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A cryptic new species of bulbul from Borneo

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Summary.—Cream-vented Bulbul *Pycnonotus simplex* of Borneo was previously considered to be polymorphic in iris colour, having either red or white (creamy-yellow) irides. Mitochondrial DNA sequence comparisons, however, indicate that white- and red-eyed Bornean individuals are not closely related to one another. Instead, white-eyed birds are sister to Ashy-fronted Bulbul *P. cinereifrons* of Palawan Island, in the south-west Philippines, and red-eyed birds are sister to white-eyed *P. simplex* of the Thai-Malay Peninsula. Consequently, we elect to treat the white-eyed Bornean population as a distinct, previously overlooked species. In respect to plumage, white- and red-eyed individuals are almost identical, varying only slightly in the amount of yellow coloration in their feathers. The two taxa are sympatric at some localities, but white-eyed individuals are rarer and more consistently associated with mature forest than red-eyed birds.

Cream-vented Bulbul *Pycnonotus simplex* is a uniformly olive-brown species that occurs from southern Indochina throughout the Sunda Islands, except Palawan in the south-western Philippines (Fig. 1). Its classification has been complicated by its variable iris colour (Hoogerwerf 1966, Mees 1986, Dickinson & Dekker 2002), which has led to a confused taxonomic history and disagreement concerning the validity of iris colour as a subspecific character (Hoogerwerf 1966, Mees 1986). Although as many as six subspecies of *P. simplex* have been named (Table 1), only three or four are currently recognised (Dickinson & Christidis 2014, Eaton *et al*. 2016, Clements *et al*. 2017). Here, we follow the classification of Dickinson & Christidis (2014) because of its thorough documentation. It lists three subspecies.

Nominate *P. s. simplex* Lesson, 1839, occurs from south-eastern Myanmar to Sumatra, the southern Natuna Islands and Borneo. Individuals on the Asian mainland and Sumatra have white to grey or yellowish-white irides (Meyer de Schauensee 1958, Mees 1986). Populations on Borneo, Billiton, and Bangka Islands have primarily red irides (Mees 1986), a distinction that caused Chasen & Kloss (1929) to treat them subspecifically as *P. s. perplexus*. Yet another subspecies, *P. s. oblitus*, was originally described from the southern Natuna Islands based on its red irides and supposedly longer, heavier bill (Deignan 1954). However, in a thorough review of the species' taxonomy, Mees (1986) noted that individuals with 'white' irides (i.e., pale yellow or creamy yellow) also occur occasionally on Borneo, often in close proximity to red-eyed individuals, and he also found no size difference between *P. s. oblitus* and specimens from Borneo. Mees agreed with Hoogerwerf (1966) that iris colour is not a reliable subspecific character in these bulbuls and treated *P. s. perplexus* and *P. s. oblitus* as junior synonyms of *P. s. simplex*. As a result, *P. s. simplex* now includes both red- and white-eyed individuals.

The second subspecies, *P. s. prillwitzi* E. J. O. Hartert, 1902, occurs on Java, but its iris colour was not noted in the original description. Later, Hoogerwerf (1996) indicated that Javan birds have red, orange or reddish-brown irides. This subspecies was described

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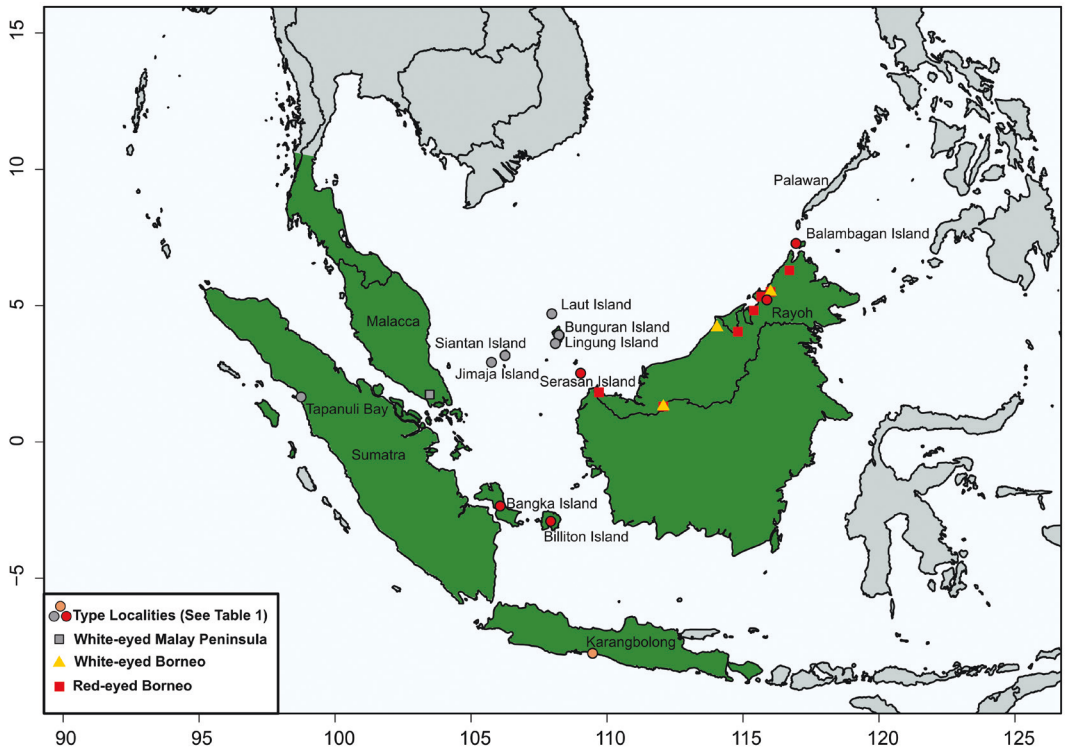

