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Revision of the systematic position of *Eucyclops bathanalicola* Boxshall et Strong, 2004, with the description of *Boxshallianus* gen.n. and Boxshallianidae fam.n.

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ABSTRACT: As part of a global revision of the genus *Eucyclops* Claus, 1895, *Eucyclops bathanalicola* Boxshall et Strong, 2004, discovered in the mantle cavity of a gastropod mollusk from Lake Tanganyika (Central Africa), was studied. This finding represents the first documented case of a copepod ectoparasite on an invertebrate host in continental waters. Significant morphological transformations in the antennal and oral appendages of the cephalosome in *E. bathanalicola* do not correspond with the diagnostic characteristics of the family Cyclopidae. The classification of this species within the genus *Eucyclops*, as proposed by the authors, obscures the taxonomic boundaries of higher systematic units. A cladistic analysis of key morphological traits separates this taxon from representatives of all families within the modern suborder Cyclopida. Based on these findings, a new monotypic genus, *Boxshallianus* gen.n., and a new family, Boxshallianidae fam.n., were established. The single species from Lake Tanganyika was assigned a new name, *Boxshallianus bathanalicola* (Boxshall et Strong, 2004) stat.n. A critical feature for the new family is the transformation of the maxilliped from a grasping organ into an unarmed, single-segmented plate (an organ of attachment). The study also discusses the necessity of revising the current systematics of cyclopid copepods.
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KEY WORDS: *Eucyclops*, *Boxshallianus*, Boxshallianidae, Cyclopida, Cyclopidae, fresh water, parasitic copepods, ectosymbiont, invertebrate host, Lake Tanganyika, taxonomy, status change.

Изменение систематического положения *Eucyclops bathanalicola* Boxshall et Strong, 2004 с описанием нового рода *Boxshallianus* gen.n. и семейства Boxshallianidae fam.n.

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РЕЗЮМЕ: При проведении ревизии мировой фауны рода *Eucyclops* Claus, 1895 был изучен *Eucyclops bathanalicola* Boxshall et Strong, 2004 из озера Танганьика (Централь-

ная Африка), найденный в мантийной полости брюхоногого моллюска. Эта находка стала первым случаем эктопаразитизма копепод на беспозвоночных хозяевах в континентальных водоемах. Значительная трансформация конечностей антеннального и ротового комплексов головного сомита *E. bathanalicola* не соответствует диагностическим признакам семейства Cyclopidae. Отнесение этого вида к роду *Eucyclops,* как было предложено авторами, размывает таксономические границы вышестоящих систематических единиц. Кладистический анализ важнейших морфологических признаков отделяет эту форму от представителей всех семейств, входящих в современный подотряд Cyclopida. На этом основании были выделены и описаны новые монотипичные род *Boxshallianus* gen.n. и семейство Boxshallianidae fam.n., куда и переносится этот таксон под именем *Boxshallianus bathanalicola* (Boxshall et Strong, 2004) stat.n. Критическим признаком для нового семейства является превращение максиллипеды из хватательного органа в невооруженную односегментную пластинку (орган прикрепления). Обсуждается необходимость ревизии существующей системы циклопид.
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КЛЮЧЕВЫЕ СЛОВА: *Eucyclops*, *Boxshallianus*, Boxshallianidae, Cyclopida, Cyclopidae, пресноводный водоем, паразитические копеподы, эктосимбионт, беспозвоночный хозяин, озеро Танганьика, таксономия, изменение статуса.

Introduction

The transition to complete or partial parasitism on aquatic invertebrates is well known in more than 200 species of Cyclopida (Crustacea: Copepoda) in both fresh and marine waters (Ho, 1994; Boxshall, Hayes, 2019). Marine parasitic cyclopids are widely distributed in association with diverse groups of marine invertebrate and vertebrate hosts in marine ecosystems (Korzhavina *et al*., 2019, 2023, 2024). In continental waters they are found much less frequently and mainly in association with fish, and in a few cases in symbiosis with invertebrates such as mollusks (Ho, Thatcher, 1989; Ho, 1998). The first and only documented case of Cyclopida ectoparasitism on invertebrates in continental waters was the discovery of a new cyclopid species described from Lake Tanganyika (Central Africa) as *Eucyclops bathanalicola* (Boxshall et Strong, 2004). Analysis of the description and illustrations provided by the authors reveals significant differences in the external structure of the cephalosome of this species compared to all other representatives of the genus. Based on its morphological features — primarily the reduction of the antennal armament, as well as the segmentation of the mandibles, maxillules, maxillae, and maxillipeds — the described species cannot be attributed to the genus *Eucyclops* Claus, 1893. Moreover, it exhibits characteristics unknown among any other representatives of the family Cyclopidae. However, in previous publications assessing the systematic position of this species, the authors classify it within the genus *Eucyclops* and the family Cyclopidae (Boxshall, Strong, 2004; Bernot *et al*., 2021). Maintaining the current classification of this species unacceptably blurs the taxonomic boundaries of both the genus *Eucyclops* and the family Cyclopidae. The aim of this study was to conduct a comprehensive comparison of the morphological differences between *Eucyclops bathanalicola* and other representatives of the genus *Eucyclops*, as well as to evaluate the potential variability of these differences across the entire family, in order to determine the necessity of revising its systematic position.

Material and methods

This study compared the morphology of all appendages in *Eucyclops bathanalicola* with the corresponding structures in the type species of the genus, *Eucyclops* (*Eucyclops*) *serrulatus* (Fischer, 1851). The observed differences were compared the full range of known appendage variations within the genus *Eucyclops* and the family Cyclopidae. The primary material consisted of the original description and illustrations

Table 1. Character matrix for families of Cyclopida.
Таблица 1. Матрица признаков для семейств Cyclopida.

