

TAXONOMIC DIFFERENTIATION AND WORLD GEOGRAPHICAL
DISTRIBUTION OF THE *EUCYCLOPS SERRULATUS* GROUP
(COPEPODA, CYCLOPIDAE, EUCYCLOPINAЕ)

BY

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ABSTRACT

The *serrulatus*-group (genus *Eucyclops*, Eucyclopinae, Cyclopidae), which includes species having a 12-segmented antennule possessing a smooth hyaline membrane on its distal three segments, caudal rami of moderate length (l/w ratio 3.5-7), and a strong inner spine on P5, is here defined and described. The species of this group also share a particular set of microcharacters on the coxopodite of P4 and on the basipodite of the antenna, which in particular includes one or two groups of fine setae (= hair-like setae) on the distal part of the caudal side. A simple numerical mapping of these microcharacters is proposed. Examination of *Eucyclops* populations collected from many locations all over the world that were identified as *Eucyclops* cf. *serrulatus* provided a set of morphological variations that allowed us to define the morphological characteristics within the *serrulatus*-group. Based on this definition of the species group, we give the composition of the *E. serrulatus* group, currently represented by 17 species and subspecies. The description of some taxa of this group is completed in particular with the microcharacters of the antennary basipodite and the P4 coxopodite. The taxonomic status of some other taxa, until now related to *E. serrulatus*, is changed as: *E. agiloides roseus* Ishida, 1997 (n. comb.); *E. macrurus baikalocorrepus* Mazepova, 1955 (n. comb.); and a key to the species of the *Eucyclops serrulatus* group is provided.

From our observations, we were able to establish that the distribution of *Eucyclops serrulatus* (Fischer, 1851) sensu stricto is restricted to the Palaearctic region. Previous data on geographical distribution of the species outside this area are critically analysed. It is hypothesized that records of *E. serrulatus* from Japan, Australia, North America, and other zoogeographical zones, could be a result of recent invasions, possibly via human activities in relation to ship transport.

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RÉSUMÉ

Le groupe *serrulatus* (genre *Eucyclops*, Eucyclopinae, Cyclopidae), qui réunit les espèces ayant une antennule à 12 segments dont les trois derniers sont pourvus d'une membrane hyaline lisse, des branches furcales de longueur modérée (rapport L/l 3,5-7), et une forte épine interne à la P5, est ici défini et décrit. Les espèces de ce groupe partagent également un ensemble particulier de microcaractères situés sur le coxopodite de P4 et sur le basipodite de l'antenne ; ce dernier, notamment, présente un ou deux groupes de longues soies fines insérées à la partie distale de la face caudale. Une cartographie numérique simple de ces microcaractères est proposée. L'examen de populations d'*Eucyclops* collectées dans différentes parties du monde et identifiées comme *Eucyclops* cf. *serrulatus* a démontré un ensemble de variations morphologiques qui ont permis de définir les caractéristiques morphologiques du groupe *serrulatus*. À partir de cette définition, nous avons pu établir la composition en espèces du groupe *E. serrulatus*, aujourd'hui représenté par 17 espèces et sous-espèces. La description de certains taxons est précisée en particulier en ce qui concerne les microcaractères du basipodite de l'antenne et du coxopodite de la P4. Le statut taxonomique de certains taxons, jusqu'à présent rattachés à *E. serrulatus* a été modifié ; c'est le cas de *E. agiloides roseus* Ishida, 1997 (n. comb.) ; *E. macrurus baikalocorrepus* Mazepova, 1955 (n. comb.) ; une clé d'identification des espèces du groupe *serrulatus* est également proposée.

À partir de ces observations, nous avons pu mettre en évidence que la répartition géographique de *Eucyclops serrulatus* (Fischer, 1851) sensu stricto est restreinte à la région Paléarctique. Les données de répartition des espèces du groupe jusqu'à présent signalées en dehors de cette région sont analysées. L'hypothèse est émise que la présence de *E. serrulatus* au Japon, en Australie, en Amérique du Nord et dans d'autres régions du monde pourrait être le résultat d'introductions récentes, peut-être liées aux activités humaines en relation avec les transports maritimes.

INTRODUCTION

The genus *Eucyclops* Claus, 1893 (Cyclopidae, Eucyclopinae) currently contains 108 species and subspecies (Dussart & Defaye, 2006, updated by D. Defaye) many of which have been insufficiently described according to current standards, and the genus itself is in need of revision. The type species of the genus, *E. serrulatus* (Fischer, 1851) was described from the vicinity of St. Petersburg and reported afterwards many times from all around the world (see Dussart & Defaye, 2006). Its cosmopolitan status remained unchallenged until some taxa that superficially looked like *E. serrulatus* were separated from the nominal species and redefined as new species (Dussart, 1986; Alekseev, 1990, 2000, 2008, 2010; Reid, 1992; Ishida, 1997, 1998, 2000, 2001, 2003). As a consequence, it is clear now that the former allegedly cosmopolitan *E. serrulatus* in fact represents a group of closely related species, some of them possibly being cryptic taxa in need to be fully described. The superspecies name “*serrulatus*-group” or “*serrulatus*-like species” was

introduced by Kiefer (1928) to group the tropical species closely related to the type species and possessing a 12-segmented antennule with a smooth hyaline membrane on the distal three segments, and a strong inner spine on P5. This species group could be the result of evolution of an ancestral form in geographically isolated, and as biotope/niche rather specific, sites (Alekseev et al., 2006). A better definition of the group thus will help to revise the whole genus.

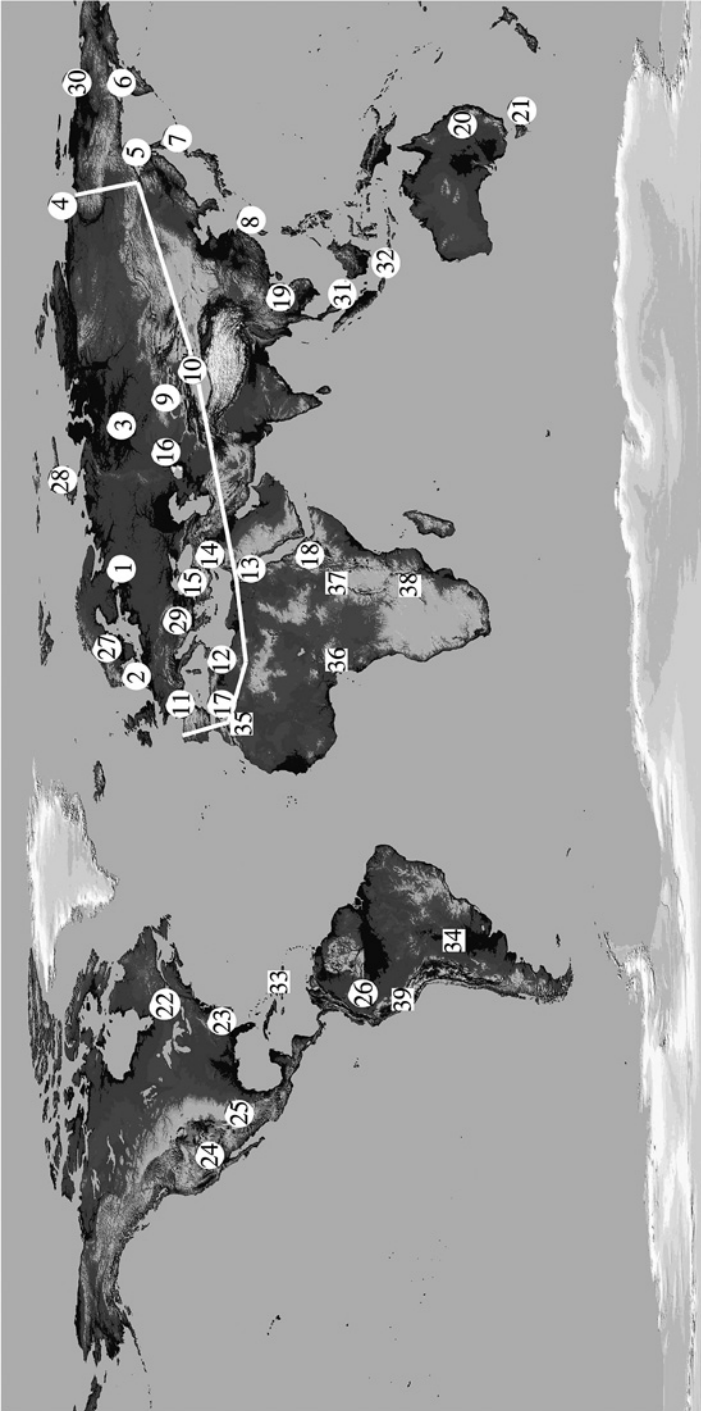
Eucyclops serrulatus (Fischer, 1851) was recently redescribed from specimens collected in the St. Petersburg area, Russia (type locality), and the classical description of the external body morphology was combined with pore signature mapping and with the nuclear small subunit (18S) ribosomal genes (Alekseev et al., 2006). *E. serrulatus* was compared in detail with some closely related species (sometimes synonymous taxa) reported from Asia, Europe, North Africa, and North America: *E. dumonti* Alekseev, 2000, *E. hadjebensis* (Kiefer, 1926), *E. speratus* Lilljeborg, 1901, *E. turcomanus* Lindberg, 1959, and *E. pectinifer* (Cragin, 1883).

In parallel, the late Dr. T. Ishida (Japan) compared *E. serrulatus* specimens collected from the type locality to the Japanese *Eucyclops* identified as *serrulatus* or cf. *serrulatus*. He could clearly show the presence of the type species in different localities (generally cold waters) from Honshu, Hokkaido, and Okinawa Island (Ishida, 2003) among the eight *Eucyclops* species at that time identified as present in Japan (*Eucyclops biwensis* Ishida, 1998, *E. euacanthus* (Sars, 1909), *E. macruroides* (Lilljeborg, 1901), *E. ohtakai* Ishida, 2000, *E. pacificus* Ishida, 2000, *E. serrulatus* (Fischer, 1851), *E. speratus* (Lilljeborg, 1901), *E. tsushimensis* Ishida, 2001).

