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Postembryonic development of males of *Polyphemus pediculus* (Linnaeus, 1761) (Cladocera: Onychopoda)

Постэмбриональное развитие самцов *Polyphemus pediculus* (Linnaeus, 1761) (Cladocera: Onychopoda)

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KEY WORDS: Crustacea, Branchiopoda, Polyphemidae, *Polyphemus*, cladocerans, ontogenesis, morphology.

КЛЮЧЕВЫЕ СЛОВА: Crustacea, Branchiopoda, Polyphemidae, *Polyphemus*, ветвистоусые ракообразные, онтогенез, морфология.

ABSTRACT: The postembryonic development of males of *Polyphemus pediculus* (Linnaeus, 1761) (Crustacea: Cladocera) was studied for the time in detail. Male postembryonic development includes two juvenile and a single mature instar. Stages differ in sizes of the testes, shape and size of penis, size of setae on the antenna I, morphology of copulatory hooks and armature of the endopodite distal segments of the first two pairs of thoracic limbs. Based on these data, it can be concluded that males of *P. pediculus* have passed through two moults during juvenile phase, as the females of this species. Morphology of two juvenile instars was studied by scanning electron microscopy and described in details for the first time.

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РЕЗЮМЕ: Впервые подробно исследовано постэмбриональное развитие самцов *Polyphemus pediculus* (Linnaeus, 1761). Развитие самцов включает в себя три возраста, из которых два — ювенильных. Постэбриональные стадии развития надежно отличаются друг от друга по размеру семенников, размеру и форме пенисов, размерам щетинок антеннул, морфологии хватательных крюков и вооружению дистальных члеников эндоподитов первых двух пар туловищных конечностей. На основании этих данных можно заключить, что самцы *P. pediculus* претерпевают две ювенильные линьки, что характерно и для самок этого вида. Впервые подробно изучено и описано внешнее морфологическое строение ювенильных самцов двух возрастов и представлены фотографии, полученные методом сканирующей электронной микроскопии.

Introduction

There are two main types of reproduction in Cladocera (Crustacea: Branchiopoda): parthenogenetic, where unfertilized eggs develop into offspring within the female brood chamber, and gamogenetic, associated with maturation of the female [Dumont, Negrea, 2002]. During the transition of a population to a sexual reproduction, males start to appear from parthenogenetic eggs. For example, in *Daphnia* Müller, 1776 (Daphniidae, Anomopoda), appearance of males in the population is triggered by the external condition changes, such as shortening of the photoperiod, lowering of temperature, or food limitation [Stross, Hill, 1965, 1968; Korovchinsky *et al.*, 2021]. The appearance of males in a population of *Daphnia* happens due to an increasing of the secretion of the terpenoid hormone methyl farnesoate by the mandibular glands [Toyota *et al.*, 2015]. Male cladocerans are smaller in size than females, they have underdeveloped brood chambers, and modified first pair of the thoracic limbs. The distal endopodite segment of the first thoracic limb is equipped with a hook, which is used to hold the female during copulation. In some cladocerans, the hook is secondarily reduced [Korovchinsky, 2004; Kotov, 2013]. Other sexual features of the males differ among representatives of different orders and families.

Males of Ctenopoda have an enlarged antenna I that bears a group of aesthetascs on the lateral side, while in females, aesthetascs are located only distally.

Males have a long serrated bristle at the distal end of the antenna I. Copulatory organs in most ctenopod males are represented by paired penises located ventro-laterally just behind the fourth pair of thoracic limbs. The absence of copulatory appendages in some genera (*Sida* Straus, 1820, *Limnosida* Sars, 1862, *Holopedium* Zaddach, 1855) is apparently a plesopmorphic trait [Korovchinsky, 2004].

Males of Anomopoda differ from females in having enlarged antenna I, the ratio of its size in males and females varies among different families. Copulatory organ is a modified part of a postabdomen, with paired gonopores in most species. Less commonly, gonopores open on special paired elevations (some *Daphnia* species) or on a non-paired penis-shaped protuberance of the postabdomen, as in *Leydigia leydigi* (Schödler, 1863) and some *Alona* species [Kotov, Sinev, 2004; Kotov, 2013]. A large single gonopore located on the postabdomen distal end is present in few cladoceran, like bosminids [Kotov *et al*., 2009].

Males of Haplopoda differ from females in the external structure of antenna I and presence of a cylindrical outgrowth on the endopodite of the first pair of limbs. The antenna I of Haplopoda males is significantly longer than those of females and bears an additional row of aesthetascs. A cylindrical protrusion covered by spines is located on the distal segment of the endopodite of the first pair of thoracic limbs, which, along with a row of protrusions on the third endopodite segment, serves to hold the female during copulation. Specialized copulatory organs are not developed in the haplopod males, and gonopores open on the ventral side of the third abdominal segment [Boykova, 2005; Korovchinsky, Boikova, 2008; Korovchinsky *et al*., 2021].

In Onychopoda, males differ from females in the structure of antenna I and the presence of a hook on the endopodite of the first pair of thoracic limbs. The size of the antenna I in males is the same as in females, but in addition to a group of aesthetascs at their distal end, antenna I sometimes is supplied by a sensitive seta. A well-developed hook is located on the distal segment of the first pair of thoracic limbs. The gonopores of onychopod males are paired and open at the tips of paired penises, located posteriorly to the fourth pair of thoracic limbs.

According to I.K. Rivier [1998], only a single genus, *Polyphemus*, belongs to the Polyphemidae family. The genus includes two species: *Polyphemus exiguu*s G.O. Sars, 1897 and *P. pediculus* (Linnaeus, 1761). *P. exiguus* is an endemic species of the Caspian Sea, while *P. pediculus* is a widely distributed freshwater species. There is currently no data available on the postembryonic development of *P. exiguus*.

Studies of *P. pediculus* has been carried out since the 18th century. Representatives of this species were among the first cladocerans described by carconologists [Kotov, 2020]. The first description of *P. pediculus* was provided by Linnaeus [1761]. Then this species was found to be distributed worldwide in freshwater bodies, and being an important part of the ecosystem. The life cycle of *P. pediculus* does not differ from that of most other cladocerans and includes two types of reproduction: parthenogenetic and sexual [Rivier, 1998].

