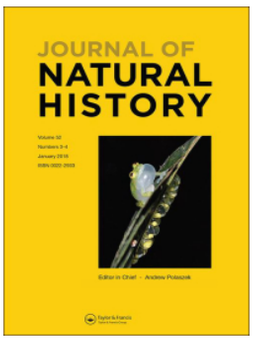

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Descriptions of seven new species of *Brueelia* Kéler 1936 (Phthiraptera: Ischnocera: Philopteridae) from North American sparrows (Aves: Passeriformes: Passerellidae), and review of host use by *Brueelia vulgata*

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ABSTRACT

Seven new species of *Brueelia* are described from North American hosts. They are: *Brueelia melospizae* sp. nov. from *Melospiza georgiana, M. lincolnii, M. melodia*, and *M. m. fallax; Brueelia californica* sp. nov. from *Melozone crissalis; Brueelia canyonica* sp. nov. from *Melozone fusca; Brueelia tenebrosa* sp. nov. from *Passerella iliaca; Brueelia chlorurae* sp. nov. from *Pipilo chlorurus; Brueelia hesperides* sp. nov. from *Pooecetes gramineus confinis; Brueelia cassiopeia* sp. nov. from *Spizella passerina arizonae* and *S. p. passerina. Brueelia vulgata* and *Brueelia angustifrons* are redescribed and illustrated. An updated host checklist of the *Brueelia*-complex species known from the Emberizidae and Passerellidae, and a key to the males of the species described herein are provided.

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Brueelia; Philopteridae; Passerellidae; North America; new species; *Brueelia vulgata*

Introduction

The *Brueelia*-complex is a large and diverse group of chewing lice that mainly parasitizes perching birds (Passeriformes) (Gustafsson and Bush 2017). This louse group is not geographically restricted, as it occurs nearly everywhere but Antarctica. However, most species of *Brueelia* have been described from passeriform birds in Europe. Only a few species have been described from North America, and most of the North American species were described over a century ago (Osborn 1896; Kellogg 1896; 1899; Kellogg and Chapman 1899; Kellogg and Mann 1912; Carriker 1902; but also Carriker 1956). This group has received little attention over the last 100 years.

Kellogg (1896) described *Nirmus vulgatus* (now *Brueelia vulgata*) from a large number of North American hosts, spanning three different host families. At an early stage, this species was thus assumed to be a host generalist, and was subsequently recorded from at least 50 host species across the world (see below). Almost without exception, these records of purported *B. vulgata* are given without any morphological comparisons,

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illustrations, measurements, or information on the existence and deposition of voucher specimens. The true identities of these records are therefore very hard to establish.

Most species in the genus *Brueelia* are host specialists, and a host range as broad as that suggested for *B. vulgata* is highly unusual within the *Brueelia*-complex. Molecular data indicate that *B. vulgata* is associated with several host species. For example, Bueter et al. (2009) and Bush et al. (2016; Figure 3e, clade I-1) showed that *B. vulgata* from the type host *Junco hyemalis* is genetically very similar to material from several other North American hosts. However, most specimens from non-American hosts included in the Bush et al. (2016) study were only distantly related to *B. vulgata*. We here redescribe *B. vulgata* from dark-eyed juncos (the type host). We also re-examine specimens of *Brueelia* from North American sparrows (Passerellidae), and confirm the association between *B. vulgata* and three host species. In addition, we identified morphologically unique material; consequently, we describe seven new species of *Brueelia* from North American sparrows.

Material and methods

Slide-mounted specimens are deposited at Field Museum of Natural History, Chicago, USA (FMNH), Natural History Museum, London, United Kingdom (NHML), Price Institute for Parasite Research, University of Utah, Salt Lake City, USA (PIPeR), or University of Minnesota, St. Paul, USA (UMSP). All studied material was mounted in Canada balsam on microscopy slides.

Specimens were examined and measured with a Nikon Eclipse E600 fitted with an Olympus DP25 camera and digital measuring software (ImageJ 1.48 v, Wayne Rasband). 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 millimetres, as ranges (mean value, when n ≥ 10). Abbreviations used: TL = total length; HL = head length (along midline); HW = head width (at temples); PRW = prothorax width; PTW = pterothorax width; AW = abdominal width (at segment V).

Morphological and setal terms and abbreviations thereof follow Gustafsson and Bush (2017; Figure 1–41), and include: *pmes – posterior mesosomal setae; ps – pleural setae; pst1–2 – parameral setae 1–2; ss – sutural setae; tps – tergal posterior setae; vms – vulval marginal setae; vos – vulval oblique setae; vss – vulval submarginal setae*. Host taxonomy follows Clements et al. (2019). Descriptions of pigmentation patterns for all species should be seen as approximate, as these often differ slightly between specimens based on preparation methods, as well as due to individual variation.

Taxonomy

Class **INSECTA** Linnaeus 1758
Order **PHTHIRAPTERA** Haeckel 1896
Suborder **Ischnocera** Kellogg 1896
Family **PHILOPTERIDAE** Burmeister 1838
Genus ***Brueelia*** Kéler 1936

Philopterus Nitzsch 1818, p. 288 (*in partim*).
Nirmus Nitzsch 1818, p. 291 (*in partim*).
Degeeriella Neumann 1906, p. 60 (*in partim*).

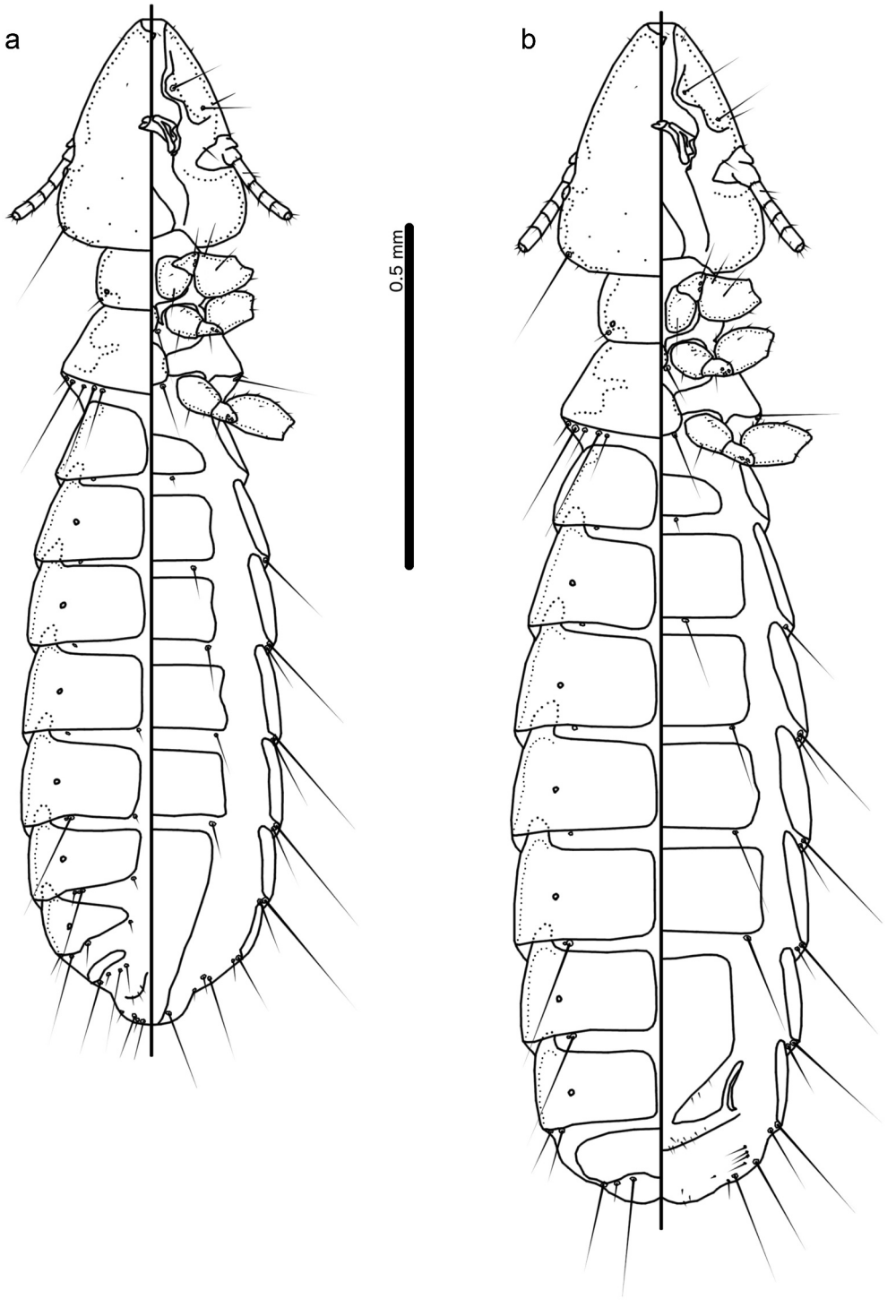

Figure 1. *Brueelia vulgata* (Kellogg 1896) ex *Junco hyemalis hyemalis* (Linnaeus 1758). (a) male habitus, dorsal and ventral views; (b) female habitus, dorsal and ventral views.

Painjunirmus Ansari 1947, p. 285.
Allobrueelia Eichler 1951, p. 36 (*in partim*).
Nigronirmus Złotorzycka 1964, p. 248.
Spironirmus, 1964, p. 261.
Serinirmus Soler Cruz et al. 1987, p. 244.
Plesionirmus Mey, 2017, p. 144.
Neosittiella, 2017, p. 149.

Type species: ***Brueelia rossittensis*** Kéler 1936, p. 257 [= *Brueelia brachythorax* (Giebel 1874, p. 134)] ex *Bombycilla garrulus garrulus* (Linnaeus 1758), by original designation.

Remarks

In addition to the species reported here, *Brueelia latiuscula* (Kellogg and Chapman, 1899) was described from Bell's sparrow *Artemisiospiza belli* (Cassin 1850). Carriker (1957) examined the holotype of this species and determined that it belongs to the *ornatissima* group typically found on hosts in the Icteridae. A second slide (EMEC-225,093) in the Kellogg collection contains a single *Brueelia* female taken from the same host species. The slide has been labelled '*N. latiusculus*', but this has been crossed out and replaced with '*ductilis*'. The hand writing appears to be Kellogg's or is at least not different from that of the rest of the label. It does not represent the same species as the holotype for *Brueelia ductilis* (Kellogg and Chapman 1899) and is not a member of the *ornatissima* group. Head shape and size of this specimen is different from any of the species treated here, but as the specimen is in poor shape and part of the abdomen is absent, it cannot be described further.

Brueelia vulgata (Kellogg 1896)

Nirmus vulgatus Kellogg 1896, p. 496
Degeeriella vulgata Kellogg [1896]; Harrison 1916, p. 126
Painjunirmus vulgata (Kellogg [1896]); Ansari 1947, p. 287
Brueelia vulgata (Kellogg, 1896); Hopkins and Clay 1952, p. 63

Type host

Junco hyemalis hyemalis (Linnaeus 1758) – dark-eyed junco.

Type locality

Lawrence, Kansas, United States.

Other hosts

Ammospiza nelsoni (Allen 1875) – Nelson's sparrow. *Junco hyemalis oreganus* (Townsend 1837) – dark-eyed junco. *Melospiza melodia* (Wilson 1810) – song sparrow. *Passerella iliaca* (Merrem 1786) – fox sparrow. *Spizelloides arborea* (Wilson 1810) – American tree sparrow. *Zonotrichia albicollis* (Gmelin 1789) – white-throated sparrow. *Zonotrichia atricapilla* (Gmelin 1789) – golden-crowned sparrow [Ref: Kellogg 1896]. *Zonotrichia leucophrys* (Forster 1772) – white-crowned sparrow. *Zonotrichia leucophrys gambellii* (Nuttall 1840) – white-crowned sparrow [Ref: Kellogg 1896].

Description

Both sexes. Head convex dome-shaped (Figure 2a), lateral margins of preantennal area slightly convex, frons narrowly flattened. Marginal carina of moderate width, much displaced and widened at osculum. Ventral anterior plate elongated triangular, anterior margin straight. Head chaetotaxy as in Figure 2a. Preantennal nodi small, not bulging. Pre- and postocular nodi moderate. Marginal temporal carina with very irregular median margin. Gular plate broadly lanceolate. Thoracic and abdominal segments as in Figure 1a–b. Head, thoracic plates, tergopleurites, and sternal and subgenital plates pale brown, only lateral tergopleurites and head carinae darker.

Male. Thoracic and abdominal chaetotaxy as in Figure 1a; *ss* present on tergopleurite V; no *tps* on tergopleurites II–VIII; *aps* absent on tergopleurite VI, present on tergopleurite VII; *ps* present on segments III. Basal apodeme broad, narrowing proximally (Figure 2b). Proximal mesosome small, flattened or rounded (Figure 2c). Mesosomal lobes wide, lateral margins distally convergent; 2 *pmes* microsetae on each side postero-lateral to gonopore; rugose area extensive. Gonopore roughly crescent-shaped. Penile arms do not reach distal margin of mesosomal lobes. Parameres slender, elongated, *pst1–2* as in Figure 2d. Measurements ex *Junco hyemalis* ssp. (n = 4): TL = 1.36–1.50; HL = 0.34–0.36; HW = 0.26–0.29; PRW = 0.16–0.18; PTW = 0.25–0.27; AW = 0.35–0.37. Measurements ex *J. h. hyemalis* (n = 2): TL = 1.44–1.50; HL = 0.33–0.34; HW = 0.26–0.27; PRW = 0.16–0.17; PTW = 0.26–0.27; AW = 0.38–0.39. Measurements ex *J. h. oreganus* (n = 5 except AW where n = 4): TL = 1.37–1.48; HL = 0.31–0.34; HW = 0.25–0.27; PRW = 0.15–0.17; PTW = 0.23–0.27; AW = 0.32–0.37. Measurements ex *Zonotrichia albicollis* (n = 3 except TL where n = 2): TL = 1.39–1.43; HL = 0.35; HW = 0.27–0.28; PRW = 0.17–0.18; PTW = 0.25–0.27; AW = 0.36–0.38. Measurements ex *Z. leucophrys* (n = 1): TL = 1.34; HL = 0.32; HW = 0.25; PRW = 0.16; PTW = 0.23; AW = 0.33.

Female. Thoracic and abdominal chaetotaxy as in Figure 1b; *ps* present on segment III. Lateral margins of proximal subgenital plate more or less parallel (Figure 2e), narrow connection to cross-piece. Vulval margin convergent to rounded median point (Figure 2e), with 3–4 short, slender *vms* and 3–4 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 ex *Junco hyemalis* ssp. (n = 14): TL = 1.48–1.76 (1.62); HL = 0.34–0.39 (0.37); HW = 0.27–0.31 (0.29); PRW = 0.16–0.20 (0.18); PTW = 0.26–0.30 (0.28); AW = 0.36–0.44 (0.40). Measurements ex *J. h. hyemalis* (n = 8): TL = 1.53–1.73; HL = 0.35–0.37; HW = 0.28–0.30; PRW = 0.17–0.19; PTW = 0.27–0.29; AW = 0.39–0.44. Measurements ex *J. h. oreganus* (n = 21 except PTW where n = 20, and AW where n = 19): TL = 1.49–1.85 (1.70); HL = 0.34–0.39 (0.37); HW = 0.27–0.31 (0.29); PRW = 0.16–1.20 (0.18); PTW = 0.24–0.32 (0.28); AW = 0.33–0.46 (0.41). Measurements ex *Zonotrichia albicollis* (n = 16 except TL, HL, PTW where n = 15): TL = 1.57–1.77 (1.67); HL = 0.35–0.38 (0.37); HW = 0.28–0.31 (0.29); PRW = 0.17–0.20 (0.18); PTW = 0.27–0.31 (0.29); AW = 0.38–0.44 (0.40). Measurements ex *Z. leucophrys* (n = 17): TL = 1.52–1.72 (1.62); HL = 0.35–0.38 (0.37); HW = 0.27–0.29 (0.28); PRW = 0.17–0.19 (0.18); PTW = 0.26–0.28 (0.27); AW = 0.36–0.50 (0.43).

