

# Ten new species of *Brueelia* Kéler, 1936 (Phthiraptera: Ischnocera: Philopteridae) from nuthatches (Aves: Passeriformes: Sittidae), tits and chickadees (Paridae), and goldcrests (Regulidae)

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## Abstract

Ten new species of chewing lice in the genus *Brueelia* Kéler, 1936, are described from hosts in the families Paridae, Regulidae, and Sittidae. They are: *Brueelia johnsoni* n. sp. from *Poecile sclateri eidos* (Peters, 1927); *Brueelia juniperi* n. sp. from *Baeolophus ridgwayi ridgwayi* (Richmond, 1902); *Brueelia kabulica* n. sp. from *Sitta tephronota tephronota* Sharpe, 1872; *Brueelia mpumalangensis* n. sp. from *Melaniparus niger niger* (Vieillot, 1818); *Brueelia nazae* n. sp. from *Parus cinereus caschmirensis* Hartert, 1905; *Brueelia oxyrhyncha* n. sp. from *Sitta nagaensis nagaensis* Godwin-Austen, 1874; *Brueelia picea* n. sp. from *Parus major excelsus* Buvry, 1857; *Brueelia ragusica* n. sp. from *Sitta neumayer neumayer* Michahelles, 1830; *Brueelia regulicida* n. sp. from *Regulus calendula grinnelli* Palmer, 1897; *Brueelia sittacola* n. sp. from *Sitta carolinensis carolinensis* Latham, 1790. *Brueelia regulicida* is the first *Brueelia*-complex louse to be described from the host family Regulidae. Collectively, the *Brueelia* of parid, regulid, and sittid hosts show two peculiar patterns. Firstly, lice on closely related hosts appear to be distantly related. Secondly, lice on most hosts in these families appear to be more closely related to lice on other host families than to each other. This contradicts the traditional view that *Brueelia*-complex lice on closely related hosts are themselves closely related. Potentially, the tendency of the hosts to participate in mixed-species feeding flocks may explain some of these patterns.

## Keywords

Phthiraptera, Ischnocera, *Brueelia*-complex, new species, Sittidae, Regulidae, Paridae

## Introduction

Chewing lice in the *Brueelia*-complex are found primarily on passeriform birds. Although this complex represents about 10% of known chewing louse diversity, little is known about *Brueelia*-complex lice from many passerine hosts, even those occurring in relatively well studied regions of the world (Gustafsson and Bush 2017). We here described ten new species of chewing lice in the genus *Brueelia* Kéler, 1936, from North America, Africa, Europe, and Asia. These descriptions include four species from nuthatches (Sittidae), one species a goldcrest (Regulidae), and five species from tits and chickadees (Paridae). The host families Sittidae and Paridae are both parasitized by *Brueelia* species belonging to several

different species groups, suggesting a complicated evolutionary history. The single species of *Brueelia* described from a regulid host constitutes the first known species in the *Brueelia*-complex associated with this host family.

## Materials and Methods

We examined slide-mounted specimens deposited at the Natural History Museum, London, United Kingdom (NHML), the Slovenian Museum for Natural History, Ljubljana, Slovenia (PMSL), the University of Minnesota, St. Paul, USA (UMSP), the Price Institute for Parasitological Research, University of Utah, Salt lake City, USA (PIPeR), the Field Museum for Nat-

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ural History, Chicago, USA (FMNH), or the Guangdong Institute for Applied Biological Resources (GIABR). All studied material was mounted in Canada balsam on microscopy slides. Holotypes and paratypes are deposited in these institutions as indicated for each species. Specimens were examined and measured with a Nikon Eclipse E600 fitted with an Olympus DP25 camera and digital measuring software (ImageJ 1.48v, 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 millimeters, as ranges (mean value, when  $n \geq 10$ ). We use the following abbreviations for measurements: TL = total length; HL = head length (along midline); HW = head width (at temples); PRW = prothorax width; PTW = pterothorax width; AW = abdominal width (at posterior end of segment V). We use the following terms and abbreviations for morphological structures: *aps* = accessory postspiracular seta; *as3* = anterior seta 3, *pms* = posterior mesosomal setae, *ps* = pleural seta, *psps* = principal postspiracular seta, *pst* = parameral seta, *ss* = sutural seta, *tps* = tergal posterior seta, *vms* = vulval marginal seta, *vos* = vulval oblique seta (which includes the distal slender seta median to the *vss*), *vss* = vulval submarginal seta. All of these terms and abbreviations follow Gustafsson and Bush (2017). Host taxonomy follows Clements *et al.* (2017).

## Systematics

### Phthiraptera Haeckel, 1896

### Ischnocera Kellogg, 1896

### Philopteridae Burmeister, 1838

### The *Brueelia*-complex

#### *Brueelia* Kéler, 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*).

*Nigronirmus* Złotorzycka, 1964: 248.

*Spironirmus* Złotorzycka, 1964: 261.

*Serinionirmus* Soler-Cruz, Rodríguez, Florido-Navío and Muñoz-Parra, 1987: 244.

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

#### *Brueelia* from nuthatches (Sittidae)

Only one species of *Brueelia* is presently known from nuthatches, *Brueelia conocephala* (Blagoveshtchensky, 1940).

*Brueelia conocephala* forms a very distinct species group together with at least *B. weberi* (Balát, 1982) and *B. oxyrhyncha* n. sp. The most conspicuous morphological feature

connecting these species is the peculiar head shape (Figs 1, 4). Similar head shapes are found in three other species of *Brueelia*: *Brueelia balati* Krištofik 1999 from Remizidae, *B. chalcomitreae* Najer et Sychra [in Najer *et al.*], 2012 from Nectarinidae, and *B. regulicida* n. sp. from Regulidae (see below). Other species of *Brueelia* from nuthatches and tits described here do not belong in this species group.

*Brueelia balati* is in need of redescription to establish whether the "well visible" dorsal suture (Krištofik 1999: 139) and lack of cross-piece in this species are described correctly. The former character is highly unusual in *Brueelia*, and the latter does not occur in this genus at all. However, no such suture is illustrated, and in the illustration of the female genitalia there are pigmentation dots that may suggest the presence of a cross-piece. *Brueelia chalcomitreae* may not belong to the genus *Brueelia* at all, as suggested by the apparent lack of a cross-piece and presence of accessory sternal plates on the female abdomen. In both cases, the similarities in head shape may be due to convergence. The inclusion of either of these species in the *B. conocephala* species group cannot presently be established.

#### *Brueelia conocephala* (Blagoveshtchensky, 1940) (Fig. 1)

*Degeeriella conocephala* Blagoveshtchensky, 1940: 64.

*Brueelia conocephalus* (Blagoveshtchensky), 1940; Hopkins and Clay, 1952: 54

*Brueelia conocephala* (Blagoveshtchensky, 1940); Gustafsson and Bush, 2017: 39

**Type host:** *Sitta europaea caucasica* Reichenow, 1901 – Eurasian nuthatch.

**Type locality:** Alexeyevka, Talysh Lowlands, Lenkoran Region [= Lankaran], Azerbaijan.

**Other hosts:** *Sitta europaea caesia* Wolf, 1810. *Sitta europaea rubiginosa* Tschusi et Zardny, 1905.

**Remarks:** Two separate host name are given as the type host in the original description: *Sitta europaea caucasica* Reichenow, 1901 and *S. e. rubiginosa* Tschusi et Zardny, 1905. These two names are separated by a symbol similar to "><", of unclear meaning. The same symbol was used in the English description of the species later in the same publication (*ibid.*: 87). Hopkins and Clay (1952) reproduced this symbol as two arrows, but only *S. e. caucasica* was listed as a host of *B. conocephala* by Price *et al.* (2003: 154). As both subspecies occur in the Caucasus, we assume this symbol is meant to convey that the subspecific status of the type host is uncertain. Price *et al.* (2003), by listing only one host subspecies, thus restricted the type host subspecies to *S. e. caucasica*. We provisionally list *S. e. rubiginosa* as a second host. This louse species is also known to occur on hosts referable to the subspecies *S. e. caesia* Wolf, 1801 (Touleshkov 1962, 1974), however, subspecies names were not provided for the hosts in these publications. Specimens examined by Gustafsson and

Bush (2017) further confirm the association of *B. conocephala* with *S. e. caesia*.

Here we have redrawn the female of this species from Blagoveshtchensky (1940), for easy reference (Fig. 1). As many features in the original illustration are suggested by density of dots rather than outlines of plates and internal structures, these have here been rendered as faithfully to the original as is possible.

***Brueelia oxyrhyncha* n. sp.** (Figs 2–8)

**Type host:** *Sitta nagaensis nagaensis* Godwin-Austen, 1874 – chestnut-vented nuthatch.

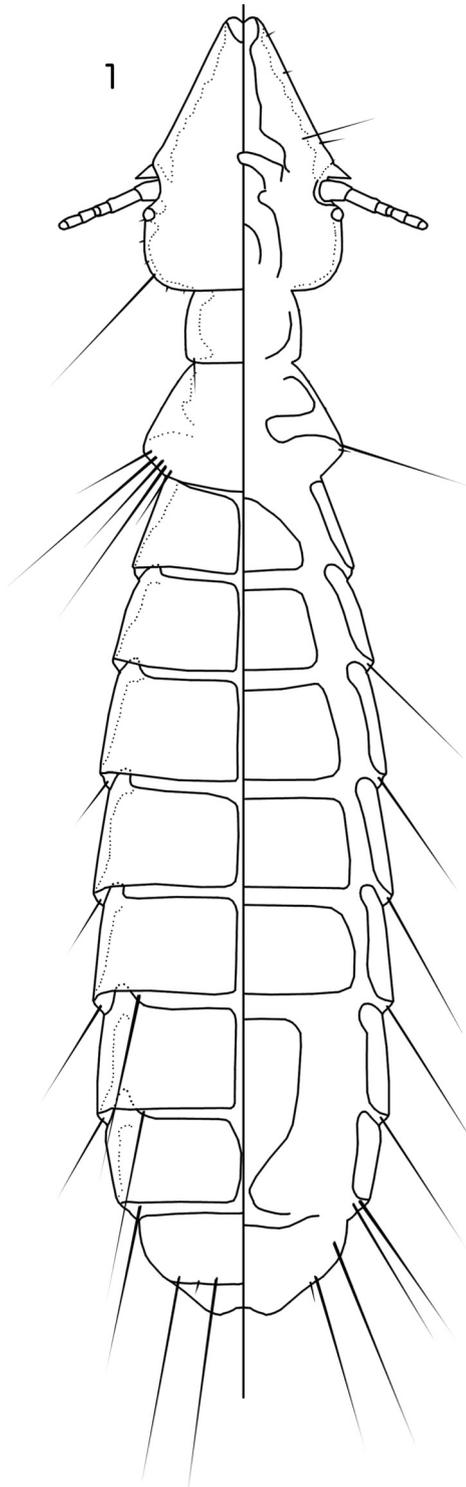
**Type locality:** Gaojingliang Village, Malipo County, Yunnan Province, China.

**Description, both sexes:** Head drop-shaped (Fig. 4), with preantennal area much elongate. Lateral margins of preantennal area slightly convex proximally, and slightly concave distally. Frons deeply concave, hyaline margin wide. Marginal carina broad, somewhat irregular in width, deeply displaced and widened at osculum. Ventral anterior plate present, longer than broad, with rounded posterior margin and flat to slightly concave anterior margin. Head chaetotaxy as in Fig. 4; *as3* apparently dorsal. Preantennal nodi slight, not bulging. Preocular nodi much larger than postocular nodi. Marginal temporal carina of irregular width. Gular plate broadly spade-shaped. Thoracic and abdominal segments as in Figs 2–3. Pigmentation very faint brown; much of preantennal head, lateral temples, pedicel and flagellomeres, proepimera, metepisterna, and lateral sections of tergopleurites pale to medium brown; only preantennal nodi and carinae of femurs and tibia dark brown.

**Male:** Thoracic and abdominal chaetotaxy as in Fig. 2; *aps* present on tergopleurites V–VII. Basal apodeme slender, not constricted medianly (Fig. 5), but with distal distortion on one side in holotype (not illustrated). Proximal mesosome short, roughly rectangular (Fig. 6). Mesosomal lobes longer than wide, with extensive rugose area in distal sections; 2 *pmes* sensilla on each side lateral to gonopore. Gonopore crescent-shaped. Penile arms long, reaching beyond distal margin of mesosome. Parameres slender (Fig. 7), elongate; *pst1–2* not visible in holotype. Measurements ( $n = 1$ ): TL = 1.51; HL = 0.38; HW = 0.32; PRW = 0.19; PTW = 0.28; AW = 0.32.

**Female:** Thoracic and abdominal chaetotaxy as in Fig. 3. Subgenital plate broad (Fig. 8), lateral margins rounded, connection to cross-plate broad. Vulval margin gently rounded, somewhat flattened medianly (Fig. 8), with 2–4 short, slender *vms* and 2–4 short, thorn-like *vss* on each side; 1–3 short, slender *vos* on each side of subgenital plate; distal *vos* median to *vss*. Measurements ( $n = 3$ , except TL and AW where  $n = 2$ ): TL = 1.72–1.83; HL = 0.41–0.44; HW = 0.35–0.38; PRW = 0.21–0.23; PTW = 0.31–0.32; AW = 0.36–0.40.

**Type material:** Holotype ♂, Gaojingliang Village, Malipo County, Yunnan Province, China, 16 Jun. 2016, X. Chu and



**Fig. 1.** *Brueelia conocephala* (Blagoveshtchensky, 1940) ex *Sitta europaea caucasica* Reichenow, 1901. Female redrawn from original illustration by Blagoveshtchensky (1940). The outlines of tergal plates, subgenital plate, tergopleural incassations and other characters interpreted from point patterns in original. Original illustration showed only dorsal side, and most ventral setae omitted in original. We have inserted the ventral setae that were illustrated in the original as closely to where the corresponding setae are located in close relatives of *B. conocephala*. Legs omitted for clarity. Scale not given in original

Y. Wu, J3114(4) (GIABR). Paratypes: 3♀, same data as holotype, except J3114(1–3) (GIABR).

**Diagnosis:** *Brueelia oxyrhyncha* n. sp. is most similar to *B. conocephala* (Blagoveshtchensky, 1940) and *B. weberi* Balát, 1982. It can be separated from both by the following combination of characters: lateral margins of preantennal head convex proximally and concave distally (Fig. 4), but almost straight in *B. conocephala* (Fig. 1) and slightly concave in *B. weberi*; temples wider in *B. oxyrhyncha* (Fig. 4) than in *B.*

*conocephala* (Fig. 1), but temples similar in *B. weberi* and *B. oxyrhyncha*; female abdominal segment VIII with 2 *ps* and trichobothrium on each side in *B. oxyrhyncha* (Fig. 3), but with 1 *ps* and trichobothrium in *B. conocephala* (Fig. 1) [abdominal chaetotaxy of *B. weberi* not mentioned by Balát (1982)]; male tergopleurite VIII with 5 *tps* in *B. oxyrhyncha* (Fig. 2), but with only two posterior setae other than the *ps* in male *B. conocephala* (see text of Blagoveshtchensky 1940; not illustrated). Males of *B. oxyrhyncha* have *ss* on tergopleurites V–

