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Morphological re-description of *Eucyclops* (*Speratocyclops*) *speratus* (Lilljeborg, 1901) (Copepoda: Cyclopoida) from the type locality, clarification of its diagnostic characters and distribution range

Морфологическое переописание *Eucyclops* (*Speratocyclops*) *speratus* (Lilljeborg, 1901) (Copepoda: Cyclopoida) из типового местонахождения, уточнение его диагностических признаков и ареала

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KEY WORDS: *Eucyclops speratus*, integrative taxonomy, cyclopid fauna, species delimitation, morhological variability, biodiversity, zoogeography, Palearctic, synonymy, identification key, Lund, Sweden.

КЛЮЧЕВЫЕ СЛОВА: *Eucyclops speratus*, интегративная таксономия, фауна циклопид, разграничение видов, морфологическая изменчивость, биоразнообразие, зоогеография, Палеарктика, синонимия, ключ для определения, Лунд, Швеция.

ABSTRACT. A detailed re-description of the external morphology of *Eucyclops* (*Speratocyclops*) *speratus* (Lilljeborg, 1901) females collected from Höje River near Lund, Sweden (the type locality), was conducted. Key characteristics of the type specimens were compared with those of several distant populations of the species across the Palearctic region. As a result, the newly described *E. sibiricus* Novikov *et al*., 2025 syn.n. was synonymized with *E.* (*Sp.*) *speratus* s.str. Distant populations of the same species from Sakhalin Island (Far East Russia) and Siberia appeared morphologically identical to specimens from Lund (Northern Europe) in all taxonomically significant macro- and micro-features. Molecular genetic differences observed for mitochondrial and nuclear genes among these distant populations suggest population polymorphism within the same widely distributed species. The modern natural range of *E.* (*Sp.*) *speratus* s.lat. is limited to the Palearctic region. An updated identification key for 10 taxa of the subgenus *Eucyclops* (*Speratocyclops*) is provided.

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РЕЗЮМЕ. Проведено детальное переописание внешней морфологии самок *Eucyclops* (*Speratocyclops*) *speratus* (Lilljeborg, 1901), собранных в реке Хёе близ Лунда, Швеция (типовое местонахождение). Ключевые характеристики типовых экземпляров были сравнены с характеристиками нескольких отдаленных популяций вида по всей Палеарктике. В результате вновь описанный *E. sibiricus* Novikov *et al*., 2025 syn.n. был синонимизирован с *E.* (*Sp.*) *speratus* s.str. Отдаленные популяции того же вида с острова Сахалин (Дальний Восток России) и из Сибири оказались морфологически идентичны образцам из Лунда (Северная Европа) по всем таксономически значимым макро- и микропризнакам. Молекулярно-генетические различия, наблюдаемые в митохондриальных и ядерных генах между этими удалёнными популяциями, свидетельствуют о популяционном полиморфизме в пределах одного широко распространённого вида. Современный естественный ареал *E.* (*Sp.*) *speratus* s.lat. ограничен Палеарктикой. Представлен обновлённый определительный ключ для 10 таксонов подрода *Eucyclops* (*Speratocyclops*).

Introduction

The subgenus *Speratocyclops* Alekseev, 2019 of *Eucyclops* Claus, 1893 was distinguished during the revision of the nominative genus based on stable features of the ornamentation of the antenna basipodite, segmentation and armature of the antennules, structure of the reduced 5th leg, and the arrangement of denticles on the caudal rami [Alekseev, Defaye, 2011; Alekseev, 2019]. The type species *Eucyclops* (*Speratocyclops*) *speratus* (Lilljeborg, 1901) was originally described from Sweden insufficiently by modern standards, and some elements of its morphology were later described from the type

Table 1. Locations and dates of sample collection of specimens of *Eucyclops* (*Speratocyclops*) *speratus* s.str. used in morphological analysis.
Таблица 1. Места и даты отбора экземпляров *Eucyclops* (*Speratocyclops*) *speratus* s.str., использованных в морфологическом анализе.

No.	Date	Sample location	Coordinates	
			N latitude	E longitude
1	16.06.2001	Höje river near Lund, Sweden	55.7021°	13.1416°
2	11.06.1997	Åland, near Mariehamn, Finland	60.1418°	19.9435°
3	10.06.1999	Tauride Garden, St. Petersburg, Russia	59.9472°	30.3696°
4	13.06.1999	Sablinka River, Leningrad Region, Russia	59.6211°	30.7435°
5	04.09.2020	Glubokoye Lake, Moscow Region, Russia	55.7516°	36.5054°
6	01.04.2002	Plön, near Schöhsee, Germany	54.1633°	10.4354°
7	17.09.2005	Sula River, Pustoviitivka, Ukraine (leg. V. Monchenko)	50.7862°	33.5578°
8	01.07.1984	Usmanka River, Voronezh, Russia	51.7375°	39.3233°
9	06.1987	Aslikul' Lake, Bashkortostan, Russia	54.2965°	54.6020°
10	5.07.2025	Bakhta River, Krasnoyarsk Krai, Russia	63.4674°	91.4092°
11	08.1997	Khuvsgul Lake, Northern Mongolia (leg. N. Kluge)	50.4956°	100.1682°
12	07.1986	Posol'skiy Sor, Baikal, Russia	51.9850°	106.1545°
13	20.08.2019	Lena River Delta (leg.A.Novikov)	72.3687°	126.4759°
14	17.07.2022	Soldatskoye Lake, Ussuriysk, Russia	43.7782°	131.9347°
15	08.2019	Minnyy Gorodok Park, Vladivostok, Russia	43.1201°	131.9369°
16	30.07.2022	Dynamo Park, Khabarovsk, Russia	48.4809°	135.0750°
17	20.07.2022	Tunaicha, Sakhalin, Russia	46.8566°	143.1068°
18	22.07.2022	Poronaysk, Sakhalin, Russia	49.2285°	143.0950°
19	27.07.2024	Tungor, Sakhalin, Russia	53.3809°	142.9509°
20	25.07.2024	Okha, Sakhalin, Russia	53.5915°	142.9343°
21	13.06.1997	Teplaya Bay (warm bay), Kurile Lake, Kamchatka, Russia (leg. D. Lajus)	51.4808°	157.1442°

locality material [Lilljeborg, 1901; Alekseev, 2024]. For comparative purposes, a more detailed description was required, which is provided in this paper.

Initially, *Eucyclops* (*Speratocyclops*) *speratus* s.str. was described as a subspecies of *Cyclops varius* (=*E.* (*E.*) *serrulatus* (Fischer, 1851)) [Lilljeborg, 1901], but Sars [1914] was the first to recognize it as a valid species. Einsle [1993] and Monchenko [1974] followed this classification, while others, including Gurney [1933] and Rylov [1948], supported its subspecies status. The matter was resolved by hybridization experiments confirming its reproductive isolation from *E.* (*E.*) *serrulatus* and other species of the genus [Monchenko *et al*., 2011]. After a recent revision, these two *Eucyclops* species were placed in different subgenera [Alekseev, 2019]. The neotype of *E.* (*E.*) *serrulatus* was described in detail from the type locality near St. Petersburg [Alekseev *et al*., 2006]. Here, we provide the first detailed description of *Eucyclops* (*Sp.*) *speratus* s.str. female based on topotype specimens collected from the type habitat — Höje River near Lund, Sweden.

Faunistic studies conducted in recent decades in the easternmost part of the Asian continent, including Sakhalin Island, Hokkaido, and Taiwan, have revealed significant differences in local populations of several cyclopoid species widely distributed across the Palearctic, particularly within the genus *Eucyclops*. This has led to the description of several new taxa [Ishida 2000, 2001; Alekseev, 2000; Alekseev, Defaye 2004; Sukhikh, Alekseev, 2015; Major *et al*., 2024]. Many of these new taxa from East Asia belong to the subgenus *Eucyclops* (*Speratocyclops*). At the start of this study, the subgenus comprised approximately 10 taxa: 3 from Europe and the rest from the East Asian region [Alekseev, 2024]. This work provides an updated identification key for the subgenus, which incorporates observed intraspecific and seasonal variability of *E.* (*Sp.*) *speratus* s.str.

