

# An extraordinary shift in life habit within a genus of cyclopoid copepods in Lake Tanganyika

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We here describe a new species of cyclopoid copepod, *Eucyclops bathanalicola* sp. nov., parasitic on a gastropod endemic to Lake Tanganyika, *Bathanalia straeleni* (Cerithioidea, Paludomidae). *E. bathanalicola* is distinguished by the possession of praecoxal claws on the maxillules, by the modified maxillae which lack any trace of an endopod on the powerful distal claw, and by the reduction of the maxillipeds to minute unarmed lobes. In the character states exhibited by the female body, antennules and swimming legs 1–5, the new species closely resembles a typical free living *Eucyclops*. The impact of the adoption of parasitism as a life habit is expressed primarily in the modification of the postmandibular mouthparts. As a member of the Cyclopidae, this species represents a unique foray into a parasitic lifestyle from an otherwise free-living group of copepods inhabiting Lake Tanganyika. This is the first record of a parasitic copepod on a mollusc host within this ancient lake and only the second family of freshwater gastropods reported to host copepods. © 2006 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2006, 146, 275–285. No claim to original US government works.

ADDITIONAL KEYWORDS: anatomy – Cyclopoida – ectoparasite – endemic – first record from nonampullariid.

## INTRODUCTION

The origin and evolution of the remarkable endemic species assemblage of Lake Tanganyika has long inspired scientists and explorers alike. In recent years, the cichlid species flock of this ancient lake has figured most prominently in morphological and molecular phylogenetic analyses (see review in Salzburger & Meyer, 2004). However, the invertebrate fauna is finally receiving the attention it deserves as a model system for studying evolutionary patterns and processes (e.g. von Sternberg & Cumberlidge, 1999; West & Michel, 2000; Park, Martens & Cohen, 2002; Michel, 2004; Wilson, Glaubrecht & Meyer, 2004).

Despite the long history of investigation on the invertebrate fauna of this lake, new species continue to be described (e.g. Martens, 1985; Morse, 1988; Tsalolikhin, 1989; Ducasse & Carbonel, 1994; Rush-ton-Mellor, 1994; Wouters & Martens, 1994, 1999;

Martin & Giani, 1995; Segers & Baribwegure, 1996; West *et al.*, 2003; Michel, 2004) and these discoveries highlight their astonishing adaptations to life in this ancient lake.

The copepod fauna of Lake Tanganyika is diverse, with the 68 species and subspecies listed by Coulter (1991) being second in species richness only to the 120 species and subspecies recorded for Lake Baikal (Boxshall & Evstigneeva, 1994). We here describe a new species of cyclopoid copepod, *Eucyclops bathanalicola* sp. nov., found to be parasitic on a species of gastropod endemic to the lake, *Bathanalia straeleni* Leloup, 1953 (Cerithioidea, Paludomidae). No parasitic copepods have been encountered previously in studies of the cerithioidean gastropods of this ancient lake.

## MATERIAL AND METHODS

The syntype series of *Bathanalia straeleni* from the Institut Royal des Sciences Naturelles de Belgique in Brussels (IRSNB) includes one lot (no. 50) containing two shells with soft bodies and shell fragments; the

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latter are apparently remnants from the soft body depicted in Leloup's (1953) paper but the soft body could not be located. As these are the only two specimens with soft bodies from the syntype series, permission to dissect only a single specimen was granted. This specimen, an adult female, yielded two mature female parasitic copepods.

The association between parasite and host was documented using a Leica MZ 12.5 binocular microscope with *camera lucida*. Dissections of the copepods were completed as temporary preparations in lactophenol. Observations were made using Differential Interference Contrast on a Leica Diaplan microscope and drawings were made via a *camera lucida*. Copepod morphological terminology follows Huys & Boxshall (1991).

## SYSTEMATICS

### FAMILY CYCLOPIDAE

#### GENUS *EUCYCLOPS* CLAUS, 1893

#### *EUCYCLOPS BATHANALICOLA* SP. NOV.

*Type material*: Holotype female undissected, stored in alcohol, IRSNB no. IG 30500; Paratype female dissected and mounted on glass slides, IRSNB no. IG 30499.

*Type locality*: Off Cape Bwana n'Denge, Democratic Republic of Congo. 1000 m offshore along the coast, trawling starting 3 miles northwest of Lugumba until in front of the Lukuga River (Station 50). Dredged from diverse substrates including mud and rocks in 20–80 m depth (translated from Leloup, 1953).

*Host*: Two ovigerous females located within inhalant region of mantle cavity in *Bathanalia straeleni*, attached to mantle floor just behind osphradium (Fig. 1).

*Etymology*: the species name is derived from *Bathanalia*, the generic name of the host, and *-icola* meaning inhabitant.

*Distribution*: Endemic to Lake Tanganyika.

### MORPHOLOGY

Female. Body cyclopiform (Fig. 2A), divided into anterior prosome and posterior urosome with prosome–urosome boundary well defined at podoplean position. Prosome comprising cephalothorax incorporating first pedigerous somite and 3 free pedigerous somites. Epimeral angles of free second to fourth pedigerous somites slightly produced. Urosome 5-segmented, comprising fifth pedigerous somite, genital double-somite formed by fusion of genital and first abdominal

somites, and 3 free abdominal somites. Fifth pedigerous somite produced laterally into paired lobes (Fig. 2B,C), each ornamented with distinctive row of long setules extending round from dorsal to lateral surfaces. Genital apparatus comprising single copulatory pore on ventral surface of genital double-somite and paired gonopores on dorsolateral surface: seminal receptacle (Fig. 2D) with broad anterior and posterior lobes, both slightly concave; anterior lobe larger than posterior. Caudal rami (Fig. 2E) about 2.3 times longer than wide: bearing six setae: seta I lacking; setal lengths, seta II – 32 µm, seta III – 56 µm, seta IV – 168 µm, seta V – 215 µm, seta VI – 78 µm, seta VII – 28 µm. Body length 1.18 mm based on two specimens.

Rostrum well developed. Nauplius eye not observed. Antennule 12-segmented (Fig. 2F); segmental homologies as follows: segment 1 (I–V) compound, segment 2 (VI–VII) double, segment 3 (VIII) free, segment 4 (IX–XI) triple, segment 5 (XII–XIII) double, segment 6 (XIV) free, segment 7 (XV–XVI) double, segment 8 (XVII–XX) compound, segment 9 (XXI–XXIII) triple, segments 10 (XXIV) and 11 (XXV) both free, segment 12 (XXVI–XXVIII) compound. Setal armature comprising: 8, 4, 2, 6, 3, 1 + spine, 2, 3, 2 + aesthetasc, 2, 2 + aesthetasc, 7 + aesthetasc. Apical aesthetasc and adjacent seta arising from common base.