Material examined

Ex Junco hyemalis hyemalis. Lectotype ♀, Lawrence, Kansas, United States, V.L. Kellogg, 238b, EMEC75460 (EMEC). *Non-types*. 2♂, 3♀, California, United States, Mar. 1939,

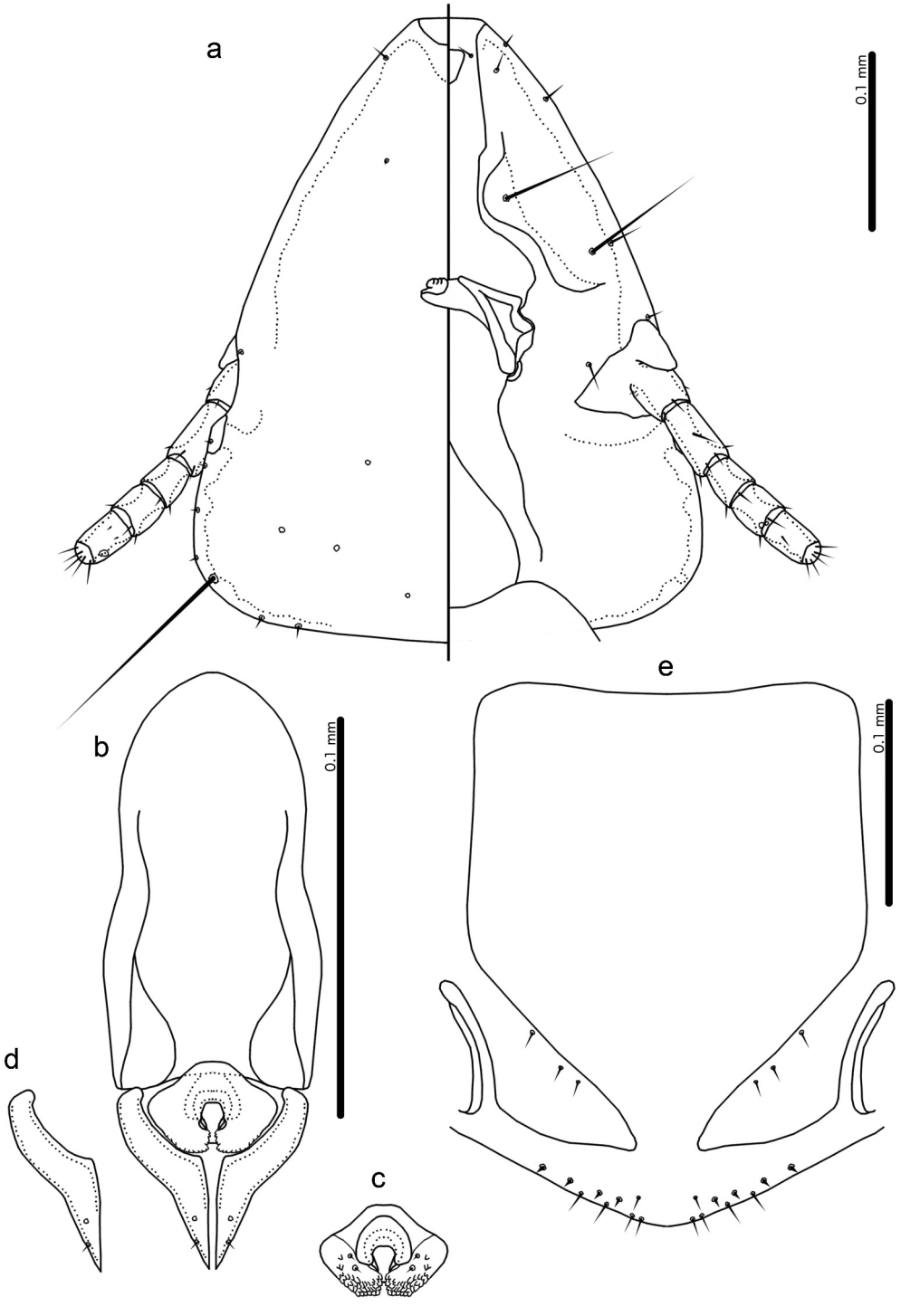

Figure 2. *Brueelia vulgata* (Kellogg 1896) ex *Junco hyemalis hyemalis* (Linnaeus 1758). (a) male head, dorsal and ventral views; (b) male genitalia, dorsal view (c) male mesosome, ventral view; (d) male paramere, dorsal view; (e) female subgenital plate and vulval margin, ventral view.

R. Meinertzhagen, 12,928 (NHML); 1♀, London Zoo, United Kingdom [label states '(Canada)', which may be origin of host], Dec. 1936, R. Meinertzhagen, 8158 (NHML); 4♀, '(Zoo)', Newfoundland, Canada, Mar. 1938, R. Meinertzhagen, 11,140 (NHML).

Ex Junco hyemalis (subspecies unknown). 4♀, Vienna, Alabama, United States, 5 March 1928 (UMSP); 1♀, McCormick Place, Chicago, Cook County, Illinois, United States, 3 April 2006, J.D. Weckstein, FMNH06-136/JDW06-04, FMNH-INS 0000 028 067, voucher for sequence Brvu.6.27.2006.28 (FMNH); 1♂, 1♀, Chevy Chase, Maryland, United Stets, 6 February 1922, E.A. Chapin, 15,634 on reverse (NHML); 5♀, Orient, Long Island, United States, 17 November 1947, R. Latham, RL-26,891, 15,635 on reverse (NHML); 1♂, 1♀, Deposit, New York, United States, 8 April 1966, S.S. Wilson, 15,631 on reverse (NHML); 2♂, 2♀, Totem Park, Juneau, Alaska, United States, 10 September 1973, 749, lot 74 3407 (NHML).

Ex J. h. oreganus. 8♂, 11♀, Iosepa, Tooele County, Utah, United States, 11 January 1965, E. & E. Branch, Dugway P/G, 7372–86 (PIPeR); 7♀, Little Granite Mountain, Dugway, Tooele County, Utah, United States, 27 October 1970, EE-700-117 (PIPeR). 2♀, same locality, 29 October 1970, EE-700-122 (PIPeR); 1♂, same locality, 29 October 1970, EE-700-121 (PIPeR); 1♀, South Cedar Mountain, Dugway P/G, Tooele County, Utah, United States, 31 January 1963, E. & E. Branch, University of Utah, JO-11-B3A (PIPeR); 2♀, V.R.S., Lbge, Alta, United States, 1 May 1956, R. Connell, Brit. Mus. 1960–443 (NHML)

Ex Zonotrichia albicollis. 4♀, Callao, Tooele County, Utah, United States, 8 October 1964, E. & E. Branch (PIPeR); 1♀, Loop, Chicago, Cook County, Illinois, United States, 5 May 2005, J.D. Weckstein, FMNH05-063/JDW05-005, FMNH-INS 000 028 104, voucher for sequence Brsp.Zoal.6.27.2006.19 (FMNH); 3♂, 11♀, Virginia, United States, Feb. 1939, R. Meinertzhagen, 12,653 (NHML).

Ex Zonotrichia leucophrys. 6♀, Dugway, Tooele County, Utah, United States, 13 May 1969, 090–72-73 (PIPeR); 6♀, Government Creek, Tooele County, Utah, United States, 4 May 1962, E. & E. Branch, University of Utah, 2 L-192 (PIPeR); 3♀, 25 miles South of Allende, Mexico, 6 April 1958, C.A. Ely, CAE-458 (PIPeR); 1♀, McCormick Place, Chicago, Cook County, Illinois, United States, 10 May 2005, J.D. Weckstein, FMNH05-091/JDW05-012, FMNH-INS 0000 028 055, voucher for sequence Brsp.Zole.6.27.2006.21 (FMNH); 1♀, Skull Valley, vicinity Dugway, Tooele County, Utah, United States, 14 October 1953, R. Porter, 213, B-655, EMEC-225,347 (EMEC); 1♂, 3♀, Sonora, Texas, United States, 21 January 1929, H.S. Peters, 13,020 (NHML).

Remarks

Kellogg (1896) described *Nirmus vulgatus* based on specimens collected from eight different host species [*Haemorhous mexicanus* (Müller, 1776), *H. purpureus* (Gmelin, 1789), *Junco hyemalis* (Linnaeus, 1758), *Melozone crissalis* (Vigors, 1839), *Pipilo maculatus* Swainson, 1827, *Turdus migratorius* Linnaeus, 1766, *Zonotrichia coronata* (Gmelin, 1789), *Zonotrichia leucophrys* (Forster, 1772)]. Subsequently, the same species has ostensibly been reported from a large number of different hosts. In total, at least 50 different bird species in three different host orders from North and South America, Africa, and Asia have been reported as hosts to *Brueelia vulgata* (*e.g.* Kellogg 1896; Kellogg and Chapman 1899; Kellogg and Kuwana 1902; Kellogg and Paine 1911; Waterston 1914; Peters 1928, 1933, 1936; Geist 1931; Brown and Wilk 1944; Ansari 1947; Woodman and Dicke 1954; Carriker 1956; Malcomson 1960; Reeves et al. 2007; Bueter et al. 2009; Bush et al. 2016). Many of

these have subsequently been described as separate species of *Brueelia*, and Price et al. (2003) only listed *Junco hyemalis* as host to *B. vulgata*. Many of these records are likely to be due to the poor original description of *B. vulgata*.

However, even the type series of *Nirmus vulgatus* contains material from a large number of hosts (Kellogg 1896). Most of this material is in poor condition, and details of chaetotaxy (particularly smaller setae such as head setae, genital setae, or *ss*), the male genitalia, and the shape of the female subgenital plate cannot be examined. Moreover, many of the specimens are female, and the male genitalia of specimens from different hosts cannot be compared. Based primarily on head shape and size, most of the other material in Kellogg's collection appears to belong to other species of *Brueelia*, and some of these are described below. A few others were described by Gustafsson and Bush (2019).

Carriker (1956) suggested *Haemorhous purpureus californicus* Baird, 1858, as the type host of *N. vulgatus*, but later (Carriker 1957) designated a female from *Junco hyemalis* as the lectotype of *Nirmus vulgatus* after having studied Kellogg's types. The lectotype is poorly preserved, but what can be seen is indistinguishable from other material from *J. hyemalis*. In addition, material from *Zonotrichia coronata* and *Z. leucophrys* is identical to material from *J. hyemalis*. As this material comes from a large number of different collections, *Zonotrichia* spp. appear to be natural hosts of *B. vulgatus*. The host genera *Junco* and *Zonotrichia* are closely related (*e.g.* Klicka et al. 2014; Bryson et al. 2016).

Both Bueter et al. (2009) and Bush et al. (2016) showed that specimens of *Brueelia* from *J. hyemalis* and several other species of sparrows are genetically very similar, and we include these species (*Passerella iliaca, Melospiza melodia, Spizelloides arborea, Zonotrichia atricapilla* and *Ammospiza nelsoni*) as natural hosts of *B. vulgata*. Note, however, that a second species of *Brueelia* occurs on some populations of *Passerella iliaca* (*Brueelia tenebrosa* sp. nov.) and *Melospiza melodia* (*Brueelia melospizae* sp. nov.). It is possible that these species of *Brueelia* and *B. vulgata* exhibit geographical specificity, as is known to occur among *Brueelia*-complex species in other host groups (Toon and Hughes 2008; Bush et al. 2009; Gustafsson and Bush 2017). More specimens from across the range of the hosts are needed to determine the geographic specificity and the frequency with which *B. vulgata* infests *P. iliaca* and *M. melodia*.

Brueelia angustifrons (Carriker 1902)

Nirmus angustifrons Carriker 1902, p. 221
Degeeriella angustifrons Carriker [1902]; Harrison 1916, p. 108
Brueelia angustifrons (Carriker, 1902); Hopkins and Clay 1952, p.53

Type host

Chondestes grammacus strigatus Swainson 1827 – lark sparrow.

Type locality

Little Bad Lands, Souix County, Nebraska, United States.

Other hosts

Chondestes grammacus grammacus (Say 1822) – lark sparrow.

Description

Both sexes. Head elongated dome-shaped (Figure 4a), lateral margins of preantennal area convex, frons rounded. Marginal carina narrow, much displaced and widened at osculum. Ventral anterior plate small, roughly oval. Head chaetotaxy as in Figure 4a. Preantennal nodi small, not bulging. Pre-ocular nodi large, post-ocular nodi moderate. Marginal temporal carina with very irregular median margin. Gular plate lanceolate. Thoracic and abdominal segments as in Figure 3a–b. Head and thorax medium brown, darker at head carinae, gular plate, and area anterior to antennal socket; sternal and subgenital plates and antero-lateral section of tergopleurites medium brown, posterior and median sections of tergopleurites pale, giving a striped appearance; pigmentation of abdomen darker in female than in male.

Male. Thoracic and abdominal chaetotaxy as in Figure 3a; *ss* absent from tergopleurite V; *tps* absent from tergopleurites II–VII; *aps* present on tergopleurites VI–VII; *ps* present on segment III. Basal apodeme narrowing anteriorly (Figure 4b). Proximal mesosome long, broad, roughly trapezoidal (Figure 4c). Mesosomal lobes unlike any other in *Brueelia*, with slender lateral thickenings, no rugose area, and 1 lateral *pmes* microseta on each side. Gonopore wide, flattened crescent-shaped with antero-lateral projections on each side; median section of gonopore slightly rugose. Penile arms minute, not reaching distal margin of mesosome. Parameres short, not elongated distally, *pst1–2* as in Figure 4d. Measurements ex *Chondestes grammacus strigatus* (n = 2): TL = 1.19–1.42; HL = 0.32–0.35; HW = 0.24–0.26; PRW = 0.15–0.16; PTW = 0.22–0.25; AW = 0.30–0.33. Measurements ex *Ch. g. grammacus* (n = 6): TL = 1.36–1.63; HL = 0.34–0.37; HW = 0.24–0.26; PRW = 0.15–0.17; PTW = 0.23–0.25; AW = 0.32–0.41.

Female. Thoracic and abdominal chaetotaxy as in Figure 3b; *ps* absent on segment III. Lateral margins of proximal subgenital plate more or less parallel (Figure 4e), narrow connection to cross-piece. Vulval margin gently rounded (Figure 4e), with 3 short, slender *vms* and 3–4 short, thorn-like *vss* on each side; 4–5 short, slender *vos* on each side of subgenital plate; distal 1 *vos* median to *vss*. Measurements ex *Chondestes grammacus strigatus* (n = 5): TL = 1.41–1.63; HL = 0.34–0.38; HW = 0.25–0.28; PRW = 0.16–0.18; PTW = 0.24–0.27; AW = 0.32–0.41. Measurements ex *Ch. g. grammacus* (n = 6): TL = 1.59–1.73; HL = 0.37–0.41; HW = 0.27–0.30; PRW = 0.17–0.19; PTW = 0.26–0.29; AW = 0.38–0.41.

Material examined

Ex Chondestes grammacus (subspecies unknown).1♂, 1♀, 25 December 1935, EWS (UMSP).

Ex Chondestes grammacus grammacus. 4♂, 4♀, Red River, near Idabel, McCurtain County, Oklahoma, United States, 13 April 1958, G.M. Sutton, GMS-13,566 (PIPeR); 2♂, 2♀, same data (NHML).

Ex Chondestes grammacus strigatus. 2♂, 4♀, North Skull Valley, Tooele County, Utah, United States, 11 June 1964, E. & E. Branch, 5360, one slide PIPeR #126 (PIPeR); 1♀, Dugway Area, Tooele County, Utah, United States, May-Jun. 1966, E. & E. Branch (PIPeR).

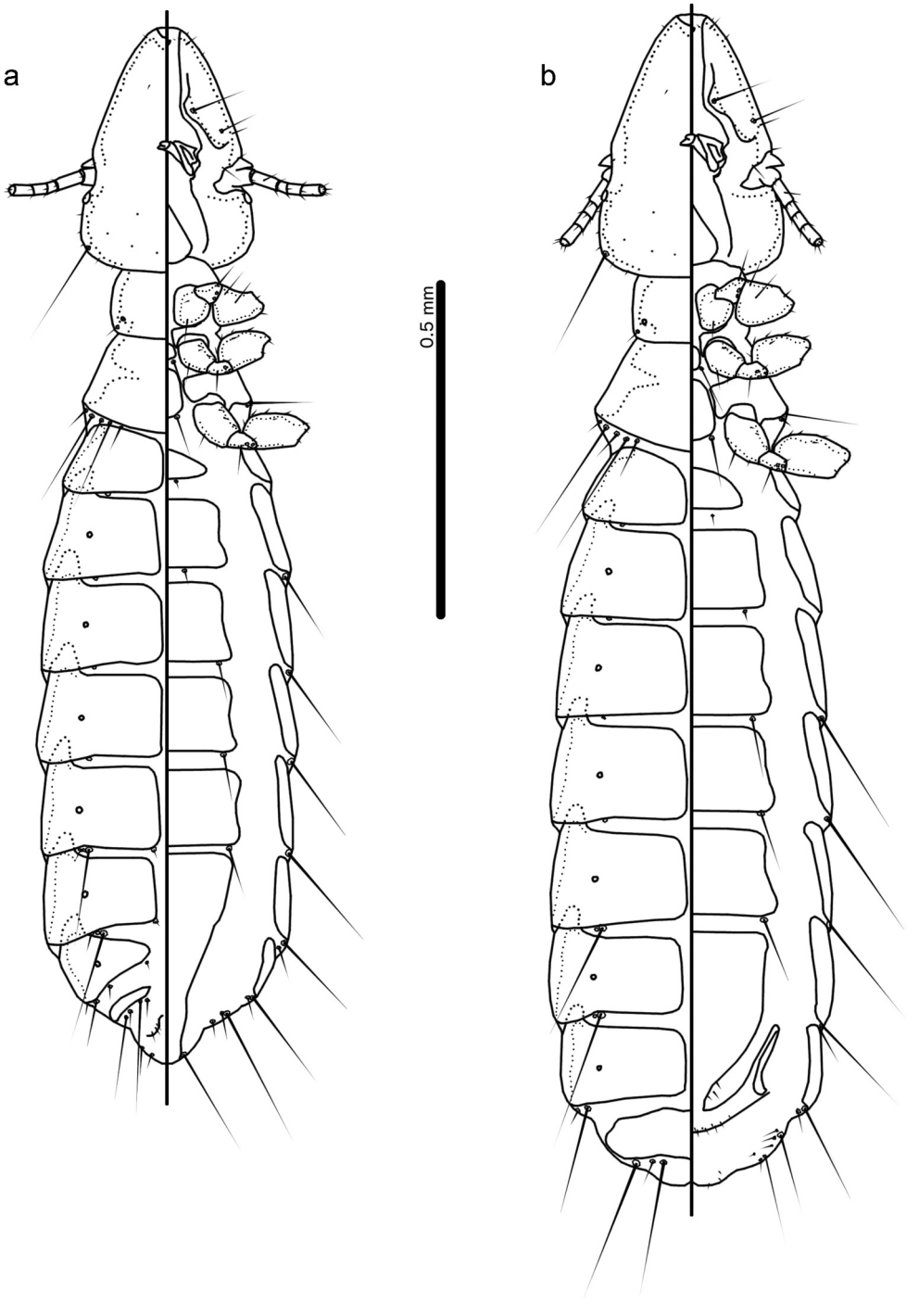

Figure 3. *Brueelia angustifrons* (Carriker 1902) ex *Chondestes grammacus strigatus* Swainson 1827. (a) male habitus, dorsal and ventral views; (b) female habitus, dorsal and ventral views.

