



Observations on the relationships of some Sundaic passerine taxa (Aves: Passeriformes) previously unavailable for molecular phylogenetic study

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Abstract

To help resolve phylogenetic and phylogeographic relationships of Southeast Asian birds, we have collected specimens in Borneo, Sumatra, and Java for phylogenetic and morphological study. Here, we compare mitochondrial ND2 gene sequences from some of these new specimens to sequences obtained in previous studies to shed light on genealogical relationships in nine passerine clades: *Erythropitta venusta/granatina/ussheri* (pittas); *Dicrurus hottentottus* (drongos); *Alophoixus* bulbuls; *Napothera*, *Turdinus* and *Pellorneum* babblers; *Anthipes* flycatchers; *Brachypteryx* shortwings; and *Myophonus* whistling thrushes. These comparisons resolve or shed substantial light on taxonomic problems in pittas, *Alophoixus*, *Napothera*, *Dicrurus*, *Brachypteryx*, and *Myophonus*, and they confirm assumed (but previously unquantified) genetic relationships within *Turdinus* and *Anthipes*. The resulting trees also allow us to (1) suggest improved taxonomic arrangements in several groups, (2) confirm the rediscovery of a “lost” species within *Napothera*, and (3) provide the basis for the description of a new subspecies of *Alophoixus*.

Keywords Borneo · Java · ND2 · Phylogeny · Phylogeography · Sumatra

Zusammenfassung

Beobachtungen zu Beziehungen einiger sundanesischer Sperlingsvogel-Taxa (Aves: Passeriformes), die bisher nicht für molekularphylogenetische Studien verfügbar waren

Um die phylogenetischen und phylogeographischen Beziehungen südostasiatischer Vogelarten zu klären, sammelten wir in Borneo, Sumatra und Java Exemplare für phylogenetische und morphologische Studien. Hier vergleichen wir die mitochondrialen ND2-Gensequenzen einiger dieser neuen Exemplare mit Sequenzen, die wir in früheren Studien erhalten haben, um die genealogischen Beziehungen zwischen neun Sperlingsvogel-Kladen zu beleuchten: *Erythropitta venusta/granatina/ussheri* (Pittas), *Dicrurus hottentottus* (Drongos), *Alophoixus*-Bülbüls, *Napothera*-, *Turdinus*- und *Pellorneum*-Drosslinge, *Anthipes*-Schnäpper, *Brachypteryx*-Kurzflügel und *Myophonus*-Pfeifdrosseln. Diese Vergleiche tragen wesentlich

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zur Lösung und Erklärung der taxonomischen Probleme bei *Pitta*, *Alophoixus*, *Napothera*, *Dicrurus*, *Brachypteryx*, und *Myophonus* bei und bestätigen die vermuteten (aber bis jetzt nicht quantifizierten) genetischen Beziehungen innerhalb von *Turdinus* und *Anthipes*. Die daraus resultierenden Stammbäume ermöglichen uns ebenfalls, (1) verbesserte taxonomische Anordnungen in mehreren Gruppen vorzuschlagen, (2) die Wiederentdeckung einer „verlorenen“ Art innerhalb der *Napothera* zu bestätigen und (3) die Grundlage für die Beschreibung einer neuen Unterart von *Alophoixus* zu liefern.

Introduction

Recent molecular studies of Southeast Asian birds have made great progress in deciphering relationships among species and populations in the region (e.g., Price et al. 2014; Moyle et al. 2016; Alström et al. 2018a; Cai et al. 2018; Ericson et al. 2019). Nevertheless, virtually all such studies lack genetic material of some taxa and, thus, can provide only a partial picture of avian diversity. This problem is particularly acute in phylogeographic studies of subspecies and populations, whose relationships are often poorly understood and whose taxonomy is often in flux (e.g., Fuchs et al. 2015; Eaton et al. 2016; Alström et al. 2018b). To provide more taxa for comparative studies of Southeast Asian birds, we have conducted more than 20 expeditions to the Greater Sunda Islands in the last 20 years. These expeditions have furnished vital genetic samples for the study of phylogeography in the region (e.g., Lim et al. 2010, 2011, 2014, 2017; Dejtaradol et al. 2015; Sheldon et al. 2015) and phylogeny of birds of the world (Shakya and Sheldon 2017; Shakya et al. 2017; Alström et al. 2018a; Cai et al. 2018; Campillo et al. 2018; Oliveros et al. 2019a, b). They have also yielded invaluable insight into Sundaic bird distribution, morphological variation, ecology, and conservation (Sheldon et al. 2009, 2010, 2013, 2014; Styring et al. 2011; Burner et al. 2016, 2018; Shakya et al. 2018).

Most recently, Louisiana State University Museum Natural Science (LSUMNS) and the University of Kansas Biodiversity Institute (KUMNH) have collaborated with the Museum Zoologicum Bogoriensis-LIPI (MZB) to obtain genetic materials of bird populations from areas in the Greater Sunda Islands for which modern specimens are almost completely nonexistent: Sumatra, Java, and Indonesian Borneo (Kalimantan). In this paper, these new specimens, combined with previously examined samples from Malaysian Borneo, the Philippines, and Indochina, allow us to estimate more comprehensively the phylogenies of nine groups of Sundaic passerines, which include some of the most taxonomically intractable species in the region.

Materials and methods

All specimens examined in this study are listed in Supplementary Table 1, with asterisks indicating newly acquired specimens/taxa and their collecting sites (shown in Fig. 1).

With respect to taxonomy, we follow the classification of Gill and Donsker (2020) but in some cases apply alternative names for clarity. In such cases, we cite the source of the alternative name. With respect to localities, most of our Sundaic sites have been described previously, i.e., all sites in Sabah, Malaysian Borneo (Sheldon et al. 2009; Sheldon 2015); all sites in Sarawak, Malaysian Borneo (Sheldon et al. 2013, 2019; Burner et al. 2016); three sites in or adjacent to Kalimantan, Indonesian Borneo—the Meratus Mountains (Shakya et al. 2018) and Maratua and Bawean islands (Burner et al. 2018); and three sites in Java—Mt. Salak, Mt. Slamet, and Mt. Ijen (Mittermeier et al. 2014). Collecting sites that have not yet been described in publications include: Siberut Island, Mentawai Islands, Sumatra, 1.72 S 99.21 E, visited in 2018; Mt. Talamau, west-central Sumatra, 0.09 N 99.96 E, visited in 2018; and Rimbo Panti Nature Reserve, west-central Sumatra, 0.35 N 100.07 E, visited in 2019.

For genetic comparisons, we sequenced the mitochondrial ND2 gene in newly acquired specimens and compared them with sequences of taxa studied previously. Although there are limitations to using a single gene in phylogenetic studies (e.g., incomplete lineage sorting, gene tree/species tree conflicts), ND2 is useful for rapid assessment of relationships because it evolves relatively quickly (Moore 1995), providing useful variation among closely related populations. It is also the one of the most commonly compared genes in phylogenetic studies of birds and, thus, is widely available in genetic archives such as GenBank.

