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# Establishment of the *Microphorella breviradia* species group, with a key to the Nearctic species groups of *Microphorella* Becker (Diptera: Dolichopodidae *sensu lato*: Parathalassiinae)

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# Abstract

The *Microphorella breviradia* species group is established for three new species from western North America, namely *Microphorella breviradia* **sp. nov.**, *M. macdonaldi* **sp. nov.** and *M. vespera* **sp. nov.**, including an identification key to species. COI mitochondrial DNA barcode sequences were obtained for two of the three species and possibly suggest the existence of additional cryptic species. The phylogenetic relationships of the *Microphorella breviradia* species group to the remainder of the *Microphorella* species groups are reviewed on a worldwide basis. A key to the four known Nearctic species groups of *Microphorella* is also provided.

Key words: new species, identification keys, classification, morphology, DNA barcodes, phylogeny

# Introduction

The empidoid subfamily Parathalassiinae is one of the basal lineages of the Dolichopodidae *sensu lato*, along with the Microphorinae (Sinclair & Cumming 2006). Worldwide the Parathalassiinae currently includes 51 described extant species in eight genera (Cumming & Brooks 2019). These genera were described as follows: *Parathalassius Mik*, 1891, *Microphorella* Becker, 1909, *Thalassophorus* Saigusa, 1986, *Plesiothalassius* Ulrich, 1991, *Amphithalassius* Ulrich, 1991, *Chimerothalassius* Shamshev & Grootaert, 2002, *Eothalassius* Shamshev & Grootaert, 2005 and *Neothalassius* Brooks & Cumming, 2016. The present generic concepts and phylogenetic relationships were analyzed morphologically by Cumming & Brooks (2019). *Microphorella* as currently recognized, was determined to be paraphyletic and polyphyletic and made up of at least 12 species groups worldwide. Cumming & Brooks (2019) indicated that four of these species groups, namely the *Microphorella* ashort R<sub>1</sub> species group, the *M. chiragra* species group and the "*Microphorella* short R<sub>1</sub> species group", occur in the Nearctic Region. We recognize Nearctic *Microphorella* on the basis of a wing with a reduced anal lobe, apically convex cell cua, a short to absent vein CuA+CuP and cell dm present, in combination with a head with a weakly developed gena, small short rounded or narrow palpus, and an arista-like stylus not lengthened (Brooks & Cumming 2011, 2012).

The purpose of this paper, the second in a series of papers revising the Nearctic species of *Microphorella*, is to describe and key the included species in the "*Microphorella* short  $R_1$  species group" (*sensu* Cumming & Brooks 2019) and formally describe the group. COI mitochondrial DNA barcode sequences are also analyzed for 74 specimens belonging to this species group. The relationship of the species group to the remainder of *Microphorella* is briefly reviewed on a worldwide basis. In addition, an illustrated key is provided to the four species groups of *Microphorella* that are present in the Nearctic Region.

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# Material and methods

This study is based on the examination of specimens that are deposited in the following institutions: California Academy of Sciences, San Francisco, USA (CAS); Canadian National Collection of Insects, Ottawa, Canada (CNC); California State Collection of Arthropods, Sacramento, USA (CSCA); Lyman Entomological Museum, Ste-Annede-Bellevue, Canada (LEMQ); Bohart Museum of Entomology, University of California, Davis, USA (UCDC); United States National Museum of Natural History, Washington D.C., USA (USNM).

Label data for primary types are cited verbatim. Labels are listed from the top label down with data from each label in quotation marks and separated by a semicolon. Lines of text on labels are delimited by a slash (/) and annotations are placed in square brackets, *i.e.*, []. The distribution maps were created with SimpleMappr (Shorthouse 2010).

Terms used for adult structures follow Cumming & Wood (2017). Homologies of the male terminalia follow Brooks & Cumming (2017, 2018) and Brooks & Ulrich (2012). Male and female terminalia dissections were macerated in 85% lactic acid heated in a microwave oven for multiple 20–60 second intervals, until muscle tissue was dissolved, with terminalia subsequently examined and illustrated in glycerin on a depression slide. Figures of male genitalia in lateral view are oriented with the anatomically dorsal and ventral parts directed towards the top and bottom of the page, respectively. This means that the left and right side of the figures refer to each side prior to the rotation and twisting caused by lateroflexion (see Sinclair & Cumming 2006, p. 48).

To provide additional evidence for species identity, numerous specimens of *Microphorella* were submitted for DNA barcoding to the Biodiversity Institute of Ontario in Guelph, ON, Canada. A single leg was removed from each specimen to obtain mitochondrial DNA barcodes (658 base pairs from the 5' end of COI). The DNA was extracted, amplified, purified and sequenced following the protocols given by Hajibabaei *et al.* (2005). Successful COI sequences were deposited in GenBank. COI sequences of >625 base pairs (bp) were analyzed with a Neighbourjoining tree (Fig. 24) created in the Barcode of Life Data Systems (BOLD) using the BOLD Aligner (Amino Acid based HMM) (Ratnasingham & Hebert 2007). For most sequenced specimens, species identities were confirmed by comparing COI sequences from males and females that clustered together with <2% genetic divergence (Hebert *et al.* 2003).

# **Systematics**

#### Microphorella breviradia species group

**Diagnosis.** The *Microphorella breviradia* species group can be distinguished from other parathalassiines by the following suite of characters: wing with short  $R_1$  vein that terminates at or before midpoint of wing (Fig. 3); mouthparts with sensory pit on palpus; male abdominal sternite 5 with short broad ventral projection; hypopygium (Figs 4, 10, 11, 14, 19, 20, 21) with epandrium and hypandrium partially fused together, right epandrial lamella greatly enlarged and comprising most of hypopygium in right lateral view, hypandrium reduced to narrow subtriangular band positioned on left side of hypopygium; female abdomen (Figs 31, 32) with 7 exposed abdominal segments, telescoping terminalia retracted into segment 7, syntergite 9+10 with acanthophorous setae (Figs 16, 17), syntergite 9+10 and sternite 10 widely separated, cercus ovoid with long apical setae (Figs 16, 32). See Cumming & Brooks (2019) for additional parathalassiine features possessed by members of this species group.

**Remarks.** The *Microphorella breviradia* species group includes three new species from western North America (described below) that share a short  $R_1$  wing vein and a distinctively modified male hypopygium. The former feature is seen in some non-Nearctic parathalassiines (*e.g.*, the *Microphorella malaysiana* species group, *Neothalassius, Chimerothalassius, Eothalassius*), but not in other known extant Nearctic species groups of *Microphorella*. There is a fossil species of *Microphorella* described from the middle Eocene Kishenehn Formation in northwestern Montana that may also belong to the *M. breviradia* species group (Greenwalt *et al.* 2022). Members of the species group are generally found along fast flowing rivers and streams (Figs 6–9). Cumming & Brooks (2019) referred to this lineage as the "*Microphorella* short  $R_1$  species group" in their phylogenetic analysis of relationships within the Parathalassiinae.