Taxon \ Character	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**
Outgroup (Misophriidae)	0	0	0	0	0	0	0	0	0	0	0	0	0
Ascidicolidae	1	1	2	1	2	1	3	1	3	3	0	0	1
Cyclopidae	1	0	1	0	0	0	4	1	1	1	0	0	0
Fratiidae	1	0	2	1	0	0	3	1	2	1	0	0	0
Boxshallianidae	1	0	2	2	0	1	4	2	3	4	0	0	0
Lernaeidae	2	2	2	2	2	1	5	2	3	2	0	0	0
Ozmanidae	2	2	2	2	2	1	5	2	3	5	1	1	1
Botryllophilidae	1	1	2	2	2	1	1	1	3	1	1	0	1
Buproridae	1	2	2	1	1	1	4	1	3	3	1	1	1
Enterognathidae	2	1	2	2	2	1	5	1	3	5	1	1	1
Enteropsidae	2	2	2	2	2	1	5	1	3	5	1	1	1
Euryteidae	0	0	1	0	0	0	4	1	1	1	0	0	0
Halicyclopidae	1	0	2	0	1	0	4	1	1	2	0	0	0
Hirodaiidae	1	1	2	?	2	2	5	2	3	4	0	0	1

of *E. bathanalicola* (Boxshall et Strong, 2004). For comparative purposes, original slides of *E.* (*E.*) *serrulatus* from its type locality (Olgin and Orlovsky ponds, Peterhof, St. Petersburg region, Russia) were examined. The identified morphological differences were further evaluated across 67 taxa of *Eucyclops*, based on the most recent revision (Alekseev, 2024).

Special attention was paid to variation in the two most diagnostically important appendages used in the current classification of the suborder into families — antennae (A2) and maxillipeds. Additional comparisons were made with other genera within the family Cyclopidae using published descriptions and data from the WoRMS taxonomic database (Walter, Boxshall, 2025).

A cladistic analysis was conducted for the families of the suborder Cyclopida, including the newly proposed family Boxshallianidae fam.n. A total of 13 morphological characters were used in the analysis:

1. A1 segmentation: at least 18-segmented (0); fewer than 18 but at least 4-segmented (1); weakly segmented or unsegmented (2).
2. Habitus: segmented with distinct prosome/urosome separation (0); without distinct separation (1); weakly segmented or unsegmented (2).
3. Exopod of antenna (A2): multisegmented (0); represented by a single seta (1) (Fig. 2B); absent (2) (Fig. 2A).
4. A2 basipodal medial setae: two setae (0) (Fig. 2B); one seta (1); absent (2) (Fig. 2A).
5. A2 endopodal segmentation: three segments (0); two (1); one (2); absent or fused with the basipod (3).
6. Terminal elements of A2: setiform (0); some transformed into spines or hooks (1); all setae absent (2).
7. Mandibular palp: biramous with a basal seta (0); biramous with naked basis (1); uniramous with several segments (2); reduced to a single segment bearing more than three setae (3); with 1–3 setae (4) (Fig. 2C, D); reduced to a single seta or absent (5).
8. Maxillular palp: biramous with ≥3 segments (0); reduced to 1–2 segments (1) (Fig. 3B); reduced to a single seta or absent (2) (Fig. 3A).
9. Maxilla segmentation: 6-segmented (0); 5- or 4-segmented (1) (Fig. 3D); 3-segmented (2); 2- or 1-segmented (3) (Fig. 3C).
10. Maxilliped segmentation: 7–8 segments (0); 3–5 segments (1) (Fig. 3F); 2 segments (2); 1 segment with setae or spines (3); 1 naked segment (4) (Fig. 3E); absent (5).
11. Swimming legs (P1–P4) endopod/exopod segmentation: all rami 2–3-segmented (0); at least one ramus of one leg reduced to a single segment or absent (1).
12. P4 Enp1 (first segment of endopod on leg 4): with inner seta (0); without inner seta or P4 Enp1 one-segmented (1).
13. P4 coxal seta: present (0); absent (1).

A data matrix was compiled (Table 1), and characters were analyzed using the Branch-and-bound algorithm in PAUP version 4.0 (Swofford, 2003). Bootstrap support values were calculated from 1,000 replicates under a parsimony criterion, with majority-rule consensus (50% cutoff).

