



PHYLOGENETIC RELATIONSHIPS OF *GUIMARAESIELLA* AND *PRICEIELLA* (PHTHIRAPTERA: ISCHNOCERA) FROM BABBLERS AND NON-BABBLERS (PASSERIFORMES)

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KEY WORDS ABSTRACT

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Phylogeny
Brueelia complex
Mixed-species flock
South China

Babblers (Passeriformes: Leiothrichidae, Pellorneidae, Timaliidae) are parasitized by more genera of lice of the *Brueelia* complex than any other group of songbirds. However, the relationships of these louse groups are poorly known. We here try to resolve the relationships between *Guimaraesiella* (*Guimaraesiella*), *Guimaraesiella* (*Cicchinella*), and their putative sister group *Priceiella* by using mitochondrial cytochrome *c* subunit 1 (*COI*), *12S*, and *16S* sequences. Our data indicate that *G. (Cicchinella)* forms a monophyletic group of lice from babblers, but the relationship between *G. (Guimaraesiella)*, *G. (Cicchinella)*, and *Priceiella* could not be resolved. Moreover, the position of the third lineage of babbler-specific lice, containing only the aberrant species *Guimaraesiella montisodalis*, is unresolved. Morphologically, this species is different from all other *Guimaraesiella* in several characters and may represent a distinct lineage. We present some data indicating that (1) the Nanling Mountain range may be a biogeographical barrier to chewing lice and (2) host participation in mixed-species feeding flocks may influence host associations in *Brueelia*-complex chewing lice.

Chewing lice in the *Brueelia* complex constitute one of the largest radiations of phthirapteran lice, occurring primarily on passeriform hosts (Gustafsson and Bush, 2017). This complex includes both genera that are known from only a single host family and genera that are widely distributed (e.g., Bush et al., 2016). This pattern is reflected on the species level, as some species are known only from a single host, some from a few closely related hosts, and some from a variety of hosts belonging to different families (Gustafsson and Bush, 2017). Host specialists and host generalists in the *Brueelia* complex may belong to the same genus, which suggests that the evolutionary history of these lice has involved both coevolution with their hosts and bouts of host switching, sometimes between distantly related hosts (Sweet et al., 2018). However, the factors that balance coevolution and host switching in the *Brueelia* complex are poorly known.

Babblers constitute a large radiation of small to medium-sized birds, most of which are found in tropical and subtropical Asia (Clements et al., 2019). Traditionally, babblers have been placed in the family Timaliidae, but more recent classification schemes based on genetic data have divided the family into 3 different families (Leiothrichidae, Pellorneidae, Timaliidae) and moved several “babbler” genera to other families (e.g., Reddy and

Cracraft, 2007; Gelang et al., 2008; Moyle et al., 2012; Oliveros et al., 2012; Cibois et al., 2018; Cai et al., 2019; Clements et al., 2019).

Collectively, the 3 babbler families are parasitized by a unique chewing louse fauna. For instance, lice of the head louse ecomorph (*sensu* Johnson et al., 2012) and lice in the genus *Menacanthus* Neumann, 1912, are largely absent from babblers despite being present on almost all other oscine passeriform families (Price et al., 2003; Mey, 2004). By contrast, babblers are collectively parasitized by more different *Brueelia*-complex louse groups than any other group of birds (Gustafsson and Bush, 2017; see our Table I). Most of the *Brueelia*-complex louse groups known from babblers are not known from any non-babbler hosts other than as occasional stragglers (Gustafsson and Bush, 2017; Table I).

The *Brueelia*-complex lice of babblers are not closely related (Bush et al., 2016; Gustafsson and Bush, 2017), and representatives of 3 of the 4 major radiations within this complex are known from babblers (Table I). This mixture of lice from these 3 radiations on babblers is also somewhat unusual; more typically, host species in a family are collectively parasitized by lice belonging to 1 or 2 of these radiations (Gustafsson and Bush,

Table 1. Host distribution of the *Brueelia*-complex louse genera on babblers. Subgenera of *Priceiella* and species groups of *Cicchinella* are here treated separately for clarity. “X” denotes presence of lice in a group on at least some members of a host family; dashes (“—”) denote that no lice of a group have been described from any host in a family. Data for distribution derive from Gustafsson and Bush (2017), Mey (2017), and Gustafsson et al. (2018a, 2018b, 2019a, 2019b, 2021c).

Louse group	Leiothrichidae	Pellorneidae	Sylviidae†	Timaliidae	Zosteropidae‡
<i>Brueelia</i> group					
<i>Brueelia</i> (“ <i>Painjunirmus</i> ”)*§	X	—	—	—	—
<i>Resartor</i> group					
<i>Ceratocista</i> *	X	—	—	—	—
<i>Resartor</i> *	X	—	X	—	—
<i>Timalinirmus</i> *	—	—	—	X	X
<i>Guimaraesiella</i> group					
<i>Camurnirmus</i> *	X	—	—	—	—
<i>Cicchinella gombakensis</i> group*	X	X	—	—	—
<i>Cicchinella sehri</i> group*	X	X	—	—	X
<i>Cicchinella tenella</i> group*	—	—	—	X	—
<i>Cicchinella</i> ?*	—	—	X	—	—
<i>Priceiella</i> s. str.*	X	—	—	—	—
<i>Thescelovora</i>	X	X	X	X	—
<i>Torosinirmus</i> *	X	—	—	—	—

* These groups are not previously known to be established on any host groups apart from those listed here.

† Only data for species traditionally considered babblers are shown. This includes the parrotbills and members of the genera *Myzornis*, *Lioparus*, *Chrysomma*, *Fulvetta*, and *Rhopophilus* (Moyle et al., 2012). Other members of this family are parasitized by either *Brueelia* Kéler, 1936, or *Guimaraesiella* s. str. Eichler, 1949 (Gustafsson and Bush, 2017).

‡ Only data for yuhinas, traditionally considered babblers, are shown. No lice in the *Brueelia* complex have been described from white-eyes (Gustafsson and Bush, 2017).

§ The position of this group in relation to *Brueelia* s. str. is presently unknown. Gustafsson and Bush (2017) treated this group as a synonym of *Brueelia* Kéler, 1936, but noted that it may be better considered a distinct species group or subgenus.

|| This represents *Guimaraesiella montisodalis*, which was not grouped with the other *Cicchinella* in our analysis and may represent an independent lineage of uncertain relationships.

2017). Moreover, host associations of the *Brueelia* complex generally follow 2 broader patterns.

In general, songbirds in the Passerida radiation are parasitized by lice in the genus *Brueelia* and its close relatives (*Brueelia* group; clades I–K in Bush et al., 2016, Figs. 2 and 3), whereas songbirds in the Corvidae radiation are parasitized by lice belonging to *Guimaraesiella* and its close relatives (*Guimaraesiella* group; clades A–H in Bush et al., 2016, Figs. 2 and 3; see also Gustafsson and Bush, 2017). This suggests that, on the broad scale, *Brueelia*-complex lice in these 2 lineages may have coradiated with their hosts. The division of most of the diversity of the *Brueelia* complex into these 2 patterns is consistent with proposed scenarios for oscine expansions from Australo-Pacific region, whether these include different routes of expansion (e.g., Jönsson and Fjeldså, 2006) or different timing of expansion (Oliveros et al., 2019).

One major exception to this is babblers, which are part of the Passerida (e.g., Barker et al., 2004; Oliveros et al., 2019) but are parasitized mainly by lice in the *Guimaraesiella* group (Gustafsson and Bush, 2017). This fits into a second general pattern of *Brueelia*-complex host associations: *Brueelia*-group lice are generally associated with more arid environments, whereas *Guimaraesiella*-group lice are typically found on birds occupying more humid areas (e.g., Takano et al., 2019). Notably, the only *Brueelia*-group lice known from babblers are the “*Painjunirmus*” group known only from babblers in the genus *Turdoides*, which occur in more dry, open country than most other babblers. Similarly, *Brueelia*-group lice parasitizing hosts in the Corvidae are generally adapted to dry regions (e.g., Gustafsson and Bush, 2019). In contrast, passeridan hosts in humid areas are generally

parasitized by lice in the *Guimaraesiella* group (e.g., Mey and Barker, 2014).

