Monograph on

Endemism in the Highlands and Escarpments of Angola and Namibia

Angola Cave-Chat *Xenocopsychus ansorgei*
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CONTENTS

Geography of the highlands and escarpments

Diversity and endemism

Birds of the highlands and escarpments of Angola and Namibia: ornithological significance, avifaunal patterns and questions requiring further study

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ABSTRACT

The highlands and escarpments of Angola and Namibia are recognised as an important region for the evolution and conservation of birds. However, no comprehensive study of the avifauna, and its potential evolutionary origins and links, has been made. As a basis for further study, we compiled a comprehensive list of birds largely confined to the region, together with details of links to nearest relatives, including birds from all relevant levels of the evolutionary process and taxonomic hierarchy (isolated populations to genera). A total of 233 Evolutionarily Significant Units (ESUs) were identified, comprised of four genera, 37 species, 71 subspecies and 121 taxa with isolated populations. The escarpment holds a richer diversity of ESUs than the Afromontane region, although most escarpment ESUs are separated from relatives by a break in the forest zone of about 320 km. Hence few Northern Escarpment ESUs are differentiated even subspecifically (15 of 111; 14%), and most (n = 92; 83%) involve isolated but undifferentiated populations. However, further south along the escarpment distinctiveness increases; 15 of 64 (23%) forest ESUs on the Central Escarpment are differentiated subspecifically. In contrast, the ESUs of the highlands are typically isolated from their nearest vicariants by a much larger gap. Although only 44 ESUs are found here, 26 of them have differentiated to the subspecies level and seven to species level. In the highlands, lower diversity is paired with a greater degree of differentiation, both of which are known to be the result of extreme isolation. Preliminary research has shown that the Angolan Afromontane forests are located in an area of high climatic stability, and that they constitute an important historical link between the montane bird communities of East Africa and the mountains of Cameroon. Our simple analysis reveals some potentially interesting patterns but relies on largely untested assumptions regarding the closest relatives of the region's significant bird taxa (ESUs). More detailed and extensive studies of the origins and relationships of key bird taxa are needed to explore whether counterintuitive patterns exist that are currently being masked.

Keywords: Angola, avifauna, endemism, escarpments, highlands, Namibia

INTRODUCTION

Congruent distribution patterns of restricted-range (< 50,000 km^2) terrestrial bird species have been used to identify key regions of bird endemism (Endemic Bird Areas (EBAs)), globally, as priorities for conservation (Stattersfield *et al*. 1998). Within Angola and Namibia there is one EBA (Western Angola; Figure 1), defined more than 20 years ago based on 14 restricted-range bird species; the updated taxonomy of BirdLife International (HBW & BirdLife International 2022) recognises seven additional relevant species. This EBA corresponds closely to the escarpment and highland zones in Angola, but also includes some areas adjacent to the escarpment along the coastal plain (Dean *et al*. 2019). There is also one 'Secondary Area' (defined as covering the range of a single restricted-range species), the 'Namibian Escarpment', based on the range of Herero chat *Namibornis herero*, which covers parts of both southern Angola and northern Namibia.

The EBA approach, however, is of limited use for understanding the evolutionary significance of regions such as the highlands and escarpments of Angola and Namibia (HEAN), as it was devised as a conservation prioritisation exercise, based on species as the only taxonomic entity considered and on the assumption that species with smaller ranges are more likely to be threatened. Although this is generally true, the method applies an arbitrary cutoff for range size that excludes several species which are endemic or near-endemic to the HEAN. The question of identifying evolutionary hotspots – regions where large numbers of distinctive taxa have evolved and are likely to evolve in the future – requires an approach that considers a region within the context of a wider area, links to other areas, evolutionary distinctiveness of taxa, and includes groups from all levels of the evolutionary process and taxonomic hierarchy (from isolated populations to genera, in this case). This was done at the species level for forest-dependent birds, globally (Buchanan *et al*. 2011); in that analysis the forests of western Angola ranked in

the highest category of impact score for their contribution to global forest bird species richness. Previous assessments (Collar & Stuart 1988, Burgess *et al*. 2004, de Klerk *et al*. 2004) all recognise the importance of the western Angolan forests to forest birds. Yet the full contribution of the Angolan–Namibian escarpment and highlands to the evolution of the African avifauna has not yet been evaluated based on current taxonomic understanding.

Allopatric speciation is regarded as the major mode of speciation in birds (Price 2008), and typically requires the condition of disjunct patches of similar habitat. Due to their topography, the HEAN have moister and cooler conditions than their lower and more arid surrounds (Fjeldså & Lovett 1997). Most bird taxa which are endemic or near-endemic to the region occur in moister habitats than found in surrounding areas; namely, forests where there are adjacent woodlands and savannas, and savannas bordered by deserts. A second important factor that may have contributed to the high levels of endemism observed in this area is long-term habitat stability (Vaz da Silva 2015); the escarpment has trapped moisture-laden coastal air against it for millennia, bringing long-term climatic stability to the area (Hall 1960, Mills 2010).

The physical structure of the escarpment varies across its length, from north to south, which impacts habitats and, consequently, birds. Eleven broad landscape units have been defined within the HEAN based on their topographical, geomorphological, ecological and climatic characteristics (Mendelsohn & Huntley 2023); we are using these landscape units in this paper. However, even within the Central