For ND2 sequencing, total genomic DNA from ethanol-preserved pectoral muscle was extracted using DNEasy® Blood and Tissue Kit (Qiagen) following the manufacturers' protocol. PCR amplifications were performed in 25 µl reactions using Taq DNA Polymerase (New England BioLabs Inc.) and ND2 primers L5215 (Hackett 1996) and HTrpC (STRI) or H6316 (Sorenson et al. 1999). Amplification consisted of 34 cycles at a denaturing temperature of 95 °C, an annealing temperature of 54 °C and an extension temperature of 72 °C. We visualized the PCR products in 1.5% agarose gel stained with SYBR® Safe DNA Gel Stain (Invitrogen). Samples were sequenced at Macrogen USA (Rockville, MD). All newly generated sequences have been submitted to GenBank (Supplementary Table 1). ND2 sequences produced in earlier studies were downloaded from GenBank (Supplementary Table 1). All sequences were assembled in Geneious 8.1.9 (Biomatters) and aligned using MUSCLE (Edgar 2004) implemented in Geneious.

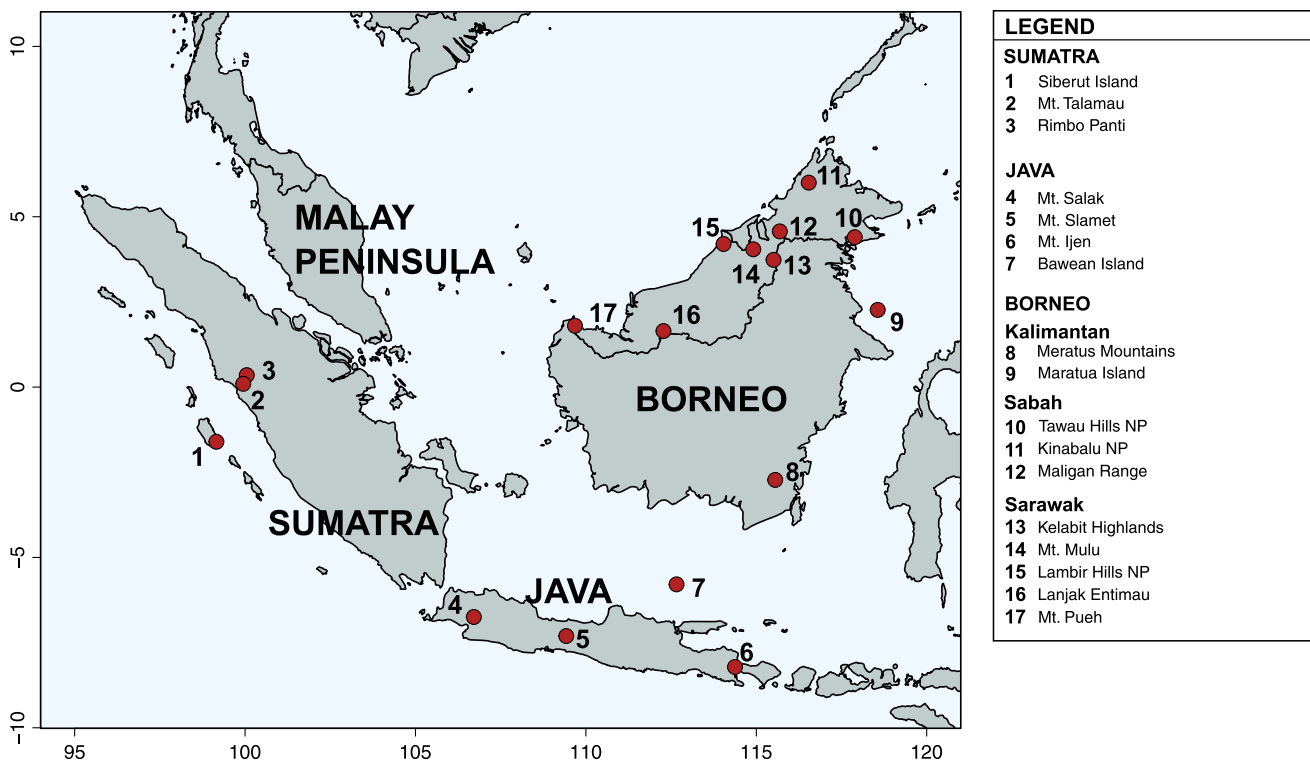


Fig. 1 Map of Sundaland showing recent sampling sites

The specimens providing new genetic material fall in nine taxonomic groups: *Erythropitta venusta/granatina/ussleri* (pittas, Pittidae); *Dicrurus hottentottus* (drongos, Dicruridae); *Alophoixus* bulbuls (Pycnonotidae); *Napothera*, *Turdinus* (Clements et al. 2019; Del Hoyo et al. 2019) and *Pellorneum* babblers (Pellorneidae); *Anthipes* flycatchers (Muscicapidae: Niltavinae); *Brachypteryx* shortwings (Muscicapidae: Saxicolinae); and *Myophonus* whistling thrushes (Muscicapidae: Saxicolinae). Relationships within these nine groups were examined by generating eight phylogenetic trees using a maximum likelihood (ML) framework in RAxML 8 (Stamatakis 2014), with 1000 non-parametric bootstrap replicates, via the CIPRES Science Gateway (Miller et al. 2010). The data were partitioned into codons and run using a GTR + GAMMA model.

For morphological comparisons of type specimens, we measured bill length (BSk—bill to skull) and tail (T5) using the methods of Eck et al. (2011); and we followed Winker (1998) in measuring wings.

Results

The eight phylogenetic trees and their sampling are as follows (“new” refers to the number of individuals for which ND2 sequences were newly generated; “old” refers to

sequences produced in previous studies): pittas (Fig. 2a), 7 new, 9 old; *Alophoixus* (Fig. 2b), 7 new, 24 old; *Turdinus* and *Pellorneum* (Fig. 2c), 19 new, 21 old; *Napothera* (Fig. 3a), 13 new, 8 old; *Brachypteryx* (Fig. 3b), 7 new, 16 old; *Myophonus* (Fig. 3c), 4 new, 5 old; flycatchers (Fig. 3d), 12 new, 38 old; and drongos (Fig. 4), 6 new, 47 old. Based on these trees, we discuss phylogenetic patterns and recommend taxonomic changes.