A significant contribution to the study of *P. pediculus* was made by L.G. Butorina, who devoted her scientific life to the description of the structure, behaviour, and ecology of this species. She found that the lifespan of males is shorter than that of females and its duration depends on the number of copulations they have. The juvenile male passes through a single moult soon after its birth, and then becomes sexually mature [Butorina, 1971]. An adult male of *P. pediculus* is smaller than an adult female and has a copulatory hook on the distal segment of its first thoracic limb. The brood pouch of the male is poorly developed, and it is filled with two enlarged testes. From the testes, two vasa deferentia extend to the small paired penises, located under the fourth pair of thoracic limbs. But there is currently no detailed description of the juvenile male in the literature.

This study aims to describe the juvenile instars of *P. pediculus* male, and contrubute to the understanding of its morphology.

Materials and Methods

Samples were collected using a plankton net in Krugloe Lake and Nizhnee Nilmozero Lake (near the White Sea Biological Station of Moscow State University, Loukhsky District, Republic of Karelia) and in Kostinsky pond (town of Korolyov, Moscow region) from July to September of 2019–2022 and fixed in 4% formaldehyde solution in distilled water. After fixation, the samples were transferred to 70% ethanol for further research and storage convenience. Additionally, some specimens were extracted from alcohol samples from a lake in Nizhny Novgorod Oblast (personal collection of A.A. Kotov).

Males of different instars were selected from the collected material under a dissective microscope. Selected specimens were placed in a drop of 70% ethanol under a cover glass. All drawings were made using a drawing apparatus attached to the high-power microscopes Leica DM250, Leica DMLS, and Olympus BX41.

All measurements were made for specimens collected from the Nizhnee Nilmozero using a drawing apparatus and the eyepiece micrometer according to the outline proposed by Mordukhai-Boltovskoy & Rivier [1987], with some modifications (Fig. 1).

For scanning electron microscopy, males were placed in permeable containers made from 1.5 ml vials covered by a plankton net with mesh size of 150 microns. The containers with males were transferred from 70% ethanol to 96% ethanol, and then to acetone, and subjected to critical point drying. Drying and sputtering with a gold and palladium blend were carried out at the Interdepartmental Laboratory of Electron Microscopy (ILEM) and at the White Sea Biological Station of MSU (WSBS MSU). JSM-6380, Camscan S-2 and JCM-7000 scanning electron microscopes were used in this study.

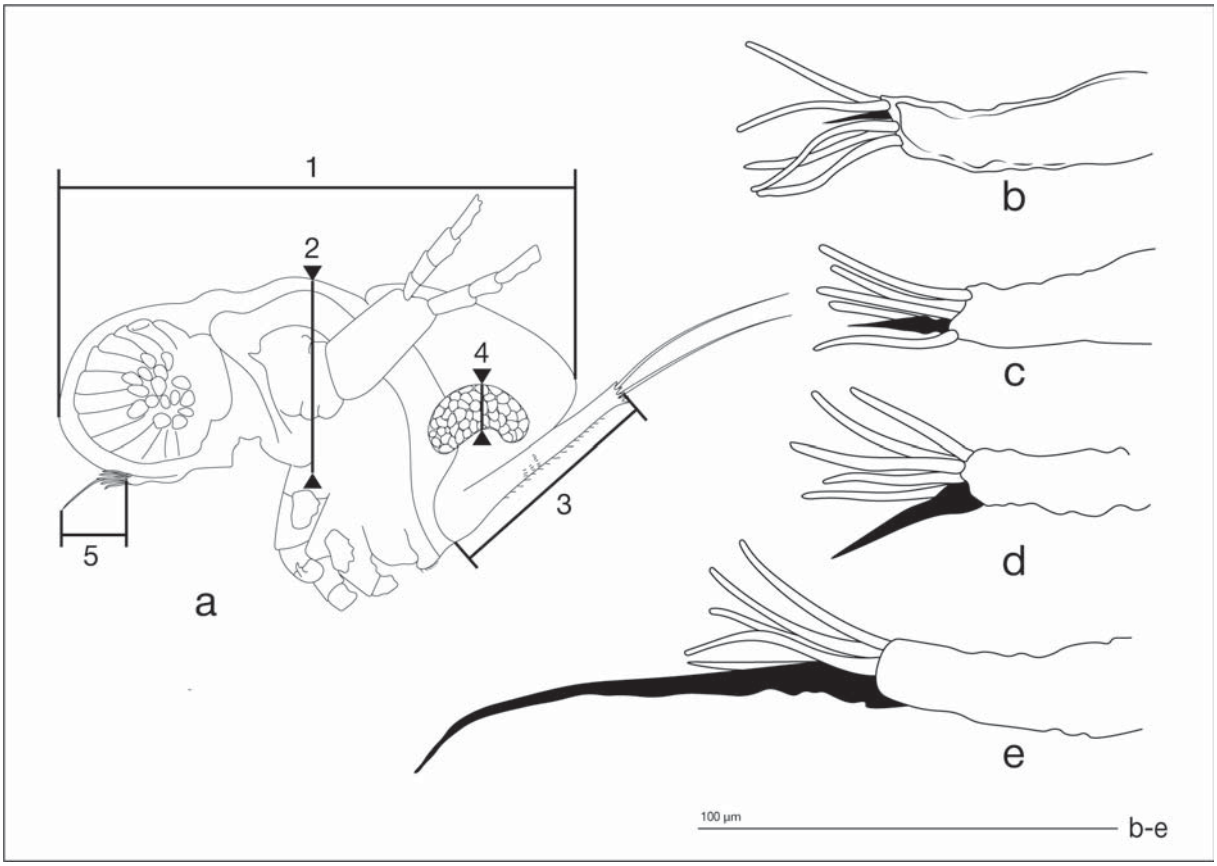

Fig. 1. *Polyphemus pediculus*: a — measurement scheme for males, 1 — body length, 2 — body width, 3 — length of the caudal spine, 4 — width of testes, 5 — length of the antenna I, b–e – antenna I, b — mature female, c — juvenile male I, d — juvenile male II, e — mature male. Scale: b–e — 0.1 mm.

