

## RESEARCH ARTICLE OPEN ACCESS

# Diversity of Chewing Lice (Insecta: Phthiraptera) in the Indo-Burma Biodiversity Hotspot

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## ABSTRACT

The diversity of birds is well documented globally. However, the same attention has generally not been given to their parasites, which comprise many times their diversity. Here, we present data from a large-scale survey of chewing lice found infesting birds in the Indo-Burma biodiversity hotspot of western Yunnan, China. A combination of morphological and phylogenies based on COI barcodes was used to assess the amount of cryptic speciation, host generalists, and variation in host associations. We examined 908 birds, representing 111 species. Overall louse prevalence was 26.3%, and 67 louse species were identified, representing 24 genera, of which 17 species have been previously described. Additionally, 41 new louse/host associations were recorded. Interestingly, *Guimaraesiella impiger* a well-known host generalist found throughout Southeast Asia was only present on three host individuals despite many of its hosts being examined. Also, *Resartor elugeus* previously reported from *Alcippe fratercula yunnanensis* in Yunnan was absent in our sampling despite examining 126 *A. f. yunnanensis*. However, *R. elugeus* was found infesting multiple *Stachyris nigriceps* in our survey. This shift in host association may be due to our sampling sites being at different elevations, but more data needs to be collected before this conclusion can be made. However, we can conclude that this is only a drop in the bucket when it comes the louse diversity of Yunnan. Additionally, the unique mountainous landscape of Yunnan coupled with the bird diversity present has created an environment for the potential of many host switching opportunities.

## 1 | Introduction

Biodiversity lies at the core of biological research, yet our knowledge of diversity often differs substantially between different taxa. For instance, one of the most well-studied groups of organisms is birds, comprising 11,131 described species [1]. Given the ease with which birds can be observed and captured, the multitude of good field guides to the avifauna of almost every part of the world, and the long tradition of ornithological research, this

number is likely to be close to the true global diversity of birds, with increases mainly due to re-evaluation of known data [2]. The number of newly discovered bird species over the last 60 years is correspondingly rather low compared to other organism groups; Brewer [3] listed only 288 new species of birds described between 1960 and 2018. In contrast, 625 species of avian chewing lice (Phthiraptera: Ischnocera, Amblycera) have been described since 2003 [4].

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Although undescribed biodiversity may be found in more boreal and well-studied areas, especially among insects and other invertebrates [5, 6], most unknown species are likely to be found in the tropics [7–10]. This is also true for larger, more obvious taxa such as birds; only 4 of the 288 new bird species listed by Brewer [3] were found in North America or boreal Eurasia. The reasons behind this pattern are complicated [11], and it is not clear if this pattern holds true for many parasitic taxa. Instead, surveys of parasite diversity across large latitudinal scales frequently find the reverse or no pattern in distribution [12–14]. Furthermore, some parasitic taxa show more complicated patterns of diversity [15, 16], and patterns may differ for different parasitic taxa infesting the same host group [17]. In some cases, these reverse patterns are associated with landscape features which may affect, for example, vector availability [18].

In contrast to many other parasitic taxa, chewing lice may be expected to follow the same diversity gradients as their hosts. Chewing lice are permanent ectoparasites, lacking free-living stages and intermediary hosts, and with few exceptions do not transfer between hosts using free-living vectors. As such, chewing louse diversity is less affected by, for example, landscape variation, although ambient humidity [19–21], host habitat size [22, 23], and possibly ambient temperature [24] may influence louse diversity in an area.

Exploring distribution patterns in chewing lice is hampered by the paucity of large-scale surveys of lice in many parts of the world, particularly in the tropics and the Global South. Although recent decades have seen the publication of broad louse surveys from, for example, Vietnam [25, 26], the Congo Basin [27], West Africa [28, 29] and parts of the Neotropics [30], synthesizing these data is hampered by several factors.

Above all, the lack of good descriptions and illustrations of most louse taxa makes morphological identification difficult, especially as most louse genera have never been revised in detail. This means that a large number of lice go unidentified at species level, and makes identification and description of new species difficult. Moreover, our lack of knowledge of inter- and intraspecific morphological variation in many louse taxa, and the traditional assumption of strict host specificity [31], means that conspecific lice parasitizing different host species may go unnoticed. Similarly, as most known louse species and most specimens collected in recent surveys lack associated DNA data, cryptic species may be overlooked. This may be particularly problematic in cases where only nymphs are collected, as data on the morphology of nymphs is rarely published.

Here, we present data from a large-scale survey of chewing lice parasitizing birds in several localities centered on Tongbiguan Township (hereafter: TBG) in western Yunnan, China. These localities are situated near the intersection of three biodiversity hotspots (conservation.org): the Indo-Burman, Himalayan, and Mountains of Southwest China hotspots. As such, the area is home to a diverse bird fauna [32], but a virtually unknown louse fauna. Only 59 louse species are known from Yunnan as a whole [33], but with over 800 recorded bird species across the province [34], and each bird species on average being parasitized by 3–5 louse species, the true louse diversity of Yunnan likely comprises over 1000 species.

In order to assess the amount of cryptic speciation, host generalists, and variation in host associations between different parts of Yunnan, we also provide COI barcode data for one louse individual of each genus from each infested bird. Although lice have traditionally been considered largely host-specific [31], recent DNA-based surveys have revealed that this is often not the case, particularly among lice parasitizing songbirds (Passeriformes) [35–40]. In particular, host participation in mixed-species flocks is suspected to increase the opportunities for host switching among lice that can transfer phoretically between hosts using hippoboscids flies [38, 41]. As most birds caught at TBG are understory songbirds that participate in these flocks, a large proportion of host generalists may be anticipated.

## 2 | Materials and Methods

### 2.1 | Sample Collection

Birds were examined for lice in December 2023, and April and May 2024. Sampling centered around TBG Township (24°36' 44.9"N 97°39'25.0"E, see Supporting Information 1: Table S1). This location belongs to the “tropical and subtropical moist broadleaf forests” biome [42], and has an elevation of ~800–1500 m. The general circumstances of the collection site have been described elsewhere [43]. Additionally, we had one non-forest site; an abandoned building that had been colonized by House Swifts (*Apus nipalensis*) in Tongbiguan, where birds were caught from a third-floor balcony.

At each site birds were caught from sunrise to early afternoon using 15–25 mist nets (3 × 12 m, 30- and 36 mm mesh sizes). Birds were handled in accordance with the protocols approved by the Institutional Animal Care and Use Committee at the University of Florida (permit 201910913 and 202200000607), and the present study was carried out in strict accordance with the Regulation for the Administration of Laboratory Animals (Decree No. 2, State Science and Technology Commission of the People's Republic of China, 14 November 1988). To collect lice each bird was fumigated in a resalable plastic bag with a cotton ball soaked in ethyl acetate. The head of each bird was left out of the bag, which was sealed on either side of the head. Additionally, a binder clip was placed on each side of the head to prevent the bird from pulling its head into the bag. A second bag was placed over the first for birds with more powerful legs that could rip the first bag apart. Each bird was fumigated for 10–20 min depending on its size, during which the bird's head was checked for lice. After fumigation, the bird was held over a tray lined with a white piece of paper and the feathers were gently ruffled. All lice that fell off were collected and stored in 95% ethanol. The fumigation bag was also checked for lice manually. Upon returning to the laboratory, lice were placed in an –80°C freezer until processed.

Birds were identified following *Birds of China* [32], but bird taxonomy follows the Clements Checklist v2024 [44] in cases where they differ. All birds were identified to species except for one individual (J4961) which could only be identified to *Phylloscopus* sp. Many Old World leaf-warblers are morphologically very similar; however, their songs are distinct and easily identifiable [45]. Unfortunately, this bird never called, therefore, we were unable to make a reliable identification to species.

## 2.2 | DNA Extraction and PCR

To facilitate identification of novel louse species one louse of each genus from every infested bird was prepared for DNA extraction by cutting halfway through the pterothorax with a new scalpel blade. DNA was extracted using DNeasy Tissue Kit (Qiagen, Shanghai, China) following the manufacture's protocol with the following changes: lice were incubated in digestion buffer for 24 h at 55°C, after Buffer AL was added samples were incubated at 70°C and only 50 µL of Buffer AE was used for each elution. After the extraction process the louse exoskeleton was retrieved and stored in ethanol to be slide mounted later. Polymerase chain reaction (PCR) were carried out using Cytiva PureTaq Ready-To-Go beads (GE Healthcare, Vienna, Austria) following the manufacture's protocol for 25 µL reactions. We targeted cytochrome oxidase subunit 1 (COI) using the primers L6625 and H7005 [46] and the thermocycle: 94°C for 2 min, 35 cycles (94°C for 30 s, 46°C for 30 s, 72°C for 30 s), 72°C for 7 min. PCR products were screened using gel electrophoresis and those that showed satisfactory bands were sent for sequencing at Tianyi Huiyuan Gene Technology, Co. Ltd. (Guangzhou, China). A complete list of sequenced specimens can be found in Supporting Information 1: Table S1.

## 2.3 | Phylogenetic Analysis

Contigs were assembled using the de novo assemble tool in Genious Prime v.2023.1.2, and the ends were trimmed. Each louse sequence was compared to published sequences in GenBank using the Basic Local Alignment Search Tool (BLAST, <https://blast.ncbi.nlm.nih.gov/Blast.cgi>), and top hits were included in subsequent phylogenetic analyses.

Each suborder of chewing lice (Ischnocera and Amblycera) was analyzed separately. Sequences were aligned using MUSCLE [47] with the default settings and checked manually. Substitution models for each tree were evaluated in MEGA11 [48], with the best models being TN93+G+I for Ischnocera, and GTR+G+I for Amblycera. Trees were constructed using Bayesian analysis in BEAST v2.7.3 [49], with the following settings: the appropriate model, Gamma category count was set to 4, Yule Model was used, Markov chain Monte Carlo (MCMC) was run for  $1 \times 10^8$  generations, and sampled every 1000 trees. The log file produced by BEAST was examined in Tracer [50] to assess MCMC for convergence. TreeAnnotator v2.7.6 was then used for tree integration, the first 10,000 trees (10%) were discarded as burn-in and a maximum clade credibility tree was constructed. Phylogenetic trees were examined using FigTree v.2.7.6 (<https://tree.bio.ed.ac.uk/software/figtree/>) and edited using inkscape v.1.4.2 (<https://inkscape.org>).

To test for the number of operational taxonomic units (OTUs), General Mixed Yule Coalescent (GMYC) was used [51]. Each louse tree generated in BEAST was imported into RStudio 2023.03.1 [52] and the "gmyc" function in the *splits* package was used to determine the number of OTUs [53]. For some data (see below), uncorrected *p*-distances were calculated using MEGA11.

