



Molecular phylogenetics of the avian feather louse *Philopterus*-complex (Phthiraptera: Philopteridae)

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ABSTRACT

The avian feather louse *Philopterus*-complex (Phthiraptera: Ischnocera: Philopteridae) currently contains 12 genera that have been grouped together because of shared morphological characteristics. Although previously lumped into a single genus (*Philopterus*), more recent morphological treatments have separated the group into several different genera. Here we evaluate the status of these genera using DNA sequence data from 118 ingroup specimens belonging to ten genera in the *Philopterus*-complex: *Australophilopterus* Mey, 2004, *Cinclosomicola* Mey 2004, *Clayiella* Eichler, 1940, *Corcorides* Mey, 2004, *Mayriphilopterus* Mey, 2004, *Paraphilopterus* Mey 2004, *Philopteroides* Mey 2004, *Philopterus* Nitzsch, 1818, *Tyrannophilopterus* Mey, 2004, and *Vinceopterus* Gustafsson, Lei, Chu, Zou, and Bush, 2019. Our sampling includes 97 new louse-host association records. Our analyses suggest that the genus *Debeauxoecus* Conci, 1941, parasitic on pittas (Aves: Pittidae), is outside of the *Philopterus*-complex, and that there is strong support for the monophyly of a group containing the remaining genera from the complex. Some diverse genera, such as *Philopterus* (*sensu stricto*) and *Mayriphilopterus* are supported as monophyletic, whereas the genera *Australophilopterus*, *Philopteroides*, and *Tyrannophilopterus* are not. The present study is the largest phylogenetic reconstruction of avian lice belonging to the *Philopterus*-complex to date and suggests that further generic revision is needed in the group to integrate molecular and morphological information.

1. Introduction

Avian chewing lice are obligate ectoparasites spending their entire life cycle on the host. They feed on feathers, dead skin, and in some cases blood of the host (Price et al., 2003). Birds have many defense mechanisms to defend themselves against parasitic lice, including preening and scratching (Bush and Clayton, 2018). Avian chewing lice are one of the most ubiquitous parasites on bird species (Price et al., 2003). Although birds are among the most well studied group of organisms in the world in terms of taxonomy and systematics (Jetz et al., 2012; Jarvis et al., 2014; Prum et al., 2016), their ectoparasitic lice are largely lacking in comprehensive systematic studies due primarily to the absence of taxonomists specializing on lice, and the difficulty of obtaining specimens for phylogenetics. Phylogenetic trees of avian lice have not only resolved issues with their systematics and taxonomy

(Cruickshank et al., 2001; Johnson et al., 2001; Bueter et al., 2009; Bush et al., 2016; Boyd et al., 2017; Kolencik et al., 2017), but have also helped to increase our understanding of coevolutionary histories (Clayton and Johnson, 2003; Johnson et al., 2018; Sweet et al., 2018; Catanach et al., 2019). These trees also shed light on the ecology, evolution, and behavior of both lice and birds (Johnson et al., 2011; Sweet and Johnson, 2018; Bush et al., 2019), and aided in understanding ecological speciation (Villa et al., 2019) and repeated adaptive diversification (Johnson et al., 2012). There are approximately 4,000 known species of chewing lice (Price et al., 2003), but there are likely many species and genera yet to be described (Mey, 2003, 2004; Valim and Weckstein, 2013).

The largest chewing louse suborder Ischnocera contains ~ 3,000 known species, with most belonging to the family Philopteridae (Price et al., 2003). In the last few decades, taxonomy of this family has

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undergone many changes that resulted in the description of groups of genera characterized as “complexes” (Clay, 1958; Johnson et al., 2002; Mey, 2004; Gustafsson and Bush, 2017). One of these large generic complexes was originally classified as the single highly diverse and globally distributed genus *Philopterus* (Price et al., 2003). *Philopterus* is associated with multiple avian host orders, including Passeriformes, Coraciiformes, Leptosomiformes, Piciformes (Mey, 2004; Valim and Palma, 2013), Galbuliformes (Valim and Linardi, 2007; Kuabara, 2019), Trogoniformes (Gustafsson et al., 2019), and Bucerotiformes (Tendeiro, 1962; Takano et al., 2019). Mey (2004) analyzed morphological variation in the complex and found that particular morphotypes matched closely with host associations, and therefore, he proposed splitting this diverse genus into 11 genera that were in general specific to particular avian host groups and morphologically unique. However, given sufficient shared morphological similarities, Mey (2004) considered these genera as part of a single *Philopterus*-complex (Mey, 2004). The morphological features that unite all members of the *Philopterus*-complex include the presence of well-developed trabeculae, the presence of preconal (pcs) and preantennal setae (pas), and antenna with the scapus (base) having a pair of curved setae (Fig. 1 in Mey, 2004: 153). Many of these genera are specific to particular host groups or geographic regions (Mey, 2004). All species within this complex are thought to be relatively sedentary and are morphologically specialized for living on the head and neck of their hosts (Clay, 1949; Mey, 2004; Valim and Palma, 2013).

