

## External Morphology of *Arcticotantulus pertzovi* (Tantulocarida, Basipodellidae), a Microscopic Crustacean Parasite from the White Sea

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**Abstract**—The material on *Arcticotantulus pertzovi*, a parasite of the harpacticoids *Bradya typica* and *Pseudobradya acuta*, was collected in the White Sea (the White Sea Biological Station, Moscow State University) in 2004–2006. The morphology of the tantulus larva, the “parthenogenetic female,” and the male was studied using SEM. The data obtained add significant details to the previous description of the species. For instance, the tantulus has at least 11 cephalic pores ( $A_I$ – $A_{IV}$ ,  $D_I$ – $D_{IV}$ ,  $L_I$ – $L_{III}$ ), while the endopod of thoracopod II has a pair of setae. A free-swimming male of *A. pertzovi* was reared for the first time for Tantulocarida. It has a cephalothorax incorporating the cephalic and two thoracic segments, 6 thoracomeres (including those of the cephalothorax) with natatory thoracopods, the 7th trunk segment with a short penis, and an unsegmented abdomen bearing furcal rami with three setae. There are four pairs of aesthetascs representing antennular rudiments. The head shield of cephalothorax is covered with cuticular ridges and bears 7 pairs of pores with setae. Both the cephalon of tantulus and cephalothorax of male lack the lattice organs, which represent the synapomorphy of the class Thecostraca. According to its morphological characteristics, *A. pertzovi* may belong to the families Deoterthridae or Basipodellidae; the former family is most probably an artificial taxon.

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Members of the class Tantulocarida are the smallest crustaceans and some of the smallest multicellular organisms in general, their size varying from 80 to 400  $\mu\text{m}$ . Although known since the beginning of the last century, they were recognized as a separate class only in 1983 (Boxshall and Lincoln, 1983). The first discovered representatives of the group, the genera *Cumonicus* Bonnier and *Microdajus* Greve, were described as parasitic isopods (Bonnier, 1903; Greve, 1965). The tantulocarid larvae were also regarded as parasitic copepods (Hansen, 1913; Becker, 1975) or as members of the superclass Maxillopoda closely related to cirripedes (Bradford and Hewitt 1980). A number of species and genera were subsequently discovered, and the class Tantulocarida now includes about 30 species classified into 20 genera and 5 families.

The tantulocarids are ectoparasites of meiobenthic crustaceans, such as Copepoda, Tanaidacea, Ostracoda, Isopoda, Cumacea, and Amphipoda. Their species are characterized by a complex life cycle with alternating sexual and parthenogenetic stages (Fig. 1) and the absence of true molts, typical of the rest of

crustaceans. The microscopic free-swimming tantulus larva (80–110  $\mu\text{m}$  long) consists of a fused cephalon (head), lacking cephalic appendages and bearing an anterior sucker-shaped oral disc, and eight trunk segments (Figs. 2a; 3a; 5c). The cephalon contains a single solid stylet, uncharacteristic of other crustaceans, rounded structures interpreted as glands (Fig. 2b), and an unpaired “funnel-shaped organ” of unknown nature. The trunk is subdivided into a thorax and a one-segmented abdomen with a furca. The thorax comprises six segments bearing biramous thoracopods and one more (the 7th) segment, which is limbless. The tantulus attaches itself to the host with the oral disc and pierces its integument with the stylet.

Further metamorphosis of the tantulus may proceed in two different ways (Fig. 1). Some larvae retain their trunk segments, between which a cuticular sac appears. This sac may form either between the 6th and the 7th trunk segments (Figs. 3c; 5d, 5e; the families Basipodellidae, Deoterthridae, Microdajidae, and Oncoerxenidae) or between the 5th and the 6th segments (Doryphallophoridae). The way of development of the

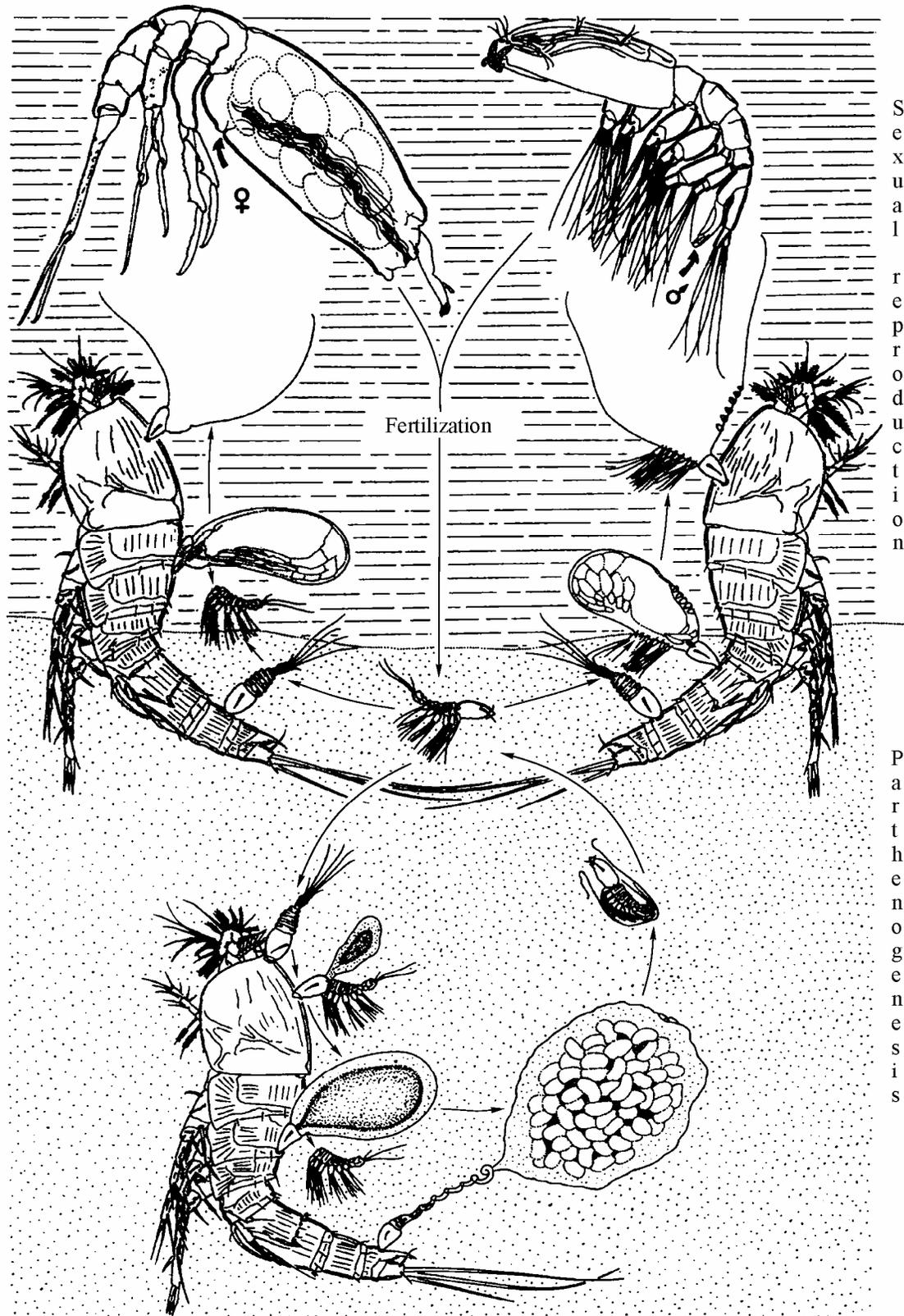
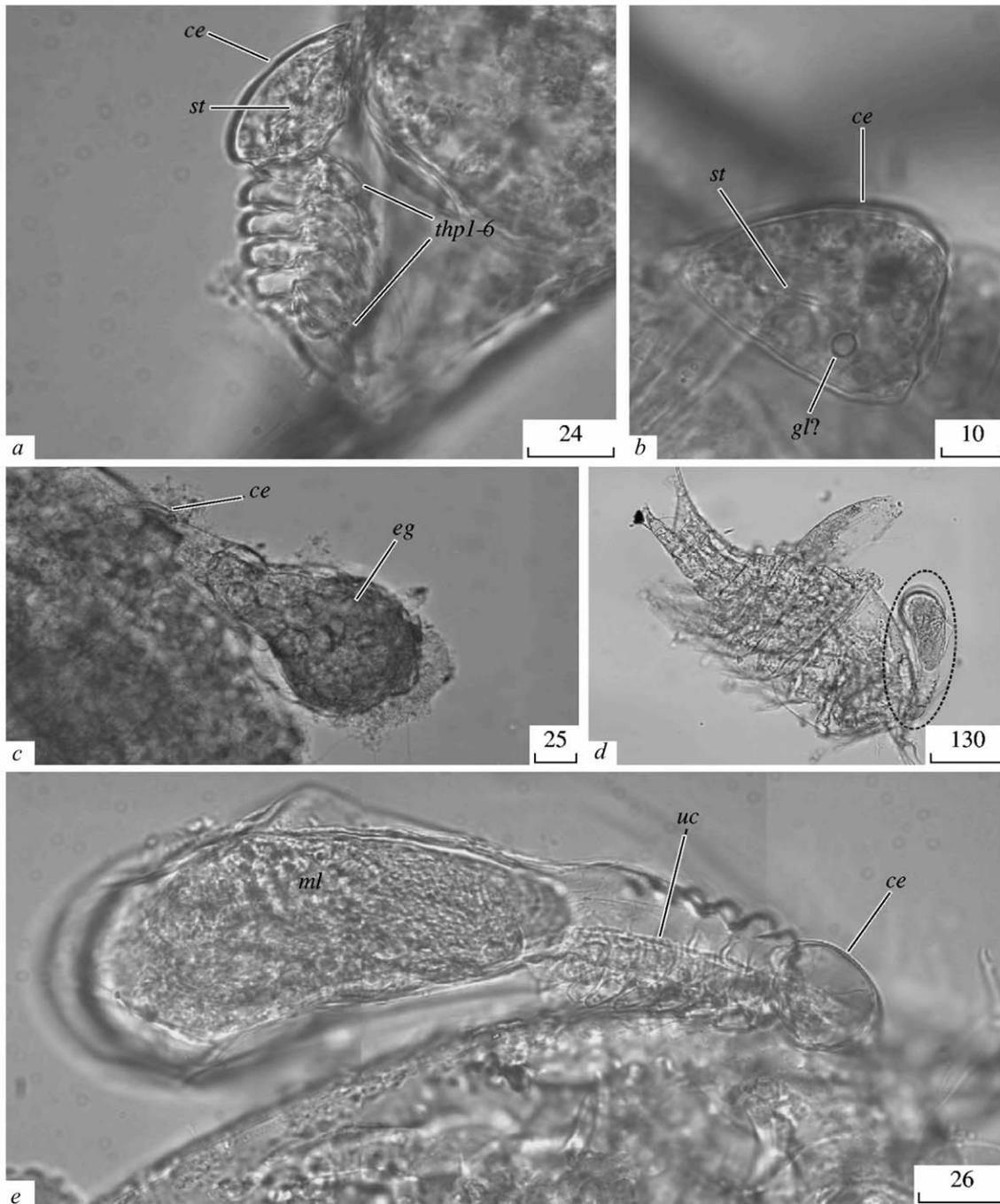