Discussion

Graceful pitta *Erythropitta venusta* (S. Müller, 1836), garnet pitta *Erythropitta granatina* (Temminck, 1830), and black-crowned pitta *Erythropitta ussheri* (Gould, 1877)

We obtained new tissues of three pitta taxa: *E. venusta* on Mt. Talamau (Sumatra); *E. granatina granatina* in Lambir Hills National Park (Sarawak); and *E. ussheri* in Tawau Hills National Park (Sabah). *Erythropitta venusta* of the Sumatran Mountains is part of a species complex containing: *E. granatina coccinea* of southern Indochina, the Malay Peninsula, and Sumatran lowlands; *E. g. granatina* of south and western Borneo; and *E. ussheri* of northeast Borneo. These taxa are medium-sized dark purplish-black birds with red underparts, a blue wing bend, and a blue stripe behind the eye (Lambert

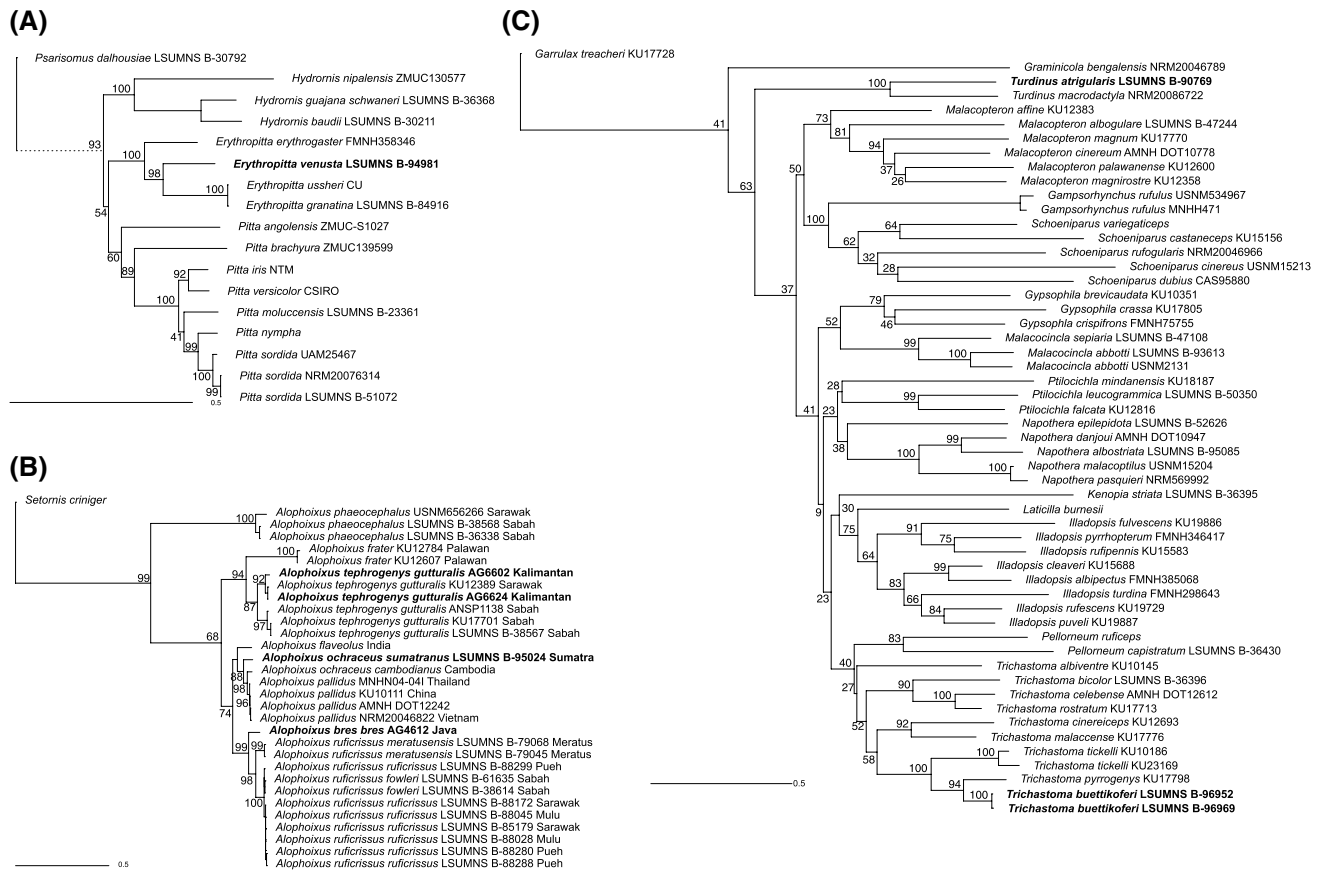


Fig. 2 Rooted maximum likelihood trees indicating mitochondrial ND2 DNA sequence relationships between relevant taxa of **a** Pittidae, **b** *Alophoixus* bulbuls, and **c** Pellorneidae, including *Turdinus* and *Pel-*

lorneum. Taxa for which new sequences were produced for this study are in bold type

and Woodcock 1996). Two taxa, *E. venusta* and *E. ussheri*, have a black crown as opposed to the red crown of *E. g. granatina* and *E. g. coccinea*. Originally, *E. ussheri* was considered a subspecies of *E. venusta* (Mayr 1979; Van Marle and Voous 1988). However, based on morphology, Rozendaal (1994) suggested that *ussheri* is more closely related to its parapatric congener on Borneo, *E. g. granatina*. Our phylogenetic tree (Fig. 2a) unfortunately lacks *E. g. coccinea*. Nevertheless, it demonstrates a relatively close relationship (for pittas) between *E. venusta* and the Bornean *E. g. granatina* and *E. ussheri* (ND2 distance, 10%). Most interestingly, we found that ND2 sequences of *E. ussheri* and Bornean *E. g. granatina* are almost identical (99.90%). Often, forest-dwelling passerines in Sabah have ND2 sequences distinct from their sister taxa elsewhere in Borneo (e.g., Lim et al. 2017; Shakya et al. 2018), but not in this case. The similarity may be the result of introgression, as the two species are thought to hybridize (MacKinnon et al. 1993).

Ochraceous bulbul *Alophoixus ochraceus* (Moore, 1858)

Fuchs et al. (2015) found *A. ochraceus* to be paraphyletic because its Indochinese subspecies are more closely related to the Indochinese puff-throated bulbul *A. pallidus* (Swinhoe, 1870) than to the *A. ochraceus* subspecies on Borneo. They also found that the two Bornean subspecies, *A. o. ruficrissus* and *A. o. fowleri*, form a clade that is sister to the grey-cheeked bulbul *A. bres* (Lesson 1832) of Java, indicating the paraphyly of *A. bres* as well. Our comparisons agree with these findings (Fig. 2b). Unfortunately, we were not able to include the data of Fuchs et al. (2015) in our study because they did not sequence ND2. However, we were able to assemble a set of key populations from across the region plus two new Sundaic populations not previously examined: *A. o. sumatranus* from Mt. Talamau (Sumatra) and the Meratus Mountains (Kalimantan) population. Our tree indicates that *A. o. sumatranus* is sister to the clade containing *A. pallidus* and *A. ochraceus* of mainland Asia rather than to the Bornean populations of

