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Preliminary assessment of community composition and phylogeographic relationships of the birds of the Meratus Mountains, south-east Borneo, Indonesia

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by Subir B. Shakya, Tri Haryoko, Ryan C. Burner, Dewi M. Prawiradilaga & Frederick H. Sheldon

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SUMMARY.—The Meratus Mountains of south-east Borneo are biogeographically interesting due to their isolation and potential endemicity. However, Meratus' birds have never been quantitatively surveyed or collected, so we know little of their community structure or taxonomy. In May 2017, we visited Mt. Besar in the Meratus range to assess its avifauna and collect specimens for phylogeographic study. Here, we report on Mt. Besar's avifauna and provide preliminary ND2sequence assessments of their relationships. We recorded 89 species, of which we collected 68 species; 17 represented distributional extensions. Mt. Besar's avian community is depauperate compared to Borneo's main mountains, and several of its species exhibit unusual elevational abundance patterns. We attribute these findings to the range's small area, low elevation, isolation from other mountains, depleted surrounding native lowland forest, and exploitation for food and pet-trading. ND2 comparisons indicate that at least 12 Meratus species exhibit population structure that merits additional phylogeographic study.

The island of Borneo is well known for its impressive avian diversity, which includes at least 373 breeding landbird and 52 endemic species, depending on classification (Dickinson & Remsen 2013, Dickinson & Christidis 2014, Sheldon et al. 2015, Eaton et al. 2016c, Clements et al. 2017). This remarkable diversity hinges on the island's wide range of habitats, from low-elevation mixed-dipterocarp, peatswamp and kerangas forests to montane moss forests and ericaceous heath. Although most of Borneo's avian diversity inhabits the lowlands, the island's montane forests are particularly important in terms of biogeographic history, not only of the island itself but the Greater Sundas as a whole (de Bruyn et al. 2014, Sheldon et al. 2015). Borneo's mountains include the main central range, which runs north-east to southwest across most of the island and features several peaks above 2,000 m in elevation, one of which, Mt. Kinabalu, reaches 4,095 m (Fig. 1). There are also numerous smaller ranges and peaks that are isolated from the main range by areas of low elevation. As a group, Borneo's mountains—especially those on the eastern side of the island—are thought to have played a key role in fomenting and preserving much of South-East Asia's avian diversity (de Bruyn et al. 2014, Sheldon et al. 2015). The mountains supported rainforest continuously during dramatic climatic changes in the Oligocene, Pliocene and Pleistocene, when colder temperatures extirpated rainforest over much of the rest of Sundaland in favour of seasonal forest and even grasslands (Bird et al. 2005, Morley 2012, Sheldon et al. 2015). However, despite the biogeographic importance of Borneo's mountains, remarkably little is known concerning the evolution and ecology of birds there, especially those occurring in mountains outside the Malaysian states of Sarawak and Sabah. This is particularly true of birds in the Meratus range of south-east Borneo. These mountains have rarely been visited by ornithologists or birdwatchers (Davison 1997, Eaton et al. 2016a), and their birds have

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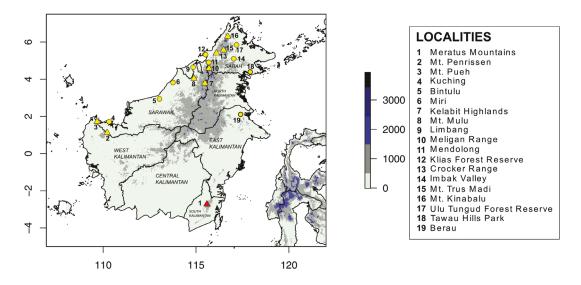


Figure 1. Map of Borneo showing the location of the Meratus and other mountain ranges.

never been surveyed quantitatively or collected for taxonomic study. As a result, we know little concerning the biogeographic relationships or community composition of the Meratus avifauna.

The Meratus Mountains are a low-elevation range skirting the south-east corner of Borneo in the Indonesian province of South Kalimantan (Fig. 1). They run north-northeast and are *c*.300 km in length and 65 km wide (Witts *et al.* 2012), with a highest point at Mt. Besar (1,901 m). The mountains consist mainly of an early Cretaceous volcanic arc and ophiolite sequence (Moss & Wilson 1998) but, like Mt. Kinabalu, they are relatively young, having arisen in the middle to late Miocene as a result of collision and subduction of continental plates on Borneo's south-eastern side (Witts *et al.* 2012). Their potential as a Pleistocene refugium and area of high endemicity has long been appreciated (MacKinnon *et al.* 1996, Gathorne-Hardy *et al.* 2002, Quek *et al.* 2007, Raes *et al.* 2009). Most forest in the Meratus Mountains is intact compared to the surrounding lowlands, but it is largely unprotected from logging and development, except the southern section, which lies within the Martapura-Pleihari Reserve (Holmes & Burton 1987, Davison 1997).

To date, only two surveys of Meratus birds have been published. Davison (1997) visited these mountains between 30 September and 10 October 1996. He identified 80 species above 800 m, expanding the known range of 21 montane specialists (*sensu* Wells 1985). Eaton *et al.* (2016a) visited the mountains on 7–10 July 2016. They observed, audio-recorded and photographed birds, identified 91 species, expanded the known range of several species, and discovered what they believed to be new species of *Cyornis* and *Zosterops*. Both expeditions approached the range from the west via Loksado (*c*.200 m) and the village of Kadayang (*c*.500 m). Davison (1997) reached close to the top of Mt. Karokangan (1,686 m), while Eaton *et al.* (2016a) reached the peak of Mt. Besar (1,901 m). Both noted that forest was heavily disturbed below 900 m, where rugged limestone outcrops appear (Davison 1997), and mildly disturbed above this elevation. The discoveries made by these two expeditions highlight the potential importance of the Meratus Mountains to understanding the evolution of avian diversity on Borneo.

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Louisiana State University Museum of Natural Science (LSUMNS) and the Museum Zoologicum Bogoriense, Indonesian Institute of Sciences (MZB), conducted a joint expedition to Mt. Besar on 1–19 May 2017. The primary purpose was to obtain molecular and morphological specimens for use in ongoing studies of Sundaic avian biogeography (e.g., Lim *et al.* 2011, Lim & Sheldon 2011, Chua *et al.* 2017, Lim *et al.* 2017, Moyle *et al.* 2017). We were also interested in the elevational distribution of birds in the Meratus Mountains, and how this distribution compares with montane communities examined elsewhere on Borneo (e.g., Harris *et al.* 2012, Burner *et al.* 2016). Here, we report on the expedition, approximate distribution of birds in the Mt. Besar region, and findings of preliminary molecular phylogeographic comparisons.

Methods

Expedition.—Our team comprised three researchers from LSUMNS (SBS, RCB, FHS), a researcher (TH) and field technician from MZB (Suparno), and a variety of local guides and porters. Like Davison (1997) and Eaton *et al.* (2016a), we approached Mt. Besar from Loksado in the Hulu Sungai Selatan regency of South Kalimantan province. We travelled from Loksado to the village of Kadayang (02°44′47″S, 115°33′20″E; 500 m), where we mistnetted birds on 1–6 May 2017. Near Kadayang, virtually all forest had been converted to (mostly overgrown) rubber, plots of hill rice, and gardens. On 6 May, we established camp on the Mt. Besar summit trail at a site known locally as 'Matupa' (02°43′30″S, 115°35′11″E; 1,150 m). We remained at this site until 19 May, setting mist-nets along the main ridge at 1,100–1,200 m and along another ridge at 1,350 m (02°43′22″S, 115°35′35″E). As noted by earlier expeditions, rubber plantation and shifting cultivation gave way to less disturbed forest at *c.*900–1,000 m. The forest above 1,000 m was largely intact, although there were some cleared areas of varying age, and footpaths were heavily trafficked by hunters armed with air guns (pellet guns) and persons seeking forest products.

Elevational records. — Avian species were sampled using mist-nets and by opportunistic observation based on visual and aural detections. Team members noted all species heard or seen during the trip, but most of our effort was directed towards mist-netting and specimen preparation.

Comparative analysis.—For morphometric comparisons we measured bill length, width and depth (all at the rear of the nares), as well as tail length, diagonal tarsus and flat wing-chord length.

We compared mitochondrial ND2 sequences of 41 species from Mt. Besar with sequences from populations in other parts of South-East Asia as available (Appendices 1-2). ND2 was used because it is the most commonly sequenced avian gene and numerous sequences were available in GenBank. When possible, we compared two individuals from each population, and included outgroups for perspective. Total genomic DNA from preserved tissues 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). 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 visualised the PCR products in 1.5% agarose gel stained with SYBR® Safe DNA Gel Stain (Invitrogen). Samples were sequenced at Macrogen USA (Rockville, MD). The ND2 sequences were assembled in Geneious 8.1.9 (Biomatters) and aligned using MUSCLE (Edgar 2004) implemented in Geneious. We generated mitochondrial gene trees using the maximum likelihood (ML) framework in RAxML 8 (Stamatakis 2014), with 1,000 bootstrap replicates, through the CIPRES Science Gateway (Miller et al. 2010).

