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Description of two new *Cisticola* species endemic to the marshes of the Kilombero floodplain of southwestern Tanzania

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The presence of two undescribed cisticola warblers in the marshes of the Kilombero floodplain in central Tanzania has been known since the 1980s and these putative new species have been illustrated in field guides on African birds, although with no formal name. Here we name both species, based on two museum specimens collected in 1961 and recently detected in a museum collection. We use these specimens to provide formal descriptions of each form and, using DNA sequence data extracted from these specimens, we place them in a broad phylogenetic framework for the genus *Cisticola*. The phylogenetic placement indicates that one of the new species is nested within a group of plain-backed duetting cisticolas and the other within the streak-backed marsh cisticolas. We use our own and public recordings to characterize the vocal repertoire of each of these new species and compare song characteristics with other members of their respective clades. Dating of nodes in the molecular phylogeny suggests that both cisticolas endemic to the Kilombero became isolated and diverged from their sister-species between 2.5 and 3.5 million years ago, long after the formation of the Eastern Arc Mountains and the Malawi Rift. We propose that both species should be classified as globally endangered, owing to immense anthropogenic pressures on the floodplain, as documented in several publications and by a recent Ramsar Advisory Mission.

Keywords: Africa, Cisticolidae, conservation, habitat selection, new species, Ramsar, wetlands.

INTRODUCTION

Although birds are generally well known at the species level, new species units are being defined through systematic revision, by combining multiple types of evidence ('integrative taxonomy'; Sangster 2009), and genuinely new species continue to be discovered (Brewer 2018). The rate of discovery of new species has been rising over the past two decades (Kennedy & Fjeldså 2020), with most new species being discovered in poorly explored mountain areas with little infrastructure, and in archipelagos (e.g. Rheindt *et al.* 2020). Only rarely are new species discovered in easily accessible places. We here present such a case where two new putative species of cisticola

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warblers (genus *Cisticola*, Cisticolidae) were discovered at the same location, close to modern infrastructure and a rural town.

The identification and classification of cisticola warblers has been problematic for both professional and amateur ornithologists because of their cryptic coloration, seasonal variation in plumage and the patchy geographical distributions of many of the 51 currently recognized species (Gill *et al.* 2020). Cisticola warblers primarily inhabit wetlands, savannah, broadleaved woodlands and upland habitats, almost exclusively in Africa. The work by Rear Admiral Hubert Lynes, published as a 673-page supplement to *Ibis* (Lynes 1930), was a milestone towards understanding species relationships and limits among the cisticolas, and his arrangement has to a large extent been confirmed by recent phylogenetic studies based on DNA data (Nguembock *et al.* 2008, 2012, Olsson *et al.* 2013, Davies 2014).

Two putative new cisticolas (*Cisticola* sp.) were, along with the Kilombero Weaver *Ploceus burnieri*, recognized in the 1980s by Eric Burnier and Neil and Liz Baker near the rural town of Ifakara, in the lowland marshes of the Kilombero (or Ruhuhu) floodplain in the Kilombero District in southwestern Tanzania, and their presence was soon confirmed (Baker & Baker 1990, 2002). The two putative new cisticola warblers were illustrated and briefly described, with no formal scientific naming, by Stevenson and Fanshawe (2002), Sinclar and Ryan (2003) and Ryan *et al.* (2006). These cisticolas have attracted many birdwatchers to the bridge across the Kilombero River (08°11′21″S, 36°41′34″E, previously a ferry site) south of Ifakara, and they have been featured in the *Handbook of Birds of the World* (Ryan *et al.* 2006: photo p. 419 and text p. 382) and on several webpages. Details about their distributions, habitat selection and population densities have even been published (Jones & John 2008, Rannestad *et al.* 2015). Moreover, they have been referred to in a number of conservation-related publications (e.g. Baker & Baker 1990, 2002, Fishpool & Evans 2001, Starkey *et al.* 2002, Dinesen 2018).

One of the putative new species, to date referred to as 'Kilombero Cisticola' (or 'Melodious Cisticola'), has been associated with Lynes' (1930) *C. nigriloris* group, or 'montane cisticolas' of Hall and Moreau (1970), alias 'duetting' or 'plain-backed cisticolas' of various field guides (e.g. Stevenson & Fanshawe 2002, Sinclar & Ryan 2003). This group comprises Chubb's *C. chubbi*, Hunter's *C. hunteri* and Black-lored Cisticola *C.nigriloris*, which replace one another in different highlands in eastern Africa and the Cameroon Mountains; thus, they occur in an ecological zone distinct from the lowland marshes of the Kilombero floodplain.

The other putative species, to date referred to as 'White-tailed Cisticola', has been associated with Lynes' (1930) *Cisticola galactotes* group, or 'marsh cisticolas' of Hall and Moreau (1970), alias 'streak-backed marsh cisticolas' (Stevenson & Fanshawe 2002, Sinclar & Ryan 2003). This group comprises the rufous-winged *C. galactotes* superspecies, which is distributed over most of Africa's savanna regions, and two more locally distributed species, Chirping Cisticola *C. pipiens* and Carruthers's Cisticola *C. carruthersi*. They are gracile birds with rather long tails, inhabiting marshy habitats and adjacent rank grass. Dickinson and Christidis (2014) retained the members of the *C. galactotes* complex as a single species, but Ryan *et al.* (2006) and Gill *et al.* (2020) recognized five species: Rufous-winged *C. galactotes*, Luapula *C. luapula*, Coastal *C. haematocephalus*, Winding *C. marginatus* and Ethiopian Cisticolas *C. lugubris*, which replace each other across different regions, in addition to the Chirping and Carruthers's Cisticolas. The distinction of each of these species was supported by the molecular phylogenetic study of Davies (2014), which suggested population divergence in the Pliocene and early Pleistocene.

Specimens of Kilombero floodplain cisticolas collected (by others) in the 1990s have subsequently been lost, but J.F. found that both forms were already represented in the collections of the Zoological Museum, at the Natural History Museum of Denmark, with specimens collected in 1961 by the late Thorkild Andersen. As part of Andersen's endeavours from 1947 to 1967 to establish a collection of all Tanzanian birds, he sailed in November 1961 along the Kilombero River (letter of December 1961 to Finn Salomonsen (bird curator at that time) in the museum archives). He obtained, among other species, one of each of the two local cisticolas, and labelled both as *Cisticola galactotes*. Because of the long delay in describing these birds based on new material, we decided (in agreement with Liz and Neil Baker) to describe these birds formally, using the two above-mentioned museum specimens as type material.

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Using DNA sequence data from toepads of these two specimens as well as detailed morphological and bioacoustic descriptions of the two putative new species, along with comparative information on related species, we here evaluate the systematic position of the two taxa hitherto known as the 'Kilombero Cisticola' and 'White-tailed Cisticola', and formally describe them. We also address the conservation status of these range-restricted forms.

METHODS

Field observations

J.F. observed both of the putative new cisticola warbler species at the site of the Kilombero Ferry on 9 December 1995 and L.D. made observations at this same site on 20–25 February 2001. These observations were made in connection with other fieldwork in the surrounding areas and were of brief duration, as we assumed that the birds were about to be described and named by others. A dedicated effort to obtain photographic and bioacoustic documentation and data on habitat use was undertaken in 2019 on 28–30 June, and on 25–28 July by L.A.H. (see Supporting Information). During the morning hours, he slowly sailed in a canoe along the banks of various river channels, listening for singing cisticolas, performing playback and landing on some river islands. During the afternoons he surveyed the surrounding river banks on foot and documented the activity and habitat use by the cisticolas. Our own data were supplemented with published information, notably from Jones and John (2008), Rannestad *et al.* (2015) and online sources, including reports from birding trips; these latter sources are not necessarily verifiable but provided valuable photos to supplement our descriptions (see 'Other material available' in the species descriptions). Comparative information about other cisticola species was gleaned from handbooks, such as Britton (1980), Urban *et al.* (1997) and Ryan *et al.* (2006).

Specimens examined

We examined all *Cisticola* specimens referable to Lynes' (1930) *nigriloris* and *galactotes* groups in the Natural History Museum of Denmark, Naturkundemuseum in Berlin and the National Museums of Kenya (see Appendix 1 for number of specimens). O.R.D. examined museum material for all *Cisticola* taxa in the collections of the Natural History Museum at Tring, UK (Davies 2014). We described plumage variation and recorded measurements of bill (to skull), wing (flattened), tail and tarsus (Svensson 1992, method 3) for different geographical populations that have been recognized as subspecies. In the description of plumages, colours written with a capital first letter denote those that match Ridgway's (1912) colour standard (which comprises a greater number of earth-toned colours than newer colour standards).

Vocalizations

Recordings of vocalizations have been obtained from public sound libraries and private sources. Sound recordings made during L.A.H.'s 2019 fieldwork were made with a Marantz PMD field recorder or Tascam DR-100MKIII recorder, with Sennheiser MKH microphones, and comprise many songs and calls of the two species (83 recordings uploaded to the website www.xeno-canto.com). Sonograms were drawn and compared using COOLEDITPRO (Syntrillium Software, Scottsdale, AZ, USA).

Molecular work

Phylogenetic relationships of cisticola warblers were studied by Davies (2014) using two mitochondrial markers (ND2, CYTB) and three nuclear markers (MB intron 2, FGB intron 5, TGFB2 intron 5; primers detailed in Table S1); the nuclear markers provided limited resolution. Sequencing was performed in both directions on an Applied Biosystems capillary sequencer and fragments of each gene were assembled in SEQUENCER 5.4.6. Toepad samples from the two specimens were extracted in a clean room and sequenced in short fragments using custom-designed primers for the introns and ND2 (Table S1). This allowed us to place the cisticolas of the Kilombero floodplain in the multi-locus phylogeny developed by Davies (2014), comprising most of the species in the genus *Cisticola*. We made use of two optimality criteria, maximum parsimony (MP) and maximum likelihood (ML), to construct a phylogenetic hypothesis of the genus *Cisticola*. The multilocus data matrix comprised 45 described species and the two putative new species, and trees were rooted with the Green Jery *Neomixis viridis*, an

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early diverging member of the Cisticolidae. Loci were aligned using MAFFT 7.471 (Katoh *et al.* 2009). The parsimony analyses were implemented using PAUP* 4.0a168 (Swofford 2002) with a heuristic search and 1000 random addition replicates with TBR branch-swapping. Node support was determined using 1000 bootstrap replicates with five random addition replicates per bootstrap replicate. For the ML analyses, we performed a joint bootstrap analysis and tree search using RAXML 8.2.10 (Stamatakis 2014) on the dataset partitioned by gene and codon position using a GTR+G model of nucleotide substitution, on the CIPRES SCIENCE GATEWAY supercomputer (Miller *et al.* 2010).

RESULTS

Distribution

Both White-tailed and Kilombero Cisticolas inhabit areas with reeds, grassland and scattered bushes within the floodplain of the Kilombero Valley in southwestern Tanzania (Fig. 1). Both type specimens were collected in the area near the present Ifakara Bridge. Judging from the rather uniform habitat across the entire Kilombero floodplain, as viewed on Google Earth and from airplane reconnaissance in 2001 (L.D.), we expect that both species exist along 70 km of floodplain extending from the southwestern (08°49′17″S, 36°02′01″E) to the northeastern section beyond the Ifakara bridge (*c.* 08°17′31″S, 37°06′00″E), with a presumed satellite population around the village of Mang'ula A, 44 km ENE of Ifakara. The elevational range extends from *c.* 240 to 305 m. However, it is possible that the Kilombero Cisticola has a smaller and patchier distribution within the floodplain (Starkey *et al.* 2002, Jones & John 2008, see Discussion), probably due to its preference for natural tall and mature *Phragmites* vegetation. The White-tailed Cisticola, in contrast, has been found in a broader range of habitats including grassland somewhat degraded by grazing from cattle and sheep. The natural vegetation of the floodplain is described by Hood *et al.* (2002; see Supporting Information).

