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Taxonomic revision of the Square-tailed Drongo species complex (Passeriformes: Dicruridae) with description of a new species from western Africa

JÉRÔME FUCHS[1,5], MORY DOUNO[2], RAURI C.K. BOWIE[3] & JON FJELDSÅ[4]

[1]*Institut Systématique Evolution Biodiversité (ISYEB), Muséum national d'Histoire naturelle, CNRS, Sorbonne Université, EPHE, 57 rue Cuvier, CP51, 75005 Paris, France.*
[2]*Centre de Gestion de l'Environnement des monts Nimba et Simandou / Ministère de l'Environnement, des Eaux et Forêts, Conakry, Guinée-Conakry.*
[3]*Museum of Vertebrate Zoology and Department of Integrative Biology, 3101 Valley Life Science Building, University of California, Berkeley, CA 94720-3160, USA*
[4]*Center for Macroecology, Evolution and Climate, Natural History Museum of Denmark, University of Copenhagen, Copenhagen, Denmark.*
[5]*Corresponding author. E-mail: fuchs@mnhn.fr*

Abstract

We describe a new species of drongo in the Square-tailed Drongo (*Dicrurus ludwigii*) complex using a combination of biometric and genetic data. The new species differs from previously described taxa in the Square-tailed Drongo complex by possessing a significantly heavier bill and via substantial genetic divergence (6.7%) from its sister-species *D. sharpei*. The new species is distributed across the gallery forests of coastal Guinea, extending to the Niger and Benue Rivers of Nigeria. We suspect that this taxon was overlooked by previous avian systematists because they either lacked comparative material from western Africa or because the key diagnostic morphological character (bill characteristics) was not measured. We provide an updated taxonomy of the Square-tailed Drongo species complex.

Key words: Dicruridae, western Africa, biometry, mitochondrial DNA, Niger River

Introduction

Determining the species limits of drongos (Family Dicruridae, Genus *Dicrurus*) is often problematic using specimens in museum collections. Most taxa are all-black, so the few diagnostic morphological characters they present has resulted in a particularly turbulent taxonomic history for this clade of passerine birds. Three primary taxonomic revisions of the Square-tailed Drongo complex (*D. ludwigii*) have been published in the past 70 years (Vaurie 1949; Clancey 1976; Fuchs *et al.* 2017a).

In a revision of the Dicruridae as a whole, Vaurie (1949) recognized two subspecies of Square-tailed Drongo, *Dicrurus ludwigii sharpei* Oustalet and *Dicrurus ludwigii ludwigii* (A. Smith). The differences between the two subspecies were attributed to "the presence in *ludwigii* and absence in *sharpei*, of white tips, or traces thereof, on the axillaries and on the small feathers along the inner bend of the wing", as well as differences in iridescence, *sharpei* being duller, dark purplish-blue whereas *ludwigii* is greenish blue-black on the upperparts. Examination of the type series of the subspecies *elgonensis* Van Someren from Sudan and north-eastern Democratic Republic of the Congo (DRC) to Uganda and western Kenya (Vaurie 1949), indicated that the plumage colour of *elgonensis* is similar to that of the subspecies *sharpei* (gloss dull purplish-blue), and unlike that of *ludwigii* (more brightly glossed and greenish-blue), so Vaurie (1949) synonymized *elgonensis* with *sharpei*, agreeing with Macdonald's (1946) independent conclusions. Vaurie (1949) also placed the subspecies *muenzneri* Reichenow (Tanzania and eastern Kenya) in synonymy with *ludwigii* (Zimbabwe, central Mozambique, Malawi, South African and southern Angola). Vaurie (1949) thus considered the subspecies *sharpei* to occur from West Africa and the Democratic Republic of the Congo (except the southeast) east to western Kenya and south to northern Angola, while he

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considered the range of *ludwigii* to be across eastern Africa, from Somalia through coastal Kenya, Tanzania, Mozambique, Zimbabwe to South Africa and westwards through Malawi, southeastern DRC, Zambia and southwestern Angola (Benguela). However, Vaurie (1949) did not have access to material from West Africa, as he only examined specimens from Cameroon, Congo, DRC and western Kenya. In addition, Vaurie's geographical sampling would not have enabled him to determine whether one or two subspecies are present in Angola (in fact, *sharpei* occurs in the north and *ludwigii* in the south; Clancey 1976).

Clancey (1976) described the subspecies *saturnus* Clancey from a male adult collected at Maubi River, Cangandala, Malanje, Angola (9°47' S, 16°41'E). The holotype of *saturnus* possesses a green rather than a strong bluish gloss, suggesting an affinity with the subspecies *ludwigii*. However, Clancey (1976) remarked that "The reduced lustre to the dorsal and ventral surfaces in *saturnus* suggest a closer affinity with the western *D. l. sharpei* than with the three eastern subspecies. However, unlike *D. l. sharpei* the sexes are dissimilar in size." In his distribution range (Figure 1A), Clancey (1976) considered *sharpei* to occur in Ndalatando (Cuanza Norte Province), 200 km west-northwest of the type locality (Cangandala) of *saturnus* and suggested that *saturnus* was "probably intergrading with *sharpei* in the north-west of its range, but not in contact with eastern taxa, i.e., *D. l. tephrogaster* and *D. l. muenzneri*." Clancey (1976) examined specimens from southeastern DRC, which he attributed to *saturnus*. Further inspection of specimens led him to conclude that specimens collected in Kenya, the eastern part of the range of *sharpei*, are indistinguishable from West African specimens, consistent with *sharpei* being broadly distributed across the lowland forests of Africa.

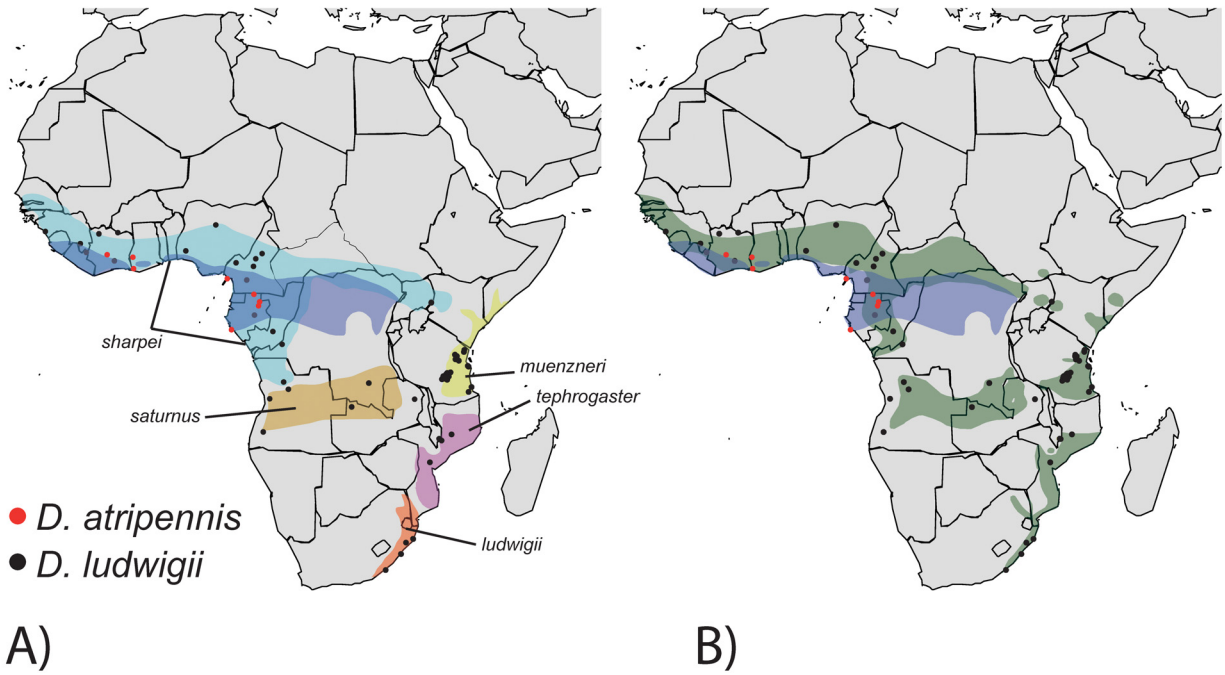

FIGURE 1. Distribution of taxa in *D. ludwigii* as inferred from **A)** Clancey (1976) and **B)** Birdlife International (2013; in green). Nomenclature follows Dickinson and Christidis (2014). Notice differences in: 1) to which subspecies individuals from NW Angola are attributed, and differences in the distribution of *sharpei* in NW Angola; 2) whether distributions of *D. l. ludwigii* and *D. l. tephrogaster* are contiguous or not; and 3) range maps in published sources do not accord well with current distributions based on sampled localities. Black dots represent the sampling *D. ludwigii* localities for individuals included in the molecular analyses. Red dots in the dark blue range in A) and B) represent the sampling localities for the *D. atripennis* individuals included in the molecular analyses.

A recent study of the Square-tailed Drongo suggested a more complicated phylogeographic pattern of the distribution of lineages, challenging traditional taxonomy (Fuchs *et al*. 2017a). First, substantial genetic divergence was recovered between the *sharpei* and *ludwigii* subspecies groups, with *D. ludwigii* recovered as not being monophyletic; the subspecies *sharpei* instead being most closely allied with the monotypic Shining Drongo *D. atripennis* Swainson. Second, the subspecies *saturnus*, as defined by Clancey (1976), was nested within *sharpei*, with limited sequence divergence from individuals sampled in Cameroon. Third, substantial genetic divergence

(Dxy: 6.6%) reflecting a pairwise distance as great as between traditionally recognized species in the genus *Dicrurus* (e.g. Dxy between *D. m. modestus* Hartlaub and *D. macrocercus* Vieillot is 6.6%), was also recovered between *sharpei* individuals sampled east and west of the Niger River. Fourth, genetic structure within the *ludwigii* subspecies groups was recovered, with *muenzneri* and *ludwigii-tephrogaster* (Dxy: 3.8%) possibly representing distinct species (Fuchs *et al*. 2017a). However, one *tephrogaster* haplotype (from Murabue, north-east of Gurue in northern Mozambique) was nested within the *muenzneri* clade, suggesting either that gene flow was occurring between *tephrogaster*/*ludwigii* and *muenzneri* or that the two lineages form a parapatric boundary in northern Mozambique. Further taxonomic conclusions were not possible in Fuchs *et al*. (2017a) because sequences from specimens representative of populations closer to type localities were not available.

Here, we clarify the taxonomic status of members of the Square-tailed Drongo species complex using new sequences obtained from further sampling of individuals from across its distribution range (Figure 1). We include sequences derived from the holotype of *saturnus* and from specimens collected close to the type locality of *elgonensis*, as well as sequences from geographically important specimens examined by Vaurie (1949) and Clancey (1976). We compare the molecular sequence data obtained with an analysis of morphological variation found across localities and, based on the results, describe a new taxon.

Methods

Molecular data. We expanded the mitochondrial data from Fuchs *et al*. (2017a) with the addition of sequences from 32 individuals, 25 of which were sampled from historical museum specimens. Our sampling of the *D. atripennis*/*D. ludwigii* superspecies complex now includes 111 individuals (Table 1). We included the holotype of the subspecies *saturnus* in the analyses, and additional specimens from Angola and Zambia were sequenced, closing important sampling gaps highlighted by Fuchs *et al*. (2017a). Extraction, PCR-amplification and DNA sequencing protocols were identical to those described in Fuchs *et al*. (2017a). Newly generated sequences were submitted to GenBank (accession numbers: MG762566-MG762597).