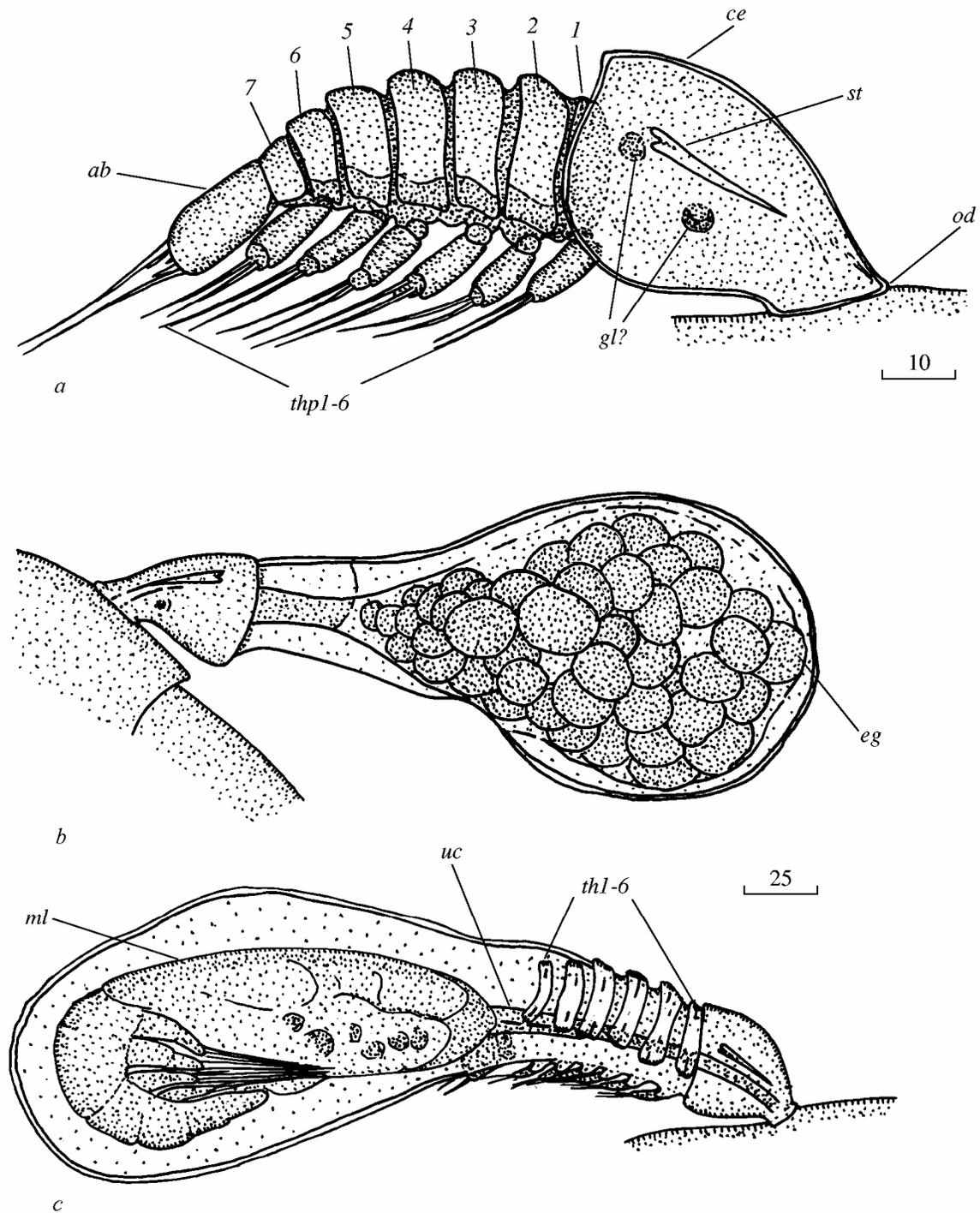
Fig. 1. The life cycle of Tantulocarida (from Huys et al., 1993).



**Fig. 2.** Morphology of *Arcticotantulus pertzovi*, light microscopy: attached tantulus larva (a), cephalon (b), “parthenogenetic female” (c), harpacticoid host with parasite attached (dotted line) (d), developing male (e); lateral (a, c–e), dorso-lateral (b) views. Scale bars in Figs. 2–9 in  $\mu\text{m}$ .

sac is the main taxonomic character in Tantulocarida. The sac soon becomes several times larger than the tantulus larva itself, and the male is formed inside its integument, obtaining nutrition via a special “umbilical” cord (Figs. 2d; 3c). The male (Fig. 9) has a cephalothorax formed by fusion of the cephalic segments and two thoracomeres and covered with a carapace

(a head shield). The remaining six segments, including the abdomen, are not fused. The male has six pairs of natatory thoracopods and an unpaired penis, located on the 7th trunk segment. The unsegmented abdomen ends with a furca. A group of saccular aestetasc, interpreted as antennular rudiments, is positioned on the anterior end of the cephalothorax. Thus,



**Fig. 3.** Morphology of *Arcticotantulus pertzovi*: tantulus larva, lateral view (trunk segments are numbered) (a), mature "parthenogenetic female," lateral view (b), and tantulus larva with developing male inside, dorso-lateral view (c).

the development of the male proceeds without noticeable molting.