Characterization and comparison of duetting (or plain-backed) cisticolas

The duetting cisticolas, recognized since Lynes' (1930) monograph and confirmed as a monophyletic group by Davies (2014), are characterized by plain backs, black lores and duetting songs (Todt 1970, Thorpe 1972). Chubb's *Cisticola C. chubbi* is represented by two subspecies *discolor* and *adametzi* in the Cameroon Highlands in western Africa, and two subspecies, *chubbi* and *marungensis*, in the highlands along the Albertine Rift, from 1000 to 2500 m, with an extension to northwestern Kenya and northern Tanzania (Urban *et al.* 1997, Baker & Mlawila 2019, and www.xeno-canto.com). In Kenya, Chubb's Cisticola overlaps at 1500 m with Hunter's Cisticola on Mt. Elgon; the latter species is in turn distributed across the highlands of Kenya and northern Tanzania, reaching 4400 m, primarily in montane forest, scrub and tall grass (Urban *et al.* 1997, Ryan *et al.* 2006). Past classifications among these species have varied (e.g. Macworth-Praed & Grant 1960, Britton 1980, Urban *et al.* 1997, Ryan *et al.* 2006, Dickinson & Christidis 2014).

The Black-lored Cisticola is distributed over much of the Rubeho and Udzungwa Highlands and highlands near the Rukwa and Malawi Rifts, extending from western Tanzania south to the Nyika and Northern Viphya Plateau of Malawi (Dowsett-Lemaire & Dowsett 2006), with one record in the Mafinga Mountains in adjacent eastern Zambia (Dowsett *et al.* 2008). The Black-lored Cisticola occupies swampy areas within or adjacent to montane forest, but also occurs in bracken, briar and grassy vegetation and in adjacent agricultural fields, observed during fieldwork by L.D., J.F. and L.A.H. There is a distinct ecological gap between its range in the Udzungwa Highlands (1100–2750 m; Fjeldså *et a*l. 2010) and that of the Kilombero Cisticola on the Kilombero floodplains (240–305 m), and we have never recorded duetting cisticolas during substantial periods of fieldwork anywhere in the habitat mosaics (which includes patches of swampy habitat) in Matundu or the West Kilombero Forests in the intervening foothills.

Morphological comparisons

All the duetting cisticolas (Appendix 1) share a fairly uniform plumage (but with faint streaks in some specimens of Hunter's Cisticola, and in juveniles of other species) with a warmer brown hue on the crown, underparts with a distinct greyish wash, being buffy white in the Kilombero Cisticola. The graduated, fan-shaped tails have black

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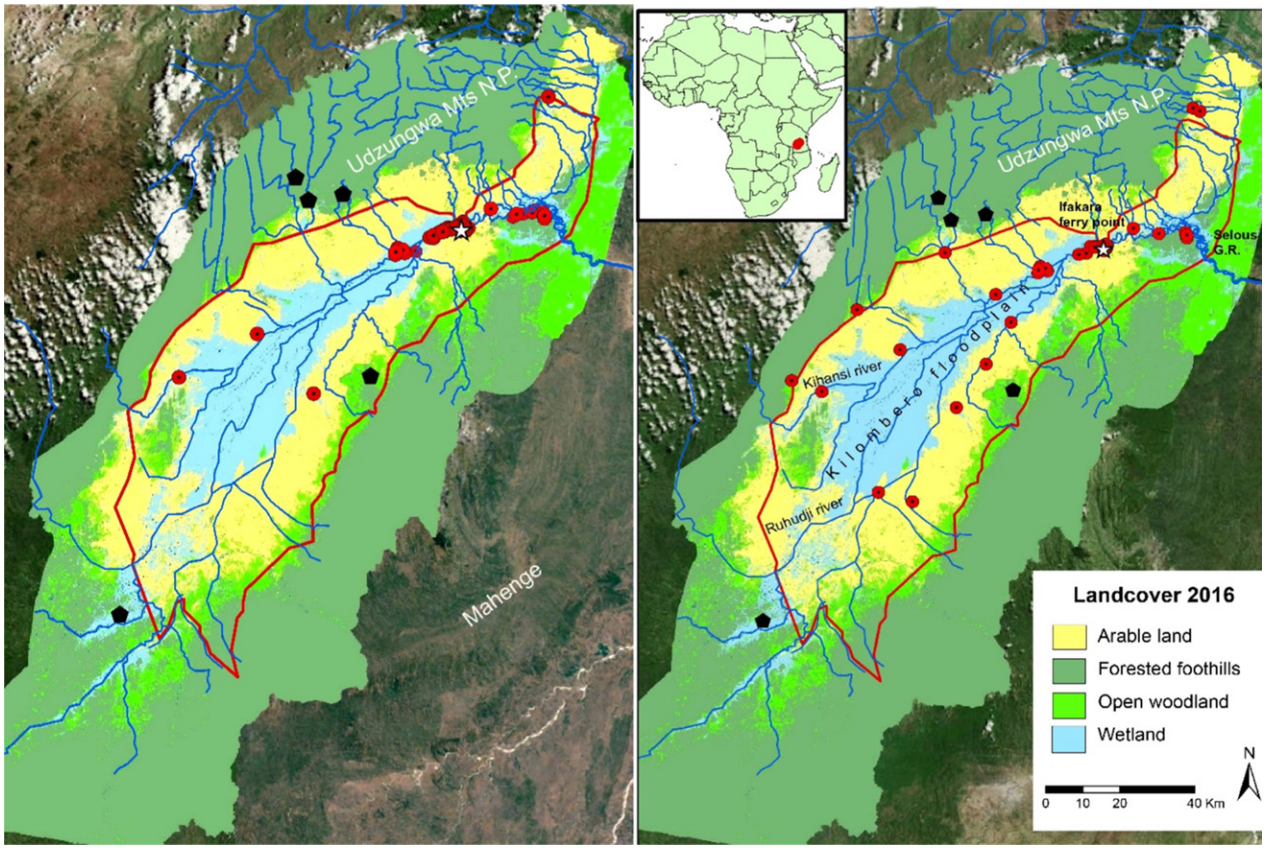

Figure 1. Maps of the Kilombero floodplain in the Kilombero and Ulanga Districts of southwestern Tanzania, with records of the Kilombero Cisticola to the left and the White-tailed Cisticola to the right (red dots marking distribution records of these cisticolas and black pentagons marking well-studied localities with humid grassland where they were not found). Records are from Jones and John (2008), Rannestad (*in litt.*) and fieldwork by J.F., L.D. and L.A.H. Map modified after Martin *et al.* (2017). The 6895 km^2 large floodplain at 240–305 m is flanked to the north by the ancient Udzungwa Mountains, which reach 2750 m in elevation, and to the south and east by the Mahenge Highlands (1300 m) and hills of the Selous Game Reserve. The bridge south of Ifakara is marked with a star. The red line delineates the Kilombero Valley Floodplain Ramsar site designated in April 2002 (Ramsar Convention on Wetlands 2002, Dinesen 2018). [Colour figure can be viewed at wileyonlinelibrary.com]

subterminal spots on all rectrices, vestigial on the central feathers but generally broad on the outer feathers. Hunter's Cisticola differs from the other duetting species, and notably from the Kilombero Cisticola, by its rather drab appearance, with mostly drab-grey underparts. The lores are dusky or benzo brown in Hunter's and black in Chubb's and Black-lored Cisticolas, but whitish in Kilombero Cisticola. Black-lored Cisticolas (notably birds from the Malawi Rift highlands) are significantly richer brown above than all other forms and rather uniform pale greyish below, except that juveniles are whitish on the central belly, more like Kilombero Cisticola.

The Kilombero Cisticola is smaller than Chubb's and Hunter's Cisticolas and these taxa are distinctly smaller than Black-lored Cisticola (wing lengths 57, 56–66, 55–65 and 59–71 mm, respectively; Appendix 2). The Kilombero Cisticola stands out by having a long, slender and slightly curved bill (Fig. 2, the longest bill of any cisticola). Judging from our single specimen and from available photos, the plumage is much paler than that of other duetting cisticolas and not as dark as illustrated by Stevenson and Fanshawe (2002) and Sinclar and Ryan (2003). It also differs from other duetting cisticolas in having a prominent white anterior supercilium and a generally pale lore often with a small dusky spot towards the eye, as well as mostly white underparts washed with cinnamon buff laterally and across the breast (see below). Pale lores with only a restricted dusky spot are

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often seen in the juveniles of other duetting cisticolas. However, most juvenile Black-lored Cisticolas have blackish lores, although less clearly demarcated, and some specimens have a pale (yellowish white) stripe along the upper lore. Field observations suggest that Kilombero Cisticolas, akin to all cisticola warbler species, can be identified by a yellowish wash to their underparts, slightly warmer tinge to the entire plumage and less well-defined dusky subterminal spots on the rectrices.

Vocalizations

The Kilombero Cisticola and its closest relatives, Chubb's, Hunter's and Black-lored Cisticolas, are those members of the genus in which pairs sing the most elaborate and precisely synchronized duets (Todt 1970, Thorpe 1972; Fig. 3). In all four species, neighbouring pairs and sometimes what appear to be other members of family groups may join in the chorus, making it difficult to assess the contribution of each sex or individual with certainty, but as Todt and Thorpe (*ibid.*) suggested, we presume that males mainly give loud pure melodic whistles, whereas females mainly give scratchy, grating or rapidly oscillating notes. Male phrases of all four species are composed of two to five notes, and phrases are repeated at a rate of 0.9–1.3/s. The female parts of the duets are mostly, but not entirely, given in the pauses between male songs. The most striking exception is Hunter's Cisticola, in which the female part of the song is a continuous, bubbling series of notes rising and falling in pitch. In all four species, a pair may repeat a particular theme 5–20 or more times through a song bout, then shift to a different theme in the next bout, males often by transposing their phrases to a different key, and females by changing the order and selection of notes. At least up to four different themes may be given by the same pair (Thorpe 1972).

Figure 2. New species of cisticola warblers from the Kilombero floodplain of Tanzania. At the top, Kilombero Cisticola (Kidenenda wa Kilombero); at the bottom White-tailed Cisticola (Kidenenda Mkia-mweupe). For both species, the bird in the front is painted after the type specimen, whereas the bird behind is based on photos of birds in more worn plumages. Watercolour painting by J.F. [Colour figure can be viewed at wileyonlinelibrary.com]

Notes in male songs of Chubb's ($n = 60$) and Hunter's Cisticolas ($n = 36$) are all clearly modulated (Fig. 3). In all 23 examined songs of Black-lored Cisticolas, the notes are completely unmodulated, resembling the ventriloquial songs of some of the ancient Australasian oscine lineages (e.g. *Ptilorrhoa*, *Eulacestoma*), and are composed of four (less commonly three) notes alternating between high and low pitch: high–low–high–low or high–low–high. Male songs of Kilombero Cisticolas ($n = 66$) are composed of three, four or five notes, of alternating pitch, but beginning with a low note: low–high–low, low–high–low–high, or low–high–low–low–high. When composed of five notes, the last two notes are a repetition of the first two and follow a loud oscillating sequence, which is presumably given by the female, and often overlaps with the following note (alternatively, this is from the male, using each side of the two syrinx halves independently; see e.g. Zollinger *et al.* 2008). The low-pitched and sometimes one of the high-pitched notes are unmodulated, closely resembling the notes in male song of Black-lored Cisticola; indeed, during a playback experiment, a Kilombero Cisticola responded vigorously to the song of the Black-lored Cisticola (F. Dowsett-Lemaire *in lit.*). The first (and the last, when the song is five notes long) of the high-pitched notes in male song of Kilombero Cisticola, however, is clearly modulated, falling distinctly in pitch during the last half or third of its duration (Figs 3 and S5). Vocal differences between Kilombero and

