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Revision of the genus *Bosmina* Baird, 1845 (Cladocera: Bosminidae), based on evidence from male morphological characters and molecular phylogenies

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The systematics of the freshwater crustacean genus *Bosmina* Baird, 1845 (Anomopoda: Bosminidae) is notoriously confused. Part of the problem stems from a lack of characters in this cyclic parthenogen. We aimed to remedy this problem by scoring male morphological characters (previously described in just a few species), and by estimating molecular phylogenies. More specifically, the goals of this investigation are: (1) a detailed description of the adult males of *Bosmina* species; (2) a study of the changes of male characters during the postembryonic development in different subgenera; (3) an analysis of the taxonomical value of male characters; and (4) the estimation of a phylogenetic tree based on male characters and genetic characters from mitochondrial 16S rDNA and nuclear rDNA-internal transcribed spacers (ITS) gene sequences. We redescribed males of ten species: *Bosmina* (*Bosmina*) *longirostris* (O. F. Müller, 1785); *Bosmina* (*Bosmina*) *liederi* De Melo & Hebert, 1994; *Bosmina* (*Sinobosmina*) *fatalis* Burckhardt, 1924; *Bosmina* (*Sinobosmina*) cf. *fatalis cyanopotamia* Burckhardt, 1924; *Bosmina* (*Liederobosmina*) *meridionalis* Sars, 1904; *Bosmina* (*Liederobosmina*) cf. *hagmanni* Stingelin, 1904; *Bosmina* (*Lunobosmina*) *oriens* (De Melo & Hebert, 1994); palaearctic *Bosmina* (*Eubosmina*) cf. *coregoni* Baird, 1857 (including the morphs '*coregoni s.s.*', '*coregoni kessleri*', '*longispina*', and '*crassicornis*'); Beringian '*Bosmina* (*Eubosmina*) cf. *longispina* Leydig, 1860'; and ***Bosmina* (*Eubosmina*) *tanakai* sp. nov.** In addition, we fully redescribe *B. (Lunobosmina) oriens* and describe ***B.* (*E.*) *tanakai sp. nov*.** (an endemic Japanese lineage of the subgenus *Eubosmina*). A cladistic analysis of 24 morphological characters of males led to a single most parsimonious tree that agreed with phylogenies based on 16S mtDNA and nuclear genes. Both the male morphological and the genetic analyses indicated that the Japanese lineage containing ***B.* (*E.*) *tanakai sp. nov*.** is divergent and unique. Thus, these approaches resolved relationships that were unresolved with female morphology. Divergent life history evolution appears to have rendered male morphology more informative than female morphology for systematic biology. We provide a key for *Bosmina* species with adequately described males. © 2009 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2009, **156**, 1–51.

ADDITIONAL KEYWORDS: 16S – anomopoda – crustacea – genetics – ITS – morphology – phylogeny – systematics.

> Hast thou seen thy fathers, Bosmina, descending in thy dreams?
>
> From the Poems of Ossian by James MacPherson

INTRODUCTION

There are several genera of Cladocera with confused systematics, but the taxonomic instability of the genus *Bosmina* Baird, 1845 (Anomopoda: Bosminidae) is legendary. Extensive phenotypic plasticity and a dearth of morphological characters has stifled taxonomic advances, despite the importance of the genus to freshwater ecosystems and paleolimnology. The discovery of head pore characters (Goulden & Frey, 1963; Kořínek, 1971; Dumont & Van de Velde, 1976) improved the taxonomic resolution, but these characters failed to resolve the majority of difficulties (Kořínek, Sacherová & Havel, 1997). Genetic investigations of the bosminids (De Melo & Hebert,

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1994; Little *et al.*, 1997; Taylor, Ishikane & Haney, 2002; Haney & Taylor, 2003) also significantly improved the taxonomy and phylogenetic understanding of the family. Still, these studies often lacked broad geographical coverage, analysis of male morphological characters, and a detailed taxonomic treatment. In less controversial anomopod taxa, a detailed treatment of males and morphology (Glagolev & Alonso, 1990; Frey, 1991; Smirnov, 1992; Smirnov, 1996; Kotov, 1999, 2000), and integrated approaches with molecular characters (e.g. Ishida, Kotov & Taylor, 2006), helped to resolve longstanding taxonomic problems. An integrated approach that explores morphological characters from males, large geographical regions, and molecular information should improve the taxonomy of bosminids.

The taxonomic value of male characters of the Cladocera has been known at the genus level for decades (Burckhardt, 1924, 1941; Brehm, 1928; Lieder, 1983b). But, for bosminids, males are usually rare (even for cyclic parthenogens), and are often unknown. Indeed, the description of rare males for a *Bosmina* species has justified special publication (Keilhack, 1904; Sergeev, 1981). Unfortunately, even where bosminid males are known, they are often inadequately described (Paggi, 1979; Kotov, 1996). The demonstration that bosminid males can be artificially induced by a juvenile hormone analogue (Kim, Kotov & Taylor, 2006) provides hope that males in many more bosminid species can be studied in detail.

The advent of genetic methods sensitive enough for small arthropods (of < 400 μm in length) such as bosminids has also yielded new characters and insights. Early genetic studies (Manning, Kerfoot & Berger, 1978; Brock, 1980) noted an association between morphology and allozyme electromorphs in *Bosmina*, hinting at the existence of cryptic species. De Melo & Hebert (1994) carried out a multilocus allozyme investigation, and revised the taxonomy of the North American bosminids with several proposed new species. Little *et al.* (1997) discovered an asexual polyploid species of *Bosmina* using allozyme information, and noted some differences in the postabdominal claw from existing Nearctic species. Taylor *et al.* (2002) later carried out a DNA sequence-based phylogenetic analysis of bosminids, and revised the subgeneric divisions in a way that was consistent with the the phylogeny and a few morphological characters (mainly from females). Haney & Taylor (2003) found that the proposed Holarctic taxon of *Bosmina longispina* Leydig, 1860 is paraphyletic, with the Palearctic *B. longispina* grouping with a phylogenetically unresolved *Eubosmina* species swarm, and with the Nearctic *B. longispina* being basal. A large part of the range of the *Eubosmina* (eastern Palearctic) remains unexamined at the genetic level. Moreover, males for these lineages have not been compared in detail.

In the present study, we aimed to further improve our understanding of bosminid relationships and taxonomy through a detailed analysis of male morphology and sequence-based genetics that includes eastern Palearctic samples.

MATERIAL AND METHODS

The males for this study were selected from preserved samples. At least ten adult males and five juvenile females of each instar from each population (if this number was available) were studied *in toto*, and then five adult males and five juvenile males of the first and second instar were dissected under a binocular stereoscopic microscope, for the study of their postabdomens and appendages. In the case of museum collections, only one or two adult males were dissected, with the permission of the collection managers. Drawings were prepared using a drawing apparatus attached to an Olympus CX41 microscope. Males from some populations were lyophilized, mounted on an aluminum stub, coated with gold, and examined under a scanning electron microscope (SEM). For *Bosmina* (*Bosmina*) *liederi* De Melo & Hebert, 1994, we have no samples with males, and so males were artificially induced in the laboratory by methyl farnesoate (MF), as previously described (Kim *et al.*, 2006).

The phylogenetic analysis of morphological characters was performed using PAUP v4.0b10 for 32-bit Microsoft Windows (Swofford, 2000), with branch-and-bound search, unordered characters, and a parsimony optimality criterion. Nonparametric bootstrapping with 100 pseudoreplicates was performed as a test of reliability.

Table 1 gives the location and species assignment for each of the specimens used in the genetic analyses. This sample is composed of *Bosmina* (*Eubosmina*) cf. *coregoni* Baird, 1857 from 17 sites; *Bosmina* (*Sinobosmina*) *fatalis* Burckhardt, 1924 from one site; *Bosmina* (*Bosmina*) *freyi* De Melo & Hebert, 1994 from 19 sites; *Bosmina* (*Liederobosmina*) cf. *hagmanni* Stingelin, 1904 from eight sites; *Bosmina* (*Bosmina*) *liederi* from 13 sites; *Bosmina* (*Bosmina*) *longirostris* (O. F. Müller, 1785) from 16 sites; *Bosmina* (*Lunobosmina*) *oriens* (De Melo & Hebert, 1994) from five sites; Nearctic *Bosmina* (*Eubosmina*) cf. *longispina* Leydig, 1860 from 17 sites; *Bosmina* (*Lunobosmina*) *tubicen* Brehm, 1953 from one site; and *Bosmina* (*Eubosmina*) *tanakai* sp. nov. from five sites.

DNA extraction was carried out using a modified Quickextract (Epicenter) protocol, where a single animal is incubated in 25 μL of extraction solution for 3 h. Polymerase chain reactions (PCR) were performed in 50-μL reactions using 5 μL of template,

Table 1. Species names, sampling locations, and abbreviations of bosminid specimens used for genetic analysis. The abbreviations are used in the phylogenetic trees presented in Figures 26 and 27

Species names	Abbreviations	Geographic name	Latitude	Longitude	Genbank accession number
°*Bosmina* (*Eubosmina*) cf. *coregoni*	FIN1	Jääsjärvi, Finland	61.7145°	26.0679°	This study
B. (*E.*) cf. *coregoni*	UK1	Derwentwater, UK	54.5939°	–3.1412°	AF484010
B. (*E.*) cf. *coregoni*	UK2	Clatto Country Park, Dundee, UK	56.4983°	–3.02833°	AY264729; AY264763
B. (*E.*) cf. *coregoni*	UK3	Ullswater, UK	54.6099°	–2.82763°	AY264727; AY264764
B. (*E.*) cf. *coregoni*	GER1	Muggelsee, Germany	52.4333°	13.6496°	AF484012
B. (*E.*) cf. *coregoni*	GER2	Okerstausee, Germany	51.8397°	10.4538°	AF482753; AF484015
B. (*E.*) cf. *coregoni*	GER3	Selenter See, Germany	54.3083°	10.4583°	AY264724; AY264756
B. (*E.*) cf. *coregoni*	IN1	Kuhn Lake, IN, USA	41.2867°	–85.6925°	AF482756; AF484011
B. (*E.*) cf. *coregoni*	IN2	Center Lake, IN, USA	41.2437°	–85.8558°	AY264725
B. (*E.*) cf. *coregoni*	NY1	Deep Lake, NY, USA	43.0217°	–77.5716°	AY264730; AY264758
B. (*E.*) cf. *coregoni*	ON1	Guelph Lake, ON, Canada	43.5953°	–80.2649°	AY264717
B. (*E.*) cf. *coregoni*	ON2	Georgian Bay, ON, Canada	45°	–81.2499°	AF482754; AF484013
B. (*E.*) cf. *coregoni*	POL1	Lake Ros, Poland	53.6735°	21.9127°	AY264719; AY264759
B. (*E.*) cf. *coregoni*	POL2	Lake Dargin, Poland	54.126°	21.7395°	AY264722; AY264760
B. (*E.*) cf. *coregoni*	POL3	Lake Hancza, Poland	54.248°	22.7997°	AY264721; AY264761
B. (*E.*) cf. *coregoni*	RUS1	Glubokoe Lake, Russia	55.7527°	36.5085°	AY264754; AY264762
B. (*E.*) cf. *coregoni*	RUS2	Lake Zuratkul, Russia	54.9121°	59.2387°	This study
Bosmina (*Sinobosmina*) *fatalis*	JPN1	Lake Suwa, Japan	36.0512°	138.084°	AF482745; AF484009
Bosmina (*Bosmina*) *freyi*	AR1	Unnamed pond, Princeton, AR, USA	34.0186°	–92.6312°	AF482736; AF484000
B. (*B.*) *freyi*	CA1	Hume Lake, CA, USA	36.7918°	–118.9068°	This study
B. (*B.*) *freyi*	CA2	Lower Blue Lake, CA, USA	39.1637°	–122.9972°	This study
B. (*B.*) *freyi*	CT1	Highland Lake, CT, USA	41.9174°	–73.0803°	This study
B. (*B.*) *freyi*	LA1	Plantation Lake, LA, USA	29.8038°	–91.7951°	AF482737; AF484001
B. (*B.*) *freyi*	MA1	Flints Pond, MA, USA	42.4299°	–71.3160°	This study
B. (*B.*) *freyi*	MA2	Ditch near Truro, MA, USA	Unknown	Unknown	This study
B. (*B.*) *freyi*	MA3	Parker Mills Pond, MA, USA	41.7685°	–70.6769°	AF482735; AF484002
B. (*B.*) *freyi*	ME1	Moose lake, ME, USA	44.0570°	–70.6740°	This study
B. (*B.*) *freyi*	ME2	Clays Pond, ME, USA	43.9860°	–70.9549°	This study
B. (*B.*) *freyi*	ME3	Jordan Pond, ME, USA	44.3228°	–68.2537°	This study
B. (*B.*) *freyi*	ME4	Long Lake, ME, USA	43.9694°	–70.6038°	This study
B. (*B.*) *freyi*	ME5	Upper Hadlock Pond, ME, USA	44.3214°	–68.2875°	This study
B. (*B.*) *freyi*	NH1	Falls Pond, NH, USA	44.0022°	–71.2781°	This study
B. (*B.*) *freyi*	NY2	Artist Lake, NY, USA	40.8854°	–72.9317°	This study
B. (*B.*) *freyi*	NY3	Great Baehre Swamp, Amherst, NY, USA	43.0158°	–78.7386°	This study
B. (*B.*) *freyi*	NY4	Payne Lake, NY, USA	43.7951°	–75.2912°	This study
B. (*B.*) *freyi*	NY5	Bond Lake, New York, USA	43.1808°	–78.9168°	AF482738; AF483999
B. (*B.*) *freyi*	ON2	Avery Lake, ON, Canada	45.1981°	–78.8059°	This study
Bosmina (*Liederobosmina*) cf. *hagmanni*	MA4	Gull Pond, MA, USA	41.956°	–70.0058°	This study
B. (*L.*) cf. *hagmanni*	MA5	Great Pond, MA, USA	41.9743°	–70.0314°	This study
B. (*L.*) cf. *hagmanni*	MA6	Halls Pond, CT, USA	41.8413°	–72.1095°	AF482750; AF484021
B. (*L.*) cf. *hagmanni*	NH2	Sunapee Lake, NH, USA	43.387°	–72.0573°	This study
B. (*L.*) cf. *hagmanni*	NY6	Swan Pond, NY, USA	40.9019°	–72.7928°	This study

Table 1. *Continued*

Species names	Abbreviations	Geographic name	Latitude	Longitude	Genbank accession number
B. (*L.*) cf. *hagmanni*	SC1	North Dike Reservoir, SC, USA	33.4076°	–80.0681°	AF482749; AF484019
B. (*L.*) cf. *hagmanni*	SC2	Swamp near Bamburg, SC, USA	33.2167°	–80.9887°	This study
B. (*L.*) cf. *hagmanni*	AR2	Paris Reservoir, AR, USA	35.27049°	–93.71973°	This study
Bosmina (*Bosmina*) *liederi*	AK1	Unnamed pond near Solomon, AK, USA	64.5962°	–164.395°	AF482739; AF484008
B. (*B.*) *liederi*	AZ1	Fool Hollow Lake, AZ, USA	34.2712°	–110.0749°	This study
B. (*B.*) *liederi*	CA2	Bass Lake, CA, USA	37.3292°	–119.5712°	This study
B. (*B.*) *liederi*	CT2	Lower Bolton, CT, USA	41.8009°	–72.4303°	AF482742
B. (*B.*) *liederi*	CT3	Halls Pond, CT, USA	41.8423°	–72.1082°	This study
B. (*B.*) *liederi*	IN4	Waldron Lake, IN, USA	41.493°	–85.4311°	This study
B. (*B.*) *liederi*	IN3	Center Lake, IN, USA	41.2455°	–85.8555°	This study
B. (*B.*) *liederi*	MI2	Hemlock Lake, MI, USA	42.0639°	–85.8066°	This study
B. (*B.*) *liederi*	NH3	Storrs Pond, NH, USA	43.7253°	–72.2644°	This study
B. (*B.*) *liederi*	NY7	Lake Ontario, NY, USA (type location)	43.3412°	–78.7194°	This study
B. (*B.*) *liederi*	NY8	Waneta Lake, NY, USA	42.4448°	–77.1003°	This study
B. (*B.*) *liederi*	ON3	Lake Erie at Leamington, ON, Canada	42.0261°	–82.6035°	AF482740; AF484007
B. (*B.*) *liederi*	WA1	Lake Washington, WA, USA	47.6512°	–122.287°	AF482741; AF484006
Bosmina (*Bosmina*) *longirostris*	AK2	Salmon Lake, AK, USA	64.9107°	–164.982°	This study
B. (*B.*) *longirostris*	AK3	Alder Pond, AK, USA	60.8065°	–148.939°	AF482744; AF484005
B. (*B.*) *longirostris*	DK1	Bagsværd Sø, Denmark (type location)	55.773°	12.4535°	This study
B (*B.*) *longirostris*	GER4	Großer Ploner See, Germany	54.1332°	10.3991°	AF482743; AF484003
B. (*B.*) *longirostris*	JPN10	Lake Aoki, Japan	36.6089°	137.8542°	This study
B. (*B.*) *longirostris*	JPN11	Lake Shikotsu, Japan	42.7066°	141.3001°	This study
B. (*B.*) *longirostris*	JPN2	Yomomarushi Ike Pond, Japan	36.8002°	137.017°	This study
B. (*B.*) *longirostris*	JPN3	Watauchi Ike Pond, Japan	36.6813°	137.09°	This study
B. (*B.*) *longirostris*	JPN4	Lake Yamanaka, Japan	35.4089°	138.8773°	This study
B. (*B.*) *longirostris*	JPN5	Ichiyanagi Numa Pond, Japan	40.9075°	141.3696°	This study
B. (*B.*) *longirostris*	JPN6	Lake Otori-Ike, Japan	38.3651°	139.829°	This study
B. (*B.*) *longirostris*	JPN7	Sainokami Ike Pond, Japan	34.4231°	136.603°	This study
B. (*B.*) *longirostris*	JPN8	Onuma Pond in Onuma Quasi-National Park, Japan	42.0123°	140.7155°	This study
B. (*B.*) *longirostris*	JPN9	Lake Ashi, Japan	35.2367°	138.9952°	This study
B. (*B.*) *longirostris*	NY9	Retaining pond, East Amherst, NY, USA	43.0277°	–78.7109°	AF484004
B. (*B.*) *longirostris*	RUS4	Glubokoe Lake, Russia	55.7527°	36.5085°	This study
Bosmina (*Lunobosmina*) oriens	CT4	Hell Hollow Pond, CT, USA	41.6373°	–71.87°	This study
B. (*Lu.*) *oriens*	MA7	Great Pond, MA, USA	42.0216°	–70.0865°	This study
B. (*Lu.*) *oriens*	MA8	Fresh Pond, Massachusetts, USA	41.67718°	–70.14877°	AF482746; AF484018
B. (*Lu.*) *oriens*	MA9	Blackwater Pond, Cape Cod, MA, USA	42.06676°	–70.19444°	AF482747; AF484016
B. (*Lu.*) *oriens*	RI1	Bowdish Reservoir, RI, USA (type location)	41.92357°	–71.77349°	AF484017; AF482748

Table 1. *Continued*

Species names	Abbreviations	Geographic name	Latitude	Longitude	Genbank accession number
Nearctic *Bosmina* (*Eubosmina*) cf. *longispina*	AK4	Unnamed pond #19 on Teller highway, AK, USA	65.0032°	–166.165°	AY264737; AY264768
Nearctic *B.* cf. *longispina*	AK5	Jerome Lake, AK, USA	60.546°	–149.576°	AY264740
Nearctic *B.* cf. *longispina*	AK6	Unnamed pond #7 on Taylor highway, AK, USA	65.2327°	–164.825°	AY264731
Nearctic *B.* cf. *longispina*	AK7	Unnamed pond #9 on Taylor highway, AK, USA	65.1742°	–164.821°	AY264732
Nearctic *B.* cf. *longispina*	AK8	Summit Lake, AK, USA	60.6319°	–149.508°	AY264742; AY264766
Nearctic *B.* cf. *longispina*	AK9	Mirror Lake, AK, USA	61.4271°	–149.415°	AY264736; AY264767
Nearctic *B.* cf. *longispina*	AK10	Unnamed pond #4–8, Nome, AK, USA	64.5588°	–165.472°	AF482755; AF484014
Nearctic *B.* cf. *longispina*	NH4	Sunapee Lake, NH, USA	43.387°	–72.0573°	This study
Nearctic *B.* cf. *longispina*	BC1	Crowman Lake, BC, Canada	50.2042°	–126.445°	AY264735
Nearctic *B.* cf. *longispina*	ME6	Green Lake, ME, USA	44.6706°	–68.5509°	AY264745
Nearctic *B.* cf. *longispina*	ME7	Philips Lake, ME, USA	44.698°	–68.6017°	AY264746
Nearctic *B.* cf. *longispina*	NWFLD1	Unnamed Pond near Cornerbrook, NF, Canada	unknown	unknown	AY264744; AY264770
Nearctic *B.* cf. *longispina*	NWT1	Unnamed lake near Paulatuk, NT, Canada	unknown	unknown	This study
Nearctic *B.* cf. *longispina*	NWT2	Unnamed lake near Franklin Bay, NT, Canada	unknown	unknown	AF482752
Nearctic *B.* cf. *longispina*	ON4	Mijinemungshing Lake, ON, Canada	47.6994°	–84.7293°	AY264751; AY264771
Nearctic *B.* cf. *longispina*	ON5	Sherborne Lake, ON, Canada	45.1901°	–78.7836°	AY264750; AY264765
Nearctic *B.* cf. *longispina*	YT1	Fox Lake, YT, Canada	61.1788°	–135.396°	AY264739; AY264769
***Bosmina* (*Eubosmina*) *tanakai* sp. nov.**	JPN15	Ichiyanagi Numa Pond, Japan (2)	40.9075°	141.3696°	This study
B.* (*E.*) *tanakai sp. nov.	JPN16	Lake Touro, Japan (4)	43.1537°	144.5080°	This study
B.* (*E.*) *tanakai sp. nov.	JPN14	Lake Akan, Japan (3)	43.4345°	144.0939°	This study
B.* (*E.*) *tanakai sp. nov.	JPN13	Lake Kussharo, Japan (2)	43.5603°	144.3387°	This study
B.* (*E.*) *tanakai sp. nov.	JPN12	Konuma Pond in Onuma Quasi-National Park, Japan (3)	41.9889°	140.6645°	This study
Bosmina (*Liederobosmina*) *tubicen*	ON6	Ril Lake, ON, Canada	45.1697°	–79.0321°	AF482751; AF484020

Existing sequences are from Taylor *et al.* (2002) and Haney & Taylor (2003).
Sequences from this study have the following Genbank Accession numbers: EU650685–EU650779.

1.5 mM $MgCl_2$ buffer, 10 μM primers, 10 mM deoxyribonucleotide triphosphates (dNTPs), and 1 U of Taq polymerase. The PCR conditions followed those of Taylor *et al.* (2002). Primers used to amplify and sequence both strands of a fragment of the 16S gene were: 16Sar (5′-CGCCTGTTTATCAAAAACATC-3′) and 16Sbr (5′-CCGGTCTGAACTCAGATCACGT-3′). The fragment of the mitochondrial large ribosomal subunit sequenced corresponds to positions 12 658–13 132 in the *Daphnia pulex* complete mitochondrial genome (Crease, 1999). Four primers were used to amplify and sequence both strands of the nuclear internal transcribed spacers (ITS), 5.8S, and D1 28S rDNA regions: 18SD, 28SD2R, 5.8SF, and 5.8SR (Taylor *et al.*, 2002). Both strands were sequenced using the ABI PRISM BigDye Terminator Cycle Sequencing Ready Reaction Kit.

Electrophoregrams were examined using Sequencher v4.5 (Gene Codes Corporation, Ann Arbor, MI, USA), and consensus sequences were assembled. Consensus sequences were aligned using MAFFT v6 (Katoh *et al.*, 2005) with a Q-INS-i strategy. GBLOCKS (Castresana, 2000) was used with the 'gaps allowed' parameter to cull unreliable sites from the alignment. Sequences were deposited in Genbank under accession numbers EU650685–EU650779. MODELTEST v3.06 (Posada & Crandall, 1998) was used to estimate the best-fitting model of nucleotide substitution for each gene region using the Akaike Information Criterion (AIC). Maximum-likelihood (ML) trees were estimated by PHYML (Guindon & Gascuel, 2003), and neighbour-joining (NJ) trees were estimated with an ML distance in PAUP 4.0 (Swofford, 2000). Nonparametric bootstrapping (1000 iterations for NJ and 100 iterations for ML) was carried out in PAUP and PHYML. Trees were visualized with Dendroscope (Huson *et al.*, 2007) and were further annotated in Keynote.

ABBREVIATIONS FOR COLLECTIONS

AAK, personal collection of A. A. Kotov, Moscow, Russia; CMN, Canadian Museum of Nature, Ottawa, Canada; DGF, collection of D. G. Frey, Support Center of the Smithsonian Institution Museum of Natural History in Suitland, MD, USA; NCMT, National Museum of Nature and Science, Tokyo, Japan; NMK, personal collection of Dr N. M. Korovchinsky, now kept at Zoological Museum of Moscow State University (MGU); NNS, personal collection of Prof. N. N. Smirnov, now kept at MGU, but not officially deposited to it; SAM, South Australian Museum, Adelaide, Australia.

ABBREVIATIONS FOR MORPHOLOGICAL STRUCTURES

aes, aesthetascs of antenna I; aml, additional male seta on antenna I; anm, anal margin of postabdomen; ass, antennular sensory seta; ave, anteroventral angle of head; css, coxal sensory setae; dbs, distal anterior seta on basal segment of antenna II; dhp, posterior dorsal head pore; dip, distal pecten of denticles on postabdominal claw; dmg, distalmost group of denticles on postabdomen; ejh, ejector hooks of limb I; fhp, frontal head pore; gnp, gonopore; idl, inner distal lobe of limb I; lhp, lateral head pore; mhp, median head pore; muc, mucro; ocd, ocular dome; odl, outer distal lobe of limb I (probably exopod); pcl, postabdominal claw; pcp, pre-claw pecten on postabdomen; poc, postaesthetasc portion of antenna I; pop, postanal portion of postabdomen; pos, postabdominal setae; prc, pre-aesthetasc portion of antenna I; prm, preanal margin of postabdomen; pvm, posterior valve margin; sav, setae at anteroventral valve margin; sdl, subdistal lobe of limb I; skz, seta kurzi; vmp, ventral margin of postabdomen.

RESULTS

SUBGENUS *BOSMINA* (*BOSMINA*) BAIRD, 1845

Eunica Koch, 1841: 23 (preoccupied name, Huebner, 1819; Lepidoptera).
Bosmina Baird, 1845: 149; Baird, 1846: 412.
Bosmina (*Bosmina*) in Lieder, 1957 (manuscript); Lieder, 1962: 317; Lieder, 1983b: 123, 126; De Melo & Hebert, 1994: 1818; Taylor *et al.*, 2002: 1494.
Bosmina (*Sinobosmina*) in De Melo & Hebert, 1994: 1820.
Garbinia Grochowski, 1910: 343.

Type species: Monoculus cornutus Jurine, 1820. When Baird (1845) established the genus *Bosmina*, it was monotypical, containing only a single species *Bosmina cornuta* (Jurine, 1820). At the same time, the author listed '*Lynceus longirostris* ? Muller' as a possible synonym of *B. cornuta*. Now, *B. cornuta* is regarded as a junior synonym of *B. longirostris*.

Subgenus diagnosis based on male characters: Distal portion of postabdomen as a tube, not inflated, preanal margin more or less depressed, with relatively long, fine setules. Gonopore opens distally. Postabdominal claw with a sharp terminal spinule. Basal pecten of denticles shifted from postabdominal claw to body of postabdomen, distal pecten consisting of short, robust denticles. Antenna I with relatively thin pre-aesthetasc portion. Copulatory hook on limb I strongly narrowing distally. On subdistal lobe of limb I, all setae located closely. Seta 2 on limb-I corm, not very short.

Comment: Numerous species, forms, and varieties of *B*. cf. *longirostris* described from Europe (see Lieder, 1996: 33–34), and from some other areas, were established on characters, such as the curvature of the female antennule, that are subject to significant intra- and interpopulation variability. In some German lakes the morphs coexist, and show overlapping but significant morphological differentiation (Kappes & Sinsch, 2002a, b). These have been regarded as separate species (*B. cornuta* and *Bosmina pellucida* Stingelin, 1895) by Kappes & Sinsch (2002a, b, 2005), but it is unknown if these morphs represent spatial polymorphisms, simple morphological polymorphisms, or cryptic invasive species. We lacked genetic evidence for more than one species of *B*. cf. *longirostris* in Europe – further studies are needed to assess the species diversity of European *longirostris*-like morphotypes.

