Zootaxa 5087 (3): 401–426
https://www.mapress.com/zt/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.5087.3.1
http://zoobank.org/urn:lsid:zoobank.org:pub:0CE51AC4-E75F-43DE-B9F5-56247B75F394

One new genus and three new species of the *Penenirmus*-complex (Phthiraptera: Ischnocera) from China, with resurrection of *Picophilopterus* Ansari, 1947

DANIEL R. GUSTAFSSON[1*], COSTICĂ ADAM[3] & FASHENG ZOU[1,2]

[1]*Guangdong Key Laboratory of Animal Conservation and Resource Utilization, Guangdong Public Laboratory of Wild Animal Conservation and Utilization, Institute of Zoology, Guangdong Academy of Sciences, 105 Xingang West Road, Haizhu District, Guangzhou, 510260, Guangdong, China.*

[2] *https://orcid.org/0000-0002-8913-5651*

[3] *"Grigore Antipa" National Museum of Natural History, Sos. Kiseleff no. 1, 011341 Bucharest, Romania.*

https://orcid.org/0000-0002-6060-4602

[*]*Corresponding author.* *kotatsu@fripost.org;* *https://orcid.org/0000-0001-8868-8310*

Abstract

Three new species of chewing lice of the *Penenirmus*-complex (Phthiraptera: Ischnocera) are described and illustrated from woodpeckers (Picidae) and barbets (Megalaimidae) occurring in China. They are: *Picophilopterus blythipici* **new species** from *Blythipicus pyrrhotis sinensis* (Rickett, 1897), *Laimoloima ruiliensis* **new genus**, **new species** from *Psilopogon asiaticus asiaticus* (Latham, 1790), and *Laimoloima tandani* **new genus**, **new species** from *Psilopogon virens virens* (Boddaert, 1783). In addition, we provide illustrations of *Picophilopterus pici sensu lato* ex *Picus canus sordidior* (Rippon, 1906), and we present evidence that justifies resurrecting the genus *Picophilopterus* Ansari, 1947 to include the species infesting woodpeckers and Neotropical barbets (Capitonidae). Also, we erect the new genus *Laimoloima* to include the species from Asian barbets (Megalaimidae). The taxonomic position of *Penenirmus* species from African barbets (Lybiidae) and honeyguides (Indicatoridae) is unresolved. An updated checklist of the species in the *Penenirmus*-complex parasitic on non-passeriform hosts is provided, including species of the genus *Turnicola* Clay & Meinertzhagen, 1938.

Key words: Phthiraptera, Ischnocera, chewing lice, new genus, new species, *Penenirmus*-complex, *Picophilopterus*, *Laimoloima*, *Turnicola*, Picidae, Megalaimidae, woodpeckers, barbets, China

Introduction

The *Penenirmus*-complex is a small group of morphologically similar species that parasitise primarily perching birds (Passeriformes), but also woodpeckers and allies (Piciformes). In most recent treatments (*e.g.* Price *et al.* 2003), almost all species are placed in one heterogeneous genus: *Penenirmus* Clay & Meinertzhagen, 1938a. Several groups of species within *Penenirmus sensu lato* have been proposed as distinct genera (*e.g.* Złotorzycka 1964), but these genera are currently poorly described and not clearly differentiated from *Penenirmus sensu stricto*. In addition, the morphological relationships between *Penenirmus sensu lato* and other louse genera are not clear either. The *Penenirmus*-complex has been often regarded as close to the *Brueelia*-complex (*e.g.* Eichler 1963; Złotorzycka 1964, 1980; Mey & Barker 2014), but Valim & Palma (2015) and Gustafsson & Bush (2017) rejected this relationship on morphological grounds. Also, genetic data do not support a close link between these two genus-complexes (*e.g.* Bush *et al*. 2016). The male genitalia of *Penenirmus* have a unique structure within the Ischnocera, and Ledger (1980: 96) stated that the genitalia of *Turnicola* Clay & Meinertzhagen, 1938b are similar to those of *Penenirmus*. The close relationship between *Penenirmus sensu lato* and *Turnicola* has been supported by the phylogeny in Johnson *et al*. (2021: fig 1) showing that, since *Turnicola* is the sister group to *Penenirmus sensu lato*, it belongs in the *Penenirmus*-complex (see Appendix 1). The genus *Debeauxoecus* Conci, 1941 may also belong in the *Penenirmus*-complex, but it has been (1) synonymised with *Philopterus* Nitzsch, 1818 (*e.g.* Price *et al*. 2003), (2) placed in the *Philopterus*-complex (Valim & Palma 2015), or (3) placed in the *Brueelia*-complex (Mey & Barker 2014), although

Accepted by R.L. Palma: 30 Oct. 2021; published: 7 Jan. 2022

the latter opinion was rejected on morphological grounds by Gustafsson & Bush (2017). We have not examined any specimens of the type species of *Debeauxoecus*, and no modern descriptions or illustrations of this genus have been published; therefore, we cannot offer an opinion regarding its morphological relationships.

Similarly, the majority of species included in *Penenirmus sensu lato* are poorly described and illustrated—in many cases only the shape of the dorsal anterior plate, the outline of the head, or a schematic overview of the male genitalia have been illustrated (*e.g.* Fedorenko & Belskaya 1979; Balát 1981). The species from passeriform hosts have never been revised. Two species found on Asian barbets (Megalaimidae) were described by Dalgleish (1967), who also listed the known *Penenirmus* from African barbets (as Capitonidae). The *Penenirmus* species from woodpeckers were treated by Eichler (1953a), Emerson & Johnson (1961) and Dalgleish (1972). Some authors have separated the species parasitic on woodpeckers in the genus *Picophilopterus* Ansari, 1947 (*e.g.* Złotorzycka 1980; Mey 1992).

In this paper, (1) we resurrect the genus *Picophilopterus* to include the species parasitic on woodpeckers (Picidae), (2) we describe the new genus *Laimoloima* for the species of the *Penenirmus*-complex which parasitise Asian barbets, and (3) we describe three new species, one belonging to *Picophilopterus* and two to *Laimoloima*, based on specimens collected in South China. In addition, we provide morphological data on a louse population from *Picus canus sordidior* (Rippon, 1906), tentatively identified as *Picophilopterus pici sensu lato*, and include an updated checklist of the known species of the *Penenirmus*-complex from non-passeriform hosts.

Material and methods

All specimens are mounted on microscope slides in either Canada balsam or Hoyer's medium, and deposited at the Institute of Zoology, Guangdong Academy of Sciences, Guangzhou, Guangdong, China (IZGAS).

Specimens were examined under a Nikon Eclipse N*i* microscope (Nikon Corporation, Tokyo, Japan). Specimens from woodpeckers were identified tentatively using the key of Emerson & Johnson (1961) and that of Dalgleish (1972). Specimens from barbets were compared to the illustrations and descriptions published by Dalgleish (1967), because no key to these species has been published. Illustrations were drawn by hand, using a drawing tube. Line drawings were scanned, collated, and edited in GIMP (www.gimp.org). Considering that many abdominal setae have been broken in all specimens examined, the lengths of many setae are approximate, but the numbers of illustrated setae are accurate

Measurements were made from live images in NIS-Elements (Nikon Corporation, Tokyo, Japan). All measurements are given in millimeters (as ranges). 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, unless otherwise noted).

Terminology and abbreviations for most structural and setal characters follows Gustafsson & Bush (2017); abbreviations used for setal characters are shown in Figs 1, 1a–c, 3, 6 (except setae that are absent), and include: *ads = anterior dorsal seta*; *as1–3 = anterior setae 1–3*; *avs3 = anterior ventral seta 3*; *hs = hyaline seta* [of tarsi]; *mts1–3 = marginal temporal setae 1–3*; *pas = preantennal seta*; *pns = postnodal seta*; *pos = preocular seta*; *pst1–2 = parameral setae 1–2*; *s3–7 = sensilla 3–7* [of the postantennal head]; *sts = sternal setae*. Terminology of leg setae follow Gustafsson *et al*. (2019, 2020: fig. 88) and are constructed using the following formula: 1) leg section: *c = coxa*; *f = femur*; *t = trochanter*; *tb = tibia*; *tr = tarsus*; 2) Roman numeral I–III designating leg pair; 3) setal position: *a = anterior seta*; *b = sensilla basiconica*; *d = dorsal seta*; *dm = distal marginal seta*; *p = posterior marginal seta*; *s = sensillus*; *sf = spiniform seta*; *spn = spine of the thumb-like process*; *th = tactile hair*; *v = ventral seta*; 4) setal number (1–5). Host taxonomy and nomenclature follow Clements *et al*. (2019).

Systematics

PHTHIRAPTERA Haeckel, 1896

Phthiraptera Haeckel 1896: 703.

Ischnocera Kellogg, 1896

Ischnocera Kellogg, 1896: 63.

Philopteridae Burmeister, 1838

Philopteridae Burmeister, 1838: 422.

Penenirmus-complex

Included genera
***Penenirmus* Clay & Meinertzhagen, 1938**
Penenirmus Clay & Meinertzhagen, 1938a: 73.
Alaudinirmus Złotorzycka, 1964: 273.
Panurinirmus Złotorzycka, 1964: 270.
Paranirmus Złotorzycka, 1964: 275.
Pleurinirmus Złotorzycka, 1964: 275.
***Picophilopterus* Ansari, 1947**
Picophilopterus Ansari, 1947: 265.
***Laimoloima* new genus**
***Turnicola* Clay & Meinertzhagen, 1938**
Turnicola Clay & Meinertzhagen, 1938b: 278. **[1]**
[1] Included based on the phylogeny in Johnson *et al*. (2021: fig. 1).

Remarks. No clear definition of the *Penenirmus*-complex has been published, but Mey (1992) suggested that the absence of the head seta *pos* is a good synapomorphy for *Penenirmus* + *Picophilopterus*. This seta appears to be present in *Penenirmus rafflesi* Dalgleish, 1967 [now in *Laimoloima*] and *pos* is also absent in the distantly related *Acronirmus* Eichler, 1953b (Gustafsson & Bush 2017). Therefore, it is not a good character to group *Penenirmus* with *Picophilopterus*. The structure of the male genitalia is perhaps a better character to define this complex, but a thorough redescription of *Turnicola* is needed before useful morphological characters which would link *Turnicola*, *Penenirmus*, *Picophilopterus* and *Laimoloima* can be identified.

Picophilopterus Ansari, 1947

Type species: *Picophilopterus tuktola* Ansari, 1947: 265 [= *Pediculus pici* Fabricius, 1798: 571] (by original designation).

Diagnosis. There are no good published illustrations to distinguish *Picophilopterus* from *Penenirmus* morphologically, especially regarding male genitalia, features of the head and its chaetotaxy. However, based on specimens available to us, the comparison between the two genera published by Mey (1992) and the redescription of the type species of *Penenirmus* by Sychra *et al*. (2014), these genera can be separated by the following characters: (1) *Penenirmus* lacks the ventral horns (VH in Figs 6, 8) in the male endomere, which are present in *Picophilopterus* ("sharp pointed lateral projection" of Carriker 1963: 33; "endomeralen Skleritpaar" of Mey 1992: 50); (2) *Picophilopterus* lacks the dorsal postantennal suture, but is present in *Penenirmus* (Figs 3–4); (3) the antero-median indentations of the tergopleurites present in at least some *Penenirmus* are lacking in *Picophilopterus* (Figs 1–2); (4) at least the type of *Penenirmus* has multiple *sts* on each of segments II–VI, but species of *Picophilopterus* generally only have one *sts* on each side, except for *Picophilopterus campephili* (Eichler, 1953a) that has two *sts* on each side (see Dalgleish 1972: figs 7–8).

Carriker (1963) suggested that the structure of the preantennal head and the number and lengths of the abdominal setae would separate these genera; however, even between species where the head shape differs significantly, the structure and chaetotaxy appear to be largely the same, and the numbers of dorsal abdominal setae appear to

overlap among species of the two genera. The ventral "elongated lateral sclerites bearing three minute, spine-like setae" mentioned as a generic character for *Picophilopterus* by Carriker (1963: 33) differ only in shape between *Picophilopterus* and *Penenirmus* [compare our illustrations with those of Sychra *et al*. (2014)], and the shape of the "three minute, spine-like setae" is different even among species of *Picophilopterus*.

Mey (1992) suggested that the shape of the ventral carina separates these genera, but this is not the case for *Picophilopterus blythipici* **n. sp.** or for the specimens of *Picophilopterus pici sensu lato* we have examined. Differences in the size and shape of the coni suggested by Mey (1992) may be more useful, but we have not seen enough species of either genus to evaluate this feature adequately. Mey (1992) also suggested that the relative length of the *os* compared to *mts1* and *mts3* separates *Picophilopterus* from *Penenirmus*, but this is not true for all *Picophilopterus* [including *P. serrilimbus* (Burmeister, 1838) illustrated by Mey (1992)].

