



## A revision of the subgenus *Eurycercus* (*Eurycercus*) Baird, 1843 emend. nov. (Cladocera: Eurycercidae) in the Holarctic with the description of a new species from Alaska

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### Abstract

Frey (1975) subdivided the genus *Eurycercus* Baird, 1843 (Cladocera: Eurycercidae) into three subgenera: *E. (Eurycercus)* s.str., *E. (Bullatifrons)* Frey, 1975 and *E. (Teretifrons)* Frey, 1975. We conducted a revision of the subgenera *Eurycercus (Eurycercus)* and *E. (Bullatifrons)* in the Holarctic based on the morphology of parthenogenetic females and a phylogeny of cytochrome c oxidase subunit I (COI) sequences. The following six species are found to be valid: *E. lamellatus* (O. F. Müller, 1776); *E. macracanthus* Frey, 1973; *E. pompholygodes* Frey, 1975; *E. microdontus* Frey, 1978; *E. longirostris* Hann, 1982; *E. nipponica* Tanaka & Fujuta, 2002. The separation of *E. vernalis* Hann, 1982 from *E. longirostris* lacks morphological and genetic justification, so *E. vernalis* is a junior synonym of *E. longirostris*. A new species, *E. beringi* sp. nov., was found in several localities in Alaska, U.S.A. Its characters are intermediate between two subgenera sensu Frey (1975): a median keel is expressed, but only in the posterior portion of the carapace dorsum (while it is absent in *E. (Bullatifrons)* and passes through all the dorsum in *Eurycercus* s.str.); the dorsal head pores are located on the bubble-like projection (a character of the subgenus *E. (Bullatifrons)*, but the latter is sitting on a prominent transverse fold (character of the subgenus *Eurycercus* s.str.). The COI tree also does not support separation of the subgenus *E. (Bullatifrons)* from *E. (Eurycercus)*, while separation of *E. (Teretifrons)* is well-supported. So, we propose to avoid a separation of *E. (Bullatifrons)* and regard all the species previously placed there as belonging to the subgenus *E. (Eurycercus)* emend. nov. We also demonstrated that *E. macracanthus*, *E. pompholygodes*, *E. longirostris* and *E. nipponica* have much broader distributional ranges than previously known.

**Key words:** Branchiopoda, Anomopoda, taxonomy, new species, revision

### Introduction

Understanding biodiversity is among the central problems of current applied biology (Dumont 2005). Many studies have aimed to estimate the number of species in regions and in the world (e.g. the FADA project attempted to calculate a general species number for different freshwater groups in the major biogeographical zones (Balian *et al.* 2008)). But reliable estimates of species diversity are made difficult by taxonomic problems. Cladocerans (Crustacea: Branchiopoda), for example, are a typical arthropod group with such taxonomic problems - a fact that may have contributed to the underestimation of species diversity by 2–4 times (Forró *et al.* 2008). Cladoceran species are the most poorly studied of the taxonomic ranks (Korovchinsky 1996). Nevertheless, progress has been made by recent detailed revisions based on morphology (Korovchinsky 2004; Van Damme & Dumont 2008; Kotov 2009; Sinev 2009; Kotov *et al.* 2010a, 2011; Van Damme *et al.* 2011) and on a combined morphological-molecular approach (Kotov *et al.* 2006, 2009).

The family Eurycercidae Kurz, 1875 sensu Dumont & Silva-Briano, 1998 (Cladocera: Anomopoda) is comprised of a single genus *Eurycercus* Baird, 1843 with three subgenera. Individuals from this genus are the largest in size for the anomopods — up to 6 mm in length. For most of the twentieth century, *Eurycercus* was regarded to be comprised of only two species: *Eurycercus lamellatus* O. F. Müller, 1785 and *Eurycercus glacialis* Lilljeborg, 1887

(Frey 1971; Smirnov 1971). However, Frey (1973a–b, 1975, 1978) and Hann (1982, 1990) described five more species and predicted the existence of several more. Still only one species, *E. lamellatus*, was thought to be present in the Neotropics. Frey (1975) based the subgeneric distinctions on head pore morphology and the number of midgut loops.

Recently we started a global revision of the genus *Eurycercus* (Bekker *et al.* 2010; Bekker 2011). We found three different neotropical species belonging to two subgenera: *E. (Eurycercus) cf. lamellatus*, *E. (Bullatifrons) meridionalis* Bekker, Kotov & Elmoor-Loureiro, 2010 and *E. (Bullatifrons) dumonti* Bekker, Kotov & Elmoor-Loureiro, 2010. The appearance of *E. (Eurycercus) cf. lamellatus* in Brazil could be a result of human introductions, while the other two are apparently Neotropical endemics. *Eurycercus norandinus* Aranguren, Monroy et Gaviria, 2010 was published two months before us by a group of Columbian investigators (Aranguren *et al.* 2010), rendering *E. dumonti* a junior synonym of *E. norandinus*.

Cladoceran species diversity is expected to be greater in the Holarctic than in the tropics (Forró *et al.* 2008). However, freshwater ecosystems are threatened in the Holarctic and large areas have recently been altered by human activity. The following formal taxa belonging to all three subgenera sensu Frey (1975) have been recorded for the Holarctic:

*Eurycercus lamellatus* (O. F. Müller, 1785);  
*Eurycercus laticaudatus* (Fischer, 1848);  
*Eurycercus glacialis* Lilljeborg, 1887;  
*Eurycercus polyodontus* var. *goplanus* Dybowski et Grochowski, 1895 (nomen nudum);  
*Eurycercus polyodontus* Dybowski et Grochowski, 1898;  
*Eurycercus macracanthus* Frey, 1973;  
*Eurycercus microdontus* Frey, 1978;  
*Eurycercus pompholygodes* Frey, 1975;  
*Eurycercus longirostris* Hann, 1982;  
*Eurycercus vernalis* Hann, 1982;  
*Eurycercus nigracanthus* Hann, 1990;  
*Eurycercus nipponica* Tanaka & Fujita, 2002.

Our study aimed for a complete taxonomic revision of Holarctic *Eurycercus* based on morphological (parthenogenetic females) and molecular evidence.

## Material and methods

Original samples collected by us were taken using different small-sized (about 20–30 cm in diameter) plankton nets which were hauled through macrophytes and over near-shore substrates in different types of water bodies. Then each whole sample was filtered through with a mesh size range of about 30–100 mm. All filtered matter was washed to a flask with 95% alcohol and fragments of plant material were removed by small-sized forceps. Also we used numerous samples collected by many different persons using various methods of sampling and preservation. In Fig. 1 we represented only samples for which the geographic coordinates were initially known, or subsequently obtained from our colleagues, or from ‘Google Earth’ ([www.google.com/earth/index.html](http://www.google.com/earth/index.html)) and Russian ‘Yandex Maps’ ([www.maps.yandex.ru](http://www.maps.yandex.ru)) portals.

For determination, specimens were selected from preserved samples under a binocular stereoscopic microscope, and studied under an optical microscope in a drop of a glycerol-formaldehyde mixture. At least two parthenogenetic females from each locality (if possible) were dissected under a stereoscopic microscope for the study of appendages and postabdomen. Drawings were prepared using a camera lucida attached to Olympus BX 41 or Olympus CX 41 microscope.

Our anatomical terminology for *Eurycercus* is explained by Bekker *et al.* (2010). For the system of seta enumeration see previous papers by Kotov (2000, 2009). The homologies of different limb parts of the Anomopoda are explained by Smirnov & Kotov (2010).

Unfortunately, alcohol samples with *E. pompholygodes* were unavailable. Several populations of all other species were used for a genetic analysis (Table 1).

**TABLE 1.** Species names, sampling localities, and abbreviations of euryceroid specimens used for genetic analysis. The abbreviations are used in the phylogenetic tree presented in Fig. 12. Sequences from this study have the following GenBank accession numbers: JQ288022-JQ288084.

Species	Sample number	Abbreviation	Country	State	Locality	N	E	Genbank
<i>Eurycercus beringi</i> sp. nov.	AAK M-1117	USA_AK1a-b	U.S.A.	Alaska	See list of samples	64,88071	-163,6872	This study
<i>Eurycercus beringi</i> sp. nov.	AAK M-1118	USA_AK2	U.S.A.	Alaska	See list of samples	64,86812	-163,6927	This study
<i>Eurycercus beringi</i> sp. nov.	AAK M-1119	USA_AK3a-c	U.S.A.	Alaska	See list of samples	64,87424	-163,6947	This study
<i>Eurycercus beringi</i> sp. nov.	AAK M-1123	USA_AK4a-b	U.S.A.	Alaska	See list of samples	64,51325	-165,4057	This study
<i>Eurycercus beringi</i> sp. nov.	DJT no number	USA_AK5	U.S.A.	Alaska	See list of samples	64,56033	-165,4872	This study
<i>Eurycercus beringi</i> sp. nov.	AAK M-1116	USA_AK6	U.S.A.	Alaska	See list of samples	65,0475	-166,184	This study
<i>Eurycercus glacialis</i>		CAN_MBI	Canada	Manitoba	Tundra pond	58,77	-93,87	GenBankDQ310652
<i>Eurycercus glacialis</i>	AAK 2010-007	GRN1a-b	Greenland (Denmark)		Unnamed shallow pond (<1m), near Kangerlussuaq	67,1481	-50,0795	This study
<i>Eurycercus glacialis</i>	AAK 2010-008	GRN2	Greenland (Denmark)		Unnamed lake with narrow rocky shelf near Kangerlussuaq	67,1294	-50,1658	This study
<i>Eurycercus glacialis</i>	AAK M-1115	USA_AK7a-d	U.S.A.	Alaska	Kodiak#2: Shallow pond in sitka spruce temperate rainforest	57,82949	-152,351	This study
<i>Eurycercus lamellatus</i>	DJT 3-254	FIN1a-d	Finland	Lapin lääni	E8 pond near Muono #2	67,7897	23,6387	This study
<i>Eurycercus lamellatus</i>	AAK M-1418	FRA1a-b	France	Champagne-Ardenne	Nogent, Seine	48,50444	3,493889	This study
<i>Eurycercus lamellatus</i>	AAK M-1419	FRA2a-e	France	Île-de-France	Mare pont Monteuil	48,50417	3,495833	This study
<i>Eurycercus lamellatus</i>	AAK M-0782	MON1a-c	Mongolia	Olgii Aimag	A affluen of unnamed small river, region of Hoton-Nuur Lake, Mongolian Altai	48,548	88,46861	This study

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TABLE 1. (continued)

Species	Sample number	Abbreviation	Country	State	Locality	N	E	Genbank Accession number
<i>Eurycerus lamellatus</i>	AAK M-0783	MON2a-b	Mongolia	Olgii Aimag	A bay with vegetation, Hurgan Nuur	48,53542	88,48175	This study
<i>Eurycerus lamellatus</i>	AAK M-0772	MON3a-b	Mongolia	Khovd Aimag	A bay with vegetation, upstream of the Bulgan Gol (River)	47,08692	91,02839	This study
<i>Eurycerus lamellatus</i>	AAK M-0758	MON4	Mongolia	Uvs Aimag	A small puddle, left bank of Dzabhan Gol (River)	47,528	95,834	This study
<i>Eurycerus lamellatus</i>	AAK M-0788	MON5	Mongolia	Huvsgul Aimag	A pool with vegetation, a oxbow of the Delger Muren (River)	49,48756	100,3582	This study
<i>Eurycerus lamellatus</i>	AAK M-1019	RUS_ARK2a-d	Russia	Arkhangelsk Area	River Pinega near Golubino	64,694	43,396	This study
<i>Eurycerus lamellatus</i>	AAK M-1384	RUS_BUR1a-d	Russia	Buryat Autonomous Republic	Kotovo Cove, Chivyrkuy Bay, Lake Baikal	53,63433	108,9714	This study
<i>Eurycerus lamellatus</i>	AAK M-1233	RUS_KOS1	Russia	Kostroma Area	A swampy floodplain of River Kondoba, affluent of Unzha River	58,2243	44,3098	This study
<i>Eurycerus lamellatus</i>	AAK M-1231	RUS_KOS2	Russia	Kostroma Area	Puddles, remainder of the Pormich River	58,1951	44,3135	This study
<i>Eurycerus lamellatus</i>	AAK M-0948	RUS_MOS1	Russia	Moscow Area	Lake Glubokoe	55,75361	36,50417	This study
<i>Eurycerus lamellatus</i>	AAK M-0351	RUS_OMS1	Russia	Omsk Area	River Osh near village of Znamenskoe	57,12192	73,7506	This study
<i>Eurycerus lamellatus</i>	AAK M-0938	RUS_PEN2	Russia	Penza Area	A small lake on left side of Sosnovka-Ahuny road, vicinities of Penza	53,1739	45,0767	This study
<i>Eurycerus lamellatus</i>	AAK M-0594	RUS_PSK1a-c	Russia	Pskov Area	Lakhta Bay, Chudskoe Lake	58,49669	27,87267	This study

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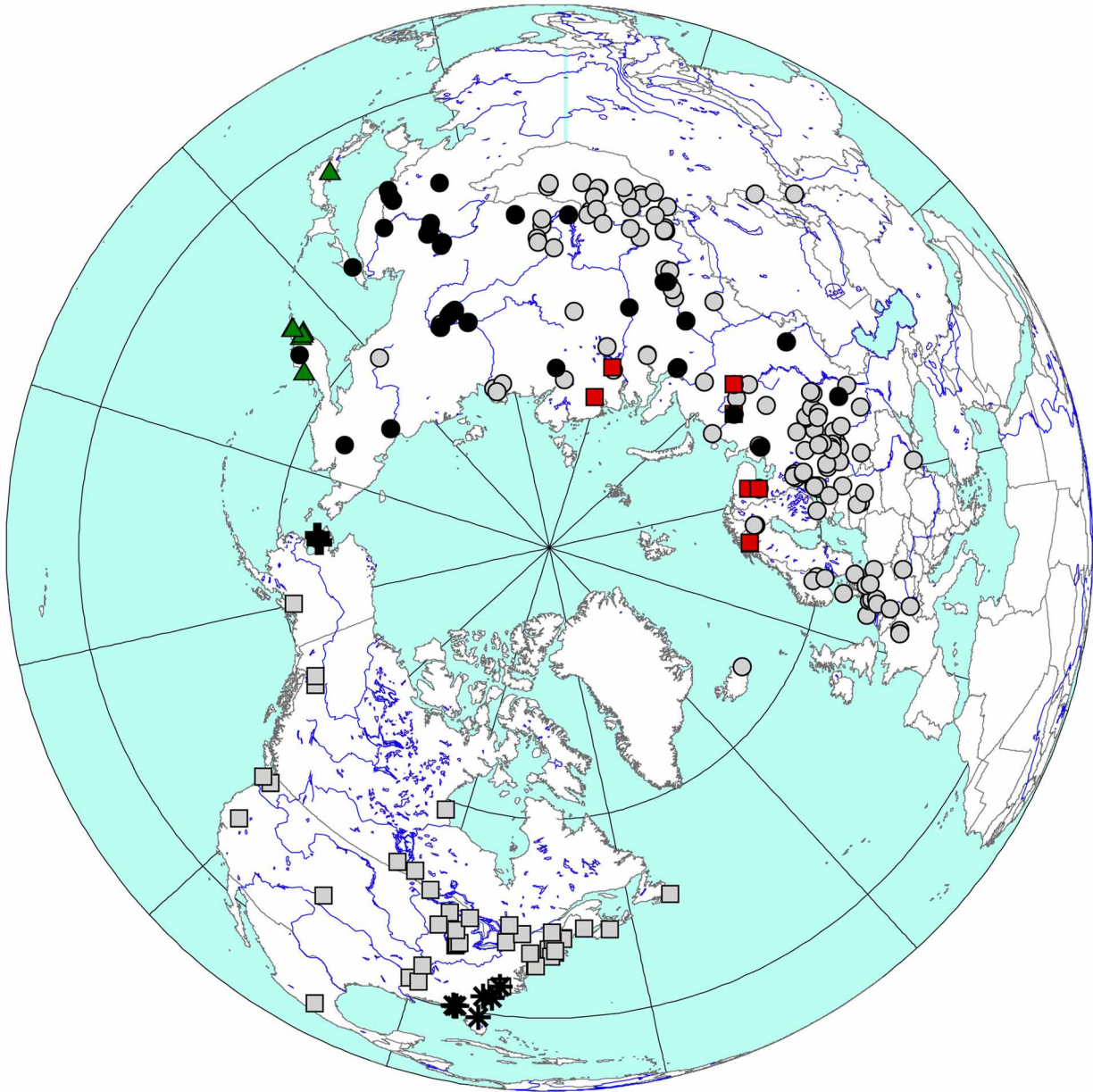
TABLE 1. (continued)

Species	Sample number	Abbreviation	Country	State	Locality	N	E	Genbank Accession number
<i>Eurycercus lamellatus</i>	AAK M-0589	RUS_PSK2	Russia	Pskov Area	Shchukinskoe Lake	56,60228	29,23992	This study
<i>Eurycercus lamellatus</i>	AAK M-0732	RUS_TAI1a-c	Russia	Taimyr Autonomous Area	A tundra pool, Khatanga	71,985	102,5472	This study
<i>Eurycercus lamellatus</i>	AAK M-0575	RUS_YAM1a-c	Russia	Yamalo-Nenets Autonomous Area	Un-named lake 1 in	66,0602	72,00614	This study
<i>Eurycercus lamellatus</i>	AAK M-0578	RUS_YAM2a-b	Russia	Autonomous Area	Nadymsky Gorodok, Lake 2 in Nadymsky	66,2208	72,04506	This study
<i>Eurycercus lamellatus</i>	AAK M-0956	RUS_YAR1	Russia	Autonomous Area	Gorodok	58,05335	38,26405	This study
<i>Eurycercus longirostris</i>		CAN_MB2a-k	Canada	Manitoba	Volga Ples, Rybinsk Water Reservoir	58,672	-94,161	GenBankJN233 928-233936
<i>Eurycercus longirostris</i>		CAN_MB3a-b	Canada	Manitoba	Burntwood River	55,82	-97,92	GenBankDQ310 651
<i>Eurycercus longirostris</i>	DJT 3-618	CAN_BCI	Canada	British Columbia	See list of samples	59,955	-132,024	This study
<i>Eurycercus longirostris</i>	DJT 3-625	CAN_YT1a-e	Canada	Yukon	See list of samples	60,4478	-133,603	This study
<i>Eurycercus longirostris</i>	AAK M-1128	USA_IN1	U.S.A.	Indiana	See list of samples	41,08	-85,9	This study
<i>Eurycercus longirostris</i>	AAK M-1124	USA_IN2	U.S.A.	Indiana	See list of samples	41,3647	-85,6775	This study
<i>Eurycercus longirostris</i>	DJT 20-129	USA_NC1a	U.S.A.	North Carolina	See list of samples	35,475	-79,075	This study
<i>Eurycercus longirostris</i>	DJT 20-004	USA_PA1a-b	U.S.A.	Pennsylvania	See list of samples	41,4154	-75,3162	This study
<i>Eurycercus longirostris</i>	DJT 20-037	USA_RI1a	U.S.A.	Rhode Island	See list of samples	41,9242	-71,7826	This study

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TABLE 1. (continued)

Species	Sample number	Abbreviation	Country	State	Locality	N	E	Genbank Accession number
<i>Euryceerus cf. longirostris</i>	DJT 3-759	CAN_NL1a-c	Canada	Newfoundland and Labrador	Ocean Pond	47,4442	-53,4118	This study
<i>Euryceerus cf. longirostris</i>	DJT 20-037	USA_R11b-c	U.S.A.	Rhode Island	Bowditch Reservoir	41,9242	-71,7826	This study
<i>Euryceerus macracanthus</i>	AAK M-1034	RUS_ARK1	Russia	Arkhangelsk Area	See list of samples	64,59211	42,85503	This study
<i>Euryceerus macracanthus</i>	AAK M-0930	RUS_PEN1	Russia	Penza Area	See list of samples	53,1727	45,0744	This study
<i>Euryceerus macracanthus</i>	AAK M-1277	RUS_PRI1	Russia	Primorski Territory	See list of samples	44,93052	131,9764	This study
<i>Euryceerus macracanthus</i>	AAK M-0578	RUS_YAM2c	Russia	Yamalo-Nenets Autonomous Area	See list of samples	66,2208	72,04506	This study
<i>Euryceerus microdonthus</i>	DJT 20-129	USA_NC1b	U.S.A.	North Carolina	Lake Carolina	35,475	-79,075	This study
<i>Euryceerus nigracanthus</i>	DJT 20-115	CAN_NL2a-c	Canada	Newfoundland and Labrador	Pond-G	49,4931	-56,4655	This study
<i>Euryceerus nipponica</i>	DJT 4-237	JPN1	Japan	Nagano	See list of samples	36,5557	137,8408	This study
<i>Euryceerus nipponica</i>	DJT 4-236	JPN2a-b	Japan	Nagano	See list of samples	36,6089	137,8542	This study
<i>Euryceerus nipponica</i>	AAK M-1344	RUS_KAM1	Russia	Kamchatka Area	See list of samples	52,92075	157,1527	This study
<i>Euryceerus</i> sp. nov.		CAN_MB2la-i	Canada	Manitoba	Weir Channel, Churchill	58,672	-94,161	GenBankGU689244, GU689246-GU689254, JN233937



**FIGURE 1.** Distribution of species from the subgenus *Eurycercus* (*Eurycercus*) **emend. nov.** in the Holarctic according to our original samples—no literature data included. *E. lamellatus*—grey circles. *E. macracanthus*—black circles. *E. pompholygodes*—solid quadrates (red in electronic version). *E. microdontus*—black stars. *E. longirostris*—grey quadrates. *E. nipponica*—solid triangles (green in electronic version). *E. beringi* **sp. nov.**—black crosses.