In other tantulus larvae, all the trunk segments are shed out and only the cephalon remains. This event can be regarded as modified molting, because the larval cephalon with which the parasite attaches itself

does not molt. The cuticular sac starts growing directly from the posterior part of the cephalon (Figs. 2c; 3b; 5d, 5e). This sac contains either parthenogenetic eggs (which develop from some, still unknown, cells of the cephalon) or a female. The parthenogenetic eggs develop into tantulus larvae, which get out of the sac and

infect new hosts. This is a parthenogenetic life cycle (Fig. 1). The stage in which the parthenogenetic eggs develop is referred to as “parthenogenetic female.” However, this term is incorrect because the typical molt is absent and the egg sac develops from the larval cephalon.

The developing female, like the male, obtains nutrition via a special cord. It has a cephalothorax formed by fusion of the cephalic and (probably) two thoracic segments, followed by two segments with biramous thoracopods, three segments without appendages, and the furca (Fig. 1). The anterior end bears unsegmented cylindrical antennulae. The putative unpaired copulatory pore probably lies ventrally at the level of the first thoracic segment. The eggs are formed inside the cephalothorax of the female, where the gonad appears to be located. The sexual stages leave the host and get into the environment, probably for fertilization; this event, however, has never been observed.

Judging from the body segmentation pattern, the tantulocarids belong to the superclass Maxillopoda. They are characterized by a reduction of cephalic appendages, except for the rudimentary antennulae in the sexual stages. It is therefore difficult to establish the phylogenetic relations between Tantulocarida and other crustaceans. Still, the position of the male and female gonopores indicates that this group may be related to the class Thecostraca (Boxshall and Lincoln, 1987; Huys et al., 1993b). The anatomy of tantulocarids remains completely unknown.

The White Sea species *Arcticotantulus pertzovi* Kornev, Tchesunov et Rybnikov 2004, parasitic on the harpacticoids *Bradya typica* Boeck and *Pseudobradya acuta* Sars, was recently described based on light microscopical observations (Kornev et al., 2004). Our data add a significant amount of detail to the morphology of this species. In addition, the morphology of the free-swimming male is described below for the first time.

#### MATERIALS AND METHODS

The material including different life stages of *A. pertzovi* was collected near the White Sea Biological Station of Moscow State University (66°31'41"N, 33°11'08"E) in 2004–2007. The sediment samples were obtained with a hyperbenthic Ockerman dredge from depths of 25–50 m and rinsed through a 50- $\mu$ m sieve. The hosts of tantulocarids are typical inhabitants of pelite silt meiobenthic communities. The infested

harpacticoids were maintained in culture to obtain the sexual stages of tantulocarids. The material was fixed in formalin or glutaraldehyde. Glycerol-mounted preparations were studied using a WILD light microscope. For electron microscopy, the material was post-fixed in 2% OsO<sub>4</sub>. The specimens for SEM were dehydrated in an alcohol series and acetone and critical-point dried in CO<sub>2</sub>. The preparations were then sputter-coated with platinum–palladium mixture and examined on JEOL JSM-6380LA microscope at operating voltages of 15–20 kV.

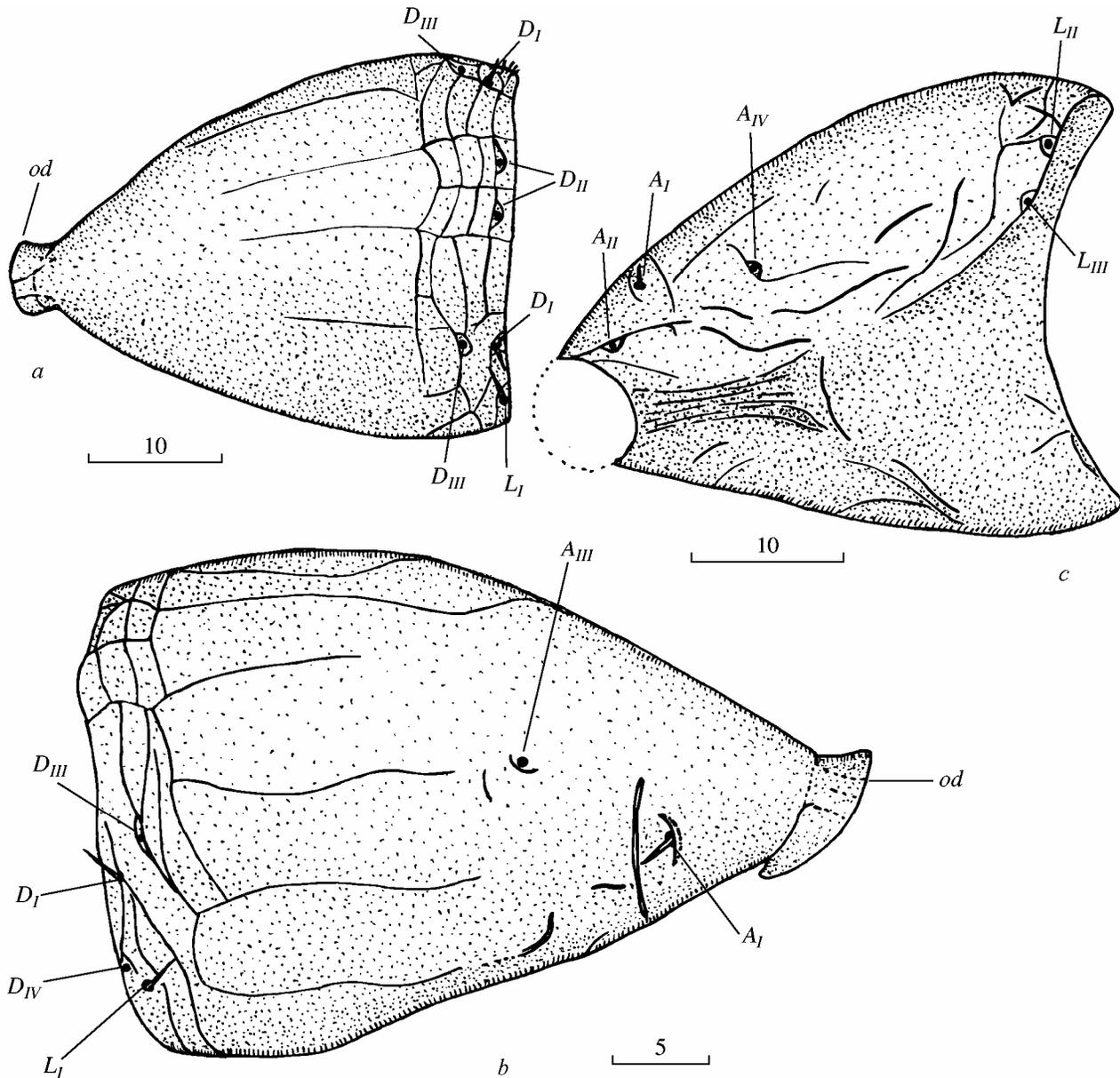
#### RESULTS

##### External morphology of the tantulus larva (Figs. 2a, 2b; 3a; 4; 5a, 5c; 6a, 6b; 7; 8).

The total length of the tantulus larva is only about 80  $\mu$ m, one half of which (~ 40  $\mu$ m) is accounted for by the cephalon, and the other, by the trunk segments, the abdomen being the longest (about 14  $\mu$ m).

The cephalon (Figs. 3a; 4; 6a, 6b, 6e, 6f) is triangular, narrowing anteriorly, semicircular in cross-section. The rounded oral disk (about 7–8  $\mu$ m in diameter) is located on the anterior end (Figs. 4a, 4b; 6a). The head shield has longitudinal and transversal cuticular ridges, which concentrate at the posterior margin, forming dorsally four transversal rows of tetragonal “plaques” (Figs. 4a, 4b; 6d). The sparse long and symmetrical longitudinal ridges (four dorsal and four lateral ones) extend to the middle of the head shield (Figs. 4a, 4b; 6d); the dorsal and lateral surfaces of the anterior portion of cephalon have no ridges except for a pair of transversal ones, located in the anterior third, behind the pore with a seta (Figs. 4b; 6a, 6b). The ventral surface of the cephalon has sparse irregular ridges and is rugose at the anterior end (Figs. 4c; 6f). There are 11 pairs of cephalic pores surrounded with cuticular ridges; they have a non-uniform distribution (Figs. 4; 6) described by the formula  $A_I-A_{IV}$ ,  $D_I-D_{IV}$ ,  $L_I-L_{III}$ , where the anterior, dorsal, and lateral pores are designated as *A*, *D*, and *L*, respectively. The median and ventral pores, typical of some tantulocarid species (Huys et al., 1993a, 1993b, 1997), were not observed in our material. The cephalic pores belong to two types: those with a single simple seta (*A<sub>I</sub>*, *D<sub>I</sub>*, *L<sub>I</sub>*) and simple pores without setae.