Figure 1. Map of Sundaland showing range of Cream-vented Bulbul *Pycnonotus simplex* with labelled type localities of subspecies from Table 1 and the collecting sites of *P. simplex* specimens whose ND2 was sequenced.

as brighter overall than other subspecies, with greener upperparts and more yellowish underparts (Hartert 1902). The third subspecies, *P. s. halizonus* Oberholser, 1917, which includes *P. s. axanthinus* Oberholser, 1932, as a junior synonym, occurs on the northern Natuna and Anamba Islands. It was described as having white irides and being larger than individuals from Borneo or the Thai-Malay Peninsula (Oberholser 1917).

Recent work has shown that iris colour actually can be an important trait for differentiating bulbul taxa that previously were considered conspecific based on similarities in plumage and vocalisations (Garg *et al*. 2016). On Borneo, two common bulbul species that are similar in plumage and voice to each other and to *P. simplex* are readily distinguished by their eye coloration. Whereas *P. simplex* has dark red, creamy or white irides, Red-eyed Bulbul *P. brunneus* has a distinctly orange or two-toned iris (red at the edge and orange towards the centre) and Spectacled Bulbul *P. erythropthalmos* has a dark red iris surrounded by an eye-ring of yellow skin. Based on these observations, eye colour would appear to play a key role in recognition among some bulbul species.

In the course of genetic comparisons for ongoing studies of Bornean bird biogeography and phylogeography (e.g., Sheldon *et al*. 2015, Lim *et al*. 2017, Shakya *et al*. 2018), we discovered that red- and white-eyed *P. s. simplex* on Borneo are not members of the same species. They are not even sister taxa. White-eyed individuals—although remarkably similar to red-eyed birds in plumage—are members of a distinct species.

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TABLE 1
Past and current names of *Pycnonotus simplex* populations.

Name	Current Designation (based on Dickinson & Christidis 2014)	Journal	Localities in original description	Iris colour in original description
P. simplex Lesson, 1839	*P. s. simplex*	*Rev. Zool*. 2: 167	'Sumatra'	-
Microtarsus olivaceus Moore, 1854	*P. s. simplex*	*Cat. Birds Mus. East India Co*. 1: 249	'Malacca'	-
P. olivaceus chloeodis Oberholser, 1912	*P. s. simplex*	*Smiths. Misc. Coll*. 60(7): 11	'Tapanuli Bay, north-western Sumatra'	-
P simplex perplexus Chasen & Kloss, 1929	*P. s. simplex*	*J. Orn*., Ergänzungsb. 2: 116	'Balembangan Island (Sabah, type locality) 'Rayoh' (Sabah)	crimson/ chrome/scarlet
P. simplex oblitus Deignan, 1954	*P. s. simplex*	*J. Wash. Acad. Sci*. 44: 124	'Pulau Serasan, southern Natuna Islands' (type locality) 'western Borneo' 'Billiton and Bangka Islands'	red
P. prillwitzi E. J. O. Hartert, 1902	*P. s. prillwitzi*	*Novit. Zool*. 9: 561	'Karangbolong, S. Java'	*
P. simplex halizonus Oberholser, 1917	*P. s. halizonus*	*Bull. US Natl. Mus*. 98: 43	'Pulo Jimaja, Anamba Islands' (type locality) 'Pulo Siantan'	white
P. simplex axanthinus Oberholser, 1932	*P. s. halizonus*	*Bull. US Natl. Mus*. 159: 78	'Bunguran Island, Natuna Islands, South China Sea' (type locality) 'Pulo Laut' 'Pulo Lingung'	white

* Iris colour was not stated in Hartert's description, but specimens from Java have red, orange or reddish-brown irides (Hoogerwerf 1966).

Methods

We compiled a dataset of mitochondrial ND2 (NADH dehydrogenase subunit 2) sequences of 15 *P. simplex* individuals from Borneo (11 red-eyed and four white-eyed) and one from the Thai-Malay Peninsula (white-eyed), as well as outgroup sequences of four *P. brunneus*, two Ashy-fronted Bulbuls *P. cinereifrons*, nine Olive-winged Bulbuls *P. plumosus*, one *P. erythropthalmos*, one Straw-headed Bulbul *P. zeylanicus* and two Buff-vented Bulbuls *Iole charlottae* (Table 2). These outgroups were selected based on a recent phylogenetic study of the Pycnonotidae (Shakya & Sheldon 2017). Sequences were either newly generated or obtained from GenBank. For newly generated sequences, we extracted total genomic DNA from frozen or alcohol-preserved samples using a DNEasy Blood and Tissue Kit (Qiagen, Hilden, Germany) following the manufacturer's protocol. PCR amplifications of ND2 were performed using primer pairs L5215 (Hackett 1996) and HTrpC (STRI) as described in Shakya & Sheldon (2017). Sequences were aligned using MUSCLE (Edgar 2004), and maximum-likelihood (ML) tree searches were conducted using RAxML v8 (Stamatakis 2014) with the GTRGAMMA model for three partitions corresponding to each codon position. A total of 1,000 non-parametric bootstraps was run to obtain branch support values in the best tree generated from RAxML.