# Key to males of species of the Microphorella breviradia species group

1	Head with face broad, nearly twice width of anterior ocellus at narrowest point (Fig. 5); fore tarsomere 5 with tuft of long dorsal setae
-	Head with face narrow, about width of anterior ocellus at narrowest point (Fig. 2); fore tarsomere 5 with shorter dorsal setae
2	Hypopygium with basiventral projection(s) on right dorsal surstylar lobe (Figs 11, 12, 13); phallus long and tubular, bearing
	very slender process medially (Fig. 10)
-	Hypopygium without basiventral projections on right dorsal surstylar lobe (Fig. 20); phallus stout and bifid, bearing thick pro-
	cess ventrally (Fig. 19)

# *Microphorella breviradia* sp. nov.

(Figs 1–4, 6, 7, 10–18, 22, 31, 32) urn:lsid:zoobank.org:act:586BABF9-B7D3-4B6B-8520-DD789B48DC44

**Type material. HOLOTYPE**  $\delta$  labelled: "USA:CA: El Dorado Co./ South Fork American River/ Eagle Rock river access/ N38°46'34.6" W120°16'00.7"/ 18.vii.2012, J.M. Cumming"; "CNC487253 [printed on both sides]"; "Legs removed/ for DNA/ analysis [green label]"; "HOLOTYPE/ *Microphorella breviradia*/ Cumming & Brooks [red label]" (CNC). **PARATYPES: USA: California:** Same data as holotype except, CNC487205, CNC487212, CNC487213, CNC487217, CNC487220, CNC487225, CNC487226, CNC487229, CNC487230, CNC487231, CNC487232, CNC487234, CNC487235, CNC487236, CNC487237, CNC487238, CNC487255, CNC487256 (14 $\delta$ , 4 $\circ$ , CNC); same data except, S.E. Brooks, CNC DIPTERA # 192164, CNC DIPTERA # 192165, CNC DIPTERA # 192166, CNC DIPTERA # 192167, CNC DIPTERA # 192172, CNC DIPTERA # 192173, CNC DIPTERA # 192174, CNC DIPTERA # 192175, CNC DIPTERA # 192176, CNC DIPTERA # 192177, CNC DIPTERA # 192178, CNC DIPTERA # 192179, CNC DIPTERA # 192180, CNC487206, CNC487210, CNC487211, CNC487214, CNC487215, CNC487216, CNC487218, CNC487222, CNC487224, CNC487239, CNC487241, CNC487242, CNC487243, CNC487244, CNC487245, CNC487246, CNC487248, CNC487249, CNC487251, CNC487252, CNC487254, CNC487270, CNC487277, CNC487278, CNC487279, CNC487280 (34 $\delta$ , 14 $\circ$ , A $\circ$ , CNC).

Other material examined. MEXICO: Baja California: Sierra San Pedro Martir NP [ca 31°00'N 115°33'W], 17 km E park entrance, 2900 m, 7.ix.1980, D.D. Wilder (2∂, 11♀, CAS); same data except, La Grulla, 6900 ft, 12.vi.1953, P.H. Arnaud, Jr (3∂, 3♀, CAS); same data except, Rancho Viejo, 7000 ft, 13.vi.1953 (2∂, CAS); same data except, 14.vi, 1953 (12, CAS). USA: California: Alpine County: along Disaster Creek [ca 38°26'N 119°45'W], T7N R20E Sec. 26, 11.vii.1977, D.D. Wilder (153, 19, CAS); same data except, 11.vii.1977 (33, CAS); along Little Teton Creek [*ca* 38°22'N 119°49'W], T6N R19E Sec. 12, 12.vii.1977, D. Wilder (22♂, 16♀, CAS); El Dorado County: same data as holotype (1763, 87, CNC); same data as holotype except, S.E. Brooks (2033, 102, CNC); same data except, Eagle Rock Picnic Area, 38°46.58'N 120°16.01'W, 1384 m, sweep, 14.viii.1999, J. Savage (13, LEMO); Fresno County: Sierra NF, along Pitman Crk, nr Big Crk [ca 37°12'N 119°13'W], 1500 m, T8SR25E Sec. 28, 2.viii.1979, D.D. Wilder (44♂, 63♀, CAS); Huntington Lake, Bolsillo Crk [*ca* 37°19'N 119°02'W], 10.vii.1984, J.F. MacDonald (1<sup>3</sup>, CNC); Madera County: Chiquito Crk 0.25 mi. below Upper Chiquito Campground [ca 37°30'N 119°24'W], 6820 ft, 11.viii.1971, H.B. Leech (1♂, CAS); Mariposa County: Summerdale Forest Camp, on Big Creek [*ca* 37°29'N 119°38'W], 1520 m, 27.vi.1973, P.H. Arnaud, Jr (1∂, USNM); Mono County: Leavitt Meadows [*ca* 38°19'N 119°33'W], 2470 m, 23.vii.1966, P.H. Arnaud, Jr (3♂, 3♀, USNM); same data except, 25.vii.1966 (1♂, USNM); Riverside County: Idyllwild [ca 33°44'N 116°42'W], 7.vii.1940, A.L. Melander (1♂, USNM); San Jacinto Mountains, Black Mountain Creek, 11 km NW Idyllwild [ca 33°48'N 116°45'W], 1535 m, 1.vii.1968, P.H. Arnaud, Jr (33, 39, USNM); San Bernardino County: Crestline [ca 34°14'N 117°17'W], 4.vii.1942, A.L. Melander (23, USNM); same data except, 13.vii.1944 (13, USNM); S Fork Santa Ana River [ca 34°10'N 116°49'W], 16.vi.1945, A.L. Melander (13, 19, USNM); same data except, 19.vi.1945 (13, USNM); same data except, vic. Melander Cabin, 1950 m, 2.vii.1968, P.H. Arnaud, Jr (10♂, 7♀, CAS); Upper Santa Ana River [*ca* 34°10′N 116°49′W], 2.vii.1950, A.L. Melander (1♂, USNM); same data except, Lost Creek, 29.vii.1948 (1♀, USNM); San Diego County: Palomar Observatory Campground [ca  $33^{\circ}20'N$  116°52'W], 25–27.vi.1968, P.H. Arnaud, Jr (1 $\bigcirc$ , CAS); same data except,

26.vi.1968, 1524 m (7♂, 5♀, USNM; 1♂, 2♀, CAS); same data except, 27.vi.1968, 1525 m (2♂, 1♀, USNM); Shasta County: W boundary Castle Crags SP [ca 41°08'N 122°19'W], 17.vii.1980, D.D. Wilder (953, 149, CAS); Montgomery Crk [ca 40°50'N 121°55'W], 2.viii.1970, P.H. Arnaud, Jr (2∂, 2♀, CAS); Siskiyou County: Klamath NF, East Fork Campground [ca 41°09'N 123°06'W], along E Fork of S Fork of Salmon R., 4.vii.1978, D.D. Wilder (2Å, CAS); Klamath NF, along Fish Lake Creek [ca 41°12'N 122°58'W], 21.vii.1980, D.D. Wilder (1Å, CAS); Klamath NF, along Portuguese Peak Trail [ca 41°22'N 123°23'W], T11N R7E Sec. 4, 2.vii.1978, D.D. Wilder (333),  $9^{\circ}$ , CAS); Klamath NF, along first 2.5 mi. of Wooley Crk Trail [*ca* 41°22'N 123°25'W], T12N R7E Sec. 29 & 31, 3.vii.1978, D.D. Wilder (5♂, 7♀, CAS); Shasta Springs [*ca* 41°14′N 122°15′W], vii.1915, A.L. Melander (3♂, 1<sup>Q</sup>, USNM); Tehama County: Battle Creek Campground, South Fork Battle Creek [*ca* 40°20'N 121°37'W], 1460 m, 12.viii.1977, P.H. Arnaud, Jr (13, CAS); Tuolumne County: along Clark Fork River [ca 38°23'N 119°48'W], T6N R19E Sec. 14, 11.vii.1977, D. Wilder (11♂, 1♀, CAS); along Deadman Crk [*ca* 38°19′N 119°42′W], 8000 ft, 12.vii.1977, D. Wilder (5 , CAS); Pinecrest [ca 38°11'N 119°59'W], 9.vii.1947, Acc. No. 258, P.H. Arnaud, Jr (63, 19, USNM); same data except, 15.vii.1947 (13, USNM); same data except, 1.viii.1947, Acc. No. 297 (19, USNM); same data except, 19.vii.1948 (16<sup>3</sup>, USNM); same data except, 21.vii.1948 (1<sup>3</sup>, USNM); same data except, 27.vii.1948 (13, USNM); Trinity County: Goldfield Campground, Boulder Creek [ca 41°06'N 122°46'W], 926 m, 15.viii.1980, P.H. Arnaud, Jr (13, USNM); Shasta NF, Boulder Creek nr Coffee Crk Rd [ca 41°06'N 122°46'W], 19.vii.1980, D.D. Wilder (2♂, CAS); Yosemite [*ca* 37°52′N 119°32′W], 13.vi.1935, A.L. Melander (1♂, USNM).