Phylogenetic analyses. We used BEAST 1.8 to reconstruct the relationships among unique *Dicrurus* haplotypes. The nucleotide substitution model (HKY + G) was selected using Topali (Milne *et al*. 2009). We used the 'strict clock' option and used the rate of divergence estimated for ATP6 (0.026 subs/site/myr/lineage; normal distribution centered on 0.026, standard deviation 0.0025) by Lerner *et al*. (2011).

Molecular species delimitation methods. We used the Bayesian implementation of the general mixed Yule-coalescent model (bGMYC 1.0; Reid & Carstens 2012) to delimit species with our molecular data. This implementation is an extension of the GMYC model (Pons *et al*. 2006) that incorporates gene tree uncertainty by sampling over the posterior distribution of sampled gene trees. We obtained a posterior distribution of ultrametric gene trees of the unique *D. atripennis-D. ludwigii* mitochondrial haplotypes using BEAST v1.8 (Drummond & Rambaut 2007) under an uncorrelated lognormal clock model (0.026 s/s/l/myr, standard deviation = 0.0025). We ran MCMC for 10^7 iterations with sampling of parameters and topologies every 10^3 iterations. The first 10% of the samples from the posterior distribution were removed as the burnin period. We analysed 100 topologies sampled randomly from the posterior distribution and used the default setting in bGMYC. We ran the MCMC chains for $5*10^4$ iterations, with a burnin of $4*10^4$ iterations, and sampled parameters every one hundred iterations.

As an alternative to the bGMYC, we used the Multi-rate Poisson Tree Processes for single-locus species delimitation, as implemented in mPTP (Kapli *et al*. 2017) using both the maximum likelihood and Markov chain Monte Carlo algorithms. We performed the analyses using both the single and multiple rates options. As an input topology, we used a maximum likelihood tree reconstructed using RAxML (RAxML black box, http://embnet.vital-it.ch/raxml-bb/; Stamatakis *et al*. 2008) and a GTR + G model.

Biometric measurements. Jérôme Fuchs (JF) measured five biometric characters: of these, culmen length (bill tip to notch in skull); bill width (at anterior edge of nostril); bill height (at anterior edge of nostril) and tarsus length were measured using a caliper (to the nearest 0.1 mm); and flattened wing-chord using a wing-rule (to the nearest mm). Both the left and right tarsi and wing-chords were measured, with the average retained for further analyses. In cases where the tarsus was broken or one of the wings was missing primaries, we only retained one measurement, the longest for the wing-chord. In total we obtained biometric data from 76 specimens (Supplementary Table 1) spanning the distribution of the species complex.

TABLE 1. List of the *Dicrurus* samples used in the phylogenetic analyses. Georeferencing for FMNH 318618–318620 was based on Mayr & Peters (1999); further georeferencing was done using ACR (2014).Country codes are the Alpha-2 codes from the International Organization for Standardization (source: https://www.iso.org/obp/ui/#search/code/)

Species	subspecies	Institution	Tissue/Ring /Voucher Number	Locality	Latitude	Longitude	Country
ludwigii	*ludwigii*	MVZ	160409	Dwesa Reserve	-32.304	28.829	ZA
ludwigii	*ludwigii*	MVZ	JF2673	Entumeni Forest, 12Km from Eshowe	-28.887	31.377	ZA
ludwigii	*ludwigii*	MVZ	JF2675	Entumeni Forest, 12Km from Eshowe	-28.887	31.377	ZA
ludwigii	*ludwigii*	MVZ	CV37680	Futulala Park, St Lucia	-28.433	32.267	ZA
ludwigii	*ludwigii*	MVZ	JF912	Pennington and Umdoni Golf	-30.309	30.751	ZA
ludwigii	*ludwigii*	MVZ	JF923	Pennington and Umdoni Golf	-30.309	30.751	ZA
ludwigii	*ludwigii*	MVZ	JF986	Pennington and Umdoni Golf	-30.309	30.751	ZA
ludwigii	*muenzneri*	ZMUC	143102	Amani Nature Reserve	-5.100	38.613	TZ
ludwigii	*muenzneri*	ZMUC	143105	Amani Nature Reserve	-5.100	38.613	TZ
ludwigii	*muenzneri*	ZMUC	143112	Amani Nature Reserve	-5.100	38.613	TZ
ludwigii	*muenzneri*	ZMUC	123459	Gombero 1750 m, Nguu	-5.467	37.483	TZ
ludwigii	*muenzneri*	ZMUC	138108	Kanga Forest Reserve	-5.983	37.700	TZ
ludwigii	*muenzneri*	ZMUC	122421	Katemele Forest	-8.133	36.017	TZ
ludwigii	*muenzneri*	ZMUC	121937	Kawemba Forest	-8.150	36.033	TZ
ludwigii	*muenzneri*	ZMUC	121938	Kawemba Forest	-8.150	36.033	TZ
ludwigii	*muenzneri*	ZMUC	137617	Kilindi Forest, Nguu Mts	-5.567	37.567	TZ
ludwigii	*muenzneri*	ZMUC	136513	Kilombero West Forest	-8.192	36.683	TZ
ludwigii	*muenzneri*	ZMUC	121877=136512	Kilombero West Forest	-8.192	36.683	TZ
ludwigii	*muenzneri*	ZMUC	123460	Lulago, Nguu mts.	-5.650	37.650	TZ
ludwigii	*muenzneri*	ZMUC	121127	Lutindi, Mt. Nilo	-4.867	38.633	TZ
ludwigii	*muenzneri*	ZMUC	119246	Mhonda 700 m	-6.217	37.967	TZ
ludwigii	*muenzneri*	MVZ	A99725	Mt Nilo Peak, East Usambara	-4.869	38.65	TZ
ludwigii	*muenzneri*	ZMUC	137066	Nambiga Forest	-8.583	36.483	TZ
ludwigii	*muenzneri*	ZMUC	140400	Ndundulu forest reserve, Matumbo camp	-7.800	36.500	TZ
ludwigii	*muenzneri*	ZMUC	138762	Ndundulu Forest Reserve, Waller's Camp, Udzungwa Mts, 1550 m	-7.800	36.500	TZ
ludwigii	*muenzneri*	ZMUC	138763	Ndundulu Forest Reserve, Waller's Camp, Udzungwa Mts, 1550 m	-7.800	36.500	TZ

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TABLE 1. (Continued)

Species	subspecies	Institution	Tissue/Ring /Voucher Number	Locality	Latitude	Longitude	Country
ludwigii	*muenzneri*	ZMUC	138778	Ndundulu Forest Reserve, Waller's Camp, Udzungwa Mts, 1550 m	-7.800	36.500	TZ
ludwigii	*muenzneri*	ZMUC	140432	Ndundulu, Matumbo juu	-7.800	36.500	TZ
ludwigii	*muenzneri*	ZMUC	119468	Ngarama forest, Lindi; inland of Mtwara	-9.500	39.550	TZ
ludwigii	*muenzneri*	ZMUC	147791	Ngologoro mts, Udzungwa mts 1100 m, Iringa	-7.690	36.890	TZ
ludwigii	*muenzneri*	ZMUC	147792	Ngologoro mts, Udzungwa mts 1100 m, Iringa	-7.690	36.890	TZ
ludwigii	*muenzneri*	ZMUC	132870	Nguru South Forest Reserve	-6.050	37.550	TZ
ludwigii	*muenzneri*	ZMUC	136199	Nguru South Forest Reserve	-6.050	37.550	TZ
ludwigii	*muenzneri*	ZMUC	136209	Nguru South Forest Reserve	-6.050	37.550	TZ
ludwigii	*muenzneri*	ZMUC	137454	Nguru South Forest Reserve	-6.050	37.550	TZ
ludwigii	*muenzneri*	ZMUC	121065	Nkubege Coastal Forest	-6.950	39.167	TZ
ludwigii	*muenzneri*	ZMUC	121095	Nkubege Coastal Forest	-6.950	39.167	TZ
ludwigii	*muenzneri*	ZMUC	121096	Nkubege Coastal Forest	-6.950	39.167	TZ
ludwigii	*muenzneri*	ZMUC	133158	Nyamiwono, Ukami forest	-7.883	36.400	TZ
ludwigii	*muenzneri*	ZMUC	133255	Nyamiwono, Ukami forest	-7.883	36.400	TZ
ludwigii	*muenzneri*	ZMUC	141041	Pugu Forest	-6.883	39.083	TZ
ludwigii	*muenzneri*	ZMUC	141043	Pugu Forest	-6.883	39.083	TZ
ludwigii	*muenzneri*	ZMUC	141055	Pugu Forest	-6.883	39.083	TZ
ludwigii	*muenzneri*	ZMUC	141056	Pugu Forest	-6.883	39.083	TZ
ludwigii	*muenzneri*	ZMUC	119465	Rondo Forest	-10.100	39.183	TZ
ludwigii	*muenzneri*	ZMUC	122632	Udzungwa Scarp	-8.367	35.967	TZ
ludwigii	*muenzneri*	ZMUC	123639	Udzungwa Scarp	-8.367	35.967	TZ
ludwigii	*muenzneri*	ZMUC	116142	Uhafiwa	-8.517	35.867	TZ
ludwigii	*muenzneri*	ZMUC	124059	Uhafiwa	-8.517	35.867	TZ
ludwigii	*muenzneri*	ZMUC	124099	Uhafiwa	-8.517	35.867	TZ
ludwigii	*muenzneri*	ZMUC	121652	Uhafiwa 1390 m	-8.517	35.867	TZ
ludwigii	*muenzneri*	ZMUC	133281	Vigolo Juu Forest	-7.883	36.400	TZ

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TABLE 1. (Continued)