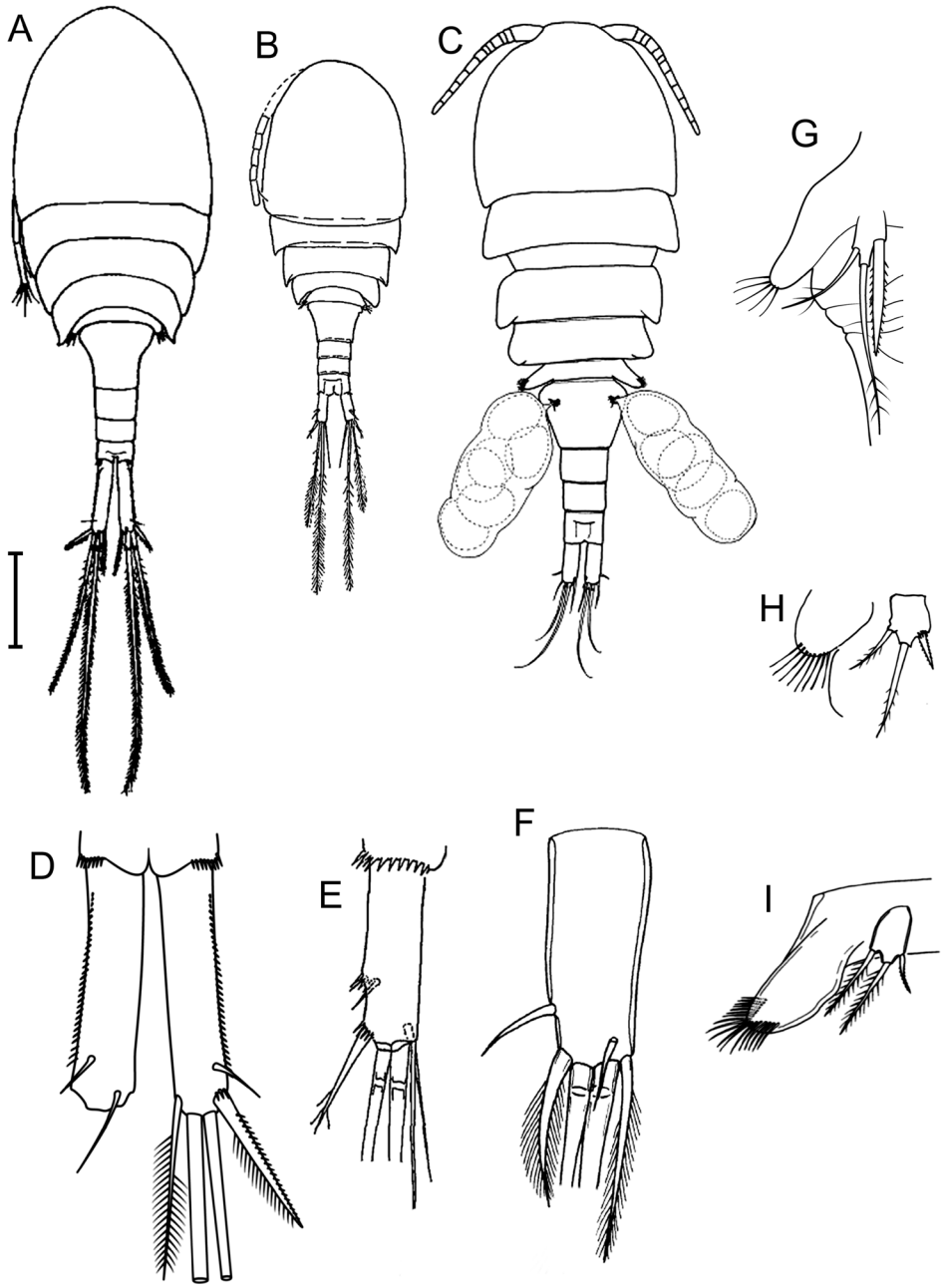

Fig. 1. Distinctive features of the external structure of *Eucyclops* (*E.*) *serrulatus* (Fischer, 1851) (A, D, G — after Alekseev *et al*., 2006), *Eucyclops* (*Macrurocyclops*) *neocaledoniensis* Dussart, 1984 (B, E, I — after Alekseev, 2024), and *Boxshallianus bathanalicola* (Boxshall et Strong, 2004) stat.n. (C, F, I — after Boxshall, Strong, 2004). A–C — general view; D–F — caudal rami; G–I — P5. Scale bar: 200 μm.

Рис. 1. Особенности внешнего строения *Eucyclops* (*E.*) *serrulatus* (Fischer, 1851) (A, D, G — по Alekseev *et al*., 2006), *E.* (*Macrurocyclops*) *neocaledoniensis* Dussart, 1984 (B, E, I — по Alekseev, 2024) и *Boxshallianus bathanalicola* (Boxshall et Strong, 2004) stat.n. (C, F, I — по Boxshall, Strong, 2004). A–C — общий вид; D–F — каудальные ветви; G–I — P5. Масштаб: 200 мкм.

Results

A sequential comparison of all morphological structures in *E.* (*E.*) *serrulatus*, the type species for the genus *Eucyclops*, and in *E. bathanalicola* is illustrated in figures below (Figs 1–4). The most important differences (indicated by arrows in the ectoparasitic species) are as follows:

Antenna basipodites have lost their armament: two medial and exopodal setae are missing, and the second segment of the endopodite has a reduced number of setae (5 instead of 9). The entire appendage on both sides lacks ornamentation, so characteristic of the genus *Eucyclops* (Fig. 2A).

Mandibular palp with 2 instead of 3 setae (Fig. 2C).

Maxillulae with significantly reduced armament, and maxillary palp reduced to a single seta (Fig. 3A).

Maxillae have lost most of their segmentation, with the terminal segments and setae modified into a single large claw, and the total number of appendages is significantly reduced (Fig. 3C).

Maxillipeds have been reduced to a single plate and completely lack armament (Fig. 3E).

Legs P1–P5 of *E. bathanalicola* are armed with the same number of setules/spines as *E.* (*E.*) *serrulatus*. However, the spines and segments are significantly reduced in length (Fig. 4B, D, F, H). The outgrowth of the basipodite P4, which is characteristically triangular in the genus *Eucyclops*, has a double tip in *E. bathanalicola* (Fig. 4H, arrow).

Caudal lateral *serra* is completely absent in *E. bathanalicola* (Fig. 1F). This feature is observed in several subterranean species of the subgenera *Eucyclops* (*Subterrocyclops*), *Eucyclops* (*Macrurocyclops*), and *Eucyclops* (*Mrazekicyclops*).

Variations in the number of segments and setules within the genus *Eucyclops* are presented in Table 2. These variations are minor and include changes in the number of setae on the second segment of the antennal endopodite (ranging from 7 to 9) and a reduction in the number of antennule segments to 11.

In representatives of several genera of the family Cyclopidae inhabiting subterranean biotopes, a reduction of A2 exopodal seta has been observed. The aforementioned transformations of the appendages in the cephalon region — particularly the reduction of the maxillipeds, which are crucial for the successful capture of food in free-living species — have not been found in any of the described taxa, except for *E. bathanalicola*.

The retention of *E. bathanalicola* within the family Cyclopidae blurs the taxonomic boundaries of this family, necessitating the establishment of a new genus and a new family to accommodate this species.

The cladistic analysis resulted in six equally parsimonious trees, each with a length of 41 steps, a consistency index (CI) of 0.70, and a retention index (RI) of 0.77. Based on these six trees, a strict consensus tree (Fig. 5) was generated with 100% bootstrap support for all clades, confirming the separation of *E. bathanalicola* from the family Cyclopidae into an independent clade within the suborder Cyclopida.

Boxshallianus **gen.n**.

Type species. *Boxshallianus bathanalicola* (Boxshall et Strong, 2004) **stat.n**.

DIAGNOSIS. Female. Body cyclopiform, slightly flattened in dorsoventral direction, with first pediger fused to cephalosome. Second to fourth pedigers (thoracic somites 1–3) are separate. Urosome five-segmented, with dense hair-like setae laterally on fourth free thoracic somite.

Genital double somite as long as broad, with mouth-shaped *receptaculum seminis* similar in shape to that of *Eucyclops* species. Caudal rami relatively short, armed with six setae, resembling those of most free-living species. Lateral seta short and positioned close to distal end of ramus. Among terminal setae, two middle setae are the longest.

