University of Cape Town

Doctoral Thesis

Taxonomy, phylogeny and biogeography of cisticolas (*Cisticola* spp.)

Author:
Owen R. Davies

Supervisors:
Prof. Timothy M. Crowe
Prof. Rauri C. K. Bowie

University of Cape Town

A thesis submitted in fulfilment of the requirements for the degree of Doctor of Philosophy

in the

Faculty of Science
DST/NRF Centre of Excellence at the
Percy FitzPatrick Institute of African Ornithology
Department of Biological Sciences

November 2014

The copyright of this thesis vests in the author. No quotation from it or information derived from it is to be published without full acknowledgement of the source. The thesis is to be used for private study or non-commercial research purposes only.

Published by the University of Cape Town (UCT) in terms of the non-exclusive license granted to UCT by the author.

University of Cape Town

Declaration of Authorship

I, Owen R. Davies, declare that this thesis titled, 'Taxonomy, phylogeny and biogeography of cisticolas (*Cisticola* spp.)' and the work presented in it is my own, unless otherwise stated. Apart from the guidance received from my supervisors, assistance from all institutions and individuals in this dissertation is acknowledged. This dissertation has not been previously submitted for the degree at this or any other university and I therefore present it for examination for the degree of Ph.D. I hereby grant the University free license to reproduce the above thesis in whole or in part, for the purpose of research.

Signed: _____

Date: _____

"With the loss of their chief, all the birds claimed to be the new king. Confident in his abilities, the vulture suggested a competition; whichever bird that could fly the highest, would be the king of the birds. When all the other birds had dropped to earth, exhausted, the vulture remained soaring high. While the vulture was claiming victory, a tiny Cloud Cisticola emerged from its hiding place amongst the vultures feathers and soared higher than the vulture could manage, shouting 'I am king'. The Cloud Cisticola realised that the rest of the birds were unhappy with this trickery and quickly dropped to earth and hid in a snake hole."

— Traditional Xhosa folklore

Abstract

Faculty of Science
DST/NRF Centre of Excellence at the
Percy FitzPatrick Institute of African Ornithology
Department of Biological Sciences

Doctor of Philosophy

Taxonomy, phylogeny and biogeography of cisticolas (*Cisticola* spp.)

by Owen R. Davies

A review of the genus *Cisticola* was published in 1930 by Rear-admiral Lynes. While subsequent authors have modified Lynes' original groupings, his work remains the basis for modern syntheses of cisticolas. This study tests Lynes' hypotheses by analysing data that he presented in his review and with measurement and plumage data collected from museum specimens. Lynes' groupings were well recovered (98%) when data captured from his review were analysed phenetically, suggesting that he grouped species mostly by similarity. In contrast, when morpho-behavioural data were analysed using cladistic methods, many of his groupings were not monophyletic and the resultant cladogram had very little nodal support due to their highly conservative morphology. To resolve the structure of the genus and the relationships within it, two mitochondrial and four nuclear regions were sequenced from toe-pad samples taken from museum specimens. The molecular analyses included 44 of the 49 currently recognised species and represents the most taxon-dense molecular phylogeny of the genus. The resultant phylogeny separates species into five main clades, but many of Lynes' groupings were not monophyletic and there was also very little support for more recent groupings. Vocalisation analyses indicated that frequency components of songs were correlated with habitat type and body size. These correlations, though, disappeared when phylogeny was controlled for indicating that phylogenetic history rather than habitat preference influenced song character distribution. Some song types are mismatched to their environment, and some sympatric sister species appear to give similar calls. Cisticolas may overcome these attenuation and identification difficulties with behavioural adaptations and aerial displays. The biogeographic distribution of closely related species does not agree with many of the previously proposed hypotheses and a dated phylogeny estimates that most of the diversification in the genus has occurred within the last five million years. Most of the mean divergence date estimates correlated with periods of climate variability and episodes during which there is evidence for high lake levels in Africa, rather than correlating with Plio-Pleistocene glaciation, offering evidence that open habitats may have become fragmented during extremes of both arid and humid climates.

Acknowledgements

The historical work of Rear-admiral Hubert Lynes must surely be acknowledged first and foremost; without his huge effort and detailed descriptions I would not have had a foundation upon which to build this thesis. I must thank Prof. Timothy M. Crowe and Prof. Rauri Bowie for their guidance and supervision as well as their financial and technical support with data collection and analyses. I am indebted to the Director of research at the Museum of Natural History in Stockholm, Dr. Per G. P. Ericson, as well as the head of the Molecular Systematics Laboratory, Dr. Pia Eldenäs, for allowing me access to their laboratory facilities and additional financial and technical support during my trip to Sweden. A huge amount of effort was made by Dr. Martin Irestedt who offered technical assistance to me in the Molecular Systematics Laboratory and passed on his skills by taking the time to teach me the technical expertise required to successfully sequence DNA from samples collected from old museum specimens, an invaluable skill which I have been able to bring back to South Africa and consequently reproduce successful DNA extractions of museum specimens in local laboratories. In addition to the technical assistance, I must thank Martin for going out of his way to be hospitable and welcoming to me from the moment I arrived in Sweden, including inviting me for birding trips and social events; hopefully I shall be able to return the favour one day. Many hours of fieldwork were spent with Dr. Jérôme Fuchs and Dr. Graeme Oatley who passed on their knowledge of skinning, field preparation and taxidermy of birds. I could not have asked for two nicer people to spend time with in the bush. Thanks to Dr. Jérôme Fuchs and Ms. Lisa Nupen for assisting with molecular analyses and Dr. Patrick R. A. Lindop for his hospitality and Mr. Charles Owen, Dr. Hanneline Smit-Robinson and Dr. Ben Smit for additional assistance in the field. Thanks to Dr. Fenton Cotterill for many hours of discussion and to Mr. Mike Mills for access to his vocalisation recordings. Thanks must go to Prof. Peter Ryan for his comments on various drafts of this manuscript, as well as Assoc. Prof. Sugnet Lubbe of the Statistical Sciences department at the University of Cape Town, Prof. François Husson of the Applied Mathematics department of Agrocampus Ouest in France and Mr. Toby Goodworth for their invaluable input and patient guidance in the statistical analyses, particularly with multiple factor and multiple correspondence analyses. Thank you also to Assoc. Prof. Rebecca R. Ackermann at the Archaeology Department at the University of Cape Town for her assistance with the analyses and interpretation of geometric morphometric data. Thanks must also be extended to the staff of Natural History Museum at Tring for their hospitality and assistance with their cisticola collections, particularly senior curator of birds Mark Adams and collections manager Dr. Robert Prys - Jones. Thanks to Ms. Petra Muller, Mr. Chris Tobler, Ms. Tania Jansen and Ms. Hilary Buchanan and the rest of the administrative and support staff at the Percy FitzPatrick Institute

of African Ornithology and the Department of Biological Sciences at the University of Cape Town for their help in the logistics and planning of my various trips both locally and abroad. Thanks to my family for financial and emotional support, including my fiancée Ms. Jennifer Waters for her continued support, patience and the invaluable comments and corrections made to thesis drafts. Thanks also to the late Prof. Phil A. R. Hockey for support, conversation and inspiration. The majority of the financial support for this project was provided by the South African Department of Science and Technology (DST)/National Research Foundation (NRF) Centre of Excellence at the Percy FitzPatrick Institute of African Ornithology and the Clancey Trust.

Contents

List of Figures

List of Tables

Dedicated to my late father, whose family commitments unfortunately halted the pursuit of his Ph.D., this is for you dad.

Summary

Historically, the taxonomy and systematics of cisticolas has been clouded by confusion, with seasonal variations in plumage or geographic variants often being classified as separate species or genera. In 1930, Rear-Admiral Lynes, unsatisfied with the state of taxonomy in this genus, published his Review of the genus *Cisticola* in which he presented detailed species accounts and offered a much needed reclassification, ordering species into groups of closely related birds. Even after this herculean effort, confusion persists and is reflected in the subsequent reshuffling and modification of initial groupings. This, combined with the addition of newly described taxa, has resulted in little consensus amongst the recent literature with respect to groupings and even in the species-level classifications. Lynes' conclusions were reinterpreted in a biogeographical context that suggested that the groups could be better thought of as 'super-species' and 'species complexes' of closely related sister-species, making modifications to the original groupings to reflect this idea and to include newly described species. Some of these later modifications were contested and it was argued that they did not contain the most closely related taxa with authors suggesting alternative hypotheses. The most recent review on the genus, though, maintained that Lynes' work remains an important starting point for modern research on the systematics of cisticolas.

I therefore set out to determine the utility of various characters (including plumage colour, measurements, vocalisations and molecular data including mitochondrial and nuclear DNA regions) in resolving cisticola systematics and test the grouping and super-species hypotheses that continue to form the basis of our understanding of the genus. While Lynes provided detailed notes on the plumage and measurement characteristics of each species, he used his intuition and familiarity with the birds in the field, rather than what would be considered formal analyses, to reach his conclusions. To test Lynes' conclusions, plumage and measurement data was captured from the descriptions he presented in his review and formally analysed. As colour perception is influenced by the context in which they are viewed (with colours appearing different depending on surrounding colours and shades), Lynes' plumage assessments may have been somewhat subjective. To reduce subjectivity and assess what influence these characters might have on phylogenetic relationships, a digital method was employed to capture colour data empirically off standardised digital images independent from the illusionary perceptual effects of context. To reanalyse mensural characters, 16 264 measurements were taken from 2033 specimens housed at the Natural History Museum at Tring, including specimens that were collected by Lynes himself. Analyses on these data demonstrated that plumage and measurement characters were useful for differentiating between the species groups as defined by Lynes (1930), particularly when these data were analysed

phenetically. In contrast, the groups, and the relationship amongst them, were poorly resolved when these data were analysed using cladistics methods. This was due to the fact that many species look very similar to each other, with regional intraspecific variation sometimes being greater than variation between recognised species.

Molecular data analyses helped to resolve the phylogenetic relationships amongst species and species groups and this study presents the first molecular phylogeny on the genus. Analyses included two mitochondrial gene regions, NADH dehydrogenase subunit 2 (ND2) and cytochrome B (CYTB), and four nuclear gene regions, β-fibrinogen gene, intron 5 (FIB 5), myoglobin intron II (MYO), glyceraldehyde-3-phosphodehydrogenase intron 11 (G3PDH) and transforming growth factor beta 2 (TGF-β2), obtained mostly from toe-pad samples of museum specimens. Sampling effort was concentrated on obtaining ND2 sequences, as this region showed both a good level of sequence diversity and a high success rate in amplification and sequencing. Molecular data was obtained from 121 individuals representing 44 of the 49 currently recognised species. Many of the species groupings proposed by Lynes were not recovered by the molecular analyses, neither were most of the proposed 'super-species' and 'species complexes'. This study provides evidence that many of these groups do not represent monophyletic clades of sister species, even after recent reshuffling, and that such groupings might obscure relationships within the genus.

Vocalisations and song structure are good characters for differentiating amongst species. The frequency components of the songs differed between habitat types, with higher pitched songs occurring more frequently in open habitat types. Songs, though, were also seemingly influenced by the size of the singing birds. Many of the correlations of habitat and size with song frequency characteristics disappeared when phylogeny was controlled for, indicating that evolutionary history rather than habitat preference influenced character distribution, with birds potentially overcoming poor acoustic performance in a given habitat with behavioural adaptations, such as aerial displays. These displays may be crucial in the advertisement of species identity between closely related species that share similar call types and occur in sympatry.

The biogeography of cisticolas provided insight into the evolution of open habitat types across Africa. A dated phylogeny indicated that many speciation events within the genus coincided with recently hypothesised periods of high climate variability and correlated with time periods during which there is evidence of high lake levels in Africa over the past five million years, offering evidence that open habitats may have become fragmented during extremes of both arid and humid climates.

In conclusion, the main value of the historical work on the genus remains in the detailed descriptions of taxa, but the groupings were based mostly on overall similarity, a practice that was common at the time. Rather than relying purely on morphology and what are ultimately slight differences amongst a group of very similar looking birds, this study included molecular data to determine relationships within the genus and provides little support for the proposed groups. The results of this thesis have also identified cryptic molecular diversity and indicate that such diversity may be hidden by morphological similarity throughout the genus; I therefore call for renewed interest into the study of cisticolas, where increased sampling resolution is sure to offer interesting results in terms of biodiversity and the study of the evolution of life history traits, mating strategy, vocalisations and habitat dynamics.

Chapter 1

Status quo ante: Taxonomic history of the genus *Cisticola*

1.1 Introduction

The genus *Cisticola* is one of the largest within the Cisticolidae, a family that was erected for members of the Old World warblers (Sylviidae) primarily restricted to Africa (Olsson et al., 2013; Sibley and Alquist, 1991). The genus comprises a large number of mostly small, drab, brown passerine birds with highly conservative plumage and morphology, making them notoriously difficult to identify.

Common names are included in the initial instance but scientific names are used throughout to ease comparisons with the sequence of historical descriptions, particularly with subspecific lists.

1.1.1 *Morphology*

In form, cisticolas have short rounded wings possessing 10 primary feathers, with the outermost primary feather typically reduced in length. Tail length varies greatly across the genus, but all have 12 retrices forming a moderately graduated or rounded tail shape. The variation in tail length seems to be correlated with the importance of aerial displays, with those that exhibit high altitude displays possessing short tails and those with low altitude, or perched, displays having relatively longer tails (Ryan, 2006). Cisticolas generally have slender bills, typical of their primarily insectivorous diet, with bill size ranging from short and slender to the somewhat thicker and more robust bill of the largest species (Ryan, 2006). Toes are typically passerine, with one rearward and three

forward facing toes (anisodactyly); the middle forward facing toe is generally the longest, with most but not all cisticolas having the inner toe longer than the outer toe (Ryan, 2006).

1.1.2 *Sexual dimorphism*

Cisticolas are generally small and of a slender build, with most weighing less than 10 grams. The size ranges from the diminutive *C. nana* (Tiny Cisticola) weighing about 5 grams to the larger, more robustly built *C. natalensis* (Croaking Cisticola), weighing about 25 grams. Males are often larger than females, with a wing length often around 10% longer and a mass up to 40-50% heavier than females in the highly dimorphic species such as *C. natalensis* (Ryan, 2006). In breeding season, male cisticolas are often less streaked on the upper-side than females, and often possess a darker bill and palate, though these characters can exhibit intraspecific variation (Lynes, 1930).

1.1.3 *Breeding and seasonal plumage variation*

Many cisticolas, especially males, exhibit seasonal differences in plumage colour and pattern, with colours (particularly of the crown) generally becoming darker and less streaked in the breeding season. Tail length often varies greatly between seasons, becoming about 13% shorter during the breeding season in males, and about 11% shorter in females of those populations with seasonally distinct plumages (Ryan, 2006). In the males of *C. exilis* (Golden-headed Cisticola), where the breeding tail length is around 30% shorter than in the non-breeding season, it has been shown that tail length could be under strong sexual selection with shorter tailed males attracting more females and fledging more chicks (Balmford et al., 2000). The increased breeding success of shorter tailed males was attributed to shorter tails improving high-speed flight performance during aerial displays and the acquisition of higher quality territories through male competition (Balmford et al., 2000). Intraspecific differences in seasonal plumage are often as great, if not greater, than interspecific plumage differences between currently recognised species (Lynes, 1930).

Cisticolas are generally solitary, territorial breeders, with the exception of *C. exilis* and *C. juncidis* (Zitting Cisticola); perhaps both *C. aridulus* (Desert Cisticola) and *C. ayresii* (Wing-snapping Cisticola), which might be polygamous at least some of the time (Ryan, 2006); and *C. chiniana* (Rattling Cisticola), where a coalition of males seems to hold and defend communal territories (Carlson, 1986). Cisticolas breed in favourable conditions when there is an abundance of food and young grass for nest building, which

generally occurs at the onset of the rains (Lynes, 1930; Ryan, 2006). Areas that experience near perennial rains, such as the tropics, are home to populations of cisticola that do not exhibit the seasonal variation in plumage shown by conspecifics outside of tropical latitudes (Lynes, 1930). These differences in plumage seasonality can obscure the relationships within and amongst species (Lynes, 1930).

Cisticolas are related to the tailorbirds (*Orthotomus*: Nguembock et al. (2007); Olsson et al. (2013)), so named because of their habit of sewing together their nests, and like tailorbirds, cisticolas also weave together grass and leaves into a closed, covered nest (Ryan, 2006). The shapes of these nests vary within the genus and fall into three main types: 1) the 'soda-bottle', unique to the wide-ranging *C. juncidis*; 2) the 'tailored-ball', made of sewn-together leaves and common to *C. erythrops* (Red-faced Cisticola), *C. cantans* (Singing Cisticola), *C. rufus* (Rufous Cisticola) and sometimes *C. exilis*; and 3) the 'ball-shape' nest that is common to the remainder of the genus and can be further categorised into deep- and oval-ball shaped nests (Lynes, 1930). Cisticolas lay between two and five eggs per clutch and eggs are highly variable in colour, which may be a result of parasite avoidance as cisticola nests are often the target of the Cuckoo Finch (*Anomalospiza imberbis*) across large parts of their range (Spottiswoode and Stevens, 2011).

1.1.4 *Juvenile plumage*

There is a large variation in juvenile plumage, with juveniles of some populations having a yellow wash over the underside. This character is common, but highly unstable, with nestlings in the same nest being either very yellow or not yellow at all (Lynes, 1930).

1.1.5 *Habitat*

Cisticolas can be found in all available open habitat types in Africa, provided there is some sort of grass available for cover. They can be found from deserts to scrub, grasslands, savanna, reed beds and emergent vegetation in wetlands to open woodland and forest edges (Ryan, 2006). Many cisticola species exploit narrow micro-habitats allowing for as many as 11 species to co-occur within a few hundred meters of each other; often, species in view of each other are separated only by a moisture gradient from wetland grasses towards dry scrub (Ryan, 2006). In contrast, some of the wide ranging species such as *C. juncidis* exploit a range of different habitats from arid savanna to irrigated cultivation and salt marshes (Ryan, 2006), though whether these are true habitat generalists or a species complex comprising several cryptic habitat specialists

remains to be tested. Cryptic colouration is common for birds that inhabit open habitats as a means of camouflage and predator avoidance - the colour of birds often matches that of the substrate on which they forage (Chittenden et al., 2012). For example, individuals of *C. juncidis*, *C. aridulus* and *C. natalensis* that inhabit dry areas have similarly sandy-coloured and lighter-coloured plumage, and are more similar to each other than to conspecifics that are found in wetter areas.

1.1.6 *Vocalisations*

Cisticolas exhibit a much greater variety in their songs than they do in their plumage, ranging from simple trills to musical whistles, either singing alone or in duet (Ryan, 2006). In addition to interspecific differences in song, the song of some species varies across their range. Ryan (2006) gives examples of intraspecific variation in the song of *C. ayresii*, whose simple whistling song in the south of its range is different to the more warbling song common in the north of its range. Similarly, the song of *C. robustus* (Stout Cisticola) is different between northern and southern populations and the songs from populations of *C. angusticauda* (Tabora Cisticola) and *C. fulvicapilla* (Neddicky) differ in parts of their range where they co-occur (Ryan, 2006).

Research into the diversity of the songs given by two species of cisticola, *C. erythrops* (Benedict and Bowie, 2009) and *C. chiniana* (Benedict and Bowie, 2012), has also confirmed variation in songs across their respective ranges, but indicated that both have some stable song features (like fixed syllables) amongst highly variable portions. Interestingly, even though the songs of only two species have currently been looked at in detail, these two species generate song diversity in very different ways (Benedict and Bowie, 2012). The diversity found in the song of *C. erythrops* is achieved by altering the ordering of syllables and by varying song duration, whereas songs of *C. chiniana* have relatively fixed song durations and ordering, but highly variable end-phrase forms (Benedict and Bowie, 2009). This variability in song structure potentially enables the large number of morphologically similar birds to signal species identity and thereby act as a pre-mating barrier to reproduction between sympatric species (Marler, 1957; Ryan, 2006). Habitat gradients and preferences across species' ranges combined with sexual selection, morphological evolution and cultural drift may all contribute to the highly variable songs of cisticolas (Benedict and Bowie, 2012).

1.2 Taxonomic history

The confounding factors of variable seasonal plumages and intraspecific geographic variation in plumage, calls and eggs, together with the great overall interspecific similarity in shape and plumage, have resulted in the genus having a tortuous taxonomic history (for complete list see Appendix A). The taxonomic treatment of del Hoyo et al. (2006) is followed below.

1810–1830

`Taxa described: 7  Species retained: 6  Subspecies retained: 1  Rejected: 0`

Seven taxa were described with six of those currently considered to be valid species, and one accepted as a subspecies. It started with the description of *juncidis* in Europe by Rafinesque in 1810, who placed it in the genus *Sylvia*. The genus included the descriptions of *fulvicapilla* and *textrix* from South Africa while the remaining three species were placed in the genus *Malurus*.

Species described: ***juncidis*** (Zitting Cisticola), ***textrix*** (Cloud Cisticola), ***fulvicapilla*** (Neddicky), ***galactotes*** (Rufous-winged Cisticola), ***exilis*** (Golden-headed Cisticola) and ***ruficeps*** (Red-pate Cisticola).

Subspecies described: ***juncidis cisticola***.

1831–1840

`Taxa described: 4  Species retained: 1  Subspecies retained: 1  Rejected: 2`

Four taxa were described, but only one was placed in the genus *Cisticola*, two were placed in the genus *Sylvia* and turned out to be merely descriptions of a juvenile and adult of the same taxon and *juncidis cursitans* was placed in the genus *Prinia* by Major Franklin during his survey of India. Only a single species and subspecies are valid with two rejected for belonging to previously described taxa.

Species described: ***lugubris*** (Ethiopian Cisticola).

Subspecies described: ***juncidis cursitans***.

1841–1850

`Taxa described: 29  Species retained: 9  Subspecies retained: 8  Rejected: 12`

A total of 29 taxa were described during this period; the large increase was mostly thanks to the separate work of Sir A. Smith and Wahlberg in South Africa. Taxa were placed into four separate genera, with Smith and Sundevall (who described birds collected by Wahlberg) placing most in the genus *Drymoica*. Of those described, nine are valid species, eight are valid subspecies and 12 were rejected, including novel species that were named by Gould in Australia that merely reflect different seasonal plumages of the same subspecies of *exilis*.

Species described: ***tinniens*** (Levaillant's Cisticola), ***aberrans*** (Lazy Cisticola), ***cherina*** (Madagascar Cisticola), ***chiniana*** (Rattling Cisticola), ***lateralis*** (Whistling Cisticola), ***natalensis*** (Croaking Cisticola), ***rufus*** (Rufous Cisticola), ***subrufficapilla*** (Grey-backed Cisticola) and ***robustus*** (Stout Cisticola).

Subspecies described: ***juncidis terrestris***, ***fulvicapilla ruficapilla***, ***natalensis strangei***, ***juncidis uropygialis***, ***chiniana campestris***, ***exilis lineocapilla***, ***juncidis brunniceps*** and ***ruficeps scotoptera***.

1851–1860

`Taxa described: 10  Species retained: 2  Subspecies retained: 4  Rejected: 4`

A further 10 taxa were described and placed in three separate genera, including *Drymoica*, *Sylvia* and *Calamanthella*. Only two species and four subspecies are considered to be valid.

Species described: ***anonymus*** (Chattering Cisticola) and ***erythrops*** (Red-faced Cisticola).

Subspecies described: ***exilis erythrocephalus***, ***juncidis omalurus***, ***juncidis tinnabulans*** and ***exilis volitans***.

1861–1870

`Taxa described: 45  Species retained: 10  Subspecies retained: 13  Rejected: 23`

The large number of taxa described was mostly due to Heuglin's work in northeast Africa, who placed taxa in three separate genera, *Hemipteryx*, *Drymoeca* and *Cisticola*. Most of these though were rejected as merely different seasonal plumages of birds that had already been described. Of those that were placed in the genus *Cisticola*, three were from completely different genera; *Urorhipis*, *Spiloptila* and *Heliolais*. Even though more than half of those described were rejected, 10 species and 13 additional subspecies were retained.

Species described: ***brunnescens*** (Pectoral-patch Cisticola), ***ayresii***, ***troglodytes*** (Foxy Cisticola), ***haematocephala*** (Coastal Cisticola), ***marginatus*** (Winding Cisticola), ***cantans*** (Singing Cisticola), ***eximius*** (Black-backed Cisticola), ***brachypterus*** (Short-winged Cisticola), ***lais*** (Wailing Cisticola) and ***rufilatus*** (Tinkling Cisticola).

Subspecies described: ***exilis tytleri***, ***juncidis fuscicapilla***, ***exilis rusticus***, ***troglodytes ferrugineus***, ***galactotes isodactylus***, ***chiniana procerus***, ***exilis tytleri***, ***chiniana procerus***, ***lateralis antinorii***, ***cantans concolor***, ***chiniana simplex***, ***tinniens elegans*** and ***cantans swanzii***.

1871–1880

`Taxa described: 11  Species retained: 0  Subspecies retained: 4  Rejected: 7`

The genus name *Cisticola* was being used more frequently for taxa described during this period, but three were described as *Drymoeca/Drymoica* and one was placed in the genus *Melocichla*. Most descriptions were rejected, with none of the proposed species accepted and only four subspecies that were described were considered to be valid.

Species described: **None**.

Subspecies described: ***exilis semirufus***, ***marginatus amphilectus***, ***robustus angolensis*** and ***lateralis modestus***.

1881–1890

`Taxa described: 10  Species retained: 5  Subspecies retained: 3  Rejected: 2`

By this time, all but three taxa were described in the genus Cisticola, as was incana which has since been moved into its own genus. All but two taxa were accepted, including five new species and three subspecies.

Species described: ***haesitatus*** (Socotra Cisticola), ***melanurus*** (Black-tailed Cisticola), ***nana***, ***cinereolus*** (Ashy Cisticola) and ***hunteri*** (Hunter's Cisticola).

Subspecies described: ***brachypterus hypoxanthus***, ***natalensis holubii*** and ***fulvicapilla dispar***.

1891–1900

`Taxa described: 17  Species retained: 4  Subspecies retained: 6  Rejected: 7`

Following the publication of the Catalogue of the Birds in the British Museum by Sharpe in 1883, which placed most of these birds into the genus *Cisticola*, all 17 taxa described during this period were placed in the same genus. Four species and six subspecies were considered valid, with seven taxa rejected, including an *Apalis*.

Species described: ***angusticauda***, ***chubbi*** (Chubb's Cisticola), ***nigriloris*** (Black-lored Cisticola) and ***aridulus*** (Desert Cisticola).

Subspecies described: ***chiniana fischeri***, ***aberrans emini***, ***chubbi discolor*** and ***robustus nuchalis***.

1901–1910

`Taxa described: 53  Species retained: 3  Subspecies retained: 21  Rejected: 29`

By this time, the exploration of Africa was becoming much easier which resulted in many more taxa being described, with Neumann recognising the first geographic variants as a subspecies in 1904. Of the 53 described, 29 were rejected with many new descriptions merely being birds that had already been described in different seasonal plumage. Three species and 21 subspecies, described mostly from equatorial Africa, were accepted.

Species described: ***cinnamomeus*** (Pale-crowned Cisticola), ***woosnami*** (Trilling Cisticola) and ***carruthersi*** (Carruthers's Cisticola).

Subspecies described: ***aridulus lavendulae***, ***chiniana humilis***, ***brachypterus katonae***, ***erythrops sylvia***, ***natalensis argenteus***, ***marginatus nyansae***, ***cantans pictipennis***, c***inereolus schillingsi***, ***lais semifasciatus***, ***marginatus suahelicus***, ***rufilatus ansorgei***, ***chiniana heterophrys***, ***natalensis inexpectatus***, ***robustus schraderi***, ***brachypterus isabellinus***, ***aberrans petrophilus***,***cantans belli***, ***brachypterus zedlitzi***, ***cantans adamauae***, ***chubbi adametzi*** and ***aridulus kalahari***.

1911–1920

`Taxa described: 52  Species retained: 1  Subspecies retained: 16  Rejected: 35`

The large number of taxa described was thanks to a collecting expedition for American museums, where Mearns joined ex-President of the United States, Theodore Roosevelt, on the Smithsonian African Expedition to east Africa. During this time, Roberts placed all taxa that had been described from southern Africa (except for *textrix*) into the genus *Cisticola* in his 1913 review of 'The Grass Warblers of South Africa (*Cisticola* and *Hemipteryx*)'. From the 52 taxa described, only a single species and 16 subspecies were accepted, with 35 taxa being rejected.

Species described: ***bodessa*** (Boran Cisticola).

Subspecies described: ***brachypterus reichenowi***, ***exilis alexandrae***, ***cinnamomeus egregia***, ***chiniana fricki***, ***textrix major***, ***aberrans minor***, ***lais monticola***, ***erythrops niloticus***, ***juncidis normani***, ***exilis equicaudatus***, ***chiniana frater***, ***cantans muenzneri***, ***erythrops pyrrhomitra***, ***fulvicapilla silberbaueri***, ***juncidis neuroticus*** and ***tinniens perpullus***.

1921–1930

`Taxa described: 61  Species retained: 4  Subspecies retained: 35  Rejected: 22`

More confusion arose when Roberts altered his 1913 treatment that grouped all taxa into the genus *Cisticola*, and split taxa into eight separate genera and five new subgenera in his 'Review of the Nomenclature of South African Birds' published in 1922. When Rear-Admiral Lynes attempted to correctly classify birds that he had identified on a trip to Darfur, he had great difficulty and found that the works available to him were inadequate in presenting the correct relationships and nomenclature. To remediate these issues, Lynes set out to categorise and better order the group, which at the time comprised 173

species and 54 different subspecies. Between 1926 and 1927, Lynes embarked on an eight-month tour of Africa to become acquainted with as many of the birds as possible during their breeding season, so that he could use knowledge of their plumages and behaviour to improve their classification. In addition to the collection of over a thousand specimens during his trip to Africa, Lynes also managed to collect together 250 Type specimens from institutions around the world so that he could examine them comparatively in the British Museum of Natural History. From this, Lynes proposed that 154 taxa and 40 species all be included in a single genus, *Cisticola*, rather than following Roberts' revised nomenclature, a decision which would have resulted in the genus being broken up into 13 or 14 separate genera and seven subgenera. Lynes suggested rather that the relationships between species might be better understood by grouping them into nine main groups.

Species described: ***aberdare*** (Aberdare Cisticola), ***bulliens*** (Bubbling Cisticola), ***guinea*** (Dorst's Cisticola) and ***pipiens*** (Chirping Cisticola).

Subspecies described: ***exilis diminutus***, ***ayresii mauensis***, ***brunnescens nakuruensis***, ***tinniens oreophilus***, ***exilis courtoisi***, ***brunnescens lynesi***, ***robustus santae***, ***robustus omo***, ***juncidis malaya***, ***brachypterus ankole***, ***bulliens bulliens***, ***lais distinctus***, ***ayresii entebbe***, ***chiniana fortis***, ***natalensis huambo***, ***subruficapilla jamesi***, ***natalensis katanga***, ***brachypterus kericho***, ***erythrops lepe***, ***brachypterus loanda***, ***aridulus lobito***, ***woosnami lufira***, ***lais maculatus***, ***lais mashona***, ***ruficeps mongalla***, ***erythrops nyasa***, ***aberrans nyika***, ***eximius occidens***, ***juncidis perennius***, ***aridulus tanganyika***, ***natalensis tonga***, ***brunnescens wambera***, ***marginatus zalingei***, ***chiniana ukamba***, ***chiniana victoria***, ***aberrans admiralis*** and ***subruficapilla namaqua***.

1931–1940

`Taxa described: 25  Species retained: 3  Subspecies retained: 19  Rejected: 3`

There was less confusion in the years following the publication of Lynes' review and Lynes' continued to work on the genus, describing 12 additional taxa. The geographic variation within the genus was becoming better understood with local variants being named as subspecies. Three species and 19 subspecies were accepted.

Species described: ***dambo*** (Dambo Cisticola), ***njombe*** (Churring Cisticola) and ***luapula*** (Luapula Cisticola).

Subspecies described: ***aberrans bailunduensis***, ***lais namba***, ***textrix bulubulu***, ***eximius winneba***, ***ayresii gabun***, ***chubbi marungensis***, ***textrix marleyi***, ***aberrans***

lurio, ***robustus awemba***, ***exilis polionotus***, ***pipiens congo***, ***fulvicapilla lebombo***, ***juncidis salimalii***, ***dambo kasai***, ***subruficapilla windhoekensis***, ***subruficapilla karasensis***, ***juncidis constans***, ***cinnamomeus midcongo*** and ***ayresii imatong***.

1941–1950

`Taxa described: 7  Species retained: 0  Subspecies retained: 4  Rejected: 3`

In preparation for the publication of a checklist of birds in Zambia, C. White described two taxa that had previously remained nameless.

Species described: **None**.

Subspecies described: ***chiniana emendates***, ***njombe mariae***, ***tinniens shiwae*** and ***aridulus perplexus***.

1951–1960

`Taxa described: 9  Species retained: 0  Subspecies retained: 7  Rejected: 2`

Species described: **None**.

Subspecies described: ***tinniens dyleffi***, ***juncidis leanyeri***, ***fulvicapilla hallae***, ***aridulus caliginus***, ***chiniana smithersi***, ***ayresii itombwensis*** and ***textrix anselli***.

1961–1970

`Taxa described: 10  Species retained: 1  Subspecies retained: 5  Rejected: 4`

The publication of Hall and Moreau's 'Atlas of Speciation of African Passerine Birds' in 1970 contained a great deal of information regarding the distribution of cisticolas, and attempted to better understand the speciation of the genus by following the groups of Lynes, but interpreting them as species-groups or super-species that included those species that had been described subsequent to (Lynes, 1930). The 'Atlas' modified some assemblages to reflect newly described species, such as the discovery of the subspecies *lurio* (which seemed to be a linking form between taxa that Lynes believed to be separate species) – namely *C. aberrans* and *C. emini* – and grouped some of the ungrouped species, such as *C. ruficeps* and *C. nana*. Hall and Moreau (1970) noted that some of Lynes' groupings were followed tentatively as it was difficult to determine which characters he used to distinguish his groups (Hall and Moreau, 1970, map 198).

Species described: ***restrictus*** (Tana River Cisticola).

Subspecies described: ***chiniana bensoni***, ***lais oreobates***, ***aridulus traylori***, ***subruficapilla newtoni*** and ***pipiens arundicola***.

1971–1980

`Taxa described: 8  Species retained: 0  Subspecies retained: 6  Rejected: 2`

In his systematic list, Wolters (1982) proposed to again split the genus into multiple genera and subgenera, suggesting that taxa be divided into six genera made up of 15 subgenera. This was not followed by Clancey and others who described eight additional taxa, six of which were accepted as subspecies.

Species described: **None**.

Subspecies described: ***fulvicapilla dexter***, ***juncidis nigrostriatus***, ***rufilatus vicinior***, ***brunnescens mbangensis***, ***bodessa kaffensis*** and ***juncidis laveryi***.

1981–1990

`Taxa described: 7  Species retained: 0  Subspecies retained: 4  Rejected: 3`

Clancey continued his prodigious taxonomic work and described most of the seven subspecies that were proposed in the 1980s.

Species described: **None**.

Subspecies described: ***fulvicapilla dumicola***, ***aridulus eremicus***, ***chiniana mbeya*** and ***chiniana keithi***.

1991–2000

`Taxa described: 6  Species retained: 0  Subspecies retained: 1  Rejected: 5`

The genus' convoluted taxonomic history continued to cause confusion in the early 1990s when Chappuis and Erard described a new species and named it *C. dorsti* (Chappuis and Erard, 1991), which was initially confused with the *mongolla* subspecies of *C. ruficeps*. It was soon suggested that it was actually the same as an existing subspecies, *C. ruficeps guinea*, described by (Lynes, 1930). Differences in vocalisations, habitat preferences

and non-breeding plumage eventually resulted in it being raised to species level as *C. guinea* and attributed to Lynes. The publication of Birds of Africa in 1997 (Urban et al., 1997) provided a brief review of the recently described taxa, synonymising 14 names and recognising a further seven including the separation of the subspecies *lepe* from the rest of *C. erythrops*, the specific separation between *C. brunnescens* and *C. cinnamomeus* and the elevation of the subspecies *angolensis* to species level separate from *C. robustus*, a suggestion that was subsequently retracted. Relationships within the genus were still unclear and, while natural groupings similar to those suggested by Lynes' could be identified, the links between them were not understood. In Birds of Africa, Tye (1997) recognised some of the super-species proposed by Hall and Moreau (1970) but modified or rejected others. For example he argued that *C. erythrops* and *C. cantans* exhibited too much overlap in range to be considered a super-species, and that the plumage differences between *C. nana* discounted it from inclusion in the *ruficeps* super-species.

Species described: **None**.

Subspecies described: ***bulliens septentrionalis***.

2001–Present

The species-level classifications remained unsettled, with Hustler (2001) suggesting that birds recognised as *C. galactotes* be separated into five separate species, and supported Sibley (1996) hypothesis that *C. luapula* be recognised as a separate species. In 2003, Sinclair and Ryan listed *C. galactotes* separate from *C. marginatus* in 'Birds of Africa south of the Sahara' (Sinclair and Ryan, 2003). Ryan provided the most recent summary of the genus in 'Handbook of the Birds of the World' (del Hoyo et al., 2006) and outlined taxa whose specific status was unresolved, ultimately following Lynes' groupings by placing newly described taxa into his groups. Ryan (2006) agreed that until molecular tools are used to investigate relationships within the genus, Lynes (1930) groups remain a useful starting point for studies on the genus.

While there have been recent reviews of the current understanding of the genus, all of the work to date has been based on what are fundamentally slight differences amongst a group of very similar birds. Confusion about the status of many species and subspecies persists as a result, and the extent of this uncertainty becomes obvious when reading through the species accounts of Ryan (2006), who notes that: *Cisticola erythrops lepe* is sometimes considered to be a separate species as it is reported to be sympatric with *C. erythrops sylvia* around the Marungu Mountains in the Democratic Republic of Congo. *Cisticola chubbi adametzi* and *C. chubbi discolor* are also sometimes considered to be

separate species, but seem to be vocally similar to eastern subspecies of *C. chubbi*. *Cisticola aberrans petrophilus* and *C. aberrans admiralis* are sometimes treated as separate species because of their spotted tail pattern and habitat preferences. The affinity of an isolated subspecies *C. aberrans bailunduensis* in Angola is uncertain. *Cisticola restrictus* is possibly an aberrant *C. cinereolus* or a hybrid between *C. cinereolus* and *C. chiniana*. *Cisticola subruficapilla windhoekensis* and *C. subruficapilla newtoni* populations are discontinuous with the rest of the subspecies and might represent a separate species. *Cisticola lais distinctus* is sometimes treated as a separate species and affinities of subspecies found in northeast South Africa and in the Chimanimani Mountains in Zimbabwe need to be clarified. *Cisticola galactotes*, *C. marginatus*, *C. lugubris*, *C. pipiens* and *C. haematocephala* are all sometimes considered to be conspecific. *Cisticola robustus* is often considered to be conspecific with *C. aberdare*, with the subspecies *C. robustus robustus* and *C. robustus omo* perhaps closer to that species than with the remaining subspecies, the affinity of the subspecies of populations in the Republic of Congo uncertain. The status of the subspecies *angolensis* is also uncertain as some consider it a separate species based on vocal differences. *Cisticola angusticauda* is often treated as conspecific with *C. fulvicapilla*. *Cisticola melanurus* is sometimes placed in a separate genus, *Apalis*, but also sometimes thought to be conspecific with *C. angusticauda*. *Cisticola juncidis* is often considered conspecific with *C. haesitatus* and the subspecific identity of populations in south New Guinea is uncertain. *Cisticola textrix textrix* in the southern Cape is sometimes regarded as a separate species because of its streaked plumage. Populations of *C. eximius* in the Republic of Congo are sometimes considered a separate subspecies based on plumage and vocalisation differences. The subspecific identity of *C. dambo* in Gabon is unclear. *Cisticola brunnescens* and *C. cinnamomeus* are often considered conspecific, but occur in sympatry in the Democratic Republic of Congo. The subspecies *gabun* of *C. ayresii* might also belong to *C. brunnescens*. Coastal populations of *C. cinnamomeus* in southern Mozambique and north-eastern South Africa are sometimes described as a separate subspecies or species. In addition there are two seemingly new species in the Kilombero Swamps of Tanzania that remain undescribed; the 'Kilombero Cisticola' which seems similar to *C. nigriloris* but lives in lowland swamps rather than montane grasslands, and the 'White-tailed Cisticola', which seems to be similar to the other marshland cisticolas in the *C. marginatus* complex, but has white edges to the outer tail feathers and lacks sub-terminal spots on its tail. All totalled, Ryan (2006) lists 204 terminal taxa including 49 named species.

Confusion exists even at the group level; a review of group structure and the potential relationships between them was well summarised by Ryan (2006). The nine 'natural groupings' are made up of: 1) the **juncidis group**, comprising four small, streaky-backed species that inhabit grasslands and have a low, simple aerial display. This group

includes: *C. juncidis*, *C. haesitatus*, *C. cherina* and *C. aridulus*; 2) the **textrix group**, comprising six small, streaky-backed species that also inhabit grasslands, often together with members of the previous group, but differ in having much shorter tails and much higher and more elaborate aerial displays. This group includes: *C. textrix*, *C. ayresii*, *C. brunnescens*, *C. cinnamomeus*, *C. dambo* and *C. eximius*. It is thought that the single species that does not occur in Africa, *C. exilis*, is most similar to members of this group (although it does show similarities to the juncidis group); 3) the **natalensis and robustus group**, comprising three large, streaky-backed species with limited aerial display and includes: *C. robustus*, *C. aberdare* and *C. natalensis*; 4) the **subruficapilla group**, comprising species that have a streaked back and a medium to long tail that inhabit scrub and open woodland, including: *C. subruficapilla*, *C. lais*, *C. restrictus* and *C. rufilatus*. The other 'bush-loving' species, *C. cinereolus*, *C. chiniana* (and presumably *C. bodessa*) and *C. njombe* show similarities to each other and to the previous group, with *C. chiniana* having a call similar to the lateralis group. Three smaller species, *C. ruficeps*, *C. guinea* and *C. nana*, are also similar to the subruficapilla group and the previous species, but may also be close to group 5) the **brachyptera group** is a complex group comprising small, plain-backed species with mostly short tails, but differing from each other in plumage colour and outermost primary feather shape. The brachyptera group includes: *C. brachypterus*, *C. fulvicapilla*, *C. angusticauda*, *C. rufus* and *C. troglodytes*. The distinctive *C. aberrans* is perhaps most similar to the previous group; 6) the **lateralis group**, comprising four similar looking plan-backed species with long tails and a range of habitat preferences including rocky hills, savannas and forest edges, including: *C. lateralis*, *C. anonymus*, *C. bulliens* and *C. woosnami*; 7) the **nigriloris group**, comprising large birds that are found in mountainous habitats and have black lores and duetting calls, including: *C. nigriloris*, *C. chubbi* and *C. hunteri* and potentially the undescribed 'Kilombero Cisticola'; 8) the two secretive species *C. cantans* and *C. erythrops*, which form their own group even though they exhibit a large degree of sympatry and are close to the previous group in plumage. They are also similar to members of group 9) the **galactotes group**, comprising streaky-backed species with long tails that prefer marshy habitats. This group includes: *C. marginatus*, *C. galactotes*, *C. lugubris*, *C. haematocephala*, *C. pipiens* and *C. carruthersi* and potentially the undescribed 'White-tailed Cisticola'. Another marsh species, *C. tinniens*, is sometimes placed in the previous group, but shows greater variation in habitat preference and shows some similarities in size and shape to the subruficapilla group.

Efforts to interpret morphology, behaviour and vocalisations have had limited success in determining the relationships within the genus. However, whereas broad-scale molecular studies on the family Cisticolidae support the monophyly of the genus *Cisticola*, the internal structure of the genus remains unknown as only a few species from the genus

have been included in analyses (Nguembock et al., 2012, 2007; Olsson et al., 2013, eight, six and six species respectively).

Cisticolas may often be overlooked for study because their drab plumage makes them seem superficially uninteresting, but they offer the opportunity to answer a host of interesting questions. Molecular work would open up simultaneous investigations into the evolution of open habitats across Africa as well as testing the 'super-species' hypothesis proposed by Hall and Moreau (1970), which remains to be tested for open habitat birds (Fuchs et al., 2011). The large number of species, high diversity in song types and high species turnover in relatively small areas make cisticolas good candidates for testing hypotheses of song evolution.

The influence that the Pleistocene climate variation had on avian diversity in Africa remains poorly understood, with hypotheses such as the 'refuge hypothesis' (Chapin, 1932; Crowe and Crowe, 1982; Diamond and Hamilton, 1980; Hall and Moreau, 1970; Mayr and O'Hara, 1986; Moreau, 1952) proposing that variability during this period caused forest fragmentation and allopatric speciation, though more recent studies on forest birds suggest that much of their speciation was much older than the Pleistocene (Beresford, 2002; Bowie et al., 2004b; Fjeldså, 1994; Njabo et al., 2008; Roy, 1997; Roy et al., 2000). A study on very closely related species and subspecies complexes of Olive Sunbirds (Bowie et al., 2004a) supported the idea that evidence for Pleistocene diversification may more likely be found among conspecific populations and subspecies (Hewitt, 1996; Klicka and Zink, 1997). The detailed accounts of subspecific variation within cisticolas, combined with their preference for open habitats, offers the potential for understanding the influence that climactic variation had on the evolution of open habitat birds. This, in turn, might reveal evidence of the expansion of non-forest habitats during periods where forests contracted, providing new opportunities for the radiation of non-forest groups during the Pleistocene epoch (Fjeldså and Bowie, 2008; Voelker et al., 2012).

The aim of the following chapters is to assess Lynes' review to gain insight into the basis of some of his groupings and conclusions and reassess the morpho-behavioural data using modern techniques; to produce the first molecular phylogeny of the genus which will enable us to test some of the groupings that have been proposed over the years and clear up the confusion surrounding the relationships amongst and between taxa; to identify the selective pressures acting on their vocalisations and songs; determine what their biogeography and speciation patterns can tell us about their evolution and the evolution of open habitats of Africa; and build on the great work that has been done on the genus in the past to lay a solid foundation for what will hopefully be renewed interest in future detailed investigations into the diversity, evolution and biogeography of cisticolas.

Chapter 2

Cisticolas? They all look the same to me – The problem of similarity. An assessment of Lynes' (1930) review on the genus and a reassessment of morpho-behavioural data using phenetic and cladistics methods

2.1 Introduction

The genus *Cisticola* is one of the most taxonomically and phylogenetically enigmatic assemblages in the class Aves. This is because the numerous putative terminal taxa are, on a superficial level, remarkably uniform in morphology. Indeed, seasonal and geographical variation in plumage within some species exceeds that between species (Ryan, 2006). This has resulted in a plethora of taxa being proposed over the decades, many of which have been subsequently synonymised or rejected (Chapter 1).

In an attempt to make sense of this systematic confusion, Lynes (1930) produced a monograph on the genus which remains the starting point for modern research on the systematics of cisticolas (Ryan, 2006). However, since Lynes' research was conducted decades before the development of modern phenetic and cladistic approaches to systematics, his conclusions were based on subjective assessments of an array of quantitative and qualitative characters.

Lynes gathered all but three of the then 250 type specimens under one roof in the British Museum of Natural History to make comparisons. He also selected a specimen from the British Museum collection to match each type specimen in terms of sex, age, season, locality, etc. and labelled these paratypes. Lynes presented his classification both in a linear sequence (Appendix B) and a diagrammatic 'phylogenetic' representation (Figure 2.1). The latter essentially amounts to an ordination in which the relative positions of the group circles 'convey something approaching an idea of the birds' relationships to one another, as based on the sum of all their characters' (Lynes, 1930, p. 71). Seven

species (broken circles in Figure 2.1) were not placed into groups because Lynes considered them to be linking forms, or simply difficult to place without spoiling the structure of his groupings and reducing the nature of the relationships between the other species.

The present study re-analyses the data presented in Lynes' review using modern, phenetic and cladistic methods to interpret and test the validity of his conclusions. Specifically, his proposed relationships within the genus which grouped taxa into nine main groups are tested, and the relationships of those taxa originally unplaced by Lynes are assessed.

2.2 Methods

Traditional character data

Information was captured and coded for each taxon from the descriptions presented in Lynes (1930), resulting in 92 qualitative characters (Appendix C, locations in Figure 2.2). Morphometric data were captured from specimens housed at the Natural History Museum at Tring. Meristic data included: culmen length from tip of culmen to skull insertion; bill width and height at nares; wing length; length of primary feathers 9 and 10 from tip of feather to insertion of shaft; tarsus length from base of the toes to inner bend of the tibiotarsal articulation and tail length from the base of the tail to the tip of the longest feathers. Specimens measured included types and paratypes that were matched by Lynes to the original type specimens and ± 10 individuals of 125 putative species and subspecies (± five of each sex). In all, 16 264 measurements were taken from 2033 individuals, all in breeding plumage. All measurements were taken with digital callipers accurate to 0.03 mm. A wing rule was used to position tail and wing measurements, but readings were captured by using the digital callipers in combination with the wing rule. Sexual size dimorphism was calculated using wing length. Measurements (with the exception of the ratio of lengths of the two outermost primary feathers, wing length and sexual dimorphism) were divided by wing length to reduce the effect of size. Wing length was used as a measure of size since (Lynes, 1930, p. 30) Lynes suggested it makes for a good index of comparative size within the genus. Plumage and other qualitative characters (Appendix C) were coded non-additively.

Digital character data

To reduce character subjectivity, I attempted to remove vague character definitions and ambiguous character state delineations by capturing plumage characteristics objectively. Four additional measurements were made on scaled digital images of the 10th primary

feather to characterise its shape. These measurements were the widths of the feather along 25%, 50% and 75% of its length, and the distance of the point of maximum width from the tip of the feather (Figure 2.3). They were captured digitally using tpsDig2 version 2.16 (Rohlf, 2010) calibrated to the correct scale and divided by the total length of primary feather 10 to reduce the effects of overall feather size. To get an objective measure of plumage colour, colour values were captured from digital images taken of males in breeding plumage in each putative terminal taxon represented in the collections housed at NHM Tring. Digital images were captured with a Nikon D3000 in RAW format (effective camera resolution ∼118 ppcm) under the same artificial lighting conditions using the fluorescent white balance setting. Images were imported into Adobe Photoshop CS2 version 9.0 in the 'LAB' colour mode. L*a*b* (LAB hereafter) colour theory is built upon the Munsell (1912) colour system, the Hunter (1948) colour space and the CIE (French Commission international de l'éclairage) 1976 colour space (detailed in CIE (1986)). It was designed by the International Commission on Illumination to best approximate human vision, which has been shown to be a valid proxy for avian colour perception outside of the UV spectrum (Seddon et al., 2010).

LAB colour space lends itself well to this kind of study as it is standardised and not device- dependent; the assigned colour value is unique to that colour, whereas RGB (Red, Green and Blue) and CMYK (Cyan, Magenta, Yellow and Key) colours may change appearance depending on the monitor or printer on which you are viewing them. This makes LAB colour more appropriate for comparisons across platforms and studies. LAB colour space is much larger than the gamut of monitor and printer displays and can more accurately match human perception of colours than can be displayed. The colour value is made up of three separate values: one for lightness (L), red-greenness (A) and blue-yellowness (B) respectively, and as a result these values can be plotted and compared on a 3D xyz scatter graph making the visualisation and justification for assigning character codes to colours easier to appreciate.

The standardisation of LAB colour makes it a widely used metric in industrial colour management to show: how far off a print or proof is from the original (e.g. in industries that manufacture plastics, textiles, inks, paints, graphic arts, etc.); how much a monitor or printer or other device drifts from original colours; how appropriate or effective a particular colour profile would be for proofing or printing, as a method to remove the subjectivity involved in determining these colour differences.

To determine the differences between two colours, a formula called delta-E was developed and, while there are a few slight variations to the equation out there, the values remain comparable if a single equation is chosen, stated explicitly and used consistently (Berns,

2000). In this study, the CIE2000 delta-E equation of colour difference was employed (Lou et al., 2001) using the program DeltaE (version 0.3, Boscarol (2008)).

This equation was used to help eliminate the illusionary perceptual effects that differing contexts and textures have on colours and contrasts, such as the 'Corrugated Plaid' and 'Checker Shadow Illusion' effect of Adelson (1993, 2006), and the Chubb Illusion (Chubb et al., 1989), which demonstrate that two identical colours can look different to each other depending on what colours surround them (for examples see Appendix D, and Lotto (2011)). Images were colour corrected with a colour calibration chart (McCamy et al., 1976) to ensure that the colours in each image were comparable to each other. LAB colour values were captured for the bill, chin, throat, breast, belly, sides, flanks, thighs, the skin of the ventral surface of the legs, the culmen, head top feather centres, head top feather borders, back feather centres, back feather borders, rump and upper tail coverts (Figure 2.4). The LAB colour values were taken after an 'average blur' was applied in Photoshop to a small area (∼60x60 pixels) within the location of interest. This averaging was done to avoid obtaining highly variant colour values from digital images where, due to the nature of the way that digital images are created, the colour selected can differ vastly depending on which pixel the selection tool covers, even if the pixels are adjacent (e.g. Appendix F.1).

Character scoring

As each LAB colour is defined by three values, colours were plotted for each character in 3D space using CHROMiX ColorThink version 2.1.2 (CHROMiX, 2006) to help visualise character scoring of similar colours. Classification of colours was attempted by performing a principal component analysis (PCA) on the LAB values using STATISTICA10 (Statsoft, 2011) to maximise colour variation in three dimensions along a two dimensional plane to facilitate scoring. The values of the first principal component (PC1) were displayed on a histogram and categorised using STATISTICA10 to optimise the distribution of the data points into normally distributed categories. These categories were projected onto the CHROMiX 3D scatterplot to visualise groupings that maximised variance between them. It became apparent from this method that colours were grouping because of their similarity in 'lightness/darkness' rather than their 'basal' colour. In an attempt to overcome this issue, the above steps were redone using only the 'A' and 'B' values to visualise categorisation separation along chromaticity regardless of luminance (L), i.e. to cause similar 'types' of colours to group together regardless of their lightness/darkness (Appendix F).

Feather shape: geometric morphometrics

The shape of the outermost primary feather was captured from digital images (of feathers *in situ*) and imported into tpsDig2 version 2.16 (Rohlf, 2010) where a scaled curve of the outline was created and converted to semi-landmark data comprising 120 points using tpsUtil version 1.46 (Rohlf, 2010). These data were Procrustes transformed and a Relative Warp Analysis was performed using PAST version 2.04 (Hammer et al., 2001). Centroid size was calculated using GMTP version 2.1 (Taravati, 2010).

