European Journal of Taxonomy 790: 1–52
https://doi.org/10.5852/ejt.2022.790.1641
ISSN 2118-9773
www.europeanjournaloftaxonomy.eu
2022 · Gustafsson D.R. *et al.*

Monograph

urn:lsid:zoobank.org:pub:E3ED109B-70C8-414D-A245-6E3590C9E5B5

New species of *Philopterus* Nitzsch, 1818 (Ischnocera: Philopteridae), with notes on *Cypseloecus* Conci, 1941

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Abstract. We describe and illustrate eight new species of chewing lice in the genus *Philopterus* Nitzsch, 1818, parasitic on hosts in the bird families Cardinalidae, Chloropseidae, Hirundinidae, Icteridae, Motacillidae, Paridae, and Vangidae from China, Peru, South Africa, Thailand, and the USA. They are: *Philopterus coriaceus* sp. nov. from *Molothrus oryzivorus oryzivorus* (Gmelin, 1788); *P. hebes* sp. nov. from *Chloropsis aurifrons inornata* Kloss, 1918 and *C. cochinchinensis kinneari* Hall & Deignan, 1956; *P. micropunctatus* sp. nov. from *Anthus hodgsoni* Richmond, 1907; *P. afropari* sp. nov. from *Melaniparus cinerascens cinerascens* (Vieillot, 1818); *P. pseudhirundo* sp. nov. from *Pseudhirundo griseopyga* Sundevall, 1850; *P. sinensis* sp. nov. from *Hemipus picatus capitalis* (Horsfield, 1840); *P. stansburyensis* sp. nov. from *Pheucticus melanocephalus melanocephalus* (Swainson, 1827); and *P. trepostephanus* sp. nov. from *Tephrodornis virgatus fretensis* Robinson & Kloss, 1920 and *T. v. mekongensis* Meyer de Schauensee, 1946. *Philopterus hebes* sp. nov. constitutes the first record of the genus *Philopterus* from the Chloropseidae. We also provide some notes on the morphology and status of *Cypseloecus* Conci, 1941.

Keywords. Phthiraptera, Philopteridae, *Philopterus*, *Cypseloecus,* new species.

Gustafsson D.R., Najer T., Zou F. & Bush S.E. 2022. New species of *Philopterus* Nitzsch, 1818 (Ischnocera: Philopteridae), with notes on *Cypseloecus* Conci, 1941. *European Journal of Taxonomy* 790: 1–52. https://doi.org/10.5852/ejt.2022.790.1641

Introduction

The *Philopterus* complex (Phthiraptera: Ischnocera) comprises several genera of chewing lice, all of which appear to be 'head louse' ecomorphs (Johnson *et al*. 2012). The majority of the species parasitize songbirds (Passeriformes), but a small number of species parasitize hosts in the orders Coraciiformes, Galbuliformes, and Trogoniformes (Mey 2004; Gustafsson *et al*. 2019). The complex contains 224 species, of which 193 are currently placed in the genus *Philopterus* Nitzsch, 1818 sensu Mey 2004 (Price *et al*. 2003; Mey 2004; Valim 2006; Cicchino 2007; Sychra *et al.* 2010, 2011; Najer *et al.* 2012a, 2012b, 2016, 2020a; Valim & Palma 2013; Gustafsson & Bush 2014, 2017; Gustafsson *et al.* 2019).

Comparatively little work has been done to elucidate the relationships of lice within the genus *Philopterus*. In the most comprehensive treatment thus far, Złotorzycka (1964) and Złotorzycka & Lucińska (1975, 1976) separated groups based largely on host associations; they considered the genus *Philopterus* to be limited to the species parasitizing corvid hosts (Corvidae), and the genus *Cypseloecus* Conci, 1941 was limited to species parasitizing swallows (Hirundinidae). All other species were placed in the genus *Docophorulus* Eichler, 1944. Złotorzycka & Lucińska (1975, 1976) further divided both *Philopterus* and *Docophorulus* into species groups; however, these treatments only considered European species, and thus do not cover the vast majority of the diversity of this near-global group. Moreover, the morphological characters that underpin the Złotorzycka-Lucińska (1975, 1976) classification are often of dubious usefulness, which is exacerbated by the fact that few other detailed descriptions and illustrations of these species have been published. In most cases, comparisons with type specimens are necessary for identification of the species included in this classification system.

Hopkins & Clay (1952) and Price *et al.* (2003) considered most proposed genera in this group to be synonymous with *Philopterus*. However, Mey (2004) resurrected several genera based on morphological arguments, and described several new genera in the complex. Moreover, recent genetic data suggest that the genus *Philopterus*, as currently circumscribed, is paraphyletic (Najer *et al*. 2020b), with the genera *Tyranniphilopterus* Mey, 2004 and *Philopteroides* Mey, 2004 possibly nested inside *Philopterus*.

A thorough revision of the *Philopterus* complex based on morphological and genetic data is sorely needed. Such an undertaking is beyond the scope of this study; however, we identify, describe and illustrate several morphological characters that are likely to prove useful in understanding relationships among taxa in the complex. For example, the structure of the mesosome is highly variable between species, suggesting that male genital characters may be useful for finding and delimiting species groups within the genus. In contrast, most somatic and setal characters of the species in *Philopterus* are quite conserved, which may indicate evolutionary relationships among more distantly related species (see below).

Here we describe eight new species of *Philopterus* belonging to different groups within this genus. For all species, we have made a special effort to describe and illustrate key morphological characteristics to facilitate identification, and to lay a solid taxonomic foundation that can be used in the future formation of species groups within the genus *Philopterus*. We do not propose any new species groups here, but we note that the species parasitizing swallows are morphologically distinct and the genus *Cypseloecus* should be resurrected, either as a subgenus of *Philopterus* or as a separate genus.

Material and methods

Slide-mounted specimens were examined with Nikon Eclipse E600 and Nikon Eclipse TI-E light microscopes (Nikon, Tokyo, Japan). Illustrations were made through the same microscopes, fitted with a drawing tube or Andor Clara camera (Oxon, United Kingdom), then collated and edited in GIMP (www.gimp.org) and NIS Elements 4.50.00 LO (Nikon, Tokyo, Japan) using an Intuos 3 PTZ-1230 tablet (Wacom, China). Measurements were made from photos taken with the same microscope with

an Olympus DP25 camera and digital measuring software (ImageJ ver. 1.48, Wayne Rasband). All measurements are given in millimetres, as ranges (mean value, when n ≥ 10). Dimensions taken and abbreviations thereof follow Najer *et al*. (2016), and include:

ADPL = dorsal anterior plate length (at midline)
ADPW = dorsal anterior plate width
AL = abdominal length (at midline)
ANW = anterior notch width
APLL = dorsal anterior plate lateral length
AW = abdominal width (at segment V)
GL = genital length (in male)
GW = genital width (in male)
HL = head length (at midline, including hyaline margin)
HW = head width (at temples)
PAL = preantennal length
PAW = preantennal width (at base of coni)
PMCL = premarginal carina length
POL = postantennal length (at midline)
PRL = prothoracic length
PRW = prothoracic width
PTL = pterothoracic length (at midline)
PTW = pterothoracic width
SGPW = subgenital plate width (in female)
TL = total length (at midline, including hyaline margin)
TPVL = tergal plate V length
TRL = trabeculum length
TRW = trabeculum width

Morphological and setal terms and their abbreviations follow Clay (1951), Mey (1994), Najer *et al.* (2016), and Gustafsson & Bush (2017). Names for setal characters are given in *italics*, whereas abbreviations for structural characters are given in upper-case. Tergal, pleural, and sternal setae were counted on each side separately, and counts given here denote setae on one side only; these normally differ between the sides of the same specimen as well as between specimens. Note that the trichobothria and thorn-like setae of the pterothorax and trichobothria of abdominal segment VIII of both sexes are not included in the setal counts, as these are constant throughout the *Philopterus* complex. For clarity, some pleural setae were illustrated on the dorsal side; however, as the lateral margins of the abdomen are typically non-sclerotized, the exact location of these setae depends on the position of the mounted specimen. In some cases, single pleural setae are situated on the postero-lateral corner of the tergopleurite or in an unsclerotized invagination of this corner. Abbreviations for setal characters follow Gustafsson & Bush (2017) and include:

ads = anterior dorsal seta
as1–3 = anterior setae 1–3
avs1–3 = anterior ventral setae 1–3
dsms = dorsal submarginal seta
mds = mandibular seta
mts1–5 = marginal temporal setae 1–5
os = ocular seta
pas = preantennal seta
pcs = preconal seta
pos = preocular seta

pts = posttemporal seta
s1–4 = sensilla 1–4
vsms1–2 = ventral submarginal setae 1–2

Head setae discussed in the text are indicated in Fig. 3.

Host taxonomy follows Clements *et al*. (2019).

All specimens are deposited at the following institutions:

MFN = Museum für Naturkunde, Berlin, Germany
NHMUK = Natural History Museum, London, UK
PIPR = Price Institute for Parasite Research, University of Utah, Salt Lake City, USA
USNM = National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA

Order Phthiraptera Haeckel, 1896
Superfamily Ischnocera Kellogg, 1896
Family Philopteridae Burmeister, 1838
Philopterus complex

Genus ***Philopterus*** Nitzsch, 1818

Philopterus Nitzsch, 1818: 288.
Docophorus Nitzsch, 1818: 289 (in partim).
Cypseloecus Conci, 1941: 126.
Debeauxoecus Conci, 1941: 126.
Docophorulus Eichler, 1944: 80.
Bitrabeculus Uchida, 1948: 317.
Prunellides Złotorzycka & Eichler, 1984: 219, figs 1–3.

Type species

Pediculus ocellatus Scopoli, 1763, ex *Corvus corone* Linnaeus, 1758, by subsequent designation (Neumann 1906).

Geographical distribution

As currently circumscribed (Mey 2004), likely global apart from Antarctica, but poorly known in the Southern Hemisphere.

Host associations

As currently circumscribed (Mey 2004), widely distributed across hosts in the Passeriformes. A single species (*Philopterus solus* Tendeiro, 1962) has been described from a bucerotiform host, but Mey (2004: 200) doubted the authenticity of this record.

Remarks

All species described herein key to the genus *Philopterus* in the key of Mey (2004), based on having both trabecula and coni, an extensive hyaline margin, dorsal anterior plates that are longer than wide, and ventral carinae that are not recurved towards the preantennal nodi. However, other characters are quite variable among the species described here, and ascertaining homologous structures can be difficult, especially in the male genitalia. Moreover, one distinguishing character of *Philopterus* in Mey's key is the similarity in the length of the *os, pos,* and *mts1–3*; yet, the relative lengths of these setae vary in the species treated here. The number and position of sensilla of the postantennal head also vary between

species. Most likely, this variation corresponds to deep divisions between different groups of *Philopterus* sensu Mey (2004), some of which may ultimately be considered different genera or subgenera.

Many species of *Philopterus* are inadequately described, with much of the description being based on measurements, and most of the illustrations being of characters of limited taxonomic value (prosternal plates, shape of trabecula, single tergopleurites with only some of the setae illustrated). Finding suitable species to compare potential new species with is, therefore, often difficult. Here, we primarily compare our new species with other species from the same, or a closely related host family. In cases where known species of *Philopterus* on the same host family are clearly very different (e.g., *Philopterus afropari* sp. nov.), or where no species of *Philopterus* were described from the same host family, we expanded our comparison to species from other host families, principally ones in the same geographical region. In some cases (e.g., *Philopterus hebes* sp. nov.), no closely related species of *Philopterus* were identifiable.

We also referred to the species groups proposed by Złotorzycka & Lucińska (1976); however, these species group are of limited use as they only include Central European species of *Philopterus*. Moreover, the morphological characters on which these species groups are based are sometimes hard to interpret, differ somewhat between species groups, and are of limited or unknown phylogenetic utility. Finally, all illustrations and descriptions in Złotorzycka's publications (e.g., Złotorzycka & Lucińska 1976) are partial and poor, and not all species are illustrated. Nevertheless, the partial revisions of *Philopterus* in Złotorzycka & Lucińska (1976) and Złotorzycka (1964) are the only published attempts to structure the species in *Philopterus*.

Philopterus hebes sp. nov.
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Figs 1–6; Tables 1–4

Diagnosis

It is difficult to ascertain which species of *Philopterus* is most similar to *P. hebes* sp. nov. The broad and relatively short preantennal head of *P. hebes* sp. nov. is reminiscent of that of *P. chilchil* Ansari, 1955 [ex *Turdoides caudata caudata* (Dumont, 1823); see Ansari (1958) for an illustration; type specimens of *P. chilchil* are presumed lost (Naz *et al*. 2020)]. Both *P. hebes* sp. nov. and *P. chilchil* have very broad dorsal anterior plates with broad posterior extensions. However, the illustrations of *P. chilchil* published by Ansari (1958) are inadequate to compare the two species properly; for instance, the subgenital plate and many head setae are absent in Ansari's illustration and not described in detail in the text. The male genitalia of *P. chilchil* are poorly illustrated and not described. From what can be seen in Ansari's illustrations, *P. hebes* sp. nov. can be separated from *P. chilchil* by the following characters: distal mesosome broadly triangular with pointed distal end in *P. chilchil*, but rounded with concave lateral margins in *P. hebes* sp. nov. (Figs 4–5); proximal mesosome extensive, with concave lateral margins and convex proximal margin in *P. chilchil,* but simple, with convergent convex lateral margins in *P. hebes* sp. nov. (Fig. 5); hyaline margin apparently very narrow and weakly concave in *P. chilchil*, but extensive, with moderate concavity in median section in *P. hebes* sp. nov. (Figs 1–3). Closer comparison of the genitalia of both sexes and chaetotaxy will have to await the redescription of *P. chilchil*.

A similar head shape is also found in *Philopterus vittati* Ansari, 1955 [ex *Lanius vittatus* Valenciennes, 1826; see Ansari (1956) for illustration; holotype presumed lost (Naz *et al*. 2020)]. These two species can be separated by the following characters: posterior extension of dorsal anterior plate narrow in *P. vittati*, but broad in *P. hebes* sp. nov. (Fig. 3); hyaline margin less extensive in *P. vittati* than in *P. hebes* sp. nov. (Fig. 3); female abdominal segments IV–V with 3 *sts* on each side in *P. hebes* sp. nov. (Fig. 2), but with 4 *sts* on each side in *P. vittati* (n = 3 and 5, respectively); female abdominal segment VI with 2 *sts* on each side in *P. hebes* sp. nov. (Fig. 2), but with 4 *sts* on each side in *P. vittati*; lateral accessory sternites present on abdominal segments II–VI and central sternal plate present on segment VI in

P. vittati, but central sternal plates absent and lateral accessory sternal plates not visible (but may be poorly sclerotized) in *P. hebes* sp. nov. (Fig. 2). The male of *P. vittati* is unknown, and the species is in need of redescription before a more complete comparison can be made.

Etymology

The species name is derived from the Latin '*hebes*' for 'blunt', referring to the shape of the preantennal area.

Material examined

Holotype

THAILAND • ♂; Chaiyaphum Province, Phukhieo, Ban Nan Khun; 11 Dec. 1952; R.E. Elbel leg.; ex *Chloropsis aurifrons inornata*; "RE-876–888, RT-B-17528"; NHMUK.

Paratypes

THAILAND • 1 ♀; same collection data as for holotype; NHMUK • 3 ♂♂, 3 ♀♀; Kamphaeng-Phet Province, Khanu, Salok Bat Ban Thung Chuak; 24 Jun. 1953; same collector and host as for holotype; "RE-2741, RT-B-21644"; PIPR.

Other material

THAILAND • 1 ♀; Loei Province, Tha Li Ban Muang Khai; 17 Jan. 1955; same collector as for holotype; ex *Chloropsis cochinchinensis kinneari*; "RE-4504, B-31119"; PIPR.

Type host

Chloropsis aurifrons inornata Kloss, 1918 – golden-fronted leafbird (Chloropseidae).

Other host

Chloropsis cochinchinensis kinneari Hall & Deignan, 1956 – blue-winged leafbird.

Description

Head shape and chaetotaxy as in Fig. 3, preantennal area very broad. Hyaline margin wide, not extending much lateral to marginal carina, concave medianly. Dorsal anterior plate roughly pentagonal, anterior margin shallowly concave, lateral corners rounded. Ventral anterior plate wide, shallowly crescent-shaped. Posterior margin of dorsal preantennal suture unclear in examined specimens. Coni slender, curved posteriorly. Gular plate small. Thoracic and abdominal segments as in Figs 1–2. Measurements as in Table 1.

Male

Thoracic and abdominal chaetotaxy as in Fig. 1 and Tables 2–4. Central sternal plates absent, lateral accessory plates present on segments II–VI. Basal apodeme slender, widening slightly anteriorly (Figs 4–5). Mesosome as in Figs 4–5, with 3 stout setae on each side. Parameres short, blunt (Figs 4–5), with *pst1–2* both apical.

Female

Thoracic and abdominal chaetotaxy as in Fig. 2 and Tables 2–4. Central sternal plates absent, lateral accessory plates not clearly visible. Subgenital plate and vulval margin as in Fig. 6; chaetotaxy as in Fig. 6 and Table 3. Subvulval plates with notch on lateral margin.

Remarks

Apart from size, no significant differences were found between specimens from the two host species. *Philopterus hebes* sp. nov. constitutes the first description of a species in the *Philopterus* complex, as well as the first ischnoceran louse, from hosts in the Chloropseidae.

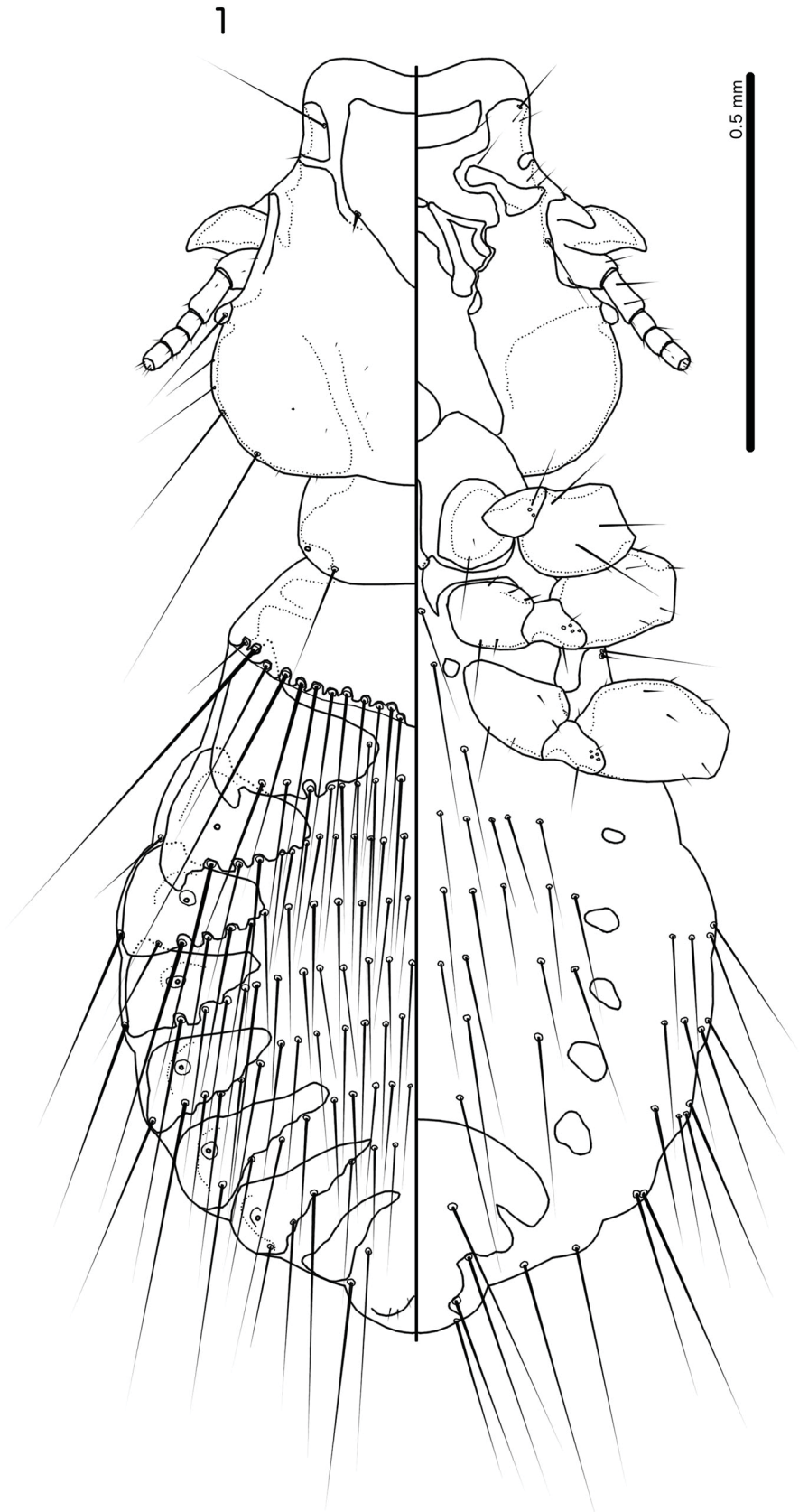


Fig. 1. *Philopterus hebes* sp. nov. ex *Chloropsis aurifrons inornata* Kloss, 1918, male habitus, dorsal and ventral views.