Рис. 1. *Polyphemus pediculus*: a — схема измерений самца, 1 — длина тела, 2 — ширина тела, 3 — длина каудального выроста, 4 — максимальная ширина семенника, 5 — длина первой антенны, b–e — 1-я антенна, b — взрослая самка, c — ювенильный самец 1-го возраста, d — ювенильный самец 2-го возраста, e — взрослый самец. Масштаб: b–e — 0,1 мм.

Results

Finally, we have differentiated two juvenile instars in the postembryonic development of *P. pediculus* male. They differ from each other in the size of body and testes, length of a sensitive seta located on the distal end of the antenna I (Fig. 1), and the degree of development of the hooks on the distal segment of the endopodite of the first pair of thoracic limbs (Fig. 2). Structure of the basal segment of the endopodite and the structure of the exopodite of the first pair of thoracic limbs do not differ from those in females. The sensitive seta on the antenna I is absent in females. Juvenile instars differ from adults in smaller size of body and testes, length of antenna I setae, and underdeveloped copulatory hooks. Also, juvenile males lack penises, while they can be found under the fourth pair of thoracic limbs in adult males.

Male I

Material: About 30 males I from all sampling sites.

Description: Length is 385–509 µm. Height is 295–465 µm. Length of caudal spine 236–346 µm. Posterior margin of the carapace is slightly convex, the seminal vesicles are visible in the underdeveloped genital chamber (Fig. 3). Width of the seminal vesicles is 16–33 µm. On the distal edge of the antenna I (between the aesthetascs), there is a single sensitive seta (Fig. 1). The length of the seta is slightly shorter than that of the aesthetascs and ranges from 18–47 µm. On the distal endopodite segment of the first pair of thoracic limbs, there is a noticeable tubercle, which is the anlagen of the hook. In addition to it, there are four setae on the distal segment and the shortest seta being approximately half the length of the longest one (Figs 2, 4).

Male II

Material: About 70 males II from all sampling sites.

Description: Length is 458–647 µm. Height is 385–502 µm. Length of caudal spine is 276–451 µm. The posterior carapace margin is slightly more convex than in males I, the brood pouch is underdeveloped, paired testes are visible, and its width is 25–142 µm. There is one seta on the distal edge of the antenna I (Fig. 1). Length of the antenna I seta is 47–62 µm, approximately equal to slightly longer than the length of the aesthetascs. A broad and blunt hook is located on the

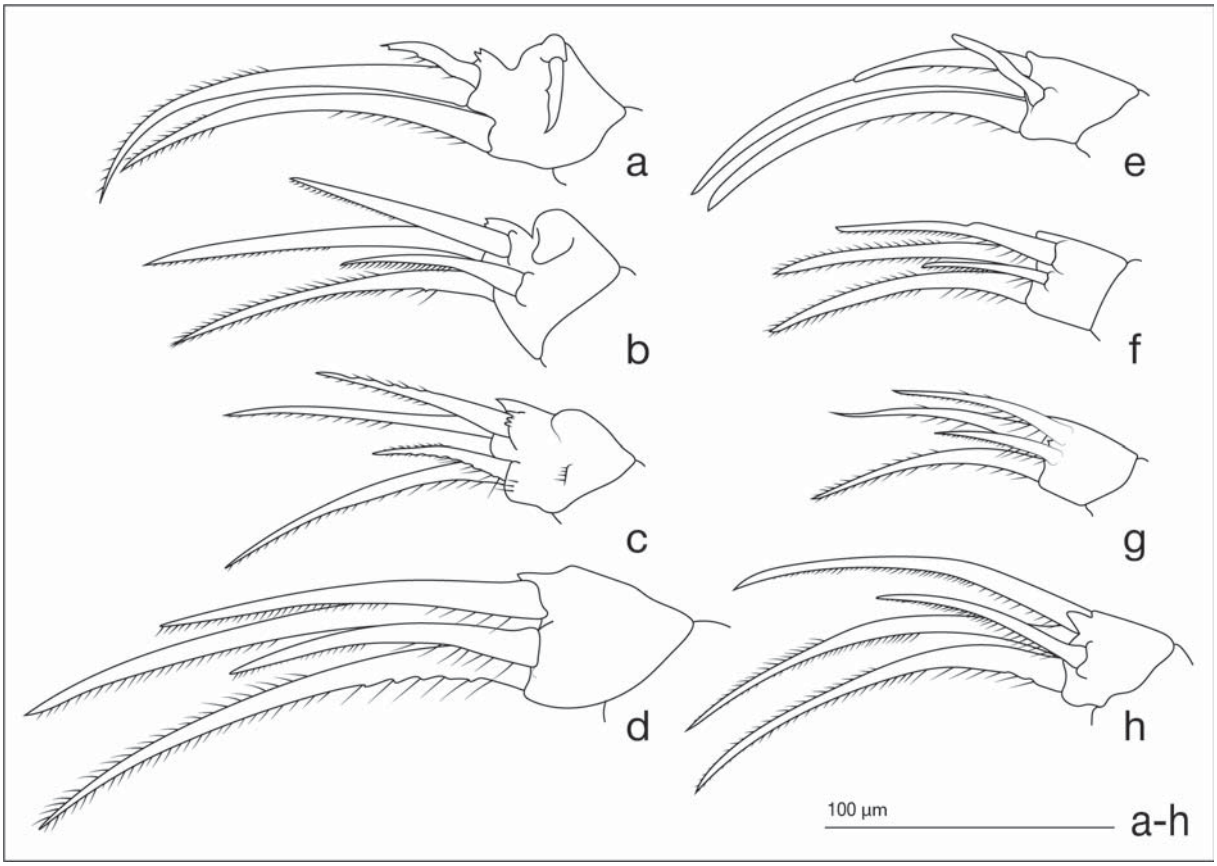

Fig. 2. Distal segments of the endopodite of the thoracic limbs of *Polyphemus pediculus*: a–d — the 1st thoracic limbs, e–h — the 2nd thoracic limbs; a, e — mature male, b, f — juvenile male II, c, g — juvenile male I, d, h — mature female. Scale: 0.1 mm.

