

THE GENUS *BRUEELIA* (PHTHIRAPTERA: ISCHNOCERA: PHILOPTERIDAE) OF NORTH AMERICAN JAYS AND ALLIES (AVES: PASSERIFORMES: CORVIDAE), WITH DESCRIPTIONS OF FIVE NEW SPECIES

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KEY WORDS ABSTRACT

Phthiraptera	Five new species of chewing lice in the genus <i>Brueelia</i> K��ler, 1936, are described from North American
<i>Brueelia</i> -Complex	jays and allies. They are <i>Brueelia mexicana</i> n. sp. from <i>Aphelocoma woodhouseii cyanotis</i> Ridgway,
New Species	1887; <i>Brueelia bonnevillensis</i> n. sp. from <i>Aphelocoma woodhouseii nevadae</i> Pitelka, 1945; <i>Brueelia</i>
Corvidae	<i>diblasiae</i> n. sp. from <i>Cyanocitta stelleri frontalis</i> (Ridgway, 1873); <i>Brueelia tempestwilliamsae</i> n. sp.
North America	from <i>Gymnorhinus cyanocephala</i> Wied-Neuwied, 1841; <i>Brueelia mcnewae</i> n. sp. from <i>Nucifraga columbiana</i> (Wilson, 1811). An identification key to the <i>Brueelia</i> on corvid hosts is provided.

The majority of species in the chewing louse genus *Brueelia* K  ler, 1936, infest hosts belonging to the Passerides (parvorder) radiation of songbirds (Price et al., 2003; Gustafsson and Bush, 2017). This radiation includes some of the larger families of passeriform birds, such as muscicapid flycatchers, thrushes, warblers, babblers, finches, sparrows, and buntings (Barker et al., 2004). However, a small number of *Brueelia* species are found on hosts in the Corvidae (parvorder) radiation (sensu J  nsson et al., 2016). In particular, *Brueelia* species are found on 2 widely distributed Corvidae families: crows and allies (Corvidae) and shrikes (Laniidae). The small number of *Brueelia* species known from corvid hosts are not morphologically similar to each other and do not appear to be closely related. This suggests that they originate from several, likely relatively recent, colonization events from Passerides hosts. However, our understanding of the evolutionary history of these lice is limited by our poor understanding of their morphology and phylogenetic relationships, as well as poor sampling from many of the families of Old World Corvidae.

Here we review the *Brueelia* s. str. species of North American corvids, based on new material, and on material examined by Ansari (1956, 1957) and Williams (1986). Ansari (1956) reviewed the *Brueelia* of the Corvidae, and judged material from New World scrub-jays [*Aphelocoma californica californica* (Vigors, 1839)] and Steller's jays [*Cyanocitta stelleri frontalis* (Ridgway, 1873)] to be indistinguishable from *Brueelia deficiens* (Piaget, 1885) found on

Old World Iberian magpies [*Cyanopica cooki* (Bonaparte, 1850)]. Similarly, Williams (1986) identified material on New World Clark's nutcrackers [*Nucifraga columbiana* (Wilson, 1811)] and pinyon jays (*Gymnorhinus cyanocephalus* Wied-Neuwied, 1841) as *B. deficiens*. Although the specimens we have examined from these New World hosts are similar to each other, they represent 5 different species. Moreover, none of these species are conspecific with *B. deficiens*, which appears to be limited to the type host in the Old World. We, therefore, describe here 5 new species of *Brueelia* from 4 New World species of jays and allies: *Brueelia tempestwilliamsae* n. sp. (Figs. 1–7), *Brueelia diblasiae* n. sp. (Figs. 8–14), *Brueelia mcnewae* n. sp. (Figs. 15–21), *Brueelia bonnevillensis* n. sp. (Figs. 22–28), and *Brueelia mexicana* n. sp. (Figs. 29–35). In addition, we provide a key to aid in the identification of these 5 New World species.

MATERIALS AND METHODS

Slide-mounted specimens are deposited at the Natural History Museum, London, United Kingdom (NHML), or the Price Institute for Parasite Research, University of Utah, Salt Lake City, Utah (PIPeR). All studied material was mounted in Canada balsam on microscope slides. Specimens were examined and measured with a Nikon Eclipse E600 microscope (Nikon, Belmont, California) fitted with an Olympus DP25 camera (Olympus, Center Valley, Pennsylvania) and digital measuring software (ImageJ 1.48v, Wayne Rasband, <https://imagej.nih.gov/>). Illustrations were drawn by hand, using a drawing tube. Line drawings were scanned, collated, and edited in GIMP (www.gimp.org). All measurements are given in millimeters, as ranges (mean value, when $n \geq 10$). Abbreviations used: TL = total length; HL = head length (along

Version of Record, first published online with fixed content and layout, in compliance with ICZN Arts. 8.1.3.2, 8.5, and 21.8.2 as amended, 2012. ZooBank publication registration: urn:lsid:zoobank.org:pub:CA00FD85-CED6-404B-8CF4-78B958FCAB30.

Table I. The lice of the genus *Brueelia* K  ler, 1936, known from hosts in the family Corvidae. Host taxonomy follows Clements et al. (2019).

Host species	Louse species
<i>Aphelocoma woodhouseii cyanotis</i> Ridgway, 1887	<i>Brueelia mexicana</i> n. sp.
<i>Aphelocoma woodhouseii nevadae</i> Pitelka, 1945	<i>Brueelia bonnevillensis</i> n. sp.
<i>Cyanocitta stelleri frontalis</i> (Ridgway, 1873)	<i>Brueelia diblasiae</i> n. sp.
<i>Cyanopica cooki</i> Bonaparte, 1850	<i>Brueelia deficiens</i> (Piaget, 1885)
<i>Gymnorhinus cyanocephalus</i> Wied- Neuwied, 1841	<i>Brueelia tempestwilliamsae</i> n. sp.
<i>Nucifraga columbiana</i> (Wilson, 1810)	<i>Brueelia mcnewae</i> n. sp.
<i>Ptilostomus afer</i> (Linnaeus, 1766)	<i>Brueelia moreli</i> Ansari, 1957
	<i>Brueelia zohrae</i> Ansari, 1956
<i>Zavattariornis stresemanni</i> Moltoni, 1938	<i>Brueelia zavattariornis</i> Ansari, 1956

midline); HW = head width (at temples); PRW = prothorax width; PTW = pterothorax width; AW = abdominal width (at segment V).

Morphological terms and abbreviations thereof follow Gustafsson and Bush (2017), and include *aps* = accessory post-spiracular seta; *pms* = posterior mesosomal setae; *ps* = paratergal seta; *psps* = principal post-spiracular seta; *pst1–2* = parameral setae 1–2; *tps* = tergal posterior setae; *vms* = vulval marginal setae; *vms* = vulval oblique setae (including setae situated median to *vss*); *vss* = vulval submarginal setae. Abbreviations for setal characters are given in italic type. Host taxonomy follows Clements et al. (2019). A complete checklist of the lice of the genus *Brueelia* known from the Corvidae is given in Table I.