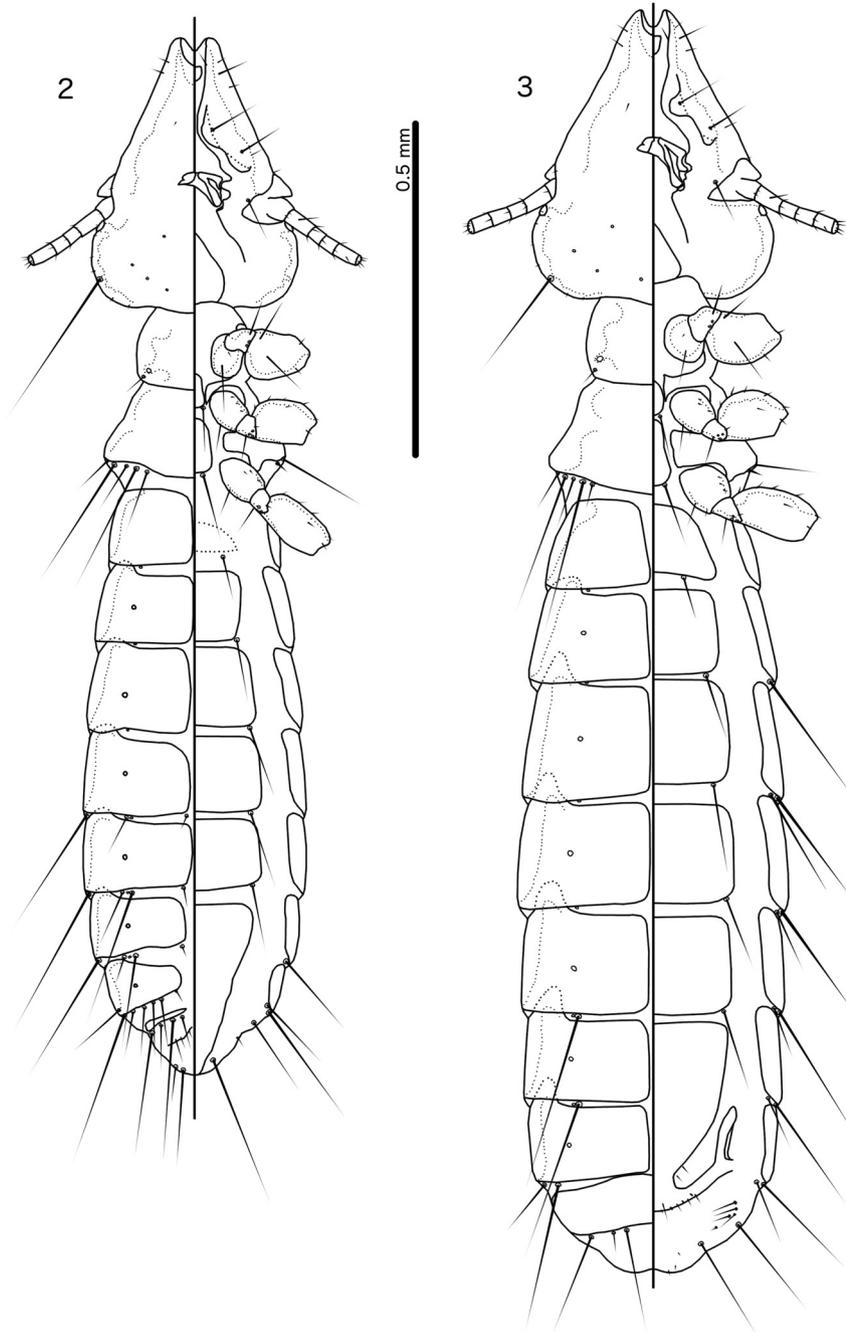
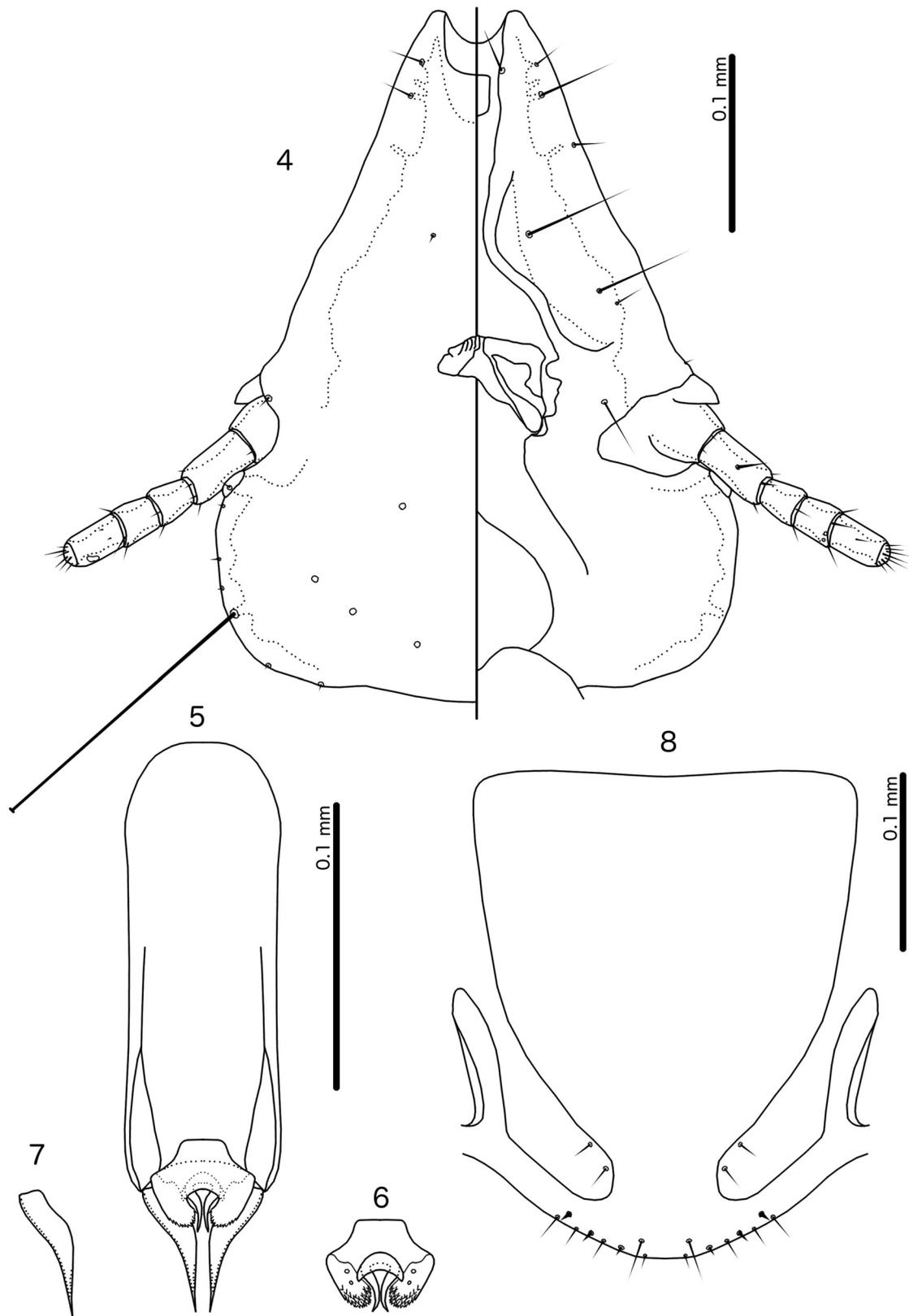


Fig. 2–3. *Brueelia oxyrhyncha* n. sp. ex *Sitta nagaensis nagaensis* Godwin-Austin, 1874. 2 – male habitus, dorsal and ventral views. 3 – female habitus, dorsal and ventral views



**Fig. 4–8.** *Brueelia oxyrhyncha* n. sp. ex *Sitta nagaensis nagaensis* Godwin-Austin, 1874. **4** – male head, dorsal and ventral view. **5** – male genitalia, dorsal view. **6** – male mesosome, ventral view. **7** – male paramere, dorsal view. **8** – female subgenital plate and vulval margin, ventral view. Abbreviations used: *as3* = anterior seta 3; *dsms* = dorsal submarginal seta

VII (Fig. 2), but no such setae are mentioned by Blagoveshtchensky (1940).

**Etymology:** The species epithet is constructed from Greek "*oxús*" for "sharp, acute" and "*rhunkhos*" for "bill". This is in references to the more elongate and narrow preantennal head of this species, compared to *Brueelia conocephala* (Blagoveshtchensky, 1940).

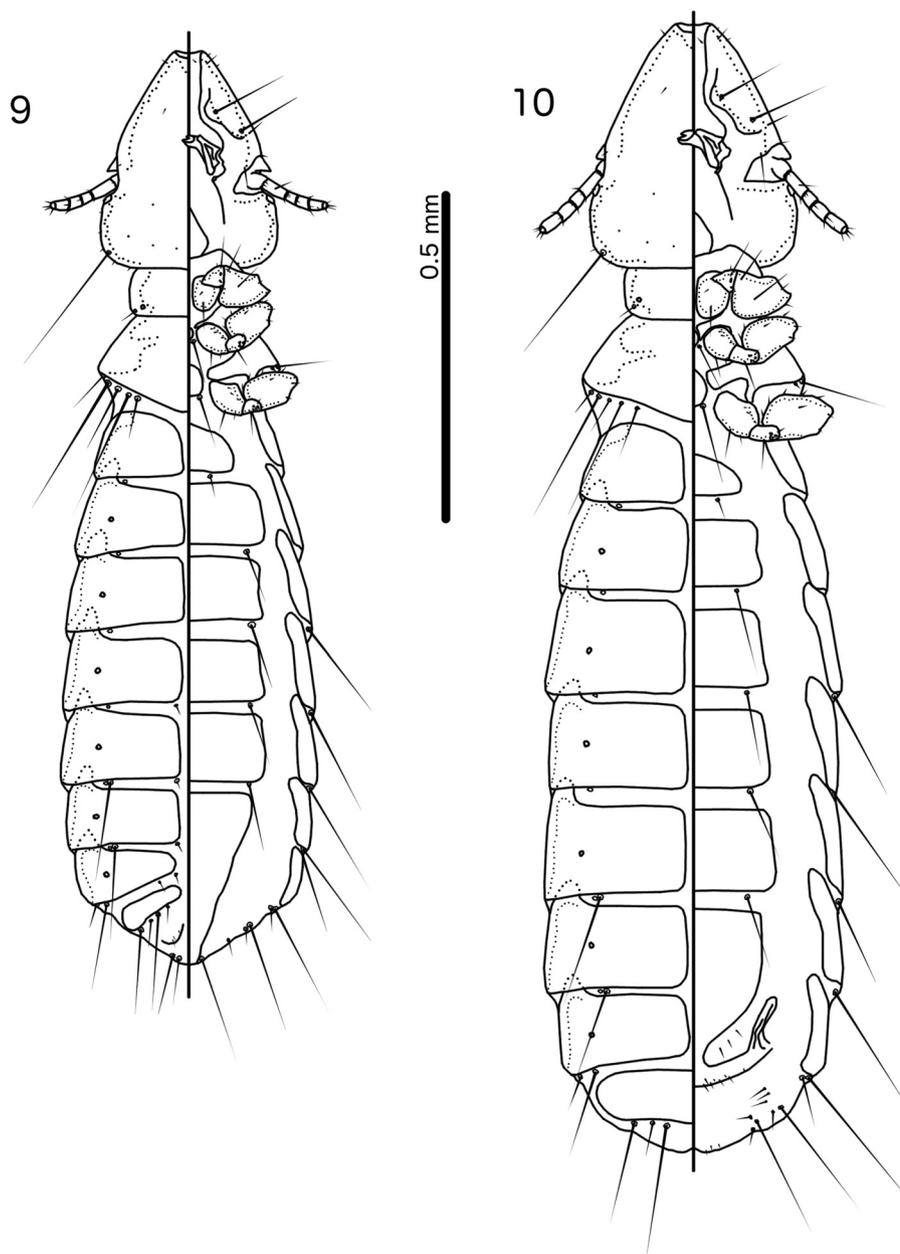
**Remarks:** The hosts of *B. conocephala* and *B. oxyrhyncha* are closely related, and their status as separate species has not always been clear (Dickinson 2006). We here follow Clements *et al.* (2017) where they are treated as separate species.

***Brueelia sittacola* n. sp.** (Figs 9–15)

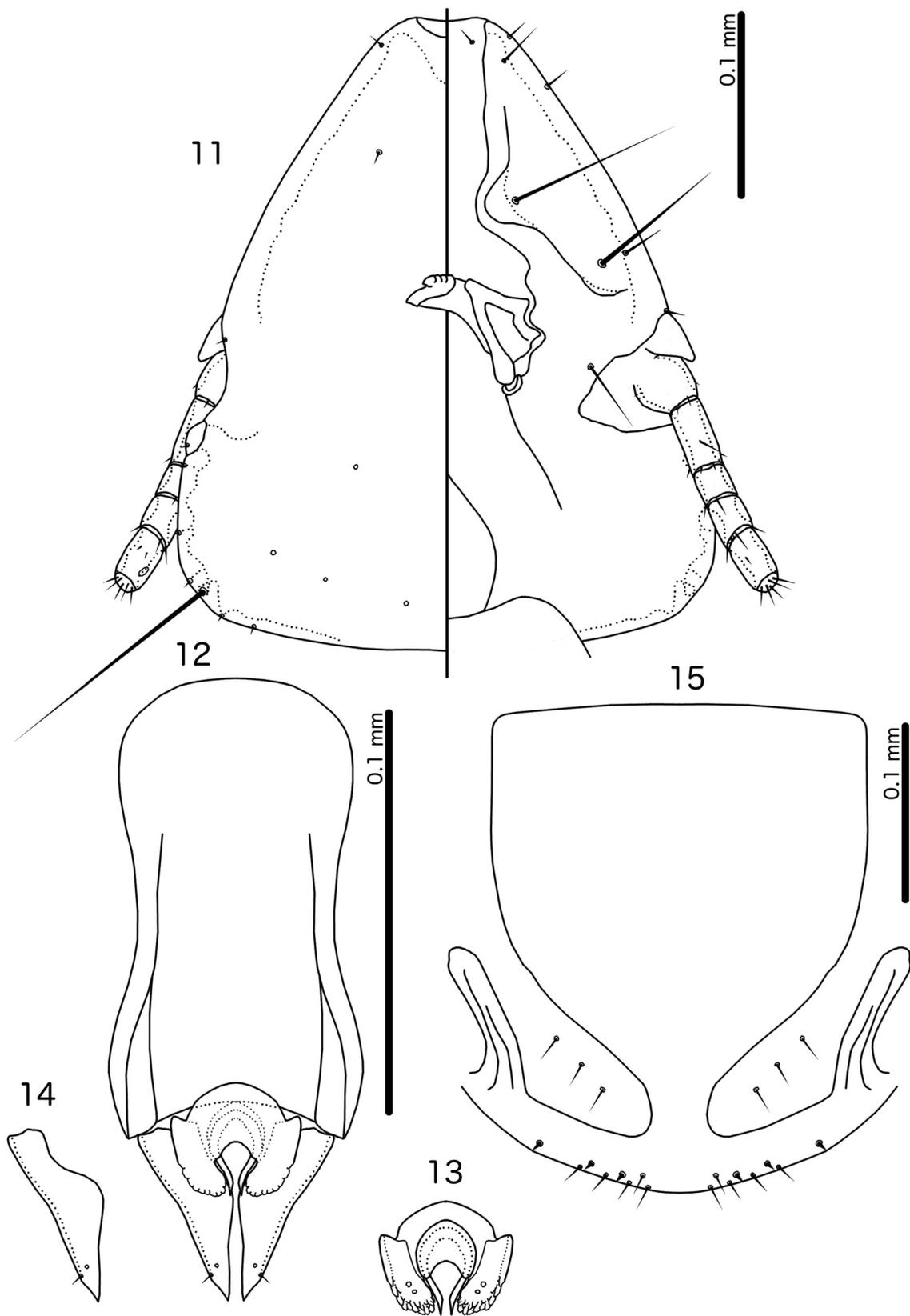
**Type host:** *Sitta carolinensis carolinensis* Latham, 1790 – white-breasted nuthatch.

**Type locality:** Carlos Avery, Minnesota, United States.

**Description, both sexes:** Head flat dome-shaped (Fig. 11), lateral margins of preantennal head straight or slightly convex, frons flattened to slightly concave. Marginal carina moderate, more or less even in width, deeply displaced and much widened at osculum. Ventral anterior plate absent. Head chaetotaxy as in Fig. 11. Preantennal nodi small, not bulging. Preocular nodi much larger than postocular nodi. Marginal



**Fig. 9–10.** *Brueelia sittacola* n. sp. ex *Sitta carolinensis carolinensis* Latham, 1790. **9** – male habitus, dorsal and ventral views. **10** – female habitus, dorsal and ventral views



**Fig. 11–15.** *Brueelia sittacola* n. sp. ex *Sitta carolinensis carolinensis* Latham, 1790. **11** – male head, dorsal and ventral view. **12** – male genitalia, dorsal view. **13** – male mesosome, ventral view. **14** – male paramere, dorsal view. **15** – female subgenital plate and vulval margin, ventral view

temporal carina very irregular in width. Gular plate slenderly lanceolate. Thoracic and abdominal segments as in Figs 9–10. Pigmentation very pale, mostly translucent, but marginal and marginal temporal carinae, head nodi, proepimera, metepisterna, pleural thickenings, medium brown; sternal and subgenital plates pale brown.

**Male:** Thoracic and abdominal chaetotaxy as in Fig. 9; *aps* absent on all segments. Basal apodeme wide, constricted at mid-length (Fig. 12). Proximal mesosome broad, short, rounded (Fig. 13). Mesosomal lobes broad and long; rugose area extensive along lateral and distal margins; 2 *pmes* sensilla on each side postero-lateral to gonopore. Gonopore broadly crescent-shaped. Penile arms long, reaching to or beyond distal margin of mesosome. Parameres elongate, stout; *pst1–2* as in Fig. 14. Measurements (n = 3 except AW where n = 2): TL = 1.34–1.36; HL = 0.33–0.35; HW = 0.27; PRW = 0.17; PTW = 0.25–0.28; AW = 0.36–0.39.

**Female:** Thoracic and abdominal chaetotaxy as in Fig. 10. Anterior subgenital plate with gently rounded lateral margins (Fig. 15); connection to cross-piece narrow. Vulval margin gently rounded (Fig. 15), with 3–4 short, slender *vms* and 2–4 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 = 10, except TL where n = 8, HL where n = 9, and AW where n = 7): TL = 1.54–1.68; HL = 0.35–0.38; HW = 0.29–0.31 (0.30); PRW = 0.17–0.20 (0.19); PTW = 0.26–0.31 (0.29); AW = 0.39–0.45.

**Type material:** Holotype ♂, Carlos Avery, Minnesota, United States, 14 Dec. 1957, J.R. Beer, 66–234 (UMSP). Paratypes: 2♂, 10♀, same data as holotype (UMSP).

**Diagnosis:** *Brueelia sittacola* n. sp. is most similar to *B. regulicida* n. sp. These two species can be separated by the following characters: *tps* present on male tergopleurite VII in *B. regulicida* (Fig. 30), but absent in *B. sittacola* (Fig. 9); *ps* present on abdominal segment III in both sexes in *B. regulicida* (Figs 30–31), but absent in *B. sittacola* (Figs 9–10); frons narrower in *B. regulicida* (Fig. 32) than in *B. sittacola* (Fig. 11); basal apodeme narrower in *B. regulicida* (Fig. 33) than in *B. sittacola* (Fig. 12); mesosome shorter, with a smaller gonopore and more extensive rugose area in *B. regulicida* (Fig. 34) than in *B. sittacola* (Fig. 13). For a comparison between *B. sittacola* and *B. johnsoni* n. sp., which are also very similar, see this species, below.

**Etymology:** The specific name constructed from the genus name of the type host (*Sitta* Linnaeus, 1758), combined with Latin "*-incola*" for "inhabitant".

### *Brueelia kabulica* n. sp. (Figs 16–22)

**Type host:** *Sitta tephronota tephronota* Sharpe, 1872 – Persian nuthatch.

**Type locality:** Kabul, Afghanistan.

**Description, both sexes:** Head flat dome-shaped (Fig. 18), lateral margins of preantennal area convex, frons rounded.

Marginal carina narrow, slightly irregular, deeply displaced and somewhat widened at osculum. Ventral anterior plate absent. Head chaetotaxy as in Fig. 18. Preantennal nodi wide, not bulging. Preocular nodi larger than postocular nodi. Marginal temporal carina moderate, somewhat irregular. Gular plate slenderly lanceolate. Thoracic and abdominal segments as in Figs 16–17. Base pigmentation translucent, only marginal carina, margins of antennal sockets, head nodi, anterior marginal temporal carina, and proepimera a darker, yet still pale, brown.