Description. ***Both sexes.*** Head rounded trapezoidal (Fig. 3), preantennal area differing in shape between species. Hyaline margin without marginal sclerotisation, and limited laterally to frons. Marginal carina interrupted medianly and laterally. Dorsal preantennal suture completely surrounds dorsal anterior plate and reaches lateral margin of head near site of *as1*; suture may extend posteriorly along midline posterior to dorsal anterior plate. Ventral anterior plate present. Ventral carina divided medianly, extended anteriorly to approach or reach frons. Head chaetotaxy as in Fig. 3; *pas* and *pos* absent; *avs3* not displaced anteriorly, situated near bend of ventral carina; *mts2* macroseta or microseta; *s5–7* absent. Dorsal postantennal suture absent. Gular plate present, often with central decoration. Thoracic and abdominal segments as in Figs 1–2. Claws of all feet of dissimilar size (Figs 1a–c), and tarsus I of all feet with small, flattened hyaline seta on median margin (*hs* in Figs 1a–c). Tergopleurites II–VII and IX+X in male and II–IX+X in female medianly continuous. Sternites present but lightly sclerotised.

Male. Subgenital plate formed from sternal plates VII–VIII, may reach distal margin of abdomen (Fig. 1). Genital opening clearly dorsal, posterior end of abdomen strongly sclerotised. Basal apodeme long, tongue-like (Fig. 5). Parameres fused to basal apodeme; *pst1* sensilla, *pst2* microsetae, in some species very stout. Endomere elongated, with postero-lateral extensions on which three slender setae are situated on each side. Ventrally, endomere has paired horn-like projections (Fig. 6). Distal endomere elongated. Lateral to endomere are paired elongated plates of unknown derivation, each with three small setae at about middle of length; anteriorly these plates appear to be fused to basal apodeme, but this is not clear in specimens examined. Distal to endomere, median to the parameres, is a hyaline section of the genitalia which is poorly visible. The lateral extent of this section is not visible, and for clarity only distal margin is illustrated; no setae are visible on this margin in specimens examined.

Female. Subgenital plate formed from sternal plate VII only (Fig. 2), bulging posteriorly along midline, but not reaching or approaching vulval margin. Subvulval plates present. In species examined by us, lightly sclerotised plates are present near vulval margin (Fig. 9). Vulval chaetotaxy with multiple long, slender setae marginally, microsetae submarginally forming convergent rows near midline, and scattered setae present between vulval margin and subgenital plate.

Host distribution. Piciformes: Capitonidae and Picidae.

Geographical range. All continents, except for the Australo-Papuan Region and Antarctica, where there are no woodpeckers or Neotropical barbets.

Remarks. Dalgleish's (1972) extensive synonymy of described taxa and expansion of the known host ranges of several species of *Picophilopterus* (as *Penenirmus*) are based primarily in similarities in abdominal chaetotaxy. Other characters, such as head shape and limited details of the male genitalia, suggest that many of the species considered junior synonyms by Dalgleish (1972) are in fact distinct species, including *P. caurensis* Carriker, 1963, *P. rivollii* Carriker, 1963 and *P. tuktola* Ansari, 1947. A thorough revision of the genus *Picophilopterus* is needed to establish whether or not the wide host associations reported by Dalgleish (1972) are accurate. Here, we follow the species-level taxonomy of Dalgleish (1972) and Price *et al*. (2003).

In addition, redescriptions of species from non-picid hosts are needed to establish the limits of *Picophilopterus*. In the phylogeny of Johnson *et al*. (2021: fig 1), *Penenirmus jungens* (Kellogg, 1896b) is separated from a large clade including many specimens identified as *Penenirmus auritus* (Scopoli, 1763), one of each of *P. arcticus* (Carriker, 1958), *P. marginatus* Tendeiro, 1958, *P. pici* and *P. zumpti* Tendeiro, 1961, plus several as *Penenirmus* sp. [we regard most of these taxa as belonging to *Picophilopterus*]. To reflect these results into the taxonomy of the complex, the species from honeyguides and some African barbets (Lybiidae) may need to be included in *Picophilopterus* in order for this genus to be monophyletic, but we believe there are still not sufficient available data to do so. Similarly, *Penenirmus zumpti*, and *P. leucomelan* Tendeiro, 1961 are morphologically close enough to *Picophi-*

lopterus to be included in this genus, but we refrain from making these transfers until these species are properly redescribed. Judging from its original description, *Penenirmus marginatus* appears to be distinct, and not close to either *Picophilopterus* or the species parasitising African barbets.

The correct generic position of *Penenirmus jungens* is not clear, although we have tentatively placed it in *Picophilopterus*. The keys of Emerson & Johnson (1961) and Dalgleish (1972) indicate that this species is morphologically close to other species of *Picophilopterus*; however, these keys are based mainly on abdominal chaetotaxy, which may not be useful to separate genera in the *Penenirmus*-complex. Furthermore, Emerson & Johnson's (1961: figs 6, 14, 24) illustrations of *P. jungens*, *i.e.* the dorsal anterior plate, the pterothoracic margin and the vulval margin, are characters which may not vary sufficiently among the genera of the *Penenirmus*-complex to allow placing *P. jungens* with certainty.

More species of the *Penenirmus*-complex need to be properly redescribed to establish whether the species from African barbets and honeyguides should be included in *Picophilopterus*, or if these species and *P. jungens* should be placed in separate new genera.

Included species

Picophilopterus arcticus (Carriker, 1958: 168) [in *Penenirmus*].
Picophilopterus auritus (Scopoli, 1763: 383) [in *Pediculus*].
Docophorus superciliosus Burmeister, 1838: 427.
Docophorus californiensis Kellogg, 1896b: 483.
Docophorus evagans Kellogg, 1896b: 480.
Penenirmus fiebrigi Eichler, 1953a: 240.
Penenirmus peusi Eichler, 1953a: 242.
Penenirmus varius Emerson, 1953: 134.
Penenirmus auritus aurifrons Carriker, 1956: 37.
Penenirmus serrilimbus asyndesmus Emerson & Johnson, 1961: 40.
Penenirmus serrilimbus pileatus Emerson & Johnson, 1961: 40.
Picophilopterus pici caurensis Carriker, 1963: 35.
Picophilopterus pici rivollii Carriker, 1963: 35.
Penenirmus silesiacus Złotorzycka, 1964: 273.
Picophilopterus blythipici **new species.**
Picophilopterus campephili (Eichler, 1953a: 239) [in *Penenirmus*] **new combination.**
Picophilopterus heteroscelis (Nitzsch, 1866: 118) [in *Nirmus*] **new combination.**
Pediculus pici Schrank, 1803: 188. Not *Pediculus pici* Fabricius, 1798.
Philopterus kumagera Uchida, 1949: 544.
Picophilopterus jungens (Kellogg, 1896b: 481) [in *Docophorus*]. **[1]**
Penenirmus villosus Emerson & Johnson, 1961: 41.
Picophilopterus maculipes (Piaget, 1880: 661) [in *Docophorus*] **new combination.**
Picophilopterus pici (Fabricius, 1798: 571) [in *Pediculus*].
Docophorus scalaris Burmeister, 1838: 427.
Docophorus macrotrichus Kolenati, 1858: 248.
Picophilopterus tuktola Ansari, 1947: 265.
Picophilopterus sitzendorfensis Mey [in Złotorzycka], 1980: 129. **[2]**
Picophilopterus serrilimbus (Burmeister, 1838: 427) [in *Docophorus*].

[1] In the phylogeny of Johnson *et al*. (2021: fig 1), *P. jungens* was not nested in the clade which we regard as *Picophilopterus sensu stricto*. However, based on published descriptions and illustrations, it cannot be separated morphologically from our concept of *Picophilopterus*. Hence, its placement in *Picophilopterus* here is tentative, pending a detailed redescription of the species.

[2] In the checklist of Price *et al.* (2003: 211), *Picophilopterus sitzendorfensis* is attributed to "Złotorzycka, 1980: 127", but author, date and page number are all incorrect. Złotorzycka (1980) explicitly attributed this name to "Mey, 1979". No thorough description and holotype designation were published until Mey (1992), who attributed it to "Mey in Złotorzycka, 1980", and stated that Złotorzycka had had access to a first draft of his manuscript before the publication of her book. Złotorzycka (1980) did not refer to any specimens, which was not necessary for availability of new taxa before 2000 (I.C.Z.N. 1999). Therefore, the correct citation of this name is as given above.

***Picophilopterus blythipici* new species**
(Figs. 1–3, 5–6, 9)

Type host. *Blythipicus pyrrhotis sinensis* (Rickett, 1897)—bay woodpecker (Picidae).

Type locality. Nanling Reservation, Ruyang County, Guangdong Province, China.

Diagnosis. *Picophilopterus blythipici* is morphologically close to *P. pici* and *P. auritus*. However, it can be separated from *P. pici* by the following characters: temples broader and more rounded, preantennal area more elongated and with more concave lateral margins in *P. blythipici* (Fig. 3) than in *P. pici* (Fig. 4); ventral horns of male endomere slender and clearly divided medianly into one horn on each side in *P. blythipici* (Fig. 6), but broader and joined distally to form a plate-like structure in *P. pici* (Fig. 8); proximal endomere proportionately longer and broader in *P. blythipici* (Fig. 6) than in *P. pici* (Fig. 8); male tergopleurites IV–VI each with two tergocentral setae on each side in *P. blythipici* (Fig. 1), but with three tergocentral setae on each side in *P. pici*.

Picophilopterus blythipici can be separated from *P. auritus* by the following characters: preantennal area more elongated and slender in *P. blythipici* (Fig. 3) than in *P. auritus*; male tergopleurite II medianly continuous in *P. auritus*, but medianly interrupted in *P. blythipici* (Fig. 1); male tergopleurite VII with two tergocentral setae on each side in *P. blythipici* (Fig. 1), but with one tergocentral seta on each side in *P. auritus*; female tergopleurite IX+X with one seta on each side in *P. blythipici* (Fig. 2), but with three setae on each side in *P. auritus*; horn-like projections of male mesosome positioned more anteriorly in *P. blythipici* than in *P. auritus*.

Description. ***Both sexes.*** Head rounded, trapezoidal (Fig. 3), preantennal area slender with shallow concave lateral margins and deeply concave frons. Marginal carina broad. Dorsal anterior plate longer than wide. Dorsal preantennal suture extended posteriorly along midline posterior to dorsal anterior plate. Preantennal nodi large. Head chaetotaxy as in Fig. 3. Gular plate with extensive central rugose area. Thorax, abdomen and chaetotaxy as in Figs 1–2.

Male. Tergopleurite IX+X sublaterally with 2–3 long setae clustered close together. Subgenital plate reaches distal margin of abdomen, but with distal end diffuse in some males examined. Genitalia as Figs 5–6; basal apodeme slender, widening considerably towards the distal end (Fig. 5); endomere elongated, with dorsal and ventral horns clearly separated (Fig. 6); chaetotaxy as in Figs 5–6; proximal end of endomere tapering and similar to that in *P. pici sensu lato* (fig. 8), but differs among specimens; distal end of endomere slender; parameres short and stout; *pst1–2* as in Fig. 6.