## 2.4 | Morphological Louse Identification

For morphological identification each louse was slide mounted. In preparation for slide mounting the gut was dissected out and the exoskeleton placed in clove oil for 30 min up to 24 h before it was slide mounted in Canada balsam and allowed to cure at room temperature for 30 days. All slides were deposited at the Institute of Zoology, Guangdong Academy of Sciences, Guangzhou, China. Specimens were examined through a Nikon Eclipse Ni microscope (Nikon Corporation, Tokyo, Japan) and identified to genus level and, when possible, species level using the keys, illustrations, and descriptions provided by Clay [54], Rheinwald [55], Ledger [56], Price [57], Price et al. [58, 59], Gustafsson and Bush [60, 61], Gustafsson and Zou [62], and Gustafsson et al. [33, 63–72].

## 2.5 | Further Investigation of *Menacanthus*

Based on a combination of genetic and morphological identification many of the *Menacanthus* specimens were identified as *Menacanthus eurysternus* [73]; however, during the OTU analysis these specimens were separated into multiple clades. In order to get a clearer picture into the genetic relationships among these specimens we made another tree containing only *Menacanthus* samples. In addition to our samples, we included samples from GenBank specifically, all sequences identified as *Menacanthus eurysternus*, and two sequences of every named *Menacanthus* species. A phylogenetic tree was constructed following the same method as above using the model TN93+G+I.

## 3 | Results

A total of 908 birds were examined for chewing lice, representing 7 orders, 34 families, and 111 bird species. The four most caught bird species were: *Alcippe fratercula yunnanensis* ( $n = 125$ ), *Leiothrix argentauris* ( $n = 123$ ), *Stachyris nigriceps* ( $n = 49$ ), and *Schoeniparus dubius* ( $n = 48$ ). Of the caught birds, 47 bird species representing 3 orders, and 24 families were never found to be infested with chewing lice (Supporting Information 2: Table S2).

Louse specimens were morphologically identified to species when possible, using published descriptions and identification keys (see above). However, for taxa where detailed illustrations and descriptions are lacking, or where the actual diversity is much higher than the described diversity, we relied on genetic characteristics, including BLAST searches and OTU analyses. Each OTU found was considered its own species unless otherwise stated. Genetic sequences were successfully amplified from all lice except one specimen, a *Myrsidea* (J4858-1) from *Brachypteryx cruralis*. For GenBank accession numbers see Supporting Information 1: Table S1.

The overall prevalence of chewing lice was 23.3%, and a total of at least 67 chewing louse species were collected, when *Menacanthus eurysternus* is treated as a single species (see below). Of these, 17 have been described before, leaving 74.6% of species undescribed. However, some of the undescribed *Guimaraesiella*, *Priceiella*, and *Myrsidea* species have previously been reported in phylogenetic studies [38, 40, 74], and in these studies have been identified by numbers (i.e., *Guimaraesiella* (Ci.) sp. 1). For



consistency, we build on the same numbering system used in previous studies, meaning that in some cases numbers are skipped here (e.g., *Myrsidea* sp. 3–10, which were not collected in TBG).

Of the 213 hosts that were infested with lice, 56 individuals (26.3%) were parasitized by more than one species of lice; 50 individuals were infested with two species of lice, four individuals with three species of lice, one individual with four species of lice, and one individual with five species of lice (Supporting Information 3: Table S3). The host individuals most often parasitized by more than one louse species were *Turdus dissimilis* (10 of 15 birds; 66.7%), and *Trochalopteron milnei* (9 of 25 birds; 36%).

### 3.1 | Ischnocera

A total of 36 species of Ischnocera, representing 19 genera were collected. Of these, 12 species were previously described, and 6 species have been previously reported (Table 1). The overall prevalence of Ischnoceran lice was 13.0%, and 32 new host records were observed (Table 1).

The majority of the Ischnoceran specimens collected belong to the *Brueelia*-complex *sensu* Gustafsson and Bush [60] all of which grouped together within a monophyletic clade with high support (Figure 1). Within the *Brueelia*-complex the *Resartor*-group *sensu* Gustafsson et al. [70] formed a monophyletic clade containing the genera *Resartor*, *Timalinirmus*, and *Turdinirmus*. Also placed in this clade was the one specimen of *Mirandofures*, which is otherwise considered to be part of the *Brueelia*-group; however, this placement had no support. The rest of the *Brueelia*-group, comprising three species of the genus *Brueelia*, formed a monophyletic clade with high support.

The majority of the collected specimens belonged to the *Guimaraesiella*-group within the *Brueelia*-complex (Figure 1), being represented by four genera, two of which were represented by multiple subgenera. First, a single species each of *Traihoriella* and *Olivinirmus* were collected (Table 1), of which the *Olivinirmus* specimens represent an undescribed species. The genus *Priceiella* was represented by two species in the subgenus *P.* (*Camurnirmus*) and one species in the subgenus *P.* (*Thescelovora*). The remaining 11 species all belong to the genus *Guimaraesiella*: one member of the subgenus *G.* (*Dicrurobates*), six species of the subgenus *G.* (*Cicchinella*), and four species of the subgenus *G.* (*Guimaraesiella*).

Within the *Guimaraesiella*-group, *Priceiella* was recovered as monophyletic with high support, as was a clade containing all *Guimaraesiella* specimens except *G.* (*Dicrurobates*); the placement of *G.* (*Dicrurobates*) as sister to *Olivinirmus* received no support. No relationships above-species level within the main *Guimaraesiella* clade received any support, except that *G.* (*Ci.*) *mcgrewi* was placed as sister to an undescribed species in the same subgenus, with high support (Figure 1). Within *Priceiella*, species identified morphologically as *P.* (*T.*) *austini* and *P.* (*T.*) *catanachei* were placed in the same OTU, but are considered separate species here.

Outside the *Brueelia*-complex, only two genera were represented by more than one species: *Philopterus* and *Degeeriella*. Relationships among non-*Brueelia*-complex lice can therefore not be assessed here. However, the two representatives of the

*Oxylipeurus*-complex grouped together, as did the two representatives of the *Penenirmus*-complex and the three representatives of the *Degeeriella*-complex. By contrast, the two representatives of the Goniididae were not grouped together, but almost all the deeper relationships in the non-*Brueelia*-complex clades lack support (Figure 1).

### 3.2 | Amblycera

A total of 31 species (when *M. eurysternus* is treated as a single species, see below) representing four genera were collected. Of these only five species have been previously described, and three species have been previously reported (Table 2). The overall prevalence of amblyceran lice was 16.4%, and nine new host records were observed (Table 2).

Each of the four genera form their own monophyletic clade, with the majority of lice belonging to the genus *Myrsidea* (Figure 2). The genus *Ricinus* was represented by three species, collectively receiving good support, whereas *Menacanthus* received no support, and *Dennysus* was represented by a single species. The relationship among these four genera is unresolved (Figure 2). Based on the OTU analysis, 20 species of *Myrsidea* were collected. Several above-species clades within *Myrsidea* were supported in our analysis; however, as most of the species-level clades represent undescribed species, or species that cannot be identified based on either the published descriptions and illustrations or the state of the specimens (e.g., only nymphs collected, see Supporting Information 1: Table S1 for samples that contain only nymphs), little can be said about these relationships. Notably, almost half of the clades contain specimens collected from more than one host, indicating that some of these *Myrsidea* species may not be as host specific as commonly thought.

Within *Menacanthus*, our OTU analysis suggested nine species were obtained. The only specimen collected from a non-passeriform host was placed as sister to the remaining *Menacanthus* specimens; whereas the overall *Menacanthus* clade was not supported, the passeriform-*Menacanthus* clade was (Figure 2). Notably, three of the *Menacanthus* clades suggested in our OTU analysis were identified morphologically as *Menacanthus eurysternus*. To investigate this further, we combined our *Menacanthus* data with 74 sequences of *M. eurysternus* and 22 sequences of other *Menacanthus* species obtained from GenBank, and reran our analyses with this dataset (Figure 3, Table 3).

The *Menacanthus*-focused analysis produced a phylogenetic tree with three main clades (Figure 3), of which two contained specimens collected during this study. First, all specimens of *Menacanthus* from galliform hosts grouped together (Clade I), including our *Menacanthus* sp. 6; this clade received no support, and was placed as sister to the other two main clades, again with no support. One clade (Clade II) contained only specimens obtained from other studies, whereas most specimens from both our original data set and those obtained from GenBank formed a third clade (Clade III), which included *M. eurysternus*.

*Menacanthus eurysternus* was suggested to comprise 8 different clades in our OTU analysis, of which one (OTU G) is widely separated from the others (Figure 3). Whereas this species is uploaded to GenBank under the name *M. eurysternus*, it derives from a publication in which the species is discussed under the

**TABLE 1** | Ischnoceran lice collected from birds caught in Tongbiguan Township, Yunnan, China, including louse identification, host association, and prevalence.

