New species of *Braggia* (Hemiptera: Aphididae) on buckwheat in western North America

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Abstract—Species of *Braggia* Gillette and Palmer (Hemiptera: Aphididae: Aphidinae: Aphidini) feed on various buckwheat, *Eriogonum* Michx. (Polygonaceae), species in western North America. Two new species, *Braggia columbiana* Pike **n. sp**. from Washington and Oregon and *Braggia longicauda* Pike **n. sp.** from Washington, Oregon, and northern California, are proposed. Descriptions, diagnoses, illustrations, mitochondrial cytochrome *c* oxidase subunit 1 ''barcode'' sequences, a key to the species of *Braggia*, and notes on biology, distribution, and parasitoid associations are provided.

Résumé—Les espèces de *Braggia* Gillette et Palmer (Hemiptera: Aphididae: Aphidinae: Aphidini) se nourrissent de diverses espèces d'*Eriogonum* Michx. (Polygonaceae) dans l'ouest de l'Amérique du Nord. Nous proposons deux nouvelles espèces, *Braggia columbiana* Pike **n. sp.** des états de Washington et d'Oregon et *Braggia longicauda* Pike **n. sp.** du Washington, de l'Oregon et du nord de la Californie. Nous fournissons des descriptions, des illustrations, des séquences des "codes à barres" COI et une clé des espèces de *Braggia*, ainsi que des notes sur leur biologie, leur répartition et leurs associations de parasitoïdes.

[Traduit par la Rédaction]

Introduction

Aphids classified in the genus *Braggia* Gillette and Palmer are known only from western North America and feed and reproduce strictly on buckwheat (*Eriogonum* Michx., Polygonaceae). Morphologically they are similar to aphids in the genus *Aphis* L.: typically they have marginal tubercles on abdominal segments I and VII, with the latter positioned posteroventral of the spiracle.

The genus *Braggia* was established by Gillette and Palmer (1929) based on *B. echinata* Gillette and Palmer and characterized by short antennae, processus terminalis subequal to basal length of ultimate antennal segment, reticulated dorsum with heavily set coarse blunt rodlike setae, and semicircular

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cauda. As species and subspecies were added to *Braggia* (Hottes 1950; Hille Ris Lambers 1966) the descriptive concept of the genus was broadened. Recently, Blackman and Eastop (2006) characterized the genus as having a combination of short processus terminalis, short siphunculi, very short and broad cauda, and strongly reticulated dorsum with variably developed dark sclerotization.

We describe two new species of *Braggia* initially discovered along the eastern slopes and foothills of the Cascade Mountains and the upper reaches of the Columbia River Gorge (Washington State, United States of America). Descriptions, illustrations, biology, distribution, DNA sequence information, parasitoid associations, diagnoses, and a key to species of *Braggia* are provided.

Materials and methods

Species descriptions and character measurements are based on specimens from the authors' field collections (specimens are deposited mainly in the Prosser collections at Washington State University, Prosser (WSU)) and comparison with known species in other collections, including holdings of the Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa (CNC); Colorado State University, Fort Collins (CSU); Essig Museum of Entomology, University of California, Berkeley (EME); Museum National d'Histoire Naturelle, Paris, France (MNHN); North Carolina State University, Raleigh (NCSU); Oregon State University, Corvallis (OSU); University of Idaho, Moscow (UI); Utah State University, Logan (USU); National Museum of Natural History Aphidoidea Collection, Beltsville, Maryland (USNM); and the private collection of A.S. Jensen, Moses Lake, Washington (ASJ).

Aphids were field-collected in the United States of America from various species of *Eriogonum* from a range of sites in Washington State and a limited number of sites in California, Colorado, Montana, Oregon, Utah, and Wyoming. Specimens were preserved in 70%–95% ethanol, then later cleared and slide-mounted in Canada balsam following Foottit and Maw (2000) or Hille Ris Lambers (1950) with modifications by D. Voegtlin (Illinois Natural History Survey, Champaign) (see Pike *et al.* 1991).

New species were identified on the basis of morphological characters, DNA sequence data, host range, distribution, and comparison with known species of *Braggia*. Descriptive terminology follows Foottit and Richards (1993) and Pike *et al*. (2003).

The following abbreviations are used in the species accounts. Aphid morphs: al, alate vivipara; ap, aptera vivipara; im, immature; m, alate male; ov, ovipara. Morphological characters: ABD, abdomen or abdominal; ANT, antenna; ASI, ASII, etc., antennal segment I, II, etc.; BVI, basal length of ultimate antennal segment (part up to and including primary rhinarium); bdIII, basal diameter of antennal segment III; FT, frontal antennal tubercles; L/W, length/width ratio; PT, processus terminalis of ultimate antennal segment (*i.e*., part beyond primary rhinarium); 2° RHIN, antennal secondary rhinaria; SIPH, siphunculus; URS, ultimate rostral segment (penultimate and ultimate segments, IV + V). Others: CG, campground; coll., collector; Cr., creek; Dr., Drive; E, east; Exp., Experimental; FR, forest road; Ft, Fort; Hwy, Highway; Mt, Mount; Mtns, Mountains; N, north; Rd, road; S, south; W, west. Identifying letters in authors' collection codes are as follows unless otherwise indicated: G, G. Graf; K, K.S. Pike (*e.g*., 97G176).

Illustrations of aphids were hand-drawn from images taken with a DEC13M digital eyepiece camera through a Zeiss Axiolab compound microscope; morphological measurements (all in millimetres; for orientation of structures measured see Figs. 1–29) and comparisons (see Tables 1 and 2) were derived from image-measuring software by D. Allison (Pike *et al*. 2005).

Sequence data for mitochondrial cytochrome *c* oxidase subunit 1 (COI) (5′-end; "DNA barcoding" region) of exemplar specimens from various collections were compared with those for other species of *Braggia* and representative species of *Aphis* (for a list of species see Table 3) as an indication of molecular coherence and distinctness of the new species relative to currently recognized

Table 1. Measurements, counts, and comparisons of features of *Braggia columbiana* and *B. eriogoni* on species of *Eriogonum* in western North America.

		Aptera vivipara[a]		Alate vivipara[a]	
	Braggia columbiana (holotype)	*Braggia columbiana* (n = 28)	*Braggia eriogoni* (n = 87)	*Braggia columbiana* (n = 26)	*Braggia eriogoni* (n = 24)
Measurement (mm)[b]					
Body	2.31	2.16 (1.41–2.56)	1.62 (1.05–2.10)	2.16 (1.86–2.52)	1.64 (1.38–2.10)
Head (width)	0.53	0.50 (0.42–0.55)	0.41 (0.33–0.49)	0.45 (0.39–0.51)	0.39 (0.33–0.43)
ASI-VI	1.60	1.43 (1.10–1.69)	1.01 (0.61–1.31)	1.52 (1.22–1.79)	1.19 (0.95–1.39)
ASIII	0.47	0.41 (0.30–0.48)	0.29 (0.14–0.42)	0.48 (0.38–0.58)	0.38 (0.31–0.46)
ASIV	0.29	0.27 (0.19–0.34)	0.18 (0.09–0.27)	0.28 (0.20–0.33)	0.21 (0.15–0.25)
ASV	0.25	0.23 (0.16–0.29)	0.16 (0.08–0.21)	0.24 (0.18–0.28)	0.18 (0.11–0.21)
BVI	0.13	0.12 (0.10–0.15)	0.11 (0.08–0.13)	0.12 (0.10–0.14)	0.11 (0.09–0.14)
PT	0.31	0.26 (0.18–0.31)	0.16 (0.11–0.22)	0.27 (0.22–0.34)	0.20 (0.16–0.26)
bdIII	0.03	0.03 (0.02–0.04)	0.02 (0.02–0.03)	0.03 (0.02–0.04)	0.02 (0.02–0.03)
URS	0.23	0.22 (0.19–0.24)	0.16 (0.13–0.19)	0.21 (0.18–0.23)	0.16 (0.13–0.18)
URS (basal width)	0.05	0.06 (0.04–0.08)	0.05 (0.03–0.07)	0.05 (0.04–0.08)	0.05 (0.04–0.06)
Thorax					
Hind femur	0.76	0.67 (0.47–0.81)	0.43 (0.24–0.57)	0.61 (0.50–0.74)	0.45 (0.34–0.54)
Hind tibia	1.30	1.16 (0.84–1.39)	0.74 (0.41–0.99)	1.17 (0.98–1.37)	0.83 (0.67–0.95)
Hind tarsus	0.15	0.14 (0.11–0.16)	0.11 (0.09–0.14)	0.14 (0.13–0.16)	0.12 (0.10–0.14)
Hind tarsus (width)[c]	0.03	0.03 (0.02–0.03)	0.03 (0.02–0.03)	0.02 (0.02–0.03)	0.02 (0.02–0.03)
Hind-tibial seta[d]	0.05	0.04 (0.03–0.06)	0.04 (0.02–0.06)	0.04 (0.03–0.05)	0.04 (0.03–0.05)
Abdomen					
Cauda	0.14	0.13 (0.09–0.16)	0.09 (0.05–0.13)	0.13 (0.11–0.15)	0.10 (0.07–0.12)
Cauda (basal width)	0.18	0.17 (0.13–0.22)	0.14 (0.12–0.19)	0.15 (0.14–0.18)	0.13 (0.11–0.15)
SIPH	0.20	0.19 (0.10–0.26)	0.13 (0.06–0.20)	0.13 (0.09–0.18)	0.11 (0.06–0.18)
SIPH (basal width)	0.17	0.15 (0.10–0.20)	0.07 (0.05–0.12)	0.11 (0.08–0.14)	0.06 (0.03–0.07)
Count					
ASIII 2° RHIN	6	6.7 (0.0–15.0)	4.5 (0.0–22.0)	27.4 (23.0–32.0)	15.5 (8.0–25.0)
ASIV 2° RHIN	8	8.0 (3.0–12.0)	4.4 (1.0–10.0)	10.4 (7.0–16.0)	6.3 (3.0–12.0)
ASV 2° RHIN	2	3.4 (0.0–7.0)	1.2 (0.0–5.0)	4.3 (2.0–6.0)	1.9 (0.0–5.0)
Caudal setae	15	8.7 (5.0–15.0)	5.2 (3.0–8.0)	7.8 (5.0–11.0)	5.1 (4.0–7.0)
URS accessory setae	2	2.0 (2.0–2.0)	2.0 (1.0–3.0)	2.0 (1.0–3.0)	2.2 (2.0–4.0)
Tarsal segment I chaetotaxy	2–2–2	2–2–2	3–3–3, 3–3–2, or 3–2–2	2–2–2	3–3–2 or 3–2–2
Comparison					
ANT/body	0.69	0.67 (0.51–0.83)	0.63 (0.47–0.83)	0.71 (0.62–0.84)	0.73 (0.63–0.86)
(ASIV+V)/ASIII	1.16	1.23 (1.06–1.34)	1.20 (0.94–1.47)	1.07 (0.92–1.17)	1.02 (0.91–1.17)
Cauda (L/W)	0.78	0.75 (0.50–0.89)	0.60 (0.40–0.85)	0.83 (0.68–1.02)	0.77 (0.63–0.96)
Hind tarsus (L/W)	5.04	5.35 (4.14–6.19)	4.54 (3.57–5.40)	5.92 (4.97–6.48)	5.32 (4.52–6.42)
PT/BVI	2.41	2.17 (1.77–2.90)	1.55 (1.03–2.08)	2.28 (1.84–2.97)	1.74 (1.42–2.48)
PT/ASIII	0.66	0.64 (0.55–0.74)	0.59 (0.34–0.83)	0.57 (0.43–0.67)	0.52 (0.43–0.71)
URS (L/W)	4.39	4.01 (2.81–5.89)	3.55 (2.15–4.75)	4.08 (2.91–5.05)	3.52 (2.47–4.37)
URS/hind tarsus	1.57	1.56 (1.40–1.76)	1.43 (1.13–1.94)	1.51 (1.40–1.77)	1.28 (1.13–1.56)
BVI/SIPH basal width	0.74	0.85 (0.59–1.23)	1.59 (0.91–2.42)	1.16 (0.85–1.63)	2.22 (1.42–3.36)