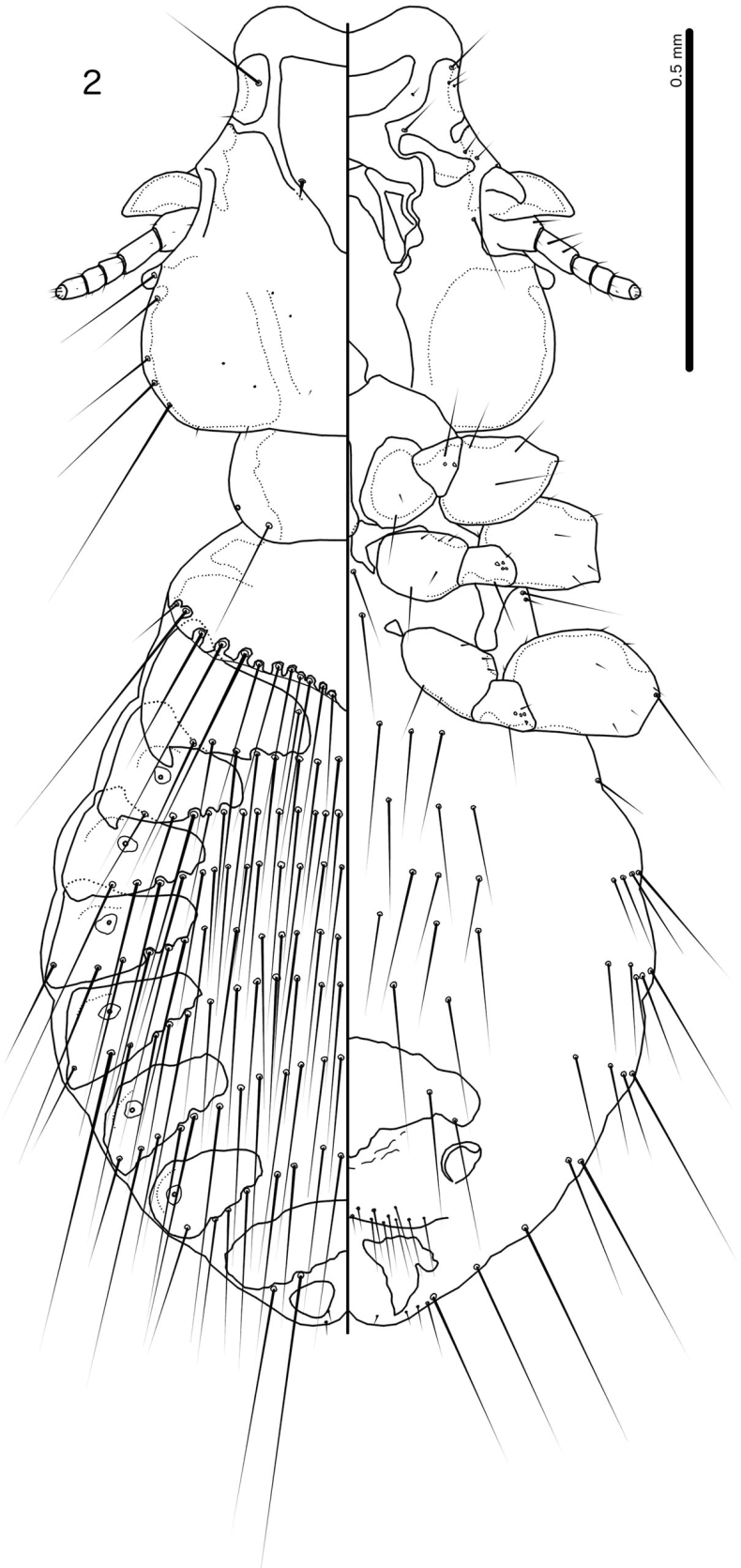
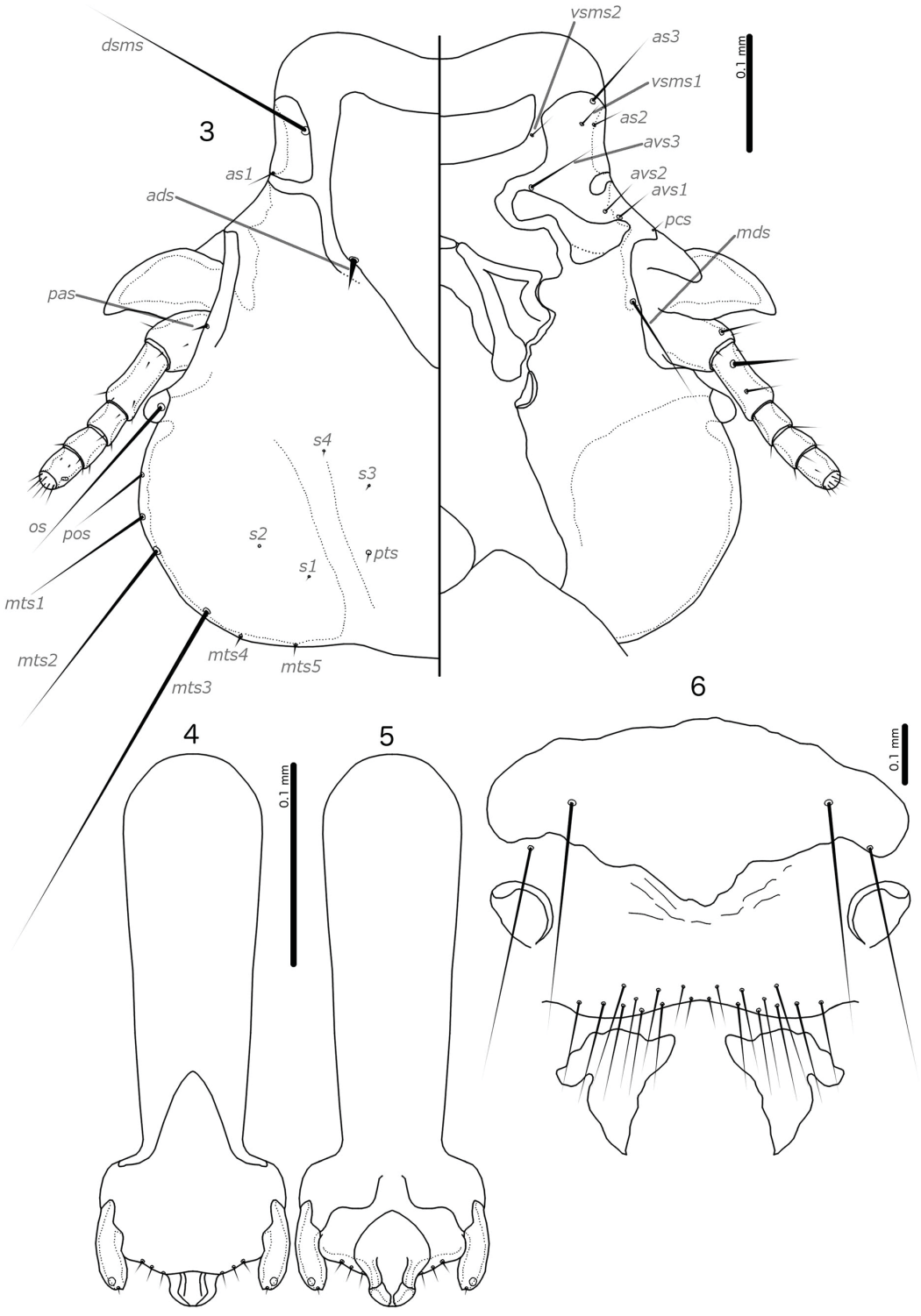


Fig. 2. *Philopterus hebes* sp. nov. ex *Chloropsis aurifrons inornata* Kloss, 1918, female habitus, dorsal and ventral views.



Figs 3–6. *Philopterus hebes* sp. nov. ex *Chloropsis aurifrons inornata* Kloss, 1918. **3**. Male head, dorsal and ventral views. **4**. Male genitalia, dorsal view. **5**. Male genitalia, ventral view. **6**. Female subgenital plate, vulval margin, and subvulval plates, ventral view. Abbreviations: *ads* = anterior dorsal seta; *as1–3* = anterior setae 1–3; *avs1–3* = anterior ventral setae 1–3; *dsms* = dorsal submarginal seta; *mds* = mandibular seta; *mts1–5* = marginal temporal setae 1–5; *os* = ocular seta; *pas* = preantennal seta; *pcs* = preconal seta; *pos* = preocular seta; *pts* = posttemporal seta; *s1–4* = sensilla 1–4; *vsms1–2* = ventral submarginal setae 1–2.

Table 1. Measurements (in millimetres) of *Philopterus hebes* sp. nov. and *P. micropunctatus* sp. nov. Some dimensions (e.g., APLL, TPVL) are measured on both sides of the body, and intervals may therefore be given even if only one specimen was examined. Abbreviations: ADPL = dorsal anterior plate length (at midline); ADPW = dorsal anterior plate width; AL = abdominal length (at midline); ANW = anterior notch width; APLL = dorsal anterior plate lateral length; AW = abdominal width (at segment V); GL = genital length (in male); GW = genital width (in male); HL = head length (at midline); HW = head width (at temples); PAL = preantennal length; PAW = preantennal width (at base of coni); PMCL = premarginal carina length; POL = postantennal length (at midline); PRL = prothoracic length; PRW = prothoracic width; PTL = pterothoracic length (at midline); PTW = pterothoracic width; SGPW = subgenital plate width (in female); TL = total length (at midline); TPVL = tergal plate V length; TRL = trabeculum length; TRW = trabeculum width.

		***Philopterus hebes* sp. nov.**			***Philopterus micropunctatus* sp. nov.**	
		Chloropsis aurifrons inornata		*C. cochinchinensis kinneari*	*Anthus hodgsoni*	
		♂♂ (n = 4) [1]	♀♀ (n = 5) [2]	♀ (n = 1) [3]	♂ (n = 1)	♀♀ (n = 4)
Total	**TL**	1.55–1.68	1.63–2.17	2.10	1.38	1.56–1.74
Head	**HL**	0.52–0.55	0.53–0.63	0.60	0.50	0.51–0.53
	HW	0.52–0.54	0.54–0.64	0.61	0.47	0.48–0.51
	ANW	0.27–0.30	0.28–0.33	0.32	0.18	0.18–0.19
	ADPL	0.21–0.23	0.23–0.29	0.27	0.27	0.26–0.28
	ADPW	0.19–0.20	0.19–0.33	0.23	0.15	0.16
	APLL	0.14–0.17	0.15–0.19	0.18–0.19	0.17–0.18	0.18–0.19
	PMCL	0.07	0.07–0.08	0.08–0.09	0.10	0.10–0.11
	PAL	0.12–0.14	0.12–0.16	0.15	0.16	0.18
	PAW	0.28–0.36	0.37–0.45	0.43	0.31	0.31–0.33
	POL	0.28–0.30	0.29–0.35	0.33	0.25	0.25–0.27
	TRL	0.11–0.12	0.11–0.13	0.12–0.13	0.10	0.09–0.11
	TRW	0.05–0.06	0.05–0.07	0.05–0.06	0.04	0.04
Thorax	**PRL**	0.13–0.14	0.13–0.17	0.14	0.11	0.11–0.15
	PRW	0.32–0.37	0.33–0.38	0.37	0.29	0.29–0.33
	PTL	0.19–0.21	0.21–0.22	0.24	0.16	0.16–0.17
	PTW	0.46–0.49	0.48–0.58	0.57	0.40	0.44–0.46
Abdomen	**AL**	0.66–0.81	0.77–1.16	1.13	0.63	0.75–0.95
	AW	0.73–0.84	0.78–0.99	0.98	0.56	0.61–0.73
	TPVL	0.13–0.14	0.14–0.19	0.18–0.19	0.09–0.10	0.12
Genitals	**GL**	0.24–0.29	–	–	0.20	–
	GW	0.10	–	–	0.08	–
	SGPW	–	0.42–0.49	–	–	0.35

[1] For PTW, n = 3 due to disruption of lateral margin of pterothorax in one specimen. For PTL, n = 3 as the posterior margin of the pterothorax is completely obscured by gut content in one specimen.
[2] For SGPW, n = 4 as subgenital plate is obscured by gut content in one specimen.
[3] Subgenital plate partially obscured by gut content and not measured.

Table 2. Thoracic and abdominal chaetotaxy of the species of *Philopterus* Nitzsch, 1818 described in this paper. Only tergal seta are included here; for sternal setae, see Table 3; for pleural setae, see Table 4. Anterior margin of tergopleurite II has 1 seta on each side in all species, which is not listed in the table. Numbers denote the numbers of setae on one side of the abdomen only; for setal counts in the entire setal row of each segment, these numbers thus need to be doubled. Abbreviation: *mms* = marginal mesometathoracic setae.

Louse	Sex	Thoracic	Tergal							
		mms	II	III	IV	V	VI	VII	VIII	IX+X
Philopterus afropari sp. nov.	♂	9–11	6–8	9–10	10–12	10–12 [3]	10–12 [3]	9–10	4–6	1
	♀	9	7–8	10–12	10–12	10–12	10–12	9–10	6	2
Philopterus coriaceus sp. nov.	♂	11–12	10	9–11	9–11	9–11	9–11	7–8	3–5	1
	♀	11–12	10	10–12	10–12	10–12	10	7–8, 10 [1]	4–6	1–2 [2]
Philopterus hebes sp. nov.	♂	11–12	8	11–12	11–12	11–12	11–12	7–9	5–6	2
	♀	11–12	8–10	12–13	12–13	12–13	12–13	12–13	8	3
Philopterus micropunctatus sp. nov.	♂	9–10	7–8	8–9	8–9	8–9	8–9	8–9	5–6	1
	♀	9–11	8–10	8–10	8–10	11–12	9–11	9	5–7	1
Philopterus pseudhirundo sp. nov.	♂	10	8	7–8	9–10	9–10	8	7	4–5	1
	♀	9	6	7–9	9–10	10–11	7–8	5	4–5	1
Philopterus sinensis sp. nov.	♂	8–9	7	8–9	6–7 [4]	8	6–8 [4]	6–7	4–5	1
	♀	9–10	6	7–8	7–8	9–10	7–8	7–8	5	1
Philopterus stansburyensis sp. nov.	♂	11–13	10–11	10–11	10–11	10–11	8–12	8–10	5	1
	♀	14–15	10–11	11–13	12–14	11–13	10–12	10–11	5–7	1
Philopterus trepostephanus sp. nov.	♂	9–11	7–8	7–9	9–10	9–10	9–10	7–9	4–5	1
	♀	10–11	7–8	9	10–11	10–11	9–10	7–8	4–5	2

[1] 7–8 in one examined female, 10 in the other.
[2] In addition, there is 1 seta on each side at the anterior end of this segment.
[3] One male with 8 setae on one side of these segments.
[4] Setal rows of these segments have significant gaps, indicating that 1–2 setae may be absent in the single examined male, but present if more males were examined. These numbers are thus preliminary.

Philopterus micropunctatus sp. nov.
urn:lsid:zoobank.org:act:2A337930-2324-465E-95D6-8F7EC902C9ED
Figs 7–12; Tables 1–4

Diagnosis

Several species of *Philopterus* have been described from motacillid hosts; however, few of them are adequately described or illustrated. Złotorzycka & Lucińska (1976) erected the *P. passerinus* species group based on size, the shape of the trabecula, the shape and chaetotaxy of the male subgenital plate, and the size of the male parameres. They placed *Philopterus passerinus* (Denny, 1842) (ex *Motacilla alba* Linnaeus, 1758), *P. pavidus* (Złotorzycka, 1964) (ex *Motacilla flava* Linnaeus, 1758), *P. vultuosus* Złotorzycka, 1964 (ex *Anthus trivialis trivialis* (Linnaeus, 1758)), and *P. hanzaki* Balát, 1955 (ex *Anthus spinoletta spinoletta* (Linnaeus, 1758)) in this group. The other two known species from motacillid hosts, *P. irkutensis* Fedorenko, 1985 (ex *Anthus richardi* Vieillot, 1818) and *P. subitus* Fedorenko, 1985 (ex *Motacilla cinerea* Tunstall, 1771) may also be closely related to the *P. passerinus* group, based on the shape of the parameres and trabecula in the original descriptions. However, a complete revision of the *Philopterus* species on motacillid hosts is sorely needed.

Table 3. Abdominal and vulval chaetotaxy of the species of *Philopterus* Nitzsch, 1818 described in this paper. Only sternal setae are listed here; for tergal setae, see Table 2; for pleural setae, see Table 4. Numbers denote the numbers of setae on one side of the abdomen only; for setal counts in the entire setal row of each segment, these numbers thus need to be doubled.

Louse	Sex	Sternal								Vulval		
		II	III	IV	V	VI	VII	VIII	IX+X	Long	Medium	Short
Philopterus afropari sp. nov.	♂	3–4	3–4	4–5	4–5	4–5	1	1	1	–	–	–
	♀	3–4	4–5	4–5	4–5	4–5	2	0	0	3–7	0	0–2
Philopterus coriaceus sp. nov.	♂	5–6	5–6	5–6	4–5	4–5	1	1	1	–	–	–
	♀	6	6–7	5–6	4–5	4	2	0	0	8–10	0–1	2–4
Philopterus hebes sp. nov.	♂	3–5	3–5	3–5	2	1	1	1	1	–	–	–
	♀	2–3	2–3	2–3	2–3	2–3	2–3	0	0	7–8	0	2–3
Philopterus micropunctatus sp. nov.	♂	4–5	6	6	5	5	1	1	1	–	–	–
	♀	3–5	4–6	4–6	4–6	4–6	2	0	0	3	2–3	1–3
Philopterus pseudhirundo sp. nov.	♂	4–5	7–8	5–6	5–6	4	1	1	1	–	–	–
	♀	5	5–7	6–7	6–7	6–7	2	0	0	5	0	3–4
Philopterus sinensis sp. nov.	♂	3–4	6	4–5	4–5	4–5	1	1	1	–	–	–
	♀	4	6	6	5	5	2	0	0	4	0	3–4
Philopterus stansburyensis sp. nov.	♂[2]	3–4	3–4	3–4	2	2–3	1	1	1	–	–	–
	♀[3]	4–5	3–5	4–5	3–4	3–5	2	0	0	6–8	0–1[4]	1
Philopterus trepostephanus sp. nov.	♂	4–5	4–5[1]	4–5	4–5	4–5	1	1	2–3	–	–	–
	♀	3	5–6	5–6	4–5	4–5	2	0	0	5–6	0	3–4

[1] One specimen with 7 sternal setae on one side. Segments V–VI with additional, shorter sternal setae lateral to those associated with the sternal plate.

[2] Two examined specimens with many sternal setae seemingly absent, and more material is necessary to confirm chaetotaxy of this species.

[3] Two of three examined specimens with many sternal setae absent; the numbers mostly derived from single specimen.

[4] All examined specimens with 1 medium seta on the left side and none on the right side.

The most distinctive character of *P. micropunctatus* sp. nov. is the elongated preantennal head and very long dorsal anterior plate (Fig. 9). The fragmented 'dots' between the female subvulval plates in *P. micropunctatus* sp. nov. (Fig. 12) are not found in any other species in the *P. passerinus* group we have examined. The shape of the head and dorsal anterior plate separates *P. micropunctatus* sp. nov. from *P. irkutensis*, *P. subitus*, *P. passerinus*, and *P. vultuosus*. Balát's (1955) only illustration of *P. hanzaki* is of the dorsal anterior plate, which is shorter than that of *P. micropunctatus* sp. nov. and with a differently shaped posterior projection. No illustration of *P. pavidus* has ever been published, and Eichler's text description (in Eichler 1953, as *Docophorus passerinus* Denny, 1842; Złotorzycka's replacement name *P. pavidus* was based on this description) does not contain enough detail to separate *P. pavidus* from any other *Philopterus*, regardless of host.

Etymology

The species name is derived from the Greek '*mikro*' for 'small' and the Latin '*punctatus*' for 'dotted', referring to the many small dots median to the subvulval plates.

Table 4. Abdominal chaetotaxy of the species of *Philopterus* Nitzsch, 1818 described in this paper. Only pleural setae are listed here; for tergal setae, see Table 2; for sternal setae, see Table 3. Numbers denote the numbers of setae on one side of the abdomen only; for setal counts in the entire setal row of each segment, these numbers thus need to be doubled. Abbreviations: ant. = anterior end; post. = posterior end.

Louse	Sex	Pleural								
		II	III	IV	V	VI	VII	VIII	IX+X (ant.)	IX+X (post.)
Philopterus afropari sp. nov.	♂	0	1	3–4	3–4	4–5	3–4	2	1	0
	♀	0	1	4	4	4	3	2	1	3
Philopterus coriaceus sp. nov.	♂	0	1	4–5	4–5	3–4	2–3	2	1	0
	♀	0	1	4	4	4	2–3	2	1	3
Philopterus hebes sp. nov.	♂	0	1	5–6	5–6	5–6	3	2	1	0
	♀	0	1	4–5	4–5	4–5	3	2	1	3–4
Philopterus micropunctatus sp. nov.	♂	0	1	3	3–4	4	3	2	1	0
	♀	0	1	4–5	4–5	4–5	2–3	2	1	2
Philopterus pseudhirundo [1] sp. nov.	♂	0	1	4–5	5	5	4	2	1	0
	♀	0	1	5–7	5–7	5–7	3	3	1	3
Philopterus sinensis sp. nov.	♂	0	0	2–3	2–3	4	4	3	0	0
	♀	0	0	3	3	4	4	3	1	3
Philopterus stansburyensis sp. nov.	♂	0	1	3–4	2–4	2–6	1–3	2–3	1	0
	♀	0	1	4–5	5–8	5–6	3–5	2–3	1	3
Philopterus trepostephanus sp. nov.	♂	0	0	4	4	5	4	3	1	0
	♀	0	0	4	4	5	4	4	1	3

[1] Segments V–VI with additional, shorter sternal setae lateral to those associated with the sternal plate; on segment IV of single examined male these are closer to the pleural setae, and these setae are therefore here included in the count of pleural setae on all segments.

Material examined

Holotype

THAILAND • ♂; Nan Province, Bun Yun, Pang Nam Un; 21 Jan. 1953; R.E. Elbel and H.G. Deignan leg.; ex *Anthus hodgsoni*; "RE-2103, RT-B-17720"; NHMUK.

