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Research article

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Redescription and taxonomic notes on *Cyclops bohater* Koźmiński, 1933 and *Cyclops lacustris* G.O. Sars, 1863 (Arthropoda, Crustacea), with an identification key to the *Cyclops* species of Fenno-Scandinavia

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Abstract. The studies of *Cyclops* O.F. Müller, 1776 have more than two centuries of tradition in Fenno-Scandinavia, yet, basic taxonomic questions remain unresolved and the limits of the distributional area are very poorly understood in the majority of the taxa (11+) occurring in the region. Based on the types and other materials we redescribe two species, *C. lacustris* G.O. Sars, 1863 and *C. bohater* Koźmiński, 1933, the latter being reported here for the first time from Fenno-Scandinavia; lectotypes of both species have been designated herein. Setulation characters of the antennal coxobasis- and maxillary palp setae and P1 medial spine, as well as the spine formula of the terminal exopodal segments of the swimming legs (3433) in the adult female distinguish *C. lacustris* and *C. bohater* from their congeners. An identification key is provided to the *Cyclops* species of Fenno-Scandinavia, including information about both the female and male morphology. Although the limited material does not allow us to define the species range limits, our data nevertheless support a Northern European distribution in *C. lacustris*, and Northern and Central European distribution in *C. bohater*, while the records from the southern Palearctic need further verification.

Key words. Cyclopidae, morphology, zoogeography, freshwater, Europe.

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Introduction

Cyclops O.F. Müller, 1776, frequently being a dominant component of the zooplankton in the cold temperate and Arctic lakes, has been the focus of various fields of biology (Koźmiński 1927, 1933; Wierzbicka 1934; Lindberg 1957; Einsle 1975, 1985, 1996a; Elgmork & Halvorsen 1998; Krajíček *et al.* in press). Nevertheless, in several representatives of the genus very basic taxonomical issues have hitherto remained unresolved, and the geographic distribution of most species is poorly known.

Table 1. *Cyclops* species of Fenno-Scandinavia (Herbst 1951; Lindberg 1957; Einsle 1968, 1996a; Silfverberg 1999; Boxshall & Defaye 2013; this paper). + = species present; ? = expected in Denmark, as the species occurs in northern Germany and Scandinavia; (1) = this paper; (2) = unpublished data of MH; * = *Cyclops abyssorum divulsus* Lindberg, 1956 is here considered as a junior synonym of *Cyclops divergens* Lindberg, 1936; ** = the records may refer to more than one species.

	Denmark	Norway	Sweden	Finland
<i>C. abyssorum</i> G.O. Sars, 1863	?	+	+	+
<i>C. bohater</i> Koźmiński, 1933	?		+ (1) (Largen)	
<i>C. divergens</i> Lindberg, 1936*	+ (Bornholm)		+ (2) (Lund)	
<i>C. furcifer</i> Claus, 1857**	?		+	+
<i>C. insignis</i> Claus, 1857	+	+	+	+
<i>C. kikuchii</i> Smirnov, 1932			+ (2) (Lund)	
<i>C. kolensis</i> Lilljeborg, 1901	?		+	+
<i>C. lacustris</i> G.O. Sars, 1863		+	+	+
<i>C. scutifer</i> G.O. Sars, 1863		+	+	+
<i>C. strenuus</i> Fischer, 1851	+	+	+	+
<i>C. vicinus</i> Uljanin, 1875	+	+	+	+

Morphometric characters based on the adult female morphology and used until the eighties of the last century in *Cyclops* taxonomy are not so helpful in the identification of the male and larvae. Also, certain morphometric and body shape traits (e.g., body length, relative width of the cephalothorax, pedigers 4 and 5, P4 enp3, and relative length of the caudal rami and caudal setae) show seasonal and/or environment-dependent variation within species (Einsle 1969, 1975; Elgmork & Halvorsen 1998), or in other cases they fail to separate evolutionary lineages that diverged in ecological, cytogenetic and enzyme electrophoretic characteristics (Einsle 1996b). Morphology nonetheless is a powerful tool in species delineation when the characters are extended to the surface microstructures of the limbs and somites, as it has been demonstrated in all recently revised cyclopid genera (papers pertaining to *Cyclops*: Einsle 1985; Brandl & Lavická 2002; Hołyńska & Dahms 2004; Hołyńska 2008).

The predominantly Palearctic *Cyclops* (31 putative species) is represented by at least 11 species in Fenno-Scandinavia (Table 1).

The aim of our paper is to redescribe two species occurring in Fenno-Scandinavia, *C. lacustris* G.O. Sars, 1863 and *Cyclops bohater* Koźmiński, 1933, based on original material from the type localities and other specimens from different parts of the species ranges, and to provide a (partial) revision of the geographic distributional data. Updated morphological information, supplemented with an identification key to all reported and expected species of *Cyclops* in Fenno-Scandinavia, may significantly facilitate the limnological studies in the region, and is also needed for a comprehensive phylogenetic reconstruction of the evolutionary history of the genus.

Material and methods

Qualitative and morphometric characters were examined in the types and other specimens of *C. bohater* (adult ♀ and ♂, and copepodid IV instar) and *C. lacustris* (adult ♀ and ♂, and copepodid IV–V instars) collected in Northern and Central Europe. The collecting sites are listed in the species descriptions. Most of the specimens were observed and measured in glycerine, and for a few microscope slides (Kiefer Collection, Karlsruhe; Sars Collection, Oslo) the mounting medium was unknown to us. Telescoping somites were measured separately and summed for total body length (Koźmiński 1936). Width of a

segment was measured across its widest part. Drawings were made using a camera lucida attached to Olympus BX 50 or Nikon Ci-L compound microscopes.

Morphological abbreviations (caudal setae are coded according to Huys & Boxshall 1991)

A1	= Antennule
A2	= Antenna
Abd	= Abdomen
Ae	= Aesthetasc
Caudal seta I	= Anterolateral accessory
Caudal seta II	= Anterolateral
Caudal seta III	= Posterolateral
Caudal seta IV	= Outer terminal
Caudal seta V	= Inner terminal
Caudal seta VI	= Terminal accessory
Caudal seta VII	= Dorsal
CIV–CV	= Fourth to fifth copepodid instar
Enp1–3	= First to third endopodal segment
Exp1–3	= First to third exopodal segment
Mxl	= Maxillule
P1–P4	= First to fourth swimming leg

Institutional abbreviations:

IDD	= private collection of Ina Dimante-Deimantovica
MIZ	= Museum and Institute of Zoology PAS, Warsaw
NHMUK	= Natural History Museum, London
SMNK	= Staatliches Museum für Naturkunde, Karlsruhe
ZMLU	= Zoological Museum, Lund University
ZMO	= Zoological Museum, Oslo

Results

Taxonomy

Phylum Arthropoda von Siebold, 1848
Subphylum Crustacea, Brünnich, 1772
Subclass Copepoda Milne-Edwards, 1840
Order Cyclopoida Burmeister, 1835
Family Cyclopidae Rafinesque, 1815
Genus *Cyclops* O.F. Müller, 1776

***Cyclops bohater* Koźmiński, 1933**
Figs 1–6

Cyclops bohater Koźmiński, 1933: 105–106, 111–113, 123–124, 135, 138–139, figs 5–6, pl. 3, tab. 3.

Cyclops bohater – Lindberg 1957: 96–97, fig. 55. — Einsle 1975: 100–102, 147, fig. 3; 1993: 136–137, fig. 80; 1996a: 28–31, fig. 18. — ? Stanković & Ternjej 2007: 189–199, figs 2–12, tab. 2. — Deimantovica 2010 (part) (records from Lake Brigene only).

non *Cyclops bohater ponorensis* Naidenow & Pandurski, 1992: 27–30, fig. 1, tabs 1–2; synonymized by Pandurski (1997) as *C. abyssorum divergens* Lindberg, 1936.

non *Cyclops bohater* – Deimantovica 2010: 216–222, figs 2–5, tabs 1, 3–4.

Type material

Lectotype (designated here)

POLAND: ♀, Wigry lakes, ~132 m a.s.l., Lake Okrażle (~0.14 km² surface area) close to the southern bay of Lake Wigry proper, 54°01' N, 23°01' E, 1 Mar. 1927, leg. and det. Z. Koźmiński (NHMUK 2016. 38).

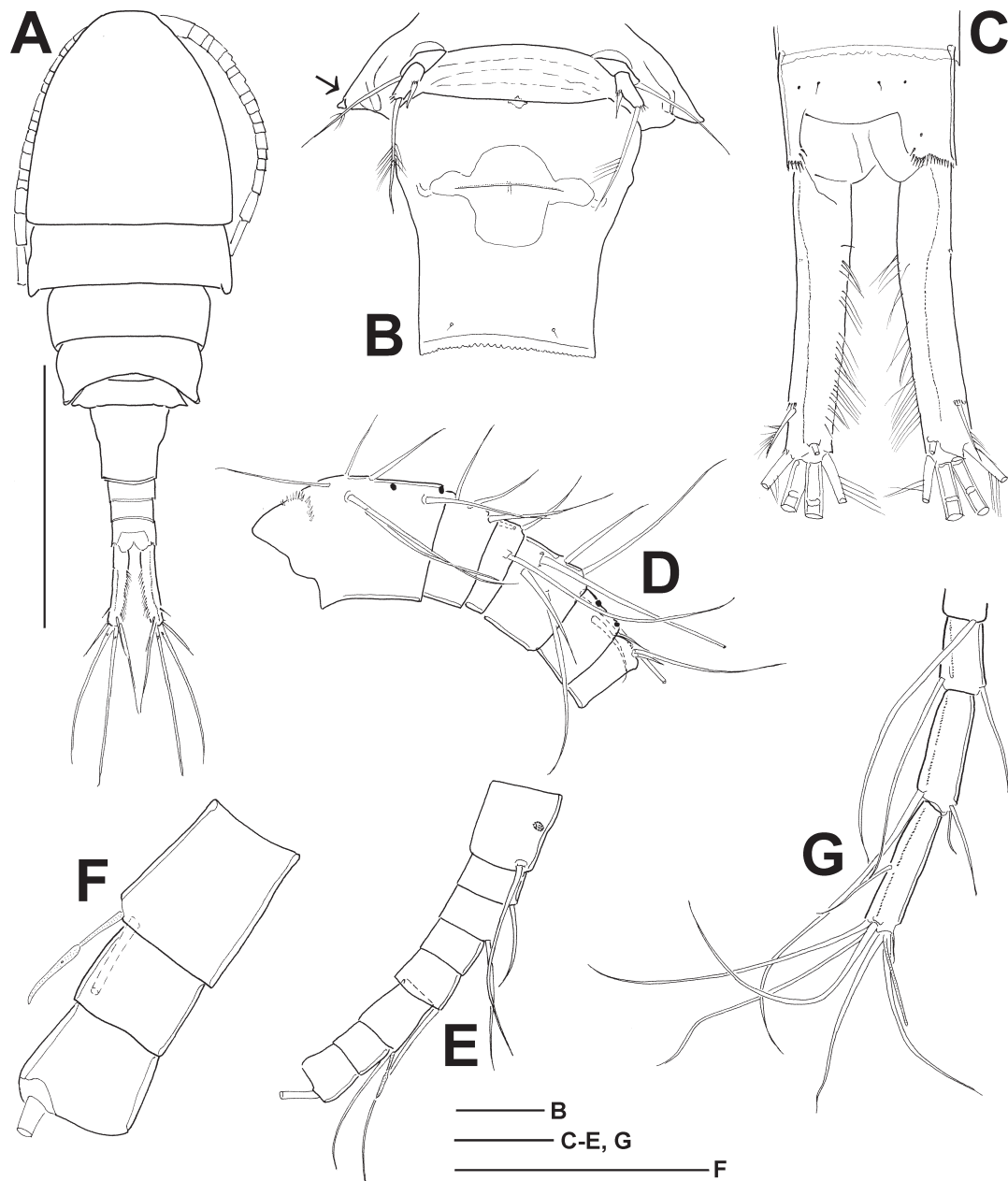


Fig. 1. *Cyclops bohater* Koźmiński, 1933, ♀. **A.** Habitus, dorsal. **B.** Pediger 5 and genital double-somite, ventral, arrow points to lateral “wing-like” protrusion of pediger 5. **C.** Anal somite and caudal rami, dorsal. **D–G.** Antennule, ventral. **D.** Segments 1–6 (I–XIV). **E.** Segments 7–14 (XV–XXIII). **F.** Segments 12–14 (XXI–XXIII). **G.** Segments 15–17 (XXIV–XXVIII). Except for A (NHMUK 2016. 39) all drawings show the lectotype (NHMUK 2016. 38). Scale bars: A = 1 mm; B–G = 100 µm.