SYSTEMATICS

Phthiraptera Haeckel, 1896

Ischnocera Kellogg, 1896

Philopteridae Burmeister, 1838

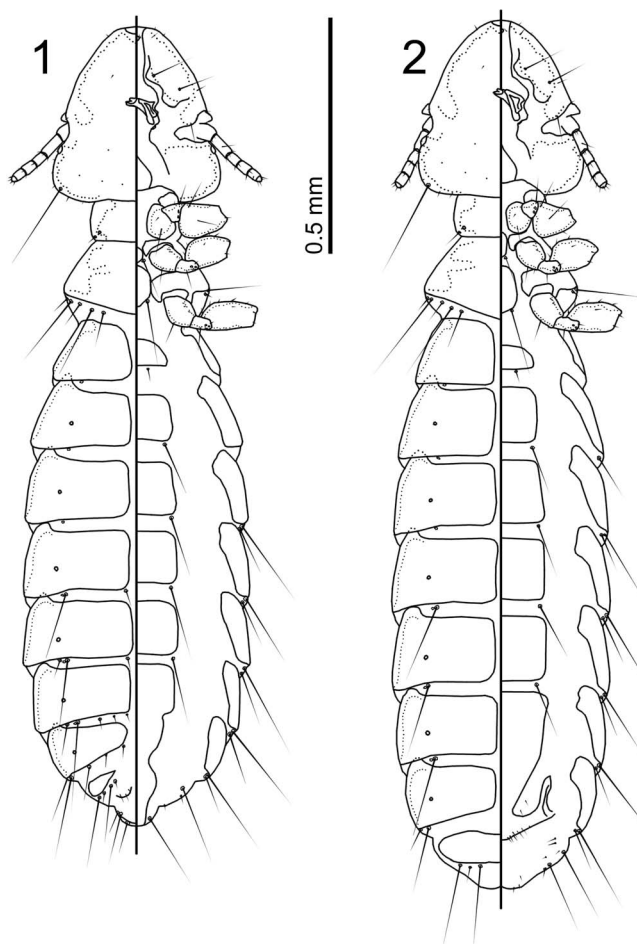
***Brueelia*-complex sensu Gustafsson and Bush, 2017**

***Brueelia* K  ler, 1936**

Philopterus Nitzsch, 1818 (288) (in partim); *Nirmus* Nitzsch, 1818 (291) (in partim); *Degeeriella* Neumann, 1906 (60) (in partim); *Painjunirmus* Ansari, 1947 (285); *Allobrueelia* Eichler, 1951 (36) (in partim); *Nigrinirmus* Zotorzycka, 1964 (248); *Spironirmus* Zotorzycka, 1964 (261); *Serinirmus* Soler Cruz et al., 1987 (244); *Plesionirmus* Mey, 2017 (144); *Neosittiella* Mey, 2017 (149).

Remarks

The 5 species described here can all be separated from the species of *Brueelia* from Old World corvids (including *B. deficiens*) by the following characters: tergopleurite V of both sexes with *psps* in all New World species, but without *psps* (but may have *aps*) in Old World species; proximal mesosome with distal constriction (e.g., Fig. 5) in New World species, but without such constriction in Old World species. We here erect the informal *Brueelia tempestwilliamsae* species group to contain these 5 species; no other species belonging to this group have been described.



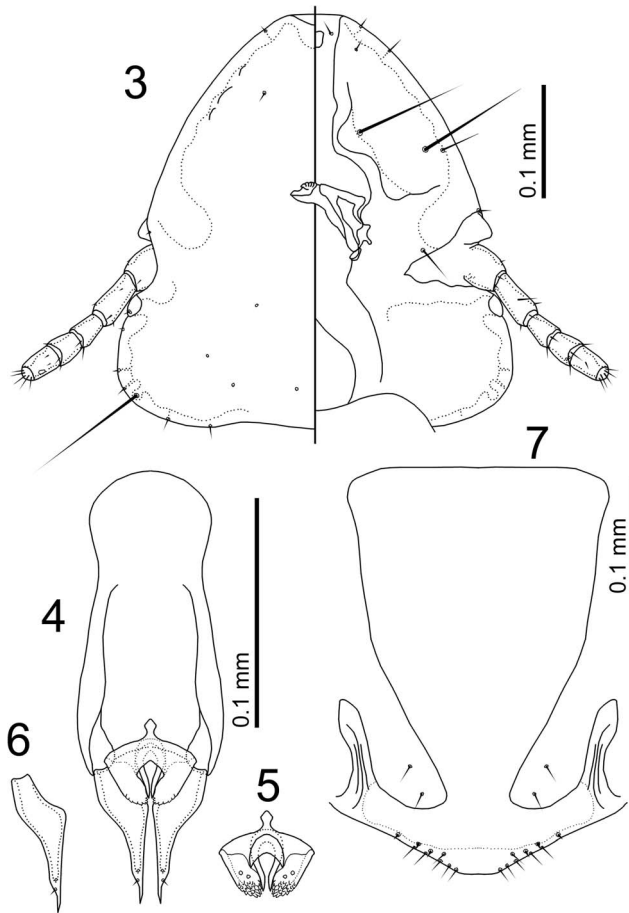
Figures 1, 2. *Brueelia tempestwilliamsae* n. sp. from *Gymnorhinus cyanocephala* Wied-Neuwied, 1841. (1) Male habitus, dorsal and ventral view. (2) Female habitus, dorsal and ventral view.

DESCRIPTION

***Brueelia tempestwilliamsae* n. sp.**

(Figs. 1–7)

Diagnosis (male): Head flat dome-shaped (Fig. 3), lateral margins of preantennal head convex, frons slightly flattened (more flattened in females than in males). Marginal carina of moderate width compared with other species in the genus, median margin undulated; carina much displaced and slightly widened at osculum. Ventral anterior plate slightly longer than wide. Head chaetotaxy as in Figure 3. Preantennal nodi large, bulging. Pre- and post-ocular nodi large. Marginal temporal carina with irregular median margin. Gular plate broadly lanceolate. Thoracic and abdominal segments and chaetotaxy as in Figure 1; tergopleurite V without *aps*; abdominal segment III without *ps*. Basal apodeme constricted at mid-length, proximal half often slightly narrower than distal half (Fig. 4). Proximal mesosome minute (Fig. 5), exact shape variable among specimens. Mesosomal lobes broad, rugose area extensive; 2 *pms* sensilla on each side, postero-lateral to gonopore. Gonopore crescent-shaped. Penile arms long, not reaching distal margin of mesosome. Parameres elongate, stout proximally, *pst1–2* as in Figure 6. Measurements as in Table II.



Figures 3–7. *Brueelia tempestwilliamsae* n. sp. from *Gymnorhinus cyanocephala* Wied-Neuwied, 1841. (3) Male head, dorsal and ventral view. (4) Male genitalia, dorsal view. (5) Male mesosome, ventral view. (6) Male paramere, dorsal view. (7) Female subgenital plate and vulval margin, ventral view. (Figures 4–6 share the lower left scale bar.)

Female: As male, except: thoracic and abdominal chaetotaxy as in Figure 2; abdominal segment III with *ps*. Subgenital plate slenderly trapezoidal, lateral margins convex (Fig. 7), with broad connection to cross-piece. Vulval margin bulging medially, in some specimens somewhat flattened (Fig. 7), with 4–5 short, slender *vms* and 2–4 short, thorn-like *vss* on each side; 2–4 short, slender *vos* on each side of subgenital plate; distal 1 *vos* median to *vss*. Measurements as in Table II.

Taxonomic summary

Type host: *Gymnorhinus cyanocephala* Wied-Neuwied, 1841, pinyon jay.

Type locality: Clover creek, Tooele County, Utah.

Type material: Holotype ♂, Clover creek, Tooele County, Utah, 6 May 1969, 09078 (NHML). Paratypes 1 ♀, same data as holotype (NHML); 8 ♂, 17 ♀, same data as holotype (PIPeR); 1 ♂, 2 ♀, same locality, 7 May 1969, 09081 (PIPeR); 4 ♂, 3 ♀, St. John, Tooele County, Utah, 10 November 1964, E. and E. Branch, Tooele County, Utah, 10 November 1964, E. & E. Branch (PIPeR); 1 ♂, Keg Mountains, Tooele County, Utah, March 1965, E. & E. Branch (PIPeR); 2 ♀, Colorado, December 1900, R. Meinertzhagen, 3094 (NHML).

ZooBank registration: urn:lsid:zoobank.org:act:69EA8D4E-1892-4BAA-8C43-3C301FA4DE05.

Etymology: The specific name is in honor of Terry Tempest Williams (previously at the Natural History Museum of Utah and the University of Utah) in recognition of her long and steadfast work to make the public realize the importance of the environment and the beauty of the desert. Much of her work in writing and advocacy has concerned the deserts and “waste” lands of the Great Basin, North America, which is the home of the pinyon jay and consequently of *B. tempestwilliamsae*.