Bush et al. (2016) published the most comprehensive phylogeny of *Brueelia*-complex lice to date, but this phylogeny included only 3 of the genera of lice known from babblers: *Guimaraesiella* Eichler, 1949, *Priceiella* Gustafsson and Bush, 2017, and *Resartor* Gustafsson and Bush, 2017. Of these, the genera *Guimaraesiella* and *Priceiella* were placed close together (Bush et al., 2016, Figs. 3a–b, clades A–C), but their relationship was not resolved. Morphologically, these 2 genera are well separated by characters of the preantennal head and male genitalia (Gustafsson and Bush, 2017; Gustafsson et al., 2018b, 2019a). Moreover, the *Guimaraesiella* species on babblers have been separated into a distinct subgenus, *Cicchinella* Gustafsson et al., 2019a, which is further divided into 3 species groups (Gustafsson et al., 2019a). Only 1 species of *Cicchinella* was included in the phylogeny of Bush et al. (2016), and the monophyly of this subgenus was therefore based on morphological characters only.

The relationships between *Cicchinella*, *Priceiella*, and *Guimaraesiella* have implications for the larger-scale coevolutionary history of babblers and their *Brueelia*-complex lice. Each combination of these 3 groups implies different scenarios. More data, including nuclear genes, will be needed to resolve their relationships and the evolutionary history of the group. However, the complete absence of *Brueelia*-group lice from any babbler species in South China in our samples (D. R. Gustafsson and F. Zou, unpubl. data) implies that potential ancestral *Brueelia*-group lice parasitizing babblers have been replaced entirely by *Guimaraesiella*-group lice through 1 or more colonization events, followed by extensive radiation of *Cicchinella* and *Priceiella* on

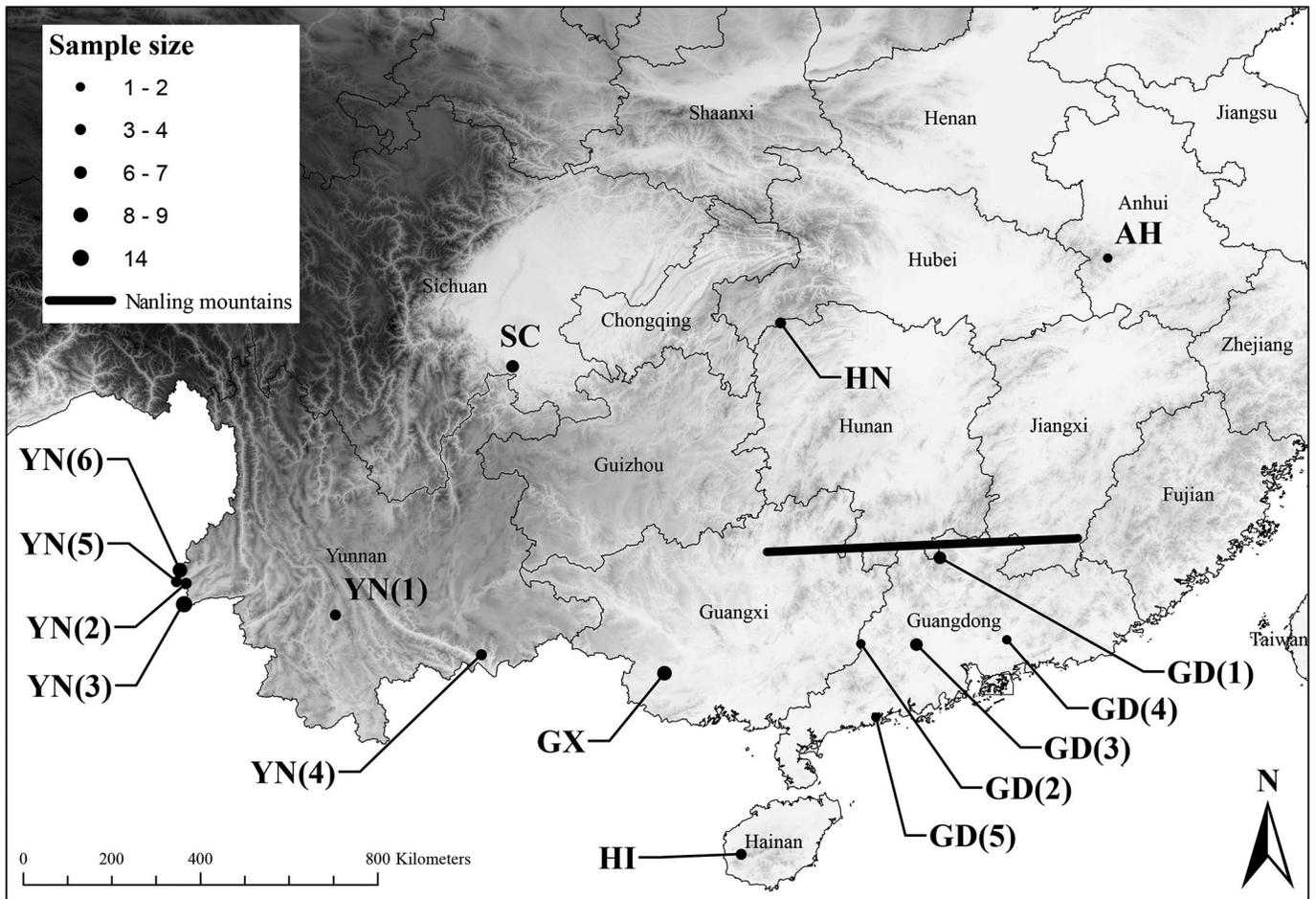


Figure 1. Map of South China, showing the sampling localities for specimens sequenced in this study. Province abbreviations used: AH = Anhui; GD = Guangdong; GX = Guangxi; HI = Hainan; HN = Hunan; SC = Sichuan; YN = Yunnan. For more detailed locality information, see Table II, in which the same numbering system is used. The size of black circles corresponds to the sample number from this site. The black line symbolizes the approximate position and direction of the Nanling Mountains; the actual mountain range is broader than this and comprises several ridges and massifs, as well as encompasses the collection locality GD(1), which is on the south slope.

babblers. The morphological differences between *Priciella* and *Cicchinella* suggest that at least 2 separate colonization events probably occurred.

Babblers are frequent participants in mixed-species feeding flocks (e.g., Chen and Hsieh, 2002; Kotagama and Goodale, 2004; Zou et al., 2011), which may explain the distribution of some of the louse groups known from these hosts (Gustafsson et al., 2018b, 2019a). Transfer from 1 host to another typically happens only when 2 host individuals are in physical contact with each other (e.g., Hillgarth, 1996; Brooke, 2009). Presumably, regular proximity and interaction between birds in a mixed-species feeding flock would increase the opportunity for louse transfer between different species. Mixed-species feeding flocks may also increase the opportunity to louse transfer via phoresy on hippoboscids (Harbison et al., 2009; Bartlow et al., 2016), because lice that are capable of phoresy are much better at transmitting to new hosts than lice that are not phoretic (Harbison et al., 2008). However, even if participation in mixed-species feeding flocks may explain the relative homogeneity of the *Brueelia*-complex louse fauna parasitizing the different groups of babblers, it does not explain why these louse groups are absent

from non-babbler hosts, which also frequently participate in the same flocks (e.g., Zou et al., 2011). Presently, only a single species of louse belonging to the groups listed in Table I has been described from a non-babbler host (Gustafsson and Bush, 2017), and virtually no babbler-specific lice were found on non-babbler hosts among the ~30,000 specimens of *Brueelia*-complex lice the last author has examined over the last 9 years (D. R. Gustafsson, unpubl. data). This is all the more remarkable as the prevalence of *Brueelia*-complex lice on non-babblers is often low in Southeast Asia (e.g., Gustafsson et al., 2019b), which suggests that babbler-specific lice transferring to non-babbler hosts in the same flocks could often find open niches where they would not be competing for resources with host-specific lice.

We sampled lice in the genera *Guimaraesiella* and *Priciella* from babblers and non-babblers across South China to address 3 questions: (1) What is the phylogenetic relationship between *Priciella* and *Guimaraesiella*? (2) Do the 3 species groups of *Cicchinella* form a monophyletic group? and (3) Do babbler-specific groups of lice ever occur on non-babblers participating in the same mixed-species flocks?