PCA and DFA

To assess the variation in mensural characters, a PCA was performed using PRIMER 5 (Clarke and Gorley, 2006) using the seven measurement characters. In order to determine their utility in characterizing Lynes' groupings, discriminant functions analyses (DFA) were performed using MYSTAT12 version 12.02.00 (Software, 2008) with priors computed from group sizes with specimens assigned *a priori* to groups. Initially the DFA included only those specimens that were placed into groups by (Lynes, 1930). A cluster analysis (UPGMA, Euclidean distance) informed placement of individuals that were not grouped by Lynes, these groups were then assigned to Lynes' groups a posteriori in a second DFA.

MCA

A multiple correspondence analysis (MCA) was performed on categorical data using the 'ca' package implemented in R version 3.0.1 (R-Core-Team, 2013), a biplot was produced using the 'rowgreen' map which utilises standardised units (Nenadic and Greenacre, 2007). Characters or taxa with missing data were omitted from the analysis. The 'cluster' package (Maechler et al., 2013) was used to calculate the Gower-metric (Gower, 1971) and perform a cluster analysis. The Gower-metric was used as it has been found to cope with nearly all forms of character coding, including multistate and quantitative coding, and can measure the similarity between individuals based on logically distinct kinds of variation (Gower, 1971).

Cladistic analysis of data captured from Lynes' monograph

A cladistic analysis was performed on the categorical scored data captured from Lynes (1930). A 126 taxon x 92 character matrix was analysed using TNT (Goloboff et al., 2003) with the eight measurement characters (wing length, difference in breeding tail length, leg size, sexual dimorphism, ratio between two outermost primary feathers, bill length, bill strength and bill curve) coded as additive and the remaining 84 plumage and behaviour characters coded as non-additive. While bill strength and bill curve are

not well defined by /citeLynes30 the former appears to be a combination of bill height and width, while the latter character seems to be an estimate of curvature along the saggital plane of the culmen. Only taxa that appeared in Lynes' review were included in the analysis. A 'traditional search' was run using the TBR swapping algorithm.

(L)AB score analyses

A multiple factor analysis (MFA) was performed on combined continuous and categorical data (Appendix G) using the 'FactoMineR' (Husson et al., 2013) package in R to visualise specific and subspecific variation in morphology and plot the partial points indicating how the position of each subspecies on the plot reacts to each type of data, the data point is plotted in the barycentre between the position of where the point would be if the data were analysed separately, with the solid line indicating the position using the continuous measurement data alone, and the dashed line indicating the position of the individual if only the categorical data were measured. Cluster analyses were performed on separate data partitions using the 'cluster' package in R as detailed above.

Cladistic analyses on mensural, behavioural and (L)AB colour data

As all data were collected by the author, additional taxa that were described subsequent to Lynes (1930) review could be included in the analysis. Measurement and colour data were first analysed separately to determine the influence of each partition on tree topology and then analysed as a combined dataset. The combined dataset resulted in a 214 taxon x 54 character matrix that was analysed using TNT (Goloboff et al., 2003). Continuous characters were analysed as such, following Goloboff et al. (2006), where quantitative characters were transformed into discrete ranges with the standard error as the measure of variance. Qualitative characters were treated as non-additive. Correlated qualitative characters were coded as missing to reduce potential effects of character reinforcement. For example, if head-top markings were coded as 'absent', the degree of striping was coded as 'missing' rather than '0'. As species differ in their degree of sexual dimorphism, only adult male individuals were considered for morphometric comparisons between groups. Life-history characters such as nest type, display habits and habitat type were included in the dataset with the four additional measurements of the outermost primary feather described in Figure 2.3 (for full list of characters included see Appendix G. A 'traditional search' was run using the TBR swapping algorithm with the Socotra Warbler Incana incana selected as the out-group, as recent molecular work has shown it to be closely related to cisticolas (Nguembock et al., 2007).

2.3 Results

PCA on mensural data

A principal component analysis on measurements resulted in the first two principal components (PCs) accounting for 92% of the total morphometric variance among cisticolas. Individuals cluster in two distinct clusters (Figure 2.5) with principal component loadings being correlated with tail length, the proportional difference between the two outermost primary feathers (P10/P9) and wing length (Table 2.1).

DFA on mensural data

A discriminant functions analysis of individuals classified into Lynes' groups indicated significant differences between Lynes' proposed groups (Wilks' Lambda = 0.008, d.f. = 7,8,661, $p < 0.005$), and demonstrates that the groupings can be distinguished using morphometric data with 76% of individuals being correctly classified a posteriori. The first two discriminant functions account for 93.2% of the total discrimination, with factor loadings being strongly correlated with wing length, the proportional difference between the two outermost primary feathers (P10/P9) and tail length (Table 2.2). Those individuals that were incorrectly placed were primarily either individuals from the brachyptera group being classified with the juncidis group (and vice versa) or individuals from the cantans & erythrops group being placed with the galactotes group (and vice versa).

A cluster analysis on all individuals and the seven morphometric measurements informed the classification of taxa that were unplaced by Lynes into his existing groups. Once these taxa were assigned to groups *a priori*, a DFA correctly classified 78% of individuals into Lynes' groups (Table 2.3).

Posterior probabilities calculated in the DFA indicate that individuals of *C. exilis* fit best with those in the brachyptera group, with an average probability of 70%. Individuals of *C. chiniana* are placed with the lateralis group (84%), *C. nana* with the brachyptera group (83%), *C. cinereolus* with the lateralis group (44%), *C. ruficeps* with the subruficapilla group (56%), *C. tinniens* with the subruficapilla group (98%), and *C. aberrans* with the cantans & erythrops group (74%). A cluster analysis using data captured from Lynes (1930) placed 97% of taxa correctly, recovering all of Lynes' groups except for the lateralis group. The analysis clustered *C. exilis* between the juncidis and textrix groups and *C. nana* together with *C. aberrans* closest to the brachyptera group. The unplaced *C. ruficeps* was closest to *C. tinniens*, with both clustering near the subruficapilla group

and *C. chiniana* clustered with *C. cinereolus* between some of the members of the lateralis group and the nigriloris group (Figure 2.6).

MCA on data captured from Lynes' monograph

An MCA on those data captured from Lynes (1930) had a total inertia of 0.527, with dimension 1 accounting for 16.4% and dimension 2 accounting for 9.7% of the total inertia. Characters with the highest influence on these dimensions are rump colour (mass = 0.0912, inertia = 0.0215), pectoral patch (mass = 0.0415, inertia = 0.0173), head-top colour (mass = 0.0652, inertia 0.017) and feather borders colour (mass = 0.043, inertia = 0.017) (Figure 2.7). The MCA biplot of the first two dimensions visualises 26.2% of the variation and shows the juncidis, robusta & natalensis and textrix groups separated from the rest along the x-axis, mostly because of the colour of their rump, back streaking and proportional tail length (Figure 2.7).

Geometric morphometrics of feather shape

The analysis of the shape of primary feather 10 recovered the three main shapes identified by Lynes (1930), as well as many intermediates, where the trajectories of each cluster appeared vertical and separated mostly along the x-axis (Figure 2.8a). When relative Warp 1 scores were plotted against centroid sizes divided by the overall length of the primary feather, all shapes clustered together (Figure 2.8b).

Cladistic analysis of data captured from Lynes' monograph

The cladistic analysis (best score hit 471 times, best score = 1273, replicates = 50 000, Figure 2.9) of categorical data captured from Lynes (1930) showed that the textrix group is polyphyletic, with *C. exilis* nested within it. The juncidis and brachyptera groups were recovered as paraphyletic and sister to the textrix group. The subruficapilla, lateralis, cantans & erythrops and galactotes groups were all recovered as polyphyletic. Trees collapsed into a polytomy when resampling for Jack-knife or Bootstrap values.

MFA of combined mensural and (L)AB colour data

The first two dimensions account for 25.6% of the variation, with measurement variables accounting for most of the observed variation of these axes. Species separated along the x-axis mostly by tail length (correlation = 1.061, $\cos^2$ = 0.53), P10/P9 (correlation = 0.914, $\cos^2$ = 0.79) and wing length (correlation = 0.729, $\cos^2$ = 0.774), and separate along the y-axis mostly by bill length (correlation = 0.807, $\cos^2$ = 0.22) and tarsus length (correlation = 0.709, $\cos^2$ = 0.096) (Figure 2.10). MFA plots of subspecies showed a high degree of intraspecific variation (Appendix H).

Cluster analyses of combined morpho-behavioural data

Cluster analyses performed on measurement data, colour data and behavioural/habitat data separately resulted in mixed groupings of taxa. Species with similar proportions were clustered together in the analysis of measurement data alone, resulting in subspecies being separated from each other (Figure 2.11). When colour data were analysed, subspecies were clustered together more often than in the analyses of measurement data, but some taxa (e.g. subspecies of *C. tinniens*) remain scattered, clustering with more similarly coloured individuals than with conspecifics (Figure 2.12). The clustering by behavioural/habitat data clusters taxa by their shared associations with grassland, scrub, open savanna woodland, woodland and marshland, their display behaviour and their nest architecture (Figure 2.13).

Cladistic analyses of morpho-behavioural data

A cladistics analysis of measurement (best score = 286.241, replicates = 15 000, Figure 2.14), colour (best score = 927, replicates = 15 000, Figure 2.15) and behavioural/habitat data (best score= 85, replicates = 15 000, Figure 2.16) alone grouped conspecific taxa but produced trees with imbalanced topology or low clade structure, with all trees collapsing into polytomies when resampled for Jack-knife or Bootstrap support values.

Results from a cladistic analysis of combined quantitative measurements and objective plumage scores recovered three of Lynes' groups as monophyletic, namely the galactotes, cantans & erythrops and robusta & natalensis groups, the nigriloris group as paraphyletic and the remaining groups all as polyphyletic (best score = 1550.843, replicates = 15 000, Figure 2.17). Trees collapsed into polytomy when resampling with only Jack-knife or Bootstrap support values for terminal taxa.

2.4 Discussion

Characters

The principal component analysis on measurement data revealed that wing length (i.e. overall size), the length of the tail and the proportional lengths of the outermost primary feathers best described the measurement variation within the genus (Table 2.1). The same variables had the highest influence on the results of the discriminant functions analysis (Table 2.2), indicating that Lynes used the characters that capture most of the variation within cisticolas to discriminate between his groups. The first principal component axis was mostly influenced by tail length and the proportional difference between the lengths of the two outermost primary feathers. In his review, Lynes notes

that proportional tail length is varied in the genus and says that it is a useful character in determining differences between closely related species. But, while he makes no special mention of its role in the formation of his groupings in the main body of text, tail length is used in his '*Key to Groups*' (Lynes, 1930, p. 70–73). In contrast, Lynes states that the relative lengths of the two outermost primary feathers 'is a character of great importance' (Lynes, 1930, p. 47), and compares proportional percentages between groups in the text and makes special note of it in his detailed drawings (Lynes, 1930, plate II). The MCA on scored categorical data captured from Lynes (1930) identified characters that describe the colour of the dorsal surface/back of the birds as accounting for the most variation between taxa (Figure 2.7). It seems counterintuitive that colour had such a big influence when analysing a genus of birds that are notorious for being all so similarly brown, but Lynes took great care to try to highlight, categorise and record even minute differences in colouration and shading between taxa. Throughout the text, Lynes (1930) makes reference to the shape of the outermost primary feather, which he classifies into three main types, 'acute', 'blade' and 'scimitar' shaped, which he details in his drawings (Plate XIX) along with two intermediates and lists which groups are characterised by each feather type. A geometric morphometric analysis on the shape of the first primary feather recovered these feather shapes as well as many intermediates, but their plot trajectory for each type appeared vertical when relative warp 1 was plotted against centroid size; this indicates that any shape variation is largely allometric and primarily a function of size. This is confirmed by the mixed nature of the plot when data points are scaled by size. MFA analyses on combined measurement and AB scored data showed that measurement data accounted for most of the variation captured in the first two dimensions, indicating that birds differ by their proportions more than by their conservative plumage colours.

Taxa

While a plot of the first two dimensions of the MCA accounts for only 26% of the total inertia, a diagrammatic representation of the group centroid positions in the MCA biplot (Figure 2.18) is similar to the diagram presented by Lynes (Lynes, 1930, p. 17, redrawn in Figure 2.1). The juncidis, robusta & natalensis and textrix groups are together on the opposite side of the graph to the nigriloris and lateralis groups, with the galactotes and subruficapilla groups placed between them. The position of cantans & erythrops between the nigriloris and galactotes groups was the same as in Lynes (1930), the placement of *C. exilis* near textrix, *C. tinniens* near galactotes and subruficapilla was also similar, and, while *C. chiniana* near lateralis was the same as suggested by Lynes, its proposed position close to subruficapilla was not recovered by the MCA. The proximity of the brachyptera group to the galactotes group was different to that suggested by

Lynes (1930), as was the position of the unplaced *C. nana* and *C. ruficeps*.

A cluster analysis of the data captured from Lynes (1930) recovered all of his suggested groups, with only a few members of the lateralis group not clustering together. In his account of the lateralis group, Lynes (1930) notes that the 'consistency of our lateralis group may not be quite up to the standard of the others' (p. 276) and that, even though the species included in the group show a great variation in sexual dimorphism in size, they are best presented together.

Lynes (1930) identified that, while following a linear sequence, there could be considered two main assemblages based on their average characteristics. The first includes the small, stripe-backed species of open country, namely *C. juncidis*, *C. textrix* and *C. aridulus*. The second assemblage included the larger plan- or striped-backed species found in the savannas, from the subruficapilla group to the robusta & natalensis group, two assemblages which Lynes had thought to have diverged over a fairly long period of time. There appear to be two main assemblages along the x-axis of the PCA scatter plot. The first assemblage includes the textrix and juncidis groups and the second starts with the subruficapilla group and ends with the robusta & natalensis group. The brachyptera group falls somewhere in-between, a position where Lynes' suggested that it might be placed, but he refrained from placing it there as he did not think that it improved the understanding of relationships between the other groups (Lynes, 1930, p. 457).

The cladistic analysis performed on data captured from Lynes (1930) produced trees with low overall support, and the majority-rule consensus tree recovered many of his groups as either poly- or paraphyletic and, with the exception of *C. tinniens* and *C. exilis*, failed to place those taxa that were unplaced by Lynes (1930) in positions near where he suggested. This could be due to his method of categorising similarity between taxa not being appropriate for cladistic analyses, the potential over-categorisation of plumage colours, assumptions about the importance of characters (unequal weighting of characters such as primary feather shape) or the inclusion of an outgroup taxon in this analysis.

MFA ordinations indicate that measurement variables contribute the most to the variation observed between species when the first two dimensions are plotted, but these only account for about a quarter of the observed variance in the dataset. When measurement, colour and behavioural/habitat data for all subspecies were plotted, there was often as much variation within species as between species (Appendix H). The relative positions of taxa in the species MFA (Figure 2.10) support many of those listed in Ryan (2006), for example *C. cinereolus*, *C. chiniana* and *C. njombe* are close to *C. ruficeps*, *C. nana*,

C. lais and *C. rufilatus*. The position of *C. brachypterus* near *C. rufus* and *C. troglodytes* also agrees with Ryan (2006), as does the proximity of *C. tinniens* to *C. subruficapilla*. There is also some support for the grouping of *C. ayresii gabun* with *C. brunnescens* as it groups closer to the latter species than to conspecifics in the subspecies MFA plots (Appendix H).

The cluster analyses performed on measurement and AB scored data grouped taxa by similarity, but because of the great overall similarity within the genus, intraspecific variations resulted in conspecifics not clustering together but rather with taxa that share proportions, colour or habitat preferences. This phenetic approach is not desirable as grouping by similarity ignores differences between ancestral and derived character states. Cladistic analyses were performed to reduce the influence of derived characters on the grouping of taxa; this resulted in conspecifics grouping together, but produced imbalanced tree topologies with low clade structuring (Figures 2.14, 2.15 and 2.16). The cladogram produced by combining these data grouped the majority of what are currently considered to be conspecific taxa and provided a structure to the relationships between and amongst groups in the genus, and recovered the galactotes, cantans & erythrops and robusta & natalensis groups as monophyletic; the remaining groups were again recovered as either poly- or paraphyletic. While the analysis placed *C. tinniens* with the subruficapilla group, the placement of the other unplaced taxa differed to those suggested by Lynes (1930) and placed them in unexpected positions in the tree, e.g. *C. cinereolus* with *C. nana* in-between members of the brachyptera group.

2.5 Conclusions

Lynes' contributed enormously to the understanding of the genus *Cisticola*, and, while the present study shows that many of his conclusions were accurate given the data and techniques available to him at the time, the pitfalls of interpreting these types of data to determine relationships within such a morphologically conservative genus remain. The high congruence between the cluster analysis and Lynes' groupings indicated that, like many pre-cladistic phylogeneticists, he did not distinguish between the importance of synapomorphy and symplesiomorphy and that he perhaps thought more like a pheneticist, basing his groupings mostly on overall similarity. The AB analyses attempted to avoid grouping of colours because of their similarity on lightness/darkness by ignoring the luminance values of the colours with the assumption that the inherent chromaticity of a colour is more informative. Cladistic analyses on these data, though, also failed to determine strongly supported, clear relationships between groups, indicating that morpho-behavioural data may not be sufficient to determine the phylogenetic structure

and relatedness between taxa given the high overall similarity of birds in the genus. The main value of the review by Lynes (1930) remains in the descriptions of the taxa included, the detail of which will ensure the worth and utility of his work for future research on the genus.

2.6 Figures and Tables

TABLE 2.1: Summary statistics of the principal component analysis performed on measurements of 869 individuals.

PC	Eigen values	% Variation	Cum. % variation
1	276	73	73
2	72.6	19.2	92.2
3	21.3	5.6	97.9

Character	PC1	PC2	PC3
Tail length	-0.821	0.512	0.249
Wing length	-0.245	-0.701	0.597
P10/P9	-0.514	-0.486	-0.666

TABLE 2.2: Discriminant functions analysis of individuals that Lynes assigned to groups (omitting those which he left unplaced; n = 670) correctly assigned 76% to his groupings. With wing length, proportional length of the outermost primaries (P10/P9) and tail length having the most influence on his groupings.

Jack-knifed Classification Matrix

Lynes' group	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**% correct**
1 Brachyptera group	55	-	-	-	-	-	-	-	4	73
2 Cantans & erythrops pair	-	42	19	-	2	4	-	1	-	62
3 Galactotes group	-	18	51	-	2	5	-	4	-	64
4 Juncidis group	28	-	-	93	-	-	-	-	5	74
5 Lateralis group	-	3	7	-	61	-	-	3	-	82
6 Nigriloris group	-	4	2	-	1	11	-	3	-	52
7 Robustus & natalensis pair	-	-	2	-	5	-	76	-	-	92
8 Subruficapilla group	-	-	4	-	1	5	-	53	-	84
9 Textrix group	6	-	-	8	-	-	-	-	66	83
Total	89	67	85	117	72	25	76	64	75	**76**

Lambda	0.008
d.f.	(7, 8, 661)
Approx. F-ratio	92.94
d.f.	(56, 3532)
p-value	0

Continued on next page

Table 2.2 – *Continued from previous page*

Character	**F-to-remove**	**Tolerance**
Wing length	181.2	0.665
Tail length	66.88	0.891
P10/P9	51.01	0.869
Bill length	36.15	0.589
Bill height	23.15	0.711
Tarsus length	19.54	0.758
Bill width	4.717	0.781

Eigenvalues

13.118 2.651 0.737

Cumulative Proportion of Total Dispersion

0.775 0.932 0.975

Canonical Discriminant Functions : Standardised by Within Variances

Character	**1**	**2**	**3**
Wing length	0.95	-0.39	0.17
Tail length	0.13	0.68	-0.43
P10/P9	0.51	0.27	0.05
Bill length	0.27	0.24	0.88
Bill height	0.23	-0.53	-0.32
Tarsus length	0.11	-0.09	0.56
Bill width	0.13	-0.08	-0.12

TABLE 2.3: The results from a discriminant functions analysis including individuals that were unplaced by Lynes (n = 869), but were assigned to his groupings based on their position in a cluster analysis (UPGMA, Euclidean distance), resulted in 78% of individuals being classified to his groups.

Jack-knifed Classification Matrix

Lynes' group	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**% correct**
1 Brachyptera group	101	-	-	16	-	-	-	3	4	81
2 Cantans & erythrops pair	-	59	15	-	3	3	-	8	-	67
3 Galactotes group	-	16	48	-	6	5	-	5	-	60
4 Juncidis group	36	-	-	85	-	-	-	-	5	67
5 Lateralis group	-	1	9	-	143	1	2	4	-	89

Continued on next page

Table 2.3 – *Continued from previous page*

6 Nigriloris group	-	4	2	-	4	10	-	1	-	48
7 Robustus & natalensis pair	-	-	1	-	8	-	81	-	-	90
8 Subruficapilla group	3	1	5	-	1	4	-	86	-	86
9 Textrix group	7	-	-	8	-	-	-	-	65	81
Total	147	81	80	109	165	23	83	107	74	**78**

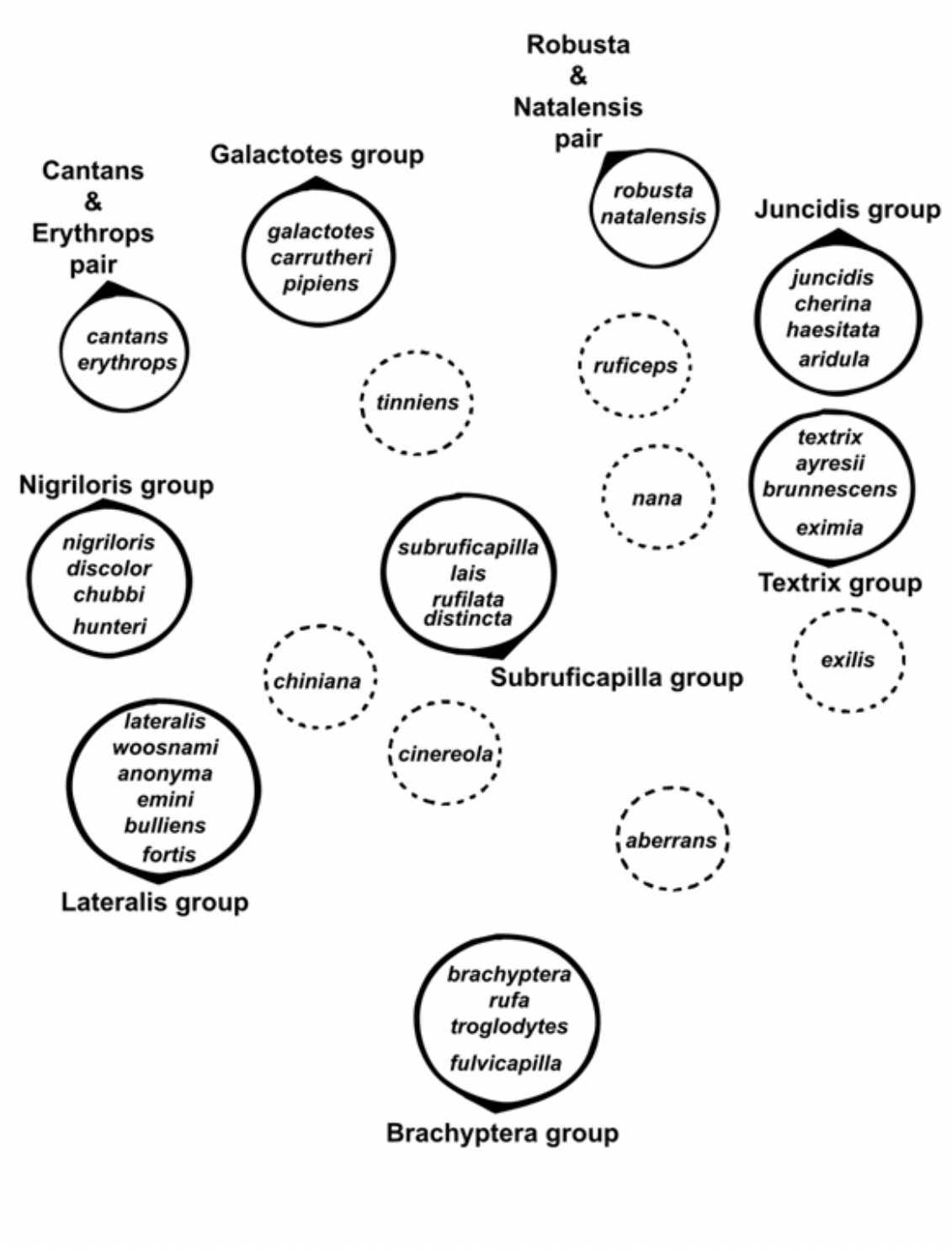


FIGURE 2.1: Lynes' diagrammatic representation depicting his proposed relationships between groups of cisticolas based on the sum of all their characters. The spacing is only roughly proportional to relatedness. Broken line circles indicate taxa unplaced by Lynes. Image modified from Lynes (1930).

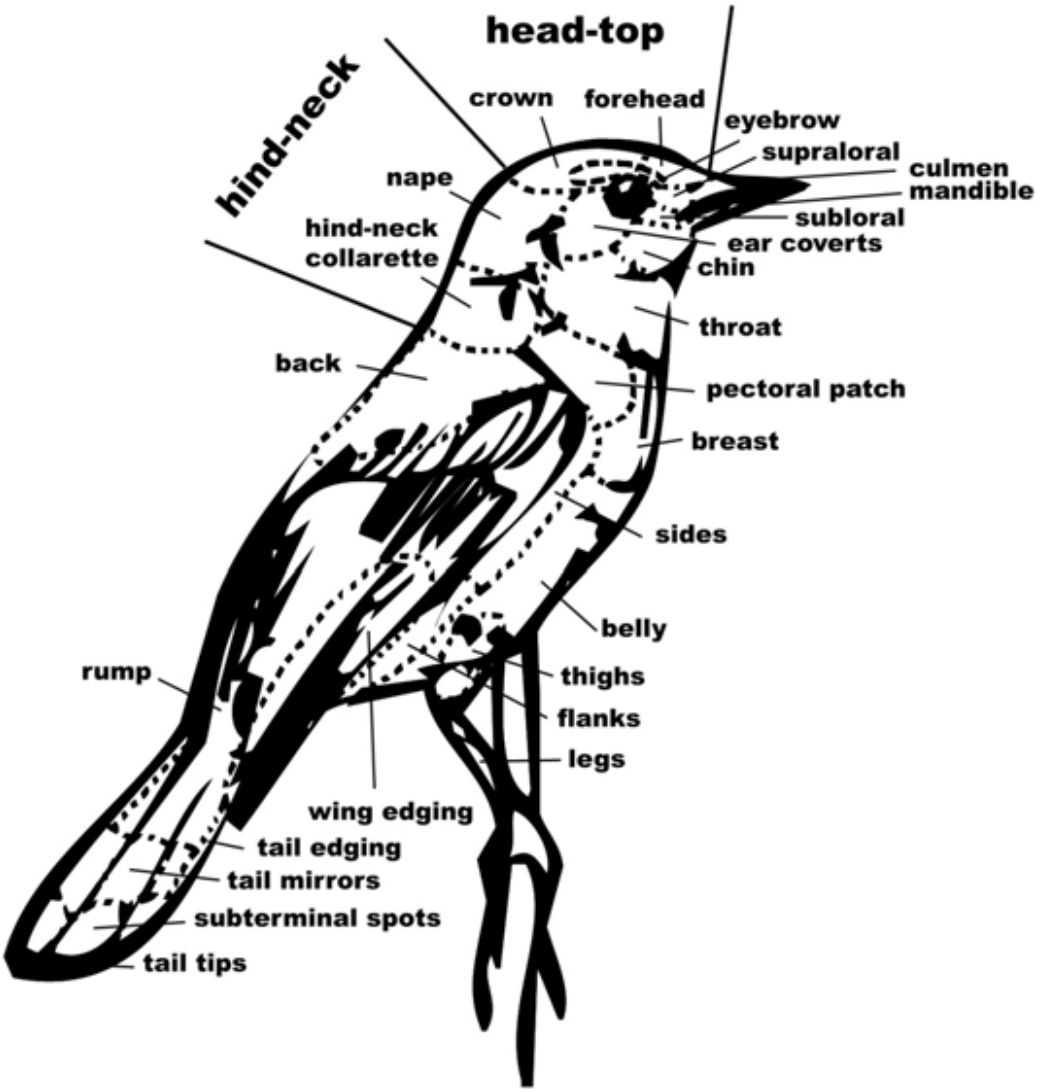


FIGURE 2.2: Positions of characters mentioned in the data matrix (Appendix C) captured from Lynes (1930).

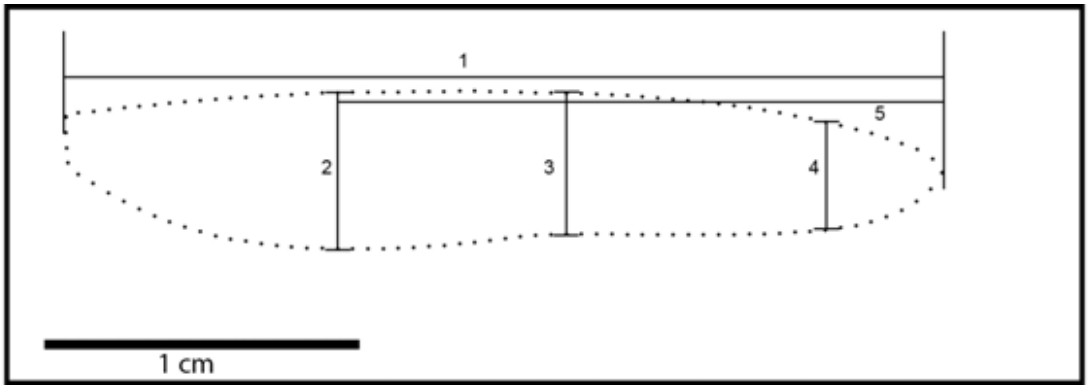


FIGURE 2.3: Measurements taken from the outermost primary feather, including 1: total length, 2, 3 and 4: width at fixed points and 5: length from tip to widest point. Measurements were captured digitally using tpsDig2 (Rohlf, 2010, version 2.16) calibrated to the correct scale; here the scale bar = 1cm.

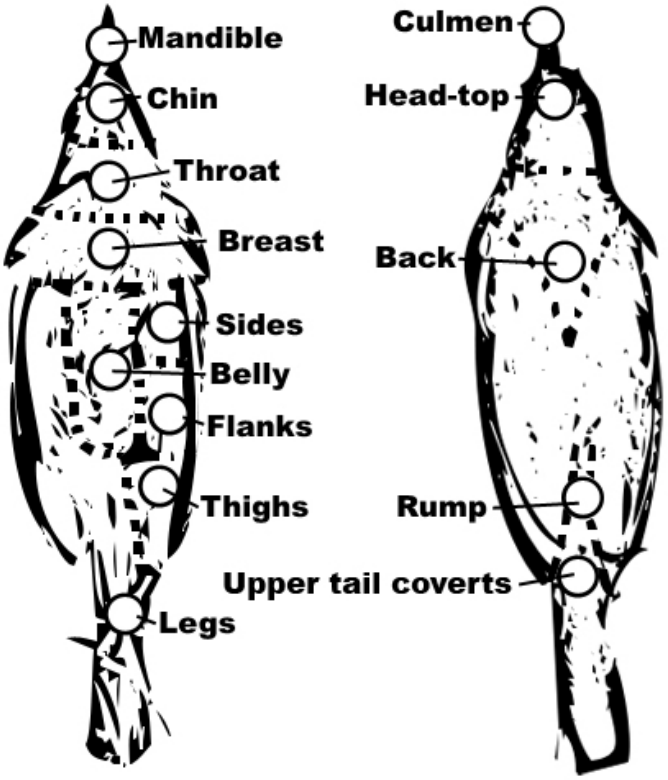


FIGURE 2.4: Locations from where colour values were captured for AB analyses. As digital images can be composed of differently coloured pixels adjacent to each other, an area roughly the size of the circles in this image (60 x 60 pixels) was selected and the average colour of the pixels within the selected area was captured. For small locations like the bill and legs, these areas were placed over a smaller area.

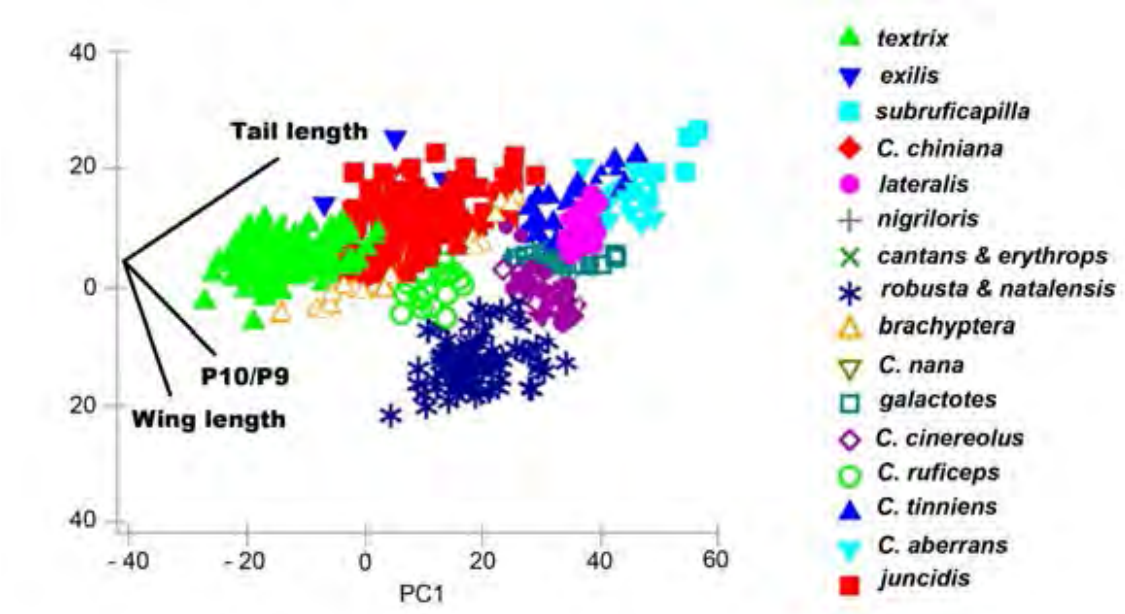


FIGURE 2.5: Scatter plot of the first two principal component axes that account for 92.2% of the variation (n = 869); the characters with the most influence on those principal components are tail length, wing length and the ratio of the outermost primary feathers.

FIGURE 2.6: Cluster analysis based on the Gower metric (Gower, 1971) calculated from a matrix of 125 terminal taxa and 66 categorical characters captured from Lynes (1930, Appendix B). Ninety-seven percent of taxa were placed into Lynes' groups. Taxa marked with a dot were incorrectly placed.

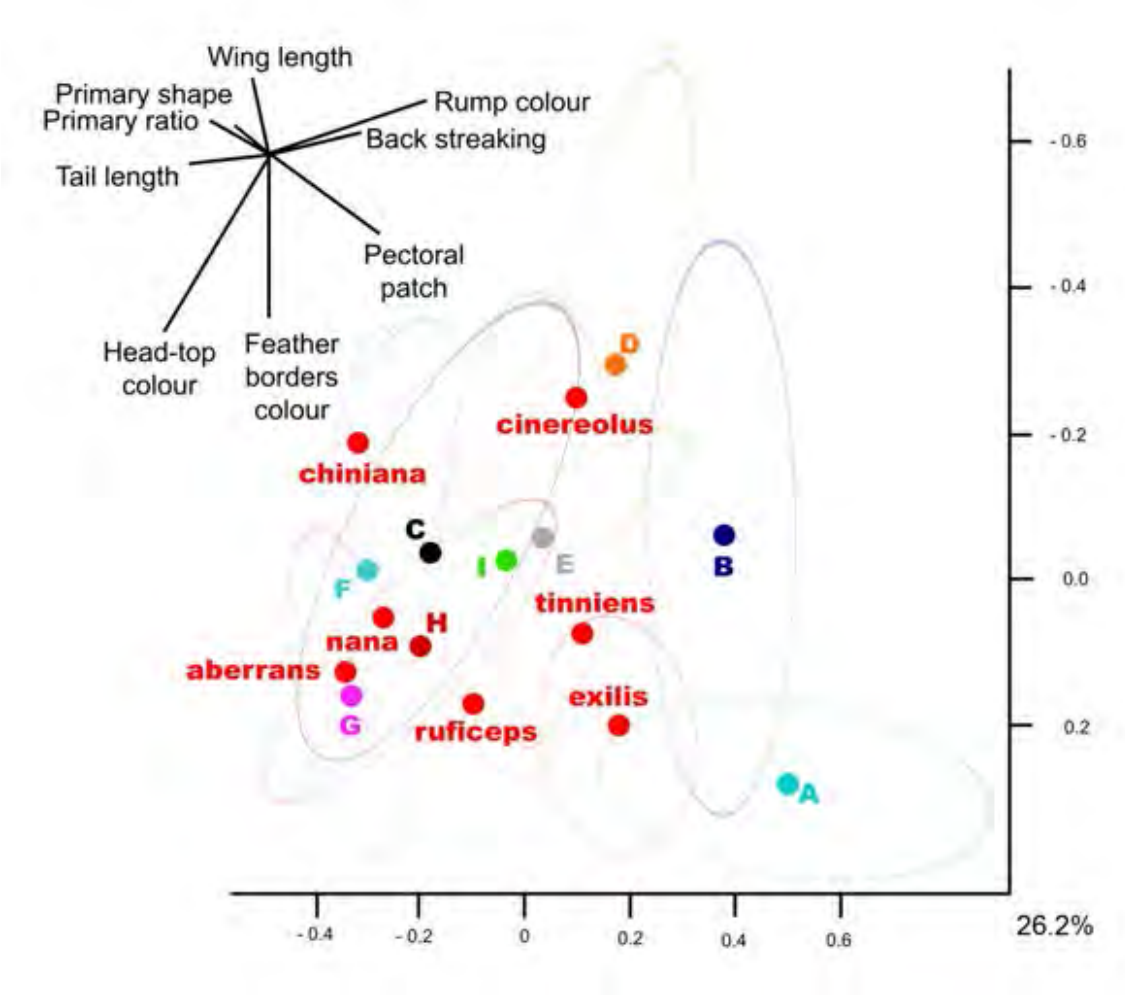
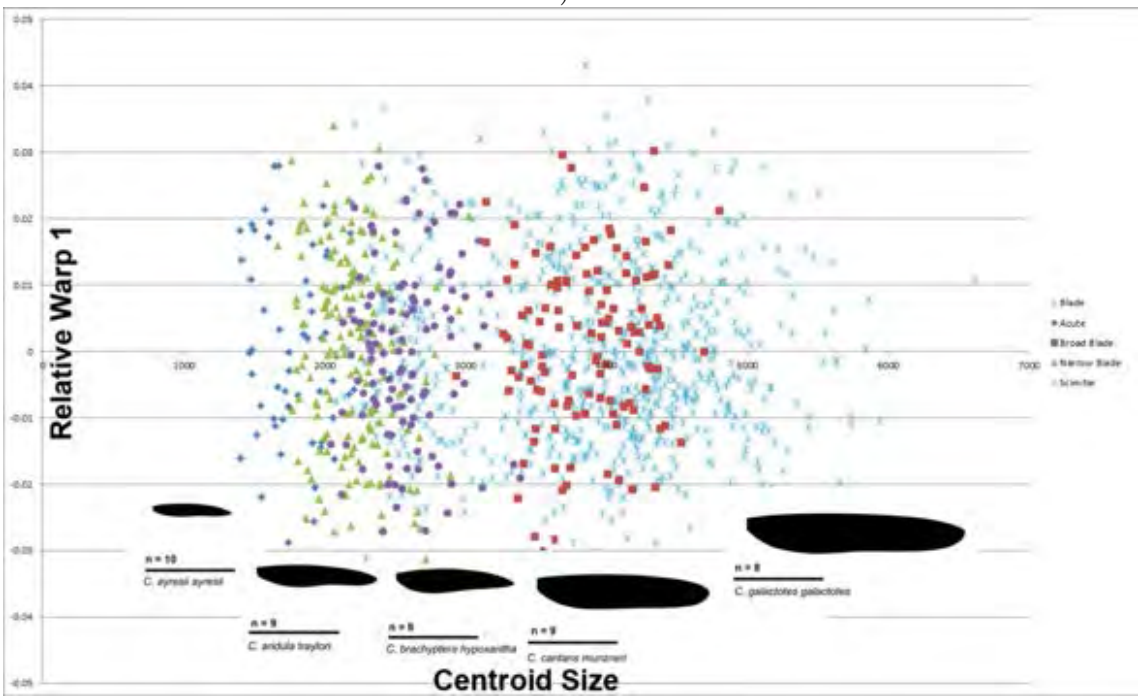


FIGURE 2.7: Plot of group centroids along the first two dimensions of a multiple correspondence analysis on categorical data captured from Lynes (1930). The analysis had a total inertia of 0.527, the x-axis accounts for 16.4% of the total inertia and is correlated mostly with rump colour (mass = 0.0912, inertia = 0.0215) and the y-axis accounts for a further 9.7% of inertia and is correlated with colour of the dorsal side, namely the characters of the head-top (mass = 0.0652, inertia 0.017) and feather borders colour (mass = 0.043, inertia = 0.017, total inertia of plot = 26.2%). A - Textrix group, B - Juncidis group, C - Brachyptera group, D - Robusta & natalensis pair, E - Subruficapilla group, F - Lateralis group, G - Nigriloris group, H - Cantans & erythrops group and I - Galactotes group.

a)



b)

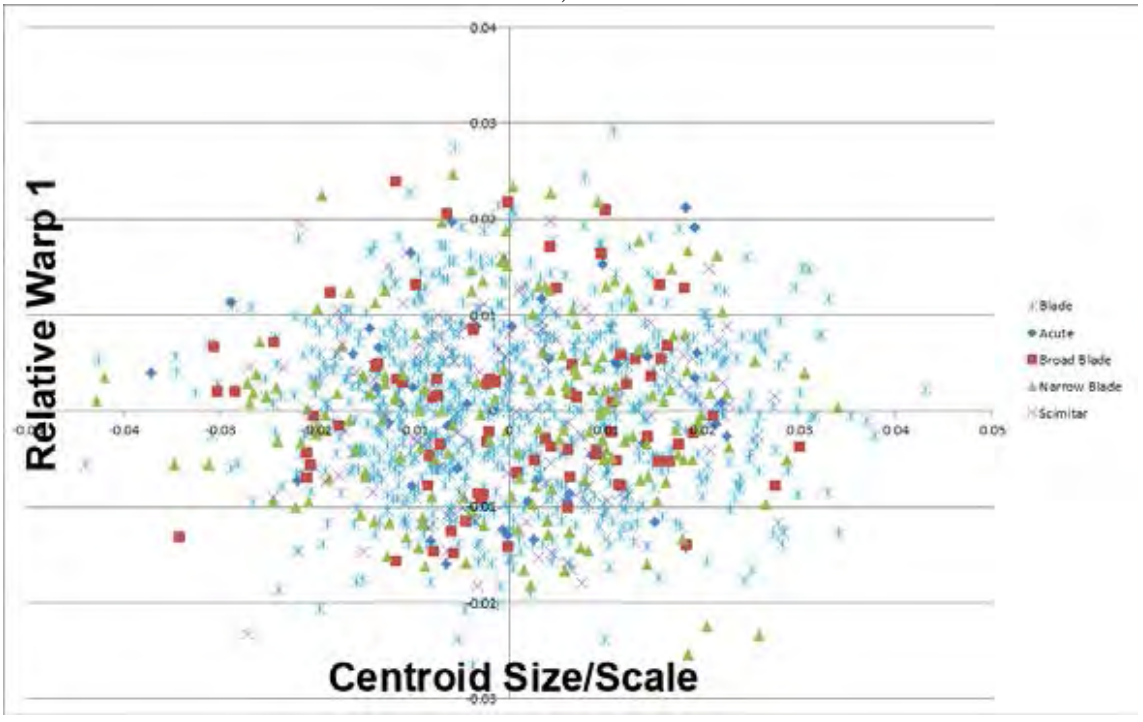


FIGURE 2.8: a) Scatterplot of the Relative Warp 1 score plotted against centroid size showing a separation along the x-axis of the main feather types, and a large distributional spread of the 'blade' shape which acted as a holdall in Lynes (1930) descriptions. Shapes of P1 were generated with tpsDig2 from digitised outlines made up from landmark data comprising 120 points using tpsUtil version 1.46 (Rohlf, 2010). A consensus shape was then computed from these landmark data using tpsTree version 1.21 (Rohlf, 2010) for each taxon. b) Scatterplot of the Relative Warp 1 score plotted against the centroid size divided by the length of the first primary feather to account for size.

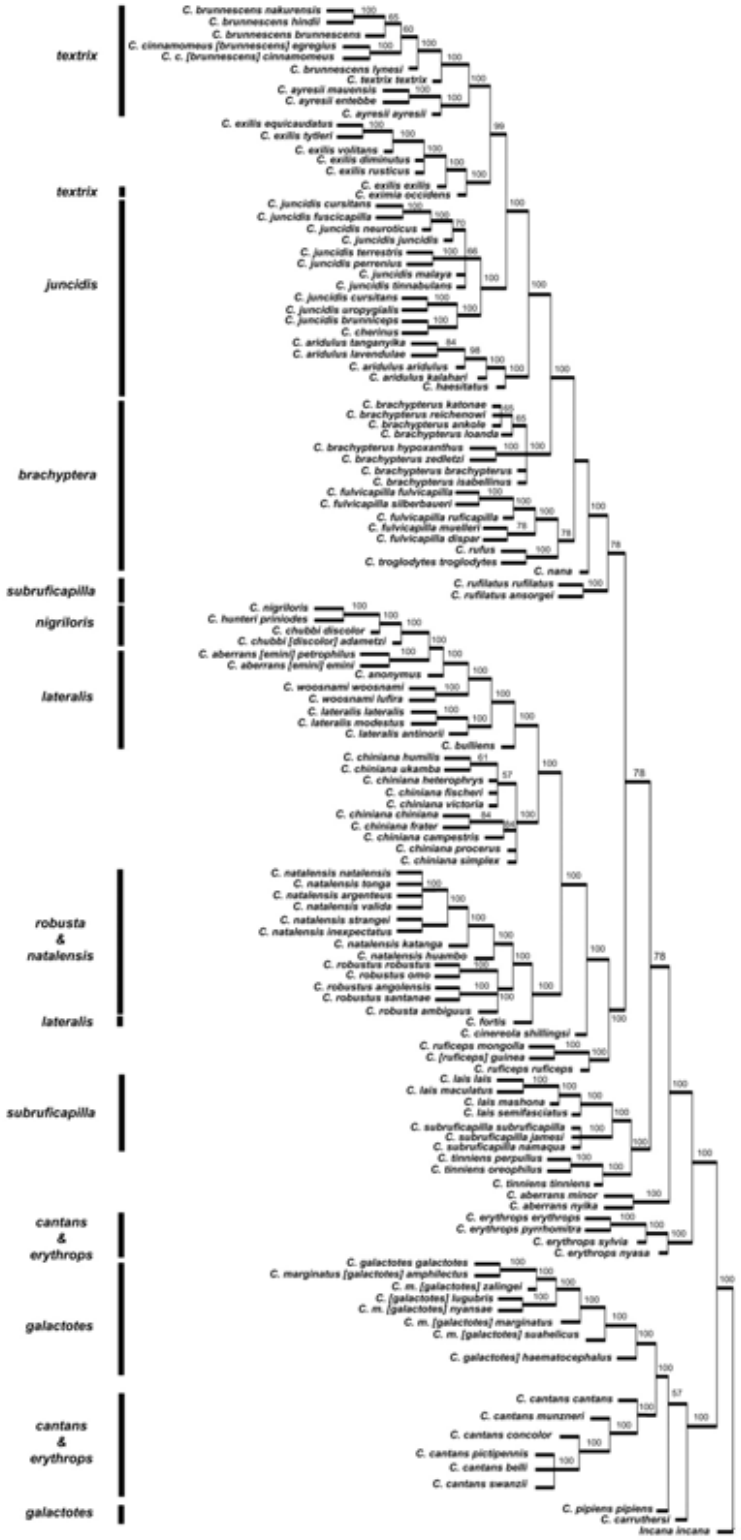


FIGURE 2.9: Majority rule tree of 1998 trees (best score = 1273, 50 000 replicates, CI = 0.249, RI = 0.749) obtained from the analysis of categorical data captured from Lynes (1930). Branch values below 50% collapsed.

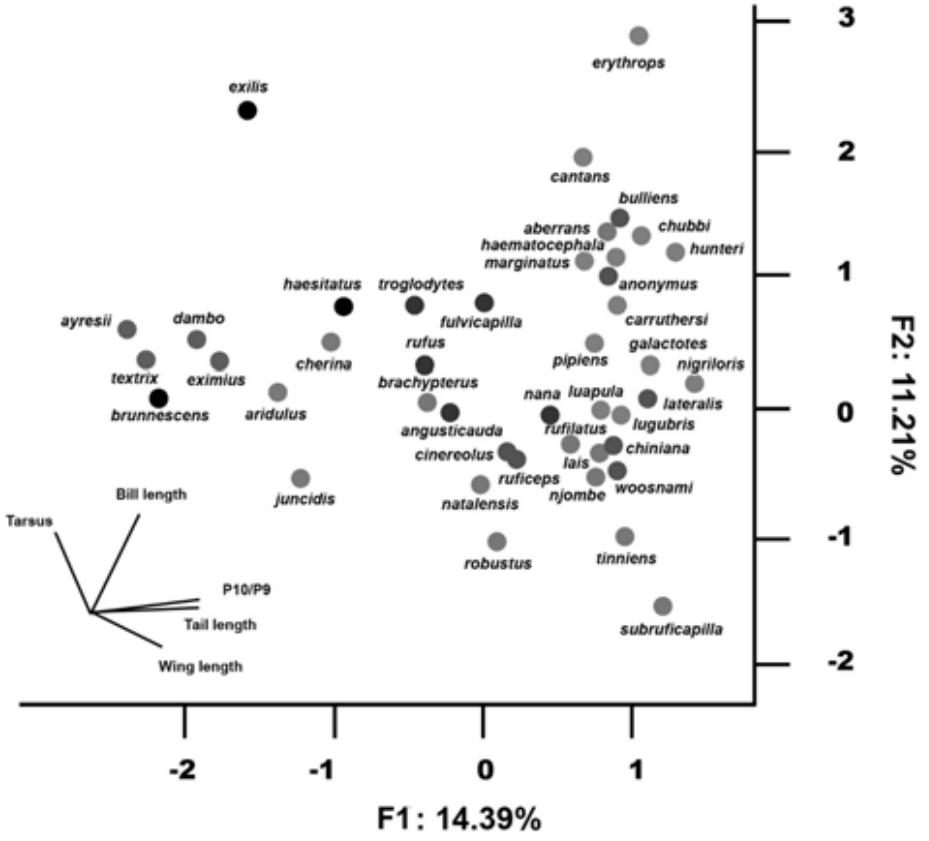


FIGURE 2.10: Results from a multiple factor analysis of combined measurements and AB scored data; the first two axes accounted for 25.6% of the total variation. Species separated along the x-axis mostly by tail length (correlation = 1.061, $\cos^2 = 0.53$), P10/P9 (correlation = 0.914, $\cos^2 = 0.79$) and wing length (correlation = 0.729, $\cos^2 = 0.774$), and separated along the y-axis mostly by bill length (correlation = 0.807, $\cos^2 = 0.22$) and tarsus length (correlation = 0.709, $\cos^2 = 0.096$).

FIGURE 2.11: Average linkage cluster analysis of measurement data using Euclidian distance.

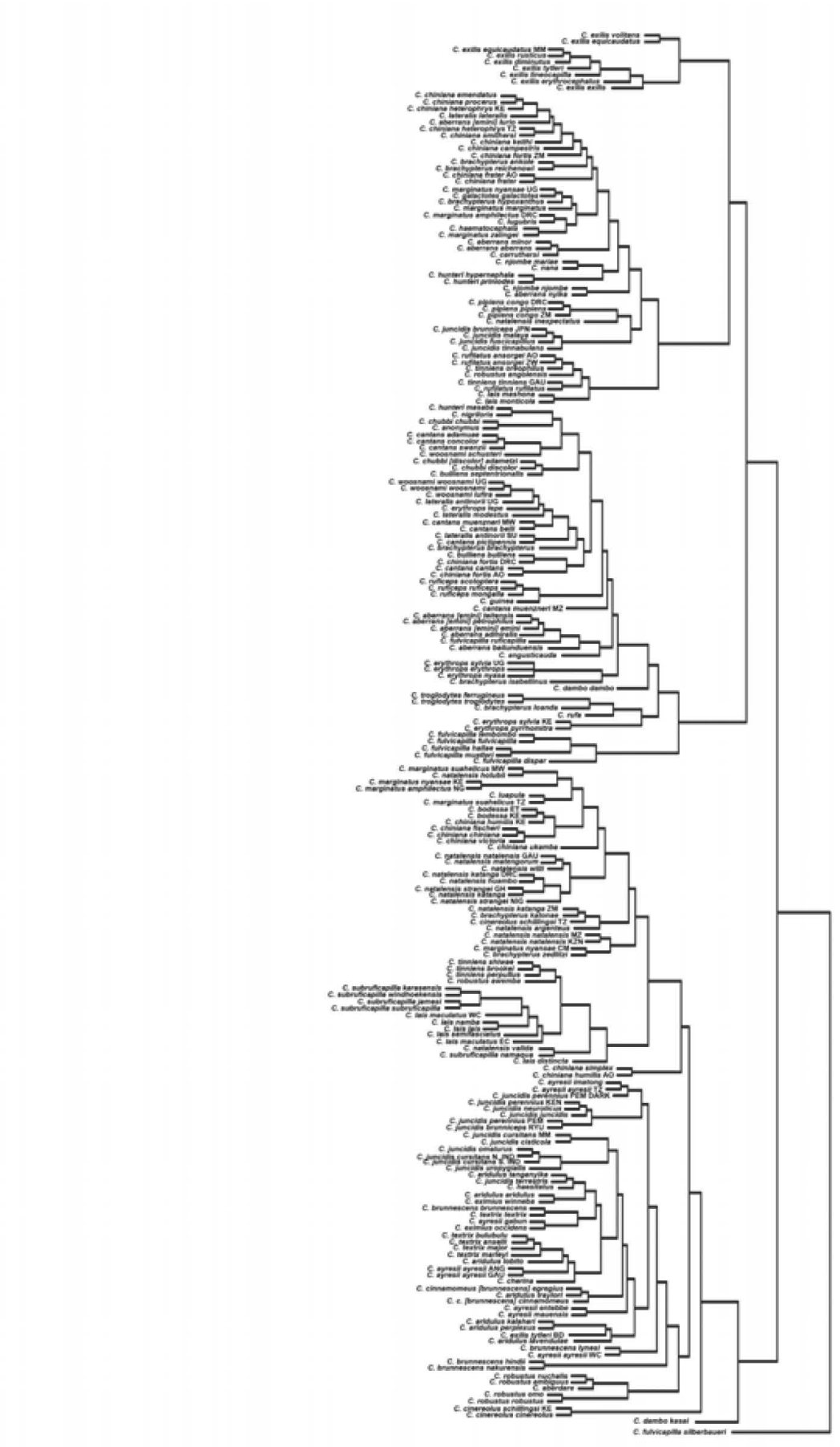


FIGURE 2.12: Average linkage cluster analysis of colour data using Euclidian distance.