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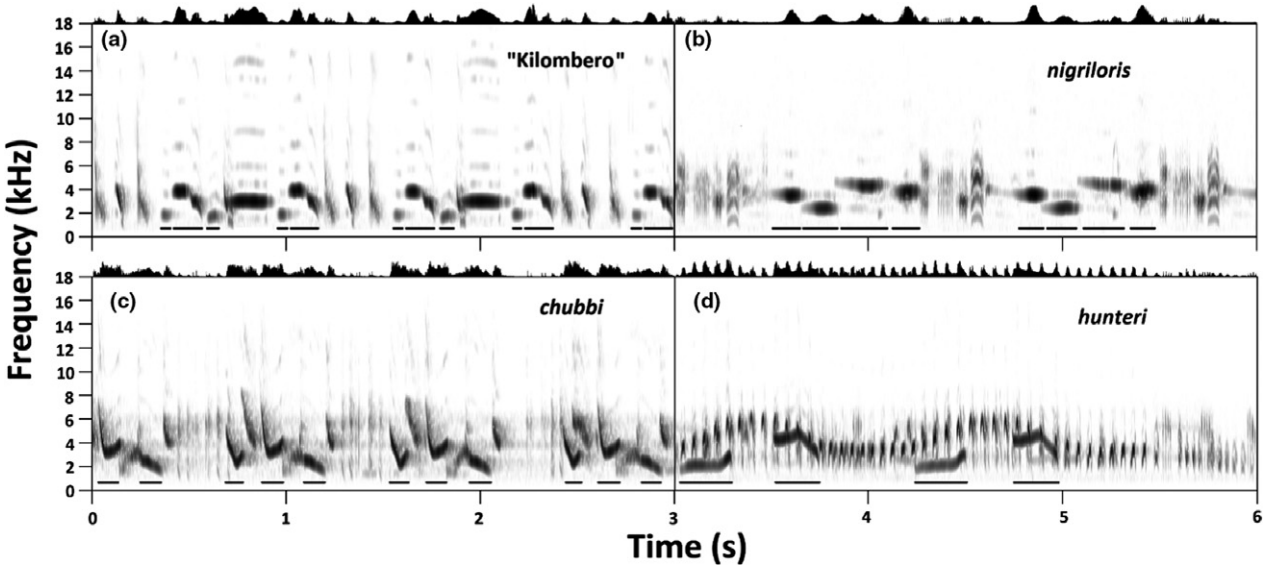

Figure 3. Duets of members of the *Cisticola* [*hunteri*] clade. (a) Kilombero Cisticola (XC511355). (b) Black-lored Cisticola (ML24604). (c) Chubb's Cisticola (XC453429). (d) Hunter's Cisticola (ML26049). Male contributions are indicated by horizontal or modulated bands. Note that this begins with a low note in Kilombero Cisticola but with a higher note in Black-lored Cisticola, and further that the last part of the second and terminal notes in Kilombero Cisticolas are modulated, with a sudden fall in pitch (see Fig. S5 for details).

Black-lored Cisticolas are also evident in the buzzy female calls (Fig. 4). The average pace and standard deviation of the oscillations is 249 ± 14/s (range 222–278, $n = 47$) in Kilombero and 319 ± 22/s (range 275–345, $n = 16$) in Black-lored Cisticola. In both species, female repertoires include more types of notes than in males. While some of the female vocalizations given during duets (Fig. 4) appear homologous, others might be unique to one or the other species. A variety of calls have been recorded for Kilombero Cisticola, none of them similar to recorded calls of Black-lored Cisticola (Fig. 5). Presumed alarm calls of both species are quite similar, a high-pitched, oscillating *psee* repeated at a pace of 2–3/s (Fig. S6), the oscillations, as in the buzzy notes, slower paced in Kilombero Cisticola (170–246/s, $n = 5$) than in the Black-lored Cisticola (291–313/s, $n = 4$). Further playback experiments with Black-lored Cisticola in Kilombero Cisticola habitat should be an aim of future work.

Molecular results

Based on the sequence data, the Kilombero Cisticola was recovered as sister to Black-lored Cisticola as part of the duetting clade (with 100% bootstrap support, both for MP and ML; Fig. 6). Based on divergence at the ND2 locus, the Kilombero Cisticola differed by 7.60% from Black-lored Cisticola and by more than 9.5% from Chubb's and Hunter's Cisticola, which in turn differed by *c.* 6.5% (cyt-b data were not available for all species for comparison). These sequence divergence values are uncorrected parsimony distances.

Characterization and comparison of the streak-backed marsh cisticolas

These are rather small and gracile birds with fairly long and graduated tails, with greyish upperparts streaked with black, rufous-brown outer webs to the remiges and buffy white underparts. Members of the streak-backed marsh cisticolas are widely distributed across the Afrotropics, with a number of taxa replacing one another geographically, with some range overlap between Carruthers's Cisticola and subspecies *amphilectus* of the Winding Cisticola and between Luapula Cisticola and subspecies *suahelicus* and *nyansae* of the Winding Cisticola (Hall & Moreau 1970, Urban *et al.* 1997). The distribution in eastern Africa suggests that the Kilombero population falls within the broad geographical range of the form *suahelicus* of the Winding Cisticola, but outside the range of Chirping, Luapula and rufous-winged Cisticolas and probably also well separated from the Coastal

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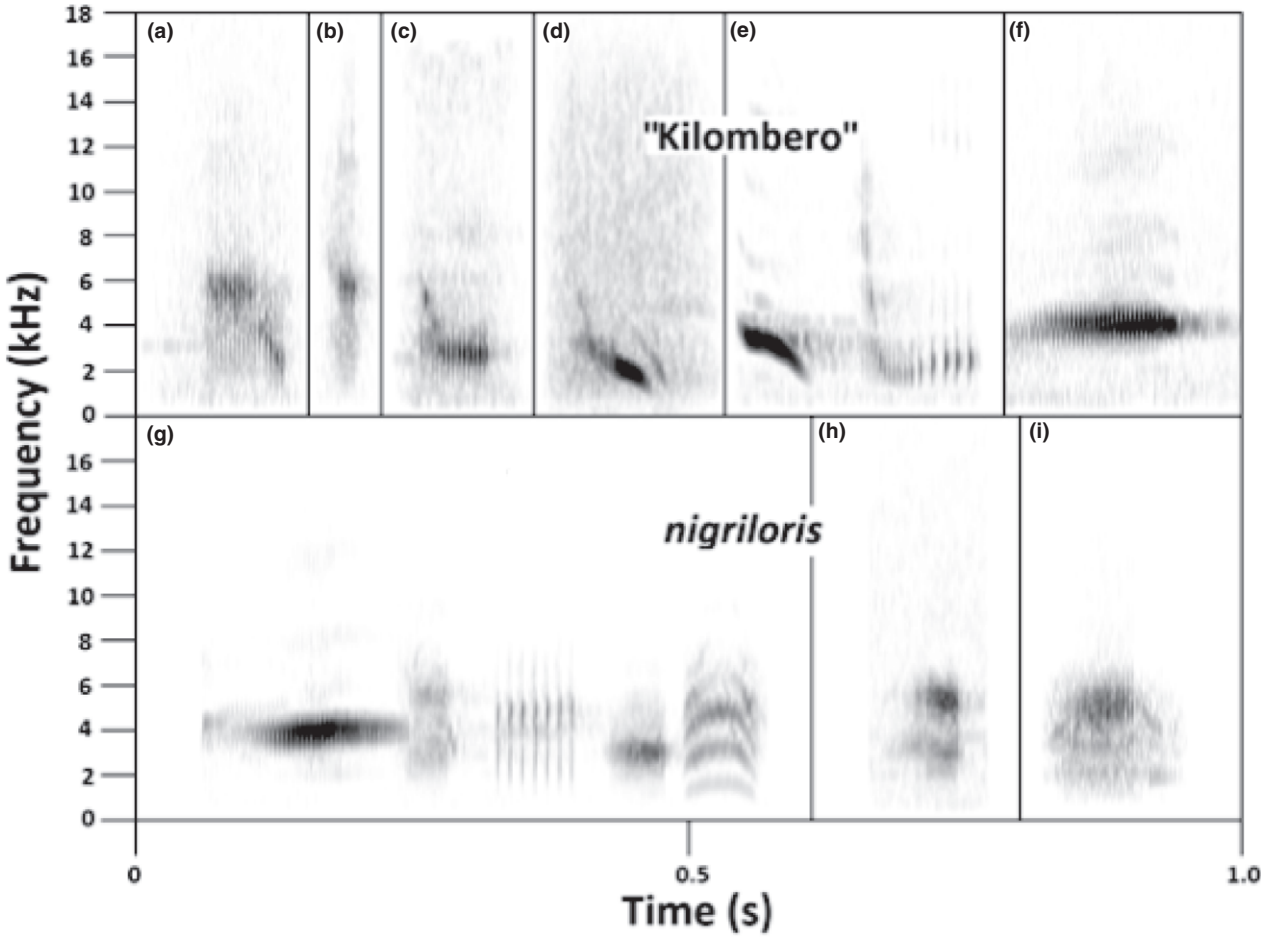

Figure 4. Female cisticola warbler vocalizations given during duets. (a–f) Kilombero Cisticola (BSL153761, BSL153762, ML135958, XC498419, XC511328, BSL153768). (g–i) Black-lored Cisticola (ML24604, ML24896, XC397960). Note that oscillations in buzzy notes of the first species are considerably slower paced than in the latter species.

Cisticola (Davies 2014). These forms are generally widespread in marshy places within scrub savanna and cultivated areas in the north, and the *suahelicus* race of the Winding Cisticola is common in the Udzungwa Highlands but with few records south of the range of the White-tailed Cisticola. The Coastal Cisticola is found along the east coast from Somalia south to the Rufiji delta in Tanzania, and there is no documented evidence of an extension towards the interior of Tanzania (N. Baker *in lit.*), where the White-tailed Cisticola occurs.

Morphological comparison

Plumage variation in the streak-backed marsh cisticolas is subtle (Appendix 1) but the White-tailed Cisticola (Fig. 2) stands out by being smaller and more dull-coloured than the other taxa (Appendices 1 and 2). The White-tailed Cisticola has a dull wood-brown wing-panel (against brighter rufous in other marsh cisticolas) and a white outer edge of the outer tail-feather, and it also differs from other related species by having more prominent white tips to the rectrices (except the two central feathers) contrasting with a broad, black subterminal band. The prominent white tips of the tail feathers give it its vernacular name.

Vocalizations

The song of the White-tailed Cisticola (eight of 37 recordings) differs markedly from songs of all other members of the C. [*galactotes*] clade (Fig. 7). It consists of a phrase of one to four (usually two or three) notes at varying pitch between 2100 and 3300 Hz, '*chi-chi-chi*' (high-pitched) or '*keek-kuck*'

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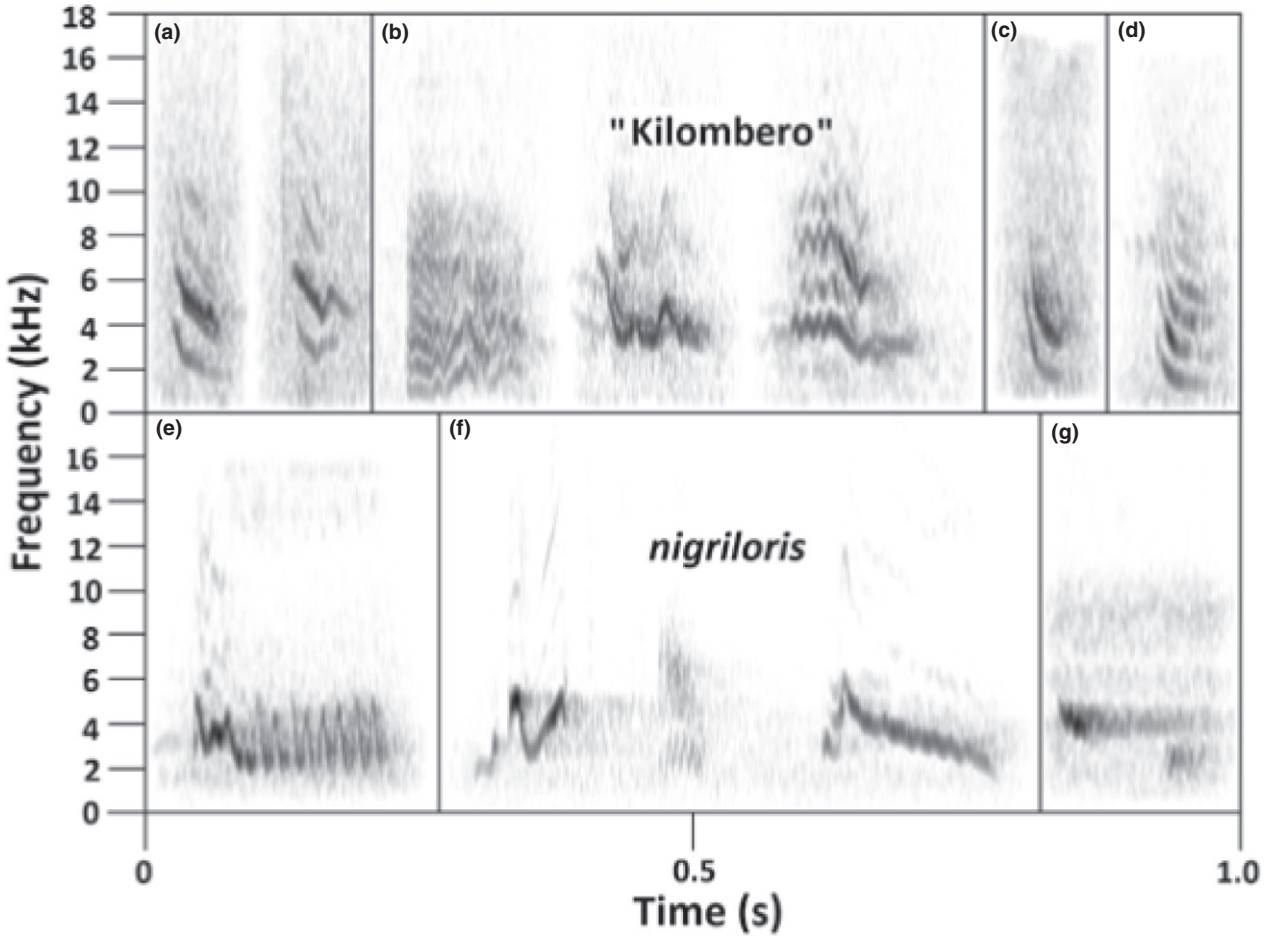

Figure 5. Cisticola warbler calls. (a–d) Kilombero Cisticola (BSL153774, BSL153775, ML135958, XC511304). (e–g) Black-lored Cisticola (XC311906a, XC311906b, XC311931).