Antennule 12-segmented, short. Antenna 4-segmented, consisting of basipodite and 3-segmented endopodite bearing 0, 1, 5, and 7 setae, respectively. Mandible consists of coxa with gnathobase armed with several blunt teeth; palp one-segmented, armed two strong, relatively short setae. Maxillule one-segmented, with three terminal claws; reduced palp represented by single seta. Maxilla reduced to large syncoxa and ends with strong claw. Maxilliped reduced to unarmed plate.

Legs 1–4 biramous with 3-segmented rami. Distal exopodite spine formula: 3/4/4/3.

Leg 5 one-segmented armed with weak inner spine and two longer setae.

Male. Unknown.

BIOLOGY. Ectoparasite of mollusk.

DISTRIBUTION. To date is known from Lake Tanganyika only (endemic?).

ETYMOLOGY. The new genus and family are named in honor of Dr. Geoffrey Boxshall (United Kingdom), one of the describers of the species examined in this study, in recognition of his outstand-

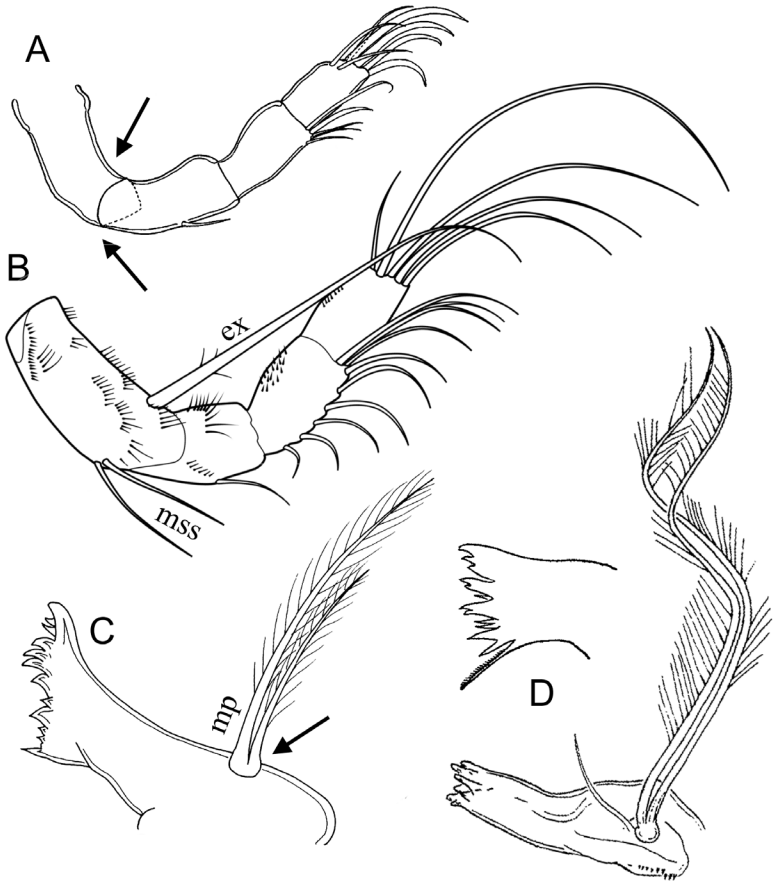

Fig. 2. Structural features of the cephalic appendages of *Boxshallianus bathanalicola* (Boxshall et Strong, 2004) stat.n. (A, C — after Boxshall, Strong, 2004) and *Eucyclops* (*E.*) *serrulatus* (Fischer, 1851) (B, D — after Alekseev, 2024). A, B — antenna; C, D — mandible (arrows indicate the main reduction of setae).
Abbreviations: ex — exopodal seta of antenna; mss — medial setae of antenna.
Рис. 2. Особенности строения конечностей головного сегмента *Boxshallianus bathanalicola* (Boxshall et Strong, 2004) stat.n. (A, C — по Boxshall, Strong, 2004) и *Eucyclops* (*E.*) *serrulatus* (Fischer, 1851) (B, D — по Alekseev, 2024). A, B — антенна; C, D — мандибула (стрелки указывают на основную редукцию щетинок).
Сокращения: ex — экзоподитная щетинка антенны; mss — медиальные щетинки антенны

ing contributions to the study of parasitic copepods in global fauna and the development of the modern taxonomic system for this group of crustaceans.

COMMENTS. A single genus of Boxshallianidae fam.n. Considering that some representatives of the family Cyclopidae exhibit transformations in individual appendages associated with adaptation to symbiosis or life in subterranean biotopes (e.g., the formation of grasping claws or the loss of part of the antennal armament), a critical feature distinguishing the new family and the new genus is the transformation of the maxilliped from a grasping organ into an unarmed, single-segment plate (an attachment organ).

Boxshallianidae **fam.n**.

Type genus. *Boxshallianus* gen.n.

DIAGNOSIS. Female. Body shape, antennule, and urosome are generally similar to those of free-living Cyclopoid. Reduced P5 has distinct shape and armament, resembling that of one of Cyclopoid genera. Antenna four-segmented, with clearly reduced setation, particularly on basipodite, which is unarmed. Mouth appendages distinctly modified for better attachment to the host's soft tissue, with setae partly reduced and partly transformed into hooks and the number of segments greatly reduced compared to free-