Paralectotypes

POLAND: 1 ♀ in alcohol (NHMUK 2016. 39) and 1 ♂ dissected (NHMUK 2016. 40), same locality and collecting date as lectotype; 1 ♀ dissected on two slides (SMNK: 4396–4397) and 1 undissected ♀

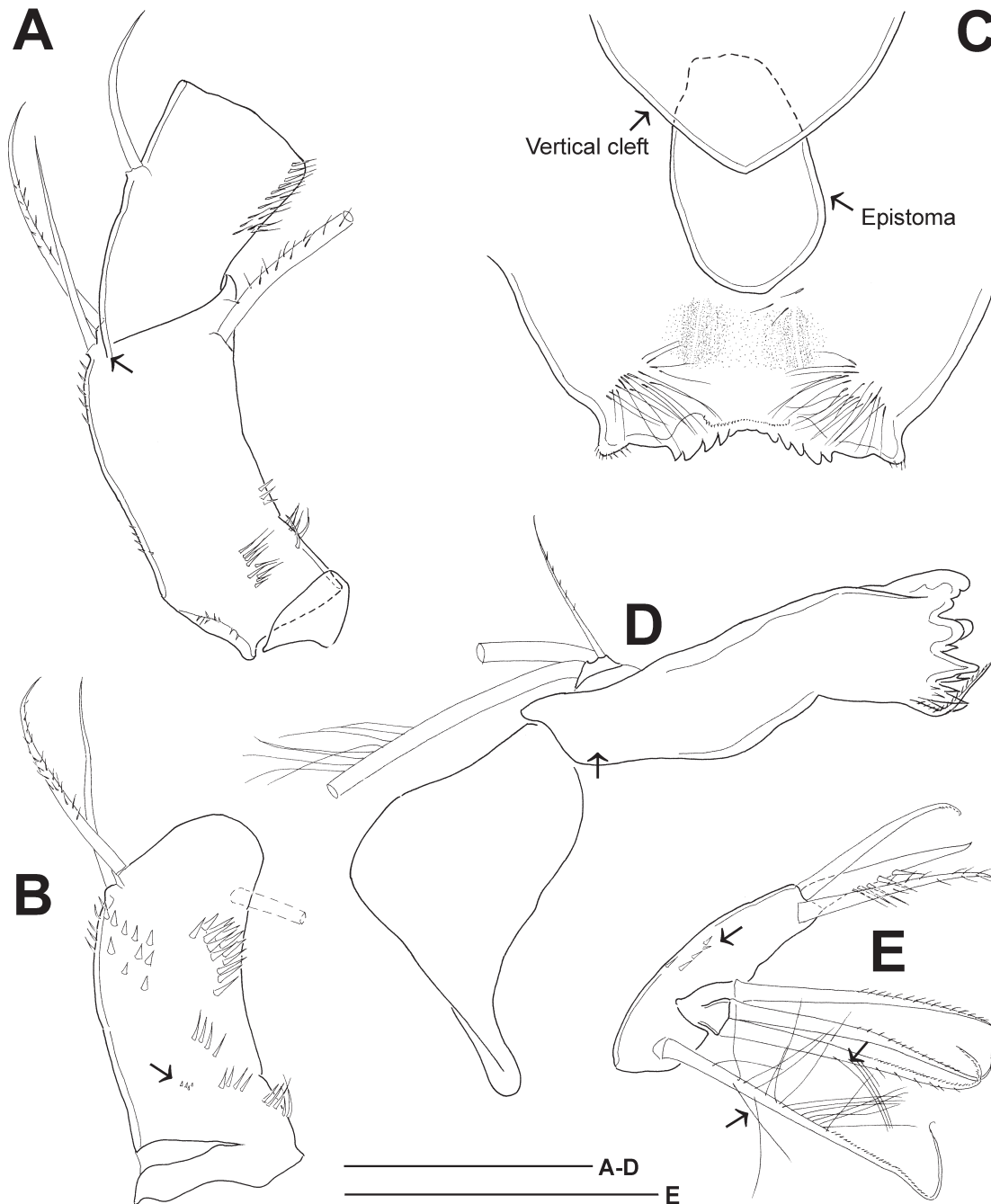


Fig. 2. *Cyclops bohater* Koźmiński, 1933, ♀. **A–B.** Surface ornamentation of antennal coxobasis. **A.** Frontal, arrow points to insertion site of long spinules missing in *C. bohater*. **B.** Caudal, arrow points to a group of spinules sometimes present. **C.** Labrum, epistoma and rostrum. **D.** Mandible, frontal, arrow points to insertion site of spinules missing in *C. bohater*. **E.** Maxillary palp, arrows point to long setules of the setae, and spinulose ornamentation of the palp. All drawings show the lectotype (NHMUK 2016.38). Scale bars: A–E = 100 µm.

(SMNK: 4398), “Wigryseen”, 54°01' N, 23°06' E, 31 Jan. 1928, leg. et det. Koźmiński, “paratype”, prep. Fr. Kiefer 13 Dec. 1939.

Other material examined

AUSTRIA: 1 ♀, Lake Wörth (Carinthia), 46°38' N, 14°09' E, 439 m a.s.l., Knut Lindberg's Collection, nr. 25, “Autriche AUT.1” (ZMLU).

LATVIA: 1 CIV ♀ toto (MIZ 2/2016/1) and 9 CIV parts (A2, Mx1, P1), Latgale region, Augshzeme, Lake Brigene, ~148 m a.s.l., 55°45' N, 26°33' E, 12 May 2008, leg. I. Deimantovica (MIZ 2/2016/2-10).

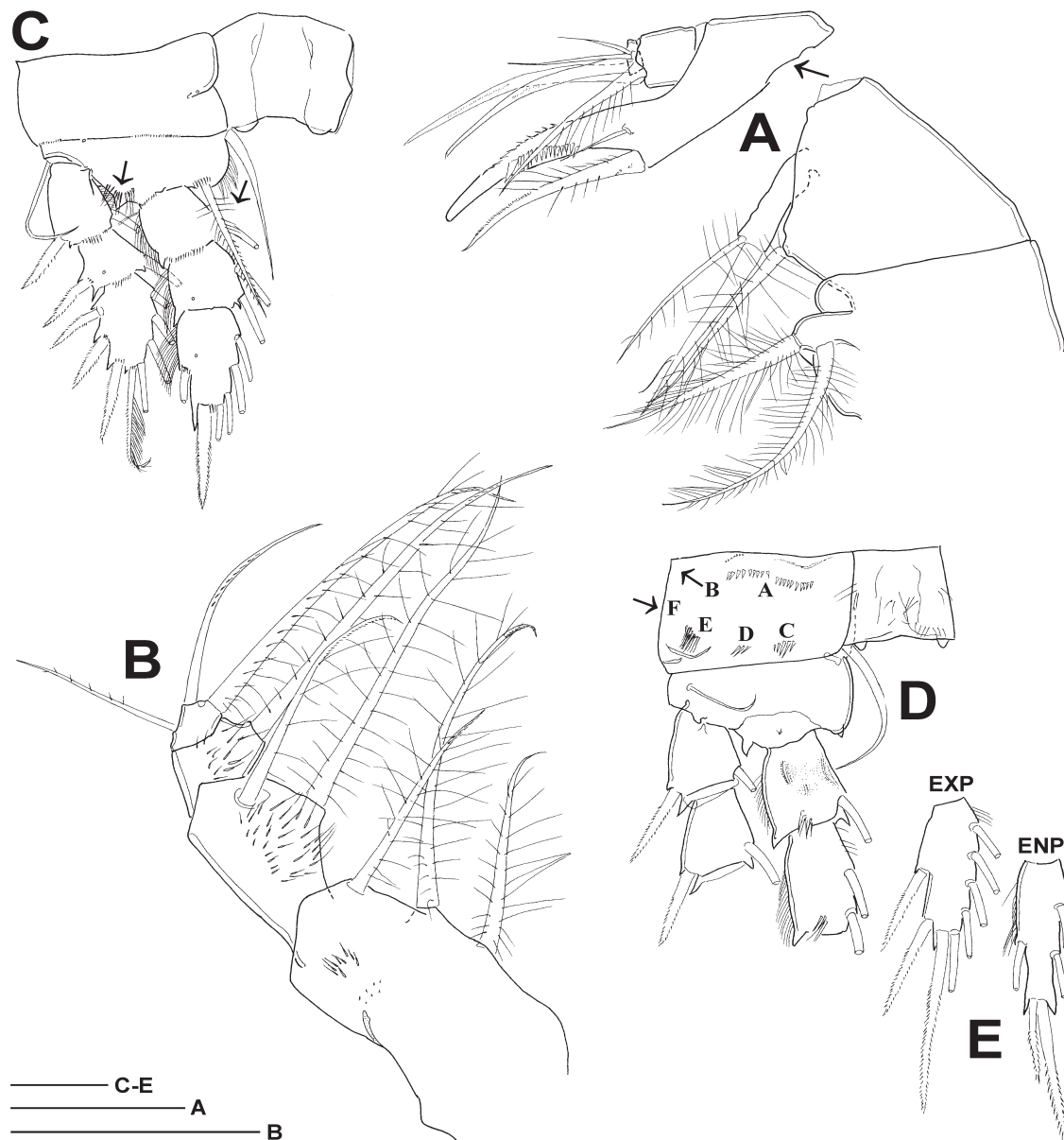


Fig. 3. *Cyclops bohater* Koźmiński, 1933, ♀. **A.** Maxilla, caudal. **B.** Maxilliped, frontal. **C.** Leg 1, frontal, arrows point to the long setules of the medial spine/seta of basipodite, and long spinules on the basipodite between the insertions of exopodite and endopodite. **D–E.** Leg 4: EXP, P4 exp 3; ENP, P4 enp3. All drawings show the lectotype (NHMUK 2016. 38). Scale bars: A–E = 100 µm.

SWEDEN: 1 ♀ (MIZ 2/2016/11), Largen, 59°35' N, 18°31' E, ~35 km NE of Stockholm, 3 Aug. 2011, leg. Oslo University; one ♀ dissected (MIZ 2/2016/12) and 1 undissected ♀ in alcohol (IDD), 3 ♂♂ dissected, same locality, 8 Nov. 2012, leg. I. Dimante-Deimantovica & B. Walseng, (MIZ 2/2016/13-15).

Description

Female

Body length 1960–2500 µm (lectotype, 2370 µm) (Fig. 1A). Cephalothorax length/width 1.05–1.14 (lectotype, 1.10), cephalothorax width/genital double-somite width 2.6–2.9 (lectotype, 2.9), prosome length/urossome length 1.5–1.8 (lectotype, 1.8). Pediger 2 (Fig. 1A) bearing distinct posterolateral lobes and conspicuously wider than succeeding somites. Pediger 5 laterally protruding, “wing-like” (Fig. 1B, arrowed).

Genital double-somite (Fig. 1B) slightly shorter than, or as long as wide. Seminal receptacle as typical in genus, transverse ridge present next to copulatory pore. Posterior margin of anal somite (Fig. 1C) with continuous row of spinules, anal sinus without surface ornamentation, anal operculum weakly developed. Caudal rami (Fig. 1C) 5.0–6.5 times as long as wide, medial margin bearing hairs. Midline crest running almost full length of ramus on dorsal surface. Few spinules present on lateral margin

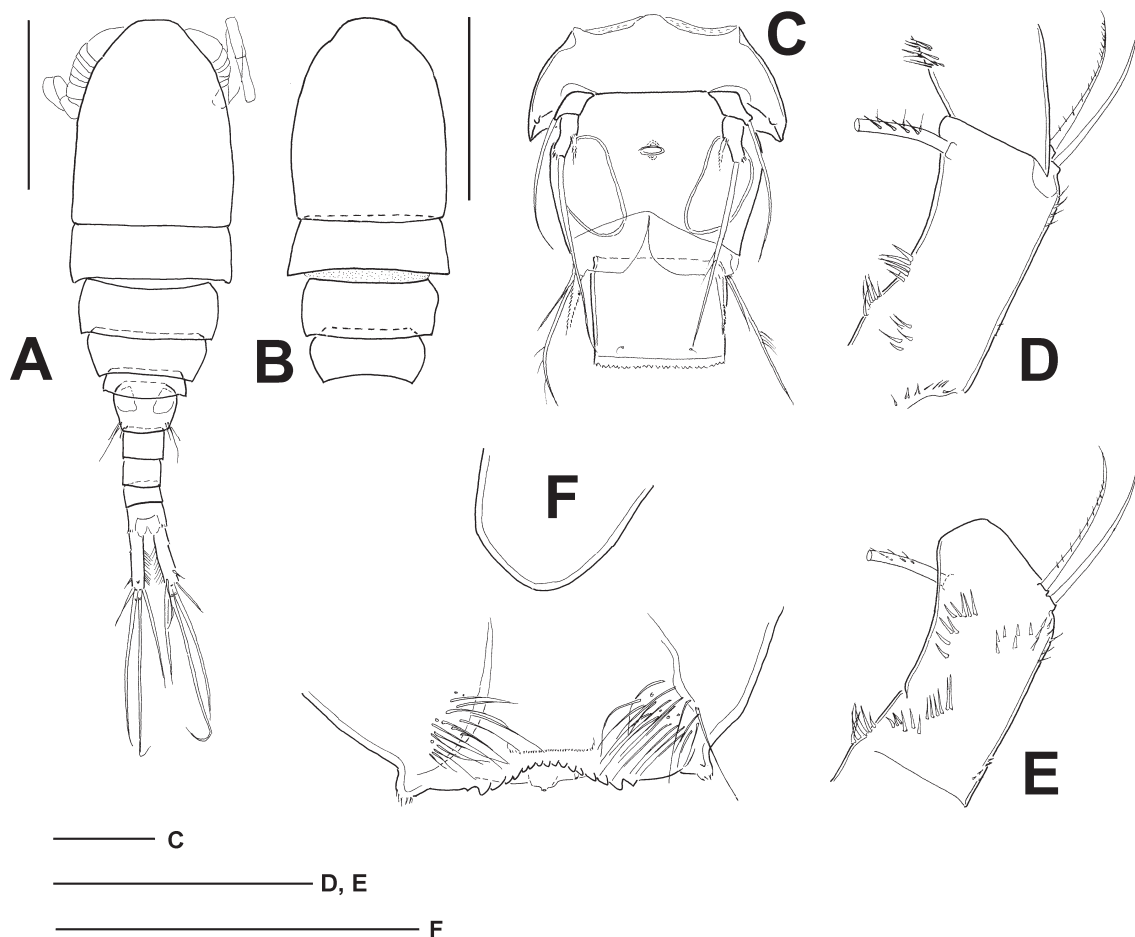


Fig. 4. *Cyclops bohater* Koźmiński, 1933, ♂. **A.** Habitus, dorsal. **B.** Prosome with distinctly wide pediger 2. **C.** Pediger 5, genital segment, and first abdominal segment, ventral. **D–E.** Antennal coxobasis. **D.** Frontal. **E.** Caudal. **F.** Labrum. Except for B (Lake Largen, Sweden – MIZ 2/2016/15) all drawings show a paralectotype (NHMUK 2016. 40). Scale bars: A–B = 500 µm; C–F = 100 µm.

in anterior third, indicating presumptive insertion site of the ancestral anterolateral accessory seta (I). Spinules also present at insertion of caudal setae II and III. Seta II inserted at distance of 0.21–0.23 ramus length measured from posterior end. Relative length of caudal setae VII, VI, V, IV, and III:

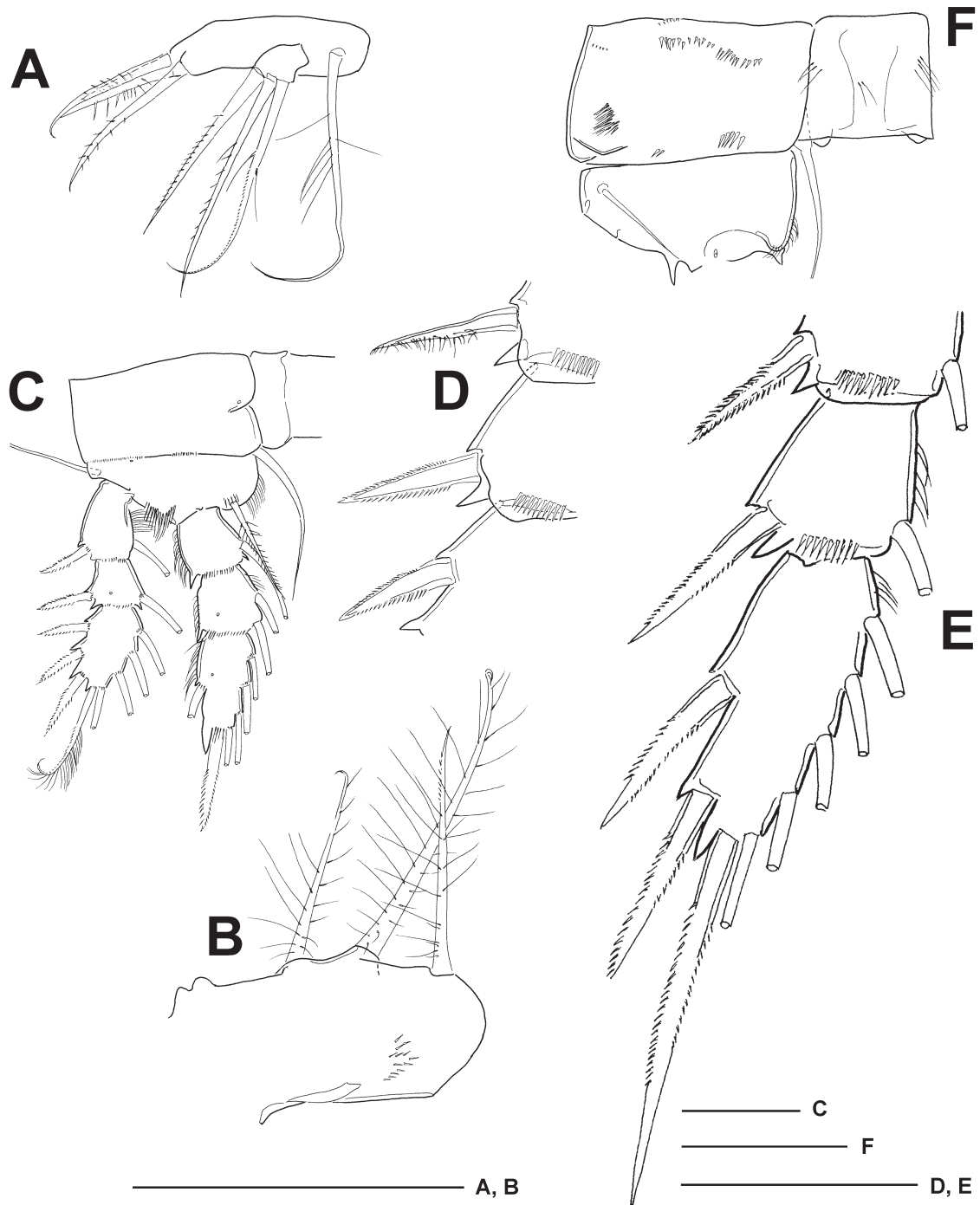


Fig. 5. *Cyclops bohater* Koźmiński, 1933, ♂. **A.** Maxillary palp. **B.** Maxilliped syncoxopodite, frontal. **C.** Leg 1, frontal. **D.** Leg 2, slender spine of first exopodal segment and robust spines of exopodal segments 2 and 3. **E.** Exopodal armature of leg 3. **F.** Leg 4 coxopodite, basipodite and intercoxal sclerite, caudal. All drawings show a paralectotype (NHMUK 2016. 40). Scale bars = 100 μ m.

1.0–1.2 (dorsal seta broken in lectotype), 1.7–2.2 (lectotype, 2.2), 3.7–4.4 (lectotype, 4.0), 2.8–3.6 (lectotype, 3.5), 1.0. Seta VI (medialmost) 1.1–1.3 (lectotype, 1.2) times as long as caudal rami, seta V (longest) 0.66–0.80 (lectotype, 0.72) times as long as urosome. Caudal setae homonomously setulose, setae IV and V with breaking plane.

Antennule (Fig. 1D–G) 17-segmented (I–V, VI–VII, VIII, IX–XI, XII–XIII, XIV, XV–XVI, XVII, XVIII, XIX, XX, XXI, XXII, XXIII, XXIV, XXV, XXVI–XXVIII) and reaching middle of pediger 2 to middle of pediger 3. Seta formula as common in plurisegmented Cyclopinae: 8, 4, 2, 6, 4, 1+sp, 2, 1, 1, 0, 1, 1+ae, 0, 1, 2, 2+ae, 7+ae. Aesthetasc on segment 12 (Fig. 1E–F) reaching distal margin of segment 13 to middle of segment 14, aesthetasc length 2.2–2.8% of body length ($n = 3$; lectotype, 2.24%). Aesthetasc on segment 16 not reaching middle of segment 17, aesthetasc length 2.1–2.7% of body length ($n = 3$; lectotype, 2.1%). Spinules only present on ventral surface of segment 1. Last three segments of antennule with hyaline membrane.

Antenna composed of coxobasis and three-segmented endopodite, and bearing 3, 1, 9 (8 in Lake Largen, Sweden – MIZ 2/2016/11) and 7 setae, respectively. Inner medial seta of coxobasis (Fig. 2A–B) with short setules, outer medial seta naked. Exopodite seta reaching beyond enp3 and bearing setules conspicuously longer in proximal than in distal section of seta. Frontal surface of coxobasis (Fig. 2A) with few spinules in $\sim 4/10$ of segment and longer spinules more proximally next to lateral margin, and distinctly long spinules in oblique/longitudinal row near middle line in proximal third of segment. Caudal surface of coxobasis (Fig. 2B) with double (single in Lake Largen, Sweden, – MIZ 2/2016/12) row of long spinules near long proximal spinules on lateral margin, elongate spinules (7–13) in longitudinal row(s) near lateral margin distally to double row, and oblique field of small spinules proximally to insertions of medial setae. Additional groups, such as small spinules medially to proximal double row (Fig. 2B, arrowed) and row of tiny spinules along presumptive proximal margin of basipodite (Lake Wörth, Austria), sometimes present.

Labrum (Fig. 2C) bearing teeth on arcuate distal margin, lateral lobes with small spinules. Distal hairs long and arranged in two groups. Epistoma and vertical cleft (Fig. 2C) naked, except for few hair-like elements on one side only next to epistoma (observed in lectotype, but missing in ♀ from Lake Wörth, Austria). Mandibular palp (Fig. 2D) with two long and one short seta, no surface ornamentation next and proximal to palp. Maxillule: setation of precoxal arthrite as typical in plurisegmented Cyclopinae. Palp with spinules (Fig. 2E, arrowed), and bearing long proximal seta, three setae on lateral lobe and three apical setae; proximal seta and at least one of lateral lobe setae with distinctly long setules (Fig. 2E, arrowed). Maxilla (Fig. 3A): precoxopodite and coxopodite fused on frontal surface but separated on caudal surface; syncoxopodite, basipodite and two-segmented endopodite with 5, 2, 2 and 3 setae, respectively. Claw-like attenuation of basipodite with spinules on both concave (inner) and convex (outer) margin. Basipodite seta inserted in front of claw-like attenuation, bearing long setules on both concave and convex edge in proximal half, and tiny spinules on convex margin in distal half of seta. Maxilliped (Fig. 3B) composed of syncoxopodite, basipodite and two-segmented endopodite with 3, 2, 1 and 3 setae, respectively. On caudal surface of basipodite spinules arranged in two groups. First endopodal segment and basipodite bearing hair-like spinules on frontal surface. Syncoxopodite frontally adorned with medium-sized or small spinules midway between median and distalmost setae, and tiny spinules more proximally next to finger-like membraneous element.

P1–P4 setation formula shown in Table 2.

Medial spine of P1 basipodite with heteronomous setulation: setules long in proximal $4/10$ (Fig. 3C, arrowed), and short spinule-like more distally. Medial spine reaching slightly beyond distal margin of enp2 to proximal $1/3$ of enp3. Long spinules (Fig. 3C, arrowed) arranged in arc on frontal surface of P1

Table 2. Armature of legs 1–4 in adult *Cyclops bohater* Koźmiński, 1933. Spines are denoted by Roman, setae by Arabic numerals. The armature on the lateral margin of any segment is given first, followed by the elements on the apical and medial margins.

	Coxopodite	Basipodite	Exopodite	Endopodite
Leg 1	0–1	1–I	I–1; I–1; II–I, 2–3	0–1; 0–2; 1–I, 1–3
Leg 2	0–1	1–0	I–1; I–1; III–I, 1–4	0–1; 0–2; 1–I, 1–3
Leg 3	0–1	1–0	I–1; I–1; II–I, 1–4	0–1; 0–2; 1–I, 1–3
Leg 4	0–1	1–0	I–1; I–1; II–I, 1–4	0–1; 0–2; 1–II–2

basipodite between insertions of exo- and endopodite. Intercostal sclerites naked on frontal and caudal surfaces in P1–P3, and sparsely pilose on caudal surface in P4. Obtuse protuberances of P4 intercostal sclerite low, hardly reaching beyond distal margin of segment, or extending well beyond it (Fig. 3D). Medial expansion of basipodite pilose in P1–P3, and naked (Fig. 3D) or bearing few short apical hairs (Lake Largen, Sweden – MIZ 2/2016/12; and Lake Wörth, Austria) in P4. Caudal surface ornamentation of P4 coxopodite (spinule groups are coded according to Einsle 1996a, see Fig. 3D) composed of: undulate line of medium-sized spinules near proximal margin (group A), with 9–16 spinules in lateral section, and 10–13 spinules in medial section; rows of spinules of unequal size along distal margin, with 3–7 spinules in medial row (group C) and 1–4 spinules in lateral row (group D); and oblique field of long spinules at laterodistal angle (group E); spinules sometimes present at lateroproximal angle (group B) (Lake Wörth, Austria) and/or lateral margin (group F) (Lake Wörth, Austria; paralectotype – SMNK: 4398). Coxopodal seta conspicuously longer (~1.9×) than height of medial expansion of basipodite. Distal margin of first and second exopodal segment of P4 naked on caudal surface (Fig. 3D), or bearing spinules. P4 enp3 2.6–2.9 times as long as wide; of apical spines medial one 1.6–2.3 times as long as lateral, and 0.94–1.10 times as long as segment.

P5 (Fig. 1B) segmentation and setation as typical in genus. Distal segment 2.0–2.3 times as long as wide. Medial spine inserted near half-length of segment (0.45–0.55 segment length measured from proximal margin), medial spine 0.5–0.9 times as long as distal segment. Lateral seta on proximal segment relatively long, 0.6–0.9 times as long as apical seta and 1.9–3.0 times as long as distal segment. Apical seta 3.1–4.0 times as long as distal segment. Spinules present at insertion of median spine and apical seta, but absent at insertion of lateral seta.

Male

Body length 1525–1685 µm (Fig. 4A), cephalothorax length/width 1.1–1.3, prosome length/urosome length 1.6–1.8. Pediger 2 without distinct posterolateral lobes, but sometimes significantly wider than succeeding prosomal segments (Lake Largen, Sweden) (Fig. 4B). Pediger 5 (Fig. 4C) laterally not protruding. Caudal rami without dorsal crest, 4.2–5.1 times as long as wide, pilose on medial margin. Short transverse row of spinules present in anterior third at presumptive insertion site of ancestral anterolateral accessory seta (I), as well as at insertion of caudal seta II and III. Seta II inserted at distance of 0.24–0.26 ramus length measured from posterior end. Relative length of caudal setae VII, VI, V, IV, and III: 1.1–1.2, 2.1–2.2, 3.4–4.0, 2.9–3.3, 1.0. Seta VI 1.6–1.8 times as long as caudal rami, seta V 0.8–0.9 times as long as urosome.

Antennule 17-segmented (verified on dorsal surface): I–V, VI–VII, VIII, IX, X, XI, XII, XIII, XIV, XV, XVI, XVII, XVIII, XIX–XX, XXI–XXIII, XXIV–XXV, XXVI–XXVIII. Armature formula 8+3ae, 4, 2, 2+ae, 2, 2, 2, 2, 1+sp+ae, 2, 2, 2, 2+ae, 2, 1+ae, 4+ae, 7+ae (setation of segment 13 and segment 17 were verified in males from Lake Largen, Sweden). Modified setae: one and two striated plates present on segment 14 and 15, respectively; and one cone-like element present on segment 14 and 15 each.

Antenna segmentation and setation as in female, except for enp2, which bears 8 or 7 setae. Spinule ornamentation of antennal coxobasis similar to that in female (Fig. 4D–E), of medial setae inner one bearing short setules and outer seta naked. Mouthparts (Figs 4F, 5A–B) similar to those in female, but bearing short setules and outer seta naked.