(low-pitched), one note usually less modulated than the other, phrases repeated every 1–2 s, loudest and highest pitched when the female is out of the male's sight, changing immediately when she appears. A secondary, rarely given song (four of 37 recordings) consists of a 0.4–0.6 s 'winding' trill at 5300–6800 Hz; notes in the trill are given at a pace of 42–61/s, slower than in trills given by Coastal Cisticola (121 ± 37 (76–169), $n = 8$), but faster than in subspecies *suahelicus* of the Winding Cisticola (29 ± 4 (23–39), $n = 19$).

The most commonly heard vocalization of the White-tailed Cisticola (20 of 37 recordings) is a creaky contact call given by both sexes. Such calls, each 0.3–1.0 s long, given alone or as a series of two to three calls – longest when given alone – and rising in pitch through much of their duration, are given by all vocally known species in the C. *galactotes* species complex except for Coastal Cisticola (Fig. 8). Many audible harmonics result in a nasal quality. Most of the volume resides on the higher harmonics at the start than on the lower harmonics later in the whistle, such that the loudest pitch descends across the whistle, although each harmonic rises. At the start of the whistle, the pitch usually rises sharply, sometimes followed by a slight drop, and at the very end it usually drops sharply. In the majority of other taxa the whistle rises linearly through most of its duration, but in the White-tailed Cisticola it forms an arch, rising until half or three-quarters through its duration, and then drops in pitch, and is also notably more nasal than in most other forms, resembling the sound of a squeaky toy. The only similarly arched and nasal calls recorded in other species in the clade were given by Chirping Cisticola

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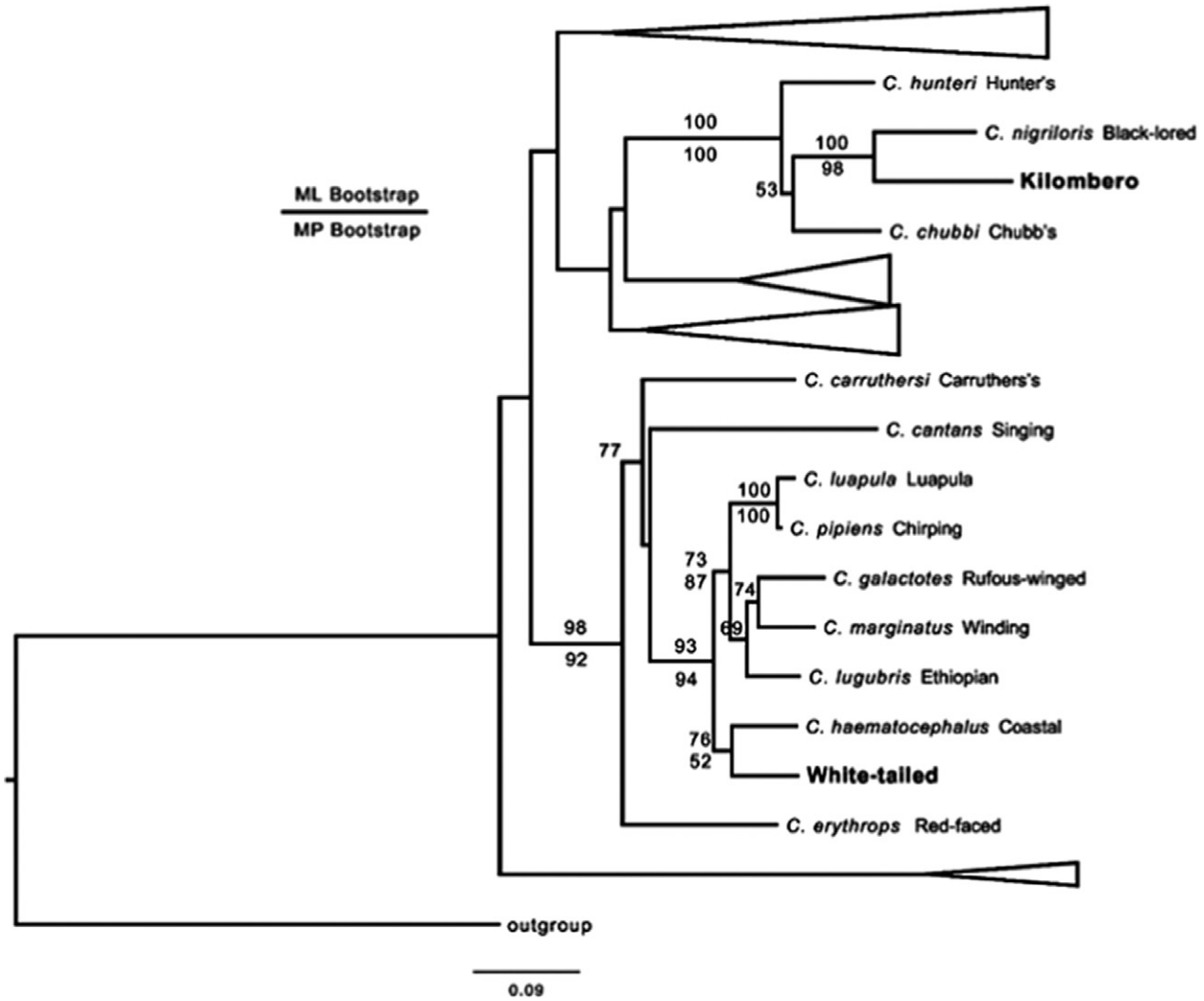

Figure 6. A simplified maximum-likelihood *Cisticola* phylogeny, where the putative new species (in bold) are placed in relation to their nearest relatives. Bootstrap support values are given at nodes. The collapsed clades indicate well-supported groups of other *Cisticola* species not closely related to the focal taxa.

(ML101190, XC339100), which usually (five of seven recordings of this call) gives a less nasal whistle that rises linearly in pitch across the duration of the call.

Other calls given by White-tailed Cisticola (Fig. 8) include a short (0.1 s) buzz of 92 oscillations per second, similar to short buzzes in songs of Coastal Cisticola (British Sound Library 195066, 198368, 198371, XC510069) but without the distinctive ending, and also much like the rapid scolding notes of C. *lugubris* (XC300128), but lower pitched (fundamental 2.4 kHz in White-tailed, 3.1–3.4 kHz in Ethiopian Cisticola); a double- or single-noted '*tick*' given in a series of 5–15 notes at a pace of 3.3–5.5/s (Fig. 9b–d), the double-noted variant somewhat resembling one of the calls of Chirping Cisticola (XC460863, 460865), but notes in the White-tailed are closer together and the loudest pitch descending rather than ascending; a 0.1-s-long '*reer*' loudest at 3.7 kHz (Fig. 9e), somewhat similar to a presumed female call of subspecies *amphilectus* of the Winding Cisticola (XC204566), but in the White-tailed the first rather than second harmonic of the call is loudest, and the start of the note is more explosive; a 0.1-s-long, sparrow-like '*chirp*' (Fig. 9f) at *c.* 4 kHz (2nd harmonic) given in series of 2–12 notes at a pace of 1.6–2.5/s (four of 37

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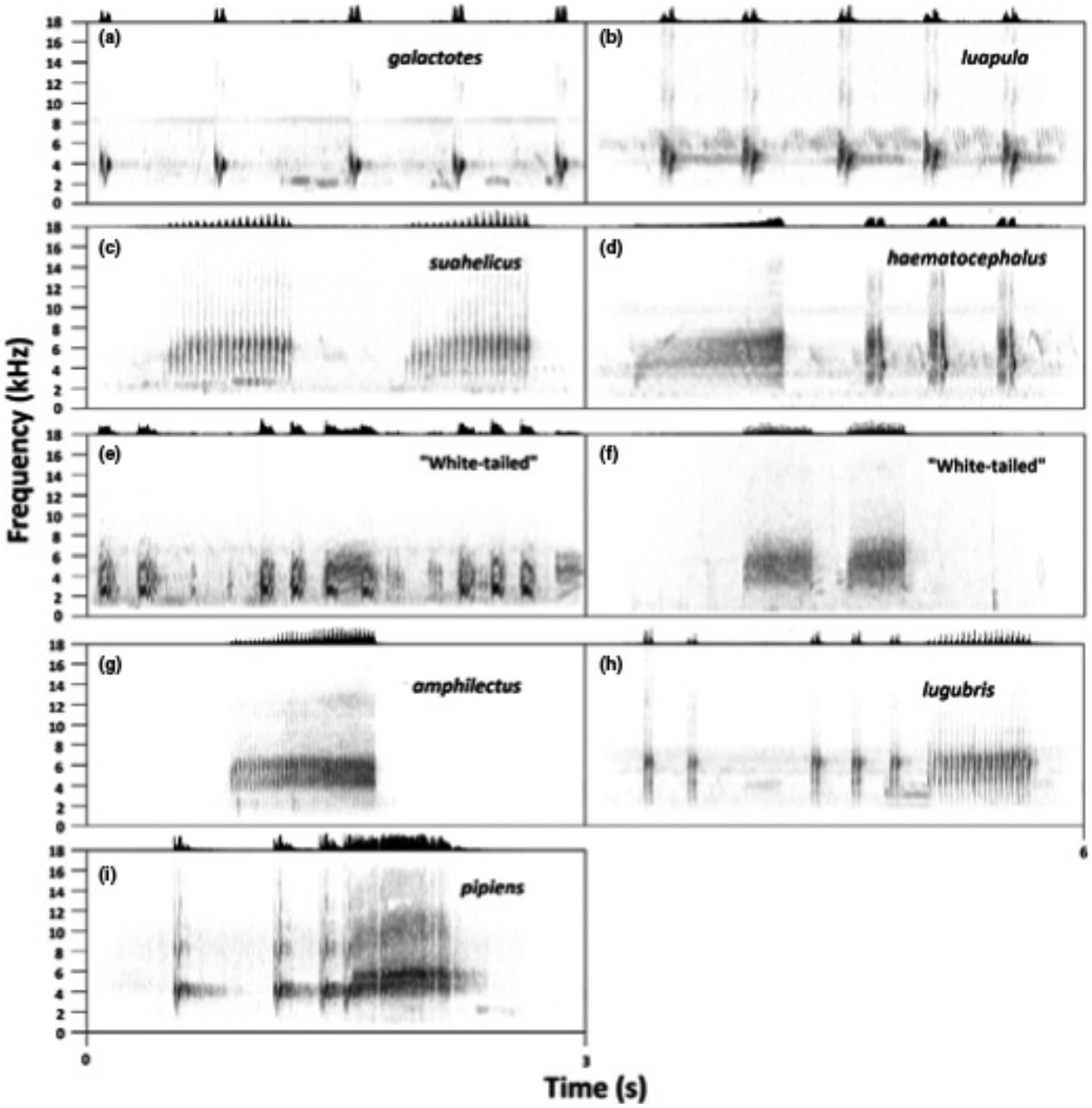

