Redefining the taxonomy of the all-black and pied boubous (*Laniarius* spp.) in coastal Kenya and Somalia

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SUMMARY.—Following the rediscovery of a form of *Laniarius* on Manda Island, Kenya, which had been treated as a melanistic morph of Tropical Boubou *Laniarius aethiopicus* for some 70 years, a detailed field study strongly indicated that it was wrongly assigned. Molecular examination proved that it is the same species as *L. (aethiopicus) erlangeri*, until now considered a Somali endemic, and these populations should take the oldest available name *L. nigerrimus*. The overall classification of coastal boubous also proved to require revision, and this paper presents a preliminary new classification for taxa in this region using both genetic and morphological data. Genetic evidence revealed that the coastal ally of *L. aethiopicus*, recently considered specifically as *L. sublacteus*, comprises two unrelated forms, requiring a future detailed study.

The black-and-white boubous—characteristic birds of Africa's savanna and wooded regions—have been treated as subspecies of the highly polytypic *Laniarius ferrugineus* (Rand 1960), or subdivided, by separating Southern Boubou *L. ferrugineus*, Swamp Boubou *L. bicolor* and Turati's Boubou *L. turatii* from the widespread and geographically variable Tropical Boubou *L. aethiopicus* (Hall & Moreau 1970, Fry *et al*. 2000, Harris & Franklin 2000). They are generally pied, with black upperparts, white or pale buff underparts, and in most populations a white wing-stripe. However, the all-black birds inhabiting bushy savanna in northern Kenya and southern Somalia have long been considered as rare morphs of Tropical Boubous in the same areas. Using molecular phylogenetic data for all relevant populations, our aim here is to clarify the relationships of these birds.

Historical context

An all-black form first collected by Fischer in 1878, was originally described as *Dryoscopus nigerrimus*, from a specimen collected at Kipini near the Tana River, Kenya (Reichenow 1879). Subsequently, Reichenow (1905) described another all-black bird from Umfudu on the Juba River, in southern Somalia, as *Laniarius erlangeri*, with reference only to it having glossier plumage than *L. leucorhynchus* (Lowland Sooty Boubou) and *L. funebris* (Slate-coloured Boubou), but without describing any differences from *nigerrimus*. Furthermore, he described a pied bird from Ganala on the lower Juba River as *L. aethiopicus somaliensis*. Van Someren (1922, 1932) questioned, using his own material from Kipini, Manda and Lamu (Kenya), and Juba (Somalia), whether *nigerrimus* and *erlangeri* were not identical species separate from *ferrugineus*. Jackson & Sclater (1938) wholly supported van Someren's comments on these all-black boubous, stating 'there can be little doubt that he is correct' and they listed *L. nigerrimus* for Kenya Colony and Italian Somaliland. Interestingly, Jackson & Sclater (1938) also felt that *L. f. somaliensis* was identical to *L. f. sublacteus* (Cassin, 1851). Despite this, Grant & Mackworth-Praed (1944) made no mention of any black forms and simply referred to the two coastal pied forms, *L. ferrugineus somaliensis* and *L. f. sublacteus.* In 1947, Stresemann, having compared a specimen of *nigerrimus* and sympatric pied birds,

decided that the former was merely a morph of *sublacteus*. White (1962) treated *erlangeri* as a race of *L. ferrugineus*, made no mention of a black morph, and did not include *nigerrimus* at all. This treatment of two colour morphs of *sublacteus* and *erlangeri* was perpetuated by Ash & Miskell (1998) and Fry *et al*. (2000). In Dickinson (2003) *erlangeri* was considered a race of *L. aethiopicus*, but with no mention of a black morph, or of *nigerrimus*. This history was more fully documented in Turner *et al*. (2011). Importantly, it emphasises the point that there was no field evidence for the decision taken by Stresemann, other than his claim that both forms occurred sympatrically at several localities.

Intrigued by Stresemann's reference to a black morph of *L. sublacteus*, which had only been found in a relatively restricted coastal area, BWF was curious as to why elsewhere throughout the extensive range of *sublacteus*, this taxon is always black above with no white in the wings and all-white underparts, with no evidence of a melanistic morph anywhere else in Kenya. BWF & NDH decided to undertake a field study on Manda Island, as the black morph has been most frequently collected there (Finch & Hunter 2010).