Mey (2004) divided the *Philopterus*-complex into five groups (A-E) on the basis of the postembryonic development of their anterior head structures (clypeal and ventral carina). Herein, Mey (2004) characterized the groups as follows: A) *Corcorides* Mey, 2004; B) *Philopterus* Nitzsch, 1818; C) *Mayrphilopterus* Mey, 2004; D) a group comprised of the genera *Australphilopterus* Mey, 2004, *Cinclosomicola* Mey, 2004, *Paraphilopterus* Mey, 2004, *Philopteroides* Mey, 2004, *Trirabeculus* Uchida, 1948, and *Tyranniphilopterus* Mey, 2004; and E) a group comprised of *Cincloecus* Eichler, 1951 and *Clayella* Eichler, 1940.

Since Mey's (2004) revision, there have been additional changes to the taxonomy of the *Philopterus*-complex, including descriptions of several new species (Valim, 2006; Cicchino, 2007; Najer et al., 2012a,b; Valim and Palma, 2013; Gustafsson and Bush, 2014; Najer et al., 2016), and one new genus *Vinceopterus* Gustafsson, Lei, Chu, Zou, and Bush, 2019 (Gustafsson et al., 2019). However, the phylogenetic relationship of these genera remains uncertain, and therefore, the status of various genera or species-groups is questionable. For example, the taxonomic status of the genus *Debeauxoecus* Conci, 1941, which had previously been synonymized with *Philopterus* (Price et al., 2003) and Valim and Palma (2015) later suggested that this genus should be recognized as a separate genus and included it as a member of the *Philopterus*-complex. In another taxonomic study of a specific *Philopterus*-complex member, in this case the genus *Philopteroides*, Najer et al. (2016) suggested that “*beckeri* species-group may prove to be artificial after more species are discovered and described” due to the morphological variation found among members of this group (e.g. the larger size of *Philopteroides gigas* Najer, Gustafsson, and Sychra, 2016 as compared to other members of this group).

Based on these recent morphological studies, it is clear that the *Philopterus*-complex contains more genera and species with broader geographic and host range than previously thought. Although there have been several taxonomic revisions at both the higher level and species level for the *Philopterus*-complex, this group has received much less attention from the standpoint of molecular phylogenetic data. The only prior molecular phylogenetic study (Najer et al., 2021) had limited taxonomic sampling, including samples of only three genera and 20 species from this complex. Thus, to understand the composition and status of genera within the *Philopterus*-complex, DNA sequence data with comprehensive taxonomic sampling would be an important advance. Here we reconstruct the phylogeny of ten genera and 118 specimens belonging to the *Philopterus*-complex and three specimens from the enigmatic genus *Debeauxoecus*, using mitochondrial and nuclear gene

sequences. We use this phylogeny to clarify the phylogenetic relationships within this group and evaluate the generic limits based on generic monophyly. We further examine these complexes in terms of host relationships and geographic distributions to build a comprehensive picture of the evolutionary history of lice in the *Philopterus*-complex.

2. Materials and methods

2.1. Samples

We examined a total of 118 specimens belonging to ten genera of the *Philopterus*-complex and additional three specimens from genus *Debeauxoecus*. These specimens were collected from 112 avian host species from 40 bird families, 14 countries, and 5 continents (Table S1). For avian host taxonomy we used the IOC Bird World List v10.1 (Gill et al., 2020). The methods for louse collection follow those from Bush et al. (2016), using either ethyl acetate fumigation for euthanized bird specimens or dusting with pyrethrum powder for live birds (Clayton and Drown, 2001; Bueter et al., 2009). Samples were stored in Eppendorf tubes filled with 95% ethanol and stored at -80°C in an ultracold freezer. We selected representatives of seven genera as outgroups (Table S1) based on prior studies that indicate their close relationship to the *Philopterus*-complex (Cruickshank et al., 2001; Johnson et al., 2018; de Moya et al., 2019).