Other new species of *Eucyclops* from Central Asia and Spain, were recently distinguished on the basis of microcharacters while only *E. serrulatus* had previously been reported from those regions (Alekseev, 2000, 2008). These new data on the systematics of *Eucyclops* led us to analyse the taxonomic differences and the geographical distribution of the *Eucyclops* species within the *serrulatus*-group. The major target of this paper, therefore, is to define the group more accurately, using a set of characters which will hopefully be useful to better describe the species within the genus *Eucyclops*.

MATERIAL

For the purpose of morphological research on and description of the type species of the *serrulatus*-group, we collected *Eucyclops serrulatus* from terra



typica in the Orlov Pond (type of water body) Town Peterhoff, 18 km west of St. Petersburg, Russia (60°00'N 30°55'E), in May–June 1999. The material was deposited as the dissected female neotype, catalogue number 55032, a male allotype (55033), and alcohol-preserved material under N 96-03-16 in the Federal Collection, Zoological Institute of the Russian Academy of Sciences, St. Petersburg. Twenty female paratypes, ethanol preserved, were deposited in the copepod collection (MNHN-Cp6029) of the Muséum national d'Histoire naturelle, Paris.

Specimens of *E. serrulatus* from two other distant sites in Central Europe (Ghent, Belgium, 51°05'N 31°25'E) and in Siberia (vicinity of Tumen, 57°15'N 66°05'E) were used for comparison with the type population. These three populations of *E. serrulatus* were found to hybridize in experimental conditions involving pairwise trials (Alekseev et al., 2006).

To evaluate the distribution of *E. serrulatus* around the world, extensive material (i.e., samples containing *Eucyclops* species) of varied geographical origin was examined (fig. 1).

Morphological characters were also studied in specimens from Kiefer's collection, kept in Karlsruhe, Germany. More than 50 *Eucyclops* species and

Fig. 1. Mapping of sampling sites for species of the *Eucyclops serrulatus* (Fischer, 1851) species group (in parentheses, name of collector). 1, pond in St. Petersburg, Russia, type locality; 2, pond in Ghent, Belgium; 3, pond in Tumen, western Siberia, Russia; 4, the Lena River delta, north-western Siberia, Russia (Dr. E. Abramova, donation); 5, Khanka Lake, Russia-China; 6, Kronozkoe Lake, Kamchatka peninsula, Russia; 7, lakes and rivers, Hokkaido Island, Japan (Dr. T. Ishida donation); 8, pond in Taipei, Taiwan; 9, Lake Baikal and nearest lakes and rivers, Russia; 10, lakes and rivers, Mongolia; 11, Albufera lake, Valencia, Spain; 12, pond and springs, Tunis (Dr. H. Dumont donation); 13, the Nile River near Cairo, Egypt; 14, ponds and springs, Israel (Dr. B. Dussart donation); 15, river in Antalya, Turkey (Dr. C. Fernando donation); 16, pond near Aral Lake, Uzbekistan; 17, spring in the Atlas Mountains, Morocco (from Dr. F. Kiefer collection); 18, the Nile River, upstream, Ethiopia; 19, springs, ponds and rivers in Nam-Nao National Park, Thailand; 20, University pond in Cleveland, Australia (Dr. D. Lajus donation); 21, lakes, ponds and rivers, Central and Northern Tasmania; 22, Lake Ontario, Canada; 23, pond in Florida, USA (Dr. B. Kuperman donation); 24, ponds near San-Diego, California, U.S.A. (Dr. B. Kuperman donation); 25, lakes in Mexico, Mexico; 26, ponds, small rivers in Quito, Ecuador; 27, pond in Oslo, Norway; 28, lakes in Novaya Zemlya, Russia (Dr. V. Bulion donation); 29, lakes in caves near Ljubljana, Slovenia (Dr. A. Brancelj donation); 30, Tchaun River, coast of East-Siberian Sea, Russia (Dr. E. Strelezkaja donation); 31, small lake in city park of Kuala-Lumpur, Malaysia; 32, pond in Jakarta, Indonesia; 33, Laguna Rincon, Haiti, F. Kiefer collection; 34, San Bernardino, Paraguay, F. Kiefer collection; 35, Saba be Rabat, Morocco, F. Kiefer collection; 36, Akonolinga, Jounde and volcanic lake, Cameroun, F. Kiefer collection; 37, Kinangop, Kenya, F. Kiefer collection; 38, Lake Malawi, F. Kiefer collection; 39, Lake Titicaca, Peru, F. Kiefer collection. Square indicates samples from Prof. Kiefer's collection in Karlsruhe, Germany. The area north of the marked line is the area with confirmed records of *E. serrulatus*.

TABLE I
Eucyclops specimens from Kiefer's collection used in this study

Species	Slide reference number	Locality as indicated on slide labels
<i>E. agiloides</i> (Sars, 1909)	852	Vulkensee, Cameroon
<i>E. bondi</i> Kiefer, 1934	2394	Laguna Rincon, Haiti
<i>E. delachauxi</i> (Kiefer, 1925)	248, 249, 253	Huaron, Peru, Lake Naticocha, Peru
<i>E. glaber</i> Kiefer, 1935	2252	Kinangop, Kenya
<i>E. neumani titicacae</i> Kiefer, 1957	5754	Lake Titicaca, Peru
<i>E. prionophorus</i> Kiefer, 1931	3103, 3104	San Bernadino, Paraguay
<i>E. vandouwei</i> (Brehm, 1909)	517	Akonolinga, Yaoundé, Cameroon
<i>E. serrulatus</i> (Fischer, 1851)	840	Sabe be Rabat, Morocco
<i>E. s. hadjebensis</i> (Kiefer, 1926)	835	Oued Guigon, Morocco

more than 200 slides were there examined, including the holotypes of 20 *Eucyclops* species described by Kiefer himself (Franke, 1989). Among 51 *Eucyclops* species from Kiefer's collection only 9 taxa (20%) belong to the *serrulatus*-group. All these *serrulatus*-group species were studied and are presented here in detail (table I).

METHODS

Three to five females of each population collected in the field (see list in legend of fig. 1) were dissected and placed on slides in a drop of lactic acid or in glycerol for observation under a microscope equipped with Nomarski optics and 1000× maximal magnification (Zeiss IMAGER A1). Drawings were made at 400-1000× with a Leitz Medilux compound microscope equipped with a camera lucida. The observation of some fine details was performed with a scanning electron microscope. Digital photographs were taken using a compound microscope Zeiss IMAGER A1 fitted with a Canon photo camera, at 12 Mp resolution. For micropatterns on both sides of the antennary basipodite we applied the numerical scheme based on an accumulation in one picture of most micropatterns of these appendages known in cyclopids (fig. 2) (Alekseev et al., 2006). For mapping rows of spinules and setules on the coxopodite and intercoxal plate of P4, we followed Einsle's (1985) method, slightly modified (fig. 2) (Alekseev et al., 2006).

The following characters (with abbreviations used) were examined in most specimens studied:

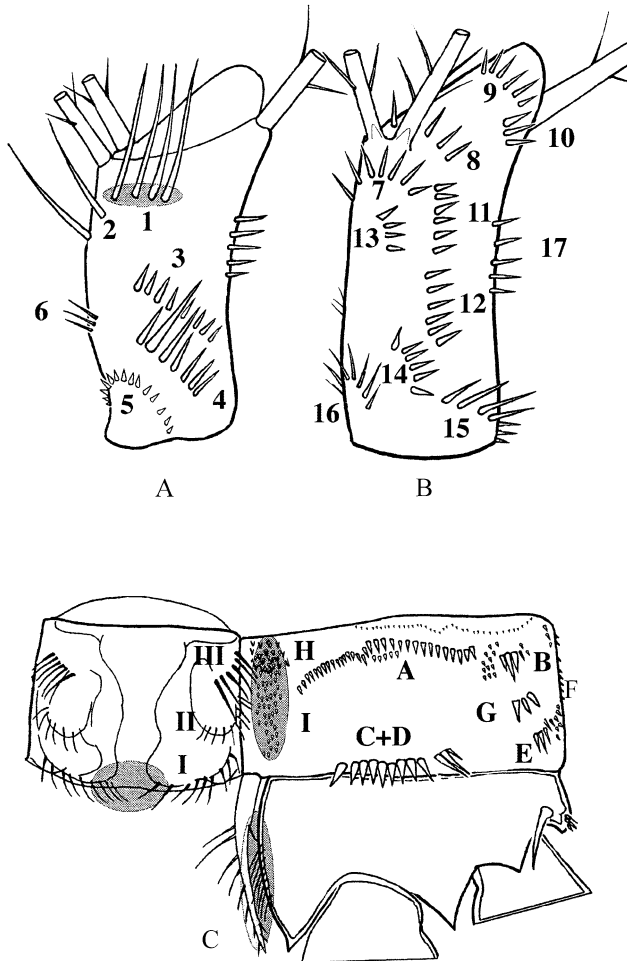


Fig. 2. Mapping of microcharacters in *Eucyclops*. A, basipodite of antenna, caudal side; B, same, frontal side; C, swimming leg 4, caudal side of coxopodite and intercoxal plate.