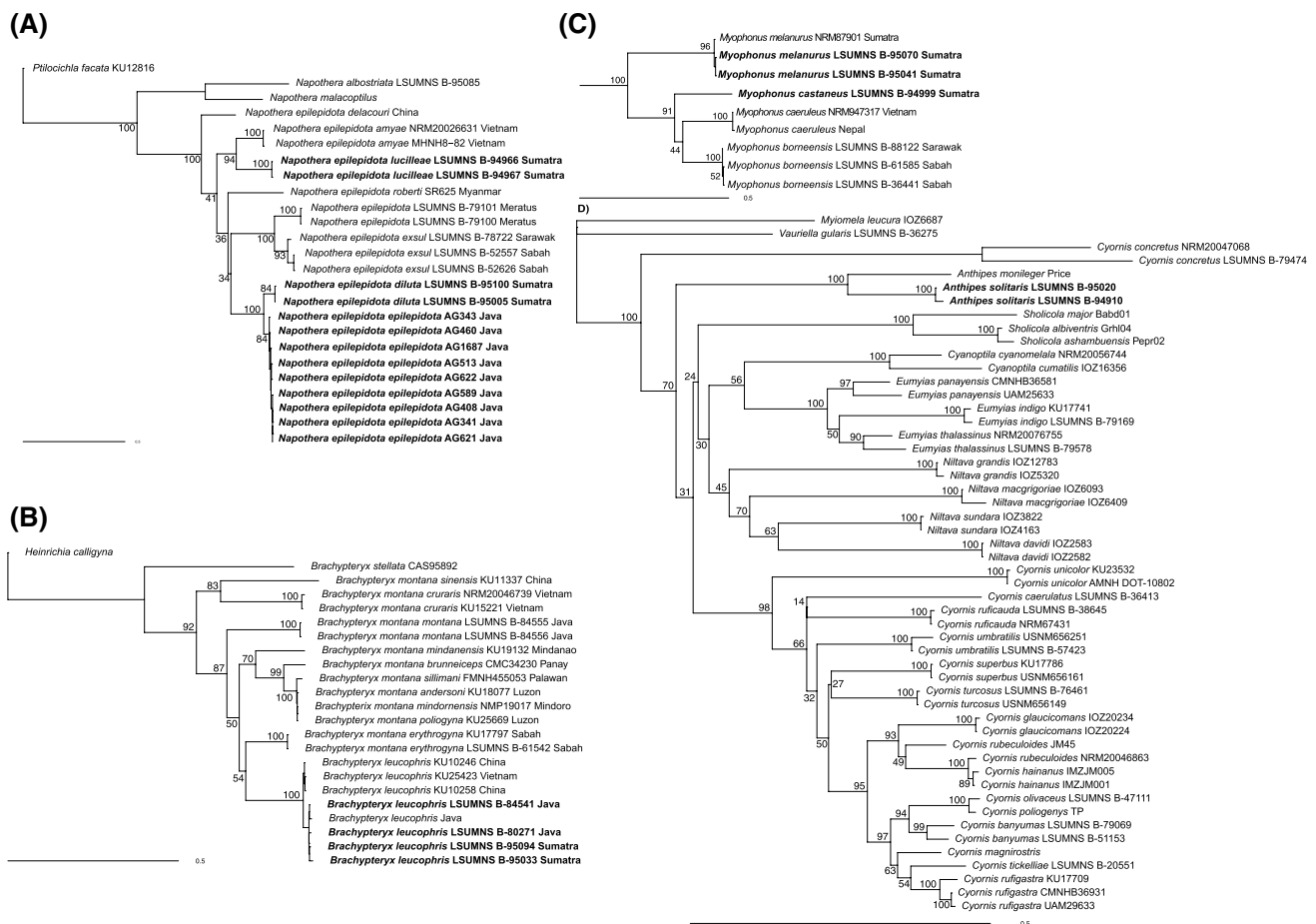


Fig. 3 Rooted maximum likelihood trees indicating mitochondrial ND2 DNA sequence relationships between various taxa of **a** *Napothera* wren-babblers, **b** *Brachypteryx* shortwings, **c** *Myophonus*

whistling thrushes, and **d** *Cyornis* flycatchers. Taxa for which new sequences were produced for this study are in bold type

A. ochraceus. It also indicates that Kalimantan's Meratus population is sister to the Bornean *A. o. ruficrissus/fowleri*, but sufficiently distinct in plumage and ND2 divergence (ca. 4.5%) to warrant separate subspecies status. Thus, following the classification of Del Hoyo et al. (2019) instead of Gill and Donsker (2020), we propose the following:

Alophoixus ruficrissus meratusensis ssp. nov.

L S I D — u r n : l s i d : z o o b a n k . o r g : a c t : 8 8 5 7 C 7 5 4 - 7 6 1 5 - 4 C 5 B - A E 2 8 - 2 D 4 1 3 D 0 8 0 D A 8 .

Holotype: Study skin, Museum Zoologicum Bogoriense (MZB No. 35541), Bogor, Indonesia; tissue MZB 35541/LSUMNS B-79057; adult male; Indonesia, Kalimantan Selatan Province, Hulu Sungai Selatan Regency, summit trail to Mt. Besar, 2.7249 S 115.5863 E, 1150 m asl; habitat moderately disturbed montane forest; collected 8 May 2017;

prepared by Frederick H. Sheldon (FHS), original catalog number FHS 1134 (Fig. 5a).

Description of holotype: We follow Smithe (1975) for color nomenclature and definitions, with color designations capitalized. Forehead and crown scaly, feathers grayish olive (Color 43), more brownish olive (Color 29) towards the crest. Lore to ear coverts glaucous (Color 79). Chin to throat white. Breast and sides of the body citrine (Color 51) with a yellow tinge, becoming straw yellow (Color 56) towards and on the belly. Undertail coverts cinnamon-rufous (Color 40). Upperparts, from nape to back, between olive green (Color 46) to olive green (Auxiliary, Color 48). Upper tail coverts raw umber (Color 23). Tail between reddish fuscous (Color 21) and burnt amber (Color 22), with raw umber edging and a lighter underside. Primaries dark grayish brown (Color 20), secondaries much lighter. The wing edges olive green (Auxiliary, Color 48). Soft part colors (specimen label):