2.2. DNA extraction and sequencing

DNA extraction protocol follows Bush et al (2016), using either the Qiagen DNeasy micro-kit (Valencia, California, USA) or the Qiagen DNeasy tissue kit (Valencia, California, USA). Following the extraction, each individual louse specimen was mounted on microscope slides using Canada Balsam method described by Palma (1978). Price et al. (2003) or other subsequent publications on genera from the *Philopterus*-complex were used for genus or species level identifications of slide mounted specimens. 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 factor 1- α (EF-1 α , 347 bp), which are both coding sequences. The PCR amplification protocols for both loci follow those in 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-1 α . Amplifications were then purified as described in Bueter et al. (2009). Purified products were cycle-sequenced using ABI Big Dye 3.1 kit (Applied Biosystems, Foster City, California) with the same primers used during amplification (Bueter et al., 2009). Reactions were cleaned with an ethanol-EDTA precipitation and resuspended in Hi-Di formamide and then run on an ABI Prism 3730 DNA sequencer (Applied Biosystems). Forward and reverse sequences were reconciled and edited, and primers removed using the software Sequencher v4.5 (Genecodes CO., Ann Arbor, Michigan). The final consensus sequences were aligned in SeaView v4.7 (Gouy et al., 2010) using clustal omega (Sievers et al., 2011) and verified by eye, and then both fragments were concatenated resulting in 729 bp alignment length.

2.3. Phylogenetic reconstruction

To find the partitioning scheme with the best fit model of molecular evolution, we used PartitionFinder v.2.1.1 (Lanfear et al., 2017). This process accounts for variation among sites due to differences in the rate of evolution by selecting appropriate models of molecular evolution for partitions of the alignment with similar evolutionary histories. We ran PartitionFinder (PF) using the following settings: branch lengths linked, testing all-models using the AICc model selection, and we tested models for each locus and codon position.

We used two different approaches for phylogenetic reconstruction. First, we conducted a maximum likelihood (ML) analysis using RAXML

v8.2 (random accelerated maximum likelihood; Stamatakis, 2014) using GTR + G model and a rapid bootstrapping method with 1,000 bootstraps. We conducted Bayesian analysis (BA) MrBayes v3.2 (Ronquist et al., 2012) using five partitions with four different models (GTR + G: Subset1 [1–379\3]; GTR + I + G: Subset2 [2–379\3] and Subset3 [3–379\3]; SYM + I + G: Subset4 [382–729\3, 380–729\3]; and HKY + I + G: Subset5 [381–729\3]), and two parallel runs for 20 million generations with four Markov chains and sampling in every 1,000 generations for a total of 20,000 parameter point estimates. We removed 10% of trees as burnin after checking for stationarity and estimating the number of burn-in generations using Tracer v1.7.1 (Rambaut et al., 2018). We visualized all trees in FigTree v1.4.4 (<https://github.com/rambaut/figtree/>) and rooted with the outgroup species *Colipeurus radiatus* (Neumann, 1912).

3. Results

This study reconstructs the largest molecular phylogeny for avian lice in the *Philopterus*-complex to date with data for 121 samples (including 3 samples from the enigmatic genus *Debeauxoecus*) collected from 112 avian host species belonging to 40 avian host families. Our dataset includes 97 new louse-host associations (Table S1) which were previously not reported in Price et al. (2003) or other subsequent publications on genera from the *Philopterus*-complex or genus *Debeauxoecus* (Mey, 2004; Valim, 2006; Cicchino, 2007; Najer et al., 2012a,b, 2016, 2021; Valim and Palma, 2013; Gustafsson and Bush, 2014; Light et al., 2016; Kuabara, 2019). In total, we successfully amplified and sequenced COI from 126 lice and EF-1 α from 122 lice, including outgroup samples. Both ML and BA analysis resulted in phylogenetic trees with very similar topologies, with slightly higher support values from the BA (Fig. 1). Generally, we found a pattern of lower support at the backbone of the tree and higher support for more terminal nodes.

