

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/357382432>

# Revision of the Genus *Mesocyclops* Sars 1914 (Copepoda, Cyclopidae) of the World Fauna

Article in *Biology Bulletin* · December 2021

DOI: 10.1134/S1062359021080021

---

CITATION

1

---

READS

99

1 author:



**Victor Alekseev**

Zoological Institute, Saint Petersburg, Russia

108 PUBLICATIONS 1,333 CITATIONS

SEE PROFILE

Some of the authors of this publication are also working on these related projects:



Special Issue "Biological Invasion of Fish Parasites and other Aquatic Dangerous Species" [View project](#)

## Revision of the Genus *Mesocyclops* Sars 1914 (Copepoda, Cyclopidae) of the World Fauna

V. R. Alekseev\*

Zoological Institute, Russian Academy of Sciences, St. Petersburg, 199034 Russia

\*e-mail: alekseev@zin.ru

Received March 15, 2020; revised March 25, 2020; accepted April 10, 2020

**Abstract**—The genus *Mesocyclops* Sars 1914, which has hitherto contained too many nominal species, is divided into four subgenera based on the morphological and habitat characteristics. The subgenus *Neomesocyclops* subgen. n. comprises species almost exclusively living in the New World. The single exception is *M. (N.) tenuisaccus* (Sars 1927), described from South Africa, which may prove to be a junior synonym of *M. (N.) annulatus* (Wierzejski 1892), from South America, and could have appeared in Africa as a result of anthropogenic invasion from the New World. The subgenus *Tethymesocyclops* subgen. n. includes species the distributions of which coincide with the borders of the former subcontinent Gondwana, or rather, the coast of the Tethys Sea, during the separation of Gondwana from Laurasia. These two subgenera contain species with a seta on the inner outgrowth of the basal segment of the first swimming leg pair. This seta is absent in all representatives of the nominative subgenus *Mesocyclops* s. str. with bare caudal rami and last thoracic somite, as well as in the new subgenus *Pilosomesocyclops* subgen. n., which has hairs on these structures. Most species of the latter two subgenera live in water bodies of the Old World. Along with a detailed characterization of the identified subgenera, a new species is described: *Mesocyclops (Neomesocyclops) frankfiersi* sp. n. As part of the revision, species in the two largest subgenera, *Neomesocyclops* subgen. n. and *Pilosomesocyclops* subgen. n., are further divided into three sections by the presence of hair-like structures on the last thoracic somite and/or caudal rami. Sections are named after the first species described that shows these characters. Such a structure of the genus makes it possible to simplify significantly the determination of species in the world fauna and, in the future, to supplement the keys after new taxa are described. Compared to the latest faunal overview by Reid and Ueda, the keys presented are extended to the 12 taxa described in the years following the publication of that guide.

**Keywords:** copepods, taxonomy, faunistics, zoogeography, new species, subgenus

**DOI:** 10.1134/S1062359021080021

### INTRODUCTION

The genus *Mesocyclops* Sars (Copepoda: Cyclopidae) is rich in species, and the process of describing new forms continues very intensively, which has led to the need for frequent revisions of the genus (Kiefer, 1981; Van de Velde, 1984; Alekseev, 2002; Holynska, 2003). The species diversity of this genus is based, on the one hand, on its worldwide distribution. As the paradigm of cosmopolitanism is replaced by the concept of twin or super species, uniting closely related but isolated groups of morphologically similar forms (Kiefer, 1981) with the ensuing isolation options (mountain building, movement of continents, formation of glaciers and their melting), the number of described species has increased significantly.

On the other hand, the ecological community has given increased attention to this genus in the past century, due to the noticeable role that it plays everywhere in the pelagic ecosystems of continental water bodies

(Gophen, 1984; Alekseev, 2002; Reid and Ueda, 2003; Meleg et al., 2012).

The latest revision of the *Mesocyclops* world fauna by M. Holynska (Holynska, 2003) brought together over 60 species of the genus. During study of the phylogenetic relationships, the number of taxa considered, including subspecies, was over 70 (Holynska, 2006). It is very difficult to work with such an array of species within the framework of one undivided genus; moreover, due to the ongoing active description of new taxa, primarily from poorly studied regions of Southeast Asia and South and North America, the last key of the world fauna of the genus compiled by Holynska (Holynska, 2003) is outdated. Important works on the phylogenetic structure of the genus *Mesocyclops* (Holynska, 2006; Wyngaard et al., 2010) confirmed both the validity of many barely distinguishable forms and the monophyly of the genus, but did not resolve the issue of simplifying the identification keys. Due to the increased incidence of intercon-

tinental biological invasions and the observed dispersal of tropical taxa into the water bodies of higher latitudes, caused by climate change in recent years (Alekseev et al., 2009, 2020; Fefilova et al., 2014; Montoliu et al., 2015), the issue of carrying out a cardinal revision of this genus has become very relevant.

Shortly before the release of the key, edited by J. Reid and H. Ueda (Reid and Ueda, 2003), I carried out a preliminary analysis of this genus. The analysis showed the complex structure of this genus and stable differences in the morphology, which are quite well related to the modern distribution of species across continents (Alekseev, 2002). Such a ratio of the morphological and geographical divergence could well be reduced to at least four subgenera. In recent years, such a division has not been made, which complicates further progress in the study of the genus. The present work was carried out to solve these and other accumulated taxonomic and systematic problems of the genus *Mesocyclops*.

In the course of this revision of the genus and its division into subgenera, the material of the island fauna was studied. In this material, collected by me earlier from the area of the Atlantic coast of Mexico, a new species for science was discovered and is described below.

## MATERIALS AND METHODS

This work used significant material collected personally by the author during expeditions across Russia (from Kaliningrad to Kamchatka and from the Lena delta to Tuva) and in the following countries: Germany (1992, Lake Constance; 1996, 2000–2003, the Holstein lakes, the Rhine River, the Oder River, and other rivers flowing into the North Sea), Mongolia (1995, Gobi lakes; 2000, Lake Khuvsgul, Tuul and Selenga rivers), Spain (2005, Guadalquivir River, Seville; 2006–2013, 2019, reservoirs of Castile and Valencia), Canada (1997, water bodies of the province of Ontario; 1998–2000, 2016–2017, lakes in the province of Quebec), United States (1996, Lake Erie; 2016, lakes of Central Park, New York, type material for the subgenus *Neomesocyclops* subgen. n. from the Great Lakes), Mexico (2009, reservoirs in the cities of Mexico City and Aguascalientes; 2011, Yucatan Peninsula and Cozumel Island), Singapore (1998), Ethiopia (2003, watersheds and upper reaches of the White and Blue Nile), Malaysia (2009, Malay Peninsula; 2011, Borneo Island), Egypt (2003, Nile near Cairo), Tunisia (2002, coastal water bodies of the Atlas Mountains), Turkey (2012–2019, rivers and lakes of the Anatolian coast), Laos (2013, Mekong River), Cambodia (2013, Mekong catchment), Vietnam (2011, Saigon River; Mekong delta; 2013, city ponds in Da Nang and Hanoi), Thailand (2002, Khon Kaen city; 2013, Mekong River catchment), Indonesia (2009, Jakarta, Java), China (2011, ponds and rivers in Beijing and Shanghai; 2013, the Yellow River, the Pearl River,

Hainan Island), Taiwan (2005–2009, Sun Moon Lake, reservoirs throughout the island), Japan (2010, Kyoto, Hiroshima, Tokyo). All material was deposited in the federal collection of the Zoological Institute, Russian Academy of Sciences, no. 96-03-16.

This work also used material from the collections of tropical zooplankton by Prof. F. Kiefer (storage location is the Museum of Natural History, Karlsruhe, Germany), C. H. Fernando (University of Singapore Museum, Singapore), H. Dumont (Department of Hydrobiology, University of Ghent, Belgium), and B. Dussart (Natural History Museum, Paris, France). Collectively, the reviewed material covers all continents and the most important bodies of water in most countries of the world.

To identify species and describe new subgenera and the type species, permanent preparations were made for them by the method of Prof. Kiefer, for which the organisms dissected in glycerin were covered with cover glasses with wax legs, and a glycerin drop, occupying no more than a quarter of the total area, was surrounded with Canadian balsam with air displacement from all sides. If these conditions are met, after the balsam hardens, which takes about two weeks, the preparation can be stored indefinitely. Photographing, sketching, and study of the morphology of taxonomically important structures of copepods was carried out on microscopes using oil and water immersion at a magnification up to  $\times 1200$ , Nomarski optics (with magnification up to  $\times 800$ ), and a laser confocal microscopy with natural luminescence of chitin (magnification up to  $\times 1000$ ). Drawings were drawn in pencil and outlined with capillary markers 0.1–0.15 mm thick, scanned with a resolution of at least 600 dpi, and scaled and edited using the Adobe Photoshop CS5 computer program.

The publication is registered in the Zoobank database under the LSID number: urn:lsid:zoobank.org:pub:2235D007-2FCE-436C-A1B1-E33A2361B854.

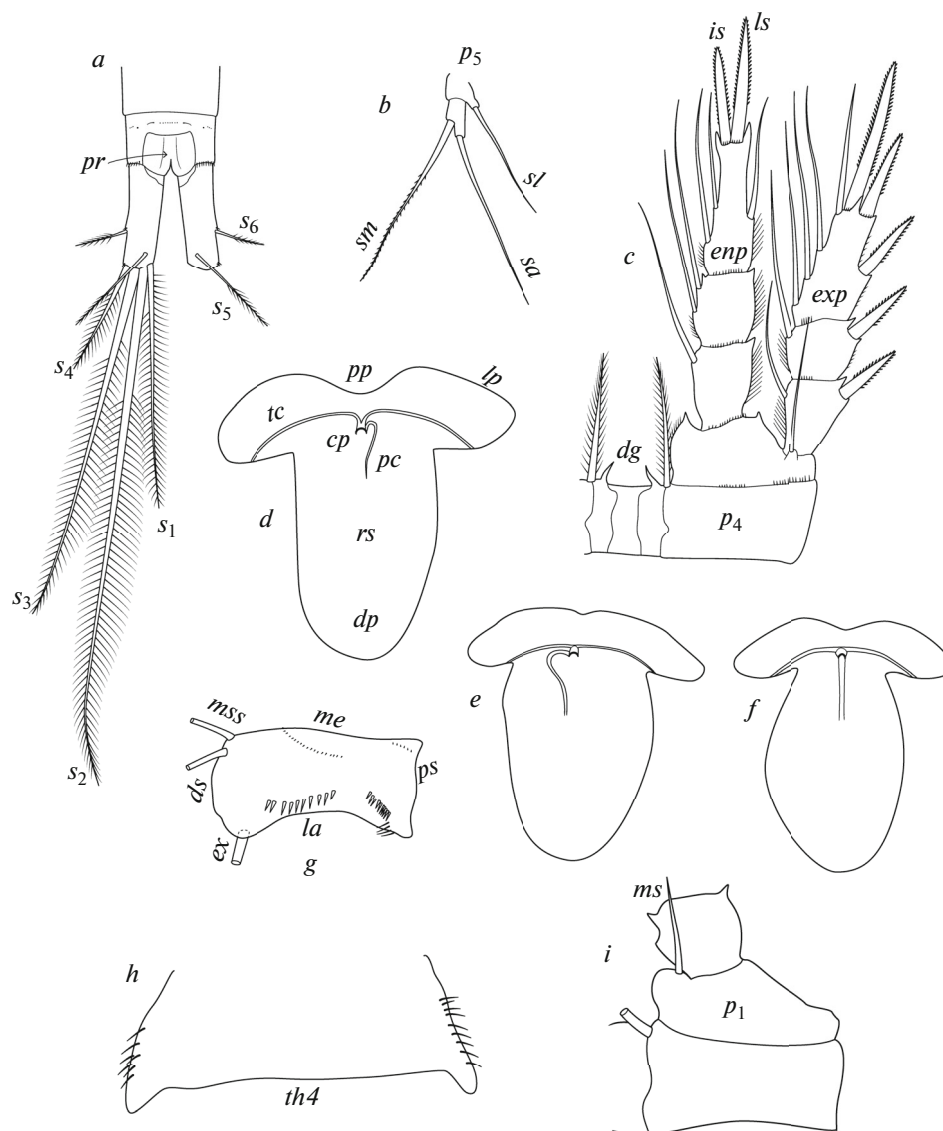
## Characters, terms, and abbreviations used (Fig. 1)

The most important in identifying and describing species of this genus are the following morphological characters observed in sexually mature females (the abbreviations used are given in parentheses):

Antennules (A1): length relative to the prosoma, construction of the hyaline plate on the distal segment.

Antennae (A2): ornament of spinules and hairs on the basipodite (Bas) and the number of setae on the second segment of the endopodite (Enp2); (*me*) medial, (*la*) lateral, (*ds*) distal, (*ps*) proximal edges; (*mss*) medial setae, (*ex*) exopod seta.

