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Microdajus tchesunovi sp. n. (Tantulocarida, Microdajidae) – A new crustacean parasite of from the White Sea

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ABSTRACT

A new species of Tantulocarida, *Microdajus tchesunovi* sp. n., was found on tanaid host, *Typhlotanais* sp. of the family Nototanaidae, collected from silty sediment in the Kandalaksha Bay in the White Sea. Several tantulus larvae, developing males at different stages of metamorphosis, and early stages of parthenogenetic females were found attached to different sites of their hosts. Ultrastructure of the new species was studied with SEM. *Microdajus tchesunovi* sp. n. can be easily distinguished from other species of the genus *Microdajus* Greve by the presence of a pair of longitudinal dorsal lamellae at the anterior end of the cephalon. It is also characterized by the presence of an endopod seta on the sixth thoracopod and the absence of thoracopodal endites. A morphological comparison of species of the family Microdajidae is presented in tabular form.

1. Introduction

Tantulocaridans are minute ectoparasitic crustaceans found on meobenthic, benthic, or even hyperbenthic crustacean hosts such as Copepoda, Tanaidacea, Ostracoda, Cumacea and Amphipoda. Tantulocaridans were first discovered at the beginning of the 20th century and were initially interpreted as parasitic isopods (Bonnier, 1903; Greve, 1965), parasitic copepods (Hansen, 1913; Becker, 1975) or as members of the superclass Maxillopoda closely related to cirripedes (Bradford and Hewitt, 1980). A new class Tantulocarida was established only in 1983 (Boxshall and Lincoln, 1983). Currently tantulocaridans are linked with Thecostraca on account of the presence of a median penis in the seventh trunk segment of the male and the putative position of the female's gonopore on the first thoracic segment (Boxshall and Lincoln, 1987; Huys et al., 1993).

Tantulocarida are characterised by a very complicated life cycle (Huys et al., 1993) apparently with alternation of parthenogenetic and sexual stages developed from free-swimming tantulus larvae that attach to the host by their oral disc. They also do not undergo typical crustacean molts. The proposed life cycle was reconstructed from bits of the life cycles of several tantulocaridan species, but no single species has been demonstrated to have all the alternative developmental pathways. Currently, Tantulocarida include about 30 species assigned to 20 genera and 5 families.

The family Microdajidae was established by Boxshall and Lincoln (1987) to comprise two species of genus *Microdajus* Greve 1965. Since then, three more species have been added, including *Xenalytus scotophilus* (Grygier and Sieg, 1988; Boxshall et al., 1989; Huys, 1991; Boxshall, 1996; Table 1 herein).

Previously, several specimens of an undefined tantulocaridan species from the White Sea were briefly reported as *Microdajus* sp. (Kornev, 2004). We collected additional abundant material, which enabled us to describe a new species of *Microdajus* and study its ultrastructure. In this paper we also give an account on systematics and taxonomy of the family Microdajidae. *Microdajus tchesunovi* is the second tantulocaridan species described from the White Sea, after the basipodellid tantulocaridan *Arcticotantulus pertzovi* (Kornev et al., 2004; Kolbasov et al., 2008).

2. Materials and methods

The material including different life stages of *Microdajus* sp. n. was collected near the White Sea Biological Station of Moscow State University (Velikaya Salma Strait, Kandalaksha Bay) in July–August, 2006–2008. Sediment samples were obtained with a hyperbenthic Ockerman dredge from depths of 20–50 m and rinsed through a 50-μm sieve. The material was fixed in formalin

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Table 1
Main characteristics of tantulus larvae of species of family Microdajidae.

Species	Body length of tantulus larva, μm	Cephalic pore formula	Cephalic lamellae	Thoracopod 6 (exopod + endopod) setation	Thoracopod endites	Abdomen ornamentation	Hosts	Locality	Depth, m	References
Microdajus aporosus	–	D_I, L_I	Few posterio-dorsal	1 + 1	Absent	No information	*Meromonakantha macrocephala*	Ross Sea	568	Grygier and Sieg (1988)
Microdajus gaelicus	120	? ('a line of pores' at posterior margin and L_I)	Absent	1 + 0	Absent	No information	*Typhlotanais pulcher*	West coast of Scotland	2884– 897	Boxshall and Lincoln (1987)
Microdajus langi	115	A_I, $D_{I(?)}$, D_{II}, D_{III}, $D_{IV(?)}$, $L_{I(?)}$	Several oblique posterior	1 + 0	Present (with one spine)	Regular, setiform denticles	*Anarthrura simplex, Haplocope angusta, Leptognathia attenuata, L. breviremis, L. gracilis, Typhlotanais aequiremis*	North-east Atlantic	22–120	Greve (1965, 1988), Boxshall and Lincoln (1987), Sieg (1986), Grygier and Sieg (1988), Boxshall et al. (1989), Huys (1991)
Microdajus pectinatus	88	A_I, A_{II}, D_{II}, $D_{IV(?)}$, L_I	Absent	1 + 0	Present (with one spine)	Combs of long, sharp denticles ventrally	*Typhlotanais sp.*	West coast of Scotland	2175–540	Boxshall et al. (1989)
Microdajus tchesunovi sp.n.	77	A_I, D_I, D_{II}, L_I	Two anterior longitudinal	1 + 1	Absent	Small, irregular denticles	*Typhlotanais sp.*	White Sea	20–100	Kornev (2004); herein
Xenalytus scotophilus	98	A_I, A_{III}, A_{IV}, D_I, D_{II}, D_{IV}, L_I, L_{II}, L_{III}	Longitudinal (3 pairs), transverse (2 pairs)	1 + 0	Present (with two spines)	Irregular, tiny longitudinal lamellae	Unknown	Mediterranean (Ligurian Sea)	160	Huys (1991)

or glutaraldehyde. Five specimens of different life stages including the holotype (a tantulus larva) were mounted in glycerol on glass slides and examined using a WILD light microscope. Line drawings were made using oil immersion on an Olympus BX 51 microscope using Nomarski differential interference contrast microscopy. About 10 individuals of different stages were selected for scanning electron microscopy. This material was postfixed in 2% OsO_4, then dehydrated in an alcohol series and acetone, and critical point dried in CO_2. The preparations were then sputter-coated with a platinum–palladium mixture and examined on JEOL JSM-6380LA microscope at operating voltages of 15–20 kV.

Taxonomy
Class Tantulocarida Boxshall and Lincoln, 1983
Family Microdajidae Boxshall and Lincoln, 1983
Genus *Microdajus* Greve, 1965
Microdajus tchesunovi Kolbasov & Savchenko, new species (Figs. 1–7)

2.1. Material examined

More than 40 individual tantulocaridans representing different life-cycle stages (tantulus larvae, parthenogenetic females and developing males) attached to different parts of the body of *Typhlotanais* sp. (Crustacea, Tanaidacea, Nototanaidae). Type locality: the White Sea (66°31′41″ N, 33°11′08″ E), depths 20–50 m, pelite silt. The holotype and fourteen paratypes are deposited in the Zoological Museum of Moscow State University under registration numbers Mj. 2 (holotype) and Mj. 3 (paratypes). A CD-ROM containing all the digital SEM photographs of the specimens has also been deposited there for permanent reference.