Remarks

Brueelia tempestwilliamsae is most similar to *B. diblasiae* n. sp. with which it shares the following characters: head broad (Figs. 3, 10); female abdominal segment III with *ps* (Figs. 2, 9); proximal mesosome very small (Figs. 5, 12); gonopore crescent-shaped

Table II. Measurements of the species of *Brueelia* von K  ler, 1936, described here.

Louse species	S*	AW*	HL*	HW*	PRW*	PTW*	TL*
<i>B. tempestwilliamsae</i>	M (n = 15)	0.44–0.53 (0.49)	0.36–0.40 (0.38)	0.33–0.36 (0.35)	0.19–0.21 (0.20)	0.30–0.34 (0.32)	1.60–1.79 (1.69)
	F (n = 25)†	0.46–0.66 (0.56)	0.37–0.45 (0.41)	0.34–0.40 (0.37)	0.19–0.23 (0.21)	0.32–0.39 (0.35)	1.79–2.15 (1.97)
<i>B. diblasiae</i>	M (n = 7)‡	0.38–0.41	0.36–0.38	0.33–0.36	0.20–0.22	0.30–0.34	1.64–1.84
	F (n = 9)§	0.42–0.53	0.38–0.41	0.36–0.39	0.22–0.24	0.34–0.38	1.90–2.18
<i>B. mcnewae</i>	M (n = 3)	0.51–0.57	0.39–0.40	0.34–0.36	0.21–0.22	0.34–0.36	1.77–1.85
	F (n = 5)	0.47–0.57	0.41–0.43	0.39–0.42	0.22–0.25	0.36–0.40	1.88–2.03
<i>B. bonnevillensis</i>	M (n = 10)	0.43–0.48 (0.46)	0.38–0.41 (0.39)	0.33–0.35 (0.34)	0.19–0.21 (0.20)	0.29–0.31 (0.30)	1.73–1.85 (1.79)
	F (n = 18)	0.42–0.54 (0.48)	0.40–0.44 (0.42)	0.35–0.38 (0.36)	0.20–0.22 (0.21)	0.31–0.35 (0.33)	1.99–2.17 (2.08)
<i>B. mexicana</i>	M (n = 16)	0.29–0.46 (0.37)	0.35–0.37 (0.36)	0.29–0.33 (0.31)	0.17–0.19 (0.18)	0.25–0.31 (0.28)	1.50–1.69 (1.59)
	F (n = 18)#	0.43–0.53 (0.48)	0.37–0.43 (0.40)	0.31–0.36 (0.33)	0.18–0.21 (0.19)	0.27–0.33 (0.30)	1.68–2.01 (1.79)

* Abbreviations used: AW = abdominal width (at segment V); *B.* = *Brueelia*; HL = head length (at midline); HW = head width (at temples); n = number of specimens measured; PRW = prothoracic width; PTW = pterothoracic width; S = sex; TL = total length (at midline). Numbers in parentheses are means, given only when n > 10.

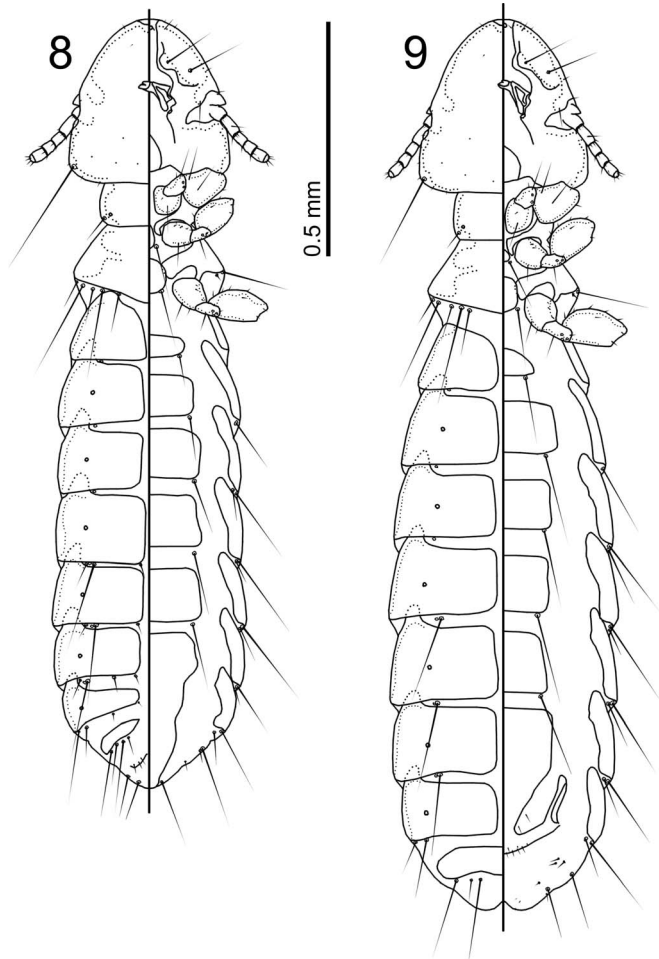
† N = 24 for AW.

‡ N = 5 for TL and N = 4 for AW.

§ N = 5 for AW.

|| N = 15 for TL and N = 13 for AW.

N = 17 for TL, PRW, and AW.



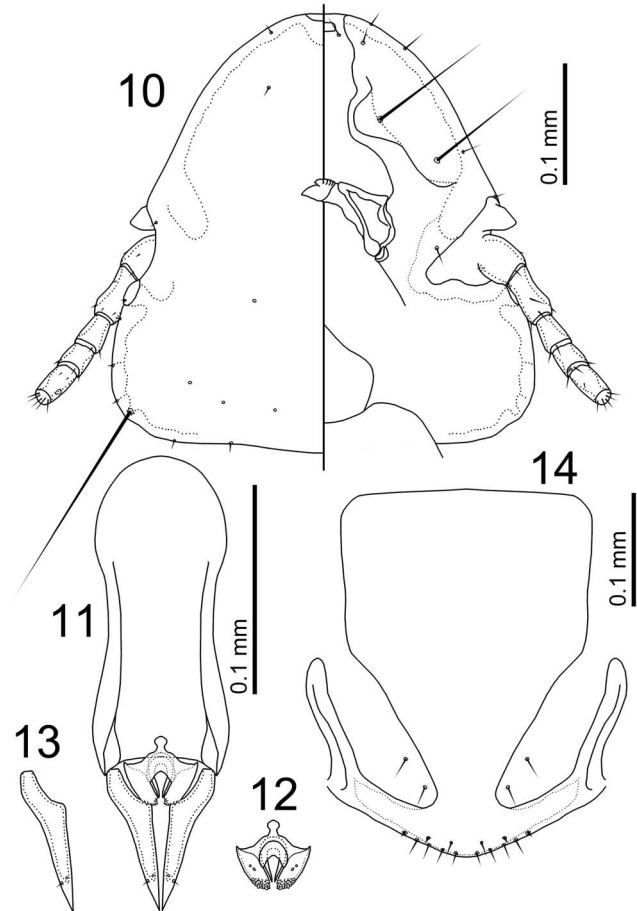
Figures 8, 9. *Brueelia diblasiae* n. sp. from *Cyanocitta stelleri frontalis* (Ridgway, 1873). (8) Male habitus, dorsal and ventral view. (9) Female habitus, dorsal and ventral view.

(Figs. 5, 12). These 2 species can be separated by the following characters: male tergopleurite V without *aps* in *B. tempestwilliamsae* (Fig. 1), but with *aps* in *B. diblasiae* (Fig. 8); male abdominal segment III without *ps* in *B. tempestwilliamsae* (Fig. 1), but with *ps* in *B. diblasiae* (Fig. 8); mesosome proportionately larger in *B. tempestwilliamsae* (Fig. 4) than in *B. diblasiae* (Fig. 12); preantennal head more broadly rounded in *B. diblasiae* (Fig. 10) than in *B. tempestwilliamsae* (Fig. 3).