Figure 1. Heads of pied and all-black boubous (*Laniarius*), photographed on Manda Island, Lamu District, Kenya, April 2010; above *sublacteus* and below *nigerrimus*, with the vertical line marking the anterior margin of the eyes (Brian W. Finch)
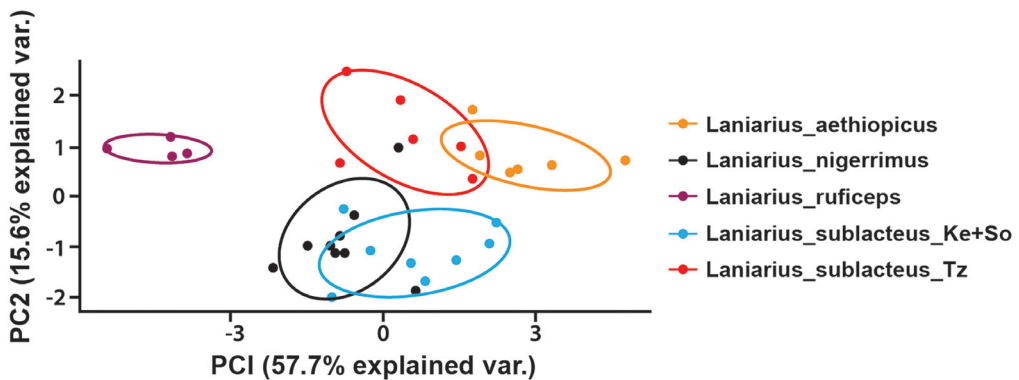

Figure 2. Morphological variation among boubous of East Africa, based on measurements taken by JF & P. Z. Marki. Principal Component 1 represents size (mainly wing and tail); PC2 represents bill parameters. '*Laniarius sublacteus*_Ke+So' comprises specimens from Kenya, as well as two genetically similar birds from Somalia, which, however, differ by having a short white wing-stripe. '*Laniarius sublacteus*_Tz' comprises Tanzanian specimens, formally referred to as '*sublacteus*' but representing another clade (see Conclusions). *L. aethiopicus* represents large birds from the Somali highlands.
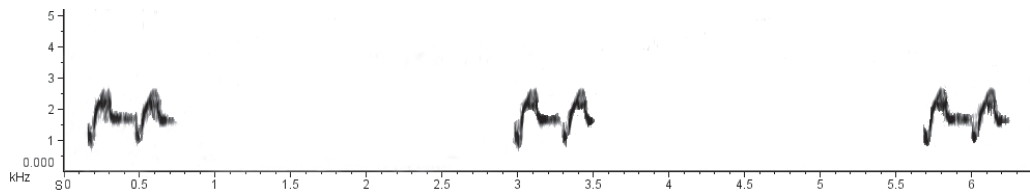
Figure 3a. Sonogram of the explosive two-noted call produced by the all-black *Laniarius nigerrimus*, recorded on Manda Island, Lamu District, Kenya, on 25 April 2010, by Brian W. Finch, using a Sony TCM 200DV recorder and Sennheiser directional microphone. Sonogram created using Raven Lite 1.0 for Windows, and background subsequently cleaned in Photoshop.
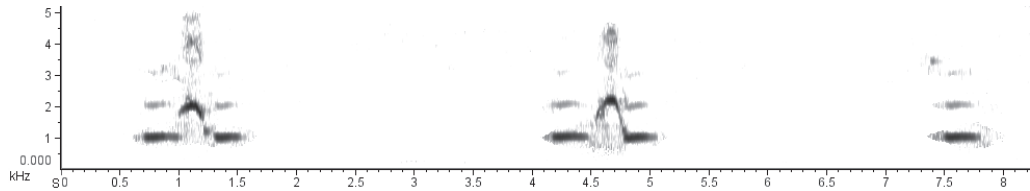

Figure 3b. Sonogram of the three-noted 'bell-like' calls of the East Coast Boubou *Laniarius sublacteus*, recorded on Manda Island, Lamu District, Kenya, on 25 April 2010, by Brian W. Finch, using a Sony TCM 200DV recorder and Sennheiser directional microphone. Sonogram created using Raven Lite 1.0 for Windows, and background subsequently cleaned in Photoshop.

Reappraisal of *Laniarius nigerrimus* based on field and museum studies

Observations were made by BWF & NDH on Manda Island (02º15'S, 40º54'E) from early morning on 25 April 2010 (Finch & Hunter 2010, Turner *et al*. 2011). Almost immediately a deep, throaty call was heard and recorded. The sound was completely unfamiliar to both observers, and on playback an all-black boubou ascended atop a bare tree. After several minutes in the open, it answered the playback with a completely different, and novel, ringing call. On recording this and playing it back, the bird became far more active and flew to the top of another acacia, calling from an open perch. Three very different calls were recorded, all alien to us, and none of them remotely like those produced by the familiar *sublacteus* present at the same locality. Fifteen playback experiments, involving ten pairs of *sublacteus* and five pairs of all-black birds, were undertaken. Using recordings made *in situ* of both forms yielded no response to calls of the other form, although the birds persistently responded to their own calls. This experiment was repeated ten months later in the same area with identical results. BWF & NDH noted that the all-black boubous remained in pairs, mainly in the upper strata of the scrubby woodland, were 'extrovert' (frequently assuming exposed perches, as opposed to the skulking behaviour of the *sublacteus* pairs) and were observed to perform an aerial, parachuting display. Sonograms of the main vocalisations, originally published in Turner *et al*. (2011), are reproduced as Fig. 3.