Species	subspecies	Institution	Tissue/Ring /Voucher Number	Locality	Latitude	Longitude	Country
ludwigii	*saturnus*	DNSM	20518 (holotype)	Maubi River, Cangandala	-9.783	16.683	AO
ludwigii	*saturnus*	FMNH	224624	Gabela, 15 km S, Cuanza Sul	-10.960	14.371	AO
ludwigii	*saturnus*	FMNH	224633	Huila, 15 km S, Huila	-15.111	13.563	AO
ludwigii	*saturnus*	MNHN	ZO 1957-104	Mubale, Parc National de l'Upemba	-9.000	26.750	CD
ludwigii	*saturnus*	MNHN	ZO 1957-105	Katongo, Parc National de l'Upemba	-9.000	26.750	CD
ludwigii	*saturnus*	FMNH	205665	Muzyatama, 4700 ft, Lundazi, Eastern	-11.017	32.450	ZM
ludwigii	*saturnus*	FMNH	219776	Mwinilunga, North Western	-12.000	24.583	ZM
ludwigii	*sharpei*	FMNH	220966	Duque de Braganca, 25 km N, 15 km E, Malanje	-8.874	16.086	AO
ludwigii	*sharpei*	FMNH	220971	Duque de Braganca, 25 km N, 15 km E, Malanje	-8.874	16.086	AO
ludwigii	*sharpei*	MCCI	3370	Cascades, Forêt Classé du Comoé-Leraba, Camp de Chasse	9.750	-4.583	BF
ludwigii	*sharpei*	FMNH	318618	Nkiene	-4.167	15.917	CD
ludwigii	*sharpei*	FMNH	318619	Nkiene	-4.167	15.917	CD
ludwigii	*sharpei*	FMNH	318620	Nkiene	-4.167	15.917	CD
ludwigii	*sharpei*	FMNH	213547	Djambala, Bateke Plateau, 2400 ft, Plateaux	-2.547	14.753	CG
ludwigii	*sharpei*	FMNH	285741	Mandinani, mts E	9.617	-6.950	CI
ludwigii	*sharpei*	MNHN	ZO 1969-239	Lamto	6.217	-5.017	CI
ludwigii	*sharpei*	FMNH	273111	Sangmélima, Sud	2.936	11.986	CM
ludwigii	*sharpei*	FMNH	273112	Sangmélima, Sud	2.936	11.986	CM
ludwigii	*sharpei*	FMNH	273114	Yoko, Centre	5.536	12.321	CM
Ludwigii	*sharpei*	FMNH	273115	Yoko, Centre	5.536	12.321	CM
ludwigii	*sharpei*	UCLA	KN98196	Tibati	6.80	12.613	CM
ludwigii	*sharpei*	UCLA	KN99579	Ngoundaba Ranch	7.130	13.420	CM
ludwigii	*sharpei*	BMNH	1966.16.5812	Bamenda	5.970	10.158	CM
ludwigii	*sharpei*	BMNH	1966.16.5814	Bamenda	5.970	10.158	CM
ludwigii	*sharpei*	MNHN	ZO 2005-1232				CM

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TABLE 1. (Continued)

Species	subspecies	Institution	Tissue/Ring /Voucher Number	Locality	Latitude	Longitude	Country
ludwigii	*sharpei*	FMNH	189397	Yaoundé, Centre	3.836	11.522	CN
ludwigii	*sharpei*	PFIAO (M. Melo)	G3M17				GA
ludwigii	*sharpei*	MNHN	ZO 2014-017	Forest edge, close to Dhôti Village, Sous-Préfecture de Khorira	9.885	-13.631	GN
ludwigii	*sharpei*	MNHN	ZO 2014-019	Forest edge, close to Dhôti Village, Sous-Préfecture de Khorira	9.885	-13.631	GN
ludwigii	*sharpei*	MNHN	ZO 1960-3561	Sérédou	8.383	-9.300	GN
ludwigii	*sharpei*	FMNH	200522	Mt Elgon, Western	1.133	34.550	KE
ludwigii	*sharpei*	FMNH	186842	Ganta	7.286	-8.531	LR
ludwigii	*sharpei*	FMNH	186843	Ganta	7.286	-8.531	LR
ludwigii	*sharpei*	NHMO	BI-29140	Ibadan	7.483	3.883	NG
ludwigii	*sharpei*	NHMO	BI-29153	Ibadan	7.483	3.883	NG
ludwigii	*sharpei*	BMNH	1964.15.2	Anara Forest, Kaduna	10.707	7.637	NG
ludwigii	*sharpei*	MNHN	ZO 1947-430	Mwinilunga	-12.000	24.583	ZM
ludwigii	*tephrogaster*	FMNH	447934	Likhubula Forestry Camp, Mulanje Mt, Mulanje	-15.942	35.502	MW
ludwigii	*tephrogaster*	FMNH	447933	Rua River Valley, above Lujeri Tea Estate, Mulanje Mt, Mulanje	-15.974	35.653	MW
ludwigii	*tephrogaster*	FMNH	447935	Rua River Valley, above Lujeri Tea Estate, Mulanje Mt, Mulanje	-15.974	35.653	MW
ludwigii	*tephrogaster*	MVZ	RCKB1371	Tinyade Estate, Mulanje Mt	-15.945	35.543	MW
ludwigii	*tephrogaster*	FMNH	481439	Gorongosa Mt, Montane Forest Camp, Sofala Province	-18.897	34.359	MZ
ludwigii	*tephrogaster*	FMNH	481440	Gorongosa Mt, Montane Forest Camp, Sofala Province	-18.897	34.359	MZ
ludwigii	*tephrogaster*	FMNH	481438	Gorongosa Mt, Murombodzi Waterfall Camp, Sofala Province	-18.897	34.359	MZ
ludwigii	*tephrogaster*	FMNH	438648	Murabue, 6 km N, 10.8 km E Gurue	-15.400	37.067	MZ
ludwigii	*tephrogaster*	FMNH	438649	Murabue, 6 km N, 10.8 km E Gurue	-15.400	37.067	MZ
atripennis		UCLA	KN20172	Parc National de la Marahoué	7.025	-5.947	CI

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TABLE 1. (Continued)

Species	subspecies	Institution	Tissue/Ring /Voucher Number	Locality	Latitude	Longitude	Country
atripennis		LSUMNS	B-27116	Fako District, Small Mount Cameroon, above Etome	4.020	9.070	CM
atripennis		MNHN	ZO 1983-749	Bélinga, Makokou, Ogoué Ivingo	1.132	13.117	GA
atripennis		MNHN	ZO 1983-746	Bélinga, Makokou, Ogoué Ivingo	1.132	13.117	GA
atripennis		MNHN	ZO 1983-747	Lata, Makokou CNRS	0.633	12.983	GA
atripennis		USNM	630795	Louango National Park	-2.340	9.598	GA
atripennis		USNM	630796	Louango National Park	-2.340	9.598	GA
atripennis		USNM	630808	Louango National Park	-2.340	9.598	GA
atripennis		FMNH	389435	Minvoul, 31 km ESE, along IOBT trail (PK 29), 600 m	2.069	12.401	GA
atripennis		KUNHM	110972	Ankasa Conservation Area	5.282	-2.640	GH
atripennis		KUNHM	110971	Ankasa Conservation Area	5.282	-2.640	GH
atripennis		LSUMNS	B-45252	26 km SW Goaso	6.710	-2.730	GH
Outgroups							
adsimilis	*adsimilis*	DNSM	39462				ZA
adsimilis	*divaricatus*	NHMO	Nig12_1360				NG
adsimilis	*fugax*	FMNH	447943				MW
aeneus		MNHN	4-3A				TH
balicassius	*abraensis*	ZMUC	119543				PH
bracteatus		UWBM	68045				PG
forficatus	*forficatus*	FMNH	430202				MG
leucophaeus		MNHN	ZO 2013-106				LA
macrocercus		UWBM	85103				MP
modestus	*atactus*	LSUMNS	B-45271				GH
modestus	*modestus*	MNHN	BE06847				ST
paradiseus		MNHN	JF1776				VN
remifer		MNHN	JF1897				VN

We performed a principal component analysis (PCA) on the five variables using the *prcomp* function in R.3.0.1 (R Core Team 2013). As some of our taxa are represented by a limited number of individuals, we tested for significant differences among populations using the non-parametric Mann-Whitney-Wilcoxon test in R.3.0.1 (R Core Team 2013). Culmen length measurements for 11 additional specimens were provided by G. Boano (MCCI) and M. Adams (NHM). We performed the Mann-Whitney-Wilcoxon tests with and without these additional specimens.

Results

Molecular analyses. The tree obtained from the phylogenetic analyses of unique ATP6 haplotypes recovered three primary clades within the *D. atripennis*/*D. ludwigii* superspecies (Figure 2). The first clade comprised *D. atripennis* individuals (PP: 1.0) within which there is strong genetic structure corresponding to Upper (C1) and Lower Guinea Forest (C2) clades, separated by the Dahomey Gap (Fuchs *et al*. 2017a). The second clade (Clade A) consisted of all individuals sampled in Tanzania (*D. l. muenzneri*), Mozambique (*D. l. muenzneri*, *D. l. tephrogaster, D. l. saturnus*), southern Malawi (*D. l. tephrogaster*), South Africa (*D. l. ludwigii*), Zambia (*D. l. saturnus*) and southern Angola (*D. l. saturnus*). The third clade (Clade B) consisted of all individuals sampled in Liberia, Ivory Coast, Guinea, Burkina Faso, Nigeria, Cameroon, Gabon, parts of northern Angola (*D. l. sharpei*), Kenya (*D. l. elgonensis*), and the Katanga region of DR Congo [theoretically *D. l. saturnus* according to current classifications, e.g. Dickinson & Christidis (2014)]. As in Fuchs *et al*. (2017a), *D. ludwigii sensu lato* was not monophyletic since *D. l. sharpei/D. l. elgonensis* is more closely related to *D. atripennis* than to the southern and eastern population of *D. ludwigii,* although this topology did not receive statistical support (PP: 0.61).

Clade A is comprised of four lineages with a strong geographic and taxonomic component. The first lineage (*muenzneri*, PP: 1.0) consists of all individuals attributed, based on distribution, to the subspecies *muenzneri*, and one individual from northern Mozambique attributed within the range of the subspecies *tephrogaster.* The *muenzneri* lineage was sister (PP: 1.0) to the clade comprising the subspecies *D. l. saturnus* (southern Angola, Zambia, northern Mozambique), *D. l. tephrogaster* (central and northern Mozambique) and *D. l. ludwigii* (eastern South Africa). Of note is that *muenzneri* and *saturnus* mtDNA haplotypes have been sampled at the same locality (Gurue, northern Mozambique), within the traditionally delineated range of *D. l. tephrogaster.* The subspecies *saturnus* is the first lineage to branch off (PP: 1.0) and is sister to the clade formed by the individuals representing the subspecies *ludwigii* and *tephrogaster* (PP: 1.0). Clade B was divided into two primary lineages (PP: 1.0) with a strong biogeographic component, with the Niger/Benue river system being the biogeographic divide that separated the two primary Clade B lineages. The first of these two lineages (clade B1) includes all individuals sampled in Liberia, Ivory Coast, Guinea, Burkina Faso, and Nigeria (*D. l. sharpei*); two subclades (B1a and B1b) within clade B1 delimit populations distributed on either side of the Dahomey Gap. The second (clade B2) lineage consists of all individuals sampled in Cameroon, Gabon, northern Angola (*D. l. sharpei*), Kenya (*D. l. elgonensis*) and southeastern DRC (*D. l. saturnus*). Fine-scale genetic structure is found within Clade B2 (clades B2a, PP: 0.83 and B2b, PP: 0.89), but genetic differentiation is limited and the two subclades do not have any clear geographic component. Hence, the phylogenetic data suggest that the subspecies *D. l. sharpei* is not monophyletic, as *D. l. elgonensis* and parts of *D. l. saturnus* are nested within it.

Subspecies *saturnus*, as defined by Clancey (1976; Figure 1), includes individuals that belong to both clades A and B, as DNA sequences derived from specimens collected in southeastern DR Congo are nested within *D. l. sharpei*. However, inclusion of the *D. l. saturnus* holotype (DNSM 20518) in the analyses leads to the suggestion that *D. l. saturnus* is more closely related to the eastern and southern African subspecies of *D. ludwigii*.