Both phylogenetic analyses supported the monophyly of the *Philopterus*-complex, excluding the genus *Debeauxoecus* (Figs. 1, S1). Both ML bootstrapping and BA posterior probability indicated strong support for several major lineages within this complex and many of these strongly supported clades are found in particular biogeographic regions. Interestingly, the genus *Philopterus* (*sensu stricto*) is found all over the world (Fig. 1) and is the only genus from the *Philopterus*-complex with a worldwide distribution. Moreover, even within the genus *Philopterus* (*sensu stricto*) (Fig. 1, clade B) there are two clades, each mainly corresponding to Old World and New World species. The majority of genera in the *Philopterus*-complex form reciprocally monophyletic clades, including the diverse genera *Philopterus* (*sensu stricto*) and *Mayrhiphlopterus*. However, the recovered topology indicates that the genera *Australophilopterus*, *Philopteroides*, and *Tyranniphilopterus* may be paraphyletic, although some of these relationships are not highly supported. Among taxa currently considered as *Philopteroides*, there are major clades such as the well-recognized *mitsusui* species-group, parts of which are strongly supported. For *Tyranniphilopterus* there are two separate clades rendering this genus paraphyletic, but the basal support for the paraphyly of these clades is weak. One clade is divided into two well-supported sub-clades, one of these found mainly on New World flycatchers (Tyrannidae) and ant-shrikes (Thamnophilidae) and the other found mainly on New World manakins (Pipridae), but also with some species on flycatchers and cotingas (Cotingidae). The second clade of *Tyranniphilopterus*, from New World flycatchers appears to be sister to *Clayiella* from motmots (Momotidae). Lastly, although there are only three specimens from the genus *Australophilopterus* included in our analyses, one species, *Australophilopterus* sp. from *Melloria quoyi* (Lesson and Garnot, 1827), groups together with lice from the avian host genus *Corcorides*, rendering *Australophilopterus* paraphyletic. Another *Australophilopterus* species is sister to the sole representative of the genus *Paraphilopterus*, furthering the complexity of paraphyly for the genus *Australophilopterus*.

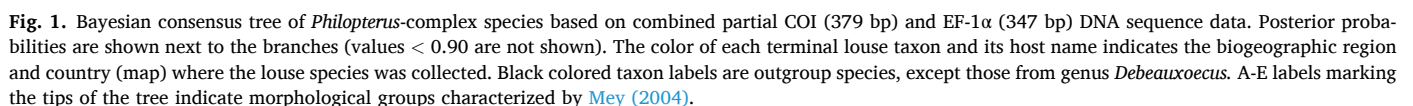
We compared our results with Mey's (2004) concept of five groups in

the *Philopterus*-complex, based on the postembryonic development of the anterior head structures. We found that most of Mey's (2004) groups form clades in the phylogenetic tree with the exception of group D, which is scattered throughout the tree (Fig. 1). Mey (2004) suggested that group A was the earliest diverging lineage, whereas group E was the most recently diverged. Our phylogeny does not necessarily support this hypothesis. The recently described genus *Vinceopterus* (Gustafsson et al., 2019) was not studied by Mey (2004) and thus there was not a hypothesis about the relationship of this taxon to others in the complex. Although *Vinceopterus* is morphologically most similar to *Clayiella* it appears to be phylogenetically distinct from *Clayiella* and is sister to all other *Philopterus*-complex genera except for *Mayrhiphlopterus* (Fig. 1).

4. Discussion

Our study provides extensive taxon sampling for a molecular phylogenetic reconstruction of the *Philopterus*-complex. The phylogenetic analyses provided high support for the more recent nodes and major clades, including well-defined genera (Fig. 1). However, there is poor support for relationships among these genera and for deeper level relationships. This pattern of resolution, with strongly supported major clades and terminal nodes but weakly supported basal relationships, is commonly found in louse phylogenies built with Sanger sequencing data from one or a few gene fragments (Bush et al., 2016; Kolencik et al., 2022). To resolve this issue and clarify the basal nodes, genomic scale data will likely be necessary as has been shown by phylogenomic studies of other louse groups (Boyd et al., 2017; Johnson et al., 2018; Sweet et al., 2018; Johnson et al., 2021). Our analyses recovered the *Philopterus*-complex as a major clade with strong support (posterior probability 97%; Fig. 1). This clade includes all genera previously described to belong to this complex that were available to us (Mey, 2004; Valim and Palma, 2015), except for *Debeauxoecus*.

