FIVE NEW SPECIES OF *GUIMARAESIELLA* (PHTHIRAPTERA: ISCHNOCERA) FROM BROADBILLS (AVES: PASSERIFORMES: CALYPTOMENIDAE, EURYLAIMIDAE)

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Abstract: Five new species of *Guimaraesiella* Eichler, 1949, are described and illustrated from hosts in the Eurylaimidae and Calyptomenidae. They are: *Guimaraesiella khlongkhlungensis* **n. sp.** from *Corydon sumatranus laoensis* Meyer de Schauensee, 1929; *Guimaraesiella latirostris* **n. sp.** from *Eurylaimus ochromalus* Raffles, 1822;

Guimaraesiella cyanophoba **n. sp.** from *Cymbirhynchus macrorhynchus malaccensis* Salvadori, 1874 and *C. m. siamensis* Meyer de Schauensee & Ripley, 1940; *Guimaraesiella altunai* **n. sp.** from *Calyptomena viridis caudacuta* Swainson, 1838; *Guimaraesiella forcipata* **n. sp.** from *Eurylaimus steerii steerii* Sharpe, 1876. These represent the first species of *Guimaraesiella* described from the Calyptomenidae and Eurylaimidae, as well as the first species of this genus described from the Old World suboscines.

KEY WORDS: Phthiraptera, Ischnocera, Philopteridae, *Brueelia*-complex, *Guimaraesiella*, Eurylaimidae, Calyptomenidae, broadbill, new species

Ischnoceran chewing lice belonging to the *Brueelia*-complex are widely distributed across the oscine passeriforms (Gustafsson & Bush, 2017). By contrast, suboscine passeriforms are generally parasitized either by lice belonging to other complexes (*e.g.* the *Rallicola*- or *Degeeriella*-complexes; Carriker, 1956; Somadder and Tandan, 1977; summarized in Table 1) or by lice belonging to genera closely related to the *Brueelia*-complex (Bush et al., 2016), but not part of this complex as defined by Gustafsson & Bush (2017). Most of the chewing louse genera occurring on suboscine hosts are not known from hosts in other groups. For instance, the genus *Debeauxoecus* Conci, 1941 is only known from hosts in the Pittidae, and the genera *Furnaricola* Carriker, 1944, *Furnariphilus* Price and Clayton, 1995, *Formicaricola* Carriker, 1957, and *Formicaphagus* Carriker, 1957, are all known only from New World suboscines. In general, oscine and suboscine passeriforms are thus parasitized by lice belonging to different groups, reflecting the basal division between the oscines and the suboscines within Passeriformes (Barker et al. 2004).

The principal exception to this general rule are the few species of *Brueelia* Kéler, 1936, and *Guimaraesiella* Eichler, 1949, known from a small number of furnariid and tyrannid hosts (*e.g.* Carriker, 1963; Cicchino, 1981, 1983). These are all typical representatives of their respective genera, and may be derived from comparatively recent host switches from oscine to suboscine hosts. Morover, Gustafsson & Bush (2017) described the genus *Psammonirmus* for a single *Brueelia*-complex species from a eurylaimid host, *Serilophus lunatus* (Gould, 1834). No representative of this species was included in the phylogeny of the *Brueelia*-complex of Bush et al. (2016), and the genus is not morphologically close to any other genus in this complex, and thus hard to place.

We here describe five additional species of chewing lice from the Eurylaimidae and the Calyptomenidae that challenge this general pattern. All five species are typical members of *Guimaraesiella* Eichler, 1949, and are morphologically similar to the type species of the genus, *Guimaraesiella papuana* (Giebel, 1879).

MATERIAL AND METHODS

Examined specimens are deposited in the Berenice Pauahi Bishop Museum, Honolulu, Hawaii (BPBM), Natural History Museum, London, United Kingdom (NHML), Oklahoma State University, Stillwater, Oklahoma (OSUS), University of Minnesota, St. Paul, Minnesota (UMSP), Zoological Institute of Russian Academy of Sciences (ZIN) as indicated below under each species. All specimens are slide-mounted in Canada balsam. Drawings were done through a drawing tube, and edited in GIMP (www.gimp.org).

Terminology and abbreviations for setal, structural and genitalic characters follow Gustafsson and Bush (2017). Measurements (Table 2) are given in millimeters for the following dimensions: TL = total length (along midline); HL = head length (along midline); HW = head width (at temples); PRW = prothoracic width; PTW = pterothoracic width; AW = abdominal width (at segment V). Host taxonomy follows Clements et al. (2018).

DESCRIPTION

PHTHIRAPTERA Haeckel, 1896

Ischnocera Kellogg, 1896

Philopteridae Burmeister, 1838

The *Brueelia*-complex

***Guimaraesiella* Eichler, 1949**

Nirmus Nitzsch, 1818: 291 (*in partim*).

Degeeriella Neumann, 1906: 60 (*in partim*).

Brueelia Kéler, 1936: 257 (*in partim*).

Xobugirado Eichler 1949: 13.

Allobrueelia Eichler, 1951: 36 (*in partim*).

Allobrueelia Eichler, 1952: 74 (near-verbatim redescription).

Allonirmus Złotorzycka, 1964: 263.

Nitzschnirmus Mey & Barker, 2014: 101.

Callaenirmus Mey, 2017: 92.

Philemoniellus Mey, 2017: 145.

Type species. *Docophorus subalbicans* Piaget, 1885: 6 [= *Docophorus papuanus* Giebel, 1879: 475], by original designation.

Remarks. Gustafsson et al. (2019a) recently described the subgenus *Guimaraesiella* (*Cicchinella*) for species of *Guimaraesiella* parasitizing babblers. All species described here are members of the nominal subgenus, *Guimaraesiella* (*Guimaraesiella*). Within this subgenus, we here establish an informal "core *Guimaraesiella*" group, which consists of all those species found in clade A-1 of the phylogeny of Bush et al. (2016; fig. 3), as well as those more closely related to this group than to other groups within *Guimaraesiella*. All species described here are part of this "core" *Guimaraesiella* group.

Morphological characterization of this group is difficult, due to high variation in many characters. However, typical members of this group are similar to the type species [*G. papuana* (Giebel, 1874)], which was redescribed and illustrated by Gustafsson and Bush (2017; 224–231, figs 354–360). In particular, the following characters are typical for this group: dorsal preantennal suture does not separate dorsal anterior plate; female subgenital plate lacks complete cross-piece (but may have lateral submarginal bulges or extensions); ventral sclerite of mesosome with single anterior extension; gonopore terminal; mesosome without rugose nodi.

The only described Southeast Asian species of "core" *Guimaraesiella* that have at least slightly concave lateral margins of the preantennal area are *Guimaraesiella papuana* (Giebel, 1879), *G. cucphuongensis* (Najer [in Najer et al.] 2012), and *Guimaraesiella wallacei* (Mey and Barker, 2014); *Olivinirmus borneensis* Mey, 2017, may also belong to this group, but its generic position cannot be determined unambiguously from the original description. None of these species are particularly similar morphologically to the species treated here; for instance, with the exception of *G. papuana* all these species have shorter and blunter preantennal areas. *Guimaraesiella papuana* can be separated from all species described here by the much simpler structure of the male mesosome and by the absence in *G. papuana* of *ps* on male abdominal segment IV (see Gustafsson and Bush, 2017).

The genus *Guimaraesiella* is in great need of revision, and the majority of the morphological variation we have seen within this genus is in undescribed species. We therefore do not presently give this group a formal name. More detailed examinations of the variation and relationships within this genus are in preparation, and we therefore do not provide a complete list of species included in the "core" group here. Further examples of the morphological variation within this "core" group can be found in Gustafsson et al. 2019b.

***Guimaraesiella khlongkhlungensis* n. sp.**

(Figs 1–7)

Description *Both sexes:* Head broadly trapezoidal (Fig. 3), lateral margins of preantennal head slightly concave, frons broadly concave. Marginal carina of moderate, irregular, width, interrupted laterally and submedianly. Dorsal preantennal carina reaching *dsms*, *ads*, and lateral head margins, extending slightly median to *ads*. Ventral anterior plate somewhat elongated. Dorsal anterior plate not separate, longer than wide. Head chaetotaxy as in Fig. 3. Preantennal nodi moderate, bulging. Preocular nodi much larger than minute postocular nodi. Marginal temporal carina narrow, of even width. Gular plate broadly with median point. Thoracic and abdominal segments as in Figs 1–2. Leg seta *fI-v4* absent.

Male: Thoracic and abdominal chaetotaxy as in Fig. 1; *ps* present on segment III; *aps* present on tergopleurite IV in some specimens, but not illustrated here; *aps* present on tergopleurite V; tergopleurite VIII with three setae on each side (not counting trichobothrium). Basal apodeme with slightly concave lateral margins (Fig. 4). Proximal mesosome substantially overlapping basal apodeme, anterior margin flat, antero-lateral corners with blunt hooks. Ventral sclerite with one anterior extension; chaetotaxy as in Fig. 5. Distal mesosome without noticeable lateral lobes, lateral margins almost parallel. Gonopore roughly quadratic, lateral margins serrated. Parameral heads rounded; parameral blades short, convergent, distal ends slightly elongated; *pst1–2* as in Fig. 6.