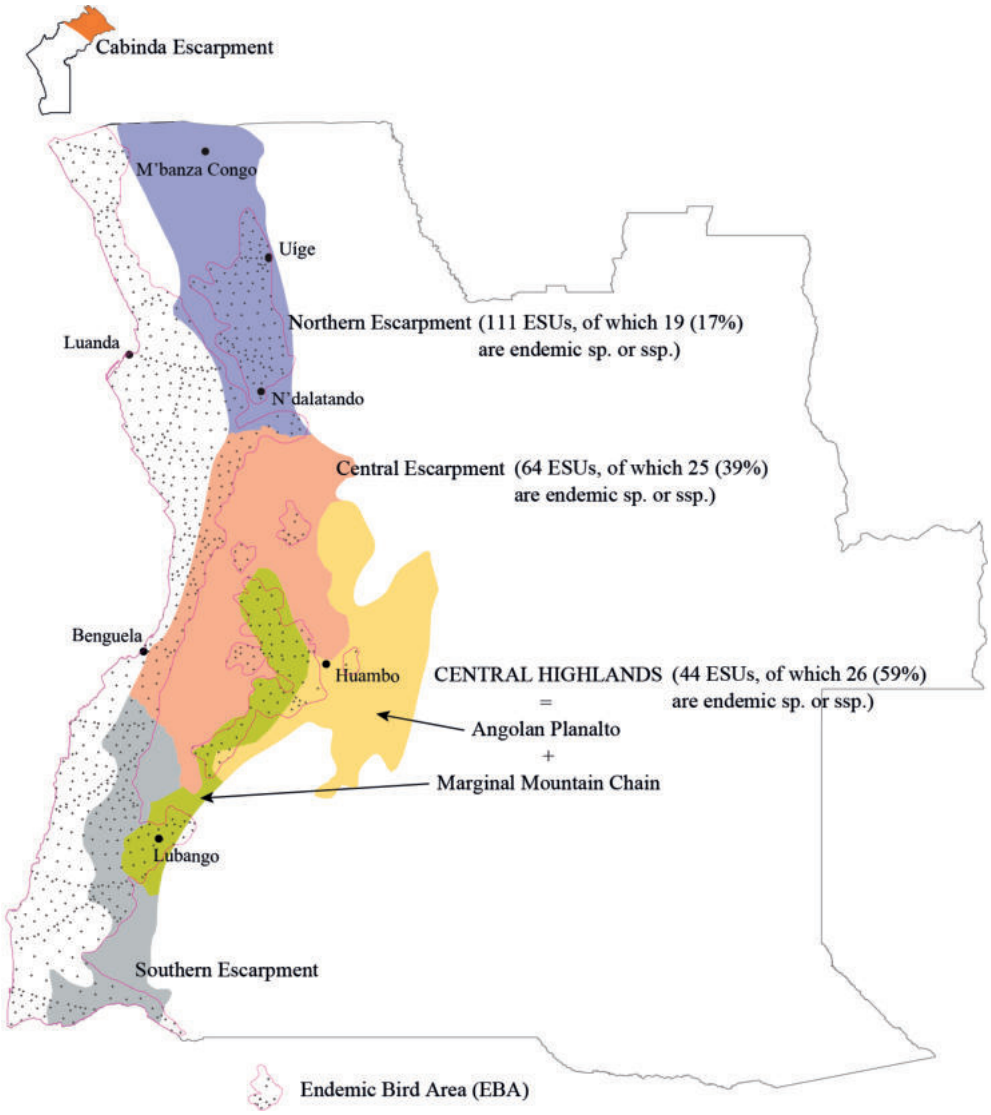

Figure 1: *Key avifaunal areas in Angola that fall within the highlands and escarpments of Angola and Namibia that are mentioned in the text. The escarpment, in its broadest sense, is divided into three main zones: Northern (purple), Central (pink) and Southern (grey). Notice the proximity of the escarpment to the Central Highlands along the Central and Southern escarpment. Also notice the decrease in the number of Evolutionarily Significant Units (ESUs) from north to south, along the escarpment, but the concurrent increase, especially in relative terms, in ESUs that are endemic species or subspecies.*

Escarpment landscape there are three distinctive forest bird communities linked to different types of forest habitats (Mills 2010).

The significance of the Angolan escarpment for the evolution of birds was studied by Hall (1960), who identified three groups of closely related birds that display different patterns of distribution relative to the escarpment. She identified three biological zones, namely the Escarpment Zone (a wedge of richer habitats on the escarpment), the *Acacia* Zone (arid savanna, including grasslands and mopane woodlands, along the coastal plain) and the *Brachystegia* Zone (miombo woodland on the plateau). The groups of birds identified were: (i) birds with a representative form in the Escarpment Zone and in either, or both, of the other zones; (ii) birds with representative forms in the *Brachystegia* and *Acacia* zones partly isolated from each other by the Escarpment Zone; and (iii) species endemic or nearly endemic to the Escarpment Zone. These groups demonstrate that the escarpment is both a centre of evolution, with taxa at different stages of evolutionary separation (groups i and iii), and a biological barrier between the more arid habitats of the coast and plateau (group ii). However, Hall (1960) did not address the distinctiveness of the escarpment in the wider context of lowland tropical forests, of which they are an outlier, and how the avifauna of the escarpment relates to that of other similar forests of the Congo Basin. Nor did she look at variation in the avifaunal composition along the escarpment, from north to south.

In this review, we assess the contribution of the HEAN to the evolution of the avifauna of the region.

METHODS

To identify potentially significant components of the avifauna for evolutionary study (here called Evolutionarily Significant Units or ESUs; Moritz 1994), we drew up a comprehensive list of birds confined or largely confined to the HEAN, using a cutoff of two-thirds of the global range or population size overlapping with the study area. This recognises that birds which currently have wider ranges, but whose distributions are centred on the study area, may be useful in understanding the biogeography of the region; they are likely to have evolved here and expanded their ranges more recently. We applied the aforementioned definition generously and without mapping in detail the ranges of the relevant birds (many of which are poorly known for Angola), and we included species which come close to matching the criteria using any dataset. While we recognise that the two-thirds cut-off is arbitrary, we believe that it is the most useful starting point for elucidating the contribution of the region (which also has arbitrarily defined borders) to the evolution of birds, and its links to other regions. Contra the general definition used in this work, we excluded Cabinda from our assessment of escarpment birds, largely because the forests and birds of Cabinda form a contiguous part of the main block of Congo Basin forests and bird populations. Consequently, there are no endemic taxa or isolated populations of birds known in Cabinda.

Each taxon that met these criteria was considered to be an ESU. For each one, we roughly estimated its degree of confinement to the study area, list whether it is an escarpment and/or montane species, list its closest relative based on best knowledge and give its distance of isolation to its sister taxon. Although the gap between the main Congo Basin forest block (immediately north of the Congo River) and the Northern Escarpment forest is rather small, at about 320 km, it constitutes a significant barrier to forest-restricted species, which tend to be highly sedentary. As such, many Congo Basin forest birds fail to cross it (based on our best knowledge) and, likewise, several Northern Escarpment forest species are not found in the nearby Congo Basin block (e.g., white-collared oliveback *Nesocharis ansorgei* and scaly-breasted illadopsis *Illadopsis albipectus*).

From this assessment flows a summary of bio-geographic links to other bird communities, and priorities for further study. Although birds are one of the best-known taxonomic groups of Angola, there are still large gaps in knowledge in basics, such as the distribution and status of many species (Dean *et al*. 2019), which could impact the overall assessment.

RESULTS

Overview of avifauna

Among the bird communities of the region, we identified 233 ESUs that are associated with the HEAN (Appendix 1). We defined the escarpment in its broadest sense here, to include moister habitats at the base and top of the escarpment that would not exist without the topography of the escarpment, and similar habitats that extend into the more arid adjacent areas along rivers where the occurrence of bird populations would be unlikely without the influence of the escarpment. We also included moister montane habitats; the isolated Afromontane forests, grasslands and shrublands.

Most significant among these ESUs are four monospecific genera which are endemic to the region, namely *Achaetops* (rockrunner), *Lanioturdus* (white-tailed shrike), *Namibornis* (Herero chat) and *Xenocopsychus* (Angola cave chat) (Appendix 1). These endemic genera are a consequence of divergence events predating the Plio-Pleistocene, the period typically associated with most bird speciation events that have led to much of the current African avifauna (Beresford *et al*. 2005). Interestingly, although Namibia

and southern Angola contribute little to the total number of ESUs of the study region, these four genera are all endemic to the Southern Escarpment. Thus, despite its relative lack of importance in terms of numbers of ESUs, this section of the escarpment contributes significantly to the overall evolutionary distinctiveness of the escarpment region. Additionally, Hartlaub's spurfowl *Pternistis hartlaubi* is basal to all other members of that genus, and Swierstra's francolin *P. swierstrai*, together with the other, extralimital, montane species, is part of an ancient radiation within the genus (Mandiwana-Neudani *et al*. 2019).

Next in significance are 37 taxa regarded as full species, none of which occurs exclusively in Namibia, although nine are found in Namibia and Angola. A few of these species also indicate links to the north (Gabon and Congo), and some species have distributions which extend onto the plateau of Angola, although these are generally confined to the higher-lying areas on its western margin.