At the same time, several other species from the subgenus *B*. (*Bosmina*) have been discovered in North America (De Melo & Hebert, 1994) and Asia (Kořínek, Saha & Bhattacharya, 1999), although they were initially incorrectly placed in the subgenus *Sinobosmina*. Recent molecular data (Taylor *et al.*, 2002) and the present analysis on males confirmed the position of *B. liederi* and *B. freyi* in the subgenus *Bosmina s.s.* Moreover, our morphological analysis (see cladogram) indicates that *Bosmina tripurae* Kořínek, Saha & Bhattacharya, 1999 is also a member of *Bosmina s.s.* Previous authors (Lieder, 1983b; De Melo & Hebert, 1994; Kořínek *et al.*, 1999) assigned species to the subgenus *Sinobosmina* when the lateral head pore was located near the edge of the head shield. But, the extreme lateral position of the head pore is a peculiarity of *B. longirostris* only, and *B. tripurae* has a pore located at a small distance from the edge of the head shield, as in the *Sinobosmina*. Combined genetic and morphological analyses of more *Sinobosmina* and Palearctic *Bosmina* specimens are necessary to further test the reliability of the lhp position for separating *Sinobosmina* and *Bosmina*.

Unfortunately, we have no males of *B. freyi*. In addition, there are some other undescribed species in North America (Little *et al.*, 1997; Kim *et al.*, 2006). So, our investigation is only a first step in the revision of the subgenus in North America.

Bosmina (Bosmina) longirostris (O. F. Müller, 1776), *Figures 1–4*

Lynceus longirostris O. F. Müller, 1776: 199; O. F. Müller, 1785: 76–77; pl. 10, figs 7, 8.
Bosmina longirostris (O. F. Müller) in Baird 1850: 105–106; P. E. Müller, 1867: 146; pl. 3, figs 8, 9; Lilljeborg, 1901: 225–236; pl. 30, figs 13–16; pl. 31, figs 1–18; pl. 32, figs 1–3; Keilhack, 1908: 444–445; figs 4–7; Uéno, 1927: 285–287; pl. 26, fig. 15a–f; Burckhardt, 1941: 130–141; figs 6, 7, 10, 11, 17, 25, 26, 28; Šrámek-Hušek, Strašcraba & Brtek, 1962: 277–280; fig. 101; Margaritora, 1983: 32–34; fig. 18A–G; Margaritora, 1985: 56–60; figs 25, 26; Sars, 1993: 79–80; pl. 61; Alonso, 1996: 248–251; figs 111–112.
Bosmina (*Bosmina*) *longirostris* (O. F. Müller) in Flössner, 1972: 214–217; figs 100, 101; Lieder, 1983b: 126; figs 1, 7a, 8a; Negrea, 1983: 219–225; figs 88–90.
Bosmina longirostris-curvirostris Fischer in Keilhack, 1909: 52; figs 127, 128.
Garbinia adriani Grochowski, 1910: 343, text – figs a–b.
?*Bosmina pellucida* Stingelin, 1895: 229, figs 22, 23.
Not *Bosmina* (*Bosmina*) *longirostris* in Chiang Sieh-chin & Du Nan-shan, 1979: fig. 110C; De Melo & Hebert, 1994: 1818–1819; fig. 10.

Material (males): Belgium. Duck pond near Ghent University, collected on 21 October 1997 by K. Van Damme and 5 November 1997 by A. A. Kotov, AAK 2002-177.

Germany. Globsow See, Berlin, collected on 27 October 1998 by M. Abashanin, AAK 2004–027.

Norway. A bog lake near Oslo, collected on 7 September 1990 by N. N. Smirnov, AAK 2004–028.

Russia (European). Lake Glubokoe, Ruza District, Moscow Area, collected on 1 December 1996 by A. A. Kotov, AAK 2004–043; Sterlazhij Pond, Zvenigorod District, Moscow Area, collected on 10 October 1999 by A. A. Kotov, AAK 2004–008; Istra Water Reservoir, Moscow Area, collected on 30 June 1980 by N. N. Smirnov, AAK 2004–025. A pond near main office of the Teberda Nature Reserve, Karachayevo-Cherkess Autonomous Republic, collected on 1 July 1980 by V. Spiridonov, AAK 2004–022.

Iraq. Zafaraniya, collected on 28 January 1974 by N. N. Smirnov, AAK 2004–034.

Diagnosis of adult male (Figs 1, 2, 3A–D): Body elongated, humped, head elevated above dorsum of valve, dorsum posteriorly almost straight, posterior margin of valves (pvm) short, almost straight. Head large, anteroventral angle (ave) well-defined, but not projected as a rostral wrinkle; distalmost extremity of head slightly projected as an ocular dome (ocd). Frontal head pore (fhp) somewhat dorsally to base of antenna I, lateral head pore (lhp) immediately near, somewhat inflated lateral edge of head shield (as in female), median head pore (mhp) somewhat posterior to ocular dome. Mucro (muc) relatively long, with ventral incisions; seta kurzi (skz) long, a series on long setae (sav) at anteroventral portion of valve. Postabdomen elongated, its ventral margin (functionally oriented towards the top of the animal because abdomen strongly bent!) straight (vmp), preanal margin (prm) deeply depressed, distalmost portion of preanal margin projected distally, with numerous series of relatively long, fine, setules; anal margin (anm) straight, located in a depression. Postanal

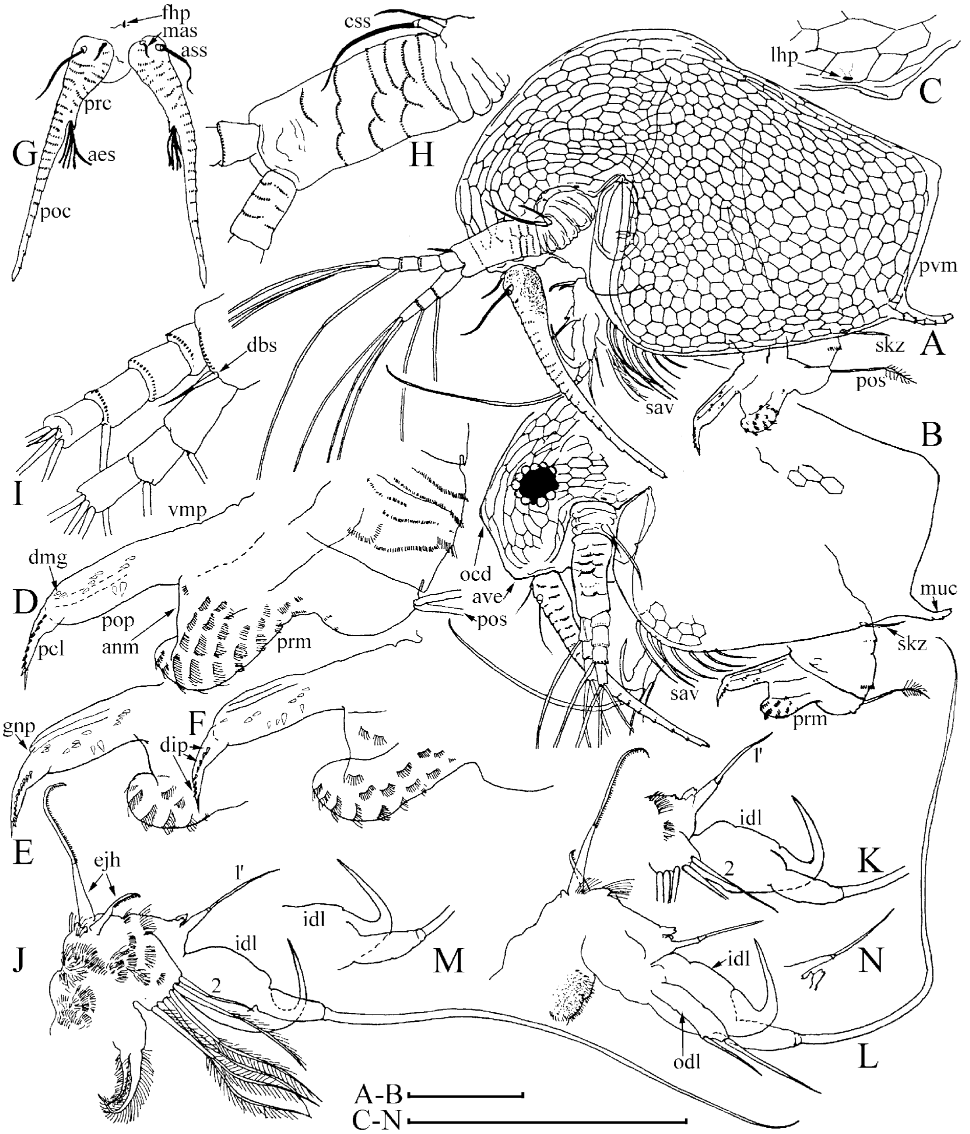

Figure 1. *Bosmina* (*Bosmina*) *longirostris*: adult male from a duck pond near Ghent University, Belgium. A, B, general view; C, lateral head pore; E, F, postandomen; G, antennae I, anterior view; H, antenna II, posterior view; I, distal portion of antenna II, anterior view; J, limb I, inner view; K–M, distal portion of limb I; N, subdistal lobe. See text for a list of morphological abbreviations. Scale bars: 100 μm.

portion of postabdomen (pop) as long tube, blunt distally, supplied with groups of distinct denticles. Dorsalmost group (dmg) of few denticles apparently a remainder of proximal pecten of postabdomen in female (but, perhaps there are other denticles that are also homologous with this pecten). A solitary gonopore (gnp) opens distally. Postabdominal claw (pcl) shortened (as compared with female), but relatively slender for the subgenus, bent in middle, with pointed tip supplied with a distal spinule, distal pecten (dip) as a series of relatively robust denticles. Postabdominal setae (pos) shorter than preanal margin of postabdomen. Antenna I jointed with head, slightly S-shaped and regularly arched in anterior view, its base thick, pre-aesthetasc portion (prc) regularly narrowing distally, postaesthetasc (poc) portion thin, almost straight. Antennular sensory seta (ass) very long, located at a short distance from basal end of antenna I; male seta short (aml), located on a small pedestal near its base; nine aesthetascs (aes), slender, subequal in size. Anterior and lateral surface of antenna I with transverse series of small denticles. Antenna II as in female, but with two sensory setae on coxal part (css) (in contrast to female with a single

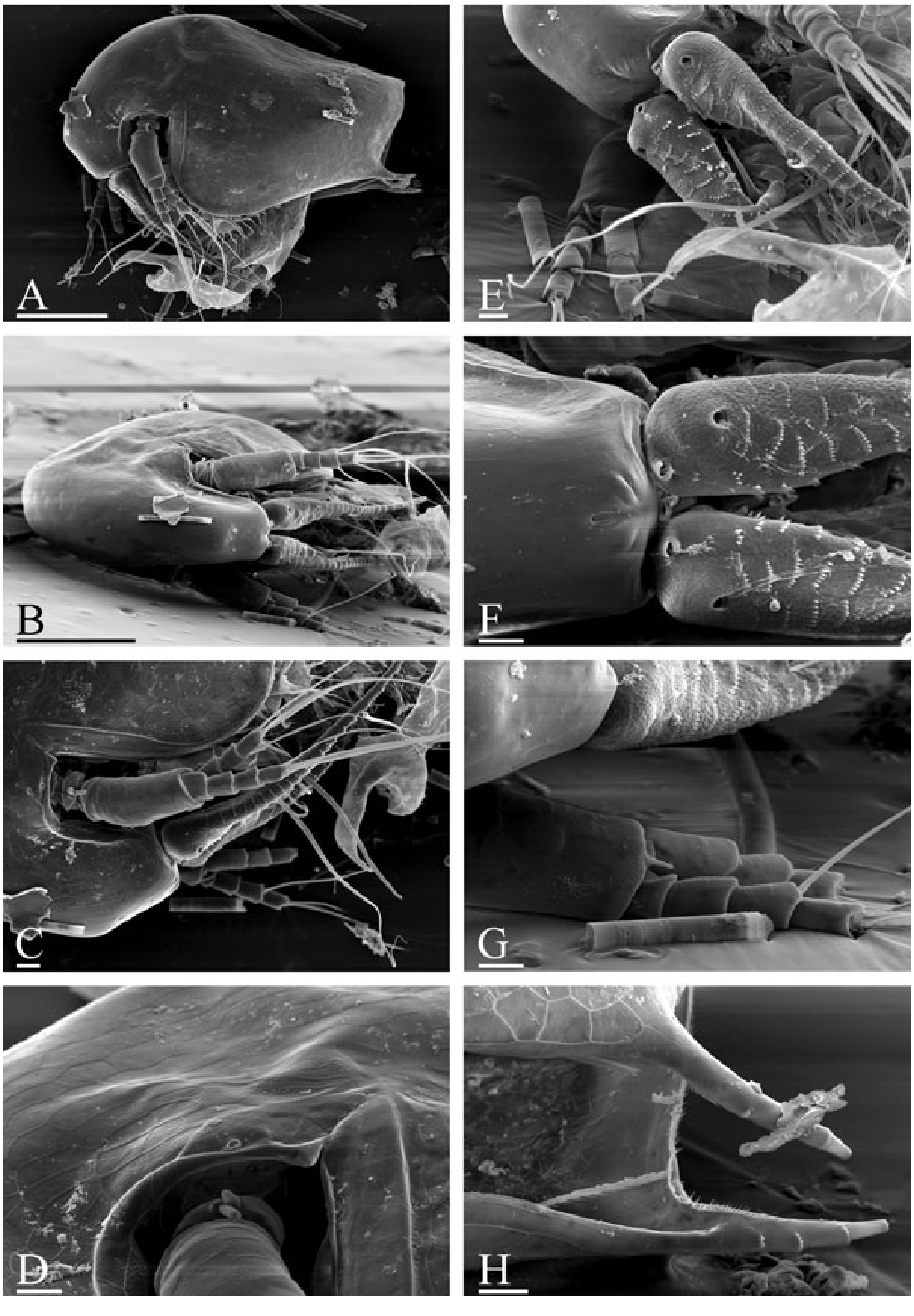

Figure 2. *Bosmina* (*Bosmina*) *longirostris*: adult male from a duck pond near Ghent University, Belgium. A, lateral view; B, anterior view; C, head; D, lateral head pore; E, F, rostrum; G, antenna II; H, mucro. Scale bars: 100 µm for (A, B); 10 µm for (C–H).

seta), and one of them very long, reaching, or projecting behind, the middle of the basal segment. Distal anterior seta (dbs) of middle size (approximately as long as basal segment of three-segmented branch), located on anterior surface of distal segment, near distal end of distal segment. Limb I with additional groups of setules on posterior (i.e. inner) surface. Outer distal lobe (odl) as an elongated lobe with two setae of different size. Inner distal lobe (idl) strongly inflated, sometimes with a slight, smooth projection on basal portion, its distal portion bottle-shaped, terminating as a long, naked seta. Copulatory hook

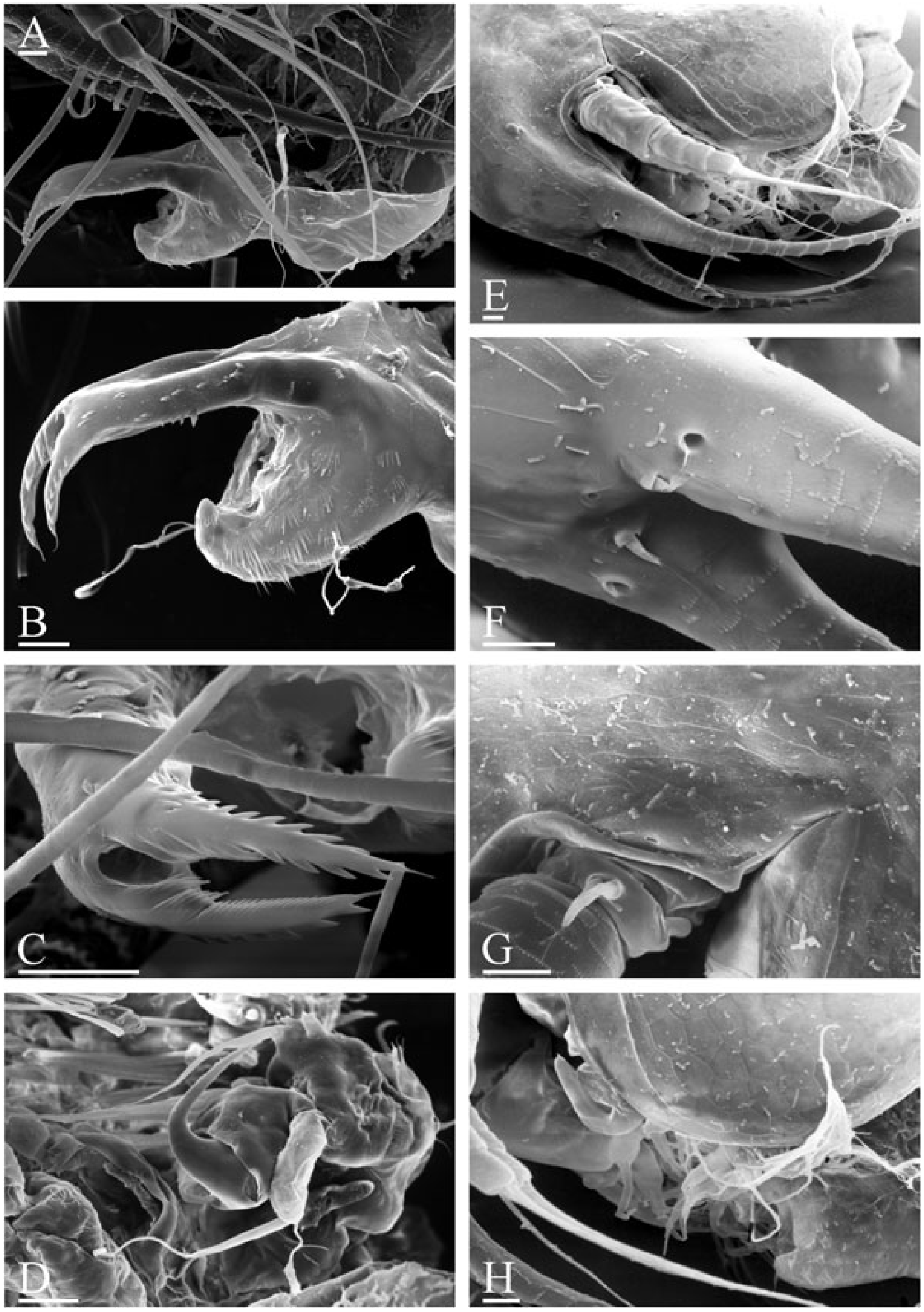

Figure 3. *Bosmina* (*Bosmina*) *longirostris*: adult male from a duck pond near Ghent University, Belgium (A–D), and juvenile male II from Lake Glubokoe, Moscow Area, Russia (E–H). A, B, postabdomen; C, tip of postabdomen in distal view; D, distal portion of limb I; E, F, rostrum; G, lateral head pore and coxal portion of antenna II; H, postabdomen and copulatory hook on limb I. Scale bar: 10 μm.

relatively small, not recurved to a parallel position with the idl, regularly tapering distally, tip of hook as a sharp spine, without setules. Subdistal lobe (sdl) slightly projected, with a single long, bisegmented seta (1′) and two closely located rudimentary setae. Seta 2 relatively long for genus, about half the length of more basal seta. Ejector hooks (ejh) of greatly different size.

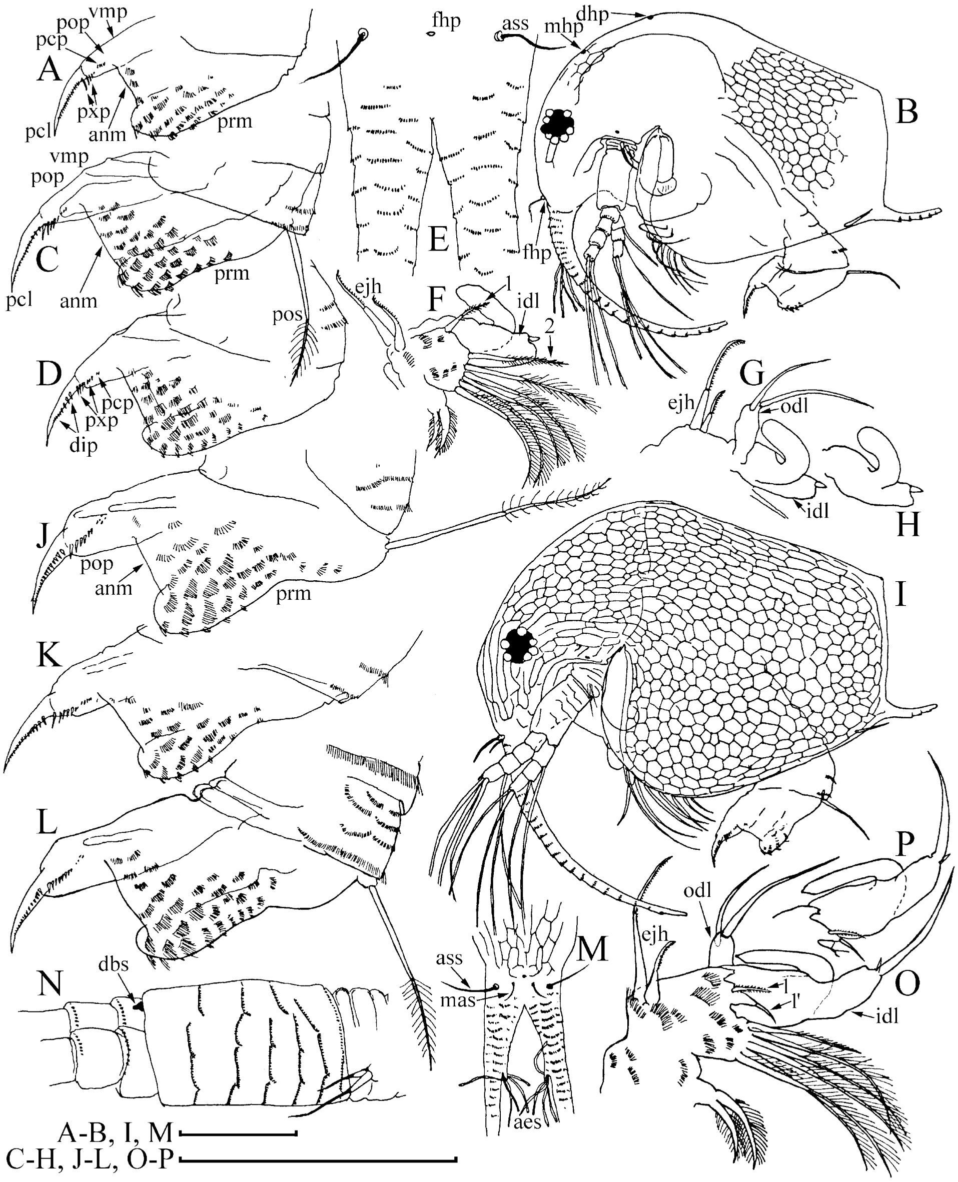

Figure 4. *Bosmina* (*Bosmina*) *longirostris*: from a duck pond near Ghent University, Belgium. A, postabdomen of juvenile female; B, juvenile male I, lateral view; C, D, postabdomen of juvenile male I; E, rostrum and antennae I of juvenile male I; F, limb I of juvenile male I, inner view; G, H, distal portion of limb I of juvenile male I; I, juvenile male II, lateral view; J–L, postabdomen of juvenile male II; M, rostrum and antennae I of juvenile male II; N, antenna II of juvenile male II; O, limb I of juvenile male II, inner view; P, distal portion of juvenile male II. See text for a list of morphological abbreviations. Scale bars: 100 µm.

Postembryonic development: Newborn males (and females) of *Bosmina* and other Anomopoda moult soon after (from several seconds to minutes) release from the brood pouch, and the first juvenile instar begins (Kotov, 1996, 1997a; Kotov & Boikova, 2001).

Juvenile male I (Fig. 4B–H) has a body shape similar to the juvenile female I. Posterior dorsal head pore (dhp) present only in females and males of instar I, fully disappearing in instar II. Postabdomen relatively similar to that in female (Fig. 4A), but with preanal margin slightly depressed, ventral margin somewhat inflated, and paired rudimentary gonoduct visible through cuticle, although gonopore absent. Postabdominal claw as in female, with distal, proximal (pxp) and pre-claw (pcp) pectens on female type. Antennae I fused with rostrum, only a pair of sensory setae (which apparently are parts of antennae I) on 'rostrum', frontal head pore at level of these setae.

Antenna II with two short sensory setae on coxal portion (in contrast to female with one seta), whereas a rudiment of distal anterior seta on basal segment absent. Limb I with odl of female type, idl (greatly reduced and lacking setae in female) small, subquadrangular, with a rudimentary seta, copulatory hook short and thick, subdistal lobe not projected, with a single seta 1 (as in female).

Juvenile male II (Figs 3E–H, 4I–P) has a body shape that is also similar to the juvenile female II, posterior dorsal head pore absent. Postabdomen with concave preanal margin and thick, tube-shaped postanal portion, and rudimentary gonoduct reaching half the length of postanal portion, although gonopore absent. Postabdominal claw shorter than in female II, distal pecten consists of denticles increasing in thickness proximally, proximal pecten shifted from claw lateral surface to postanal portion of postabdomen, consisting of numerous spinules, pre-claw pecten greatly reduced. Antennae I fused with rostrum, which is supplied with a pair of antennular sensory setae and a pair of male setae, somewhat dorsally to first pair, frontal head pore on middle line, dorsal to level of male setae. Antenna II with two sensory setae of unequal size on coxal portion, with a rudimentary distal anterior seta present. Limb I with odl of female type, idl large (but smaller than in adult), elongated, with a seta approximately as long as idl, and another rudimentary seta, copulatory hook longer, but thick, with triangular tip; subdistal lobe projected, with seta 1, and two other setae. Most probably, seta 1 is greatly reduced in size in adult males, whereas only seta 1′ is well developed.

As with chydorids, bosminids have two juvenile instars in male development. This instar number is fixed (apparently unaffected by food or other conditions). The transition to the adult (third) instar is usually accompanied by the greatest ontological changes in morphology. Just after this ecdysis, antenna I develops a joint separating it from the head, and all additional setae and hairs strongly increase in size (Lilljeborg, 1901; Kotov, 1996). It is likely that the adult males lack a moult beyond instar III.

Comments: Males of *B. longirostris* have been described several times previously (Sars, 1993; Alonso, 1996), but the postembryonic development remains unknown. Lilljeborg's (1901) schematic illustrations of the male II habitus were not detailed enough to discuss the development of the male characters.

Uéno (1927) found a morphologically typical *B. longirostris* in Japan. But Tanaka (2000) described an adult male of '*B. longirostris*' from Japan with a strange, extremely short and blunt postabdominal claw, and an exceptionally long copulatory hook on limb I. Populations from Japan must be re-examined; they may belong to another species (there is also a chance of introduction from North America, where the subgenus is more diverse). Chiang Sieh-chin & Du Nan-shan (1979) illustrated the male of *B. fatalis* or *B. tripurae* under the name '*B. longirostris*'.

De Melo & Hebert (1994) reported females of '*B. longirostris*' with very fine and long setules on the base of the postabdominal claw from Hume Lake (California, USA). This determination seems to be dubious: perhaps this population belongs to a species that differs from *B. longirostris* sp. str. Indeed, our sampling from this location revealed specimens that group in the *B. freyi* clade. However, we have not compared the setules of specimens from the two sampling dates, and it is possible that we have sampled something different from the '*B. longirostris*' described by De Melo & Hebert (1994).

Bosmina (Bosmina) liederi De Melo & Hebert, 1994, *Figure 5*

Bosmina (*Sinobosmina*) *liederi* De Melo & Hebert, 1994: 1823; fig. 13A–C.

Material: Artificially obtained males from the addition of MF in laboratory culture, initially from Bass Lake, CA, USA, AAK 2004-092.

Differences from B. (B.) longirostris: Body less humped, posterior margin of valve high. Denticles in all series on postanal portion of postabdomen: minute. Postabdominal claw thick, with relatively blunt tip [supplied with a distal spinule, as in *B.* (*B.*) *longirostris*]. Antenna I characteristically S-shaped in anterior view. Antenna II with short sensory setae on coxal portion, and a short distal anterior seta (not reaching distal end of the first endopod segment, or distal end of the second exopod segment).

Comments: Unfortunately, only a single population of *B.* (*B.*) *liederi*, well-differentiated from *B.* (*B.*) *longirostris* genetically, and with artificially induced males, was studied. Although Kim *et al.* (2006) found that artificial induction leads to the appearance of morphologicaly normal, instead of monstrous, males, our list of differences between species must be checked by examination of several other populations of *B.* (*B.*) *liederi*.