We also examined and measured skin specimens in the collections of the Louisiana State University Museum of Natural Science (LSUMNS), Baton Rouge, LA, and the Western Foundation of Vertebrate Zoology (WFVZ), Camarillo, CA, USA. Specifically, we measured bill length (from the nares to the tip), bill width (at nares), bill depth (at nares),

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TABLE 2
Specimen, tissue, and GenBank numbers of taxa included in phylogenetic analyses.

Species[1]	Specimen No.	Tissue No.	Locality[2]	Iris colour	GenBank No.
Pycnonotus simplex	LSUMZ 176482	LSUMNS B-47018	Serinsim, Sabah	red	MK298052
Pycnonotus simplex	LSUMZ 176485	LSUMNS B-47164	Klias Forest Reserve, Sabah	red	MK298053
Pycnonotus simplex		LSUMNS B-52090	Johor, Malay Peninsula	brown*	MK298054
Pycnonotus simplex	LSUMZ 186302	LSUMNS B-58561	Pueh, Sarawak	red	MK298055
Pycnonotus simplex	LSUMZ 181682	LSUMNS B-61611	Ulu Kimanis, Sabah	red	MK298056
Pycnonotus simplex		LSUMNS B-88077	Mt. Mulu National Park, Sarawak	red	MK298059
Pycnonotus simplex		LSUMNS B-88418	Ahmad Takong, Lawas, Sarawak	red	MK298060
Pycnonotus simplex	USNM 656154		Batang Ai National Park, Sarawak	red	MH908199
Pycnonotus simplex	USNM 656156		Batang Ai National Park, Sarawak	red	MH908200
Pycnonotus simplex	USNM 656168		Batang Ai National Park, Sarawak	red	MH908211
Pycnonotus simplex	USNM 656277		Batang Ai National Park, Sarawak	red	MH908312
Pycnonotus simplex	USNM 656279		Batang Ai National Park Sarawak	red	MH908314
Pycnonotus pseudosimplex	KU 113008	KU 17777	Ulu Kimanis, Sabah	light yellow	GU112671
Pycnonotus pseudosimplex	LSUMZ 181671	LSUMNS B-61615	Ulu Kimanis, Sabah	pale yellow	MK298057
Pycnonotus pseudosimplex	LSUMZ 188187	LSUMNS B-84971	Lambir Hills National Park, Sarawak	creamy yellow	MK298058
Pycnonotus pseudosimplex	USNM 656157		Batang Ai National Park, Sarawak	light yellow	MH908201
Pycnonotus brunneus		LSUMNS B-36341	Crocker Range National Park HQ, Keningau, Sabah	orange	DQ402233
Pycnonotus brunneus		LSUMNS B-47074	Serinsim, Sabah	orange	MK298042
Pycnonotus brunneus	LSUMZ 179308	LSUMNS B-57043	Samarakan, Tatau District, Sarawak	orange	MK298043
Pycnonotus brunneus		LSUMNS B-79723	Sebako, Mt. Pueh, Sarawak	orange	MK298044
Pycnonotus plumosus		LSUMNS B-23354	Membakut, Sabah	red	DQ402239
Pycnonotus plumosus		LSUMNS B-47033	Serinsim, Sabah	red	MK298046
Pycnonotus plumosus	LSUMZ 176502	LSUMNS B-47151	Klias Forest Reserve, Sabah	red	MK298047
Pycnonotus plumosus		LSUMNS B-52242	Niah National Park, Sarawak	red	MK298048
Pycnonotus plumosus	LSUMZ 186219	LSUMNS B-58541	Mt. Pueh, Sarawak	red	MK298049
Pycnonotus plumosus	LSUMZ 186220	LSUMNS B-58562	Pueh village, Sarawak	red	MK298050
Pycnonotus plumosus		LSUMNS B-88202	Mt. Penrissen, Sarawak	red	MK298051
Pycnonotus plumosus	KU 112990	KU 17707	Inobang, Sabah	red	GU112686
Pycnonotus plumosus		M0099	Singapore	red	KT321611
Pycnonotus cinereifrons	KU 99194	KU 12660	Palawan	chestnut	GU112684
Pycnonotus cinereifrons	KU 110303	KU 12806	Palawan	red	GU112685
Pycnonotus erythropthalmos	LSUMZ 188188	LSUMNS B-85012	Lambir Hills National Park, Sarawak	red	MK298045
Pycnonotus zeylanicus		LSUMNS B-23321	Lumat, Sabah	red	DQ402240
Iole charlottae	KU 113005	KU 17765	Ulu Kimanis, Sabah	white	GU112690
Iole charlottae	USNM 656293		Batang Ai National Park, Sarawak	white	MH908328

*Juveniles have brown eyes, which eventually become white on the Thai-Malay Peninsula (Wells 2007).
[1]Classification follows Dickinson & Christidis (2014).
[2]Sites in Sabah are described in Sheldon (2015).