Female: Thoracic and abdominal chaetotaxy as in Fig. 2; abdominal segment III with 1 *ps* on each side. Vulval margin (Fig. 7) slightly convex. Subgenital plate broad distally, with narrow submarginal bulges; 0–4 short, slender *vms* and 4–6 short, thorn-like *vss* on each side; 3–5 short, slender *vos* on each side of subgenital plate, the most distal *vos* median to *vss*.

Taxonomic summary

Type host: Corydon sumatranus laoensis Meyer de Schauensee, 1929 – dusky broadbill.

Type locality: Ban Hua Thanon, Khlong Khlung, Kamphaeng-Phet, Thailand.

Specimens deposited: **Holotype** ♂, Ban Hua Thanon, Khlong Khlung, Kamphaeng-Phet, Thailand, 3 Apr. 1953, R.E. Elbel & H.G. Deignan, RE-2357, RT-B-17855 (OSUS).

Paratypes. 3♂, 4♀, same data as holotype (OSUS).

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

ZooBank registration:

Remarks. *Guimaraesiella khlongkhlungensis* **n. sp.** is most similar to *G. altunai* **n. sp.** and *G. latirostris* **n. sp.**, with which it shares the following characters: preantennal area broad (Figs 3, 10, 24); *aps* present on male tergopleurite V (Figs 1, 8, 22); proximal mesosome substantially overlapping with basal apodeme (Figs 4, 11, 25). *Guimaraesiella khlongkhlungensis* can be separated from both of these species by the following characters: *ps* present on male abdominal segment III in *G. khlongkhlungensis* (Fig. 1), but absent in *G. latirostris* (Fig. 8) and *G. altunai* (Fig. 22); male tergopleurite VIII with three posterior setae on each side, not counting trichobothrium (Fig. 1), but with only two setae on each side in *G. latirostris* (Fig. 8) and *G. altunai* (Fig. 22); *ps* present on female abdominal segment III in *G. khlongkhlungensis* (Fig. 2), but absent in *G. latirostris* (Fig. 9) and *G. altunai* (Fig. 23); proximal mesosome with flat anterior margin and bluntly hooked antero-lateral corners in *G. khlongkhlungensis* (Fig. 5), but with convergent anterior margin and rounded antero-lateral corners in *G. latirostris* (Fig. 12) and *G. altunai* (Fig. 26).

***Guimaraesiella latirostris* n. sp.**

(Figs 8–14)

Description *Both sexes:* Head broadly trapezoidal (Fig. 10), lateral margins of preantennal head convex posteriorly and slightly concave anteriorly, frons broadly concave. Marginal carina of broad, of irregular width, interrupted laterally and submedianly. Dorsal preantennal carina reaching *dsms, ads,* and lateral head margins, not extending median to *ads*. Ventral anterior plate roughly trapezoidal. Dorsal anterior plate not separate, longer than wide. Head chaetotaxy as in Fig. 10. Preantennal nodi large, bulging. Preocular nodi much larger than minute postocular nodi. Marginal temporal carina very narrow, of even width. Gular plate with median point. Thoracic and abdominal segments as in Figs 8–9. Leg seta *fI-v4* absent.

Male: Thoracic and abdominal chaetotaxy as in Fig. 8; *ps* absent on abdominal segment III; *aps* present on tergopleurite V; tergopleurite VIII with two setae on each side (not counting trichobothrium). Basal apodeme broad, with slightly concave lateral margins (Fig. 11). Proximal mesosome substantially overlapping basal apodeme, rounded to median point (more pronounced than illustrated here in some specimens), with rounded antero-lateral corners. Distal mesosome with gently rounded margins, mesosomal lobes not noticeable. Ventral sclerite with single anterior extension, almost reaching anterior margin of mesosome (Fig. 12) and small rugose area medianly near distal margin; chaetotaxy as in Fig. 12. Gonopore displaced anteriorly, roughly rounded in outline, lateral margins serrated. Parameral heads with medio-posterior angle; parameral blades short, slender; *pst1–2* as in Fig. 13.

Female: Thoracic and abdominal chaetotaxy as in Fig. 9; *ps* absent on abdominal segment III. Distal subgenital plate poorly visible in examined specimens, and here illustrated approximately; submarginal extensions likely more slender than illustrated; distal end broad (Fig. 14). Vulval margin gently rounded, slightly flattened medianly, with 3 short, slender *vms* and 5–7 short, thorn-like *vss* on each side; 4–6 short, slender *vos* on each side of subgenital plate; distal 1–2 *vos* median to *vss*.

Taxonomic summary

Type host: Eurylaimus ochromalus Raffles, 1822 – black-and-yellow broadbill.

Type locality: Khao Phappha, Banna, Phatthalung, Thailand.

Material deposited: **Holotype** ♂, Khao Phappha, Banna, Phatthalung [as Phatalung], Thailand, 20 Aug. 1955, B. Lekagul, SE2591 [marked with black dot on slide] (BPBM).

Paratypes. 5♂, 4♀, same data as holotype (BPBM).

Etymology: The specific name is derived from Latin "*lata*" for "broad" and "*rostres*" for "beak", referring to the broad preantennal area of this species.

ZooBank registration:

Remarks Host identification is uncertain on the slide labels; we tentatively accept the given host as the type host.

Guimaraesiella latirostris **n. sp.** is most similar to *G. altunai* **n. sp.**, with which it shares the following characters: *aps* present on male tergopleurite V (Figs 8, 22); *ps* absent on male abdominal segment III (Figs 8, 22); male tergopleurite VIII with two posterior setae on each side (not counting trichobothrium; Figs 8, 22); female abdominal segment IV with two *ps* on each side (Figs 9, 23); proximal mesosome convergent to median point (Figs 12, 26). These two species can be separated by the following characters: preantennal area proportionately shorter and broader in *G. latirostris* (Fig. 10) than in *G. altunai* (Fig. 24); ventral sclerite of male mesosome almost reaches anterior margin of mesosome in *G. latirostris* (Fig. 12), but not in *G. altunai* (Fig. 26); lateral margins of mesosome gently rounded in *G. latirostris* (Fig. 12), but with distinct bulge at mid-length in *g. altunai* (Fig. 26); distal margin of ventral sclerite rugose in *G. latirostris* (Fig. 12), but not in *G. altunai* (Fig. 26); gonopore more rounded in outline and situated farther anterior in *G. latirostris* (Fig. 12) than in *G. altunai* (Fig. 26). Females best separated on head shape, as vulval chaetotaxy overlaps between the two species.

***Guimaraesiella cyanophoba* n. sp.**

(Figs 15–21)

Description *Both sexes:* Head broadly trapezoidal (Fig. 17), lateral margins of preantennal head slightly concave, frons broadly concave. Marginal carina of moderate, irregular, width, interrupted laterally and submedianly. Dorsal preantennal carina reaching *dsms, ads,* and lateral head margins. Ventral anterior plate large, rounded triangular. Dorsal anterior plate not separate, longer than wide. Head chaetotaxy as in Fig. 17. Preantennal nodi large, bulging. Preocular nodi much larger than minute postocular nodi. Marginal temporal carina very narrow, of even width. Gular plate with median point. Thoracic and abdominal segments as in Figs 15–16. Leg seta *fI-v4* absent.

Male: Thoracic and abdominal chaetotaxy as in Fig. 15; posterior margin of mesometathorax normally with 5–6 setae on each side, but in one specimen with 9 setae on each side; *ps* absent on abdominal segment III; *aps* absent in tergopleurites IV–V; tergopleurite VIII with 2 setae on each side (not counting trichobothrium). Anterior end of basal apodeme not clearly visible in examined specimens; lateral margins more or less parallel, but bulging proximally (Fig. 18). Proximal mesosome substantially overlapping with basal apodeme (Fig. 18); anterior margin roughly flat, antero-lateral corners with slight rectangular bulges (exact shape differs between specimens). Ventral sclerite with single anterior extension not reaching near anterior margin of mesosome; distal end not rugose; chaetotaxy as in Fig. 19. Distal mesosome with convex mesosomal lobes. Gonopore roughly quadratic in outline, antero-median part slightly rugose, lateral margins serrated. Parameral heads with several small bulges (Fig. 20); parameral blades short, stout; *pst1–2* as in Fig. 20.

Female: Thoracic and abdominal chaetotaxy as in Fig. 16; posterior margin of mesometathorax with 5–7 setae on each side; *ps* absent on abdominal segment III. Subgenital plate broad distally, with slender submarginal extensions (Fig. 21). Vulval margin gently rounded, with 3–4 short, slender *vms* and 4–8 short, thorn-like *vss* on each side; 6–8 short, slender *vos* on each side of subgenital plate; 1–2 distal *vos* median to *vss*.