Antenna (Fig. 4A) uniramous; with coxa and basis indistinctly separated; coxa-basis unarmed; endopod 3-segmented; first endopodal segment with 1 inner margin seta, second segment with 5 setae (setae V to IX using terminology of Boxshall & Evstigneeva, 1994), third segment with 7 setae; exopodal seta absent.

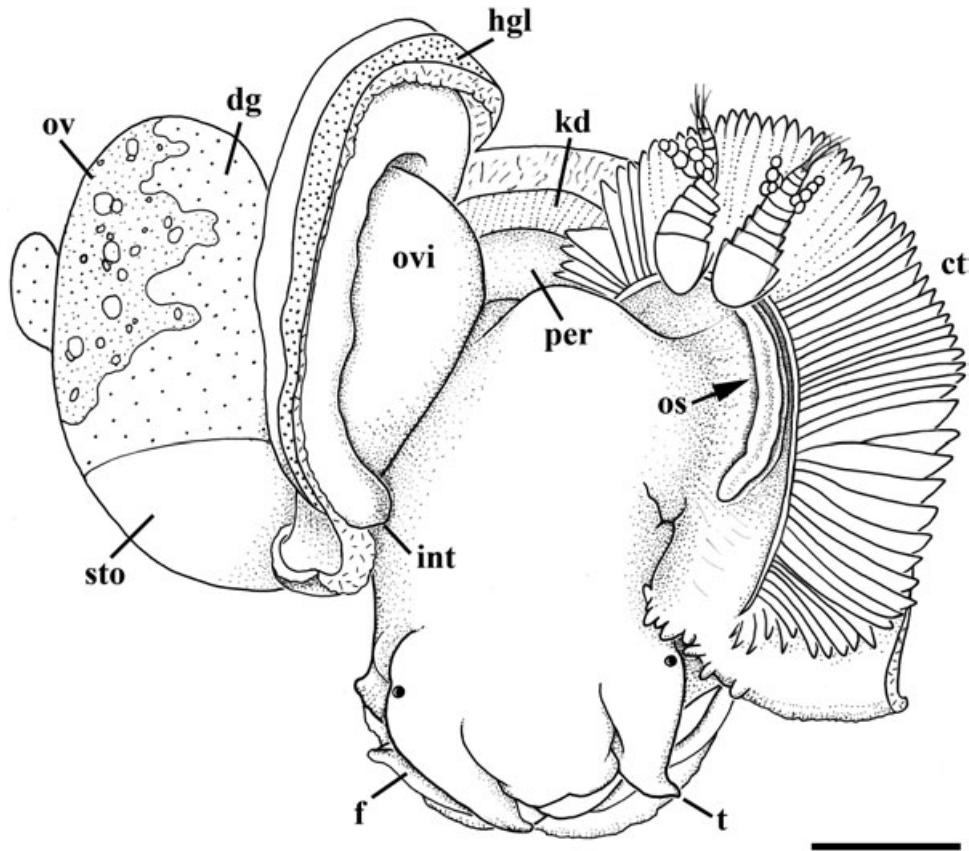
Mandible (Fig. 3A) comprising coxa with well developed gnathobase bearing numerous blades along oblique margin, and reduced palp consisting of vestigial segment bearing 2 sparsely plumose setae; lacking tiny third seta.

Maxillule modified (Fig. 3B); large praecoxa with powerfully developed arthrite produced into 2 curved terminal claws and third, smaller subterminal claw showing traces of articulation at base; palp represented by single seta on distal surface.

Maxilla 2-segmented (Fig. 3C); praecoxa and coxa fused to form syncoxa; inner margin produced into irregular lobate processes in proximal half; distally bearing single seta and vestigial distal coxal endite with 2 apical setae; basis drawn out into powerful apical claw; endopod entirely lacking.

Maxilliped reduced to unarmed, rounded lobe (Fig. 4B).

Swimming legs 1–4 biramous, with 3-segmented rami (Figs 3D,E, 4C,D). Intercoxal sclerites present in legs 1–4; free posterior margins smoothly rounded, lacking any setular ornamentation on either surface. Spine and seta formula as follows:



**Figure 1.** Position of *Eucyclops bathanalicola* sp. nov. within the mantle cavity of its host, *Bathanalia straeleni*. Scale bar, 1 mm. Abbreviations: ct, ctenidium; dg, digestive gland; f, foot; hgl, hypobranchial gland; int, intestine; kd, kidney; os, osphradium; ov, ovary; ovi, pallial oviduct; per, pericardium; sto, stomach; t, cephalic tentacle.

	coxa	basis	exopodal segments	endopodal segments
leg 1	0-1	1-I	I-1; I-1; III,I,4	0-1; 0-1; 1,I +1,3
leg 2	0-1	1-0	I-1; I-1; III,I,5	0-1; 0-1; 1,I +1,3
leg 3	0-1	1-0	I-1; I-1; III,I,5	0-1; 0-2; 1,I +1,3
leg 4	0-1	1-0	I-1; I-1; II,I,5	0-1; 0-2; 1,II,2

Outer margin spines on exopods short. Inner spine on basis of leg 1 short and stout, absent on right leg of paratype but present on both sides of holotype. Inner margin of basis of legs 2-4 ornamented with row of setules; coxa of leg 2 with outer spinule row. Inner margin of first exopodal segment of legs 1-4 with row of setules. Inner distal spine on third endopodal segment of leg 4 spiniform but lacking marginal serrations.

Fifth legs comprising 1 free segment (Fig. 2D) about 1.6 times longer than wide; bearing inner spine, apical seta and outer seta; both setae plumose; inner spine 12.9 µm, shorter than segment (18.6 µm), ornamented with tiny serrations.

Leg 6 represented by 2 stout spines and a seta (broken in figured specimen) carried along oblique opening of genital operculum (Fig. 2C).