DNA extraction was carried out after air-drying to remove ethanol. We used a modified Quicextract (Epicentre) protocol where a single animal is ground by a Kontes micropestle in 10  $\mu$ L of extraction solution and then incubated in a final volume of 80  $\mu$ L of extraction solution for three hours at 60°C. Proteinase-K in the extraction solution was denatured by a two minute incubation at 98°C. DNA extractions were then frozen until exposed to PCR reactions. Standard PCR was carried out using Go Taq reagent mix (Promega) with primers from the COI region of the mitochondrial genome (Folmer *et al.* 1998). DNA sequencing was carried out by the High throughput DNA sequencing lab at the University of Washington (Seattle). Sequences were assembled and edited using Geneious 5 software. To assess PCR artifacts (e.g. amplification of recent pseudogenes of mitochondrial genes) we shotgun sequenced an individual of *E. glacialis* from Kodiak Island Alaska using 454 Titanium next generation sequencing (University at Buffalo). The COI region of the assembled (non-PCR) mitochondrial genome was used in the present study.

DNA sequences were aligned and translated to verify a continuous open reading frame. As there were no apparent indels, alignment was trivial. Maximum Likelihood (ML) analysis was implemented in two different ways: RAxML-HPC BlackBox on the Cipres Scientific gateway using the default GTR+G model with partitioning according to the three codon positions; and Phyml 3.0 with Seaview using a subtree pruning and reconnection search algorithm with five random starting trees and a GTR+I+G substitution model. Reliability was assessed by nonparametric bootstrapping in RAxML and approximate likelihood ratio tests (a nonparametric Shimodaira-Hasegawa-like procedure) in Seaview. Reliability values were plotted onto the best ML phylogram using Figtree.

**Information about the material examined is presented below as follows: locality, date of sampling, collector, number of sample (latitude, longitude)** (N—degree with decimals, E—degree with decimals). States of large and intensively collected countries (Russia, U.S.A. and Canada) are given in alphabetical order instead of their geographical position.

### Abbreviations for museum collections:

CMN	Canadian Museum of Nature, Ottawa, Canada.
DGF	Collection of D. G. Frey, Support Center of USNM in Suitland, Maryland, U.S.A. (accession number of whole DGF is USNM 403774).
MGU	Zoological Museum of Moscow State University, Moscow, Russia.
NHM	The Natural History Museum, London, United Kingdom.
NMK	Personal collection of N. M. Korovchinsky, Moscow, Russia.
NNS	Personal collection of N. N. Smirnov, Moscow, Russia.
NNS MGU	slides of N. N. Smirnov officially deposited to MGU.
USNM	The Smithsonian Institution Museum of Natural History, Washington, D.C., U.S.A.
ZIN	Zoological Institute of Russian Academy of Sciences, St. Petersburg, Russia.

## Results

### Morphological descriptions

#### Subgenus *Eurycercus* (*Eurycercus*) Baird, 1843 emend. nov.

Subgenus *Eurycercus* (*Eurycercus*) Baird, 1843 plus subgenus *E. (Bullatifrons)* Frey, 1975, p. 292–294; Kotov *et al.* 2010b, p. 234.

**Type species.** *Lynceus lamellatus* O. F. Müller, 1776 = *Eurycercus lamellatus* (O. F. Müller, 1776) now (Baird 1843).

**Diagnosis. Parthenogenetic female.** Body from strongly compressed laterally to almost incompressible, without median dorsal keel (Fig. 2A), with median keel passes through whole carapace dorsum and actually begins on the head behind head pores (Fig. 2C, arrow), or with median keel present only in posterior portion of carapace dorsum (Fig. 2E). Dorsal head pores on a bubble-like projection located immediately on head shield (Fig. 2A–B), or on a transverse fold in posterior portion of head shield with an indentation behind it (Fig. 2C–D), or on bubble-like projection located on a transverse fold (Fig. 2E–F), but never of a flat head shield itself. Labral keel of different size and shape. The intestine has a single loop; a posterior intestinal caecum is present.

**Comments.** In our understanding, the separation of the subgenus *E. (Bullatifrons)* from the subgenus *E. (Eurycercus)* by Frey (1975) was incorrect. See explanations in the Discussion section.

#### *Eurycercus lamellatus* (O. F. Müller, 1776)

*Lynceus lamellatus* O. F. Müller, 1776, p. 199; O. F. Müller 1785, p. 73–74, Pl.9, figs 4–6.

*Eurycercus lamellatus* (O. F. Müller) in Baird 1843, p. 88–89, Pl. 2, figs 1–8; Baird 1850, 124–125, Pl. 15, figs 1, 1a–l; Lilljeborg 1901, p. 385–393, Figs 59–60; Behning 1941, p. 241–244, Fig. 102; Herbst 1962, p. 78, Fig. 53a–e; Šrámek-Hušek *et al.* 1962, p. 313–314, Fig. 115; Flössner 1972, p. 268–272, Figs 127–128; Negrea 1983, p. 232–235, Fig. 94; Margaritora 1983, p. 101, Figs 6C, 8C, 10B, 64; Margaritora 1985, p. 203–206, Fig. 82A, C–H (not B!); Duigan & Frey 1987, p. 241–247, Pls

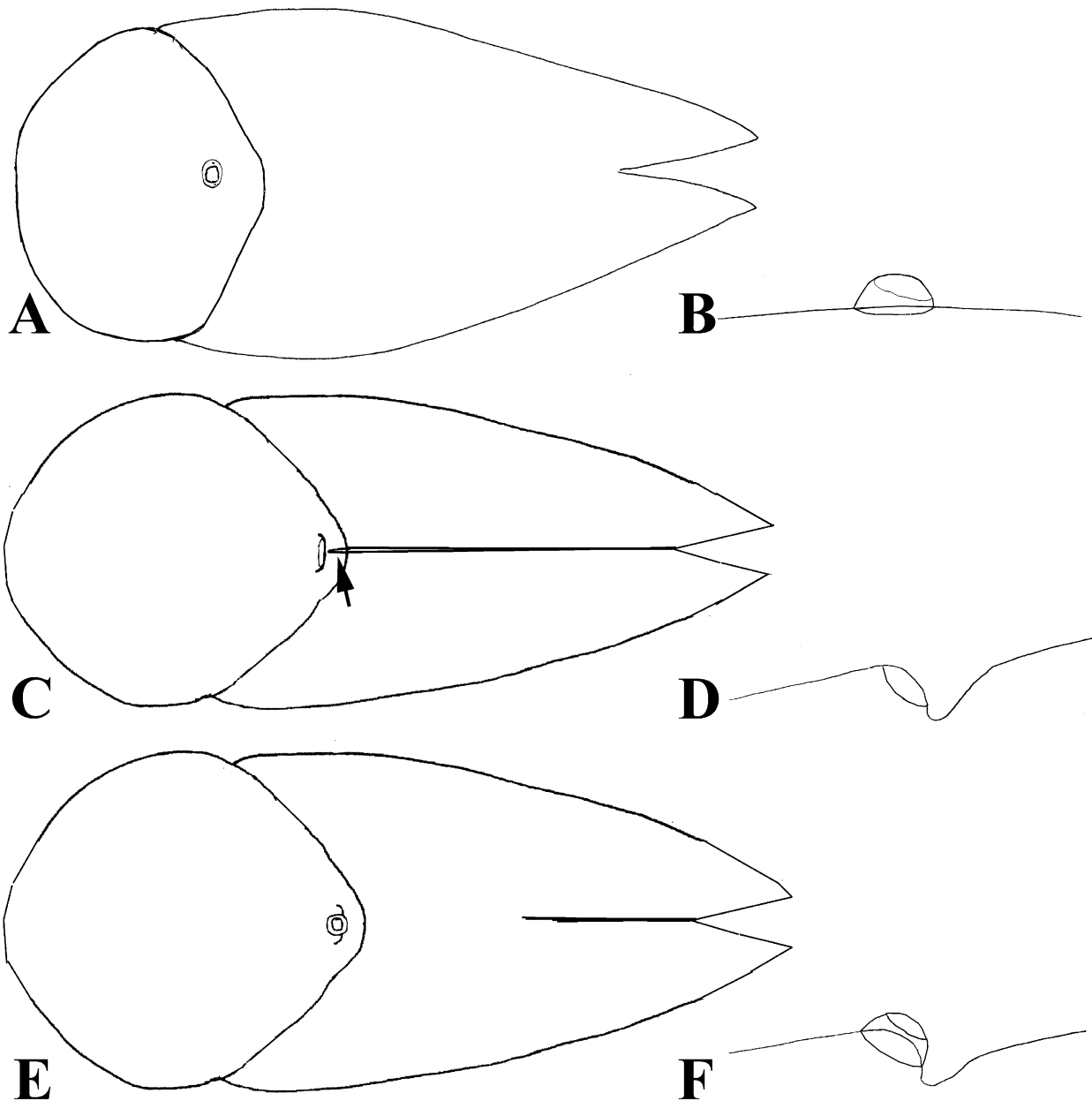


A–B; Sars 1993, p. 115–116, Fig. 85; Røen 1995, p. 193–195, Figs 89, 90A; Alonso 1996, p. 254–257, Figs 113–114; Silva-Briano 1998, p. 48–50, Figs 89–100; Flössner 2000, p. 224–227, Fig. 85; Kotov 2000, p. 160–170, Figs 1–94; Hudec 2010, p. 266, Figs 63, 63a; Kotov *et al.* 2010b, p. 234–235, Fig. 137(1–8).

*Lynceus laticaudatus* Fischer, 1848, p. 187–188, Pl. 8, figs 4–7; Fischer 1850, p. 4 (= *L. lamellatus*); Leydig 1860, p. 209.

*Eurycercus lamellatus* (Fischer) in Schödler 1862, p. 9–10.

*Eurycercus polyodontus* Dybowski & Grochowski, 1898, p. 36–37, Fig. 2 (Dybowski & Grochowski 1894, p. 380—Nomen nudum; Dybowski & Grochowski 1895, p. 149—Nomen nudum).



**FIGURE 2.** Characteristic traits of different species of *Eurycercus* (*Eurycercus*) **emend. nov.** A–B, *E. longirostris*, dorsal view and dorsal head pores in lateral view. C–D, *E. lamellatus*, dorsal view and dorsal head pores in lateral view. E–F, *E. beringi* **sp. nov.**, dorsal view and dorsal head pores in lateral view. Rather schematic, not to scale.

**Type locality.** No information on the exact locality is present in the first description (O. F. Müller 1776) and in the author’s redescription (O. F. Müller 1785). But it is known that most of Müller’s taxa were described from “Frederiksdal, located slightly north-west of Copenhagen between Fuersø and Bagsvaeds Sø” (Frey 1980), Denmark.

**Type material.** Apparently lost (Frey 1980).

**Material examined here.** Many parthenogenetic, ephippial females and males from Denmark, Iceland, Fin-

land, Norway, France, Germany, The Netherlands, Czech Republic, Lithuania, Belarus, Ukraine, different Areas of European and Asian Russia, Kirghizia, Tajikistan and Mongolia (Fig. 1). A full list will be represented in a special future publication concerning a revision of the *lamellatus*-like forms worldwide.

**Diagnosis. Parthenogenetic female.** Dorsal head pores on a transverse fold in posterior portion of head shield with an indentation behind it. In anterior view, body moderately compressed laterally, median keel passes through whole carapace dorsum and actually begins on the head behind head pores. Rostrum long. Ocellus minute. Lateral head pore elongated along longitudinal body axis. Labrum with a large median keel, terminating in an angled apex protruding beyond distal end of antenna I. Postabdomen with sub-parallel dorsal and ventral margins, preanal teeth pointed. Spines at base of pre-claw portion predominantly single. Antenna I with antennular sensory seta arising in middle. Denticles in rows encircling antennular surface relatively large and numerous. On antenna II, spine situated on proximal segment of exopod equal or longer than second segment. Limb I IDL with a hook-like seta only somewhat thicker than longest seta, smallest seta not very short. IDL with distal, proximal, marginal (which is relatively reduced) and basal group spinules. Eight setae in filter plate II, 9 setae in filter plate III; 9 setae in filter plate IV, 8 setae in filter plate V.

**Most recent redescrptions.** See Alonso (1996), Kotov (2000), Hudec (2010).

**Comments.** In the synonymy we try to represent only recent and relatively recent publications, where the determination of *E. lamellatus* was really adequate (i.e. when head pore region was accurately illustrated). Unfortunately, descriptions and illustrations in many previous publications were lacking important traits. Keeping in mind the possibility to find *E. pompholidodes* and *E. macracanthus* in Europe, we need to be critical of determinations of *E. lamellatus* in such papers, even when the authors are well-known cladocero-logists (i.e. Schödler 1862; Müller P.E. 1867; Hellich 1877; Matile 1890; Wesenberg-Lund 1894). Some authors redrew pictures by Lilljeborg (1901) to illustrate specimens from geographically distant populations. Taxonomic assignment of such redrawn specimens is uncertain. See extensive comments in Smirnov (1971) and Frey (1971).

**Distribution.** *E. lamellatus* is widely distributed in the Palaearctic from Spain in the West up to the Anadyr basin (Streletskaia 2010) in the East. Records from Chukot Peninsula, Kamchatka Peninsula and Alaska (Tash & Armitage 1967; Kurenkov 2005) could belong to some other species described below. At least, we did not see this species in our material from Beringia East of the Kolyma River. The southern border is not well-known, populations from India and Tibet (Frey, 1971) could belong to a congeneric species.

Margaritora (1985, Fig. 82B) represented a drawing of a male of "*E. lamellatus*" with a bubble-like projection in region of head pores, but it could be inadequate drawing. At present, it seems that only *E. lamellatus* occurs in Central and South Europe.

**Ecology.** See detailed analysis by Flössner (2000).

### ***Eurycercus macracanthus* Frey, 1973**

Figs 3–4

*Eurycercus macrocanthus* Frey, 1973, p. 225–248, Figs 1–2, 5–10, 23, 25–26, 28–30, 33–34, 37, 40–41, 44–45, 48–51, 61–62; Chen *et al.* 1995, p. 68–69, Figs 1–12.

*Eurycercus macracanthus* Frey, 1973, p. 593; Kotov *et al.* 2011, p. 136–138, Fig. 4.

**Type locality.** "Two small ponds in the flood plain of the Amur River across the river from Khabarovsk" (Frey 1973), Jewish Autonomous Region, Russia. There is no chance to locate exact ponds according to such comments among numerous floodplain water bodies in that region. Approximate geographic coordinates: 48.53, 134.98.

**Type material. Holotype.** A parthenogenetic female 1.50 mm long in alcohol, NHM 1972.4.18.5.

**Paratypes (all from type locality).** Two parthenogenetic females in alcohol (NHM 1972. 4. 18. 3–4); one parthenogenetic female in glycerine jelly (NHM 1972.4.18.1). Two exuviae in polyvinyl lactophenol (NHM 1972.4.18.2). One parthenogenetic female and one exuvium on slides, NNS MGU 63–64 (in Frey's paper they have accession numbers NN 54383-54384, but the numeration was subsequently changed); one parthenogenetic female and one exuvium, ZIN, accession numbers 16 and 64, respectively in Frey (1973). Some other specimens were kept in the DGF.

**Material examined here:** *Russia. Amur Area.* Affluents of the Zeya River, coll. in 2006 by N. G. Sheveleva, NNS 2009-030; Lake Khasan, the plain of Zeya river, coll. in 20.07.2006 by N. G. Sheveleva, NNS 2009-036

(53.4870, 126.9428); Lake Malaya Sazanka near town of Svobodny, coll. in 2006 by N. G. Sheveleva, NNS 2009-040 (51.1602, 128.1057); Lake Mukhinka, oxbow water body of the Zeya River near Mukhinka, coll. in 01.09.2005 by N. G. Sheveleva, AAK 2006-023 (50.5605, 127.6481); Lake Teploe, coll. in 2006 by N. G. Sheveleva, NNS 2009-037 (51.4474, 128.3738); Mouth of the Birma River, coll. in 2006 by N. G. Sheveleva, NNS 2009-043 (51.4713, 128.4374); Mouth of the Iver River, coll. in 2006 by N. G. Sheveleva, NNS 2009-044 (51.74, 128.88); Mouth of the Ulunga River, coll. in 2006 by N. G. Sheveleva, NNS 2009-042 (53.45, 126.86); Small water bodies near Zeya Water Reservoir dam, coll. in 2006 by N. G. Sheveleva, NNS 2009-033-35 (53.7308, 127.2696); Zeya Water Reservoir, coll. in 2006 by N. G. Sheveleva, NNS 2009-029 (53.7527, 127.3050); Zeya Water Reservoir near dam, coll. in 18.07.2006 by N. G. Sheveleva, NNS 2009-028 (53.7768, 127.2842). *Arkhangelsk Area*. A small marshy lake, Pinega Forest Reserve, coll. in 22.07.2009 by E. I. Bekker, AAK M-1034 (64.5921, 42.8550). *Chelyabinsk Area*. Uruzan' Pond, town of Uruzan', coll. in 07.08.2006 by A. A. Kotov, AAK M-0322 (54.8583, 58.4469). *Chita Area*. Sandy mine lake, town of Chita, coll. in 01.09.1991, NNS 1999-035 (52.0, 113.5). *Chukot Autonomous Area*. A puddle in the Region of the Anadyr River, coll. by E. A. Streletskaya, AAK 1999-076 (65, 171); A water body in the Anadyr River basin, №311, 6-134-72, coll. by E. A. Streletskaya, NNS 1999-015; Lake Verkhnee, Kolyma Region, coll. in 1981 by E. A. Streletskaya, NNS 1999-014. *Irkutsk Area*. Kurma Bay, Irkutsk Water Reservoir, coll. in 2010, AAK M-1849 (52.2499, 104.3001). *Jewish Autonomous Region*. Small ponds in the flood plain of the Amur River across the river from Khabarovsk, coll. in 07.08.1971 by D. G. Frey, NNS MGU 0016, 0063-0064 (48.53, 134.98). *Kamchatka Area*. A tundra Lake near Lake Tsentral'noje, Caldera Uzon coll. in 28.08.1995 by Y. R. Galimov, AAK 2007-311 (54.49, 160.0); Lake Tsentral'noje, Caldera Uzon, coll. in 29.08.1995 by Y. R. Galimov, AAK 2007-310 (54.4961, 159.9833). *Khanty-Mansi Autonomous Area*. A lake in Posiolok Divniy, town of Nizhnevartovsk, coll. in 23.07.2005 by A. A. Kotov, AAK 2005-321 (60.9236, 76.4935). *Komi Autonomous Republic*. Kurja near Schel'jajur, coll. in 10.08.1982 by AAK 1999-079 (65.33, 53.4); Lake Bezymian'noje, near the Schugor River, coll. in 24.07.1970 by V. N. Shubina, NMK 1712. *Krasnoyarsk Territory*. A lake near Mirnoe, coll. in 17.07.2011 by E. Y. Demidova (62.34, 89,1); *Penza Area*. A big lake, Sosnovka locality, vicinities of Penza, coll. in 31.05.2009 by E. I. Bekker, AAK M-1064 (53.1731, 45.0755); a lake fully covered by vegetation, locality Montazhny, vicinities of Penza, coll. in 24.10.2009 by E. I. Bekker, AAK M-1071-73 (53.218, 45.125); a roadside lake along new road, locality Sosnovka, vicinities of Penza, coll. in 05.2009 by E. I. Bekker, AAK M-0939 (53.1727, 45.0744); a small lake covered by *Stratiotes aloides*, on left side of Sosnovka-Ahuny road, vicinities of Penza, coll. in 05.2009 by E. I. Bekker, AAK M-0940 and AAK M-0930 (53.1727, 45.0744); Degtyarniy Zaton, a tributary of River Sura near village Sosnovka, vicinity of Penza, coll. in 04.10.1992 by A. O. Bienkowski & M. J. Orlova-Bienkowskaja, AAK 1999-073 (53.1759, 45.0561); 1st lake near Kordon 95, road to Akhuny, locality Sosnovka, vicinities of Penza, coll. in 08.07.2009 by E. I. Bekker, AAK M-1061 (53.1727, 45.0738). *Primorski Territory*. A big oxbow lake, the River Razdol'naya walley near town of Ussuriysk, coll. in 17.09.2010 by N. M. Korovchinsky, AAK M-2071 (43.8374, 131.8521); a small, almost dried pond, the River Razdol'naya walley near village of Razdol'noye, coll. in 19.09.2010 by N. M. Korovchinsky, AAK M-2081 (45.54, 131.89); a channel with filamentous algae, area of Lake Khanka, coll. in 11.09.2009 by N. M. Korovchinsky, NMK 2970-2971 (44.9305, 131.9764); a small swamp near the Manchzhurka River, area of Lake Khanka, coll. in 10.09.2009 by N. M. Korovchinsky, NMK 2946 (44.7961, 131.9985); a swamp on another side of road from Ilyinskoe Lake, area of Lake Khanka, coll. in 10.09.2009 by N. M. Korovchinsky, NMK 2949 (44.9211, 131.9642). *Sakhalin Area*. An oxbow lake of the Tym' River, coll. in 31.08.1999 by D. Zavarzin, NMK 2433 (50.9, 142.7). *Taimyr Autonomous Area*. A lake near river Kotuikan, coll. in 4.08.2011 by V. E. Fedosov (70.6928, 105.5169). *Tomsk Area*. Lake Kotets (locally named Chemuldo), coll. in 13.07.2005 by A. A. Kotov, AAK M-0114 (57.7364, 83.6171); Lake Svetloe near River Chulym, coll. in 14.07.2005 by A. A. Kotov, AAK M-0122 and AAK 2005-285 (57.8178, 84.1841). *Yakutia Autonomous Republic*. Lake Mutnoe, upper stream of the Markha River, coll. in 21.09.2010 by A. I. Klimovskiy, AAK M-1921; A lake, remain of the Suola River, coll. in 25.08.2010 by A. A. Kotov, AAK M-1944 (62.0986, 130.1494); A lake, remainder of the Tuima River, coll. in 29.08.2010 by A. A. Kotov, AAK 2011-049 (62.3368, 131.2744); an oxbow lake, River Khandyga, right bank of the Aldan River, coll. in 26.08.2010 by A. A. Kotov, AAK 2011-039 (63.112, 134.0446); A puddle near the Aldan River, coll. in 27.08.2010 by A. A. Kotov, AAK 2011-042 (63.0262, 134.0453); a swamp, right side of the "Kolyma" Federal Road near crossing with the Suola River, coll. in 25.08.2010 by A. A. Kotov, AAK M-1945 (62.0993, 130.1467); Lake Atlasovka near town of Yakutsk, coll. in 24.08.2010 by A. A. Kotov, AAK M-1938 (61.9670, 129.6204); a small lake near Lake Bolshaya Chabyda, coll. in 02.09.2010 by A. A. Kotov and A. I. Klimovsky, AAK M-1980 (61.9837; 129.3848); A swamp