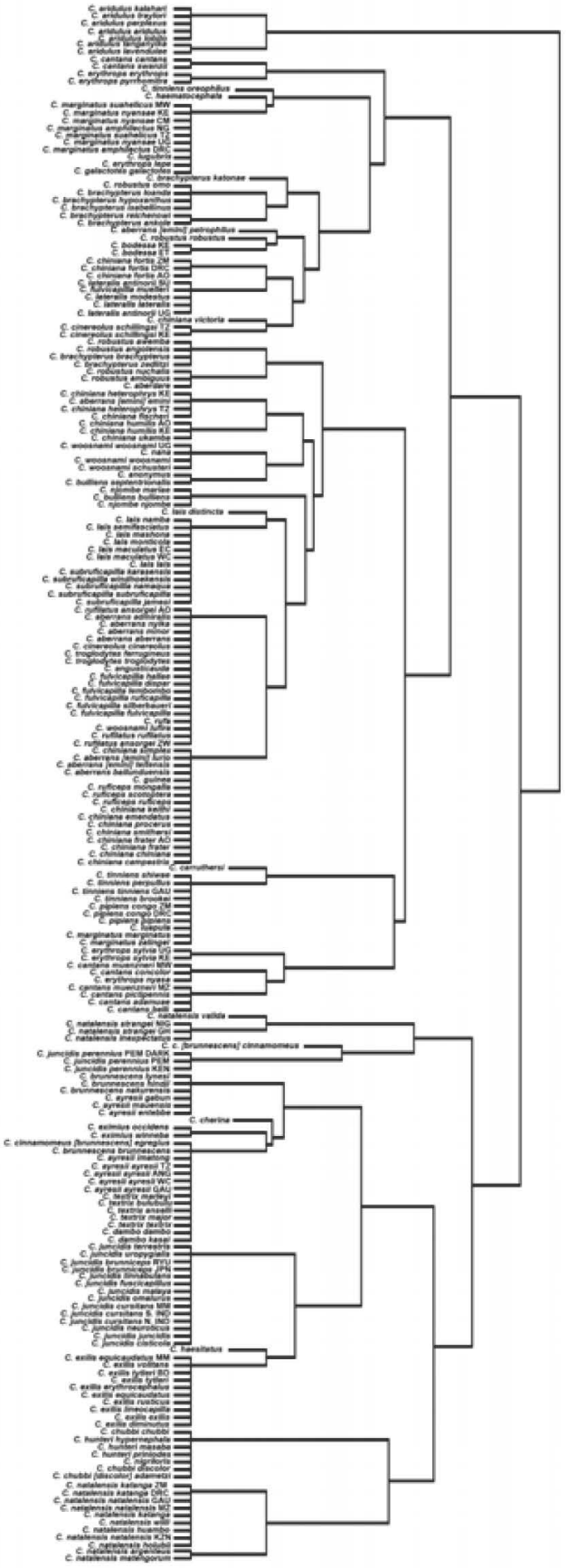


FIGURE 2.13: Average linkage cluster analysis of behavioural/habitat data using Euclidian distance.

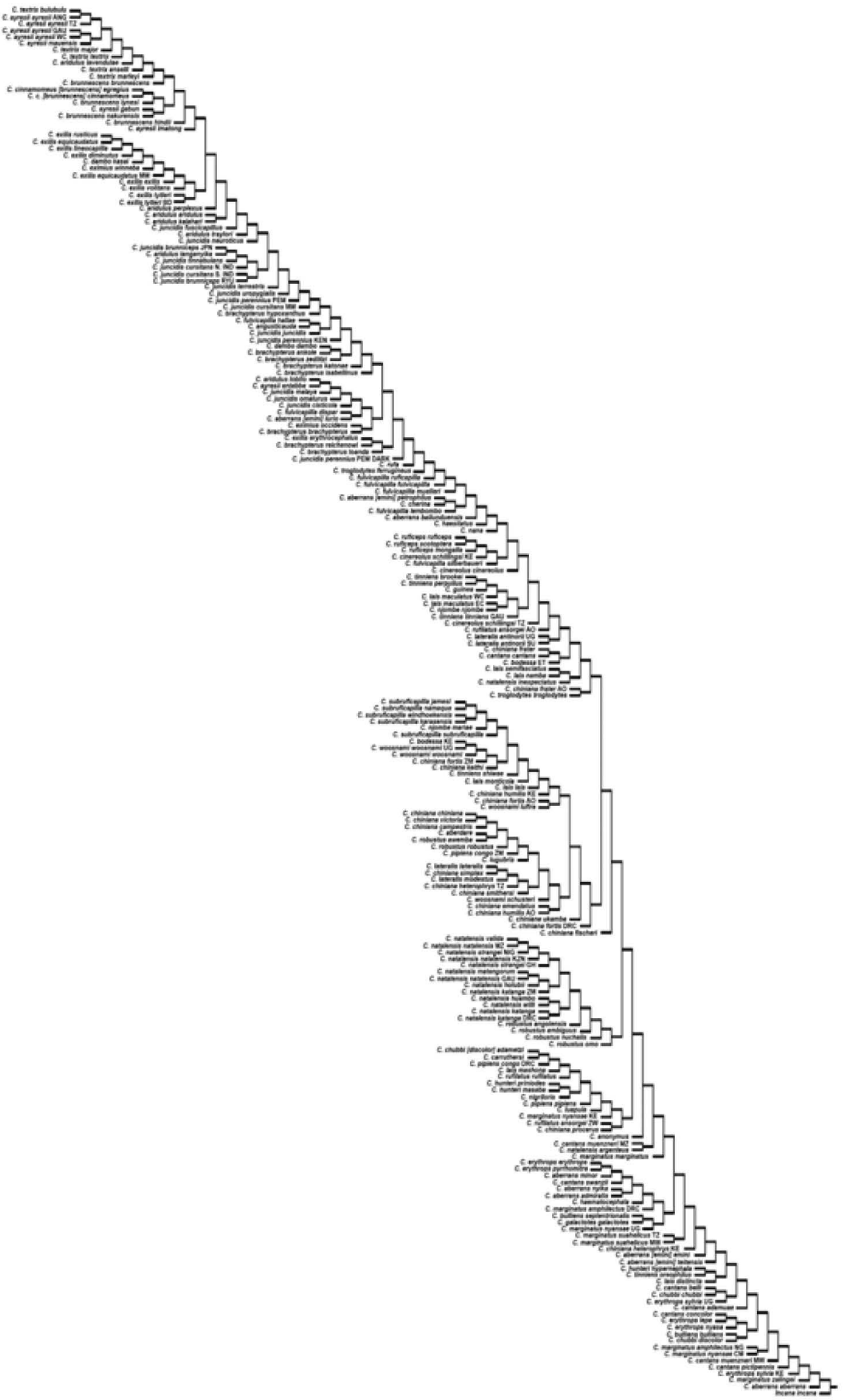


FIGURE 2.14: Best score tree from cladistic analysis of measurement data (best score = 286.241, replicates = 15 000, CI = 0.251, RI = 0.833).

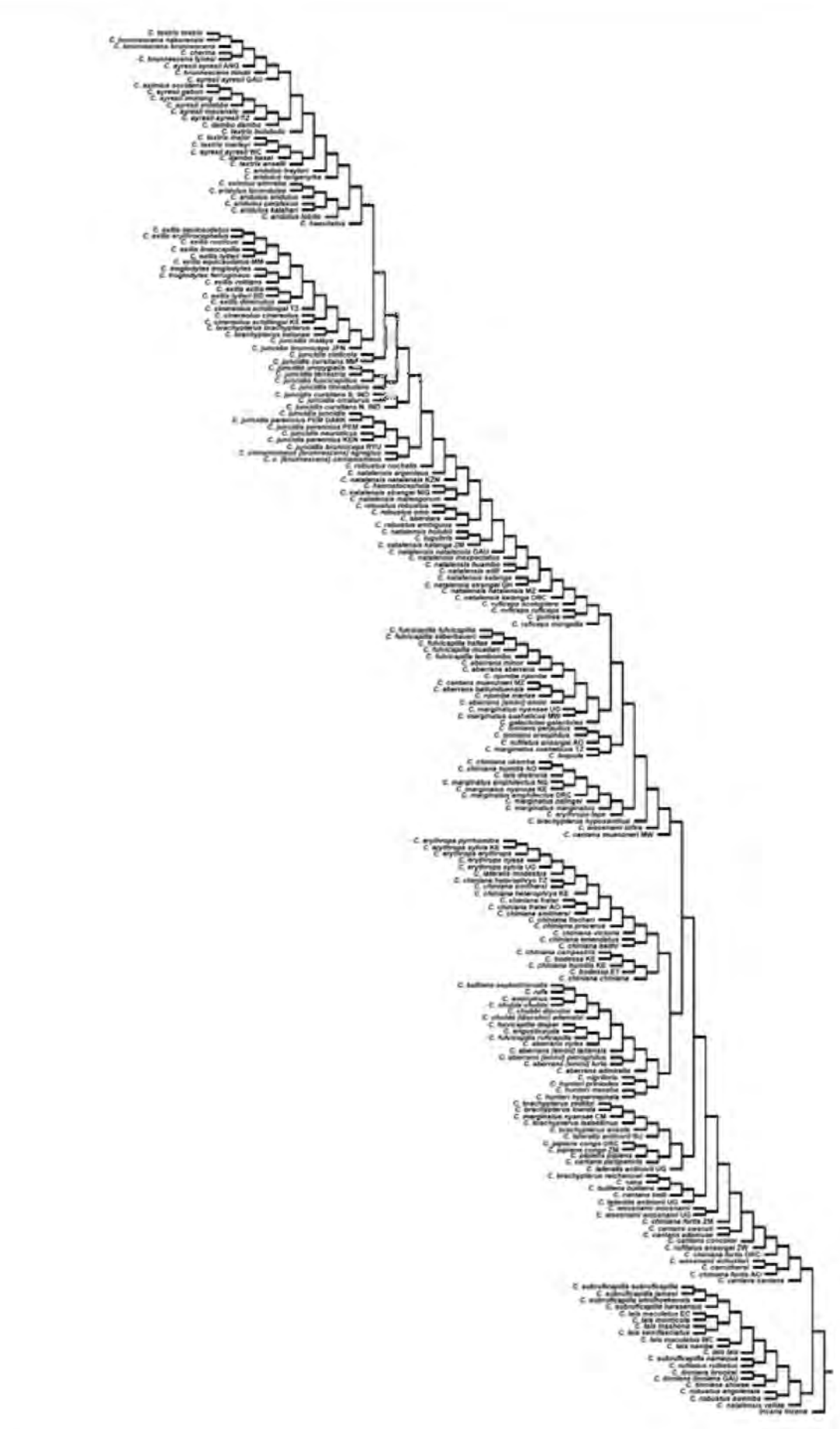


FIGURE 2.15: Best score tree from cladistic analysis of colour data (best score = 927, replicates = 15 000, CI = 0.070, RI = 0.635).

FIGURE 2.16: Best score tree from cladistic analysis of behavioural/habitat data (best score= 85, replicates = 15 000, CI = 0.306, RI = 0.902).

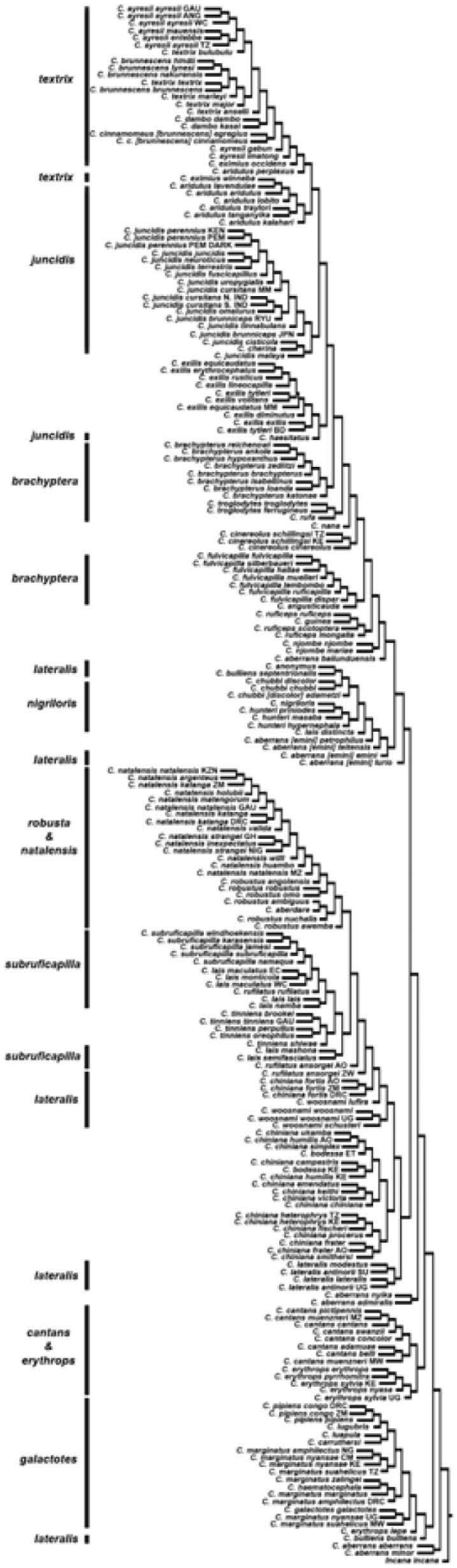


FIGURE 2.17: Best score tree from cladistic analysis of combined data (best score = 1550.843, replicates = 15 000, CI = 0.096, RI = 0.66).

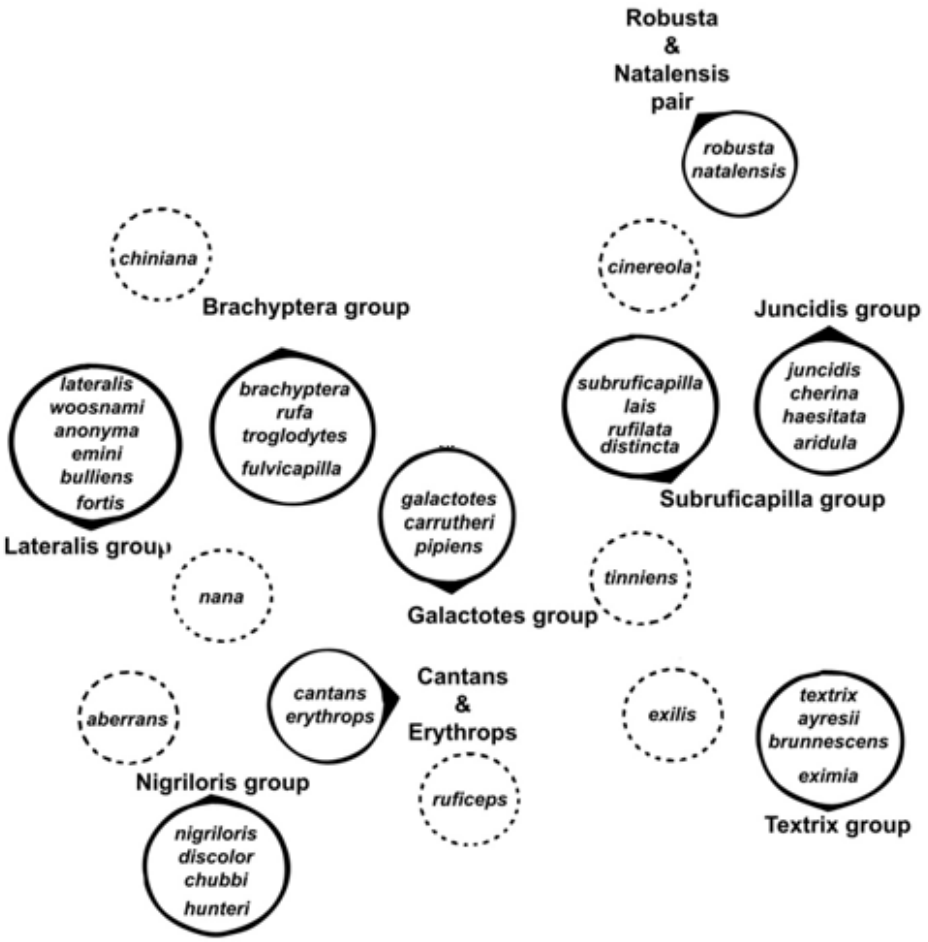


FIGURE 2.18: Diagrammatic representation of the centroid positions along the first two dimensions of the multiple correspondence analysis performed on all data captured from Lynes (1930). The spacing is only roughly proportional to the distance between centroids. Broken line circles indicate taxa unplaced by Lynes (1930), stylised to match Lynes' original depiction of group relationships (Lynes, 1930, p. 71).

Chapter 3

Molecular phylogeny of cisticolas

3.1 Introduction

The genus *Cisticola* is one of the most species rich genera of birds and, while it has representatives in Australia and Asia, its diversity is centered in Africa: Of the 50 or so species currently recognised, all but one are found in the open habitats of Africa and surrounding islands (Ryan, 2006). Despite their widespread distribution and local abundance, they have been poorly studied and the structure of the genus and patterns of diversity within the genus remain largely unknown.

The high degree of overall morphological similarity within the genus results in a poorly supported phylogeny, with trees collapsing into polytomies when these data are analysed using cladistics methods (Chapter 2). Lynes (1930) used his familiarity with these birds to hypothesise on the genetic relatedness between some species in his review of the genus *Cisticola* in 1930, where he stated that: '*C. exilis* and *C. eximia* are extremely alike, and the likeness is so much more than merely superficial that the comparatively near genetic affinity of the species cannot be doubted' (Lynes, 1930, chapter III, p. 181) and, while contemplating the taxonomic position of the lateralis and nigriloris groups, he noted that they were: 'linked genetically with the subruficapilla group' through *C. chiniana* and followed by *C. cantans* and *C. erythrops* 'without any great genetic jump' (Lynes, 1930, chapter III, p. 344). Lynes (1930) proposed nine groups of species that he considered to be closely related and contemplated the relationships amongst them and proposed likely positions of ungrouped taxa (Chapter 2, Figure 2.1 and Appendix B).

Hall and Moreau (1970) suggested some changes to Lynes' groupings and added some

taxa that had been described during the time between the two publications and proposed that Lynes' classification consisted of 'superspecies' and 'species-groups'. 'Superspecies' were defined as species immediately descended from a common ancestor with non-overlapping ranges or local habitats, i.e. allopatric sister-species. 'Species-groups' would be those closely related species whose ranges overlap. The changes included: the addition of *C. cinereolus* to the subruficapilla group and the tentative inclusion of *C. restrictus*; the grouping of *C. chiniana* and *C. njombe* into a superspecies (which they suggested was closely related to the subruficapilla group); the grouping of *C. ruficeps* and *C. nana* into a superspecies and the addition of *C. tinniens* to the galactotes group, suggesting that it was particularly close to *C. carruthersi* (Hall and Moreau, 1970, p. 174).

Tye (1997) recognised most of the groupings but argued that *C. cantans* and *C. erythrops* do not constitute superspecies because of a large degree of range overlap. Similarly, the ranges of *C. bodessa* and *C. chiniana* show significant overlap and Tye (1997) disagreed with the grouping of *C. njombe* with these species. Tye (1997) agreed with the grouping of *C. tinniens* with the rest of the marsh dwelling species but disagreed with the grouping of *C. nana* and *C. ruficeps*. Tye (1997) went on to suggest that *C. brachypterus*, *C. melanurus* and the fulvicapilla superspecies were close to the rufus superspecies and that *C. nana* probably did not form a superspecies with *C. ruficeps* due to differences in size and plumages.

Ryan (2006) summarised the most recent grouping considerations (detailed in Chapter 1), agreeing with many of the groups and suggesting some associations for the ungrouped taxa, noting the similarities of *C. cinereolus*, *C. chiniana* and *C. njombe* to each other and the subruficapilla group and commenting on the similarity of the calls of *C. chiniana* with the lateralis group. Ryan (2006) also noted the similarity between *C. ruficeps* and *C. nana* with all the previous species and the brachyptera group. He suggested that *C. aberrans* was also most similar to the brachyptera group. The similarity between *C. erythrops* and *C. cantans* with the lateralis group and the galactotes group was also listed, as well as the similarities shared between *C. tinniens* and both the galactotes and subruficapilla groups (Ryan, 2006).

In his summary, Ryan (2006) called for detailed molecular work to be done on the family in general, as well as more specifically under the species descriptions of many members of the genus *Cisticola*, e.g. in the descriptions of the marsh dwelling cisticolas, namely *C. galactotes*, *C. marginatus*, *C. luapula*, *C. lugubris* and *C. haematocephala*.

Molecular studies published on the family Cisticolidae have only included a few cisticolas ((Nguembock et al., 2012, 2007; Olsson et al., 2013, eight, six and six species respectively); while these studies have helped resolve the placement of cisticolas within the Cisticolidae – with Olsson et al. (2013) placing them sister to the Socotra Warbler (*Incana incana*), Winifred's Warbler (*Scepomycter winifredae*) and the Black-faced Rufous Warbler (*Bathmocercus rufus*) – the structure within the genus remains poorly understood.

The purpose of this study is to provide a more detailed resolution of the structure and relationships within the genus with the most taxon-dense analysis of mitochondrial and nuclear DNA of cisticolas to date, with particular focus on the marsh cisticolas, and constitutes the first attempt at testing the proposed groupings and taxon associations using genetic material. As the first study on African bird species to be conducted at such broad geographic scales, we aim to test some of the 'superspecies' hypotheses of Hall and Moreau (1970) for open habitat birds, which remain untested (Fuchs et al., 2011).

3.2 Methods

Taxon sampling

Because of the widespread distribution of cisticolas and the obvious logistical difficulties associated with the continent-wide sampling of Africa, toe-pads were taken from museum specimens housed at the Natural History Museum at Tring and the Swedish Museum of Natural History. Toe-pads were obtained from 73 individuals representing 41 terminal taxa (species or subspecies) and we had access to fresh material for an additional 48 samples representing 21 terminal taxa and an out-group species. We obtained material from 121 individuals (Figure 3.1) representing 44 of the 49 currently recognised in-group species (Ryan, 2006). Sub-specific sampling was performed on the marsh dwelling species to better determine the diversity within the group, and also on the Kenyan subspecies of *C. chiniana* for comparisons with *C. restrictus*. We used *Neomixis viridis* as the out-group taxon as recent molecular work on the family Cisticolidae place it basal to the cisticola clade (Nguembock et al., 2012, 2007).

DNA extraction

To account for the age of the samples and the hardened nature of the toe-pads in comparison to fresh material, both the DNeasy Tissue Kit (Qiagen) manufacturer's instructions and the protocol outlined in Irestedt et al. (2006) were slightly modified to

increase yield. Toe-pad samples were allowed to soak in distilled water for 10 minutes to soften the material before being cut up into smaller pieces. I added 180μl Buffer ATL, 20μl Proteinase K and 20μl DTT (dithiothreitol) to each sample and briefly pulsed on a mix vortex before incubating at 38 °C overnight. After incubation, 200μl Buffer AL was added to each sample and then pulsed on a mix vortex before another brief incubation on a 72 °C heat block for 10 minutes and 200μl of 96-100% ethanol was added to each sample, which were then left for 5 minutes at room temperature. Lysate was transferred into mini elute columns and spun in a centrifuge at 8000rpm for 1 minute, 500μl of Buffer AW1 was added to each sample and then spun again at 8000rpm for 1 minute, 500μl of Buffer AW2 was added and samples were spun at 8000rpm for 1 minute. Columns were then spun at 14 000 rpm for 3 minutes to dry. We then added 120μl of Buffer AE at the final elution stage to ensure that a high enough concentration and volume of product was available for multiple PCR runs. Samples were left at room temperature for 1 minute before a final spin in the centrifuge at 14 000 rpm for 1 minute.

PCR amplification

Toe-pads from old study skins contain mostly degraded or short fragments of DNA (Irestedt et al., 2006). I therefore designed internal primer combinations that amplified short, overlapping DNA sequences between 200–250 bp long to increase amplification success and reduce the risk of contamination (Irestedt et al., 2006; Ohlson et al., 2012). Internal primers were designed from a template of DNA extracted from fresh material and carefully designed to have similar melting temperatures ($60-65$ °C salt adjusted). Melting temperatures and potential for hairpin loop formation were checked using the online Oligo Calc tool (`www.basic.northwestern.edu/biotools/OligoCalc.html`). To avoid primer combinations that form primer dimers, all primers were checked using Amplify version 3.1 for Mac (Engels, 1993). I used GE Healthcare™ illustra™ Hot Start Mix RTG PCR beads with initial annealing temperatures for the first cycles about $1-2$ °C below the melting temperature of the primer with the lowest melting temperature (Irestedt et al., 2006). The cycle started with 95 °C for 5min, followed by four cycles of 95 °C for 30s, $55-57$ °C for 30s, 72 °C, and another four-cycle phase and one 36–40 cycle phase with identical temperatures and intervals, except that the annealing temperatures were reduced to $53-55$ °C, $51-53$ °C and $48-50$ °C with the thermocycling program ended with 72 °C for 5min. PCR products were checked using gel electrophoresis on 0.7g agar+50ml TBE buffer+GelRed™ in gels; if some fragments failed to amplify, temperatures of the thermocycling program were dropped by 1 °C and a cycle added to the PCR protocol, or DNA was increased from 2μl to 3μl. Primer sequences are listed in Table 3.1. Two separate sets of primers were designed to sequence cytochrome B as we were not satisfied with the performance of the first set in some PCR reactions.

Sequencing

We sequenced two mitochondrial gene regions, NADH dehydrogenase subunit 2 (ND2) and cytochrome B (CYTB), and four nuclear gene regions, β-fibrinogen gene, intron 5 (FIB5), myoglobin intron II (MYO), glyceraldehyde-3-phosphodehydrogenase intron 11 (G3PDH) and transforming growth factor beta 2 (TGF-β2). Sequences were obtained from all toe-pad samples with good overall success, but some regions failed to amplify for certain individuals regardless of changes to primer design and PCR protocol (Figure 3.2). We concentrated our efforts on sampling ND2 as it showed both a good level of sequence diversity and a high success rate in amplification and sequencing. Sequencing was performed in an ABI PRISM 3100 (Applied Biosystems) automated sequencer using BigDye ® version 1.1. Sequence fragments (contigs) were trimmed and assembled using SEQMAN II™ (DNASTAR Inc.). Positions where the nucleotide could not be determined with certainty were coded as missing data for mtDNA and IUPAC codes were used for heterozygous nuDNA bases, sequences were aligned using MegAlign (DNASTAR Inc.).

Phylogenetic inferences

Parsimony analyses were performed on each gene region separately and combined in a concatenated dataset using a traditional search with 10 000 replicates in TNT (Goloboff et al., 2003). Nodal support was calculated using Jack-knife resampling (Farris et al., 1996) and 1 000 replicates. We also used Bayesian inference to estimate the phylogeny using a concatenated data set of both mitochondrial and nuclear data using BEAST version 1.7.5 (Drummond et al., 2012). The models for nucleotide substitutions used in the analyses were selected for each gene individually using the Akaike Information Criterion (Akaike, 2006) in the program MODELTEST version 2.3 (Posada and Crandall, 1998) in conjunction with PAUP*4.0b10 (Swofford, 1998). We applied the models determined by MODELTEST 2.3 for each partition in the Bayesian analysis using BEAUti version 1.7.5 (Drummond et al., 2012) and ran for 150 million generations, sampling every 15 000 generations. Results from the Bayesian MCMC runs were analysed using Tracer version 1.5 (Rambaut and Drummond, 2009), convergence and mixing were assessed visually by observing trace plots to ensure that they displayed a relatively constant mean and variance. Tree information was summarised using TreeAnnotator version 1.7.5 (Drummond et al., 2012) using a burn-in of 100 and visualised using FigTree version 1.4.0 (Rambaut, 2012). Phylogenetic hypotheses were tested by making topological comparisons of trees using the Kishino-Hasegawa (KH) (Kishino and Hasegawa, 1989) and Shimodaira-Hasegawa (SH) (Shimodaira and Hasegawa, 1999) tests in PAUP*4.0b10 (Swofford, 1998). Comparisons were made between unconstrained ND2 trees and trees where the monophyly

of Lynes' groups was forced using BEAUti version 1.7.5 (Drummond et al., 2012) and analysed as above.

3.3 Results

Variation in the molecular data set

We obtained full (1041 bp) ND2 sequences from all fresh samples and some toe-pad samples, while partial (∼888 bp) ND2 sequences were obtained from the majority of the toe-pad samples (Figure 3.2 for sequence details for each individual). We obtained partial (∼890 bp) CYTB sequences from 46 samples representing 19 terminal taxa of the marsh dwelling cisticolas, full FIB5 sequences (plus small pieces of flanking exons for a total of 566 bp) from 52 samples representing 32 terminal taxa, 306 bp of G3PDH from 34 samples representing 17 terminal taxa, partial (∼620 bp) MYO sequences from 23 samples representing 22 terminal taxa and ∼616 bp TGF-β2 sequences from 60 samples representing 34 terminal taxa. When these data were combined, the concatenated file included 122 individuals and 4058 bp (maximum number of bases excluding missing data = 3642 bp for *C. lugubris* [BMNH 1929.11.15.66]). ND2 sequences contained 502 conserved sites, 539 variable sites and 484 parsimony-informative sites, a single most parsimonious tree was recovered with a tree length of 801 (CI = 0.286, RI = 0.793). CYTB contained 657 conserved sites, 233 variable sites and 178 parsimony-informative sites, five MP trees were recovered with a tree length of 158 (CI = 0.588, RI = 0.869). FIB5 contained 495 conserved sites, 71 variable sites and 25 parsimony-informative sites, 49 MP trees were recovered with a tree length of 44 (CI = 0.955, RI = 0.951). G3PDH contained 301 conserved sites and only five variable sites and four pasimony-informative sites, resulting in a CI and RI of 1.00. MYO contained 585 conserved sites, 35 variable sites and eight parsimony-informative sites, 23 MP trees were recovered with a tree length of 23 (CI = 0.956, RI = 0.916). TGF-β2 contained 480 conserved sites, 97 variable sites and 37 parsimony-informative sites, 60 MP trees were recovered with a tree length of 16 (CI = 0.937, RI = 0.875).

Uncorrected pairwise distances between species ranged from 3.2–18.3% in ND2 (*C. anonymus* vs. *C. textrix/C. ayresii*); 3.5–10.2% in CYTB (*C. tinniens* vs. *C. haematocephala*); 0–4.0% in FIB5 (*C. juncidis* vs. *C. exilis/C. natalensis*); 0–0.7% in G3PDH (*C. lugubris* vs. *C. pipiens/C. marginatus*); 0–2.7% in MYO (*C. exilis* vs. *C. rufus/C. robustus*) and 0–5.8% in TGF-β2. Six indels were found in TGF-β2; a 5 bp insertion shared between *C. dambo*, *C. exilis*, *C. eximius* and *C. juncidis*; a 4 bp insertion shared between *C. cinereolus*, *C. rufilatus* and *C. luapula*; a 4 bp insertion shared between *C.*

haematocephala, *C. melanurus*, *C. nana*, *C. rufus* and *C. troglodytes*; a 4 bp insertion in *C. juncidis*; a 23 bp insertion in *C. angusticauda*; and a 7 bp insertion in *C. rufus*. The prior selection of substitution models by MODELTEST 2.3 supported GTR+I+Γ for ND2, CYTB and TGF-β2, HKY for FIB5, F81 for G3PDH, and HKY+I for MYO.

Phylogenetic reconstructions

Parsimony analyses on the separate nuclear datasets failed to resolve internal structure within the genus with only a few basal nodes supported after Jack-knife analyses (Figures 3.3, 3.4, 3.5, 3.6 and 3.7) as overall sequence variation was low in these regions. Topological tests indicated that the two hypotheses differed in their fit to the ND2 dataset (Figure 3.8). The unconstrained tree had a shorter length and had a significantly preferred topology than the tree produced by the constrained analysis that forced the monophyly of Lynes' groups (constrained: TL = 2618, -ln L = 13240.32; unconstrained: TL = 2506, -ln L = 12999.36, diff. -ln L = 240.96, KH test $p < 0.001$, SH test $p < 0.001$). Parsimony analysis on ND2 recovered relationships between sister-species with high Jack-knife support values (Figure 3.9) with tip nodes also being supported in the marsh dwelling cisticolas by CYTB (Figure 3.10), resulting in slightly higher resolution and Jack-knife support for these nodes in the concatenated dataset (Figure 3.11). Bayesian analyses on the concatenated dataset produced a tree with the same topology as the strict consensus maximum parsimony tree with high posterior probabilities on internal nodes (Figure 3.12), placing *C. exilis* at the base of a tree with five main clades, which could be further divided into a number of sub-clades (Figure 3.14). The first clade was supported by ND2 and the concatenated parsimony (Figures 3.9 and 3.11) and Bayesian analyses (highlighted green/labeled 1 in Figure 3.14). It comprised the small grassland species and could be further divided into two sub-clades that included *C. juncidis*, *C. cherina* and *C. aridulus* (Figure 3.14, 1a) together with *C. dambo*, *C. eximius*, *C. textrix* and *C. ayresii* (Figure 3.14, 1b). The second clade was supported by the Bayesian and concatenated parsimony analyses (Figures 3.11 and highlighted orange/labeled 2 in Figure 3.14); it included the two large *C. natalensis* and *C. robustus* together with *C. [lais] distinctus*, *C. subruficapilla*, *C. lais*, *C. rufilatus* and *C. aberrans*. The third clade (highlighted blue/labeled 3 in Figure 3.14) was supported by Bayesian and parsimony analyses on ND2 and concatenated data (Figures 3.9, 3.11 and 3.12). It comprised *C. erythrops*, *C. cantans*, *C. carruthersi* and *C. luapula*, together with *C. galactotes* and Kenyan and Tanzanian samples of *C. marginatus*, a species which was not recovered as monophyletic in any of the Bayesian or parsimony analyses on ND2 or concatenated data (Figures 3.9, 3.11 and 3.12), *C. haematocephala*, *C. pipiens* and *C. lugubris* and samples of *C. marginatus* from Uganda, Sudan, Nigeria and Sierra Leone. The fourth clade (highlighted pink/labeled 4 in Figure 3.14) was supported by Bayesian

and parsimony analyses of ND2 and concatenated data (Figures 3.9, 3.11 and 3.12) and included *C. brachypterus* and *C. njombe* grouping with *C. tinniens* (Figure 3.14, 4a) and a sub-clade including *C. nigriloris*, *C. hunteri* and *C. chubbi* (Figure 3.14, 4b). The fifth clade (highlighted yellow/labeled 5 in Figure 3.14) was supported by the Bayesian analysis and parsimony analysis of ND2 (Figures 3.9 and 3.12) and was recovered in the strict consensus tree of concatenated data, but the node between the sub-clades collapsed under Jack-knife resampling (Figure 3.11). It included the grouping of *C. troglodytes* and *C. rufus* together with *C. nana*, *C. angusticauda*, *C. melanurus* and *C. fulvicapilla* (Figure 3.14, 5a) and a sub-clade that included *C. ruficeps*, *C. cinereolus*, *C. lateralis*, *C. woosnami*, *C. anonymus*, *C. bulliens*, *C. restrictus*, *C. chiniana* and *C. bodessa* (Figure 3.14, 5b).

3.4 Discussion

Lynes' textrix, juncidis, natalensis and robustus, nigriloris and galactotes groups (Lynes, 1930) were recovered as monophyletic in the Bayesian analysis (Figure 3.12) but the remaining four groups (cantans and erythrops pair, lateralis, brachyptera and subruficapilla groups) were poly- or paraphyletic and his suggested positions of ungrouped taxa were generally not supported.

The tree that resulted from an unconstrained analysis of ND2 data provided a significantly better fit to the dataset than when the monophyly of Lynes' groups was forced (Figure 3.8). As Lynes relied heavily on morphological characters to inform his groupings, this suggests that character convergence within the genus may have obscured the phylogenetic relationships between and amongst species. This convergence in morphological characters can also explain the incongruity between the molecular phylogeny and phylogenetic analyses performed on morphological data collected from museum specimens in Chapter 2. Lynes (1930) considered similarity in size, habitat preference, leg strength, the shape of the outermost primary feather and back striping in the formation of his groups. Morphological similarity, such as plain or patterned (striped) backs, is also used to group species in field guides (such as Sinclair and Ryan (2003)) to aid identification, but this does not reflect phylogenetic relationships within the genus. The problem of convergence is exacerbated due to the high degree of overall morphological similarity within the genus and the fact that differentiation between species is often based on what are fundamentally subtle differences in colouration or form.

Lynes (1930) grouped *C. cantans* and *C. erythrops* due to their similar size, mostly plain-back, affinity for thick overgrown habitats and their above average leg strength; while they are closely related they do not form a monophyletic group.

Lynes' lateralis group comprised *C. lateralis*, *C. anonymus*, *C. woosnami* and *C. bulliens*, which were all from central Africa and shared similar colouration and overall size; these species would form a monophyletic group with the inclusion of the pattern-backed *C. chiniana*, a species which Lynes (1930) considered to be a linking form between the lateralis and subruficapilla groups. The proposed brachyptera group was based largely on their small size, preference for open woodland habitats, plain back, weak legs and scimitar shaped outermost primary feathers while *C. rufilatus* was placed within the subruficapilla group due to similarity in seasonal plumages, location and proportionally weak legs. The subruficapilla group would be monophyletic with the inclusion of *C. aberrans*, birds characterised by stronger legs, a different shape of the outermost primary feather and preference for somewhat more woodland environments.

By plotting morphological characters and habitat preference onto a phylogeny generated from combined morphological, behavioural and molecular datasets, it became apparent that many of the characters that were considered by Lynes (1930) to be important taxonomic characters are symplesiomorphic or convergent traits (Figure 3.13). For example the distinction between plain- or pattern-backed species does not offer much insight into thy phylogenetic relationships between all species exhibiting those characters, as plain-backed species are found dotted throughout the phylogeny and sometimes more closely related to birds with heavy streaking than to other plain-backed species (e.g. the close relationship between *C. erythrops* and the galactotes group). Striping, streaking and patterning on the back may be convergently evolved by taxa that inhabit habitats that contain verticle elements in their structure, such as grass stalks, reeds, sedges or thorny scrubland. Leg strength is correlated with overall size, with larger birds such as *C. robustus* and *C. natalensis* having the largest, strongest legs, but there is also adaptive diversification of this trait to habitat, for example *C. carruthersi* has weaker legs than the rest of the galactotes group but has proportionally longer toes which may facilitate easier movement through the *Papyrus* stalks and leaves that this species prefers. Habitat preference does not run true for each clade, with multiple adaptations to thorny scrubland (e.g. *C. lais* and *C. chiniana*) and the movement into marshland-type habitats has happened independently at least twice with members of the galactotes group and *C. tinniens* both preferring these emergent environments. The shape of the outermost primary feather can be compared with the categorisation of these shapes made by Lynes (1930). The large variation in shape across the genus was dealt with in Chapter 2 and can be attributed to geometric scaling with size rather than phylogenetic proximity, with the large variation making categorisation into discrete shapes difficult, for example the different categorisation of *C. aberrans* and *C. rufilatus* or the distinction between blade- and narrow-blade shaped feathers in the juncidis and textrix groups, amongst others (Figure 3.13).

Despite similarities in behaviour, morphology and habitat preferences, the suggestion of Hall and Moreau (1970) to include *C. cinereolus* and *C. restrictus* with the subruficapilla group was not supported here, with both rather more closely related to *C. chiniana* as suggested by Ryan (2006). The grouping of *C. njombe* with *C. chiniana* into a superspecies by Hall and Moreau (1970) was also not supported, nor was their close association with the subruficapilla group even though they share many similarities. These results affirmed the rejection of this superspecies by Tye (1997). Hall and Moreau (1970) said that their grouping of *C. ruficeps* and *C. nana* into a superspecies was 'particularly tentative' and a close relationship between these two species was not recovered in this analysis. The position of *C. tinniens* with either the galactotes group (Hall and Moreau, 1970; Ryan, 2006; Tye, 1997) or close to the subruficapilla group (Lynes, 1930; Ryan, 2006) was not supported, with this analysis placing it closer to *C. njombe* and *C. brachypterus*. The position of *C. nana* with members of the brachyptera group is consistent with Hall and Moreau (1970) and Ryan (2006) notes on their similarity, and the proximity of the majority of this group with the fulvicapilla group and *C. melanurus* as supported by Tye (1997), as well as the inclusion of *C. angusticauda* by Hall and Moreau (1970). The placement of *C. brachypterus*, separate from the rest of the brachyptera group, is not too surprising as this group was also only 'tentatively' followed by Hall and Moreau (1970), who commented on their differences in colour and pattern and the difficulty in appreciating the field characteristics that Lynes may have used to group them together, but the close relationship of this species with *C. tinniens* and *C. njombe* was unanticipated. Also somewhat unexpectedly, this analysis placed the rather enigmatic *C. aberrans* with those species of the subruficapilla group, with Ryan (2006) suggesting that it was perhaps more similar to members of the brachyptera group. Samples of *C. [lais] distinctus*, which Lynes (1930) described as a separate species, are placed between *C. robustus/C. natalensis* and the subruficapilla group, and are distinct from samples of *C. lais* which are often considered to be conspecific due to their vocal similarity (Ryan, 2006). The grouping of *C. angusticauda* with *C. nana* was somewhat unexpected. While Lynes (1930) commented on their near relationship, more recent authors have considered it to be closer to *C. melanurus* or even conspecific with *C. fulvicapilla* (Benson and Irwin, 1964; Dowsett and Dowsett-Lemaire, 1980; Irwin, 1991). This study supported the field observations of Mills et al. (2011) who concluded that *C. angusticauda* should rather be considered as a separate species.

This analysis placed *C. erythrops* and *C. cantans* basal to the galactotes group, a placement that supports Ryan (2006) who noted the similarities amongst these species. The galactotes group was recovered as monophyletic, with *C. carruthersi* following from the previous two species. The group then splits with *C. luapula*, *C. galactotes* and

Kenyan/Tanzanian specimens of *C. marginatus*, forming a clade separate from *C. haematocephala*, *C. pipiens*, *C. lugubris* and specimens of *C. marginatus* from Uganda, Sudan and Sierra Leone. The separation of *C. luapula* from other members of the group offers genetic support for the recognition of this species based on vocalisation and plumage differences (Hustler, 2001; Sibley, 1996), with about 3.2% difference in ND2 and 3.7% difference in CYTB from its closest relative (*C. galactotes*). Morphologically, specimens of *C. marginatus* from east Africa tend to have a less rufous wash on their head than specimens from Kenya and Tanzania.

Samples were taken from subspecies of *C. chiniana* surrounding the Tana River area to test the hypothesis that *C. restrictus* might be an aberrant form of *C. cinereolus* or a hybrid between *C. chiniana* and *C. cinereolus*. This species is known from very few specimens and only a handful of localities in eastern Kenya, but has not been officially recorded since 1972 (Ryan, 2006). There was a particular interest to investigate the genetic affinity of *C. restrictus*, as the Royal Society for the Protection of Birds (RSPB) was reassessing the conservation status of this species at the time and contacted the authors in this regard. This analysis rejects the hypothesis that *C. restrictus* is an aberrant *C. cinereolus* and recovered about a 5.1% difference in ND2 between *C. restrictus* and local subspecies of *C. chiniana*, which average about 2.9% difference from each other. In addition to this molecular divergence, *C. restrictus* is also morphologically distinct from the local subspecies of *C. chiniana*, being smaller, paler and having no rufous wing panel Ryan (2006). These differences together support the current recognition of *C. restrictus* as a valid species.

3.5 Conclusions

The phylogeny obtained from the Bayesian analysis represents the best estimate of the structure of the genus *Cisticola* to date and the relationships between the species appear to be well supported by the posterior probabilities and shared topology with the strict consensus maximum parsimony analysis.

This study presents the most taxon-inclusive phylogenetic analysis on the genus to date and gives evidence for the splitting of *C. marginatus* into two species, one including the west African subspecies (*C. m. marginatus/amphilectus/zalingei*) and a second that includes the east African subspecies (*C. m. nyansae/suahelicus*). There is also a case for the elevation of *C. lais distinctus* to full species rank and, while this study provides little support for the recognition of *C. bodessa* as anything more than a subspecies of *C. chiniana*, additional samples are required to rule out effects of potential hybridisation and to better determine validity of the species.

There is still a lot of work to do on the genus regarding specific and subspecific rank; in addition to the inclusion of samples from *C. aberdare*, *C. guinea*, *C. haesitatus*, *C. brunnescens*, *C. cinnamomeus* and the as yet undescribed 'Kilombero' and 'White-tailed' cisticolas, samples from the subspecies *C. ayresii gabun*, *C. cinnamomeus taciturnus*, *C. chubbi adametzi*, *C. chubbi discolor*, *C. aberrans emini*, *C. aberrans petrophilus*, *C. aberrans admiralis*, *C. subruficapilla newtoni*, *C. subruficapilla windhoekensis* and *C. robustus angolensis* should be included in future phylogenetic analyses to determine their status and placement in the genus. An investigation into the various subspecies of the wide-ranging *C. juncidis* should also be considered.

The low level of molecular diversity observed in the nuclear regions that were sequenced for this study may indicate a fairly rapid and recent radiation of the genus diversifying with the availability of novel open habitats in Africa. While movement into similar habitat types has occured multiple times on the phylogenetic tree, many sister species appear to occupy the same habitat type and occur in sympatry, even breeding within sight of each other (e.g. *C. textrix* and *C. ayresii*). The following two chapters will investigate the diversification of the genus in the context of historical climate change and African open habitat evolution and the influences of habitat, size and phylogeny on the song characteristics of cisticolas, as songs and displays are potentially important for species recognition and the maintainence of species boundaries in such similar looking birds.

3.6 Figures and Tables

TABLE 3.1: List of primers used in this study. Those without references were developed by this study.

Primer	Sequence	Reference
NADH dehydrogenase subunit 2 (ND2)		
L5219-Met	CCCATACCCCGAAAATGATG	Sorenson et al. (1999)
ND2-CistOD-F2	CCACTAATCTCAAAATCCCACCA	
ND2-CistOD-R2	TCTGGAAATCAGAAGTGGAATGG	
ND2-CistOD-F3	TCCTAACTTCAGCCCTAGCAAT	
ND2-CistOD-R3	GGCTAGGATTTTTCGGATTTGTGT	
ND2-CistOD-F4	CTAGGAGGATGAATAGGACTAAAC	
ND2-CistOD-R4	AGTGCGGGTGCTTTTGTTCATG	
ND2-CistOD-F5	CAAAGTATCAAAACTATCAACCCTAAT	
ND2-CistOD-R5	AGTGTGATTGTTGCACAGTATGC	
Cytochrome B (CYTB)		
Cytb-CistOD-F1	GCCATACATTACACAGCAGACAC	
Cytb-CistOD-R1	ACCTACGAAGGCGGTTGCTAT	
Cytb-CistOD-F2	CAAAGAAACGTGAAACGTAGGAGT	
Cytb-CistOD-R2	ACGAATGGAAGGAGGAAGTGGA	
Cytb-CistOD-F3	GACAATCCAACCCTCACCCGA	
Cytb-CistOD-R3	CTAGGCTGGCTAGGGGGAT	
Cytb-CistOD-F4	ACAAAAGACATCCTAGGATTCGCA	
Cytb-CistOD-R4	ATAAGGAAGAGGACTAGGACGGA	
Cytb-CistOD-F5	CAAATAAACTAGGAGGAGTACTAGC	
Cytb-CistOD-R5	GACTAGAATGATTATGAAGTAGGTGA	
Cytochrome B (CYTB) set b		
CytB-CistOD-F1b	AGCAGACACTTCCCTAGCCT	
CytB-CistOD-R1b	TAACCTACGAAAGCGGTTGCTAT	
CytB-CistOD-F2b	AAGAAACTTGAAATATTGGAGTAATCC	
CytB-CistOD-R2b	AGGAGGAAGTGGATGGCGAA	
CytB-CistOD-R3b	TGCGAATCCTAGAATGTCTTTTGT	
CytB-CistOD-F4b	GTGACAAAATCCCATTCCACCC	
CytB-CistOD-R4b	AGTTTGTTTGGGATGGATCGTAG	
CytB-CistOD-F5b	CCACACATCAAACCCGAATGATA	
CytB-CistOD-R5b	AGAAGATTGGCTACTAGGGTTCA	
Myoglobin intron II (MYO)		
Myo2	GCCACCAAGCACAAGATCCC	Heslewood et al. (1998)

Continued on next page

Table 3.1 – *Continued from previous page*

Primer	**Sequence**	**Reference**
MYO-CistOD-R1	TCTAAACTTGGATATTCACATACCATTT	
MYO-CistOD-F2	TGTGCAAGCAGGAGGCATAGAA	
MYO-CistOD-R2	ACTCTAAAATTGTATGTCCCTTGTG	
MYO-CistOD-F3	ATTACATAAGGACTCCCAGTGACT	
MYO-CistOD-R3	CTGATCTGCTTCATAACCTTGAG	
MYO-CistOD-F4	AAAAGTGGAAAGGGCCATGGTC	
Myo3F	GCAAGGACCTTGATAATGACTT	Slade et al. (1993)
β-fibrinogen gene, intron 5 (FIB5)		
Fib5	CGCCATACAGAGTATACTGTGACAT	Fuchs et al. (2004)
Fib-CistOD-R1	TGACCTTAACAAGACTTCCCCAA	
Fib-CistOD-F2	ACTTGGTAATTAAACCTGATTGACTTA	
Fib-CistOD-R2	GGTGGAAAAAGCAGAACTTGAAG	
Fib-CistOD-F3	ACCCTGCTCCAATGCACTTG	
Fib-CistOD-R3	AACTTCACCTCAGGACCAGAG	
Fib-CistOD-F4	GAAACAGTGAAGGACCTGCTG	
Fib6	GCCATCCTGGCGATTCTGAA	Fuchs et al. (2004)
Transforming growth factor beta 2 (TGF-β2)		
TGF5	GAAGCGTGCTCTAGATGCTG	Bures et al. (2002)
TGFB-CistOD-F3	CACCTTCACTTTGTTCATCTACTC	
TGFB-CistOD-R3	CACAAAAATTCTCAACTAAATCAAATCAAT	
TGFB-CistOD-F4	TAAGCATTCCTGTAATAGCTGTCAT	
TGF6	AGGCAGCAATTATCCTGCAC	Bures et al. (2002)
Glyceraldehyde-3-phosphodehydrogenase intron 11 (G3PDH)		
G3P-CistOD-F2	ACTGTGGAGTGAGATTGCTTCTT	
G3P-BRC	ATGCCAGCACCCGCATCAAAGGTGGA	

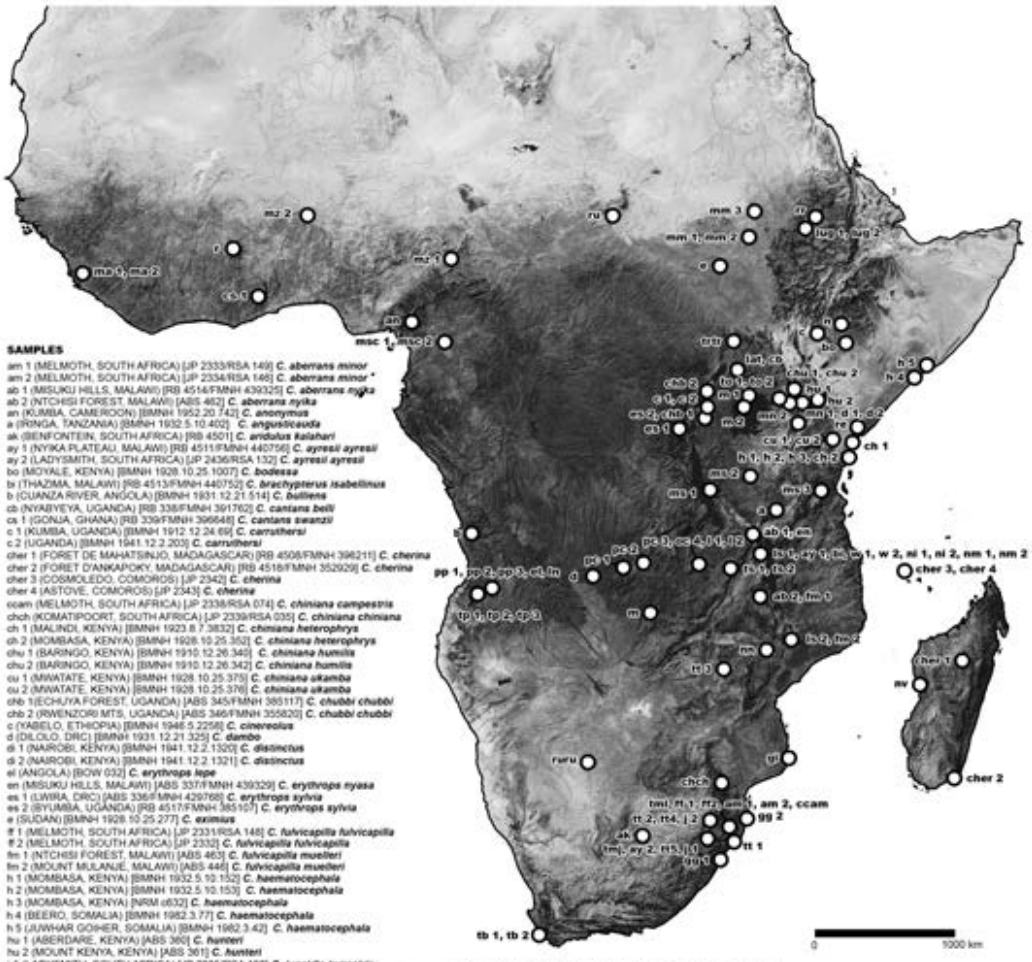


FIGURE 3.1: Sampling localities of molecular data used in this study. Samples not included in this figure include *C. exilis exilis* [BMNH 1964.17.325] collected from Victoria, Australia and *C. juncidis juncidis* [BMNH 1949.whi.1.11309] collected from Sicily, Italy.