[a]Measurements are given as the mean with the range in parentheses.
[b]Segment lengths are measured, unless otherwise indicated (ANT, antenna; AS, antennal segment; 2° RHIN, secondary rhinaria; bdIII, basal diameter of antennal segment III; BVI, base of antennal segment VI; L/W, length/width ratio; PT, processus terminalis; SIPH, siphunculus; URS, ultimate rostral segment.
[c]Measured at the midpoint of the segment.
[d]The longest seta, measured near the midpoint of the segment.

Table 2. Measurements, counts, and comparisons of features of *Braggia longicauda* and *B. urovaneta* on species of *Eriogonum* in western North America.

		Aptera vivipara[a]		Alata vivipara[a]	
	Braggia longicauda (holotype)	*Braggia longicauda* (n = 63)	*Braggia urovaneta* (n = 43)[b]	*Braggia longicauda* (n = 24)	*Braggia urovaneta* (n = 3)
Measurement (mm)[c]					
Body	2.25	2.21 (1.46–2.85)	1.48 (1.08–1.85)	2.27 (1.40–2.71)	1.60 (1.33–1.82)
Head (width)	0.51	0.47 (0.38–0.54)	0.40 (0.34–0.44)	0.46 (0.38–0.51)	0.41 (0.39–0.42)
ASI-VI	1.76	1.58 (0.95–2.24)	0.93 (0.67–1.16)	1.76 (1.43–2.08)	0.97 (0.65–1.23)
ASIII	0.49	0.44 (0.23–0.66)	0.26 (0.17–0.40)	0.48 (0.39–0.59)	0.33 (0.29–0.38)
ASIV	0.35	0.32 (0.15–0.46)	0.17 (0.10–0.24)	0.34 (0.26–0.45)	0.19 (0.16–0.21)
ASV	0.33	0.29 (0.17–0.40)	0.15 (0.10–0.20)	0.32 (0.25–0.38)	0.18 (0.16–0.18)
BVI	0.17	0.15 (0.11–0.20)	0.11 (0.08–0.16)	0.17 (0.14–0.20)	0.12 (0.11–0.12)
PT	0.27	0.24 (0.18–0.34)	0.15 (0.11–0.19)	0.28 (0.21–0.33)	0.21 (0.18–0.23)
bdIII	0.03	0.03 (0.02–0.04)	0.02 (0.02–0.03)	0.03 (0.02–0.04)	0.02 (0.02–0.02)
URS	0.19	0.17 (0.13–0.24)	0.14 (0.10–0.16)	0.17 (0.13–0.22)	0.15 (0.14–0.18)
URS (basal width)	0.08	0.07 (0.05–0.09)	0.05 (0.04–0.07)	0.07 (0.05–0.10)	0.05 (0.04–0.05)
Thorax					
Hind femur	0.86	0.77 (0.47–0.98)	0.39 (0.26–0.51)	0.77 (0.60–0.93)	0.42 (0.36–0.48)
Hind tibia	1.48	1.32 (0.82–1.71)	0.72 (0.44–0.93)	1.45 (1.19–1.73)	0.81 (0.69–0.91)
Hind tarus	0.22	0.21 (0.17–0.26)	0.12 (0.09–0.15)	0.23 (0.20–0.24)	0.12 (0.11–0.13)
Hind tarsus (width)[d]	0.03	0.03 (0.02–0.03)	0.03 (0.02–0.03)	0.03 (0.02–0.03)	0.02 (0.02–0.02)
Hind-tibial seta[e]	0.03	0.03 (0.02–0.04)	0.02 (0.01–0.03)	0.03 (0.02–0.04)	0.03 (0.02–0.04)
Abdomen					
Cauda	0.19	0.17 (0.13–0.23)	0.10 (0.08–0.12)	0.16 (0.13–0.21)	0.10 (0.09–0.11)
Cauda (basal width)	0.17	0.14 (0.10–0.20)	0.11 (0.08–0.14)	0.13 (0.10–0.16)	0.09 (0.07–0.12)
SIPH	0.16	0.12 (0.06–0.21)	0.14 (0.09–0.18)	0.11 (0.06–0.19)	0.14 (0.09–0.22)
SIPH (basal width)	0.11	0.09 (0.05–0.13)	0.09 (0.06–0.11)	0.07 (0.05–0.09)	0.08 (0.06–0.10)
Count					
ASIII 2° RHIN	0.0	0.0 (0.0–0.0)	0.1 (0.0–2.0)	10.9 (8.0–14.0)	11.5 (7.0–16.0)
ASIV 2° RHIN	0.0	0.0 (0.0–0.0)	0.0 (0.0–0.5)	0.1 (0.0–1.0)	3.0 (0.0–6.0)
ASV 2° RHIN	0.0	0.0 (0.0–0.0)	0.0 (0.0–0.0)	0.0 (0.0–0.0)	0.5 (0.0–1.0)
Caudal setae	7.0	6.5 (4.0–11.0)	7.4 (5.0–10.0)	6.8 (4.0–9.0)	7.3 (7.0–8.0)
URS accessory setae	2.0	2.1 (0.0–4.0)	2.0 (1.0–2.0)	2.1 (0.0–4.0)	2.0 (2.0–2.0)
Tarsal segment I chaetotaxy	3–3–3	3–3–3	3–3–3, 3–3–2, or 3–2–2	3–3–3	3–3–3 or 3–3–2
Comparison					
ANT/body	0.78	0.72 (0.55–0.90)	0.64 (0.49–0.97)	0.78 (0.67–1.09)	0.61 (0.40–0.77)
(ASIV+V)/ASIII	1.39	1.39 (1.20–1.61)	1.25 (0.96–1.60)	1.36 (0.66–1.53)	1.12 (1.03–1.22)
PT/BVI	1.58	1.60 (1.30–1.94)	1.40 (0.76–1.91)	1.61 (1.37–1.94)	1.86 (1.63–1.97)
PT/ASIII	0.54	0.57 (0.43–0.84)	0.62 (0.38–0.94)	0.57 (0.51–0.70)	0.65 (0.61–0.70)
URS (L/W)	2.50	2.57 (1.77–3.25)	2.75 (1.90–3.73)	2.57 (1.43–3.78)	3.46 (2.89–4.35)
URS/hind tarsus	0.86	0.80 (0.64–1.02)	1.19 (0.80–1.51)	0.75 (0.60–0.95)	1.27 (1.20–1.39)
Hind tarsus (L/W)	7.36	7.42 (5.97–9.06)	4.65 (3.03–5.95)	8.57 (7.64–9.56)	5.25 (4.95–5.48)

[a]Measurements are given as the mean with the range in parentheses.
[b]Includes data on 20 specimens of *B. urovaneta* subsp. *pachysiphon*.
[c]Segment lengths are measured, unless otherwise indicated. For an explanation of abbreviations see Table 1.
[d]Measured at the midpoint of the segment.
[e]The longest seta, measured near the midpoint of the segment.

Table 3. Material used for DNA (mitochondrial cytochrome *c* oxidase subunit 1) sequence comparisons.

	Collection code[a]	BOLD specimen ID	GenBank accession No.
Aphis craccivora Koch	—	CNC No. HEM056007	EU710308
Aphis farinosa Gmelin	—	CNC No. HEM055912	EU701331
Aphis gossypii Glover	—	CNC No. HEM050491	EU701395
Aphis helianthi Monell	—	CNC No. HEM010099	EU701429
Aphis lupini Gillette and Palmer	—	CNC No. HEM039463	EU701445
Aphis middletonii Thomas	—	CNC No. HEM051479	EU701449
Aphis nerii B. de Fonscolombe	—	CNC No. HEM012610	EU701470
Aphis pomi de Geer	—	CNC No. HEM033921	EU701478
Aphis varians Patch	—	CNC No. HEM026140	EU701507
Braggia agathona (Hottes)	A8K201	CNC No. HEM061776	GQ377862
	A8K203	CNC No. HEM061782	GQ377861
	A8K204	CNC No. HEM061783	GQ377860
	A8K208	CNC No. HEM061784	GQ377859
Braggia columbiana n. sp. (“*Braggia* sp. B” of Foottit *et al.* 2008)	A4K032	CNC No. HEM052545	EU701543
	A6K076	CNC No. HEM059785	FJ429939
	A7G019	CNC No. HEM058030	FJ429940
	A7K106	CNC No. HEM058085	FJ429941
	A5K057	CNC No. HEM113559	FJ429942
Braggia echinata (Gillette and Palmer)	A8K202	CNC No. HEM061780	GQ377863
Braggia eriogoni eriogoni (Cowen)	A6K085	CNC No. HEM055868	EU701538
	—	CNC No. HEM028589	EU701539
	—	CNC No. HEM026463	EU701540
	—	CNC No. HEM033259	EU701541
	A7K076	CNC No. HEM058074	FJ429943
	A7K061	CNC No. HEM058069	FJ429944
	A7K068	CNC No. HEM058072	FJ429945
	A7G044	CNC No. HEM059784	FJ429946
	A7G091	CNC No. HEM058041	FJ429947
	A7G095	CNC No. HEM058042	FJ429948
	A7G096	CNC No. HEM058043	FJ429949
	A7G011	CNC No. HEM058027	FJ429950
	A8K113	CNC No. HEM061765	GQ377866
	A8K144	CNC No. HEM061773	GQ377865
	A8K145	CNC No. HEM061774	GQ377864
Braggia longicauda n. sp. (“*Braggia* sp. A” of Foottit *et al.* 2008)	A4K031	CNC No. HEM052544	EU701542
	A7K100	CNC No. HEM058081	FJ429951
	A7K105	CNC No. HEM058084	FJ429952
	A7K109	CNC No. HEM058086	FJ429953
	A6K175	CNC No. HEM114012	FJ429954
	A6K176	CNC No. HEM114013	FJ429955
	A7G008	CNC No. HEM058026	FJ429956
	A7G016	CNC No. HEM058028	FJ429957
Braggia urovaneta urovaneta (Hottes)	—	CNC No. HEM054158	EU701545
	A5K176	CNC No. HEM113654	EU701546
	A5K190	CNC No. HEM113666.2	FJ429958
	A8K211	CNC No. HEM061785	GQ377867
Braggia urovaneta pachysiphon Hille Ris Lambers	—	CNC No. HEM054170	EU701544

Note: Full collection data for all samples are available on the Barcode of Life Data System (BOLD) (Ratnasingham and Hebert 2007). Sequence data are available on BOLD as well as on GenBank. *Aphis* sequences and some *Braggia* sequences are from Foottit *et al.* (2008).