on Shestakovka stream originated from Lake Bolshaya Chabyda, coll. in 02.09.2010 by A. A. Kotov and A. I. Klimovsky, AAK M-1988 (61.9377, 129.4120); Lake Bolshaya Chabyda, coll. in 02.09.2010 by A. A. Kotov and A. I. Klimovsky, AAK M-1984 (61.9884, 129.3794); Lake Suordakh, left bank of the Aldan River, coll. in 27.08.2010 by A. A. Kotov, AAK M-1958 (63.0737, 133.9702); Lake Tiungulju, coll. in 25.08.2010 by A. A. Kotov, AAK M-1946 (62.18029, 130.6640); Lake 1 on Melnikova Island, the Lena River, coll. in 22.08.2010 by A. A. Kotov, AAK M-1933 (63.8530, 127.4713); Lake 2 on Melnikova Island, the Lena River coll. in 22.08.2010 by A. A. Kotov, AAK 2011-021 (63.8512, 127.4738); River Muna, left affluent of the Lena River, coll. in 08.2003 by V. A. Sokolova, NMK 2484; an oxbow lake 2, near Nizhnekolymsky, south bank of the Kolyma River, coll. by A. I. Klimovskiy, AAK M-1912 (68.5356, 160.9348). *Yamalo-Nenets Autonomous Area*. A puddle near unnamed lake in Nadymsky Gorodok, 31 km from the River Nadym mouth, coll. in 17.07.2007 by A. B. Savinetsky, AAK M-0574 (66.0599, 72.0048); Lake 2 in Nadymsky Gorodok, 31 km from Obskaya Guba, coll. in 17.07.2007 by A. B. Savinetsky, AAK M-0578 (66.2208, 72.0451); un-named lake 1 in Nadymsky Gorodok, 31 km from Obskaya Guba, coll. in 17.07.2007 by A. B. Savinetsky, AAK M-0573 (66.0602, 72.0061).

*China*. Nen River, Loakan zi, Jilin Province, coll. in 07.06.1973 by C. Sieh-chih, DGF 6306 (45.53, 124.28). Lake Malaga, Xiuganmeng, coll. in 20.05.1988, AAK 1999-081 and NNS 1998-226

**Diagnosis. Parthenogenetic female.** Dorsal head pores on a bubble-like projection located immediately on head shield. In anterior view, body wide, not compressed laterally, median dorsal keel absent. Rostrum short. Ocellus minute. Lateral pore small, rounded. Labrum with a medium-sized median keel, terminating in a broadly rounded apex not reaching distal end of antenna I. Postabdomen with sub-parallel dorsal and ventral margins, preanal teeth pointed. Spines at base of pre-claw portion predominantly doubled. Antenna I with antennular sensory seta arising in middle. Denticles in rows encircling antennular surface especially small. On antenna II, spine situated on proximal segment of exopod somewhat shorter than second segment. Limb I IDL with a remarkably strong hook-like seta, the smallest IDL seta especially fine and short. IDL with 5–7 distal spinules, 11–16 proximal spinules, 7–9 marginal spinules and 2–4 basal spinules. Eight setae in filter plate II, eight-nine setae in filter plate III; eight-nine setae in filter plate IV, 8 setae in filter plate V.

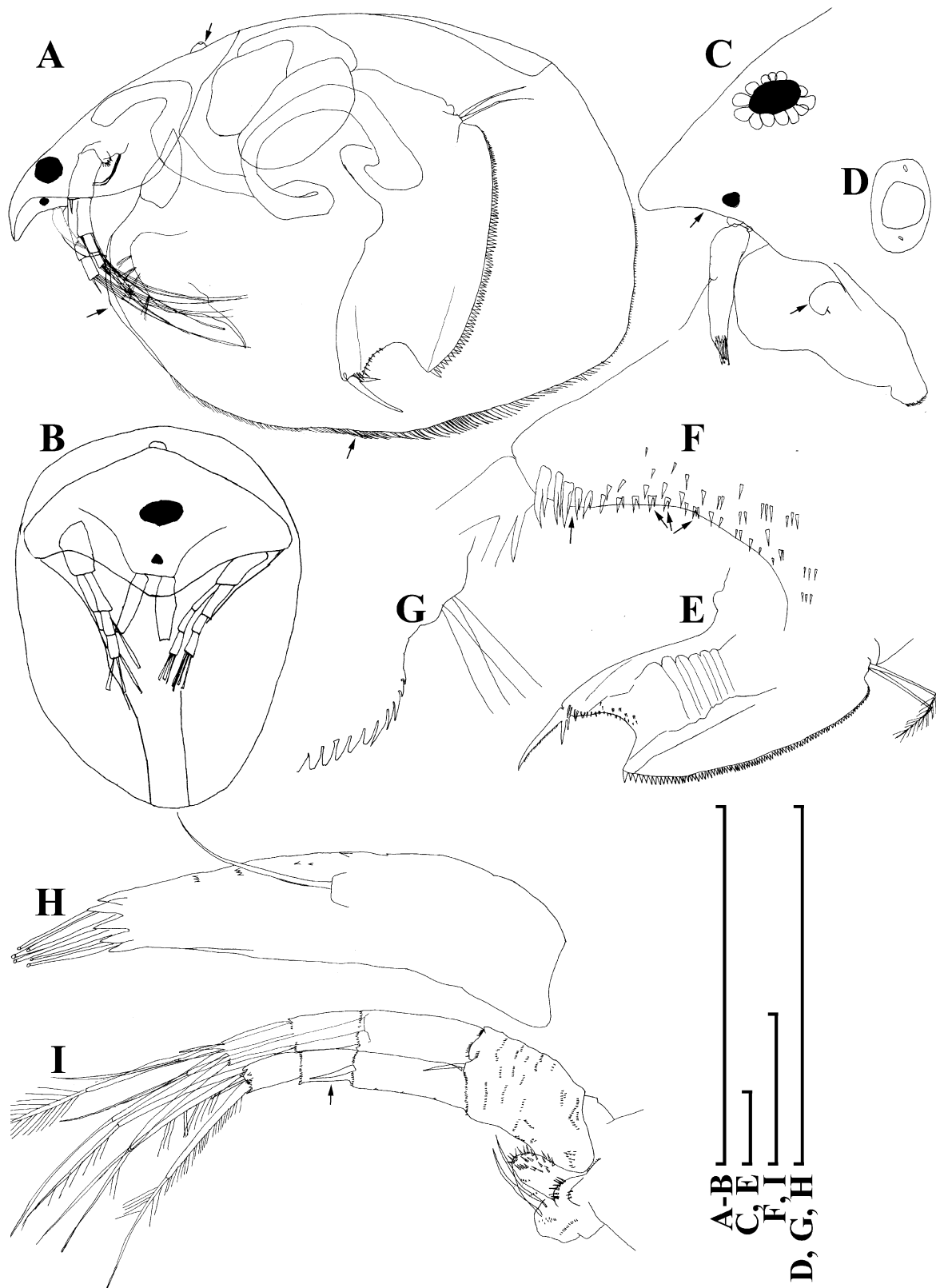
**Full redescription. Parthenogenetic female.** In lateral view body sub-ovoid in larger females (Fig. 3A), maximum height of the body in its middle portion (BH/BL= 0.52–0.57 in juveniles and 0.66 in largest adults). Dorsal margin evenly convex, interrupted only by a bubble-like projection with head pore (Fig. 3A, arrow). Postero-dorsal angle more or less rounded in both adults and juveniles. Posterior margin slightly convex, smoothly rounded, postero-ventral angle broadly rounded. In larger adults ventral margin with a slight prominence immediately anterior to the margin middle (Fig. 3A, arrow). In anterior view, body wide, not compressed laterally, maximum width of body at level of mandibular articulation, median dorsal keel completely absent (Fig. 3B). Intestine has a single loop, posterior intestinal caecum present. Few eggs in brood pouch.

*Head* large, with dorsal margin regularly arched from rostrum to region of dorsal head pores. Border line between head shield and valves obscure in preserved animals. Rostrum relatively short. Frontal head pore as transverse split, located somewhat anterior to the bases of antenna I on the ventral surface of the head (its position is marked by an arrow in Fig. 3C). Compound eye rather large, located near dorsal margin of head markedly closer to the rostral extremity than to the head pores. Ocellus small, located at antenna I base. A single major “head pore” (dorsal organ) as a ringed, sub-oval field of special cuticle located on a dorsal bubble (Fig. 3D). Lateral pore minute, circular and located at either side of major pore, closely to it.

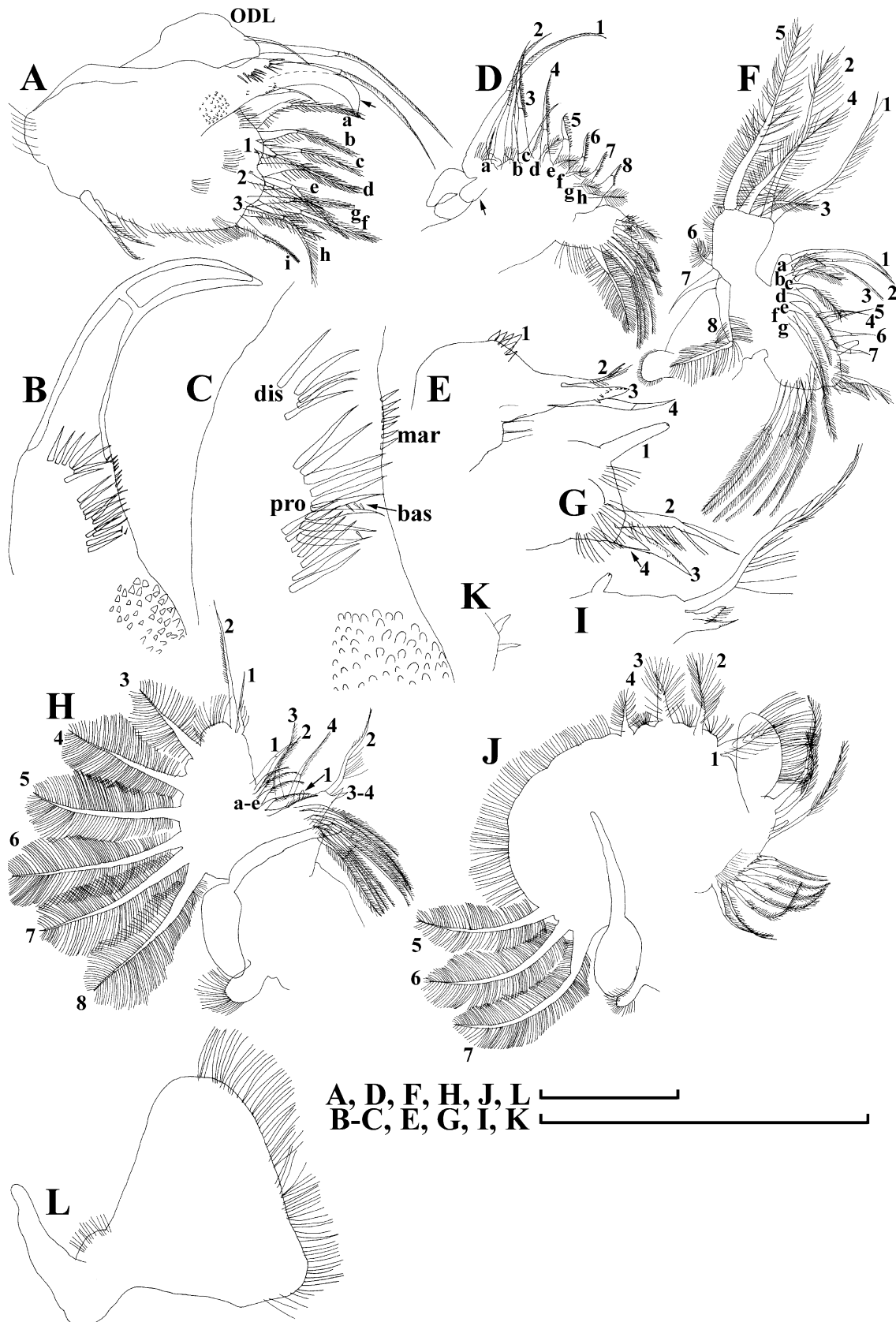
*Labrum* fleshy body, with a medium-sized median keel, terminating in a broadly rounded apex (Fig. 3C), keel anterior margin slightly convex, without setulation, posterior margin almost straight. Distal labral plate with short setulation. Paired lateral projections on labrum well-developed, horn-like, with apices directed anterior (Fig. 3C, arrow).

*Valves* generally ovoid (VL/BL= 0.80–0.90 in both juveniles and largest adults), with very obscure, almost invisible reticulation. Antero-ventral portion of valves slightly prominent, with a special narrow flap (Fig. 3A, arrow). Continuous row of setae along ventral rim of valves, the anterior most members short, setae then sharply increasing in size posterior to the prominence on ventral margin, and finally gradually decreasing in size to postero-ventral valve portion. Postero-ventral angle with a row of thin spinules. This row continues to ventral portion of posterior margin.

*Thorax* without external traces of segmentation, with six limb pairs. Abdomen thick; no abdominal projections on dorsal part of all segments.



**FIGURE 3.** *Eurycercus macracanthus*, parthenogenetic female from a small lake covered by *Stratiotes aloides*, on left side of Sosnovka-Ahuny road, vicinities of Penza, Penza Area (A); small water bodies near Zeya Water Reservoir dam, Amur Area (B); Lake Bezymiannoje, near the Schugor River, Komi Autonomous Republic (C); Degtyarniy Zaton, a tributary of River Sura near village Sosnovka, vicinity of Penza, Penza Area (D, F, H, I); Lake Svetloe near River Chulyim, Tomsk Area (G, E), all in Russia. A, lateral view. B, anterior view. C, head, lateral view. D, head pores. E, postabdomen. F, its distal portion. G, its basal portion. H, antenna I. I, antenna II. Scale bar denotes 1 mm (A–B); 0.1 mm (C–H).



**FIGURE 4.** *Eurycercus macracanthus*, limbs of parthenogenetic female from Lake Svetloe near River Chulym, Tomsk Area (A–B, D–K); Degtyarniy Zaton, a tributary of River Sura near village Sosnovka, vicinity of Penza, Penza Area (C); mouth of the Ulunga River, Amur Area (L), all in Russia. A, Limb I. B–C, inner distal lobe. D, limb II. E, distal armature of its gnathobase. F, limb III. G, distal armature of its gnathobase. H, limb IV. I, distal armature of its gnathobase. J, limb V. K, distal armature of its gnathobase. L, limb VI. Scale bar denotes 0.1 mm.

*Postabdomen* as a large (PL/BL= 0.44–0.46), relatively broad (PH/PL= about 0.43 in juveniles and 0.48–0.50 in adults), flattened plate with sub-parallel dorsal and ventral margins (Fig. 3E). Anus opening distally; thus whole slightly convex dorsal margin represents preanal margin of postabdomen. Dorso-distal (preanal) angle well expressed, distal anal embayment relatively deep, dorsal portion of distal (=anal) margin straight to slightly concave. Postanal angle rounded (Fig. 3F, arrow). Pre-claw portion of postabdomen as a conical prominence. Ventral margin of postabdomen slightly convex. Armature of the preanal margin as a series of preanal teeth, slightly and fluently increasing in size in distal direction; a small gap lacking any teeth at base of postabdominal setae (Fig. 3G); teeth in middle of preanal margin with sharp tips (NT= 90–92); distal most tooth somewhat larger than the others, located just on dorso-distal angle of postabdomen (Fig. 3E). On postanal and anal margins of postabdomen there are crescentic clusters of spines (homologues of postanal teeth of chydorids), distalmost members particularly large, predominantly clustered, teeth at base of pre-claw portion (=at distal part of anal margin) short, predominantly doubled (Fig. 3F, arrows). Sub-parallel rows of minute setules on whole lateral surface of postabdomen (not represented in Fig. 3E due to their minute size). Postabdominal setae short (less than half of preanal margin length), bisegmented, distal segment shorter than basal one and bilaterally setulated (Fig. 3E). Setae located on a distinct, nut-like base (Fig. 3G). Postabdominal claw relatively robust (CL/PL= 0.23–0.25); with massive base; weakly and evenly tapered in distal direction, and slightly curved. Two basal spines, first (distal) long (DS/CL= 0.33–0.47), second (basal) short (BS/CL=0.2–0.27; BS/DS = about 0.6), located dorsally immediately at base of claw.

*Antenna I* (antennule) relatively short (AL/BL= 0.08–0.10; AL/DA=2.8–4.0); with maximal width in basal half, with its distal 2/3 evenly tapering distally (Fig. 3H); protruding beyond tip of rostrum. Slender antennular sensory seta about half of antenna I length, arising at antenna I middle. Nine bisegmented aesthetascs with pointed teeth around them. No setules at anterior margin of antenna I. Numerous short rows of minute denticles encircling antennular surface.