1. Antennule (A1): number of segments, presence and structure of hyaline membranes on distal three segments;
2. Antenna (A2): micropatterns on frontal and caudal sides of basipodite (fig. 2A, B);
3. Swimming legs 1-4 (P1-P4): spine formula of distal segments of exopodites (Exp); for exopodite and endopodite (Enp) of P4: relative lengths of distal segment, spines, and setae; micropatterns of the caudal side of the coxopodite of P4, setation of the coxopodal spines, presence of fine setae on intercoxal plate, and inner outgrowth on basipodite of P4 (fig. 2C);

4. Legs 5-6 (P5–P6): relative length of the inner spine, the segment itself, and two setae;
5. Genital double somite (GDS): length/width ratio; shape of the seminal receptacle;
6. Last urosomite: shape of anal operculum; spinules on both sides of proximal edge;
7. Caudal rami: length/width ratio; presence of fine setae and denticles on surface, relative length of lateral row of spinules (= serra according to Dussart & Defaye's (2005) definition and their size; length ratios of the caudal setae. Caudal setae named as follows: II — anterolateral (lateral) caudal seta; III — posterolateral (outermost) caudal seta; IV — outer terminal (terminal median external) caudal seta; V — inner terminal (terminal median internal) caudal seta; VI — terminal accessory (innermost) caudal seta; VII — dorsal seta. Numerical system for the setae from Huys & Boxshall (1991) and terminology after Dussart & Defaye (1995).

RESULTS

Here below, we present a morphological description of the *serrulatus* species group, based on the diagnosis of the type species for this group, *Eucyclops serrulatus* (Fischer, 1851) s.s. For this purpose, we used the data already described in Alekseev et al. (2006). These authors gave a full description of this species, including some results on hybridizations between different morphological types and distant populations, an analysis of pore signatures, and an analysis of the nucleotide sequence in the small subunit 18-S ribosomal RNA.

Description of species of the *serrulatus*-group (based on *Eucyclops serrulatus* morphology)

In **bold face**, we indicate the more important characters that distinguish the species of the *serrulatus*-group from the other *Eucyclops* species with, in addition, some remarks in parentheses on their variation among those other species.

Female. — Body colour rusty brown, rarely dark brown or greyish. Full length without caudal seta from 800 to 1700 μm . Cephalosome as long as wide, maximum width close to posterior margin. Last somite of prosome with lateral group of short setules. Genital double somite 0.7-1.2 times as long as

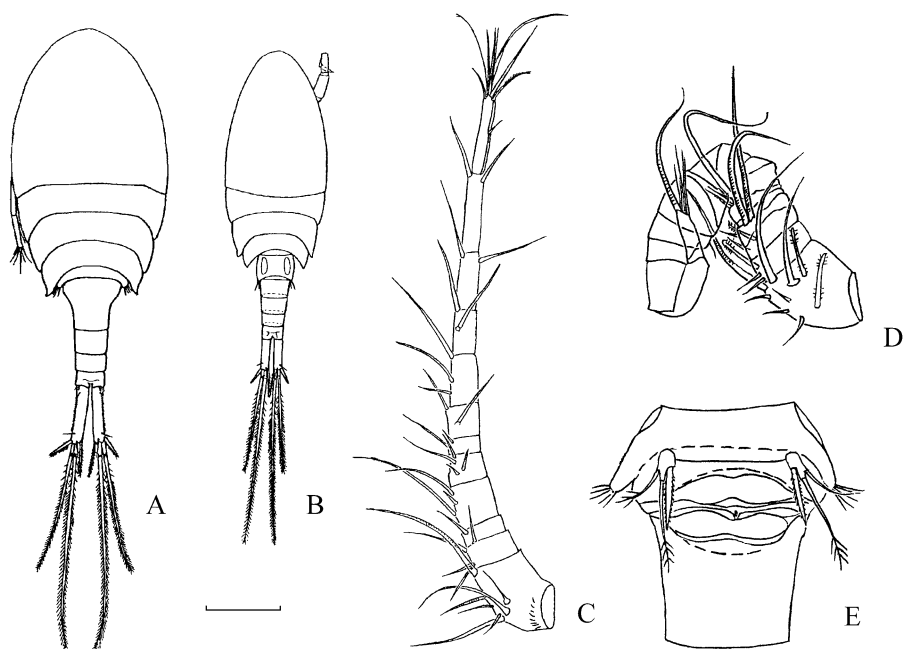


Fig. 3. *Eucyclops serrulatus* (Fischer, 1851) from the type locality. A, female, dorsal view; B, male, dorsal view; C, female antennule; D, male antennule; E, female genital double somite. Scales: A, B = 75 μm ; C = 175 μm ; D, E = 150 μm .

wide, with seminal receptacle as in fig. 3E. Caudal rami 3.5-7 times as long as wide, with longitudinal row of spinules along most of outer edge of each ramus, but partly reduced in some taxa inhabiting subterranean or spring environments (*E. romaniensis*, *E. serrulatus hadjebensis*) and never with hair-like setae or denticles on dorsal or ventral surfaces. Six setae inserted on distal part of ramus. The length proportions of the 4 terminal setae, beginning from III to VI, are, however, variable and must be used with caution for species differentiation, they are given for general information only. Dorsal seta about half the length of seta VI (in *E. pectinifer* less than half), covered with long setules on both sides; seta III: a spiny seta with dense setules on both sides, but longer on inner margin, about 3 times as long as dorsal seta yet distinctly shorter than seta VI (in *E. romaniensis* the opposite is found).

Antennule 12-segmented, with smooth membrane along 3 distalmost segments. The width of membrane varies from narrow to wide (fig. 3C). Setation of antennular segments, beginning from first, 8/4/2/6/4/2/2/3/2/3/8. First segment with curved row of spinules at its base; outermost spinules the longest.

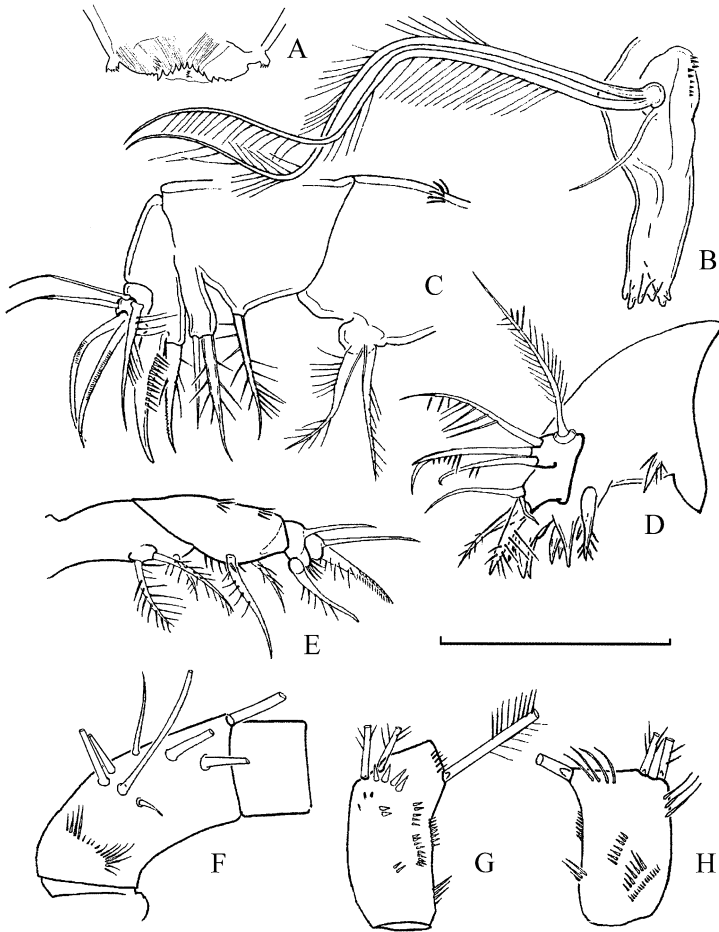


Fig. 4. *E. serrulatus* (Fischer, 1851), type locality, female, mouth appendages. A, labrum plate; B, mandible; C, maxilla; D, maxillule; E, maxilliped; F, antennule, first segment; G, basipodite of antenna, frontal side; H, basipodite of antenna, caudal side. Scale = 35 μm .

Antenna composed of 1-segmented basipodite bearing exopodite represented by a long, barbed seta and the two usual apical lateral setae, and a 3-segmented endopodite (second segment bearing nine setae). **Frontal side of basipodite A2: apical group N1 with 2-6 long setules and group N2 with variable number of the same setules (0-4) subdistally along inner margin (in some species only one of these groups can be found (in *E. pectinifer* (Cragin, 1883) the hair-like setules are replaced by strong but very long denticles); with three oblique and parallel rows of spinules (N3-5) and 2 groups of marginal spinules (N17) and (N15) (fig. 4H).**

Caudal side of basipodite A2: 3-5 strong spinules, of different length among species, subdistally (N8), groups 9 and 10 sometimes united in one row; a long row of 10-17 spinules medially (N11 + N12); N13 and N14 represented by 2 isolated groups of tiny spinules; groups 15 and 17 usually composed of long spinules and group 16 of short or even tiny denticles (fig. 4G). For numerical variation of microcharacters of antennary basipodite among species in *serrulatus* group, see table II.

Labrum (fig. 3A) with 8-12 large central teeth and with 2 groups of small teeth on lateral outgrowths. Gnathobase of mandible (fig. 4B) with 6 teeth, rudiment of endopodal segment with 2 long plumose setae, and 1 short naked seta. Maxillule (fig. 4D): praecoxal arthrite with 6 strong teeth and 2 strong setae; palp with 7 setae, surface without ornamentation.

Maxilla (fig. 4C), 4-segmented, praecoxopodite with 2 strong median setae; syncoxopodite with 2 endites; proximal endite with 1, distal endite with 2 setae; basal endite with 2 strong spines and 1 small seta near site of fusion of 2-segmented endopodite: the first segment with strong spine and slender seta; second segment with 3 elements in all. Maxilliped (fig. 4E) 4-segmented, syncoxopodite with 2 strong setae medially and 1 small seta distally. Basipodite with 2 setae of different length and ornamented with strong spinules close to proximal setae and with 2 sets of spinules medially and subdistally along outer margin. First and second endopodal segments with 2 elements each.