Taxonomic summary

Type host: Cymbirhynchus macrorhynchos malaccensis Salvadori, 1874 – black-and-red broadbill.

Type locality: Thung Nui, Satun, Thailand.

Other host: Cymbirhynchus macrorhynchus siamensis Meyer de Schauensee & Ripley, 1940 – black-and-red broadbill.

Specimens deposited: Ex *Cymbirhynchus macrorhynchus malaccensis*: **Holotype** ♂, Thung Nui, Satun, Thailand, 1 Sep. 1963, W. Songprakob & W.S. Laong, WS459 [marked with black dot on slide] (BPBM). **Paratypes.** 2♂, 1♀, same data as holotype (BPBM); 4♂, 12♀, Muang Kluang, Kapoe, Ranong, Thailand, 17 Jan. 1963, W. Songprakob, RE7013 (BPBM); 2♀, Thadindang, Phat Phayun [as Phatphayan], Phatthalung, Thailand, 25 Jul. 1962, W. Songprakob, RE6339 (BPBM). **Non-types** ex *Cymbirhynchus macrorhynchus siamensis*: 1♂, 3♀, Ban Hua Thanon, Khlong Khlung, Kamphaeng-Phet, Thailand, 6 Apr. 1953, R.E. Elbel & H.G. Deignan, RE-2384, RT-B-17871 (BPBM).

Etymology: The specific name is derived from "*kúanos*", Greek for "blue", and "*phóbos*", Greek for "fear". This refers to the large, cyan bill of the host that this louse species would have reason to fear.

ZooBank registration:

Remarks No significant differences have been found between material from the two host subspecies.

Guimaraesiella cyanophoba **n. sp.** is not very similar to any other species of *Guimaraesiella*, but may be most similar to *G. khlongkhlungensis* **n. sp.**, with which it shares the flat anterior margin of the mesosome and the roughly quadratic gonopore (Figs 5, 19). These two species can be separated by the following characters: *ps* present on male abdominal segment III in *G. khlongkhlungensis* (Fig. 1), but absent in *G. cyanophoba* (Fig. 15); *aps* present on male tergopleurite V (and in some specimens also IV) in *G. khlongkhlungensis* (Fig. 1), but absent on these segments in *G. cyanophoba* (Fig. 15); male tergopleurite VIII with two setae on each side (not counting trichobothrium) in *G. cyanophoba* (Fig. 15), but with three setae on each side in *G. khlongkhlungensis* (Fig. 1); antero-lateral corners of mesosome with bluntly rectangular corners in *G. cyanophoba* (Fig. 19; in some specimens broader than illustrated here), but with bluntly hooked corners in *G. khlongkhlungensis* (Fig, 5).

Guimaraesiella altunai n. sp.

(Figs 22–28)

Description *Both sexes:* Head broadly trapezoidal (Fig. 24), lateral margins of preantennal head slightly concave, frons broadly concave. Marginal carina of moderate, irregular, width, interrupted laterally and submedianly. Dorsal preantennal carina reaching *dsms, ads,* and lateral head margins, not extending median to *ads*. Ventral anterior plate large, rounded triangular. Dorsal anterior plate not separate, longer than wide. Head chaetotaxy as in Fig. 24. Preantennal nodi moderate, bulging. Preocular nodi much larger than minute postocular nodi. Marginal temporal carina narrow, of even width. Gular plate with median point. Thoracic and abdominal segments as in Figs 22–23. Leg seta *fI-v4* absent.

Male: Thoracic and abdominal chaetotaxy as in Fig. 22; *ps* absent of abdominal segment III; *aps* present on tergopleurite IV; Tergopleurite VIII with two setae on each side (not counting trichobothrium). Basal apodeme with concave lateral margins (Fig. 25). Proximal mesosome substantially overlaps basal apodeme, anterior margin convergent to median point, antero-lateral corners rounded. Ventral sclerite not reaching near anterior margin of mesosome; distal section not rugose; chaetotaxy as in Fig. 26. Mesosomal lobes bulging at about mid-length of distal mesosome. Gonopore broader than long, roughly trapezoidal, lateral margins serrated. Parameral heads slightly extended medio-posteriorly (Fig. 27); parameral blades stout, short; *pst1–2* as in Fig. 27.

Female: Thoracic and abdominal chaetotaxy as in Fig. 23; *ps* absent on abdominal segment III. Distal subgenital plate poorly visible in examined specimens, and here illustrated approximately; submarginal extensions likely more slender than illustrated (Fig. 28); distal end broad. Vulval margin bulging medianly, with 2–3 short, slender *vms* and 6–7 short, thorn-like *vss* on each side; 3–4 short, slender *vos* on each side of subgenital plate; distal 1–2 *vos* median to *vss*.

Taxonomic summary

Type host: Calyptomena viridis caudacuta Swainson, 1838 – green broadbill.

Type locality: Terengganu, Malaysia.

Specimens deposited: Ex *Calyptomena viridis caudacuta*: **Holotype** ♂, 102˚ 40' E, 5˚ 28' N, elev. 140 ft., Terengganu [as Trengganu], Malaysia, 24 Mar. 1974, Gn. Lawit Expedition, Brit. Mus. 1974-2 (NHML). **Paratypes.** 1♂, 4♀, same data as holotype (NHML). **Non-types.** Ex *Calyptomena viridis* ssp.: 2♂, no locality ["Java" stated on slide, but this is outside the range of the host], M.M. (NHML). Ex *C. v. caudacuta*: 1♀, Thung Nui, Satun [as Saton], Thailand, 12 Sep. 1963, W. Songprakob & W.S. Laong, WS503 (UMSP).

Etymology: The specific name is in honor of Juan Altuna (previously in the Clayton/Bush Lab, at the University of Utah), in recognition of his considerable contributions to our understanding of the biology and evolution of chewing lice.

ZooBank registration:

Remarks. *Guimaraesiella altunai* **n. sp.** is most similar to *G. latirostris* **n. sp.**, with which it shares the following characters: *aps* present on male tergopleurite V (Figs 8, 22); *ps* absent on male abdominal segment III (Figs 8, 22); male tergopleurite VIII with two posterior setae on each side (not counting trichobothrium; Figs 8, 22); female abdominal segment IV with two *ps* on each side (Figs 9, 23); proximal mesosome convergent to median point (Figs 12, 26). These two species can be separated by the following characters: preantennal area proportionately shorter and broader in *G. latirostris* (Fig. 10) than in *G. altunai* (Fig. 24); ventral sclerite of male mesosome almost reaches anterior margin of mesosome in *G. latirostris* (Fig. 12), but not in *G. altunai* (Fig. 26); lateral margins of mesosome with distinct bulge at mid-length in *g. altunai* (Fig. 26), but gently rounded in *G. latirostris* (Fig. 12); distal margin of ventral sclerite with rugose area in *G. latirostris* (Fig. 12), but smooth in *G. altunai* (Fig. 26); gonopore more rounded in outline and situated farther anterior in *G. latirostris* (Fig. 12) than in *G. altunai* (Fig. 26). Females best separated on head shape, as vulval chaetotaxy overlaps between the two species.

Guimaraesiella forcipata n. sp.

(Figs 29–35)

Description *Both sexes:* Head rounded truncated triangular (Fig. 31), lateral margins of preantennal area convex, frons very narrowly but deeply concave. Marginal carina broad, of irregular width, interrupted laterally and submedianly. Dorsal preantennal carina reaching *dsms, ads,* and lateral head margins, not extending median to *ads*. Ventral anterior plate large, elongated. Dorsal anterior plate not separate, longer than wide. Head chaetotaxy as in Fig. 31. Preantennal nodi large, bulging. Preocular nodi larger than minute postocular nodi. Marginal temporal carina very narrow, of even width. Gular plate with median point. Thoracic and abdominal segments as in Figs 29–30. Leg seta *fI-v4* absent.

Male: Thoracic and abdominal chaetotaxy as in Fig. 29; *ps* absent on abdominal segment III; *aps* absent on tergopleurite V; tergopleurite VIII with two setae on each side (not counting trichobothrium). Basal apodeme broad, narrowing distally (Fig. 32). Proximal mesosome almost flat, barely or not overlapping with basal apodeme. Ventral sclerite broad, with flattened anterior end almost reaching proximal margin; distal section diffuse medially, and with undulating postero-lateral margins; chaetotaxy as in Fig. 33. Mesosomal lobes slight, distal third of mesosome much narrower than proximal section. Gonopore large, roughly oval in outline, with serrated lateral margins. Parameral heads small (Fig. 34); parameral blades long, stout, slightly extended distally; *pst1–2* as in Fig. 34.

Female: Thoracic and abdominal chaetotaxy as in Fig. 30; *ps* absent on segment III. Subgenital plate diffuse distally in all examined material, and illustrated approximately; submarginal extensions likely narrower than illustrated (Fig. 35). Vulval margin gently rounded, with 3–4 short, slender *vms* and 8–10 short, thorn-like *vss* on each side; 6–7 short, slender *vos* one each side of subgenital plate; 1–2 distal *vos* median to *vss*.