De Melo & Hebert (1994) erroneously placed this species in the subgenus *Sinobosmina*, based on information on the mobility of the allozyme products of a few alleles in North American species from different subgenera. Subsequently, Taylor *et al.* (2002) proposed that *B. liederi* is a member of the subgenus *Bosmina* s. str., and the sister species to *B.* (*B.*)

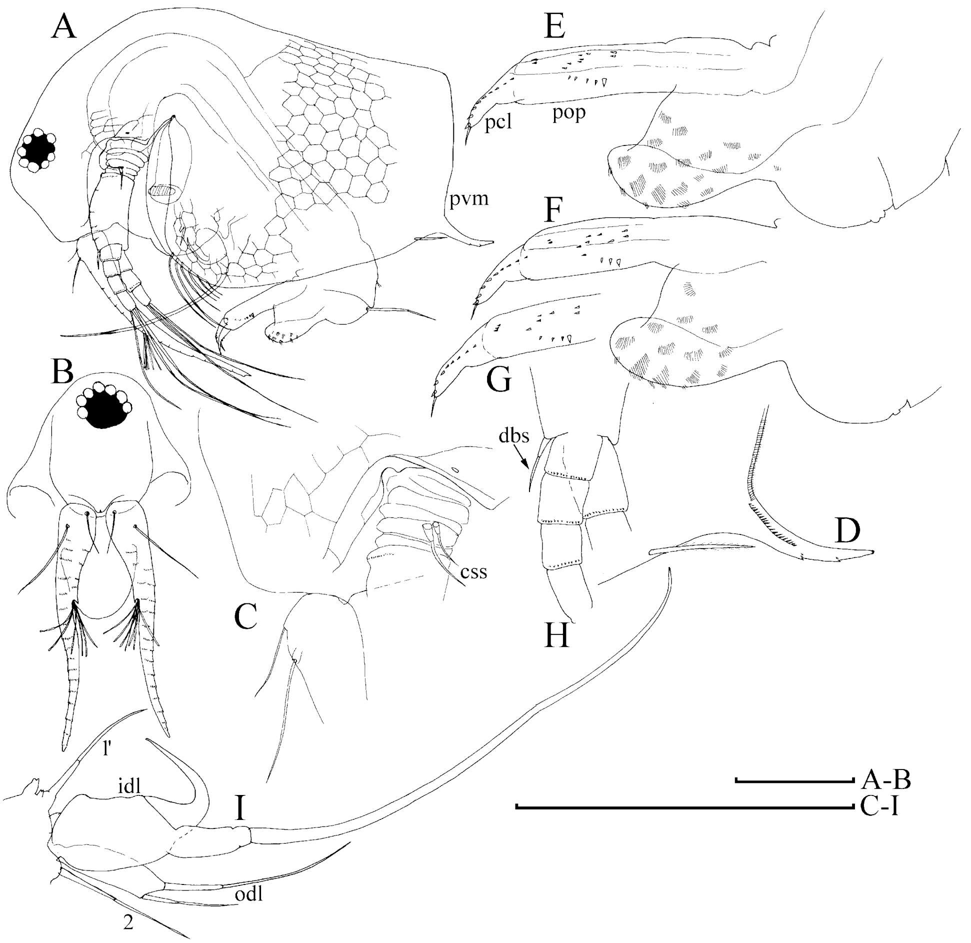

Figure 5. *Bosmina* (*Bosmina*) *liederi*: artificially induced adult male, cultured initially from Bass Lake near Lake Erie, Ontario, Canada. A, B, lateral and anterior view; C, head, lateral view; D, mucro, inner view; E–G, postabdomen; H, antenna II, external view; I, distal portion of limb I. See text for a list of morphological abbreviations. Scale bars: 100 µm.

longirostris. Our expanded sampling of this clade (using specimens from the type region and from Asia) and detailed morphological analyses support the sister-species relationship of *B.* (*B.*) *liederi* and *B.* (*B.*) *longirostris*.

Bosmina (Bosmina) tripurae Kořínek, Saha & Bhattacharya, 1999
Bosmina cf. *japonica* Poppe & Richard, 1890 in Kořínek, 1971: 292–294; figs 10F–H, 11A–D.
Bosmina tripurae Kořínek *et al.*, 1999: 241–247; figs 1A–D, 2A–F, 3A–G, 4A–D.
Not *Bosmina japonica* Poppe & Richard, 1890: 76–77.

Source of information: The description of Kořínek *et al.* (1999). Some important details (i.e. gonopore position and pattern of denticles on postanal portion of postabdomen) are not described or illustrated.

Diagnosis of adult male: Body relatively high, not humped, dorsum in posterior half slightly convex, posterior margin especially high. Head large, anteroventral angle well defined, but not projected; distalmost extremity of head slightly projected as an ocular dome. Frontal head pore somewhat dorsal to base of antenna I, lateral head pore at a small distance from lateral edge of head shield (as in female). Mucro relatively long, seta kurzi long, a series of long setae at the anteroventral portion of valve. Postabdomen elongated, its ventral margin slightly convex, preanal margin moderately depressed, distalmost portion of preanal margin (dorsodistal angle) not projected distally, with numerous series of relatively long, fine, setules; anal margin straight, not within a depression. Postanal portion massive, blunt distally, supplied with groups of denticles of pattern unclear from the author's illustrations. Dorsalmost group of about seven or eight denticles, a remainder of a proximal pecten of the postabdominal claw, apparently continues as a distal pecten on postabdominal claw. Gonopore not illustrated. Postabdominal claw relatively thin, slender, regularly curved, with distal spinule, and with distal pecten as a series of robust denticles. Antenna I articulated at the attachment site to the head, probably straight in anterior view, its pre-aesthetasc portion regularly narrowing distally, post-aesthetasc portion thin, almost straight. Antennular sensory seta short, located at a distance from base; male seta short, located on a minute pedestal. Antenna II with two sensory setae on coxal part, which are shorter than sensory setae of *B.* (*B.*) *longirostris*. Distal anterior seta short, as long as basal segment of four-segmented branch. Limb I with additional groups of setules on inner surface. Strongly inflated idl, with a slight projection on basal portion, its distal portion bottle-shaped, terminating as a long, naked seta. Copulatory hook relatively small, recurved to a parallel position with the idl, regularly tapering distally, tip of hook blunt, with a ridge. Subdistal lobe large, with single long seta and two closely located rudimentary setae. Ejector hooks different in size by 1.5 times.

Comments: The species was first described as *B.* cf. *japonica* Poppe & Richard, 1890 from India (Kořínek, 1971), but Kořínek stated that the male of this animal is markedly different from males of *B.* (*B.*) *longirostris* and *B.* (*S.*) *fatalis*. Kořínek *et al.* (1999) described the adult male of this species, and placed it in the subgenus *Sinobosmina*, based on the position of the lateral head pore, structure of male postabdomen, and copulatory hook. But, according to our re-evaluation of the genus system, we reveal that this species is a primitive member of the subgenus *Bosmina* sp. str., instead of *Sinobosmina*. Most of the differentiation of *B.* (*B.*) *tripurae* from *B.* (*B.*) *longirostris*, i.e. unhumped body, high posterior margin, massive postanal portion of postabdomen, absence of an anal depression, proximal pecten apparently continues as distal pecten on postabdominal claw, short sensory setae on coxal part, and short distal sensory seta on basal segment of antenna II, and smaller difference in size of ejector hooks, are apparent plesiomorphies of *B.* (*B.*) *tripurae*.

SUBGENUS *BOSMINA* (*SINOBOSMINA*) LIEDER, 1957 *SENSU* LIEDER, 1962

Bosmina Sinobosmina Lieder, 1957: manuscript name; Lieder, 1962: 317; Lieder, 1983b: 126–127; Taylor *et al.*, 2002: 1494.
Not *Bosmina* (*Sinobosmina*) in De Melo & Hebert, 1994: 1820.

Type species: Bosmina fatalis Burckhardt, 1924 (Lieder, 1962). It is necessary to say that Lieder's (1957) dissertation, which is regarded as a first description of the subgenus, is a manuscript only. So, the valid typification was only made in 1962 (Lieder, 1962: 317).

Subgenus diagnosis based on male characters: Distal portion of postabdomen as a short tube, not inflated, preanal margin slightly depressed, with relatively long, fine setules. Gonopore opens distally. Postabdominal claw relatively short and thick, without a terminal spinule. Basal pecten of denticles not shifted from postabdominal claw to body of postabdomen, distal pecten consisting of fine denticles. Antenna I with relatively thin pre-aesthetasc portion. Distinct basal projection on idl. On subdistal lobe of limb I, all setae located closely. Seta 2 on limb I not very short.

Comment: After removing *B.* (*B.*) *liederi*, *B.* (*B.*) *freyi* (Taylor *et al.*, 2002) and *B.* (*B.*) *tripurae* (see above) from *Sinobosmina*, Lieder's (1983b) proposed distribution of the subgenus *Bosmina* seems to be correct. Burckhardt (1924) described *B. fatalis* with three different variations (*megalolimnetis*, *cyanopotamia*, and *supolites*), but failed to designate the nominotypical variation. Subsequently, Brehm (1925) and Manujlova (1964) described a form from the subgenus with a very short posterior margin and antenna I pointed anteriorly, *Bosmina amemiyai* Brehm, 1925 and *Bosmina praeliaris* Manujlova, 1964.

Bosmina (Sinobosmina) fatalis Burckhardt, 1924, *Figures 6 and 7*

Bosmina fatalis Burckhardt, 1924: 235–237, 240–241; fig. 10, 1–17 (except var. *cyanopotamia*); Burckhardt, 1941: 130–141; figs 5, 19, 24, 30.
Bosmina (*Sinobosmina*) *fatalis* Burckhardt, in Kořínek, 1971: 289–292; figs 9A–F, 10A–G; Lieder, 1983b: 127; figs 2, 7b, 8b; Kotov, 1997b: 29; fig. 3; Tanaka, 2000: 118–120; figs 7–9.
?*Bosmina longirostris* (Müller) in Chiang Sieh-chin & Du Nan-shan, 1979: fig. 110C.

Material: China. Taihu Lake near Shanghai (type locality), Jiantsu Province, collected on 10 September 1993 by Guo Xiaoming, AAK 2004-032; Honqzehu Lake, Jiantsu Province, collected in September–October 1990 by Guo Xiaoming, AAK 2004-030 and AAK 2004-031.

Russia. Lake Khanka, Primorski Territory, collected on 28 September 1932 by the Amur Expedition, NNS 1997-196.

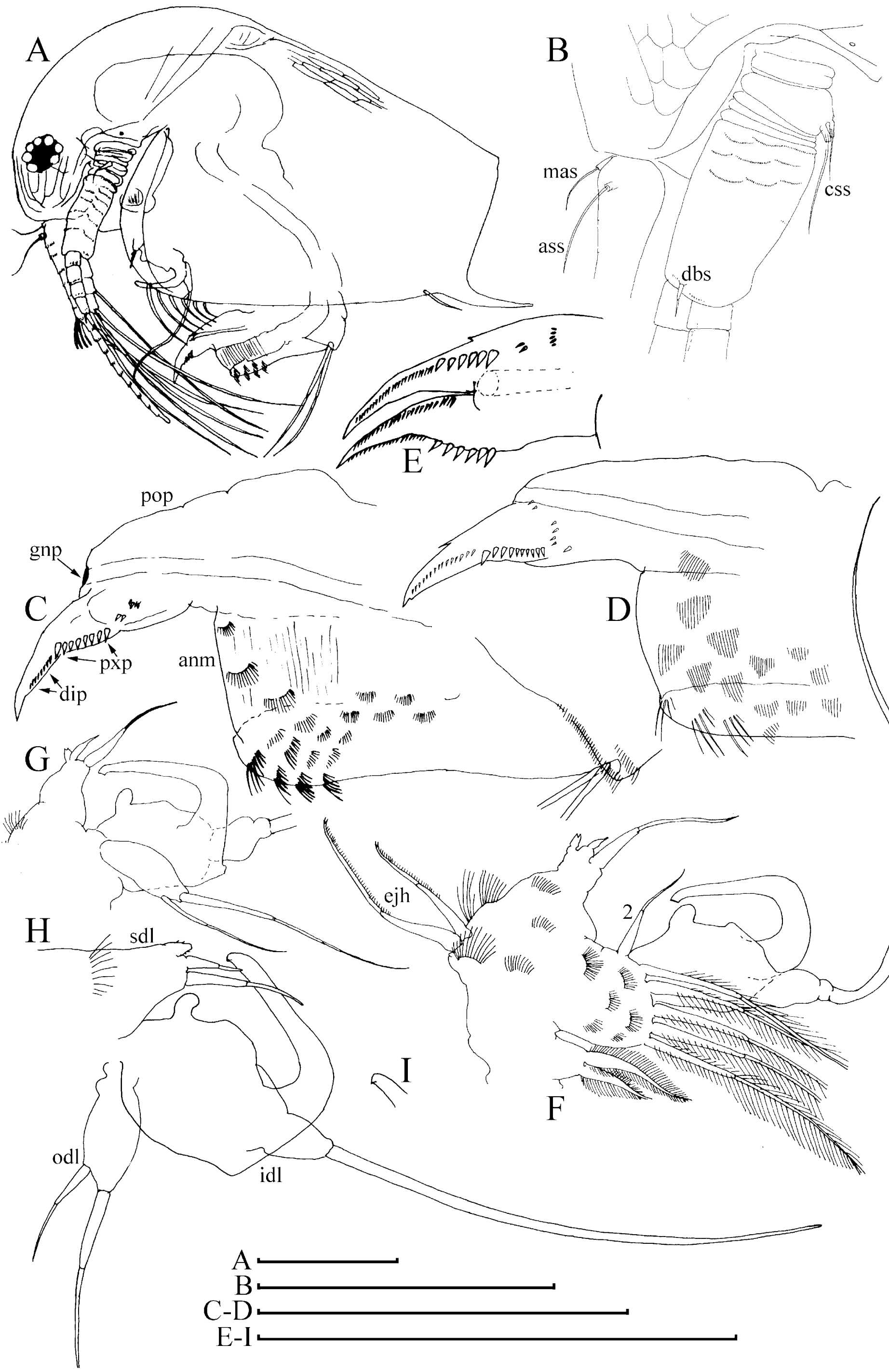

Figure 6. *Bosmina* (*Sinobosmina*) *fatalis*: adult male from Hongzehu Lake, Jiantsu Province, China. A, lateral view; B, head, lateral view; C, D, postabdomen, lateral view; E, distal portion of postabdomen, dorsal view; F, limb I, inner view; G, H, distal portion of limb I, external view; I, tip of copulatory hook on limb I. See text for a list of morphological abbreviations. Scale bars: 100 μm.

Diagnosis of adult male (Fig. 6): Body elongated, dorsum posteriorly almost straight, posterior margin of valves short. Head large, anteroventral angle rounder; distalmost extremity of head without ocular dome. Lateral head pore at a distance from lateral edge of head shield, in a bifurcation of reticulation (as in female). Mucro long, seta kurzi long, a series of long setae at anteroventral portion of valve. Postab-

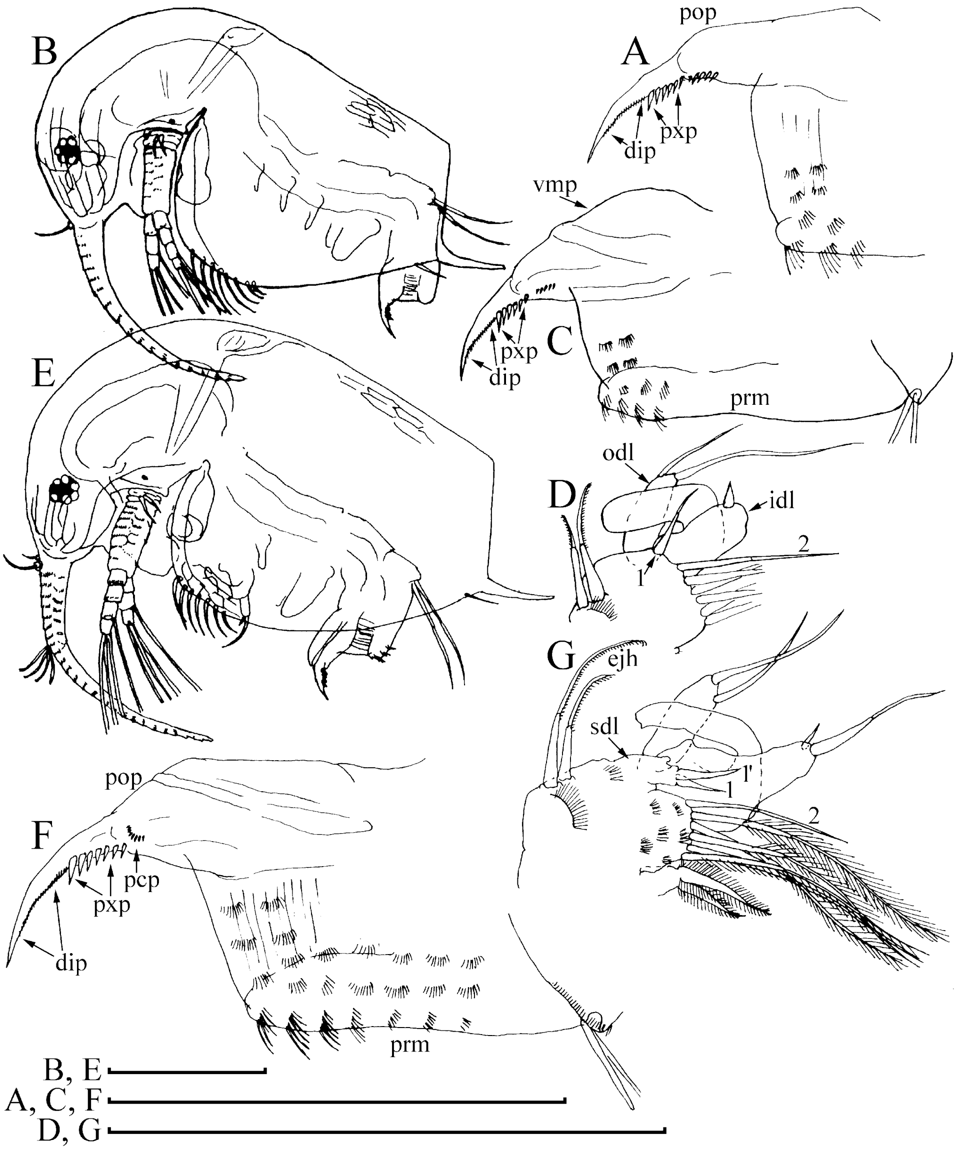

Figure 7. *Bosmina* (*Sinobosmina*) *fatalis*: from Hongzehu Lake, Jiantsu Province, China. A, postabdomen of juvenile female; B, juvenile male I, lateral view; C, postabdomen of juvenile male I; D, limb I of juvenile male I; E, juvenile male II; F, postabdomen of juvenile male II; G, limb I of juvenile male II. See text for a list of morphological abbreviations. Scale bars: 100 μm.

domen massive, ventral margin straight to slightly convex, preanal margin slightly concave, dorsodistal angle not projected, anal margin slightly convex, no anal depression. Postanal portion of postabdomen as a tube, but remarkably shorter than in *Bosmina* sp. str., blunt distally, supplied with a series of small denticles near base of claw. Singular gonopore opens distally. Postabdominal claw short, thick, without distal spinule, distal pecten as a series of small denticles, proximal pecten with more robust denticles. Antenna I articulated at the attachment site to the head, with inflated base, regularly narrowing distally, slightly bent in lateral view. Antennular sensory seta long, located relatively closely to base; male seta short, located on a small pedestal. Antenna II with two sensory setae on coxal part: one of them very long, reaching the middle of the basal segment. Distal anterior seta shorter than basal segment of three-segmented branch. Limb I with a broad idl possessing a distinct process on its basal portion. Distal portion of idl relatively short, terminating in a long, naked seta. Copulatory hook large and thick, slightly tapering, ending with a ridged tip. The hook terminates near the process on the idl, but because of the ridged tip sometimes appears to be truncated. Subdistal lobe projected, with two long setae (it is not fully clear which one is 1 or 1′) and a rudimentary seta. Seta 2 less than half of the length of the more basal seta. Ejector hooks strongly different in size.

Postembryonic development: Juvenile male I (Fig. 7B–D) body shape similar to juvenile female I. In contrast with female (Fig. 7A), postabdomen with slightly depressed preanal margin, and remarkably inflated ventral portion, a rudimentary gonoduct only reaches the level of the anus, although the gonopore is absent. Postabdominal claw as in female, with distal, proximal, and pre-claw pectens of the female type. Antenna I fused with rostrum, only a pair of sensory setae on rostrum. Antenna II with two short sensory setae of subequal size on coxal portion, no rudiment of distal anterior seta. Limb I with odl of female type, idl small, subovoid, with a rudimentary seta, copulatory hook short and thick, subdistal lobe not projected, with a single seta 1 (as in female).

Juvenile male II (Fig. 7E–G) body shape also similar to juvenile female II. Postabdomen with slightly depressed preanal margin, postanal portion short and massive, rudimentary gonoduct close to tip, as compared with male I, although gonopore absent. Postabdominal claw slightly shorter than in female II, distal pecten with fine setules, proximal pecten with denticles more robust, as compared with female II, pre-claw pecten as a transverse series of setules (in contrast with female, where it continues as the proximal pecten). Antenna I fused with rostrum; antennular sensory seta long, a short male seta somewhat dorsally to it. Antenna II with two sensory setae of different size on coxal portion, and with a rudiment of distal anterior seta present. Limb I with an odl of female type, idl large (but smaller than in the adult), conically narrowing distally, with a seta approximately as long as the idl, and with a second rudimentary seta, copulatory hook longer and thinner than in male II, with a truncated tip, subdistal lobe projected, with two setae of equal size (1 and 1′), and with a small rudimentary third seta. Seta 2 longer than half of the length of the more basal seta.

Comments: Previously, adult males were described by Burckhardt (1924, 1941).

Bosmina (Sinobosmina) cf. fatalis cyanopotamia Burckhardt, 1924,
Figure 8
Bosmina fatalis var. *cyanopotamia* Burckhardt, 1924: 241; fig. 10.
Bosmina amemiyai Brehm, 1925: 271–273, text – fig.
Bosmina praeliaris Manujlova, 1964: 286–287; fig. 157, 1–9.
Bosmina (*Sinobosmina*) *fatalis praeliaris* Manujlova in Kořínek, 1971: 292; fig. 10A–G.
Bosmina (*Sinobosmina*) *cyanopotamia* var. *praeliaris* Manujlova in Rivier, 1998: 376–380; figs 1–4.

Material: Russia. Lake Bolon, Khabarovsk Territory, Far East of Russia, collected on 12 August 1930 by the Amur Expedition, AAK 2004-029; Lake Udil, Far East of Russia, collected on 13 October 1930 by the Amur Expedition, AAK 2004-099.

Differences of adult male: It differs from *B.* (*S.*) *fatalis* in the massive anteroventral portion of head, less numerous denticles in proximal pecten on postabdominal claw, antenna I folded against the ventral margin of the body, a finer distal anterior spine on basal segment of antenna II, a shorter seta on idl (less then three lengths of the copulatory hook) and a rudimentary second seta (1 or 1′?) on subdistal lobe.

Comments: In the first description of *B. praeliaris*, Manujlova (1964) schematically illustrated an adult male of *Sinobosmina*-type. Subsequently, some authors regarded *B. praeliaris* as a junior synonym or a variation of *Bosmina cyanopotamia* Buckhardt, 1924 (Lieder, 1983b; Rivier, 1998). Kořínek (1971) said that *B.* (*S.*) *fatalis* has a subspecies *B.* (*S.*) *fatalis praeliaris*. It is demonstrated that anteriorly projected antenna I is only characteristic of summer females from *cyanopotamia*-like populations, whereas winter females have the ‘normal’ antenna of the *fatalis*-type (Lieder, 1983b; Rivier, 1998). At the same time, even these winter females have a very short preanal margin (Rivier, 1998), which can be a key character for the discrimination between two forms. We found that the male of *B. fatalis cyanopotamia* is also different from that of *B. fatalis s.s.* in a series of traits, although the consistency of these differences is not completely clear. It is quite possible that the former is a subspecies of the latter, if not a separate species, but this idea must be checked by studying further populations and investigating the molecular phylogeny of the *Sinobosmina* clade.

SUBGENUS *BOSMINA* (*LIEDEROBOSMINA*) BRTEK, 1997

Bosmina (*Liederobosmina*) nomen novum in Brtek, 1997: 16.
Bosmina (*Neobosmina*) Lieder, 1957: manuscript name; Lieder, 1962: 317; Lieder, 1983b: 127–128; De Melo & Hebert, 1994: 1818.

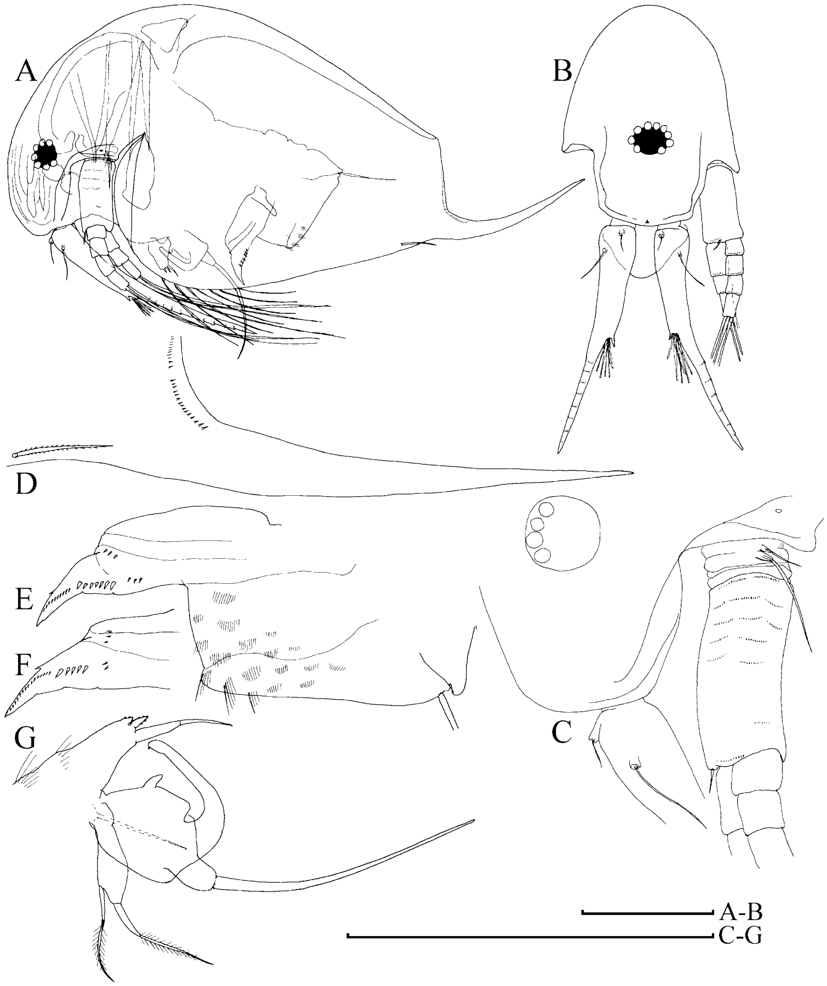

Figure 8. *Bosmina* (*Sinobosmina*) cf. *fatalis cyanopotamia*: adult male from Lake Bolon, Khabarovsk Territory, Asian Russia. A, B, lateral view; C, head, lateral view; D, mucro, inner view; E, postabdomen; F, distal portion of postabdomen; G, distal portion of limb I. Scale bars: 100 μm.

Eubosmina (*Neobosmina*) in Taylor *et al.*, 2002: 1494.

Type species: Bosmina hagmanni Stingelin, 1904 (Lieder, 1962).

Subgenus diagnosis based on male characters: Distal portion of postabdomen remarkably inflated, preanal margin from slightly depressed to convex, with relatively long, fine setules. Gonopore opens subdistally. Postabdominal claw long, without a terminal spinule. Basal pecten of denticles not shifted from postabdominal claw to body of postabdomen, consisting of thin spines, distal pecten consisting of fine setules. Antenna I with widened pre-aesthetasc portion, normally additionally expanded near aesthetascs. On subdistal lobe of limb I there is a small seta located at a distance from two others. Seta 2 on limb I is short.