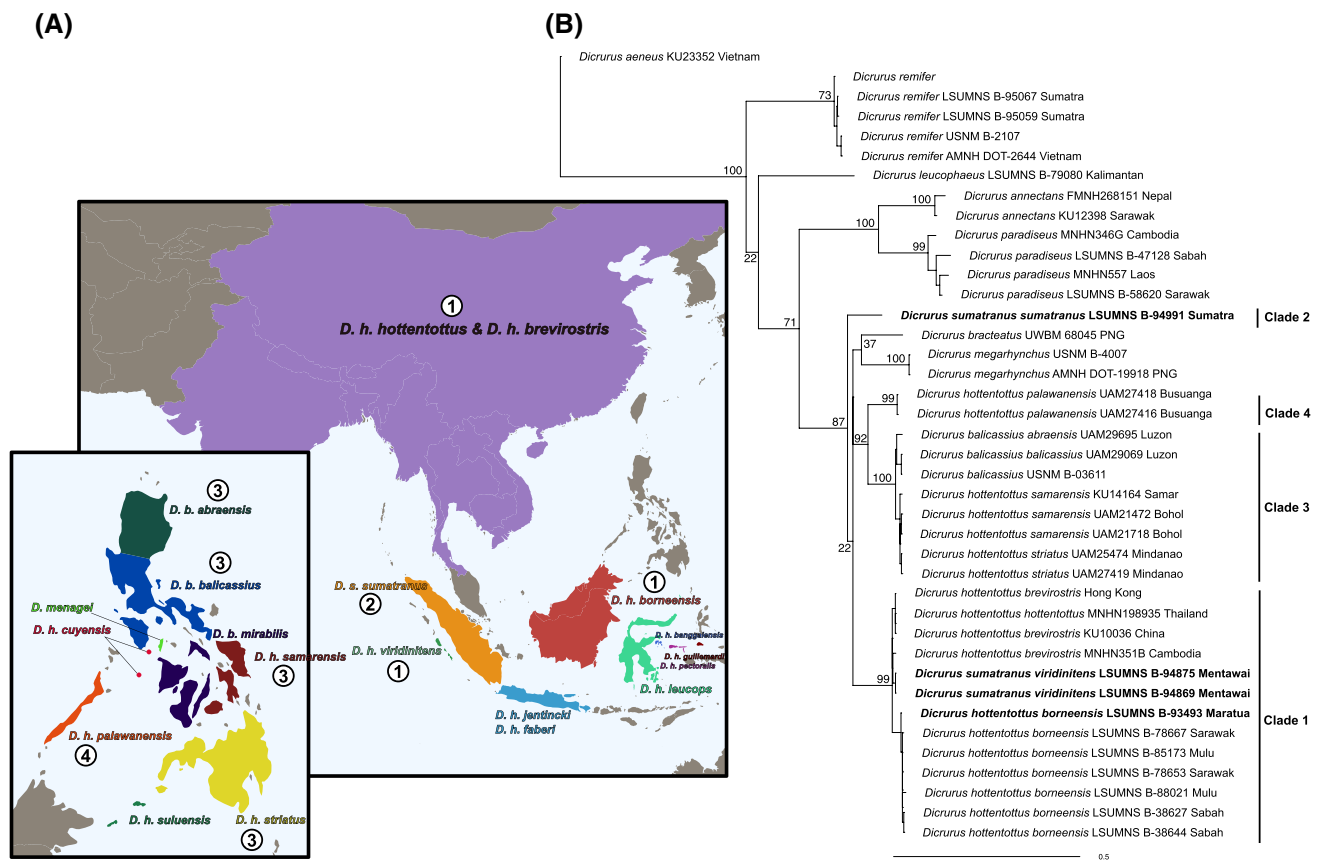


Fig. 4 **a** Map showing ranges of subspecies of *Dicurus hottentottus*, *D. sumatranus*, *D. menagei*, and *D. balicassius*. Taxa without associated clade numbers were not sampled in this study. **b** Rooted maximum likelihood trees indicating mitochondrial ND2 DNA sequence

relationships between various populations and species of Dicuridae. Taxa for which new sequences were produced for this study are in bold type

maxilla dark gray, mandible gray, legs and toes light brown, iris brownish red.

Measurement of type: See Table 1.

Diagnosis: There is no sexual dimorphism in coloration.

Figure 5 compares *A. ruficrissus meratusensis*, *A. r. ruficrissus*, *A. ochraceus sumatranus*, and *A. tephrogenys gutturalis*, respectively. Taxic differences are described below:

Alophoixus ruficrissus meratusensis versus *A. r. fowleri/ruficrissus*.

Alophoixus ruficrissus meratusensis is distinguished from *A. r. fowleri* and *A. r. ruficrissus* by having: the crown greyish olive versus greyish brown; a shorter crest; the breast and belly yellow versus uniform light drab (Color 119C) to drab gray (Color 119D) with an olive tinge; the upperparts tinted markedly olive, including the wing edges; the wings blackish with olive edging versus brownish; the upper tail

coverts darker brown versus more rufous; and the undertail coverts cinnamon versus rufous. *A. r. meratusensis* also tends to be smaller than *A. r. fowleri*, especially in the wing and tail length (Table 1).

Alophoixus ruficrissus meratusensis versus *A. ochraceus sumatranus*.

Alophoixus ruficrissus meratusensis and *A. o. sumatranus* are similar in appearance and size. However, the former tends to have shorter wings and tail than the latter; its underparts are a lighter yellowish olive versus a dark brownish without any yellow tinge; and its wings are a little darker than those of *A. o. sumatranus*.

Alophoixus ruficrissus meratusensis versus *A. tephrogenys gutturalis*.

Alophoixus ruficrissus meratusensis differs from *A. tephrogenys gutturalis* in having: the forehead and crown grayish olive versus brown; upperparts olive versus brownish; wings



Fig. 5 **a** Ventral, dorsal, and side views of holotype of *Alophoixus ruficrissus meratusensis* ssp. nov. **b** ventral, **c** dorsal, and **d** side views of specimens of, from left to right, *A. r. ruficrissus*, *A. ochraceus sumatranus*, *A. r. meratusensis* paratype (MZB 35412), and *A. tephrogenys gutturalis*

and uppertail coverts darker brown with olive edgings on the feathers versus lighter brownish cinnamon with cinnamon edging; undertail coverts darker versus lighter cinnamon; and underparts bright yellow versus buff-greyish olive. Males of both subspecies are similar in size; however, wings and tails of female *A. r. meratusensis* are longer than those of *A. t. gutturalis* (Table 1).

Alophoixus ruficrissus meratusensis versus *A. tephrogenys tephrogenys*.

Alophoixus ruficrissus meratusensis differs from *A. tephrogenys tephrogenys* by being larger, especially in length of wings and tail (Table 1), and in having: upperparts darker versus lighter; forehead and crown grayish olive versus uniformly brown; and upper side of rectrices uniformly dark brown versus pale brownish olive.

Paratypes: MZB No. 35542 (adult female) and MZB No. 35543 (adult male) collected at the same locality as the holotype; MZB No. 35412/LSUMZ 198198 (adult female) collected nearby (Indonesia, Kalimantan Selatan Province, Hulu Sungai Selatan Regency, Kadayang, 2.7465 S 115.5555 E, 500 m asl).

Etymology: This new subspecies of *A. ruficrissus* is named for the locality where the type series was collected, the Meratus Mountains. As far as we know, *A. r. meratusensis* is restricted to this mountain range and is unlikely to occur elsewhere. The Meratus Mountains form an isolated range in southeastern Kalimantan that seems to have acted as a refuge for montane birds in a region of otherwise low elevation (Shakya et al. 2018).