Molecular species delimitation methods. The molecular species delimitation method bGMYC, using the mitochondrial haplotypes only, indicated that the current diversity at the species level in the *D. atripennis*-*D. ludwigii* species complex is underestimated, with five versus the present two species recognized at the 0.05 threshold. The five lineages that may represent biological species correspond to: 1) *D. l. muenzneri*; 2) *D. l. ludwigii* (including *D. l. tephrogaster* and part of *D. l. saturnus*); 3) *D. l. sharpei* east of the Niger River; 4) *D. l. sharpei* west of the Niger River; and 5) *D. atripennis*.

The mPTP analyses recovered strikingly different results. Using either a single or multi-rate Poisson process had a strong impact on the number of putative species delimited, either 9 or 19, respectively. There was no

difference between the maximum likelihood and Markov chain Monte Carlo algorithm results and the only significant parameter was single versus multiple rates. Unrealistic results were recovered under both mPTP rate modes, for example, *D. remifer* (Temminck) and *D. aeneus* Vieillot were considered conspecific under the single rate model, whereas *D. atripennis* was split into three species under the multiple rate model analyses. However, consistent with the bGMYC analyses, for both the single and multi-rate models the following lineages were delimited: 1) *D. l. sharpei* lineages distributed on either side of the Niger River were considered to be significantly distinct at the species level; and 2) *D. l. muenzneri*, *D. l. ludwigii* and *D. l. tephrogaster* were considered conspecific. Hence, both the bGMYC and mPTP algorithms recognized at least four putative species: 1) *D. atripennis*; 2) *D. sharpei* west of the Niger River; 3) *D. sharpei* east of the Niger River; and 4) *D. ludwigii* (including *muenzneri, saturnus* and *tephrogaster*). The primary discrepancy between the two species delimitation algorithms is whether *D. l. muenzneri* is classified as a species or a subspecies.

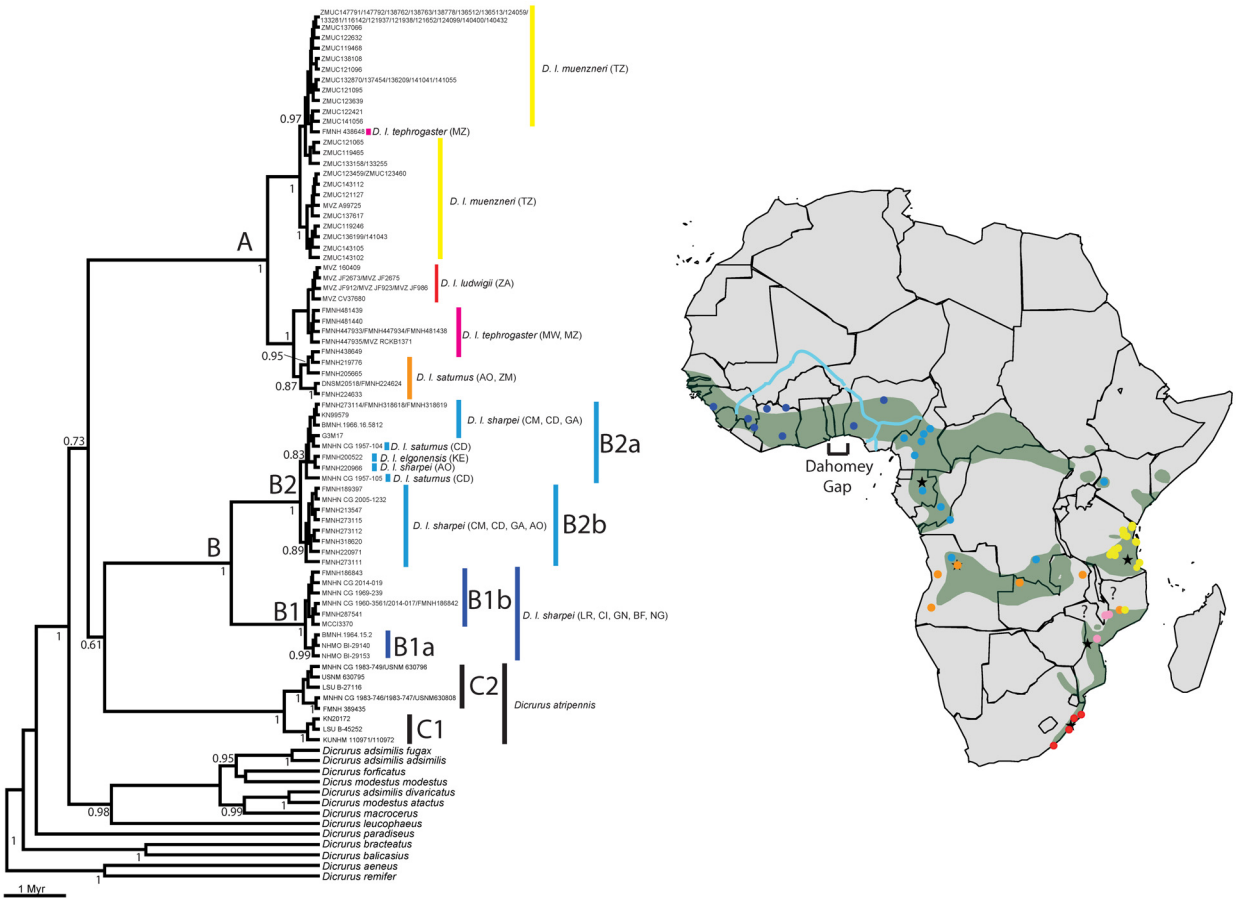

FIGURE 2. Phylogenetic relationships among the unique haplotypes. Sampling points are indicated in colors that refer to the mitochondrial lineages. Locations of type localities are indicated by the stars. Color code: dark blue: *D. occidentalis* sp. nov.; light blue: *D. l. sharpei*; orange: *D. l. saturnus*; pink: *D. l. tephrogaster*; red: *D. l. ludwigii*; yellow: *D. l. muenzneri.* Question marks indicate areas in Mozambique where isolated populations may occur (see Discussion) but where subspecific allocation is unknown. The location of the Dahomey Gap is indicated as well as the location of the Niger/Benue River systems (blue course).

Biometry. The analyses of individual measurements (Table 2, Figure 3, Supplementary Table 1) give four major findings, as follows. First, no significant biometric differentiation exists between the *D. atripennis* individuals distributed across the Dahomey Gap/Niger River (culmen length W=71.5, P=0.32; bill width W=54.5, p=0.12; bill height W=37, P=0.84, tarsus length W=68.5 P=0.09; wing chord W=62.5 P=0.66). Second, the most reliable biometric measurements to discriminate *D. atripennis* from any *D. ludwigii* population are bill height and wing length (Figure 3). Third, significant differences exist in bill characteristics between the *D. l. sharpei* populations distributed west and east of the Niger/Benue River system (culmen length: J.F. measurements only: west clade B2: mean: 23.2 mm, range: 21.9–23.9 mm, east clade B1: mean: 21.0 mm, range: 20.3–21.8 mm; Mann-

Whitney-Wilcoxon test, W = 0, P = 0.0034; all culmen length data: west clade B2: mean: 23.0 mm, range: 21.8–23.9 mm, east clade B1: mean: 20.9 mm, range: 20.0–21.8 mm; Mann-Whitney-Wilcoxon test, W = 0.5, P = $6*10^{-5}$; bill width W = 8.5, P = 0.027; bill height W = 8.5, P = 0.044) but not for tarsus length (W=21, P=0.45) and wing chord (W=24.5, P=0.73). Fourth, *D. l. ludwigii* and *D. l. muenzneri* could not be separated by the biometric data we collected (culmen length W=31, P=0.14; bill width W=51, P=0.88; bill height W=20, P=0.16, tarsus length W=74.5 P=0.30; wing chord W=69.5, P=0.46). We did not compare *D. l. saturnus* as this taxon was only represented by one individual in the biometric data set.

The PCA indicated that *D. l. sharpei* populations distributed west and east of the Niger/Benue River system could be discretely separated based on multivariate analyses from all other *Dicrurus* taxa within the *D. ludwigii* species complex (Figure 4). As in the univariate analyses, no separation could be made using the multivariate analyses between *D. l. muenzneri* and *D. l. ludwigii.*

Based on the genetic divergence (Dxy: 6.6%, Da: 6%) and discrete differences in some biometric measurements (culmen length, bill width, bill height), we here describe a new species that we name:

TABLE 2. Average/ standard deviation and minimum-maximum for five biometric characters for each lineage recognized at the 0.9 level by the bGMYC analyses. The morphological characters are culmen length, bill width at nostril, bill height at nostril, tarsus length (average of the left and right tarsus when possible) and wing chord (average of the left and right chords when possible). All characters but wing length were measured to the nearest 0.1 mm. Wing length was measured to the nearest 0.5 mm.

Lineage	Culmen length	Bill Width	Bill Height	Tarsus Length	Wing Chord
atripennis (West Dahomey Gap)	23.2/0.2(22.9–23.6) (n=5)	6.6/0.3 (6.0–7.1) (n=4)	7.2 /0.25 (6.7–7.3) (n=5)	15.9 /0.1 (15.8–16.1) (n=4)	111.8/3.4 (108.0–118.0) (n=5)
atripennis (East Dahomey Gap)	23.6/0.7 (22.2-24.8) (n=22)	7.0/0.3 (6.3-7.4) (n=18)	7.1/0.2 (6.7-7.5) (n=16)	16.3/0.4 (15.5-17.2) (n=22)	112.6/2.3 (106.5-118.5) (n=22)
sharpei (west of Niger River)	J.F. only 23.2/0.8 (21.9–23.9) (n=7) All measurements 22.0/0.7 (21.8-23.9) (n=9)	7.1/0.3 (6.5–7.4) (n=7)	6.4/0.1 (6.2–6.7) (n=7)	16.15/0.3 (15.7–16.6) (n=7)	106.6/1.7 (104.0–110.0) (n=7)
sharpei (east of Niger River)	J.F. Only: 21.0/0.4 (20.3–21.8) (n=7) All measurements 20.9/0.5 (20.0–21.8) (n=17)	6.4/0.5 (5.8–7.1) (n=8)	5.8/0.4 (5.3–6.6) (n=7)	16.0/0.30 (15.3–16.6) (n=8)	106.1/1.2 (103.0–108.0) (n=8)
ludwigii	22.3/0.4 (21.6–22.7) (n=4)	6.5/0.2 (6.3–6.8) (n=4)	6.5/0.1 (6.4–6.7) (n=3)	16.4/0.04 (16.2–17.1 (n=4)	100.60/1.10 (99.0–102.0) (n=4)
saturnus	21 (n=1)	6.8 (n=1)	6.6 (n=1)	16.15 (n=1)	106.5 (n=1)
muenzneri	21.8/0.6 (20.7–23.5) (n=29)	6.5/0.2 (6.1–6.9) (n=27)	6.3/0.2 (5.7–6.8) (n=27)	16.7/0.3 (15.8–17.7) (n=28)	103.9/5.3 (95.0–115.0) (n=28)

***Dicrurus occidentalis*, Fuchs, Douno, Bowie, and Fjeldså, sp. nov.**

Holotype. MNHN ZO 1960-3561 Female adult. Collected by Raymond Pujol and Jean Roché on 18 December 1959 in Sérédou, Poste 5 (Geo-referenced a posteriori: latitude: 8.383, longitude: -9.300), Macenta Prefecture, Nzérékoré Region, Guinea.