Swimming legs 1-4 (fig. 5) with 3-segmented rami, spinal (Roman numerals) and setal (Arabic numerals) formula as follows:

	Coxopodite	Basipodite	Exopodite	Endopodite
Leg 1	0-I	1-I	I-1; I-1; III-5	0-1; 0-2; 1,I,4
Leg 2	0-I	1-0	I-1; I-1; IV-5	0-1; 0-2; 1,I,4
Leg 3	0-I	1-0	I-1; I-1; IV-5	0-1; 0-2; 1,I,4
Leg 4	0-I	1-0	I-1; I-1; III-5	0-1; 0-2; 1,II,2

Setae on all segments of P1–P4 uniformly seta-like, not constricted, flanked with series of long setules on both edges. The setules at least twice as long as the distance between them. Inner edge of basipodite of P1–P4 usually with group of long setules. Intercoxal plate of P1 (fig. 5A) with two protuberances, a transversal row of small denticles around midway, and two groups of thin spinules on main body of protuberances, not extending beyond their edges. Intercoxal plates of P2–P3 also with protuberances on free edge and with groups of setules as shown in fig. 5B, C. Distal segment of Enp P4 elongated, 2.2-2.8 times as long as wide, with 2 strong apical spines; inner spine 1.2-1.5 times as long as outer spine. **Coxopodite of P4 (fig. 5D) with strong inner**

TABLE II

Pattern of microcharacters of the antennary basipodite in the studied species of the *Eucyclops serrulatus* (Fischer) group. Latin names in **bold** correspond to specimens from Kiefer's collection. Numeration of patterns corresponds to fig. 2A–B; Roman numerals, hairs; Arabic numerals, denticles; –, character missing; ?, structure not observed

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
<i>E. serrulatus</i> A	VI–VIII	I–II	8-9	7-8	12-16	1-4	4-5	–	5-8	–	5-6	6-8	–	5-8	4-5	–	10-13
type locality																	
<i>E. serrulatus</i> B	V–IX	III–IV	7	9	13	4-5	3-4	–	5-6	–	5-6	7	2	3-4	4-5	–	9-10
type locality																	
<i>E. serrulatus</i> A	IV	I–II	6-10	8-9	15-18	?	4	–	6-7	–	5-6	6-7	4	3-6	6-7	–	8-12
Oslo, Norway																	
<i>E. serrulatus hadjebensis</i>	VI	I–II	7	9	12	?	5	–	2	2	7	6	–	–	8	–	7-10
<i>E. romaniensis</i>	X	III	6	7	15	10	4	–	5	5	5	5	–	–	7	–	8
<i>E. albuferensis</i>	VII	III	8	3	3	7	10	5	3	5	6	6	5	7	7	6	18
<i>E. agiloides</i>	II–VI	0	–	6-8	7-9	–	6	3-6	4	2	5-6	3-6	–	–	4-6	10	5-8
<i>E. miracleae</i>	IV	III	7	6	–	3	4	6	7	4	6	8	–	4	5	–	10
<i>E. agiloides roseus</i>	V–VI	II–III	8	–	12	–	6	5	5	4	6	6	–	3	6	7	12
<i>E. arcanus</i>	VI	–	8-10	7-8	20-24	6	4	3	5	5	5-7	10-12	3-5	6-8	3-6	4-6	10-12
<i>E. borealis</i>	II	–	5	5	11	5	7	4	3	2	5	11	–	11	–	15	4
<i>E. delachauxi</i>	V	4	4	6	16	6	5	3	4	3	9	6	10	3	6	2	8
<i>E. glaber</i>	V	3	?	?	?	?	?	?	?	?	?	?	?	?	?	4	10
<i>E. neumani titicacae</i>	III	–	7	6	2	5	6	?	3	3	5	4	5	5	4	8	9
<i>E. pacificus</i>	VII	VIII	5	5	23	11	3	4	4	10	8	7	3	5	10	5	8
<i>E. pectiniifer</i>	VII	5	7	7	18	2	7	8	3	4	5	11	–	4	6	7	11
<i>E. procerus</i>	IV–V	–	0-3	8-11	8-14	–	9	7	9	3	5	7	7	4	7	11	8-9
<i>E. vandonwei</i>	III–IV	IV	5-6	6	11	–	0-2	1	1-2	4	5	6	–	0-4	5-7	2-3	5-8
NOT <i>serrulatus</i> -group																	
<i>E. speratus</i>	–	–	–	7	12	–	5-8	–	3	7	3-5	4-5	–	2-5	4-6	5	10-12
<i>E. dumonti</i>	–	–	–	7	15	–	4-7	–	6-8	8	8-9	4-5	5-8	6	–	–	10-12

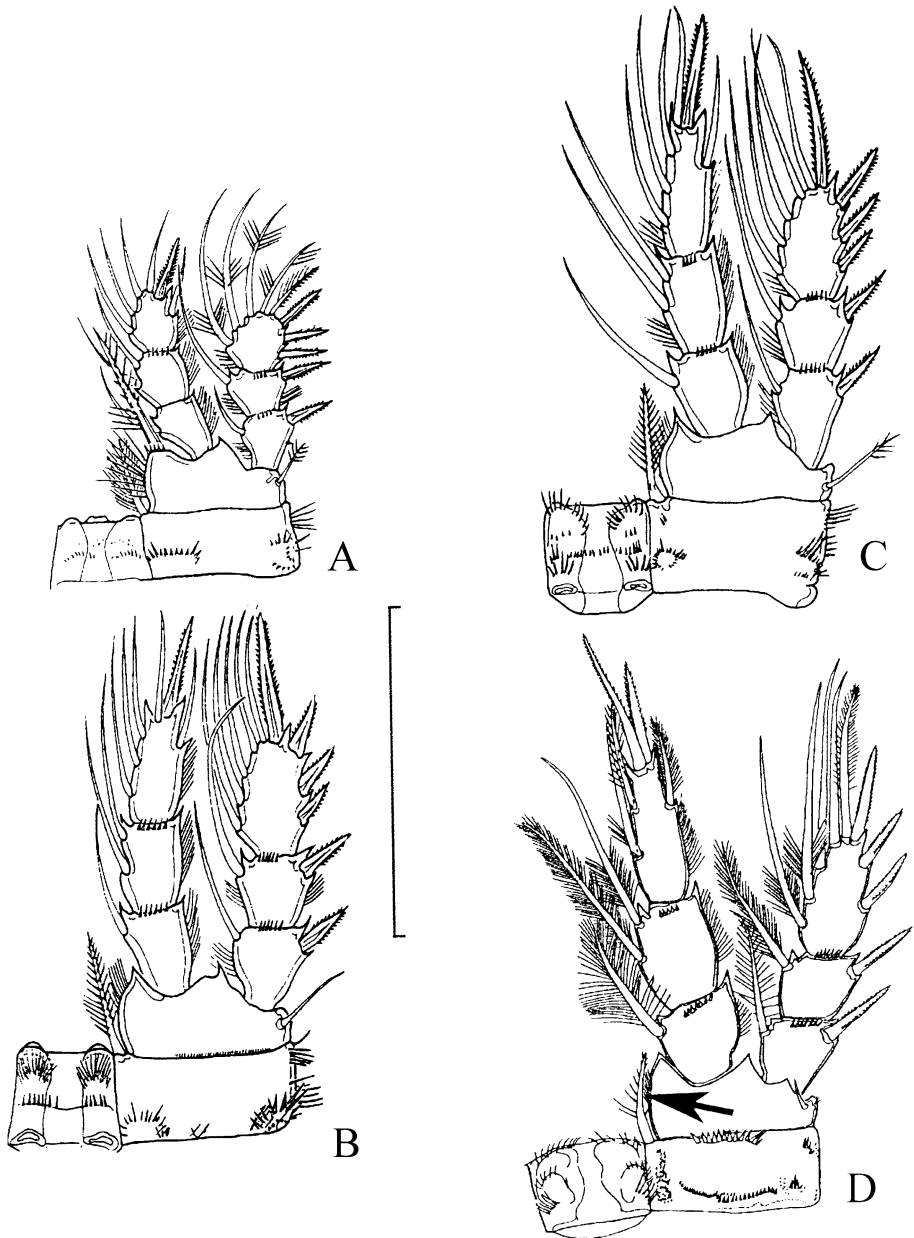


Fig. 5. *E. serrulatus* (Fischer, 1851), type locality, female swimming legs. A, P1; B, P2; C, P3; D, P4. Arrow indicates a gap in hair-like setae at inner side of coxal spine. Scale = 50 μ m.

spine, dense hair-setae on inner side, and in many species with large gap among short hair-like setae on inner side (fig. 4D, arrow). Posterior side of coxopodite with tiny spinules on inner side, not organized in groups, and groups of spinules and setules, giving the formula A-B-C + D-E-H (fig. 5D). Intercoxal plate of P4 (fig. 5D) with protuberances wide but not protruding beyond free edge of plate; group of hair-like, long setules along edge, 2 groups of setules and spinules on main body of plate. For variation of microcharacters in coxopodite of P4 among different species in the *serrulatus*-group, see table III.

P5 (fig. 6A) 1-segmented, **with wide and strong inner spine**, and 2 setae; outer seta subequal in length to spine, middle seta about 1.1-2 times as long as spine. Even in a tiny population, we found a significant variation in spine/setae ratio (see fig. 6A).

Male. — Body length 650-1100 μm . Cephalosome 1.1-1.5 times as long as wide, with maximal width near to its posterior end. Last somite of prosome smooth, last urosomal somite with a row of denticles on caudal side. Caudal rami (fig. 6E) 3.8-5 times as long as wide, without lateral spinules. Slender innermost terminal seta (VI) about twice the length of spine-like outermost seta (III). Lateral seta (II) shifted to dorsal side, with several spinules at base. Dorsal seta (VII) near insertion of innermost seta (VI), about 0.8 times as long as outermost seta.