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Results

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Expedition.-We recorded 89 species on Mt. Besar (Appendix 1), of which 68 were collected. Of the species recorded, 17 were new for the Meratus Mountains (marked with double asterisks in Appendix 1). Most notable among these was Bornean Spiderhunter Arachnothera everetti, the first record of this species outside Borneo's main mountain chain (Mann 2008, Brickle et al. 2010, Burner et al. 2016, Moyle et al. 2017). Its occurrence in the Meratus Mountains mirrors Bornean Leafbird Chloropsis kinabaluensis, which until it was discovered in the Meratus Mountains by Eaton et al. (2016a) was also thought to be restricted to Borneo's main mountain chain (Mann 2008, Moyle et al. 2011, 2017). Two of our 'new' Meratus records, Black-backed Dwarf Kingfisher Ceyx erithaca and Pin-tailed Parrotfinch Erythrura prasina, were anticipated by Davison (1997) from discussions with villagers. Some usually easily detected species recorded by Davison (1997) were not found by us or by Eaton et al. (2016a), most notably Helmeted Hornbill Buceros vigil, Oriental Magpie-Robin Copsychus saularis, White-rumped Shama C. malabaricus and Grey-cheeked Bulbul Alophoixus bres. These species are highly sought by hunters and pet traders (Eaton et al. 2016b), and probably have been extirpated from the area we visited.

Elevational records.—Elevational ranges of most species detected on Mt. Besar were within the limits known from other parts of Borneo. However, some patterns of species occurrence appeared unusual. Several species that are common at the same elevations in similar forest in other parts of Borneo were absent or found in low numbers on Mt. Besar. These include species that are generally common and conspicuous at 500 m, such as Greybellied Bulbul Pycnonotus cyaniventris, Spectacled Bulbul P. erythropthalmos, Yellow-bellied Bulbul Alophoixus phaeocephalus, Fluffy-backed Tit-Babbler Macronus ptilosus, Rufousfronted Babbler Cyanoderma rufifrons, Rufous-crowned Babbler Malacopteron magnum and Short-tailed Babbler Pellorneum malaccense. Other 'missing' species were Rufouswinged Philentoma Philentoma pyrhoptera, Green Iora Aegithina viridissima, Blyth's Paradise Flycatcher Terpsiphone affinis and Pale Blue Flycatcher Cyornis unicolor. Another unusual feature of the bird community at 500-1,200 m was that its commonest species (based on capture and incidental observations) was Hill Blue Flycatcher Cyornis banyumas, which is generally uncommon and restricted to a narrow submontane elevational band in other parts of Borneo. Other slope specialists that are principally montane elsewhere in Borneo but occurred in unusually large numbers at 500 m on Mt. Besar were Grey-throated Babbler Stachyris nigriceps and Temminck's Babbler Pellorneum pyrrogenys. Their abundance near Kadayang was remarkable. At higher elevation, c.1,300–1,400 m, some usually scarce species were remarkably common, e.g., Bornean Stubtail Urosphena whiteheadi. In contrast, a species that is generally common and easy to mist-net in the main Bornean mountain range, Chestnut-hooded Laughingthrush Ianthocincla treacheri, was rarely seen and only occasionally heard (see Discussion).

Genetic and morphological comparisons.-Of the 41 Meratus species whose ND2 we compared, 23 were not obviously distinct from populations sampled elsewhere on Borneo, i.e., their phylogeographic trees had little branching structure, and their ND2 divergence values averaged less than 1%: Plaintive Cuckoo Cacomantis merulinus, Rufous Piculet Sasia abnormis, Malaysian Pied Fantail Rhipidura javanica, White-throated Fantail R. albicollis, Spotted Fantail R. perlata, Ashy Drongo Dicrurus leucophaeus, Bornean Treepie Dendrocitta cinerascens, Ashy Bulbul Hemixos flavala, Mountain Leaf Warbler Phylloscopus trivirgatus, Yellow-breasted Warbler Seicercus montis, Rufous-tailed Tailorbird Orthotomus sericeus, Scaly-crowned Babbler Malacopteron cinereum, Brown Fulvetta Alcippe brunneicauda, Pellorneum pyrrogenys, Ianthocincla treacheri, Rufous-chested Flycatcher Ficedula dumetoria,

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Little Pied Flycatcher *F. westermanni*, Eyebrowed Jungle Flycatcher *Vauriella gularis*, *Chloropsis kinabaluensis*, Chestnut-crested Yuhina *Yuhina everetti*, *Arachnothera everetti*, Little Spiderhunter *A. longirostra* and Purple-naped Spiderhunter *A. hypogrammicum*. In six cases, we did not possess an adequate number of specimens or sequences to speculate on patterns of population structure: Bornean Barbet *Psilopogon eximius*, Grey-chinned Minivet *Pericrocotus solaris*, Blyth's Shrike-Babbler *Pteruthius aeralatus*, *Urosphena whiteheadi*, Mountain Tailorbird *Phyllergates cucullatus* and Indigo Flycatcher *Eumyias indigo*. However, the remaining 12 species exhibited phylogeographic patterns worthy of further work. We depict these patterns in Fig. 2 and describe them briefly below, but caution that population genetic parameters have not been examined in detail. Also, note that mitochondrial trees sometimes indicate incorrect population structure (see Bornean examples in Lim *et al.* 2017, Manthey *et al.* 2017). The rooted trees in Fig. 2, therefore, are intended only as preliminary guides for future investigation.

Bornean Whistler *Pachycephala hypoxantha.*—Meratus individuals form a clade separate from other Bornean individuals, but divergence between the populations is not large (*c*.1%).

Ochraceous Bulbul *Alophoixus ochraceus.*—The Meratus population differs by 4.5% from both *A. o. ruficrissus* (Sabah specimens) and *A. o. fowleri* (Sarawak specimens), which are also distinct genetically from each other (Chua *et al.* 2017). All three populations differ in plumage (Table 1). The Sabah and Sarawak populations lack yellow pigment in their plumage, causing them to appear distinct from other populations of *A. ochraceus*. Indeed, the Meratus individuals look more like Sumatran than northern Bornean birds, raising the possibility of multiple invasions of Borneo. Confusion is also wrought by paraphyly of *A. ochraceus* and Grey-cheeked Bulbul *A. bres* as traditionally constituted; *A. ochraceus* of Sabah is sister to *A. bres* of Java (Fuchs *et al.* 2015, Collar 2017). *A. ochraceus* and *A. bres* populations among all of the Greater Sundas and the Malay Peninsula should be compared before their scientific names are revised.

Lemon-bellied White-eye Zosterops chloris.-This is one of the taxa identified as a new species by Eaton et al. (2016a). ND2 comparisons with 45 other species of white-eyes, including the genera Zosterops, Lophozosterops, Speirops and Chlorocharis (mostly from Moyle et al. 2009), reveal the Meratus population to be most closely related to Z. chloris (ND2 divergence 2.69%). This finding makes general biogeographic sense, because Z. chloris occurs from Wallacea west across some islands of the Java Sea to Karimata and Belitung (van Balen 2017). The occupied islands include Kalambau and Solombo Besar near the south-east corner of Borneo (Clements et al. 2017). However, Z. chloris generally occurs at low elevations and in coastal habitats, whereas the Meratus population is montane. As such, the Meratus population appears to fill a potential ecological gap left by the absence of montane white-eye species that occupy mountains in other parts of Borneo: Black-capped White-eye Z. atricapilla, Mountain Black-eye Chlorocharis emiliae and Pygmy White-eye Oculocincta squamifrons. None of these species seems to occur in the Meratus range, leaving the high-elevation forest open for invasion and occupation by Z. chloris. We have not yet performed a morphological analysis for lack of specimens from other populations, but plumage of the Meratus birds appears much like that in photographs of other populations (Fig. 3). Given the large number of Z. chloris populations across the Java Sea and Wallacea, extensive study will be required to determine more precise phylogeographic relationships of the Meratus birds.

Bold-striped Tit-Babbler *Mixornis bornensis.*—Genetic comparisons of the Meratus population indicate it is closest to individuals from Sarawak and western Sabah (Meligan range) (ND2 divergence 0.55%) than to those in the rest of Sabah and mid-eastern Kalimantan (Berau) (ND2 divergence 3.33%). However, this species displays greater mtDNA

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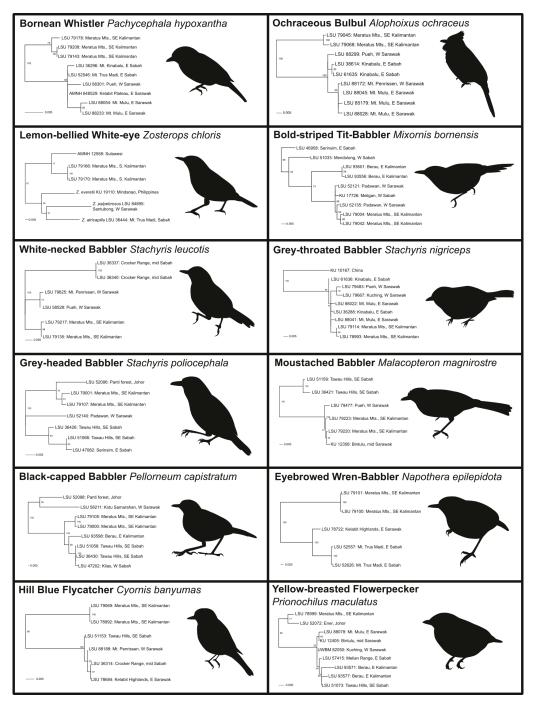


Figure 2. Rooted maximum likelihood trees indicating mtDNA-ND2 relationships between Meratus and other populations (in some cases species) for 12 species exhibiting marked genetic patterns. Bootstrap values are reported next to respective nodes.

than nuclear DNA structure on Borneo (Lim *et al.* 2017). It also has complex relationships with Pin-striped Tit-Babbler *M. gularis* (Cros & Rheindt 2017), its closest relative outside of

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TABLE 1 Plumage colour variation in Ochraceous Bulbul Alophoixus ochraceus and Grey-cheeked Bulbul A. bres from the Meratus Mountains and other parts of Borneo.