The remainder of the ESUs can be divided into 71 recognised subspecies and 121 taxa with isolated populations which are not regarded as differentiated subspecifically. Together, these two groups are the most informative for understanding links to other regions, not only because of their larger sample size but also because close relatives can generally be assumed as the geographically nearest vicariant.

Of the subspecies, several have parapatric sister taxa whose differences are questionable and may, on reassessment, be found not to constitute ESUs. Similarly, other subspecies may be found to meet specific status in future assessments.

Among the ESUs represented by isolated populations, the vast majority are escarpment species with modest gaps in their range to their nearest vicariant; usually c. 320 km between the Northern Escarpment and the main Congo Basin. Given the small gaps in distribution, some gene flow is likely to persist between these populations and their vicariants, reducing the probability of them evolving along their own evolutionary trajectories. A few ESUs, however, mostly montane taxa, are isolated from closest relatives by more than 1,000 km. One can reasonably assume that gene flow is likely to be inversely proportional to gap size and so a significant proportion of these highly isolated populations may be reassessed to be independent subspecies or species in future or will evolve along independent trajectories and become genetically and phenotypically more isolated from their vicariants with time (Fjeldså & Bowie 2008).

Links to other avifaunas

First, when considering the escarpment and highlands as separate entities, it is apparent that the two areas have independent bird faunas with independent origins, although there are complicating factors. Foremost of these is the proximity between montane habitats and the escarpment in certain parts of Angola, especially within the Marginal Mountain Chain at Lubango and the Central Escarpment at Cumbira. This meeting of the two ecoregions at the top of the escarpment blurs their separation. Significantly, at Cumbira, typical lowland forest birds with links to the Congo Basin, such as buff-throated apalis *Apalis rufogularis,* and montane specialists, such as grey apalis *A. cinerea*, with links to distant montane areas, live within earshot of one another. Just above the treeline, at the same site, one also finds arid zone escarpment representatives with links to the south, such as rockrunner *Achaetops pycnopygius* and mountain wheatear *Myrmecocichla monticola*. The Central Escarpment is a particularly heterogenous area where montane habitats, lowland forest, arid escarpment and plateau miombo woodlands come together in a small area to form a region of great biological complexity.

To clarify the distinction between escarpment and highlands from an ornithological perspective, we defined any species which is absent from the main highlands (Serra do Môco and Serra da Namba region) as being an escarpment species, and any species that occurs in the main highlands but is absent from the main escarpment (generally around 700 masl) as a highland species. Only 13 of the ESUs occur in both the escarpment and highlands zones, including Angola cave chat *Xenocopsychus ansorgei* (Mount Soque and on isolated hills away from the escarpment such as around Serra da Neve), red-faced crimsonwing *Cryptospiza reichenovii* and Angola naked-faced barbet *Gymnobucco vernayi* (Serra da Namba and Cumbira). The remaining 220 taxa can be attributed to either the escarpment (n = 170) or highlands (n = 50).

The escarpment, as a whole, holds a much richer diversity of ESUs than the Afromontane region (see also Mills 2010, Mills *et al*. 2011, 2013). The vast majority of escarpment ESUs are separated from relatives by a break in the forest zone of about 320 km, between the northern tip of Pingano (the northernmost ridge of the Northern Escarpment) and the main Congo Basin forest block just north of the Congo River mouth (Figure 2). However, within this gap there are several patches of forest along rivers and in small pockets that almost certainly facilitate the movement of individuals between the two areas, and thus enhance gene flow. As a consequence, there are very few Northern Escarpment ESUs that are differentiated specifically or subspecifically from their nearest vicariants in the Congo Basin. Of a total

of 111 ESUs, just 15 are endemic subspecies (14%), of which only one is confined to the Northern Escarpment, and four are endemic species (4%), of which only one is confined to the Northern Escarpment (Braun's bushshrike *Laniarius brauni*). By contrast, the majority of ESUs (n = 92; 83%) involve isolated populations along the northern scarp. The proportion of the ESUs that have differentiated specifically or subspecifically – indicative of an absence or restriction of gene flow – is thus relatively small.

From north to south along the escarpment, however, specific and subspecific distinctiveness increases (Figure 1). Of the 64 forest ESUs that occur on the Central Escarpment (south of the Cuanza River), 15 are differentiated at the subspecies level (23%), including two which are endemic to the Central Escarpment, and 10 at the species level (16%), including three species endemic to the Central Escarpment. The remaining ESUs (n = 39; 61%) are of taxa with isolated populations. In Angola's Southern Escarpment, forest bird species are largely absent and the avifaunal connection to the Congo Basin is lost almost entirely.

In contrast to the escarpment zone, the ESUs of the Central Highlands (Figure 1, and equivalent to the combined Angolan Planalto and Marginal Mountain Chain of Mendelsohn and Huntley (2023)) are typically isolated from their nearest vicariants by a much larger distributional gap (typically more than 1,500 km). Although only 44 ESUs are found here, 26 (59%) of them have differentiated to the subspecies level and seven to species level. Thus, only a quarter of ESUs in the Central Highlands remain undifferentiated (n = 11; i.e., representing an