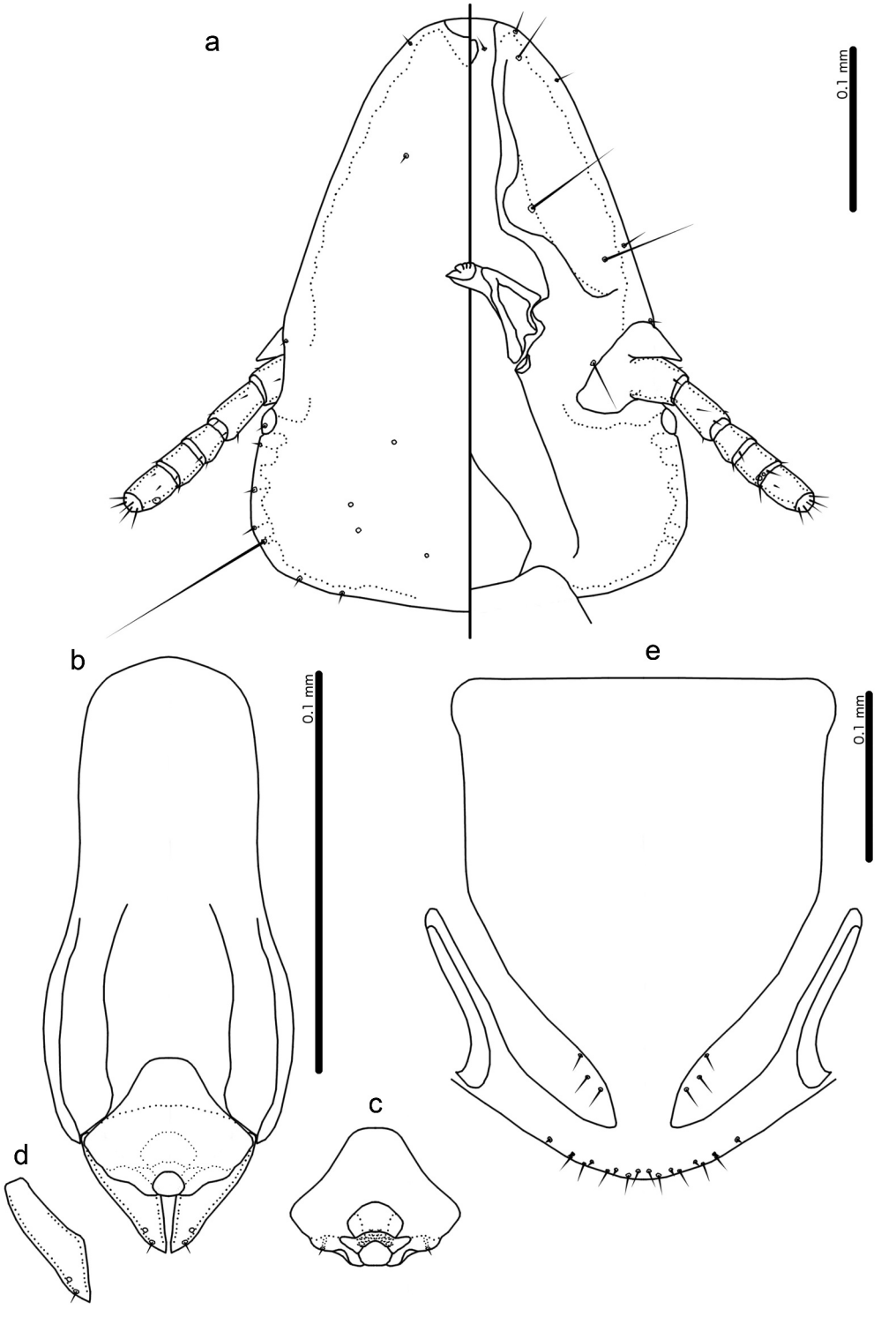

Figure 4. *Brueelia angustifrons* (Carriker 1902) ex *Chondestes grammacus strigatus* Swainson 1827. (a) male head, dorsal and ventral views; (b) male genitalia, dorsal view (c) male mesosome, ventral view; (d) male paramere, dorsal view; (e) female subgenital plate and vulval margin, ventral view.

Remarks

Carriker's (1902) original illustration appears to be drawn from an individual with a laterally compressed head, which results in the differences in head shape between his illustrations and ours.

Brueelia hesperides sp. nov.

Type host

Pooecetes gramineus confinis Baird 1858 – vesper sparrow.

Type locality

Little Davis Mountain, Tooele County, Utah, United States.

Diagnosis

Brueelia hesperides sp. nov. is most similar to *B. angustifrons*, with which it shares the following characters: head elongated dome-shaped (Figures 4a and 6a); mesosomal lobes much reduced (Figures 4c and 6c); gonopore flattened crescent-shaped (Figures 4c and 6c); *ss* absent from male tergopleurite V (Figures 3a and 5a); *aps* present on male tergopleurite VI (Figures 3a and 5a); *ps* absent from female abdominal segment III (Figures 3b and 5b). The two species can be separated by the following characters: *tps* present on male tergopleurite VII in *B. hesperides* (Figure 5a), but absent in *B. angustifrons* (Figure 3a); gonopore with antero-lateral projections in *B. angustifrons* (Figure 4c), but without such projections in *B. hesperides* (Figure 6c); mesosomal lobes narrowly rounded with slight rugosity near latero-distal margins in *B. hesperides* (Figure 6c), but widely angular and without rugose area in *B. angustifrons* (Figure 4c); parameres elongated in *B. hesperides* (Figure 6d), but not in *B. angustifrons* (Figure 4d); *ps* present on male abdominal segment III in *B. angustifrons* (Figure 3a), but absent in *B. hesperides* (Figure 5a). There is virtually no overlap in total length in males of these two species, but females are of similar size. Female vulval chaetotaxy overlaps between species, but females can be separated by head shape (Figures 3b and 5b) and pigmentation patterns (see below).

Description

Both sexes. Head elongated dome-shaped (Figure 6a), lateral margins of preantennal area convex, frons rounded to slightly flattened. Marginal carina slender, much displaced and widened at osculum. Ventral anterior plate large, elongate, rounded. Head chaetotaxy as in Figure 6a. Preantennal nodi slender, not bulging. Pre-ocular nodi large, post-ocular nodi moderate. Marginal temporal carina with very irregular median margin. Gular plate broadly lanceolate. Thoracic and abdominal segments as in Figure 5a–b. Base pigmentation pale brown, with head carinae, margins of antennal socket, proepimera, metepisterna, and lateral margins of tergopleurites medium brown.

Male. Thoracic and abdominal chaetotaxy as in Figure 5a; *ss* absent from tergopleurite V; *tps* present on tergopleurite VII; *aps* present on tergopleurites VI–VII; *ps* absent from abdominal segment III. Basal apodeme narrowing proximally (Figure 6b). Proximal mesosome broad, roughly trapezoidal (Figure 6c). Mesosomal lobes slender, rounded, with

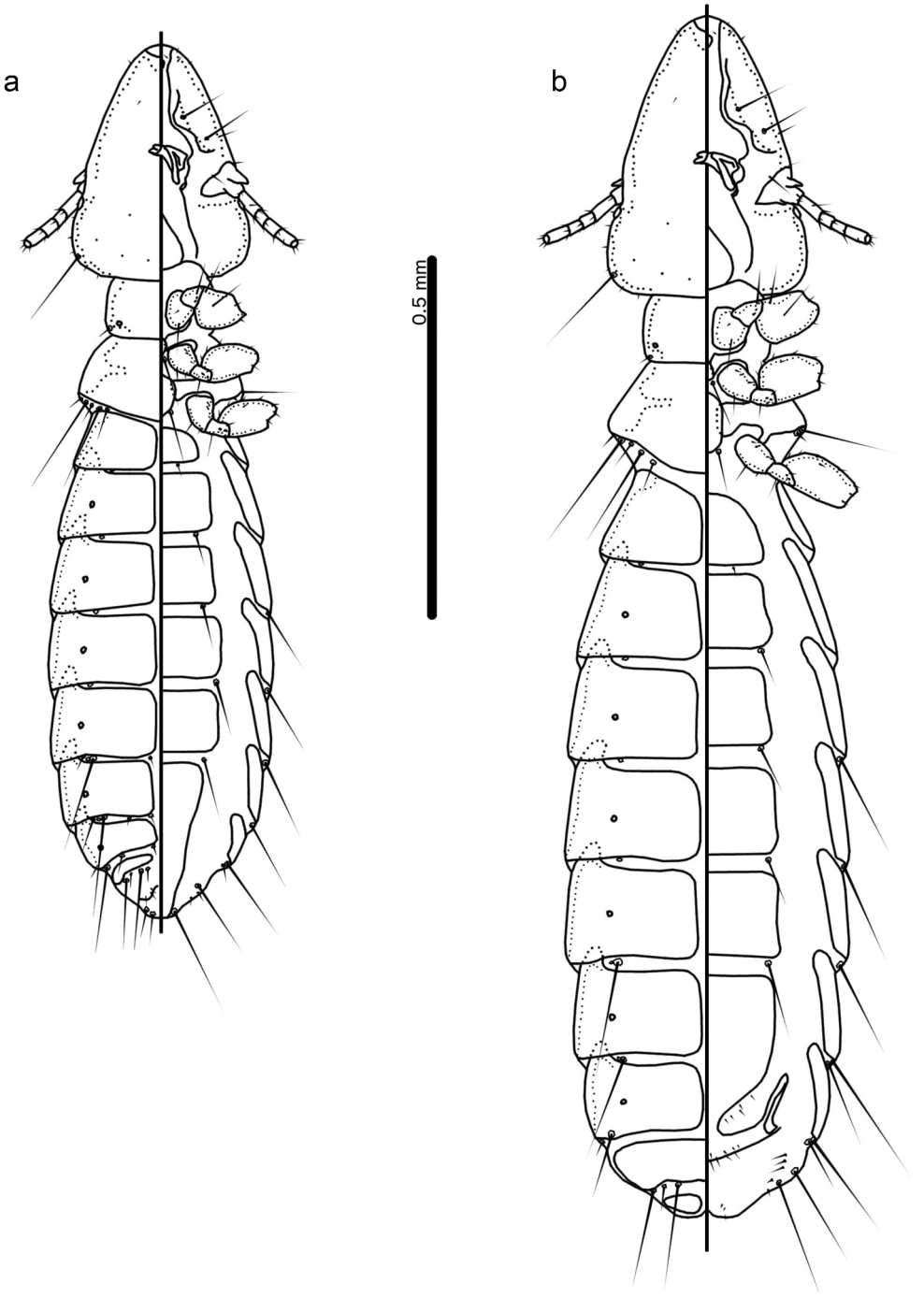

Figure 5. *Brueelia hesperides* sp. nov. ex *Pooecetes gramineus confinis* Baird 1858. (a) male habitus, dorsal and ventral views; (b) female habitus, dorsal and ventral views.

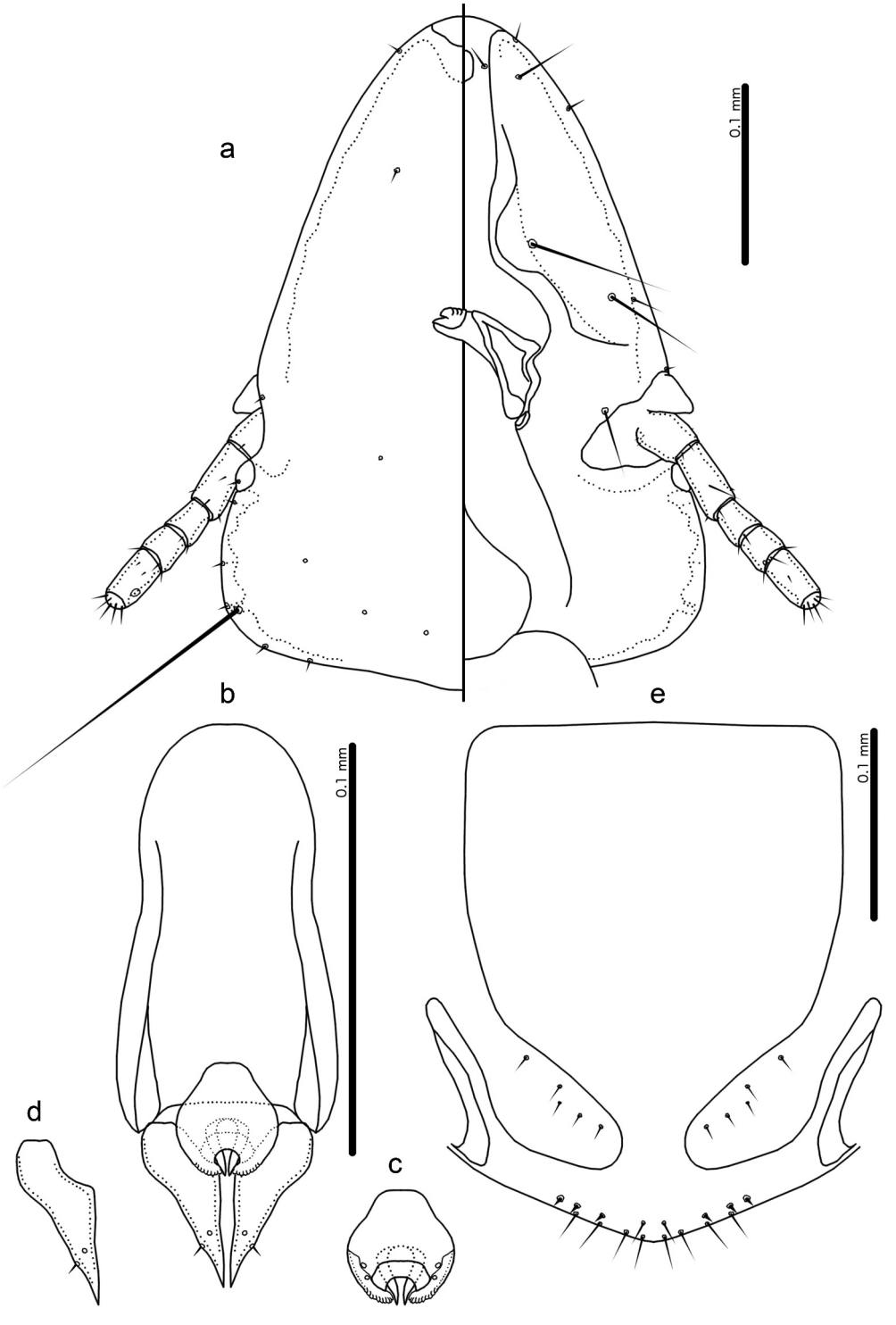

Figure 6. *Brueelia hesperides* sp. nov. ex *Pooecetes gramineus confinis* Baird 1858. (a) male head, dorsal and ventral views; (b) male genitalia, dorsal view (c) male mesosome, ventral view; (d) male paramere, dorsal view; (e) female subgenital plate and vulval margin, ventral view.

narrow lateral thickenings and restricted rugose area near postero-lateral margins; 2 *pmes* sensilla on each side lateral to gonopore. Gonopore flattened crescent-shaped. penile arms long, reaching to distal margin of mesosome. Parameres broad, elongated, *pst1–2* as in Figure 6d. Measurements (n = 2): TL = 1.26–1.37; HL = 0.35–0.36; HW = 0.25; PRW = 0.16; PTW = 0.24–0.25; AW = 0.31–0.33.

