New Genus and Two New Species of Chewing Lice from Southeast Asian Trogons (Aves: Trogoniformes), with a Revised Key to the Philopterus*-complex*

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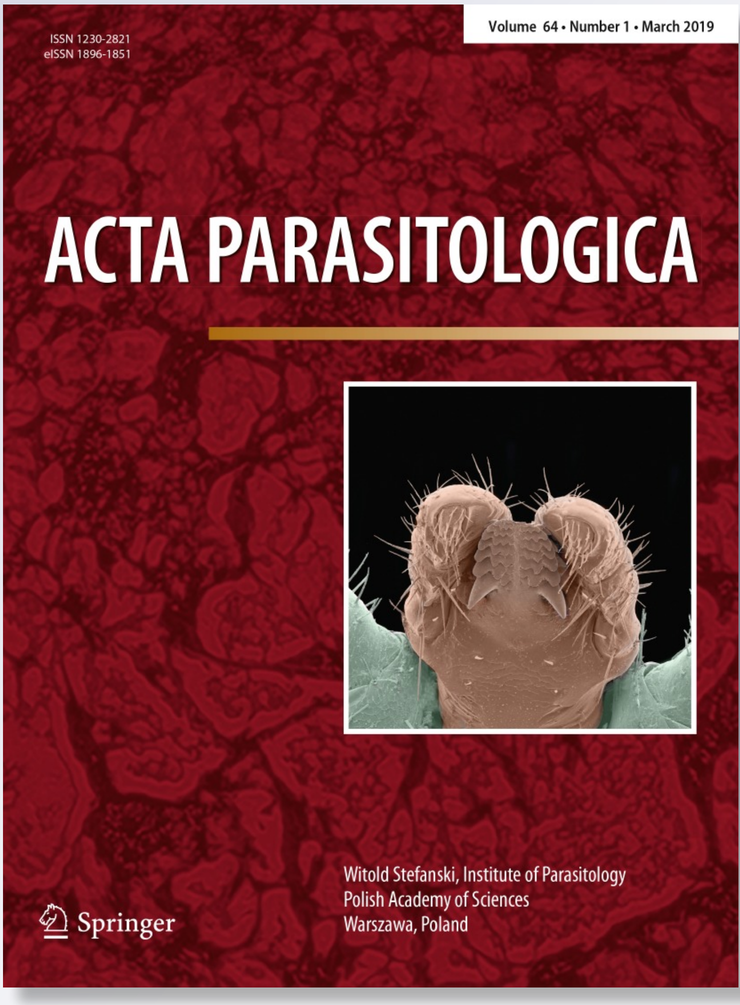

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ORIGINAL PAPER

New Genus and Two New Species of Chewing Lice from Southeast Asian Trogons (Aves: Trogoniformes), with a Revised Key to the *Philopterus*-complex

Daniel R. Gustafsson[1] · Lujia Lei[1] · Xingzhi Chu[1] · Fasheng Zou[1] · Sarah E. Bush[2]

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Abstract
Purpose To describe a new genus and two new species of chewing lice from Southeast Asian trogons (Trogoniformes). These lice belong in the *Philopterus*-complex.
Methods Slide-mounted lice were examined in a light microscope, illustrated by means of a drawing tube, and described using standard procedures.
Results The new genus and species were successfully described.
Conclusions The genus *Vinceopterus* n. gen. is described from two species of Southeast Asian trogons (Trogoniformes: *Harpactes*). It presently comprises two species: *Vinceopterus erythrocephali* n. sp. from three subspecies of the Red-headed Trogon *Harpactes erythrocephalus* (Gould, 1834), and *Vinceopterus mindanensis* n. sp. from two subspecies of the Philippine Trogon *Harpactes ardens* (Temminck, 1826). *Vinceopterus* belongs to the *Philopterus*-complex, and thus likely constitutes a genus of head lice. *Vinceopterus* is the second new genus of chewing lice discovered on Southeast Asian trogons in recent years, the first genus of presumed head lice on trogons worldwide, and the fifth genus of chewing lice known from trogons globally. A translated and revised key to the *Philopterus*-complex is provided, as well as notes on the various chewing lice genera known from trogons.

Keywords Phthiraptera · Philopteridae · *Philopterus*-complex · Trogoniformes · New genus · New species

Introduction

Lice in the *Philopterus*-complex are specialized for life on the heads of their hosts [1, 2]. These lice occur mainly on perching birds (Passeriformes), but some genera also occur on hosts in the Coraciiformes and Galbuliformes [2]. Another species in the complex was recorded as being from a host in the Bucerotiformes: *Philopterus*[?] *solus* Tendeiro 1962 [3]; however, Mey [2] doubted the authenticity of this host record.

The relationships between many species in the *Philopterus*-complex are poorly known, and most species are today placed in the large and heterogeneous genus *Philopterus* Nitzsch 1818 [4] ([2, 5]). However, over the last two decades several new genera have been recognized within this complex, and the host distributions and morphological variation in the complex have been explored in several publications [2, 6–10]. Yet, the host associations of several genera within the *Philopterus*-complex have not been thoroughly investigated, and many host families have not yet been examined for *Philopterus*-complex lice [2]. Additional data regarding louse diversity, host associations, and geographical distribution are needed to reach a more comprehensive understanding of this enigmatic complex.

We here describe the first species in the *Philopterus*-complex from trogons (Trogoniformes), adding a new host order to the distribution of this complex. This constitutes the fifth genus of ischnoceran lice known from trogons, and the second genus of lice discovered on Asian trogons in recent years [11]. The discovery of this new genus, *Vinceopterus*

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n. gen., was unexpected, as no other *Philopterus*-complex lice are known from trogons. The two species described here show some morphological similarities to the genus *Clayiella* Eichler 1940 [12], known from Neotropical motmots (Momotidae) and Madagascan cuckoo-rollers (Leptosomatidae).

Materials and Methods

We examined slide-mounted specimens deposited at the Price Institute for Parasitological Research (PIPeR), University of Utah, Salt Lake City, USA, as well as lice from China deposited at the Guangdong Institute for Applied Biological Resources, Guangzhou, China (GIABR). All examined materials were mounted in Canada balsam on microscopy slides. Holotypes and paratypes are deposited at the Natural History Museum, London (NHML) or in PIPeR, as indicated below. Specimens were examined and measured with a Nikon Eclipse E600 fitted with an Olympus DP25 camera and digital measuring software (ImageJ 1.48v, Wayne Rasband). Illustrations were drawn by hand, using a drawing tube. Line drawings were scanned, collated, and edited in GIMP (www.gimp.org). All measurements are given in millimeters, following [9]. Morphological terminology and head chaetotaxy follow [13] as adapted by [2, 14] (Fig. 3a). Terminology of head sensilla follows [15] (Fig. 3a).

Leg chaetotaxy follows [11] for proximal leg segments (Figs. 6, 7). We here extend the conventions proposed by [9] and [11] to include the tibiae and tarsi of all three legs. Some setae and features of the distal leg segments have been named to correspond to those proposed by [16]; note, however, that some setae of the anopluran leg do not occur in *Vinceopterus*. Our abbreviations follow [16], with a few exceptions: we retain the abbreviation *s* for sensilla only, as in [15] and [11], and use *sf* for *spiniform setae*. We use *b* for a set of very short setae near the *tactile hair* (*th1*), following [16]; however, these setae are hair-like rather than cone-shaped in *Vinceopterus*, and these setae may not be homologous. It should be noted that the homologies of setae between different suborders of lice are not always clear. Here, we present a starting point for comparisons of leg setae among chewing lice, but we do not necessarily consider similarities as positive statements of homologies.

Host taxonomy follows [17].

Systematics

PHTHIRAPTERA Haeckel, 1896 [18].

Ischnocera Kellogg, 1896a [19].

Philopteridae Burmeister, 1838 [20].

Philopterus-complex.

Vinceopterus Gustafsson, Lei, Chu, Zou, and Bush, new genus.

Type species: *Vinceopterus erythrocephali* Gustafsson, Lei, Chu and Zou, new species, ex *Harpactes erythrocephalus yamakanensis* Rickett 1899.

Diagnosis: *Vinceopterus* n. gen. keys to couplet 8 in the key of [2], placing it near *Clayiella* and *Cincloecus* Eichler, 1951 [21]. Neither of the choices given in the key fits *Vinceopterus*: it has shorter, poorly developed, coni like *Cincloecus*, but a deeply concave and medianly sclerotized hyaline margin like *Clayiella*. In gross morphology, *Vinceopterus* is also most similar to *Clayiella*, having large rounded lateral lobes of the hyaline margin, a similarly shaped dorsal anterior plate, and a broad, roughly quadratic preantennal head.