| Louse species                                  | Host species                                  | Host family     | Number of hosts examined | Prevalence (number of hosts infested) |
|------------------------------------------------|-----------------------------------------------|-----------------|--------------------------|---------------------------------------|
| <i>Traihoriella binhchauensis</i>              | <i>Psilopogon asiaticus</i>                   | Megalaimidae    | 3                        | 33.3% (1)                             |
| <i>Brueelia leiae</i>                          | <i>Alcurus striatus</i> <sup>d</sup>          | Pycnonotidae    | 1                        | 100% (1)                              |
|                                                | <i>Alophoixus flaveolus</i> <sup>d</sup>      | Pycnonotidae    | 6                        | 83.3% (5)                             |
|                                                | <i>Ixos maclellandii</i>                      | Pycnonotidae    | 3                        | 33.3% (1)                             |
|                                                | <i>Pycnonotus xanthorrhous</i> <sup>d</sup>   | Pycnonotidae    | 5                        | 20% (1)                               |
|                                                | <i>Rubigula flaviventris</i> <sup>d</sup>     | Pycnonotidae    | 2                        | 100% (2)                              |
| <i>Brueelia</i> sp. 1 <sup>a</sup>             | <i>Pycnonotus cafer</i>                       | Pycnonotidae    | 8                        | 25% (2)                               |
| <i>Brueelia</i> sp. 2 <sup>a</sup>             | <i>Rhipidura albicollis</i>                   | Rhipiduridae    | 17                       | 5.9% (1)                              |
| <i>Guimaraesiella</i> (G.) <i>impiger</i>      | <i>Alcippe yunnanensis</i> <sup>d</sup>       | Leiotherichidae | 125                      | 0.8% (1)                              |
|                                                | <i>Anthipes monileger</i>                     | Muscicapidae    | 20                       | 5% (1)                                |
|                                                | <i>Leiothrix argenteauris</i> <sup>d</sup>    | Leiotherichidae | 123                      | 0.8% (1)                              |
| <i>Guimaraesiella</i> (G.) sp. 1 <sup>c</sup>  | <i>Turdus dissimilis</i> <sup>d</sup>         | Turdidae        | 15                       | 60% (9)                               |
| <i>Guimaraesiella</i> (G.) sp. 3 <sup>c</sup>  | <i>Geokichla citrina</i>                      | Turdidae        | 1                        | 100% (1)                              |
|                                                | <i>Pellorneum ruficeps</i> <sup>d</sup>       | Pellorneidae    | 6                        | 16.7% (1)                             |
| <i>Guimaraesiella</i> (G.) sp. 4 <sup>c</sup>  | <i>Brachypteryx leucophris</i> <sup>d</sup>   | Muscicapidae    | 4                        | 25% (1)                               |
|                                                | <i>Cyornis whitei</i>                         | Muscicapidae    | 21                       | 23.8% (5)                             |
|                                                | <i>Myiomela leucura</i> <sup>d</sup>          | Muscicapidae    | 20                       | 10% (2)                               |
| <i>Guimaraesiella</i> (Ci.) <i>mcgrewi</i>     | <i>Alcippe yunnanensis</i> <sup>d</sup>       | Leiotherichidae | 125                      | 2.4% (3)                              |
|                                                | <i>Muscicapa muttui</i> <sup>d</sup>          | Muscicapidae    | 8                        | 12.5% (1)                             |
|                                                | <i>Stachyris nigriceps</i> <sup>d</sup>       | Timaliidae      | 49                       | 4.1% (2)                              |
| <i>Guimaraesiella</i> (Ci.) <i>yuhinae</i>     | <i>Heterophasia gracilis</i> <sup>d</sup>     | Leiotherichidae | 2                        | 50% (1)                               |
|                                                | <i>Leiothrix argenteauris</i>                 | Leiotherichidae | 123                      | 0.8% (1)                              |
|                                                | <i>Liocichla ripponi</i> <sup>d</sup>         | Leiotherichidae | 6                        | 33.3% (2)                             |
|                                                | <i>Trochalopteron milnei</i> <sup>d</sup>     | Leiotherichidae | 25                       | 12% (3)                               |
| <i>Guimaraesiella</i> (Ci.) sp. 1 <sup>c</sup> | <i>Alcippe yunnanensis</i> <sup>d</sup>       | Leiotherichidae | 125                      | 1.6% (2)                              |
| <i>Guimaraesiella</i> (Ci.) sp. 2 <sup>b</sup> | <i>Heterophasia gracilis</i> <sup>d</sup>     | Leiotherichidae | 2                        | 50% (1)                               |
| <i>Guimaraesiella</i> (Ci.) sp. 3 <sup>a</sup> | <i>Leiothrix argenteauris</i>                 | Leiotherichidae | 123                      | 1.6% (2)                              |
|                                                | <i>Schoeniparus dubius</i>                    | Pellorneidae    | 48                       | 25% (12)                              |
| <i>Guimaraesiella</i> (Ci.) sp. 4 <sup>a</sup> | <i>Cyanoderma chrysaeum</i>                   | Timaliidae      | 22                       | 18.2% (4)                             |
|                                                | <i>Cyanoderma ruficeps</i>                    | Timaliidae      | 5                        | 20% (1)                               |
|                                                | <i>Schoeniparus dubius</i>                    | Pellorneidae    | 48                       | 2.1% (1)                              |
| <i>Guimaraesiella</i> (D.) <i>regis</i>        | <i>Gampsorhynchus rufulus</i> <sup>d</sup>    | Pellorneidae    | 5                        | 20% (1)                               |
| <i>Priceiella</i> (T.) <i>austini</i>          | <i>Actinodura egertoni</i> <sup>d</sup>       | Leiotherichidae | 17                       | 5.9% (1)                              |
|                                                | <i>Gampsorhynchus rufulus</i> <sup>d</sup>    | Pellorneidae    | 5                        | 60% (3)                               |
|                                                | <i>Leioptila annectens</i> <sup>d</sup>       | Leiotherichidae | 4                        | 25% (1)                               |
|                                                | <i>Stachyris nigriceps</i> <sup>d</sup>       | Timaliidae      | 49                       | 12.2% (6)                             |
| <i>Priceiella</i> (T.) <i>catanachei</i>       | <i>Actinodura egertoni</i> <sup>d</sup>       | Leiotherichidae | 17                       | 5.9% (1)                              |
|                                                | <i>Pomatorhinus phayrei</i> <sup>d</sup>      | Timaliidae      | 1                        | 100% (1)                              |
| <i>Priceiella</i> (Ca.) <i>lindquistae</i>     | <i>Ianthocinclia rufogularis</i> <sup>d</sup> | Leiotherichidae | 1                        | 100% (1)                              |

(Continues)

TABLE 1 | (Continued)

| Louse species                              | Host species                               | Host family     | Number of hosts examined | Prevalence (number of hosts infested) |
|--------------------------------------------|--------------------------------------------|-----------------|--------------------------|---------------------------------------|
|                                            | <i>Pterorhinus caerulatus</i> <sup>d</sup> | Leiotherichidae | 5                        | 20% (1)                               |
|                                            | <i>Pterorhinus merulensis</i> <sup>d</sup> | Leiotherichidae | 1                        | 100% (1)                              |
| <i>Priceiella</i> (Ca.) sp. 1 <sup>b</sup> | <i>Erythrogonys gravivox</i>               | Timaliidae      | 8                        | 12.5% (1)                             |
| <i>Olivinirmus</i> sp. 1 <sup>a</sup>      | <i>Dendrocitta formosae</i>                | Corvidae        | 1                        | 100% (1)                              |
| <i>Resartor elugeus</i>                    | <i>Leiothrix argentauris</i> <sup>d</sup>  | Leiotherichidae | 123                      | 0.8% (1)                              |
|                                            | <i>Leiothrix lutea</i> <sup>d</sup>        | Leiotherichidae | 16                       | 6.3% (1)                              |
|                                            | <i>Liocichla ripponi</i> <sup>d</sup>      | Leiotherichidae | 6                        | 16.7% (1)                             |
|                                            | <i>Stachyris nigriceps</i> <sup>d</sup>    | Timaliidae      | 49                       | 16.3% (8)                             |
| <i>Resartor novofacies</i>                 | <i>Trochalopteron milnei</i>               | Leiotherichidae | 25                       | 20% (5)                               |
| <i>Timalinirmus</i> sp. 1 <sup>a</sup>     | <i>Yuhina flavicollis</i>                  | Zosteropidae    | 21                       | 9.5% (2)                              |
| <i>Mirandofures</i> sp. 1 <sup>a</sup>     | <i>Lonchura punctulata</i>                 | Estrildidae     | 8                        | 12.5% (1)                             |
| <i>Turdinirmus</i> sp. 1 <sup>a</sup>      | <i>Alcippe yunnanensis</i>                 | Leiotherichidae | 125                      | 0.8% (1)                              |
|                                            | <i>Zoothera dixonii</i>                    | Turdidae        | 1                        | 100% (1)                              |
| <i>Reticulipeurus longistylus</i>          | <i>Arborophila rufogularis</i>             | Phasianidae     | 1                        | 100% (1)                              |
| <i>Megalipeurus</i> sp. 1 <sup>a</sup>     | <i>Arborophila rufogularis</i>             | Phasianidae     | 1                        | 100% (1)                              |
| <i>Columbicola</i> sp. 1 <sup>a</sup>      | <i>Macropygia unchall</i>                  | Columbidae      | 1                        | 100% (1)                              |
| <i>Degeeriella</i> sp. 1 <sup>a</sup>      | <i>Accipiter trivirgatus</i>               | Accipitridae    | 1                        | 100% (1)                              |
|                                            | <i>Accipiter virgatus</i>                  | Accipitridae    | 1                        | 100% (1)                              |
| <i>Cuculicola</i> sp. 1 <sup>a</sup>       | <i>Accipiter virgatus</i>                  | Accipitridae    | 1                        | 100% (1)                              |
| <i>Picophilopterus</i> sp. 1 <sup>a</sup>  | <i>Picumnus innominatus</i>                | Picidae         | 2                        | 50% (1)                               |
| <i>Penenirmus</i> sp. 1 <sup>a</sup>       | <i>Certhia manipurensis</i>                | Certhiidae      | 4                        | 25% (1)                               |
| <i>Philopterus</i> sp. 1 <sup>a</sup>      | <i>Dicrurus remifer</i>                    | Dicruridae      | 2                        | 50% (1)                               |
| <i>Philopterus</i> sp. 2 <sup>a</sup>      | <i>Turdus dissimilis</i>                   | Turdidae        | 15                       | 13.3% (2)                             |
| <i>Goniocotes</i> sp. 1 <sup>a</sup>       | <i>Arborophila rufogularis</i>             | Phasianidae     | 1                        | 100% (1)                              |
| <i>Goniodes</i> sp. 1 <sup>a</sup>         | <i>Arborophila rufogularis</i>             | Phasianidae     | 1                        | 100% (1)                              |

Note: Annotation beside louse species names denote the source of the unidentified species number: <sup>a</sup>This paper, <sup>b</sup>Grossi et al. [40], and <sup>c</sup>Tian et al. [38]. It should be noted that *Priceiella* (Ca.) sp. 1 and *Guimaraesiella* (Ci.) sp. 2 in this paper were referred to as *Priceiella* (Ca.) sp. nov. and *Guimaraesiella* (Ci.) sp. nov., respectively, by Grossi et al. [40], but are here numbered for clarity. <sup>d</sup>Beside host species indicates a new louse/host association. Abbreviations: Ca., *Camurnirmus*; Ci., *Cicchinella*; D., *Dicrurorobates*; G., *Guimaraesiella*; T., *Thescelovora*.

name *Menacanthus brelihi* Balát, 1958 [75]; this name is adopted here following their recommendation. The remaining OTUs form a monophyletic clade with good support. Within this clade, our TBG *Menacanthus* specimens fell into one of two clades, as our OTU analysis placed *M. eurysternus* B, and *M. eurysternus* C from the main analysis into the same OTU. Tongbiguan specimens of *Menacanthus* not identified to *M. eurysternus* were separated into five clades in our analysis, none of which were placed together with specimens obtained from GenBank.

### 3.3 | Prevalence

The prevalence for every louse/host association was calculated (Tables 1, 2; since the reliability of prevalence depends strongly on sample size, samples of 10 or fewer examined individuals (arbitrary threshold) are not discussed further). Prevalence values varied widely among examined hosts, with the most

prevalent louse species being *Myrsidea* sp. 23 from *Trochalopteron milnei* (84%), *Myrsidea* sp. 11 and *Guimaraesiella* (G.) sp. 1 from *Turdus dissimilis* (both 60%), *Menacanthus eurysternus* B also from *Turdus dissimilis* (40%), and *Myrsidea* sp. 22 on *Actinodura egertoni* (29.4%). For both Amblycera and Ischnocera, most host species for which at least 10 individuals were examined had louse prevalences below 10%.

## 4 | Discussion

Yunnan is a popular destination for bird watchers attracted by the high diversity of birds known from this province [76, 77]. However, much less is known about the louse fauna associated with Yunnanese birds. Gustafsson et al. [78] published the only detailed survey of lice from two localities in south-central Yunnan, situated in other mountain ranges than those around TBG.



**FIGURE 1** | Phylogenetic reconstruction of Ischnoceran lice collected from birds caught in Tongbiguan Township, Yunnan, China inferred by BEAST, with node posterior probabilities > 0.95 displayed. Gray bars beside taxon names indicate the results of the operational taxonomic unit analysis. In parentheses is the voucher number (i.e., J1234-5; J1234 refers to the bird individual and 5 refers to the louse). *G.* = *Guimaraesiella*; *Ci.* = *Cicchinella*; *D.* = *Dicruobates*; *T.* = *Thescelovora*; *Ca.* = *Camurnirmus*.