Female. Thoracic and abdominal chaetotaxy as in Figure 5b; *ps* absent from abdominal segment III. Lateral margins of proximal subgenital plate more or less parallel (Figure 6e), with intermediate connection to cross-piece. Vulval margin convergent to rounded median point (Figure 6e), with 3–4 short, slender *vms* and 3–4 short, thorn-like *vss* on each side; 4–6 short, slender *vos* on each side of subgenital plate; distal 1 *vos* median to *vss*. Measurements (n = 8): TL = 1.42–1.73; HL = 0.34–0.39; HW = 0.25–0.28; PRW = 0.15–0.18; PTW = 0.24–0.28; AW = 0.33–0.39.

Etymology

The specific name is derived from the '*Esperídes*', the nymphs of the sunset in Greek mythology, and daughters of Hesperos, the Evening Star. This is a reference to the English name of the type host, the Vesper Sparrow.

Material examined

Ex Pooecetes gramineus confinis: Holotype ♂, Little Davis Mountain, Tooele County, Utah, United States, 18 May 1964, E. & E. Branch, 5217 (NHML). Paratypes. 4♀, same data as holotype (NHML); 2♀, Sewerline, vicinity of Dugway valley, Tooele County, Utah, United States, 15 April 1953, W.G. Denzer, 265-B-173 (PIPeR); 2♀, same locality, 15 April 1953, W.G. Denzer, 193-B-174 (NHML); 1♂, 1♀, no locality, 25 December 1935, 'E.W.S.', 509 (UMSP).

Brueelia californica sp. nov.

Type host

Melozone crissalis (Vigors 1839) – California towhee.

Type locality

California, United States.

Diagnosis

Brueelia californica sp. nov. is most similar to *Brueelia canyonica* sp. nov., with which it shares the following characters: *aps* absent from male tergopleurites VI–VII (Figures 7a and 9a); *ss* present on male tergopleurite V (Figures 7a and 9a); *ps* absent on male abdominal segment III (Figures 7a and 9a), but present on female abdominal segment III (Figures 7B and 9b); gonopore broad (Figures 8c and 10c); rugose area of mesosomal lobes confined to posterior margin (Figures 8c and 10c). The two species can be separated by the following characters: proximal mesosome narrowly rounded in *B. californica* (Figure 8c), but broadly rounded in *B. canyonica* (Figure 10c); gonopore with concave antero-lateral corners in *B. californica* (Figure 8c), but with rounded antero-lateral margins in *B. canyonica* (Figure 10c).

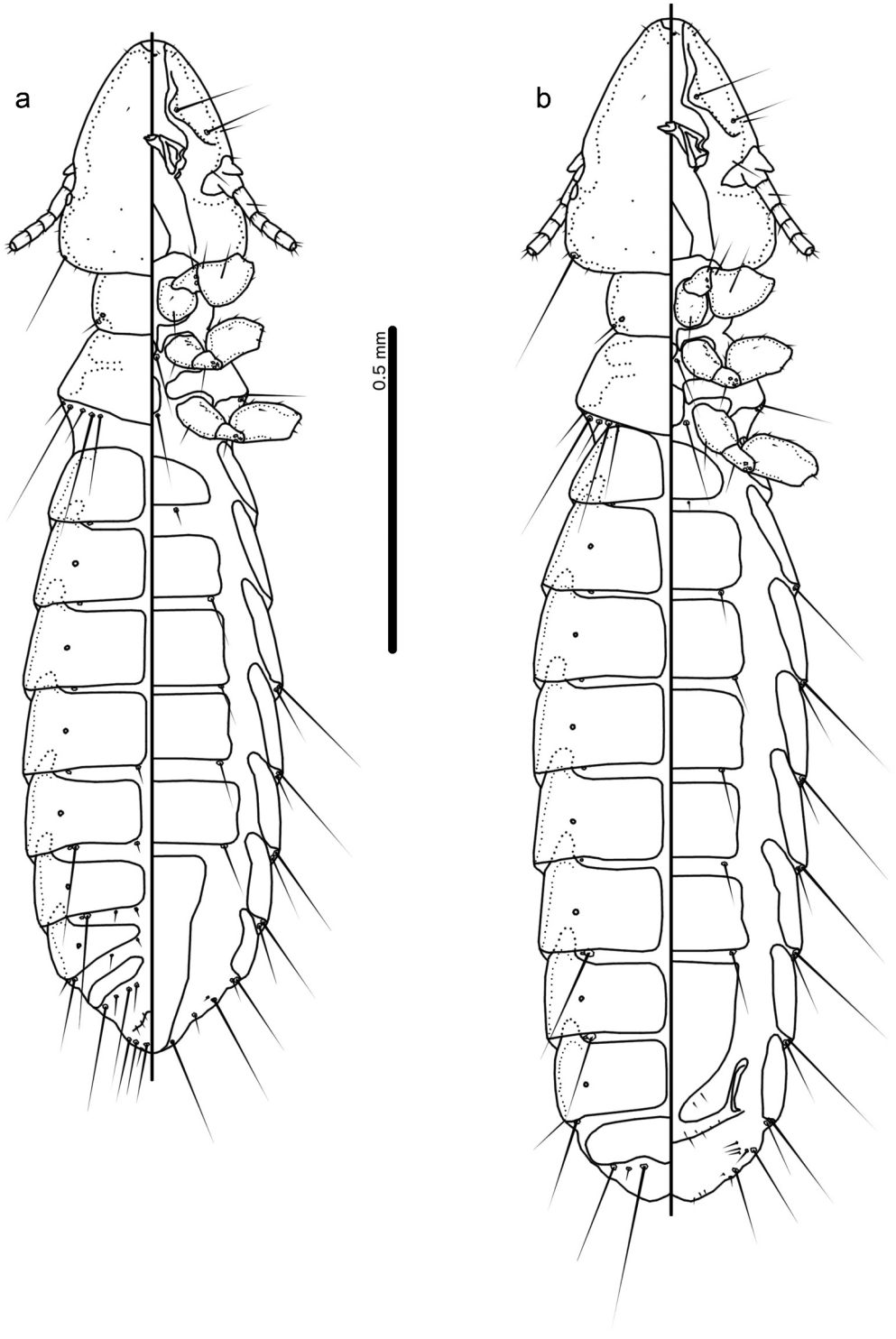

Figure 7. *Brueelia californica* sp. nov. ex *Melozone crissalis* (Vigors 1839). (A) male habitus, dorsal and ventral views; (b) female habitus, dorsal and ventral views.

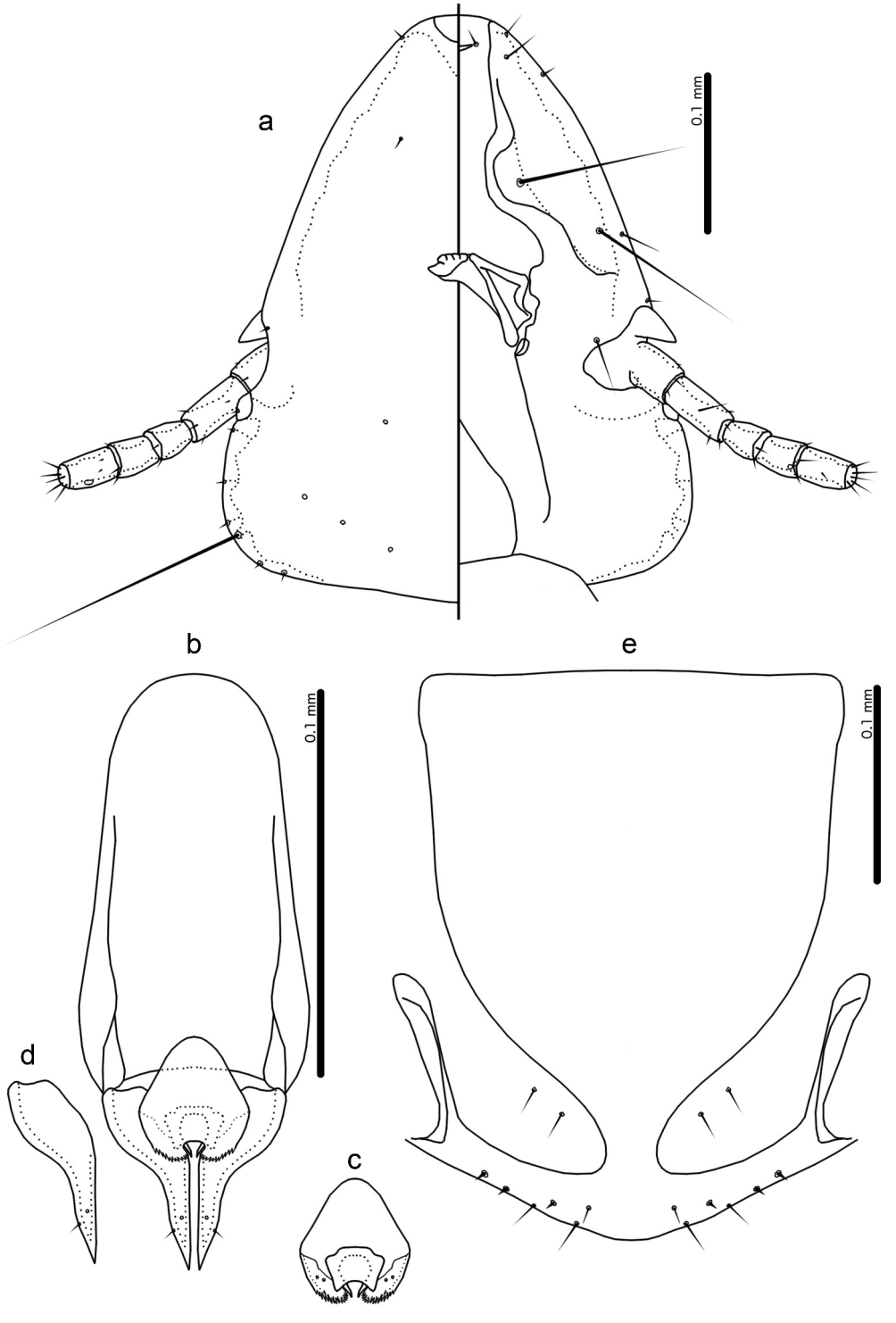

Figure 8. *Brueelia californica* sp. nov. ex *Melozone crissalis* (Vigors 1839). (a) male head, dorsal and ventral views; (b) male genitalia, dorsal view (c) male mesosome, ventral view; (d) male paramere, dorsal view; (e) female subgenital plate and vulval margin, ventral view.

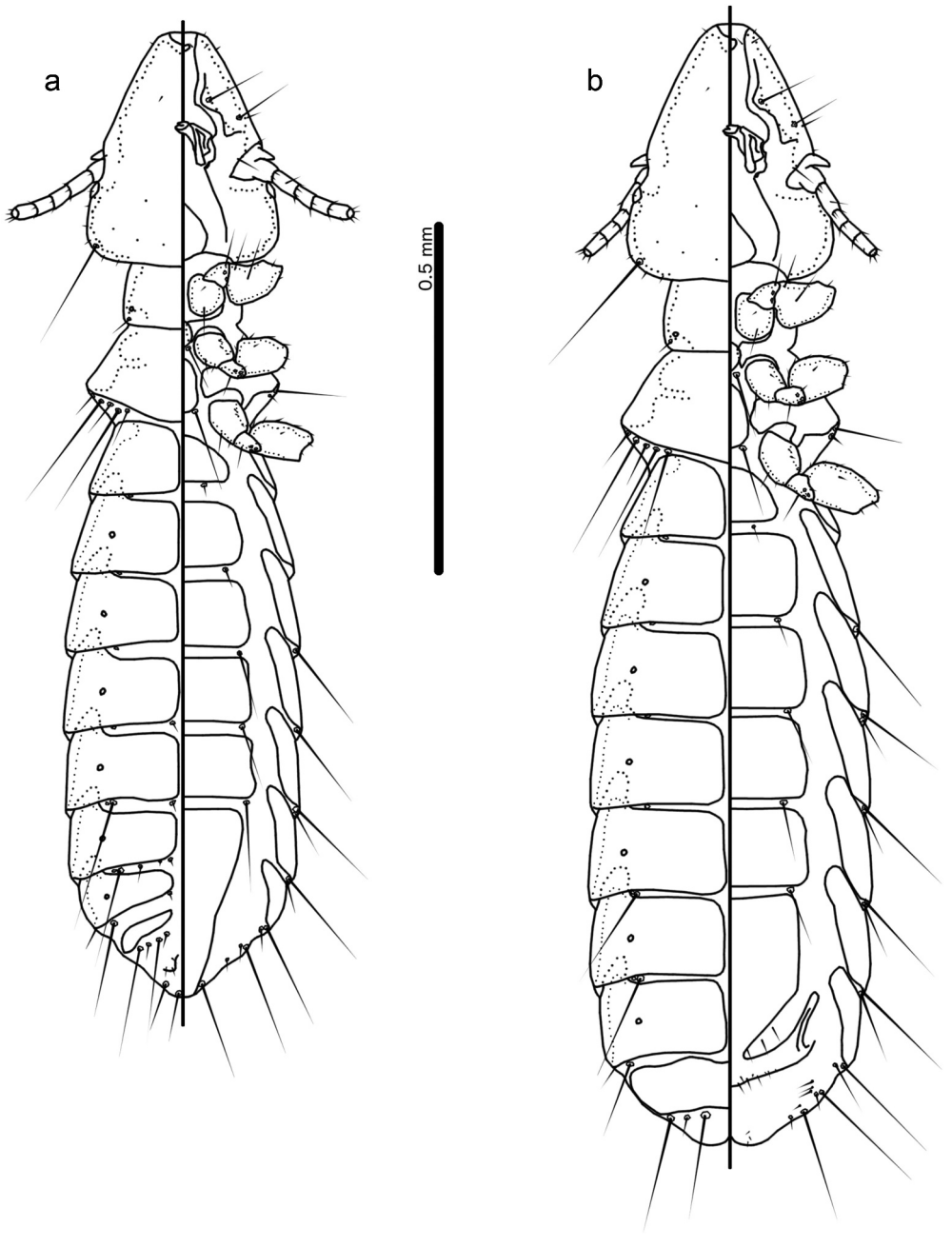

Figure 9. *Brueelia canyonica* sp. nov. ex *Melozone fusca* (Swainson 1827). (a) male habitus, dorsal and ventral views; (b) female habitus, dorsal and ventral views.

