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ORIGINAL ARTICLE

A new species of *Diaphanosoma* Fischer, 1850 (Crustacea: Branchiopoda: Sididae) inhabits lakes of the western United States of America

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ABSTRACT

Diaphanosoma edmondsoni *sp. nov. (Cladocera: Sididae) is described based on material from several lakes in Washington, California, and Montana, USA. It differs from all other known species of the genus in having a specific combination of traits: a head with conspicuously protruding dorsal part, comparatively small eye shifted ventrally, specific armament of postero-ventral valve margin, lack of thorn(s) near posterior valve margin, comparatively long distal basal spine of postabdominal claws of slightly variable shape, and occasional presence of additional large spines on the claws. This is the first endemic species of the genus (and also of the family Sididae and order Ctenopoda) recorded in the western part of North America and, along with some other cladocerans, it forms a group of taxa highlighting this region as one of the regional hot-spots of endemic aquatic fauna.*

Key words: Diaphanosoma*; new species; description; lakes; Western USA.*

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Abbreviations:

ad, adult parthenogenetic females; AnL, length of swimming antennae; BL, body length; DE, diameter of eye; DGF, collection of Professor D.G. Frey (now in Smithsonian Institution, Natural History Museum Support Center, Maryland, USA); D, diagonals of molar surface; en, endopodite; ep, epipodite; ex, exopodite; Fb, fishbones of molar surface; gam, gamogenetic females with resting eggs; HH, head height; HL, head length; I, large, two-segmented, setulated seta on outer distal corner of gnathobases of tl I - tl V; i, small outer gnathobasic seta near seta I; J, modified thorn-like, naked, hooked seta on distal corner of gnathobases of tl III - tl V; j, small outer curved gnathobasic seta near seta I; mx I, maxillula; mx II, maxilla; *n,* number of filtering setae of endopodite and gnathobase of thoracic limbs; ND, number of denticles of postero-ventral valve margin; p, nonsetulated seta on proximal corner of gnathobases of tl II - tl V; Pa, pales of molar surface; Pe, pegs of molar surface; tl I - tl VI, thoracic limbs of first - sixth pairs, UpBrL, length of upper antennal branch (exopodite).

INTRODUCTION

In North America, the first representatives of the genus *Diaphanosoma* Fischer (syn. *Daphnella* Baird) were poorly described as separate species (Birge, 1879; Herrick, 1879), *D. exspinosa* (Birge, 1879) and *D. winchelli* (Herrick, 1879). Later they were synonymized with the European *D. brachyurum* (Liévin, 1848) and *D. leuchtenbergianum* Fisher, 1850 (Birge, 1918; Brooks, 1959, 1966; Pennak, 1978) and for a long time only these two species were recorded in the region.

Only in the 1980s, the first American native species of the genus, *D. birgei* Kořínek (Kořínek, 1981), was described and *D. leuchtenbergianum* considered a synonym. Later on, brief investigations of the extensive collection of late Professor D.G. Frey revealed four undescribed species and two species new to North American fauna (Korovchinsky, 2002, 2004a, 2005). In particular, it was stated that forms close to *D. brachyurum* and *D. birgei,* more numerous and more readily available throughout the eastern United States, constitute in fact two species groups to be further studied. To date, seven species have been described in North American inland waters. Most of the occurrence localities of the recorded taxa are situated in the eastern and southern parts of the United States whereas the western part of the country remained unexplored in respect to detailed investigation of this genus.

Close investigation of a small set of samples, collected in lakes of the western United States, most of which were kindly placed at the disposal of the author by late Professor W.T. Edmondson and his colleagues (University of Washington, Seattle, USA), has revealed a new species, as described herein. Recently, these samples were supplemented by another more extensive set of samples from Lake Washington kindly sent by Ms. A.H. Litt. These samples were collected from 1957 till 2013 and contained numerous parthenogenetic and gamogenetic individuals which allowed checking the long-term species persistence in the lake and expand its description.

METHODS

Specimens for this study were obtained from the following lakes in the western United States:

i) Lake Sammamish, King Co., Washington State, 13.9.1976, leg. W.T. Edmondson, 37 ad, 4 juv.
ii) Lake Washington, King Co., Washington State, 29.10.1957, 9 ad, 6 males; 10.9.1958, 17 ad; 12.11.1958, 6 ad, 6 males; 20.6.1969, 21 ad, 6 juv; 21.10.1968, 5 ad, 3 gam, 6 males; 14.7.1972, 17 ad; 27.10.1972, 3 ad, 7 gam, 6 males, 1 juv male; 13.10.1981, numerous ad, 1 male (deformed); June 1990, 10 ad; 5.5.1992, many ad; 18.5.1993, 3 ad; 28.6.2003, 8 ad; 21.10.2003, 6 ad, 5 gam, 9 males; 6.11.2007, 5 ad, 2 males; 10.10.2013, 21 ad, 7 gam, 12 males, leg. W.T. Edmondson and A.H. Litt.
iii) Lake Cushman, Mason Co., Washington State, no date, 12 ad, leg. W.T. Edmondson and A.H. Litt
iv) Lake Alva, Missoula Co., Montana State, 9.10.1977, 1 ad, leg. D.G. Frey (DGF-4411);
v) Vicinity of San Francisco, California State, no locality, no date, 1 ad.