Paratypes

THAILAND • 1 ♀; same collection data as for holotype; NHMUK • 3 ♀♀; same collection data as for holotype; PIPR.

Type host

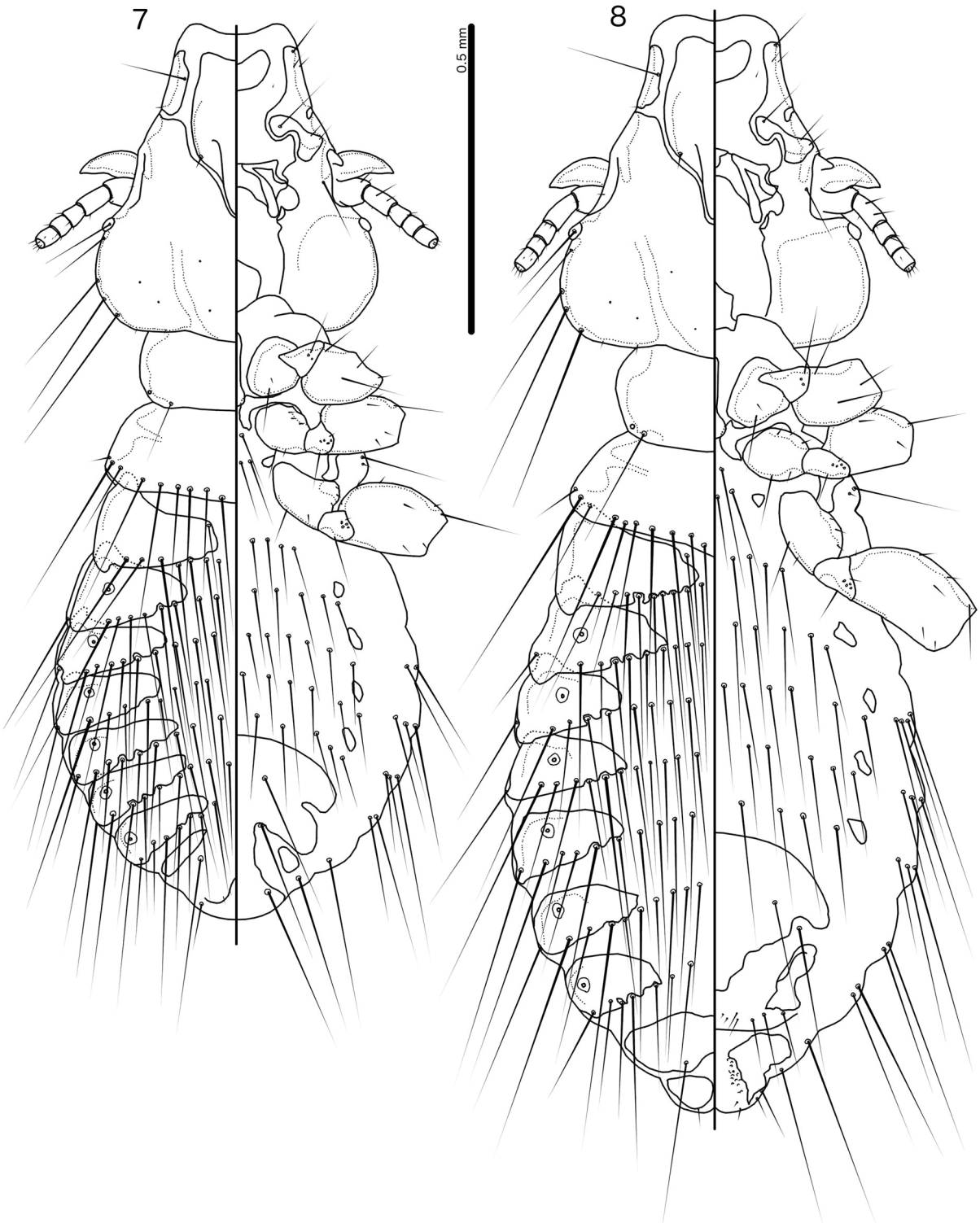
Anthus hodgsoni Richmond, 1907 – olive-backed pipit (Motacillidae).

Description

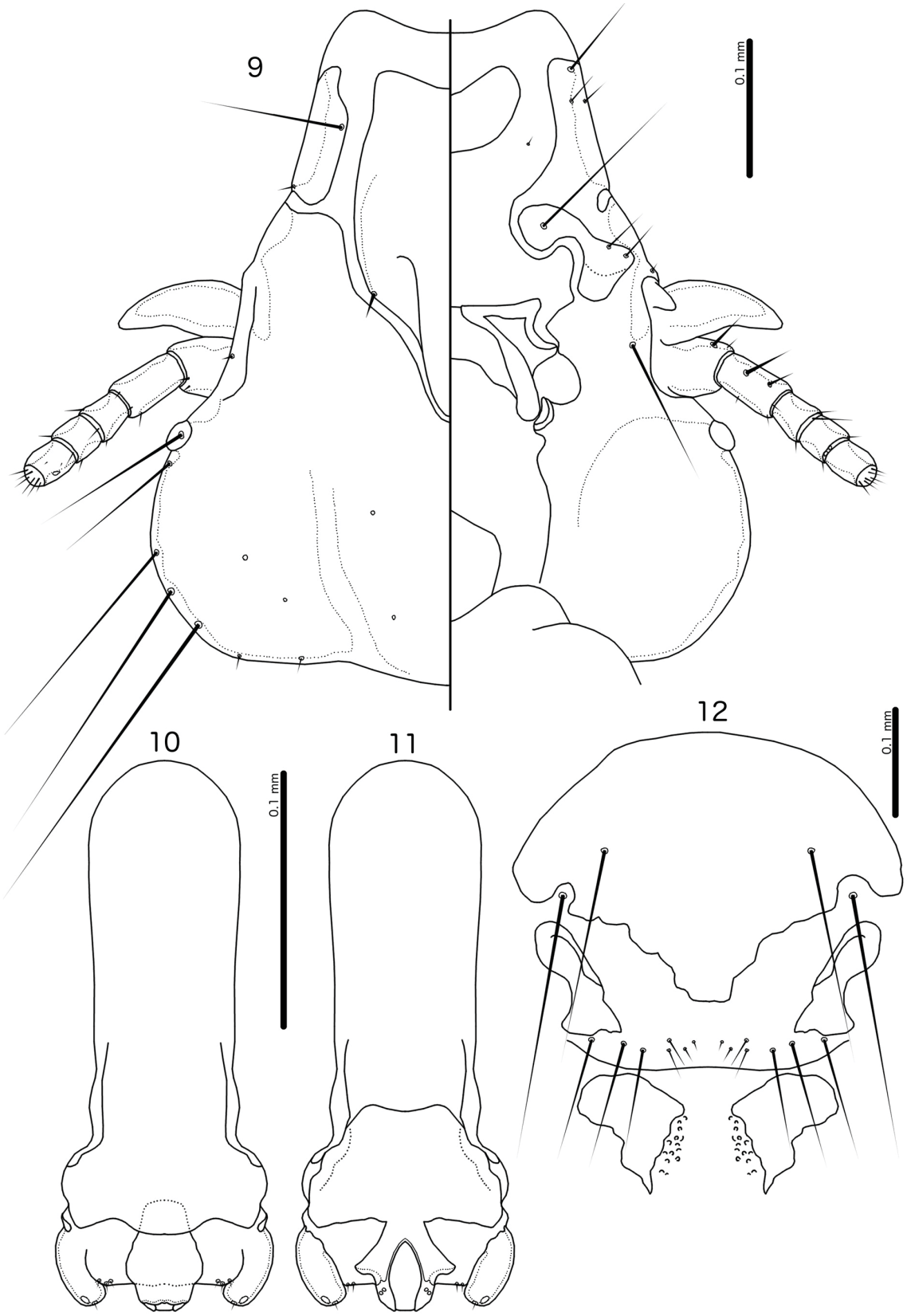
Head shape and chaetotaxy as in Fig. 9, preantennal area moderately broad. Hyaline margin wide, slightly concave medianly, not extending much lateral to marginal carina. Dorsal preantennal plate long, narrowing gently posteriorly, with distinct lateral thickenings along much of lateral margins anterior to *ads*. Ventral anterior plate bluntly crescent-shaped. Coni small, pointed posteriorly. Thoracic and abdominal segments as in Figs 7–8. Measurements as in Table 1.

Male

Thoracic and abdominal chaetotaxy as in Fig. 7 and Tables 2–4. Central sternal plates absent on segments II–VI. Lateral accessory plates present on segments III–VI. Subgenital plate broad, but diffuse distally and illustrated approximately. Basal apodeme short and slender (Figs 10–11). Mesosomal thickening



Figs 7–8. *Philopterus micropunctatus* sp. nov. ex *Anthus hodgsoni* Richmond, 1907. **7**. Male habitus, dorsal and ventral views. **8**. Female habitus, dorsal and ventral views.



Figs 9–12. *Philopterus micropunctatus* sp. nov. ex *Anthus hodgsoni* Richmond, 1907. **9**. Male head, dorsal and ventral views. **10**. Male genitalia, dorsal view. **11**. Male genitalia, ventral view. **12**. Female subgenital plate, vulval margin, and subvulval plates, ventral view.

truncated oval; mesosome with 3 microsetae on each side (Fig. 10). Gonopore bluntly lanceolate, with wide, roughly triangular sclerotization anterior and lateral to opening, proximally fused to basal apodeme; 2 sensilla on each side of gonopore. Parameres short and stocky (Figs 10–11); *pst1–2* as in Fig. 10.

Female

Thoracic and abdominal chaetotaxy as in Fig. 8 and Tables 2–4. Central sternal plates absent on segments II–VI. Lateral accessory plates present on segments III–VI. Subgenital plate as in Fig. 12; lateral sclerotizations of vulval area extended posteriorly to approach vulval margin; in one female also extended anteriorly to fuse with subgenital plate. Vulval margin more or less straight, chaetotaxy as in Fig. 12 and Table 3. Subvulval plates slender distally, with many small fragmentary dots between plates as in Fig. 12.

Philopterus afropari sp. nov.

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Figs 13–18; Tables 2–5

Diagnosis

Philopterus afropari sp. nov. is not similar to any species of *Philopterus* known from Holarctic parid hosts, which are all characterized by having the dorsal anterior plate with pointed postero-lateral corners near *ads* on each side, 3–4 setae on each side on the posterior margin of the pronotum, and a long and narrow basal apodeme (Fedorenko & Vasjukova 1985; Mey 1988, 1994). In contrast, *P. afropari* sp. nov. lacks the pointed corners of the dorsal anterior plate, has only one posterior seta on each side of the pronotum, and has a broader basal apodeme. No species of *Philopterus* has been described from other African parids.

Philopterus afropari sp. nov. is somewhat similar to *P. solus* Tendeiro, 1962, another African species associated with a host in the Bucerotiformes (*Rhinopomastus cyanomelas schalowi* Neumann, 1900). These two species share the following characters: hyaline margin wide but relatively short; dorsal anterior plate broadly trapezoidal; coni small with concave anterior margins; male subgenital plate with at least 2 lateral lobes on each side and a lateral accessory sternal plate on abdominal segment IX+X (fused with subgenital plate in one specimen examined in Tendeiro 1962). Most notably, the gonopore of both species is of similar shape and the ventral section of the mesosome is largely indistinguishable from the distal basal apodeme in both species; dorsally, the mesosome of *P. afropari* sp. nov. (Fig. 16) appears to be similar to the dark section of the distal basal apodeme in Tendeiro's photo of *P. solus*, but this section is not clearly illustrated by Tendeiro (1962), and the photo is of poor quality.

These two species can be separated by the following characters: *os* and *pos* of more or less equal length in *P. afropari* sp. nov. (Fig. 15), but *pos* much longer than *os* in *P. solus*; preantennal head longer and more slender in *P. afropari* sp. nov. (Fig. 15) than in *P. solus*; central sternal plates evidently absent in males of *P. solus*, but present in males of *P. afropari* sp. nov. (Fig. 13); lateral lobes of male subgenital plate of roughly equal size in *P. solus*, but posterior lobe much larger than anterior lobe in *P. afropari* sp. nov. (Fig. 13); basal apodeme in *P. solus* with clear central thickenings presumably associated with the endophallus, but no such structures visible in *P. afropari* sp. nov. (Figs 16–17); central posterior extension of the female subgenital plate more prominent in *P. afropari* sp. nov. (Fig. 18) than in *P. solus*. Note that *P. solus* is in need of a more detailed redescription before a complete comparison between these two species can be made.

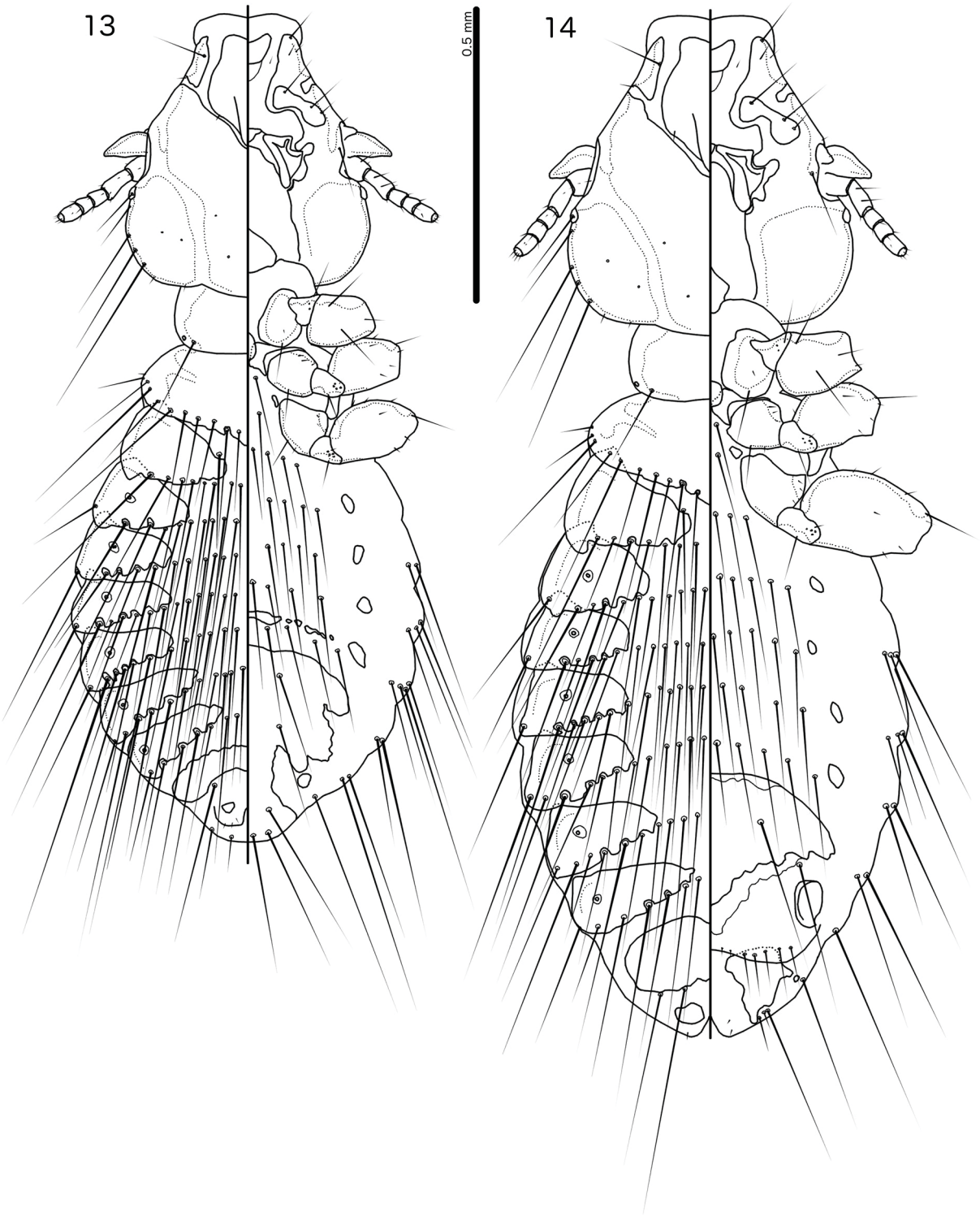
Etymology

The specific name refers to the fact that this is the first species of the *Philopterus* complex described from African parids.

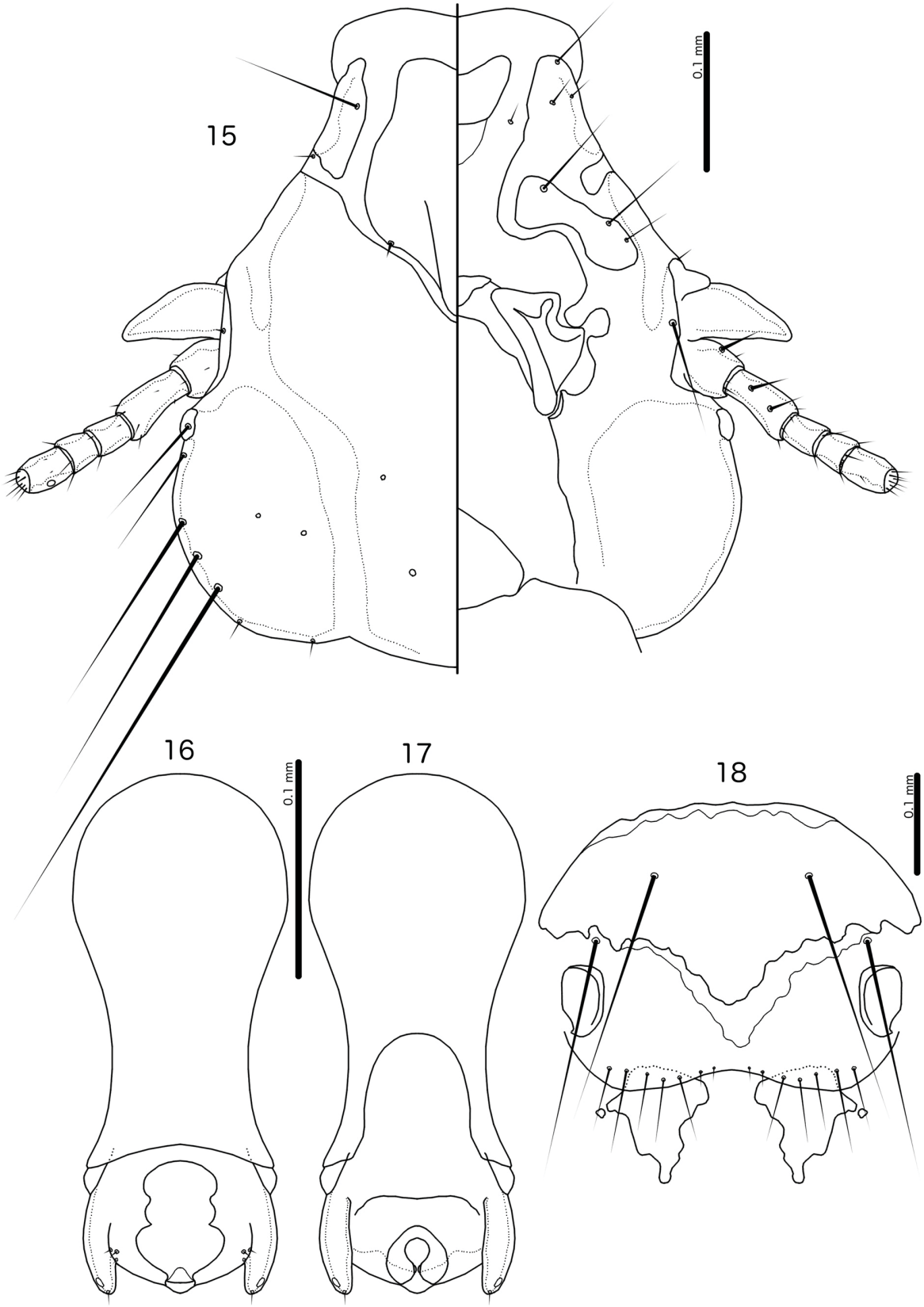
Material examined

Holotype

SOUTH AFRICA • ♂; Transvaal, Potchefstroom; 27 Jul. 1952; [F.] Zumpt leg.; ex *Melaniparus cinerascens cinerascens* (as *Parus cinerascens*); "I.N. 1373/29"; MFN.



Figs 13–14. *Philopterus afropari* sp. nov. ex *Melaniparus cinerascens cinerascens* (Vieillot, 1818). **13**. Male habitus, dorsal and ventral views. **14**. Female habitus, dorsal and ventral views.



Figs 15–18. *Philopterus afropari* sp. nov. ex *Melaniparus cinerascens cinerascens* (Vieillot, 1818). **15**. Male head, dorsal and ventral views. **16**. Male genitalia, dorsal view. **17**. Male genitalia, ventral view. **18**. Female subgenital plate, vulval margin, and subvulval plates, ventral view.

Table 5. Measurements (in millimetres) of *Philopterus afropari* sp. nov., *P. sinensis* sp. nov., and *P. trepostephanus* sp. nov. Some dimensions (e.g., APLL, TPVL) are measured on both sides of the body, and intervals may therefore be given even if only one specimen was examined. Abbreviations: ADPL = dorsal anterior plate length (at midline); ADPW = dorsal anterior plate width; AL = abdominal length (at midline); ANW = anterior notch width; APLL = dorsal anterior plate lateral length; AW = abdominal width (at segment V); GL = genital length (in male); GW = genital width (in male); HL = head length (at midline); HW = head width (at temples); PAL = preantennal length; PAW = preantennal width (at base of coni); PMCL = premarginal carina length; POL = postantennal length (at midline); PRL = prothoracic length; PRW = prothoracic width; PTL = pterothoracic length (at midline); PTW = pterothoracic width; SGPW = subgenital plate width (in female); TL = total length (at midline); TPVL = tergal plate V length; TRL = trabeculum length; TRW = trabeculum width.