*Antenna II* relatively short (Fig. 3I). Several projections on its external surface in coxal region. On one of them with two bisegmented setae, unequal in length, next projection with semi-circular row of setules; distalmost projection inflated, with numerous strong spinules. Massive basal segment with a relatively long seta distally on anterior surface and rows of short denticles. Both branches with elongated segments, basal most members particularly elongated; all segments with rows of short denticles. Setae 0-0-3/1-1-3; both apical and lateral setae long, clearly bisegmented, with long hairs on both basal and distal segments. Spines 1-0-1/0-0-1. No additional spines on distal parts of any segments of either branch. Length of apical spines and of segments from which they arise, sub-equal; length of spine situated on proximal segment of exopod somewhat shorter than length of second segment (Fig. 3I, arrow).

*Mandibles* relatively elongated, articulated with integument between head shield and valves.

*Maxilla I* with three densely setulated setae and a fourth short seta-like structure (as it was described for *E. lamellatus* by Kotov (2000). *Maxilla II* absent in adults and in juveniles (Fryer 1963; Kotov 1996).

*Limb I* large, epipodite without a finger-like projection (not represented in Fig. 4A). Two accessory setae, unequal in size and setulated in distal parts, are the distal most structures of the distal portion of limb I (also not represented in Fig. 4A). Outer distal lobe with 2 setae of very unequal size on its top (Fig. 4A, ODL). Inner distal lobe (Fig. 4A, IDL) with three bisegmented setae, named as clasping hooks in term of Fryer (1963), generally decreasing in size towards endites, among them, a remarkable especially strong hook-like seta (Fig. 4A, arrow). It is necessary to note that the relative size of this hook varies strongly among populations, but in any case the base of this seta occupies the whole top of the IDL in contrast to all other species (Fig. 4B–C), although their hook sometimes is also relatively large. Also the IDL supplied with 4 groups of spinules, named here after Hann (1982): long distal spinules (5–7 in largest adults, Fig. 4C, dis), long proximal spinules (pro, 11–16 in largest adults), short marginal spinules (mar, 7–9 in largest adults) and very short basal spinules (bas, 2–4 in largest adults); a field of minute denticles on IDL basally, named as grinding tubercles by Frey (1975). Endite III with three setulated, bisegmented posterior setae of similar size (a–c), and a setulated, stiff anterior seta 1 with a small sensillum near its base. Endite II with three posterior setae (d–f) analogous to those on eIII, and a stiff, setulated anterior seta 2, a very small sensillum near its base. Endite I with 3 posterior setae (g–i), and a stiff anterior seta 3. Two ejector hooks anteriorly on outer portion of limb corm. Well-developed maxillar process, earlier shown in embryos to be a remainder of gnathobase I (Kotov 1996), bearing three slender, fully and densely setulated setae on inner side of limb base (not represented in Fig. 4A).

*Limb II* with ovoid epipodite bearing a relatively short finger-like projection; exopodite as a small lobe (Fig. 4D, arrow). At inner side of limb, a row of eight stiff marginal scrapers (Fig. 4D, 1–8); setae 1–2 with more delicate feathering, setae 3–8 with relatively robust denticle. Posteriorly on limb corm 8 soft setae: distal most one (a) short;

next two ones (b–c) longest, relatively stout, armed in distal portions by short setules; basal most ones (d–h) similarly feathered by long hairs. Distal armature of gnathobase with four setae, one of them a minute sensillum (Fig. 4E, 1), located far from the others, a row of denticles (about 5 in largest adults) near it. Filter plate with 8 long, densely setulated setae; distal most seta of filter plate clearly smaller than the others, second-third ones slightly shorter than others. Additional bunch of setules basal to filter plate.

*Limb III* with a small pre-epipodite and a relatively large epipodite lacking a finger-like projection (Fig. 4F). Exopodite flat, smaller than those of limbs IV–V. Distally, five setae of unequal size (Fig. 4F, 1–5), lateral group consists of three setae (6–8, armature of seta 7 not represented), setae 8 especially long. Distal portion of inner limb part forms a partly isolated lobe, distal endite *sensu* Kotov (1999, 2000), external endite *sensu* Dumont & Silva-Briano (1998) with three bisegmented anterior setae (1–3). Basal endite, internal endite *sensu* Dumont & Silva-Briano (1998) larger than distal endite. Marginally, a row of 4 stiff setae (4–7). Seven long soft setae of subequal size (a–g) on limb corm posteriorly. Gnathobase weakly demarcated from basal endite, distal armature with 4 members, one of them (Fig. 4G, 1) a large, bottle-shaped sensillum located far from the others. Nine-eight setae in filter plate.

*Limb IV* with pre-epipodite as a setulated hillock; epipodite large, ovoid, with a long finger-like projection (Fig. 4H). Exopodite oval, with two distal, relatively stout, bisegmented setae of unequal size, armed by short setules (1–2), other six setae feathered bilaterally by very long hairs (3–8). Marginally on inner limb face, a row of four stiff anterior setae (1–4). Seta 1 slightly shorter, setae 2–4 approximately of equal size, setulated distally. Posteriorly, five soft setae (a–e) with subequal length. Distal armature of gnathobase with 4 members (1–4). One of them a long, bisegmented seta, densely feathered in distal part (2), two others small (3–4), a large, bottle-shaped sensillum (1) is a fourth member of gnathobasic armature (similar to limb III). Filter plate IV with 8–9 setae, middle ones slightly longer than marginal ones.

*Limb V* with pre-epipodite as a setulated hillock; epipodite with a long finger-like projection (Fig. 4J). Exopodite very large, with four short distal (1–4) and three large lateral (5–7) setae. Inner portion of limb with a protruding flap-like distal projection, fringed by long setules. Three marginal setae on inner face of limb, distal member slightly protruding behind distal endopodite projection, a sensillum near basalmost seta. Gnathobase with two small setae (Fig. 4K). Filter plate with 8 setae.

*Limb VI* triangular-shaped, with epipodite supplied with a relatively long finger-like projection and a bunch of setules somewhat distal to it; its inner margin setulated (Fig. 4L).

**Ephippial female, Male.** Unknown

**Length.** 0.90–1.73 mm in our material; 0.54–2.05 mm according to Frey (1973).

**Comments.** Frey's (1973) publication was a pioneering effort in the *revision of Eurycerus*. After description of several closely related species it is necessary to improve the diagnosis of *E. macracanthus* keeping in mind newly discovered characters discriminating this taxon from its congeners.

**Distribution.** The taxon was regarded as an endemic of the Amur basin (Frey 1973). Now it is obvious that this species is widely distributed in the northern Palaearctic from Far East to the Volga River basin in European Russia. In the Amur and the Lena basins *E. macracanthus* is the most common species of *Eurycerus*.

**Ecology.** After our study, it is obvious that *E. macracanthus* occurs in water bodies of very different types, from small puddles and shallow swamps to large lakes and artificial reservoirs. The most common habitat in Siberia is an oxbow lake of any size. We think that it occurs in small temporary pools only if they are partly dried remains of larger water bodies formed during spring flooding. *E. macracanthus* is found in the macrophyte patches in the rivers themselves.

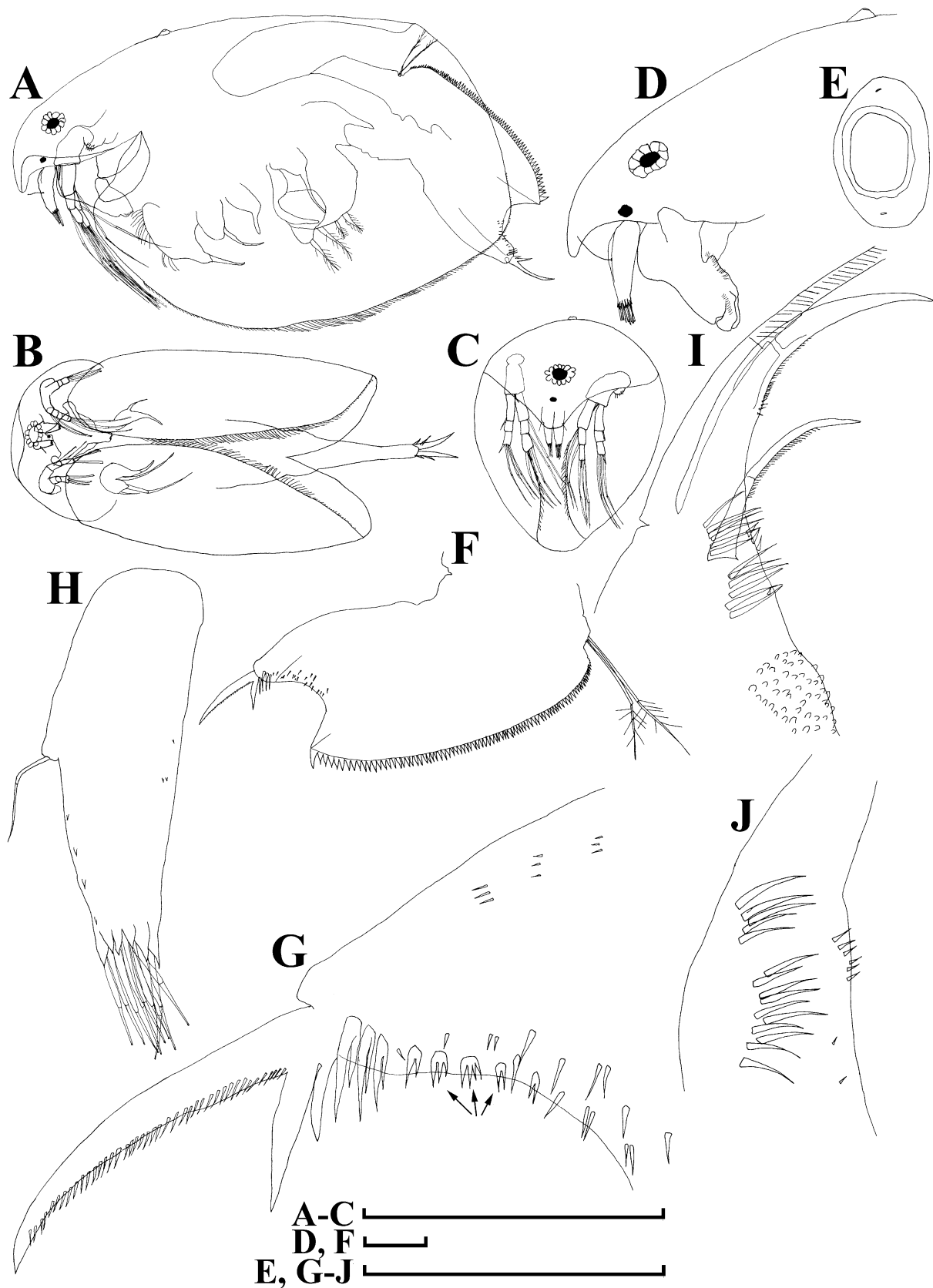
### ***Eurycerus pompholygodes* Frey, 1975**

Fig. 5

*Eurycerus pompholygodes* Frey, 1975, p. 270–284, Figs 1–31; Kotov *et al.* 2010b, p. 234–235, Fig. 137(12–14).

**Type locality.** "Bythotrepes Pond, located about 1 km northwest of the limnological station at Kuokkel and about 5 km north of Björkstugan at the west end of Tome Träsk in Swedish Lapland" (Frey 1975). Approximate geographic coordinates: 68.4, 18.4





**FIGURE 5.** *Eurycercus pompholygodes*, parthenogenetic female from Lake №6 near River Tareya, a tributary of River Pyasina, Taimyr Autonomous Area, Russia. A, lateral view. B, ventral view. C, anterior view. D, head. E, head pores. F, postabdomen. G, its distal portion. H, antenna I. I–J, inner distal lobe of limb I. Scale bar denotes 1 mm (A–C); 0.1 mm (D–J).

**Type material. Holotype.** A parthenogenetic female 1.92 mm long in alcohol, NHM 1973.845.

**Paratypes.** Two parthenogenetic females in alcohol, one parthenogenetic female on a slide in glycerine jelly, and three exuviae mounted individually in polyvinyl lactophenol on the same slide, NHM 1973.846-849. One parthenogenetic female in alcohol, one parthenogenetic female on a slide in glycerine jelly, and three exuviae mounted individually in polyvinyl lactophenol on the same slide, USNM 143768. One parthenogenetic female and three exuviae in polyvinyl lactophenol on the same slide (ZIN, accession numbers 2656 and 2667), one parthenogenetic female and three exuviae in polyvinyl lactophenol on the same slide, ZIN (ZIN, accession numbers 2658 and 2659). Some other specimens were kept in the D. G. FREY collection in Bloomington, now they are in USNM (accession number of whole DGF is USNM 403774).

**Material examined here:** *Sweden.* Small pond ca. 8 m within 100 m of Abisko Turiststation, coll. in 20.07.1972 by D. G. Frey, DGF 3260 (68.358, 18.783); Bythotrephes pond, north of Kuokkel, Abisko, coll. in 27.07.1972 by D. G. Frey, DGF 3268 (68.4, 18.4)

*Russia. Komi Autonomous Republic.* A bay of the Kozhim-Yu River, Pechora-Ilych National Reserve, coll. in 20.07.2010 by A. A. Kalinin, AAK M-1619 (63.1514, 59.0225); Kurja near Scheljajur, coll. in 10.08.1982, AAK 1999-043 (65.33, 53.4). *Murmansk Area.* A small lake near the Belomorskaya Biological Station of Moscow State University, coll. in 08. 1995 by A. Yu. Sinev, AAK 2004-020 (66.5, 33.1); Lake Bolshoy Vudjavr, coll. in 01.08.2009, AAK M-1404 (67.6306, 33.673). *Taimyr Autonomous Area.* A tarn at Talnah, coll. in 11.08.1974 by Y. I. Chernov, AAK 1999-075 and AAK 1999-049 (69.5, 88.4); Lake №6, River Tareya, a tributary of River Pyasina, coll. in 11.08.1974 by Y. I. Chernov, AAK 1999-074 (73.3, 90.8).

**Diagnosis. Parthenogenetic female.** Dorsal head pores on a bubble-like projection located immediately on head shield. In anterior view, body wide, not compressed laterally, median dorsal keel absent. Rostrum relatively long. Ocellus minute. Lateral head pore elongated. Labrum with a relatively small median keel, broadly rounded, reaching only half of antenna I length. Postabdomen with sub-parallel dorsal and ventral margins, preanal teeth pointed. Spines at base of pre-claw portion predominantly clustered. Antenna I with antennular sensory seta arising in middle. Denticles in rows encircling antennular surface especially small. On antenna II, spine situated on proximal segment of exopod somewhat shorter than second segment. Limb I IDL with a remarkably strong hook-like seta, the smallest IDL seta especially fine and short. IDL with 6–4 distal spinules, 6–10 proximal spinules, 3–6 marginal spinules and 1–2 basal spinules. Eight setae in filter plate II, 8 setae in filter plate III; 9 setae in filter plate IV, 8 setae in filter plate V.

**Full description of parthenogenetic female, ephippial female, male.** See Frey (1975).

**Short redescription. Parthenogenetic female.** In lateral view (Fig. 5A) body in larger females ovoid (BH/BL=0.60–0.66), but in juveniles more sub-rectangular, than in other species. Dorsal margin interrupted by a dorsal bubble bearing head pores. In anterior of ventral view, body wide, not compressed laterally, median dorsal keel is absent (Fig. 5B–C). Intestine has a single loop, posterior intestinal caecum present. Few eggs in the brood pouch.

*Head* with short rostrum (Fig. 5D). A single major “head pore” as a ringed, sub-oval field of special cuticle; a minute, elongated lateral pore located at either side of major pore, closer to it (Fig. 5E).

*Labrum* with a small, rounded median keel, reaching only about middle of antenna I (Fig. 5A, D).

*Armature of valve* margin as in previous species (VL/BL = 0.81–0.86), with sub-parallel dorsal and ventral margins (Fig. 5F).

*Postabdomen.* Distal anal embayment shallow. Armature of the preanal margin as a series of preanal teeth (NT about 83), distalmost tooth remarkably larger than others; small gap lacking any teeth at base of postabdominal setae; teeth in middle of preanal margin with sharp tips. Distalmost postanal teeth on pre-claw portion long, thin, predominantly double, teeth on pre-claw portion shorter, generally clustered (doubled or tripled) (Fig. 5G, arrows). Postabdominal claw robust (CL/PL = 0.26–0.30); first (distalmost) basal spine long (DS/CL = 0.36–0.50), second (basalmost) spine short (BS/CL = 0.18–0.25; BS/DS about 0.5).

*Antenna I* (Fig. 5H) short relatively body length (AL/BL = 0.11–0.13), but protruding greatly beyond labral keel and tip of rostrum; elongated (AL/DA = 2.3–3.3), triangular in cross section. Antennular sensory seta arising near the middle of the antenna I. Denticles in rows encircling antennular surface especially small, ridges on the body of antenna I absent.

*Antenna II.* Spine situated on proximal segment of exopod somewhat shorter than length of second segment.

*Limb I* with IDL supplied with three bisegmented setae generally decreasing in size towards endites, among them, a strong hook-like seta, but not too large like one in *E. macracanthus*. IDL supplied with 4–6 long distal

spinules, 6–10 long proximal spinules, 3–6 short marginal spinules and 1–2 very short basal spinules. Other limbs as in previous species, filter plate III with 9–10 setae, IV and V limbs with 8 setae.

**Size.** 0.69–01.67 in our material, 0.62–2.36 according to Frey (1975).

**Comments.** It is a well-defined Arctic-Subarctic taxon with a characteristic short labral keel.

**Distribution.** This taxon was known only from Swedish Lapland (Frey 1975) and a few localities in Norway (Hessen & Walseng 2008). Now it is clear that *E. pompholygodes* occurs in the north of European Russia and even on the Taimyr Peninsula. The range could reach the eastern part of the Siberian Subarctic.

**Ecology.** Frey (1975, p. 265–266) wrote that the species is present in the waters bodies where "water has a low concentration of electrolytes, tends to be acidic, and quite frequently has a perceptible humic color", and that it sometimes co-occurs with *E. lamellatus*. We found that *E. pompholygodes* is present in subarctic water bodies of different types: tundra ponds of different size, small or large lakes, and bays of rivers.

### ***Eurycercus microdontus* Frey, 1978**

*Eurycercus microdontus* Frey, 1978, p. 8–22, Figs 2–17, 19–28, 30–35.

**Type locality.** "Lake June in Winter, Highlands Co., Florida" (Frey 1978), USA. Approximate geographic coordinates: 27.3, -81.4.

**Holotype.** A parthenogenetic female 1.67 mm long in alcohol, USNM 151210.

**Paratypes.** Two parthenogenetic females in alcohol and one mounted in glycerine jelly, USNM 151210. Two parthenogenetic females in alcohol and one in glycerine jelly, NHM 1974. 716-718. All other specimens and exuvial fragments in DGF.

**Material examined here.** Many females from U.S.A. (Florida, South Carolina and North Carolina). Full list will be represented in a special future publication concerning a revision of the *lamellatus*-like forms worldwide.

**Diagnosis. Parthenogenetic female.** Dorsal head pores on a transverse fold in posterior portion of head shield with an indentation behind it. In anterior view, body strongly compressed laterally, median keel sharp, passes through whole carapace dorsum and actually begins on the head behind head pores. Dorsal margin of head flattened between compound eye and head pore region. Rostrum short. Ocellus minute. Lateral head pore small, rounded. Labrum with a median keel of moderate size, terminating in a widely rounded apex reaching distal end of antenna I. Postabdomen with sub-parallel dorsal and ventral margins, preanal teeth pointed. Spines at base of pre-claw portion predominantly clustered. Antenna I with antennular sensory seta arising in middle. Denticles in rows encircling antennular surface small. On antenna II, spine situated on proximal segment of exopod shorter than second segment. Limb I IDL with a hook-like seta markedly thicker than longest seta, the smallest IDL seta short. IDL with distal, proximal, marginal and basal group spinules. Eight setae in filter plate II, 9 setae in filter plate III; 9 setae in filter plate IV, 8 setae in filter plate V.

**Full description.** See Frey (1978).

**Comments.** It is a characteristic taxon from the south of the U.S.A., and is the most laterally compressed among all species of the genus.

**Distribution.** Southern states of the U.S.A. The species is recorded from North Carolina, South Carolina, Georgia, Florida, Louisiana and Texas (Frey 1978).