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wing-chord length, tail length and tarsus length. We did not re-examine type specimens of *P. simplex* subspecies because original or revisional descriptions of subspecies outside Borneo distinguished them from Bornean red- and white-eyed individuals either by plumage colour or size (Oberholser 1917, Hoogerwerf 1966, Mees 1986). Also, plumage colour in specimens of *P. simplex* changes rapidly with age (Hoogerwerf 1966) and, thus, re-examination of plumage at this stage would be uninformative.

Results

Genetic comparisons indicate that white- and red-eyed *P. simplex* from Borneo do not form a monophyletic group (Fig. 2). Red-eyed Bornean birds are sister to white-eyed birds from the Thai-Malay Peninsula, whereas white-eyed Bornean birds are sister to *P. cinereifrons* of Palawan. ND2 sequences of white-eyed Bornean birds differ by a mean 14% from red-eyed Bornean birds and 12% from *P. cinereifrons*. Compared to these relatively large distances, ND2 of red-eyed Bornean birds differs by just 4% from white-eyed *P. simplex* of the Thai-Malay Peninsula.

Mensural data from museum skins indicate similarity in most dimensions between red-eyed and white-eyed individuals (Table 3). Wing, tail and tarsus lengths did not differ

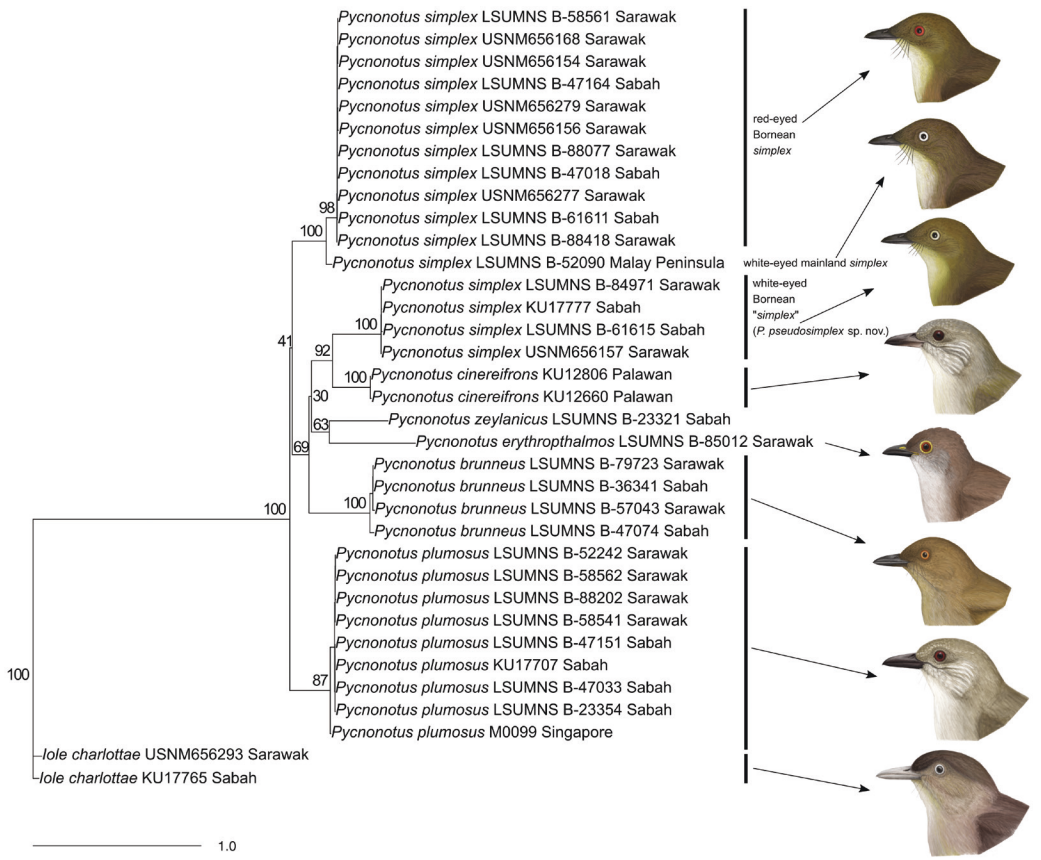

Figure 2. Maximum likelihood tree generated from mitochondrial ND2 sequences. Numbers adjacent to branches indicate bootstrap support. Illustrations of heads of each species are shown to the right (depictions by Subir B. Shakya).

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TABLE 3
Measurements of the new species and *P. s. simplex* from Borneo.

