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A distinctive new species of flowerpecker (Passeriformes: Dicaeidae) from Borneo

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ABSTRACT

The enigmatic 'Spectacled Flowerpecker'—a probable new bird species from the island of Borneo—was first sighted in the Danum Valley of Sabah, Malaysia in 2009. However, the absence of a holotype specimen has prevented its formal scientific description. Since then only a handful of reports from widely disparate localities across the island have emerged, all from lowland sites and often in close association with fruiting mistletoe. Here, we report the long-awaited capture of a specimen of this putative new species and confirm its morphological and molecular distinctiveness as a novel species in the genus *Dicaeum*.

Key words: *Dicaeum*, holotype, canopy, mistletoe, specialist

INTRODUCTION

The vast and ancient tropical forests of Borneo are a globally important center for biodiversity (De Bruyn *et al.* 2014). Situated within the Greater Sunda Archipelago in Southeast Asia, the island serves as an area of endemism for many taxonomic groups, with new taxa of plants and animals still routinely being discovered. One such group is the flowerpeckers (Dicaeidae)—a family of small, frugivorous passerine birds—whose range extends from the northernmost regions of Indomalaya to Australasia. Borneo sits within the core of the family's distribution, with 13 of the 48 currently known and accepted species occurring on the island, surpassed only by nearby Sumatra (16 species) and the Philippines (15 species) (Gill & Donsker 2019). With the exception of one montane endemic (*Dicaeum monticolum*), Borneo's flowerpeckers favor lowland elevations, inhabiting a wide variety of forest and edge habitats throughout the island where they are often closely associated with hemiparasitic aerial mistletoe (Cheke *et al.* 2019).

In 2009 DPE reported on the discovery of a potential new species of flowerpecker from the Danum Valley in the lowlands (180m asl) of Sabah in northeastern Malaysian Borneo (Fig. 1) (Edwards *et al.* 2009). The bird appeared among several other species of flowerpecker foraging on a patch of fruiting mistletoe (likely *Macrosolen cochinchinensis* (Lour.) Tiegh. (Loranthaceae), as inferred from photos) in a tree along the canopy walkway of the Borneo Rainforest Lodge. Their report and photographs documented a bird species with the clear proportions and bill shape of a flowerpecker, uniform gray plumage save for a white stripe from throat to vent, and conspicuous white eye-arcs giving the bird a uniquely "spectacled" appearance. The authors felt confident that these characters distinguished it from any other species currently known from Borneo. Attempts to locate additional individuals were unsuccessful, and the species eluded observation for years thereafter. However, the prospect of an entirely new species of bird, likely the first for Borneo in over 100 years, led to considerable excitement in the scientific and birdwatching communities, and garnered the attention of global media outlets (Braun 2010, Doyle 2010, Walton 2010). Unfortunately, the lack of a holotype specimen prevented the species from being scientifically described and formally named (Collar 2009, Peterson 2014).

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It was not until August 2014 that another individual of this putative new species was found and photographed, this time in the Labi Hills Forest Reserve in Brunei, followed shortly thereafter by a pair of photographed observations in September 2014 from the Maliau Basin of Sabah (Fig. 1) (Sykes & Loseby 2015). Additional sightings early the following year, this time hundreds of kilometers south in the Bukit Batikap Protection Forest in Central Kalimantan, dramatically extended the bird's known range to south of the central montane spine of Borneo, demonstrating that the species could potentially be encountered anywhere in the island's extensive lowland forests (Boyd *et al*. 2016, Fischer *et al*. 2016).

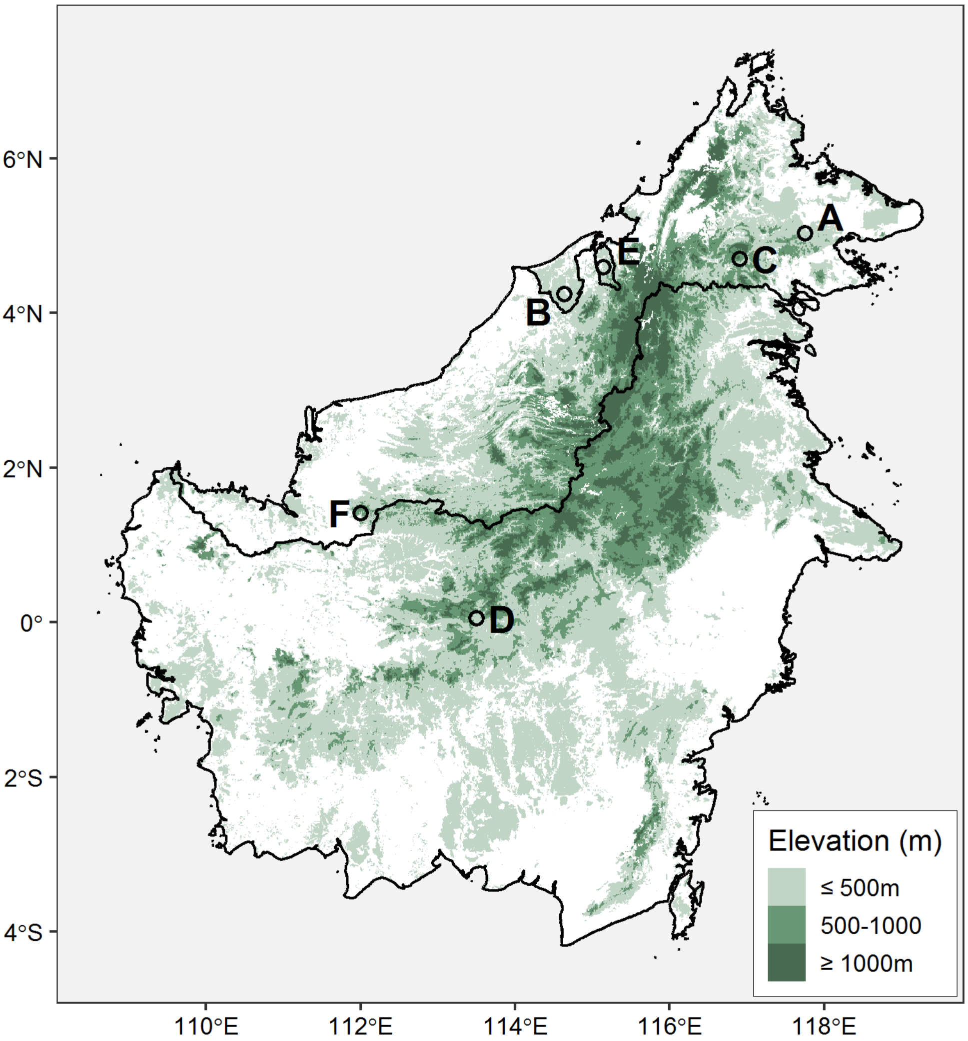

FIGURE 1. Map of Borneo depicting reported localities of the new flowerpecker species. A) Danum Valley Conservation Area, Sabah, Malaysia; B) Labi Hills Forest Reserve, Brunei; C) Maliau Basin Conservation Area, Sabah, Malaysia; D) Bukit Batikap Protection Forest, Kalimantan, Indonesia; E) Belalong Canopy Walkway, Brunei; and F) Lanjak Entimau Wildlife Sanctuary, Sarawak, Malaysia. Forest cover shaded in green, with shading varying by elevational band. Forest cover obtained from Gaveau *et al.* (2016), and SRTM elevational dataset obtained from Jarvis *et al.* (2008). Non-forest shaded in white, the majority of which represents deforested areas converted to agriculture.