2.2. Diagnosis (based on tantulus larva)

Microdajus with cephalon with two dorsal anterior lamellae only. Cephalic pore formula as follows: A_I, D_I, D_{II}, L_I. Trunk tergites smooth, lacking ornamentation. All thoracopods lacking medial endites. Thoracopod 6 biramous, with 2 unequal setae. Abdomen with small, irregular denticles. Host: tanaid of the genus *Typhlotanais* (Fig. 1A).

3. Description

3.1. Tantulus larva

Body comprising cephalon, 6 pedigerous thoracic segments, and two-segmented urosome (Figs. 1A, B and 3C). Total length of paratype excluding furcal setae 77.6 μm (Fig. 3C). Cephalon triangular, tapering anteriorly, ca. 40 μm long and 30 μm wide (Figs. 2A, B and 4A, C, E). Cephalic shield smooth, with only two short dorsal, longitudinal lamellae anteriorly (Figs. 2B and 4C, D). Cephalic pore formula A_I, D_I, D_{II}, L_I. Pores A_I, D_I, L_I containing setae (Figs. 2A, B and 4A–F), D_{II} pores hidden by posteriormost margin and observed only in separated cephalon (Figs. 2A, B and 4E, F), enclosed in circlet of cuticular ornamentation. Ventrolateral margins of cepahlon with narrow membranous extensions in anterior half (Fig. 2A). Oral disk round or slightly oval, about 25 μm in diameter, lateral sides covered with a sheathing membrane or cuticular folds (2A; 3D). Ventral side of oral disk completely covered with cement, and structure of ventral surface thus not observed except for tiny aperture (ca. 1 μm in diameter) in the center (Fig. 5A and B), showing the position of mouth opening. Oral disk with elongated posterior part (Figs. 2A and 4A). Ventral surface of cephalon without pores, smooth, except for the trian-

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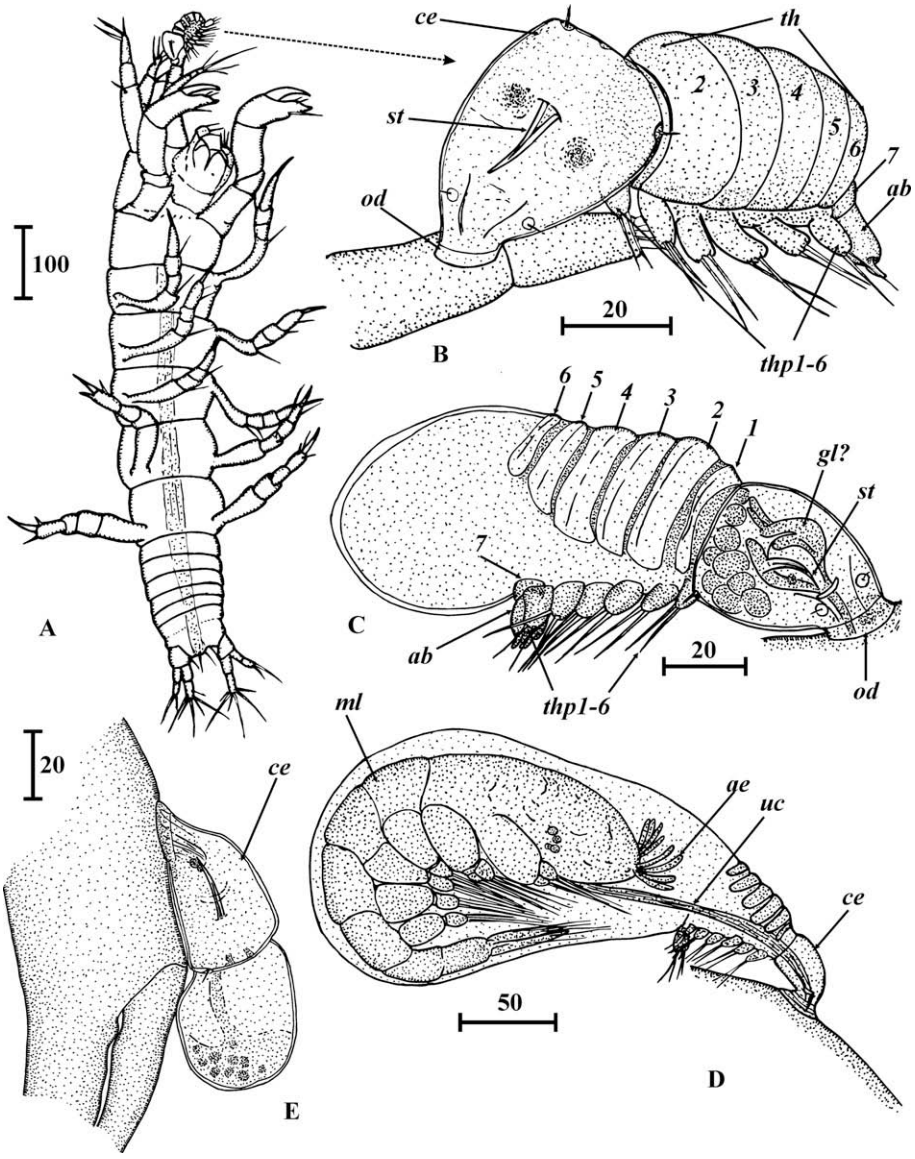

Fig. 1. Morphology of different stages of *Microdajus tchesunovi*. (A) Tantulus attached to second antenna of host; (B) tantulus, general view, dorsolateral (tergites of trunk segments numbered); (C) expanded tantulus, containing male at early stage of development, general view, lateral (tergites of trunk segments numbered); (D) developing male inside trunk sac, lateral; (E) early stage of "parthenogenetic" female, lateral. Abbreviations: *ab*, abdomen; *ae*, aestetascs; *ce*, cephalon; *gl*, glandular structures; *ml*, male; *od*, oral disk; *st*, stylet; *th*, thorax; *thp1–6*, thoracopods; *uc*, umbilical cord. Scale bars in μm.