**Male:** Thoracic and abdominal chaetotaxy as in Fig. 16; *aps* present on tergopleurites IV–VII. Basal apodeme rectangular (Fig. 19), in all examined specimens indistinct anteriorly and here illustrated approximately. Proximal mesosome broadly rounded, broader than long (Fig. 20). Mesosomal lobes moderate, rounded; rugose area small, limited to medio-posterior margins; 2 *pmes* sensilla on each side postero-lateral to gonopore. Gonopore arched, longer than wide. Penile arms long, reaching to posterior margin of mesosome. Parameres elongate, stout (Fig. 21); *pst1–2* as in Fig. 21. Measurements (n = 5, except AW where n = 2): TL = 1.51–1.61; HL = 0.37–0.38; HW = 0.28–0.29; PRW = 0.18–0.19; PTW = 0.26–0.31; AW = 0.44.

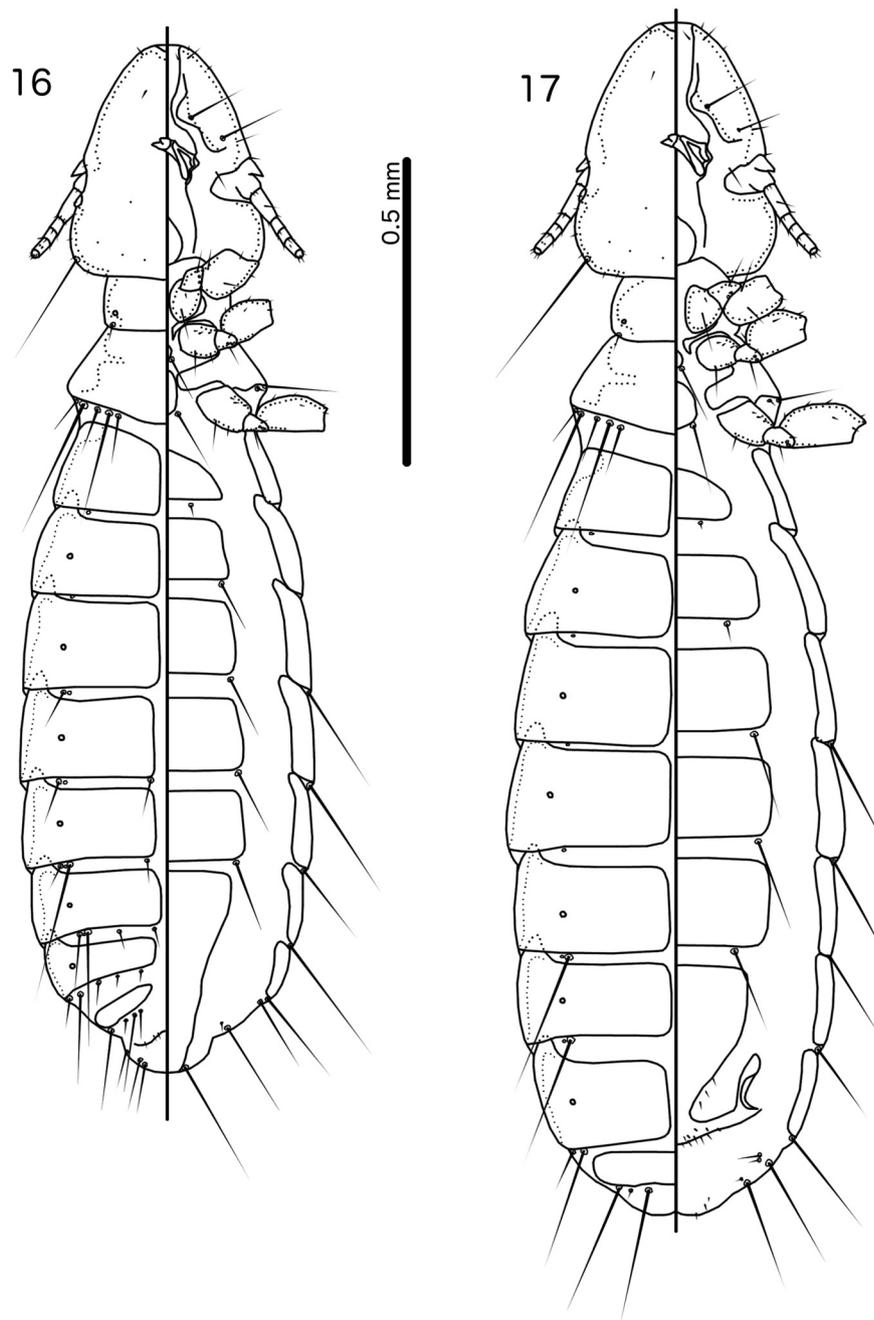
**Female:** Thoracic and abdominal chaetotaxy as in Fig. 17. Subgenital plate trapezoidal, with convex lateral margins and broad connection to cross-piece (Fig. 22). Vulval margin distinctly bulging in median section (Fig. 22), with 3–5 short, slender *vms* and 2–4 short, thorn-like *vss* on each side; 2–4 short, slender *vos* on each side of subgenital plate; distal 1 *vos* median or slightly posterior to *vss*. Measurements (n = 11, except TL where n = 10, and AW where n = 4): TL = 1.81–1.93 (1.86); HL = 0.39–0.42 (0.41); HW = 0.31–0.33 (0.32); PRW = 0.19–0.20 (0.20); PTW = 0.29–0.33 (0.31); AW = 0.44–0.51.

**Type material** [host as *Sitta neumayer*]: Holotype ♂, Kabul [Afghanistan], Apr. 1937, R. Meinertzhagen, 9632–33 (NHML). Paratypes: 4♂, 11♀, same data as holotype (NHML).

**Etymology:** The species epithet is derived from the type locality.

**Diagnosis:** *Brueelia kabulica* n. sp. is most similar to *B. ragusica* n. sp. However, there are several differences between these two species, suggesting that they may not be closely related. These differences include: ventral anterior plate present in *B. ragusica* (Fig. 25), but absent in *B. kabulica* (Fig. 18); proximal mesosome gently rounded in *B. kabulica* (Fig. 20), but elongate in *B. ragusica* (Fig. 27); frons flattened in *B. ragusica* (Fig. 25), but rounded in *B. kabulica* (Fig. 18). The general shape of the head (Figs 18, 25), width of the marginal carina (including the width of the displaced section at the osculum), and the distal mesosome (Figs 20, 27) are also different between these two species. Females of *B. ragusica* are best separated from females of *B. kabulica* on head shape (Figs 17, 24) and the structure of the preantennal area (Figs 18, 25).

**Remarks:** All examined material is excessively cleared, and exact outlines of tergal and sternal plates are often hard to dis-



**Fig. 16–17.** *Brueelia kabulica* n. sp. ex *Sitta tephronota tephronota* Sharpe, 1872. **16** – male habitus, dorsal and ventral views. **17** – female habitus, dorsal and ventral views

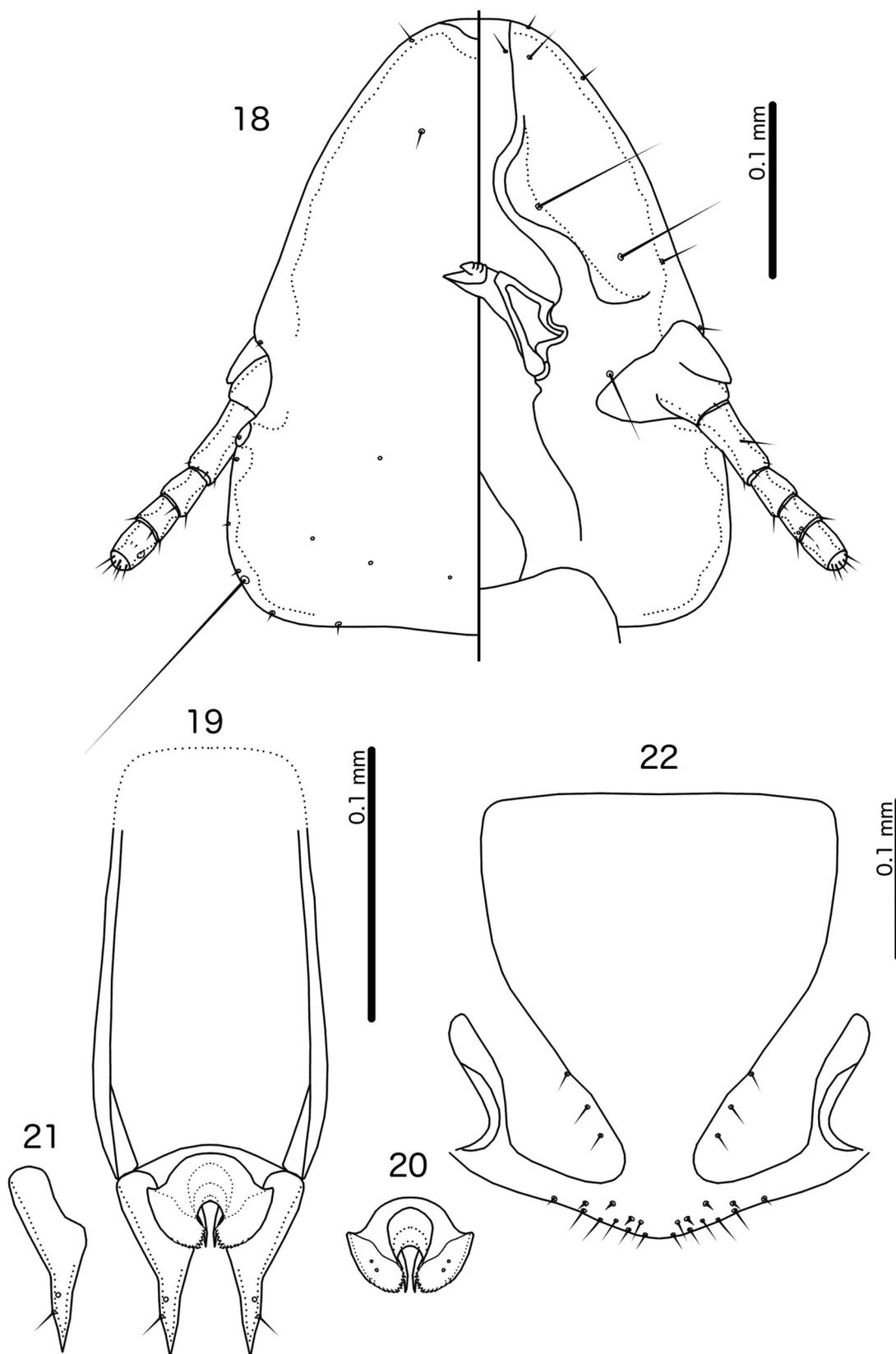
cern. In particular, the female subgenital plate is almost entirely cleared and its edges are not clearly visible in all examined specimens. It is here illustrated as close as possible to what can be seen in the examined specimens.

***Brueelia ragusica* n. sp.** (Figs 23–29)

**Type host:** *Sitta neumayer neumayer* Michahelles, 1830 – rock nuthatch.

**Type locality:** Dubrovnik, Croatia.

**Description, both sexes:** Head rounded trapezoidal (Fig. 25), lateral margins of preantennal area slightly convex, frons broadly flattened. Marginal carina moderate in width, slightly irregular, broadly but shallowly displaced and much widened at osculum. Ventral anterior plate present, elongate crescent-shaped. Head chaetotaxy as in Fig. 25. Preantennal nodi wide, slightly bulging. Preocular nodi much larger than postocular nodi. Marginal temporal carina slender, irregular. Gular plate lanceolate. Thoracic and abdominal segments as in Figs 23–24. Base pigmentation largely translucent, with marginal and



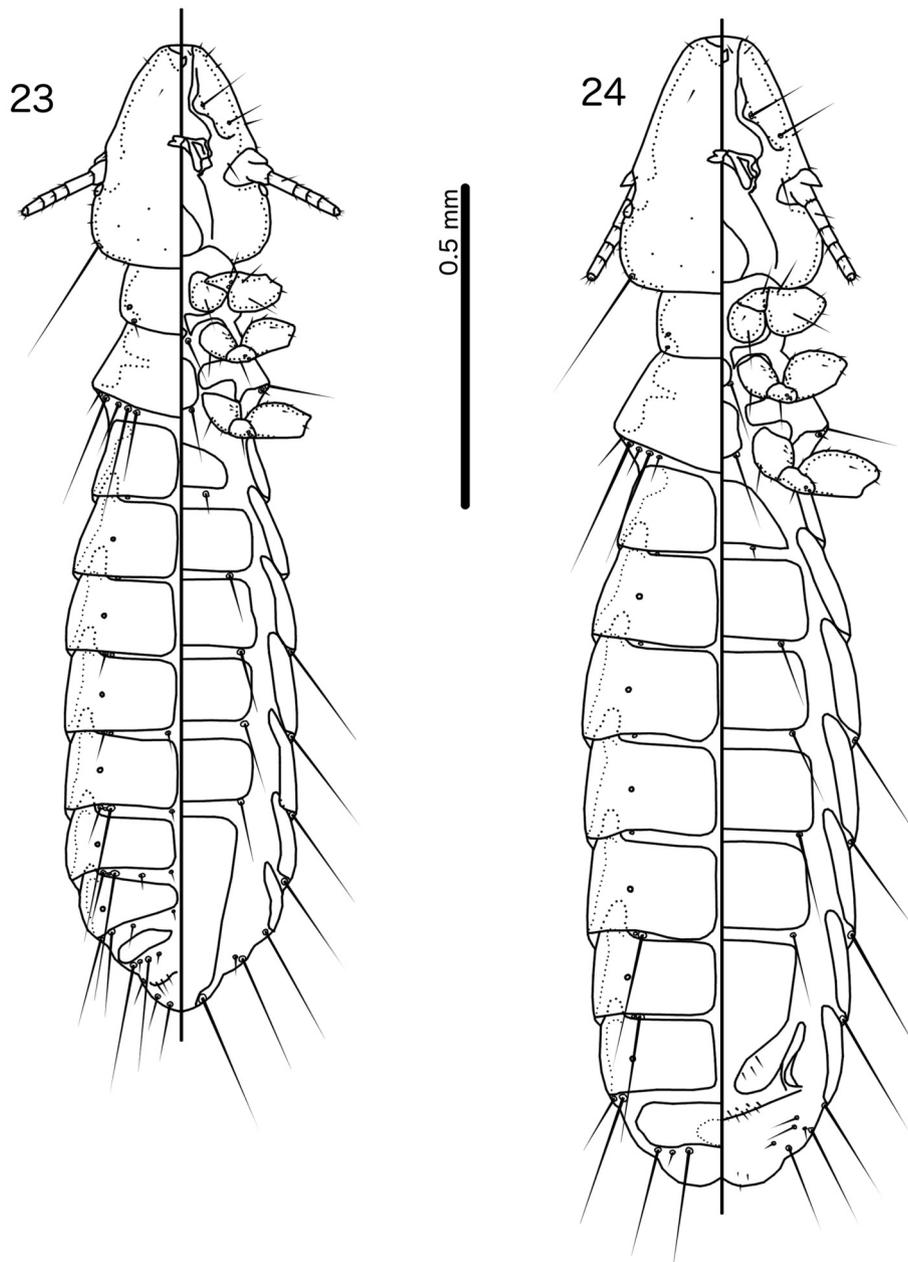
**Fig. 18–22.** *Brueelia kabulica* n. sp. ex *Sitta tephronota tephronota* Sharpe, 1872. **18** – male head, dorsal and ventral view. **19** – male genitalia, dorsal view. **20** – male mesosome, ventral view. **21** – male paramere, dorsal view. **22** – female subgenital plate and vulval margin, ventral view

marginal temporal carinae, head nodi, and posterior margin of antennal socket medium brown; proepimera, metepisterna, pleural thickenings, and sternal and subgenital plates pale brown. Female with pale brown spot on posterior margin of tergopleurite VIII as in Fig. 24.