**Problematic material examined. USA: California:** San Bernardino County: 2.6 mi E of Seven Oaks, Santa Ana R., 34°11′0.1″N 116°52′12.1″W, 1770 m, 11.vi.2016, J.M. Cumming, CNC576977 (1♂, CNC, see "Remarks"); same data except, S.E. Brooks, CNC574674 (1♂, CNC, see "Remarks"); same data except, S.E. Brooks, CNC574674 (1♂, CNC, see "Remarks"); same data except, 11–12.vi.2016, YPT, Cumming & Brooks, CNC576726 (1♂, CNC).

**Diagnosis.** Males of *M. breviradia* **sp. nov.** are distinguished from those of *M. macdonaldi* **sp. nov.** and *M. vespera* **sp. nov.** by the following combination of features: narrow face (Fig. 2); right dorsal surstylar lobe with basiventral projection(s) (Figs 11, 12, 13); phallus long, tubular and C-shaped (Fig. 10). Males of *M. breviradia* **sp. nov.** are morphologically variable (see "Remarks"), compared to the known material of the other two species, and some specimens can be further distinguished by the following features: hind femur with ventral setae up to 2X femur width; hind tibia with short erect setae on anterior and ventral surfaces; right epandrial lamella elongated with anterior end subconical and strongly projected (Fig. 13). Females of *M. breviradia* **sp. nov.** appear to be indistinguishable from those of *M. macdonaldi* **sp. nov.** and *M. vespera* **sp. nov.** 

**Description. Male** (Figs 1–4, 10–15): Body length 1.38–1.62 mm, wing length 1.43–1.67 mm. **Head** (Figs 1, 2): Largely blue-grey pruinose with dark brown to black ground colour; slightly broader than thorax in dorsal view, ovoid in lateral view; usually slightly broader than high in anterior view, wider in occasional specimens (about 1.3X broader than high); setae mostly black, paler on occiput laterally and on postgena ventrally. Ocellar triangle conspicuous. Vertex with greenish-bronze reflections. Occiput dark, concave on upper median part. Eyes covered with short ommatrichia, slightly longer near ventral margin; medial edge of eye with weak emargination adjacent to antenna; ommatidia of uniform size. Frons over 2X broader than high, widening above. Face narrow, about subequal to width of anterior ocellus at narrowest point in middle. Face and clypeus concolorous, grey pruinose. Clypeus not separated from face, as high as broad, apical margin weakly produced medially. Setae of head well differentiated: 1 pair of inclinate fronto-orbitals well-separated from base of antenna; 1 pair of lateroclinate anterior ocellars; 1 pair of small posterior ocellars; 1 pair of strong inclinate inner verticals (sometimes referred to as postocellars); 2-4 pairs of lateroclinate outer verticals, anterior and posterior pair usually stronger; upper postocular setae short and uniserial, longer and more scattered ventrally; postgena with longer scattered setae around edge of mouth-opening. Antenna entirely brown to dark brown, inserted above middle of head in profile; scape short, funnel-shaped; pedicel subequal in length to scape, spheroidal with subapical circlet of setulae; postpedicel elongate, 2.1–3.2X longer than wide, conical and gradually tapered distally to broader basally and more abruptly narrowed distally, clothed in fine setulae; arista-like stylus 1.2–1.7X length of postpedicel, with minute hairs. Palpus dark brown, short and narrow, slightly over 2X longer than wide, with 1–2 lateral setulae and 1 long preapical seta. Proboscis brown, short, projecting ventrally. Gena narrow. Thorax (Fig. 1): Dorsum pruinose, dull metallic blue-grey with strong greenish-bronze coloration on posterior 2/3–3/4 (including scutellum), to mostly bronze; pleura pruinose, dull metallic blue-grey with light metallic green and bronze reflections; setae black. Mesoscutum moderately arched, prescutellar depression present. Prosternum fused with proepisternum forming precoxal bridge. Proepisternum with a few setulae. Postpronotal lobe distinct with a few small setae. Mesonotum shield-shaped in dorsal view, slightly longer than

wide. Acrostichal setae biserial, short, sometimes sparse, not extended onto prescutellar depression; other thoracic setae well differentiated, each side of mesonotum with: 6 dorsocentrals (posteriormost seta stronger), 1 strong presutural supra-alar (posthumeral), 3 postsutural supra-alars, sparse acrostichal-sized setae intermixed with supraalars, 2 strong notopleurals, 1 strong postalar. Scutellum broadly subtriangular with one strong seta per side. Mesopleuron bare. Halter pale brown. Legs (Fig. 1): Coxae dark brown to dark grey-brown and mainly concolorous with thorax; femora dark brown to dark grey-brown; trochanters, tibiae and tarsi dark brown; coxae with pale setae; trochanters, femora, tibiae and tarsi with brown to pale brown setae; setae of femora, tibiae and tarsi short, except hind femur with series of long ventral setae; tarsal claws, pulvilli and empodium normally developed on all legs. Foreleg: Coxa with anterior surface setose, apical setae longer; femur subequal in length to tibia; tibia with apical comb-like row of short setae on anterior surface; tarsus subequal in length to tibia; tarsomere 1 subequal to combined length of tarsomeres 2-4; tarsomeres 2-4 decreasing in length apically; tarsomere 5 somewhat enlarged, subequal to combined length of tarsomeres 3 and 4, broad, with short dorsal setae. *Midleg*: Coxa with 2 anterolateral setae and a few anterior setae along apical margin; femur subequal in length to tibia; tibia with relatively strong anteroapical seta; tarsus slightly to distinctly shorter than tibia, tarsomere 1 subequal to combined length of tarsomeres 2–5; tarsomeres 2-4 decreasing in length apically; tarsomere 5 slightly shorter than tarsomere 2. *Hindleg*: Coxa with 2 setae on lateral surface; femur slightly longer than tibia, with series of long pale to light brown ventral setae (longest setae up to 2X femur width in some specimens); tibia often slightly bowed outwardly, some specimens also with erect setae on anterior and ventral surfaces, with apical comb-like row of closely-spaced setae on posterior surface; tarsus distinctly shorter than tibia (about 0.6–0.7X tibia length); tarsomere 1 subequal to combined length of tarsomeres 2-4, tarsomere 2-4 gradually decreasing in length apically, tarsomere 5 subequal in length to tarsomere 3. Wing (Fig. 3): With brownish tinge, veins dark brown, about 2.4X longer than wide. Pterostigma absent, membrane entirely covered with minute microtrichia, alula absent. Costa circumambient. Extreme anterior base of costa with strong anterodorsal seta. Anterior section of costa (between base and  $R_{4+5}$ ) bearing double row of spine-like setae, setae of ventral row stronger. Posterior section of costa (i.e. beyond  $R_{4+5}$ ) with setae finer and longer. Longitudinal veins complete, reaching wing margin, except CuA+CuP (anal vein) extending halfway to wing margin, Sc faint apically. R<sub>1</sub> short, terminating before midpoint of wing. Base of Rs originating opposite humeral crossvein. R<sub>2+3</sub> subparallel with  $R_1$  in basal 1/3, straight and parallel with  $R_{4+5}$  in distal part.  $R_{4+5}$  straight.  $M_1$  nearly straight with gentle posterior curve apically. M<sub>2</sub> and M<sub>4</sub> nearly straight and subparallel beyond cell dm. Costal section between M<sub>1</sub> and M<sub>2</sub> longer than costal section between M<sub>2</sub> and M<sub>4</sub>. CuA rounded. Short r-m crossvein present in basal portion of wing, distal to base of R<sub>4+5</sub>. Crossvein bm-m incomplete. Cell dm present, closed by base of M<sub>2</sub> and dm-m crossvein, cell extending to middle of wing. Cells br, bm and cua in basal fourth of wing. Cells bm and cua broader than br. Cell cua closed, ovoid. Anal lobe not developed. Calypter with fine pale setae. Abdomen (Figs 1, 4, 10–15): Dark brown with grey tinge. Abdominal plaques usually visible on lateral margins of tergites and sternites 2–4; tergite 2 with transverse band of plaques visible anteriorly. Tergites 1-6 and sternites 2-5 with short setae along posterior surface (setae tiny on sternite 5), otherwise mostly bare, sternite 6 bare. Segment 7 bare. Segment 1 reduced and very short; segments 2–4 mostly symmetrical with simple tergites and sternites, segment 2 relatively long; segments 5–7 narrowed and laterally compressed to form cavity on right side for hypopygium. Sternite 5 with short broad ventral projection. Segment 7 tubular. Sternite 8 round and setose, forming dome-like cap over anterodorsal region of hypopygium (Fig. 14); tergite 8 narrow, U-shaped. Hypopygium (Figs 4, 10-15): Mainly dark brown. Lateroflexed to right, inverted with posterior end directed anteriorly,  $\frac{1}{3}-\frac{1}{2}$  length of abdomen, asymmetrical, foramen not formed. Epandrium divided into separate left and right lamellae. Left epandrial lamella (Fig. 10) trifurcate with surstylar lobes and ventral epandrial process projecting posteriorly, ventral edge fused with hypandrium but margin distinct. Left ventral epandrial process present, articulated at base, elongate, broadened in middle portion, narrowed apically with acute hooked apex, dorsal margin with pair of small setae near mid-length. Left surstylus bilobed with dorsal and ventral lobes separated by deep U-shaped cleft through which the left postgonite lobe protrudes (Fig. 10). Dorsal lobe of left surstylus large and broad (covering base of cercus), dorsal edge with concave basal emargination (Fig. 14) and rounded subapical protrusion bordering lateroventral margin of left cercus, apical margin rounded with several strong setae (Fig. 10), lacking prensiseta. Ventral lobe of left surstylus narrow, as long as dorsal lobe, with long apical seta and small seta below. Right epandrial lamella (Figs 4, 11–14) greatly enlarged, bowl-shaped, relatively short to elongate (compare Figs 11-13), comprising most of hypopygium in right lateral view; dorsal edge with broad concave emargination bordering lateroventral margin of right cercus; anterior end broadly rounded and weakly projected to subconical and strongly projected (compare Figs 11-13);