Taxonomic summary

Type host: Eurylaimus steerii steerii Sharpe, 1876 – wattled broadbill.

Type locality: Malaita, Mindanao, Philippines.

Specimens deposited: **Holotype** ♂, Malaita, Mindanao, Philippines, SUBBM-1099 (BPBM). **Paratypes.** 6♂, 3♀, same data as holotype (BPBM); 2♂, 4♀, same locality, SUBBM-1102 (BPBM).

Etymology: The species name is derived from "*forcipatus*", Latin for "pincer-shaped", referring to the narrow and highly convergent frons of this species.

ZooBank registration:

Remarks. In some specimens there appears to be a slight thickening of the median section of the hyaline margin, similar to that seen in *e.g. Philopteroides*. This thickening is absent in other specimens, and may be due to a folding of the hyaline margin during mounting. Fresh specimens are needed to establish the true nature of this character.

No described species of *Guimaraesiella* appear to be morphologically similar to *Guimaraesiella forcipata* **n. sp.**, and we have not seen any similar species among the approximately 100 undescribed species we have examined. This species can be separated from all described species of *Guimaraesiella* by the unique head shape (Fig. 31) and the short, almost quadratic mesosome (Fig. 33) not or only barely overlapping with the basal apodeme (Fig. 32).

DISCUSSION

The hosts of all five species described here are representatives of the Old World suboscines. As such, they are more closely related to groups of birds that typically are not parasitized by *Brueelia*-complex lice, than to the other hosts of the "core" *Guimaraesiella* (Barker et al. 2004). The five species described here are all morphologically typical for the "core" *Guimaraesiella* (Clade A-1 in fig. 3 of Bush et al., 2016). Specimens of *Guimaraesiella* from eurylaimid hosts were placed near the type species of *Guimaraesiella* in this phylogeny. The head shape, extent of dorsal preantennal suture, and the shape of the male genitalia and lack of complete cross-piece in the female genitalia are all consistent with this placement.

The placement of *Guimaraesiella* specimens from eurylaimid hosts deep inside a clade comprising *Guimaraesiella* from oscine hosts (Bush et al., 2016) may indicate that these are the descendants of a successful host switch from an oscine to a suboscine host. However, as the species described here are not very similar morphologically (in particular *G. forcipata* **n. sp.**), more than one host switch may be involved. Moreover, the hosts belong to two different families, which are not closely related within the Eurylaimides (e.g. Moyle et al., 2006; Selvatti et al., 2016). The Calyptomenidae are more closely related to the Pittidae, which are not known to be parasitized by any lice in the *Brueelia*-complex (Table 1). This also suggests that multiple host switches may have occurred from oscine to suboscine hosts in Southeast Asia. The majority of “core” *Guimaraesiella* are known from canopy-feeding birds, many of which participate in mixed-species feeding flocks. This also applies to the hosts of the species described here, but not to the Pittidae. Potentially, participation in mixed-species feeding flocks may have facilitated these host switches; however, no detailed study on the effect of mixed-species feeding flocks on chewing louse distribution has been published.

Notably, Sychra et al (2014) recently published a case of natural host switching between a pycnonotid host and *Cymbirhynchus macrorhynchus* in Vietnam. This may strengthen the argument that the louse fauna of Asian broadbills is at least partially derived from unrelated hosts. More studies of the louse fauna of Southeast Asian hosts are sorely needed to determine whether or not host switching – including between distantly related hosts – is common in the Old World tropics.

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References

Barker, F. K., Cibois, A., Schikler, P., Feinstein, J. and Cracraft, J. 2004. Phylogeny and diversification of the largest avian radiation. Proceedings of the National Academy of Science of the U.S.A. 101: 11040–11045.

Burmeister, H. 1838. Mallophaga Nitzsch. Handbuch der Entomologie, Berlin 2: 418–443.

Bush, S. E., Weckstein, J. D., Gustafsson, D. R., Allen, J., DiBlasi, E., Shreve, S. M., Boldt, R., Skeen, H. R. and Johnson, K. P. 2016. Unlocking the black box of feather louse diversity: a molecular phylogeny of the hyper-diverse genus *Brueelia*. Molecular Phylogenetics and Evolution 94: 737–751.

Carriker, M. A., Jr. 1944. Studies in Neotropical Mallophaga—No IV. New genera and species. Boletin de Entomologica Venezolana 3: 65–104.

Carriker, M. A., Jr. 1956. Estudios sobre Mallophaga Neotropicales (XIV) (Piojos de las Cotingidae). Revista de la Academia Colombiana de Ciencias 9: 365–380.

Carriker, M. A., Jr. 1957. Studies in Neotropical Mallophaga. XVI: bird lice of the suborder Ischnocera. Proceedings of the United States National Museum 106: 409–439.

Carriker, M. A., Jr. 1963. Neotropical Mallophaga (Insecta) miscellany, No. 13. Revista Brasileira e Biologia 23: 293–316.

Cicchino, A. C. 1981 Contribucion al conocimiento de los malofagos argentines. X. Cuatro nuevas especies del género *Brueelia* Keler, 1936 parasitas de Furnariidae (Aves: Passeriformes). Revista de la Sociedad Entomologica Argentina 40: 31–40.

Cicchino, A. C. 1983. Especies nuevas o poco conocidas del genero *Brueelia* Keler, 1936 (Mallophaga: Philopteridae) parasitas de Passeriformes, Piciformes y Trogoniformes (Aves) Americanos. Revista de la Sociedad Entomologica Argentina 42: 283–303.

Cicchino, A. C. and Valim, M. P. 2008. Three new species of *Formicaphagus* Carriker, 1957 (Phthiraptera, Ischnocera, Philopteridae), parasitic on Thamnophilidae and Conopophagidae (Aves, Passeriformes). Zootaxa 1949: 37–50.

Clements, J. F., Schulenberg, T. S., Iliff, M. J., Roberson, D., Fredericks, T. A., Sullivan, B. L. and Wood, C. L. 2017. The eBird/Clements checklist of birds of the world: v2016. Available from: http://www.birds.cornell.edu/clementschecklist/download/ (Accessed 17 July 2018).

Conci, C. 1941. Nuovi genera di Mallofagi. Bollettino della Societa Entomologica Italiana 73: 126–127.

Eichler, W. 1949. Phthirapterorum nova genera. Bolletino della Società Entomologica Italiana 79: 11–13.

Eichler, W. 1951. Die Federlinge der Drosseln. *In* Bedeutung der Vogelwelt in Forschung und Praxis – Zusammenstellung der Vortrage gehalten auf der Ersten Ornithologen-Tagung in der Deutschen Demokratischen Republik am 21 und 22 Oktober 1950 in Leipzig. Leipzig, Germany, p. 29–47.

Eichler, W. 1952. Notulae Mallophagologicae. XXVI. *Rhombiceps* n. g. und andere neue Federlingsgattungen. Zoologische Anzeiger 149: 74–78.

Enout, A. M. J., Lobato, D. N. C., Diniz, F. C. and Antonini, Y. 2012. Chewing lice (Insecta, Phthiraptera) and feather mites (Acari, Astigmata) associated with birds of the Cerrado in Central Brazil. Parasitology Research 111: 1731–1742.

Giebel, C. 1874. Insecta Epizoica. Die auf Säugethieren und Vögeln schmarotzenen Insecten nach Chr. L. Nitzsch's Nachlass bearbeitet. Otto Wigand, Leipzig, xvi + 308 p. + 20 plates.

Giebel, C. 1879. Einige von Herrn Dr. Meyer, Director des Zoologischen Museums in Dresden, auf den Südseeinseln gesammelte Philopteren oder Federlinge. Zeitschrift für die Gesammten Naturwissenschaften, Halle 52: 474–475.

Gustafsson, D. R. and Bush, S. E. 2017. Morphological revision of the hyperdiverse *Brueelia*-complex (Insecta: Phthiraptera: Ischnocera: Philopteridae) with new taxa, checklists and generic key. Zootaxa 4313: 1–443.

Gustafsson, D. R., Clayton, D. H. and Bush, S. E. 2019a. Twelve new species of *Guimaraesiella* (Phthiraptera: Ischnocera: Philopteridae) from "babblers" (Passeriformes: Leiothrichidae, Pellorneidae, Timaliidae) with a description of a new subgenus and a key to its species. Zootaxa 4543: 451–497.

Gustafsson, D. R., Oslejskova, L., Najer, T., Sychra, O. and Zou, F. 2019b. Redescriptions of thirteen species of chewing lice in the *Brueelia*-complex (Phthiraptera, Ischnocera, Philopteridae), with one new synonymy and a neotype designation for *Nirmus lais* Giebel, 1874. Deutsche Entomologische Zeitschrift 66: 17–39.

Haeckel, E. 1896. Systematische Phylogenie. 2. Theil. Systematische Phylogenie der wirbellose Thiere (Invertebrata). Verlag von Georg Reiner, Berlin, 720 p.

