fig. 1) is provisionally identified as *Styloptocuma angustatum* (Jones, 1984) (Nannastacidae) on the basis of the presence of the fairly long pseudorostrum upturned at about 45°, the unarmed carapace (except for hair sensilla), the absence of serrations and spines on the pereon and pleon, and the relative proportions of the uropodal peduncles and rami (Jones, 1984). The specimen is slightly smaller (3.4 mm) than the adult female holotype (3.5 mm) described by Jones (1984). The last pair of pereopods is indicated by a ventral expansion (limb bud) on pereonite 5 (Fig. 1B), suggesting that the specimen is a manca II stage (Gerken & Martin, 2014).

Description of tantulus larva: Body consisting of cephalon covered by dorsal shield, 6 pedigerous somites and 2-segmented limbless urosome; body length 175 µm (Fig. 1B).

Cephalon (Fig. 2A, B; 3A) distinctly tapering towards anteriorly located oral disc; dorsal and lateral surfaces ornamented with 4 pairs of longitudinal epicuticular lamellae extending from posterior end of cephalon to base of oral disc; 2 additional pairs of shorter lamellae discernible in dorsal aspect, longest one extending to position of A_{III} pore; middorsal longitudinal lamella shortest, connected by short transverse ones; ventral surface of cephalon with pair of median papillae (Fig. 3A) and series of longitudinal surface ridges separated by fine reticulations. Cephalic shield about 1.6 times as long as maximum width (81 µm × 50 µm), representing 46% of total body length; posterolateral corners slightly produced, inrolled ventrally; posterior margin slightly sinuous in dorsal aspect. Oral disc about 28 µm in diameter, anteroventrally positioned; partly covered anteriorly by membranous extension of cephalon (Fig. 2B). Cephalon bearing 15 pairs of integumental pores; anterior zone with 5 pairs (A_{I-V}), posteriodorsal zone with 4 pairs (D_{I-IV}), lateral zone with 5 pairs (L_{I-V}); ventral surface with single pair of pores (V_I) at about halfway along shield length. Sensilla emerging from pores A_I, D_I L_I. Median pores (M) not observed. Cephalic stylet very thin, delicate; nearly straight except for curved base; 55 µm long; hollow at base. No other internal

Table 1. Current classification, known stages, body length (based on tantulus larva, in µm), and distribution of valid species of Tantulocarida. T, tantulus larva; P, parthenogenetic female; F, adult sexual female; f, sexual female at early stage of development; M, sexual male, either at an early stage of development or fully developed. [1] Type material re-examined by Lincoln & Boxshall (1983) and Huys (1990a); [2] originally described as *Austrotantulus lincolni* Boxshall, 1988; transferred by Huys (1990a), who redescribed the species; [3] Knudsen *et al.* (2009: fig. 17C) observed one attached sac-like individual containing a large mass of mostly undifferentiated tissue instead of developing eggs; the expression of what appears to be the presumptive abdomen suggests that they were dealing with a potential sexual female at an early stage of development; two additional individuals displaying a similar trunk sac with undifferentiated tissue inside (Knudsen *et al.*, 2009: fig. 16A, B) are most likely early stage parthenogenetic rather than developing sexual females; [4] type material re-examined by Boxshall & Lincoln (1983) and Huys *et al.* (1997); [5] re-examined by Boxshall & Lincoln (1987), Grygier & Sieg (1988), and Boxshall *et al.* (1989); [6] originally described as *Deoterthron aselloticola* Boxshall & Lincoln, 1983; transferred by Huys (1990a); [7] originally described as *Deoterthron megacephala* Lincoln & Boxshall, 1983; transferred by Huys (1990a); [8] originally described as *Deoterthron harrisoni* Boxshall & Lincoln, 1987; transferred by Huys (1990a).

Family/genus/species	Stages	Length	Distribution
Cumoniscidae Nierstrasz & Brender à Brandis, 1923			
Cumoniscus			
C. kruppi	T	100	Isle of Capri, Bay of Biscay
Deoterthron Bradford & Hewitt, 1980			
D. dentatum Bradford & Hewitt, 1980 [1]	T	135	NW of Chatham Island
D. lincolni (Boxshall, 1988) [2]	TM	113	Tasmania, Bass Strait
Boreotantulus Huys & Boxshall, 1988			
B. kunzi Huys & Boxshall, 1988	T	98	SW Sweden, Skagerrak
Dicrotrichura Huys, 1989			
D. tricincta Huys, 1989	T	83	Ligurian Sea
Campyloxiphos Huys, 1990a			
C. dineti Huys, 1990a	T	95	Cape Basin off Namibia
Coralliotantulus Huys, 1990b			
C. coomansi Huys, 1990b	TM	94	Great Barrier Reef
Aphotocentor Huys, 1991			
A. styx Huys, 1991	T	110	Ligurian Sea
A. kolbasovi **sp. nov**	T	175	Brazil, Campos Basin
Tantulacus Huys, Funch Andersen & Kristensen, 1992			
T. hoegi Huys, Funch Andersen & Kristensen, 1992	T	150	Faroe Bank
T. karolae Mohrbeck, Martínez Arbizu & Glatzel, 2010	T	85	Drake Passage
T. dieteri Mohrbeck, Martínez Arbizu & Glatzel, 2010	T	90	Drake Passage
T. longispinosus Mohrbeck, Martínez Arbizu & Glatzel, 2010	T	130	Drake Passage
T. coroniporus Martínez Arbizu & Petrunina, 2017	T	140	Argentinian abyssal plain
Itoitantulus Huys, Ohtsuka, Boxshall & Itô, 1992			
I. misophricola Huys, Ohtsuka, Boxshall & Itô, 1992	TPFM	156	Okinawa, Philippine Sea
Amphitantulus Boxshall & Vader, 1993			
A. harpiniacheres Boxshall & Vader, 1993	TPM	132	central northern North Sea
Arcticotantulus Kornev, Tchesunov & Rybnikov, 2004			
A. pertzovi Kornev, Tchesunov & Rybnikov, 2004	TPM	100	White Sea
A. kristenseni Knudsen, Kirkegaard & Olesen, 2009	TPfM [3]	147–192	E Greenland
Basipodellidae Boxshall & Lincoln, 1983			
Basipodella Becker, 1975			
B. harpacticola Becker, 1975 [4]	TPM	85	Peru-Chile (Atacama) Trench
B. atlantica Boxshall & Lincoln, 1983	P	?	SW of Azores
Stygotantulus Boxshall & Huys, 1989			
S. stocki Boxshall & Huys, 1989	TM	94	Canary Islands, Lanzarote
Nipponotantulus Huys, Ohtsuka, Boxshall & Itô, 1992			
N. heteroxenus Huys, Ohtsuka, Boxshall & Itô, 1992	TPM	82	Okinawa
Polynyapodella Huys, Møbjerg & Kristensen, 1997			
P. ambrosei Huys, Møbjerg & Kristensen, 1997	TPM	120	E Greenland
P. thieli Martínez Arbizu & Petrunina, 2017	T	115	Cape Verde abyssal plain
Rimitantulus Huys & Conroy-Dalton, 1997			
R. hirsutus Huys & Conroy-Dalton, 1997	TM	108	Galapagos Rift
Hypertantulus Ohtsuka & Boxshall, 1998			
H. siphonicola Ohtsuka & Boxshall, 1998	PFM	?	W Japan
Serratotantulus Savchenko & Kolbasov, 2009			
S. chertoprudae Savchenko & Kolbasov, 2009	T	76	Southern Indian Ocean
Microdajidae Boxshall & Lincoln, 1987			
Microdajus Greve, 1965			

Table 1. Continued

Family/genus/species	Stages	Length	Distribution
M. langi Greve, 1965 [5]	TPM	110–120	SW Norway, SW Sweden, W Scotland, Northern Ireland, E England, northern North Sea
M. gaelicus Boxshall & Lincoln, 1987	TP	120	Rockall Trough
M. pectinatus Boxshall, Huys & Lincoln, 1988	TM	94	Rockall Trough
M. aporosus Grygier & Sieg, 1988	M	?	Ross Sea, Drake Passage
M. tchesunovi Kolbasov & Savchenko, 2010	TPM	78	White Sea
Xenalytus Huys, 1991			
X. scotophilus Huys, 1991	T	98	Ligurian Sea, Drake Passage
Doryphallophoridae Huys, 1990a			
Doryphallophora Huys, 1990a			
D. aselloticola (Boxshall & Lincoln, 1983) [6]	T	149	Tasman Sea
D. megacephala (Lincoln & Boxshall, 1983) [7]	T	177	Tasman Sea, Drake Passage
D. harrisoni (Boxshall & Lincoln, 1987) [8]	TPM	130	Rockall Trough
Paradoryphallophora Ohtsuka & Boxshall, 1998			
P. inusitata Ohtsuka & Boxshall, 1998	PM	?	Kumano Trough
Onceroxenidae Huys, 1990a			
Onceroxenus Boxshall & Lincoln, 1987			
O. birdi Boxshall & Lincoln, 1987	TPM	100	Bay of Biscay
O. curtus Boxshall & Lincoln, 1987	P	?	NW of Ireland

structures preserved inside cephalon (Fig. 2A, B) except stylet and cuticular lining of anterior mouth tube.