The application of molecular genetic methods, assessments of population isolation age, and genome divergence levels, unsupported by morphological differences in some cases, complicates further expansion of the fauna study due to excessive synonymy [Novikov *et al*., 2025]. This work, based on materials from Europe and East Asia (the Baikal region, Kamchatka, Sakhalin Island, and Japan), focuses on further investigation of the composition, zoogeography, and origin of the *Eucyclops* (*Speratocyclops*) fauna. It also addresses the applicability of new taxonomic traits and the use of molecular genetic methods for cope-

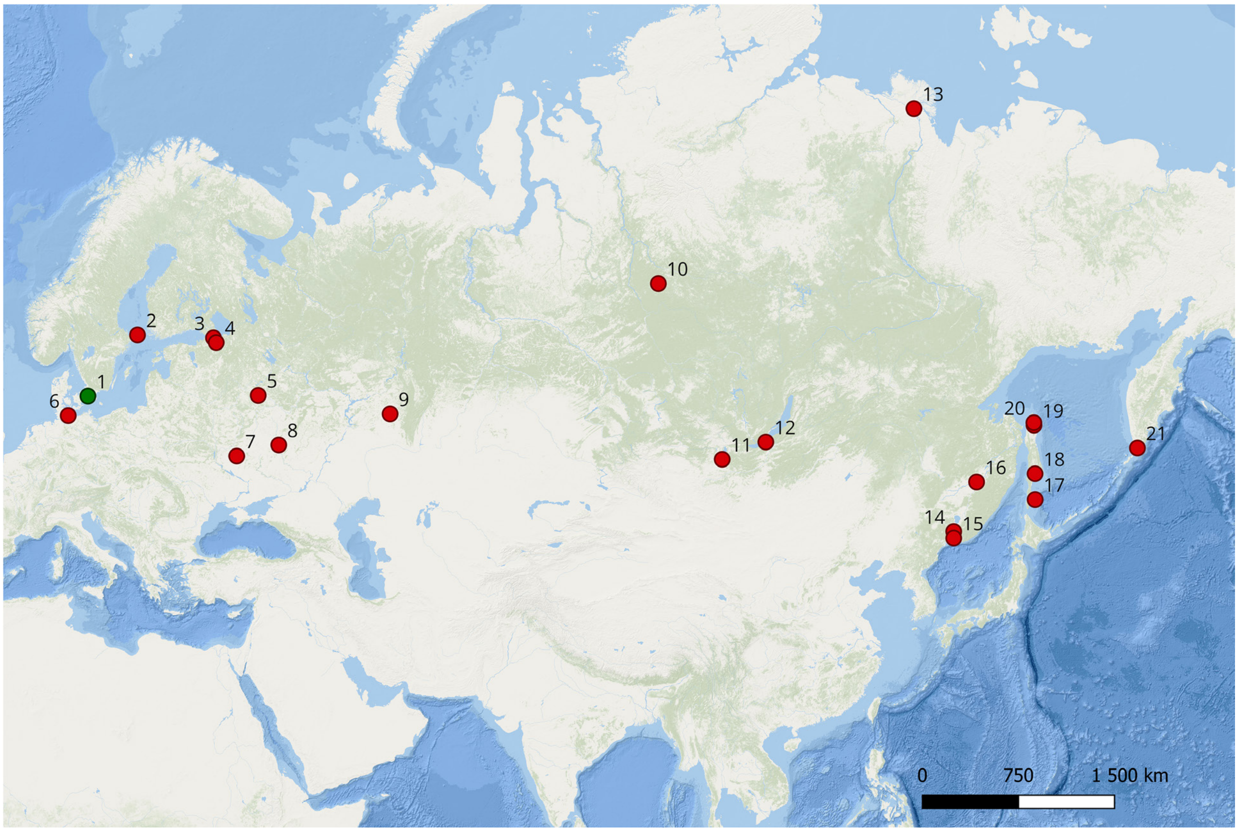

Fig. 1. Localities of *Eucyclops* (*Speratocyclops*) *speratus* s.str. specimens used for morphological analysis. Numbers correspond to Table 3. Green circle indicates the type locality.

Рис. 1. Места находок представителей *Eucyclops* (*Speratocyclops*) *speratus* s.str., использованных для морфологического анализа. Номера соответствуют табл. 1. Типовое местонахождение обозначено зеленым кружком.

pods within the framework of the rules established by the International Code of Zoological Nomenclature.

Material and methods

1. Morphology. The morphology and armature of all limbs were described for the type population of *E.* (*Sp.*) *speratus* using three topotype specimens collected from the type habitat near Lund, Northern Sweden. Specimen slides deposited in the federal collection of the Zoological Institute of the Russian Academy of Sciences (Russia). To study morphological variability and estimate the range of distribution, specimens from geographically dispersed populations of the Palearctic were studied (Table 1, Fig.1).

The structure of the recently described *Eucyclops sibiricus* Novikov *et al*. 2025 was analyzed based on its original description [Novikov *et al*., 2025] and a female paratype kindly provided by the authors.

Morphological structures were observed under Zeiss Axio A1 compound microscope. For morphological analysis, organisms were placed on a glass slide in a drop of glycerol, dissected, covered with a cover glass on plasticine legs, measured, photographed and sketched. To study and draw the ornamentation of structures, they were pressed with a cover glass and studied under oil immersion. The drawings were made with a drawing apparatus and processed in Adobe Illustrator CC 2017.

The specimens are deposited in the Federal Collection of the Zoological Institute of the Russian Academy of Sciences.

Abbreviations: Bas — basipodite; CR — caudal rami; Enp, Exp — endopodite, exopodite; InS — inner spine; IS — innermost caudal seta; L/W — length-to-width ratio; OS — outermost caudal seta; OutS — outer spine; P1–P6 — legs 1–6.

2. Genetic analysis. Mitochondrial cytochrome oxidase I (COI), 12S rRNA and nuclear ITS1-5.8S rRNA-ITS2, and 18S rRNA gene fragments were used in the analysis. All DNA sequences were obtained by the authors, except for material from Great Britain and Eastern Siberia, which was retrieved from GenBank (Table 2). A total of 10 adult *Eucyclops* specimens were analyzed for the mtCOI gene fragment (532 bp), 8 for the 12S rRNA gene fragment (397 bp), 4 for ITS1-5.8S rRNA-ITS2 (592 bp), and 4 for the 18S rRNA gene fragment (397 bp). All sequences were deposited in GenBank under the accession numbers: CO1 — PX387045; 12SrRNA — PX387084–PX387096; 18SrRNA — PX387104–PX387108; nITS — PX387097– PX387101.

Sequences were aligned using the CLUSTAL W algorithm [Thompson *et al*., 1994] implemented in BIOEDIT v.7.2 [Hall, 1999], with manual editing of ambiguous sites.

3. Analysis of sequences and phylogeny reconstruction. The level of nucleotide differences among species was calculated using the Tamura-Nei model in MEGA 11 [Tamura *et al*., 2021]. The best-fitting models of nucleotide substitution for mitochondrial and nuclear datasets were selected in jModelTest v. 2.1.7 based on likelihood scores for 88 different models under the Akaike Information Criterion (AICc) [Posada, 2008].

Phylogeny reconstruction was performed separately for each locus (COI, 12S rRNA, nITS, and 18S rRNA), and a joint COI-12S rRNA-nITS consensus tree was constructed using maximum parsimony (MP). For COI gene fragment analysis, maximum likelihood (ML) and the General Time Reversible

Table 2. Locations and dates of sample collection of specimens of *Eucyclops* (*Speratocyclops*) *speratus* s.str. and additional material used in molecular analysis.

Таблица 2. Места и даты сбора экземпляров *Eucyclops* (*Speratocyclops*) *speratus* s.str. и дополнительного материала, использованных в молекулярном анализе.

Specimens ID	Sample location	Coordinates		Date
		N latitude	E longitude	
E.speratus 720	Volgograd reservoir, Russia	48.9984°	44.8315°	02.09.2020
E.serrulatus	Orlovsky Pond, St. Petersburg, Russia	59.8669°	29.9377°	25.06.2009
E.speratus T13	Aleksandrovka village, Tulun district, Irkutsk region, Russia	55.3905°	100.8231°	25.07.2021
E.speratus K1-6, 23-51, 23-52	Kuitun District, Irkutsk Region, Russia	54.3472°	101.5286°	06.2021
E.denticulatus; E.speratus 23-50; E. a. roseus 23-42	Sakhalin Island, Russia	51.7981°	143.1250°	25.07.2022
E.speratus	Zeneva Lake, Zeneva	46.2003°	6.140°	5.03.2016
E speratus	Vladivostok, Russia	43.1201°	131.9369°	08.2019
E. delongi	Vaigach Island	70.0366°	59.4817°	2012
E. arcanus arcticus; E. delongi	Lena Delta, Russia	55.3905°	100.8231°	04.2014
E. a. roseus M1	Akgel Lake, Dagestan, Russia	42.9602°	47.5422°	07.2010

model with gamma rate distribution (G) and without invariable sites (I) were applied in MEGA 11 [Tamura *et al.*, 2021].

Taxonomy

Eucyclops (*Speratocyclops*) *speratus* (Lilljeborg, 1901)
Figs 1–4; Tables 1, 3.