Table 1 Summary of measurements of *Alophoixus* taxa

Species	Bill length (mm)				Wing (mm)				Tail (mm)				Mass (g)
	Range		Average		Range		Average		Range		Average		
	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	
<i>A. ruficristatus meratusensis</i> (N=4, M=2, F=2)	22.3–22.4	19.7–20.5	22.4	20.1	104.7–106.6	100.2–100.9	105.6	100.5	91.0–94.0	83.0–89.0	92.5	86.0	41.0–44.5
<i>A. ruficristatus fowleri</i> (N=4, M=3, F=1)	20.6–22.7	22.0	22.2	22.0	106.9–112.1	110.5	110.0	110.5	91.0–100.0	101.0	95.0	101.0	45.0
<i>A. ochraceus sumatranus</i> (N=8, M=4, F=4)	21.1–22.2	21.6–22.7	21.7	22.1	109.0–120.5	98.2–103.5	113.4	104.8	93.0–98.0	90.0–101.0	96.5	95.3	40.0–50.0
<i>A. tephrogenys gutturalis</i> (N=8, M=4, F=4)	23.0–23.8	21.4–22.4	23.4	21.9	104.6–109.7	98.4–103.9	106.4	100.7	82.0–86.0	77.0–85.0	84.8	80.5	39.0–59.0
<i>A. tephrogenys tephrogenys</i> (N=8, M=4, F=4)	21.0–22.5	19.8–21.0	21.6	20.3	93.6–101.8	87.4–93.0	98.2	91.9	66.0–84.0	72.0–76.0	77.8	75.3	NA

All specimens were measured by MI at the Museum Zoologicum Bogoriense
N total number of specimens, *M* male specimen, *F* female specimen

Habitat: Overgrown rubber at 500 m to moderately disturbed montane forest at 1150 m (Shakya et al. 2018).

Sumatran babbler *Pellorneum buettikoferi* (Vorderman, 1892)

A Sumatran endemic, *P. buettikoferi* was not available to Cai et al. (2018) in their reconstruction of ground-babbler (Pellorneinae) phylogeny. We obtained three specimens at Rimbo Panti (Sumatra) and found it to be the sister of Temminck's babbler *P. pyrrogenys*, restricted to Java and Borneo, at an ND2 distance of ca. 7% (Fig. 2c). Vocal and plumage differences between *P. pyrrogenys*, *P. buettikoferi* and buff-breasted babbler *P. tickelli* are discussed in detail by Wells et al. (2001).

Black-throated wren-babbler *Turdinus atrigularis* (Bonaparte, 1850)

Little is known about *T. atrigularis*, an endemic, mature forest species of Borneo. We compared ND2 of a specimen from Lanjak Entimau (Sarawak) to sequences used by Cai et al. (2018) in their ground-babbler phylogeny. Their tree included large wren-babbler *T. macrodactylus* (Strickland, 1844), whose tissue came from a specimen obtained in a bird market on Bali (hence, lacking locality information). We found *T. atrigularis* to be the sister of *T. macrodactylus* at an ND2 distance of ca. 14% (Fig. 2c). Citing Gelang et al. (2009), who originally discovered the distinction between *Turdinus* and *Napothera*, Cai et al. (2018) reserved *Turdinus* for *T. macrodactylus*, while assuming that the morphologically similar *T. atrigularis* also belonged in this genus. Our comparisons confirm that assumption.

Eye-browed wren-babbler *Napothera epilepidota* (Temminck, 1828)

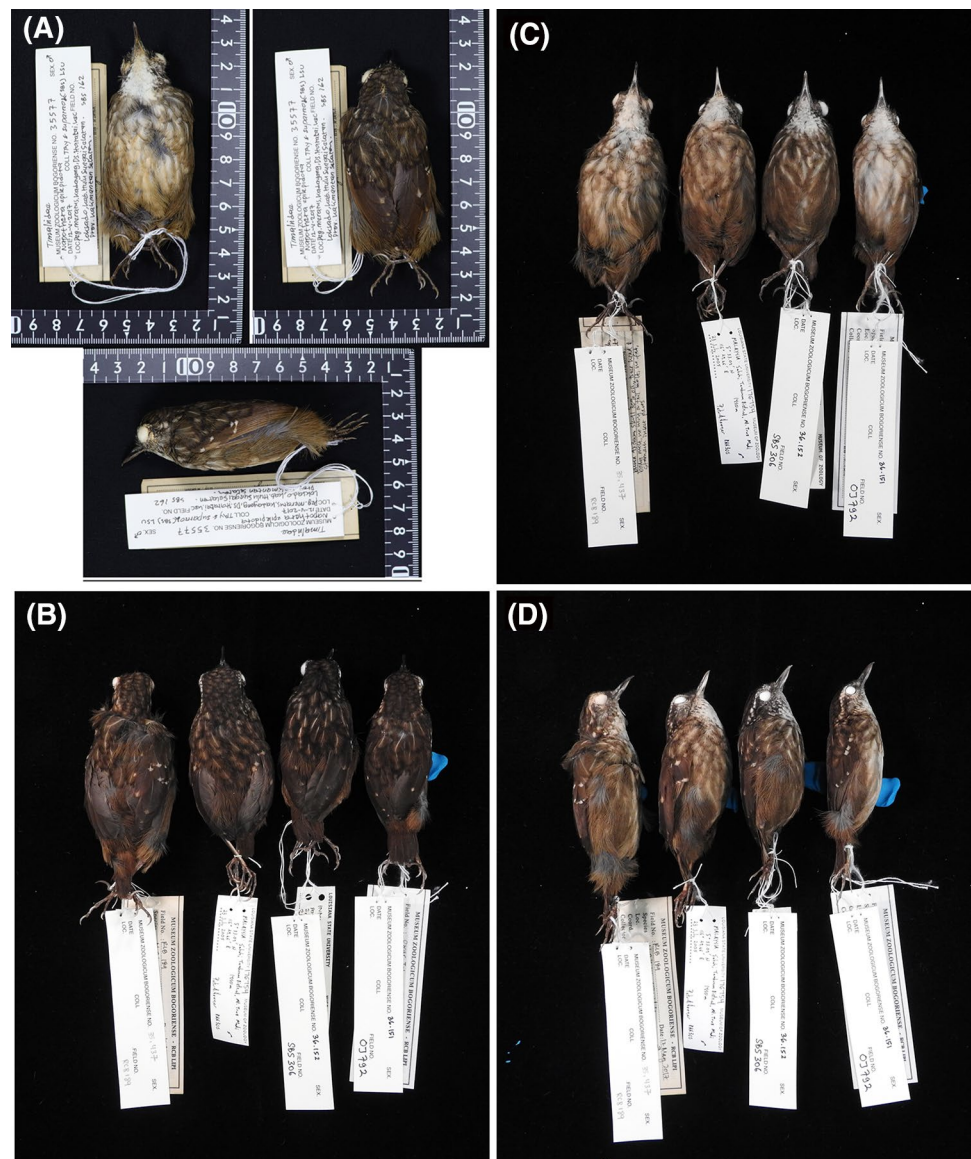
Meyer de Schauensee and Ripley (1939) reported on two species of wren-babblers from the mountains of Aceh Province, North Sumatra, in the collection of the Academy of Natural Sciences of Philadelphia (now Drexel University). One of these was *N. epilepidota* (Temminck, 1828), characterized by relatively dark underparts with white longitudinal streaks. They considered this species to comprise the Javan subspecies *epilepidota* and the Sumatran subspecies *diluta* and *mendeni* (the latter is now considered a junior synonym of *diluta*). The other species was *N. exsul* (Sharpe, 1888), characterized as having relatively pale and scalloped underparts. At the time, *N. exsul* consisted of most mainland Asian populations of what is now considered *N. epilepidota*, plus the Bornean subspecies *exsul*. Meyer de Schauensee and Ripley (1939) noted that these two species were collected on the same mountain and segregated by elevation, *N. exsul*

occurred from 1500–2500 ft. (~450 to 750 m) and *N. epilepidota diluta* at 3600 ft. (~1100 m). They named the lower elevation taxon *N. exsul lucilleae*. Subsequently, Deignan et al. (1964) considered the difference between *lucilleae* and *diluta* to be individual variation, treated *lucilleae* as a junior synonym of *diluta*, and merged them and all other subspecies of *N. exsul* and *N. epilepidota* into a single species: *N. epilepidota*.