Comment: Neobosmina Lieder, 1957 *sensu* Lieder, 1962 is a junior homonym of *Neobosmina* Cameron, 1906 (Insecta: Hymenoptera) (Brtek, 1997). Instead of the Lieder's taxon, the name *Liederobosmina* Brtek, 1997 was proposed. Paggi (1979) revised the subgenus in South America, and De Melo & Hebert (1994) revised the subgenus in North America. However, the second paper is subject to criticism: type (or topotype) material was not studied, and so De Melo & Hebert's determinations of species were very provisional.

Our reconsideration of the *Liederobosmina* systematics in North and South America will be published in a separate paper. At this point we only have males of *Bosmina meridionalis* Sars, 1904 and *B. hagmanni*.

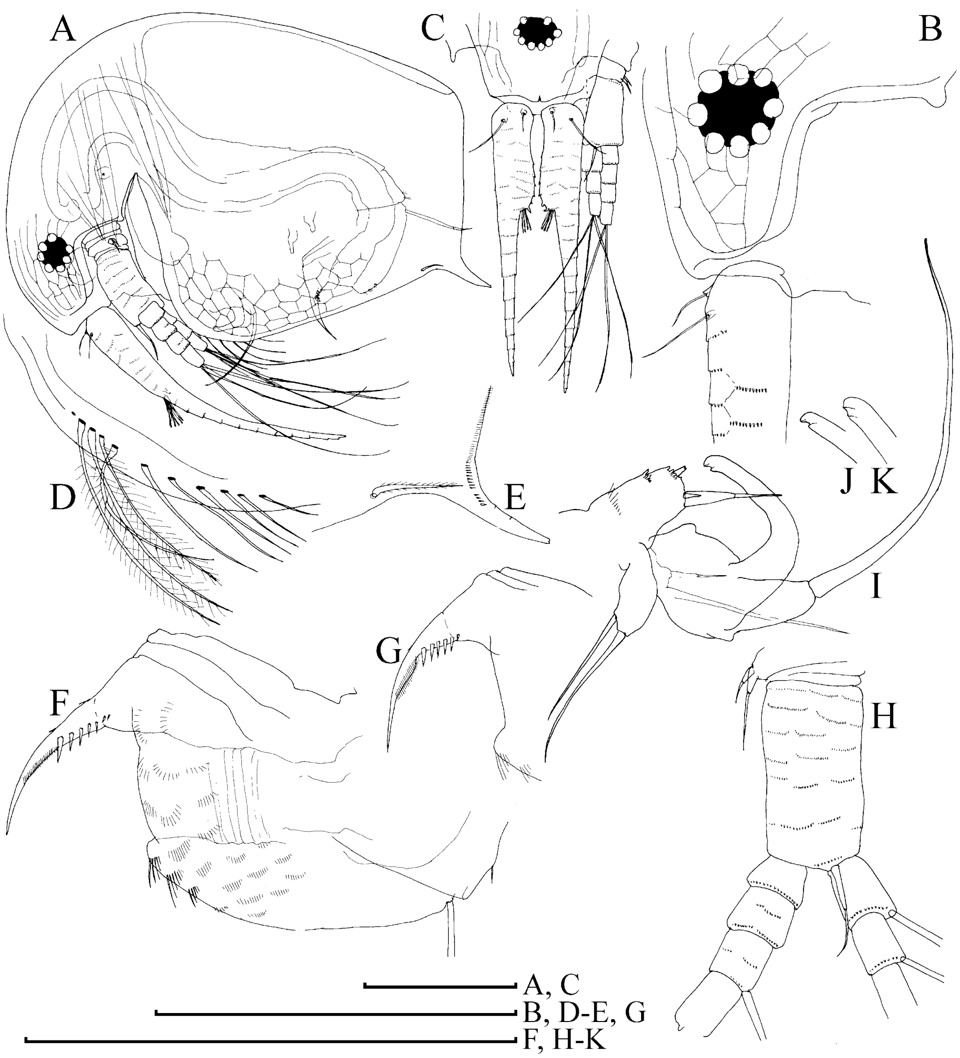

Figure 9. *Bosmina* (*Liederobosmina*) *meridionalis*: adult male from a waterhole 22 km from Pedrika on road to Dalhousie, South Australia (A–F, H–J), and from Rainbow Lake, Kosciusko National Park, New South Wales, Australia (G, K). A, lateral view; B, C, head, lateral and anterior views; D, anteroventral portion of valve, inner view; E, mucro, inner view; F, postabdomen; G, postabdominal claw; H, antenna II, anterior view; I, limb I; J, K, tip of copulatory hook on limb I. Scale bars: 100 μm.

Bosmina (Liederobosmina) meridionalis Sars, 1904, *Figures 9 and 10*
Bosmina meridionalis Sars, 1904: 63–632; pl. 34, fig. 3a–c.
Bosmina (*Neobosmina*) *meridionalis* Sars in Kořínek, 1971: 286–289; fig. 8A–F; Kořínek, 1983: 89–90; figs 104–107; Kořínek, Sacherová & Havel, 1997: 15; figs 2C, 4F.
Bosmina (*Neobosmina*) *chilensis* Daday in Lieder, 1983b: 128 (part).

Material: Australia. Rainbow Lake, Kosciusko National Park, New South Wales, collected in April 1991 by V. F. Matveev, AAK 1998-048; Stock Dam near Anakie, Queensland, collected on 18 July 1974 by B. V. Timms, AAK 2004-035; waterhole 22 km from Pedrika on road to Dalhousie, South Australia, collected on 04 May 1976 by W. Zeidler, SAM C5860; dam 35 km North of William Creek, South Australia, collected in May 1976 by W. Zeider, SAM C5939.

Diagnosis of adult male (Fig. 9): Body relatively high, dorsum regularly arched from anteriormost point to posterodorsal angle, posterior margin of valves high. Head with distinct anteroventral angle, although no wrinkle there, anterior portion of rostrum straight, an ocular dome absent. In anterior view, rostrum truncated, frontal head pore opens immediately on rostral

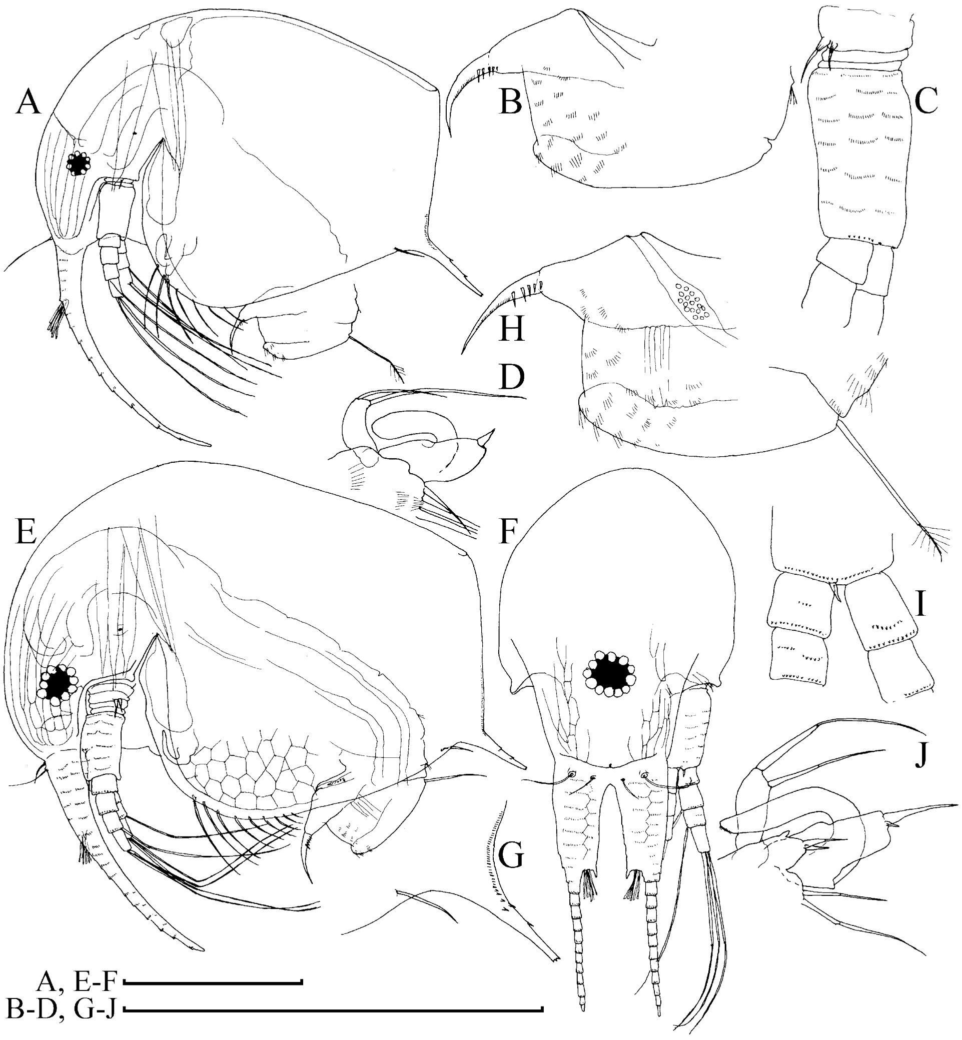

Figure 10. *Bosmina* (*Liederobosmina*) *meridionalis*: juvenile male from waterhole 22 km from Pedrika, South Australia. A, juvenile male I, general view; B, postabdomen of juvenile male I; C, antenna II of juvenile male I, external view; D, distal portion of limb I of juvenile male I; E, F, juvenile male II, lateral and anterior view; G, mucro of juvenile male II, inner view; H, postabdomen of juvenile male II; I, distal portion of basal segment of antenna II of juvenile male II; J, distal portion of limb I of juvenile male II. Scale bars: 100 μm.

'fold' (anteroventral angle of head). Lateral head pore at a great distance from lateral edge of head shield. Mucro long, seta kurzi short, a series of long setae at anteroventral portion of valve. Postabdomen massive, ventral margin humped, preanal margin characteristically convex, dorsodistal angle slightly projected, anal margin straight. Postanal portion of postabdomen short, conical, blunt distally, without spinules except for a pre-claw group of up to two spinules, but sometimes this group is completely reduced. Gonoduct thick, gonopore opens on dorsal side, on anterior 'slope' of ventral margin, far from distal end of postabdomen. Postabdominal claw long, slender, without a distal spinule, distal pecten as a series of minute setules, proximal pecten with few relatively large denticles. Antenna I regularly bent in lateral view, in anterior view, its pre-aesthetasc portion thick, with concave inner margin, whereas distal half thin, straight, regularly narrowing distally. Antennular sensory seta long, male seta short, located on a minute pedestal. Antenna II with two short sensory setae on coxal part. Distal anterior seta long, reaching half of second segment of endopod. Limb I bears idl with a relatively small basal portion supplied with a low hillock, and a conical distal portion terminating as a long, naked seta. Copulatory hook relatively large and thick, not recurved to a parallel position with the idl, tip of hook incised. Subdistal lobe large,

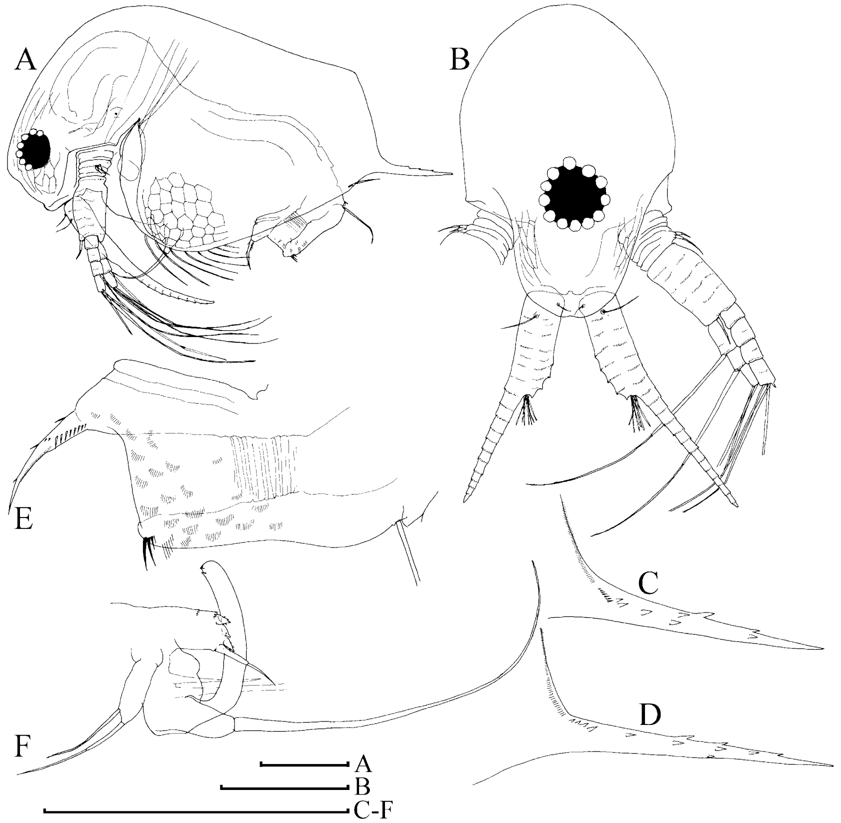

Figure 11. *Bosmina* (*Liederobosmina*) *hagmanni*: adult male from Lago Cristalino, Ipiranga, lower Rio Negro, Amazonas, Brazil. A, B, lateral and anterior view; C, D, mucro; E, postabdomen; F, distal portion of limb I. Scale bars: 100 μm.

with a long seta, a rudimentary seta near it, and another rudimentary seta at a distance from the two aforementioned setae.

Postembryonic development: Juvenile male I (Fig. 10A–D) body shape similar to juvenile female I. Postabdomen with convex preanal margin and inflated ventral portion, a rudimentary gonoduct terminating far from the level of the anus, although the gonopore is absent. Postabdominal claw long, with distal and proximal pectens on female type. Antenna I fused with rostrum, only a pair of long antennular sensory setae on rostrum. Antenna II with two short sensory setae on coxal portion, whereas there is no rudimentary distal anterior seta. Limb I with idl small, subovoid, with a single rudimentary seta, copulatory hook short and thick, subdistal lobe not projected, with a single seta 1 (as in female).

Juvenile male II (Fig. 10E–J) with body shape as in juvenile female II. Postabdomen with slightly convex preanal margin, ventral side inflated, rudimentary gonoduct does not reach the level of the anus, although located closer to anus than in male I. Postabdominal claw long, distal pecten with fine setules, proximal pecten with few slender spinules, pre-claw pecten absent. Antenna I fused with rostrum, with a long sensory seta and a short male seta at the same level. Antenna II with two short antennular sensory setae on coxal portion, and a rudimentary distal sensory seta on the basal segment. Limb I with idl large (but smaller than in the adult), its distal portion subquadrangular, with a seta shorter, as in adult, and a second rudimentary seta; copulatory hook robust, with blunt tip bearing fine setules, subdistal lobe small, with two setae of different lengths, and a small rudimentary third seta at a distance from the aforementioned pair.

Comments: Most probably, there is only a single species of *B.* (*Liederobosmina*) in Australia [although recently a representative of *B.* (*Bosmina*) has been found; A. A. Kotov, unpubl. data]. Kořínek (1971, 1983) schematically illustrated the adult male of this species, similar to that described above, including the characteristic convex preanal margin.

Bosmina (Liederobosmina) cf. *hagmanni* Stingelin, 1904, *Figures 11 and 12*
Bosmina hagmanni Stingelin, 1904: 582–583; pl. 20, figs 5, 6.

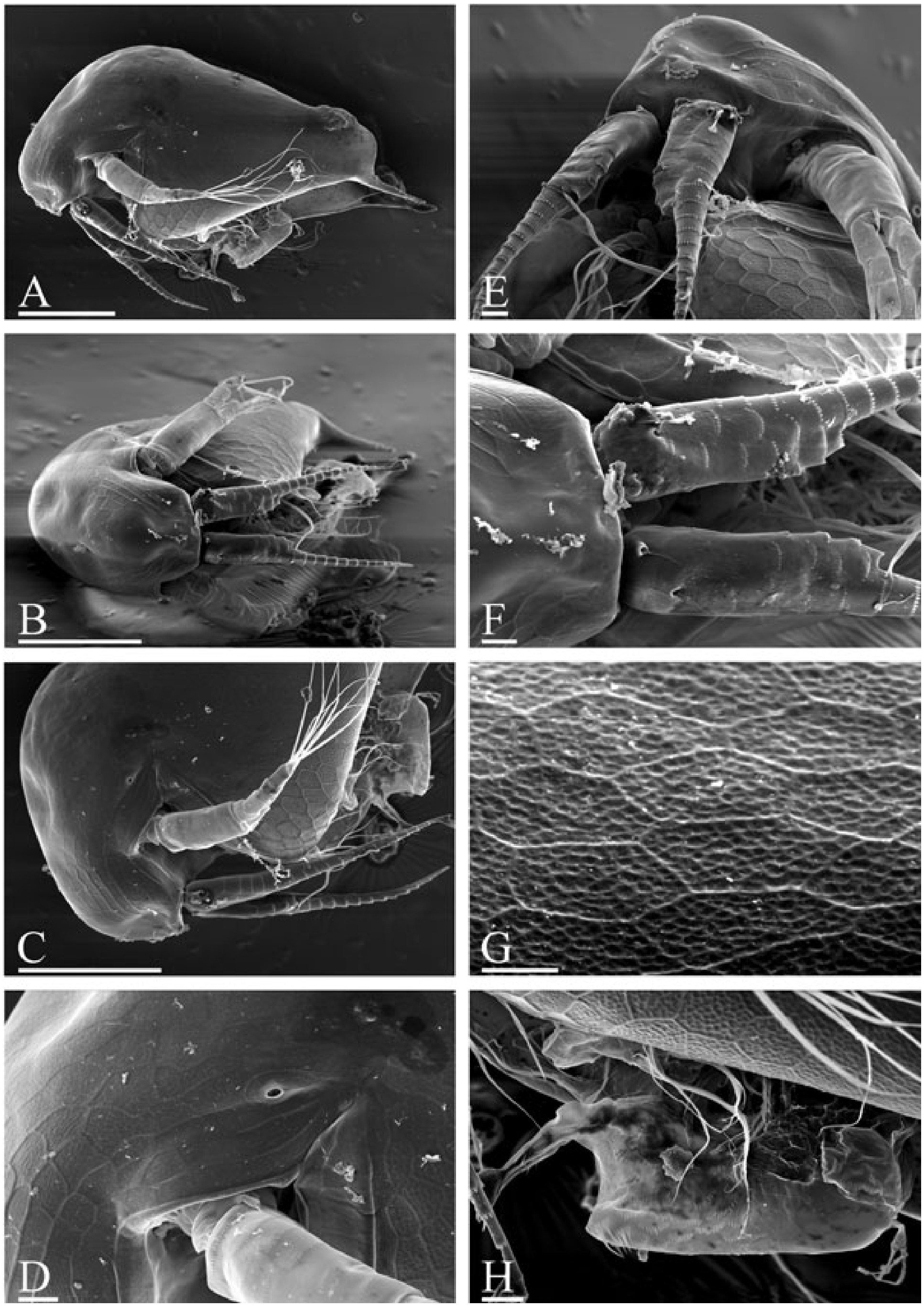

Figure 12. *Bosmina* (*Liederobosmina*) *hagmanni*: adult male from Lago Cristalino, Brazil. A, lateral view; B, anterior view; C, head; D, lateral head pore; E, F, rostrum; G, sculpture of valves; D, postabdomen. Scale bars: 100 μm for (A, C); 10 μm for (D, H).

Bosmina (*Neobosmina*) *hagmanni* Stingelin in Kořínek, 1971: 286; fig. 7C; De Melo & Hebert, 1994: 1818; fig. 8A, B.
Eubosmina hagmanni (Stingelin) in Deevey & Deevey, 1971: 209–213; pl. 1, fig. 4a, b; pl. 4, figs 1–6.
Bosmina (*Neobosmina*) *chilensis* Daday in Lieder, 1983b: 128 (part).
Eubosmina (*Neobosmina*) *hagmanni* Stingelin in Taylor *et al.*, 2002: 1491.

Material: Brazil. Lago Cristalino, Amazonas, collected on 20 September 1974 by G.-O. Brandorff, AAK 1999-066; Rio Negro near Manaus, Ponta Negra, Amazonas, collected on 26 March 1974 by G.-O. Brandorff, AAK 2002-136; Rio Tapajyz, Pará, collected on 14 January 1948 by V. Koste, AAK 2002-139; Lago Timby, Tapajys region, Pará, collected on 11 January 1948 by V. Koste, NMK 0860.

Short diagnosis of adult male: Dorsum of valves slightly concave in posterior half, posterior margin very short. Reticulation distinct, with a sculpture consisting of minute depressions within each cell. Ocular dome present, rostrum in anterior view rounded, rostral wrinkle or fold more or less developed. Preanal margin of postabdomen slightly concave, a group of a few robust setules at dorsodistal angle. Postabdominal claw with between eight and ten slender spinules in the proximal pecten. Distal anterior seta on basal segment of antenna II shorter than basal segment of endopod. Tip of copulatory hook on limb I with two ridges.

Comments: This may be a group of cryptic species (V. Kořínek, pers. comm.), so we are not sure about the relationships of our populations with those described by Stingelin (1904). Deevey & Deevey (1971) and then De Melo & Hebert (1994) reported this species as common in North America.

Two other South American species
Source: Description by Paggi (1979).

Differences of Bosmina (Liederobosmina) chilensis Daday, 1902: Bosmina (*Liederobosmina*) *chilensis* differs from other species of the subgenus in males having: (1) distinct preocular depression; (2) anteroventral angle of head not elevated, with distinct doubled fold on rostrum; (3) a single incision on tip of copulatory hook; (4) idl with a short seta.

Differences of Bosmina (Liederobosmina) huaronensis Delachaux, 1918: Bosmina (*Liederobosmina*) *huaronensis* differs from other species of the subgenus in males having: (1) no preocular depression; (2) elevated anteroventral angle of head, without doubled fold on rostrum; (3) two fine ridges on tip of copulatory hook; (4) idl with a long seta.

Comments: See key for determination of species.

SUBGENUS *BOSMINA* (*LUNOBOSMINA*) TAYLOR *ET AL.*, 2002

Eubosmina (*Lunobosmina*) Taylor *et al.*, 2002: 1494.

Type species: Bosmina (*Eubosmina*) *oriens* De Melo & Hebert, 1994, typified by monotypy, case 68.3 of ICZN (2000).

Subgenus diagnosis based on male characters: Distal portion of postabdomen as in female, not inflated, preanal margin slightly depressed, with relatively long, fine setules. Gonopore opens subdistally. Postabdominal claw long, without a terminal spinule. Basal pecten of denticles not shifted from postabdominal claw to body of postabdomen, consisting of thin spines, distal pecten consisting of short, fine setules. Antenna I with widened pre-aesthetasc portion. A seta located at a distance from two others on the subdistal lobe of limb I. Seta 6 on limb I short.

Comment: The sole species of the subgenus, *B. oriens*, has a lateral head pore of the '*Eubosmina*' type. But, *B. oriens* is the most primitive member of the '*Eubosmina–Liederobosmina*' clade because it has a non-specialized postabdomen (an uninflated and a non-conical distal end with a gonopore located far from the distal end). Because of these traits, the postabdomen of *B. oriens* is more primitive than those of *Eubosmina*, *Liederobosmina*, or *Sinobosmina*. Also, *B. oriens* has a primitive, thick tip of the copulatory hook, in contrast to the elaborated tip of *Liederobosmina*. So, although *B. oriens* might be the distant sister lineage to *Liederobosmina*, the subgenus *Lunobosmina* retains several plesiomorphic characters.

Bosmina (Lunobosmina) oriens (De Melo & Hebert, 1994)
Figures 13–16
Eubosmina longispina (Leydig, 1860) in Deevey & Deevey, 1971: 206–209; pl. 1: fig. 3a, b; pl. 3, fig. 3a–d (part).
Bosmina (*Eubosmina*) *oriens* De Melo & Hebert, 1994: 1815–1818, fig. 6G, H.
Eubosmina (*Lunobosmina*) *oriens* De Melo & Hebert in Taylor *et al.*, 2002: 1494.

Type locality: 'A lake located on the north side of highwayhighway 44, 3 km east of the Rhode Island–Connecticut state line 41°55′N; 71°45′W)' (De Melo & Hebert, 1994), Rhode Island, USA. This body of water is locally named Bowdish Reservoir.

Type material: Holotype. A parthenogenetic female, CMN. Paratypes. ten adult and six juvenile females, CMN.

Material
Populations containing males: USA. Hell Hollow Pond, Connecticut, AAK 2004-051 (the former artificially induced by adding MF to the culture, see Kim *et al.*, 2006).

Canada. Pond on highway 1, 2.9 km east of Little Harbor junction, Newfoundland, collected on 4 September 1984 by D. G. Frey, DGF 7092; Barren Pool,

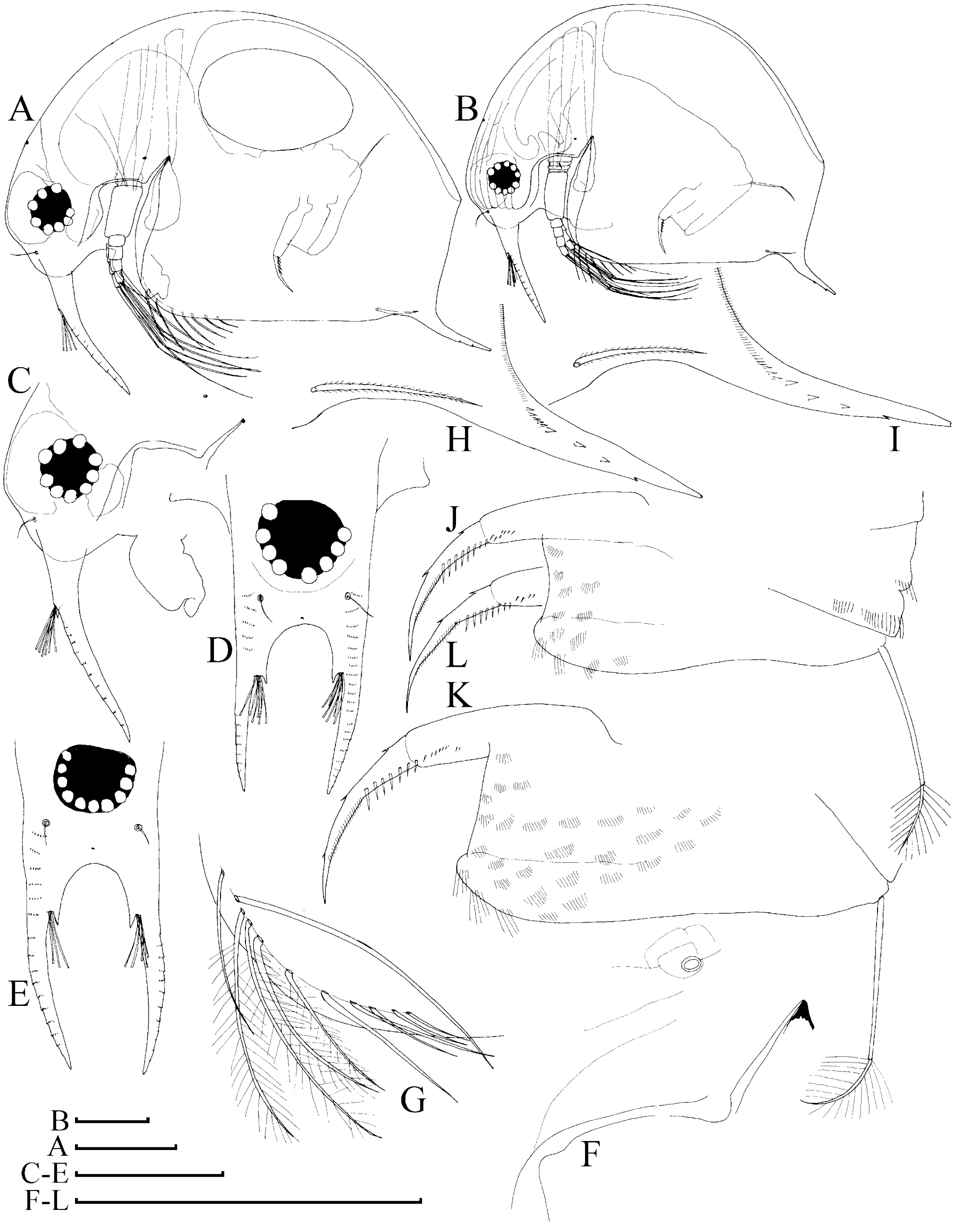

Figure 13. *Bosmina* (*Lunobosmina*) *oriens*: adult female from a pond on highway 1, 2.9 km east of Little Harbor junction, Newfoundland, Canada. A, B, lateral view; C, head, lateral view; D, E, head, anterior view; F, region of lateral head pore; G, setae at anteroventral portion of valve, inner view; H, I, mucro, inner view; J, K, postabdomen, lateral view; L, postabdominal claw. Scale bars: 100 μm.