[a]Collection codes correspond to collection numbers in material examined listed in the text.

species. Specimen processing and primer details follow Foottit *et al.* (2008). Sequence and collection/taxonomic information for each specimen was entered in the Barcode of Life Data System (BOLD) (Ratnasingham and Hebert 2007). All sequences obtained in this study have been deposited in GenBank (for accession numbers see Table 3). Voucher specimens from the same colonies as sequenced specimens are deposited in WSU or CNC.

Pairwise nucleotide sequence divergences were calculated using the Kimura two-parameter model of base substitution (Kimura 1980); a neighbour-joining tree (Saitou and Nei 1987) was used to illustrate relationships among taxa and population samples. Although distance calculations are based on a particular evolutionary model, the neighbour-joining tree (Fig. 33) represents phenetic sequence divergences among samples, not a phylogenetic hypothesis.

All aphid parasitoids (Hymenoptera) associated with *Braggia* species were reared from individually isolated field collections held in semi-transparent plastic containers on clipped foliage at ambient laboratory temperatures ranging from 20 to 23 ℃ for 30 days. Vouchers are deposited in WSU collections and were identified by P. Starý, K. Pike, and G. Graf using various keys (Smith (1944), Gibson *et al.* (1997), and Pike *et al.* (1997, 2000*b*) for *Aphelinus* Dalman (Aphelinidae) and *Diaeretiella* Starý, *Ephedrus* Haliday, and *Lysiphlebus* Förster (Braconidae); Dessart (1972), Takada (1973), and Fergusson (1980) for *Dendrocerus* Ratzeburg (Megaspilidae); Andrews (1978) for *Alloxysta* Förster, *Lytoxysta* Keiffer, and *Phaenoglyphis* Förster (Charipidae); Gibson *et al.* (1997) for *Asaphes* Walker and *Pachyneuron* Walker (Pteromalidae)), and by comparison with paratypes (*Ephedrus clavicornis* Pike and Starý) and other verified specimens.

Results

Previously described species

Braggia agathona (Hottes, 1950)

All from *Eriogonum corymbosum* Benth. and deposited in WSU unless otherwise indicated. **UNITED STATES OF AMERICA. Colorado:** Mesa Co., Gateway, 27-viii-1948, 14-ix-1948, and 1, 19-x-1948, coll. F.C. Hottes (1 al Type (USNM); 19 ap paratypes, 12 im (CSU); 6 ap, 2 ov morphotypes, 1 m allotype (USNM); 8 ap, 3 im (USU)). **UTAH:** Duchesne Co., Hwy 87, 8 mi. N of Hwy 40, 9-ix-2008, on *Eriogonum* sp., coll. K.S. Pike and L. Pike (1 ap (A8K204)); Wasatch Co., Hwy 40, 10 mi. E of Strawberry Reservoir (3 ap, 1 im (A8K201)) and Hwy 40 and Current Cr. (4 ap (A8K202)), 9-ix-2008, coll. K.S. Pike and L. Pike; Uintah Co., Hwy 121, 20 mi. W of Vernal, 10-ix-2008, *Eriogonum* sp., coll. K.S. Pike and L. Pike (3 ap (A8K208)).

Braggia deserticola deserticola Hille Ris Lambers, 1966

UNITED STATES OF AMERICA. California: Los Angeles Co., 15 mi. E of Gorman, 28-iv-1976, on *Eriogonum* sp., coll. N.N. Youssef and G.F. Bohart (1 al, 1 ap (NCSU), 1 ap (USU)); Monterey Co., Alder Cr., 7-viii-1962, on *Eriogonum* sp., coll. E. Schlinger (3 al (EME)); Riverside Co., Aguanga, 17-i-1964, and Riverside, 14-i-1964, on *E. fasciculatum* Benth., coll. R.C. Dickson and D. Hille Ris Lambers (1 ap, 1 al paratypes (EME), 1 ap paratype (MNHN)). **MEXICO.** 1.2 mi. N of Ensenada, 17-iv-1981, on *E. fasciculatum*, coll. G. Remaudière (5 ap, 1 im (MNHN)).

Braggia deserticola thanatophila Hille Ris Lambers, 1966

UNITED STATES OF AMERICA. California: Inyo Co., 7 mi. E of Big Pine, Tollhouse Springs, 16-vii-1961, on *Eriogonum* sp., coll. R. van den Bosh (2 al, 1 ap paratypes (EME)); Santa Barbara Co., Hwy 154, 5 mi. E of Goleta, 2-ii-1966, on *E. fasciculatum*, coll. C. Lagace (2 al, 2 ap (EME)).

Braggia echinata (Gillette and Palmer, 1929)

UNITED STATES OF AMERICA. Colorado: Larimer Co., Ft Collins, 7-vi-1916, 8-vii-1917, and 6, 12-x-1916, on *Eriogonum* sp., coll. L.C. Bragg (1 ap Holotype (USNM); 12 ap and 5 al paratypes (CSU), 1 ap (USNM)), and 12-x-1948, on *Eriogonum* sp., coll. F.C. Hottes (1 ap

(USNM)). **Utah:** Wasatch Co., Hwy 40 and Current Cr., 9-ix-2008, on *E. corymbosum*, coll. K.S. Pike and L. Pike (16 ap (A8K202)).

Braggia eriogoni (Cowen, 1895)

All from *Eriogonum heracleoides* Nutt. and deposited in WSU unless otherwise indicated. **UNITED STATES OF AMERICA. California:** El Dorado Co., near South Lake Tahoe, along Hwy 50 and Country Club Rd (4 al, 3 ap (A2K086)), Sawmill Rd (2 ap, 3 im (A2K085)), and Pioneer Rd (1 al, 2 ap (A2K092)), 19-vi-2002, on *E. compositum* Dougl. *ex* Benth. and *E. strictum* Benth.; Santa Barbara Co., Santa Cruz Island, 8-v-2006, on *E. arborescens* Greene, coll. D.G. Miller (2 al, 13 ap (A6K085)). **Colorado:** Larimer Co., Rocky Mtns, 17-vii-1998, on *E. umbellatum* Torr., coll. L. Boydston (1 al, 9 ap (98L024, -027, -029, -036 to -038). **Idaho:** Franklin Co., Cub River Canyon, Thomas Spring area, 22-vi-1979, coll. G.F. Knowlton (2 ap, 1 im (USU)); Franklin Basin, 6-viii-1966, on *Eriogonum* sp., coll. G.F. Knowlton and H. Stroyan (2 ap (USU)); Geneva, 27-vi-1996, on *Eriogonum* sp. (96K132). **Montana:** Gallatin Co., along Gallatin River near Big Sky, on *Eriogonum* sp. (1 al, 1 ap (96K119)). **Oregon:** Lane Co., H.J. Andrews Exp. Forest, 20-x-1995, on *Eriogonum* sp., coll. A.S. Jensen (1 al (ASJ)); Umatilla Co., Emigrant Spring, 7-vii-1991 and 20-v-1992, coll. G. Reed (1 al, 4 ap (ASJ)); 5 mi. S of Battle Mountain State Park, 13-vi-2007 (11 ap (A7K061)); near Lehman Hot Springs, 13-vi-2007 (3 al, 10 ap (A7K068)); Union Co., near Starkey, 13-vi-2007 (6 al, 2 ap (A7K076)). **Utah:** Box Elder Co., Willard Basin and Willard Peak, 30-viii-1962, coll. G.F. Knowlton (1 ap, 9 im (USU)); Duchesne Co., near White Rock, 6 mi. W on Ute 7 Rd, 10-ix-2008, *ex E. racemosum* Nutt., coll. K.S. Pike and L. Pike (1 ap (A8K211)). **Washington:** Adams Co., Potholes area, 4-x-2003, on *Eriogonum* sp., coll. A.S. Jensen (1 al male, 3 ap, 5 ov, 3 im (ASJ)); Asotin Co., FR 40, 1.7 mi. from FR 44, 11-vii-1996, coll. T. Miller (1 ap (96T246)); FR 40 and FR 44 junction, 19-vii-1996, on *Eriogonum* sp., coll. T. Miller (1 ap (96T317)); FR 44, 12 mi SW of Wildlife Area, 18-vii-1996, on *Eriogonum* sp., coll. T. Miller (1 al (96T311)); Montgomery Ridge Rd, mile-marker 13.6, 18-vii-1995, on *Eriogonum* sp., coll. T. Miller (1 al, 1 ap (95T260)); Mt Misery, 22-viii-1996, coll. T. Miller (1 ap (96T481)); Schumaker Rd, mile-marker 8, 18-vii-1995, errant on *Cirsium arvense* (L.) Scop. (1 al (95T267)); Benton Co., Rattlesnake Hills, Anderson Ranch, 8-vi-1995 (4 al (95G154)); Columbia Co., FR 46 on ridge above Bluewood, 1-viii-2007 (1 al, 20 ap (A7G095, A7G096, respectively)); 1 mi. E of FR 64 and FR 46 junction, 1-viii-2007 (5 ap (A7G091)); Douglas Co., Chief Joseph Dam, 9-ix-1997, on *E. niveum* Dougl. *ex* Benth. (1 al, 1 ap (97K015)); Ferry Co., near Curlew Lake, Trout Cr., W of Curlew Rd, 13-vii-2007 (2 al, 11 ap (A7G011)), and Hwy 21 at Curlew Lake, 9-vii-2008 (2 al, 2 ap, 1 im (A8K145)); 4 mi. W of Deer Pass on Boulder Cr. Rd, 9-vii-2008 (2 al, 4 ap, 1 im (A8K144)); Franklin Co., Juniper Dunes Wilderness, 23-v-1995, errant on *Achillea millefolium* L. (1 al, 1 ap (95G082)); Palouse Falls, 15-v-2004, on *Eriogonum* sp., coll. A.S. Jensen (1 al (ASJ)); Garfield Co., Central Ferry, 21-vi-1991, host unknown (1 al (91K001)); Thorp, 1-viii-2001, on *E. elatum* Dougl. *ex* Benth. (14 al (A1G245)); Klickitat Co., Bickleton, 7-vi-1994, coll. K. Pike and P. Starý (6 al, 6 ap, 1 im (94/94)); near Bickleton, Cemetery Rd, 1 mi. from Bickleton−Mabton Hwy, 18-vi-1997, on *Eriogonum* sp. (4 ap (97G106)); Old Gile Ranch, 31-v-1995 (1 al, 1 ap (95G099)); Cleveland, 18-vi-1996 (1 al (96K111)); Hwy 14, 10 mi. NE of Roosevelt, 5-iv-1999, on *Eriogonum* sp. (1 ap (99K001)) and W of Alderdale, 14-v-1996, on *E. niveum* (1 ap (96G031)); Kittitas Co., Manastash Rd, 19-vii-2007 (3 ap (A7G044)); Lincoln Co., 4 mi. N of Davenport on Hwy 25, 7-vii-2008, coll. K.S. Pike and L. Pike (2 al, 4 ap (A8K113)); Spokane Co., Tyler, 18-vi-2003 (1 al, 2 ap (A3K064)); Yakima Co., Glade Rd, Donaho Ranch, 7-vii-1997 (1 ap (97G221)) and 0.5 mi. E of Ranch, on *E. microthecum* Nutt. (1 ap (98G065)); Hwy 12 near junction with Hwy 410, 12-ix-2001, on *E. elatum* (7 ap, 16 im (A1G304)); Yakama Nation, Mill Cr. Guard Station, 30-v-1995, on *E. thymoides* Benth. (1 al, 2 ap, 1 im (95K028)). **Wyoming:** Carbon Co., Medicine Bow National Forest,