Kéler, S. von 1936. Über einige Mallophagen aus Rossitten. Arbeiten in morphologische und taxonomische Entomologie von Berlin-Dahlem 3: 256–264.

Kellogg, V. L. 1896. New Mallophaga II, from land birds, together with an account of mallophagous mouth-parts. Proceedings of the California Academy of Science 2: 431–458.

Kuabara, K. M. D. and Valim, M. P. 2017. New records of chewing lice (Insecta, Phthiraptera) from Brazilian birds (Aves) collected by Helmut Sick (1910–1991). Revista Brasileira de Entomologia 61: 146–161.

Mey, E. 2004. Zur Taxonomie, Verbreitung und parasitophyletischer Evidenz des *Philopterus*-Komplexes (Insecta, Phthiraptera, Ischnocera). Ornithologische Anzeiger 43: 149–203.

Mey, E. 2017. [2016] Neue Gattungen und Arten aus dem *Brueelia*-Komplex (Insecta, Phthiraptera, Ischnocera, Philopteridae s. l.). Rudolstädter naturhistorische Schriften 22: 85–215.

Mey, E. and Barker, S. C. (2014) Eine neue auf den Feenvögeln (Irenidae) lebende *Brueelia*-Art (Insecta, Phthiraptera, Ischnocera, Philopteridae), nebst Anmerkungen zur Gattung *Brueelia* Kéler, 1936 sensu lato. Rudolstädter naturhistorische Schriften 19: 73–114.

Meyer, M. J., Price, R. D. and Johnson, K. P. 2008 A new species of *Picicola* Clay and Meinertzhagen, 1938 (Phthiraptera: Ischnocera) parasitic on the rufous-sided broadbill (Passeriformes: Eurylaimidae) in Ghana. Zootaxa 1762: 63–68.

Moyle, R. G., Chesser, R. T., Prum, R. O., Schikler, P. and Cracraft, J. 2006. Phylogeny and evolutionary history of Old World suboscine birds (Aves: Eurylaimides). American Museum Novitates 3544: 1–22.

Najer, T., Sychra, O., Hung, N. M., Capek, M., Podzemny, P. and Literak, I. 2012. New species and new records of chewing lice (Phthiraptera: Amblycera and Ischnocera) from bulbuls (Passeriformes: Pycnonotidae) in Vietnam. Zootaxa 3357: 37–48.

Neumann, L. G. 1906. Notes sur les Mallophages. Bulletin de la Société zoologique de France 31: 54–60.

Nitzsch, C. L. 1818. Die Familien und Gattungen der Thierinsekten (Insecta epizoica); als ein Prodromus einer Naturgeschichte derselben. E.F. Germar's Magazin der Entomologie 3: 261–318.

Piaget, E. 1885. Les Pédiculines. Assai Monographique. Supplément. E.J. Brill, Leide. xvi + 200 pp., 17 pls.

Price, R. D. and Clayton, D. H. 1995. A new genus and three new species of chewing lice (Phthiraptera: Philopteridae) from Peruvian ovenbirds (Passeriformes: Furnariidae). Proceedings of the Entomological Society of Washington 97: 839–844.

Price, R. D., Hellenthal, R. A., Palma, R. L., Johnson, K. P. and Clayton, D. H. 2003. The Chewing Lice. World Checklist and Biological Overview. Illinois Natural History Survey Special Publication 24, Champaign, x + 501 p.

Sánchez-Montes, S., Colunga-Salas, P., Álvarez-Castillo, L., Guzmán-Vornejo, C. and Montiel-Parra, G. 2018. Chewing lice (Insecta: Phthiraptera) associated with vertebrates in Mexico. Zootaxa 4372: 1–109.

Selvatti, A. P., Galvão, A., Pereira, A. G., Gonzaga, L., P. and de Moraes Russo, C. A. 2016. An African origin of the Eurylaimides (Passeriformes) and the successful diversification of the ground-foraging pittas (Pittidae). Molecular Biology and Evolution 34: 483–499.

Somadder, K. and Tandan, B. K. 1977. Degeerielline Ischnocera (Insecta: Phthiraptera) of the Pittidae. Oriental Insects 11: 113–138.

Soto-Patiño, J., Londoño, G. A., Johnson, K. P., Weckstein, J. D., Avendaño, J. E., Catanach, T. A., Sweet, A. D., Cook, A. T., Jankowski, J. E. and Allen, J. 2018. Composition and distribution of lice (Insecta: Phthiraptera) on Colombian and Peruvian birds: new data on louse-host associations in the Neotropics. Biodiversity Data Journal 6: e21635 [30 p.]

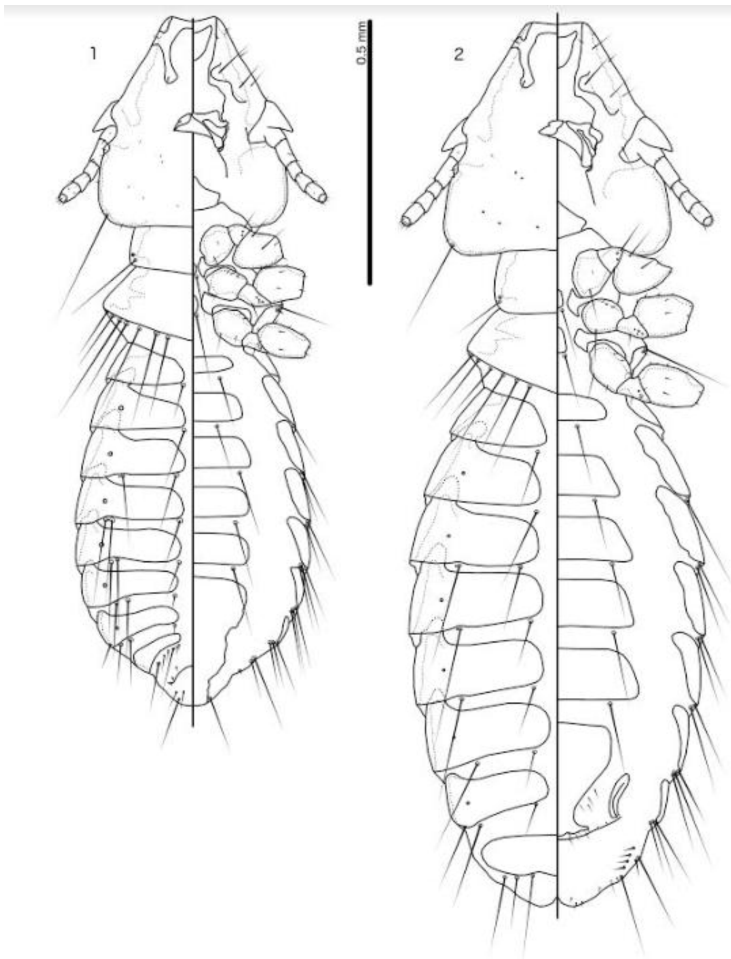
Sychra, O., Literák, I., Čapek, M., and Havlíček, M. 2006. Chewing lice (Phthiraptera) from typical antbirds and ground antbirds (Passeriformes: Thamnophilidae, Formicariidae) from Costa Rica, with descriptions of three new species of the genera *Formicaphagus* and *Myrsidea*. Zootaxa 1206: 47–61.

Sychra, O., Najer, T., Kounek, F., Hung, N. M., Tolstenkov, O. O. 2014. *Myrsidea claytoni* (Phthiraptera: Menoponidae) from *Cymbirhynchus macrorhynchus* (Passeriformes: Eurylaimidae): a case of natural host switching. Journal of Parasitology 100: 280–283.