Species	Museum	No.	Sex	Locality[1]	Iris colour[2]	Mass (g)	Wing-chord length (mm)	Tail length (mm)	Culmen length (from nares) (mm)	Culmen width (at nares) (mm)	Culmen depth (at nares) (mm)	Tarsus length (mm)
sp. nov.	WFVZ	38747	M	Bole River, Sabah	straw	19.0	74	67.3	9.1	3.6	4.3	21.6
sp. nov.	WFVZ	38775	M	Saliwangan, Sabah	pale yellow	18.0	76	70.5	9.3	3.9	4.1	19.4
sp. nov.	WFVZ	38742	F	Bole River, Sabah	cream dark yellow	18.1	73	72.4	8.6	3.7	4.3	17.9
sp. nov.	WFVZ	38778	F	Saliwangan, Sabah	pale yellow	12.4	71	62.8	8.5	3.4	3.5	19.6
sp. nov.	WFVZ	38743	M	Bole River, Sabah	cream yellow	20.8	72	76.9	8.7	3.9	3.9	17.0
sp. nov.	WFVZ	38746	F	Bole River, Sabah	creamy yellow	17.6	73	65.9	8.6	3.1	3.9	17.4
sp. nov.	WFVZ	38754	M	Megatai (Mangkatai), Sabah	pale yellow	21.2	76	73.8	9.4	3.6	4.5	16.2
sp. nov.	WFVZ	38776	M	Saliwangan, Sabah	pale yellow	16.0	77	71.6	8.4	3.5	3.6	19.3
sp. nov.	WFVZ	38782	F	Saliwangan, Sabah	pale yellow	15.0	76	69.4	8.8	3.7	3.7	19.5
sp. nov.	WFVZ	38780	M	Saliwangan, Sabah	straw yellow	17.9	75	70.3	9.3	3.7	3.8	17.5
sp. nov.	LSUMZ	188187	M	Lambir Hills National Park, Sarawak	cream yellow	17.6	76	67.9	9.4	4.3	4.2	19.2
sp. nov.	LSUMZ	181671	F	Ulu Kimanis, Sabah	pale yellow	19.9	69	65.2	8.6	3.8	4.3	20.1
					Mean	**17.8**	**74.0**	**69.5**	**8.9**	**3.7**	**4.0**	**18.7**
					SD	**2.4**	**2.3**	**3.8**	**0.4**	**0.3**	**0.3**	**1.5**
simplex	LSUMZ	188186	M	Lambir Hills National Park, Sarawak	red	20.0	71	67.3	9.0	4.4	4.6	18.1
simplex	LSUMZ	187653	F	Kelabit Highlands, Sarawak	red	19.0	71	70.2	9.2	4.0	4.1	19.1
simplex	LSUMZ	187654	F	Kelabit Highlands, Sarawak	red	18.5	74	71.2	8.5	3.8	4.3	16.9
simplex	LSUMZ	181670	M	Ulu Kimanis, Sabah	red	21.1	77	72.9	9.4	3.6	4.8	15.8
simplex	LSUMZ	176482	M	Serinsim, Sabah	red	20.8	75	71.7	9.5	3.7	4.3	18.5
simplex	LSUMZ	181681	M	Ulu Kimanis, Sabah	red	19.1	79	73.9	9.7	4.0	4.7	20.1
simplex	LSUMZ	176484	M	Klias Forest Reserve, Sabah	red	19.2	78	67.0	9.6	4.4	4.9	18.9
simplex	LSUMZ	176486	F	Klias Forest Reserve, Sabah	red	24.6	74	68.4	9.1	4.1	4.4	20.2
simplex	LSUMZ	177789	F	Ulu Tungud Forest Reserve, Sabah	red	22.0	76	68.9	9.0	4.5	4.6	19.1
simplex	LSUMZ	181715	F	Tatau, Sarawak	red	24.0	74	73.4	9.9	4.3	4.3	20.4
simplex	LSUMZ	187650	F	Kelabit Highlands, Sarawak	red	19.7	74	74.7	9.2	4.1	4.4	18.1
					Mean	**20.7**	**74.8**	**70.9**	**9.3**	**4.1**	**4.5**	**18.6**
					SD	**2.0**	**2.4**	**2.6**	**0.4**	**0.3**	**0.2**	**1.3**

[1]Sites in Sabah are described in Sheldon (2015).
[2]Iris colour from specimen labels.

significantly. However, red-eyed birds appear to be slightly heavier than white-eyed birds: red, mean 20.7 ± 2.0 g (n = 11); white, mean 17.8 ± 2.4 g (n = 12). Red-eyed birds also appear to have slightly larger bills in all dimensions. No incidental biological circumstances appear to cause the size differences; e.g., the mass variation does not result from more breeding females in one taxon than the other.

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Discussion

Taxonomy.—Genetic comparisons using mitochondrial ND2 sequences reveal that white- and red-eyed individuals of *P. simplex* from Borneo are not members of the same species. Their segregation by iris colour is backed by a deep ND2 sequence divergence (14%). Red-eyed Bornean birds are sister to white-eyed *P. s. simplex* of the Thai-Malay Peninsula at 4% ND2 divergence, whereas white-eyed Bornean birds are sister to *P. cinereifrons* of Palawan at 12% ND2 divergence. The perfect association of ND2 haplotype with iris colour across the region where the two morphotypes co-occur suggests assortative mating and the absence of mitochondrial gene introgression. For the red-eyed Bornean population, iris colour difference is adequate for recognition as a separate subspecies (*P. s. perplexus*; Chasen & Kloss, 1929, Eaton *et al.* 2016), or possibly even species, from white-eyed *P. s. simplex* of the Thai-Malay Peninsula and Sumatra. Because the two taxa are relatively closely related in respect to ND2 distance, species-level reclassification should depend on future research into gene flow and song. Plumage variation is unlikely to be helpful because of the similarity between these populations and the tendency for colours to change in museum specimens (Hoogerwerf 1966, Mees 1986). For the white-eyed Bornean population, its large genetic distance from *P. cinereifrons* and distinct morphology (Fig. 2) are sufficient to recognise it as a species.