Over the next two hours we made a detailed description of the differences between the all-black form and *sublacteus*. The differences in morphology, behaviour, vocalisations and habitat are fully described in Finch & Hunter (2010). Among the morphological differences, structurally *nigerrimus* differs from *sublacteus* in bill depth and length. The bill is shorter than *sublacteus*, which results in a much deeper appearance and is very easy to gauge, even in the field; *nigerrimus* has a bill that is equal to or slightly shorter than the distance between the base of the maxilla and the eye. In *sublacteus*, the long and slender-looking bill is obviously far greater than the distance between the base of the maxilla and the eye

TABLE 1

Details of specimens sampled for genetic analyses.

All-black birds

Museum[1] registration no.	Lab no.	Locality	Collection date	# Sequences generated	# unique sequence reads mapping to reference mito-genome	Mean read length[2]	Mean-fold sequence coverage	Fragments recovered[3]
FMNH 200871	B02	Juba, southern Somalia	March 1923	15,341,937	11,872	100	47x	ND2 + ATP6
NMK 12622	B07	southern Somalia	May 1916	9,999,735	6,715	100	22x	ND2 + ATP6
NMK 12619	B08	Manda Island, Kenya	April 1916	11,920,211	6,426	100	21x	ND2 + ATP6
NMK 12617	B09	Manda Island, Kenya	April 1916	9,945,138	4,901	40	14x	ND2
NMK 11650	B10	near Balad, southern Somalia	Jan. 1954	23,266,600	10,090	100	40x	ND2 + ATP6
NMK 12618	B11	Manda Island, Kenya	April 1916	14,878,764	7,562	100	24x	ND2 + ATP6

Black-and-white birds

Museum[1] registration no.	Lab no.	Locality	Collection date	# Sequences generated	# unique sequence reads mapping to reference mito-genome	Mean read length[2]	Mean-fold sequence coverage	Fragments recovered[3]
FMNH 200949	B01	Juba, southern Somalia	March 1923	13,841,061	9,684	100	35x	ND2 + ATP6
FMNH 200950	B03	Juba, southern Somalia	April 1923	21,281,091	13,360	100	55x	ND2 + ATP6
NMK 12487	B04	Mkoi, Manda Island, Kenya	May 1916	15,338,000	7,116	100	24x	ND2 + ATP6
NMK 12498	B05	Kilifi, north Kenya coast	April 1959	28,812,753	14,886	100	64x	ND2
NMK 11614	B06	Kilifi, north Kenya coast	April 1959	28,357,111	15,451	100	67x	ND2 + ATP6

[1] FMNH = Field Museum of Natural History, Chicago; NMK = National Museums of Kenya, Nairobi
[2] Because of the sequencing chemistry used, 100 bp is the max. read length achievable. The true mean length of mtDNA fragments in the extracts is almost certainly greater.
[3] mtDNA fragments as reported in Nguembock *et al*. (2008)

(Fig. 1). In *nigerrimus* the eye appears to be set back further on the head, and the difference could suggest different feeding strategies.

The differences observed in the field are supported by a principal components analysis (see Fig. 2) undertaken by JF & P. Z. Marki. The analysis utilised specimens in Kenya National Museums (Nairobi), American Museum of Natural History (New York), Field Museum of Natural History (Chicago) and Museum für Naturkunde (Berlin). Altogether,

208 specimens from East Africa were examined and Fig. 2 illustrates segregation for 32 specimens for which a full set of measurements were taken, comprising: culmen length to skull, depth and width of bill at level of anterior edge of nostrils, tarsus, hind toe with nail, wing length (flattened against a ruler), length from carpal joint to tip of outer secondary, tail length and length of outer rectrix.

To summarise, not only do the all-black boubous appear glossier and smaller than *sublacteus*, they remain in pairs, inhabit a different vegetation stratum, are not skulking, possess entirely different vocalisations (calls are ringing, but not bell-like, suggesting gonoleks), and an aerial display. Based on this, BWF & NDH concluded that they appeared to belong to a completely different grouping within *Laniarius*. Thus, the van Someren (1922, 1932) hypothesis that the all-black boubous from Manda and Somalia represent the same species needed to be tested molecularly, as recommended by Turner *et al*. (2011, 2013). Nevertheless, Dickinson & Christidis (2014) tentatively elected to award specific status to the all-black birds under the name Coastal Boubou *L. nigerrimus* on the basis of the two just-mentioned papers.