Thoracic somites 1–6 (Fig. 2A, B) each provided with well-developed tergite and pair of thoracopods; becoming gradually narrower towards major body articulation with urosome. First tergite much narrower than others, largely concealed beneath posterior rim of cephalon; lacking surface ornamentation. Surface of tergites 2–6 with distinct polygonal ornamentation consisting of short longitudinal and transverse ridges; posterolateral angles rounded in lateral aspect (Fig. 2B).

Thoracopod 1 (Fig. 3D) with unsegmented protopod bearing medial endite with coupling spine and vestigial seta; anterior surface, outer margin with fine spinulation. Endopod relatively short; represented by digitiform segment, with proximal part swollen halfway along its length, distal part bifid apically, ending in spatulate process; outer margin with 2 basally inflated, fine setae. Exopod 2-segmented with both segments about equally wide; proximal segment without armature or ornamentation; distal segment with 2 strong (inner one spiniform and curved) and 2 fine terminal setae.

Thoracopod 2 (Fig. 3E) with unsegmented protopod bearing medial endite with coupling spine and vestigial seta; inner distal corner produced into pointed process; anterior surface, outer margin with fine spinulation. Endopod well developed, distinctly longer than in thoracopod 1; represented by digitiform segment, with proximal part swollen halfway along its length, distal part bifid apically, ending in spatulate process; outer margin with 2 fine setae halfway along the segment length. Exopod 2-segmented; proximal segment without armature or ornamentation; distal segment slightly wider than proximal one, with 2 strong and 2 fine terminal setae.

Thoracopods 3–5 (Fig. 3F) similar, with large, unsegmented, subrectangular protopod bearing medial endite with coupling spine and vestigial seta; inner distal corner produced into pointed process; anterior surface and outer margin with fine spinulation. Endopod 1-segmented, elongated, slender, distinctly more curved outwardly than in thoracopod 2; represented by digitiform segment, with proximal part slightly inflated, distal part bifid apically, ending in spatulate process; outer margin with 2 unequal, fine setae halfway along the segment. Exopod 2-segmented; proximal segment without armature or ornamentation; distal segment distinctly wider than proximal one, with 2 strong and 3 fine terminal setae.

Thoracopod 6 (Fig. 3G) uniramous, comprising single, subrectangular protopodal segment; lacking endite, but with 2 coupling spinules; row of fine spinules along medial margin; inner distal corner slightly attenuated; outer margin stepped, with 3 rows of fine spinules; with 2 basally fused long setae, inner seta shorter than outer, curved inwardly; common base of setae with few minute spinules.

Urosome (Figs 2; 3B, C) consisting of small seventh thoracic somite and large unsegmented abdomen; about 32 µm in length. Seventh thoracic somite tapering anteriorly, separated from preceding somite by distinct arthrodial membrane dorsally (Fig. 3C); with pair of longitudinal lamellae dorsolaterally, few connecting minor lamellae laterally. Abdomen longer than wide, 25 µm long; with 4 distinct, transverse lamellae, all of which continuous except for third being interrupted midventrally; dorsal, lateral, ventral surfaces with short longitudinal lamellae (Figs. 2; 3B, C), those in posterior third particularly prominent laterally, dorsally, each ending in small pointed processes on posterior abdominal border; ventral posterior margin with pair of larger spinous processes (Fig. 3B, C). Caudal rami small, each with short lateral seta (discrete at base) and 2 long composite setae apically (fused at base to ramus), consisting of short proximal, swollen, styliform part and long distal, setiform part.

Sexual adults and parthenogenetic female: Unknown.

Etymology: The new species is dedicated to Dr. Gregory A. Kolbasov (Moscow State University), mentor of the senior author, in recognition of his contributions to the taxonomy, morphology, and biology of Tantulocarida.

Nomenclatural statement: A life science identifier (LSID) number was obtained for the new species: urn:lsid:zoobank.org:pub:7FFE7CA2-712D-45A5-B464-F1719D94232C.

DISCUSSION

Tantulocarida on cumacean hosts

The most widely used classification of Tantulocarida (Huys, 1990a) recognizes five families, based on trunk sac formation during male development in addition to other characters, but recent contributions suggest that Cumoniscidae (formerly Deoterthridae; see Boyko & Boxshall, 2018), containing the

Table 2. Literature records of Tantulocarida, including host group/species and depth (in m). Records based exclusively on tantulus stages from the temporary meiobenthos or unidentified stages from the meroplankton are listed as "free-living" in chronological order. LP, lava pool; –, depth not specified. [1] Mature parthenogenetic female caught off La Réunion, probably belonging to Basipodellidae; [2] Huys *et al.* (1994) listed the host as an undescribed genus and species of Cyclopinidae (Cyclopininae). Martínez Arbizu (2001) identified the host as a member of his newly established family Psammocyclopinidae; [3] Kolbasov (2007, 2009) identified the hosts as *Bradya* sp. and *Pseudobradya* sp. Kornev & Tchesunov (2005) had previously reported this species from the White Sea but did not identify the host harpacticoid; [4] The host was originally identified as a member of the Cletodidae but the habitus SEM photograph provided by Savchenko & Kolbasov (2009: fig. 2A) shows that it belongs to the Canthocamptidae, most likely to the genus *Pyrocletodes* Coull, 1973; [5] Parthenogenetic female collected from the Kuril-Kamchatka Trench; [6] The host copepods were identified by Schriever in Grygier & Sieg (1988) which was overlooked by Boxshall & Lincoln (1983) who claimed that their examination revealed that the different host species represented at least two harpacticoid families. Depth data are from Becker (1979) for station 157 and Becker (1974) for station 179. Note that the depth given for this locality in Becker (1979) and Boxshall & Lincoln (1983) is wrong. Bradford & Hewitt (1980) erroneously stated that the host of this species was *Pseudomesochra minor* Becker, 1974; [7] The host was identified as *Stenhelia* sp. by Boxshall (1988) and as *Stenhelia* (*Delavalia*) sp. by Huys (1990a); [8] The hosts (with parthenogenetic females) were collected in the plankton with a multi(plankton)net at least 2,200 m from the bottom in the Kuril-Kamchatka Trench; [9] Developing male collected from the Kuril-Kamchatka Trench; [10] Kornev (2004) first recorded this species as an unidentified member of Basipodellidae on *Pseudobradya* sp. from 60–100 in Kandalaksha Bay (White Sea); [11] According to Huys *et al.* (1997) the conspecificity of the sexual female with the type material from Japan (Huys *et al.*, 1992b) requires confirmation; [12] Originally named as an undescribed species of *Haploniscus* by Lincoln & Boxshall (1983); the species name was revealed by Boxshall (1988) after its description by his co-author; [13] Originally named as an undescribed species of *Hydroniscus* by Boxshall & Lincoln (1983); the species name was revealed by Boxshall (1988) after its description by his co-author; [14] Collected in the Kuril-Kamchatka Trench; [15] Infested specimens in the collections of the Bergen Museum. The host was listed as *Leptognathia gracilis* (Krøyer, 1842); [16] Tantulus larva collected south of Jan Mayen, probably belonging to *Microdajus* sp.; [17] Originally identified as *Typhlotanais pulcher* Hansen, 1913; [18] Tantulus larva collected east of Iceland, probably belonging to *Microdajus* sp.; [19] This species was recorded by Kornev (2004) as *Microdajus* sp. on an unidentified tanaid at 60–100 m depth in the White Sea (Kandalaksha Bay); it was also reported as "a new species of Microdajidae" by Kolbasov (2007); [20] Collected in the Ligurian Sea and formally described by Huys (1989, 1991); [21] Collected in the Weddell Sea; [22] Collected in the Barents Sea; [23] Collected in the Laptev Sea along two depth transects (30–3,400 m); [24] Collected in the Peru Basin (DISCOL experiment site); see Vopel & Thiel (2001) for depth data; [25] Collected from the Great Meteor Seamount (see also George, 2001); see Pfannkuche *et al.* (2000) for depth data; [26] Collected in the Drake Passage between South America's Cape Horn and the South Shetland Islands of Antarctica; [27] Collected W of Svalbard (79° N, 4° E); [28] Collected in the Clarion Clipperton Fracture Zone; [29] Collected from the Porcupine Abyssal Plain, NE Atlantic; [30] Collected from the Seine Seamount, NE Atlantic; [31] Collected in the NE Atlantic at approximately 40° N, 26° W (near Azores); [32] Collected in the Southern Ocean at approximately 52° S, 0° E; [33] Collected in the Ligurian Sea (NW Mediterranean); [34] Collected in the N Atlantic (Iceland Basin, Irminger Basin, Norwegian Sea, Denmark Strait); [35] Captured by metabarcoding and DNA barcoding of individual larvae combined (i.e. total barcoding) and also detected by microscopy; material collected in the Clarion Clipperton Fracture Zone; [36] Collected from the Great Meteor Seamount.

