Integrative and Comparative Biology Advance Access published May 22, 2009

Serratotantulus chertoprudae gen. et sp. n. (Crustacea, Tantulocarida, Basipodellidae): A new tantulocaridan from the abyssal depths of the Indian Ocean

Alexandra S Savchenko* and Gregory A Kolbasov[1,†]

*Department of Invertebrate Zoology, Faculty of Biology, Moscow State University, Moscow 119992, Russia;
†Department of Invertebrate Zoology, White Sea Biological Station, Faculty of Biology, Moscow State University, Moscow 119992, Russia

Synopsis A single tantulus larva was found at the abyssal depth of the Indian Ocean attached to a harpacticoid host of the family Cletodidae. It represents a new genus and species of Tantulocarida, family Basipodellidae. Its ultrastructure was studied with SEM. This genus can be easily distinguished from the other genera of Basipodellidae by the pore pattern, bilobed oral disk with strong longitudinal ridges and the posterior projection of the cephalic shield. A morphological analysis of two related families Basipodellidae and Deothertridae shows that they represent polyphyletic taxa and need further revision.

Introduction

Although tantulocaridans were discovered in the beginning of the 20th century, they were described as a separate class only in 1983 (Boxshall and Lincoln 1983). These smallest ectoparasitic crustaceans are characterized by lack of true molts typical of the other crustaceans and by a complex life cycle with both sexual and parthenogenetic phases (Huys et al. 1993). Currently the class Tantulocarida comprises about 30 species arranged into 20 genera and five families. They are ectoparasites of meiobenthic crustaceans such as Copepoda, Tanaidacea, Ostracoda, Cumacea, and Amphipoda. The free-swimming tantulus larva uses its oral disc to attach itself to the host and then pierces the host's integument with an unpaired stylet.

For a long time the phylogenetic position of Tantulocarida was in doubt. They were interpreted as isopods (Bonnier 1903; Greve 1965) and copepods (Hansen 1913; Becker 1975). Currently tantulocaridans are linked with Thecostraca on account of the presence of a median penis in the seventh trunk somite of the male and because of the position of the female's gonopore on the first thoracic somite (Boxshall and Lincoln 1987; Huys et al. 1993).

The phylogenetic relationships between tantulocridan families and genera are still unclear. Two main families Basipodellidae and Deoterthridae can not be distinguished based on their diagnoses; rather these families are paraphyletic (Kolbasov et al. 2008). Almost nothing is known about the internal anatomy of Tantulocarida. Due to their minute size more SEM and TEM investigations are needed to improve the accuracy of descriptions.

The collections of deep sea meiobenthic fauna held by the Zoological Institute of the Russian Academy of Sciences (St Petersburg) was examined and one specimen of tantulocaridan attached to its harpacticoid host was found. It belongs to a new genus and species of the family Basipodellidae. The holotype was investigated using SEM.

Material and methods

During a survey of the collections of the Zoological Institute (St Petersburg), a single tantulus larva was found attached to the abyssal harpacticoid host of the family Cletodidae. The host was fixed with 70% ethanol. The copepod specimen with the tantulus larva was mounted on a slide in glycerol and studied with an Olympus BX51 light compound microscope. For SEM investigation it was dehydrated in acetone and critical-point-dried in CO_2. The dried specimen was sputter-coated with gold and examined at 15 kV accelerating voltage with a HITACHI S405A in Moscow.

From the symposium "The Biology of the Parasitic Crustacea" presented at the annual meeting of the Society for Integrative and Comparative Biology, January 3–7, 2009, Boston, Massachusetts.
[1]E-mail: gakolbasov@gmail.com
Integrative and Comparative Biology, pp. 1–8
doi:10.1093/icb/icp023

Taxonomy

Class: Tantulocarida Boxshall and Lincoln, 1983
Family: Basipodellidae Boxshall and Linkoln, 1983
Genus: *Serratotantulus* Savchenko & Kolbasov gen. n.
Serratotantulus chertoprudae Savchenko & Kolbasov, new species (Figs. 1–4)

Material examined

One tantulus larva (holotype) on a harpacticoid host of the family Cletodidae (ca. 1.5-mm long, Fig. 2A), found by G. A. Kolbasov during a survey of the collections of the Zoological Institute (St Petersburg). Type locality: SRV 'Vityaz', 1959, Indian Ocean, st. 4645, (16° 09′S; 67° 32′E), 3121 m, silicious foraminiferan slit. The holotype, mounted on an SEM stub, is deposited in the Zoological Museum of Moscow State University (no. Mj. 1). A CD-ROM containing all the digital SEM photographs of the specimen has also been deposited there for permanent reference.