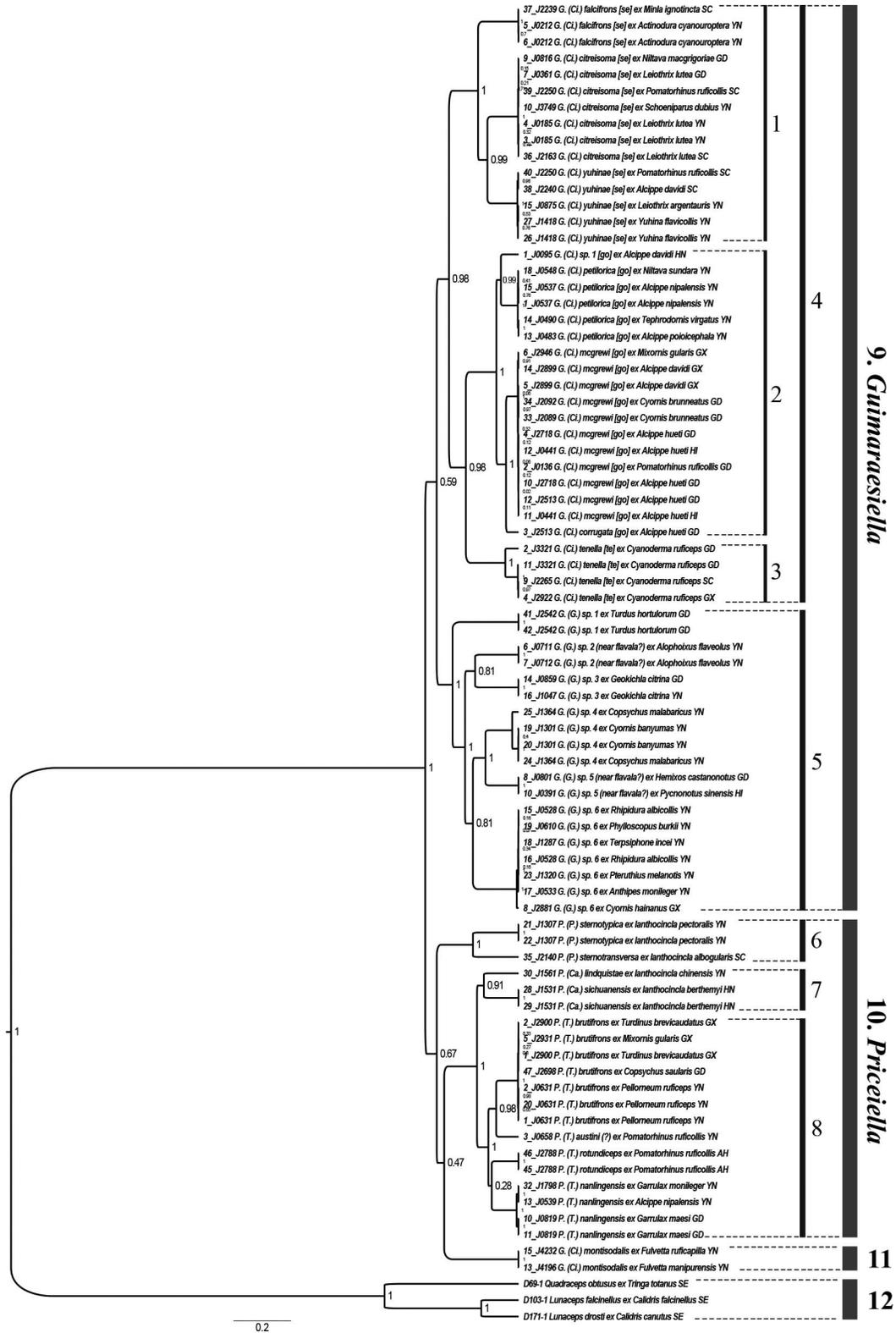


Figure 2. Phylogenetic reconstruction of *Guimaraesiella*, *Cicchinella* and *Priceiella* inferred by BEAST v1.10.4, with node posterior probabilities shown in smaller font. Identification numbers of taxa (e.g., 37_J2239) correspond to data in Table III. Locality data are given only to province level in the tree (country level for outgroups). Numbered groups correspond to taxa discussed in the text: 1 = *Guimaraesiella* (*Cicchinella*) *sehri* species group; 2 = *Guimaraesiella* (*Cicchinella*) *gombakensis* species group; 3 = *Guimaraesiella* (*Cicchinella*) *tenella* species group; 4 = *Guimaraesiella* (*Cicchinella*); 5 = *Guimaraesiella* (*Guimaraesiella*) [= *Guimaraesiella* s. str.]; 6 = *Priceiella* (*Priceiella*) [= *Priceiella* s. str.]; 7 = *Priceiella* (*Camurnirmus*); 8 = *Priceiella* (*Thescelovora*); 9 = *Guimaraesiella* s. lat.; 10 = *Priceiella* s. lat.; 11 = *Guimaraesiella* (?) *montisodalis*; 12 = Outgroups.

Table II. Summary of collection localities for samples used in this study. For the location of each sampling locality, see Figure 1.

Abbreviation	Province	Locality
AH	Anhui	Baiguo Village, Zhubo Town, Yuexi County
GD(1)	Guangdong	Babaoshan Management Station, Nanling National Nature Reserve
GD(2)	Guangdong	Tongle Nature Reserve, Yunan County
GD(3)	Guangdong	Dinghushan National Nature Reserve, Zhaoqing City
GD(4)	Guangdong	Xiangtoushan National Nature Reserve
GD(5)	Guangdong	Xitou Town, Yangxi County
GX	Guangxi	Guanghe Village, Zuozhou Town, Jiangzhou District, Chongzuo City
HI	Hainan	Hainan Houmaling Provincial Nature Reserve
HN	Hunan	Badagong Mountain National Nature Reserve, Sangzhi County, Zhangjiajie City
SC	Sichuan	Laojun Mountain Nature Reserve, Pingshan County, Yibin City
YN(1)	Yunnan	Ailao Mountain National Nature Reserve
YN(2)	Yunnan	Pingshan Village, Husa Township, Longchuan County, Dehong Prefecture
YN(3)	Yunnan	Weijiao Village, Huyu Township, Ruili City, Dehong Prefecture
YN(4)	Yunnan	Dawei Mountain Nature Reserve, Pingbian, Honghe Prefecture
YN(5)	Yunnan	Hongbeng River, Yingjiang County, Dehong Prefecture
YN(6)	Yunnan	Rongshuwang Highway, Daonong Village, Nabang Township, Yingjiang County, Dehong Prefecture

MATERIALS AND METHODS

Birds were caught and fumigated for lice in several localities across South China during 2012–2021 (Fig. 1; Table II) using mist nets following the methods outlined by Gustafsson et al. (2019b). Louse specimens were stored in 95% ethanol in a –80 C freezer at the Institute of Zoology, Guangdong Academy of Sciences (IZGAS), Guangdong, China. Hosts were identified using MacKinnon and Phillipps (2000) or Arlott (2017); host taxonomy has been updated to conform with Clements et al. (2019). Lice were identified to genus and subgenus level following the key of Gustafsson and Bush (2017). At least 1 louse specimen (typically 1 male and 1 female) identified as *Guimaraesiella* or *Priceiella* from each host species was selected for DNA extraction. When possible, lice were identified to species level using the keys and descriptions of Gustafsson et al. (2018b, 2019a, 2021a).

Selected lice (Table III) were cut halfway through the prothorax and extracted for DNA using the DNeasy Blood and Tissue Kit (Qiagen, Shanghai, China) following the manufacturer's instructions. Exoskeletons were retrieved from the extraction fluid and slide mounted in Canada balsam as vouchers, following Palma (1978) and Gustafsson et al. (2019b). Vouchers are deposited in the collection at IZGAS.

Amplification and sequencing of 3 mitochondrial markers (*COI*, *12S*, *16S*) were attempted, following Gustafsson and Olsson (2012). However, *16S* was rarely amplified; instead, we designed new louse-specific *16S* primers based on sequences from a *Myrsidea* mitochondrial genome sequence (GenBank accession number MW199174.1) and specimen 25_J1364 *Guimaraesiella* (see Table II), using Primer Premier 6 (Premier Biosoft, San Francisco, California). These new primer sequences are 16S03F (5'-CAATACTGGCTTGCATGT-3') and 16S03R (5'-GATA-GAACTGACCTGACTTAC-3'). The reaction program for these new primers is the following: pre-denaturation at 94 C for 3 min; denaturation at 94 C for 30 sec; annealing at 47 C for 45 sec; extension at 72 C for 30 sec; and after 40 cycles, extension at 7 C for 7 min. The sequences obtained with the new primers are generally about 20 bp longer than those obtained by 16SAR and 16SBR and were therefore trimmed to the same length during alignment (see below). PCRs were performed using Cytiva

PureTaq Ready-To-Go beads (GE Healthcare, Vienna, Austria), following the manufacturers' instructions. All PCR products were tested on an ethidium bromide gel. Samples showing satisfactory bands were sent for sequencing using the same primers as for PCR to Tianyi Huiyuan Gene Technology, Co. Ltd. (Guangzhou, China).