Host group/(sub)order/species	Tantulocaridan species	Depth	Reference
AMPHIPODA			
Amphilochidea			
Harpinia antennaria Meinert, 1890	*Amphitantulus harpiniacheres*	80	Boxshall & Vader (1993)
		107	O'Reilly (2006)
COPEPODA			
Calanoida			
Paracyclopia sp.	*Nipponotantulus heteroxenus*	46–49	Huys *et al.* (1994)
Pseudocyclopia sp.	*Nipponotantulus heteroxenus*	46–49	Huys *et al.* (1994)
Pseudocyclopiidae sp. indet.	*Nipponotantulus heteroxenus*	46–49	Huys *et al.* (1994)
Canuelloida			
Canuellidae gen. et sp. indet.	*Stygotantulus stocki*	LP	Boxshall & Huys (1989)
Canuellidae gen. et sp. indet.	Tantulocarida sp. indet. [1]	4,050	Huys (1991)
Longipedia scotti Sars, 1903	*Coralliotantulus coomansi*	35	Huys (1990b)
Cyclopoida			
Psammocyclopinidae sp. [2]	*Nipponotantulus heteroxenus*	46–49	Huys *et al.* (1994)
Harpacticoida			
Amphiascus sp.	*Nipponotantulus heteroxenus*	46–49	Huys *et al.* (1994)
Argestoides prehensilis Huys & Conroy-Dalton, 1997	*Rimitantulus hirsutus*	2,494	Huys & Conroy-Dalton (1997)
Bradya sp.	*Arcticotantulus kristenseni*	100–200	Knudsen *et al.* (2009)
Bradya typica Boeck, 1873	*Arcticotantulus pertzovi*	25–50	Kolbasov *et al.* (2008), Petrunina & Kolbasov (2012), Petrunina *et al.* (2014, 2018) [3]
		40–90	Kornev & Chertoprud (2008)
Canthocamptidae gen. et sp. indet. [4]	*Serratotantulus chertoprudae*	3,121	Savchenko & Kolbasov (2009)
Cervinia sp.	*Polynyapodella ambrosei*	450	Huys *et al.* (1997)
Cerviniella sp.	Tantulocarida sp. indet. [5]	8,894–9,541	Petrunina *et al.* (2016)
Cylindropsyllus laevis Brady, 1880	*Boreotantulus kunzi*	20	Huys & Boxshall (1988)
Dahmsopottekina peruana (Becker, 1979)	*Basipodella harpacticola*	4,100	Becker (1975) [6]
Delavalia sp. [7]	*Deoterthron lincolni*	22	Boxshall (1988), Huys (1990a)
Metahuntemannia magniceps Becker, 1979 or *D. peruana*	*Basipodella harpacticola*	5,000	Becker (1975) [6]
Nudivorax sp.	Tantulocarida sp. indet. [8]	3,000–5,900	Petrunina *et al.* (2016)
Miraciidae sp. indet.	Tantulocarida sp. indet.	–	George (2001)

Table 2. Continued

Host group/(sub)order/species	Tantulocaridan species	Depth	Reference
Parameiropsis sp.	Tantulocarida sp. indet. [9]	7,135	Petrunina *et al.* (2016)
Paramesochridae gen. et sp. indet.	*Nipponotantulus heteroxenus*	46–49	Huys *et al.* (1994)
Peresime abyssalis Dinet, 1974	*Campyloxiphos dineti*	4,100	Huys (1990a)
Pseudobradya sp.	*Arcticotantulus pertzovi*	60	Kornev *et al.* (2004) [10]
Pseudobradya acuta Sars, 1904	*Arcticotantulus pertzovi*	25–50	Kolbasov *et al.* (2008), Petrunina & Kolbasov (2012), Petrunina *et al.* (2014) [3]
Robertgurneya sp.	Tantulocarida sp. indet.	–	Martínez Arbizu & Schminke (2000)
Stenocaris sp.	*Nipponotantulus heteroxenus*	46–49	Huys *et al.* (1994)
Styracothorax gladiator Huys, 1993	*Itoitantulus misophricola* [11]	2,050	Huys (1993), Huys *et al.* (1993b)
Syrticola intermedius Huys & Ohtsuka, 1993	*Nipponotantulus heteroxenus*	46–49	Huys & Ohtsuka (1993), Huys *et al.* (1994)
Tetragonicipitidae sp. indet. (? *Tetragoniceps*)	*Nipponotantulus heteroxenus*	46–49	Huys *et al.* (1994)
Tisbidae sp. indet.	*Basipodella atlantica*	~3,000	Boxshall & Lincoln (1983)
Unidentified tisbidimorph species	*Stygotantulus stocki*	LP	Boxshall & Huys (1989)
Family indeterminable	*Basipodella harpacticola*	4,100	Becker (1975) [6]
Misophrioida			
Misophriopsis okinawensis Ohtsuka, Huys, Boxshall & Itô, 1992	*Itoitantulus misophricola*	167	Huys *et al.* (1992b), Ohtsuka (1993)
Misophrioida sp. indet.	Tantulocarida sp. indet.	–	George (2001)
Siphonostomatoida			
Asteropontoides sp. indet.	*Hypertantulus siphonicola*	95	Ohtsuka & Boxshall (1998)
Asterocheridae spp. indet.	*Hypertantulus siphonicola*	128	Ohtsuka & Boxshall (1998)
Cumacea			
Leuconidae sp. indet.	*Cumoniscus kruppi*	1,000	Bonnier (1903), Lo Bianco (1903)
		306–307	Huys *et al.* (1993a)
Diastylis lucifera (Krøyer, 1837)	?*Cumoniscus kruppi*	–	O'Reilly (2006)
Eudorella sp.	Tantulocarida sp. indet.	2,786	Cortes & Bolaño (2017)
Styloptocuma angustatum (Jones, 1984)	*Aphotocentor kolbasovi* **sp. nov.**	1,050	present account
Isopoda			
Asellota			
Haploniscus tangaroae Lincoln, 1985 [12]	*Doryphallophora megacephala*	1,386	Lincoln & Boxshall (1983)
Hydroniscus lobocephalus Lincoln, 1985 [13]	*Doryphallophora aselloticola*	3,250–3,340	Boxshall & Lincoln (1983)
Macrostylis magnifica Wolff, 1962	*Doryphallophora harrisoni*	1,993–2,907	Boxshall & Lincoln (1987)
Haploniscidae spp. indet.	*Paradoryphallophora inusitata*	2,027–2,035	Ohtsuka & Boxshall (1998)
Macrostylidae sp. indet.	Tantulocarida sp. indet.	5,484–5,679	Petrunina *et al.* (2016) [14]
Ostracoda			
Myodocopida			
Metavargula mazeri Kornicker, 1979	*Deoterthron dentatum*	384	Bradford & Hewitt (1980)
Tanaidacea			
Tanaidomorpha			
Akanthophoreus gracilis (Krøyer, 1842)	*Microdajus langi*	–	Boxshall & Lincoln (1987) [15]
		7–64	O'Reilly (2006)
Anarthrura simplex Sars, 1882	*Microdajus langi*	120–130	Greve (1988)
Haplocope angusta Sars, 1882	*Microdajus langi*	120–130	Greve (1965)
Leptognathia zezinae Kudinova-Pasternak, 1973	*Onceroxenus curtus*	2,513–2,907	Boxshall & Lincoln (1987)
Leptognathia breviremis (Lilljeborg, 1864)	*Microdajus langi*	120–130	Greve (1965, 1988), Boxshall & Lincoln (1987)
		45–64	Grygier & Sieg (1988, 1989)
		120	Boxshall *et al.* (1989)
		–	Sieg (1986)
		–	Huys (1991)
	Tantulocarida sp. indet. [16]	1,834	Hansen (1913)
Leptognathiopsis attenuata Holdich & Bird, 1986	*Microdajus langi*	22	Boxshall & Lincoln (1987)
Meromonakantha macrocephala (Hansen, 1913)	*Microdajus aporosus*	568	Grygier & Sieg (1988, 1989)
Paranarthrura insignis Hansen, 1913	*Onceroxenus birdi*	2,187–4,190	Boxshall & Lincoln (1987)
Pulcherella pulcher (Hansen, 1913) [17]	*Microdajus gaelicus*	2,884–2,897	Boxshall & Lincoln (1987)