Vinceopterus can be separated from *Clayiella* by the following characters [based on [2] and examinations of two species of *Clayiella* from motmots]: median sclerotization of hyaline margin narrower than dorsal anterior plate in *Clayiella*, but about as wide as dorsal anterior plate in *Vinceopterus* (Figs. 3a, 5a); coni elongated in *Clayiella*, but short and rounded in *Vinceopterus* (Figs. 3a, 5a); marginal carina without median indentations in *Clayiella*, but with median indentations in *Vinceopterus* (Figs. 3a, 5a); *mts2* macrosetae in *Clayiella*, but short setae in *Vinceopterus* (Figs. 3a, 5a); male genitalia distinct, with lateral margins distally divergent in *Clayiella*, but lateral margins parallel in *Vinceopterus* (Figs. 3b, c, 5b, c); *Clayiella* lacks central sternal plates on abdominal segments II–VI in both sexes, but in *Vinceopterus* there are central sternal plates on segments II–VI in males (Figs. 2a, 4a), and at least on segment VI in females (in *V. erythrocephali* also on segment V; Figs. 2b, 4b); female genital margin with > 10 mesosetae on each side in *Clayiella* (female of *C. dreophila* Mey 2004 [2] unknown), but with only 5 mesosetae on each side in *Vinceopterus* (Figs. 3d, 5d);

Description: *Both sexes.* Head morphology similar to other lice in the *Philopterus*-complex (Figs. 3a, 5a). Marginal carina interrupted medianly and with narrowing near anterior end of recurved ventral carina. Hyaline margin wide, forming lateral lobes arising lateral to *as2*; median section of hyaline margin with wide sclerotization. Dorsal preantennal suture present, completely surrounding dorsal anterior plate and with lateral extensions that do not reach lateral margin of head. Dorsal anterior plate with posteromedian elongation (Fig. 8a, b). Ventral anterior plate present, wide. Ventral carinae interrupted medianly forming clypeo-labral suture; lateral sections recurved, anterior end nearly reaching lateral head margin near *avs1*. Mandibles with one auricular process each (Fig. 1c, d). Trabecula present. Coni small. Antennae sexually monomorphic. Eyes not extended posteriorly. Temporal carinae present. Gular plate generally small, triangular in shape but with irregular

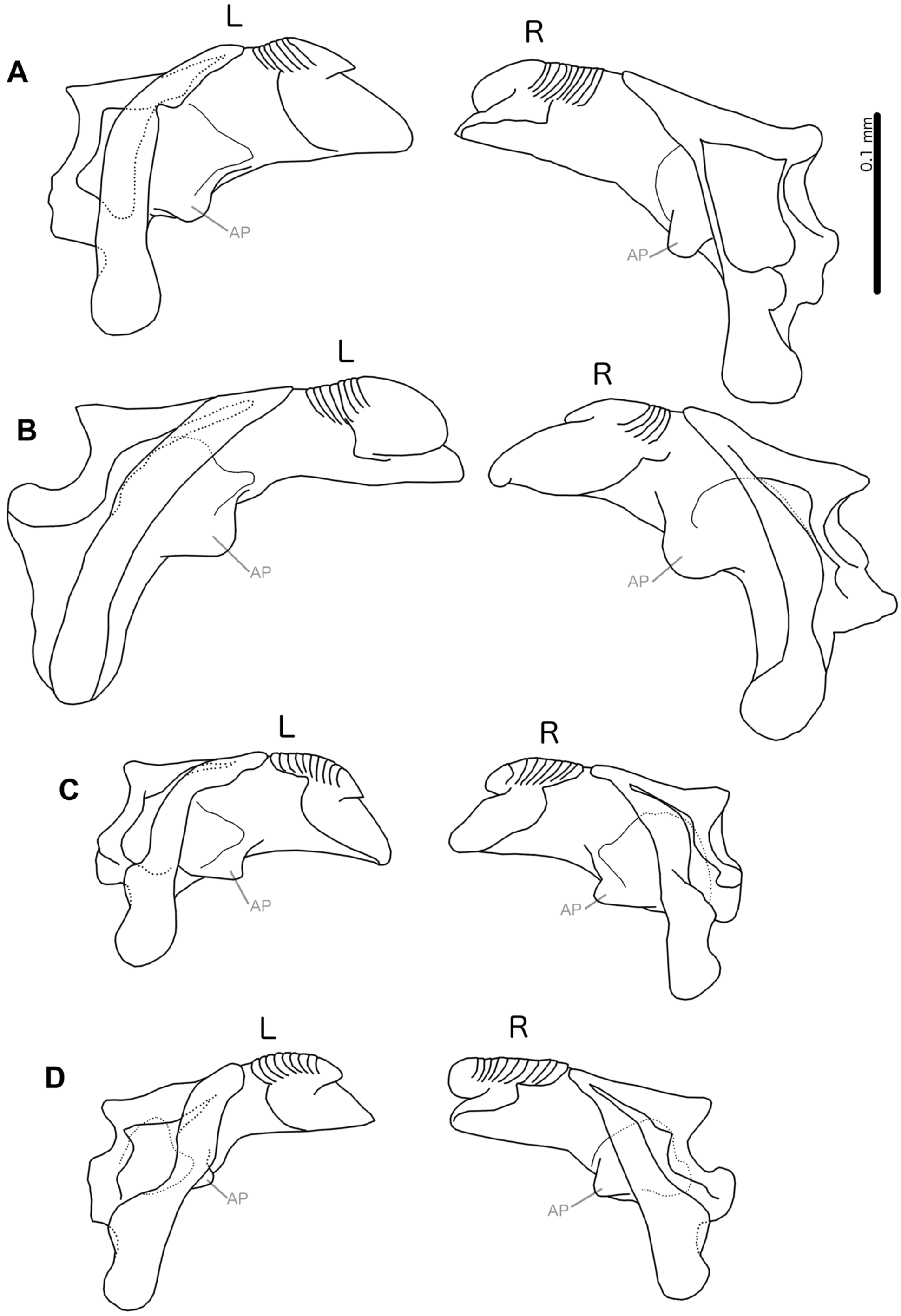

Fig. 1 Female mandibles of two species of *Clayiella* Eichler, 1940 [12], and two species of *Vinceopterus* n. gen. **a** *Clayiella prionitis* (Denny, 1842) [22]. **b** *Clayiella baryphthenga* (Carriker, 1963) [28]. **c** *Vinceopterus erythrocephali* n. sp. **d** *Vinceopterus mindanensis* n. sp. Mandibles overlap in specimens, and are illustrated separated for clarity. All mandibles drawn to same scale. *AP* auricular process (tentatively identified), *L* left mandible, *R* right mandible

margins. Head chaetotaxy as in Fig. 3a; *as2* and *as3* dorsal; *pns* and *s4* present; *os*, *mts1* and *mts3* macrosetae.

Thoracic and abdominal segments and chaetotaxy as in Figs. 2a, b, 4a, b. Lateral *marginal mesometanotal setae* (*mms*) separated from median *mms* by clear gap. Tergopleurites reduced medianly, not reaching ventral side of abdomen, except in segment VIII of some specimens. Tergopleurites II–IX + X in male and II–VIII in female divided medianly and female tergopleurite IX + X medianly continuous. Central sternal plates present on at least some segments in both sexes, but number and extent variable between specimens in both species. Accessory sternal plates present on segments III–VI, but not visible on segment II in any examined specimens. Abdominal chaetotaxy relatively sparse compared to other *Philopterus*-complex genera. Thorn-like setae of

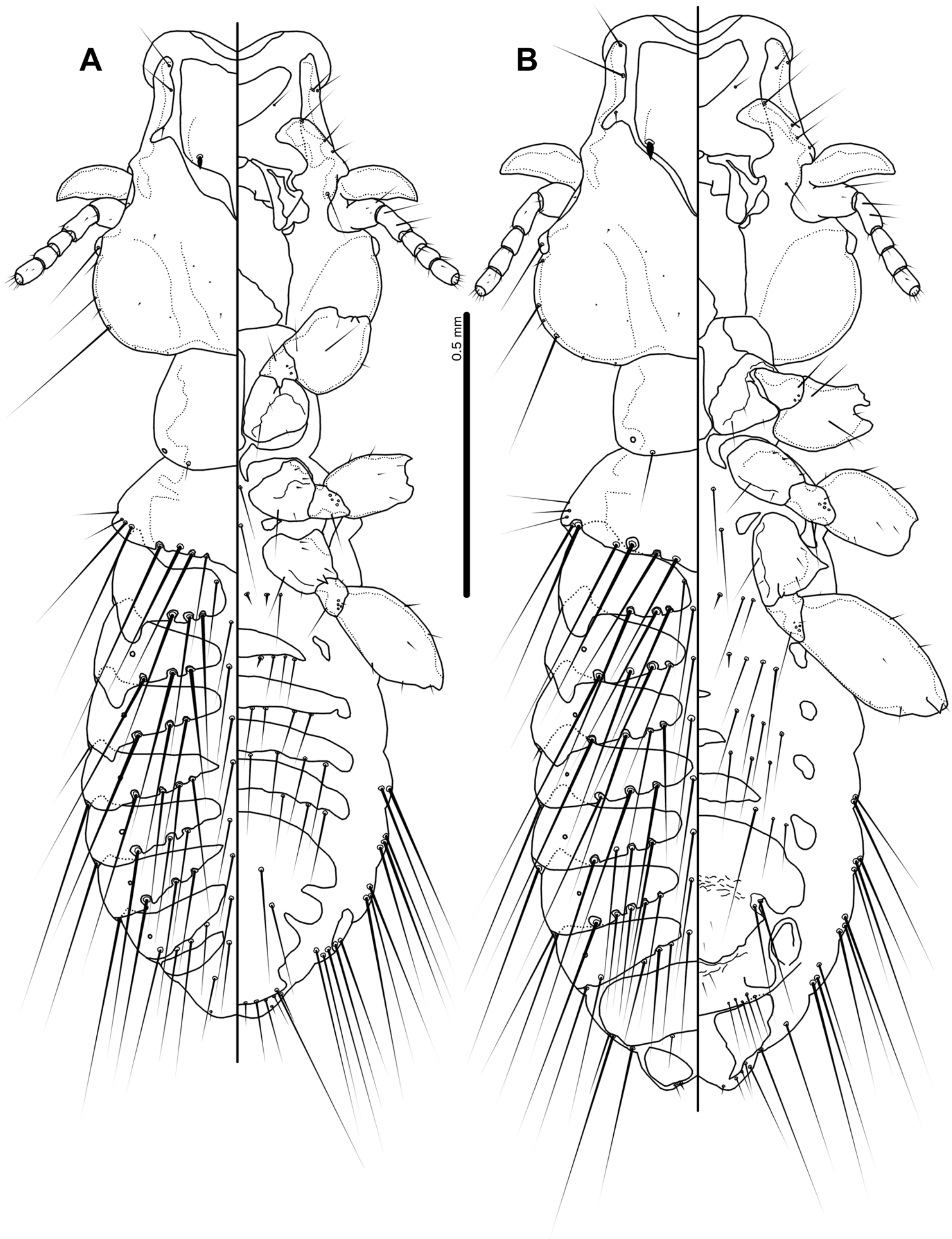

Fig. 2 *Vinceopterus erythrocephali* n. sp. ex *Harpactes erythrocephalus yamakanensis*. **a** Male habitus, dorsal and ventral views. **b** Female habitus, dorsal and ventral views

sternites variable between specimens of same species, and often variable between sides of same specimen.