SYNONYMY. *Cyclops varius* var. *speratus* Lilljeborg, 1901; *Cyclops agilis speratus*: Gurney, 1933; *Leptocyclops speratus*: Sars G.O., 1914; *Eucyclops serrulatus* var. *speratus*: Rylov, 1948; *Eucyclops speratus*: Monchenko, 1974; Einsle, 1993; Alekseev *et al*., 2006; Dussart, Defaye, 2006; *Eucyclops* (*Speratocyclops*) *speratus*: Alekseev, 2019, 2024.

Recent younger synonym: *Eucyclops sibiricus* Novikov *et al*., 2025, **syn.n**.

TYPE LOCALITY. Höje River, near Lund, Sweden.

HOLOTYPE. Not found.

MATERIAL. Topotype specimens (3 females) from the type locality collected in June 2002; specimens from various Palearctic populations (see Table 1).

DESCRIPTION. FEMALE (topotype). Total length (excluding caudal setae) 1154–1246 μm. Cephalosome oval in front, about as long as broad, maximum width at the level of the lower 25% of the length. Prosome about 1.3 times as long as urosome. Th1–3 free somites smooth; Th4 with long setulae laterally. Genital double-somite about as long as broad (L/W=1.0–1.1), wider anteriorly then sharply narrow (Wmax/Wmin~1.7); *receptaculum seminis* (Fig. 3A) mouth-shaped, typical of the genus. Anal operculum weakly developed. Caudal rami (Fig. 2B) parallel, with L/W ratio about 5.8–6.3; with lateral *serra* occupying 59–78% of lateral edge length; *serra* composed of small sub-equal spinules not increasing in size distally. Lateral seta about as long as ramus width. Outermost spiniform seta with spinules on outer edge and hairs on inner edge, about 0.4 times as long as ramus length, inserted close to other terminal seta, with set of large spinules in base. Dorsal seta short, 0.7–0.8 times as long as outermost seta. Innermost seta plumose, 1.2–1.4 times as long as outermost one. Length ratio of caudal median setae 1.6. Relative lengths of caudal setae (outermost to innermost): 1.0/4.5–4.9/6.9–7.6/1.2–1.4.

Antennule (Fig. 3I) 12-segmented, reaching middle or posterior border of Th1, with smooth or very finely serrated hyaline membrane on three distal segments. 1st segment with proximal group of short denticles and distal row of long spinules. Segment setal formula (proximal to distal): 1(8) / 2(4) / 3(2) / 4(6) / 5(4) / 6(2) / 7(2) / 8(3) / 9(2+aesthetasc) / 10(2) / 11(2+aesthetasc) / 12(7+aesthetasc).

Antenna (Fig. 3B) consists of basipodite with two medial setae and one long exopodite seta, and three endopodite segments with setal formula 1, 9, 7. Basipodite on caudal surface without distal groups of setulae in N1, 2 positions; other groups of spinules NN3, 4, 5, 6, 17 as in Fig. 3E; on frontal surface: NN7, 8, 9, 10, 11, 12, 14, 15 as in Fig. 3C, D.

Labrum represented by wide plate with free margin bearing large blunt teeth between lateral projections armed with small denticles. Mandible (Fig. 3G, H) consists of long plate with palp armed with two long feathered and one short naked setae; on opposite side from palp there are two rows of setulae; gnathobase with group of long spinules, feathered seta, and blunt teeth of different sizes. Maxillule (Fig. 2F) composed of unclearly segmented syncoxa bearing 3 distal claw-like projections and 8 setae; two-segmented palp armed with 7 setae of different lengths; surface of palp bears several tiny denticles. Maxilliped (Fig. 3F) 4-segmented, setal formula 3/2/1/3 (proximal to distal); 2nd segment ornamented with two lateral rows and two medial rows of long setulae; 3rd segment bearing medial group of long setulae. Maxilla 5-segmented, setal formula 2/3/2+1claw/2/3, ornamentation as in Fig. 4A.

Swimming legs P1–P4 biramous with 3-segmented endo- and exopodites; distal exopodites with formula of spines: 3/4/4/3, setae: 5/5/5/5; distal endopodites with formula of spines: 1/1/1/2, setae: 5/5/5/3.

P1 (Fig. 4B) basipodite inner spine plumose with strong setulae; this spine reaches distal edge of Enp3. Caudal surface of intercoxal plate with two median rows of tiny denticles. Inner

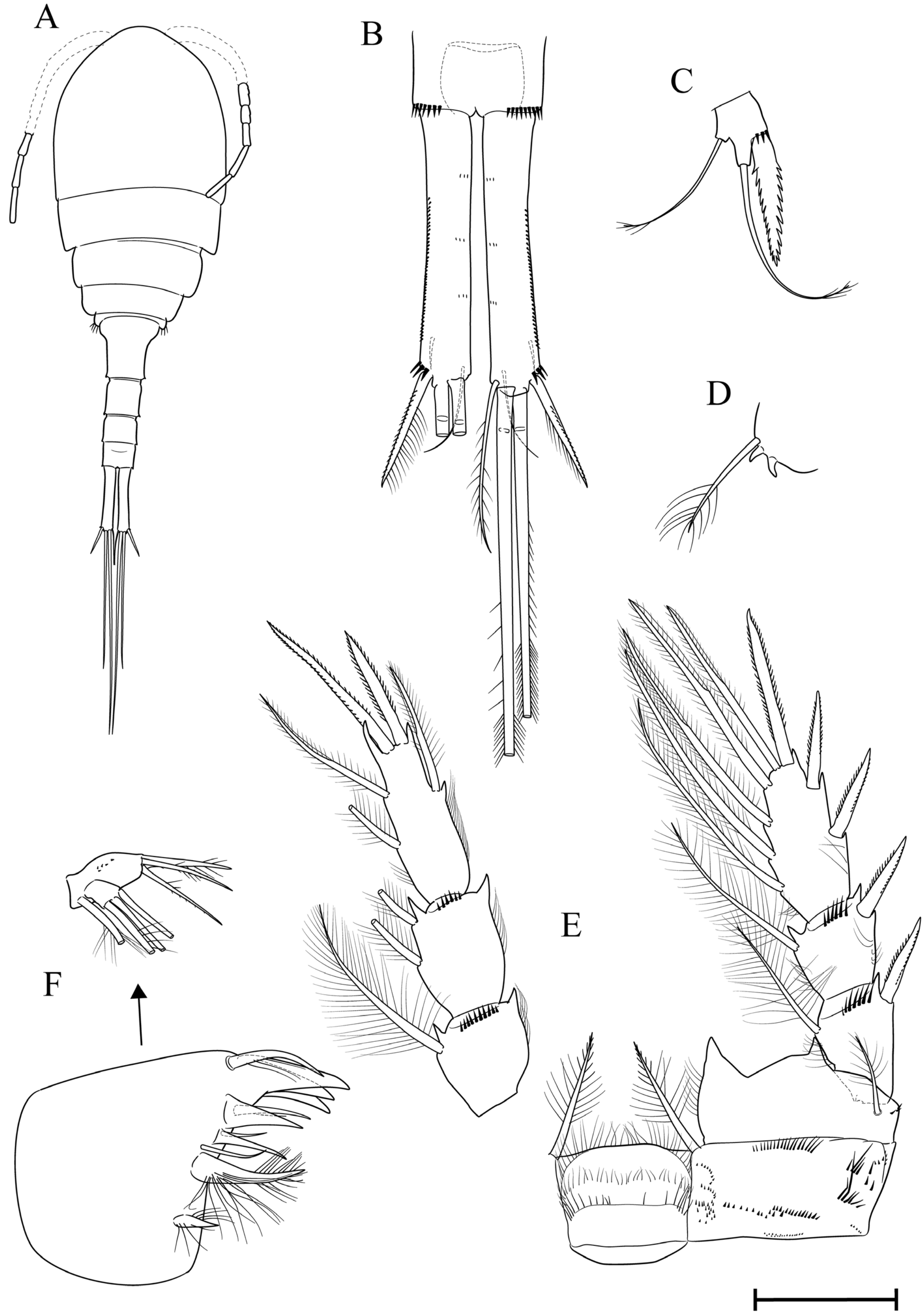

Fig. 2. *Eucyclops* (*Speratocyclops*) *speratus* (Lilljeborg, 1901), Sweden. Topotype, female. A — habitus; B — caudal rami, ventral; C — P5; D — P6; E — P4, caudal; F — maxillule. Scale bar: A — 300; B — 70; C–F — 50 µm.

Рис. 2. *Eucyclops* (*Speratocyclops*) *speratus* (Lilljeborg, 1901), Швеция. Топотип, самка. A — габитус; B — каудальные ветви, вентрально; C — P5; D — P6; E — P4, каудально; F — максиллула. Масштабная линейка: A — 300; B — 70; C–F — 50 мкм.