1.4 km west of Rocky River bridge, west of Colinet, Newfoundland, collected on 9 September 1984 by D. G. Frey, DGF 7121; Fen Pool, east side of road from Cape St. Mary's to highway 100, Newfoundland, collected on 11 September 1984 by D. G. Frey, DGF 7135a; a body of water near highway 1, Newfoundland, collected in September 1984 by D. G. Frey, DGF 7167-II; bog pool 12, Barrents near Daggett's Round Pond near Bavline, north of St. John's, Newfoundland, collected on 24 September 1984 by D. G. Frey, DGF 7186; Pine Hill Pond, Terra Nova National Park, Newfoundland, collected on 30 September 1984 by D. G. Frey, DGF 7202; Peskowesk Lake, east of where canoes are put in, Kefimkujik National Park, Nova Scotia, collected on 13 October 1984 by D. G. Frey, DGF 7280.

Parthenogenetic populations: USA. Bowdish Resevoir (type locality), Rhode Island, collected in June 2004 by D. J. Taylor & A. A. Kotov, AAK 2005-236-237; Hell Hollow Pond, Connecticut, collected in June 2004

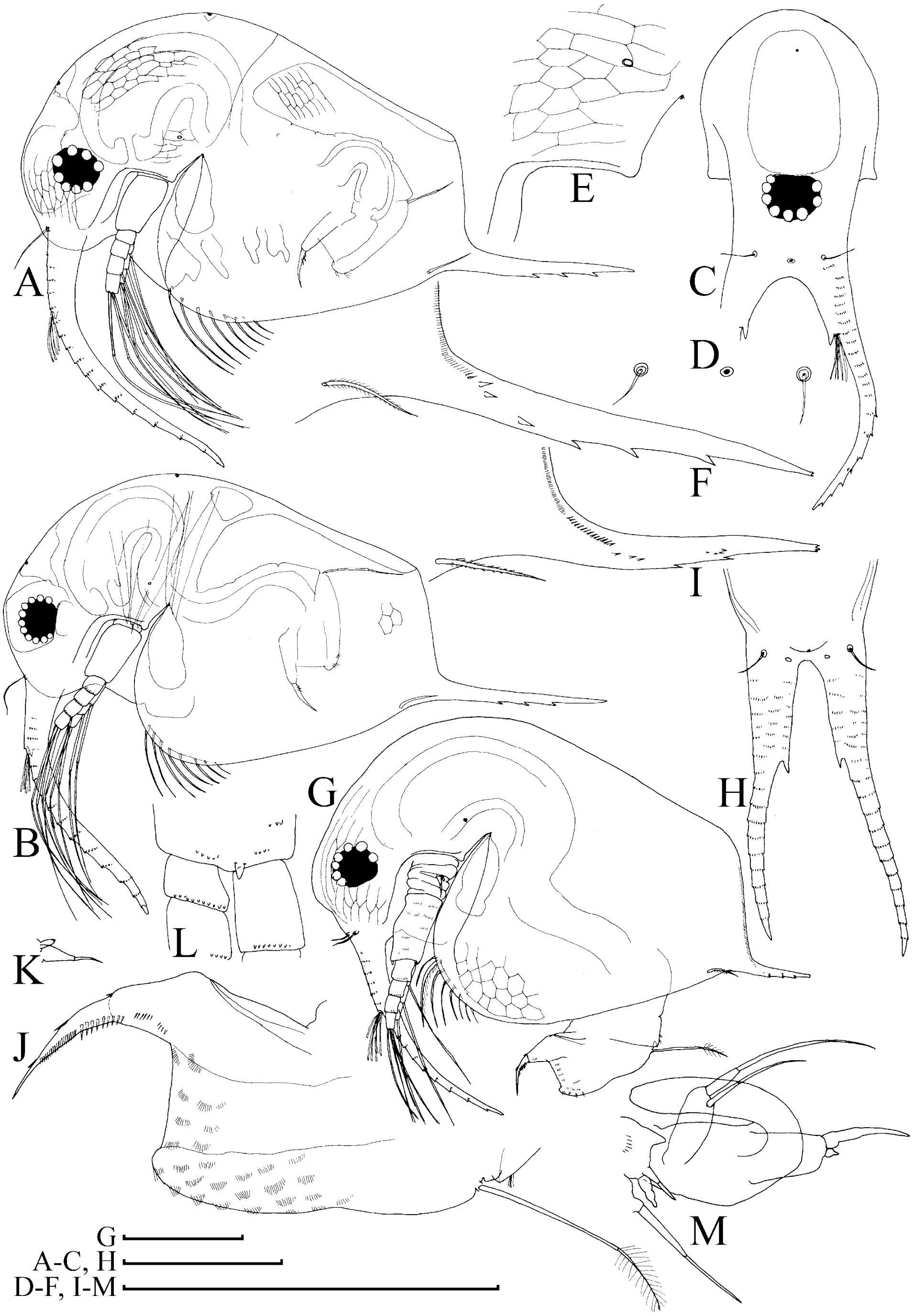

Figure 14. *Bosmina* (*Lunobosmina*) *oriens*: juvenile female from a pond on highway 1, Newfoundland, Canada (A, C–F), and from Great Pond, Cape Cod, Massachusetts, USA (B); juvenile male II from Hell Hollow Pond, Connecticut, USA (G–M). A, B, general view of juvenile female; C, anterior view of juvenile female; D, antennular sensory setae and frontal head pore of juvenile female; E, lateral head pore of juvenile female; F, mucro of juvenile female; G, juvenile male II, general view; H, head of juvenile male II, anterior view; I, mucro of juvenile male II, inner view; J, postabdomen of juvenile male II; K, setae at coxal part of antenna II of juvenile male II; L, rudimentary sensory seta at distal segment of antenna II of juvenile male II; M, distal portion of limb I of juvenile male II. Scale bars: 100 μm.

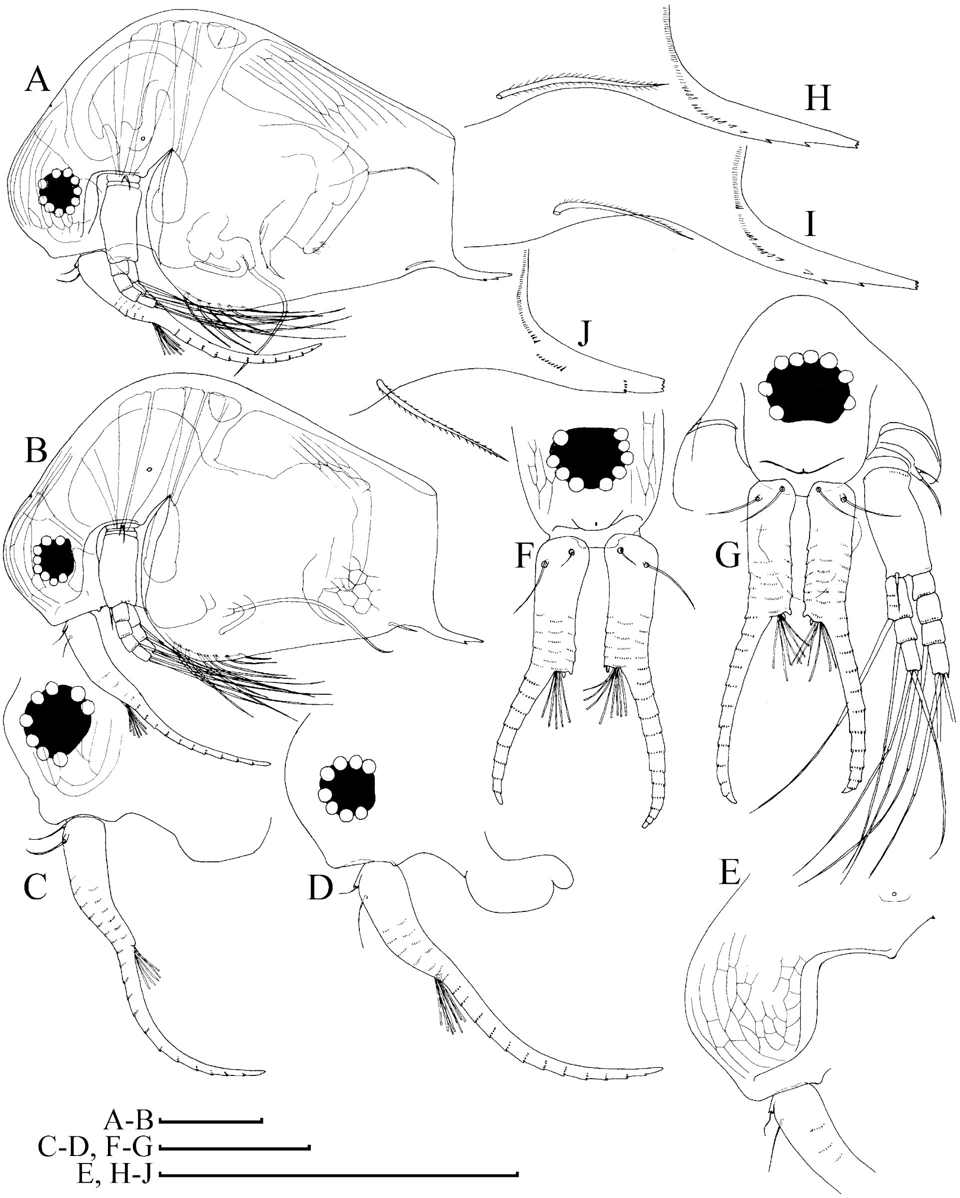

Figure 15. *Bosmina* (*Lunobosmina*) *oriens*: adult male from a pond on highway 1, Newfoundland, Canada (A, B, D–F, H, I), and from Hell Hollow Pond, Connecticut, USA (C, G, J). A, B, lateral view; C–E, head, lateral view; F, G, head, anterior view; H–J, mucro, inner view. Scale bars: 100 μm.

by D. J. Taylor & A. A. Kotov, AAK 2005-238-239; Fresh Pond, Dennis, Massachusetts, collected in June 2004 by W. Piel & A. A. Kotov, AAK 2005-258; Great Pond, Cape Cod, Massachusetts, collected in June 2004 by W. Piel & A. A. Kotov, AAK 2005-251; Pond 3, Three ponds, Long Island, New York, collected in June 2006 by D. J. Taylor & A. A. Kotov, AAK 2005-209.

Canada. Roadside Lake, highway 333, 0.8 km east of East Dover, Nova Scotia, collected on 21 October 1984 by D. G. Frey, DGF 7300.

Redescription

Adult parthenogenetic female (Fig. 13): Body wide in anterior view, short and wide in lateral view, dorsal margin in general regularly curved from distalmost extremity to posterodorsal angle, posterior margin straight, its height about half of the body height, ventral margin almost straight, with a depression anterior to mucro. Reticulation very obscure, both on head and on valves. Head with well-developed ocular dome, and consequently with a distinct preocular depression that is obvious in lateral view, rostrum

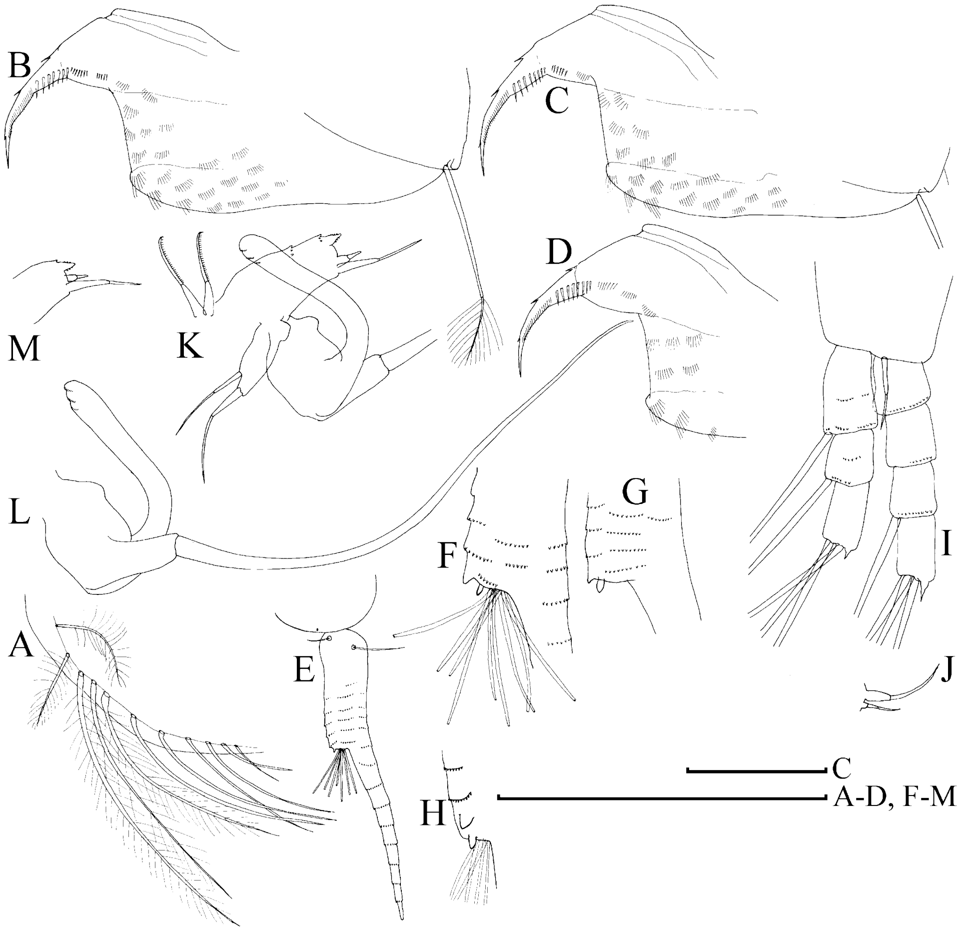

Figure 16. *Bosmina* (*Lunobosmina*) *oriens*: adult male from a pond on highway 1, Newfoundland, Canada (B–E, G, I–M), and from Hell Hollow Pond, Connecticut, USA (A, F, H, J). A, setae at anteroventral portion of valve, inner view; B–D, postabdomen; E, antenna I, anterior view; F, G, region of aesthetasc location, anterior view; H, region of aesthetasc location, inner view; I, antenna II, anterior view; J, sensory setae at coxal part of antenna II. Scale bars: 100 μm.

blunt, regularly arched. Frontal head pore small, located closely to ventral margin of head (as seen from anterior side), and significantly ventral to level of antennular sensory setae. Median head pore minute, located posteriorly to ocular dome. Fornices well-developed, covering coxal part of antenna II. Lateral head pore small, with a raised ring-like margin, located at a great distance from ventral margin of head shield, above level of mandibular articulation. Compound eye very large. Labrum as a fleshy appendage lacking significant projections, distal labral plate small. Ventral valve margin with a series of stout setae, the bases of which are located on its internal surface, the more anterior setae supplied with long setules. Seta kurzi with small setules, located on internal side of valve anterior to the aforementioned depression near the mucro, which is strong and long even in large adults, with a truncated tip and one or two incisions on the ventral side, sometimes the incisions are completely absent. On inner side of mucro, there are few relatively strong denticles, as a continuation of a series of setules at the posterior valve margin.

Thorax relatively long, with six limb pairs, abdomen short, with transverse rows of setules. Postabdomen strongly compressed laterally, with width approximately equal along entire length, and with ventral (functionally dorsal!) margin slightly convex. Preanal margin long, slightly concave, with few groups of setules distally. Sides of postabdomen supplied with series of finer setules. Distal (anal) margin nearly directly truncated, posterodorsal angle as a small projection. Postanal portion as a cylindrical projection bearing paired postabdominal claws. Each claw regularly bent, with three denticles on convex (ventral) margin and two pectens on concave (dorsal) margin: distal pecten consists of fine setules, whereas proximal pecten consists of between seven and nine rather strong, sparsely located teeth. Near the claw on the postanal portion of the postabdomen there is a third, pre-claw pecten of minute denticles. Postabdominal seta shorter than preanal margin, with its distal segment about two times shorter than distal one, supplied with fine, long setules.

Antenna I fused with rostrum, rather short, its length from tip to tip of rostrum about 0.3–0.4 body lengths. Antennular (frontal) sensory seta located on rostrum in region of preocular depression. Free (not incorporated in rostrum) part of antenna I consists of a pre-aesthetasc portion, fused with rostrum, and post-aesthetasc portion, the presence of which is a unique synapomorphy of *Bosmina*. Pre-aesthetasc portion straight, regularly narrowing in anterior view, with an internal spine near a flat site of the aesthetasc bases. Nine aesthetascs that are delicate, slightly differing in size, with the longest somewhat shorter than the pre-aesthetasc free portion. Post-aesthetasc portion directed ventrally and somewhat posteriorly, slightly curved in lateral and anterior views. Both portions supplied with crossing series of fine denticles.

Antenna II typical for the genus, with six pairs of thoracic limbs, and with morphology indistinguishable from that in other species (Kotov, 1996).

Juvenile female (Fig. 14A–F): Body more compressed laterally and more elongated in lateral view, with obvious reticulation. Ocular dome less developed, especially in instar I; median head pore as in adult, posterior dorsal head pore presents in instar I. Lateral head pore closer to mandibular articulation. Mucro long, with several denticles at ventral margin. Antenna I longer (especially its post-aethetasc portion), strongly curved in lateral and anterior view, head pore at level of antennular sensory setae.

Ephippial female: In lateral view habitus similar to adult parthemogenetic female, a longitudinal fold on dorsal part of valves of large ephippial females, a median fold on top of dorsum, so dorsum is triangular in cross section.

Adult male (Figs 15 and 16): Body relatively high, dorsum posteriorly slightly concave, posterior margin of valves of moderate height. Head large, anteroventral angle projected; distalmost extremity of head with slight ocular dome or without it. Lateral head pore at a long distance from lateral edge of head shield. Mucro long, seta kurzi long, a series of long setae at anteroventral portion of valve. Postabdomen massive, ventral margin straight, preanal margin slightly concave, dorsodistal angle slightly projected, anal margin straight, in a small anal depression. Postanal portion of postabdomen short, conical, blunt distally, supplied with series of fine spinules, spinules in a pre-claw group somewhat larger than rest. Single gonopore opens on dorsal side, far from distal end. Postabdominal claw long, slender, without distal spinule, distal pecten as a series of fine setules, proximal pecten with slender denticles. Antenna I with base not inflated, regularly narrowing distally, characteristically E-shaped. Sensory seta long, male seta long, located on a minute pedestal. Antenna II with two short sensory setae on coxal part. Distal sensory seta long, reaching distal end of basal segment of endopod. Limb I with idl strongly inflated, with a low hillock on the basal portion, and with its distal portion relatively short, terminating as a long, naked seta. Copulatory hook relatively large and thick, not recurved to a parallel position with the idl, tip of hook blunt, with fine setules. Subdistal lobe massive, with a long seta, a rudimentary seta near it, and another rudimentary seta at a distance from the two aforementioned setae.

Juvenile male I: Not studied.

Juvenile male II (Fig. 14G–M): Body shape as in juvenile female II, with a slight ocular dome. Postabdomen with slightly depressed preanal margin, postanal portion slightly inflated, rudimentary gonoduct that does not reach the level of anus. Postabdominal claw long, distal pecten with fine setules, proximal pecten with slender teeth, pre-claw pecten with fine setules. Antenna I fused with rostrum, with a sensory seta and a short male seta approximately at the same level. Antenna II with two short sensory setae on coxal portion, and a rudiment of distal sensory seta. Limb I with idl large (but smaller than in adult), its distal portion subovoid, with a seta approximately as long as distal portion, and with a second rudimentary seta; copulatory hook robust, with blunt tip, subdistal lobe small, with two setae of equal lengths, and a massive hillock (a rudiment of the third seta).

Size: Females, 380–630-μm long; adult males 465–510-μm long.

Distribution: This is a species with a relatively local distribution on the Atlantic Coast of the USA and Canada.

Comments: The species was briefly described by Deevey & Deevey (1971) as *Eubosmina longispina*: they illustrated the adult males bearing characteristic E-shaped antenna I (Fig. 15C, D). Later, Kotov (1996) noted that the male described by Deevey & Deevey had a postabdomen of the *Neobosmina*-type (now *Liederobosmina*) – very different from the beveled postabdomen of the males from European

Bosmina (*Eubosmina*) *longispina*. De Melo & Hebert (1994) created a new species based largely on allozyme evidence, without examination of the males. The DNA sequence-based phylogeny of Taylor *et al.* (2002) indicated a distant relationship of *B. oriens* with *B. longispina*, and they created a new subgenus *Eubosmina* (*Lunobosmina*) containing *B. oriens*. However, Taylor *et al.* (2002) also proposed that the '*B. longispina*' of Deevey & Deevey (1971) was actually *B. oriens*. Later, Kim *et al.* (2006) induced males of *B. oriens* and confirmed that the unusual male antenna I indeed unites *B. oriens* with *B. longispina sensu* Deevey & Deevey (1971). Our more detailed analysis of male morphology further supports the opinion that *B. oriens* is the species that Deevey& Deevey termed North American *B. longispina*. We note that endemic *B. longispina*-like species do exist in North America in addition to *B. oriens*.

The morphology of parthenogenetic females of the common North American species of subgenera *Eubosmina* and *Liederobosmina* have not been well studied. Previous authors concentrated on such characters as the length of the mucro or of antenna-I (Lieder, 1991), instead of attempting to find other characters that are less vulnerable to the influence of ecological factors. Females of *B. oriens* are difficult to discern from females of North American *Bosmina* (*Eubosmina*) sp. *Bosmina oriens* does seem to possess a relatively large mucro and relatively strong denticles on its inner side that are absent in the *Eubosmina*. In contrast, males are easily diagnosed after scoring the characteristic E-shaped antenna I and a unique, primitive postabdomen.

SUBGENUS *BOSMINA* (*EUBOSMINA*) SELIGO, 1900

Bosmina Eubosmina Seligo, 1900: 67; Lieder, 1962: 317; Lieder, 1983a: 202–203; Lieder, 1983b: 128–134; De Melo & Hebert, 1994: 1812 (part, except of *oriens*). *Eubosmina* (*Eubosmina*) in Taylor *et al.*, 2002: 1494.

Type species: Bosmina coregoni Baird, 1857. When Seligo (1900) described his new taxon, as well as in his subsequent paper (Seligo, 1928), he discussed many species of *Bosmina* (*Eubosmina*), without selecting a type species. Lieder (1962) said that the subgenus includes '*B. coregoni* s. lat.': this sentence can probably be regarded as a typification of this genus-group name by a subsequent author (case 69 of ICZN, 2000).

Subgenus diagnosis based on male characters: Postabdomen conically tapering distally, not inflated, preanal margin in general straight, with very short setules. Gonopore opens distally. Postabdominal claw long, without a terminal spinule. Basal pecten of denticles not shifted from postabdominal claw to body of postabdomen, consisting of large, robust teeth, distal pecten consisting of long, fine setules. Antenna I with widened pre-aesthetasc portion. On subdistal lobe of limb I, a seta located at a distance from two others. Seta 2 on limb I very short.

Comments: This is the subgenus with the most confusion in the Bosminidae. About 100 (!) described nominal taxa of the genus *Bosmina* can be attributed to this subgenus. Previous proposals on introgressive hybridization (Lieder, 1956, 1983a, 1996) have lacked evidence, but ecologically plastic characters certainly contribute to the species problem. Now the subgenus needs to be revised.

Palaearctic *Bosmina (Eubosmina)* cf. *coregoni* Baird, 1857,
Figs 17–19
Bosmina coregoni Baird, 1857: 21, 24.

Previous descriptions with information on males: Norman & Brady, 1867: 7–8; figs 1, 2 (*B. longispina*); P. E. Müller, 1870: 150–151; pl. 2, figs 3–8 ; pl. 3, fig. 11 (*Bosmina diaphana* P.E. Müller, 1867); Stenroos, 1895: 25–26; figs 11–15 (*Bosmina brevispina* Lilljeborg, 1890 in Sars, 1890); Lilljeborg, 1901: 237–256; pl. 32, figures 4–13; pl. 33, figs 1–12; pl. 34, figs 1–12; pl. 35, figs 1–9; pl. 36, figs 1–12; pl. 37, figs 1–7 (*Bosmina obtusirostris* Sars, 1861); 256–259; pl. 37, figs 8–9; pl. 38, figs 1–2 (*Bosmina longicornis* Schoedler, 1865); 259–269; pl. 38, figures 3–17; pl. 39, figs 1–8; pl. 40, figures 1–10 (*B. longispina*); 269–274; pl. 40, fig. 11; pl. 41, figs 1–7 (*Bosmina insignis* Lilljeborg, 1901); 275–284; pl. 41, figs 8, 9; pl. 42, figs 1–9; pl. 43, figs 1–9; pl. 44, figs 1, 2 (*Bosmina mixta* Lilljeborg, 1901); 284–298; pl. 44, figs 2–8; pl. 45, figs 1–11; pl. 46, figs 1–6; pl. 47, figs 1–8; pl. 48, figs 1–6 [*B. coregoni*]; 298–304; pl. 48, figs 7, 8; pl. 49, figs 1–12; pl. 50, figs 1, 2 (*Bosmina crassicornis* Lilljeborg, 1887); 304–308; pl. 50, figs 3–12; pl. 51, figs 1–5 [*Bosmina globosa* Lilljeborg, 1901]; Keilhack, 1904: 564; text – fig. (*Bosmina coregoni gibbera* Schoedler, 1863); Keilhack, 1908: 448; figs 12, 13 (*B. coregoni gibbera*); Zykoff, 1906: 479; figs 1, 2 (*B. insignis*); Keilhack, 1909: fig. 118 (*coregoni–lilljeborgii*); Apstein, 1910: 11–12; figs 20–21 (*Bosmina maritima* P. E. Müller, 1867); Burckhardt, 1941: 130–141; figs 3, 4, 12–15, 13′, 15′, 18, 21–23, 29 (*B. coregoni*); Purasjoki, 1958: 23–26; fig. 4 (*Bosmina coregoni maritima* P. E. Müller, 1867); Šrámek-Hušek *et al.*, 1962: 280–284; fig. 102 (*coregoni* morph *coregoni*, *coregoni* m. *longispina*, *coregoni* m. *poppei*, *coregoni* m. *longicornis*); Semenova, 1970: 50–51; figs a, b, v (*B. coregoni*); Flössner, 1972: 218–224; figs 102–104 [*B.* (*E.*) *longispina*]; 225–232; figs 106–108 [*B.* (*E.*) *coregoni*];

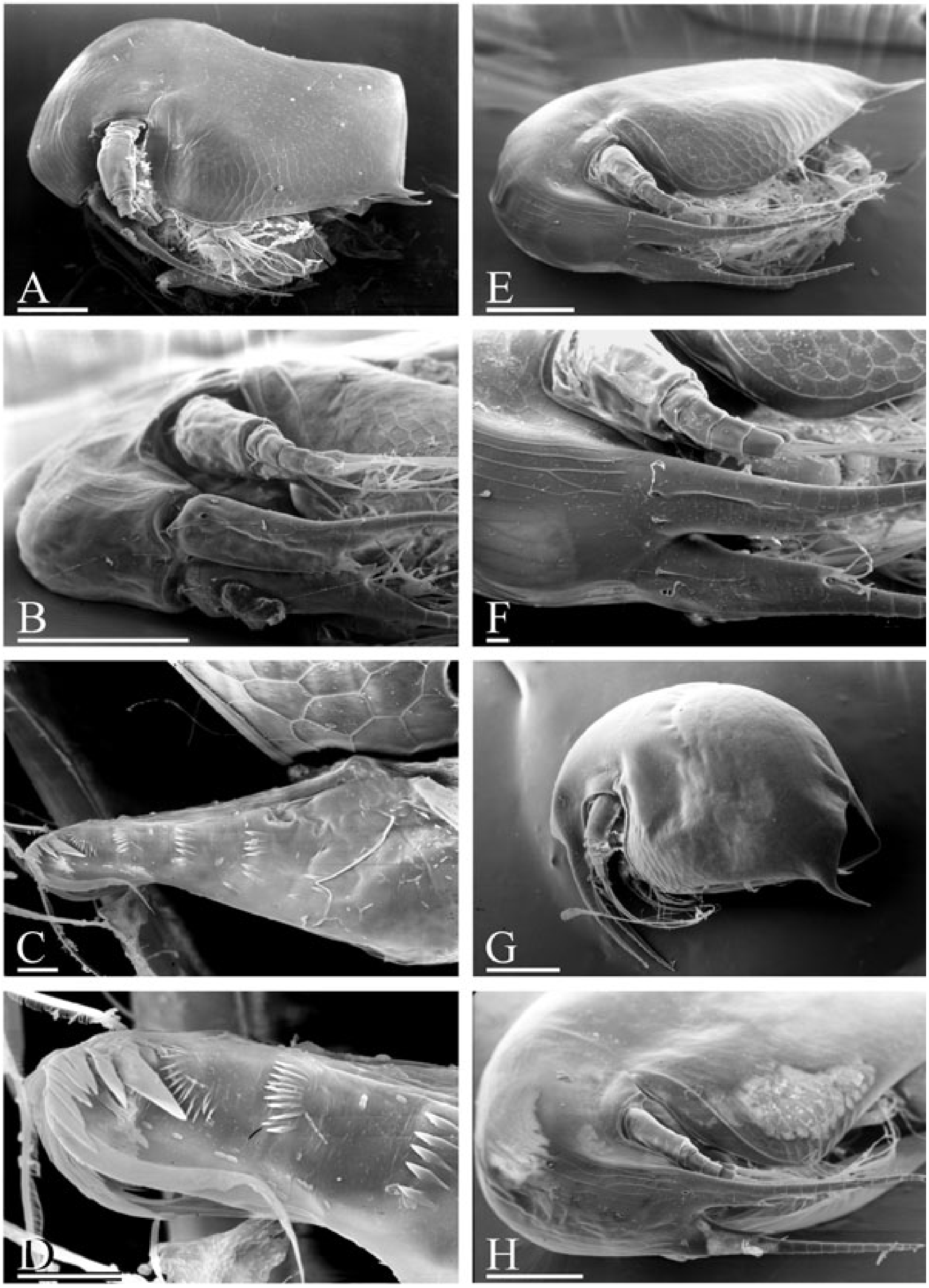

Figure 17. *Bosmina* (*Eubosmina*) cf. *longispina*: from a lake in tundra, Tareya, Taimyr Autonomous Area, Asian Russia. A, adult male; B, head of adult male, anteroventral view; C, D, postabdomen and its distal portion; E, juvenile male II; F, head of juvenile male II, anteroventral view; G, adult parthenogenetic female, general view; H, head of adult parthenogenetic female, anteroventral view. Scale bars: 100 μm for (A, B, E, G, H); 10 μm for (C, D, F).