Description

Both sexes. Head convex dome-shaped (Figure 8a), lateral margins of preantennal area convex, frons rounded to slightly flattened. Marginal carina moderate, deeply displaced and slightly widened at osculum; median margin undulated. Ventral anterior plate very

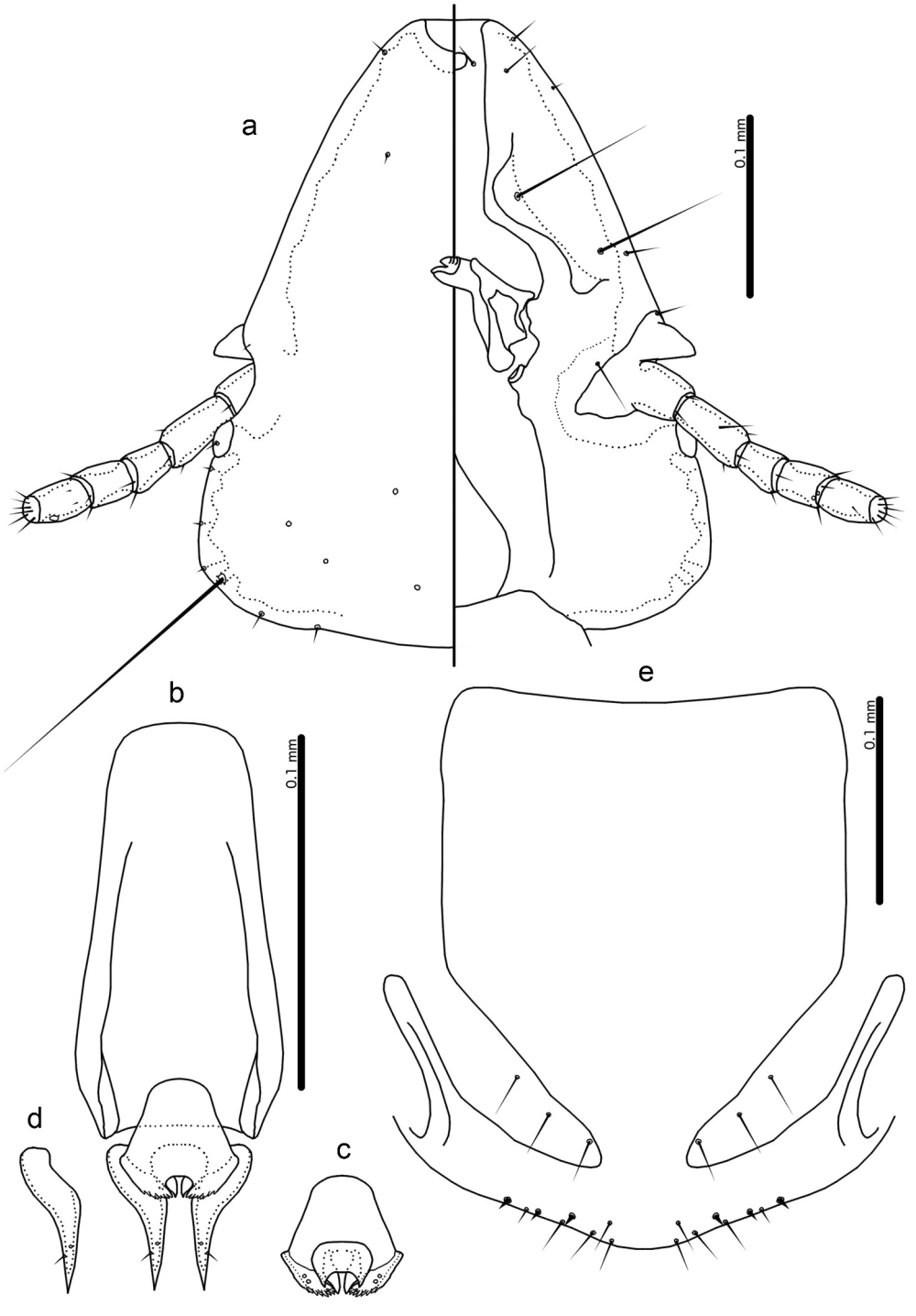

Figure 10. *Brueelia canyonica* sp. nov. ex *Melozone fusca* (Swainson 1827). (a) male head, dorsal and ventral views; (b) male genitalia, dorsal view (c) male mesosome, ventral view; (d) male paramere, dorsal view; (e) female subgenital plate and vulval margin, ventral view.

small, crescent-shaped. Head chaetotaxy as in Figure 8a. Preantennal nodi slender, not bulging. Pre- and post-ocular nodi moderate. Marginal temporal carina with irregular median margin. Gular plate lanceolate. Thoracic and abdominal segments as in Figure 7a–b. Head medium brown with marginal and marginal temporal carinae, margins of antennal socket, and anterior half of gular plate darker; thoracic and abdominal segments pale brown, with proepimera, metepisterna, lateral margins of tergopleurites IV–VIII, and sternal plates IV–VI and subgenital plate medium brown.

Male. Thoracic and abdominal chaetotaxy as in Figure 7a; *ss* present on tergopleurite V; *tps* present on tergopleurite VII; *aps* absent on tergopleurites II–VII; *ps* absent from abdominal segment III. Basal apodeme narrowing anteriorly (Figure 8b). Proximal mesosome narrowly rounded, long (Figure 8c). Mesosomal lobes slender, rounded, with rugose area limited to posterior margin; 2 *pmes* sensilla on each side of gonopore. Gonopore shaped as in Figure 8c, with concave anterolateral corners. Penile arms do not reach distal margin of mesosome. Parameres broad, elongated, *pst1–2* as in Figure 8d. Measurements (n = 3, except TL, where n = 2): TL = 1.49–1.52; HL = 0.36; HW = 0.28–0.29; PRW = 0.17–0.18; PTW = 0.27–0.28; AW = 0.36–0.39.

Female. Thoracic and abdominal chaetotaxy as in Figure 7b; *ps* present on abdominal segment III. Lateral margins of subgenital plate slightly convergent distally (Figure 8e), with narrow connection to cross-piece. Vulval margin gently rounded (Figure 8e), with 2–3 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 (n = 52, except AW, where n = 51): TL = 1.55–1.79 (1.68); HL = 0.38–0.41 (0.39); HW = 0.30–0.33 (0.31); PRW = 0.19–0.21 (0.20); PTW = 0.27–0.32 (0.30); AW = 0.36–0.47 (0.42).

Etymology

The specific name is derived from the type locality, California.

Material examined

Ex Melozone crissalis [as *Pipilo fuscus crissalis*]: Holotype ♂, California [United States], Mar. 1939, R. Meinertzhagen, 12814 (NHML). *Paratypes*. 1♂, 54♀, same data as holotype (NHML). *Non-types*. 1♂, same data as holotype (NHML).

Remarks

One male on same slide as type series with dissected genitalia much unlike those of the other two males. Other characters are similar to the two males included in the type series. As we cannot tell whether this specimen has aberrant genitalia, or if they were somehow distorted during dissection, we do not count this specimen as a paratype. The holotype and paratype males are not dissected. All specimens are mounted on the same slide.

Brueelia canyonica sp. nov.

Type host
Melozone fusca (Swainson 1827) – canyon towhee.

Type locality
Las Vacas, Coahuila, Mexico.

Diagnosis
Brueelia canyonica sp. nov. is most similar to *Brueelia californica* sp. nov., with which it shares the following characters: *aps* absent from male tergopleurites VI–VII (Figures 7a and 9a); *ss* present on male tergopleurite V (Figures 7a and 9a); *ps* absent on male abdominal segment III (Figures 7a and 9a), but present on female abdominal segment III (Figures 7b and 9b); gonopore broad (Figures 8c and 10c); rugose area of mesosomal lobes confined to posterior margin (Figures 8c and 9c). These two species can be separated by the following characters: proximal mesosome narrowly rounded in *B. californica* (Figure 8c), but broadly rounded in *B. canyonica* (Figure 10c); gonopore with concave antero-lateral corners in *B. californica* (Figure 8c), but with rounded antero-lateral margins in *B. canyonica* (Figure 10c).

Description
Both sexes. Head convex dome-shaped (Figure 10a), lateral margins of preantennal head slightly convex, frons flattened to slightly concave. Marginal carina moderate, deeply displaced and slightly widened at osculum; median margins undulated. Ventral anterior plate small, roughly rectangular. Head chaetotaxy as in Figure 10a. Preantennal nodi slender, slightly bulging. Pre- and postocular nodi moderate. Marginal temporal carina with very irregular median margin. Gular plate lanceolate. Thoracic and abdominal segments as in Figure 9a–b. Base pigmentation very pale, except marginal carina, margins of antennal socket, marginal temporal carina, proepimera, metepisterna, and lateral margins of tergopleurites III–VIII with brown pigmentation.

Male. Thoracic and abdominal chaetotaxy as in Figure 9a; *ss* present on tergopleurite V; *tps* absent on tergopleurites II–VII in holotype, but present on tergopleurite VII in paratype; *aps* absent on tergopleurites II–VII in holotype, but present on tergopleurite VII in paratype; *ps* absent on abdominal segment III. Basal apodeme narrowing anteriorly (Figure 10b). Proximal mesosome broad, anterior margin slightly convex, overall shape roughly trapezoidal (Figure 10c). Mesosomal lobes wide, angular, with rugose area limited to distal margin; 2 *pmes* sensilla on each side of gonopore. Gonopore broad, distal margin concave, anterior margin convex. Penile arms nearly reach distal margin of mesosome. parameres slender, elongated, *pst1–2* as in Figure 10d. Measurements (n = 3): TL = 1.35–1.53; HL = 0.33–0.36; HW = 0.26–0.27; PRW = 0.16–0.18; PTW = 0.26–0.28; AW = 0.34–0.40.

Female. Thoracic and abdominal chaetotaxy as in Figure 9b; *ps* present on abdominal segment III. Lateral margins of proximal subgenital plate more or less parallel (Figure 10e),

with wide connection to cross-piece. Vulval margin gently rounded, bulging slightly at median (Figure 10e), with 2–4 short, slender *vms* and 3–4 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 (n = 5): TL = 1.58–1.74; HL = 0.36–0.39; HW = 0.28–0.29; PRW = 0.19; PTW = 0.28–0.31; AW = 0.38–0.45.

Etymology

The specific name is derived from the Spanish '*cañon*' for 'gorge', referring to the English name for the type host and the common habitat of the host species.

Material examined

Ex Melozone fusca [as *Pipilo fuscus*]: Holotype ♂, Las Vacas, Coahuila, Mexico, 31 July 1958, C.A. Ely, CAE-738 (NHML). *Paratypes*. 2♀, same data as holotype (NHML); 1♂, 2♀, same data as holotype (PIPeR); 1♀, same locality, 5 August 1958, C.A. Ely, CAE-765 (PIPeR).

Brueelia chlorurae sp. nov.

Type host

Pipilo chlorurus (Audubon 1839) – green-tailed towhee.

Type locality

Dugway Proving Grounds, Tooele County, Utah, United States.

Diagnosis

Brueelia chlorurae sp. nov. is most similar to *Brueelia californica* sp. nov., with which it shares the following characters: *tps* present on male tergopleurite VII (Figures 7a and 11a); *ss* present on male tergopleurite V (Figures 7a. and 11a); *ps* absent on male abdominal segment III (Figures 7a and 11a), but present on female abdominal segment III (Figures 7b and 11b); proximal mesosome elongate (Figures 8c and 12c); gonopore broad (Figures 8c and 12c); parameres elongated (Figures 8d and 12d). These two species can be separated by the following characters: *aps* present on male tergopleurite VII in *B. chlorurae* (Figure 11a), but absent in *B. californica* (Figure 7a); proximal mesosome with concave lateral margins in *B. chlorurae* (Figure 12c), but straight lateral margins in *B. californica* (Figure 8c); antero-lateral corners of gonopore concave in *B. californica* (Figure 8c), but convex in *B. chlorurae* (Figure 12c); distal parameres broader in *B. chlorurae* (Figure 12d) than in *B. californica* (Figure 8d); connection between subgenital plate and cross-piece broad in *B. chlorurae* (Figure 12e), but narrow in *B. californica* (Figure 8e).

Description

Both sexes. Head broadly drop-shaped (Figure 12a), lateral margins of preantennal area slightly convex, frons concave to flat. Marginal carina slender, deeply displaced and slightly widened at osculum. Ventral anterior plate small, triangular, in some specimens more elongated. Head chaetotaxy as in Figure 12a. Preantennal nodi slender, not bulging. Pre- and postantennal nodi moderate. Marginal temporal carina with irregular median margin. Gular plate lanceolate. Thoracic and abdominal segments as in Figure 11a–b. Base

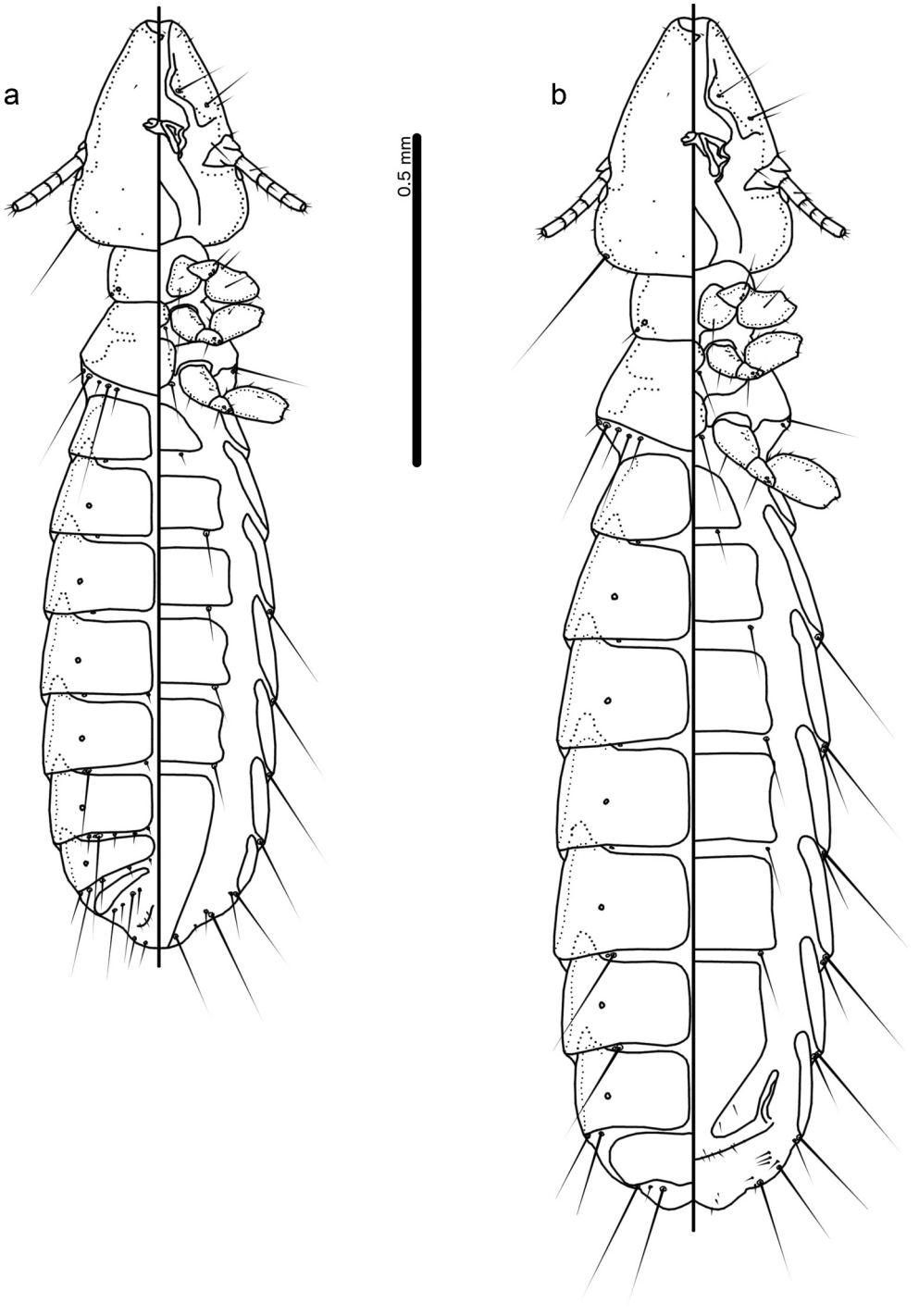

Figure 11. *Brueelia chlorurae* sp. nov. ex *Pipilo chlorurus* (Audubon 1839). (a) male habitus, dorsal and ventral views; (b) female habitus, dorsal and ventral views.

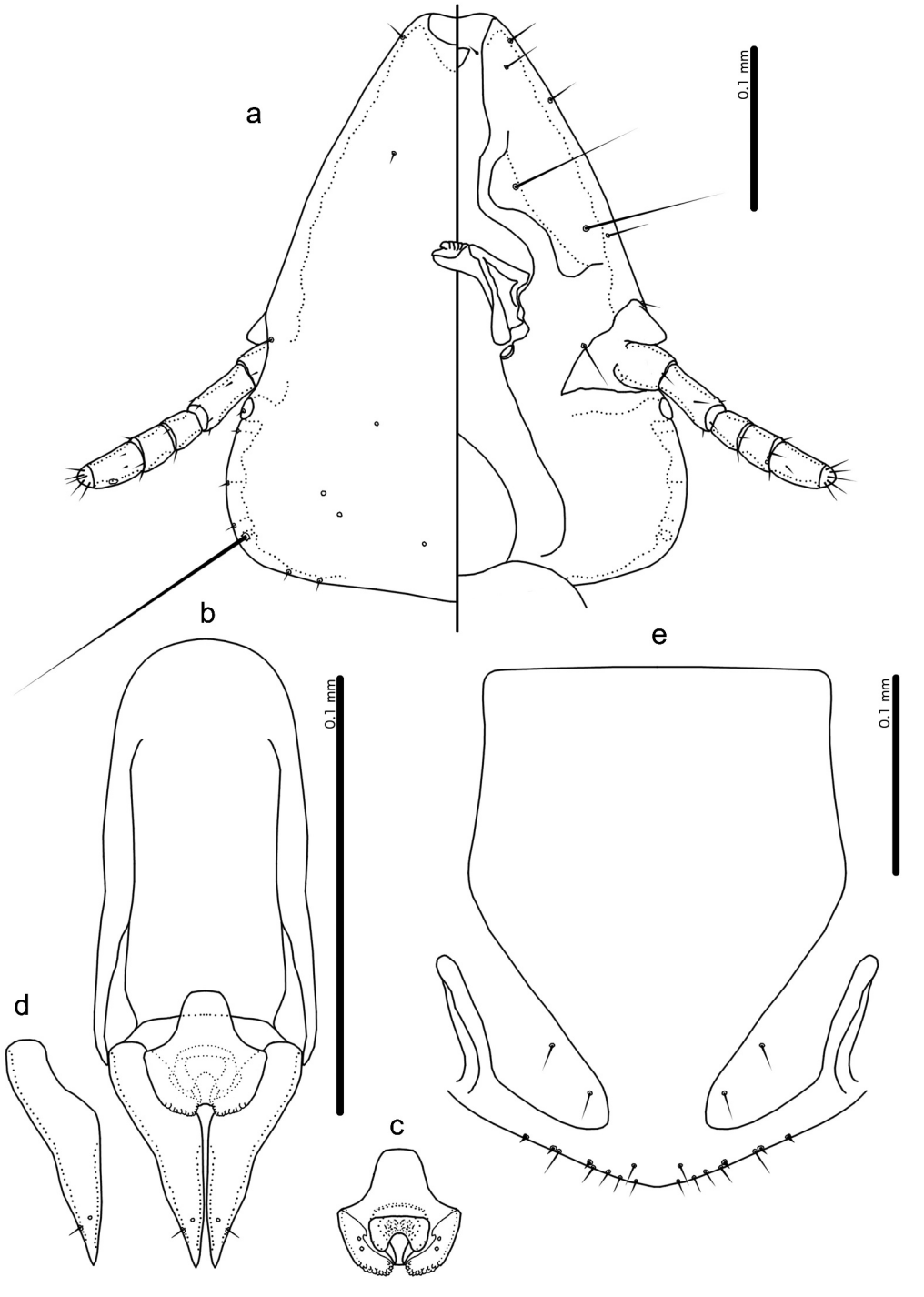

Figure 12. *Brueelia chlorurae* sp. nov. ex *Pipilo chlorurus* (Audubon 1839). (a) male head, dorsal and ventral views; (b) male genitalia, dorsal view (c) male mesosome, ventral view; (d) male paramere, dorsal view; (e) female subgenital plate and vulval margin, ventral view.

pigmentation pale yellow; sternal and subgenital plates, metepisterna, and gular plate pale brown; marginal and marginal temporal carinae, margins of antennal sockets, proepimera, and lateral margins of tergopleurites medium brown.