gular wrinkled area centrally (Fig. 5A). Cephalic stylet slightly curved downwards (14–16 μm long), medially positioned in the cephalon (Fig. 1B and C). Several globular and glandular-like structures observed in posterior and medial parts of cephalon respectively (Fig. 1C). Trunk segments 1–7 with distinct tergites (Figs. 1B, C and 3B, C; Fig. 5C) lacking any ornamentation. The first tergite narrow, notched centrally, totally concealed under cephalic shield in tantulus larva (Fig. 5D), only visible in metamorphosed tantulus containing developing male (Figs. 1C, 3B and 5D). Tergite 2 the widest, width of the following tergites gradually decreasing towards seventh segment. Thoracic segment 1 with trapezoidal fold (sternite) in front of thoracopod 1 (Fig. 6A). Thoracic segments 1–6 bearing biramous thoracopods without medial endites (Figs. 1B, C, 3B–D and 6A–E). Thoracopods 1–5 have similar morphology; protopods nearly rectangular, wider than long, swollen anteroposteriorly with sharp denticles at distal end and on lateral margins (Figs. 2C, D and 6A–E). Rami attached closely to the inner side of protopod; each represented by a small, stub-shaped segment with single terminal biserrate seta, approximately equal in exopod and endopod (Figs. 2C, D and 6A–E). In thoracopods 2–5, rami somewhat embedded in protopods (Figs. 2D and 6C). Endopodal setae of thoracopods 2–5 with modified claw-like tip and bearing enlarged, thorn-like denticule at one third of length from base (Figs. 2D and 6D, E). Thoracopod 6 with cylindrical protopod, ramal segments reduced, bearing one terminal biserrate seta each; exopodal seta more than twice as long as endopodal seta (Figs. 2E and 6F). Urosome consisting of two unequal segments (2.4 μm and 12.8 μm long). First segment (seventh trunk segment) smooth, without ornamentation (Figs. 5C). Second segment (abdomen) with small, sharp, irregularly arranged denticles on ventral and lateral sides, dorsal surface smooth (Figs. 2F; Fig. 7A–D). Furcal rami distinct, longer than wide, armed with one terminal seta and two outer lateral setae inserted at base of each ramus (Figs. 2F and 7A–C). In all studied specimens terminal setae were short (5–7 μm) and smooth (Figs. 2F and 7A–C), in

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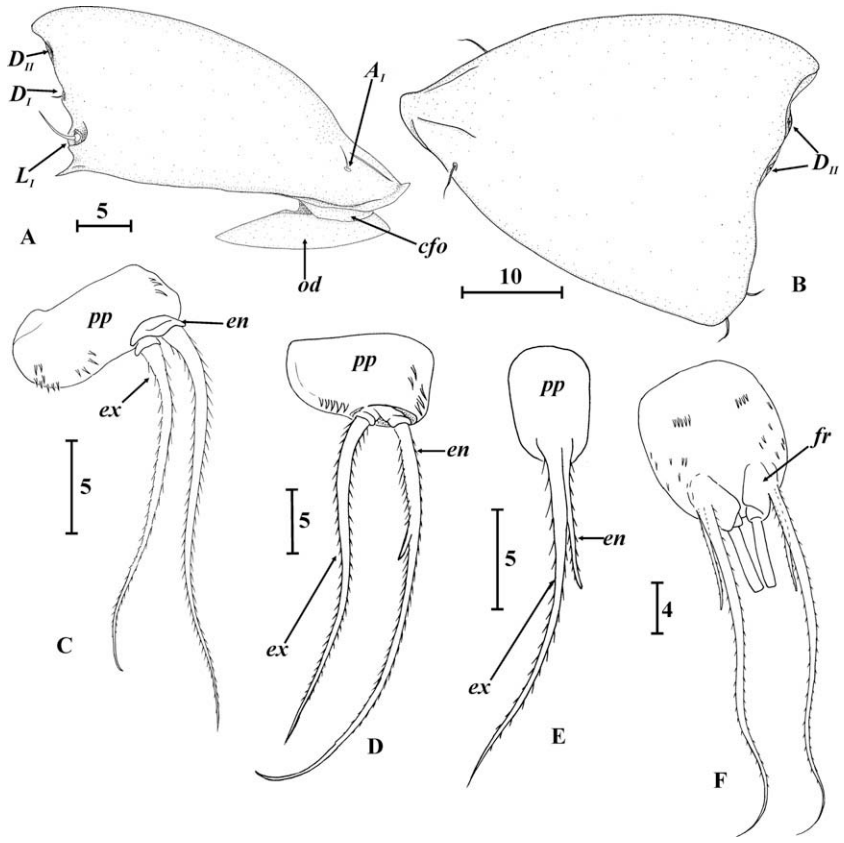

Fig. 2. *Microdajus tchesunovi*, external morphology of tantulus (cephalon, thoracopods and abdomen). (A) Cephalon, lateral view; (B) cephalon, dorsolateral view; (C) thoracopod 1, anterior view; (D) thoracopod 3, anterior view; (E) thoracopod 6, anterior view; (F) abdomen with furcal rami, ventral view. *Abbreviations:* A_I, D_I, D_{II}, L_I, cephalic pores; *cfo*, cuticular folds; *en*, endopod; *ex*, exopod; *fr*, furcal ramus; *od*, oral disc; *pp*, protopod. Scale bars in μm.

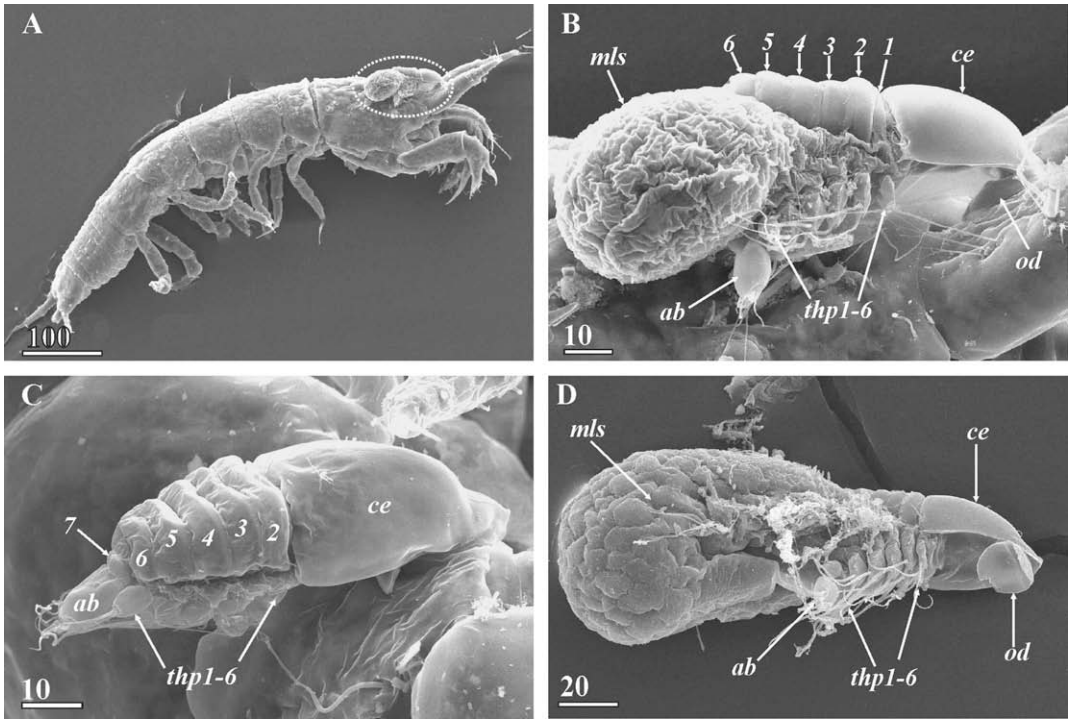

Fig. 3. *Microdajus tchesunovi*, general morphology of different stages. (A) Expanded tantulus with developing male (indicated by dotted oval) attached to host, lateral view; (B) general view of expanded tantulus with developing male from "A" (tergites of trunk segments numbered), lateral; (C) tantulus, general view (tergites of trunk segments numbered), dorsolateral; (D) expanded tantulus with developing male, general view, ventrolateral. *Abbreviations: ab*, abdomen; *ce*, cephalon; *mls*, sac with male inside; *od*, oral disc; *thp1–6*, thoracopods. Scale bars in μm.