First pair of swimming legs (P1): presence/absence of seta on the inner (medial) outgrowth of the basipodite and its covering with hairs; (*ms*) the inner seta of basipodite.



**Fig. 1.** Characters of the greatest importance in the taxonomy of the genus *Mesocyclops* and their designation: (a) ornamentation of caudal rami and ratio of caudal setae; (b) ratio of P5 setae; (c) structure of P4; (d) seminal receptacle, V-shape; (e, f) T-shaped seminal receptacles with curved and straight pore canals; (g) frontal ornamentation of A2; (h) the presence of lateral hairs on last thoracic somite; and (i) the presence of an inner seta of basipodite P1.

Fourth pair of swimming legs (P4): length and shape of outgrowths (*dg*) on the distal edge of the connecting plate of the coxa (intercoxal sclerite, CoxP1), the ratio of the length and the greatest width of the distal segment of the endopodite (Enp3P4), the ratio of the lengths of the outer (*ls*) and inner (*is*) terminal spines of this segment (*lo/li*), the ratio of the length of the outer spine to the length of the segment itself (*lo/Ls*), the presence of spinules on the outer edges of the first (proximal) segment of the exopodite (Exp1P4).

Rudimentary fifth pair of legs (P5): the ratio of the lengths of the medial (inner) spine (*sm*) and the termi-

nal (apical) seta (*sa*) of the distal segment, as well as the ratio of the lengths of the medial spine of the distal segment and the lateral seta (*sl*) of the basal segment.

Last free thoracic somite (Th4): presence/absence of hair-like setae along the outer edge.

Genital urosomal double somite (GDS): ratio of length to maximum width; the form of the seminal receptacle (RS); shape and direction of curvature of the pore canal (*pc*), lateral arms (*lp*) and the angle at which the transverse canals (*tc*) are connected (sharp angle is V-shaped, straight angle is T-shaped); (*pp*) proximal part, (*dp*) distal part, (*cp*) copulatory pore.

Caudal rami (CR): presence/absence of hairs or spinules on the inner surface; length-to-width ratio (L/W); the ratio of the lengths of the innermost and outermost setae; the ratio of the lengths of the dorsal and the outermost setae; the ratio of the lengths of the innermost seta and the branch (li/Lcr); the presence of spinules at the attachment place of the lateral (*s6*) and outermost (*s4*) setae; proctodeum (*pr*).

## RESULTS AND DISCUSSION

### Genus *Mesocyclops* Sars 1914

#### Analysis of the world fauna of the genus *Mesocyclops*

Representatives of the genus *Mesocyclops* have been registered everywhere on all continents except Antarctica (Dussart and Defaye, 2006). At one time, this was associated with the isolation of the cosmopolitan species *M. leuckarti* (Claus 1857), which has now split into more than 15 species (Holynska, 2003). In the last revision of the genus, the number of valid species was reduced to 66 (Holynska, 2003). *Mesocyclops arakh-lensis* Alekseev 1993 was reduced by Holynska (Holynska, 2003) to a younger synonym of *M. leuckarti*; however, according to the results of hybridization experiments, these taxa proved to be genetically isolated (author's data, unpublished). The features I found later in the structure of the endopodites of the fourth pair of swimming legs make it easy to distinguish them (see the key of the genus *Mesocyclops*) (Alekseev, 1993, 1998). Together with 11 new species described over the past 17 years, including *M. frankfi-ersi* sp. n., the number of species of this genus is currently 78. It seems quite likely that in the near future we should expect a further expansion of the species composition of this ancient (judging by the worldwide distribution) genus, which is already clearly overloaded. Analysis of the morphology and distribution of species by the cardinal points allows me to propose a completely logical grouping of species according to some stable and easily found morphological characters, which can be used to divide the genus into subgenera.

The first such grouping was carried out according to the presence or absence of a seta on the inner outgrowth of the basal segment of the first pair of swimming legs. On this basis, representatives of the genus fall into two groups, which was noted a long time ago (Alekseev, 2002). Further division within these groups proceeds according to the absence or presence of hair-like structures on the lateral surface of the fourth free thoracic somite and/or on the inner surface of the caudal branches.

As a result, the following four subgenera are distinguished in the genus:

(1) Representatives of the type subgenus *Mesocyclops* (*Mesocyclops*) have no inner seta on basepodite P1 and no hairs on Th4 and CR.

(2) Representatives of the subgenus *Mesocyclops* (*Pilosomesocyclops*) subgen. n. have no inner seta on basepodite P1, but have hairs on Th4 and/or CR.

(3) Representatives of the subgenus *Mesocyclops* (*Neomesocyclops*) subgen. n. have an inner seta on basepodite P1 and hairs on Th4 and/or CR.

(4) Representatives of the subgenus *Mesocyclops* (*Tethymesocyclops*) subgen. n. have an inner seta on basepodite P1, but no hairs on Th4 and CR.

The largest subgenera (with hairs on Th4 and/or CR) can be divided into three natural morphological groups or sections, based on easily observable features: the presence of hairs on Th4 and CR at the same time, or on one of these structures only. These sections, named after the first of the species described with such features, were used to compose the keys and allow me not only to simplify the keys for the subgenus, but also to make some predictions about the prospect of expanding their species composition. In particular, sections such as *reidae* and *edax* in the newly distinguished subgenus *Mesocyclops* (*Neomesocyclops*) subgen. n., as well as *pseudospinosus* from the *Mesocyclops* (*Pilosomesocyclops*) subgen. n., contain one or two species and, apparently, the number of taxa in these sections is greatly underestimated, primarily due to the tropical and equatorial faunas.

It should be noted that most of the species that belong to the newly isolated subgenus *Mesocyclops* (*Neomesocyclops*) subgen. n., were described from the Neotropics, which also justifies its formation. The subgenus *Mesocyclops* (*Tethymesocyclops*) subgen. n. (with an inner seta on the basipodite P1 and without hairs on Th4 and caudal branches) has the largest number of representatives found in the Old World, namely in Africa, India, and Australia, which, according to the theory of continental drift, about 100 million years ago were part of the single continent of Gondwana. *M. sondoongensis* Tran et Holynska 2015, recently described from groundwater in Vietnam, is quite possibly a relict species of the island fauna of the Tethys Sea, which, due to the convergence of continental plates of the Asian and Indian continents, ended up in the Asian continental platform. The existing models of the movement of continental plates confirm this (Besse, 1995).

The likely mechanism for the appearance of representatives of the neotropical subgenus *Neomesocyclops* in the Old World could have been the transportation of water between continents, initially drinking water, in periodically refreshed barrels of the sailing fleet, and later, since 1860, in the bilge water and in the ballast compartments of ships. Described from South Africa, *M. tenuisaccus* (Sars 1927), down to the smallest detail, is similar to the mass South American species *M. annulatus* (Wierzejski 1892), and could well have come to Africa from Latin America, which was the basis of the slave trade and the transportation of slaves to the plantations of the New World for several centu-

ries. A similar assumption was also made by Holynska as a result of phylogenetic studies (Holynska, 2006). The introduction of invasive species of the subgenus *Mesocyclops* in the opposite direction was noted in recent works: finds of *M. ogunnus* in Brazil (Peixoto et al., 2010) and *M. pehpeiensis* in North America (Montoliu et al., 2015; Connolly et al., 2019).

#### Key for identifying the subgenera of the genus *Mesocyclops*

1. Basipodite P1 has no seta on the inner outgrowth.....(2)
  - Basipodite P1 has a seta on the inner outgrowth.....(3)
2. The lateral surface of Th4 and the medial surface of the CR are not covered with hairs.....*Mesocyclops* (*Mesocyclops*)
  - The lateral surface of Th4 and/or the medial surface of the CR are covered with hairs.....*Mesocyclops* (*Pilosomesocyclops*) subgen. n.
3. The lateral surface of Th4 and/or the medial surface of the CR are covered with hairs.....*Mesocyclops* (*Neomesocyclops*) subgen. n.
  - The lateral surface of Th4 and the medial surface of the CR are not covered with hairs.....*Mesocyclops* (*Tethymesocyclops*) subgen. n.

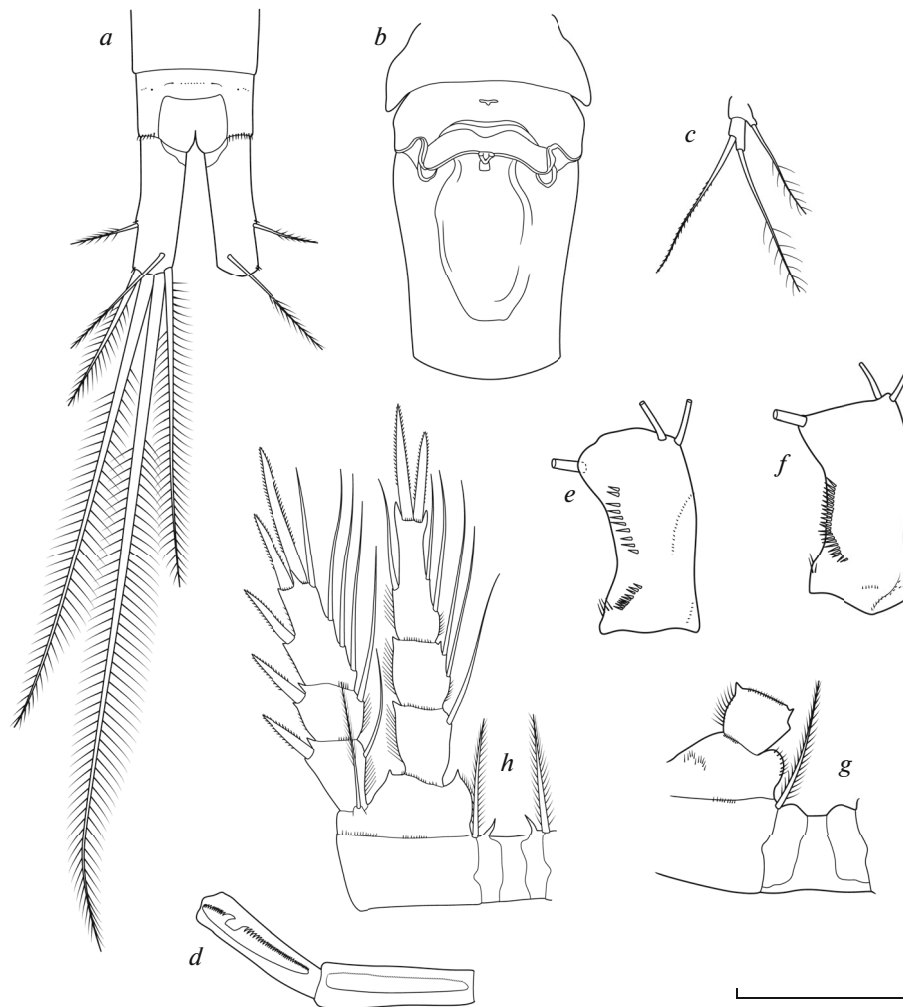
#### Subgenus *Mesocyclops* (*Mesocyclops*)

**D i a g n o s i s.** The subgenus includes species with the following combination of characters: basipodite P1 without seta on the inner outgrowth; hairs on the lateral surface of the fourth free somite of the thorax and on the inner side of the caudal branches are absent; occasionally, instead of them, short spinules, denticles, or pits are found. The representative of the subgenus *M. leuckarti* is also a type species for the entire genus, which in the recent past was considered a cosmopolitan species. The subgenus includes 17 species, described mainly from the water bodies of Europe and North Asia (four species), Australia (three species), Africa (two species), Southeast Asia, including China and Japan (eight species), and North America (two species). No species of this subgenus has been shown for South America. The type species *M. leuckarti* was redescribed in great detail during the last revisions (Van de Velde, 1984; Dahms and Fernando, 1993). Below is a brief description of it, as it is necessary for the isolation of a new subgenus. The type species is *M. (M.) leuckarti* (Claus 1857).