Sequences were assembled in Seqman Pro 7.1.0 (DNASTar Inc., Madison, Wisconsin) and checked manually to rule out mismatches between forward and reverse sequencing results for each gene and each individual. Sequences were aligned in MEGA X using ClustalW and MUSCLE (Edgar, 2004; Larkin et al., 2007; Kumar et al., 2018). Substitution models for each gene were evaluated in MEGA X; the best model for the *COI* data was GTR+G+I, and for each of the *12S* and *16S* data sets the best model was HKY+G. The 3 aligned and partitioned genes were imported into BEAST v1.10.4 (Suchard et al., 2018), with default settings except for the options of linked trees, separated clock models for each gene, 4 Gamma Categories under the strict clock, and constant size of coalescence. Markov chain Monte Carlo (MCMC) tests were run for 5×10^8 generations and sampled every 5,000 generations. We used the Tree Annotator v1.10.4 (Suchard et al., 2018) for tree integration and discarded the first 10,000 trees as "burnin." The output tree from Tree Annotator was imported to FigTree v1.4.3 (Rambaud, 2006) for figure illustration. Genetic distances were calculated for the *COI* gene for each group of taxa separately (*Priceiella*, *Guimaraesiella* (*Guimaraesiella*), and *Guimaraesiella* (*Cicchinella*)) in MEGA X.

RESULTS

Our analysis resulted in a single tree (Fig. 2), in which both *Cicchinella* (Fig. 2; Group 4) and *Guimaraesiella* (Fig. 2; Group 5) were recovered as monophyletic with high support. Within *Cicchinella*, all 3 species groups (Fig. 2; Groups 1–3) are monophyletic with high support; the *gombakensis* and *tenella* species groups are sister groups, and the *sehri* species group is sister to *gombakensis+tenella*. *Priceiella* (Fig. 2; Group 10) was not recovered as monophyletic, but all 3 included subgenera of *Priceiella* were monophyletic (Fig. 2; Groups 6–8). A fourth lineage (Fig. 2; Group 11), containing only *Guimaraesiella*

Table III. Collection and sequence information for specimens included in this study. J-numbers refer to host individuals, whereas the initial numbers in the voucher number sequence is the sample number of the individual louse specimen. Thus, 5_J0212 and 6_J0212 refer to 2 lice collected from the same host specimen. Abbreviations used in genus names: *Ca* = *Camurnirmus*; *Ci.* = *Cicchinella*; *G.* = *Guimaraesiella*; *P.* = *Pricieliella*; *T.* = *Thescelovora*. Abbreviations used for collection localities: AH = Anhui; GD = Guangdong; GX = Guangxi; HI = Hainan; HN = Hunan; SC = Sichuan; YN = Yunnan; *Quadriceps*-complex outgroups were collected in Sweden (SE). For the location of each sampling locality, see Table I and Figure 1. Host taxonomy follows Clements et al. (2019); for brevity, host subspecies are not given. Louse species that could not be positively identified as any described species are denoted as “sp. #” or “sp. nov. #”; the latter represent taxa that are under review elsewhere but that had not been published at the time of submission of this paper. Specimens denoted “sp. #” may also represent new species but could not be positively identified as the specimens were nymphal, female, distorted, or broken or had key characters obscured.

Taxon information		Sequence data				
Louse species	Host species	Voucher no.	Locality	COI	12S	16S
<i>Guimaraesiella</i>						
Subgenus <i>Cicchinella</i>						
<i>G. (Ci.) sehri</i> species group						
<i>G. (Ci.) falcifrons</i>	<i>Minla ignotincta jerdoni</i>	37_J2239	SC	OL514089	OL527791	OL527869
<i>G. (Ci.) falcifrons</i>	<i>Actinodura cyanouroptera wingatei</i>	5_J0212	YN(4)	OL514045	OL527747	OL527825
<i>G. (Ci.) falcifrons</i>	<i>Actinodura cyanouroptera wingatei</i>	6_J0212	YN(4)	OL514046	OL527748	OL527826
<i>G. (Ci.) citreisoma</i>	<i>Niltava macgrigoriae macgrigoriae</i>	9_J0816	GD(1)	OL514065	OL527767	OL527845
<i>G. (Ci.) citreisoma</i>	<i>Schoeniparus dubius intermedius</i>	10_J3749	YN(1)	OL514103	OL527805	OL527883
<i>G. (Ci.) citreisoma</i>	<i>Leiothrix lutea yunnanensis</i>	4_J0185	YN(4)	OL514044	OL527746	OL527824
<i>G. (Ci.) citreisoma</i>	<i>Leiothrix lutea yunnanensis</i>	3_J0185	YN(4)	OL514043	OL527745	OL527823
<i>G. (Ci.) citreisoma</i>	<i>Leiothrix lutea kwangtungensis</i>	7_J0361	GD(1)	OL514047	OL527749	OL527827
<i>G. (Ci.) citreisoma</i>	<i>Leiothrix lutea lutea</i>	36_J2163	SC	OL514088	OL527790	OL527868
<i>G. (Ci.) citreisoma</i>	<i>Pomatorhinus ruficollis reconditus</i>	39_J2250	SC	OL514091	OL527793	OL527871
<i>G. (Ci.) yuhinae</i>	<i>Pomatorhinus ruficollis reconditus</i>	40_J2250	SC	OL514092	OL527794	OL527872
<i>G. (Ci.) yuhinae</i>	<i>Alcippe davidi davidi</i>	38_J2240	SC	OL514090	OL527792	OL527870
<i>G. (Ci.) yuhinae</i>	<i>Leiothrix argentauris vernayi</i>	15_J0875	YN(2)	OL514069	OL527771	OL527849
<i>G. (Ci.) yuhinae</i>	<i>Yuhina flavicollis rouxi</i>	27_J1418	YN(2)	OL514080	OL527782	OL527860
<i>G. (Ci.) yuhinae</i>	<i>Yuhina flavicollisrouxi</i>	26_J1418	YN(2)	OL514079	OL527781	OL527859
<i>G. (Ci.) gombakensis</i> species group						
<i>G. (Ci.)</i> sp. 1	<i>Alcippe davidi davidi</i>	1_J0095	HN	OL514041	OL527743	OL527821
<i>G. (Ci.) petilorica</i>	<i>Alcippe nipalensis*</i>	15_J0537	YN(6)	OL514040	OL527742	OL527820
<i>G. (Ci.) petilorica</i>	<i>Alcippe nipalensis*</i>	1_J0537	YN(6)	OL514028	OL527730	OL527808
<i>G. (Ci.) petilorica</i>	<i>Alcippe poioicephala haringtoniae</i>	13_J0483	YN(5)	OL514051	OL527753	OL527831
<i>G. (Ci.) petilorica</i>	<i>Niltava sundara denotata</i>	18_J0548	YN(6)	OL514056	OL527758	OL527836
<i>G. (Ci.) petilorica</i>	<i>Tephrodornis virgatus jugans</i>	14_J0490	YN(5)	OL514052	OL527754	OL527832
<i>G. (Ci.) mcgrewi</i>	<i>Mixornis gularis lutescens</i>	6_J2946	GX	OL514102	OL527804	OL527882
<i>G. (Ci.) mcgrewi</i>	<i>Alcippe davidi schaefferi</i>	14_J2899	GX	OL514039	OL527741	OL527819
<i>G. (Ci.) mcgrewi</i>	<i>Alcippe davidi schaefferi</i>	5_J2899	GX	OL514032	OL527734	OL527812
<i>G. (Ci.) mcgrewi</i>	<i>Cyornis brunneatus</i>	33_J2089	GD(2)	OL514085	OL527787	OL527866
<i>G. (Ci.) mcgrewi</i>	<i>Cyornis brunneatus</i>	34_J2092	GD(2)	OL514086	OL527788	OL527867
<i>G. (Ci.) mcgrewi</i>	<i>Alcippe hueti hueti</i>	4_J2718	GD(3)	OL514031	OL527733	OL527811
<i>G. (Ci.) mcgrewi</i>	<i>Alcippe hueti hueti</i>	10_J2718	GD(3)	OL514035	OL527737	OL527815
<i>G. (Ci.) mcgrewi</i>	<i>Alcippe hueti rufescentior</i>	12_J0441	HI	OL514050	OL527752	OL527830
<i>G. (Ci.) mcgrewi</i>	<i>Alcippe hueti rufescentior</i>	11_J0441	HI	OL514049	OL527751	OL527829
<i>G. (Ci.) mcgrewi</i>	<i>Pomatorhinus ruficollis reconditus</i>	2_J0136	GD(1)	OL514042	OL527744	OL527822
<i>G. (Ci.) mcgrewi</i>	<i>Alcippe hueti hueti</i>	12_J2513	GD(3)	OL514037	OL527739	OL527817
<i>G. (Ci.) mcgrewi</i>	<i>Alcippe hueti hueti</i>	3_J2513	GD(3)	OL514030	OL527732	OL527810
<i>G. (Ci.) tenella</i> species group						
<i>G. (Ci.) tenella</i>	<i>Cyanoderma ruficeps davidi</i>	2_J3321	GD(4)	OL514029	OL527731	OL527809
<i>G. (Ci.) tenella</i>	<i>Cyanoderma ruficeps davidi</i>	11_J3321	GD(4)	OL514036	OL527738	OL527816
<i>G. (Ci.) tenella</i>	<i>Cyanoderma ruficeps davidi</i>	9_J2265	SC	OL514034	OL527736	OL527814
<i>G. (Ci.) tenella</i>	<i>Cyanoderma ruficeps davidi</i>	4_J2922	GX	OL514100	OL527802	OL527880
Subgenus <i>Guimaraesiella</i> s. str.						
<i>G. (G.)</i> sp. 1	<i>Turdus hortulorum</i>	41_J2542	GD(3)	OL514093	OL527795	OL527873
<i>G. (G.)</i> sp. 1	<i>Turdus hortulorum</i>	42_J2542	GD(3)	OL514094	OL527796	OL527874
<i>G. (G.)</i> sp. 2 (near <i>flavala</i> ?)	<i>Alophoixus flaveolus burmanicus</i>	6_J0711	YN(3)	OL514062	OL527764	OL527842
<i>G. (G.)</i> sp. 2 (near <i>flavala</i> ?)	<i>Alophoixus flaveolus burmanicus</i>	7_J0712	YN(3)	OL514063	OL527765	OL527843
<i>G. (G.)</i> sp. 3	<i>Geokichla citrina</i> ssp.	14_J0859	GD(5)	OL514068	OL527770	OL527848
<i>G. (G.)</i> sp. 3	<i>Geokichla citrina</i> ssp.	16_J1047	YN(5)	OL514070	OL527772	OL527850