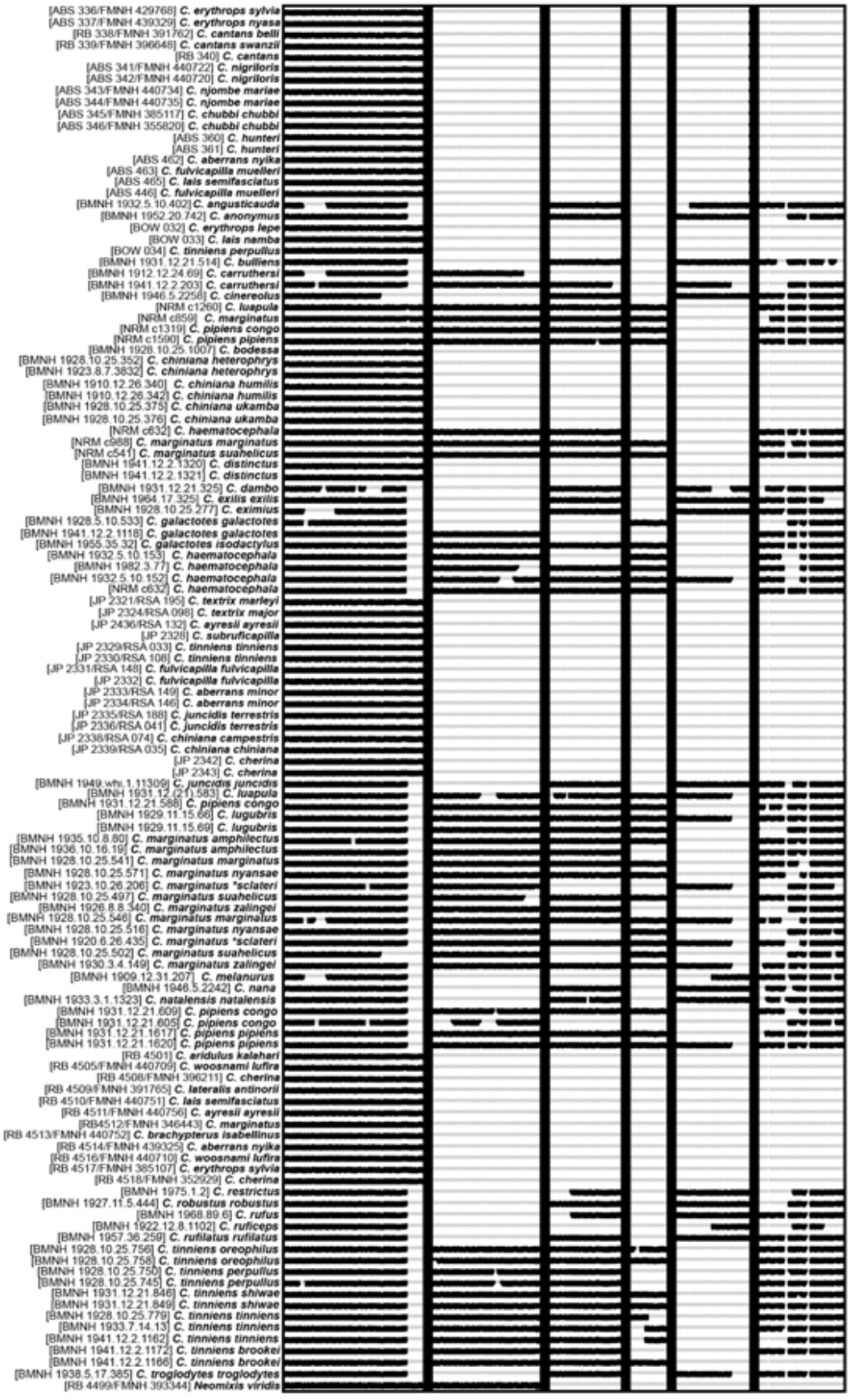


FIGURE 3.2: Distribution of sequence data obtained for each sample. The first column represents the ND2 region, the second column is for CYTB, FIB5, G3PDH, MYO and the last column is TGF-β2. Gaps represent missing data.

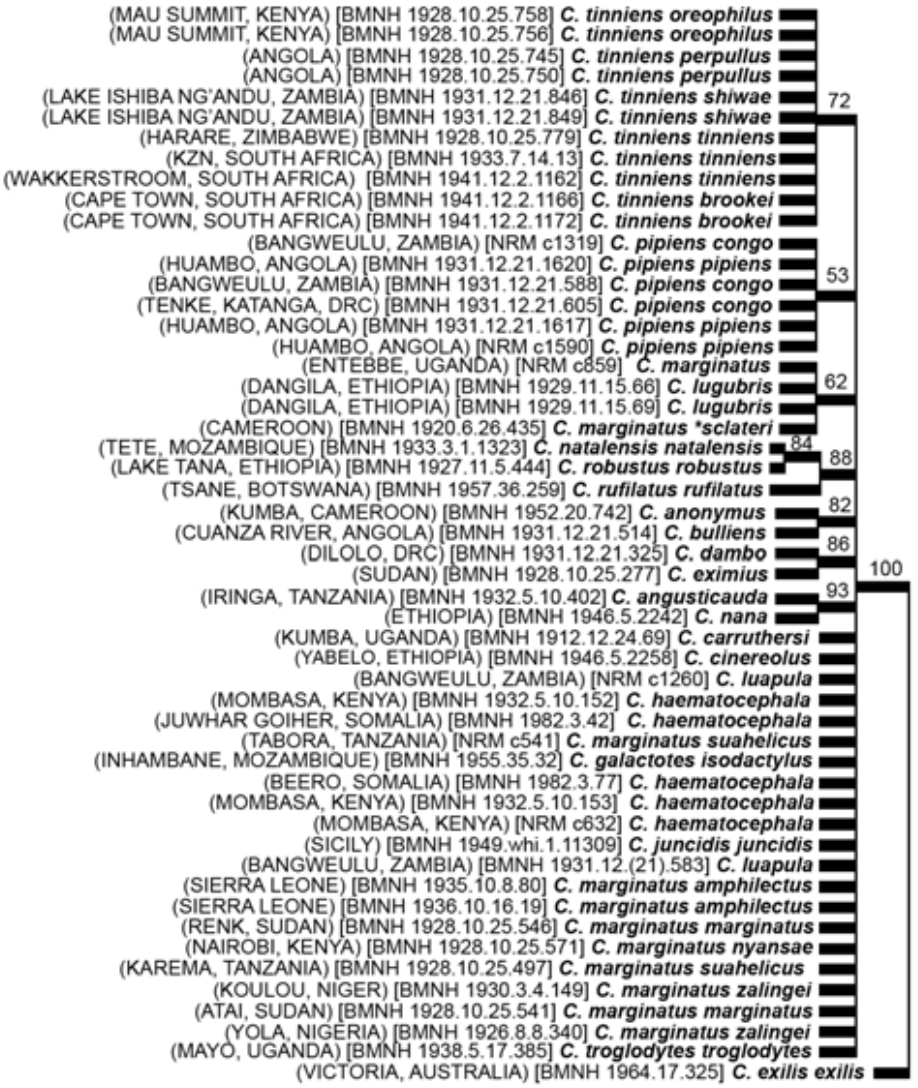


FIGURE 3.3: Results from a parsimony analysis of the β-fibrinogen gene, intron 5 (FIB5) nuclear region run in TNT (Goloboff et al., 2003, 10 000 replicates), showing Jack-knife values obtained from resampling (1 000 replicates, CI = 0.955, RI = 0.951).

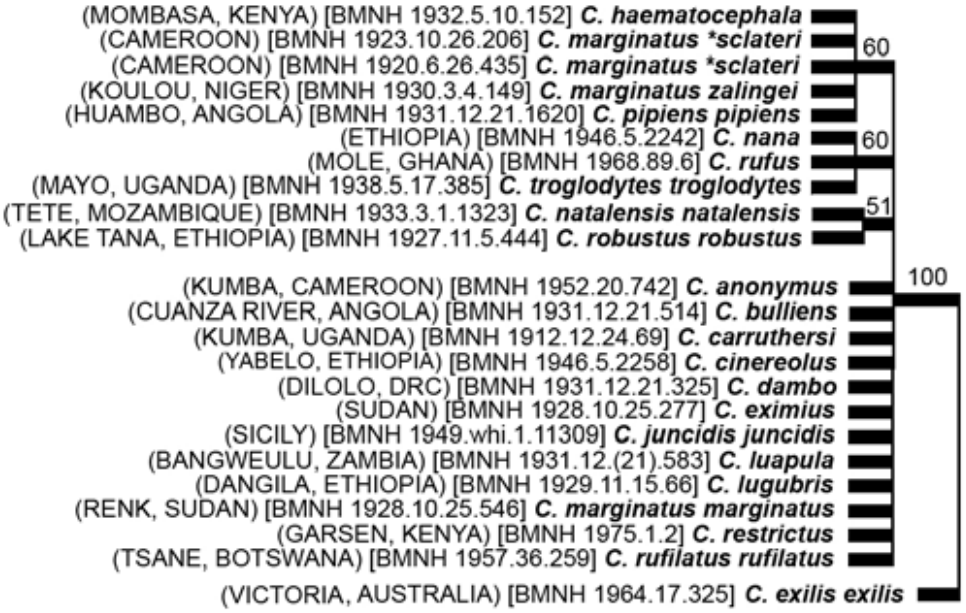


FIGURE 3.4: Results from a parsimony analysis of the myoglobin intron II (MYO) nuclear region run in TNT (Goloboff et al., 2003, 10 000 replicates), showing Jack-knife values obtained from resampling (1 000 replicates, CI = 0.956, RI = 0.916).

FIGURE 3.5: Results from a parsimony analysis of the glyceraldehyde-3-phosphodehydrogenase intron 11 (G3PDH) nuclear region run in TNT (Goloboff et al., 2003, 10 000 replicates), showing Jack-knife values obtained from resampling (1000 replicates, CI = 1.00, RI = 1.00).

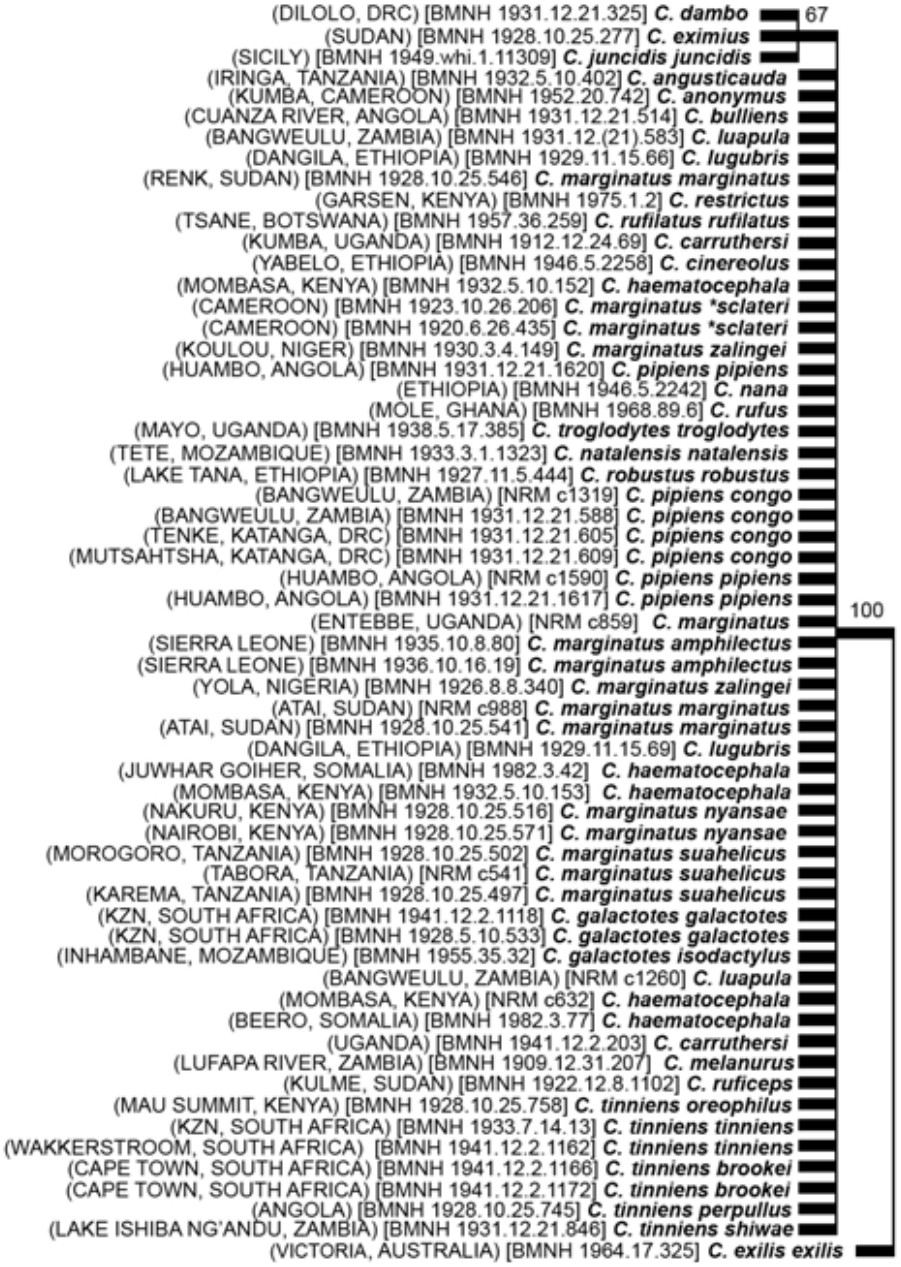


FIGURE 3.6: Results from a parsimony analysis of the transforming growth factor beta 2 (TGF-β2) nuclear region run in TNT (Goloboff et al., 2003, 10 000 replicates), showing Jack-knife values obtained from resampling (1 000 replicates, CI = 0.937, RI = 0.875).

FIGURE 3.7: Results from a parsimony analysis of the combined nuclear data obtained from TNT (Goloboff et al., 2003, 10 000 replicates), showing Jack-knife values obtained from resampling (1 000 replicates, CI = 0.733, 0.798).

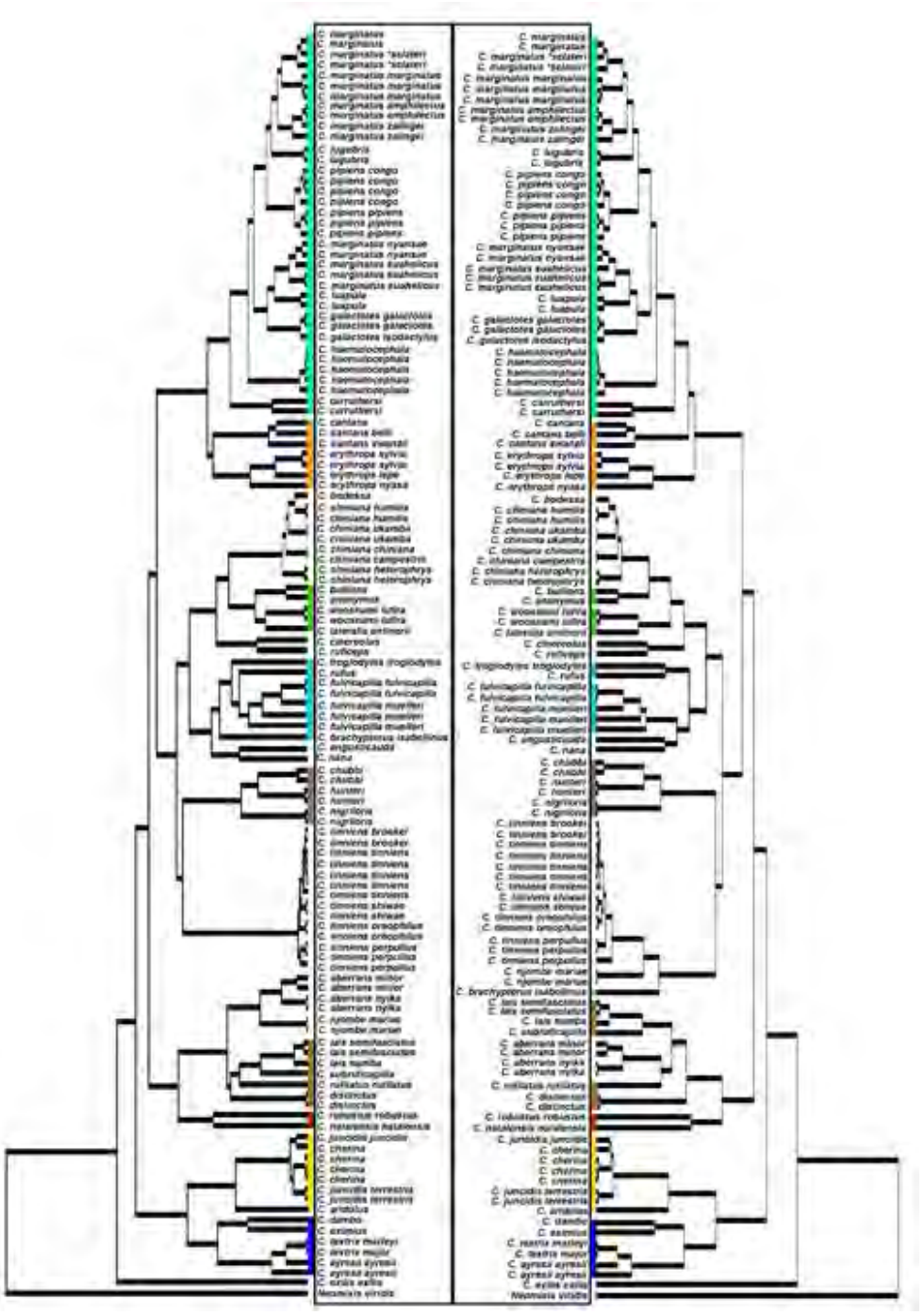


FIGURE 3.8: Topological comparison between trees in which the monophyly of Lynes' groupings were forced (left) and unconstrained (right). Topological tests indicated that the unconstrained tree was a significantly better fit to the ND2 dataset (constrained: TL = 2618, -ln L = 13240.32; unconstrained: TL = 2506, -ln L = 12999.36, diff. -ln L = 240.96, KH test $p < 0.001$, SH test $p < 0.001$). Coloured bars indicate the position of Lynes' groups.

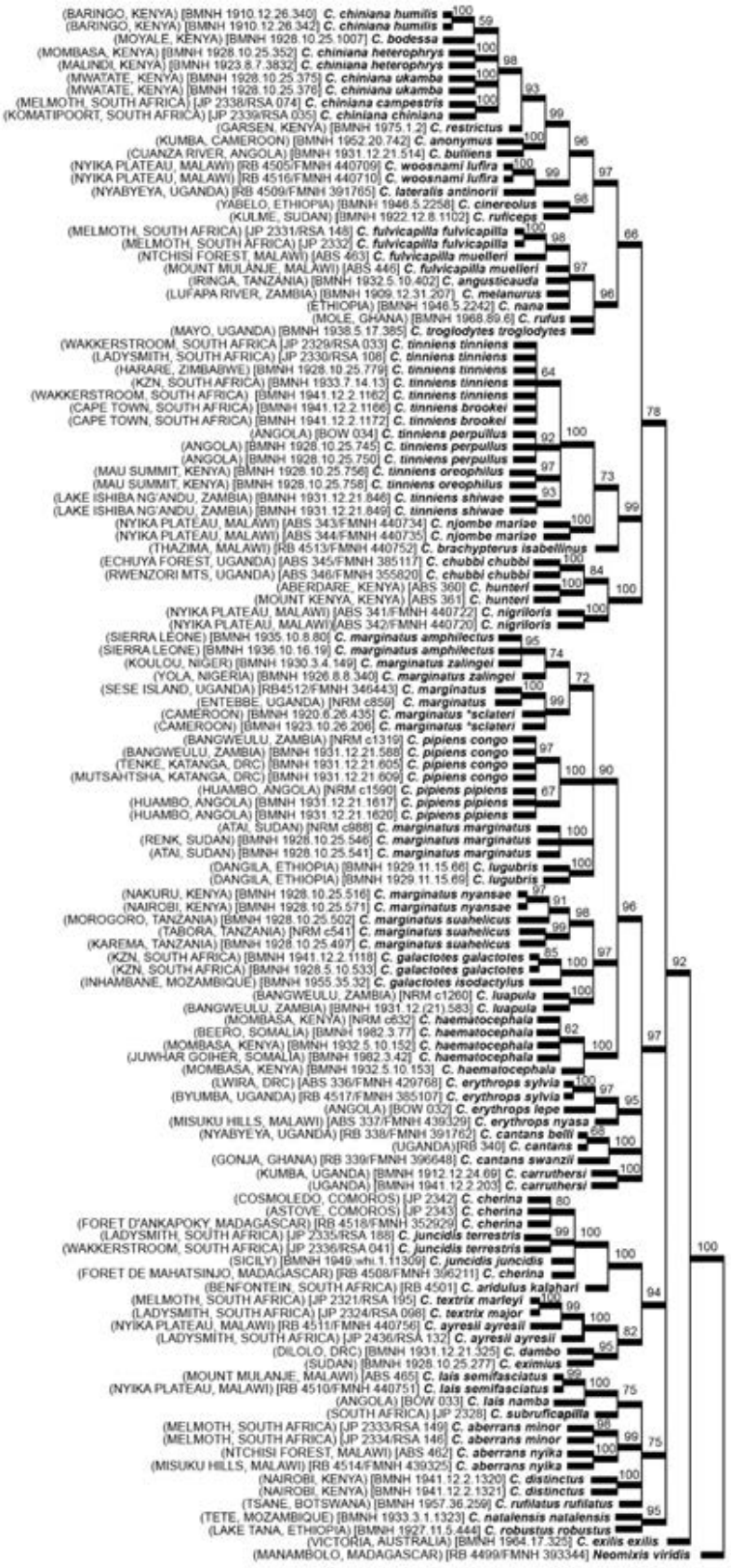


FIGURE 3.9: Results from a parsimony analysis of the NADH dehydrogenase subunit 2 (ND2) mitochondrial region run in TNT (Goloboff et al., 2003, 10 000 replicates), showing Jack-knife values obtained from resampling (1 000 replicates, CI = 0.286, RI = 0.793).

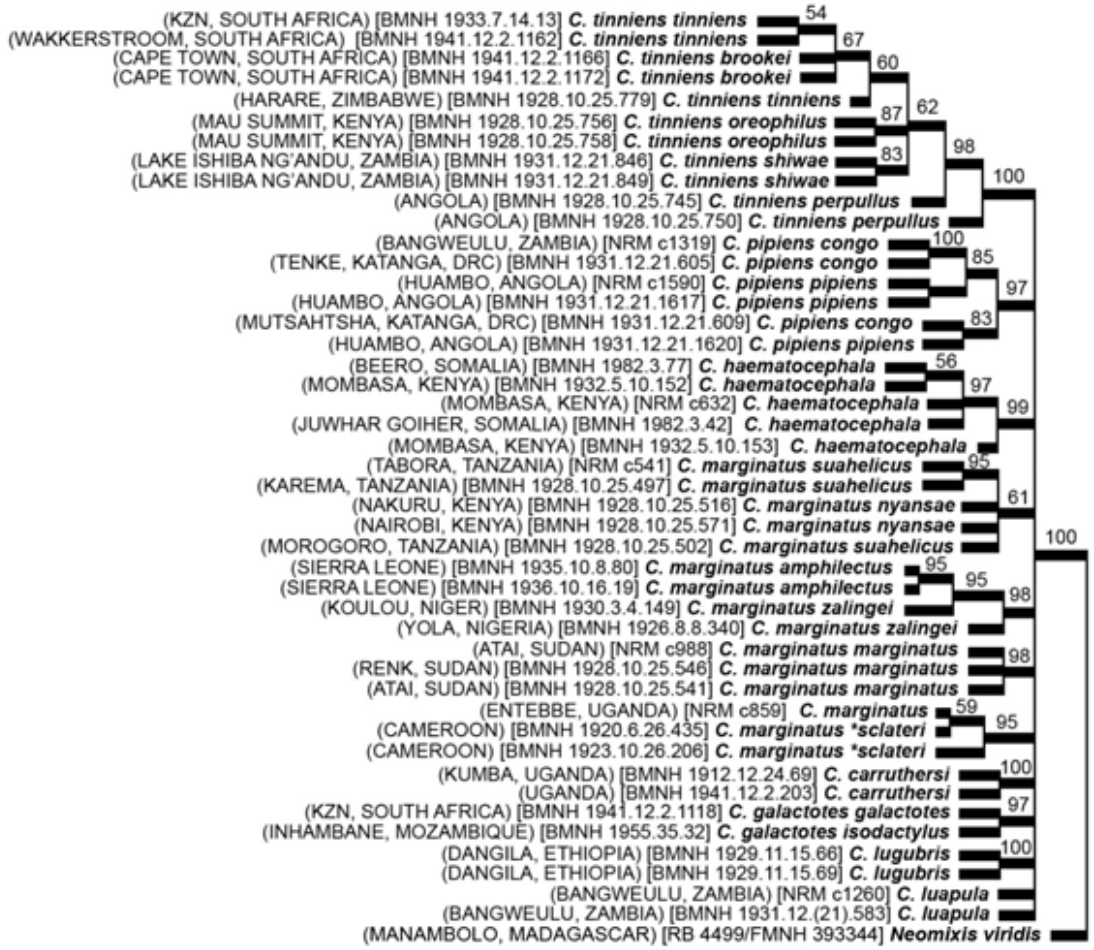


FIGURE 3.10: Results from a parsimony analysis of the cytochrome B (CYTB) mitochondrial region run in TNT (Goloboff et al., 2003, 10 000 replicates), showing Jackknife values obtained from resampling (1 000 replicates, CI = 0.588, RI = 0.869).

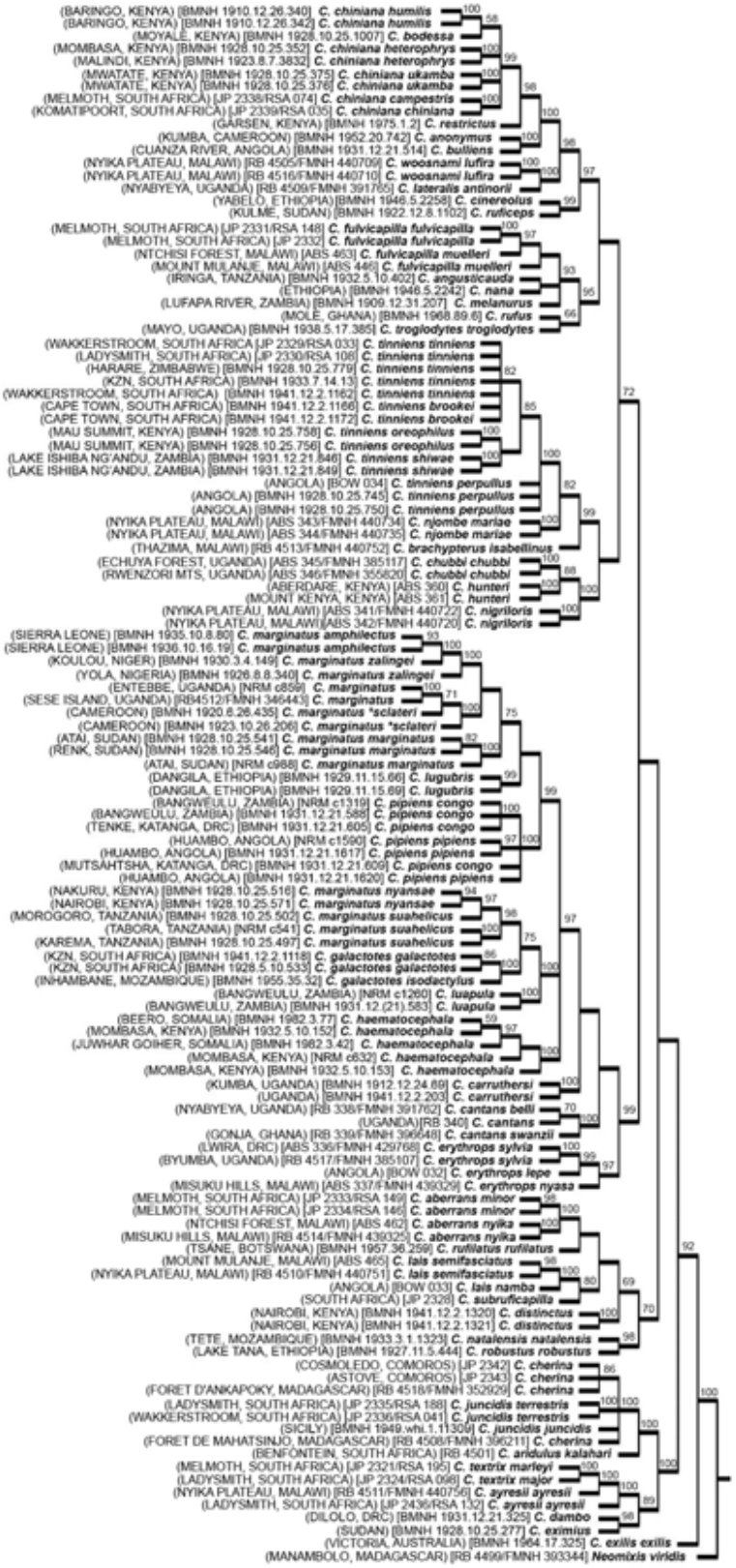


FIGURE 3.11: Results from a parsimony analysis of the concatenated dataset including all mitochondrial and nuclear regions run in TNT (Goloboff et al., 2003, 10 000 replicates), showing Jack-knife values obtained from resampling (1 000 replicates, CI = 0.286, RI = 0.793).

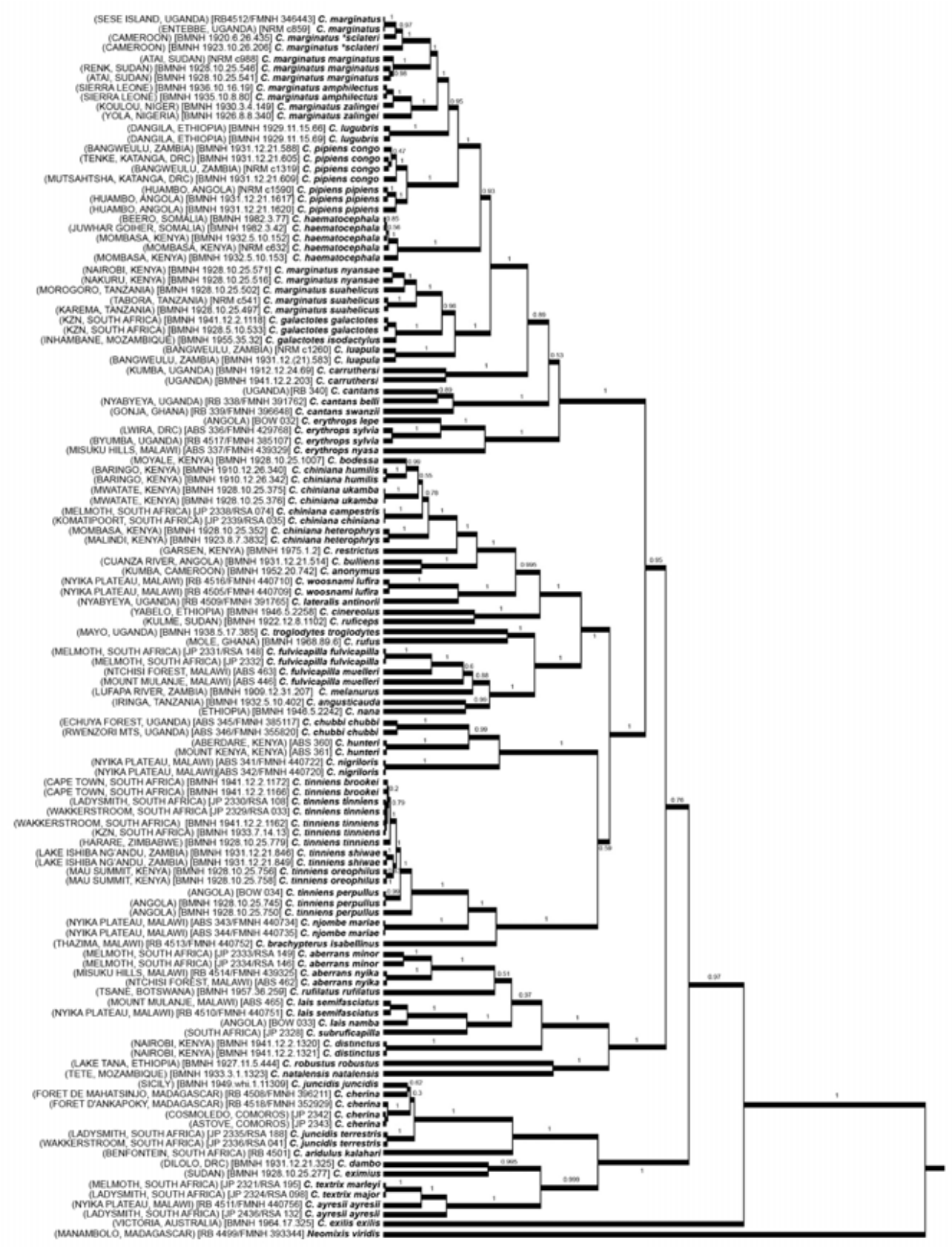


FIGURE 3.12: Results and posterior probabilities from a Bayesian analysis using the concatenated dataset including different models for each gene region (GTR+I+Γ for ND2, CYTB and TGF-β2, HKY for FIB5, F81 for G3PDH, and HKY+I for MYO determined by MODELTEST 2.3) and run for 150 million generations.

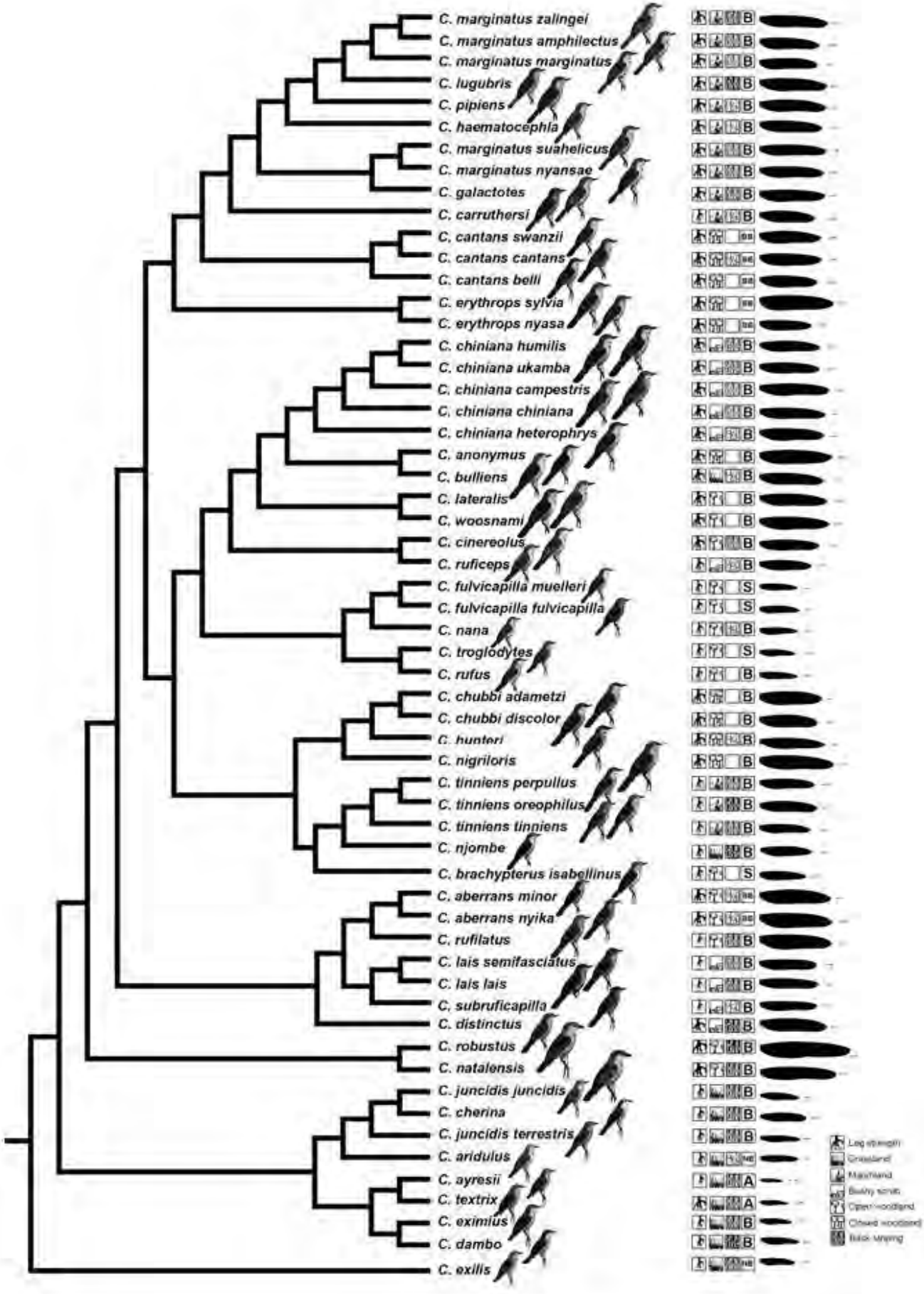


FIGURE 3.13: Morphological characters and habitat preference plotted on an MP tree of total combined morphological, behavioural and molecular datasets. A - acute, B - blade, NB - narrow blade, BB - broad blade, S - scimitar shaped primary feather.

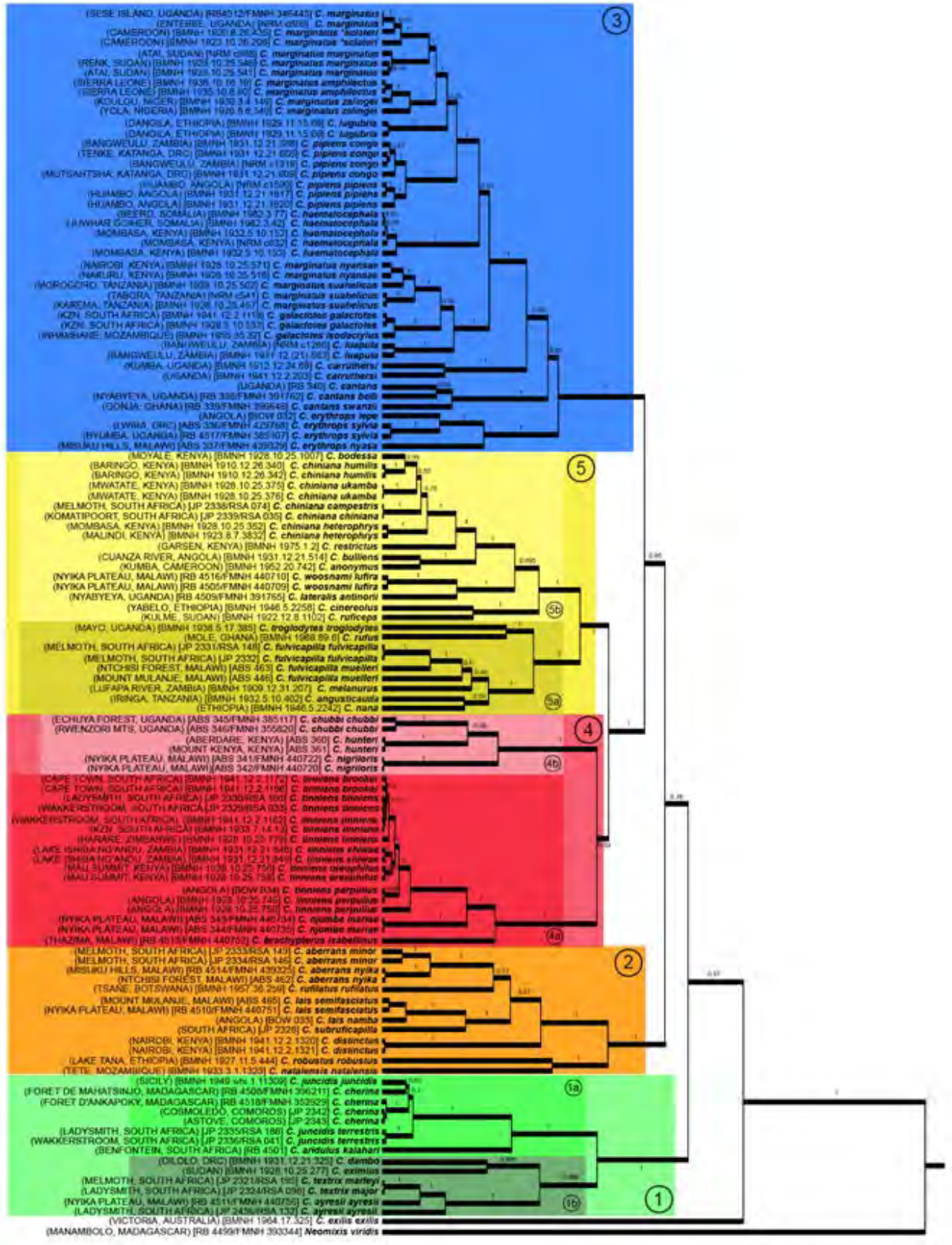


FIGURE 3.14: Coloured clades superimposed on the tree obtained from a Bayesian analysis using the concatenated dataset including different models for each gene region (GTR+I+Γ for ND2, CYTB and TGF-β2, HKY for FIB5, F81 for G3PDH, and HKY+I for MYO determined by MODELTEST 2.3) and run for 150 million generations.

Chapter 4

Habitat, size and evolution as predictors of song characteristics in cisticolas

4.1 Introduction

The evolution of bird song differs to that of morphological characters in its complexity. In oscine passerines, songs are learned (Catchpole and Slater, 1995; Kroodsma, 1982, 2004; Slabbekoorn and Smith, 2002; Slater, 1989) and learning errors or cultural drift might allow for greater variation (Payne, 1996). There may also be a sexually selected advantage to generate variation to advertise individual fitness (Slabbekoorn and Smith, 2002) and a requirement to differentiate between closely related species (Becker, 1982; Seddon, 2005), but the level of this diversification is also constrained by the need to maintain species identity and recognition by conspecifics (Price, 2008).

As songs are used for species recognition and the attraction of mates, the advertisement of fitness and the establishment and defence of breeding territories, it should follow that songs that most effectively communicate these functions are favoured. The efficacy of communication, though, is influenced by the physical properties of the environment through the acoustic effects of spherical-spreading, frequency attenuation, irregular amplitude fluctuations and reverberations off surfaces constraining the transmission of signals (Wiley, 1991; Wiley and Richards, 1982). The acoustic properties of songs may be strongly influenced by habitats, with low frequencies being favoured overall by attenuating less over distance in any habitat, and especially favoured in more cluttered habitats as high frequencies are scattered more easily by foliage (Morton, 1975; Wiley,

1991). The length of notes is thought to be constrained by the amount of reverberation in a habitat (Tubaro and Segura, 1995), therefore birds that live in more closed habitats with many scattering surfaces such as leaves and branches should avoid high frequencies to reduce attenuation, avoid broadband and frequency modulated songs and keep their notes short to avoid reverberation (Badyaev and Leaf, 1997) (i.e. low frequency, short whistles), whereas birds in more open habitats, with fewer frequency constraints, should use more broadband or modulated songs to avoid degradation through amplitude fluctuation (Morton, 1975; Wiley and Richards, 1982) (i.e. trills). The acoustic properties of songs may be further constrained by body size, with smaller birds being unable to produce the lowest frequency sounds (Ryan and Brenowitz, 1985) and confounded by phylogenetic relatedness, making inter-habitat variation difficult to appreciate as there may be an unequal distribution of either different sized birds (Ryan and Brenowitz, 1985) or closely related taxa amongst the various habitat types (Wiley, 1991).

This study aims to examine the effects that phylogeny, habitat preference and body size have on the acoustic properties of the songs given by cisticolas. Now that a phylogeny is available, cisticolas are well suited to this kind of investigation as they exhibit very similar plumage and morphology but a high degree of song variation. The genus is also highly speciose, with members varying greatly in size (5–30 grams), and occupying a variety of different habitats. This study tests the hypotheses that song frequencies correlate negatively with body mass and that lower frequency, less frequency modulated, narrow band calls are favoured in habitats with more clutter.

4.2 Methods

Taxon sampling and recordings

Songs were obtained from a variety of sources including online libraries (AVoCet, British Library of Wildlife Sounds, Macaulay, Xeno-canto), private collections (Mike Mills) and personal recordings. In total, a collection of recordings was amassed totalling 11 hours, 32 minutes and 39 seconds and represented 37 species (for species list and length of recording for each taxon see Figure 4.1). As many of these recordings were not made by the authors, songs that could not be identified and unrecognised ambiguous call types were excluded from analyses. Personal recordings were made using a RODE NTG-2 directional shotgun microphone in a wind exclusion blimp connected to a Marantz PMD-660 solid state recorder at a sampling rate of 44100 Hz.

Data and analysis

Differentiation between calls (alarm, contact) and display/territorial songs was based on their description in Ryan (2006) and, while both element types were sampled (Figure 4.1), only data obtained from songs were included in these analyses (Figure 4.2). Songs were visualised with Sonic Visualiser version 1.8 (`www.sonicvisualiser.org`) and measurements were made from Hanning spectrograms with a Fourier transformation window of 1024 samples. Measurements were made for the element duration (DUR), the minimum frequency (FMIN), the maximum frequency (FMAX), the bandwidth or frequency range (FRNG) and the fundamental frequency or frequency of maximum power (MAXPWR), which was measured after visualising the waveform and the corresponding spectrum distribution at the peaks on the waveform (Figure 4.3). A maximum of 10 of each of the elements were measured if they were present in the recording and averaged, recording their standard deviation (Supplementary Data). In cases where only a single incidence of an element type was present, that was still measured and included in these analyses. Measurements were differentiated between subspecies based on their recording location but these were lumped together by species, except for *C. marginatus* which was not recovered as monophyletic in the phylogeny (Chapter 3). Habitats were ordered by the density of reflective surfaces or structural clutter, and divided into five groups: grassland, scrubland, open woodland, woodland and marshland (Wiley, 1991); habitat preferences were assigned following Lynes (1930) and Ryan (2006). Species that occupy a variety of habitats were assigned to whichever habitat they occurred in with the most clutter, i.e. if a species occurs in open, scattered woodland and more closed woodland, then it would be assigned to the latter. Wing length was used as a proxy for size; while this may not work well outside the genus, Lynes (1930) notes that it is a good index of comparative size within cisticolas (ch. III p. 30).

Phylogenetic independent contrasts were calculated using the 'ape' package (Paradis et al., 2004) implemented in R (R-Core-Team, 2013) using a phylogeny generated from a Bayesian analysis using a combined nuclear and mitochondrial dataset in BEAST version 1.7.5 (Drummond et al., 2012) run for 150 million generations, sampling every 15 000 generations. Multiple regressions of contrasts were calculated through the origin (Felsenstein, 1985). Principal component analyses were performed using the 'FactoMineR' package (Husson et al., 2013), while ANOVA/ANCOVA and linear regressions were performed using the 'Rcmdr' package (Fox, 2005) implemented in R. Measurements were log-transformed for analyses.

4.3 Results

Mean FMIN showed a general decreasing trend as habitat clutter increased (Figure 4.4a) with the highest frequency in the grassland (2544 Hz) and the lowest average minimum frequency in the marsh (1976 Hz). Mean FMAX showed the same trend (Figure 4.5a), with the mean maximum frequency in grassland (6358 Hz) and scrubland (6603 Hz) being higher than the frequencies in scattered woodland (5790 Hz), woodland (5841 Hz) and marshland (5921 Hz). Mean FRNG (Figure 4.6a) was highest in scrubland (4283 Hz) and marshland (3944 Hz) with species often employing broadband trills in these environments. Frequency of maximum power decreases with increasing habitat clutter (Figure 4.7a), with the highest FMIN values occurring in grassland (4798 Hz) and scrubland (4745 Hz) and the lowest occurring in scattered woodland (4029 Hz), woodland (4137 Hz) and marshland (4117 Hz). Mean element duration, DUR, shows an increasing trend with the increase in habitat clutter (Figure 4.8a), with notes given in grassland shorter (0.18 s) than those in scrubland (0.25 s), scattered woodland (0.29 s), woodland (0.30 s) and marshland (0.29 s). When these measurements are plotted with their variance, these trends become less appreciable (Figures 4.4b, 4.5b, 4.6b, 4.7b and 4.8b) with an ANOVA (Table 4.1) showing that FMIN was significantly different between grassland and marshes ($p = 0.003$), and FMAX was significantly different between scrubland and open- ($p = 0.004$) and closed woodland ($p = 0.002$). The ANOVA also shows that MAXPWR differed significantly between the two least cluttered habitats and the remaining habitats (Table 4.1) and that DUR was significantly different between grassland and scrubland. An ANCOVA revealed that FMIN and DUR were significantly correlated with both habitat and wing length but there were no interaction effects (Table 4.2). In the regressions of phylogenetic independent contrasts through the origin, these relationships all but disappeared with no statistically significant differences in the acoustic properties of songs between habitats (Figures 4.4c, 4.5c, 4.6c, 4.7c, and 4.8c). The linear regression of FMIN showed a significant ($p = 0.004$) negative correlation ($R2 = 0.2486$) with wing length (Figure 4.4d), and a positive correlation ($p = 0.008$, $R2 = 0.1505$) of DUR (Figure 4.8d), but, in the regressions of phylogenetic independent contrasts, these correlations again disappeared (Figures 4.4e and 4.8e). In a principal component analysis on these variables, the first two principal components accounted for 74.74% of the total variation with habitat separating mostly due to MAXPWR and FMIN (Figure 4.9) and phylogenetic clades separating mostly by FMIN and FRNG (Figures 4.10 and 4.11). Principal component analyses of species within clades revealed a large amount of overlap in acoustic variables (Figure 4.12). If songs that contain trill-type elements evolved early in the diversification of the genus, evolution away from this song type would have had to have occurred in at least four separate occasions (Figure 4.13).

4.4 Discussion

Perhaps the most surprising result was that the overall variation in songs seemed phylogenetically conserved across the genus; the similarity in song characteristics between closely related species was contrary to the authors expectation and may highlight the importance of unique ordering of elements, timing and context of delivery and differential mating displays between species within clades.

For example the two sister species, *C. ayresii* and *C. textrix*, both inhabit short grasslands and the two species are sympatric in northern South Africa and Lesotho, where they often breed alongside one another. While they share similar tonal songs, their delivery differs in that *C. ayresii* introduces its song with a few elements of the same tone before a volley of broad-band ticks, while *C. textrix* introduces its song with elements of different tones before the onset of broad-band ticks often given at a quicker tempo than those of *C. ayresii* (Figure 4.2). These subtle differences may work in concert with differing display flights in order to advertise species identity as *C. ayresii* incorporates wing-snapping into its displays, a behaviour that has not been observed in *C. textrix* (Lynes, 1930).

Another closely related member of the textrix group, *C. eximius*, exhibits wing-snapping in its displays and is sympatric with *C. ayresii* in parts of Uganda and Kenya, but the song of *C. eximius* is more bell-like and the flight display differs between the two species as *C. ayresii* wing-snaps during a steep descent before landing in the grass; *C. eximius* in contrast dives with its wings closed and pulls out of the dive once or twice, raising a few meters before terminating the display by dropping into the grass (Ryan, 2006). The two species also seem to occupy slightly different habitats with *C. eximius* preferring less well drained habitats than *C. ayresii*, potentially reducing the incidence of direct contact between the two species.

C. juncidis and *C. cherina* have mostly identical calls but are not sympatric. *C. aridulus* is sympatric with *C. juncidis* throughout much of its range and, while they share some song elements such as broad-band ticks, their display differs; *C. aridulus* incorporates wing-snaps into a erratic display flight, while during regular flight display *C. juncidis* exhibits a more level cruising flight and seldom incorporates snapping unless alarmed (Ryan, 2006). These differences in song structure and display may enable the two species to breed alongside one another in the same habitat but maintain species boundaries.

C. robustus and *C. natalensis* are often separated by altitude, but breed alongside each other in parts of their range (such as Angola and Equatorial East Africa). The two species share common element types but differential ordering of shared song elements and addition of novel elements may allow for the sympatry of these sister species, particularly

if combined with different display strategies as *C. natalensis* has been recorded to more readily take to the air during displaying than *C. robustus* (Ryan, 2006).

C. subruficapilla and *C. lais* share many vocal similarities, both in the elements that they utilise and in their trill-like song (Figure 4.2). While similar in overall song structure, the two can be distinguished in the field by their songs as *C. lais* has a faster delivery of the trill-type element (Ryan, 2006). Their behaviour also differs, with *C. lais* exhibiting tail-flicking more often than *C. subruficapilla*. The ranges of the two overlap along the south-east coast of South Africa, but at the local level the two occupy different habitats; *C. lais* prefers more grassy slopes with scattered bushes while *C. subruficapilla* prefers scrubland with bare ground between grassy tufts.

Variation in habitat preference also exists between *C. aberrans* and *C. rufilatus* with the former found predominantly on steep rocky slopes with proximal woodland, or rocky outcrops in *Brachystegia* woodland and the latter preferring the edge matrix of woodland and savanna grassland with scattered trees and bushes (Ryan, 2006). The ranges of *C. erythrops* and *C. cantans* overlap quite significantly and both share similar calls but the latter prefers somewhat drier habitat at higher elevations than *C. erythrops*. *C. pipiens* is sympatric with *C. luapula* and shares the extended trill-type song common to the marsh cisticolas, but *C. luapula* often delivers a longer version than *C. pipiens*, with the latter occupying a somewhat different habitat niche, favouring taller vegetation in wetter areas than *C. luapula* (Ryan, 2006). Similarly *C. carruthersi* overlaps with *C. marginatus*, but the two species are largely separated by habitat preference where they occur in sympatry, with *C. carruthersi* preferring tall *Papyrus* and *C. marginatus* remaining on the edges of the *papyrus* beds.

The calls of *C. woosnami* and *C. lateralis* are quite different, with *C. woosnami* delivering an extended trill increasing in intensity, whereas the trill of *C. lateralis* consists of slightly different elements (Figure 4.2). These two species also prefer slightly different habitats with *C. woosnami* preferring somewhat wetter areas than *C. lateralis* in areas where they overlap (Ryan, 2006). The dry savanna dwelling *C. bulliens* shares similar songs to *C. anonymus*, but the latter prefers grassy clearings in forests and plantations (Ryan, 2006). *C. bodessa* and *C. chiniana* share similar calls and, while *C. bodessa* is thought to prefer wetter habitats and more sloping ground to those areas preferred by *C. chiniana*, there are areas such as Nichisar National Park in Ethiopia where they occupy similar habitats (Ryan, 2006). As the samples included in this study were not well differentiated genetically, more work on *C. bodessa* would be required to better understand the specific differences between the two species as genetic relationships might be confuscated by hybridisation.

