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Cryptic genera, cryptic species: phylogeny of the genus *Philopteroides* Mey, 2004, sensu lato, with descriptions of two new genera and one new species

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Abstract

Closely related chewing lice in the *Philopterus*-complex are typically morphologically homogeneous, with the most significant differences often being in the male genitalia. However, in many groups within this complex the male genitalia are reduced and lacking one or more element, with the remaining components often at least partially fused. This is not least the case in the genus *Philopteroides* Mey, 2004, in which the male mesosome is often reduced and other characters are largely homogeneous throughout the genus. A phylogeny of the group based on a combination of mitochondrial and nuclear genes suggests that the species presently placed in *Philopteroides* belong to three different clades, which do not form a monophyletic group together. We here redefine *Philopteroides* morphologically, and describe two of these clades as new genera: *Stasiasticopterus* **n. gen.** for the species on bulbuls, and *Coronedax* **n. gen.** for species on monarch flycatchers. These genera can be separated from each other and from *Philopteroides* only by some characters of the male genitalia, but possibly also by characters of the preantennal head and female genitalia. In addition, we describe a new species of *Coronedax*, *Coronedax longiceps* **sp. n.** and provide an overview of the morphology of the male genitalia in the three genera treated.

Key words

1.   Introduction

The *Philopterus*-complex (sensu Mey 2004) constitutes a small, morphologically rather homogeneous, group of ischnoceran lice that are adapted to the "head louse" niche (Johnson et al. 2012). The majority of lice in this group parasitize passeriform hosts, but exceptions are known (Tendeiro 1962; Mey 2004; Gustafsson et al. 2019a). For most of the 20th century, this group has been considered to consist of a single genus, *Philopterus* Nitzsch, 1818, by most authors (e.g., Hopkins & Clay 1952); however, some authors separated smaller groups as different gen-

era, often on a poorly established morphological basis (e.g., Eichler 1963; Złotorzycka 1964). In the latest general checklist to the chewing lice of the world, these proposed genera were all synonymized with *Philopterus* (Price et al. 2003).

In a groundbreaking study on the classification of this complex, Mey (2004; fig. 4) showed that structural characters of the preantennal area may be useful for broader divisions of the complex. Using this and other characters, Mey (2004) overhauled our understanding of the *Philopterus*-complex and showed that the group is divisible if more careful attention is paid to structural characters. The classification proposed by Mey (2004) has not been challenged in subsequent publications on the group (e.g., Valim & Palma 2013; Gustafsson & Bush 2014; Najer et al. 2020a; Kolencik et al. 2022), and most of the genera he proposed seem to be robust enough to stand the test of time (but see e.g., Valim & Palma 2013; Kolencik et al. 2022).

However, several of the structural groups suggested by Mey (2004) corresponded to multiple genera, meaning that these characters need to be combined with other characters for correct genus-level identification. This becomes problematic as many known species are poorly described and illustrated, and crucial characters in e.g., the preantennal area or male genitalia have never been published. Moreover, some characters (e.g., patterns of abdominal chaetotaxy) are largely the same across most groups within this complex (Mey 2004; Gustafsson et al. 2022a). In other cases, characters such as the secondary sclerotization of the hyaline margin may have evolved multiple times independently (Gustafsson et al. 2022a).

Given these difficulties, it is not surprising that molecular analyses of lice in the *Philopterus*-complex have repeatedly shown that many genera are paraphyletic and consist of several distinct clades separated by very long branches. For instance, based on *COI* data, Najer et al. (2020a) found the genera *Philopteroides* Mey, 2004, and *Tyranniphilopterus* Mey, 2004, nested inside the genus *Philopterus* Nitzsch, 1818, s. lat. Kolencik et al. (2022) found *Australophilopterus* Mey, 2004, *Philopteroides* Mey, 2004, and *Tyranniphilopterus* to be paraphyletic, and identified numerous other groups that did not fit into any of the genera considered valid by Mey (2004). Ren et al. (2023) also found *Philopteroides* to be separated into several clades.

Here, we use a combination of genetic and morphological data to look closer at the genus *Philopteroides*. This genus is distributed across numerous host families from Africa, South Asia, and the Australo-Papuan region (Valim & Palma 2013), most of which are not yet described (DRG, pers. obs.). Najer et al. (2020a) and Ren et al. (2023) found that the species parasitizing bulbuls (Pycnonotidae) form a distinct group, which in the phylogeny of Kolencik et al. (2022) was placed close to some African and Bornean specimens from other host families. Kolencik et al. (2022) and Ren et al. (2023) also found a second group of lice identified as *Philopteroides* from a variety of mainly Australo-Papuan hosts, which Kolencik et al. (2022) called the "*mitsusui* species-group",

following Valim & Palma (2013). We examine the morphological variation among these clades, and revisit the generic circumscription of *Philopteroides*, which leads to the description of two new genera, *Coronedax* **gen. n.**, and *Stasiasticopterus* **gen. n.**, as well as a new species, *Coronedax longiceps* **sp. n.**

2. Material and methods

2.1. Specimen acquisition and identification

Birds were caught and fumigated for lice in several localities across South China during 2012–2021 using standard mist nets (net size: 2×6 m; 2×12 m) following the methods outlined by Gustafsson et al. (2019b); see Ren et al. (2023) for exact collection localities. Hosts were identified using MacKinnon & Phillipps (2000) or Arlott (2017); host taxonomy has been updated to conform with Clements et al. (2021).

Lice were stored in a –80°C freezer at the Institute of Zoology, Guangdong Academy of Sciences (IZGAS), Guangdong, China. Voucher specimens (see below) were identified to genus by DRG level using the key of Gustafsson et al. (2019a). All specimens of *Philopteroides* from bulbuls were identified by DRG using the key of Gustafsson et al. (2022b); note that many specimens represent new species, following Ren et al. (2023), and could not be identified with this key.

2.2. DNA extraction and sequencing

Specimens of *Philopteroides* were obtained from seven of the 20 species of bulbuls occurring in China, representing 5 of the 7 genera of bulbuls in this country; most of these sequences were previously published by Ren et al. (2023). Additional sequences of *Philopteroides* specimens and other members of the *Philopterus*-complex, as well as some outgroup taxa, were obtained from GenBank, originating from Kolencik et al. (2022), Light et al. (2016) and Catanach et al. (2019). Only taxa for which both *COI* and *EF-1α* were available on GenBank were added. All specimens used in our analyses are listed in Table 1.

Selected lice (Table 1) were cut halfway through the pterothorax and extracted for DNA using the DNeasy Blood and Tissue Kit (Qiagen, Shanghai, China) following the manufacturer's instructions except that extractions were left in 55°C water baths for 24 hours, and only 50µℓ were used for each elution. Exoskeletons were retrieved from the extraction fluid and slide mounted in Canada balsam as vouchers, following Palma (1978). Vouchers are deposited in the collection at IZGAS. Two gene loci were amplified and sequenced – a fragment of the mitochondrial cytochrome oxidase subunit I (*COI*, 379 bp) and a fragment of the nuclear gene elongation

Table 1. Collection and sequence information for specimens included in this study. Apart from some new EF-1a sequences, all genetic sequences were obtained from GenBank. Louse identification follows the information on GenBank for non-Chinese specimens, and has not been verified.

Louse species	Host species	Voucher No.	Locality	*COI* accession No.	*EF-1α* accession No.
Alcedoecus chelicutii	*Halcyon chelicuti*	Alsp.Hache.7.1.2014.16	Malawi	MK526914	MK570262
Alcedoecus delphax	*Dacelo novaeguineae*	Alsp.Danov.8.27.2014.3	Australia	MK526927	MK570258
Alcedoecus sp.	*Todiramphus sanctus*	Alsp.Tosan.8.27.2014.4	Australia	MK526926	MK570260
Australophilopterus curviconus	*Strepera graculina*	Ausp.Stgr.9.19.2011.9	Australia	OM363070	OM304396
Australophilopterus sp.	*Prinodura newtoniana*	Ausp.Prne.9.17.2011.12	Australia	OM363069	OM304395
Clayiella sp.	*Baryphthengus martii*	Clpr.4.4.2011.22	Peru	OM363072	OM304398
Clayiella sp.	*Baryphthengus martii*	Clpr.4.4.2011.23	Peru	OM363073	OM304399
Corcorides biocellatus	*Struthidea cinerea*	Corsp.Stci.9.17.2011.16	Australia	OM363076	OM304402
Corcorides inopinatus	*Corcorax melanorhamphos*	Corsp.Come.9.17.2011.14	Australia	OM363075	OM304401
Cuculicola sp.[1]	*Cercococcyx olivinus*	1379.2	Democratic Republic of Congo	KU187328	KU187360
Cuculoecus sp.	*Cercococcyx olivinus*	1379.1	Democratic Republic of Congo	KU187329	KU187372
Mayriphilopterus sp.	*Monasa morpheus*	Masp.Momo.3.3.2011.21	Brazil	OM363092	OM304418
Mayriphilopterus sp.	*Notharchus hyperrynchus*	Masp.Nohy.4.4.2011.28	Peru	OM363093	OM304419
Paraphilopterus sp. [2]	*Amblyornis macgregoriae*	Ausp.Amma.9.19.2011.5	Papua New Guinea	OM363067	OM304393
Coronedax graciliceps **n. sp.**	*Terpsiphone incei*	J1124 1103F3	China	OP476477	OR529496
Coronedax graciliceps **n. sp.**	*Terpsiphone incei*	J1124 1103M2	China	OP476474	OR529497
Coronedax sp.	*Hypothymis azurea*	J2882 1103N	China	OP476469	OR529499
Coronedax sp.	*Hypothymis azurea*	J1793M	China	OR528779	OR529500
Coronedax sp.	*Terpsiphone rufiventer*	Phosp.Teru.9.19.2011.13	Ghana	OM363118	OM304441
Coronedax sp.	*Terpsiphone rufiventer*	340.1	Democratic Republic of Congo	KU187313	KU187367
Coronedax sp.	*Terpsiphone mutata*	Phosp.Temu.9.17.2011.22	Madagascar	OM363117	OM304440
Philopteroides sp.	*Aethopyga saturata*	J0242 1103F1	China	OP476479	OR529493
Philopteroides sp.	*Arachnothera magna*	J1040 1103F2	China	OP476478	OR529494
Philopteroides sp.	*Arachnothera magna*	J1040 1103M1	China	OP476472	OR529495
Philopteroides sp.	*Arachnothera magna*	J0507 1103N1	China	OP476471	OR529498
Philopteroides sp.	*Climacteris melanurus*	Phosp.Clme.9.19.2011.21	Australia	OM363101	OM304426
Philopteroides sp.	*Climacteris picumnus*	Phosp.Clpi.9.17.2011.13	Australia	OM363102	OM304427
Philopteroides sp.	*Ptilotula plumula*	Phosp.Lipl.9.17.2011.19	Australia	OM363104	OM304429
Philopteroides sp.	*Kempiella flavovirescens*	Phosp.Mifl.9.19.2011.7	Papua New Guinea	OM363105	OM304430
Philopteroides sp.	*Cinnyris mediocris*	Phosp.Neme.6.9.2011.29	Kenya	OM363106	OM304431
Philopteroides sp.	*Cinnyris reichenowi*	Phosp.Nere.6.9.2011.26	Kenya	OM363107	OM304432
Philopteroides sp.	*Peneothello cyanus*	Phosp.Pecy.9.19.2011.2	Papua New Guinea	OM363108	OM304433
Philopteroides sp.	*Petroica goodenovii*	Phosp.Pego.9.17.2011.15	Australia	OM363109	OM304434
Philopteroides sp.	*Plectorhyncha lanceolata*	Phosp.Plla.9.17.2011.18	Australia	OM363113	OM304436
Philopteroides sp.	*Ptiloprora guisei*	Phosp.Ptgu.9.19.2011.6	Papua New Guinea	OM363115	OM304438
Philopteroides sp.	*Xanthotis flaviventer*	Phsp.Xafl.9.19.2011.17	Papua New Guinea	OM363157	OM304480
Philopteroides sp.?	*Chlamydochaera jeffreyi*	Phosp.Chje.6.9.2011.13	Malaysia	OM363100	OM304425
Philopteroides sp.?	*Batis molitor*	Tysp.Bamo.6.9.2011.6	Malawi	OM363160	OM304483
Philopteroides sp.?	*Eugerygone rubra*	Tysp.Euru.9.19.2011.4	Papua New Guinea	OM363165	OM304487
Philopteroides sp.?	*Grallina cyanoleuca*	Phsp.Grcy.9.17.2011.10	Australia	OM363134	OM304456
Philopterus linariae	*Zonotrichia leucophrys*	Phsp.Zole.6.9.2011.16	USA	OM363159	OM304482
Philopterus sp.	*Psalidoprogne albiceps*	Phosp.Psal.6.9.2011.11	Malawi	OM363114	OM304437
Philopterus sp.	*Geokichla gurneyi*	Phsp.Zogu.6.9.2011.14	Malawi	OM363158	OM304481
Stasiasticopterus flavala	*Ixos mcclellandii*	J0295 1028F3	China	OP476490	OR529481