Рис. 2. Дистальные членики эндоподитов туловищных конечностей *Polyphemus pediculus*: a–d — 1-я пара туловищных конечностей, e–h — 2-я пара туловищных конечностей; a, e — взрослый самец, b, f — ювенильный самец 2-го возраста, c, g — ювенильный самец 1-го возраста, d, h — взрослая самка. Масштаб: 0,1 мм.

distal segment of the endopodite of the first pair of thoracic limbs, the length of which is approximately equal or slightly less than half the length of the distal segment. There are also four setae on the distal segment, with the shortest seta being approximately half the length of the longest one (Figs 2, 3). Paired genital openings are located posteriorly to the fourth pair of thoracic limbs, they situated on small protuberances (Fig. 5).

Adult male

Material: About 150 mature males from all sampling points.

Description: Length is 553–840 µm. Height is 345–498 µm. Length of caudal spine is 233–424 µm. Posterior margin of the carapace is more convex than in juvenile males but less pronounced compared to that of adult parthenogenetic females, and the brood pouch is underdeveloped. There is a single seta on the distal edge of the antenna I (Figs 1, 3). The length of this seta is 1.5–3 times longer than the length of the aesthetascs and ranges from 47–142 µm. A thin hook, tapered at the end and with 1–2 spines, is located on the distal segment of the endopodite of the first pair of thoracic limbs (Figs 2, 3). The length of the hook is slightly smaller or half the length of the distal segment. There are three setae on the distal segment, with the shortest being approximately four times shorter than the longest. Paired penises are located posteriorly to the fourth pair of thoracic limbs, and the genital openings are situated on the inner surface. The distal surface of the penis is covered with setae, and length of the penis is approximately half the length of the fourth pair of thoracic legs (Figs 6, 7).

Discussion

Immediately after release from the mother brood pouch, a cladoceran embryo casts off the last embryonic membrane [Kotov, Boikova, 2001]. Following Kotov & Boikova, I do not regard such freshly released, but not moulted, embryo as a separate stage of the postembrionic development, this is the last phase of the embryogenesis, while postembryonic development starts just from the casting off the last embryonic membrane.

All three instars of the postembryonic development of *P. pediculus* males are well distinguished from each other by the degree of development of the hooks of the distal segments of the endopodites of the first pair of

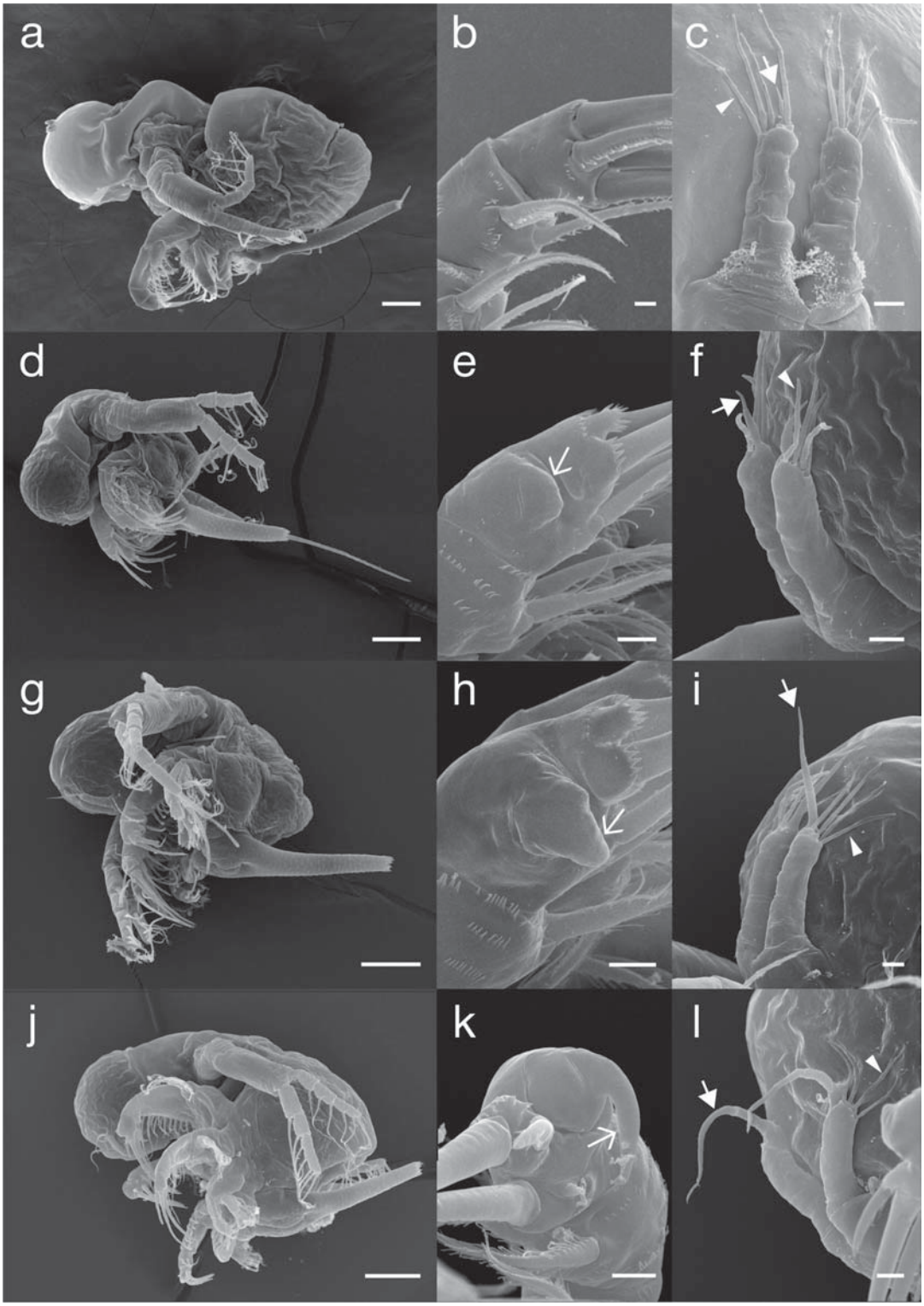

Fig. 3. Males and a female of *Polyphemus pediculus*: a–c — adult parthenogenetic female, d–f — juvenile male I, g–i — juvenile male II, j–l — mature male, a, d, g, j — general view from the lateral side, b, e, h, k — distal segment of the endopodite of the 1st thoracic limb, c, f, i, l — antennae I, thin arrows — male hook, thick arrow — antennular seta, arrowhead — aestetasks. Scales: a, d, g, j — 0.1 mm, b–c, e–f, h–i, k–l — 0.01 mm.