C. chubbi and *C. hunteri* are largely parapatric but *C. chubbi* generally display in more open areas (Lynes, 1930). These two duetting species might allow for maintenance of species boundaries through visual cues and slight differences in plumage between the species or accuracy and timing of the duet. *C. angusticauda* and *C. fulvicapilla* differ slightly in habitat preference in areas of overlap, with the former preferring tall *Brachystegia* woodland and the latter preferring scrubby woodland, but it is also thought that the songs of *C. angusticauda* differ in pitch and pace in areas of overlap with *C. fulvicapilla* (Ryan, 2006). More recordings in these areas would help determine the nature of the vocal differences between *C. angusticauda* and *C. fulvicapilla*, similarly those of *C. melanurus* in areas of overlap with *C. fulvicapilla*.

While correlations between bill morphology and vocal traits (such as frequency bandwidth) have been identified in Darwin's Finches (Podos, 2001) and Woodcreepers (Derryberry et al., 2001), there was no correlation between the song characters or bill morphology metrics (bill height, bill width, bill length or the product thereof) collected in this study. In the graphs of the mean values for FMIN, FMAX, FRNG and DUR, more open habitats had the highest FMIN (Figure 4.4a), FMAX (Figure 4.5a) and MAXPWR (Figure 4.7a), with values decreasing as you move towards habitats with more reflective surfaces, which supports the prediction that lower frequencies are favoured in these habitats (Badyaev and Leaf, 1997). Element duration, on the other hand, seemed to show an inverse relationship, with longer durations in closed habitats (Figure 4.8a). While element duration appeared to increase with increased habitat clutter in contrast to predictions, this result was mostly due to the fact that, compared to the birds in open habitats that produce a number of short broadband ticks, any narrow-band whistles would have a longer duration. By plotting these results with their variation, these patterns became less obvious (Figures 4.4b, 4.5b, 4.7b and 4.8b). The PCA plot of habitats shows grassland and scrubland separating from the other habitats mostly by having a higher FMIN, FMAX and MAXPWR, but some overlap existed amongst the groups (Figure 4.9). An ANOVA indicated that only grassland and marshland had significantly different FMIN values (Table 4.1), and DUR only differed significantly between grassland and scrubland with elements in the rest of the habitats having similar duration to each other. The fundamental frequency or frequency of maximum power (MAXPWR) was significantly lower in more closed habitats than open habitats, with elements in grassland and scrubland having significantly higher MAXPWR than open woodland, woodland and marshland (Table 4.1). But, as wing length was significantly inversely correlated with FMIN (Figure 4.4d), and to a lesser extent with MAXPWR (Figure 4.7d), and significantly correlated with DUR (Figure 4.8d), it could be argued that these results were caused by an unequal distribution of different sized birds in each

habitat (Ryan and Brenowitz, 1985) as the average wing length in grasslands was significantly lower than in other habitats (50 mm vs. 59.3 mm, t-stat = -4.5, $p < 0.001$). In addition, many of the small, open habitat species share a close evolutionary history and when phylogeny is controlled for, wing length seemed to have less influence on FMIN than habitat ($p = 0.218$ vs. $p = 0.0547$, Figures 4.4c and 4.4e). Habitat had a very slight, but not statistically significant, negative correlation with FMAX (Figure 4.5c) and MAXPWR (Figure 4.7c) after correcting for phylogeny, and the frequency of maximum power still seemed to be somewhat correlated with wing length after correcting for phylogeny, even if with a small R^2 value this correlation was not significant at the 5% level ($p = 0.062$, $R^2 = 0.0078$, Figure 4.7e). While wing length appeared to be correlated with element duration ($p = 0.008$, $R^2 = 0.15$, Figure 4.8d), which would make theoretical sense if larger birds have larger lung capacity and are able to expend more energy over a longer period, but this correlation disappeared completely after accounting for phylogeny ($p = 0.941$, $R^2 = 0.0001$, Figure 4.8e).

For an example of the influence of habitat vs. size on song acoustics; one of the smallest species, *C. fulvicapilla*, is found in a variety of habitats including the understory of woodland and thickets and produces relatively low frequency, narrow band whistles (Figure 4.2), indicating that it is possible for small cisticolas to produce the kinds of songs that are predicted to work well in cluttered habitats. Interestingly, the frequency of the songs of this species seems to be variable across its range and a recording from Wilderness outside George in South Africa showed birds calling at around 5 kHz, and a recording from another coastal city, Port Elizabeth just 300 km away, had a lower frequency, perhaps to avoid masking by a strong band of insect noise also present in the recording at 5 kHz (Supplementary Data). Such an influence on song by insects has been noted for another small warbler, the Green Hylia (*Hylia prasina*); see Kirschel et al. (2009).

While clades separate along principal component axes, these are influenced by the size distributions and habitat preferences of the member species within each clade (Figure 4.10). There was a large amount of overlap in the acoustic properties of songs within clades (Figure 4.12), with species identity perhaps more commonly communicated through unique, fixed notes as described in *C. erythrops* (Benedict and Bowie, 2009) and *C. chiniana* (Benedict and Bowie, 2012), with individual variation generated through either the order of elements (*C. erythrops*) or variable end phrases given after fixed notes (*C. chiniana*). Element structure or behavioural displays rather than fundamental acoustic characteristics (i.e. character displacement) may be employed to communicate species identity.

The small species that produce broadband songs might be constrained to open habitats,

as these sounds perform poorly in closed habitats. The small grassland species such as those in the textrix and juncidis groups might have adopted behavioural adaptations, such as their high altitude displays, to overcome the reduced ability of the higher frequency songs to travel extended distances even in the absence of clutter. The song structure in the marsh cisticolas seems at odds to what would be predicted, as broadband trills and rapid modulation should be selected against, but birds in the habitat with the most vegetative clutter and the highest number of reflective surfaces (leaves of reeds) have the longest, most broadband trills (*C. marginatus/C. pipiens* etc.) or rapidly modulated warbles (*C. tinniens*) (Figure 4.2). These songs are sometimes given in flight above the reeds, potentially compensating for the attenuation problems associated with these types of calls in such closed habitat by altering their behaviour and offering their songs above the level of clutter. Alternatively, some of these species have been recorded at densities of over 30 birds per hectare (see *C. carruthersi* in Ryan (2006)) and the high abundance of individuals might mean that long distance signalling is either not required or not advantageous. More localised transmission might serve to reduce chances of the signal being intercepted by eavesdropping parasites, such as the brood parasitic Cuckoo-finch/Parasitic Weaver (*Anomalospiza imberbis*). A trade-off might exist between broadcast distance and eavesdropping potential (Borncoraglio and Saino, 2007). Trills might be found in a variety of habitats if the common ancestor of these species made trill-like songs (Figure 4.13).

The species that inhabit secondary growth in forest clearings that also have trill elements in their songs (e.g. *C. anonymus*, *C. bulliens*) might not need to transmit their calls over long distances through the cluttered forest, but potentially only to the other side of the clearing and therefore attenuation and reverberation factors might not come into play. Those species whose songs contain trill elements and inhabit dense undergrowth (e.g. *C. chubbi* and *C. hunteri*) avoid repeating elements of the same frequency in quick succession, and therefore reverberation, by having slower, narrowband and frequency modulated trills made up of a rising and falling succession of short elements in non-overlapping frequency bands. This may offer enough redundancy in the signal to counteract losses through reverberation and offer an opportunity to deliver maximum power through a wider frequency range, aiding long distance communication through intensity modulation (Richards and Wiley, 1980). The female generally gives this call and pairs probably defend territories together (Ryan, 2006). In contrast, the males' call is a long, frequency modulated whistle, which should perform poorly in cluttered environments but they may overcome habitat constraints and reverberation behaviourally by instigating close-quarter duets for courtship displays.

As many of the recordings were not made by the author, unrecognised elements or songs

may have been left out of the analyses, decreasing the chance of an accurate and comprehensive repertoire library being compiled in this study, as uncommon call types may have been discarded or not have been present in species with a low number of recordings. Once more comprehensive recordings have been collected and repertoire sizes calculated, the high variation in sexual dimorphism across the genus could potentially offer insight into the evolution of song complexity if used as a proxy for sexual selection (Mahler and Gil, 2009; Price and Lanyon, 2004), as the species in the genus with the largest degree of sexual dimorphism in size (approx. 20% in *C. chiniana*) has also been shown to have an enormous repertoire (Benedict and Bowie, 2012). Playback experiments could also reveal that all species within the genus operate within an acceptable window for transmission over the desired distances, as many species are locally abundant and the relative overall differences between the various acoustic properties of songs seems relatively slight.

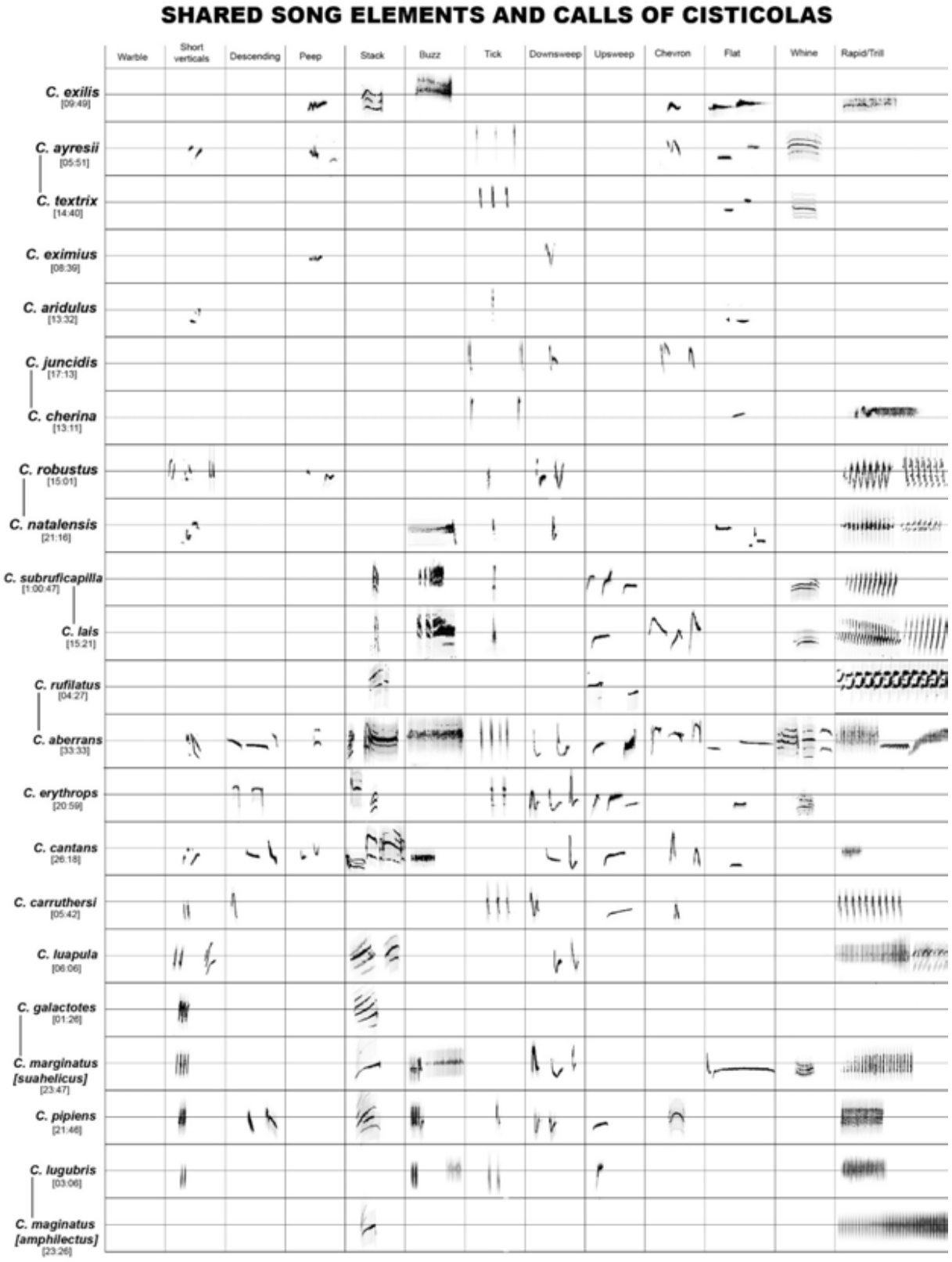
4.5 Conclusions

These analyses demonstrate that, while some acoustic characteristics seem dependent on habitat, the effects are confounded by body size and phylogenetic history, and, if phylogenies are not taken into account when doing comparative studies on bird song across species, the results can potentially be misleading if different lineages are on different evolutionary trajectories. Cisticolas potentially overcome the constraints that body size and habitat place on their songs with behavioural adaptations, such as aerial displays, giving calls above clutter or duetting. With the identification of sister species, it is hoped that more detailed recordings of songs and displays of sympatric species may reveal greater insight into how the similarity of acoustic characters within clades does not become problematic to the maintenance of species boundaries in areas where they overlap.

4.6 Figures and Tables

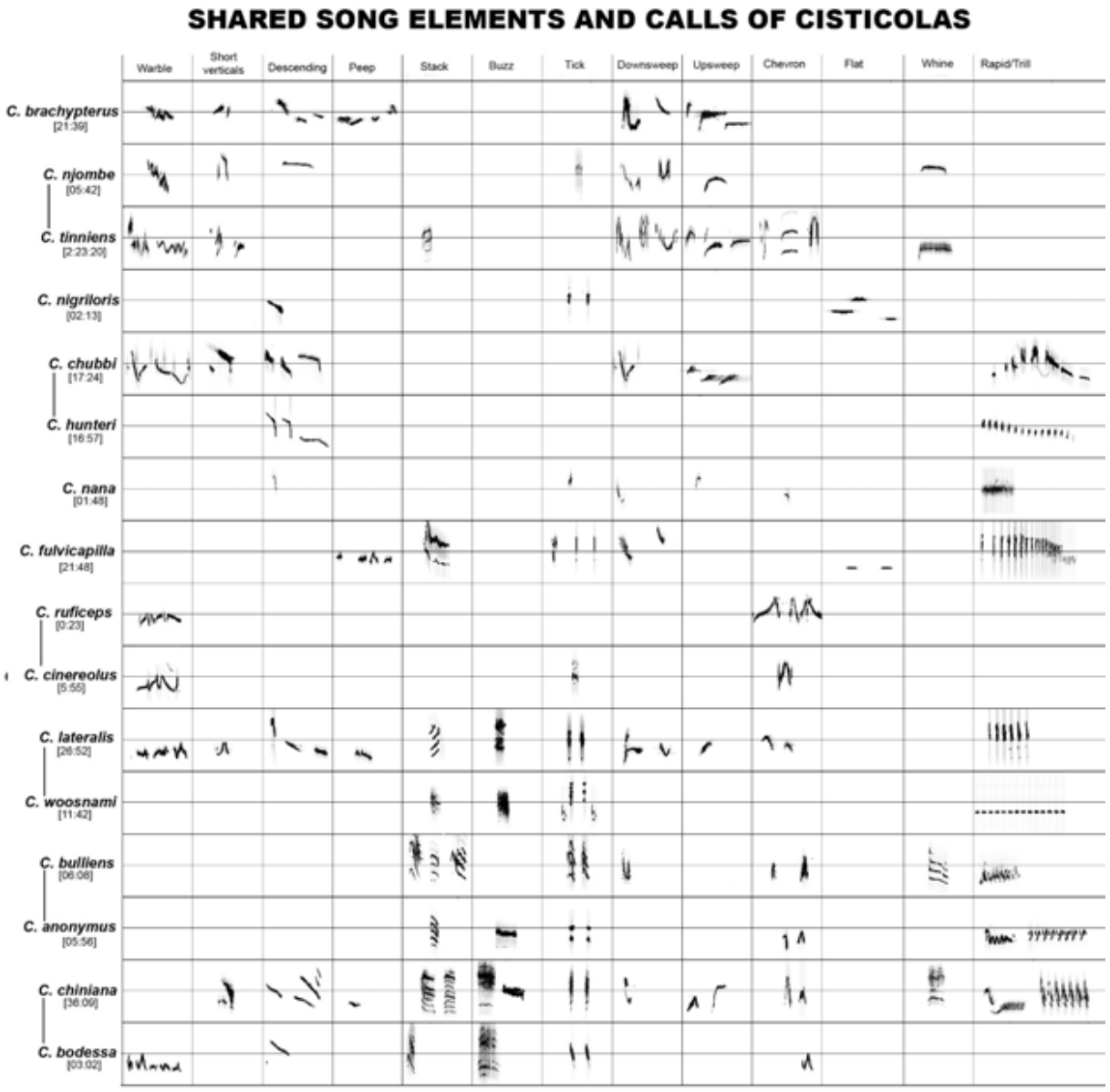
Continued on next page.

FIGURE 4.1: Common call and song elements recorded from each species broken down into general descriptive categories. Species names connected with a line indicate sister-species and numbers in square brackets represent the total recording length obtained.



(A) *figure 4.1 continued on next page*

(B) *figure 4.1 continued*



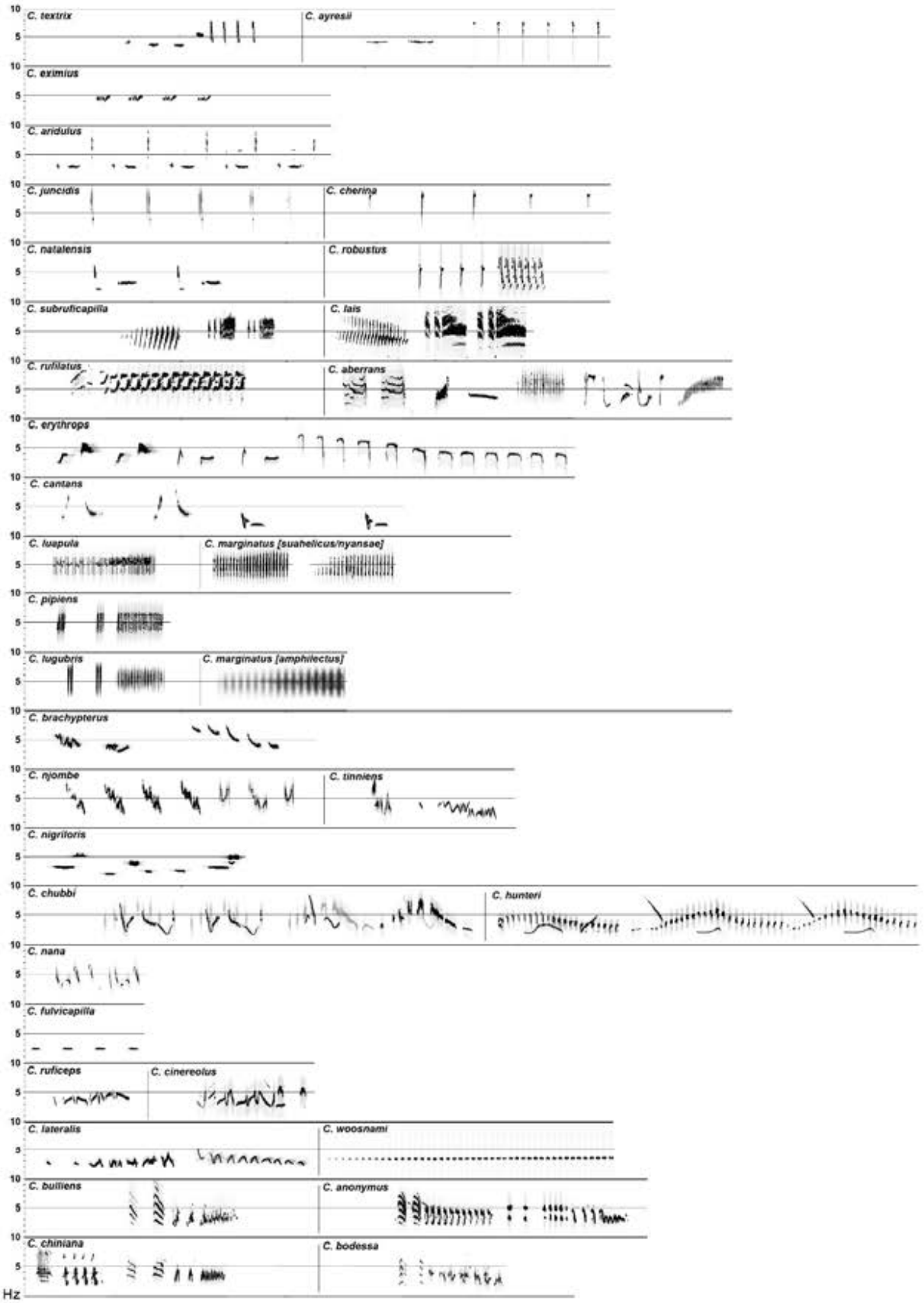


FIGURE 4.2: Common song types of cisticolas in phylogenetic order and grouped by sister-species.

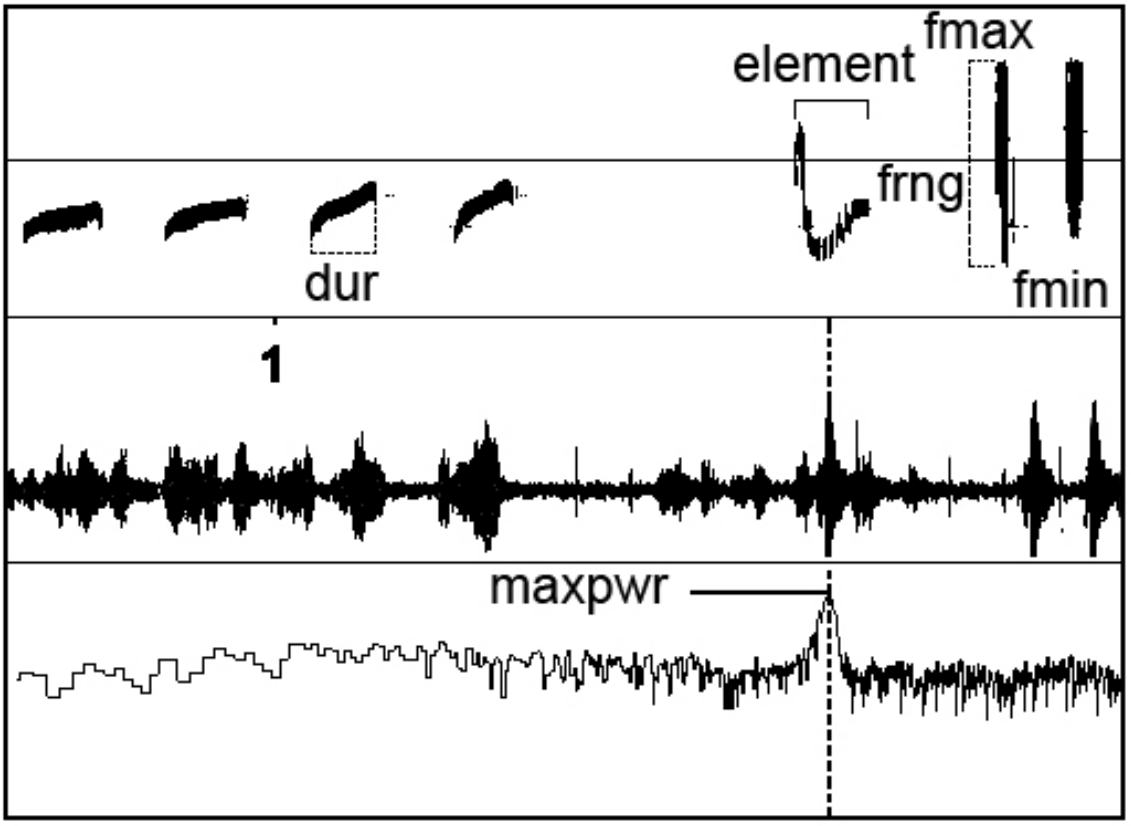
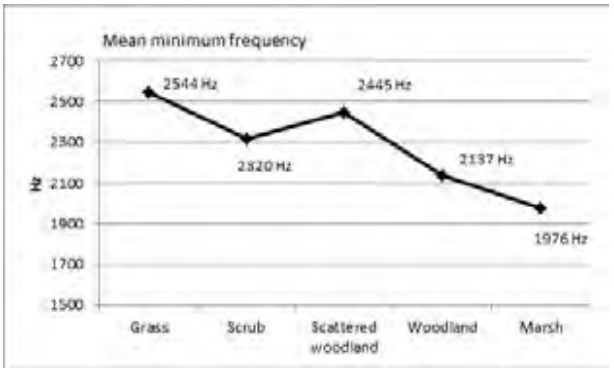
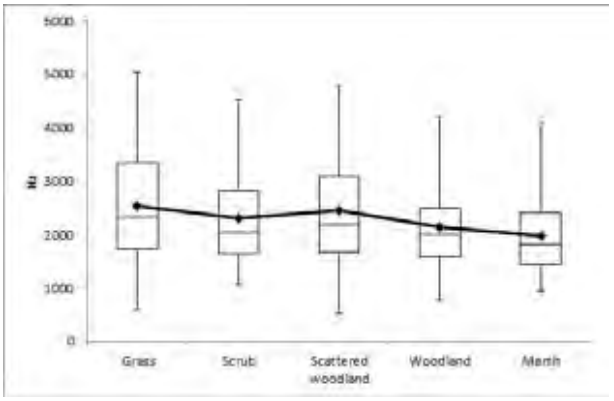


FIGURE 4.3: Measurements taken from sonograms and spectrograms including element duration (DUR), minimum frequency (FMIN), maximum frequency (FMAX), frequency range (FRNG) and frequency of maximum power (MAXPWR) which were measured after visualising power spectrogram and the distribution of frequencies.

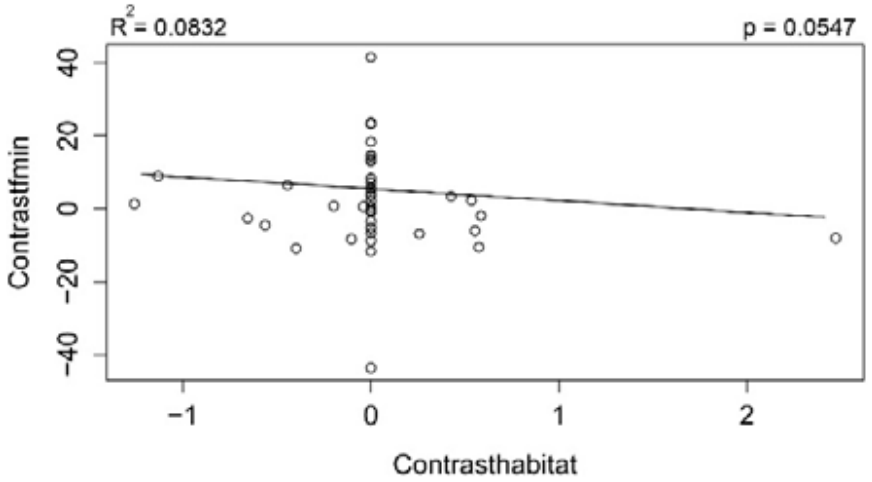
FIGURE 4.4: Minimum frequency graphs.



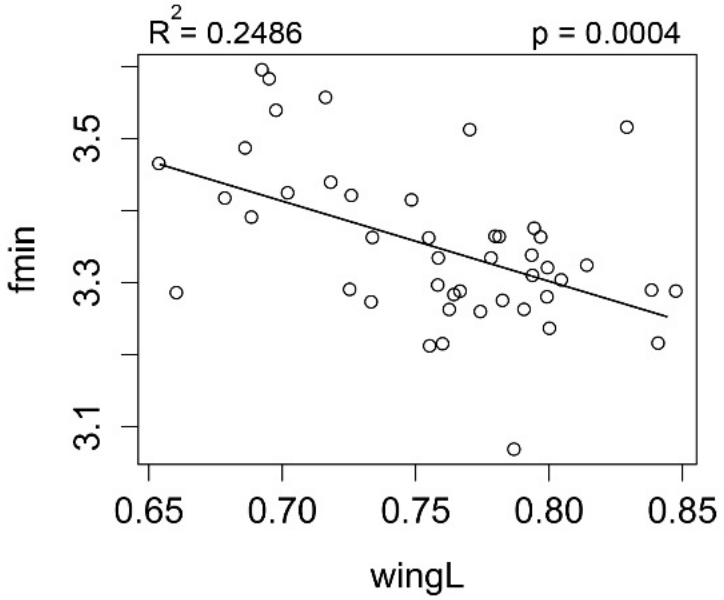
(A) Mean minimum frequency per habitat type.



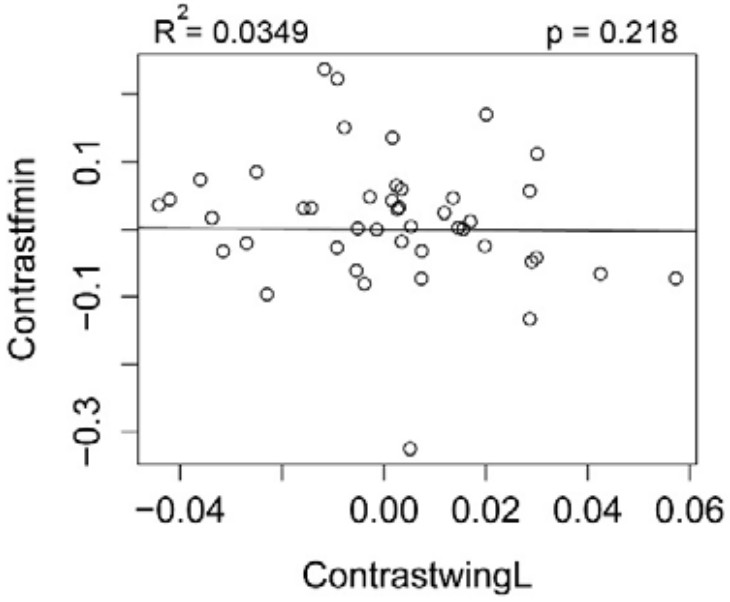
(B) Box-and-whisker plot of minimum frequency per habitat showing variation.



(C) Phylogenetic independent contrasts of minimum frequency plotted through the origin against habitat type. *Figure continued on next page*

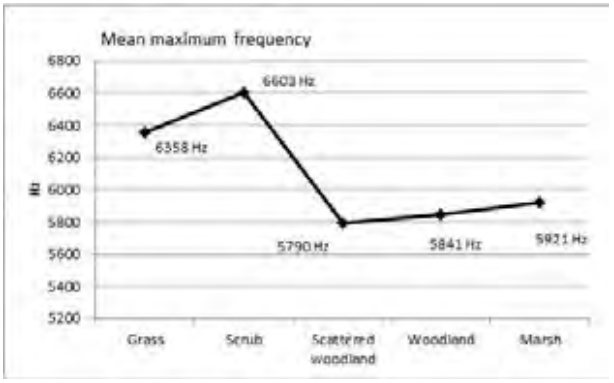


(D) Linear regression of minimum frequency plotted against wing length.

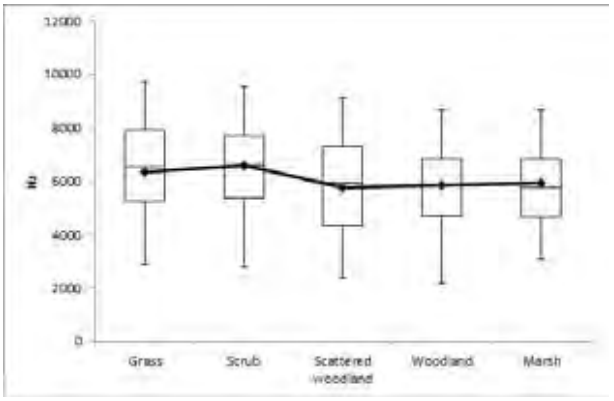


(E) Phylogenetic independent contrasts of minimum frequency plotted through the origin against wing length.

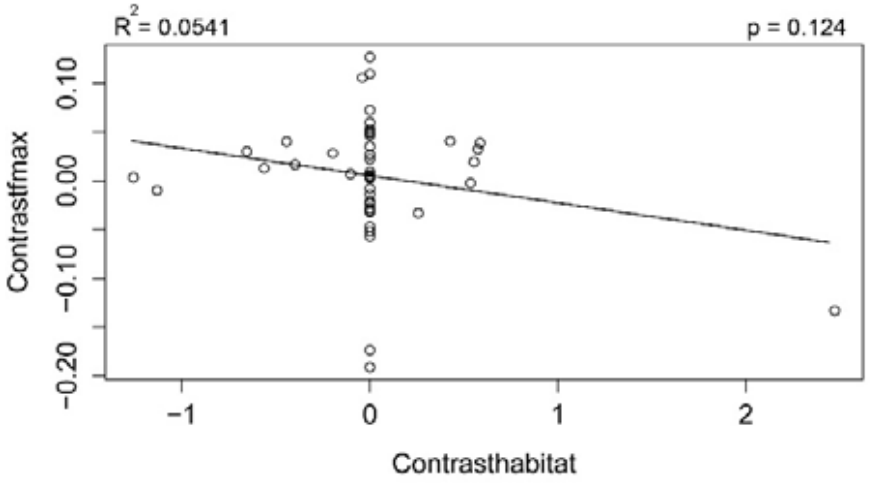
FIGURE 4.5: Maximum frequency graphs.



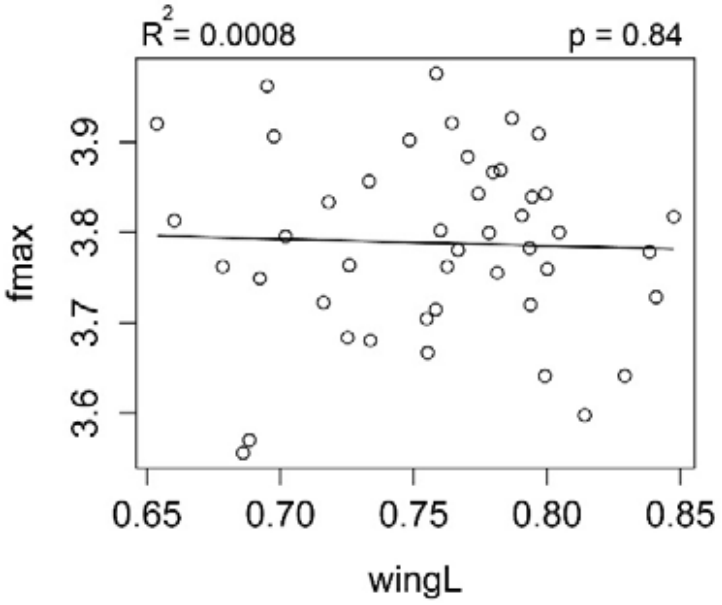
(A) Mean maximum frequency per habitat type.



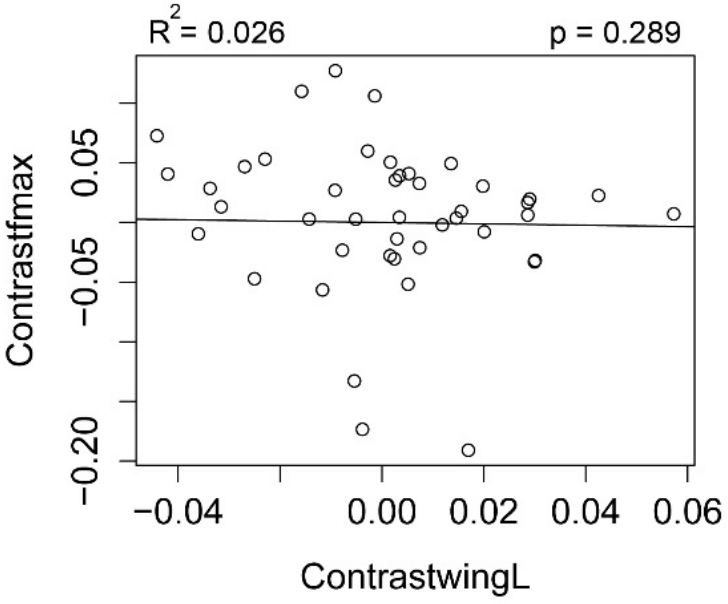
(B) Box-and-whisker plot of maximum frequency per habitat showing variation.



(C) Phylogenetic independent contrasts of maximum frequency plotted through the origin against habitat type. *Figure continued on next page*

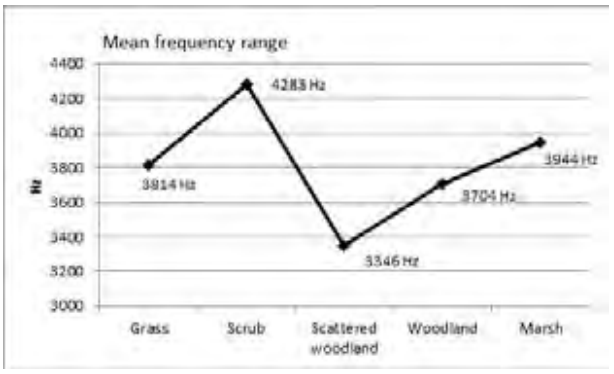


(D) Linear regression of maximum frequency plotted against wing length.

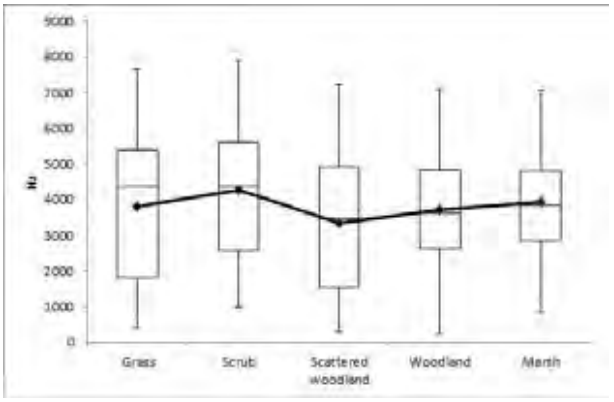


(E) Phylogenetic independent contrasts of maximum frequency plotted through the origin against wing length.

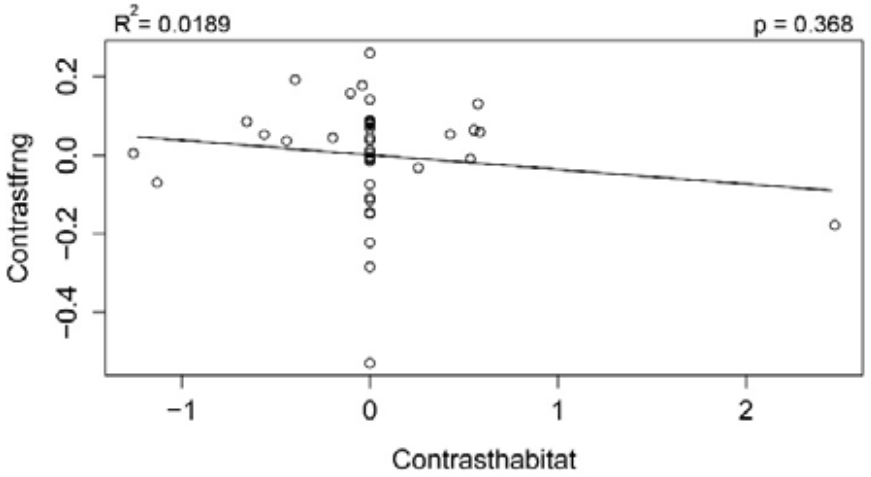
FIGURE 4.6: Frequency range graphs.



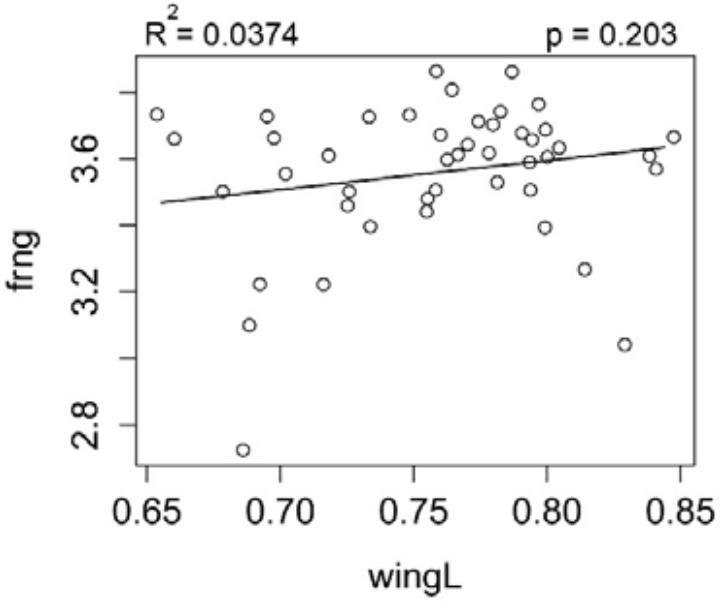
(A) Mean frequency range per habitat type.



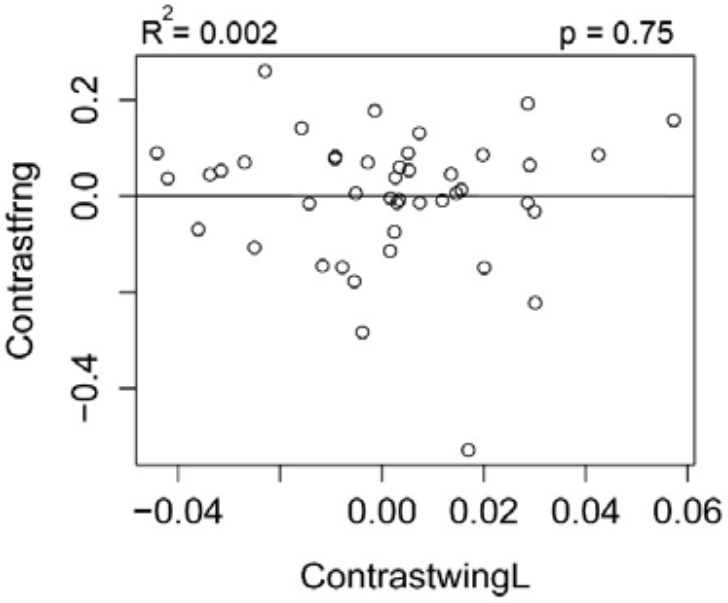
(B) Box-and-whisker plot of frequency range per habitat showing variation.



(C) Phylogenetic independent contrasts of frequency range plotted through the origin against habitat type. *Figure continued on next page*

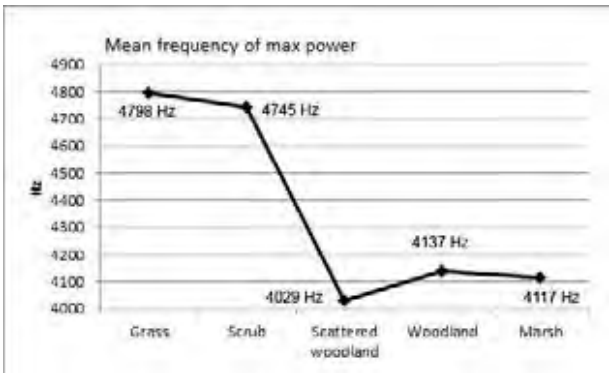


(D) Linear regression of frequency range plotted against wing length.

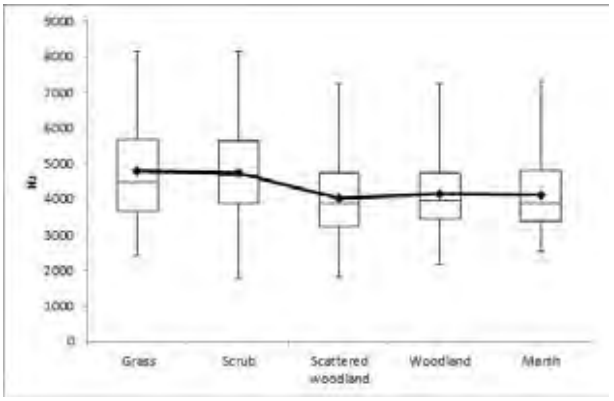


(E) Phylogenetic independent contrasts of frequency range plotted through the origin against wing length.

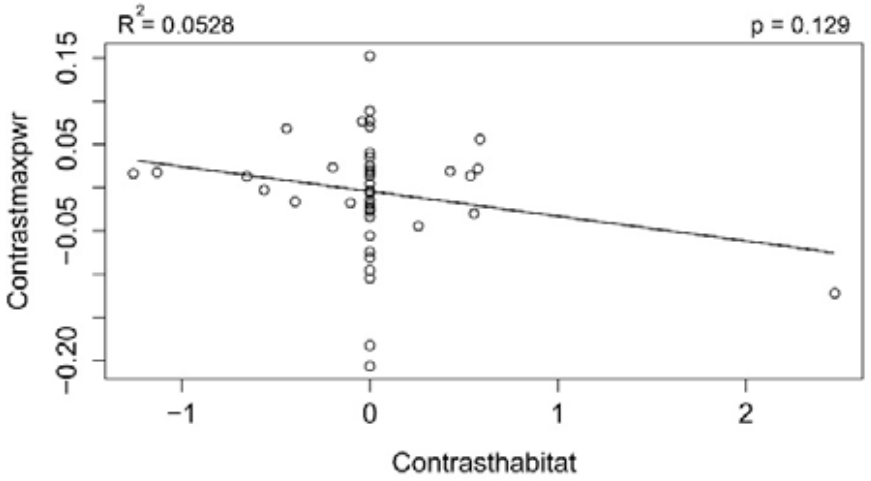
FIGURE 4.7: Frequency of maximum power graphs.



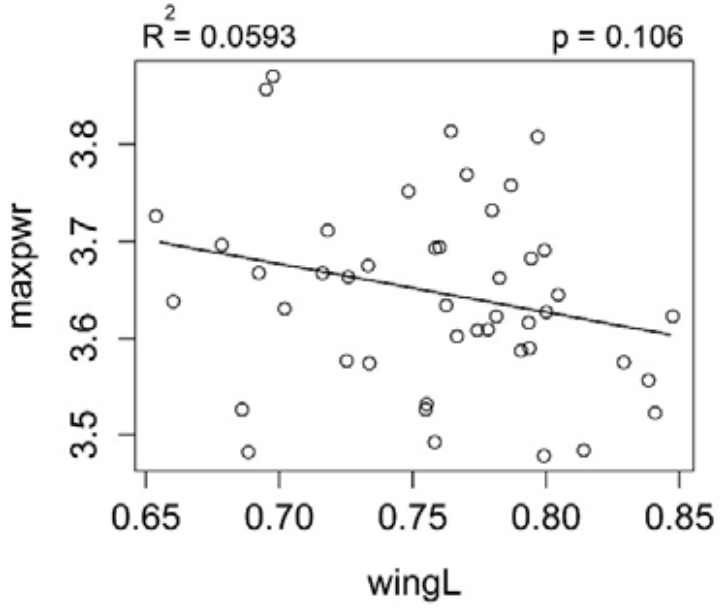
(A) A) Mean frequency of maximum power per habitat type.



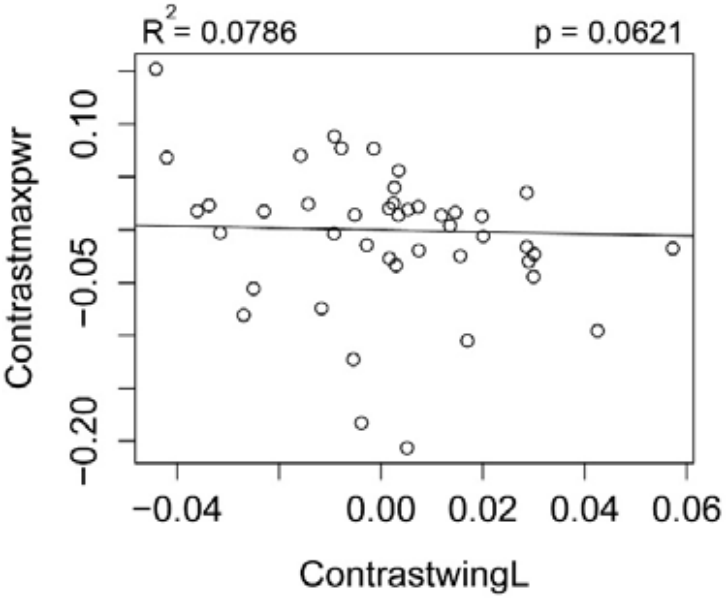
(B) Box-and-whisker plot of frequency of maximum power per habitat showing variation.



(C) Phylogenetic independent contrasts of frequency of maximum power plotted through the origin against habitat type. *Figure continued on next page*

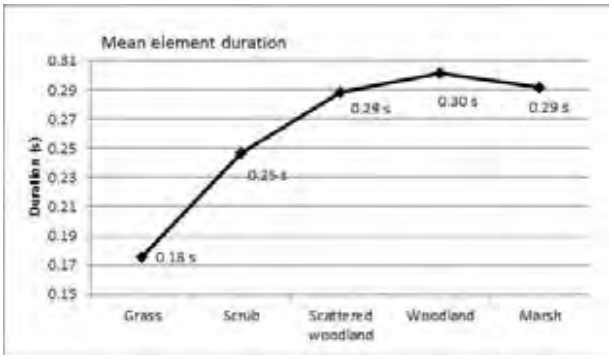


(D) Linear regression of frequency of maximum power plotted against wing length.

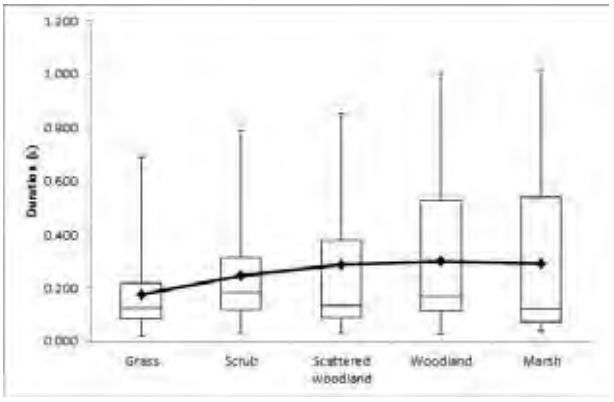


(E) Phylogenetic independent contrasts of frequency of maximum power plotted through the origin against wing length.

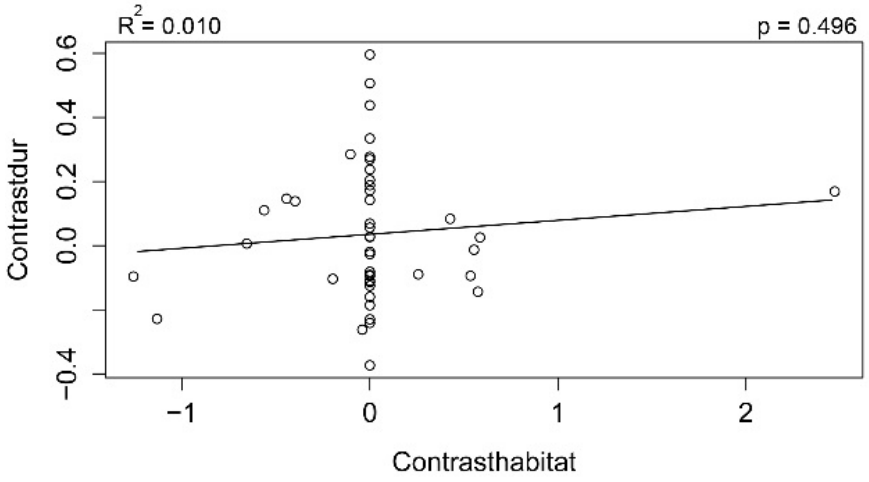
FIGURE 4.8: Element duration graphs.



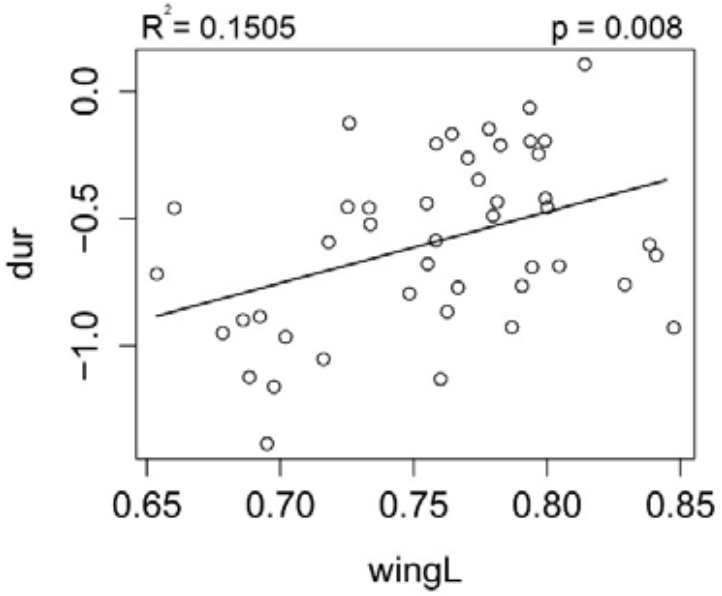
(A) Mean element duration per habitat type.



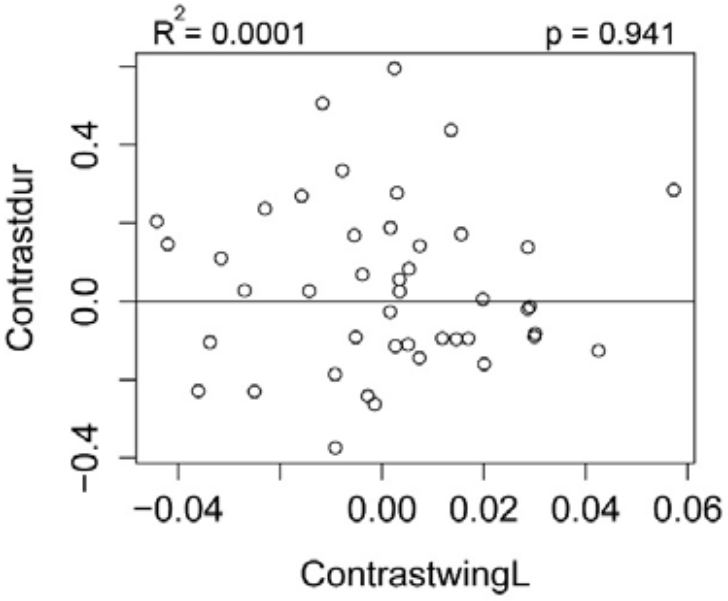
(B) Box-and-whisker plot of element duration per habitat showing variation.



(C) Phylogenetic independent contrasts of element duration plotted through the origin against habitat type. *Figure continued on next page*



(D) Linear regression of element duration plotted against wing length.



(E) Phylogenetic independent contrasts of element duration plotted through the origin against wing length.