Table 2. Continued

Host group/(sub)order/species	Tantulocaridan species	Depth	Reference
Typhlotanais aequiremis (Lilljeborg, 1864)	*Microdajus langi*	120–130	Greve (1965), Boxshall & Lincoln (1987)
Typhlotanais variabilis (Hansen, 1913)	Tantulocarida sp. indet. [18]	1,372	Hansen, (1913)
Typhlotanais sp.	*Microdajus pectinatus*	2,175–2,540	Boxshall *et al.* (1989)
Typhlotanais sp.	*Microdajus tchesunovi* [19]	20–50	Kolbasov & Savchenko (2010), Petrunina & Kolbasov (2012), Petrunina et al. (2014, 2018)
Unidentified juvenile tanaid	*Microdajus langi*	113	Boxshall & Lincoln (1987)
FREE-LIVING			
Unknown	*Dicrotrichura tricincta*	1,220	Huys (1989)
Unknown	*Aphotocentor styx*	760	Huys (1991)
Unknown	*Xenalytus scotophilus*	160	Huys (1991)
Unknown	Tantulocarida sp. indet.	160–1,220	Soetaert *et al.* (1991) [20]
Unknown	Tantulocarida sp. indet.	339–1,958	Herman & Dahms (1992) [21]
Unknown	*Tantulacus hoegi*	260	Huys *et al.* (1992a)
Unknown	Tantulocarida sp. indet.	534	Martínez Arbizu (1997) [22]
Unknown	Tantulocarida sp. indet.	–	Martínez Arbizu *et al.* (1998) [23]
Unknown	Tantulocarida sp. indet.	4,040–4,170	Ahnert & Schriever (2001) [24]
Unknown	Tantulocarida sp. indet.	295–3,074	George & Schminke (2002) [25]
Unknown	Tantulocarida sp. indet.	2,875–5,194	Gutzmann *et al.* (2004) [26]
Unknown	Tantulocarida sp. indet.	1,200–5,500	Hoste *et al.* (2007) [27]
Unknown	Tantulocarida sp. indet.	4,877–5,042	Mahatma (2009) [28]
Unknown	Tantulocarida sp. indet.	4,850	Kalogeropoulou *et al.* (2010) [29]
Unknown	*Amphitantulus* sp.	3,650	Mohrbeck *et al.* (2010) [26]
Unknown	Basipodellidae sp.	3,650–5,190	Mohrbeck *et al.* (2010) [26]
Unknown	Deoterthridae sp. 1	2,875	Mohrbeck *et al.* (2010) [26]
Unknown	Deoterthridae sp. 2	2,875	Mohrbeck *et al.* (2010) [26]
Unknown	*Dicrotrichura* sp. 1	3,954–5,194	Mohrbeck *et al.* (2010) [26]
Unknown	*Dicrotrichura* sp. 2	2,893	Mohrbeck *et al.* (2010) [26]
Unknown	*Dicrotrichura* sp. 3	3,954	Mohrbeck *et al.* (2010) [26]
Unknown	*Doryphallophora megacephala*	5,194	Mohrbeck *et al.* (2010) [26]
Unknown	*Doryphallophora* sp. 1	3,650	Mohrbeck *et al.* (2010) [26]
Unknown	*Doryphallophora* sp. 2	2,289	Mohrbeck *et al.* (2010) [26]
Unknown	*Hypertantulus* sp. 1	3,954	Mohrbeck *et al.* (2010) [26]
Unknown	*Hypertantulus* sp. 2	5,190	Mohrbeck *et al.* (2010) [26]
Unknown	*Hypertantulus* sp. 3	2,900	Mohrbeck *et al.* (2010) [26]
Unknown	*Itoitantulus* sp. 1	3,954	Mohrbeck *et al.* (2010) [26]
Unknown	*Itoitantulus* sp. 2	2,875	Mohrbeck *et al.* (2010) [26]
Unknown	*Microdajus aporosus*	2,893–3,958	Mohrbeck *et al.* (2010) [26]
Unknown	*Microdajus* sp.	3,797	Mohrbeck *et al.* (2010) [26]
Unknown	*Paradoryphallophora* sp.	3,797	Mohrbeck *et al.* (2010) [26]
Unknown	*Tantulacus dieteri*	2,893	Mohrbeck *et al.* (2010) [26]
Unknown	*Tantulacus karolae*	3,614	Mohrbeck *et al.* (2010) [26]
Unknown	*Tantulacus longispinosus*	3,797–5,190	Mohrbeck *et al.* (2010) [26]
Unknown	*Tantulacus* sp. 1	2,875–3,954	Mohrbeck *et al.* (2010) [26]
Unknown	*Tantulacus* sp. 2	3,650–5,194	Mohrbeck *et al.* (2010) [26]
Unknown	*Tantulacus* sp. 3	5,194	Mohrbeck *et al.* (2010) [26]
Unknown	*Tantulacus* sp. 4	3,797	Mohrbeck *et al.* (2010) [26]
Unknown	*Tantulacus* sp. 5	2,875–2,917	Mohrbeck *et al.* (2010) [26]
Unknown	*Tantulacus* sp. 6	2,900	Mohrbeck *et al.* (2010) [26]
Unknown	*Tantulacus* sp. 7	2,875–2,917	Mohrbeck *et al.* (2010) [26]
Unknown	*Tantulacus* sp. 8	3,650	Mohrbeck *et al.* (2010) [26]
Unknown	*Tantulacus* sp. 9	3,797	Mohrbeck *et al.* (2010) [26]
Unknown	*Tantulacus* sp. 10	2,875–3,958	Mohrbeck *et al.* (2010) [26]
Unknown	*Tantulacus* sp. 11	5,190	Mohrbeck *et al.* (2010) [26]
Unknown	*Xenalytus scotophilus*	2,289–3,954	Mohrbeck *et al.* (2010) [26]
Unknown	Tantulocarida sp. indet.	210	Büntzow (2011) [30]