Diagnosis (based on tantulus larva)

Cephalic shield ornamented with two pairs of longitudinal lamella connected by numerous transverse lamellae, with tapering protrusion on the posteroir margin. Cephalic pore formula as follows: D_I, D_{IV}; L_I; A_{II}, A_{IV}, (probably D_{II}). Oral disk bilobed posteriorly, with a pair of strong anterior

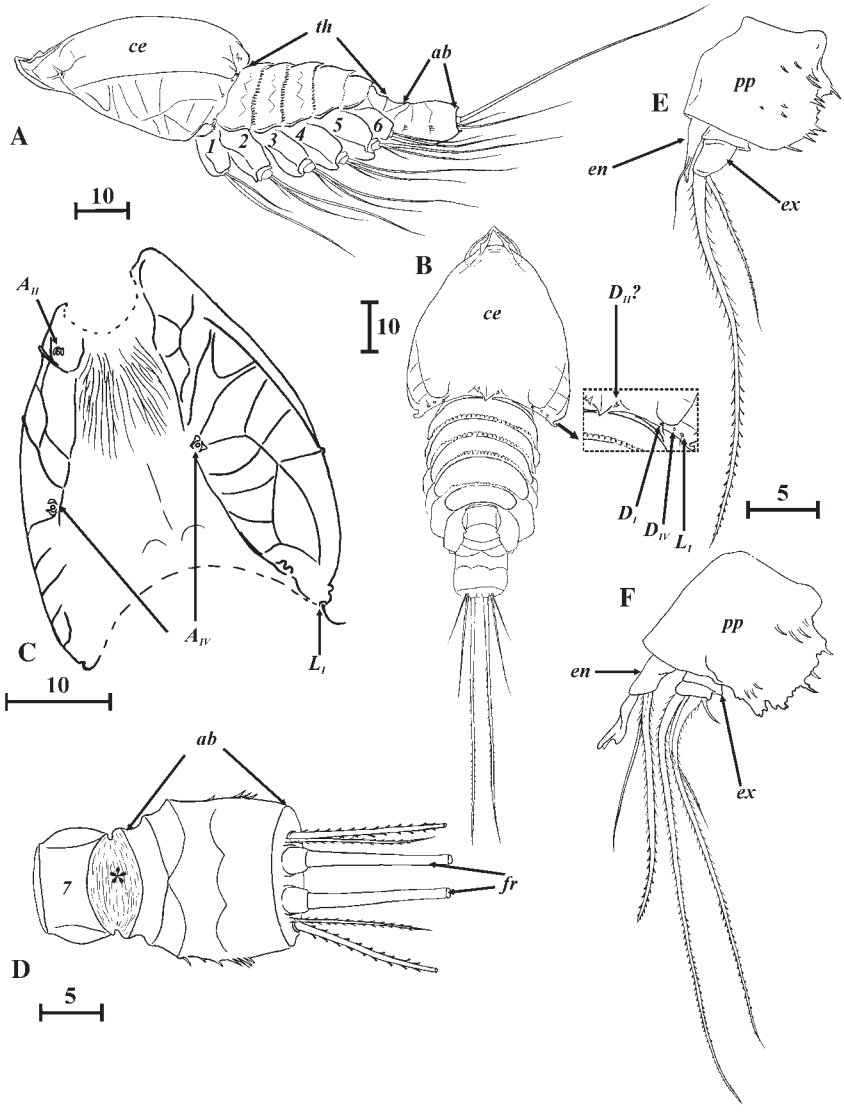

Fig. 1 General morphology of the tantulus of *Serratotantulus chertoprudae*. (**A**) Lateral view of tantulus (thoracopods numbered), (**B**)dorsal view of tantulus (enlarged) showing the distribution of pores, (**C**)ventro-lateral view of cephalon, (**D**) dorsal view of abdomen with furcal rami (articulation zone between abdomen and seventh somite "7" indicated by an asterisk), (**E** and **F**) Thoracopods I and II respectively. A_{II}, A_{IV}, D_I, D_{II}, D_{IV}; L_I, cephalic pores; *ab*, abdomen; *ce*, cephalon; *en*, endopod; *ex*, exopod; *fr*, furcal rami; *pp*, protopod; *th*, thorax. Scale bars in micrometer.