#### Description of the type species *Mesocyclops* (*Mesocyclops*) *leuckarti* (Claus 1857)

**F e m a l e** (Fig. 2). Body length without setae 700–1300 µm. The fourth free thoracic somite is devoid of hairs. The length and width of the genital double somite are 1.2–1.5 : 1. It is also hairless. The seminal receptacle has wide, relatively short lateral arms, slightly curved downward, and a wide lower section. The pore canal is very short, wide and curved inward (seems straight ventrally). Caudal rami are smooth, without hairs, rather long, length-to-width ratio 3–4. Spinules are present at the insertion sites of the lateral and outermost setae. The terminal setae are strong and densely covered with hairs; the ratio of their lengths beginning with the outermost one is 1/2.5–2.9/3.1–3.8/2–2.6. The dorsal seta is shorter than the outermost one. The largest of the caudal setae is shorter than the urosoma. Antennule is 17-segmented, reaching the third thoracic somite; its terminal segment bears a wide sawtooth hyaline membrane with one large notch in the middle. Antennae with three-segmented endopodite; basipodite on both sides bears only the main groups of denticles (Figs. 2e, 2f). Second segment of endopodite with seven setae. The mouth appendages are of a typical cyclopoid structure. Swimming legs 1–4 pairs are two-branched and three-segmented. Basipodite of the first pair without setae on inner outgrowth. Intercoxal sclerite without ornamentation; legs of the fourth pair with long pointed rod-shaped outgrowths on the outer edge (Fig 2h). The distal segment of the endopodite of the fourth pair is long and narrow, with a length-to-width ratio of about three, at the end with two strong spines, the inner one slightly shorter than the outer one. Rudimentary P5 two-segmented, basal segment with a short, hair-covered seta, terminal segment elongated at the end with an apical hair-covered seta slightly longer than the strong medial spine-like seta.

**M a l e.** Body length without terminal setae 750–950 µm. Spermatophores are light yellow. Prosoma and urosome are in a ratio of 1.8 : 1; the ratio of the cephalosome length to width is 1.25 : 1. The fourth free thoracic somite is hairless. Caudal branches are shorter than in females, without hairs on the inner surface. Spinules are present at the insertion sites of the lateral and outermost setae. The geniculating antennulae are 14-segmented, grasping type. The second segment of the endopodite of the antenna has seven setae. The structure of the swimming legs is the same as that of the female. Rudimentary fifth pair: apical seta longer than spine-like medial seta; seta of the basal segment noticeably shorter than both appendages of the distal segment. The sixth rudimentary pair is represented by a wide plate with three appendages, of which the inner spine is almost as long as the middle one and almost half as long as the outer seta.



**Fig. 2.** *Mesocyclops (Mesocyclops) leuckarti* (Claus 1857): (a) caudal rami, dorsally; (b) genital somite; (c) P5; (d) distal segments of A1; (e) basipodite A2, caudal; (f) basipodite A2, frontal; (g) P5; and (h) P4. Scale ( $\mu\text{m}$ ): (a–c, g, h) 100; (d) 70; (e, f) 60 (after Van de Velde, 1984).

**Distribution.** The Palearctic (?), to the east of Lake Baikal is possibly replaced by closely related species (Alekseev, 1998).

**Key for identifying species of the subgenus *Mesocyclops* (*Mesocyclops*)**

1. The innermost seta of the caudal branches (*s1*) is very short, no more than 1.5 times as long as the outermost one (*s4*).....(2)
  - The innermost seta is longer.....(3)
2. The distal segment of the P4 endopodite is very short, with L/W of about 1.8; RS is V-shaped.....*M. (M.) brevisetosus* Dussart et Sarnita 1987 (Indonesia, Kalimantan)
  - This segment is longer (L/W 2.2–2.5); RS is T-shaped.....*M. (M.) yena* Holynska 1998 (Vietnam)

3. Inner spine P5 is very short, less than half the length of the apical seta; outgrowths of the P4 intercoxal sclerite are short and rounded.....*M. (M.) cuttacuttiae* Dumont et Maas 1985 (Australia)

- This spine is noticeably longer, the outgrowths are pointed.....(4)
- 4. Medial outgrowth of P4 basipodite without hairs.....(5)
  - Medial outgrowth of basipodite P4 with hairs.....(6)
- 5. Caudal surface of basipodite A2 with distal field of small spinules at the base of medial setae; behind the horseshoe-shaped copulatory pore there are two round pores.... *M. (M.) papuensis* Van de Velde 1987 (New Guinea, Australia, Indonesia)
  - Caudal surface of basipodite A2 without similar field of spinules; behind the horseshoe-shaped copu-

latory pore there is one round pore or none.....*M. (M.) pehpeiensis* Hu 1943 (China, Uzbekistan + Europe and Americas as invader)

6. The hairs on the medial outgrowth of P4 are located proximally, while distally there is a row of small spinules.....*M. (M.) kieferi* Van de Velde 1984 (Africa)

– The hairs on the medial outgrowth P4 are located distally.....(7)

7. Intercoxal sclerite P4 with hairs on the caudal surface.....*M. (M.) salinus* Onabamiro 1957 (Africa)

– P4 intercoxal sclerite without hairs.....(8)

8. The P4 coxal spine is short and does not reach the distal end of the medial outgrowth of the basipodite.....*M. (M.) restrictus* Dussart et Fernando 1985 (Myanmar)

– P4 coxal spine long, extending beyond the distal end of basipodite outgrowth.....(9)

9. Caudal surface of basipodite A2 with oblique row of spinules located in the middle at the medial margin.....(10)

– Caudal surface of A2 basipodites without a similar row.....(15)

10. On the caudal surface of A2, at the base of the medial setae, there is a group of small spinules and a triangular field of small spinules proximal to it.....*M. (M.) fer-jemurami* Holynska et Nam 2000 (wells in Vietnam)

– There are no spinules on the caudal surface of A2 at the base of the medial setae.....(11)

11. Caudal rami are relatively short,  $L/W < 3$  *M. (M.) pescei* Petkoski 1986 (Bahamas)

– Caudal rami are longer,  $L/W > 3$ .....(12)

12. The pore canal is long and narrow, with a lateral curvature.....*M. (M.) yesoensis* Ishida 1999 (Japan, Malaysia)

– This canal is very short and wide, seems straight when viewing the specimen strictly ventrally.....(13)

13. Spine P5 is noticeably shorter than the apical seta and is approximately equal in length to the lateral one *M. (M.) bodanicola* Kiefer 1929 (Europe, large postglacial lakes)

– This spine is equal to the apical seta and distinctly longer than the lateral seta.....(14)

14. Caudal rami are relatively short,  $L/W < 4$ ; all segments of ExpP4 along the outer edge with hairs.....*M. (M.) leuckarti* (Claus 1857) (Palaeartic?)

– Caudal rami are longer,  $L/W > 4$ ; the first (proximal) segment of ExpP4 along the outer edge with strong spinules.....*M. (M.) arakhlensis* Alekseev 1993 (Transbaikalia)

15. A2 enp2 with seven or eight setae; crustacean size 0.7–0.8 mm; on the caudal surface of A2, the lateral row is strongly reduced and consists of 2–7 small spinules....*M. (M.) tobae* Kiefer 1933 (Sumatra, Indonesia)

– A2 enp2 with 6 setae; the size of the crustacean is 0.9–1.2 mm; on the frontal surface of A2, the lateral row consists of about ten large spines....*M. (M.) americanus* Dussart 1985 (Canada)

Subgenus *Mesocyclops (Pilosomesocyclops)* subgen. n.

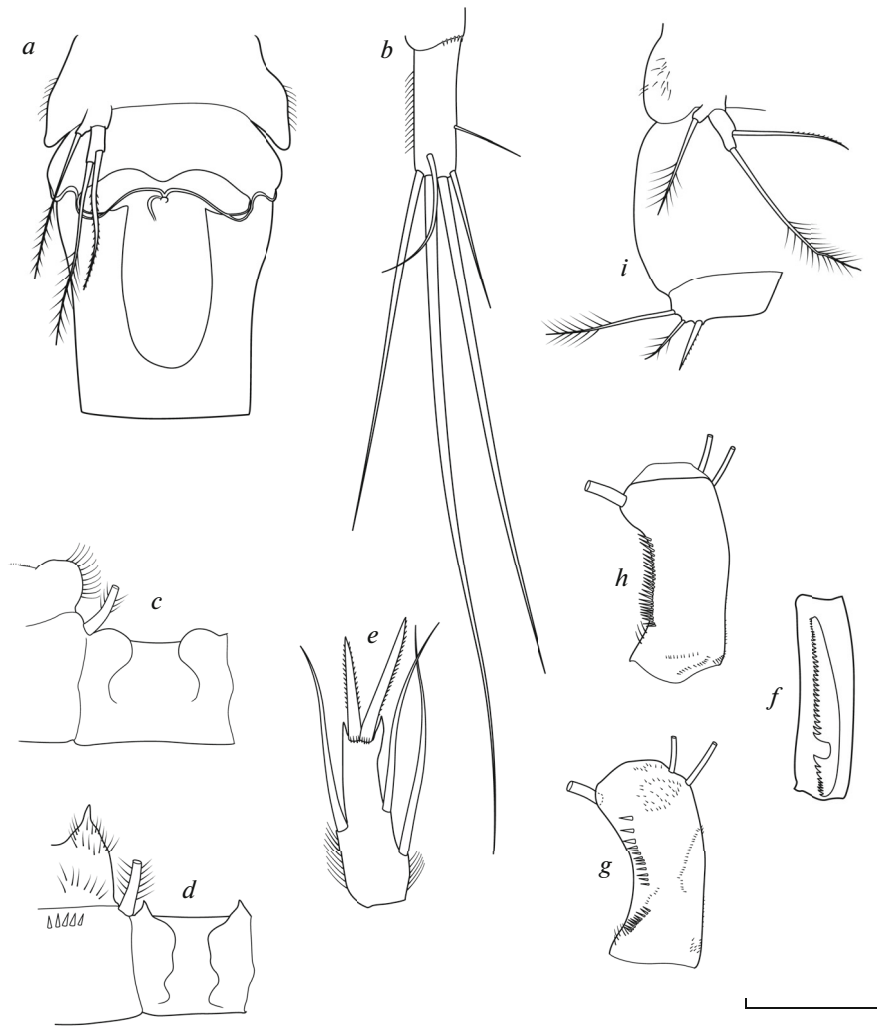
Zoobank LSID: urn:lsid:zoobank.org:act:4673BFF6-62CE-4219-B5E5-3074E60286AA

**D i a g n o s i s.** The richest subgenus in terms of the number of taxa. It includes 35 species that lack a seta on the inner outgrowth of basipodite P1, but have hairs on the lateral surface of the fourth thoracic somite and/or on the inner edge of the caudal rami, which determined its name (*pilosus* (lat.), hairy). Due to the large number of species described, this subgenus is subdivided into three sections on the basis of easily observed characters: the *aspericornis* section (nine species in the tropics of the Old World), the *pseudospinosus* section (two species in South East Asia), and the *thermocyclopoides* section (24 species, almost all from the tropics and subtropics of the Old World). The last, largest, section can also be divided into three subsections of 6–10 species each (indicated in the common key). The resulting system of keys greatly facilitates the identification of already known species and the identification of taxa new to science. The type species for the subgenus *M. (P.) aspericornis* (Daday 1906) is widespread in almost all tropical and subtropical countries of the Old World. It was redescribed in great detail by I. Van de Velde during the revision of the genus (Van de Velde, 1984), and its description is given briefly on the basis of her description, because it is absent in my collection.

**Description of the type species of the subgenus *Mesocyclops (Pilosomesocyclops) aspericornis* (Daday 1906) comb. n.**

**F e m a l e** (Fig. 3). Body length without caudal setae 1100–1600  $\mu\text{m}$ . Along the outer edge of the fourth free thoracic somite with a group of hairs. The length and width of the genital double somite are 1.1–1.3 : 1. The seminal receptacle with wide and long lateral arms slightly curved downward and a wide lower section. The pore canal is curved to the right. Caudal rami along inner surface covered with dense hairs, length-to-width ratio 2.7–3.6, lateral seta attached almost one-third of ramus length. Spinules are present at the insertion sites of the lateral and outermost setae. The terminal setae are strong and densely covered with hairs, the ratio of their lengths beginning with the outermost one: 1/2.5–3.8/5.5–6.8/2.6–3.4. Dorsal seta equal to outermost seta, largest of caudal setae equal to or 1.3 times as long as urosome. Antennule 17-segmented, reaching the second thoracic somite; its terminal segment bears a wide sawtooth hyaline membrane with one very deep incision. Antennae with three-segmented endopodite; basipodite on the frontal side, in addition to the main groups of spinules, has





**Fig. 3.** *Mesocyclops (Pilosomesocyclops) aspericornis* (Daday 1906): (a) genital somite; (b) caudal ramus; (c) P1; (d) P4; (e) P4 Enp3; (f) A1, distal segment; (g) basipodite A2, caudal; (h) basipodite A2, frontal; (i) P5 and P6, male. Scale ( $\mu\text{m}$ ): (a, b) 100; (c–e, g–i) 65; (f) 40 ((a–h) after Van de Velde, 1984; (i) after Holynska, 2000).

a wide field of small spinules at the insertion of the medial setae, as well as a group of tiny spinules between the lateral and medial rows of spines. The second segment of the endopodite of the antennae in populations from the New (as invader) and Old Worlds with different numbers of setae (from 7 to 9), which probably indicates the composite character of this taxon. The mouth appendages are of a typical cyclopoid structure, and along with the antennae, they are often covered with small pits. The swimming legs of the first to fourth pairs are two-branched and three-segmented. Basipodite of first pair without seta on inner outgrowth, but covered with dense long hairs. The coxal plate of P4 without hairs, with conical pointed outgrowths on the distal edge. The distal segment of the endopodite of P4 is long and narrow (L/W 2.5–3), at the end with two strong spines, the inner one is 1.1–1.5 times longer than the outer one and noticeably

shorter than the segment. Rudimentary P5 two-segmented, basal segment with long hair-covered seta, distal segment at the end with hair-covered apical seta, which is 1.1–1.6 times longer than strong medial spine-like seta, which in turn is equal to the lateral seta of the basal segment.