Antennule (fig. 3D) 14-segmented with 6 setae and 3 aesthetascs on first segment. Segments 2, 3, 4, 6, and 10 also with aesthetascs.

Antennary basipodite basically as in female, with 4-6 long setules posteriorly corresponding to groups N1 and N2; anteriorly with 3 rows of strong spinules and an additional row of spinules subdistally.

Morphology of mouthparts and P1 basically as in female.

Coxopodites and intercoxal plates of P1 to P3 with apical setules. Inner edge of basipodite of P4 (fig. 6B) with short setules. Coxopodite of P4 with strong spine, bearing 8-10 stiff inner hair-like setae and 2-3 hair-like setae at apex and 1 at base of spine, so also with a gap in those setae at the outer margin (fig. 6B, arrow). Coxopodite of P4 (fig. 6B) also with a narrow row of small spinules on its inner side and several groups of spinules (corresponding to A-B-C + D-F) posteriorly. Intercoxal plate of P4 (fig. 6B) with small protuberances, strong hair-like setae on free edge, and 3 groups of setules on both sides. Distal segment of endopodite of P4 about 2.2-3.2 times as long as wide, with inner spine as long as segment and always longer than outer spine. P5 (fig. 6C) with inner spine slightly shorter than in female, outer seta as long as spine, middle

TABLE III

Pattern of microcharacters of the P4 coxopodite recorded in the studied *Eucyclops* species. Latin names in **bold** correspond to specimens from Kiefer's collection. Numeration of patterns corresponds to fig. 2C; Y, present; N, absent; ?, character not seen; -, character missing; H, hairs; LH, long hairs; SH, short hairs; * consists of two groups; **D, denticle

Species	A	B	C+D	E	F	G	H	J	I	II	III	Gap on coxopodal spine	Hair-like setae on basipodite
<i>E. serrulatus</i> A	Y	4-5	12	2-4	N	N	Y	Y	LH	SH	LH	Y	Y
type locality													
<i>E. serrulatus</i> B	Y	5	12-14	3	N	N	Y	Y	SH	SH	LH	Y	Y
type locality													
<i>E. serrulatus</i> A	Y	5	14	3-4	N	N	Y	Y	SH	SH	LH	Y	Y
Norway													
<i>E. serrulatus</i> Ghent	Y	4	13	2	N	N	Y	Y	H	H	H	Y	Y
<i>E. s. hadjebensis</i>	Y	5	10-11	2	N	N	Y	Y	LH	LH	LH	Y	Y
<i>E. romaniensis</i>	Y	4	8-11	4-5	N	N	Y	Y	LH	LH	LH	N	Y
<i>E. aglroides</i>	Y	0	4 + 5*	4	Y	N	Y	Y	D**	D**	D**	N	Y
<i>E. miracleae</i>	Y	6	20	4	Y	N	Y	Y	LH	LH	LH	Y	Y
<i>E. a. roseus</i>	Y	6	18	4	Y	N	Y	Y	LH	LH	LH	N	?
<i>E. albuferensis</i>	Y	5	15	5	Y	N	Y	Y	LH	LH	LH	Y	Y
<i>E. arcanus</i>	Y	6	16	4	Y	Y	Y	Y	LH	SH	LH	N	Y
<i>E. bondi</i>	Y	5	-	4	Y	Y	Y	Y	D*	SH	LH	Y	Y

TABLE III
(Continued)

Species	A	B	C+D	E	F	G	H	J	I	II	III	Gap on coxopodal spine	Hair-like setae on basipodite
<i>E. borealis</i>	Y	3	13	6	N	Y	Y	Y	LH	SH	LH	Y	Y
<i>E. delachauxi</i>	Y	3-4	21	5	Y	N	Y	N	SH	SH	SN	Y	?
<i>E. glaber</i>	Y	4	3 + 9*	4	N	Y	Y	Y	SH	SH	LH	Y	Y
<i>E. neumani titicacae</i>	Y	4	20	4	Y	N	Y	Y	LH	LH	LH	Y	N
<i>E. pacificus</i>	Y	3	5 + 17*	7	Y	Y	Y	Y	LH	SH	LH	N	Y
<i>E. pectiniifer</i>	Y	5	10	6	Y	N	Y	Y	LH	SH	LH	N	Y
<i>E. prionophorus</i>	Y	4	6	?					LH	SH	LH	Y	Y
<i>E. procerus</i>	Y	3	20	0	Y	N	Y	Y	H	H	H	N	Y
<i>E. vandonwei</i>	Y	4	11	5	Y	N	?	Y	H	H	H	N	Y
NOT serrulatus													
<i>E. speratus</i>	Y	5	27	8	N	N	Y	Y	LH	H	LH	N	Y
<i>E. dumonti</i>	Y	2-3	10-12	2	N	N	Y	Y	SH	SH	SH	N	N

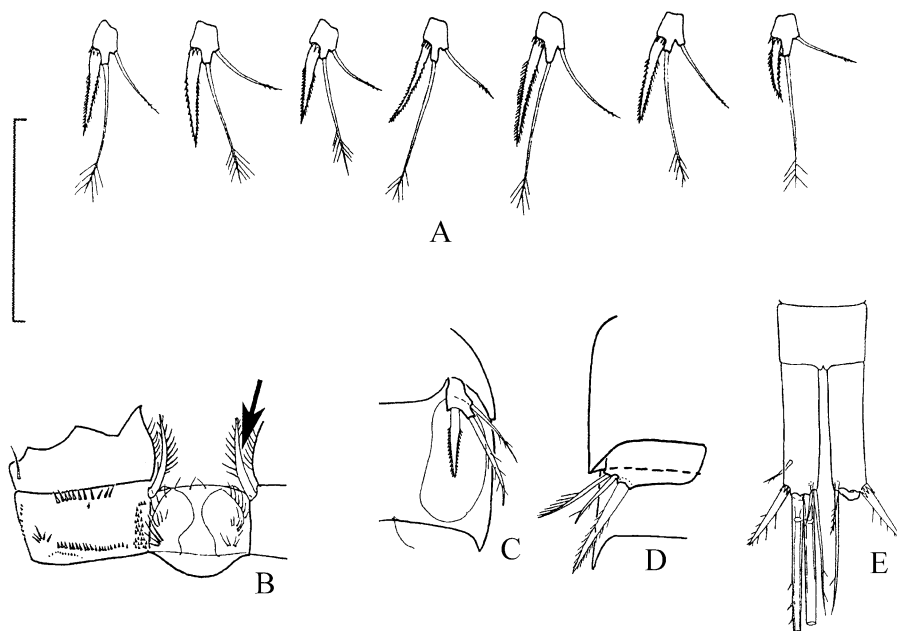


Fig. 6. *E. serrulatus* (Fischer, 1851), type locality. A, variation in female P5 structure; B, male intercoxal plate and coxopodite of P4, arrow indicates a gap in hair-like setae at inner side of coxa spine; C, male P5; D, male P6; E, male caudal rami, dorsal view. Scale = 50 μ m.

seta significantly longer than spine. P6 (fig. 6D) with inner spine and two setae with variable length proportions.

Intrapopulation variation in the type population of *Eucyclops serrulatus*

There appeared to be appreciable variation among the specimens from the locus typicus as well as in other populations of the species and in other species of the *serrulatus*-group. We identified three morphotypes, based on the type population (*E. serrulatus* s. stricto) from St. Petersburg (Alekseev et al., 2006).

Type A, with plumose setae on the endopodite and exopodite segments of P1–P4, and innermost and outermost setae of the caudal rami with dense long setules. Intercoxal plate of P4 with dense long setules, sometimes as long as half of the plate's width. At some distance from seta I, the setules are much longer than the distance between them. For variation of microcharacters of the antennary basipodite and coxopodite of P4 in type A, see tables II and III.

Type B, with a few short setules on caudal setae III and VI; characterized by a reduction in length of the setules of the exopodal and endopodal setae of P4, and also of the setae of the caudal rami. Distal half of setae of Enp3P4 and

most setae of Exp3P4 blade-shaped, narrowed, and with much shorter setules on distal part than on proximal part. Intercoxal plate of P4 with short marginal setules of about 1/3 or less the membrane width. For microcharacters of the antennary basipodite as well of the P4 coxopodite in type B: see table III.

Type C (pitted form). In the caudal setae, a configuration similar to that of form A is found, but this form is provided with a pitted integument on the cephalosome, urosome, caudal rami, and first antennae.

In the Peterhoff ponds, Type C was rare during spring (15%) but became more frequent in fall (40%). Types A and B were most abundant in spring (about 40% each), hybrids between these three types dominated during summer and fall.

The specimens of these three groups can live together at the same time in the same waterbody and easily hybridize in both laboratory experiments and in the field. The possible reasons for the coexistence of these types had been discussed in Alekseev et al. (2006). In several other species belonging to the *serrulatus*-group, such as *E. delachauxi* and *E. prionophorus*, similar inter-population variability exists. In some cases, such variations were significant enough to attribute specimens of the same species to different species, which is not justified. Some examples of such misinterpretation were discussed by Alekseev et al. (2006).

Species included in the *serrulatus*-group

The *serrulatus*-group includes species having a 12-segmented antennule, with a smooth hyaline membrane at the distal three segments. Caudal rami 3.5-7 times as long as wide, with **longitudinal row of spinules (serra) along most of outer edge of each ramus, but partly reduced in some taxa inhabiting subterranean or spring environments and never with hair-like setules or denticles on dorsal or ventral surfaces**. P5 with strong inner spine. They also have one or two groups of spinules on the distal part of the frontal side of the basipodite of antenna (fig. 2A, groups 1 and 2). Many species of the *serrulatus*-group have the coxopodal spine of P4 with a clear gap in the hair-like spinules at the outer edge of the spine (fig. 2C).