posterior end with large dorsal surstylar lobe, small ventral surstylar lobe and ventral conical projection; fused with hypandrium along left margin (Fig. 10). Right ventral epandrial process absent. Right surstylus bilobed with dorsal and ventral lobes separated by cleft through which right postgonite lobe protrudes (Fig. 11). Dorsal lobe of right surstylus large and overlapping ventral lobe, dorsoapical margin rounded to broadly pointed with 3 strong submarginal setae, ventral margin with 1 or 2 basiventral projections and 3 strong marginal setae, lacking prensiseta. Ventral lobe of right surstylus short and broad, with a few marginal setae, mostly covered by dorsal lobe of surstylus. Hypandrium (Fig. 10) reduced to narrow subtriangular band, only visible from left side of hypopygium, with 2 tiny setae near apex. Postgonite with basal internal portion cradling base of phallus and ejaculatory apodeme; left and right postgonite lobes asymmetrical, protruding out from between dorsal and ventral lobes of surstylus. Left postgonite lobe (Fig. 10) narrow and strap-like, apex with narrow dorsal projection bearing a few small setae. Right postgonite lobe (Figs 10, 11, 14) large with expanded complex trilobate apex, bearing prominent thick seta near base of apical lobes. Phallus (Fig. 10) long and tubular, C-shaped, with very slender process medially on right side. Ejaculatory apodeme short and keel-like. Hypoproct (Figs 11, 14) projected as a pair of short asymmetrical lobes directly below cerci, left lobe short and globular with apical setae, right lobe longer and digitiform with apical setae. Cerci (Figs 11, 14, 15) asymmetrical; left cercus broad basally bearing 1 strong seta, with lateroventral margin fitting into dorsal concavity at base of dorsal surstylar lobe, distal portion narrowed and bent laterally, apex compressed laterally and rounded with pair of strong setae; right cercus broad basally bearing 1 strong seta, with lateroventral margin fitting into dorsal concavity near base of dorsal surstylar lobe, evenly tapered distally, with apex narrow (Fig. 14) or expanded and truncate (Fig. 15).

**Female** (Figs 16–18, 31, 32): Body length 1.19–1.67 mm, wing length 1.36–1.67 mm. Similar to male except as follows: **Head:** Face broader, nearly twice width of anterior ocellus at narrowest point in middle. **Legs:** *Foreleg*: Tarsomere 5 smaller with fewer dorsal setae. *Midleg*: Tarsus subequal in length to tibia. *Hindleg*: Femur with short indistinct setae ventrally; tibia straight, without erect setae; tarsus slightly shorter than tibia. **Abdomen** (Figs 31, 32): Tapering posteriorly, apical segments retractable into segment 7. *Terminalia* (Figs 16–18): Tergite 7 U-shaped and mostly desclerotized medially, with setae posteriorly, sternite 7 weakly sclerotized with setae posteriorly; tergite 8 medially divided, narrowly fused with sternite 8 anterolaterally; syntergite 9+10 medially divided into subrect-angular hemitergites, with three acanthophorite setae on each side, widely separated from sternite 10; sternite 10 desclerotized medially; cercus ovoid with several rather long setae, apical seta longest; spermathecal duct unsclerotized, with broad, ridged sperm pump in basal part and textured spherical terminal expansion.

**Distribution.** This new species is known from northern California, USA south to Baja California, Mexico (Fig. 22).

**Etymology.** The species name refers to the short  $R_1$  wing vein in both males and females, a feature shared by all three members of the *M. breviradia* species group.

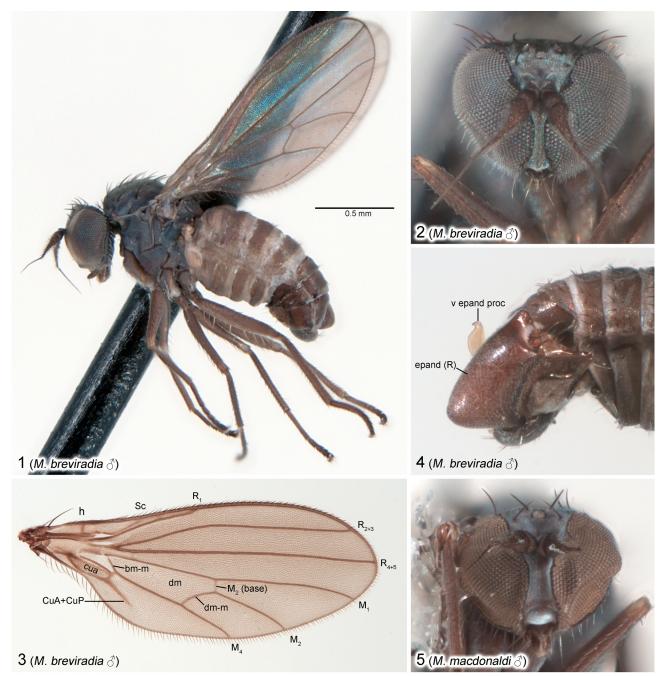
**Remarks.** DNA barcode sequences were obtained and analyzed for 67 specimens (both males and females) of *M. breviradia* (Fig. 24). All were from the type locality of Eagle Rock, American River in central California (Figs 6, 7) and all clustered together with less than 2% genetic divergence from each other. However, these specimens, particularly males, exhibit considerable morphological variation in overall body size, width of the head, length of ventral setae on the hind femur, chaetotaxy of the hind tibia, and in the shape of the right epandrial lamella. This entire *M. breviradia* cluster appears to represent a morphologically variable species, which remains genetically separate from the *M. vespera* cluster (*M. macdonaldi* was not sequenced, see below). Two additional male specimens from Seven Oaks, southern California (CNC576977, CNC574674) that are sympatric (Figs 22, 23) and morphologically similar to *M. breviradia*, did not cluster with either *M. breviradia* or *M. vespera*, indicating that more sampling and sequencing is required to resolve whether these specimens should be included in this variable species concept or represent additional new cryptic species.