Male. Leg chaetotaxy as in Fig. 6. Subgenital plate with indentations at lateral margins of segments VII and VIII. Genitalia typical for *Philopterus*-complex (Figs. 3b, c, 5b, c), simple, with all elements apparently fused. Mesosome with diffuse anterior margin, here illustrated approximately. Setae of male genitalia not clearly visible in most examined material, but appears to consist of 1–2 setae on the posterior margin of the genitalia lateral to the mesosome. Setae of distal parameters short, not clearly visible except as apertures in examined specimens.

Female: leg chaetotaxy as in Fig. 7. Abdominal sternites reduced compared to male. Subgenital plate, vulval chaetotaxy, and subvulval plates as in Figs. 3d and 5d. Subgenital plate with lateral indentation at posterior margin of segment VII. Posterior margin of subgenital plate irregular, not reaching near vulval margin. Central setae of subgenital plate scattered. Vulval margin with 5 macrosetae on each side; in some specimens, shorter setae indistinguishable from the scattered setae are present on or near the vulval margin between the macrosetae. Subvulval plates unclear in anterior end, and here illustrated tentatively.

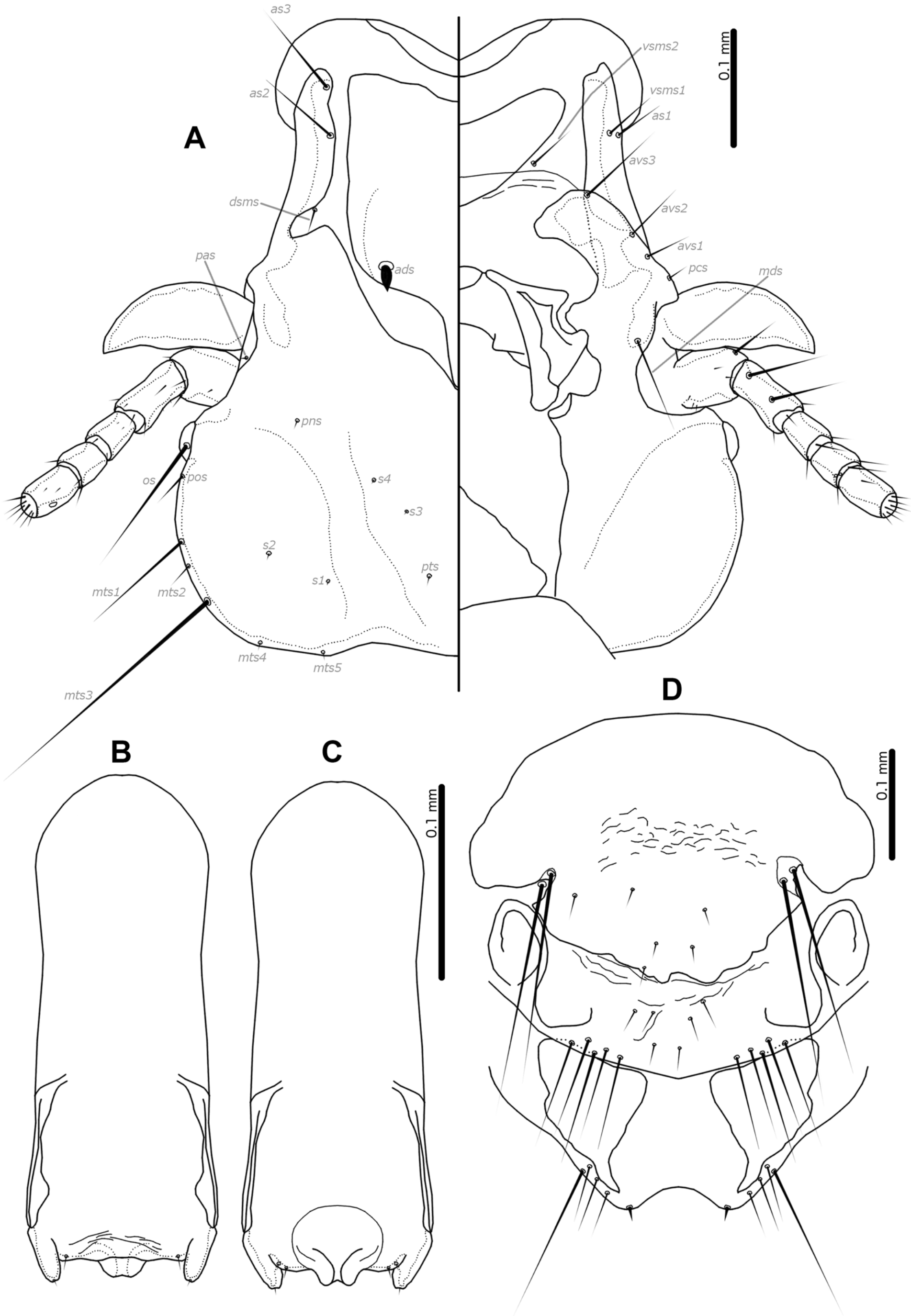

Fig. 3 *Vinceopterus erythrocephali* n. sp. ex *Harpactes erythrocephalus yamakanensis*. **a** Male head, dorsal and ventral views. **b** Male genitalia, dorsal view. **c** Male genitalia, ventral view. **d** Female subgenital plate, vulval margin, and subvulval plates, ventral view. *ads* anterior dorsal seta, *as1–3* anterior setae 1–3, avs1–3 anterior ventral setae 1–3, *dsms* dorsal submarginal seta, *mds* mandibular seta, *mts1–5* marginal temporal setae 1–5, *os* ocular seta, *pas* preantennal seta; *pcs* preconal seta, *pns* postnodal seta; *pos* preocular seta; *pts* posttemporal seta; *s1–4* sensilla 1–4, *vsms1–2* ventral submarginal setae 1–3

Host distribution: *Vinceopterus* is presently known only from two species of trogons in the genus *Harpactes* Swainson, 1853.

Geographical range: *Vinceopterus* is known from South China, Thailand, and the Philippines, suggesting that it is found throughout the range of the South-East Asian trogons; however, no specimens from India or Indonesia have been examined.

Etymology: *Vinceopterus* is a portmanteau, derived from Dr. Vincent Smith (Natural History Museum, London; NHML) and the ischnoceran head louse genus *Philopterus* Nitzsch, 1818 [4] (ultimately derived from Greek "*phílos*" for "friend of", and "*pterón*" for "wing"). We name this genus in honor of Vince in recognition of his many contributions to louse research, as well as his support of and friendship to DRG over the years. Gender: masculine.

Remarks: variation in the shape of the mandibles is poorly known in Ischnocera, and mouthparts are often illustrated incompletely or schematically. Kellogg [23] described the so-called basal and quadrangular processes (terminology from [24, 25]) at the base of the left and right mandible, respectively. These processes serve as muscle attachment points [23, 26]. In addition to these processes, Qadri [25] noted that there may be additional processes "in the middle of the cutting surfaces", so-called "auricular processes". No examples of taxa with auricular processes were mentioned by Qadri [25] and the processes were neither illustrated nor described in detail.

We observed processes consistent with Qadri's description of auricular processes (AP in Fig. 1a, c) in *Vinceopterus* and in two species of *Clayiella*. In both genera, the basal and quadrangular processes appear to be absent on both mandibles (Fig. 1a–d). In contrast, basal and quadrangular processes were observed in several species each of *Philopterus* s. lat. and *Philopteroides* Mey 2004 [2] (not illustrated). Characters of the mandibles may ultimately be useful taxonomic characters; however, caution is warranted as Rheinwald [27] showed that amblyceran mouthparts may be very different within a given genus due to differences in feeding ecology.

It is unclear what function, if any, these auricular processes may have. They appear to be soft, and as such, they seem unlikely to be involved in cutting off parts of the feather during eating; however, they could function as muscle attachment points. A survey of the shape and structure of the mandibles across Ischnocera is sorely needed to establish which genera possess these auricular processes, possible functions, and whether or not they are of taxonomic value. As ischnoceran lice use their mandibles both for feeding and for attachment to the host, it is somewhat surprising that no such review already exists.

The auricular processes are not visible in the illustrations of *Clayiella* spp. by Carriker [28] and Mey [2]. The mandibles of both species of *Clayiella* are illustrated in Fig. 1a, b, based on specimens in the PIPeR collection. For comparison, mandibles of both species of *Vinceopterus* are illustrated in Fig. 1c, d.