Figure 7. Songs of members of the streak-backed marsh cisticolas. (a) Rufous-winged Cisticola (Gibbon 2003 cut 1). (b) Luapula Cisticola (BSL07920). (c) Subspecies *suahelicus* of Winding Cisticola (XC430163). (d) Coastal Cisticola (XC510071). (e,f) White-tailed Cisticola (XC499005 and BSL153756). (g) Subspecies *amphilectus* of Winding Cisticola (Chappuis 2002 cut 1). (h) Ethiopian Cisticola (XC210042). (i) Chirping Cisticola (BSL07924). 'Winding' or buzzy trills occur in songs of species in all three groups but are missing in the southern forms, which give songs of repeated chirps, single-noted in Red-winged, and double-noted in Luapula Cisticola. Recordings of *C. m. marginatus* were not available. White-tailed Cisticola only rarely gives a trill. Its common song is a repeated, two- to three-note phrase '*keek-kuck*'.

recordings); a scratchy, 0.04-s-long, double-noted scold '*r-r*' (Fig. 9g) given in series of four to six notes at a pace of 10/s, resembling the flush call of a Fieldfare *Turdus pilaris*; another scratchy, but single-noted call (Fig. 6h) given at a pace of 5/s; and a single '*chiu*' (Fig. 9i) dropping sharply in

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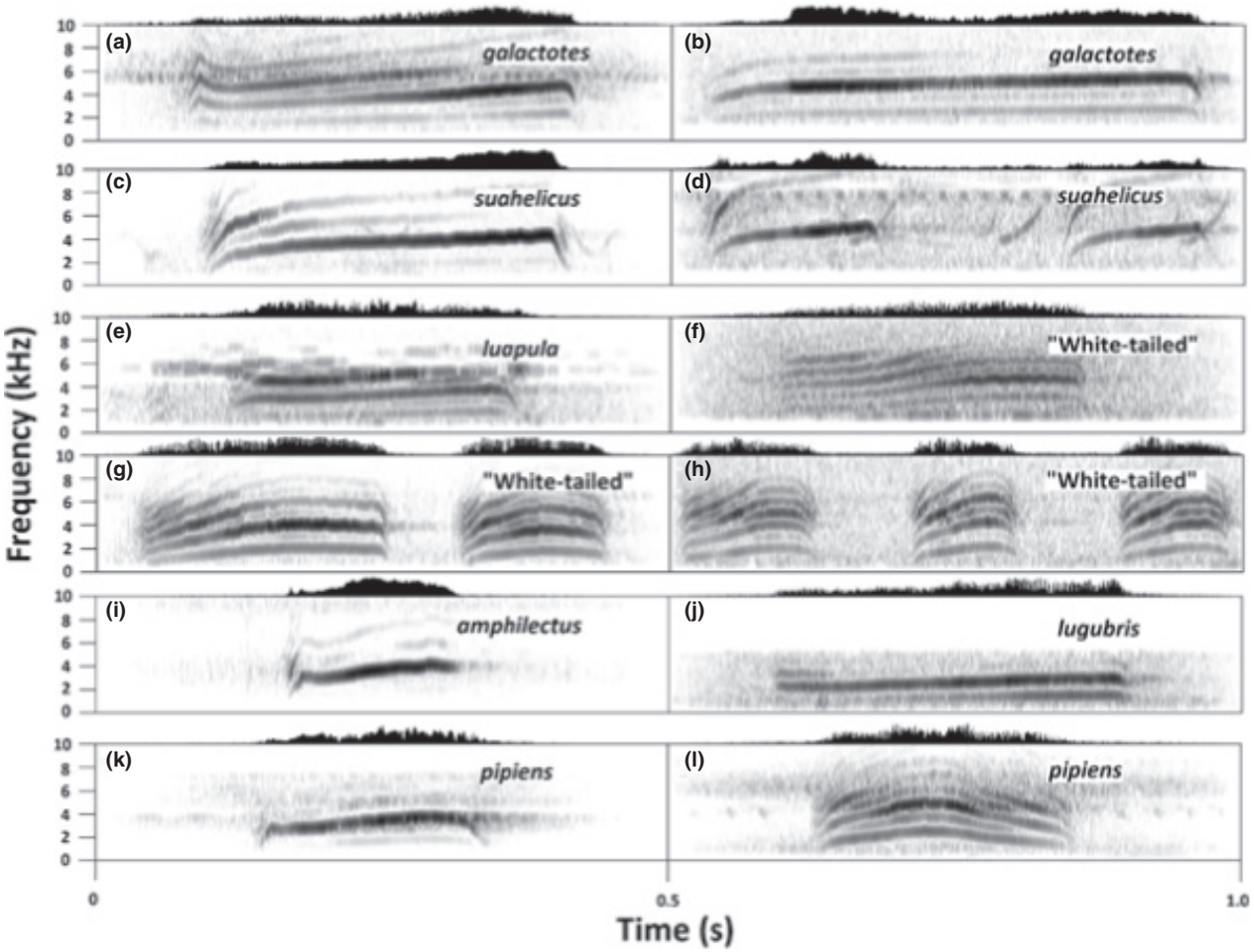

Figure 8. Creaky calls of the *Cisticola* [*galactotes*] clade. These calls are given by all members of the clade except for Coastal Cisticola. (a, b) Red-winged Cisticola (BSL137148, XC452901). (c, d) Subspecies *suahelicus* of Winding Cisticola (ML88126, ML14391). (e) Luapula Cisticola (XC247179). (f–h) White-tailed Cisticola (XC494988, XC499010, XC511380). (i) Subspecies *amphilectus* of Winding Cisticola (XC454661). (j) Ethiopian Cisticola (XC305989). (k, l) Chirping Cisticola (XC339100, XC339103).

pitch. Most of these calls of White-tailed Cisticola do not resemble vocalizations given by any other member of the C. [*galactotes*] clade.

Playback with songs of Winding Cisticola in the Kilombero floodplain caused a vocal response by White-tailed Cisticola but the responding bird never moved out of its core habitat to confront the apparent 'intruder'.

Molecular results

Analysis of our DNA sequence data recovered the White-tailed Cisticola as sister to the Coastal Cisticola within the larger clade of streak-backed marsh cisticolas comprising: Chirping, Luapula, rufous-winged, Winding and Ethiopian Cisticolas (Fig. 6). These seven taxa together comprise a species-complex of closely related forms that are sister to the plain-backed Singing Cisticola *Cisticola cantans*, and all eight are sister to Carruthers's Cisticola. The White-tailed Cisticola is genetically closest to the Coastal Cisticola with a 4.31% sequence divergence in the ND2 gene, and this divergence is greater than that between Winding and Ethiopian Cisticolas at 3.38%, and similar to that between Ethiopian and Chirping Cisticolas at 4.50% and Chirping and Winding Cisticolas, also at 4.50%. The uncorrected parsimony sequence divergence between the eight members of the species complex above, including the White-tailed

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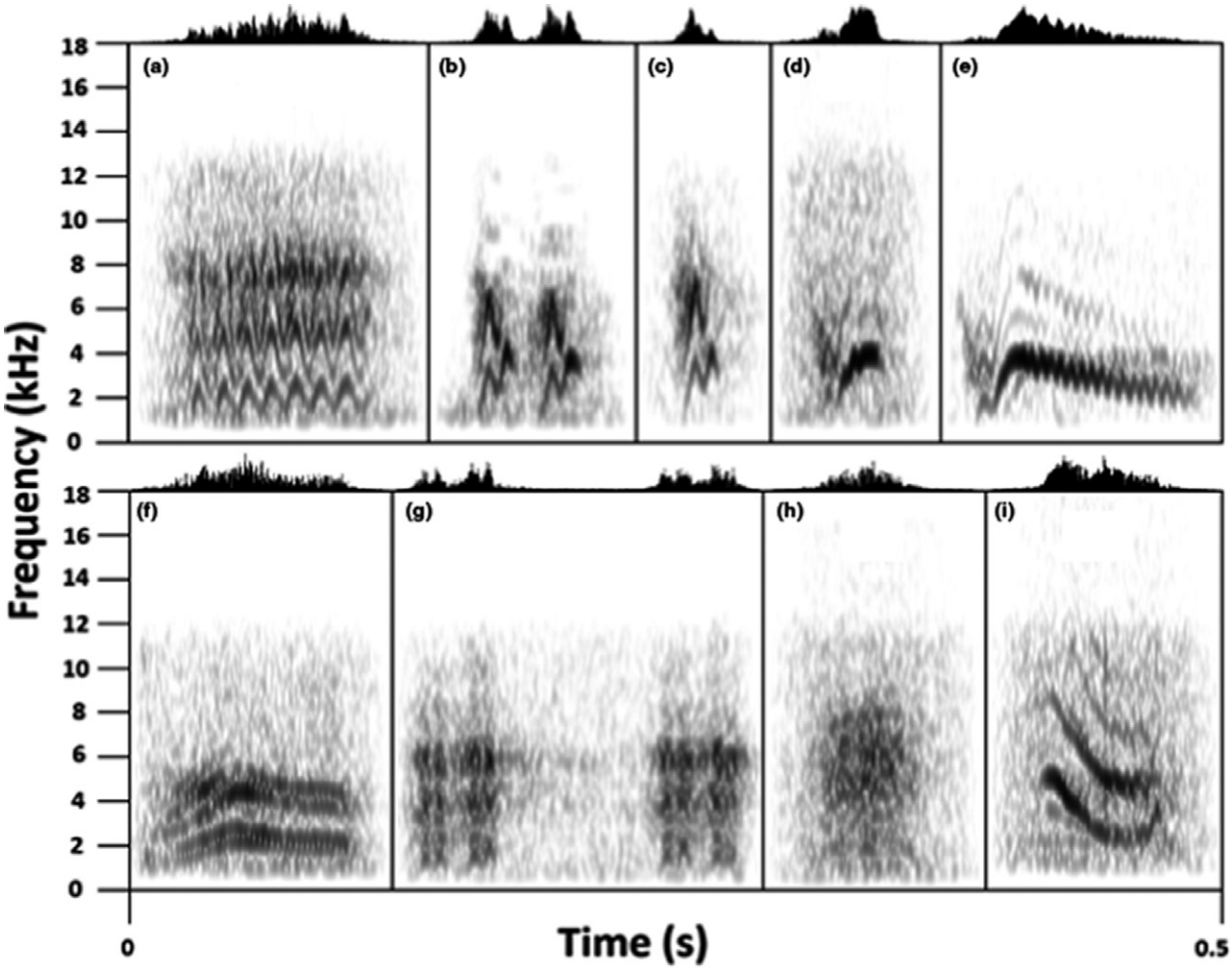

Figure 9. Calls of White-tailed Cisticola: (a) short buzz (BSL153779); (b–d) double- and single-noted '*tick*'s (TZA15_091395_047, BSL153779, BSL153777); (e) '*reer*' (BSL153781); (f) sparrow-like '*chirp*' (XC511376); (g) scratchy, double-noted scold '*r-r*' (BSL153778); (h) scratchy single-noted call (ML135955); (i) '*chiu*' (BSL153757). Most of these calls do not resemble vocalizations given by any other member of the *C.* [*galactotes*] clade.

Cisticola and Singing Cisticola, varies between 8 and 9%.

TAXONOMIC CONCLUSION

As outlined above, the two cisticolas of the Kilombero floodplain were found to be morphologically and vocally diagnosable and genetically distinctive from other cisticola taxa. Using rates of molecular evolution calculated by Lerner *et al.* (2011) for the Hawaiian honeycreeper radiation, Davies (2014) and R.C.K.B. (unpubl. data) estimated divergence times among the duetting cisticolas to have occurred over the past 3.5 Mya, and among streak-backed marsh cisticolas over the past 3.0 Mya. Such molecular clock estimates, based on rates of nucleotide base substitutions, have inherent uncertainties, but with the poor avian fossil record from the tropics, such approaches are often the only means to estimate divergence dates among lineages. The genetic divergence between the Kilombero Cisticola and its sister-species is greater than that between Hunter's and Chubb's Cisticolas, which are in contact on Mt. Elgon on the Kenya–Uganda border, replacing each other elevationally but co-occurring at 1500–1550 m (see Fuchs *et al.* 2011 for a similar case of apparently secondary contact and elevational replacement of sibling species of greenbuls). The White-tailed Cisticola showed a degree of sequence

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divergence from its sister-species that is similar to the divergence among most other species of marsh streak-backed cisticolas.