# Microphorella macdonaldi sp. nov.

(Figs 5, 23) urn:lsid:zoobank.org:act:07E499E7-A2B0-4A7F-A129-9F3B486D583F

**Type material. HOLOTYPE**, *d* labelled: "CA.Huntington L. [ca. 37°13'N 119°14'W]/ Kaiser C. 2700m/ Fresno Co.17.VIII/ J. MacDonald 1984"; "84-0079"; "Microphorella/ ornatipes/Det. J.F. MacDonald"; "HOLOTYPE/ *Microphorella macdonaldi*/ Cumming & Brooks [red label]" (CNC). **PARATYPES: USA: California:** Same data

as holotype (1 $\bigcirc$ , CNC); same data as holotype except, Rancheria C., 2600m, 20.viii.1984 (1 $\bigcirc$ , CNC); same data as holotype except, Midge C., 2200m, 13.viii.1984 (1 $\bigcirc$ , CNC); Bolsillo Creek at Bolsillo Campground, SW of Mono Hot Springs, 2270 m, 8.viii.1975, Paul H. Arnaud, Jr. (1 $\bigcirc$ , 2 $\bigcirc$ , CAS); Madera County: Chiquito Creek, 0.25 mi below Upper Chiquito Campground, 6820 ft, 11.viii.1971, Hugh B. Leech (2 $\bigcirc$ , CAS).



**FIGURES 1–5.** *Microphorella breviradia* **sp. nov.** and *M. macdonaldi* **sp. nov.** (males). **1.** Habitus of *M. breviradia* **sp. nov.**, left lateral view. **2.** Head of *M. breviradia* **sp. nov.**, anterior view (CNC487231). **3.** Wing of *M. breviradia* **sp. nov.**, anterior view (CNC487241). **4.** Abdomen of *M. breviradia* **sp. nov.**, right lateral view (CNC1155716). **5.** Head of *M. macdonaldi* **sp. nov.**, anterior view (holotype). Abbreviations: bm-m-basal medial crossvein; cua—anterior cubital (=anal) cell; CuA+CuP—anterior branch of cubital vein + posterior branch of cubital vein; dm—discal medial cell; dm-m-discal medial crossvein; epand—epandrium; h—humeral crossvein; M<sub>1</sub>, M<sub>2</sub>, M<sub>4</sub>—medial veins; (R)—right; R<sub>1</sub>, R<sub>2+3</sub>, R<sub>4+5</sub>—radial veins; Sc—subcostal vein; v epand proc—ventral epandrial process.



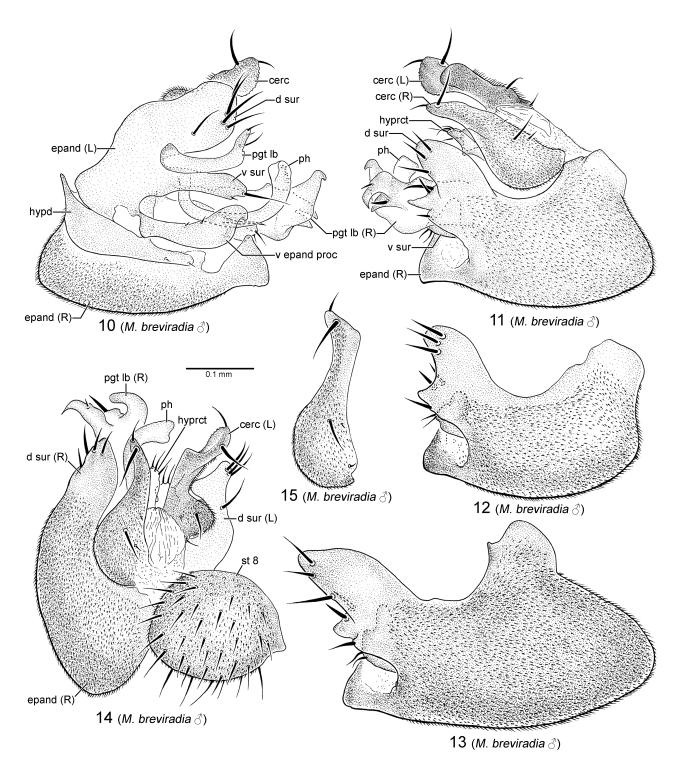
**FIGURES 6–9.** Collection localities and habitats of the *Microphorella breviradia* species group. **6–7.** South Fork of American River (Eagle Rock), California, *M. breviradia* **sp. nov.** type locality (first author pictured in Fig. 7). **8–9.** West Fork of Patrick Creek, California, *M. vespera* **sp. nov.** type locality.

**Diagnosis.** Males of *M. macdonaldi* **sp. nov.** are distinguished by their broad face (Fig. 5) and long dorsal setae on fore tarsomere 5, in contrast to males of *M. breviradia* **sp. nov.** and *M. vespera* **sp. nov.**, which both have a narrow face (as in Fig. 2) and shorter dorsal setae on fore tarsomere 5. The hypopygial morphology of *M. macdonaldi* **sp. nov.** is similar to some specimens of *M. breviradia* **sp. nov.** (see Figs 10, 11). Females of *M. macdonaldi* **sp. nov.** appear to be indistinguishable from those of *M. breviradia* **sp. nov.** and *M. vespera* **sp. nov.** 

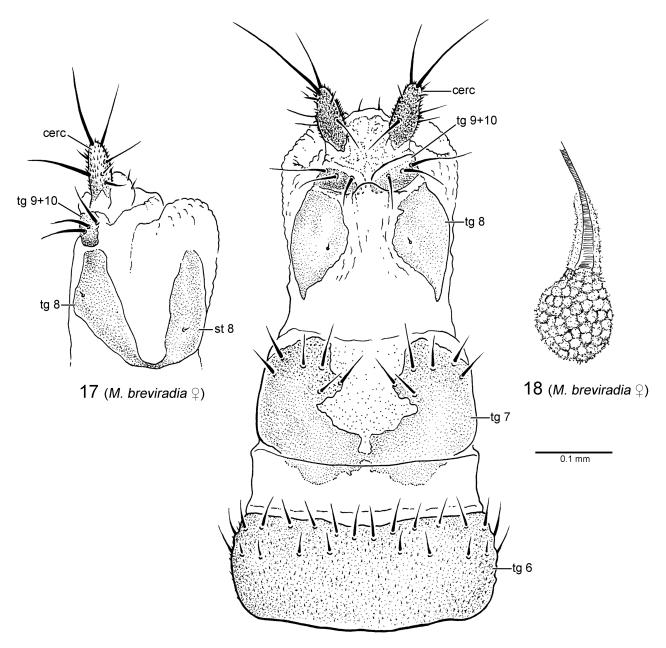
**Description. Male** (Fig. 5): Body length 1.40–1.43 mm, wing length 1.67–1.78 mm. Similar to *M. breviradia* **sp. nov.** except as follows: **Head** (Fig. 5): Slightly broader than high in anterior view, not wider in occasional specimens. Face broader, nearly twice width of anterior ocellus at narrowest point in middle. Antenna with postpedicel slightly shorter, about 2X longer than wide, conical and gradually tapered distally; arista-like stylus slightly longer, about 2X length of postpedicel. **Thorax:** Dorsum and pleura with brighter metallic blue-grey coloration, dorsum with reduced greenish-bronze region posteriorly. **Legs:** Femora and tibiae dark grey-brown. *Foreleg:* Tarsomere 5 slightly larger, with tuft of longer dorsal setae. *Hindleg:* Femur with series of ventral setae pale, as long as femur width; tibia straight, without erect setae; tarsus slightly shorter than tibia (>0.7X tibia length). **Abdomen:** Dark brown with bluish grey tinge. *Hypopygium:* Right epandrial lamella with anterior end slightly projected. Dorsal lobe of right surstylus with 2 basiventral projections and 3 strong marginal setae on ventral margin (similar to Fig. 11). Right cercus with apex narrow (similar to Fig. 14).