The description and designation of generic diversity within the *Philopterus*-complex was based mainly on head features and the ontogenetic development of the ventral head carinae (Mey, 2004). Nevertheless, all recently described species in this complex correspond to morphologically distinct characters of the imagoes (Mey, 2004; Valim and Linardi, 2007; Valim and Palma, 2013; Gustafsson and Bush, 2014; Gustafsson et al., 2019; Takano et al., 2019). Price et al. (2003) synonymized *Debeauxoecus*, which occurs on Old World pittas (Pittidae) with the genus *Philopterus*. Later, Valim and Palma (2015) suggested that due to the morphological and genetic similarities between *Debeauxoecus* and other complex members, that it should be included in the *Philopterus*-complex. The genus *Debeauxoecus* has the typical rounded body shape of a head louse and well-developed trabecula (*sensu* Clay, 1946), which would place it morphologically in the *Philopterus*-complex (*sensu* Mey, 2004). From the morphological point of view, *Debeauxoecus* has trabecula and lacks a conus, a combination of characters also found in the genus *Mayrhiphlopterus*. The sclerotization on the hyaline margin in the frontal head region is absent in some genera (e.g. *Mayrhiphlopterus*, *Paraphilopterus*, *Philopterus*) and present in others (e.g. *Clayiella*, *Philopteroides*, *Tyranniphilopterus*). When present, the sclerotization is restricted to the middle of the hyaline margin (not over 1/3 of hyaline margin's entire width), whereas in *Debeauxoecus* this sclerotization is wider (at least 2/3 of hyaline margin). Only the species of *Tyranniphilopterus* that are parasitic on cotingas have such a wide band of sclerotization (Mey, 2004), but in the specimens studied, the sclerotization in *Debeauxoecus* seems to be wider. Based on morphological analyses, Valim and Palma (2015) placed *Debeauxoecus* inside the *Philopterus*-complex. However, in our analysis of the present molecular dataset with extensive taxonomic sampling, *Debeauxoecus* is clearly outside of the *Philopterus*-complex, grouping with other outgroup genera (Fig. 1), despite the morphology of *Debeauxoecus* being typical of a "*Philopterus* louse." Gustafsson et al. (2022) also considered the possibility that *Debeauxoecus* may be a member of the *Penenirmus*-complex. However, our results indicate that *Debeauxoecus* is more closely related to



Craspedorrhynchus von K  ler, 1938 and *Cuculoecus* Ewing, 1926, than to *Penenirmus* Clay & Meinertzhagen, 1938. More sampling of these and related genera is needed to further clarify the phylogenetic position of *Debeauxoecus*.

For genera in the *Philopterus*-complex where we have sampled more than one species, our analysis recovered a tree with the genera *Philopterus* (*sensu stricto*), *Clayiella*, *Corcorides*, and *Mayrphilopterus* as all monophyletic (Fig. 1). The first molecular study of the genus *Mayrphilopterus* found that this genus was monophyletic as in our study, and five of the eight clades in the phylogeny are composed of five unpublished new species (Kuabara, 2019). The specimens not identified to species level in our study agree with the arrangement of the new species proposed by Kuabara (2019). Most of the clades recovered in our study are the same as those found by Kuabara (2019), with differences in the arrangement of the clades with a low branch support.

Our phylogenetic results indicated three cases of paraphyletic genera as currently defined: *Philopteroides*, *Tyranniphilopterus*, and *Australophilopterus* (Fig. 1). While *Philopteroides* is a well-studied genus from a taxonomic perspective (Mey, 2004; Najer et al., 2012a, 2016, 2021; Valim and Palma, 2013), only one of these studies has included molecular data. The molecular phylogenetic study of Najer et al. (2021) that included only six species of *Philopteroides*, found that these species grouped into a single clade, but this study did not include any *Philopteroides* species from Africa or Australasia. We found that *Philopteroides* is potentially paraphyletic and that well supported clades of “*Philopteroides*” were made up of species from the same biogeographic regions, with one clade containing samples exclusively from Africa and another mainly containing Australasian taxa with a few African species. The current taxonomy of *Philopteroides* follows Valim and Palma (2013) who identify two separate species-groups within this genus, based on the shape of the head, which is triangular in the *mitsusui* group and trapezoidal in the *beckeri* group. The results of our phylogenetic analyses support the separation of “*Philopteroides*” into these two species-groups, with support for monophyly of the *mitsusui* species group. In our molecular tree, the *beckeri* species group appeared as the sister taxon of *Philopterus* (*sensu stricto*), but this basal relationship is weakly supported. These morphologically based groups also appear to correspond to the same geographical distribution as identified in the molecular phylogeny, where the species from *beckeri* group occur in the “Old World” (Africa, Madagascar, Malaysia) and most of the species from *mitsusui* group are found in the Australasian region (Australia and Papua New Guinea). It is likely that the genus *Philopteroides* will need to be split into at least two separate genera but additional data that provides higher support at basal nodes is needed to put the generic limits in this group into a stronger phylogenetic context.