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Plumage tract	A. ochraceus (Meratus)	A. ochraceus ruficrissus/ fowleri (Sabah and Sarawak)	Alophoixus bres (Sabah and Sarawak)
Crown and nape	Grey	Greyish brown	Rufous-brown
Back and rump	Olive-green	Olive-brown	Olive-green
Tail	Dark reddish brown	Dark reddish brown	Dark reddish brown
Wings	Brown with green edges	Dark reddish brown	Dark reddish brown
Throat	White	White	White
Breast and flanks	Bright olive-green	Greyish brown	Pinkish brown
Belly	Lemon-yellow	Pale yellowish brown	Pale yellow
Vent	Yellowish brown	Rufous	Yellowish brown



Figure 3. Lemon-bellied White-eyes *Zosterops chloris* from: (A) the Meratus Mountains (J. C. Eaton); (B) Tukangbesi Islands, south-east Sulawesi, *Z. c. flavissimus* (J. C. Eaton); and (C) Lore Lindu National Park, central Sulawesi, *Z. c. mentalis* (D. Beadle)

Borneo, decreasing the reliability of conclusions based on a few mtDNA comparisons of a limited sample of specimens.

White-necked Babbler *Stachyris leucotis*. — The Meratus, Sarawak and Sabah populations appear to form distinct clades. ND2 distances are: Meratus–Sarawak 1%, Meratus–Sabah 3% and Sabah–Sarawak 3%. The substantial divergence separating Sabah's population from the others is consistent with many other species (Lim *et al.* 2010, 2011, Lim & Sheldon 2011, Lim *et al.* 2017).

Grey-throated Babbler *Stachyris nigriceps.*—The Meratus population appears distinct from western Sarawak and north-eastern populations (ND2 divergence 4%; also see Chua *et al.* 2017).

Grey-headed Babbler *Stachyris poliocephala.*—Like White-necked Babbler *S. leucotis,* this lowland species exhibits marked divergence among Meratus, Sarawak and Sabah populations (ND2 divergence 2.3%) (Lim *et al.* 2011).

Moustached Babbler *Malacopteron magnirostre.*—The population-genetic structure of Borneo's *Malacopteron* species has never been assessed. Meratus and Sarawak populations appear to be closely related and quite distinct from birds in eastern Sabah (ND2 divergence 5.81%). The pattern in this species suggests a connection between western and southern Bornean populations and, again, a distinct history for the north-east population (Lim *et al.* 2010, 2011, Lim & Sheldon 2011, Lim *et al.* 2017).

Black-capped Babbler *Pellorneum capistratum.*—The Meratus population is distinct from others in Borneo (average ND2 divergence 7.2%), and Sabah and Sarawak populations are distinct from one another as well (ND2 divergence 11.2%) (Lim *et al.* 2011).

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Eyebrowed Wren-Babbler *Napothera epilepidota.*—Few tissues of this species are available for genetic assessment. However, the three Bornean populations we compared are remarkably different from one another genetically, in the order of 7%. We did not obtain sufficient specimen material to judge morphological differences.

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Hill Blue Flycatcher *Cyornis banyumas.*—This taxon is one of two possibly new species mentioned by Eaton *et al.* (2016a). ND2 comparisons indicate that the Meratus population is monophyletic with *C. banyumas* and divergent by 3.27% from other Bornean populations that have been sampled (i.e., in Sabah and on Mt. Mulu in eastern Sarawak). Morphometric comparisons indicate that Meratus individuals are larger overall in size and have larger bills than those from Borneo's central mountain chain (Table 2). The orange breast of Meratus males also grades into a whiter belly and their black chin is much reduced compared to male *C. banyumas* from Mt. Mulu and Sabah. As with *Z. chloris*, thorough phylogeographic comparisons across the entirety of Sundaland will be required to establish the phylogeographic position of the Meratus population.

Yellow-breasted Flowerpecker *Prionochilus maculatus.*—Our single Meratus specimen is relatively distinct genetically from other Bornean populations and closer to a Peninsular Malaysian bird. Better sampling will be required to tell if this unexpected relationship is well supported and what it implies for Bornean populations.

Discussion

Avifaunal characteristics. – Compared to Borneo's central mountain chain, the Meratus forest bird community has distinctive features. At 500 m, some common lowland species are absent (e.g., *Pycnonotus erythropthalmos, Macronus ptilosus* and *Pellorneum malaccense*), whereas species normally uncommon at this elevation are abundant (e.g., *Stachyris nigriceps, Pellorneum pyrrogenys* and *Cyornis banyumas*). At higher elevations, 1,100–1,400 m, some species that are usually common are uncommon (e.g., *Ianthocincla treacheri*), and others that are typically uncommon are remarkably common (e.g., *C. banyumas, Urosphena whiteheadi*). Moreover, at this higher elevation, many montane species are completely absent, including numerous Bornean endemics such as Whitehead's Trogon Harpactes whiteheadi, Whitehead's Broadbill *Calyptomena whiteheadi* and Whitehead's Spiderhunter *Arachnothera juliae*.

Several interacting factors probably contribute to these patterns. First, the Meratus range is relatively small in area, low in elevation and isolated from other mountain ranges. Simply as a function of size, elevation and location, i.e., by the expectations of island biogeography, the Meratus Mountains should lack a complete montane avifauna. Second,

Population	Culmen length	Culmen width	Culmen depth	Tail	Tarsus	Wing
Meratus (mean)	10.63	5.87	4.53	64.78	20.48	78.83
Meratus (s.d.)	0.37	0.25	0.35	2.86	1.24	2.19
Sabah and Sarawak (mean)	9.68	5.48	3.86	61.20	17.98	72.80
Sabah and Sarawak (s.d.)	0.22	0.31	0.14	1.43	1.32	1.60
T-test P value	0.001	0.038	0.003	0.024	0.009	0.001

TABLE 2

Size comparison between six specimens of Meratus and five specimens of Sabah and Sarawak populations of Hill Blue Flycatcher *Cyornis banyumas,* including males and females. T-test values show significance of differences between the two groups. All measurements in mm.

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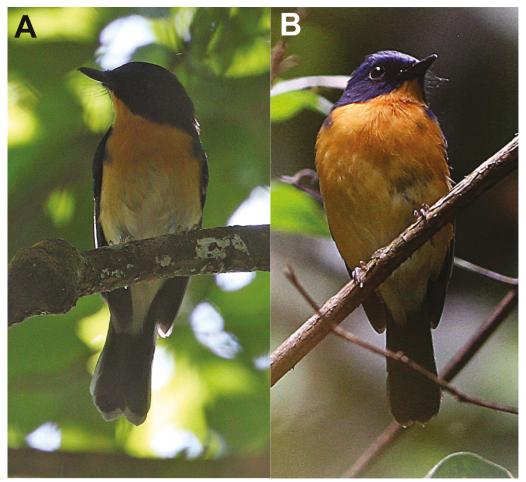


Figure 4. Male Hill Blue Flycatchers (*Cyornis banyumas*) from: (A) the Meratus Mountains (J. C. Eaton) and (B) Poring, Sabah, *C. b. montanus* (J. C. Eaton)

native lowland forest surrounding the Meratus Mountains has been replaced mostly by plantations: oil palm at low elevation, rubber and mixed-use forest at higher elevation (up to 900 m). Thus, the lowland forest avifauna that would normally contribute to the Meratus community at 500 m and above has largely been depleted. Montane species such as Stachyris nigriceps and Cyornis banyumas may be filling this low-elevation species void. There may also be a Massenerhebung effect driving montane species to lower elevation (Bruijnzeel et al. 1993). Third, the local human population appears to depend heavily on small birds for protein. Virtually every villager we encountered in the forest was carrying an air gun (pellet gun) and was shooting small birds and mammals for food. Unlike shotgun ammunition, air gun ammunition is inexpensive and, thus, these guns can be used economically to hunt animals that individually yield small amounts of food. The guns are also quiet when fired, and do not disturb wildlife. We observed hunters climbing fruiting fig trees and shooting numerous barbets at a sitting. This type of hunting pressure might explain the paucity of pigeons, trogons, laughingthrushes, drongos, Alophoixus bulbuls and other mid-sized species in the area we visited. Finally, hornbill-ivory hunters and pet traders appear to have extirpated Buceros vigil, Copsychus saularis, C. malabaricus and Alophoixus bres in the

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Kadayang area, and may be influencing numbers of other popular cagebird species (e.g., laughingthrushes and leafbirds).