**Female:** Body length 1.38–1.49 mm, wing length 1.73–1.79 mm. Similar to male except as follows: **Head:** Face more linear, not narrowed in middle. **Thorax:** Dorsum mostly dull greenish-bronze. **Legs:** *Foreleg*: Tarsomere 5 smaller with fewer dorsal setae. *Hindleg*: Femur with short indistinct setae ventrally. **Abdomen:** Similar to *M. breviradia* **sp. nov.** 

**Distribution.** This new species is known from the Sierra Nevada Mountains in central California, USA (Fig. 23).



FIGURES 10–15. Hypopygium of *Microphorella breviradia* sp. nov. 10. Hypopygium, left lateral view (CNC DIPTERA # 192173). 11. Hypopygium, right lateral view (CNC DIPTERA # 192173). 12. Right epandrial lamella, right lateral view (CNC DIPTERA # 192167). 13. Right epandrial lamella, right lateral view (CNC487206). 14. Hypopygium and sternite 8, dorsal view (CNC DIPTERA # 192173). 15. Right cercus, dorsal view (CNC487206). Abbreviations: cerc—cercus; d sur—dorsal lobe of surstylus; epand—epandrium; hypd—hypandrium; hyprct—hypoproct; (L)—left; pgt lb—postgonite lobe; ph—phallus; (R)—right; v epand proc—ventral epandrial process; v sur—ventral lobe of surstylus.



16 (*M. breviradia* ♀)

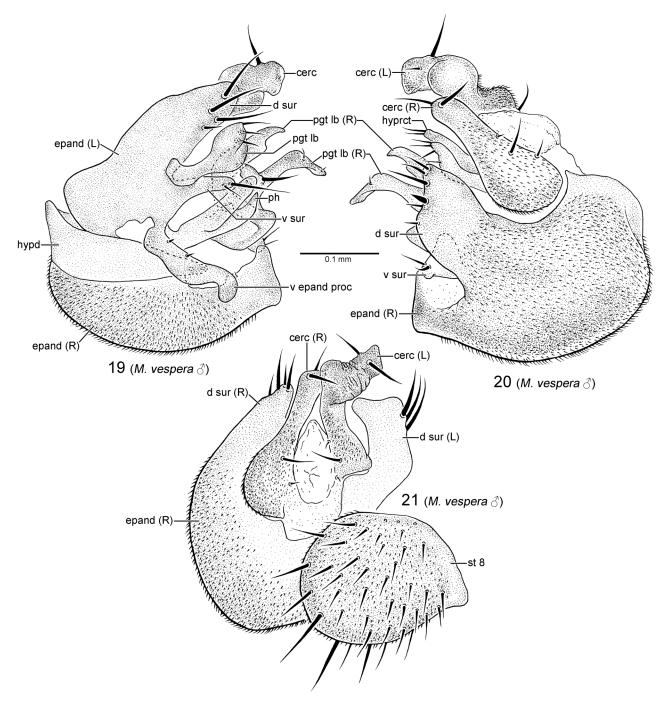
FIGURES 16–18. Female terminalia of *Microphorella breviradia* sp. nov. 16. Terminalia, dorsal view (CNC487214). 17. Terminalia, lateral view (CNC487214). 18. Spermatheca, lateral view (CNC487218). Abbreviations: cerc—cercus; st—sternite; tg—tergite.

**Etymology.** This species is named after the late John F. MacDonald of Purdue University, West Lafayette, Indiana. John was primarily a specialist on Hemerodromiinae, who collected many other valuable Empidoidea, including much of the type series of this new species. His empidoid collection now resides in the CNC.

**Remarks.** No barcode sequences were obtained from the small number of specimens known for this species. The width of the male face in *M. macdonaldi* is relatively broad compared with the narrower face of males of *M. breviradia* or *M. vespera*, resembling the wider face found in *M. breviradia* species group females. Although a broader face is one of the demasculinization features described by Runyon (2022) for nematode infected Dolichopodidae, it does not appear to be the case for males of *M. macdonaldi*, which show no signs of nematode infection.

*Microphorella vespera* sp. nov. (Figs 19–21, 23) urn:lsid:zoobank.org:act:A769BA44-14E6-4FEA-B0A0-536992476C23

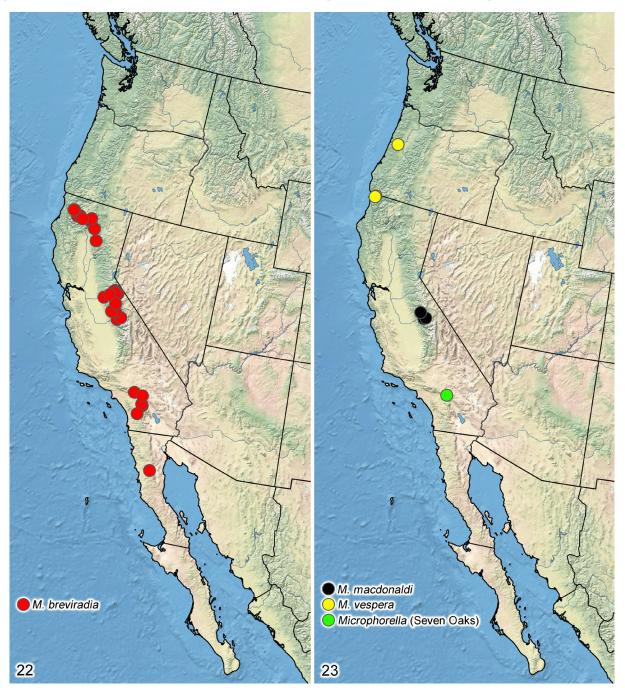
**Type material. HOLOTYPE** ♂ labelled: "USA: CA: Del Norte Co./ West Fork of Patrick Crk./ N41°55′03″ W123°51′28″/ 3.VI.2009, S.E. Brooks"; "HOLOTYPE/ *Microphorella vespera*/ Cumming & Brooks" [red label] (CNC). **PARATYPES: USA: California:** Same data as holotype (2♂, 2♀, CNC); same data as holotype except,