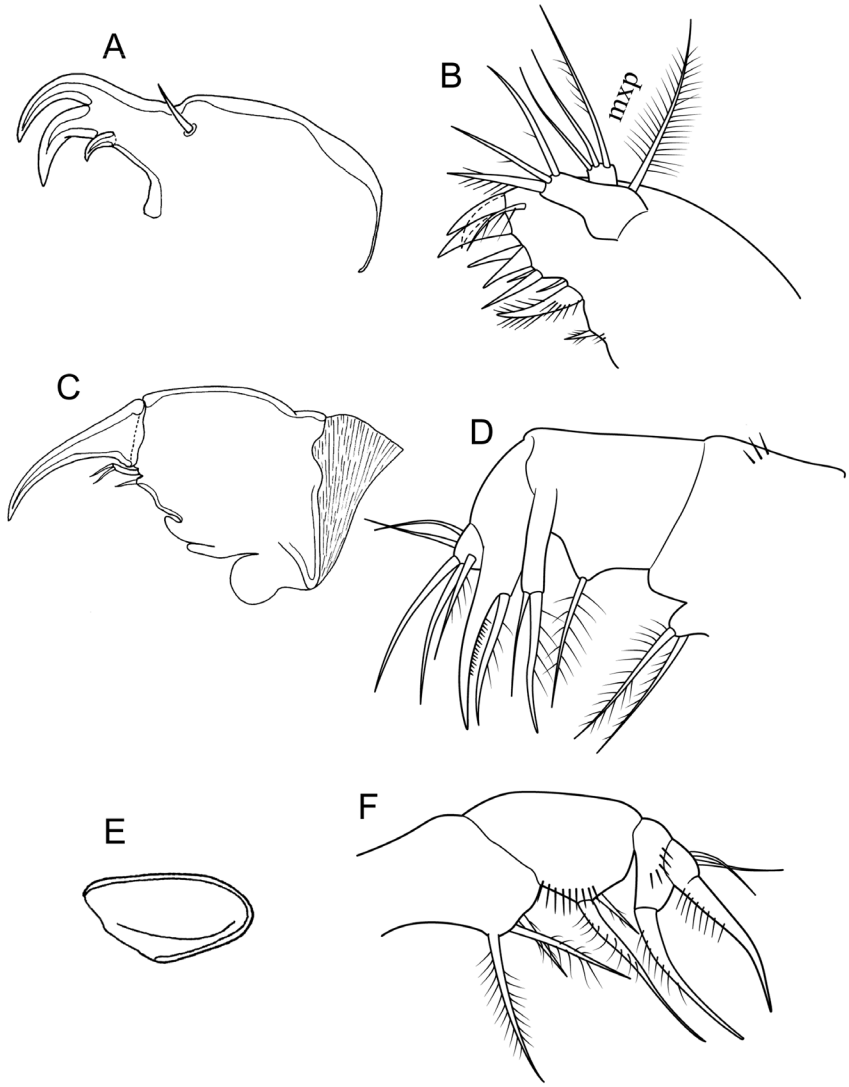

Fig. 3. Structural features of the cephalic appendages of *Boxshallianus bathanalicola* (Boxshall et Strong, 2004) stat.n. (A, C, D — after Boxshall, Strong, 2004) and *Eucyclops* (*E.*) *serrulatus* (Fischer, 1851) (B, D, F — after Alekseev, 2024) (continued). A, B — maxillule; C, D — maxilla; E, F — maxilliped.
Abbreviations: mxp — maxillular palp.
Рис. 3. Особенности строения конечностей головного сегмента *Boxshallianus bathanalicola* (Boxshall et Strong, 2004) stat.n. (A, C, D — по Boxshall, Strong, 2004) и *Eucyclops* (*E.*) *serrulatus* (Fischer, 1851) (B, D, F — по Alekseev, 2024) (продолжение). A, B — максиллула; C, D — максилла; E, F — максиллипеда.
Сокращения: mxp — пальп максиллулы.

living forms. Maxilliped always one-segmented and unarmed, representing the most reduced mouthpart. This family can be distinguished from others by the unique combination of unarmed antennal basipodite and unarmed maxilliped reduced to a single segment.

BIOLOGY. Ectoparasite of mollusks in continental waters.

COMMENTS. At the moment, it is a monotypic family with a single genus *Boxshallianus* gen.n. and a single species *Boxshallianus bathanalicola* (Boxshall et Strong, 2004) stat.n. The new family is characterized by a unique combination of 13 morphological parameters (summarized in Table 1) that distinguish it from the other 12 families. While similar in the degree of max-