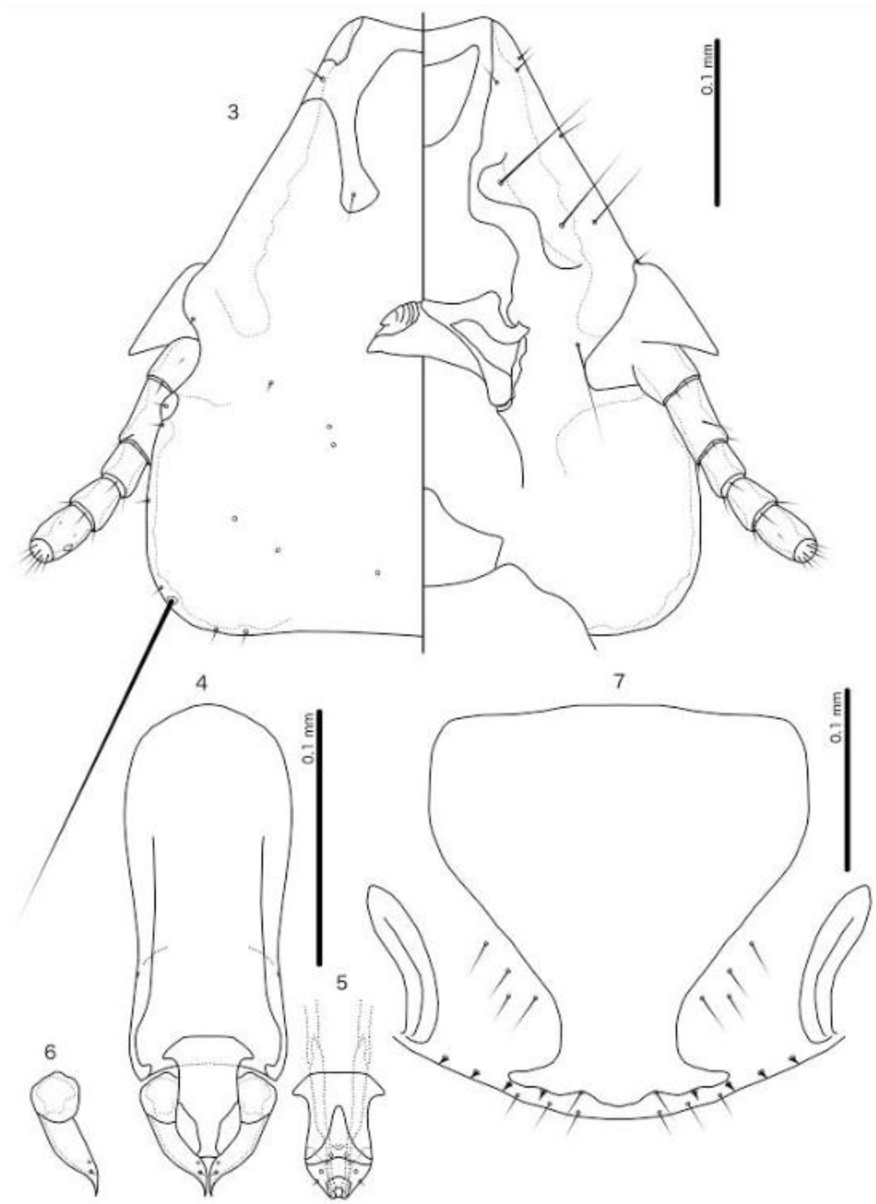
Valim, M. P. and Weckstein, J. D. 2012. Two new species of *Cotingacola* Carriker, 1956 (Phthiraptera: Ischnocera: Philopteridae) from Amazonian Brazil, with comments on host-specificity. Systematic Parasitology 81: 159–167.

Złotorzycka, J. 1964. Mallophaga parasitizing Passeriformes and Pici. II. Brueeliinae. Acta Parasitologica Polonica 12: 239–282.

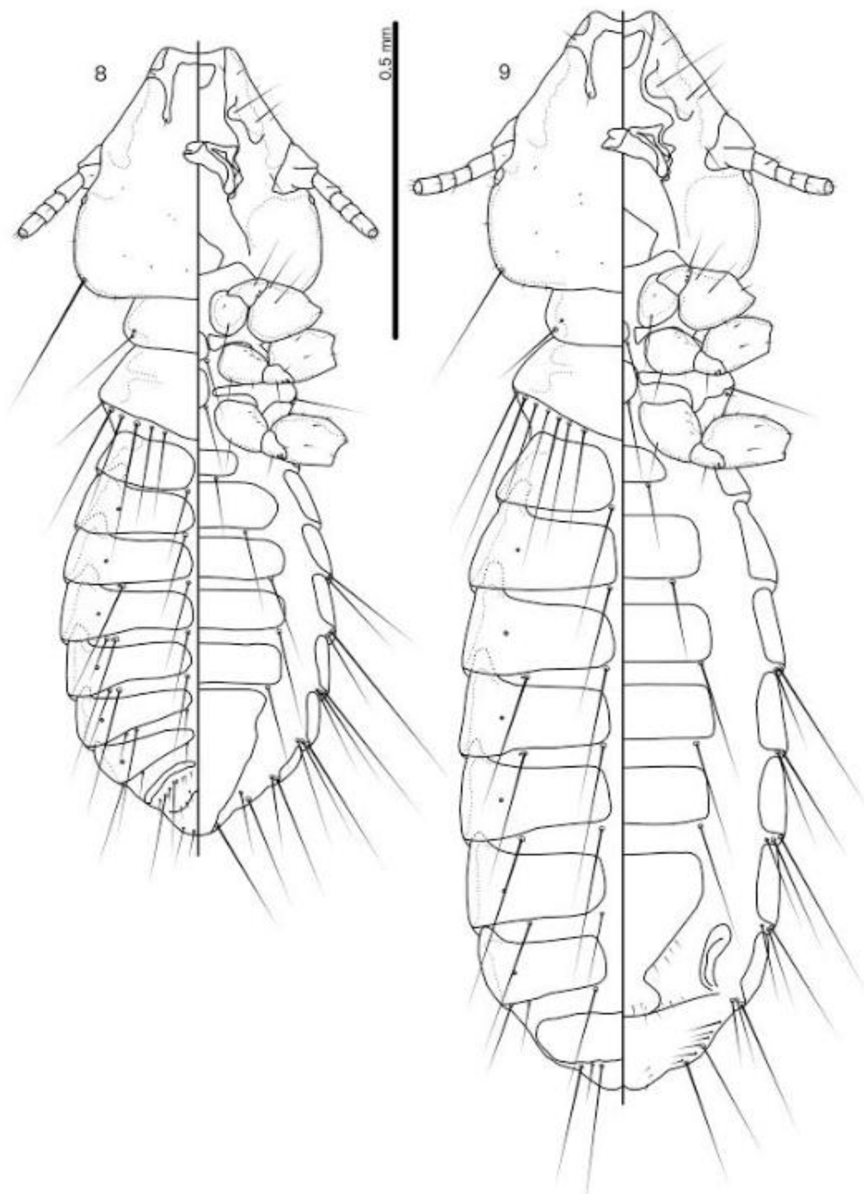
FIGURES and FIGURE LEGENDS



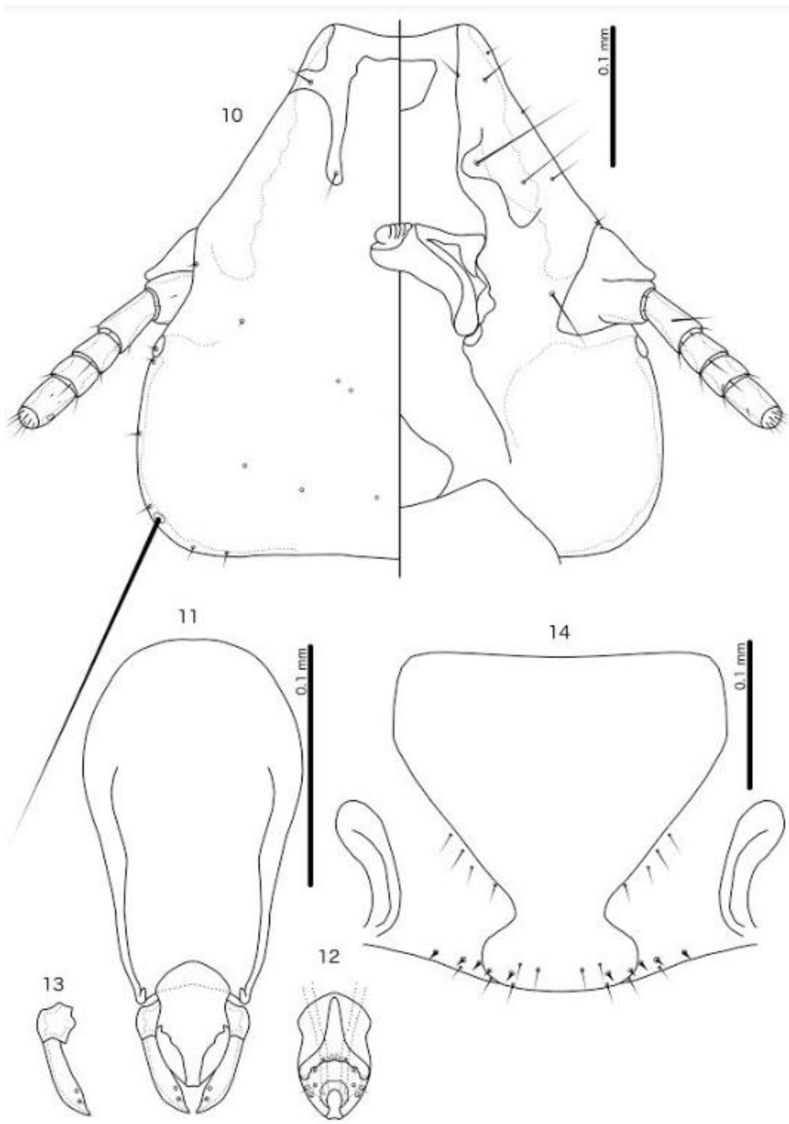
Figures 1–2. *Guimaraesiella khlongkhlungensis* **n. sp.** ex *Corydon sumatranus laoensis* Meyer de Schauensee, 1929. **(1)** Male habitus, dorsal and ventral views. **(2)** Female habitus, dorsal and ventral views.