Table III. Continued.

Taxon information				Sequence data		
Louse species	Host species	Voucher no.	Locality	COI	12S	16S
<i>G. (G.)</i> sp. 4	<i>Copsychus malabaricus macrourus</i>	25_J1364	YN(6)	OL514078	OL527780	OL527858
<i>G. (G.)</i> sp. 4	<i>Copsychus malabaricus macrourus</i>	24_J1364	YN(6)	OL514077	OL527779	OL527857
<i>G. (G.)</i> sp. 4	<i>Cyornis banyumas whitei</i>	19_J1301	YN(3)	OL514072	OL527774	OL527852
<i>G. (G.)</i> sp. 4	<i>Cyornis banyumas whitei</i>	20_J1301	YN(3)	OL514073	OL527775	OL527853
<i>G. (G.)</i> sp. 5 (near <i>flavala?</i>)	<i>Hemixos castanonotus canipennis</i>	8_J0801	GD(1)	OL514064	OL527766	OL527844
<i>G. (G.)</i> sp. 5 (near <i>flavala?</i>)	<i>Pycnonotus sinensis hainanus</i>	10_J0391	HI	OL514048	OL527750	OL527828
<i>G. (G.)</i> sp. 6	<i>Rhipidura albicollis celsa</i>	15_J0528	YN(6)	OL514053	OL527755	OL527833
<i>G. (G.)</i> sp. 6	<i>Rhipidura albicollis celsa</i>	16_J0528	YN(6)	OL514054	OL527756	OL527834
<i>G. (G.)</i> sp. 6	<i>Phylloscopus burkii</i>	19_J0610	YN(3)	OL514057	OL527759	OL527837
<i>G. (G.)</i> sp. 6	<i>Terpsiphone incei</i>	18_J1287	YN(3)	OL514071	OL527773	OL527851
<i>G. (G.)</i> sp. 6	<i>Pteruthius melanotis melanotis</i>	23_J1320	YN(3)	OL514076	OL527778	OL527856
<i>G. (G.)</i> sp. 6	<i>Anthipes monileger leucops</i>	17_J0533	YN(6)	OL514055	OL527757	OL527835
<i>G. (G.)</i> sp. 6	<i>Cyornis hainanus hainanus</i>	8_J2881	GX	OL514033	OL527735	OL527813
Priceiella						
Subgenus Priceiella s. str.						
<i>P. (P.) sternotypica</i>	<i>Ianthocincla pectoralis pingi</i>	21_J1307	YN(3)	OL514074	OL527776	OL527854
<i>P. (P.) sternotypica</i>	<i>Ianthocincla pectoralis pingi</i>	22_J1307	YN(3)	OL514075	OL527777	OL527855
<i>P. (P.) sternotransversa</i>	<i>Ianthocincla albobularis eoa</i>	35_J2140	SC	OL514087	OL527789	OL527865
Subgenus Camurnirmus						
<i>P. (Ca.) lindquistae</i>	<i>Ianthocincla chinensis lochmia</i>	30_J1561	YN(3)	OL514083	OL527785	OL527863
<i>P. (Ca.) sichuanensis</i>	<i>Ianthocincla berthemyi</i>	28_J1531	HN	OL514081	OL527783	OL527861
<i>P. (Ca.) sichuanensis</i>	<i>Ianthocincla berthemyi</i>	29_J1531	HN	OL514082	OL527784	OL527862
Subgenus Thescelovora						
<i>P. (T.) brutifrons</i>	<i>Turdinus brevicaudatus stevensi</i>	1_J2900	GX	OL514098	OL527800	OL527878
<i>P. (T.) brutifrons</i>	<i>Turdinus brevicaudatus stevensi</i>	2_J2900	GX	OL514099	OL527801	OL527879
<i>P. (T.) brutifrons</i>	<i>Mixornis gularis lutescens</i>	5_J2931	GX	OL514101	OL527803	OL527881
<i>P. (T.) brutifrons</i>	<i>Copsychus saularis saularis</i>	47_J2698	GD(3)	OL514097	OL527799	OL527877
<i>P. (T.) brutifrons</i>	<i>Pellorneum ruficeps shanense</i>	20_J0631	YN(3)	OL514058	OL527760	OL527838
<i>P. (T.) brutifrons</i>	<i>Pellorneum ruficeps shanense</i>	1_J0631	YN(3)	OL514059	OL527761	OL527839
<i>P. (T.) brutifrons</i>	<i>Pellorneum ruficeps shanense</i>	2_J0631	YN(3)	OL514060	OL527762	OL527840
<i>P. (T.) austini</i> (?)	<i>Pomatorhinus ruficollis similis</i>	3_J0658	YN(3)	OL514061	OL527763	OL527841
<i>P. (T.) rotundiceps</i>	<i>Pomatorhinus ruficollis reconditus</i>	45_J2788	AH	OL514095	OL527797	OL527875
<i>P. (T.) rotundiceps</i>	<i>Pomatorhinus ruficollis reconditus</i>	46_J2788	AH	OL514096	OL527798	OL527876
<i>P. (T.) nanlingensis</i>	<i>Garrulax monileger monileger</i>	32_J1798	YN(5)	OL514084	OL527786	OL527864
<i>P. (T.) nanlingensis</i>	<i>Alcippe nipalensis*</i>	13_J0539	YN(6)	OL514038	OL527740	OL527818
<i>P. (T.) nanlingensis</i>	<i>Garrulax maesi maesi</i>	10_J0819	GD(1)	OL514066	OL527768	OL527846
<i>P. (T.) nanlingensis</i>	<i>Garrulax maesi maesi</i>	11_J0819	GD(1)	OL514067	OL527769	OL527847
Incerta sedis						
<i>G. (Ci.) montisodalis</i>	<i>Fulvetta ruficapilla sordidior</i>	15_J4232	YN(1)	OL514105	OL527807	OL527885
<i>G. (Ci.) montisodalis</i>	<i>Fulvetta manipurensis tonkinensis</i>	13_J4196	YN(1)	OL514104	OL527806	OL527884
Outgroups						
<i>Lunaceps falcinellus</i>	<i>Calidris falcinellus falcinellus</i>	D103-1	SE	JN900091	JN900206	JN900167
<i>Lunaceps drosti</i>	<i>Calidris canutus canutus</i>	D171-1	SE	JN900107	JN900221	JN900180
<i>Quadraceps obtusius</i>	<i>Tringa totanus totanus</i>	D69-1	SE	OL514089	OL527791	OL527869

* Arlott (2017) and Clements et al. (2019) do not list *A. nipalensis* as breeding in China, but it is listed by Zheng (2017). The collection locality (Yingjiang County, Dehong Prefecture, Yunnan Province) is right at the border of the range of *A. nipalensis* outlined by Arlott (2017). None of the present authors participated in the collection trip to Dehong when these samples were collected, and this host association would need to be verified by future collection trips.