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Biogeographic issues.-Knowledge of Sundaic rainforest bird phylogeography is confined mainly to studies of populations in Malaysian Borneo (Sabah and Sarawak). Although restricted geographically, these studies provide hypotheses against which to judge the results of our preliminary genetic comparisons of Meratus bird populations. Studies in Malaysian Borneo indicate that lowland populations of birds in Sarawak are often more closely related to those in western Sundaland (Malay Peninsula and Sumatra) than to populations in Sabah (Sheldon et al. 2009, Lim et al. 2010, 2011, Lim & Sheldon 2011, Lim et al. 2017). This pattern, combined with molecular estimates of divergence dates, suggests that Sabah's lowland birds were isolated (one or more times) from populations in western Sundaland, probably in rainforest refugia during global glacial events early in the Pleistocene (e.g., 1-2 million years ago) when most of central Sundaland was subaerial and covered by dry or seasonal forest (Sheldon et al. 2015). Similarly, studies suggest that Bornean populations of montane taxa, such as Chloropsis kinabaluensis, Bornean Forktail Enicurus leschenaulti borneensis and Arachnothera everetti, were isolated in rainforest refuges in north-east Borneo from congeneric populations in western Sundaland early in the Pleistocene (Moyle et al. 2005, 2011, 2017). During the more recent Pleistocene, glaciation events apparently had a different effect on Sundaic habitats; instead of reducing rainforest cover in Sundaland, they increased it, causing greater habitat connectivity among islands and the mainland (Cannon et al. 2009, Raes et al. 2014). Genetic comparisons suggest that, concomitant with this recent increase in rainforest coverage, several western Sundaic bird populations invaded Borneo and occupied the western lowlands, pushing or restricting endemic Bornean populations to the east or into the mountains. These dynamics caused the marked parapatry witnessed today between populations in the lowlands of Sarawak and Sabah (e.g., between White-rumped Shama Copsychus malabaricus suavis in Sarawak and White-crowned Shama C. m. stricklandii in Sabah) and between populations in the lowlands and mountains of Borneo (e.g., White-crowned Forktail Enicurus leschenaulti frontalis in the lowlands and Bornean Forktail E. l. borneensis at higher elevation) (Sheldon et al. 2015, Moyle et al. 2017). Using these biogeographic scenarios as a foundation, we can put our preliminary phylogeographic comparisons of Meratus birds into context and identify the requirements of future investigations.

One of the most interesting discoveries of this study is the occurrence of Chloropsis kinabaluensis and Arachnothera everetti in the Meratus Mountains (also see Eaton et al. 2016a). Previously these species were known only from north-eastern portions of the main Bornean mountain range, e.g., Mulu, Crocker Range and Menyapa Mountains (Mann 2008, Brickle et al. 2010, Burner et al. 2016, Moyle et al. 2017). Their presence in the Meratus Mountains suggests that early Bornean Pleistocene rainforest refuges occurred not just in Sabah (Sheldon 2016) but also in mountains and adjacent lowlands near the coast across much of eastern Borneo. This hypothesis is supported by paleo-habitat data (Morley 2012), paleo-habitat modelling (Cannon et al. 2009, Lim et al. 2011, Manthey et al. 2017) and phylogeographic studies (Quek et al. 2007, Chua et al. 2015).

Some of our preliminary ND2 comparisons suggest that lowland species in the Meratus Mountains are more closely related to western Sarawak or even western Sundaic populations than to north-east Bornean populations (e.g., Malacopteron magnirostre, Stachyris leucotis and Prionochilus maculatus). This pattern could result from the same phenomenon causing similarity between Sarawak and western Sundaic populations: invasion of Borneo from the west during recent global glacial events when the islands and mainland were connected by suitable habitat. Recent invasion of Borneo might also explain the genetic

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difference between montane birds in the Meratus Mountains and those in northern Borneo (e.g., *Alophoixus ochraceus, Pellorneum pyrrogenys, Napothera epilepidota* and *Cyornis banyumas*). Invasion from Sumatra is possible for all four of these species; the last three could have arrived from Java. A faunal connection between Java and south-east Borneo is especially likely, given proximity. Several open- or dry-habitat taxa are shared between Java and Borneo, e.g., Red-breasted Parakeet *Psittacula alexandri*, Savanna Nightjar *Caprimulgus affinis, Copsychus saularis* and Scarlet-headed Flowerpecker *Dicaeum trochileum* (e.g., Mees 1996, Phillipps & Phillipps 2014). More importantly for Meratus populations, preliminary genetic comparisons of some taxa from Borneo's central mountain chain, e.g., swiftlets (*Collocalia*), spiderhunters (*Arachnothera*) and forktails (*Enicurus*), suggest they are closest to Javan populations (Moyle *et al.* 2005, 2008, 2011). Thus, it is reasonable to expect that some birds in the Meratus Mountains will have at least as much, or greater, affinity with Javan populations than with other Bornean populations.

Overall, understanding the biogeographic significance of genetic and morphological divergence in both lowland and montane populations of the Meratus Mountains will require phylogeographic comparisons with populations of Java, Sumatra and even Peninsular Malaysia, as well as the rest of Borneo. For *Zosterops chloris*, it will require comparisons with populations across the Java Sea and Wallacea.

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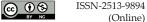
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Scientific name ^a	English name ^a	Elev	Elevation, this study [®]			Eaton et al.	
	English name	500 m	1,150 m	1,350 m	(1997) ^c	(2017)	
Rollulus rouloul	Crested Partridge					х	
Spilornis cheela	Crested Serpent Eagle	х			х	х	
Nisaetus alboniger	Blyth's Hawk-Eagle					х	
Lophotriorchis kienerii	Rufous-bellied Eagle					х	
Macropygia ruficeps	Little Cuckoo-Dove		х		х	х	
Chalcophaps indica	Asian Emerald Dove	х			х		
Treron olax**	Little Green Pigeon		х				
Ducula badia	Mountain Imperial Pigeon				х		
Centropus sinensis	Greater Coucal	х			х		
Centropus bengalensis	Lesser Coucal				х		
Phaenicophaeus curvirostris	Chestnut-breasted Malkoha	s					
Cacomantis merulinus*	Plaintive Cuckoo	s			х		
Cacomantis variolosus	Brush Cuckoo					х	

Appendix 1: List of bird species recorded in the Meratus Mountains

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Scientific name ^a	English name ^a	Elevation, this study ^b				Eaton et al.
	me English name 500 m 1,150 m 1,350 r		1,350 m	(1997) ^c	(2017)	
Surniculus lugubris	Square-tailed Drongo-Cuckoo		х		х	
Cuculus micropterus	Indian Cuckoo		х		х	
Cuculus lepidus	Sunda Cuckoo		х	s	х	х
Otus spilocephalus	Mountain Scops Owl					х
Bubo sumatranus	Barred Eagle-Owl					х
Glaucidium brodiei	Collared Owlet		s			х
Batrachostomus poliolophus	Short-tailed Frogmouth				х	х
Lyncornis temminckii	Malaysian Nightjar				х	
Rhaphidura leucopygialis	Silver-rumped Needletail				х	
Collocalia affinis	Plume-toed Swiftlet				х	
Aerodramus sp.	swiftlet sp.	х			х	х
Cypsiurus balasiensis	Asian Palm Swift	х				х
Harpactes diardii	Diard's Trogon	s				х
Harpactes oreskios**	Orange-breasted Trogon		s			
Berenicornis comatus**	White-crowned Hornbill		х			
Buceros vigil	Helmeted Hornbill				х	
Buceros rhinoceros	Rhinoceros Hornbill		х		х	х
Anorrhinus galeritus	Bushy-crested Hornbill		х		х	х
Rhyticeros undulatus	Wreathed Hornbill		х		х	х
Alcedo euryzona**	Blue-banded Kingfisher	s				
Ceyx erithaca**	Black-backed Dwarf Kingfisher	s				
Lacedo pulchella	Banded Kingfisher	5			х	х
Actenoides concretus	Rufous-collared Kingfisher				x	X
Nyctyornis amictus	Red-bearded Bee-eater	s			x	
Merops viridis	Blue-throated Bee-eater	5			x	
Psilopogon duvaucelii	Blue-eared Barbet				x	х
Psilopogon eximius	Bornean Barbet		s		А	x
Psilopogon mystacophanos	Red-throated Barbet	s	3		х	А
Psilopogon monticola	Mountain Barbet	3	s	х	x	х
Psilopogon chrysopogon	Gold-whiskered Barbet		3	~	x	x
Sasia abnormis*	Rufous Piculet	c.	c.	X		
Dendrocopos moluccensis		s	s	х	x	х
Dendrocopos canicapillus	Sunda Woodpecker				x	X
Picus miniaceus	Grey-capped Woodpecker				х	x
	Banded Woodpecker					x
Picus puniceus Picus mentalis	Crimson-winged Woodpecker		-			x
	Checker-throated Woodpecker		s			х
Meiglyptes tristis**	Buff-rumped Woodpecker		s			
Blythipicus rubiginosus	Maroon Woodpecker		s		х	х
Loriculus galgulus	Blue-crowned Hanging Parrot					х
Calyptomena viridis	Green Broadbill		х		х	х
Psarisomus dalhousiae**	Long-tailed Broadbill		S			
Eurylaimus javanicus	Banded Broadbill		х		х	
Eurylaimus ochromalus	Black-and-yellow Broadbill	х			х	х
Hydrornis schwaneri	Bornean Banded Pitta				х	х
Gerygone sulphurea	Golden-bellied Gerygone	х			х	х
Hemipus picatus	Bar-winged Flycatcher-Shrike				х	х
Pericrocotus solaris*	Grey-chinned Minivet		S			х
Pachycephala hypoxantha*	Bornean Whistler		s	s		х
Pteruthius aeralatus*	Blyth's Shrike-Babbler		s	S	х	х