In *E. serrulatus* s. stricto, many general morphological characters as well as body proportions vary among local populations and with the seasons, so using them for taxonomic purposes in the *serrulatus*-group is problematic. The use of qualitative microcharacters provides many additional discriminating elements, because such microcharacters exhibit a very low variability in relation to the ambient ecological conditions (Alekseev et al., 2006). According to

these characters, we consider the *E. serrulatus* species group to be composed of the following taxa:

– *E. serrulatus* s. stricto and the subspecies *E. serrulatus hadjebensis* (Kiefer, 1926); *E. romaniensis* Alekseev, 2010;

– *E. agiloides* (Sars, 1907), *E. miracleae* Alekseev, 2010, *E. agiloides roseus* Ishida, 1997 (**comb. nov.**);

– *E. albuferensis* Alekseev, 2008, *E. arcanus* Alekseev, 1990, *E. bondi* Kiefer, 1934, *E. borealis* Ishida, 2001, *E. delachauxi* (Kiefer, 1925), *E. glaber* Kiefer, 1935, *E. neumani titicacae* (Kiefer, 1957); *E. pectinifer* (Cragin, 1883); *E. prionophorus* Kiefer, 1931, *E. procerus* Dussart, 1981; *E. vandouwei* (Brehm, 1909).*)

Eucyclops serrulatus s. stricto and its subspecies can be separated from other closely related taxa within the *serrulatus*-group by a set of microcharacters that includes:

– antennary basipodite, at caudal side, **always with two groups of long hair-like setae** placed between insertion sites of lateral setae and on inner lateral (= medial) margin, **with three parallel rows of hair-like setules placed obliquely in central part and also with two groups of spinules and hair-like setae on lateral side**; on the frontal side this segment with a group of strong denticles on apex, a long row of 10-17 relatively small spinules in the central part, and two groups of 2 spinules each, as shown in fig. 4G;

– P4: inner edge of basipodite with a group of long hair-like setae; coxopodite always with a strong spine **bearing sparse hair-like setae or with a large gap among short and strong hair-like setae/spinules on inner side**; caudal side of coxopodite with two groups of long hair-like setae located close to lateral margin, with numerous tiny spinules on inner side; with long rows of strong denticles (10-17) at distal side of the segment, as shown in fig. 2C; intercoxal plate with small prominences and three rows of long hair-like setae and small denticles as shown in fig. 3; apical spine of exopodite very often as long as other spines and usually shorter than the segment itself;

– P5 with strong inner spine and short outer seta of subequal length; caudal rami with a long (sometimes asymmetrically reduced) serra (= row of denticles) along outer edge and without hair-like setae/spinules on surface.

The subspecies can be distinguished from *E. serrulatus* s. stricto using differences in the following characters, which have proved to be constant: caudal rami with asymmetrically reduced serra (*E. s. hadjebensis*); proportion

*) Another species *Eucyclops chilensis* Suárez-Morales & Walsch, 2009 will have to be added to the *serrulatus*-group (see Menu-Marqué & Locascio de Mitrovich, this volume).

of III/VI caudal setae (*E. romaniensis* Alekseev, 2010; *E. s. suecicus* Lindberg, 1950); setae/spine ratio in P5 (*E. s. chiliensis* Löffler, 1961). In contrast, variations in microcharacters not specific for the *E. serrulatus* group, as the basipodite of the A2 and the coxopodite of P4, together with general morphological characters, and, of course, along with the exclusion of sympatric distribution, would be the more common way for discriminating new subspecies.

We note that we could not observe differences in the structure of the mouthparts, another character very discriminating in some cyclopoid genera as *Mesocyclops* and *Thermocyclops*, i.e., the shape and structure of the female seminal receptacle. In all females examined, the seminal receptacle shows the same shape: located in the anterior half of the genital double somite; consisting of an anterior part slightly bilobed in its anterior margin; this anterior part a little narrower than the distal part; this distal part of about the same size and with its posterior margin bilobed; and extending on each side towards the P6. Copulatory pore in central position situated at same level as the suture chord, on the right, and delimiting the two parts of the seminal receptacle. No striking difference could be observed in the *serrulatus*-group.

Distribution area of *Eucyclops serrulatus*

The examination of the present material allowed to define the distribution of the *E. serrulatus* group and of the other species of *Eucyclops* over the various localities sampled:

We found *E. serrulatus* sensu stricto mainly in countries/sites in the Palearctic (table I). Four other *Eucyclops* species that do not belong to the *serrulatus*-group (i.e., *E. denticulatus* (Graeter, 1903), *E. macruroides* (Lilljeborg, 1901), *E. macrurus* (Sars, 1863), and *E. speratus* (Lilljeborg, 1901)) usually coexisted with *E. serrulatus* in the same habitats. These species are probably the most common cyclopoids in fresh surface waters of the Palearctic and are included sometimes under different, synonymous names in the most common identification keys to cyclopoids in this region (Gurney, 1933; Dussart, 1969; Monchenko, 1974; Alekseev, 1995). We did not find *Eucyclops* species among cyclopoids collected in Novaya Zemlya (Northern-Arctic Ocean) and Antarctica. The northernmost site among our samples with confirmed presence of *E. serrulatus* is the River Lena delta (close to the Polar Circle). The records on the presence of *E. serrulatus* on Arctic islands, including Iceland, Greenland, and Novaya Zemlya (Monchenko, 1974) should be re-examined.

In some places along the Palearctic border, along with *E. serrulatus* s.s. we found other *Eucyclops* taxa belonging to the *serrulatus*-group that we consider to indicate the boundaries of the area occupied by *E. serrulatus* s.s.

Europe

E. serrulatus s. stricto is the only species of the *serrulatus*-group living probably everywhere from Iceland to Slovenia in surface waters of the European continent.

In lake Albufera, near Valencia, Spain, we found along with *E. serrulatus* s. stricto a group of species presumably of African origin: *E. miracleae* Alekseev, 2010, which is taxonomically close to *E. agiloides roseus* from lake Victoria, Central Africa; *E. albuferensis* Alekseev, 2008 which is close to *E. vandouwei* (Brehm, 1909) from Cameroun, and *E. romaniensis* Alekseev, 2010, close to *E. serrulatus hadjebensis* from Morocco. Professor B. H. Dussart (cf. Dussart, 1969) in fact, had predicted that species of cyclopoids closely related to the African fauna might be discovered on the Iberian peninsula.

Another species of the *serrulatus*-group, *E. roseus* Ishida, 1997, was described from Japan but later collected by us in a stream near Oldenburg (Germany) and in Lake Victoria, Kenya (Ishida, 1998). Judged from the antennule morphology and the microcharacters of the antennary basipodite, this taxon belongs to the species *E. agiloides* and must be considered a subspecies of *E. agiloides*, as *E. agiloides roseus* comb. nov.

Hereafter a brief complement to the description of the *E. agiloides* from the type locality (Malawi lake, Africa) is given: caudal rami short ($l/w < 4$) and parallel, with long serra of large spinules on outer edge of rami (fig. 7A). Antennula with wide, wavy hyaline membrane at distal segment (fig. 7E). Antennal basipodite on caudal side with one to two groups of long hair-like spinules in position 1-2 (fig. 7D). This clearly confirms that *E. agiloides* belongs to the *serrulatus*-group. At its frontal side, the basipodite shows a large group of strong spinules on the distal side of the segment and several other groups of spinules in the proximal part of the segment (fig. 7C). Coxopodal spine of P4 with long hairs and without a gap at outer sides (fig. 7B).

The distribution area of the species *E. agiloides* are the tropics and subtropics. Therefore, *E. agiloides roseus* comb. nov. might possibly have been introduced into Germany via ships, i.e., water transport, from Africa by German troops during the Second World War.

North Africa

Morocco. — We re-examined *E. serrulatus hadjebensis* from a sample that we collected from a spring at the type locality (Atlas Mountains); those specimens quite well matched the original description (Kiefer, 1926), except

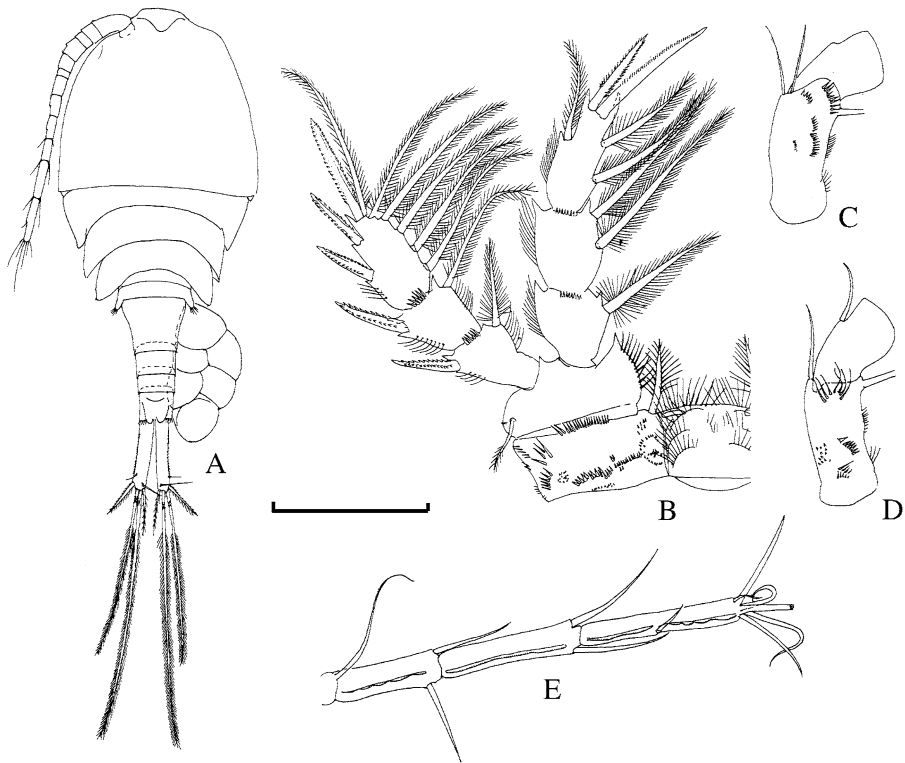


Fig. 7. *Eucyclops agiloides* (Sars, 1909), female, from a small river, tributary of Lake Malawi, Mozambique. Sample from Prof. F. Kiefer collection. A, total view, dorsal side; B, leg 4; C, antennary basipodite, anterior side; D, antennary basipodite, posterior side; E, distal segments of antennule. Scales: A = 250 μm ; B, E = 75 μm ; C, D = 50 μm .

for the longer caudal rami. Most of the microcharacters in this subspecies, particularly the armament of the antennary basipodite and the structure of the P4 coxopodal spine, are close to those of *E. serrulatus* from the type locality. In some ponds and small rivers in Morocco, *E. serrulatus* s. stricto was also collected but the two taxa were never found together (V. R. Alekseev, unpubl. data).