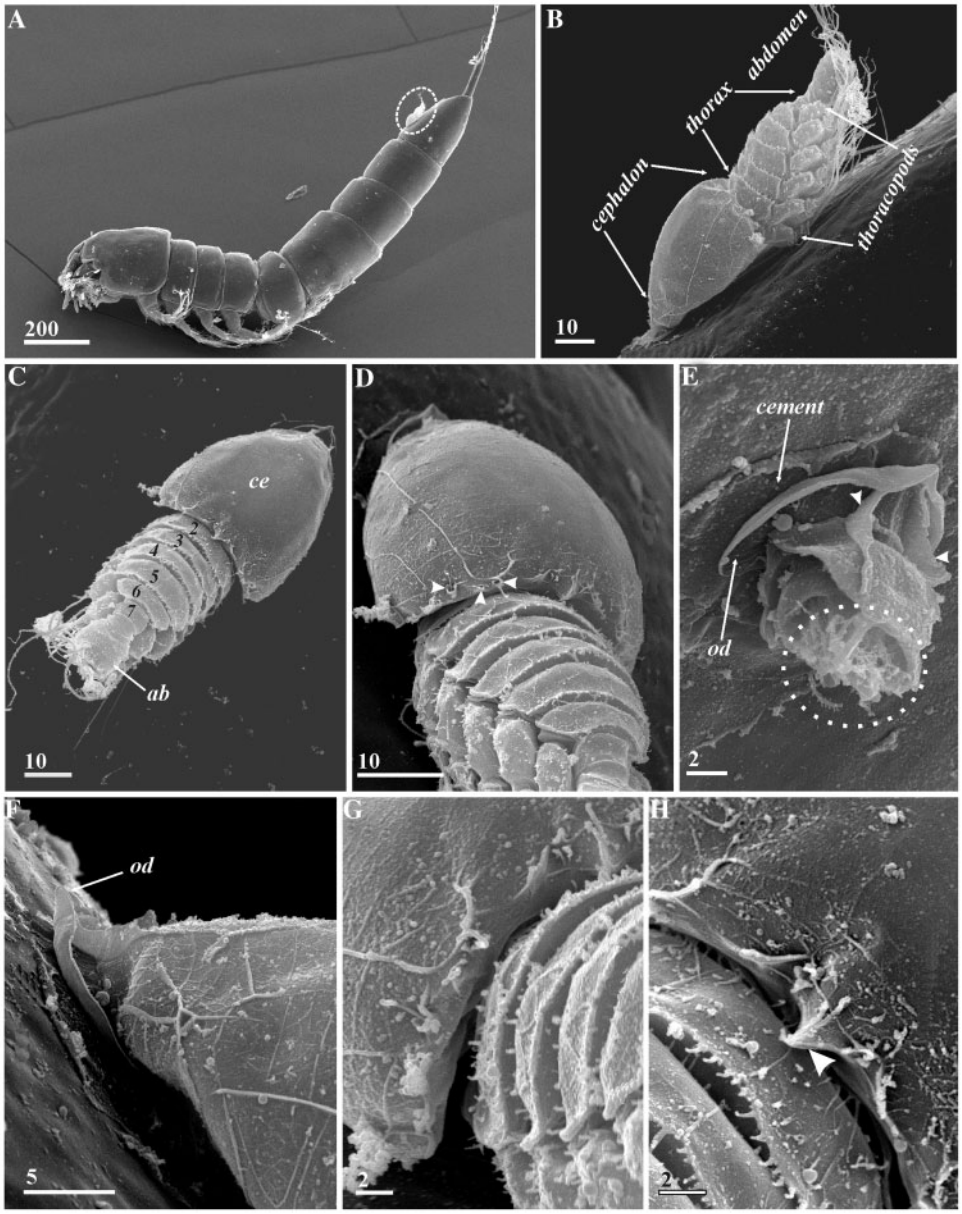

Fig. 2 External morphology of tantulus of *Serratotantulus chertoprudae*. (**A**) Host with attached tantulus (indicated by dotted oval line), lateral view, (**B**) lateral view of tantulus, (**C**) dorsal view of tantulus (thoracic tergites numbered), (**D**) dorsolateral view of cephalon and thorax (posterior cephalic pores indicated by arrowheads), (**E**) dorsolateral view of oral disk (body of tantulus removed; anterior cuticular ridges indicated by arrowheads, area indicated by dotted outline detailed in Fig. 3E), (**F**) lateral view of anterior part of cephalon with oral disk, (**G**) posterior–lateral part of cephalon, (**H**) tapering medial projection (indicated by arrowhead) on the dorsal side of the posterior margin of the cephalon. *ab*, abdomen; *ce*, cephalon; *od*, oral disk. Scale bars in micrometer.