***Brueelia diblasiae* n. sp.**

(Figs. 8–14)

Diagnosis (male): Head broadly flat dome-shaped (Fig. 10), lateral margins of preantennal head convex, frons rounded. Marginal carina of moderate width, median margin only slightly undulated; carina shallowly displaced and widened at osculum. Ventral anterior plate small, wider than long. Head chaetotaxy as in Figure 10. Preantennal nodi large, bulging. Pre- and post-ocular nodi large. Marginal temporal carina with irregular median margin. Gular plate broadly lanceolate. Thoracic and abdominal segments and chaetotaxy as in Figure 8; tergopleurite V with *aps*; abdominal segment III with *ps*. Basal apodeme slender, constricted at mid-length (Fig. 11). Proximal mesosome



Figures 10–14. *Brueelia diblasiae* n. sp. from *Cyanocitta stelleri frontalis* (Ridgway, 1873). (10) Male head, dorsal and ventral view. (11) Male genitalia, dorsal view. (12) Male mesosome, ventral view. (13) Male paramere, dorsal view. (14) Female subgenital plate and vulval margin, ventral view. (Figures 11–13 share the lower left scale bar.)

minute to small (Fig. 12), in some specimens more similar to that of *B. bonnevillensis* n. sp. (Fig. 26). Mesosomal lobes broad, rugose area extensive; 2 *pms* sensilla on each side postero-lateral to gonopore. Gonopore crescent-shaped. Penile arms long, not reaching distal margin of mesosome. Parameres elongated, slender, *pst1*–2 as in Figure 13. Measurements as in Table II.

Female: As male, except: thoracic and abdominal chaetotaxy as in Figure 9; abdominal segment III with *ps*. Subgenital plate pentagonal, lateral margins angular (Fig. 14), with broad connection to cross-piece. Vulval margin gently rounded (Fig. 14), with 3–4 short, slender *vms* and 2–3 short, thorn-like *vss* on each side; 3–4 short, slender *vos* on each side of subgenital plate; distal 1 *vos* median to *vss*. Measurements as in Table II.

Taxonomic summary

Type host: *Cyanocitta stelleri frontalis* (Ridgway, 1873), Steller's jay.

Type locality: California.

Type material: Holotype ♂, California, March 1939, R. Meinertzhagen, 12929 (NHML) [marked with a black dot on slide, dissected genitalia marked with black dot]. Paratypes 1 ♂,

same data as holotype (NHML); 6♂, 12♀, same data as holotype, except 12930 (NHML).

ZooBank registration: urn:lsid:zoobank.org:act:2F07776C-CD5D-4E9F-BB2D-9381522E788A.

Etymology: The species epithet is in honor of Dr. Emily DiBlasi (University of Utah), in recognition of her work on the population genetic structure of avian parasites.

Remarks

Brueelia diblasiae is most similar to *B. tempestwilliamsae*, with which it shares the following characters: head broad (Figs. 3, 10); female abdominal segment III with *ps* (Figs. 2, 9); proximal mesosome very small (Figs. 5, 12); gonopore crescent-shaped (Figs. 5, 12). These 2 species can be separated by the following characters: male tergopleurite V with *aps* in *B. diblasiae* (Fig. 8), but without *aps* in *B. tempestwilliamsae* (Fig. 1); male abdominal segment III with *ps* in *B. diblasiae* (Fig. 8), but without *ps* in *B. tempestwilliamsae* (Fig. 1); mesosome proportionately smaller in *B. diblasiae* (Fig. 12) than in *B. tempestwilliamsae* (Fig. 4); preantennal head more broadly rounded in *B. diblasiae* (Fig. 10) than in *B. tempestwilliamsae* (Fig. 3).

Brueelia mcnewae n. sp.

(Figs. 15–21)

Diagnosis (male): Head broadly flat dome-shaped (Fig. 17), lateral margins of preantennal head markedly convex, frons rounded to slightly flattened medially. Marginal carina of moderate width, median margin undulating; carina shallowly displaced and much widened at osculum. Ventral anterior plate rounded. Head chaetotaxy as in Figure 17. Preantennal nodi large, bulging. Pre- and post-ocular nodi large. Marginal temporal carina wide, of roughly equal width throughout. Gular plate squat. Thoracic and abdominal segments and chaetotaxy as in Figure 15; *aps* absent on tergopleurite V; *ps* present on abdominal segment III. Basal apodeme slender, constricted at mid-length (Fig. 18). Proximal mesosome broadly rounded, constricted distally. Mesosomal lobes wide, rugose area restricted to near distal and median margins; 2 *pms* sensilla on each side of gonopore. Gonopore roughly quadratic, distal margin concave. Penile arms short, not reaching distal margin of mesosome. Parameres tapering gently, elongated, *pst1*–2 as in Figure 20. Measurements as in Table II.

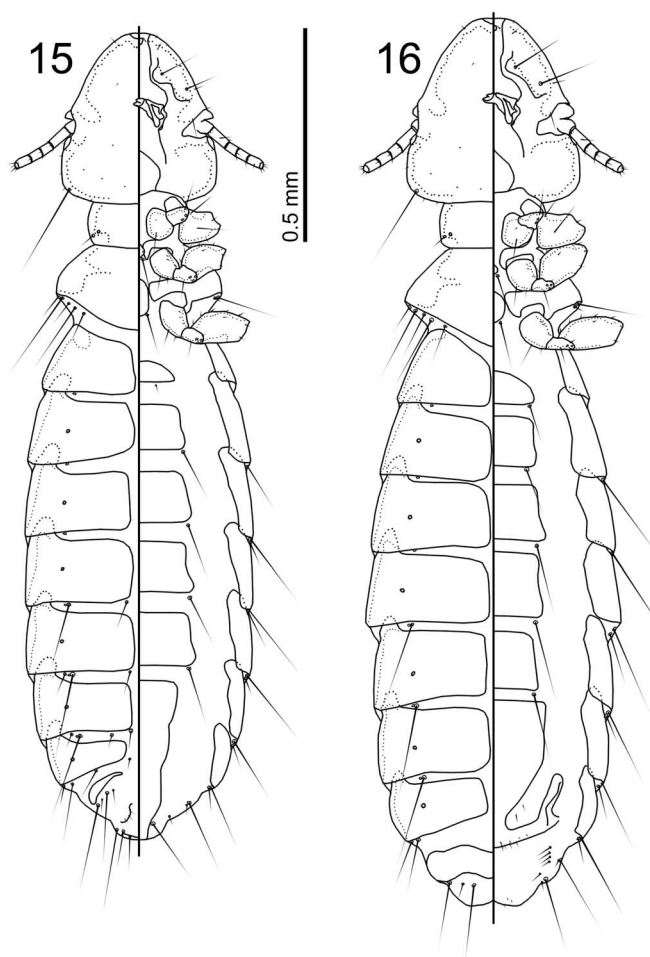
Female: As male, except: thoracic and abdominal chaetotaxy as in Figure 16; *ps* present on abdominal segment III. Subgenital plate slenderly pentagonal, lateral margins angular (Fig. 21). Vulval margin gently rounded (Fig. 21), with 3–4 short, slender *vms* and 2–3 short, thorn-like *vss* on each side; 3–4 short, slender *vos* on each side of subgenital plate; distal 1 *vos* median to *vss*. Measurements as in Table II.

Taxonomic summary

Type host: *Nucifraga columbiana* (Wilson, 1811), Clark's nutcracker.

Type locality: Mount Pinos, Ventura County, California.

Type material: Holotype ♂, Mount Pinos, Ventura County, California, 13 November 1987, M.M.A., 68 (NHML). Paratypes 1♂, 1♀, same data as holotype (NHML); 1♂, 1♀, no data, PIPeR



Figures 15, 16. *Brueelia mcnewae* n. sp. from *Nucifraga columbiana* (Wilson, 1810). (15) Male habitus, dorsal and ventral view. (16) Female habitus, dorsal and ventral view.