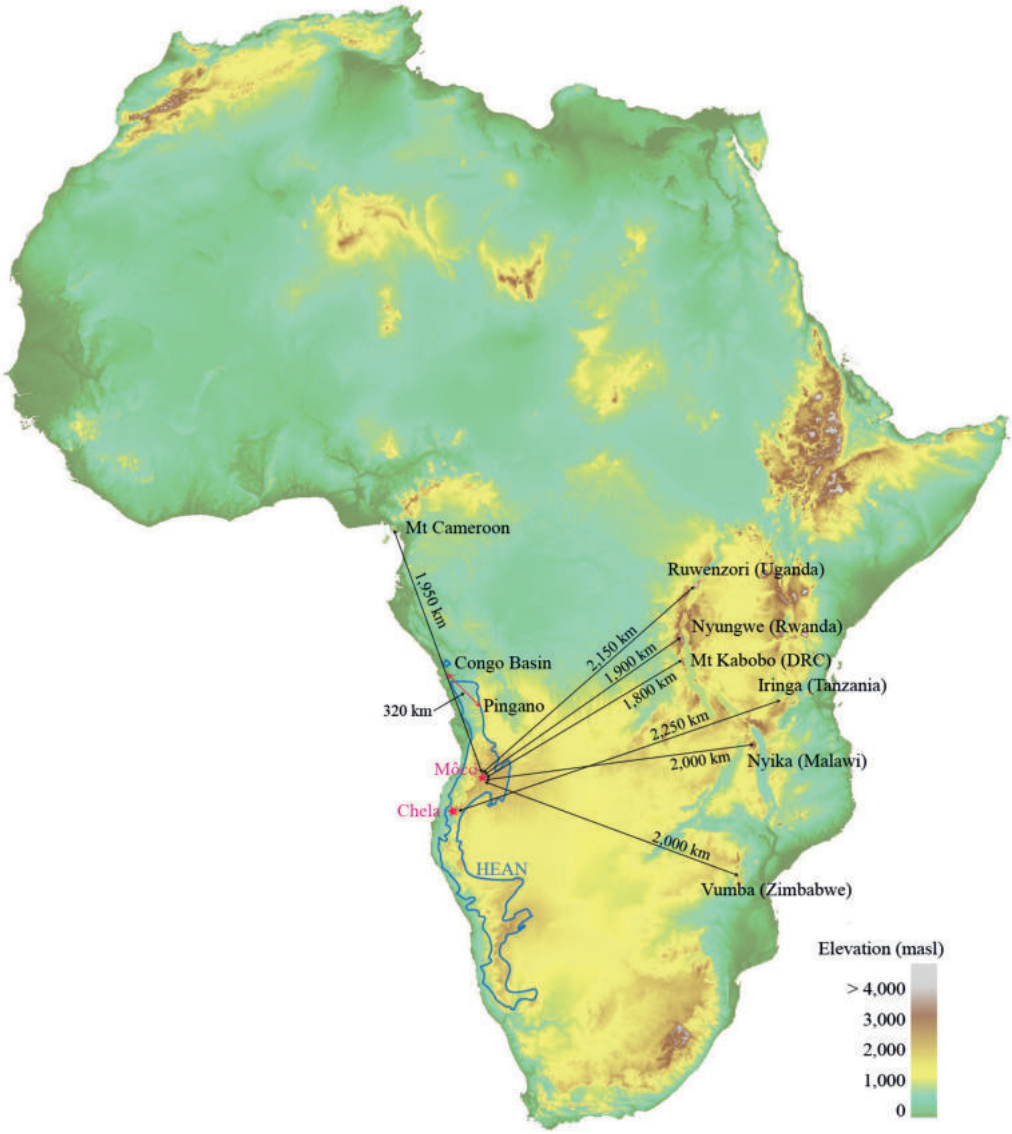

Figure 2: *Key links of the avifauna of the highlands and escarpments of Angola and Namibia (HEAN) region to other regions within Africa. The highlands (of which Serra do Môco is the highest point) lie at least 1,800 km from other Afromontane centres, whereas the gap between the Northern Escarpment and Congo Basin forests is much smaller.*

isolated population). Here the lower diversity is paired with a greater degree of differentiation, both of which are known to be the result of extreme isolation. The Afromontane forests of west-central Angola comprise the most isolated centre of the Afromontane archipelago biome (see White 1978), separated by more than 1,700 km from other similar habitats (Vaz da Silva 2015). Because of the mixed botanical composition of the Afromontane forests of Angola, they were not included in White's (1978) original definition of this phytochorion (or biome) based on plant communities. Nevertheless, their bird communities clearly identify them as belonging to the Afromontane biome (Dowsett 1986, Dowsett-Lemaire & Dowsett 1998). The number of endemics species entirely confined to these forests is small, but many subspecies, and ESUs more generally, are present (Appendix 1; Mills *et al*. 2011, 2013). Preliminary research – combining molecular data, ecological niche modelling, and the reconstruction of past climates and associated habitats – has shown that the small Angolan Afromontane forests are located in an area which has experienced high climatic stability across several glacial cycles (Vaz da Silva 2015). They also constitute an important historical link between the montane bird communities of East Africa and the mountains of Cameroon. White (1981), using plants as a model and Afromontane isolates as signals of historical connectedness (stepping stones), found evidence for a stronger link between the Ethiopian and Cameroonian highlands via a route south of the Congo Basin, via Angola, (named the Southern Migratory Track) rather than the more direct route that lies north of the Congo Basin. Dowsett-Lemaire and Dowsett (1998) found similar evidence for some birds, including two Angolan species, evergreen forest warbler *Bradypterus lopezi* and grey apalis *Apalis cinerea*. For species such as African hill babbler *Pseudoalcippe abyssinica* and Bocage's akalat *Sheppardia bocagei*, populations were isolated in the Angola mountains from very early on and are likely to constitute distinct species (Vaz da Silva 2015).

GAPS IN KNOWLEDGE

The simple analysis presented here reveals some potentially interesting patterns but relies on largely untested assumptions regarding the closest relatives of the region's significant bird taxa (ESUs). Even for taxa with published phylogenies, many are based on small sample sizes or incomplete taxon sampling. For example, rockrunner was found to be sister to Cape grassbird *Sphenoeacus afer* in one study (Beresford *et al*. 2005), whereas a second study found Cape grassbird to be sister to African moustached warbler *Melocichla mentalis* (Fregin *et al*. 2012); neither study sampled all three taxa, and so the actual relationships among the three species remains unresolved. More detailed and extensive studies of the origins and relationships of key bird taxa are needed to explore whether counterintuitive patterns exist that are currently being masked. Of special interest would be seemingly similar taxa that are assumed to be, but are not, most closely related to their geographically nearest vicariants (such as is the case with northern fiscal *Lanius humeralis* and southern fiscal *L. collaris*; Fuchs *et al*. 2011), and morphologically well-differentiated taxa that appear unrelated to nearby taxa but which actually share a common ancestor (for example, the montane white-eyes *Zosterops* spp. of East Africa; Cox *et al*. 2014).

Although bird endemism in Angola and Namibia is mostly concentrated in their highlands (escarpment and Afromontane forests), we know very little about the factors that have driven bird speciation here. Molecular data, sampled across most or all ESUs at the population level, should be obtained to elucidate the biogeography of the bird communities associated with this region (Kahindo *et al*. 2007). This alone would allow a comprehensive understanding of the diversification history of the avifauna of the highlands of Africa, highlight the dynamics of the interactions between different montane regions and between different parts of the Angolan escarpment and the Congo Basin, as well as the role of the cyclical climatic changes associated with the Plio-Pleistocene glaciations of the northern hemisphere (e.g., Voelker *et al*. 2010).

A preliminary study using five Afromontane forest bird species occurring in Angola has demonstrated the potential of genetic data to shed light on past evolutionary history (Vaz da Silva 2015). For the avifauna of the Angola escarpment, an obvious starting point would be to test the diversification hypotheses clearly put forward by Hall (1960). Ideally, this would be achieved as an 'umbrella project', built up from MSc and PhD projects carried out by Angolan and Namibian students.

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Appendix 1: *Significant bird taxa (Evolutionarily Significant Units) of the greater escarpment and highlands regions of Angola and Namibia, ranked in order of evolutionary/taxonomic significance. Taxonomy follows the International Ornithological Congress (IOC) World Bird List (Gill* et al. *2023) and all species listed by IOC are included. Additional species recognised by Handbook of the Birds of the World (HBW) and BirdLife International (HBW & BirdLife International 2022) are added, plus a few species based on recently published taxonomies that have not yet been assessed by world lists. None of our own taxonomic assessments affect the taxon list, although we do make comments where appropriate. Column heading abbreviations as follows: Ass = Percentage range association with the escarpment and highlands (67% minimum), M = Montane species, E = Escarpment species and D = Distance (km) to nearest extant relative, followed by the location of the relative (DRC = Democratic Republic of the Congo).*