Рис. 3. Самцы и самки *Polyphemus pediculus*: a–c — взрослая партеногенетическая самка, d–f — ювенильный самец 1-го возраста, g–i — ювенильный самец 2-го возраста, j–l — взрослый самец, a, d, g, j — общий вид с боковой стороны, b, e, h, k — дистальный членик эндоподита 1-й пары туловищных конечностей, c, f, i, l — 1-я антенна, тонкие стрелки — хватательный крюк самца, утолщенные стрелки — щетинка 1-й антенны, треугольные указатели — эстетаски. Масштаб: a, d, g, j — 0,1 мм, b–c, e–f, h–i, k–l — 0,01 мм.

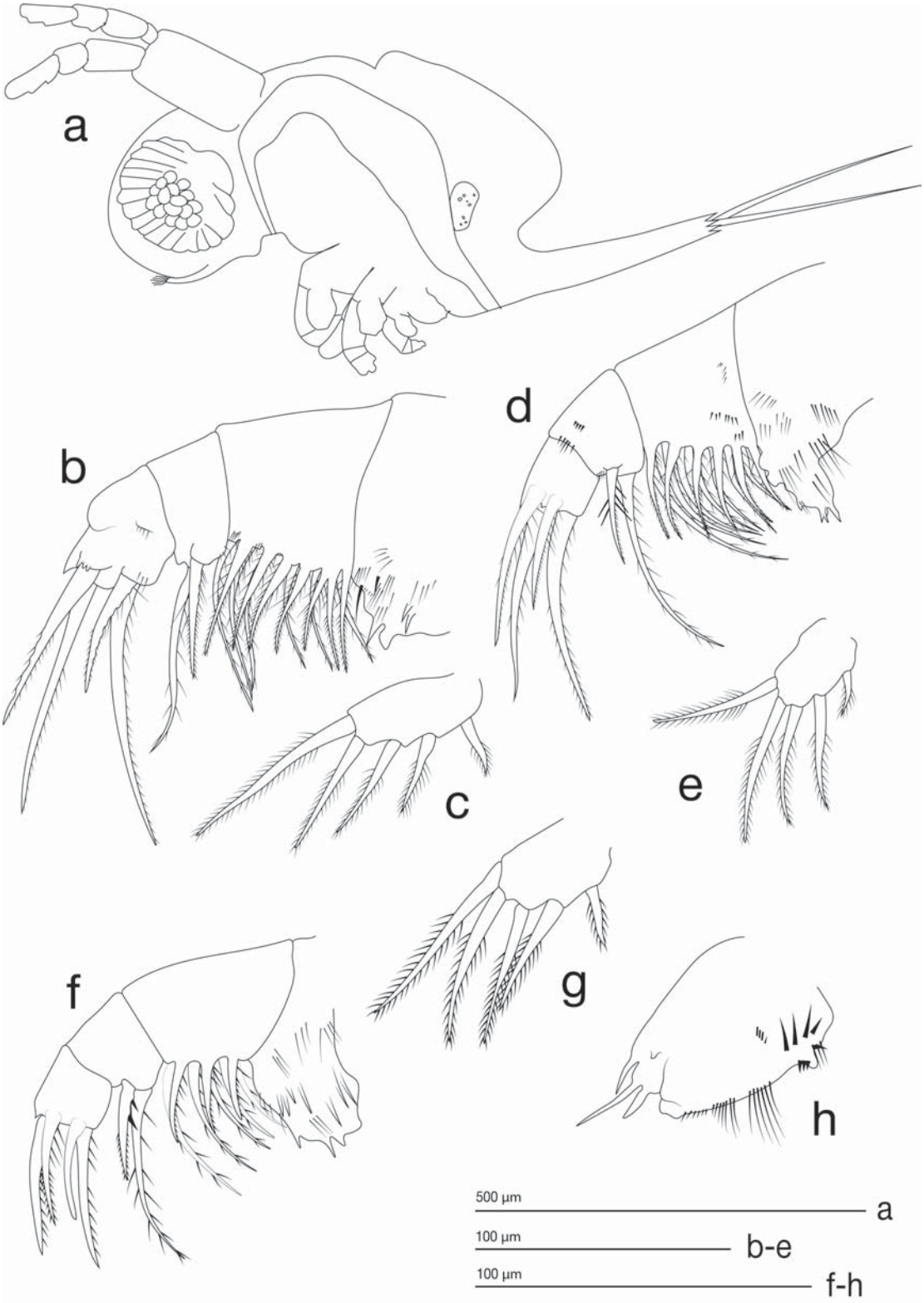

Fig. 4. Juvenile male I of *Polyphemus pediculus*: a — general view from the lateral side, b — endopodite of the 1st thoracic limb, c — exopodite of the 1st thoracic limb, d — endopodite of the 2nd thoracic limb, e — exopodite of the 2nd thoracic limb, f — endopodite of the 3rd thoracic limb, g — exopodite of the 3rd thoracic limb, h — the 4th thoracic limb. Scales: a — 0.5 mm, b–h — 0.1 mm.

Рис. 4. *Polyphemus pediculus*, ювенильный самец 1-го возраста *Polyphemus pediculus*: a — общий вид с боковой стороны, b — эндоподит 1-й пары туловищных конечностей, c — экзоподит 1-й пары туловищных конечностей, d — эндоподит 2-й пары туловищных конечностей, e — экзоподит 2-й пары туловищных конечностей, f — эндоподит 3-й пары туловищных конечностей, g — экзоподит 3-й пары туловищных конечностей, h — 4-я пара туловищных конечностей. Масштаб: a — 0,5 мм, b–h — 0,1 мм.