**Ecology.** Frey (1978) reported this taxon only from lakes, but he also said that "the smaller water bodies, such as ponds, back-waters, slow streams, etc., particularly those with an abundance of macrophytes, and hence some protection against predation by fishes, will yield many records of the species when they are studied intensively" (Frey 1978, p. 24). Our study confirms this idea as we also found *E. microdontus* in ponds.

### ***Eurycercus longirostris* Hann, 1982**

Figs 6–7

*Eurycercus longirostris* Hann, 1982, p. 587–595, Figs 1–25; Elías-Gutiérrez *et al.* 1997, p. 65, 67–68, Figs. 9–13; Bekker *et al.* 2010, p. 2501, Fig. 12.

*Eurycercus vernalis* Hann, 1982, p. 595–596.

**Type locality.** "Big Turkey Lake, Lagrange Co" (Hann 1982), Indiana, U.S.A. Approximate geographic coordinates: 41.59, -85.19.

**Holotype.** A parthenogenetic female, 1.44 mm, in alcohol, USNM 181893.

**Paratypes.** A parthenogenetic female on a slide in glycerine jelly, USNM 181895. Two parthenogenetic females in alcohol, and one parthenogenetic female in glycerine jelly on a slide, NHM 1980.371, 1980.372. A parthenogenetic female in alcohol, and one parthenogenetic female in glycerine jelly on a slide, CMN C-1981-217. An ephippial female in glycerine jelly, USNM 181896. "In addition, one exuvia mounted in polyvinyl lactophenol on a slide has been deposited in each of the three museums listed above. All other specimens are in the author's collection" (Hann 1982).

**Allotype.** A mature male in glycerine jelly, USNM 181894.

**Material examined here:** *Canada. British Columbia.* Morei Lake, coll. in 02.07.2005 by M. Belyaeva & S. Ishida, DJT 3-618 (59.955, -132.024). *Manitoba.* Fish House Pond, Boat dock at Delta Marsh Field Station, coll. in 19.09.1982 by M. M. Boucherle, DGF 6770 (49.97, -98.29); Weir Channel, Churchill, coll. in 16.08.2006 by M. Eñías-Gutiérrez, AAK M-0898 and AAK M-0891 (58.672, -94.161). *Newfoundland and Labrador.* Ocean Pond, coll. in 03.07.2005 by L.J. Hovind & M. Faustova, AAK M-0487 (47.4442, -53.4118). *Nova Scotia.* A lake, west side of Hgy. 349, 0.5 miles N of Williamswood/Harrietsfield boundary, coll. in 31.10.1984 by D. G. Frey, DGF 7328 (44.55, -63.64). *Ontario.* Pond 3 miles E Manitoba/Ontario border, on Trans-Canada Hwy, coll. in 29.08.1974 by D. G. Frey, DGF 3660 (49.73, -95.11); Pond on Opeongo Road, Algonquin Park, coll. in 08.10.1982 by S & F, DGF 6446 (45.56, -78.6); Sydenham Lake, Sydenham, coll. in 11.10.1982 by S & F, DGF 6490 (44.4226, -76.5559). *Yukon.* Squanga Lake, coll. in 02.07.2005 by M. Belyaeva & S. Ishida, DJT 3-624, DJT 3-625 and AAK M-0477 (60.4478, -133.603).

*U.S.A. Alaska.* Birch Lake, Anchorage, coll. 8.08.2011 by D. J. Taylor, A. A. Kotov, M. Ballinger & A. Medeiros, DJT20\_2011\_Ancourage\_04 (61,14558, -149,9384). *California.* CPR Pond 2, coll. in 01.05.2001 by E. Gallo, AAK 2007-319; Lower Twin Lake in Robinson, Creek Valley, coll. in 12.09.1965 by D. G. Frey, DGF 1726 (40.5066, -121.3639). *Colorado.* Poned Brooklet near Upper Red Rock Lake, coll. in 02.09.1975 by D. G. Frey, DGF 1704 (40.0816, -105.5412). *Connecticut.* Beach Pond, coll. in 14.06.2004 by D. J. Taylor & A. A. Kotov, AAK 2005-234 (41.5837, -71.7222). *Indiana.* Hammond Lake, coll. in 29.10.2006 by S. Ishida & K. Kim, AAK M-1124 (41.3647, -85.6775); Oliver Lake, coll. in 25.11.1966 by D. G. Frey, DGF 2342 (41.5724, -85.4051); Silver Lake, coll. in 29.10.2006 by S. Ishida & K. Kim, AAK M-1128 (41.08, -85.9). *Maine.* Meddybemps Lake, Hgy. 119, Moosehorn Wildlife Refuge, coll. in 09.11.1984 by G. Frey, DGF 7346 (45.07, -67.37); Sebago Lake, coll. in 11.08.1966 by D. G. Frey and 09.1981 by D. B. Berner, DGF 1911, DGF 1874 and AAK 1999-103 (43.778, -70.518). *Massachusetts.* Pequot Pond, coll. in 26.06.2004 by A. A. Kotov & W. Piel, AAK M-0076 (42.18, -72.692). *Michigan.* Douglas Lake, Marl Bay, coll. in 29.07.1961 by D. G. Frey, DGF 0295 (45.58, -84.69); Hamilton Lake, coll. in 07.07.1966 by D. G. Frey, DGF 1857 (45.7551, -87.7854); Twin Lake, coll. in 31.01.1975 by D. G. Frey, DGF 0303 (43.3676, -86.1716). *Minnesota.* Newton Lake in BWCA near Ely, coll. in 08.08.1979 by D. G. Frey, DGF 5250 (47.9768, -91.7273). *Mississippi.* Pearl River System, Chien's Sta. 3, 1.2 miles SW of jct. 411 on State Road 12 near McCool, coll. in 09.05.1974 by D. G. Frey, DGF 3413 (33.21, -89.36); Roadside ditch, Hwy 39W, ca. 4 miles S of Indianola, coll. in 13.03.1978 by D. G. Frey, DGF 4583 (33.5, -90.6). *New Hampshire.* Otter Pond near Sunapee Lake, coll. in 24.06.2004 by W. Piel & A. A. Kotov, AAK 2005-255 (43.4303, -72.0587); Sunapee Lake at Brich Point, coll. in 24.06.2004 by W. Piel & A. A. Kotov, AAK 2005-264-265 (43.3756, -72.07). *New York.* Fishpond near Atlantic city Reservoir, coll. in 01.05.1995 by H. Segers, AAK 1998-014 (39.44, -74.55); Lake Erie, coll. in 25.06.2006 by L. Hovind, AAK M-0272 (42.8503, -78.8742); Pond 3, Brigantine National Wildlife Refuge, coll. in 08.05.1995 by H. Segers, AAK 1998-016 (39.4, -74.4); Round Pond, Long Island, coll. in 12.06.2004 by D. J. Taylor & A. A. Kotov, AAK 2005-223 (40.9857, -72.2914). *North Carolina.* Lake Carolina, coll. in 07.06.2005 by L.J. Hovind, DJT 20-129 (35.475, -79.075); Pages Lake, coll. in 18.08.1958 by P. Patterson, DGF 0050 (35.1379, -79.4304); Panther Lake, 02.03.1979 by D. G. Frey, DGF 3759 (35.5678, -78.6955). *Pennsylvania.* Swingle Road Pond, coll. in 11.06.2004 by D. J. Taylor & A. A. Kotov, DJT 20-004 (41.4154, -75.3162); Swingle Road Pond, coll. in 06.2004 by D. J. Taylor & A. A. Kotov, AAK 2005-219 (41.4154, -75.3162). *Rhode Island.* Bowdish Reservoir, coll. in 14.06.2004 by D. J. Taylor & A. A. Kotov, AAK 2005-236 and DJT 20-037 (41.9242, -71.7826). *Tennessee.* Pool between road and Reelfoot Lake, 1 mile N of Dods, Tennessie Nat. Wildlife Ref., coll. in 11.10.1974 by D. G. Frey, DGF 3427 (36.4, -89.4). *Vermont.* Crystal Lake, coll. in 26.03.1975 by D. G. Frey, DGF 2600 (44.7338, -72.1539). *Washington.* Green Lake, Seattle, coll. in 22.10.1983 by D. G. Frey, DGF

6695 (47.6784, -122.3381); Slough, upper end of Lake Quinault, Rain Forest Camp, Olympic Peninsula, coll. in 27.06.1978 by D. G. Frey, DGF 4895 (47.49, -123.85). *Wisconsin*. Fox Lake, coll. in 23.06.1956 by D. G. Frey, DGF 0248 (43.5822, -88.919).

*Mexico. State of Mexico*. Lake La Luna, in the crater of the volcano Nevado de Toluca, coll. in 04.06.1994 by M. Elías-Gutiérrez, AAK 2002-106 (19.1036, -99.7556).

**Diagnosis. Parthenogenetic female.** Dorsal head pores on a bubble-like projection located immediately on head shield. In anterior view, body wide, not compressed laterally, median dorsal keel absent. Rostrum relatively long. Ocellus of moderate size. Lateral head pore circular. Labrum with a moderate median keel, with broadly rounded apex, reaching distal end of antenna I length. Postabdomen with sub-parallel dorsal and ventral margins, preanal teeth pointed. Spines at base of pre-claw portion predominantly single. Antenna I with antennular sensory seta arising somewhat basally to middle. Denticles in rows encircling antennular surface relatively large. On antenna II, spine situated on proximal segment of exopod equal to or somewhat shorter than second segment. Limb I IDL with a strong hook-like seta, the smallest IDL seta especially fine and short. IDL with about 4–11 distal spinules, 3–15 proximal spinules, 1–11 marginal spinules and 0–12 basal spinules. Eight setae in filter plate II, 9 setae in filter plate III; 9 setae in filter plate IV, 8 setae in filter plate V.

**Short redescription. Parthenogenetic female.** In lateral view body sub-ovoid in larger females (Fig. 6A), maximum height of the body in its middle portion (BH/BL = 0.57–0.59). Dorsal margin interrupted only by a bubble-like head pore. In anterior view, body wide, not compressed laterally, maximum width of body at level of mandibular articulation. Median dorsal keel is absent. A single midgut loop, posterior intestinal caecum present. Few eggs in the brood pouch.

*Head* large, with well expressed, relatively long rostrum (Fig. 6B). The anterior portion of headshield (= portion anterior to level of mandibular articulation) more than two times larger than posterior one, broadly rounded, with slightly projected rostral region (Fig. 6C). A single major “head pore” as a ringed, sub-oval field of special cuticle located on a dorsal bubble. A small, circular lateral pore located at either side of major pore, closer to it (Fig. 6D). Labrum fleshy body, with a medium-size median keel, terminating in a broadly rounded apex (Fig. 6B) and with paired lateral horn-like projections (Fig. 6E).

*Valves* generally ovoid (VL/BL = 0.78–0.87), armature of posterior valve margin as in previous species (Fig. 6F–H).

*Postabdomen* large (PL/BL = 0.41–0.44), relatively broad (PH/PL = 0.48–0.56), with sub-parallel dorsal and ventral margins (Fig. 6I). Distal anal embayment shallow. Armature of the preanal margin as a series of preanal teeth (NT = 87–98); distalmost tip somewhat larger than others; small gap lacking any teeth at base of postabdominal setae; teeth in middle of preanal margin with sharp tips. Distalmost postanal teeth long, clustered; teeth at base of pre-claw portion mainly single (Fig. 6J, arrows). Postabdominal setae as in previous species. Postabdominal claw relatively robust (CL/PL = 0.22–0.24); basal spines, first (distal) long (DS/CL = 0.30–0.47), second (basal) short (BS/CL = 0.13–0.22; BS/DS = 0.38–0.44).

*Antenna I* (Fig. 6K) relatively short (AL/BL = 0.10–0.11; AL/DA = 2.86–3.42), triangular in cross section; protruding beyond tip of rostrum. Antennular sensory seta relatively short (about third of antenna I length), arising basally to antenna I middle. Nine bisegmented aesthetascs, with pointed teeth around them. Numerous short rows of relatively large denticles encircling antennular surface.

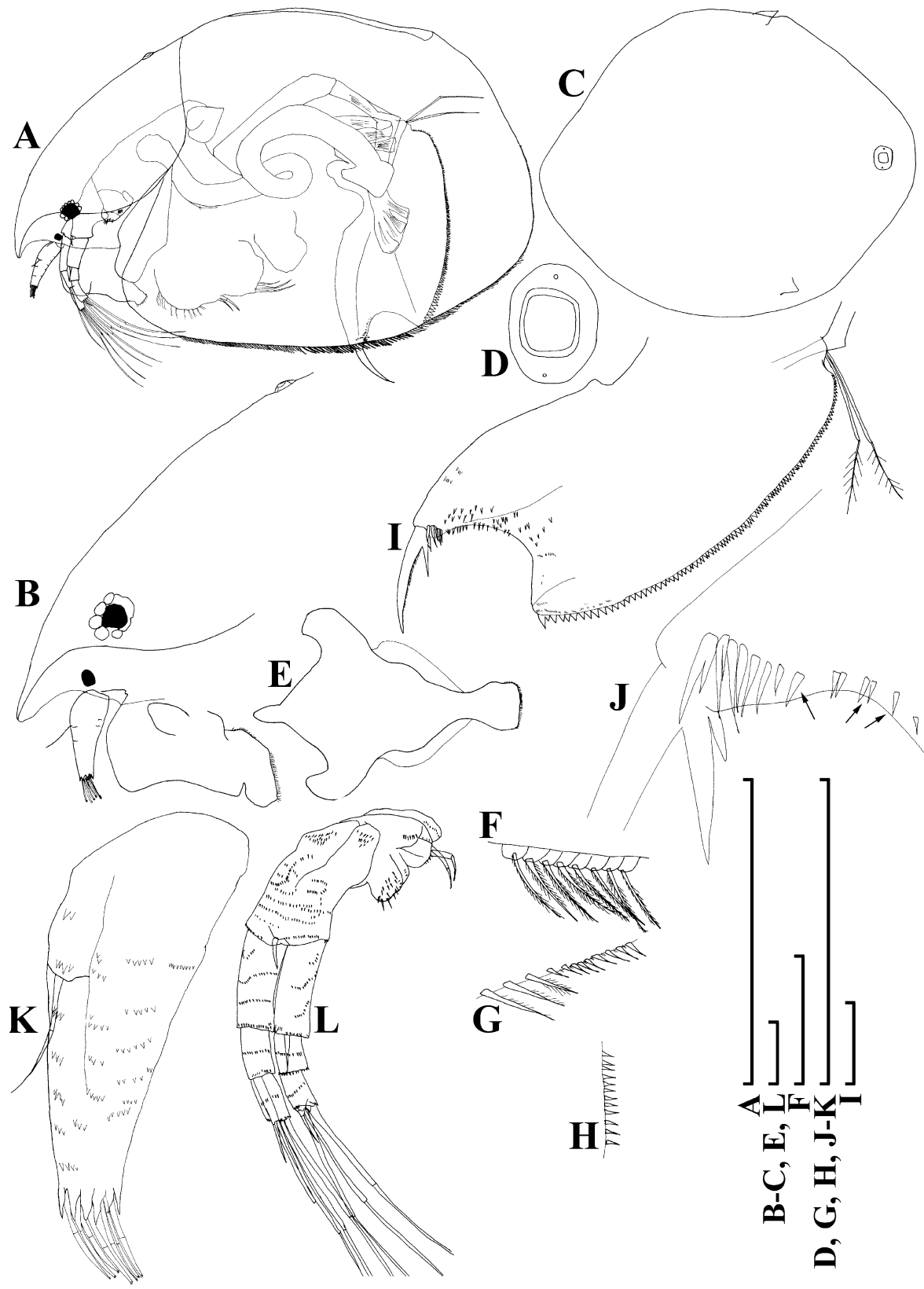
*Antenna II* relatively short; spine situated on proximal segment of exopod somewhat shorter than or equal to length of second segment (Fig. 6L). Setae 0-0-3/1-1-3; spines 1-0-1/0-0-1.

*Thoracic limbs* (Fig. 7A–L) basically similar with those in *E. macracanthus*, some differences described below. Limb I with IDL with a strong hook-like seta (Fig. 7A–D), but not so large as in *E. macracanthus*. In contrast to the latter, the smallest seta of IDL stronger in *E. longirostris*. IDL with long distal spinules (4–11), long proximal spinules (3–15), short marginal spinules (1–11) and short basal spinules (0–12). On exopodite III seta 7 short, eight soft setae on inner limb portion (Fig. 7G). On exopodite IV seta 1 relatively long (Fig. 7I). On exopodite V setae 5–7 increasing in size distally (Fig. 7J). Filter plate of gnathobase III, IV with 9 setae, and limb V with 8 setae.

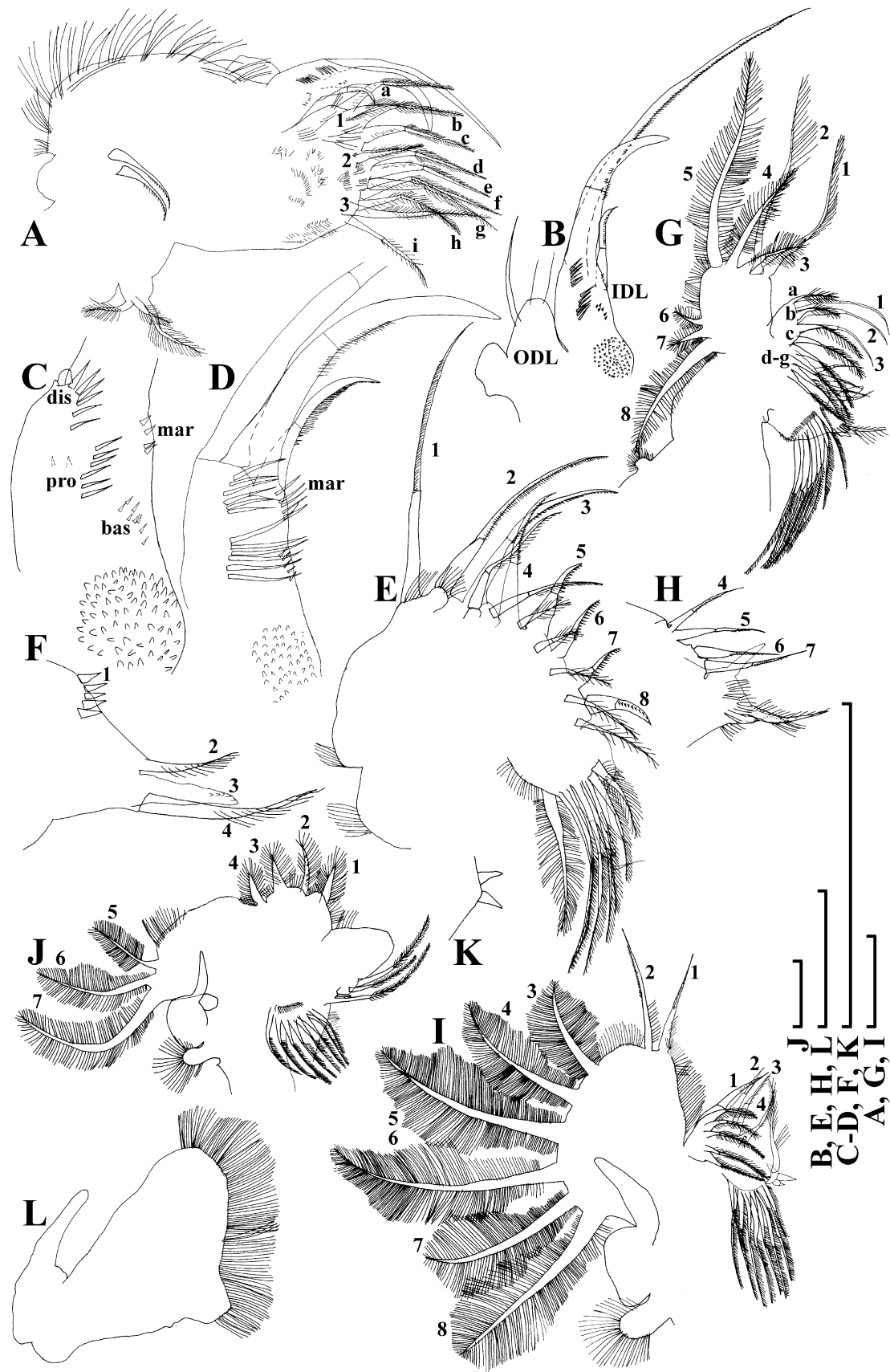
**Ephippial female, male.** See Hann (1982).