Table 2. Continued

Host group/(sub)order/species	Tantulocaridan species	Depth	Reference
Unknown	Tantulocarida sp. indet.	2,720–2,875	Büntzow (2011) [31]
Unknown	Tantulocarida sp. indet.	2,964–2,995	Veit-Köhler *et al.* (2011) [32]
Unknown	Tantulocarida sp. indet.	2,347	Guidi-Guilvard & Dallot (2014) [33]
Unknown	Tantulocarida sp. indet.	303–4,068	Rose *et al.* (2015) [21]
Unknown	*Tantulacus coroniporus*	5,726	Martínez Arbizu & Petrunina (2017)
Unknown	*Polynyapodella thieli*	5,102	Martínez Arbizu & Petrunina (2017)
Unknown	Tantulocarida sp. indet.	~4,500	Pape *et al.* (2017) [28]
Unknown	Tantulocarida sp. indet.	1,240–2,749	Ostmann & Martínez Arbizu (2018) [34]
Unknown	*Arcticotantulus* sp.	abyssal	Kersten *et al.* (2019) [35]
Unknown	Tantulocarida sp. indet.	–	Richter & George (2019) [36]
Unknown	Tantulocarida sp. indet.	–	Petrunina *et al.* (2019) [14]
Unknown	Tantulocarida sp. indet.	6,516–8,735	Schmidt *et al.* (2019) [14]

cumacean-associated type genus *Cumoniscus* Bonnier, 1903, and Basipodellidae are possibly paraphyletic or polyphyletic (Kolbasov *et al.*, 2008; Savchenko & Kolbasov, 2009; Petrunina & Kolbasov, 2012). Kolbasov *et al.* (2008) explicitly questioned the monophyly of the Cumoniscidae, recognizing that only three of its genera, *Cumoniscus*, *Deoterthron* Bradford & Hewitt, 1980, and *Amphitantulus* Boxshall & Vader, 1993, could be placed in a separate taxon. Although no supporting evidence was given for this claim it appears to be based (Kolbasov *et al.*, 2008: table on p. 1205) on the absence of "circular folds" (transverse surface lamellae) on the abdomen and the lack of "denticles" (although paired minute spinous processes have been reported for *D. lincolni* (Boxshall, 1988); see Huys, 1990a) along its dorsal posterior margin, both of which are characters of questionable phylogenetic significance.

Cumoniscus kruppi Bonnier, 1903 was first recognized as a tantulocaridan by Boxshall & Lincoln (1987) based on Bonnier's (1903) description of a parthenogenetic female from an unidenified leuconid cumacean in the vicinity of the island of Capri, Tyrrhenian Sea (western Mediterranean), and placed in Tantulocarida *incertae sedis*. The species was subsequently redescribed by Huys *et al.* (1993a) based on a newly collected damaged tantulus larva from the Bay of Biscay near Arcachon, France. The assumed conspecificity of both records was based solely on the identity of the host which represented a new genus of Leuconidae characterized by 3-segmented inner rami on the uropods. O'Reilly (2006) reported a developing male tantulus attached to the carapace of *Diastylis lucifera* (Krøyer, 1837) (Diastylidae) in the Minch on the northwestern coast of Scotland and tentatively identified it as ?*C. kruppi*; this identification was not based on morphological evidence but on the grounds that *C. kruppi* was the only species known at that time to utilize a cumacean host. Cortes & Bolaño (2017) recorded a male tantulus at an early stage of development on the carapace of an unidentified species of *Eudorella* Norman, 1867 (Leuconidae) collected at 2,786 m 85 km north of Barranquilla, Colombia; this species was not assigned to any family and placed in the *incertae sedis* category.

Huys *et al.* (1993a) assigned *Cumoniscus* to Deoterthridae (= Cumoniscidae), primarily on the basis of the morphology of the swimming legs and the absence of a rostrum. At that time *C. kruppi* differed from other members of the family by the arrangement of the cephalic pores, the presence of minute curved spinules along the inner margin of the endopods of legs 2–5, and the reduced armature of leg 6 (Huys *et al.*, 1993a). Our specimen from the Campos Basin differs from *C. kruppi* in all these characters, in addition to others, suggesting that it belongs to a different genus.

The systematics of Tantulocarida has traditionally been based on the morphology of the tantulus larva, and to a lesser extent host utilization, except in cases where the adult male at a late stage of development is known (e.g., Boxshall & Lincoln, 1987; Boxshall *et al.*, 1988; Boxshall & Huys, 1989; Huys, 1990b; Huys *et al.*, 1994, 1997; Ohtsuka & Boxshall, 1998; Kolbasov *et al.*, 2008; Knudsen *et al.*, 2009; Kolbasov & Savchenko, 2010). Since the formal recognition of the subclass in 1983, the great majority of the genera were typically established for single species on the basis of differences in larval characters such as the patterns of the cephalic pores and the armature of the swimming legs, and the surface ornamentation of the cephalic shield, pedigerous somites, and abdomen. In the absence of alternative testable evidence (e.g., adult morphology, molecular sequence data) this approach inevitably led to an inflation of taxa at the generic level and is reflected in the high number of monotypic genera (currently 15 out of 23; Table 1). Intrageneric variation in cephalic pore arrangement, body surface ornamentation, and/or thoracopodal armature has been documented since for various genera, including *Arcticotantulus* Kornev, Tchesunov & Rybnikov, 2004 (Kolbasov *et al.*, 2008; Knudsen *et al.*, 2009), *Polynyapodella* Huys, Møbjerg & Kristensen, 1997 (Huys *et al.*, 1997; Martínez Arbizu & Petrunina, 2017) and *Tantulacus* Huys, Funch Andersen & Kristensen, 1992 (Huys *et al.*, 1992a; Mohrbeck *et al.*, 2010; Martínez Arbizu & Petrunina, 2017), demonstrating the limitations of such characters for delimiting generic boundaries.

Aphotocentor kolbasovi **sp. nov**. has a unique swimming leg setal formula, displaying the highest number of setation elements ever reported for leg 1. The only other species possibly exhibiting two setae on the endopod of this leg is *Arcticotantulus kristenseni* Knudsen, Kirkegaard & Olesen, 2009 but this observation requires confirmation (Table 3). The cephalic shield of the new species is exceptionally large, representing 46% of the total body length. Similarly elongated cephalic shields have only been reported in a few members of Cumoniscidae, such as *Itoitantulus misophricola* Huys, Ohtsuka & Boxshall, 1992b (47% of the total body length), and the Doryphallophoridae, such as *Doryphallophora megacephala* (Lincoln & Boxshall, 1983) (51%), and *D. harrisoni* (Boxshall & Lincoln, 1987) (53%); however, the shape of these shields in dorsal aspect is distinctly different. The presence of paired papillae on the midventral surface of the cephalon has not been recorded before in tantulocaridan larvae. Except for the asymmetrically arranged median pores (M) observed on either side of the dorsal midline in some tantulocaridans (Huys *et al.*, 1992b, 1993a, b, 1997), the new species exhibits the full complement of cephalic pores, including the anterior pore (A_V), which has been observed previously in only *Cumoniscus kruppi*, *I. misophricola*, and *Nipponotantulus heteroxenus* Huys, Ohtsuka & Boxshall, 1994 (Huys *et al.*, 1993a,b, 1994). The new species exhibits conspicuous surface ornamentation on the pedigerous somites, consisting of a polygonal pattern