Table IV. Genetic distances (percentage) of the mitochondrial cytochrome *c* subunit 1 gene within and between species of *Guimaraesiella* (*Cicchinella*), including *Gu. (Ci.) montisodalis*. Dashes represent taxa where only 1 specimen was analyzed, and within-species distances are therefore not calculated.

	<i>Gu. (Ci.) falcifrons</i>	<i>Gu. (Ci.) citreisoma</i>	<i>Gu. (Ci.) yuhinae</i>	<i>Gu. (Ci.) sp. 1</i>	<i>Gu. (Ci.) petilorica</i>	<i>Gu. (Ci.) mcgrewi</i>	<i>Gu. (Ci.) corrugata</i>	<i>Gu. (Ci.) tenella</i>	<i>Gu. (Ci.) montisodalis</i>
<i>Gu. (Ci.) falcifrons</i>	0.0–0.3								
<i>Gu. (Ci.) citreisoma</i>	16.6–18.8	0.0–0.3							
<i>Gu. (Ci.) yuhinae</i>	17.6–18.8	13.3–14.3							
<i>Gu. (Ci.) sp. 1</i>	24.7–25.1	18.7–19.0	0.0–1.1	—					
<i>Gu. (Ci.) petilorica</i>	23.6–25.2	21.2–22.0	22.1–23.3	13.5–14.5	0.0–0.8				
<i>Gu. (Ci.) mcgrewi</i>	22.5–23.3	19.5–20.3	21.4–22.2	9.5–9.8	11.6–12.2	0.0–0.3			
<i>Gu. (Ci.) corrugata</i>	22.8–23.3	19.9–20.3	21.4–22.2	9.8	11.9–12.2	0.0–0.3	—		
<i>Gu. (Ci.) tenella</i>	18.3–19.1	18.8–19.6	15.6–17.0	17.8–18.2	18.3–19.9	18.1–18.5	18.1–18.5	0.0–0.8	
<i>Gu. (Ci.) montisodalis</i>	20.7–21.1	19.3–19.7	16.9–17.7	23.2	23.2–23.6	23.2–23.6	23.6	18.1–19.3	0.0

montisodalis, was nested inside *Priceiella*, but this placement received no support. Rerunning the analysis with the same settings, but omitting *Guimaraesiella montisodalis*, had largely no effect on the major clades of the tree and their support (Supplemental Fig. S1). Within *Priceiella*, *Camurnirmus* (Fig. 2; Group 7) and *Thescelovora* (Fig. 2; Group 8) are sister groups, but the relationships between this pair, *Priceiella* s. str., and *Guimaraesiella montisodalis* is unresolved.

Genetic divergences in the *COI* marker were similar between all 3 groups (Tables IV–VI), with within-species distances being between 0.0 and 2.2%, and between-species distances generally being between 15 and 25% for all 3 groups examined. The main exceptions are the species in the *G. (Ci.) gombakensis* species group, in which between-species distances were below 10%. *COI* distances between *G. (Ci.) mcgrewi* and *G. (Ci.) corrugata* were indistinguishable from within-species distances of the former.

DISCUSSION

Our analysis resulted in a fairly well-resolved tree, in which all species-level taxa previously identified were found to be monophyletic. Genetic distances based on the *COI* marker between species were generally 15.0–25.0% (Tables IV–VI), whereas those within species were generally below 2.0%. However, between-species distances were lower than 10% in the *G. (Ci.) mcgrewi* species group (Table IV). These patterns are consistent with those seen in other groups of lice (e.g., Gustafsson and Olsson, 2012). No appreciable differences in the *COI* marker were found between *G. (Ci.) gombakensis* and *G. (Ci.) corrugata*, but these 2 taxa differ substantially morphologically. The lower genetic distances among species in the *G. (Ci.) gombakensis* species group may reflect the complicated relationships of their hosts (Zou et al., 2007; Song et al., 2009).

Relationships between *Guimaraesiella*, *Cicchinella*, and *Priceiella*

Babblers are part of the Passerida radiation of songbirds, which are widely distributed across all continents except Antarctica (Clements et al., 2019). Generally, birds in this radiation are parasitized by lice in the *Brueelia* group (Gustafsson and Bush, 2017); however, many exceptions are known. For instance, many Neotropical Passerida are parasitized by *Guimaraesiella* (e.g., Thraupidae; Cicchino, 1983; Valim and Palma, 2006). More typically, a passeridan host species that is parasitized by

Guimaraesiella-group lice is also parasitized by *Brueelia*-group lice (e.g., thrushes, bulbuls, starlings; Gustafsson and Bush, 2017).

Babblers are somewhat apart, in that *Brueelia*-group lice are unknown from all genera of babblers except *Turdoides* (Gustafsson and Bush, 2017; Mey, 2017; Gustafsson et al., 2018a, 2018b, 2019a; Table I). This host genus is aberrant among babblers, as it is not associated with rainforests and other humid areas, but is more typical of scrubland, savannah, and drier country. As such, babblers are a good example of the pattern that lice in the *Brueelia* group seem to be more common in dry-country hosts, whereas those in the *Guimaraesiella* group seem to be more closely connected to more humid areas.

The overall distribution of *Brueelia*-complex lice on Passerida, babblers, and *Turdoides* suggests that if *Brueelia*-group lice occurred on ancestral babblers, these have now been almost completely replaced by *Guimaraesiella*-group lice. Where, when, and how this happened is unknown, and unlikely to be known in the future, given the sparse fossil record of chewing lice (Dalgleish et al., 2006). However, phylogenetic data have the potential to indicate whether it is likely that the current *Guimaraesiella*-group fauna on babblers originates from 1 or more colonization events. For instance, a sister-group relationship between *Cicchinella* and *Priceiella* species found on babblers would suggest that the present fauna likely derived from a single colonization event followed by radiation. By contrast, if, e.g., species of *Cicchinella* found on babblers are scattered throughout *Guimaraesiella*, this would indicate that multiple colonization events were involved.

Our data set is not sufficient to resolve the relationships between *Cicchinella*, *Guimaraesiella*, and *Priceiella*; moreover, only *Cicchinella* and *Guimaraesiella* were recovered as monophyletic with good support (Fig. 2; Groups 4 and 5). Some specimens of *Cicchinella* were recovered from non-babbler hosts, but no specimens from babblers were nested inside *Guimaraesiella* s. str. This may indicate that *Cicchinella* derives from a single colonization event, followed by radiation on babblers and occasional transfers from babblers to non-babblers. However, our samples of *Guimaraesiella* are limited and do not include several of the larger clades of *Guimaraesiella* found by Bush et al. (2016).

Priceiella was not supported as monophyletic in our data set, although each of the 3 subgenera included had high support (Fig. 2; Groups 6, 7, and 8). Possibly this was influenced by the unresolved placement of *Guimaraesiella montisodalis*, but the removal of this species did not significantly increase the support

Table V. Genetic distances (percentage) of the mitochondrial cytochrome *c* subunit 1 gene within and between species of *Guimaraesiella* (*Guimaraesiella*).

	<i>Guimaraesiella</i> (G.) sp. 1	<i>Guimaraesiella</i> (G.) sp. 2	<i>Guimaraesiella</i> (G.) sp. 3	<i>Guimaraesiella</i> (G.) sp. 4	<i>Guimaraesiella</i> (G.) sp. 5	<i>Guimaraesiella</i> (G.) sp. 6
<i>Guimaraesiella</i> (G.) sp. 1	0.0					
<i>Guimaraesiella</i> (G.) sp. 2	22.1	0.0				
<i>Guimaraesiella</i> (G.) sp. 3	23.1	16.2	0.0			
<i>Guimaraesiella</i> (G.) sp. 4	20.8	16.1	18.7	0.0		
<i>Guimaraesiella</i> (G.) sp. 5	25.4	18.3	20.3	14.9	0.0	
<i>Guimaraesiella</i> (G.) sp. 6	20.2–20.4	17.7–18.5	18.8–19.2	17.1–17.8	16.9–18.5	0.0–1.1

for *Priceiella* s. lat. (Fig. S1). Morphology suggests that *Priceiella* is monophyletic, and the genus was recovered as monophyletic with high support by Bush et al. (2016, Fig. 3c, clade B). This suggests that more data, including nuclear data, are needed to test the monophyly of *Priceiella*.