**TABLE 2** | Amblyceran lice collected from birds caught in Tongbiguan Township, Yunnan, China, including louse identification, host association, and prevalence.

| Louse species                         | Host species                                | Host family       | Number of hosts examined | Prevalence (number of hosts infested) |
|---------------------------------------|---------------------------------------------|-------------------|--------------------------|---------------------------------------|
| <i>Menacanthus eurysternus</i> A      | <i>Leiothrix argentauris</i> <sup>c</sup>   | Leiothrichidae    | 123                      | 1.6% (2)                              |
|                                       | <i>Pomatorhinus ruficollis</i> <sup>c</sup> | Timaliidae        | 22                       | 4.5% (1)                              |
| <i>Menacanthus eurysternus</i> B      | <i>Anthipes monileger</i> <sup>c</sup>      | Muscicapidae      | 20                       | 5% (1)                                |
|                                       | <i>Cyornis whitei</i> <sup>c</sup>          | Muscicapidae      | 21                       | 4.8% (1)                              |
|                                       | <i>Niltava sundara</i> <sup>c</sup>         | Muscicapidae      | 13                       | 7.7% (1)                              |
|                                       | <i>Orthotomus sutorius</i> <sup>c</sup>     | Cisticolidae      | 4                        | 25% (1)                               |
|                                       | <i>Turdus dissimilis</i>                    | Turdidae          | 15                       | 40% (6)                               |
|                                       | <i>Arachnothera magna</i>                   | Nectariniidae     | 13                       | 7.7% (1)                              |
| <i>Menacanthus</i> sp. 1 <sup>a</sup> | <i>Machlolophus spilonotus</i>              | Paridae           | 3                        | 33.3% (1)                             |
|                                       | <i>Psittiparus gularis</i>                  | Paradoxornithidae | 1                        | 100% (1)                              |
| <i>Menacanthus</i> sp. 2 <sup>a</sup> | <i>Leiothrix argentauris</i>                | Leiothrichidae    | 123                      | 1.6% (2)                              |
| <i>Menacanthus</i> sp. 3 <sup>a</sup> | <i>Phylloscopus pulcher</i>                 | Phylloscopidae    | 7                        | 14.3% (1)                             |
| <i>Menacanthus</i> sp. 4 <sup>a</sup> | <i>Schoeniparus dubius</i>                  | Pellorneidae      | 48                       | 2.1% (1)                              |
| <i>Menacanthus</i> sp. 5 <sup>a</sup> | <i>Alophoixus flaveolus</i>                 | Pycnonotidae      | 6                        | 83.3% (5)                             |
|                                       | <i>Rubigula flaviventris</i>                | Pycnonotidae      | 2                        | 50% (1)                               |
| <i>Menacanthus</i> sp. 6 <sup>a</sup> | <i>Arborophila rufogularis</i>              | Phasianidae       | 1                        | 100% (1)                              |
| <i>Ricinus</i> sp. 1 <sup>a</sup>     | <i>Phylloscopus poliogenys</i>              | Phylloscopidae    | 2                        | 50% (1)                               |
|                                       | <i>Phylloscopus valentini</i>               | Phylloscopidae    | 7                        | 14.3% (1)                             |
| <i>Ricinus</i> sp. 2 <sup>a</sup>     | <i>Erpornis zantholeuca</i>                 | Vireonidae        | 1                        | 100% (1)                              |
| <i>Ricinus</i> sp. 3 <sup>a</sup>     | <i>Cyornis whitei</i>                       | Muscicapidae      | 21                       | 14.3% (3)                             |
| <i>Myrsidea argentauris</i>           | <i>Leiothrix argentauris</i>                | Leiothrichidae    | 123                      | 4.9% (6)                              |
| <i>Myrsidea dukguni</i>               | <i>Stachyris nigriceps</i> <sup>c</sup>     | Timaliidae        | 49                       | 2% (1)                                |
| <i>Myrsidea sultanpurensis</i>        | <i>Cyanoderma chrysaeum</i> <sup>c</sup>    | Timaliidae        | 22                       | 4.5% (1)                              |
| <i>Myrsidea</i> sp. 2 <sup>b</sup>    | <i>Alcippe yunnanensis</i>                  | Leiothrichidae    | 125                      | 18.4% (23)                            |
| <i>Myrsidea</i> sp. 11 <sup>b</sup>   | <i>Arachnothera magna</i>                   | Nectariniidae     | 13                       | 7.7% (1)                              |
|                                       | <i>Turdus dissimilis</i>                    | Turdidae          | 15                       | 60% (9)                               |
| <i>Myrsidea</i> sp. 16 <sup>b</sup>   | <i>Ixos mccllellandii</i>                   | Pycnonotidae      | 3                        | 66.7% (2)                             |
| <i>Myrsidea</i> sp. 21 <sup>a</sup>   | <i>Schoeniparus dubius</i>                  | Pellorneidae      | 48                       | 27.1% (13)                            |
|                                       | <i>Stachyris nigriceps</i>                  | Timaliidae        | 49                       | 2% (1)                                |
| <i>Myrsidea</i> sp. 22 <sup>a</sup>   | <i>Actinodura egertoni</i>                  | Leiothrichidae    | 17                       | 29.4% (5)                             |
|                                       | <i>Phylloscopus poliogenys</i>              | Phylloscopidae    | 2                        | 50% (1)                               |
|                                       | <i>Rhipidura albicollis</i>                 | Rhipiduridae      | 17                       | 5.9% (1)                              |
| <i>Myrsidea</i> sp. 23 <sup>a</sup>   | <i>Geokichla citrina</i>                    | Turdidae          | 1                        | 100% (1)                              |
|                                       | <i>Pellorneum ruficeps</i>                  | Pellorneidae      | 6                        | 16.7% (1)                             |
|                                       | <i>Trochalopteron milnei</i>                | Leiothrichidae    | 25                       | 84% (21)                              |
| <i>Myrsidea</i> sp. 24 <sup>a</sup>   | <i>Gampsorhynchus rufulus</i>               | Pellorneidae      | 5                        | 80% (4)                               |
| <i>Myrsidea</i> sp. 25 <sup>a</sup>   | <i>Heterophasia gracilis</i>                | Leiothrichidae    | 2                        | 100% (2)                              |
| <i>Myrsidea</i> sp. 26 <sup>a</sup>   | <i>Liocichla ripponi</i>                    | Leiothrichidae    | 6                        | 66.7% (4)                             |
|                                       | <i>Pycnonotus cafer</i>                     | Pycnonotidae      | 8                        | 12.5% (1)                             |

(Continues)



TABLE 2 | (Continued)

| Louse species                       | Host species                        | Host family    | Number of hosts examined | Prevalence (number of hosts infested) |
|-------------------------------------|-------------------------------------|----------------|--------------------------|---------------------------------------|
|                                     | <i>Trochalopteron milnei</i>        | Leiothrichidae | 25                       | 4% (1)                                |
| <i>Myrsidea</i> sp. 27 <sup>a</sup> | <i>Pterorhinus caerulatus</i>       | Leiothrichidae | 5                        | 20% (1)                               |
| <i>Myrsidea</i> sp. 28 <sup>a</sup> | <i>Alcippe yunnanensis</i>          | Leiothrichidae | 125                      | 0.8% (1)                              |
|                                     | <i>Cyanoderma chrysaeum</i>         | Timaliidae     | 22                       | 22.7% (5)                             |
|                                     | <i>Cyanoderma ruficeps</i>          | Timaliidae     | 5                        | 40% (2)                               |
| <i>Myrsidea</i> sp. 29 <sup>a</sup> | <i>Rubigula flaviventris</i>        | Pycnonotidae   | 2                        | 50% (1)                               |
| <i>Myrsidea</i> sp. 30 <sup>a</sup> | <i>Pycnonotus flavescens</i>        | Pycnonotidae   | 1                        | 100% (1)                              |
| <i>Myrsidea</i> sp. 31 <sup>a</sup> | <i>Alcippe yunnanensis</i>          | Leiothrichidae | 125                      | 0.8% (1)                              |
|                                     | <i>Rhipidura albicollis</i>         | Rhipiduridae   | 17                       | 5.9% (1)                              |
| <i>Myrsidea</i> sp. 32 <sup>a</sup> | <i>Alcurus striatus</i>             | Pycnonotidae   | 1                        | 100% (1)                              |
| <i>Myrsidea</i> sp. 33 <sup>a</sup> | <i>Abroscopus albogularis</i>       | Cettiidae      | 9                        | 11.1% (1)                             |
| <i>Myrsidea</i> sp. 34 <sup>a</sup> | <i>Leiothrix argentauris</i>        | Leiothrichidae | 123                      | 0.8% (1)                              |
|                                     | <i>Myiomela leucura</i>             | Muscicapidae   | 20                       | 5% (1)                                |
| <i>Dennyus hirundinis</i>           | <i>Apus nipalensis</i> <sup>c</sup> | Apodidae       | 23                       | 26.1% (6)                             |

Note: Annotation beside louse species name denotes the source of the unidentified species number: <sup>a</sup>This Paper, and <sup>b</sup>Grossi et al. [40]. <sup>c</sup>Beside host species indicates a new louse/host association.

However, other smaller reports have been published, especially in taxonomic papers [68]. In total, 59 species of ischnoceran lice are known from Yunnan [33], which likely represents a fraction of the true diversity. The number of Amblycera recorded from Yunnan is presently unknown; Gustafsson et al. [78] recorded only two taxa identified to species level, but many more to genus level, principally in the genus *Myrsidea*.

Our OTU analysis of the COI-based phylogenies performed here indicates that we collected a total of 68 louse species, all from a small area in Dehong Prefecture, western Yunnan. However, morphologically a total of 69 louse species are separable, as our OTU analysis places *Priceiella* (*T.*) *austini* and *P.* (*T.*) *catanachei* in the same OTU, with low genetic distances between subclades (p-distance = 0.0123, S.E.  $\pm$  0.0054). Of these, only 17 could be identified to species level using a combination of morphology and COI barcodes; additional clades recovered here may correspond to known species, which cannot be identified due to, for example, poor species descriptions, lack of COI barcodes, or because our specimens are only nymphal or distorted during the mounting process. Notably, of the 17 species positively identified here, only five were previously known from Yunnan [33]; *Brueelia leiae* [69], *Guimaraesiella* (*Ci.*) *yuhinae* [66], *Priceiella* (*Ca.*) *lindquistae* [64], *Priceiella* (*T.*) *austini* [64], and *Resartor elugeus* [67]. At least three species (*Guimaraesiella* [*Dicruobates*] *regis* [61]; *Resartor novofacies* [79]; *Reticulipeurus* [*Forcipurellus*] *longistylus* [62]) represent new records for China. Moreover, almost all species of *Myrsidea* collected represent undescribed species, which will be treated in more detail elsewhere.