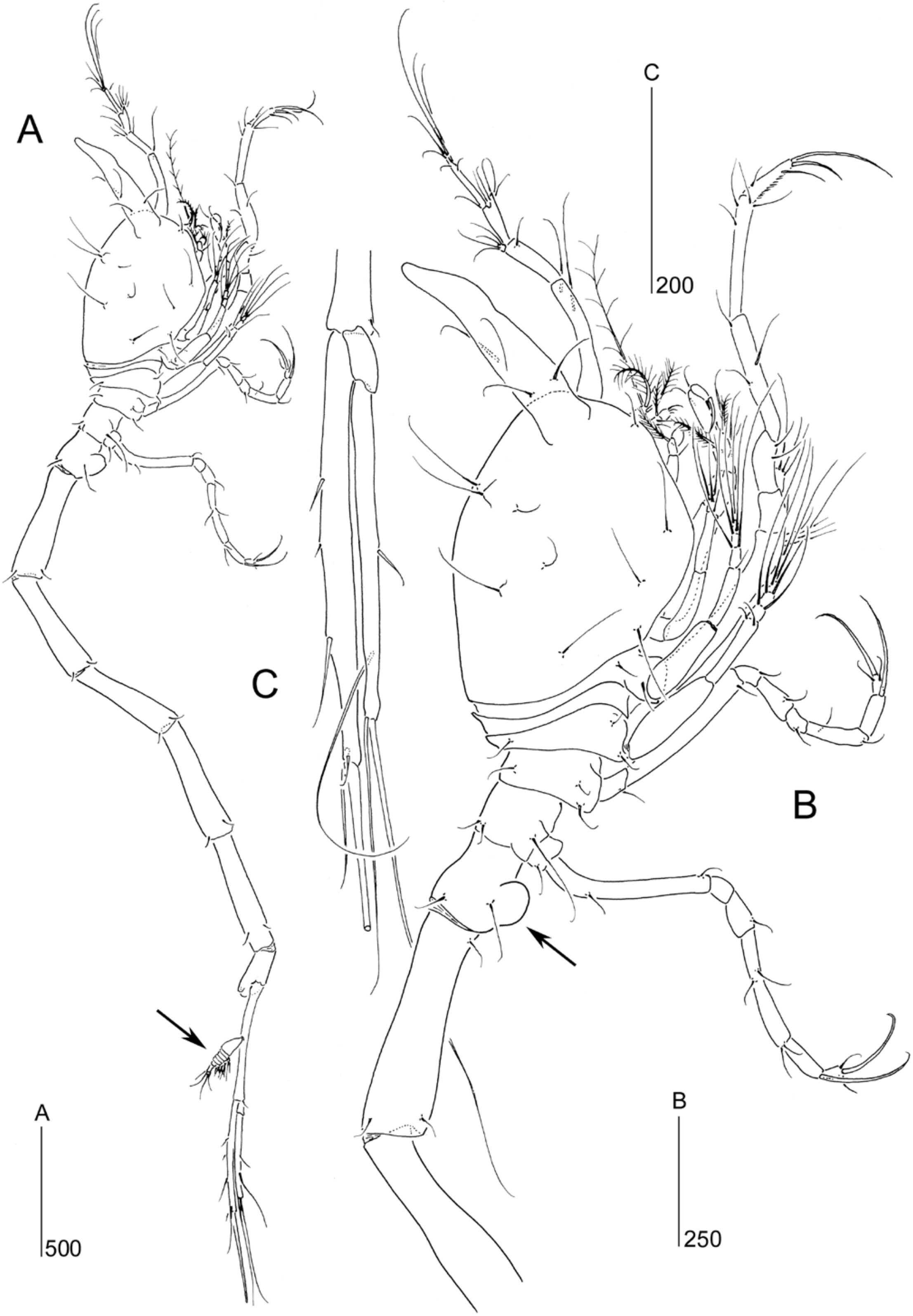

Figure 1. *Styloptocuma angustatum* (Jones, 1984), manca II stage. Habitus, lateral, with tantulus larva (indicated by arrow) attached to right uropod (**A**); close-up of cephalopereon, lateral (limb bud of pereopod 5 indicated by arrow) (**B**); right uropod, lateral (proximal two-thirds of peduncle omitted) (**C**).

of epicuticular lamellae. Similar thoracic ornamentation patterns have been recorded in *Basipodella* Becker, 1975 and *Hypertantulus* Ohtsuka & Boxshall, 1998 in Basipodellidae, *Boreotantulus* Huys & Boxshall, 1988, *Campyloxiphos* Huys, 1990a, b (Huys, 1990a), *Coralliotantulus* Huys, 1990a, b (Huys, 1990b) and *Aphotocentor* in Cumoniscidae, and some members of *Doryphallophora* Huys, 1990a, b (Huys, 1990a), *Arcticotantulus*, and *Tantulacus* (Table 3). The tantulus of *A. kolbasovi* is one of the largest larvae reported

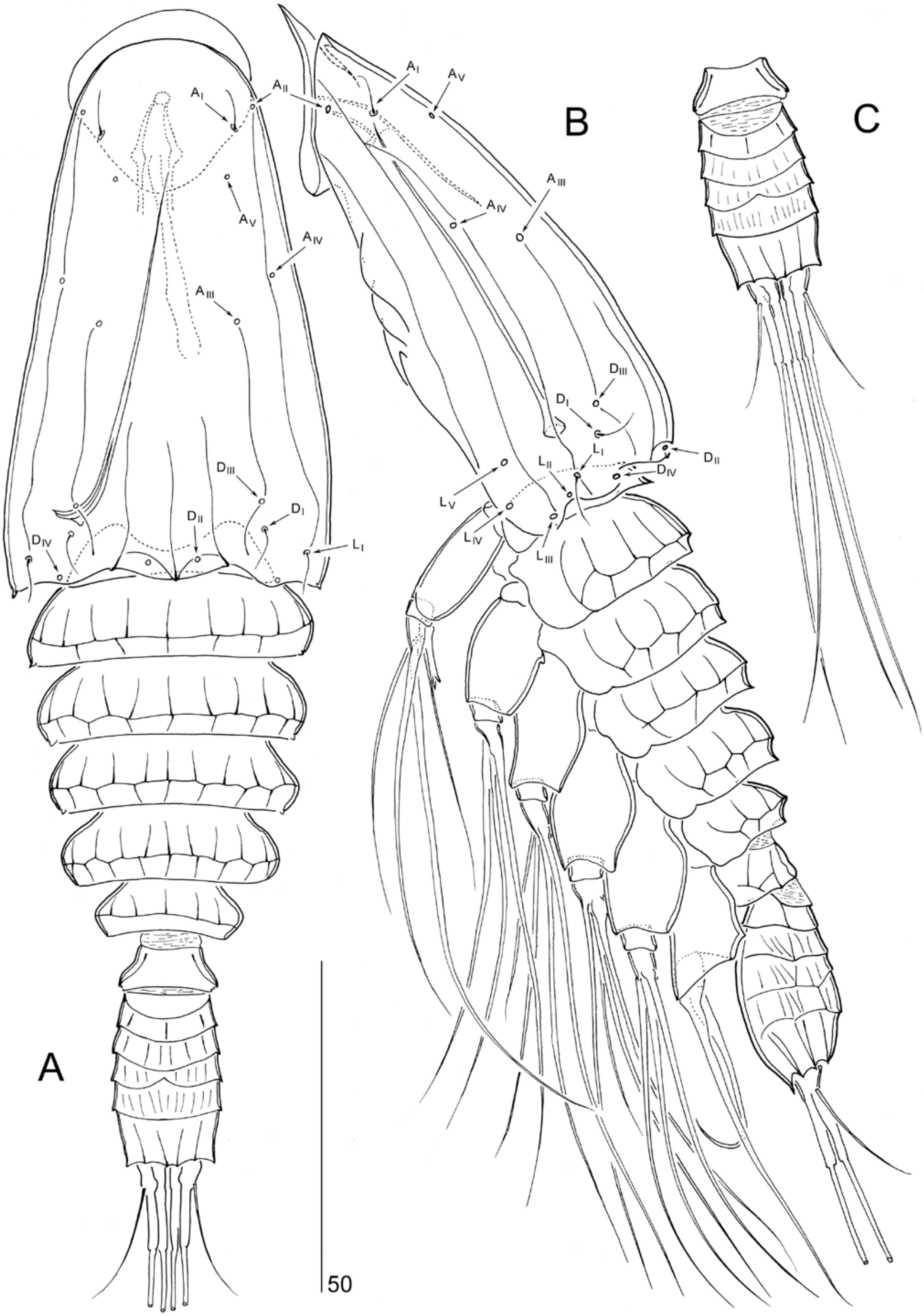

Figure 2. *Aphotocentor kolbasovi* **sp. nov.**, holotype tantulus larva. Habitus, dorsal (**A**), lateral (**B**); urosome with caudal ramus setae drawn at full length, dorsal (**C**). Cephalic stylet in A and B drawn in solid lines to highlight the delicate aspect of the structure. Cuticular lining of anterior mouth tube indicated by dotted lines. Pores indicated by arrows (A, anterior group; D, dorsal group; L, lateral group).

in Tantulocarida. Only the tantuli of *Doryphallophora megacephala* (177 μm), which parasitize an isopod host, and some larvae of *Arcticotantulus kristenseni*, reported from a harpacticoid copepod (147–192 μm), are known to have a larger body size.