		Philopterus afropari		***Philopterus sinensis***		***Philopterus trepostephanus***			
		Melaniparus cinerascens cinerascens		*Hemipus picatus picatus*		*Tephrodornis virgatus fretensis*		*Tephrodornis virgatus mekongensis*	
		♂♂ (n=6)	♀♀ (n=6)	♂ (n=1)	♀ (n=1)	♂♂ (n=2)	♀ (n=1)	♂♂ (n=4)	♀♀ (n=4)
Total	**TL**	1.32–1.37	1.59–1.69	1.45	1.75	1.41–1.50	1.83	1.42–1.52	1.63–1.83
Head	**HL**	0.45–0.48	0.52–0.53	0.46	0.46	0.49	0.53	0.50–0.54	0.52–0.55
	HW	0.40–0.44	0.46–0.48	0.42	0.41	0.45	0.50	0.46–0.50	0.50–0.52
	ANW	0.14–0.16	0.17–0.18	0.19	0.17	0.22	0.23	0.22–0.25	0.24–0.25
	ADPL	0.18–0.19	0.20–0.22	0.24	0.22	0.22–0.23	0.24	0.24–0.27	0.26–0.27
	ADPW	0.13–0.14	0.15–0.17	0.15	0.15	0.16	0.18	0.16–0.18	0.17–0.19
	APLL	0.14–0.16	0.15–0.16	0.13–0.14	0.13–0.14	0.14–0.16	0.15	0.15–0.16	0.16–0.17
	PMCL	0.07–0.08	0.08–0.09	0.07	0.07	0.07–0.08	0.08–0.09	0.08	0.08–0.09
	PAL	0.16–0.17	0.16–0.19	0.16	0.15	0.14–0.15	0.16–0.18	0.17	0.16–0.18
	PAW	0.31–0.34	0.34–0.37	0.33	0.30	0.32	0.35	0.34–0.36	0.37–0.38
	POL	0.23–0.25	0.26–0.28	0.23	0.24	0.24	0.27	0.26–0.27	0.28–0.29
	TRL	0.09	0.10	0.09–0.10	0.09–0.10	0.10	0.10–0.11	0.09–0.11	0.09–0.11
	TRW	0.04	0.04–0.05	0.04	0.05	0.04–0.05	0.05	0.05	0.05
Thorax	**PRL**	0.09–0.11	0.11–0.13	0.11	0.11	0.11–0.12	0.14	0.12–0.14	0.12–0.16
	PRW	0.23–0.24	0.26–0.27	0.16	0.16	0.28	0.31	0.28–0.30	0.30–0.31
	PTL	0.14–0.17	0.17–0.19	0.18	0.17	0.19–0.20	0.22	0.15–0.19	0.20–0.22
	PTW	0.35–0.37	0.41–0.42	0.37	0.39	0.40–0.41	0.48	0.41–0.43	0.46–0.47
Abdomen	**AL**	0.60–0.65	0.78–0.86	0.70	0.97	0.62–0.70	0.94	0.64–0.66	0.78–0.94
	AW	0.56–0.62	0.68–0.71	0.60	0.72	0.58–0.70	0.67	0.60–0.65	0.72–0.80
	TPVL	0.10–0.11	0.13–0.14	0.12–0.13	0.13–0.14	0.12–0.14	0.16–0.17	0.12–0.14	0.15–0.16
Genitals	**GL**	0.23–0.25	–	0.23	–	0.22–0.23	–	0.22–0.23	–
	GW	0.08–0.09	–	0.10	–	0.10	–	0.09	–
	SGPW	–	0.37–0.39	–	0.35	–	–[1]	–	0.39–0.41

[1] Subgenital plate partially obscured by gut content in single examined female, and not measured.

Paratypes

SOUTH AFRICA • 1 ♂, 4 ♀♀; same collection data as for holotype; MFN • 4 ♂♂, 2 ♀♀; same collection data as for holotype but 24 Apr. 1952; "I.N. 1373/28"; MFN.

Type host

Melaniparus cinerascens cinerascens (Vieillot, 1818) – ashy tit (Paridae).

Description

Head shape and chaetotaxy as in Fig. 15, preantennal area broad. Hyaline margin wide, extending laterally beyond marginal carina, shallowly concave medianly. Dorsal anterior plate broad, trapezoidal, with broad, blunt posterior extension. Ventral anterior plate roughly triangular, with shallowly concave anterior margin. Coni small, distal end in some specimens curved slightly anteriorly. Gular plate small, irregular. Thoracic and abdominal segments as in Figs 13–14. Measurements as in Table 5.

Male

Thoracic and abdominal chaetotaxy as in Fig. 13 and Tables 2–4. Tergopleurite IX+X medianly continuous. Abdominal segments II–V with no central sternal plate, but with lateral accessory plates; segment VI with narrow, typically very fragmented central sternal plate and large lateral accessory plates. Subgenital plate with 3 lateral lobes on each side and small lateral accessory plate of segment IX+X. Basal apodeme broad (Figs 16–17), much constricted at mid-length. Mesosomal thickening large, with sinuous lateral margins and distal thickening (Fig. 16); 3 microsetae on each side of mesosome. Gonopore large (Fig. 17), widening distally. Parameres fused to basal apodeme, slender; *pst1–2* as in Fig. 17.

Female

Thoracic and abdominal chaetotaxy as in Fig. 14 and Tables 2–4. Subgenital plate as in Fig. 18, with more weakly sclerotized sections on anterior and posterior ends. Vulval margin concave medianly (Fig. 18), chaetotaxy as in Fig. 18 and Table 3. Subvulval plate large, irregularly triangular, often with minute accessory plate laterally.

Philopterus sinensis sp. nov.

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Figs 19–24; Tables 2–5

Diagnosis

Philopterus sinensis sp. nov. does not appear to be morphologically close to any other known species of the genus, but is somewhat similar to *P. trepostephanus* sp. nov., with which it shares the following characters: *mts1* relatively short in male (Figs 19, 25), but longer in female (Figs 20, 26); gonopore with postero-lateral bulges, each of which is associated with 2 microsetae (Figs 23, 29); female genital setae displaced anteriorly from vulval margin (Figs 24, 30), particularly the more median setae; abdominal segment III without *ps* in both sexes (Figs 19–20, 25–26).

These two species can be separated by the following characters: head sensillus *s4* present in *P. trepostephanus* sp. nov. (Fig. 27), but absent in *P. sinensis* sp. nov. (Fig. 21); female subgenital plate with flattened posterior margin in *P. sinensis* sp. nov. (Fig. 24), but with bulging posterior margin in *P. trepostephanus* sp. nov. (Fig. 30); male mesosome with extensive ventral plate in *P. trepostephanus* sp. nov. (Fig. 29), but without such a plate in *P. sinensis* sp. nov. (Fig. 23); central sternal plates present on abdominal segments II–VI in *P. sinensis* sp. nov. (Fig. 19), but only on segment VI in *P. trepostephanus* sp. nov. (Fig. 25); male subgenital plate with deep indentation posterior to setae, and with small accessory plate inside this indentation, in *P. trepostephanus* sp. nov. (Fig. 25), but without such an indentation or plate in *P. sinensis* sp. nov. (Fig. 19).

Etymology

The specific epithet is derived from the type locality.

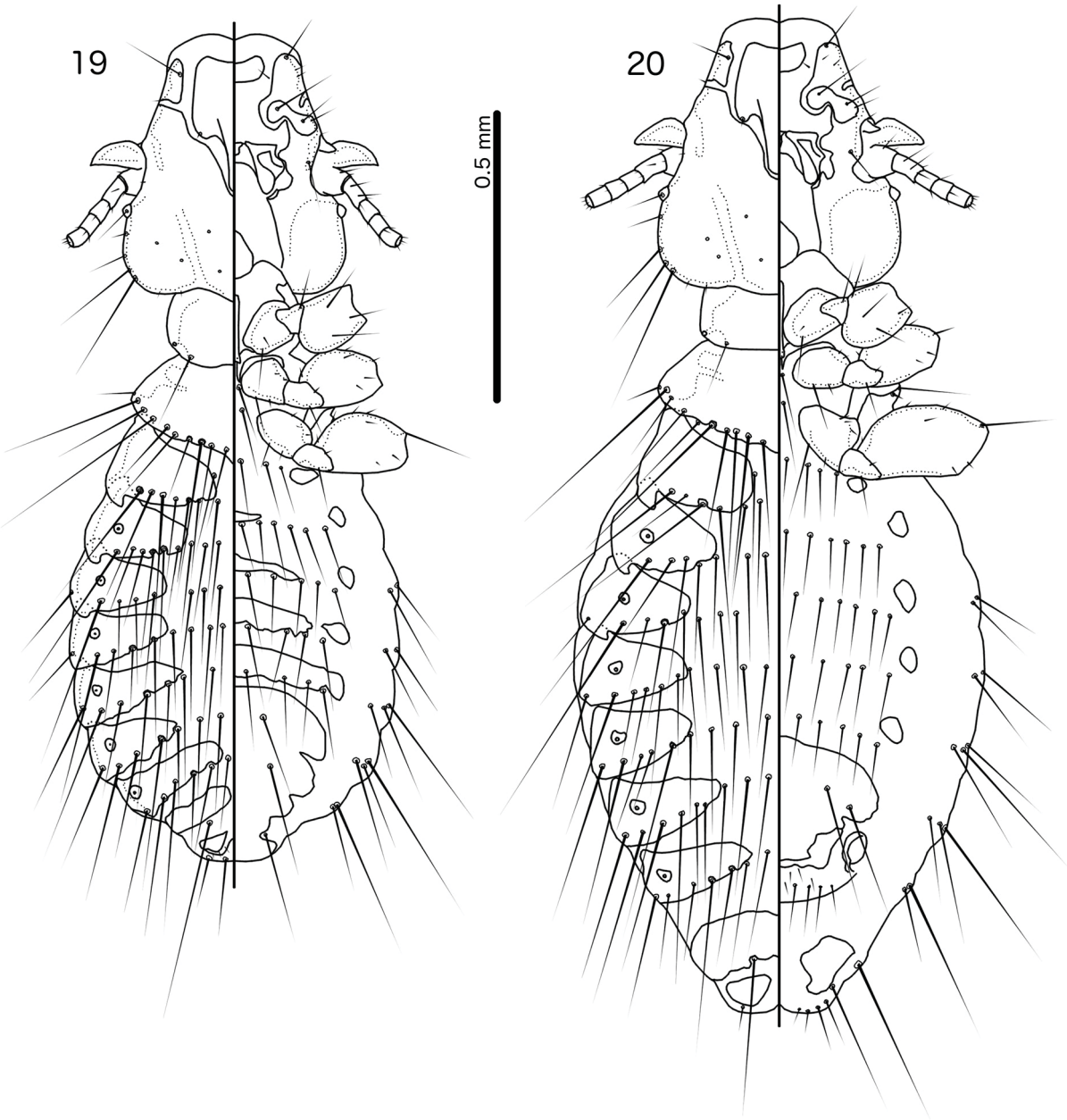
Material examined

Holotype

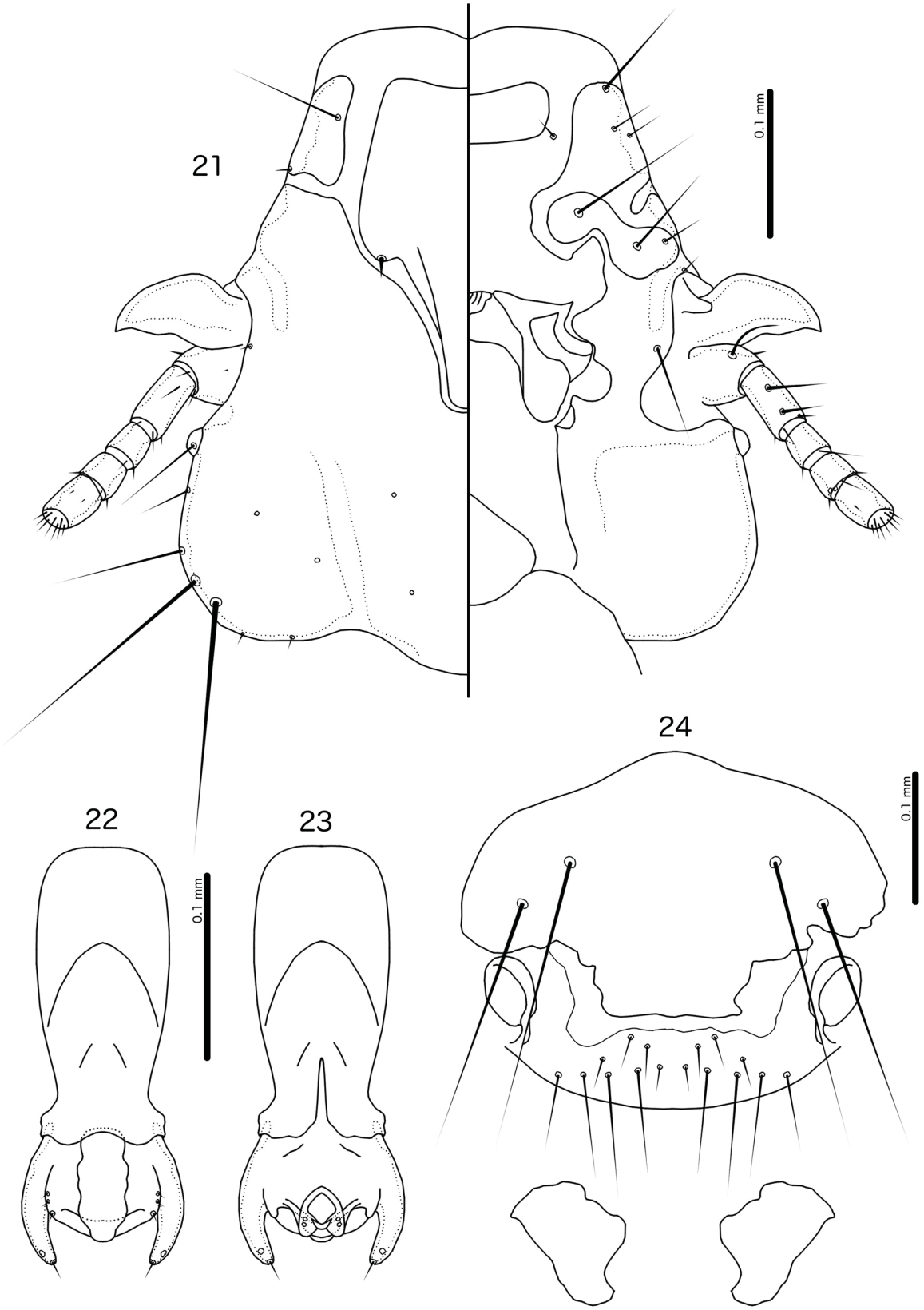
CHINA • ♂; Guanxi Province, Jingxin County; 5 Oct. 2004; S.E. Bush leg.; ex *Hemipus picatus capitalis*; "ATP-2004-161, P-559"; NHMUK.

Paratype

CHINA • 1 ♀; same collection data as for holotype; NHMUK.



Figs 19–20. *Philopterus sinensis* sp. nov. ex *Hemipus picatus capitalis* (Horsfield, 1840). **19**. Male habitus, dorsal and ventral views. **20**. Female habitus, dorsal and ventral views.



Figs 21–24. *Philopterus sinensis* sp. nov. ex *Hemipus picatus capitalis* (Horsfield, 1840). **21**. Male head, dorsal and ventral views. **22**. Male genitalia, dorsal view. **23**. Male genitalia, ventral view. **24**. Female subgenital plate, vulval margin, and subvulval plates, ventral view.

Type host

Hemipus picatus capitalis (Horsfield, 1840) – bar-winged flycatcher-shrike (Vangidae).

Description

Head shape and chaetotaxy as in Fig. 21, preantennal area wide. Hyaline margin broad, not extending laterally beyond marginal carina, shallowly indented medianly. Dorsal anterior plate almost square, with broad, blunt posterior extension. Ventral anterior plate near-rectangular, wide and short, with slightly concave anterior margin. Coni small, curved slightly anteriorly. Gular plate small, irregular. Thoracic and abdominal segments as in Figs 19–20. Measurements as in Table 5.

Male

Thoracic and abdominal chaetotaxy as in Fig. 19 and Tables 2–4. Abdominal segment II without central sternal plate but with lateral accessory plates; segments III–V with small to wide central sternal plates and lateral accessory plate on each side; segment VI with wide central sternal plate fused to lateral accessory plates. Subgenital plate broad, lateral notches small, lateral sternal plate of segment IX+X fused to subgenital plate. Basal apodeme broad (Figs 22–23), constricted in distal half. Mesosomal thickening oblong, irregular; 3 microsetae on each side of mesosome. Gonopore with convergent anterior margin and bulbous distal extensions (Fig. 23), 2 sensilla on each side of gonopore. Parameres fused to basal apodeme, long, slender; *pst1–2* as in Figs 22–23.

Female

Thoracic and abdominal chaetotaxy as in Fig. 20 and Tables 2–4. Central sternal plates absent, lateral accessory plates present on segments II–VI. Subgenital plate and vulval margin as in Fig. 24, chaetotaxy as in Fig. 24 and Table 3. Subvulval plates partially obscured by gut content, but appear to be broad, blunt distally.

Philopterus trepostephanus sp. nov.
urn:lsid:zoobank.org:act:BA72A2B0-545C-434F-8820-152AB279A3CA
Figs 25–30; Tables 2–5

Diagnosis

Apart from the similarity between *Philopterus trepostephanus* sp. nov. and *P. sinensis* sp. nov. outlined under the latter species (see above), *P. trepostephanus* sp. nov. does not appear to be morphologically close to any other known species of the genus. The species morphologically closest to *P. trepostephanus* sp. nov. may be *P. petrescuae* Adam in Sychra *et al*., 2011 (ex *Dicrurus hottentottus* (Linnaeus, 1766)). These two species share the following characters: hyaline margin extends lateral to *as1* (Fig. 27); ventral sclerite of male mesosome with lateral extensions (Fig. 29); long vulval setae far anterior to the vulval margin (Fig. 30); gonopore extensive, collar-shaped. These two species can be separated by the following characters: lateral extensions of ventral mesosomal sclerite in distal half in *P. trepostephanus* sp. nov. (Fig. 29), but in proximal half in *P. petrescuae*, and the overall shape of this sclerite also differs between these species; coni with recurving anterior 'hooks' in *P. petrescuae*, but without such hooks in *P. trepostephanus* sp. nov. (Fig. 27); central sternite absent on male abdominal segment VI in *P. petrescuae*, but present in *P. trepostephanus* sp. nov. (Fig. 25); lateral lobes of hyaline margin more extensive in *P. petrescuae* than in *P. trepostephanus* sp. nov. (Fig. 27); dorsal anterior plate (ignoring posterior extension) longer than wide in *P. petrescuae*, but about as wide as long in *P. trepostephanus* sp. nov. (Fig. 27); macrosetae of female subgenital plate all situated on plate in *P. trepostephanus* sp. nov. (Fig. 30), but lateral setae on each side situated lateral to plate in *P. petrescuae*.

Etymology

The species name is constructed from '*trepo*', Greek for 'I turn', and '*stephanos*', Greek for 'crown, wreath'. This refers to the shape of the gonopore, with its anterio-lateral hooks.

Material examined

Holotype

THAILAND • ♂; Songkhla Province, Muang, Thung Wang; 4 Sep. 1963; W. Songprakob [as Songphabob] and W. Suwan Laong leg.; ex *Tephrodornis virgatus fretensis*; "WS-471"; NHMUK.

Paratypes

THAILAND • 1 ♀; same collection data as for holotype; NHMUK • 1 ♂; same collection data as for holotype; PIPR.

Non-type material

THAILAND • 3 ♂♂, 3 ♀♀; Loei Province, Thali, Ban Muang Khai; 26 Jan. 1955; R.E. Elbel leg.; ex *Tephrodornis virgatus mekongensis*; "RE-4564, RT-B-31145"; PIPR • 1 ♂, 1 ♀; same collection data as for preceding; "RE-4563, RT-B-31144"; PIPR.

Type host

Tephrodornis virgatus fretensis Robinson & Kloss, 1920 – large woodshrike (Vangidae).

Other host

Tephrodornis virgatus mekongensis Meyer de Schauensee, 1946.

Description

Head shape and chaetotaxy as in Fig. 27, preantennal area broad. Hyaline margin broad, extending laterally beyond marginal carina, shallowly concave medianly. Dorsal anterior plate roughly quadratic, with shallowly concave anterior margin and broad posterior extension. Ventral anterior plate roughly semicircular, with slightly concave anterior margin. Coni moderate, slender, pointed posteriorly. Gular plate large. Thoracic and abdominal segments as in Figs 25–26. Measurements as in Table 5.

Male

Thoracic and abdominal chaetotaxy as in Fig. 25 and Tables 2–4. Central sternal plates absent on segments II–V, present and broad on segment VI. Lateral accessory plates present on segments II–VI. Subgenital plate broad anteriorly, narrowing markedly on segment IX+X, widening distally; lateral accessory plates present on abdominal segment IX+X, of about same size as other lateral accessory plates. Basal apodeme short, slender, constricted at mid-length (Figs 28–29). Mesosomal thickening long, rounded anteriorly, with slight lateral bulges. Mesosome with 3 microsetae on each side (Fig. 28). Gonopore as in Fig. 29, broad and with prominent distal lobes; 2 microsetae on each side of gonopore. Parameres elongated, slender; *pst1–2* as in Figs 28–29.

Female

Thoracic and abdominal chaetotaxy as in Fig. 26 and Tables 2–4. Central sternal plates absent on segments II–VI. Lateral accessory plates present on segments II–VI. Subgenital plate and vulval margin as in Fig. 30, chaetotaxy as in Fig. 30 and Table 3. Subvulval plates broad.