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Scientific name ^a	English name ^a	Elevation, this study ^b			Davison	Eaton et al.	
	English hame	500 m 1,150 m		1,350 m	(1997)°	(2017)	
Erpornis zantholeuca	White-bellied Erpornis					х	
Dicrurus leucophaeus*	Ashy Drongo		s	s		х	
Rhipidura perlata*	Spotted Fantail		s		х	х	
Rhipidura javanica* **	Malaysian Pied Fantail	s					
Rhipidura albicollis*	White-throated Fantail		s	s	х	х	
Hypothymis azurea	Black-naped Monarch					х	
Platylophus galericulatus	Crested Jay		х		х	х	
Dendrocitta cinerascens*	Bornean Treepie		s	х		х	
Corvus enca	Slender-billed Crow				х		
Hirundo tahitica	Pacific Swallow				х		
Culicicapa ceylonensis	Grey-headed Canary-Flycatcher		s			х	
Sitta frontalis	Velvet-fronted Nuthatch			s		х	
Pycnonotus atriceps	Black-headed Bulbul	х			х	х	
Pycnonotus squamatus	Scaly-breasted Bulbul				x	x	
Pycnonotus goiavier	Yellow-vented Bulbul	s			x		
Pycnonotus brunneus	Red-eyed Bulbul	-			x		
Alophoixus ochraceus*	Ochraceous Bulbul	s	s		x	х	
Alophoixus bres	Grey-cheeked Bulbul	0	5		x	Х	
Hemixos flavala*	Ashy Bulbul		х	s	x	х	
Ixos malaccensis	Streaked Bulbul		A	3	А	x	
Urosphena whiteheadi*	Bornean Stubtail			s		x	
Abroscopus superciliaris	Yellow-bellied Warbler	s	s	3	х	x	
Phyllergates cucullatus*	Mountain Tailorbird	5	5	s	x	x	
Phylloscopus trivirgatus*	Mountain Leaf Warbler			s	x		
Seicercus montis*	Yellow-breasted Warbler		X			x	
	Dark-necked Tailorbird		х	s	х	x	
Orthotomus atrogularis						x	
Orthotomus ruficeps	Ashy Tailorbird	s			x	x	
Orthotomus sericeus*	Rufous-tailed Tailorbird	S			x	х	
Prinia flaviventris	Yellow-bellied Prinia	S			х		
Yuhina everetti*	Chestnut-crested Yuhina		s	s		х	
Zosterops palpebrosus	Oriental White-eye				đ	х	
Zosterops everetti	Everett's White-eye				x ^d		
Zosterops chloris*	Meratus White-eye			s	X ^e	х	
Mixornis bornensis*	Bold-striped Tit-Babbler	S			х	х	
Cyanoderma erythropterum**	Chestnut-winged Babbler		х				
Pomatorhinus montanus	Chestnut-backed Scimitar Babbler	s	s	s	х	х	
Stachyris nigriceps*	Grey-throated Babbler	S	s	х	х	х	
Stachyris poliocephala*	Grey-headed Babbler	S			Х		
Stachyris leucotis* **	White-necked Babbler			S			
Malacopteron magnirostre*	Moustached Babbler	s				х	
Malacopteron cinereum* **	Scaly-crowned Babbler	s					
Pellorneum capistratum* **	Black-capped Babbler	s					
Pellorneum pyrrogenys*	Temminck's Babbler	S	s	х	х	х	
Napothera epilepidota* **	Eyebrowed Wren-Babbler		s				
Alcippe brunneicauda*	Brown Fulvetta		s			х	
lanthocincla treacheri*	Chestnut-hooded Laughingthrush		s		х	х	
Irena puella	Asian Fairy Bluebird		s		х	х	
Copsychus saularis	Oriental Magpie-Robin				х		
Copsychus malabaricus	White-rumped Shama				х		

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0 1 114	w that a	Elevation, this study ^b			Davison	Eaton et al.
Scientific name ^a	English name ^a	500 m	1,150 m	1,350 m	(1997) ^c	(2017)
Cyornis banyumas*	Meratus Flycatcher	s	s	х	х	x
Cyornis superbus	Bornean Blue Flycatcher					х
Eumyias indigo*	Indigo Flycatcher		s			х
Eumyias thalassinus	Verditer Flycatcher					х
Vauriella gularis*	Eyebrowed Jungle Flycatcher		s	s	х	х
Brachypteryx montana	White-browed Shortwing					х
Enicurus leschenaulti	White-crowned Forktail	х			х	
Enicurus ruficapillus	Chestnut-naped Forktail				х	
Ficedula westermanni*	Little Pied Flycatcher		s		х	х
Ficedula dumetoria* **	Rufous-chested Flycatcher		s			
Chlamydochaera jefferyi	Fruit-hunter					х
Gracula religiosa	Common Hill Myna				х	
Chloropsis kinabaluensis*	Bornean Leafbird		s			х
Prionochilus maculatus*	Yellow-breasted Flowerpecker	s				х
Prionochilus xanthopygius	Yellow-rumped Flowerpecker					х
Dicaeum trigonostigma	Orange-bellied Flowerpecker	s			х	х
Dicaeum monticolum	Black-sided Flowerpecker				х	х
Chalcoparia singalensis	Ruby-cheeked Sunbird					х
Anthreptes malacensis	Plain-throated Sunbird				х	х
Leptocoma brasiliana	Van Hasselt's Sunbird					х
Aethopyga temminckii	Temminck's Sunbird		s	s	х	х
Aethopyga siparaja	Crimson Sunbird				х	
Arachnothera longirostra*	Little Spiderhunter	s			х	х
Arachnothera hypogrammicum*	Purple-naped Spiderhunter	s				х
Arachnothera flavigaster**	Spectacled Spiderhunter			s		
Arachnothera modesta	Grey-breasted Spiderhunter					х
Arachnothera everetti* **	Bornean Spiderhunter	s	s	х		
Erythrura prasina**	Pin-tailed Parrotfinch	s				
Lonchura fuscans	Dusky Munia	s			х	х

^a = Classification follows Clements *et al.* (2017).

^b = s: specimen records, x: other records.

^c = Migrants recorded by Davison (1997) have been omitted.

^d = Identified as Zosterops everetti or perhaps Z. palpebrosa by Davison (1997)

^e = Identified as Z. atricapilla by Davison (1997).

* = Species for which ND2 was sequenced in this study.
** = New records for the Meratus Mountains.

Appendix 2: List of ND2 sequence-samples compared for this study, classified according to Clements et al. (2017).

Tissue No.*	Genus	Species	Locality	GenBank No.
LSUMNS B-51117 / AMNH DOT 15123	Cacomantis	sonneratii	Tawau Hills Park, Sabah	KJ455342
LSUMNS B-79648	Cacomantis	sonneratii	Kuching, Sarawak	MG546353
LSUMNS B-47009	Cacomantis	merulinus	Mt. Kinabalu, Sabah	MG546349
LSUMNS B-47049	Cacomantis	merulinus	Mt. Kinabalu, Sabah	MG546350
LSUMNS B-58630	Cacomantis	merulinus	Mt. Pueh, Sarawak	MG546351
LSUMNS B-79020	Cacomantis	merulinus	Meratus Mountains, South Kalimantan	MG546352
UWBM 67474	Cacomantis	merulinus	Sumatra, Indonesia	KJ455341
LSUMNS B-51190	Psilopogon	eximius	Tawau Hills Park, Sabah	MG546418
LSUMNS B-79082	Psilopogon	eximius	Meratus Mountains, South Kalimantan	MG546419