Following another gap in observations, at least one individual was spotted and photographed at the Belalong Canopy Walkway in the Temburong District of Brunei in May 2017, its appearance coinciding with a mass fruiting of nearby Loranthaceous mistletoe plants (Fig. 1) (Ong 2018). From this handful of observations, the 'Spectacled Flowerpecker' was beginning to reveal itself as an elusive but widely distributed bird species that had somehow evaded scientific description. Its frequent association with hemiparasitic mistletoe has led some to speculate that the bird is a secretive canopy dweller with a highly specialized foraging ecology, potentially nomadic tendencies, and low population densities; but the real reasons for the bird's confounding scarcity remains a mystery (Edwards *et al.* 2009, Phillips & Phillips 2014, Sykes & Loseby 2015, Boyd *et al*. 2016).

In early 2019 (24 March–7 April), an ornithological field expedition led by members of the Smithsonian Institution (CMM and JRS) and the Sarawak Forestry Corporation (RR) surveyed the Lanjak Entimau Wildlife Sanctuary (LEWS) of Sarawak as part of a series of field surveys to characterize and document avian biodiversity in the lowland forests of Sarawak. On 31 March, a female individual of this putative new species was captured in a mistnet and preserved as a scientific specimen. The bird was immediately discernible from other flowerpeckers in the study area and expressed all of the characteristic features described by previous observers and as depicted in field guide illustrations (Phillips & Phillips 2014, Myers 2016). In addition to a traditional museum skin specimen, various anatomical, diet, and genetic samples were saved for preservation and analysis.

Here, we formally confirm and describe this bird as a distinctive new species of flowerpecker, for which we propose the following name:

***Dicaeum dayakorum*, species novum**
Spectacled Flowerpecker
urn:lsid:zoobank.org:act:5F5CF534-8023-45B0-809F-0A6A5949A8D4

Holotype.—Study skin and partial skeleton, Smithsonian Institution, National Museum of Natural History, USNM 663246; tissues preserved in dimethyl sulfoxide (DMSO) buffer and later housed in gaseous nitrogen at the NMNH Biorepository (AK7DC13, AK7DC14, AK7DC15, AK7DC18); tongue, stomach and fecal samples saved; prepared by C.M.M., original field number CMM 5719; adult female; Malaysia: Sarawak; Lanjak Entimau Wildlife Sanctuary, 01°24’48”N, 112°00’16”, 350 m asl; GenBank sequences: MN416066 (ND2), MN416068 (ND3), MN416067 (TGFb2).

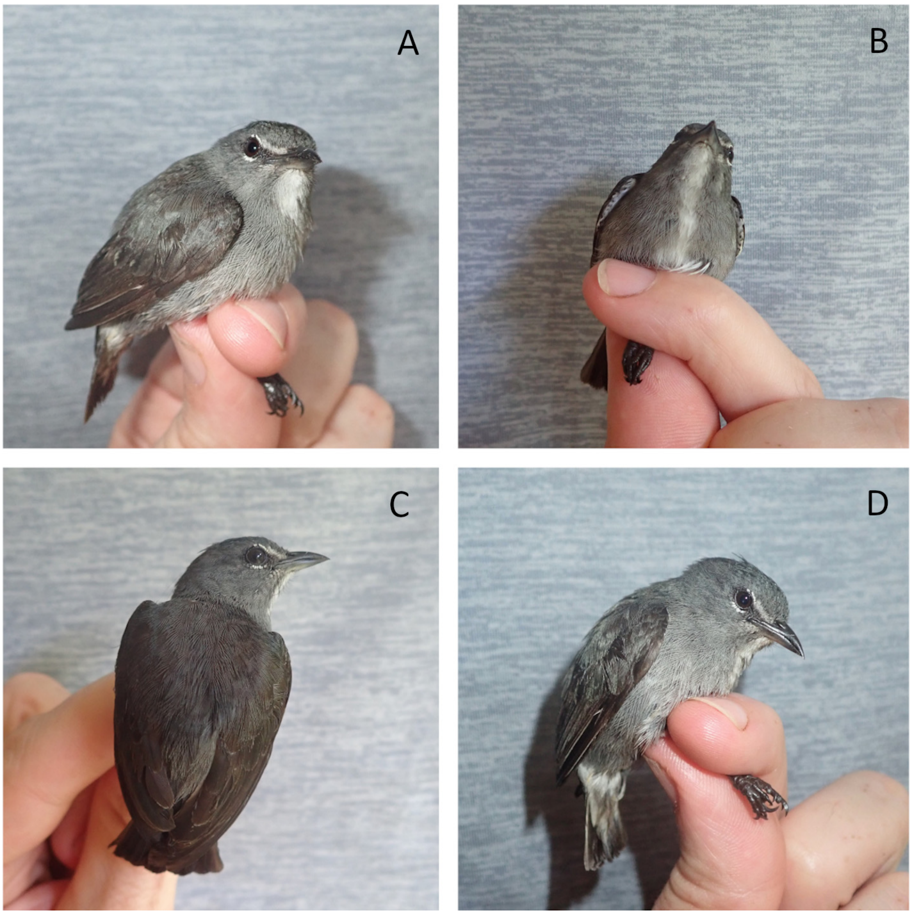

FIGURE 2. Images of *Dicaeum dayakorum* (USNM 663246) immediately after capture on 31 March 2019 at the Lanjak Entimau Wildlife Sanctuary, Sarawak, MYS; showing views of (A) side with views of throat and forehead, (B) ventral/underparts, (C) dorsal/upperparts, and (D) side with views of vent and undertail coverts.

Diagnosis.—Phenotypically assignable to the genus *Dicaeum* Cuvier, 1816, by short thin bill, specialized (bifid and semi-tubular) tongue morphology (Fig. 4), and a greatly reduced outermost primary feather (Mayr & Amadon 1947, Salomonsen 1960a,b, Morioka 1992). Diagnosable as distinct from other species of *Dicaeum* by the following combination of characters; (1) rows of white orbital feathers above and below the eye, forming thin, but conspicuous white arcs; (2) entirely gray and white plumage coloration with no evidence of carotenoid pigments in the adult plumage; (3) short distal bill length (6 mm from nares to bill tip). Field observations indicate that the eye-arcs of putative males are even more strongly expressed than in the female holotype. The strong white eye-arcs of *D. dayakorum* are unique in Dicaeidae, although traces of pale eye-arcs are known to be present in female and juvenile plumages of a few other species (e.g. *D. monticolum*, *D. agile*, *D. pygmaeum*). Red and yellow carotenoid pigments are evident in the plumage of most species of *Dicaeum*. The apparent lack of these pigments in the adult female holotype and field observations of putative adult males sets *D. dayakorum* apart from most of its congeners.