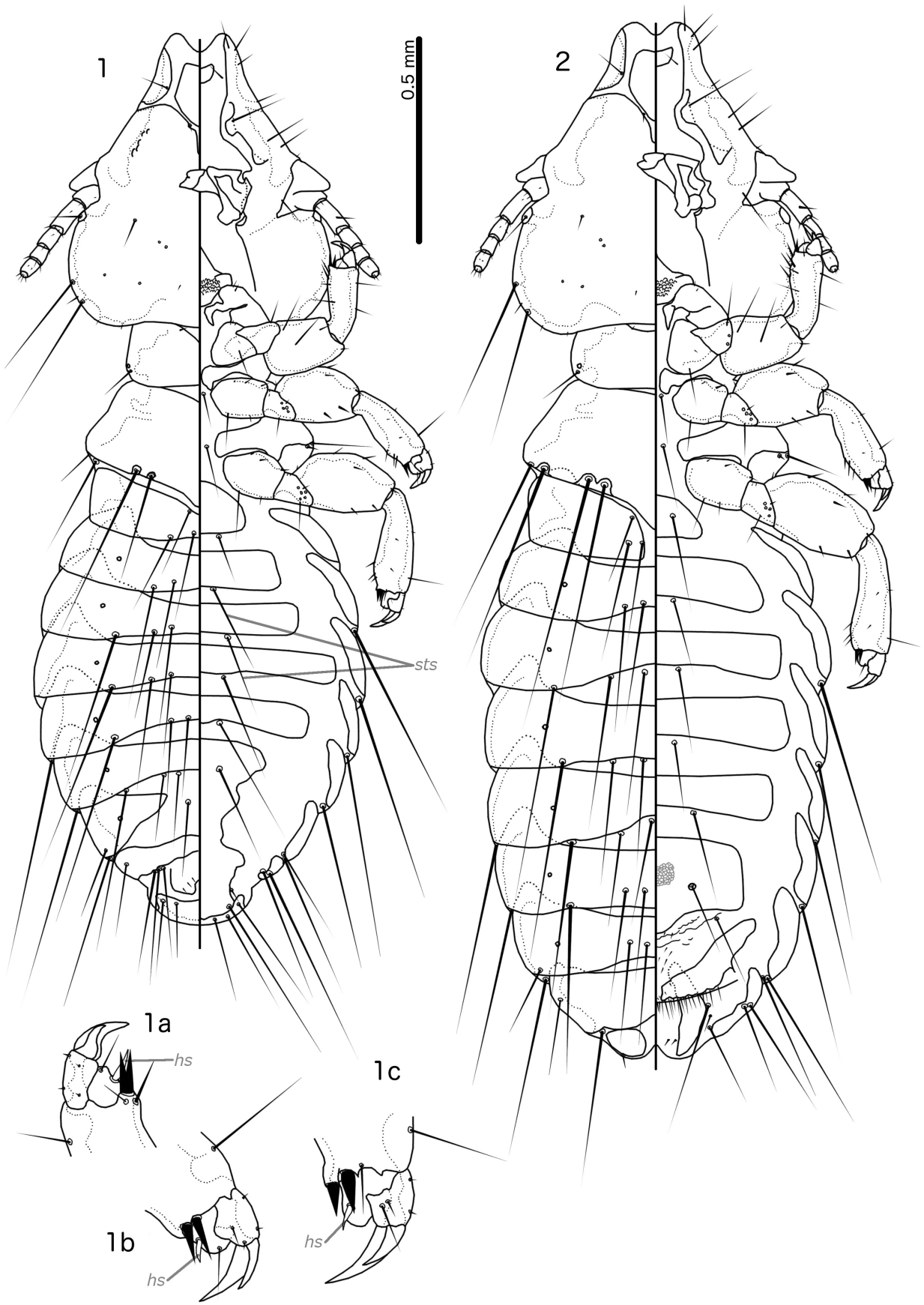
Female. Subgenital plate roughly rectangular, with medio-posterior margin bulging distally (Fig. 9); central part of subgenital plate often with faint reticulation; area posterior to subgenital plate wrinkled. Vulval margin gently rounded, with vulval marginal plates present on each side, seemingly unconnected medianly, but in some specimens there are additional sclerotised areas between these plates (not illustrated). Five sets of setae associated with subgenital plate and vulval area: one macroseta on each side situated on subgenital plate; one macroseta on each side situated just posterior to subgenital plate; 6–7 short, slender setae scattered in area between subgenital plate and vulval marginal plates; 4–6 microsetae in convergent rows median to vulval marginal plates; 17–22 (one specimen with 12 on one side) long, slender setae along vulval margin (some may be submarginal).

Type material. Ex ***Blythipicus pyrrhotis sinensis*: Holotype** ♂, Nanling Reservation, elev. 1200–1225 m, Ruyang County, Guangdong Province, China, 23 Nov. 2012, Nanling Bird Research Team, bird J0150, GD-PHTH-00123 (IZGAS). **Paratypes:** 5♂, 1♀, same data as holotype, GD-PHTH-00124–00136 (IZGAS).

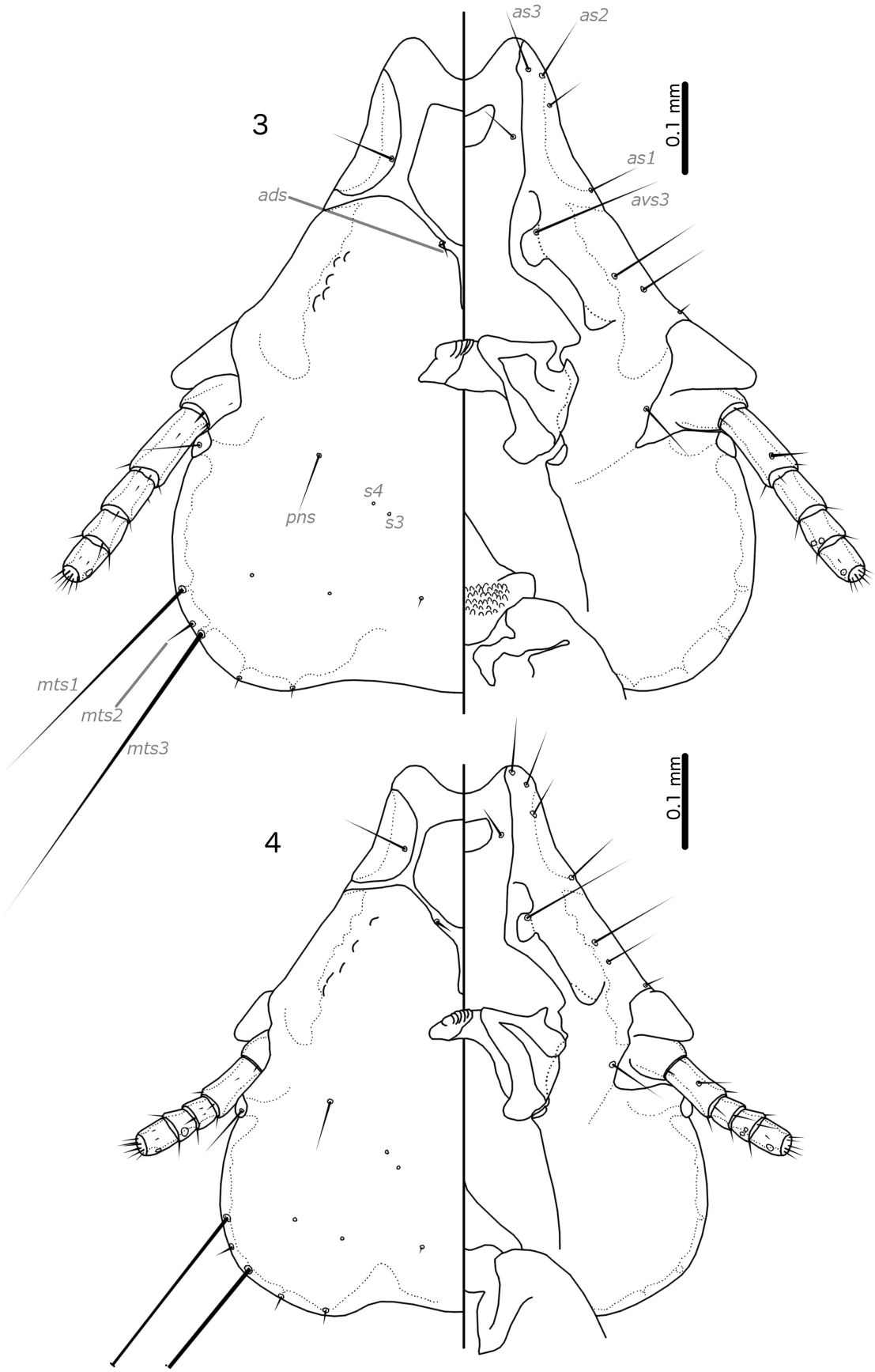
Non-types: 2 nymphs, same data as holotype, GD-PHTH-00137–00138 (IZGAS).

Etymology. The species epithet is derived from the generic name of the host.

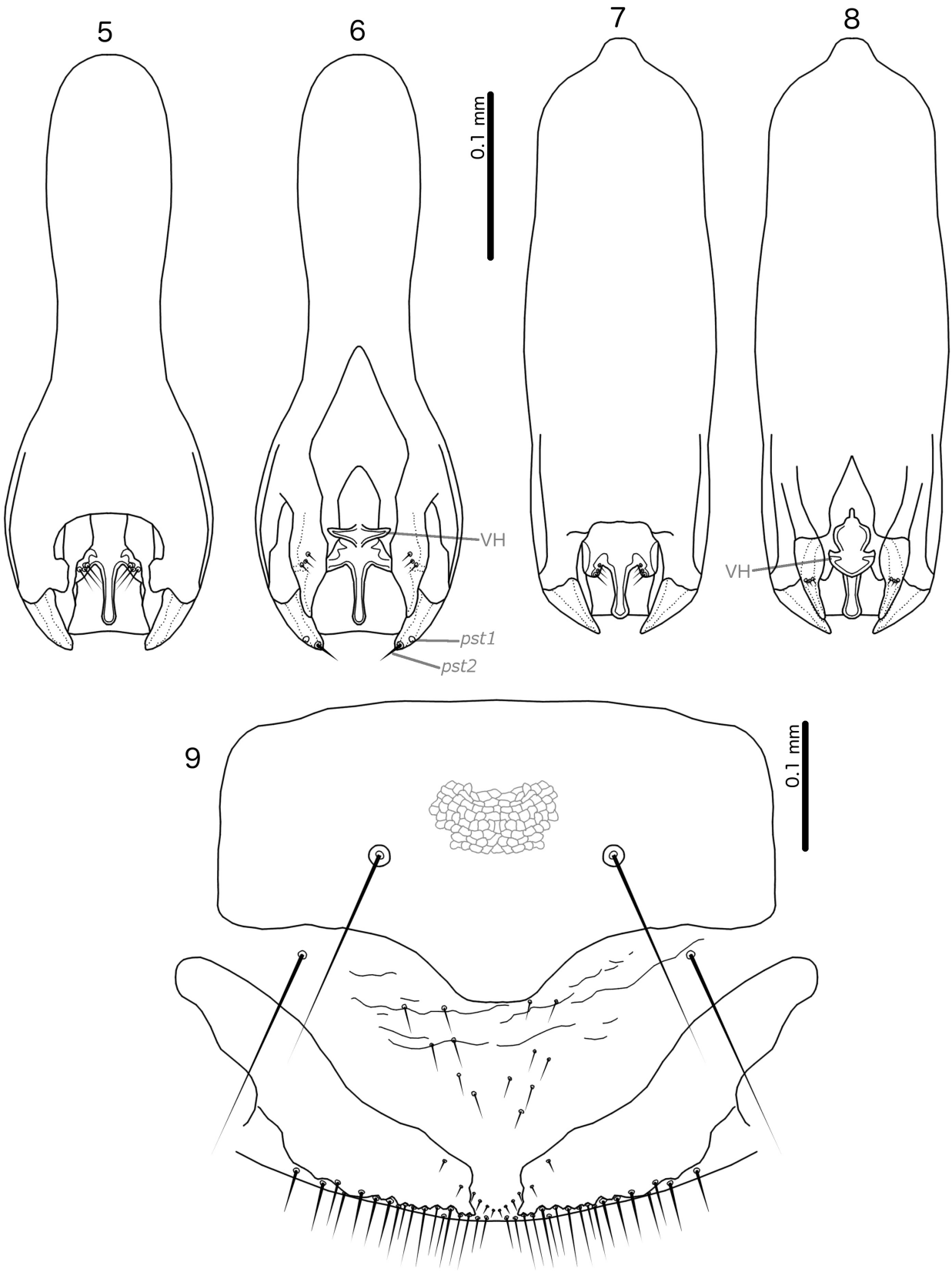
Remarks. Dalgleish (1972) included specimens from *Blythipicus pyrrhotis pyrrhotis* (Hodgson, 1837) from Nepal in *Penenirmus pici* (Fabricius, 1798) but, using Dalgleish's (1972) key, our specimens key out to *Penenirmus auritus* based on abdominal chaetotaxy. Using the key in Emerson & Johnson (1961), our specimens key out to couplet 4, but do not fit either alternative due to differences in female chaetotaxy, and males cannot be accurately identified in this key. As neither Emerson & Johnson (1961) nor Dalgleish (1972) illustrated or described the male genitalia in detail, our comparisons were made with specimens we studied and identified as *Picophilopterus pici sensu lato* from *Picus canus sordidior* (see below). Comparisons with *P. auritus* are based on the redescription of this species by Clay & Hopkins (1960), based on the neotype.



FIGURES 1–2. *Picophilopterus blythipici* **n. sp. 1,** male habitus, dorsal and ventral views **1a,** ventral view distal leg I. **1b,** ventral view of distal leg II. **1c,** ventral view of distal leg III. **2,** female habitus, dorsal and ventral views. Abbreviations: *hs—hyaline seta* (white); *sts—sternal setae*.



FIGURES 3–4. Male head, dorsal and ventral views. **3,** *Picophilopterus blythipici* **n. sp. 4,** *Picophilopterus pici* (Fabricius, 1798) *sensu lato* ex *Picus canus sordidior*. Abbreviations: *ads—anterior dorsal seta*; *as1–3—anterior setae 1–3*; *avs3—anterior ventral seta 3*; *mts1–3—marginal temporal setae 1–3*; *pns—postnodal seta*; *s3–4—sensilla 3–4*.