Battle Cr., 4-vii-2004, coll. A.S. Jensen (8 ap (ASJ)); Teton Co., Alta, 27-vi-1996, on *Eriogonum* sp. (1 al, 1 ap (96K119)).

Braggia uncompahgrensis Hottes, 1950

UNITED STATES OF AMERICA. Colorado: Mesa Co., Gateway, 19-x-1948, coll. F.C. Hottes (ap vivipara, Type (USNM)), 16, 27-viii, 14-ix, 1, 19-x-1948 (12 ap, allo-, morpho-, and paratypes (USNM); 15 ap, 2 im paratypes (CSU)), and 12-viii-1960, on *E. corymbosum*, coll. F.C. Hottes and C.F. Smith (6 ap (UI), 2 ap (USNM), 2 ap (USU)). **Utah:** Uintah Co., Bonanza, 10-ix-1976, on *Eriogonum* sp., coll. G.F. Knowlton and G.E. Bohart (1 ap (USU)).

Braggia urovaneta urovaneta (Hottes, 1950)

UNITED STATES OF AMERICA. Colorado: Mesa Co., Hwy 141, Unaweep Canyon N of Gateway, 24-viii-1948, on *Eriogonum* sp., coll. F.C. Hottes (al vivipara, Type (USNM)), 24, 25, 27-viii-1948, 1, 19-x-1948, and 1-xi-1948, on *Eriogonum* sp. (ap, al, m, ov allo-, morpho-, or topo-types (USNM)), 10-x-1952 (2 ap (EME)), and 12-viii-1960, coll. F.C. Hottes and C.F. Smith (5 ap, 2 al (NCSU); 1 al, 5 ap (UI); 1 al, 1 ap (USNM); 1 al, 3 ap, 1 im (USU)); 10 mi. from Gateway, John Brown Rd, 30-viii-2005, on *E. racemosum*, coll. K.S. Pike and R. Hammon (2 al, 5 ap, 4 im (A5K176)); Uncompahgre Plateau, top of 6.3 Rd, 1-ix-2005, on *E. racemosum,* coll. K.S. Pike and R. Hammon (1 al, 8 ap, 3 im (A5K190)). **Idaho:** Power Co., American Falls, 19-vi-1973, from pan trap, coll. G.W. Bishop (1 al (USNM)). **Utah:** Duchesne Co., Uinta Canyon, 21-vii-1966, on *E. racemosum*, coll. G.F. Knowlton (2 al, 4 ap, 1 im (UI); ap, al (USNM); 1 ap (USU)); near White Rock, 6 mi. W on Ute 7 Rd, 10-ix-2008, *ex E. racemosum*, coll. K.S. Pike and L. Pike (1 al, 6 ap, 1 im (A8K211)).

Braggia urovaneta pachysiphon Hille Ris Lambers, 1966

UNITED STATES OF AMERICA. California: Alameda Co., Berkeley, Botanical Gardens, 30-x-1963, coll. D. Hille Ris Lambers (2 al, 4 ap (EME); 6 al, 9 ap (MNHN)); Los Angeles Co., Catalina Island, 9-xii-2003, on *Eriogonum* sp., coll. A.S. Jensen (3 al, 9 ap, 2 im (ASJ)); Siskiyou Co., Meadow Cr., 10-viii-1962, on *Eriogonum* sp. coll. J. Schuh and B. Peters (im (USNM)).

New species

Braggia columbiana Pike, new species

(Figs. 1−11, 31; Table 1)

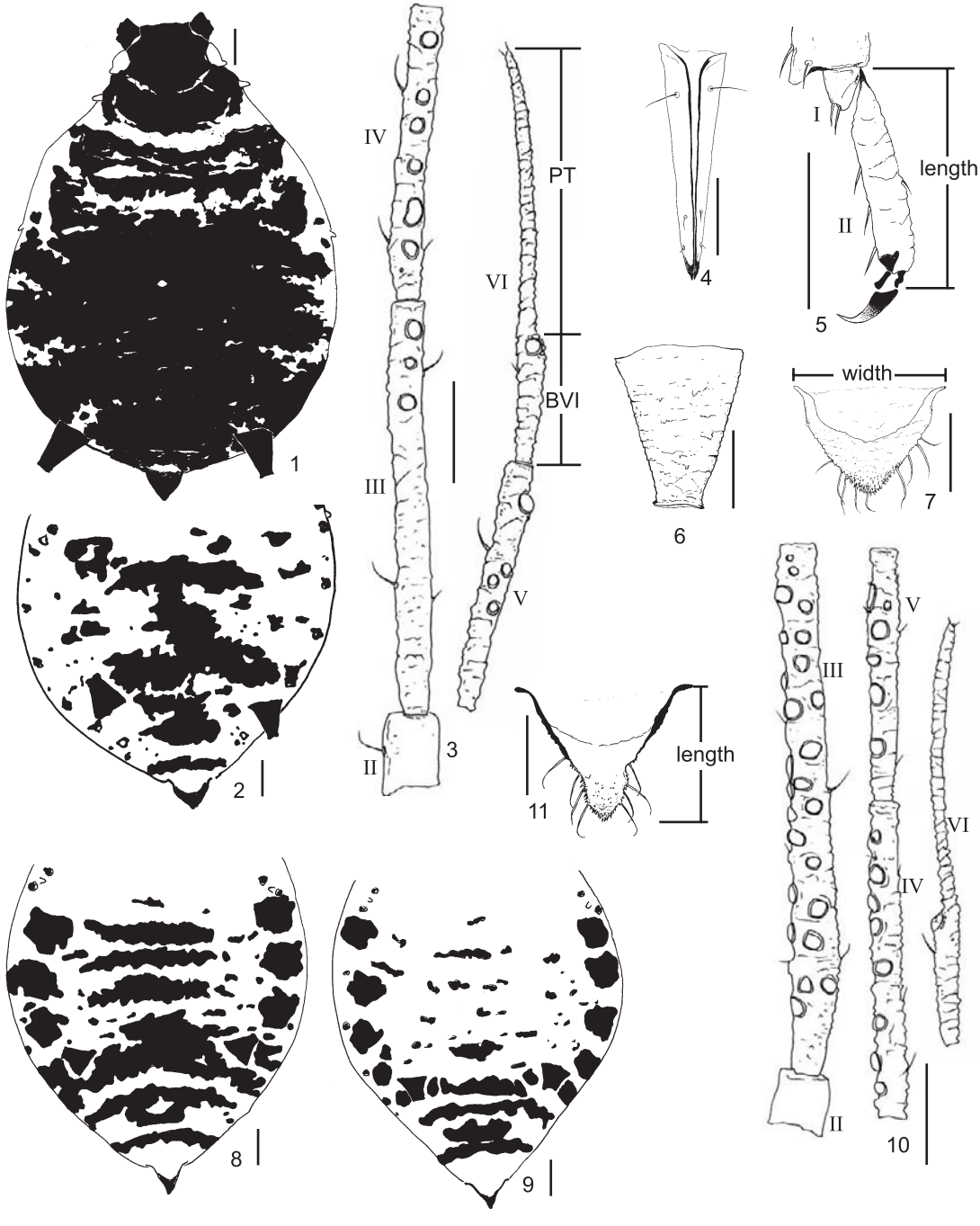
Specimens examined

Holotype (aptera vivipara): **UNITED STATES OF AMERICA. Washington:** Klickitat Co., Columbia Gorge, Catherine Creek (45.7563N, 120.6155W), 12-v-2006, on *Eriogonum compositum*, coll. K.S. Pike (A6K076, deposited in USNM; holotype designation on slide marked in bold red capital letters). *Paratypes*: Paratype designation on slide in bold blue capital letters. **Washington:** Klickitat Co., Columbia Gorge, Catherine Cr. (45.7563N, 120.6155W), 12-v-2006, on *E. compositum* (5 al, 5 ap (A6K076, part in CNC, USNM, and WSU)); Yakima Co., 20 mi N of Naches (46.6957N, 120.9240W), 27-vi-2007, on *E. compositum* (5 al, 14 ap (A7K106, part in CNC, USNM, and WSU)).