Description of Holotype.—Alphanumeric codes follow Munsell (1990) and capitalized color names are approximate and follow Smithe (1975). Upperparts (forehead, crown, back, rump) Dark Neutral Gray (N3.5/0) becoming less dark on cheeks (N4/0) and darker on wing coverts and wing remiges (N3/0). Eye arcs clean white and conspicuous, but thin, extending only marginally past the first row of orbital feathers. Supraloral line faded-white extending from just past the orbital to the base of the nares. Submoustacial stripe faded-white, becoming more diffuse away from the bill. Malar and sides of throat Medium Neutral Gray (N5/0). Center of throat white, forming a stripe that narrows slightly below the throat (to 3.5mm wide) and extending down to the vent. Sides and flanks Medium Neutral Gray (N5/0) with pale-brownish undertones. Pectoral tufts and wing lining clean white. Thighs Dark Neutral Gray (N3.5/0) with pale edgings. The white coloration from the ventral line extends onto the undertail coverts, where it is indistinctly mottled or stained darker. Ventral surface of rectrices Dark Neutral Gray (N3/0), with dorsal surface darker, almost appearing black (N2.5/0).

Soft part colors photographed and recorded at the time of collection: irides dark brown, maxilla black, mandible gray with dark tip, tarsi and feet black. No molt, little fat, skull 100% pneumatized, ovary 6 x 4 mm and granular, oviduct slightly enlarged, no bursa of Fabricius present. Stomach contained parts of a small jumping spider (*Salticidae*). Mistletoe seeds (Loranthaceae) were recovered from the lower large intestine (Fig. 5).

Measurements: mass 7.8 g; tarsus length 11.8 mm; wingchord 48.4 mm; tail length 24 mm; length of tenth primary 5.5 mm; bill width 3.6 mm; bill depth 3.3 mm; bill length from nares 6.0 mm; exposed culmen 8.0 mm (Appendix Table 1).

Paratypes.—No specimens other than the holotype were obtained and no additional specimens are known to exist.

Etymology.—We name *Dicaeum dayakorum* in honor of the Dayak people of Borneo. Their immense knowledge of the flora and fauna of their homeland forests is irreplaceable and crucial to future conservation efforts of Borneo's endemic ecosystems.

The English name of 'Spectacled Flowerpecker' is assigned as proposed by Edwards *et al.* (2009), and refers to the broken eye-ring that is this species' most characteristic and easily recognized plumage feature. This name also has the benefit of established usage in the ornithological and birdwatching community.

REMARKS

Phylogenetic relationships.—To infer phylogenetic placement of *D. dayakorum* within the Dicaeidae we sequenced DNA from the holotype to place it in the framework of a previous phylogenetic study of the family by Nyári *et al.* (2009). We downloaded sequence data from that study posted to GenBank, which included the nicotinamide adenine dinucleotide dehydrogenase subunit 2 (ND2, 1034 bp), ND subunit 3 (ND3, 351 bp), and the transforming growth factor beta 2 (TGFb2, 542 bp) for 30 species of flowerpecker and 11 outgroup species (10 sunbirds and 1 leafbird; Appendix Table 2). Genomic DNA was isolated from DMSO preserved tissues of the holotype specimen (USNM 663246). The DNA extraction was performed at the Smithsonian Laboratories of Analytical Biology (LAB) using a fully automated phenol-chloroform genomic extraction machine (Gene Prep, AutoGen, Holliston, MA). PCR products were amplified for all three coding regions (ND2, ND3, and TGFb2) using GoTaq® G2 Hot Start Master Mix (Promega Corporation) with additional BSA (New England BioLabs, 50 mM stock solution) and magnesium chloride (Bioline, Biolase DNA Polymerase, London, UK). The annealing temperature for ND2 was 57°C, and

59°C for ND3 and TGFb2. PCR products were cleaned and visualized on a 1% agarose gel. Cycle-sequencing was performed using ABI Prism® BigDyeTM Terminator (v3.1 chemistry, ThermoFisher Scientific, Waltham, MA) for both forward and reverse directions. The products were purified using SephadexTM (GE Healthcare Bio-Sciences Corp., Pittsburgh, PA) spin columns before submitting for sequencing on an ABI 3730 xl DNA analyzer at the LAB facilities. Raw sequences were visualized and quality-trimmed using Sequencher (version 5.4.6; Gene Codes Corporation, Ann Arbor, MI).

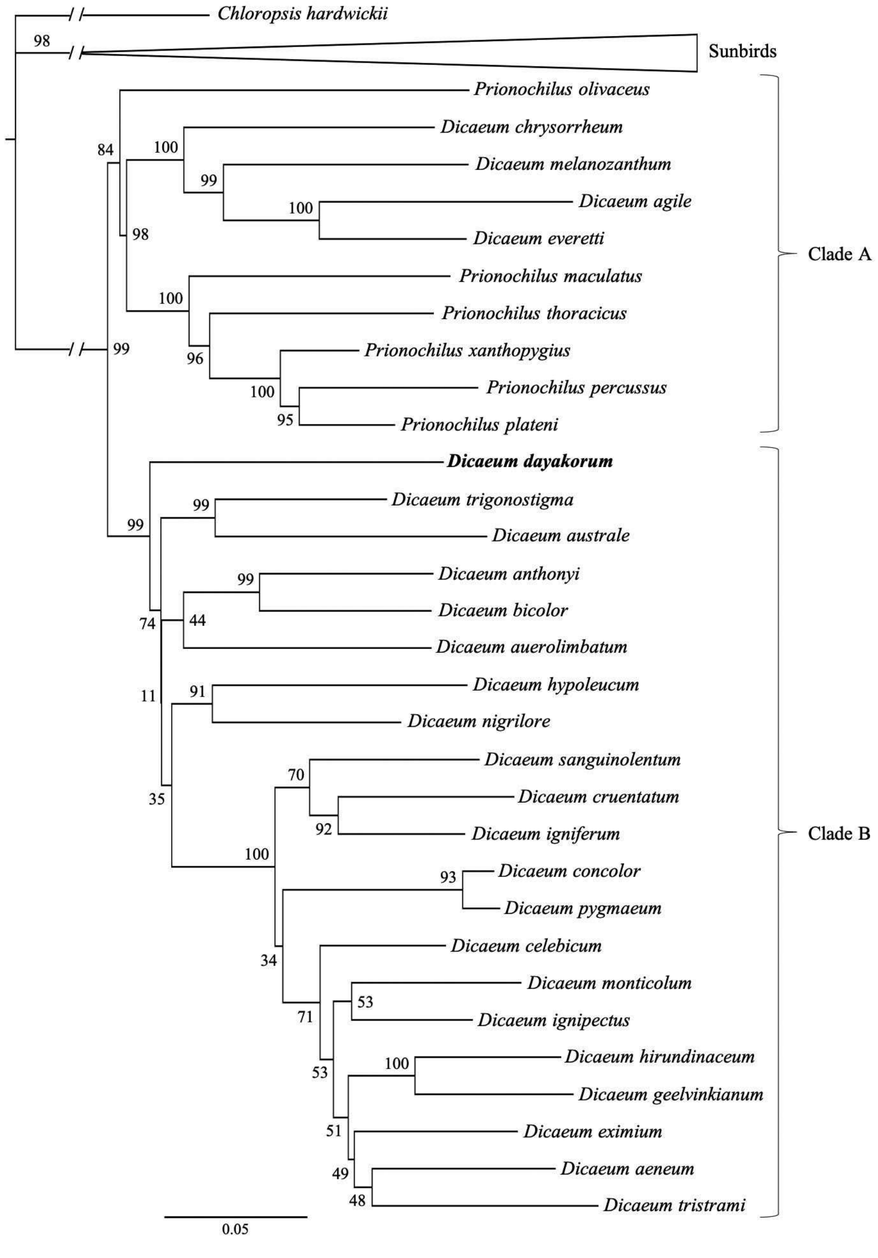

FIGURE 3. Maximum likelihood tree from the aligned and concatenated genes ND2, ND3, TGFb2 (1,909 bp) showing the placement of *Dicaeum dayakorum* (in bold) in relation to other members of the Dicaeidae. Bootstrap support values from the ML analysis are indicated at the nodes.