Remarks

Specimens from the two host subspecies differ slightly in head shape and size (specimens from *Tephrodornis virgatus mekongensis* are generally larger than specimens from *T. v. fretensis*; Table 5) and abdominal chaetotaxy (specimens from *T. v. mekongensis* typically have more tergal setae per segment than those from *T. v. fretensis*), but some specimens from *T. v. mekongensis* have the same abdominal chaetotaxy as material from the type host subspecies, and most measurements overlap somewhat. The

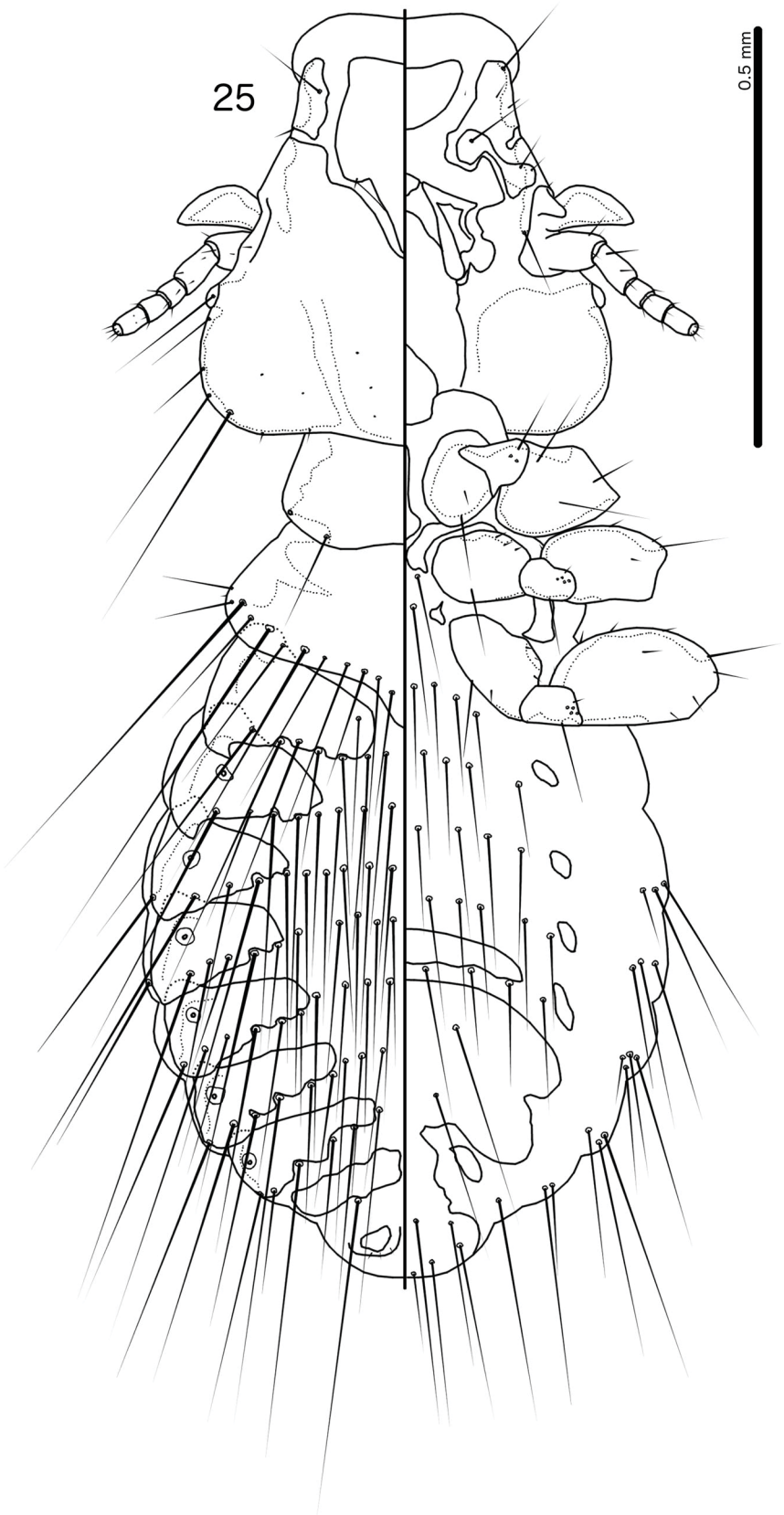


Fig. 25. *Philopterus trepostephanus* sp. nov. ex *Tephrodornis virgatus fretensis* Robinson & Kloss, 1920, male habitus, dorsal and ventral views.

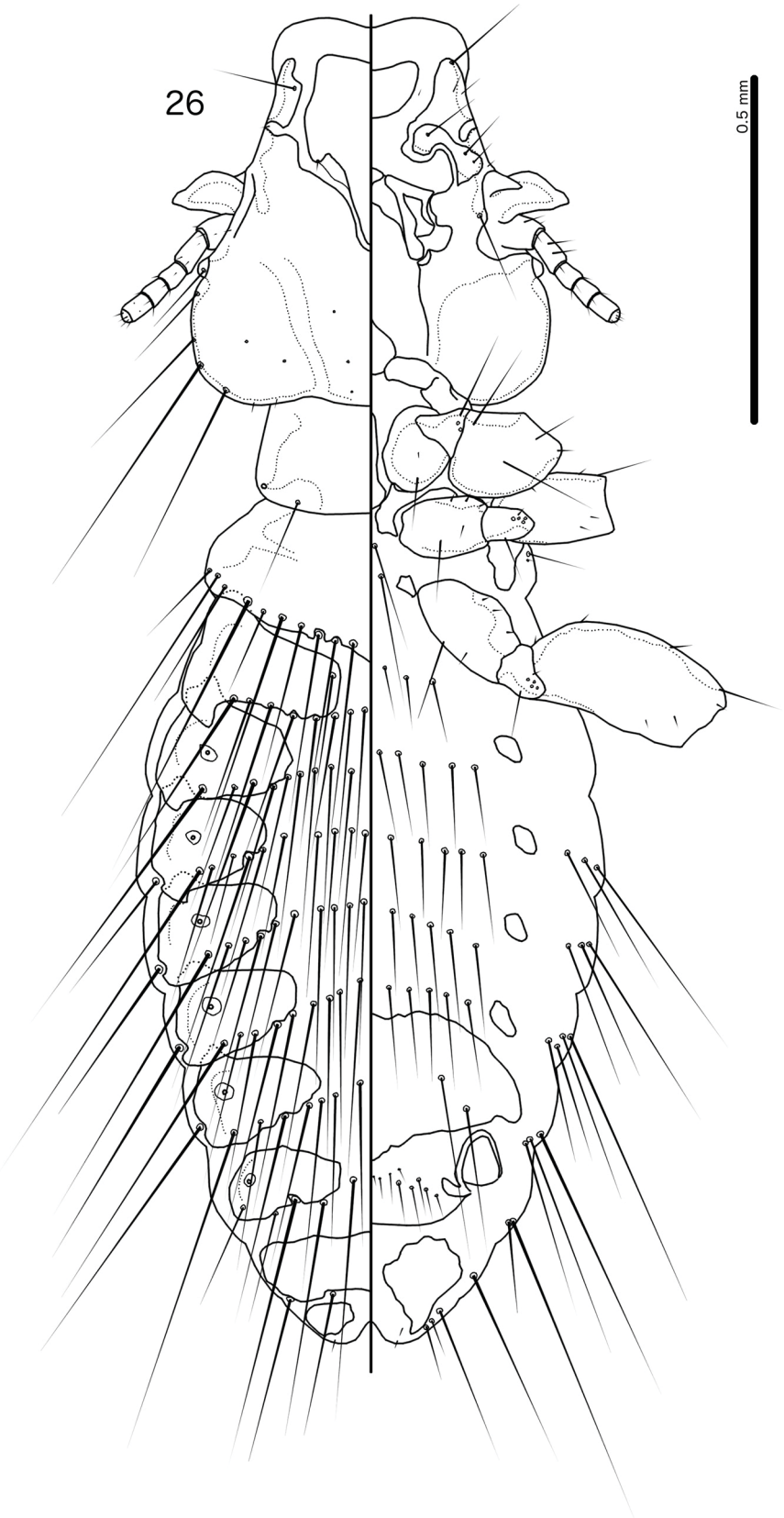
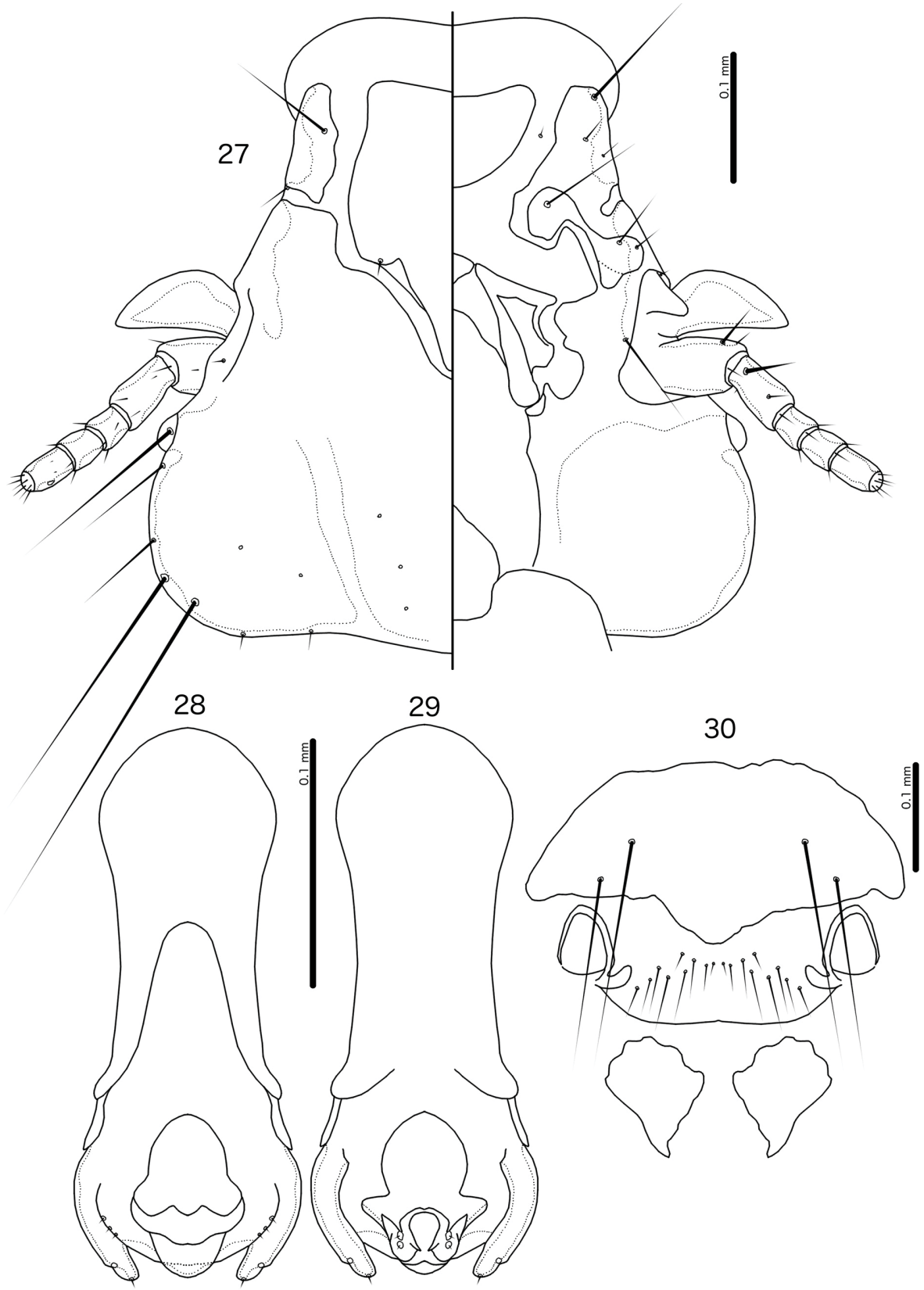


Fig. 26. *Philopterus trepostephanus* sp. nov. ex *Tephrodornis virgatus fretensis* Robinson & Kloss, 1920, female habitus, dorsal and ventral views.



Figs 27–30. *Philopterus trepostephanus* sp. nov. ex *Tephrodornis virgatus fretensis* Robinson & Kloss, 1920. **27**. Male head, dorsal and ventral views. **28**. Male genitalia, dorsal view. **29**. Male genitalia, ventral view. **30**. Female subgenital plate, vulval margin, and subvulval plates, ventral view.

ranges of the two known host subspecies are separated by a gap in distribution in peninsular Thailand (Robson 2006). We tentatively consider all specimens from both host subspecies conspecific.

Philopterus stansburyensis sp. nov.
urn:lsid:zoobank.org:act:DB198892-3BCC-4D00-988C-EAFE8E446B7A
Figs 31–36; Tables 2–4, 6

Diagnosis

The only previously known species of *Philopterus* from a cardinalid host is *P. cardinalis* Piaget, 1880 (ex *Paroaria coronata* (Miller, 1776)); this species is poorly described and illustrated, and has never been redescribed. We have examined 3 specimens (1 ♂, 2 ♀♀) collected by Piaget and labeled as *P. cardinalis* (NHMUK 010712725–27); however, none of them is in good enough condition to allow proper morphological redescription. An adequate comparison between *P. cardinalis* and *P. stansburyensis* sp. nov. must await the redescription of new specimens of *P. cardinalis*.

The male genitalia of *P. stansburyensis* sp. nov. and the absence of sternal plates in the Colorado specimens resemble conditions in *P. confusio* Ansari, 1955 (ex *Turdus fulviventris* Sclater, 1857). These two species can be separated by the following characters: the posterior projection of dorsal anterior plate short and narrow (shorter than the plate itself) in male of *P. stansburyensis* sp. nov. (Fig. 33), but long and wide (longer than the plate itself) in male of *P. confusio* (Ansari 1955: fig. 7a); lateral slits separating sternites VII and VIII of male subgenital plate long, reaching almost to setal apertures in *P. stansburyensis* sp. nov. (Fig. 31), but short, just slightly cut out from lateral margin of plate in *P. confusio* (Ansari 1955: fig. 7c); female subgenital accessory plates oval or pear-shaped, pointed anteriorly in *P. stansburyensis* sp. nov. (Fig. 36), but horizontally elongated, pointed medioposteriorly in *P. confusio* (Ansari 1955: fig. 7f); vulval setae become shorter medianly and are placed in one row in *P. stansburyensis* sp. nov. (Fig. 36), but all are short and placed in two rows in *P. confusio* (Ansari 1955: fig. 7g). Note that all these comparisons are based on illustrations given by Ansari (1955), which may be of limited reliability.

Etymology

The specific name is derived from the type locality.

Material examined

Holotype

USA • ♂; Utah, Tooele County, Stansbury Mountains, Hickman Canyon; alt. 7000 ft [2134 m]; 24 Jun. 1969; ex *Pheucticus melanocephala melanocephala*; "09084"; NHMUK.

Paratypes

USA • 1 ♂, 3 ♀♀; Colorado; 1967; J.A. Allen leg.; same host as for holotype; mounted by R.C. Dalgleish; "1367"; USNM.

Type host

Pheucticus melanocephalus melanocephalus (Swainson, 1827) – black-headed grosbeak (Cardinalidae).

Description

Head shape and chaetotaxy as in Fig. 33, preantennal area broad. Hyaline margin wide, extending laterally beyond marginal carina. Dorsal anterior plate as in Fig. 33. Ventral anterior plate semi-circular, with slightly concave anterior margin. Coni large, blunt, with round posterior margins, pointing posterolaterally. Gular plate small and narrowly pointed, displaced anteriorly. Thoracic and abdominal segments and chaetotaxy as in Figs 31–32 and Tables 2–4. Measurements as in Table 6.

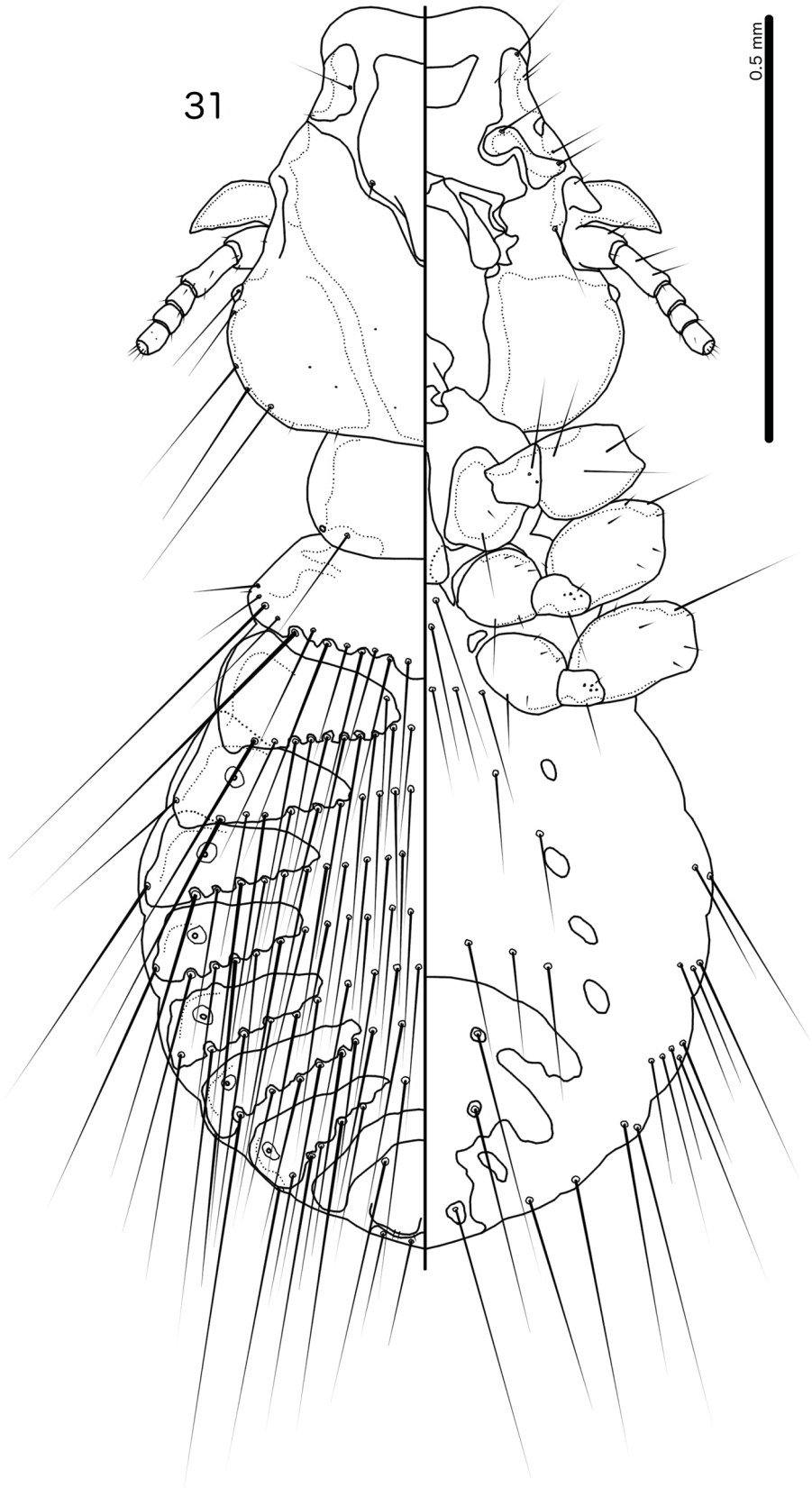


Fig. 31. *Philopterus stansburyensis* sp. nov. ex *Pheucticus melanocephalus melanocephalus* (Swainson, 1827), male habitus, dorsal and ventral views.