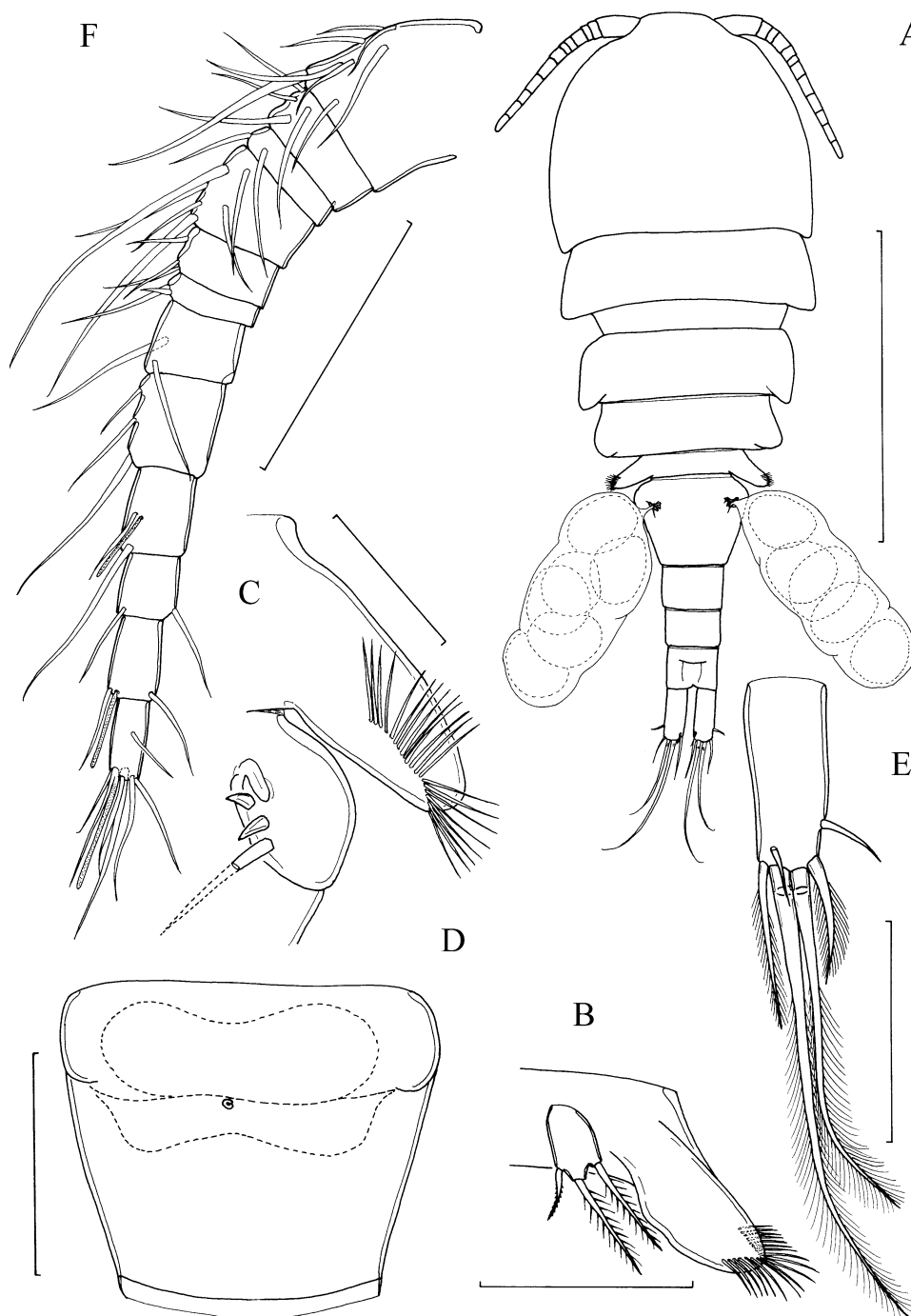
Egg sacs paired (Fig. 2A), containing 5 or 6 eggs.

Male unknown.

## DISCUSSION

### ANATOMY AND AFFINITY OF *EUCYCLOPS BATHANALICOLA* SP. NOV.

The subfamily Eucyclopinae currently comprises ten genera (Boxshall & Halsey, 2004) but the one-segmented fifth swimming leg bearing three setal elements, as exhibited by the new species, is shared with six genera: *Eucyclops*, *Afrocyclops* Sars, 1927, *Tropocyclops* Kiefer, 1927, *Homocyclops* Forbes, 1897, *Paracyclops* Claus, 1893 and *Ochridacyclops* Kiefer, 1937. The shape of the free segment of the fifth leg is shared only with the first three of these, *Eucyclops*, *Afrocyclops* and *Tropocyclops*.



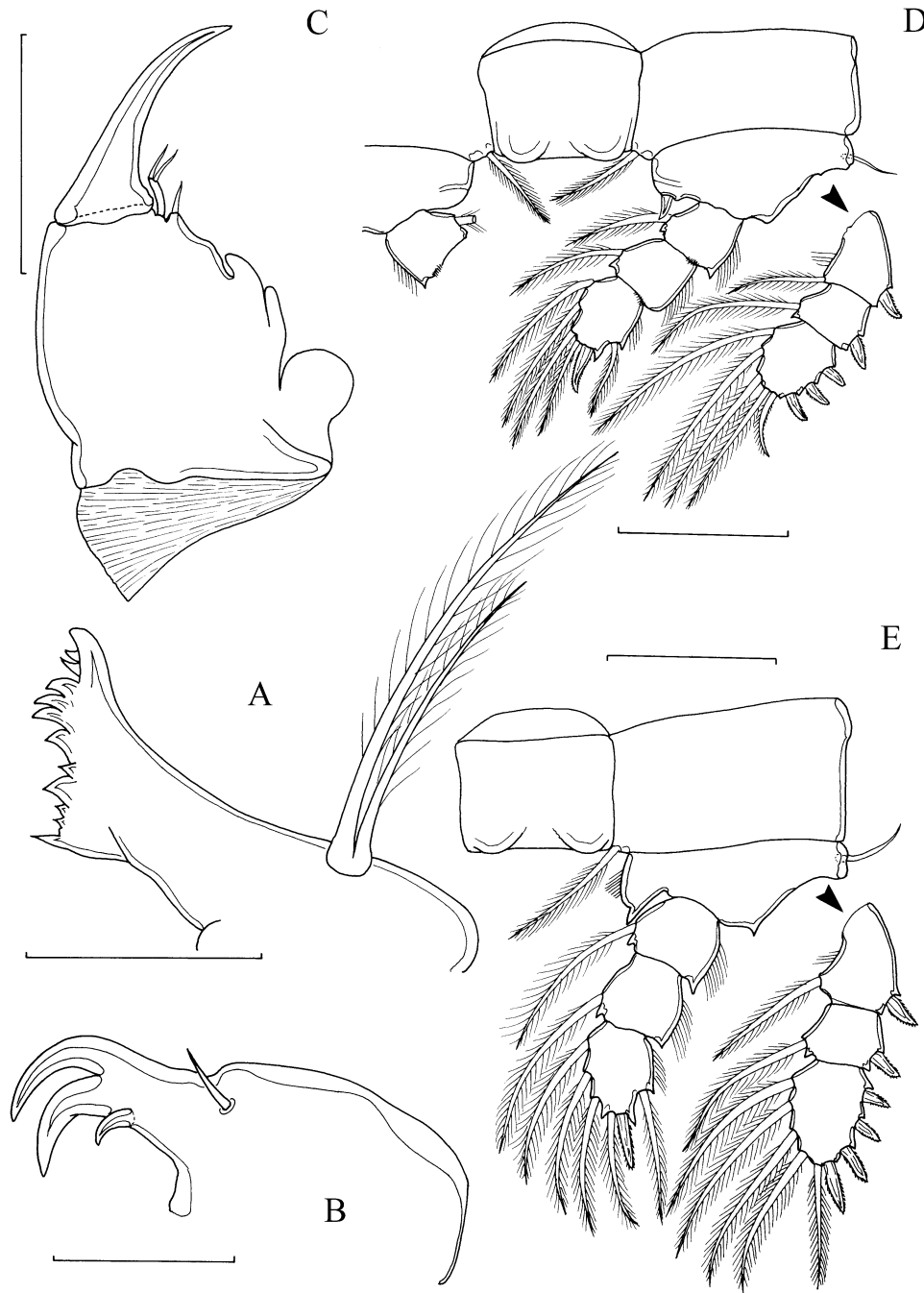
**Figure 2.** *Eucyclops bathanalicola* sp. nov. paratype female. A, habitus, dorsal; B, fifth leg *in situ* on left side of fifth pedigerous somite, ventral; C, right genital aperture, sixth leg and right side of fifth pedigerous somite, dorsal; D, genital double-somite, ventral showing copulatory pore and extent of seminal receptacle (dotted lines); E, right caudal ramus, dorsal; F, antennule. Scale bars: A, 0.5 mm, B–C, 50 µm, D–F, 100 µm.