Other material

All from *E. compositum* and deposited in WSU unless otherwise indicated. **Oregon:** Umatilla Co., Milton−Freewater, Harris Park, 11-vi-1996 (1 al, 1 ap (96G234)). **Washington:** Columbia Co., Skyline Dr., 8-vii-2005, on *E. umbellatum* (2 al, 5 ap (A5G078)); Grant Co., Rd 14 and Rd 5 NE, v-2003, on *Eriogonum* sp., coll. A.S. Jensen (6 ap, 1 im (ASJ)); King Co., Stampede Pass, 8-viii-2005 (1 al, 1 ap (96G446)); Kittitas Co., Ellensburg Canyon, Umtanum Cr., 26-v-2008, on basal leaves of *E. elatum* (1 al, 3 ap (A8G030)); Hwy 821, mile-marker 23.5, 26-v-2008 (4 al, 8 ap (A8G025, A8G027, A8G028)); Lost Lake Trail, 6-viii-1997 (1 al, 1 ap (97G326), 1 al, 1 ap (97G350)); 3 mi. S of Colockum Ridge Rd, 2-vii-1997 (1 al, 1 ap

Figs. 1–11. *Braggia columbiana*. 1–7, aptera vivipara: 1, adult with extensive dorsal pigmentation; 2, abdomen with reduced dorsal pigmentation; 3, antennal segments II−VI; 4, ultimate rostral segment; 5, hind tarsus; 6, siphunculus; 7, cauda; 8–11, alate vivipara: 8, 9, abdominal dorsal pigmentation, showing extensive and reduced patterns, respectively; 10, antennal segments II−VI; 11, cauda (PT, processus terminalis of ultimate antennal segment; BVI, basal segment VI). Scale bars = 0.1 mm.



(97G190), 1 al, 1 im (A7G193)); Reecer Cr., 27-vii-1998 (7 al, 5 ap (98K024)); Reecer Cr. Grade, 7-vii-1998 (1 al, 1 ap (98G098), 1 al (98G103)); Taneum Cr. Rd, 19-vii-2007 (6 al, 3 ap (A7G019)); Taneum Lake Trail, 11-ix-1997 (1 al (97G42)); Taneum Spring, 3-x-2002 (1 ap (A2K276)); Klickitat Co., Hwy 14, W of Alderdale, 14-v-1996 (1 al, 1 ap (96G035), 2 ap (96G039)) and 0.6 mi. W of Drano Lake, 26-v-2000, on *Eriogonum* sp. (1 ap, 3 im (A5K057)); Klickitat Rd and Outlet Cr., 4-v-2000, on *Eriogonum* sp. (5 ap (A0K039)); near Bickleton, 1 mi. E, 5-vi-1998 (1 al, 1 ap (98G067)), Box Springs, 29-vi-1997 (2 al, 1 ap (97G176)), Cemetery Rd, 18-vi-1997 (3 ap (97G109), 8 al (97G110)), and Old Gile Ranch, 31-v-1998, on *E. umbellatum* (1 ap (95G098), 2 ap (95G100)); Yakima Co., Bethel Ridge Rd, 24-vi-1998, on *E. umbellatum* and *Eriogonum* sp. (4 al, 1 ap (98G123), 3 al, 2 ap (98G125)); Darland Mtn summit, 29-vii-2008, on *E. pyrolifolium* Hook. (4 ap (A8G126); Little Naches River Rd, 28-vi-1997, on *E. strictum* (1 al, 1 ap (97G290)); near Chinook Pass, 0.5 mi. E of summit, 4-ix-2007 (1 al, 6 ap (A7G225)), near Hause CG, 15-vi-1996, on *E. elatum* (1 ap (96K105)), Wenas Lake, 1 mi. S, 11-vi-1997, on *Eriogonum* sp. (4 ap (97G060)), and Yellow Rose CG, Hwy 12, 16-vi-2004 (8 ap, 2 im (A4K032, part in CNC, USNM, and WSU)); Satus Pass, Boundary Rd, 6-vi-2000 (2 al, 2 ap (A0K049)); Yakama Nation, along Klickitat River, 7-vi-1995 (1 ap (95G126)) and Lower Mill Cr., 25-v-1996 (1 ap (95K051)).

Etymology

The species is named after the Columbia River Gorge, the type locality.

Diagnosis

Braggia columbiana is most similar morphologically to *B. eriogoni* (Fig. 30) but is distinguished from all subspecies of *B. eriogoni* by size (adults usually >2 mm *vs.* usually <2 mm), longer URS (0.19–0.24 *vs.* 0.12–0.19 mm), and tarsus I chaetotaxy (2–2–2 *vs.* 3–3–3, 3–3–2, or 3–2–2). Comparative biometric data for the two species (aptera and alate viviparae) are given in Table 1. See the key to distinguish *B. columbiana* from other species of *Braggia*.

Description

Aptera vivipara (Figs. 1–7, 31)

In life, black or blackish brown with white or whitish gray pattern on dorsum; appendages brownish black to brown except for pale basal half of ASIII, front femora, and middle areas of tibia, and semi-pale cauda. Dorsal integument faintly to moderately reticulate on head and ABD dorsum. Body length 1.41–2.56 mm; head width across eyes 0.42–0.55 mm; ANT short, 0.51–0.83 × body length; FT weakly developed; setae on head and ABD stout, tapering, pointed or blunt, usually >1.50 × bdIII; longest seta on ASIII (0.02–0.05 mm) slightly longer than bdIII; 2° RHIN usually on ASIII, -IV, and -V; PT about 2 × BVI (range 1.77–2.90 × BVI); rostrum extending to metacoxa; URS long (0.19–0.24 mm), length >2 × segment width, with 2 accessory setae; pronotum with marginal tubercles; hind-femur length 0.47–0.81 mm, hind-tibia length 0.84–1.39 mm, hind tarsus II length 0.11–0.16 mm; tarsal I chaetotaxy 2–2–2; claws simple; empodial setae acuminate, not quite reaching tip of claws. ABDI and VII with marginal tubercles; SIPH 0.10–0.26 mm long, imbricated, subcylindrical, tapering (narrower at apex than base), and flanged; cauda wider than long (L/W = 0.50–0.89), with a total of 5–15 setae. For a full range of morphological measurements and comparisons, including values for the holotype, see Table 1.

Alate vivipara (Figs. 8–11)

Morphological features generally similar to those of aptera vivipara (see Table 1). ANT with 2° RHIN on III (>20), IV, and V; ABD terga with definite pigmented marginals and usually transverse stripes.

Ovipara and male

Not observed.

DNA characterization

GenBank accession numbers for sequences of COI, 5′-end (DNA barcode), are given in

Table 3. Specimen CNC No. HEM059785 is from the type locality. Comparisons with other samples of *Braggia* (Fig. 33) indicate that specimens of *B. columbiana* form a tight cluster well separated from other species evaluated (species comparisons were limited to available fresh or suitably preserved specimens). The maximum within-species divergence (percent difference) is 0.62%, while the mean distance from the most similar species (*B. eriogoni*) is 3.05% (Table 4).

Biology, hosts, and distribution

The species is monoecious on *Eriogonum* species, predominantly *E. compositum* (72% of collections), less commonly *E. umbellatum* Torr. (19%), and infrequently *E. elatum, E. pyrolifolium* Hook., and *E. strictum* Benth. It is presently known only from Oregon and Washington, having been found along the eastern slopes and foothills of the Washington Cascade Mountains, the upper areas of the Columbia River Gorge, and the Blue Mountains, at elevations ranging from 35 to 1670 m. Aptera and alate viviparae occur from about mid-May to mid-September.

Parasitoids (Table 5)

Lysiphlebus testaceipes (Cresson) (Hymenoptera: Braconidae) was the predominant parasitoid reared. The associated secondary parasitoids were a mix of species from several genera of Hymenoptera (*Alloxysta*, *Lytoxysta*, *Phaenoglyphis*, *Dendrocerus*, *Asaphes*, and *Pachyneuron*).

Braggia longicauda Pike, new species

(Figs. 12–29, 32; Table 2)

Specimens examined

Holotype (aptera vivipara): **UNITED STATES OF AMERICA. Washington:** Yakima Co., 15 mi. N of Naches (46.6957N, 120.9240W), 27-vi-2007, on *Eriogonum elatum*, coll. K.S. Pike (A7K100, deposited in USNM; holotype designation on slide marked in bold red capital letters). *Paratypes*: Paratype designation on slide in bold blue capital letters. **Washington:** Yakima Co., 15 mi. N of Naches (46.6957N, 120.9240W), 27-vi-2007,

Table 4. Summary of pairwise distances between samples (percent difference in mitochondrial cytochrome *c* oxidase subunit 1 sequences) between *Braggia* species (above the diagonal), maximum observed within-species divergence (on the diagonal), and minimum observed distances between samples of *Braggia* species and representative *Aphis* species (right-hand column).

	Braggia agathona	*Braggia columbiana*	*Braggia echinata*	*Braggia eriogoni*	*Braggia longicauda*	*Braggia urovaneta*	Nearest *Aphis* specimen
Braggia agathona ($n = 4$)	1.71	3.30–4.10 (3.54 ± 0.24)	4.76–4.92 (4.88 ± 0.70)	0.77–1.70 (1.13 ± 0.27)	4.60–5.26 (4.85 ± 0.24)	3.13–4.10 (3.73 ± 0.30)	6.41 (*A. varians*)
Braggia columbiana ($n = 6$)		0.62	5.76–5.92 (5.8 ± 0.70)	2.65–3.29 (3.05 ± 0.15)	4.61–4.93 (4.67 ± 0.71)	3.45–4.75 (4.19 ± 0.41)	6.73 (*A. middletoni*)
Braggia echinata ($n = 1$)			na	4.26–4.59 (4.42 ± 0.96)	6.61 (6.61 ± 0)	4.44–4.93 (4.83 ± 0.20)	7.10 (*A. helianthi*)
Braggia eriogoni ($n = 15$)				0.31	4.76–5.09 (4.90 ± 0.11)	3.29–4.10 (3.71 ± 0.24)	6.22 (*A. middletoni*)
Braggia longicauda ($n = 8$)					0	3.95–4.96 (4.40 ± 0.27)	7.10 (*A. farinosa*)
Braggia urovaneta ($n = 5$)						1.39	5.59 (*A. varians*)

Note: Between-species values are given as the range, followed by the mean ± standard deviation in parentheses, for all pairwise comparisons of the two species. *Braggia urovaneta* includes *B. u. urovaneta* and *B. u. pachysiphon* (na, not available).

Table 5. Primary and secondary parasitoids associated with the aphids *Braggia columbiana*, *B. eriogoni*, and *B. longicauda* in the western United States of America.