Species	Ass	M	E	Closest relative	D	Location of relative
GENERA						
White-tailed shrike *Lanioturdus torquatus*	100	–	E	Western black-headed batis *Batis erlangeri* (Jonsson *et al*. 2016)	500	N Angola
Rockrunner *Achaetops pycnopygius*	100	–	E	African moustached warbler *Melocichla mentalis* (Fregin *et al*. 2012) or Cape grassbird *Sphenoeacus afer* (Beresford *et al*. 2005)	0 or 1,000	Parapatric/SW South Africa
Angola cave chat *Xenocopsychus ansorgei*	100	M	E	White-throated robin-chat *Dessonornis humeralis* (Zhao *et al*. 2023)	1,650	S Botswana
Herero chat *Namibornis herero*	100	–	E	Clade of fiscal flycatcher *Melaenornis silens* and silverbird *Empidornis semipartitus* (Zhao *et al*. 2023)	500	NW South Africa
SPECIES						
Finsch's francolin *Scleroptila finschi*	70	M	–	Possibly Whyte's francolin *Scleroptila whytei* (Mandiwana-Neudani *et al*. 2019)	500	NW Zambia
Hartlaub's spurfowl *Pternistis hartlaubi*	90	–	E	Clade of all other *Pternistis* francolins (Mandiwana-Neudani *et al*. 2019)	0	Sympatric
Swierstra's francolin *Pternistis swierstrai*	100	M	–	Clade of most other *Pternistes* francolins (Mandiwana-Neudani *et al*. 2019)	0	Sympatric
Grey-striped francolin *Pternistis griseostriatus*	100	–	E	Scaly francolin *P. squamatus* (Mandiwana-Neudani *et al*. 2019)	320	Cabinda
Red-crested turaco *Tauraco erythrolophus*	100	–	E	White-crested turaco *Tauraco leucolophus* (Perktas *et al*. 2020)	2,000	Cameroon
Red-backed mousebird *Colius castanotus*	100	M	E	Assumed speckled mousebird *C. striatus* or white-backed mousebird *C. colius*	0 or 100	Parapatric/far N Namibia
Violet wood hoopoe *Phoeniculus damarensis*	75	–	E	Green wood hoopoe *P. purpureus* (Cooper *et al*. 2001)	0	Sympatric
Monteiro's hornbill *Tockus monteiri*	75	–	E	Clade of several other *Tockus* spp. (Gonzalez *et al*. 2013)	0	Sympatric
Angola naked-faced barbet *Gymnobucco vernayi*	100	M	E	Assumed naked-faced barbet *G. calvus angolensis*	100	N Scarp of Angola
White-bellied barbet *Lybius leucogaster*	100	–	E	Assumed white-headed barbet *L. leucocephalus*	2,500	C Tanzania
Western black-backed barbet *Lybius minor*	75	M	E	Assumed eastern black-backed barbet *L. macclounii*	0	Parapatric
Rüppell's parrot *Poicephalus rueppellii*	75	–	E	Clade of all other *Poicephalus* parrots (Coetzer *et al*. 2015)	0	Sympatric
Angola batis *Batis minulla*	70	–	E	Assumed other central African forest *Batis* spp., e.g., West African batis *B. occulta*	250	C Gabon
White-fronted wattle-eye *Platysteira albifrons*	100	–	E	Brown-throated wattle-eye *P. cyanea* (Jonsson *et al*. 2016)	0	Parapatric
Monteiro's bushshrike *Malaconotus monteiri*	100	–	E	Assumed grey-headed bushshrike *M. blanchotii*	0	Parapatric
Braun's bushshrike *Laniarius [luehderi] brauni*	100	–	E	Assumed Luhder's bushshrike *L. luehderi*	320	Cabinda
Gabela bushshrike *Laniarius [luehderi] amboimensis*	100	–	E	Assumed Braun's bushshrike and/or Luehder's bushshrike	100	N Scarp of Angola
Gabela helmetshrike *Prionops gabela*	100	–	E	Assumed Retz's helmetshrike *P. retzii*	200	Plateau of Angola

Species	Ass	M	E	Closest relative	D	Location of relative
Carp's tit *Melaniparus carpi*	75	–	E	Assumed southern black tit *M. niger*	0	Parapatric
Pale-olive greenbul *Phyllastrephus fulviventris*	90	–	E	Assumed other relatives members of Genus *Phyllastrephus*	0	Sympatric
Angola white-throated greenbul *Phyllastrephus [albigularis] viridiceps*	100	–	E	Assumed white-throated greenbul. *P. albigularis*	320	Congo Basin
Pulitzer's longbill *Macrosphenus pulitzeri*	100	–	E	Assumed Kretschmer's longbill *M. kretschmeri*	2,100	SW Tanzania
Bubbling cisticola *Cisticola bulliens*	90	–	E	Assumed chattering cisticola *C. anonymus*, with which most likely conspecific	0	Parapatric
Huambo cisticola *Cisticola bailunduensis*	100	M	–	Short-winged cisticola *C. brachypterus* (Mills *et al*. in prep.)	0	Sympatric
Hartert's camaroptera *Camaroptera harterti*	100	–	E	Assumed grey-backed camaroptera *C. brevicaudata*	0	Parapatric
Bare-cheeked babbler *Turdoides gymnogenys*	100	–	E	Assumed other members of genus *Turdoides*	0	Sympatric
Angola yellow white-eye *Zosterops quanzae*	75	M	E	Clade including southern yellow white-eye *Zosterops anderssoni* (Martins *et al*. 2020)	0	Parapatric
Benguela long-tailed starling *Lamprotornis benguelensis*	100	–	E	Cunene long-tailed starling *L. violacior* and Meves's long-tailed starling *L. mevesii*	200	SW Plateau of Angola/SE Angola
Cunene long-tailed starling *Lamprotornis violacior*	100	–	E	Benguela long-tailed starling *L. benguelensis* and Meves's long-tailed starling *L. mevesii*	100	Base of S Scarp/SE Angola
Angola slaty flycatcher *Melaenornis brunneus*	100	M	–	Clade of other slaty flycatchers (Voelker *et al*. 2016)	2,000	NE Zambia/Albertine Rift
Gabela akalat *Sheppardia gabela*	100	–	E	Assumed Tanzanian montane *Sheppardia*	2,500	Probably C Tanzania
Rufous-tailed palm thrush *Cichladusa ruficauda*	70	–	E	Assumed collared palm thrush *C. arquata*	1,000	SW Zambia
Bocage's sunbird *Nectarinia bocagii*	75	M	–	Assumed Tacazze sunbird *N. tacazze*	2,100	N Tanzania
Ludwig's double-collared sunbird *Cinnyris ludovicensis*	100	M	–	Clade of other double-collared sunbirds, excluding Whyte's double-collared sunbird *C. whytei* (Bowie *et al*. 2016)	0	Sympatric
Golden-backed bishop *Euplectes aureus*	100	–	E	Yellow-crowned bishop *E. afer* (Prager *et al*. 2008)	0	Sympatric
Angola swee waxbill *Coccopygia bocagei*	100	M	–	Assumed swee waxbill *C. melanotis*	2,000	NE South Africa
Cinderella waxbill *Estrilda thomensis*	100	–	E	Assumed grey waxbill *E. perreini*	200	Parapatric
SUBSPECIES						
Orange River francolin *Scleroptila levalliantoides jugularis*	75	–	E	Conspecifics (Mandiwana-Neudani *et al*. 2019)	0	Parapatric
Red-necked spurfowl *Pternistis a. afer*	100	–	E	Red-necked spurfowl excluding *P. a. cranchii* (Mandiwana-Neudani *et al*. 2019)	2,000	E Zimbabwe/E Zambia
Rwenzori nightjar *Caprimulgus ruwenzorii koesteri*	100	M	–	Conspecifics	2,000	NE Zambia/Albertine Rift
Horus swift *Apus horus fuscobrunneus*	100	–	E	Conspecifics	300	CW Angola
African green pigeon *Treron calvus ansorgei*	100	–	E	Conspecifics	0	Parapatric