Description of holotype: Colour designations from Smithe (1975; corresponding number in parentheses) when relevant. Forehead black, nape, back, chin, abdomen, breast and throat black with iridescent blue-green, rump close to INDIGO (73), flanks and sides MEDIUM NEUTRAL GRAY (84), rectrices, primaries and secondaries most similar to DUSKY BROWN (19) when examined individually.. The ATP6 sequence derived from the holotype (GenBank accession number: KX133856) was identical to those obtained from the paratype MNHN ZO 2014-017 and FMNH 186842 (non-type specimen), collected in Ganta, Liberia.

Measurements of holotype: Left/right tarsus: 16.6/16.5 mm, left/right wing-chord: 105/ 105 mm, culmen length: 23.9 mm, bill width at anterior end of nostril 7.1 mm, bill depth at anterior end of nostril 6.3 mm.

Paratypes: MNHN ZO 2014-017 Female, adult, collected by M.D. and J.F. within a forest close to a 'garden' (latitude 9.88543, longitude: -13.63058, elevation 26 m) near Dhôti Village, Sous Préfecture de Khorita, Préfecture de Dubréka, Région de Kindia, Guinea, on 5 March 2014. Specimen prepared by J.F. (JF3561), mass 25.0 g, skull pneumatisation 75%, gonads not developed (smooth ovary), no fat deposition, and no evidence of molt; iris color orange-red. Measurements: left/right tarsus 16.4/16.8 mm; left/right wing-chord 104/104 mm; culmen length 22.4 mm; bill-width at anterior end of nostril 7.4 mm; bill-depth at anterior end of nostril 6.5 mm. The ATP6 sequence of the paratype MNHN ZO 2014-017 (Genbank Number: KX133904) is identical to that of the holotype.

MNHN ZO 2014-019 Male, adult. Collected by M.D. and J.F. within a forest close to a 'garden' (latitude 9.88543, longitude: -13.63058, elevation 26 m) near Dhôti Village, Sous Préfecture de Khorita, Préfecture de Dubréka, Région de Kindia, Guinea, on 5 March 2014. Specimen prepared by J.F. (JF3563), mass 24.0 g; skull pneumatisation 100% (adult), testes symmetric, 5 X 3 mm, no fat deposition, and no evidence of molt, iris color red. Measurements: left/right tarsus 16.4/16.2 mm; left/right wing chord 105/105 mm; culmen length 22.8 mm; bill width at anterior end of nostril 7.0 mm; bill depth at anterior end of nostril 6.3 mm. The ATP6 sequence of the paratype MNHN ZO 2014-019 (Genbank Number: KX133905) differs by two substitutions (0.29%) from the holotype MNHN ZO 1960-3561 and paratype MNHN ZO 2014-017.

Supplementary material examined. Additional material examined is listed in Table 3.

Etymology. The name *occidentalis* refers to the species' geographic distribution across western Africa.

English Name: We propose the name Western Square-tailed Drongo.

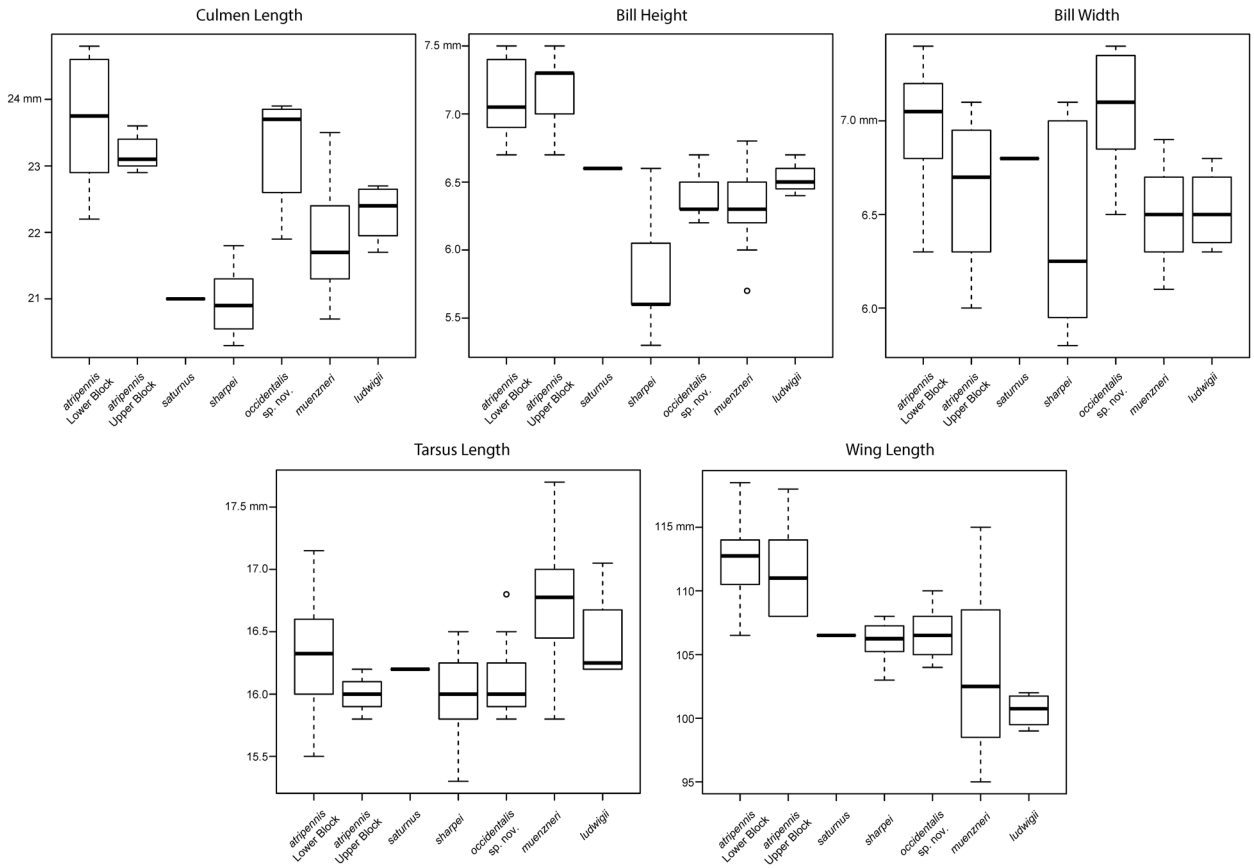

FIGURE 3. Boxplots of the five morphological characters measured by J.F. for the primary lineages from the *D. atripennis*/*D. ludwigii* superspecies.

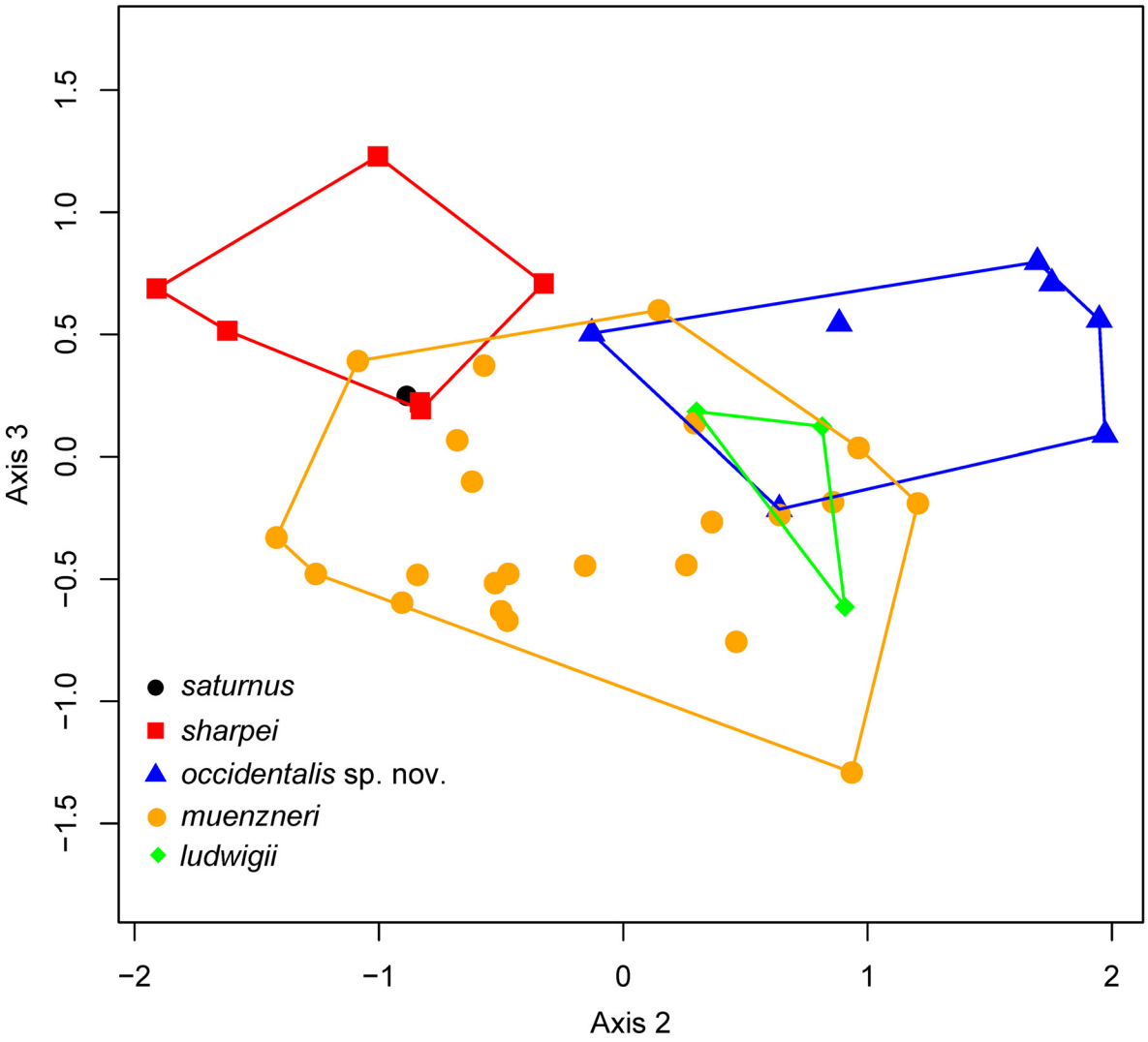

FIGURE 4. Plot of axes 2 and 3 of the Principal Component Analysis (PCA) for the taxa of *D. ludwigii sensu lato*.