*clops* and *Tropocyclops*. Of these, *Tropocyclops* differs in the form of the seminal receptacle: the anterior part of the seminal receptacle is typically produced anterolaterally into paired, horn-like lobes. The new species

shares the same simple form of seminal receptacle with both *Eucyclops* and *Afroscyclops*.

*Eucyclops* and *Afroscyclops* are very similar and their validity has never been tested by phylogenetic



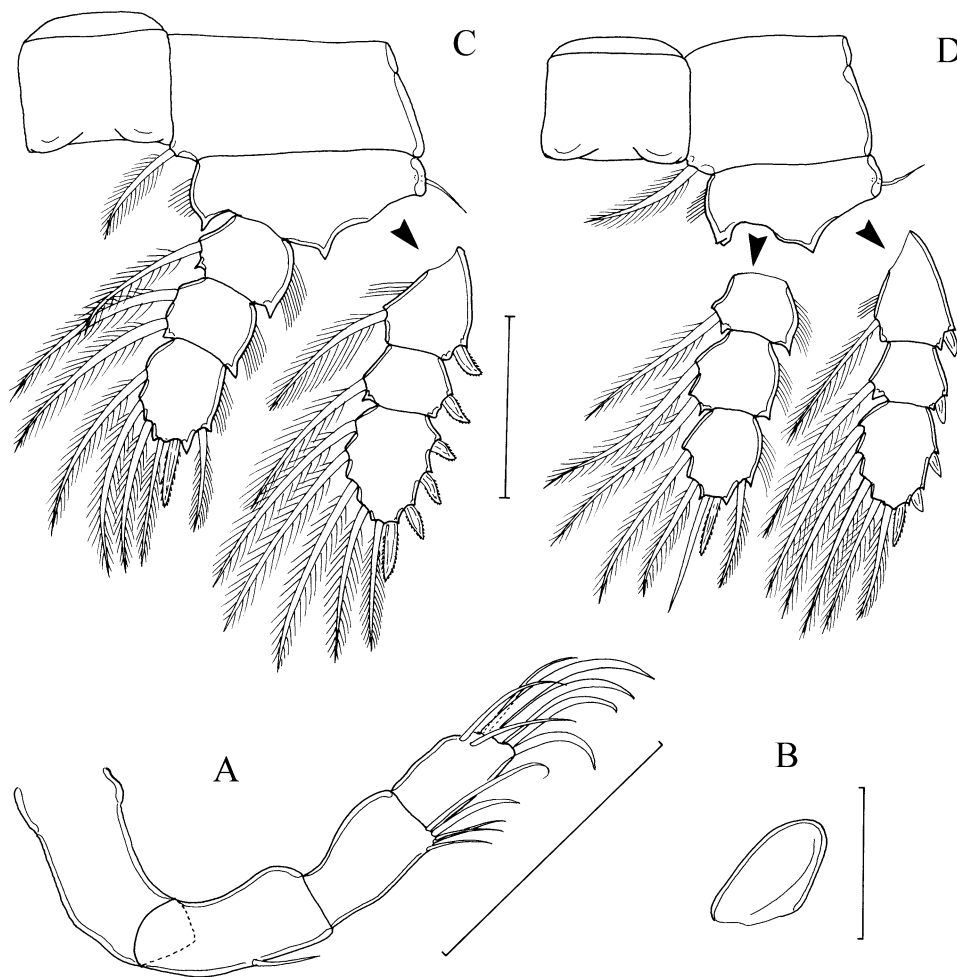


**Figure 3.** *Eucyclops bathanalicola* sp. nov. paratype female. A, mandible; B, maxillule; C, maxilla; D, left leg 1, intercoxal sclerite and base of endopod of right leg, anterior view showing lack of inner spine on right basis; E, left leg 2 and intercoxal sclerite, anterior. All scale bars: 50 µm.

analysis, but they have traditionally been distinguished on the shape of the margin of the basis of the fourth legs (Dussart & Defaye, 2001). In *Eucyclops* species, the inner distal angle of the basis of leg 4 is produced into a spinous process whereas in *Afrocylops* species, this margin is rounded. The inner angle of the basis of the new species is produced into a

spinous process with a bifid tip: it is not rounded and is therefore classified as a *Eucyclops*.

Twelve species of *Eucyclops* have previously been reported from Lake Tanganyika (Dussart & Defaye, 1985), of which six are endemic and another two are found only in Lake Tanganyika plus Lake Malawi (Table 1). *Eucyclops* is a large genus with over 80



**Figure 4.** *Eucyclops bathanalicola* sp. nov. paratype female. A, antenna; B, vestigial maxilliped; C, left leg 3 and intercoxal sclerite, anterior; D, Left leg 4 and intercoxal sclerite, anterior. Scale bars: A, 100 µm, B–D, 50 µm.

described species, all of which are free-living and are epibenthic or planktonic with normally developed maxillules and maxillae. The specimens described here were firmly attached to the host by means of the praecoxal claws of the maxillules and the distal claws of the maxillae. These claws were deeply embedded into the host tissue and serve as the primary attachment mechanism. The new species is atypical in its short caudal rami (most *Eucyclops* species have rami more than four times longer than wide). The possession of an inner spine on leg 5 that is shorter than the free segment is also an atypical character state, shared with at least four species known from the lake. It shares both this short spine and the complete absence of an outer longitudinal row of spinules on the caudal ramus only with *E. angustus* Sars, 1909 and *E. laevimargo* Sars, 1909. The available data on the lacustrine species listed in Table 1 are limited: for most, the mouthparts have never been described. Given the lack of the male and the absence of such

data, we are unable to estimate the phylogenetic relationships of *E. bathanalicola* sp. nov., but we hypothesize that its sister group might lie within the small cluster of *Eucyclops* species known from the East African Rift Valley lakes, characterized by a short spine on the fifth leg and the lack of spinule rows on the caudal rami.