Louse species	Host species	Voucher No.	Locality	*COI* accession No.	*EF-1α* accession No.
Stasiasticopterus flavala	*Hemixos flavala*	J1063 1028F5	China	OP476481	OR529482
Stasiasticopterus flavala	*Hemixos flavala*	J1063 1028M3	China	OP476483	OR529483
Stasiasticopterus flavala	*Hemixos castanonotus*	J2606 1028F7	China	OP476486	OR529486
Stasiasticopterus flavala	*Hemixos castanonotus*	J0830 1028M2	China	OP476489	OR529487
Stasiasticopterus flavala	*Hemixos castanonotus*	J0830 1028F4	China	OP476484	OR529488
Stasiasticopterus kayanobori?	*Spizixos semitorques*	J0102	China	OP476492	OR529478
Stasiasticopterus kayanobori?	*Spizixos semitorques*	J0102 1028M1	China	OP476485	OR529479
Stasiasticopterus sp. 4	*Hypsipetes leucocephalus*	J0258 1028F2	China	OP476491	OR529480
Stasiasticopterus sp. 4	*Hypsipetes leucocephalus*	J1195 1028M4	China	OP476482	OR529489
Stasiasticopterus sp. 5	*Ixos mcclellandii*	J4155 1029M3	China	OP476480	OR529492
Stasiasticopterus sp. 5	*Alophoixus flaveolus*	J0493 1028F6	China	OP476487	OR529484
Stasiasticopterus sp. 5	*Alophoixus flaveolus*	J0493 1028M5	China	OP476488	OR529485
Stasiasticopterus sp. 5	*Alophoixus pallidus*	J3023 1029M1	China	OP476475	OR529491
Stasiasticopterus sp. 5	*Alophoixus pallidus*	J2991 1029F1	China	OP476476	OR529490
Stasiasticopterus sp.	*Arizelocichla milanjensis*	Phosp.Anmi.6.9.2011.20	Malawi	OM363099	OM304424
Stasiasticopterus sp.	*Arizelocichla fuscicdps*	Phosp.Pyte.6.9.2011.12	Malawi	OM363116	OM304439
Stasiasticopterus sp.	*Hypsipetes madagascariensis*	Phosp.Hyma.9.17.2011.21	Madagascar	OM363103	OM304428
Stasiasticopterus sp.	*Phyllastrephus icterinus*	Phosp.Phic.9.19.2011.11	Ghana	OM363110	OM304435
Stasiasticopterus sp.	*Phyllastrephus albigularis*	1672.1	Democratic Republic of Congo	KU187320	KU187368
Stasiasticopterus sp.	*Bleda syndactylus*	1713.1	Democratic Republic of Congo	KU187323	KU187369
Stasiasticopterus sp.	*Stizorhina fraseri*	1765.1	Democratic Republic of Congo	KU187325	KU187370
Stasiasticopterus sp.	*Eurillas virens*	278.1	Democratic Republic of Congo	KU187318	KU187371
Strigiphilus sp.	*Megascops guatemalae*	Stcru.1.27.1999.10	Mexico	AF545767	AF320467
Tyranniphilopterus caiolukasi	*Tolmomyias sulphurescens*	Tysp.Tosu.10.1.2011.16	Panama	OM363184	OM304506
Tyranniphilopterus sp.	*Tyrannus melancholicus*	Tysp.Tyme.10.1.2011.2	Panama	OM363185	OM304507
Vinceopterus sp.	*Harpactes kasumba*	Phsp.Haka.9.19.2011.22	Malaysia	OM363135	OM304457

[1] Identity of this specimen is uncertain. In the analysis where this sequence was originally published (Light et al. 2016) it was nested within the *Degeeriella*-complex, which is the expected placement of this genus.

[2] This specimen likely represents *Paraphilopterus knutieae* Gustafsson & Bush, 2014, but was left unidentified by Kolencik et al. (2022).

factor 1-alpha (*EF-1α*, 347 bp). PCR conditions followed those outlined by Bush et al. (2016), using primers L6625 and H7005 (Hafner et al., 1994) for *COI*, and EF1-For3 and EF1-Cho10 (Danforth and Ji, 1998) for *EF-1α*.

PCRs were performed using Cytiva PureTaq Ready-To-Go beads (GE Healthcare, Vienna, Austria), following the manufacturer's instructions. Samples showing satisfactory bands on an electrophoresis gel were sent for sequencing using the same primers as for PCR to Tianyi Huiyuan Gene Technology, Co. Ltd. (Guangzhou, China). Sequences were assembled in Seqman Pro 7.1.0 (DNAStar Inc., Madison, Wisconsin) and checked manually to rule out mismatches between forward and reverse sequencing results for each gene and each individual.

2.3. Phylogenetic reconstruction

Sequences were aligned separately in MEGA 11 using ClustalW and MUSCLE (Edgar, 2004; Larkin et al.

2007; Kumar et al. 2018). Substitution models for each gene were evaluated in MEGA 11; the best model for *COI* was GTR+G, and for *EF-1α* was TN93+G,. The 2 aligned and partitioned genes were imported into and concatenated by BEAST v1.10.4 (Suchard et al. 2018), with the default strict clock prior and a Yule speciation process prior, using random starting trees, with the options of linked trees, separated clock models for each gene, 4 Gamma Categories under the strict clock, and constant size of coalescence. Markov chain Monte Carlo (MCMC) tests were run for 1×10^8 generations and sampled every 1000 generations. We used Tree Annotator v1.10.4 (Suchard et al. 2018) for tree integration and discarded the first 10,000,000 trees as "burnin." The output tree from Tree Annotator was imported to FigTree v1.4.3 (http://tree.bio.ed.ac.uk/software/figtree) for figure illustration and edited in Adobe Illustrator 2021.

Figure 1. Phylogeny of the *Philopterus*-complex based on the mitochondrial *COI* and nuclear *EF-1α* genes generated in BEAST v1.10.4. Nodes with posterior probabilities of 1.0 are marked with asterisks (*), whereas nodes with posterior probabilities >0.95 are marked with circlets (°); all unmarked clades received posterior probabilities of <0.95. Louse voucher numbers are reduced compared to Table 1 for simplicity; voucher numbers are given only when disambiguation is necessary. For information on the collection locality of all specimens, see Table 1. The three genera of the *Philopteroides* morpho-group are named to the right, along with numbered clades discussed in the text. Within Clades II–III, specimens derived from African hosts are marked with gray circles after the name.

2.4. Illustration and description

Slide-mounted voucher specimens were examined with a Nikon Eclipse N*i* (Nikon Corporation, Tokyo, Japan), with a drawing tube attached for making illustrations. Drawings were scanned, then compiled and edited in GIMP (www.gimp.org). Measurements (all in mm) were made from live images in NIS-Elements (Nikon Corporation, Tokyo, Japan) for the following dimensions: AW = abdominal width (at segment V); HL = head length (at midline); HW = head width (at widest point of temples); PRW = prothoracic width; PTW = pterothoracic width; TL = total length (at midline).

Morphological terms used and their abbreviations used follow Clay (1951), Mey (1994, 2004), Gustafsson & Bush (2017); abbreviations include: *aps* = accessory postspiracular seta; *as1* = anterior seta 1; *lpmes* = lateral posterior mesosomal seta; *mms* = marginal mesometanotal setae; *mts1, 3* = marginal temporal setae 1, 3; *os* = ocular seta; *pns* = postnodal seta; *ppss* = pronotal post-spiracular seta; *ps* = paratergal seta; *psps* = principal postspiracular seta; *pst1–2* = parameral setae 1–2; *pts* = posttemporal seta; *s1–4* = sensilla 1–4 of dorsal postantennal head; *sts* = sternal seta; *tps* = tergal posterior seta; *vms* = vulval marginal setae; *vss* = vulval submarginal setae. These terms are indicated in the relevant figures.