**Male.** Body length without terminal setae 750–950  $\mu\text{m}$ . There are few hairs along the outer edge of the fourth free thoracic somite. Spermatophores are large, bean-shaped. Caudal rami are shorter than in females (L/W 2.6–3.4), without hairs on the inner surface; spinules are present at the insertion sites of the lateral and outermost setae. The dorsal seta is approximately equal to the outermost one. The geniculating antennules are 14-segmented, grasping type. Antennae and other mouth appendages, as in females, often with pits, but the second segment of the endopodite of the antenna with six setae. The structure of the swimming

legs is the same as that of the female. Rudimentary fifth pair: apical seta 1.5 times longer than the spine-like medial seta; the seta of the basal segment is slightly shorter than the medial seta of the distal segment. The rudimentary sixth pair is represented by a wide plate with a strong inner spine, the middle seta almost equal in length, and the outer seta twice as long as spine.

**Distribution.** The species was described from Indonesia (Sumatra Island) and was later found everywhere in the tropics, which allowed the authors of the reports to designate its range as pantropic (Reid and Sanders, 1986; Suárez-Morales et al., 2011). Given the significant differences in morphology, especially for populations from the Old and New Worlds, this conclusion seems unlikely and is based either on the existence of a cluster of sister species-twins, or on the processes of bioinvasion, or both together. To obtain a decisive answer to these questions, it is necessary to conduct large-scale molecular genetic and morphological studies.

**Key for sectioning the subgenus *Mesocyclops* (*Pilosomesocyclops*) subgen. n.**

1. Hairs are present both on the lateral surface of the fourth thoracic somite and on the inner surface of the caudal rami section *aspericornis*

– Hairs are present only on one of these structures (2)

2. Hairs are present at the inner surface of the CR.....section *pseudospinosus*

– Hairs are present on the lateral surface of the Th4.....section *thermocyclopoides*

**Key for identifying the species of the section *aspericornis***

1. The crustaceans are rather large; the length of the females is 1.1–1.6 mm.....(2)

– The crustaceans are small; females are less than 1.1 mm long.....(6)

2. The genital somite with RS of T-shape (Figs. 1e, 1f) .....(3)

– The RS shape is different *M. (P.) aspericornis* (Daday 1906) (Pantropic?)

3. Basipodites A2 on the caudal side with a group of large spinules distally closer to the base of two medial setae....*M. (P.) kayi* Holynska et Brown 2003 (Burma)

– Basipodites A2 without such spinules.....(4)

4. The caudal surface of the P4 intercoxal sclerite has two rows of hairs.....*M. (P.) pilosus* Kiefer 1930 (Southeast Asia)

– P4 intercoxal sclerite is hairless.....(5)

5. The caudal rami have spinules at the insertion site of the outermost setae; CR L/W is less than three.....*M. (P.) spinosus* Van de Velde 1984 (Africa)

– Spines are absent on the caudal rami at the site of attachment of the outermost seta; CR L/W is more than three.....*M. (P.) mariae* Guo 2000 (China)

6. Basipodites A2 on the caudal side with a group of large spinules distally near the medial setae.....*M. (P.) geminus* Holynska 2000 (Kali-mantan)

– Basipodites A2 on the caudal side with a group of small spines near the medial setae.....(7)

7. P4 intercoxal sclerite without hairs.....*M. (P.) microlasius* Kiefer 1981 (Philippines)

– P4 intercoxal sclerite with hairs on the caudal surface.....(8)

8. P4 intercoxal sclerite outgrowths are short; medium-sized crustaceans (0.9–1.1 mm).....*M. (P.) dadayi* Holynska 1997 (India)

– P4 intercoxal sclerite outgrowths are long; very small crustaceans (0.7–0.8 mm).....*M. (P.) insulensis* Dussart 1982 (Madagascar)

**Key for identifying species of the *pseudospinosus* section**

1. The pore canal RS is strongly curved; CR with hairs on the proximal part of the inner surface and spinules on the distal part; outgrowths on the P4 intercoxal sclerite are wide..... *M. (P.) pseudospinosus* Dussart et Fernando 1988 (Indonesia)

– The pore canal RS is slightly curved; CR with hairs on the proximal part of the inner surface and without spinules on the distal part; outgrowths on the P4 intercoxal sclerite are narrow..... *M. (P.) shenzhenensis* Guo 2000 (South China and Central Vietnam)

**Key for identifying the subsections and species of the *thermocyclopoides* section**

1. In the seminal receptacle, transverse canals meet at the copulatory pore at an acute angle (V-shape).....(2) (subsection *woutersi*)

– Canals meet at an obtuse or almost straight angle...(14)

2. The dorsal surface of the last thoracic somite is not covered with dense hairs apart from a few sensilla.....(3)

– The dorsal surface of the last thoracic somite is covered with hairs.....(6)

3. Spinules are absent on CR at the attachment place of the lateral and outermost setae.....*M. (P.) woutersi* Van de Velde 1987 (New Guinea, Australia, Indochina)

– The CR has spinules at the attachment place of the lateral and/or outermost setae.....(4)

4. Dorsal surface of A1 segments without pits; eight pores behind P6.....*M. (P.) dissimilis* Defaye et Kawabata 1993 (Japan, Eastern Siberia, China)

– A1 with pits on the dorsal surface of segments 1, 4; six pores behind P6 (5)

5. The inner spine of P4 Enp3 is shorter than or equal to the outer one; outgrowths on the P4 intercoxal sclerite are small, blunt, or sharp.....*M. (P.) brooksi* Pesce, De Laurentiis et Humphreys 1996 (Australia)

– The inner spine of P4 Enp3 equal to or longer than the outer one; outgrowths on the P4 intercoxal sclerite are long and sharp.....*M. (P.) acanthoramus* Holynska et Brown, 2003 (Australia)

6. There are no spinules on the CR at the insertion site of the lateral and outermost setae.....(7)

– The CR has spinules at the insertion site of the lateral and/or outermost setae.....(8)

7. CR L/W 2.9–4.5; A2 caudally with a lateral row of 13–19 spinules, caudally 21–28 spinules.....*M. (P.) granulatus* Dussart et Fernando 1988 (Pakistan, India, Myanmar)

– CR L/W 3.0–3.5; there is a “pseudosomite” between the last thoracic segment and the genital somite; A2 frontally with a lateral row of 10–14 spines, caudally 22–26 spinules.....*M. (P.) arcanus* Defaye 1995 (Israel)

8. The genital somite dorsally covered with hairs.....(9)

– The genital somite dorsally not covered with hairs (11)

9. The genital somite is ventrally covered with hairs.....*M. (P.) pubiventris* Holynska et Brown, 2003 (partially) (Australia)

– The genital somite is ventrally not covered with hairs.....(10)

10. A2 Caudal surface with a row of large spinules at the place of insertion of the medial setae; P4 Enp3 L/W 3.0–3.9.....*M. (P.) notius* Kiefer 1981 (Australia)

– A2 Caudal surface with a field of small spinules at the place of attachment of the medial setae; P4 Enp3 L/W 2.4–2.7.....*M. (P.) medialis* Defaye 2001 (New Caledonia)

11. CR ventral surface in the distal quarter at the medial edge with a row of long spinules.....*M. (P.) francisci* Holynska 2000 (Malaysia)

– There are no such spinules on CR.....(12)

12. A2 Enp2 with nine setae; P4 CoxPl outgrowths are obtuse; hairs on the dorsal surface of last thoracic somite are short and located near the distal border.....*M. (P.) roberti* Holynska et Stoch 2012 (Fiji)

– A2 enp2 with seven setae; P4 CoxPl outgrowths are sharp; the dorsal surface of last thoracic somite is covered with long hairs.....(13)

13. CR with spinules at the place of attachment of both lateral and outermost setae; A2 frontal surface with a lateral row of 11–12 spinules.....*M. (P.) friendorum* Holynska 2000 (Indonesia)

– CR with spinules only at the outermost setae; A2 Caudal surface with a lateral row of 13–16 spinules.....*M. (P.) parentium* Holynska 1997 (India)

14. The pore canal of RS is straight or slightly curved.....(15) (subsection *aequatorialis*)

– This canal is strongly curved.....(22) (subsection *ogunnus*)

15. CR has spinules at the attachment place of the lateral and/or outermost setae.....(16)

– Neither the lateral nor the outermost setae have spinules on CR.....(21)

16. There are rows of hairs on the caudal surface of the P4 CoxPl.....(17)

– The P4 CoxPl has no hairs.....(18)

17. A2 basipodite caudal surface with a group of large spinules at the insertion site of the medial setae and several spinules at Exp, the lateral row consists of approximately 18–20 spinules; CR L/W 2.3–2.5; CR dorsal seta is shorter than the outermost one; P4 CoxPl outgrowths are small.....*M. (P.) jakartensis* Alekseev 2013 (Indonesia)

– Ornamentation on the A2 basipodite caudal surface is different; CR L/W 2.7–3.4; CR dorsal seta is longer than the outermost one; P4 CoxPl outgrowths are long ..... *M. (P.) major* Sars 1927 (Africa)

18. Th4 dorsal surface is covered with hairs *M. (P.) dussarti* Van de Velde 1984 (West Africa)

– This surface is not covered with hairs.....(19)

19. A2 basipodite caudal surface without a field of small spinules at the insertion site of the medial setae; P5 apical seta is 1.6–2.0 times as long as the medial spine ..... *M. (P.) aequatorialis aequatorialis* Kiefer 1929 (Africa, Madagascar)

– A2 basipodite frontal surface with such field of small spinules in this place; P5 apical seta is 1.1–1.5 times as long as the medial spine.....(20)

20. CR inner middle seta (s2) is slightly shorter or equal to the length of the urosome (0.9–1.0: 1); behind P6 there are six or eight pores; RS pore canal is straight and wide..... *M. (P.) aequatorialis similis* Van de Velde 1984 (Africa, Uzbekistan)

– This seta of CR is slightly longer than the urosome (1.1–1.5 : 1); there are six pores behind P6; RS pore canal is slightly curved and thin.....*M. (P.) affinis* Van de Velde 1987 (New Guinea, Indochina)

21. P4 intercoxal sclerite with rows of hairs on the caudal surface; P4 CoxPl outgrowths are large and sharp; A2 basipodite caudal surface without spinules at the insertion site of the medial setae; CR L/W 2.6–2.8; genital segment L/W is approximately 1.1.....*M. (P.) bosumtwii* Mirabdullayev, Sanful et Frempong 2007 (West Africa)

– There are no hairs on the P4 CoxPl, the outgrowths are small and obtuse; A2 basipodite frontal surface with a group of large spinules; CR L/W 2.9–3.6; genital segment L/W 1.3–1.5.....*M. (P.) thermocyclopoides* Harada 1931 (partially)

22. CR without spinules at the insertion place of the lateral and outermost setae.....(23)

– CR with spinules at the insertion place of the lateral and/or outermost setae (24)

23. A2 basipodite frontal surface with a group of large spinules at the insertion site of the medial setae.....*M. (P.) thermocyclopoides* Harada 1931 (partially)

– A2 basipodite Caudal surface with a field of small spinules in this place.....*M. (P.) isabellae* Dussart et Fernando 1988 (India)

24. The dorsal surface of the last thoracic somite is covered with hairs.....(25)

– The dorsal surface of the last thoracic somite is not covered with hairs.....(26)

25. A2 basipodite Caudal surface with a field of small spinules at the place of attachment of the medial setae.....*M. (P.) pubiventris* Holynska et Brown, 2003 (partially) (Australia)

– A2 basipodite frontal surface with a row of long spinules in this place.....*M. (P.) ogunnus* Onabamiro 1957 (Africa, Southeast Asia)

26. Anal somite proctodeum with a group of short spinules proximally and long spinules distally; the dorsal surface of the genital somite is not covered with hairs.....*M. (P.) augusti* Papa et Holynska 2013 (Philippines)

– There are no such spinules on the proctodeum; the dorsal surface of the genital somite is covered with hairs.....*M. (P.) australiensis* (Sars 1908) (Australia)

#### Subgenus *Mesocyclops (Tethymesocyclops)* Alekseev subgen. n.

Zoobank LSID: urn:lsid:zoobank.org:act:A56349FD-F455-4B50-85DE-69DB67A51803

**D i a g n o s i s.** This group of species has a seta on the outgrowth of the basipodite P1 and lack of hairs on the lateral surface of the last thoracic somite and inner surface of the caudal rami. This subgenus unites 11 species known from India (+Ceylon Island), Africa (+Madagascar Island), Australia (+New Zealand and New Guinea), southern Mexico, and underground waters of Vietnam. Most of these finds occur on continents that were part of the southern supercontinent of Gondwana, or rather, on the part of them that made up the coast of the Tethys Sea during the period of separation of Gondwana from Laurasia. It is possible that the modern distribution of the species of this subgenus throughout the world was associated with the subsequent division of this supercontinent into Africa, Australia, India, and South America. Species of this subgenus have not yet been found in the water bodies of the last continent, which makes it possible for the author to predict their detection there in the foreseeable future.