Specimens were examined under a Lomo MBS dissecting microscope and an Olympus BX 51 compound microscope with a *camera lucida*. Body measurements were performed according to Korovchinsky (2004b). Three females from the former sample were dissected to investigate the structure of thoracic limbs and mandibles. Molar structure of mandibles was described according to Edwards (1980) terminology. Mandibles were mounted on an aluminium stub, coated with gold and examined under a scanning electron microscope VEGA TESCAN at the A.N. Severtsov Institute of Ecology and Evolution.

DESCRIPTION

***Diaphanosoma edmondsoni* sp. nov.**

Etymology. The species is named in honour of the outstanding limnologist, the late W.T. Edmondson, Professor Emeritus of Washington University (USA), who supplied the author of the paper with material from lakes of western United States.

Type locality. Lake Sammamish, King Co., Washington State, USA.

Body measurements of specimens from three populations are presented in Tab. 1.

Parthenogenetic female. Body oval-elongated with head of moderate to large size (length 34.5-44.8% and height 18.9-26.3% of body length), having massive and strongly protruding dorsal part (Fig. 1a). Eye comparatively small (4.8-7.2% of body length) situated closer to the ventral head margin (Fig. 1a). Antennules small and situated ventrally with nine small aesthetascs and rather long sensory seta (Fig. 1b).

Swimming antennae of moderate length (63.9-76.5% of body length), with upper branch (exopodite) either not reaching or almost reaching the posterior valve margin (82.5-117.6% of length of basipodite) (Fig. 1a). Their basipodite is massive, with thin, hardly visible dorsal seta on its basal part (Fig. 1c), small, sharp spine on the outer side of its apical end (Fig. 1d), small spine-like seta (Fig. 4j) and distally setulated comparatively long setae on the dorsal and inner side of this end, respectively (Fig. 1k). Proximal segment of upper two-segmented antennal branch has rather large apical spine (Fig. 1 e-f), while that of the distal segment of the branch is considerably longer

Tab. 1. Measurements of body size and body part proportions and number of denticles of postero-ventral valve margin (ND) for three populations of *Diaphanosoma edmondsoni* [in each column from top to down: range (R), mean (M), standard deviation (SD), coefficient of variability (CV)].

BL (mm)	HL:BL (%)	HH:BL (%)	DE:BL (%)	AnL:BL (%)	UpBrL:BasL (%)	ND
Lake Sammamish, n=15						
1.33-1.82	38.9-44.8	20.2-26.3	4.8-5.9	63.9-76.2	86.5-105.0	13-23
1.57	41.3	22.6	5.4	70.6	95.6	17.2
	1.8	1.6	0.4	3.6	5.6	
	4.3	6.9	6.6	5.1	5.9	
Lake Cushman, n=12						
0.85-1.12	34.5-38.3	18.9-25.7	4.9-5.7	64.2-74.5	88.9-117.6	8-13
0.93	36.3	21.1	5.5	68.2	104.4	11.0
	1.2	1.2	0.4	3.3	9.1	
	3.3	5.7	6.5	4.8	8.7	
Lake Washington, n=16						
1.14-1.57	35.4-44.4	20.5-25.8	5.6-7.2	65.5-76.5	82.5-106.5	13-22
1.35	41.6	23.6	6.7	69.9	93.6	17.3
	2.3	1.4	0.7	2.8	6.6	
	5.4	5.9	10.9	4.0	7.0	