3. Results

3.1. Phylogenetic analysis

Our analysis resulted in a tree in which the trabeculum-bearing genera (*Philopterus*-complex sensu Mey 2004) formed a monophyletic group, to the exclusion of closely related genera (Fig. 1). This clade is basally divided between the *Mayriphilopterus* Mey, 2004, parasitizing hosts in the Galbuliformes, and all other *Philopterus*-complex lice, parasitizing mainly hosts in the Pas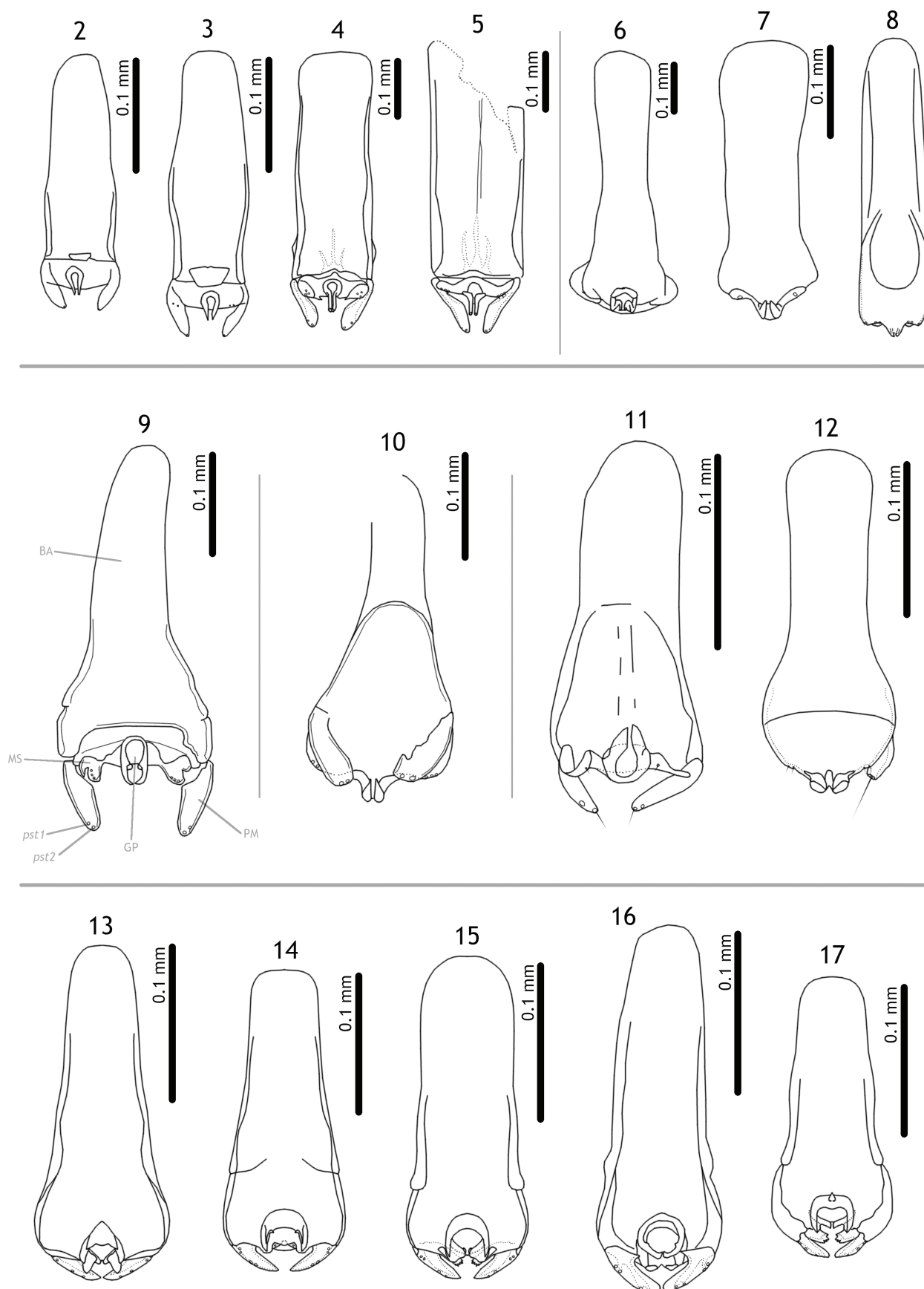seriformes, but also the genera *Clayiella* (parasit-izing motmots; Coraciiformes) and *Vinceopterus* (parasitizing trogons; Trogoniformes). Most of the relationships between genera within the *Philopterus*-complex are unresolved, and both *Tyranniphilopterus*, *Philopteroides* and *Australophilopterus* are recovered as paraphyletic.

Specimens of *Philopteroides* were placed in three larger clades, although the relationship between these clades were not clear (Fig. 1). Two of these clades are here described as new genera, *Coronedax* **new genus** and *Stasiasticopterus* **new genus**. For convenience, these three genera together are here referred to as the "*Philopteroides* morpho-group", which is not intended to indicate any close relationship between them. Four samples identified by Kolencik et al. (2022) as belonging to *Philopteroides* were placed outside the three main clades here, but as we have not examined these samples, their generic placement is unresolved; none of these three samples were identified to species level by Kolencik et al. (2022).

The first clade (Clade I; Fig. 1) comprises samples of *Philopteroides* from a variety of hosts, including honeyeaters (Meliphagidae), Australasian robins (Petroicidae), sunbirds and spiderhunters (Nectariniidae), and treecreepers (Climacteridae). Although the type species of *Philopteroides* was not included in this phylogeny, previous studies of specimens from honeyeaters (DRG, unpublished data) indicate that this group likely represents *Philopteroides* s. str.; alternatively, *Philopteroides* s. str. is not represented in any clade of this tree, and has not yet been sampled. The geographical range of these samples covers Asia and the Australo-Papuan region, but the clade is not divided geographically as the Asian samples are nested inside the Australo-Papuan samples. The Asian samples are all from Nectariniidae, but these do not form a monophyletic clade, as specimens from *Aethopyga saturata* are nested inside a clade of lice from various Australo-Papuan birds. Most of the relationships within this clade received no support, and the relationships between *Philopteroides* s. str. and its inferred closest relatives (*Clayiella*, *Tyranniphilopterus* s. lat) also received no support.

The second clade (Clade II; Fig. 1) comprises the specimens from bulbuls, which are here described as the ge-

Figures 2–17. Comparison of the male genitalia of some species of *Philopteroides* Mey, 2004, *Coronedax* **gen. n.**, and *Stasiasticopterus* **gen. n.** All figures redrawn from their original descriptions (Tandan 1955; Mey 2004; Valim & Palma 2013), unless otherwise noted. Illustrations have been rescaled to be roughly the same size. Illustrations are in ventral view, unless otherwise noted. No illustrations of the genitalia have ever been published for *Philopteroides lineatus* (Giebel, 1874), *Philopteroides mitsusui* (Uchida, 1948), or *Stasiasticopterus kayanobori* (Uchida, 1948). **2** *Philopteroides novaezelandiae* Mey, 2004. **3** *Philopteroides xenicus* Mey, 2004. **4** *Philopteroides fuliginosus* Valim & Palma, 2013. **5** *Philopteroides macrocephalus* Valim & Palma, 2013. **6** *Philopteroides gigas* Najer et al., 2016. **7** *Philopteroides sinancorellus* Najer et al., 2016. **8** *Philopteroides sclerotifrons* (Tandan, 1955); no scale in original. **9** *Philopteroides pilgrimi* Valim & Palma, 2013. **10** *Philopteroides beckeri* (Mey, 2004) (redrawn from Valim & Palma 2013). **11** *Coronedax terpsiphoni* (Najer & Sychra [in Najer et al.], 2012a). **12** *Coronedax longiceps* **sp. n. 13** *Stasiasticopterus longiclypeatus* (Gustafsson et al., 2022b). **14** *Stasiasticopterus holosternus* (Gustafsson et al., 2022b). **15** *Stasiasticopterus haerixos* (Gustafsson et al., 2022b). **16** *Stasiasticopterus flavala* (Najer & Sychra [in Najer et al.], 2012a. **17** *Stasiasticopterus cucphuongensis* (Mey, 2004) (redrawn from Gustafsson et al. 2022b). Bold grey lines signify the generic divisions used here; narrow grey lines signify groups that are morphologically different from the type species of the respective genera, but where there is insufficient data to propose addition (e.g., subgeneric) limits. The two species here considered incerta sedis are placed in separate groups, pending further investigations. — Abbreviations used: BA = basal apodeme; GP = gonopore; MS = mesosome; *lpmes* = lateral posterios mesosomal setae; PM = parameres; *pst1–2* = parameral setae 1–2 (2 distal to 1).

Figures 2–8, 0.1 mm scale bars.

Figures 9–12, 0.1 mm scale bars. Labels: BA, MS, pst1, pst2, GP, PM.

Figures 13–17, 0.1 mm scale bars.

nus *Stasiasticopterus*. This clade includes samples from both African and Asian bulbuls, but samples from the two continents do not form reciprocally monophyletic clades. Instead, samples from African-endemic host genera form two clades, and samples from Asia and the African representative of the genus *Hypsipetes* forms a third clade. The relationship among these three clades is unresolved. Specimens from the African *Batis molitor* and the Asian

Table 2. Morphological comparison of *Philopteroides* s. str., *Coronedax* **new genus**, and *Stasiasticopterus* **new genus**. Species here considered incerta sedis have not been included in the evaluation of these characters. Note that the description of *Philopteroides* s. str. here only refers to those species that have parameres (Figs 2–5), as the status of the paramere-less species is unclear.

Character	*Philopteroides* Mey, 2004	*Coronedax* new genus	*Stasiasticopterus* new genus
Mesosome	Prominent, rectangular or at least broadly following distal margin of basal apodeme	Reduced to distal margin of basal apodeme	Reduced, typically visible as vague dorsal plate only
Gonopore	Subterminal, with distinct posterior appendages	Terminal	Ventral, with complicated sclerotized margins and in some species with fringed distal appendages
Parameres	Widening distally, loosely articulated, moderately sclerotized	Of equal width, loosely articulated, poorly sclerotized	Narrowing distally, strictly convergent, strongly sclerotized
Parameral seta 2	Apical, sensillum or microseta	Apical, mesoseta	Subapical, sensillum or microseta
Sternal setae	At least 2 macrosetae on each side on segments II–VI	Only 1 macroseta on each side on segments II–VI	At least 2 macrosetae on each side on segments II–VI
Uncertain characters			
Dorsal preantennal suture	Not reaching lateral margin of head	Not reaching lateral margin of head	Reaching lateral margin of head
Marginal carina	Not interrupted laterally	Not interrupted laterally	Interrupted laterally in some species?
Vulval chaetotaxy	Generally with numerous long lateral setae (*vms*?) and numerous short central setae (*vss*?)	With few long, lateral setae (*vms*?) and no short, central setae	Generally with numerous long lateral setae (*vms*?) and numerous short central setae (*vss*?)

Chlamydochaera jeffreyi are placed as sister to *Stasiasticopterus*, but these specimens have not been examined.

The third clade (Clade III; Fig. 1) comprises the specimens from monarch flycatchers, which are here described as the genus *Coronedax*. The deepest divergence within this clade is between specimens from Africa and specimens from Asia, with specimens from Asian *Terpsiphone incei* being more closely related to specimens from Asian *Hypothymis azurea* than to specimens from other *Terpsiphone* hosts from Africa. This clade appears closely related to single specimens from another monarch flycatcher, *Grallina cyanoleuca*, and the petroicid *Eugerygone rubra*. As these specimens have not been examined, they are not here considered part of *Coronedax*.

3.2. Morphological analysis

The structure of the male genitalia of specimens and published illustrations of lice in the *Philopteroides* morpho-group fall into three categories (Figs 2–17; Table 2).

Group one includes species in which the mesosome is prominent, roughly rectangular, and with a gonopore that has elongated projections distally; moreover, the parameres are long, less restricted in their flexibility, and lack prominent apical setae (Figs 2–5). This group corresponds to the specimens in Clade I in Fig. 1, and represent *Philopteroides* s. str.

Group two includes species in which the mesosome is much reduced ventrally, but may be visible as a plate dorsally, and with a prominent gonopore of varying structure, that may project distally and may be associated with rugose median projections; moreover, the parameres are more intensely sclerotized, restricted to be highly convergent distally, and lack apical setae (Figs 13–17). This group corresponds to Clade II in Fig. 1, and represent the new genus *Stasiasticopterus*.

Group three includes species in which the mesosome is reduced to at most a thickening of the distal margin of the basal apodeme, and the gonopore lacks distal projections; moreover, the parameres are long and slender, less restricted in their flexibility, and have prominent apical setae (Fig. 12). This group corresponds to the specimens in Clade III in Fig. 1, and represent the new genus *Coronedax*.