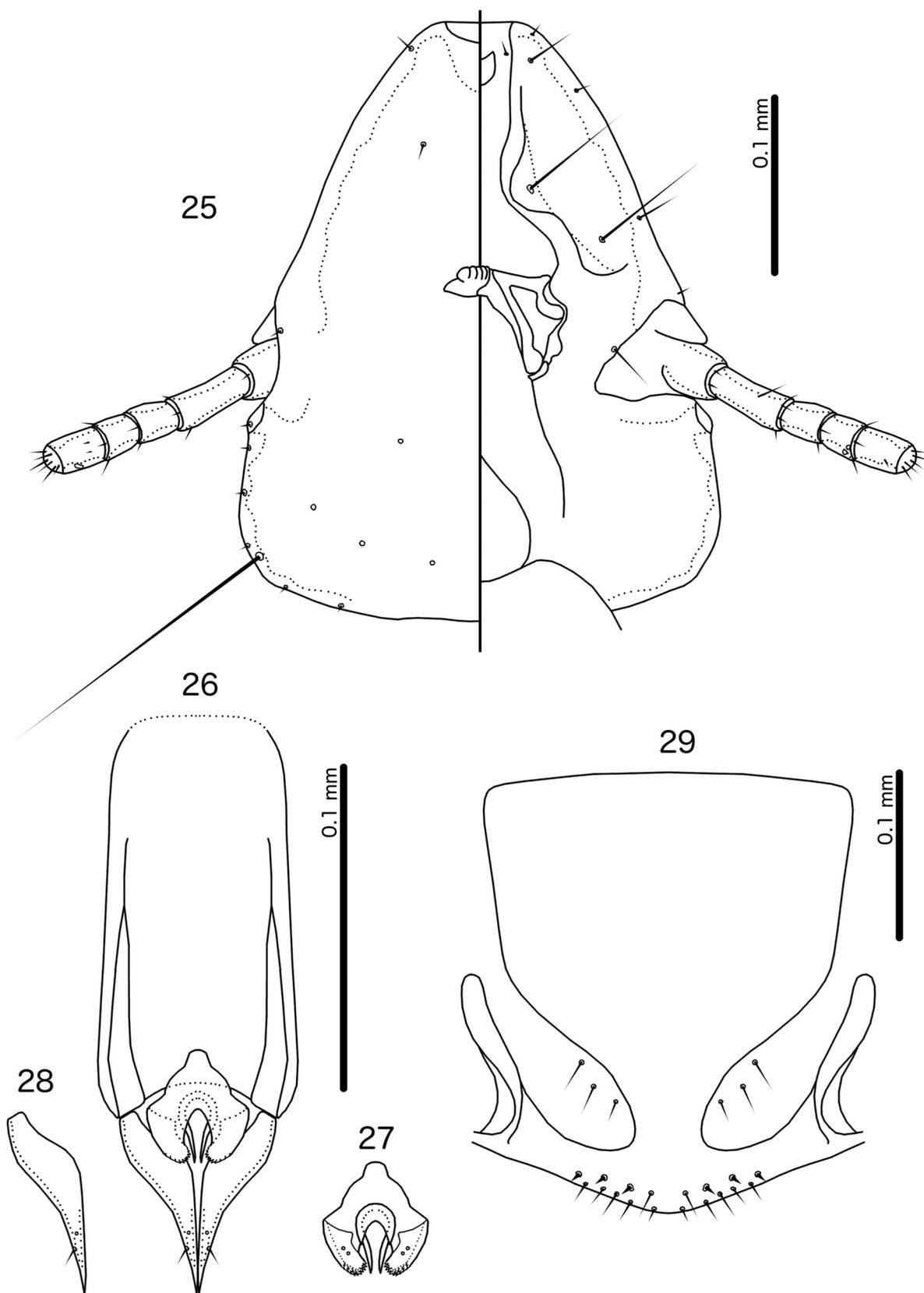
**Male:** Thoracic and abdominal chaetotaxy as in Fig. 23; *aps* present on tergopleurites IV–VII. Basal apodeme with straight lateral margins that converge slightly anteriorly (Fig. 26); anterior end diffuse in all examined specimens, and here illustrated approximately. Proximal mesosome longer than wide, with proximal constriction (Fig. 27). Mesosomal lobes with slight rugose area, restricted to posterior and median margins;

2 *pms* sensilla on each side postero-lateral to gonopore. Gonopore arches, slender. Penile arms long, reaching near or to distal margin of mesosome. Parameres elongate, slender distally (Fig. 28); *pst1–2* as in Fig. 28. Measurements (n = 5): TL = 1.43–1.49; HL = 0.34–0.35; HW = 0.27–0.29; PRW = 0.17–0.18; PTW = 0.27–0.29; AW = 0.35–0.37.

**Female:** Thoracic and abdominal chaetotaxy as in Fig. 24. Subgenital plate shaped as in Fig. 29, with clearly bulging lateral margins and broad connection to cross-piece. Vulval margin convergent to rounded median point (Fig. 29), with 3–6 short, slender *vms* and 3–4 short, thorn-like *vss* on each side; 3–4 short, slender *vos* on each side of subgenital plate;



**Fig 23–24.** *Brueelia ragusica* n. sp. ex *Sitta neumayer neumayer* Michahelles, 1830. **23** – male habitus, dorsal and ventral views. **24** – female habitus, dorsal and ventral views



**Fig 25–29.** *Brueelia ragusica* n. sp. ex *Sitta neumayer neumayer* Michahelles, 1830. **25** – male head, dorsal and ventral view. **26** – male genitalia, dorsal view. **27** – male mesosome, ventral view. **28** – male paramere, dorsal view. **29** – female subgenital plate and vulval margin, ventral view

distal 1 *vos* median to *vss*. Measurements ( $n = 8$ , except TL and HL where  $n = 7$ ): TL = 1.70–1.77; HL = 0.38–0.40; HW = 0.30–0.34; PRW = 0.19–0.21; PTW = 0.30–0.33; AW = 0.39–0.43.

**Type material:** Holotype ♂, Dubrovnik, Dalmatia, Croatia, 1968, A. Lesinger, IM-10201 (PMSL). Paratypes: 3♂, 7♀, same data as holotype except IM-10201–12 (PMSL); 1♂, Baćinska jezera [as Baćinsko jezero], Croatia, 2 May 1974, S. Brelih, IM-11520 (PMSL).

**Etymology:** The species epithet is derived from the Roman name for Dubrovnik, Ragusa.

**Diagnosis:** Most similar to *B. kabulica* n. sp., see diagnosis of this species above.

### *Brueelia* from Regulidae

No species in the *Brueelia*-complex have previously been described from hosts in the Regulidae.

The head shape of *B. regulicida* n. sp. is similar to that of species in the *B. conocephala* species group, but the preantennal area is not as prolonged as in the other known species in this group. We presently do not include this species in the *B. conocephala* group.

### *Brueelia regulicida* n. sp. (Figs 30–36)

**Type host:** *Regulus calendula grinnelli* Palmer, 1897 – ruby-crowned kinglet.

**Type locality:** California, United States.

**Description, both sexes:** Head rounded triangular (Fig. 32), lateral margins of preantennal area more or less straight, highly convergent anteriorly, frons concave. Marginal carina narrow, more or less regular in width, deeply displaced and slightly widened at oculus. Ventral anterior plate absent. Head chaetotaxy as in Fig. 32. Preantennal nodi slender, not bulging. Pre-ocular nodi larger than postocular nodi. Marginal temporal carina of very irregular width. Gular plate spade-shaped. Thoracic and abdominal segments as in Figs 30–31. All examined specimens dyed red before mounting, and true pigmentation patterns unknown. Head and thorax appears darker than abdomen, lateral tergopleurites and sternal plates darker than median tergopleurites.

**Male:** Thoracic and abdominal chaetotaxy as in Fig. 30; *aps* absent on all tergopleurites (2 examined males have *aps* on one side of segment VII); *ps* present on abdominal segment III–VII. Basal apodeme slender, not constricted at mid-length (Fig. 33). Proximal mesosome short, rounded to flattened (Fig. 34). Mesosomal lobes broad, intensely rugose on most of ventral surface; 2 *pmes* sensilla on each sidelateral to gonopore. Gonopore widely crescent-shaped. Penile arms short, not reaching distal margin of mesosome. Parameres elongate, stout; *pst1–2* as in Fig. 35. Measurements ( $n = 4$ ): TL = 1.45–1.51; HL = 0.32–0.33; HW = 0.27–0.28; PRW = 0.17–0.18; PTW = 0.26–0.27; AW = 0.37–0.40.

**Female:** Thoracic and abdominal chaetotaxy as in Fig. 31; *ps* present on abdominal segment III. Anterior subgenital plate roughly square-shaped, lateral margins roughly straight (Fig. 36), connection to cross-piece narrow. Vulval margin clearly rounded (Fig. 36), with 3–4 short, slender *vms* and 3–5 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 ( $n = 10$  except TL where  $n = 8$ ): TL = 1.62–1.68; HL = 0.32–0.35 (0.34); HW = 0.26–0.29 (0.28); PRW = 0.17–0.19 (0.18); PTW = 0.25–0.28 (0.27); AW = 0.38–0.43 (0.41).

**Type material:** [host as *Regulus calendula cinerascens*]: Holotype ♂, California, United States, Feb. 1939, R. Meinentzhagen, 12800 (NHML) [marked with black dot on slide]. Paratypes: 5♂, 8♀, same data as holotype (NHML).

**Etymology:** Specific name is derived from the host genus, *Regulus* Cuvier, 1800, meaning "little king", with the ending "*cida*" from Latin "*caedo*" for "cut, hew, kill".

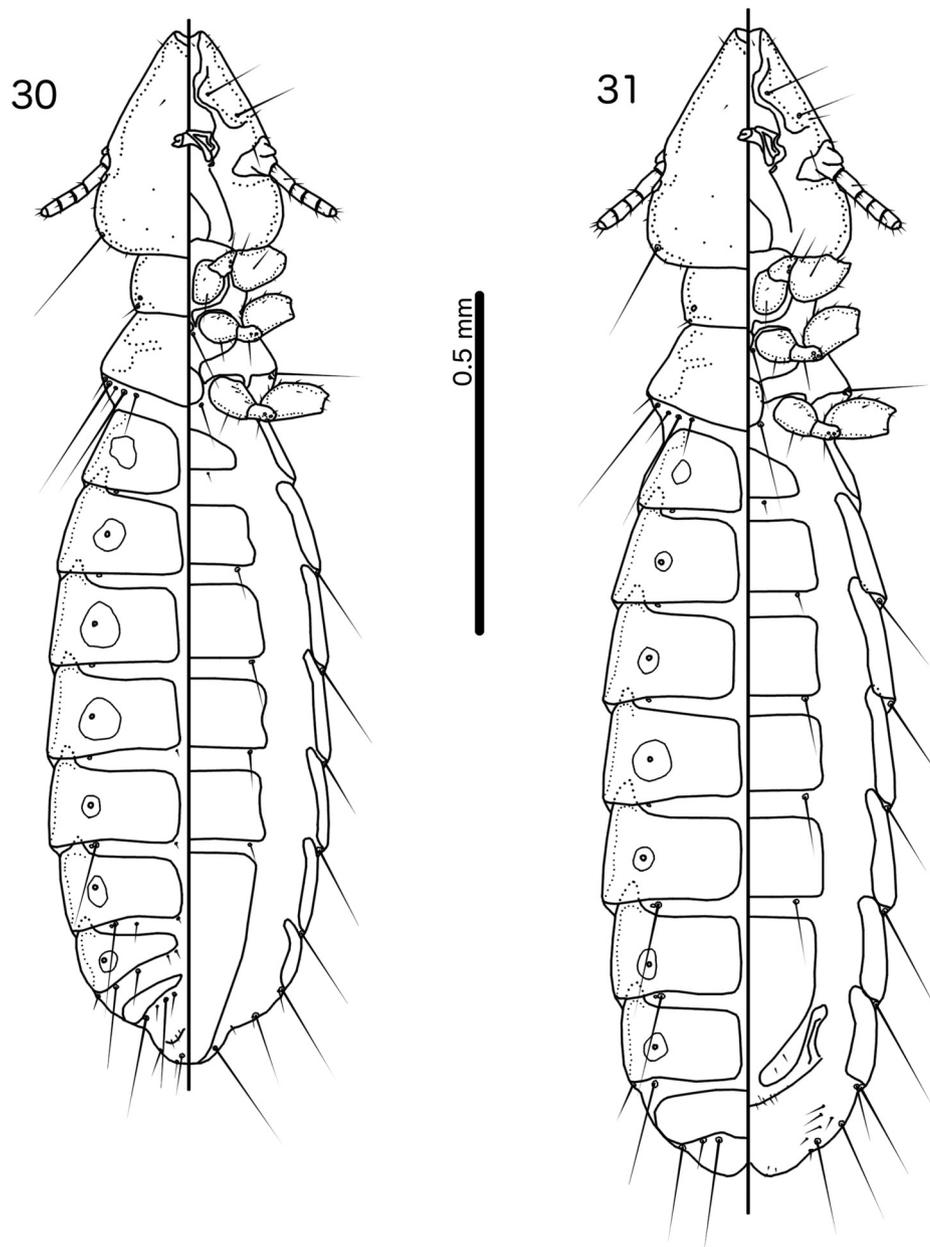
**Diagnosis:** The head shape of *Brueelia regulicida* n. sp. is reminiscent of that of members of the *B. conocephala* species group (see above). However, there are few other characters that suggest a close relationship between *B. regulicida* and the *B. conocephala* species group. Overall, *B. regulicida* is most similar *Brueelia sittacola* n. sp. These two species can be separated by the following characters: *tps* present on male tergopleurite VII in *B. regulicida* (Fig. 30), but absent in *B. sittacola* (Fig. 9); *ps* present on abdominal segment III in both sexes in *B. regulicida* (Figs 30–31), but absent in *B. sittacola* (Figs 9–10); frons narrower in *B. regulicida* (Fig. 32) than in *B. sittacola* (Fig. 12); basal apodeme narrower in *B. regulicida* (Fig. 33) than in *B. sittacola* (Fig. 13); mesosome shorter, with a smaller gonopore and more extensive rugose area in *B. regulicida* (Fig. 34) than in *B. sittacola* (Fig. 14).

**Remarks:** One reviewer of this manuscript suggested that the clear areas around the spiracle openings may be a result of the mounting process. All examined specimens appear to have been cleared with KOH and then dyed red, which may have highlighted the differences in pigmentation between these cleared areas and the rest of the tergopleurite. We have seen many other species of *Brueelia*-complex lice in which similar clear areas occur, even in specimens that have not been cleared with KOH or dyed red. It is therefore unclear whether or not these clear areas actually exist. We include these circles here, as this is how the specimens examined appear, but note that in fresh specimens, these circles may be absent.

### *Brueelia* from Paridae

Two species of *Brueelia* have previously been described from hosts in the Paridae: *Brueelia longifrons* Carriker, 1956, from *Poecile atricapilla* (Linnaeus, 1766), and *Brueelia weberi* Balát, 1982 from *Parus major major* Linnaeus, 1758.

Both Kéler (1939) and Séguy (1944) mentioned *Cyanistes caeruleus* (Linnaeus, 1758) as a host of *Acronirmus gracilis*



**Fig. 30–31.** *Brueelia regulicida* n. sp. ex *Regulus calendula grinnelli* Palmer, 1897. **30** – male habitus, dorsal and ventral views. **31** – female habitus, dorsal and ventral views

(Burmeister, 1838). Kéler (1939) ascribed this host record to L. Picaglia, but we have been unable to locate this record in Picaglia's publications. Kéler believed that Picaglia's specimen derived from a straggler. We do not consider *C. caeruleus* as a host of any known species of *Brueelia*.

Rékási (1993) listed *Brueelia breieri* [= misspelling for *breueri* Balát, 1955] from both *C. caeruleus* and *Sitta europaea* Linnaeus, 1758. This species normally occurs on European greenfinch *Chloris chloris* (Linnaeus, 1758), and this host record was likely a misidentification, but we have not seen Rékási's material.

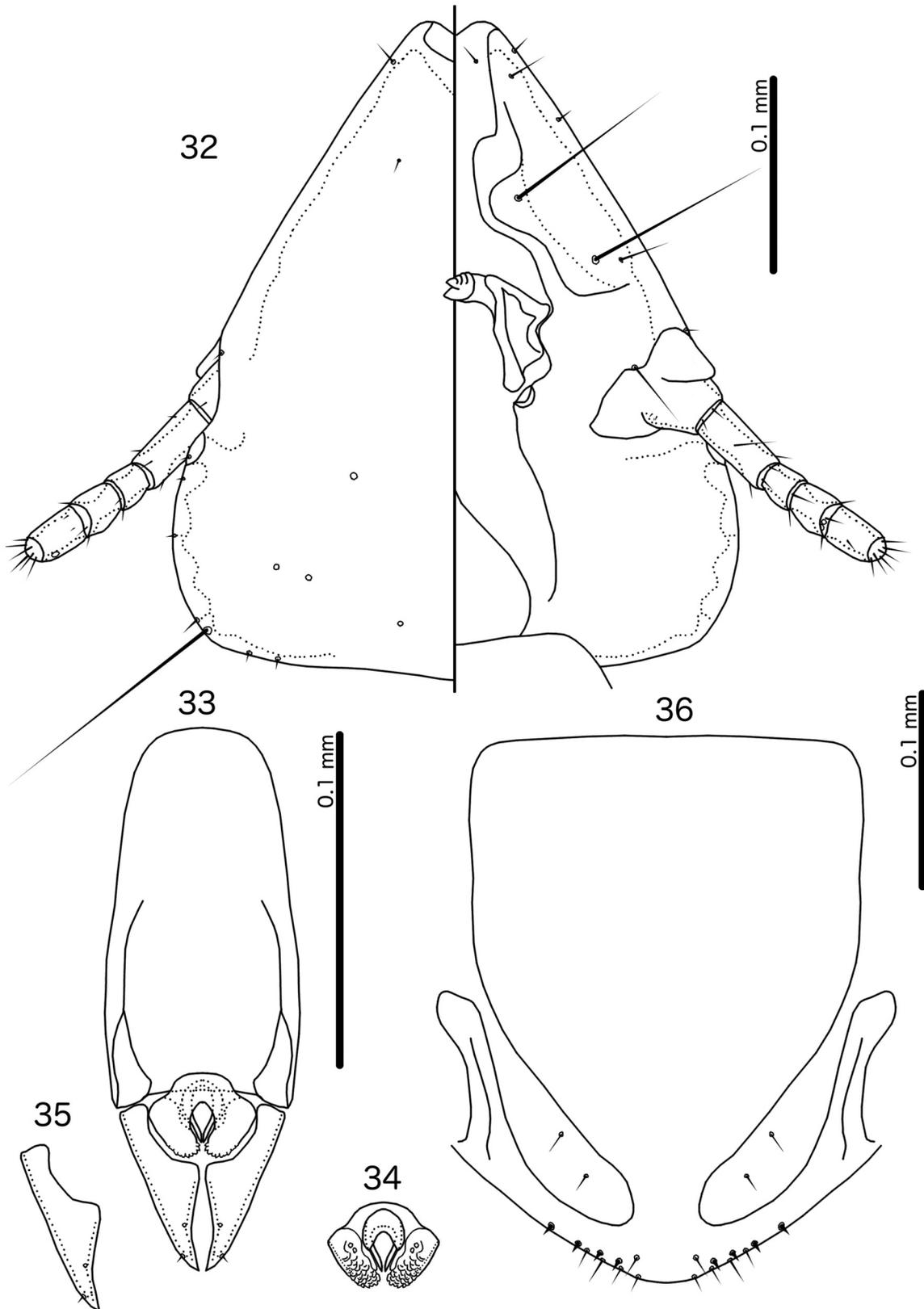
#### ***Brueelia longifrons* Carriker, 1956**

*Brueelia longifrons* Carriker, 1956: 81

**Type host:** *Parus atricapillus longicaudatus* Harris = *Poecile atricapillus atricapillus* (Linnaeus, 1766) – black-capped chickadee.