Egypt. — We found *E. agiloides* but not *E. serrulatus* in the Nile delta near Cairo.

Asia

Israel. — We recorded several taxa of the *serrulatus*-group in this country, that differ from the type description and are close to *E. agiloides*. The latter species, described from Lake Malawi, was later found at many locations in

Africa, Europe, and Asia (see Dussart & Defaye, 2006, for a review). Two subspecies of *E. agiloides* have been discriminated from the nominal form: *E. agiloides roseus* and *E. miracleae*. Here again, a brief addition to the description of the *E. agiloides* from the type locality is given:

Caudal rami short ($l/w < 4$) and parallel with long a row of large spinules on outer edge of rami (fig. 7A). Antennule with wide, wavy, hyaline membrane on distal segment (fig. 7E). Antennal basipodite on caudal side with 1-2 groups of long hairs in position 1-2 (fig. 7D). This clearly confirms that *E. agiloides* belongs to the *serrulatus*-group. At the frontal side, this basipodite shows a large group of strong denticles on the distal side of the segment and several other groups of denticles in the proximal part of the segment (fig. 7C). Coxopodal spine of P4 with long hairs and without a gap at the outer sides (fig. 7B).

E. agiloides and its subspecies seem to substitute *E. serrulatus* and its subspecies in the tropics.

Turkey. — *E. cf. agiloides* and *E. cf. serrulatus* were found together in a small river near Antalya, which might represent the limit of the distribution area of *E. serrulatus* in Asia in south-western direction.

Afghanistan. — We examined 10 *Eucyclops* females from a sample collected by Lindberg at the type locality of *Eucyclops turcomanus* Lindberg, 1959. Their main characters fitted the original description of this species by Lindberg (Alekseev et al., 2006). However, most microcharacters on the antennary basipodite and the coxopodite of P4 match those of *E. serrulatus* Fischer Type B. So, in contrast to our previous conclusion (Alekseev et al., 2006) we instate *Eucyclops turcomanus* Lindberg, 1959 as a junior synonym of *E. serrulatus* s. stricto. Thus, *E. serrulatus* s. stricto inhabits also the Irano-Turanian province of the Palaearctic, at least up to that locality.

Uzbekistan. — In a sample from a rain pool near the Aral Sea, we found a single specimen of a *Eucyclops* sp. belonging to the *serrulatus*-group. This identification is based on the morphology of the coxopodal spine of P4 and on the micropatterns of the basipodite of the antenna. *Eucyclops* sp., when compared to *E. serrulatus* s. stricto, shows a long row (about 40) of small denticles on the distal side of the coxopodite of P4, whereas *E. serrulatus* s.s. has only 14-20 such denticles (groups C + D). Furthermore, in this specimen, the oblique rows on the caudal side of the basipodite of the antenna are reduced and there are additional groups of denticles on the frontal side, including a group of hairs organized in a circular pattern. This taxon is possibly a new species but because only one female was collected, it will not be described until more specimens, including males, will be available.

Russia. — Females of *E. serrulatus* s. stricto have been found practically everywhere in European Russia: from Arkhangel'sk in the north to the Caucasus in the south, and in western and central Siberia, including the Angara and Enisey rivers and their tributaries. In Lake Baikal and in lakes of the Amur River system, *Eucyclops arcanus* Alekseev, 1990, a species belonging to the *serrulatus*-group, was collected together with *E. serrulatus* s. stricto (tables II, III). *E. arcanus* was also found in some lakes in Mongolia (Alekseev, 1990), in Japan (Ishida, 2000), and in Thailand (Alekseev & Sanoamuang, 2006). *Eucyclops baikalocorrepus* Mazepova, 1955 was later considered a subspecies of *E. serrulatus* by Mazepova (1978), and named as *E. serrulatus baikalocorrepus* Mazepova, 1955. This taxon has a short spine at P5, distal segments of the antennule missing a hyaline membrane, caudal rami 6.4-8.2 times as long as wide, without serra, and subequal distal spines at Enp3 of P4 (Mazepova, 1978). These characters better fit the description of *E. macrurus*, as reported by Monchenko (1974) than that of *E. serrulatus*, and accordingly should be moved to be a subspecies of the former, as *E. macrurus baikalocorrepus* **comb. nov.**

To the East of Lake Baikal, we did not find *E. serrulatus* any longer. By contrast, in lakes and small rivers of the Amur River catchment, we discovered at least two new taxa (*Eucyclops* sp. 2 and *Eucyclops* sp. 3).

In north-eastern Siberia, east of the Lena River, a new taxon of the *serrulatus*-group (*Eucyclops* sp. 4) is probably present (in the River Chaun, E. Y. Strelezkaya, pers. comm.).

In Lake Khanka (Russia and China), *E. serrulatus* appeared to be replaced by a *E. cf. agiloides* that shows some differences with *E. a. roseus* comb. nov. (*Eucyclops* sp. 5).

Mongolia. — In lakes of western Mongolia, we found *E. serrulatus*. In the eastern Mongolian lakes, this species was replaced by *E. arcanus*, *E. pacificus* Ishida, 2000, and *E. cf. agiloides* (*Eucyclops* sp. 6).

Japan. — Ishida (2000, 2001) described several species belonging to the *serrulatus*-group from Lake Biwa and small rivers in Hokkaido: *E. pacificus* and *E. borealis*, belong to the *serrulatus*-group. *E. ohtakai* Ishida, 2000 is rather close to *E. serrulatus* and its taxonomic position should be better defined, possibly as a subspecies of *E. serrulatus*. We found specimens similar to *Eucyclops cf. pacificus*, in Kronozkoe Lake, Kamchatka and in the Razdolnaja River, a tributary of Lake Khanka, in the River Amur catchment.

Outside of the Palearctic

Taiwan. — In rice fields and in temporary fish ponds of Taiwan (in the tropical part of the island), we found *E. serrulatus* Fischer (introduced?) along with another form (*Eucyclops* sp. 7), with obvious denticles on the 11th and 10th segments of the antennule and a smooth hyaline membrane at the distal segments of the 12-segmented antennule (it is not clear if the membrane is present only on the last one or on the last three segments) but with the antennary basipodite as in the *serrulatus*-group, bearing long setules at positions 1 and 2. This taxon has other small differences and possibly represents a new species.

Thailand. — In Thailand, we found three species of *Eucyclops*: *E. arcanus* (mentioned above), *E. pacificus*, *E. cf. serrulatus* (*Eucyclops* sp. 8) (cf. Alekseev & Sanoamuang, 2006).

Australia. — In a pond of the University campus in Newcastle, along with *E. australensis* Morton, 1990, we found specimens of *E. cf. serrulatus* that are morphologically very close to Type A of *E. serrulatus* s.s. This type of *E. serrulatus* is very common in temporary waterbodies, so likely producing diapausing stages resistant to desiccation. This stage can be transported from coastal areas to the pond by aquatic birds. We hypothesize that via a long chain of events, the presence of *E. serrulatus* s.s. in Australia might be a result of a human-mediated invasion, possibly with fresh water transports by ships.

Tasmania. — *E. cf. serrulatus* was found in some lakes along with *E. nicholli* Brehm, 1950, possibly as a human mediated invasion of *E. serrulatus* s.s.

North America. — In Canada, *E. serrulatus* s. stricto was found in Lake Ontario (invasion?) together with *E. pectinifer* and *E. prionophorus*. In the U.S.A., the *serrulatus*-group is represented by *E. prionophorus*, *E. bondi*, *E. neumani* (Pesta, 1927) and *E. delachauxi*, and possibly *E. conrowae* Reid, 1992, whose membership to this group needs to be confirmed based on a detailed redescription of the antennary basipodite. *Eucyclops cf. serrulatus* was found at a few isolated sites in California and in Florida and might reveal to be an invasive species in the U.S.A. derived from *Eucyclops serrulatus* from Europe.

South America. — In Ecuador, we recorded a *Eucyclops* sp. 7 with a specific combination of microcharacters of the basipodite of the antenna (group 1 present, group 2 missing, very long denticles on 7 and 9) and with an anal plate

of peculiar morphology. This population could be ascribed to a new species of the *serrulatus*-group.

In synthesis, we did not find *E. serrulatus* s.s. in any sample from the following countries: Ethiopia, Niger, Kenya, Cameroun, Malaysia, Indonesia, Mexico, or Ecuador. Other species of the *serrulatus*-group were found there instead of *Eucyclops serrulatus*. In central and southern African countries, the *serrulatus*-group was represented by *E. agiloides*, *E. glaber*, and *E. vandouwei*.