Comparisons of other morphological characters are inconclusive. Potentially, the dorsal preantennal suture reaches the lateral margin of the preantennal head at the site of anterior seta 1 only in Clade II species (*Stasiasticopterus*), but this character is not illustrated in sufficient detail in all described species to evaluate. The ventral chaetotaxy may separate *Coronedax* from other genera, but this is also not conclusive. Female specimens cannot presently be identified to genus level, until the variation of in morphology of the dorsal preantennal suture and the ventral abdominal chaetotaxy have been examined in more detail.

4. Systematics

PHTHIRAPTERA Haeckel, 1896: 703

Ischnocera Kellogg, 1896: 63

Philopteridae Burmeister, 1838: 422

***Philopterus*-complex**

Philopteroides Mey, 2004

Philopterus Nitzsch, 1818: 288 in partim.
Docophorus Nitzsch, 1818: 289 in partim.

Bitrabeculus Uchida, 1948: 317 in partim.
Philopteroides Mey, 2004: 173.
Tyranniphilopterus Mey, 2004: 178 in partim.

Type species. *Philopteroides novaezelandiae* Mey, 2004: 174, by original designation.

Diagnosis. With the data provided herein, a redefinition of the genus *Philopteroides* is necessary. Essentially, most of the characters used by Mey (2004) to diagnose the genus are still valid, but here we restrict the genus to contain only those species in which the genitalia are of the same type as in the type species. Specifically: species in which the mesosome is broad, rectangular (or at least widely following distal margin of basal apodeme) (Figs 2–5); gonopore with distal extensions that protrude beyond the distal margin of the mesosome; parameres not densely sclerotized, somewhat lobe-like, not strongly convergent, and without apical mesoseta; in some species parameres are apparently absent (see below) (Figs 6–8).

In general, known species of *Philopteroides* all seem to have dorsal preantennal suture not reaching lateral margin of the head, and marginal carina being indented but not interrupted laterally, but this needs to be confirmed for some species. Females of *Philopteroides* have a large number of short, central setae (*vss*?) on the vulval margin, and numerous longer setae (*vms*?) sublaterally. The homology of these setae compared to the rest of Ischnocera are uncertain, and require further study.

Host associations. Known from numerous host families (see Table 3).

Geographical range. All known species are Australo-Papuan or Indo-Malayan.

Included species. See Table 3.

Remarks. As noted by Mey (2004), Tandan (1955) illustrated the genitalia of *Philopterus sclerotifrons* Tandan, 1955, without parameres (Fig. 8), which is unlike the type species of *Philopteroides*, but similar to the species described by Najer et al. (2016) (Figs 6, 7. We have not examined any specimens of *Ph. sclerotifrons*, but have seen a single male of another undescribed species from a sunbird, which is similar to *Ph. sclerotifrons*. In this male, the genitalia are partially obscured by gut content, but appear to be lacking clear parameres. Specimens from two species of sunbirds were nested inside *Philopteroides* s. str. in our phylogeny. The lack of parameres needs to be confirmed with additional samples, and the relationship between the paramere-less species and the paramere-bearing species needs further evaluation. For the present, we retain the paramere-less species in *Philopteroides*, but consider them atypical, and do not include characters from these species in the genus-level comparisons below.

Philopteroides pilgrimi Valim & Palma, 2013, has male genitalia of the same type as the type species of *Philopteroides* (cf. Figs 2–5, 9), and probably belongs to this genus. However, the female genitalia lack the central short setae (*vss*?; see Valim & Palma 2013: fig. 9), which is more typical of the genus *Coronedax* (see below). If these are very short in this species, they may have been overlooked; no specimen of *Ph. pilgrimi* was examined. We here retain *Ph. pilgrimi* in *Philopteroides*, but note that a reexamination of the species is necessary.

Philopteroides beckeri (Mey, 2004), originally placed in the genus *Tyranniphilopterus* is also here retained in the genus *Philopteroides*; however, this placement is more tentative. Mey (2004) illustrated the male genitalia of this species without parameres, similar to e.g., *Ph. sclerotifrons* (cf. Fig. 8 with Mey 2004: fig. 29d). However, when Valim & Palma (2013) reexamined the type specimens, they found that the parameres are present in this species but folded under the mesosome and attached to the basal apodeme much farther anterior than in most other species in the morpho-group (reproduced in Fig. 10). Overall, the male genitalia of this species resemble those of *Coronedax* (Figs 11, 12) more than those of any other species of *Philopteroides* (Figs 2–8). However, sternal chaetotaxy, head shape, and the lack of elongated *pst2* in *Ph. beckeri* separate it from *Coronedax*. Possibly this species represents either the sister clade to *Coronedax* or the sister clade to *Stasiasticopterus* in our tree (Fig. 1). As this mosaic of characters complicates any assessment of the placement of this species within the *Philopteroides* morpho-group, we presently consider *Philopteroides beckeri* to be incerta sedis within *Philopteroides* s. lat.

The two species described by Najer et al. (2016) from New Guinean berrypeckers are difficult to place presently, not least because the two species are so different from each other. The male genitalia appear to lack or have much reduced parameres (Figs 6, 7), similar to species of *Philopteroides* from sunbirds (Fig. 8), but in overall shape of the male genitalia and in the broad heads they are more similar to those of the *beckeri*-species group, in which they were originally placed. Presumably, as more species of the *Philopteroides* morpho-group are described, the relationships of these two species with the rest of the morpho-group may be clarified. No genetic data are available for either species. They are here considered to belong to *Philopteroides* until more is known about this group.

Stasiasticopterus Ren, Tian, Grossi, Zou & Gustafsson gen. n.

https://zoobank.org/F1CA7ED4-6DB8-492B-B370-197D5A531CD1

Bitrabeculus Uchida, 1948: 317 in partim.
Philopteroides Mey, 2004: 173 in partim.

Type species. *Philopteroides flavala* Najer & Sychra [in Najer et al.], 2012a.

Table 3. Classification of the species previously placed in *Philopteroides*, along with host information. Type species of each genus are denoted with an asterisk (*).

Louse taxon	Type host	Host family	Notes
***Philopteroides* Mey, 2004**			
Philopteroides fuliginosus Valim & Palma, 2013	*Rhipidura fuliginosa placabilis* Bangs, 1921	Rhipiduridae	
Philopteroides gigas Najer et al., 2016	*Paramythia montium* De Vis, 1892	Paramythiidae	[1]
Philopteroides lineatus (Giebel, 1874)	*Arachnothera longirostra* (Latham, 1790)	Nectariniidae	
Philopteroides macrocephalus Valim & Palma, 2013	*Petroica macrocephala macrocephala* (Gmelin, 1789)	Petroicidae	
Philopteroides mitsusui (Uchida, 1948)	*Myzomela rubrata dichromata* Wetmore, 1919	Meliphagidae	[2]
Philopteroides novaezelandiae Mey, 2004*	*Acanthisitta chloris chloris* (Sparrman, 1787)	Acanthisittidae	
Philopteroides pilgrimi Valim & Palma, 2013	*Gerygone igata igata* (Quoy & Gaimard, 1830)	Acanthizidae	[3]
Philopteroides sclerotifrons (Tandan, 1955)	*Cinnyris asiaticus asiaticus* (Latham, 1790)	Nectariniidae	
Philopteroides sinancorellus Najer et al., 2016	*Oreocharis arfaki* (Meyer, 1874)	Paramythiidae	[1]
Philopteroides xenicus Mey, 2004	*Xenicus longipes longipes* (Gmelin, 1789)	Acanthisittidae	
***Coronedax* new genus**			
Coronedax longiceps **new species** *	*Terpsiphone incei* (Gould, 1852)	Monarchidae	
Coronedax terpsiphoni (Najer & Sychra [in Najer et al.], 2012b) **new combination**	*Terpsiphone viridis* (Müller, 1776)	Monarchidae	
***Stasiasticopterus* new genus**			
Stasiasticopterus cucphuongensis (Mey, 2004) **new combination**	*Pycnonotus finlaysoni eous* Riley, 1940	Pycnonotidae	
Stasiasticopterus flavala (Najer & Sychra [in Najer et al.], 2012a) **new combination** *	*Hemixos flavala* Blyth, 1845	Pycnonotidae	
Stasiasticopterus haerixos (Gustafsson et al. 2022b) **new combination**	*Ixos mcclellandii* (Swinhoe, 1861)	Pycnonotidae	
Stasiasticopterus holosternus (Gustafsson et al., 2022b) **new combination**	*Pycnonotus goiavier goiavier* (Scopoli, 1786)	Pycnonotidae	
Stasiasticopterus kayanobori (Uchida, 1948) **new combination**	*Spizixos semitorques cinereicapillus* Swinhoe, 1871	Pycnonotidae	[4]
Stasiasticopterus longiclypeatus (Gustafsson et al. 2022b) **new combination**	*Hypsipetes everetti samarensis* Rand & Rabor, 1959	Pycnonotidae	
Incerta sedis			
Philopteroides beckeri (Mey, 2004)	*Platysteira cyanea nyansae* Neumann, 1905	Platysteiridae	[5]

[1]   These two species, from mountain endemics of New Guinea, are difficult to place in the present classification. They appear to be similar to both *Philopteroides* and *Coronedax*, but the parameres are much reduced or absent, and the dorsal preantennal suture appears to reach the lateral margin of the head. We here retain them in *Philopteroides*, but note that as more species of this genus are described, this may need to be reevaluated.

[2]   This species cannot be satisfactorily placed based on the original description and illustrations of Uchida (1948) and is in need of redescription. Notably, other species known from honeyeaters all fall within *Philopteroides* as defined here, but as many of Uchida's specimens appear to be contaminations or stragglers, this cannot be assumed.

[3]   The female vulval chaetotaxy and the shape of the male genitalia (Fig. 9) is similar to that of *Philopteroides*, and the sternal chaetotaxy of *Ph. pilgrimi* is similar to that of *Coronedax*. However, no specimens were examined, and the species has never been fully illustrated. Notably, the original illustration does not show any long apical setae of the parameres (Valim & Palma 2013; fig. 33). Possibly, *Ph. pilgrimi* is close to the unidentified species from *Eugerygone rubra* that was placed as a sister to *Coronedax* in our phylogeny.

[4]   Placed in *Stasiasticopterus* based on host associations and the fact that specimens from the same host from the Chinese subspecies *Spizixos semitorques semitorques* Swinhoe, 1861 belong to this genus. However, the species cannot be identified satisfactorily based on Uchida's description and illustration (Gustafsson et al. 2022b) and is in need of redescription.

[5]   The placement of this species is uncertain. The male genitalia, as illustrated by Valim & Palma (2013; fig. 31), suggests that it may be close to *Coronedax*, but the sternal abdominal chaetotaxy is dissimilar to that of other *Coronedax* [cf. Mey (2004; fig. 29) and Figs. 18, 19]. A reexamination of the type material is necessary before this species can be placed in the present classification.

Diagnosis. Species in *Stasiasticopterus* **gen. n.** can be separated from species of *Philopteroides* by the following combination of characters: 1) mesosome broad (rectangular or of more irregular shape), and clearly delineated ventrally in *Philopteroides* (Figs 2–5), but completely fused to basal apodeme and visible only as vague dorsal plate in *Stasiasticopterus* (Figs 13–17); 2) gonopore simple, extended distally in *Philopteroides* (Figs 2–5), but more complicated, with numerous small thickenings and ridges in *Stasiasticopterus* (Figs 13–17); 3) parameres fleshy, loosely articulated with basal apodeme and not strongly convergent in *Philopteroides* (Figs 2–5), but smaller, harder, tightly convergent in *Stasiasticopterus* (Figs 13–17); 4) male tergopleurite IX+X medially continuous in *Philopteroides*, but medially interrupted in *Stasiasticopterus*.