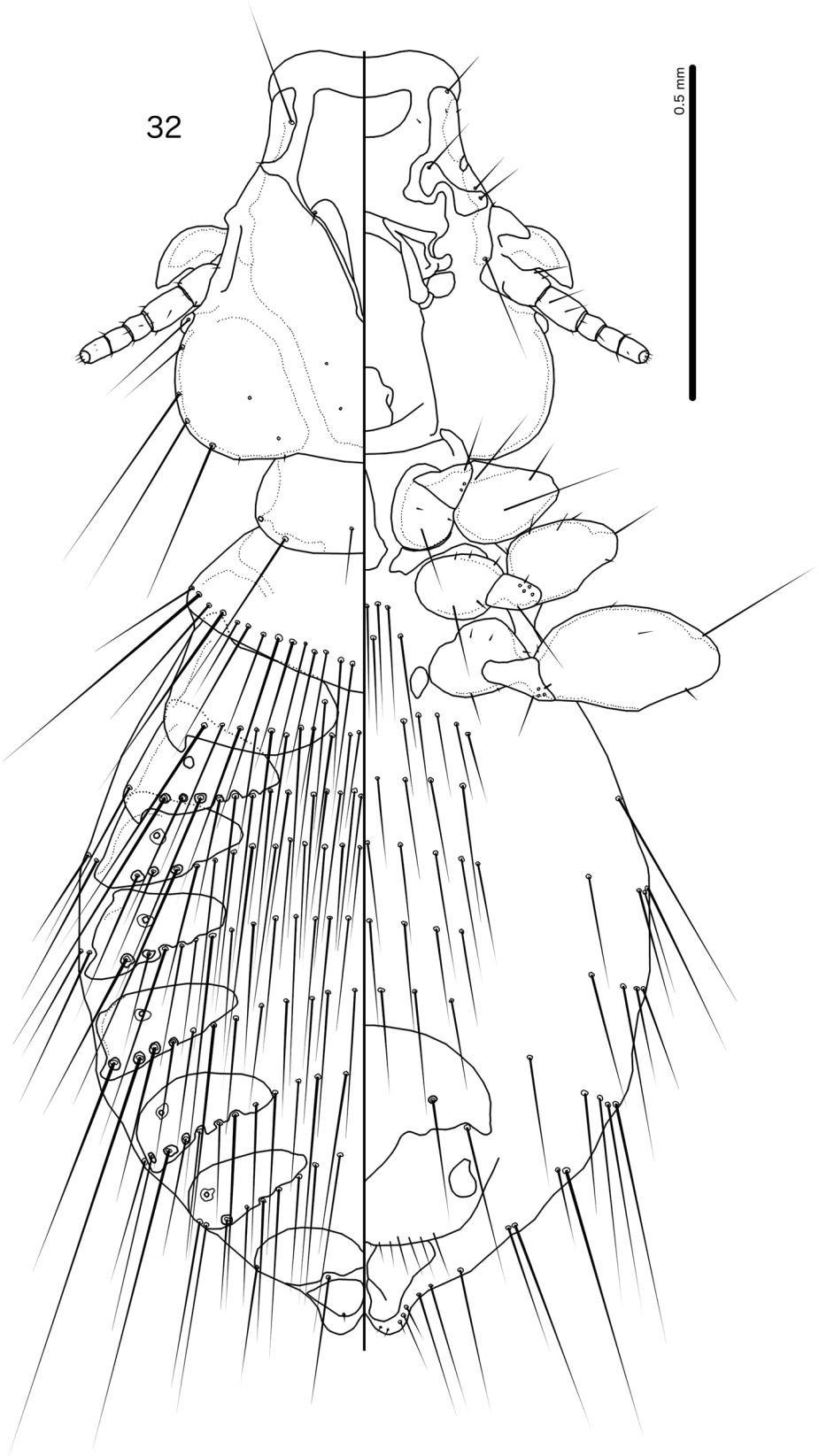
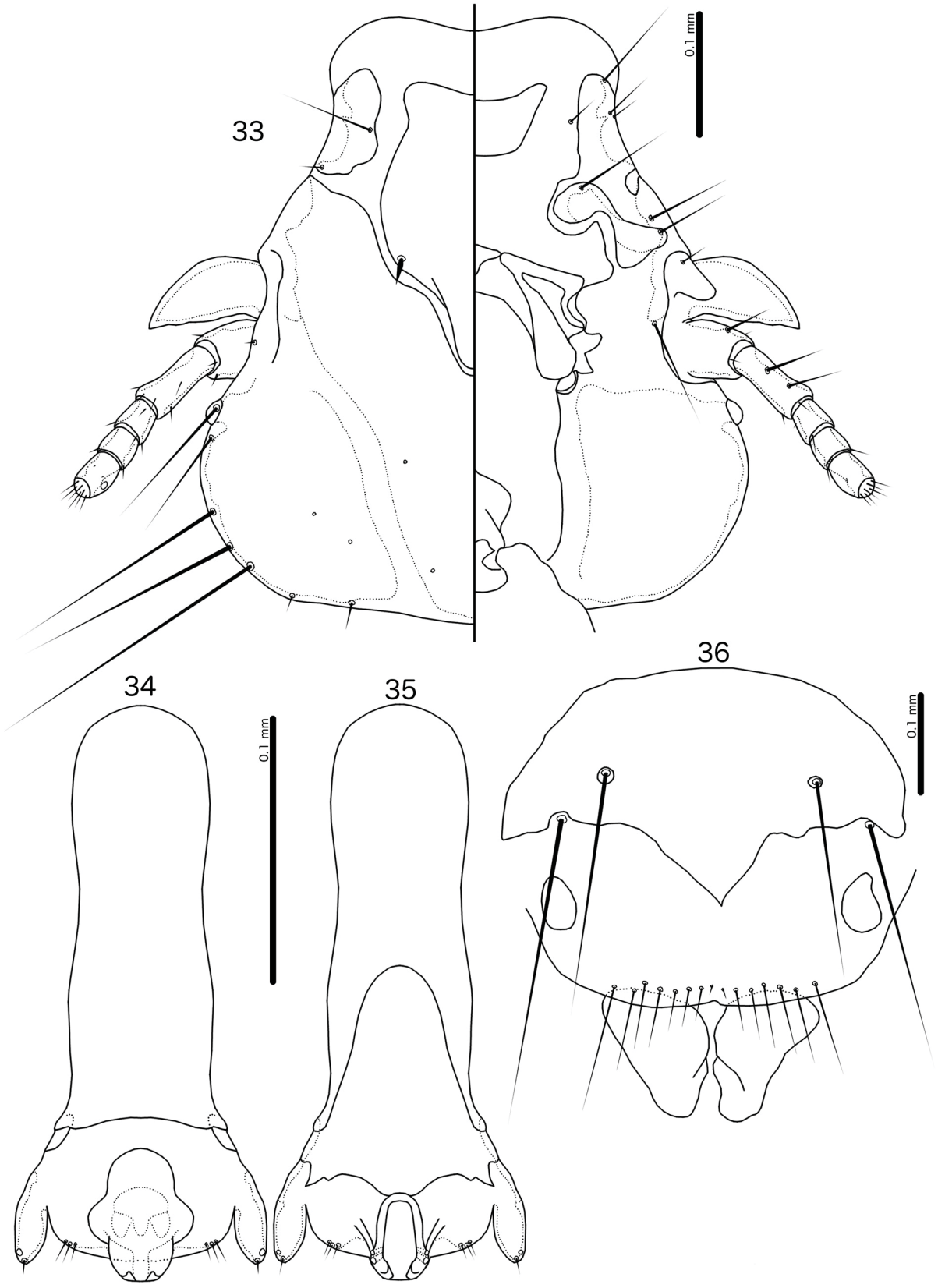


Fig. 32. *Philopterus stansburyensis* sp. nov. ex *Pheucticus melanocephalus melanocephalus* (Swainson, 1827), female habitus, dorsal and ventral views.



Figs 33–36. *Philopterus stansburyensis* sp. nov. ex *Pheucticus melanocephalus melanocephalus* (Swainson, 1827). **33**. Male head, dorsal and ventral views. **34**. Male genitalia, dorsal view. **35**. Male genitalia, ventral view. **36**. Female subgenital plate, vulval margin, and subvulval plates, ventral view.

Table 6. Measurements (in millimetres) of *Philopterus stansburyensis* sp. nov., *P. coriaceus* sp. nov., and *P. pseudhirundo* sp. nov. Some dimensions (e.g., APLL, TPVL) are measured on both sides of the body, and intervals may therefore be given even if only one specimen was examined. Abbreviations: ADPL = dorsal anterior plate length (at midline); ADPW = dorsal anterior plate width; AL = abdominal length (at midline); ANW = anterior notch width; APLL = dorsal anterior plate lateral length; AW = abdominal width (at segment V); F = female; GL = genital length (in male); GW = genital width (in male); HL = head length (at midline); HW = head width (at temples); M = male; PAL = preantennal length; PAW = preantennal width (at base of coni); PMCL = premarginal carina length; POL = postantennal length (at midline); PRL = prothoracic length; PRW = prothoracic width; PTL = pterothoracic length (at midline); PTW = pterothoracic width; SGPW = subgenital plate width (in female); TL = total length (at midline); TPVL = tergal plate V length; TRL = trabeculum length; TRW = trabeculum width.

		***Philopterus stansburyensis* sp. nov.**		***Philopterus coriaceus* sp. nov.**		***Philopterus pseudhirundo* sp. nov.**	
		Pheucticus melanocephalus melanocephalus		*Molothrus oryzivorus oryzivorus*		*Pseudhirundo griseopyga*	
		♂♂ (n=2)	♀♀ (n=3)	♂♂ (n=2)	♀♀ (n=2)	♂ (n=1)	♀ (n=1)
Total	**TL**	1.42–1.61	1.81–1.90	1.76–1.89	1.95–2.17	1.22	1.47
Head	**HL**	0.51–0.56	0.61	0.59–0.65	0.65–0.71	0.40	0.42
	HW	0.47–0.51	0.57–0.58	0.58–0.63	0.62–0.69	0.36	0.38
	ANW	0.21–0.24	0.25–0.26	0.24–0.27	0.25–0.26	0.10	0.11
	ADPL	0.23–0.28	0.31–0.33	0.26–0.31	0.28–0.33	0.18	0.20
	ADPW	0.16–0.18	0.20	0.17–0.19	0.18–0.20	0.10	0.11
	APLL	0.15–0.18	0.19–0.20	0.19–0.20	0.20	0.14–0.16	0.15–0.16
	PMCL	0.07–0.09	0.09–0.10	0.11–0.12	0.11–0.12	0.09–0.10	0.10
	PAL	0.16–0.19	0.20–0.21	0.19–0.21	0.21–0.22	0.17–0.18	0.17
	PAW	0.36–0.39	0.43	0.39–0.42	0.42–0.45	0.25	0.27
	POL	0.26–0.27	0.29–0.30	0.28–0.32	0.32–0.36	0.20	0.22
	TRL	0.11–0.13	0.13–0.14	0.13–0.15	0.14–0.15	0.08	0.09
	TRW	0.05	0.06	0.06–0.07	0.06–0.07	0.04	0.04–0.05
Thorax	**PRL**	0.12–0.16	0.14–0.17	0.16–0.17	0.16–0.18	0.10	0.12
	PRW	0.29–0.30	0.32–0.33	0.34–0.35	0.37–0.39	0.24	0.25
	PTL	0.14–0.18	0.22	0.18–0.20	0.22–0.24	0.16	0.16
	PTW	0.40–0.48	0.52–0.54	0.49	0.51–0.56	0.35	0.37
Abdomen	**AL**	0.66–0.72	0.85–0.94	0.81–0.88	0.92–1.05	0.57	0.77
	AW	0.65–0.72	0.75–0.85	0.73	0.76–0.89	0.54	0.61
	TPVL	0.08–0.11	0.12–0.15	0.13–0.14	0.17	0.09–0.10	0.11
Genitals	**GL**	0.19–0.21	–	0.30–0.31	–	0.19	–
	GW	0.08–0.09	–	0.10–0.11	–	0.08	–
	SGPW	–	0.39–0.43	–	0.45	–	0.31

Male

Thoracic and abdominal chaetotaxy as in Fig. 31 and Tables 2–4. Tergite IX+X medianly continuous. Central sternal plates absent on segments II–VI. Holotype with lateral accessory sternal plates on each side of segments III–VI, but in specimens from Colorado these lateral accessory sternal plates not visible. Subgenital plate with deep lateral notches and elongated lateral accessory plate on segment IX+X. Basal apodeme long, slender (Figs 34–35). Mesosomal thickening diffuse, with wide extensions distally; 3 microsetae on each side of mesosome. Gonopore elongate, rounded (Fig. 35), with 2 sensilla on lateral margins near distal ends. Parameres completely fused to basal apodeme, slender, with *pst1–2* as in Figs 34–35.

Female

Thoracic and abdominal chaetotaxy as in Fig. 32 and Tables 2–4. Gular plate trilobal, with blunt anterior margin. Central sternal plates absent on segments II–VI. Lateral accessory sternal plates not visible. Subgenital plate and vulval margin as in Fig. 36, lateral accessory plates on segment IX+X small and oval. Vulval chaetotaxy as in Fig. 36 and Table 3; vulval setae longest laterally, gradually shortening medianly, with minute median pair. Subvulval plates broadly triangular, with rounded anterior margin.

Philopterus coriaceus sp. nov.

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Figs 37–42; Tables 2–4, 6

Diagnosis

Finding the closest known relative of *Philopterus coriaceus* sp. nov. is difficult. This species is set apart from almost all other known *Philopterus* complex species by the presence of a pair of setae on the anterior margin of female tergopleurite IX+X. To our knowledge, this seta is only present in some species of *Mayriphilopterus* Mey, 2004. All of the species in this genus are Neotropical, but none of them occur on passeriforms.

However, *P. coriaceus* sp. nov. does not key to *Mayriphilopterus* in the key of Mey (2004), and can be separated from this genus by the following characters: coni present in *P. coriaceus* sp. nov. (Fig. 39), but absent (possibly highly reduced) in *Mayriphilopterus*; hyaline margin with thickened setae in *Mayriphilopterus*, but without such setae in *P. coriaceus* sp. nov. (Fig. 39); area between subgenital plate and vulval margin with a large number of small setae in *Mayriphilopterus*, but without such setae in *P. coriaceus* sp. nov. (Fig. 42). It thus seems unlikely that *P. coriaceus* sp. nov. is closely related to *Mayriphilopterus*.

Only two species of *Philopterus* are previously known from icterid hosts: *Philopterus quiscali* Osborn, 1896 (ex *Quiscalus quiscula* (Linnaeus, 1758)) and *Philopterus agelaii* Osborn, 1896 (ex *Agelaius phoeniceus* (Linnaeus, 1766)). No detailed descriptions or illustrations of either of these species have been published, and both species are in need of redescription.

From Osborn's descriptions of both species, and the illustration of *P. quiscali* (*P. agelaii* not illustrated in Osborn 1896, but said to be similar to *P. quiscali*), these two species can be separated from *P. coriaceus* sp. nov. by the following characters: preantennal head proportionately wider in *P. quiscali* than in *P. coriaceus* sp. nov. (Fig. 39); dorsal anterior plate with broad posterior extension in *P. quiscali,* but with slender posterior extension in *P. coriaceus* sp. nov. (Fig. 39); tergopleurites of *P. quiscali* extending only about halfway to midline of abdomen on each side, whereas those of *P. coriaceus* sp. nov. are much longer in both sexes, almost reaching midline in more posterior segments in male. Chaetotaxy is not given for either *P. quiscali* or *P. agelaii*, but Osborn's illustration of *P. quiscali* has only apertures for 6 setae illustrated on each of the tergopleurites of segment II. In *P. coriaceus* sp. nov. there are 8 setae placed on each of the tergopleurites of this segment in both sexes (Figs 37–38); however, the number of

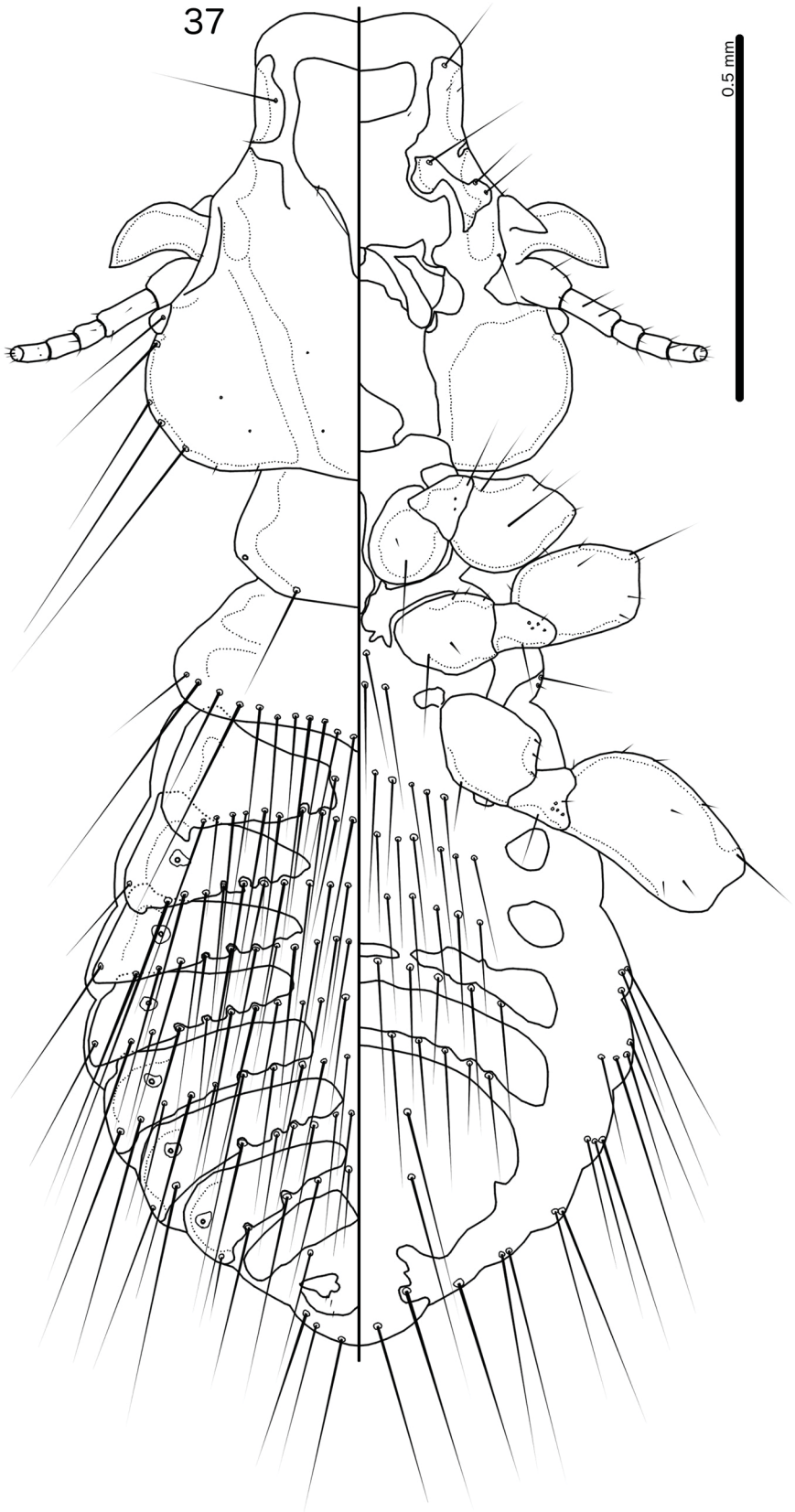


Fig. 37. *Philopterus coriaceus* sp. nov. ex *Molothrus oryzivorus oryzivorus* (Gmelin, 1788), male habitus, dorsal and ventral views.

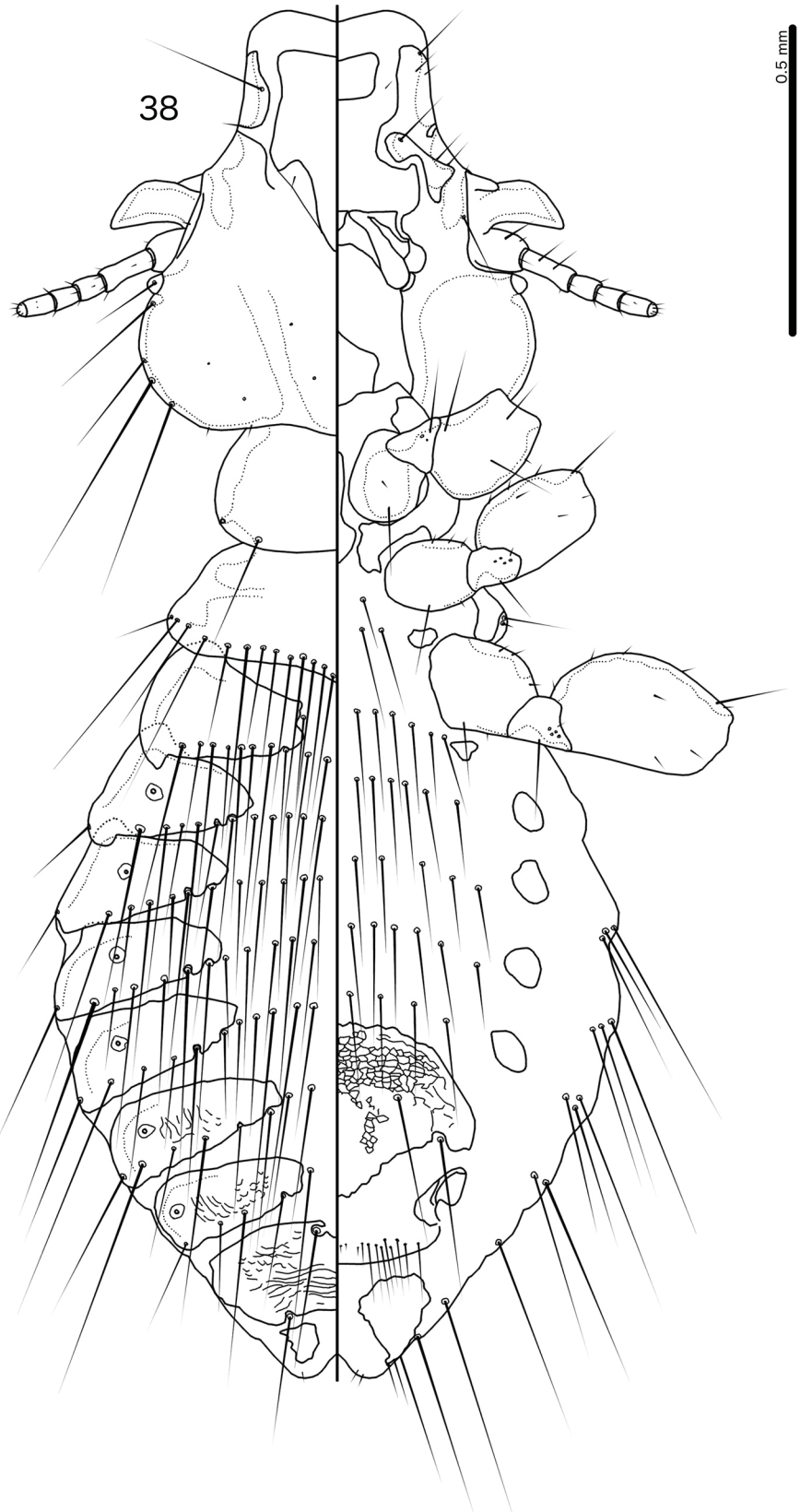


Fig. 38. *Philopterus coriaceus* sp. nov. ex *Molothrus oryzivorus oryzivorus* (Gmelin, 1788), female habitus, dorsal and ventral views.

setae situated median to the tergopleurites in *P. quiscali* is unknown. In specimens of *P. agelaii* deposited at the NHMUK, there are 7–8 setae on each side in females and 8–9 setae on each side in males, which overlap with the number of setae in *P. coriaceus* sp. nov.; one seta on each side is situated median to the tergopleurites in both sexes of the NHMUK specimens of *P. agelaii*. In addition, Osborn (1896: 220) mentioned "brown spots on each segment back to the eighth [= IX+X]; those on the sixth segment [= VII] form the outer portion of the genital patch." Osborn (1896) further stated that the "lateral spots" of *P. agelaii* are "small, rather elongated, oblique"; it is not clear whether he was describing the male or the female, but his illustration is of a male. We interpret these spots as the overlap of the median section of the tergopleurites with either the lateral accessory sternal plates (in segments II–VI) or the subgenital plate (segments VII–XI+X). This overlap often shows as darker brown spots than the rest of the tergopleurite. This suggests that the central sternal plates are absent on segments II–VI in *P. quiscali* and *P. agelaii*, whereas these are present on male segments V–VII in *P. coriaceus* sp. nov. (Fig. 37).