Species	Ass	M	E	Closest relative	D	Location of relative
Southern yellow-billed hornbill *Tockus leucomelas elegans*	100	–	E	Conspecifics	0	Parapatric
Crowned hornbill *Lophoceros a. alboterminatus*	100	–	E	Conspecifics	0	Parapatric
Olive bee-eater *Merops superciliosus alternans*	100	–	E	Conspecifics	1,000	SW Zambia
Naked-faced barbet *Gymnobucco calvus congicus*	75	–	E	Conspecifics	320	Cabinda
Anchieta's barbet *Stactolaema anchietae rex*	75	M	–	Conspecifics	0	Parapatric
Western green tinkerbird *Pogoniulus coryphaea angolensis*	100	M	–	Conspecifics	1,900	Albertine Rift/Cameroon
Green-backed honeybird *Prodotiscus zambesiae lathburyi*	100	M	–	Conspecifics	0	Parapatric
Elliot's woodpecker *Dendropicos elliotii gabela*	100	–	E	Conspecifics	320	Congo Basin
Rosy-faced lovebird *Agapornis roseicollis catumbella*	100	–	E	Conspecifics	0	Parapatric
Margaret's batis *Batis m. margaritae*	100	M	–	Conspecifics	500	NW Zambia
Eastern yellow-bellied wattle-eye *Platysteira a. ansorgei*	100	–	E	Conspecifics	800	S Gabon
Grey-headed bushshrike *Malaconotus blanchoti citrinipectus*	100	–	E	Conspecifics	0	Parapatric
Pink-footed puffback *Dryoscopus a. angolensis*	70	–	E	Conspecifics	800	S Gabon
Swamp boubou *Laniarius bicolor guttatus*	90	–	E	Conspecifics	200	Plateau of Angola and coast of Gabon
Dusky tit *Melaniparus funereus gabela*	100	–	E	Conspecifics	600	S DRC
Sabota lark *Calendulauda sabota ansorgei*	100	–	E	Conspecifics	0	Parapatric
Rufous-naped lark *Mirafra africana occidentalis*	100	–	E	Conspecifics	0	Parapatric
Angola lark *Mirafra a. angolensis*	100	M	–	Conspecifics	0	Parapatric
Long-billed crombec *Sylvietta rufescens ansorgei*	100	–	E	Conspecifics	0	Parapatric
Green crombec *Sylvietta virens tando*	90	–	E	Conspecifics	320	Congo Basin
Laura's woodland warbler *Phylloscopus l. laurae*	100	M	–	Conspecifics	500	NW Zambia
Evergreen forest warbler *Bradypterus lopezi boultoni*	100	M	–	Conspecifics	1,200	NC Zambia
Little rush warbler *Bradypterus baboecala benguellensis*	100	M	–	Conspecifics	0	Parapatric
Wailing cisticola *Cisticola lais namba*	100	M	–	Conspecifics	2,000	E Zambia/SW Tanzania

Species	Ass	M	E	Closest relative	D	Location of relative
Chirping cisticola *Cisticola p. pipiens*	100	M	–	Conspecifics	0	Parapatric
Croaking cisticola *Cisticola natalensis huambo*	90	M	–	Conspecifics	0	Parapatric
Desert cisticola *Cisticola aridulus lobito*	80	–	E	Conspecifics	0	Parapatric
Cloud cisticola *Cisticola textrix bulubulu*	75	M	–	Conspecifics	500	W Zambia
Banded prinia *Prinia bairdii heinrichi*	100	–	E	Conspecifics	320	W DRC
Buff-throated apalis *Apalis rufogularis brauni*	100	–	E	Conspecifics	100	N Scarp, but outside Angola in S DRC
Buff-throated apalis *Apalis rufogularis angolensis*	100	–	E	Conspecifics	250	C Scarp, but outside Angola in S DRC
Grey apalis *Apalis cinerea grandis*	100	M	–	Conspecifics, but could be brown-headed apalis *A. alticola*	2,000	If former, Cameroon/Albertine Rift, if latter, parapatric
Miombo wren-warbler *Calamonastes undosus huilae*	75	M	–	Conspecifics	0	Parapatric
Barred wren-warbler *Calamonastes fasciolatus pallidior*	100	–	E	Conspecifics	0	Parapatric
Brown illadopsis *Illadopsis fulvescens dilutior*	100	–	E	Conspecifics	320	Congo Basin
Black-faced babbler *Turdoides melanops angolensis*	100	–	E	Conspecifics	0	Parapatric
African thrush *Turdus pelios bocagei*	90	–	E	Conspecifics	0	Parapatric
Forest scrub robin *Cercotrichas leucosticta reichenowi*	100	–	E	Conspecifics	2,000	E DRC
Kalahari scrub robin *Cercotrichas paena benguellensis*	100	–	E	Conspecifics	0	Parapatric
Brown-chested alethe *Chamaetylas poliocephala hallae*	100	–	E	Conspecifics	320	W DRC
White-browed robin-chat *Cossypha heuglini subrufescens*	70	M	E	Conspecifics	0	Parapatric
Bocage's akalat *Sheppardia b. bocagei*	100	M	–	Conspecifics	500	NW Zambia
Mountain wheatear *Myrmecocichla monticola nigricauda*	100	M	–	Conspecifics	200	SW Angola
Familiar chat *Oenanthe familiaris angolensis*	100	–	E	Conspecifics	0	Parapatric
Carmelite sunbird *Chalcomitra f. fuliginosa*	95	–	E	Conspecifics	0	Parapatric
Bronzy sunbird *Nectarinia kilimensis gadowi*	100	M	–	Conspecifics	2,000	NE Zambia/E Zimbabwe/Albertine Rift
Purple-banded sunbird *Cinnyris b. bifasciatus*	75	–	E	Conspecifics	800	NE Namibia
Oustalet's sunbird *Cinnyris o. oustaleti*	100	M	–	Conspecifics	2,000	NE Zambia