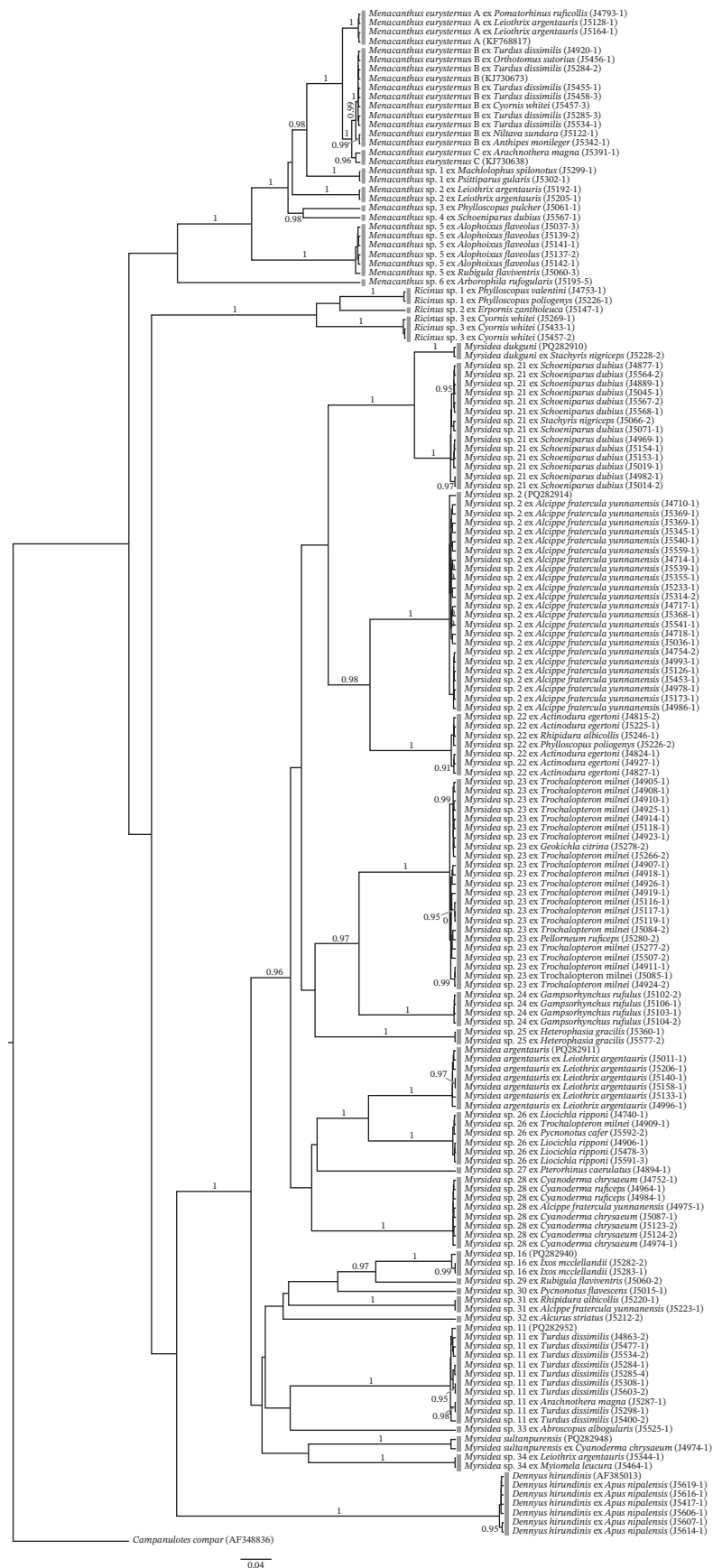
#### 4.1 | Prevalence

Prevalence of lice was generally low for host species with a sample size of 10 or more, with most louse species having a prevalence of

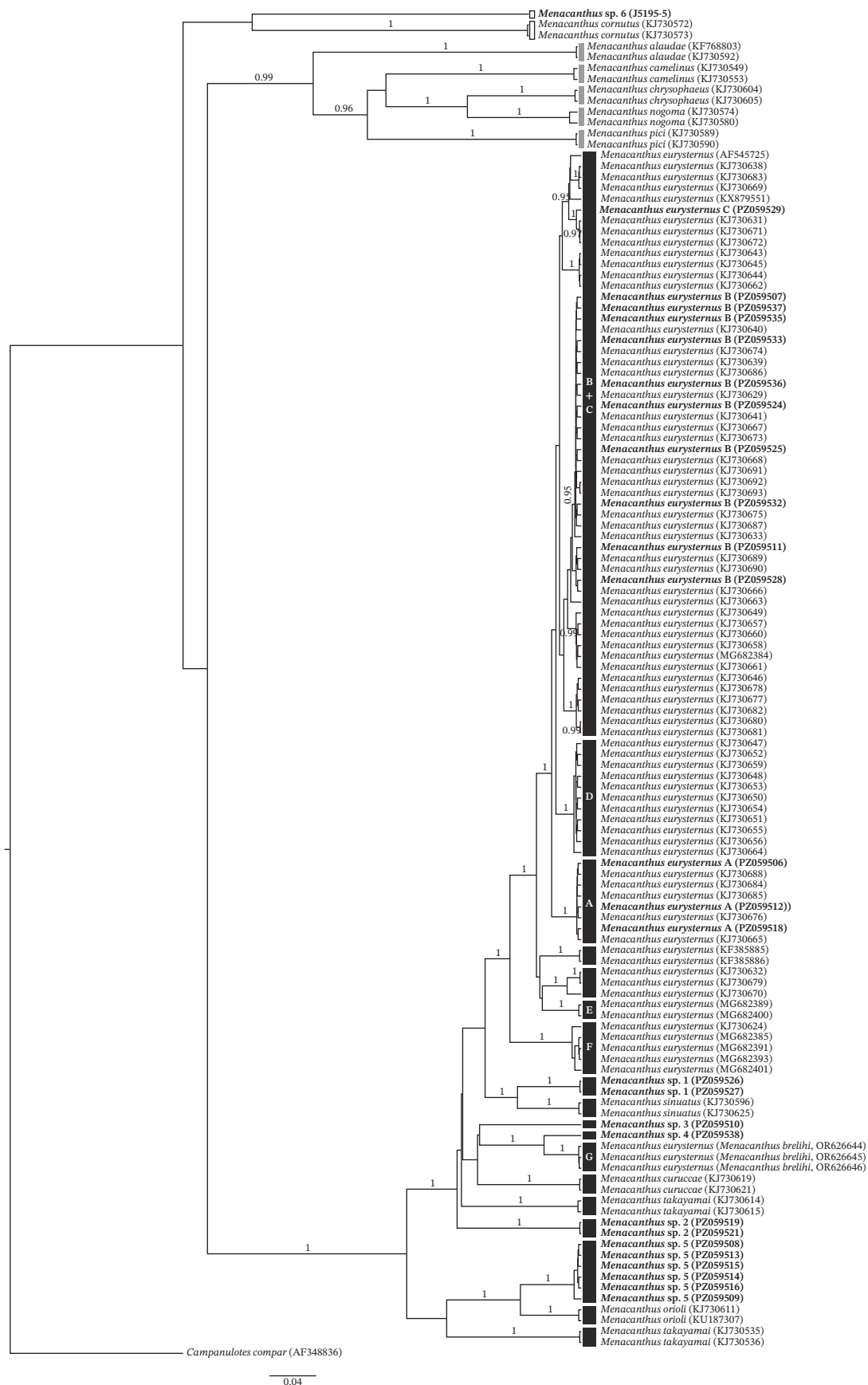
10% or less (Tables 1, 2). Notably, prevalence was generally higher for larger-bodied birds examined, such as *Trochalopteron milnei* or *Turdus dissimilis*. This is in contrast to the report by Gustafsson et al. [78], in which most resident songbirds with more than 10 individuals examined had prevalence values over 25%.

Possibly, differences in prevalence between the two sampling areas in these studies may be related to the time of year. Gustafsson et al. [78] sampled their non-migratory hosts in the early autumn, in the post-breeding season, whereas the samples for this study were obtained either in the winter of 2023 or the spring of 2024, both in the non-breeding season or early breeding season. The relationship between collecting season and prevalence and abundance is poorly known for chewing lice. Some studies suggest strong seasonality for a range of louse taxa [80–86] but this may differ between different species of lice on the same host [87, 88]. Moreover, ambient humidity, temperature and possibly other, yet unidentified, factors may influence prevalence, abundance, and community composition of lice [19, 89]. The low number of data points (3: December, April/May, and August/September) available for the Yunnanese bird louse fauna makes speculation on possible influence by seasonality on prevalence premature; even more so as we have reason to believe that louse species may differ on the same host within and between the localities sampled (see below).

Unfortunately, published data from other localities in tropical and subtropical Asia are limited. Najer et al. [25, 26] examined a range of birds in Vietnam, but sample size for each host species is generally low, and few host species overlap between their data and ours, making comparisons difficult. Most other published prevalence data from the region are limited to one or a few host species [84, 90], and no general overview has been published. Presumably, patterns of prevalence related to, for example, ambient humidity, temperature, and perhaps elevation may be revealed in the future, when more data have been published.



**FIGURE 2** | Phylogenetic reconstruction of Amblyceran lice collected from birds caught in Tongbiguan Township, Yunnan, China inferred by BEAST, with node posterior probabilities > 0.95 displayed. Gray bars beside taxon names indicate the results of the operational taxonomic unit analysis. In parentheses is the voucher number (i.e., J1234-5; J1234 refers to the bird individual and 5 refers to the louse).



**FIGURE 3** | Phylogenetic reconstruction of *Menacanthus* collected from birds caught in Tongbiguan Township, Yunnan, China and sequences obtained from Genbank inferred by BEAST, with node posterior probabilities > 0.95 displayed. Colored bars beside taxon names indicate the results of the operational taxonomic unit analysis. Color indicates the clades referenced in the text; white: Clade I, gray: Clade II, and black: Clade III. Letters in the black bars refer to the OTUs referenced in the text. In parentheses is the Genbank accession number. Bolded sequences indicate lice collected for this study.