Etymology

The specific name is derived from Latin '*coriaceo*' for 'leather-like', referring to the colour and texture of the abdominal plates.

Material examined

Holotype

PERU • ♂ (marked with black dot on slide); Hacienda Amazonia, near Atalaya, Department of Madre de Dios; 4 Nov. 1985; S.M. Lanyon leg.; ex *Molothrus oryzivorus oryzivorus* (as *Scaphidura oryzivora*); "1032"; NHMUK.

Paratypes

PERU • 1 ♂, 2 ♀♀; same collection data as for holotype; NHMUK.

Type host

Molothrus oryzivorus oryzivorus (Gmelin, 1788) – giant cowbird (Icteridae).

Description

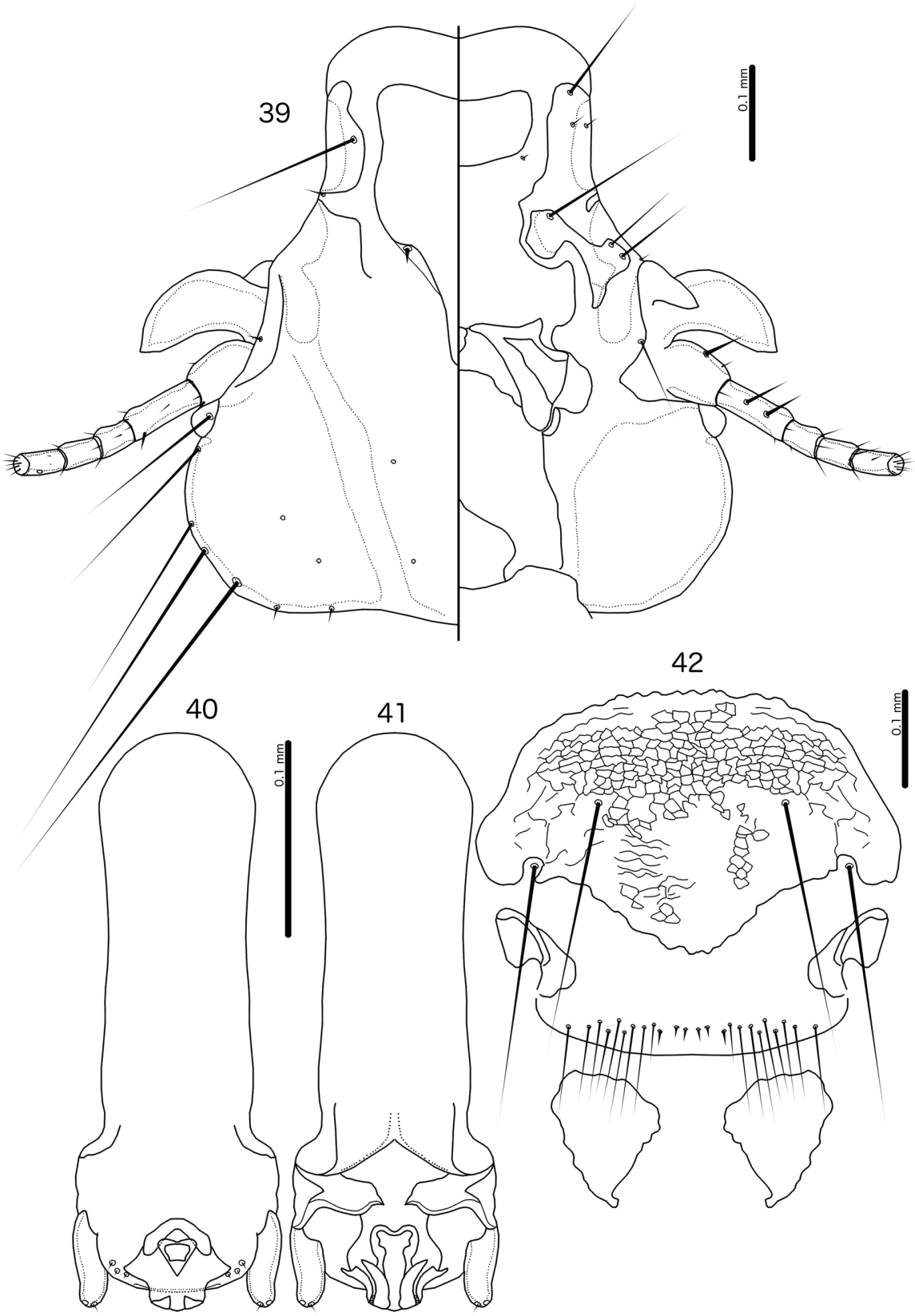
Head shape and chaetotaxy as in Fig. 39, preantennal area broad. Hyaline margin broad, shallowly concave medianly, extending laterally slightly beyond marginal carina. Dorsal preantennal plate narrowing gently posteriorly, *ads* situated in transparent section. Ventral anterior plate roughly trapezoidal, anterior margin concave. Coni long, broad, pointed posteriorly. Gular plate large, irregular. Thoracic and abdominal segments as in Figs 37–38. Measurements as in Table 6.

Male

Thoracic and abdominal chaetotaxy as in Fig. 37 and Tables 2–4. Tergopleurite VIII interrupted medianly. Central sternal plates absent from segments II–IV, present but fragmented on segment V, and present on segment VI. Lateral accessory plates present on segments II–IV, present and fused to central sternal plates on segments V–VI. Subgenital plate large, lateral incisions shallow or absent, lateral accessory plate of segment IX+X fused to subgenital plate. Basal apodeme long, rectangular (Figs 40–41). Mesosomal thickening about as broad as long, laterally pointed on dorsal side, with roughly crescent-shaped sclerotization in anterior end and triangular sclerotization centrally; 3 microsetae on each side of mesosome. Gonopore bilobed anteriorly, distal part as in Fig. 41. Parameres short, stocky (Figs 40–41); *pst1–2* as in Figs 40–41.

Female

Thoracic and abdominal chaetotaxy as in Fig. 38 and Tables 2–4. Tergopleurites VI–IX+X with slight to extensive reticulation median to spiracle openings. Central sternal plates absent on segments



Figs 39–42. *Philopterus coriaceus* sp. nov. ex *Molothrus oryzivorus oryzivorus* (Gmelin, 1788). **39**. Male head, dorsal and ventral views. **40**. Male genitalia, dorsal view. **41**. Male genitalia, ventral view. **42**. Female subgenital plate, vulval margin, and subvulval plates, ventral view.

II–VI. Lateral accessory plates present on segments II–VI. Subgenital plate as in Fig. 42, reticulation prominent. Lateral sclerotizations of vulval area extended to vulval margin, chaetotaxy as in Fig. 42 and Table 3; short vulval setae thorn-like. Subvulval plates broad, roughly triangular, each with small postero-median projection.

Remarks

Philopterus coriaceus sp. nov. is only the third species of *Philopterus* described from icterid hosts. This is surprising, as hosts in this family have been examined extensively, and many other species of ischnoceran lice are known from icterid hosts (e.g., Cicchino 1990, 2004; Cicchino & Castro 1996; Valim & Palma 2012). However, two previous studies have found comparatively low infestation rates of *Philopterus* on icterid hosts: 11.5% of examined red-winged blackbirds, *Agelaius phoeniceus* (Linnaeus, 1766) (Spory 1965) and 4.1% of brown-headed cowbirds, *Molothrus ater* (Boddaert, 1783) (Hahn *et al*. 2000).

The lack of records of *Philopterus* complex lice on icterid hosts may be related to the presence of lice of the genus *Bizarrifrons* Eichler, 1938 on some icterid hosts. This genus belongs to the *Brueelia* complex (Valim & Palma 2012; Gustafsson & Bush 2017) and is also considered to belong to the 'head louse ecomorph'. Competition may influence the distribution of these lice, but more ecological information is needed to assess any potential interactions between these species.

Both *P. agelaii* and *P. quiscali* are in need of redescription before an adequate comparison between these species and *P. coriaceus* sp. nov. can be made. It is not clear what gender of *P. quiscali* was described by Osborn (1896); however, Emerson (1960) noted that only one female and a nymph are present in Osborn's collection at Ohio State University, Columbus, Ohio. Emerson (1960) designated the female as the lectotype, stating that a female was illustrated. This seems incorrect, as the illustrated specimen has a rounded terminal abdomen and no medianly continuous tergopleurite, suggesting that it is a male. If so, the illustrated male is likely lost.

Philopterus pseudhirundo sp. nov.
urn:lsid:zoobank.org:act:5D816C2B-A805-4804-ABEB-9C90AC672D3F
Figs 43–48; Tables 2–4, 6

Diagnosis

Philopterus pseudohirundo sp. nov. belongs to the same group as other species of *Philopterus* known from hirundinid hosts (see Table 7). Of these, only *P. excisus* Nitzsch, 1818 (ex *Delichon urbicum* (Linnaeus, 1758)), and *P. microsomaticus* Tandan, 1955 (ex *Hirundo rustica rustica* Linnaeus, 1758), were illustrated and described in sufficient detail for an adequate comparison to be made. Characters supporting this relationship include the strongly bilobed hyaline margin (Fig. 45), the somewhat splayed distal male genitalia (Figs 46–47), and the general shape of the head (Fig. 45).

Philopterus pseudhirundo sp. nov. can be separated from *P. excisus* by the following characters (see Tandan (1955) and Clay & Hopkins (1960) for partial illustrations and redescriptions of *P. excisus*): preantennal area longer and narrower in *P. pseudhirundo* sp. nov. than in *P. excisus*; abdominal segments IV–V in male *P. excisus* with 6–8 pleural setae on each side, but with only 4–5 pleural setae on each side in *P. pseudhirundo* sp. nov. (Fig. 43); male sternal plate V interrupted medianly in *P. excisus,* but medianly continuous in *P. pseudhirundo* sp. nov.; distal margin of male genitalia (ignoring gonopore) convex in *P. excisus*, but concave in *P. pseudhirundo* sp. nov. (Figs 46–47); mesosome with wide angular lateral margins in *P. excisus*, but with slender rounded lateral margins in *P. pseudhirundo* sp. nov. (Fig. 47); parameres reach about as far distally as mesosome in *P. excisus*, but much father distally in

P. pseudhirundo sp. nov. (Figs 46–47); anterior end of mesosome in *P. excisus* different in shape from that of *P. pseudhirundo* sp. nov. (Fig. 46).

Philopterus pseudhirundo sp. nov. can be separated from *P. microsomaticus* by the following characters: male tergopleurite II with 4–7 (typically 6) setae on each side in *P. microsomaticus*, but with 8 setae on each side in *P. pseudhirundo* sp. nov. (Fig. 43); male genitalia with concave distal margin (ignoring gonopore) in *P. pseudhirundo* sp. nov. (Figs 46–47), but with protruding distal end in *P. microsomaticus*; mesosome protruding distally to parameres in *P. microsomaticus*, but not in *P. pseudhirundo* sp. nov. (Figs 46–47); anterior margin of dorsal mesosome with blunt angle in *P. microsomaticus*, but with acute angle in *P. pseudhirundo* sp. nov. (Fig. 46).

The sclerotized median section of the hyaline margin was not mentioned by either Tandan (1955) or Clay & Hopkins (1960); however, in specimens of *P. microsomaticus* we have examined, the sclerotized median section is evident. Presumably, this character also occurs in other species of *Philopterus* from hirundinid hosts, but this has to be verified.

Etymology

The specific name is derived from the type host genus.

Material examined

Holotype

NO LOCALITY • ♂; South Africa?; 5 Jun. 1950; [F.] Zumpt leg.; ex *Pseudhirundo griseopyga* (as *Hirundo griseopygia*); "S-125, I.N. 1373/26"; MFN.

Paratype

NO LOCALITY • 1 ♀; same collection data as for holotype; MFN.

Type host

Pseudhirundo griseopyga Sundevall, 1850 – gray-rumped swallow (Hirundinidae).

Description

Head shape and chaetotaxy as in Fig. 45, preantennal area narrow. Hyaline margin wide, extending laterally beyond marginal carina, deeply concave medianly; weak sclerotization in mid-section. Dorsal anterior plate elongated, shape as in Fig. 45. Ventral anterior plate small, anterior margin deeply concave. Coni small, blunt, directed laterally. Gular plate short, broad. Thoracic and abdominal segments as in Figs 43–44. Measurements as in Table 6.

Male

Thoracic and abdominal chaetotaxy as in Fig. 43 and Tables 2–4. Medianly continuous sternal plates present on segments V–VI, lateral accessory plates present on segments II–IV. Basal apodeme slender (Figs 46–47), widening markedly in distal end. Mesosome as in Fig. 47, with 3 microsetae on each side. Parameres short, blunt (Figs 46–47), with *pst1–2* apical.

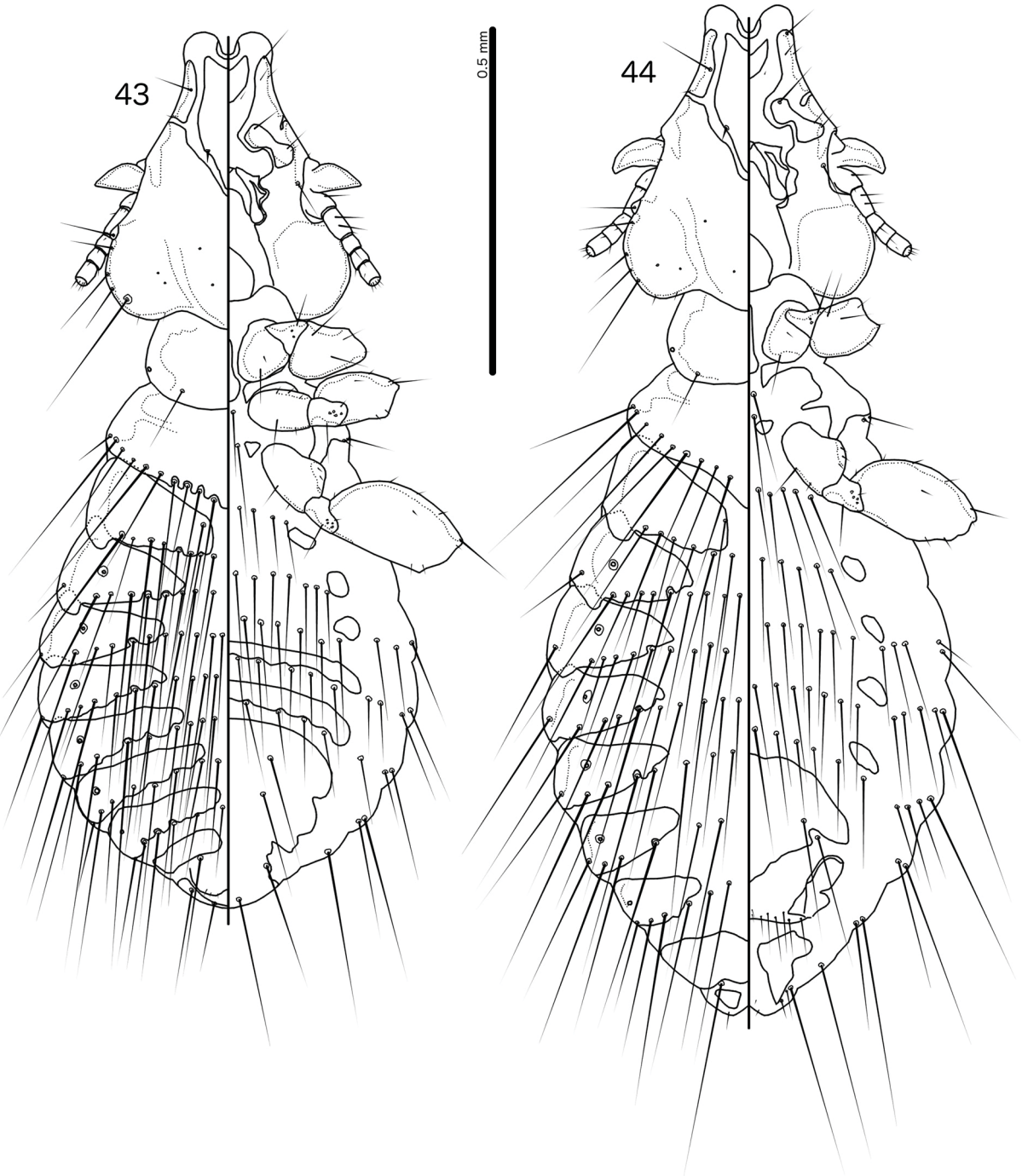
Female

Leg II on both sides of the only examined female missing or distorted, not illustrated. Thoracic and abdominal chaetotaxy as in Fig. 44 and Tables 2–4. Central sternal plates absent, lateral accessory plates present on segments III–VI. Subgenital plate and vulval margin as in Fig. 48; chaetotaxy as in Fig. 48 and Table 3. Lateral sclerotizations of vulval area extended to vulval margin. Subvulval plates elongated triangular.

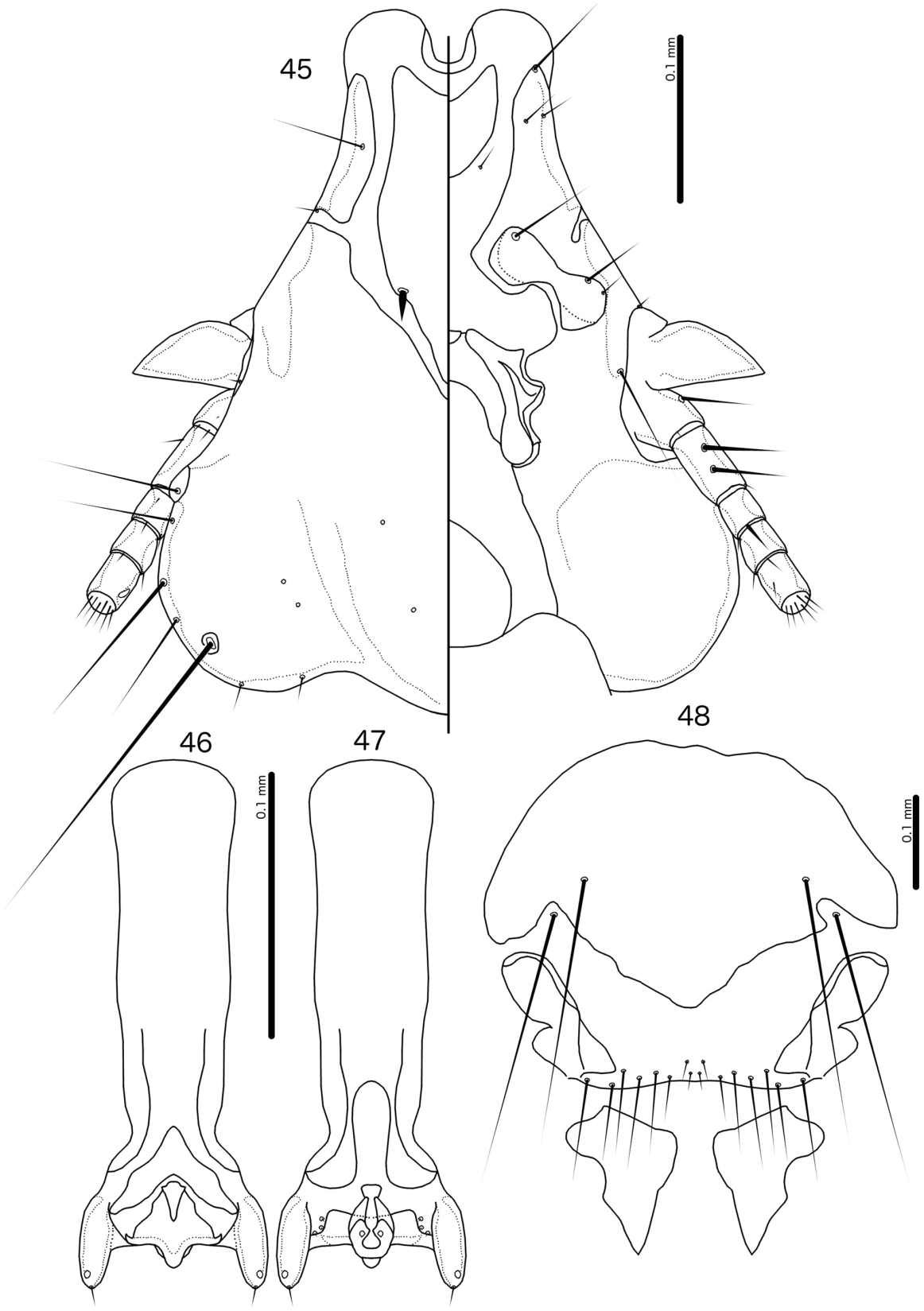
Remarks

The collection locality is not given on the slide, but the host is restricted to Africa (Turner & Rose 1994), and Zumpt's collections are otherwise mainly from South Africa (Ledger 1980).