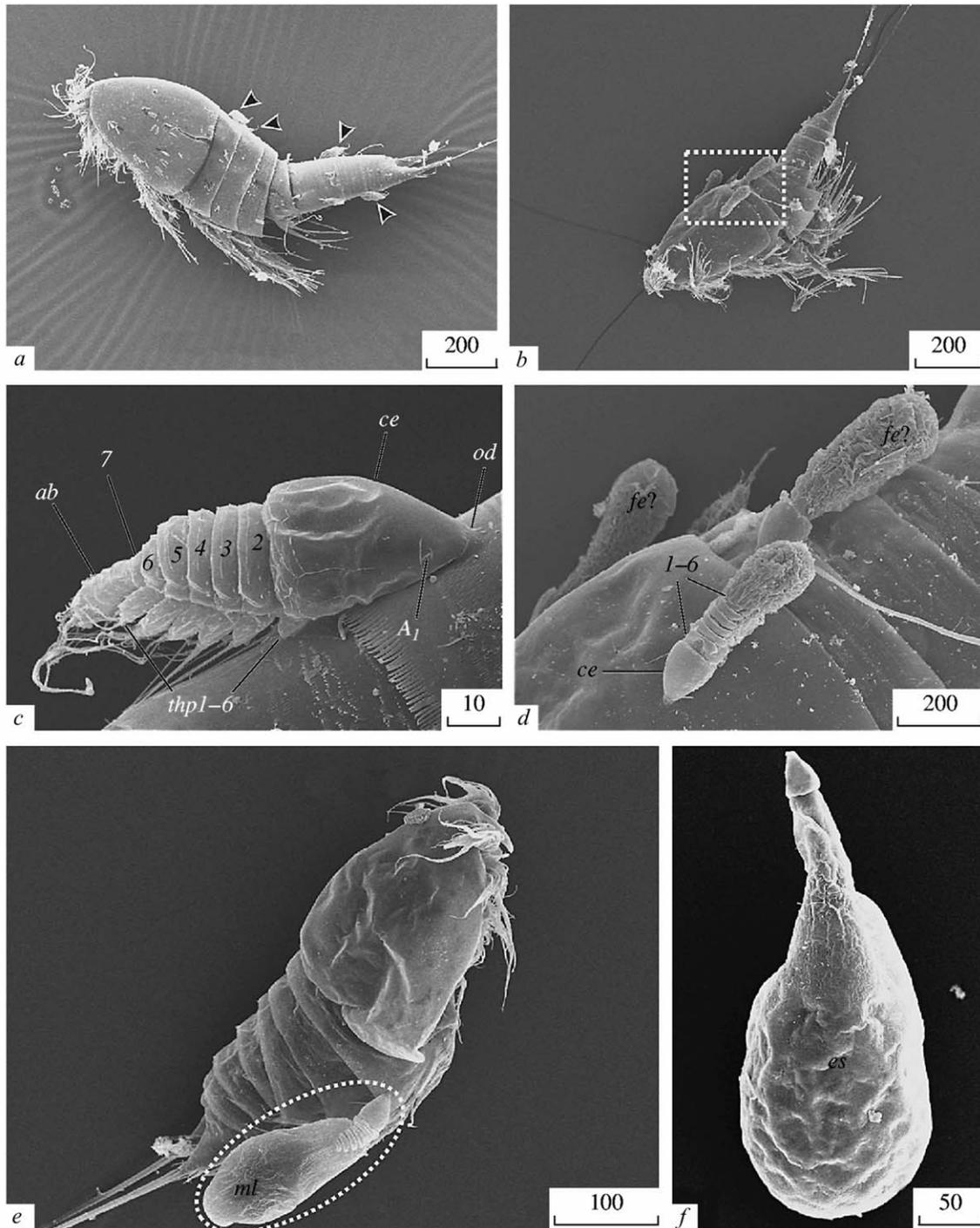
The thorax (Figs. 3a; 5c; 7a, 7b, 7e) consists of six segments with thoracopods and the 7th segment with no appendages; it is not entirely clear if this segment



**Fig. 4.** External morphology of cephalon of *Arcticotantulus pertzovi*: dorsal (a), lateral (b), and ventrolateral (c) surfaces (place of oral disk shown with dotted line).

really belongs to the thorax rather than abdomen. Dorsally and laterally the segments are covered with well-developed tergites, and tetragonal pleural sclerites are located at the bases of all the thoracopods. The tergite surface is smooth, with only one transversal cuticular ridge (Figs. 7a, 7b). The first thoracic segment in the larva is narrow, covered dorsally by the cephalon (Figs. 3a; 1a, 1b); its tergite has an irregular shape with a median incision at the anterior margin (Figs. 6c, 6d). The thoracic segments decrease gradually in size from the 2nd (the largest) to the 7th (the smallest). The 7th segment bears a pair of small lateral outgrowths, or epaulets, bent onto the dorsal surface (Fig. 7d).

The cylindrical abdomen has five concentric, irregularly shaped folds, with rows of fine spinules located along the 3rd, 4th, and 5th folds (Figs. 7a, 7c, 7d). The 3rd and the 4th folds almost touch in the median portion of the dorsal surface; the 5th fold has a median incision (Fig. 7d). The posterior margin of the abdomen has nine symmetric styloid processes with double or triple tips, located on the dorsal and lateral surfaces (Figs. 7c, 7d). The furcal rami are short, one-segmented, and most probably bear three setae: an outer subterminal seta, which is short and simple, a terminal one, long and bearing setulae, and an inner terminal one, which consists of