Male. Thoracic and abdominal chaetotaxy as in Figure 11a; *ss* present on tergopleurite V; *tps* present on tergopleurite VII; *aps* absent on tergopleurite VI, present on tergopleurite VII; *ps* absent on abdominal segment III. Basal apodeme broad, slightly narrowing proximally (Figure 12b). Proximal mesosome elongated, slender, with concave lateral margins (Figure 12c). Mesosomal lobes broad, rounded; rugose area restricted to near distal and median margins; 2 *pmes* sensilla on each side of gonopore. Gonopore broad, roughly rectangular, but distal margin deeply concave; median section of gonopore with slight rugosity. Parameres stout, elongated, *pst1–2* as in Figure 12d. Measurements (n = 4): TL = 1.36–1.38; HL = 0.34–0.36; HW = 0.26–0.27; PRW = 0.16–0.17; PTW = 0.24–0.25; AW = 0.32–0.35.

Female. Thoracic and abdominal chaetotaxy as in Figure 11b; *ps* present on abdominal segment III. Proximal subgenital plate with concave lateral margins (Figure 12e), with broad connection to cross-piece. Vulval margin convergent to blunt median point (Figure 12e), with 4–5 short, slender *vms* and 3–4 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 (n = 24 except TL, HL, AW where n = 23): TL = 1.58–1.79 (1.66); HL = 0.36–0.40 (0.38); HW = 0.27–0.30 (0.28); PRW = 0.17–0.19 (0.18); PTW = 0.25–0.28 (0.27); AW = 0.27–0.44 (0.39).

Etymology

The specific name is derived from the specific name of the type host.

Material examined

Ex Pipilo chlorurus: Holotype ♂, GPI-3, Dugway Proving Grounds, Tooele County, Utah, United States, 15 May 1964, E. & E. Branch, EE-5198 (NHML). *Paratypes*. 1♀, same data as holotype (NHML); 2♂, 2♀, same data as holotype (PIPeR); 16♀, Clover Creek, Tooele County, Utah, United States, 1 May 1969, 09077 (PIPeR); 1♀, North Skull Valley, Tooele County, Utah, United States, 1 May 1963, E. & E. Branch, Cc-3E-161 (PIPeR); 1♀, White Rock Spring, Tooele County, Utah, United States, 12 May 1965, University of Utah, 00301 (PIPeR); 1♂, 4♀, 10 miles W of Dugway, Tooele County, Utah, United States, 3 May 1962, E. & E. Branch, Cc-135 (PIPeR).

Remarks

Two of four examined males have one *ps* on one side of segment III. This has not been illustrated.

Brueelia cassiopeia sp. nov.
(Figures 13–14)

Type host

Spizella passerina arizonae Coues 1872 – chipping sparrow.

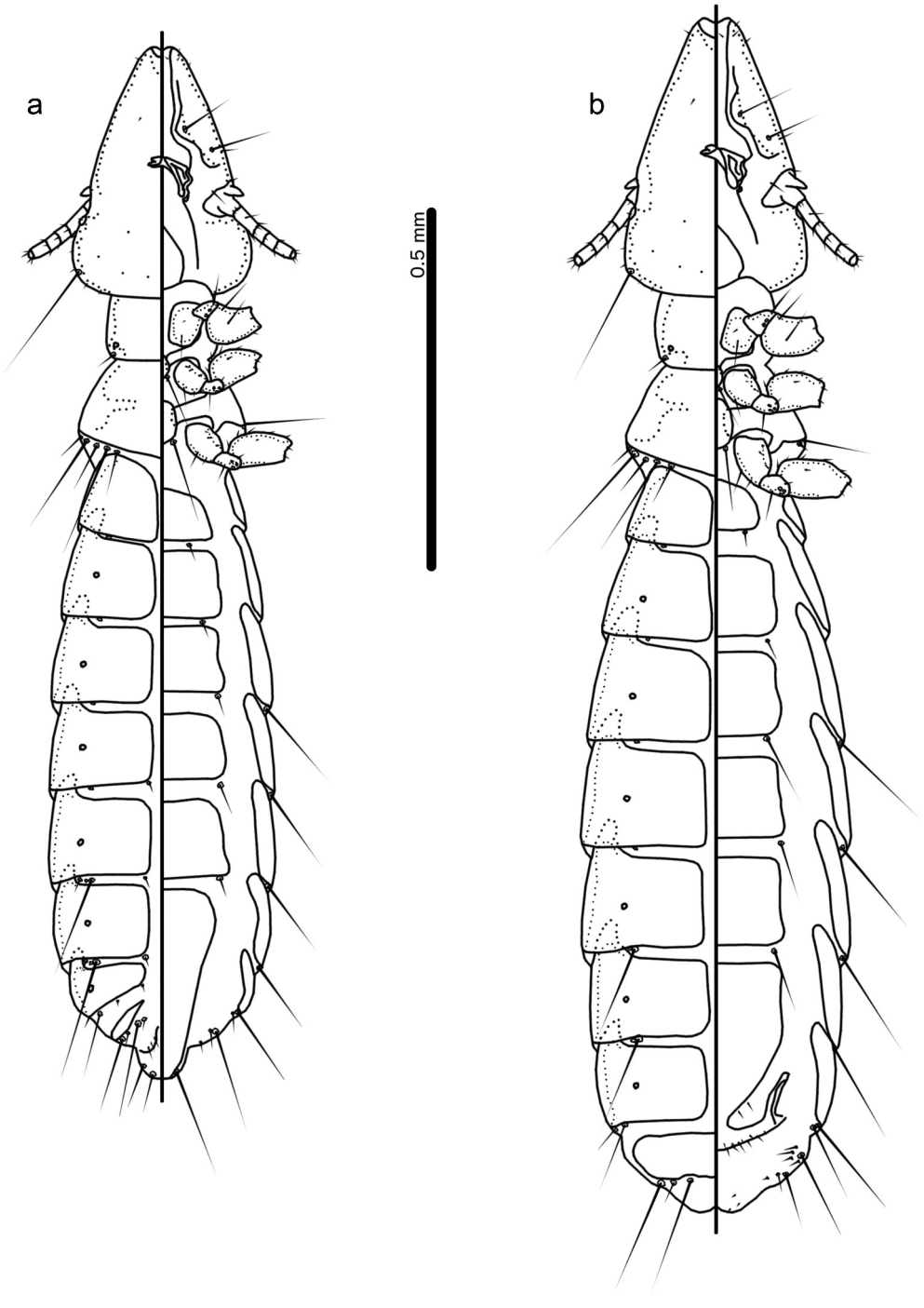

Figure 13. *Brueelia cassiopeia* sp. nov. ex *Spizella passerina arizonae* Coues 1872. (a) male habitus, dorsal and ventral views; (b) female habitus, dorsal and ventral views.

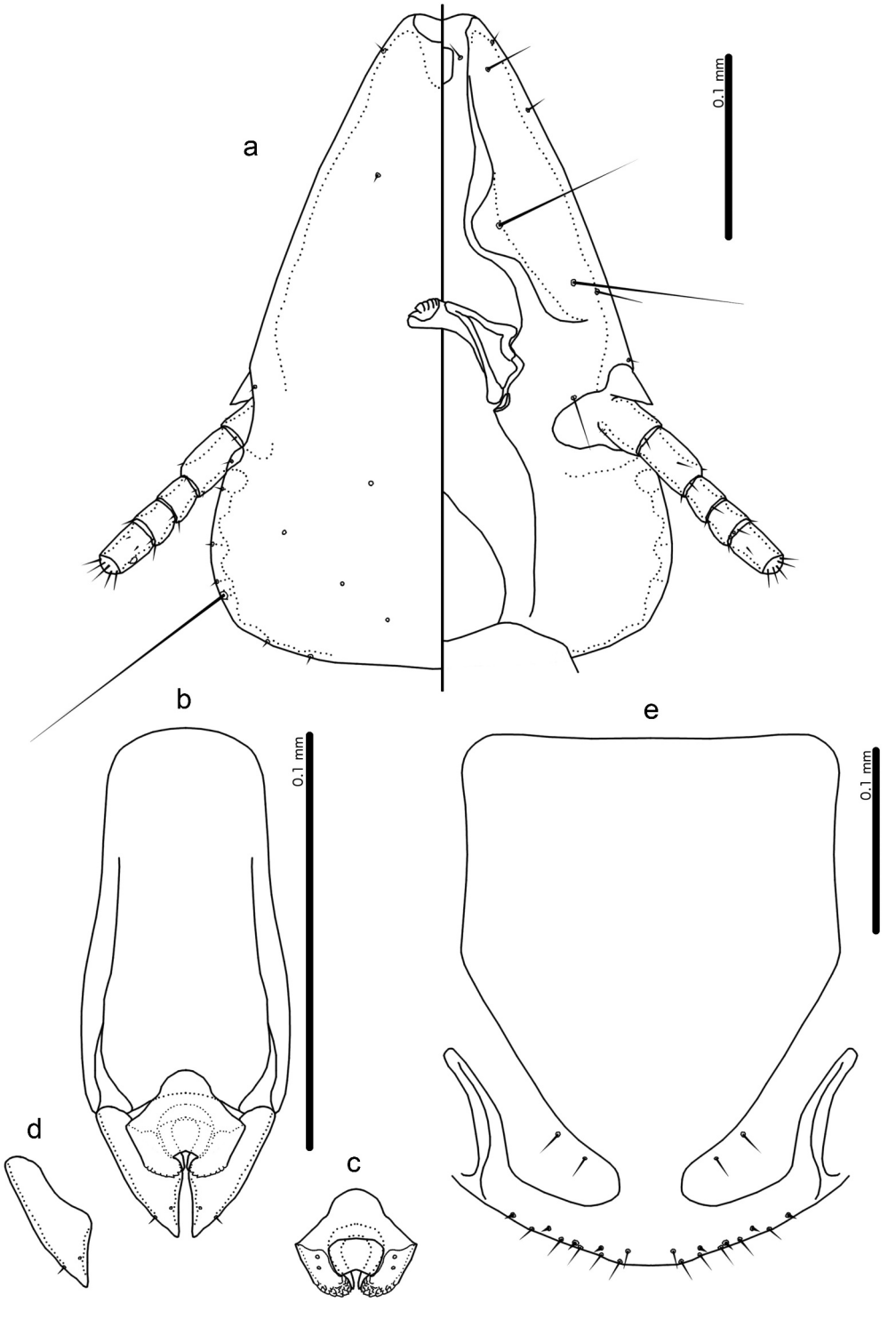

Figure 14. *Brueelia cassiopeia* sp. nov. ex *Spizella passerina arizonae* Coues 1872. (a) male head, dorsal and ventral views; (b) male genitalia, dorsal view (c) male mesosome, ventral view; (d) male paramere, dorsal view; (e) female subgenital plate and vulval margin, ventral view.

Type locality
California, United States.

Other hosts
Spizella passerina passerina (Bechstein 1798) – chipping sparrow.

Diagnosis
Brueelia cassiopeia sp. nov. is most similar to *B. angustifrons* (Carriker 1902) and *B. hesperides* sp. nov., with which it shares the following characters: *tps* absent from male tergopleurite VII (Figures 3a, 5a, 13a); *aps* present on male tergopleurites VI–VII (Figures 3a, 5a, 13a); *ps* absent from female abdominal segment III (Figures 3b, 5b, 13b). *Brueelia cassiopeia* is more similar to *B. hesperides*, with which it shares the following characters not found in *B. angustifrons: ps* absent from male abdominal segment III in *B. cassiopeia* (Figure 13a) and *B. hesperides* (Figure 5a), but present in *B. angustifrons* (Figure 3a); gonopore with antero-lateral extensions in *B. angustifrons* (Figure 4c), but without such extensions in the other two species (Figures 6c and 14c); rugose area present on mesosome in *B. hesperides* (Figure 6c) and *B. cassiopeia* (Figure 14c), but absent in *B. angustifrons* (Figure 4c). *Brueelia cassiopeia* can be separated from *B. hesperides* by the following characters: *ss* present on male tergopleurite V in *B. cassiopeia* (Figure 13a), but absent in *B. hesperides* (Figure 5a); proximal mesosome rounded in *B. cassiopeia* (Figure 14c), but flat in *B. hesperides* (Figure 6c); parameres elongated in *B. hesperides* (Figure 6d), but short in *B. cassiopeia* (Figure 14d); gonopore roughly rectangular with shallowly concave posterior margin in *B. cassiopeia* (Figure 14c), but broadly crescent-shaped, with deeply concave posterior margin in *B. hesperides* (Figure 6c).

Description
Both sexes. Head elongated drop-shaped (Figure 14a), lateral margins of preantennal head flat to slightly convex, in some specimens longer than illustrated, and with distal section slightly concave, frons flat to slightly concave. Marginal carina slender, deeply displaced and widened at osculum. Ventral anterior plate elongated. Head chaetotaxy as in Figure 14a. Preantennal nodi slender, not bulging. Pre- and postocular nodi moderate. Marginal temporal carina with irregular median margin. Gular plate lanceolate. Thoracic and abdominal segments as in Figure 13a–b. Base pigmentation pale brown; marginal and marginal temporal carinae, margins of antennal sockets, proepimera, metepisterna, and lateral margins of tergopleurites dark brown; sternal and subgenital plates and lateral section of tergopleurites medium brown. All pigmentation darker in female than in male.