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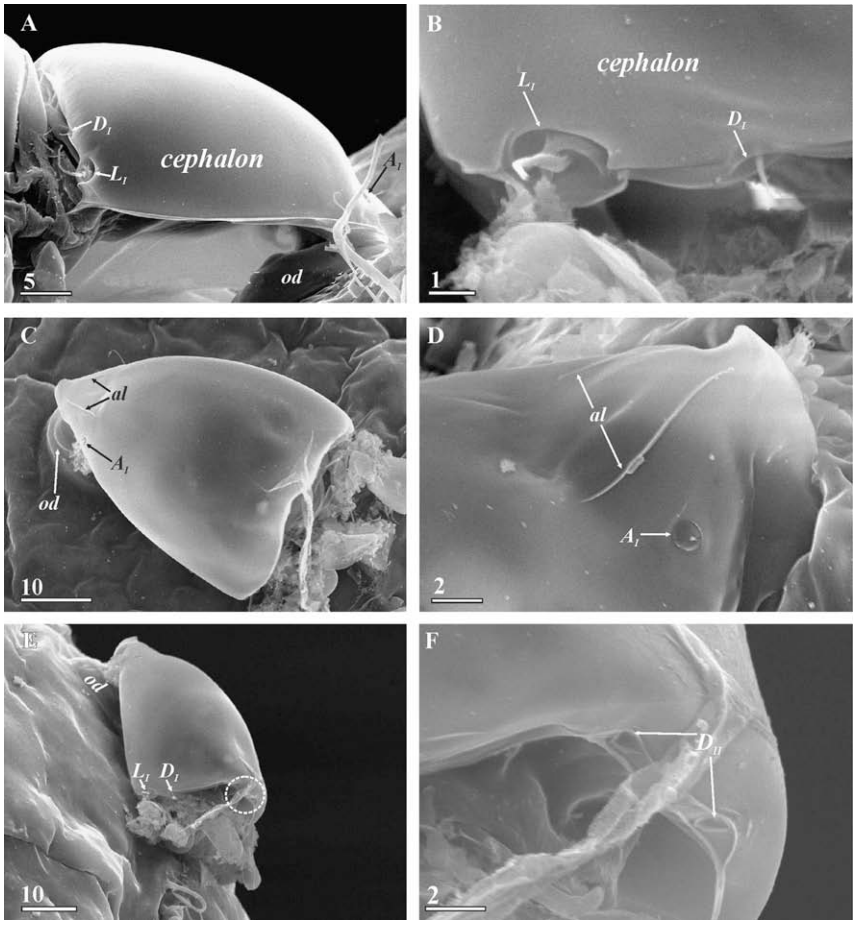

Fig. 4. *Microdajus tchesunovi*, external morphology of cephalon. (A) Cephalon, lateral; (B) pores on posteriolateral margin of cephalic shield; (C) cephalon, dorsal; (D) anterior part of cephalon, dorsolateral; (E) cephalon, posterolateral (location of DII pores indicated by dotted circle); (F) DII pores on posterior margin of cephalon. *Abbreviations:* A_I, D_I, D_{II}, L_I, cephalic pores; *al*, anterior lamellae; *od*, oral disc. Scale bars in μm.

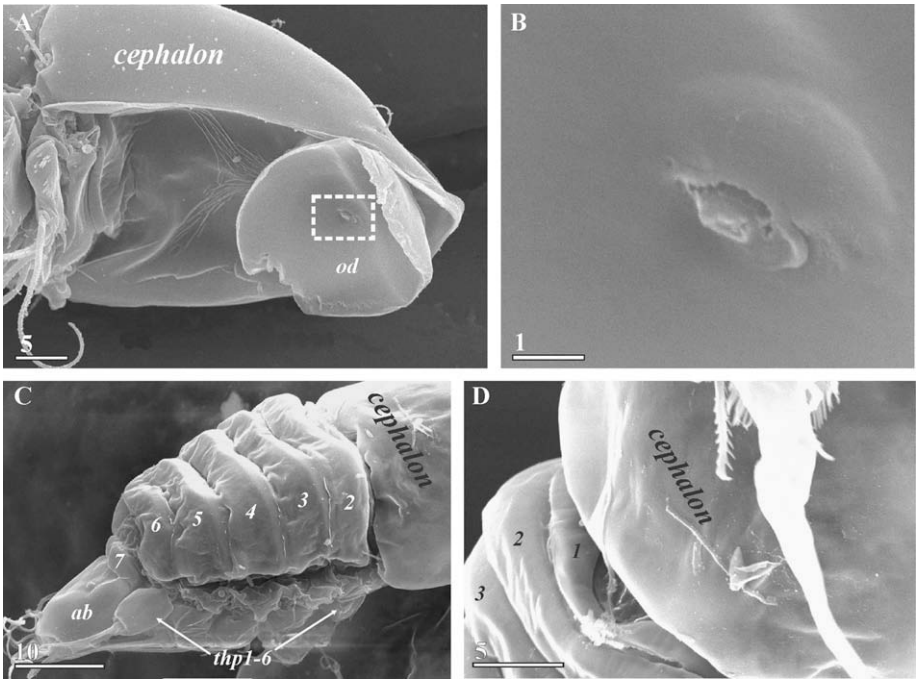

Fig. 5. *Microdajus tchesunovi*, external morphology of oral disk and trunk segments. (A) Cephalon, ventrolateral (position of mouth opening on oral disk indicated by dotted rectangle); (B) opening (mouth) on ventral surface of oral disk; (C) hindbody (tergites of trunk segments 1–7 numbered), lateral; (D) tergite of trunk segment 1 (tergites of trunk segments numbered), dorsal. *Abbreviations: ab*, abdomen; *od*, oral disc; *thp1–6*, thoracopods. Scale bars in μm.