Sequences of the holotype were aligned with the rest of the dataset (42 taxa in total) using the MAFFT plugin (version 7.388; Katoh & Standley 2013) implemented in Geneious Prime 2019.1.3 (https://www.geneious.com, accessed on 28 June 2019). The multiple sequence alignments for each of the three loci were visually inspected and manually curated when necessary. As ND2 and ND3 represent portions of the same mitochondrial gene, both matrices were concatenated into a dataset of 1,383 bp. The individual datasets for both ND and TGFb2 genes were trimmed to remove characters not suited for phylogenetic inference using BMGE (Criscuolo & Gribaldo 2010) with a sliding window size of three, a maximum entropy threshold and gap rate cut-off of 0.5, and a minimum block size of five. We estimated nucleotide substitution models for individual genes using ModelFinder (Kalyaanamoorthy *et al.* 2017) implemented in IQ-TREE (version 1.6.11 Nguyen *et al.*, 2014). We then concatenated the multiple sequence alignments for both genes, resulting in a matrix of 1,909 bp, and performed a Maximum Likelihood analysis with partitions using IQ-TREE, allowing the program to find the best-fit partitioning scheme possible to merge partitions (Chernomor *et al.* 2016). The Maximum Likelihood analysis was replicated with 1000 ultrafast bootstrap iterations (Hoang *et al.* 2017) by resampling partitions and then sites within resampled partitions, as recommended by Gadagkar *et al.* (2005). To detect incongruences in the topology of trees built from different organelles (i.e., nuclear vs. mitochondrial sequences), we performed ML analyses using only the concatenated ND2 and ND3 loci representing mitochondrial DNA, and the TGFb2 representing nuclear DNA. We estimated models of nucleotide substitutions for each of these loci and conducted a ML analysis using IQ-TREE with 1000 bootstrap replications as described above. Bayesian Inference (BI) analyses were conducted in MrBayes (version 3.2.6; Ronquist *et al.* 2012) using the CIPRES Science Gateway web server (Miller *et al.* 2010). The BI was conducted using two separate four Markov Chain Monte Carlo (MCMC) analyses with 10,000,000 generations and sampling every 1000 generations. The first 25% of sample trees ("burn-in period") were removed and a majority rule (> 50%) consensus tree was built. We estimated pairwise sequence divergences of raw mtDNA from the ND2-ND3 concatenated matrix using the Kimura 2-parameter distance model (Kimura, 1980) with a Gamma distribution (Gamma parameter: 5) in MEGAX (version 10.1.0 Kumar *et al.* 2018). We also conducted a Poisson tree processes (PTP) species delimitation test with a subset of the taxa including all species of *Dicaeum* and *Prionochilus* with *Chloropsis* as outgroup, using a MCMC analysis with 100,000 generations with a burn-in period of 50% and a thinning of 100 (Zhang *et al.* 2013).

Topologies of the ML and BI phylogenetic trees largely mirror those found in Nyári *et al.* (2009), and place *D. dayakorum* at a basal position of the "core" *Dicaeum* clade (Clade B *sensu* from Nyári *et al.* 2009) with high support (99% bootstrap support and 1.00 posterior probability in the in the ML and BI analyses, respectively; Figure 3). The topology from the concatenated ML tree is largely congruent with the trees built using the two individual genes. However, as each of these individual datasets have fewer phylogenetically informative sites, the resultant trees show several unresolved nodes with low support values, especially at deep branches. The only notable discrepancy is the weak placement of *D. dayakorum* as sister to *D. australe* (74% bootstrap support) in the tree constructed from the TGFb2 gene.

Morphology and voice.—We took standard morphological measurements from the holotype, along with several of the most closely related species (as per our molecular analyses), and similar/co-occurring species of *Dicaeum* for comparison (Appendix Table 1).

Classic taxonomic treatments of the Dicaeidae focused on morphological characters such as bill shape, tongue morphology, and relative length of the outermost primary. *D. dayakorum* displays a relatively small and slender bill similar to that of *D. monticolum* and *D. cruentatum*, and distal bill length is at the low end of the range for the genus. The culmen is moderately arched downward and slight serrations are present along the edge of the distal half of both maxilla and mandible. The base is relatively wide compared to the tip and rictal bristles are reduced.

As opposed to the triangular, non-tubular tongues shown by members of *Prionochilus*, 1841, many members of *Dicaeum* have specialized tongues with tubular structures and deeply bifid tips (Morioka 1992). Tongue morphologies in this genus are often distinctive, reflecting varying degrees of specialization between frugivory and nectarivory (Mayr & Amadon 1947, Morioka 1992). The tongue and hyoid of the holotype were preserved in aqueous formaldehyde and later transferred to ethanol. Examination revealed an overall structure that is not atypical for *Dicaeum*. The tongue has a triangular, fleshy base extending approximately halfway up the length of the structure giving way abruptly to a narrow, straight, and deeply concave anterior portion. This latter half is horny and semi-tubular at the base, becoming increasingly translucent distally, and ending in a strongly bifid tip (Fig. 4).

One of the most reliable characters differentiating flowerpecker genera has been the length of the 10th or outermost primary, being relatively long in *Prionochilus* compared to *Dicaeum* (Mayr & Amadon 1947, Salomonsen 1960a,b). Evaluation of this character in our holotype specimen revealed it to be greatly reduced (5.5 mm), fitting with the vestigial outer primaries possessed by other members of genus *Dicaeum*.

DPE heard the putative male sing with a series of ~12 high-pitched *see* notes, rising and then falling in pitch (Edwards *et al.* 2009), but no recoding was obtained. Boyd *et al.* (2016) subsequently obtained the first and only known voice recordings of this species during their sightings of the birds in Central Kalimantan in 2015 (xeno-canto.org recordings XC239907, XC301233). The recordings reveal a simple call typical of other flowerpecker species and an accelerating trilled song of 18 notes lasting 1.5 seconds, starting with two notes at 4.8 kHz, then immediately accelerating to a trill that rises from 5.3 kHz to a maximum centered at 6.1 kHz (5.8-6.4 kHz), and falls for the last three notes to 5.7 kHz. The song thus bears similarities, but is distinctive, to other known flowerpecker songs.