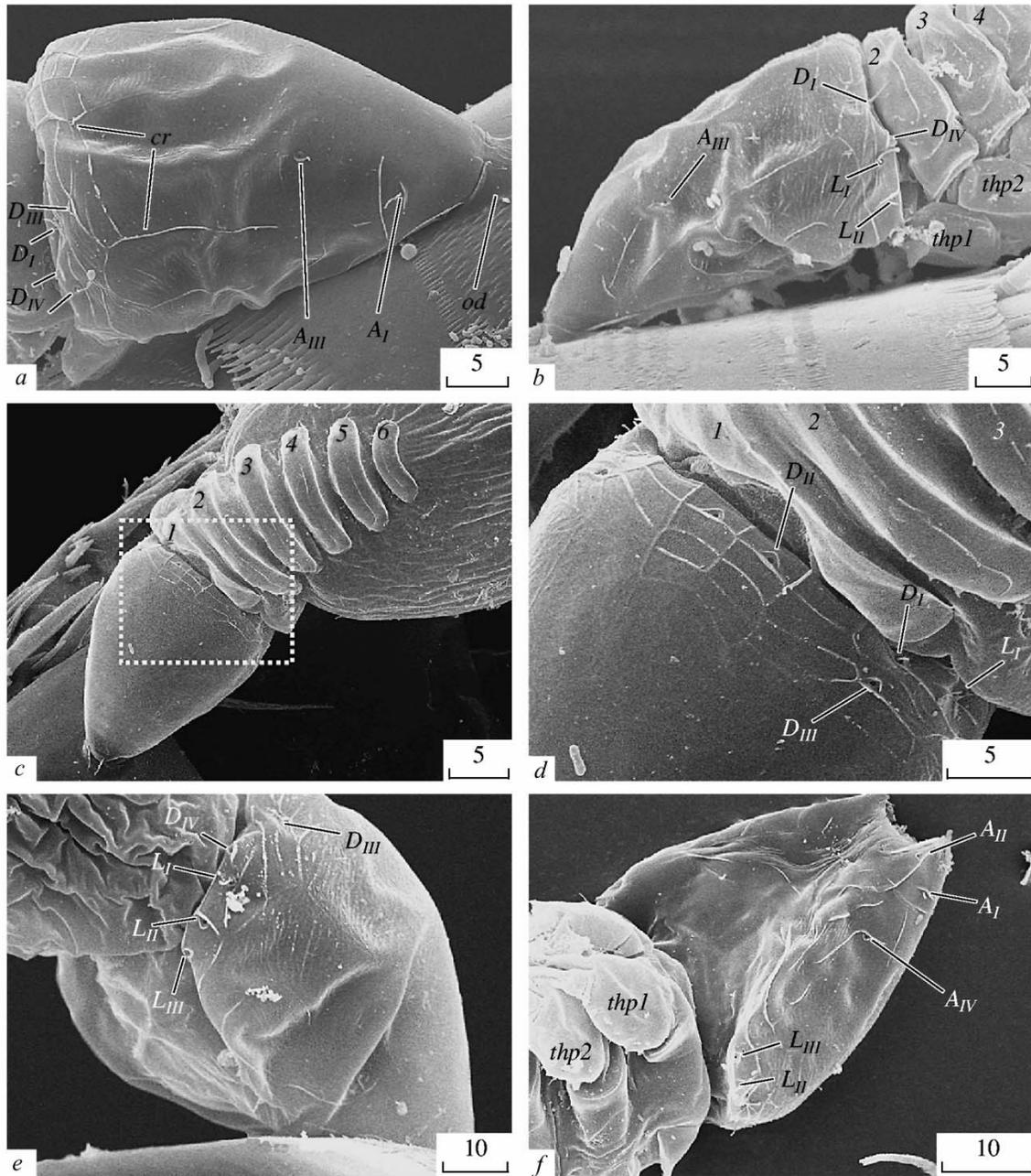


**Fig. 5.** Infested hosts and external morphology of *Arcticotantulus pertzovi*: four tantulus larvae (arrowheads) attached to host (a); host with male and “parthenogenetic females” developing on it (marked with dotted line) (b); attached tantulus larva, lateral view, with trunk segments numbered (c); enlarged fragment of b showing tantulus larvae with parthenogenetic eggs and male (early stage) developing inside them; thoracic tergites of tantulus larva numbered (d); tantulus larva with male at late development stage, dorsal view (e); mature “parthenogenetic female” detached from host, lateral view (f).

a thickened base and a long distal part bearing setulae (Figs. 7c, 7d).

The thoracopods are characterized by well-developed protopods formed by the fused coxa and

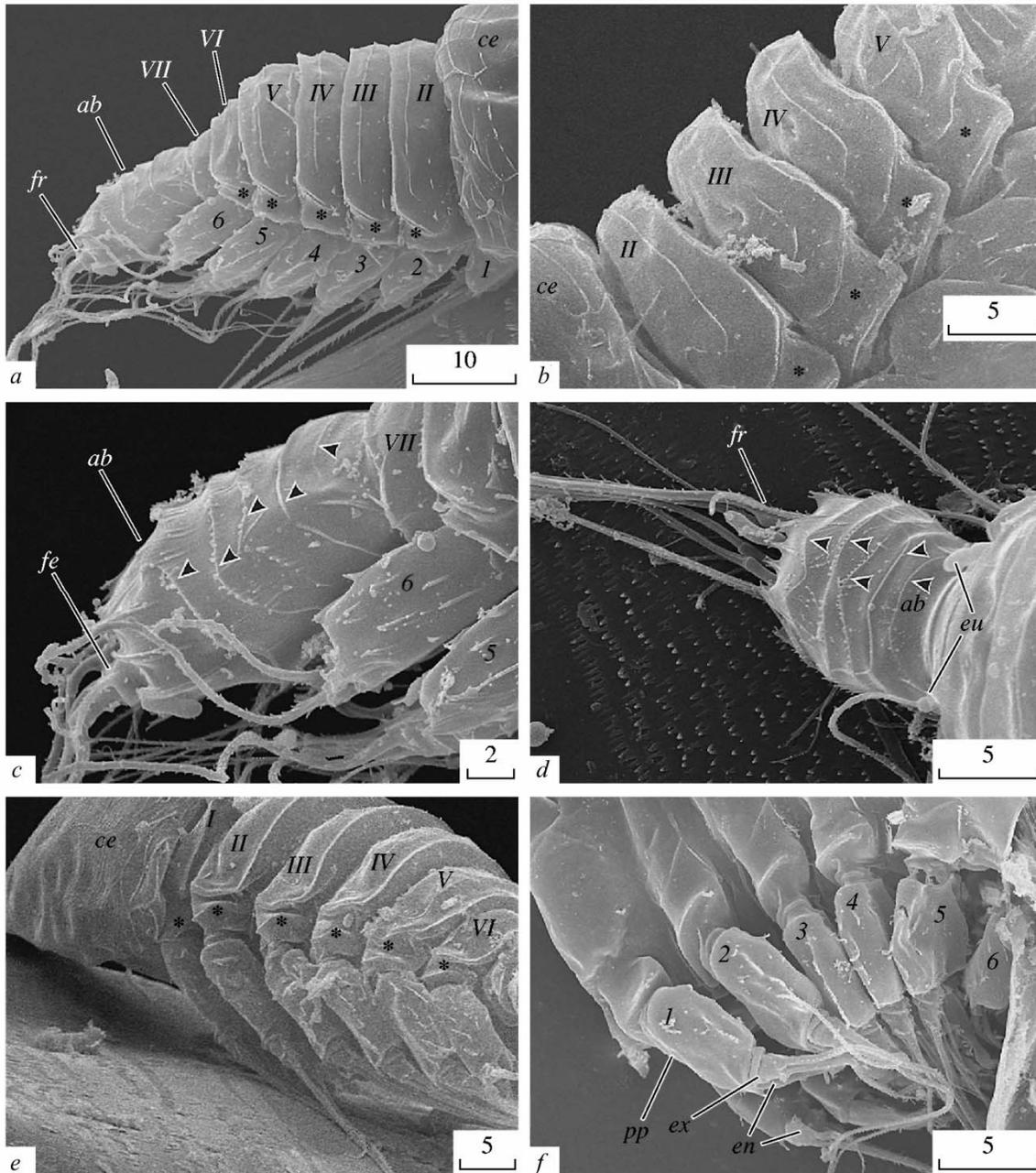
basis; thoracopods I–V are biramous, having both exo- and endopods, while thoracopod VI is uniramous, lacking an endopod (Figs. 7f, 8). The external margin of each protopod bears a row of fine cuticular spinules



**Fig. 6.** Ultrastructure of cephalon of *Arcticotantulus pertzovi*: cephalon, lateral view (a), cephalon and anterior thoracic segments (numbered), lateral view (b), cephalon and thoracic segments (numbered), dorsal view (c), enlarged fragment of c (marked with dotted line) showing posterior margin of cephalon and anterior thoracic segments (numbered), dorsal view (d), and cephalon, postero-lateral (e) and ventro-lateral (f) views.

(Fig. 8), and 1–2 spines are positioned on the posterior margin (Figs. 7a, 7f; 8d). Protopod I has a distinct spine at the inner distal corner (Figs. 7f; 8a). At the base of the protopods there are pointed triangular proximal endites with a pair of fine terminal setae (Fig. 8b). The exopods of thoracopods I–V are two-segmented: the basal segment is short and has no setae; the distal segment is longer and has one rather