**Type locality:** Douglas County, Kansas, United States.

**Remarks:** Carriker (1956) placed *Brueelia longifrons* near *Brueelia vulgata* (Kellogg, 1896). No direct comparison with *B. vulgata* was provided, and it is unclear what Carriker meant when he stated that *B. longifrons* "resembl[es] *vulgata* in some ways, [but] differs very much in others". At the time, *Brueelia*



**Fig 32–36.** *Brueelia regulicida* n. sp. ex *Regulus calendula grinnelli* Palmer, 1897. 32 – male head, dorsal and ventral view. 33 – male genitalia, dorsal view. 34 – male mesosome, ventral view. 35 – male paramere, dorsal view. 36 – female subgenital plate and vulval margin, ventral view

*vulgata* was a catch-all name for a variety of *Brueelia*-species from across the world (e.g. Geist 1931), and this statement may simply refer to the fact that both species are relatively slender.

The broadly flattened frons of *B. longifrons* (see Carriker 1956: fig. 61) resembles that of some *Brueelia* species from North American emberizids, as well as *Brueelia* from boreal motacillids, such as *B. ferianci* Balát, 1955, or *B. corydalla* Timmermann, 1950. We have not examined the holotype and only known specimen of *B. longifrons*. However, the large differences in head shape between this species and all other species of *Brueelia* known from parid hosts separates *B. longifrons* from all species treated here. We have seen several specimens (located at UMSP) of an undescribed species of *Brueelia* from the same host, *Poecile atricapillus* (Linnaeus, 1766), which is not conspecific with *B. longifrons*. This material is too poorly preserved to be described, but appears more similar to *B. juniperi* or *B. johnsoni* than to *B. longifrons*.

### *Brueelia weberi* Balát, 1982

*Brueelia weberi* Balát, 1982: 44.

**Type host:** *Parus major major* Linnaeus, 1758.

**Type locality:** Serrahn, Kreis Neustrelitz, East Germany.

**Remarks:** Balát (1982) stated that *B. weberi* is closest to *Brueelia conocephala* (Blagoveshtchensky, 1940). The stated differences between these two species are in the proportions of the head, the width of the clypeo-labral suture, the shape of the conus, the width of the antennae, and the width of the body, with *B. weberi* being more slender than *B. conocephala*. The lateral margins of the preantennal area are entirely straight in *B. conocephala* (Fig. 1), but slightly concave in the anterior end in *B. weberi*. Finally, the parameres of *B. weberi* have a more concave lateral margin than in *B. conocephala*.

We have not seen any material of *B. weberi*, but it seems that the species is indeed close to *B. conocephala*. In addition, *B. oxyrhyncha* n. sp. and possibly *B. regulicida* n. sp. also belong to this species group. The range of this species group may thus span three different host families from China, Azerbaijan, Central Europe, and North America. Notably, Balát (1982) collected this species from several host individuals in both Germany and Czech Republic, suggesting that this species may be more common than the other species of *Brueelia* known from the Paridae. No *Brueelia* were found on great tits we have examined in Sweden (n = 28 birds, unpubl. data).

### *Brueelia juniperi* n. sp. (Figs 37–43)

**Type host:** *Baeolophus ridgwayi ridgwayi* (Richmond, 1902) – juniper titmouse.

**Type locality:** Clover Creek, Tooele County, Utah, United States.

**Description, both sexes:** Head flat dome-shaped (Fig. 39), lateral margins of preantennal head slightly convex, frons concave. Marginal carina narrow, of roughly even width, deeply

displaced and widened at osculum. Ventral anterior plate absent. Head chaetotaxy as in Fig. 39. Preantennal nodi slender, not bulging. Preocular nodi much larger than postocular nodi. Marginal temporal carina narrow, irregular. Gular plate slenderly lanceolate. Thoracic and abdominal segments as in Figs 37–38. Pigmentation overall pale yellow; marginal and marginal temporal carinae and head nodi slightly darker.

**Male:** Thoracic and abdominal chaetotaxy as in Fig. 37; *aps* present on tergopleurites VI–VII; *tps* absent on tergopleurite VII. Basal apodeme roughly rectangular, slightly wider distally (Fig. 40). Proximal mesosome broad rounded (Fig. 41). Mesosomal lobes broad, oblique; rugose area extensive on ventral surface of distal end; 2 *pms* sensilla on each side later-posterior to gonopore. Gonopore with flat anterior margin, concave posterior margin, and convex lateral margins. Penile arms long, not reaching distal margin of mesosome. Parameres elongate, slender; *pst1–2* as in Fig. 42. Measurements (n = 14, except AW where n = 13): TL = 1.47–1.61 (1.54); HL = 0.34–0.36 (0.35); HW = 0.27–0.29 (0.28); PRW = 0.17–0.19 (0.18); PTW = 0.25–0.31 (0.28); AW = 0.35–0.40 (0.38).

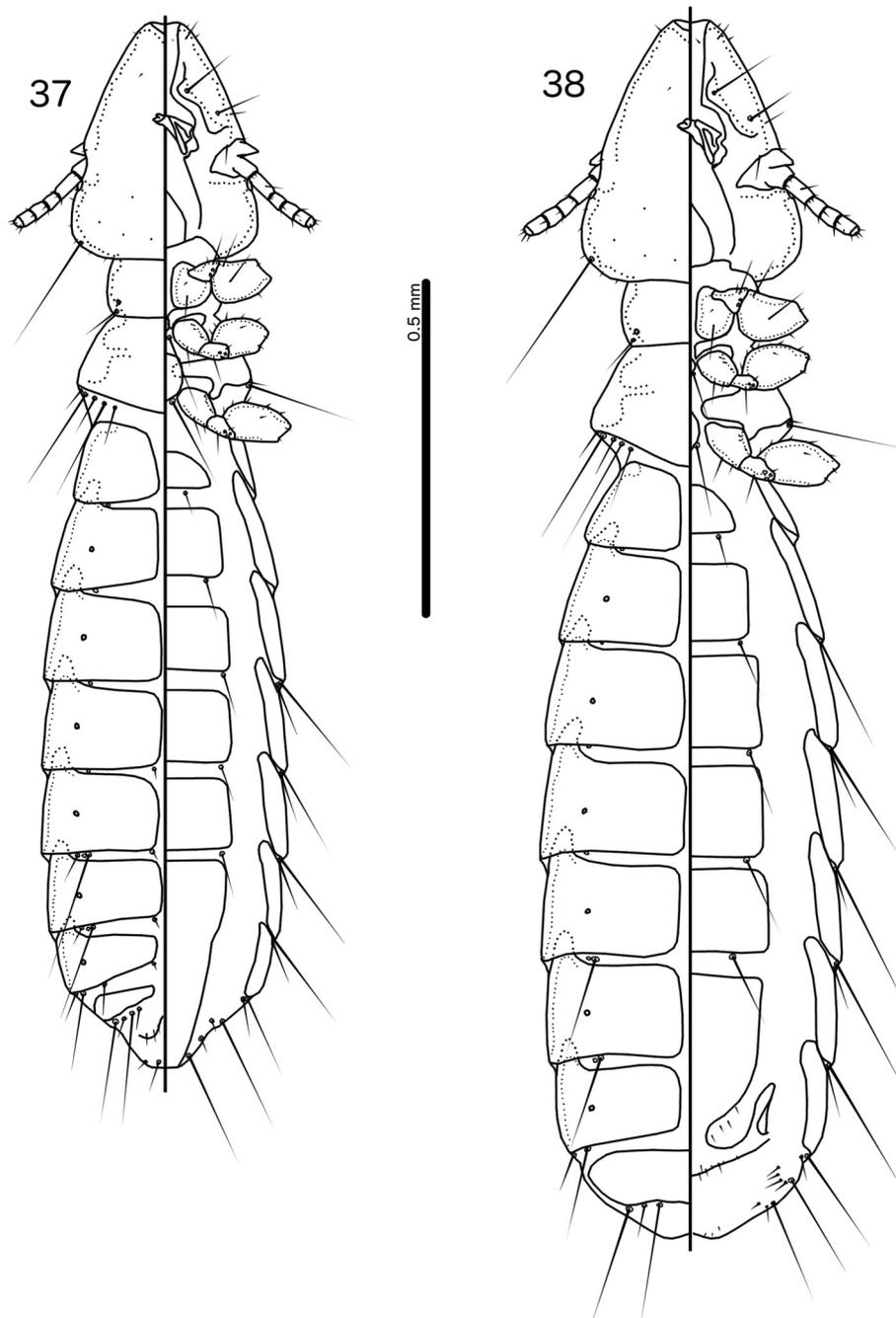
**Female:** Thoracic and abdominal chaetotaxy as in Fig. 38. Subgenital plate broad, narrowing only in distal end, and connection to cross-piece broad (Fig. 43). Vulval margin convergent to median point (Fig. 43), with 2–4 short, slender *vms* and 2–3 short, thorn-like *vss* on each side; 4–5 short, slender *vos* on each side of subgenital plate; distal 1 *vos* median to *vss*. Measurements (n = 46, except TL where n = 43, and PRW and AW where n = 45): TL = 1.64–1.96 (1.75); HL = 0.36–0.39 (0.37); HW = 0.29–0.31 (0.30); PRW = 0.19–0.21 (0.19); PTW = 0.28–0.33 (0.30); AW = 0.39–0.45 (0.42).

**Type material** [host as *Parus inornatus*]: Holotype ♂, Clover Creek, Tooele County, Utah, United States, 24 Apr. 1969, 09046 (NHML). Paratypes: 1 ♀, same data as holotype (NHML); 9 ♂, 27 ♀, same data as holotype (PIPeR); 1 ♂, 1 ♀, Broons Canyon, Tooele County, Utah, United States, Mar. 1967, E. and E. Branch, EE-074510 (PIPeR); 5 ♂, 20 ♀, Ditto Dunes, D.P.G., Tooele County, Utah, United States, 1 May 1969, E. and E. Branch, D.P.G., 09076 (PIPeR).

**Etymology:** Specific name derived from the scientific name for the juniper, *Juniperus* Linnaeus, 1758, which is the main habitat of the host.

**Diagnosis:** *Brueelia juniperi* n. sp. is most similar to *B. johnsoni* n. sp., but can be separated by the following characters: *aps* present on male tergopleurites VI–VII in *B. juniperi* (Fig. 37), but absent in *B. johnsoni* (Fig. 44); ventral anterior plate absent in *B. juniperi* (Fig. 39), but present in *B. johnsoni* (Fig. 46); gonopore with flat anterior margin in *B. juniperi* (Fig. 41), but rounded anterior margin in *B. johnsoni* (Fig. 48); parameres long and slender in *B. juniperi* (Fig. 42), but shorter and stockier in *B. johnsoni* (Fig. 49); female subgenital plate differs in shape between *B. juniperi* (Fig. 43) and *B. johnsoni* (Fig. 50).

**Remarks:** Host given as *Parus inornatus* "Plain Titmouse" on slides. This species was split into the mainly Californian *Bae-*



**Fig. 37–38.** *Brueelia juniperi* n. sp. ex *Baeolophus ridgwayi ridgwayi* (Richmond, 1902). **37** – male habitus, dorsal and ventral views. **38** – female habitus, dorsal and ventral views

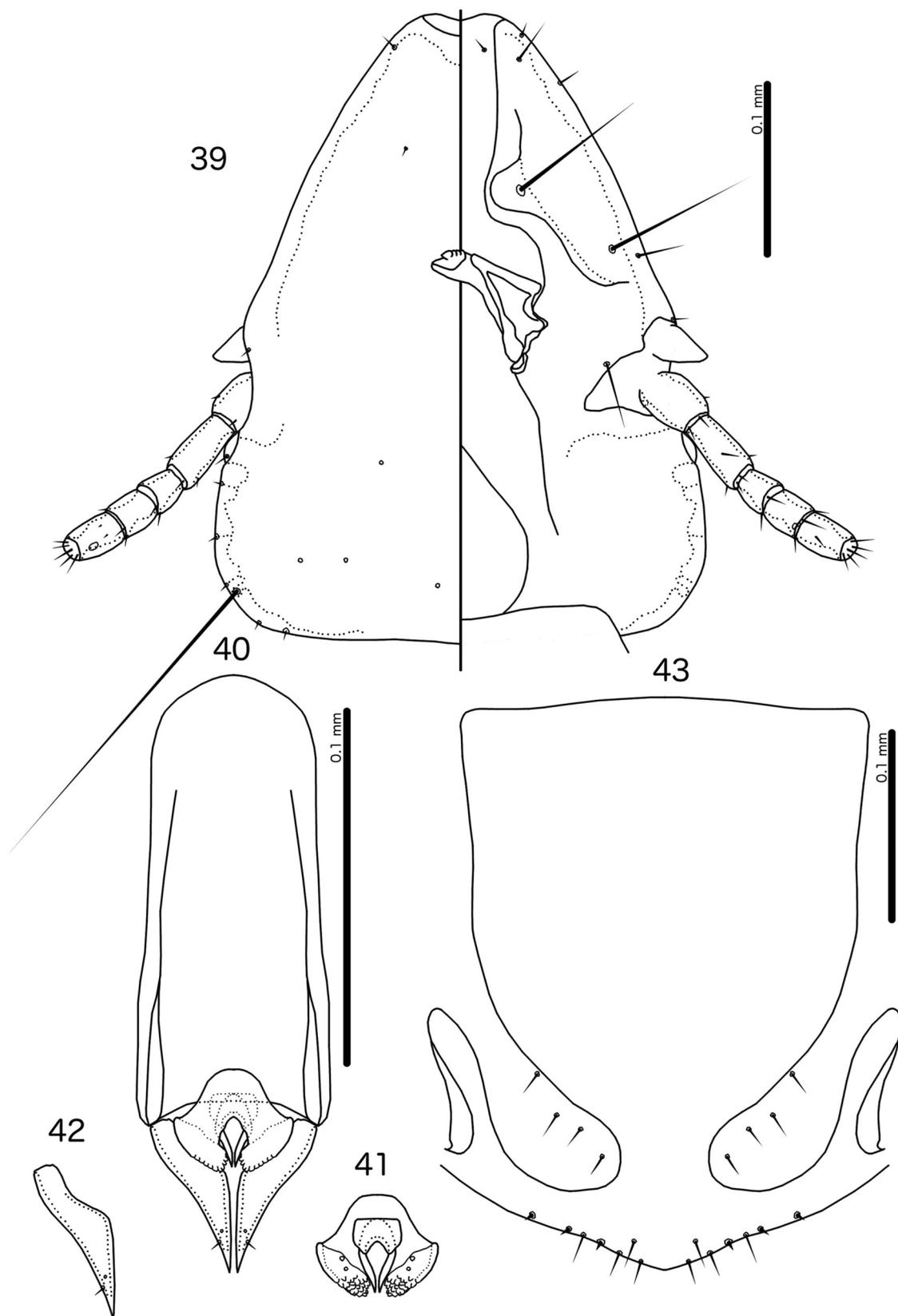
*olophus inornatus* (Gambel, 1842) and *B. ridgwayi* (Gambel, 1842) from the Great Basin and more eastern areas by the American Ornithologists' Union (1997). The latter is the correct name for the host species living in the type locality of *B. juniperi* n. sp.

***Brueelia johnsoni* n. sp.** (Figs 44–50)

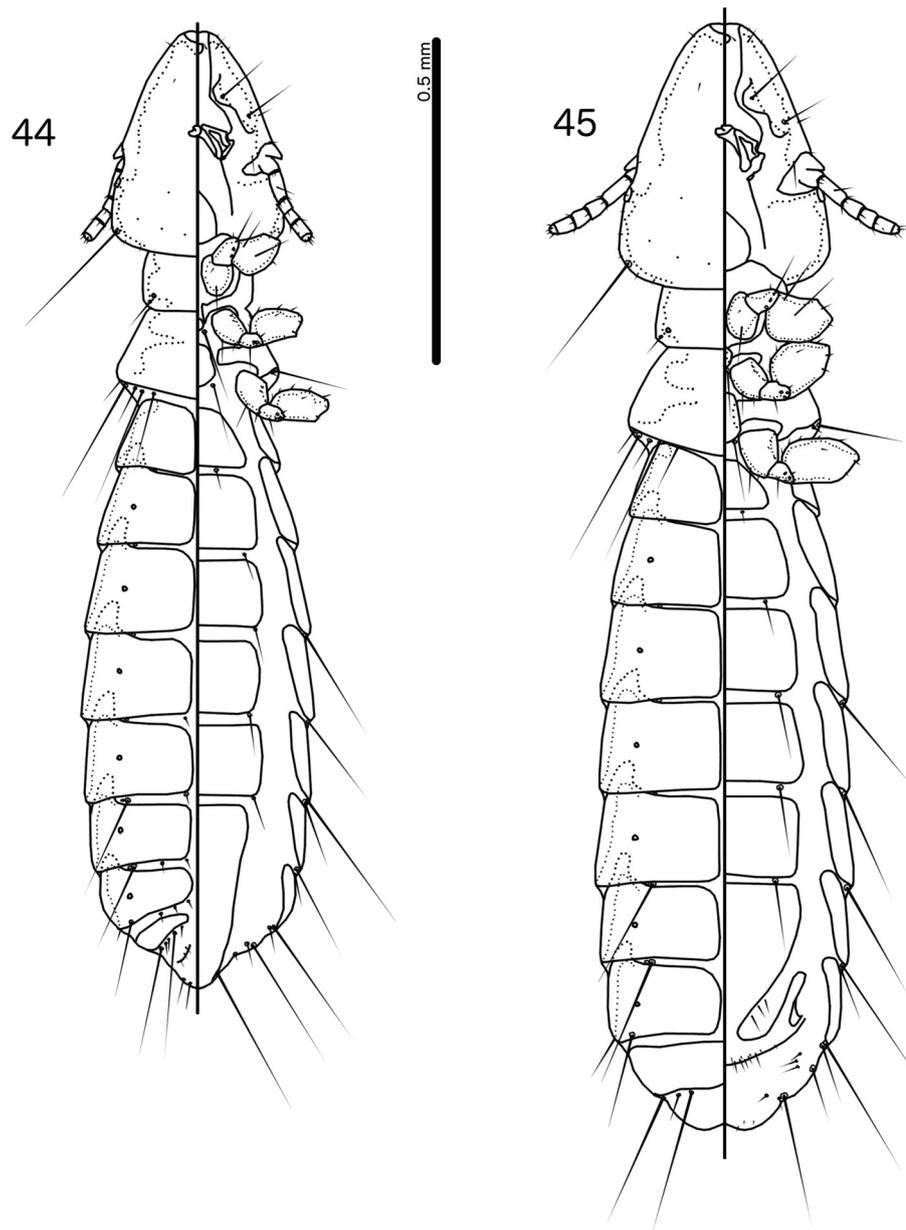
**Type host:** *Poecile sclateri eidos* (Peters, 1927) – Mexican chickadee.