Possibly, species of these two genera may be separated on preantennal characters as well. In *Stasiasticopterus*

the dorsal preantennal suture always reaches the lateral margin of the head at the site of *as1*, and the marginal carina may be divided at the same point (but this is not always clear, and the carina may be just indented in some species); this would represent state D1 in the schematics of the preantennal head published by Mey (2004). In published photos and illustrations, it seems *Philopteroides* typically represents state D2 in the same scheme, with a notched but not interrupted marginal carina, and a suture that does not reach the lateral margin of the head. Possibly, the state of the dorsal preantennal suture is a better diagnostic character than the state of the marginal carina, but more species need to be examined before this character can be evaluated properly.

Moreover, the structure of the dorsal anterior plate may consistently differ between the two genera, in that the plate is generally broader and with the posterior extension thickened and associated with internal carinae in some *Philopteroides*, but more narrow and without such thickening of the posterior elongation in *Stasiasticopterus*.

Females can presently only be identified based on the preantennal characters described above, and by genetic data. However, both preantennal characters need verification, and are not clearly illustrated for some species.

Description. Small lice of the head louse ecomorph (sensu Johnson et al. 2012). Frons deeply and narrowly emarginate, with median margin secondarily sclerotized. Dorsal preantennal suture completely surrounds dorsal anterior plate and reaches lateral margin of head at site of *as1*; plate slender with no internal carinae and with posterior elongation not thickened. Marginal carina may be interrupted at site of *as1*. Trabecula present. Antennae sexually monomorphic. Transverse carinae present. Temporal setae *os*, *mts1* and *mts3* macrosetae, *mts3* typically longer than the others. Dorsal head sensilla *s1–4*, *pts*, and *pns* present. Pro- and pterothorax not divided medially; *ppss* on posterior margin of pronotum; *mms* as continuous row on posterior margin of pteronotum. Prosternum present; mesometasternum absent. Metepisterna not sclerotized laterally. Abdomen broad, tergopleurites II–IX+X (male) or II–VIII (female) medially divided, each with rows of macrosetae on posterior margin; anterior seta of tergopleurite II present. Sternal plates variable between species, typically present on at least segments III–VI, generally broader in male than in female; accessory sternal plates present in at least some segments, in males often fused to central sternal plates at least in more posterior segments. At least some thorn-like *sts* present on most of segments II–VI. Basal apodeme slender, completely fused to mesosome; mesosome may be visible as vague plate on dorsal side, if so, never rectangular. Gonopore large, with numerous sclerites, ridges, and in some species with fringed distal extensions; mesosomal setae not visible in more species. Parameres strongly sclerotized, strongly convergent, with *pst1–2* sensilla. Female subgenital plate not reaching vulval margin; vulval margin with 1–2 rows of shorter *vss* and longer *vms*. Subvulval plates present.

For more complete illustrations of this genus, see Gustafsson et al. (2022b).

Host associations. Presently only known from bulbuls (Passeriformes: Pycnonotidae).

Geographical range. Described species only known from Asian hosts (China, Japan, Philippines, Vietnam), but undescribed species from African hosts closely related and probably belong to *Stasiasticopterus*.

Etymology. The genus name is derived from Greek "στασιαστικός" (*stasiastikós*), meaning "factious, seditious". This refers to the fact that the lice in this group are morphologically almost identical to those of *Philopteroides*, but insist on forming their own, presumably convergently evolving, clade. To this is added an ending derived from "-πτερόν" (*pterón*), Greek for "wing", and here used as an indicator of relationship with the genus *Philopterus* Nitzsch, 1818. Gender: masculine.

Included species. See Table 3.

Coronedax Ren, Tian, Grossi, Zou & Gustafsson gen. n.

https://zoobank.org/FAE0F2BC-C224-47BD-983A-55FD49FD36B8

Philopteroides Mey, 2004: 173 in partim.

Type species. *Coronedax longiceps* **new species.**

Diagnosis. Species of *Coronedax* **gen. n.** are almost indistinguishable morphologically from species of *Philopteroides*, but can be separated by the following characters: 1) mesosome distinct, broad (rectangular or of more irregular shape) in *Philopteroides* (Figs 2–5), but reduced to thickening along distal margin of basal apodeme in *Coronedax* (Figs 11, 12); 2) *parameral seta 2* sensillous in *Philopteroides* (Figs 2–5), but as distinct seta that may be almost as long as the paramere in *Coronedax* (Figs 11, 12); 3) sternal plates II–VI each with 1 thorn-like and one normal seta on each side in *Coronedax* (Figs 18, 19), but with more setae (exact numbers variable among species) in *Philopteroides*; 4) vulval margin without or with only few central short setae (*vss*?) and few long, lateral setae (*vms*?) in *Coronedax* (Fig. 23), but with numerous setae of both types in *Philopteroides*.

Description. Small lice of the head louse ecomorph (sensu Johnson et al. 2012). Frons shallowly emarginate, with median margin secondarily sclerotized (Fig. 20). Dorsal preantennal suture completely surrounds dorsal anterior plate but does not reach lateral margin of head at site of *as1*; plate broad with internal carinae and with posterior elongation thickened. Marginal carina uninterrupted laterally. Trabecula present. Antennae sexually monomorphic. Transverse carinae present. Temporal setae *os*, *mts1*

and *mts3* meso- or macrosetae, *mts3* typically longer than the others. Dorsal head sensilla *s1–3* and *pts* present, *pns* absent, *s4* present or absent. Pro- and pterothorax not divided medially (Figs 18, 19); *ppss* on posterior margin of pronotum; *mms* as continuous row on posterior margin of pteronotum. Prosternum present; mesometasternum absent. Metepisterna not sclerotized laterally. Abdomen broad, tergopleurites II–VIII medially divided, each with rows of macrosetae on posterior margin; anterior seta of tergopleurite II present. Sternal plates present on at least segments II–VI; accessory sternal plates present on segments III–VI in female, not present in male but lateral ends of central sternal plates may be modified. Each of sternal plates II–VI with one thorn-like and one normal seta on each side. Basal apodeme slender (Figs 21, 22); mesosome reduced to thickening of distal margin of mesosome; 1–2 *lpmes* on each side of gonopore (Fig. 22), typically small and may be overlooked. Gonopore simple, small. Parameres less densely sclerotized, seemingly fused proximally to basal apodeme; *pst1* sensillum, *pst2* long seta which may be as long as paramere. Female subgenital plate not reaching vulval margin (Fig. 23); vulval margin with 0–2 rows of shorter *vss* (absent in type species) and longer *vms*. Subvulval plates present.

Host associations. All known species from hosts in the Monarchidae.

Geographical range. Known from China, Democratic Republic of the Congo, and Senegal.

Etymology. The genus name is derived from "*corona*", Latin for "crown", and "*edax*", Latin for "devour". This is in reference to the name of the hosts, the Monarchidae, and the fact that these lice live on the hosts' head, essentially eating their crowns. Gender: masculine.

Included species. See Table 3.

Remarks. The male genitalia of *Coronedax terpsiphoni* (Najer & Sychra [in Najer et al.], 2012b) were illustrated in three different views in the original description (*ibid.*, figs 10–12), of which only one (Najer et al. 2012b: fig. 12) is directly comparable to the specie described here. As mentioned by Najer et al. (2012b), the distal male genitalia of this group are easily distorted, and we have here reproduced their fig. 10, to illustrate the variation possible within this genus, depending on preparation. We do not consider the genitalia illustrated by Najer et al. (2012b) to be substantially different from those of *Coronedax longiceps*.

The female genitalia of *C. terpsiphoni* have a small number of short, central setae (here tentatively interpreted as *vss*), which are absent in *C. longiceps*. In an undescribed, but poorly preserved, species of *Coronedax* we have seen from *Hypothymis azurea* (Boddaert, 1783) there appears to be only one short *vss* on each side (visible only on one side). More species of *Coronedax* need to be examined before the variation in vulval chaetotaxy, and its taxonomic significance, can be explored in more detail.

Coronedax longiceps Ren, Tian, Grossi, Zou & Gustafsson sp. n.

https://zoobank.org/794224B7-CE8B-4581-A03A-3E082A3C268B

Figures 12, 18–24

Type host. *Terpsiphone incei* (Gould, 1852) – Amur paradise flycatcher.

Diagnosis. Morphologically similar to *Coronedax terpsiphoni* (Najer & Sychra [in Najer et al.], 2012b), but can be separated by the following characters: 1) head proportionately longer and narrower in *C. longiceps* than in *C. terpsiphoni* (Figs 24, 25); 2) dorsal anterior plate more slender in *C. longiceps* than in *C. terpsiphoni* (Figs 24, 25); 3) female vulval margin of *C. terpsiphoni* with short *vss*, but these are absent in *C. longiceps* (Fig. 23); 4) male subgenital plate with only 1 macroseta on each side (on segment VII) in *C. longiceps* (Fig. 18), but with 2 macrosetae on each side (on segments VII–VIII) in *C. terpsiphoni*.

Possibly, head sensillum *s4* is absent in *C. terpsiphoni*, but these sensilla are easily overlooked and as no specimen of *C. terpsiphoni* were examined, this cannot be verified; *s4* is present in *C. longiceps*. Differences in the male genitalia between *C. longiceps* and the illustrations of Najer et al. (2012b) (Figs 11, 12) may not be diagnostic as much of the distal genitalia are largely soft, and thus affected by mounting.