longitudinal ridges. Thoracopod 1: endopod with subterminal seta, exopod distinctly two-segmented, with two terminal setae. Thoracopods 2–5 with endopod bearing two subterminal setae; exopod with three terminal and one small subterminal setae. Thoracopod six uniramous, presumably with two terminal setae. All thoracopodal and furcal setae with distinct long denticules in proximal and small pustulate/wart-shaped denticules in distal parts. Abdomen with three transverse lamellae and two tooth-like bifid projections on the ventral margin. Furcal rami with strong terminal seta and two lateral setae near the base of each ramus. Host—harpacticoid copepod of the family Cletodidae. Monotypic, type species *S. chertoprudae*.

Etymology

The generic name is composed from *serrate*, referring to setae with denticules of thoracopods and furcal

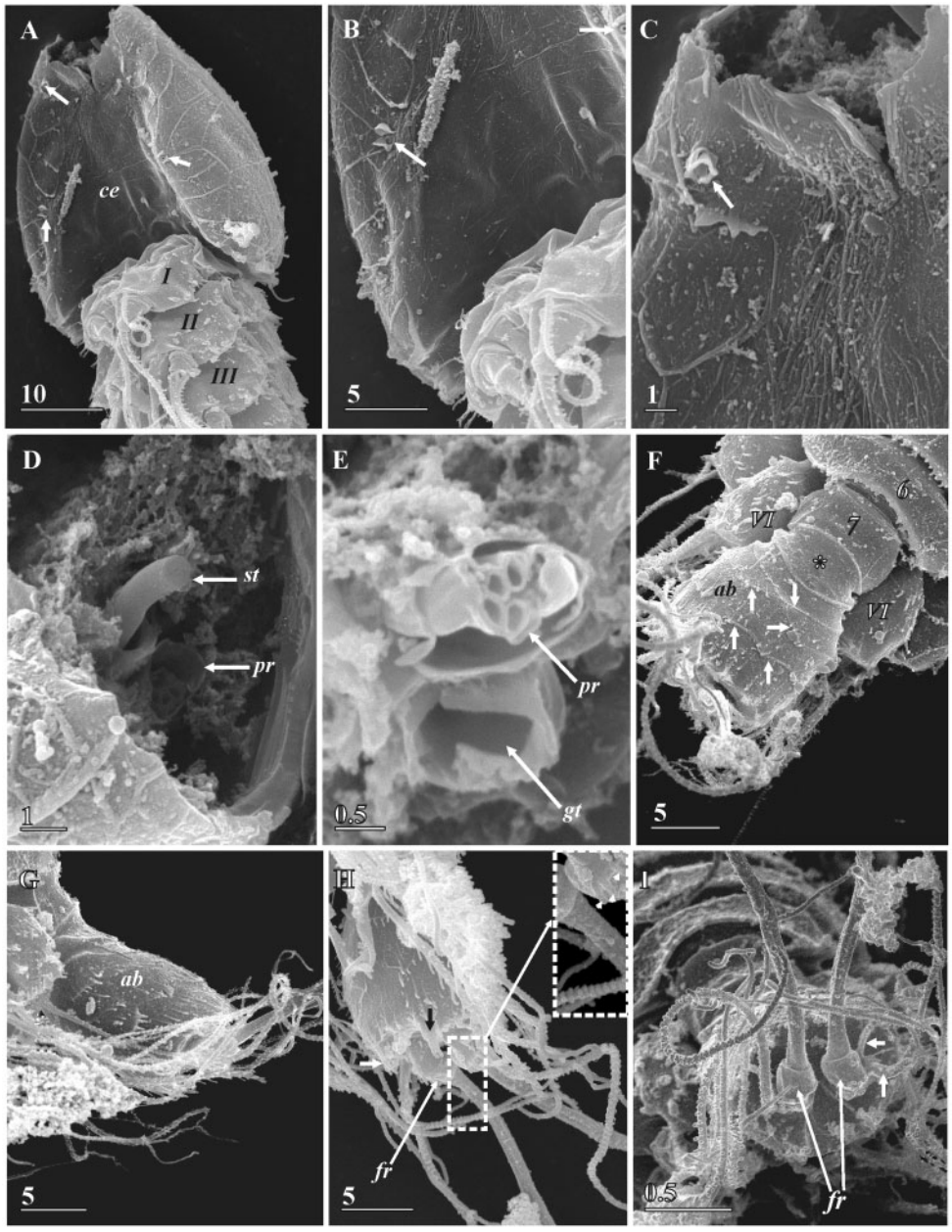

Fig. 3 External morphology of tantulus of *Serratotantulus chertoprudae* (cephalon, abdomen, and furcal rami). (**A**) Ventral view of cephalon and anterior part of thorax (oral disk remains attached to host; cephalic pores indicated by arrows; thoracopods numbered), (**B**) pores (indicated by arrows) on ventro-lateral surface of the posterior part of the cephalon, (**C**) pore (indicated by arrow) on the anterior end of the ventro-lateral surface of the cephalon, (**D**) solid tip of stylet and broken proboscis within the anterior portion of the cephalon, (**E**) proboscis with four tubular canals inside; cuticle of gut, within anteriormost portion of the cephalon, attached to the host by the oral disk (enlarged from 2E, indicated by dotted outline), (**F**) dorsal view (articulation zone between abdomen and seventh somite indicated by asterisk) of posteriormost tergites (Arabic numerals), sixth thoracopods (Roman numerals), and abdomen (three cuticular lamellae indicated by arrows), (**G**) lateral view of abdomen, (**H**) ventro-lateral view of abdomen with furcal rami (two tooth-like processes on ventral margin indicated by short arrows), rectangular area contains enlarged parts of furcal ramus with three small basal denticles (indicated by arrowheads) and seta with small postulate denticules, (**I**) furcal rami inserted onto the posterior end of the abdomen (two setae at the base of the furcal ramus indicated by short arrows). *ab*, abdomen; *ce*, cephalon; *fr*, furcal rami; *gt*, gut (cuticle); *pr*, proboscis, *st*, stylet. Scale bars in micrometer.