**Type locality:** Las Vacas, Coahuila, Mexico.

**Description, both sexes:** Head convex dome-shaped (Fig. 46), lateral margins of preantennal area convex, frons slightly concave. Marginal carina of moderate width, median margin slightly irregular, deeply displaced and much widened at frons. Ventral anterior plate present, rounded. Head chaetotaxy as in Fig. 46. Preantennal nodi wide, not bulging. Preocular nodi larger than postocular nodi. Marginal temporal carina moderate, irregular. Gular plate slenderly lanceolate. Thoracic and abdominal segments as in Figs 44–45. Base pigmentation pale



**Fig. 39–43.** *Brueelia juniperi* n. sp. ex *Baeolophus ridgwayi ridgwayi* (Richmond, 1902). **39** – male head, dorsal and ventral view. **40** – male genitalia, dorsal view. **41** – male mesosome, ventral view. **42** – male paramere, dorsal view. **43** – female subgenital plate and vulval margin, ventral view



**Fig. 44–45.** *Brueelia johnsoni* n. sp. ex *Poecile sclateri eidos* (Peters, 1927). **44** – male habitus, dorsal and ventral views. **45** – female habitus, dorsal and ventral views

yellow, with marginal and marginal temporal carina, head nodi, and proepimera pale brown.

**Male:** Thoracic and abdominal chaetotaxy as in Fig. 44; *aps* absent on all segments; *tps* present on tergopleurite VII; 2 *ps* on each side of abdominal segment VI. Basal apodeme slender, roughly rectangular, but slightly constricted at mid-length (Fig. 47). Proximal mesosome broad, rounded trapezoidal (Fig. 48). Mesosomal lobes rather slender; rugose area limited to median and distal margins; 2 *pmes* sensilla on each side, lateral to gonopore. Gonopore widely crescent-shaped. Penile arms short, not reaching distal margin of mesosome. Parameres stout, slightly elongate distally; *pst1–2* as in Fig. 49. Meas-

urements ( $n = 3$ , except TL where  $n = 2$ ): TL = 1.28–1.43; HL = 0.31–0.33; HW = 0.25–0.27; PRW = 0.16–0.17; PTW = 0.21–0.26; AW = 0.29–0.34.

**Female:** Thoracic and abdominal chaetotaxy as in Fig. 45. Subgenital plate triangular with convex lateral margins (Fig. 50), connection to cross-piece narrow. Vulval margin gently rounded with hint of flattened median point (Fig. 50), with 3–5 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 ( $n = 11$ ): TL = 1.36–1.72 (1.58); HL = 0.31–0.37 (0.35); HW = 0.26–0.30 (0.28); PRW = 0.16–0.19 (0.18); PTW = 0.23–0.28 (0.26); AW = 0.33–0.42 (0.38).

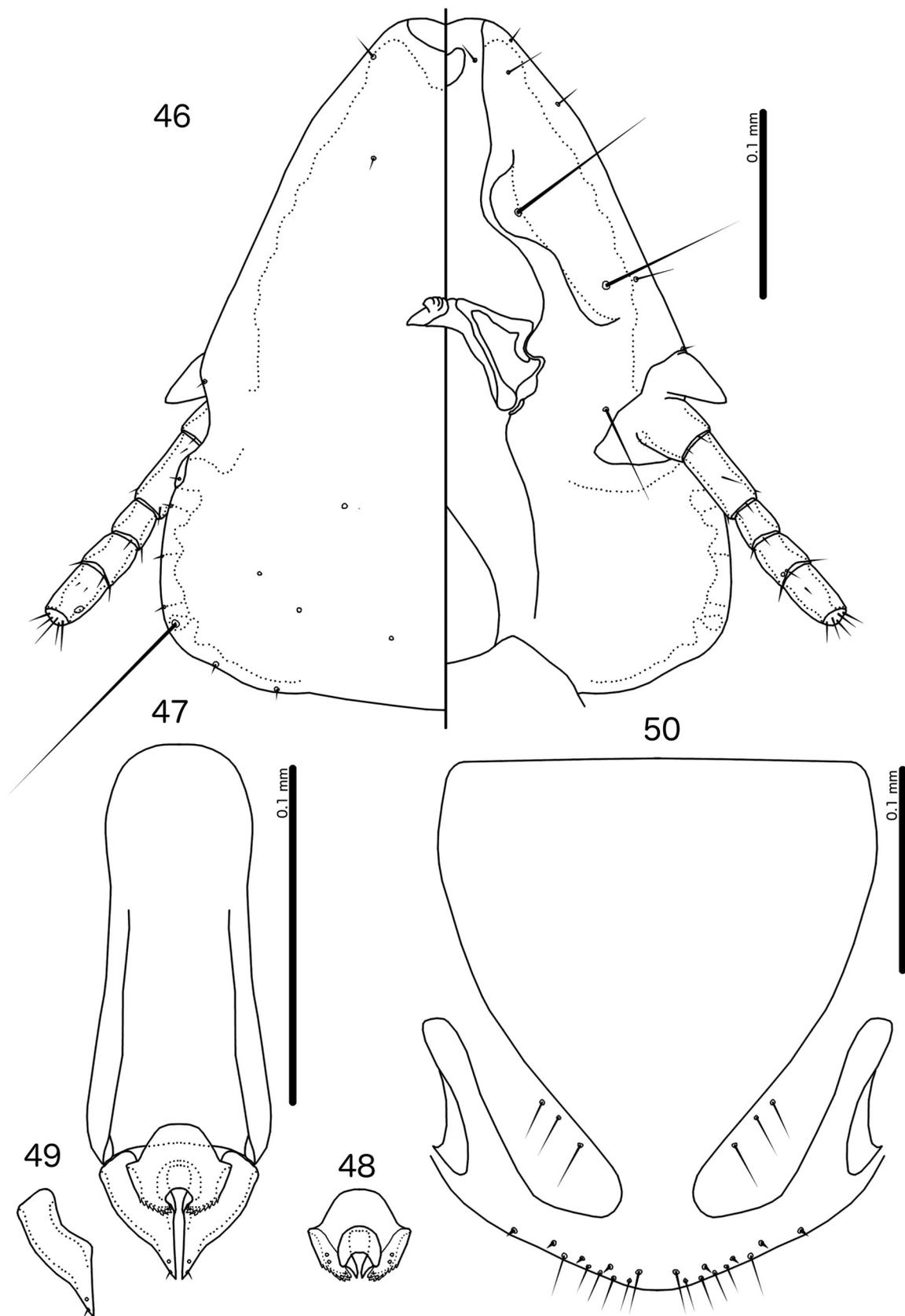


Fig. 46–50. *Brueelia johnsoni* n. sp. ex *Poecile sclateri eidos* (Peters, 1927). 46 – male head, dorsal and ventral view. 47 – male genitalia, dorsal view. 48 – male mesosome, ventral view. 49 – male paramere, dorsal view. 50 – female subgenital plate and vulval margin, ventral view

**Type material:** Holotype ♂, Las Vacas, Coahuila, Mexico, 3 Nov. 1958, C.A. Ely, CAE-1054 (NHML). Paratypes: 1 ♀, same data as holotype (NHML); 1 ♂, 1 ♀, same data as holotype (PIPeR); 1 ♂, 3 ♀, same data as holotype except CAE-1053 (PIPeR); 4 ♀, same locality, 28 Oct. 1958, C.A. Ely, CAE-1007 (PIPeR); 2 ♀, same locality, 6 Jul. 1958, C.A. Ely, CAE-608 (PIPeR); 2 ♀, same locality, 27 Jul. 1958, C.A. Ely, CAE-727 (PIPeR).

**Etymology:** *Brueelia johnsoni* is named in honour of Dr. Kevin P. Johnson (Illinois Natural History Survey, USA), in recognition of his many and varied contributions to the study of the Phthiraptera, and for good friendship and cooperation over the years.

**Diagnosis:** *Brueelia johnsoni* n. sp. is most similar to *Brueelia sittacola* n. sp. These species can be separated by the following characters: *tps* present on male tergopleurite VII in *B. johnsoni* (Fig. 44), but absent in *B. sittacola* (Fig. 9); 2 *ps* on each side of male abdominal segment VI in *B. johnsoni* (Fig. 44), but 1 *ps* on each side in *B. sittacola* (Fig. 9); ventral anterior plate present in *B. johnsoni* (Fig. 46), but absent in *B. sittacola* (Fig. 11); proximal mesosome rounded trapezoidal in *B. johnsoni* (Fig. 48), but rounded in *B. sittacola* (Fig. 13).

***Brueelia nazae* n. sp.** (Figs 51–57)

**Type host:** *Parus cinereus caschmirensis* Hartert, 1905 – cinereous tit.

**Type locality:** Peshawar, Khyber Pakhtunkhwa, Pakistan.

**Description, both sexes:** Head flat dome-shaped (Fig. 53), lateral margins of preantennal head convex, frons flattened to slightly rounded. Marginal carina moderate in width, irregular, deeply displaced and much widened at osculum. Ventral anterior plate absent. Head chaetotaxy as in Fig. 53. Preantennal nodi wide, not bulging. Pre- and postocular nodi large. Marginal temporal carina narrows conspicuously posteriorly. Gular plate broadly lanceolate. Thoracic and abdominal segments as in Figs 51–52. Base pigmentation pale yellowish brown, with marginal carina, marginal temporal carina, margins of antennal sockets, and head nodi medium to dark brown; gular plate, metepisterna, proepimera, lateral tergopleurites, female tergopleurite VIII, and subgenital plates pale brown. FIGURE 51–52

**Male:** Thoracic and abdominal chaetotaxy as in Fig. 51; *aps* present on tergopleurite V, but absent on tergopleurite IV. Basal apodeme long, roughly rectangular, with slight constriction in proximal half (Fig. 54); proximal margin diffuse in examined material and here illustrated approximately. Proximal mesosome trapezoidal to roughly square-shaped (Fig. 55). Mesosomal lobes broad and long, with rugose area extensive over distal ends; 2 *pms* sensilla on each side postero-lateral to gonopore. Gonopore broad and long, arched. Penile arms long, reaching to or almost to distal end of mesosome. Parameres stout, slightly elongate distally (Fig. 56); *pst1–2* as in Fig. 56. Measurements (n = 5): TL = 1.38–1.46; HL = 0.33–0.35; HW = 0.27–0.28; PRW = 0.17–0.18; PTW = 0.26–0.28; AW = 0.27–0.35.

**Female:** Thoracic and abdominal chaetotaxy as in Fig. 52. The lateral margins of the anterior subgenital plate are convergent, but the degree of convergence differs somewhat between specimens; a typical outline is shown in Fig. 57. Connection between subgenital plate and cross-piece moderate. Vulval margin gently curving, somewhat flattened in median section (Fig. 57), with 4–6 short, slender *vms* and 2–3 short, thorn-like *vss* on each side; 2–4 short, slender *vos* on each side of subgenital plate; distal 1 *vos* roughly median to *vss*. Measurements (n = 27, except TL where n = 24 and AW where n = 21): TL = 1.46–1.73 (1.60); HL = 0.34–0.39 (0.37); HW = 0.28–0.32 (0.30); PRW = 0.18–0.21 (0.19); PTW = 0.27–0.32 (0.29); AW = 0.31–0.43 (0.36).

**Type material:** Holotype ♂, Peshawar, [Khyber Pakhtunkhwa] Pakistan, Mar. 1937, R. Meinertzhagen, 9218 (NHML) [marked with black dot on slide]. Paratypes: 3 ♂, 16 ♀, same data as holotype (NHML); 1 ♂, 11 ♀, same locality, Mar. 1937, R. Meinertzhagen, 9189–90 (NHML).

**Etymology:** The specific epithet is in honor of the phthirapterologist Dr. Saima Naz (University of Karachi, Pakistan), in recognition of her work with the louse fauna in Pakistan and her many exemplary illustrations of new louse species.

**Diagnosis:** *Brueelia nazae* n. sp. is most similar to *B. picea* n. sp. These species can be separated by the following characters: *ss* absent on male tergopleurite V in *B. nazae* (Fig. 51), but present in *B. picea* (Fig. 58); head proportionately more slender in *B. nazae* (Fig. 53) than in *B. picea* (Fig. 60); mesosomes distinct (*cf.* Figs 55, 62); gonopore roughly trapezoidal in *B. picea* (Fig. 62), but arched in *B. nazae* (Fig. 55); female subgenital plate generally with bulging lateral margins that converge in proximal end in *B. nazae* (Fig. 57), but with roughly parallel lateral margins in *B. picea* (Fig. 64).

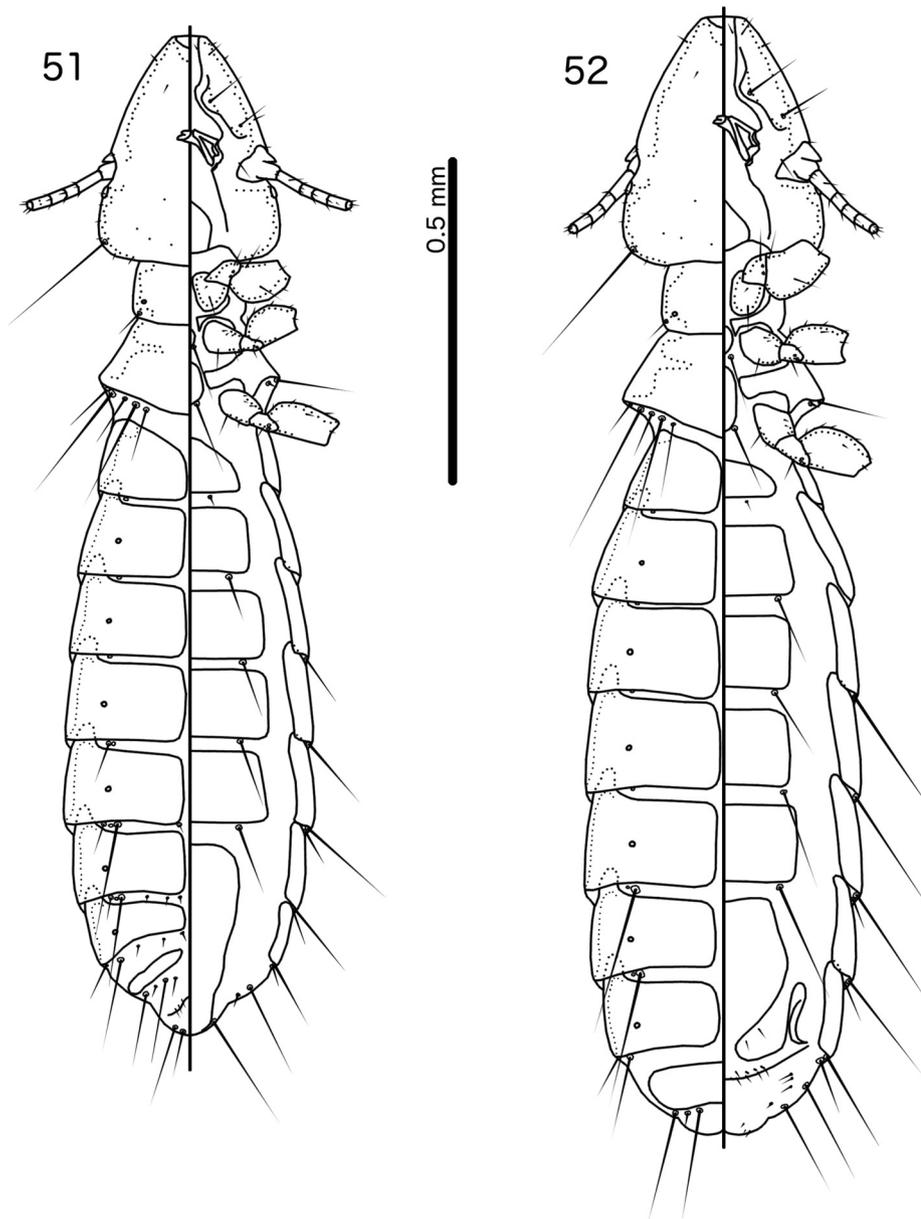
**Remarks:** *Parus cinereus* Vieillot, 1818, is often considered a separate species from *P. major* (*e.g.* Kvist *et al.* 2003; Päckert *et al.* 2005; Eck and Martens 2006), despite their genetic similarities (Gill *et al.* 2005; Johansson *et al.* 2013). The species limits in *Parus* are complicated (summarized in Päckert and Martens 2008). We here follow Clements *et al.* (2017), which separates these taxa into different species. Note that regardless of host systematics, each host taxon in this complex is parasitized by a different species of *Brueelia*.