Diagnosis. The Western Square-tailed Drongo can be distinguished from its closest and parapatric relative, Sharpe's Drongo (*D. sharpei*), by culmen length (Mann-Whitney test W = 0, P = 0.0034), bill width (W = 8.5, P = 0.03) and bill height (W = 8.5, P = 0.044) (Table 2). Based on available specimens, the Western Square-tailed Drongo could not be diagnosed by plumage characters from, Sharpe's Drongo (*D. sharpei*) (Figure 5). Yet, large genetic divergence was recovered at the studied mitochondrial locus. The new species is characterized by two substitutions in ATP6 that are fixed in *D. occidentalis* and not shared with any other drongo taxa (species or subspecies) included in this study. The two fixed substitutions are: a C-T synonymous transition at position 43 (first codon position) and an A-G transition at position 297 (third codon position) of ATP6. These two substitutions are complemented by 21 additional substitutions in ATP6 that allow differentiation from Sharpe's Drongo but that exhibit various levels of homoplasy across the full data set. In areas where the Western Square-tailed Drongo and Shining Drongo co-occur, the two species can be distinguished by plumage color on the upperparts (*D. occidentalis*: Gloss Dull Purplish Blue, *D. atripennis* Steel Green Gloss; Vaurie 1949) and bill height (*D. occidentalis*: 6.2–6.7 mm, *D. atripennis*: 6.7–7.3 mm). No other lineages from the *D. ludwigii*/*D. atripennis* species complex occur in western Africa. The newly described species can be diagnosed from other drongo species occurring in western Africa by plumage color (*D. occidentalis*: Gloss Dull Purplish Blue, *D. adsimilis divaricatus* M. H. C. Lichtenstein: Glossy Black; *D. modestus coracinus* J. P. Verreaux & J. B. E. Verreaux, Dull Velvety Black; *D. modestus atactus* Oberholser: intermediate between the gloss of *D. a. divaricatus* and the dull velvet of

D. m. coracinus; color discrimination from Vaurie 1949) and measurements (e.g. wing length: *D. occidentalis*: 104–110 mm—this study; *D. modestus atactus*: 129–140 mm, *D. modestus coracinus*: 122–138 mm; *D. adsimilis divaricatus:*122–136 mm; Vaurie 1949).

Distribution. The Western Square-Tailed Drongo inhabits secondary forest and gallery forest from coastal Guinea to Nigeria. Based on rather scattered locality records, the eastern distribution limit appears to be bounded by the Niger/Benue River system in Nigeria. Based on the sequenced specimens and our examination of specimens in museum collections, there is at present no known locality where *D. occidentalis* and *D. sharpei* co-occur (Table 3).

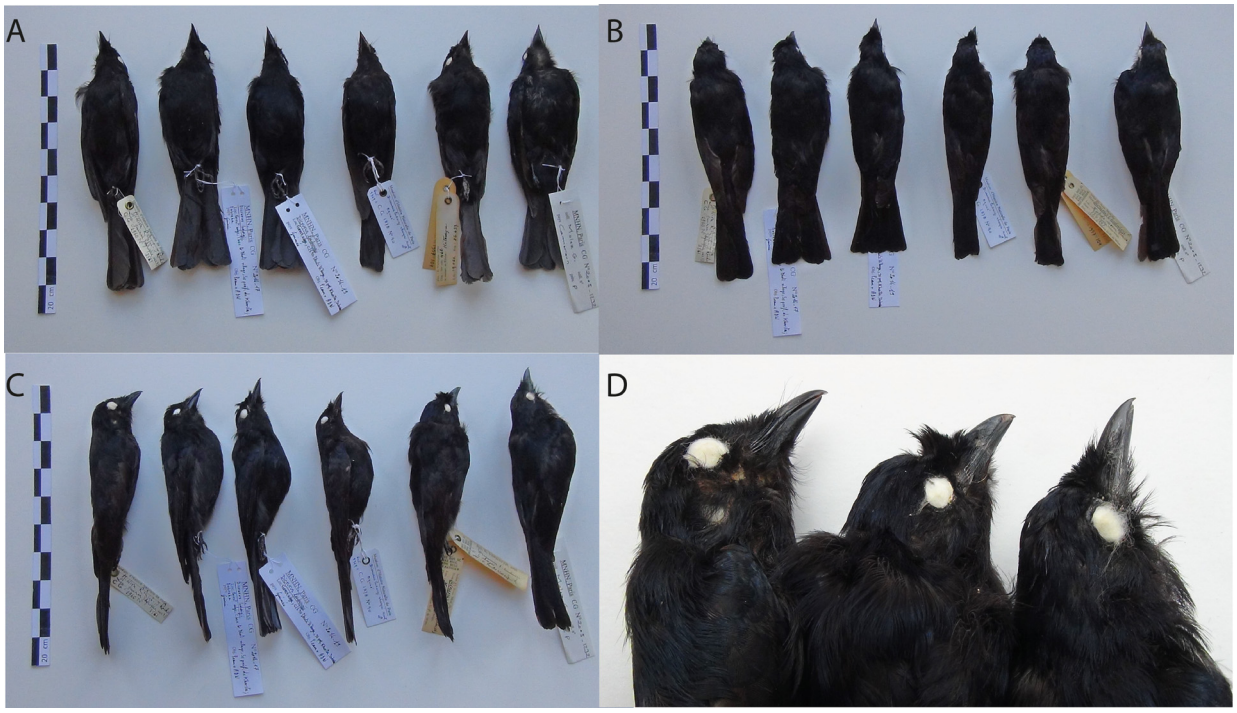

FIGURE 5. Specimens attributed to *D. occidentalis* and *D. sharpei* on ventral (A), dorsal (B) and lateral (C) views. From left to right: *D. occidentalis* MNHN ZO 1960-3561 (holotype); MNHN ZO 2014-017 (paratype); 2014-019 (paratype); *D. sharpei* MNHN ZO 1878-90; MNHN ZO 1965-881; MNHN ZO 1957-104; MNHN ZO 2005-1232. The different bill shape between *D. occidentalis* and *D. sharpei* is exemplified in (D). From left to right: *D. occidentalis* MNHN ZO 1960-3561 (holotype); *D. sharpei* MNHN ZO 1957-104; and MNHN ZO 2005-1232.

Conservation. The description of the new species reduces the former distribution of *D. sharpei* (clade B). The ranges of both species are still extensive, however, encompassing several countries. The two species have broad habitat preferences (dense woodland, secondary forest, gallery forest) that do not appear to be under immediate threat. The combination of large ranges and no immediate threat from extensive habitat transformation suggests that both species should be considered as of 'Least Concern' by the IUCN. Further work may be needed to assess connectivity and gene flow among populations of *D. occidentalis* (B1) distributed either side of the Dahomey Gap, as the mitochondrial data suggest the presence of two subclades (B1a and B1b) across this biogeographic barrier (Figure 2).

Vocalizations. We only found one vocalization of *Dicrurus occidentalis* on xeno-canto (http://www.xeno-canto.org/), a call (XC353659) from Dande, Kédougou, Sénégal (latitude: 12.3638, longitude -12.3244, 23 March 2016); we were unable to record the birds in the field ourselves. Further work is needed to describe the vocalizations of this taxon. Four recordings are deposited on xeno-canto for *D. sharpei* (Cameroon—XC99706 and XC99707; Kenya—C101207 and XC101208). *Dicrurus* are known to have large repertoires and abilities to mimic other birds (Goodale & Kotagama 2006; Flower *et al*. 2010).

Discussion

The rate of description of new bird species has accelerated over the past two decades (Fjeldså 2013), in part due to continued efforts to collect specimens by avian systematists and the development of molecular techniques (Fujita *et al.* 2012; Rocha *et al*. 2014). Collection and analysis of molecular DNA data enable detection of lineages that are difficult to distinguish using morphological data alone or when vocalizations are highly variable, not available, or include mimics (as in drongos). Our present data set represents an extension of a previous study that addressed the phylogeography of the Shining-Square-tailed Drongo superspecies complex, in which we suggested the presence of an undescribed taxon (Fuchs *et al*. 2017a). The recognition of new taxa in sub-Saharan Africa is uncommon relative to other areas around the globe (e.g. South America, Indonesia; Fjeldså 2013) and most new African taxa have come from the Lower Guinean Forest Block (Beresford *et al.* 1999; Schmidt *et al*. 2008) or the mountains of eastern and central Africa (Jensen 1983; Dinesen *et al*. 1994; Fjeldså & Kiure 2003; Beresford *et al*. 2004; Bowie & Fjeldså 2005; Fjeldså *et al*. 2006; Bowie *et al*. 2009, 2016; Voelker *et al*. 2010, 2017). All these cases underscore the need for continued collecting of voucher specimens in sub-Saharan Africa (Bates *et al*. 2004).

TABLE 3. List of verified specimens and localities attributed to *D. occidentalis* based on genetic and/or biometric data (included in the PCA). Culmen measurement for MCCI 3370 was 22.6 mm (pers. com. G. Boano) and BMNH 1964.15.2 was 21.8 mm (pers. com. M. Adams); these specimens were not included in the PCA.* after specimen number indicates blood samples. Country codes are the Alpha-2 codes from the International Organization for Standardization (source: https://www.iso.org/obp/ui/#search/code/).

Species	Museum/specimen number	Locality	Country	Latitude	Longitude	DNA	Morphology
occidentalis	MCCI 3370	Cascades, Forêt Classé du Comoé-Leraba, Camp de Chasse	BF	9.750	-4.583	X	X
occidentalis	MNHN ZO 1969-239	Lamto, Agnéby-Tiassa	CI	6.217	-5.017	X	X
occidentalis	FMNH 285741	Mandinani, mts. E	CI	9.617	-6.950	X	
occidentalis	MNHN ZO 1976-1205bis	Vallée du Bandama District, Gbeke	CI				X
occidentalis	MNHN ZO 1976-1206bis		CI				X
occidentalis	MNHN ZO 2014-017	close to Dhôti Village, Sous-Préfecture de Khorira	GN	9.885	-13.631	X	X
occidentalis	MNHN ZO 2014-019	close to Dhôti Village, Sous-Préfecture de Khorira	GN	9.885	-13.631	X	X
occidentalis	MNHN ZO 1960-3561	Sérédou	GN	8.383	-9.300	X	X
occidentalis	FMNH 186842	Ganta	LR	7.286	-8.531	X	
occidentalis	FMNH 186843	Ganta	LR	7.286	-8.531	X	
occidentalis	NHMO BI-29140*	Ibadan	NG	7.483	3.883	X	
occidentalis	NHMO BI-29153*	Ibadan	NG	7.483	3.883	X	
occidentalis	BMNH 1964.15.2	Anara Forest, Kaduna	NG	10.707	7.636	X	X
occidentalis	MNHN ZO 1983-226	Ziguinchor, Oussouyé	SN	12.490	-16.544		X

This new species of drongo was overlooked by taxonomists despite *D. occidentalis* being the morphologically most differentiated species in the *D. ludwigii-D. atripennis* complex. This is likely due to Vaurie (1949) not having access to material from western Africa and so could only examine specimens from Cameroon, Congo, DRC and western Kenya. Hence, he could not detect in his measurements the discrete variation in culmen length in *D. occidentalis* compared to *D. sharpei.* Clancey (1976), in contrast, had access to several specimens from within the range of *D. occidentalis*, but he did not measure bill length, but instead examined variation in plumage and tail length.

Taxonomy of the northern and western groups. We here describe a new taxon using biometric and genetic (mitochondrial ATP6 locus) data that clearly enable diagnosis of a discret set of characters that render *D. occidentalis* distinct from other drongo specimens collected throughout the geographical range of each of the other taxa. We included type specimens of the other taxa or, when this was not possible, specimens sampled close to type

localities. Our sampling suggests that the range of *D. occidentalis* is limited on its eastern side by the Niger-Benue River drainage, although it seems possible that it could extend to Lake Chad or to the Cameroon Volcanic Line to the east.