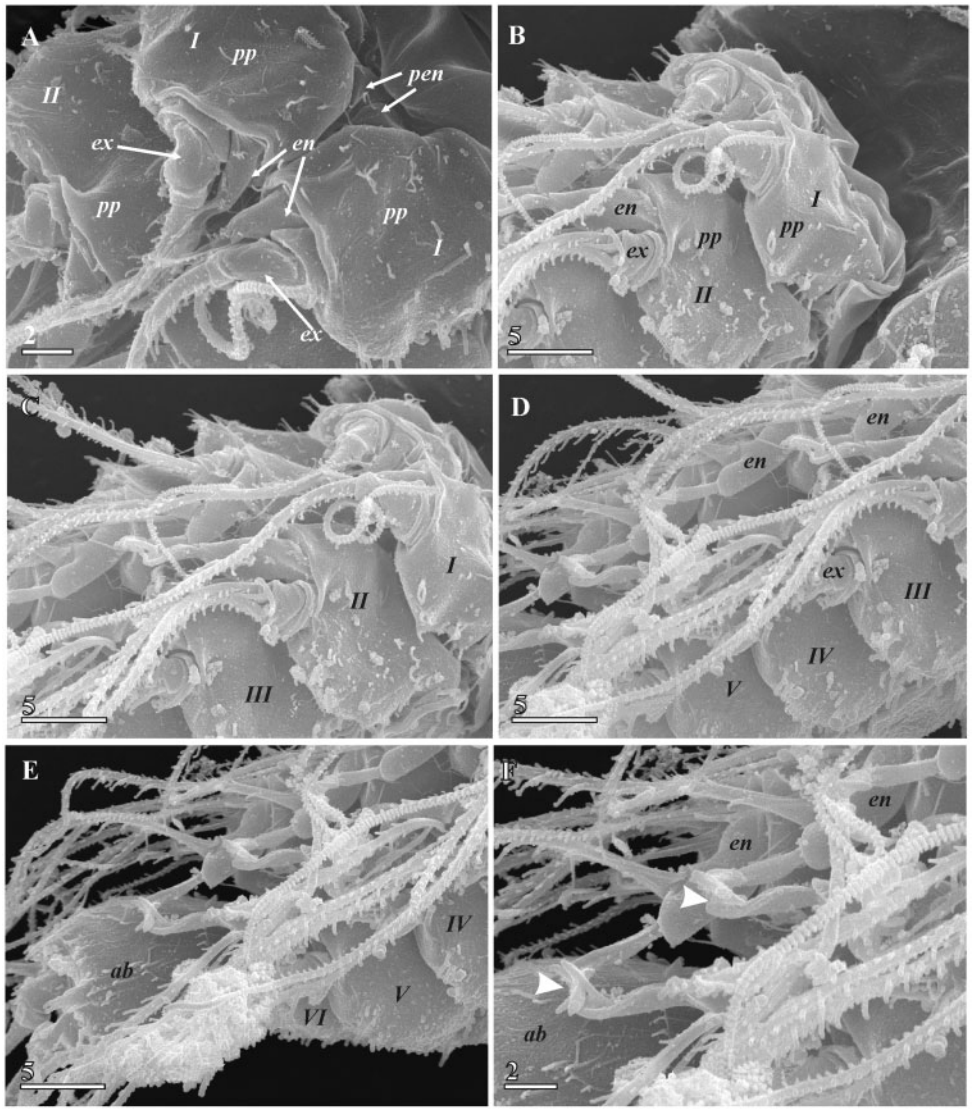

Fig. 4 Thoracopods and abdomen of tantulus of *Serratotantulus chertoprudae*. (**A** and **B**) Ventral and ventro-lateral view of Thoracopods I, II, (**C**) Thoracopods I–III, (**D**) ventro-lateral view of Thoracopods III–V, (**E**) venro-lateral view of Thoracopods IV–VI and abdomen, (**F**) joined distal forks of endopods IV and V (indicated by arrowheads). *ab*, abdomen; *en*, endopod; *ex*, exopod; *pen*, proximal endites; *pp*, protopod. Scale bars in micrometer.

rami and *tantulus*, which forms part of the name of the class Tantulocarida.

Description

Tantulus larva

Body comprising cephalon and six pedigerous thoracic somites, one limbless somite and unsegmented abdomen. Body length without furcal setae about 76 µm. Cephalon triangular tapering towards the anterior margin. It is only slightly longer than wide (l = 35.3 µm, w = 36.6 µm). Posterior margin of cephalon with tapering medial projection on the dorsal side (Figs. 1B and 2H). Posterolateral angles are curved towards the anterior side in dorsal view.

Cephalic shield is ornamented only with two pairs of longitudinal and about 18 pairs of tiny, irregular transverse lamellae running on the sides (Figs. 1A–C, 2D and E). The proximal lamella in its posterior part turns backwards, forming a semicircle; dorsal medial lamella absent (Figs. 1B and 2B–D). Triangular cuticular structure resembling a pore border, but with no pore inside, is observed in the anterior part of the shield right above the oral disk on the lateral side. It is formed as the junction of two transverse and longitudinal lamellae (Fig. 2E)