Based on the combined evidence from genetics, morphology and bioacoustics, we conclude that these two cisticolas of the Kilombero Floodplain represent independent species, which we formally describe and name below:

***Cisticola bakerorum*, species nova**

(a.k.a. Kilombero Cisticola in English and Kidenenda wa Kilombero in Kiswahili)

Holotype: ZMUC number 075795; 12 November 1961; collected at Kilombero River near Ulanga; this name does not refer to a recognized locality and may refer to the general area (N. Baker *in litt*.) but it seems plausible to believe that the collecting site was in the area near the ferry launch south of Ifakara, 8°11′S, 36°55′E, elevation *c*. 245 m (but given as 950 feet on the original label), collected in tall grass by the Kilombero River (T. Andersen *in litt*. 1961). Adult (by plumage structure) male (by original label data). The specimen is documented by digital photos available on DanBIF Multimedia (https://www.gbif.org/occurrence/455915634). GenBank accession number for ND2 is MW926527 and Zoobank registration number is http://zoobank.org/urn:lsid:zoobank.org:act:BF1F0B50-9B63-4557-B3A2-3170F9EB99C4.

Description of type specimen (Fig. 2): Forehead, crown and hind-neck Cinnamon Brown; whitish supercilium extending from base of bill to fade out just behind the eye; colour of crown grading to buffy brown on ear coverts. Back to rump and lesser wing coverts olive brown to buffy brown on terminal ciliae but with no indication of striped patterning; greater wing coverts and tertials darker, sepia brown, with snuff brown edge and feather tips. Rectrices snuff brown with a broad blackish sub-terminal band (about 5 mm, faint on the central feathers), with a more diluted pinkish buff towards the feather tips. Underparts from chin to belly whitish, actually pure white on central throat and breast but otherwise cream buff and with sides of breast, axillaries and upper sides chamois; feathers of tibiae and under tail coverts cinnamon buff. Soft parts, according to the specimen label: iris pale brown, feet flesh, bill black; in the roundskin, the upper mandible is black at the base, hessian brown towards tip, lower mandible light ivory yellow along its full length.

Measurements of the type specimen: Length (of skin) 135 mm; wing (flattened) 55.5 mm, tail 54.8 mm. P6 longest and more than twice as long as P10 (outermost; which is 21 mm long and 6.3 mm broad). Bill to skull 18.7 mm, slender and slightly curved. Tarsus 22.8 mm.

Diagnosis: Resembles the plain-backed, duetting highland cisticolas but has a diagnostic bold white supercilium above a small, dusky loral patch or stripe, and significantly longer and slenderer bill with whitish proximal part of the lower mandible. It is distinctly smaller than the related Black-lored Cisticola (Appendix 2) and inhabits a different (lowland) marsh habitat, and differs from all other duetting cisticolas by having more buffy white (not greyish) underparts. The male vocalizations during duets resemble those of Black-lored Cisticola, four alternating high- and low-pitched unmodulated whistles, but differs by beginning with a low-pitched rather than high-pitched note, and by the second note being modulated (Figs 3 and S2). Further, oscillations in buzzy calls by the female are considerably slower paced than in Black-lored Cisticola, and a variety of other calls, some of which appear to be diagnostic, were also recorded (Fig. 5).

Other material examined: No other preserved specimen appears to exist. The informal descriptions and illustrations in Stevenson and Fanshawe (2002) and Sinclar and Ryan (2003) do not refer to collected specimens or alternative reference voucher material. Photos and videos available from L.A.H.'s 2019 fieldwork and from many photos on the internet (Nik Borrow, Mikael Bauer, Charles Davies, John Drummond, Ron Eggert, Per Holmen, Angie Pattison, David Peterson, Karine van den Vust) agree well with the type description, although the upperparts and sides appear often more greyish; moreover, the bill is more bluish slate, eye rim dark brown, legs pink with the toes more greyish on the photos.

Etymology: We named this species after Neil Baker and the late Liz Baker, in recognition of their long-term efforts to document and conserve Tanzania's birdlife, which includes the exploration of the Kilombero floodplain (e.g. Baker & Baker 1990, 2002).

Distribution, habitat and ecology: The species is distributed in lowland marshes at 240–305 m asl, where it prefers flooded reedbeds and is common along the Kilombero River and the other major river channels of the Kilombero floodplain

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(Starkey *et al.* 2002, Stevenson & Fanshawe 2002, Jones & John 2008, Rannestad *et al.* 2015, L.A.H. fieldwork 2019). The Kilombero Cisticola was first recognized as a potential new species when observed in the mid-1980s in the area near the past Ifakara ferry point on the Kilombero River. Rannestad *et al.* (2015) surveyed a stretch of c. 60 km (centred on the present-day Ifakara bridge) and found it to be distributed along the Kilombero River throughout the year and generally associated with grassland (with some bushes) and reeds. However, the core habitat is dominated by tall *Phragmites mauritianus*, although the species foraging habitat may include more mixed vegetation including *Polygonum* species. Juveniles were observed in June and July 2019.

***Cisticola anderseni*, species nova**

(a.k.a. White-tailed Cisticola in English and Kidenenda Mkia-mweupe in Kiswahili)

Holotype: ZMUC number 075787; 12 November 1961; collected at Kilombero River near Ulanga; this name does not refer to a recognized locality and may refer to the general area, but it seems plausible to believe that the collecting site was in the area near the ferry launch south of Ifakara, 8°11′S, 36°55′E, 245 m (but given as 950 feet on the original label), in tall grass by the river (T. Andersen *in litt.* 1961). Adult (by plumage structure) male (by original label data). The specimen is documented by digital photos available on DanBIF Multimedia (https://www.gbif.org/occurrence/455919067). GenBank accession number for ND2 is MW926526 and Zoobank registration number is http://zoobank.org/urn:lsid:zoobank.org:act:E0A633A8-E244-4DEB-AC52-C3E4261778AB.

Description of type specimen (Fig. 2): Top of head from forehead Cinnamon Brown to Prout's Brown, and Sepia on the nape with a greyish shade on the ear-coverts; buffy whitish supercilium extending from base of bill to above the eye; mantle benzo brown or more grey towards sides, and with 2- to 3 -mm-broad Fuscous-Black central streak on each feather, but lower back and rump and upper tail-covers uniform dark grey (Quaker drab); wing-coverts fuscous broadly margined with wood-brown; tertials similar but descending secondaries and primaries less heavily pigmented benzo brown with outer webs wood-brown, giving the impression of a dull-coloured, wood-brown closed wing. Central rectrices dark greyish brown (benzo brown) with a broad (12 mm) black subterminal zone fringed with a thin (2 mm) terminal margin; the other rectrices are greyer with distinct black subterminal zone, and with clear-cut 5- to 8-mm-broad white tips; the outer rectrix also with the entire outer margin white. Lores dusky; cheeks and sides of neck and body light grey with cream-buff terminal cilia, grading to uniform pale buff on the rest of the underparts, and almost pure white on the mid-throat and vent; feathers of tibiae cinnamon. Soft parts, based on information on the label: iris pale brown; bill black to dark horn-coloured, lower mandible light ivory yellow at base, legs and feet flesh.

Measurements of the type specimen: Length (of skin) 121 mm; wing (flattened) 58.9 mm, tail 54.0 mm. P4 (from outer) longest and 22 mm longer than P1 (which is 23 mm long, 6.1 mm broad on the middle); central rectrix 19.5 mm longer than outer. Bill to skull 13.3 mm, slender and slightly curved. Tarsus 19.3 mm (Svensson 1992: method 3).

Diagnosis: Resembles other species of marsh streak-backed cisticolas but is generally more dull-coloured, notably with darker crown and with a much duller wood-brown closed wing, grey sides of body and rather buffy underparts, almost as in the Ethiopian Cisticola. The Coastal Cisticola has a rather dull-coloured crown and wing but not nearly as dark as White-tailed Cisticola, which furthermore is distinguished by its more prominent white supercilium and the very dark colour of the tail, except for the extensive and contrasting white tips to all except the two central rectrices and white outer edge to the outer rectrix. The song of White-tailed Cisticola differs distinctly from songs of all other members of the C. *galactotes* clade (Appendix 2). It consists of a phrase of usually two to three notes at varying pitches between 2100 and 3300 Hz '*chi-chi-chi*' (high-pitched) or '*keek-kuck*' (low-pitched), one note usually less modulated than the other, phrases repeated every 1–2 s. More rarely it gives a 0.4- to 0.6-s-long 'winding' trill at 5300–6800 Hz, notes in trills given at a pace of 42–61 /s, slower than in trills given by Coastal Cisticola but faster than in the taxon *suahelicus* from the surrounding landscapes. The contact calls are fairly distinct, of nasal quality, and with the pitch rising and falling, forming an arch on a spectrogram (Fig. 8); various other calls also do not resemble those given by other members of the streak-backed cisticola group (Fig. 9).

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Other material available: No other prepared specimen appears to exist. Photos available from L.A.H. and on the internet (Nik Borrow, Charles Davies, John Drummond, Ron Eggert, Johannes Fisher, Oliver Hammerlock, Per Holmen, David Peterson, Trude Peterson, Friedemann Vetter and others) are in good agreement with the type description, but in general birds in photos appear more grey on the dorsal parts of the body, indicating that the type specimen could be slightly foxed. Eye colour appears to be tawny, bill grey with pale grey proximal half of the lower mandible, with the legs and feet pink. During L.A.H.'s 2019 fieldwork, female birds were observed to have more uniform grey and less streaky upperparts, probably reflecting plumage wear during the breeding period. Two pairs were observed with young, the latter showing a yellowish wash to the underparts and even on the brightest parts of the face, thereby resembling features of other juvenile cisticola species.

Etymology: We named this species after the late Thorkild Andersen, in recognition of his efforts to document Tanzania's birdlife, including his collection in 1961 of the two specimens that serve as holotypes in this publication. His 11 741 avian specimens from Tanzania, collected over 20 years, are today deposited in six European natural history museums.

Distribution, habitat and ecology: White-tailed Cisticola is known from the Kilombero Floodplain at 240–305 m south of Ifakara in southern central Tanzania. Jones and John (2008) found it to be by far the most common cisticola in the area, recorded at 14 of 15 surveyed localities and in 81% of all (159) point count surveys. In December 1995, J.F. observed it in rather dry and sandy places with short *Phragmites* mixed with annuals and scattered dry herbs, and it was sometimes running on the ground, in a manner resembling a pipit (*Anthus*). L.A.H. found it to be more closely associated with shorter vegetation than the Kilombero Cisticola and to generally stay low in the vegetation, often foraging on the ground as indicated in Figure 2. In June, the White-tailed Cisticola was primarily found in short *Phragmites* and in mixed habitat with other grasses. It was also seen foraging in *Polygonum*. It is replaced by the Winding Cisticola (*suahelicus* ssp.) in the surrounding landscapes, including in marshy places throughout the Udzungwa area.

DISCUSSION

The Kilombero floodplain was once connected with the vast wetland habitats of the ancient Zambian Luangwa drainage system (Tiercelin & Lezzar 2002, Cotterill 2004, Stankiewicz & de Wit 2006). However, this connection was broken in the late Miocene, with the formation of the Malawi Rift. Our genetic data suggest that the cisticolas of the Kilombero floodplain are evolutionarily much too young to have been part of the fauna of this ancient wetland system, and more probably colonized the area from the adjacent highlands or from the neighbouring coastal plains.

At present, the Black-lored Cisticola inhabits highland habitat only 15–20 km away from the Kilombero floodplain, but in a markedly different elevational niche. Predictable humidity may therefore play a greater role than elevation in determining the disjunct altitudinal distribution (Bowie *et al.* 2006, Fjeldså *et al.* 2007, 2010, Johansson *et al.* 2007, Fuchs *et al.* 2011). The Coastal Cisticola resides mainly near the coast 300 km away from the Kilombero floodplain, although it is unknown how far inland it may occur. Similarly, the endemic Kilombero Weaver is closely related to the Northern Masked Weaver *Ploceus taeniopterus* and the form '*holoxanthus*' of the adjacent Selous area and coastal Tanzania (this form is currently synonymized under the Yellow Weaver *Ploceus subaureus* but is not genetically close to it; U. Olssen unpubl. data).