		Primary parasitoid[a]					Secondary parasitioid[b]					
	n^c	Ap	Dr	Eca	Ecl	Lt	n^d	Allox	Lytox	Phae	Dend	Asap	Pachy
B. columbiana	78	16 (0.8)	0 (0.0)	16 (0.8)	0 (0.0)	1877 (98.3)	44 (56.4)	52 (8.2)	37 (5.8)	45 (7.1)	14 (2.2)	8 (1.3)	477 (75.4)
B. eriogoni	30	0 (0.0)	0 (0.0)	1 (0.2)	0 (0.0)	596 (99.8)	12 (40.0)	23 (13.5)	8 (4.7)	8 (4.7)	0 (0.0)	0 (0.0)	131 (77.1)
B. longicauda	38	0 (0.0)	1 (0.1)	0 (0.0)	3 (0.3)	978 (99.6)	15 (39.5)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	1 (0.4)	222 (99.6)

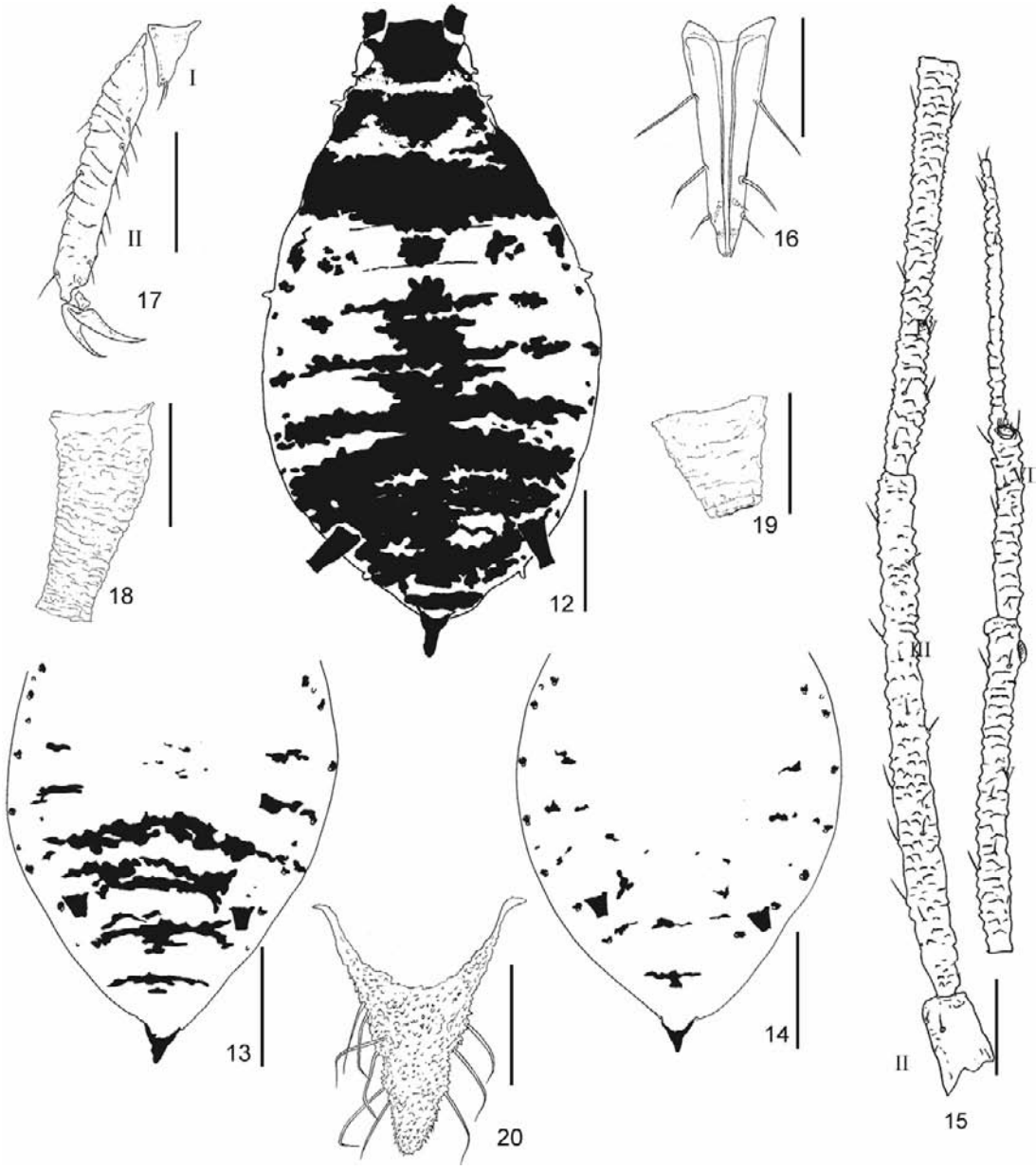
Note: Values are given as the total number reared, followed by the percentage of total rearings per aphid species in parentheses.
[a]Aphelinidae: Ap, *Aphelinus* Dalman. (Braconidae, Aphidiinae); Dr, *Diaeretiella rapae* (McIntosh); Eca, *Ephedrus californicus* Baker; Ecl, *Ephedrus clavicornis* Pike and Starý; Lt, *Lysiphlebus testaceipes* (Cresson).
[b]Charipidae, Alloxystinae: Allox, *Alloxysta* Förster; Lytox, *Lytoxysta* Keiffer; Phae, *Phaenoglyphis* Förster. Megaspilidae: Dend, *Dendrocerus* Ratzeburg. Pteromalidae: Asph, *Asaphes* Walker; Pachy, *Pachyneuron* Walker.
[c]Number of collections with reared parasitoids.
[d]Number of parasitized collections with secondary parasitoids, followed by the percentage in parentheses.

on *E. elatum*, coll. K.S. Pike (9 ap (A7K100, part in CNC, USNM, and WSU)); Klickitat Co., 1.4 mi. NW of Blockhouse (46.0569N, 121.6703W), 23-viii-2006, on *E. elatum* (4 al, 13 ap (A6K176, part in CNC, USNM, and WSU)); Yakima Co., Ahtanum, 3-vi-1994, on *E. compositum* (4 al, 7 ap (94–073, WSU)); Hwy 97, 7.5 mi. NE of Satus Pass (45.8535N, 120.9523W), 23-viii-2006, on *E. elatum*, coll. K.S. Pike and L. Pike (2 al, 9 ap (A6K175, WSU)).

Other material

All from *E. elatum* and deposited in WSU unless otherwise indicated. **California:** El Dorado Co., South Lake Tahoe near Regan Beach, 19-vi-2002 (4 al, 6 ap (A2K083)). **Oregon:** Klamath Co., Klamath Falls, 22-ix-1946, host unknown (ap, im (6 slides, USNM)). **Washington:** Kittitas Co., 10 mi. S of Ellensburg, 26-vi-1960, on *Eriogonum* sp., coll. E. Schlinger (2 al, 2 ap (EME)); Ellensburg Canyon, Big Pines CG, 7-vii-2007 (5 ap (A7G008)) and 6-vi-2008 (2 al, 4 ap, 1 im (A8G033)), and Umtanum Cr. Trail, 26-v-2008 (A8G029); Reecer Cr., 20-vi-1995 (1 al (95G213)); Taneum Cr. Rd, 3-x-2007 (9 ap (A7G016)); Taneum Spring, 3-x-1995 (1 m, 4 ov (A2K279)); Klickitat Co., Blockhouse, 7-vi-1995 (2 ap (95G141)); Yakima Co., Bear Cr. near Rimrock Lake, 9-vi-1995, coll. D. Allison (1 ap (95A006)); Ft Simcoe, 6-vi-1995, on *E. compositum* and *Eriogonum* sp. (2 al (95G117), 2 ap (95G141)); Hwy 12, 1-vii-1995 (1 al, 1 ap (95K040)), several miles W of Hwy 410 junction, 16-viii-1995, on *E. compositum*, coll. D. Allison (3 al, 4 ap (95A031)), and near Yellow Rose CG, 16-vi-2004 (4 al, 4 ap (A4K031)); Hwy 410, 1 mi. from junction with Hwy 12, 28-vii-1997 (1 al, 1 ap (97G276)); Naches, 9-vi-1994 (7 al, 1 ap, 1 im (94–139)) and 20 mi. N, 28-vii-2007 (7 ap (A7K105)); near Clear Lake, 5 mi. N, 27-vi-2007 (1 al, 6 ap (A7K109)); Oak Cr., 2 mi. from Hwy 12, 25-vi-1995, on *Eriogonum* sp., coll. L. Boydston (1 ap (95L014)); Satus Pass, 7-vi-1995, on *Eriogonum* sp. (1 al (95G142)); Wenas Rd, 2 mi. SE of Wenas Lake, 11-ix-1996 (1 ap (96G557); White Swan, 6- vi-1995, on *E. compositum* (3 al (95G111)); Windy Point CG, 3-vi-1995 (16 al, 7 ap, 2 im (95G105, part in CNC, USNM, and WSU)); Yakama

Figs. 12–20. *Braggia longicauda*, aptera vivipara: 12, adult with extensive abdominal dorsal pigmentation; 13, 14, abdomen with reduced dorsal pigmentation; 15, antennal segments II−VI; 16, ultimate rostral segment; 17, hind tarsus; 18, siphunculus, long form; 19, siphunculus, short form; 20, cauda. Scale bars: 0.5 mm (12–14); 0.1 mm (15–20).