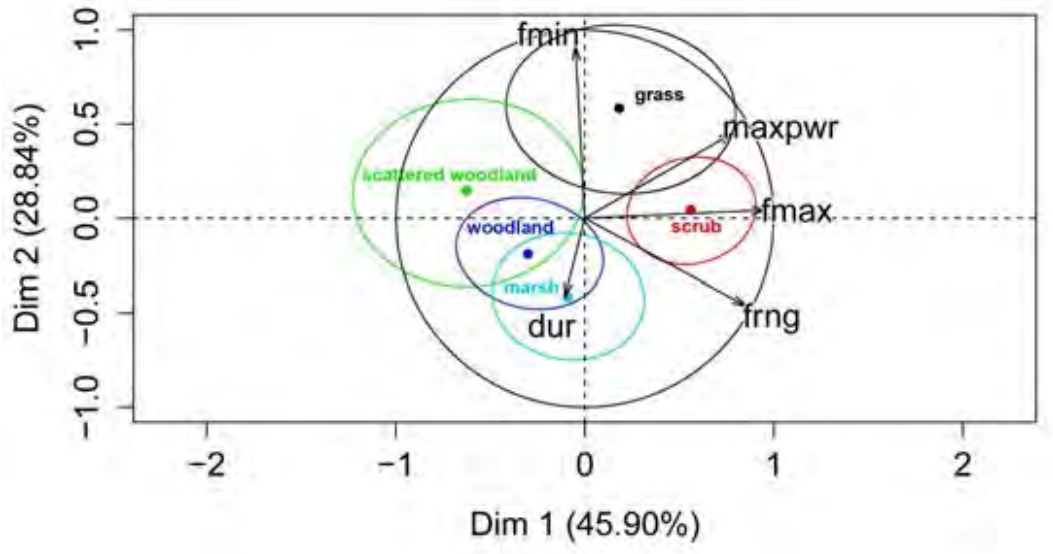


FIGURE 4.9: Principal component analysis of all acoustic variables. The first two axes account for 74.74% of the total variation with habitat types separating mostly by the FMIN and MAXPWR.

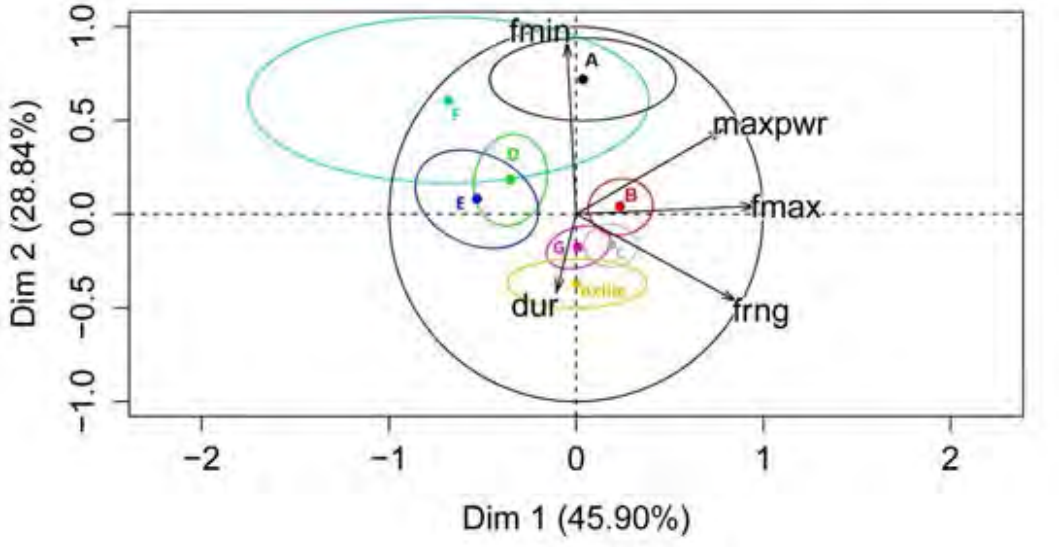


FIGURE 4.10: Principal component analysis of all acoustic variables. The first two axes account for 74.74% of the total variation with phylogenetic clades separating mostly by the FMIN and FRNG. A - *ayresii/textrix/eximius/aridulus/juncidis/cherina*; B - *robustus/natalensis/subruficapilla/lais/rufilatus/aberrans*; C - *erythrops/cantans/carruthersi/luapula/galactotes/marginatus/pipiens/lugubris*; D - *brachypterus/njombe/tinniens*; E - *nigriloris/hunteri/chubbi*; F - *nana/fulvicapilla*; G - *ruficeps/cinereolus/lateralis/woosnami/bulliens/anonymus/chiniana/bodessa*.

TABLE 4.1: Results of an ANOVA of elemental acoustic properties and habitat. Bold numbers highlight statistical significant differences at $p < 0.05$.

	fmin	**fmax**	**frng**	**maxpwr**	**dur**
grass:scrub	1	1	0.07916	1	**0.008**
grass:open woodland	1	0.49	1	**0.002**	0.83
grass:woodland	0.07	0.58	1	**0.014**	0.09
grass:marsh	**0.003**	1	0.96	**0.023**	0.54
scrub:open woodland	1	**0.004**	**0.0007**	**1.70E-04**	1
scrub:woodland	0.99	**0.002**	0.068	**0.001**	1
scrub:marsh	0.06	0.057	1	**0.003**	1
open woodland:woodland	0.98	1	0.85	1	1
open woodland:marsh	0.07	1	**0.035**	1	1
woodland:marsh	1	1	1	1	1

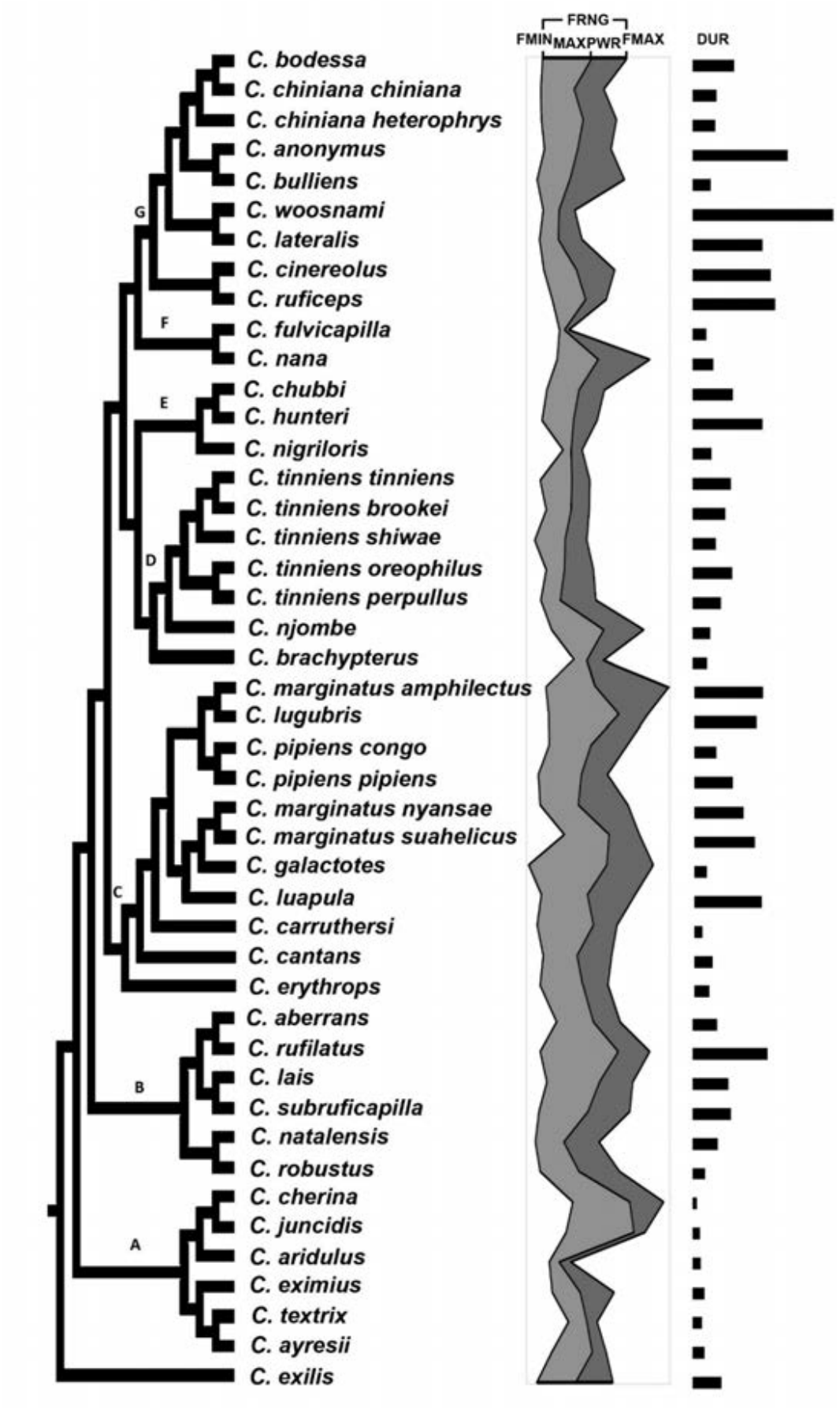
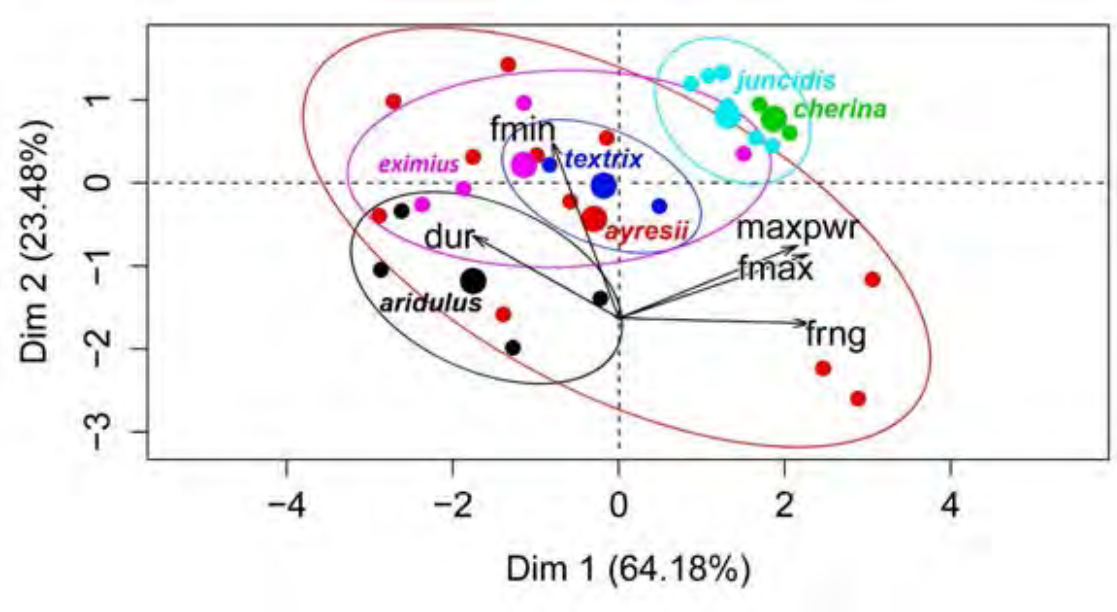


FIGURE 4.11: Acoustic properties plotted on the phylogenetic tree; letters on the tree indicate clades.

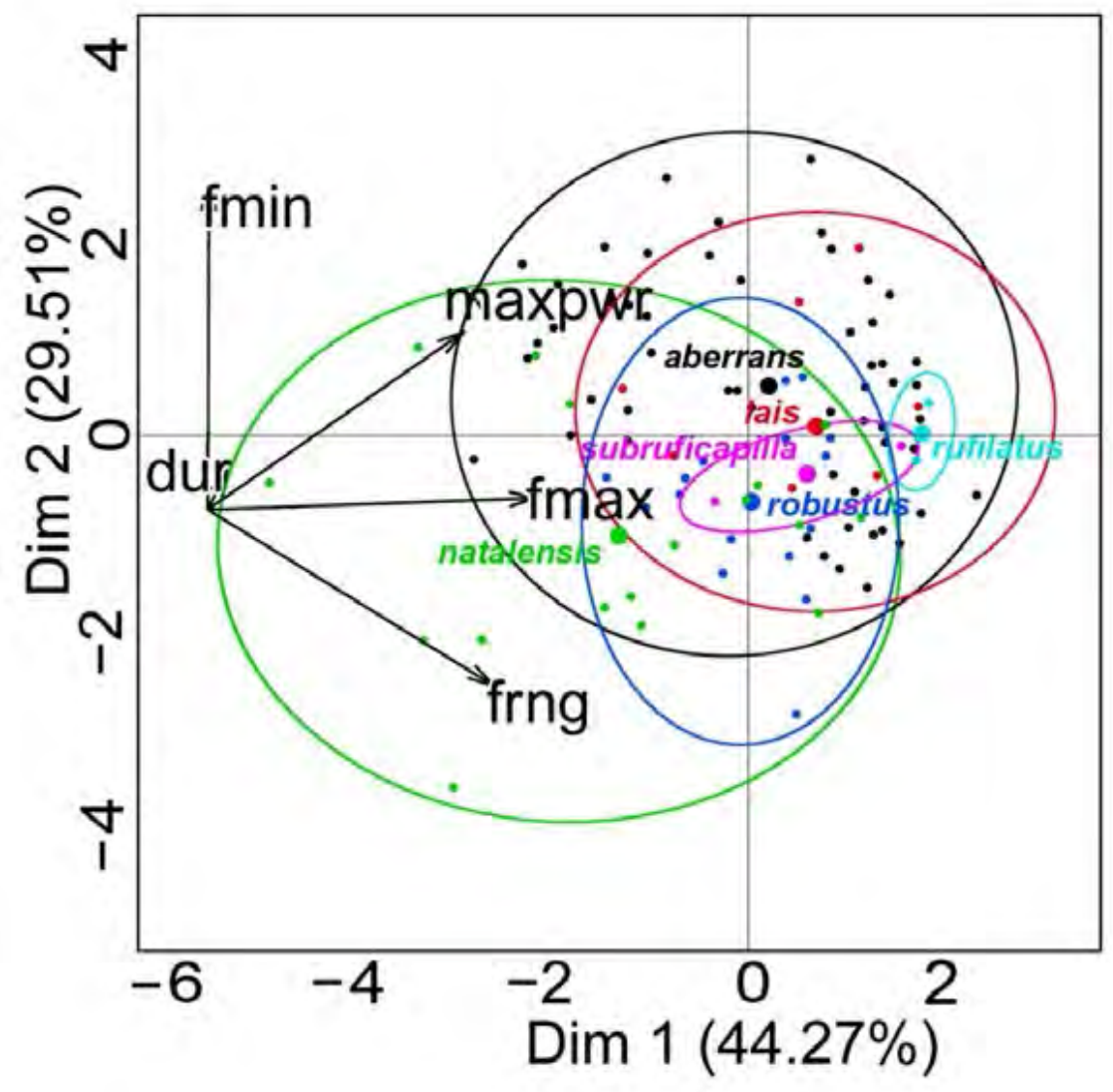
TABLE 4.2: Results of an ANCOVA of song variables in different habitats with the values log transformed. Bold numbers highlight statistical significant differences at $p < 0.05$. Entries are the F-ratios for each variable or interaction.

	Sources of variation		
Song variable	**Habitat**	**Wing length**	**Interaction**
d.f. = 5,39			
Minimum frequency (FMIN)	**3.468**	**6.126**	0.88
Maximum frequency (FMAX)	1.66	0.081	1.554
Frequency range (FRNG)	1.851	2.063	0.475
Frequency of maximum power (MAXPWR)	2.273	0.457	2.33
Duration (DUR)	**5.478**	**4.107**	0.79

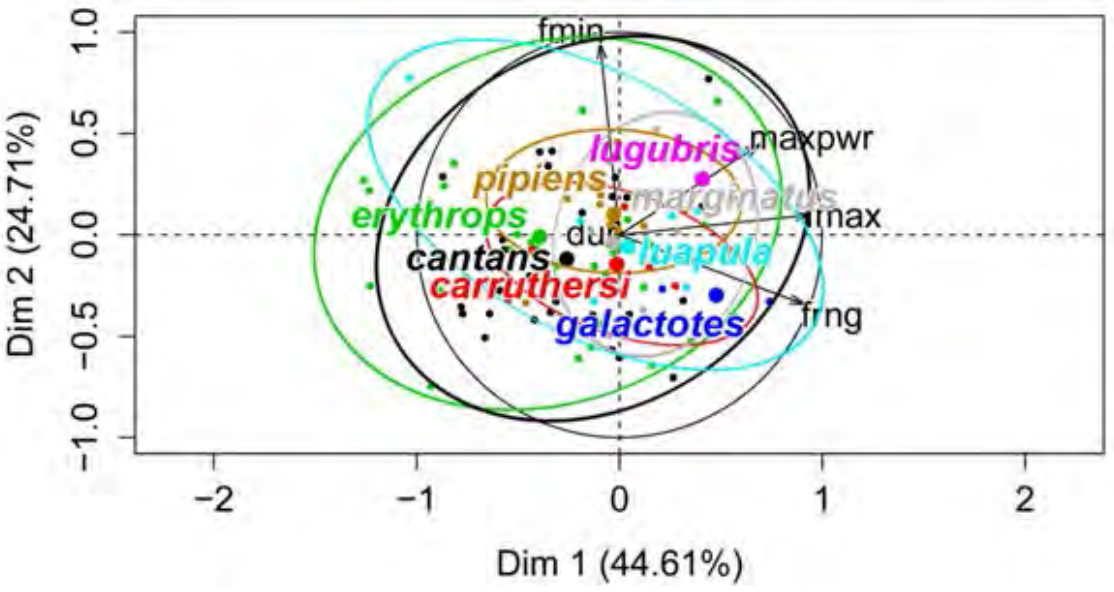
FIGURE 4.12: Principal component analyses of each clade.



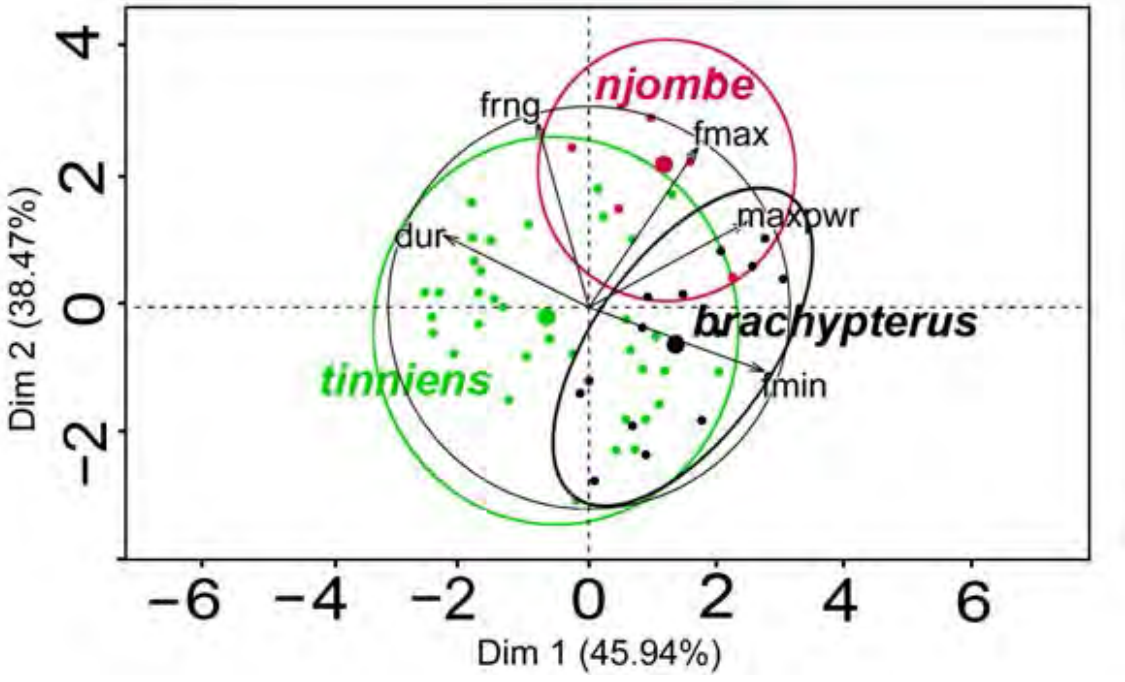
(A)



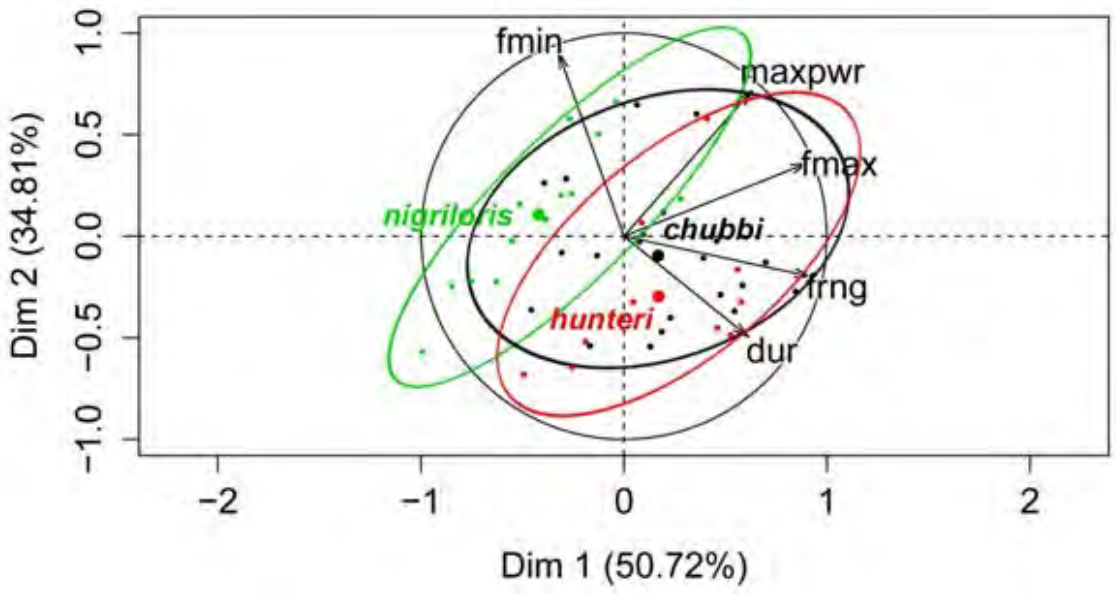
(B)


fmin
maxpwr
lugubris
pipiens
marginatus
fmax
erythrops
dur
luapula
cantans
carruthersi
frng
galactotes
Dim 2 (24.71%)
Dim 1 (44.61%)
1.0
0.5
0.0
−0.5
−1.0
−2
−1
0
1
2

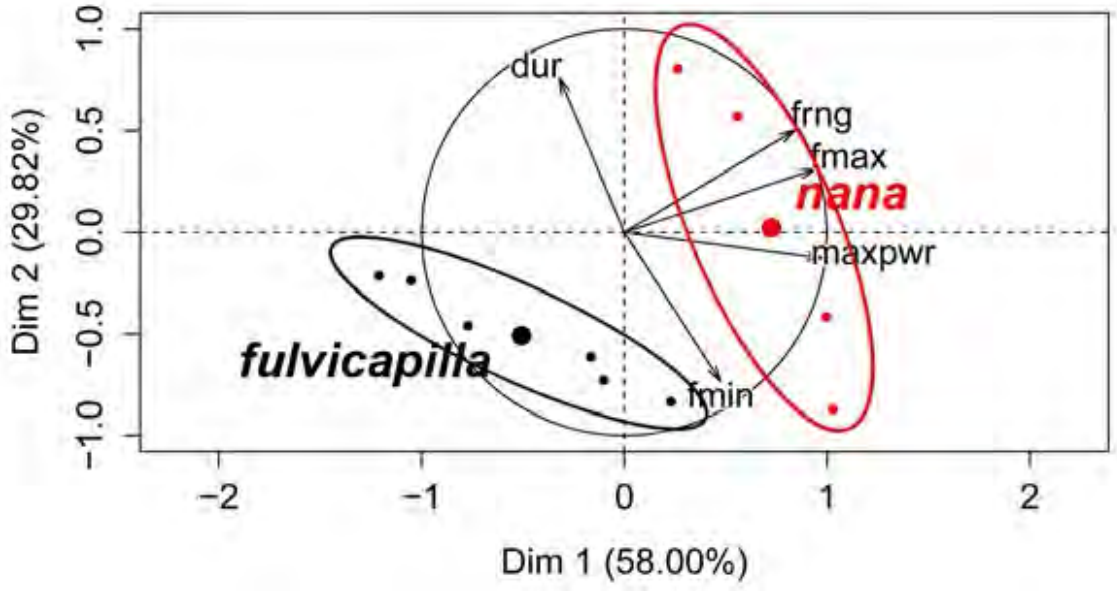
(C)


njombe
frng
fmax
maxpwr
dur
brachypterus
tinniens
fmin
Dim 2 (38.47%)
Dim 1 (45.94%)
4
2
0
−2
−6
−4
−2
0
2
4
6

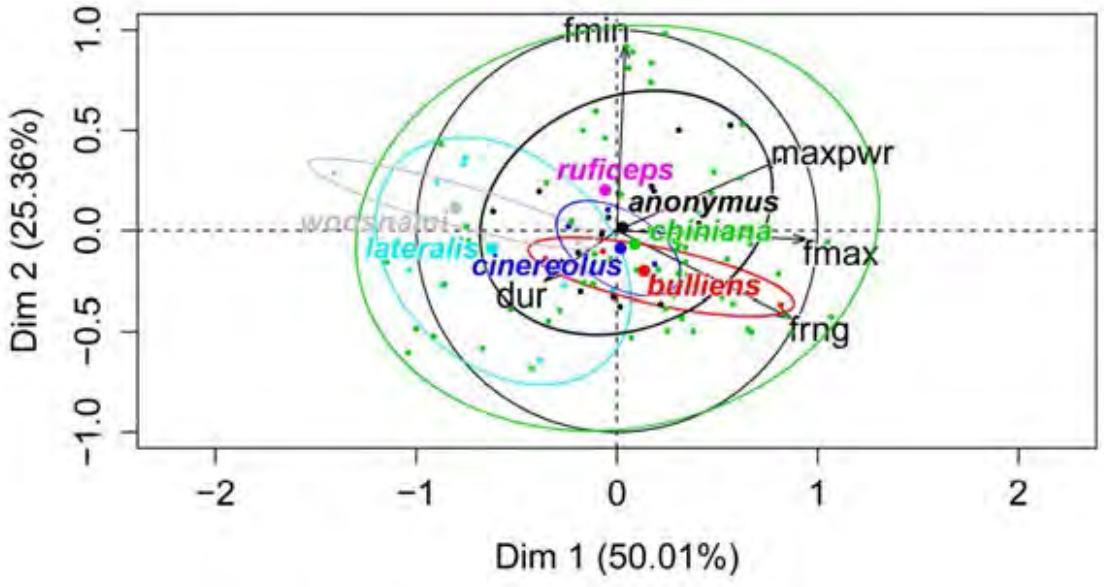
(D)


fmin
maxpwr
fmax
nigriloris
chubbi
frng
hunteri
dur
Dim 2 (34.81%)
Dim 1 (50.72%)
1.0
0.5
0.0
−0.5
−1.0
−2
−1
0
1
2

(E)


dur
frng
fmax
nana
maxpwr
fulvicapilla
fmin
Dim 2 (29.82%)
Dim 1 (58.00%)
1.0
0.5
0.0
−0.5
−1.0
−2
−1
0
1
2

(F)


fmin
maxpwr
ruficeps
anonymus
chiriana
fmax
wrocsnalbi
lateralis
cinereolus
bulliens
dur
frng
Dim 2 (25.36%)
Dim 1 (50.01%)
1.0
0.5
0.0
−0.5
−1.0
−2
−1
0
1
2

(G)

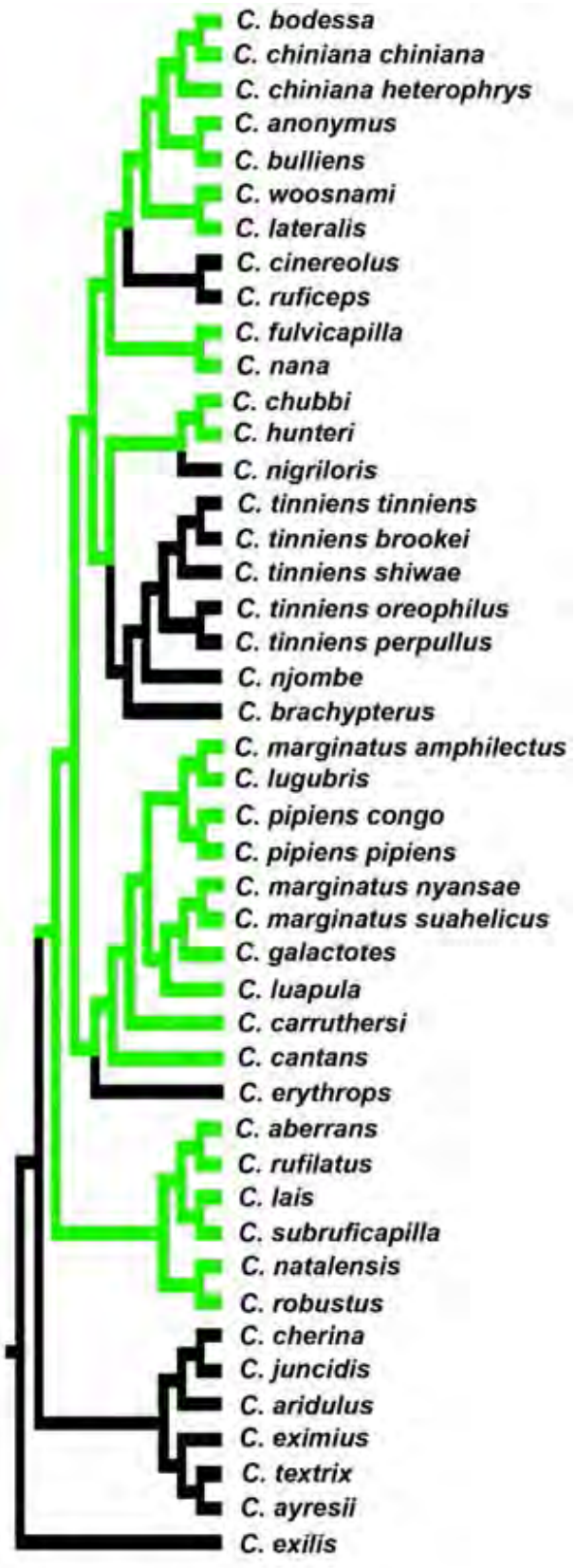


FIGURE 4.13: Required evolutionary steps if an early common ancestor had evolved trill-type songs (green). Such a distribution would explain why some trill songs are maintained in closed habitat where they are predicted to perform poorly; such a reconstruction would require the evolution away from trills to have occurred in at least four separate occasions.

Chapter 5

Climate variability driving speciation in cisticolas?

Cisticola biogeography, evolution and correlation with the Pulsed Climate Variability hypothesis

5.1 Introduction

The idea that the fragmentation of previously continuous distributions can isolate species into refugia is by no means a new one and was first proposed by Forbes (1846) to account for the disjunct distributions of plants in Europe (Mayr and O'Hara, 1986). Darwin recognised that glaciation may be responsible for the isolation of the same species of plants and animals in distant locations and regretted not expanding upon this idea (Darwin, 1958). The refuge theory was revived by Mayr (1963), who suggested that climate change in the Pleistocene, specifically the advancing ice sheets, could have provided a means of isolation and thereby facilitated speciation of temperate zone populations in refugia of suitable habitat (Mayr and O'Hara, 1986). It soon became clear that glaciation-induced Pleistocene climate variation could also be responsible for vegetation shifts in the tropics and subtropics, and various authors argued that isolation due to resulting vegetative barriers between previously continuous ranges could have initiated speciation (Brown et al., 1974; Chapin, 1932; Crowe and Crowe, 1982; Diamond and Hamilton, 1980; Haffer, 1974; Hamilton, 1976; Keast, 1961; Mayr and O'Hara, 1986; Moreau, 1952; Snow, 1974; Vanzolini and Williams, 1970). These ideas, coupled with compelling evidence for the African climate becoming cooler and drier, and the resulting vegetative shift from closed canopy forest to open savanna during the Pleistocene (Bonnefille, 1983; deMenocal, 1995; Hamilton, 1976; Livingstone, 1975, 1993), made an intuitive argument for the forest refuge hypothesis to be an important mechanism driving the speciation of forest biota. Some authors have argued for the importance of montane forests in speciation over time (Fjeldså and Bowie, 2008; Jetz et al., 2004; Tolley et al.,

2011; Voelker et al., 2010) and others have suggested locations of refugia in lowland forest as being of particular importance during the arid phases of the Pleistocene (Crowe and Crowe, 1982; Nichol, 1999). While the Pleistocene refuge theory has had 'paradigmatic rank' (Fjeldså and Lovett, 1997) for over two decades, it has been contested by authors arguing that many rainforest species predate the Pleistocene (Amorim, 1991; Fjeldså, 1994; Hackett, 1993). Various other studies of the African forest biota have indicated similar trends of pre-Pleistocene diversification, including African greenbuls (*Andropadus*; Roy (1997), forest robins and akalats (*Stiphrornis*; Beresford and Cracraft (1999), *Sheppardia*; Roy et al. (2000), and *Sheppardia/Alethe*; Beresford (2003); Voelker et al. (2010)), forest adapted *Begonia* species (Plana, 2003), forest adapted soft-furred mice (*Praomys* complex; Lecompte et al. (2002), forest shrews (*Sylvisorex*; Querouil et al. (2003)) and forest trees (Annonaceae; Couvreur et al. (2008)), amongst others.

The influence that the Pleistocene climate variation had on the diversity of African fauna (particularly birds) therefore remains poorly understood, causing debate on whether it caused an increase or even a decrease in speciation (Fjeldså, 1994), but a study on closely related species and subspecies complexes of Olive Sunbirds (*Nectarinia olivacea*, Bowie et al. (2004b)) supported the idea that evidence for Pleistocene diversification may more likely be found among conspecific populations and subspecies (Hewitt, 1996; Klicka and Zink, 1997). In addition, the effects of Pleistocene climate variation on the speciation of African birds might be found in open habitat species rather than the forest species that have been the primary focus of study to date.

There has been a great deal of interest in determining what paleoclimactic changes have occurred in the last 5 million years as climate and habitat dynamics during this period are believed to have had an important influence on the evolution of hominids (Finlayson, 2005; O'Brien and Peters, 1999). As a result, various hypotheses have been proposed as drivers of speciation and evolution in Africa over this period, including the savanna hypothesis in which Dart (1925) suggested that bipedalism and brain size were products of savanna life, though subsequent data revealed that savannas may not have been the predominant habitat at the time or location of these adaptations (Cerling, 1992; Senut et al., 2001). The Turnover Pulse hypothesis noted that bursts of biotic change from woodland to savanna bovids occurred during short, distinct time periods of climate shifts (Vrba, 1985, 1995, 2000) but a reanalysis indicated that the turnover in species was more gradual (Behrensmeyer et al., 1997; Bobe et al., 2002). Evidence from the analyses of Saharan dust in marine records seemed to support the aridification of Africa during the time of northern hemisphere glaciation resulting in the formulation of the Aridification hypothesis (deMenocal, 1995, 2004) which proposed three distinct increases in aridity at 2.8 ($\pm$ 0.2) MYA, 1.7 ($\pm$ 0.1) and 1 ($\pm$ 0.2) as drivers of shifts from woodland to

savanna and associated speciation. Again, this hypothesis invoked fairly rapid effects of glaciation on the climate but it has been shown that these glaciation events were a more gradual process occurring over a longer period (Bartoli et al., 2005) and reanalyses of the data (Trauth et al., 2009) have challenged the proposed shifts towards drier and more variable climates at 2.8 MYA (Trauth et al., 2010). The analyses of more recent data has resulted in the formulation of the Pulsed Climate Variability hypothesis (Trauth et al., 2010) which modifies and adds to the earlier Variability Selection hypothesis, which emphasised the importance of climate instability for speciation (Potts, 1996, 1998). The Pulsed Climate Variability hypothesis links tectonic processes and global influences of atmospheric and ocean currents to climate variability, habitat fragmentation and speciation, and invokes periods of relatively stable environments (allowing for the increase and spread of populations over the landscape) being punctuated by spikes of highly variable climate conditions fragmenting populations or driving adaptation and diversification (Donges et al., 2011). This hypothesis promotes a Plio-Pleistocene African climate characterised by pulses of significantly wetter and more variable climate fluctuations, that are mostly unrelated to the onset of northern hemisphere glaciation, as being the main drivers of speciation during this period (Trauth et al., 2010).

The extent and availability of wetland environments are also of particular interest as recent hypotheses have identified the importance of bulbs, tubers and other plant underground storage organs found in these environments as fallback foods in the evolutionary history of hominoids (Laden and Wrangham, 2005) and the ephemeral nature of these wetlands and lakes (Kingston et al., 2007) combined with periods of aridity may have had a strong influence on faunal evolution (Trauth et al., 2007). The breakup of wetlands is thought to have driven Lechwe (*Kobus* sp.) speciation through vicariance (Cotterill, 2005). Drainage evolution has also been implicated in driving vicariant speciation of some wetland avifauna, such as Swamp weavers (*Ploceus* sp.) and Swamp flycatchers (*Muscicapa* sp. Cotterill (2004)), but the timing of these events remain unclear. While investigations into the genetic divergence of biota (crocodiles, lechwe and tigerfish; see Cotterill and Goodier (2008) for a summary) found in these environments have offered great insight into geological and drainage basin evolution in southern Africa, considerable uncertainty remains. Phylogenetic comparisons of savanna and wetland species would yield interesting insights into the history of the African landscape (Broadley and Cotterill, 2004).

The concordant distribution patterns of savanna ungulates is thought to reflect the influences that the Pleistocene had on the evolution and diversification of the group, with the expansion of woodland and grassland savannas and arid-adapted C4 plants facilitating the emergence of species associated with these habitats and the expansion and

contraction of these environments during climate variation within the last 2.8 million years often being implicated in offering conditions for their speciation (Lorenzen et al., 2012). The Pleistocene has indeed been influential in the diversification of various savanna adapted groups such as the Hartebeest (*Alcelaphus buselaphus*; Flagstad et al. (2001)), African buffalo (*Syncerus caffer*; van Hooft et al. (2002)), Common warthog (*Phacochoerus africanus*; Muwanika et al. (2003)), Roan antelope (*Hippotragus equinus*; Alpers et al. (2004)), Ground squirrels (*Xerus* spp.; Herron et al. (2005)) and Giraffe (*Giraffa camelopardalis*; Brown et al. (2007)). A dated phylogeny of the Guinea multimammate mouse (*Mastomys erythroleucus*; Brouat et al. (2009)) indicated that they diversified in the Pleistocene and comparative study of the timing of the diversification of the African green monkey (*Chlorocebus*), Baboon (*Papio*), Hartebeest (*Alcelaphus*) and Common warthog (*Phacochoerus africanus*) showed that, while they also diversified in the Pleistocene, there was little concordance in the timing of cladogenesis, suggesting that multiple events were responsible for their diversification (Haus, 2013). An explanation for the discordance in diversification timing between different savanna lineages was proposed by Haus (2013), who argued that, in contrast to forest or desert habitats, savanna areas would be fragmented during extremes of both wet and dry cycles, contracting during times of extreme aridity and being separated by wetlands and forests during the wet periods. Expansions of savannas would likely be expected to occur during intermediate climate periods (Haus, 2013).

While most of our understanding about the distribution of genetic diversity in savannas relates to mammals, we are beginning to uncover the patterns in African birds. Recent findings by Voelker et al. (2012) show that diversification in savanna adapted chats (*Myrmecocichla*) occurred during a humid period in the Pliocene when forests were expanded across the continent, dividing northern and southern savanna habitats between 3–5 MYA, whereas Fuchs et al. (2012) found evidence for Pleistocene diversification in the Fiscal shrike (*Lanius collaris*) species complex.

Cisticolas are well suited to investigating the dynamics of open habitats across Africa as the genus is highly speciose, comprising about 49 species; and they are fairly sedentary, non-migratory and exhibit a pan-African distribution (Figure 5.1) with representatives in most of the major non-forest habitats from grasslands, scrub, savanna and woodland to marshland. In this study we examine the biogeography of cisticolas to provide us with greater insight into the effects of historical climate and habitat variation on the diversity of the genus and determine if there is any correlation between the patterns of speciation and any of the various proposed hypotheses thought to be driving the diversification of open habitat fauna in Africa.

5.2 Methods

We employed Bayesian inference to estimate and date the phylogeny using a concatenated data set of both mitochondrial and nuclear data using BEAST version 1.7.5 (Drummond et al., 2012). The models for nucleotide substitutions used in the analyses were selected for each gene individually using the Akaike Information Criterion (Akaike, 2006) in the program MODELTEST version 2.3 (Posada and Crandall, 1998) in conjunction with PAUP*4.0b10 (Swofford, 1998). We generated the input file in BEAUti version 1.7.5 (Drummond et al., 2012) considering the genes ND2, CYTB, FIB5, G3PDH, MYO2 and TGFB) with the substitution models selected by MrModeltest (GTR+I+Γ for ND2, CYTB and TGFB; HKY for FIB; HKY + I for MYO2, and F81 for G3PDH). A strict clock was implemented for ND2 as a Tajima's Relative Rate Test (performed with MEGA version 4.1) did not reject the null hypothesis (Tajima's D = 0.91) and a relaxed clock was implemented with an uncorrelated lognormal distribution (Ho et al., 2006) for all other genes using the Yule process. We followed the substitution rates of Lerner et al. (2011) for ND2, CYTB and TGFB to estimate divergence dates using normal prior distribution and mean mutation rates of 0.029 ($\pm$ 0.003) for ND2, 0.014 ($\pm$ 0.002) for CYTB and 0.0017 ($\pm$ 0.0003) for TGFB and allowed BEAST to estimate the mutation rates for the remaining nuclear introns using a log-normal distributed prior under default settings for each partition. MCMC analyses were run for 150 million generations, sampling every 15 000 generations. Results from the Bayesian MCMC runs were analysed using Tracer version 1.5 (Rambaut and Drummond, 2009), and tree information was summarised using TreeAnnotator version 1.7.5 (Drummond et al., 2012) using a burn-in of 1 000 and visualised using FigTree version 1.4.0 (Rambaut, 2012). Distribution maps were modified from Ryan (2006). See Chapter 3 for sample and sequence details.

5.3 Results

Of the 55 cladogenesis events that occur between 0.7–4.7 MYA, 20 (36%) are correlated with the periods identified by the Aridity hypothesis (deMenocal, 2004) as being important for speciation, whereas 28 (51%) are correlated with time intervals that show evidence for the presence of large lakes (Donges et al., 2011) and 31 (56%) are correlated with the periods of high climate variability (Donges et al., 2011). There are some periods of overlap between the hypotheses, and of those not correlated with periods of high climate variability, only three (5.5%) of the cladogenesis events are explained by those periods identified by deMenocal (2004) alone. A total of 41 of the 55 (74.5%) cladogenesis events are correlated with time intervals of large lakes and periods of high climate variability proposed by Donges et al. (2011).

Our analyses revealed that the only species of cisticola that does not occur in Africa, *C. exilis*, is the most divergent and was recovered as being basal to the African species with a Miocene estimation on its separation (Figure 5.2). Cladogenesis events occurred at 8.98, 8.28 and 7.64 million years ago (MYA) resulting in four main lineages, each of which showed initial radiation between 4–7 MYA. Clade A, comprising small grassland species, diversifies around 6.34 MYA into the juncidis and textrix groups, each subclade then splits further 4.66 and 3.82 MYA, with *C. aridulus* and *C. juncidis* diverging some 3.82 MYA (Figure 5.3). There are divergences within the textrix group at 1.86 and 1.12 MYA (Figure 5.4). Clade B shows an initial split around 6.61 MYA, with *C. natalensis* and *C. robustus* showing a deep split 4.98 MYA (Figure 5.5) and *C. distinctus* sharing a common ancestor with *C. subruficapilla/lais/rufilatus/aberrans* 4.69 MYA (Figure 5.6). These bushy/scrub dwelling species split 3.8 MYA with *C. subruficapilla* and *C. lais* diverging 2.49 MYA (Figure 5.7) and *C. rufilatus* separating from *C. aberrans* 3.3 MYA and a split within *C. aberrans* 1.44 MYA. Clade C is made up of species that prefer more rank habitats associated with moisture and contains the marsh cisticolas. After initial divergence *C. erythrops* is basal to this clade, diverging 5.11 MYA; there are intraspecific divergences within *C. erythrops* at 3 and 1.69 MYA. The divergence of *C. cantans* was estimated to be 4.82 MYA with intraspecific splits at 2.05 and 1.59 MYA. There also seems to be a divergence between the two samples of *C. carruthersi* at 1.78 MYA, with these species diverging from the rest of the marsh group 4.17 MYA (Figure 5.8). There does seem to be a northern/southern split, if somewhat obscured, within the marsh cisticolas, with *C. luapula/galactotes* and Kenyan/Tanzanian populations of *C. marginatus* splitting from *C. haematocephala/pipiens/lugubris* and West African/Ugandan populations of *C. marginatus*, with this separation occurring 3.02 MYA. Within the southern species of the marsh group, *C. luapula* separates from *C. galactotes* and *C. marginatus* at 1.99 MYA, while those two species diverged from each other around 1.63 MYA. Within the northern species, *C. haematocephala* diverged 2.75 MYA, followed by *C. pipiens* at 2.08 MYA and *C. lugubris* at 1.79 MYA, and the subspecies of *C. marginatus* from Nigeria diverged from those in Sudan 1.5 MYA (Figure 5.9), which themselves are separated from the Cameroon and Ugandan populations around 1.32 MYA. Clade D splits into two lineages 6.61 MYA, each one diversifying further fairly soon thereafter at 6.3 and 5.82 MYA. The highlands species of *C. nigriloris*, *C. chubbi* and *C. hunteri* diversify around 3.43 MYA, with *C. chubbi* and *C. hunteri* separating between the eastern and western arc mountains about 2.52 MYA (Figure 5.10). The wide-ranging lowland savanna dwelling *C. brachypterus* separates from the rather more range restricted *C. njombe* found in the montane grasslands and rank streamside vegetation north of the Rukwe rift and on the Nyika Plateau around 3.3 MYA. *C. njombe* separated from the

marsh adapted *C. tinniens* around 2.45 MYA (Figure 5.11). The two small savanna dwelling species, *C. troglodytes* from the east Sudan-Guinea biome and *C. rufus* from the west, separate around 3.66 MYA and separate from the Ethiopian and southern species around 4.43 MYA. The diminutive *C. nana*, found in the savanna and open woodlands of the Somali-Masai biome, separates from the Zambezian biome species *C. angusticauda* around 2.41 MYA (Figure 5.12). These species separate from the miombo dwelling *C. melanurus* and *C. fulvicapilla* that occur in a variety of habitats around 3.12 MYA. *C. melanurus* separated from the southerly species of *C. fulvicapilla* around 2.63 MYA, with populations of *C. fulvicapilla* diverging around 2.35 MYA and 1.42 MYA. The other main subclade consists of mostly bushveld species and begins to radiate 4.63 MYA (Figure 5.13) with *C. cinereolus*, found in the Somali-Masai savanna biome in the east, and *C. ruficeps*, found in the Sudan-Guinea savanna biome to the west of the rift, separating from each other around 2.63 MYA (Figure 5.14). Two species inhabiting savanna and open woodland, *C. lateralis* and *C. woosnami*, separate around 2.21 MYA (Figure 5.15), with *C. woosnami* preferring slightly drier habitats to the south-east of the distribution of *C. lateralis*; these species separated from the remaining species 3.91 MYA. The rest of the subclade underwent further cladogenesis at 2.77 and 2.18 MYA (Figure 5.16), with Kenyan populations of *C. chiniana* separating 1.32, 1.02 and 0.67 MYA.

5.4 Discussion

Without fossil calibration points to constrain nodes, the confidence intervals of estimated divergence times are large, and they should be interpreted cautiously; nevertheless the distribution of the estimated mean divergence dates obtained by this study are interesting as they support the hypothesis that pulses of significantly wetter and more variable climate fluctuations influenced speciation in cisticolas.

The initial radiation of the four main lineages between 4–7 MYA, and the further diversification between clades 4 and 5 (Figure 3.14), corresponds to an increase in C4 grasslands during this period and matches what was found in grassland lineages of flightless bush crickets (Voje et al., 2009) possibly as a result of adaptive speciation into newly available niches. The diversification within the textrix (4.66 MYA), subruficapilla (4.69), fulvicapilla (4.43) and ruficeps (4.63) clades occurs during a period where there is geological evidence for the presence of a wet period supporting large lakes between 4.3 and 4.7 MYA (Donges et al., 2011; Trauth et al., 2007). Cisticolas may have diversified and spread out into the expanding grassland environments and then have become fragmented or isolated by wetland or forest environments expanding during this fluvial period.

A second, shorter fluvial period has been proposed for the time between 3.9 and 4.0 MYA, a period that correlates well with the lateralis diversification (3.91 MYA) and slightly less so with the divergence of the *C. carruthersi* clade (4.17 MYA) and subruficapilla clade (3.80), and separation of *C. aridulus*, which is an arid adapted species, from *C. juncidis* (3.82 MYA). This split may have come about during a drying period that summoned the end of the high lake levels and gradial but continued aridification of Africa since the Miocene.

The estimated mean age of divergence between *C. eximius* and *C. dambo* is 3.08 MYA. The age of this split, and their north-south distribution (Figure 5.17), is similar to the pattern that Voelker et al. (2012) found in chats and interpreted as being the result of the expansion of the Afrotropical forest to the Kenyan coast separating north and south savanna belts. Both of these cisticola species favour damp areas of grassland and areas with seasonal flooding and the dating of the split is correlated with another time interval with geological evidence for large lakes and wet, humid conditions, as well as evidence for abrupt climate change (Donges et al., 2011) where a common ancestor could have been widespread and then experienced rapid fragmentation caused by climate dynamics. A similar, but less obvious pattern can be seen in the marsh cisticolas with north/south species separating at 3.02 MYA. The period between 2.95 and 3.5 MYA has been identified by Donges et al. (2011) as being the earliest of three periods of extreme climate variation and includes two periods of high lake levels between 2.95–3.2 and 3.3–3.4 MYA.

In addition to the divergence between *C. eximius* and *C. dambo* and the *C. cantans* clade mentioned above, this variable period also correlates with the diversification of *C. nigriloris* (3.43 MYA); the split of *C. rufilatus* from *C. aberrans* (3.30 MYA); divergence between *C. brachypterus* and *C. njombe/tinniens* (3.30 MYA); and the diversification of the *C. fulvicapilla* clade (3.12 MYA), with most of these cladogenesis events coinciding with high lake level periods. The divergence between the southern African dry scrubland species *C. subruficapilla* and *C. lais* (2.49 MYA) is also correlated with high lake levels between 2.5–2.7 MYA, with the Rukwa rift and Rukwa lake acting as a potential barrier during high levels between *C. njombe* and *C. tinniens* 2.45 MYA as it may have done during the earlier high levels between *C. brachypterus* and *C. njombe* 3.30 MYA. This feature may have acted as a barrier to gene flow multiple times for different taxa moving through the savanna 'arid corridor' (Balinsky, 1962; Moreau, 1952) such as the Common warthog (Haus, 2013), with divergence dates coinciding with tectonic activity in the area (Macgregor, 2015). This period, while not considered by Donges et al. (2011) to be one of high climate variability, is correlated with splits between *C. melanurus* and *C. fulvicapilla* (2.63 MYA); *C. ruficeps* and *C. cinereolus* (2.63 MYA);

C. hunteri and *C. chubbi* (2.52 MYA); *C. haematocephala* and other members of the marsh clade (2.75 MYA); *C. bulliens/anonymus* and *C. chiniana* (2.77 MYA); and *C. nana* and *C. angusticauda* (2.41 MYA) all having divergence dates within this period of proposed climatic stability, but increased tectonic activity around the East African Rift System (EARS) (Macgregor, 2015). The divergence of species between the Somali-Masai savanna dwelling *C. cinereolus* from the Sudan-Guinea dwelling *C. ruficeps* may have occurred around the eastern rift valley during a period of high lake levels causing a barrier between the two biomes 2.63 MYA, but the estimated mean date for this split also coincides with tectonic activity and the formation of a graben in the southern Gregory rift (Macgregor, 2015). In contrast, the extent of the Somali-Masai biome may have increased to join the Zambezian biome during times of climate stability and increased rainfall, and may have been punctuated by drying events that brought an end to the high lake levels 2.5 MYA.

A second period of extreme climate variability occurred between 1.6–2.25 MYA (Donges et al., 2011) and is correlated with the diversification between *C. woosnami* and *C. lateralis* (2.21 MYA); between *C. restrictus* and Kenyan populations of *C. chiniana* (2.18 MYA); within *C. cantans* populations (2.05 and 1.59 MYA); between *C. luapula* and *C. galactotes* (1.99 MYA); within populations of *C. ayresii* (1.86 MYA); between *C. lugubris* and northern populations of *C. marginatus* (1.79 MYA); within populations of *C. carruthersi* (1.78 MYA); within populations of *C. erythrops* (1.69 MYA) and between *C. galactotes* and Kenyan/Tanzanian populations of *C. marginatus* (1.63 MYA) all correlating with this time period. The diversification event that occurred within *C. ayresii* populations and populations of *C. erythrops* as well as *C. carruthersi*, between *C. galactotes* and the Kenyan/Tanzanian samples of *C. marginatus* and the separation of *C. lugubris* from the Nigerian/Sudanese/Ugandan samples of *C. marginatus* all correlated more specifically with a shorter time period within this variability that had evidence for a period of high lake levels (1.7–1.9 MYA; Donges et al. (2011)). Most of these species prefer wet vegetation, or are marshland adapted, and the common ancestors could have expanded their range during times of high humidity. In a climate that supplied the water to sustain high lake levels, these populations could have been isolated in pockets of suitable habitat during extreme climate variability and the expansion of savanna habitats around east Africa (Bobe and Behrensmeyer, 2004; Cerling et al., 1998).

The most recent period identified by Donges et al. (2011) occurred between 0.7–1.1 MYA and correlates with the divergence between *C. ayresii* and *C. textrix* samples (1.12 MYA); within *C. juncidis* and *C. cherina* (0.89, 0.75 and 0.70 MYA); within *C. lais* (0.71 MYA) and *C. chiniana* (1.15, 1.02 and 0.67 MYA); within Tanzanian populations of *C. marginatus* (0.87 MYA) and Nigerian populations (0.81 MYA); and within

populations of *C. tinniens* (0.68 MYA), with many of these correlating with another high lake level period between 0.9–1.1 MYA.