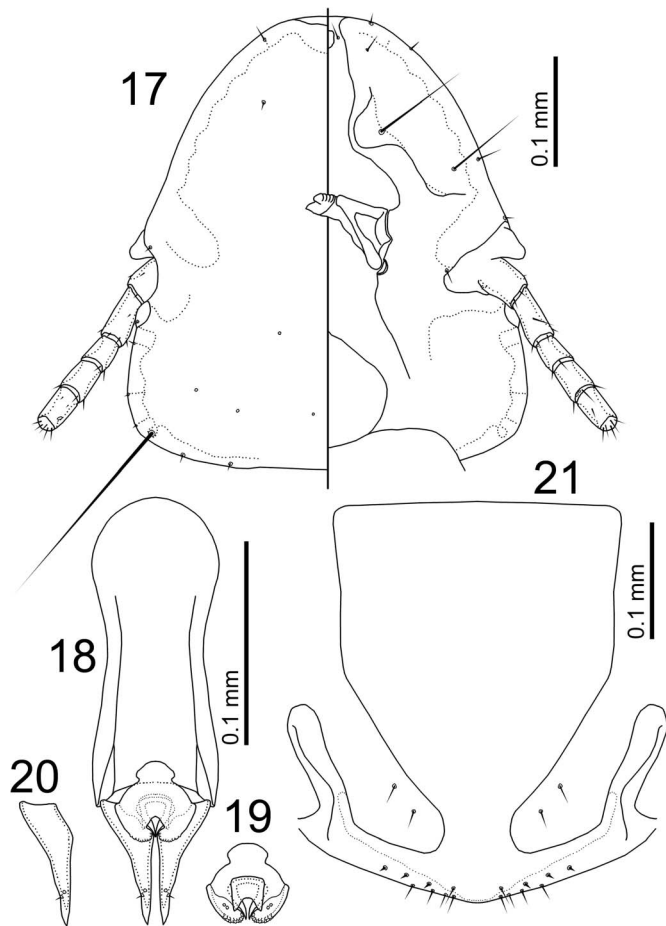
No. 12 (PIPeR); 3♀, Alberta [Canada], December 1897, R. Meinertzhagen, 3095 (NHML).

ZooBank registration: urn:lsid:zoobank.org:act:50940101-0EB2-41DC-9124-B3675627A18A.

Etymology: The specific name is in honor of Dr. Sabrina McNew (Cornell University), in recognition of her work on the ecology of host tolerance in response to parasitism.

Remarks

Brueelia mcnewae is most similar to *B. diblasiae*, with which it shares the following characters: head broad (Figs. 10, 17); *ps* present on abdominal segment III of both sexes (Figs. 9, 16); sclerotization of female subgenital plate reaches vulval margin medianly (Figs. 14, 21); basal apodeme slender, constricted at mid-length (Figs. 11, 18). These 2 species can be separated by the following characters: *aps* present on male tergopleurite V in *B. diblasiae* (Fig. 9), but absent in *B. mcnewae* (Fig. 16); proximal mesosome about as broad as gonopore in *B. mcnewae* (Fig. 19), but markedly more slender than gonopore in *B. diblasiae* (Fig. 12); in specimens where proximal mesosome is more similar to that of *B. bonnevillensis*, the gonopore is still slightly wider than the proximal mesosome, but the difference in width is not as



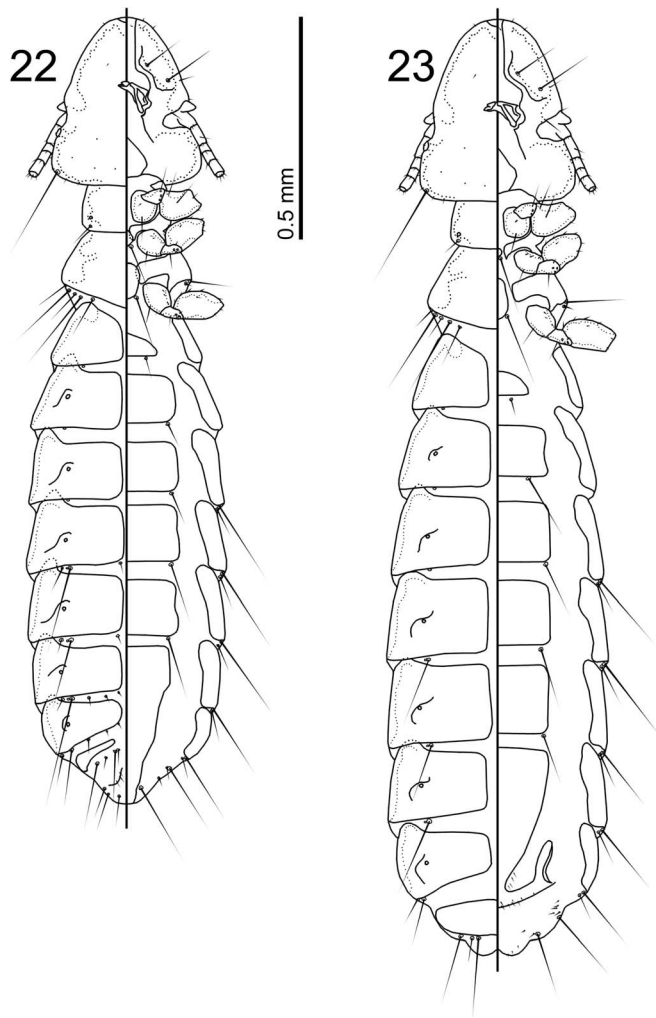
Figures 17–21. *Brueelia mcnewae* n. sp. from *Nucifraga columbiana* (Wilson, 1810). (17) Male head, dorsal and ventral view. (18) Male genitalia, dorsal view. (19) Male mesosome, ventral view. (20) Male paramere, dorsal view. (21) Female subgenital plate and vulval margin, ventral view. (Figures 18–20 share the lower left scale bar.)

pronounced); gonopore quadratic with convex distal margin in *B. mcnewae* (Fig. 19), but crescent-shaped in *B. diblasiae* (Fig. 12); lateral margins of preantennal head more pronounced convex in *B. mcnewae* (Fig. 17) than in *B. diblasiae* (Fig. 10).

***Brueelia bonnevillensis* n. sp.**

(Figs. 22–28)

Diagnosis (male): Head flat dome-shaped (Fig. 24), lateral margins of preantennal area convex, frons rounded to slightly flattened medianly. Marginal carina of moderate width, median margin undulating markedly; carina moderately displaced and widened at osculum. Ventral anterior plate not clearly visible. Head chaetotaxy as in Figure 24. Preantennal nodi large, bulging. Pre- and post-ocular nodi large. Marginal temporal carina with irregular median margin. Gular plate lanceolate. Thoracic and abdominal segments and chaetotaxy as in Figure 22; *aps* present on tergopleurite V; *ps* absent on abdominal segment III. Basal apodeme broad, narrowing anteriorly in most specimens (Fig. 25). Proximal mesosome wide, roughly quadratic, about as wide as gonopore. Mesosomal lobes moderate, rounded, rugose area restricted to near distal and median margins; 2 *pmes* sensilla on



Figures 22, 23. *Brueelia bonnevillensis* n. sp. from *Aphelocoma woodhouseii nevadae* Pitelka, 1945. (22) Male habitus, dorsal and ventral view. (23) Female habitus, dorsal and ventral view.

each side of gonopore. Gonopore broadly crescent-shaped. Penile arms long, reaching to distal margin of mesosome. Parameres elongated, broad, *pst1*–2 as in Figure 27. Measurements as in Table II.