Traditional taxonomic practice as previously employed to classify larval tantulocaridans would probably have placed *A. kolbasovi* **sp. nov** in a separate, new genus. Given the currently known range of intrageneric variation in some taxa we have elected to assign it

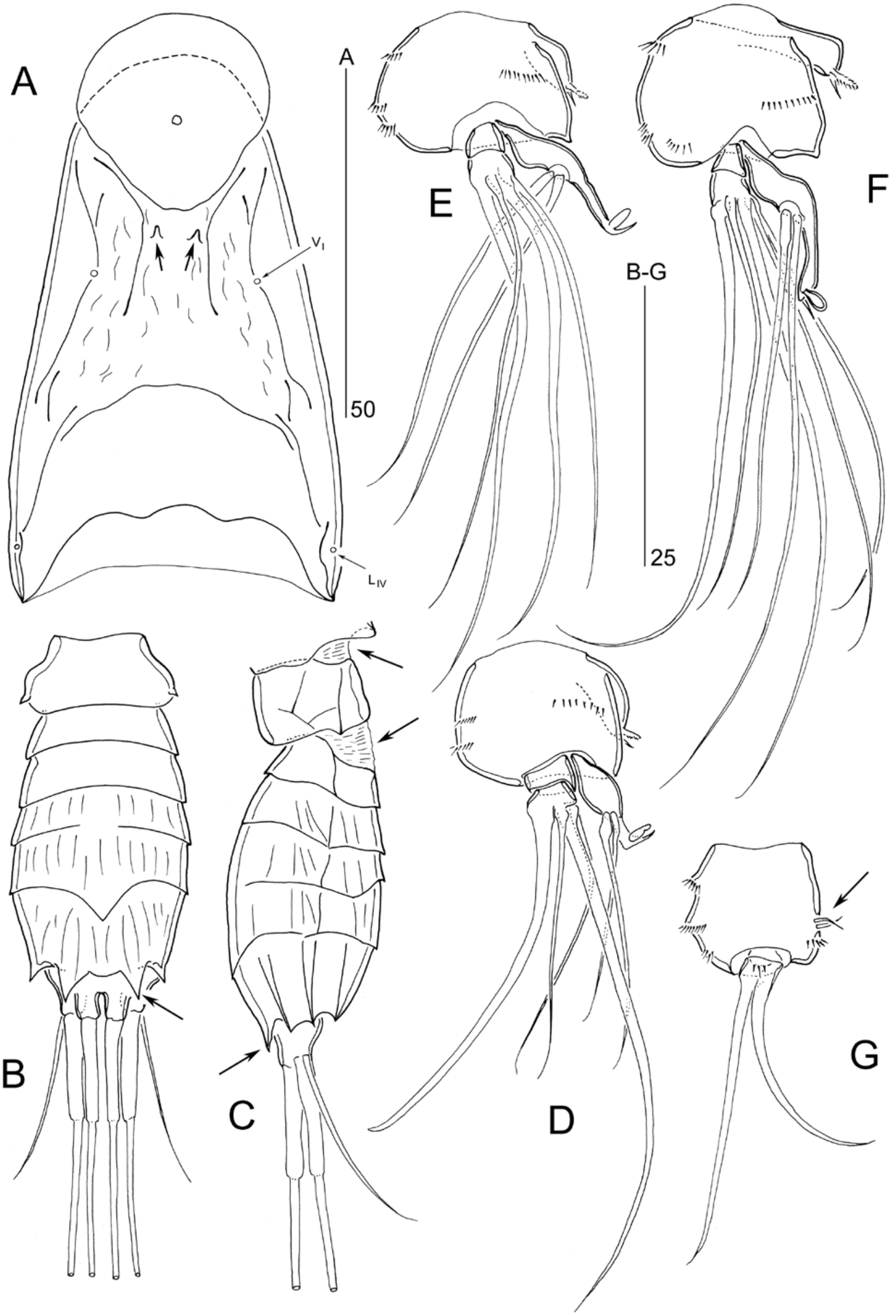

Figure 3. *Aphotocentor kolbasovi* **sp. nov.**, holotype tantulus larva. Cephalon, ventral (internal structures omitted; arrows indicating paired midventral papillae; V_I, ventral pore; L_{IV}, lateral pore) (**A**); urosome, ventral (arrow indicating ventral spinous process) (**B**); urosome, lateral (arrows indicating dorsal membranous inserts and ventral spinous process) (**C**); leg 1, anterior (**D**); leg 2, anterior (**E**); leg 3, anterior (**F**); leg 6, anterior (arrow indicating coupling spines) (**G**).

to an existing genus rather than establishing another monotypic one. The new species shows obvious similarities with *Aphotocentor styx* Huys, 1991, the type and only species of *Aphotocentor*, which was described from deep-sea mud samples taken in northwestern Calvi Bay (Corsica), Ligurian Sea (western Mediterranean). Both species share the proximally dilated setae of the terminal caudal ramus, the conspicuous polygonal surface ornamentation on the thoracic somites, small pointed dorsal processes and a large pair of ventral processes around the posterior border of the abdomen, the dorsal abdominal surface pattern consisting of four

Table 3. Swimming leg setation numbers (exopodal followed by endopodal) and presence/absence of polygonal thoracic surface ornamentation (TO) in members of Basipodellidae, Cumoniscidae, Doryphallophoridae and Onceroxenidae. Members of the Microdajidae have a strongly reduced leg armature and are consequently omitted. +, present; –, absent; ±, weakly developed or consisting of either only transverse or longitudinal lamellae. [1] There is some confusion over the correct setal numbers of legs 1 and 2. Knudsen *et al.* (2009) list four exopodal setae for leg 1 in their Table 4 but mention/illustrate only three in the text description (Knudsen *et al.*, 2009: 51) and in their Figure 5A. Their report of only one endopodal seta on leg 1 appears to be contradicted by their SEM photograph (Knudsen *et al.*, 2009: fig. 13C), which shows two confluent setae on the left endopod. *Arcticotantulus kristenseni* differs from all known tantulocaridans (except microdajid members) in possessing only one endopodal seta on leg 2; this requires confirmation as it may be based on an observational error.

	TO	Leg 1		Leg 2		Leg 3		Leg 4		Leg 5	
Basipodella harpacticola	+	2	0	4	2	4	2	4	2	4	2
Hypertantulus siphonicola	+	2	1	4	2	4	2	4	2	4	2
Nipponotantulus heteroxenus	–	2	0	3	2	3	2	4	2	4	2
Polynyapodella ambrosei	+	1	0	3	2	4	2	4	2	4	2
Polynyapodella thieli	±	1	0	3	2	4	2	4	2	4	2
Rimitantulus hirsutus	+	2	1	4	2	4	2	4	2	4	2
Serratotantulus chertoprudae	±	2	1	4	2	4	2	4	2	4	2
Stygotantulus stocki	±	2	1	4	2	4	2	4	2	4	2
Amphitantulus harpiniacheres	–	4	1	5	2	5	2	5	2	5	2
Aphotocentor kolbasovi **sp. nov.**	+	4	2	4	2	5	2	5	2	5	2
Aphotocentor styx	+	3	0	5	2	5	2	5	2	5	2
Arcticotantulus kristenseni [1]	+	3	1	4	1	4	2	4	2	4	2
Arcticotantulus pertzovi	±	4	0	4	2	4	2	4	2	4	2
Boreotantulus kunzi	+	3	1	2	2	2	2	2	2	2	2
Campyloxiphos dineti	+	2	0	4	2	4	2	4	2	4	2
Coralliotantulus coomansi	+	2	1	4	2	4	2	4	2	4	2
Cumoniscus kruppi	?	?	?	5	2	5	2	5	2	5	2
Deoterthron dentatum	–	2	1	5	2	5	2	5	2	5	2
Deoterthron lincolni	–	2	1	5	2	5	2	5	2	5	2
Dicrotrichura tricincta	–	2	0	3	2	4	2	4	2	4	2
Itoitantulus misophricola	±	2	0	4	2	4	2	4	2	5	2
Tantulacus coroniporus	+	4	1	5	2	5	2	5	2	5	2
Tantulacus dieteri	–	4	1	4	2	5	2	5	2	5	2
Tantulacus hoegi	–	4	1	4	2	4	2	5	2	5	2
Tantulacus karolae	+	4	1	4	2	5	2	5	2	5	2
Tantulacus longispinosus	–	4	1	4	2	4	2	5	2	5	2
Doryphallophora aselloticola	–	4	0	4	2	4	2	4	2	4	2
Doryphallophora harrisoni	+	4	1	4	2	4	2	4	2	4	2
Doryphallophora megacephala	–	4	1	4	2	4	2	4	2	4	2
Paradoryphallophora inusitata	–	4	1	4	2	4	2	4	2	4	2
Onceroxenus birdi	±	2	0	4	2	4	2	4	2	4	2