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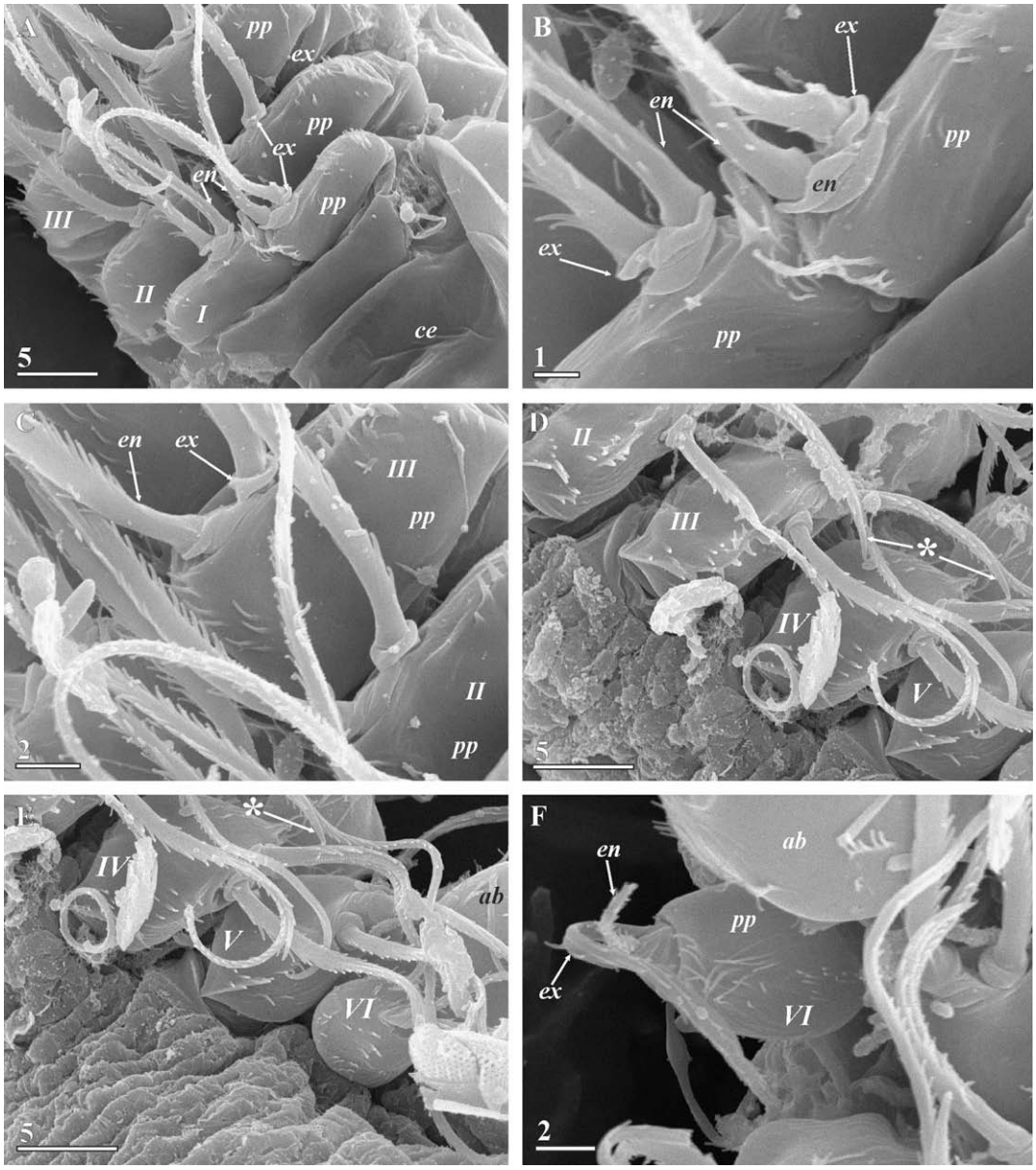

Fig. 6. *Microdajus tchesunovi*, morphology of thoracopods. (A) Thoracopods I–III, anterioventral; (B) rami of thoracopod I, anterior; (C) thoracopods II–III, anterior; (D) thoracopods II–V (thorn-shaped denticules on exopodal setae indicated with asterisk), ventrolateral; (E) thoracopods IV–VI (thorn-shaped denticules on exopodal setae indicated with asterisk), ventrolateral; (F) thoracopod VI, ventral. *Abbreviations: ab*, abdomen; *ce*, cephalon; *en*, endopod; *ex*, exopod, *pp*, protopod. Scale bars in μm.

some specimens bent upwards (Fig. 7D). Lateral setae unequal, bigger one more than three times longer than smaller one), serrate.

3.2. Male

All studied males were inside trunk sacs. Trunk sac with developing male formed posterior to sixth thoracic tergite (Figs. 1C, D and 3A, B, D). Larval tergites separated from limbs by considerable thoracic expansion, abdomen deflected to ventral side (Figs. 1C, D and 3B, D). Typical tantulocaridan male inside sac connected with host tissues via umbilical cord (Fig. 1D). Body comprising cephalothorax incorporating first and second pedigerous thoracic segments, then four free pedigerous thoracic and two abdominal segments (Figs. 8A and 9A). Total length 460 μm, cephalothorax 126 μm long. Cephalic shield ornamented with regular pattern of transverse and longitudinal lamellae, with 7 pairs of pits containing from two to six setae (Figs. 8A, B and 9A–D). These pits arranged in 5 anterior (A_1–A_5) and 2 posterior (P_1, P_2) pairs, A_1 with three, A_2, A_3, A_5 with four, A_4 with six, P_1 with two and P_2 with five setae respectively. Two clusters of 4 aesthetascs at anterior margin of cepaholothorax (Fig. 8A,B). Other cephalic appendages absent. First two thoracic segments presumably fused with cephalon bearing two pairs of biramous thoracopods. Tergites of the following thoracic segments ornamented with polygonal pattern of lamellae (Figs 8A and 9A).

Thoracopods 1–3 each consisting of large unsegmented protopod and uni-segmented rami. Thoracopod 1 with exopod longer than endopod, the former bearing five long terminal setae and one short outer subterminal seta (Fig. 8C). Endopod with four long terminal setae and one short seta at outer side (Fig. 8C). Setation of thoracopods 2–3 similar to that in thoracopod 1, but outer exopodal seta inserted terminally (Fig. 8D and E). Thoracopods 4–5 with bisegmented protopod comprising large coxa/syncoxa and smaller basis. Segmentation and setation of rami similar to those of thoracopods 1–3 (Fig. 8F and G). Thoracopod 6 uniramous, with