Because of the continued high water supply from the adjacent humidity-capturing Udzungwa highlands (Fjeldså & Bowie 2008, Linder *et al.* 2012, Dinesen 2018), all three endemics could maintain breeding populations on the Kilombero floodplain, in spite of the climatic instability in the Pliocene or early Pleistocene (deMenocal 2004, Trauth *et al.* 2007). Because of the extremely flat landscape, the floodplain undergoes extensive seasonal flooding during the peak of the rainy season (December to April) and the main rivers and oxbow lakes in the central parts of the plain therefore have permanent water even during the driest period in June (Hughes & Hughes 1992, Starkey *et al.* 2002, Dinesen 2018).

Habitat and conservation status of the cisticolas of the Kilombero wetlands

Because of its biodiversity value and important ecosystem functions, the Kilombero floodplain has

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been recognized as a Ramsar site (Dinesen 2018). It receives water from many permanent and seasonal streams from the Udzungwa Highlands in the north and west and from three larger rivers in the south, with streams joining and forming a myriad of channels in the central part of the plain (Hughes & Hughes 1992). Because of the extremely flat landscape, the Kilombero undergoes extensive seasonal flooding and may be nearly completely flooded at the peak of the rainy season (December to April), whereas in June, only the main rivers and oxbow lakes and marshy areas have permanent water (Hughes & Hughes 1992, Starkey *et al.* 2002).

Almost half of the natural vegetation of the Kilombero floodplain has been converted to agricultural land within the last 25 years and the land area under rice cultivation rapidly increased between 2004 and 2014 (Thonfeld *et al.* 2020). The human population of Tanzania has doubled over just 20 years and as an area of above-average soil fertility, the Kilombero floodplain is now targeted as a high-potential area for raising food production (Thonfeld *et al.* 2020). Moreover, massive immigration of semi-nomadic pastoralists has taken place in the last few decades (Nindi *et al.* 2014). A very large part of the floodplain seems now to be burned annually during the dry season (Wilson *et al.* 2017). Only the seasonally flooded central part of the floodplain (blue in Fig. 1) now remains with natural marsh vegetation.

Plans for damming the major Ruhudji River upstream of the floodplain (Kabigumila 2002, International Rivers, 2013) pose another serious threat and may completely alter the flood dynamics of the plains, leading to concern about maintaining fish production and sustaining the remaining wildlife. Damming of the Kihansi River from the western end of the Udzungwa Scarp has resulted in severe alternation of the largest permanent swamp (Kibasira) in the floodplain (Dinesen 2018) and may have caused the recent accelerated process of drying of this part of the floodplain.

Although many observations of the two cisticolas are from the site of the Kilombero bridge south of Ifakara, current evidence suggests that both species have, at least until recently, occurred over most parts of the floodplain, but not outside it (Jones & John 2008, Rannestad *et al.* 2015, L.A.H. fieldwork 2019).

The fieldwork suggests that the Kilombero Cisticola is quite narrowly associated with water and flooded marsh with tall reeds and sedges along the major river channels, with a preference for tall *P. mauritianus*, whereas the White-tailed Cisticola prefers shorter or more open vegetation with patches of drier habitat, where it feeds by walking on sandy ground. While this difference in habitat use may mean that the two cisticola species are affected differently by the intensive recent land-use, we propose to classify both species as Endangered (following criteria of IUCN 2019) due to an inferred population size reduction as a result of an alarming decrease in habitat quality (criterion A4 C) documented by a number of recent papers (Nindi *et al.* 2014, Wilson *et al.* 2017, Dinesen 2018, Munishi & Jewitt 2019). Only the White-tailed Cisticola has to date been reported as far north as Mang'ula A at the edge of the sugarcane plantations at the northern margin of the Kilombero plains (Jones & John 2008), which is 33 km due north of the main Kilombero River. The endemic Kilombero Weaver of the same floodplain is categorized as Vulnerable (Birdlife International 2020).

The marshes of the floodplains are home to three endemic species of birds and an endemic toad *Sclerophrys reesi*, and nine endemic species of plants, all of which are experiencing severe population declines. A Ramsar Advisory Mission in 2017, requested by the Tanzanian government, concluded that the Kilombero floodplain is under intense pressure and subject to unsustainable changes due to the current land-use practices (Wilson *et al.* 2017). There is little doubt that the floodplain and marshes are experiencing a 'change in ecological character', in the Ramsar terminology. The recommendations were clear that the integrity and flood dynamics of the marshes should be conserved, and degraded areas rehabilitated and restored following the international environmental commitments Tanzania has made, and the Tanzanian Government has accepted these recommendations. An important immediate step must be to conserve the remaining natural vegetation in the central floodplain from cultivation and to secure continued annual natural flooding by water that is not polluted by agrochemicals.

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CONFLICT OF INTEREST

None.

AUTHOR CONTRIBUTION

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ETHICAL APPROVAL

The description of new species is based on specimens from legal museum collections and imported to Denmark before international trade in wildlife was regulated.

Data Availability Statement

Specimens used in this study are detailed in the appendices, with additional information available in the online supplementary documents. DNA sequences of the new cisticola species have been deposited in GenBank under accession numbers MW926526–926527. This paper is registered in Zoobank under LSID: http://zoobank.org/urn:lsid:zoobank.org:pub:BA654F2D-3CA9-4A6F-81ED-99DA15AAB33E.

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Appendix 1. Plumage characteristics of duetting and streak-backed marsh cisticolas, based on the examined specimens in the Natural History Museum of Denmark, Naturkundemuseum in Berlin, and National Museum of Kenya. The characterization of geographical and elevational distributions is based on regional handbooks, primarily Britton (1980) and Urban *et al.* (1997).

	Kilombero Cisticola Kilombero Valley, $n = 1$	Black-lored Cisticola *C. nigriloris* Tanzania SW highlands, $n = 15$	Hunter's Cisticola *C. hunteri* "Kilimanjaro" + Kenya, $n = 71$	Chubb's Cisticola *C. chubbi chubbi* Albertine Rift Mts, $n = 10$
Crown – forehead to hind-neck	Cinnamon brown	Rich russet	Dark cinnamon brown with indistinct streaks; hue and amount of streaking variable	Snuff brown, paler on forehead
Supercilium and lore	Distinct white supercilium from bill to end of or behind eye, and dusky spot in front of eye	No white supercilium and broad black lore	No white supercilium and dark brown lore	No white supercilium and distinct black lore
Back	Uniform olive-brown	Uniform dark brown, often warm rufous	Dark snuff brown with variable reddish wash and faint streaks in some specimens	Uniform olive brown
Breast and belly	Cream buff at sides of breast but white central underparts	Mostly drab to mouse grey, but off-white centrally on throat and belly	Drab-grey side of breast and flanks and dull creamy white central underparts	Drab grey flanks, central breast creamy and belly white
Wing	Uniform sepia-brown	Dark brown flight feathers edged tawny to light brown	Dark brown flight feathers with narrow light brown to pale rufous margins	Dark brown, feathers variable edged brown to pale rufous-brown on outer webs
Bill	Long, blackish, lower mandible ivory yellow	Black, heavy and short	Black to brownish black	Stout, black, but base of lower mandible sometimes grey
Tail	Uniform Snuff Brown, dark sub-terminal band, tips creamy buff. Central feathers more uniform	Uniform dark reddish brown with sub-terminal band and creamy tips. Central feathers more uniform	Dark uniform brown with sub-terminal spots and pale tips. Central feathers more uniform	Uniform umber-brown, sub-terminal band fading towards centre, paler tips. Central feathers more uniform
Range	Restricted-range (< 7000 km^2) in the Kilombero floodplain in southwestern Tanzania at 240–300 m	Restricted-range, in southwestern Tanzania, extending to N Malawi and NE Zambia, at 1100–2550 m	Restricted-range in northern Tanzania and central to western Kenya, at 1550–4400 m	Disjunct in W Kenya, Uganda, Rwanda, Burundi, DRC and Cameroon highlands, at 850–3000 m

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Appendix 1. (continued)

	White-tailed Cisticola Kilombero Valley, $n = 1$	Coastal Cisticola *C. haematocephalus* Tanzania, $n = 4$	Winding Cisticola *C. marginatus suahelicus* Tanzania, $n = 4$	Winding Cisticola *C. marginatus nyansae* Kenya, $n = 5$
Crown – forehead to hind-neck	Cinnamon brown to Prout's Brown	Dull rufous brown, top of head and less reddish than in *nyansae*	Rufous-brown	Rufous-brown especially on forehead
Supercillium	Distinct white from bill to end of eye, eventually with indistinct dusky spot in the white lore	Indistinct superciliary and white lore	Indistinct superciliary and white lore	Rather thin whitish superciliary and dusky stripe in the white lore
Back	Grey, broadly streaked with fuscous-black, but variable	Buffy grey streaked dark brown on mantle and back slightly paler than in *nyansae*	Grey-brown broadly streaked	Grey-brown broadly streaked although less heavily than other races
Breast and belly	Creamy buff, whitish on mid-throat and vent	Creamy buff, paler on central belly and less grey compared with *nyansae*	Whitish and buff. Creamier buff and less grey flanks than in *nyansae*	Pale buff whiter on centre belly
Wing	Dark brown with rufous-buff margins forming a wood brown wing panel	Dark brown with rufous-buff margins forming a dull rufous panel, paler than *nyansae*	Dark brown with rufous margins forming rufous wing panel	Dark brown, fringed buff and especially secondaries giving a rufous patch on closed wing
Bill	Slender, grey, lower mandible with pale grey base	Black, base of lower mandible pinkish-grey	Upper mandible dark brown, lower grey brown	Upper mandible dark brown, lower grey brown
Tail	Greyish brown, with broad black sub-terminal band and broad white tips and white outer edge of lateral feather	Greyish brown with a darker sub-terminal band and pale buffy-grey tips	Uniform grey with a black sub-terminal band and whitish tips	Dull brown, tipped buff with sub-terminal dark brown band
Range	Inland, southern Tanzania, restricted-range < 7000 km^2 in Kilombero Valley, 240–305 m	Coastal S Somalia, Kenya and N Tanzania, probably below 500 m	Central Tanzania, SE DRC, N Zambia, Malawi, Mozambique, 300–1500 m	Central and East DRC, Uganda, W Kenya, at 1100–2300 m

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Appendix 2. Biometrics of duetting and streak-backed marsh cisticolas, for each taxon; our own data are followed by measurements from Urban *et al.* (1997). Note that tail-lengths of streak-backed marsh cisticolas appear to vary seasonally.

	Kilombero Cisticola	Black-lored Cisticola	Hunter's Cisticola	Chubb's Cisticola
	C. bakerorum	*C. nigriloris*	*C. hunteri*	*C. chubbi chubbi*
Measurements (mm)	Kilombero Valley	Tanzania S. highlands	'Kilimanjaro' + Kenya	Kenya
Wing				
M	57	64–68, $\bar{x}$ = 67 (n = 7); 67–71, $\bar{x}$ = 69 (n = 10)	60–62, $\bar{x}$ = 61 (n = 4); 59–65, $\bar{x}$ = 61.9 (n = 10)	58–66, $\bar{x}$ = 62 (n = 4); 60–64, $\bar{x}$ = 62.8 (n = 10)
F		59–65, $\bar{x}$ = 64 (n = 8); 63–71, $\bar{x}$ = 66.5 (n = 10)	$\bar{x}$= 58.4 (n = 5); 55–62, $\bar{x}$ = 58.9 (n = 10)	59–61, $\bar{x}$ = 60.2 (n = 3); 56–59, $\bar{x}$ = 57.5 (n = 10)
Tail				
M	55	68–80, $\bar{x}$ = 70 (n = 7); 69–76, $\bar{x}$ = 72 (n = 10)	55–69, $\bar{x}$ = 63 (n = 4); 62–71, $\bar{x}$ = 66.2 (n = 10)	60–63, $\bar{x}$ = 61 (n = 4); 60–64, $\bar{x}$ = 61.9 (n = 10)
F		46–70, $\bar{x}$ = 64 (n = 8); 66–76, $\bar{x}$ = 71.4 (n = 10)	$\bar{x}$= 60.8 (n = 4); 58–68, $\bar{x}$ = 62.4 (n = 10)	51.3–68, $\bar{x}$ = 58.1 (n = 3); 52–57.5, $\bar{x}$ = 55.4 (n = 10)
Bill				
M	18	15–18, $\bar{x}$ = 17 (n = 7); 16–16, $\bar{x}$ = 16 (n = 2)	15–16, $\bar{x}$ = 15.5 (n = 3); 14–16, $\bar{x}$ = 14.9 (n = 10)	15.9–17, $\bar{x}$ = 16.7 (n = 4); 15.5–17, $\bar{x}$ = 16 (n = 10)
F		15–17, $\bar{x}$ = 17 (n = 8); 16–16.5, $\bar{x}$ = 16.3 (n = 2)	$\bar{x}$= 13.9 (n = 5); 14–16, $\bar{x}$ = 15 (n = 10)	12.3–19, $\bar{x}$ = 16.4 (n = 3); 14.5–16, $\bar{x}$ = 15 (n = 10)
Tarsus				
M	23	28–30, $\bar{x}$ = 29 (n = 7); 24–27, $\bar{x}$ = 25.7 (n = 12)	26–30, $\bar{x}$ = 27.6 (n = 4); 24–27, $\bar{x}$ = 25 (n = 10)	25–29, $\bar{x}$ = 26.7 (n = 3); 25–26.5, $\bar{x}$ = 25.5 (n = 10)
F		28–30, $\bar{x}$ = 29 (n = 8); 23–26, $\bar{x}$ = 24.6 (n = 12)	$\bar{x}$= 25.4 (n = 5); 23–25, $\bar{x}$ = 24.4 (n = 10)	24.5–30, $\bar{x}$ = 26.6 (n = 3); 23–25, $\bar{x}$ = 24.2 (n = 10)