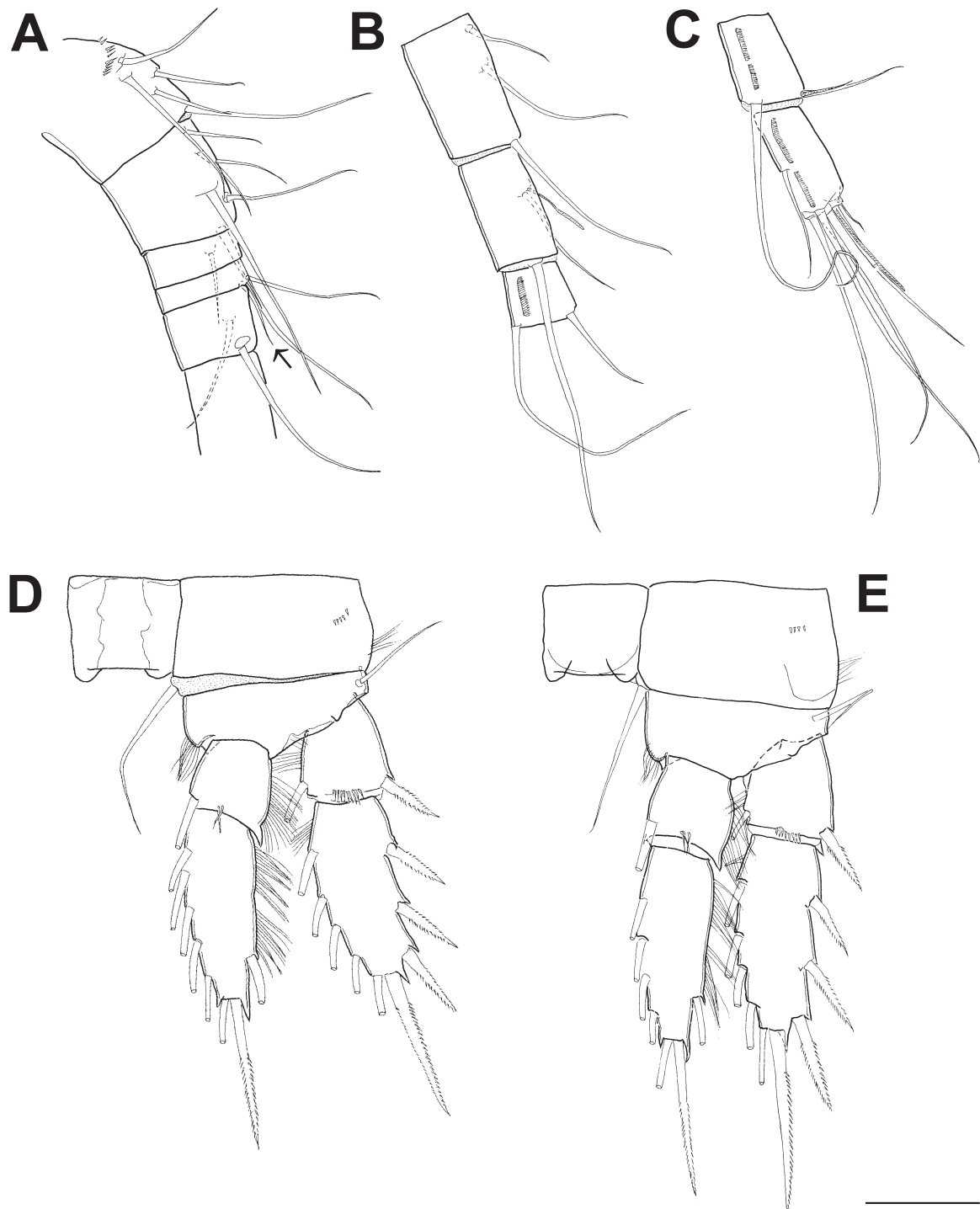


Fig. 6. *Cyclops bohater* Koźmiński, 1933, copepodid IV, ♀. **A–C.** Antennule, ventral. **A.** Segments 1–5 (I–XVI), arrow points to long anterodistal seta of ancestral segment XIV. **B.** Segments 6–8 (XVII–XXIV). **C.** Segments 9–10 (XXV–XXVIII). **D.** Leg 2, caudal. **E.** Leg 3, caudal. All drawings show specimen from Latvia (Lake Brigene – MIZ 2/2016/1). Scale bar = 100 µm.

Table 3. Armature of legs 1–4 in CIV instar of *Cyclops bohater* Koźmiński, 1933 (coding system as in Table 2).

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

spinules tiny or absent on maxillary palp, and maxilliped syncoxopodite adorned with single group of spinules midway between median and distalmost setae.

P1–P4 segmentation and setation as in female (Table 2). Medial spine of P1 basipodite (Fig. 5C) with few long setules proximally and short spinules more distally, and reaching distal margin of enp2 to proximal $\sim 1/6$ of enp3. Long spinules arranged in arc on frontal surface of P1 basipodite between insertions of exo- and endopodite. Lateral spine of P2 exp1 more slender than other spines of exopodite, and bearing long setules (Fig. 5D *cf.* Fig. 5E). Intercoxal sclerites naked in P1–P3 and sparsely pilose on caudal surface in P4. Caudal surface ornamentation of P4 coxopodite (Fig. 5F) similar to that in female, but spinules/hairs missing on lateral margin. Coxopodal seta conspicuously longer (~ 1.7 – $1.8\times$) than height of medial expansion of basipodite. Medial expansion of basipodite apically pilose in P1–P4. P4 enp3 2.9–3.2 times as long as wide. Of apical spines medial one 1.9–2.1 times as long as lateral spine and as long or slightly ($\sim 1.1\times$) longer than segment.

P5 (Fig. 4C) distal segment 2.0–2.4 times as long as wide, medial spine inserted near half-length of segment (0.47–0.58 segment length measured from proximal margin), medial spine 0.56–0.71 times as long as distal segment. Lateral seta on P5 proximal segment 0.68–0.81 times as long as apical seta and 2.9–3.6 times as long as distal segment. Apical seta 4.1–4.8 times as long as distal segment. Spinules present at insertion of median spine and apical seta, but absent at insertion of lateral seta.

P6 (Fig. 4C) composed of three elements; median- and lateral seta 0.94–1.05 times and 1.9–2.4 times as long as median spine, respectively. P6 flap naked.

Copepodid IV instar (Lake Brigene, Latvia)

Copepodid shows some important species diagnostic characters, such as: inner medial seta of antennal coxobasis with short setules and outer medial seta naked; proximal seta of maxillary palp and at least one seta of lateral lobe of palp with long setules; medial spine of P1 basipodite with few distinctly longer setules proximally and short spinules distally; long spinules arranged in arc on frontal surface of basipodite between insertions of exo- and endopodite; P5: spinules present at insertions of medial spine and apical seta, but absent at insertion of lateral seta; lateral seta (110 μm) relatively long ($0.79\times$ apical seta length).

Other features: Anal somite with continuous row of spinules along posterior margin. Caudal rami relatively short (175 μm), bearing medial hairs, longitudinal crest absent on dorsal surface. Short transverse row of robust spinules present in anterior third at presumptive insertion site of anterolateral accessory seta (I), and caudal seta II and III. Seta II (50 μm) inserted at distance of 0.31 ramus length measured from posterior margin. Length of setae VII, VI, V, IV and III, 153 μm , 260 μm , 565 μm , 425 μm , and 137 μm , respectively.

Table 4. Overview of the published records of *Cyclops bohater* Koźmiński, 1933. For comments on the data see “Discussion”. ? = dubious identification according to Maemets *et al.* 1996; * = world-catalogue or regional checklist reports without specific information on the localities and authors; n.d. = no data; E = East; N = North; S = South; W = West.

Country	Region	Habitat	Altitude (m)	References
Sweden	Central (Svealand), L. Lagen	lake	33	reported here
Estonia (?)	Peipus	lake	30	Maemets <i>et al.</i> 1996
Latvia	Latgale, L. Brigene	lake	148	Deimantovica 2010
Lithuania	Vilnius/Trakai	lakes	~100-150	Wierzbicka 1936
Ukraine	Dnieper	river		Monchenko 2003
Poland	NE: Suwalszczyzna	lakes	~130	Koźmiński 1933
	NW: Pomerania	lakes	50–135	Patalas 1954
	Central: Warsaw	clay pit pond	~80–115	Wierzbicka 1960
Germany	N: Schleswig Holstein, Lower Oder Valley	lakes and alluvial ponds	~5–45 m	Einsle 1968; Frisch 2002
	S: Lake Constance	lake	395	Einsle 1964, 1996a
Austria	N: Salzburg, Upper Austria	lakes	~480–505	Gaviria 1998
	S: Carinthia	lakes	~440–750	Einsle 1971; Gaviria 1998
Croatia	NW: Drava River basin	gravel pit lake	119	Stanković & Ternjej 2007
Switzerland	W, NE and Central: Bern, Zürich, Schwyz	lakes	~405–645	Kiefer & Einsle 1962; Kiefer 1978; Stebler 1979
*Czech Rep.	n.d.	n.d.		Dussart & Defaye 2006
France	E: French Alps	eutrophic with decomposed plants	~370–570	Dussart 1958
	W: Pays de la Loire	n.d.	~70–170	Dussart 1969
Spain	N: Burgos	lakes	~1900	Velasco <i>et al.</i> 2005
*Italy	n.d.	n.d.		Dussart & Defaye 2006
Georgia	W: Racha (L. Shaori)	dam	1105	Monchenko 1974
*Turkey	n.d.	n.d.		Ustaoglu 2004

Antennule (Fig. 6A–C) 10-segmented, homologous with ancestral segments I–V, VI–XI, XII–XIII, XIV, XV–XVI, XVII–XX, XXI–XXIII, XXIV, XXV, XXVI–XXVIII. Seta formula 5, 6, 2, 2, 2, 3, 2+ae, 2, 2+ae, 7+ae. Anterodistal seta on segment 4 (XIV), spine-like in the adult, relatively long, reaching slightly beyond distal margin of succeeding segment (Fig. 6A, arrowed). Length of aesthetascs on segment 7 (XXI–XXIII) and 9 (XXV), 60 µm and 62 µm, respectively (Fig. 6 B–C). Second endopodal segment of antenna bearing 7 setae. P1–P4 rami two-segmented (Fig. 6D–E), setation shown in Table 3.

P4: intercoxal sclerite naked, medial expansion of basipodite apically pilose; medial apical spine of endopodite much longer (3.6×) than lateral apical spine. P5 distal segment relatively short (length, 36 µm; width, 28 µm), medial spine (24 µm) inserted at distance of 0.72 segment length, measured from proximal margin. P6 armed with medial spine (50 µm) and lateral seta (81 µm).

Remarks

Cyclops bohater was originally described from Lake Wigry (max. depth 73 m, surface area 21.15 km²) and some smaller lakes (Okraęle, Długie, Muliczne and Rzepiskowe) within the vicinity of L. Wigry in the Suwałki-Augustów Lake District, NE Poland (Koźmiński 1933). The holotype of *C. bohater* was not designated in the original description (Koźmiński 1933), and we are not aware of any institution where it might be deposited. The Hydrobiological Station at Wigry Lakes, where Zygmunt Koźmiński worked and his copepod material might be left, was completely destroyed during World War II (Gieysztor 1963). We have not found any type(s) at the Museum and Institute of Zoology PAS (Warsaw) either, though

part of Koźmiński's samples (e.g., those from the Tatra Mts. and Warsaw region) are deposited here. However, some specimens from the terra typica and identified by Koźmiński himself as *C. bohater* fortunately have remained in the collections of Staatliches Museum für Naturkunde in Karlsruhe and Natural History Museum in London. The collecting data of these specimens suggest that they might constitute the material which Koźmiński's original description was based on; therefore, we selected one of those specimens as the lectotype of the species (NHMUK 2016.38). In choice of the lectotype the NHM series was preferred to the material from Karlsruhe Museum, because more characters (incl. those of the mouthparts and the morphometric traits) could be verified in the NHM specimens which were dissected by us, and the collecting data of the NHM material were fully consistent with the information provided in the original description.

Ecology

Permanent lakes and ponds, eutrophic to oligotrophic. The species is rather rare in the surface plankton, both the larvae and adult seem to prefer the deep or near-bottom waters (Koźmiński 1933, 1936; Wierzbicka 1936). The same distribution pattern was observed in a population in Lake Largen, Sweden (Dimante-Deimantovica & Walseng, unpublished data). Adults and copepodids occurred in large number in the littoral zone of a clay pit pond in Poland (Warsaw) in March, but disappeared from the littoral in late spring (Wierzbicka 1960). Einsle (1988) reported on the permanent near-shore occurrence of the species in Lake Constance (Obersee).

Cyclops bohater usually has one generation per year: reproduction from November to February, youngest copepodid instars appear early spring, copepodid V instar enters summer diapause in May and stays in the sediment on the bottom of the lake until late autumn when the larvae moult to adults. (Einsle 1988; Frisch 2002). A second summer generation appeared in the Wigry lakes (Koźmiński 1933), and Einsle (1988) also hypothesized more than one generation in the permanently littoral populations.

Distribution

Verified occurrences from Northern (Sweden, Latvia) and Central Europe (Poland, Austria) (Table 4). For a critical overview of the literature data on the geographic distribution of *C. bohater*, see the Discussion.

Cyclops lacustris G.O. Sars, 1863 Figs 7–10

Cyclops lacustris G.O. Sars, 1863: 30

Cyclops lacustris – Sars, 1914: 35–36, pl. 18. — Rylov 1948: 187–189, fig. 38, tab. 13. — Lindberg 1957: 85–87, figs 90–94, tab. 13. — Einsle 1993: 141–142, fig. 84; 1996a: 41–43, fig. 26. — Deimantovica 2010: 216–222, figs 2–5, tabs 1, 3–4.

Cyclops strenuus f. *lacustris* – Lilljeborg 1901: 31–32, pl. 2, fig. 23.

Type material

Lectotype (designated here)

SOUTHERN NORWAY: ♀, dissected on two slides labelled as “lectotypus b” and “lectotypus c”, Lake Mjøsa, 60°42' N, 11°1' E, 121 m a.s.l., surface area 369.2 km², max. depth 443 m, G.O. Sars coll., prep. Fr. Kiefer, 27 Aug. 1971 (ZMO).