FIGURES 5–9. Genitalia. **5,** male *Picophilopterus blythipici* **n. sp.**, dorsal view. **6,** male *Picophilopterus blythipici* **n. sp.**, ventral view. **7,** male *Picophilopterus pici* (Fabricius, 1798) *sensu lato* ex *Picus canus sordidior*, dorsal view. **8,** male *Picophilopterus pici* (Fabricius, 1798) *sensu lato* ex *Picus canus sordidior*, ventral view. **9,** female subgenital plate and vulval margin, *Picophilopterus blythipici* **n. sp.**, ventral view. Abbreviations: *pst1–2—parameral setae 1–2;* VH—ventral horns of endomere.

Picophilopterus pici (Fabricius, 1798) *sensu lato*
(Figs 4, 8–9)

Pediculus pici Fabricius, 1798: 571.
Docophorus scalaris Burmeister, 1838: 427.
Picophilopterus tuktola Ansari, 1947: 265.
Picophilopterus sitzendorfensis Mey [in Złotorzycka], 1980: 129.
Penenirmus pici (Fabricius, 1798); Price *et al.* 2003: 210.

Type host: *Picus viridis* Linnaeus, 1758—green woodpecker (Picidae).

Type locality. Estonia—following Clay & Hopkins (1960) designation of a neotype.

Other hosts: 25 species and subspecies of woodpeckers (Picidae); see Appendix 1.

Host in China: *Picus canus sordidior* (Rippon, 1906)—gray-headed woodpecker: **new host record**.

Material examined: 1♂, 1♀, 2 nymphs, Wudiancun, elev. 903–1080 m, Ruili County, Yunnan Province, China, 8 Jan. 2013, Y. Wu & Y. Zhang, bird J-0681, GD-PHTH-00119–00122 (IZGAS).

Remarks. This species was previously recorded from China by Chu *et al.* (2019), and this report is based on the same specimens. *Picophilopterus pici* has been recorded from at least 16 host species (Price *et al*. 2003), but it is unclear whether all louse populations are conspecific. As we show above, at least the population from *Blythipicus pyrrhotis sinensis* is not conspecific with *P. pici*. Considering that Dalgleish (1971) named as *Brueelia straminea* (Denny, 1842) a large number of dissimilar species, many of which are not closely related to each other (Gustafsson & Bush, *in prep.*), we suspect that Dalgleish (1972) overestimated the similarities among populations of *P. pici* from different hosts, and that some of these populations may prove to be different species.

The phylogeny of Johnson *et al*. (2021: fig 1) includes only one specimen of *P. pici* from *Picus canus*, nested within a large clade of species mostly named as *P. auritus*; hence, genetic variation within *P. pici* from different hosts is unknown. However, several specimens of *P. auritus* included in the same phylogeny indicate that this nominal species may represent a number of different taxa. A thorough morphological revision of *Picophilopterus* from all woodpeckers is needed to ascertain the true number of different species currently included under these two species names. As an example, here we provide illustrations of the head and male genitalia of lice from *Picus canus sordidior*, which may prove to be a different species from *P. pici sensu stricto*. Note that *pst1–2* are not visible in examined specimens, and are not illustrated; the absence of these setae would need to be confirmed in other specimens.

Laimoloima new genus

Type species: *Laimoloima tandani* **n. sp.**

Diagnosis. *Laimoloima* is morphologically closest to *Penenirmus*. For comparison, refer to figures 4 and 5 in Sychra *et al.* (2014) to see the diagnostic characters of *Penenirmus* against those of *Laimoloima* as enumerated and illustrated in this paper. These two genera can be separated by the following characters: (1) head hyaline margin with marginal sclerotisation in *Laimoloima* (Fig. 14), but without sclerotisation in *Penenirmus*; (2) hyaline margin arising laterally near *as2* and thus extending lateral to sclerotised part of frons in *Laimoloima* (Fig. 14), but restricted to median part of frons in *Penenirmus*; (3) marginal carina clearly interrupted laterally at point where dorsal preantennal suture reaches head margin in *Penenirmus*, but not interrupted at that point in *Laimoloima* (Fig. 14); (4) head seta *as3* clearly dorsal, situated on hyaline margin in *Laimoloima* (Fig. 14), but marginal and situated on sclerotised part of head in *Penenirmus*; (5) head seta *as1* clearly dorsal in *Laimoloima* (Fig. 14), but marginal in *Penenirmus*; (6) head seta *mts1* short in *Laimoloima*, and in males clearly situated ventrally [in *P. rafflesi* (Dalgleish, 1967) this seta appears to be situated near the eye, but we have not seen any specimens to confirm this character], but *mts1* is a macroseta in *Penenirmus*; (7) head seta *mts2* is a macroseta in *Laimoloima* but is short in *Penenirmus*; (8) tergopleurites II–VIII medianly separated in both sexes in *Laimoloima* (Figs 10–11), but medianly continuous (may be indented anteriorly) in *Penenirmus*; (9) ventral side of abdomen of both sexes with only one *sts* on each side in *Laimoloima* (Figs 10–11), but with multiple *sts* on each side in *Penenirmus*; (10) ventral endomere of male genitalia with posterior and anterior lobes in *Laimoloima* (Fig. 19), but without lobes in *Penenirmus*.

Description. ***Both sexes.*** Head rounded, trapezoidal (Fig. 14), preantennal area broad, relatively short, typically

with concave frons. Hyaline margin broad, arising laterally near site of *as2*, and with clear sclerotisation of margin. Marginal carina interrupted medianly but not laterally. Dorsal preantennal suture completely surrounds dorsal anterior plate; in all specimens examined, the suture extends slightly distally posterior to *ads*, as illustrated in Fig. 14, but it is not clear if this is an artifact of mounting. Ventral carina interrupted medianly, extended anteriorly but does not reach frons. Head chaetotaxy as in Fig. 14; *as1* and *as3* clearly dorsal; *pas* and *pos* absent (*pos* may be present in *B. rafflesi*); *avs3* displaced anterior from bend in ventral carina; *mts1* clearly ventral at least in males, short seta; *mts2–3* macrosetae; *s5–7* absent. Dorsal postantennal suture present, with *pns* situated in suture but *s3–4* situated medial to suture. Gular plate present, central part decorated. Thoracic and abdominal segments as in Figs 10–11. Claws of all tarsi of dissimilar size (Figs 10a–c), and segment I of all tarsi with small, flattened hyaline seta on median margin (*hs* in Figs 10a–c). Leg setae *cI-v3*, *tI-v2, fI-V4, fI-p1, fII-a2, fII-a5, fIII-a2, fIII-a5* absent; *fII-d1* and *fIII-d1* displaced toward centre of femur; *cI-v1, tbI-d1–5*, *tbI-dm1, tbII-p1–3, tbII-dm3, tbII-v2, tbIII-p1–3* long and spine-like; *tbI-v1* very long; *tbI-a1* longer than leg seta *tbI-a2*; long and slender setae here called *tbI-v3* (Fig. 10a) present medial to *tbI-spn* on ventral side; trochanter II–III each with two microsetae near anterior margin (*tII-a1–2* and *tIII-a1–2*, respectively). Tergopleurites II–VIII medianly separated in both sexes. Tergopleurite II extended into postero-lateral hook. Sternal and subgenital plates lightly sclerotised in all specimens examined, and may be absent (not illustrated).

Male. Basal apodeme long, tongue-like (Fig. 16), but anterior end diffuse in specimens examined. Parameres fused to basal apodeme, *pst1* sensilla, *pst2* microsetae, in some species very stout. Endomere elongated, with distinct lobes on both ends: distal lobes pointed, and associated with three setae each side dorsally; proximal lobes on ventral side rounded. Distal endomere elongated. Lateral to endomere are paired elongated plates of unknown derivation, each with three small setae at about mid-length; anteriorly these plates appear to be fused to basal apodeme, but this is not clear in specimens examined. Hyaline section of genitalia distal to endomere poorly visible, but one minute seta visible on the distal margin on each side; lateral extent of this hyaline section is not visible in examined specimens, and only the distal margin is illustrated.

Female. Vulval margin with numerous long, slender marginal setae and numerous long, stout submarginal setae; short, slender setae scattered on lightly sclerotised subgenital plate.

Host distribution. Piciformes: Megalaimidae.

Geographical range. Indo-Malayan region.

Etymology. The name *Laimoloima* is constructed from "*laimós*", Greek for "throat", referring to the family name of the host (Megalaimidae), and "*loimós*", Greek for "pest". Gender: feminine.

Remarks. We include in *Laimoloima* two new species, described below, and three previously described species. We have not seen any specimens of *Docophorus limbatus* Piaget, 1885 (as *Penenirmus limbatus* in Hopkins & Clay 1952: 275) from *Psilopogon corvinus* (Temminck, 1831), and the original illustration is poor. Piaget (1885: 4) states that the frons has a "coloured border", which we interpret as referring to the thin band of sclerotisation of the hyaline margin. Therefore, we tentatively include *Docophorus limbatus* Piaget, 1885 in *Laimoloima*. Furthermore, *Penenirmus rafflesi* Dalgleish, 1967 and *Penenirmus zeylanica* Dalgleish, 1967 are also included in *Laimoloima*, based on the original descriptions which, as far as it is possible to see, share all the characters of the new genus.

In Tendeiro's (1961) illustrations of *Penenirmus guineensis*, the frons appears to be sclerotised, the dorsal preantennal suture is present, and *as3* is illustrated on the dorsal side. Both, Tendeiro's (1961) photo of *P. bidentatus* with a sclerotised hyaline margin and his photo of the male genitalia of *P. guineensis* suggest a relationship with *Laimoloima*. However, in the phylogeny of Johnson *et al*. (2021: fig 1), *P. guineensis* is embedded in a clade with lice from other African barbets and a woodpecker, sister to a clade of *Penenirmus* from Passeriformes, and both clades together are sisters to all other *Penenirmus sensu lato* and *Picophilopterus*. Nevertheless, as we have not examined any specimens of any African species, we retain *P. guineensis* and *P. bidentatus* in *Penenirmus* until they can be redescribed.

In the phylogeny of Johnson *et al*. (2021), one louse belonging to the *Penenirmus*-complex from *Psilopogon chrysopogon* (Temminck, 1824) (Megalaimidae) was placed as sister to a large clade containing several species of *Picophilopterus*, as well as lice from honeyguides (Indicatoridae), Neotropical barbets (Capitonidae) and two African barbets (Lybiidae). Presumably, the specimen from *Psilopogon chrysopogon* belongs to *Laimoloima*, but its morphology is not known to confirm its taxonomic position. Although the phylogeny of Johnson *et al*. (2021) contains only one species from Asian barbets, its position would indicate that the lice of the *Penenirmus*-complex from these birds are not closely related to those from African and Neotropical barbets, and that some morphological

similarities between species of *Laimoloima* species and those from African barbets (*e.g.* the sclerotised central part of the hyaline margin) may be the result of convergent evolution.

Included species

Laimoloima limbata (Piaget, 1885: 4) **new comb.**
Laimoloima rafflesi (Dalgleish, 1967: 606) **new comb.**
Laimoloima ruiliensis **n. sp.**
Laimoloima tandani **n. sp.**
Laimoloima zeylanica (Dalgleish, 1967: 604) **new comb.**

Laimoloima tandani new species

(Figs 10–11, 14, 16–17, 20)

Type host. *Psilopogon virens virens* (Boddaert, 1783)—great barbet (Megalaimidae).

Type locality. Shunhuangshan, Xinning Village, Chaoyuan County, Hunan Province, China.

Diagnosis. Sharing the same position of *mts1* near *mts2* would suggest that *Laimoloima tandani*, *L. ruiliensis*, and *L. zeylanica* are more closely related to each other than to *L. rafflesi.* Further, the shape of the male endomere of *L. tandani* (Figs 15–16) is more similar to that of *L. zeylanica* than to that of *L. ruiliensis* (Figs 17–18). *Laimoloima tandani* can be separated from *L. zeylanica* by the following characters: (1) dorsal anterior plate gently rounded posteriorly in *L. zeylanica*, but extended posteriorly in *L. tandani* (Fig. 14), (2) preantennal area proportionately slightly shorter and broader in *L. tandani* (Fig. 14) than in *L. zeylanica*, (3) anterior lobes of male endomere of different shapes, and proportionately larger in *L. tandani* (Fig. 16) than in *L. zeylanica*, (4) parameres stouter in *L. tandani* (Figs 15–16) than in *L zeylanica*, (5) meso- and metasternum each with two setae on each side in *L. zeylanica*, but each with one seta on each side in *L. tandani* (Figs 10–11), (6) female tergopleurite II with two tergocentral setae on posterior margin in *L. tandani* (Fig. 11), but with one seta in *L. zeylanica*, (7) female tergopleurite VIII with one tergocentral seta in *L. tandani* (Fig. 11), but with two setae in *L. zeylanica*.