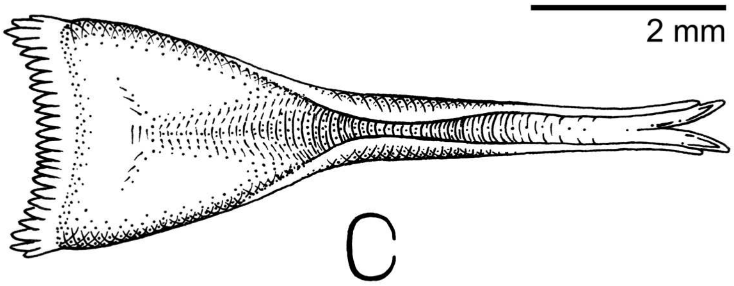

FIGURE 4. Sketch depicting the bifid, semi-tubular tongue of the holotype of *Dicaeum* dayakorum (USNM 663246). Dorsal view, distal end at right, with cross section (below) of semi-tubular portion.

Taxonomy.—Clear phenotypic distinctiveness from known species of flowerpeckers, and high confidence values from phylogenetic and species delimitation analyses of our molecular dataset, strongly support *Dicaeum dayakorum* as a new species.

Nyári *et al.* (2009) recognized two predominant molecular clades in the Dicaeidae: generally thicker-billed species with a longer outermost primary (Clade A); and generally more slender-billed species with shorter outer primaries (Clade B). These clades are roughly concordant with the two established genera of flowerpeckers, *Prionochilus* and *Dicaeum*, respectively, with the exception of four traditionally *Dicaeum* species that tend to group with Clade A (Nyári *et al.* 2009). Our independent analyses of the same molecular dataset (with the addition of USNM 663246) mirrors this arrangement, with strong support for *D. dayakorum* as sister to the core *Dicaeum* (Clade B; Fig. 3). With the added consideration of morphological characters (e.g. outer primary length and tongue morphology) that are closely (though not exclusively) associated with the core *Dicaeum* lineage, we strongly support the view of Edwards *et al.* (2009) that the new species be placed in this genus.

We recovered no clear sister taxon to *D. dayakorum* from our phylogenetic analyses (Fig. 3). Although *D. dayakorum* seems to be sister to the rest of Clade B with high support (99% ML; 1.0 BI), branches separating this and related taxa are short and support values are low (Fig. 3), indicating that more molecular data may be needed to define this relationship satisfactorily. Results from the pairwise distance analysis suggest that genetic distances between *D. dayakorum* and other basal members of Clade B are high, ranging from 14–16% (*D. anthonyi*: 16.1%; *D. auerolimbatum*: 16.8%; *D. australe*: 16.8%; *D. bicolor*: 15.6%; and *D. trigonostigma*: 14.5%). Species-level distinctiveness was further supported by the species delimitation test with a posterior probability support value of 0.99. In fact, the PTP analysis suggest that *D. dayakorum* is more distinctive at the molecular level than the rest of the 30 other flowerpecker taxa included in the Nyári *et al.* (2009) study. Although further taxon sampling is warranted, no unsampled species is a realistic candidate for conspecific status, and thus the proposed status of *D. dayakorum* as a new species will not be affected.

Ecology and distribution.—The type locality for *Dicaeum dayakorum* (USNM 663246) was characterized by tall, mixed dipterocarp forest upslope from the Nanga Segerak field station (LEWS, 350m asl). This section of forest lies at the edge of an expansive sanctuary dominated by primary lowland forest that has previously been subjected to light selective logging by local communities (Chai 1996). The immediate area of capture was a relatively open and steep section of ridgeline, possibly the site of a previous treefall or landslide in the advanced stages of succession. The location seemed to be a crossing point for birds cresting the ridge and several bird species typical of canopy or upperstory flocks were observed here near ground level (e.g *Irena puella, Psilopogon chrysopogon, Coracina fimbriata*). Documented observations depict a species with affinities for mature forest at lower elevations (30–350 m) (Edwards *et al*. 2009, Sykes & Loseby 2015, Boyd *et al.* 2016). The elevation of the sightings in the Maliau Basin are unclear (likely between 260-1100 m), but could potentially represent higher elevation limits for the species

(Sykes & Loseby 2015). The Spectacled Flowerpecker has not yet been observed in areas with significant anthropogenic disturbance and we suspect it may be very rare or absent in heavily selectively logged forest and will abandon largely deforested areas.

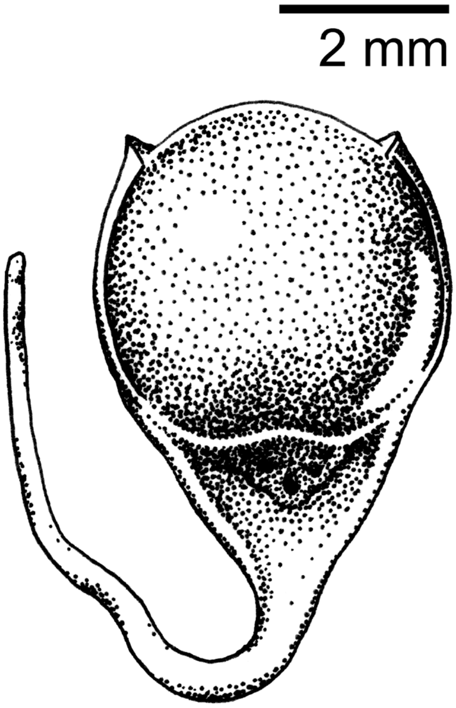

FIGURE 5. Sketch of a Loranthaceous mistletoe seed recovered from the lower gut of the holotype (USNM 663246). The sides of the seed show two longitudinal ribs which end in horn-like projections while the base depicts the uncoiled viscin aril which helps the seed attach to tree branches.

Flowerpeckers are known to feed on a wide variety of fruits, flowers, and invertebrates (Cheke *et al*. 2019). However, specialization on mistletoe fruit is one of the characteristic traits of the family, and is likely reciprocal due to their role as canopy seed dispersers (Ali 1931, Kannan 1966, Cheke *et al.* 2019). Most, if not all, flowerpecker species possess gut adaptations thought to be specifically evolved for processing mistletoe, in which the rapidly digestible berries are able to bypass the muscular ventriculus so that the seeds can be expelled intact (Desselberger 1931, Cheke *et al*. 2019). Many of the reported observations of *D. dayakorum* show it foraging in or closely associated with various species of mistletoe, often engaging in pulp-predation behavior (Boyd *et al.* 2016). A review of available photographs from these observations revealed several mistletoe species from at least two families (Loranthaceae: *Macrosolen cochinchinensis*; Santalaceae: *Ginalloa arnottiana* Korth. and *Viscum ovalifolium* DC). Examination of the holotype's gut contents found a partially digested jumping spider (*Salticidae* sp.) in the gizzard as well as mistletoe seeds in the large intestine (Fig. 5). These seeds were identified as a species of Loranthaceae upon morphological examination. However, a BLAST search of its chloroplast DNA was inconclusive. Further investigation is needed to determine which of the over 16 genera of Loranthaceae reported for Borneo can be a suitable match.