DISCUSSION

The role of micropatterns in morphological discrimination among species of the *serrulatus*-group

Among the 108 species and subspecies currently known in the genus *Eucyclops*, at least 17 taxa fit into the *serrulatus*-group description as given above (tables II, III). One can find at least one, but usually a set of *serrulatus*-like taxa that, outside of the Palaearctic region, differ from the nominal species in taxonomically valid characters. These species probably represent lineages derived from a common ancestor, when geographical barriers originating from large-scale geographic and climatic events appeared in the past. Variations in microcharacters should be analysed more precisely among different populations of *Eucyclops*, as they are allegedly important for recognizing the speciation processes within the *serrulatus*-group. In most species of the *serrulatus*-group, the same groups of spines or hair-like setules (groups 1-17) are often observed on the antennary basipodite. However, in some species, those groups are represented by spines or hair-like spinules of different size and number. The analysis of the differences both within and outside the *serrulatus*-group, especially focused on determining how stable such differences are among local populations of the same species, could be the next and very important goal for a better knowledge of *Eucyclops* taxonomy.

We found at least 8 taxa of the *serrulatus*-group (*Eucyclops* sp. 1-8) that differ from the description of *E. serrulatus* s.s. from the type locality in the microcharacters of the basipodite of the antenna and of the coxopodite of P4. Most of the species were found near the limits of the Palaearctic region, but also in Taiwan, South America, and South-East Asia. The taxonomic position of these different representatives will be analysed in a further study, but at least three should be described as new species. Some of the specimens from Israel, Morocco, Western Siberia, and Uzbekistan probably represent new

species/subspecies as well. It is highly likely that some other new species exist outside of the Palaearctic zone, from where *E. serrulatus* has been reported. A set of cryptic species likely inhabits Canada, the U.S.A., Mexico, Ecuador, Brazil, Malaysia, India, and the regions located all around the Central African Rift Valley lakes, as well as South Africa.

Distribution of *Eucyclops serrulatus* world-wide

E. serrulatus is one of the few species that for a long time was suspected to live everywhere on the Earth's continents, with the exception only of Antarctica. Taking into account our more precise analysis of morphological characters and microcharacters, a revision of the type species of the genus could be partly done herein already, but a revision of the whole genus will be necessary for a better understanding of the relationships between the species in the future.

Based on all the populations we analysed, we can give a first hypothesis of the true boundaries of the distribution of *E. serrulatus* sensu stricto, and evaluate the potential biological invasion of this species towards some countries. *E. serrulatus* sensu stricto, then, occupies a part of the Palaearctic area (see fig. 1). Its distribution range is limited in the east by eastern Siberia, in the west by the Iberian peninsula, in the north by the islands of the Arctic seas, and in the south by North Africa, Middle Asia, Turkey (in part), Iran, Afghanistan, Kazakhstan (in part), Uzbekistan (in part), and Mongolia (in part). The species is not present in the Far East, nor in South-East Asia. Several records of *E. serrulatus* outside this area are hypothesized to be the result of recent introductions, possibly in relation to human activity. This might be the case for Australia, Canada, the U.S.A. (Atlantic coast and California), Japan, Taiwan, and Thailand. This hypothesis has already been suggested by Karanovic (2005), who collected specimens of *E. serrulatus* in New Zealand, which he considered as showing no differences with the European specimens.

Molecular-genetic tests (for instance barcoding) should be applied to provide new arguments to support this hypothesis, and confirm or refute the postulated origin of the supposed *E. serrulatus* enclaves outside its natural area of distribution.

KEY TO SPECIES OF THE *EUCYCLOPS SERRULATUS* GROUP

1. Basipodite of antenna at posterior side in position 1 with group of hair-like spinules and in position 2 with group of tooth-like spinules, or without spinules at all. 2
 - Basipodite of antenna, at posterior side, with 2 groups of hairs (positions 1 and 2) 11

2. Basipodite of antenna at posterior side with 1 group of hairs (group 1), with group 2 missing 3
 - Basipodite of antenna at posterior side with group 2 transformed into teeth or very short hairs 6
3. Spine of coxopodite P4 with fine hairs at both sides 4
 - Spine of coxopodite P4 at outer margin with gap among strong spinules 5
4. Distal segments of antennule having wide hyaline membrane with wavy margin, caudal rami about 4.5-5.5 times as long as wide *E. agiloides* s.s. (G. O. Sars, 1907)
 - Distal segments of antennule with narrow hyaline membrane, caudal rami about times 6-7 times as long as wide *E. procerus* Dussart, 1981
5. Caudal rami 4.5-5.2 times as long as wide, serra composed of spinules, in length reduced to half the length of the ramus, innermost seta significantly shorter than ramus *E. borealis* Ishida, 2001
 - Caudal rami 3.4-4.0 times as long as wide, with serra composed of denticles, present all along the outer margin, innermost seta as long as ramus *E. arcanus* Alekseev, 1990
6. Distal segment of endopodite of P4 with long inner distal seta, reaching end of outer apical spine 7
 - Distal segment of endopodite of P4 with short inner distal seta, never reaching end of outer apical spine 8
7. Caudal rami naked, without serra (no denticles or spinules) *E. glaber* Kiefer, 1935
 - Caudal rami with long serra composed of denticles *E. delachauxi* (Kiefer, 1925)
8. Caudal rami with dorsal seta (seta VII) longer than outermost seta (seta IV) *E. bondi* Kiefer, 1934
 - Caudal rami with dorsal seta shorter than outermost caudal seta 9
9. Caudal rami long, 5.6-6.8 times as long as wide, with reduced row of lateral denticles *E. neumani titicacae* Kiefer, 1957*
 - Caudal rami shorter, with serra of denticles along entire outer margin of ramus 10
10. Caudal rami 5.0-5.5 times as long as wide, serra composed of denticles almost equal in length *E. pectinifer* (Cragin, 1883)
 - Caudal rami 3.5-4.5 times as long as wide, serra with denticles increasing in length and with several significantly longer denticles proximally *E. prionophorus* Kiefer, 1931
11. Three distalmost segments of antennule with wide hyaline membrane, wavy, appearing curved in dorsal view, spine of coxopodite of P4 with homogeneous fine hairs at both margins 12
 - Three distalmost segments of antennule with narrow hyaline membrane of regular shape, spine of coxopodite of P4 with gap among the strong teeth-like hairs on the outer side (*E. serrulatus* s. lato) 13
12. Spine of coxopodite of P4 short, not reaching inner notch of basipodite *E. miracleae* (Alekseev, 2010)
 - Spine of coxopodite of P4 long, always reaching inner notch of basipodite *E. agiloides roseus* Ishida, 1997 (comb. nov.)

*) We only considered the subspecies *titicacae* as we could not find appropriate information about the antennary basipodite of the nominal species *E. neumani* (Pesta, 1927).

13. Caudal rami with reduced serra composed of denticles usually present on less than half of outer margin; inner spine of P5 very strong, about as long as median seta
 *E. serrulatus hadjebensis* (Kiefer, 1926)
 – Caudal rami with well-developed serra of denticles present almost on the whole outer margin, inner spine of P5 shorter than median seta 14
14. Innermost caudal seta shorter than spine-like outermost seta
 *E. romaniensis* Aleksseev, 2010
 – Innermost caudal seta longer than or at least as long as outermost seta 15
15. Caudal rami with serra composed of denticles of regular size, basipodite of antenna on anterior side with a group of small denticles at position 9; inner spine of Enp3 P4 shorter than distal segment *E. serrulatus serrulatus* (Fischer, 1851)
 – Caudal rami with serra of very long denticles, in proximal part as long as half the ramus' width; basipodite of antenna with 1-2 rough denticles at position 9 on anterior side. Inner spine of Enp3 P4 as long as or even longer than distal segment. 16
16. Spine of P4 coxopodite with gap among teeth-like hairs at outer margin; inner spine of P5 twice the segment length *E. albuferensis* Aleksseev, 2008
 – Spine of P4 coxopodite with fine hairs homogeneously distributed on both margins; inner spine of P5 almost as long as the segment *E. vandouwei* (Brehm, 1909)

CONCLUSIONS

1. The *serrulatus*-group is composed of species having a 12-segmented antenna, with a smooth hyaline membrane at the three distal segments of the A1; caudal rami of moderate length (l/w ratio 3.5-7.0); and a strong inner spine of P5. They also present at least one or two groups of hairs on the distal part of the caudal side of antennary basipodite. In many species of this group, the inner spine of the coxopodite of P4 has a clear gap between the hairs on the outer margin.

2. A key to 17 species and subspecies belonging to the *serrulatus*-group has been provided.

3. The distribution area of *Eucyclops serrulatus* is restricted to part of the Palaearctic with some exceptions in South and East Asia. Previous data on the geographical distribution of the species around the world are revised. The records of *Eucyclops serrulatus* outside of this recognized area (in Japan, Australia, North America, and likely other zoogeographic zones) may probably be interpreted as the result of recent invasions caused by human activities. One plausible explanation could be the transport of fresh water via ship traffic. Extensive studies including molecular-genetic tests (including barcoding) should be developed to confirm or refute the origin of these *E. serrulatus* f. *typica* enclaves outside the area of distribution considered at present as the natural one. Such studies should give new insights in order

to explain how the genus could have radiated and which routes of dispersal have been followed to lead to the current distribution of the *serrulatus*-group, but also of the entire genus *Eucyclops*. The cosmopolitanism of the genus as evidenced nowadays, without considering anthropogenic actions that introduce a bias that is by no means negligible, confirms that the genus is very ancient. Further studies of phylogeography, in combination with a complete revision of the genus, would certainly yield an important advance in our knowledge of the historical pathways, both phylogenetically and zoogeographically.

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