The cephalic pore formula is D_I, D_{IV}; L_I; A_{II}, A_{IV}. Two pairs of dorsal and one pair of lateral pores are arranged along the posterior edge of the shield (Figs. 1B, 2D and G). The outermost (L_I) and

innermost (D_I) contain small setae. A pair of trilobed cuticular flaps are situated near the medial projection of the posterior margin (Figs. 1B and 2H). No obvious pores (D_{II} pores) are seen inside these petal-like structures. The ventro-lateral surface with two pairs of pores in the central (A_{IV}) and anterior (A_{II}) parts (Figs. 1C, 3A–C). They are surrounded by petal-like cuticular flaps. The ventral surface has neither pores nor lamellae, but bears numerous longitudinal striations anteriorly (Figs. 1C and 3A). The oral disk tapers anteriorly with two strong longitudinal ridges >2 μm high that continue onto the cephalon and have a transverse lamella between them (Figs. 2E and F). The posterior margin of the disk is bilobed, with lateral margins recurved upwards (Figs. 2E and F). The anterior part of the stylet is solid and ~0.77 μm in diameter, surrounded by the gut (Fig. 3D). A funnel-shaped organ/proboscis (1.3 μm in diameter) with four glandular tubes inside is situated above the cephalic stylet (Fig. 3D and E).

Thoracic somites 1–6 with well-developed tergites and paired thoracopods. Only five tergites of thoracic somites could be seen dorsally because the first one is totally hidden under the cephalic shield (Figs. 1A, B and 2B–D). The surface of tergites 2–5 is ornamented with certain pattern of tiny oblique lamellae, their posterior margins serrate.

Protopods of thoracopods are expanded, with sharp denticles along the outer margins (Figs. 1E–F and 4). The proximal endites of the protopods are hidden, and only their basal parts were observed for thoracopod 1 (Fig. 4A).