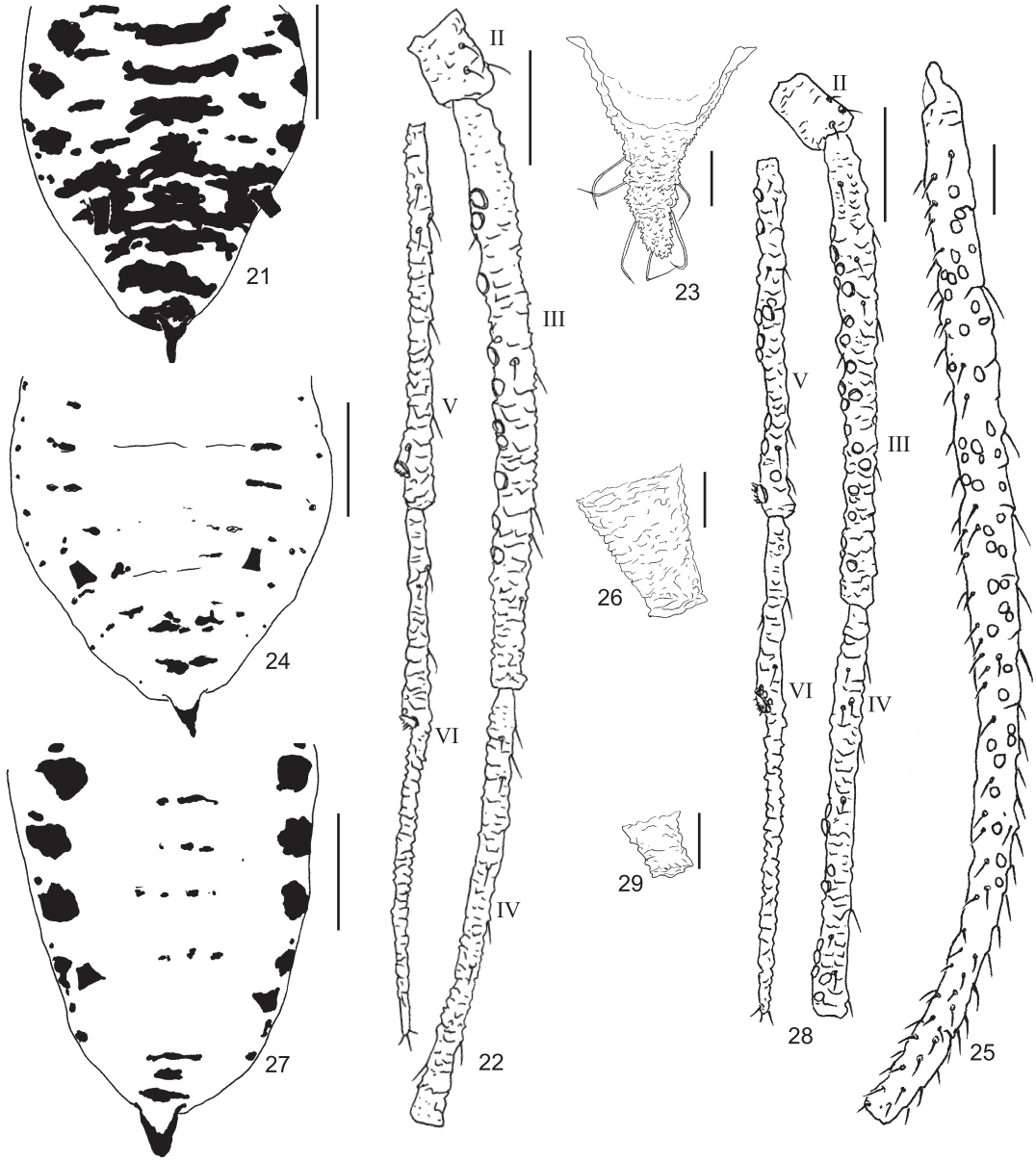


Nation, Mill Cr., 19-ix-1995 (1 ap, 4 m, 1 ov (95G605)), Cedar Cr. (1 ap, 3 ov (95G626)), on *E. compositum*, and near Signal Peak, 19-ix-1996 (1 ap (96G575).

Etymology

The name is based on the relatively long cauda of this species compared with those of other species of *Braggia*.

Figs. 21–29. *Braggia longicauda*. 21–23, alate vivipara: 21, abdomen; 22, antennal segments II−VI; 23, cauda; 24–26, aptera ovipara; 24, abdomen; 25, hind tibia with pseudosensoria; 26, siphunculus; 27–29, alate male: 27, abdomen; 28, antennal segments II−VI; 29, siphunculus. Scale bars: 0.5 mm (21, 24, and 27); 0.1 mm (22, 25, and 28); 0.05 mm (23, 26, and 29).



Diagnosis

Braggia longicauda is most similar morphologically to *B. urovaneta* but is distinguished from both subspecies of *B. urovaneta* by body size (length of apterous adult usually >2.00 mm *vs.* usually <1.50 mm), cauda length 0.13–0.23 *vs.* 0.08–0.12 mm, hind tarsus II length 6–9 *vs.* <6 × width at midpoint of segment), and tarsus I chaetotaxy 3–3–3 *vs.* usually 3–3–2 or 3–2–2 (3–3–3 in some

Figs. 30–32. Live specimens of *Braggia* species: 30, *B. eriogoni* (A3K064); 31, *B. columbiana* (A8G027); 32, *B. longicauda* (A8G029).

B. u. pachysiphon from California). *Braggia longicauda* further differs from *B. urovaneta* in its host-plant range (on *E. elatum* and *E. compositum vs. E. corymbosum*, *E. latifolium* Sm., or *E. nudum* var. *nudum* Dougl. *ex* Benth.). Comparative biometric data for the two species (aptera and alate viviparae) are given in Table 2. See the key to distinguish *B. longicauda* from other species of *Braggia*.

Description

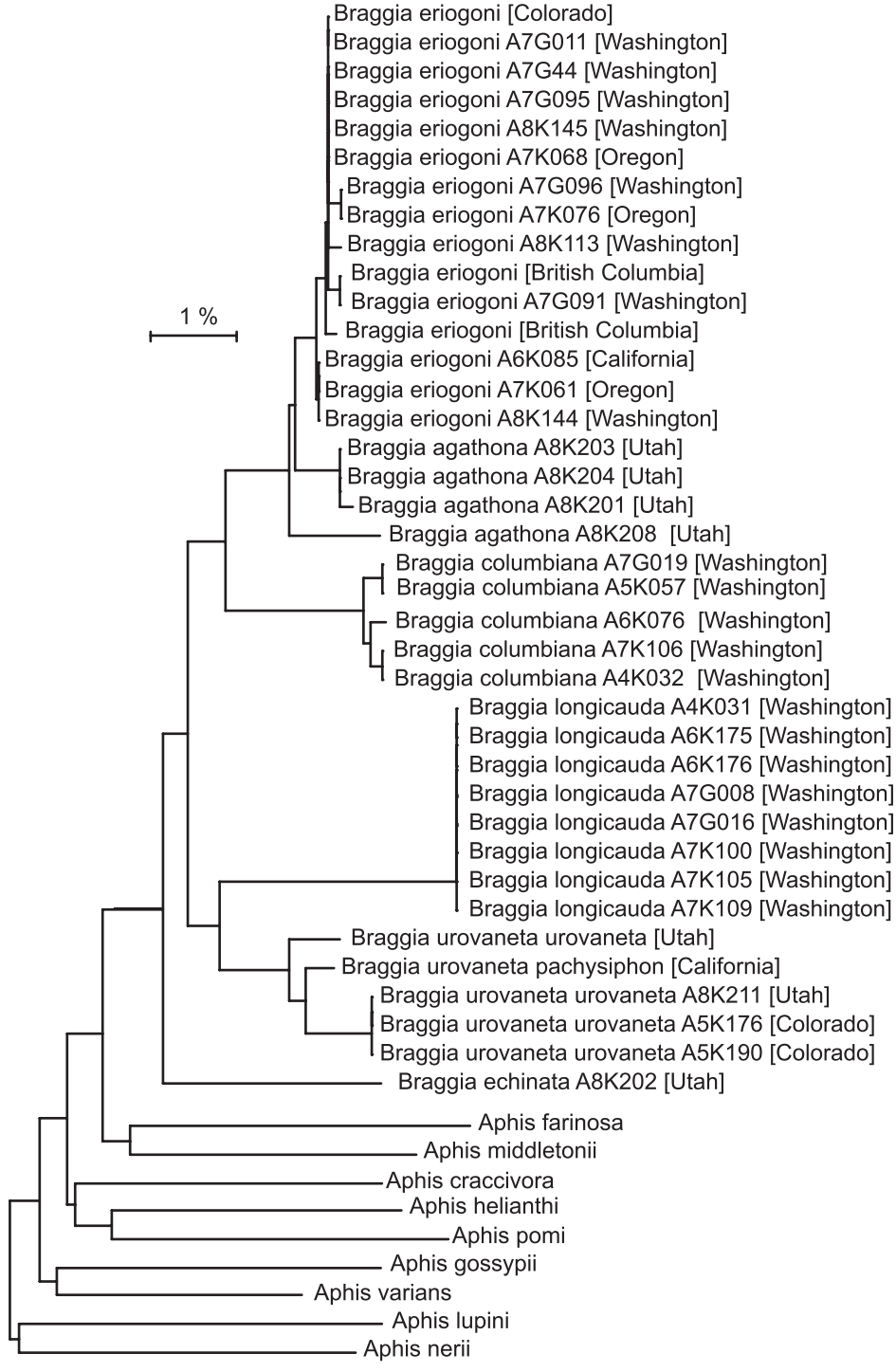
Aptera vivipara (Figs. 12–20, 32)

In life, black, blackish gray, or blackish brown with white wax powdering; appendages black to brownish black or brown except basal half or more of ASIII−V pale, basal femora pale, and middle areas of tibia sometimes paler. Dorsal integument faintly to moderately reticulate on head and ABD dorsum. Body length 1.46–2.85 mm; head width across eyes 0.38–0.54 mm; ANT short, 0.55–0.90 × body length; FT weakly developed; setae on head and ABD stout, tapering, pointed or blunt, usually longer than bdIII; longest seta on ASIII (0.016–0.031 mm long) always shorter than bdIII; ANT without 2° RHIN; PT usually >1.5 × BVI (range 1.30–1.94 × BVI); rostrum extending to metacoxa; URS length (0.13–0.24 mm) >1.75 × basal width of segment, with 0–3 accessory setae; pronotum with marginal tubercles; hind-femur length 0.47–0.98 mm, hind-tibia length 0.82–1.71 mm, hind tarsus II length 0.17–0.26 mm; tarsus I chaetotaxy 3–3–3; claws simple; empodial setae acuminate, not reaching tip of claws. ABDI and VII with marginal tubercles; SIPH relatively short, mean length 0.12 mm (range 0.06–0.21 mm), slightly imbricated, subcylindrical, tapering (narrower at apex than at base), and flanged; cauda long, L/W > 1.0 (mean 1.2, range 1.01–1.47), with 4–11 setae. For a full range of morphological measurements and comparisons, including values for the holotype, see Table 2.

Alate vivipara (Figs. 21–23)

Morphological features generally similar to those of aptera vivipara (see Table 2). Body length 1.40–2.71 mm; ANT with 2° RHIN on

Fig. 33. Neighbour-joining tree of Kimura two-parameter distances among specimens of *Braggia* and *Aphis* for cytochrome *c* oxidase subunit 1 sequences. The geographic origin of the sample is shown in brackets (all samples of *B. longicauda* and *B. columbiana* are from Washington State). The codes are collection codes as given in the ''material examined'' sections in the text and listed in Table 3.



ASIII (8–14) and ASIV (0–1); ABD terga with irregular stripes and marginals.