Deep phylogeographic breaks can occur by chance for a mitochondrial locus without geographic barriers to gene flow (Irwin 2002). Yet, the same area (Niger River/Benue drainage extending to eastern Nigeria and Lake Chad) is a putative phylogeographic break for multiple other bird taxa (e.g., *Campethera nivosa* (Swainson), *Dendropicos obsoletus* (Wagler), *Campethera punctuligera* (Wagler), and *Dicrurus adsimilis divaricatus*; Fuchs & Bowie 2015; Fuchs *et al*. 2017b, 2018). This suggests that this phylogeographic break reflects a past habitat discontinuity that has led to the formation of a suture zone, where multiple species now meet in secondary contact. The level of genetic divergence recovered between *D. occidentalis* and *D. sharpei* is of the same order of magnitude as the mitochondrial divergence among undisputed species in the *D. adsimilis* superspecies complex (*D. occidentalis*/*D. sharpei*: Dxy 6.6%; *D. forficatus*/*D. adsimilis* Dxy 6.5%; *D. modestus atactus*/*D. macrocercus* Dxy 5.4%).

According to our divergence time estimates, *D. occidentali*s and *D. sharpei* diverged about 1.3 mya. During this time, multiple climatic oscillations occurred, which could have led to isolation and divergence of populations followed by remixing of gene pools. Such a phenomenon, sometimes referred to as 'despeciation' or 'speciation in reverse', detected with the use of molecular sequence data is, now more commonly uncovered in empirical datasets (e.g. Webb *et al*. 2011; Hogner *et al*. 2012; Block *et al*. 2015). In these cases, populations come into secondary contact after having been isolated for some time and exchange genetic material. If no intrinsic or extrinsic barriers to hybridization have developed, then the two lineages will merge. This process is reflected in the mitochondrial phylogeny by the presence of two highly divergent clades that lack any geographic structure across the landscape. In other words, in despeciation, highly divergent mitochondrial haplotypes occur in sympatry across the landscape. This is clearly not what we observe in our dataset as there is strong geographic structure underlying the distribution of haplotypes. Further, the geographical position of the primary mitochondrial DNA break between *D. occidentalis* and *D. sharpei* coincides with the position of genetic breaks observed in other avian species. Finally, given the high pairwise molecular divergence between *D. occidentalis* and *D. sharpei* (Dxy: 6.6%), it is likely that cyto-nuclear incompatibilities could have evolved and may facilitate the completion of the speciation process (Hill 2017).

Indirect evidence for the possibility of 'despeciation' involving *D. sharpei* may also be present in our dataset. Indeed, we recovered two intraspecific clades within *D. sharpei* that differ from each other by more than one percent. Interestingly, individuals from both clades were recovered together in sympatry in Nkiene, DR Congo: (FMNH 318618–318619 Clade B2a, FMNH 318620 Clade B2b), suggesting that populations may have differentiated across the Lower Guinea Forest Block 'refugia' during the Pleistocene (0.7 mya) before coming into secondary contact and possibly merging. This possibility requires further research, with inclusion of additional individuals and markers.

Taxonomy of the 'southern' group. Our understanding of the taxonomy and distribution of the eastern and southern group of taxa has improved over that of Fuchs *et al*. (2017a) with the inclusion of additional samples from Angola and Zambia. Noticeably, our analyses revealed that the range of what is presently considered *D. l. saturnu*s encompass two different lineages, *D. sharpei* in southeastern DRC and northern Angola, and *D. l. saturnus* in southern Angola and Zambia. The three southern African subspecies (*saturnus*, *tephrogaster*, *ludwigii*) form distinct clades in the mitochondrial analyses, but we advocate they be retained under *D. ludwigii*, as genetic divergence is limited. Our analysis and sampling extends the range of *D. l. saturnu*s further east as the subspecies occurs in Mozambique (FMNH 436849), but restricts it to the northern part of the country and thereby indicates that all four subspecies (*muenzneri, saturnus*, *tephrogaster*, *ludwigii*) occur in Mozambique.

The currently recognized distribution of *D. l. saturnus* as conceived by BirdLife International (2013) appears to be particularly misleading in Zambia and northern Mozambique, where museum records and recent field observations (e.g., Serra Jeci area; Ryan & Spottiswoode 2003) suggest that the distribution gap is not as large as depicted and that several isolated populations may occur throughout these areas. Delineating where each of the taxa are distributed across the southern African landscape, given that all four eastern and southern African subspecies meet in Mozambique, will require additional fieldwork and collection of multi-locus genetic data. Such a study offers an important opportunity to learn more about the relative roles that morphology, song and landscape variables play as intrinsic and extrinsic drivers of lineage diversification in African drongos.

The subspecies *muenzneri* is the genetically most divergent lineage in the eastern/southern group. The two

molecular species delimitations methods we used (bGMYC and mPTP) gave slightly different conclusions. Consequently, we consider *muenzneri* to be a subspecies of *D. ludwigii.* Further sampling in the north of Mozambique is needed to understand the interactions and extent of gene flow with *D. l. tephrogaster* and *D. l. saturnus*.

Interactions between the north/eastern and eastern/southern lineages. Two non-sister taxa (*D. ludwigii* and *D. sharpei*) appear to be parapatrically distributed in Angola, southeastern DRC and Zambia, suggesting that the range of *D. l. saturnus*, as described by Clancey (1976), includes two species. Further study is needed to resolve the exact distribution of each lineage and potential interactions (hybridization, competition) between lineages. With respect to these taxa, but also for resolving taxonomic issues of many other taxa, the undertaking of specimen-based inventories in southeastern DRC and Angola would greatly improve our knowledge. Habitat may be an important factor in delimiting the distribution of these species, as *D. sharpei* appears to be mostly restricted to the southern Congolian forest-savanna mosaic, whereas *D. l. saturnus* appears to be primarily restricted to miombo woodland.

Taxonomic implications and update of Fuchs et al. *(2017a).* Based on our phylogenetic results, we here suggest that the subspecies *elgonensis*, van Someren, 1920 should be synonymized with *D. sharpei.* We also update the classification recently proposed in Fuchs *et al.* (2017a) by recognizing *D. l. tephrogaster* and moving the taxon *saturnus* to *D. ludwigii.*

***Dicrurus ludwigii* A. Smith (Common Square-tailed Drongo)**
Dicrurus ludwigii ludwigii A. Smith
Distribution: South Africa to the Limpopo River.
Dicrurus ludwigii tephrogaster Clancey
Distribution: Malawi, southern and central Mozambique.
Dicrurus ludwigii saturnus Clancey
Distribution: Angola (except northwest), northern Zambia, northern Mozambique and potentially parts of Malawi.
Dicrurus ludwigii muenzneri Reichenow
Distribution: Northern Mozambique, Tanzania, eastern Kenya, Somalia.

***Dicrurus sharpei* Oustalet** (includes *elgonensis* Van Someren) (**Sharpe's Drongo)**
Distribution: North and southeastern DRC, Uganda, southern Sudan, western Kenya, to northwestern Angola and Nigeria east of the Niger River and south of the Benue River.

***Dicrurus occidentalis* Fuchs, Douno, Bowie & Fjeldså (Western Square-tailed Drongo)**
Distribution: Senegal to Nigeria (west of the Niger River).

***Dicrurus atripennis* Swainson** (**Shining Drongo)**
Distribution: Sierra Leone to northeastern DRC.

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SUPPLEMENTARY TABLE 1. Measurement details for the specimens included in the biometric analyses. — = not applicable. Culmen measurement for MCCI and BMNH specimens were provided by G. Boano and M. Adams, respectively.

species	subspecies	Institution	Catalog Number	Culmen Length	BillWidth (nostril)	Bill Height (nostril)	Tarsus Length Left	Tarsus Length Right	Tarsus Length Average	Wing Chord Left	Wing Chord Right	Wing Chord Average	Locality	Country
atripennis		NRM	48146	22.5	7	7	16.9	16.9	16.9	108	105	106.5	Malisavo, Ituri	CD
atripennis		NRM	48149	23.2	7.3	7.5	16.9	16.9	16.9	110	110	110	Wambutti, Ituri	CD
atripennis		NRM	uncatalogued	23.8	-	—	16.3	16.3	16.3	112	112	112	Beni, Kivu	CD
atripennis		NRM	uncatalogued	24.8	7.3	—	16.8	16.8	16.8	112	112	112	Beni, Kivu	CD
atripennis		NRM	uncatalogued	24.8	—	—	16.2	16.5	16.35	113	113	113	Beni, Kivu	CD
atripennis		NRM	48143	24.7	—	—	16.5	16.5	16.5	113	113	113	Beni, Kivu	CD
atripennis		NRM	uncatalogued	24.6	6.8	6.8	16.6	16.6	16.6	113	113	113	Beni, Kivu	CD
atripennis		NRM	uncatalogued	24.8	7.2	-	16.9	17.2	17.05	113	113	113	Beni, Kivu	CD
atripennis		NRM	48148	22.8	6.8	7.4	16.3	16.3	16.3	115	113	114	Kartoushi, Ituri	CD
atripennis		NRM	48145	23.2	6.3	7.1	16.4	16.4	16.4	114	114	114	Malisavo, Ituri	CD
atripennis		NRM	48144	23.7	7.1	7.3	16.2	16.1	16.15	118	117	117.5	Beni Forest, Kivu	CD
atripennis		NRM	48142	24.7	7	-	17.2	17.1	17.15	119	118	118.5	Beni, Kivu	CD
atripennis		MNHN	ZO 1892-1139	22.8	7.4	6.7	—	15.8	15.8	108	110	109	Bangui, Bangui	CF
atripennis		MNHN	ZO 1969-240	23.4	6.6	7.3	15.8	16	15.9	114	—	114	Lamto, Agnéby-Tiassa, Lagunes	CI
atripennis		MNHN	ZO 1969-246	22.9	6.8	7	16	16.1	16.05	110	106	108	Lamto, Agnéby-Tiassa, Lagunes	CI
atripennis		MNHN	ZO 1968-1558	22.9	6.6	7.4	16.4	16.5	16.45	113	112	112.5	Kumba, Meme, Sud-Ouest	CM
atripennis		MNHN	ZO 1983-747	22.9	6.8	6.8	15.8	15.9	15.85	107	107	107	Lata-Bengoué, Ivindo, Ogooué-Ivindo	GA
atripennis		MNHN	ZO 1983-748	23.6	7.2	7	16	16.4	16.2	110	108	109	Bélinga, Ivindo, Ogooué-Ivindo	GA
atripennis		MNHN	ZO 1983-749	22.2	6.8	6.9	15.8	16	15.9	111	110	110.5	Makokou, Ivindo, Ogooué-Ivindo	GA
atripennis		MNHN	ZO 1983-752	24	-	7	16	16.3	16.15	112	112	112	Makokou, Ivindo, Ogooué-Ivindo	GA
atripennis		MNHN	ZO 1983-751	23.8	7.2	7.1	15.5	15.5	15.5	112	113	112.5	Makokou, Ivindo, Ogooué-Ivindo	GA
atripennis		MNHN	ZO 1983-746	22.2	6.3	6.9	15.8	15.8	15.8	114	114	114	Bélinga, Ivindo, Ogooué-Ivindo	GA
atripennis		MNHN	ZO 1983-750	23.8	7.2	7.4	15.7	16	15.85	118	116	117	Makokou, Ivindo, Ogooué-Ivindo	GA
atripennis		MNHN	ZO 1935-352	23.9	7.1	7.5	16.4	16.4	16.4	117	117	117	Mimongo, Ogoulou, Ngounié	GA
atripennis		MNHN	ZO 1999-851	23.1	6	6.7	—	—	—	108	108	108		GH
atripennis		MNHN	ZO 1960-3562	23.6	7.1	7.5	15.8	16.2	16	111	111	111	Sérédou, Macenta, Nzérékoré	GN