#### Description of the type species for the subgenus *Mesocyclops (Tethymesocyclops) annae* Kiefer 1930 comb. n.

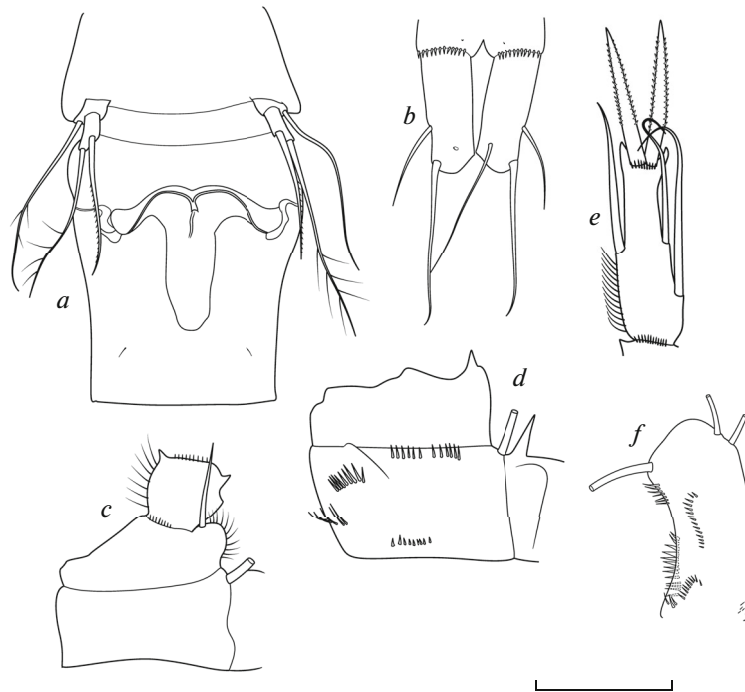
**F e m a l e** (Fig. 4). Body length without caudal setae 1200–1400 µm. No hairs along the lateral edge of the fourth free thoracic somite. The genital double somite length and width are 1.1–1.2. The seminal receptacle has wide and long lateral arms, curved downward, and a wide lower section. The pore canal is straight and long. Caudal rami without hairs, length-to-width ratio 2.2–2.5. The lateral seta is attached almost one-third of ramus length and is very long. There are no spinules on the caudal rami at the insertion sites of the lateral and outermost setae. Terminal setae are strong and densely covered with hairs, the ratio of their lengths beginning with the outermost one: 1/3.5–3.8/5.0/2.4–2.6. The dorsal seta is shorter than the outermost one; the longest of the caudal setae is equal to or slightly longer than the urosome. The antennule is 17-segmented, reaching the second thoracic somite; its terminal segment bears a wide sawtooth hyaline membrane with 2–3 deep incisions. Antennae with 3-segmented endopodite; the basipodite caudal surface with two rows of long spinules at the lateral edge and a row of small spinules on the anterior part of the medial edge, the oblique medial row is absent; the caudal side has a row of long spinules at the anterior part of the lateral edge and few spinules at the distal part of the lateral edge (near the Exp). The mouth appendages are of a typical cyclopoid structure. Swimming legs of the first to fourth pairs are two-branched and three-segmented. The basipodite of the first pair bears a seta on the inner outgrowth, which is a quarter longer than the first segment of the endopodite. The P4 intercoxal sclerite is naked, with long conical pointed outgrowths on the distal edge. The P4 Enp3 is long and narrow (about three times longer than the width), distally with two strong spines, the inner one is almost equal to the outer one and slightly shorter than the segment. Rudimentary P5 is two-segmented, the basal segment with a long lateral seta exceeding the length of the medial seta of the distal segment, the distal segment at the end with a hair-covered apical seta that is longer than the medial one.

**M a l e.** Not known.

**D i s t r i b u t i o n.** The species was described from a reservoir on the island of Madagascar.

#### Key for identifying species of the subgenus *Mesocyclops (Tethymesocyclops)* subgen. n.

1. The innermost seta of CR is less than twice as long as the outermost one.....(2)
  - This seta is at least twice as long as the outermost one.....(3)
2. P5 lateral seta is significantly longer than the medial one.....*M. (T.) yutsil* Reid in Fiers et al. 1996 (Mexico)



**Fig. 4.** *Mesocyclops (Tethymesocyclops) annae* Kiefer 1930: (a) genital somite and P5; (b) caudal rami, ventral; (c) P1; (d) coxa P4, caudal; (e) P4 Enp3; (f) basipodite A2, Caudal. Scale ( $\mu\text{m}$ ): (a, b) 100; (c–f) 65 (after Holynska, 2003).

– The ratio of the lengths of these setae is inverse.....*M. (T.) chaci* Fiers 1996 (Mexico)

3. CR with spinules at the base of the lateral and outermost setae.....*M. (T.) sondoongensis* Tran et Holynska 2015 (Vietnam)

– CR without such spinules.....(4)

4. A2 basipodite caudal surface with the lateral row of spinules that reaches the attachment place of Exp.....(5)

– This row of spinules does not reach Exp.....(7)

5. RS pore canal is long.....*M. (T.) darwini* Dussart et Fernando 1988 (Australia)

– The pore canal is short.....(6)

6. There is more than one notch on the A1 hyaline plate; P4 Enp3 L/W 2.5–2.9; female size is 1.3–1.5 mm.....*M. (T.) paludosus* Lindberg 1956 (Africa)

– There is one small notch on the A1 hyaline plate; P4 Enp3 L/W is about 3.2; female size is 1.1–1.3 mm.....*M. (T.) holynskae* Karanovic 2006 (Australia)

7. The lateral arms of RS are wide, curved back.....(8)

– RS arms are narrow, almost straight.....(10)

8. The inner outgrowth of P4 basipodite is without hairs.....*M. (T.) annae* Kiefer 1930 (Madagascar, India)

– The inner outgrowth of P4 basipodite has distal hairs (9)

9. The transverse canals of RS are connected at an almost obtuse angle; the first segment of A1 lacks ventral spinules.....*M. (T.) pseudoannae* Van de Velde 1987 (New Guinea)

– Transverse canals are connected at an acute angle; the first segment of A1 has ventral spinules.....*M. (T.) splendidus* Lindberg 1943 (India)

10. P5 lateral seta is subequal to the medial seta; CR with the central inner seta (*s*2) 4.8–5.1 times longer than the outermost (*s*4) seta, and the innermost (*s*1) seta is 2.6–2.8 times longer than the outermost (*s*4) one.....*M. (T.) dayakorum* Holynska 2000 (Indonesia)

– P5 lateral seta is shorter than the medial one; CR with *s*2 that 4.2–4.7 times as long as *s*4 and *s*1 is 2.2–2.4 times as long as *s*4.....*M. (T.) rarus* Kiefer 1981 (Africa)

Subgenus *Mesocyclops (Neomesocyclops)* Alekseev subgen. n.

Zoobank LSID: urn:lsid:zoobank.org:act:0361FD6F-1742-40E2-A213-55A19030415C

**Diagnosis.** The members of this group are clearly separated from the other species of the genus both morphologically (setae on the outgrowth of the basipodite P1 and hairs on at least one of the elements of the prosome (Th4) or urosome (CR)) and territorially (New World). The only species with these characteristics described from South Africa, *M. tenuisaccus*,

is morphologically very close to the mass form from South America, *M. annulatus*, and, in my opinion, is a bioinvasion of the latter, introduced by seafarers with drinking water during the period of the active slave trade (16th–18th centuries). Holynska also came to the conclusion about the identity of these species (Holynska, 2006). According to the combination of presence of hairs on Th4 and caudal rami, the subgenus *Neomesocyclops* subgen. n. can be divided, by analogy with the subgenus *Pilosomesocyclops* subgen. n., into three sections unequal in the number of species.

1. Hairs are present on both structures in the section *annulatus*, which includes 10–12 species, of which 11 are found in South and Central America, and one or two species are from Mexico. One species mentioned above (*M. tenuisaccus*) was described from a river in Cape Town, South Africa. Its presumably invasive appearance requires confirmation by molecular genetic methods.

2. Hairs are present only on the lateral surface of the last thoracic somite—the *reidae* section, so far includes only one species from South America.

3. Hairs are present only on the inner edge of the caudal rami—the *edax* section, includes one species. *M. edax* was described twice—from the Great Lakes of North America under this name and later as *M. nicaraguensis* from South America, from which it probably penetrated into North America after the joining of the continents.

The center of the origin and diversity of the species of this subgenus is undoubtedly South America after its separation from the African platform ~80 million years ago. Taking into account the low abundance in two sections, the identification key was composed for the subgenus in whole, which does not prevent us from returning to division into sections if more species are added.

**Description of the type species for the subgenus  
*Mesocyclops (Neomesocyclops) edax* (Forbes 1891)  
comb. n.**

An appropriate description of the holotype *M. (N.) edax* is absent despite its wide distribution in the New World, which was the reason for more detailed consideration when characterizing this as the type species for the subgenus. A topotype of a female from a zooplankton sample collected by the author in the United States in the region of one of the Great Lakes (Lake Erie) on its western shore (Wisconsin, Chicago area) was used. The described topotype no. 56055 is stored in the Federal Collection of the Zoological Institute, Russian Academy of Sciences, no. 96-03-16: section “Type collection of freshwater invertebrate species (taxonomy section).” The male variability was described using the article by Dahms and Fernando (1995).

**F e m a l e** (Fig. 5). The body length without caudal setae is 1350 (900–1450)  $\mu\text{m}$ , uncolored; the length-

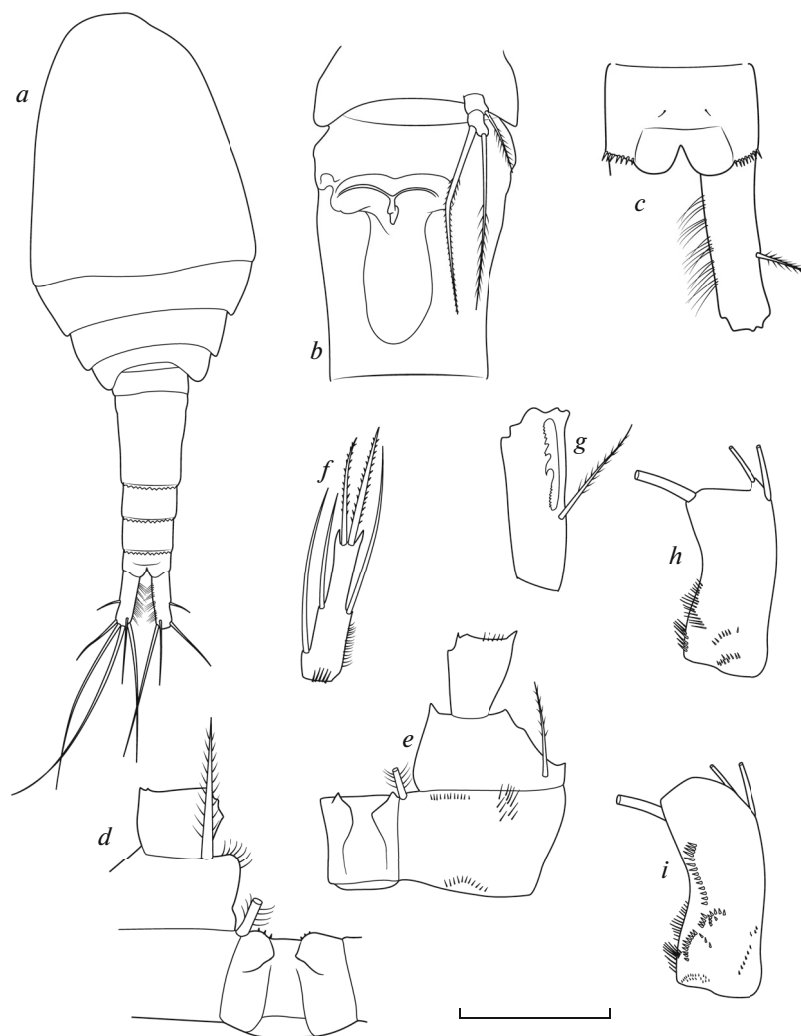
to-maximum-width ratio is ~3 (2.98). The prosome to urosome ratio is ~1.6 : 1; and the cephalosome length-to-width ratio is 1.1. There are no hairs along the outer edge of the last thoracic somite (according to Holynska (2003), individuals with a few short hairs are occasionally found, which is possibly atavism). The genital double somite length-to-width ratio is 1.4 : 1. The seminal receptacle has wide arms; its lower segment is wider and occupies about half of the area of its somite. The pore canal is short and seems straight when viewed ventrally. The caudal rami are narrow, the length-to-width ratio ~4; the lateral seta is attached at a distance of 2/5 of the ramus length from the terminal setae. Inner surface of rami with long dense hairs. The terminal setae are strong and densely covered with hairs, the ratio of their lengths beginning with the outermost seta is 1.0/2.8–3.1/3.6–4.2/2.4–2.8. The dorsal seta is appreciably (1.4 times) longer than the outermost seta; the longest caudal seta is shorter than the urosome (0.85).