Genetic analysis

Specimens.—A previous molecular study by Nguembock *et al*. (2008) already revealed rather complex relationships among the 'tropical boubous', suggesting the requirement to recognise several additional species in East Africa. For Somalia, a tissue sample from an all-black specimen grouped with the unique (black, white and yellowish) *L. liberatus* (named by Smith *et al*. 1991). Although sympatrically occurring pied specimens, initially described as *L. aethiopicus somaliensis*, were not sampled, the presence of a polymorphic species *Laniarius erlangeri* was suggested for southern Somalia. Further, the form *sublacteus* (pied but without a white wing-stripe) was pointed out as a separate species, based on samples from Tanzania, while a single sample from Arabuko-Sokoke Forest in Kenya was also genetically distinct, suggesting cryptic speciation (see Fig. 1a–d in Nguembock *et al*.). The skin collections at the National Museums of Kenya include several all-black specimens from Manda Island, as well as others from Somalia. Furthermore, the Field Museum of Natural History has one all-black and two pied specimens from the Juba Valley, southern Somalia. In total, toe-pad samples were obtained from six black and five pied specimens (Table 1). Our aims were to test if the all-black birds represent one (or more) species separate from the pied forms, and whether the pied form in southern Somalia (*somaliensis*), currently treated as a subspecies of Ethiopian or Tropical Boubou *L. aethiopicus*, differs from pied birds on the coast of northern Kenya (East Coast Boubou *L. sublacteus*).

Methodology.—DNA analyses were undertaken at the Centre for GeoGenetics, Natural History Museum of Denmark, Copenhagen. Historic and ancient samples can largely be expected to contain extremely fragmented DNA (Lindahl 1993) and therefore may not be suitable for conventional PCR-based analyses. Such problems are especially exacerbated when samples have been stored in warm climates. Additionally, analysis of degraded materials is extremely susceptible to contamination from higher quality sources of DNA (Hofreiter *et al*. 2001). Indeed, initial pilot attempts to amplify short (*c*.100 bp) sub-fragments of the sequences reported by Nguembock *et al*. (2008) using conventional PCR failed (data not shown). Therefore, we elected to generate data using an Illumina shotgun-sequencing approach, in which we would generate many millions of shotgun sequence reads per sample, then use the dataset to unearth the two mtDNA markers published by Nguembock *et al*. (2008), ATP6 and ND2. No attempt was made to recover the nuDNA marker used by Nguembock *et al*. (2008), as such analyses require much additional sequencing. To prevent contamination, the sample extractions and initial manipulations were undertaken

in the 'clean laboratories' at the Copenhagen facility dedicated to working with degraded samples. All manipulation incorporated standard ancient DNA precautions to minimise the risk of contamination, including use of new reagents, protective body suits and sterile gloves, etc. (Hofreiter *et al*. 2001).

DNA was extracted from the toe-pad samples using an extraction method developed for historic/ancient DNA. Each sample was digested overnight at 56°C in 750 µl of custom lysis buffer (0.5 M UltraPure EDTA pH 8.0, 1% SDS [sodium dodecyl sulphate], 10 mM DTT [Dithiothreitol], 1 mg/µl Proteinase K) and then spun through a centrifuge at 13,000 RPM for one minute, thereafter the supernatant was transferred to a new tube and the pellet discarded. Samples were then concentrated on 30K Amicon Millipore Ultra Centrifugal Filters (cut-off size of minimum 50 bp DNA fragments), purified using the MinElute PCR Purification Kit (Qiagen) and finally eluted in 100 µl of EB buffer. Subsequently, the DNA was converted into Illumina sequencing libraries, following the blunt-end ligation approach of Meyer & Kircher (2010). Next, libraries were PCR-amplified using unique indexed primers, prior to pooling at an equimolar ratio, and finally they were sequenced together on one lane of an Illumina HiSeq2500 sequencing run using 100 bp single-read chemistry. Subsequently, the data were analysed as follows. The raw reads from the different sequencing datasets were concatenated into a single fastq file per bird sample. Adapter Removal version 1.5.4 (Lindgreen 2012) was then used to trim adapters from the 3' end of the reads and to cut N's at the end of the sequence and low-quality nucleotides, and to discard reads that after cleaning had a length of <25bp. We then attempted to use the ATP6 nucleotide sequence of *Laniarius f. erlangeri* (NCBI identity EU554471.1) as a reference seed to mine and reconstruct the mito-genomes from all datasets. Initially, this was only successful for samples B02 and B06, so subsequently we re-attempted this reconstruction for the other samples using the now-reconstructed mito-genome from B06 as a new reference.