Paralectotypes

SOUTHERN NORWAY: 1 undissected ♀ labelled as “lectotypus a”, 1 ♂ labelled as “lectotypus d”, same locality as in lectotype, G.O. Sars coll., prep. Fr. Kiefer, 27 Aug. 1971 (both ZMO); 2 ♀♀ and 1 ♂ dissected by the authors from vial “Sars Coll. 12977” (ZMO), and 1 ♀ and 1 ♂ dissected by the

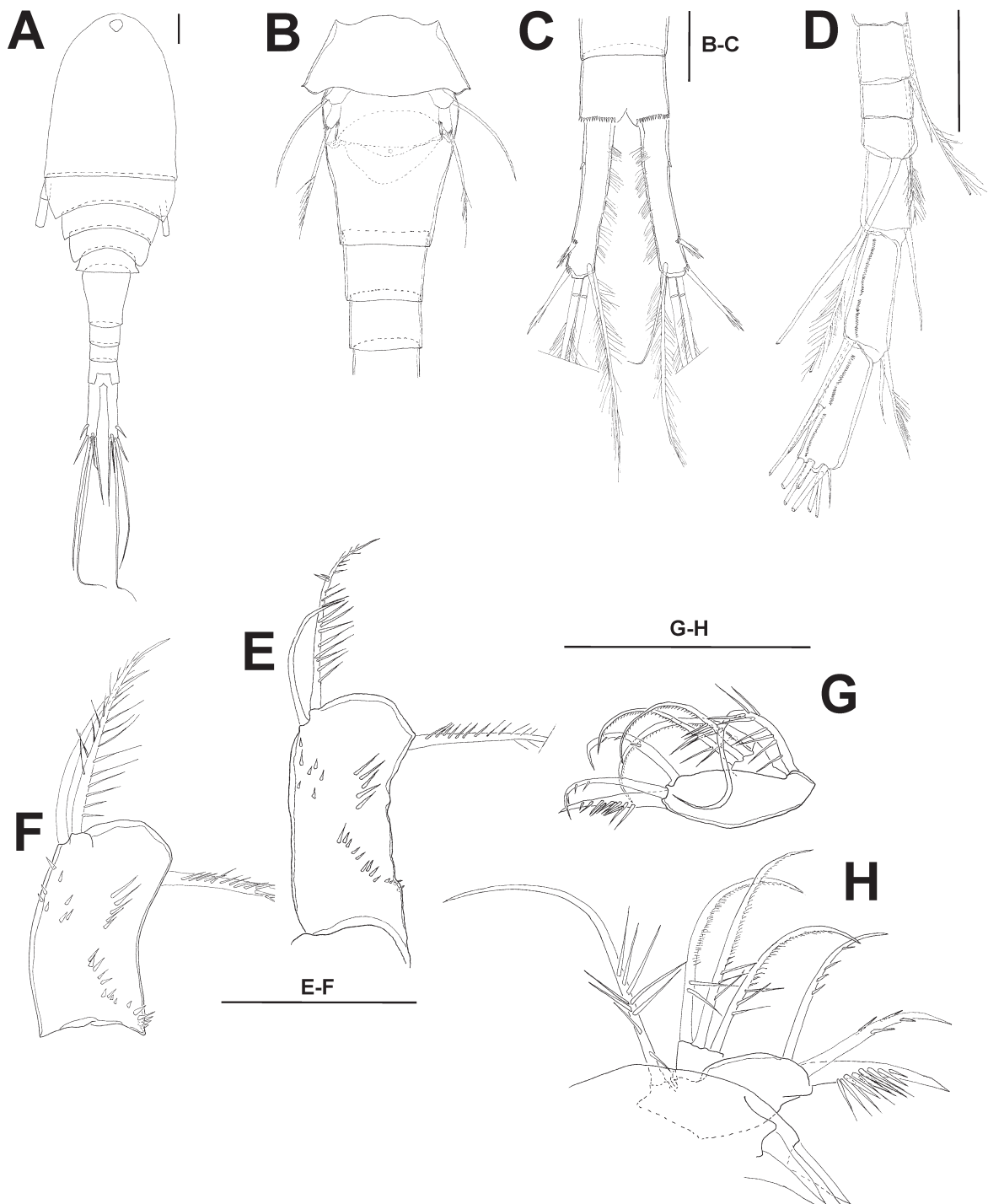


Fig. 7. *Cyclops lacustris* G.O. Sars, 1863, ♀. **A.** Habitus, dorsal (SMNK: 9567). **B–C.** Urosome, ventral (Lake Aspern, Norway – MIZ 2/2016/20). **B.** Urosomites 1–4. **C.** Anal somite and caudal rami. **D.** Antennular segments 12–17, ventral (Lake Aspern, Norway – MIZ 2/2016/20). **E–F.** Antennal coxobasis, caudal. **E.** ♀ from Lake Mjøsa, Norway (ZMO: Sars Coll. 12977 ♀-2). **F.** ♀ from Lake Aspern, Norway (MIZ 2/2016/20). **G–H.** Maxillulary palp. **G.** ♀ from Lake Mjøsa, Norway (ZMO: Sars Coll. 12977 ♀-2). **H.** ♀ from Lake Aspern, Norway (MIZ 2/2016/20). Scale bars: A–H = 100 µm.

authors from vial “Sars Coll. 12976” (ZMO); two antenna of single ♀, “*Cyclops lacustris* ♀ 2 A2 Kiefer 26.4.83, Norwegen, Mjøsen 4894, Oslo Mus. F 12977” (SMNK:11366); 1 undissected ♀ “*Cyclops lacustris* Sars, ♀ Kiefer 31 Aug. 71, Norwegen Mjøsen” (SMNK: 9567); and 2 ♀♀ dissected on two slides “*Cyclops lacustris* Sars, ♀, C. Kiefer 31 Aug. 71, Norwegen Mjøsen” (SMNK: 9568 (Abd+P5), SMNK: 9569 (A1-P4)).

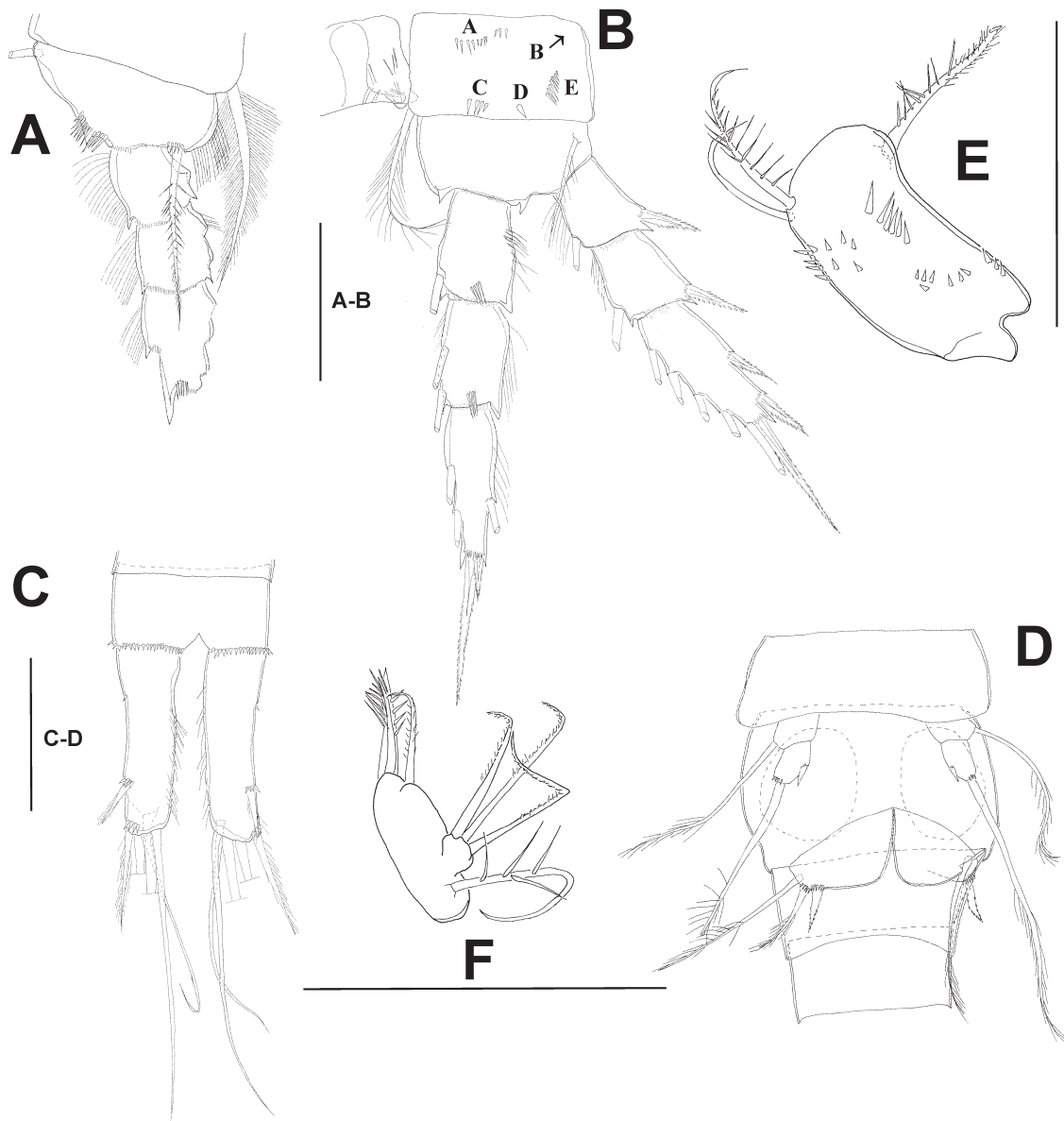


Fig. 8. *Cyclops lacustris* G.O. Sars, 1863. **A–B.** ♀. **A.** Leg 1, frontal (ZMO: lectotype designated herein). **B.** Leg 4, caudal – distal margin of the first and second exopodal segments bearing spinules on the frontal surface only (ZMO: Sars Coll. 12977 ♀-2). **C–F.** ♂. **C.** Anal somite and caudal rami, ventral (ZMO: Sars Coll. 12977 ♂-1). **D.** Urosomites 1–4, ventral (ZMO: Sars Coll. 12977 ♂-1). **E.** Antennal coxobasis, caudal (ZMO: Sars Coll. 12976 ♂-1). **F.** Maxillulary palp (ZMO: Sars Coll. 12976 ♂-1). Scale bars = 100 µm.

Other material examined

NORWAY (southern): 1 ♀, Øymarksjøen, 59°23' N, 11°39' E, 107 m a.s.l., surface area 14.3 km², max. depth 37.6 m, 18 Jul. 2012, leg. I. Dimante-Deimantovica & B. Walseng (MIZ 2/2016/16); 1 ♀, Store Le, 59°17' N, 11°48' E, 102 m a.s.l., located on the border between Norway and Sweden, surface area 136.1 km², of which 14.88 km² in Norway, max. depth 58.2 m, 2011, P.2872, leg. I. Dimante-Deimantovica & B. Walseng (MIZ 2/2016/17); 1 ♀, Aremark, 59°15' N, 11°40' E, 105 m a.s.l., surface area 7.47 km², max. depth 39.5 m, 18 Jul. 2012, leg. I. Dimante-Deimantovica & B. Walseng (MIZ 2/2016/18); 2 ♀♀, 1 ♂, Aspern, 59°9' N, 11°43' E, 105 m a.s.l., surface area 6.76 km², max. depth 46.5 m, Jul. 2011, leg. I. Dimante-Deimantovica & B. Walseng (MIZ 2/2016/19-20 and MIZ 2/2016/21, respectively).

SWEDEN: 4 ♀♀, K. Lindberg collection Lund, jar nr. 109, S. 28 (ZMLU).

LATVIA: 1 ♀ dissected (MIZ 2/2016/22) and 1 ♀ in alcohol (IDD), 1 CV ♂ parts (A2, Mx1, P1) (MIZ 2/2016/23), 2 CIV ♀♀ parts (A1, A2, Mx1, P1) (MIZ 2/2016/24-25), 4 CIV parts (A2, Mx1, P1) (MIZ 2/2016/26-29), Lake Svente, 55°51' N, 26°22' E, southeastern part of Latvia, 137 m a.s.l., surface area 7.35 km², max. depth 38 m, 30 Aug. 2007, leg. I. Deimantovica.