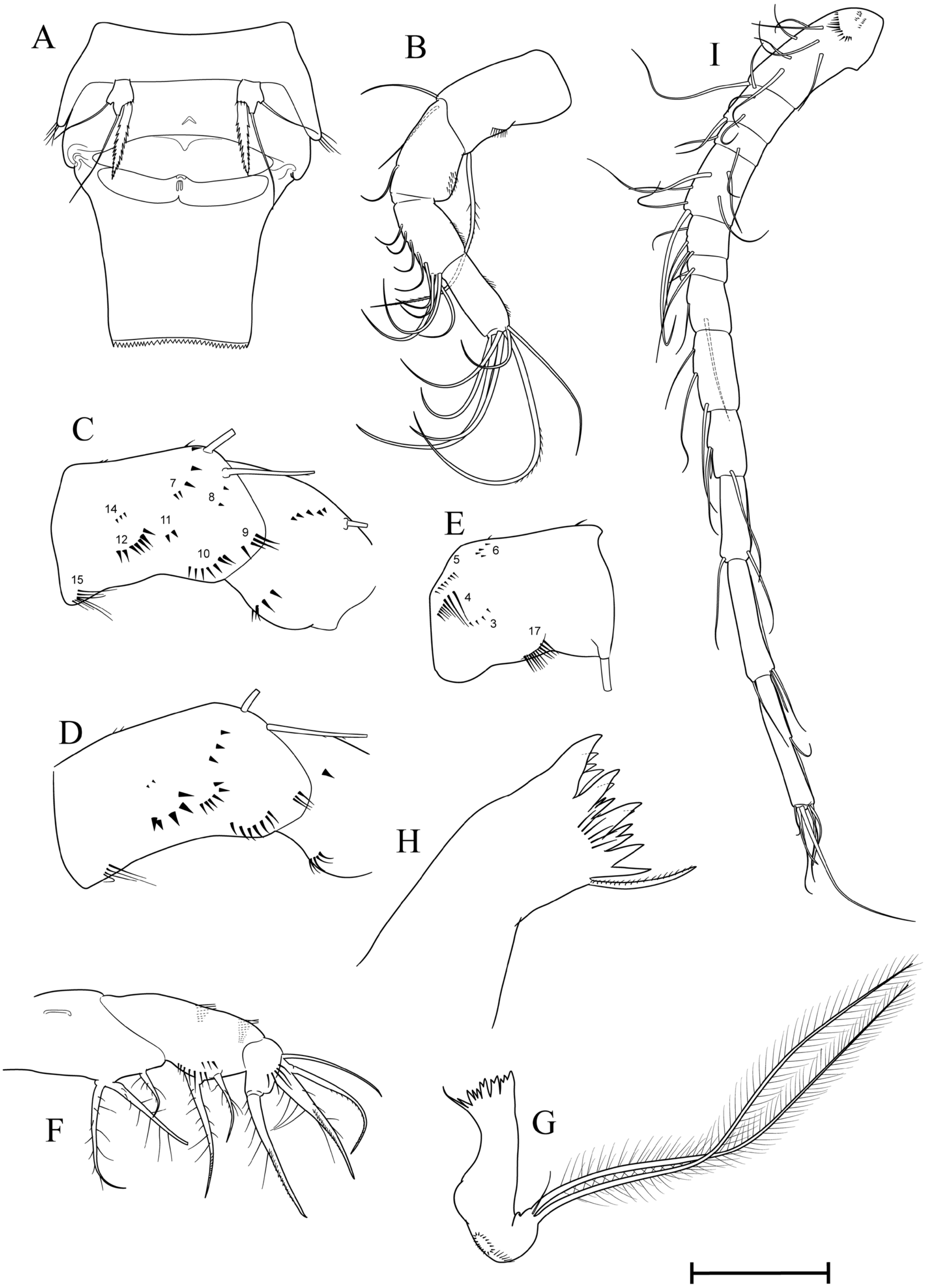

Fig. 3. *Eucyclops* (*Speratocyclops*) *speratus* (Lilljeborg, 1901), Sweden. Topotype, female (cont.). A — genital double somite; B — 2nd antenna (A2); C — A2 basipodite, frontal; D — A2 basipodite, frontal, variation; E — A2 basipodite, caudal; F — maxilliped; G — mandible; H — mandible gnathobase; I — A1. Scale bar: A, B, I — 75; C–F — 40; G — 60; H — 30 μm.

Рис. 3. *Eucyclops* (*Speratocyclops*) *speratus* (Lilljeborg, 1901), Швеция. Топотип, самка (прод.). A — двойной генитальный сомит; B — 2-я антенна (A2); C — базиподит A2, фронтально; D — базиподит A2, фронтально, вариант; E — базиподит A2, каудально; F — максиллипеда; G — мандибула; H — гнатобаза мандибулы; I — A1. Масштабная линейка: A, B, I — 75; C–F — 40; G — 60; H — 30 мкм.

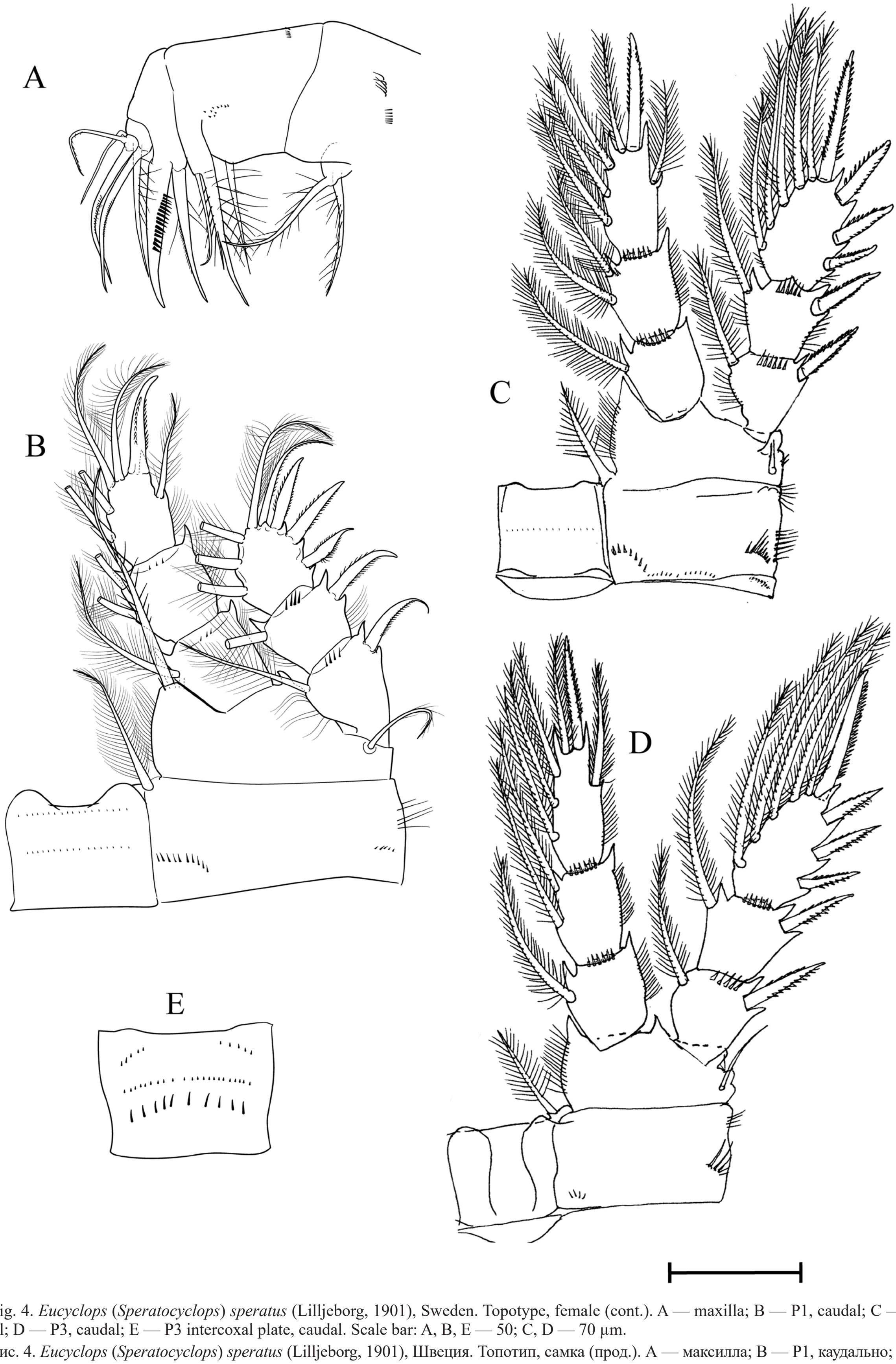

Fig. 4. *Eucyclops* (*Speratocyclops*) *speratus* (Lilljeborg, 1901), Sweden. Topotype, female (cont.). A — maxilla; B — P1, caudal; C — P2, caudal; D — P3, caudal; E — P3 intercoxal plate, caudal. Scale bar: A, B, E — 50; C, D — 70 μm.