The situation is even more complicated for the genus *Tyranniphilopterus*, with one clade grouping with species from genus *Clayiella*, albeit with weak support (Fig. 1, clade E). Interestingly, these two genera do not parasitize closely related hosts. Species of *Tyranniphilopterus* are only found on passerine birds (order Passeriformes), whereas species of *Clayiella* parasitize birds from the order Coraciiformes with one species, *Clayiella dreophila* Mey, 2004, from *Leptosomus discolor* (Hermann, 1783) (order Leptosomiformes). Both major clades of *Tyranniphilopterus* occur on New World Flycatchers (Tyrannidae), and in some cases representatives from both of these clades of *Tyranniphilopterus* are found on the same host genera (e.g. *Mionectes* and *Tolmomyias*).

The third genus in the complex, *Australophilopterus*, appears to be paraphyletic based on our analysis (Fig. 1). There are only two species of *Australophilopterus* described to date and both are from Tasmania: *A. curvicones* Mey, 2004 from *Strepera fuliginosa fuliginosa* (Gould, 1837) and *A. strepericus* Mey, 2004 from *Strepera versicolor arguta* Gould, 1846 (order Passeriformes, family Artamidae). Although we do not have samples of these two species, our study includes data from three new host records from Australia, including a species from *Strepera graculina* (Shaw, 1790). One species from the host *Melloria quoyi* (Lesson and

Garnot, 1827) is sister to a clade containing the two species from the louse genus *Corcorides*, also from Australia. *Corcorides* is highly unusual and distinctive in its morphology. One possibility is that *Corcorides* could be a highly derived morphology within *Australophilopterus*. Furthermore, it appears that *Paraphilopterus* is also embedded within *Australophilopterus*. Thus, there appears to be a clade comprising multiple Australian louse genera and to fully resolve questions regarding generic limits within this clade, additional morphological and molecular data are required from a broader diversity of louse species.

As might be expected, the geographical distribution of the hosts plays an important role in phylogenetic structure of the *Philopterus*-complex. In general, lice from the same regions group together. Only a few exceptions to this rule can be found in the genera *Philopteroides* and *Philopterus* (*sensu stricto*). However, biogeographic region also interacts with host associations in structuring the phylogenetic tree of these parasites. There are several cases where closely related louse species parasitize the same or closely related bird hosts from different regions, breaking down the biogeographic structure of the tree in select places. For example, a species of *Philopterus* from an Australasian drongo (*Dicrurus bracteatus* Gould, 1843) falls within a clade comprised of several African drongos (*Dicrurus* spp.). This pattern is well-known across various louse genera and has led many authors to use host families in louse descriptions (Price et al., 2008; Price and Johnson, 2009; Najer et al., 2012a; Gustafsson and Bush, 2014; Kolencik et al., 2017, 2018). Moreover, biogeographic regions and host families have significant phylogenetic signal for lice of the *Brueelia*-complex (Bush et al., 2016), the genus *Penenirmus* (Johnson et al., 2021), and the genus *Myrsidea* (Kolencik et al., 2022). Thus, our results in combination with prior studies, suggest that both host association and biogeography interact to structure the phylogenetic tree of the *Philopterus*-complex, as well as lice more broadly. This pattern of both host and geographic phylogenetic structure likely results from a mix of codivergence and biogeographically localized host-switching.

CRedit authorship contribution statement

Stanislav Kolencik: Conceptualization, Data curation, Formal analysis, Investigation, Project administration, Validation, Visualization, Writing – original draft, Writing – review & editing. **Kevin P. Johnson:** Conceptualization, Funding acquisition, Investigation, Project administration, Resources, Writing – original draft, Writing – review & editing. **Avery R. Grant:** Formal analysis, Writing – review & editing. **Michel P. Valim:** Data curation, Investigation, Writing – review & editing. **Kamila M.D. Kuabara:** Data curation, Investigation, Writing – review & editing. **Jason D. Weckstein:** Conceptualization, Funding acquisition, Investigation, Resources, Writing – review & editing. **Julie M. Allen:** Conceptualization, Funding acquisition, Project administration, Resources, Supervision, Validation, Writing – original draft, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

The data that support the findings of this study are available in the supplementary material of this article.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ympev.2022.107556>.

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