The endopod of thoracopod 1 is unsegmented, shorter than the exopod and has at least one subterminal seta (Figs. 1E, 4A and B). The exopod of thoracopod 1 is two-segmented, with a very short unarmed proximal segment; the distal segment has two unequal terminal setae (Figs. 1E and 4A–C). The endopods of Thoracopods 2–5 are unsegmented, elongated, with two unequal subterminal setae and one movable terminal process terminating in a modified fork-like tip which allows endopods to cling together (Figs. 1F and 4C–F). Exopods 2–5 are two-segmented, with short unarmed proximal segments, distal segments with three apical setae and one tiny seta on the outer margin (Figs. 1F and 4B–D). Thoracopod 6 could not be entirely observed but from the lateral and dorsal views, it has protopod and exopod with at least two simple apical setae (Fig. 3F and G). All the thoracopodal setae except the smaller ones of endopodites 2–5 are omniserrate. Denticules become shorter and more pustulate towards the distal part of seta (Fig. 3H).

Urosome consists of a small, limbless seventh somite, which is two times wider than long (7.7–3.8 μm) and an unsegmented abdomen. These are connected by a broad articulate cuticular membrane (Figs. 1D and 3F). The seventh somite with two longitudinal lamellae running laterally on the dorsal side (Figs. 1D and 3F). The abdomen is nearly quadrate (11–10.8 μm); its dorsal surface is ornamented with three irregular, transverse lamellae (Figs. 1D, 3F and G). Both lateral and ventral surfaces of the abdomen with sharp denticles, which may be united into scales (Figs. 3G, 4E and F). The postero-ventral margin of the urosome with two tooth-like bifid processes on the ventral side (Figs. 1D and 3H).

The furcal rami are short, with three little denticles on the ventral surface (Figs. 1D, 3H and I). Each ramus bears a single strong long seta (Figs. 1D and 3I); the distal two-thirds of it bear pustulate denticules, the proximal third is smooth (Fig. 3F and I). Two setae are inserted near the base of each ramus at the outer side (Figs. 1D and 3I).

Comparison

Currently the family Basipodellidae comprises nine species arranged in seven genera: *Basipodella*, *Stygotantulus*, *Hypertantulus*, *Polynyapodella*, *Nipponotantulus*, *Rimitantulus*, *Arcticotantulus*. The new genus has a unique cephalic pore formula within the Basipodellidae. *Serratotantulus* can be easily distinguished from *Basipodella, Nipponotantulus*, *Rimitantulus*, *Polynyapodella*, *Arcticotantulus* by the presence of seta on the endopodite of thoracopod 1. In both *Stygotantulus* and *Hypertantulus* one of the apical setae of the sixth thoracopod is modified into a recurved claw, which is absent in the new species. The new species is the first tantulocaridan with a bilobed oral disk (although it is necessary to note that the particular structure of the oral disk is difficult to observe in attached specimens) bearing two strong ridges. The central protrusion of the posterior margin of the cephalic shield is also unique for Tantulocarida.

Etymology

This species is named in honor of Dr Elena S. Chertoprud who helped us identify the harpacticoid host.

Discussion

Due to the fact that only the holotype (tantulus larva) was available for description nothing can be said about the formation of the trunk sac containing

the developing male. Still, that is considered to be one of the main distinguishing characters in tantulocaridan taxonomy (Huys 1990). Unfortunately, it can not be applied to all tantulocaridans, because a number of descriptions were based only on tantulus larval characters, so the way of trunk-sac formation was not observed. Boxshall and Huys (1989) admitted that the family Basipodellidae had been initially based on plesiomorphic characters and might therefore be paraphyletic. In fact, the distribution of tantulocarid species over the families Basipodellidae and Deoterthridae is clearly artificial, depending on the authors' bias rather than on the actual phylogenetic relations. Furthermore, according to the latest diagnoses (Boxshall 1996), two main tantulocaridan families Basipodellidae and Deoterthridae could not be distinguished at all. So their artificial or paraphyletic nature becomes apparent. Revision of the morphological criteria used for identification of the families attempted by Kolbasov et al. (2008) showed that only two (absence/presence of transverse abdominal lamellae, absence/presence of tooth-like projections on posterior margin of abdomen) out of nine characters could be used for dividing basipodellid–deoterthrid genera into two groups. The rest of the characters (7) overlap in these two families. Only three genera of the group Basipodellidae–Deoterthridae could be clearly united into a separate taxon. These are *Cumoniscus*, *Deoterthron*, and *Amphitantulus*. These genera lack transverse abdominal lamella and have no tooth-like projections on the posterior margin of the abdomen, and probably should be contained within Deothertridae. Moreover, these genera live on cumaceans, ostracods, and amphipods respectively, but not on copepods. Thus, the host's taxonomy could also be important for distinguishing tantulocaridan families.