Рис. 4. *Eucyclops* (*Speratocyclops*) *speratus* (Lilljeborg, 1901), Швеция. Топотип, самка (прод.). A — максилла; B — P1, каудально; C — P2, каудально; D — P3, каудально; E — межкоксальная пластинка P3, каудально. Масштабная линейка: A, B, E — 50; C, D — 70 мкм.

Table 3. Variability of some morphological features of *Eucyclops* (*Speratocyclops*) *speratus*.
Таблица 3. Проявление изменчивости отдельных морфологических признаков *Eucyclops* (*Speratocyclops*) *speratu*s.

Site	Region	N specim.	CR L/W	CR *serra*	CR IS/ OS	CR OS/ CR	P4 Enp3 L/W	P4 Enp3 InS/ OutS	No. of medial hairs on P4 Exp1
1	Lund, Sweden	1	6.3	II	1.3	0.4	2.7	1.4	5
		2	5.8	II	1.4	0.4	2.6	1.4	7
		3	5.9	II	1.2	0.4	2.6	1.4	5
2	Åland Finland	1	6.3	I	1.2	0.5	2.7	1.6	0
3	SPb, Russia	1	6.8	II	1.2	0.4	2.3	1.4	0
		2	6.5	II	1.1	0.4	2.5	1.4	2
		3	7.2	II	1.2	0.4	2.5	1.4	1
		4	7.0	II	1.2	0.4	2.6	1.4	0
4	Len. Obl., Russia	1	6.6	II	1.2	0.5	2.9	1.5	0
		2	6.8	II	1.2	0.4	2.5	1.4	3
5	Mos. Obl., Russia	1	5.5	I	1.2	0.5	2.8	1.3	0
6	Plön, Germany	1	6.6	III	1.5	0.4	3.3	1.4	5
		2	7.3	II	1.5	0.4	2.9	—	2
		3	7.8	III	1.3	0.4	3.2	1.3	0
7	Sula, Ukraine	1	5.0	I	1.4	0.5	2.3	1.5	0
8	Voronezh, Russia	1	5.0	I	1.4	0.5	2.5	1.5	0
9	Bashkortostan, Russia	1	7.1	II	1.4	0.4	2.8	1.5	0
10	Krasnoyarsk, Russia	1	6.2	II	1.3	0.4	2.7	1.6	10
11	N. Mongolia	1	5.7	I	1.3	0.4	2.7	1.5	10
12	SE Baikal, Russia	1	6.1	I	1.2	0.5	2.7	1.5	14
13	Lena River Delta, Russia	1	6.3	III	1.5	0.4	2.8	1.5	14
14	Ussuriysk, Russia	1	5.2	I	1.3	0.5	2.5	1.5	7
15	Vladivostok, Russia	1	5.5	I	1.2	0.5	2.4	1.6	10
16	Khabarovsk, Russia	1	5.2	I	1.1	0.5	2.0	1.5	11
17	Sakhalin, Russia	1	4.8	I	—	0.5	2.8	1.5	11
18	Sakhalin, Russia	1	4.7	I	1.2	0.5	2.7	1.5	9
19	Sakhalin, Russia	1	5.7	I	1.3	0.4	2.9	1.5	8
20	Sakhalin, Russia	1	5.9	I	1.3	0.4	2.8	1.5	10
21	Kamchatka, Russia	1	5.0	I	1.3	0.5	2.1	1.6	11
	Mean and SD		6.06 ±0.82		1.28 ±0.11	0.44 ±0.05	2.65 ±0.28	1.47 ±0.08	5.3 ±4.9
	Range		4.7–7.8		1.1–1.5	0.4–0.5	2.0–3.3	1.3–1.6	0–14

For caudal *serra*: I — reaches the CR base; II — slightly reduced (goes beyond the CR middle); III — strongly reduced (does not reach the CR middle).

Для каудальной серры: I — достигает основания CR; II — слабо редуцирована (заходит за середину CR); III — сильно редуцирована (не доходит до середины CR).

Bas outgrowths with dense long hairs. Inner coxal seta long and plumose. Spine of Exp1 without outer denticles. P2 (Fig. 4C) caudal surface of intercoxal plate with one median row of tiny denticles. P3 (Fig. 3D) caudal surface of intercoxal plate with three rows of spinules of different size (Fig. 3E).

P4 (Fig. 2E) caudal surface of intercoxal plate with three rows of setules: I — long hair-like; II — shorter hair-like; III — stronger, long and dense at sides, shorter rare at middle. Coxopodite ornamentation shown in Fig. 2E. Coxal spine/seta without gap, plumose with long thin setae proximally and gradually shortening strong spinules distally. P4 Enp3 L/W 2.6–2.7; inner spine 1.4 times longer than outer spine and 1.0–1.1 times as long as segment; distal setae reaching 2/3 of nearest spines. P4 Exp3 distal spine 1.0–1.1 times as long as segment and 1.6 times as long as adjacent spine. Distal setae of Exp and Enp modified — flattened, with hyaline membrane and shortened setules distally.

Reduced leg P5 (Fig. 2C) with elongated segment armed with strong inner spine twice longer than segment, about 3 times wider than median seta at base. Inner spine armed with large rough teeth (more rare on outer side of spine and more dense on inner side) and bearing spinules at base. Relative lengths of appendages (spine to outermost seta): 1.0/1.2–1.5/0.9–1.1.

Rudimentary leg P6 (Fig. 2D) placed laterally on genital double somite and represented by a small plate armed with two short naked spines and a plumose seta.

MALE. Not found in topotype locality.

VARIABILITY. The studied populations of *E. speratus* s.str. exhibited a broad range in the length-to-width ratio of the caudal rami (CR), from 4.7 to 7.8 (Table 3). Longer caudal rami were characteristic of cold-water populations at northern latitudes, while shorter rami were typical of warm-water populations.

The degree of reduction of the lateral *serra* varied considerably. It ranged from significant reduction, where the spinules did not extend beyond the mid-length of the caudal ramus (e.g., observed in specimens from Plön, Germany, with the *serra* occupying 13–23% of the lateral edge length, and from the Lena River Delta, Russia), to no observable reduction, where the *serra* extended to the base of the ramus (e.g., observed in all specimens from Sakhalin Island, Fig. 5). Occasionally, a gap in the *serra* was present. The typical parallel arrangement of the caudal rami was not always observed; divergence was common, particularly in specimens from Primorye and Sakhalin.

The ratio of the outermost spiniform seta length to caudal ramus length (OS/CR) was relatively constant, ranging narrowly from 0.4 to 0.5. The ratio of the lengths of the two middle caudal setae was typically 1.5–1.6 (rarely 1.3–1.4). The innermost caudal seta was invariably longer than the outermost spiniform seta, although their ratio varied from 1.1 to 1.5. The dorsal caudal seta was always shorter than the outermost seta.

The ratio of the lengths of the distal spines on the endopodite of the 4th swimming leg (P4 Enp3) was typically 1.4–1.6 (rarely 1.3), and the length-to-width ratio (L/W) of the segment itself varied noticeably from 2.0 to 3.3. The distal setae of P4 Enp3 reached from one-half to three-quarters of the length of the adjacent spine. In most, though not ubiquitous cases, the distal setae of Enp and Exp were modified; this modification was either significant (flattened, with a hyaline membrane and short setules) or slight (only shorter setules, without flattening and a membrane).

The presence of medial hairs on the first exopodite of the 4th swimming leg (P4 Exp1) varied as well. Their absence was more common in European populations, while their presence in abundance (10 or more) was frequently observed in eastern populations; however with overlap in number in specimens from both Europe and East. Variability in the ornamentation of the antennary basipodite (A2) was typically manifested in the different reduction of spine groups 7, 8, and 11. The size of the denticles on the maxillulary palp ranged from tiny (e.g., specimens from Lund) to rather large (e.g., specimens from Voronezh).

Key diagnostic features of *E. speratus* s.str. that distinguish it from other forms: relatively long caudal rami bearing lateral *serra* of small, dense teeth of subequal length; relatively short, thick outermost spine, the length of which relative to the length of the caudal rami does not exceed 0.5; A1 with a smooth or finely serrated hyaline plate; absence of hairs on the outer side of P4 Ex1; absence of setule groups N1 and 2 on the basipodite A2 and the presence of spine group 9 composed of rather long spinules; the presence of 1–2 rows of teeth on the palp of the maxillula (from tiny, barely distinguishable to rather large); the nature of the plumage of the coxal spine of P4; long thin hair-like setules along the distal edge of the intercoxal plate of P4; wide spine of P4 with large teeth.