**TABLE 3** | Collection information about the *Menacanthus* specimens used in the construction of the *Menacanthus* phylogeny.

| OTU | Louse species                           | Host species                         | Host family   | Collection location | Accession number |
|-----|-----------------------------------------|--------------------------------------|---------------|---------------------|------------------|
| B+C | <i>Menacanthus eurysternus</i>          | <i>Sturnus vulgaris</i>              | Sturnidae     | Sweden              | KJ730645         |
| B+C | <b><i>Menacanthus eurysternus</i> B</b> | <i>Orthotomus sutorius</i>           | Cisticolidae  | China               | J5456-1          |
| B+C | <i>Menacanthus eurysternus</i>          | <i>Pica pica</i>                     | Corvidae      | France              | KJ730638         |
| B+C | <i>Menacanthus eurysternus</i>          | <i>Pica pica</i>                     | Corvidae      | France              | KJ730669         |
| B+C | <i>Menacanthus eurysternus</i>          | <i>Pica pica</i>                     | Corvidae      | France              | KJ730683         |
| B+C | <i>Menacanthus eurysternus</i>          | <i>Emberiza fucata</i>               | Emberizidae   | Japan               | KJ730673         |
| B+C | <i>Menacanthus eurysternus</i>          | <i>Emberiza personata</i>            | Emberizidae   | Japan               | KJ730631         |
| B+C | <i>Menacanthus eurysternus</i>          | <i>Carpodacus erythrinus</i>         | Fringillidae  | Czech Republic      | KJ730663         |
| B+C | <i>Menacanthus eurysternus</i>          | <i>Coccothraustes coccothraustes</i> | Fringillidae  | Japan               | KJ730633         |
| B+C | <i>Menacanthus eurysternus</i>          | <i>Fringilla coelebs</i>             | Fringillidae  | Sweden              | KJ730646         |
| B+C | <i>Menacanthus eurysternus</i>          | <i>Fringilla coelebs</i>             | Fringillidae  | Sweden              | KJ730677         |
| B+C | <i>Menacanthus eurysternus</i>          | <i>Fringilla coelebs</i>             | Fringillidae  | Sweden              | KJ730678         |
| B+C | <i>Menacanthus eurysternus</i>          | <i>Fringilla coelebs</i>             | Fringillidae  | Sweden              | KJ730680         |
| B+C | <i>Menacanthus eurysternus</i>          | <i>Fringilla coelebs</i>             | Fringillidae  | Sweden              | KJ730681         |
| B+C | <i>Menacanthus eurysternus</i>          | <i>Fringilla coelebs</i>             | Fringillidae  | Sweden              | KJ730682         |
| B+C | <i>Menacanthus eurysternus</i>          | <i>Lybius torquatus</i>              | Lybiidae      | unknown             | AF545725         |
| B+C | <b><i>Menacanthus eurysternus</i> B</b> | <i>Anthipes monileger</i>            | Muscicapidae  | China               | J5342-1          |
| B+C | <b><i>Menacanthus eurysternus</i> B</b> | <i>Cyornis whitei</i>                | Muscicapidae  | China               | J5457-3          |
| B+C | <i>Menacanthus eurysternus</i>          | <i>Melaenornis silens</i>            | Muscicapidae  | South Africa        | MG682384         |
| B+C | <b><i>Menacanthus eurysternus</i> B</b> | <i>Niltava sundara</i>               | Muscicapidae  | China               | J5122-1          |
| B+C | <b><i>Menacanthus eurysternus</i> C</b> | <i>Arachnothera magna</i>            | Nectariniidae | China               | J5391-1          |
| B+C | <i>Menacanthus eurysternus</i>          | <i>Hypsipetes amaurotis pryeri</i>   | Pycnonotidae  | Japan               | KJ730671         |
| B+C | <i>Menacanthus eurysternus</i>          | <i>Hypsipetes amaurotis pryeri</i>   | Pycnonotidae  | Japan               | KJ730672         |
| B+C | <i>Menacanthus eurysternus</i>          | <i>Sitta europaea</i>                | Sittidae      | Japan               | KJ730689         |
| B+C | <i>Menacanthus eurysternus</i>          | <i>Sitta europaea</i>                | Sittidae      | Japan               | KJ730690         |
| B+C | <i>Menacanthus eurysternus</i>          | <i>Sturnus vulgaris</i>              | Sturnidae     | Slovakia            | KJ730662         |
| B+C | <i>Menacanthus eurysternus</i>          | <i>Sturnus vulgaris</i>              | Sturnidae     | Sweden              | KJ730643         |
| B+C | <i>Menacanthus eurysternus</i>          | <i>Tangara dowii</i>                 | Thraupidae    | Costa Rica          | KJ730649         |
| B+C | <i>Menacanthus eurysternus</i>          | <i>Tangara dowii</i>                 | Thraupidae    | Costa Rica          | KJ730661         |
| B+C | <i>Menacanthus eurysternus</i>          | <i>Turdus cardis</i>                 | Turdidae      | Viet Nam            | KJ730666         |
| B+C | <b><i>Menacanthus eurysternus</i> B</b> | <i>Turdus dissimilis</i>             | Turdidae      | China               | J4920-1          |
| B+C | <b><i>Menacanthus eurysternus</i> B</b> | <i>Turdus dissimilis</i>             | Turdidae      | China               | J5284-2          |
| B+C | <b><i>Menacanthus eurysternus</i> B</b> | <i>Turdus dissimilis</i>             | Turdidae      | China               | J5285-3          |
| B+C | <b><i>Menacanthus eurysternus</i> B</b> | <i>Turdus dissimilis</i>             | Turdidae      | China               | J5455-1          |
| B+C | <b><i>Menacanthus eurysternus</i> B</b> | <i>Turdus dissimilis</i>             | Turdidae      | China               | J5458-3          |
| B+C | <b><i>Menacanthus eurysternus</i> B</b> | <i>Turdus dissimilis</i>             | Turdidae      | China               | J5534-1          |
| B+C | <i>Menacanthus eurysternus</i>          | <i>Turdus merula</i>                 | Turdidae      | Sweden              | KJ730686         |
| B+C | <i>Menacanthus eurysternus</i>          | <i>Turdus merula</i>                 | Turdidae      | Sweden              | KJ730691         |
| B+C | <i>Menacanthus eurysternus</i>          | <i>Turdus merula</i>                 | Turdidae      | Sweden              | KJ730693         |
| B+C | <i>Menacanthus eurysternus</i>          | <i>Turdus merula</i>                 | Turdidae      | Sweden              | KJ730629         |

(Continues)



TABLE 3 | (Continued)

| OTU | Louse species                           | Host species                      | Host family    | Collection location | Accession number |
|-----|-----------------------------------------|-----------------------------------|----------------|---------------------|------------------|
| B+C | <i>Menacanthus eurysternus</i>          | <i>Turdus merula</i>              | Turdidae       | Sweden              | KJ730639         |
| B+C | <i>Menacanthus eurysternus</i>          | <i>Turdus merula</i>              | Turdidae       | Sweden              | KJ730640         |
| B+C | <i>Menacanthus eurysternus</i>          | <i>Turdus merula</i>              | Turdidae       | Sweden              | KJ730641         |
| B+C | <i>Menacanthus eurysternus</i>          | <i>Turdus nigrescens</i>          | Turdidae       | Costa Rica          | KJ730657         |
| B+C | <i>Menacanthus eurysternus</i>          | <i>Turdus nigrescens</i>          | Turdidae       | Costa Rica          | KJ730658         |
| B+C | <i>Menacanthus eurysternus</i>          | <i>Turdus nigrescens</i>          | Turdidae       | Costa Rica          | KJ730660         |
| B+C | <i>Menacanthus eurysternus</i>          | <i>Turdus pallidus</i>            | Turdidae       | Japan               | KJ730674         |
| B+C | <i>Menacanthus eurysternus</i>          | <i>Turdus pallidus</i>            | Turdidae       | Japan               | KJ730675         |
| B+C | <i>Menacanthus eurysternus</i>          | <i>Turdus pallidus</i>            | Turdidae       | Japan               | KJ730687         |
| B+C | <i>Menacanthus eurysternus</i>          | <i>Turdus pilaris</i>             | Turdidae       | Sweden              | KJ730667         |
| B+C | <i>Menacanthus eurysternus</i>          | unknown                           | Unknown        | China               | KX879551         |
| B+C | <i>Menacanthus eurysternus</i>          | unknown                           | Unknown        | unknown             | KJ730692         |
| B+C | <i>Menacanthus eurysternus</i>          | unknown                           | unknown        | unknown             | KJ730668         |
| B+C | <i>Menacanthus eurysternus</i>          | unknown                           | unknown        | Sweden              | KJ730644         |
| D   | <i>Menacanthus eurysternus</i>          | <i>Mimus saturninus</i>           | Mimidae        | Brazil              | KJ730664         |
| D   | <i>Menacanthus eurysternus</i>          | <i>Chlorospingus ophthalmicus</i> | Passerellidae  | Costa Rica          | KJ730652         |
| D   | <i>Menacanthus eurysternus</i>          | <i>Chlorospingus ophthalmicus</i> | Passerellidae  | Costa Rica          | KJ730653         |
| D   | <i>Menacanthus eurysternus</i>          | <i>Chlorospingus ophthalmicus</i> | Passerellidae  | Costa Rica          | KJ730654         |
| D   | <i>Menacanthus eurysternus</i>          | <i>Tangara dowii</i>              | Thraupidae     | Costa Rica          | KJ730650         |
| D   | <i>Menacanthus eurysternus</i>          | <i>Turdus grayi</i>               | Turdidae       | Costa Rica          | KJ730647         |
| D   | <i>Menacanthus eurysternus</i>          | <i>Turdus grayi</i>               | Turdidae       | Costa Rica          | KJ730648         |
| D   | <i>Menacanthus eurysternus</i>          | <i>Turdus grayi</i>               | Turdidae       | Costa Rica          | KJ730651         |
| D   | <i>Menacanthus eurysternus</i>          | <i>Turdus grayi</i>               | Turdidae       | Costa Rica          | KJ730655         |
| D   | <i>Menacanthus eurysternus</i>          | <i>Turdus grayi</i>               | Turdidae       | Costa Rica          | KJ730656         |
| D   | <i>Menacanthus eurysternus</i>          | <i>Turdus grayi</i>               | Turdidae       | Costa Rica          | KJ730659         |
| A   | <b><i>Menacanthus eurysternus</i> A</b> | <i>Leiothrix argenteauris</i>     | Leiothrichidae | China               | J5128-1          |
| A   | <b><i>Menacanthus eurysternus</i> A</b> | <i>Leiothrix argenteauris</i>     | Leiothrichidae | China               | J5164-1          |
| A   | <b><i>Menacanthus eurysternus</i> A</b> | <i>Pomatorhinus ruficollis</i>    | Timaliidae     | China               | J4793-1          |
| A   | <i>Menacanthus eurysternus</i>          | <i>Zosterops japonicus</i>        | Zosteropidae   | Japan               | KJ730665         |
| A   | <i>Menacanthus eurysternus</i>          | <i>Zosterops japonicus</i>        | Zosteropidae   | Japan               | KJ730676         |
| A   | <i>Menacanthus eurysternus</i>          | <i>Zosterops japonicus</i>        | Zosteropidae   | Japan               | KJ730684         |
| A   | <i>Menacanthus eurysternus</i>          | <i>Zosterops japonicus</i>        | Zosteropidae   | Japan               | KJ730685         |
| A   | <i>Menacanthus eurysternus</i>          | <i>Zosterops japonicus</i>        | Zosteropidae   | Japan               | KJ730688         |
| H   | <i>Menacanthus eurysternus</i>          | <i>Pycnonotus blanfordi</i>       | Pycnonotidae   | Viet Nam            | KF385886         |
| H   | <i>Menacanthus eurysternus</i>          | <i>Pycnonotus finlaysoni</i>      | Pycnonotidae   | Viet Nam            | KF385885         |
| I   | <i>Menacanthus eurysternus</i>          | <i>Emberiza schoeniclus</i>       | Emberizidae    | Japan               | KJ730670         |
| I   | <i>Menacanthus eurysternus</i>          | <i>Passer domesticus</i>          | Passeridae     | Sweden              | KJ730632         |
| I   | <i>Menacanthus eurysternus</i>          | <i>Passer domesticus</i>          | Passeridae     | Sweden              | KJ730679         |
| E   | <i>Menacanthus eurysternus</i>          | <i>Pycnonotus nigricans</i>       | Pycnonotidae   | South Africa        | MG682389         |
| E   | <i>Menacanthus eurysternus</i>          | <i>Curruca subcoerulea</i>        | Sylviidae      | South Africa        | MG682400         |