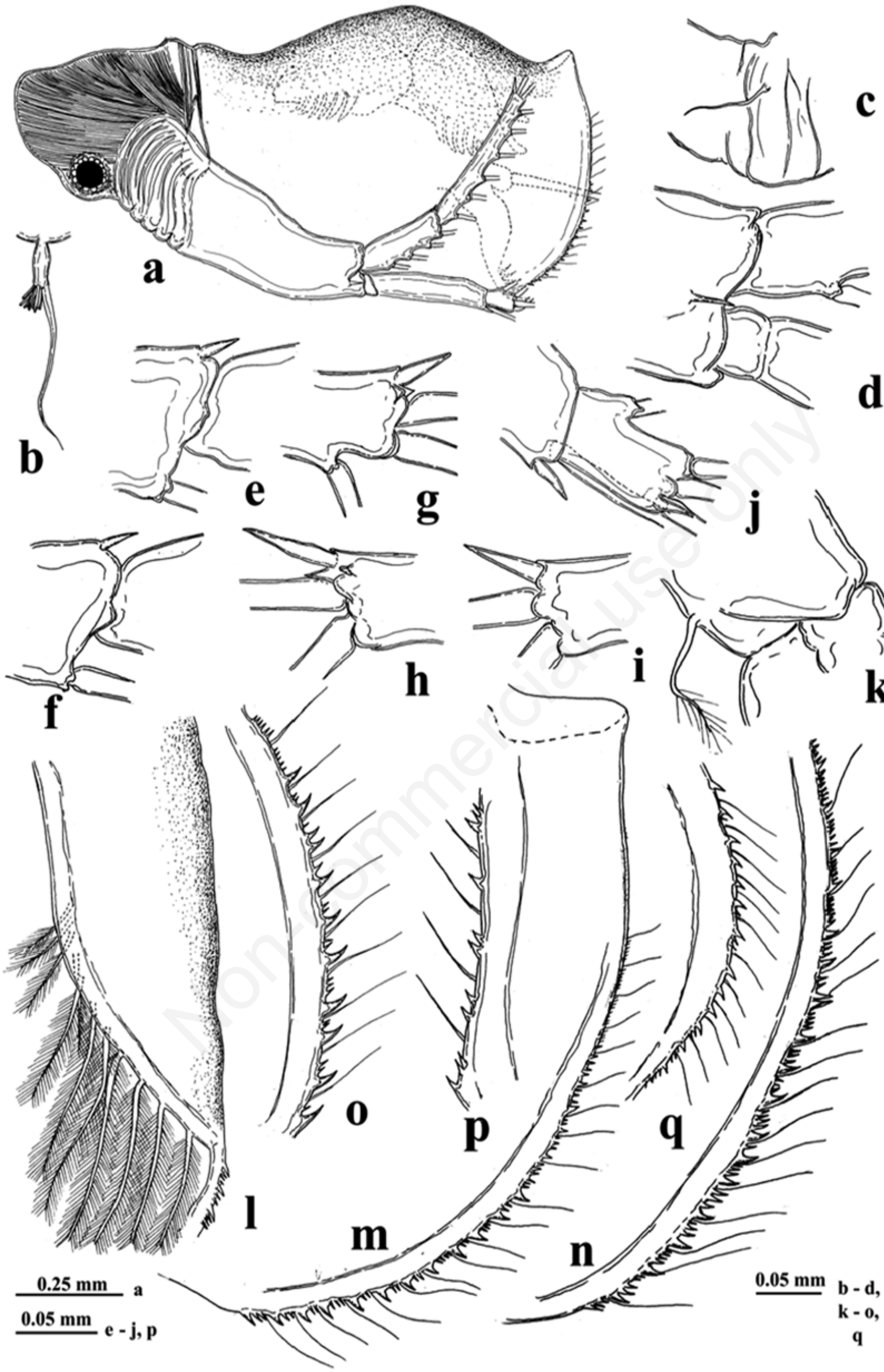

Fig. 1. *Diaphanosoma edmondsoni* sp. nov., females from Lake Sammamish (a-j, l-n), Lake Cushman (k,o) and from the vicinity of San Francisco (p,q). a) Female, general lateral view. b) Antennule. c) Seta on dorsal side of basal part of antennal basipodite. d) Distal part of antennal basipodite, outer side. e,f) Distal part of proximal segment of upper antennal branch (exopodite). g,h,i) Apical part of distal segment of upper antennal branch. j) Distal part of lower antennal branch (endopodite). k) Seta on inner distal side of antennal basipodite. l) Ventral valve fold; m-q) Armament of postero-ventral valve margin.

and has two, inner and outer, outgrowths near it (Fig. 1 g-h) [sometimes the latter are absent (Fig. 1i)]. Lower antennal branch (endopodite) with one seta and one spine on the end of the long middle segment and four setae and smaller spine on the small terminal segment (Fig. 1j). Formula of antennal setae: 4-8/0-1-4.

Mouthparts consist of mandibles, maxillules, and maxillae. Right mandible (Fig. 2b) with elongated-oval molar plate, having one large conical thorn (peg - Pe) posteriorly, a row of about six conical prominences (pales - Pa) along dorsal margin which soon disappear and then appear again on the anterior margin of the molar plate as a number of thin prominences. Ventral margin of the mandible apparently lacks any prominences; central part concave with parallel rows of diagonals (D) with perforated margin. Left mandible (Fig. 2a) wider, with more or less triangular molar plate, having three outgrowths posteriorly (pegs - P), one large more or less rectangular and distally branched and two small conical (another case, pegs were represented by three thinner, conical and apically branched outgrowths). The neighbouring outgrowth (fishbone - Fb) is distally widened bearing prominences apically. Pales are represented by a group of small, thin, partly fused prominences, forming almost the entire ventral molar margin. The central part of the molar surface has rows of diagonals, composed of numerous densely situated small prominences posteriorly and with the entire perforated plate anteriorly. Maxillules (mx I) with 8-9 densely situated feathered setae and one smaller naked seta incurved forward (Fig. 3a). Maxillae (mx II) with uneven apical margin situated just near the base of tl I (Fig. 3a).