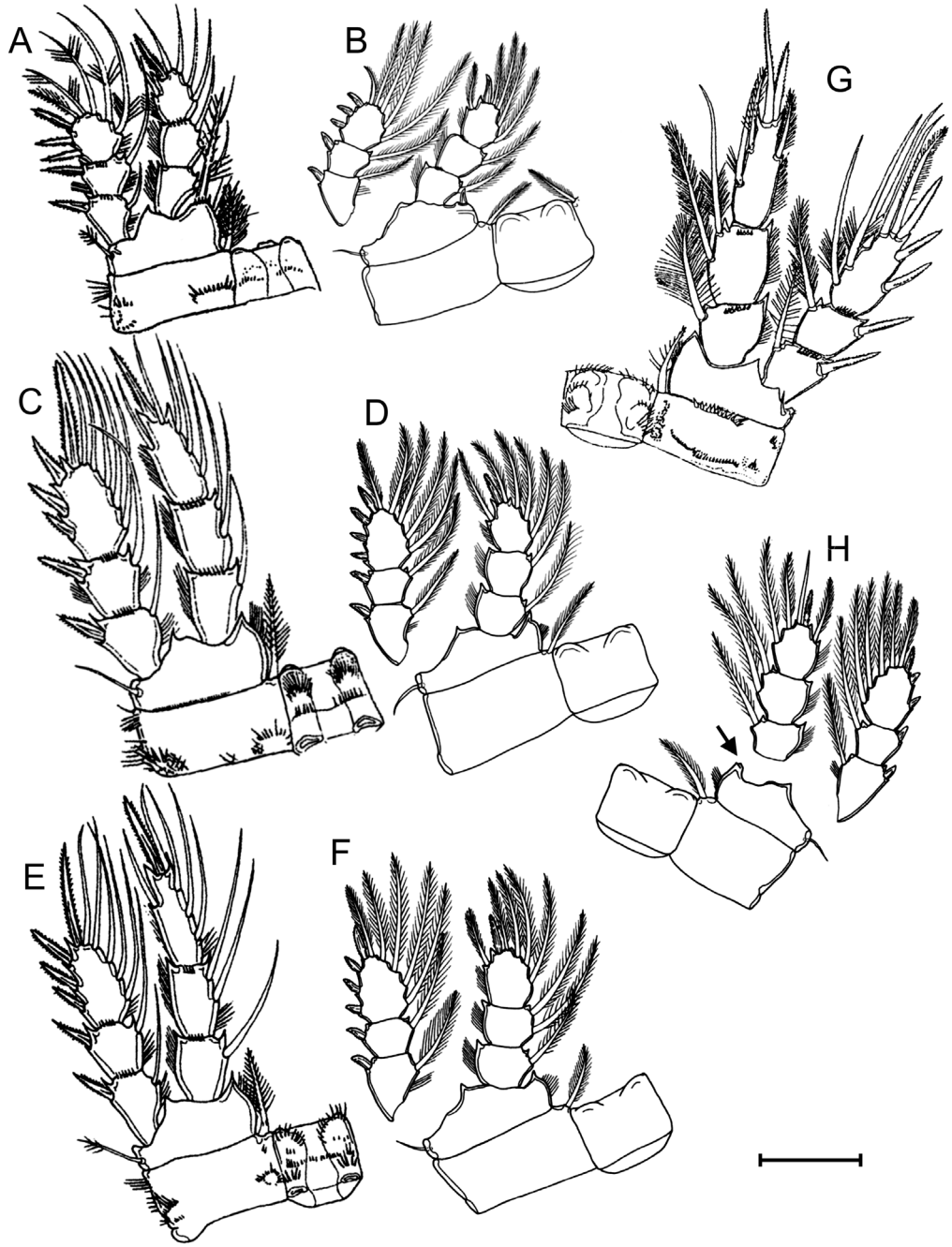

Fig. 4. Structure of the swimming appendages of *Eucyclops* (*E.*) *serrulatus* (Fischer, 1851) (A, C, E, G — after Alekseev, 2006) and *Boxshallianus bathanalicola* (Boxshall et Strong, 2004) stat.n. (B, D, F, H — after Boxshall, Strong, 2004). A, B — P1; C, D — P2; E, F — P3; G, H — P4. Scale bar: 50 μm.

Рис. 4. Строение плавательных конечностей *Eucyclops* (*E.*) *serrulatus* (Fischer, 1851) (A, C, E, G — по Alekseev, 2006) и *Boxshallianus bathanalicola* (Boxshall et Strong, 2004) stat.n. (B, D, F, H — по Boxshall, Strong, 2004). A, B — P1; C, D — P2; E, F — P3; G, H — P4. Масштаб: 50 мкм.

Table 2. Segmentation and setation of the antennal and mouth appendages of *Boxshallianus bathanalicola* (Boxshall et Strong, 2004) stat.n., *Eucyclops* (*E.*) *serrulatus* (Fischer, 1851), the genus *Eucyclops*, and the family Cyclopidae.

Таблица 2. Сегментация и сетация конечностей антеннального и ротового комплексов *Boxshallianus bathanalicola* (Boxshall et Strong, 2004) stat.n., *Eucyclops* (*E.*) *serrulatus* (Fischer, 1851), рода *Eucyclops* и семейства Cyclopidae.

Appendages	*Boxshallianus bathanalicola*	*Eucyclops serrulatus*	Genus *Eucyclops*	Fam Cyclopidae
Antennule segments	12	12	11–12	6-18
Antenna segments	4	4	4	4
Antenna setation	0/1/5/7	3/1/9/7	3/1/7–9/7	2–3/1/4–9/6–7
Mandibular palp setation	2	3	3	1–3
Maxillular palp setation	1	7	7	5–7
Maxilla segments	2	5	5	4–5
Maxilliped segments	1	4	4	3–4

illiped reduction, members of the family Hirodaiidae have advanced further in their adaptation to parasitism, having lost the generic characteristics of free-living forms that are still retained in Boxshallianidae fam.n. In contrast, representatives of Fratiidae, which remain closely related to *Halicyclops*, do not exhibit such a significant reduction in their mouth appendages.

Discussion

Cyclopoid copepods often transition to parasitic relationships with larger organisms. The primary evolutionary trends in this regard are evident in a series of forms that partially rely on hosts during the final stage of development (e.g., Ergasilidae). In these cases, sexually mature females attach to the host after fertilization, utilizing it for the production of sexual products, protection from predators, and survival during unfavorable seasons, such as winter. All preceding developmental stages, from naupliar to advanced copepodites, occur in a free-living state (Thatcher, 2006).

The newly described family likely represents the initial stage of transition to ectoparasitism, in which only one of the mouth structures — the maxillipeds — undergoes radical restructuring, transforming into a plate for firmer attachment, possibly through suction to the host's tissues. Other head appendages involved in attachment, primarily the antennae, retain their basic segmentation or exhibit partial reduction, but lose a significant portion of their armament. The distal elements of the armament (in maxillulae and maxillae) are transformed into claw-like appendages, which enable them to penetrate deeper into the host tissues. Such a method of attachment most likely proves sufficient to hold inside gastropods, which, unlike fish, do not make sudden movements and whose ability to free themselves from ectoparasites is determined only by the intake or release of small portions of water.

The reduction of the maxillipeds from a multisegmented limb, armed with strong bristles, to a smooth plate that facilitates attachment to the host, crucially changes the nature of the feeding of these animals (Monakov, 2003). With such changes, according to Dollo's principle, a return from ectoparasitism to a free-living way of life becomes impossible (Dollo, 1893).

A unique feature of crustaceans at this stage of adaptation to ectoparasitism is the retention of the general body configuration, as well as the structure of the swimming legs and abdomen, which largely correspond to the characteristics of the genus (in this case, *Eucyclops*) from which this taxon undoubtedly diverged. The preservation of locomotor structures — such as the swimming legs — in this species is reminiscent of Ergasilidae, which live independently of hosts for most of their life cycle.