**Length.** 1.17–2.00 mm in our material.

**Comments.** Hann (1982) described two species, *E. longirostris* and *E. vernalis*, and concluded that there are no evident morphological differences between them. Only ontogenetic changes were found to be different, as



**FIGURE 6.** *Eurycercus longirostris*, parthenogenetic female from CPR WDS, California, U.S.A. (A, C, D, F, G, H, K, L); Oliver Lake, Indiana, U.S.A. (B, E, I); Lake La Luna, in the crater of the volcano Nevado de Toluca, State of Mexico, Mexico (J). A, lateral view. B, head. C, head shield. D, head pores. E, labrum, ventral view. F, setae at anterior portion of valves. G, setae at postero-ventral portion of valve. H, armature of valve posterior margin. I, postabdomen. J, its distal portion. K, antenna I. L, antenna II. Scale bar denotes 1 mm (A); 0.1 mm (B-I).



**FIGURE 7.** *Eurycercus longirostris*, limbs of parthenogenetic female from CPR WDS, California, USA (A–C, E–K); Lake La Luna, in the crater of the volcano Nevado de Toluca, State of Mexico, Mexico (D, L). A, limb I. B, its distal portion. C–D, inner distal lobe. E, limb II. F, distal armature of its gnathobase. G, limb III. H, its inner-distal portion. I, limb IV. J, limb V. K, distal armature of its gnathobase. L, limb VI. Scale bar denotes 0.1 mm.

revealed by a statistical analysis of the instar variability. Unfortunately, such ontogenetic differences are difficult to interpret and diagnose. We concluded that the patterns of instar variability found by Hann (1982) lack discreteness when more populations are examined (Bekker 2011). So, we believe that absence of any diagnostic traits of Hann's (1982) two taxa is due to their synonymy.

We found a small divergence of *COI* sequences among populations from distant points of the USA, including Indiana (the type locality of *E. longirostris*) and North Carolina (the type locality of *E. vernalis*). We found a separate sub-clade in Rhode Island and Newfoundland, but its separation from *E. longirostris* could not be associated with Hann's (1982) separation of *E. longirostris* and *E. vernalis*.

Note that the opinion of Hann (1982) is influenced by Frey's (1982b) idea that populations of cladocerans in southern and northern regions of North America become reproductively isolated as their timing of gamogenesis diverges (in autumn in the North and in spring in the South), which leads to speciation. It is presently unclear if there are good examples of this mode of speciation in cladocera. Geographic clades are commonly found in cladocerans, but these are often West-East, not South-North (Taylor *et al.* 1998). For genetically differentiated north-south species, it is unclear if differences in the timing of reproduction are a cause or an effect of speciation (Constanzo & Taylor 2010).

Case 24.2.1 of ICZN (2000) proposed that "When the precedence between names or nomenclatural acts cannot be objectively determined, the precedence is fixed by the action of the first author citing in a published work those names or acts and selecting from them; this author is termed the "First Reviser"". We followed this code, and *Eurycercus vernalis* Hann, 1982 is found by us to be a junior synonym of *E. longirostris* Hann, 1982.

**Distribution.** It is a remarkable fact that the southernmost populations of *E. longirostris* occur in Central Mexico (Elías-Gutiérrez *et al.* 1997, 2008) which is the southernmost portion of the Nearctic, while in nearby Neotropical Mexico, Belize and Guatemala (Elías-Gutiérrez *et al.* 2006, 2008), Central America and the West Indies (Frey 1982a) *E. longirostris* is almost certainly absent. There is a big gap in the distribution of *Eurycercus* south to Central Mexico until Columbia (see Aranguren *et al.* 2010; Bekker *et al.* 2010). So, the taxa of *Eurycercus* might be subdivided into the Nearctic and the Neotropical.

We know that *E. longirostris* s.str. is widely distributed through whole U.S.A. and southern Canada (Hann & Karrow 1984; Chengalath 1987; Lemke & Benke 2004) and present even in Churchill (Manitoba, Canada) (Jeffery 2011) and the Yukon Territories (our data). But more Canadian populations need to be studied to further assess species diversity. At least, the molecular data suggests a more complicated situation (see two clades in the *COI* chapter in this article).

**Ecology.** It is widely distributed in water bodies of different types. We found that two "species" according to Hann (1982) appear to belong to a sole taxon. The range of thermal preferences of *E. longirostris* is quite wide as evidenced by a record from subarctic Churchill.

## ***Eurycercus nipponica* Tanaka & Fujita, 2002**

Figs 8–9

*Eurycercus nipponica* Tanaka & Fujita, 2002, p. 13, Pl. 5: figs 1–2, Pl. 6: figs 1–2, Pl. 7: figs 1–6; Tanaka *et al.* 2004, p. 172.

**Type locality.** "Lake Utonai-numa" (Tanaka & Fujita 2002) = Unonaito-numa, Hokkaido, Japan. Approximate geographic coordinates: 42.70, 141.71.

**Holotype.** A female with number Y7860825, but the place of its deposition unclear, and absent in the first description (Tanaka & Fujita 2002).

**Material examined here:** *Japan.* Nagano. Aoki Ko, coll. in 06.12.2006 by S. Tanaka, DJT 4-235, DJT 4-236 (36.6089, 137.8542); Kizaki Ko, coll. in 06.12.2006 by S. Tanaka, DJT 4-237 (36.5557, 137.8408).

*Russia. Kamchatka Area.* A bay of Kurilskoe Lake, coll. in 08.2009 by A. A. Kotov, AAK 2009-104 (51.41754, 157.0459); A swampy area near Travianoy Cape, Kurilskoe Lake, coll. in 08.2009 by A. A. Kotov, AAK 2009-103 (51.4172, 157.0454); A swampy area (with a fresh bear trail in time of sampling) near Travianoy Cape, Kurilskoe Lake, coll. in 16.08.2009 by A. A. Kotov, AAK M-1352 (51.4165, 157.0450); Tundra lake 1 near Kurilskoe Lake, coll. in 16.08.2009 by A. A. Kotov, AAK M-1353 (51.4101, 157.0490); Tundra lake 4 near Kurilskoe Lake, coll. in 16.08.2009 by A. A. Kotov, AAK M-1357 (51.4090, 157.0517); A forest puddle 1 near the Plotnikova River, coll. in 13.08.2009 by A. A. Kotov, AAK M-1344 (52.9208, 157.1527); A forest puddle 2 near the



Bystraya River, coll. in 08.2009 by A. A. Kotov, AAK 2009-093 (52.9264, 156.6012); An affluent of the Bystraya River, coll. in 08.2009 by A. A. Kotov, AAK 2009-094 and AAK M-1376 (52.9304, 156.6031); Bolshaya River near the KamchatNIRO station, coll. in 13.08.2009 by T. N. Travina, AAK 2009-079 (52.7612, 156.2647); Small lake near Lake Azabachje on Cape Ivashka, coll. in 02.10.1985, NNS 1999-008, NNS 1999-017 and AAK 1999-077 (56.16, 161.85).

**Diagnosis. Parthenogenetic female.** Dorsal head pores on a bubble-like projection located immediately on head shield. In anterior view, body wide, not compressed laterally, median dorsal keel absent. Rostrum relatively long. Ocellus small. Lateral head pore minute, circular. Labrum with a large median keel, terminating in an angled apex, reaching distal end of antenna I. Postabdomen with sub-parallel dorsal and ventral margins, preanal teeth pointed. Spines at base of pre-claw portion predominantly single. Antenna I with antennular sensory seta arising somewhat basally to middle. Denticles in rows encircling antennular surface relatively large. On antenna II, spine situated on proximal segment of exopod equal to or somewhat shorter than second segment. Limb I IDL with a strong hook-like seta, the smallest IDL seta especially short. IDL with about 11 distal spinules, about 8 proximal spinules, about 6 marginal spinules and about 10 basal spinules. Eight setae in filter plate II, 8 setae in filter plate III; 8 setae in filter plate IV, 8 setae in filter plate V.

**Short redescription. Parthenogenetic female.** In lateral view body sub-ovoid in larger females (Fig. 8A), maximum height of the body in its middle portion (BH/BL= 0.50–0.66). Dorsal margin interrupted only by a bubble-like head pore. In anterior or ventral view, body wide, not compressed laterally (Fig. 8D), maximum width of body at level of mandibular articulation, median dorsal keel absent. Intestine has a single loop, posterior intestinal caecum present. Few eggs in the brood pouch.

*Head* with short rostrum (Fig. 8E). A single major “head pore” as a ringed, sub-oval field of special cuticle located on a dorsal bubble. A minute, circular lateral pore located at either side of major pore, closer to it (Fig. 8F).

*Labrum* fleshy body with paired lateral horn-like projections, a large median keel terminating in an angled apex (Fig. 8E).

*Valves* generally ovoid (VL/BL= 0.84–0.96), as in previous species.

*Postabdomen* large (PL/BL= 0.27–0.43), relatively broad (PH/PL= 0.45–0.46), with sub-parallel dorsal and ventral margins (Fig. 8G). Distal anal embayment very shallow. Armature of the preanal margin as a series of preanal teeth (NT=101); small gap lacking any teeth at base of postabdominal setae (Fig. 8I); teeth in middle of preanal margin with sharp tips, distalmost tooth equal to or somewhat larger than others. Distalmost postanal teeth particularly large, predominantly clustered, teeth at base of pre-claw portion (=at distal part of anal margin) predominantly single (Fig. 8H, arrows). Postabdominal claw relatively robust (CL/PL= 0.16–0.24); basal spines, first (distal) long (DS/CL= 0.25–0.38), second (basal) short (BS/CL= 0.13–0.25; BS/DS= 0.43–0.60).

*Antenna I* relatively short (AL/BL = 0.10–0.14; AL/DA=3.0–3.6 in adults), triangular in section; protruding greatly beyond tip of rostrum. Antennular sensory seta relatively short (about third of antenna I length), arising somewhat basally to antenna I middle (Fig. 8J). Nine bisegmented aesthetascs, with pointed teeth around them. No setules at anterior margin of antenna I. Numerous rows of minute denticles encircling antennular surface. Antenna II relatively short. On antenna II, spine situated on proximal segment of exopod somewhat shorter than length of second segment (Fig. 8K). Setae 0-0-3/1-1-3; spines 1-0-1/0-0-1.

*Limbs* in general as in previous species (Fig. 9A–J). IDL of limb I with a remarkable strong hook-like seta, but not so large as in *E. macracanthus*, smallest seta very small, as in the latter (Fig. 9A–B). IDL with long distal spinules (about 11 in largest adults), long proximal spinules (8 in largest adults), short marginal spinules (6 in largest adults) and short basal spinules (10 in largest adults). On exopodite III seta 7 somewhat longer than seta 6 (Fig. 9E). On exopodite IV both setae 1 and 2 short (Fig. 9G). On exopodite V setae 5–6 slightly increasing in size basally. Filter plate of gnathobase III–V limbs with 8 setae.

**Ephippial female.** Body more compressed laterally, with median dorsal keel (Fig. 8B–C).

**Male.** Unknown

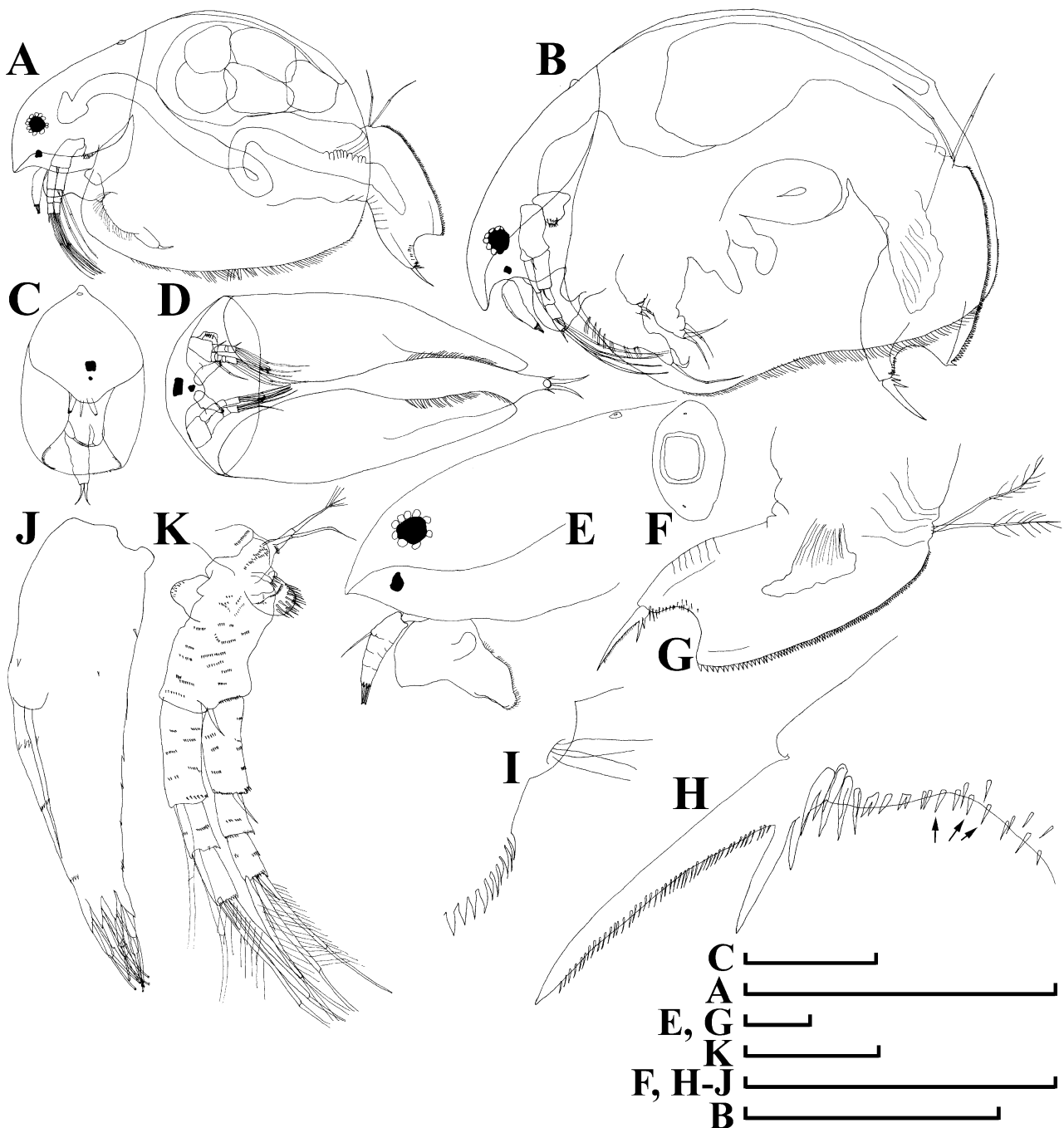
**Length.** 0.69–2.00 mm in our material, up to 3 mm according to Tanaka & Fujita (2002).

**Comments.** Smirnov (1998: p. 81) said that “Easternmost Siberia is also distinguished by the presence of ... an undescribed species of *Eurycercus*”. As we found, this taxon has been formally described as *E. nipponica* Tanaka & Fujita, 2002 based on samples from Japan (Tanaka & Fujita 2002). The author’s diagnosis was lacking any helpful information on the taxon discrimination from other species, but it is obvious from the author’s drawings and photos that: (1) the labral keel is very large and has an angled apex; (2) the head pores are located on a bubble-like projection

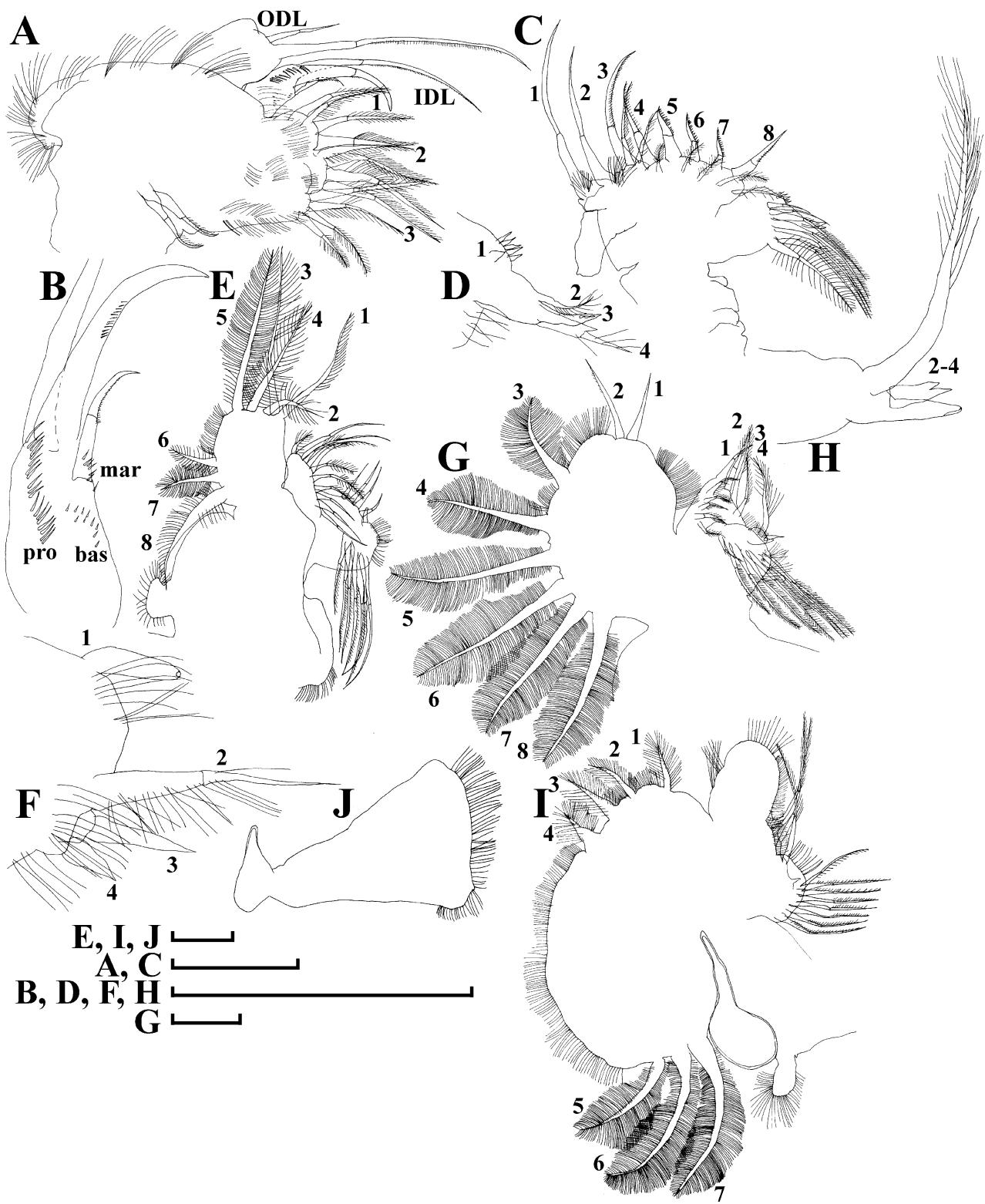
(not represented by the authors in their drawings, but see in their photo in Plate 7 (fragment 1); (3) the preanal teeth on the pre-claw portion are mainly singular. After our redescription, it is clear that this is a valid species.

**Distribution.** *E. nipponica* was known from Japan (Tanaka & Fujita 2002; Tanaka *et al.* 2004) – we found it also in Kamchatka (see Fig. 1). The species could be present in Sakhalin Island, Kurile Islands and, Chukotka Peninsula.

**Ecology.** Mostly, it is present in relatively large lakes and smaller water bodies associated with them (i.e. connected during a spring flooding time). The species is found in very shallow flooded grasslands, but, as in case of *E. macracanthus*, we think that it could be found in temporary water bodies only as the remains of a larger water body formed by spring flooding. It is present in the vegetation patches in rivers themselves.



**FIGURE 8.** *Eurycercus nipponica*, female from a swampy area (with a fresh bear trail in time of sampling) near Travianoy Cape, Kurilskoe Lake, Kamchatka Area, Russia A, parthenogenetic female, lateral view. B–C, ephippial female, lateral and anterior view. D, parthenogenetic female, ventral view. E, head. F, dorsal head pores. G, postabdomen. H, its distal portion. I, its basal portion. J, antenna I. K, antenna II. Scale bar denotes 1 mm (A–D); 0.1 mm (E–K).