Ovipara (Figs. 24–26)

Body length 1.50–2.50 mm; ANT without 2° RHIN; hind tibia with 30–65 pseudosensoria; ABD terga largely membranous; SIPH length 0.08–0.10 mm; other features similar to those of aptera vivipara.

Male (Figs. 27–29)

Body length 1.40–1.70 mm; ANT with 2° RHIN on ASIII (9–32), IV (13–22), and V (9–10); winged; ABD with distinct marginal pigmentation and light dorsal spinal and posterior pigmentation; SIPH short, 0.04–0.05 mm; other features similar to those of alate vivipara.

DNA characterization

For GenBank accession numbers for sequences of mitochondrial COI, 5′-end (DNA barcode) see Table 3. Specimen CNC No. HEM058081 is from the type locality. Comparisons with other samples of *Braggia* (Fig. 33) indicate that specimens of *B. longicauda* are well separated from other species evaluated (species comparisons were limited to available fresh or suitably preserved specimens). All specimens have identical sequences; the mean distance (percent difference) from the most similar species (*B. urovaneta*) is 4.4% (Table 4).

Biology, hosts, and distribution

The species is holocyclic monoecious on *Eriogonum* species, predominantly the stems of *E. elatum* (80% of collections) and less frequently *E. compositum* (20%). Aptera and alate viviparae occur from late May to early October; oviparae and males occur from mid-September to mid-October. It is found along the eastern slopes and foothills of the Cascade Mountains (Washington State), Klamath Falls (Oregon), and South Lake Tahoe (California) at elevations ranging from 370 to 1910 m.

Parasitoids (Table 5)

Lysiphlebus testaceipes was the predominant primary parasitoid, constituting 99.6% of the primary population present. Secondary parasitoids were pteromalids, mainly in the genus *Pachyneuron*.

Key to species of *Braggia* (aptera vivipara)

1 Dorsal setae thick, rodlike to spinelike, arising from tuberculate bases >0.012 mm in height. Colorado and Utah 2

— Dorsal setae not thick, rodlike to spinelike, with short, less pronounced bases. Distribution variable, may include Colorado and Utah 3

2(1) Dorsal setae rodlike, with blunt-rounded apices . . . . . *B. echinata*

— Dorsal setae tapering, with thin-rounded apices . . . . . *B. uncompahgrensis*

3(1) Dorsal setae inconspicuous, length maximally equal to bdIII; ABDVII marginal tubercles apparently absent; SIPH length <0.05 × body length and equal to or less than basal width; tarsus I chaetotaxy 2–2−2; ASIII setae short and sparse, <0.75 × bdIII; cauda short, length <0.5 × width; on *Eriogonum fasiculatum* Benth. California (includes *Braggia deserticola thanatophila* on *Eriogonum* sp.) . . . . . *B. deserticola*

— Dorsal setae mainly longer than bdIII; ABDVII marginal tubercles present; SIPH length ≥0.05 × body length (if <0.05 × body length, then not with the above combination of characters); other features variable. 4

4(3) ASIII and (or) IV with 2° RHIN; cauda length/width ratio (L/W) < 0.75 5

— ASIII and (or) IV without 2° RHIN (if 1 or 2 present (rare, <3%), then cauda L/W >0.75) 7

5(4) URS length ≥0.19 mm (range 0.19–0.24 mm), tarsus I chaetotaxy 2–2–2; on *E. compositum*, *E. umbellatum*, *E. elatum*, *E. pyrolifolium*, and *E. strictum*. Oregon and Washington . . . . . *B. columbiana*

— URS length usually <0.19 mm, tarsus I chaetotaxy variable (if URS length ≥0.19 mm (rare, <3%), then tarsus I chaetotaxy 3–3–3, 3–3–2, or 3–2–2) 6

6(5) Tarsus I chaetotaxy 2–2–2, and setae on ASIII sparse and shorter than bdIII; on *E. corymbosum*. Colorado and Utah . . . . . *B. agathona*

— Tarsus I chaetotaxy 3–3–3, 3–3–2, or 3–2–2 and longest setae on ASIII equal to or shorter than bdIII; on *Eriogonum* spp. Western North America (includes *Braggia eriogoni atra* Hille Ris Lambers and *B. e. californica* (Hille Ris Lambers)) . . . . . *B. eriogoni*

7(4) Cauda length ≥0.13 mm (range 0.13–0.23 mm); hind-tarsus length 6–9 × width at midpoint of segment; on *E. elatum* and *E. compositum*. Northern California, Oregon, and Washington . . . . . *B. longicauda*

— Cauda length ≤0.12 mm (range 0.08–0.12 mm); hind-tarsus length 3–6 × width at midpoint of segment; on *E. corymbosum* in Colorado, Idaho, and Utah and *E. latifolium* or *E. nudum* var. *nudum* in California (includes *Braggia urovaneta pachysiphon*) . . . . . *B. urovaneta*

Discussion

The general morphological similarities of *B. columbiana* and *B. longicauda* (despite the relatively long cauda of the latter) to other *Braggia* species, together with their strict host relationship on *Eriogonum* species, support the placement of these two species in *Braggia*.

Four species, each subdivided into subspecies, were classified in *Braggia* by Hille Ris Lambers (1966): *B. echinata* (subspp. *echinata* and *uncompahgrensis*), *B. deserticola* (subspp. *deserticola* and *thanatophila*), *B. eriogoni* (subspp. *agathona*, *atra*, *californica*, and *eriogoni*), and *B. urovaneta* (subspp. *pachysiphon* and *urovaneta*). Subsequent reclassification of species in the genus by Remaudière and Remaudière (1997) and our addition of two new species have resulted in a complement of eight species, with three divided into subspecies: *B. agathona*, *B. columbiana*, *B. echinata*, *B. deserticola* (subspp. *deserticola* and *thanatophila*), *B. eriogoni* (subspp. *atra*, *californica*, and *eriogoni*), *B. longicauda*, *B. uncompahgrensis*, and *B. urovaneta* (subspp. *pachysiphon* and *urovaneta*).

The geographic ranges of *Braggia eriogoni atra* and *B. e. californica* fall within the range of the nominate subspecies and differ from it in details of setal length and form. The subspecies of *B. deserticola*, both restricted to southern California, differ in coloration and exhibit subtle differences in appendage lengths. The subspecies of *B. urovaneta* are recognized mainly by differences in rostral length and distribution (*pachysiphon* in California, *urovaneta* in Colorado, Utah, and Idaho). Further justification of these subspecies is required, but presently there are not enough good-quality specimens or geographic material of most of the subspecies with which to do a balanced evaluation or revision.

Among aphids in general, mean intraspecific sequence divergence is about 0.2% (almost always <1.5%) and the distance between congeneric species generally ranges from 1% to 13%, but as low as 0.46% for a few species pairs (Foottit *et al.* 2008). The geographic range of *B. columbiana* (Washington and Oregon) is encompassed by that of the species that it most closely resembles, *B. eriogoni* (British Columbia south to southern California, east to Colorado). Intraspecific COI sequence divergence of these two morphologically defined species within samples is low, <0.62% (Table 4, Fig. 33), in contrast to 3% divergence between the two species. Samples of *B. columbiana* are in fact more distinct from samples of *B. eriogoni* than are samples of *B. agathona*, currently recognized as a distinct species. Sequence data are thus consistent with these species designations.

Similarly, sequence divergence between samples of *B. longicauda* and samples of *B. urovaneta*, the species most similar to it, is about 4%, in contrast to the 1.4% divergence observed within *B. urovaneta* (including *B. u. pachysiphon*) (Table 4, Fig. 33).

More than 200 species of buckwheat are recognized in the western United States of America (Reveal 2003), but only 20 have been specifically linked with species of *Braggia*. *Braggia columbiana* and *B. longicauda* are each commonly associated with just a few species of *Eriogonum*. Most other described *Braggia* species are similarly narrow in their host range. One exception is *B. eriogoni*; it feeds on at least 17 different *Eriogonum* species (Palmer 1952; Hille Ris Lambers 1966; Blackman and Eastop 2006; unpublished data)

The geographic distribution of the two new species described here may be more extensive than is currently recognized, and may extend across the full range of the preferred hosts. *Eriogonum compositum* (preferred by *B. columbiana*) is found from northern California to Mount Rainier, Washington, east through south-central and southeastern Washington State; *E. elatum* (preferred by *B. longicauda*) is widely distributed on dry, often open slopes from northern and eastern California and northern Nevada north to eastern Washington State (Stokes 1932; Reveal 1976).

The *Braggia* species on buckwheat are not of economic importance. At times, certain *Braggia* species may become unusually abundant, but there is no apparent injury to the host. However, *Braggia* species may be useful as a host source for the primary parasitoid *Lysiphlebus testaceipes*, which is broadly oligophagous and an important agent for natural biological control of many economically important aphids in the region, including *Aphis craccivora* Koch on *Asparagus* L. (Liliaceae) and alfalfa and clover (*Medicago* L. and *Trifolium* L., Fabaceae); *A. fabae* Scopoli on beans (Fabaceae); *A. pomi* de Geer and *A. spiraecola* Patch on apple (*Malus* Mill., Rosaceae); *Brachycorynella asparagi* (Mordvilko) on asparagus; *Brevicoryne brassicae* (L.) on canola (*Brassica* L., Brassicaceae); *Diuraphis noxia* (Kurdjumov) on wheat and barley (*Triticum* L. and *Hordeum* L., Poaceae); *Myzus cerasi* (F.) on cherry (*Prunus* L., Rosaceae); *M. persicae* (Sulzer) on peach (*Prunus persica* (L.) Batsch, Rosaceae) and potato (*Solanum tuberosum* L., Solanaceae); *Phorodon humuli* (Schrank) on hops (*Humulus lupulus* L., Cannabaceae); *Rhopalosiphum insertum* (Walker) on apple; and *Rhopalosiphum padi* (L.), *R. maidis* (Fitch), *Schizaphis graminum* (Rondani), and *Sitobion avenae* (F.) on small grains (Poaceae) (Pike *et al*. 2000*a*).

Although buckwheat is not found in close proximity to many of the region's crops, it harbours hosts (*e.g.*, *Braggia* spp.) of *L. testaceipes*. Various *Eriogonum* species (including *E. compositum*) have been successfully cultivated by nurseries for use as native landscape ornamentals and are suitable for erosion control (Nicholls 2002). The plants are often low-maintenance, produce abundant flowers, and are excellent sources of nectar for bees and butterflies (Nicholls 2002; Reveal 2003). *Eriogonum* species might also be useful in landscape plantings to enhance the presence and action of *L. testaceipes* in nearby crops (Starý and Pike 1998).

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