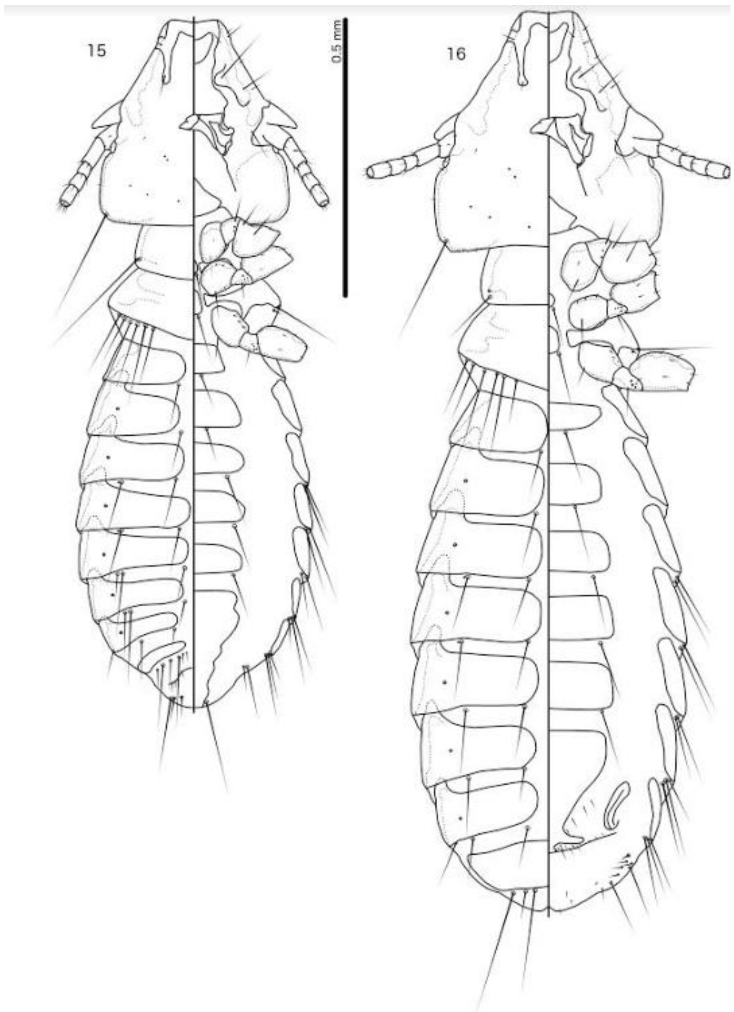
Figures 3–7. *Guimaraesiella khlongkhlungensis* **n. sp.** ex *Corydon sumatranus laoensis* Meyer de Schauensee, 1929. **(3)** Male head, dorsal and ventral views. **(4)** Male genitalia, dorsal view. **(5)** Male mesosome, ventral view. **(6)** Male paramere, dorsal view. **(7)** Female subgenital plate and vulval margin, ventral view.



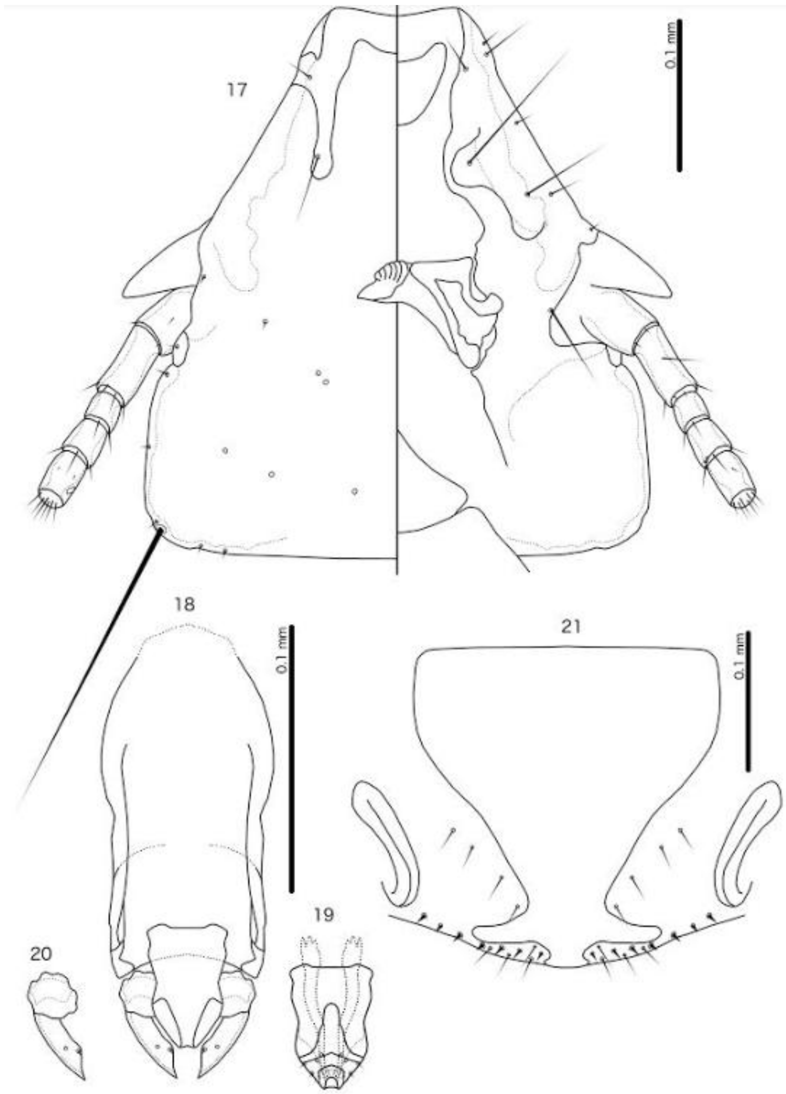
Figures 8–9. *Guimaraesiella latirostris* **n. sp.** ex *Eurylaimus ochromalus* Raffles, 1822. **(8)** Male habitus, dorsal and ventral views. **(9)** Female habitus, dorsal and ventral views.



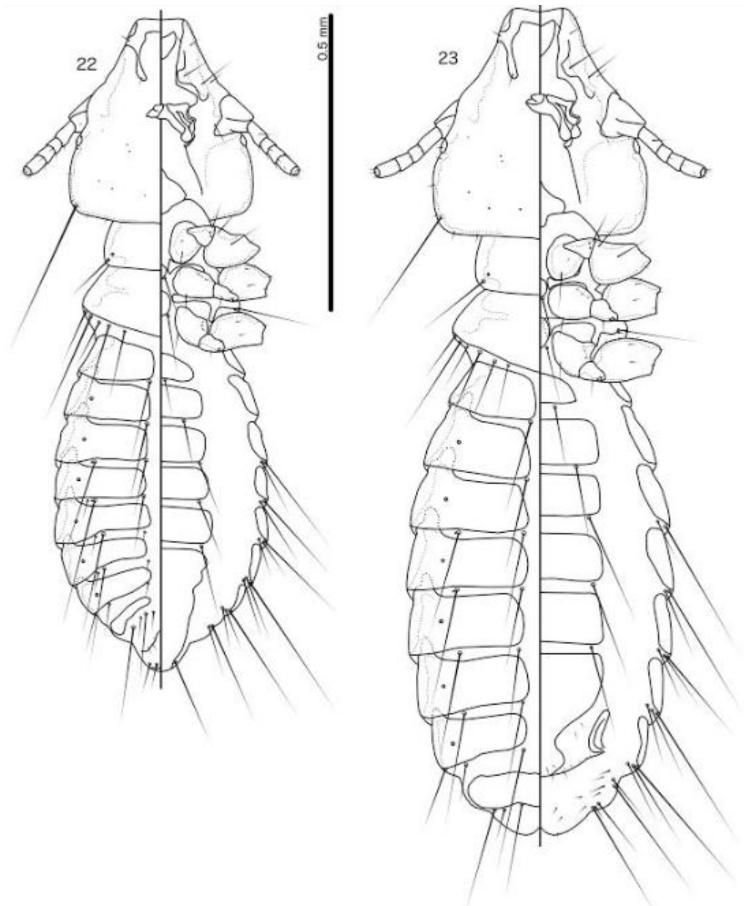
Figures 10–14. *Guimaraesiella latirostris* **n. sp.** ex *Eurylaimus ochromalus* Raffles, 1822. **(10)** Male head, dorsal and ventral views. **(11)** Male genitalia, dorsal view. **(12)** Male mesosome, ventral view. **(13)** Male paramere, dorsal view. **(14)** Female subgenital plate and vulval margin, ventral view.