There are no other taxa whose names apply to the Bornean white-eyed population. *P. simplex* subspecies have been described from Sumatra, the Anamba Islands, the northern Natuna Islands, the southern Natuna Islands, Java, and northern Borneo (Table 1, Fig. 1). Iris colour and size connect white-eyed populations of Sumatra and mainland Asia in subspecies *simplex* (Fig. 1). Larger size distinguishes the white-eyed subspecies *halizonus* (including its junior synonym *axanthinus*) of the Anamba and northern Natuna Islands from other white-eyed populations: e.g., mean wing length for *halizonus* 83.6 mm (n = 4) vs. 74 mm (n = 12) for Bornean white-eyed individuals. The red-eyed subspecies on the southern Natuna Islands (*oblitus*) belongs with Borneo's red-eyed population based on iris colour, size and plumage (Mees 1986). Eye colour of the Javan population (*prillwitzi*) varies from red to orange or red-brown, and its plumage is more distinctive than any other population of *P. simplex*, including red- and white-eyed Bornean populations (Hoogerwerf 1966). Apart from these taxa of *P. simplex*, there is no evidence that early taxonomists confused other species of similar-looking bulbuls with the white-eyed Bornean population of *P. simplex*. *Pycnonotus brunneus* has two subspecies*: P. b. brunneus* (including *P. b. zaphaeus*) and *P. b. zapolius*. Both of these were described as having red irides. *P. erythropthalmos* (including *P. e. salvadorii*, sometimes recognised for Borneo) has a red iris with a yellow eye-ring. Because no name applies to the Bornean white-eyed population, we name it:

Pycnonotus pseudosimplex, sp. nov.
Cream-eyed Bulbul

Holotype.—Study skin, Louisiana State University Museum of Zoology (LSUMZ 188187), Baton Rouge; tissue, LSU Museum of Natural Science (LSUMNS B-84971); adult male; Malaysia, Sarawak, Miri Division, Miri, Lambir Hills National Park, 04°12′N, 114°25′E; elevation *c*.120 m (from Google Earth); habitat: secondary forest continuous with old-growth hill forest; collected 23 April 2013; prepared by Frederick H. Sheldon (FHS), original catalogue number FHS 1022; photo by John Mittermeier (Fig. 3A); GenBank accession no. MK298058.

Diagnosis.—The iris of *P. pseudosimplex* is creamy yellow instead of crimson-red as in Cream-vented Bulbul *P. s. simplex* of Borneo. Its plumage also differs from that of *P. s. simplex*

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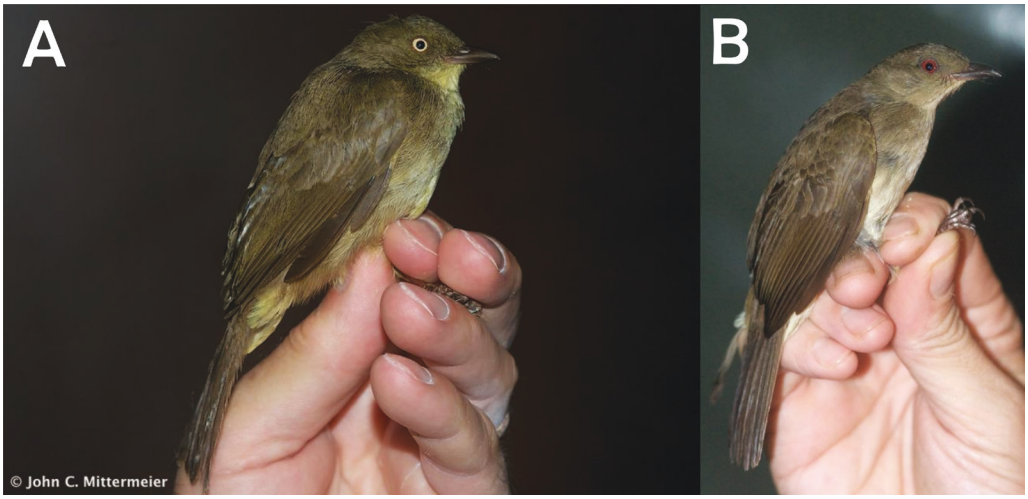

Figure 3. Photographs from Lambir Hills National Park, Miri Division, Sarawak, Malaysia of (A) Cream-eyed Bulbul *Pycnonotus pseudosimplex* sp. nov., and (B) Cream-vented Bulbul *P. simplex* (© John C. Mittermeier)

in being yellower on the throat and vent, creating greater contrast with the darker breast and flanks. From *P. cinereifrons*, *P. pseudosimplex* differs in being much smaller: *P. cinereifrons* mean 31.7 g (n = 3); *P. pseudosimplex* mean 20.7 g (n = 11). *P. cinereifrons* also has an olive tinge to the leading edge of its remiges, which is especially obvious on the folded wings of specimens (similar to *P. plumosus* of Borneo). From *P. brunneus*, *P. pseudosimplex* differs in having a white iris instead of an orange or two-toned iris. Similarly, *P. erythropthalmos* differs in having a dark red iris and a circle of yellow skin around the eyes.