The leg setae of *Vinceopterus* are more similar to those found in the *Brueelia*-complex [11] than those reported for the genus *Philopteroides* [9]. Only three setae and sensilla found in *Vinceopterus* were not found in any member of the *Brueelia*-complex: *tI-v2*, *tII-s7*, and *tIII-s7*. Some setae found in the *Brueelia*-complex are apparently absent in *Vinceopterus* (*cI-a4, fI-p2, fI-dm4, fI-v4, fII-a5, fII-dm2, fIII-a5*); however, these may be absent only in the specimens examined. This close correspondence between the leg chaetotaxy of *Vinceopterus* and the *Brueelia*-complex suggests that leg chaetotaxy may be conserved throughout large parts of the Ischnocera. Additional studies into the patterns of leg chaetotaxy are sorely needed to evaluate their use as taxonomic characters.

Included species:

Vinceopterus erythrocephali n. sp.

Vinceopterus mindanensis n. sp.

Vinceopterus erythrocephali Gustafsson, Lei, Chu, Zou, and Bush, new species.

(Figures 1c, 2, 3, 6, 7, 8a).

Type host: *Harpactes erythrocephalus yamakanensis* Rickett 1899—red-headed trogon.

Other hosts: *Harpactes erythrocephalus erythrocephalus* (Gould 1834). *Harpactes e. helenae* Mayr 1941.

Type locality: Jingxi County, Guangxi Province, China.

Description, both sexes: Head shape as in Fig. 3a. Antero-lateral lobes of hyaline margin extensive. Dorsal anterior plate with narrow posterior extension (Fig. 8a). Preantennal nodi narrow. Head chaetotaxy typical for genus (Fig. 3a). Thoracic and abdominal segments as in Figs. 2a, b. Leg chaetotaxy as in Figs. 6, 7. All legs distorted or partially destroyed in single examined male from type host subspecies. A complete reconstruction of all three pairs of legs is shown in Figs. 2a and 6, but exact insertion of legs II–III tentative. Legs of single male from *H. e. erythrocephalus* largely consistent with Fig. 6, but specimen seems to lack several dorsal setae of leg II.

Male: Thoracic and abdominal chaetotaxy as in Fig. 2a; thorn-like sternal setae typically limited to segments II–III, but variable between specimens and between sides of same specimen. Sternal plates present on abdominal segments III–VI. Male genitalia as in Figs. 3b, c. Lateral margins of distal basal plate more or less straight. Mesosome with broadly rounded anterior end, but exact border somewhat diffuse in specimens. Genital setae very small, primarily visible as apertures. Measurements as in Table 1.

Female: Thoracic and abdominal chaetotaxy as in Fig. 2b; thorn-like sternal setae typically limited to segments II–III, but variable between specimens and between sides in same specimen. Sternal plates present on abdominal segments IV–VI in 3 females and on segments V–VI in 4 females. Subgenital plate as in Fig. 3d, with weak reticulation in mid-section; 2 macrosetae on each side on segment VII; 8–16 short setae scattered in area between distal subgenital plate and vulval margin; vulval margin with 4–5 mesosetae on each side. Distal margin of subgenital plate irregularly shaped. Lateral notches of subgenital plate present, but differ between specimens, and do not reach macrosetae in all examined females. Subvulval plates not clear anteriorly in examined specimens, and here illustrated tentatively; 3 mesosetae and 1 macroseta on each side lateral to distal subvulval plate. Anal opening with 1 ventral thorn-like seta, 1 dorsal thorn-like seta, and 1 dorsal short seta on each side. Measurements as in Table 1.

Table 1 Measurements of *Vinceopterus erythrocephali* n. sp. and *Vinceopterus mindanensis* n. sp

	V. erythropteri n. sp.					*V. minadanensis* n. sp.		
	H. e. yamakanensis		*H. e. erythrocephalus*		*H. e. helenae*	*H. a. ardens*		*H. a. linae*
	Male	Female	Male	Female	Female	Male	Female	Female
N	1[1]	3	1	3	1[2]	2[3]	1	4[4]
as3	0.034–0.058	0.045–0.054	0.035–0.042	0.044–0.061	0.045	0.034–0.060	0.033–0.036	0.037–0.053
dsms	0.0047–0.0067	0.0064–0.011	0.0060	0.0049–0.017	0.015	0.0095–0.10	0.010–0.011	0.006–0.011
pas	0.0044	0.0032–0.0048	0.0037	0.0028–0.0038	–	0.0037–0.0047	0.0053	0.0044
pcs	0.0076	0.0092–0.014	0.0075–0.0082	0.0056–0.011	–	0.0074–0.010	0.011–0.012	0.0054–0.0096
ADPL	0.17	0.18–0.19	0.15	0.18–0.19	0.17	0.15–0.17	0.17	0.16–0.17
ADPW	0.14	0.14–0.15	0.13	0.14–0.19	0.14	0.13	0.14	0.13–0.15
APLL	0.12	0.13	0.11	0.13–0.14	0.12	0.12	0.13	0.12–0.14
ANW	0.16	0.16–0.17	0.14	0.17	0.17	0.14–0.15	0.15	0.15–0.17
PMCL	0.093	0.10–0.11	0.080	0.10–0.11	0.083	0.83–0.89	0.99	0.10–0.11
PAL	0.13	0.13	0.11	0.13–0.14	0.12	0.12–0.13	0.13	0.077–0.140
PAW	0.24	0.26	0.23	0.27	0.25	0.26	0.27	0.25–0.28
TRL	0.079–0.086	0.082–0.089	0.066–0.074	0.086–0.092	0.076–0.085	0.067–0.071	0.071–0.073	0.055–0.079
TRW	0.040–0.043	0.038–0.045	0.032–0.033	0.037–0.048	0.036–0.040	0.036–0.040	0.032–0.039	0.037–0.040
POL	0.17	0.19–0.20	0.16	0.21	0.18	0.18	0.21	0.19–0.21
HL	0.34	0.37–0.38	0.34	0.38–0.39	0.35	0.35	0.39	0.36–0.38
HW	0.33	0.36–0.37	0.31	0.38	0.36	0.36	0.39	0.37–0.41
PW	0.20	0.21	0.18	0.22	0.20	0.20–0.21	0.23	0.21–0.23
PTL	0.13	0.13–0.15	0.11	0.14–0.16	–	0.15	0.16	0.14–0.15
PTW	0.28	0.31–0.32	0.29	0.33–0.34	–	0.30	0.36	0.30–0.33
AL	0.49	0.56	0.49	0.57–0.70	–	0.49	0.69	0.52–0.68
AW	0.35	0.39–0.41	0.37	0.42–0.44	0.39	0.40	0.49	0.36–0.41
TPVL	0.084	0.095–0.096	0.082	0.097–0.010	0.095	0.076–0.085	0.11	0.089–0.110
SGPW	–	0.24–0.25	–	0.27–0.28	0.23	–	0.28	0.22–0.27
GL	0.18	–	0.19	–	–	0.18–0.20	–	–
GW	0.068	–	0.067	–	–	0.071–0.072	–	–
TL	–	1.16–1.18	1.02	1.21–1.33	–	1.19	1.33	1.09–1.31

All measurements are in millimeters. Ranges given for setae and trabecula even in cases where only one specimen was measured, as these characters occur in pairs; where no ranges are given, seta on one side of head broken or absent. Abbreviations follows [9], and include: ADPL—dorsal anterior plate median length; ADPW—dorsal anterior plate width; AL—abdominal length; AW—abdominal width; ANW—anterior notch width; APLL—dorsal anterior plate lateral length; *as3—anterior seta* 3; *dsms—dorsal submarginal seta*; GL—male genitalia length; GW—male genitalia width; HL—head length; HW—head width; PAL—preantennal head length; PAW—preantennal head width; *pas—preantennal seta*; *pcs—preconal seta*; PMCL—premarginal carina length; POL—postantennal head length; PTL—pterothoracic length; PTW—pterothoracic width; PW—prothoracic width; SGPW—female subgenital plate width; TL—total length; TPVL—tergal plate V length; TRL—trabecula length; TRW—trabecula width. Genus abbreviations used: *H.* = *Harpactes*; *V.* = *Vinceopterus*

[1] Single male with head separated from body and TL, therefore, not measured

[2] Small setae not visible due to crystallization of Canada balsam. Pterothorax and abdominal segment II ruptured during mounting. PTL, PTW, AL, and TL could, therefore, not be measured

[3] N = 1 for PTW, AL, AW, and TL

[4] N = 1 for *pas*, and N = 3 for POL

Type material: Holotype ♂ ex *Harpactes erythrocephalus yamakanensis*: Jingxi County, Guangxi Province, China, 20 Sep. 2004, S.E. Bush, AN-281, P#101 (NHML). Paratypes ex *H. e. yamakanensis*: 1♀, same data as holotype (NHML). 2♀, same data as holotype (PIPeR).