Male. Thoracic and abdominal chaetotaxy as in Figure 13a; *ss* present on tergopleurite V; *tps* absent on tergopleurites II–VII; *aps* present on tergopleurites VI–VII; *ps* absent on abdominal segment III. Basal apodeme narrowing slightly anteriorly (Figure 14b). Proximal mesosome elongated, rounded, lateral margins concave (Figure 14c). Mesosomal lobes wide, rugose area extensive; 2 *pmes* sensilla on each side of gonopore. Gonopore broad, roughly rectangular, distal margin shallowly concave. Penile arms short, not reaching distal margin of mesosome. Parameres broad, not elongated, *pst1–2* as in Figure 14d. Measurements ex *Spizella passerina arizonae* (n = 2): TL = 1.40; HL = 0.35–0.36; HW = 0.24;

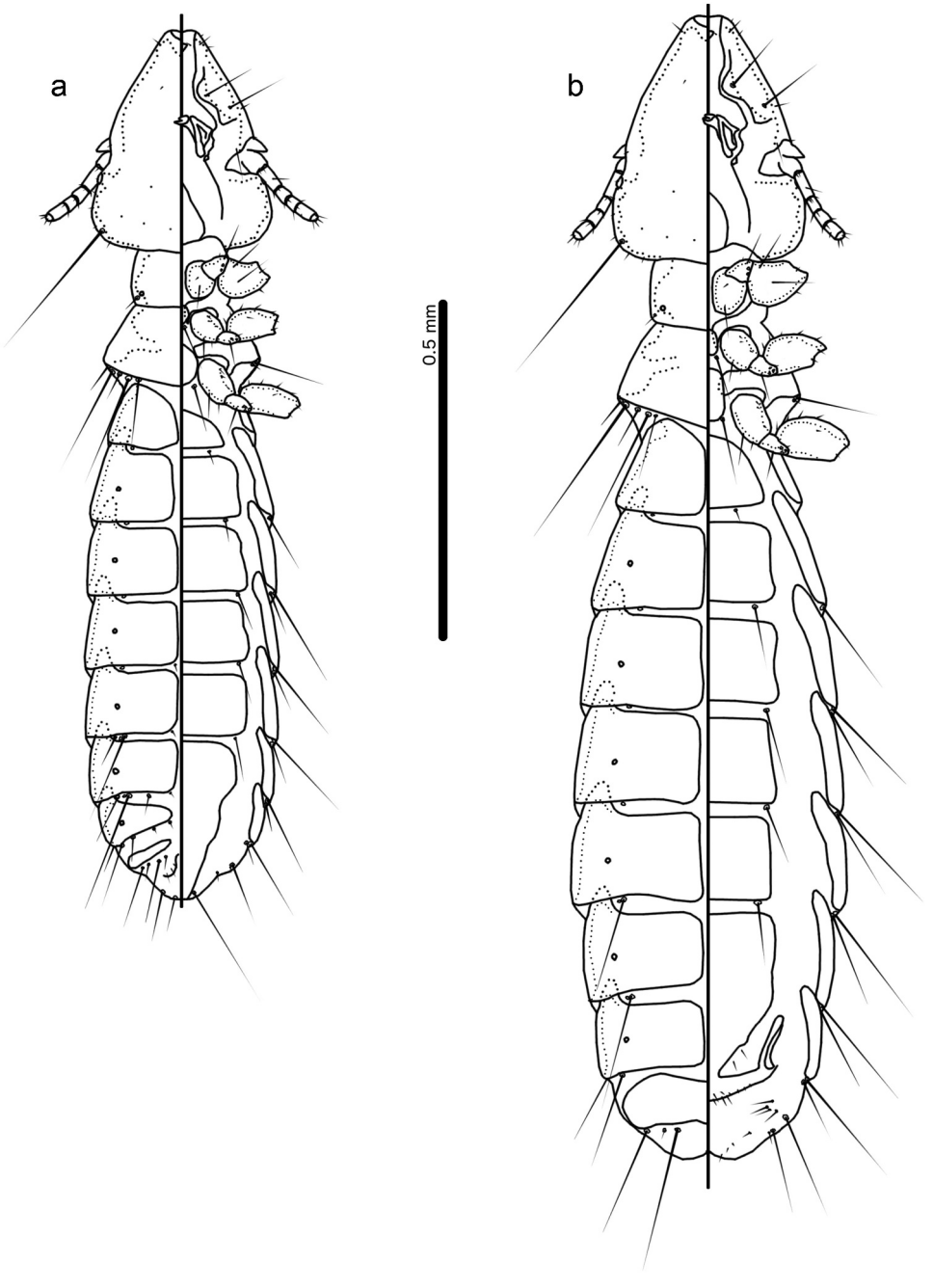

Figure 15. *Brueelia melospizae* sp. nov. ex *Melospiza melodia fallax* (Baird 1854). (a) male habitus, dorsal and ventral views; (b) female habitus, dorsal and ventral views.

PRW = 0.15–0.16; PTW = 0.22–0.23; AW = 0.30–0.31. Measurements ex *S. p. passerina* (n = 3): TL = 1.19–1.26; HL = 0.30–0.31; HW = 0.22–0.23; PRW = 0.13–0.14; PTW = 0.20–0.21; AW = 0.27–028.

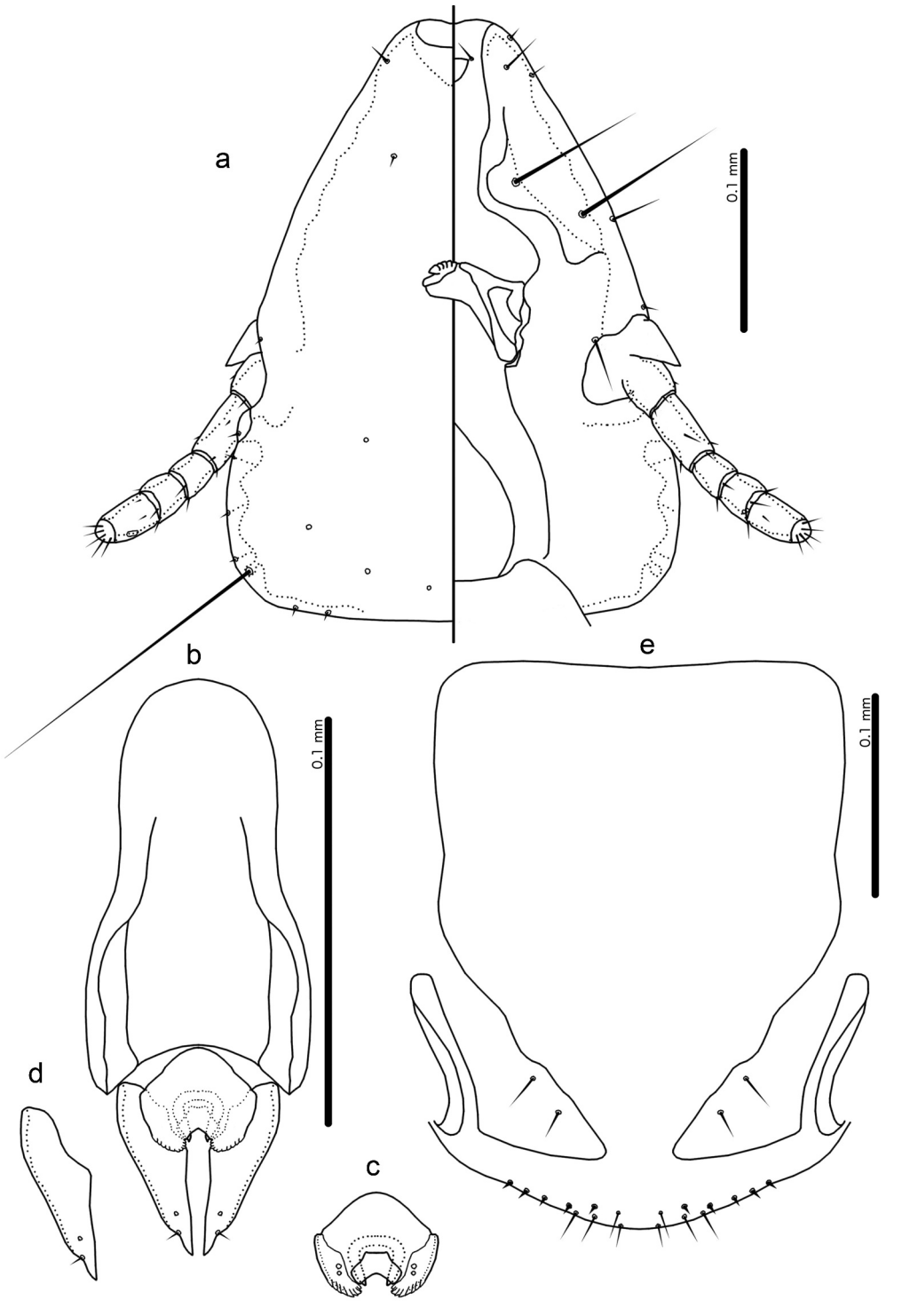

Figure 16. *Brueelia melospizae* sp. nov. ex *Melospiza melodia fallax* (Baird 1854). (a) male head, dorsal and ventral views; (b) male genitalia, dorsal view (C) male mesosome, ventral view; (d) male paramere, dorsal view; (e) female subgenital plate and vulval margin, ventral view.

Female. Thoracic and abdominal chaetotaxy as in Figure 13b; *ss* absent on abdominal segment III. Lateral margins of proximal subgenital plate concave to roughly parallel (Figure 14e), with narrow connection to cross-piece. Vulval margin gently rounded to slightly flattened medianly (Figure 14e), with 4–5 short, slender *vms* and 3–4 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 ex *Spizella passerina arizonae* (n = 16): TL = 1.63–1.79 (1.71); HL = 0.37–0.40 (0.38); HW = 0.25–0.27 (0.26); PRW = 0.16–0.17 (0.17); PTW = 0.25–0.27 (0.26); AW = 0.3–0.38 (0.35). Measurements ex *S. p. passerina* (n = 6 except TL and AW where n = 5): TL = 1.53–1.73; HL = 0.36–0.38; HW = 0.25–0.26; PRW = 0.15–0.17; PTW = 0.22–0.26; AW = 0.31–0.39.

Etymology

Brueelia cassiopeia is named after Queen Cassiopeia of Ethiopia, who was considered very beautiful, an attribute that applies equally well to the host of *B. cassiopeia* sp. nov., as well as to the louse itself.

Material examined

Ex Spizella passerina arizonae: Holotype ♂, California [United States], Mar. 1939, R. Meinertzhagen, 13,019 (NHML) [marked with black border on slide]. *Paratypes*. 1♂, 16♀, same data as holotype (NHML).

Ex *S. p. passerina*. *Paratypes*. 4♀, Las Vacas, Coahuila, Mexico, 4 July 1958, C.A. Ely, CAE-600 (PIPeR); 2♂, 1♀, Basswood Lake, Minnesota, United States, 30 June 1959, J.R. Beer (UMSP); 1♀, same locality, 16 July 1963, J.R. Beer (UMSP); 2♂, 2♀, same locality, 18 July 1959, J.R. Beer (UMSP); 1♂, same locality, 22 July 1959, J.R. Beer (UMSP).

Brueelia melospizae sp. nov.

Type host

Melospiza melodia fallax (Baird 1854) – song sparrow.

Type locality

Arizona, United States.

Other hosts

Melospiza georgiana (Latham 1790) – swamp sparrow. *Melospiza lincolnii* (Audubon 1835) – Lincoln's sparrow.

Diagnosis

Brueelia melospizae sp. nov. is most similar to *Brueelia vulgata* (Kellogg 1896), with which it shares the following characters: *ps* present on abdominal segment III in both sexes (Figure 1a–b, 15A–B); *ss* present on male tergopleurite V (Figure 1a, 15a); *aps* present on male tergopleurite VII (Figure 1a, 15a); head shape (Figure 2a, 16A); shape of the female subgenital plate (Figure 2e, 16e). These two species can be separated on the following characters: *tps* present on male tergopleurite VII in *B. melospizae* (Figure 15a), but absent in *B. vulgata* (Figure 1a); *aps* present on male tergopleurite VI in *B. melospizae* (Figure 15a),

but absent in *B. vulgata* (Figure 1a); gonopore smaller and with flattened anterior margin in *B. melospizae* (Figure 16c), but larger and with rounded anterior margin in *B. vulgata* (Figure 2c); rugose area of mesosomal lobes more restricted in *B. melospizae* (Figure 16c) than in *B. vulgata* (Figure 2c).

Description

Both sexes. Head rounded trapezoidal (Figure 15a), lateral margins of preantennal head convex, except distal extreme concave in some specimens, frons flattened to slightly concave. Marginal carina of moderate width, much narrowed in distal section, deeply displaced and widened at osculum. Ventral anterior plate broad, roughly triangular. Head chaetotaxy as in Figure 16a. Preantennal nodi slender, slightly bulging. Pre- and postocular nodi large. Marginal temporal carina with irregular median margin. Gular plate broadly lanceolate. Thoracic and abdominal segments as in Figure 15A–B. Base pigmentation pale brown; marginal carina, margins of antennal sockets, marginal temporal carina, proepimera, metepisterna, and lateral margins of tergopleurites dark brown, almost black in some specimens; sternal and subgenital plates, lateral sections of tergopleurites, and distal margin of female tergopleurite IX+X medium brown.

Male. Thoracic and abdominal chaetotaxy as in Figure 15A; *ss* present on tergopleurite V; *tps* present on tergopleurite VII; *aps* present on tergopleurites VI–VII; *ps* present on abdominal segment III. In many specimens *ss* of tergopleurites V–VI much longer than *ss* on more posterior segments, reaching between 1/3 and ½ the length of the next tergopleurite. Basal apodeme wide distally, narrowing conspicuously proximally (Figure 16B). Proximal mesosome short, gently rounded (Figure 16C). Mesosomal lobes wide, gently rounded; rugose area limited to distal and median margins; 2 *pmes* sensilla on each side lateral to gonopore. Gonopore shaped as in Figure 16C, with flattened anterior margin slightly extended proximally. Penile arms short, not reaching distal margin of mesosome. Parameres broad, stout distally, *pst1–2* as in Figure 16D. Measurements ex *Melospiza melodia* (n = 11 except TL where n = 9): TL = 1.19–1.38; HL = 0.32–0.35; HW = 0.25–0.28; PRW = 0.15–0.17; PTW = 0.22–0.25; AW = 0.29–0.35. Measurements ex *M. lincolnii* (n = 2): TL = 1.28–1.40; HL = 0.33–0.34; HW = 0.25; PRW = 0.16; PTW = 0.23; AW = 0.35–0.36.

Female. Thoracic and abdominal chaetotaxy as in Figure 15B; *ps* present on abdominal segment III. Lateral margins of proximal subgenital plate slightly concave to roughly parallel (Figure 16E), with narrow connection to cross-piece. Vulval margin gently rounded to slightly flattened medially (Figure 16E), with 3–4 short, slender *vms* and 4–6 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 ex *Melospiza melodia* (n = 37): TL = 1. 54–1.75 (1.65); HL = 0.35–0.39 (0.37); HW = 0.28–0.40 (0.30); PRW = 0.17–0.19 (0.18); PTW = 0.26–0.29 (0.28); AW = 0.28–0.42 (0.35). Measurements ex *M. lincolnii* (n = 15): TL = 1.55–1.74 (1.64); HL = 0.35–0.38 (0.37); HW = 0.27–0.30 (0.29); PRW = 0.17–0.19 (0.18); PTW = 0.26–0.29 (0.27); AW = 0.38–0.42 (0.40). Measurements ex *M. georgiana* (n = 1): TL = 1.75; HL = 0.36; HW = 0.27; PRW = 0.19; PTW = 0.27; AW = 0.38.

Etymology

The specific name is derived from the generic name of the three hosts, genus *Melospiza* Baird, 1858.

Material examined

Ex Melospiza melodia fallax: Holotype ♂, Arizona [United States], Mar. 1939, R. Meinertzhagen, 13,123–26 (NHML) [marked with black circle on slide]. *Paratypes*. 11♂, 44♀, same data as holotype (NHML); 2♀, Basswood Lake, Minnesota, United States, 15 July 1959, J.R. Beer (UMSP); 3♂, 2♀, same data except 16 July 1959 (UMSP).

Ex Melospiza georgiana. 1♀, McCormick Place, Chicago, Cook County, Illinois [United States], 5 May 2005, J.D. Weckstein, FMNH05-070, JDW05-002, FMNH-INS 0000 028 102, voucher specimen for sequence Brsp.Mege.6.27.2006.17 (FMNH).

Ex Melospiza lincolnii. 2♂, 15♀, Dugway, Tooele County, Utah, Unites States, 25 May 1971, E. & E. Branch, D.P.G., 71-0-0008 (PIPeR); 1♀, Sewerline, vicinity of Dugway, Tooele County, Utah, United States, 15 April 1953, W.G. Denzer, 192-B-175 (PIPeR); 1♀, 4 miles NE of Camelback Mountain, vicinity of Dugway, Tooele County, Utah, United States, 13 April 1953, R.D. Porter, 222-B-160 (PIPeR).

Remarks

Brueelia melospizae was represented in the phylogeny of Bush et al. (2016) by a specimen from *M. georgiana* (specimen 59, clade I-1, Figure 3e). This specimen was placed close to specimens from *Geothlypis trichas* (Linnaeus, 1766), *M. lincolnii, Seiurus aurocapilla* (Linnaeus 1766), and *Icterus galbula* (Linnaeus 1758). Other specimens of *Brueelia* from *S. auricapilla* we have examined are not conspecific with *B. melospizae*, and all other specimens from *Icterus* spp. we have examined belong to the *ornatissima* group, which morphologically different from all species treated here. We have seen no additional specimens from *G. trichas*. It, therefore, cannot be excluded that these specimens from *G. trichas, S. aurocapilla*, and *I. galbula* are stragglers. However, the closest relative of *B. melospizae* in the Bush et al. (2016) phylogeny is *Brueelia anamariae* Cicchino 1980, which is also morphologically different from *B. melospizae*. This may suggest that morphological similarity is not always a good predictor of close relationships in *Brueelia*. We do not presently include any host species other than *Melospiza* spp. as hosts of *B. melospizae*. More specimens are needed to determine whether *Brueelia melospizae* occurs naturally on other hosts, or if these records are the result of e.g. straggling.

Brueelia tenebrosa sp. nov.
(Figure 17–18)

Type host

Passerella iliaca (Merrem 1786) – fox sparrow.

Type locality

Sullivan Canyon, Los Angeles County, California, United States.