MOLECULAR ANALYSIS. Genetic analysis of *Eucyclops* (*Speratocyclops*) *speratus* s.str. was conducted across its Palearctic range, from Sakhalin Island and Vladivostok through Lake Baikal to European locales near Volgograd, St. Petersburg, and Lake Geneva.

Mitochondrial DNA sequences (COI) revealed a split between Siberian and European populations, with 17.6% mean nucleotide divergence. At the same time, both major clades exhibited substantial internal heterogeneity, illustrating significant intraspecific polymorphism. Within Europe, the Volgograd and St. Petersburg populations differed by 3%. Within the Siberian clade, divergences ranged from 4.8 to 7.5%, with a specimen from Vladivostok showing the highest divergence. A comparison of populations from the Lena Delta and Sakhalin Island showed a COI divergence of 13.7%, while their nuclear (nITS) divergence was markedly lower at 1.3%, indicating long-term isolation and interpopulation genetic polymorphism.

Analysis of the 12S rRNA gene, used for broader comparison, showed lower overall divergence. Divergence between British [Hamrova *et al*., 2012] and Sakhalin populations was 4.4%, and between British and Lake Geneva populations was 3.6%. In contrast, the divergence between Lake Geneva and Sakhalin populations was minimal at 0.4%.

Nuclear (nITS) sequences from Baikal and European (St. Petersburg, Lake Geneva) populations also separated into European and Siberian subclades, with an 8.1% divergence between them. Divergence within the Siberian subclade was low (0.3–0.6%), and minimal within the European subclade.

Based on the results of joint 12S-CO1-nITS phylogenetic analysis of species within the subgenus *Eucyclops* (*Speratocyclops*), we note that all studied specimens of *Eucyclops* (*Speratocyclops*) *speratus* s.str. from various localities form a single monophyletic group represented by two clades (Fig. 6). Specimens from the Baikal vicinity (Putorana Plateau, referred to as *E. sibiricus* by Novikov *et al*., [2025]) grouped within the clade containing specimens from Sakhalin Island and Vladivostok, forming a subclade distinct from European representatives, indicating geographically determined population groupings. The nucleotide differences between two above mentioned forms across the gene regions 12S rRNA, COI, and nITS amounting to 26.5, 11.6, and 2.3%, respectively.

Eucyclops (*Denticyclops*) *taiwanensis* Sukhikh et Alekseev, 2015 forms a distinct clade including organisms from Taiwan and China according to BLAST identification in GenBank. The species yet remains closely related to the clade encompassing *E.* (*Sp.*) *speratus* populations with high Bootstrap support according to CO1 gene analysis (Fig. 1).

Two other species within the subgenus, *E.* (*Sp.*) *arcanus* Alekseev, 1990 (Lake Baikal vicinity) and *E.* (*Sp.*) *delongi* Alekseev *et al*., 2019 (Lena Delta), were clearly genetically differentiated from *E.* (*Sp.*) *speratus* s.str.

Extending these observations, we also present the first genetic data for *E.* (*Sp.*) *delongi* from the Lena Delta and Vaygach Island, and for *E.* (*Sp.*) *arcanus* from Siberia. The two species are morphologically and genetically similar, forming a large common clade on the joint gene tree with two corresponding subclades (see Fig. 6). The genetic divergence between them was 25.4% (12S rRNA), 2.9% (nITS), and 0.4% (18S rRNA).

E. (*Sp.*) *arcanus* itself comprised two lineages: one from the Baikal vicinity and Sakhalin Island, and another from the Lena Delta, with divergences of 13.6% (12S rRNA) and 1.7% (nITS). Preliminary morphological assessment suggests the Lena Delta specimens correspond to *E.* (*Sp.*) *arcanus arcticus*.

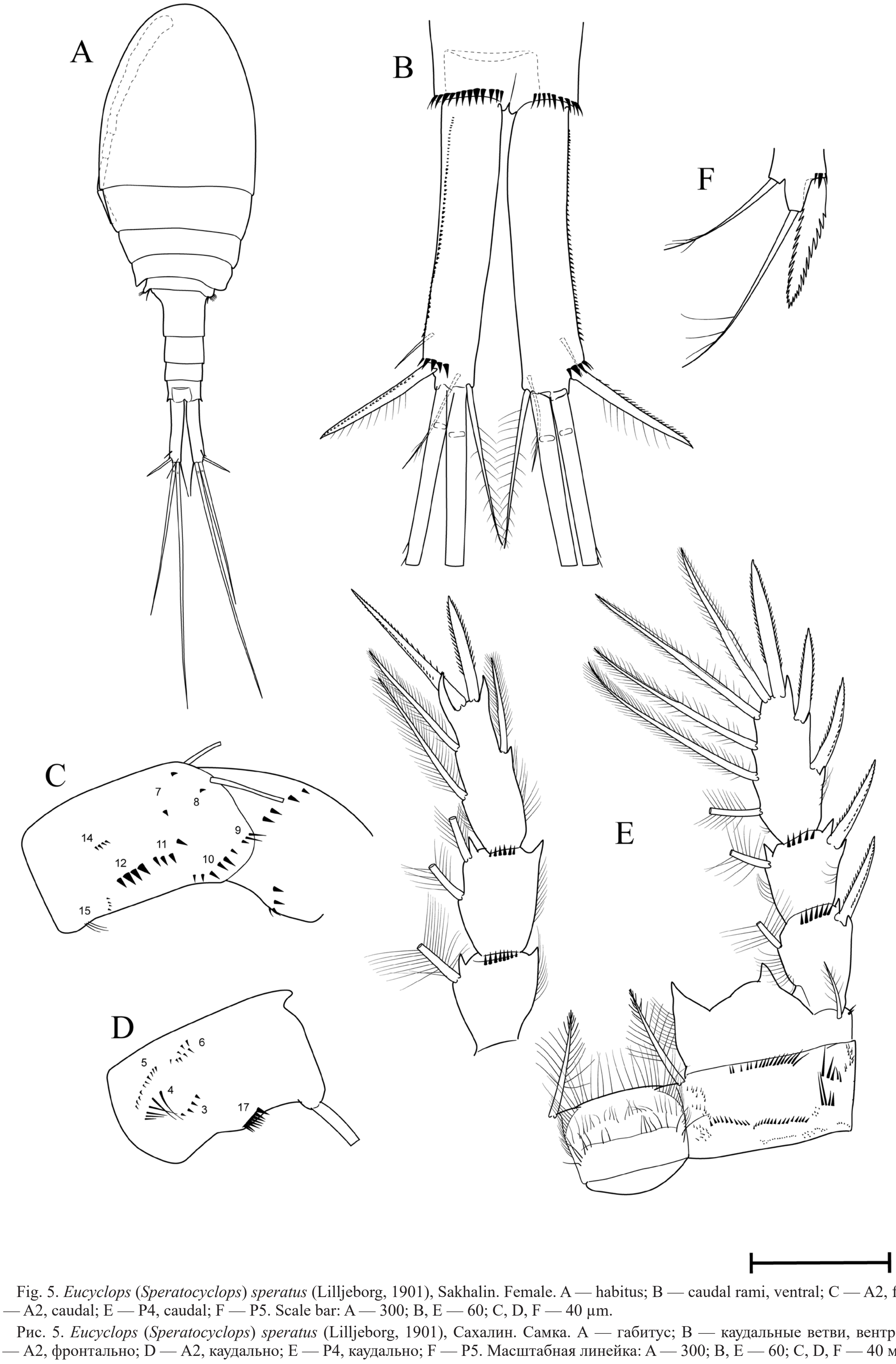

Fig. 5. *Eucyclops* (*Speratocyclops*) *speratus* (Lilljeborg, 1901), Sakhalin. Female. A — habitus; B — caudal rami, ventral; C — A2, frontal; D — A2, caudal; E — P4, caudal; F — P5. Scale bar: A — 300; B, E — 60; C, D, F — 40 μm.

Рис. 5. *Eucyclops* (*Speratocyclops*) *speratus* (Lilljeborg, 1901), Сахалин. Самка. A — габитус; B — каудальные ветви, вентрально; C — A2, фронтально; D — A2, каудально; E — P4, каудально; F — P5. Масштабная линейка: A — 300; B, E — 60; C, D, F — 40 мкм.