This new species is a fascinating mosaic: in body form, in the segmentation pattern of the antennules and antennae, in the vestigial mandibular palp, in the segmentation and setation of the swimming legs and in the shape and armature of the fifth leg, it can readily be classified as a typical member of the subfamily Eucyclopinae, whereas the maxillules and maxillae of the new species are highly modified and the maxillipeds are vestigial. The maxillule is unique in the presence of powerful medial claws on the praecoxa. The maxillary palp in cyclopids usually comprises a coxa, basis and endopod, with the exopod represented by an isolated surface seta (Boxshall & Halsey, 2004).

**Table 1.** Species of *Eucyclops* recorded from Lake Tanganyika

Species	Female body length (mm)	CR L : W	Leg 5 spine	CR lateral spinule row	Distribution	Data source
<i>E. bathanalicola</i>	1.18	2.3 : 1	short	absent	LT endemic	Present account
<i>E. angustus</i>	0.82	6.6 : 1	short	absent	LT and LM	Sars (1909)
<i>E. laevimargo</i>	0.85–1.05	6.2 : 1	short	absent	LT endemic	Sars (1909); Lindberg (1951)
<i>E. semiserratus</i>	0.86	5.5 : 1	short	distal half	LT endemic	Sars (1909)
<i>E. ciliatus</i>	0.86	4.8 : 1	short	entire	LT endemic	Sars (1909)
<i>E. agiloides</i>	0.90	4.2 : 1	long	entire	Africa, Asia	Sars (1909)
<i>E. caparti</i>	0.92–0.94	4.1 : 1	long	absent	LT endemic	Lindberg (1951)
<i>E. dubius</i>	0.62	5.0 : 1	long	absent	LT and LM	Sars (1909)
<i>E. euacanthus</i>	0.76–0.79	4.6 : 1	long	entire	Africa, Asia	Sars (1909); Lindberg (1951)
<i>E. paucidentatus</i>	0.86	3.6 : 1	long	distal half	LT endemic	Lindberg (1951)
<i>E. rarispinus</i>	0.75–0.85	3.5 : 1	medium	distal half	LT endemic	Sars (1909); Lindberg (1951)
<i>E. serrulatus</i>	0.80–1.45	~5.0 : 1	long	entire	cosmopolitan	Dussart (1969)
<i>E. sublaevis</i>	0.95–1.20	6.9 : 1	long	distal half	S.Africa, LT	Sars (1927); Lindberg (1951)

CR, caudal rami; L : W, mean length : width ratio; LT, Lake Tanganyika; LM, Lake Malawi. Length of spine on leg 5: short = shorter than segment, medium = about as long as segment, long = longer than segment. Shaded background groups those species with a short spine on leg 5 and lacking a lateral spinule row on the caudal ramus.

The entire palp in this new species is represented by a single naked seta. The maxillae are also modified, with the basis forming a well developed claw, and the entire endopod is lost, as are the enditic setae from the basis. Together, the maxillules and maxillae appear to form a powerful and specialized attachment mechanism and nothing like these modifications exists anywhere within the Cyclopidae. The profound modification of these two limbs is interpreted here as evidence of obligate parasitism, at least in the female.

The reduction of the maxilliped to an unarmed lobe has been reported in the cyclopoid genus *Smirnoviella* Monchenko, 1977 (Monchenko, 1977a), and Monchenko (1977b) also reported the complete lack of maxillipeds in a related genus *Colpocyclops* Monchenko, 1977. However, study of new material of *Colpocyclops* (C.E.F. Rocha, pers. comm.) has revealed the presence of lobate vestiges in this genus. Both these genera are derived forms belonging to the subfamily Halicyclopinae, and we infer that the loss of functional maxillipeds is convergent.

A few species of Cyclopidae from the genera *Ochridacyclops* and *Diacyclops* Kiefer, 1927, including *Diacyclops spongicola* Mazepova, 1961 and *Diacyclops incolotaenia* Mazepova, 1950, are known to live in association with sponges in Lake Ohrid and in Lake Baikal (Kiefer, 1937; Mazepova, 1978), although *Ochridacyclops* and *D. incolotaenia* are commonly found away from any host. In each case, however, the degree of modification is considerably less than in the new species: no praecoxal claws are present on the maxillules, the maxilla retains its typical format with well developed syncoxal endites and an endopod, and a

normal four-segmented maxilliped is present. The nature of the relationship in these sponge-associates has not yet been investigated, but it is interesting to note that these shifts into a symbiotic life mode by cyclopids have all occurred in ancient lakes with relatively diverse faunas.

#### HOST

Very little is known about the ecology and distribution of the host species, *Bathania straeleni*. Searches through many major museums or collections of historical importance (Museum of Comparative Zoology, Harvard; Museum National d'Histoire Naturelle, Paris; National Museum of Natural History, Washington DC; The Natural History Museum, London; Museum für Naturkunde, Humboldt Universität, Berlin; Danish Bilharziasis Laboratory, Charlottenlund) have revealed only limited shell material for its congener, *B. howesi*, and no material for *B. straeleni*. Apart from two shells collected by L. Stappers in the collections of the IRSNB (Leloup, 1953), the only other known museum material of *B. straeleni* was collected during the hydrobiological exploration of the lake conducted by the IRSNB from 1946 to 1947.

According to Leloup's detailed report on the gastropods collected during this expedition, specimens of *Bathania straeleni* were collected from 13 stations along all shores of Lake Tanganyika. Only a single station yielded living animals (No. 50), which were dredged in 20–80 m depth near the mouth of the Lukuga River along the shore of the Democratic Republic of Congo. The living specimens were dredged

from diverse substrates including mud and rocks. Other localities reported substrates including black mud, sand, sandy mud, rocks or stones; they were dredged or trawled at depths ranging from 0.5 m to 70 m, but yielded only empty shells. Thus, the species apparently prefers deeper water habitats (e.g. Dart-velle & Schwetz, 1948; Leloup, 1953). *Bathanalia straeleni* is a small species and is typically less than 12.0 mm in height (Leloup, 1953), whereas its congener, *B. howesi*, can reach 25.0 mm in height (Brown, 1994). Later accounts relating to this genus have relied heavily on information provided by Leloup (e.g. Brown, 1994) or have provided no new data (West *et al.*, 2003).