The new genus is placed in the family Basipodellidae because of its distinct transverse cuticular lamellae on the dorsal side of the abdomen and the tooth-like projections on the posterior margins of the abdomen. The new species parasitizes harpacticoid copepods that represent hosts for all basipodellids.

Serratotantulus has distal digitiform processes of endopodites 2–5 distinctly separated from the basal segment. They could be interpreted either as modified setae or as distal endopodal segments. The first explanation seems to be more accurate. In this case, the endopodal morphology is most plesiomorphic within the basipodellid–deoterthrid clade. In all other basipodellid–deoterthrid tantulocaridans this terminal seta is probably attached to the segment by a hidden supracuticular articulation.

Tantulocaridans are widespread crustaceans. They were found in cold and warm waters in both Southern and Northern hemispheres. The range in depth is also remarkable: they live from shallow water in the subtidal zone to the abyssal. The new species is the second from the family Basipodellidae to inhabit the abyssal zone. The first, *Basipodella harpacticola* Becker, was found in the Peruvian Trench at depths of 2000–5000 m (Becker 1975). *Serratotantulus* is the second tantulocaridan reported from the Indian Ocean. The first record (an unidentified tantulocaridan) was mentioned by Huys (1991).

Serratotantulus is the smallest described tantulocaridan (76 μm in length) and is even smaller than *Dicrotrichura tricincta* Huys, 1989 [~83 μm (Huys 1989)].

Funding

This work was financially supported by the Russian Foundation for Basic Research [grants no. 06-04-48921, 09-04-00916].

Acknowledgments

We are indebted to Dr Elena S. Chertoprud, who identified a harpacticoid host. GAK also thanks Prof. Jeffrey D. Shields and Dr Christopher B. Boyko for an invitation to take part in the SICB Meeting in 2009. We also thank the Editor Harold Heatwole and our reviewers for critical remarks which helped us to improve this manuscript.

References

Becker KH. 1975. *Basipodella harpacticola* n. gen., n. sp. (Crustacea, Copepoda). Helgoländer wissenschaftliche Meeresuntersuchungen 27:96–100.

Bonnier J. 1903. Sur deux types nouveaux d'Epicarides parasites d'un Cumacé et d'un Schizopode. Compte rendu hebdomadaire des séances de l'Académie des sciences, Paris 136:102–3.

Boxshall GA. 1996. Classe des Tantulocarides (Tantulocarida Boxshall & Lincoln, 1983). Traité de Zoologie T. VII. F. II. Crustacés. 399–408.

Boxshall GA, Lincoln RJ. 1983. Tantulocarida, a new class of Crustacea ectoparasitic on other crustaceans. J Crustacean Biol 3:1–16.

Boxshall GA, Lincoln RJ. 1987. The life cycle of the Tantulocarida (Crustacea). Philos Trans R Soc Lond B Biol Sci 315:267–303.

Greve L. 1965. A new epicaridean from western Norway, parasite on Tanaidacea. Sarsia 20:15–19.

Hansen HJ. 1913. Crustacea Malacostraca II., IV. The order Tanaidacea. Danish Ingolf-Expedition 3:1–145.

Huys R. 1989. *Dicrotrichura tricincta* gen. et spec. nov.: a new tantulocaridan (Crustacea: Maxillopoda) from Mediterranean deep waters of Corsica. Bijdragen tot de Dierkunde 59:243–9.

Huys R. 1990. *Campyloxiphos dineti* gen. et spec. nov. from Namibia and the redefinition of the Deoterthridae Boxshall and Lincoln (Crustacea: Tantulocarida). J Nat Hist 24:415–32.

Huys R. 1991. Tantulocarida (Crustacea: Maxillopoda): a new taxon from the temporary meiobenthos. Pubblicazioni della Stazione Zoologica di Napoli I: Marine Ecol 12:1–34.

Huys R, Boxshall GA, Lincoln RJ. 1993. The tantulocaridan life cycle: the circle closed? J Crustacean Biol 13:432–42.

Kolbasov GA, Sinev AY, Tchesunov AV. 2008. External morphology of *Arcticotantulus pertzovi* (Tantulocarida, Basipodellidae), a microscopic crustacean parasite from the White Sea. Entomol Rev 88:1192–207 (Original Russian text published in Zoologicheskii Zhurnal 2008. 87:1437–52).