Description. Head structure and chaetotaxy as in Fig. 20; head long and slender; dorsal anterior plate slender (Fig. 20); head sensillum *s4* present; *os* much shorter than *mts3*; *mts1* intermediate in length between *os* and *mts3*. Thoracic and abdominal segments and chaetotaxy as in Figs 18, 19. Male abdominal chaetotaxy: *ss* present on segments II–VIII; *tps* present on segments II–VIII (2 on each side on II–VI, 1 on each side on VII–VII); *psps* present on segments III–VII; *aps* absent; *ps* present on segments IV–VIII. Female abdominal chaetotaxy: *ss* present on segments II–VIII; *tps* present on segments II–VIII (1 on each side); *psps* present on segments III–VII; *aps* absent; *ps* present on segments IV–VIII. Central sternal plates present on segments II–VI in both sexes; accessory sternal plates absent in male (but some central sternal plates with modified lateral ends) and present on segments III–VI in female. Each of sternal plates II–VI in both sexes with 1 thorn-like and 1 normal seta on each side; on segments II–V thorn-like setae median to normal setae, but on VI thorn-like setae lateral to normal setae. Basal apodeme slender, not conspicuously thickened laterally, bulging distally (Fig. 21). Mesosome as mainly dorsal thickening of distal mesosome centrally; 2 *lpmes* microsetae visible on each side. Gonopore reduced, extending slightly beyond distal margin of basal apodeme, with slight nodi distally (Fig. 22). Parameres completely fused to basal apodeme proximally, soft and flexible, may be displaced dorsally; *pst1* sensillum, *pst2* distal seta, as
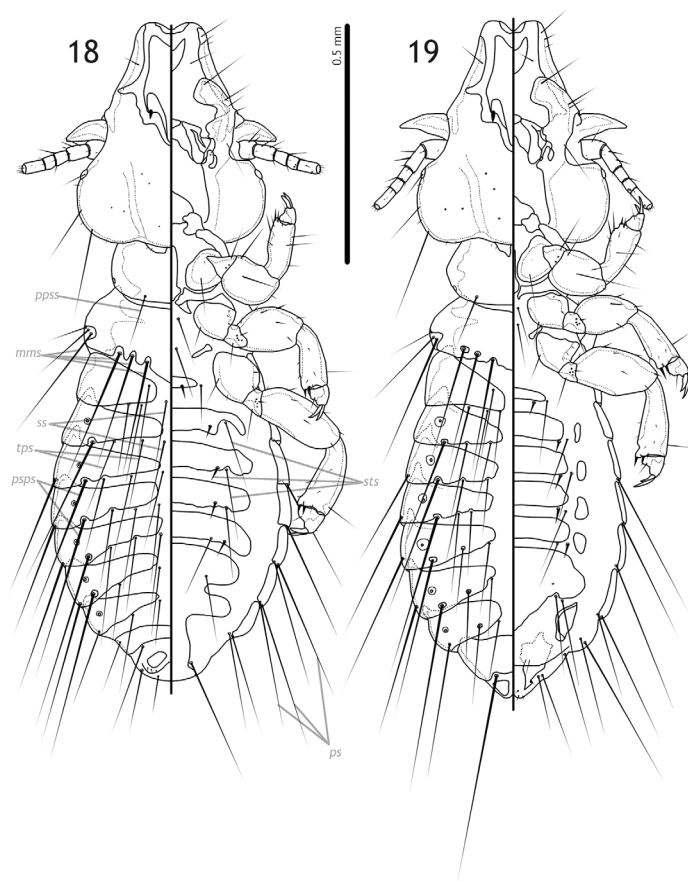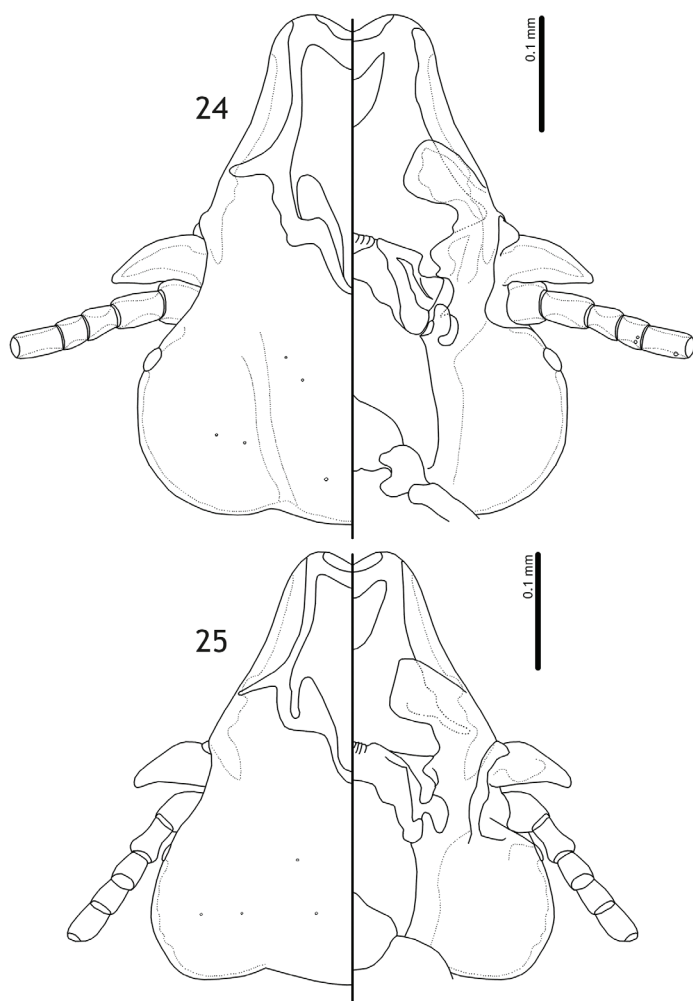
Figures 18, 19. *Coronedax longiceps* **sp. n. 18** male habitus, dorsal and ventral views. **19** female habitus, dorsal and ventral views. — Abbreviations used: *mms* = marginal mesometanotal setae; *ppss* = pronotal post-spiracular seta; *ps* = paratergal setae; *psps* = principal post-spiracular setae; *ss* = sutural setae; *sts* = sternal setae; *tps* = tergal posterior setae.
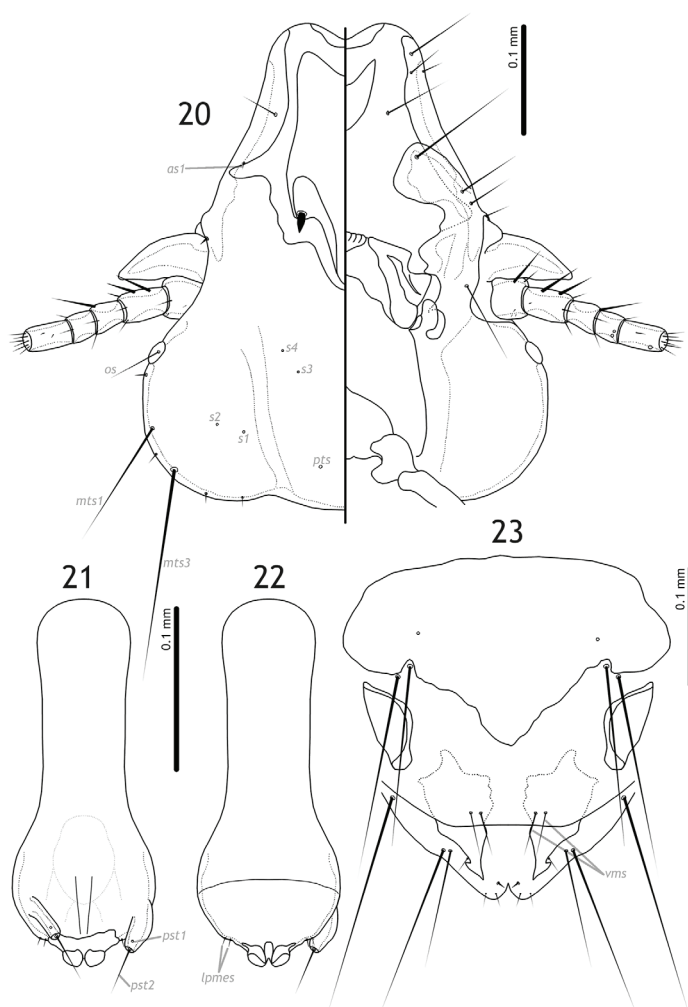
Figures 20–23. *Coronedax longiceps* **sp. n. 20** male head, dorsal and ventral views. **21** male genitalia, dorsal view. **22** male genitalia, ventral view. **23** female subgenital plate, vulval margin, and post-vulval area, ventral view. Male genitalia are illustrated asymmetrically as in holotype specimen, to indicate the "looseness" of the parameres. — Abbreviations used: *as1* = anterior seta 1; *lpmes* = lateral posterior mesosomal seta; *mts1, 3* = marginal temporal setae 1, 3; *os* = ocular seta; *pst1–2* = parameral setae 1–2; *pts* = posttemporal seta; *s1–4* = sensilla 1–4 of dorsal postantennal head; *vms* = vulval marginal setae.

Figures 24, 25. Comparison in shape and proportions of head in species of *Coronedax* **gen. n. 24** male head of *Coronedax longiceps* **sp. n. 25** female head of *Coronedax terpsiphoni* (Najer & Sychra [in Najer et al.], 2012b) (redrawn from original description to same scale as Fig. 24). Setae and some other characters illustrated by Najer et al. (2012b) have been omitted for clarity.

long as paramere. Female subgenital plate with triangular extension distally (Fig. 23). Vulval margin bulging, with 2 *vms* mesosetae on each side. Subvulval plates roughly triangular.

Measurements. Male (n =3, except for TL, where n = 1 and PW where n = 2): TL = 1.26; HL = 0.39–0.41; HW = 0.35–0.37; PRW = 0.22–0.26; PTW = 0.31–0.35; AW = 0.41–0.48. Female (n = 1, total length not measured due to breakage in pterothorax): HL = 0.42; HW = 0.37; PRW = 0.25; PTW = 0.30; AW = 0.41.

Etymology. Specific name derived from "*longus*", Latin for "long", and "*-ceps*", Latin for "-headed", referring to the relatively long head of this species compared to the only other known member of the genus.

Type specimens. Holotype ♂, CHINA: Yunnan Province, Banna Prefecture, Mengla County, primary forest near Xinhuikuan and Manpa villages, 6 Jun. 2013, coll. D. Su & Y. Zhao, bird ID: J1124, louse ID: GD-PHTH-901 (IZGAS). **Paratypes:** 2♂, 1♀, same data as holotype, louse ID: GD-PHTH-00899–900, 902 (IZGAS).

5. Discussion

5.1. The *Philopterus*-complex

Species and genus delimitation in the *Philopterus*-complex are notoriously difficult. For instance, whereas patterns of abdominal chaetotaxy can often be used to delimit taxa in the *Brueelia*-complex (e.g., Gustafsson & Bush 2017), *Philopterus*-complex lice almost uniformly have setal rows on all tergopleurites and sternal plates (e.g., Mey 2004; Najer et al. 2016, 2020b; Gustafsson et al. 2022a). The numbers of setae in these rows may be different between species, but often constitute ranges with individual variations that may overlap between species; at the genus level, few useful chaetotaxy characters are known. Similar homogeneity can be found in many other character sets, such as the overall structure of the head and the female genitalia.

Other morphological elements, such as the male genitalia, are often much reduced, so that characters can be difficult to compare. For instance, reduction in parameres is found both in *Mayriphilopterus* (see Mey 2004)

and *Philopteroides* s. lat (see Tandan 1955; Najer et al. 2016; Figs 6–8), and possibly elsewhere. Similarly, the female subgenital plate is almost uniformly reduced to the same general shape in many genera of the *Philopterus*-complex, and female vulval chaetotaxy is both homogeneous and reduced compare to that of many other louse groups (see e.g., Gustafsson & Bush 2017; Gustafsson et al. 2020).

Moreover, several characters seem to have evolved convergently several times. For instance, the secondary sclerotization of the hyaline margin is known from several distantly related genera (cf. Mey 2004 with Kolencik et al. 2022) and may even occur on subgroups within genera that otherwise lack this character (e.g., *Philopterus* species on swallows; Gustafsson et al. 2022a). Several distantly related groups in the phylogeny of Kolencik et al. (2022) also have similar preantennal structure (Mey 2004); notably, *Mayriphilopterus* Mey, 2004, was placed as a sister group to the rest of the *Philopterus*-complex in the phylogeny of Kolencik et al. (2022) as well as in our phylogeny (Fig. 1), but the preantennal structure in this genus is the same as in *Philopterus*, which is deeply nested inside the complex (Mey 2004; Kolencik et al. 2022).