As stated above, the female copepods were found attached within the inhalant region of the mantle cavity. No males were found within the mantle cavity, but as the material is over 50 years old, any free males may have become dislodged during the intervening time. Upon dissection of the host, no copepods were found within the haemocoel.

#### COPEPODS IN LAKE TANGANYIKA

The majority of copepods reported from Lake Tanganyika are free-living omnivores and/or predators feeding mainly on algae, small zooplankton and cyanobacteria (Haberyan, 1985; Sarvala *et al.*, 2003). They are important members of the zooplankton community (e.g. Kurki *et al.*, 1999; Vuorinen *et al.*, 1999) as they represent a key player in pelagic food webs in the lake (Dumont, 1994; Bahananga, Diamani & Kabungo, 1996), especially as prey for some species of the spectacular array of endemic fishes (Kondo, 1986).

Several parasitic copepods have also been described from, or recorded from the lake (Fryer, 1968), including the ergasilids *Ergasilus megacheir* (Sars, 1909), *E. macrodactylus* (Sars, 1909), *E. kandti* van Douwe, 1912 and *E. flaccidus* Fryer, 1965, and the lernaeids *Afrolernaea longicollis* Fryer, 1956, *Lernaea barnimi-ana* (Hartmann, 1865), *L. bistricornis* Harding, 1950, *L. haplocephala* (Cunnington, 1914), *L. diceracephala* (Cunnington, 1914), *Lamproglana clariae* Fryer, 1956, *L. hemprichii* von Nordmann, 1832, *L. monodi* Capart, 1944 and *Ophiolernaea longa* (Harding, 1950). All these parasites exclusively utilize fishes as hosts and are drawn from large parasitic lineages.

#### FRESHWATER PARASITIC COPEPODS

Copepods occur in virtually every kind of aquatic habitat and exhibit enormous variety in mode of life. About half of the 11 500 known species of copepods live in symbiotic association with metazoan hosts, although the nature of the symbiotic relationship is not always known. Copepods have shifted into para-

sitism independently in numerous different lineages (Kabata, 1979; Huys & Boxshall, 1991). These parasitic lineages vary in size from entire orders, such as the Siphonostomatoida, to families, or to a few genera within a family, such as the Tisbidae (Boxshall & Halsey, 2004). The occurrence of a single parasitic species within a large and well defined, free living clade is, however, extremely rare.

Relatively few families of copepods have successfully colonized fresh water (Boxshall & Jaume, 2000) and only ten families of freshwater Copepoda contain symbiotic species. Four of these families are parasitic exclusively on vertebrate hosts. The Lernaeidae is a relatively speciose family, comprising about 120 species (Ho, 1998), all parasites of freshwater fishes, although there are rare reports of lernaeids from amphibians such as frog tadpoles (Stunkard & Cable, 1931). The Lernaeopodidae comprises over 270 species but only one clade within the large family has radiated in freshwater (Kabata, 1979). This clade comprises 38 species in seven genera, of which *Salmincola* Wilson, 1915 is the largest, and they occur on a range of fish hosts, including silurids, cyprinids and coregonids as well as salmonids and acipenserids. One genus of the family Dichelesthidae parasitizes the anadromous sturgeons, migrating between fresh and marine waters, and the large family Caligidae similarly contains a single freshwater species, *Caligus lacustris* Steenstrup & Lütken, 1861, among several hundreds of marine and a few brackish water species. The Ergasilidae comprises over 260 nominal species and occurs across all salinity regimes from fresh to marine. Ergasilids have free living developmental stages and only the adult females become parasitic, after mating; they typically utilize fishes as hosts.

On freshwater invertebrates, copepods are most commonly found as commensal epibionts living in association with, for example, freshwater crayfishes (Chappuis, 1926; Boshko *et al.*, 1977; Boshko, 1978; Reid, 2001), freshwater medusae (Humes, 1953) or sponges (Mazepova, 1978; Boxshall & Evstigneeva, 1994). However, copepods parasitic on freshwater invertebrates are rare. The only copepods described to date as parasitic from freshwater invertebrates exclusively use molluscan hosts and include species in the family Ergasilidae living on the gills of freshwater bivalves in the genus *Anodonta* (Unionoidea) (Titir & Chernogorenko, 1982; Chernysheva, 1988; Pekkarinen, 1993; Taskinen & Saarinen, 1999; Saarinen & Taskinen, 2003), and species in the Ozmanidae Ho & Thatcher, 1989.

The family Ozmanidae includes only two species that live as endo- and ectoparasites of snails in the family Ampullariidae (Ho & Thatcher, 1989; Gamarra-Luque *et al.*, 2004). At the time of its description, *Ozmana haemophila* Ho & Thatcher, 1989 – discov-



ered within the haemolymph of *Pomacea maculata* (Caenogastropoda, Ampullariidae) – represented the first record of a freshwater gastropod harbouring parasitic copepods. Since that time, few additional reports have been published on copepods associated with freshwater gastropods. One described a second species in the Ozmanidae associated with *Pomacea canaliculata* (Ampullariidae) in the Plata and Amazon basins of South America (Gamarra-Luque *et al.*, 2004). In addition, an unidentified species of harpacticoid was described living in association with *Lanistes carinatus* (Ampullariidae) in Egypt (El-Bahy, 1998). However, the precise nature of this association was not investigated, although it was characterized as having no ill effect on the host and may simply be a commensal relationship.

Thus, the present description represents a rare account of a freshwater copepod parasitic on an invertebrate host, the first record from a host in the freshwater Cerithioidea, as well as the first report from a nonampullariid host. It also represents a unique foray into an obligate parasitic life mode in the otherwise free living Cyclopidae; although the order Cyclopoida (*sensu* Huys & Boxshall, 1991) is almost certainly paraphyletic, in addition to the Chitinophilidae, Mantiidae and Ozmanidae, the Cyclopidae can be added to the list of cyclopoid families that utilize molluscs as hosts (see Discussion in Huys *et al.*, 2002). As such, this discovery highlights yet another intriguing facet of the endemic fauna of Lake Tanganyika.

## CONCLUSIONS

*Eucyclops bathanalicola* is distinguished by the possession of praecoxal claws on the maxillules and the reduction of the maxillular palp, by the modified maxillae which lack any trace of an endopod on the powerful distal claw, and by the reduction of the maxillipeds to minute unarmed lobes. It is thus, highly modified for a parasitic life habit. As a member of the genus *Eucyclops* within the family Cyclopidae, this species represents a unique foray into a parasitic lifestyle from an otherwise free living group of copepods living in Lake Tanganyika. This is the first record of a copepod parasite on a snail within this ancient lake and represents only the third record of a copepod parasite on a freshwater snail.