Description of holotype.—Approximate colour names used for description, with standard colour names from Ridgway (1912) and alphanumeric colour codes from Munsell (1950) in parentheses. Crown, nape and back uniform olive-brown (Olive Brown; 5Y3/4) becoming yellower on rump and uppertail-coverts (Dresden Brown; 2.5Y4/4). Tail dark brown (Chestnut Brown; 10YR3/2). Cheeks similar in colour to crown (Olive Brown; 5Y3/4) with paler shaft-streaks to feathers. Throat pale yellow (Olive Buff; 5Y8.5/4); breast slightly darker than throat with darker olive-brown diffuse streaks (5Y4/2). Flank feathers olive (Light Brownish Olive; 2.5Y5/6). Undertail feathers cream-coloured (Naples Yellow; 5Y7/6). Wing like tail (Chestnut Brown; 10YR3/2) with olive-yellow edges. Soft part colours recorded on collection: bill black; iris creamy yellow; legs and toes dark brown. No moult; testis 2 × 1 mm, skull: 100% ossified; stomach: full of fruit with 1 mm-long seeds.

Measurements of type.—See Table 3.

Paratypes.—We designate 11 paratypes, which include specimen LSUMZ 181671 and ten specimens held at WFVZ: 38742, 38743, 38746, 38747, 38754, 38775, 38776, 38778, 38780, 38782 (listed in Table 3). The paratypes were collected in various parts of Sabah, Malaysian Borneo (unlike the holotype, which was taken in Sarawak, Malaysian Borneo). Measurements of all paratypes and their iris colours are reported in Table 3.

Etymology.—For more than 100 years this species has been confused with *P. simplex*, i.e., since Carl Lumholtz collected the first white-eyed specimen in 'Boeloengan' (Balungan Regency) along the Kayan River in eastern Kalimantan, Indonesian Borneo, in 1914 (Lumholtz 1920, Voous 1961). Apart from eye colour, the two species are almost indistinguishable; hence, we refer to the new species as 'false' or 'pseudo' *simplex*. The common name, Cream-eyed Bulbul, describes the main identifying character of the new

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species. It also evokes a time when *P. simplex* was known as the White-eyed Brown Bulbul, as opposed to the Red-eyed Brown Bulbul *P. brunneus* of Borneo (Smythies 1960).

Habitat.—*P. simplex* and *P. pseudosimplex* appear to be sympatric in mature forest interior and edge. Individuals of both species whose DNA was compared in this study were collected in the same localities during recent years: viz., Ulu Kimanis, Crocker Range National Park, Sabah, in 2008; Lambir Hills National Park, Sarawak, in 2013; and Batang Ai National Park, Sarawak, in 2018 (Fig. 1, Table 2). Both taxa were also mist-netted together in the early 1980s elsewhere in Sabah: at Bole River, Saliwangan Baru, and Mangkatai (Megatai) (localities described in Sheldon 2015). Although previous authors have stated that white- and red-eyed individuals co-occur throughout Borneo (Hoogerwerf 1966, Mees 1986), our experience and specimen records suggest that white-eyed individuals are considerably rarer and perhaps more habitat-restricted. *P. simplex* occurs to 1,100 m (Kelabit Highlands) and in several forest types of varying quality: good-soil dipterocarp, *kerangas* and peatswamp; primary, secondary, and heavily disturbed forest; and plantations. We have found *P. pseudosimplex* (only by mist-netting) to 500 m (Ulu Kimanis) near the edge of mature good-soil dipterocarp, and in *kerangas* forest nearer to sea level.

Morphology and voice.—Given their distinct ancestry, the striking similarity in plumage between *P. simplex* and *P. pseudosimplex* is remarkable. This is particularly true in specimens, less so in photographs (Fig. 3). They also closely resemble other species of brown bulbuls on Borneo to which they are not especially closely related: Red-eyed Bulbul and Spectacled Bulbul (Fig. 2). Perhaps these species are strongly selected for the cryptic advantage of dull brown plumage, but that observation does not hold for other bulbuls that occasionally occupy forest-edge habitat, such as Black-headed *P. atriceps* and Yellow-vented Bulbuls *P. goiavier*, which are both much more brightly coloured.

We are unaware of any vocal differences between *P. simplex* and *P. pseudosimplex*, although we would expect some. *P. simplex* is far more common than *P. pseudosimplex* and thus more likely to be represented in sound archives, but without accompanying iris colour data it is currently impossible to know which species is vocalising in recordings. In general, all of Borneo's brown bulbuls have similar songs that are not as distinctive (to the human ear) as Black-headed, Yellow-vented, or other species of bulbuls. Although vocalisations are certainly important, eye colour might be the main trait for species recognition among brown bulbuls. This has been observed in Streak-eared Bulbul *P. blanfordi* of Indochina and the Thai-Malay Peninsula (Garg *et al*. 2016). A large mitochondrial distance occurs between two vocally and visually similar subspecies, *P. b. blanfordi* and *P. b. conradi*, which are also most easily distinguished by iris colour: *P. b. blanfordi* has dark red irides, whereas *P. b. conradi* usually has dark grey irides (Garg *et al*. 2016). On Borneo, field comparisons of *P. pseudosimplex* with other brown bulbuls—especially how the species use their markedly distinct eye colours—are likely to yield rich information on the behavioural ecology of an otherwise generally under-appreciated group of birds.