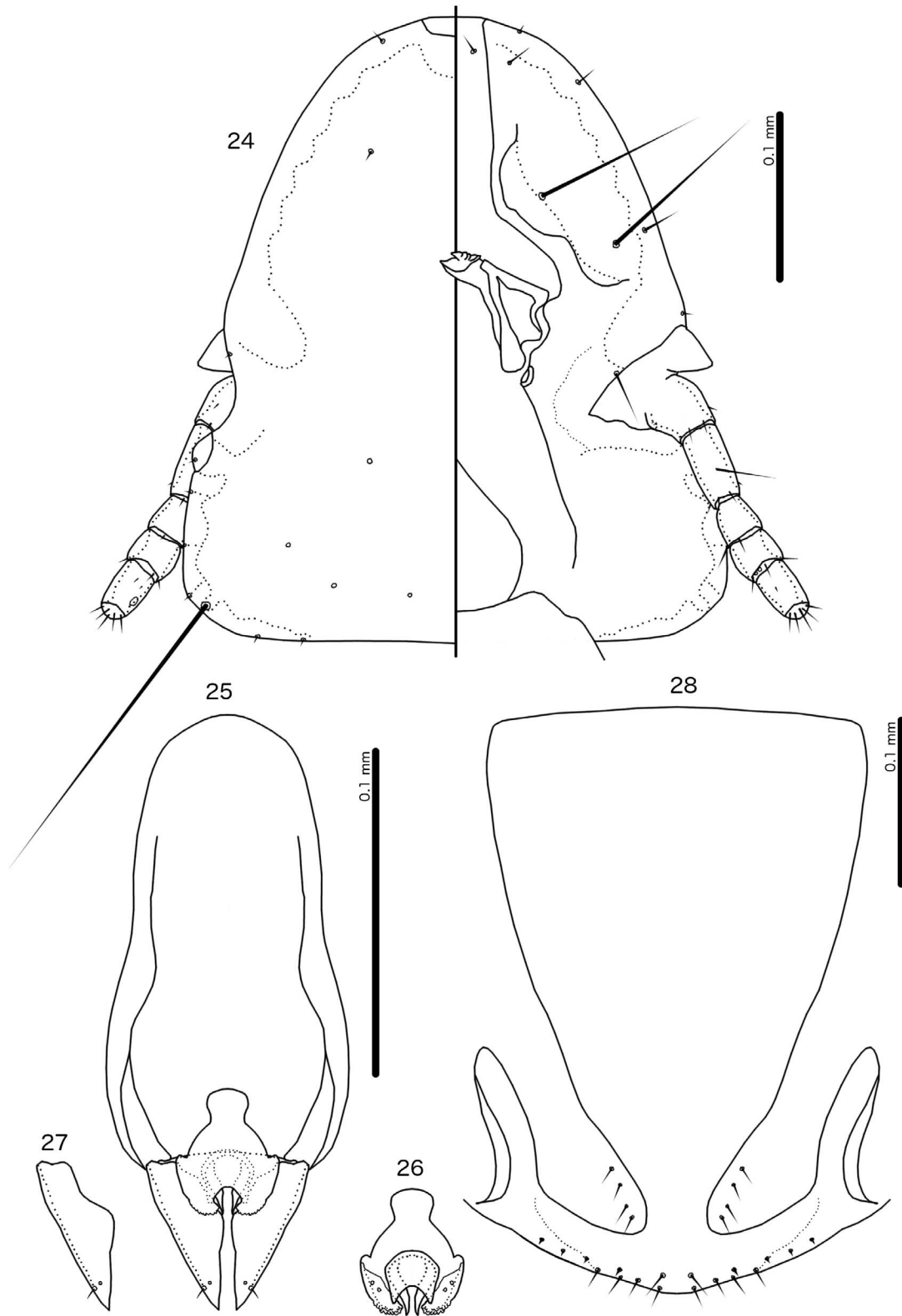
Female: As male, except thoracic and abdominal chaetotaxy as in Figure 23; *ps* absent on abdominal segment III. Subgenital plate roughly triangular, lateral margins convex (Fig. 28), with narrow connection to cross-piece. Vulval margin gently rounded (Fig. 28), with 3–4 short, slender *vms* and 3–5 short, slender *vss* on each side; 4–5 short, slender *vos* on each side of subgenital plate; distal 1 *vos* median to *vss*. Measurements as in Table II.

Taxonomic summary

Type host: *Aphelocoma woodhouseii nevadae* Pitelka, 1945, Woodhouse's scrub-jay.

Type locality: Granite Creek Canyon, Deep Creek Mountains, Juab County, Utah.

Type material: Holotype ♂, Granite Creek Canyon, Deep Creek Mountains, Juab County, Utah, 23 June 1964, EE-5415



Figures 24–28. *Brueelia bonnevillensis* n. sp. from *Aphelocoma woodhouseii nevadae* Pitelka, 1945. (24) Male head, dorsal and ventral view. (25) Male genitalia, dorsal view. (26) Male mesosome, ventral view. (27) Male paramere, dorsal view. (28) Female subgenital plate and vulval margin, ventral view. (Figures 25–27 share the lower left scale bar.)

(NHML). Paratypes 1♀, same data as holotype (NHML); 10♂, 18♀, same data as holotype (PIPeR).

ZooBank registration: urn:lsid:zoobank.org:act:3F0A69EE-F859-4155-8C80-C60FE2F93C45.

Etymology: Specific name refers to Lake Bonneville, the prehistoric lake that covered large parts of Utah during the Pleistocene, including the type locality.

Remarks

Brueelia bonnevillensis is most similar to *B. mexicana* n. sp., with which it shares the following characters: head relatively slender (Figs. 24, 31); *ps* absent from abdominal segment III in both sexes (Figs. 22–23, 29–30); connection between female subgenital plate and cross-piece slender (Figs. 28, 35); proximal mesosome about as broad as gonopore (Figs. 26, 33); parameres broad (Figs. 27, 34). These 2 species can be separated by the following characters: *aps* present on male tergopleurite V in *B. bonnevillensis* (Fig. 22), but absent in *B. mexicana* (Fig. 29); preantennal head more rounded in *B. bonnevillensis* (Fig. 24) than in *B. mexicana* (Fig. 31); proximal mesosome nearly quadratic in *B. bonnevillensis* (Fig. 26), but wide and with pointed anterior margin in *B. mexicana* (Fig. 33); posterior margin of gonopore deeply concave and postero-lateral corners flaring in *B. mexicana* (Fig. 33), but distal margin only shallowly concave, and postero-lateral corners parallel to slightly convergent in *B. bonnevillensis* (Fig. 26).

Brueelia mexicana n. sp.

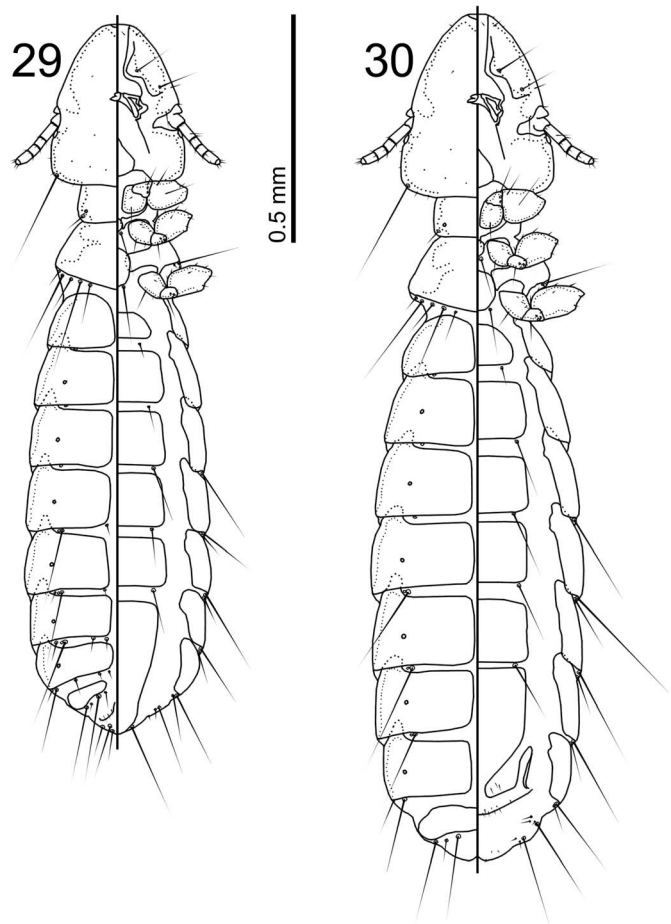
(Figs. 29–35)