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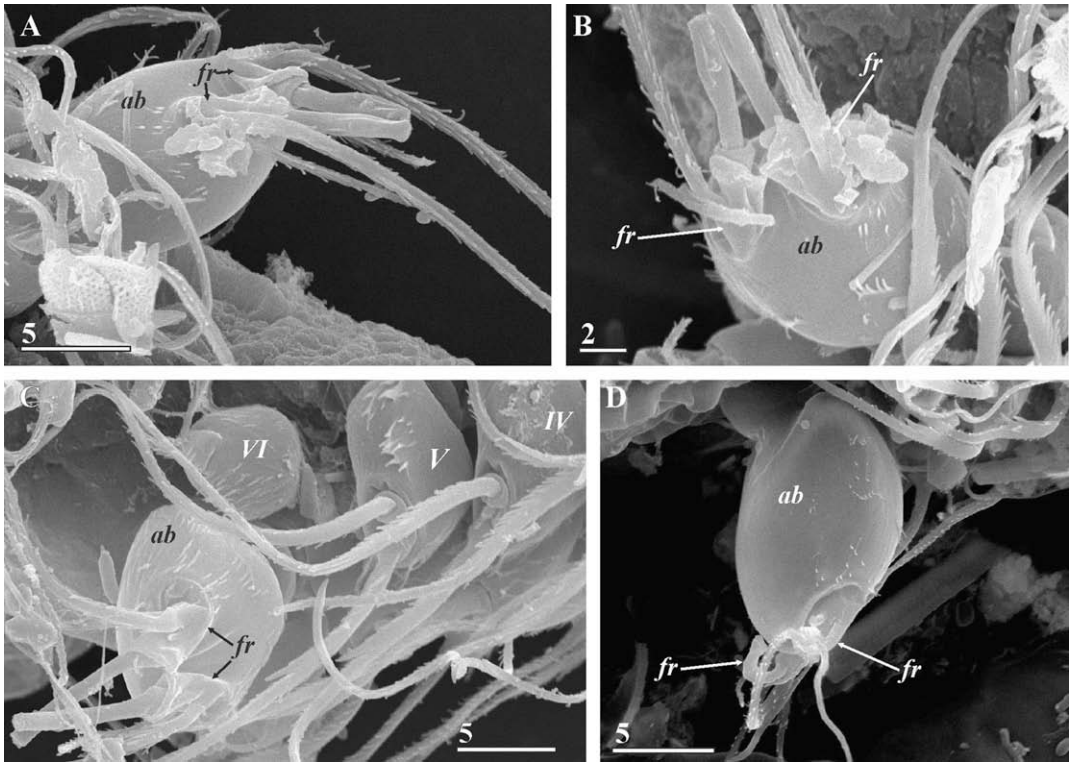

Fig. 7. *Microdajus tchesunovi*, morphology of abdomen. (A) Abdomen, lateral; (B) abdomen, posterioventral; (C) abdomen, posterioventral (thoracopods IV–VI numbered); (D) abdomen, dorsolateral. *Abbreviations: ab*, abdomen; *fr*, furcal rami. Scale bars in μm.

unsegmented protopod (Fig. 8H). Distal segment presumably representing exopod, with 5 long subequal terminal setae and shorter outer seta. Two setiform protrusions or "brush setae" of proximal part on inner margin of protopods were found only in thoracopod 2 (Fig. 8D). Their absence/presence in other thoracopods could not be observed due to imperfect condition of the material.

First abdominal (seventh trunk) segment about 13 μm long. Second abdominal segment, presumably representing telson (26 μm long), bearing furcal rami about 45 μm long (Fig. 8I). Posterior margins of furcal rami without setae, possibly underdeveloped. Unpaired medial penis (57 μm long), attached to distal part of ventral extension of first abdominal (seventh trunk) segment (Fig. 8I). Distal part of penis slightly curved, ventral surface concave.

3.3. "Parthenogenetic" female

All "parthenogenetic" females were present only at their early stages of development (Fig. 1E). We could not confirm whether their final habitus differs much from those of other *Microdajus* species having large, oval brood sac with long and narrow neck.

3.3.1. Comparison

Tantulus larva of *Microdajus tchesunovi* differs from other species of the genus in the presence of two anterior dorsal cephalic lamellae. The new species differs from *M. gaelicus, M. pectinatus* and *M. langi* in having an endopodal seta on thoracopod 6. Both *M. langi* and *M. pectinatus* possess medial endites that are absent in *M. tchesunovi* and two other species of the genus (Table 1). Abdomen of the newly described species bears only small, irregular denticles and lacks regular setiform denticles of *M. langi* and combs of long, sharp denticles of *M. pectinatus*.

Adult males have yet been discovered for 3 species of *Microdajus*: *M. pectinatus, M. aporosus* and *M. langi*. Male of the new species can be readily distinguished from these three species by the unsegmented protopod of thoracopod 6. Both *M. pectinatus*, *M. aporosus* have two-segmented protopod of thoracopod 3 which is different about the new species.

4. Discussion

A cephalic pore formula was introduced by Boxshall and Vader (1993) to describe the pore pattern of the basipodellid genus *Amphitantulus*. This pore formula was later applied to all subsequently described species of the families Basipodellidae, Deoterthridae and Doryphallophoridae (Boxshall, 1996; Ohtsuka and Boxshall, 1998; Kornev et al., 2004; Savchenko and Kolbasov, 2009). Despite several limitations this formula is currently the only way to homologize and compare cephalic pore pattern among different tantulocaridan taxa. As yet, only a few pores can be homologized throughout the Tantulocarida. These are the A_I, D_I and L_I pores, which have setae inside and are similarly located on cephalon. In this paper for the first time the cephalic pore formula is applied to microdajid species (Table 1).

Species of the genus *Microdajus* have a smaller number of cephalic pores (two to six pairs) than the other microdajid genus, *Xenalytus*, the sole species of which has nine pairs of pores (Table 1), *Microdajus* spp. also have the smallest number among tantulocarid taxa. All species of *Microdajus* have a low number of both cephalic pores and lamellae. Microdajids differ from other tantulocaridans in their reduced, unsegmented rami of the thoracopods consisting of small, stub-shaped segments with a single terminal seta each. However, there are some differences in interpretation of thoracopodal segmentation among species of *Microdajus*. It is difficult to trace a segmentation of rami for *M. langi* and *M. gaelicus*, which have a couple of ramal setae inserted in unsegmented protopod (Boxshall and Lincoln, 1987). Thoracopods of *M. aporosus* have similar morphology with *M. langi* and *M. gaelicus*,