Shell with arched dorsal side and conspicuous dorso-posterior angle (Fig. 1a). Valves with high posterior margin smoothly connected with ventral margin and forming a comparatively narrow inflexion bearing 10-12 long, finely setulated setae, the proximal of which are shortened and sit submarginally (Fig. 1l). Postero-ventral valve margin armed with a row of 8-23 large primary denticles; 1-4, more often 2-3 smaller denticles, diminishing in size dorsally, and one long, thin setula-like seta between each two of these primary denticles (Fig. 1 m-q, Fig. 2 c-g, Fig. 4 k,l) [some intermediate denticles can be rather large, almost equal in size to the large primary denticles (Fig. 2 d,e)]. Ventral denticles are larger (Fig. 2 d,e) while dorsal ones are smaller and intermediate denticles are more numerous (5-8) (Fig. 2f). Posterior valve margin with rows of marginal and submarginal spinules and some setule-like setae (1m). No inner thorn(s) near posterior margin.

Six pairs of thoracic limbs, all with epipodites. Their structure and armament are described in Tab. 2. Exopodite of tl I comparatively narrow at its end (Fig. 3 b,c), tl II to tl VI exopodite widened terminally (Fig. 3 e,h). Endopodites of tl I - tl V inconspicuously subdivided into four segments, the proximal is the largest, bearing numerous filtering setae (20-37), while the three terminal segments have from three to eight such setae each. Terminal segment from tl I to tl V and subterminal segment from tl II to tl V also with outer seta each, similar to those of the exopodite, of which the former one is especially long (Fig. 3 b,e, arrowed). Small, naked seta above the row of filtering setae of tl I (Fig. 3 b, ns). Gnathobase of tl I (Fig. 3d) with an inner row of seven to nine two-segmented, finely setulated filtering setae and outer row of one large two-segmented seta on its distal corner (I) and two small neighbouring setae (i and j), the latter of which is strongly curved. Gnathobases of tl II - tl V are larger, bearing 25-34 filtering setae, one small naked seta proximally (p), and one long, two-segmented seta distally with rough setules (I) (Fig. 3e); an additional modified naked, hooked seta (J) near the previous one is also present (tl III - tl V) (Fig. 3f). Tl VI small and strongly modified (Fig. 3 g,h). Its exopodite reduces up to the terminal plate and is armed with five terminal (two of them with conical thorns near their bases) and one lateral setae. Endopodite with seven similar setae and one thorn. Gnathobase with two long setae and three thorns of different sizes and shapes.

Postabdomen cone-shaped with rather long postabdominal setae (39.8-48.2% of body length) and rows and groups of spinules on its lateral and dorsal sides (Fig. 2h). Terminal claws with three basal spines, the distal spine is conspicuously longer than others and may be slightly wavy (Fig. 2i-m). Sometimes an additional spine sits near one, two or even all three primary claws (Fig. 2k-m, arrowed). Rows of spinules are situated above the basal spines and

Tab. 2. Data on structure and armament of thoracic limbs of *Diaphanosoma edmondsoni* from Lake Sammamish, King. Co., Washington State, USA, 13 September 1976 (for explanations of abbreviations, see above and Fig. 3).

Limb pairs	Exopodite (apical+lateral setae)	Endopodite	Gnathobase	Epipodite
I	5+6	(*n*7+1)+(*n*4)+(*n*4)+(*n*35-37)	(*n*7-9)+I+i+j	+
II	6+5	(*n*7-8+1)+(*n*4+1)+(*n*4)+(*n*32)	(*n*30-34+p)+I	+
III	6+5	(*n*8+1)+(*n*4+1)+(*n*4)+(*n*29)	(*n*29+p)+I+J	+
IV	6+5	(*n*6+1)+(*n*4+1)+(*n*4)+(*n*27)	(*n*25+p)+I+J	+
V	5+4	(*n*5+1)+(*n*3+1)+(*n*4)+(*n*20)	(*n*25+p)+I+J	+
VI	5+1	7+one thorn	2+three thorns	+