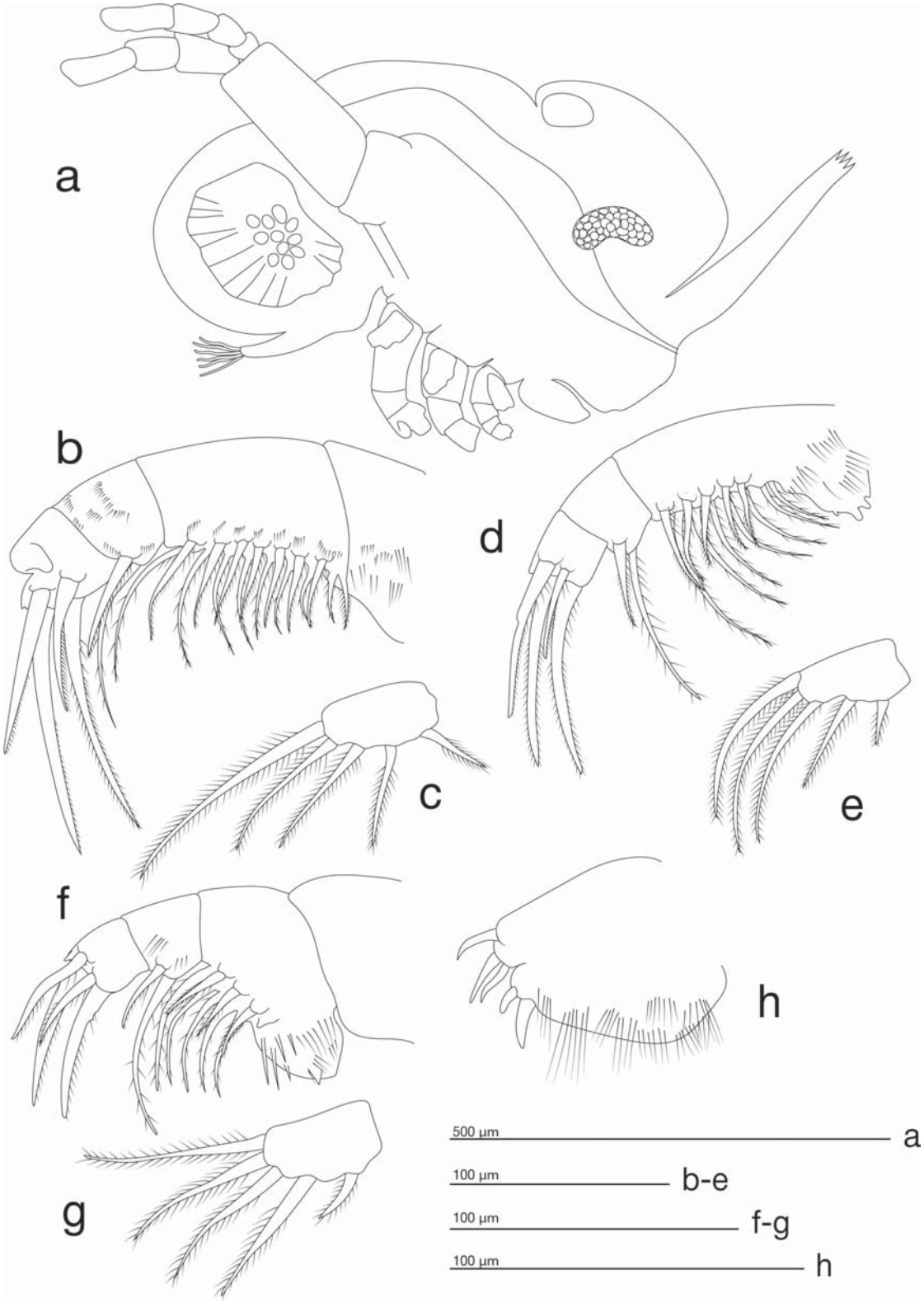

Fig. 5. Juvenile male II of *Polyphemus pediculus*: a — general view from the lateral side, b — endopodite of the 1st thoracic limb, c — exopodite of the 1st thoracic limb, d — endopodite of the 2nd thoracic limb, e — exopodite of the 2nd thoracic limb, f — endopodite of the 3rd thoracic limb, g — exopodite of the 3rd thoracic limb, h — the 4th thoracic limb. Scales: a — 0.5 mm, b–h — 0.1 mm.

Рис. 5. *Polyphemus pediculus*, ювенильный самец 2-го возраста: a — общий вид с боковой стороны, b — эндоподит 1-й пары туловищных конечностей, c — экзоподит 1-й пары туловищных конечностей, d — эндоподит 2-й пары туловищных конечностей, e — экзоподит 2-й пары туловищных конечностей, f — эндоподит 3-й пары туловищных конечностей, g — экзоподит 3-й пары туловищных конечностей, h — 4-я пара туловищных конечностей. Масштаб: a — 0,5 мм, b–h — 0,1 мм.