It is quite apparent by these lists of shared divergence ages that distinct bursts of diversification and radiation occurred at similar times across lineages and habitat preferences, showing a great deal of correlation with the 'epochs of interest' predicted by the Pulsed Climate Variability hypothesis (Donges et al., 2011; Trauth et al., 2010). The influence of the Pleistocene variability does seem to be largely found amongst closely related species and between intraspecific populations, as predicted by Bowie et al. (2004b), and most of the cladogenesis events correlate with periods of high climate variability, suggesting that in times of climate stability birds in open habitats have been able to increase their populations and expanded their range only to have periods of high climate variability fragment populations and provide opportunity for allopatric speciation or adaptive radiation into a dynamic mosaic of habitats. Many of the cladogenesis events not only correlate with climate variability, but notably with periods with high lake levels suggesting that climates that could maintain these large lakes have influenced the speciation cisticolas rather than the periods of aridity that have previously been invoked to drive speciation in savanna habitats. Comparative phylogeographic studies of savanna species should be re-evaluated against this paradigm, especially those species which show splits that correlate with the arid corridor.

5.5 Conclusions

The timing of the diversification of cisticolas seems to correlate well with tectonic activity and climate variability but the current distributions of cisticola species do not show as elegant a pattern as many of the savanna mammals. This somewhat obscured pattern might be due to secondary expansion of range after initial speciation, but a more intensively sampled survey may reveal better resolution for some concordant patterns of genetic diversity with other groups and vicariance events to be more easily identified and appreciated.

5.6 Figures and Tables

Continued on next page.

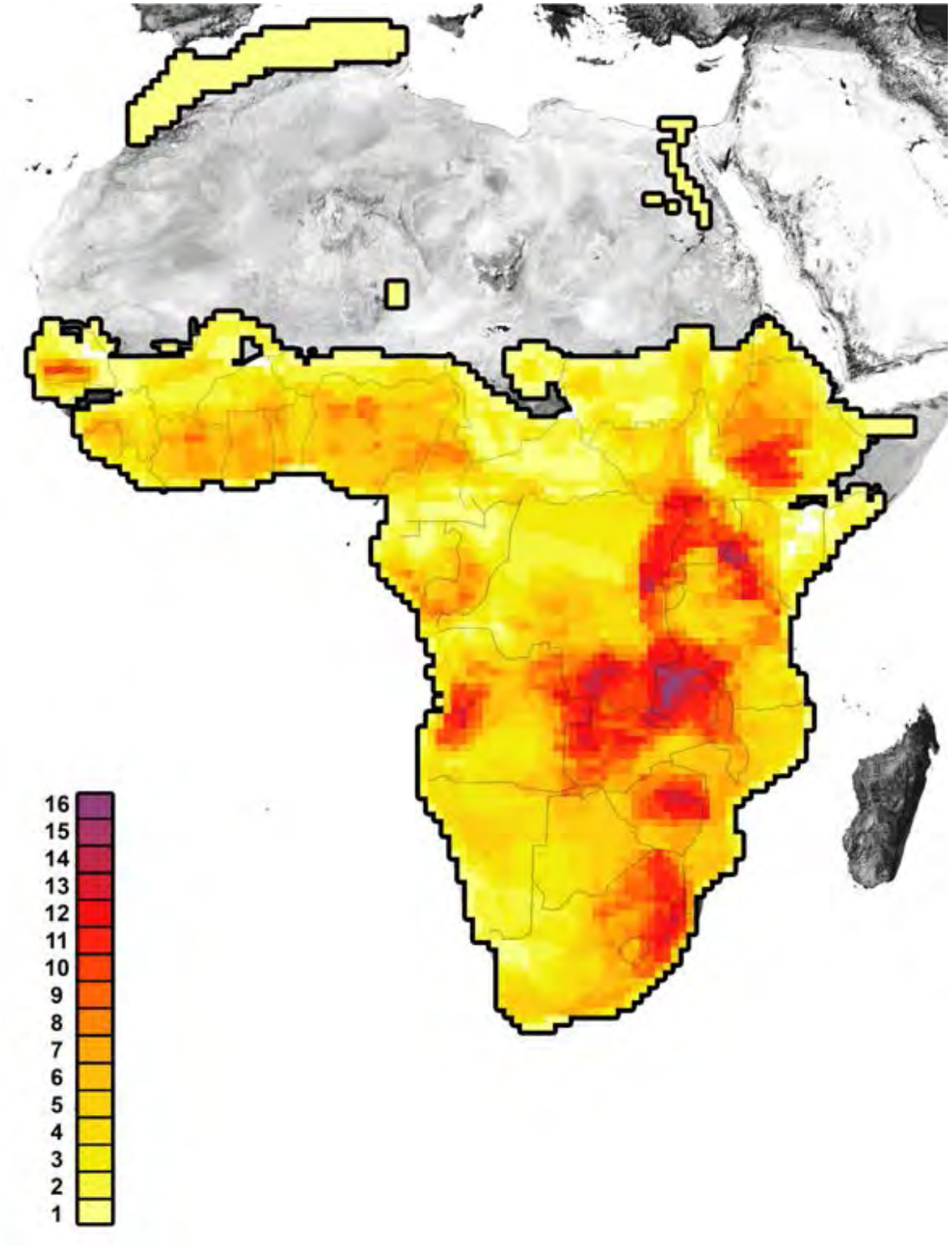


FIGURE 5.1: Species richness of cisticolas across Africa.

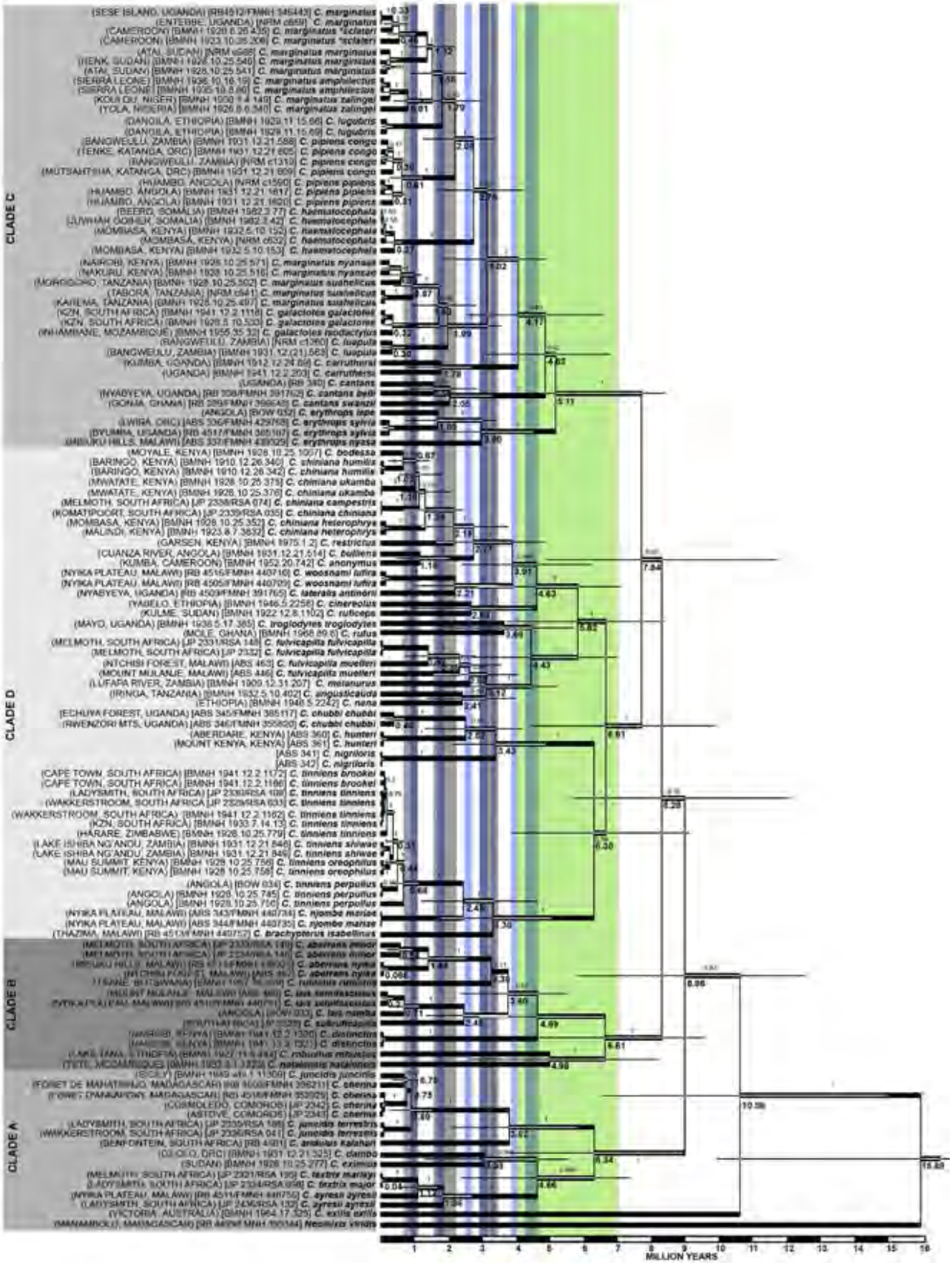


FIGURE 5.2: Dated phylogeny indicating posterior probabilities, mean divergence ages and 95% error bars. Green bar indicates time of expansion of C4 grasses (Voje et al., 2009), grey bars indicate periods of extreme climate variability and blue bars indicate times of high lake levels (Donges et al., 2011).

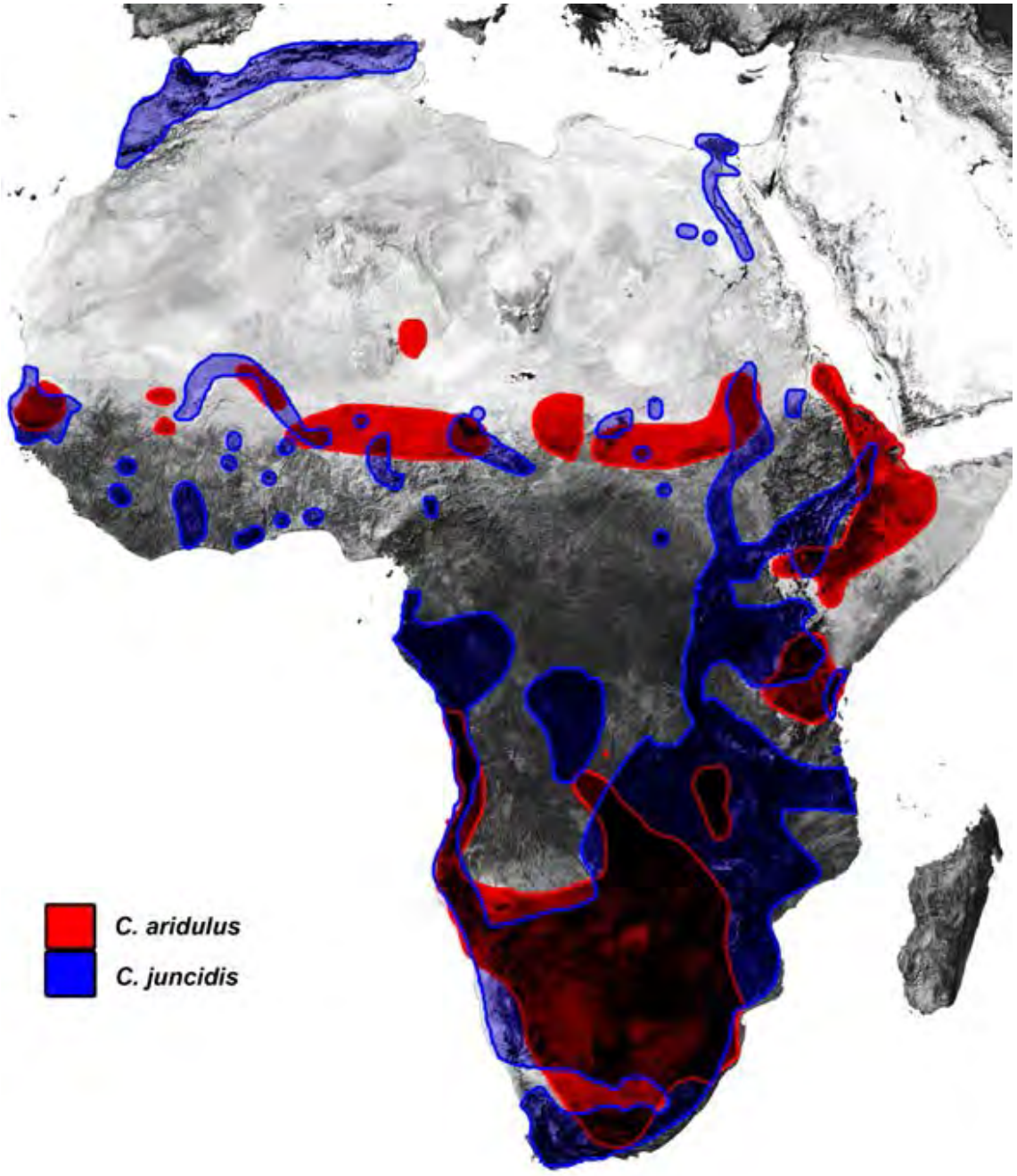


FIGURE 5.3: Distribution map of *C. aridulus* and *C. juncidis*; mean date of divergence was 3.82 MYA with *C. aridulus* favouring drier habitats than *C. juncidis*.

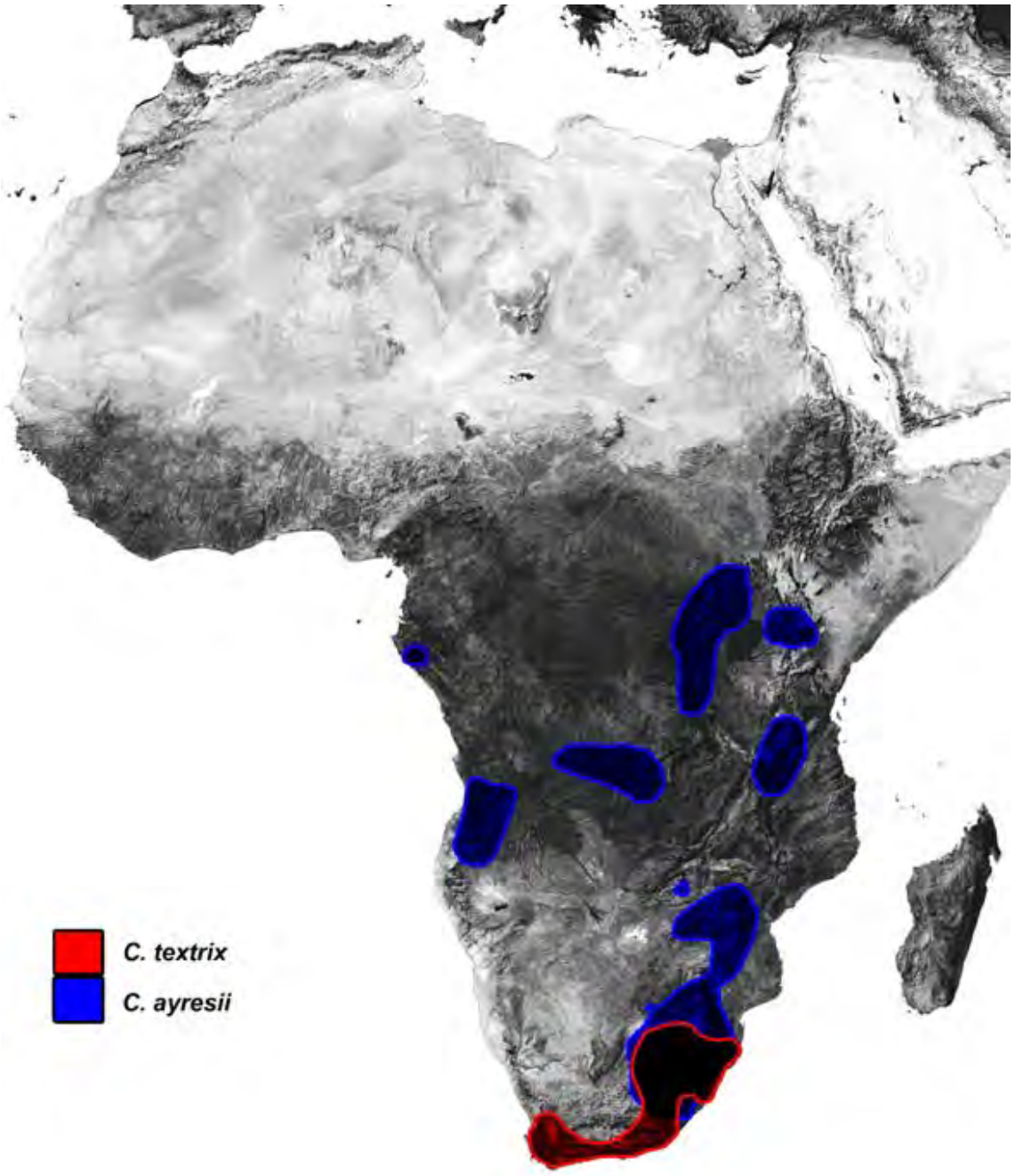


FIGURE 5.4: Distribution map of *C. textrix* and *C. ayresii*; with a split occurring around 1.12 MYA.

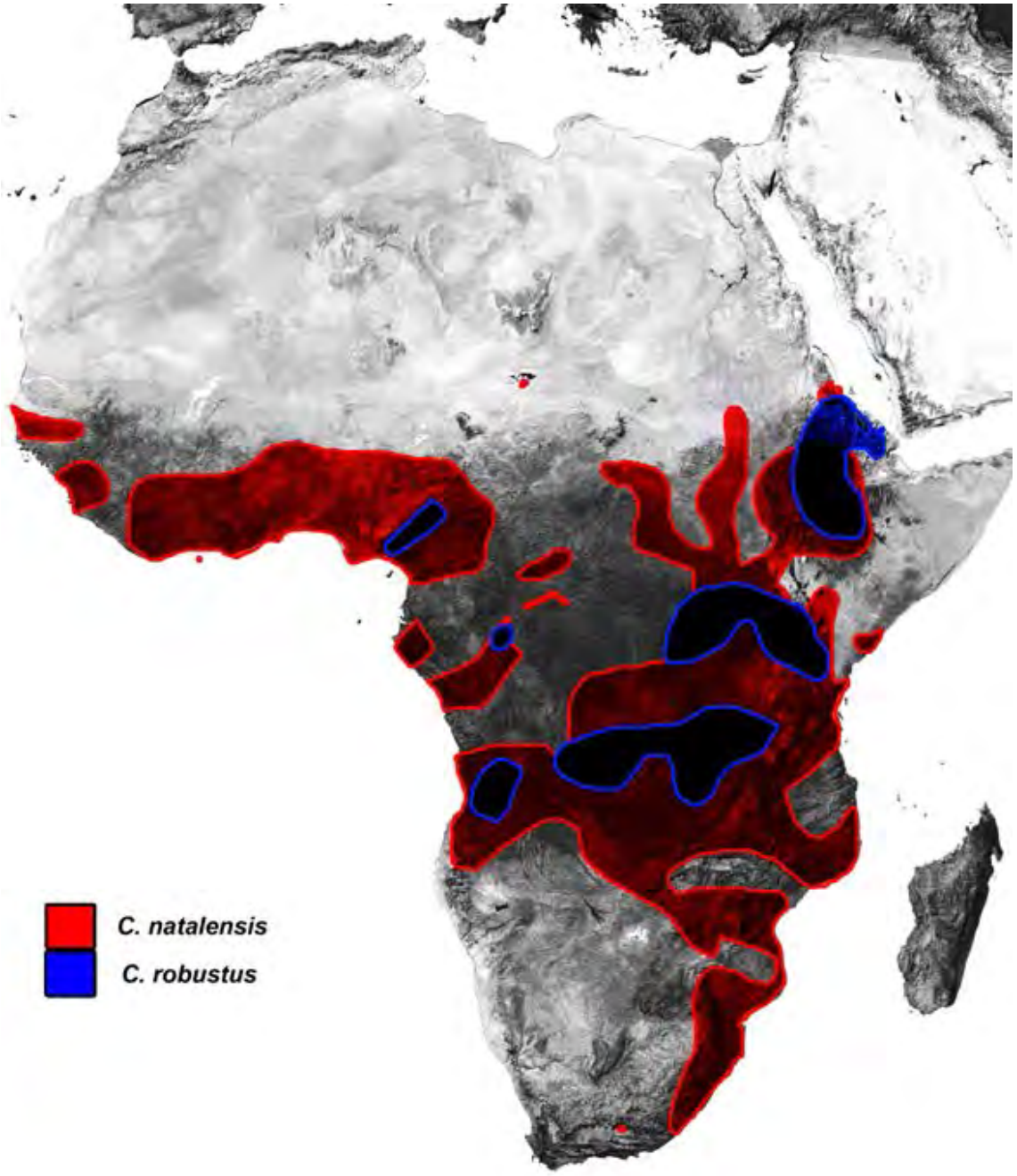


FIGURE 5.5: Distribution of *C. natalensis* and *C. robustus*; these two species diverged an estimated 4.89 MYA.

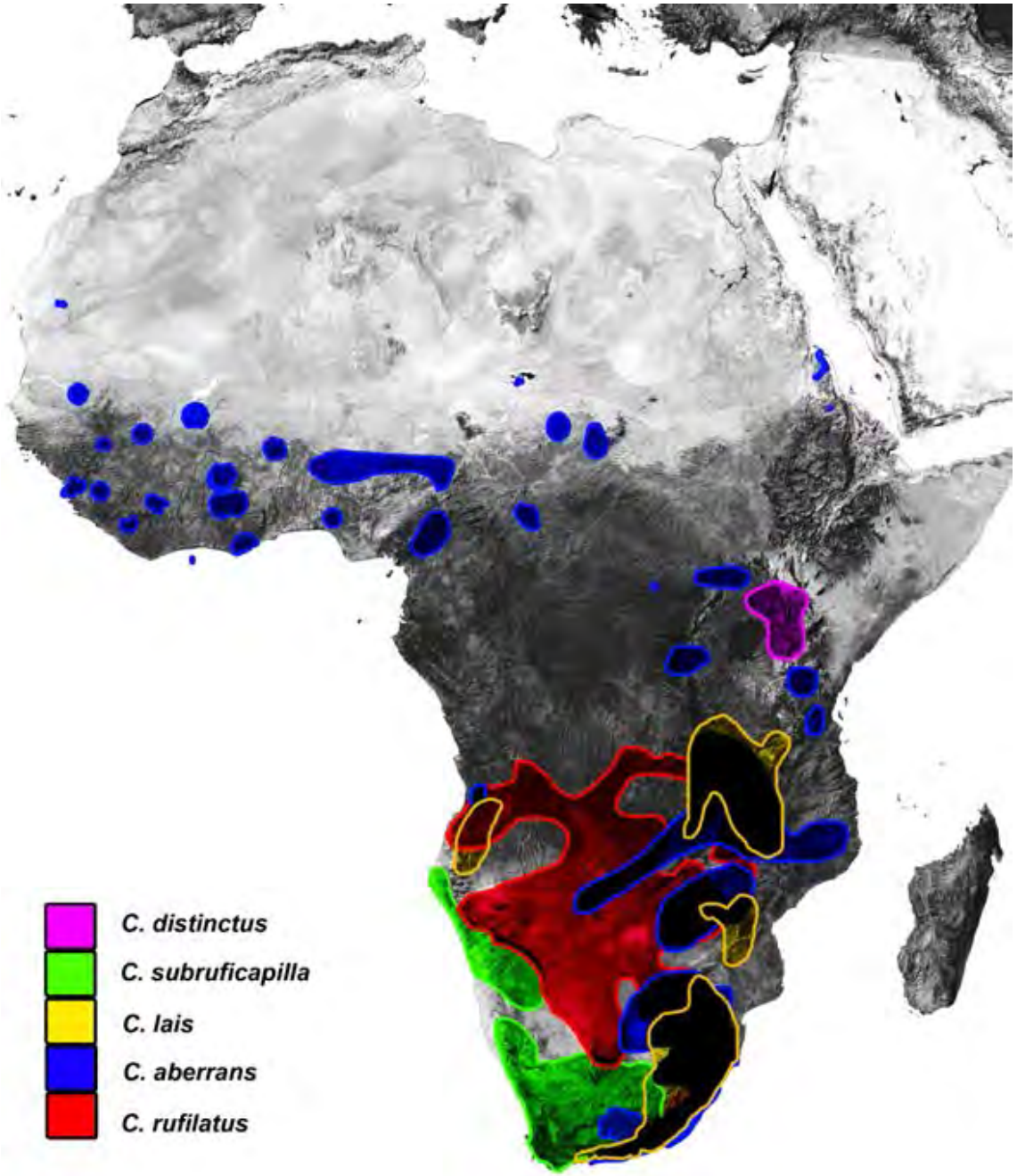


FIGURE 5.6: Distribution of the subruficapilla group showing a southern distribution of many species, with *C. [l]. distinctus* diverging around 4.69 MYA during a period of high lake levels.

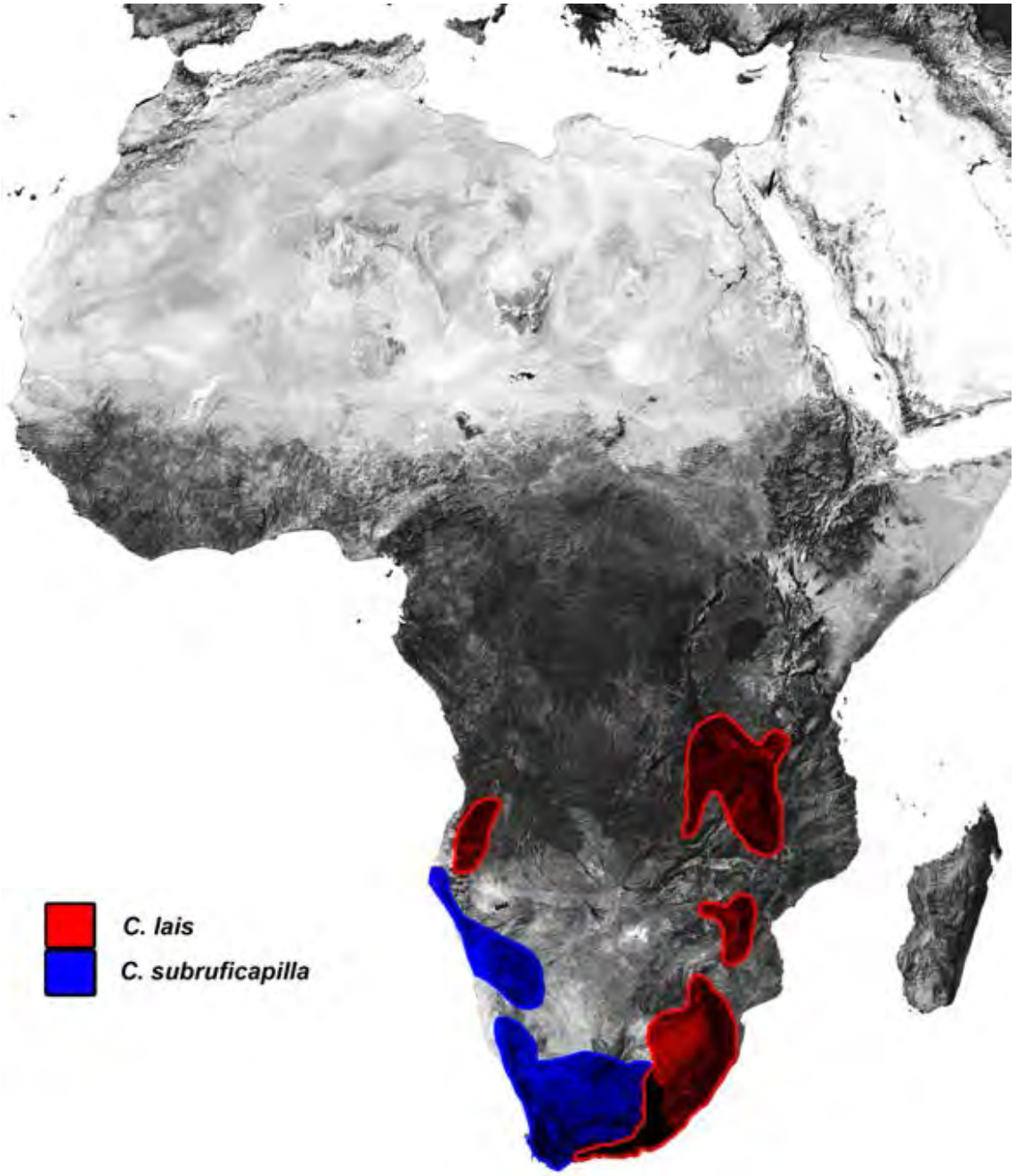


FIGURE 5.7: Distribution of *C. lais* and *C. subruficapilla*, two scrubland dwelling species which diverged at an estimated 2.49 MYA.

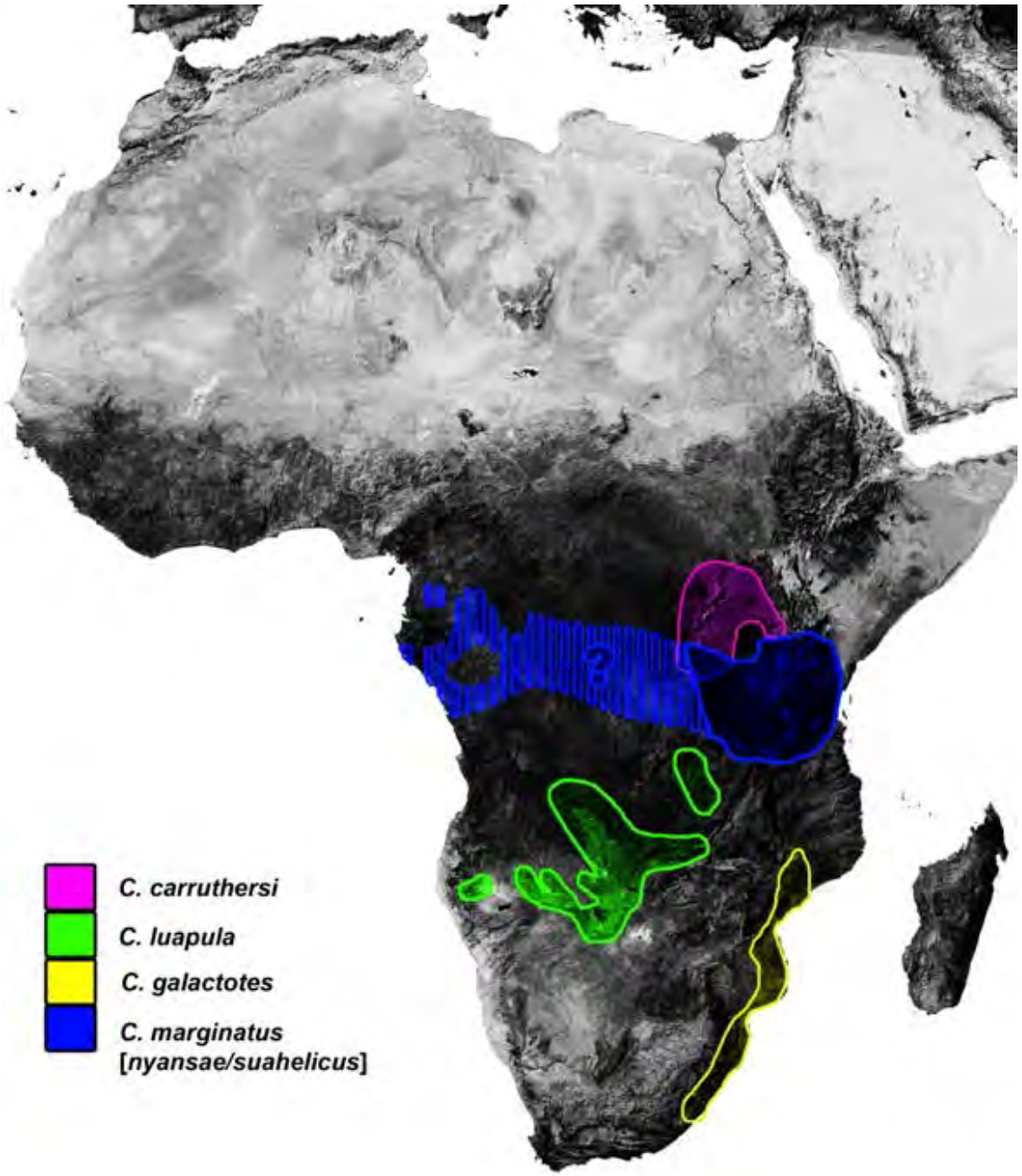


FIGURE 5.8: Distribution map of *C. carruthersi*, *C. luapula*, *C. galactotes* and Kenyan/Tanzanian members of *C. marginatus*. The area of uncertain distribution is due to this area formerly being considered to be part of the range of *C. marginatus nyansae*, but specimens collected in Uganda are more closely related to those in western Africa than to those in Kenya; the affinity of birds in this area is therefore unknown. Divergence between *C. luapula* and *C. galactotes* occurred around 1.99 MYA, and the divergence between *C. galactotes* and *C. marginatus* occurred around 1.68 MYA.

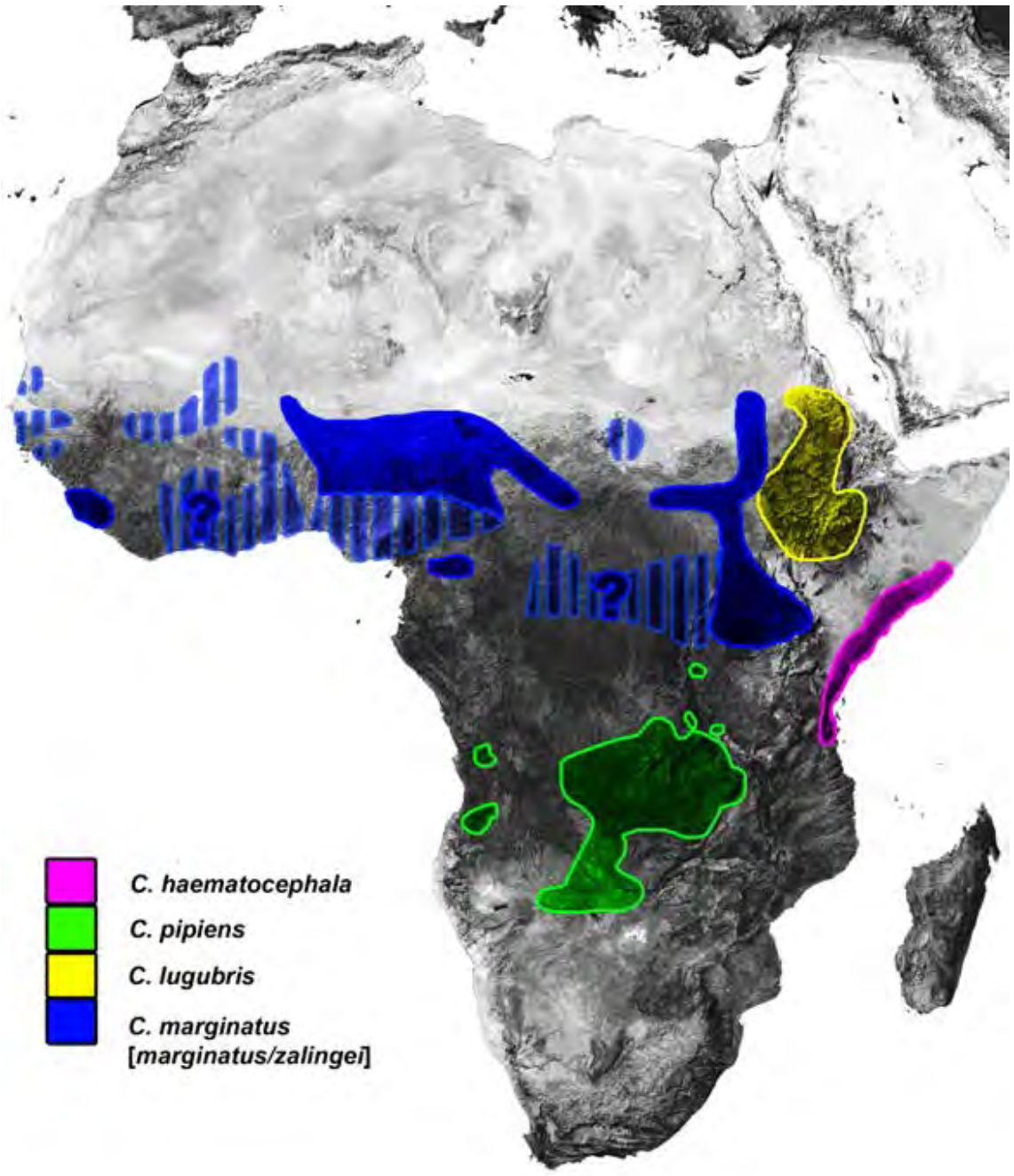


FIGURE 5.9: Distribution map of *C. haematocephala*, *C. pipiens*, *C. lugubris* and northern and western populations of *C. marginatus*. The divergence of *C. haematocephala* occurred 2.75 MYA and the divergence between *C. pipiens* and *C. lugubris* occurred 1.79 MYA followed by *C. marginatus* 1.50 MYA.

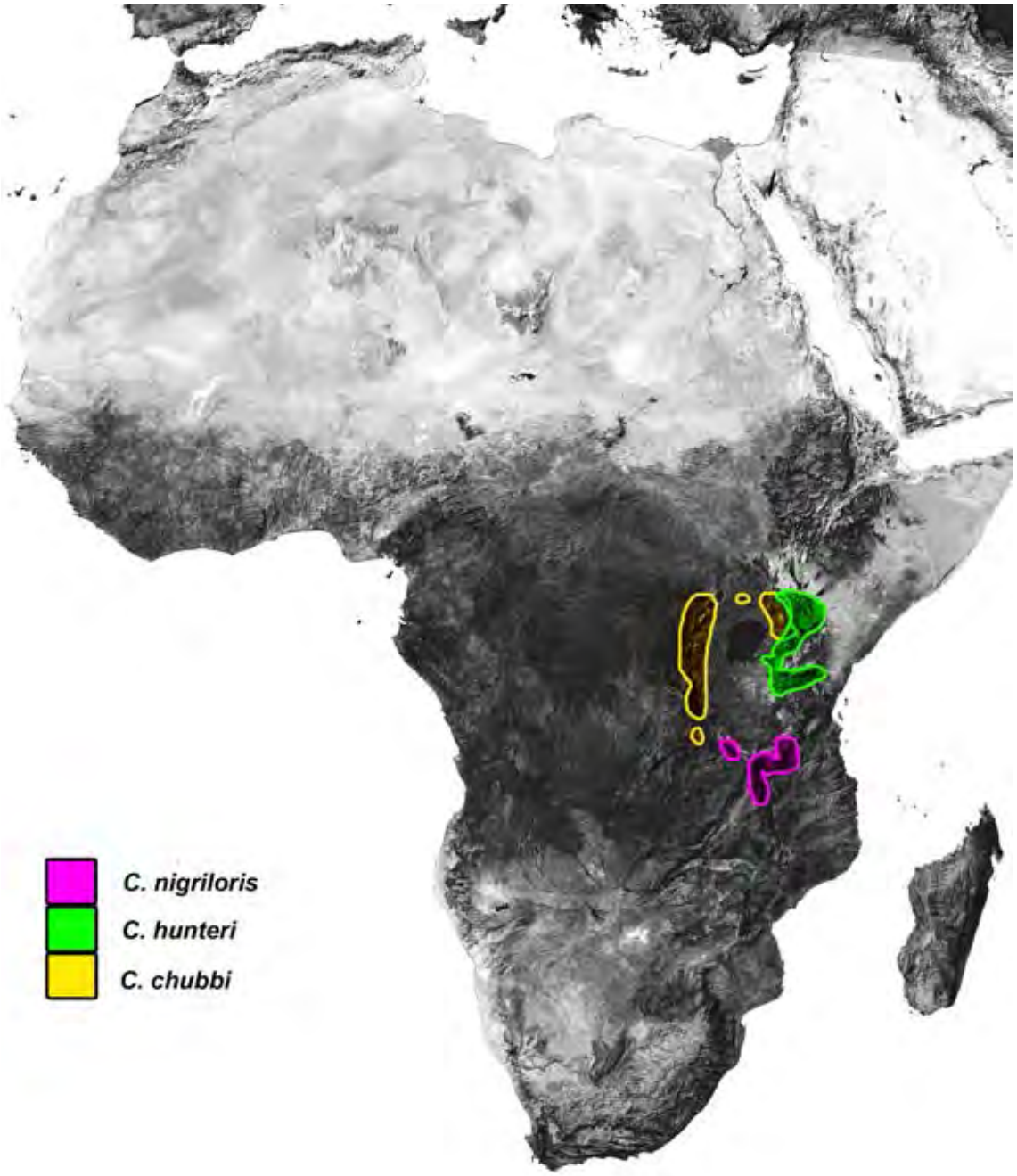


FIGURE 5.10: Distribution map of *C. nigriloris*, *C. hunteri* and *C. chubbi*. Initially *C. nigriloris* diverged at 3.43 MYA, followed by the separations of *C. hunteri* and *C. chubbi* estimated at 2.52 MYA.

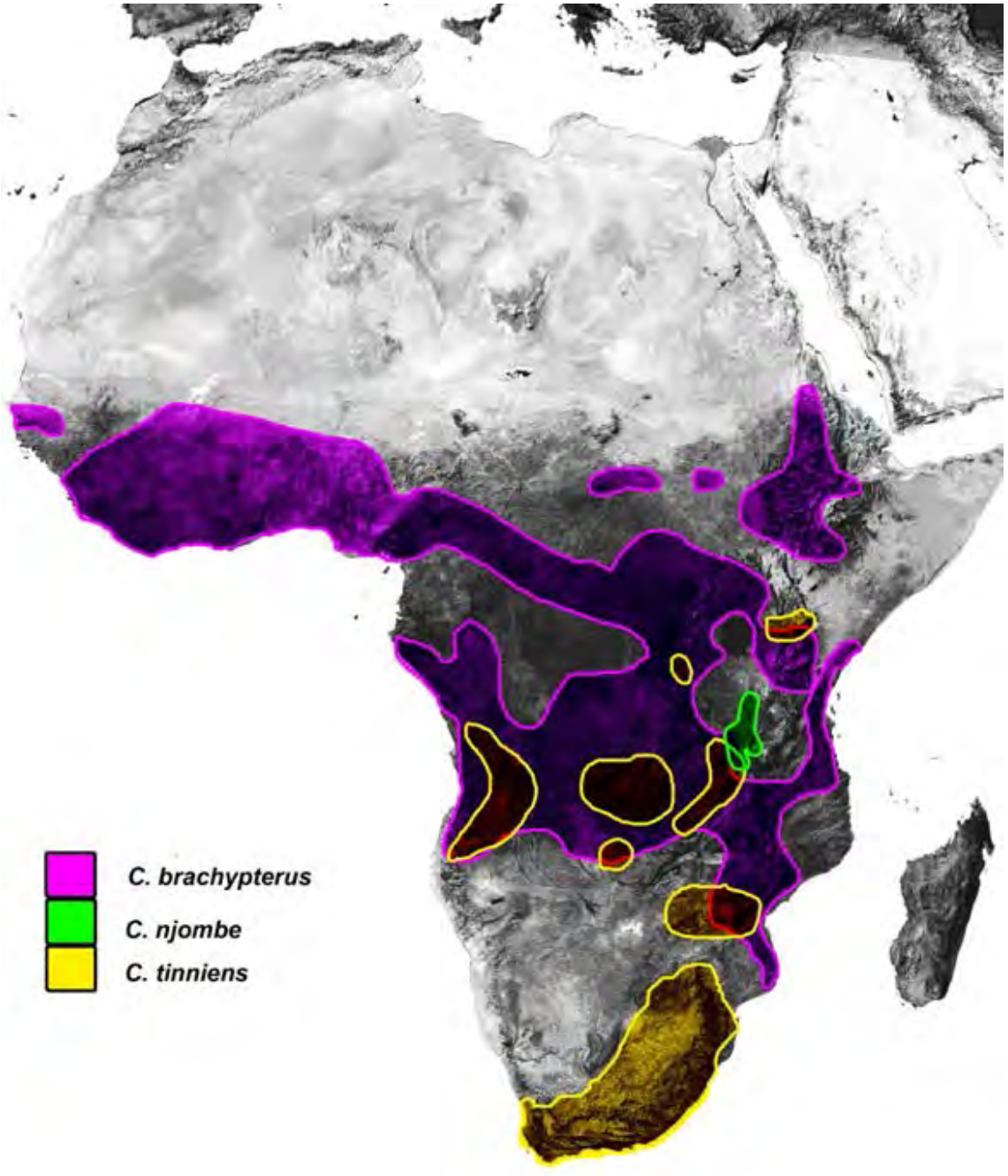


FIGURE 5.11: Distribution map of *C. brachypterus*, *C. njombe* and *C. tinniens*. The divergence between *C. brachypterus* and *C. njombe* occurred 3.30 MYA, while *C. njombe* and *C. tinniens* separated 2.45 MYA. These events may have occurred around Rukwa Rift and could have restricted geneflow in other taxa between eastern and southern Africa multiple times.

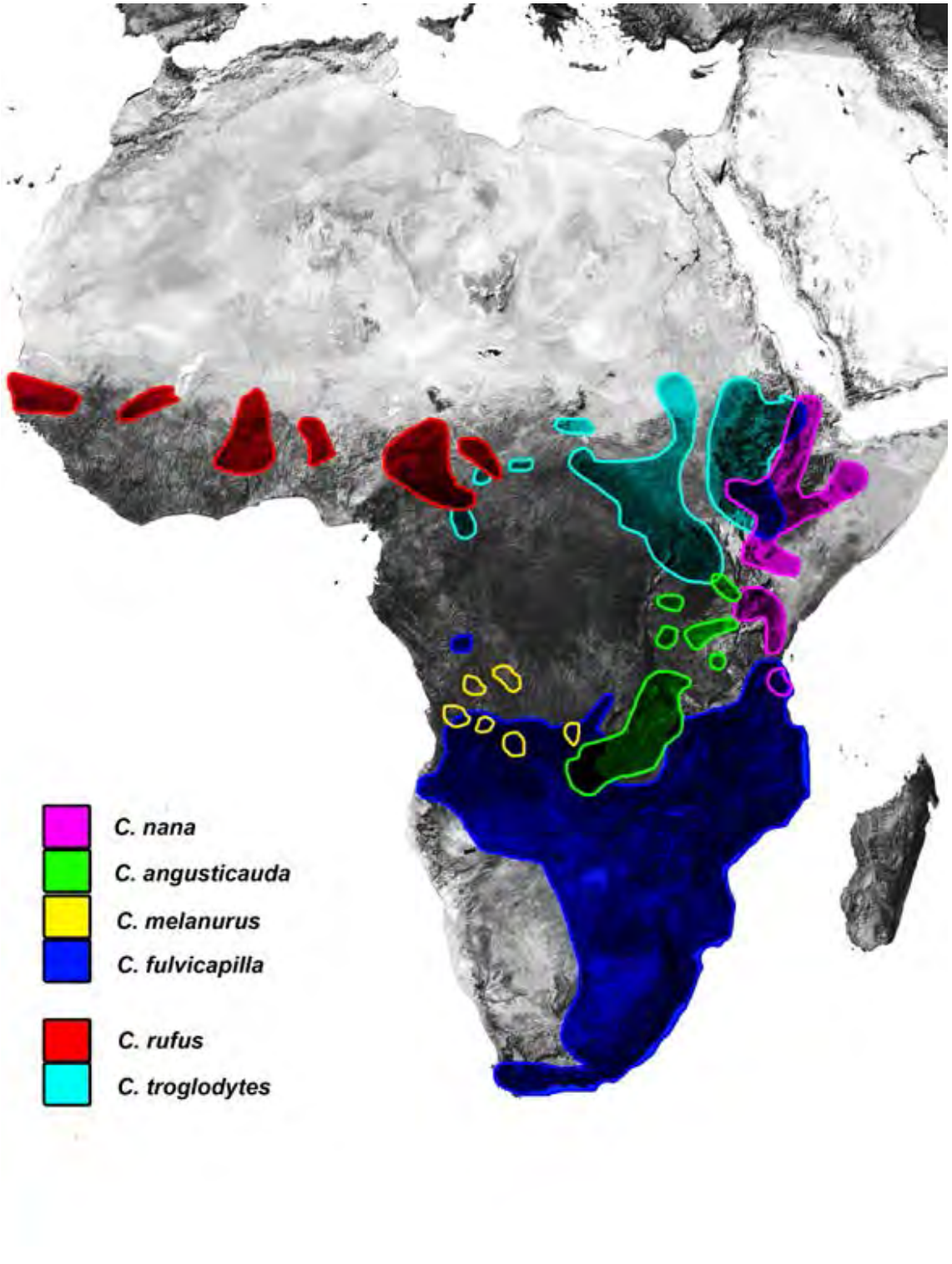


FIGURE 5.12: Distribution map of *C. nana*, *C. angusticauda*, *C. melanurus*, *C. fulvicapilla*, *C. rufus* and *C. troglodytes*. Two species in the northern savanna belt, *C. troglodytes* and *C. rufus*; separated around 3.66 MYA and *C. nana*, from the Somali-Masai biome, separated from the Zambezian biome species *C. angusticauda* around 2.41 MYA.

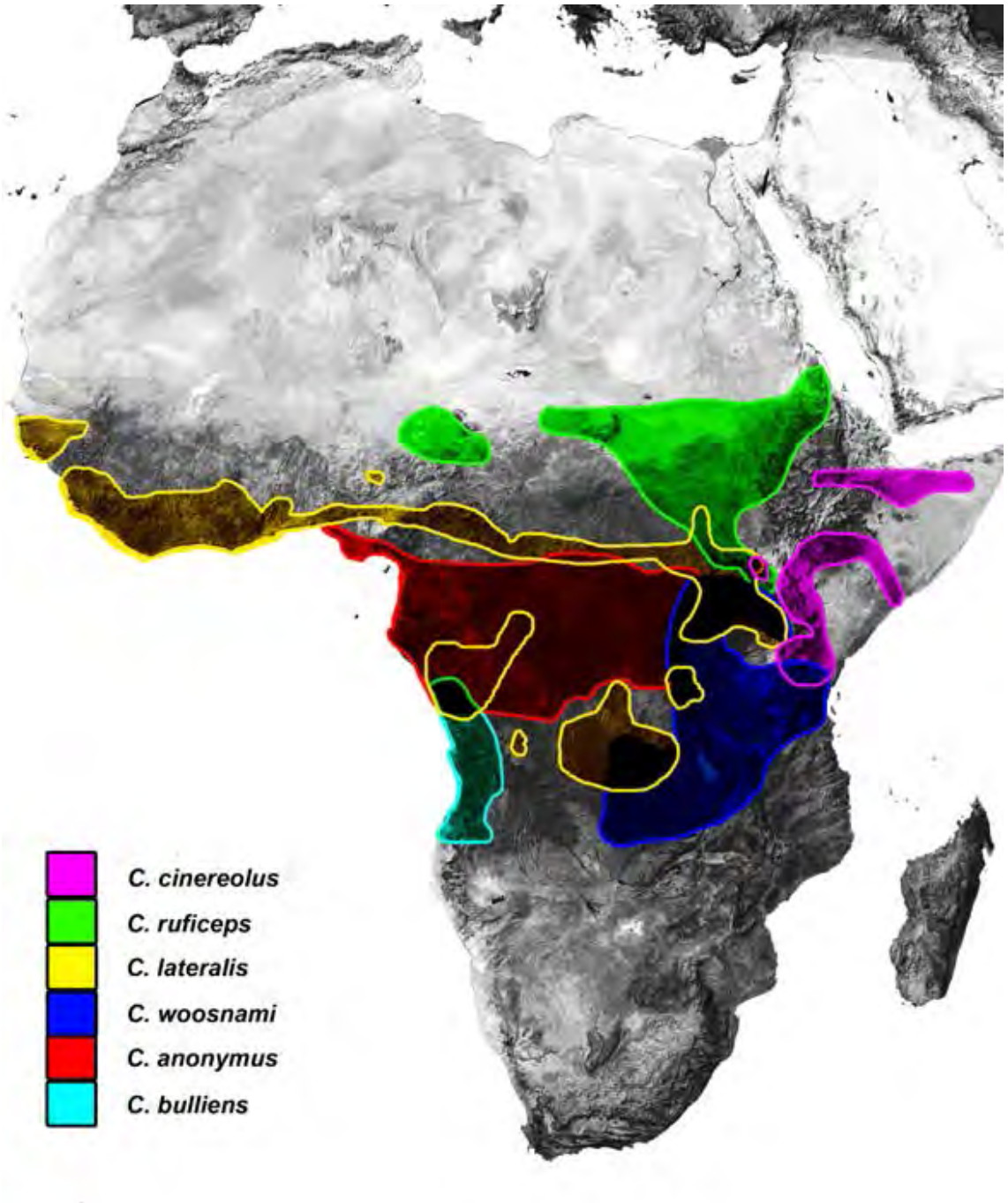


FIGURE 5.13: Distribution maps of *C. cinereolus*, *C. ruficeps*, *C. lateralis*, *C. woosnami*, *C. anonymus* and *C. bulliens*; the initial divergence of this clade (not showing *C. chiniana*) occurred 4.63 MYA.