Other material ex *Harpactes erythrocephalus erythrocephalus*: 2♀, Luonlo Mountain, Kosathon Ban Malo, Dansai, Loei, Thailand, 28 Mar. 1954, R.E. Elbel and B. Lekagul, RE-3508, B-22716 (PIPeR). 1♂, ♀, Krading Mountain, Wangsaphun Srithani, Loei, Thailand, 1 Jan. 1954, R.E. Elbel and B. Lekagul, RE-3252, B-22640 (PIPeR). Ex *H. e.*

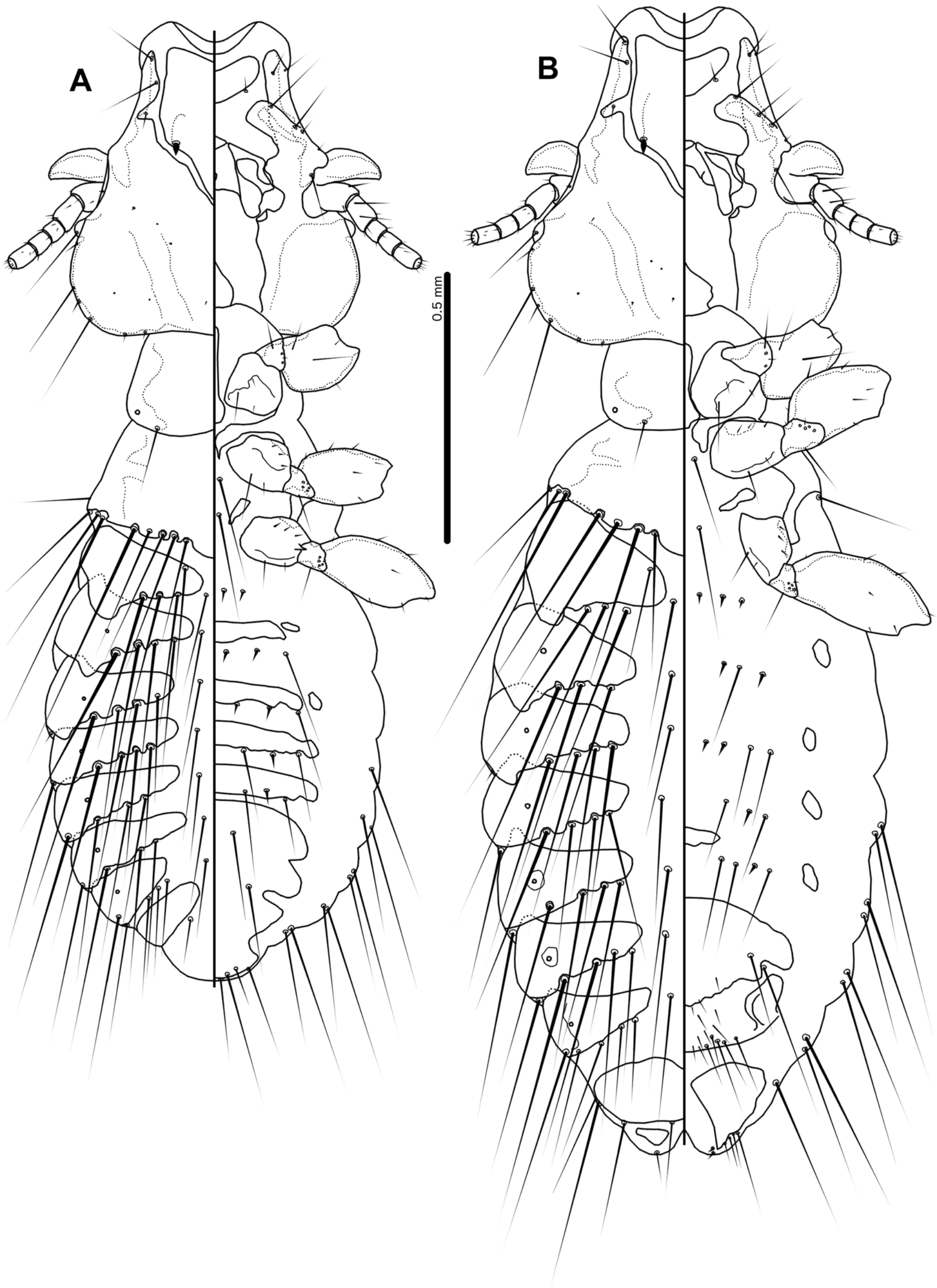

Fig. 4 *Vinceopterus mindanensis* n. sp. ex *Harpactes ardens ardens*. **a** Male habitus, dorsal and ventral views. **b** Female habitus, dorsal and ventral views

helenae: 1♀, Danong, Nanbang, Yingjian County, Dehong State, Yunnan Province, China, 30 Dec. 2012, Yuchun Wu and Yanhua Zhang, J0571 (GIABR).

Diagnosis: *Vinceopterus erythrocephali* can be separated from *V. mindanensis* n. sp. by the following characters: hyaline margin thicker in *V. erythrocephali* (Fig. 3a) than in *V. mindanensis* (Fig. 5a); dorsal anterior plate more square-shaped, with a very narrow posterior elongation in *V. erythrocephali* (Fig. 8a) unlike *V. mindanensis* (Fig. 8b); central sternal plates present on female abdominal segments IV–VI in *V. erythrocephali* (Fig. 2b), but only on segment VI in *V. mindanensis* (Fig. 4b), however these plates may be very small and poorly sclerotized, and thus may be easily overlooked; both sexes of *V. erythrocephali* have more pleural setae on segments VI–VIII than in *V. mindanensis* (*cf.* Figs. 2a, b, 4a, b); thorn-like sternal setae are generally limited to segments II–III in *V. erythrocephali* (Fig. 2a, b), but found on segments II–VI in *V. midnanensis* (Fig. 4a, b), however some individual variation in this characters can be seen; ventral mesosome larger and more rounded in *V.*

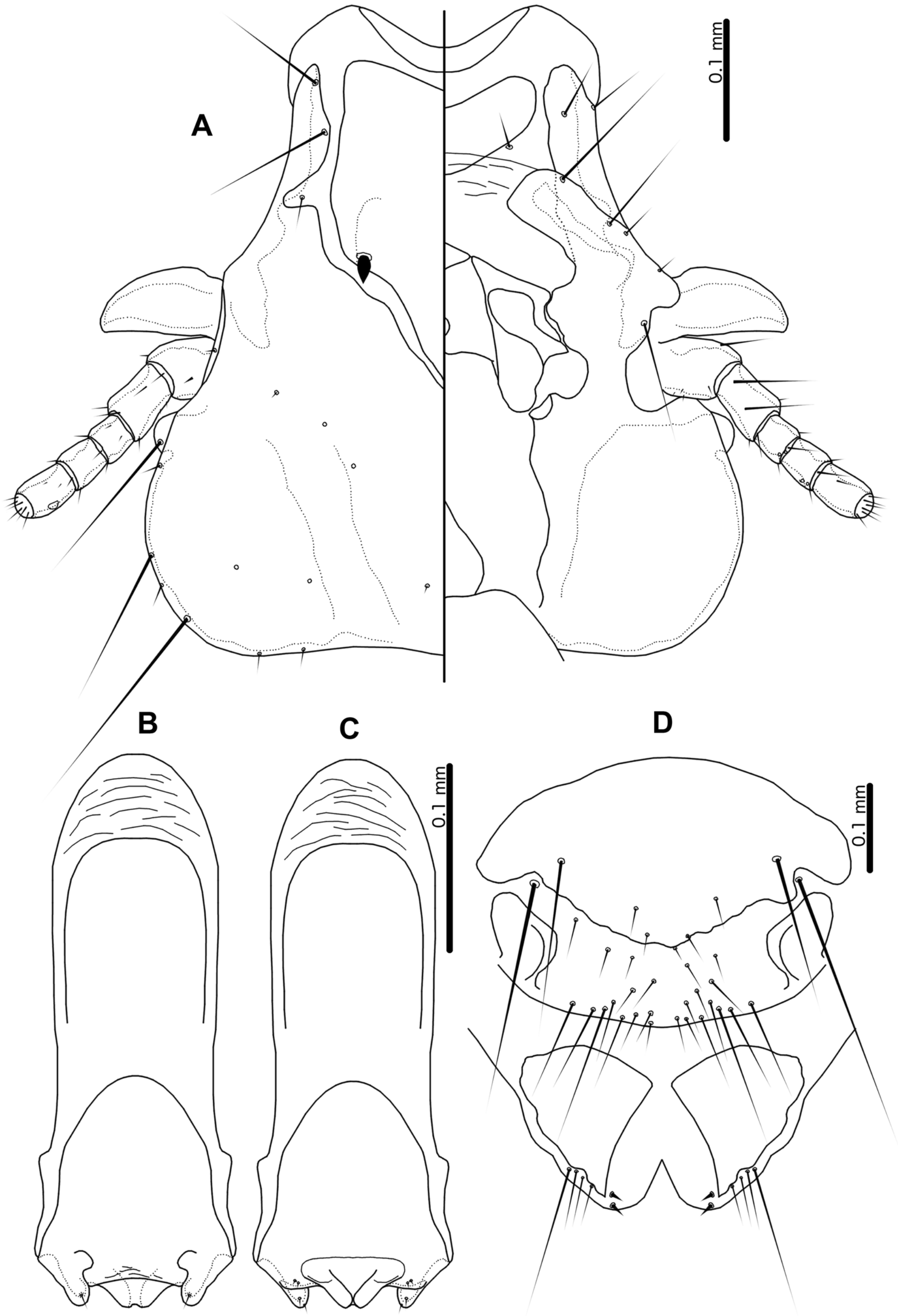

Fig. 5 *Vinceopterus mindanensis* n. sp. ex *Harpactes ardens ardens*. **a** male head, dorsal and ventral views. **b** Male genitalia, dorsal view. **c** Male genitalia, ventral view. **d** Female subgenital plate, vulval margin, and subvulval plates, ventral view

erythrocephali (Fig. 3c) than in *V. mindaneneis* (Fig. 5c); posterior section of female subgenital plate more extensive in *V. erythrocephali* (Fig. 3d) than in *V. mindanensis* (Fig. 5d); female subgenital plate with weak reticulation in central part in *V. erythrocephali* (Fig. 3d), but without such reticulation in *V. mindanensis* (Fig. 5d); female from type host subspecies of *V. erythrocephali* with fewer scattered setae of the genitalia (8–12; Fig. 3d) compared to *V. mindanensis* (15–21; Fig. 5d), but material of *V. erythrocephali* from *H. e. erythrocephalus* overlap slightly in setal counts (13–16; not illustrated).