(Continues)

TABLE 3 | (Continued)

| OTU | Louse species                   | Host species                      | Host family       | Collection location | Accession number |
|-----|---------------------------------|-----------------------------------|-------------------|---------------------|------------------|
| F   | <i>Menacanthus eurysternus</i>  | <i>Cisticola lais</i>             | Cisticolidae      | South Africa        | MG682385         |
| F   | <i>Menacanthus eurysternus</i>  | <i>Prinia flavicans</i>           | Cisticolidae      | South Africa        | MG682401         |
| F   | <i>Menacanthus eurysternus</i>  | <i>Prinia subflava</i>            | Cisticolidae      | Senegal             | KJ730624         |
| F   | <i>Menacanthus eurysternus</i>  | <i>Pycnonotus tricolor</i>        | Pycnonotidae      | South Africa        | MG682391         |
| F   | <i>Menacanthus eurysternus</i>  | <i>Turdus libonyana</i>           | Turdidae          | South Africa        | MG682393         |
| J   | <b><i>Menacanthus</i> sp. 1</b> | <i>Psittiparus gularis</i>        | Paradoxornithidae | China               | J5302-1          |
| J   | <b><i>Menacanthus</i> sp. 1</b> | <i>Machlolophus spilonotus</i>    | Paridae           | China               | J5299-1          |
| K   | <i>Menacanthus sinuatus</i>     | <i>Cyanistes caeruleus</i>        | Paridae           | Sweden              | KJ730596         |
| K   | <i>Menacanthus sinuatus</i>     | <i>Poecile palustris</i>          | Paridae           | Czech Republic      | KJ730625         |
| G   | <i>Menacanthus eurysternus</i>  | <i>Panurus biarmicus</i>          | Panuridae         | Slovakia            | OR626644         |
| G   | <i>Menacanthus eurysternus</i>  | <i>Panurus biarmicus</i>          | Panuridae         | Slovakia            | OR626645         |
| G   | <i>Menacanthus eurysternus</i>  | <i>Panurus biarmicus</i>          | Panuridae         | Slovakia            | OR626646         |
| L   | <i>Menacanthus curuccae</i>     | <i>Acrocephalus schoenobaenus</i> | Acrocephalidae    | Slovakia            | KJ730619         |
| L   | <i>Menacanthus curuccae</i>     | <i>Acrocephalus schoenobaenus</i> | Acrocephalidae    | Slovakia            | KJ730621         |
| M   | <i>Menacanthus takayamai</i>    | <i>Drepanorhynchus reichenowi</i> | Nectariniidae     | Kenya               | KJ730614         |
| M   | <i>Menacanthus takayamai</i>    | <i>Drepanorhynchus reichenowi</i> | Nectariniidae     | Kenya               | KJ730615         |
| N   | <b><i>Menacanthus</i> sp. 2</b> | <i>Leiothrix argentea</i>         | Leiothrichidae    | China               | J5192-1          |
| N   | <b><i>Menacanthus</i> sp. 2</b> | <i>Leiothrix argentea</i>         | Leiothrichidae    | China               | J5205-1          |
| O   | <b><i>Menacanthus</i> sp. 5</b> | <i>Alophoixus flaveolus</i>       | Pycnonotidae      | China               | J5037-3          |
| O   | <b><i>Menacanthus</i> sp. 5</b> | <i>Alophoixus flaveolus</i>       | Pycnonotidae      | China               | J5137-2          |
| O   | <b><i>Menacanthus</i> sp. 5</b> | <i>Alophoixus flaveolus</i>       | Pycnonotidae      | China               | J5139-2          |
| O   | <b><i>Menacanthus</i> sp. 5</b> | <i>Alophoixus flaveolus</i>       | Pycnonotidae      | China               | J5141-1          |
| O   | <b><i>Menacanthus</i> sp. 5</b> | <i>Alophoixus flaveolus</i>       | Pycnonotidae      | China               | J5142-1          |
| O   | <b><i>Menacanthus</i> sp. 5</b> | <i>Rubigula flaviventris</i>      | Pycnonotidae      | China               | J5060-3          |
| P   | <i>Menacanthus oriolis</i>      | <i>Eurillas latirostris</i>       | Pycnonotidae      | Congo Basin         | KU187307         |
| P   | <i>Menacanthus oriolis</i>      | <i>Eurillas latirostris</i>       | Pycnonotidae      | Kenya               | KJ730611         |
| Q   | <i>Menacanthus takayamai</i>    | <i>Locustella luscinioides</i>    | Locustellidae     | Slovakia            | KJ730535         |
| Q   | <i>Menacanthus takayamai</i>    | <i>Locustella luscinioides</i>    | Locustellidae     | Slovakia            | KJ730536         |
| R   | <i>Menacanthus cornutus</i>     | <i>Gallus gallus</i>              | Phasianidae       | Czech Republic      | KJ730572         |
| R   | <i>Menacanthus cornutus</i>     | <i>Gallus gallus</i>              | Phasianidae       | Czech Republic      | KJ730573         |
| S   | <i>Menacanthus alaudae</i>      | <i>Plocepasser mahali</i>         | Ploceidae         | South Africa        | KF768803         |
| S   | <i>Menacanthus alaudae</i>      | <i>Plocepasser mahali</i>         | Ploceidae         | South Africa        | KJ730592         |
| T   | <i>Menacanthus camelinus</i>    | <i>Lanius collurio</i>            | Laniidae          | Sweden              | KJ730549         |
| T   | <i>Menacanthus camelinus</i>    | <i>Lanius collurio</i>            | Laniidae          | Sweden              | KJ730553         |
| U   | <i>Menacanthus chrysophaeus</i> | <i>Emberiza schoeniclus</i>       | Emberizidae       | Japan               | KJ730605         |
| U   | <i>Menacanthus chrysophaeus</i> | <i>Emberiza spodocephala</i>      | Emberizidae       | Japan               | KJ730604         |
| V   | <i>Menacanthus nogoma</i>       | <i>Calliope calliope</i>          | Muscicapidae      | Japan               | KJ730580         |
| V   | <i>Menacanthus nogoma</i>       | <i>Larvivora sibilans</i>         | Muscicapidae      | Viet Nam            | KJ730574         |
| W   | <i>Menacanthus pici</i>         | <i>Picus viridis</i>              | Picidae           | Sweden              | KJ730589         |
| W   | <i>Menacanthus pici</i>         | <i>Picus viridis</i>              | Picidae           | Sweden              | KJ730590         |

(Continues)

TABLE 3 | (Continued)

| OTU | Louse species                   | Host species                   | Host family    | Collection location | Accession number |
|-----|---------------------------------|--------------------------------|----------------|---------------------|------------------|
| X   | <b><i>Menacanthus</i> sp. 3</b> | <i>Phylloscopus pulcher</i>    | Phylloscopidae | China               | J5061-1          |
| Y   | <b><i>Menacanthus</i> sp. 4</b> | <i>Schoeniparus dubius</i>     | Pellorneidae   | China               | J5567-1          |
| Z   | <b><i>Menacanthus</i> sp. 6</b> | <i>Arborophila rufogularis</i> | Phasianidae    | China               | J5195-5          |

Note: Louse names that are bolded indicate specimens that were collected in the present study. Non-bolded louse names indicate sequences that were obtained from GenBank. Letters indicate operation taxonomic unit (OTU).

#### 4.2 | Host Associations and Mixed Species Flocks

Of the 17 species of *Brueelia*-complex lice obtained from more than one host individual in this study, a total of 13 species (76.5%) were collected from more than one host species (Figure 1; Table 1). For *Menacanthus*, that proportion is 4 of 6 (66.7%) and for *Myrsidea* 8 of 13 (61.5%). In some cases, a single specimen of a louse species was found on a different host species than the others (e.g., *Myrsidea* sp. 21; *Myrsidea* sp. 11), indicating that our specimens may derive from contaminations during catching or handling.

In some cases, such contaminations may be straightforward to identify. For instance, in the examples mentioned above, the *Myrsidea* sp. 11 specimen from *Arachnothera magna* was collected shortly after two *Turdus dissimilis*, both infested with *Myrsidea* sp. 11, were handled, suggesting contamination. In other cases, natural straggling may be a better explanation; for instance, over 8 h of catching and fumigating separate the *Myrsidea* sp. 21 collected from *Stachyris nigriceps* from the previous *Schoeniparus dubius* being infested with the same louse species. Similarly, both samples of *G. (Cicchinella)* sp. 3 collected from *Leiothrix argentea* were obtained on days when no lice of this species were found on any *S. dubius*. Moreover, the only member of the subgenus *G. (Dicruobates)*, normally found on drongos, we collected was from a babbler; no drongos were caught during the entire field trip, and *G. rufulus* was the only bird species caught at that locality. In all these three cases, natural straggling or previously unrecorded host generalism are more probable explanations than contamination.

Whereas lice in the genus *Guimaraesiella* and some other *Brueelia*-complex lice are known to be able to switch hosts through phoretic attachment to hippoboscids flies [41], this is presently not known for any species of *Myrsidea*. Instead, lice of this genus are generally considered host specific, with 80% of species being monoxenous [37]. Nevertheless, host specificity does not imply cospeciation, as shown by numerous phylogenetic analyses of *Myrsidea* in which host switches are apparent [40, 91–93]. Moreover, natural host switching and polyxeny have been documented in different species of *Myrsidea* [37, 94]. The mechanisms behind such host switching, if not related to phoresy, are presently unknown.

Host participation in mixed-species feeding flocks may increase the frequency of opportunities for host switching. Indirect data supporting this has been published for numerous groups of bird lice [38, 40, 95–98], and artificial transfer experiments have shown that there may be no barriers to host switching at least between similarly-sized hosts [99]. Although most of the cases in our data where a single louse OTU was recovered from multiple

host species involve hosts that regularly participate in the same mixed-species flocks in the TBG are (pers. obs.), we were unable to establish whether the exact birds involved were in mixed-species flocks. However, as such flocks may be somewhat fluid, with birds joining and leaving occasionally [100], such data may not be informative.