Description

Female

Body length 1375–1800 µm (the female here designated as lectotype was originally dissected by F. Kiefer, and no data are available on the morphometric traits of the prosome and the total body length). Cephalothorax length/width 1.1–1.3, cephalothorax width/genital double-somite width 2.6–2.8,

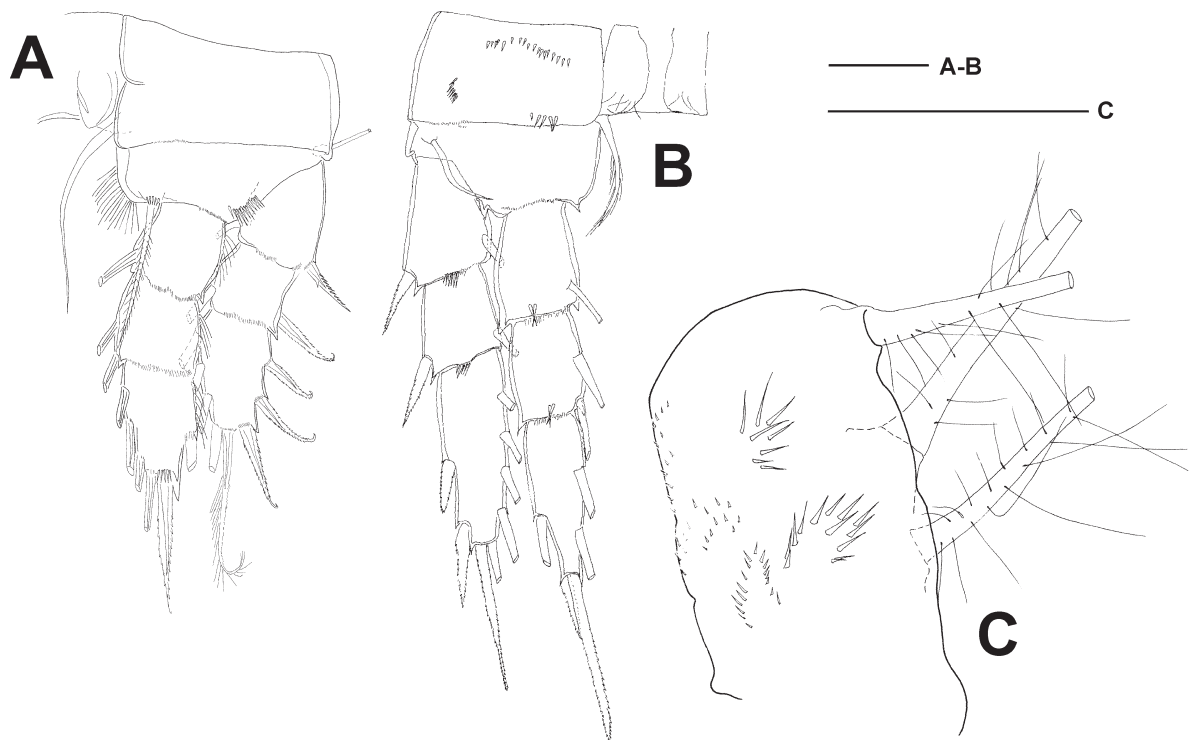


Fig. 9. A–B. *Cyclops lacustris* G.O. Sars, 1863, ♂ (ZMO: Sars Coll. 12976 ♂-1). **A.** Leg 1, frontal. **B.** Leg 4, caudal. **C.** *Cyclops vicinus* Uljanin, 1875, maxilliped syncoxopodite, frontal (Lake Østensjøvann, Norway – MIZ 2/2016/30). Scale bars = 50 µm.

prosome length/urosome length 1.4–1.7. Pediger 2 (Fig. 7A) without distinct posterolateral lobes, and not wider than succeeding somites. Pediger 5 not protruding laterally (Fig. 7B vs. Fig. 1B).

Genital double-somite (Fig. 7B) longer than its greatest width. Seminal receptacle (Fig. 7B) as typical in genus, transverse ridge present next to copulatory pore. Posterior margin of anal somite with continuous row of spinules, anal sinus without surface ornamentation, anal operculum weakly developed. Caudal rami (Fig. 7C) length/width 4.3–7.5 (lectotype, 4.9), medial margin bearing hairs. Midline crest running almost full length of ramus on dorsal surface. Few spinules present on lateral margin in anterior third, indicating presumptive insertion site of anterolateral accessory seta (I). Spinules also present at insertion of caudal setae II and III. Caudal seta II inserted at distance of 0.20–0.26 ramus length measured from posterior end (lectotype, 0.25). Relative length of caudal setae VII, VI, V, IV, and III: 1.2–2.0 (lectotype, 1.5), 1.8–2.6 (lectotype, 2.3), 3.7–6.0 (lectotype, 5.3), 3.2–4.9 (lectotype, 4.0), 1.0. Seta VI (medialmost) 1.0–1.4 (lectotype, 1.35) times as long as caudal rami, seta V (longest) 0.63–1.0 (lectotype, 0.95) times as long as urosome. Caudal setae homonomously setulose, setae IV and V with breaking plane.

Antennule reaching middle of pediger 3, segmentation and setation pattern as in *C. bohater*. Aesthetasc on segment 12 (Fig. 7D) reaching middle to distal margin of segment 14; aesthetasc length 2.9–3.6% of body length (n = 10; no data on lectotype). Aesthetasc on segment 16 reaching near insertion site of medial seta of segment 17 (approx. middle of terminal segment); aesthetasc length 2.6–3.6% of body length (n = 9; no data on lectotype). Spinules only present on ventral surface of segment 1. Last three segments of antennule with hyaline membrane.

Antenna composed of coxobasis and three-segmented endopodite, and bearing 3, 1, 9 and 7 setae, respectively. Inner medial seta of coxobasis (Fig. 7E–F) with long setules, outer medial seta naked. Exopodite seta reaching beyond enp3 and bearing setules conspicuously longer in proximal than in distal section of seta. On frontal surface of coxobasis, spinules (4, 5) present in ~4/10 of segment and group of longer spinules appear more proximally next to lateral margin, few long spinules usually present in oblique/longitudinal row near middle line in proximal third of segment (for similar pattern see Fig. 2A). Caudal surface of coxobasis (Fig. 7E–F) with double row of long spinules near long proximal spinules on lateral margin, long and thin spinules (5–7) in longitudinal row near lateral margin, and oblique field of small spinules proximally to insertions of medial setae.

Labrum with distal teeth in arc, lateral lobe with small spinules. Distal hairs long and arranged in two groups. Epistoma and vertical cleft naked. Segmentation and setation of mandible, maxillule, maxilla and maxilliped as in *C. bohater*. No cuticular ornamentation present next and proximally to mandibular palp. Maxillulary palp usually without spinules (Fig. 7G) (spinules absent in lectotype). Proximal seta and at least one (sometimes two or all three) of lateral lobe setae of maxillulary palp with distinctly long setules (Fig. 7G–H). Claw-like attenuation of basipodite of maxilla with spinules on both concave (inner) and convex (outer) margin. Basipodite seta inserted in front of claw-like attenuation with long setules on both concave and convex edge in proximal half, and tiny spinules on convex edge in distal half (for similar pattern see Fig. 3A). Maxilliped: first endopodal segment bearing long and thin spinules on frontal surface; basipodite with spinules arranged in two groups on caudal surface and long and thin spinules on frontal surface; syncoxopodite frontally adorned with small spinules midway between median and distalmost setae, tiny spinules sometimes present (Sweden, ♀-2) near finger-like membranous element (for similar pattern see Fig. 3B).

P1–P4 setation formula same as in *C. bohater* (Table 2). Medial spine of P1 basipodite (Fig. 8A): setules distinctly longer near base of seta and becoming abruptly shorter towards distal end, or length of setules almost gradually decreasing (lectotype). Medial spine reaching beyond distal margin of enp2 up to middle of enp3. Long spinules arranged in arc on frontal surface of P1 basipodite between insertions of

exo- and endopodite. Intercoxal sclerites naked on frontal and caudal surfaces in P1–P3, and sparsely pilose on caudal surface in P4. Obtuse protuberances of P4 intercoxal sclerite low, slightly extending beyond distal margin of segment (Fig. 8B). Medial expansion of basipodite usually pilose in P1–P3 and naked in P4; basipodite sometimes naked in P2–P4 (Sars Coll. 12977 ♀-1) or pilose in all swimming legs (Sweden, ♀-2). Caudal surface ornamentation of P4 coxopodite (Fig. 8B) composed of several groups of spinules (groups are coded according to Einsle 1996a): A – with 6–9 spinules in medial section and 5–10 spinules in lateral section; B – few spinules (5), group sometimes absent; C – 5–7 spinules, sometimes accompanied with 2–4 spinules directly above former row; D – usually single spinule, sometimes group of spinules (7 + 1); E – 5–8 spinules. P4 coxopodal seta conspicuously longer (1.6–2.1×; lectotype, 1.6×) than height of medial expansion of basipodite. On caudal surface, distal margin of first and second exopodal segment of P4 naked or bearing spinules. P4 enp3 2.8–3.8 (lectotype, 3.0) times as long as wide; of apical spines medial one 2.2–3.8 (lectotype, 3.4) times as long as lateral and 0.8–1.1 (lectotype, 0.95) times as long as segment.

P5 (Fig. 7B) segmentation and setation as typical in genus. Distal segment 1.9–2.3 times as long as wide. Medial spine inserted near half-length of segment (0.47–0.64 segment length measured from proximal margin; 0.60 segment length in lectotype), medial spine 0.33–0.62 (lectotype, 0.37) times as long as distal segment. Lateral seta on proximal segment relatively long, 0.70–0.90 (lectotype, 0.70) times as long as apical seta and 2.5–4.0 (lectotype, 2.5) times as long as distal segment. Apical seta 3.3–4.6 (lectotype, 3.6) times as long as distal segment. Spinules present at insertion of median spine and apical seta, but absent at insertion of lateral seta.

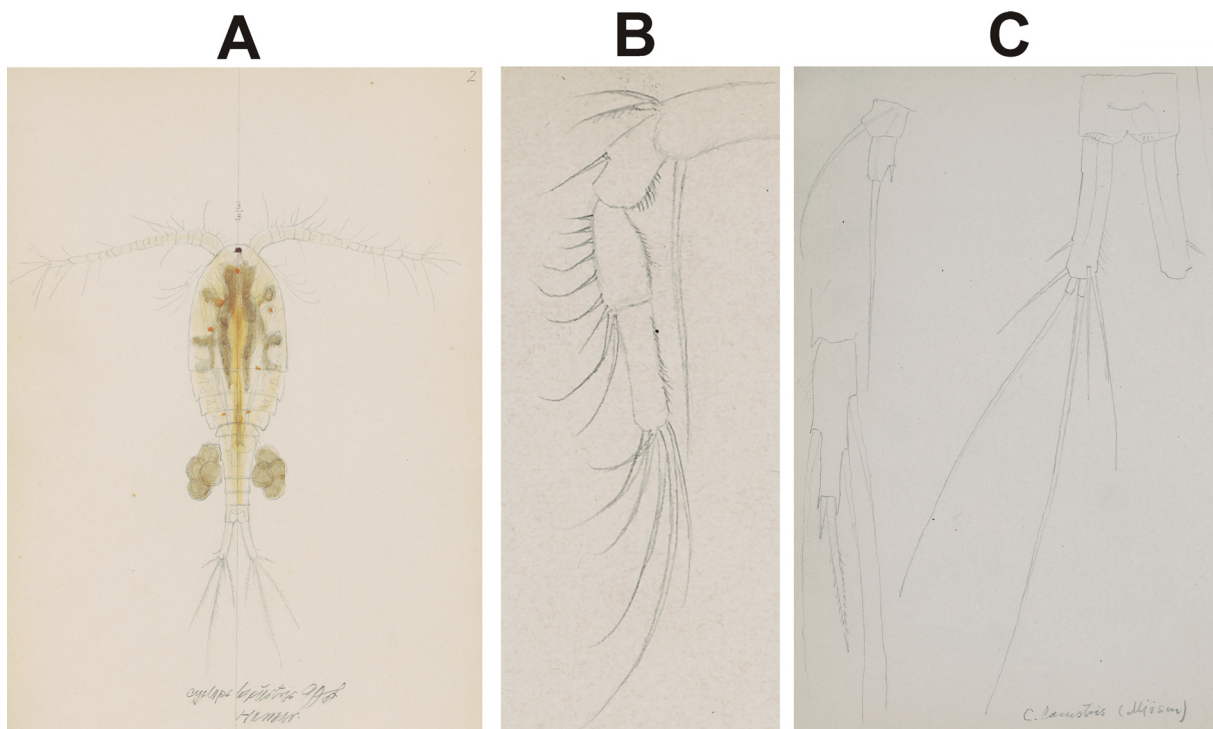


Fig. 10. Original drawings of *Cyclops lacustris*, made by G.O. Sars (Archives of the National Library of Norway, archive items – Ms.Fol. 1109: 333; Ms.Fol. 1109: 421). **A.** Habitus, dorsal. **B.** Antenna, caudal – note the long setules on the inner medial seta of the coxobasis. **C.** Leg 5, third endopodal segment of leg 4, and caudal rami with setae. All drawings show specimens from Lake Mjøsa, Norway.

Male

Body length 1135–1325 μm , cephalothorax length/width 1.3–1.4, prosome length/urosome length ca 1.6. Pediger 5 laterally not protruding. Caudal rami (Fig. 8C) without dorsal crest, 3.5–5.1 times as long as wide, pilose on medial margin. Short transverse row of spinules present in anterior third at presumptive insertion site of ancestral anterolateral accessory seta (I). Spinules also present at insertion of caudal seta II and III. Caudal seta II inserted at distance of 0.26–0.30 ramus length measured from posterior end. Relative length of caudal setae VII, VI, V, IV, and III: 1.8–2.5, 2.3–2.8, 4.1–5.4, 3.3–4.4, 1.0. Seta VI 1.5–1.7 times as long as caudal rami, seta V 0.81–0.98 times as long as urosome.

Antennule 17-segmented, but two terminal segments (ancestral segment XXV and compound segment XXVI–XXVIII) fused on ventral surface. Armature formula as in *C. bohater*. Antenna segmentation and setation as in female, except for enp2, which has 8 setae. Spinule ornamentation of antennal coxobasis (Fig. 8E) similar to that in female, inner medial seta bearing long setules, outer seta naked. Mouthparts similar to those in female. Lateral lobe setae of maxillulary palp sometimes lacking long setules (Fig. 8F). Maxilliped syncoxopodite bearing small spinules midway between median and distalmost setae (verified in male from Lake Aspern, Norway).

P1–P4 segmentation and setation as in *C. bohater* (Table 2.). Medial spine of P1 basipodite usually with homonomous setulation (Fig. 9A) and exceeding distal margin of enp2; distinctly long setules sometimes present near base of seta (Lake Aspern, Norway). Long spinules arranged in arc on frontal surface of P1 basipodite between insertions of exo- and endopodite. Lateral spine of P2 exp1 more slender than other spines of exopodite, bearing long setules. Intercoxal sclerites naked in P1–P3 and sparsely pilose on caudal surface in P4. Caudal surface ornamentation of P4 coxopodite composed of groups A, C and E; group B sometimes present (Lake Aspern, Norway) (Fig. 9B *cf.* Fig. 8B). Coxopodal seta ca 1.5 \times longer than height of medial expansion of basipodite. Medial expansion of basipodite apically pilose in P1–P3, naked (paralectotype – Sars Coll. 12976) or pilose (paralectotype – Sars Coll. 12977; Lake Aspern, Norway) in P4. P4 enp3 2.7–3.3 times as long as wide. Of apical spines medial one 2.5–3.7 times as long as lateral spine, as long or slightly ($\sim 1.1\times$) longer than segment.