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Tissue No.*	Genus	Species	Locality	GenBank No
LSUMNS B-79194	Psilopogon	eximius	Meratus Mountains, South Kalimantan	MG546420
LSUMNS B-36374	Sasia	abnormis	Tawau Hills Park, Sabah	MG546474
LSUMNS B-36380	Sasia	abnormis	Tawau Hills Park, Sabah	DQ479158
LSUMNS B-36428	Sasia	abnormis	Tawau Hills Park, Sabah	DQ188163
LSUMNS B-52131	Sasia	abnormis	Padawan, Sarawak	MG546475
LSUMNS B-58509	Sasia	abnormis	Mt. Pueh, Sarawak	MG546476
LSUMNS B-79019	Sasia	abnormis	Meratus Mountains, South Kalimantan	MG546477
LSUMNS B-79061	Sasia	abnormis	Meratus Mountains, South Kalimantan	MG546478
LSUMNS B-88097	Sasia	abnormis	Mt. Mulu, Sarawak	MG546479
LSUMNS B-88107	Sasia	abnormis	Mt. Mulu, Sarawak	MG546480
LSUMNS B-93562	Sasia	abnormis	Berau, East Kalimantan	MG546481
LSUMNS B-93600	Sasia	abnormis	Berau, East Kalimantan	MG546482
LSUMNS B-51210	Pericrocotus	solaris	Guangdong, China	JQ864472
LSUMNS B-52683	Pericrocotus	solaris	Mt. Trus Madi, Sabah	MG590020
LSUMNS B-79096	Pericrocotus	solaris	Meratus Mountains, South Kalimantan	MG590021
LSUMNS B-79142	Pericrocotus	solaris	Meratus Mountains, South Kalimantan	MG590022
AMNH 648529	Pachycephala	hypoxantha	Kelabit Highlands, Sarawak	GQ494105
LSUMNS B-36296	Pachycephala	hypoxantha	Mt. Kinabalu, Sabah	
LSUMNS B-52546	Pachycephala	hypoxantha	Mt. Trus Madi, Sabah	MG546432
LSUMNS B-79143	Pachycephala	hypoxantha	Meratus Mountains, South Kalimantan	MG546433
LSUMNS B-79178	Pachycephala	hypoxantha	Meratus Mountains, South Kalimantan	MG546434
LSUMNS B-79208	Pachycephala	hypoxantha	Meratus Mountains, South Kalimantan	MG546435
LSUMNS B-88054	Pachycephala	hypoxantha	Mt. Mulu, Sarawak	MG546436
LSUMNS B-88233	Pachycephala	hypoxantha	Mt. Mulu, Sarawak	MG546437
LSUMNS B-88301	Pachycephala	hypoxantha	Mt. Pueh, Sarawak	MG546438
LSUMNS B-52675	Pteruthius	aeralatus	Mt. Trus Madi, Sabah	MG546454
LSUMNS B-79081	Pteruthius	aeralatus	Meratus Mountains, South Kalimantan	MG546455
LSUMNS B-79214	Pteruthius	aeralatus	Meratus Mountains, South Kalimantan	MG546456
LSUMNS B-36475	Dicrurus	leucophaeus	Mt. Trus Madi, Sabah	MG546371
LSUMNS B-52560	Dicrurus	leucophaeus	Mt. Trus Madi, Sabah	MG546372
LSUMNS B-79080	Dicrurus	leucophaeus	Meratus Mountains, South Kalimantan	MG546372 MG546373
LSUMNS B-79134	Dicrurus	leucophaeus	Meratus Mountains, South Kalimantan	MG546374
LSUMNS B-79564	Dicrurus	leucophaeus	Kuching, Sarawak	MG546375
LSUMNS B-88044	Dicrurus	leucophaeus	Mt. Mulu, Sarawak	MG546376
LSUMNS B-88295	Dicrurus	leucophaeus	Mt. Pueh, Sarawak	MG546377
LSUMNS B-38596	Rhipidura	perlata	,	MG546377 MG546468
LSUMNS B-57451	,	perlata	Imbak Valley, Sabah	GQ145409
LSUMNS B-57451 LSUMNS B-74749	Rhipidura Blinidura	1	Ulu Tungud Forest Reserve, Sabah	
	Rhipidura	perlata	Mt. Mulu, Sarawak	MG546469
LSUMNS B-79054	Rhipidura	perlata	Meratus Mountains, South Kalimantan	MG546470
LSUMNS B-79070	Rhipidura	perlata	Meratus Mountains, South Kalimantan	MG546471
LSUMNS B-79480	Rhipidura	perlata	Kuching, Sarawak	MG546472
LSUMNS B-88071	Rhipidura	perlata	Mt. Mulu, Sarawak	MG546473
KU 17717	Rhipidura	javanica	Padas Damit, Sabah	JN546011
LSUMNS B-46972	Rhipidura	javanica	Mt. Kinabalu, Sabah	GQ145404
LSUMNS B-58663	Rhipidura	javanica	Mt. Pueh, Sarawak	MG546463
LSUMNS B-79018	Rhipidura	javanica	Meratus Mountains, South Kalimantan	MG546464
LSUMNS B-79254	Rhipidura	javanica	Limbang, Sarawak	MG546465
LSUMNS B-93595	Rhipidura	javanica	Berau, East Kalimantan	MG546466
LSUMNS B-93602	Rhipidura	javanica	Berau, East Kalimantan	MG546467
KU 13977	Rhipidura	nigritorquis	Camiguin, Philippines	JN546013

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Tissue No.*	Genus	Species	Locality	GenBank No
KU 10230	Rhipidura	albicollis	Guangxi, China	GQ145386
LSUMNS B-36474	Rhipidura	albicollis	Mt. Trus Madi, Sabah	GQ145387
LSUMNS B-52563	Rhipidura	albicollis	Mt. Trus Madi, Sabah	MG546457
LSUMNS B-79050	Rhipidura	albicollis	Meratus Mountains, South Kalimantan	MG546458
LSUMNS B-79098	Rhipidura	albicollis	Meratus Mountains, South Kalimantan	MG546459
LSUMNS B-88121	Rhipidura	albicollis	Mt. Pueh, Sarawak	MG546460
LSUMNS B-88230	Rhipidura	albicollis	Mt. Mulu, Sarawak	MG546461
LSUMNS B-88238	Rhipidura	albicollis	Mt. Mulu, Sarawak	MG546462
LSUMNS B-38662	Dendrocitta	cinerascens	Mt. Kinabalu, Sabah	MG546364
LSUMNS B-61577	Dendrocitta	cinerascens	Meligan Range, Sabah	MG546365
LSUMNS B-78702	Dendrocitta	cinerascens	Kelabit Highlands, Sarawak	MG546366
LSUMNS B-79092	Dendrocitta	cinerascens	Meratus Mountains, South Kalimantan	MG546367
LSUMNS B-79129	Dendrocitta	cinerascens	Meratus Mountains, South Kalimantan	MG546368
LSUMNS B-88039	Dendrocitta	cinerascens	Mt. Mulu, Sarawak	MG546369
LSUMNS B-88245	Dendrocitta	cinerascens	Mt. Mulu, Sarawak	MG546370
LSUMNS B-38614	Alophoixus	ochraceus	Mt. Kinabalu, Sabah	DQ402229
LSUMNS B-61635	Alophoixus	ochraceus	Mt. Kinabalu, Sabah	KY547863
LSUMNS B-79045	Alophoixus	ochraceus	Meratus Mountains, South Kalimantan	MG546336
LSUMNS B-79068	Alophoixus	ochraceus	Meratus Mountains, South Kalimantan	MG546337
LSUMNS B-85179	Alophoixus	ochraceus	Mt. Mulu, Sarawak	KY547847
LSUMNS B-88028	Alophoixus	ochraceus	Mt. Mulu, Sarawak	KY547848
LSUMNS B-88045	Alophoixus	ochraceus	Mt. Mulu, Sarawak	KY547844
LSUMNS B-88172	Alophoixus	ochraceus	Mt. Penrissen, Sarawak	KY547868
LSUMNS B-88299	Alophoixus	ochraceus	Mt. Pueh, Sarawak	MG546338
KU 15140	Hemixos	flavala	Kyi Tan, Myanmar	GU112648
LSUMNS B-38649	Hemixos	flavala	Mt. Kinabalu, Sabah	KY547905
LSUMNS B-38659	Hemixos	flavala	Mt. Kinabalu, Sabah	DQ402224
LSUMNS B-79173	Hemixos	flavala	Meratus Mountains, South Kalimantan	MG546392
LSUMNS B-79203	Hemixos	flavala	Meratus Mountains, South Kalimantan	MG546393
LSUMNS B-88173	Hemixos	flavala	Mt. Penrissen, Sarawak	KY547908
LSUMNS B-88235	Hemixos	flavala	Mt. Mulu, Sarawak	MG546394
LSUMNS B-88254	Hemixos	flavala	Mt. Mulu, Sarawak	MG546395
LSUMNS B-88289	Hemixos	flavala	Mt. Pueh, Sarawak	MG546396
LSUMNS B-88303	Hemixos	flavala	Mt. Pueh, Sarawak	
		juuouu whiteheadi	,	MG546397
KU 17730 LSUMNS B-61550	Urosphena Urosphena	whiteheadi whiteheadi	Meligan Range, Sabah	MG546498
	Urosphena		Meligan Range, Sabah	MG546499
LSUMNS B-79133	Urosphena	whiteheadi	Meratus Mountains, South Kalimantan	MG546500
LSUMNS B-79200	Urosphena	whiteheadi	Meratus Mountains, South Kalimantan	MG546501
KU 21046	Phyllergates	cucullatus	Luzon, Philippines	JX006118
LSUMNS B-52577	Phyllergates	cucullatus	Mt. Trus Madi, Sabah	JX006119
LSUMNS B-79210	Phyllergates	cucullatus	Meratus Mountains, South Kalimantan	MG546445
LSUMNS B-52702	Phylloscopus	trivirgatus	Mt. Kinabalu, Sabah	MG546446
LSUMNS B-61581	Phylloscopus	trivirgatus	Meligan Range, Sabah	MG546447
LSUMNS B-79165	Phylloscopus	trivirgatus	Meratus Mountains, South Kalimantan	MG546448
LSUMNS B-79167	Phylloscopus	trivirgatus	Meratus Mountains, South Kalimantan	MG546449
429247	Phylloscopus	trivirgatus	Philippines	FJ173457
LSUMNS B-36278	Seicercus	montis	Mt. Kinabalu, Sabah	MG546483
LSUMNS B-52597	Seicercus	montis	Mt. Trus Madi, Sabah	KY547975
LSUMNS B-61549	Seicercus	montis	Meligan Range, Sabah	MG546484
LSUMNS B-79159	Seicercus	montis	Meratus Mountains, South Kalimantan	MG546485