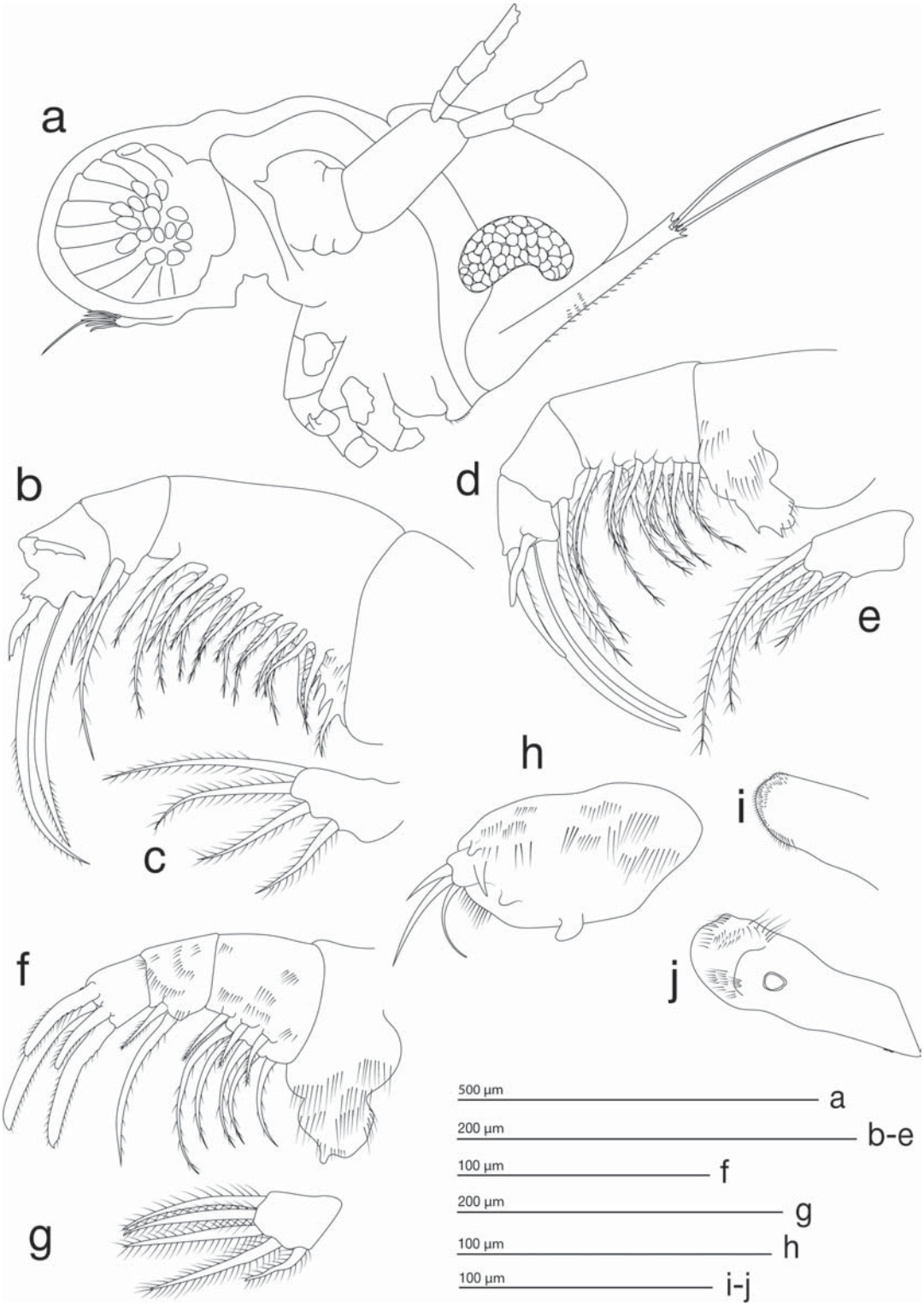

Fig. 6. Mature male of *Polyphemus pediculus*: a — general view from the lateral side, b — endopodite of the 1st thoracic limb, c — exopodite of the 1st thoracic limb, d — endopodite of the 2nd thoracic limb, e — exopodite of the 2nd thoracic limb, f — endopodite of the 3rd thoracic limb, g — exopodite of the 3rd thoracic limb, h — the 4th thoracic limb, i — penis, lateral view, j — penis, ventral view. Scales: a — 0.5 mm, b–e, g — 0.2 mm, f, h, i–j — 0.1 mm.

Рис. 6. *Polyphemus pediculus*, взрослый самец: a — общий вид с боковой стороны, b — эндоподит 1-й пары туловищных конечностей, c — экзоподит 1-й пары туловищных конечностей, d — эндоподит 2-й пары туловищных конечностей, e — экзоподит 2-й пары туловищных конечностей, f — эндоподит 3-й пары туловищных конечностей, g — экзоподит 3-й пары туловищных конечностей, h — 4-я пара туловищных конечностей, i — пенис, вид сбоку, j — пенис, вид с брюшной стороны. Масштаб: a — 0,5 мм, b–e, g — 0,2 мм, f, h, i–j — 0,1 мм.