P5 (Fig. 8D) distal segment 1.6–1.9 times as long as wide, medial spine inserted near half-length of segment (0.5–0.6 segment length measured from proximal margin), medial spine 0.41–0.50 times as long as distal segment. Lateral seta on P5 proximal segment 0.60–0.74 times as long as apical seta and 3.0–4.2 times as long as distal segment. Apical seta 5.0–6.0 times as long as distal segment. Spinules present at insertion of median spine and apical seta, but absent at insertion of lateral seta.

P6 (Fig. 8D) composed of three elements; median and lateral seta 1.1–1.4 times and 3.0–4.3 times as long as median spine, respectively. P6 flap naked.

Morphology of the species diagnostic characters in the late copepodid instars (Lake Svente, Latvia)

Antennule segmentation and setation in CIV instar as in *C. bohater*. Inner medial seta of antennal coxobasis with conspicuously long setules, outer medial seta naked in CIV and CV; second endopodal segment with 7 and 8 setae in CIV and CV (male), respectively. Long setules present on proximal seta of maxillulary palp and at least one seta of lateral lobe of maxillulary palp both in CIV female and CV male. Setulation of medial spine of P1 basipodite homonomous or heteronomous (few longer setules present proximally) in CIV, and heteronomous in CV male (verified in single specimen).

Remarks

The species was originally described from two large lakes (Mjøsa (or Mjøsen) and Tyrifjord) in Norway; a holotype was not designated by the author (Sars 1863). The Zoological Museum in Oslo holds the syntypes of *C. lacustris* collected by Sars from Lake Mjøsa, comprising alcohol material and few

microscope slide preparata made by F. Kiefer; the fate of the original material from Tyrifjord is unknown to us. Other parts of the Sars legacy, such as notes, manuscript drafts and unpublished drawings, are kept in the archives of the National Library of Norway. The first description of the species was part of a two-volumed hand-written manuscript (archive item Ms. Fol. 1109: 613) entitled “Om de i Christiania’s Omegn forekommende Ferskvandskrebsdyr. I og II” (On the freshwater crustaceans occurring in the vicinity of Christiania) and devoted to the Cladocera, Copepoda and Ostracoda; this work as a whole has never been published. In the archives we did not manage to identify the drawings of *C. lacustris* which Sars might have added to the above mentioned manuscript; in any case, the published description of the species (Sars 1863) did not contain illustrations. Nevertheless, the published diagnosis, the illustrations that later appeared in the monograph of the Crustacea of Norway (Sars 1914) and some fine pencil drawings of *C. lacustris* from Lake Mjøsa (Fig. 10A–C; date of origin of these drawings is unknown), deposited in the archives, allow us to identify the species with great certainty.

Kiefer (1978) provided drawings of the female habitus and the third endopodal segment of leg 4 of the “lectotypus” of *C. lacustris*, which most likely show one of the two females that he selected from among the syntypes as “lectotype” in the early seventies. These two females (one dissected on two slides, and one undissected specimen) plus one male, all of which were labelled by Kiefer as “lectotypus”, are deposited in the Zoological Museum in Oslo. As the lectotype designation by Kiefer is invalid (only one specimen can be chosen as the lectotype, ICZN art. 74.1), we designated the lectotype of *C. lacustris* herein, which is the dissected female labelled by Kiefer as lectotypus “B” (containing Abd+P5) and “C” (containing A1–P4).

Ecology

Cyclops lacustris is a true limnetic species, mostly known from comparatively large and deep oligotrophic to slightly eutrophic lakes. Adult individuals are generally found in the epilimnion, close to the surface (Sars 1914); however, the species has also been recorded down to 20 m depth and deeper (Rylov 1948). In Lake Mjøsa a significant part of the population has been found in deep waters. The vertical distribution depends on the season and developmental stage (Huitfeldt-Kaas 1946; Jarl Eivind Løvik, unpublished data).

In Norway *C. lacustris* often co-occurs with typical glacial relict species (Spikkeland *et al.* 2012). In 2006, when *C. lacustris* was evaluated for the Norwegian Red List database, it was only known from Lake Mjøsa and got included in the Red List as a critically endangered species, threatened by eutrofication (incl. oxygen decrease) and water temperature increase due to the global warming. Later, by applying new micro-characters in species identification, *C. lacustris* was discovered in several other lakes in SE Norway. The new finds indicated that the species had a wider distribution in the country than was thought before. At the moment the Red List status of *C. lacustris* in Norway has been changed from endangered to least concern (Bjørn Walseng, personal communication). The example of *C. lacustris* illustrates how alpha taxonomy may contribute to a better understanding of the actual geographic distribution of and environmental threats to a species.

Distribution

Verified occurrences from Northern Europe (Norway, Sweden, Latvia) (Table 5). For an overview of the literature data on the geographic distribution of *C. lacustris*, see the Discussion.

Table 5. Overview of the published records of *Cyclops lacustris* G.O. Sars, 1863, including the forms *C. l. suecicus* Lindberg, 1957 and *C. l. finlandicus* Lindberg, 1957. For comments on the data see “Discussion”. * = there are no recent records of the species; ** = records that need further verification; n.d. = no data; E = East; N = North; S = South; W = West.

Country	Region	Habitat	Altitude (m)	References
Norway	SE: L. Mjøsa, L. Tyrifjord *, L. Store Le, L. Øymarksjøen, L. Rødenesjøen, L. Aspern, L. Femsjø, L. Skulerudsjøen, L. Rømsjøen, L. Aremark (1)	lakes	~70–140	Sars 1863, 1914; Spikkeland <i>et al.</i> 2012; (1) (this paper).
Sweden	South (Götaland) and Central (Svealand), – incl. the largest lakes Vänern, Vättern, Mälaren	lakes	~15–270	Lilljeborg 1901; Lindberg 1957
Finland	S: L. Lohjanjärvi	lake	30	Lindberg 1957
	lakes from both the southern and northern (Finnish Lapland) regions	lakes	–	Silfverberg 1999
Latvia	E: L. Svente L. Ilzas- Geranimova, L. Raznas, L. Baltas, L. Kustaru	lakes	130–170	Line 1966; Deimantovica 2010
Estonia	n.d.	lakes.	n.d.	Monchenko 1974
Russia	NW: L. Onega, L. Ladoga	lakes	~4–130	Rylov 1948,
	Several lakes from former Karelo-Finnish SSR			
	SW: Volgograd reservoir, Veselovsky reservoir	n.d.	n.d.	Monchenko 1974
	S Siberia: Lower Multinskoe Lake in Altai	lake	1710	Rylov 1948
	W Siberia: Lower Ob	river	n.d.	Yukhneva 1970
Belarus**	NE Siberia: Kolyma	river	n.d.	Monchenko 1974
	S: Pripyat river basin	n.d.	n.d.	Monchenko 1974
Poland**	NE: L. Kolje, L. Perty (Suwalszczyzna)	lakes	~150	Karabin & Ejsmont-Karabin 1993
Germany**	N: L. Plön (Schleswig- Holstein)	lake	18	Herbst 1951
France**	n.d.	n.d.	n.d.	Boxshall & Defaye 2013
Spain**	n.d.	n.d.	n.d.	Boxshall & Defaye 2013
Ukraine**	SW: Dniester,	river		Monchenko 1974
	S: Lower Dnieper valley	river, liman	–	Monchenko 1974
Georgia**	Abkhazia	lake		Derevenskaya & Mingazova 2015
Turkey**	n.d.	n.d.		Ustaoglu 2004
Uzbekistan **	E: Kattakurgan (Zeravshan River valley)	reservoir	503–543	Monchenko 1974
Kazakhstan **	N: Kokshetau district	lakes	n.d.	Monchenko 1974
Kirgystan **	N: Chu River valley	n.d.	n.d.	Monchenko 1974
	Orto Tokoy	reservoir	n.d.	Monchenko 1974
“Caspian Sea basin” **	n.d.	n.d.	n.d.	Monchenko 2003

Identification key to the *Cyclops* species of Fenno-Scandinavia:

Character states are diagnostic both in the adult female and male (♀, ♂), or in the adult female (♀) only.

1. P1: spinules absent or tiny on frontal surface of basipodite near distal margin between insertions of exo- and endopodite (♀, ♂)2
 - P1: arc (or group) of large spinules present on frontal surface of basipodite near distal margin between insertions of exo- and endopodite (♀, ♂) (Fig. 3C, arrowed)5

2. Pediger 4 with wing-like posterolateral protrusions, that is pediger 4 wider than pediger 3 (width measured as distance between posterolateral angles of the somite) (♀). Intercoxal sclerites of P1–P3 (and usually also P4) naked on caudal surface (♀). Mandibular coxopodite with group of large spinules near palp on frontal surface (♀, ♂) (site is arrowed in Fig. 2D)3
 - Pediger 4 without wing-like posterolateral protrusions, that is pediger 4 narrower than pediger 3 (width measured as distance between posterolateral angles of the somite) (♀). Intercoxal sclerite of P3 (sometimes also P2) with hairs on caudal surface, P4 intercoxal sclerite caudally naked or pilose (♀). Mandibular coxopodite without spinules near palp (Fig. 2D) (♀, ♂)4

3. Antennal coxobasis: spinules small or sometimes absent on frontal surface at mediodistal angle of segment (site is shown by arrow in Fig. 2A) (♀, ♂); inner medial seta with long setules (for a similar setulation pattern see Fig. 7E–F) (♀, ♂). Frontal surface of maxilliped syncoxopodite with a distal (midway between insertions of median and distal seta) and proximal (midway between insertions of median and proximal seta) group of long spinules, and smaller spinules arranged in nearly ellipse line laterally to proximal group of long spinules; scattered tiny spinules sometimes also present near lateral margin (♀, ♂) (Fig. 9C)*C. vicinus* Uljanin, 1875
 - Antennal coxobasis: spinules large on frontal surface at mediodistal angle of segment (♀, ♂); setules absent or short on inner medial seta (♀, ♂). Frontal surface of maxilliped syncoxopodite with two groups of long spinules only: distal group (midway between insertions of median and distal seta) and proximal group (midway between insertions of median and proximal seta) (♀, ♂)*C. kikuchii* Smirnov, 1932

4. Antennule usually 17-segmented (18, 17, 16, and 14-segment states were found in *C. furcifer caspicus* Lindberg, 1942 from a saline marsh in Golestan Prov., Iran) (♀). Anterolateral (II) caudal seta inserted at distance of 0.18–0.23 ramus length measured from posterior end (♀). Maxillary palp: long setules present almost at full length of proximal seta and one (proximalmost) seta of lateral lobe (♀, ♂). P4 coxal seta slender: seta thickness and setulation similar to those in corresponding setae of P1–P3 (♀)*C. furcifer* Claus, 1857
 - Antennule 14-segmented (♀). Anterolateral (II) caudal seta inserted at distance of 0.24–0.29 ramus length measured from posterior end (♀). Maxillary palp: proximal seta and lobe setae without long setules (♀, ♂). P4 coxal seta usually swollen at its base (seta thicker than corresponding setae in P1–P3), and setules of seta short and robust (♀)*C. insignis* Claus, 1857

5. Maxillary palp: proximal seta bearing long setules (♀, ♂) (shown by arrow at bottom in Fig. 2E) ...6
 - Maxillary palp: proximal seta without long setules (♀, ♂)10

6. Maxillary palp: at least one of the lateral lobe setae also bearing long setules (♀) (Fig. 2E)7
 - Maxillary palp: lateral lobe setae lacking long setules (♀)9

7. Antennal coxobasis: inner medial seta with long setules (♀, ♂) (Fig. 7E–F). Dorsal (VII) caudal seta 1.2–2.1 times as long as posterolateral (III) caudal seta (♀)*C. lacustris* G.O. Sars, 1863

- Antennal coxobasis: inner medial seta naked or bearing short setules (♀-♂). Dorsal (VII) caudal seta shorter or just slightly longer (max. 1.2×) than posterolateral (III) caudal seta (♀)8
- 8. P1 basipodite: medial spine proximally bearing long setules/spinules (♀, ♂) (Fig. 3C, arrowed). Terminal accessory (VI) caudal seta longer than caudal ramus (♀). Dorsal caudal seta as long or slightly longer than posterolateral (III) caudal seta (♀). Caudal surface ornamentation of P4 coxopodite: group “E” present (Fig. 3D) (♀) ***C. bohater*** Koźmiński, 1933
- P1 basipodite: medial spine with tiny spinules only (♀, ♂). Terminal accessory (VI) caudal seta shorter than caudal ramus (♀). Dorsal caudal seta usually shorter than posterolateral (III) caudal seta (♀). Caudal surface ornamentation of P4 coxopodite: group “E” absent or present (*cf.* Fig. 3D) (♀) ***C. heberti*** Einsle, 1996
(Occurrence of the species is expected in Fenno-Scandinavia.)
- 9. Maxillary palp with transverse row or large spinules near base of palp and field of tiny spinules more apically (♀, ♂) ***C. divergens*** Lindberg, 1936
(Synonyms: *C. abyssorum divulsus* Lindberg, 1956 and *C. singularis* Einsle, 1996)
- Maxillary palp naked or if spinules present they are tiny and scattered (♀, ♂) ***C. abyssorum*** G.O. Sars, 1863
- 10. Pediger 4 with wing-like posterolateral protrusions, that is pediger 4 wider than pediger 3 (width measured as distance between posterolateral angles of the somite) (♀). Anterolateral (II) caudal seta inserted at distance of $>1/3$ ramus length, measured from posterior end (♀). P5, proximal (first) segment: spinules absent at insertion of lateral seta (♀, ♂). Male antennule: first segment with single (distal) aesthetasc ***C. scutifer*** G.O. Sars, 1863
- Pediger 4 with or without wing-like posterolateral protrusions, that is pediger 4 wider or narrower than pediger 3 (width measured as distance between posterolateral angles of the somite) (♀). Anterolateral (II) caudal seta inserted at distance of $<1/3$ ramus length, measured from posterior end (♀). P5, proximal (first) segment: spinules usually present at insertion of lateral seta (♀, ♂). Male antennule: first segment with three aesthetascs 11
- 11. Spine formula on terminal exopodal segments of P1–P4, 2-3-3-3 (♀) ... ***C. kolensis*** Lilljeborg, 1901
- Spine formula on terminal exopodal segments of P1–P4, 3-4-3-3 (♀) 12
- 12. P4 coxopodite seta reaching distinctly beyond distalmost point of medial expansion of P4 basipodite (♀, ♂). Intercoxal sclerites of P1–P3 naked, P4 intercoxal sclerite caudally pilose (♀). P5, distal (second) segment: apical seta long, 2.7-4.2 times as long as segment (♀). Caudal surface ornamentation of P4 coxopodite: groups “B” and “E” usually absent (for coding of the spinule groups see Fig. 3D) (♀, ♂) ***C. strenuus*** Fischer, 1851
- P4 coxopodite seta not reaching beyond distalmost point of medial expansion of P4 basipodite (♀, ♂). Intercoxal sclerites of P3–P4 (sometimes also P2) with hairs on caudal surface (♀). P5, distal (second) segment: apical seta short, 1.6–2.3 times as long as segment (♀). Caudal surface ornamentation of P4 coxopodite: groups “B” and “E” present (for coding of the spinule groups see Fig. 3D) (♀, ♂) ***C. sibiricus*** Lindberg, 1949
(This species has often been confounded with *C. strenuus*. *Cyclops sibiricus* is distributed in Siberia and arctic North America; its westernmost occurrence is so far known from the Yamal Peninsula (Lindberg 1957); occurrence in arctic Fenno-Scandinavia is possible.)