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LSUMNS B-79216	Seicercus	montis	Meratus Mountains, South Kalimantan	MG546486
LSUMNS B-88115	Seicercus	montis	Mt. Pueh, Sarawak	KY547972
LSUMNS B-88278	Seicercus	montis	Mt. Pueh, Sarawak	MG546487
LSUMNS B-88300	Seicercus	montis	Mt. Pueh, Sarawak	MG546488
KU 17792	Orthotomus	sericeus	Crocker Range, Sabah	JN826602
LSUMNS B-36370	Orthotomus	sericeus	Crocker Range, Sabah	KJ865188
LSUMNS B-51034	Orthotomus	sericeus	Mendolong, Sabah	KJ865189
LSUMNS B-58160	Orthotomus	sericeus	Miri, Sarawak	KJ865180
LSUMNS B-58183	Orthotomus	sericeus	Miri, Sarawak	KJ865179
LSUMNS B-74736	Orthotomus	sericeus	Mt. Mulu, Sarawak	MG546425
LSUMNS B-74766	Orthotomus	sericeus	Mt. Mulu, Sarawak	MG546426
LSUMNS B-79005	Orthotomus	sericeus	Meratus Mountains, South Kalimantan	MG546427
LSUMNS B-79109	Orthotomus	sericeus	Meratus Mountains, South Kalimantan	MG546428
LSUMNS B-93551	Orthotomus	sericeus	Berau, East Kalimantan	MG546429
LSUMNS B-93604	Orthotomus	sericeus	Berau, East Kalimantan	MG546430
KU 17756	Yuhina	everetti	Meligan Range, Sabah	JN826709
LSUMNS B-36290	Yuhina	everetti	Mt. Kinabalu, Sabah	FJ460779
LSUMNS B-79163	Yuhina	everetti	Meratus Mountains, South Kalimantan	MG546507
LSUMNS B-79193	Yuhina	everetti	Meratus Mountains, South Kalimantan	MG546508
LSUMNS B-88025	Yuhina	everetti	Mt. Mulu, Sarawak	KY548027
LSUMNS B-88190	Yuhina	everetti	Mt. Penrissen, Sarawak	KY548030
LSUMNS B-88237	Yuhina	everetti	Mt. Mulu, Sarawak	MG546509
LSUMNS B-88279	Yuhina	everetti	Mt. Pueh, Sarawak	MG546510
LSUMNS B-84895	Zosterops	palpebrosus	Santubong, Sarawak	MG546511
LSUMNS B-36444	Zosterops	atricapilla	Mt. Trus Madi, Sabah	FJ460802
KU 19110	Zosterops	everetti	Mindanao, Philippines	MG546512
LSUMNS B-79166	Zosterops	chloris	Meratus Mountains, South Kalimantan	MG546513
LSUMNS B-79170	Zosterops	chloris	Meratus Mountains, South Kalimantan	MG546514
AMNH 12558	Zosterops	chloris	Sulawesi Selatan, Sulawesi	FJ460798
KU 17726	Mixornis	bornensis	Meligan Range, Sabah	JN826571
LSUMNS B-46958	Mixornis	bornensis	Mt. Kinabalu, Sabah	HQ011004
LSUMNS B-51033	Mixornis	bornensis	Mendolong, Sabah	HQ011001
LSUMNS B-52121	Mixornis	bornensis	Kuching, Sarawak	HQ011018
LSUMNS B-52135	Mixornis	bornensis	Kuching, Sarawak	HQ011017
LSUMNS B-79004	Mixornis	bornensis	Meratus Mountains, South Kalimantan	MG546404
LSUMNS B-79042	Mixornis	bornensis	Meratus Mountains, South Kalimantan	MG546405
LSUMNS B-93556	Mixornis	bornensis	Berau, East Kalimantan	MG546406
LSUMNS B-93601	Mixornis	bornensis	Berau, East Kalimantan	MG546407
KU 10167	Stachyris	nigriceps	Guangxi, China	JN826673
LSUMNS B-36288	Stachyris	nigriceps	Mt. Kinabalu, Sabah	JN826674
LSUMNS B-61636	Stachyris	nigriceps	Mt. Kinabalu, Sabah	KY547978
LSUMNS B-78993	Stachyris	nigriceps	Meratus Mountains, South Kalimantan	MG546494
LSUMNS B-79114	Stachyris	nigriceps	Meratus Mountains, South Kalimantan	MG546495
LSUMNS B-79483	Stachyris	nigriceps	Mt. Pueh, Sarawak	KY548009
LSUMNS B-79667	Stachyris	nigriceps	Mt. Penrissen, Sarawak	KY547999
LSUMNS B-88022	Stachyris	nigriceps	Mt. Mulu, Sarawak	KY547993
LSUMNS B-88041	Stachyris	nigriceps	Mt. Mulu, Sarawak	KY547996
LSUMNS B-36426	Stachyris	poliocephala	Tawau Hills Park, Sabah	HQ011178
LSUMNS B-47082	Stachyris	poliocephala	Mt. Kinabalu, Sabah	HQ011180

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Tissue No.*	Genus	Species	Locality	GenBank No
LSUMNS B-52096	Stachyris	poliocephala	Panti Forest, West Malaysia	HQ011192
LSUMNS B-52140	Stachyris	poliocephala	Kuching, Sarawak	HQ011186
LSUMNS B-79001	Stachyris	poliocephala	Meratus Mountains, South Kalimantan	MG546496
LSUMNS B-79107	Stachyris	poliocephala	Meratus Mountains, South Kalimantan	MG546497
LSUMNS B-36337	Stachyris	leucotis	Crocker Range, Sabah	MG546489
LSUMNS B-36340	Stachyris	leucotis	Crocker Range, Sabah	JN826671
LSUMNS B-58528	Stachyris	leucotis	Mt. Pueh, Sarawak	MG546490
LSUMNS B-79135	Stachyris	leucotis	Meratus Mountains, South Kalimantan	MG546491
LSUMNS B-79217	Stachyris	leucotis	Meratus Mountains, South Kalimantan	MG546492
LSUMNS B-79625	Stachyris	leucotis	Kuching, Sarawak	MG546493
KU 12358	Malacopteron	magnirostre	Samarakan, Sarawak	JN826585
LSUMNS B-36421	Malacopteron	magnirostre	Tawau Hills Park, Sabah	FJ460778
LSUMNS B-51159	Malacopteron	magnirostre	Tawau Hills Park, Sabah	MG546414
LSUMNS B-79220	Malacopteron	magnirostre	Meratus Mountains, South Kalimantan	MG546415
LSUMNS B-79223	Malacopteron	magnirostre	Meratus Mountains, South Kalimantan	MG546416
LSUMNS B-79477	Malacopteron	magnirostre	Mt. Pueh, Sarawak	MG546417
KU 12320	Malacopteron	cinereum	Samarakan, Sarawak	IN826583
LSUMNS B-38552	Malacopteron	cinereum	Tawau Hills Park, Sabah	MG546408
LSUMNS B-51118	Malacopteron	cinereum	Tawau Hills Park, Sabah	MG546409
LSUMNS B-74719	Malacopteron	cinereum	Mt. Mulu, Sarawak	MG546410
LSUMNS B-79077	Malacopteron	cinereum	Meratus Mountains, South Kalimantan	MG546411
LSUMNS B-79492	Malacopteron	cinereum	Kuching, Sarawak	MG546412
LSUMNS B-88095	Malacopteron	cinereum	Mt. Mulu, Sarawak	MG546413
LSUMNS B-36430	Pellorneum	capistratum	Tawau Hills Park, Sabah	FJ460772
LSUMNS B-47202	Pellorneum	capistratum	Klias Forest Reserve, Sabah	HQ011068
LSUMNS B-51058	Pellorneum	capistratum	Tawau Hills Park, Sabah	HQ011069
LSUMNS B-52098	Pellorneum	capistratum	Panti Forest, West Malaysia	HQ011077
LSUMNS B-58211	Pellorneum	capistratum	Kota Samarahan, Sabah	HQ011077 HQ011074
LSUMNS B-79000	Pellorneum	capistratum	Meratus Mountains, South Kalimantan	MG546439
LSUMNS B-79105	Pellorneum	capistratum	Meratus Mountains, South Kalimantan	MG546440
LSUMNS B-93598	Pellorneum	capistratum	Berau, East Kalimantan	MG546441
KU 17798	Pellorneum	pyrrogenys	Mt. Kinabalu, Sabah	JN826614
LSUMNS B-36316	Pellorneum	,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,	Crocker Range, Sabah	KY547936
LSUMNS B-78985	Pellorneum	pyrrogenys	Meratus Mountains, South Kalimantan	MG546442
LSUMNS B-78985	Pellorneum	pyrrogenys	Meratus Mountains, South Kalimantan	MG546443
LSUMNS B-88033	Pellorneum	pyrrogenys	Mt. Mulu, Sarawak	KY547943
LSUMNS B-88042	Pellorneum	pyrrogenys	Mt. Mulu, Sarawak	K 1547945 KY547944
		pyrrogenys	,	
LSUMNS B-88132	Pellorneum	pyrrogenys	Mt. Penrissen, Sarawak	KY547937
LSUMNS B-88166	Pellorneum	pyrrogenys	Mt. Penrissen, Sarawak	KY547949
LSUMNS B-88294	Pellorneum	pyrrogenys	Mt. Pueh, Sarawak	MG546444
LSUMNS B-52557	Napothera	epilepidota	Mt. Trus Madi, Sabah	JN826601
LSUMNS B-52626	Napothera	epilepidota	Mt. Trus Madi, Sabah	MG546421
LSUMNS B-78722	Napothera	epilepidota	Kelabit Highlands, Sarawak	MG546422
LSUMNS B-79100	Napothera	epilepidota	Meratus Mountains, South Kalimantan	MG546423
LSUMNS B-79101	Napothera	epilepidota	Meratus Mountains, South Kalimantan	MG546424
KU 17766	Alcippe	brunneicauda	Crocker Range, Sabah	JN826469
LSUMNS B-36359	Alcippe	brunneicauda	Crocker Range, Sabah	FJ460770
LSUMNS B-78700	Alcippe	brunneicauda	Kelabit Highlands, Sarawak	MG546332
LSUMNS B-79053	Alcippe	brunneicauda	Meratus Mountains, South Kalimantan	MG546333
LSUMNS B-79221	Alcippe	brunneicauda	Meratus Mountains, South Kalimantan	MG546334