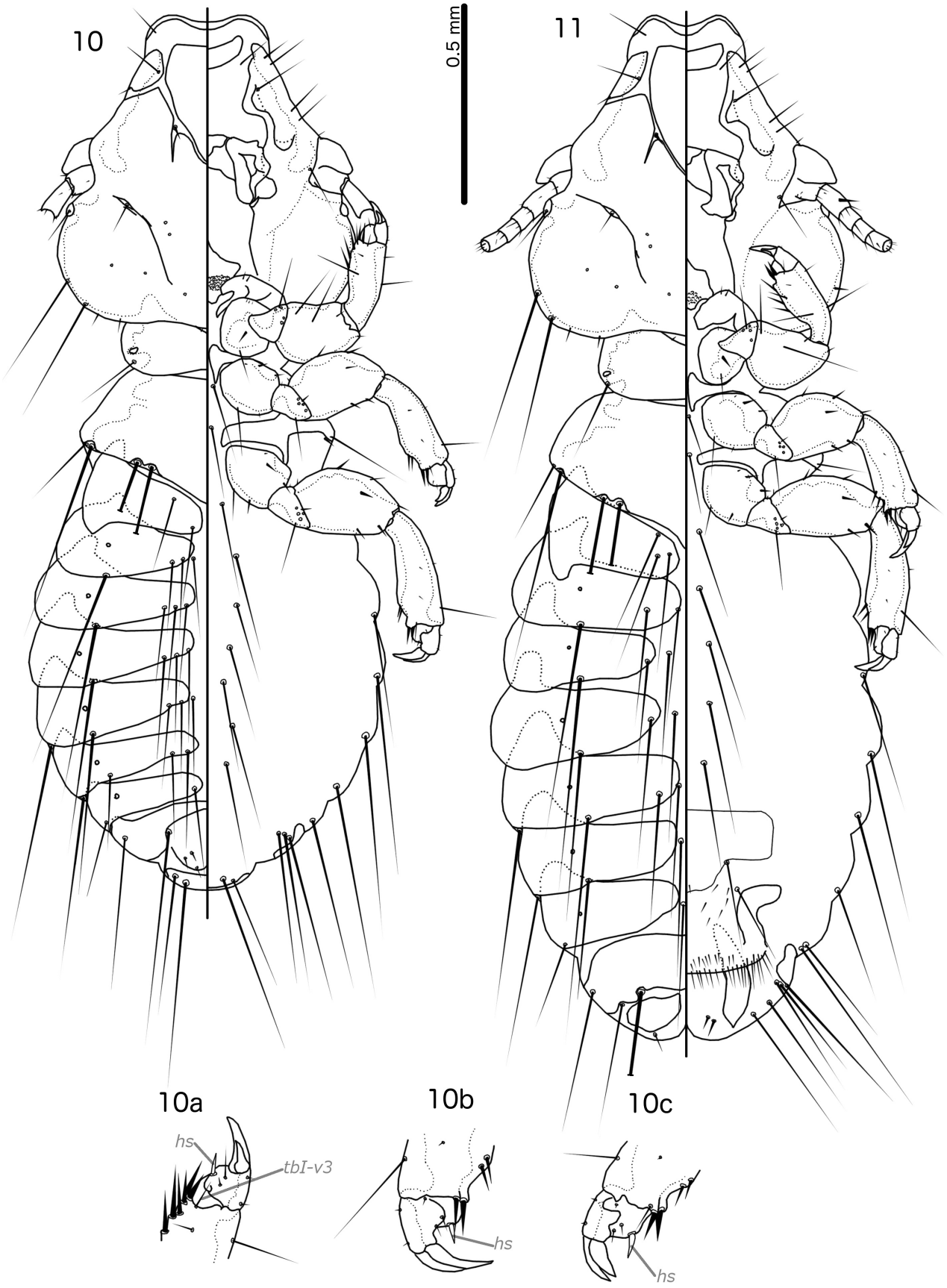
Description. ***Both sexes.*** Head rounded trapezoidal (Fig. 14), frons broad and slightly concave, lateral margins of preantennal head slightly concave. Dorsal anterior plate roughly triangular, longer than wide. Dorsal preantennal suture diffuse posterior to *ads*, and illustrated approximately. In both specimens examined, the dorsal preantennal suture extends posteriorly from *ads*; this may be an artifact of mounting but, as it is similar in both specimens, we illustrated it as described. Marginal carina broad. Head chaetotaxy as in Fig. 14; chaetotaxy of antennae as in Figs 14a–b. Dorsal postantennal suture present, widened around aperture of *pns*. Gular plate with extensive rugose area centrally. Thoracic and abdominal segments and chaetotaxy as in Figs 10–11; sternal plates lightly sclerotised, and not illustrated.

Male. Subgenital plate lightly sclerotised, and not illustrated. Tergopleurites III–VI each with three tergocentral setae on each side; tergopleurite VII with two tergocentral setae on each side. Anterior end of basal apodeme diffuse, and not illustrated; distal section with more or less parallel lateral margins, but bulging lateral margins distally (Fig. 16). Endomere longer than wide, with prominent rounded antero-lateral lobes ventrally and pointed postero-lateral lobes. Endomeral chaetotaxy as in Figs 16–17. Distal endomere asymmetrical in one examined specimen. Parameres short and broad; *pst1–2* as in Fig. 17.

Female. Subgenital plate weakly sclerotised, and here illustrated approximately (Fig. 20). Vulval margin with 14–19 long, slender setae marginally and 9–11 long, stout setae submarginally on each side; 1–2 macroseta associated with subgenital plate on each side, and 5–7 short, slender setae on each side in area between subgenital plate and vulval margin. Subvulval plates diffuse distally in one examined female, and illustrated approximately.

Type material. Ex ***Psilopogon virens virens*****: Holotype** ♂, Shunhuangshan, Xinning Village, elev. 814–855 m, Chaoyuan County, Hunan Province, China, 31 Aug. 2018, X. Chu & L. Lei, bird J3634, GD-PHTH-00139 (IZGAS). **Paratype:** 1♀, same data as holotype, GD-PHTH-00140 (IZGAS).

Etymology. The species epithet honours the late Bhup Kishore Tandan (formerly at the University of Lucknow, India). In our opinion, Tandan was one of the greatest phthirapterists of the 20th century, and his published illustrations and descriptions of, especially, Asian chewing louse taxa should be considered a benchmark to strive toward by all chewing louse taxonomists.



FIGURES 10–11. *Laimoloima tandani* **n. sp. 10,** male habitus, dorsal and ventral views. **10a,** ventral view distal leg I. **10b,** ventral view of distal leg II. **10c,** ventral view of distal leg III. **11,** female habitus, dorsal and ventral views. Abbreviation: *hs—hyaline seta* (*white*).

Remarks. Since the holotype has one antenna medianly distorted and the other with flagellomeres I–III fused (Fig. 14), we provide illustrations of the female antennae (Figs 14a–b) to depict the chaetotaxy of the antennae of *B. tandani* accurately, which is indistinguishable from that of males of *B. ruiliensis*; this suggests that there may be no differences between the antennal chaetotaxy of males of the two species. Also, some head and abdominal setae are broken on both sides of the holotype, hence they are illustrated approximately, based on the length of the same seta in the female.

Laimoloima ruiliensis new species

(Figs 12–13, 15, 18–19, 21)

Type host. *Psilopogon asiaticus asiaticus* (Latham, 1790)—blue-throated barbet (Megalaimidae).

Type locality. Wudiancun, Ruili County, Yunnan Province, China.

Diagnosis. *Laimoloima ruiliensis* can be separated from *L. zeylanica* and *L. tandani* by having a proportionately shorter preantennal area (Fig. 15) and from *L. rafflesi* by the position of *mts1* near *mts2* rather than near posterior margin of eye. The shape of the male endomere suggests that *L. ruiliensis* is closer to *L. zeylanica* than to *L. tandani*.

Furthermore, *Laimoloima ruiliensis* can be separated from *L. zeylanica* by the following characters: dorsal anterior plate with rounded posterior margin in *L. zeylanica*, but with tapering posterior margin in *L. ruiliensis* (Fig. 15); male tergopleurites III–IV with two tergocentral setae on each side in *L. ruiliensis* (Fig. 12), but with three tergocentral setae on each side in *L. zeylanica*; female tergopleurites V–VI each with three tergocentral setae on each side in *L. ruiliensis* (Fig. 13), but with two setae on each side in *L. zeylanica*; male genitalia of *L. zeylanica* are illustrated without much detail by Dalgleish (1967: fig. 4), but the general shape of the endomeres and thickness of their distal sections differ between the two species (Fig. 19).

Description. ***Both sexes.*** Head rounded trapezoidal (Fig. 15), frons slightly concave, lateral margins of preantennal area concave. Dorsal preantennal plate tapering to blunt posterior point. Dorsal preantennal suture diffuse in posterior end, and illustrated approximately. Marginal carina broad. Head chaetotaxy as in Fig. 15. Dorsal postantennal suture present, widened around aperture of *pns*. Gular plate with extensive rugose area centrally. Thoracic and abdominal segments and chaetotaxy as in Figs 12–13; sternal and subgenital plates lightly sclerotised, and not illustrated.

Male. Tergopleurites II–III each with two tergocentral setae on each side; tergopleurites V–VII each with three tergocentral setae on each side. Anterior end of basal apodeme diffuse, and not illustrated; distal section with parallel lateral margins converging distally (Fig. 18). Endomere with lateral extensions at midline dorsally; endomere with moderate, somewhat angular anterior lobes and pointed posterior lobes ventrally (Fig. 19). Endomeral chaetotaxy as in Figs 18–19. Parameres short and broad; *pst1–2* as in Fig. 19.

Female. Vulval margin with 11–13 long, slender, marginal setae, and 8–11 long, stout, submarginal setae on each side; two macroseta associated with lightly sclerotised subgenital plate on each side, and four short, slender setae on each side in area between subgenital plate and vulval margin. Subvulval plates elongate, widening distally (Fig. 21).

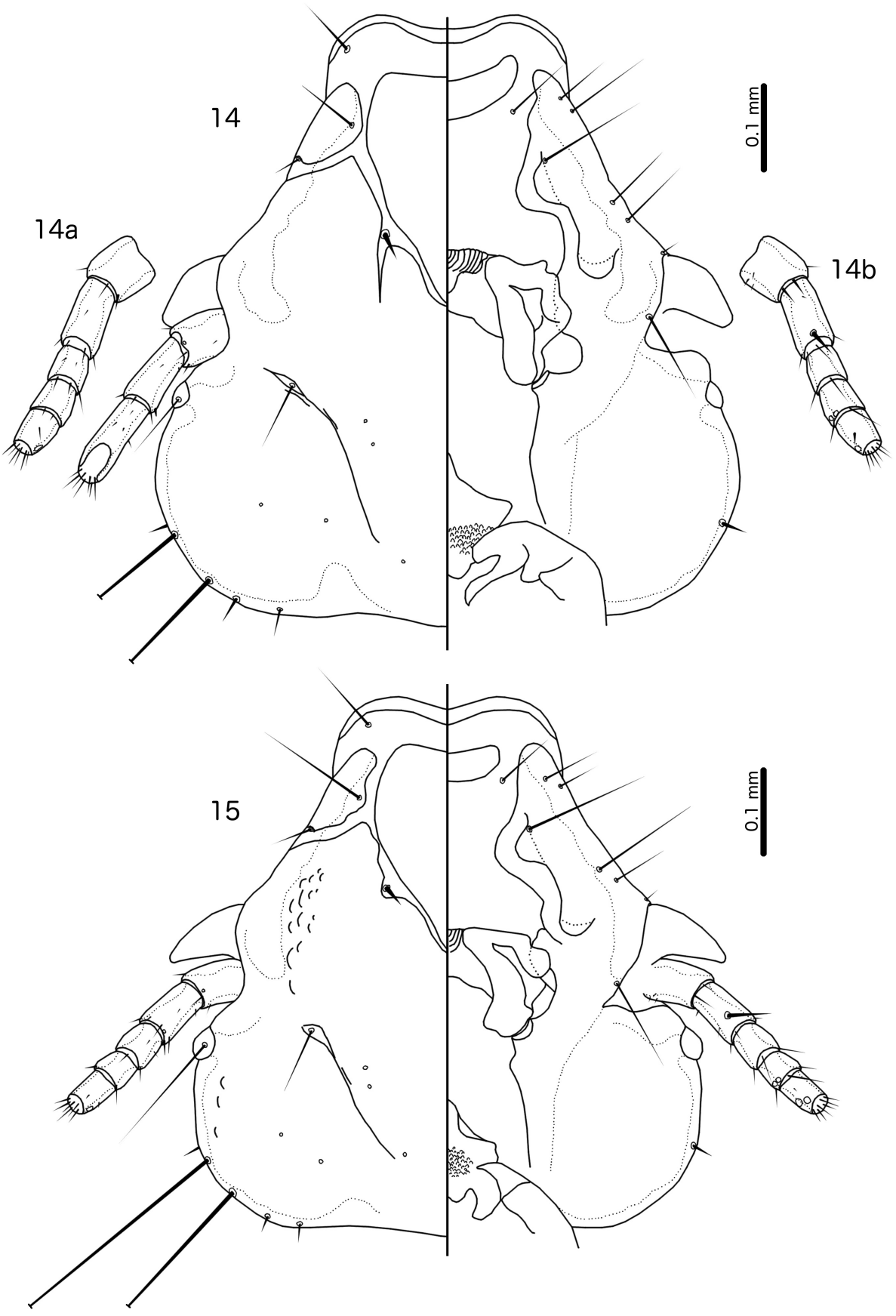
Type material. Ex ***Megalaima asiaticus asiaticus*: Holotype** ♂, Wudiancun, elev. 903–1080 m, Ruili County, Yunnan Province, China, 9 Jan. 2013, Y. Wu & Y. Zhang, bird J0697, GD-PHTH-00141 (IZGAS). **Paratypes:** 1♂, 2♀, same data as holotype, GD-PHTH-00142–00144 (IZGAS).