To reconstruct the mito-genomes, we first created a manifest file for MIRA 4 (http://www.chevreux.org/projects_mira.html), in which we specified the reads as the cleaned reads and the reference as either the *Laniarius f. erlangeri* ATP6 sequence or the B06 assembled sequence described above. Subsequently, we used MIRA 4 to generate an initial mapping assembly that was then used by the MITObim pipeline (Hahn *et al*. 2013). Specifically, the maf file created by MIRA 4 was used for the baiting and iterative mapping using the MITObim.pl script. The reconstructed mitochondrial genome was taken from the unpadded fasta file within the final iteration directory. We used miraconvert to create a consensus sequence of ambiguous SNPs in the assembly. Finally, we annotated the reconstructed mitochondrial genomes using the MITOS (Bernt *et al*. 2013) web server, and downloaded amino acids for the annotated sequences. These were mined for the final ND2 and ATP6 genes to compare with the reference dataset published by Nguembock *et al*. (2008). For phylogenetic reconstruction, we added the ND2 and ATP6 gene datasets to the data matrix produced by Nguembock *et al*. (2008), then aligned each region using MAFFT (Katoh 2013). The resulting alignments were each converted into phylip format using the perl script Fasta2Phylip (Mullins Lab, Univ. of Washington), following which a phylogeny was reconstructed independently for each region using RAxML (Stamatakis 2014) under the GTR+GAMMA model of evolution with 100 bootstrap replicates. Due to our inability to recover both regions from all historic samples, we did not attempt a concatenated analysis of both genes.

Results

Between 9.9 and 28.8 million sequence reads were generated per DNA extract, which after filtering provided average coverage of the mitochondrial genomes between 14 and

Figure 4a. Maximum Likelihood phylogeny of ATP6 mitochondrial DNA subfragments showing the relative placement of the samples studied in the context of the dataset published by Nguembock *et al*. (2008). Sample B09 was not included due to unsuccessful recovery of the ATP6 marker for this sample. Bootstrap support values relevant to the key samples are indicated.
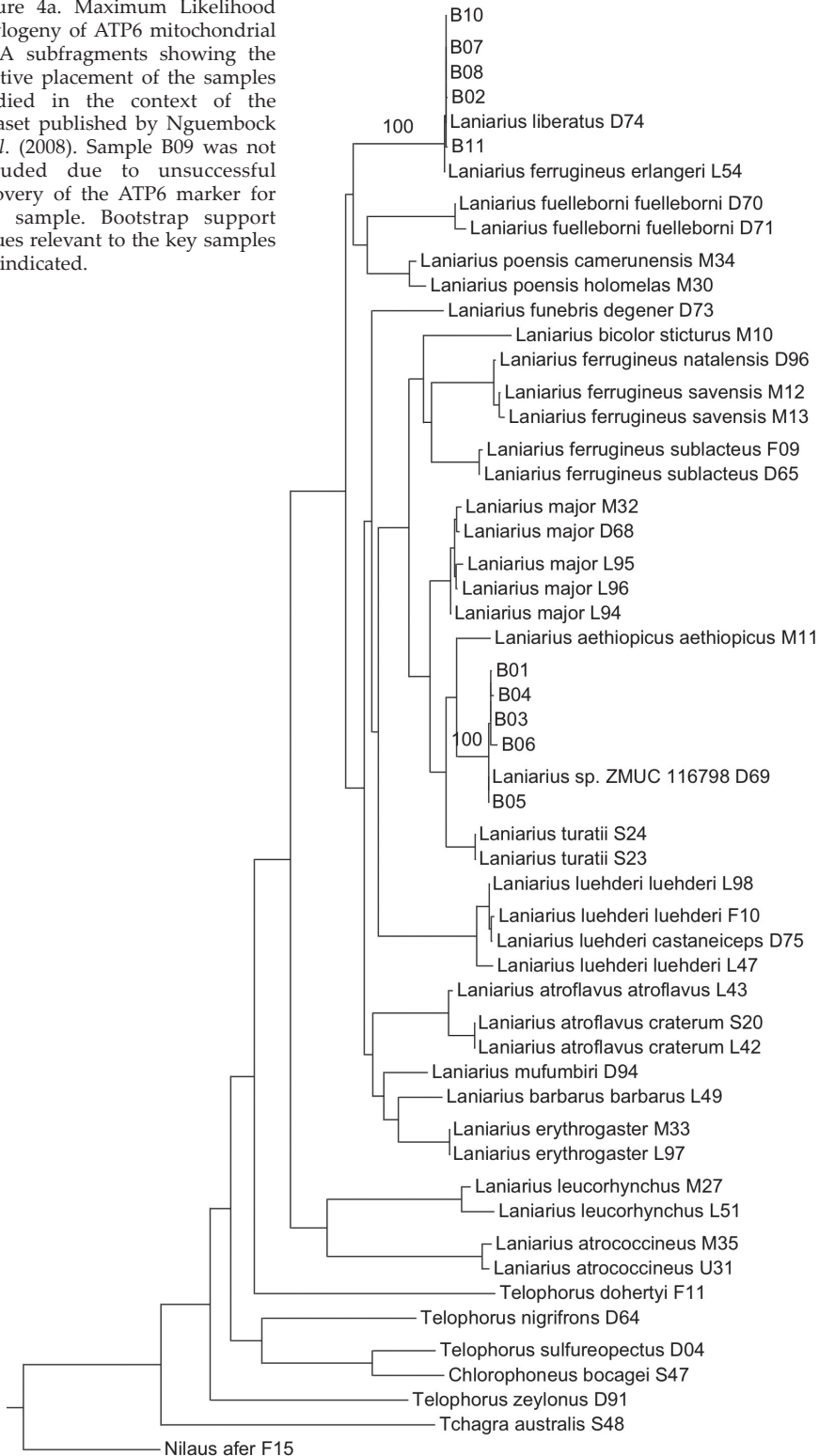
B10
B07
B08
B02
Laniarius liberatus D74
B11
Laniarius ferrugineus erlangeri L54
100
Laniarius fuelleborni fuelleborni D70
Laniarius fuelleborni fuelleborni D71
Laniarius poensis camerunensis M34
Laniarius poensis holomelas M30
Laniarius funebris degener D73
Laniarius bicolor sticturus M10
Laniarius ferrugineus natalensis D96
Laniarius ferrugineus savensis M12
Laniarius ferrugineus savensis M13
Laniarius ferrugineus sublacteus F09
Laniarius ferrugineus sublacteus D65
Laniarius major M32
Laniarius major D68
Laniarius major L95
Laniarius major L96
Laniarius major L94
Laniarius aethiopicus aethiopicus M11
B01
B04
B03
B06
100
Laniarius sp. ZMUC 116798 D69
B05
Laniarius turatii S24
Laniarius turatii S23
Laniarius luehderi luehderi L98
Laniarius luehderi luehderi F10
Laniarius luehderi castaneiceps D75
Laniarius luehderi luehderi L47
Laniarius atroflavus atroflavus L43
Laniarius atroflavus craterum S20
Laniarius atroflavus craterum L42
Laniarius mufumbiri D94
Laniarius barbarus barbarus L49
Laniarius erythrogaster M33
Laniarius erythrogaster L97
Laniarius leucorhynchus M27
Laniarius leucorhynchus L51
Laniarius atrococcineus M35
Laniarius atrococcineus U31
Telophorus dohertyi F11
Telophorus nigrifrons D64
Telophorus sulfureopectus D04
Chlorophoneus bocagei S47
Telophorus zeylonus D91
Tchagra australis S48
Nilaus afer F15