Sergeev, 1981 (coregoni maritima); Lieder 1983a: 209–211; figs 28–30 [*B.* (*E.*) *longispina longispina*]; 213–214; fig. 64 [*B.* (*E.*) *mixta kessleri* Uljanin, 1874]; 215–216; fig. 88, 94; pl. 3, fig. 2 [*B.* (*E.*) *mixta cederstroemi* Schoedler, 1865]; 223–224; pl. IV, fig. 1 [*B.* (*E.*) *coregoni thersites*]; Negrea, 1983: 227–229; fig 92 [*B.* (*E.*) *longispina*]; Margaritora, 1985: 61–64; fig. 27 (*E. coregoni*); 64–66, fig. 28 (*E. longispina*); Sars, 1993: 82–83; pl. 62–63 (*B. obtusirostris*); Hudec, 1995: 293–295; pl. 1 [*B.* (*E.*) *longicornis kessleri*]; Kotov, 1996: 188–194; figs 1–5 [*B.* (*E.*) *longispina*]; Lord *et al.*, 2006: pl. 1 [*B.* (*E.*) *coregoni gibbera*].

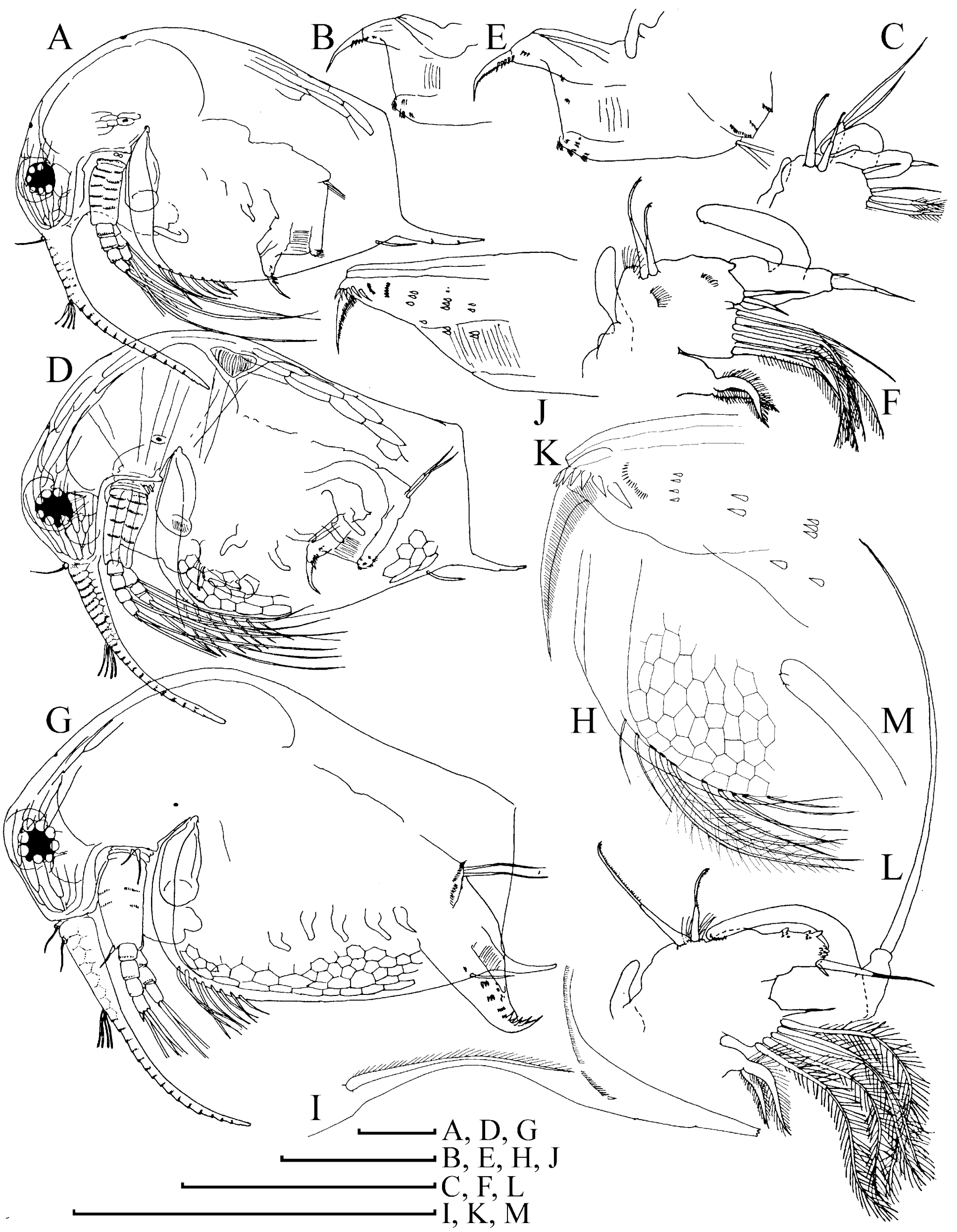

Figure 18. *Bosmina* (*Eubosmina*) cf. *longispina*: male from a lake in tundra, Tareya, Taimyr Autonomous Area, Asian Russia. A, juvenile male I, lateral view; B, postabdomen of juvenile male I; C, distal portion of limb I of juvenile male I, inner view; D, juvenile male II, general view; E, postabdomen of juvenile male II; F, limb I of juvenile male II, inner view; G, adult male (third instar), general view; H, anteroventral portion of valve of adult male, inner view; I, mucro of adult male, inner view; J, postabdomen of adult male; K, distal portion of adult male; L, limb I of adult male, inner view; M, tip of copulatory hook of adult male. Scale bars: 100 μm.

Material

'Bosmina coregoni sp. str.': Russia (European). Lake Khotavets, Darwin National Reserve, Vologda Area, collected on 3 October 1994 by V. I. Lazareva, AAK 2004–005; a small un-named lake near Petrokrepost train station, Leningrad Area, collected on 16 September 2004 by A. A. Kotov, AAK M-034.

'Bosmina coregoni kessleri': Russia (European). Lake Glubokoe, Ruza District, Moscow Area, collected in September–December of 1994–1998 by A. A. Kotov, AAK 2004-040-043.

'Bosmina longispina' (including 'obtusirostris' and 'lacustris' morphs): Norway. MjIIIsa, east side,

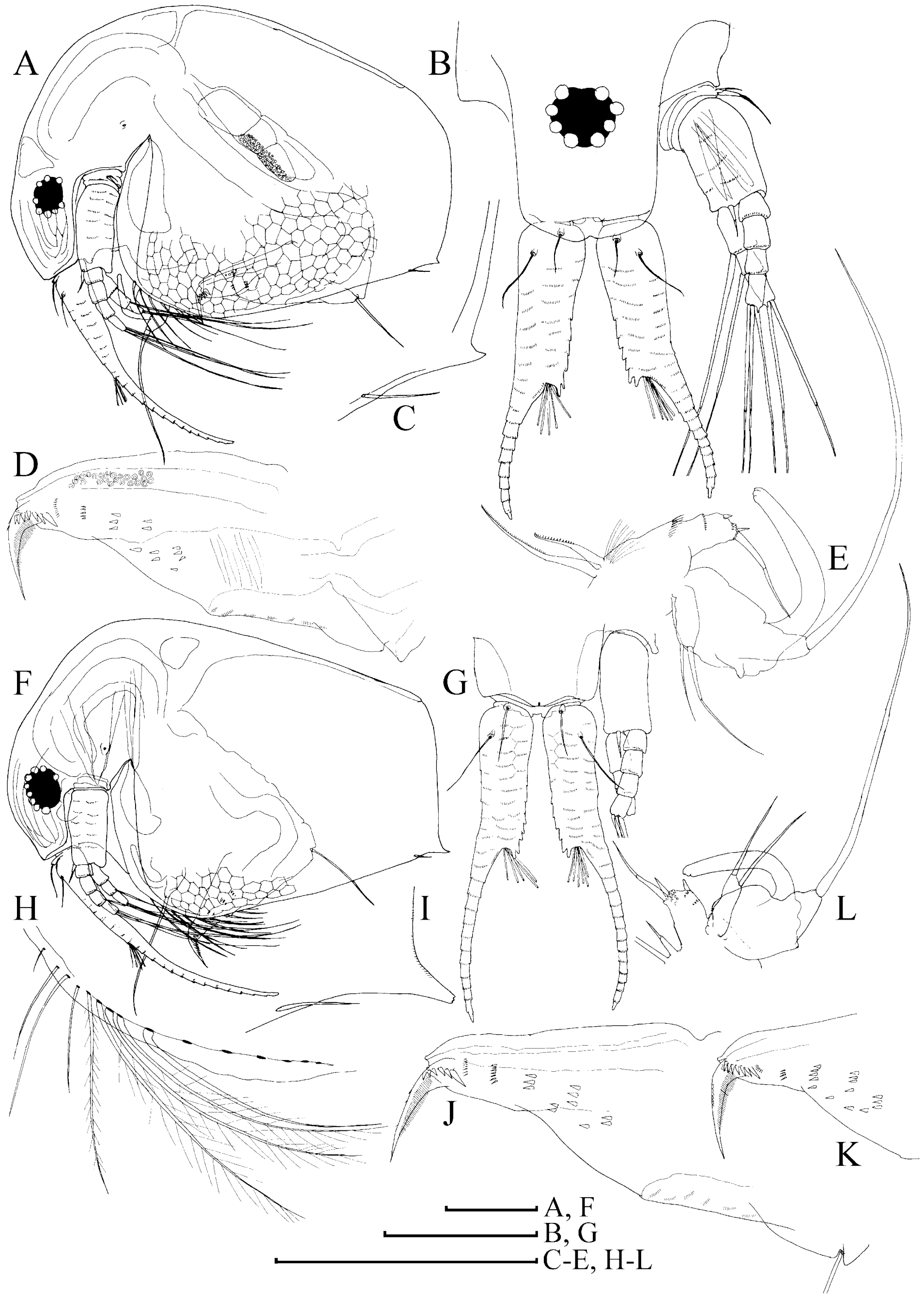

Figure 19. Adult male of *Bosmina* (*Eubosmina*) cf. *crassicornis*: from Bratsk Water Reservoir, Irkutsk Area, Asian Russia (A–E). Adult male of *Bosmina* (*Eubosmina*) cf. *kessleri*: from Lake Glubokoe, Ruza District, Moscow Area, European Russia (F–L). A, general view; B, head in anterior view; C, mucro; D, postabdomen; E, distal portion of limb I; F, general view; G, head in anterior view; H, setae at anteroventral portion of valve; I, mucro; J, K, postabdomen; L, distal portion of limb I. Scale bars: 100 μm.

collected on 8 August 1965 by D. G. Frey, DGF 1632; Gelggojervi, Troms, collected on 27 August 2004 by D. J. Taylor & S. Ishida, AAK M-456.

Iceland. A small lake near Asbyrgi, Northern Iceland, collected on 19 August 1977 by N. N. Smirnov (see Kotov, 1996).

Ireland. Lough Leane, collected on 7 October 1985 by D. G. Frey, DGF 7628.

Finland. Kilpisjärvi, Lapin Lääni, collected on 27 August 2004 by D. J. Taylor & S. Ishida, AAK M-457.

Russia (European). Vodoprovodnoe Lake, Verkhnee Yershovskoe Lake, and a small un-named lake, territory of the Belomorskaya Biological Station of Moscow State University, Murmansk Area, collected in August 1995 by A. Yu. Sinev, AAK 2003-006, AAK 2004-018-020; Un-named lake 2, Rybachiy Peninsula, Murmansk Area, collected in August 2003 by Y. Galimov, AAK M-394; Lake Kumitchevo, Pinega Region, Arkhangelsk Area, collected on 15 August 2004 by N. Bayanov, NMK 2491; several bog lakes near Petrozavodsk, Karelian Autonomous Republic, collected from July 1970 to July 1971 by Z. I. Fillimonova, AAK 2004-026, NNS 1997-159-160; Ladoga Lake immediately at the source of the Neva River, Leningrad Area, collected on 16 September 2004 by A. A. Kotov, AAK M-031; Rybinsk man-made lake at Mologa station, Yaroslavl Area, collected on 18 October 1994, AAK 2004-021; Lake Dubrovskoje, Darvin Reserve, Vologda Area, collected in September 1994 by V. I. Lazareva, AAK 2004-023.

Russia (Asian). Several lakes in tundra, Tareya, Taimyr Autonomous Area, collected in July–August 1969 by Yu. I. Chernov, AAK 1999-051, AAK 2004-003, AAK 2004-004; a small lake in tundra, Talnakh, Taimyr Autonomous Area, collected on 11 August 1974, AAK 2004-016; Teletskoye Lake near Iogatch, Altai Territory, collected on 1 September 2002 by O. S. Burmistrova, NMK 2516; Lake Leprindo, Chita Area, collected on 27 August 1998 by N. G. Sheveleva, AAK 2004-016.

'Bosmina crassicornis': Russia (Asian). Rybinsk Water Reservoir, Yaroslavl Area, collected on 25 September 2007 by V. I. Lazareva, NMK 2685; Bratsk Water Reservoir, Irkutsk Area, collected on 10 November 1998 by N. G. Sheveleva, AAK 2004-017.

Diagnosis of adult male (Figs 17A–D, 18G–M, 19): In all studied morphotypes, the male characters are more 'generalized' compared with female characters, i.e. (1) body less deep, lacking a hump; (2) if antenna I is very long in the female (*B. coregoni gibbera*), it is comparatively shorter in the male; by contrast, if the female antenna I is short (*B. crassicornis*), it is comparatively longer in the male; (3) if mucro is very long in the female (*B. longispina*), it is comparatively shorter in the male; by contrast, if mucro is short (*B. coregoni kessleri*) in the female, it is longer in males. In *B. crassicornis* the female has no mucro, but there is a small mucro in its male. As a result, males of all morphotypes are remarkably more similar in general appearance than are the females.

Dorsum from regularly arched from anteriormost point to posterodorsal angle (*B. crassicornis*) to concave (*B. longispina* and *B. kessleri*), posterior margin of valves high. Head with distinct anteroventral angle, anterior portion of rostrum straight or slightly concave, ocular dome absent or ill-defined. In anterior view, rostrum truncated. Lateral head pore at a great distance from lateral edge of head shield. Mucro of different length, seta kurzi short, a series of long setae at anteroventral portion of valve. Postabdomen elongated, with its ventral margin in general straight or slightly convex, preanal margin relatively short, with a slight depression, dorsodistal angle well-defined, anal margin aslant truncated. Postanal angle well-defined, postanal portion of postabdomen slightly narrowing towards distal end, blunt distally, where a single gonopore opens. There are several groups of relatively robust denticles on the postanal and middle portion of the postabdomen. Postabdominal claw long, bent, regularly narrowing distally, distal pecten as a row of numerous, long, fine setules, proximal pecten with several (normally between six and ten) relatively large teeth. Antenna I regularly bent in lateral view; in anterior view, its basal portion thick, with straight or slightly concave, serrated inner margin, wereas distal half thin, regularly bent and narrowing distally. Sensory seta long and male seta long: located on a marked pedestal. Antenna II with two short sensory setae on coxal part. Distal sensory seta short, not reaching distal end of basal segment of endopod. Limb I bears idl with an inflated basal portion, without a hillock basally, and with a conical distal portion terminating as a long, naked seta. Copulatory hook large and thin, not recurved to a parallel position with the idl, tip of hook with two ridges. Subdistal lobe large, with a long seta 1, a rudimentary setae near it, and another rudimentary seta at a distance from the two aforementioned setae; seta 2 very short.

Postembryonic development: Juvenile male I (Fig. 18A–C) body shape similar to juvenile female I, and with posterior dorsal head pore present. Postabdomen with slightly convex preanal margin and slightly inflated ventral portion, a rudimentary gonoduct terminating far from the level of the anus, although the gonopore is absent. Postabdominal claw long, with distal and proximal pectens on female type, pre-claw pecten present. Antenna I fused with rostrum, only a pair of long sensory setae on rostrum. Antenna II with two short sensory setae on coxal portion, whereas there is no rudiment of anterior sensory seta. Limb I with idl small, subovoid, with a single rudimentary seta, copulatory hook short and thick, subdistal lobe not projected, with a single seta 1 (as in female).

Juvenile male II (Figs 17E, F, 18D–F) body shape as in juvenile female II. Postabdomen with straight to slightly concave preanal margin, ventral side inflated, rudimentary gonoduct reaches the level of the anus. Postabdominal claw long, distal pecten with fine setules, proximal pecten with a few slender spinules, pre-claw pecten with a few spinules. Antenna I fused with rostrum, which has a long sensory seta and a short male seta at the same level. Antenna II with two short sensory setae on coxal portion, and with a rudiment of a distal anterior seta. Limb I with idl large (but smaller than in adult), its distal portion conical, with a short seta and a second rudimentary seta; copulatory hook robust, with blunt tip bearing small denticles, subdistal lobe small, with two setae (1 and 1′) of somewhat different lengths, and a small rudiment of the third seta.

Comments. The species status of several of the studied populations is controversial. No specific primary and secondary sexual traits were found in males of the aforementioned 'species'. It is clear that several forms are very closely related, and the paleolimnology and genetic distances suggest postglacial origins (Haney & Taylor, 2003). Detailed genetic analysis of coexisting morphs and perhaps breeding studies are needed to further assess the species status of this relatively young group.

De Melo & Hebert (1994) proposed that *B. maritima* from North America is a valid species that is genetically distant from other *Eubosmina*. The presence of this species in North America seems to be a consequence of its introduction from Europe (Haney & Taylor, 2003). It is unknown if the North American *B. maritima* re-evolved from invading *B.* (*E.*) cf. *coregoni* in North America, or if it represents an independent introduction of a Eurasian morphotype. Presently there are no morphological characters to distinguish saline populations (*B. maritima*) from *B. longispina*.

Nearctic '*Bosmina* cf. *longispina*'
Figure 20
Material: A pond in Nome, Alaska, USA, collected on 26 September 2003 by D. J. Taylor, AAK 2004-052.

Differences of adult male: Male of Nearctic '*B. longispina*' differ from European eubosminids in having: (1) a larger distance between base of antenna I and anteroventral angle of head; (2) very large compound eye; (3) an especially thin distal portion of idl; (4) a depression on the tip of the copulatory hook.

Comments: Our note on the difference of Beringian Nearctic males from the Palaearctic males is based on only a single studied Nearctic population. But, there is a chance that we found some traits that are important for the eubosminid systematics beyond female characters. It is possible that the Nearctic '*B. longispina*' belongs to another, undescribed species, as was proposed by Haney & Taylor (2003). If Beringian and Atlantic Nearctic species belong to a single species, then this species must be named *Bosmina* (*Eubosmina*) *striata* Herrick, 1882.

Bosmina (Eubosmina) tanakai sp. nov.,

Figures 21–24
Bosmina coregoni seligoi forma Rühe in Uéno, 1933: 309–310; pl. 10, figs 9, 10.
Bosmina coregoni obtusirostris Sars in Uéno, 1938b: 285.
Bosmina (*Eubosmina*) *longispina* Leydig in Tanaka, 2000: 120–123; figs 10, 11.
?*Bosmina coregoni* Baird in Uéno, 1938a: 15–18, figs 20–33; Uéno, 1968: fig. 1J.
Not *Bosmina amemiyai* Brehm, 1925: 271–273; text – fig.
Not *Bosmina coregoni yezoensis* Uéno, 1933: 310; pl. 10, figs 11 and 12.

Etymology: This species is dedicated to Prof. S. Tanaka, a Japanese cladocerologist, who determined this species as *B. longispina*, but made the first adequate drawings of males of Japanese *Eubosmina*, and remarked on their differences from European representatives (Tanaka, 2000).

Type locality: Ichiyanagi Numa Pond (40.912434°N, 141.365243°E), Rokkasho Village, Aomori Prefecture, Japan. The type series was collected on 29 November 2006 by S. Ishida.

Type material
Holotype: Ephippial female in 90% alcohol, MGU Ml 65. Label of the holotype: '*Bosmina tanakai* sp. nov., 1 eph. fem. from Ichiyanagi Numa Pond, Aomori Prefecture, Japan, collected on 28 November 2006 by S. Ishida, HOLOTYPE'.

Allotype: Adult male, MGU Ml 66.

Paratypes: 30 parthenogenetic and ephippial females, MGU Ml 67; ten adult males, MGU Ml 68; 30 females and ten adult males, AAK M-299; 30 females, NCMT-Cr 17918; 30 males, NCMT-Cr 17917.

Other material studied (all from Japan): Lake Akan, Kushiro, Hokkaido Prefecture, collected in November 2006 by S. Ishida; Lake Touro, Shibecha, Hokkaido Prefecture, collected in November 2006 by S. Ishida; Lake Kussharo, Teshikaga, Hokkaido Prefecture, collected in November 2006 by S. Ishida; Konuma Pond, Nanae, Hokkaido Prefecture, collected in November 2006 by S. Ishida.

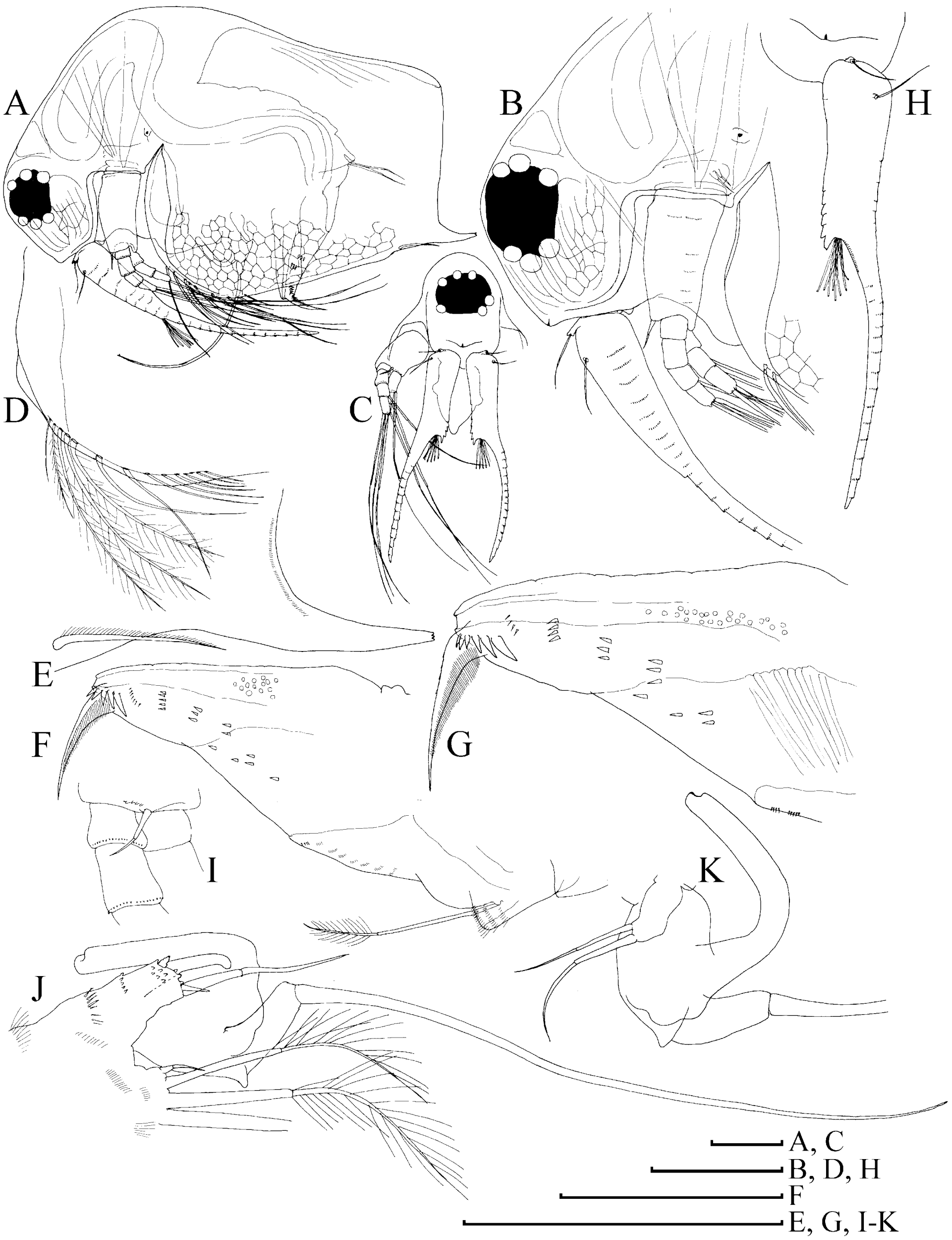

Figure 20. *Bosmina* (*Eubosmina*) cf. *longispina*: adult male from a pond in Nome, Alaska, USA. A, lateral view; B, C, head in lateral and anterior view; D, setae at anteroventral portion of valve, inner view; E, mucro, inner view; F, G, postabdomen; H, antenna I, anterior view; I, proximal portion of basal segment of antenna II; J, K, distal portion of limb I in inner (anterior) and external (posterior) view. Scale bars: 100 μm.

Diagnosis: Adult females without ocular dome, anterior surface of head almost flat, in lateral view, antenna I looks like a continuation of anterior head margin. Adult male with head lacking ocular dome, frontal head pore as a short longitudinal split, opens on a special tubercle on ventral surface of head, its postabdomen relatively massive, postanal angle absent, postabdominal claw with two or three robust proximal denticles.