The degree to which *D. dayakorum* is dependent on mistletoe is an important question that remains to be evaluated. The partially tubular tongue structure (Fig. 3), the presence of arthropod material in the stomach, and observations of the species foraging on *Medinella* (Melastomataceae) berries suggest a diet similar to that of other flowerpeckers in which a mistletoe-dominated diet is supplemented to some extent by nectarivory, general frugivory, and arthropod predation. The role of diet specialization on habitat preference and distribution is poorly known (Reif *et al.* 2016). The various species of mistletoe that the bird has been observed to consume are ubiquitous species of Southeast Asia that likely occur widely throughout Borneo where mature forests persist (Beaman *et al.* 2001, 2004). However, the patchy distributions of mature mistletoe plants (Aukema 2004), and seasonality of fruit (Barea & Watson 2007) suggest that the distribution of this resource is likely sparse and ephemeral. These factors, along with competition for fruit resources from other mistletoe specialists—especially other species of flowerpeckers as noted in the initial report by Edwards *et al.* (2009)—may have a limiting effect on population density. All other aspects of the bird's life-history, including breeding biology, phenology, and vagility, remain undocumented.

Conservation.—Extrapolation of range based on documented localities of occurrence (Fig. 1) and the bird's currently known foraging ecology suggest that *D. dayakorum* has a widespread distribution, with the potential to occur anywhere in the extensive lowlands of Borneo where suitable habitat exists. The pattern of occurrences suggests a bird that is patchily distributed, possibly even nomadic while following shifts in an ephemeral food source. It is also possible that the core distribution of the species has yet to be discovered. However, the considerable scarcity of these observations, despite documented occurrence in relatively well-explored areas (e.g. Danum Valley) is more difficult to explain and may be compounded by low population densities and difficulty of detection owing to the bird's small size, dull coloration, and canopy dwelling tendencies.

Given our current lack of information on processes governing the distribution of this species, the potential effects of habitat fragmentation and disturbance should not be underestimated. However, our discovery of the species in Lanjak Entimau Wildlife Sanctuary—an approximately 187,000 ha. tract of protected lowland/hill forest managed by the Sarawak Forestry Corporation—is a reason to be hopeful (Guntavid *et al.* 1997). We see no reason why *D. dayakorum* would not occur throughout the sanctuary's pristine forests, or the contiguous Batang Ai National Park to the south. Although further surveys of the area are needed to assess habitat and mistletoe prevalence. Lowland forests such as this are the heart of Borneo's ecosystems. Sadly, these sanctuaries are under increasing threat with the encroachment of intensive selective logging and unsustainable agricultural practices, including widespread conversion of lowland forest to oil palm (Wilcove *et al.* 2013). It should also be noted that the indigenous Iban Dayak inhabitants of the region are the primary facilitators of conservation upkeep and protection. The imperilment and continued diminishment of these traditional longhouse communities is an underappreciated threat to the protection of these vital areas.

Many questions remain regarding the distribution, population dynamics, and ecology of the Spectacled Flowerpecker. Though the species may have once enjoyed a historical distribution of relative continuity throughout the lowland forests of Borneo, its current distribution has almost certainly become increasingly fragmented and diminished. We are hopeful that the formal scientific description of this exciting new species will help to underscore the importance of Borneo's lowland forests as an area of ecological significance and future discovery.

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LITERATURE CITED

Ali, S. (1931) The role of sunbirds and flowerpeckers in the propagation and distribution of the tree-parasite, *Loranthus longiflorus* Dest., in the Konkan (W. India). *Journal of the Bombay Natural History Society*, 35, 144–149.

Aukema, J. (2004) Distribution and dispersal of desert mistletoe is scale-dependent, hierarchically nested. *Ecography*, 27, 137–144.
https://doi.org/10.1111/j.0906-7590.2004.03640.x

Barea, L.P. & Watson, D.M. (2007) Temporal variation in food resources determines onset of breeding in an Australian mistletoe specialist. *Emu*, 107, 203– 209.
https://doi.org/10.1071/MU07003

Beaman, J.H., Anderson, C. & Beaman, R.S. (2001) *The plants of Mount Kinabalu. Volume 4*. Natural History Publications (Borneo) Shn. Bhd., Kota Kinabalu. 570 pp.

Beaman, J.H. & Anderson, C. (2004) *The plants of Mount Kinabalu. Volume 5*. Natural History Publications (Borneo) Shn. Bhd., Kota Kinabalu. 609 pp.

Boyd, N.S., Phillipps, Q. & Fischer, J.H. (2016) The first record of the undescribed "spectacled flowerpecker"(species novum) for Indonesia. *Kukila*, *19*, 42–49.

Braun, D.M. (2010) Meet Spectacled Flowerpecker, the world's newest bird species. National Geographic Society. Available from: https://blog.nationalgeographic.org (accessed 24 June 2019)

Chai, P.P.K. (1996) Development of Lanjak Entimau Wildlife Sanctuary as a Totally Protected Area Phase I, The Management Plan. Kuching L.M.P. Co, Malaysia. 138 pp.

Cheke, R., Mann, C. & Bonan, A. (2019) Flowerpeckers (Dicaeidae). *In*: del Hoyo, J., Elliott, A., Sargatal, J., Christie, D.A. & de Juana, E. (eds.). Handbook of the Birds of the World Alive. Lynx Editions, Barcelona. Avaliable from: https://www.hbw.com/node/52349 (Accessed 25 Jun. 2019)

Chernomor, O., von Haeseler, A. & Minh, B. Q. (2016) Terrace aware data structure for phylogenomic inference from supermatrices. *Systematic Biology*, 65 (6), 997–1008.
https://doi.org/10.1093/sysbio/syw037

Collar, N.J. (2009) New species in photographs: risks, rights and responsibilities. *BirdingASIA*, 12, 36–37.

Criscuolo, A. & Gribaldo, S. (2010) BMGE (Block Mapping and Gathering with Entropy): a new software for selection of phylogenetic informative regions from multiple sequence alignments. *BMC Evolutionary Biology*, 10 (1), 210.
https://doi.org/10.1186/1471-2148-10-210

De Bruyn, M., Stelbrink, B., Morley, R.J., Hall, R., Carvalho, G.R., Cannon, C.H., van den Bergh, G., Meijaard, E., Metcalfe, I., Boitani, L., Maiorano, L., Shoup, R. & von Rintelen, T. (2014) Borneo and Indochina are major evolutionary hotspots for Southeast Asian biodiversity. *Systematic Biology*, 63 (6), 879–901.
https://doi.org/10.1093/sysbio/syu047

Desselberger, H. (1931) Der verdauungskanal der Dicaeiden nach gestalt und funktion. *Journal of Ornithology*, 79 (3), 353–370.
https://doi.org/10.1007/BF01953010

Doyle, A. (2010) "Spectacled flowerpecker" bird found in Borneo. Reuters. Available from: https://www.reuters.com (accessed 24 Jun. 2019)

Edwards, D.P., Webster, R.E. & Rowlett, R.A. (2009) 'Spectacled Flowerpecker': a species new to science discovered in Borneo?. *BirdingASIA*, 12, 38–41.

Fischer, J.H., Boyd, N.S., Maruly, A., Van Der Kaaden, A.S., Husson, S.J. & Sihite, J. (2016) An inventory of the avifauna of the Bukit Batikap Protection Forest, Central Kalimantan, Indonesia. *Forktail*, (32), 26–35.