Figure 4b. Maximum Likelihood phylogeny of ND2 mitochondrial DNA subfragments showing the relative placement of the samples studied in the context of the dataset published by Nguembock *et al.* (2008). Bootstrap support values relevant to the key samples are indicated.
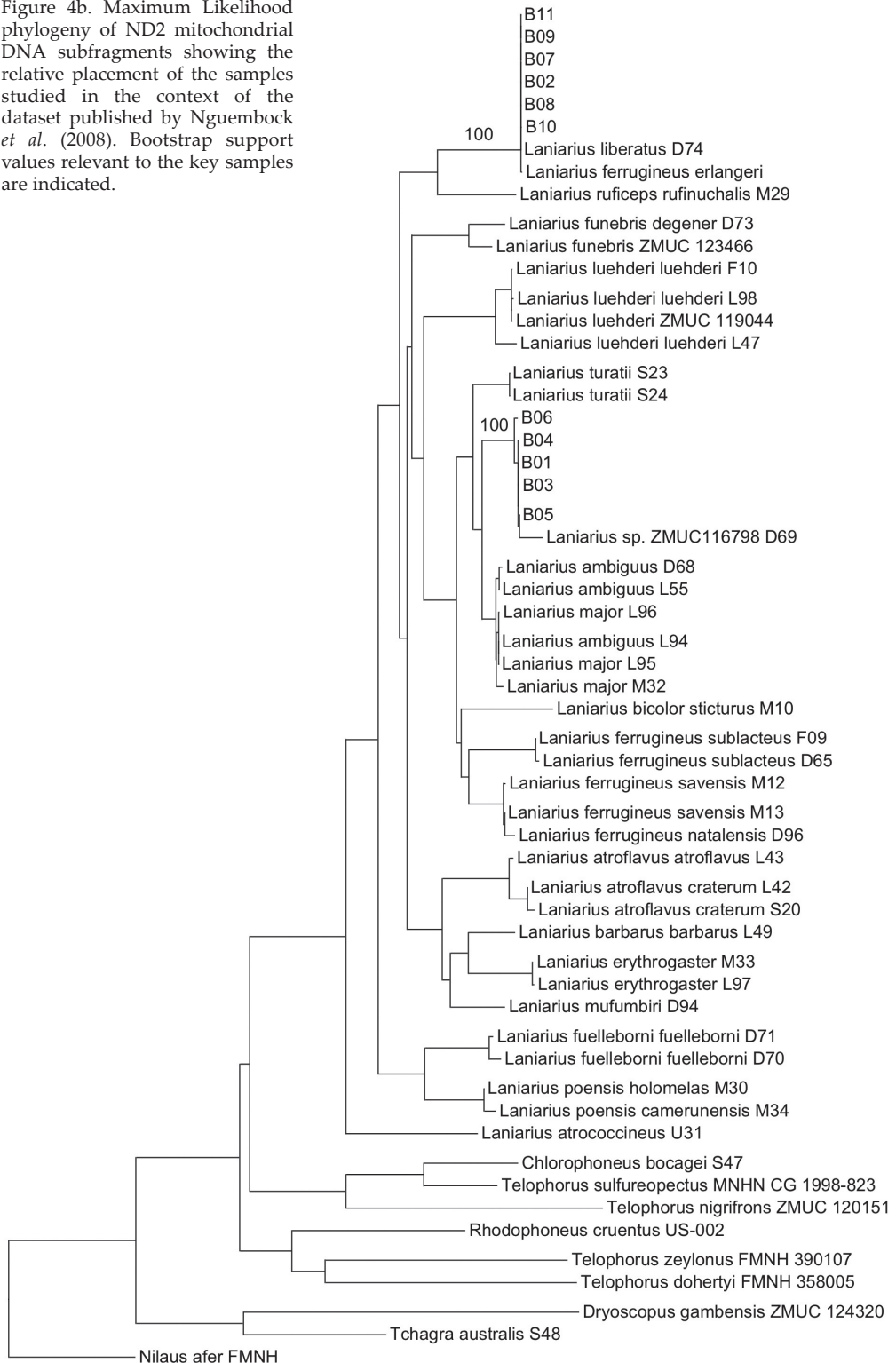
67x (Table 1). After trimming the adaptors, the mean read length for most samples was 100, reflecting the max. length that the sequencing chemistry permitted, suggesting that most DNA fragments in the samples were probably longer than this. We recovered ND2 and ATP6 sequence from all samples except B09, in which the ATP6 sequence was too poor to enable reliable sequencing. All new ND2 and ATP6 sequences have been accessioned in GenBank (accession nos. KU905020–KU905040).