Etymology: the specific epithet is derived from the type host specific name.

Remarks: male specimen from *Harpactes e. erythrocephalus* has a smaller head and more extensive central sternal plates than male from *H. e. yamakanensis*, females from

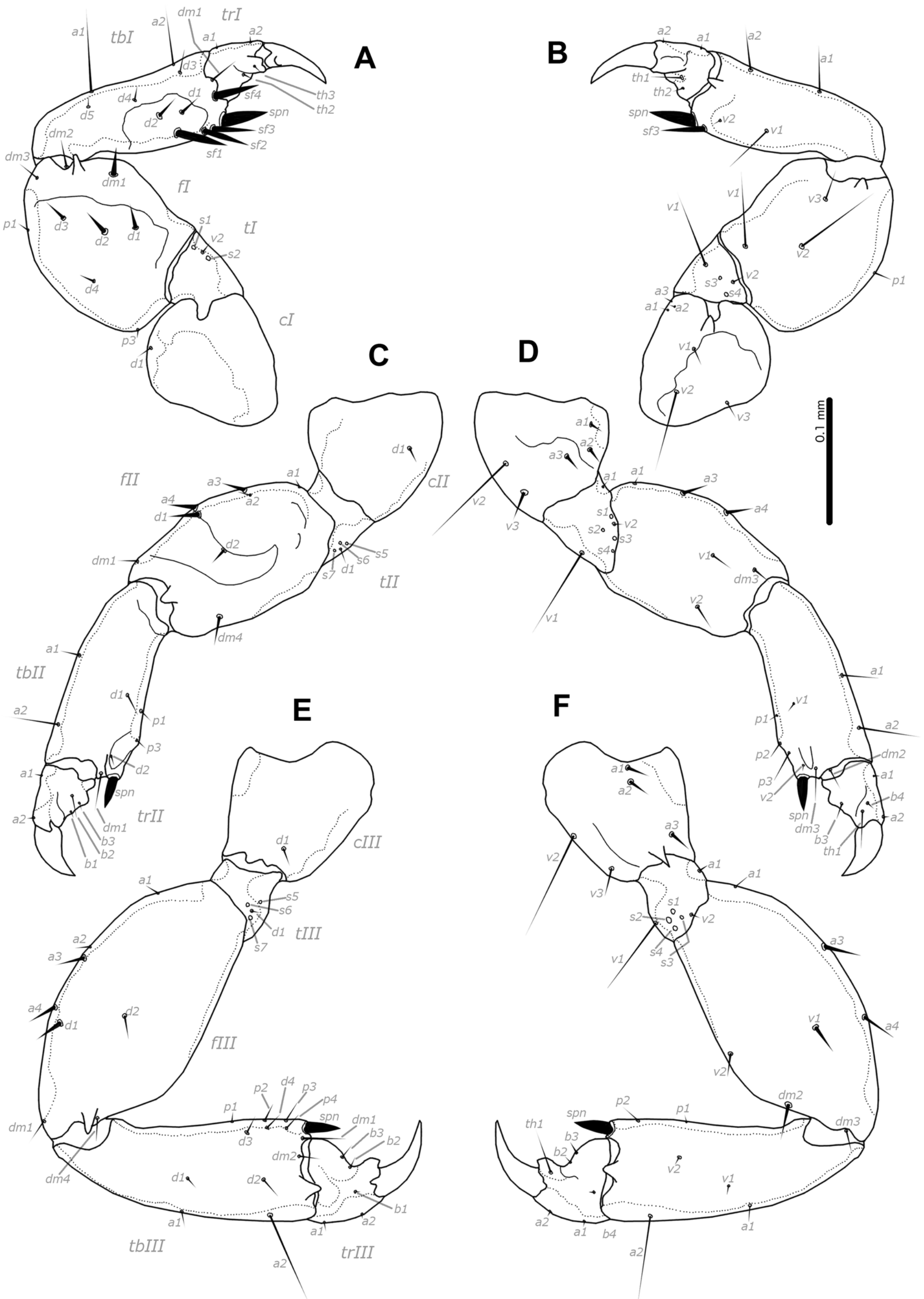

Fig. 6 Male legs of *Vinceopterus erythrocephali* ex *Harpactes erythrocephalus yamakanensis*. **a** leg I, dorsal view. **b** Leg I, ventral view. **c** Leg II, dorsal view. **d** Leg II, ventral view. **e** Leg III, dorsal view. **f** Leg III, ventral view. Note that leg II has been twisted on both sides in single examined male, and exact placement of setae of coxa and trochanter are here illustrated as seen in specimens. All legs drawn at the same scale. Name of individual setae formed by combining the leg segment (including number) with the setal number as in [11]. Setae *tbI-dm2* and *tbI-b1–3* not visible in examined specimens, but may be present. Abbreviations used for leg segments: *cI–III* coxa I–III, *fI–III* femur I–III, *tI–III* trochanter I–III, *tbI–III* tibia I–III, *trI–III* tarsus I–III. Abbreviations used for setal numbers: *a1–5* anterior setae 1–5, *b1–3* sensilla basiconica 1–4, *d1–5* dorsal setae 1–5, *dm1–4* distal marginal setae 1–4, *p1–3* posterior marginal setae 1–3, *s1–7* sensilla 1–7, *sf1–4* spiniform setae 1–4, *spn* spine of the thumb-like process, *th1–3* tactile hairs 1–3, v1–3 ventral setae 1–3

subspecies *H. e. erythrocephalus* have more scattered setae of the female subgenital plate (13–16 in material from *H. e. erythrocephalus* and 8–12 in material from *H. e. yamakanensis*). Given the small number of specimens involved, we do not presently consider these differences taxonomically significant. However, as more material becomes available, it may be necessary to reevaluate the species limits of *Vinceopterus* on different subspecies of *H. erythrocephalus*. It should be noted that different subspecies of *H. erythrocephalus* are parasitized by different species of *Harpactrox* [11]; the same may hold true in the genus *Vinceopterus*.

Vinceopterus mindanensis Gustafsson, Lei, Chu, Zou, and Bush, new species.

(Figures 1d, 4, 5, 8b).

Type host: *Harpactes ardens ardens* (Temminck 1826)—Philippine trogon.

Other host: *Harpactes ardens linae* Rand and Rabor 1959.