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SUPPLEMENTARY TABLE 1. (Continued)

species	subspecies	Institution	Catalog Number	Culmen Length	BillWidth (nostril)	Bill Height (nostril)	Tarsus Length Left	Tarsus Length Right	Tarsus Length Average	Wing Chord Left	Wing Chord Right	Wing Chord Average	Locality	Country
atripennis		MNHN	ZO 1999-850	23	—	7.3	15.8	15.8	15.8	118	118	118		LR
ludwigii	*ludwigii*	ZMUC	AVES-48.442	22.7	6.6	6.5	17	17.1	17.05	100	100	100		MZ
ludwigii	*ludwigii*	NRM	555002	21.7	6.4	—	16.2	16.2	16.2	99	99	99	Port Natal (Durban), KwaZulu-Natal	ZA
ludwigii	*ludwigii*	NRM	90148135	22.6	6.8	6.7	16.3	16.3	16.3	102	102	102	Port Natal (Durban), KwaZulu-Natal	ZA
ludwigii	*ludwigii*	NRM	90148136	22.2	6.3	6.4	16.2	—	16.2	102	101	101.5	Port Natal (Durban), KwaZulu-Natal	ZA
ludwigii	*muenzneri*	ZMUC	AVES-100475	23.5	6.2	6.2	16.7	16.7	16.7	112	112	112	Ndundulu Forest, Kilolo District, Iringa Region	TZ
ludwigii	*muenzneri*	ZMUC	AVES-103521	22.4	6.7	6.7	16.8	17.1	16.95	114	114	114	Amani	TZ
ludwigii	*muenzneri*	ZMUC	AVES-103522	22.5	6.4	6.6	17.2	17.2	17.2	108	108	108	Amani	TZ
ludwigii	*muenzneri*	ZMUC	AVES-103523	21.5	6.9	6.3	—	15.8	15.8	—	—	—	Amani	TZ
ludwigii	*muenzneri*	ZMUC	AVES-074743	22.7	6.3	6.5	—	16.3	16.3	96	96	96	Mikindani	TZ
ludwigii	*muenzneri*	ZMUC	AVES-074744	21.1	6.4	-	16.8	—	16.8	96	96	96	Mikindani	TZ
ludwigii	*muenzneri*	ZMUC	AVES-074745	20.7	6.7	6.3	16.2	15.9	16.05	101	100	101	Mikindani	TZ
ludwigii	*muenzneri*	ZMUC	AVES-074746	22.5	6.3	6	—	—	—	99	99	99	Mikindani	TZ
ludwigii	*muenzneri*	ZMUC	AVES-074747	22.5	6.5	6.2	—	16.7	16.7	100	100	100	Mikindani	TZ
ludwigii	*muenzneri*	ZMUC	AVES-074748	21.8	—	6.7	17	16.8	16.9	98	100	98	Mikindani	TZ
ludwigii	*muenzneri*	ZMUC	AVES-074749	21.8	6.8	6.5	15.8	—	15.8	97	97	97	Mikindani	TZ
ludwigii	*muenzneri*	ZMUC	AVES-074750	22.7	6.6	6.8	17.7	17.7	17.7	101	101	101	Mikindani	TZ
ludwigii	*muenzneri*	ZMUC	AVES-074751	21.8	—	—	16.6	16.6	16.6	95	95	95	Mikindani	TZ
ludwigii	*muenzneri*	ZMUC	AVES-091851	22.9	6.6	6.3	16.7	16.7	16.7	107	107	107	Nambiga Teak Nursery	TZ
ludwigii	*muenzneri*	ZMUC	AVES-100476	20.7	6.3	6	16.8	17.1	16.95	103	103	103	Ndundulu Forest, Kilolo District, Iringa Region	TZ
ludwigii	*muenzneri*	ZMUC	AVES-100482	20.7	6.1	6.3	16.8	16.7	16.75	109	109	109	Ndundulu Forest, Kilolo District, Iringa Region	TZ
ludwigii	*muenzneri*	ZMUC	AVES-100480	21.7	6.4	6.2	17	17	17	111	111	111	Ndundulu Forest, Kilolo District, Iringa Region	TZ
ludwigii	*muenzneri*	ZMUC	AVES-100481	21.6	6.5	6.5	16.5	16.7	16.6	115	114	115	Ndundulu Forest, Kilolo District, Iringa Region	TZ
ludwigii	*muenzneri*	ZMUC	AVES-100478	21.3	6.5	6.3	15.9	16.2	16.05	102	103	102	Nguru South Forest Reserve	TZ
ludwigii	*muenzneri*	ZMUC	AVES-102252	20.8	6.6	6.5	17	17	17	99	105	99	Pugu Hills	TZ
ludwigii	*muenzneri*	ZMUC	AVES-102253	21.3	6.6	6	16.5	16.8	16.65	107	107	107	Pugu Hills	TZ
ludwigii	*muenzneri*	ZMUC	AVES-102254	21.4	6.8	6.6	17	17.3	17.15	106	106	106	Pugu Hills	TZ
ludwigii	*muenzneri*	ZMUC	AVES-102255	21.3	6.7	6.3	17	17	17	102	102.5	102	Pugu Hills	TZ
ludwigii	*muenzneri*	ZMUC	AVES-100477	21.5	6.4	6.3	17.1	17.1	17.1	106	104	106	Ukami Forest	TZ

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SUPPLEMENTARY TABLE 1. (Continued)

species	subspecies	Institution	Catalog Number	Culmen Length	BillWidth (nostril)	Bill Height (nostril)	Tarsus Length Left	Tarsus Length Right	Tarsus Length Average	Wing Chord Left	Wing Chord Right	Wing Chord Average	Locality	Country
ludwigii	*muenzneri*	ZMUC	AVES-100479	21.2	6.2	5.7	17	17	17	103	101	103	Ukami Forest	TZ
ludwigii	*muenzneri*	ZMUC	AVES-074752	22	6.7	6.3	16.2	16.4	16.3	97	-	97	Uluguru Mts.	TZ
ludwigii	*muenzneri*	ZMUC	AVES-074753	21.1	6.3	6.3	16.3	—	16.3	98	98	98	Uluguru Mts.	TZ
ludwigii	*muenzneri*	ZMUC	AVES-091849	22.4	6.9	6.6	16.7	16.9	16.8	111	112	111	West of Ruipa river, West Kilombero Forest Reserve, Morogoro	TZ
ludwigii	*muenzneri*	ZMUC	AVES-091850	22.2	6.1	6.2	16.9	17	16.95	115	114	115	West of Ruipa river, West Kilombero Forest Reserve, Morogoro	TZ
ludwigii	*saturnus*	MNHN	ZO 1947-430	21	6.8	6.6	16.1	16.2	16.15	106	107	106.5	Mwinilunga, Mwinilunga, North-Western	CM
ludwigii	*sharpei*	MCCI	3370	22.6	—	—	—	—	—	—	—	—	Cascades, Forêt Classé du Comoé-Leraba, Camp de Chasse	BF
ludwigii	*sharpei*	MNHN	ZO 1957-104	21.8	6.3	5.8	15.6	15.8	15.7	106	106	106	Mubale	CD
ludwigii	*sharpei*	MNHN	ZO 1957-105	20.6	5.8	—	—	16.2	16.2	103	103	103	Katongo	CD
ludwigii	*sharpei*	MNHN	ZO 1965-881	20.3	6	5.6	15.8	15.8	15.8	108	107	107.5	Sibiti, Sibiti, Lékoumou	CG
ludwigii	*sharpei*	MNHN	ZO 1965-882	21.4	5.9	5.6	16.2	16.3	16.25	106	107	106.5	Sibiti	CG
ludwigii	*sharpei*	MNHN	ZO 1969-239	23.9	6.5	6.2	15.5	15.8	15.65	108	108	108	Lamto, Agnéby-Tiassa, Lagunes	CI
ludwigii	*sharpei*	MNHN	ZO 1976-1205bis	21.9	6.9	6.3	16	16.1	16.05	109	107	108	Bouaké, Gbeke, Vallée du Bandama	CI
ludwigii	*sharpei*	MNHN	ZO 1976-1206bis	23.8	7.4	6.7	15.9	16	15.95	106	107	106.5		CI
ludwigii	*sharpei*	MNHN	ZO 2005-1232	21.2	7	5.3	16.6	16.5	16.55	105	105	105		CM
ludwigii	*sharpei*	BMNH	1966.16.5812	20.3	—	—	—	—	—	—	—	—	Bamenda	CM
ludwigii	*sharpei*	BMNH	1966.16.5814	21.2	—	—	—	—	—	—	—	—	Bamenda	CM
ludwigii	*sharpei*	MNHN	ZO 1947-599	20.9	7.1	6.3	-	15.3	15.3	107	107	107	Lastoursville, Mouloundou, Ogooué-Lolo	GA
ludwigii	*sharpei*	MNHN	ZO 1878-90	20.5	6.2	5.6	16	16	16	106	105	105.5	Ogooué	GA
ludwigii	*sharpei*	MNHN	ZO 1884-630	—	7	6.6	16	—	16	108	108	108	Franceville, Mpassa, Haut-Ogooué	GA
ludwigii	*sharpei*	MNHN	ZO 2014-17	22.4	7.4	6.5	16.4	16.8	16.6	104	104	104	Doti, Dubréka, Kindia	GN
ludwigii	*sharpei*	MNHN	ZO 2014-19	22.8	7	6.3	16	16.4	16.2	105	105	105	Doti, Dubréka, Kindia	GN
ludwigii	*sharpei*	MNHN	ZO 1960-3561	23.9	7.1	6.3	16.6	16.5	16.55	105	105	105	Sérédou, Macenta, Nzérékoré	GN
ludwigii	*sharpei*	BMNH	1955.59.180	20	—	—	—	—	—	—	—	—	Enugu	NG
ludwigii	*sharpei*	BMNH	1955.59.181	21.6	—	—	—	—	—	—	—	—	Enugu	NG
ludwigii	*sharpei*	BMNH	1955.59.183	20.6	—	—	—	—	—	—	—	—	Enugu	NG
ludwigii	*sharpei*	BMNH	1966.16.5806	21.6	—	—	—	—	—	—	—	—	Enugu	NG
ludwigii	*sharpei*	BMNH	1966.16.5807	20.6	—	—	—	—	—	—	—	—	Enugu	NG
ludwigii	*sharpei*	BMNH	1966.16.5808	20.6	—	—	—	—	—	—	—	—	Enugu	NG
ludwigii	*sharpei*	BMNH	1966.16.5810	20.7	—	—	—	—	—	—	—	—	Okposi, Ogoja Prov	NG
ludwigii	*sharpei*	BMNH	1964.15.2	21.8	—	—	—	—	—	—	—	—	Anara Forest, Kaduna	NG
ludwigii	*sharpei*	MNHN	ZO 1983-226	23.7	7.3	6.5	16.3	15.8	16.05	110	110	110	Oussouye, Oussouye, Ziguinchor	SN