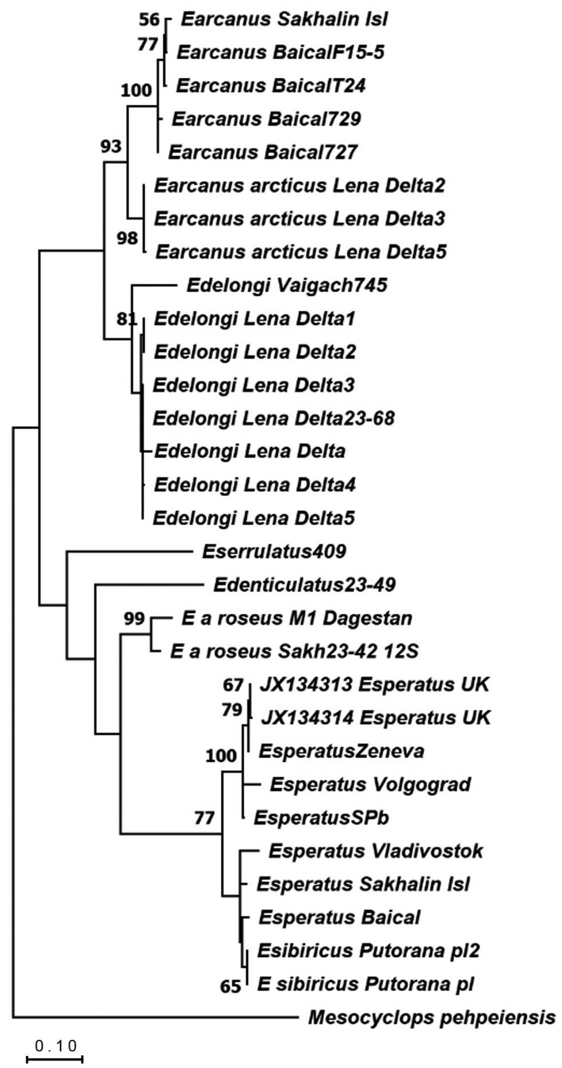

Fig.6. Maximum likelihood phylogram of *Eucyclops* (*Speratocyclops*) species on the concatenated 12SrRNA-CO1-nITS set using 30 sequences constructed with the GTR+G model. Node statistical support is reported as bootstrap values. Accession numbers are given before the species name.

Рис.6. Филогенетическое дерево для 30 последовательностей видов *Eucyclops* (*Speratocyclops*) построенное методом максимального правдоподобия с использованием объединенного набора генов 12SrRNA-CO1-nITS и модели GTR+G. Статистическая поддержка узлов отображается в виде значений бутстрепа. Регистрационные номера указаны перед названием вида.

The Lena Delta population of *E.* (*Sp.*) *delongi* was represented by four haplotypes, showing high haplotype diversity (Hd = 0.806 ± 0.089) and low nucleotide diversity (Pi = 0.02985). A specimen from Vaygach Island, confirmed as *E.* (*Sp.*) *delongi*, differed from the Lena Delta population by 9.7% (12S rRNA) and 3.3% (nITS), though it appeared on the common tree without a clear topological reference to the species.

DISCUSSION. This study provides the first comprehensive morphological re-description of *Eucyclops* (*Speratocyclops*) *speratus* based on topotype material from its type locality near Lund, Sweden. Our analysis of geographically dispersed populations across the Palearctic reveals that *E.* (*Speratocyclops*) *speratus* s.str. is a morphologically variable yet well-defined species. Despite considerable intraspecific polymorphism in mitochondrial and nuclear DNA, the morphological features examined exhibit continuous, overlapping gradients across the Palearctic.

This includes the number of medial hairs on the first exopodite of the fourth swimming leg (P4 Exp1), a character proposed as the primary diagnostic feature for *E. sibiricus*. As demonstrated in Table 3, this character is highly variable, ranging from 0 to 14 hairs across the species' range. Critically, this variation is present even within the topotype population from Sweden, where individuals were found with 5 and 7 hairs — values that close and overlap with those observed in populations from the Far East. Therefore, in strict morphological terms, *E. sibiricus* lacks fixed, reliable autapomorphies that would allow for its consistent diagnosis and identification separate from *E.* (*Sp.*) *speratus* s.str.

The International Code of Zoological Nomenclature requires a species to be based on a definable character basis. A formal description based solely on genetic distances, unsupported by consistent morphological or ecological distinctions, creates significant practical problems for identification and compromises the stability of the taxonomic framework. We therefore contend that the description of *E. sibiricus* was premature. Nevertheless, the detailed description provided by Novikov *et al*. [2025] offers valuable insight into the intraspecific polymorphism of *E.* (*Sp.*) *speratus*.

The observed genetic patterns across the Palearctic reveal a complex phylogeographic history for *Eucyclops* (*Spe.*) *speratus*. This pattern of high mitochondrial polymorphism alongside morphological stasis is a hallmark of significant intraspecific diversity, rather than evidence for cryptic speciation. The case of the Eastern Siberian population (described as *E. sibiricus*) is a prime example of this phenomenon. Despite its genetic distinction, it lacks diagnostic morphological autapomorphies and clusters within the monophyletic group of *E. speratus* in our analysis. This, in our view, illustrates a critical principle of integrative taxonomy: genetic distance alone, without corroborating evidence from morphology or other independent lines of data (e.g., hybridization experiments), is insufficient to justify the description of a new species. The description of *E. sibiricus* appears to be a result of this reverse process, creating an unnecessary junior synonym.

The morphological and genetic patterns observed in *E. speratus* invite a phylogeographic hypothesis. The distribution of variable characters appears loosely correlated with the maximum extent of Pleistocene glaciations in Europe. This may suggest a complex history of population fragmentation into glacial refugia, followed by post-glacial recolonization. Under this model, northern Europe, including Scandinavia, could have been recolonized from eastern refugia (e.g., in Siberia), explaining the morphological similarity between Swedish and Siberian populations. Central and southern Europe may have been repopulated from southern refugia (e.g., the Balkans or Iberia), as shown for other aquatic invertebrates [Csapó *et al*., 2020]. Contact zones between these recolonizing lineages would be expected to exhibit high variability and hybridization, potentially explaining the wide spectrum of character states we observe. This model, however, remains a testable hypothesis that requires validation through higher-density genetic sampling.

Minor differences are evident in the proportions of the caudal rami, which are often more divergent and somewhat shorter in eastern populations compared to those from Lund and St. Petersburg. However, similar variations occur in summer populations of *E.* (*Sp.*) *speratus* s.str. from central Russia (e.g., the Voronezh region) that are identical in other traits. These differences appear to be seasonal, a phenomenon well-documented in many cyclopoid species. *E.* (*Sp.*) *speratus* s.str. with shortened furcae was found in several isolated summer populations on Sakhalin Island, in a Kamchatka population from a warm bay with thermal vents, and on Hokkaido Island, Japan.

From a practical standpoint, the synonymization of *E. sibiricus* with *E. speratus* is necessary to restore a workable taxonomic system, while the observed variations are best interpreted as population-level polymorphism and perhaps ecophenotypic plasticity within a single, widely distributed species. Thus *Eucyclops* (*Speratocyclops*) *speratus* (Lilljeborg, 1901) is a single, morphologically variable species with a Palearctic distribution. The reported genetic differences do not currently warrant taxonomic recognition in the absence of diagnosable morphological support.

The genetic differences observed between European and Siberian populations are expected given their geographic distance. Similar interpopulation patterns have been described for other species within the genus and for representatives of other copepod families, such as harpacticoids and calanoids [Sukhikh *et al*., 2016; Kochanova *et al*., 2021; Fefilova *et al*., 2020], across the Palearctic region. Parallel findings for species groups in this area have been partially described in studies by Mayor *et al*. [2024] and Novikov *et al*. [2025].

In evolutionarily old taxa, the level of genetic divergence considered significant for taxonomy can vary considerably [Cádiz *et al*., 2018]. When assessing genetic data, it is crucial to remember that percentage divergence reflects the time since lineage separation and does not, by itself, demonstrate reproductive isolation. Perhaps the main value of this discussion is to highlight the need for a critical approach when using genetic distance as the primary criterion for taxonomy [Carstens *et al*., 2013].

DISTRIBUTION of *E.* (*Sp.*) *speratus.* Among the available materials, populations showing morphological features of *Eucyclops* (*Speratocyclops*) *speratus* were found in water bodies across the Palearctic. In Europe, the species ranges from Arkhangelsk in the north to France (Marseille) and Spain (Valencia) in the south. Records from Afghanistan, Iran, and especially India need confirmation. The northernmost record in Asia is Ob'-Taz Bay in Western Siberia, while the southern limit extends to the Fergana Valley (Bukhara) and the Aral Sea region (Kazakhstan). In Eastern Siberia, the species has been recorded in the Lena Delta (Ust-Lensky Nature Reserve) and on the Putorana Plateau [Novikov *et al*., 2025] in the north; Posolski Bay, Southern Baikal, and the Tola River (Mongolia) in the south. In the Far East, it was found on Kamchatka (Petropavlovsk-Kamchatsky vicinity), in Primorsky Krai (Vladivostok), on Sakhalin Island (see Fig.1). According to Ishida's data, the species is common on Hokkaido. At the southwestern edge of its range, the species represented by the subspecies *E.* (*Sp.*) *speratus azorensis* (Defaye et Dussart, 1991) (Azores, Northern Africa — Holynska *et al*., [2021]).