It is perhaps notable that, in many cases, host generalists in the *Brueelia*-complex were recovered from birds of similar size; for instance, all three hosts infested by *Pr. (Ca.) lindquistae* are large-bodied laughingthrushes, whereas all hosts infested by *G. (Cicchinella)* sp. 4 and *G. (Ci.) mcgrewi* were small-bodied babblers. However, this is not always the case, as species like *G. (Guimaraesiella)* sp. 4 and *P. (T.) austini* were both recovered from host species of very different sizes. Moreover, *Menacanthus eurysternus* B was recovered from both large-bodied thrushes and some of the smallest-bodied host species examined (*Orthotomus sutorius* and *Anthipes monileger*). This is in contrast to the results from artificial transfer studies of pigeon lice, which found that lice transferred between hosts of very different body size did not generally survive [99]. This raises questions about how generalizable the results from artificial transfer studies are for other groups of lice, particularly amblyceran lice or ischnoceran lice of the body louse or “generalist” ecomorphs. These groups of lice would not be expected to have body sizes correlated to host sized (Harrison’s rule; [101]), as their microhabitat niches and host defense escape mechanisms are different from wing lice. Transfer experiments of lice belonging to different families or microhabitat niches between non-pigeon hosts of different sizes are much needed to establish how flexible chewing lice are in their host choice.

#### 4.3 | Biogeography

The environmental factors that shape the geographical distribution of lice are poorly known, with most published studies focusing on ambient humidity [19]. Although cases are known where physical geography may constrain louse populations, such examples are generally continental in scale [102–104], with few examples known where more local geographical features (e.g., rivers, mountain ranges) form barriers to lice [27, 68, 105]. Although the overall resolution of the geographical range of lice in Yunnan is limited, outlines of some patterns worthy of further investigation can be seen in our data.

First, the louse species *Guimaraesiella ailaoshanensis* was described from *S. dubius* in the Ailaoshan mountain range in central Yunnan by Gustafsson et al. [78], where it occurred at a prevalence of 47%. *Schoeniparus dubius* is one of few host species examined both here and by Gustafsson et al. [78], and notably the

species of *Guimaraesiella* collected from *S. dubius* in the TBG area is not the same species as that in the Ailaoshan range, based on morphology. Tian et al. [38] included one sample from *S. dubius* from the same locality as *G. ailaoshanensis*, finding it to be nearly identical to *Guimaraesiella citreisoma*, commonly known from *Leiothrix lutea*; whether these two species should be considered synonymous will be addressed elsewhere. Here, we note that the within-group uncorrected *p*-distances of both the *G. citreisoma* specimens published by Tian et al. [38] and the *G. (Cicchinella)* sp. 3 specimens included here are both 0.001%, whereas between-group distances are 3.88%, sufficient to place them in different OTUs under the setting used here, particularly given the morphological differences.

Secondly, Gustafsson et al. [78] described *Resartor elugeus* based on specimens collected in the Ailaoshan range, reportedly at a prevalence of 100% of four examined *Alcippe fratercula yunnanensis*. Despite having examined 126 *A. f. yunnanensis* in the TBG area, no specimens of any species of *Resartor* were obtained from this host (Table 1). *Resartor* belongs to a group of lice in the *Brueelia*-complex suspected to be adapted to high elevations, which is likely a proxy for some other, presently unknown, environmental factor [70]. The Ailaoshan samples were all collected at an altitude of 2360 m, whereas the TBG samples are from around 1500 m, with the exception of the Badui locality which is at around 800 m. One possibility is thus that *R. elugeus* does not occur below a certain elevation.

However, strangely *Resartor elugeus* was obtained in the TBG area from multiple specimens of *Stachyris nigriceps* and occasionally from some other host species (Table 1; Figure 1). Sequences of *R. elugeus* from the type locality have been compared with those obtained from *S. nigriceps* in the TBG area, and found to be nearly identical (data not shown), indicating that this is not a case of cryptic speciation. Instead, it would appear that there is a geographical difference in host preference between Ailaoshan (*A. f. yunnanensis*) and the TBG area (*S. nigriceps*). No specimens of *S. nigriceps* were examined in Ailaoshan [78], which is at the upper limit of the altitudinal range for this species [32].

Notably, *S. nigriceps* were caught at many of the TBG localities situated around 1500 m, but also at the Badui locality at 800 m. In total, 37 *S. nigriceps* were caught at around 1500 m, whereas 12 were caught at around 800 m. The prevalence of *R. elugeus* at 1500 m is 21.6%, whereas no *R. elugeus* were collected at the lower elevation. As only a single locality at a lower elevation was used, it is possible that a broader survey of lower-elevation localities in the TBG area would result in *R. elugeus* being found at lower elevations as well. The other *Resartor* species collected in this study, *R. novofacies*, was collected at both the 1500 m localities (3 of 22 birds; prevalence 13.6%) and at Badui (2 of 4 birds; prevalence 50.0%), showing that at least some species of *Resartor* occur at lower elevation.

Finally, we note the nearly complete absence of *Guimaraesiella impiger* in the TBG area, collected from only three host individuals of three different species. This louse species was recently described as having an extensive geographical and host range, being known from across south China, the Philippines, Singapore, and Malawi [98]. Many of the known hosts of this super-generalist louse species were caught at TBG, and the species is previously known from the general area [98]. The paucity of this

species in our samples is puzzling, especially as two of the three records here are from novel hosts. *Guimaraesiella impiger* is particularly associated with flycatchers (Muscicapidae, 13 of 32 known host species) [98], but in our samples from the TBG area, flycatchers were generally not infested by lice (Supporting Information 1: Table S1), or were infested with the undescribed *G. (Guimaraesiella)* sp. 4 instead (Table 1; Figure 1). This species, and potential interactions between it and *Guimaraesiella impiger*, will be discussed elsewhere.

More fine-grained investigations of the spatial distribution of lice in Yunnan are needed before these patterns can be analyzed in detail. However, as rivers have been shown to form barriers for lice elsewhere [27, 105], it is possible that the many rivers and mountain ranges running through Yunnan form distributional barriers to some groups of lice, even if the hosts are largely unaffected. Similar differences have been reported in *Myrsidea* from Yunnan and Sichuan by Grossi et al. [40] and in *Priceiella* on different sides of the Nanling Mountains in South China by Gustafsson et al. [68]. Whether rivers or mountain ranges are working as barriers to gene flow between louse populations in Yunnan, and if so, which are the most important barriers, needs further research.

#### 4.4 | Myrsidea and Menacanthus

The amblyceran fauna of birds caught in the TBG area is dominated by the genera *Myrsidea* and *Menacanthus* (Figure 2), with most amblyceran samples belonging to the former genus. Moreover, whereas several *Myrsidea* species were found at high prevalence, none of the *Menacanthus* species collected can be said to be common in the TBG area, with most species only being collected a single time from a host (Table 2). This difference in diversity is expected, as species of *Myrsidea* generally are host-specific, whereas *Menacanthus* contains numerous species that are widely distributed across many host species, including many cases where hosts in multiple families are involved [58]. Similarly, *Myrsidea* appears to be more common in previous collections in China and Southeast Asia [25, 26, 78, 106].

However, almost none of the *Menacanthus* OTUs collected in the TBG area could be identified to species level using the key of Price [57]. In many cases, specimens are morphologically similar to known species, but differ in details of, for example, chaetotaxy, shape of the gular plate, etc. Moreover, specimens identified as *Menacanthus eurysternus*—a known super-generalist louse [58]—were placed in different OTUs in our analysis. We therefore ran a separate analysis consisting of our *Menacanthus* specimens as well as all representatives of *Menacanthus eurysternus*, and at least two representatives of all other species of *Menacanthus* found on GenBank.

The results of the *Menacanthus*-specific phylogeny (Figure 3) indicate that *Menacanthus eurysternus* as currently circumscribed likely consists of several species. Specimens identified as *M. eurysternus* were divided into eight different OTUs, of which one represents *M. balati* [75]. Of the seven other OTUs, the specimens collected at TBG were represented in two: an OTU that combined *M. eurysternus* B and C from our main Amblycera analysis, and an OTU that includes all our specimens of *M. eurysternus* A. This discrepancy in OTU delimitations between the two data sets, despite using the same setting, makes



us wary of interpreting the results for *M. eurysternus* before more data has been analyzed. However, it is notable that some clades appear to be limited to certain host groups or geographical regions. For instance, *M. eurysternus* D comprises only specimens from the Neotropics and *M. eurysternus* E and F are all from Africa (Table 3). Similarly, *M. eurysternus* A contains only specimens collected from closely related babblers and white-eyes [107]. By contrast, the *M. eurysternus* B+C clade contains specimens from across most of the known range of *M. eurysternus*, and from a multitude of different host families, echoing the findings of Martinů et al. [35].

Notably, among the *Menacanthus* specimens collected at TBG not identified as *M. eurysternus* group, none were placed in the same OTUs as any of the known species of *Menacanthus* available on GenBank. This may not be significant, as sequences are only available for a handful of the ~100 species of *Menacanthus* currently accepted as valid [58]. However, several of the species collected at TBG key to known species in the key of Price [57]. For instance, *Menacanthus* sp. 1 keys to *M. sinuatus* and *Menacanthus* sp. 5 keys to *M. orioli*. In each case, GenBank specimens identified to *M. sinuatus* and *M. orioli*, respectively, form sister clades to our specimens. The GenBank specimens of *M. sinuatus* are both from boreal hosts, whereas those of *M. orioli* are from African hosts, hinting at geographical patterns of cryptic speciation.

Clearly more data is needed on *Menacanthus* species across the world, including both known and unknown species. Our data from the TBG area indicates that there may be a large undiscovered diversity of *Menacanthus* in Yunnan, and that many of the species in this group may be relatively rare, compared to the more prevalent *Myrsidea*. Finally, morphological data is needed to establish whether different clades of *M. eurysternus* constitute cryptic species, or if useful morphological characters have been overlooked. From a preliminary survey of the specimens available to us, the key to *Menacanthus* on songbirds by Price [57] is in part very vague, particularly in characters leading to *M. eurysternus*. A larger revision of the genus is sorely needed.

## 5 | Conclusions

The previously unknown diversity of chewing lice in a small part of Yunnan Province, China, indicates that the region's status as a biodiversity hotspot extends also to parasitic animals. Among our collections from a small area in western Yunnan, only five of 67 collected species were previously known from Yunnan, and that the majority of the collected species are undescribed. This echoes the several estimates of vast unexplored louse diversity in other parts of the world [98, 108, 109]. Moreover, it highlights the necessity for more parasitological research in Yunnan and the greater biodiversity hotspot of which it is part.

Although published comparative data is limited, our data from the TBG area indicate that there are differences in, for example, louse prevalence and host associations across Yunnan, the outlines of which can just barely be seen. Most interestingly, the finding that some louse species are associated with different hosts in different localities (*Resartor elugeus*) and the suggestion that

some geographical features may act as distributional barriers to lice needs further investigation.

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## Conflicts of Interest

The authors declare no conflicts of interest.

## Data Availability Statement

Sampling and collection data can be found in Supporting Information 1: Table S1 of the supporting information section; including GenBank accession numbers.

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### Supporting Information

Additional supporting information can be found online in the Supporting Information section.

[Supporting Information 1](#). Table S1: Collection information and GenBank accession number.

[Supporting Information 2](#). Table S2: Bird species from which no lice were obtained during this study.

[Supporting Information 3](#). Table S3: Host individuals examined that were infested with more than one louse species.