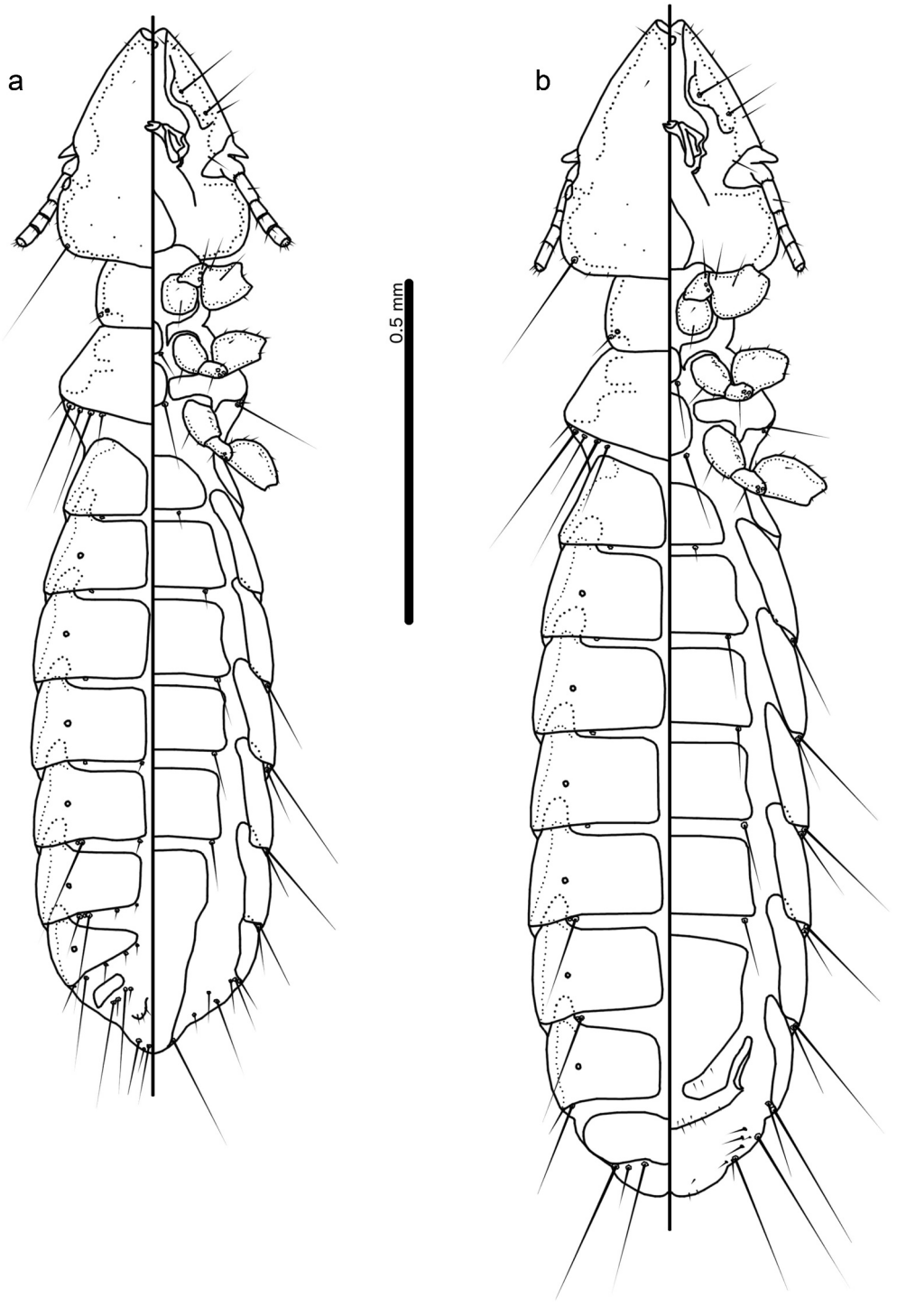

Figure 17. *Brueelia tenebrosa* sp. nov. ex *Passerella iliaca* (Merrem 1786). (a) male habitus, dorsal and ventral views; (b) female habitus, dorsal and ventral views.

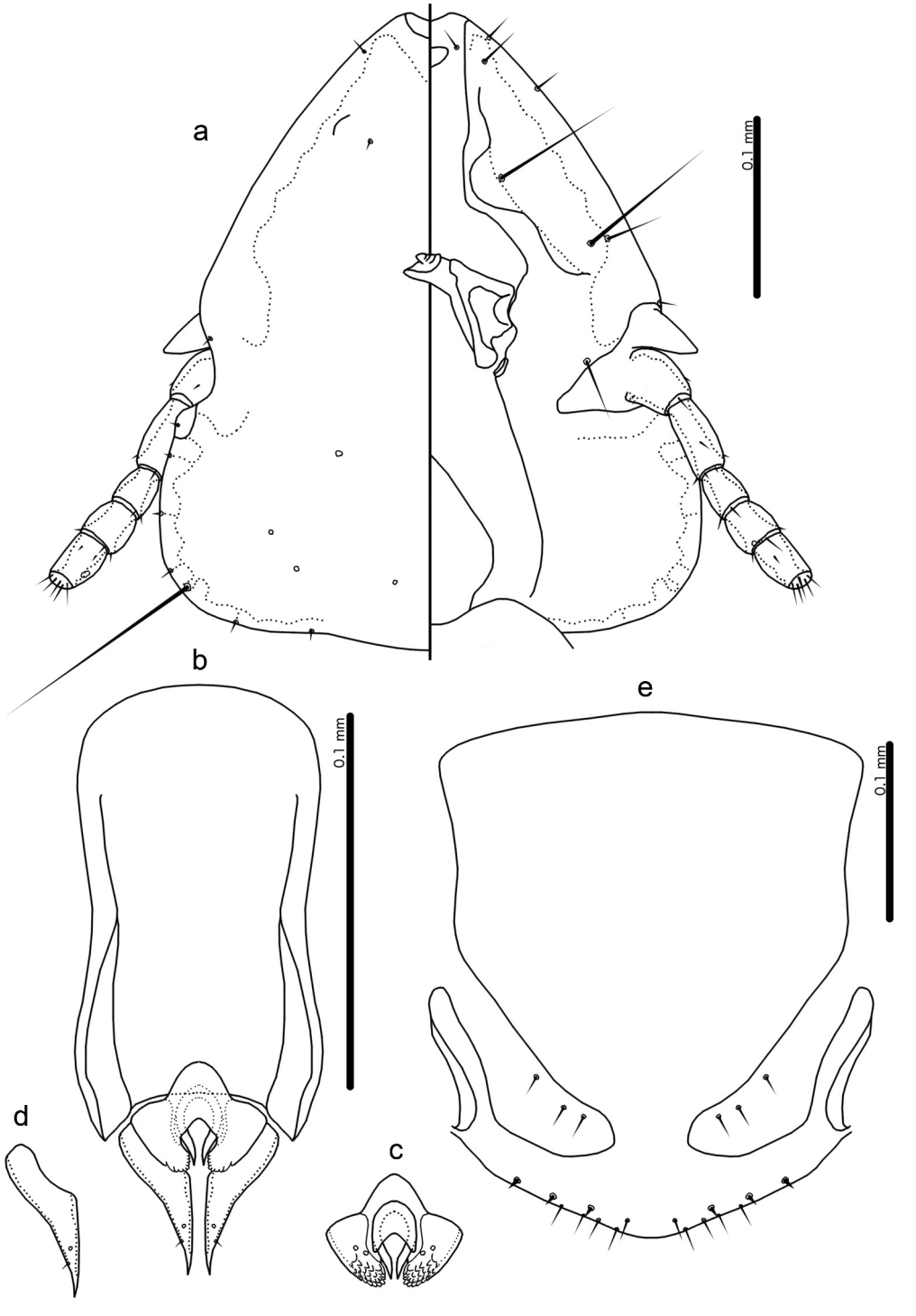

Figure 18. *Brueelia tenebrosa* sp. nov. ex *Passerella iliaca* (Merrem 1786). (a) male head, dorsal and ventral views; (b) male genitalia, dorsal view (c) male mesosome, ventral view; (d) male paramere, dorsal view; (e) female subgenital plate and vulval margin, ventral view.

Diagnosis

Brueelia tenebrosa sp. nov. is most similar to *B. melospizae* sp. nov., with which it shares the following characters: *ss* present on male tergopleurite V (Figure 15a, 17a); *tps* and *aps* present on male tergopleurite VII (Figure 15a, 17a). These two species can be separated by the following characters: *aps* absent on male tergopleurite VI in *B. tenebrosa* (Figure 17a), but present in *B. melospizae* (Figure 15a); *ps* absent on male abdominal segment III in *B. tenebrosa* (Figure 17a), but present in *B. melospizae* (Figure 15a); preantennal head proportionately broader and shorter in *B. tenebrosa* (Figure 18a) than in *B. melospizae* (Figure 16a); proximal mesosome narrower in *B. tenebrosa* (Figure 18c) than in *B. melospizae* (Figure 16c); rugose area of mesosome more extensive in *B. tenebrosa* (Figure 18c) than in *B. melospizae* (Figure 16c); parameres slender in *B. tenebrosa* (Figure 18d), but stout in *B. melospizae* (Figure 16d). Females best separated on head shape and pigmentation patterns (see below).

Description

Both sexes. Head convex dome-shaped (Figure 18a), lateral margins of preantennal area convex, frons flat to slightly concave. Marginal carina broad, width irregular, much displaced and widened at osculum. Ventral anterior plate small, crescent-shaped to triangular. Head chaetotaxy as in Figure 18a. Preantennal nodi large, bulging. Preocular nodi large, postocular nodi moderate. Marginal temporal carina with irregular median margin. Gular plate broadly lanceolate. Thoracic and abdominal segments as in 17A–B. Base pigmentation yellowish brown; marginal and marginal temporal carinae, head nodi, margins of antennal sockets, anterior end of gular plate, proepimera, metepisterna, sternal and subgenital plates, and most of tergopleurites except central area around spiracle opening darker.

Male. Thoracic and abdominal chaetotaxy as in Figure 17a; *ss* present on tergopleurite V, *tps* and *aps* present on tergopleurite VII, *tps* absent from tergopleurite VI; *ps* absent from abdominal segment III. Basal apodeme broad, constricted at mid-length, but widening anteriorly (Figure 18b). Proximal mesosome somewhat elongated, narrowly rounded (Figure 18c). Mesosomal lobes wide, angular; rugose area covers most of ventral surface of lobes in distal end; 2 *pmes* sensilla on each side lateral to gonopore. Gonopore long, crescent-shaped. Penile arms short, not reaching distal margin of mesosome. Parameres elongated, slender, *pst1–2* as in Figure 18d. Measurements (n = 7 except TL where n = 6): TL = 1.47–1.62; HL = 0.35–0.38; HW = 0.30–0.32; PRW = 0.18–0.21; PTW = 0.28–0.32; AW = 0.36–0.42.

Female. Thoracic and abdominal chaetotaxy as in Figure 17b; *ps* present on abdominal segment III. Lateral margins of proximal subgenital plate concave (Figure 18e), with broad connection to cross-piece. Vulval margin gently rounded (Figure 18e), 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 (rarely 2 on one side) *vos* median to *vss*. Measurements (n = 21): TL = 1.67–1.81 (1.74); HL = 0.37–0.41 (0.39); HW = 0.31–0.34 (0.33); PRW = 0.19–0.22 (0.20); PTW = 0.29–0.36 (0.33); AW = 0.38–0.44 (0.41).

Etymology

Specific name derived from Latin '*tenebrosus*' for 'dark', referring to the extensive dark pigmentation of this species.

Material examined

Ex Passerella iliaca (subspecies unknown): Holotype ♂, Sullivan Canyon, Los Angeles County, California, United States, 19 March 1985, M.A. Marin, 4 (NHML). *Paratypes*. 1♂, 6♀, same data as holotype (NHML); 5♂, 15♀, Virginia [United States], Feb. 1939, R. Meinertzhagen, 12,639 (NHML).

Discussion

Kellogg (1896) originally described *Nirmus vulgatus* from eight different host species belonging to three different families. Subsequently, at least 50 other host species of this species have been reported (see Remarks under *B. vulgata*). Most of these early host reports are likely due to the very general description of *Nirmus vulgatus*, and the assumption that the species is widely distributed on many different hosts. Apart from the material treated here, we have examined *Brueelia* from a range of hosts from across the world, including specimens from many of the hosts reported to be parasitised by *B. vulgata*. No specimens identified as *B. vulgata* has been found, other than those from *Zonotrichia* spp. and *Junco hyemalis*. Rather than the wide host range of this species proposed by earlier authors, our study indicated that *B. vulgata* is limited to a small number of closely related North American sparrows. This pattern of restricted host specificity is consistent with that of most other species of feather lice in the *Brueelia*-complex.

Sometimes the patterns of host associations in *Brueelia* are straightforward. Closely related host species are often parasitised by closely related lice, a pattern consistent with Fahrenholz' rule (Eichler 1940). Although there are some exceptions, Fahrenholz' rule generally seems to apply among the *Brueelia* species found on passerellid hosts. For example, three bird species in the genus *Melospiza* are parasitised by the same species of louse (*B. melospizae*). This louse species is also morphologically similar to *Brueelia* spp. on related hosts in the genera *Pooecetes* Baird 1858, *Pipilo* Vieillot 1816, and *Melozone;* Reichenbach 1850. Similarly, the bird genera *Chondestes* Swainson 1827 and *Spizella*; Bonaparte 1832 are closely related, and the *Brueelia* from these hosts are morphologically similar. These host genera are also closely related to the genus *Aimophila;* Swainson 1837. We have examined a single, poorly preserved male *Brueelia* from *A. ruficeps* (Cassin 1852), which also has *tps* on tergopleurite VII, an elongated mesosome, and a large gonopore, similar to the *Brueelia* species known from *Melospiza, Pooecetes*, and *Pipilo*. Finally, *Zonotrichia* spp. and *Junco hyemalis* are closely related birds (Klicka et al. 2014), and both morphological patterns (as described above) and molecular data (Bueter et al. 2009; Bush et al. 2016) support the treatment of lice on these birds as conspecific.

This is in contrast to the patterns of host associations seen in many other groups of hosts parasitised by *Brueelia*-complex lice. For instance, Gustafsson and Bush (2015) reported species in the *Brueelia clara* species group from hosts belonging to different parvorders. Gustafsson et al. (2018; 2019a, 2019b) described cases where morphologically similar species of *Brueelia* parasitise hosts belonging to different families. Conversely, closely related hosts are sometimes parasitised by morphologically dissimilar species of

Brueelia. For instance, the *Brueelia* species parasitising nuthatches (Sittidae) appear to belong to three different morphological groups (Gustafsson et al. 2018). Discordant host associations may be more common than once thought. Indeed, in the phylogeny of Bush et al. (2016), there are only few examples of multi-species clades of *Brueelia* s. str. where all hosts belong to the same host family. Thus far, we have examined specimens from only 14 of the 43 passerellid hosts living in North America, and all of the specimens we examined were from regions north of US–Mexico border. Examination of more specimens from a greater geographic distribution are needed to rigorously establish whether the overall patterns of host associations in *Brueelia* on passerellid hosts follows Fahrenholz's law, or some other evolutionary or ecological pattern.

1. Mesosome entirely without rugose area, but with microsetae on postero-lateral margin (Figure 4c) ..... *Brueelia angustifrons* (Carriker 1902)
   - Mesosome with at least posterior margin rugose, no microsetae on postero-lateral margin 2
2. At least 1 *tps* present on each side on tergopleurite VII 3
   - No *tps* present on tergopleurite VII 8
3. Abdominal segment III with 1 *ps* on each side (Figure 15a) ..... *Brueelia melospizae* sp. nov.
   - Abdominal segment III without *ps* 4
4. Tergopleurite V without *ss* (Figure 5a); tergopleurite VI with *aps* (Figure 5a) ..... *Brueelia hesperides* sp. nov.
   - Tergopleurite V with *ss*; tergopleurite VI without *aps* 5
5. Proximal mesosome narrow (Figure 12C, 18C) 6
   - Proximal mesosome broad (Figures 8c, 10c) 7
6. Gonopore roughly rectangular with deeply concave distal margin and rugose central section (Figure 12c); parameres stout (Figure 12d) ..... *Brueelia chlorurae* sp. nov.
   - Gonopore elongated crescent-shaped, without rugose central section (Figure 18c); parameres slender (Figure 18d) ..... *Brueelia tenebrosa* sp. nov.
7. Anterior head rounded (Figure 8a); proximal mesosome gently rounded (Figure 8c); antero-lateral corners of gonopore concave (Figure 8c) *Brueelia californica* sp. nov.
   - Anterior head flattened (Figure 10a); proximal mesosome broadly flattened (Figure 10c); antero-lateral margins of gonopore convex (Figure 10c) ..... *Brueelia canyonica* sp. nov.
8. Tergopleurite VI with *aps* (Figure 13a); head narrow (Figure 14a); abdominal segment III without *ps* (Figure 13a) ..... *Brueelia cassiopeia* sp. nov.
   - Tergopleurite VI without *aps* (Figure 1a); head broader (Figure 2a); abdominal segment III with *ps* (Figure 1a) ..... *Brueelia vulgata* (Kellogg 1896)

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Disclosure statement

No potential conflict of interest was declared by the authors.

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