Based on these observations, *E.* (*Sp.*) *speratus* along with *E.* (*E.*) *serrulatus* s.lat., appears to be widely distributed within the Palearctic. Monchenko's [1974] view of the species as a cosmopolitan is clearly exaggerated. All previous reports of *E.* (*Sp.*) *speratus* occurrence outside this region are likely based on unclear taxonomic criteria and require verification.

On the other hand, during recent revisions of species previously considered cosmopolitan, Western researchers questioned its presence in the Far East of Asia. Ishida & Hiruta [1999] first reliably recorded the species in Lake Harutori in Kushiro, and later confirmed its distribution in Japanese waterbodies including Lake Akan, wetlands in Kushiro and Tomakomai, and rivers near Iwanai. The southernmost known record so far is a tributary of the Chigusa River in Mikazuki town, Hyogo Prefecture. In all these locations, as well as on Sakhalin Island, *E.* (*Sp.*) *speratus* s.lat. is represented by a form with shortened furcae.

With the exception of these questionable records, most representatives of the subgenus *Eucyclops* (*Speratocyclops*) are currently known from the Palearctic, with the highest taxonomical diversity found in North-Eastern Asia. The status of *E. troposperatus*, described from Java (Indonesia) — a region with centuries of maritime trade with Europe — also remains uncertain and warrants validation including molecular genetic analysis. All reports of the subgenus occurring south of the Himalayas require re-evaluation. This suggests that the possible origin of both the type species and the subgenus lies in Western Laurasia, after separation from the North American plate approximately 50 million years ago.

The morphological revision of the nominate species revealed a widespread occurrence of individuals with short caudal rami (likely summer forms) in natural populations of *E.* (*Sp.*) *speratus*, which necessitates some adjustments to the recently published identification key for this subgenus [Alekseev, 2024]. Hereafter an updated key that solves the problem is provided.

IDENTIFICATION KEY FOR *EUCYCLOPS* (*SPERATOCYCLOPS*) TAXA

1. CR with very long outermost spiniform seta, ~ 0.7–0.8 times as long as CR length 2

– CR with shorter outermost spiniform seta, < 0.7 times as long as CR length.. 4

2. P4 Exp3 distal spine ~ 1.2 times as long as nearest proximal spine........................... *E.* (*Sp.*) *dumonti* Alekseev, 2000
[Eastern Siberia, Mongolia, China, Thailand]

– P4 Exp3 distal spine ~ 1.7 times as long as nearest proximal spine.. 3

3. P4 Enp3 distal setae rather short, reaching middle of nearest spines; P4 Exp3 distal spine slightly longer than segment and about as long as distal seta......................................
.... *E.* (*Sp.*) *arcanus arcanus* Alekseev, 1990
[Central and Eastern Siberia, Kamchatka]

– P4 Enp3 setae longer; P4 Exp3 distal spine shorter than segment and almost twice shorter than distal seta ....
.... *E.* (*Sp.*) *arcanus arcticus* Alekseev, 2022
[The River Lena delta, tundra lakelets in Northern Europe, Arctic zone in Palearctic?]

4. CR with innermost seta shorter than outermost spiniform seta; P4 coxal seta with short setules with gap on outer side..
......*E.* (*Sp.*) *leschermoutouae* Alekseev et Defaye, 2004
[well in Balearic Islands, Europe]

– CR with innermost seta subequal or longer than outermost seta; P4 coxal seta without gap.................................... 5

5. P4 intercoxal plate distal row with rather short strong dense spinules ....
..*E.* (*Sp.*) *delongi* Alekseev, Abramova et Chaban, 2019
[East Siberia]

– P4 intercoxal plate distal row with thin hair-setules........ 6

6. P4 Exp3 distal spine ~ 1.3 times as long as nearest proximal spine.. 7

– P4 Exp3 distal spine more than 1.4 times longer than nearest proximal spine 8

7. P4 Exp3 distal spine ~ 0.6 times as long as segment; P4 coxal seta on inner margin with long setulae proximally and shorter spinules distally, outer margin with short setules
......*E.* (*Sp.*) *speratus azorensis* Defaye et Dussart, 1991
[Azores, Northern Africa]

– P4 Exp3 distal spine ~ 0.8 times as long as segment; P4 coxal seta homogenously plumose with dense thin hairs.........
.... *E.* (*Sp.*) *troposperatus* Alekseev et Yusoff, 2013
[Java, Indonesia]

8. P4 IntCox distal margin with rare short hairs; P4 Exp3 distal spine ~ 0.7 times as long as segment............................. .... *E.* (*Sp.*) *productus* Kiefer, 1939 [Tibetan Plateau, Asia]
– P4 IntCox distal margin with long dense hairs; P4 Exp3 distal spine > 0.7 times as long as segment........................... 9
9. P5 with thin, but long inner spine; P4 Exp3 distal spine about 0.8–0.9 times as long as segment; maxillular palp without denticles 10
– P5 with wide inner spine; P4 Exp3 distal spine about 0.9–1.1 as long as segment; maxillular palp with few denticles11
10. Dorsal caudal seta longer than outermost seta............... ....*E.* (*Sp.*) *biwensis biwensis* Ishida, 1998 [Lake Biwa, Japan]
– Dorsal caudal seta shorter than outermost seta................. .... *E.* (*Sp.*) *biwensis ohtakai* Ishida, 2000 [Japan].
11. Caudal rami long, L/W ratio about 5.5 and more .... *E.* (*Sp.*) *speratus speratus* (Lilljeborg, 1901) [Palearctic, wintertime and high altitude populations]
– CR shorter, with L/W ratio < 5.5 .... *E.* (*Sp.*) *speratus speratus* (Lilljeborg, 1901) [Palearctic, summertime low altitude populations]

Conclusion

A detailed redescription of females of *Eucyclops* (*Speratocyclops*) *speratus* s.str. from the type locality provides a morphological basis for distinguishing this species from other members of the subgenus, using a combination of classical and micro-morphological features of limb armature and ornamentation. This work provides a foundation for further revision of the subgenus *Speratocyclops*.

Contrary to its previous status as a cosmopolitan species, *E.* (*Sp.*) *speratus* s. lat. is confined to the Palearctic. It is currently represented by two subspecies: the nominate form, *E.* (*Sp.*) *speratus speratus*, whose range spans the Eurasian Palearctic, and *E.* (*Sp.*) *speratus azorensis*, found on the Azores islands and along the Mediterranean coast of North Africa.

Our analysis of 21 populations across the Palearctic reveals that all proposed morphological characters for distinguishing *E. sibiricus* fall within the continuous range of variation displayed by topotype specimens of *E.* (*Sp.*) *speratus* s.str. In the absence of fixed, reliable morphological autapomorphies, and in accordance with the principle of diagnostic species delimitation, we synonymize *Eucyclops sibiricus* Novikov *et al*., 2025 syn.n. with *Eucyclops* (*Speratocyclops*) *speratus* (Lilljeborg, 1901).

The phylogeographic pattern within its range suggests a complex postglacial recolonization history. Northern Europe, including Scandinavia and the British Isles, was likely recolonized by lineages from eastern refugia (e.g., Siberia), while central and southern Europe were repopulated by lineages from southern refugia (e.g., the Balkans, Iberia). This hypothesis is supported by the observed morphological and genetic polymorphism across the species' range, but requires validation through higher-density genetic sampling.

The distribution of the entire subgenus *Speratocyclops* appears to be limited to the Palearctic. Historical records of *E.* (*Sp.*) *speratus* from the Americas, Central, and Southern Africa require confirmation through modern taxonomic methods; they likely represent misidentifications of other species or localized anthropogenic introductions, similar to those documented for *E.* (*E.*) *serrulatus*.

The center of biodiversity for the subgenus is considered to be in Eastern Siberia (the Beringian region), where approximately half of its valid taxa were first described.

The updated identification key for the subgenus incorporates insights into intraspecific and seasonal variability of key taxonomic characters, enabling more reliable differentiation among all currently recognized taxa.

Compliance with ethical standards

Conflict of interest: The authors declare that they have no conflict of interest.

Ethical approval: No ethical issues were raised during our research.

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