The antennule is 17-segmented, reaching the second thoracic somite; its terminal segment bears a wide hyaline membrane with two or three notches, and the first segment is ornamented with a long row of strong hairs along with seven setae. The antennae have a three-segmented endopodite; the basipodite on both sides bears only the main lateral groups of denticles. The second segment of the endopodite of the antennae bears nine setae. The mouth appendages have a typical structure of cyclopides.

The swimming legs of the first to fourth pairs are two-branched and three-segmented. P4 intercoxal sclerite with short blunt outgrowths on the distal edge; the coxal seta is very long and densely covered with hairs. The basipodite of P1 on the inner outgrowth has a long, well-discernible seta. The distal segment of the endopodite of P4 is long and narrow, with two strong spines, the inner one being slightly longer than the outer one, but noticeably shorter than the segment.

The rudimentary fifth pair is two-segmented, with a structure typical for the genus; the basal segment has a long hair-covered seta; the distal segment is elongated, with a thin hair-covered apical seta, which is slightly shorter than the strong medial spinulose seta.

**M a l e** (Fig. 6). The body length without the terminal setae is 884  $\mu\text{m}$ , varying from 600 to 900  $\mu\text{m}$  in different populations. The spermatophores are large, reddish. The prosome to urosome ratio is ~1.8 : 1, with a cephalosome length-to-width ratio of ~1.25 : 1. There are no hairs along the outer edge of the last thoracic somite. The caudal rami are short, and the length-to-width ratio is 2.7, varying from 2.2 to 2.8. The lateral seta is attached almost in the middle of the outer edge of the caudal rami. Inner edge of caudal rami with long hairs, beginning with the proximal third and thickening in the distal direction. The terminal setae are rather long and densely covered with hairs. The dorsal seta is noticeably longer than the



**Fig. 5.** *Mesocyclops* (*Neomesocyclops*) *edax* (Forbes 1891): (a) general view; (b) genital somite and P5; (c) anal somite and caudal ramus, dorsal; (d) P1; (e) P4; (f) P4 Enp3; (g) A1, distal segment; (h) basipodite A2, frontal; (i) basipodite A2, caudal. Scale ( $\mu\text{m}$ ): (a) 100; (b) 120; (c–f) 100; (g–i) 65 ((a, c) after Dahms and Fernando, 1995; (b, g) after Reid and Moreno, 1999; (d, e, f, h, i) original).

outermost seta, but shorter than the innermost seta. The longest caudal seta is nearly equal to the urosome. The geniculating antennules are 14-segmented. The antennae and other mouth appendages are similar in structure and armament to those of females. P1 basipodite inner outgrowth with a long seta, reaching the distal edge of the second segment of the endopodite. The structure of other swimming legs is the same as in the female, but the endopodite of P4 is slightly shorter. The latter length-to-width ratio is 3.1–3.4; at the end, it has almost equal spines, both being shorter than the segment. P5 apical seta is longer than the spinulose medial seta of the distal segment; the lateral seta of the basal segment is noticeably shorter than both appendages. The rudimentary sixth pair is represented by a wide plate with three appendages, of which the inner spine is almost as long as the middle seta and half the outer seta in length.

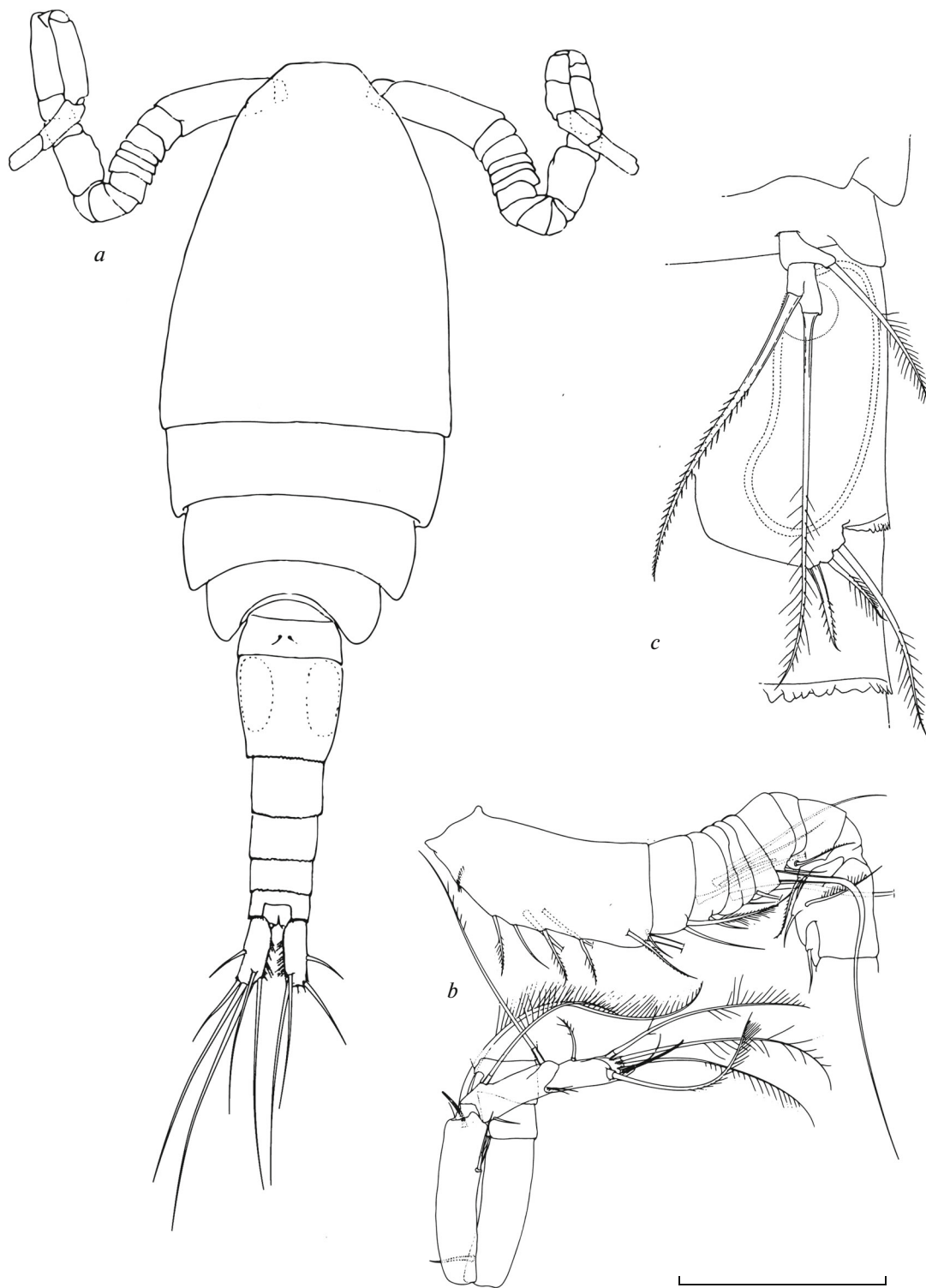
**Distribution.** The species has been shown for lake-like water reservoirs in North America and as *M. nicaraguensis*, recognized as its synonym, for Central and South America (Reid and Ueda, 2003).

**Description of the new species *Mesocyclops* (*Neomesocyclops*) *frankfiersi* Alekseev subgen. n., Alekseev sp. n.**

Zoobank LSID: urn:lsid:zoobank.org:act:452772F5-ECBF-405F-90AB-C67972E67907

**Type habitat.** The location of the type population is Cozumel Island, Atlantic coast of Mexico; the type water reservoir is rain puddles among the palm thickets at the southern tip of the island. The material was collected by the author in June 2011.





**Fig. 6.** *Mesocyclops (Neomesocyclops) edax* (Forbes 1891), male: (a) general view, (b) geniculating antennule, (c) P5 and P6. Scale ( $\mu\text{m}$ ): (a) 200; (b) 120; (c) 70 (after Dahms and Fernando, 1995).



**Type series.** Holotype no. 56123, female specimen, placed on one slide. Paratype no. 56124, male specimen on one slide; paratypes no. 56125, 12 females and 8 males in a vessel with pure glycerin, stored in the Federal collection of the Zoological Institute, Russian Academy of Sciences, no. 96-03-16 in the section "Type collection of aquatic invertebrates of the taxonomy section."

**Description.** Female (holotype no. 56123) (Figs. 7, 8). The body length without caudal setae is 980  $\mu\text{m}$ . The body is colored brown; the color disappears during storage in alcohol and is obviously due to the color of palm leaf litter. The prosome-to-urosome ratio is  $\sim 2 : 1$ ; and the cephalosome length-to-width ratio is  $1.1 : 1$ . There are hairs along the outer edge of the fourth free thoracic somite.

The genital double somite length-to-width ratio is  $1.1 : 1$ . The seminal receptacle has rather wide lateral arms turned downward and a very narrow middle distal part. The pore canal is rather long and curved to the left. The caudal rami have a length-to-width ratio of  $\sim 3.2$  ( $3.1-3.3$ ); the lateral seta is attached at a distance of about one-third of the terminal setae. On the inner surface of the rami, there are long, but rather sparse hairs. The terminal setae are strong and densely covered with hairs; the ratio of their lengths beginning with the outermost seta is  $1/4.7-5.1/6.5-7.4/3.3-3.7$ . The dorsal seta is  $1.15-1.25$  times as long as the outermost one, the longest of the caudal setae is  $1.35$  times as long as the urosome.

The antennule is 17-segmented and reaches the middle of the second thoracic somite when folded; its terminal segment bears a wide hyaline membrane reaching the base of the middle seta, with one large and two narrow notches. The antennae have a three-segmented endopodite. The ornamentation on the frontal surface of the basipodite is as follows: a proximal row of long spinules along the lateral edge; distal to it is a row of 7-9 shorter spinules and a row of 8-9 spinules not reaching the base of Exp. On the medial side, there is a transverse proximal row of tiny spinules and two groups of small spinules distal from it. The ornamentation on the caudal side of the basipodite consists of a proximal group of long spinules, a long lateral row of 14-16 spinules, and a distal row of spinules at the base of Exp. The second segment of the endopodite of the antennae bears nine setae. The mouth appendages have a structure typical for cyclopides.

Maxillula of complex structure, distally with 4 pairs of teeth and sensilla; gnathopod smooth with 7 setae of different length and thickness. Maxillae four-segmented, powerful; setae on segments arranged in pairs. Maxillipeds after antennae are the longest, they are also four-segmented, with 2-3 setae, distally covered with strong hairs, the first and second segments on the inner side with a row of long strong hairs.