Species groups of *Cicchinella*

Cicchinella and the 3 species groups it comprises were originally defined morphologically (Gustafsson et al., 2019a). In our data set, each of the 3 species groups is monophyletic with good support (Fig. 2, Groups 1–3), and together these form a monophyletic group with good support (Fig. 2, Group 4), indicating that the subgenus *Cicchinella* may be monophyletic. However, apart from the specimens of *Cicchinella*, all *Guimaraesiella* specimens included here are part of *Guimaraesiella* s. str. (core group *sensu* Gustafsson et al., 2019c). We were unable to obtain sequences from the 2 other described subgenera (*Mohoaticus* Mey, 2017, and *Dicrurobates* Gustafsson and Bush, 2020). The latter subgenus was included in the phylogeny of Bush et al. (2016, Fig. 3c, clade C) and not placed close to the specimens of *Cicchinella* (Bus et al. 2016, clade A-5).

Guimaraesiella montisodalis was originally described as close to *Guimaraesiella tenella*, based primarily on preantennal characters and the presence of prominent lateral rugose nodi on the male mesosome (Gustafsson et al., 2019b). In our data set, *G. montisodalis* is not placed close to any other species of *Guimaraesiella*, but its placement is unresolved (Fig. 2, Group 11). Morphologically, this species differs from all other *Cicchinella* by having a terminal gonopore, but morphology does not suggest a close relationship with any other group of *Guimaraesiella* examined here. In particular, no morphological characters suggest a close relationship between *G. montisodalis* and *Priceiella*, which were placed together in our analysis, albeit with no support. This species must for now be considered *incerta sedis* within the *Guimaraesiella* group until more data has been analyzed and its position can be clarified.

Host associations

In total, 11 of the 23 species-level clades of *Guimaraesiella* s. lat. and *Priceiella* include specimens from more than 1 host species. In some cases, these may be due to straggling or contamination in the field; however, at least some of these may represent genuine cases where the same species of louse naturally occurs on more than 1 host species. For instance, comparisons of *COI* sequences of *Guimaraesiella* sp. 6 indicate that this species is the same as the top-most clade of *Guimaraesiella* in the phylogeny of Bush et al. (2016). In that study, this undescribed species of *Guimaraesiella*

was recovered from 25 different host species in 12 families from across the Old World tropics and Australia. As there are no overlaps in host associations for this species in our data set and that of Bush et al. (2016), this is a species that has a remarkably large host range; moreover, we have seen slide-mounted specimens of *Guimaraesiella* from at least 20 other Southeast Asian host species that cannot be separated morphologically from voucher specimens of the sequences used by Bush et al. (2016), indicating that the real host range may be even larger. Similar degrees of host generalism is not previously known from either *Priceiella* or *Cicchinella*, although *Priceiella orichalca* Gustafsson et al. (2018b) was described based on specimens from 5 different host species, and some other species of both groups are known from more than 1 host species (Gustafsson et al., 2018b, 2019a). Notably, most of the hosts of *Guimaraesiella* sp. 6 are relatively small-bodied birds that occur in humid tropical forests at least part of the year, and many of them also participate in mixed-species flocks.

Except for singletons and *G. tenella*, all species of *Cicchinella* included in our data set involved records from more than 1 host species. Most of these cases involve host species that co-occur in mixed-species feeding flocks. In 1 case (*Guimaraesiella* (*Ci.*) *yuhinae*; Fig. 2, Group 1), all specimens are from different host species, except for 2 specimens taken from the same host individual.

Notably, lice in the *gombakensis* group of *Cicchinella* (Fig. 2, Group 2) are often found on hosts other than *Alcippe* spp., and lice from *Alcippe* spp. include 2 samples that are not in the *gombakensis* species group (specimens 38_J2240; Fig. 2, Group 1, and 13_J0539; Fig. 2, Group 8). *Alcippe* spp. are often indicated as the pilot or nuclear species of such flocks (e.g., Chen and Hsieh, 2002; Hsieh and Chen, 2011; Zhang et al., 2013; Zou et al., 2018), and at least some of the hosts of *gombakensis* species group lice (Fig. 1, Group 2) in our data set are also frequent participants in flocks lead by *Alcippe* spp. (Zou et al., 2011; D. R. Gustafsson, pers. obs.). As flocks lead by *Alcippe* spp. may include many other birds (e.g., Zou et al., 2011), *gombakensis* species group lice might be expected from more non-babbler host species in the future.

The many records of otherwise babbler-specific lineages on non-babbler hosts are remarkable, given the seeming lack of such records among other specimens we have examined (e.g., Bush et al., 2016; Gustafsson and Bush, 2017). This lack of records may have several causes. First, *Priceiella* and *Cicchinella* have been recognized as distinct taxonomic units only in recent years (Gustafsson and Bush, 2017; Gustafsson et al., 2019a), and older published records from non-babbler hosts may refer to either of these groups. Second, specimens of these genera are not always easy to separate under stereomicroscopes, especially if only

Table VI. Genetic distances (percentage) of the mitochondrial cytochrome *c* subunit 1 gene within and between species of *Priceiella*. Dashes represent taxa where only 1 specimen was analyzed, and within-species distances are therefore not calculated.

	<i>P. (P.) sternotypica</i>	<i>P. (P.) sternotransversa</i>	<i>P. (Ca.) lindquistae</i>	<i>P. (Ca.) sichuanensis</i>	<i>P. (T.) brutifrons</i>	<i>P. (T.) austini (?)</i>	<i>P. (T.) rotundiceps</i>	<i>P. (T.) nanlingensis</i>
<i>P. (Priceiella) sternotypica</i>	0.0							
<i>P. (P.) sternotransversa</i>	20.3	—						
<i>P. (Camurnirmus) lindquistae</i>	19.4	19.1	—					
<i>P. (Ca.) sichuanensis</i>	22.6	23.6	21.6	0.0				
<i>P. (Thescelovora) brutifrons</i>	19.3–19.7	24.3–24.7	18.6–18.9	17.8–18.1	0.0–0.3			
<i>P. (T.) austini (?)</i>	18.1	20.9	16.6	18.9	15.4–15.7	—		
<i>P. (T.) rotundiceps</i>	17.9	21.2	19.7	21.3	19.0–19.3	14.1	0.0	
<i>P. (T.) nanlingensis</i>	22.7–23.1	22.8–24.0	17.9–19.0	19.1–19.6	17.8–18.5	15.2–15.9	17.3–18.4	0.0–2.2

females are available, as the cross-piece that separate *Cicchinella* from *Guimaraesiella* s. str. may be poorly sclerotized or pigmented. Finally, such occurrences may be rare in nature; the specimens we have obtained may be the result of our targeted sampling of mixed-species flocks and babblers in South China for almost a decade. Further collections of lice from non-babblers, and more detailed examinations of our specimens, are needed to establish how common these kinds of occurrences are. Notably, only in a single case did we recover the same species of *Cicchinella* from 2 conspecific non-babbler hosts (*G. (Ci.) mcgrewi* from 2 different *Cyornis brunneatus*; Fig. 2, Group 2, samples J2089 and J2092). These were collected at the same locality the same day, but no *Alcippe* spp. were examined that day, suggesting that the records may represent a locally established population of *Cicchinella* on a flycatcher.

In our data set *Priceiella* s. str. and *Camurnirmus* were both represented by either singletons or male/female louse pairs derived from the same host individual (Fig. 1, Groups 6 and 7). Of the 4 species of *Thescelovora* included in our data set, 2 were recovered from multiple host species (Fig. 1, Group 8). Species in *Priceiella* s. str. and *Camurnirmus* are almost exclusively known from larger-bodied (>20 cm) laughingthrushes, whereas subgenus *Thescelovora* has a broader range of host body sizes, although most known hosts are smaller-bodied (<20 cm) (Gustafsson and Bush, 2017; Gustafsson et al., 2018b, 2021b). Interestingly, this pattern of lice on larger-bodied hosts generally being more host-specific than lice on smaller-bodied hosts exactly parallels the situation in the distantly related shorebird louse genus *Lunaceps* Clay and Meinertzhagen, 1939 (Gustafsson and Olsson, 2012).