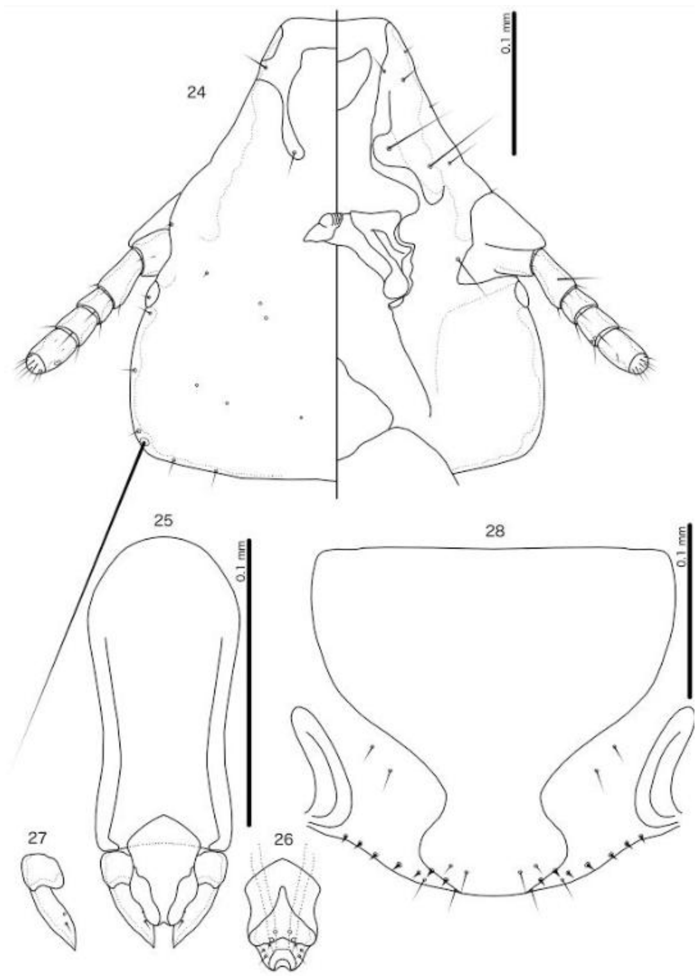
Figures 15–16. *Guimaraesiella cyanophoba* **n. sp.** ex *Cymbirhynchus macrorhynchus malaccensis* Salvadori, 1874. **(15)** Male habitus, dorsal and ventral views. **(16)** Female habitus, dorsal and ventral views.



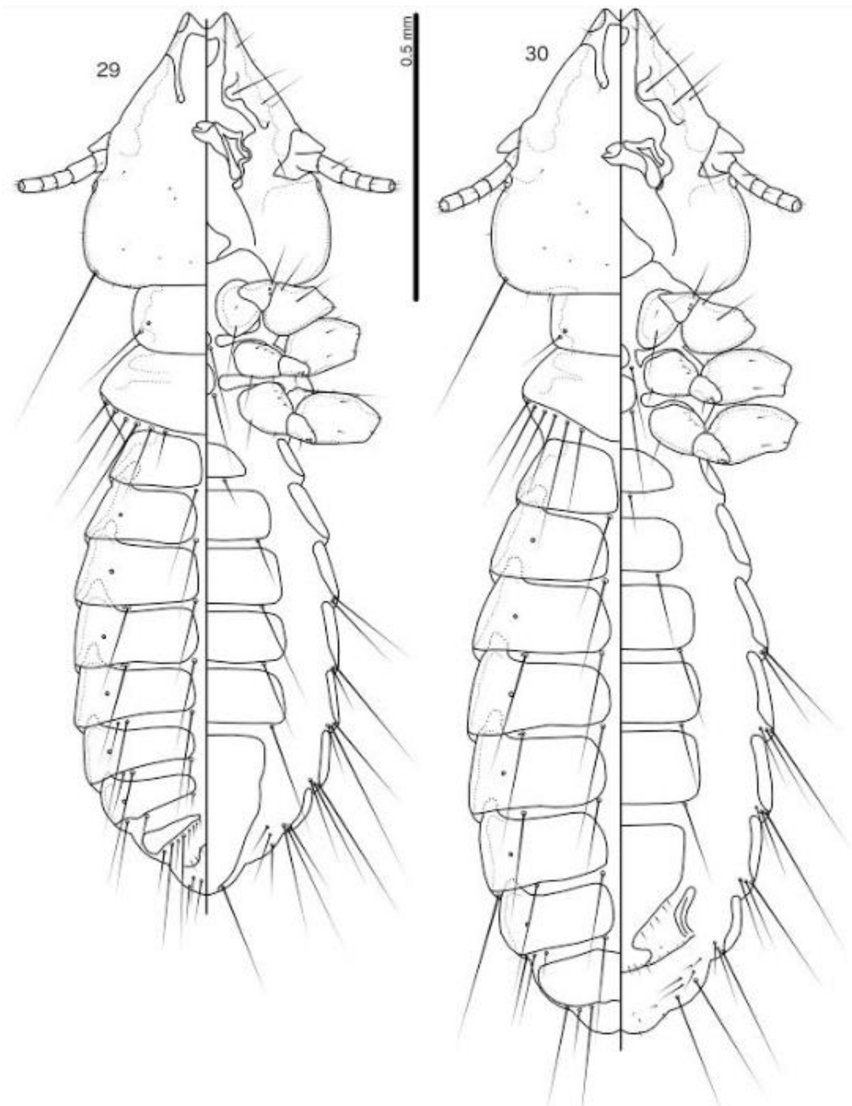
Figures 17–21. *Guimaraesiella cyanophoba* **n. sp.** ex *Cymbirhynchus macrorhynchus malaccensis* Salvadori, 1874. **(17)** Male head, dorsal and ventral views. **(18)** Male genitalia, dorsal view. **(19)** Male mesosome, ventral view. **(20)** Male paramere, dorsal view. **(21)** Female subgenital plate and vulval margin, ventral view.



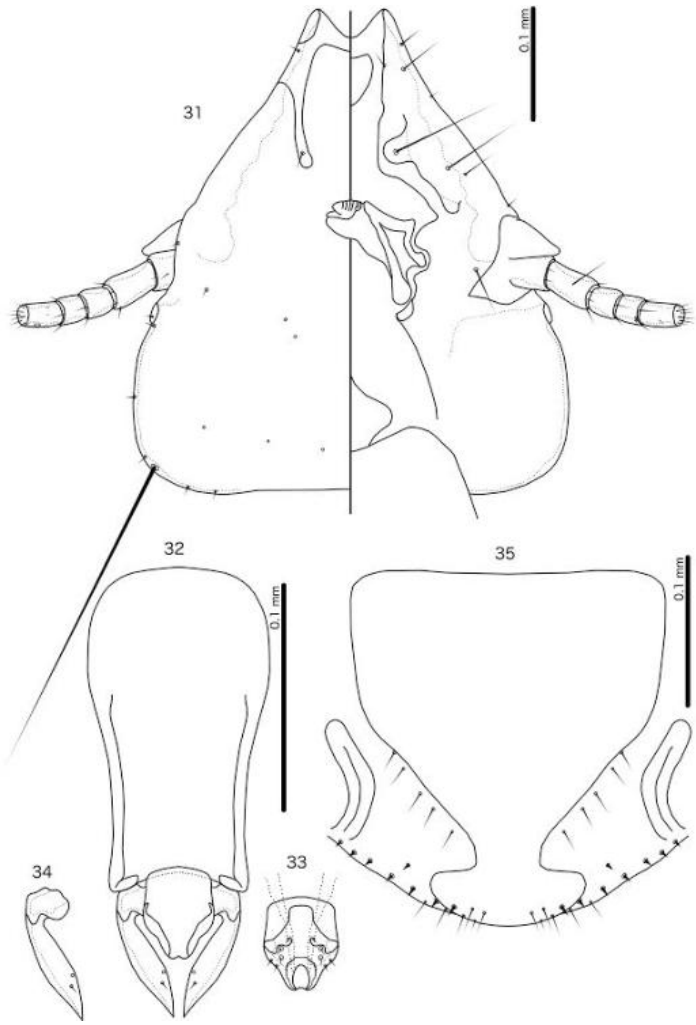
Figures 22–23. *Guimaraesiella altunai* **n. sp.** ex *Calyptomena viridis caudacuta* Swainson, 1838. **(22)** Male habitus, dorsal and ventral views. **(23)** Female habitus, dorsal and ventral views.



Figures 24–28. *Guimaraesiella altunai* **n. sp.** ex *Calyptomena viridis caudacuta* Swainson, 1838. **(24)** Male head, dorsal and ventral views. **(25)** Male genitalia, dorsal view. **(26)** Male mesosome, ventral view. **(27)** Male paramere, dorsal view. **(28)** Female subgenital plate and vulval margin, ventral view.



Figures 29–30. *Guimaraesiella forcipata* **n. sp.** ex *Eurylaimus steerii steerii* Sharpe, 1876. **(29)** Male habitus, dorsal and ventral views. **(30)** Female habitus, dorsal and ventral views.



Figures 31–35. *Guimaraesiella forcipata* **n. sp.** ex *Eurylaimus steerii steerii* Sharpe, 1876. **(31)** Male head, dorsal and ventral views. **(32)** Male genitalia, dorsal view. **(33)** Male mesosome, ventral view. **(34)** Male paramere, dorsal view. **(35)** Female subgenital plate and vulval margin, ventral view.