The results of our phylogenetic analyses were generally consistent with those of Nguembock *et al*. (Fig. 4a,b), although some differences can be observed. We caution that the focus of our analysis serves only to establish the non-monophyly of *nigerrimus* and *sublacteus* using a neutral maternally inherited genetic marker that has worked well across birds for such specific questions, and unlike Nguembock *et al*. (2008) we did not attempt to analyse any nuclear genes. Therefore, our tree is not intended to accurately represent phylogenetic relationships in the wider context of the groups. With respect to our central questions, the phylogeny indicates that the five all-black individuals that we sampled clustered with high bootstrap support with the single all-black bird sampled (L54) by Nguembock *et al*. (2008) and the uniquely plumaged specimen named as *L. liberatus*. Concerning *liberatus*, Nguembock *et al*. (2008) concluded that the single specimen represents a plumage aberration of the all-black form and is not a hybrid. We agree with that conclusion and reaffirm that *liberatus* be treated as a synonym of *L. nigerrimus*. The all-black birds collected in Kenya and Somalia grouped into one clade, and differed considerably from the pied individuals, which constitute a separate clade.

The pied forms analysed here form a subclade separate from that containing the two Tanzanian samples of '*sublacteus*' in Nguembock *et al*. (2008). More intriguing is that the subclade containing our pied forms also clustered with high bootstrap support with an individual from Arabuko-Sokoke Forest in Kenya (ZMUC 116978), which lies just north of Kilifi. Because this was the only coastal sample from Kenya sampled by the Nguembock *et al*. (2008) analysis and it did not group with the two *sublacteus* specimens from Tanzania, they questioned if there might be yet another boubou species occurring in the forest. Our analyses indicated that the Arabuko-Sokoke sample forms parts of the same subclade as Somalian and Kenyan pied specimens, whereas the Tanzanian *sublacteus* samples grouped with the phenotypically quite different *L. ferrugineus*.

Conclusions

Laniarius nigerrimus.—As indicated by our field work and confirmed by genetic analysis, it can be concluded that the all-black birds found in the Juba and Shabeelle valleys, Somalia, and on Manda Island, Kenya, represent a single species, separate from any of the pied forms. The hypothesis that this all-black form represents a morph of any pied boubou species can therefore be rejected. The bird referred to as '*erlangeri*' (= *nigerrimus*) is almost monomorphic, with *liberatus* representing an apparently one-off variant under present knowledge. The species can be diagnosed as being all black (except concealed grey sub-apical spots on the fluffy rump feathers, with a bluish gloss; bill length to skull 22.8–23.3 mm, wing (flattened against the ruler) 84.0–93.8 mm, tail 79.3–90.5 mm, and tarsus 27.7–32.2 mm.