The mechanics behind the success or failure of interspecies transfers of lice are still poorly known, but the impact of host size is comparatively well known. Bush and Clayton (2006) found that transfers worked best when hosts were of similar size. Transfers to smaller hosts may fail because of differences in interbarb space of feathers, which is known to be correlated with louse size in many birds (Johnson et al., 2005; Harnos et al., 2017). The failure of transfers to larger hosts has no satisfactory answer but may be related to difficulties in finding mates on a larger host (Bush and Clayton, 2006) or reduced locomotion speed (Villa et al., 2019).

However, neither of these explanations seems sufficient to understand why transfers between similar-sized hosts appear to be more common among small-bodied hosts than among large-bodied hosts. We have no data to evaluate whether interbarb spaces are significantly different among similar-sized, large-bodied laughingthrushes. Interbarb space is strongly correlated

with overall body size in pigeons (Johnson et al., 2005), which suggests that neither the space itself nor locomotion speed connected to interbarb space would be very different in similar-sized laughingthrushes. If lice on babblers use chemical clues to find mates and these are diluted on larger hosts (Bush and Clayton, 2006), this may still be a factor. However, as many lice in the *Brueelia*-complex are specialists for certain feather tracts (Baum, 1968; Mey, 1982), it would seem likely that the area on the host's body over which the chemical trail is diluted may be rather small, even on larger-bodied hosts. After all, the lice manage to find mates on their natural hosts, even if these are large-bodied.

Potentially, the vertical distribution of the hosts may be a factor. Laughingthrushes tend to forage on the ground or in the understory (e.g., Bušina et al., 2017), whereas smaller babblers tend to have a wider vertical range of foraging, including at rather high elevations (e.g., Srinivasan et al., 2012; Mansor and Ramli, 2017). In many cases, laughingthrushes are also reported to form different kinds of flocks than smaller, midstory or canopy birds (e.g., King and Rappole, 2001; Srinivasan et al., 2012); detailed reports of such flock almost always contain only 1 species of laughingthrush, suggesting that they may also be more species-specific (e.g., King and Rappole, 2001; but see Zou et al., 2011; Bušina et al., 2017). Moreover, smaller-bodied babblers appear to be more commonly participate in mixed-species flocks than larger-bodied laughingthrushes (e.g., Zou et al., 2011).

Together, these aspects of host ecology may suggest the outlines of a partial answer. Larger-bodied laughingthrushes may tend to form flocks that do not contain other babblers, and these flocks may be more species-specific, containing only 1 or a few species of laughingthrush. This may tend to give babbler-specific lice fewer opportunities to transfer from 1 laughingthrush species to another, compared to lice that live on smaller-bodied hosts that more often occur in babbler-rich flocks. Moreover, since the volume of forest that the laughingthrushes forage in is mainly ground and understory, larger birds may need to be more spread out than smaller-bodied hosts in the midstory, reducing the opportunities for transfer further. More louse data from laughingthrushes is needed to establish whether these factors influence the apparently low rate of louse transmission between hosts.

Alternatively, if the prevalence and abundance of lice are lower on smaller-bodied hosts, local extinction of lice may be more common on smaller-bodied hosts than on larger-bodied hosts. This may tend to produce open niches on smaller birds, which lice capable of host switching can exploit; on larger-bodied birds, such

opportunities would be rarer. However, it is unclear whether prevalence and abundance, in general, are lower for smaller-bodied babblers in South China (D. R. Gustafsson and F. Zou, unpubl. data).

Biogeography

The geographic distribution of lice is poorly known. Some louse species appear to occur across the range of their hosts (e.g., *Columbicola columbae* (Linnaeus, 1758); Adams et al., 2005), but this is not always the case (Clay, 1964; Edwards, 1965). In some cases, there appear to be environment-mediated limits to the range of a louse but not the host (e.g., Bush et al., 2009); these limits may be compounded by interspecies competition on the same host (Malenke et al., 2011; Gustafsson and Zou, 2020). Insular birds may also have a depauperate louse fauna compared to mainland relatives (Literák et al., 2015; Regolin et al., 2015), and similar effects may be seen in noninsular birds living in fragmented habitats (Bush et al., 2013).

The impact of geographical barriers on the distribution of lice is less well known. Light et al. (2016) reported that conspecific birds on opposite sides of the Congo River may be parasitized by different species of lice; this is consistent with data showing that major tributaries of the Amazon may be significant barriers to lice (Weckstein, 2004). In general, any barrier that restricts the movements of the hosts may limit the distribution of the lice on that host. Our data include 2 possible examples of this.

Lice from *Pomatorhinus ruficollis* are scattered across the tree, with 3 species of *Cicchinella* and 2 species of *Thescelovora* being recovered from this host. All previous records of *Guimaraesiella*-group lice from *Pomatorhinus* spp. have been from the subgenus *Thescelovora* (Gustafsson et al., 2019a), and the records of *Cicchinella* may all represent stragglers, particularly as 1 host was parasitized by 2 different species of *Cicchinella* (Fig. 2, Group 1, host J2250). However, contamination in the field is unlikely, as none of the other host species in either of those clades were caught at that locality at that date; the only hosts caught were *Cyanoderma ruficeps*, *Suthora verreauxi*, and *Lioparus chrysotis*.

The 2 species of *Thescelovora* from *P. ruficollis* correspond to morphological differences (Gustafsson et al., 2018b, 2021b) that support that 2 species of *Thescelovora* occur on this host. *Priceiella* (*T.*) *austini* appears to be the more widely distributed species, as we have seen specimens from Yunnan, Guangdong, and Guangxi provinces (Gustafsson et al., 2018b; Fig. 2; D. R. Gustafsson, unpubl. data). *Priceiella* (*T.*) *rotundiceps* is limited to Anhui in our samples, but sampling data from North of the Nanling mountains are limited; the Nanling range is a known biogeographical barrier for many taxa (e.g., Shih et al., 2011; Li et al., 2019; Liang et al., 2020). Moreover, *P. ruficollis* from central China is genetically distinct from populations in Yunnan and the area south of the Nanling Mountains (Dong et al., 2014; Reddy et al., 2015), paralleling the split between the *Thescelovora* lice in these localities.

Similarly, the only sample from *Alcippe* spp. from north of the Nanling Mountains (Hunan; specimen J0095) is parasitized by a different lineage of *Cicchinella* from the specimens from south of this range (Fig. 2, Group 2). However, in this case, there may be a mismatch between the phylogeny of the host and the phylogeny of the lice. *Alcippe* from Hunan and central China (*A. davidi davidi*) is closely related to specimens from Guangxi and Vietnam (*A.*

davidi schaefferi; Zou et al., 2007; Song et al., 2009), but in our data specimens from Guangxi are conspecific with specimens from Guangdong (*A. hueti hueti*) and Hainan (*A. hueti rufescentior*). More detailed studies are needed, including more data from the populations of central China, but potentially this suggests that the Nanling Mountains may have formed a barrier to the dispersal of *Cicchinella* even if the hosts have not been affected by the barrier. More data are also needed from other hosts that occur on both sides of the Nanling range.

CONCLUSION

Our broad sampling of lice from babblers and non-babblers across South China has revealed several interesting results. The *Cicchinella* and *Priceiella* faunas of South China appear to contain both host-specific and host-generalist species, and both groups include species that appear to be geographically restricted and species that appear to occur across the range of their hosts. This is similar to published data from other groups of lice on passerine hosts, including both ischnoceran (e.g., Bush et al., 2016; Najer et al., 2020) and amblyceran lice (e.g., Martinů et al., 2015; Sychra et al., 2021). Similar mixed patterns are also known from lice of other host groups (e.g., Johnson et al., 2002, 2011; Gustafsson and Olsson, 2012; Escalante et al., 2016; Catanach et al., 2017) and appear to be the norm in chewing lice.

However, more data are needed to resolve the deeper nodes in this radiation and determine the relationships between *Cicchinella*, *Guimaraesiella*, and *Priceiella*, as well as the position of *G. montisodalis*. Better resolution, and coevolutionary analysis, may allow us to understand the apparent switch between the *Brueelia*-group lice expected on babblers based on their phylogenetic position in Passerida and the *Guimaraesiella*-group lice that occur on almost all babblers. Combined with further collections, this may also help solve questions about what factors facilitate or limit the establishment of lice on novel hosts under natural conditions.

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