On Mt. Talamau (Sumatra), we collected two morphotypes of *N. epilepidota* that differ in appearance and segregate by elevation, just as described by Meyer de Schauensee and Ripley (1939). Lighter scalloped individuals match the description of *lucilleae* and occur at lower elevation (900–1100 m) and darker streaked individuals match *diluta* and occur at higher elevation (1300–1600 m; Fig. 6). We also examined the original specimens at the

Academy of Natural Sciences and they support the morphological division, although their quality is poor. When we compared ND2 sequences of the two morphotypes to populations from Borneo and mainland Asia, we discovered the two taxa on Talamau differ by 11% in their ND2 sequences and are not sister taxa (Fig. 3a). However, sampling available from mainland Asia is so poor that it is impossible to determine relationships of most *N. epilepidota* subspecies (of ten mainland subspecies, we compared sequences of only three: *roberti*, *amya*, and *delacouri*). Moreover, the genetic differences among the subspecies we were able to compare ranges from 8 to 15% ND2 divergence, so it is likely that *N. epilepidota* actually comprises several distinct species. At this stage, we know only that *diluta* (Sumatra) and *epilepidota* (Java) are sister taxa, that *lucilleae* (Sumatra) and *amya* (Vietnam) likely belong in

Fig. 6 **a** Ventral, dorsal, and side views of *Napothera exsul* from the Meratus Mountains. **b** dorsal, **c** ventral, and **d** side views of specimens of, from left to right, *N. exsul* from the Meratus Mountains (second individual), *N. exsul* from NE Borneo, *N. epilepidota diluta*, and *N. roberti lucilleae*



the same clade, and that samples spanning Borneo (*exsul*) are monophyletic and distinct from the other subspecies (ND2 12–14%).

Based on the sympatry of *diluta* and *lucilleae* in Sumatra (Meyer de Schauensee and Ripley 1939; this study) and their morphological and genetic differences as well as the limited structure in our tree (Fig. 3a), we suggest the following (provisional) taxonomic changes.

1. *Napothera epilepidota* (Temminck, 1828) should be restricted to *N. epilepidota epilepidota* of Java and *N. epilepidota diluta* of Sumatra. It is characterized by dark underparts with white streaks. The common name would remain eyebrowed wren-babbler.
2. *Napothera exsul* (Sharpe, 1888) should be resurrected for *N. e. exsul* of Borneo. *Napothera exsul* differs from *N. epilepidota* (#1 above) by being considerably paler above; it differs from members of the *N. roberti* group (#3 below) by having greater streaking in its underparts. As a common name, we suggest Whitehead's wren-babbler because there is no simple plumage character that uniquely describes *N. exsul* (some *N. roberti* populations are also pale) nor does it inhabit a well-defined Bornean locality or habitat, other than mountains. The names mountain wren-babbler (*Turdinus crassus*) and Bornean wren-babbler (*Ptilocichla leucogrammica*) are already in use. John Whitehead collected the first specimens of this species and his name is universally associated with endemic montane birds of Borneo.
3. *Napothera roberti* (Godwin-Austen and Walden, 1875) may be used as a convenient, though likely polyphyletic, holding place for *N. epilepidota lucilleae* of Sumatra and the subspecies of mainland Asia until better sampling is available. This group is characterized by white-scalloped underparts. Considerable morphological variation occurs among its subspecies, especially between *roberti* and *guttaticollis* (Meyer de Schauensee and Ripley 1939), but without genetic data it is currently not possible to discern relationships among them. Some subspecies, including *guttaticollis*, *roberti*, *granti*, and *lucilleae*, may each constitute distinct species. The common name for *N. roberti* would be Austen's wren-babbler (Baker 1915).

The population of *N. exsul* from the Meratus Mountains (Kalimantan) is distinct genetically from the north and central Bornean populations (7%) and may warrant subspecies rank. However, the two existing skins from this population are both of juvenile birds. Without adult individuals for appropriate morphological comparisons, we refrain from naming the population. Nonetheless, we describe the plumage below:

Description of juvenile *Meratus Napothera exsul* based on MZB 35437/LSUMZ 198269 (Fig. 6a):

Approximate names of the colors used in the description, with standard color names from Ridgway (1912) and alphanumeric color codes from Munsell (1950) in parentheses. Upperparts dark brown (argus brown; 10YR3/6). Feathers on the head and back with black edges and prominent buffy shafts (cream buff; 10YR8/4), giving the head and back a striped appearance. Wings and tail similar in color to upperparts (argus brown; 10YR3/6). Secondary coverts with white spots. A white superciliary stripe runs from the lores to the side of head. Auriculars paler brown than head (orange buff; 7.5YR6) with black edges. Throat white tinged buff. Breast buffy brown (cinnamon buff; 7.5YR7/8) with dark edges and paler centers, giving the breast a striped appearance. Belly and flank feathers are darker brown (Antique Brown; 7.5YR3/4) with more prominent longitudinal stripes on feathers. Undertail coverts like the breast but with less prominent paler regions in center. Soft part colors recorded on collection: iris gold; feet and tarsi dark gold; bill, upper mandible black, lower mandible gray.

Measurement: weight: 18 g, bill length: 16.47 mm, wing: 54.47 mm, tarsus: 22.66 mm.

White-browed shortwing *Brachypteryx montana* (Horsfield, 1821) and lesser shortwing *Brachypteryx leucophris* (Temminck, 1828)

The classification of *B. montana* is notably unsettled. Dickinson and Christidis (2014) treat the 14 morphologically distinct populations of *B. montana* as subspecies, whereas other classifications split *B. montana* into as many as six species (e.g., Del Hoyo et al. 2019), consistent with recent genetic comparisons showing that some subspecies are highly divergent (Alström et al. 2018b; Kyriazis et al. 2018). As with other species in the region, it is difficult to resolve the taxonomic relationships within the *B. montana* complex because of sparse sampling.

Using new material of *B. montana erythrogyna* from the Maligan Range (Sabah) and *B. m. montana* from Purbalingga (Java), and new material of *B. leucophris leucophris* from Slamet and Ijen Reserves (Java) and Mt. Talamau (Sumatra), we generated a phylogenetic tree consisting of several populations of both species (Fig. 3b). In agreement with previous studies (Kyriazis et al. 2018), we found *B. montana* to be paraphyletic, with *B. leucophris* embedded within it. *B. leucophris* may be sister to the Bornean *B. m. erythrogyna*, although resolution in that part of the tree is poor. We also recovered a distinct Philippine clade and a mainland Asian clade. These clades have diverged by 8–12% in ND2 from one another.