Non-types: 2 nymphs, same data as holotype, GD-PHTH-00145–00146 (IZGAS).

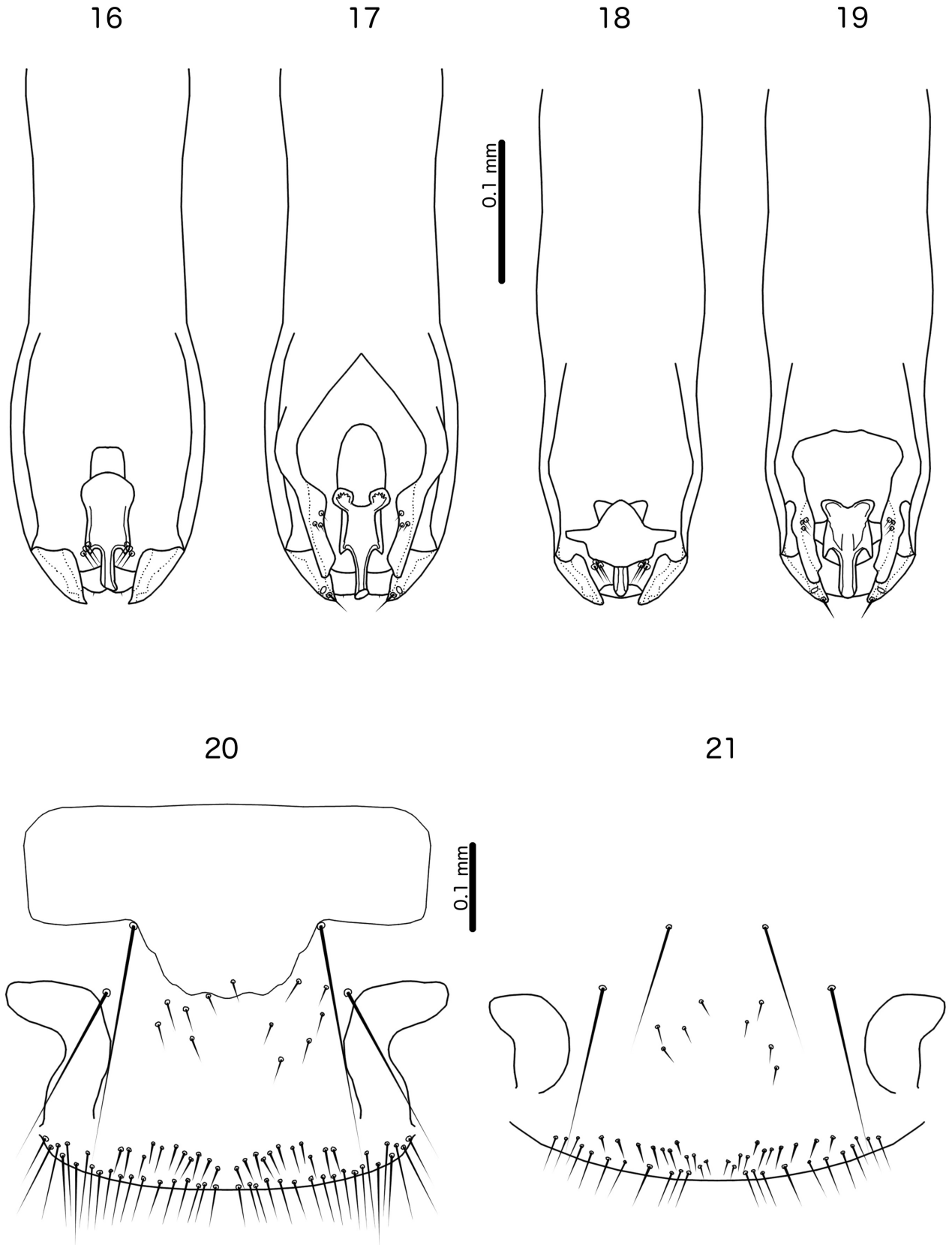
Etymology. The species epithet is derived from the type locality.

Remarks. The male genitalia are partially obscured by gut content in the holotype, hence illustrations are based on the paratype male; the parts of the genitalia that can be seen in the holotype are identical to those of the paratype.

FIGURES 12–13. *Laimoloima ruiliensis* **n. sp. 12,** male habitus, dorsal and ventral views. **13,** female habitus, dorsal and ventral views. Note: Since some abdominal setae are broken on both sides of all specimens examined, their lengths are illustrated approximately.



FIGURES 14–15. Head, dorsal and ventral views. **14,** male *Laimoloima tandani* **n. sp. 14a,** female antenna, dorsal view. **14b,** female antenna, ventral view. **15,** male *Laimoloima ruiliensis* **n. sp.**



FIGURES 16–21. Genitalia. **16,** *Laimoloima tandani* **n. sp.**, male dorsal view. **17,** *Laimoloima tandani* **n. sp.**, male ventral view. **18,** *Laimoloima ruiliensis* **n. sp.**, male dorsal view. **19,** *Laimoloima ruiliensis* **n. sp.**, male ventral view. **20,** *Laimoloima tandani* **n. sp.**, female subgenital plate and vulval margin, ventral view. **21,** *Laimoloima ruiliensis* **n. sp.**, female vulval margin, ventral view.

Discussion

The *Penenirmus*-complex is among the least known groups of ischnoceran lice, in particular the demarcation of its genera and their relationships, as well as their relationship as a group to other groups of ischnoceran lice. In our opinion, the complex is so morphologically diverse that it cannot be contained in one genus. Besides the species here placed in *Picophilopterus* and *Laimoloima*, at least four other groups within *Penenirmus sensu lato* may deserve to be recognised as separate genera. Based on the phylogeny of Johnson *et al*. (2021) and published morphological data of species in this group (*e.g.* Tendeiro 1961, 1962), the lice from honeyguides would comprise a new genus, *Picophilopterus jungens* would need another genus, as well as each of the two different clades of lice from African barbets. Alternatively, the lice from honeyguides and some from African barbets could be included in *Picophilopterus*, depending on how generic boundaries are chosen as defined by the clades.

Furthermore, several of the species here placed in *Picophilopterus* need to be redescribed and their taxonomic placement reassessed, in particular *P. auritus* and *P. pici*. The revision by Dalgleish (1972) is based almost entirely on abdominal chaetotaxy, ignoring male and female genitalic characters, head shape, and other potentially useful defining features. Differences in head shape and male genitalia among specimens presumably belonging to the same species (*Penenirmus auritus*) as reported by Emerson (1953), Emerson & Johnson (1961), Carriker (1963), Dalgleish (1972) and González-Acuña *et al*. (2014) appear to be too ample to regard them as intraspecific variation. We expect that a thorough revision of *Picophilopterus* will reveal that the characters used by Dalgleish (1972) should be considered as species-group characters, and that the diversity of species within this genus is much greater than currently accepted.

Acknowledgements

This study was funded by the National Natural Science Foundation of China [Grant number 31961123003], the Foreign Young Talent Plan (QN20200130012), the Introduction of Full-Time High-Level Talent Fund of the Institute of Zoology, Guangdong Academy of Sciences (GIABR-GJRC201701), the Pearl River Talent Recruitment Program, Guangdong Province [Grant number 2019QN01N968], and the Introduction of Full-Time High-Level Talent Fund of the Institute of Zoology, Guangdong Academy of Sciences [Grant number GIABR-GJRC201701]. These agencies had no influence in the design or execution of this study, and we declare no conflict of interest. We thank Xingzhi Chu, Lujia Lei, Yuchun Wu and Yanhua Zhang (formerly at IZGAS) for collecting the specimens studied in this paper. We are indebted to Ricardo Palma (Museum of New Zealand, Wellington, New Zealand) for his valuable advice and revision of the first draft of this paper, and to Terry D. Galloway (Department of Entomology, University of Manitoba, Winnipeg, Manitoba, Canada) for many helpful comments that improved this paper.

References

Ansari, R.A.M. (1947) Mallophaga (Ischnocera) infesting birds in the Punjab (India). *Proceedings of the National Institute of Science, India*, 13, 253–303.

Balát, F. (1981) New species of biting lice (Mallophaga) of the genera *Penenirmus* and *Rostrinirmus*. *Folia Parasitologica*, 28, 161–168.

Burmeister, H. (1838) Mallophaga. *In*: *Handbuch der Entomologie*. *2 (1)*. Enslin, Berlin, pp. 418–443.

Bush, S.E., Weckstein, J.D., Gustafsson, D.R., Allen, J., DiBlasi, E., Shreve, S.M., Boldt, R., Skeen, H.R. & 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.
https://doi.org/10.1016/j.ympev.2015.09.015

Carriker, M.A. Jr. (1903) Mallophaga from birds of Costa Rica, Central America. *University Studies* [*University of Nebraska*], 3, 123–197, 9 pls.

Carriker, M.A. Jr. (1956) Report on a collection of Mallophaga, largely Mexican (Part II). *The Florida Entomologist*, 39, 19–43 + 69–84 + 119–132.
https://doi.org/10.2307/3492776

Carriker, M.A. Jr. (1958) On a small collection of Mallophaga from the United States, with descriptions of three new species. *Proceedings of the Entomological Society of Washington* 60, 167–174.

Carriker, M.A. Jr. (1963) New and little known Mallophaga from Venezuelan birds (Part II). *Memoria de la Sociedad de Ciencias Naturales La Salle*, 23 (64), 5–42.

Chu, X., Dik, B., Gustafsson, D.R., Che, X., Zhang, Q. & Zou, F. (2019) The influence of host body size and food guild on prevalence and mean intensity of chewing lice (Phthiraptera) on birds in Southern China. *Journal of Parasitology*, 105, 334–344.
https://doi.org/10.1645/17-137

Clay, T. & Hopkins, G.H.E. (1960) The early literature on Mallophaga (Part IV, 1787–1818). *Bulletin of the British Museum (Natural History) Entomology*, 9, 1–61, 6 pls.
https://doi.org/10.5962/bhl.part.27551

Clay, T. & Meinertzhagen, R. (1938a) Two new genera of Mallophaga. *The Entomologist*, 71, 73–76.

Clay, T. & Meinertzhagen, R. (1938b) New genera and species of Mallophaga. *The Entomologist*, 71, 275–279.

Clements, J.F., Schulenberg, T.S., Iliff, M.J., Roberson, D., Fredericks, T.A., Sullivan, B.L. & Wood, C.L. (2019) The eBird/Clements checklist of birds of the world. Version 2019. Available from: http://www.birds.cornell.edu/clementschecklist/download/ (accessed 23 September 2019)

Conci, C. (1941) Nuovi generi de Mallofagi (nota preliminare). *Bollettino della Societá Entomologica Italiana*, 73, 126–127.

Dalgleish, R.C. (1967) Two new species of *Penenirmus* (Mallophaga: Ischnocera) from Asian barbets (Piciformes, Capitonidae). *The Canadian Entomologist*, 99 (6), 604–606.
https://doi.org/10.4039/Ent99604-6

Dalgleish, R.C. (1971) The *Brueelia* (Mallophaga: Ischnocera) of the Picidae (Aves: Piciformes). *Journal of the New York Entomological Society*, 79, 139–146.

Dalgleish, R.C. (1972) The *Penenirmus* (Mallophaga: Ischnocera) of the Picidae (Aves: Piciformes). *Journal of the New York Entomological Society*, 80, 83–104.

Denny, H. (1842) *Monographia Anoplurorum Britanniae or, an essay on the British species of parasitic insects belonging to the order of Anoplura of Leach, with the modern divisions of the genera according to the views of Leach, Nitzsch, and Burmeister, with highly magnified figures of each species*. Henry G. Bohn, London, xxiv + 262 pp., 26 pls.
https://doi.org/10.5962/bhl.title.137104

Eichler, W. (1953a) Mallophagen-Synopsis. XXIV. Genus *Penenirmus* (incl. *Picophilopterus*). *Zoologischer Anzeiger*, 150, 235–245.

Eichler, W. (1953b) Von Alexander König gesammelte Federlinge. I. Von Singvögeln und Spechten. *Bonner zoologische Beiträge*, 4, 333–343.