No material has been seen from either of the other two proposed host species in this complex, *Parus minor* Temminck et Schlegel, 1848, and *P. bokharensis* Lichtenstein, 1823, nor from the only other member of the genus, *Parus monticolus* Vigors, 1831. Collections from these hosts would be very valuable for trying to understand the evolutionary history of *Brueelia* on *Parus* tits.

***Brueelia picea* n. sp.** (Figs 58–64)

**Type host:** *Parus major excelsus* Buvry, 1857 – great tit.

**Type locality:** Morocco.

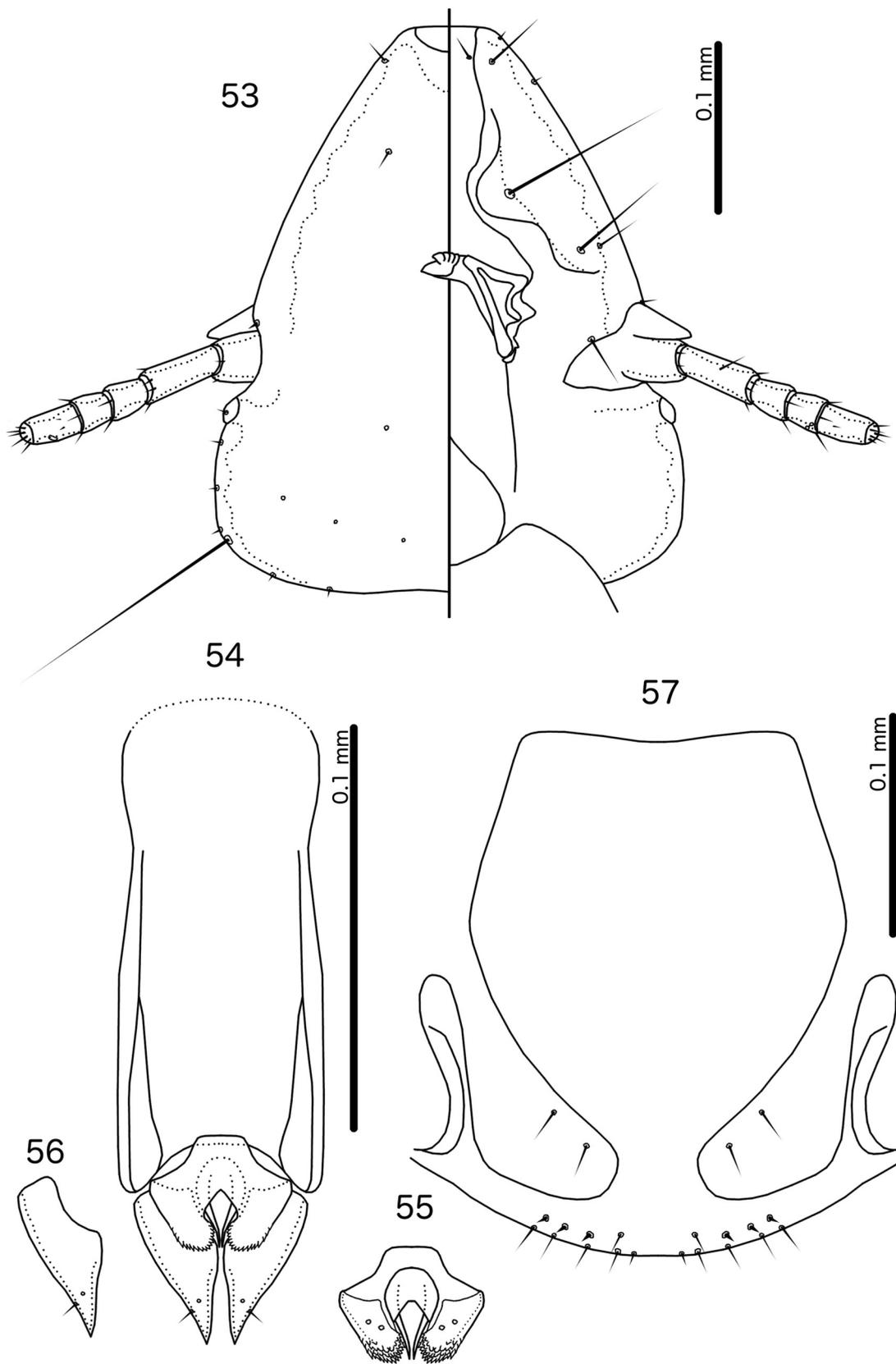


**Fig. 51–52.** *Brueelia nazae* n. sp. ex *Parus cinereus cacshmirensis* Hartert, 1905. **51** – male habitus, dorsal and ventral views. **52** – female habitus, dorsal and ventral views

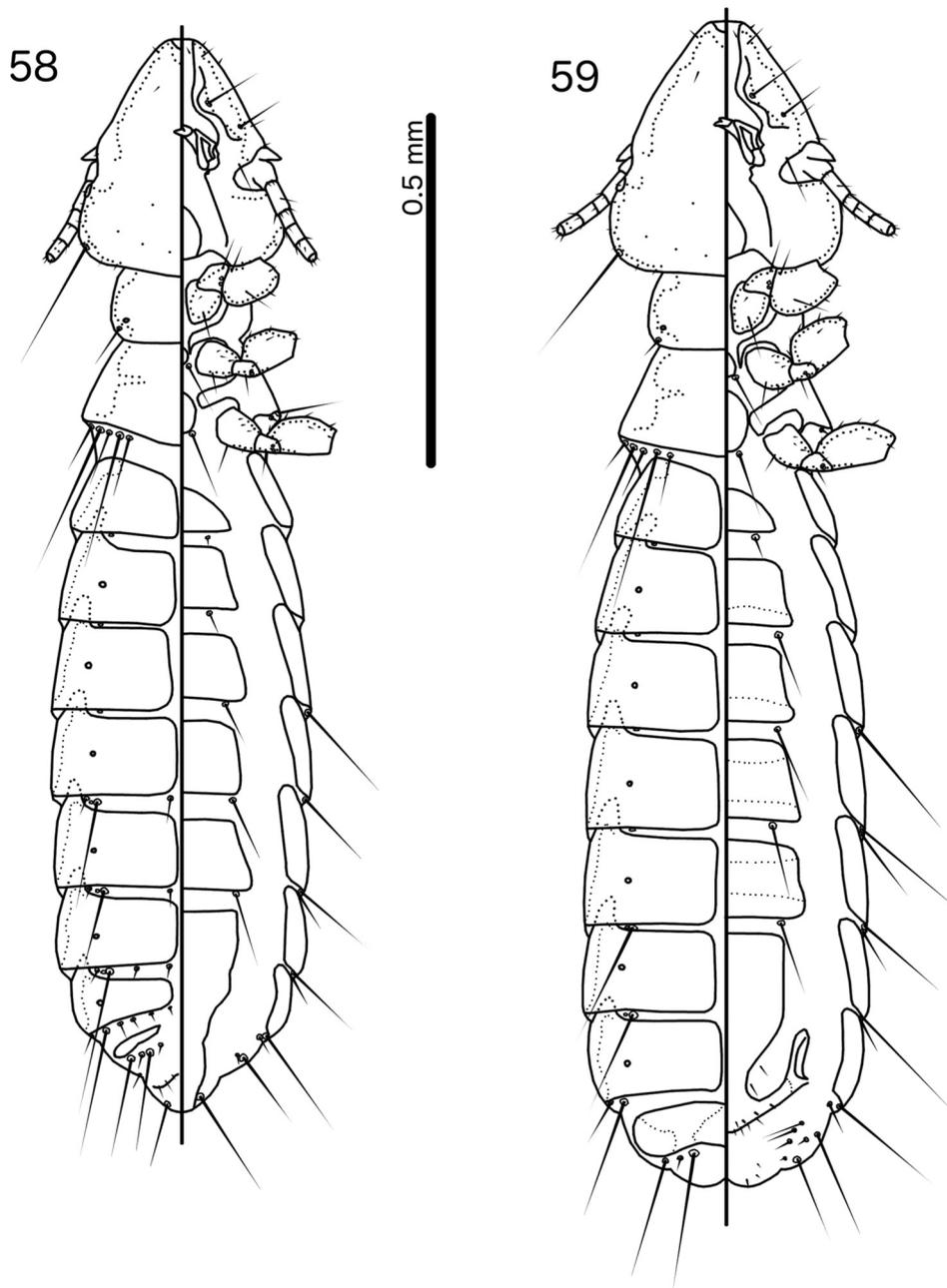
**Description, both sexes:** Head broad, rounded triangular (Fig. 60), lateral margins of preantennal area straight or slightly convex, frons flattened to slightly concave. Marginal carina broad, irregular, deeply displaced and much widened at osculum. Ventral anterior plate absent. Head chaetotaxy as in Fig. 60. Preantennal nodi wide, bulging. Pre- and postocular nodi large. marginal temporal carina broad, very irregular. Gular plate lanceolate. Thoracic and abdominal segments as in Figs 58–59. Base pigmentation faintly yellow, translucent; lateral head margins, head nodi, margins of antennal socket, proepimera, metepisterna, pleural thickenings, and lateral tergopleurites dark brown; gular plate, meso- and metasternal plates, and subgenital plates medium brown or darker; sternal

plates II–IV with medium brown posterior margin; sternal plates V–VI with medium brown anterior and posterior margins; female tergopleurite VIII with medium brown median and lateral sections, as in Fig. 59.

**Male:** Thoracic and abdominal chaetotaxy as in Fig. 58; *aps* present on tergopleurite V, but absent on tergopleurite IV. Basal apodeme rounded proximally, with constriction around mid-point (Fig. 61). Proximal mesosome rounded trapezoidal, lateral margins slightly concave (Fig. 62). Mesosomal lobes longer than wide, small; rugose area slight, limited to distal margin; 2 *pmes* sensilla on each side postero-lateral to gonopore. Gonopore with somewhat rectangular anterior margin and shallowly concave posterior margin. Penile arms short.



**Fig. 53–57.** *Brueelia nazae* n. sp. ex *Parus cinereus caeshmirensis* Hartert, 1905. **53** – male head, dorsal and ventral view. **54** – male genitalia, dorsal view. **55** – male mesosome, ventral view. **56** – male paramere, dorsal view. **57** – female subgenital plate and vulval margin, ventral view



**Fig. 58–59.** *Brueelia picea* n. sp. ex *Parus major excelsus* Buvry, 1857. **58** – male habitus, dorsal and ventral views. **59** – female habitus, dorsal and ventral views

Parameres stout, slightly elongate distally (Fig. 63); *pst1*–2 as in Fig. 63. Measurements (n = 10): TL = 1.37–1.53 (1.45); HL = 0.31–0.34 (0.33); HW = 0.27–0.29 (0.28); PRW = 0.17–0.19 (0.18); PTW = 0.26–0.28 (0.27); AW = 0.33–0.38 (0.35).

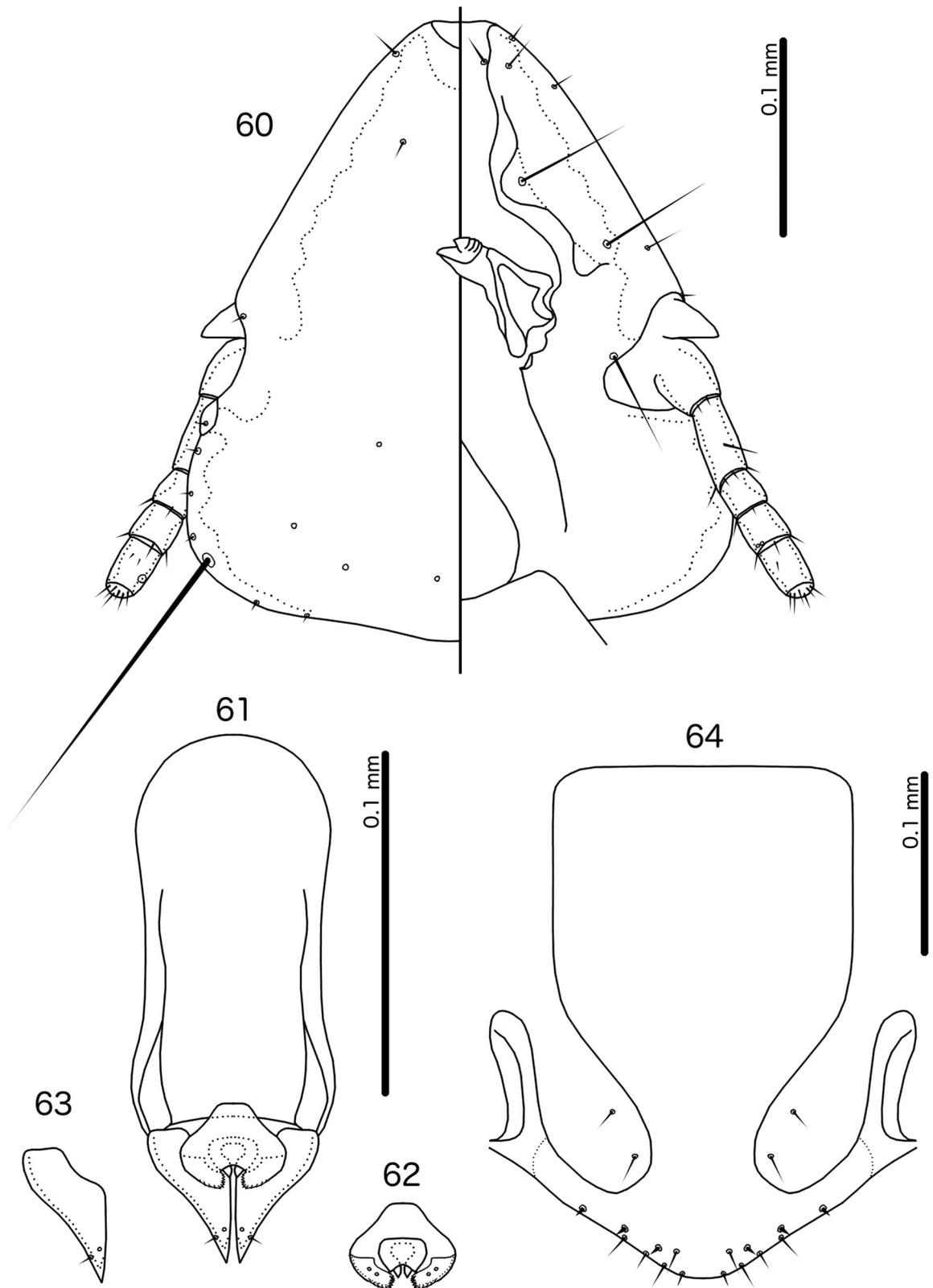
**Female:** Thoracic and abdominal chaetotaxy as in Fig. 59. Subgenital plate slender, more or less rounded rectangular, with very broad connection to cross-piece (Fig. 64). Vulval margin highly convergent into broadly rounded or slightly flattened median point (Fig. 64), with 3–4 short, slender *vms* and 2–3 short, thorn-like *vss* on each side; 3–4 short, slender *vos* on each side of submarginal plate; distal 1 *vos* median to median

*vss*. Measurements (n = 21): TL = 1.58–1.84 (1.71); HL = 0.35–0.38 (0.36); HW = 0.31–0.34 (0.32); PRW = 0.20–0.22 (0.21); PTW = 0.29–0.32 (0.31); AW = 0.36–0.45 (0.41).

**Type material:** Holotype ♂, Morocco, Nov. 1938, R. Meinertzhagen, 12003 (NHML) [encircled in black on slide]. Paratypes: 9♂, 21♀, same data as holotype (NHML).

**Etymology:** The specific epithet is derived from Latin "*piceus*" for "pitch black", referring to the very dark lateral margins of the abdomen and head.

**Diagnosis:** *Brueelia picea* n. sp. is most similar to *B. nazae* n. sp. These species can be separated by the following charac-



**Fig. 60–64.** *Brueelia picea* n. sp. ex *Parus major excelsus* Buvry, 1857. **60** – male head, dorsal and ventral view. **61** – male genitalia, dorsal view. **62** – male mesosome, ventral view. **63** – male paramere, dorsal view. **64** – female subgenital plate and vulval margin, ventral view

ters: *ss* present on male tergopleurite V in *B. picea* (Fig. 58), but absent in *B. nazae* (Fig. 51); head proportionately broader in *B. picea* (Fig. 60) than in *B. nazae* (Fig. 53); proximal mesosome, mesosomal lobes and gonopore have different shapes in the two species (Figs 55, 62); female subgenital plate generally with bulging lateral margins that converge in proximal end in *B. nazae* (Fig. 57), but with more or less parallel lateral margins in *B. picea* (Fig. 64); vulval margin strongly arched in *B. picea* (Fig. 64), but more gently rounded or with flattened median section in *B. nazae* (Fig. 57).