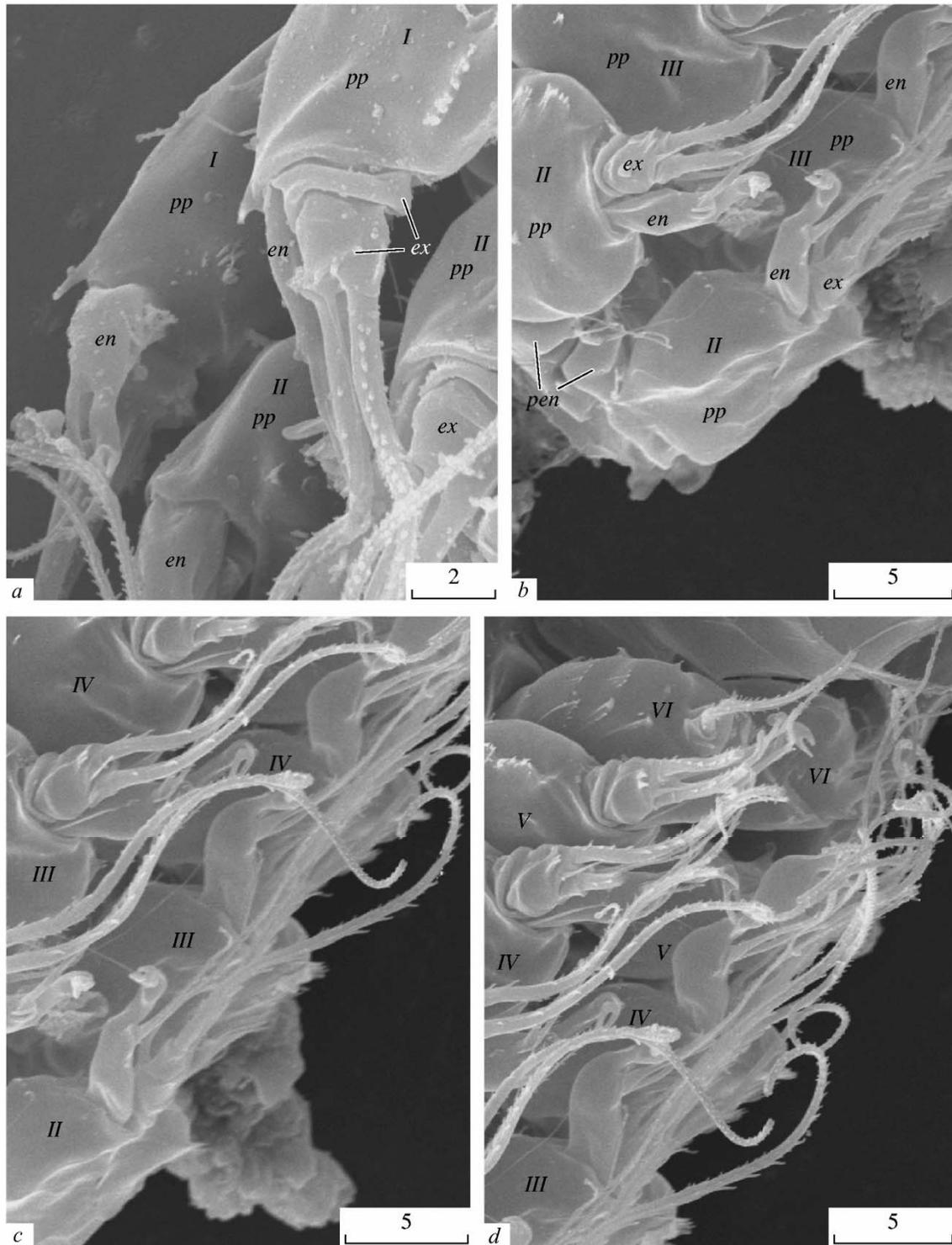
short, simple subterminal seta and a pair of long terminal ones, bearing setulae, with a fine, rudimentary simple seta in between (Fig. 8). The exopod of thoracopod VI is one-segmented and has a pair of terminal setae with setulae (Figs. 7c; 8d). The endopods are one-segmented, elongated, and end with a curved fork; endopods II–V bear a pair of subterminal setae, which are absent on endopod I (Fig. 8).



**Fig. 7.** Ultrastructure of thorax, abdomen, and thoracopods of tantulus larva of *Arcticotantulus pertzovi*: trunk, lateral view, with segments numbered in Roman, thoracopods numbered in Arabic, and pleural sclerites marked with asterisks (a); thoracic tergites (numbered), lateral view, with pleural sclerites marked with asterisks (b); abdomen and furcal rami, lateral (c) and dorsal view (d), with circular folds of abdomen marked with arrowheads, 7th trunk segment and posterior thoracopods numbered in Roman and Arabic, respectively; thorax, postero-lateral view, with segments numbered and pleural sclerites marked with asterisks (e); thoracopods (numbered), lateral view (f).

The “parthenogenetic female” (Figs. 2a; 3b; 5d, 5f) develops in the way typical of all tantulo-carids. The cuticular sac in which several dozens of parthenogenetic eggs (Figs. 2c; 3b) develop into the tantulus larvae starts growing directly from the cephalon after all the trunk segments have been shed. At early stages of development (about 100 μm

long), the sac is pear-shaped with a dilated posterior end, and covered with rugose cuticle (Fig. 5d). In mature individuals the sac is about 350 μm long, including a narrow proximal portion (neck) about 90 μm long and a dilated distal portion about 260 μm long, covered with smooth cuticle (Fig. 5f).

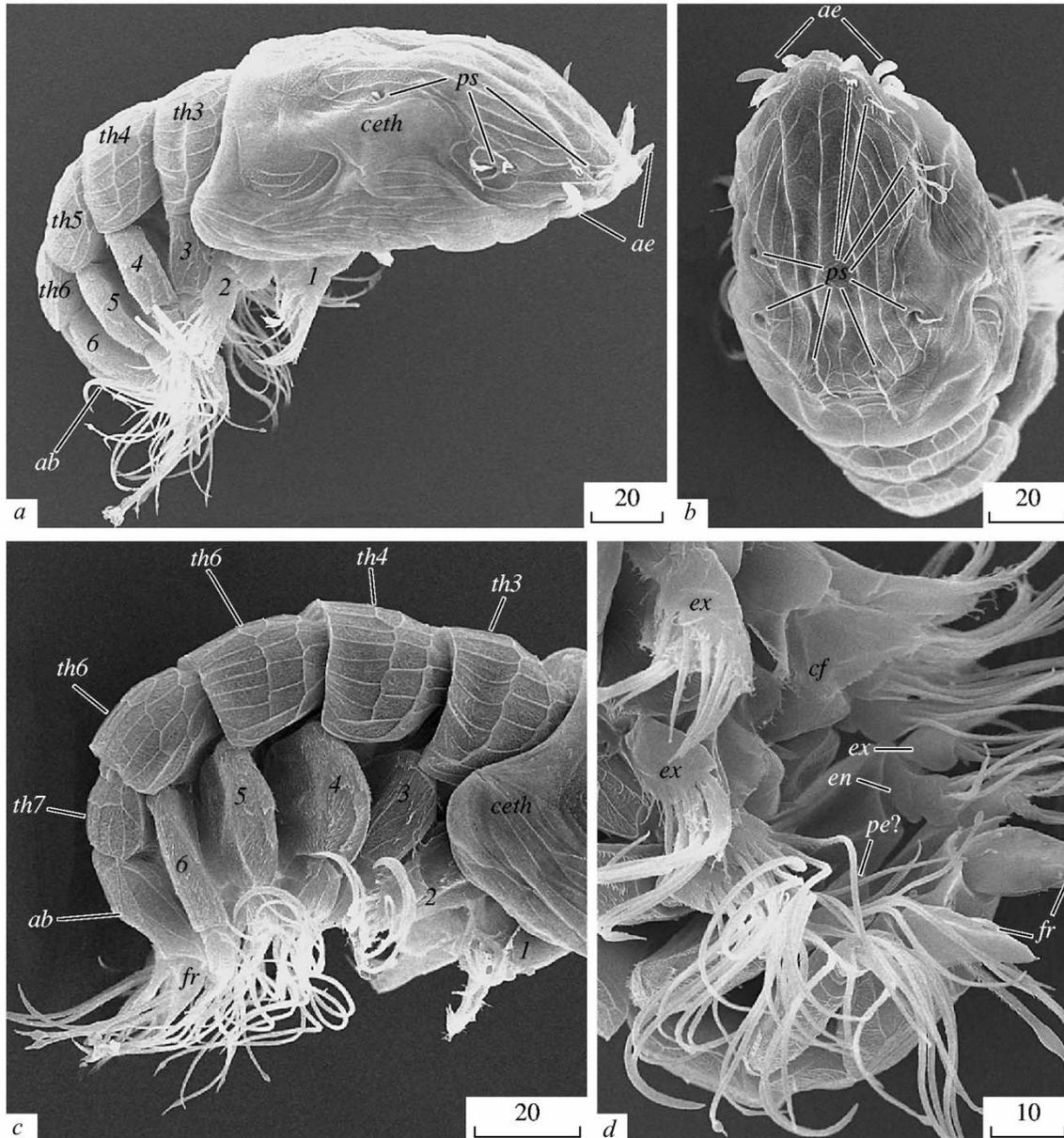


**Fig. 8.** Ultrastructure of thoracopods (numbered) of tantulus larva of *Arcticotantulus pertzovi*: thoracopods I (a), II and III (b), III and IV (c), and IV–VI (d).

**Preliminary data on the male** (Figs. 2e; 3c; 9).

The development of the male proceeds in the way typical of Tantulocarida. The male develops inside the sac, a special enlargement of the body of the tantulus

larva (Figs. 2e; 3f; 5e). The sac starts growing between the 6th and the 7th thoracic tergites and may reach 200  $\mu\text{m}$  in length. The male obtains nutrition from the special “umbilical cord” extending from its anterior



**Fig. 9.** Morphology of male of *Arcticotantulus pertzovi*: total lateral view, with thoracopods numbered (a), cephalothorax, dorsal view (b), trunk, lateral view (c), and thoracopods and abdomen, ventro-lateral view (d).

end to the anterior end of the tantulus larva (Figs. 2e; 3c). This cord evidently serves for transport of nutrients obtained from the host. The posterior end of the developing male is bent under the anterior portion of the body. The mature male breaks the sac wall and gets out into the water.