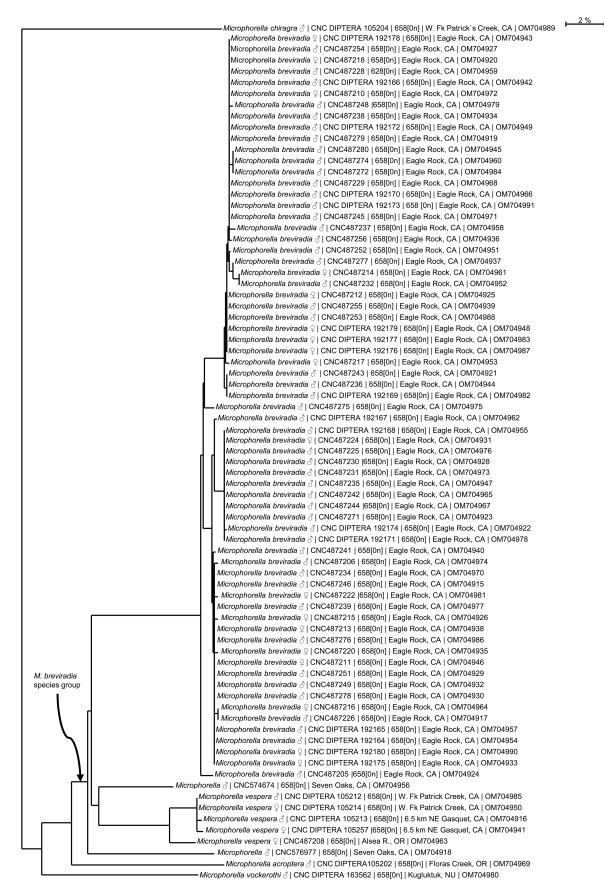
**FIGURES 19–21.** Hypopygium of *Microphorella vespera* **sp. nov.** (CNC DIPTERA # 105212). **19.** Hypopygium, left lateral view. **20.** Hypopygium, right lateral view. **21.** Hypopygium and sternite 8, dorsal view. Abbreviations: cerc—cercus; d sur—dorsal lobe of surstylus; epand—epandrium; hypd—hypandrium; hyprct—hypoproct; (L)—left; pgt lb—postgonite lobe; ph—phallus; (R)—right; v epand proc—ventral epandrial process; v sur—ventral lobe of surstylus.

J.M. Cumming (1 $\Diamond$ , CNC); same data as holotype except, J.M. Cumming, CNC DIPTERA 105212, 105214 (2 $\Diamond$ , CNC); same data as holotype except, 31.v.2009, J.M. Cumming (1 $\Diamond$ , 1 $\heartsuit$ , CNC); same data as holotype except, 31.v-3.vi.2009, YPT, J.M. Cumming & S.E. Brooks (2 $\Diamond$ , 1 $\heartsuit$ , CNC); ca 6.5 mi NE Gasquet nr Cold Spring Mountain, N41°52'15" W123°53'21", S.E. Brooks, CNC DIPTERA 105257 (1 $\heartsuit$ , CNC); same data except, J.M. Cumming, CNC DIPTERA 105213 (1 $\Diamond$ , CNC). **Oregon:** Benton County: North Fork Alsea R., nr. fish hatchery, N44°25'14.0" W123°33'47.8", 115 m, 5.vii.2014, S.E. Brooks, CNC 487208 (1 $\heartsuit$ , CNC, see "Remarks").

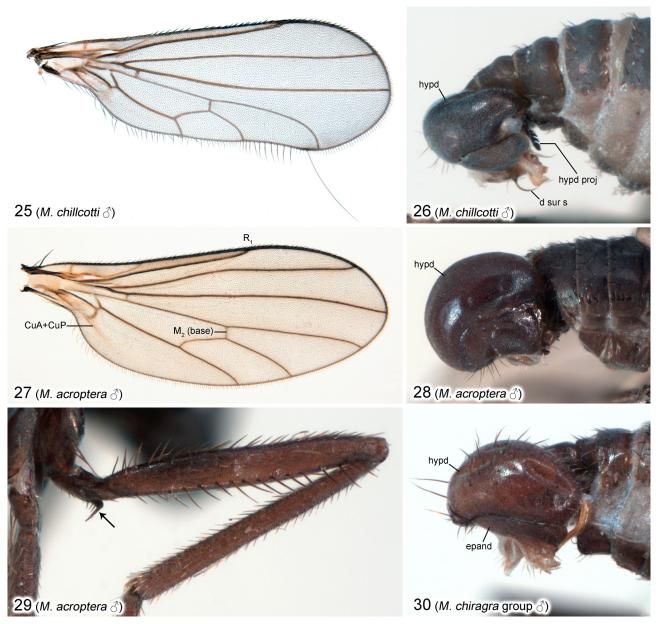
**Diagnosis.** Males of *M. vespera* **sp. nov.** are distinguished from those of *M. breviradia* **sp. nov.** and *M. mac-donaldi* **sp. nov.** by the following combination of features: narrow face (similar to Fig. 2); right dorsal surstylar lobe without basiventral projection(s) (Fig. 20); phallus short, stout and bifid (Fig. 19). Females of *M. vespera* **sp. nov.** appear to be indistinguishable from those of *M. breviradia* **sp. nov.** and *M. macdonaldi* **sp. nov.** 



FIGURES 22–23. Known geographical distribution of the *Microphorella breviradia* species group. 22. *M. breviradia* sp. nov. 23. *M. macdonaldi* sp. nov., *M. vespera* sp. nov. and specimens from Seven Oaks, California (see "Remarks" in text under *M. breviradia* sp. nov.).



**FIGURE 24.** Neighbour-joining tree of 74 specimens of the *M. breviradia* species group and three outgroup specimens, including unique voucher number, sequence length, geographic locality and GenBank number.



**FIGURES 25–30.** Males of the *Microphorella chillcotti*, *M. acroptera* and *M. chiragra* species groups. **25.** Wing of *M. chillcotti* Brooks & Cumming, right lateral view. **27.** Wing of *M. acroptera* Melander. **28.** Abdomen of *M. acroptera* Melander, right lateral view. **29.** Left hind leg of *M. acroptera* Melander, anterior view (arrow indicating spine-bearing tubercle on trochanter). **30.** Abdomen of *Microphorella* sp. 15 (*M. chiragra* species group), right lateral view. Abbreviations: CuA+CuP—anterior branch of cubital vein + posterior branch of cubital vein; d sur s—dorsal lobe of surstylus seta; epand—epandrium; hypd—hypandrium; hypd proj—hypandrial projection;  $M_2$ —second medial vein;  $R_1$ —first radial vein.

**Description. Male** (Figs 19–21): Body length 1.25–1.57 mm, wing length 1.38–1.41 mm. Similar to *M. breviradia* **sp. nov.** except as follows: **Head:** Slightly broader than high in anterior view, not wider in occasional specimens. Antenna with postpedicel conical and gradually tapered distally; arista-like stylus slightly shorter, 0.8–1.1X length of postpedicel. **Thorax:** Usually 6 dorsocentrals (one male paratype apparently with 5). **Legs:** *Midleg*: Tarsus subequal in length to tibia. *Hindleg*: Femur with series of ventral setae at most as long as femur width; tibia straight, without erect setae; tarsus slightly shorter than tibia (>0.7X tibia length). **Wing:**  $R_1$  terminating near midpoint of wing. **Abdomen:** *Hypopygium* (Figs 19–21): Left ventral epandrial process narrowed preapically with apex expanded and rounded, dorsal margin with pair of small setae in basal half. Right epandrial lamella with anterior end broadly rounded and weakly projected; posterior end with broad ventral conical projection. Dorsal lobe of

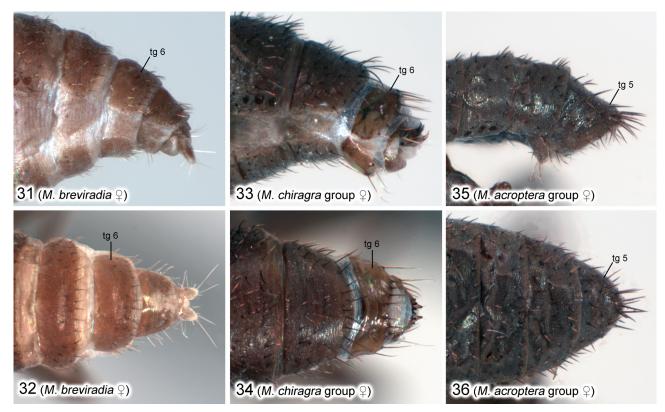
right surstylus with dorsoapical margin broadly pointed with several strong marginal setae, ventral margin broadly rounded, without basiventral projections. Left postgonite lobe narrow basally, apical half enlarged with broad dorsal projection bearing a few small setae. Phallus stout and bifid, bearing thick process ventrally. Hypoproct with left lobe expanded basally, both lobes with apical setae. Left cercus slightly broadened basally, distal portion strongly bent laterally and wrinkled, apex compressed laterally and subrectangular. Right cercus with apex slightly expanded and broadly rounded.