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## REFERENCES

- Bahananga J-M, Diamani B, Kabungo K. 1996.** Physico-chemical preferences of the zooplankton and notes on the predominance of a carnivorous copepod in Lake Tanganyika. *African Journal of Ecology* **34**: 86–89.
- Boshko EG. 1978.** Parazyty i simbioty rechnogo raka *Astacus (Pontastacus) leptodactylus* Esch. r. Uda (Dneprovski bassen). In: Markevich AP, ed. *Problemy gidro-parazitologii*. Kiev: Naukova Dumka, 16–20. (In Russian).
- Boshko EG, Koval VP, Marchenkov FS, Tarnovskij VS. 1977.** Fauna zhabrovoi porozhnini richkovikh rakiv r. Suli (Dnirovskii basein). *Visnyk Kyivskoho Universytetu Seriya Biologichna* **19**: 112–114. (In Ukrainian with Russian and English summaries).
- Boxshall GA, Evstigneeva TD. 1994.** The evolution of species flocks of copepods in Lake Baikal: a preliminary analysis. In: Martens K, Goddeeris B, Coulter G, eds. *Speciation in ancient lakes. Archiv für Hydrobiologie, Ergebnisse der Limnologie* **44**: 235–245.
- Boxshall GA, Halsey SH. 2004.** *An introduction to copepod diversity*. London: The Ray Society.
- Boxshall GA, Jaume D. 2000.** Making waves: the repeated colonization of fresh water by copepod crustaceans. *Advances in Ecological Research* **31**: 61–79.
- Brown DS. 1994.** *Freshwater snails of Africa and their medical importance*. Revised, 2nd edn. London: Taylor & Francis.
- Chappuis PA. 1926.** Harpacticiden aus der Kiemenhöhle des Flusskrebsses. *Archiv für Hydrobiologie* **17**: 515–520.
- Chernysheva NB. 1988.** On the identity of *Paraergasilus rylovi* and *P. markevichi* (Copepoda, Ergasilidae). *Parazitologiya* **22**: 428–431.
- Coulter G. 1991.** *Lake Tanganyika and its life*. Oxford: Oxford University Press.
- Dartevelle E, Schwetz J. 1948.** Le lac Tanganika. *Mémoires Institut Royal Colonial Belge* **14** (5): 1–118, pl. I–VI.
- Ducasse O, Carbonel P. 1994.** Cytherideinae (Crustacea, Ostracoda) recents du Lac Tanganyika. *Archeocyprideis tuberculata* n. gen., n. sp. systematique, distribution, ecologie. *Revue de Micropaleontologie* **37**: 97–112.
- Dumont HJ. 1994.** Ancient lakes have simplified pelagic food webs. In: Martens K, Goddeeris B, Coulter G, eds. *Speciation in ancient lakes. Archiv für Hydrobiologie, Ergebnisse der Limnologie* **44**: 223–234.
- Dussart BH. 1969.** *Les copépodes des eaux continentales d'Europe occidentale*. Tome II: *Cyclopoides et biologie*. Paris: Boubée & Cie.
- Dussart BH, Defaye D. 1985.** *Répertoire mondial des crustacés copépodes des eaux intérieures*. II. *Cyclopoides*. Paris/Bordeaux: Centre National de la Recherche Scientifique.
- Dussart BH, Defaye D. 2001.** *Introduction to the Copepoda*, 2nd edn. *Guides to the identification of the microinvertebrates of the continental waters of the world*. Dumont HJF, ed. Leiden: Backhuys Publishers.
- El-Bahy NM. 1998.** Parasitological aspects of *Lanistes carinatus* (Olivier, 1804, Cyclostoma) snails and their role in trans-