Diagnosis (male): Head flat dome-shaped (Fig. 31), lateral margins of preantennal head convex, frons flattened. Marginal carina of moderate width, median margin undulating; carina shallowly displaced and widened at osculum. Ventral anterior plate not visible. Head chaetotaxy as in Figure 31. Preantennal nodi large, bulging. Pre- and post-ocular nodi large. Marginal temporal carina slender, median margin more or less regular. Gular plate lanceolate. Thoracic and abdominal segments and chaetotaxy as in Figure 29; *aps* absent on tergopleurite V; *ps* absent on abdominal segment III. Basal apodeme slender, only slightly constricted at mid-length (Fig. 32). Proximal mesosome wide, rounded triangular, broader than gonopore (Fig. 33). Mesosomal lobes slender, rounded, rugose area extensive; 2 *pms* sensilla on each side lateral to gonopore. Gonopore as in Figure 33. Penile arms short, not reaching distal margin of mesosome. Parameres broad, tapering distally, elongated, *pstl*–2 as in Figure 34. Measurements as in Table II.

Female: As male, except: thoracic and abdominal chaetotaxy as in Figure 30; *ps* absent on abdominal segment III. Subgenital plate roughly pentagonal (Fig. 35), with narrow connection to cross-piece; sclerotization pale but does not appear to reach vulval margin as in Figure 35. Vulval margin gently rounded to slightly flattened medially (Fig. 35), with 3–4 short, slender *vms* and 2–4 short, thorn-like *vss* on each side; 3–5 short, slender *vos* on each side of subgenital plate; distal 1 *vos* median to *vss*. Measurements as in Table II.

Taxonomic summary

Type host: *Aphelocoma woodhouseii cyanotis* Ridgway, 1887, Woodhouse's scrub-jay.



Figures 29, 30. *Brueelia mexicana* n. sp. from *Aphelocoma woodhouseii cyanotis* Ridgway, 1887. (29) Male habitus, dorsal and ventral view. (30) Female habitus, dorsal and ventral view.

Type locality: Las Vacas, Coahuila, Mexico.

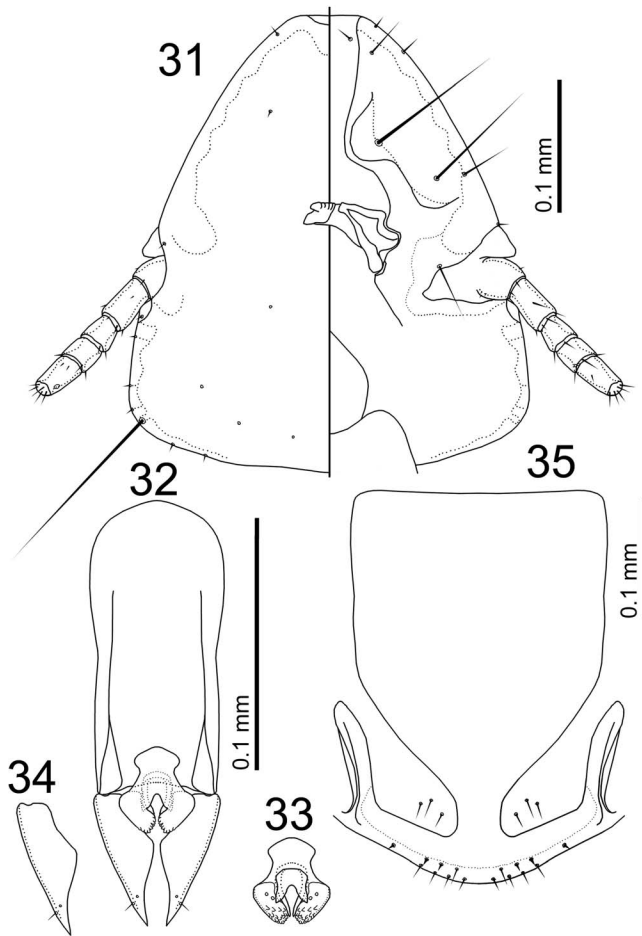
Type material: Holotype ♂, Las Vacas, Coahuila, Mexico, 30 June 1958, C.A. Ely, CAE-573 (NHML). Paratypes 1♀, same data as holotype (NHML); 9♂, 18♀, same data as holotype (PIPeR); 4♂, 2♀, same locality, 21 October 1958, C.A. Ely, CAE-971 (PIPeR); 2♂, 2♀, same data (NHML).

ZooBank registration: urn:lsid:zoobank.org:act:19515E4B-62FD-4387-B20D-54E307B75AE4.

Etymology: Specific name derived from the type locality.

Remarks

Brueelia mexicana is most similar to *B. bonnevillensis*, with which it shares the following characters: head relatively slender (Figs. 24, 31); *ps* absent from abdominal segment III in both sexes (Figs. 22–23, 29–30); connection between female subgenital plate and cross-piece slender (Figs. 28, 35); proximal mesosome about as broad as gonopore (Figs. 26, 33); parameres broad (Figs. 27, 34). These 2 species can be separated by the following characters: *aps* absent on male tergopleurite V in *B. mexicana* (Fig. 29), but present in *B. bonnevillensis* (Fig. 22); preantennal head more rounded in *B. bonnevillensis* (Fig. 24) than in *B. mexicana* (Fig. 31); proximal mesosome nearly quadratic in *B. bonnevillensis* (Fig. 26), but wide and with pointed anterior margin in *B. mexicana*



Figures 31–35. *Brueelia mexicana* n. sp. from *Aphelocoma woodhouseii cyanotis* Ridgway, 1887. (31) Male head, dorsal and ventral view. (32) Male genitalia, dorsal view. (33) Male mesosome, ventral view. (34) Male paramere, dorsal view. (35) Female subgenital plate and vulval margin, ventral view. (Figures 32–34 share the lower left scale bar.)

(Fig. 33); gonopore with deeply concave distal margin and flaring postero-lateral corners in *B. mexicana* (Fig. 33), but with shallowly concave distal margin and parallel or slightly convergent postero-lateral corners in *B. bonnevillensis* (Fig. 26).

DISCUSSION

Lice in the genus *Brueelia* occur mainly on hosts in the Passerides radiation (Gustafsson and Bush, 2017). However, a small number of species in this genus are known from hosts in the Corvidae radiation, particularly from hosts in the families Corvidae (Table III) and Laniidae. The *Brueelia* species known from these 2 host families are morphologically dissimilar and do not appear to be closely related (D.R. Gustafsson and S.E. Bush, unpubl. data). This suggests that the *Brueelia* populations found on laniid and corvid hosts have originated from at least 2 independent colonization events, sometime after these bird lineages diverged approximately 40 million years ago (Jönsson and Fjeldså, 2006).

However, a single colonization event may not be sufficient to explain the diversity of *Brueelia* species lice on corvid hosts. The 5 species described from North American hosts here are morpho-

Table III. Host associations of *Brueelia*-complex lice on corvid hosts. Dash (—) denotes host genera from which no *Brueelia*-complex lice are known. Host taxonomy follows Clements *et al.* (2019), and host genera are arranged in the same order as Clements *et al.* (2019), to give a rough indication about their relationships. Louse numbers and taxonomy follow Gustafsson and Bush (2017), but include the species described as new here and by Mey (2017).