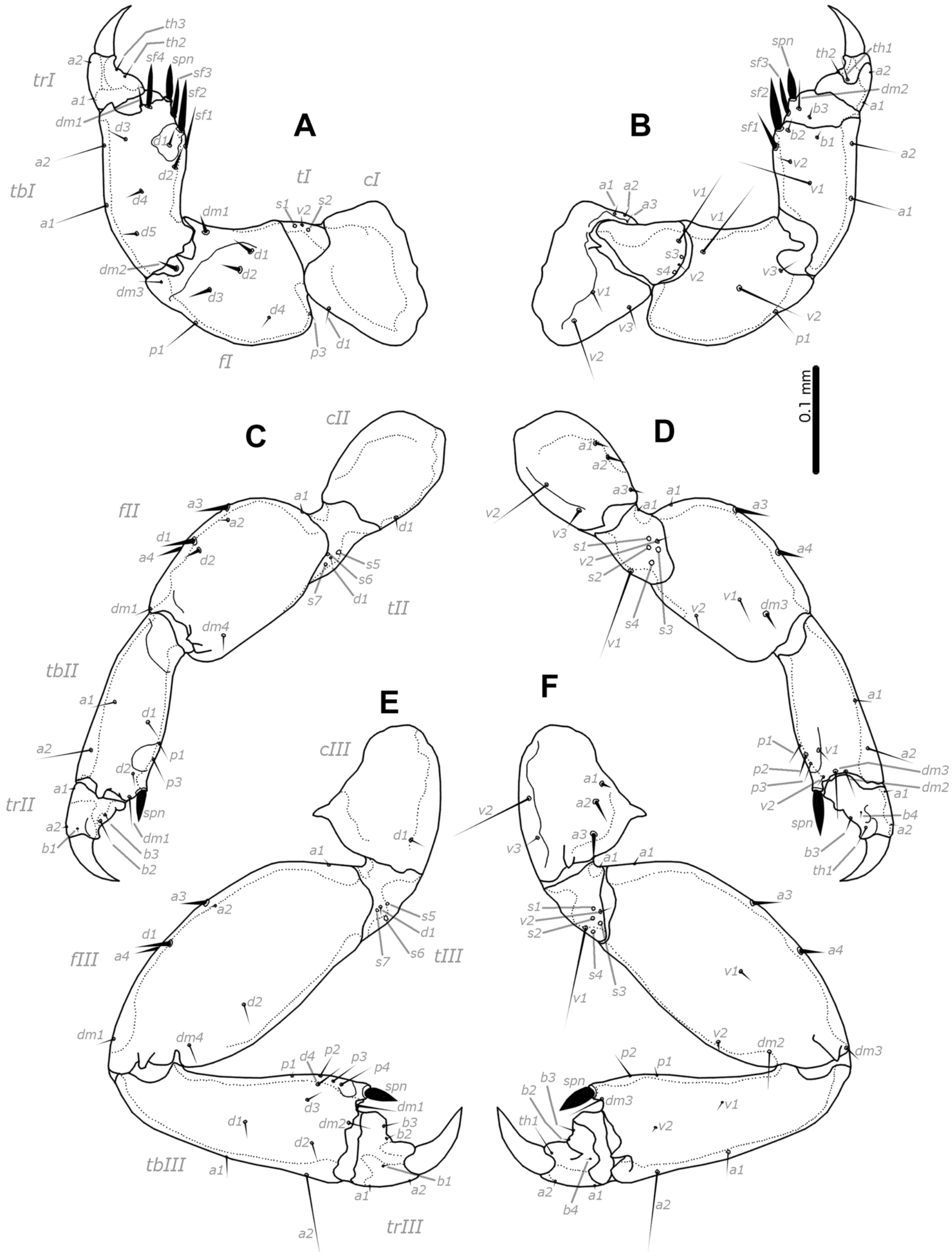

Fig. 7 Female legs of *Vinceopterus erythrocephali* ex *Harpactes erythrocephalus yamakanensis*. **a** Leg I, dorsal view. **b** Leg I, ventral view. **c** Leg II, dorsal view. **d** Leg II, ventral view. **e** Leg III, dorsal view. **f** Leg III, ventral view. All legs drawn at the same scale. Name of individual setae formed by combining the leg segment (including number) with the setal number as in [11]. Abbreviations used for leg segments: *cI–III* coxa I–III, *fI–III* femur I–III, *tI–III* trochanter I–III, *tbI–III* tibia I–III, *trI–III* tarsus I–III. Abbreviations used for setal numbers: *a1–5* anterior setae 1–5, *b1–3* sensilla basiconica 1–4, *d1–5* dorsal setae 1–5, *dm1–4* distal marginal setae 1–4, *p1–3* posterior marginal setae 1–3, *s1–7* sensilla 1–7, *sf1–4* spiniform setae 1–4, *spn* spine of the thumb-like process, *th1–3* tactile hairs 1–3, *v1–3* ventral setae 1–3

Type locality: Tucay E-el, Mindanao, Philippines.

Description, both sexes: Head shape as in Fig. 5a. Anterolateral lobes of hyaline margin not as thick as in *V. erythrocephali* n. sp.. Dorsal anterior plate with broad posterior extension (Fig. 8b). Preantennal nodi comparatively wide. Head chaetotaxy typical for genus (Fig. 5a). Thoracic and abdominal segments as in Figs. 4a, b. Leg chaetotaxy roughly as in *Vinceopterus erythrocephali* (Figs. 6, 7), but exact placement of setae varies slightly. Leg II and distal leg III distorted or broken off in both examined males. Chaetotaxy of remaining similar to *V. erythrocephali*, and here illustrated tentatively.

Male: thoracic and abdominal chaetotaxy as in Fig. 4a; thorn-like sternal setae found on segments II–VI in at least some specimens, but varies between specimens and between sides of same specimen. Sternal plates present on abdominal segments IV–VI in both males; in one male sternal plate is also present on segment III, but this cannot be confirmed in the second male, as the abdomen is broken on this segment. Male genitalia as in Figs. 5b, c. Lateral margins of distal basal plate with characteristic distal bulge and concave section. Mesosome with seemingly flattened anterior end, but exact border somewhat diffuse in specimens. Genital setae

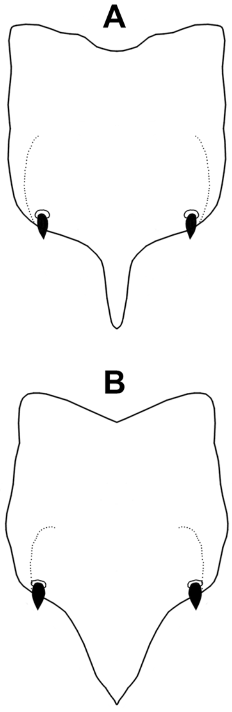

Fig. 8 Dorsal anterior plates of **a** *Vinceopterus erythrocephali* ex *Harpactes erythrocephalus yamakanensis*, and **b** *Vinceopterus mindanensis* n. sp. ex *Harpactes ardens ardens*

visible in specimens, as in Figs. 5b, c. Measurements as in Table 1.

Female: Thoracic and abdominal chaetotaxy as in Fig. 4b; thorn-like sternal setae found on segments II–VI in at least some specimens, but varies between specimens and between sides of same specimen. Sternal plates present only on abdominal segment VI. Subgenital plate as in Fig. 5d, with no visible reticulation; 2 macrosetae on each side on segment VII; 15–21 short setae scattered in area between distal subgenital plate and vulval margin; vulval margin with 4–5 mesosetae on each side. Distal margin of subgenital plate broadly rounded, with irregularly notched posterior margin. Lateral notches of subgenital plate always reach the lateral macroseta on each side, but not the median macroseta. Subvulval plates not clear anteriorly in examined specimens, and here illustrated tentatively; 3 mesosetae and 1 macroseta on each side lateral to distal subvulval plate. Anal opening with 2 ventral thorn-like setae and 1 dorsal short seta on each side. Measurements as in Table 1.

Type material: Holotype ♂ ex *Harpactes ardens ardens*: Tucay E-el, Mindanao, Philippines, no date or collector, SUBBM-1507 (NHML). Paratype ex *H. a. ardens*: 1♀, same data as holotype (NHML). 1♂, Balisong, Mindanao, Philippines, no date or collector, SUBBM-1170 (PIPeR).

Other material ex *Harpactes ardens linae*: 4♀, Tambis Burauen, Mt. Lobi Range, Leyte Island, Philippines, 4 May 1964, P.S. Rabor, B152 (PIPeR).

Diagnosis: See under *V. erythrocephali* n. sp., above.

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

Remarks: there is some variation in both the number of female tergopleural setae and scattered setae of the female genitalia between specimens form the two host subspecies. In general, specimens from *H. a. linae* have fewer genital setae but more tergopleural setae. As one of the females from *H. a. linae* is more similar to that from *H. a. ardens*, we presently consider these differences to represent intraspecific variation.

Clayiella Eichler, 1940 [12].

Remarks: To illustrate the mandibles of two species of *Clayiella* accurately, we also examined the following specimens:

Non-type material: *Clayiella prionitis* (Denny 1842) [22] [?] [as *Philopterus prionitis*] ex *Baryphthengus ruficapillus*: 3♂, 2♀,Cerro de Pantiacolla, elev. 680 m, Department of Madre de Dias, Peru, 8 Nov. 1985, D.H. Clayton (PIPeR).

Clayiella baryphthenga (Carriker 1963) [28] [as *Philopterus baryphthenga*] [?] ex *Baryphthengus martii*: 1♀, Alajvela, Cerro Montezuma, Costa Rica, 6 May 1986, M.A. Marin, 517 (PIPeR).

In both cases, these lice are from non-type hosts, and would constitute new host records for *C. prionitis* and *C. baryphthenga*. However, as the genus *Clayiella* has never been revised, and the descriptions of most species are inadequate, we do not consider these records to be definitely identified.

Discussion

Trogons form a morphologically distinct order of birds distributed across most tropical regions of the world [29]. Fossil birds recognized as early trogoniforms are known from 47 to 54 MYA [30–32]. Trogons appear to have no close living relatives [33], and the deeper relationships of trogons are not clear, with different data sets giving conflicting results [29, 34, 35].

Many authors have suggested that chewing lice could be used as an aid to the classification of the hosts in cases where the evidence from the hosts themselves is contradictory or insufficient to resolve their relationships (e.g., [36–39]). As the generic limits of lice have often been established based on their host relationships, the utility of chewing louse distribution for resolving host relationships is often limited [40]. Systematic approaches based on molecular data have the potential to break free from the circular reasoning that plagued earlier louse taxonomists. Indeed, this approach has been applied to other host–louse systems with interesting results. In some cases, lice act as "heirlooms" and follow the evolutionary history of their hosts [41]. In other cases,

Table 2 Host and geographic distribution of the five ischnoceran chewing louse genera known from trogons

Host genus	Geographical region	*Brueelia*-complex lice	*Degeeriella*-complex lice	*Philopterus*-complex lice
Apaloderma Swainson 1833	Afrotropics	–	*Trogoniella* Tendeiro, 1960 [42]	–
Apalharpactes Bonaparte 1854	Indomalaya	*Harpactrox* Gustafsson and Bush [11]	–	–
Euptilotis Gould 1858	Neotropics	–	–	–
Harpactes Swainson 1833	Indomalaya	*Harpactrox* Gustafsson and Bush [11]	–	*Vinceopterus* **n. gen.**
Pharomachrus La Llave 1832	Neotropics	*Guimaraesiella* Eichler [43]	*Trogoninirmus* Eichler, 1944 [44]	–
Priotelus Gray 1840	Neotropics	–	–	–
Trogon Brisson 1760	Neotropics	*Guimaraesiella* Eichler [43]	*Trogoninirmus* Eichler [44]	–

No amblyceran lice are presently known from any species of trogon. Host ranges and taxonomy are from [17], except *Apalharpactes* is recognized as valid, following [45]. Chewing louse distributions collated from [5, 11, 48] and the present study. Dashes (—) denotes that no lice belonging to this complex are presently known from this host genus, rather than positive statements that no lice from this complex exist on the host genus. Future research may well find more groups of lice on many of these host genera. No chewing lice of any genus are presently known from the Neotropic trogon genera *Euptilotis* and *Priotelus*

however, lice have switched hosts, which provide information about historical interspecific interactions [37, 39].

With the description of *Vinceopterus*, five genera of ischnoceran chewing lice are known from trogons (Table 2). In the future, a systematic study of these genera based on molecular data should provide several independent views of their host' ecological and evolutionary history. We here briefly discuss the chewing lice of all trogons.