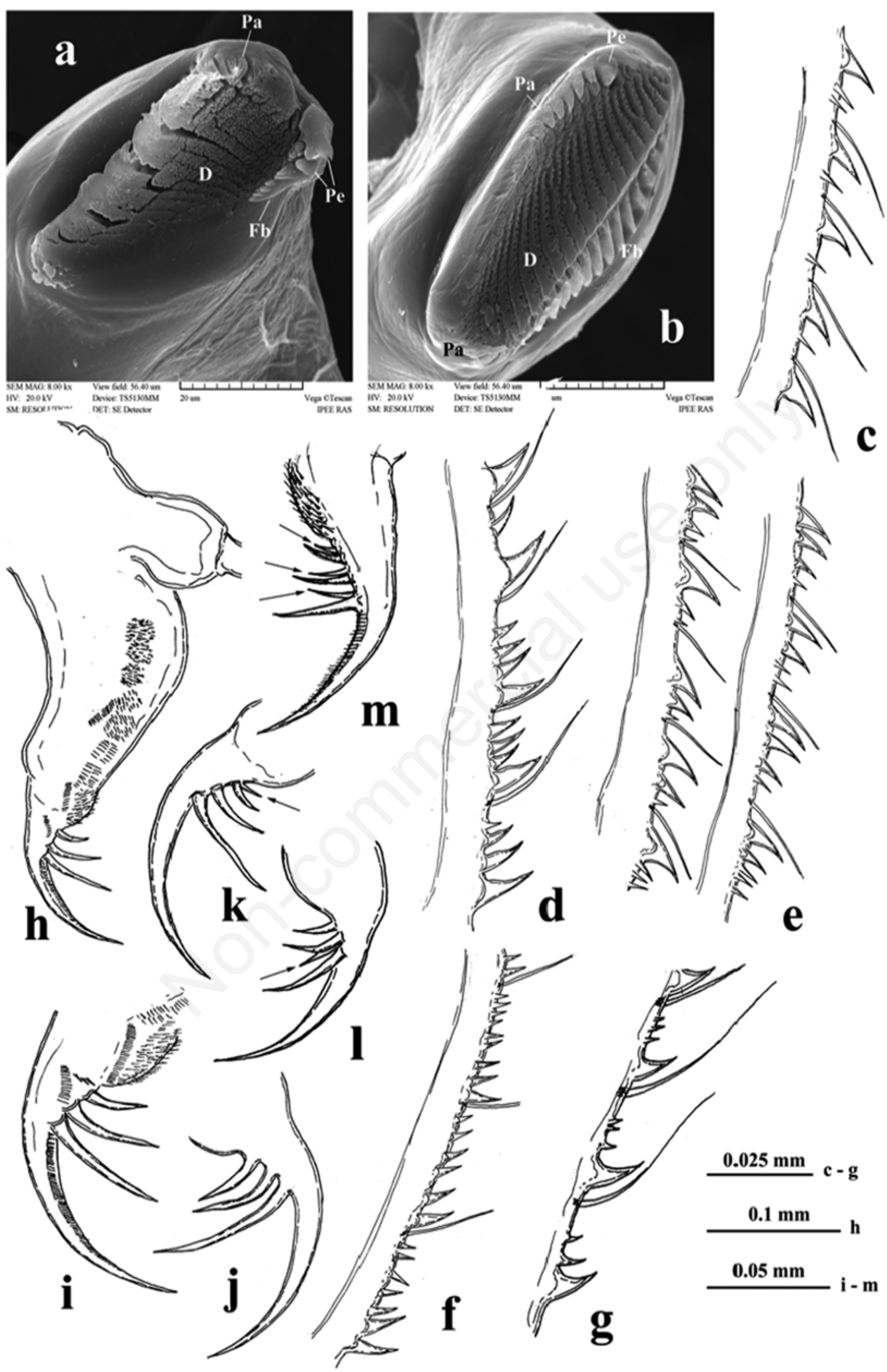

Fig. 2. *Diaphanosoma edmondsoni* sp. nov., females from Lake Sammamish (a-j, l-n), Lake Cushman (k), Lake Washington (l), and Lake Alva (g, m). a) Molar plate of left mandible. b) Molar plate of right mandible. c-e, g) Denticles of lower part of postero-ventral valve margin. f) Denticles of upper part of postero-ventral valve margin. h) Postabdomen, lateral view. i-m) Postabdominal claws.

distally along the outer lateral side of claws (Fig. 2 h,i).

Body length 0.85-1.82 mm. The size of parthenogenetic eggs of female with body length 1.28 mm is 0.34 x 0.21 mm.

Gamogenetic female. They differed from parthenogenetic females only in presence of dark resting eggs in brood pouches. The latter varied in their size from 0.25 x 0.19 to 0.32 x 0.21 mm.

Body length 1.18-1.44 mm.

Male. The main diagnostic traits, head shape, structure and armament of branches of swimming antennae, margin of shell valves, and postabdomen, as in females (Fig. 4a). Antennules (Fig. 4b) long (~54.2-62.7% of body length) and distally armed with numerous densely situated setules. Basipodite of swimming antennae with large spine on its outer distal end (Fig. 4c). Copulatory appendages long, tube-like, evenly tubular or slightly narrowing distally (21.1-26.9% of body length) (Fig. 4 d,e). Endopodite of tl I bears apically strong hook with tiny denticles along its inner concave margin and rather long naked seta-like outgrowth, while laterally it is armed internally with filtering setae and externally with three spine-like naked setae (Fig. 4 f,g). Juvenile males possess short antennules (35.5-48.4% of body length) and copulatory appendages (8.9-15.7% of body length).

Body length 1.04-1.33 mm.

Morphological variability. As seen from Tab. 1, the body size of specimens from different populations can differs significantly as it is evident from the comparison of specimens from three lakes. The latter from Lake Cushman are conspicuously smaller than those from Lake Sammamish and Lake Washington, which are large, reaching up to 1.82 mm. The intra- and interpopulation variability of some structures is rather high. It is of special interest, that the length of the antennal exopodite may be slightly shorter or longer than that of basipodite. In general, the antennal exopodite seems comparatively shorter in specimens from Lake Sammamish and Lake Washington *vs.* those from Lake Cushman. This does not correlate with the presence of a larger head in specimens from two former lakes and smaller head in the latter one.