The swimming legs of the first to fourth pairs are two-branched and three-segmented. The P4 inter-

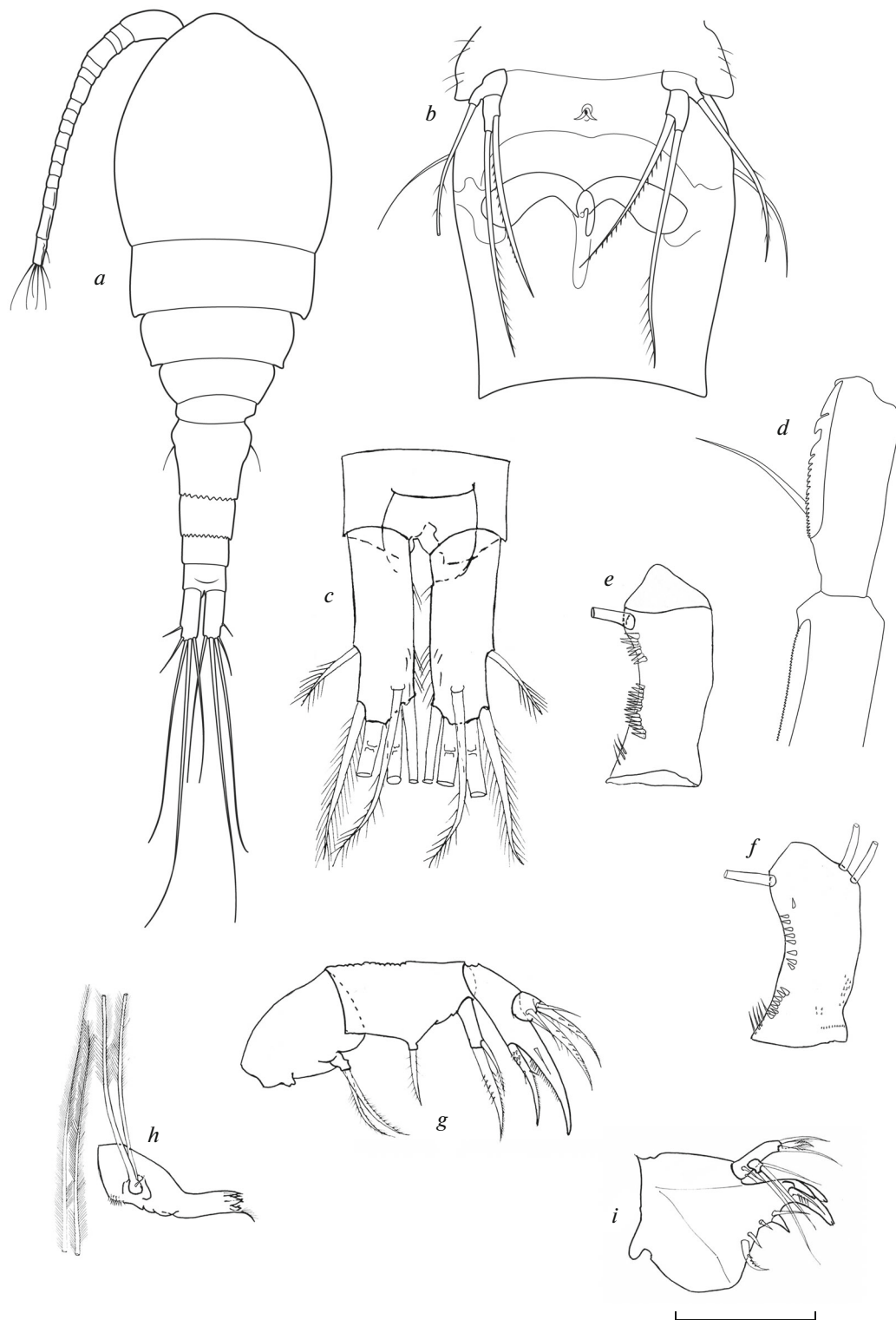
coxal sclerite with caudal hairs and, on the distal edge, has rather long, pointed outgrowths, which are wide at the base; the coxal seta is rather long, densely covered with hairs. The basipodite of P1 has short seta on the inner outgrowth, barely reaching the distal edge of the first segment of the endopodite. The distal segment of the endopodite of P4 is long and narrow (the length-to-width ratio is 2.6) with two strong, almost equal spines, the inner one being (1.1 times) stronger than the outer one and both spines being shorter than the segment. The terminal setae of this segment extend beyond the middle of the spines nearest to them.

The rudimentary P5 is two-segmented with a structure typical of the genus; the basal segment is short and flattened with a long hair-covered seta; the distal segment is elongated rod-shaped with an apical seta noticeably longer than the inner spinulose seta, which, in turn, is almost equal to the seta of the basal segment. The egg sacs contain a small number (20-30) of large eggs.

**Male.** (Paratype no. 56124) (Fig. 9). The body length without terminal setae is 650  $\mu\text{m}$ . The color is brownish. The spermatophores are large, broad oval, reddish or orange in color. The prosome-to-urosome ratio is  $\sim 2 : 1$ ; the cephalosome length-to-width ratio is  $\sim 1$ . There are no hairs at the lateral edge of the fourth free thoracic somite.

The length of the genital somite is approximately equal to its width. The caudal rami are short, the length-to-width ratio being 2.7 (varying from 2.2 to 2.8); the lateral seta is attached almost at the level of the distal third part of the outer edge of the rami. The dorsal seta is noticeably longer than the outermost one, but shorter than the innermost one. The terminal setae are rather long and densely covered with hairs; the innermost seta is 2.5 times as long as the outermost one. The caudal rami lack hairs at the inner edge. The geniculating antennulae are 14-segmented, of the grasping type. The structure of the antennae and other mouth appendages generally resembles the structure of those for the female. The swimming legs are generally the same as those of the female. P1 basipodite outgrowth with a short spine, which is half the length of that for the female and reaches only to the middle of the first segment of the endopodite. P4 has a structure similar to that for the female; its intercoxal sclerite has pointed outgrowths with a wide base. The formula of denticles and hairs on the caudal side of the coxopodite is similar to that of the female. Intercoxal sclerites of all swimming legs is hairless. The fifth pair of swimming legs differs from that of the female in the longer spinulose medial seta of the distal segment. The rudimentary sixth pair has the form of a wide flap with three appendages, of which the inner spine and the middle seta are almost equal, and the outer seta is 1.7 times as long.

**Distribution.** The new species is still known only from the type habitat. It belongs to the species-rich section *annulatus* of the subgenus *Neomesocy-*



**Fig. 7.** *Mesocyclops (Neomesocyclops) frankfiersi* sp. n., female: (a) general view; (b) genital somite and P5; (c) caudal rami, dorsal; (d) A1, distal segments; (e) basipodite A2, frontal; (f) basipodite A2, caudal; (g) maxilla; (h) mandible; (i) maxillule. Scale ( $\mu\text{m}$ ): (a) 200; (b, c) 100; (d–i) 40.

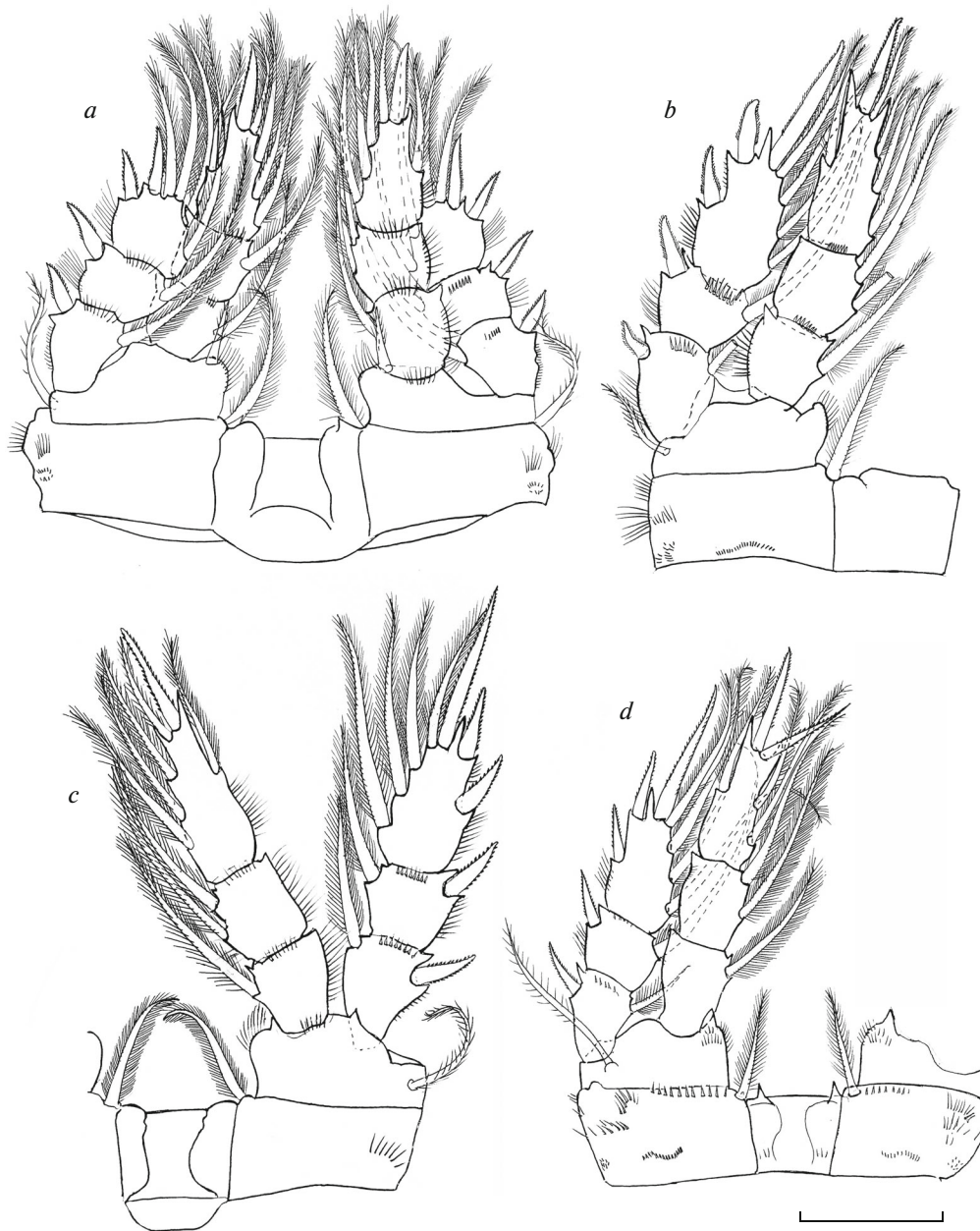


Fig. 8. *Mesocyclops (Neomesocyclops) frankfiersi* sp. n., female (continue): (a) P1, (b) P2, (c) P3, (d) P4. Scale 40  $\mu$ m.

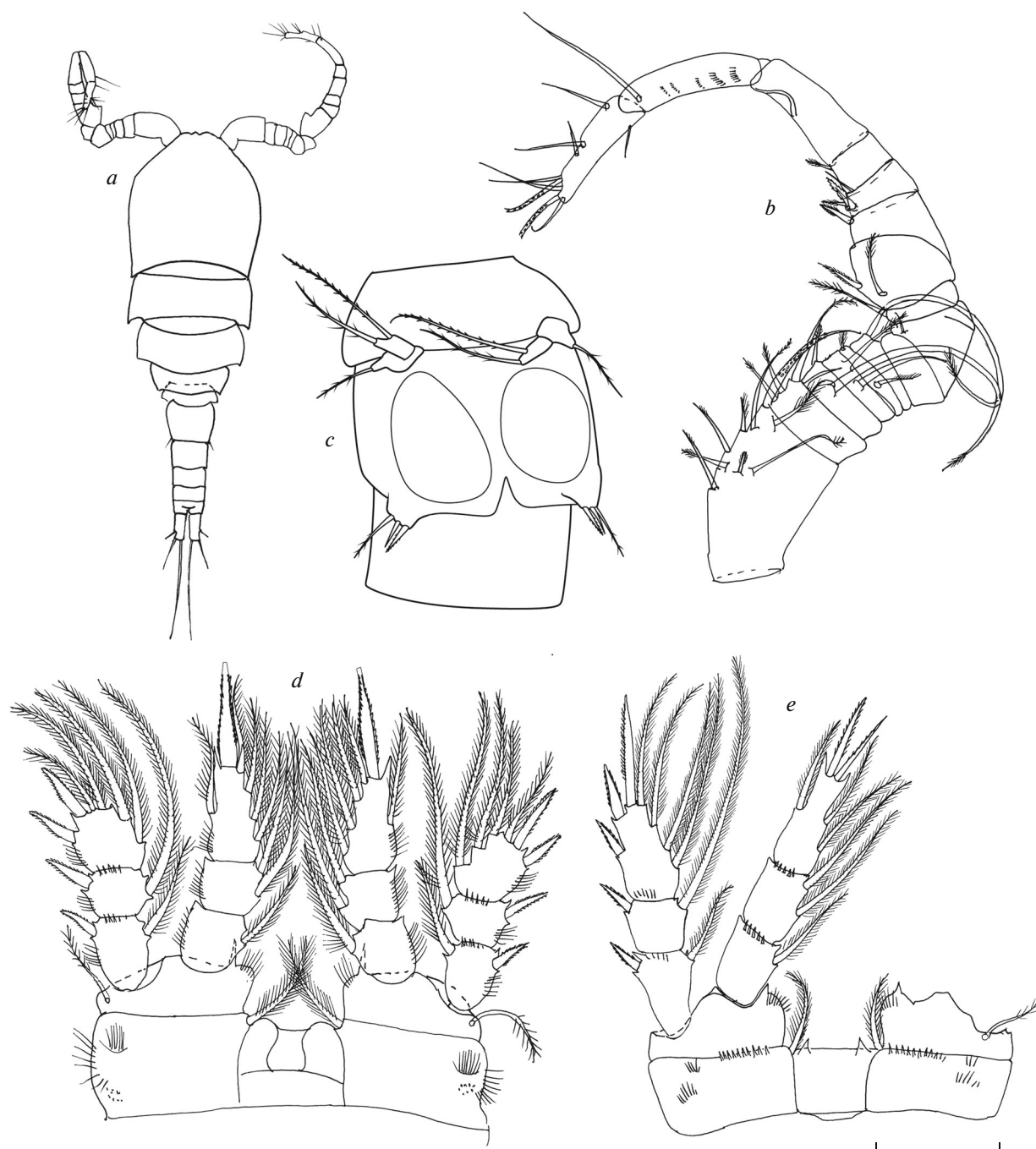
*clops*, all representatives of which inhabit the waters of South and North America.