Description

Adult parthenogenetic female (Figs 21, 22): Body short and wide in lateral view, dorsal margin in general regularly curved from distalmost extremity to posterodorsal angle, posterior margin straight, with height about half of body height, ventral margin almost straight, with a very shallow depression anterior to mucro. Reticulation very obscure, both on head and on valves. Head with or without traces of an

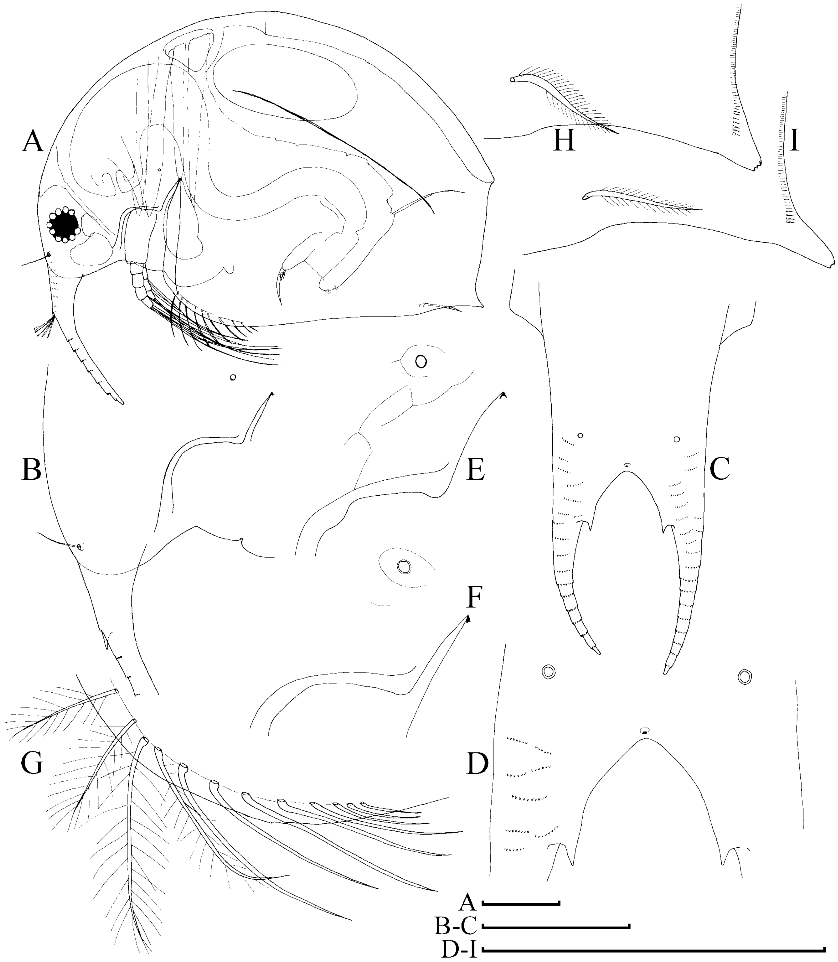

Figure 21. ***Bosmina*** **(*Eubosmina*)** ***tanakai*** **sp. nov.**: ephippial female from Ichiyanagi Numa Pond, Aomori Prefecture, Japan. A, lateral view; B, head, lateral view; C, D, head, anterior view; E, F, region of lateral head pore; G, setae at anteroventral portion of valve; H, I, mucro, inner view. Scale bars: 100 μm.

ocular dome, preocular depression absent, anterior surface of head almost flat, in lateral view, antenna I looks like a continuation of anterior head margin. Frontal head pore as a short transverse split, with specially chitinized dorsal side, located closely to ventral margin of head, significantly ventral to level of antennular sensory setae. Lateral head pore small, located at a great distance from ventral margin of head shield, somewhat above level of the mandibular articulation. Compound eye of moderate size. Labrum as a fleshy appendage, distal labral plate small. Ventral valve margin with a series of stout setae, the bases of which are located on its internal surface, with the more anterior setae supplied with long setules. Seta kurzi with fine, long setules; mucro short in large adults, without incision on ventral side and with tip supplied with minute tubercles. On inner side of posterior margin, a continuous row of setules, with the ventralmost setules of this row located on the mucro, and somewhat stronger than the rest.

Postabdomen strongly compressed laterally, with width approximately equal along all of its length, and with ventral margin straight. Preanal margin long, slightly concave, with a distal group of setules larger than other setules on dorsal side of postabdomen. Distal (anal) margin nearly directly truncated, posterodorsal angle as a distinct projection. Postanal portion as a cylindrical projection bearing paired postabdominal claws. Each claw regularly bent, with three denticles on convex (ventral) margin and two pectens on concave (dorsal) margin, distal pecten consists of numerous fine setules, whereas proximal pecten consists of between five and seven rather strong, sparsely located teeth, no pre-claw pecten was found. Postabdominal seta shorter than preanal margin.

Antenna I fused with rostrum, rather short. Antennular (frontal) sensory seta located on rostrum, closer to compound eye than to its tip. Pre-aesthetasc portion wide, regularly narrowing in anterior view, an

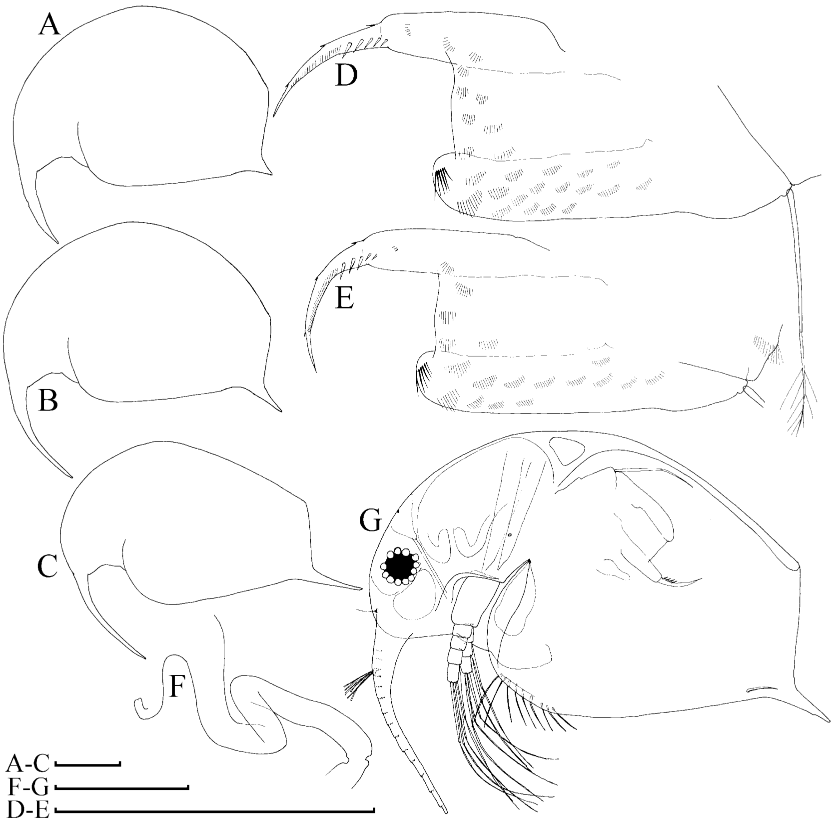

Figure 22. ***Bosmina* (*Eubosmina*) *tanakai* sp. nov.**: female from Ichiyanagi Numa Pond, Aomori Prefecture, Japan (A, D–G), and from Konuma (B) and Kussharo (C), Hokkaido Prefecture, Japan. A–C, body outline of large adult; D, E, postabdonem of large adult; F, midgut with loops of an atypical specimen; G, juvenile female. Scale bars: 100 μm.

internal spine near a flat site of aesthetasc bases. Nine aesthetascs delicate, slightly differing in size, longest being about half of the pre-aesthetasc-free portion. Post-aesthetasc portion directed ventrally and somewhat posteriorly, slightly curved in lateral and anterior view. Both portions supplied with a crossing series of fine denticles.

Antenna II and thoracic limbs as for the genus.

An atypical specimen with midgut supplied with loops, more characteristic of the Chydoridae (Smirnov, 1971), was found in the type locality (Fig. 22F). It is interesting that previously Uéno (1927) found an atypical *B.* (*B.*) *longirostris* with a mudgut loop.

Variability: In the type locality of *B.* (*E.*) *tanakai sp. nov*., the adult female has relatively short antenna I and mucro (Figs 21A, H, I, 22A), but these were significantly longer in other populations studied (Fig. 22B, C). Tanaka (2000) also described '*B. longispina*' from Japan with an even longer antenna I and mucro. In some of our populations, adult females had more elongated bodies and their antennas I projected more strongly backwards, as compared with the population from the type locality (Fig. 22C), these populations are superficially similar to European '*Bosmina reflexa* Seligo, 1900'.

Juvenile female (Fig. 22G): Body more elongated in lateral view. Mucro longer than in adults, but also without denticles at ventral margin. Antenna I longer, strongly curved in lateral and anterior view.

Ephippial female (Fig. 21A): Differs from parthenogenetic female in having a longitudinal fold on dorsal part of valves, and a median fold on top of dorsum.

Adult male (Figs 23, 24): Body elongated, dorsum regularly convex from anteriormost extremity to posterodorsal angle, posterior margin straight, of moderate height. Head with well-defined, but not projected, anteroventral angle; no traces of ocular dome. Frontal head pore as a short longitudinal split: opens on a special tubercle on ventral surface of head. Lateral head pore at a long distance from lateral edge of head shield, relatively close to mandibular articulation. Mucro short, with small denticles in its inner side,

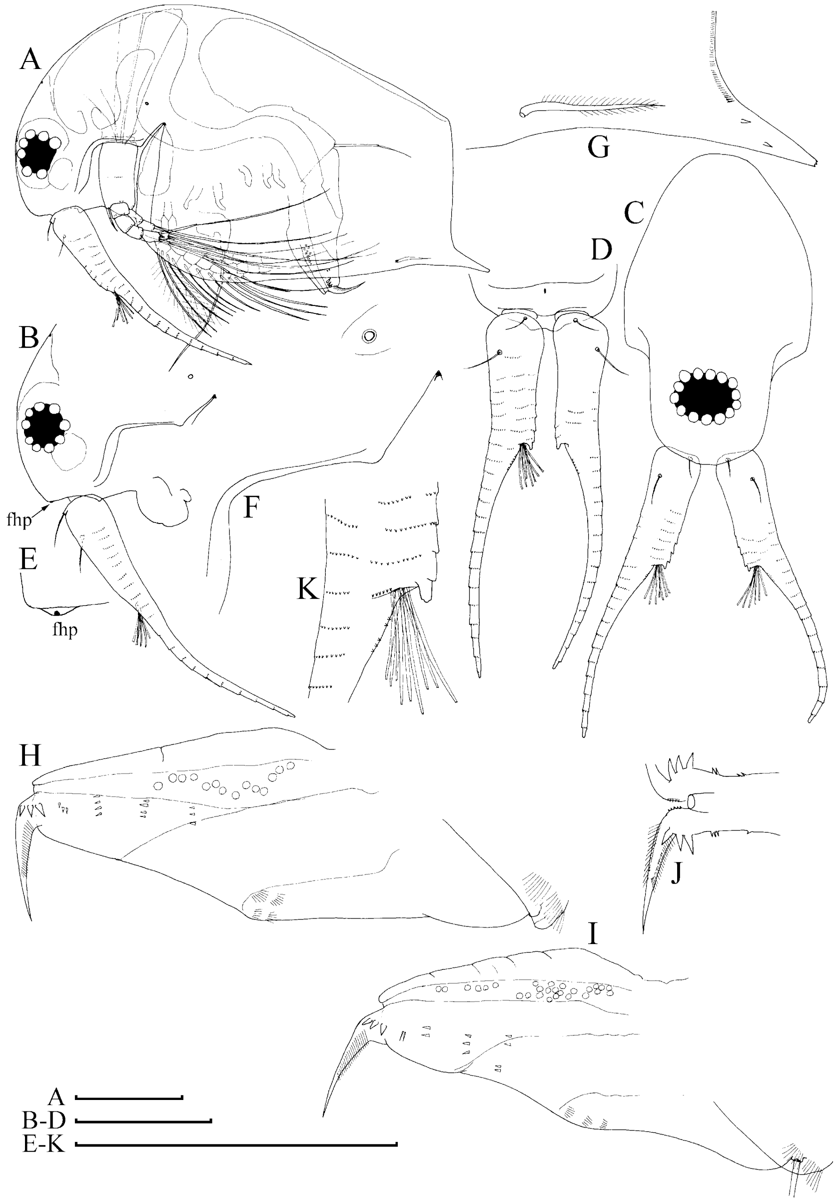

Figure 23. ***Bosmina* (*Eubosmina*) *tanakai* sp. nov.**: adult male from Ichiyanagi Numa Pond, Aomori Prefecture, Japan. A, general view; B, head, lateral view; C, D, head, anterior view; E, frontal head pore; F, region of lateral head pore; G, mucro, inner view; H, I, postabdomen, lateral view; J, distal end of postabdomen, ventral view; K, aesthetasc region of antenna I. Scale bars: 100 μm.

and seta kurzi setulated; a series of long setae at anteroventral portion of valve. Postabdomen relatively massive, its ventral margin straight, preanal margin slightly to moderately concave, dorsodistal angle slightly projected, anal margin slightly concave, postanal angle absent. Postanal portion of postabdomen short, conical, blunt distally, with singular gonopore on distal end. Postabdominal claw long, slender, without a distal spinule, distal pecten as a series of fine setules, proximal pecten with two or three robust proximal denticles. Antenna I slightly S-shaped in lateral view, with a wide pre-aesthetasc portion, particularly inflated near joint with rostrum. Sensory seta long, male seta short, located on a minute pedestal. Antenna II with two short sensory setae on coxal part. Distal anterior seta relatively short, not reaching distal end of basal segment of endopod. Limb I idl with a low hillock on basal portion, distal portion of which relatively short, terminating as a long, naked seta. Copulatory hook

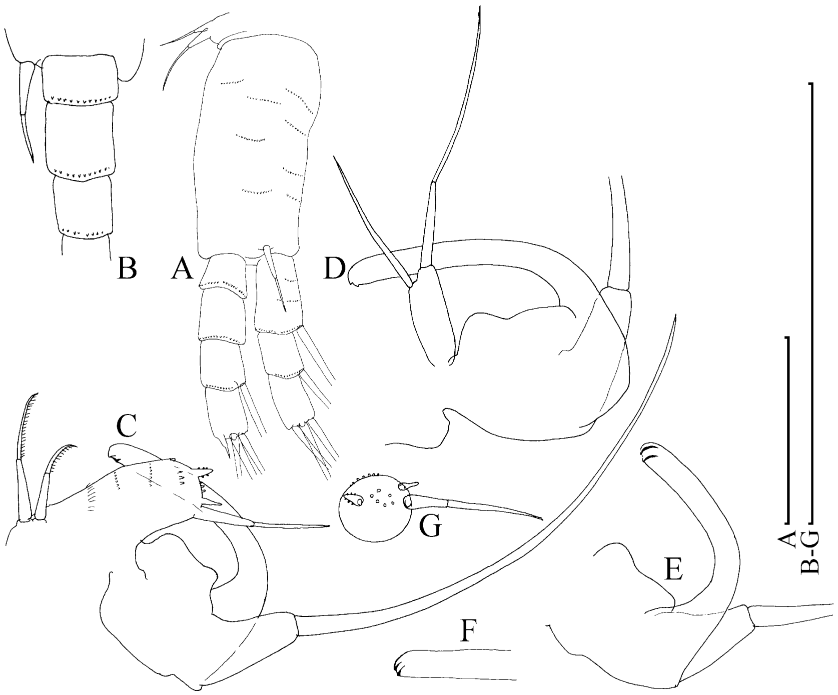

Figure 24. ***Bosmina*** **(*Eubosmina*)** ***tanakai*** **sp. nov.**: adult male from Ichiyanagi Numa Pond, Aomori Prefecture, Japan. A, antenna II; B, distal anterior seta; C–E, limb I; F, tip of copulatory hook; G, subdistal lobe in distal view. Scale bars: 100 µm.

relatively large and thick, not recurved to a parallel position with the idl, and with tip of hook blunt, with two ridges. Subdistal lobe, seta 1, and seta 2 as in *B. longispina*.

Juvenile males: Not found, because all studied gamogenetic populations were greatly advanced in a gamogenetic mode of reproduction, containing only adults.

Size: Holotype 615-µm long, females 370–650-µm long; allotype 510-µm long, adult males 465–540-µm long. According to Tanaka (2000), female 400–1700-µm long, male 300–600-µm long, but the maximum size of the female seems to be overestimated.

Differential diagnosis: At this time, the morphological differentiation of parthenogenetic females of *B.* (*E.*) *tanakai sp. nov*. and other *Eubosmina* species is difficult, and needs further investigation. At the same time, males of *B.* (*E.*) *tanakai sp. nov*. are unique for the subgenus in having a short postanal portion without postanal angle, and with only about three teeth in the proximal pecten on the postabdominal claw.

Distribution: According to recent information, this species is apparently present in Hokkaido, Eastern Honshu, and, most probably, in the Kurile Islands and Sakhalin Island (Uéno, 1938a, b). In numerous samples from the Far East of Russia, we found only members of the subgenera *Sinobosmina* (see above) and *Bosmina* sp. str.: no eubosminids were found. It is unlikely that the species range extends to eastern Beringia, because Haney & Taylor (2003) only detected a Nearctic clade in the extreme west of Alaska.

Comments: Three species of *Bosmina* were described from Japan: *B. japonica* Poppe & Richard, 1890, *B. amemiyai* and *B. coregoni yezoensis*.

Our examination of Richard's samples demonstrated that Poppe & Richard (1890) described a representative of *B. longirostris* group, an apparent member of *Bosmina s.s.*, *B. amemiyai* Brehm, 1925, is an apparent member of the subgenus *Sinobosmina*, namely a junior synonym of *B.* (*S.*) *fatalis cyanopotamia*. Tanaka (2000) listed *B. yezoensis* Uéno (1933) as a junior synonym of *B. longispina*, placing it in the *Eubosmina*, but this opinion seems to be incorrect. Uéno (1933) illustrated *B.* (*S.*) *fatalis*, a *Sinobosmina* representative. An analogous point of view was presented by Kořínek (1971). No valid *Eubosmina*-like

Table 2. Descriptions of the morphological characters of adult males used in cladistic analysis

1. Ocular dome: absent (0); present (1).
2. Gonopode: subdistal (0); distal (1).
3. Postabdomen: not tapering distally (1).
4. Postabdomen: with massive postanal portion (0); with distal portion as short tube (1); with distal portion as a long tube (2).
5. Distal part of tapering postabdomen: massive (0); slender (1).
6. Postabdomen ventral margin: inflated (1).
7. Postabdomen distal part: not inflated (0); strongly inflated with wide gonopore (1).
8. Anus: not in anal depression (0); within a deep depression (1).
9. Preanal margin: without a deep depression (0); with a deep depression (1).
10. On preanal margin: setules of normal size (0); only very small setules (1).
11. Denticles on sides of postabdomen: absent (0); robust, in short rows (1); with a series along ventral margin (2).
12. Postabdominal claw: long (0); shortened (1).
13. Proximal pecten: located on postabdominal claw (1); removed from claw to postanal part (1); as a cown of strong teeth at claw base (2).
14. Denticles of basal pecten on claw: small (0); very large (1).
15. Distal pecten on claw: with short, fine setules (0); with very long setules (1); with robust denticles (2).
16. Postabdominal claw: without a terminal spinule (0); with a terminal spinule (1).
17. Antenna I: with relatively thin pre-aesthetasc portion (0); with specially widened pre-aesthetasc portion (1).
18. Coxal sensory setae on antenna II: short (0); long (1).
19. Hook on limb I: large, recurved to a parallel position with inner distal lobe of limb I (0); small, not recurved (1).
20. Tip of copulatory hook on limb I: blunt (0); as a sharp spinule (1); abrupted (2).
21. Tip of hook on limb I: with setules (0), without setules (1).
22. On inner distal lobe of limb I: projection in basal portion very small or absent (0); strong projection present (1).
23. On subdistal lobe of limb I: third seta rudimentary (1); third seta rudimentary and far from two others (2).
24. On limb I: seta 2 relatively long (0); seta 2 very short (1).

species exists from Japan, China, or from the Far East of Russia, so the Japanese *Eubosmina* represents a new species.

Tanaka (2000) noted that the proximal pecten of Japanese '*Eubosmina*' tapers in length compared with the more even length of other *Eubosmina*; so, he understood the unique status of Japanese populations. *Bosmina* (*E.*) *tanakai* sp. nov. was determined by Uéno (1933, 1938a, b) to be yet another variety of *B.* (*E.*) *coregoni*. However, genetic study (see below) has revealed that each Japanese *Eubosmina* population belongs to a single closely related genetic lineage, consistent with a single species. Most probably, the very different morphotypes of parthenogenetic females described by Uéno (1938a, b) also belong to the same species.

We had samples from both Lake Kawaguchi (type locality of *B. amemiyai*) and Lake Tôro-ko (type locality of *B. yezoensis*), but again, both of these taxa are apparently members of the subgenus *Sinobosmina*. Recently, both of these water bodies were occupied with *B.* (*E.*) *tanakai sp. nov.*, which differs substantially in morphology from *Sinobosmina* species. The species composition in these lakes has apparently changed, probably as a result of anthropogenic effects. Species replacement of this nature has been demonstrated by Tanaka (2000) for other Japanese water bodies. Paleolimnological studies would help to sort out the species transitions in Japanese lakes during the Anthropocene.

CLADISTIC MORPHOLOGICAL PHYLOGENY

A description of the characters analysed is given in Table 2; the data matrix is given in Table 3. Unfortunately, most of the male characters analysed are missing or are too variable in representatives of the closest family Chydoridae, a potential outgroup. The other potential outgroup, *Bosminopsis*, is also a very distant relative of *Bosmina* (Taylor *et al.*, 2002), and is perhaps not even a member of the Bosminidae (see discussion in Kotov, 1997b). So, we reconstructed a hypothetical proto-male of *Bosmina* (with all characters in the plesiomorphic state) as an artificial outgroup.

Cladistic analysis with the artificial ancestor as outgroup, and all characters unordered, yielded a single most parsimonious tree (tree length, TL = 31; consistency index, CI = 0.968; retention index, RI = 0.988). A bootstrap test resulted in a tree with the same topology (Fig. 25). The genus *Bosmina* apparently consists of two main, well-supported

Table 3. Data matrix of 24 morphological characters used in the cladistic analysis

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
longirostris	1	1	0	2	0	0	0	1	1	0	2	1	1	0	2	1	0	1	1	1	1	0	1	0
liederi	1	1	0	2	0	0	0	1	1	0	2	1	1	0	2	1	0	1	1	1	1	0	1	0
tripurae	1	1	0	1	0	0	0	0	0	0	9	1	1	0	2	1	0	9	0	0	0	0	1	0
fatalis	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	2	0	1	0	0
cf. *fatalis cyanomotamia*	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	2	0	1	0	0
meridionalis	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2	1
hagmanni	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2	1
chilensis	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2	1
huaronensis	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2	1
oriens	9	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2	1
'longispina' (Europe)	0	1	1	0	1	0	0	0	0	1	1	0	2	1	1	0	1	0	0	0	0	0	2	1
coregoni	0	1	1	0	1	0	0	0	0	1	1	0	2	1	1	0	1	0	0	0	0	0	2	1
'crassicornis'	0	1	1	0	1	0	0	0	0	1	1	0	2	1	1	0	1	0	0	0	0	0	2	1
'longispina' (Alaska)	0	1	1	0	1	0	0	0	0	1	1	0	2	1	1	0	1	0	0	0	0	0	2	1
***tanakai* sp. nov.**	0	1	1	0	0	0	0	0	0	1	1	0	2	1	1	0	1	0	0	0	0	0	2	1
Ancestor	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

groups of subgenera, the *Bosmina* sp. str. + *Sinobosmina* versus the *Liederobosmina* + *Lunobosmina* + *Eubosmina*.

Recently accepted subgenera are also well supported. But, *B.* (*B.*) *tripurae* and *B.* (*B.*) *liederi* are both members of *Bosmina* sp. str. instead of *Sinobosmina*. The grouping of *Lunobosmina* with *Liederobosmina* has low support, but is in agreement with the nuclear DNA (see below). *Bosmina* (*E.*) *tanakai* sp. nov. is a basal member of the *Eubosmina* clade.

DNA SEQUENCE BASED PHYLOGENIES

Details about the regions amplified and the gene boundaries are given in Taylor *et al.* (2002). Gblocks culled the mtDNA alignment from 482 sites to 446 sites, and the nrDNA alignment from 1200 to 1131 sites. Hierarchical model fitting indicated that the transversion model with invariable sites and the gamma estimate of among-site rate variation (TVM + I + G) had the best fit for the mtDNA data, and the generalized time reversible model with an invariable sites parameter (GTR + I) had the best fit for the nuclear rDNA. The TVM has four base frequency parameters, four transversion substitution parameters, and one transition parameter. The GTR model has six substitution parameters and four base frequency parameters.

The mtDNA trees and nuclear rDNA trees (Figs 26, 27) reveal similar topologies to the morphological tree, with the subgenera being well supported (more specimens of *Sinobosmina* are needed to confirm their genetic monophyly). The *Liederobosmina*/*Lunobosmina* clade is split up in the mtDNA tree, but this placement is weakly supported. Another difference between the mtDNA tree and the identical morphology/nrDNA topology is the placement of *Sinobosmina*. In the mtDNA tree, *Sinobosmina* is placed within the *Bosmina*, but with the other data, *Sinobosmina* is placed as a sister group to *Bosmina*. In all methods *B.* (*E.*) *tanakai sp. nov*. is a distant sister group (14% with mtDNA and 2.2% with nrDNA) to the other *Eubosmina*.

DISCUSSION

GENERAL COMMENTS ON THE GENUS PHYLOGENY

Our most novel phylogenetic findings are that a morphologically based tree, with several male characters, agrees well with the sequence-based trees, and that the *Eubosmina* from Japan form a distantly related sister group to the other Holarctic *Eubosmina*.

Burckhardt (1924) grouped *coregoni* + *fatalis* (= *Eubosmina* + *Sinobosmina*) versus *longirostris* (= *Bosmina* sp. str.). Subsequently it was accepted

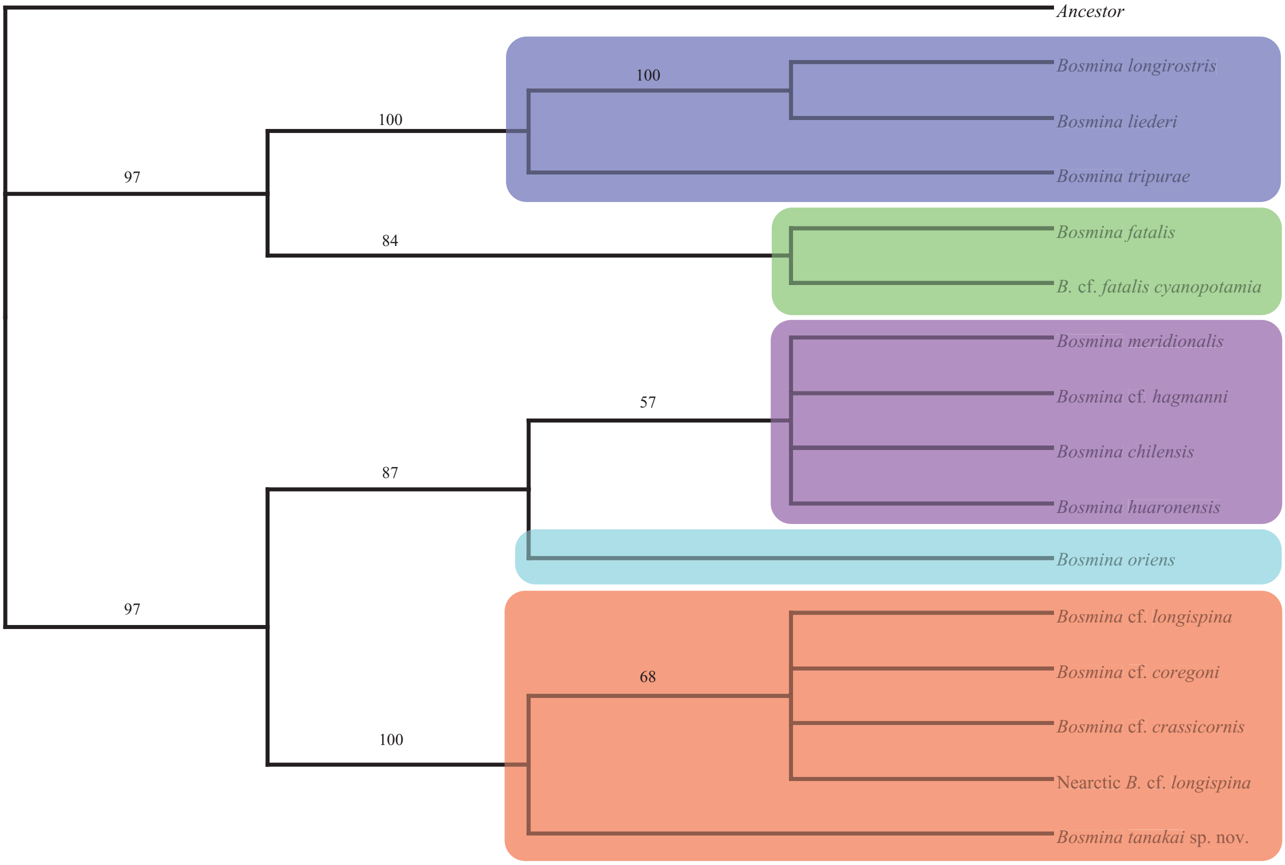

Figure 25. The 50% majority rule bootstrap tree based on the maximum parsimony analysis of morphological characters for bosminids. The numbers above the branches indicate clade support estimated by nonparametric bootstrapping. The boxes indicate the subgenera (from top to bottom; subgenera are indicated by coloured boxes in the online version of this article) *Bosmina* (blue), *Sinobosmina* (green), *Liederobosmina* (purple), *Lunobosmina* (turquoise), and *Eubosmina* (red).

that *B.* (*S.*) *fatalis* was an 'intermediate' taxon between *B. (B.) longirostris* (*Bosmina* sp. str.) and *B.* (*E.*) cf. *coregoni* (Goulden & Frey, 1963; Uéno, 1968). But, Lieder (1982, 1983a, b) said that *Eubosmina* was a sister group of *Neobosmina* (now *Liederobosmina*), whereas *Bosmina* sp. str. was an 'archaic type'.