Species	Ass	M	E	Closest relative	D	Location of relative
Thick-billed weaver *Amblyospiza albifrons tandae*	90	–	E	Conspecifics	800	W Zambia/Cameroon
Dark-backed weaver *Ploceus bicolor amaurocephalus*	100	–	E	Conspecifics	800	NE Angola
Red-headed malimbe *Malimbus rubricollis praedi*	100	–	E	Conspecifics	320	W DRC
Black bishop *Euplectes gierowii gierowii*	90	–	E	Conspecifics	1,900	Albertine Rift
Yellow bishop *Euplectes capensis angolensis*	70	M	–	Conspecifics	0	Parapatric
Fan-tailed widowbird *Euplectes axillaris quanzae*	100	–	E	Conspecifics	500	E Angola
White-winged widowbird *Euplectes albonotatus asymmetrurus*	80	–	E	Conspecifics	800	W Zambia
Grey-headed nigrita *Nigrita canicapillus angolensis*	100	–	E	Conspecifics	320	Cabinda
Dusky twinspot *Euschistospiza c. cinereovinacea*	100	M	–	Conspecifics	1,900	Albertine Rift
Jameson's firefinch *Lagonosticta rhodopareia ansorgei*	100	–	E	Conspecifics	800	NE Namibia
Common waxbill *Estrilda astrild angolensis*	100	M	–	Conspecifics	0	Parapatric
Nicholson's pipit *Anthus nicholsoni palliditinctus*	100	M	–	Conspecifics	0	Parapatric
Nicholson's pipit *Anthus nicholsoni moco*	100	M	–	Conspecifics	200	SW Angola
Black-faced canary *Crithagra capistrata hildegardae*	100	M	E	Conspecifics	0	Parapatric
Yellow-crowned canary *Serinus flavivertex huillensis*	100	M	–	Conspecifics	2,000	NE Zambia
Cape bunting *Emberiza capensis bradfieldi*	75	–	E	Conspecifics	0	Parapatric
Cape bunting *Emberiza capensis nebularum*	100	–	E	Conspecifics	0	Parapatric
ISOLATED POPULATIONS						
Western crested guineafowl *Guttera v. verreauxi*	100	–	E	Conspecifics	300	C Angola
Hartlaub's duck *Pteronetta hartlaubii*	100	–	E	Conspecifics	320	Cabinda
Freckled nightjar *Caprimulgus tristigma lentiginosus*	75	M	E	Conspecifics	500	W South Africa
Scarce swift *Schoutedenapus m. myoptilus*	100	M	–	Conspecifics	2,000	NE Zambia/E Zimbabwe/ Albertine Rift
Böhm's spinetail *Neafrapus b. boehmi*	100	–	E	Conspecifics	500	NW Zambia
Mottled swift *Tachymarptis a. aequatorialis*	100	M	–	Conspecifics	800	Zimbabwe/E Zambia
Fernando Po swift *Apus [barbatus] sladeniae*	100	M	–	Conspecifics	2,000	Cameroon
Great blue turaco *Corythaeola cristata*	100	–	E	Conspecifics	320	Cabinda
Green turaco *Tauraco persa persa*	100	–	E	Conspecifics	320	Cabinda
Gabon coucal *Centropus anselli*	100	–	E	Conspecifics	320	Cabinda
Blue yellowbill *Ceuthmochares aereus*	100	–	E	Conspecifics	320	Cabinda

Species	Ass	M	E	Closest relative	D	Location of relative
Dusky long-tailed cuckoo *Cercococcyx mechowi*	100	–	E	Conspecifics	320	Cabinda
Olive long-tailed cuckoo *Cercococcyx olivinus*	100	–	E	Conspecifics	320	Cabinda
Double-banded sandgrouse *Pterocles bicinctus ansorgei*	100	–	E	Conspecifics	0	Parapatric
Afep pigeon *Columba unicincta*	100	–	E	Conspecifics	320	Cabinda
African olive pigeon *Columba arquatrix*	100	M	–	Conspecifics	500	NW Zambia
Western bronze-naped pigeon *Columba iriditorques*	100	–	E	Conspecifics	320	Cabinda
Lemon dove *Columba larvata*	100	–	E	Conspecifics	500	NW Zambia
Congo serpent eagle *Circaetus spectabilis*	100	–	E	Conspecifics	320	Cabinda
Crowned eagle *Stephanoaetus coronatus*	100	–	E	Conspecifics	320	Cabinda
Rufous-breasted sparrowhawk *Accipiter r. rufiventris*	100	M	–	Conspecifics	2,000	NE Zambia
Augur buzzard *Buteo augur*	75	M	E	Conspecifics	800	NW Zimbabwe
Bar-tailed trogon *Apaloderma vittatum*	100	M	–	Conspecifics	2,000	NE Zambia/Albertine Rift
Eastern piping hornbill *Bycanistes sharpii*	100	–	E	Conspecifics	320	Cabinda
Black-casqued hornbill *Ceratogymna atrata*	100	–	E	Conspecifics	320	Cabinda
Blue-throated roller *Eurystomus gularis*	100	–	E	Conspecifics	320	Cabinda
Chocolate-backed kingfisher *Halcyon badia*	100	–	E	Conspecifics	320	Cabinda
Blue-breasted kingfisher *Halcyon malimbica*	100	–	E	Conspecifics	320	Cabinda
African dwarf kingfisher *Ispidina lecontei*	100	–	E	Conspecifics	320	Cabinda
White-bellied kingfisher *Corythornis leucogaster*	100	–	E	Conspecifics	320	Cabinda
Black bee-eater *Merops gularis*	100	–	E	Conspecifics	320	Cabinda
Speckled tinkerbird *Pogoniulus scolopaceus*	100	–	E	Conspecifics	320	Cabinda
Red-rumped tinkerbird *Pogoniulus atroflavus*	100	–	E	Conspecifics	320	Cabinda
Yellow-throated tinkerbird *Pogoniulus subsulphureus*	100	–	E	Conspecifics	320	Cabinda
Hairy-breasted barbet *Tricholaema hirsuta angolensis*	75	–	E	Conspecifics	320	Cabinda
Eastern yellow-billed barbet *Trachyphonus purpuratus*	100	–	E	Conspecifics	320	Cabinda
Cassin's honeybird *Prodotiscus insignis*	100	–	E	Conspecifics	320	Cabinda
Willcocks's honeyguide *Indicator willcocksi*	100	–	E	Conspecifics	320	Congo Basin
Least honeyguide *Indicator exilis*	100	–	E	Conspecifics	320	Cabinda
African piculet *Sasia africana*	100	–	E	Conspecifics	320	Cabinda
Buff-spotted woodpecker *Campethera nivosa*	100	–	E	Conspecifics	320	Cabinda

Species	Ass	M	E	Closest relative	D	Location of relative
Brown-eared woodpecker *Campethera caroli*	100	–	E	Conspecifics	320	Cabinda
Yellow-crested woodpecker *Chloropicus xantholophus*	100	–	E	Conspecifics	320	Cabinda
Olive woodpecker *Dendropicos griseocephalus ruwenzori*	100	M	–	Conspecifics	800	NE Angola
Red-fronted parrot *Poicephalus gulielmi*	100	–	E	Conspecifics	320	Cabinda
African pitta *Pitta a. angolensis*	100	–	E	Conspecifics	320	Cabinda
Chestnut wattle-eye *Platysteira castanea*	100	–	E	Conspecifics	320	Cabinda
Black-necked wattle-eye *Platysteira chalybea*	100	–	E	Conspecifics	500	C Gabon
Many-coloured bushshrike *Chlorophoneus multicolor batesi*	100	–	E	Conspecifics	500	Gabon
Bocage's bushshrike *Chlorophoneus bocagei*	100	–	E	Conspecifics	320	W DRC
Gorgeous bushshrike *Telophorus v. viridis*	100	M	E	Conspecifics	800	W Zambia
Petit's cuckooshrike *Campephaga petiti*	100	–	E	Conspecifics	320	Cabinda
Purple-throated cuckooshrike *Campephaga quiscalina*	100	–	E	Conspecifics	320	Cabinda
Mackinnon's shrike *Lanius mackinnoni*	100	–	E	Conspecifics	320	W DRC
Black-winged oriole *Oriolus nigripennis*	100	–	E	Conspecifics	320	W DRC
Blue-headed crested flycatcher *Trochocercus nitens*	100	–	E	Conspecifics	320	Cabinda
Bates's paradise flycatcher *Terpsiphone batesi bannermani*	100	–	E	Conspecifics	320	Congo Basin
African blue flycatcher *Elminia longicauda*	100	–	E	Conspecifics	320	Congo Basin
Ashy tit *Melaniparus cinerascens benguelae*	100	–	E	Conspecifics	0	Parapatric
Yellow-throated nicator *Nicator vireo*	100	–	E	Conspecifics	320	Congo Basin
Slender-billed greenbul *Stelgidillas gracilirostris*	100	–	E	Conspecifics	320	Congo Basin
Plain greenbul *Eurillas curvirostris*	100	–	E	Conspecifics	320	Congo Basin
Yellow-whiskered greenbul *Eurillas latirostris*	100	–	E	Conspecifics	320	Congo Basin
Swamp palm bulbul *Thescelocichla leucopleura*	100	–	E	Conspecifics	320	Congo Basin
Red-tailed bristlebill *Bleda syndactylus*	100	–	E	Conspecifics	320	Congo Basin
Brazza's martin *Phedina brazzae*	90	M	–	Conspecifics	0	Sympatric
White-throated blue swallow *Hirundo nigrita*	100	–	E	Conspecifics	320	Congo Basin
Forest swallow *Petrochelidon fuliginosa*	100	–	E	Conspecifics	800	S Gabon
Yellow longbill *Macrosphenus flavicans*	100	–	E	Conspecifics	320	Congo Basin