Conci (1941) described the genus *Cypseloecus* for the *Philopterus* species on swallows (Hirundinidae) and swifts ("Cypseli" = Apodiformes); however no *Philopterus* complex lice occur on swifts, and the name is thus a misnomer. This erroneous host range may be a result of earlier authors believing



Figs 43–44. *Philopterus pseudhirundo* sp. nov. ex *Pseudhirundo griseopyga* Sundevall, 1850. **43**. Male habitus, dorsal and ventral views. **44**. Female habitus, dorsal and ventral views.



Figs 45–48. *Philopterus pseudhirundo* sp. nov. ex *Pseudhirundo griseopyga* Sundevall, 1850. **45**. Male head, dorsal and ventral views. **46**. Male genitalia, dorsal view. **47**. Male genitalia, ventral view. **48**. Female subgenital plate, vulval margin, and subvulval plates, ventral view.

Pediculus hirundinis Schrank, 1803 (= *Philopterus hirundinis* (Schrank, 1803)) to be the same as *Pediculus hirundinis* Linnaeus, 1758 (= *Dennyus hirundinis* (Linnaeus, 1758)). Clay & Hopkins (1950, 1960) showed that these names refer to different species, of which only the latter occurs on swifts. To date, nine species of *Philopterus* have been described from swallows (Table 7), all of which fall into the "*Cypseloecus*" group; if the genus *Cypseloecus* Conci, 1941 is resurrected, all the species listed here should be included in that genus based on their descriptions and published illustrations.

Hopkins & Clay (1952), Price *et al*. (2003), and Mey (2004) considered *Cypseloecus* inseparable from *Philopterus*. Mey (2004) stated that the only notable character of this group is the bilobed state of the hyaline margin. We here describe a new species of *Philopterus* from a swallow, *P. pseudhirundo* sp. nov. This species exhibits several characteristics that seem to indicate that the *Philopterus* from swallows may be more different from *Philopterus* s. str. than previously believed. However, the relationships within *Philopterus* s. lat. are poorly known, and it is not clear which morphological characters are useful for the delimitation of groups within *Philopterus* s. lat.

The most distinctive character of the "*Cypseloecus*" group is the preantennal area. Compared to most other species of *Philopterus*, the preantennal area is narrow and elongated in "*Cypseloecus*," with a deeply concave frons and distinctly bilobed hyaline margin. As can be seen in the species of *Philopterus* described here, the shape of the preantennal area and the hyaline margin vary greatly between different species in the genus (cf., e.g., Figs 3, 9, 39). In most of the *Philopterus* from corvid hosts (including the type species, *P. ocellatus*; see Price & Hellenthal 1998), the frons is more or less flat, convex, or only slightly concave. Even in species of *Philopterus* where the frons is concave (e.g., Fig. 3), the lateral parts of the hyaline margin do not form distinct, narrow lobes as in "*Cypseloecus*".

In *P. pseudhirundo* sp. nov., the central part of the hyaline margin is sclerotized (Fig. 45), which makes the head superficially resemble that of many species of *Philopteroides* Mey, 2004. However, this character is not illustrated or mentioned in the descriptions of any other species in "*Cypseloecus*." We have examined some specimens of *P. microsomaticus* at the Museum of Natural History, University of Wroclaw, Poland. These all have a median sclerotization similar to that of *P. pseudhirundo* sp. nov. Presumably, this sclerotization occurs in other species of "*Cypseloecus*" as well, but we have not examined any of them. No other species of *Philopterus* from other host families have this sclerotization, but it occurs in many other genera in the *Philopterus* complex (Mey 2004).

The male genitalia are also distinct in "*Cypseloecus*," with a rather flat distal margin of the mesosome and somewhat flaring parameres (Figs 45–46). This is unlike the genitalia of most other species described here, which have a more rounded distal margin of the mesosome and more convergent parameres (e.g., Figs 22–23). However, the type species of *Philopterus*, and most other species from corvid hosts, have genitalia that are more similar to those of "*Cypseloecus*" than to most of the other species described here. Moreover, some species of *Philopterus* on non-hirundinid hosts have genitalia that are intermediate between the two types (e.g., *P. stansburyensis* sp. nov.; Figs 34–35). Too little is known about the more detailed structure of the mesosome and other parts of the genitalia in the *Philopterus* complex to make a more detailed comparison.

In our opinion, these differences are not sufficient, based on our current knowledge, to recognize *Cypseloecus* as a distinct genus within the *Philopterus* complex, but are perhaps sufficient to recognize it as a subgenus within *Philopterus*. Potentially, at least three groups are involved: *Philopterus* s. str. from corvid hosts, with simple hyaline margin, typically short preantennal areas, and splayed male genitalia; "*Cypseloecus*" from hirundinid hosts, with a deeply bilobed hyaline margin with median sclerotization, slender and elongated preantennal area, and splayed genitalia; and *Philopterus* s. lat. (=? *Docophorulus* Eichler, 1944) from other hosts, with an intermediate hyaline margin, typically short preantennal areas,

Table 7. Checklist of the known distribution of species of the genus *Philopterus* Nitzsch, 1818 on swallows (Hirundinidae). Type host species are indicated by an asterisk (*).

Louse species	Host species	Remark
Philopterus breviformis (Kellogg & Kuwana, 1902)	**Progne modesta* Gould, 1839	1
Philopterus dathei (Eichler in Niethammer, 1956)	**Tachycineta albiventer* (Boddaert, 1783)	
Philopterus diasi Tendeiro, 1958	**Hirundo smithii smithii* Leach & Koenig, 1818	2
Philopterus domesticus (Kellogg, 1896)	**Progne subis* (Linnaeus, 1758)	
Philopterus excisus Nitzsch, 1818	**Delichon urbicum* (Linnaeus, 1758)	3
	Petrochelidon spilodera (Sundevall, 1815)	4
	Riparia riparia (Linnaeus, 1758)	5
Philopterus major (Kellogg, 1896)	**Petrochelidon pyrrhonota* (Vieillot, 1817)	6
	Tachycineta bicolor (Vieillot, 1808)	
Philopterus microsomaticus Tandan, 1955	*Cecropsis abyssinica* (Guérin-Méneville, 1843)	7
	Hirundo neoxena Gould, 1842	8
	**Hirundo rustica rustica* Linnaeus, 1758	9
Philopterus pseudhirundo **sp. nov.**	**Pseudhirundo griseopyga* Sundevall, 1850	
Philopterus tropicalis Carriker, 1956	*Stelgidopteryx ruficollis* (Vieillot, 1817)	10
	**Stelgidopteryx serripennis* (Audubon, 1838)	
Philopterus sp.	*Progne chalybea* (Gmelin, 1789)	11
	Progne dominicensis (Gmelin, 1789)	11
	Progne tapera fusca (Vieillot, 1817)	11
	Progne tapera tapera (Linnaeus, 1766)	11

Remarks:

1) Kellogg & Kuwana (1902) reported this species from two non-hirundinid hosts from the Galápagos Islands. These records are most probably the result of human contamination, as discussed by Palma (1994) and Palma & Peck (2013). A lectotype of this species was designated by Palma & Peck (2013).
2) Ledger (1980) considered this species a synonym of *P. microsomaticus* based on similarities in measurements. Price *et al*. (2003) listed it as a valid species.
3) Redescribed and partially illustrated by Clay & Hopkins (1960). Additional illustrations in Tandan (1955).
4) Złotorzycka *et al*. (1999).
5) Balát (1966).
6) Price *et al*. (2003) listed both hosts as type hosts, thus overlooking that Carriker (1957) selected a lectotype and designated *Petrochelidon pyrrhonota* as the type host of *P. major*. No illustration of this species has been published, and the description is very short and unhelpful. This species urgently needs redescription.
7) Ledger (1980).
8) Palma & Barker (1996).
9) Records of *P. excisus* from *Hirundo rustica* have here tentatively been interpreted as *P. microsomaticus*; however, none of this material has been examined for this study, and both *P. excisus* and *P. microsomaticus* may occur on *H. rustica* in different parts of the range.
10) Clayton *et al*. (1992).
11) Carriker (1956).

and convergent parameres. Most likely, the morphological variation in this latter group is sufficient to recognize further subgeneric or generic groups, some of which may not be recognizable based on published illustrations and descriptions. We do not propose any taxonomic changes at the genus level here, but note that a more thorough revision of *Philopterus* is needed. Such a revision should, in our opinion, include a consideration of resurrecting *Cypseloecus* as at least a subgenus within *Philopterus*.

Discussion

With the eight species described here, the numbers of known species in the *Philopterus* complex and the genus *Philopterus* (including *Cypseloecus*) are 224 and 193, respectively. All species of the complex described since the publication of the checklist in Price *et al*. (2003) are listed in Table 8. However, the number of species that can reliably be identified from published descriptions and illustrations is far lower. In general, somatic and setal characters appear to be rather uniform in *Philopterus*. For instance, all species described here have setal rows on abdominal segments II–VII in both sexes, but the number of setae typically overlaps between species. This suggests that these may be useful to separate closely related species, but less useful to establish relationships between distantly related species. Similarly, the head chaetotaxy is essentially the same in all species described here and varies little within the *Philopterus* complex in general, with the exception of some preantennal setae. Moreover, apart from differences in the development of the ventral and marginal carinae (Mey 2004), the head structure shows less variation within the *Philopterus* complex than in, e.g., the *Brueelia*, *Oxylipeurus*, and *Degeeriella* complexes.

This relative homogeneity in setal and somatic characters means that the characters that are usually illustrated for species of *Philopterus* in the published literature (e.g., outlines of heads, dorsal anterior plates, subgenital plates, etc.) are of little use to determine which species are closely related. In contrast, the differences in the structure and complexity of the male genitalia are evident from the species described here (cf., e.g., *P. afropari* sp. nov. (Figs 16–17) and *P. coriaceus* sp. nov. (Figs 40–41)). The size, shape, and structure of the mesosome, the location and presence or absence of mesosomal setae, the length and shape of the parameres, and the overall structure of the basal apodeme all vary between the species described here. In some cases, the structures seen in one species appear to have no counterpart in other species (e.g., the ventral plates near the anterior end of the mesosome in *P. coriaceus* sp. nov.; Fig. 41). This variation suggests that male genitalia may be the key to assessing the relationships among species of *Philopterus* and in evaluating whether or not this genus is monophyletic. Many of the details of the male genitalia illustrated here (e.g., mesosomal sensilla) are generally only visible at high magnifications using oil immersion and phase contrast. Limitations in microscope technology may explain why male genitalia have rarely been illustrated in sufficient detail to be of much use in the past. Notably, many of the characters used to establish species groups within *Philopterus* by Złotorzycka & Lucińska (1975, 1976) are from the male genitalia.

Moreover, it is presently difficult to assess patterns of host associations in *Philopterus*. Mey (2004) summarized the known host distributions of the *Philopterus* complex genera. Some of the gaps in his summary have now been filled (e.g., *Tyranniphilopterus* on Polioptilidae (Cicchino 2007); *Philopteroides* on Rhipiduridae (Valim & Palma 2013)), and the discovery of the new genus *Vinceopterus* Gustafsson *et al*., 2019 on trogons fell outside the framework of his summary. Nevertheless, few species of *Philopterus* have been described since 2004 (Table 8), and the outline published by Mey (2004) largely holds true today.

Mey's summary suggests that *Philopterus* as currently defined parasitizes a wide range of hosts representing most of the major radiations of passeriforms. However, the genus is not known from any suboscine hosts, and it appears to be largely replaced by *Tyranniphilopterus* in many primarily Neotropical host families and by *Philopteroides* in many exclusively Old World tropical host families; the correct placement of some poorly known *Philopterus* species from the Australo-Papuan region may also be questionable. The bulk of the species in *Philopterus* are thus found on host families that occur in the Holarctic. Notably, both *Philopteroides* and *Philopterus* are distributed across the two main radiations of Passeriformes, Corvides and Passerida, which may hint at a rich history of host switching in the evolution of the *Philopterus* complex. However, determining any such patterns of host switching or co-evolution will require a thorough revision of *Philopterus*. Useful characters to identify groups

Table 8 (continued on next 2 pages). Species of the *Philopterus* Nitzsch, 1818 complex described since the publication of the checklist in Price *et al.* (2003), with their host associations. The list also includes a few species that have been transferred to the *Philopterus* complex since 2003 (in Gustafsson & Bush 2017). In cases where a louse species is known from more than one host species or subspecies, the type host species or subspecies is indicated by an asterisk (*).

Louse species	Host species	Host group
Australophilopterus curviconus Mey, 2004	*Strepera fuliginosa fuliginosa* (Gould, 1837)	Passeriformes: Artamidae
Australophilopterus strepericus Mey, 2004	*Strepera versicolor arguta* Gould, 1846	Passeriformes: Artamidae
Cinclosomicola punctatica Mey, 2004	*Cinclosoma punctatum dovei* Mathews, 1912	Passeriformes: Cinclosomatidae
Clayiella dreophila Mey, 2004	*Leptosomus discolor discolor* (Hermann, 1783)	Leptosomiformes: Leptosomidae
Corcorides biocellatus Mey, 2004	*Struthidea cinerea cinerea* Gould, 1837	Passeriformes: Corcoracidae
Corcorides inopinatus Mey, 2004	*Corcorax melanorhamphos melanorhamphos* (Vieillot, 1817)	Passeriformes: Corcoracidae
Mayriphilopterus brevicephalus Mey, 2004	*Jacamerops aureus isidori* Deville, 1849	Galbuliformes: Galbulidae
Mayriphilopterus ernsti Mey, 2004	*Monasa morphoeus peruana* Sclater, 1856	Galbuliformes: Bucconidae
Mayriphilopterus galbulicus Mey, 2004	*Galbula cyanescens* Deville, 1849	Galbuliformes: Galbulidae
Mayriphilopterus nystalicus Mey, 2004	*Nystalus maculatus striatipectus* (Sclater, 1854)	Galbuliformes: Bucconidae
Paraphilopterus knutieae Gustafsson & Bush, 2014	*Amblyornis macgregoriae kombok* Schodde & McKean, 1973	Passeriformes: Ptilonorhynchidae
	Amblyornis macgregoriae nubicola Schodde & McKean, 1973 *	Passeriformes: Ptilonorhynchidae
	Archboldia sanfordi (Mayr & Gilliard, 1950)	Passeriformes: Ptilonorhynchidae
Paraphilopterus meyi Gustafsson & Bush, 2014	*Cnemophilus macgregorii macgregorii* De Vis, 1890 *	Passeriformes: Cnemophilidae
	Cnemophilus macgregorii sanguineus Iredale, 1948	Passeriformes: Cnemophilidae
Paraphilopterus styloideus Mey, 2004	*Corcorax melanorhamphos* (Vieillot, 1817)	Passeriformes: Corcoracidae
Philopteroides beckeri (Mey, 2004)	*Platysteira cyanea nyansae* Neumann, 1905	Passeriformes: Platysteiridae
Philopteroides cucphuongensis Mey, 2004	*Pycnonotus finlaysoni eous* Riley, 1940	Passeriformes: Pycnonotidae
Philopteroides flavala Najer & Sychra in Najer *et al*., 2012b	*Hemixos flavala* Blyth, 1845	Passeriformes: Pycnonotidae
Philopteroides fuliginosus Valim & Palma, 2013	*Rhipidura fuliginosa placabilis* Bangs, 1921	Passeriformes: Rhipiduridae

Table 8 (continued).

Louse species	Host species	Host group
Philopteroides gigas Najer *et al.*, 2016	*Paramythia montium brevicauda* Mayr & Gilliard, 1954	Passeriformes: Paramythiidae
	Paramythia montium montium De Vis, 1892 *	Passeriformes: Paramythiidae
Philopteroides macrocephalus Valim & Palma, 2013	*Petroica macrocephala macocephala* (Gmelin, 1789)	Passeriformes: Petroicidae
Philopteroides novaezelandiae Mey, 2004	*Acanthisitta chloris chloris* (Sparrman, 1787)	Passeriformes: Acanthisittidae
Philopteroides pilgrimi Valim & Palma, 2013	*Gerygone igata* (Quoy & Gaimard, 1830)	Passeriformes: Acanthizidae
Philopteroides sinancorellus Najer *et al.*, 2016	*Oreocharis arfaki* (Meyer, 1875)	Passeriformes: Paramythiidae
Philopteroides terpsiphoni Najer & Sychra in Najer *et al.*, 2012a	*Terpsiphone viridis* (Statius Müller, 1776)	Passeriformes: Monarchidae
Philopteroides xenicus Mey, 2004	*Xenicus longipes longipes* (Gmelin, 1789)	Passeriformes: Acanthisittidae
Philopterus aenas (Piaget, 1885)	*Motacilla alba* Linnaeus, 1758	Passeriformes: Motacillidae
Philopterus afropari **sp. nov.**	*Melaniparus cinerascens cinerascens* (Vieillot, 1818)	Passeriformes: Paridae
Philopterus capitis (Ansari, 1955)	*Copsychus fulicata cambaiensis* (Latham, 1790)	Passeriformes: Muscicapidae
Philopterus chilchil (Ansari, 1955)	*Turdoides caudata caudata* (Dumont, 1823)	Passeriformes: Timaliidae
Philopterus coriaceus **sp. nov.**	*Molothrus oryzivorus oryzivorus* (Gmelin, 1788)	Passeriformes: Icteridae
Philopterus gustafssoni Najer *et al.*, 2020	*Regulus ignicapillus* (Temminck, 1820)	Passeriformes: Regulidae
	Regulus regulus (Linnaeus, 1758)	Passeriformes: Regulidae
	Regulus regulus azoricus Seebohm, 1883	Passeriformes: Regulidae
	Regulus regulus buturlini von Loudon, 1911	Passeriformes: Regulidae
	Regulus regulus regulus (Linnaeus, 1758) *	Passeriformes: Regulidae
	Regulus regulus sanctaemariae Vaurie, 1954	Passeriformes: Regulidae
	Regulus regulus tristis Pleske, 1892	Passeriformes: Regulidae

Table 8 (continued).

Louse species	Host species	Host group
Philopterus hebes **sp. nov.**	*Chloropsis aurifrons inornata* Kloss, 1918 *	Passeriformes: Chloropseidae
	Chloropsis cochinchinensis kinneari Hall & Deignan, 1956	Passeriformes: Chloropseidae
Philopterus micropunctatus **sp. nov.**	*Anthus hodgsoni* Richmond, 1907	Passeriformes: Motacillidae
Philopterus nigellatus Mey, 2004	*Xenopirostris polleni* (Schlegel, 1868)	Passeriformes: Vangidae
Philopterus petrescuae Adam in Sychra *et al*., 2011	*Dicrurus hottentottus* (Linnaeus, 1766)	Passeriformes: Dicruridae
Philopterus pseudhirundo **sp. nov.**	*Pseudhirundo griseopyga* Sundevall, 1850	Passeriformes: Hirundinidae
Philopterus sinensis **sp. nov.**	*Hemipus picatus capitalis* (Horsfield, 1840)	Passeriformes: Vangidae
Philopterus stansburyensis **sp. nov.**	*Pheucticus melanocephalus melanocephalus* (Swainson, 1827)	Passeriformes: Cardinalidae
Philopterus trepostephanus **sp. nov.**	*Tephrodornis virgatus mekongensis* Meyer de Schauensee, 1946	Passeriformes: Vangidae
	Tephrodornis virgatus fretensis Robinson & Kloss, 1920	Passeriformes: Vangidae
Tyranniphilopterus caiolukasi Valim, 2006	*Tolmomyias sulphurescens* (Spix, 1825)	Passeriformes: Tyrannidae
Tyranniphilopterus delicatulus Mey, 2004	*Elaenia albiceps modesta* Tschudi, 1844	Passeriformes: Tyrannidae
Tyranniphilopterus polioptilus Cicchino, 2007	*Polioptila dumicola dumicola* (Vieillot, 1817)	Passeriformes: Polioptilidae
Tyranniphilopterus toledo Sychra in Sychra *et al*., 2010	*Chiroxiphia linearis* (Bonaparte, 1838)	Passeriformes: Pipridae
Tyranniphilopterus venezuelensis Mey, 2004	*Myiodynastes maculatus maculatus* (Statius Müller, 1776)	Passeriformes: Tyrannidae
Vinceopterus erythrocephali Gustafsson *et al*., 2019a	*Harpactes erythrocephalus erythrocephalus* (Gould, 1834)	Trogoniformes: Trogonidae
	Harpactes erythrocephalus helenae Mayr, 1941	Trogoniformes: Trogonidae
	Harpactes erythrocephalus yamakanensis Rickett, 1899 *	Trogoniformes: Trogonidae
Vinceopterus mindanensis Gustafsson *et al*., 2019a	*Harpactes ardens ardens* (Temminck, 1826) *	Trogoniformes: Trogonidae
	Harpactes ardens linae Rand & Rabor, 1959	Trogoniformes: Trogonidae

within *Philopterus* will need to be detected and evaluated before specimens used either for molecular or morphological analysis can be properly identified. The male genitalia appear to constitute an excellent source for such characters, but these need to be better described for almost all known species in the *Philopterus* complex.

Acknowledgements

This research was funded by grant 36/07 1.4 from the Swedish Taxonomic Initiative, grant NSF-DEB-1050706, NSF 1926738, the Introduction of Full-Time High-Level Talent Fund of the Guangdong Academy of Sciences grant 2018GDASCX-0809, GDAS Special Project of Science and Technology Development grants 2017GDASCX-0107 and 2018GDASCX-0107, and GIABR-GJRC201701, and the Pearl River Talent Recruitment Program of Guangdong Province, grant 2019QN01N968. These agencies had no influence in the design or execution of this study, and we declare no conflict of interest. Two anonymous reviewers provided helpful comments during the review of this manuscript, for which we are very grateful.

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Manuscript received: 7 December 2020
Manuscript accepted: 18 November 2021
Published on: 4 February 2022
Topic editor: Nesrine Akkari
Desk editor: Danny Eibye-Jacobsen