The definitive male is about 260  $\mu\text{m}$  long. Its body consists of a cephalothorax, free thoracic segments, and an abdomen (Fig. 9a). The cephalothorax is about 110  $\mu\text{m}$  long; it consists of the fused cephalic and two thoracic segments and is covered with a head shield

dorsally and laterally (Figs. 9a, 9b). The first six thoracic segments, including those fused with the cephalon, bear well-developed natatory thoracopods (Figs. 9a, 9c). The 7th trunk (thoracic?) segment has no thoracopods but bears a rudimentary blunt ventral outgrowth, interpreted as a penis (Fig. 9d).

The anterior end of the male body bears paired bunches of aestetasci (four in each), originating directly from the body surface and probably representing antennular rudiments (Figs. 9a, 9b). The cephalic appendages are absent. The head shield is covered with

distinct symmetrical cuticular ridges forming polygonal cells. The surface of the head shield has noticeable single or double pores with setae (Figs. 9a, 9b), located symmetrically except for an unpaired pore lying on the left side of the shield in its middle portion. The double pores are located at the anterior margin and at 1/3 the shield length from it. One pair of single pores lies in the middle part of the shield, and the other is shifted to its posterior margin. Thus, the head shield has six or seven (if we consider the unpaired pore as an abnormality and assume that a symmetrical pore should be present on the right side) pairs of pores. The structures resembling the lattice organs of Thecostraca are absent.

The free thoracic segments have well-developed tergites, whose entire surface is covered with cuticular ridges forming tetragonal (less frequently polygonal, especially on the posterior segments) cells arranged in three transversal rows (Fig. 9c). The segments decrease in size from the 3rd to the 7th.

The thoracopods have well-developed, large protopods covered with numerous fine cuticular spinules (Fig. 9c). The first five pairs of thoracopods are biramous; their unsegmented exopods bear six setae with setulae, which are larger in the posterior pairs. The endopods are two-segmented, their basal segment has no setae, and the distal one bears 5 setae with setulae. Thoracopods VI are uniramous; their exopods most probably bear 5 setae (Fig. 9d). The inner surfaces of anterior thoracopods are underlain by a thin cuticular fold with a fringed margin (Fig. 9d).

The abdomen is unsegmented, elongate, about 26  $\mu\text{m}$  long. It is covered with cuticular ridges, and its posterior end bears lancet-shaped, unsegmented furcal rami about 15  $\mu\text{m}$  long. Each ramus bears 3 subterminal setae covered with setulae, and originating from their dorsal surface (Figs. 9c, 9d).

## DISCUSSION

Our studies of the morphology of tantulus larvae of *A. pertzovi* add new details to the description of this species based on light microscopy (Kornev et al., 2004).

First of all, we have obtained more precise information concerning the number and structure of the cephalic pores. The cephalic pore formula was originally believed to be  $A_{III}, D_I, D_{IV}, L_I$ , even though the presence of only four pairs of head pores would be a unique feature for Tantulocarida. In reality, *A. pertzovi*

possesses at least 11 pairs of cephalic pores ( $A_I-A_{IV}, D_I-D_{IV}, L_I-L_{III}$ ). This set and morphology of pores is typical of tantulocarids from the families Basipodellidae and Deoterthridae (Huys, 1990; Boxshall and Vader, 1993; Huys et al, 1993, 1997; Ohtsuka and Boxshall, 1998). We have also demonstrated the presence of setae on the endopod of thoracopods II and the presence of three well-developed and one rudimentary seta on the exopods of thoracopods I–V. The thoracic tergites have a transversal cuticular ridge, while the abdomen is characterized by five, rather than six, cuticular folds.

It was previously noted that *A. pertzovi* occupied an intermediate position between the families Basipodellidae and Deoterthridae, because the sac enveloping the male had a very small additional anterior dilation between the cephalon and the first tergite (Kornev et al., 2004). The cited authors originally assigned *A. pertzovi* to the family Basipodellidae, for the reason that the species *Rimitantulus hirsutus* Huys et Conroy-Dalton 1997, also showing a small additional dilation of the sac, had been placed into that family (Huys and Conroy-Dalton, 1997). However, the description of the sac of *R. hirsutus* refers to an early stage of the male development. On the contrary, *A. pertzovi* lacks an additional dilation even at a late stage of male maturation, and should therefore be assigned to the family Deoterthridae by this character.

In fact, the distribution of tantulocarid species over these two families is clearly artificial, depending on the authors' bias rather than on the actual phylogenetic relations. G.A. Boxshall and R. Huys (1989) admitted that the family Basipodellidae had been initially based on plesiomorphic characters and might therefore be paraphyletic. One of the cited authors (Huys, 1990) noted in his revision of Deoterthridae that even though the main sac in Basipodellidae was formed behind the 6th tergite, it also revealed a dilation between the cephalon and the 1st tergite that was absent in Deoterthridae. After a rostrum was described in *Basipodella* (Boxshall and Lincoln, 1983), R. Huys (1990) mentioned the presence of a rostrum as a character shared by all members of Basipodellidae. However, the subsequently described species of other genera, also placed in the family Basipodellidae, have no rostrum. Quite naturally, the subsequent diagnoses of Basipodellidae included a state of his character that was directly opposed to that observed in the nominotypical genus! Comparison of the most recent diagnoses proposed for the two families (Boxshall, 1996)

reveals no difference between them. Basipodellidae: tantulus larva without rostrum. Rami of thoracopods well-developed. Urosoma two-segmented, with circular striation. Male sac formed behind the 6th thoracic tergite. Urosoma of male two-segmented, with cylindrical caudal rami bearing setae. Penis well-developed, curved, with large apical opening. Deoterthridae: tantulus larva without rostrum. Rami of thoracopods well-developed. Urosoma two-segmented. Male sac formed behind the 6th thoracic tergite. Urosoma of male two-segmented, with cylindrical furcal rami bearing setae. Penis well-developed, curved, with large apical opening.

This is not surprising. Seven genera of Tantulocarida have been placed in Basipodellidae, and ten genera, in Deoterthridae (table). We have compiled a table in which all the genera from both families can be compared by nine principal morphological characters (table). As can be seen from the table, many characters (cephalic pore formulas, morphology of thoracopods and abdomen) overlap in species from the two families. There are several characters, namely the presence of circular abdominal folds and the structure of the posterior dorsal margin of abdomen, according to which these species can be subdivided into two groups. According to these characters, only the genera *Amphitantulus*, *Cumoniscus*, and *Deoterthron* can be grouped together in a separate taxon. An additional dilation of the sac is a character known for some but not all genera (there is no information for the genera described from attached tantulus larvae). In addition, this character is not correlated with abdominal morphology.

All the above facts indicate that a serious revision of tantulocarids of the group Basipodellidae–Deoterthridae is necessary.

The different development stages of males were described for only several species of tantulocarids: *Coralliotantulus coomansi* (Huys, 1990b), *Deoterthron lincolni* (Boxshall, 1988), *Doriphallophora harrisoni* (Boxshall et Lincoln, 1987), *Itoitantulus miso-phricola* Huys, Ohtsuka et Boxshall, 1992, *Microdajus aporosus* Grygier et Sieg, 1988, *Microdajus langi* Greve, 1965, *Microdajus pectinatus* Boxshall, Huys et Lincoln 1989, *Onceroxenus birdi* Boxshall et Lincoln, 1987, *Paradoryphallophora inusitata* Ohtsuka et Boxshall, 1998, and *Stygotantulus stocki* Boxshall et Huys, 1989 (Boxshall and Lincoln, 1987; Boxshall, 1988; Grygier and Sieg, 1988; Boxshall and Huys, 1989;

Boxshall et al., 1989; Huys et al., 1992; Ohtsuka and Boxshall, 1998). All the males examined were immature and remained inside the cuticular sacs of the tantulus larvae. The morphology of males at later development stages (removed from the sacs) was studied in more or less sufficient detail for six species: *C. coomansi*, *D. harrisoni*, *M. aporosus*, *M. langi*, *M. pectinatus*, *P. inusitata*, and *S. stocki*. G.A. Kolbasov was the first to obtain a mature free-swimming male of a tantulocarid (*A. pertzovi*) and study the definitive morphology of this stage. The preliminary data are included in this communication, and the results of a detailed morphological study will be published separately.