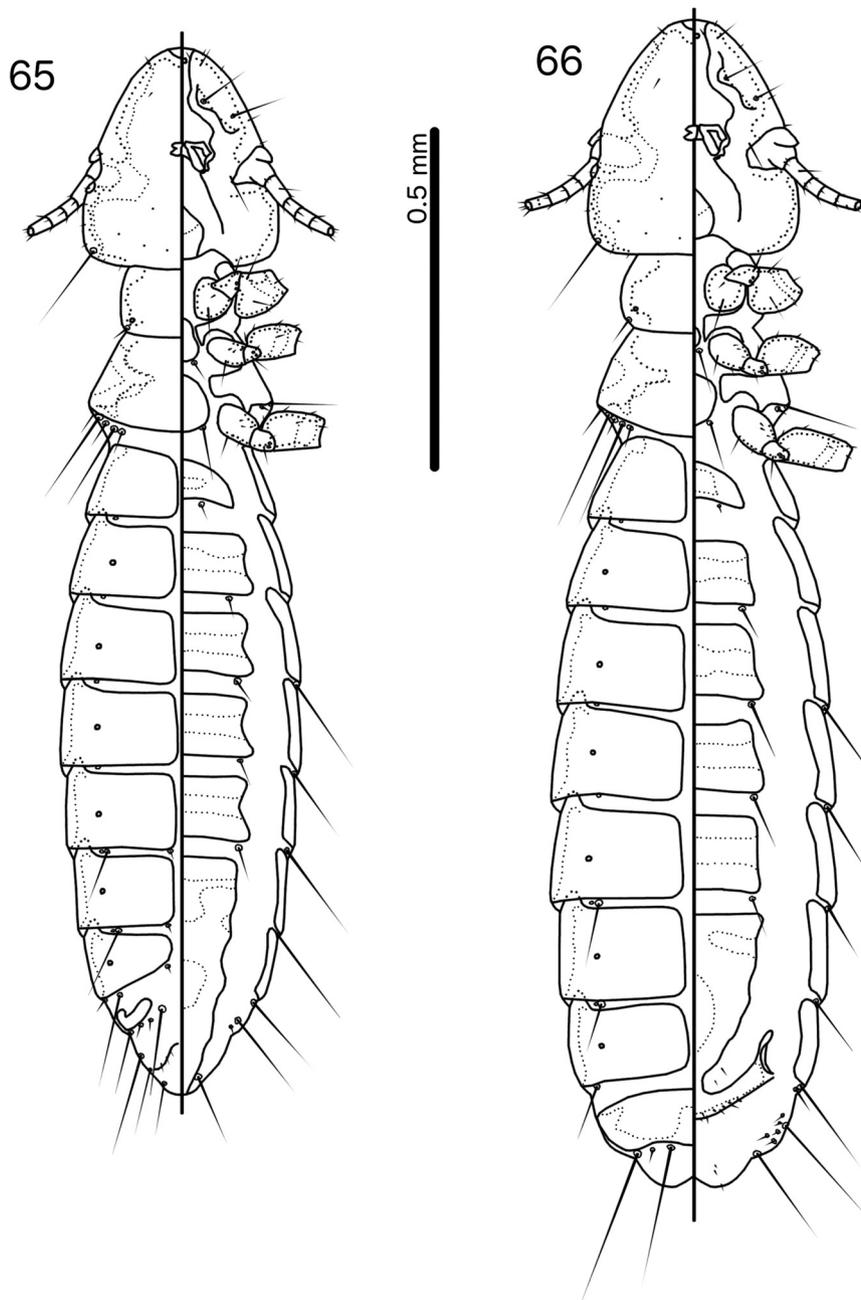
**Remarks:** Slide with holotype and paratypes also contain three nymphs.

*Brueelia mpumalangensis* n. sp. (Figs 65–71)

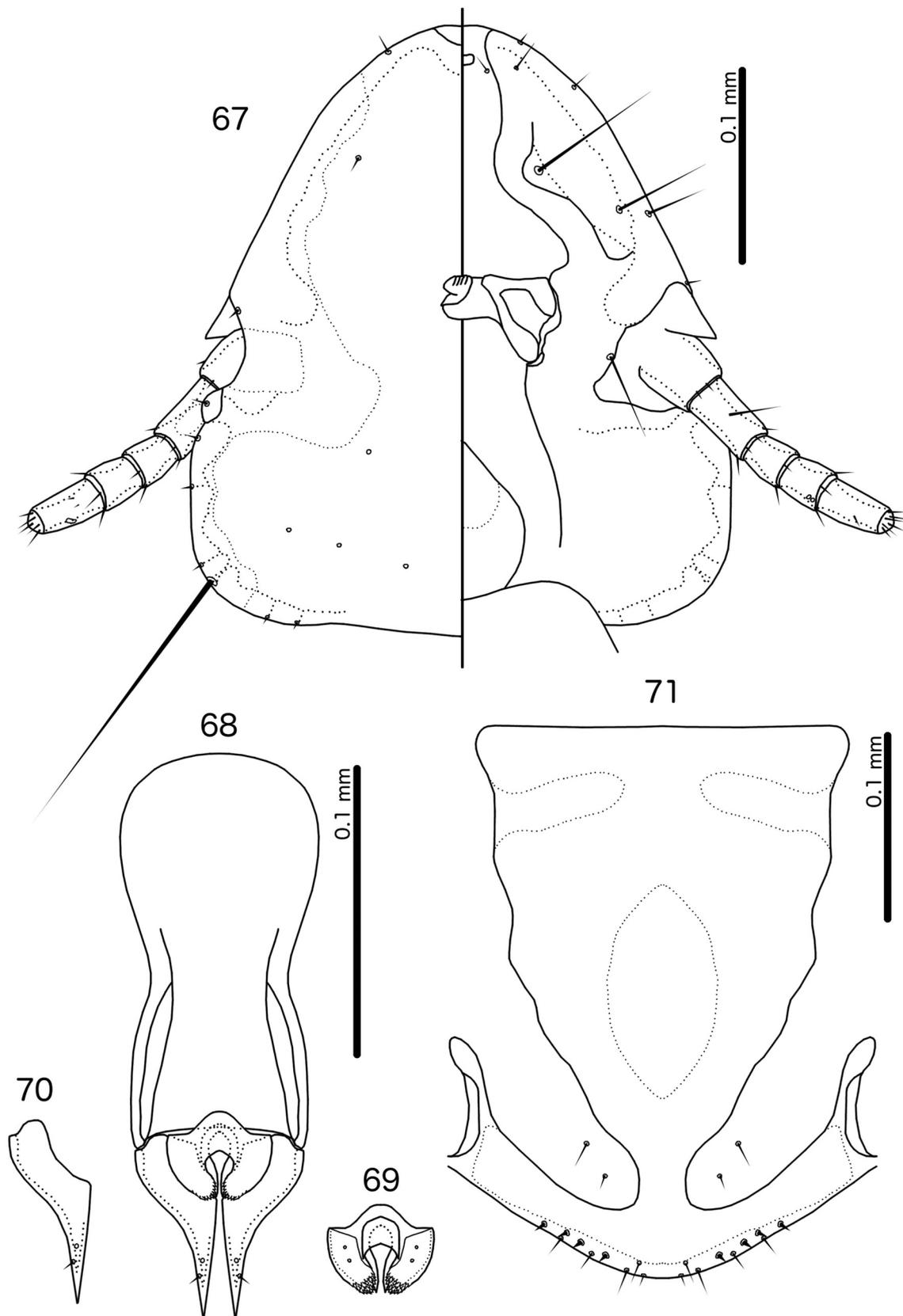
**Type host:** *Melaniparus niger niger* (Vieillot, 1818) – southern black tit.

**Type locality:** Mpumalanga, South Africa.

**Description, both sexes:** Head broad, rounded triangular (Fig. 67), lateral margins of preantennal area convex, frons



**Fig. 65–66.** *Brueelia mpumalangensis* n. sp. ex *Melaniparus niger niger* (Vieillot, 1818). **65** – male habitus, dorsal and ventral views. **66** – female habitus, dorsal and ventral views



**Fig. 67–71.** *Brueelia mpumalangensis* n. sp. ex *Melaniparus niger niger* (Vieillot, 1818). **67** – male head, dorsal and ventral view. **68** – male genitalia, dorsal view. **69** – male mesosoma, ventral view. **70** – male paramere, dorsal view. **71** – female subgenital plate and vulval margin, ventral view

rounded. Marginal carina moderate in width, with more or less even median margin; deeply displaced but not widened as osculum. Ventral anterior plate small, roughly rectangular. Head chaetotaxy as in Fig. 67. Preocular nodi large, bulging. Pre- and postocular nodi similar in size. Marginal temporal carina wide, irregular. Gular plate lanceolate. Thoracic and abdominal segments as in Figs 65–66. Base pigmentation translucent, however areas of head outlined by narrow dotted line in Fig. 67 dark brown; proepimera, metepisterna, meso- and metasternal plates, nodi and bands of legs, pleural thickenings, anterior and posterior margins of sternal plates also dark brown.

**Male:** Thoracic and abdominal chaetotaxy as in Fig. 65; *aps* absent on all tergopleurites. Pigmentation of subgenital plates as in Fig. 65. Basal apodeme rounded anteriorly, with deep constriction at about mid-length (Fig. 68). Proximal mesosome small, gently rounded (Fig. 69). Mesosomal lobes long but slender; rugose area extensive over medio-distal section; 2 *pms* sensilla on each side lateral to gonopore. Gonopore arched, with rounded or slightly pointed proximal margin. Penile arms long, reaching to or near distal margin of mesosome. Parameres much elongate distally (Fig. 70); *pst1–2* as in Fig. 70. Measurements ( $n = 2$ , except PRW where  $n = 1$ ): TL = 1.42–1.47; HL = 0.32; HW = 0.28–0.29; PRW = 0.18; PTW = 0.24–0.27; AW = 0.28–0.34.

**Female:** Thoracic and abdominal chaetotaxy as in Fig. 66. Pigmentation of subgenital plates as in Fig. 71. Subgenital plate irregularly triangular, with narrow connection to cross-piece (Fig. 71). Vulval margin strongly arched (Fig. 71), with 3–4 short, slender *vms* and 4–5 short, thorn-like *vss* on each side; 3 short, slender *vos* on each side of subgenital plate; distal 1 *vos* median to *vss*. distal margin of crosspiece translucent. Measurements ( $n = 3$ , except TL where  $n = 2$ ): TL = 1.59–1.66; HL = 0.33–0.37; HW = 0.30–0.31; PRW = 0.19–0.20; PTW = 0.27–0.28; AW = 0.38–0.39.

**Type material:** Holotype ♂, Mpumalanga, South Africa, 6 Aug. 1998, K. Johnson (NHML). Paratypes: 1 ♀, same data as holotype (NHML); 1 ♀, same data as holotype, voucher specimen for sequence Brsp.Panig.2.10.1999.5 (PIPeR); 1 ♂, Khuta Maji, elev. 1170 ft., –10.8667, 33.45, Vwaza Marsh, Vwaza Wildlife Reserve, Malawi, 13 Oct. 2009, J.D. Weckstein, host MLW-3645, FMNH-468312, specimen FMNH-INS-0000-029-054, voucher specimen for sequence Brsp.Pani.2.9.2011.32 (FMNH).

**Etymology:** The specific epithet is derived from the type locality.

**Diagnosis:** *Brueelia mpumalagensis* n. sp. belongs to the same strikingly pigmented group as *B. plocea* (Lakshminarayana, 1968), *B. cantans* Sychra [in Sychra *et al.*], 2010a, *B. quelea* Sychra et Barlev [in Sychra *et al.*], 2010b, and *B. aguilarae* Gustafsson et Bush, 2017. The most similar species to *B. mpumalagensis* appears to be *B. aguilarae*. These species can be separated by the following characters: *aps* absent on male tergopleurites VI–VII in *B. mpumalagensis* (Fig. 65), but present in *B. aguilarae*; preantennal area broadly

rounded in *B. mpumalagensis* (Fig. 67), but narrowly trapezoidal in *B. aguilarae*; proximal mesosome very small in *B. mpumalagensis* (Fig. 69), but larger in *B. aguilarae*; female subgenital plate with roughly oval, isolated translucent area in distal end in *B. mpumalagensis* (Fig. 71), but with slender translucent area continuous with near-transversal translucent band in anterior end in *B. aguilarae*.

## Discussion

Chewing lice in the *Brueelia*-complex typically have low infestation rates (*e.g.* Ash 1960; Fowler and Williams 1985; Mey 1994), especially among small-bodied hosts. Thus, it is not surprising that there are few reports of lice in this complex from hosts in the Paridae, Regulidae, and Sittidae (Touleshkov 1962, 1974; Rékási 1993; Bush *et al.* 2016). *Brueelia*-complex lice were not found in most surveys of hosts in these three families (*e.g.* Blagoveshtchensky 1951; Balát 1958, 1981; Ash 1960; Rékási 1973; Mey 1977; Ilieva 2005; Adam 2007; Adam *et al.* 2009; Dik *et al.* 2013, 2017).

Formerly, two species of *Brueelia* were known to parasitize hosts in the Paridae, and only one species was known to parasitize hosts in the Sittidae. Our descriptions add an additional four species from hosts in the Paridae, four species from hosts in the Sittidae, and the first record of *Brueelia* from a regulid host. To date, *Brueelia*-complex lice are known to be associated with just over 13% of the 96 species in these three families. Future sampling of birds in these families are quite likely to reveal undiscovered louse diversity.

The morphological affinities of *Brueelia* species described here suggest a complicated evolutionary history. Intriguingly, some of the hosts in these three families appear to be parasitized by closely related species of *Brueelia*, even though the hosts themselves are not closely related (Barker 2004; Barker *et al.* 2004; Gill *et al.* 2005; Alström *et al.* 2006, 2013; Johansson *et al.* 2013). Two general patterns can be discerned. However, it must be stressed that the vast majority of species in each of these host families have never been sampled for *Brueelia*-complex lice, and these patterns may be artifacts of the low number of *Brueelia* species known from these host families.

**Pattern 1:** Species of *Brueelia* on closely related hosts are morphologically distinct and do not appear to be closely related. For instance, the *Brueelia* species from large, mainly ground-living, species of nuthatches (*B. ragusica* n. sp. and *B. kabulica* n. sp.) are very different from the species from smaller, tree-living, hosts in the *B. conocephala* group in head shape and other characters. In particular *B. kabulica* is similar to several undescribed species of *Brueelia* from finches and other hosts (Gustafsson and Bush, *in prep.*). Like *B. kabulica*, these other *Brueelia* species are all from host species that occur in arid or mountainous areas in Central Asia and the Middle East. More research is needed to determine whether these similarities in morphology are due to a close relationship or to convergence.

In another example, we here describe two species of *Brueelia* from hosts in the Great Tit complex: *B. nazae* n. sp. and *B. picea* n. sp. Neither of these species appears to be closely related to the only other *Brueelia* known from a host in the same complex, *B. weberi*. *Brueelia weberi* and *B. picea* are recorded from geographically separated subspecies of the same host species, *Parus major* Linnaeus, 1758. *Brueelia nazae* is from a closely related host species that is often regarded as conspecific with *P. major* (see Remarks under *P. nazae*). Notably, the two *Brueelia* species from warmer regions (Morocco, Pakistan) are more similar to each other than either is to the more boreal species from Central Europe.

**Pattern 2:** Closely related species of *Brueelia* are found on distantly related hosts. For example, *Brueelia conocephala*, *B. weberi*, *B. oxyrhyncha* n. sp., and possibly *B. regulicida* n. sp. form a group of *Brueelia* species characterized by their peculiar head shape. Only two other known species of *Brueelia* have similar head shapes: *Brueelia balati* Krištofik, 1999, and *Brueelia chalcomitrae* Najer et Sychra [in Najer *et al.*], 2012. The *Brueelia conocephala* group thus occurs on at least two distantly related host families (Sittidae, Paridae) and potentially on another three (Regulidae, Remizidae, Nectarinidae).

In another example, all three known *Brueelia* species from North American parids may be more closely related to *Brueelia* species found on other host families than they are to each other. Notably, neither *B. johnsoni* n. sp. nor *B. juniperi* n. sp. is particularly similar to the only other *Brueelia* species known from a North American chickadee, *Brueelia longifrons* Carriker, 1956. This latter species is more similar to *Brueelia* from boreal pipits and wagtails (Motacillidae). Similarly, both *Brueelia sittaicola* n. sp. and *B. johnsoni* both exhibit a complete lack of *aps* in males, which is a rare condition in *Brueelia* (Gustafsson and Bush 2017). However, this condition is also found in *Brueelia anamariae* Cicchino, 1980 from *Troglodytes aedon* (Vieillot, 1809) and in some undescribed species of *Brueelia* from North American cardinalids (Gustafsson and Bush, *in prep.*). *Brueelia juniperi* has *aps* on male tergopleurites VI–VII, suggesting that this species is not close to *B. johnsoni* and *B. sittaicola*. Both the abdominal chaetotaxy and the shape of the male genitalia of *B. juniperi* are reminiscent of those of some undescribed species of *Brueelia* from North American finches and sparrows (Gustafsson and Bush, *in prep.*).

In yet another example, *Brueelia mpumalangensis* n. sp. from an Africa parid is likely closely related to species on mainly African ploceids and estrildids, and was placed close to some of these species in the phylogeny of Bush *et al.* (2016; as *Brueelia* sp. from *Parus niger*, fig. 3e, clade I-2). *Brueelia mpumalangensis* may be the result of a successful host switch from a ploceid host to a parid host. Both *Melaniparus niger* and the host of the closest relative of *B. mpumalangensis* in the phylogeny of Bush *et al.* (2016) are known to participate in mixed-species flocks (Thompson and Ferguson 2007).

Movements of lice between unrelated host species that participate in mixed-species flocks could potentially explain many of the unusual host relationships within the genus

*Brueelia*. Members of all three host families treated here regularly participate in mixed-species flocks in both boreal Eurasia (Morse 1978; Mönkkönen *et al.* 1996), North America (Morse 1970; Hutto 1987), southern Asia (Chen and Hsieh 2002; Zou *et al.* 2011) and Africa (Thompson and Ferguson 2007). Opportunities for lateral transmission between *e.g.* sittiid and parid hosts could thus be frequent. The effects of participation of hosts in mixed-species flocks on the distribution and relationships of chewing lice is poorly known. Different genera of lice on shorebirds behave very differently despite the opportunities for transfer between hosts being even more frequent in shorebirds than in perching birds (Gustafsson and Olsson 2012, 2017; Yamagishi *et al.* 2014). Ecological research focusing on the movement of lice among birds participating in mixed-species host flocks is sorely needed.

Finally, these patterns suggest that *Brueelia*-complex lice on closely related hosts cannot be assumed to be closely related. This has implications for both revisions of *Brueelia*-complex lice, and for descriptions of new species. It is often convenient to circumscribe a revision based on hosts associations, and to compare new species only with those parasitizing the same host family. However, examples such as those outlined above show that this may not be sufficient. In both new descriptions and revisions, species should be compared with other species that are morphologically similar, regardless of host associations, rather than only species that parasitize the same host family.

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