- mission of parasitic diseases to animal and man. *Assiut Veterinary Medical Journal* **38**: 230–282.
- Fryer G. 1968.** The parasitic Crustacea of African freshwater fishes: their biology and distribution. *Journal of Zoology* **156**: 45–95.
- Gamarra-Luque CD, Vega IA, Koch E, Castro-Vazquez A. 2004.** Intrahost distribution and transmission of a new species of cyclopoid copepod endosymbiotic to a freshwater snail, *Pomacea canaliculata* (Caenogastropoda, Ampullariidae) from Argentina. *Biocell* **28**: 155–164.
- Haberyan KA. 1985.** The role of copepod fecal pellets in the deposition of diatoms in Lake Tanganyika. *Limnology and Oceanography* **30**: 1010–1023.
- Ho J-S. 1998.** Cladistics of the Lernaieidae (Cyclopoida), a major family of freshwater fish parasites. *Journal of Marine Systems* **15**: 177–183.
- Ho J-S, Thatcher VE. 1989.** A new family of cyclopoid copepods (Ozmanidae) parasitic in the hemocoel of a snail from the Brazilian Amazon. *Journal of Natural History* **23**: 903–911.
- Humes AG. 1953.** Two new semiparasitic harpacticoid copepods from the coast of New Hampshire. *Journal of the Washington Academy of Sciences* **43**: 360–373.
- Huys R, Boxshall GA. 1991.** *Copepod evolution*. London: The Ray Society.
- Huys R, Lopez-Gonzalez PJ, Roldan E, Luque AA. 2002.** Brooding in cocculiniform limpets (Gastropoda) and familial distinctiveness of the Nucellicolidae (Copepoda): Misconceptions reviewed from a chitonophilid perspective. *Biological Journal of the Linnean Society* **75**: 187–217.
- Kabata Z. 1979.** *Parasitic copepoda of British fishes*. London: The Ray Society.
- Kiefer F. 1937.** Ein neuer Cyclopide (Crust. Copepoda) aus dem Ochridasee. *Zoologischer Anzeiger* **120**: 137–143.
- Kondo T. 1986.** Feeding habits of *Lamprologus savoryi* (Teleostei: Cichlidae) with reference to its social behaviour. *Physiology and Ecology Japan* **23**: 1–15.
- Kurki H, Vuorinen I, Bosma E, Bwebwa D. 1999.** Spatial and temporal changes in copepod zooplankton communities of Lake Tanganyika. *Hydrobiologia* **407**: 105–114.
- Leloup E. 1953.** Gastéropodes. In: *Exploration hydrobiologique du Lac Tanganika (1946–47). Résultats scientifiques* Vol. 3 (4). 1–272. Bruxelles.
- Lindberg K. 1951.** Cyclopides (Crustacés Copépodes). In: *Exploration hydrobiologique du Lac Tanganika (1946–47). Résultats scientifiques*. Vol. 3 (2). 45–91. Bruxelles.
- Martens K. 1985.** *Tanganyikacypridopsis* gen. n. (Crustacea, Ostracoda) from Lake Tanganyika. *Zoologica Scripta* **14**: 221–230.
- Martin P, Giani N. 1995.** Two new species of *Epirodilus* (Oligochaeta, Tubificidae) from Lake Nyasa and Tanganyika (East Africa), with redescrptions of *E. slovenicus* and *E. michaelsoni*. *Zoologica Scripta* **24**: 13–19.
- Mazepova GF. 1978.** Tsiklopy ozera Baikal. *Trudy Limnologicheskogo Instituta (Akad. Nauk SSSR, Sibirskoe Otdel.)* **28** (49): 1–144. (In Russian).
- Michel AE. 2004.** *Vinundu*, a new genus of gastropod (Cerithioidea: 'Thiaridae') with two species from Lake Tanganyika, East Africa, and its molecular phylogenetic relationships. *Journal of Molluscan Studies* **70**: 1–19.
- Monchenko VI. 1977a.** On a strong modified new copepod (*Colpocyclops dulcis* gen. et sp. n.) (Crustacea, Cyclopidae). *Vestnik Zoologii* **1977** (6): 25–32. (In Ukrainian with English summary).
- Monchenko VI. 1977b.** *Smirnoviella reducta* gen. et sp. n. (Crustacea, Copepoda) from the Dniestr estuary (Black Sea basin). *Zoologicheskii Zhurnal* **56** (9): 1402–1406. (In Russian with English summary).
- Morse JC. 1988.** A new species of *Ceraclea* (Athripsodina) (Trichoptera: Leptoceridae) from Lake Tanganyika. *Revue de Zoologie Africaine* **102**: 43–45.
- Park LE, Martens K, Cohen AS. 2002.** Phylogenetic relationships of *Gomphocythere* (Ostracoda) in Lake Tanganyika, East Africa. *Journal of Crustacean Biology* **22**: 15–27.
- Pekkarinen M. 1993.** Reproduction and condition of unionid mussels in the Vantaa River, south Finland. *Archiv für Hydrobiologie* **127**: 337–357.
- Reid JW. 2001.** A human challenge: discovering and understanding continental copepod habitats. *Hydrobiologia* **453/454**: 201–226.
- Rushton-Mellor SK. 1994.** The genus *Argulus* (Crustacea: Branchiura) in Africa: two new species, *A. fryeri* and *A. gracilis*, the previously undescribed male of *A. brachypeltis* Fryer and the identity of the male described as *A. ambloplites* Wilson. *Systematic Parasitology* **28**: 23–31.
- Saarinén M, Taskinen J. 2003.** Reduction in the level of infection of the bivalve *Anodonta piscinalis* by the copepod *Paraergasilus rylovi* using high temperature and low oxygen. *Journal of Parasitology* **89**: 1117–1167.
- Salzburger W, Meyer A. 2004.** The species flocks of East African cichlid fishes: recent advances in molecular phylogenetics and population genetics. *Naturwissenschaften* **91**: 277–290.
- Sars GO. 1909.** Zoological results of the Third Tanganyika Expedition conducted by Dr. W.A. Cunningham, F.Z.S., 1904–05. Report on the Copepoda. *Proceedings of the Zoological Society of London*, **1909**: 31–77.
- Sars GO. 1927.** The freshwater Entomostraca of the Cape Province. Part 3: Copepoda. *Annals South African Museum, Cape Town* **25**: 85–149.
- Sarvala J, Badende S, Chitamwebwa D, Juvonen P, Mwape L, Molsa H, Mulimbwa N, Salonen K, Tarvainen M, Vuorio K. 2003.** Size-fractionated  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  isotope ratios elucidate the role of the microbial food web in the pelagial of Lake Tanganyika. *Aquatic Ecosystem Health and Management* **6**: 241–225.
- Segers H, Baribwegure D. 1996.** On *Lecane tanganyikae* new species (Rotifera: Monogononta, Lecanidae). *Hydrobiologia* **324**: 179–182.
- von Sternberg R, Cumberlidge N. 1999.** A cladistic analysis of *Platythelphusa* A. Milne-Edwards, 1887, from Lake Tanganyika, East Africa (Decapoda: Potamoidea: Platythelphusidae) with comments on the phylogenetic position of the group. *Journal of Natural History* **33**: 493–511.

- Stunkard HW, Cable RM. 1931.** Notes on a species of *Lernaea* parasitic in the larvae of *Rana clamitans*. *Journal of Parasitology* **18**: 92–97.
- Taskinen J, Saarinen M. 1999.** Increased parasite abundance associated with reproductive maturity of the clam *Anodonta piscinalis*. *Journal of Parasitology* **85**: 559–588.
- Titar VM, Chernogorenko MI. 1982.** Novyi vid rode. *Paraergasilus* Markewitsch, 1937 (Copepoda: Ergasilidae) u *Anodonta piscinalis* Nils. (Mollusca: Unionidae). In: Polyan-skij YI, ed. *Parazyti parazitozy cheloveka i zhivotnykh. Sbornik nauchnykh trudov*. Kiev: Naukova Dumka, 214–218. (In Russian with English summary).
- Tsalolikhin S. 1989.** New nematode species in Tanganyika Lake. *Zoologicheskii Zhurnal* **68**: 8–16.
- Vuorinen I, Kurki H, Bosma E, Kalangali A, Molsa H, Lindqvist OV. 1999.** Vertical distribution and migration of pelagic Copepoda in Lake Tanganyika. *Hydrobiologia* **407**: 115–121.
- West K, Michel E. 2000.** The dynamics of endemic diversification: molecular phylogeny suggests an explosive origin of the thiarid gastropods of Lake Tanganyika. *Advances in Ecological Research* **31**: 331–354.
- West K, Michel E, Todd J, Brown D, Clabaugh J. 2003.** *The gastropods of Lake Tanganyika. Diagnostic key, classification and notes on the fauna*. Dorchester: Dorset Press.
- Wilson AB, Glaubrecht M, Meyer A. 2004.** Ancient lakes as evolutionary reservoirs: evidence from the thalassoid gastropods of Lake Tanganyika. *Proceedings of the Royal Society of London, Biology Sciences* **1538**: 529–536.
- Wouters K, Martens K. 1994.** Contribution to the knowledge of the *Cyprideis* species flock (Crustacea: Ostracoda) of Lake Tanganyika, with the description of three new species. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique Biologie* **64**: 111–128.
- Wouters K, Martens K. 1999.** Four new species of the *Cyprideis* species flock (Crustacea: Ostracoda) of Lake Tanganyika. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique Biologie* **69**: 67–82.