Gadagkar, S.R., Rosenberg, M.S. & Kumar, S. (2005) Inferring species phylogenies from multiple genes: concatenated sequence tree versus consensus gene tree. *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution*, 304 (1), 64–74.
https://doi.org/10.1002/jez.b.21026

Gaveau, D.L.A., Salim, M. & Arjasakusuma, S. (2016) Deforestation and industrial plantations development in Borneo. Center for International Forestry Research (CIFOR), V2.
https://doi.org/10.17528/CIFOR/DATA.00049

Gill, F & Donsker, D. (Eds) (2019) IOC World Bird List (v9.2).
https://doi.org/10.14344/IOC.ML.9.2

Guntavid, J.P., Julaihi, L.C.J. & Supardiyono (1997) Ethnobotany. *In*: Kuswanda, M.P., Chai, P. & Jaya, I.N.S. (Eds.) ITTO Borneo Biodiversity Expedition 1997 Scientific Report. Collaboration between the Governments of Indonesia and Malaysia and International Tropical Timber Organization (ITTO), Yokohama, pp. 140–154.

Hoang, D.T., Chernomor, O., Von Haeseler, A., Minh, B.Q. & Vinh, L.S. (2017) UFBoot2: improving the ultrafast bootstrap approximation. *Molecular Biology and Evolution*, 35 (2), 518–522.
https://doi.org/10.1101/153916

Jarvis, A., Reuter, H.I., Nelson, A. & Guevara, E. (2008) *Hole-filled SRTM for the globe Version 4*. Available from the CGIAR-CSI SRTM 90m Database. Available from http://srtm.csi.cgiar.org. (19 August 2019)

Kalyaanamoorthy, S., Minh, B.Q., Wong, T.K., von Haeseler, A. & Jermiin, L.S. (2017) ModelFinder: fast model selection for accurate phylogenetic estimates. *Nature Methods*, 14 (6), 587.
https://doi.org/10.1038/nmeth.4285

Kannan, P. (1966) *Ornithophily: A preliminary study of the reciprocal association between flowerbirds and birdflowers as observed in and around Bombay*, M. Sc. Thesis, University of Bombay, India.

Katoh, K. & Standley, D.M. (2013) MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution*, 30 (4), 772–780.
https://doi.org/10.1093/molbev/mst010

Kimura, M. (1980) A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. *Journal of Molecular Evolution*, 16, 111–120.
https://doi.org/10.1007/BF01731581

Kumar, S., Stecher, G., Li M., Knyaz C. & Tamura, K. (2018) MEGA X: Molecular Evolutionary Genetics Analysis across computing platforms. *Molecular Biology and Evolution,* 35(6),1547–1549.
https://doi.org/10.1093/molbev/msy096

Mayr, E. & Amadon, D. (1947) A review of the Dicaeidae. *American Museum Novitates*, no. 1360, 1–32.

Miller, M.A., Pfeiffer, W. & Schwartz, T. (2010) "Creating the CIPRES Science Gateway for inference of large phylogenetic trees" in Proceedings of the Gateway Computing Environments Workshop (GCE), 14 Nov. 2010, New Orleans, LA pp 1–8.
https://doi.org/10.1109/GCE.2010.5676129

Morioka, H. (1992) Tongue of two species of Prionochilus from the Philippines, with notes on feeding habits of flowerpeckers (Dicaeidae). *Japanese Journal of Ornithology*, 40 (3), 85–91.
https://doi.org/10.3838/jjo.40.85

Munsell, A.H. (1990) *Munsell Soil Color Charts.* Kollmorgen Instruments, Inc., Baltimore Maryland,

Myers, S. (2016) *Birds of Borneo, Second Edition*. Bloomsbury Publishing, London, 336pp.

Nguyen, L.T., Schmidt, H.A., von Haeseler, A. & Minh, B.Q. (2014) IQ-TREE: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution*, 32 (1), 268–274.
https://doi.org/10.1093/molbev/msu300

Nyári, Á.S., Peterson, A.T., Rice, N.H. & Moyle, R.G. (2009) Phylogenetic relationships of flowerpeckers (Aves: Dicaeidae): Novel insights into the evolution of a tropical passerine clade. *Molecular Phylogenetics and Evolution*, 53 (3), 613–619.
https://doi.org/10.1016/j.ympev.2009.06.014

Ong, S. (2018) High Up in the Borneo Canopy, a Likely New Bird Species Lurks. National Audubon Society. Available from: https://www.audubon.org (accessed 24 June 2019)

Peterson, A.T. (2014) Type specimens in modern ornithology are necessary and irreplaceable. *The Auk: Ornithological Advances*, 131 (3), 282–286.
https://doi.org/10.1642/AUK-13-204.1

Phillipps, Q. & Phillipps, K. (2014) *Phillipps' Field Guide to the Birds of Borneo*, *Third Edition*. John Beaufoy Publishing, Oxford, 372 pp.

Reif, J., Hořák, D., Krištín, A., Kopsová, L. & Devictor, V. (2016) Linking habitat specialization with species' traits in European birds. *Oikos*, 125 (3), 405–413.
https://doi.org/10.1111/oik.02276

Ronquist, F., Teslenko, M., Van Der Mark, P., Ayres, D.L., Darling, A., Höhna, S, Larget, B., Liu, L., Suchard, M.A. & Huelsenbeck, J.P. (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, 61 (3), 539–542.
https://doi.org/10.1093/sysbio/sys029

Salomonsen, F. (1960a) Notes on flowerpeckers (Aves, Dicaeidae) 1. The genera *Melanocharis, Rhamphocharis, and Prionochilus*. *American Museum Novitates* no.1990, 1–28.

Salomonsen, F. (1960b) Notes on flowerpeckers (Aves, Dicaeidae) 2. The primitive species of the genus *Dicaeum*. *American Museum Novitates* no. 1991, 1–38.

Smithe, F.B. (1975) *Naturalist's color guide*. American Museum of Natural History.

Sykes, B. & Loseby, T. (2015) More on Borneo's 'Spectacled'Flowerpecker. *BirdingASIA*, *23*, 126–127.