In parallel to this, published descriptions and illustrations of many species in the *Philopterus*-complex are often inadequate to establish which genus they belong to. For instance, of the eleven species of *Philopterus* s. lat described by Złotorzycka (1964), rough outlines of the male genitalia are given only for four, none of which are detailed enough to be identifiable or placeable in the classification of Mey (2004). Only the dorsal anterior plate is illustrated for all species, but the utility of this character for species delimitation has never been evaluated; moreover, its utility for genus-level classification is probably very limited. Poorly described species like these constitute a large part of the species in the *Philopterus*-complex, making assessments of taxon limits difficult without reexamining type specimens.

Any investigation into taxon limits in the *Philopterus*-complex thus must be seen against a background of very low morphological variation in some characters, and convergence or reduction in others. Even if potentially distinct morphological characters are found in a specimen, it is often difficult to assess what this specimen may be related to, due to the lack of adequate comparative illustrations (see Gustafsson et al. 2022a). More than for many other recently revised groups of Ischnocera, the classification of the *Philopterus*-complex may benefit from the use of genetic data to supplement what few morphological characters can be found.

Here, we have detailed one such investigation, in which genetic and morphological characters come together to separate three distinct group within the *Philopterus*-complex. These three groups are "cryptic" in the sense that most morphological characters except the male genitalia are either homogeneous (e.g., most chaetotaxy), reduced (e.g., female subgenital plate, some elements of the male genitalia), or seemingly convergent (e.g., sclerotization of frons, preantennal structure) in all three groups. Due to the limited number of species of each genus available

for analysis, and the lack of sequence data for most described species, the placement of many species is uncertain, and the variation in e.g., the parameres within some groups is unknown (e.g., the lack of parameres in some *Philopteroides*; Figs 6–8). It is not clear whether females of these groups can at all be separated, depending on where e.g., *Philopteroides beckeri* and *Ph. pilgrimi* are placed (see above).

Moreover, species within some of these genera are remarkably homogeneous. Ren et al. (2023) showed that specimens they considered congeneric in some cases belonged to several distinct genetic clades, and the new species described here, *Coronedax longiceps*, can be separated from the only other known species in the genus by a range of morphological characters, each of which is rather minor when seen in isolation. Genetic data for *C. terpsiphoni* has not been published, but genetic data from other African members of this group, previously identified as morphologically close to *C. terpsiphoni* (Light et al. 2016), is distinct. It seems likely that other members of these three genera, and of the *Philopterus*-complex as a whole, will be similarly homogeneous morphologically, but clearly separable genetically. This echoes the findings in several other studies on various groups of lice, where morphologically homogeneous specimens have been separated by long branches, and sometimes even been paraphyletic (e.g., Johnson et al. 2003, 2021; Gustafsson & Olsson 2012; Martinů et al. 2015; Escalante et al. 2016).

5.2. Identity of *Philopteroides* s. str.

It should be noted that the type species of *Philopteroides* has not been examined genetically, and the voucher specimens of the sequences published by Kolencik et al. (2022) have not been examined by us. We have previously examined *Philopteroides* morpho-group specimens from over two dozen species of honeyeaters (DRG, unpublished data), which have all belonged to one of three morpho-types with regards to the male genitalia (Figs 26–28). The first morphotype (Fig. 26) is the same, or close to, that of the type species of *Philopteroides*, but notably with reduced parameres compared to described species (Figs 2–5). The second morphotype (Fig. 27) resembles the paramere-less group within *Philopteroides* (Figs 6–8) but apparently have stout lateral setae instead of parameres; it is not clear whether these setae represent *lpmes* or *pst2*, or some other seta, nor if parameres are actually present but much reduced in length. The third morpho-group (Fig. 28) is without parameres and lateral setae, but resemble other species of *Philopteroides* as defined here regarding the overall shape of the genitalia (e.g., Fig. 8).

There thus appears to be a wide diversity of *Philopteroides* species from honeyeaters, almost none of which are described. The only described species, *Philopteroides mitsusui* (Uchida, 1948), is poorly known, and its genitalia were not illustrated or described by Uchida (1948). All specimens we have examined fall into the variation of what we here consider *Philopteroides*, and seem to
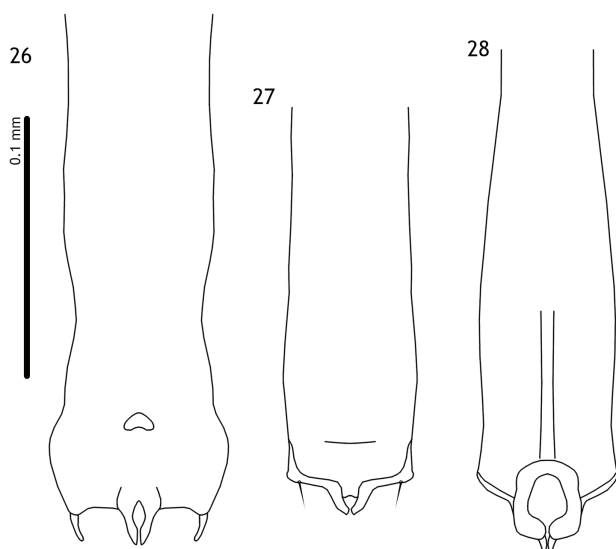
Figures 26–28. Male genitalia (ventral view) from three undescribed species of *Philopteroides* Mey, 2004 (sensu lato), parasitizing honeyeaters. **26** *Philopteroides* sp. ex *Anthochaera carunculata* (Shaw, 1790). **27** *Philopteroides* sp. ex *Gavicalis virescens* (Vieillot, 1817. **28** *Philopteroides* sp. ex *Melithreptus lunulatus* (Vieillot, 1802). Note that some detail may be missing in these figures compared to the actual specimens, as they were drawn at a lower magnification and at a time when the illustrator (DRG) was less experienced in both louse morphology and illustration. They are included here for comparative purposes only, and are not intended to be useful for identification. All figures at same scale.

straddle the variation among the known species with regards to the presence or absence of parameres. A more extensive examination of lice on honeyeaters is needed to establish whether they form a monophyletic group, as implied by the genetic data (Kolencik et al. 2022; Fig. 1). By comparison, the lice in the *Brueelia*-complex parasitizing honeyeaters are known to fall into at least three genera (Valim & Palma 2015; Mey 2017).

Here, we tentatively consider the specimens in Clade I (Fig. 1) to represent *Philopteroides* s. str. However, more studies are needed to establish whether this is the case, or if these specimens actually represent a fourth, unnamed, genus. In any case, based on morphology of the male genitalia, the type species of *Philopteroides* does not fall within either of the genera described as new here.

5.3. Relationships within the *Philopteroides* morpho-group

The relationships between the three genera in the *Philopteroides* morpho-group are ambiguous. *Philopteroides* has been divided into two species groups, the "*mitsusui*" and "*beckeri*" groups (Valim & Palma 2013), which differ mainly by the shape of the head and preantennal area; the *mitsusui* species group includes the type species of *Philopteroides*. Valim & Palma (2013) placed all species except two in the *mitsutsui* species group, and Najer et al. (2016) added two more species supposedly

belonging to the *beckeri* species group; Gustafsson et al. (2022b) stated that all the species they treated belonged to the *mitsusuit* species-group. These placements of species described after 2013 were based on the perceived differences in head shape between the *mitsusui* and *beckeri* species-groups. Here, the *mitsusui* species-group likely falls within the genus *Philopteroides* (see above), but the placement of the *beckeri* species group is unknown.

Light et al. (2016) included specimens here placed in both *Stasiasticopterus* and *Coronedax*, which formed a monophyletic group in their *COI+EF-1α* dataset; however, no other *Philopterus*-complex species were included, and the relationship between these two groups could thus not be evaluated. Similarly, Najer et al. (2020a) included only specimens of what is here called *Stasiasticopterus*, which all formed a single clade. In the more taxon-rich phylogeny of Kolencik et al. (2022) recovered two clades of lice in the *Philopteroides* morpho-group, which they identified as representing the *mitsusui* and *beckeri* species-groups. The majority of the clade they identified as the *beckeri* species-group is the one here described as *Stasiasticopterus*, which may not represent the *beckeri* species-group, as the species from bulbuls lack the morphological characters associated with this group (cf. Mey 2004; Valim & Palma 2013; Gustafsson et al. 2022b). Possibly, the undescribed species from platysteirid and turdid hosts placed as sister to *Stasiasticopterus* (Fig. 1; Kolencik et al. 2022) may represent the *beckeri* species group, but the structure of the male genitalia in *Ph. beckeri* (Fig. 10) may be more similar to those of *Coronedax* (Figs 11, 12).

The relative position of the three genera in the *Philopteroides* morpho-group has varied between analyses (Figs 29–32). In the phylogenies of Kolencik et al. (2022; *COI*, *EF-1α*) and Ren et al. (2023; *COI*, *hyp*, *TMEDE6*) the groups here called *Philopteroides* and *Coronedax* were placed as sisters, with *Stasiasticopterus* more distantly related to both. Here, based on *COI* and *EF-1α* but with a denser taxon sampling in these groups (particularly in *Stasiasticopterus*), we find no statistical support for the placement of any of the three genera in the *Philopteroides* morpho-group within the *Philopterus*-complex (Fig. 1). More molecular markers are needed to resolve the deeper nodes of the *Philopterus*-complex tree. Moreover, more morphological data is needed to evaluate whether the specimens marked "*Philopteroides*?" in Fig. 1 belong to *Stasiasticopterus* or *Coronedax*, respectively, or if the morphological differences are sufficient to consider these separate, undescribed, genera.