**FIGURE 9.** *Eurycercus nipponica*, limbs of parthenogenetic female from a swampy area (with a fresh bear trail in time of sampling) near Travianoy Cape, Kurilskoe Lake, Kamchatka Area, Russia A, limb I. B, inner distal lobe of limb I. C, limb II. D, its distal armature. E, limb III. F, distal armature of its gnathobase. G, limb IV. H, distal armature of its gnathobase. I, limb V. J, limb VI. Scale bar denotes 0.1 mm.

***Eurycercus beringi* sp. nov.**

Figs 10–11

*Eurycercus* sp. nov. in Bekker 2011, Table 1.

**Etymology.** The taxon is named in honor of Vitus Jonassen Bering (1681–1741), the leader of the First and the Second Russian Kamchatka Expeditions, who discovered the Bering Strait, Alaska, and the Aleutian and Commander Islands. Now this region is named “Beringia”.

**Type locality.** Council #05: a roadside pond <1.5 m deep, 10 X 25 m, Seward Peninsula, Alaska, U.S.A. Geographic coordinates: 64.8807 N 163.6872 W. The type series was collected in 05.08.2006 by D. J. Taylor,

**Holotype.** A parthenogenetic female in 90%, MGU MI 108. Label of the holotype: “*Eurycercus beringi* sp. nov., 1 parthenogenetic female from Council #05: a roadside pond (64.88071°N, 163.6872°W), Seward Peninsula, Alaska, USA, coll. in 05.08.2005 by D. J. Taylor, HOLOTYPE”.

**Paratypes.** Eight parthenogenetic females in in 90%, MGU MI 109. Eight parthenogenetic females in in 90%, AAK M-1117. All paratypes are from the type locality.

**Other material excluded from type series in Alaska, U.S.A.:** Nome Road #06: Roadside pond <1 m deep, coll. in 06.08.2005 by D. J. Taylor, DJT (64.5603, -165.4870); Nome #07: A pond 80x55 m, coll. in 05.08.2005 by D. J. Taylor, AAK M-1121 (64.5604, -165.4872); Nome #10: A pond 20x30 m, coll. in 06.08.2005 by D. J. Taylor, AAK M-1120 (64.6226, -165.4111); Nome #11: Unnamed pond 8 X 5m, coll. in 06.08.2005 by D. J. Taylor, AAK M-1123 (64.5133, -165.4057); 2011\_Nome 03, coll. in 03.08.2011 by D. J. Taylor, A. A. Kotov, M. Ballinger & A. Medeiros (64.55368, -165.4499); 2011\_Nome 05, coll. in 03.08.2011 by D. J. Taylor, A. A. Kotov, M. Ballinger & A. Medeiros (64.56152, -165.4899); 2011\_Nome 13, coll. in 03.08.2011 by D. J. Taylor, A. A. Kotov, M. Ballinger & A. Medeiros (64.51241, -165.4224); 2011\_Nome 15, coll. in 03.08.2011 by D. J. Taylor, A. A. Kotov, M. Ballinger & A. Medeiros (64.49419, -165.3753); 2011\_Nome 17, coll. in 03.08.2011 by D. J. Taylor, A. A. Kotov, M. Ballinger & A. Medeiros (64.49532, -165.3728); 2011\_Nome 18, coll. in 03.08.2011 by D. J. Taylor, A. A. Kotov, M. Ballinger & A. Medeiros (64.4891, -165.3326); Council Road #10: A tundra pond 21.54 X 17.58 m, coll. in 05.08.2005 by D. J. Taylor, AAK M-1118 (64.8681, -163.6927); Council #11: Large (65 X 54 m) tundra pond, coll. in 05.08.2005 by D. J. Taylor, AAK M-1119 (64.8742, -163.6947); 2011\_Council 07, coll. in 29-07-2011 by D. J. Taylor, A. A. Kotov, M. Ballinger & A. Medeiros (64.87984, -163.6878); 2011\_Council 09, coll. in 29.07.2011 by D. J. Taylor, A. A. Kotov, M. Ballinger & A. Medeiros (64.87365, -163.692); 2011\_Council 11, coll. in 29.07.2011 by D. J. Taylor, A. A. Kotov, M. Ballinger & A. Medeiros (64.86829, -163.6937); 2011\_Council 17, coll. in 02.08.2011 by D. J. Taylor, A. A. Kotov, M. Ballinger & A. Medeiros (64.82822, -163.6795); 2011\_Council 18, coll. in 02.08.2011 by D. J. Taylor, A. A. Kotov, M. Ballinger & A. Medeiros (64.64355, -164.3562); 2011\_Council 25, coll. in 02.08.2011 by D. J. Taylor, A. A. Kotov, M. Ballinger & A. Medeiros (64.8777, -163.6893). Teller Road #07: Roadside pond <1m deep, coll. in 04.08.2005 by D. J. Taylor, AAK M-1116 (65.0475, -166.1840); 2011\_Teller 13, coll. in 28.07.2011 by D. J. Taylor, A. A. Kotov, M. Ballinger & A. Medeiros (64.56004, -165.4736); 2011\_Pilgrim Road 01, coll. in 27.07.2011 by D. J. Taylor, A. A. Kotov, M. Ballinger & A. Medeiros (65.08334, -164.9122); 2011\_Pilgrim 03, coll. in 27.07.2011 by D. J. Taylor, A. A. Kotov, M. Ballinger & A. Medeiros (65.08134, -164.891); 2011\_Pilgrim 04, coll. in 27.07.2011 by D. J. Taylor, A. A. Kotov, M. Ballinger & A. Medeiros (65.08067, -164.8887); 2011\_Pilgrim 703, coll. in 04.08.2011 by D. J. Taylor, A. A. Kotov, M. Ballinger & A. Medeiros (65.08895, -164.9228). 2011\_Glacial Lake 992, coll. in 01.08.2011 by D. J. Taylor, A. A. Kotov, M. Ballinger & A. Medeiros (64.82653, -165.6725).

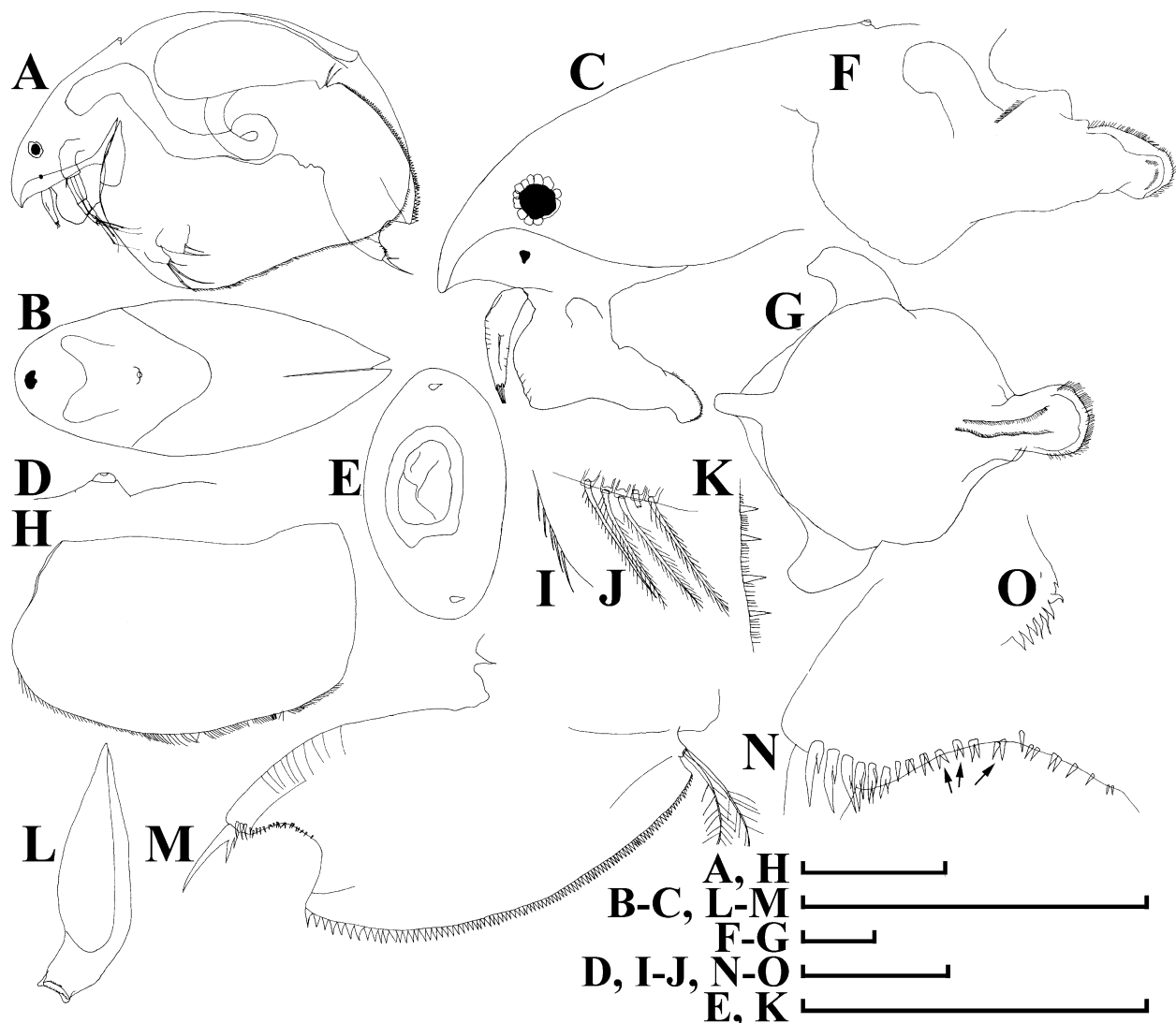
**Short diagnosis. Parthenogenetic female.** Dorsal head pores on a bubble-like projection located on a transverse fold. In anterior view, body moderately compressed laterally, median dorsal keel present only in a posterior portion of the valves. Rostrum short. Ocellus small. Lateral head drop-shaped. Labrum with a large median keel, with angled apex, reaching distal end of antenna I length. Postabdomen subovoid, preanal teeth pointed. Spines at base of pre-claw portion predominantly doubled. Antenna I with antennular sensory seta arising in middle. Denticles in rows encircling antennular surface small. On antenna II, spine situated on proximal segment of exopod somewhat shorter than second segment. Limb I IDL with a strong hook-like seta, the smallest IDL seta short. IDL with about 9 distal spinules, about 14 proximal spinules, about 13 marginal spinules and about 17 basal spinules. Eight setae in filter plate II, 9 setae in filter plate III; 8 setae in filter plate IV, 8 setae in filter plate V.

**Description. Parthenogenetic female.** Body sub-ovoid in lateral view body (Fig. 10A), maximum height of the body in its middle portion (BH/BL= 0.66–0.71). Dorsal margin in general convex, but interrupted by a promi-

ment transverse fold, bearing also a bubble-like projection with head pores. Postero-dorsal angle well expressed, posterior margin slightly convex, postero-ventral angle broadly rounded. In larger adults ventral margin with a slight prominence immediately anterior to the margin middle. In anterior or dorsal view, body somewhat compressed laterally (Fig. 10B), maximum width of body at level of mandibular articulation. Median dorsal keel present only in a posterior portion of the valves. Intestine has a single loop, posterior intestinal caecum present.

*Head* large, with dorsal margin regularly arched from rostrum to region of dorsal head pores (Fig. 10C). Border line between head shield and valves obscure in preserved animals in lateral view, but quite distinct in dorsal view (Fig. 10B). Rostrum short. Compound eye rather large, located near dorsal margin of head markedly closer to rostral extremity than to head pores. Ocellus small, located at antennule base, closer to eye than to tip of rostrum. A single major “head pore” as a ringed, sub-oval field of special cuticle located on aforementioned dorsal bubble (as *E. macracanthus*), oriented somewhat posterior, this bubble sites on a prominent transverse fold (as a *E. lamellatus*) (Fig. 10D–E). Lateral pore minute, drop-shaped and located at either side of major pore, closer to it.

*Labrum* fleshy, with a large median keel (Fig. 10F), terminating in a well-developed apex, which seems to be angular (although not too strongly angular as in *E. lamellatus*), keel anterior margin convex, without setulation, posterior margin almost straight. Distal labral plate with rich setulation. Paired lateral projections on labrum well-developed, horn-like, with apexes directed anterior (Fig. 10G).



**FIGURE 10.** *Eurycercus beringi* sp.nov., parthenogenetic female from Council #05: a roadside pond <1.5 m deep, 10 X 25 m, Seward Peninsula, Alaska, U.S.A. A, lateral view. B, dorsal view. C, head. D–E, head pores, lateral and dorsal view. F–G, labrum, lateral and ventral view. H, valve. I, setae at antero-ventral valve portion. J, setae at postero-ventral valve portion. K, armature of valve posterior margin. L, mandible. M, postabdomen. N, its distal portion. O, its basal portion. Scale bar denotes 1 mm (A–C, H, L–M); 0.1 mm (D–G, I–K, N–O).

*Valves* generally ovoid (VL/BL= 0.73–0.86), with very obscure reticulation. Antero-ventral portion of valves slightly prominent, with a special narrow flap (Fig. 10H). Continuous row of setae along ventral rim of valves, in anterior portion they are short (Fig. 10I), then sharply increasing in size posterior to the prominence on ventral margin (Fig. 10J), and finally gradually decreasing in size to postero-ventral valve portion. Postero-ventral angle with a row of spinules, with minute setules between them. This row continues to ventral portion of posterior margin (Fig. 10K).

*Thorax, abdomen* as in previous species.

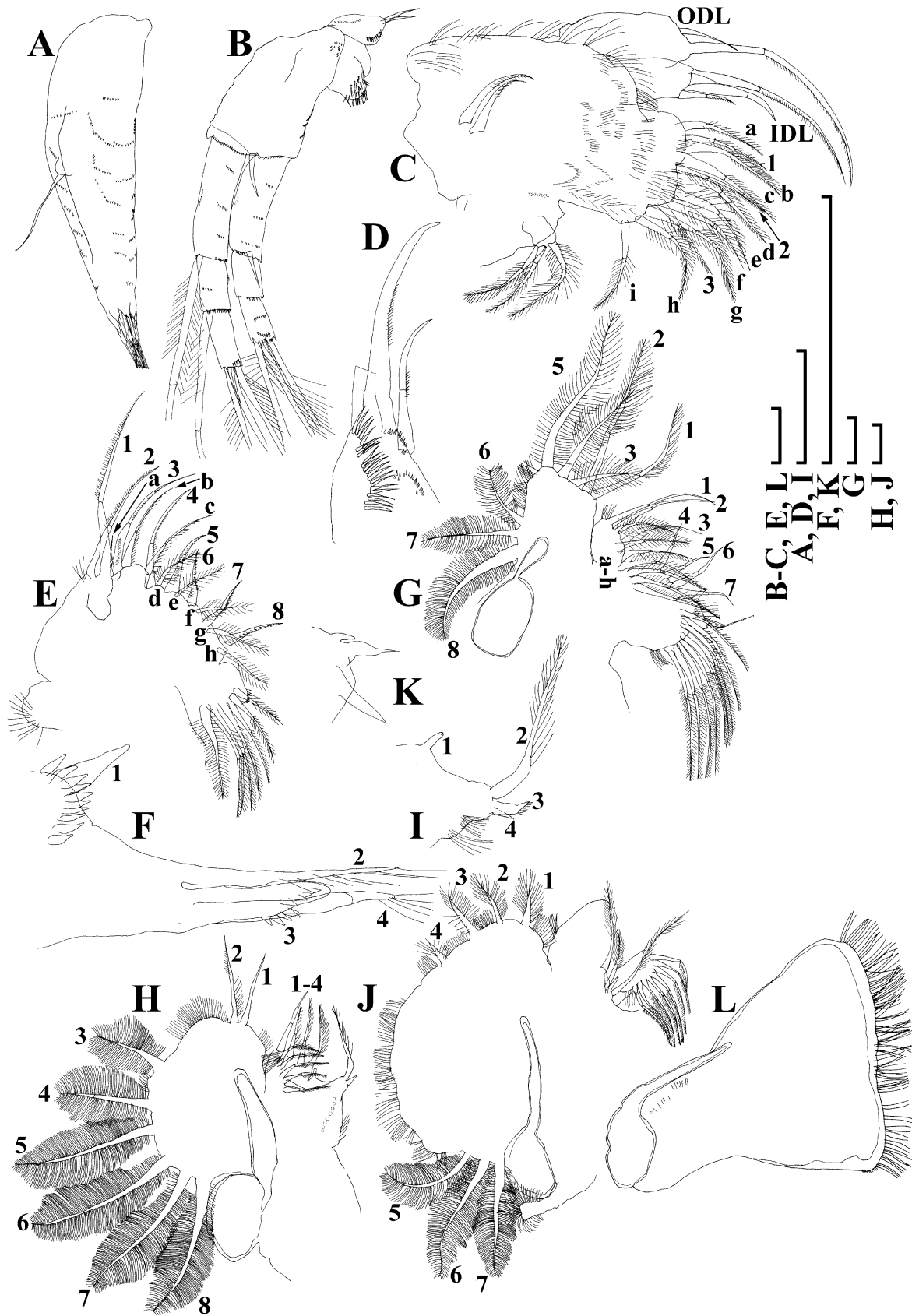
*Postabdomen* as a large (PL/BL= 0.37–0.45), relatively broad (PH/PL= 0.38–0.49), flattened plate (Fig. 10M). It is more ovoid, than in previous species, with dorsal and ventral margins coming together distally. Dorso-distal (preanal) angle well expressed, distal anal embayment deep, dorsal portion of distal (=anal) margin slightly concave. Postanal angle obtuse, rounded (Fig. 10N). Pre-claw portion of postabdomen as a conical prominence. Ventral margin of postabdomen slightly convex. Armature of the preanal margin as a series of preanal teeth, slightly and fluently increasing in size in distal direction; a gap lacking any teeth at base of postabdominal setae (Fig. 10O); teeth in middle of preanal margin with sharp tips (NT= 97); distal most tooth somewhat larger than the others, located just on dorso-distal angle of postabdomen. On pre-claw portion of postabdomen there are crescentic clusters postanal teeth, distalmost members particularly large, predominantly clustered, teeth at base of pre-claw portion short, predominantly doubled (Fig. 10N, arrows). Sub-parallel rows of minute setules on whole lateral surface of postabdomen (not represented in Fig. 10M due to their minute size). Postabdominal setae short (less than third of preanal margin length), bisegmented, distal segment slightly shorter than basal one and bilaterally setulated. Setae located on a distinct, nut-like base. Postabdominal claw relatively robust (CL/PL= 0.13–0.25); with massive base; weakly and evenly tapered in distal direction, and slightly curved. Two basal spines, first (distal) long (DS/CL= 0.30–0.43), second (basal) short (BS/CL= 0.15–0.27; BS/DS= 0.34–0.60), located dorsally immediately at base of claw.

*Antenna I* relatively short (AL/BL = 0.1; AL/DA=2.85–3.94); with maximal width in basal half, with its distal 2/3 portion evenly tapering distally (Fig. 11A); protruding greatly beyond tip of rostrum (Fig. 10C). Slender antennular sensory seta relatively short (about third of antenna I length), arising approximately in antenna I middle. Nine bisegmented aesthetascs, with pointed teeth around them. Numerous short rows of minute denticles encircling antennular surface. *Antenna II* relatively short (Fig. 11B). In coxal region, a projection with two bisegmented setae, unequal in length, next projection with semi-circular row of setules and a distalmost projection with numerous strong spinules. Massive basal segment with a relatively long seta distally on anterior surface, and rows of short setules. Both branches with elongated segments, basal most members particularly elongated; all segments with rows of short setules. Setae 0-0-3/1-1-3; both apical and lateral setae long, clearly bisegmented, with long hairs on both basal and distal segments. Spines 1-0-1/0-0-1. No additional spines on distal parts of any segments of either branch. Length of apical spines and of segments from which they arise sub-equal; spine situated on proximal segment of exopod shorter than second segment.

*Mandible* (Fig. 10L), *maxilla I*, *maxilla II* as in previous species.

*Limb I* large. Epipodite (not represented in Fig. 11C) without a finger-like projection. Two accessory setae, unequal in size and setulated in distal parts, are the distal most structures of the distal portion of limb I (also not represented in Fig. 11C). ODL distally with 2 setae of very unequal size. IDL with three bisegmented setae, one of them a remarkable relatively strong hook-like seta (but less strong as *E. macracanthus*), the smallest IDL seta short. IDL supplied with long distal spinules (about 9 in largest adults), long proximal spinules (about 14 in largest adults), short marginal spinules (about 13 in largest adults) and short basal spinules (about 17 in largest adults); a field of minute denticles on IDL basally. Endite III with three setulated, bisegmented posterior setae of similar size (a–c), and a setulated, stiff anterior seta 1. Endite II with three posterior setae (d–f) and a stiff, setulated anterior seta 2, a very small sensillum near its base. Endite I with 3 posterior setae (g–i), and a stiff anterior seta 3. Two ejector hooks anteriorly on outer portion of limb corm. Well-developed maxillar process bearing three slender, fully and densely setulated setae on inner side of limb base.