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Genus	Species	Locality	GenBank No
Alcippe	brunneicauda	Mt. Pueh, Sarawak	MG546335
Ianthocincla	mitrata	Sumatra, Indonesia	MG546390
Ianthocincla	treacheri	Meligan Range, Sabah	JN826518
Ianthocincla	treacheri	Mt. Trus Madi, Sabah	FJ460776
Ianthocincla	treacheri	Kelabit Highlands, Sarawak	KY547901
Ianthocincla	treacheri	Meratus Mountains, South Kalimantan	MG546391
Ianthocincla	treacheri	Mt. Mulu, Sarawak	KY547902
Ianthocincla	treacheri	Mt. Mulu, Sarawak	KY547903
Cyornis	banyumas	Crocker Range, Sabah	MG546358
Cyornis	banyumas	Tawau Hills Park, Sabah	MG546359
Cyornis	banyumas	Kelabit Highlands, Sarawak	MG546360
Cyornis	banyumas	Meratus Mountains, South Kalimantan	MG546361
Cyornis	banyumas	Meratus Mountains, South Kalimantan	MG546362
Cyornis	banyumas	Mt. Penrissen, Sarawak	MG546363
Eumyias	indigo	Meligan Range, Sabah	MG546378
Eumyias	indigo		MG546379
Eumyias	indigo	Mt. Mulu, Sarawak	MG546380
Vauriella	gularis	Mt. Kinabalu, Sabah	MG546502
Vauriella	0	Meratus Mountains, South Kalimantan	MG546503
Vauriella	0	Meratus Mountains, South Kalimantan	MG546504
Vauriella	0	Mt. Mulu, Sarawak	MG546505
Vauriella	0	Mt. Mulu, Sarawak	MG546506
Ficedula	westermanni	Mindanao, Philippines	DO674452
Ficedula	westermanni	11	MG546386
Ficedula	westermanni	Meratus Mountains, South Kalimantan	MG546387
Ficedula	westermanni	,	MG546388
Ficedula	westermanni	Mt. Mulu, Sarawak	MG546389
Ficedula	dumetoria	,	DQ674458
Ficedula	dumetoria	-	MG546381
Ficedula	dumetoria	0	MG546382
Ficedula	dumetoria	Meratus Mountains, South Kalimantan	MG546383
Ficedula	dumetoria	Mt. Penrissen, Sarawak	MG546384
Ficedula	dumetoria	Mt. Mulu, Sarawak	MG546385
Chloropsis	kinabaluensis	Tawau Hills Park, Sabah	MG546354
,	kinabaluensis	,	MG546355
	kinabaluensis	,	MG546356
,	kinabaluensis		MG546357
,	maculatus	· · · · · · · · · · · · · · · · · · ·	GQ145275
			HQ011104
		,	HQ011115
			HQ011112
		-	MG546450
			MG546451
			MG546451 MG546452
		,	MG546453
		,	HQ011114
			JN126640
	0	-	JN126643
Arachnothera	longirostra	Mt. Kinabalu, Sabah	MG546343
	Alcippe Ianthocincla Ianthocincla Ianthocincla Ianthocincla Ianthocincla Ianthocincla Ianthocincla Ianthocincla Cyornis Cyornis Cyornis Cyornis Cyornis Cyornis Eumyias Eumyias Eumyias Eumyias Eumyias Eumyias Vauriella Vauriella Vauriella Vauriella Ficedul	AlcippebrunneicaudaIanthocinclamitrataIanthocinclatreacheriIanthocinclatreacheriIanthocinclatreacheriIanthocinclatreacheriIanthocinclatreacheriIanthocinclatreacheriIanthocinclatreacheriIanthocinclatreacheriIanthocinclatreacheriIanthocinclatreacheriCyornisbanyumasCyornisbanyumasCyornisbanyumasCyornisbanyumasCyornisbanyumasCyornisbanyumasCyornisbanyumasCyornisbanyumasCyornisbanyumasCyornisbanyumasCyornisbanyumasEumyiasindigoEumyiasindigoEumyiasindigoVauriellagularisVauriellagularisVauriellagularisVauriellagularisFicedulawestermanniFicedulawestermanniFiceduladumetoriaFiceduladumetoriaFiceduladumetoriaFiceduladumetoriaFiceduladumetoriaFiceduladumetoriaFiceduladumetoriaFiceduladumetoriaFiceduladumetoriaFiceduladumetoriaFiceduladumetoriaFiceduladumetoriaFiceduladumetoriaFiceduladumetoria	AlcippebrunneicaudaMt. Pueh, SarawaklanthocinclamitrataSumatra, IndonesialanthocinclatreacheriMeligan Range, SabahlanthocinclatreacheriMt. Trus Madi, SabahlanthocinclatreacheriMt. Trus Madi, SarawaklanthocinclatreacheriMeratus Mountains, South KalimantanlanthocinclatreacheriMt. Mulu, SarawaklanthocinclatreacheriMt. Mulu, SarawakCyornisbanyumasCrocker Range, SabahCyornisbanyumasKelabit Highlands, SarawakCyornisbanyumasMeratus Mountains, South KalimantanCyornisbanyumasMeratus Mountains, South KalimantanCyornisindigoMeratus Mountains, South KalimantanCyuriellagularisMt. Mulu, SarawakVauriellagularisMt. Mulu, SarawakVauriellagularisMt. Mulu, SarawakVauriellagularisMt. Pueh, SarawakFicedulawestermanniMeratus Mountains, South KalimantanFicedulawestermanniMt. Pueh, SarawakFiceduladumetoriaKg. Makanitan, SabahFiceduladumetoriaMt. Pueh, SarawakFiceduladumetoriaMt. Pueh, SarawakFicedula

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Tissue No.*	Genus	Species	Locality	GenBank No.
LSUMNS B-57069	Arachnothera	longirostra	Bintulu, Sarawak	IN126684
LSUMNS B-74742	Arachnothera	longirostra	Mt. Mulu, Sarawak	MG546344
LSUMNS B-78987	Arachnothera	longirostra	Meratus Mountains, South Kalimantan	MG546345
LSUMNS B-79043	Arachnothera	longirostra	Meratus Mountains, South Kalimantan	MG546346
LSUMNS B-93535	Arachnothera	longirostra	Berau, East Kalimantan	MG546347
LSUMNS B-93538	Arachnothera	longirostra	Berau, East Kalimantan	MG546348
LSUMNS B-38549	Arachnothera	hypogrammicum	Tawau Hills Park, Sabah	JF956935
LSUMNS B-47081	Arachnothera	hypogrammicum	Mt. Kinabalu, Sabah	HQ010965
LSUMNS B-51127	Arachnothera	hypogrammicum	Tawau Hills Park, Sabah	HQ010972
LSUMNS B-52085	Arachnothera	hypogrammicum	Bukit Hanta Forest Reserve, West Malaysia	HQ010989
LSUMNS B-74741	Arachnothera	hypogrammicum	Mt. Mulu, Sarawak	MG546398
LSUMNS B-78991	Arachnothera	hypogrammicum	Meratus Mountains, South Kalimantan	MG546399
LSUMNS B-79046	Arachnothera	hypogrammicum	Meratus Mountains, South Kalimantan	MG546400
LSUMNS B-88102	Arachnothera	hypogrammicum	Mt. Mulu, Sarawak	MG546401
LSUMNS B-93541	Arachnothera	hypogrammicum	Berau, East Kalimantan	MG546402
LSUMNS B-93547	Arachnothera	hypogrammicum	Berau, East Kalimantan	MG546403
UWBM 81984	Arachnothera	hypogrammicum	Kubah National Park, Sarawak	HQ010983
AMNH 648559	Arachnothera	everetti	Sarawak	JF956980
LSUMNS B-36309	Arachnothera	everetti	Crocker Range, Sabah	JF956951
LSUMNS B-36402	Arachnothera	everetti	Tawau Hills Park, Sabah	JF956974
LSUMNS B-78752	Arachnothera	everetti	Kelabit Highlands, Sarawak	MG546339
LSUMNS B-79021	Arachnothera	everetti	Meratus Mountains, South Kalimantan	MG546340
LSUMNS B-79213	Arachnothera	everetti	Meratus Mountains, South Kalimantan	MG546341
LSUMNS B-88259	Arachnothera	everetti	Mt. Mulu, Sarawak	MG546342
KU 17801	Arachnothera	everetti	Mt. Kinabalu, Sabah	JF956920

* AMNH = American Museum of Natural History, New York; FMNH = Field Museum of Natural History, Chicago; KU = University of Kansas Museum of Natural History, Lawrence; LSUMNS = Louisiana State University Museum of Natural Science, Baton Rouge; and UWBM = University of Washington Burke Museum, Seattle.

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