Measurements (mm)	White–tailed Cisticola	Coastal Cisticola	Winding Cisticola	Winding Cisticola
	C. anderseni	*C. haematocephalus*	*C. marginatus suahelicus*	*C. marginatus nyansae*
	Kilombero Valley	Tanzania	Tanzania	Kenya
Wing				
M	58.9	51–51, $\bar{x}$ = 51 (n = 2); 55–57, $\bar{x}$ = 56.5 (n = 6)	$\bar{x}$ = 56.5 (n = 1); 58–62, $\bar{x}$ = 60.6 (n = 8)	$\bar{x}$ = 61.6 (n = 4); 60–64, $\bar{x}$ = 62.2 (n = 8)
F		48 (n = 1); 49–52, $\bar{x}$ = 50.5 (n = 6)	56.5 (n = 1); 52–57, $\bar{x}$ = 53.9 (n = 8)	$\bar{x}$ = 56 (n = 1); 53–59, $\bar{x}$ = 57 (n = 8)
Tail				
M	54	$\bar{x}$ = 47.2 (n = 2); 50–55, $\bar{x}$ = 51.8 (n = 6)	$\bar{x}$ = 49.5 (n = 1); 46–61, $\bar{x}$ = 49.7 br. (n = 4), $\bar{x}$ = 57.7 non–br. (n = 4)	$\bar{x}$ = 60.8 (n = 4); 49–64, $\bar{x}$ = 54.1 (n = 8)
F		44.8 (n = 1); 48–52, $\bar{x}$ = 50 (n = 6)	$\bar{x}$ = 44.8 (n = 1); 46–51, $\bar{x}$ = 47 br. (n = 4), $\bar{x}$ = 48.5 non–br. (n = 4)	54 (n = 1); 43–56, $\bar{x}$ = 50.1 (n = 7)
Bill				
M	13.3	$\bar{x}$ = 13.4 (n = 2); 15–17, $\bar{x}$ = 15.8 (n = 5)	$\bar{x}$ = 14.7 (n = 1); 14–16, $\bar{x}$ = 15.4 (n = 8)	15–17, $\bar{x}$ = 16 (n = 4); 14–18, $\bar{x}$ = 16.4 (n = 8)

(continued)

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Appendix 2. (continued)

Measurements (mm)	White–tailed Cisticola	Coastal Cisticola	Winding Cisticola	Winding Cisticola
	C. anderseni	*C. haematocephalus*	*C. marginatus suahelicus*	*C. marginatus nyansae*
	Kilombero Valley	Tanzania	Tanzania	Kenya
F		11.6 (n = 1); 14–15, $\bar{x}$ = 14.8 (n = 6)	$\bar{x}$ = 14 (n = 2); 14–15, $\bar{x}$ = 14.7 (n = 8)	15 (n = 1); 14–16, $\bar{x}$ = 15.6 (n = 8)
Tarsus				
M	19.3	$\bar{x}$ = 22.7 (n = 2); 22–22, $\bar{x}$ = 22 (n = 6)	$\bar{x}$ = 25.5 (n = 1); 22–24, $\bar{x}$ = 22.7 (n = 8)	23.5–25, $\bar{x}$ = 24.3 (n = 4); 22–26, $\bar{x}$ = 24.1 22.9 (n = 8)
F		22.7 (n = 1); 20–22, $\bar{x}$ = 21.2 (n = 6)	$\bar{x}$ = 21.9 (n = 2); 19–22, $\bar{x}$ = 21.2 (n = 8)	21–23, $\bar{x}$ = 22.1 (n = 8)

APPENDIX 3

Acronyms for sound libraries used are: British Sound Library (BSL; https://sounds.bl.uk/), Macaulay Library (ML; https://www.macaulaylibrary.org/), Xeno-Canto (XC; https://www.xeno-canto.org/). Published recordings (Chappuis 2002, Gibbon 2003) are listed under References. Unpublished recordings are available upon request from recordist Michael Mills (michael@birdingafrica.com). Following the ND2 phylogenetic tree of Davies (2014), birds from Kenya except the Lake Victoria area are included in the taxon *suahelicus*. No recording of nominate *C. m. marginatus* from the White Nile in Sudan and South Sudan was available

C. galactotes (including *isodactylus*) (8): **Mozambique**: BSL137148, XC201332, 452901; **South Africa**: ML80688, XC408045; **Country?**: Gibbon (2003) 3 cuts.

C. luapula (including *schoutedeni* and *stagnans*) (11): **Botswana**: ML88126; **Namibia**: XC185626; **Zambia**: BSL07920, 25751, 26263, 26264, M. Mills, five unpublished (ZMB16_022492-96).

C. (*marginatus*) *suahelicus* (35): **Kenya**: BSL18179, 22160, 27817, 30058, 30080, 48810, 48811, 198295, 198297, 198304, 199214, ML14391, 14392, 14393, 14394, XC247179, 247198, 247216, 247326, 375345, 375346, 376079, 401966, 403557, 420354, 420355, 420356; **Tanzania**: BSL7921, XC33986, 430162, 430163, 430164, 436372, 436508, 450327.

C. haematocephalus (13): **Kenya**: BSL30051, 180378, 195066, 198365, 198366, 198368, 198371, M. Mills 1 unpublished (KEN11_071082); **Somalia**: BSL24060; **Tanzania**: XC510068, 510069, 510070, 510071.

C. anderseni: **Tanzania** (37): BSL153756, 153757, 153769, 153770, 153771, 153772, 153777, 153778, 153779, 153780, 153781, ML135955, M. Mills, 1 unpublished (TZA15_091395), XC494988, 499003, 499004, 499005, 499006, 499007, 499008, 499009, 499010, 511338, 511371, 511373, 511374, 511376, 511377, 511378, 511379, 511380, 511513, 511514, 511517, 511518, 511521, 511522.

C. marginatus amphilectus (including *nyansae* and *zalingei*) (45): **Angola**: M. Mills, four unpublished (AGO11_042941-44); **Benin**: XC204564, 204565, 204566, 288071, 288072, 288244, 454660, 454661; **Cameroon**: XC375031; **Chad**: Chappuis (2002, cut 2); **DR Congo**: ML1025; **Ivory Coast**: Chappuis (2002, cut 1), ML53006, 53007, XC255037, 350100, 350101; **Kenya**: BSL100994, 196758, 196760, 196832, 197071, 197072, 197074, 197300, 197499, M. Mills, 1 unpublished (KEN05_010124), XC396245, 73415; **Rwanda**: XC48350, 76608; **Senegal**: XC343738; **Uganda**: XC116736, 117143, 148556, 157105, 157106, 217562, 217563, 217566, 288726.

C. lugubris (12): **Ethiopia**: M. Mills, 3 unpublished (ETH14_041124, ETH14_041359-60), ML100328, XC210039, 210040, 210042, 300126, 300127, 300128, 305989, 410335.

C. pipiens (incl. *congo* and *arundinicola*) (33): **Angola**: BSL213053, 213054, 213055, 213056, 213057, 213058; **Botswana**: XC158072; **Burundi**: ML94704, XC71354 (originally misidentified as *C. marginatus*); **Namibia**: XC460863, 460865; **Tanzania**: ML101186, 101188, 101190, 101191; **Zambia**: BSL07924, 07925, 17463, 17464, ML24893, XC339099, 339100, 339101, 339102, 339103, 508841, M. Mills, 3

unpublished (ZMB19_111336-37, ZMB19_111354); **Zimbabwe**: BSL69045; **Country?**: Gibbon (2003) three cuts.

C. chubbi (including *chubbi*, *discolor*, *adametzi*) (62): **Cameroon**: ML212400, 534808, 534818, 534842, 534845, 534847, 537098, XC120759, 121049, 121091, 48925, 99119, 99120, 99121, 99122, 99123, 99124, 99125, 99126; **DR Congo**: ML1013, 1289, XC103933, 105604; **Kenya**: ML14373, 14374, 14375, 23159, 24636, 26071, XC205752, 396444, 396446, 396447, 453427, 453428, 453429, 453430, 62961, 98717; **Rwanda**: XC153957, 48366, 75613, 75614, 83847; **Uganda**: ML24685, 26303, XC113292, 233056, 233076, 233077, 233078, 233079, 233080, 233780, 234731, 234735, 235938, 236854, 266021, 266271, 470844, 76939.

C. hunteri (44): **Kenya**: ML14395, 14396, 14397, 14398, 14399, 14500, 14501, 14502, 14503, 14504, 20446, 53575, XC131989, 131990, 196092, 289555, 299758, 344762, 398570, 444578, 450352, 450353, 450354, 455653, 470592, 470593; **Tanzania**: ML17973, 17975, 17979, 23910, 23915, XC449338, 449339, 449340, 449342, 449343, 449344, 449346, 449347, 449349, 96691, 96692; **Country?**: ML26049, 26050.

C. bakerorum (79): **Tanzania**: BSL153758, 153759, 153760, 153761, 153762, 153763, 153764, 153765, 153766, 153767, 153768, 153771, 153773, 153774, 153775, 153776, ML135954, 135956, 135958, XC494987, 498412, 498413, 498414, 498415, 498416, 498417, 498418, 498419, 511302, 511304, 511306, 511308, 511311, 511312, 511314, 511315, 511316, 511317, 511320, 511322, 511323, 511324, 511326, 511328, 511329, 511330, 511332, 511333, 511334, 511335, 511336, 511339, 511340, 511341, 511342, 511344, 511345, 511347, 511349, 511350, 511352, 511355, 511357, 511360, 511361, 511363, 511365, 511366, 511368, 512015, 512016, 512017, 512018, 512019, 512020, 512021, 512022, 512023, 512024.

C. nigriloris (31): **Malawi**: ML83268, 83269, 83271, 83273, XC311906, 311927, 311929, 311931, 395920, 395921, 397958, 397959, 397960, 397961, 96999; **Tanzania**: ML14509 (originally misidentified as *C. hunteri*), 49642, 49643, XC116201, 429723, 444293, 444294, 459256, 459257, 49841; **Zambia**: ML24896, 161773; **Country?**: ML24602, 24604, 28062, 28063 (originally misidentified as *C. chubbi*).

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Supinfo S1 Habitats of the Kilombero floodplain

Figure S1 Typical habitat for Kilombero Cisticola on both right and left side of a river channel.

Figure S2 Typical Kilombero Cisticola habitat with very tall, dense and flowering *Phragmites* along a smaller side river. Persons and canoes serve to illustrate the size of the plants.

Figure S3 Habitat of White-tailed Cisticola with shorter grass, but in the background tall and mature *Phragmites* reeds that constitute typical Kilombero Cisticola habitat.

Figure S4 Recently cleared floodplain with the first crop emerging.

Figure S5 Male parts of duets.

Figure S6 *Cisticola* alarm calls.

Table S1 List of primers used in this study.

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