*Limb II* with ovoid epipodite lacking a finger-like projection; exopodite as a small lobe (Fig. 11E). At inner side of limb, a row of eight stiff scrapers; setae 1–2 with more delicate feathering, setae 3–8 with relatively robust denticle. Posteriorly on limb corm 8 soft setae: distal most one (a) short; next two ones (b–c) longest, basal most ones (d–h) similarly feathered by long hairs. Distal armature of gnathobase with four setae, one of them a relatively large sensillum (Fig. 11F, 1), located far from the others, a row of denticles (about 10 in largest adults) crossing



**FIGURE 11.** *Eurycercus beringi* sp.nov., head and thoracic appendages of parthenogenetic female from Council #05: a roadside pond <1.5 m deep, 10 X 25 m, Seward Peninsula, Alaska, U.S.A. A, antenna I. B, antenna II. C, limb I. D, inner distal lobe of limb I. E, limb II. F, distal armature of its gnathobase. G, limb III. H, limb IV. I, distal armature of its gnathobase. J, limb V. K, distal armature of its gnathobase. L, limb VI. Scale bar denotes 0.1 mm.

near it. Filter plate with 8 long, densely setulated setae; distal most seta of filter plate clearly smaller than the others, second-third ones slightly shorter than others.

*Limb III* with relatively large epipodite bearing a finger-like projection (Fig. 11G). Exopodite flat, distally, five setae of unequal size (Fig. 11G, 1–5); lateral group consists of three setae (6–8) increasing in size basally. Distal endite with three bisegmented anterior setae (1–3), basal endite with 4 stiff setae (4–7). Seven long soft setae of subequal size (a–h) on limb corm posteriorly. Gnathobase weakly demarcated from basal endite, distal armature with 4 members as in previous species. Nine setae in filter plate.

*Limb IV* with epipodite large, ovoid, bearing a finger-like projection (Fig. 11H). Exopodite oval, with two distal, relatively long, bisegmented setae of unequal size, armed by short setules (1–2), other six setae feathered bilaterally by very long setules (3–8). Marginally on inner limb face, a row of four stiff anterior setae (1–4). Seta 1 long, setae 2–4 approximately of equal size, feathered by long setules in distal part. Posteriorly, five soft setae with subequal length. Distal armature of gnathobase with 4 members (Fig. 11I, 1–4). One of them a long, bisegmented seta, densely feathered in distal part (2), two others small (3–4), a large, bottle-shaped sensillum (1) is a fourth member of gnathobasic armature (similar to limb III). Filter plate IV with 8 setae, middle ones longer than marginal ones.

*Limb V* with pre-epipodite as a setulated hillock; epipodite with a finger-like projection (Fig. 11J). Exopodite very large, with four short distal (1–4) and three large lateral (5–7) setae. Inner portion of limb with a protruding flap-like distal projection, fringed by long setules. Three marginal setae on inner face of limb, distal member slightly protruding behind distal endopodite projection, a sensillum near basalmost seta. Distal armature of gnathobase with three members (Fig. 11K). Filter plate with 8 setae.

*Limb VI* triangular-shaped, with epipodite bearing a long finger-like projection and a row of setules somewhat distal to it; its inner margin setulated (Fig. 11L).

**Ephippial female, male.** Unknown

**Length.** Parthenogenetic females 0.77–2.66 mm, holotype 2.04 mm.

**Comments.** This is the most specific taxon of the subgenus, combining characters of Frey's subgenera *E. (Eurycercus)* and *E. (Bullatifrons)*. It means that previously it could be misidentified as *E. lamellatus* or *E. longirostris-vernalis*.

**Distribution.** *E. beringi* **sp. nov.** has been found definitively only on the Seward Peninsula in northwest Alaska. However, there are several records of "*E. lamellatus*" from arctic Alaska and southwest Alaska (Frey 1971) that have the same medial antenna I seta position as *E. beringi* (Reed 1962). So there is a good chance that *E. beringi* is common and widespread in Alaska and perhaps even beyond this state.

**Ecology.** This species is very common and widespread on the Seward Peninsula in oxbow ponds, roadside ditch ponds, small tundra ponds and even among the emergent plants of a glacial lake (Salmon Lake). The species occurs in standing waters on mixed tundra-taiga and on tundra. *E. beringi* **sp. nov.** was missing however from the high conductivity ponds near the Pilgrim hot springs and near the Safety Sound. *E. beringi* **sp. nov.** sometimes co-occurs with the less common *E. glacialis*. It also occurs when different predators of cladocerans are abundant (fish in Salmon Lake; *Chaoborus* and *Heterocope* in ponds).

### Key for determination of adult parthenogenetic females of the Holarctic species of *Eurycercus* (*Eurycercus*) emend. nov.

- |   |  |   |
|---|--|---|
| 1 | Dorsal head pores lack a bubble-like projection and are located on a prominent transverse fold (indentation); a median keel passes through whole carapace dorsum . . . . .   | 2   |
| - | Dorsal head pores possess a bubble-like projection and are located on a prominent transverse fold (indentation) or on a flat head shield; a median keel is completely absent or expressed only in the posterior portion of the carapace dorsum . . . . . | 3   |
| 2 | Small (seldom as large as 2 mm), body very strongly compressed laterally, dorsal margin of head flattened or even slightly concave between compound eye and median head pore, the smallest seta IDL very short . . . . .                                 | <i>E. microdontus</i> Frey, 1978          |
| - | Large species, body moderately compressed laterally, dorsal margin of head regularly convex, the smallest seta of IDL of moderate size . . . . .   | <i>E. lamellatus</i> (O. F. Müller, 1776) |
| 3 | Bubble-like projection on prominent transverse fold, median keel present in posterior portion of carapace dorsum . . . . .   | <i>E. beringi</i> <b>sp. nov.</b>         |
| - | Bubble-like projection on flat head shield, median keel absent . . . . .   | 4   |
| 4 | Median labral keel short, reaching approximately middle of antenna I . . . . .   | <i>E. pompholygodes</i> Frey, 1975        |
| - | Median labral keel large, approximately reaching tip of antenna I . . . . .  | 5   |
| 5 | Apex of median labral keel distinctly angled . . . . .   | <i>E. nipponica</i> Tanaka & Fujita, 2002 |



-	Apex of median labral keel rounded . . . . .	6
6	Hook-like seta on IDL especially strong, its base occupies the whole top of IDL . . . . .	<i>E. macracanthus</i> Frey, 1973
-	Hook-like seta on IDL not so strong, its base occupies only a part of top of IDL . . . . .	<i>E. longirostris</i> Hann, 1982

## The COI phylogeny

Fig. 12

The species identified by classical morphological taxonomy were generally associated with well-supported phylogenetic clades. One exception was *E. nipponica*, which was distinct from *E. longirostris*, but with weak support. Another exception was the *Eurycerus* cf. *longirostris* reported from Churchill, Manitoba (Jeffery *et al.* 2011). This species appears to be a sister group with *E. glacialis* and only distantly related to *E. longirostris*. *E. beringi* **sp. nov.** and *E. macracanthus* appear to be distantly related sister species. As with the morphological assessment, the subgenera appear to be broken up by the positions of the two new species *E. beringi* **sp. nov.** and *Eurycerus* cf. *longirostris*. The sequence of *E. glacialis* determined by non-PCR methods turned out to be identical to that determined by PCR methods, indicating that there is unlikely to be a universal pseudogene artifact in the data. Moreover, the open reading frame is preserved as expected from a functional mitochondrial gene.

## Discussion

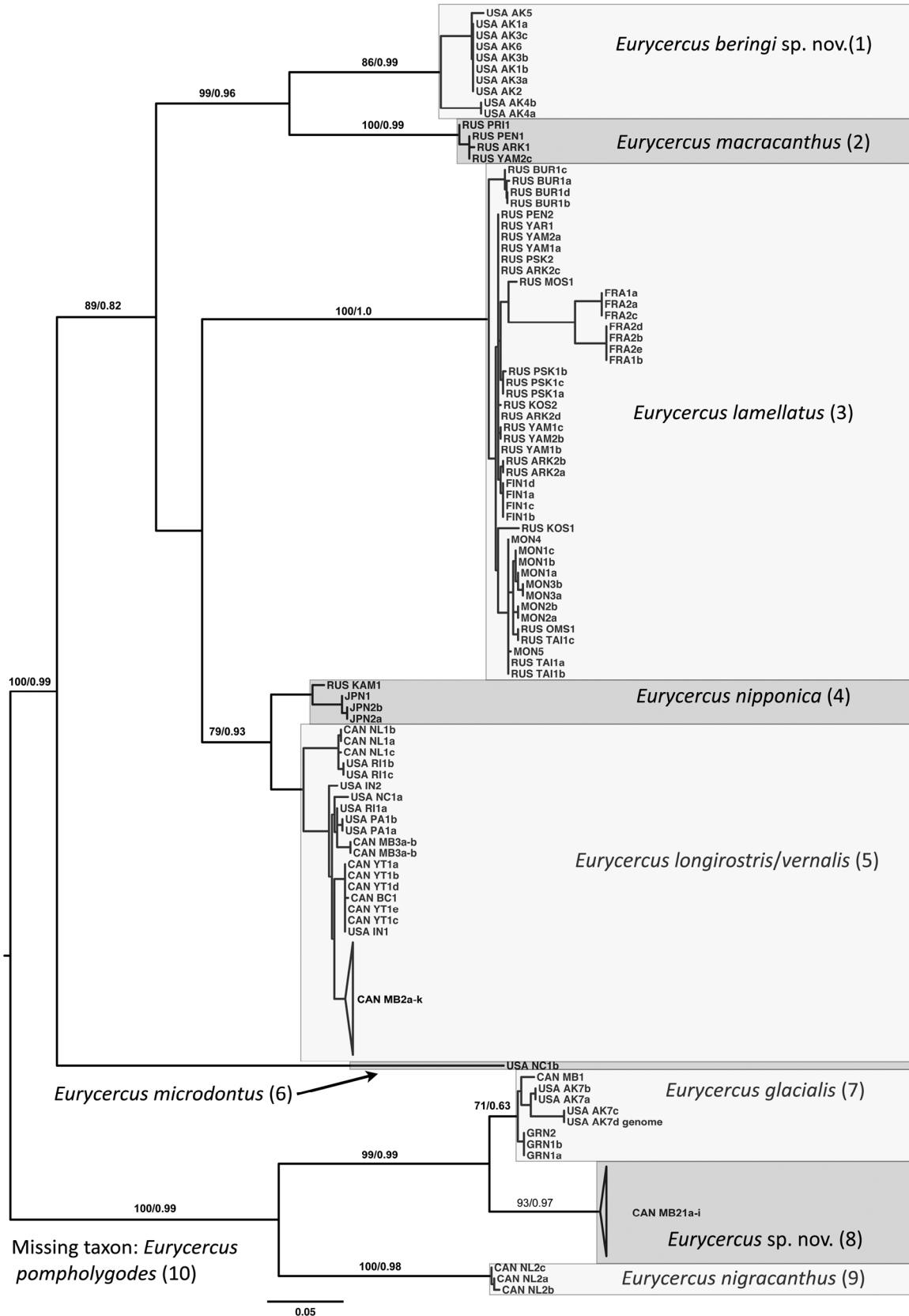
Our results indicate that there are at least ten species of the genus *Eurycerus* in the Holarctic. We describe one new species in detail and identify another likely new species that requires description. Surprisingly, at least half of the species diversity is found in the northern latitudes of the Holarctic. Unfortunately, the unexpected diversity is located in a region where standing waters are undergoing rapid massive losses from permafrost melting, increased evaporation, vegetation changes, and other warming-related processes. Usually, the biotic damages for the loss of Alaskan and Siberian standing waters are couched in terms of harm to waterfowl. Our discovery of northern diversity in *Eurycerus* is a reminder that endemic arctic and subarctic crustaceans will also have suffered extensive population losses from the dramatic disappearance of surface waters.

Another unexpected result is that the three described subgenera of *Eurycerus* are disrupted by the morphological characters of the new species and by the phylogeny that we present.

Now we can confidently say that the species diversity of Holarctic *Eurycerus* was underestimated, even keeping in mind that the two species described by Hann (1982) in reality comprise a single species. Two previously described species, *E. macracanthus* and *E. pompholygodes*, which were recorded from very limited areas of the Palaearctic (Frey 1973a, 1975; Chen *et al.* 1995; Hessen & Walseng 2008; Kotov *et al.* 2011), are found by us to have very wide distributional ranges (i.e. present in both Europe and Asia). Note that any previous records of *E. macracanthus* from Pacific Asia lack illustrations (Streletskaia 2010) and need to be verified, because both *E. nipponica* and *E. beringi* **sp. nov.** might also be found there.

We found that two other taxa, *E. nipponica* and *E. beringi* **sp. nov.**, have a more limited distribution (Japan-Kamchatka-Alaska and Alaska), in the former Beringian region. Until the last decade, this area was poorly studied by cladoceran investigators. For example, the main approach of the “anti-cosmopolitanism” publications by David Frey’s (1982c, 1988) concerning the Holarctic was to compare populations of “the same” taxon from Europe and Atlantic portion of North America, while the whole Asian Palaearctic went without study. Only a few specific taxa were described from the Far East of Russia and Japan (Frey 1973a–b; Korovchinsky 1979; Smirnov 1998) until the beginning of the XXI century, when these territories started to be one of main sources of newly described taxa for morphologists (Korovchinsky 2009; Korovchinsky & Sheveleva 2009; Sinev *et al.* 2009; Smirnov & Sheveleva 2010; Kotov & Sinev 2011) and new phylogroups for molecular biologists (Ishida & Taylor 2007; Belyaeva & Taylor 2009; Xu L. *et al.* 2010; Xu S. *et al.* 2010). Our present publication is the next step in the study of taxa from the easternmost Palaearctic combining morphological and molecular approaches that proved successful in revising the *Daphnia curvirostris* group (Ishida *et al.* 2006; Kotov *et al.* 2006) and the subgenus *Bosmina* (*Eubosmina*) (Kotov *et al.* 2009).

Although *E. macracanthus* is widely distributed in Palaearctic, the center of its distribution is probably located in the Lena and Amur basins (where it is the most common species), while in Western Siberia and European Russia it is a relatively rare taxon. We can assume that this species colonized de-glaciated territories from Eastern Siberia relatively recently.



**FIGURE 12.** Phylogram based on an alignment of mitochondrial COI sequences for the genus *Eurycerus*. The tree is mid-point rooted and based on the best ML tree found in PhyML 3.0 (see text). Support values are from nonparametric bootstrap and from approximate likelihood ratio tests. Values less than 70 or 0.7 are not shown. The scale bar represents substitutions per site based on a GTR+I+G model. Proposed species are numbered. See Table 1 for Genbank Accession numbers.

**Critique of the subgeneric differentiation according to Frey (1975).** Our results both from the COI phylogeny and morphology confirm the separation of the subgenus *Eurycercus* (*Teretifrons*), but strongly compromise the further subgeneric differentiation according to Frey (1975). Frey (1975) listed three main diagnostic characters of the subgenera (Table 2). Even *E. nipponica*, being "*Bullatifrons*" and weakly separated from *E. longirostris* in the COI tree, bears an "angled" labral keel in contrast to other similar forms. But even more destructive for Frey's (1975) subgenera is a remarkable new taxon, *E. beringi* **sp.nov.**, which possesses a combination of Frey's main "diagnostic" characters.

Our COI tree has strong support for many nodes but is incompletely resolved. The position of *E. lamellatus* is, for example, poorly supported. But, the very unusual *E. beringi* **sp. nov.** is grouped together (and with a good support) with *E. macracanthus*, the type species of the subgenus *E. (Bullatifrons)*. The known species of the subgenus *E. (Eurycercus)* sensu Frey (1975), *E. lamellatus* and *E. microdontus*, apparently do not form a monophyletic taxon. Although a more thorough phylogenetic estimate of the genus awaits nuclear evidence, our morphological and genetic results challenge the correctness of Frey's subgeneric differentiation.

So, we propose for the genus *Eurycercus* to use only two subgenera: *E. (Eurycercus)* emend. nov., combining two Frey's subgenera, and *E. (Teretifrons)*. But even in this subdivision there are some problems with Frey's diagnostic characters! We found that *E. (T.) cf. nigracanthus* in reality has dorsal head pores located on a very low "pancake"-like projection, not immediately on the head shield surface as Hann (1990) suggested, placing this taxon to the subgenus *E. (Teretifrons)*. Also *E. nigracanthus* has a relatively short antenna I as compared with *E. (T.) glacialis*, but relatively long antenna I is regarded as a character of *E. (Teretifrons)* (Frey, 1975). So, a single good character uniting all species of the subgenus *E. (Teretifrons)* is an apomorphic double loop of the mid gut, which is, unfortunately, difficult to discern in fixed specimens. Apparently the diagnosis of the subgenus *E. (Teretifrons)* needs to be emended in future studies.

**Species diagnostic characters in *Eurycercus*.** Bekker (2011) analyzed characters previously regarded as taxonomically important for *Eurycercus* and concluded that Hann's (1982) species differentiation based on morphometric statistics is somewhat problematic for the genus. In general, weakly oligomerized series of morphological structures are less valuable for taxonomy than strongly oligomerized structures (Smirnov & Kotov 2010). Among quantitative characters, only the number of the spinules on the IDL proved informative. At the same time, differences in the number of such spinules among populations are insufficient to warrant taxonomic revisions. It is necessary to take into consideration, that Frey's (1973a, 1975) descriptions were insufficiently detailed to characterize the spinules of the IDL (i.e., basal spinules were missed in *E. macracanthus*). This lack of detail appears to have led to incorrect conclusions about species differences and group numbers based on the IDL. The relative size of these spinules works for species determination in some cases, i.e. for discrimination of two South American taxa (Bekker *et al.* 2010), but in *E. longirostris* there are populations with both long and short spinules.

The most informative characters for species diagnosis in *Eurycercus* are from the labral keel, which is strongly variable among species, from very short and rounded to large and angled. In the chydorids, characters of the labral keel are found to be helpful for different genera (Fryer 1968; Dumont & Silva-Briano 2000).

**Remaining gaps in taxonomic knowledge.** Even after a series of our publications (Bekker *et al.* 2010; Bekker 2011 and this study), *E. (Eurycercus)* some regions of the World are poorly studied:

- 1) South Africa, where *Eurycercus* cf. *lamellatus* (see Harding 1961) is apparently a new, distinct species (Frey 1993; Smirnov, pers. comm.);
- 2) Tibetan and Himalayan populations of *E. cf. lamellatus* (see Venkataraman 2001), which could represent a separate taxon;
- 3) Mediterranean area and North Africa (Frey 1971), where most probably only *E. lamellatus* s. str. is present;
- 4) Northern Canada, where "*Bullatifrons*"-like populations are quite common (Chengalath 1987), but we had no good material to analyze them accurately. The clade of "Atlantic *E. cf. longirostris*" could be a part of a more complicated pattern of taxa.

There is a chance to find more species in South America because only a few populations from this continent have been revised (Bekker *et al.*, 2010). Finally, a global revision of *E. (Teretifrons)* needs to be done. Many previous records and descriptions (Cushman 1908; Tash & Armitage 1967) cannot presently be assigned to valid taxa.

**TABLE 2.** Differentiation between parthenogenetic females of the subgenera *E. (Eurycercus)* and *E. (Bullatifrons)* according to Frey (1975) and intermediate characters of *E. nipponica* and *E. beringi* **sp. nov.**

Character	Subgenus <i>E. (Eurycercus)</i>	subgenus <i>E. (Bullatifrons)</i>	<i>E. nipponica</i>	<i>E. beringi</i> <b>sp. nov.</b>
Medial keel on valves	Present	Absent	Absent	Present in posterior portion, but absent in anterior portion
Dorsal head pores	On a transverse fold, with an indentation immediately posterior	On a special bubble, located on flat head surface	On a special bubble, located on flat head surface	On a bubble, which is located on a transverse fold, with an indentation immediately posterior
Labral keel	With prominent apex ("angled")	Rounded	With prominent apex ("angled")	With prominent apex ("angled")

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