L. 'erlangeri'.—The suggestion that this name refers to a polytypic species is proven incorrect, as *L. aethiopicus somaliensis*, a pied form with a short white wing-stripe, is genetically identical to the northern Kenyan population of *sublacteus*, although the latter has no hint of a wing-stripe. Nguembock *et al*. (2008), who did not sample any black individuals from Kenya, accepted Stresemann's (1947) view that they are a melanistic form of *sublacteus*.

Our study reveals that inclusion of *somaliensis* with northern Kenyan *sublacteus* results only in a pied and essentially not a polymorphic form.

Nomenclature.—Given that the all-black birds in Somalia and Kenya represent the same species, protocol demands that their scientific name should be that bestowed by Reichenow (1879), i.e. *Laniarius nigerrimus*. The name *erlangeri* is a junior synonym, as it was not introduced until 1905. This leaves the question of an appropriate English name. Although Dickinson & Christidis (2014) coined Coastal Boubou for *nigerrimus*, we prefer Manda Boubou. Firstly, our work on Manda Island was critical to unravelling this taxonomic conundrum. Secondly, the boubou's range is limited, it being currently known in Kenya only from Manda Island and just inland of Ras Tenewi (on the mainland coast 25–30 km south-west of Manda), and the valleys of Juba and Shabeelle in Somalia. Given the military conflict in Somalia and the very widespread use of illegal charcoal to fund this, *L. nigerrimus* may be under real threat from habitat loss. In Kenya, Manda forms part of the Lamu archipelago, the location for a new commercial port development. Currently, Manda Island still supports good habitat for the boubou, but it is largely unprotected. There is an urgent need to establish a conservation unit there. Naming the species for Manda should hopefully give impetus to establishing such a reserve, which is likely to prove easier than at Ras Tenewi.

Pied forms.—Conventionally, *Laniarius sublacteus* refers to the pied boubou that occurs on the coast of Kenya from Boni Forest at the border with Somalia to slightly south of Dar es Salaam, in Tanzania, and inland to Makindu, Taita, the North Pare Mountains, the Usambaras, Ulugurus and Mpwapwa (Britton 1980), a range subsequently extended to include the Rubeho and eastern Udzungwa Mountains in central Tanzania (Fjeldså *et al*. 2010). Similarly, *L. aethiopicus somaliensis* refers to the pied boubou of the Juba Valley in Somalia. Our analysis indicates that there is no genetic difference between *somaliensis* and *sublacteus sensu stricto* occurring north from Kilifi, Kenya, including the Arabuko-Sokoke specimen included in Nguembock *et al*. (2008). However, when we combine our results with those of Nguembock *et al*. (2008) with respect to their two *sublacteus* specimens from Tanzania, at Kwizu, South Pare Mountains (in secondary forest at 04°07'S, 37°51'E, at *c*.1,400 m) and Korogwe District, West Usambara Mountains (Ambangulu Tea Estate, 14.5 km north-west of Korogwe), they fall into a different subclade. Therefore, the *sublacteus* group contains two distinct forms, which finding clearly demands further research.

To correctly name the northern population of '*sublacteus*', we are faced with a dilemma. Having ascertained that the range ascribed to *sublacteus* is occupied by two different forms, which one is represented by the type specimen of *sublacteus*? This specimen is at the Academy of Natural Sciences, Philadelphia, and was described in 1851. Its provenance is confused, with 'Eastern Africa' (Cassin 1851, Sclater 1930), 'Mombasa' (Grant & Mackworth-Praed 1944, Mackworth-Praed & Grant 1955, 1960) and 'Lamu' (Grant & Mackworth-Praed 1947) all having been suggested. As the true origin is vague and apparently contradictory, the only solution would appear to be a genetic assessment to determine whether it belongs to the northern or southern clade.

Turner *et al*. (2013) already suggested that work was needed to determine if the pied boubous south of Mombasa and inland are separate from those north of Mombasa, as their vocalisations appear to differ. In this respect, note that Fig. 3b represents the pied boubou found from Kilifi northwards. The sonogram depicts the typical three-noted call, which is given in duet. The male utters the first note, the female the second one and the male the third. When the female does not issue the second note, the male does not respond. There does not appear to be much variation in this duet, unlike some boubous such as *L.*

aethiopicus major. However, this vocalisation may prove to be just one significant indicator, when future study of the *sublacteus* group is undertaken.

The previous treatment of Tropical Boubou *L. aethiopicus* and Erlanger's Boubou *L. erlangeri* has been shown by Nguembock *et al*. (2008) and by us to be an over-simplification. For Somalia and the East African coast, it is now pertinent to recognise five species: *L. aethiopicus* (northern Somalia), *L. nigerrimus* (southern Somalia and northern Kenya coast), *L. sublacteus* (comprising two unrelated taxa, one of them unnamed, along the southern Somalian, Kenyan and Tanzanian coasts) and *L. mossambicus* (southern Tanzania, previously also treated as a subspecies of *L. aethiopicus*).

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