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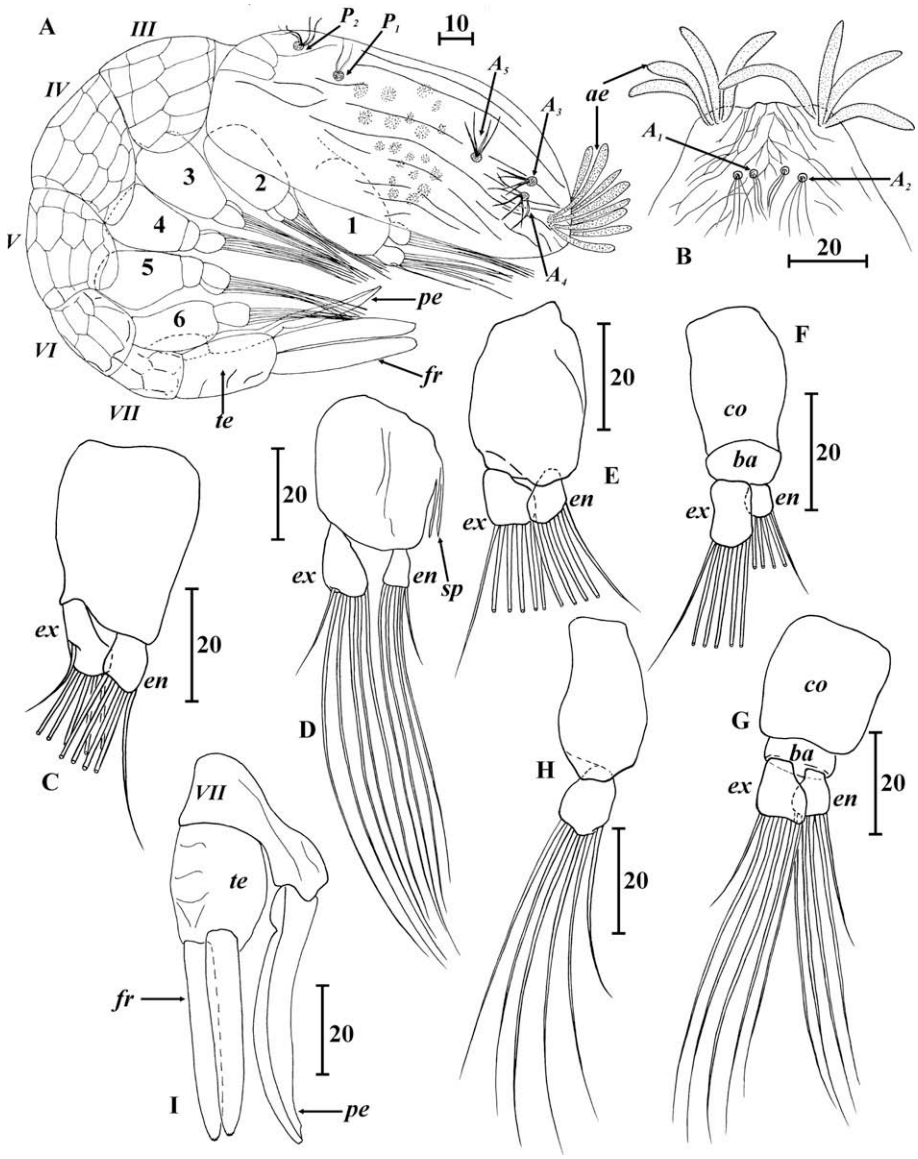

Fig. 8. *Microdajus tchesunovi*, external morphology of male. (A) General view, lateral (tergites of trunk segments numbered in Roman, thoracopods numbered in Arabic); (B) anterior part of cephalic shield, dorsal view; (C–H) thoracopods 1–6 respectively; (I) posterior part of hindbody (seventh trunk segment and telson). *Abbreviations: ae*, aestetascs, A_1–A_5, anterior pits with setae of cephalic shield; *ba*, basis; *co*, coxa/syncoxa; *en*, endopod; *ex*, exopod; *fr*, furcal rami; P_1, P_2, posterior pits with setae of cephalic shield; *pe*, penis; *sp*, setiform protrusions; *te*, telson. Scale bars in μm.

the protopods armed with two equal setae, arising from oval socket (Grygier and Sieg, 1988). Thoracopods of *M. pectinatus* have small ramal segments with apical seta, thoracopod 1 is characterized by a bisegmented protopod with a short but distinct basis (Boxshall et al., 1989). In *M. tchesunovi* a basal fold may be interpreted both as a proximal part of wrinkled endopod, as it is in our description, or as a reduced basis partially fused with ramal segments. However, in other crustaceans the basis is rather fused with coxa than with rami. Besides short ramal segments of thoracopods 2–5 of *M. tchesunovi* seem to be inserted directly in unsegmented protopods. Thus, the morphology of thoracopod needs to be thoroughly studied using TEM. The significant reduction of rami may represent an autapomorphy of the Microdajidae in comparison with the states found in the Basipodellidae and Deoterthridae (Kolbasov et al., 2008; Savchenko and Kolbasov, 2009). These, like all other tantulocaridans, have multi-segmented rami. Microdajidae are thus judged to constitute a monophyletic taxon. Probably with their highly reduced thoracic appendages they can also be treated as the most advanced tantulocaridan family.

There are several differences in the armament of furcal rami in the species of *Microdajus*. All species of the genus have three sensory elements (setae) on each furcal ramus, except *M. aporosus* with four (Grygier and Sieg, 1988). Perhaps Grygier and Sieg (1988) erroneously interpreted a large sharp denticle on ventral edge as a short sensillum/seta, so *M. aporosus* also may have three furcal setae. This species also has a shorter baton-shaped seta on both rami, similarly to the short terminal seta described herein for the furcal rami of *M. tchesunovi*. Grygier and Sieg (1988) suggested such a baton-shaped seta may have been a broken long seta. But the presence of similar setae in all studied specimens of the new species suggests that this is a natural form. Thus, *M. aporosus* and *M. tchesunovi* may differ from other species of the genus in this character.

Males have been described for several species of tantulocaridans: *Coralliotantulus coomansi, Deoterthron lincolni, Doriphallophora harrisoni*, *Itoitantulus misophricola*, *Microdajus aporosus*, *M. langi*, *M. pectinatus*, *Onceroxenus birdi*, *Paradoryphallophora inusitata, Stygotantulus stocki,* and *Arcticotantulus pertzovi* (Boxshall and

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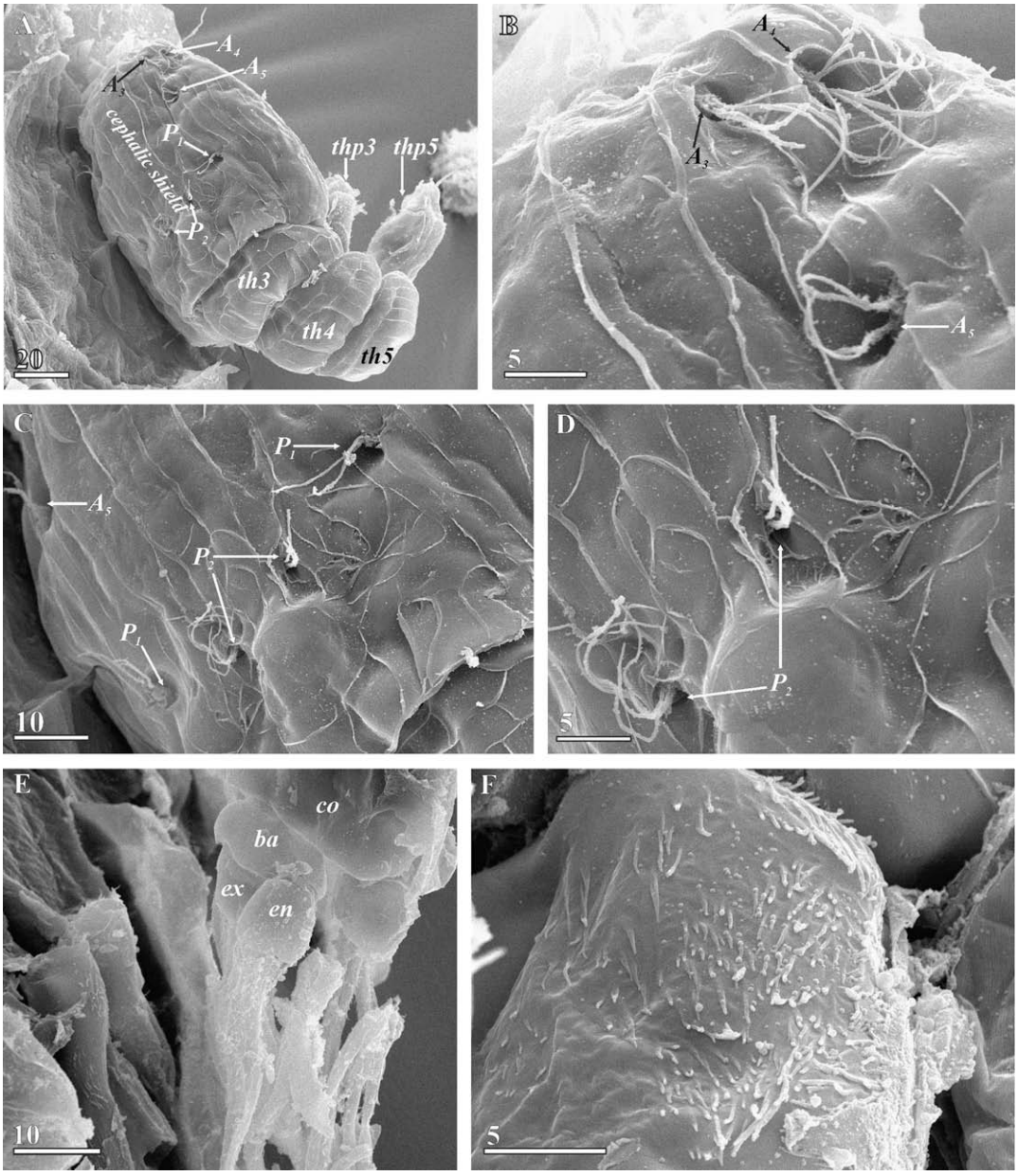