continuous transverse lamellae, and the spinular ornamentation on the protopods of legs 2–6. The two tiny spinules along the outer margin reported in *A. styx* proved upon re-examination of the type material to be spinular rows. The assignment of the new species to *Aphotocentor* is arbitrary and may have to be re-evaluated should a wider molecular sampling of tantulocaridans and new material (including adults) of the species become available. The latter can be differentiated from *A. styx* by the length and shape of the cephalic shield, the setal armature of legs 1 (4 exopodal and 2 endopodal *versus* 3 and 0) and 2 (4 exopodal *versus* 5), the ventral pattern of surface lamellae on the abdomen, the shape of the paired ventral processes around the posterior abdominal margin (spinous *versus* finely serrated), body size (175 *versus* 110 μm), and the relative length and robustness of the cephalic stylet.

The cumacean host of *A. kolbasovi* was originally described as *Cumella angustata* Jones, 1984 based on material collected off the coast of Recife, at 943–1007 m depth. Jones (1984) considered *Styloptocuma* Băcescu & Muradian, 1974 a junior subjective synonym of *Cumella* Sars, 1865. Watling (1991) concluded that the former could be a subgenus of the latter, while Holthuis (1992) subsequently accepted it as a valid genus (see also ICZN, 1994). The generic status of the name *Styloptocuma* now appears to have been generally recognised (Petrescu, 2000; Watling & Gerken, 2019). Except for the present record from 1,050 m depth in the Campos Basin, *Styloptocuma angustatum* has not been reported again since its original description (S. Gerken, personal communication).

Species diversity, distribution, and host utilization

Based on recent meiobenthic surveys it would be difficult to overstate the ubiquity and species diversity of tantulocaridans. They can be extremely abundant locally in deep-sea environments, both in terms of individuals and species. For example, Veit-Köhler *et al.* (2011) recorded a density of 119 ind.69.4 cm^{-2} at 2,965 m depth in the Southern Ocean and Mohrbeck *et al.* (2010) identified 33 putative species in 15 deep-water stations in the Drake Passage (Shackleton Fracture Zone) (Table 2). Tantulocaridans show an immense vertical distribution ranging from anchialine lava pools (Boxshall & Huys, 1989) and coral reefs (Huys, 1990b) to the deepest hadal depressions in excess of 9,500 m depth (Petrunina *et al.*, 2016) (Table 2).

Except for Cumoniscidae, which utilizes primarily copepods but also cumaceans, amphipods, and ostracods as hosts, species belonging to the same family typically seem to be restricted to a single host category (Table 2). Based on current data, most tantulocaridans appear to show a high level of host specificity. Notable exceptions are *Nipponotantulus heteroxenus* which has been reported from nine copepod hosts (Huys & Ohtsuka, 1993; Huys *et al*., 1994), *Microdajus langi* Greve, 1965 from six tanaid hosts (Greve, 1965, 1988; Sieg, 1986; Boxshall & Lincoln, 1987; Boxshall *et al*., 1989; Grygier & Sieg, 1988, 1989; Huys, 1991), and *Basipodella harpacticola* Becker, 1975 from three copepod hosts (Becker, 1975). Two members of Cumoniscidae, *Itoitantulus misophricola* and *Arcticotantulus pertzovi* Kornev, Tchesunov & Rybnikov, 2004, and two basipodellids, *Stygotantulus stocki* Boxshall & Huys, 1989 and *Hypertantulus siphonicola* Ohtsuka & Boxshall, 1998 are known from two copepod hosts each (Boxshall & Huys, 1989; Huys *et al*., 1992b, 1993b; Huys, 1993; Ohtsuka, 1993; Ohtsuka & Boxshall, 1998; Kornev *et al*., 2004). Most hosts are epibenthic or hyperbenthic living in a habitat where chance encounter is highest since it is probable that infection takes place at or around the sediment-water interface. Preliminary results of a more recent survey, however, reported harpacticoid copepods (Aegisthidae) parasitized by tantulocaridans (including parthenogenetic females) collected in the plankton at least 2,200 m from the bottom in the Kuril-Kamchatka Trench, northwestern Pacific (Petrunina *et al*., 2016).

False records of tantulocaridans

Schiaparelli *et al*. (2015) claimed to have found three tantulus larvae on the pleopods of the amphipod *Lepidepecreella debroyeri* Schiaparelli, Alvaro, Kilgallen, Scinto & Lörz, 2015 (Lysianassida, Lepidepecreellidae) collected from Terra Nova Bay (Ross Sea, Antarctica). This would have been only the third tantulocaridan record from an amphipod host (cf. Boxshall & Vader, 1993; O'Reilly, 2006); however, their SEM photograph (Schiaparelli *et al*., 2015: fig. 11c) shows several features indicating that they were dealing with a different group of ectoparasitic crustaceans. The body is distinctly flattened dorsoventrally and appears to consist of a cephalon (or possibly cephalothorax) and at least seven discrete somites. There is no evidence of an oral disc and the cephalon appears to possess a series of eight filamentous structures originating from the ventrolateral margin. The first six (thoracic?) somites each have paired elongated appendages, which are positioned laterally and therefore clearly discernible in dorsal aspect. A similar pair of appendages originates from the posterolateral corners of the head region, possibly indicating that the first pedigerous somite is incorporated to form a cephalothorax. Based on the scale bar provided by the authors, the larvae are at least 550 µm long which greatly exceeds the known size range of tantuli reported so far (76–192 µm) (Table 1). Disregarding the highly modified duplorbid Rhizocephala which live in the brood pouch of isopods and cumaceans (Høeg & Rybakov, 1992), the only other crustaceans that utilize peracarids as hosts are either members of Epicaridea (Isopoda), with some species belonging to the Podasconidae known to parasitize amphipods (Giard & Bonnier, 1895), or Nicothoidae (Copepoda), which includes two genera, *Rhizorhina* Hansen, 1892 and *Sphaeronella* Salensky, 1868, that contain species associated with amphipod hosts (Hansen, 1892, 1897). The larval stages of both groups, however, are radically divergent from the specimens of Schiaparelli *et al*. (2015). Although the latter superficially resemble some of the immature free-living forms of bathypelagic epicarideans reported from the Antarctic (Schultz, 1977), it is highly unlikely that they belong to this group (C. Boyko, personal communication).

Mantha *et al*. (2013) reported several tumour-like anomalies on the exoskeleton of planktonic cyclopoid copepods around hydrothermal vent fluids off northeastern Taiwan. Their speculation that the spiny protrusions observed on the exoskeleton of *Oncaea* spp. (Mantha *et al*., 2013: fig. 5D) probably represent tantulocaridan infections is entirely unfounded since tantulocaridans do not alter the external surface of the host. Al-Aidaroos & Mantha (2018) recorded similar morphological abnormalities on planktonic copepods in the central Red Sea, some of which they attributed to tantulocaridan infections. The protrusion illustrated on the prosome of *Labidocera* sp. (Al-Aidaroos & Mantha, 2018: fig. 4E), however, shows no evidence for such an origin.

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