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References:

Chasen, F. N. & Kloss, C. B. 1929. Some new birds from North Borneo. *J. Orn*. 77: 106–121.

Clements, J. F., Schulenberg, T. S., Iliff, M. J., Roberson, D., Fredericks, T. A., Sullivan, B. L. & Wood, C. L. 2017. The eBird / Clements Checklist of birds of the world: V2017. Cornell Lab of Ornithology, Ithaca, NY.

Deignan, H. G. 1954. Five new races of bulbuls (Pycnonotidae) from southern Asia. *J. Wash. Acad. Sci*. 44: 123–125.

Dickinson, E. C. & Christidis, L. (eds.) 2014. *The Howard and Moore complete checklist of the birds of the world*, vol. 2. Fourth edn. Aves Press, Eastbourne.

Dickinson, E. C. & Dekker, R. W. R. J. 2002. Systematic notes on Asian birds. 25. A preliminary review of the Pycnonotidae. *Zool. Verhand*. 340: 93–114.

Eaton, J. A., van Balen, S., Brickle, N. W. & Rheindt, F. E. 2016. *Birds of the Indonesian archipelago: Greater Sundas and Wallacea*. Lynx Edicions, Barcelona.

Edgar, R. C. 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acid Res*. 32: 1792–1797.

Garg, K. M., Tizard, R., Ng, N. S. R., Cros, E., Dejtaradol, A., Chattopadhyay, B., Pwint, N., Päckert, M. & Rheindt, F. E. 2016. Genome-wide data help identify an avian species-level lineage that is morphologically and vocally cryptic. *Mol. Phyl. & Evol*. 102: 97–103.

Hackett, S. 1996. Molecular phylogenetics and biogeography of tanagers in the genus *Ramphocelus* (Aves). *Mol. Phyl. & Evol*. 5: 368–382.

Hartert, E. 1902. On birds from Pahang, eastern Malay Peninsula. *Novit. Zool*. 9: 537–580.

Hoogerwerf, A. 1966. On Moore's olive bulbul (*Pycnonotus simplex* subspp.). *Bull. Brit. Orn. Cl*. 86: 56–60.

Lim, H. C., Gawin, D. F., Shakya, S. B., Harvey, M. G., Rahman, M. A. & Sheldon, F. H. 2017. Sundaland's east-west rain forest population structure: variable manifestations in four polytypic bird species examined using RAD-Seq and plumage analyses. *J. Biogeogr*. 44: 2259–2271.

Lumholtz, C. 1920. *Through central Borneo: an account of two years' travel in the land of the head-hunters between the years 1913 and 1917*. Charles Scribner's Sons, New York.

Mees, G. F. 1986. A list of the birds recorded from Bangka Island, Indonesia. *Zool. Verhand*. 232: 1–174.

Meyer de Schauensee, R. M. 1958. The birds of the Island of Bangka, Indonesia. *Proc. Acad. Nat. Sci. Phil*. 110: 279–299.

Munsell, A. H. 1950. *Munsell book of color*. Munsell Color Co., Inc., Baltimore, MA.

Oberholser, H. C. 1917. The birds of the Anamba Islands. *Bull. US Natl. Mus*. 98: 1–75.

Ridgway, R. 1912. *Color standards and color nomenclature*. Privately published, Washington DC.

Shakya, S. B. & Sheldon, F. H. 2017. The phylogeny of the world's bulbuls (Pycnonotidae) inferred using a supermatrix approach. *Ibis* 159: 498–509.

Shakya, S. B., Haryoko, T., Burner, R. C., Prawiradilaga, D. M. & Sheldon, F. H. 2018. Preliminary assessment of community composition and phylogeographic relationships of the birds of the Meratus Mountains, south-east Borneo, Indonesia. *Bull. Brit. Orn. Cl*. 138: 45–66.

Sheldon, F. H. 2015. Gazetteer and site-based history of the ornithology of Sabah, Malaysian Borneo. *Occ. Pap. Mus. Nat. Sci. Louisiana State Univ*. 86: 1–91.

Sheldon, F. H., Lim, H. C. & Moyle, R. G. 2015. Return to the Malay Archipelago: the biogeography of Sundaic rainforest birds. *J. Orn*. 156: 91–113.

Smythies, B. E. 1960. *The birds of Borneo*. Oliver & Boyd, London.

Stamatakis, A. 2014. RAxML version 8: a tool for phylogenetic analysis and post-analysis for large phylogenetic trees. *Bioinformatics* 30: 1312–1313.

Voous, K. H. 1961. Birds collected by Carl Lumholtz in eastern and central Borneo. *Zool. Mus., Univ. of Oslo Contrib.* 71: 127–180.

Wells, D. R. 2007. *The Birds of the Thai-Malay Peninsula*, vol. 2. Christopher Helm, London.

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