**Female:** Body length 1.23–1.35 mm, wing length 1.32–1.54 mm. Similar to male except as follows: **Head:** Face broader, nearly twice width of anterior ocellus at narrowest point in middle. **Legs:** *Hindleg*: Femur with short indistinct setae ventrally. **Abdomen:** Similar to *M. breviradia* **sp. nov.** 

**Distribution.** This new species is known from the Coast Range of central Oregon and northern California, USA (Fig. 23).

**Etymology.** From the Latin word *vesper* meaning west, in reference to the western Nearctic distribution of this species.

**Remarks.** One female specimen (CNC487208) from Alsea River in Oregon, which appears morphologically identical to other specimens of *M. vespera*, yielded a barcode sequence with slightly greater than 2% genetic divergence (*i.e.*, 2.67%) from the remainder of the *M. vespera* barcode cluster that contained both males and females from northern California (Fig. 24). Although the reason for this increase in genetic divergence is unknown, it could be due to factors such as differences in initial specimen preservation, or a lack of sampling and sequencing of specimens between both the California and Oregon geographic localities.



FIGURES 31–36. Female abdomens of the *Microphorella breviradia*, *M. chiragra* and *M. acroptera* species groups. 31. *M. breviradia* sp. nov., left lateral view. 32. *M. breviradia* sp. nov., dorsal view. 33. *Microphorella* sp. 1 (*M. chiragra* species group), left lateral view. 34. *Microphorella* sp. 1 (*M. chiragra* species group), dorsal view. 35. *Microphorella* sp. 8 (*M. acroptera* species group), left lateral view. 36. *Microphorella* sp. 8 (*M. acroptera* species group), dorsal view. Abbreviation: tg—tergite.

# Key to the species groups of Microphorella in the Nearctic Region

1 Wing with  $R_1$  vein short, terminating at or before midpoint of wing (Fig. 3); female syntergite 9+10 with acanthophorous setae (Figs 16, 17, 31, 32); male terminalia with right epandrial lamella greatly enlarged and comprising most of hypopygium in right lateral view (Figs 4, 11, 20), hypandrium reduced to narrow subtriangular band, only visible from left side of hypopygium (Figs

10, 19) ..... M. breviradia species group Wing with R<sub>1</sub> vein long, terminating beyond midpoint of wing (Figs 25, 27); female syntergite 9+10 with acanthophorous spines (Figs 33, 34); male terminalia with right epandrial lamella smaller than hypandrium in right lateral view, hypandrium 2 Wing with vein CuA+CuP absent; male wing with long apicoventral seta on hind margin (Fig. 25); male fore tibia and tarsomere 1 with row of posterior comb-like setae; male mid trochanter and mid femur each with strong basiventral seta; hypopygium with elongate medial hypandrial projection and dorsal surstylar lobe with strong sickle-shaped seta (Fig. 26); female abdominal tergite 5 medially with some slender submarginal setae, tergite 6 mainly glaborous ... M. chillcotti species group Wing with vein CuA+CuP extending slightly beyond cell cua, sometimes faint (Fig. 27); male wing without long apicoventral seta on hind margin; male fore tibia and tarsomere 1 without comb-like setae; male mid trochanter and mid femur each without strong basiventral seta; hypopygium without elongate medial hypandrial projection and dorsal surstylar lobe without strong sickle-shaped seta (Figs 28, 30); female abdominal tergite 5 or 6 usually with either stout median or stout marginal setae (Figs 3 Male hind trochanter with spine-bearing tubercle (Fig. 29); male terminalia with bare hypandrium (Fig. 28); female abdominal tergite 5 usually with cluster of stout median setae (Figs 35, 36), female abdominal tergite 6 without row of stout marginal setae Male hind trochanter without spine-bearing tubercle; male terminalia with setose hypandrium (Fig. 30); female abdominal tergite 5 without cluster of stout median setae, female abdominal tergite 6 usually with row of stout marginal setae (Figs 33, 34) 

# Discussion

The *M. breviradia* species group is distinguished by several characters, including uniquely modified synapomorphic male terminalia with a greatly enlarged right epandrial lamella in conjunction with a narrow reduced hypandrium positioned on left side of hypopygium. Most of the remaining diagnostic characters also occur elsewhere within the Parathalassiinae. Some of these features, such a short R<sub>1</sub> vein and a hypopygium with the epandrium and hypandrium partially fused together, are generally not found in groups that are currently classified within Microphorella (except the *M. malaysiana* species group, see Shamshev & Grootaert 2004). In the phylogenetic analysis of the Parathalassiinae by Cumming & Brooks (2019), Microphorella was determined to be both paraphyletic and polyphyletic, and made up of at least 12 species groups worldwide. Also, there was no evidence in their analysis that the four Nearctic species groups of *Microphorella* form a single monophyletic group. The *M. breviradia* species group (as the "Microphorella short R<sub>1</sub> species group") was found to be more distantly related to various groups of Microphorella than to some other groups of Parathalassiinae (e.g., Eothalassius). However, the relationships presented by Cumming & Brooks (2019) were only partially resolved and each of the Microphorella species groups analyzed were left within Microphorella in their preliminary classification. Decisions on eventual ranking of the M. brevira*dia* species group and other species groups of *Microphorella*, either as separate genera or possible subgenera within Microphorella, should wait as stated by Cumming & Brooks (2019), for discovery of additional morphological and molecular evidence on phylogenetic relationships within the Parathalassiinae.

The included species in the *M. breviradia* species group are generally restricted to fast flowing rivers and streams in western North America. Fast flowing rivers and streams are poorly collected habitats for small flies throughout this region, and given the huge number of unsampled localities it can be expected that further new species await discovery. Future description of any additional species diversity will test the definition of the *M. brevira-dia* species group and all the included species concepts described herein.

# Acknowledgements

We thank the following curators and their respective institutions for loan of specimens: Stephanie Boucher (LEMQ); Lynn Kimsey and Steven Heydon (UCDC); Allen Norrbom and Norm Woodley (USNM); Michelle Trautwein and Charles Griswold (CAS). We are grateful to Steve Gaimari (CSCA) for arranging collecting permits for us with the California Department of Parks and Recreation and the California Department of Fish and Wildlife. Thanks also to Jessica Hsiung (CNC) who skillfully inked the illustrations of male and female terminalia. Jeff Skevington (CNC) kindly assisted with sequence interpretation and editing. We would like to acknowledge our colleague, Jade Savage (Bishop's University, Sherbrooke, Quebec), whose single male specimen of *M. breviradia*, which she collected in 1999 from Eagle Rock, alerted us to the existence of this unique species group and notable collection locality. Justin

Runyon (U.S. Forest Service, Bozeman, Montana) and Renato Capellari (Instituto Federal do Triângulo Mineiro, Uberaba, Brazil) kindly reviewed the manuscript.

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