At the same time, the number of denticles on postero-ventral valve margin correlates with body size. The specimens from Lake Washington are also comparatively large (body length reaches up to 1.57 mm), bearing 13-22 denticles on postero-ventral valve margin. The shape and number of these denticles vary, being similar to those of specimens from Lake Sammamish or closer (Fig. 4k, l) to those in specimens from Lake Cushman and Lake Alva whose intermediate denticles are smaller. In a single specimen from the vicinity of San Francisco, the armament of postero-ventral valve margin differ from those previously described, having only one, rarely two small intermediate denticles and sometimes lack them all together (Fig. 1 p, q).

The armament of the postabdominal claws is characterized by presence of unusually long distalmost basal spine, variable in shape. It is of special interest that in some specimens from one to three of these spines may have a smaller spine very close to its base (Fig. 2 k-m). This is an unique feature which has to date not been observed in other *Diaphanosoma* species.

Type material.

Holotype - a female from Lake Sammamish, 13.09.1976, coll. W. Edmondson with body length 1.41 mm deposited in the collection of type material of the Zoological Museum of M.V. Lomonosov Moscow State University (№ Ml 140); paratypes - three parthenogenetic females from the same sample and one gamogenethic female and two males from Lake Washington, 21.10.1968, coll. A. Litt in the same collection (two tubes № Ml 141-1 and Ml 141-2), other paratypes are deposited in the author's collection.

Differential diagnosis. *D. edmondsoni* sp. nov. differs from all other known species of the genus in having a specific combination of traits: 1) a head with conspicuously protruding dorsal part, 2) comparatively small eye shifted ventrally, 3) specific armament of postero-ventral valve margin, 4) lack of thorn(s) near posterior valve margin, 5) a comparatively long distal basal spine of postabdominal claws of slightly variable shape and occasional presence of additional spines on the claws. Among North American species, this new species mostly resembles *D. birgei* s. str., which possesses a similar protruding head shape and armament of postero-ventral valve margin. But the latter differs in presence of inner thorns near posterior valve margin and details of armament of postero-ventral valve margin which consists of a number of large denticles widening basally with only 1-3 small denticles between them, which sometimes may be absent (in the latter respect, the specimens of *D. edmondsoni* from Lake Cushman, Lake Alva and especially from the vicinity of San Francisco remind *D. birgei*).

DISCUSSION

The body size of *D. edmondsoni,* is unusually large, reaching up to 1.82 mm, which exceeds that of the pelagic *D. dubium* Manuilova, 1964 (max. 1.54 mm) and comparable with the larger *Limnosida frontosa* Sars, 1862 (up to 2.0 mm, rarely more). Among diaphanosomas, only *D. senegal* Gauthier, 1951 appears to be larger, however, it prefers small tropical water bodies with intermittent regime, including temporary ones (Korovchinsky, 2004b). Such a large body size is unusual because *D. edmondsoni* was under the high predation pressure (see Eggers, 1978). At least in part this may be explained by morphological and behavioral adaptations of the species. Large protruding head and powerful swimming antennae of *D. edmondsoni* are similar to those of *D. dubium* and some other pelagic