Eichler, W. (1963). Klassen und Ordnungen des Tierreichs. Fünfter Band: Arthropoda. III. Abteilung: Insecta. 7. Buch. b) Phthiraptera. 1. Mallophaga. *In*: Bronns H.G. (Ed.), Akademische Verlagsgesellschaft Geest & Portig K.-G., Leipzig, vii + 291 pp.

Emerson, K.C. (1953) New North American Mallophaga. *Journal of the Kansas Entomological Society*, 26, 132–136.

Emerson, K.C. & Johnson, J.C. (1961) The genus *Penenirmus* (Mallophaga) found on North American woodpeckers. *Journal of the Kansas Entomological Society*, 34, 34–43.

Fabricius, J.C. (1798) *Pediculus*. *In*: *Supplementum Entomologiae Systematicae*. Proft & Storch, Hafniae, pp. 570–571.

Fedorenko, I.A. & Belskaya, G.S. (1979) [Species of the genus *Penenirmus* (Mallophaga, Ischnocera), parasitising whinchats and wheatears]. *Vestnik Zoologii*, 1979, 22–28. [in Russian, with English summary]

Giebel, C. (1866) Die im zoologischen Museum der Universität Halle aufgestellten Epizoen nebst Beobachtungen über dieselben. *Zeitschrift für die Gesammten Naturwissenschaften*, 28, 353–397.

González-Acuña, D., Ardiles, K., Moreno, L., Muñoz, S., Vásquez, R.A., Celis C., Rozzi, R. & Cicchino, A. (2014) Lice species (Insecta: Phthiraptera) from Chilean Picidae (Aves: Piciformes). *Entomological News*, 124 (2), 109–119.
https://doi.org/10.3157/021.124.0206

Gustafsson, D.R. & 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), 1–443.
https://doi.org/10.11646/zootaxa.4313.1.1

Gustafsson, D.R., Lei, L., Chu, X., Zou, F. & Bush, S.E. (2019) New genus and two new species of chewing lice from Southeast Asian trogons (Aves: Trogoniformes), with a revised key to the *Philopterus*-complex. *Acta Parasitologica*, 64, 86–102.
https://doi.org/10.2478/s11686-018-00011-x

Gustafsson, D.R., Lei, L., Chu, X. & Zou, F. (2020) Review of Chinese species of the *Oxylipeurus*-complex (Phthiraptera: Philopteridae), with descriptions of two new genera and five new species. *Zootaxa*, 4742 (2), 201–255.
https://doi.org/10.11646/zootaxa.4742.2.1

Haeckel, E. (1896) *Systematische Phylogenie. 2. Theil. Systematische Phylogenie der wirbellosen Thiere* (*Invertebrata*). Verlag von Georg Reimer, Berlin, 720 pp.
https://doi.org/10.1515/9783111443935

Hopkins, G.H.E. & Clay, T. (1952) *A check list of the genera & species of Mallophaga.* British Museum (Natural History), London, 362 pp.
https://doi.org/10.5962/bhl.title.118844

Ilieva, M. (2009) Checklist of the chewing lice (Insecta: Phthiraptera) from wild birds in Bulgaria. *Zootaxa*, 2138 (1), 1–66.
https://doi.org/10.11646/zootaxa.2138.1.1

International Commission on Zoological Nomenclature [I.C.Z.N.] (1999) *International Code of Zoological Nomenclature*. *4th Edition*. International Trust for Zoological Nomenclature, London, xxix + 306 pp.

Johnson, K.P., Weckstein, J.D., Virrueta-Herrera, S. & Doña, J. (2021) The interplay between host biogeography and phylogeny in structuring diversification of the feather louse genus *Penenirmus*. *Molecular Phylogenetics and Evolution*, 165 (107297), 1–13.
https://doi.org/10.1016/j.ympev.2021.107297
Kellogg, V.L. (1896a) New Mallophaga, I—with special reference to a collection made from maritime birds of the Bay of Monterey, California. *Proceedings of the California Academy of Sciences*, Series 2, 6, 31–168, 14 pls.
Kellogg, V.L. (1896b) New Mallophaga, II—from land birds; together with an account of the mallophagous mouth-parts. *Proceedings of the California Academy of Sciences*, Series 2, 6, 431–548, 14 pls.
Kolenati, F.A. (1858) Zwei neue ostindische Philopteriden. *Sitzungsberichte der Mathematisch-Naturwissenschaftlichen Classe, Akademie der Wissenschaften*, 29, 247–249.
Ledger J.A. 1980. The arthropod parasites of vertebrates in Africa south of the Sahara. Volume IV. Phthiraptera (Insecta). *Publications of the South African Institute for Medical Research*, 56, 1–327.
Martín Mateo, M.P. (2006) Diversidad y distribución de las especies de Mallophaga (Insecta) en aves y mamíferos de la comunidad de Madrid. *Graellsia*, 62 (número extraordinario), 21–32.
https://doi.org/10.3989/graellsia.2006.v62.iExtra.108
Mey, E. (1992) Über einen Grauspecht-Federling aus dem Thüringer Wald und seine systematische Zugehörigkeit. *Entomologische Nachrichten und Berichte*, 36, 47–53.
Mey, E. & Barker, S.C. (2014) Eine neue auf Feenvögeln (Irenidae) lebende *Brueelia*-Art (Insecta, Phthiraptera, Ischnocera, Philopteridae), nebst Anmerkungen zur Gattung *Brueelia* Kéler, 1936 sensu lato. *Rudolstädter naturhistorische Schriften*, 19, 73–114.
Nitzsch, C.L. (1818) Die Familien und Gattungen der Theierinsekten (Insecta epizoica); als ein Prodromus einer Naturgeschichte derselben. *E.F. Germar's Magazin der Entomologie*, 3, 261–318.
Nitzsch, C.L. (1866) Die Federlinge der Sing-, Schrei-, Kletter-, und Taubenvögel. *Zeitschrift för die Gesammten Naturwissenschaften*, 27, 115–122.
Oniki, Y. (1999) Avian parasites and notes on habits of lice from Mato Grosso, Brazil. *Ilheringia, Séries Zoologia*, 86, 183–190.
Piaget, E. (1880) *Les Pédiculines. Essai monographique*. E.J. Brill, Leiden, xxxix + 714 pp., 56 pls.
Piaget, E. (1885) *Les Pédiculines. Essai Monographique. Supplement*. E.J. Brill, Leiden, xii + 200 pp., 17 pls.
Price, R.D., Hellenthal, R.A., Palma, R.L., Johnson, K.P. & Clayton, D.H. (2003) *The chewing lice: world checklist and biological overview*. *Illinois Natural History Survey Special Publication 24*. Illinois NHS, Champaign, Illinois, x + 501 pp.
Sánchez-Montes, S., Colunga-Salas, P., Álvarez-Castillo, L., Guzmán-Cornejo, C. & Montiel-Parra, G. (2018) Chewing lice (Insecta: Phthiraptera) associated with vertebrates in Mexico. *Zootaxa*, 4372 (1), 1–109.
https://doi.org/10.11646/zootaxa.4372.1.1
Schrank, F. von P. (1803) Thierlaus. *Fauna Boica, Landshut*, 3 (1), 186–194.
Scopoli, J.A. (1763) *Pediculus*. *In*: *Entomologia Carniolica exhibens insecta Carnioliae indigena et distributa in ordines*, *genera*, *species*, *varietates*, *methodo Linnaeana*. Trattner, Wien, pp. 381–386.
https://doi.org/10.5962/bhl.title.119976
Sychra, O., Kounek, F., Papousek, I., Capek, M., Cárdenas-Callirgos, J.M., Franco, S. & Literák, I. (2014) Chewing lice (Phthiraptera: Amblycera et Ischnocera) from wrens (Passeriformes: Troglodytidae), with description of a new species of *Myrsidea*. *Acta Entomologica Musei Nationalis Pragae*, 54 (1), 1–27.
Tendeiro, J. (1958) Études sur les mallophages. Sur une petite collection de mallophages prélevée au Mozambique. *Garcia de Orta*, 6 (2), 223–240, 10 pls.
Tendeiro, J. (1961) Études sur les Mallophages. Sur deux espèces et deus sous- espèces nouvelles du *Penenirmus* Th. Clay et Meinertzhagen (Ischnocera, Philopteridae) obtenues sur les Capitonidés. *Boletim Cultural de Guiné Portuguesa*, 15 (60), 785–803, 5 pls.
Tendeiro, J. (1962) Études sur les Mallophages. Observations sur des Ischnocera africains, avec description de 12 espèces et 2 sous-espèces nouvelles. *Boletim Cultural de Guiné Portuguesa*, 17 (68), 669–704.
Uchida, S. (1949) Studies on the biting-lice (Mallophaga) of Japan and adjacent territories (Suborder Ischnocera Pt. II). *Japanese Medical Journal*, 1, 535–556.
https://doi.org/10.7883/yoken1948.1.535
Valim, M.P. & Palma, R.L. (2015) A new genus and two new species of feather lice (Phthiraptera: Ischnocera) from New Zealand endemic passerines (Aves: Passeriformes). *Zootaxa*, 3926 (4), 480–498.
https://doi.org/10.11646/zootaxa.3926.4.2
Vas, Z., Rékási, J. & Rózsa, L. (2012) A checklist of lice of Hungary (Insecta: Phthiraptera). *Annales Historico-Naturales Musei Nationalis Hungarici*, 104, 5–109.
Złotorzycka, J. (1964) Mallophaga parasitizing Passeriformes and Pici. II. Brueeliinae. *Acta Parasitologica Polonica*, 12 (24), 239–282, 4 pls.
Złotorzycka, J. (1980) *Wszoły—Mallophaga, zeszyt 6, Nadrodzina Philopteroidea, rodziny: Meinertzhageniellidae, Lipeuridae, Degeeriellidae, Pseudonirmidae, Giebeliidae, Esthiopteridae i Acidoproctidae. [Chewing lice—Mallophaga 6, Superfamily Philopteroidea, families Meinertzhageniellidae, Lipeuridae, Degeeriellidae, Pseudonirmidae, Giebeliidae, Esthiopteridae i Acidoproctidae]*. *Klucze do Oznaczania Owadów Polski 15*. Panstwowe Wydawnictwo Naukowe, Warszawa and Wroclaw, 202 pp.

APPENDIX 1. Checklist of the louse species from non-passeriform hosts included in the *Penenirmus*-complex in this paper.

References to published host records are given where hosts are not listed by Dalgleish (1972) or Price *et al.* (2003). Host taxonomy follows Clements *et al.* (2019), although they treat some subspecific bird names used in louse literature as synonyms. Subspecific names of many hosts were omitted by Price *et al.* (2003), but have been included here. Species of the louse genus *Turnicola* are included in this list as part of the *Penenirmus*-complex following the phylogeny in Johnson *et al.* (2021: fig. 1). The species marked with an asterisk (*) may need to be included in *Picophilopterus*.

Louse species	Host species	**Notes/References**
Laimoloima limbata (Piaget, 1885) **n. comb.**	*Psilopogon corvinus* (Temminck, 1831)	
Laimoloima rafflesi (Dalgleish, 1967) **n. comb.**	*Psilopogon rafflesi* (Lesson, 1839)	
Laimoloima ruiliensis **n. sp.**	*Psilopogon asiaticus asiaticus* (Latham, 1790)	
Laimoloima tandani **n. sp.**	*Psilopogon virens virens* (Boddaert, 1783)	
Laimoloima zeylanica (Dalgleish, 1967) **n. comb.**	*Psilopogon zeylanicus* (Gmelin, 1789)	
Penenirmus arcus (Piaget, 1885)	*Eurystomus glaucurus afer* (Latham, 1790)	[1]
Penenirmus bidentatus Tendeiro, 1961	*Lybius bidentatus aequatorialis* (Shelley, 1889)	
	Lybius bidentatus bidentatus (Shaw, 1799)	
Penenirmus guineensis Tendeiro, 1961	*Lybius dubius* (Gmelin, 1788)	[2]
**Penenirmus leucomelan* Tendeiro, 1961	*Tricholaema leucomelas leucomelas* (Boddaert, 1783)	[2]
**Penenirmus marginatus* Tendeiro, 1958	*Indicator indicator* (Sparrman, 1777)	[3]
Penenirmus stactolaemae Tendeiro, 1962	*Stactolaema anchietae katangae* (Vincent, 1934)	
**Penenirmus zumpti* Tendeiro, 1961	*Lybius torquatus torquatus* (Dumont, 1805)	[2]
Picophilopterus arcticus (Carriker, 1958)	*Picoides arcticus* (Swainson, 1832)	
	Picoides dorsalis bacatus Baird, 1858	
	Picoides tridactylus (Linnaeus, 1758)	[4]
	Picoides tridactylus crissoleucus (Reichenbach, 1854)	
Picophilopterus auritus (Scopoli, 1763)	*Chloropicus goertae* (Muller, 1776)	[4]
	Chrysophlegma miniaceum (Pennant, 1769)	
	Chrysophlegma mineaceum malaccense (Latham, 1790)	
	Colaptes atricollis peruvianus (Reichenbach, 1854)	
	Colaptes campestris campestris (Vieillot, 1818)	
	Colaptes campestris campestroides (Malherbe, 1849)	
	Colaptes pitius (Molina, 1782)	González-Acuña *et al.* (2014)