It should be noted that morphology of the male of *A. pertzovi* largely corresponds to the descriptions of other males. The cuticular ridges are also typical of the head shield and thoracomeres of *C. coomansi*, *M. pectinatus*, *P. inusitata*, and *S. stocki*. The pores with setae appear to be characteristic of the cephalothoracic shield of all tantulocarid males. Moreover, the arrangement of the pores is nearly identical in all the species examined. Seven pairs of the same pores were described in males of *C. coomansi* (Huys, 1990b) and *M. pectinatus* (Boxshall et al., 1989); this number may be general for Tantulocarida (Huys, 1990b). The males of *D. harrisoni* and *P. inusitata* were reported to have six pairs of pores (Boxshall and Lincoln, 1987; Ohtsuka and Boxshall, 1998), the arrangement of which is similar to that observed in our species. Eight pairs of setae were reported for the carapace of *M. aporosus* (Grygier and Sieg, 1988) but the number of pores in the species was not specified (one pore may house one or two setae).

All tantulocarid males are characterized by the presence of two bunches of aestetascs (each with 4 aestetascs) at the anterior body end. The aestetascs of crustaceans are modified setae. In the sister taxon, the class Thecostraca, the aestetascs typically occur on the antennulae of free-swimming larvae (Høeg and Kolbasov, 2002; Kolbasov and Høeg, 2007), therefore it stands to reason to assume that they represent antennular rudiments in Tantulocarida (Boxshall and Lincoln, 1987; Boxshall, 1991).

All the males previously studied were characterized by a long and curved, stylet-like “penis,” located on the 7th trunk segment. At the same time, the free-swimming male of *A. pertzovi* has a rudimentary “penis.”

The main morphological characteristics of genera of the families Basipodellidae (B) and Deoterthridae (D)

Genus	Cephalic pores	Rostrum	T1	T2	T3-5	Structures on endites	Circular folds of abdomen	Posterior dorsal margin of abdomen	Additional sac dilation between cephalon and 1st thoracic tergite
<i>Arcticotantulus</i> (B)	$A_I-A_{IV}, D_I-D_{IV}, L_I-L_{III}$	absent	3 + 1-0	3 + 1-2	3 + 1-2	2 long setae	present (5)	dentate	absent
<i>Basipodella</i> (B)	$D_I, L_I$ (?)	present	2-0	3-2	3-2	1 spinule	present (4)	?	present
<i>Hypertantulus</i> (B)	$A_I-A_{IV}, D_I-D_{IV}, L_I-L_{II}$	absent	2-1	4-2	4-2	1 spinule	present (4)	dentate	present
<i>Nipponotantulus</i> (B)	$A_I-A_{IV}, D_I-D_{IV}, L_I-L_{IV}$	absent	2-0	3-2	4-2	2 spinules (T1 without endite)	present (3)	dentate	present
<i>Polyhyapodella</i> (B)	$A_I-A_{IV}, D_I-D_{IV}, L_I-L_{IV}, V_I, M$	absent	2-0	3-2	4-2	1-2 spinules	present (4)	dentate	present
<i>Rimitantulus</i> (B)	$A_I-A_{IV}, D_I-D_{IV}, L_I-L_{IV}$	absent	2 + 1-0	4 + 1-2	5-2	1 spinule	present (5)	dentate	present
<i>Stygotantulus</i> (B)	$A_I, D_{III}-D_{IV}$ (?)	absent	2-1	4-2	4-2	1-2 spinules	present (5)	dentate	present
<i>Amphitantulus</i> (D)	$A_I-A_{IV}, D_I-D_{IV}, L_I-L_{IV}, V_I$	absent	4-1	5-2	5-2	2 spinules	absent	no denticles	absent
<i>Aphotocentor</i> (D)	$A_I-A_{IV}, D_I-D_{IV}, L_I-L_{II}$	absent	3-0	5-2	5-2	2 spinules	present (5)	dentate	no data
<i>Boreotantulus</i> (D)	$A_I-A_{IV}, D_I-D_{IV}, L_I$	absent	3-1	2-2	2-2	1-2 spinules	present (3)	dentate	no data
<i>Campyloxiphos</i> (D)	$A_I-A_{IV}, D_I-D_{IV}, L_I-L_{II}$	absent	2-?	4-2	4-2	1 spinule	present (4)	dentate	no data
<i>Coralliotantulus</i> (D)	$A_I-A_{IV}, D_I-D_{IV}, L_I-L_{III}$	absent	2-1	4-2	4-2	1-2 spinules	present (5)	dentate	absent
<i>Cumoniscus</i> (D)	$A_I-A_{IV}, D_I-D_{IV}, L_I-L_{IV}, V_I$	absent	?	5-2	5-2	1 spinule	absent	no denticles	no data
<i>Deoterthron</i> (D)	$A_I-A_{IV}, D_I-D_{IV}, L_I-L_{II}$	absent	2-1	5-2	5-2	1-2 spinules	absent	no denticles	absent
<i>Dicrotrichura</i> (D)	$A_I-A_{IV}, D_I-D_{IV}, L_I-L_{II}$	absent	2-0	3-2	4-2	2 spinules	present (4)	dentate	no data
<i>Itoitantulus</i> (D)	$A_I-A_{IV}, D_I-D_{IV}, L_I-L_{III}, M_I-M_{II}$ ( $A_I-A_{IV}, D_I-D_{IV}, L_I-L_{III}, M_I$ ) <sup>*</sup>	absent	2-0	4-2	4(5)-2	2 spinules	present (5)	dentate	absent
<i>Tantulacus</i> (D)	$A_I-A_{IV}, D_I-D_{IV}, L_I-L_{III}$	absent	2*-1	4-2	5(4)-2	1-2 spinules	present (3)	dentate	no data

Notes: ? indicates the absence of data, (?) insufficient data. Two alternative formulas of the head pores are given for the genus *Itoitantulus*, because some of them cannot be reliably characterized as anterior or median. Only two setae are included for the exopodite of thoracopod I in the genus *Tantulacus*; two more setae mentioned in the description (Huys et al., 1992) are basal setulae.

The differences in the thoracopod segmentation in males should also be noted. It was previously assumed that the endopods were always unsegmented, and the protopods were two-segmented, consisting of the coxa and the basis. The species examined, however, has unsegmented protopods and two-segmented endopods. The basal segment of endopods may have been previously mistaken for the basis of protopod.

Based on the body segmentation pattern: six pairs of thoracopods on the first six thoracomeres, the penis located on the 7th trunk segment, and the female gonopore located on the 1st thoracic segment, the class Tantulocarida should be regarded as a sister taxon of the class Thecostraca (Facetotecta, Ascothoracida, Cirripedia) (Huys et al, 1993b). In addition, the sexual stages (especially males) of tantulocarids externally resemble the cypridiform larvae of thecostracans. It is therefore natural that some authors placed the tantulocarids into Thecostraca (Newman, 1992). Still, all representatives of Thecostraca are characterized by five pairs of sensory lattice organs on the head shield, which is a synapomorphy of the group (Høeg and Kolbasov, 2002). These structures are absent in all stages of Tantulocarida, which should undoubtedly 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 pores of tantulocarids and the lattice organs of thecostracans cannot be completely ruled out.

Abbreviations used in the figures: *A<sub>I-IV</sub>*, anterior pores of the cephalon; *ab*, abdomen; *ae*, aestetases; *ce*, cephalon; *ceth*, cephalothorax; *cf*, cuticular fold; *cr*, cuticular ridges; *D<sub>I-IV</sub>*, dorsal pores of the cephalon; *eg*, parthenogenetic eggs; *en*, endopod; *es*, egg sac; *ex*, exopod; *eu*, epaulets; *fe?*, probable "parthenogenetic female;" *fr*, furcal rami; *gl?*, probable glands; *L<sub>I-III</sub>*, lateral pores of the cephalon; *ml*, male; *od*, oral disk; *pe?*, probable penis; *pen*, proximal endites, *pp*, protopod, *ps*, pores with setae, *st*, stylet; *th1-6*, thoracomeres; *thp1-6*, thoracopods; *tr7*, 7th trunk segment; *uc*, "umbilical cord."

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