Species	Ass	M	E	Closest relative	D	Location of relative
Green hylia *Hylia prasina*	100	–	E	Conspecifics	320	Congo Basin
Tit hylia *Pholidornis rushiae*	100	–	E	Conspecifics	320	Congo Basin
Red-faced cisticola *Cisticola erythrops lepe*	75	M	–	Conspecifics	0	Parapatric
Pale-crowned cisticola *Cisticola c. cinnamomeus*	75	M	–	Conspecifics	1,000	NW Zambia
Wing-snapping cisticola *Cisticola a. ayresii*	100	M	–	Conspecifics	1,000	NW Zambia
Lowland masked apalis *Apalis binotata*	100	–	E	Conspecifics	1,500	NE Gabon
Black-throated apalis *Apalis j. jacksoni*	100	–	E	Conspecifics	1,900	Albertine Rift
Yellow-browed camaroptera *Camaroptera superciliaris*	100	–	E	Conspecifics	320	Congo Basin
Rufous-crowned eremomela *Eremomela badiceps*	100	–	E	Conspecifics	320	Congo Basin
Scaly-breasted illadopsis *Illadopsis albipectus*	100	–	E	Conspecifics	500	C DRC
African hill babbler *Pseudoalcippe abyssinica ansorgei*	100	M	–	Conspecifics	2,000	NE Zambia/Albertine Rift/ Cameroon
Southern hyliota *Hyliota australis slatini*	100	–	E	Conspecifics	0	Central Angola
Forest chestnut-winged starling *Onychognathus fulgidus*	100	–	E	Conspecifics	320	Congo Basin
Narrow-tailed starling *Poeoptera lugubris*	100	–	E	Conspecifics	320	W DRC
White-tailed ant thrush *Neocossyphus poensis*	100	–	E	Conspecifics	320	Congo Basin
Rufous flycatcher thrush *Stizorhina fraseri*	100	–	E	Conspecifics	320	Congo Basin
Orange ground thrush *Geokichla gurneyi otomitra*	100	M	–	Conspecifics	1,800	SE DRC
Fire-crested alethe *Alethe castanea*	100	–	E	Conspecifics	320	Congo Basin
Brown-backed scrub robin *Cercotrichas hartlaubi*	100	–	E	Conspecifics	2,000	E DRC/Cameroon
Grey-throated tit-flycatcher *Myioparus griseigularis*	100	–	E	Conspecifics	320	Congo Basin
Cassin's flycatcher *Muscicapa cassini*	100	–	E	Conspecifics	320	Congo Basin
Dusky-blue flycatcher *Muscicapa comitata*	100	–	E	Conspecifics	320	Congo Basin
Sooty flycatcher *Muscicapa infuscata*	100	–	E	Conspecifics	320	Congo Basin
Little green sunbird *Anthreptes seimundi*	100	–	E	Conspecifics	320	Congo Basin
Grey-chinned sunbird *Anthreptes tephrolaemus*	100	–	E	Conspecifics	320	Congo Basin
Green-headed sunbird *Cyanomitra verticalis*	100	–	E	Conspecifics	320	Congo Basin
Blue-throated brown sunbird *Cyanomitra cyanolaema*	100	–	E	Conspecifics	320	Congo Basin
Olive sunbird *Cyanomitra olivacea*	100	–	E	Conspecifics	320	Congo Basin
Green-throated sunbird *Chalcomitra rubescens*	100	–	E	Conspecifics	320	Congo Basin

Species	Ass	M	E	Closest relative	D	Location of relative
Olive-bellied sunbird *Cinnyris chloropygius*	100	–	E	Conspecifics	320	Congo Basin
Superb sunbird *Cinnyris superbus*	100	–	E	Conspecifics	320	Congo Basin
Black-chinned weaver *Ploceus nigrimentus*	100	M	–	Conspecifics	800	NE Angola
Black-necked weaver *Ploceus nigricollis*	100	–	E	Conspecifics	320	Congo Basin
Yellow-mantled weaver *Ploceus tricolor*	100	–	E	Conspecifics	320	W DRC
Brown-capped weaver *Ploceus insignis*	100	–	E	Conspecifics	1,900	Albertine Rift
Crested malimbe *Malimbus malimbicus*	100	–	E	Conspecifics	320	W DRC
Woodhouse's antpecker *Parmoptila woodhousei ansorgei*	100	–	E	Conspecifics	320	W DRC
White-breasted nigrita *Nigrita fusconotus*	100	–	E	Conspecifics	320	Cabinda
Chestnut-breasted nigrita *Nigrita bicolor*	100	–	E	Conspecifics	320	Cabinda
Pale-fronted nigrita *Nigrita luteifrons*	100	–	E	Conspecifics	320	Cabinda
White-collared oliveback *Nesocharis ansorgei*	100	–	E	Conspecifics	1000	S DRC/Albertine Rift
Green twinspot *Mandingoa nitidula schlegeli*	100	–	E	Conspecifics	320	W DRC
Red-faced crimsonwing *Cryptospiza reichenovii reichenovii*	100	M	E	Conspecifics	2,000	E Zimbabwe/NE Zambia/Albertine Rift
Red-headed bluebill *Spermophaga r. ruficapilla*	100	–	E	Conspecifics	320	S DRC
Landana firefinch *Lagonosticta landanae*	90	M	E	Conspecifics	0	Parapatric
Black-and-white mannikin *Lonchura bicolor*	100	–	E	Conspecifics	320	Congo Basin
Magpie mannikin *Lonchura fringilloides*	100	–	E	Conspecifics	500	Gabon
Dusky indigobird *Vidua funerea* (Dusky Twinspot parasite)	100	M	–	Conspecifics	0	Parapatric
Mountain wagtail *Motacilla clara*	100	M	E	Conspecifics	800	NE Angola
Striped pipit *Anthus lineiventris*	100	M	–	Conspecifics	800	W Zambia
Bushveld pipit *Anthus caffer*	100	M	–	Conspecifics	800	W Zambia
Thick-billed seedeater *Crithagra burtoni tanganjicae*	100	M	–	Conspecifics	1,900	Albertine Rift