It is worth noting that some representatives of the genera *Eucyclops* and *Diacyclops*, which are apparently associated with living on sponges, exhibit an even earlier form of adaptation. This adaptation is linked to the need to attach to a living substrate, specifically the transforma-

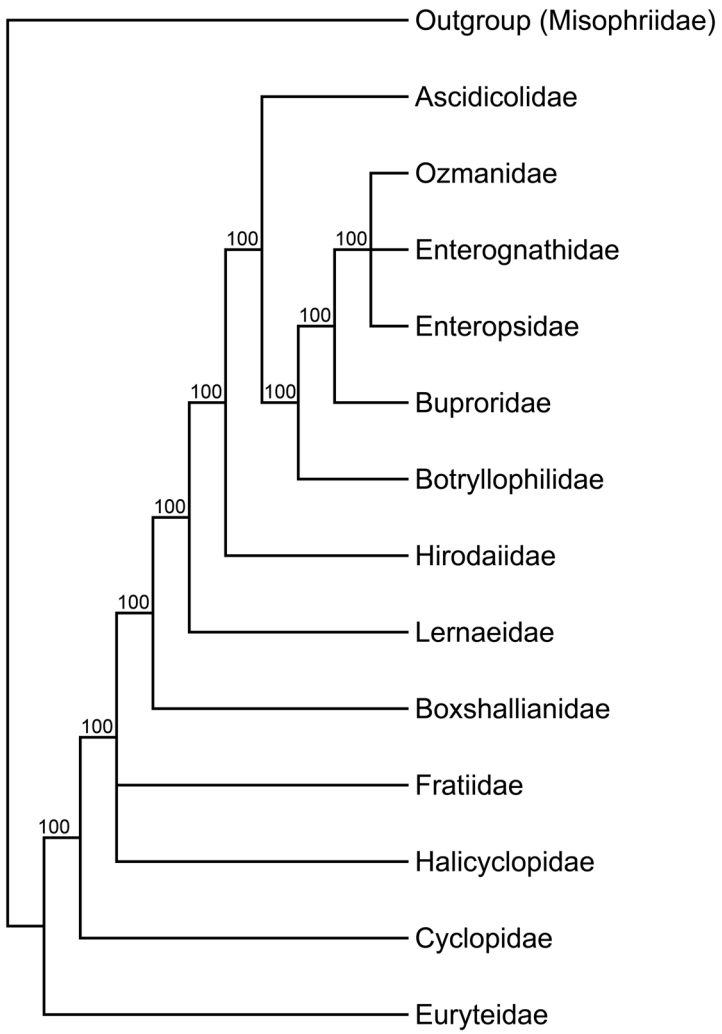

Fig. 5. Supposed position of *Boxshallianus bathanalicola* (Boxshall et Strong, 2004) stat.n., the representative of the new family Boxshallianidae fam.n., in the suborder Cyclopida. Strict consensus tree of six equally parsimonious trees (consistency index 0.70, retention index 0.77).
Рис. 5. Предполагаемое положение *Boxshallianus bathanalicola* (Boxshall et Strong, 2004) stat.n., представителя нового семейства Boxshallianidae fam.n., в подотряде Cyclopida. Строгое консенсусное дерево, построенное на основе шести равноэкономных деревьев (индекс состоятельности 0.70, индекс удержания 0.77).

tion of the terminal bristles of the antennae into strong, hook-like structures (Mazepova, 1978; Alekseev, Monchenko, 2011). However, no significant changes in other appendages, let alone a reduction of the maxillipeds, have been observed in these species.

The described taxa at the supraspecific level are neither the first nor the only examples of monotypic genera and families among parasitic cyclopids in both continental and marine ecosystems. Typically, these taxa include only a single species, suggesting a relatively short evolutionary period as a parasitic form. For instance, the genus *Ozmana* Ho et Thatcher, 1989 and the family Ozmanidae Ho et Thatcher, 1989, originally described from Amazonian mollusks, have

only recently been expanded to include a second species (Ho, Thatcher, 1989; Gamarra-Luques *et al*., 2004). The species *Fratia gaditana* Ho, Conradi et López-González, 1998 and the family Fratiidae Ho, Conradi et López-González, 1998, described from a blue ascidian in the Mediterranean Sea, exhibit significant similarities to *Boxshallianus* gen.n. The urosomite region remains almost unchanged and corresponds to the genus *Halicyclops*, while the mouth appendages, like those of *Boxshallianus* gen.n., are significantly modified and do not align with the characteristics of the family Halicyclopidae (Ho *et al*., 1998).

The monotypic nature of these families and genera may also result from the limited study of cyclopid fauna in ancient water bodies. Ancient lakes like Tanganyika are known hotspots for endemic cyclopid diversity (Boxshall, Defaye, 2008; Alekseev, 2024), yet their benthic zones remain poorly explored for parasitic associations. The stable, long-term conditions in these ecosystems could promote specialized host-parasite coevolution, particularly with sedentary invertebrates (e.g., mollusks, sponges). In ancient continental lakes such as Baikal, Biwa, and others, attention should be given to similar associations, especially among representatives of the species-rich genera Eucyclops and Diacyclops. This type of parasitism is most likely to occur in continental water bodies within tropical and equatorial climate zones, where fish reproduction — and consequently the presence of their young, the primary consumers of small invertebrates — is not seasonal. If this assumption is confirmed, it will provide grounds for expanding this family, particularly through the inclusion of species from the Rift Valley lakes in Africa (e.g., Lake Malawi), Lake Biwa in Japan, tectonic lakes in Indonesia, and Central America.

The provided characteristics of the family intentionally exclude specific details of the reduction of mouth and antennal appendages, except for two key features (A2 basipodite and maxilliped), which, in combination, distinguish it from other families within the suborder. The primary diagnostic feature of this family, in addition to parasitism, should be the retention of morphological traits characteristic of the genus, particularly in the structure of the urosomite region, including P5 and the caudal rami, alongside significant oligomerization of the armament and segmentation of the mouth appendages. Consequently, the new family may include representatives of other genera exhibiting varying degrees of mouth apparatus reduction and a relatively recent transition to parasitism on invertebrates in continental waters, primarily mollusks. In my opinion, this approach will help mitigate the excessive proliferation of monotypic families among parasitic cyclopids.

Conclusion

Eucyclops bathanalicola Boxshall et Strong, 2004, found in the mantle cavity of a gastropod mollusk from Lake Tanganyika (Central Africa), cannot be classified within the family Cyclopidae or any other family of the suborder Cyclopida. To resolve this taxonomic inconsistency, a new monotypic genus, *Boxshallianus* gen.n., and family, Boxshallianidae fam.n., were proposed and described. This parasitic taxon was transferred to the new genus under the name *Boxshallianus bathanalicola* (Boxshall et Strong, 2004) stat.n.