Host genus	Bird spp.*	Louse genus	Louse spp.†	Known host spp.‡
<i>Platysmurus</i>	1	<i>Olvinirmus</i>	1	1
<i>Perisoreus</i>	3	<i>Olvinirmus</i>	1	1
<i>Cyanolyca</i>	9	—		
<i>Calocitta</i>	2	—		
<i>Psilorhinus</i>	1	—		
<i>Cyanocorax</i>	16	<i>Olvinirmus</i>	7	7
<i>Gymnorhinus</i>	1	<i>Brueelia</i>	1	1
<i>Cyanocitta</i>	2	<i>Brueelia</i>	1	1
		<i>Olvinirmus</i>	1	1
<i>Aphelocoma</i>	7	<i>Brueelia</i>	2	2
<i>Garrulus</i>	3	<i>Olvinirmus</i>	2	2
<i>Cyanopica</i>	2	<i>Brueelia</i>	1	1
<i>Urocissa</i>	5	<i>Olvinirmus</i>	2	3
<i>Cissa</i>	4	—		
<i>Dendrocitta</i>	7	<i>Olvinirmus</i>	2	2
<i>Crypsirina</i>	2	<i>Olvinirmus</i>	1	1
<i>Temnurus</i>	1	—		
<i>Pica</i>	7	<i>Hecatrishula</i>	1	3
		<i>Olvinirmus</i>	1	1
<i>Zavattariornis</i>	1	<i>Brueelia</i>	1	1
<i>Podoces</i>	4	<i>Hecatrishula</i>	1	2
<i>Nucifraga</i>	3	<i>Brueelia</i>	1	1
		<i>Hecatrishula</i>	1	1
		<i>Olvinirmus</i>	1	1
<i>Pyrhocorax</i>	2	<i>Hecatrishula</i>	2	2
<i>Ptilostomus</i>	1	<i>Brueelia</i>	2	1
<i>Corvus</i>	44	<i>Corvonirmus</i>	19	20
		<i>Hecatrishula</i>	5	8

* Number of bird species in each genus.

† Number of louse species in each genus that are known from each host genus.

‡ Number of bird species known to host lice in each genus.

logically rather similar to each other, but they are not similar to the lice known from Old World corvids. Moreover, the *Brueelia* species known from Old World corvids are also not very similar to each other (e.g., Ansari, 1956, 1957) and seem to have originated from several separate colonization events. In the phylogeny of Bush *et al.* (2016), *Brueelia* from the African piapiac (*Ptilostomus afer*) and the New World scrub-jay (*Aphelocoma californica*) were separated, with each species more closely related to specimens from non-corvid hosts from the same continent.

The pattern of host associations of *Brueelia* on corvid hosts also suggests that several independent colonization events may be involved, rather than a single event followed by radiation. The hosts of the *Brueelia* species on corvids do not form a monophyletic group. *Cyanocitta*, *Aphelocoma*, and *Gymnorhinus* are closely related (Bonnaccorso and Peterson, 2007), and form the sister clade to the Neotropical jays in the genera *Cyanocorax*, *Psilorhinus*, and *Calocitta*. By contrast, *Nucifraga* is more closely related to the genus *Corvus* (Cibois and Pasquet, 1999; Ericson *et*

al., 2005), *Cyanopica* is more closely related to *Garrulus*, and both *Zavattariornis* and *Ptilostomus* are most closely related to *Podoces*. Lice in the genus *Brueelia* are not known from any of these other host genera; however, lice belonging to other genera in the *Brueelia*-complex are known from most of these hosts (Gustafsson and Bush, 2017; Table III). Notably, each of the species of *Nucifraga* is parasitized by lice in different genera within the *Brueelia*-complex.

The occurrence of 2 different species of *Brueelia* (*B. mexicana* and *B. bonnevillensis*) on 2 different subspecies of *Aphelocoma woodhouseii* is notable. Most commonly, different subspecies of birds are parasitized by morphologically indistinguishable populations of *Brueelia* (see checklists in Gustafsson and Bush, 2017). However, the African piapiac *Ptilostomus afer* is host to both *Brueelia moreli* Ansari, 1957, and *Brueelia zohrae* Ansari, 1956. There are few published reports of these *Brueelia* species, and their geographical range is poorly known. Both species were described from material collected in adjacent parts of the host's range (*B. moreli* from Senegal, and *B. zohrae* from Guinea-Bissau), and to our knowledge, there are no significant gaps in the distribution of the host between Senegal and Guinea-Bissau. The occurrence of 2 species of *Brueelia* on the same host species in the same region may suggest either that both louse species may occur together on the same host, or that the geographical distribution of the lice is limited to some unknown environmental factor. In one of the few examples where a species of louse has been sampled across the range of its host, Toon and Hughes (2008) showed greater genetic distances between northern and southern populations of *Olivinirmus semiannulatus* (Piaget, 1883) than between their hosts. Environmental factors, as well as chance events, may make the geographical range of lice much different from that of their hosts.

Adaptation to different environments and/or geographic isolation may influence the distribution of *Brueelia* spp. on New World corvids. Bush et al. (2009) showed that *Brueelia* “*deficiens*” on *A. californica* s. lat. occurred only in part of the host's range, being absent in less arid areas. In addition, the 2 *Brueelia* species known from *A. woodhouseii* occur on different host subspecies that are geographically isolated (Delaney et al., 2008; McCormack et al., 2010). Range modeling of *A. woodhouseii* during the Pleistocene suggests that these populations may have been isolated for a long time (Peterson et al., 2004). This long period of geographical isolation of the hosts may be sufficient to explain the occurrence of 2 different species of *Brueelia* on different host subspecies; however, environmental difference may also have contributed to divergence. Additional examined material from the Californian *A. californica* may represent a third species of *Brueelia* from this host complex, but most of this material is poorly preserved and is not described here. More louse specimens are needed from *Aphelocoma* jays across North America to further explore the host associations and geographical distribution of these lice, particularly in those parts of Mexico where several host species overlap.

KEY TO SPECIES OF *BRUEELIA* ON CORVIDAE

Vulval chaetotaxy overlapping between North American species and not diagnostic. Females of these species best separated on the shape of the head and the subgenital plate.

1. Male tergopleurite VI with at least 1 *tps* on each side ... 2
 - Male tergopleurite VI with no *tps* 4
2. Male tergopleurite IV with *ss* and *aps*; preantennal head broadly rounded or trapezoidal 3
 - Male tergopleurite IV with no *ss* and no *aps*; preantennal head slender and elongated, with almost pointed frons *Brueelia zohrae*
3. Preantennal head broadly rounded; proximal mesosome broadly rounded *Brueelia zavattariornis*
 - Preantennal head trapezoidal; proximal mesosome elongated, rounded trapezoidal *Brueelia moreli*
4. Male tergopleurite V without *psps*, but *aps* present ...
 - *Brueelia deficiens*
 - Male tergopleurite V with *psps*, *aps* present (Fig. 8) or absent (Fig. 1) 5
5. Abdominal segment III with 1 *ps* on each side in both sexes; connection between female subgenital plate and cross-piece broad (Fig. 7) 6
 - Abdominal segment III without *ps* in either sex; connection between female subgenital plate and cross-piece narrow (Fig. 35) 8
6. Proximal mesosome about as broad as gonopore (Fig. 19); gonopore roughly quadratic with concave distal margin (Fig. 19) *Brueelia mcnewae*
 - Proximal mesosome much narrower than gonopore (Fig. 5); gonopore crescent-shaped (Fig. 5) 7
7. Female subgenital plate roughly trapezoidal, sclerotization not reaching vulval margin medianly (Fig. 7); male tergopleurite V without *aps* and male abdominal segment III without *ps* (Fig. 1) *Brueelia tempestwilliamsae*
 - Female subgenital plate roughly pentagonal, sclerotization reaching vulval margin medianly (Fig. 14); male tergopleurite V with *aps* and male abdominal segment III with *ps* (Fig. 8) *Brueelia diblasiae*
8. Female subgenital plate roughly trapezoidal (Fig. 28); proximal mesosome roughly quadratic (Fig. 26); male tergopleurite V with *aps* (Fig. 22) ... *Brueelia bonnevillensis*
 - Female subgenital plate roughly pentagonal (Fig. 35); proximal mesosome rounded triangular, lateral margins flaring (Fig. 33); male tergopleurite V without *aps* (Fig. 29) *Brueelia mexicana*

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