5.4. Distribution patterns

Both new genera proposed are here considered to be limited to one host family each: Monarchidae for *Coronedax*, and Pycnonotidae for *Stasiasticopterus*. This parallels the known distribution of some other *Philopterus*-complex genera (Table 4). As more species of the *Philopteroides* morpho-group are described and examined in detail, it seems likely that further cases of host family-specific lice in this group will be discovered. This would also paral-
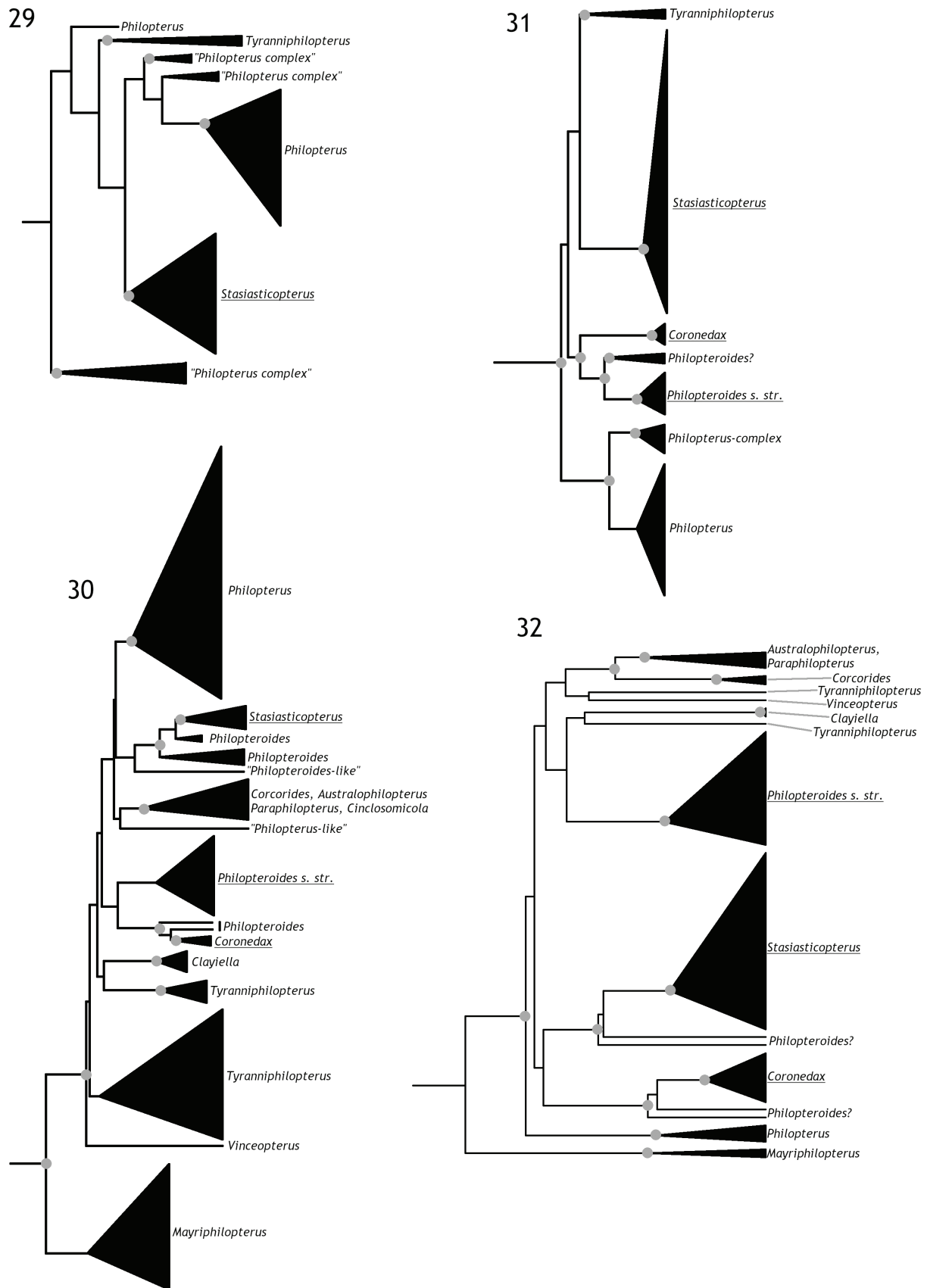
Figures 29–32. Comparison between the phylogenetic structure of the *Philopterus*-complex from four studies. Outgroups have been removed for simplicity. The names *Coronedax* **gen. n.** and *Stasiasticopterus* **gen. n.** were not used by previous studies but are used here to aid in comparisons; other genus-level taxonomy follows the original publications, except that some groups are combined together for simplicity, as they were recovered as paraphyletic in the respective phylogenies. **29** simplified version of fig. 1 of Najer et al. (2020a). **30** simplified version of fig. 1 of Kolencik et al. (2022). **31** simplified version of fig. 3 of Ren et al. (2023). **32** simplified version of Fig. 1 of the present study. Nodes that received >0.95 support are indicated by grey circles. The three genera in the *Philopteroides* morpho-group are underlined, where present.

Table 4. Host association patterns of the *Philopterus*-complex louse genera parasitizing passeriform hosts, including undescribed species included in the phylogeny of Kolencik et al. (2022). Data derived from Mey (2004), Najer et al. (2012a,b, 2016, 2020a), Valim & Palma (2013), Gustafsson & Bush (2014), Gustafsson et al. (2019a, 2022a,b), Kolencik et al. (2022), and the present study. Host families placed in square parentheses are placed close to the respective genera (Kolencik et al. 2022; Fig. 1), but have not been examined morphologically, and are placed tentatively. Host families indicated by a "(?)" after represent the two species here considered incerta sedis within the *Philopteroides* morpho-group, and families listed by Mey (2004) from which no species of *Philopteroides* have been described. Specimens identified as "*Philopterus*-like" or "*Philopteroides*-like" by Kolencik et al. (2022) are not included.

Louse genus	Known host families	Possible host families
Australophilopterus Mey, 2004 [1]	Cracticidae	[Ptilonorhynchidae?]
Cincloecus Eichler, 1951	Cinclidae	
Cinclosomicola Mey, 2004	Cinclosomatidae	
Corcorides Mey, 2004	Corcoracidae	
Coronedax **new genus**	Monarchidae	[Petroicidae?]
Paraphilopterus Mey, 2004	Cnemophilidae, Corcoracidae, Ptilonorhynchidae	
Philopteroides Mey, 2004	Acanthisittidae, Climacteridae, Meliphagidae, Nectariniidae, Paramythiidae, Petroicidae, Rhipiduridae	Acanthizidae (?), Ifritidae (?), Melampittidae (?), Pachycephalidae (?), Platysteiridae (?)
Philopterus Nitzsch, 1818 [2]	Over 30 known; see Mey (2004); Najer et al. (2020b); Gustafsson et al. (2022a); Kolencik et al. (2022)	
Stasiasticopterus **new genus**	Pycnonotidae	[Bernieridae?] [Platysteiridae?] [Turdidae?]
Tritrabeculus Uchida, 1948	Campephagidae	
Tyranniphilopterus Mey, 2004 [1]	Cotingidae, Parulidae, Pipridae, Thamnophilidae, Tityridae, Tyrannidae	
[1] These genera were found to be paraphyletic by Kolencik et al. (2022) and the present study.		
[2] This genus was found to be paraphyletic by Najer et al. (2020a), and consists of two deeply separated sister-clades by Kolencik et al. (2022).		

lel the situation in the *Brueelia*-complex, which is distributed across more or less the same bird groups as the *Philopterus*-complex, and which comprises a mixture of host family specialists and more widely distributed genera (Gustafsson & Bush 2017).

Notably, in both the *Brueelia*- and *Philopterus*-complexes there appear to be a concentration of more specialist genera occurring on hosts that are limited to the Australo-Papuan and Indo-Malayan regions, but a lowered diversity in the Neotropics and in more boreal areas (cf. Mey 2004; Gustafsson & Bush 2017; Table 4). This likely mirrors the extensive early radiation of passeriform birds in Gondwana and what is today the Australo-Papuan region (e.g., Barker et al. 2004; Jønsson et al. 2008, 2016; Aggerbeck et al. 2014). The estimated ages for the radiation out of this area for both the Passerida and the Corvides (~40–45 Mya; Barker et al. 2004; Jønsson & Fjeldså 2006) predates the estimated age of the *Brueelia*-complex (~30 Mya; Johnson et al. 2018), but no estimation of the age of the *Philopterus*-complex has been published. While estimating the radiation dates of ischnoceran lice reliably is difficult, due to the lack of fossil evidence, it is possible that much of the currently known diversity of ischnoceran lice on passeriform hosts post-dates the time when these hosts left their inferred region of origin. The more widely distributed radiations within each louse complex may thus represent the lice that were present on the host lineages that left the Australo-Papuan region, whereas the more specialist louse genera may represent those that parasitized hosts that remained behind. Presumably, as more species of *Philopterus*-complex lice are described, these patterns may become clearer.

Several of the host families of the *Philopteroides* morpho-group genera are distributed across a large portion of the Old World tropics, from Australia through South Asia to much of Africa (Clements et al. 2021). The number of species for which DNA sequences or morphological data are available is still very limited; for instance, with the exception of lice from sunbirds and allies (Nectariniidae), the known geographical distribution of *Philopteroides* s. str. as defined here is largely limited to the Australo-Papuan region (Table 3). Presumably this will change as more species are described, as some host families from which *Philopteroides* s. str. are known occur more widely (e.g., Rhipiduridae).

However, even among the few species that are included in our analyses, a few potentially significant patterns can be seen. For instance, bulbuls are divided into an African and a largely Asian clade, but members of the latter clade have subsequently recolonized Africa several times (Shakya & Sheldon 2017). Ren et al. (2023), using only Asian louse species and different genetic markers, found some louse clades to contain only specimens parasitizing one host radiation, but at least one clade contained lice from a mixture of host radiations; moreover, although not all relationships between their four clades were resolved, there was no indication of a basal division following the division in the host phylogeny. In our analysis, *Stasiasticopterus* is divided into three clades, but the relationship between these is unresolved. Two clades (S2 and S3 in Fig. 1) comprise only specimens from Africa, which are placed in the "Africa" clade of Shakya & Sheldon (2017). The third clade (S1 in Fig. 1) contains all species of *Stasiasticopterus* from Asian hosts, as well as a single spec-

imen from an African host; notably, this African host is one of those that have colonized Africa from Asia, and is nested deeply inside the "Asia" clade of Shakya & Sheldon (2017).

Fewer specimens of *Coronedax* are available for analysis. However, Asian and African species of *Coronedax* appear to be separated into different clades, despite both clades containing specimens parasitizing *Terpsiphone* spp. All the hosts of the included species of *Coronedax* are in Clade A of Monarchidae (sensu Andersen et al. 2015); the host genera of these species are sister taxa (Fabre et al. 2012; Andersen et al. 2015). The discrepancy between host associations and louse phylogeny may be an artefact of the few species included, but may also be a result of the complicated biogeographical history of these flycatchers (Fabre et al. 2012). The sister group of *Coronedax* as defined here is also from monarch flycatchers, but specimens from a petroicid host is also closely related to these, suggesting that the true host range of *Coronedax* may be wider than suggested here.

The partial overlap in available gene sequences between different data sets makes reconciliation of patterns in different studies difficult. However, at least in *Coronedax* and *Stasiasticopterus*, it would appear that host biogeography may have helped shape the radiation patterns in lice. Biogeographical patterns are less obvious in *Philopteroides* s. str., as most specimens included in our analysis are derived from the Australo-Papuan region. The few samples from outside this region in our analysis are all from nectariniid hosts from China and Africa, but the exact placement of these specimens within *Philopteroides* received little support.

5.5. Conclusions

Based on published phylogenies (Najer et al. 2020a; Kolencik et al. 2022; Ren et al. 2023; Fig. 1), a substantial amount of genus-level diversity remains to be discovered within the *Philopterus*-complex. Several genera appear to be paraphyletic, and even within presumably monophyletic genera, significant morphological differences may exist. However, these differences may be limited to single character sets, particularly the male genitalia (Figs. 2–8). This suggests that much of the diversity of the *Philopterus*-complex may be hidden, especially in cases where only females are known. Descriptions of new taxa in this complex should be accompanied by detailed illustrations of dorsal and ventral features of the male genitalia, so that they may be placed accurately in future revisions of the group.

Species-level circumscription and identification may be even more difficult, although detailed illustrations of male genitalia and other characters may help differentiating species (Gustafsson et al. 2022a). In some cases, traditionally illustrated characters such as the head shape, shape of the dorsal anterior plate, and setal counts may be useful, but the utility of these characters on larger scales needs evaluation. Najer et al. (2020b) considered specimens from several different host species conspecific,

even if there was some variation in e.g., the shape of the dorsal anterior plate. Ultimately, at least *COI* sequences may be necessary to supplement morphological data for species descriptions in the *Philopterus*-complex.

6. Conflict of interest

The authors declare no conflict of interest.

7. Acknowledgements

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