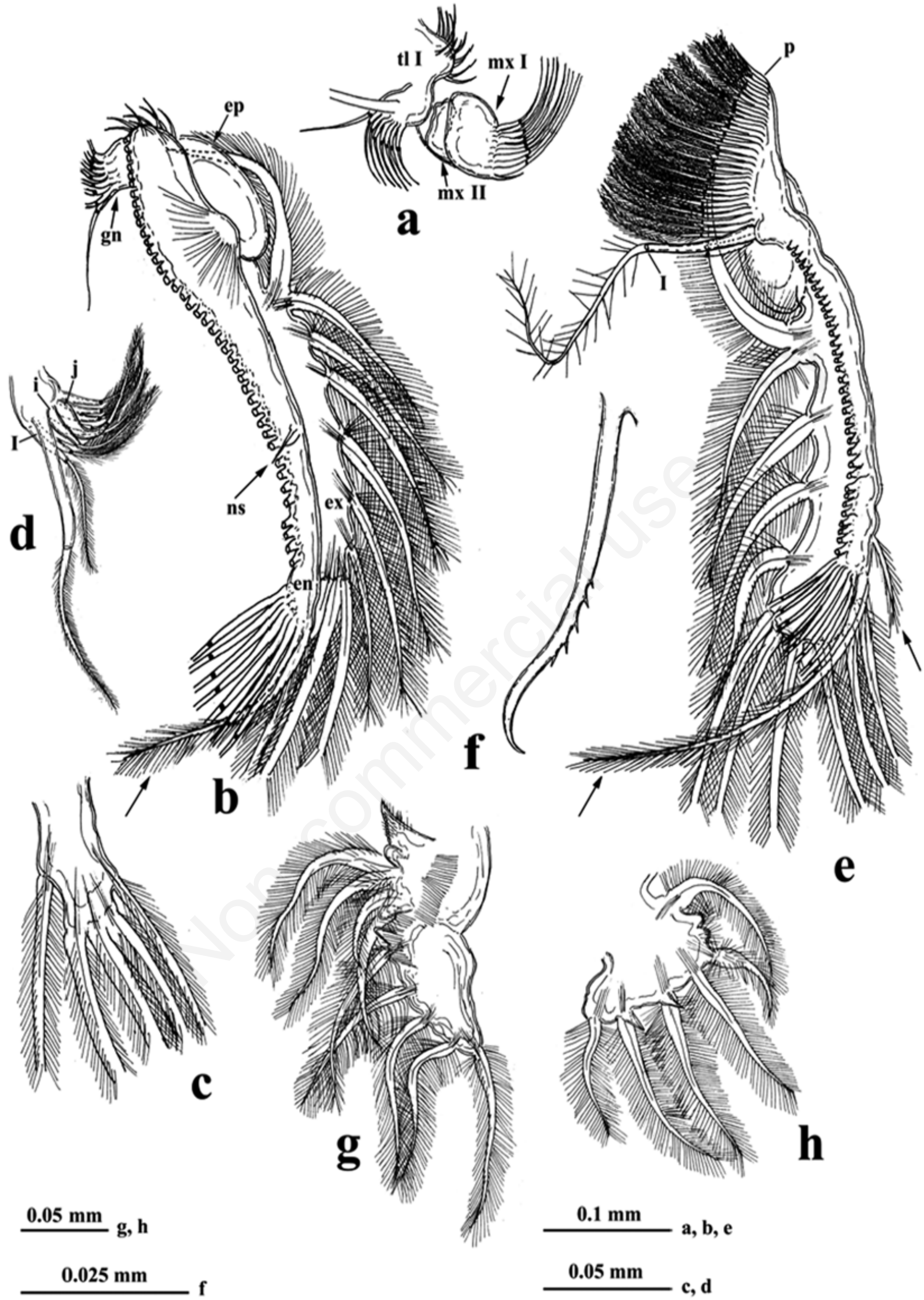

Fig. 3. *Diaphanosoma edmondsoni* sp. nov., females from Lake Sammamish. a) Maxillula (mx I) and maxilla (mx II) near the base of tl I. b) Thoracic limb of first pair (tl I). c) End of exopodite of tl I. d) Gnathobase of tl I, outer view. e) Thoracic limb of second pair (tl II). f) Hooked seta of distal outer corner of gnathobase. g) Endopodite and gnathobase of thoracic limb of sixth pair (tl VI). h) Exopodite of thoracic limb of sixth pair (tl VI).

diaphanosomas, considered good swimmers. The animals can escape predators by means of combination of soaring and fast movements (see Korovchinsky, 1990, 2004b).

D. edmondsoni is only the second *Diaphanosoma* whose mandibles have been studied. The structure of mandibular molar plates was first investigated in the Australian *D. hamatum* Korovchinsky et Timms (Korovchinsky and Timms, 2011). In general, the molar structure of the right and left mandibles of these species look similar with only minor differences, while the rest of body structure is quite different. For example, the thoracic limbs, the endopodites of which in contrast to those of some other members of the genus, are seen as inconspicuously subdivided in four segments. Also, the male structures (antennules, apical hook of tl I, copulatory appendages) do not demonstrate any specificity.

In spite of numerous investigation of lakes inhabited by *D. edmondsoni,* especially Lake Washington, the members