.....continued on the next page

APPENDIX 1. (Continued)

Louse species	Host species	**Notes/References**
	Colaptes punctigula striatigularis (Chapman, 1914)	
	Colaptes punctigula ujhelyii (Madarasz, 1912)	
	Colaptes rivolii atriceps (Sclater & Salvin, 1876)	
	Colaptes rivolii brevirostris (Taczanwoski, 1875)	
	Colaptes rivolii meridae (Chapman, 1923)	
	Colaptes rivolii rivolii (Boissonneau, 1840)	
	Colaptes rubiginosus alleni (Bangs, 1902)	
	Colaptes rubiginosus yucatanensis (Cabot, 1844)	
	Dendrocopos atratus (Blyth, 1849)	
	Dendrocopos darjellensis (Blyth, 1845)	
	Dendrocopos hyperythrus hyperythrus (Vigors, 1831)	
	Dendrocopos leucotos (Bechstein, 1802)	
	Dendrocopos leucotos leucotos (Bechstein, 1802)	
	Dendrocopos macei macei (Vieillot, 1818)	
	Dendrocopos major major (Linnaeus, 1758)	[4] [5]
	Dendrocopos major pinetorum (Brehm, 1831)	
	Dendrocopos syriacus (Hemprich & Ehrenberg, 1833)	
	Dryobates albolarvatus (Cassin, 1850)	
	Dryobates arizonae (Hargitt, 1886)	
	Dryobates callonotus major (Berlepsch & Taczanowski, 1884)	
	Dryobates dingus (Sclater & Salvin, 1877)	
	Dryobates fumigatus (Orbigny, 1841)	
	Dryobates kirkii cecilii (Malherbe, 1849)	
	Dryobates minor minor (Linnaeus, 1758)	[6]
	Dryobates passerinus modestus (Zimmer, 1942)	[7]
	Dryobates pubescens (Linnaeus, 1758)	
	Dryobates pubescens medianus (Swainson, 1832)	
	Dryobates scalaris cactophilus (Oberholser, 1911)	[8]

.....continued on the next page

APPENDIX 1. (Continued)

Louse species	Host species	**Notes/References**
	Dryobates stricklandi (Malherbe, 1845)	
	Dryobates villosus (Linnaeus, 1766)	
	Dryobates villosus extimus (Bangs, 1902)	
	Dryobates villosus harrisi (Audubon, 1838)	
	Dryobates villosus hyloscopus (Cabanis & Heine, 1863)	
	Dryobates villosus jardinii (Malherbe, 1845)	Carriker (1903)
	Dryocopus lineatus (Linnaeus, 1766)	
	Dryocopus lineatus similis (Lesson, 1847)	
	Dryocopus pileatus abieticola (Bangs, 1898)	
	Dryocopus pileatus pileatus (Linnaeus, 1758)	
	Dendrocoptes medius (Linnaeus, 1758)	
	Eubucco bourcierii (Lafresnaye, 1845)	
	Jynx torquilla torquilla Linnaeus, 1758	
	Melanerpes aurifrons aurifrons (Wagler, 1829)	
	Melanerpes aurifrons grateloupensis (Lesson, 1839)	
	Melanerpes candidus (Otto, 1796)	
	Melanerpes carolinus (Linnaeus, 1758)	
	Melanerpes chrysogenys (Vigors, 1839)	
	Melanerpes cruentatus (Boddaert, 1783)	
	Melanerpes erythrocephalus (Linnaeus, 1758)	
	Melanerpes formicivorus angustifrons Baird, 1870	Sánchez-Montes *et al*. (2018)
	Melanerpes formicivorus bairdi Ridgway, 1881	
	Melanerpes formicivorus flavigula (Malherbe, 1849)	
	Melanerpes formicivorus formicivorus (Swainson, 1827)	
	Melanerpes hoffmannii (Cabanis, 1862)	Carriker (1903)
	Melanerpes hypopolius (Wagler, 1829)	
	Melanerpes lewis (Gray, 1849)	
	Melanerpes superciliaris nyeanus (Ridgway, 1886)	

.....continued on the next page

APPENDIX 1. (Continued)

Louse species	Host species	**Notes/References**
	Melanerpes uropygialis (Baird, 1854)	
	Micropternus brachyurus phaioceps (Blyth, 1845)	
	Micropternus brachyurus squamigularis (Sundevall, 1866)	
	Piculus flavigula (Boddaert, 1783)	
	Picumnus aurifrons Pelzeln, 1870	
	Picumnus cinnamomeus Wagler, 1829	
	Picumnus innominatus Burton, 1836	
	Picumnus olivaceus Lafresnaye, 1845	
	Picus chlorolophus Vieillot, 1818	
	Sphyrapicus nuchalis Baird, 1858	
	Sphyrapicus ruber (Gmelin, 1788)	
	Sphyrapicus ruber daggetti Grinnell, 1901	
	Sphyrapicus thyroideus (Cassin, 1852)	
	Sphyrapicus varius (Linnaeus, 1766)	
	Yungipicus moluccensis (Gmelin, 1788)	
	Yungipicus kizuki (Temminck, 1836)	
Picophilopterus blythipici **n. sp.**	*Blythipicus pyrrhotis sinensis* (Rickett, 1897)	
Picophilopterus campephili (Eichler, 1953a) **n. comb**.	*Campephilus magellanicus* (King, 1827)	
Picophilopterus heteroscelis (Nitzsch, 1866) **n. comb.**	*Dryocopus martius* (Linnaeus, 1758)	
	Dryocopus martius martius (Linnaeus, 1758)	
Picophilopterus jungens (Kellogg, 1896b)	*Colaptes auratus luteus* Bangs, 1898	[9]
	Colaptes auratus collaris Vigors, 1829	
	Colaptes auratus cafer (Gmelin, 1788)	
	Colaptes chrysoides mearnsi Ridgway, 1911	
	Colaptes pitius (Molina, 1782)	
	Colaptes rupicola Orbigny, 1841	
	Dryobates villosus audubonii (Swainson, 1832)	
	Dryobates villosus orius (Oberholser, 1911)	

.....continued on the next page

APPENDIX 1. (Continued)

Louse species	Host species	**Notes/References**
	Dryobates villosus villosus (Linnaeus, 1766)	
Picophilopterus maculipes (Piaget, 1885) **n. comb.**	*Picus* sp.	
Picophilopterus pici (Fabricius, 1798)	*Blythipicus pyrrhotis pyrrhotis* (Hodgson, 1837)	
	Blythipicus rubiginosus (Swainson, 1837)	
	Chrysocolaptes guttacristatus (Tickell, 1833)	
	Chrysophlegma flavinucha flavinucha (Gould, 1834)	[10]
	Chrysophlegma flavinucha pierrei Oustalet, 1889	
	Chrysophlegma mentale humii Hargitt, 1889	
	Dinopium benghalense benghalense (Linnaeus, 1758)	
	Dinopium benghalense puncticolle (Malherbe, 1845)	
	Dinopium javanense (Ljungh, 1797)	
	Dinopium javanense intermedium (Blyth, 1845)	
	Dinopium javanense javanense (Ljungh, 1797)	
	Dryocopus javensis feddeni (Blyth, 1863)	
	Gecinulus grantia grantia (Horsfield, 1840)	
	Gecinulus grantia viridanus Slater, 1897	
	Mulleripicus pulverulentus harterti Hesse, 1911	
	Mulleripicus pulverulentus pulverulentus (Temminck, 1826)	
	Picus canus Gmelin, 1865	[4]
	Picus canus canus Gmelin, 1865	
	Picus canus hessei Gyldenstolpe, 1916	
	Picus canus sordidior (Rippon, 1906)	new host record
	Picus chlorolophus Vieillot, 1818	
	Picus erythropygius (Elliot, 1865)	
	Picus squamatus squamatus Vigors, 1831	
	Picus vaillantii (Malherbe, 1847)	
	Picus viridis Linnaeus, 1758	[11]
	Picus vittatus Vieillot, 1818	

.....continued on the next page

APPENDIX 1. (Continued)

Louse species	Host species	**Notes/References**
Picophilopterus serrilimbus (Burmeister, 1838)	*Jynx ruficollis* Wagler, 1830	
	Jynx torquilla Linnaeus, 1758	
	Jynx torquilla torquilla Linnaeus, 1758	
Turnicola angustissimus (Giebel, 1866)	*Turnix nigricollis* (Gmelin, 1789)	
	Turnix suscitator (Gmelin, 1789)	
Turnicola nigrolineatus (Piaget, 1885)	*Turnix sylvaticus dussumier* (Temminck, 1828)	
Turnicola platyclypeatus (Piaget, 1880)	*Turnix suscitator rufilatus* Wallace, 1865	

[1] No modern redescription of this species has been published, and the host may be erroneous. Hopkins & Clay (1952) and Price *et al.* (2003) included it in *Penenirmus*, and we here retain it in this genus until it has been redescribed, although this species may prove to be a straggler.

[2] The descriptions and illustrations of Tendeiro (1961, 1962) of species from African barbets (Lybiidae) indicate a similarity to *Laimoloima*, in particular, the clearly sclerotised hyaline margin of *Penenirmus guineensis*, as shown in his photos and drawings. However, these two groups were not placed together in the phylogeny of Johnson *et al.* (2021), in which *P. guineensis* appeared nested with specimens from other African barbets. By contrast, Tendeiro's (1961) photos and drawings suggest that *Penenirmus zumpti* and *P. leucomelan* may belong in *Picophilopterus*, a position supported by the phylogeny in Johnson *et al*. (2021), where *P. zumpti* is sister to *Penenirmus* from *Tricholaema leucomelas*, the type host of *P. leucomelan*. Here, we retain *P. zumpti* and *P. leucomelan* in *Penenirmus*, until these species are properly redescribed.

[3] *Penenirmus marginatus* differs from all other *Penenirmus* in head shape, and may represent a separate genus. Since we have not examined any specimens of *P. marginatus*, we retain it in *Penenirmus* until it has been redescribed.

[4] The phylogenetic tree in Johnson *et al*. (2021: fig. 1) shows a large clade formed by lice from 17 woodpecker species, 12 identified as *Penenirmus auritus* (including one from the type host), one as *Penenirmus arcticus* (from *Picoides tridactylus*), one as *Penenirmus pici* (from *Picus canus*) and three as *Penenirmus* sp. In addition, imbedded among these 17 branches, there are five specimens of *Penenirmus* sp. from five species of Neotropical barbets (Capitonidae). The high degree of structure in this large clade suggests that at least some of these specimens belong to species of *Picophilopterus*, and that the host distribution of *Picophilopterus auritus* may be more limited than that shown in Price *et al*. (2003: 209). No morphological data were given by Johnson *et al.* (2021) and we have not examined their specimens. Moreover, the specimen of *P. auritus* (from the type host) and that of *P. pici* form a clade sister to all remaining specimens of the large clade, suggesting that lice from the other hosts may not belong to *P. auritus sensu stricto*. Therefore, we have not included host records published by Johnson *et al*. (2021) in this Appendix.

[5] Specimens from Spain reported by Martín Mateo (2006) are most likely from the host subspecies *Dendrocopos major hispanus* (Schluter, 1908).

[6] Specimens from Spain reported by Martín Mateo (2006) are most likely from the host subspecies *Dryobates minor buturlini* Hartert, 1912. Records from Hungary listed by Vas *et al*. (2012) may be from host the subspecies *Dryobates minor hortorum* (Brehm, 1831).

[7] Specimens reported from Mato Grosso (Brazil) by Oniki (1999) may be from the host subspecies *Dryobates passerinus olivinus* (Natterer & Malherbe, 1845).

[8] Dalgleish (1972) listed two host subspecies, *Dryobates scalaris giraudi* and *D. s. symplectus*, which are regarded as junior synonyms of *Dryobates scalaris cactophilus* by Clements *et al*. (2019).

[9] In the phylogeny of Johnson *et al*. (2021: fig. 1), *Penenirmus jungens* (from the type host) was not placed close to other members of *Picophilopterus* as defined here.

[10] Dalgleish (1972) listed two host subspecies, *Chrysophlegma flavinucha archon* and *C. flavinucha lyeli*, which are regarded as junior synonyms of *Chrysophlegma flavinucha flavinucha* by Clements *et al*. (2019).

[11] Specimens from Spain reported by Martín Mateo (2006) are most likely from the host subspecies *Picus viridis sharpei* (Saunders, 1872). Records from Bulgaria listed by Ilieva (2009) are likely to be from the host subspecies *Picus viridis karelini* Brandt, 1841.