According to our cladisic analysis, the genus *Bosmina* is completely subdivided into two main branches: *Bosmina* sp. str. + *Sinobosmina* versus *Eubosmina* + *Liederobosmina* + *Lunobosmina*. This point of view agrees with the nuclear and mtDNA sequence based phylogenies. The differing placements of some of the long branches leading to *Sinobosmina*, *Liederobosmina*, and *Lunobosmina* in the mtDNA tree are either unsupported (a common result when comparing genes; Taylor & Piel, 2004) or are the result of an unidentified bias. Taylor *et al.* (2002) noted that the mtDNA tree topology of *Bosmina* was sensitive to the model used. Additional genes and samples of *Sinobosmina* may remedy the mtDNA problem. The nrDNA tree appears to be better at resolving the deeper branches than the mtDNA, which is a common pattern (Taylor *et al.*, 2002). We propose that the nrDNA/morphology tree represents the best-supported phylogenetic hypothesis for the group.

Lieder's (1983b) opinion on *B.* (*B.*) *longirostris* as an 'archaic' member of the genus is apparently incorrect. In contrast, the male of this species seems to be very advanced, having the maximum number of apomorphic characters among all of species of the genus. Also, female characters such as a longer rostrum (i.e. represented by more fused bases of antennae I), and a lateral head pore located maximally closer to the ventral margin of the head shield, are apparent apomorphies. In addition, the extreme success of *B.* (*B.*) *longirostris* in the Holarctic water bodies contradicts the idea of this species as an archaic bosminid.

Although we found clear differences between bosminid males, our re-evaluation of their morphology demonstrated that some previously proposed 'differences' were illusory. Kotov (1996) found sensory setae on the coxal portion of antenna II in

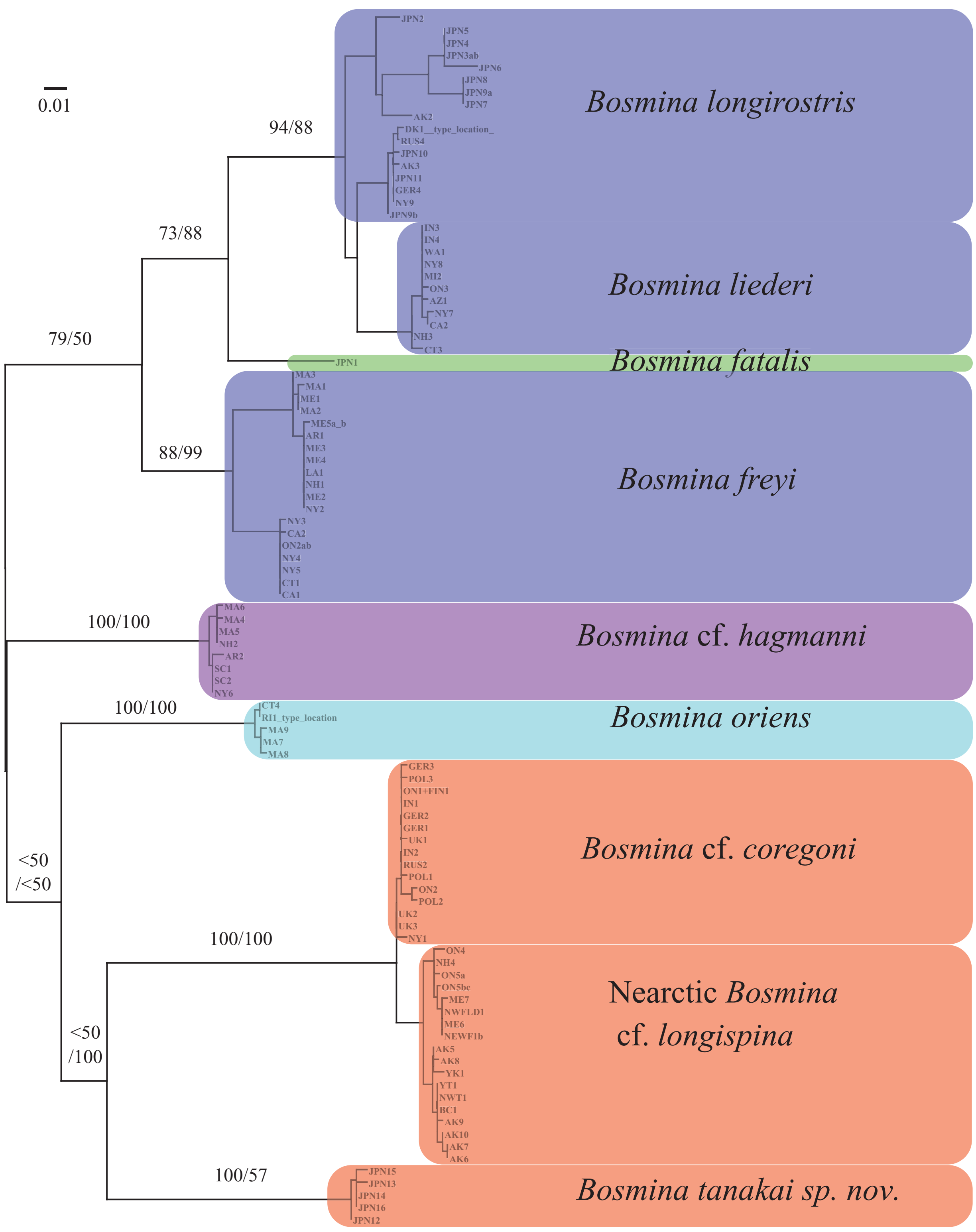

Figure 26. Maximum likelihood (ML) phylogram based on 16S rDNA mitochondrial sequences for bosminids. The numbers above the branches indicate clade support estimated by the nonparametric bootstrapping using neighbour-joining and ML methods. The colours indicate subgenera and the population abbreviations are given in Table 1 (lowercase letters indicate different specimens from the same site). The boxes indicate the subgenera (from top to bottom; see Fig. 25 for subgeneric colour scheme of boxes in the online version of this article) *Bosmina*, *Sinobosmina*, *Bosmina, Liederobosmina*, *Lunobosmina*, and *Eubosmina*.

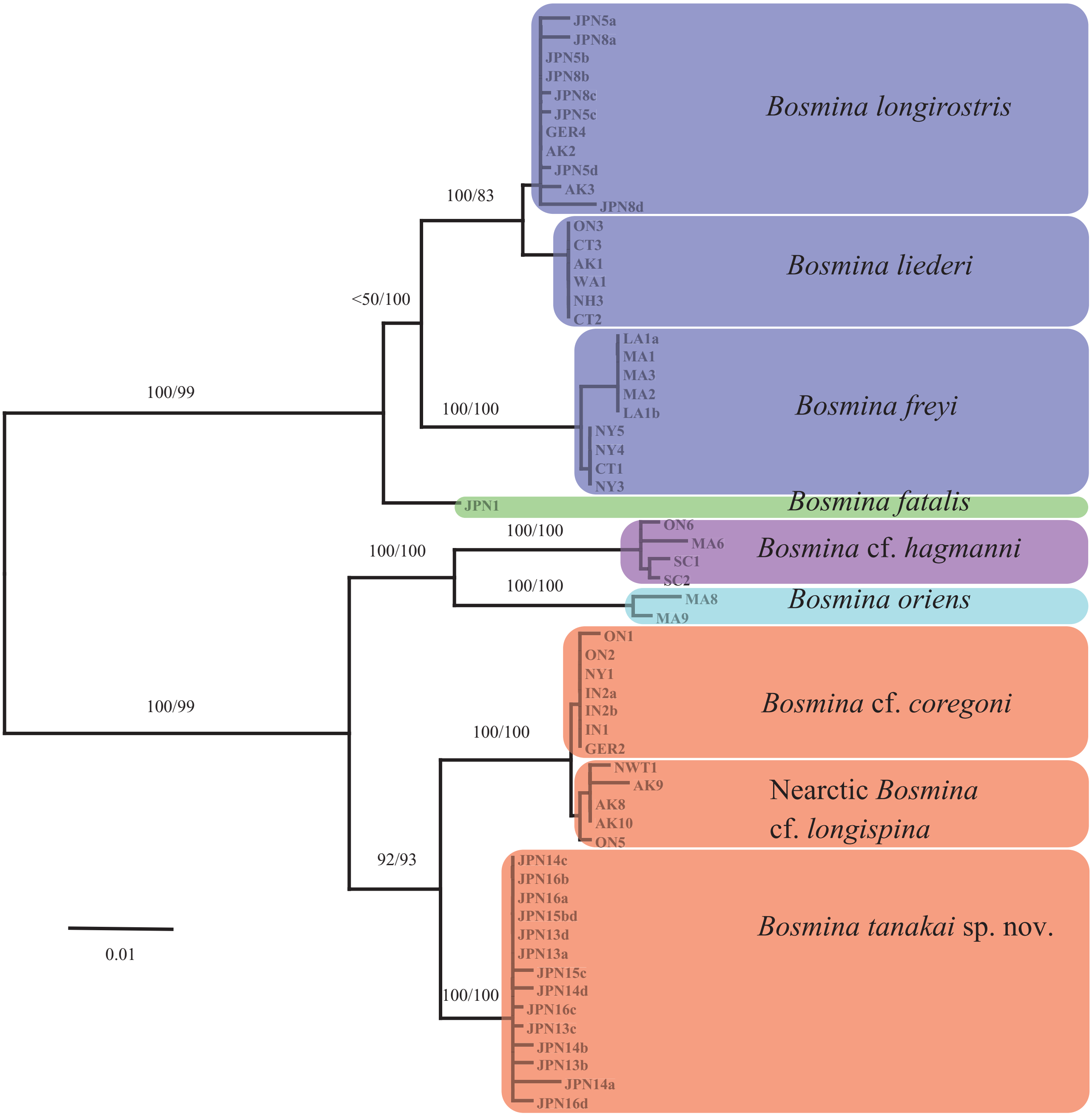

Figure 27. Maximum likelihood (ML) phylogram based on partial 18S rDNA, internal transcribed spacer (ITS)-1, ITS-2, and partial 28S rDNA nuclear sequences for bosminids. The numbers above the branches indicate clade support estimated by the nonparametric bootstrapping using neighbour-joining and ML methods. The population abbreviations are given in Table 1 (lowercase letters indicate different specimens from the same site). The boxes indicate the subgenera (from top to bottom; see Fig. 25 for subgeneric colour scheme of boxes in the online version of this article) *Bosmina*, *Sinobosmina*, *Liederobosmina*, *Lunobosmina*, and *Eubosmina*.

B. longispina, but had doubts of their presence in other subgenera, with reference to the illustrations of Paggi (1979). Now it is clear that the adult males of all of the subgenera have an identical set of sensory setae. Previous authors missed these setae in their descriptions and illustrations.

Earlier authors (Deevey & Deevey, 1971; Taylor *et al.*, 2002) regarded *Eubosmina* Seligo, 1900 as a separate genus. Indeed, two well-defined clades exist within the genus, and the designation of genera is arbitrary. But, morphological differences between *Bosmina* and '*Eubosmina*' are extremely small when compared with the differences between the genera of other anomopods. Parthenogenetic females of the *Bosmina* clade (*Bosmina* + *Sinobosmina*) and the '*Eubosmina*' clade (*Eubosmina* + *Lunobosmina* + *Liederobosmina*) seriously differ in the position of the lateral head pore only, whereas other characters are almost or exactly identical in the two clades, or, in contrast, are too variable within each clade to be regarded as a consistent character of generic rank. At the same time, females of different species from another dominant planktonic genus, *Daphnia*, frequently have a long list of morphological differences (Glagolev & Alonso, 1990; Ishida *et al.*, 2006).

The adult males differ markedly in the more advanced (in male morphology) representatives (*Eubosmina* and *Bosmina* sp. str.), whereas in the more basal members of the same clades (*Lunobosmina* in first case and *Sinobosmina* in second case), the males are significantly more similar. Kotov (1995, 1997a) analysed thoracic limbs in all subgenera (with the exception of *Lunobosmina*, which was not described at that time), and found that all species have an absolutely identical set of setae on each limb. We have used the weak morphological differentiation to justify the single-genus approach in our taxonomy.

TRACES OF EVOLUTIONARY MODIFICATIONS IN POSTEMBRYONIC DEVELOPMENT

During copulation, the adult male of *Bosmina* hooks the movable antennae I under the medial keel on the valve of the ephippial female, its hook on the limb I forces the valve of the female open, and the postabdomen is inserted into the egg chamber (Kerfoot & Peterson, 1980). Possibly, two pairs of sensory setae on antenna I sense the sculpture on the ephippum, and thus allow the male to choose a 'correct' female (i.e. mature, ephippial female of the same species). We speculate that the sensory arrangement of the antenna II, the setae on limb I, and of the postabdomen are also important in the species determination by the male.

Bosminids show strong morphological differentiation between males and females, compared with other cladocerans. Kotov (1996: 195) declared that the evolution of the gamogenetic generation of *Bosmina* 'went the way of an amplification of distinctions between males and females'. It was also found that juvenile males of *Bosmina* (*Eubosmina*) have characters similar to adult females of *B.* (*Liederobosmina*). Indeed, studying juvenile males we can find in their morphology some ancestral characters, and trace some events in the evolution of males within the genus.

1. The shift of the gonopores into a distalmost position and their fusing. In the adult state, the males of the subgenera *B.* (*Liederobosmina*), and *B.* (*Lunobosmina*) have subdistal gonopores. In contrast, juvenile males I and II of all studied species have subdistal gonopores (or terminal points of gonoducts, it these have no openings). The terminal points of the gonoducts in males II are located distal to those of males I. So, a shift of gonopores towards the distal end of the postabdomen takes place during development. This shift is likely to reflect former evolutionary transformations, where the gonopore becomes more distal. Analogous evolution of the gonopore position in ontogenesis is described in chydorids (Smirnov, 1971).
2. The shift of the prominal pecten of the postabdominal claw to the body of the postabdomen. This shift is maximally visible in *B.* (*B.*) *longirostris*. In observing juvenile males of this species we concluded that the dorsal row of denticles on the distal portion of the postabdomen is a remnant of the proximal pecten.
3. Reduction of number and size of setae on the subdistal lobe. Males II of all species have three setae on this lobe, with two of them normally developed. In adult males, there is only a single normally developed seta, whereas the other setae are rudimentary [with the exception of *B.* (*S.*) *fatalis* in which the second seta is also relatively large]. Pro-bosminids apparently have three normally developed setae on this lobe.
4. Disappearance of the second seta on the idl. In males of *B. longispina* (see Kotov, 1996), *B.* (*S.*) *fatalis*, and *B.* (*Lu.*) *oriens*, there is a small second seta on idl, that completely disappears in adult males. This seta was likely to be present on the idl of the ancestor of bosminids. In other anomopods, there are more setae on the idl, up to four, e.g. in males of *Eurycercus* (see Smirnov, 1971; Kotov, 2000).
5. Modification of the tip of the copulatory hook. Juvenile males II are immature and unable to copulate with females (Purasjoki, 1958). Nevertheless, the tips of their copulatory hooks are sometimes modified. For example, the hook of male II in *B.* (*B.*) *longirostris* is similar to that in adult *B.* (*S.*) *fatalis*. The hook of male II in *B.* (*Li.*) *meridionalis* is supplied with setules, as in adult *B.* (*Lu.*) *oriens*. We think that these similarities are reflections of relationships between subgenera: the ancestor of *B. (B.) longirostris* had the hook of the *fatalis* type, whereas the ancestor of *B.* (*Li.*) *meridionalis* had the hook of the *oriens* type.

Males and females of the second bosminid genus, *Bosminopsis* Richard, 1895, have a postabdomen of similar structure (Kotov, 1997c). Postabdomens in females and males of ancestral bosminids were, probably, similar (Kotov, 1996). In the two main clades within the genus, *Bosmina* sp. str. + *Sinobosmina* versus *Eubosmina* + *Liederobosmina* + *Lunobosmina*, independent, and sometimes analogous, modifications took place: elongation of distal part of postabdomen, shifting of the gonopores towards the distalmost position and their fusing, removal of basal pecten from lateral surface of postabdominal claw to its base, or to the body of postabdomen, thickening of denticles in the basal pecten, and elaboration of tip of the copulatory hook on limb I.

HOMOLOGY OF LIMB-I PARTS IN *BOSMINA* AND OTHER ANOMOPODS

Olesen, Martin & Roessler (1996: 306) state that 'the homologies are uncertain' for the distal portion of limb I in the *Bosmina* male. But, this opinion was based on previous undetailed descriptions and inaccurate figures, as well as on a superficial analysis of the limb–I morphology within the order Anomopoda. As a result, the orientation of limb I appears mixed: in Figures 13c, e, and f some of the internal endites on limb I were marked as 'exopod'. Difficulties with homologies appear to result from the orientation problem.

Still, there are also some problems with the homology of the more basal portions of female limb I in *Bosmina* and other anomopods caused by the fusing of endites in *Bosmina* (Kotov, 1996, 1997b). But, the homology of the distal portion of limb I in the *Bosmina* male is relatively straightforward.

The outermost projection on the male limb I is the outer distal lobe (Fig. 1L: odl), which is a well-recognized limb part in Chydoridae (Smirnov, 1971, 1996; Kotov, 2000), Macrothricidae (Smirnov, 1992; Kotov, 1999), and Daphniidae (Ishida *et al.*, 2006; Kotov, Ishida & Taylor, 2006). There were some doubts in its homology with the exopod I of large branchiopods (Kotov, 1999), but the pattern of expression of the *Distalless* gene in *Daphnia* (Shiga *et al.*, 2002: fig. 1) can be regarded as evidence of such homology. Apparently, another remainder of the exopod of limb I is an accessory seta, present in some chydorids (Kotov, 2000). *Eurycercus* is a unique anomopod with two accessory setae (Smirnov, 1971). But, in *Bosmina*, traces of the accessory seta are absent.

The next projection is the inner distal lobe, bearing the copulatory hook in all anomopods. It is interesting that in the female of *Bosmina* this lobe is very reduced (Kotov, 1997b), whereas in the adult male it is very large (Fig. 1J–M). As it was said above, in the majority of the anomopods the idl is supplied with more numerous setae (up to four), and the presence of the second seta on idl in the juvenile male is evidence of the fact that the number of setae on this lobe was reduced in bosminids.

A further projection is the subdistal lobe, which has a less clear homology. The limb I of males of chydorids and macrothricids is supplied with a so-called copulatory brush seta, and is associated with a copulatory brush of numerous setules (Kotov, 1999, 2000; Sinev & Kotov, 2000). The copulatory brush is opposed to the copulatory hook, and is necessary for a successful clasping of the female valve during mating (Van Damme & Dumont, 2006). *Bosmina* and *Bosminopsis* are the only two genera in which this seta is present in the female, and is located on a special lobe in the male (in *Bosminopsis* this lobe is also present in females!). In addition, in juvenile males of *Bosmina* there are two setae on the subdistal lobe. It is possible that the subdistal lobe is the remainder of a special endite, which is reduced in the rest of the anomopods.

TWO DIFFERENT DIRECTIONS OF MORPHOLOGICAL EVOLUTION

Haney & Taylor (2003) demonstrated the lack of morphological and genetic covariation in the subgenus *Eubosmina*. Indeed, populations were grouped according to their phylogeny and according to their regions (Holarctic, Atlantic Nearctic, and Beringian Nearctic), instead of according to morphotype (*coregoni*, *longispina*, or others). In the present paper we have identified the most genetically divergent regional clade, *B.* (*E.*) *tanakai sp. nov*. from Japan. Unlike the other members of *Eubosmina*, the morphology does concur with genetics in identifying this lineage as the most divergent of the subgenus. Thus, *B.* (*E.*) *tanakai sp. nov*. represents another case where male characters appear to provide more evolutionary information than female characters.

Specifically, female characters such as the length of antenna I (more accurately, length of its post-aesthetasc portion) and the length of the mucro appear to be phylogenetically unreliable. We found that *B. (E.) tanakai sp. nov*. forms a continuum of morphological variability of these characters, analogous to that in Palearctic *Eubosmina*. It is quite possible that female structures with antipredation roles such as those of the mucro and antenna I arose independently. Using only female characters led some authors (Uéno, 1938a, b; Tanaka, 2000) to assign *B.* (*E.*) *tanakai sp. nov*. to a taxa previously described from Europe (*longispina* or *coregoni*).

The differences in the number of informative male and female morphological characters is partly a reflection of the differing life histories of males and females. Males have shorter lifespans than females, and there appears to be less investment in feeding structures and more investment in reproductive structures. Males stop moulting after the third instar, and the moult proceeds regardless of food levels. Females undergo numerous moults, and will delay moulting under low food conditions. Continued moulting permits females the opportunity to grow defensive structures as the environment changes. So, females exhibit much more phenotypic plasticity than males in body shape and defensive structures (Kerfoot & Peterson, 1980; Hellsten, Lagergren & Stenson, 1999), and this plasticity confuses the taxonomy. Kairomones from predators frequently stimulate female bosminids to produce long projections, which are elements of an antipredator morphology (Hellsten *et al.*, 1999). Some populations of *Bosmina* (i.e. the *gibbera* morph) develop hypertrophic antipredator defenses, such as dorsal humps and extremely long antennae I, whereas their males lack these defenses. Lord *et al.* (2006) also proposed that 'sexual dimorphism derives from different costs of hydrodynamic drag and selection for mobility in males'.

The life of an adult male seems largely connected with a single task: sexual reproduction. Protective morphology (Kerfoot, 1977; Dodson, 1984) is less developed or is even nearly absent in males. Indeed, even feeding structures seem to be reduced in males, and are replaced by reproductive modifications. For example, the postabdomen is converted to a copulatory organ in males [with shortened postabdominal claws, as in *B.* (*B.*) *longirostris*], and is presumably less efficient for the cleaning of filtering limbs than the postabdomen of females. Limb I of males is modified for clasping during copulation, and presumably reduces the feeding efficiency compared with the limb I of females. So, the male provides a suite of weakly plastic sensory and copulatory structures that are absent in females, and many of the variable female characters are highly plastic because they are inducible defensive structures. The divergent strategies thus yield more informative morphological characters in males than in females. Bosminids are not unique anomopods in having similar females and divergent males – an analogous situation is described for chydorids (Smirnov, 1971; Van Damme & Dumont, 2006).

JAPAN AS A 'HOT SPOT' FOR CLADOCERAN RELICTS

Ishida *et al.* (2006) state that 'Japan may represent an important area for cladoceran diversity because it probably lacked permafrost during the Pleistocene and, unlike much of Beringia, represented a refugium for temperate species'. Several new endemic taxa have been found in Japan (Kotov & Tanaka, 2004; Ishida *et al.*, 2006) and nearby regions (Kotov *et al.*, 2006). More specific Japanese endemics, i.e. several new lineages of *Daphnia*, await description (Ishida *et al.*, unpubl. data). *Bosmina* (*E.*) *tanakai* sp. nov. was found several times by Japanese authors (Uéno, 1938b; Tanaka, 2000), but they did not understand that they had a new species, and determined it as 'European' *B.* (*E.*) cf. *coregoni* or *B. longispina*. Our investigation revealed that this is a separate species, which is known only from the northern parts of the Japanese Archipelago. We recommend that all Japanese populations of cladocerans be tested for conspecificity to Holarctic species by direct comparisons of male morphology and genetic structure.

PERSPECTIVES FOR FURTHER STUDIES

Our study reveals the necessity of examining males for bosminid taxonomy. The discrimination between the subgenera *Bosmina* and *Sinobosmina* based on the position of the female head pore (immediately near the edge of the head shield vs. at a small distance from the edge, in a bifurcation of reticulation) needs further testing. So, at present, it is very difficult to discriminate these two subgenera using female characters.

At this point, descriptions of males are missing from several species. In addition, the variability of some characters between different populations of a species must be studied further. Studies of the fine details of female morphology are also still wanting. Female head pores and postabdominal claw structures warrant more attention than the more commonly variable defensive structures in bosminids. But, we believe that our preliminary data are important for understanding the comparative morphology, phylogeny, and systematics of the genus *Bosmina*. Even by analysing previous descriptions of males we can find differences of described animals from 'traditional' species, as in the case of '*B. longispina*' in Deevey & Deevey (1971), or in Tanaka (2000). Unfortunately, the level of morphological descriptions of bosminids, even in recent publications, is frequently poor, and needs to be radically improved. We believe that artificial induction of males can be an important tool to improve the situation.

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KEY TO SPECIES WITH ADEQUATELY DESCRIBED ADULT MALES

1(10). Postanal part of postabdomen elongated, cylindrical, postabdominal claw thick, shortened as compared with female; antenna I with relatively thin pre-aesthetasc portion……………see below
2(5). Postabdominal claw with two pectens of denticles, without distal spinule, a large projection on side of idl I……………subgenus *Bosmina* (*Sinobosmina*), see below.
3(4). Antenna I not folded close to ventral margin of the body, with a long second seta on subdistal lobe……………*Bosmina* (*Sinobosmina*) *fatalis*.
4(3). Antenna I folded close to ventral margin of the body, with a rudimentary second seta on subdistal lobe……………*Bosmina* (*Sinobosmina*) *fatalis cyanopotamia*.
5(2). Postabdominal claw with a single pecten of denticles, with distal spinule, and either no projection or a low projection on the side of idl I……………subgenus *Bosmina* (*Bosmina*), see below.
6(7). Preanal margin of postabdomen slightly depressed, tip of copulatory hook blunt……………*Bosmina* (*Bosmina*) *tripurae*.
7(6). Preanal margin of postabdomen strongly depressed, tip of copulatory hook as a sharp spine……………see below
8(9). Posterior margin of valve high, postabdominal claw thick, with relatively blunt tip, all denticles on distal potion of postabdomen minute……………*Bosmina* (*Bosmina*) *liederi*.
9(8). Posterior margin of valve low, postabdominal claw slender, with pointed tip, denticles on distal potion of postabdomen relatively large……………*Bosmina* (*Bosmina*) *longirostris*.
10(1). Postanal part of postabdomen inflated or conically narrowing, postabdominal claw long; antenna I with widened pre-aesthetasc portion……………see below.
11(12). Postanal portion inflated slightly, antenna I in lateral view strongly E-shaped and curved……………subgenus *Bosmina* (*Lunobosmina*) [with single species *Bosmina* (*Lunobosmina*) *oriens*].
12(11). Other postanal portion, antenna I not curved……………see below.
13(20). Postanal part of postabdomen inflated, postabdominal claw with relatively small denticles in first pecten……………subgenus *Bosmina* (*Liederobosmina*), see below.
14(17). Ocular dome distinct.
15(16). Tip of copulatory hook with a single incision……………Bosmina (*Liederobosmina*) *chilensis*.
16(15). Tip of copulatory hook with two minute ridges……………*B*. (*Liederobosmina*) *hagmanni*.
17(14). Ocular dome absent……………see below.
18(19). Postabdomen with markedly convex preanal portion……………*B*. (*Liederobosmina*) *meridionalis*.
19(18). Postabdomen with almost straight preanal portion……………*B*. (*Liederobosmina*) *huaronensis*.
20(13). Postanal part of postabdomen conically narrowing, postabdominal claw with large denticles in first pecten……………subgenus *Bosmina* (*Eubosmina*), see below.
21(22). Postanal portion of postabdomen massive, postanal margin continues along anal margin, with a few (two or three) denticles at claw base……………***Bosmina* (*Eubosmina*) *tanakai* sp. nov.**
22(21). Postanal portion of postabdomen relatively thin, postanal margin makes a distinct obtuse angle with anal margin, with many (more than five) denticles at claw base……………see below.
23(24). Eye large, copulatory hook with a depression at its tip……………Beringian '*Bosmina* cf. *longispina*'.
24(23). Eye small, copulatory hook without depression on tip……………Palaearctic '*Bosmina* cf. *coregoni*' (*coregoni*, *longispina*, *thersithes*, and *crassicornis*).

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