Brown-winged whistling thrush *Myophonus castaneus* (RG Wardlaw-Ramsay, 1880)

Distinct forms of the Sunda whistling thrush *Myophonus* occur on each of the Sunda landmasses: Java (*glaucinus*), Borneo (*borneensis*), Sumatra (*castaneus*), and the Malay Peninsula (*robinsoni*). Some authors, including Dickinson and Christidis (2014), consider each population to be a subspecies of *M. glaucinus*. Others, including Collar (2004), Eaton et al. (2016), Del Hoyo et al. (2019), and Gill and Donsker (2020), consider each population to be a distinct species. We obtained new samples of *M. borneensis* and *M. castaneus*, but unfortunately not *M. glaucinus* or *M. robinsoni*, for ND2 comparison. Our tree (Fig. 3c) suggests that *M. borneensis* may be more closely related to blue whistling thrush *M. caeruleus* (Temminck, 1822) of mainland Asia, Sumatra, and Java than to *M. castaneus* (the tree is not well resolved in this respect). Because of this, we concur that each taxon should be recognized as a distinct species. The relationships of the Javan *glaucinus* and Malayan *robinsoni* remain to be determined.

Rufous-browed flycatcher *Anthipes Solitaris* (S. Müller, 1836)

Based on morphological similarities, Vaurie (1953) placed *A. solitaris* with white-gorgeted flycatcher *A. monileger* (Hodgson, 1845) in the “*Anthipes* group” of *Ficedula*. Subsequent phylogenetic analyses that included *A. monileger* but not *A. solitaris* found that *Anthipes* lies outside *Ficedula* (Outlaw and Voelker 2006; Sangster et al. 2010). Until now, the sister relationship of *A. solitaris* and *A. monileger* has been assumed. Comparisons of a new specimen of *A. solitaris* from Mt. Talamau (Sumatra) confirm that assumption (Fig. 3d).

Hair-crested drongo *Dicrurus hottentottus* (Linnaeus, 1766) and Sumatran drongo *Dicrurus sumatranus* (RG Wardlaw-Ramsay, 1880)

Dicrurus hottentottus forms a species complex that reaches from the Himalayas, through Sundaland, the Philippines and Wallacea, to Australia (Fig. 4a). The assignment of subspecies is based mainly on the morphological study of Vaurie (1949) but varies among classifications and uncertainty about intraspecific and interspecific relationships is substantial (Dickinson and Christidis 2014; Eaton et al. 2016; Clements et al. 2019; Gill and Donsker 2020). For example, the Maratua Island population (Kalimantan) is included in *D. h. suluensis* (Rocamora et al. 2009; Eaton et al. 2016), but Clements et al. (2019) and Dickinson and Christidis (2014) place it in *D. h. borneensis*. Populations from Sumatra (*D. sumatranus*), Tablas Island (*D. menagei*), and Wallacea (*D.*

densus) have alternately been split or lumped with *D. hottentottus* depending on classification.

We compared new *D. hottentottus* material from Mt. Kinabalu (Sabah), Mt. Mulu (Sarawak), the Kelabit Highlands (Sarawak), Maratua Island (Kalimantan), Mt. Talamau (Sumatra), and Siberut Island (Sumatra) with existing ND2 sequences (Fig. 4b). The tree indicates that *D. hottentottus* as currently classified is paraphyletic with the Balicassiao *D. balicassius* (Linnaeus, 1766). To simplify discussion of the tree, we have divided the taxa into four clades based on topology.

Clade 1 includes the nominate *D. h. hottentottus* and a migratory subspecies *D. h. brevirostris*, both from mainland Asia, along with *D. sumatranus viridinitens* of the Mentawai Islands, and *D. h. borneensis* of Borneo and Maratua Island. The Sumatran population *D. s. sumatranus* constitutes clade 2 and is genetically distinct from members of clade 1 (7–8% ND2 divergence). A biogeographically interesting aspect of clade 2 is that the population on Siberut in the Mentawai Islands is not sister to the adjacent Sumatran population, but instead is closer to populations on Borneo and mainland Asia. A disjunct relationship was recognized by Vaurie (1949), who hypothesized that the Mentawai population was derived by dispersal from Sulawesi via the islands of the Java Sea. He believed the Sumatran population derived by dispersal from the Lesser Sundas (Flores and Lombok). Unfortunately, our study lacks samples from Java, the Lesser Sundas and Java Sea islands, so Vaurie’s hypothesis remains to be tested.

Clades 3 and 4 comprise several Philippine taxa. Clade 3 includes *D. balicassius* of the northern Philippines and *D. h. samarensis* and *D. h. striatus* of the southern Philippines. The Palawan subspecies *D. h. palawanensis* constitutes Clade 4. Vaurie (1949) distinguished *D. hottentottus* from *D. balicassius* based on the appearance and complexity of feather ornaments. Genetic data, however, suggest a close relationship between *D. hottentottus* subspecies of the southern Philippines and *D. balicassius* of the northern Philippines. It is possible, however, that this closeness arises as a result of mtDNA introgression. A more extensive set of comparisons using nuclear loci is required to confirm *D. hottentottus* relationships within the Philippines Islands.

As noted, the *D. hottentottus* species complex extends through Wallacea to Australia, thus many taxa in the group are beyond the scope of this study. Based on our comparisons, however, we suggest the following (limited) taxonomic changes:

1. Elevate short-tailed Drongo *D. h. striatus* (including *D. h. samarensis*) of the southern Philippines to species status or include it as a subspecies of *D. balicassius*.
2. Elevate Palawan Drongo *D. h. palawanensis* (probably including *D. menagei* and *D. h. cuyensis*) to species sta-

tus. Rocamora et al. (2009) present arguments for treating *D. menagei* as a separate species.

3. Remove the Mentawai subspecies *viridinitens* from Sumatran Drongo *D. sumatranus*.
4. Maintain or place the following subspecies within hair-crested Drongo: *D. h. hottentottus*, *D. h. brevirostris*, *D. h. viridinitens*, and *D. h. borneensis*. This species would for the time being include additional extralimital taxa.

Conclusions

ND2 sequence comparisons provide only preliminary estimates of genealogical relationships (see Lim et al. 2017; Campillo et al. 2018, for examples of ND2 limitations in the study of Bornean taxa), but nevertheless add a quantitative element to the difficult process of assigning taxonomic positions. Their contribution is especially useful for studies of Southeast Asian taxa, given the complexity of geological and geographic events.

Unfortunately, despite increased sampling provided by recent work in Sumatra, Java, and Kalimantan, we were still unable to compare all necessary taxa in most groups examined. Even so, we have moved closer to that goal and, in the process, clarified several relationships. We have also obtained samples for future taxonomic and evolutionary studies. Ultimately, documenting the key features of avian diversification in the Southeast Asia, including the investigation of population size changes, rates of gene flow, and timing of key events, will require better sampling through extensive fieldwork and the application of next-generation DNA technology.

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