The diagnosis of the new family, which includes continental cyclopids that have transitioned to ectoparasitism on mollusks, is based on the retention of morphological traits characteristic of the genus in the urosome structures, alongside significant oligomerization of the armament and segmentation of the cephalosome appendages. This includes the inevitable loss of the grasping function of the maxillipeds. The new family may eventually encompass representatives of other genera and species of cyclopids exhibiting similar reductions in the mouth apparatus, which have relatively recently — but irreversibly — transitioned to ectoparasitism on invertebrates in continental waters, primarily mollusks.

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References

Alekseev V.R. 2024. Genera *Eucyclops* Claus, 1893, *Isocyclops* Kiefer, 1957 and *Stygocyclops* Pleša, 1971

(Copepoda: Cyclopoida). Identification guide of the world fauna // Arthropoda Selecta. Suppl. No.6. 201 p.

Alekseev V.R., Dumont H.J., Pensaert J., Baribwegure D., Vanfleteren J.R. 2006. A redescription of *Eucyclops serrulatus* (Fischer, 1851) (Crustacea: Copepoda: Cyclopoida) and some related taxa, with a phylogeny of the *E. serrulatus*-group // Zoologica Scripta. Vol.35. No.2. P.123–147. https://doi.org/10.1111/j.1463-6409.2006.00223.x

Alekseev V.R., Monchenko V.I. 2011. [Species diversity of Cyclopida in Caspian Sea basin] // V.R. Alekseev, S.Ya. Tsalolikhin (ed.). Biologicheskoe raznoobrazie vodnykh bespozvonochnykh kontinental'nykh vodoemov. St. Petersburg: Zoological Institute RAS. P.157–164 [in Russian].

Barnes R.D. 1982. Invertebrate Zoology. Philadelphia, PA: Holt-Saunders International. 692 p.

Bernot J.P., Boxshall G.A., Crandall K.A. 2021. A synthesis tree of the Copepoda: integrating phylogenetic and taxonomic data reveals multiple origins of parasitism // PeerJ. Vol.9. Art.e12034. https://doi.org/10.7717/peerj.12034

Boxshall G.A., Defaye D. 2008. Global diversity of copepods (Crustacea: Copepoda) in freshwater // Hydrobiologia. Vol.595. P.195–207. https://doi.org/10.1007/s10750-007-9014-4

Boxshall G., Hayes P. 2019. Biodiversity and taxonomy of the parasitic Crustacea // N.J. Smit, N.L. Bruce, K.A. Hadfield (eds.). Parasitic Crustacea. Springer. P.73–134. https://doi.org/10.1007/978-3-030-17385-2_3

Boxshall G.A., O'Reilly M. 2015. The first parasitic copepod from a scaphopod mollusc host // Syst. Parasitol. Vol.90. No.2. P.113–124. https://doi.org/10.1007/s11230-014-9537-9

Boxshall G.A., Strong E.E. 2006. An extraordinary shift in life habit within a genus of cyclopid copepods in Lake Tanganyika // Zool. J. Linn. Soc. Vol.146. No.2. P.275–285. https://doi.org/10.1111/j.1096-3642.2006.00206.x

Dollo L. 1893. The laws of evolution // Bull. Soc. Bel. Geol. Paleontol. Vol.7. P.164–166.

Gamarra-Luques C.D., Vega I.A., Koch E., Castro-Vazquez A. 2004. Intrahost distribution and transmission of a new species of cyclopoid copepod endosymbiontic to a freshwater snail, *Pomacea canaliculata* (Caenogastropoda, Ampullaridae) from Argentina // Biocell. Vol.28. No.2. P.155–164. https://doi.org/10.32604/biocell.2004.28.155

Ho J.S. 1994. Origin and evolution of the parasitic cyclopoid copepods // International journal for parasitology. Vol.24. No.8. P.1293–1300.

Ho J.S. 1998. Cladistics of the Lernaeidae (Cyclopoida), a major family of freshwater fish parasites // J. Mar. Syst. Spec. Vol.15. No.1–4. P.177 –183.

Ho J.S., Conradi M., López-González P.J. 1998. A new family of cyclopoid copepods (Fratiidae) symbiotic in the ascidian (*Clavelina dellavallei*) from Cádiz, Spain // J. Zool. Vol.246. P.39–48.

Ho J.S., Thatcher V.E. 1989. A new family of cyclopoid copepods (Ozmanidae) parasitic in the hemocoel of a snail from the Brazilian Amazon // J. Nat. Hist. Vol.23. No.4. P.903–911.

Korzhavina O.A., Grishina D.Y., Chen X., Fontaneto D., Ivanenko V.N. 2023. Diving into Diversity: Copepod Crustaceans in Octocoral Associations // Diversity. Vol.15. Art.1140. https://doi.org/10.3390/d15111140

Korzhavina O.A., Gubareva N.V., Kitashov A.V., Britayev T.A., Ivanenko V.N. 2024. From Microscale Interactions to Macroscale Patterns in Copepod–Crinoid Symbiosis // Animals. Vol.14. Art.877. https://doi.org/10.3390/ani14060877

Korzhavina O.A., Hoeksema B.W., Ivanenko V.N. 2019. A review of Caribbean Copepoda associated with reef-dwelling cnidarians, echinoderms and sponges // Contrib. Zool. Vol.88. No.3. P.297–349. https://doi.org/10.1163/18759866-20191411

Mazepova G.F. 1978. [Cyclopoids of Lake Baikal] // Trudy Limnol. Inst. Sibirsk. Otdel. AN SSSR. Vol.28. 143 p. [In Russian]

Monakov A.V. 2003. Feeding of Freshwater Invertebrates. Ghent: Kenobi Publications. 373 p.

Thatcher V.E. 2006. Amazon fish parasites. Vol.1. Sofia: Pensoft Publishers. 508 p.

Swofford D.L. 2003. PAUP. Phylogenetic Analysis Using Parsimony (and Other Methods). Version 4. Sinauer Associates, Sunderland, Massachusetts.

Walter T.C., Boxshall G. 2025. World of Copepods Database. Cyclopida. Online at: https://www.marinespecies.org/aphia.php?p=taxdetails&id=1381344, accessed on 13.03.2025.

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