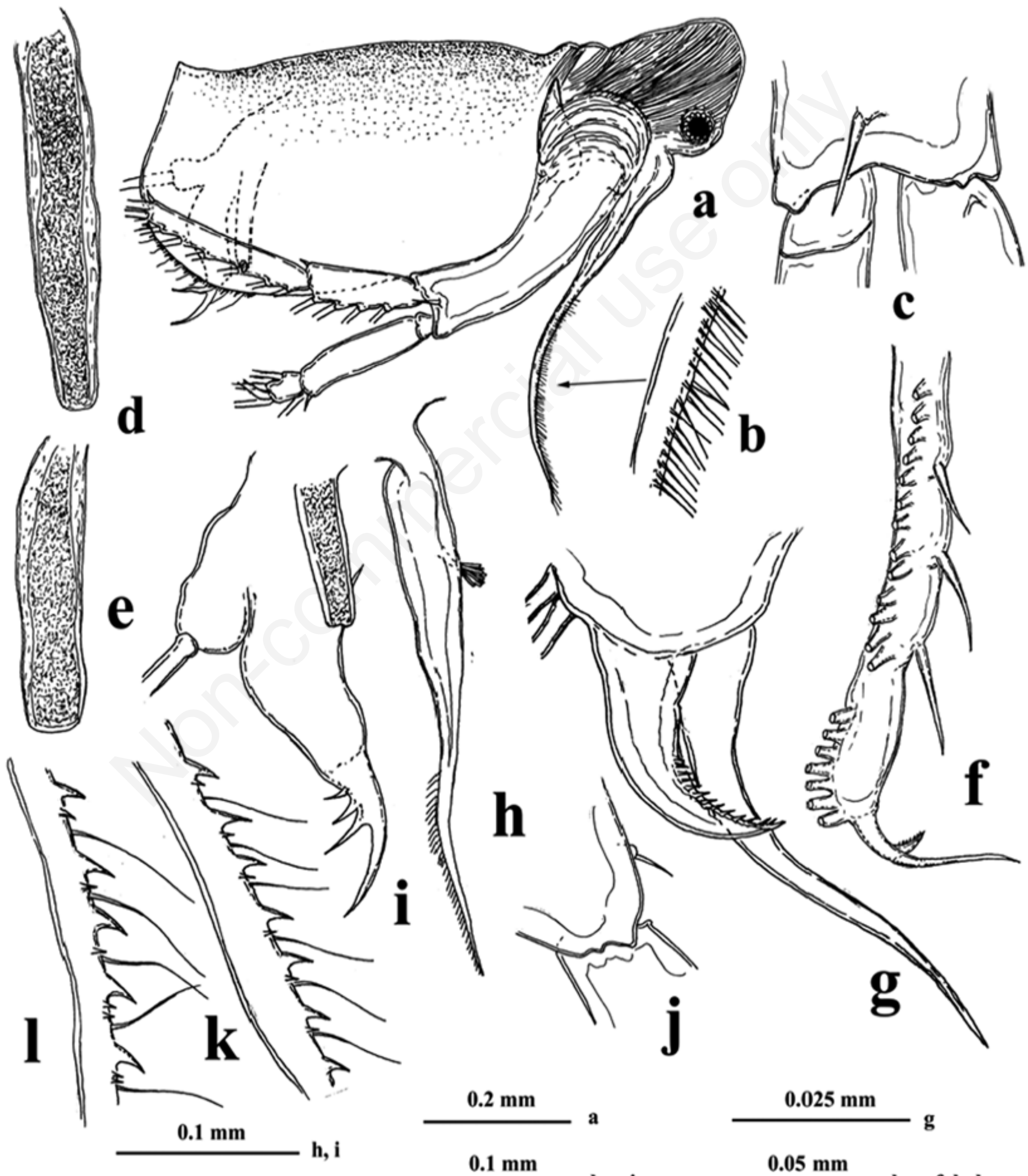

Fig. 4. *Diaphanosoma edmondsoni* sp. nov., males (a-i) and females (j-l) from Lake Washington. a) General lateral view. b) Armament of distal part of antennule. c) Distal part of antennal basipodite, outer side. d,e) Copulatory appendages. f) Distal part of male's tl I. g) Apical hook of male's tl I. h) Antennules of juvenile male. i) Copulatory appendage of juvenile male. j) Short spine-like seta on dorsal side of basipodital distal end. k,l) armament of postero-ventral valve margin.

of the genus, which at times dominated the summer zooplankton until 1974 and were simply called *Diaphanosoma* or *D. leuchtenbergianum* Fischer, (later changed to *D. birgei* – A.H. Litt, *personal communication*), did not attract much attention (Welch *et al*., 1973; Eggers, 1978; Edmondson and Litt, 1982; Hampton *et al*., 2006). Based on limited data of the present investigation, it is possible to conclude that the species under consideration is an inhabitant of the pelagic zone of large lakes. It is probably monocyclic because the gamogenetic females and males are present in October-November and designate the only period of gamogenetic reproduction. According to the investigated set of long-term monitoring samples from Lake Washington, it was possible to trace that this species permanently occurs in the lake since 1957 till present.

It may be supposed that *D. edmondsoni* occurs only in the western United States after investigation of about 200 samples with diaphanosomas from the eastern and southern parts of the USA (Korovchinsky, 2002, 2005), that contained mostly members of *D. brachyurum* and *D. birgei* species groups. At the same time, much more material is needed to evaluate more precisely the conspecificity of remote *D. edmondsoni* populations from Montana and California.

The information on cladoceran fauna of the western part of North America is limited. However, some taxa are known to be specific to this region, such as, the representatives of the family Dumontiidae from Oregon (Santos-Flores and Dodson, 2003), species of *Chydorus* (Frey, 1985), and some Daphniidae (Kořinek and Hebert, 1996; Taylor et al., 1999; Orlova-Bienkowskaja, 2001) and Bosminidae (Haney and Taylor, 2003). The finding of the first endemic species of the genus *Diaphanosoma* emphasizes the zoogeographical significance of the region under consideration and should stimulate further investigation of its aquatic fauna.

CONCLUSIONS

A new species of the genus *Diaphanosoma, D. edmondsoni* sp. nov., was found occurring in several large lakes in the western United States of America. It differs from all other known species of the genus in having a specific combination of traits. This is the first endemic species of the genus recorded in the western part of North America, and its biology remains poorly known. Together with some other cladocerans they form a group of taxa highlighting this region as one of the regional hot-spots of endemic aquatic fauna.

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