Walton, D. (2010) New bird species found in rainforests of Borneo. BBC. Available from: http://news.bbc.co.uk (accessed 24 June 2019)

Wilcove, D.S., Giam, X., Edwards, D.P., Fisher, B. & Koh, L.P. (2013) Navjot's nightmare revisited: Logging, agriculture and biodiversity in Southeast Asia. *Trends in Ecology and Evolution* 28: 531–540.
https://doi.org/10.1016/j.tree.2013.04.005

Zhang, J., Kapli, P., Pavlidis, P. & Stamatakis, A. (2013) A general species delimitation method with applications to phylogenetic placements. *Bioinformatics*, 29 (22), 2869–2876.
https://doi.org/10.1093/bioinformatics/btt499

APPENDIX TABLE 1. Morphological measurements from the holotype and other selected Dicaeidae species. Female specimens only included. All specimens from the USNM collections.

	bill width (mm)	bill depth (mm)	nares to bill tip (mm)	exposed culmen (mm)	wingchord (mm)	tail length (mm)	tarsus length (mm)
D. dayakorum	**3.6**	**3.3**	**6.0**	**8.0**	**48.4**	**24**	**11.8**
	(n=1)	(n=1)	(n=1)	(n=1)	(n=1)	(n=1)	(n=1)
D. trigonostigma	3.4±0.1	2.8±0.1	7.8±0.3	9.7±0.3	45.7±0.6	20.4±0.4	12.8±0.2
	(n=9)	(n=8)	(n=9)	(n=10)	(n=10)	(n=9)	(n=10)
D. anthonyi	4.6±0.1	4.3±0.3	7.1±0.4	9.8±0.5	54.6±0.3	25.3±0.6	14.6±0.6
	(n=4)	(n=2)	(n=4)	(n=3)	(n=3)	(n=4)	(n=4)
D. bicolor	4.0±0.2	3.8±0.1	5.9±0.1	7.4±0.2	50.0±0.9	21.7±0.70	13.7±0.5
	(n=7)	(n=6)	(n=7)	(n=7)	(n=7)	(n=7)	(n=7)
D. aureolimbatum	3.8±0.1	3.6±0.1	6.1±0.1	7.8±0.1	47.6±0.8	23.7±0.7	12.6±0.2
	(n=10)	(n=10)	(n=10)	(n=10)	(n=10)	(n=10)	(n=10)
D. hypoleucum	3.1±0.1	3.0±0.04	8±0.3	10.1±0.5	49.6±0.8	22.2±0.6	13.8±0.4
	(n=10)	(n=10)	(n=10)	(n=10)	(n=10)	(n=10)	(n=10)
D. nigrilore	3.6±0.1	3.0±0.1	8.6±0.4	11.1±0.3	53.2±0.9	25.8±0.7	15.2±0.5
	(n=8)	(n=6)	(n=8)	(n=8)	(n=8)	(n=8)	(n=8)
D. cruentatum	3.0±0.2	2.7±0.06	6.9±0.4	8.8±0.4	44.1±0.6	21.6±0.6	11.5±0.3
	(n=10)	(n=10)	(n=10)	(n=10)	(n=10)	(n=10)	(n=10)
D.monticolum	2.7±0.3	2.9±0.1	6.7±0.1	8.2±0.3	43.9±1.6	20.5±1.0	12.1±0.2
	(n=2)	(n=2)	(n=2)	(n=2)	(n=2)	(n=2)	(n=2)

APPENDIX TABLE 2. Accession numbers for the three genomic regions (ND2, ND3, and TGFb2) used in this study per species. Sequences generated here are marked in bold. The rest of the data was generated by Nyári *et al.* (2009) and retrieved from Genbank (https://www.ncbi.nlm.nih.gov/genbank/).

	ND2	**ND3**	**TGFb2**
Flowerpeckers (Ingroup):			
Dicaeum aeneum (Pucheran, 1853)	GQ145285	GQ145243	GQ145327
Dicaeum agile (Tickell, 1833)	GQ145306	GQ145264	GQ145348
Dicaeum anthonyi (McGregor, 1914)	GQ145283	GQ145241	GQ145325
Dicaeum aureolimbatum (Wallace, 1865)	GQ145288	GQ145246	GQ145330
Dicaeum australe (Hermann, 1783)	GQ145305	GQ145263	GQ145347
Dicaeum bicolor (Bourns & Worcester, 1894)	GQ145284	GQ145242	GQ145326
Dicaeum celebicum (Müller, 1843)	GQ145289	GQ145247	GQ145331
Dicaeum chrysorrheum (Temminck, 1829)	GQ145277	GQ145235	GQ145319
Dicaeum concolor (Jerdon, 1840)	GQ145297	GQ145255	GQ145339
Dicaeum cruentatum (Linnaeus, 1758)	GQ145278	GQ145236	GQ145320
Dicaeum dayakorum, sp. nov.	MN416066	MN416068	MN416067
Dicaeum everetti (Sharpe, 1877)	GQ145307	GQ145265	GQ145349
Dicaeum eximium (Sclater, 1877)	GQ145303	GQ145261	GQ145345
Dicaeum geelvinkianum (Meyer, 1874)	GQ145279	GQ145237	GQ145321
Dicaeum hirundinaceum (Shaw, 1792)	GQ145267	GQ145225	GQ145309
Dicaeum hypoleucum (Sharpe, 1876)	GQ145286	GQ145244	GQ145328
Dicaeum igniferum (Wallace, 1864)	GQ145287	GQ145245	GQ145329
Dicaeum ignipectus (Blyth, 1843)	GQ145304	GQ145262	GQ145346

......*continued on the next page*

APPENDIX TABLE 2. (Continued)

	ND2	**ND3**	**TGFb2**
Dicaeum melanozanthum (Blyth, 1843)	GQ145270	GQ145228	GQ145312
Dicaeum monticolum (Sharpe, 1887)	GQ145299	GQ145257	GQ145341
Dicaeum nigrilore (Hartert, 1904)	GQ145296	GQ145254	GQ145338
Dicaeum pygmaeum (von Kittlitz, 1833)	GQ145302	GQ145260	GQ145344
Dicaeum sanguinolentum (Temminck, 1829)	GQ145281	GQ145239	GQ145323
Dicaeum trigonostigma (Scopoli, 1786)	GQ145266	GQ145224	GQ145308
Dicaeum tristrami (Sharpe, 1884)	GQ145300	GQ145258	GQ145342
Prionochilus maculatus (Temminck, 1836)	GQ145275	GQ145233	GQ145317
Prionochilus olivaceus (Tweeddale, 1877)	GQ145282	GQ145240	GQ145324
Prionochilus percussus (Temminck, 1826)	GQ145269	GQ145227	GQ145311
Prionochilus plateni (Blasius, 1888)	GQ145293	GQ145251	GQ145335
Prionochilus thoracicus (Temminck, 1836)	GQ145272	GQ145230	GQ145314
Prionochilus xanthopygius (Salvadori, 1868)	GQ145280	GQ145238	GQ145322
Sunbirds (Outgroup):			
Aethopyga boltoni (Mearns, 1905)	GQ145301	GQ145259	GQ145343
Aethopyga christinae (Swinhoe, 1869)	GQ145290	GQ145248	GQ145332
Aethopyga duyvenbodei (Schlegel, 1871)	GQ145295	GQ145253	GQ145337
Aethopyga primigenia (Hachisuka, 1941)	GQ145292	GQ145250	GQ145334
Aethopyga siparaja (Raffles, 1822)	GQ145294	GQ145252	GQ145336
Anthreptes rectirostris (Shaw, 1812)	GQ145273	GQ145231	GQ145315
Arachnothera longirostra (Latham, 1790)	GQ145268	GQ145226	GQ145310
Cinnyris jugularis (Linnaeus, 1766)	GQ145271	GQ145229	GQ145313
Cinnyris superbus (Shaw, 1809)	GQ145291	GQ145249	GQ145333
Cyanomitra obscura (Jardine, 1843)	GQ145298	GQ145256	GQ145340
Leafbird (Outgroup):			
Chloropsis hardwickii (Jardine & Selby, 1830)	GQ145276	GQ145234	GQ145318