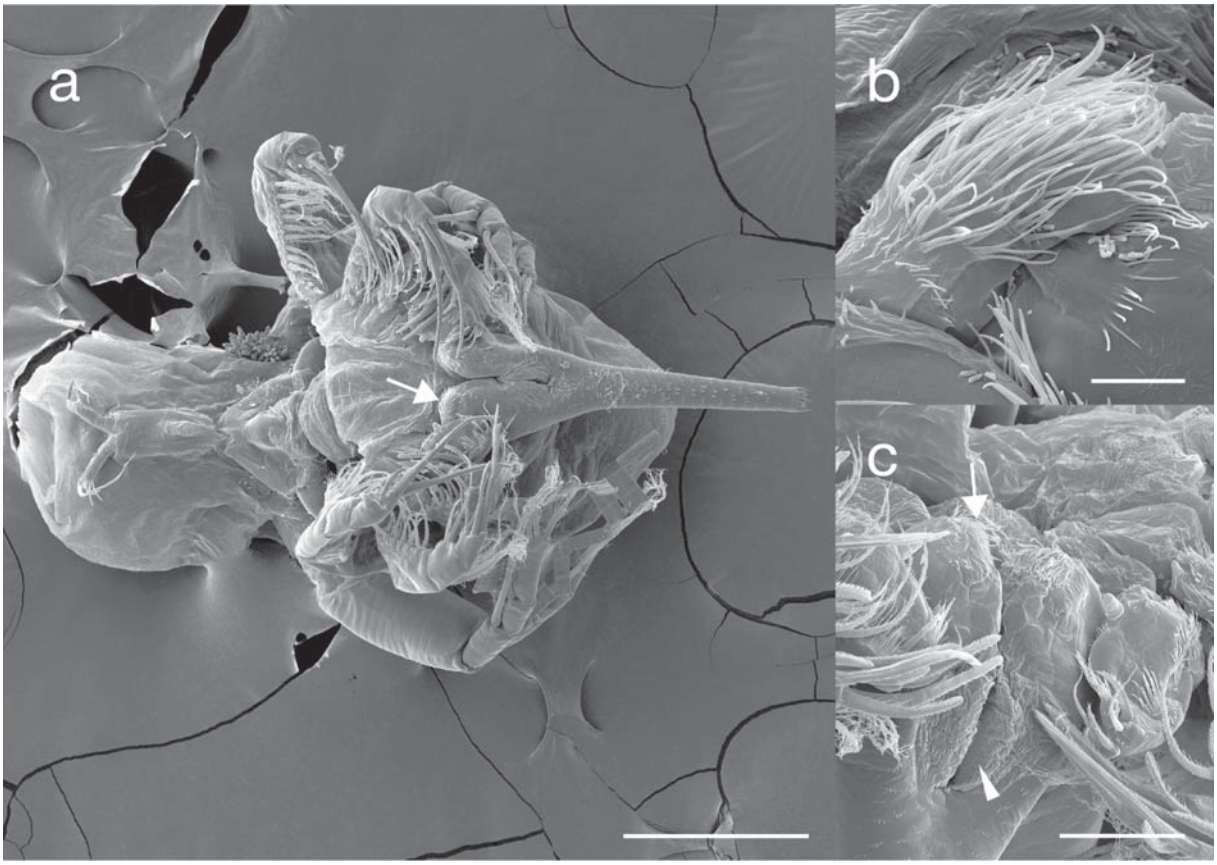

Fig. 7. Mature male of *Polyphemus pediculus*: a — general view from the ventral side, b — penis, c — postabdomen, arrow — penis, arrowhead — anus. Scales: a — 0.2 mm, b — 0.01 mm, c — 0.05 mm.

Рис. 7. *Polyphemus pediculus*, взрослый самец: a — общий вид с боковой стороны, b — пенис, c — постабдомен, стрелка – пенис, треугольный указатель — анальное отверстие. Масштаб: a — 0,2 мм, b — 0,01 мм, c — 0,05 мм.

thoracic limbs, and by the degree of development of the antenna I setae. The sizes of males I and juvenile females I coincide, indicating that there are no earlier stages of the postembryonic development in *P. pediculus* males.

According to Sinev & Degtyareva [2019], postembryonic development of the podonid males includes three instars, two of which are juvenile. These three instars of the podonid males are distinctly distinguished from each other by the degree of development of hooks and the number of setae located on the distal segment of the first pair of thoracic limbs. In addition, with each subsequent moult, penis shape and size is changed.

The postembryonic development of *P. pediculus* is similar to that of Podonidae males, both include three ages. As in Podonidae, *P. pediculus* males I have no hook on the distal segment of the endopodite of the first thoracic limb. Instead, there is a noticeable tubercle that is an anlagen of the hook. In the males II of both Podonidae and *P. pediculus*, the hook exists but is undeveloped. Mature males possess a long and thin copulatory hook.

The number of setae on the distal segment of the endopodite of the first thoracic limbs varies among Podonidae, for example in *Pleopis polyphemoide*s (Leuckart, 1859). In the first juvenile instar, the distal segment of the endopodite of the first thoracic appendage carries four long setae, in the second juvenile instar there are two long and one short setae, while in adult males, there are only two long setae. Male of *Evadne nordmanni* Loven, 1836 of all instars carry only two long setae on the distal segment of the endopodite of the first thoracic limbs. The number of distal setae on the endopodite of the first thoracic limbs of *P. pediculus* males (Polyphemidae) only changes as a result of the second postembryonic moult. The distal segments of the endopodites of the first thoracic limbs of juvenile males in both the first and second instar carry four setae each, with the size ratio of the setae remaining constant. In adult males, the first distal seta is completely absent, and the second one is significantly reduced. Therefore, the distal segment of the endopodite of the first thoracic limbs of adult males carries three setae, with one of them being about four times shorter than the other two.

The number of distal setae on the endopodites of the second pair of limbs does not differ between adult and juvenile males. In juvenile males I and II, there are four setae on the distal segment of the second pair of limbs, two of which are long, one being approximately

five-sixths the length of the long setae, and another one is short, half the length of the long setae. In adult males, the distal segment of the second pair of thoracic legs has two long setae and two short setae, one of which is half the length of the long setae, and the other is four times shorter.

The number and relative lengths of the distal setae of the third pair of limbs are constant for males of all instars. The armature of the fourth pair of legs also remains unchanged during whole postembryonic development.

The penises of males of the Podonidae are well-developed and are noticeable even in the instar I. The size of the penises increases with each postembryonic moult: in males I, the length of the penis barely reaches the length of the fourth pair of thoracic legs, penises of juvenile males II are equal in length to the fourth pair of thoracic legs, and the penises of adult males are longer than the fourth pair of thoracic limbs. The penises of males of *P. pediculus* are noticeably smaller and are only formed at the sexually mature age. Juvenile males I lack both penises and genital pores. In males II, paired smooth bumps with genital pores appear on the postabdomen above the anal opening. The penises of adult males are elongated, with a broad, rounded distal end, covered with numerous long sensilla, and are located above the postabdomen, adjacent to it. The length of the penises is significantly shorter than the length of the fourth pair of thoracic legs.

The hook is formed in *P. pediculus* males in the same way as in Podonidae. In males I, a well-defined bump appears on the outer part of the distal endopodite segment of the first pair of thoracic limbs, which is the beginning of the future hook. After moulting, a wide and blunt protrusion appears in the place of the bump in males II, the distal part of which is isolated and located along the inner surface of the limb. The length of the future hook at this stage does not exceed half the width of the distal endopodite segment. In mature (instar III) males, the hook elongates and thins, acquiring one or two additional spines in the middle and one at the distal end of the hook. The surface of the distal endopodite segment under the hook is smooth and does not supplied with an additional armature. In juvenile males, there are the anlagen of the hook and four distal setae on the distal endopodite segment of the first pair of limbs appears at the same time. The number of distal setae coincides in juvenile males I and females. As in Podonidae, the hook is a protrusion of the leg itself, not a modified seta [Sinev, Degtyareva, 2019].

Development of the primary sexual features in *P. pediculus* male was insufficiently studied and still is requires further investigation. The results of present study showed that the gradual increase in the size of the testes can be observed using the light microscopy, but the changes in the structure of the genital glands can be determined only using the histological methods.

The secondary sexual features of *P. pediculus* males coincide with those of other Cladocera and develop gradually and sequentially throughout the whole postembryonic development.

Conclusion

Postembryonic development of *P. pediculus* male includes two juvenile instars and a single adult instar. These stages are reliably distinguishable from each other, which allows us to confidently say that after emerging from the mother's brood chamber, males undergo two juvenile moults, which is also typical for parthenogenetic females of this species [Butorina 1971].

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COMPLIANCE WITH ETHICAL STANDARDS

Statement on the welfare of animals. This article does not contain any studies involving animals performed by any of the authors.

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