Fig. 9. *Microdajus tchesunovi*, external ultrastructure of male. (A) Cephalic shield and anterior part of trunk, dorsolateral view (posterior part of trunk removed); (B) anterior pits with setae (A_{3-5}) of cephalic shield; (C) pairs of posterior pits with setae ($P_{1,2}$) of cephalic shield; (D) pair of posteriormost pits with setae (P_2) of cephalic shield; (E) thoracopod 5, distal part; (F) proximal part of protopod 3. *Abbreviations:* A_{3-5}, anterior pits with setae of cephalic shield; *ba*, basis; *co*, coxa/syncoxa; *en*, endopod; *ex*, exopod; P_1, P_2, posterior pits with setae on cephalic shield; *th3–5*, tergites of thoracic segments 3–5; *thp3,5*, thoracopods 3, 5. Scale bars in μm.

Lincoln, 1987; Boxshall, 1988; Grygier and Sieg, 1988; Boxshall and Huys, 1989; Boxshall et al., 1989; Huys et al., 1993; Ohtsuka and Boxshall, 1998; Kolbasov et al., 2008). All these males, except those of A. pertzovi, which were studied in the free-swimming stage, were immature and were removed from the cuticular sacs of the tantulus larvae. Morphology of males was studied in more or less sufficient detail for seven species: *C. coomansi*, *D. harrisoni*, *M. aporosus*, *M. langi*, *M. pectinatus*, *P. inusitata*, *S. stocki*, and *A. pertzovi*. The morphology of *M. tchesunovi* males largely corresponds to the descriptions of other males. The cuticular ridges are also typical of the cephalic shield and thoracomeres of *C. coomansi*, *M. pectinatus*, *P. inusitata*, *S. stocki*, and *A. pertzovi*. The pits with setae appear to be characteristic of the cephalic shield of all tantulocarid males. Moreover, the arrangement of the pits is nearly identical in all the species examined. Seven pairs of pits were described in males of *C. coomansi* (Huys, 1990), *M. pectinatus* (Boxshall et al., 1989) and *A. pertzovi* (Kolbasov et al., 2008), and they have similar location to that observed in *M. tchesunovi*. This number of cephalic pits may be general for Tantulocarida (Huys, 1990). Males of *D. harrisoni* and *P. inusitata* were reported to have six pairs of pits (Boxshall and Lincoln, 1987; Ohtsuka and Boxshall, 1998). Eight pairs of setae were reported for the carapace of *M. aporosus* (Grygier and Sieg, 1988), but the number of pits for these setae was not specified, because one pit may house one or two setae.

All tantulocarid males are characterized by the presence of two clusters of four aestetascs at anterior body end. The aestetascs of crustaceans are modified setae. In the sister taxon, the class Thecostraca, the aestetascs always occur on the antennules of free-swimming cypridiform larvae (Høeg and Kolbasov, 2002; Kolbasov and Høeg, 2007), therefore it stands to reason that they represent modified antennules in Tantulocarida (Boxshall and Lincoln, 1987; Boxshall, 1991).

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The majority of previously studied males are characterized by a long and curved, stylet-shaped penis, located on the seventh trunk segment (Boxshall and Lincoln, 1987; Boxshall, 1988; Boxshall and Huys, 1989; Boxshall et al., 1989; Huys et al., 1993; Ohtsuka and Boxshall, 1998). The shape of the penis in *M. tchesunovi* is similar to that in other males of the genus *Microdajus*.

Based on the following body segmentation pattern: six pairs of thoracopods, the penis located on the seventh trunk segment, and the putative female gonopore located on the first thoracic segment, the class Tantulocarida should be regarded as a sister taxon of the class Thecostraca (Facetotecta, Ascothoracida, Cirripedia) (Huys et al., 1993). In addition, the sexual stages, especially males, of tantulocaridans externally resemble the cypridiform larvae of thecostracans. However, all representatives of Thecostraca are characterized by five pairs of sensory lattice organs on the cephalic shield, which is a synapomorphy of the group (Høeg and Kolbasov, 2002). These structures are absent in all stages of Tantulocarida, which is why it should be regarded as a separate taxon. It should be noted that the lattice organs of thecostracans are derivatives of the naupliar setae positioned in special pores (Rybakov et al., 2003). Thus, a homology between the seta-bearing pits of tantulocaridans and the lattice organs of thecostracans cannot be completely ruled out.

Microdajus is the only tantulolocaridan genus comprising as more as four species (Table 1). Although tantulus larvae of all of them lack a developed pattern of longitudinal and transverse cephalic lamellae and have a low number of cephalic pores, they distinctly fall into two groups (Table 1). The first group includes species without endopodal seta on the sixth thoracopod. These are *M. gaelicus*, *M. langi* and *M. pectinatus*. The second group includes two species, *M. aporosus* and *M. tchesunovi*, which both have one endopodal seta on the sixth thoracopod and lack medial endites. Moreover, these species may differ from others in having short baton-shaped setae of the furcal rami. We suggest these groups should have generic ranks and their phylogenetic position with respect to other tantolocaridan taxa should be reviewed using more morphological characters.

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