Discussion

In the genus only three species, *C. bohater*, *C. lacustris* and *C. heberti* Einsle, 1996, share the characteristic setulation of the maxillary palp setae, namely, long setules are present in the proximal half of the

proximal seta and at least one seta of the lateral lobe of the palp (Figs 2E, 5A, 7G–H). This feature is present not only in the adult female, but it also appears in the adult male (though with intraspecific variation in *C. lacustris*) and copepodid instars (data on CIV and CV) in these species. Both the adult (female and male) and copepodid instars (data on CIV and CV) of *Cyclops lacustris* can be distinguished from *C. bohater* and *C. heberti* by the conspicuously long setules on the inner medial seta of the antennal coxobasis (Figs 7E–F, 8E vs. Figs 2A–B, 4D–E). *Cyclops heberti* differs from *C. bohater* in the lack of long setules on the medial spine of the P1 basipodite (copepodid and adult instars, both sexes), and the relatively short caudal seta VI (seta VI/caudal ramus length <1) in the adult female.

The terra typica of *C. bohater* is located in the coldest part of Poland (Kupryjanowicz 2007), mirrored in the presence of boreal elements in the region; northerly distributed *Cyclops* species, such as *C. scutifer*, *C. abyssorum* (boreo-alpine/montane) and *C. kolensis* occur in Lake Wigry and its neighbourhood. The geographic occurrence data (Table 4) seem to indicate a lowland in the north and montane in the south pattern, in a region with humid continental climate with warm summer (warmest month average below 22 °C but above 10 °C) and cold winter (coldest month average below -3 °C) (Peel *et al.* 2007). Geographic range limits of the species are poorly understood. Einsle (1996a) wrote that *C. bohater* occurred in Asia, yet except for the record (without information on the locality) from Turkey (Ustaoğlu 2004), we failed to find any publication describing Asian occurrence. The presence of *C. bohater* in Italy is questioned by Pesce (“Checklist of the Italian Copepods” <http://www.lucioPesce.net/copepods/>). Western and Southern Europe, and Western Asia, with hot summer and/or mild winter, are home to another species, *C. divergens*, which by its large body size and the appearance of posterolateral lobes on pediger 2 might be confounded with *C. bohater* (e.g., in the Ponor Mts, Bulgaria; Pandourski 1997). Also the “*tatricus*” ecotype of *C. abyssorum* (as to the taxonomical status of the “*tatricus*” form, we followed Einsle 1969, 1996a), characterized by the distinct posterolateral lobes on pediger 2, may approach the lower bound of the body length in *C. bohater*, as it was observed in a few high mountain lakes of the Pyrenees (Dussart 1979). Though the large body and the posterolateral lobes on pediger 2 still remain part of the character set that is diagnostic to *C. bohater*, other characters are also needed to unambiguously identify the species. *Cyclops bohater*, *C. abyssorum* and *C. divergens* have identical setulation on the proximal seta of the maxillulary palp (i.e. long setules are present in the proximal half of the seta); however, in *C. bohater* long setules are also present on one or more setae of the lateral lobe of the maxillulary palp (Figs 2E, 5A), while the lateral lobe setae lack long setules in *C. abyssorum* and *C. divergens*. In *C. abyssorum* setules are sometimes (rarely) present on the proximalmost seta of the lateral lobe (e.g., in 2 ♀♀, SMNK: 6306 and 8467, collected in Lake Constance and labelled by F. Kiefer as “*C. abyssorum bodanus*”), but they are much shorter ($\sim\frac{1}{3}$ of the length of the setules on the proximal seta of the maxillulary palp) than those in *C. bohater* ($\sim\frac{3}{4}$ of the length of the setules on the proximal seta of the maxillulary palp).

Relative length of the terminal accessory (VI) caudal seta in comparison to the caudal ramus length can also be a helpful taxonomic character. There is a large variation in this trait in *C. abyssorum* (0.82–1.4) and *C. divergens* (0.73–1.1) (Holyńska 2008), yet in all the specimens of *C. bohater* that we have seen so far, caudal seta VI was longer than the caudal ramus. Therefore, we speculate that those *Cyclops* forms in which this index is less than one (e.g., in Thonon in the French Alps – see table II in Dussart 1958) might be not conspecific with *C. bohater*.

In the male, a useful diagnostic character is the relative length of the median seta of P6, which is as long as the medial spine of P6 in *C. bohater*, while it is distinctly longer than the medial spine in *C. divergens* (1.4–2.3 times) and *C. abyssorum* (1.1–1.9 times).

The species range limits of *C. lacustris* (Table 5) remain poorly understood as well, but the recent taxonomic literature suggests it being a predominantly northerly distributed species: Fenno-Scandinavia,

Latvia, Estonia, northwestern Russia (Lindberg 1957; Rylov 1948; Monchenko 1974; Einsle 1996a; Silfverberg 1999; Dussart & Defaye 2006; Deimantovica *et al.* 2011). *Cyclops lacustris* was also reported from two smaller lakes (Kojle, 17 ha; and Perty, 20 ha) in a limnological study in NE Poland (Karabin & Ejsmont-Karabin 1993), but the records have not been confirmed by later finds of the species. The occurrence in northern Germany (Lake Plön) is uncertain as well. In a paper about the crustaceans of the small bodies of water in Schleswig-Holstein, Herbst (1951: 491) wrote that *C. lacustris* (along with *C. abyssorum*, *C. kolensis* and *C. vicinus*) lived in the plankton of Lake Plön in the spring of 1949; however, Herbst did not mention *C. lacustris* in his later studies on the zooplankton of Lake Plön (Herbst 1953, 1955). Monchenko (1974) overviewed the taxonomical and limnological literature from the territory of the former Soviet Union (Table 5), mentioning the alleged occurrence of *C. lacustris* in the western/southwestern regions of the USSR, Central Asia and Siberia, and supposed that the species could have been transported to southern latitudes by rivers. Nonetheless, we think that all southern records, also those from France, Spain (see Boxshall & Defaye 2013) and the Caspian Sea basin (literature data cited in Monchenko 2003), need to be confirmed.

Based on morphometric differences Lindberg (1957) described two subspecies from Fenno-Scandinavia: *C. lacustris suecicus* Lindberg, 1957 from the Lakes Malären and Ylen in Sweden, and *C. l. finlandicus* Lindberg, 1957 from the Lake Lohjanjärvi in Finland. Lindberg also reported on the occurrence of *C. lacustris* s. str. (among others from Lake Stora Le, from where we also have material) and transitional forms (in Lake Vänern) between the “typical” form and *C. l. suecicus* in Sweden. Table 6 shows the variation of those morphometric characters which Lindberg used to distinguish the subspecies. We can conclude that morphometric traits of the specimens here examined from Sweden (Lindberg Coll., there is no accurate information on the locality) and Latvia are within the range found in the material from Norway. The single noticeable difference observed in the Latvian specimens is a slight decrease in the length proportion of caudal setae VI and III. However, the relative lengths of caudal setae VI and III compared to the body length in the Latvian females are at the lower bound of the range of caudal seta VI and at the upper bound of the range of caudal seta III measured in the females from Norway. Both the Malären and Ylen populations of “*C. lacustris suecicus*” differ from *C. lacustris* s. str. (Norway, Sweden, Latvia – see Table 6) in the relatively long caudal seta III (see proportions “III/body I” and “VI/III”). The Ylen population also has other differences in the P5 morphology (longer medial spine on the distal segment and shorter lateral seta on the proximal segment), while the Malären specimens are distinguished by their large body size. *Cyclops lacustris finlandicus* differs from the nominate subspecies in the large body length, wider pediger 5 and the longer caudal seta III. The types of these two subspecies were not designated in the original description (Lindberg 1957); therefore, examination of the topotype material might elucidate the taxonomic position of *C. lacustris suecicus* and *C. lacustris finlandicus*. In some older taxonomic works (e.g., Dussart 1969) the taxa originally described as *C. strenuus* var. *laevis* Losito, 1902 (Central Italy) and *C. rubens* f. *corsicana* Lindberg, 1955 (Corsica) were also treated as subspecies of *C. lacustris*. In the recent literature (Einsle 1975, 1996a; Dussart & Defaye 2006) both taxa are referred to as subspecies of *C. abyssorum*. Both the “*laevis*” and “*corsicanus*” subspecies need revision to clear up their accurate taxonomic relationships to *C. abyssorum* and its close relatives (e.g., *C. divergens*).

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Table 6. Variability of the morphometric traits in the female of *C. lacustris* G.O. Sars, 1863. The morphometric characters selected here are those which showed no or very slight overlapping between *C. lacustris lacustris* (Sweden), *C. lacustris suecicus* Lindberg, 1957 and *C. lacustris finlandicus* Lindberg, 1957 (see Lindberg 1957: 190–191). Number of the specimens examined is given in parentheses after the mean value. * = Data taken from Lindberg 1957. *C. lacustris suecicus* was described from the lakes Malären (Mal) and Ylen (Yle) in Sweden. *C. lacustris finlandicus* was described from Lake Lohjanjärvi in Finland. n.d. = no data. Underlined values are those which are distinctly out of the range of the Norwegian populations.

	<u>Mjøsa (type loc.)</u>		<u>Norway</u>		<u>Sweden</u>		<u>Latvia</u>		<u>"suecicus"</u> *		<u>"finlandicus"</u> *	
	(range)	mean	(range)	mean	(range)	mean	range	range	(range)	mean		
Body l (µm)	(1375–1545)	1488 (5)	(1375–1800)	1571 (7)	(1560–1585)	1576 (4)	1580, 1800 (2)	1787 (Yle)	2029 (Mal)	(1914–2126)	2018 (6)	
VII/body l (%)	(90–110)	100 (5)	(90–110)	99 (7)	(90–100)	97 (4)	100 (2)	94.4 (Yle)	107 (Mal)	(102–116)	109 (5)	
VII/caud r l (%)	(74–91)	85 (8)	(67–93)	83 (13)	(67–78)	73 (4)	79, 80 (2)	63.9 (Yle)	72.5 (Mal)	(72.6–79.7)	75.5 (5)	
VII/III (%)	(133–194)	149 (8)	(125–205)	153 (13)	(144–172)	155 (4)	143, 147 (2)	84.9 (Yle)	120 (Mal)	(119–154)	135 (5)	
III/body l (%)	(58–73)	67.5 (5)	(58–73)	67.9 (7)	(60–67)	62.8 (4)	69, 73 (2)	89.4 (Mal)	111 (Yle)	(75.6–95.5)	81.0 (6)	
III/caud r l (%)	(47–63)	57.7 (8)	(40–64)	54.9 (13)	(45–50)	47.3 (4)	55, 54 (2)	60.3 (Mal)	75.2 (Yle)	(47.1–63.0)	55.4 (6)	
VI/III (%)	(214–261)	228 (8)	(204–261)	227 (13)	(235–247)	240 (4)	183, 200 (2)	164 (Yle)	179 (Mal)	(205–225)	219 (6)	
P5 sp/segm (%)	(33–61)	43 (6)	(33–62)	47 (11)	(42–45)	43 (4)	50 (1)	62.8 (Mal)	80.0 (Yle)	(42.8–69.7)	59.0 (6)	
P5 lat s/ap s (%)	(70–88)	79 (2)	(70–94)	82 (7)	(72–76)	73 (3)	71 (1)	50.3 (Yle)	66.6 (Mal)	(73.3–82.5)	78.5 (5)	
P5 ap s/body l (%)	81, 105 (2)		(81–105)	90.8 (4)	(78–98)	87.5 (3)	87 (1)	84.8 (Mal)	85.4 (Yle)	(81.1–106)	96.4 (6)	
Ped5 w/body l (%)	134 (1)		(134–151)	142 (3)	(133–147)	138 (4)	146 (1)	n.d.		180, 188 (2)		

Body l = body length; **VII/body l** = length of dorsal caudal seta / body length; **VII/caud r l** = length of dorsal caudal seta / length of caudal ramus; **III/III** = length of dorsal caudal seta / length of posterolateral caudal seta; **III/body l** = length of posterolateral caudal seta / body length; **III/caud r l** = length of posterolateral caudal seta / length of caudal ramus; **VI/III** = length of terminal accessory caudal seta / length of posterolateral caudal seta; **P5 sp/segm** = length of medial spine on the distal segment of leg 5 / length of the distal segment of leg 5; **P5 lat s/ap s** = length of lateral seta on the proximal segment of leg 5 / length of apical seta on the distal segment of P5; **P5 ap s/body l** = length of apical seta on the distal segment of P5 / body length; **Ped5 w/body l** = max. width of pediger 5 / body length.

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