Brueelia-Complex Lice

The *Brueelia*-complex parasitizes most families in the Passeriformes, but a few genera are known from non-passeriform hosts [11]. This includes two genera known from trogons: *Guimaraesiella* Eichler 1949 [43], and *Harpactrox* Gustafsson and Bush, 2017 [11].

Guimaraesiella is mainly found on passeriform birds, and is widely distributed across the world [11]. The two species of *Guimaraesiella* known from trogons are both found in the Neotropics, and both are morphologically distinct, with a preantennal area that is unique within the *Brueelia*-complex [46]. However, in the abdominal chaetotaxy and structure of the male genitalia, the *Guimaraesiella* of trogons are fairly typical members of the genus [11]. Two representatives were nested deeply inside *Guimaraesiella* in the phylogeny of [47]. It thus seems most likely that the *Guimaraesiella* of Neotropical trogons are the result of a rather recent host switch, probably from a passeriform host to a trogon; however, no close relatives of the trogon *Guimaraesiella* are known [47].

Harpactrox is presently known only from the genera *Harpactes* Swainson 1833 and *Apalharpactes* Bonaparte 1854 in Southeast Asia [11, 48]. The genus is markedly different morphologically from all other genera in the *Brueelia*-complex. The folded male parameral heads, the leg chaetotaxy, and the distribution of abdominal sensilla suggest that *Harpactrox* falls within the same general group within the *Brueelia*-complex as *Guimaraesiella*. If correct, this would suggest that *Harpactrox* is also the result of a host switch, likely from a passeriform host. However, as the morphology of *Harpactrox* is so different from all other known lice in the *Brueelia*-complex, this host switch may be more ancient than the one involving the Neotropical *Guimaraesiella* lice. No representative of this genus was included in the phylogeny of [47], and no close relatives can be suggested based on morphology.

Degeeriella-Complex Lice

The *Degeeriella*-complex lice are widely distributed across a large range of bird orders, spanning most of the avian tree of life (*cf.* [49] with, e.g., [33]). Two genera are known from trogons, both of which are found only on trogons.

Trogoninirmus Eichler, 1944 [44] is known from Neotropical trogons of the genera *Pharomachrus* La Llave 1832 and *Trogon* Brisson 1760. The placement of this genus in phylogenies based on molecular data has been relatively unsupported [40, 50]. This highlights how little we understand the morphological variation and relationships within the *Degeeriella*-complex, and any conclusions about the closest relatives of *Trogoninirmus* would be premature.

The other *Degeeriella*-complex genus known from trogons is the Afrotropical *Trogoniella* Tendeiro, 1960 [42]. This genus is very poorly known, and it is not clear from the original description how this genus differs from *Degeeriella* Neumann 1906 [51]. Based on morphology, *Trogoniella* does not appear to be particularly closely related to *Troginirmus*. To our knowledge, it has not been reported after the first descriptions [42].

Philopterus-complex Lice

Vinceopterus n. gen. is the only *Philopterus*-complex louse known from trogons, and is known only from Southeast Asian trogons of the genus *Harpactes* Swainson 1833. The genus is presumably specialized for living on the host's head, similar to other *Philopterus*-complex lice [2]. No other head lice are known from African or Neotropical trogons; however, this may be due to undersampling. Interestingly, *Vinceopterus* is morphologically most similar to *Clayiella* Eichler 1940 [12]. This genus occurs on Neotropical motmots (Momotidae), but is also known from the Madagascan cuckoo roller (Leptosomatidae) [2]. The morphologically similar *Tyranniphilopterus* Mey 2004 [2], and *Mayriphilopterus* Mey 2004 [2], are both found exclusively on Neotropical hosts (Galbulidae, Bucconidae, Pipridae, Cotingidae, Tyrannidae; [2, 10]). Further examinations of Neotropical trogons are needed to establish whether *Vinceopterus* is found also in the New World.

Summary

The known chewing lice of trogons represent three distinct louse complexes, and fall into five different genera, each of which seem to be restricted to a particular geographical area. All of these complexes are widely distributed across several host orders: both the *Brueelia*- and *Philopterus*-complexes contain lice primarily found on passeriform hosts, but the *Degeeriella*-complex contains lice from over 10 host orders [2, 11, 49]. These host associations suggest that trogons have repeatedly acquired lice from non-trogon hosts. These host switches, however, appear to have happened at very different times. *Vinceopterus* (*Philopterus*-complex) and *Harpactrox* (*Brueelia*-complex) are lice on trogon hosts that are morphologically quite distinct from other genera of lice in the same complex; this morphological divergence may be a consequence of early host switched from non-trogon to trogon hosts. On the other end of the spectrum, the species of *Guimaraesiella* (*Brueelia*-complex) on trogons are quite similar to congeneric lice on non-trogon hosts, which may be indicative of a much more recent host switch. Evolution of distinct forms can, however, happen rapidly and a molecular systematic approach is needed to more clearly understand the timing and diversification of these enigmatic lice.

The species of *Vinceopterus* described here constitute the first known presumed head lice from hosts in the order Trogoniformes. This is intriguing, as head lice are typically both common and easy to collect (DRG, pers. obs.). Moreover, trogons are hole nesters, a mechanism that has been proposed to aid in the transmission of chewing lice [52]. Neotropical and African trogons have been studied fairly recently [42, 46, 53], yet no head lice have been documented. No amblyceran lice are known from trogons at all [5], making them almost unique among bird orders in the Neoaves. Possibly, our understanding of trogon chewing louse distribution and evolution is simply a result of lack of sufficient sampling. Yet, it is also possible that trogon head lice are restricted to the trogons of Southeast Asia.

Revised key to the *Philopterus*-complex

We here include a translation of the key to the *Philopterus*-complex of [2], revised to include the genus *Vinceopterus* n. gen. Data from [6–10] have been included to reflect changes in our knowledge of the *Philopterus*-complex since 2004. The genus *Debeauxoecus* Conci 1941 [54] may be part of the *Philopterus*-complex [11, 55], but its placement within Philopteridae is unclear. No representatives of genera other than *Vinceopterus* and *Clayiella* were examined for this study.

1. Both trabecula and coni present… 2.
   Trabecula present, but coni absent, or if present only rudimentary… 12
2. Hyaline margin small, as mere cone-shaped continuation of the preantennal head; frons flat or slightly convex; dorsal anterior plate wider than long, without posterior elongation … *Corcorides* Mey, 2004 [2].
   Hyaline margin considerable, broadly covering frons; frons concave (rarely flat or convex); dorsal anterior plate longer than wide, with posterior elongation … 3.
3. Ventral carinae continue to anterior end of head; *os*, *pos*, and *mts1–3* all as macrosetae of more or less equal length … *Philopterus* Nitzsch, 1818 [4].
   Ventral carinae not continuing towards anterior end of head, but recurved towards postmarginal carinae and preantennal nodi; only *os*, *mts1*, and *mts3* macrosetae of more or less equal length (but *mts2* may be macrosetae that is shorter than *mts1* and *mts3*) … 4
4. Hyaline margin confined to osculum, and does not reach lateral to marginal carina… 5.
   Hyaline margin extends lateral to marginal carina, with lateral ends being near *as2* … 6.
5. Preantennal head very narrow; hyaline margin with deep concavity at midline; marginal sclerite of hyaline margin often seemingly divided into two parts…

Philopteroides Mey, 2004 [2] (*P. mitsusui* species group).

Preantennal head broader; hyaline margin with shallow concavity at midline; marginal sclerite of hyaline margin clearly continuous medianly … *Philopteroides* Mey, 2004 [2] (*beckeri* species group).

6. Hyaline margin weakly convex; marginal carina clearly divided into pre- and postmarginal carina … *Cinclosomicola* Mey, 2004 [2].

   Hyaline margin concave medianly; marginal carina undivided … 7.

7. Terminal segment of female abdomen with paired pseudostyli, each with 1–2 distal setae … *Paraphilopterus* Mey, 2004 [2].

   Terminal segment of female abdomen without such pseudostyli … 8.

8. Eyes with posterior end elongated into point … 11.

   Eyes not elongated posteriorly … 9.

9. Preantennal head elongated and narrow, with complete head clearly longer than wide; median section of hyaline margin without marginal sclerite; hyaline margin not swelling into rounded lobes laterally … *Cincloecus* Eichler, 1951 [21].

   Preantennal head shorter, with complete head roughly as broad as long; median section of hyaline margin with marginal sclerite; lateral ends of hyaline margin swelling into rounded lobes … 10.

10. Marginal carina with indentation on median side; *mts2* short seta; male genitalia not flaring distally … *Vinceopterus* n. gen.

    Marginal carina without indentation on median side; *mts2* macrosetae, but not as long as *mts1* and *mts3*; male genitalia with characteristic flaring distally … *Clayiella* Eichler, 1940 [12].

11. Hyaline margin excessively large, with lateral ends reaching to near *as1*; median section of hyaline margin more or less straight, without sclerotization; marginal carina divided into premarginal and postmarginal carinae … *Australophilopterus* Mey, 2004 [2].

    Hyaline margin smaller, at most reaching to near *as2* laterally; median section of hyaline margin concave with sclerotization; marginal carina undivided … *Tritrabeculus* Uchida, 1948 [56].

12. Hyaline margin with median marginal sclerotization and without setae … *Tyranniphilopterus* Mey, 2004 [2].

    Hyaline margin without median marginal sclerotization, but with 2–5 setae on each side … *Mayriphilopterus* Mey, 2004 [2].

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