**Comments.** The species differs from other members of the section in the strongly reduced seta of the basal outgrowth of the first pair of swimming legs and some other details (the shape of the female pore canal, the ratio of the lengths of the appendages of the fifth pair, and the structure of the hyaline membrane of the distal segment of antennulae).

**Etymology.** The name of the species is dedicated to the memory of the Belgian taxonomist of copepods Frank Fiers, who passed away untimely on May, 2018.

**Key for identification of the species of the subgenus *Mesocyclops (Neomesocyclops)* subgen. n.**

1. Th4 with lateral hairs.....(2)
  - Th4 without lateral hairs.....*M. (N.) edax* (Forbes 1891) (North and Central America)
2. CR with hairs on inner edge.....(3)
  - CR without hairs on the medial surface.....*M. (N.) reidae* Petkovski 1986 (South and Central America)
3. P4 CoxPl without outgrowths.....(4)
  - This plate has a pair of more or less long outgrowths.....(10)



**Fig. 9.** *Mesocyclops (Neomesocyclops) frankfiersi* sp. n., male: (a) general view; (b) A1; (c) P5, P6; (d) P1; (e) P4. Scale ( $\mu\text{m}$ ): (a) 200; (b) 70; (c–e) 50.

4. RS with long and wide lateral arms; the second endopodite of A2 has nine setae.....*M. (N.) meridialis* Dussart et Frutos 1986 (South America)

– RS with narrow and short lateral arms; A2 Enp2 has seven or eight setae.....(5)

5. CR with a distal group of strong spinules ventrally.....*M. (N.) pseudomeridianus* Defaye et Dussart 1988 (French Guiana)

– There is no such group of spinules on the CR.....(6)

6. The ventral surface of the genital somite is covered with hairs.....(7)

– The ventral surface of the genital somite has only pits.....*M. (N.) evadomingoi* Gutierrez-Aguirre et Suárez-Morales 2001 (Mexico)

7. The lateral arms of RS have hilly outgrowths in the upper part.....*M. (N.) venezolanus* Dussart 1987 (South America)

– The lateral arms of RS without such outgrowths...(8)

8. CR with spinules at the site of attachment of the outermost seta.....*M. (N.) brasiliensis* Kiefer 1933 (Central and South America)

– There are no spinules at the site of attachment of the outermost seta.....(9)

9. The caudal rami are 3.3–3.7 times longer than the width.....*M. (N.) meridianus* (Kiefer 1926) (Central and South America)

– The caudal rami are ~2.9 times longer than the width.....*M. (N.) varius* Dussart 1987 (Guatemala)

10. CR rather long, the length-to-width ratio is more than five.....*M. (N.) annulatus* (Wierzejski 1892) (South America)

– CR are shorter, the L/W ratio is generally about three, rarely reaching four.....(11)

11. The seminal receptacle has wide lateral arms....(12)

– The seminal receptacle has narrow lateral arms...(13)

12. P4 intercoxal sclerite has hairs on caudal surface; the apical seta P5 does not extend beyond the lower border of the genital somite; the size of the crustacean is ~1 mm.....*M. (N.) frankfiersi* sp. nov.

– P4 intercoxal sclerite without hairs; the apical seta is very long, extending considerably beyond the lower edge of the genital somite; the size of the crustacean ranges from 1.2 to 2 mm....*M. (N.) longisetus* (Thiébaud 1912) (Central and South America)

13. Urosomites with transverse ridges.....*M. (N.) paranaensis* Dussart et Frutos 1986 (South America)

– Urosomites without transverse ridges.....(14)

14. The size of the crustacean is 0.5–0.6 mm; the medial outgrowth of basipodite P4 has only distal hairs.....*M. (N.) intermedius* Pesce 1985 (West Indies)

– The size of the crustacean is ~1 mm; the medial outgrowth of basipodite P4 has distal and proximal hairs .....*M. (N.) ellipticus* Kiefer 1936 (Central and South America)

## CONCLUSIONS

Thus, the species-rich genus *Mesocyclops* (78 species) was revised and divided into four subgenera based on the morphological features and natural habitats of their representatives. A new species *Mesocyclops (Neomesocyclops) frankfiersi* sp. n. from the water reservoirs of Cozumel Island (Mexico) was described. The key is complemented with 12 taxa (to 78 species) compared with the latest faunal summary (Ueda and Reid, 2003). The analysis of the genus suggests that there may be more species added to it. The addition of new

species is expected to be most active from the water reservoirs of South East Asia and South America.

## FUNDING

This work was supported by the Federal Program for the Study of Animal Biodiversity, Russian Academy of Sciences, project no. AAAA-A19-119020690091-0, and by the Russian Foundation for Basic Research, project no. 20-04-00035. The Federal Collection of the Zoological Institute, Russian Academy of Sciences, no. 96-03-16, was involved in its preparation.

## ACKNOWLEDGMENTS

I really appreciate all the people mentioned as donating their own materials: Prof. D. Defaye (France), Prof. H. Dumont (Belgium), Prof. C.H. Fernando (Canada), H.W. Mittmann (Germany). The author thanks O.A. Chaban for help with drawings, identification tables, and manuscript design.

## COMPLIANCE WITH ETHICAL STANDARDS

*Conflict of interest.* The author declares no conflict of interests.

*Statement on the welfare of animals.* All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

## REFERENCES

- Alekseev, V.R., The new subspecies of *Mesocyclops leuckrti* from East Siberia (Crustacea, Cyclopidae: Cyclopidae), *Zoosyst. Ross.*, 1993, vol. 2, pp. 55–58.
- Alekseev, V.R., Key to freshwater Cyclopidae of Russia and adjacent lands (Crustacea), *Zoosyst. Ross.*, 1998, vol. 7, pp. 25–43.
- Alekseev, V.R., *A Guide to Tropical Freshwater Zooplankton*, Ch. 4: *Copepoda*, Fernando, C.H., Ed., Leiden: Backhuys Publ., 2002, pp. 123–187.
- Alekseev, V.R., Abramson, N.I., and Sukhikh, N.M., Introduction of sibling species to the ecosystem of the Baltic Sea, *Dokl. Biol. Sci.*, 2009, vol. 429, no. 1, pp. 544–547.
- Alekseev, V.R., Miracle, M.R., Sahuquillo, M., and Vicente, E., Redescription of *Acanthocyclops vernalis* (Fischer, 1853) and *Acanthocyclops robustus* (Sars, 1863) from neotypes, with special reference to their distinction from *Acanthocyclops americanus* (Marsh, 1892) and its invasion of Eurasia, *Limnetica*, 2020, vol. 40. <https://doi.org/10.23818/limn.40.xx>
- Besse, J., *Continental Drift. Tectonics Observatory*, California Institute of Technology, 1995. <http://www.tectonics.caltech.edu/outreach/animations/drift.html>. Accessed September 25, 2009.
- Connolly, J.K., Watkins, J.M., Hinchey, E.K., Rudstam, L.G., and Reid, J.W., The Asian cyclopoid copepod *Mesocyclops pehpeiensis* Hu 1943 reported from the western basin of Lake Erie, *J. Great Lakes Res.*, 2019, vol. 45, pp. 196–201.



- Copepoda: Cyclopoida: genera *Mesocyclops* and *Thermocyclops*, in *Guides to the Identification of the Microinvertebrates of the Continental Waters of the World*, Reid, J.W. and Ueda, H., Eds., 2003, vol. 20, pp. 1–318.
- Dahms, H.U. and Fernando, C.H., Redescription of female and male *Mesocyclops edax* Forbes, 1891 (Copepoda: Cyclopoida), *J. Crustacean Biol.*, 1995, vol. 15, pp. 317–328.
- Dahms, H.U. and Fernando, C.H., Redescription of *Mesocyclops leuckarti* (Copepoda, Cyclopoida), including a study of its naupliar development, *Int. Rev. Gesamten Hydrobiol. Hydrogr.*, 1993, vol. 78, pp. 589–609.
- Dussart, B.H. and Defaye, D., *World Directory of Crustacea Copepoda of Inland Waters*, vol. II: *Cyclopiformes*, Leiden: Backhuys Publ., 2006.
- Fefilova, E.B., Baturina, M.A., Kononova, O.N., Loskutova, O.A., Khokhlova, L.G., and Dubovskaya, O.P., Long-term changes of aquatic communities in the Kharbeyskie Lakes, *J. Sib. Fed. Univ., Ser. Biol.*, 2014, vol. 7, no. 3, pp. 240–266.
- Gophen, M., The impact of zooplankton status on the management of Lake Kinneret (Israel), *Hydrobiologia*, 1984, vol. 113, pp. 249–258.
- Hołyńska, M., Phylogeny of mesocyclops (Copepoda: Cyclopidae) inferred from morphological characters, *Zool. J. Linn. Soc.*, 2006, vol. 147, pp. 1–70.
- Hołyńska, M., Genus *Mesocyclops* Sars, 1914, in *Copepoda: Cyclopoida. Genera Mesocyclops and Thermocyclops. Guides to the Identification of the Microinvertebrates of the Continental Waters of the World*, Reid, J.W. and Ueda, H., Eds., 2003, vol. 20, pp. 12–213.
- Hołyńska, M., Revision of the Australasian species of the genus *Mesocyclops* Sars, 1914 (Copepoda, Cyclopidae), *Ann. Zool. (Warszawa)*, 2000, vol. 50, pp. 363–447.
- Kiefer, E., Beitrag zur Kenntnis von Morphologie, Taxonomie und geographischer Verbreitung von *Mesocyclops leuckarti* auctorum, *Arch. Hydrobiol., Suppl.*, 1981, vol. 62, pp. 148–190.
- Meleg, L.N., Fiers, F., Robu, M., and Moldovan, O.T., Distribution patterns of subsurface copepods and the impact of environmental parameters, *Limnologia*, 2012, vol. 42, pp. 156–164.
- Montoliu, L., Miracle, M.R., and Elias-Gutierrez, M., Using DNA barcodes to detect non-indigenous species: the case of the Asian copepod *Mesocyclops pehpeiensis* Hu, 1943 (Cyclopidae) in two regions of the world, *Crustaceana*, 2015, vol. 88, pp. 1323–1338.
- Peixoto, R.S., Brandão, L.P.M., Valadares, C.F., and Barbosa, P.M.M., Occurrence of *Kellicottia bostoniensis* (Rousset, 1908) and *Mesocyclops ogunnus* Onabamiro, 1957 in lakes of the Middle River Doce, MG, Brazil, *Acta Limnol. Bras.*, vol. 22, pp. 356–360.
- Reid, J.W. and Moreno, D., The western and southern distribution of *Mesocyclops edax* (S.A. Forbes) (Crustacea: Copepoda: Cyclopoida), *Proc. Biol. Soc. Wash.*, 1999, vol. 112, pp. 581–591.
- Reid, J.W. and Saunders, J.F., The distribution of *Mesocyclops aspericornis* (von Daday) in South America, *J. Crustacean Biol.*, 1986, vol. 6, no. 4, pp. 820–824.
- Suárez-Morales, E., Gutiérrez-Aguirre, M.A., and Mendoza, F., The Afro-Asian cyclopoid *Mesocyclops aspericornis* (Crustacea: Copepoda) in eastern Mexico with comments on the distribution of exotic copepods, *Rev. Mex. Biodivers.*, 2011, vol. 82, no. 1, pp. 109–115.
- Van de Velde, I., Revision of the African species of the genus *Mesocyclops* Sars, 1914 (Copepoda: Cyclopidae), *Hydrobiologia*, 1984, vol. 109, pp. 3–66.
- Wyngaard, G., Holynska, M., and Schulte, J.A., Phylogeny of the freshwater copepod *Mesocyclops* (Crustacea: Cyclopidae) based on combined molecular and morphological data, with notes on biogeography, *Mol. Phylogenet. Evol.*, 2010, vol. 55, pp. 753–764.

Translated by N. Smolina