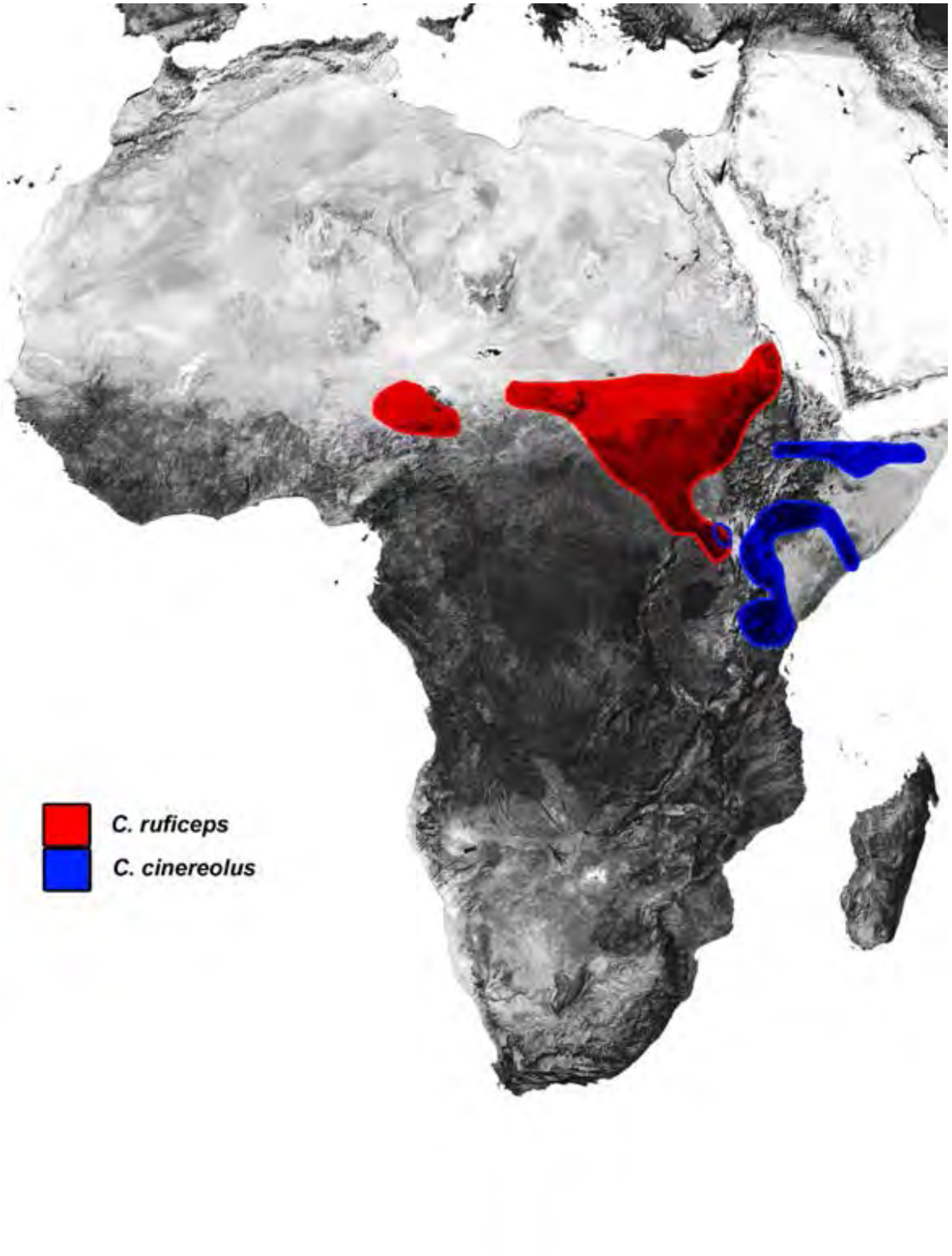


FIGURE 5.14: Distribution map of *C. cinereolus*, found in the Somali-Masai savanna biome, and *C. ruficeps*, found in the Sudan-Guinea savanna biome, separated from each other around 2.63 MYA potentially around the rift valley.

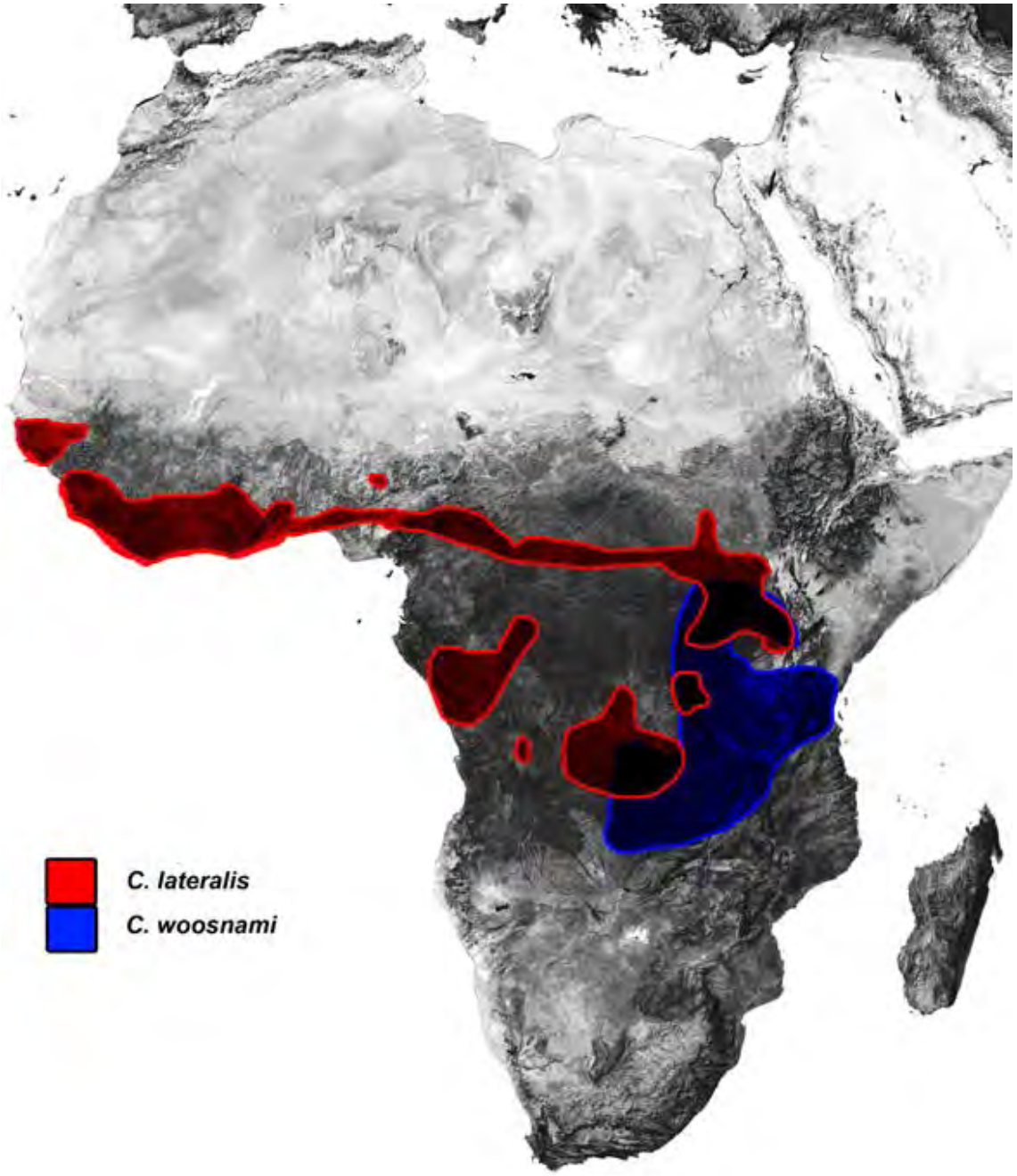


FIGURE 5.15: Distribution of *C. lateralis* and *C. woosnami* estimated to have separated around 2.21 MYA.

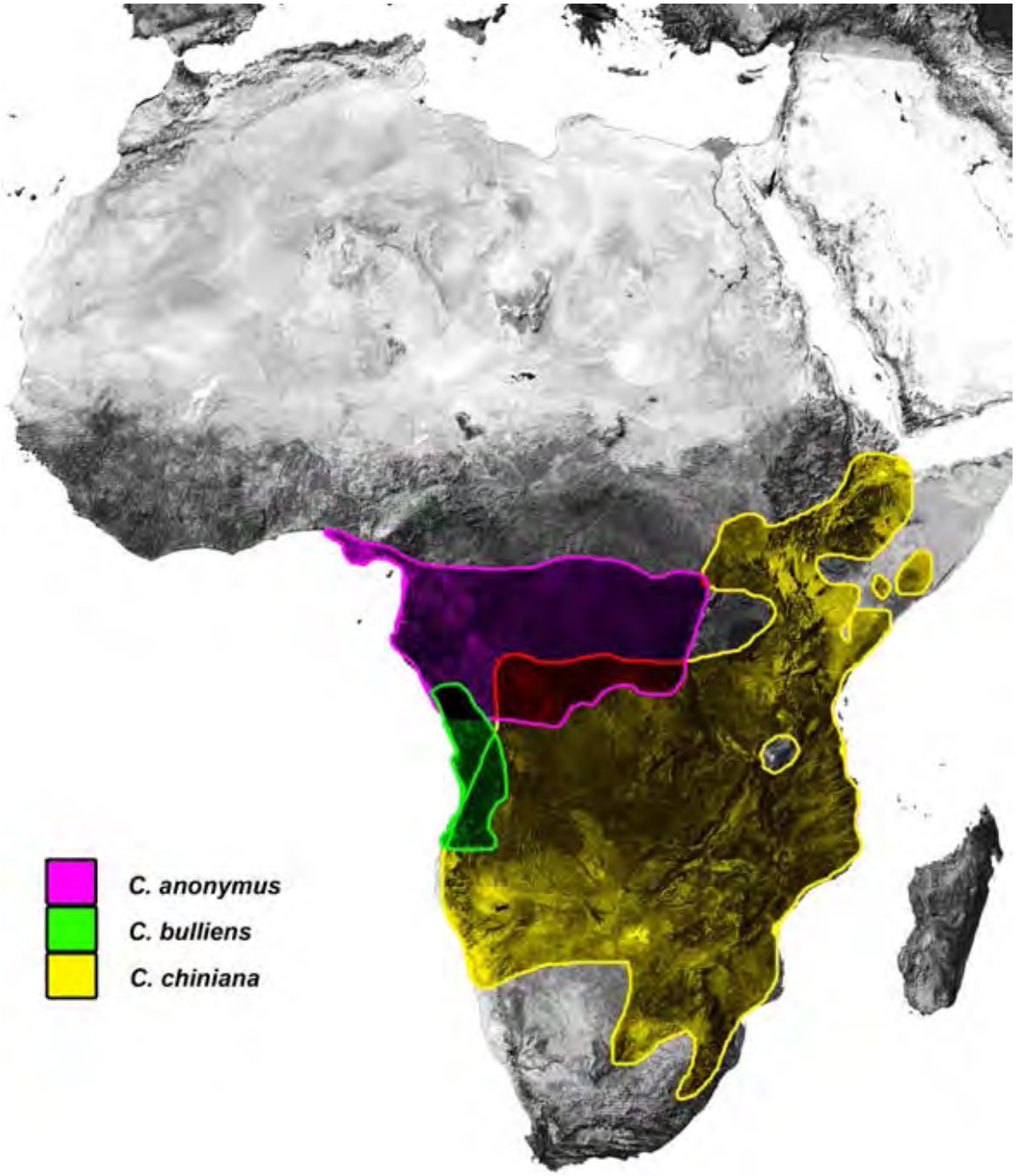


FIGURE 5.16: Distribution of *C. anonymus*, *C. bulliens* and *C. chiniana*. The divergence between *C. anonymus* and *C. bulliens* occurred 1.18 MYA, and these species shared a common ancestor with *C. restrictus* (not drawn) and *C. chiniana* 2.77 MYA.

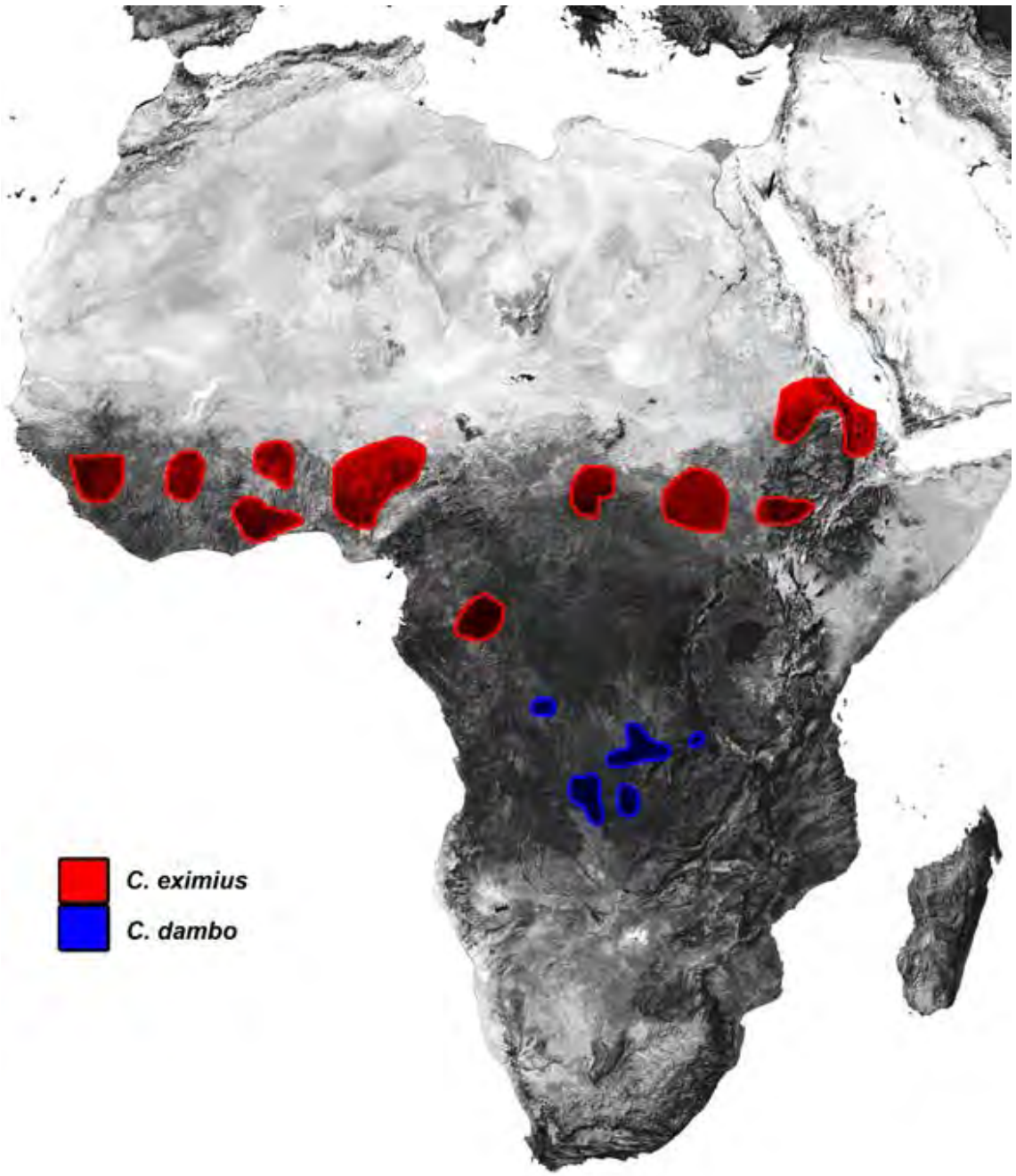


FIGURE 5.17: Distribution of *C. eximius* and *C. dambo* exhibiting a north-south divide similar to those which invoke the expansion of the equatorial forest to the Kenyan coast to separate taxa; these species diverged around 3.08 MYA during a period of high climate variability.

Chapter 6

A review of the specific status of the Tana River Cisticola (*C. restrictus*) Traylor, 1967

6.1 Introduction

While examining cisticolas in the Field Museum of Natural History, Traylor (1967) identified three specimens amongst a collection of *C. cinereolus* that appeared to represent a novel species. Three additional specimens were identified in the Los Angeles County museum that had been collected from the same location around the Tana River; Traylor (1967) described a new species, *C. restrictus*, from these six specimens. The type specimen is an adult male collected on 4 June 1932 by V.G.L van Someren from Karawa in the Tana River Delta; it is currently housed in the Field Museum of Natural History in Chicago (FMNH 200020, Traylor (1967)). The Field Museum has two additional specimens of *C. restrictus* (FMNH 200017 and 200019) that were collected from Sangole, about 125 km north of the type locality, on 3 March 1931. Two of the three specimens in the Los Angeles County Museum of Natural History were collected at Ijara (1° 34' S, 40° 31' E), some 125 km from the type locality by J.G. Williams on 20 June 1962 (LACM 55706 and 55707), with the third specimen collected at Mnazini, approximately 70 km from the type locality, by R. Destro on 22 March 1963. The collections in the Natural History Museum at Tring include two specimens collected near Garsen, about 40 km from the type locality, by A. N. Start on 12 August 1967 (BMNH 1975.1.1 and 1975.1.2). The Nairobi National Museum has a specimen of *C. restrictus* (NMK 16536/890 or 16207/890) collected from the type locality by A. Forbes Watson on 4 September 1972. Together, these nine specimens represent the sum total of all

individuals of *C. restrictus* known to exist. More recent attempts to locate the species in the field have been unsuccessful and the species has not been seen since 1972 (Ryan, 2006), prompting speculation about the validity of the taxon, which has mostly shifted into rejection (BirdLife, 2014). Several subspecies of *C. chiniana* are found around the vicinity of the Tana River (Figure 6.1) and it has been suggested that *C. restrictus* samples might be the result of hybridisation between *C. chiniana* and *C. cinereolus*, or simply an aberrant form of the latter, rather than a novel species (Ryan, 2006; Tye, 1997).

Tana River Delta in context

The Tana River Delta is a diverse area situated on the Kenyan coast and is home to more than 345 species of birds including the threatened Basra Reed Warbler (*Acrocephalus griseldis*; potentially its main wintering ground) and the near-threatened, range restricted Malindi Pipit (*Anthus melindae*) (Mireri et al., 2008). The wetlands of the delta, together with the coastline and offshore islets, often host high concentrations of water birds, with internationally important populations of at least 22 species (Ng'weno, 2008). The Tana River Delta is an Important Bird Area (IBA) and a portion has recently become Kenya's sixth Ramsar site, recognised as a wetland of international importance, representing the country's first Ramsar site that is found outside of the Rift Valley (Ndoo, 2012). In addition to the importance of the area to birdlife, the area is also home to two endangered primates (Hamerlynck et al., 2012): the Tana River Red Colobus (*Procolobus rufomitratus rufomitratus*) and the Tana River Mangabey (*Cercocebus galeritus*).

The area has received attention as it faces pressure from both the increasing local human population growth of about 3.4% per annum, which is above the national average (Odhengo et al., 2012), and from increasing interest from investors. Recently there have been commercial development proposals from over half a dozen companies including large-scale sugar and bio-fuel production, large-scale rice and maize production, industrial prawn farming, titanium mining and oil and gas exploration, as well as various large-scale infrastructural projects proposed as part of the Kenyan government's 'Vision 2030', which has targeted the Tana River basin for development (Government of the Republic of Kenya (2007)). The recent history of proposed developments in the area is complicated by politics; an attempt to outline some of these recent events will go some way towards demonstrating the uncertainty that exists about the future of the Tana River Delta.

In the 1980s and early 1990s, Coastal Aquaculture Limited possessed rights to develop

13 000 ha in the Tana River Delta to farm shrimp and build a tourist complex (Kang'aru, 2008), but land was compulsorily acquired by the government before completion, resulting in a long legal process challenging the acquisition (Kenya-Law, 1996, 2001). The company was reportedly lobbying the new government in order to restart the project and develop shrimp farms (Trent et al., 2004).

The Tana Delta Irrigation Project (TDIP) was a product of a feasibility study that was commissioned by Tana and Athi Rivers Development Authority (TARDA) in 1981 to study irrigation development in the Lower Tana River Basin. The study identified 12 000 ha as suitable for rice production under irrigation (Figure 6.2, TARDA (2012)). TARDA approached the Japanese Government to finance a rice scheme which was funded through the Japanese Bank for International Cooperation (Luke et al., 2005). The implementation of Phase 1 covering 1 763 ha was completed in October 1987; this comprised irrigation infrastructure, flood protection dykes, an estate compound and a rice mill complex (TARDA, 2012). Most of the infrastructure was, however, destroyed by the El Niño floods of 1997/98, forcing TARDA to close down farm operations and the Japanese to cease funding (Lebrun et al., 2010). In 2009/2010, TARDA, under the Economic Stimulus Program (ESP) for Emergency Food Production, rehabilitated the farm infrastructure thereby opening up 1 300 ha for rice production. TARDA was recently seeking a partner to engage in 'Agri-Business Development of the Tana Delta Irrigation Project' (TARDA, 2012) with the aims to fully rehabilitate and operate the original 1 763 ha and add an additional 4 000 ha for rice production (TARDA, 2012).

TARDA proposed sugar cane production on part of the 28 680 ha previously allocated to the TDIP (Allotment Letter reference number 106798 of January 1995, Lebrun et al. (2010)), but the allocation and ownership of this land was challenged as TARDA had no title deed (Civil Case No. 660, Lebrun et al. (2010)). The proposal included the Mumias sugar & TARDA's Tana Integrated Sugar Project (TISP), which was to utilise 20 000 ha under an irrigation system with water supply from the river (Mireri et al., 2008). This included 16 000 ha for a sugarcane plantation and a 4 000 ha out-grower system; the proposal also included an ethanol production plant and a livestock component for fattening beef cattle (Mwaniki et al., 2007). An Environmental Impact Assessment (EIA) study was done but was challenged in terms of technical and scientific weakness, omissions, errors and ambiguities as well as procedural flaws (EAWLS, 2008). Nevertheless, Kenya's National Environment Management Authority (NEMA) approved the project's EIA (Temper, 2010). A court injunction was temporarily placed on the project following lobbying by conservation groups, but the case was thrown out on a technicality in 2009 (Makutsa, 2010). While the court injunction was still in force, TARDA were

awarded the title deed for an additional 40 000 ha above the 28 000 ha from their original allotment to grow maize and rice (Figure 6.2) because Kenya was facing a drought and food emergency (Odhengo et al., 2012). Bad press surrounding the case against the project prompted the initial investors to pull out (Makutsa, 2010) and development was temporarily put on hold while a master land use plan for the delta was developed in consultation with the local communities (Temper and Martinez-Alier, 2012). The Kenyan government recently published the Tana River Delta Land Use Plan Framework (Odhengo et al., 2012) and a Strategic Environmental Assessment Scoping Report 2012 (Odhengo et al., 2012) and Mumais renewed its search for additional funding and investment for project implementation (Anyanzwa, 2012; Ciuri, 2014) and plan to break ground by August 2014 (Ciuri, 2014).

Initially another company, Mat International, was involved in a deal with TARDA to grow sugarecane, but this deal was terminated before TARDA entered into the TISP agreement with Mumias, a partnership which Mat International had sought a court order to block (Law, 2006). Mat International is in the process of acquiring 120 000 ha of land for sugarcane production, 30 000 ha of which are within the delta and the remaining 90 000 ha are from the adjacent land (Nunow, 2011). The exact location of the project is unknown but it seems to include 30 000 ha north of Garsen town in Tana River County, 30 000 ha in the adjacent Ijara County and a further 60 000ha in the neighbouring Lamu County (Mwaniki et al., 2007).

In the mid-2000s, there was growing interest in biofuels and many investors were interested in the planting of crops for fuel in the Tana River Delta. For example, a British company, G4 Industries, had proposed to plant biofuel and oil seed on 28 000 ha in the Tana River Delta (Figure 6.2), focussing on irrigated Crambe, Castor and Sunflower oil (Odhengo et al., 2012). The company withdrew their proposal over concerns about the environmental implications of operations in the Tana Delta (RSPB, 2011). There was a similar proposal in the area surrounding Malindi, where Kenya Jatropha Energy Limited, a 100% owned Kenyan subsidiary of an Italian company (Nuove Iniziative Industriali Srl), planned to clear 50 000 ha of the Dakatcha woodlands to grow the biofuel crop *Jatropha curcas*. This proposal was denied by NEMA in 2012, as a result of a study by NorthEnergy (2011) commissioned by Nature Kenya and the Royal Society for the Protection of Birds (UK) and Action Aid, which highlighted the pitfalls of the proposal. It has been suggested that NEMA may have advised developers to look for an alternative site and the company moved its machinery to a more remote part of the woodlands (RSPB, 2013). A Canadian based company, Bedford Biofuels, secured 164 000 ha in the areas surrounding the delta (Figure 6.2) for the planting of *Jatropha* and was in

the process of securing an additional 200 000 ha (Bélanger-Gulick, 2013). Initially, Bedford Biofuels produced an EIA concerning the planting of 64 000 ha, but NEMA only granted a licence to plant a 10 000 ha 'pilot' project (Ndoo, 2012). Bedford Biofuels only managed to plant 19 ha before it pulled out of the country and filed for bankruptcy (Flood, 2013). In 2008, Better Globe Forestry Limited signed a memorandum of understanding with the Witu-Nyongoro Ranch Directed Agricultural Company Limited concerning the establishment of an industrial plantation of 23 000 ha of *Jatropha* and an additional 12 000 ha out-grower scheme (Figure 6.2, Deprins (2009)). The company soon realised that the oil yield from the crop did not match the hype and, following the recommendation of an economic viability study that advised that Jatropha plantations should be avoided in Kenya (Iyama et al., 2009), the company decided to change direction and plant Mukau (*Melia volkensii*) trees for timber, *Acacia senegal* for gum Arabic and mango trees on the land (Solberg, 2010). In 2012, Better Globe Forestry finalised a lease agreement to plant 10 000 ha of Mukau and they plan to plant an estimated one million mango trees on an additional 5 000 ha (Solberg, 2012). Their nursery has around 5 000 Mukau trees and is grafting approximately 19 000 mango trees which, when planted, will represent the largest mango plantation in Kenya (Solberg, 2013a). A soil conditioner, TerraCottem®, is being used by Better Globe Forestry; this technology allows for moisture to be stored closer to the roots and allows for trees to be planted in more arid areas (Solberg, 2013b). Better Globe Forestry started developing a five-year master plan for the ranch in the view that it will be the company's main processing plant due to the proximity of the proposed port and infrastructural developments associated with Kenya's flagship 'Vision 2030' project, namely the Lamu Port and Lamu-Southern Sudan-Ethiopia Transport (LAPSSET) corridor (Solberg, 2012).

The LAPSSET corridor is one of the largest transport and infrastructure projects in Africa (Jorgic, 2013) which aims to provide a transport linkage between Kenya, South Sudan and Ethiopia, and includes the construction of a new road network, railway line and oil/gas pipeline, an oil refinery and international airport at Lamu near a new port and resort cities on the coast (Figures 6.2 and 6.3, Kasuku (2012)).

The Kenyan government was in talks with Qatar in offering 40 000 ha of land in and around the Tana River Delta for food production exchange for investment in the construction of the new port at Lamu (Mireri, 2010; Nunow, 2011). The agreement was shelved, with China Communications Construction Company recently winning a tender to start construction (Jorgic, 2013). Additional infrastructure is planned in the area; the development includes the construction of the High Grand Falls mega-dam project on the Tana River to supply hydroelectricity and water for Lamu expansions and other LAPSSET developments. Upon completion, the dam would be the second largest dam

in Africa and Kenya was in talks with China to help finance the project (Gibendi, 2014). A major power project by the Kenya Electricity Transmission Company (KETRACO) is also awaiting funding for a high voltage transmission line from Malindi through the Tana River Delta area to Garsen and on to Lamu (Odhengo et al., 2012).

Omnicane, a Mauritian sugar company, is expanding operations on the Kenyan coast with 6 880 ha of sugar cane and a new sugar processing plant (in partnership with Kwale International Sugar Company Limited (KISCOL)) near Mombasa (Kihara, 2011). The plant was set for commissioning and expected to be fully operational by mid-2014 (Mwakio, 2013), there is also potential for an 8 000 ha expansion in the Tana River Delta (Temper, 2013). In addition to the sugar production investors already in the area (Mat International, Mumias/TARDA and Omnicane/KISCOL), the Kenyan government advertised an additional processing investment opportunity of 13 000 ha of land located in the Tana River Delta as part of its 'Greenfield' investment opportunities along the LAPSSET corridor (Kenya, 2012b). This development initiative also advertises investment in mango production in the Tana River Delta including 350 ha of cultivated land and a 6 000 ha out-grower scheme (Figure 2.3, Kenya (2012a)).

Various chemical and mineral mining operations have been proposed in the area, including titanium, oil and gas exploration and the expansion of local saltworks. Tiomin Resources (now Vaaldiam Resources Incorporated of Canada) proposed the extraction of titanium from the sand dunes of the Tana River Delta as well as further south in the Kwale district, but, after failing to obtain investment from the Chinese Jinchuan Group Limited, the project stalled (Hill, 2010). Recently, Base Resources Limited of Australia acquired the Kwale project, completed the processing plant and begun titanium extraction at the site (Muchira, 2013). Base Resources also acquired all the intellectual property associated with Tiomin's mineral-sands projects in Africa and an option to purchase three further exploration projects north of Mombasa (for which confirmatory drilling has already commenced), with an option to acquire 100% of Tiomin Kenya Limited (Hill, 2010). Considering their progress in the Kwale project, it seems likely that mineral exploration in the Tana River Delta area may still be pursued by Base Resources. Various petrochemical companies have been awarded exploration blocks to prospect for oil and gas in the area (Figure 6.3); some of the onshore allocations include AZ Petroleum, CAMAC Energy, Imara Energy, EDGO, Pacific Seaboard Investments, Rift Energy, Zarara and FAR Limited/Pancontinental Oil & Gas (Gilblom, 2012).

There are already a number of salt operations in the Tana River Delta area including Mombasa Salt Works, Kensalt, Malindi Salt, Krystalline Salt, Kemu/Tana saltworks and Kurawa Industries Limited, which is looking to expand its Kurawa salt works and

aquaculture by 5 360 ha (Twahir, 2011). The proposal included the integrated aquaculture of shrimp by using *Artemia* grown in the evaporation ponds as feed for shrimp that will be farmed in reservoirs where the brine density is equal to that of sea water (Twahir, 2011). These projects and the extensive development plans that have been proposed highlight the commercial interest in the area and the large-scale nature of many of the proposals may threaten the remaining habitat of *C. restrictus* should the species exist. The highly restricted proposed range of *C. restrictus* combined with the socio-political geographic context of the species' distribution and the uncertainty surrounding the future of the Tana River Delta has renewed interest in determining the status of *C. restrictus*. Currently, *C. restrictus* is classified as Data Deficient by the IUCN Red List as a consequence of taxonomic uncertainty (Butchart and Bird, 2010); this status would surely change to Critically Endangered due to range restriction if indeed the species was validated and observed in the field. This study aims to reassess the specific status of *C. restrictus* using morphological and molecular data and outline the potential threats to the habitat in the area of the Tana River Delta.

6.2 Methods

Only the two specimens in the Natural History Museum at Tring were examined, both of which were female. The measurements obtained from these specimens differed from the measurements published by Traylor (1967). While Traylor (1967) only measured a single female individual of *C. restrictus*, measurements obtained from specimens of other species also differed from those published by Traylor (1967), suggesting that the difference between the authors and Traylor's measurements of *C. restrictus* was not simply because of natural variation and small sample size but rather because different techniques may have been used to collect measurement data, making direct comparisons between studies difficult. Measurements were therefore taken from the two *C. restrictus* specimens and a number of other cisticola species in the Natural History Museum at Tring that had been collected in the vicinity of the Tana River. Measurements included bill length (to the insertion of the skull), bill width and bill height (at the nares), wing length, the length of the outermost primary feathers, tarsus length and tail length. Measurements for male specimens were captured from Traylor (1967) but analysed separately. Measurement data were analysed using the 'FactoMineR' package (Husson et al., 2013) in R (R-Core-Team, 2013). Analyses of females were done on untransformed and transformed measurements; transformed measurements were scaled for size by dividing each measurement by wing length with measurements from the outermost primary feathers only included as a proportional length between the two to reduce correlation. Molecular data was obtained from the toe-pad of a single specimen of *C.*

restrictus (BMNH 1972.1.2) for inclusion in the analyses that included local subspecies of *C. chiniana*, *C. cinereolus* and *C. [lais] distinctus* (detailed in Chapter 3). Extractions and analyses were performed using methods outlined in Chapter 3.

6.3 Results

Morphologically, *C. restrictus* is similar to *C. cinereolus* but there are slight differences in plumage colouration between the two, with *C. restrictus* differing from *C. cinereolus* in that the feathers around the base of the nape are not whitish as in *C. cinereolus*, but rather tinged with a brownish wash. This brownish wash extends to the head-top in *C. restrictus* and this causes a contrast between the head and the rest of the back, which is somewhat more greyish in colour. This differs from *C. cinereolus* which has uniformly grey feather borders on the back all the way to the head-top and shows no such contrast in colouration. The streaking on the back is also somewhat narrower in *C. restrictus* than in *C. cinereolus*. The undersides of the two birds are also slightly different colours, with *C. restrictus* having a less buffy wash on the belly and a greyer tint on the sides and flanks than *C. cinereolus*. The tail of *C. restrictus* is tinted with a warmer brown than in *C. cinereolus*; it is also proportionately longer than in *C. cinereolus* (Traylor, 1967). *C. restrictus* has bold, black subterminal spots and buffy tips on the end of the tail (Traylor, 1967).

In comparison to the subspecies of *C. chiniana* that occurs in the area, *C. restrictus* is generally smaller and paler with less rufous on the wing edgings and has a proportionately longer tail. The subspecies of *C. chiniana* that occurs within the range of *C. restrictus*, *C. chiniana heterophrys*, does not exhibit seasonal variation in plumage, but rather has a perennial 'summer-like' plumage where the back is nearly plain dark brown with very few mottles or stripes (Lynes, 1930). This is in contrast to the stripe-backed *C. restrictus*. The more inland subspecies, *C. chiniana ukamba*, also has perennial plumage but it resembles the 'winter-like' plumage of the species and has more markings on the back than the coastal subspecies *heterophrys* (Lynes, 1930). *C. chiniana ukamba* differs from *C. restrictus* in that it is darker, with more brown on the back, and thicker stripes that appear more like mottling in comparison to the finer striping of *C. restrictus*. When comparing the morphology Traylor (1967) remarked on similarities between *C. restrictus* and *C. [lais] distinctus*, noting that they had similar patterning, colouration, tail proportions and dimorphism in size between the sexes. He maintained, though, that unless field observations of behaviour and song showed the two to be similar, they were not closely related (Traylor, 1967). The song of *C. restrictus* is reported to be similar to that of *C. chiniana* (Ryan, 2006).

Measurements of *C. restrictus* specimens most closely matched measurements obtained from female specimens of *C. cinereolus* (n = 5), particularly with respect to bill length, bill height, the length of the outermost primary and the proportional length between the outer two primary feathers (Table 6.1). A principal component analysis (PCA) on male specimens (using data captured from Traylor (1967)) resulted in *C. restrictus* positioned the closest to *C. cinereolus* in a plot of the first two principal components (Figure 6.4), which accounted for around 75.44% of the variance. Similarly, female *C. restrictus* specimens were positioned the closest to specimens of *C. cinereolus* in a plot of the first two principal components (71.18%) when measurement data were not corrected by size (Figure 6.5). A PCA on the corrected measurements from female specimens of *C. restrictus* clustered with specimens of *C. heterophrys* (Figure 6.6) when the first two principal components were plotted against each other (64.32%), indicating that *C. restrictus* has more similar proportions to *C. chiniana* than with *C. cinereolus*. Molecular analyses placed *C. restrictus* basal to the subspecies of *C. chiniana* (Chapter 3: Figure 3.14), rather than grouping with either *C. cinereolus* (9.4% sequence divergence) or *C. [lais] distinctus* (13.3% sequence divergence). The average sequence divergence between *C. restrictus* and the subspecies of *C. chiniana* was 5.1%, which is double the 2.9% average sequence divergence between subspecies of *C. chiniana* that occur in the area. Sequence divergence within *C. chiniana* ranged from a maximum of 3.2% between *C. chiniana heterophrys* and *C. chiniana humilis* and a minimum divergence of 1.3% between *C. chiniana humilis* and *C. bodessa*, which is currently regarded as a full species (Ryan, 2006).

6.4 Discussion

Given that *C. restrictus* specimens have streaked plumage that is more similar to *C. cinereolus* than to *C. chiniana heterophrys*, and that males and females cluster together with *C. cinereolus* when principal component analyses are performed on untransformed measurements, it is not unreasonable to suggest that the two species are closely related or conspecific. And, since the two female *C. restrictus* samples cluster with *C. chiniana heterophrys* samples when a PCA is performed on measurements that are corrected for size, it also seems reasonable to suggest that *C. restrictus* may be a hybrid between *C. cinereolus* and *C. chiniana heterophrys* when analysing the morphology of a limited number of individuals. Out of the 10 000 specimens examined by Lynes, he was unable to detect a single incidence of hybridisation (Lynes, 1930), so it is thought that such occurrences might be rare in the genus, with the exception of *C. angusticauda* and *C. fulvicapilla* which have been reported to hybridise in Zambia (Ryan, 2006).

It was predicted that the ND2 sequence obtained from the *C. restrictus* specimen would show a high degree of similarity to the sequences obtained from either *C. cinereolus* or *C. chiniana* specimens if it was a product of a hybridisation event between the two species due to the maternal inheritance of the complete mitochondrial genome. This pattern was not observed, as *C. restrictus* had an average sequence divergence of approximately 5.1% in comparison to *C. chiniana* and 9.4% in comparison to *C. cinereolus*. The divergence between *C. restrictus* and *C. chiniana* is similar to the sequence divergence observed between currently recognised species, for example: *C. galactotes* and *C. luapula* (4%); *C. pipiens* and *C. lugubris* (4%); *C. lateralis* and *C. erythrops* (4.1%); *C. lais* and *C. subruficapilla* (4.4%); *C. galactotes* and *C. lugubris* (4.5%); *C. lugubris* and *C. haematocephala* (5%); *C. chubbi* and *C. hunteri* (5.2%) and *C. aberrans* and *C. lais* (5.2%). The sequence divergence of *C. restrictus*, combined with morphological diagnosability, offers evidence that effort should be made to try and locate the species in the field in an attempt to determine if it still exists, and to make notes about the species' behaviour and songs if located.

While socio-political instability in the area, climate variability, saltwater intrusion and poor quality soils have contributed to the failure of many large scale projects in the area during the recent past, socio-political stability, community involvement, increased infrastructure and efficient management practices may still allow for economic development of the area, particularly if an adequate crop can be identified. A recent breakthrough in the potential use of the haplophyte, *Salicornia bigelovii*, in the production of biofuel in saline, desert environments (Cybulskaa et al., 2014) may renew biofuel investor interest in the area. Proposals such as the Sustainable Bioengineering Reseach Consortium's (SBRC) Integrated Seawater Energy and Agriculture System (ISEAS) concept aims to combine the aquaculture of shrimp with *Salicornia* production for aviation fuel by pumping saline water into a series of shrimp farms, which produce waste that enriches the salt water used to irrigate *Salicornia* crops, with runoff entering a mangrove system (Masdar, 2014). As shrimp and biofuels have both been attempted in the area, such a proposal might appear attractive as the design seems to avoid many of the difficulties that faced previous projects. Other technological advances, such as the soil conditioners already being used by projects in the area, may alleviate previous investor concerns regarding soil moisture and nutrients. Such renewed interest, combined with the large-scale developments that are already underway, are sure to place additional pressure on the environmental integrity of the area. As most of the *C. restrictus* samples were collected outside the recently designated Ramsar site, a dedicated field survey to try and establish the status of *C. restrictus* should be considered an urgent priority.

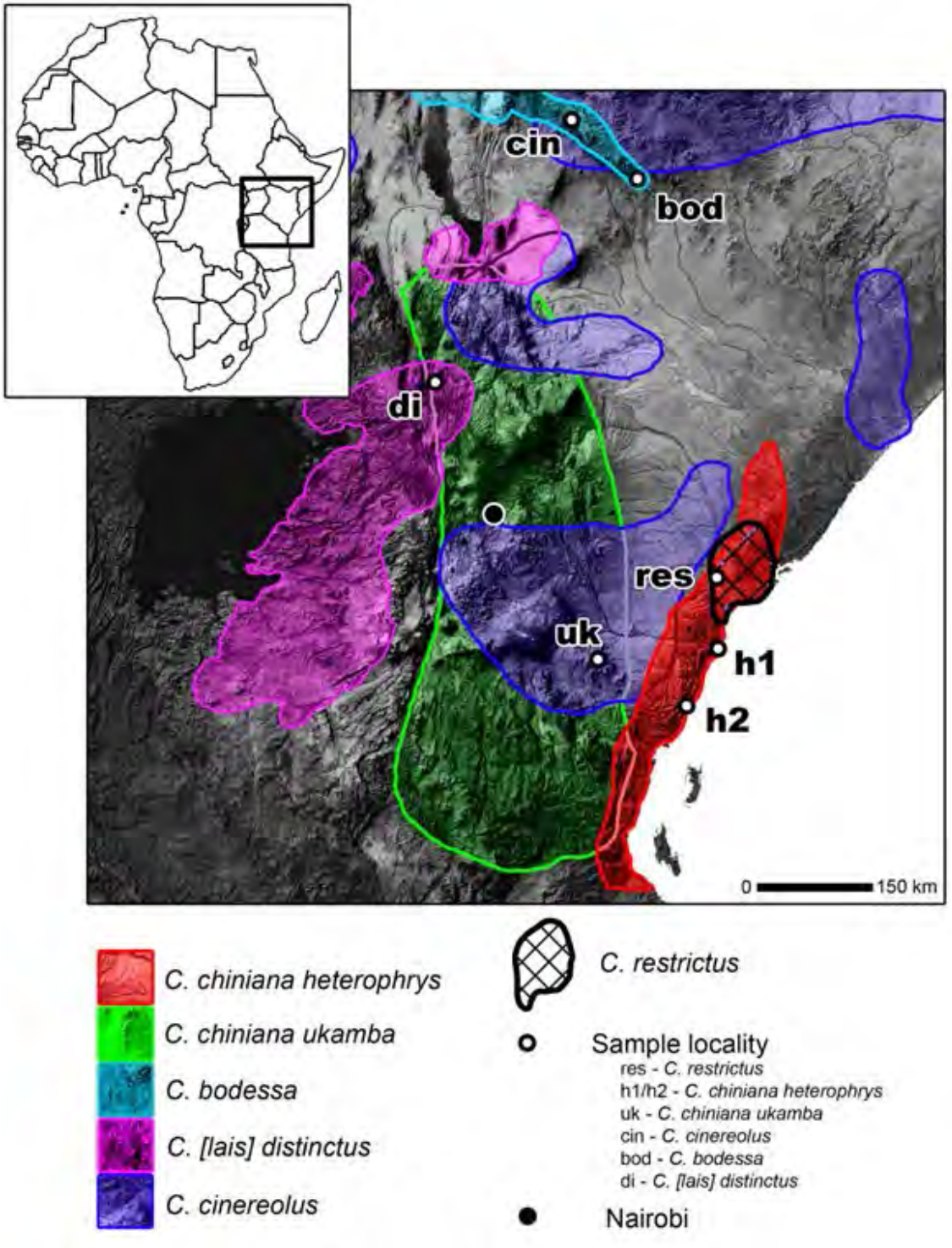


FIGURE 6.1: Distribution of *C. restrictus* (cross-hatched), *C. cinereolus* (blue), *C. [lais] distinctus* (pink), *C. bodessa* (turquoise), *C. chiniana ukamba* (green), *C. chiniana heterophrys* (red) and collection localities of measured specimens.

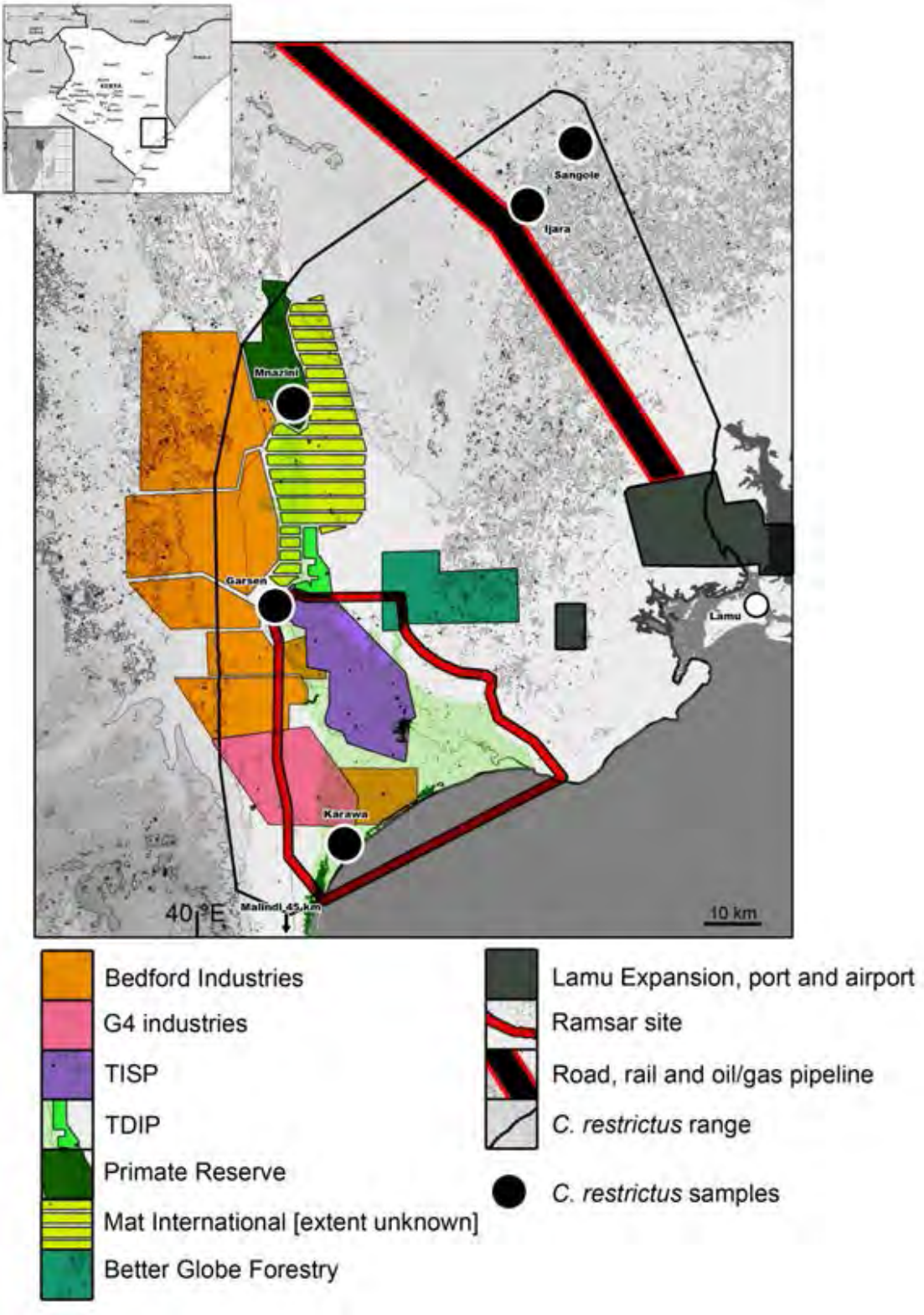


FIGURE 6.2: Recent development proposals in and around the Tana River Delta.

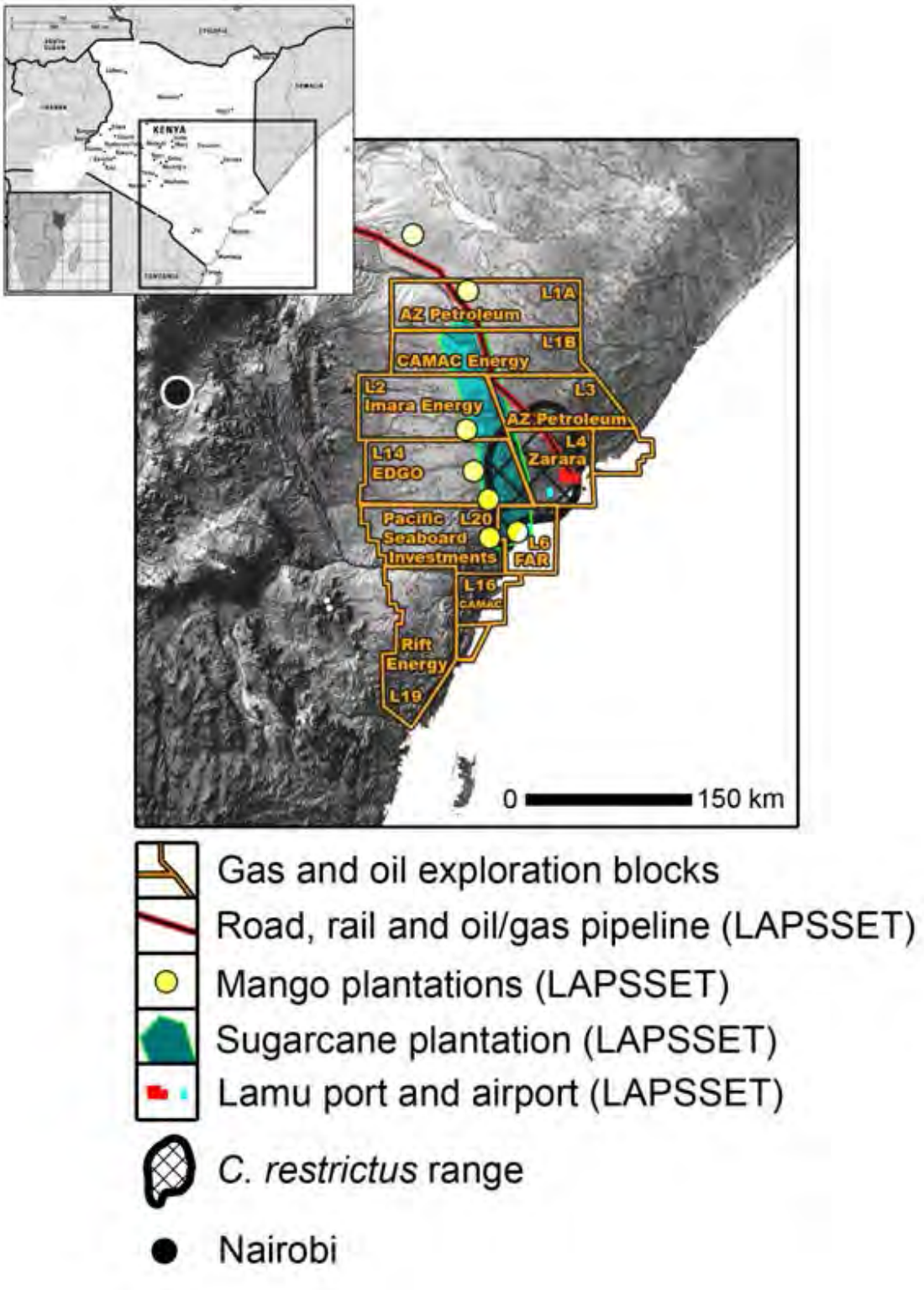


FIGURE 6.3: Exploration blocks for oil/gas prospecting in the Tana River Delta area and the proposed LAPSSET infrastructure, including a road and rail network, an oil/gas pipeline, a new seaport and international airport and areas of potential mango and sugarcane investment advertised by the Kenyan government.

Females	**n**	**WL**	**Range**	**TL**	**Range**	**Culmen**	**Range**	**TrL**	**Range**	**F/M**
C. restrictus	2	48.5	46.8 – 50.3	49.9	44.0 – 55.7	13.8	13.5 – 14.1	18.4	17.5 – 19.4	-
C. cinereolus	2	52.5	52.1 – 52.9	51.4	46.4 – 56.5	14	13.7 – 14.3	20.3	19.8 – 20.9	87%
***C. cinereolus* 2**	5	52.5	50.9 – 54	47.4	46.1 – 48.7	13.6	13.1 – 14.2	19.2	18.4 – 19.9	86%
C. chiniana ukamba	5	55.7	54.3 – 57.1	49.7	47.5 – 52.0	14.2	13.4 – 14.9	21.5	20.6 – 22.4	87%
C. chiniana heterophrys	1	49.1	-	45.5	-	13.8	-	20.6	-	80%
***C. chiniana heterophrys* 2**	5	50	48.7 – 51.4	46.9	44.5 – 49.2	14.5	14.1 – 15.0	20.5	19.2 – 21.8	81%
C. [lais] distinctus	4	56.7	55.4 – 58.0	61.7	58.8 – 64.6	14.9	14.7 – 15.2	22.6	22.0 – 23.2	94%
C. bodessa	2	58.6	47.9 – 69.2	49.9	41.6 – 58.1	14.7	13.3 – 16.2	22.6	20.7 – 24.6	93%
		BW	**Range**	**BH**	**Range**	**P10**	**Range**	**P9**	**Range**	**P10/P9**
C. restrictus	2	3	2.8 – 3.1	3.2	3.0 – 3.3	23.2	23.2 – 23.3	38.5	37.7 – 39.2	60.40%
C. cinereolus	2	3	2.7 – 3.2	3.1	2.9 – 3.3	24	23.7 – 24.7	39.9	39.2 – 40.6	60.20%
***C. cinereolus* 2**	5	2.8	2.7 – 2.9	3.2	3.0 – 3.4	24.2	22.8 – 25.5	39.8	38.7 – 40.9	60.70%
C. chiniana ukamba	5	2.8	2.6 – 3.1	3.6	3.3 – 3.8	26.2	25.0 – 27.3	43.8	42.7 – 45.0	59.70%
C. chiniana heterophrys	1	2.9	-	3.6	-	22.5	-	37.3	-	60.30%
***C. chiniana heterophrys* 2**	5	2.8	2.6 – 3.0	3.5	3.3 – 3.6	25.5	23.9 – 27.1	39.7	38.7 – 40.7	64.30%
C. [lais] distinctus	4	2.8	2.5 – 3.0	3.6	3.4 – 3.8	26.5	24.6 – 28.1	43.7	41.7 – 46.3	60.60%
C. bodessa	2	2.9	2.5 – 3.3	3.7	3.3 – 4.0	28.3	26.4 – 30.3	48	44.8 – 51.3	59%

TABLE 6.1: Measurements taken from female specimens collected around the vicinity of the Kenyan coast. WL - wing length, TL - tail length, TrL - tarsus length, F/M - sexual dimorphism, BW - bill width, BH - bill height, P 10 - outermost primary feather, P 9 primary feather nearest P 10 and P10/P9 - proportional length between the two outermost primary feathers.

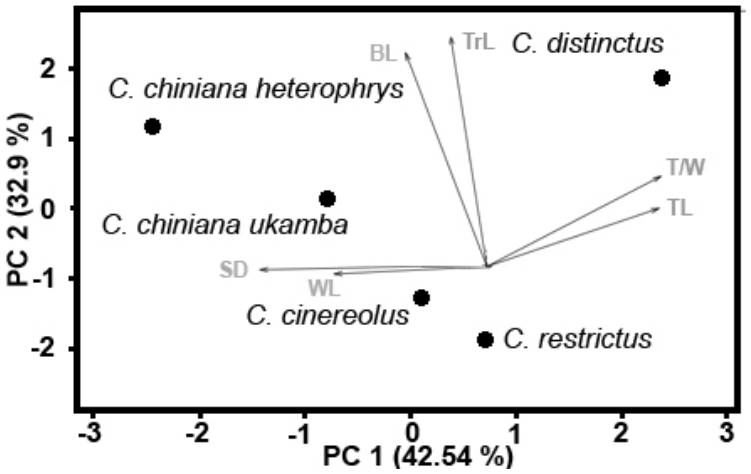


FIGURE 6.4: Principal component analysis of male *C. restrictus*, *C. chiniana heterophrys*, *C. chiniana ukamba*, *C. cinereolus* and *C. [lais] distinctus* measurements captured from Traylor (1967).

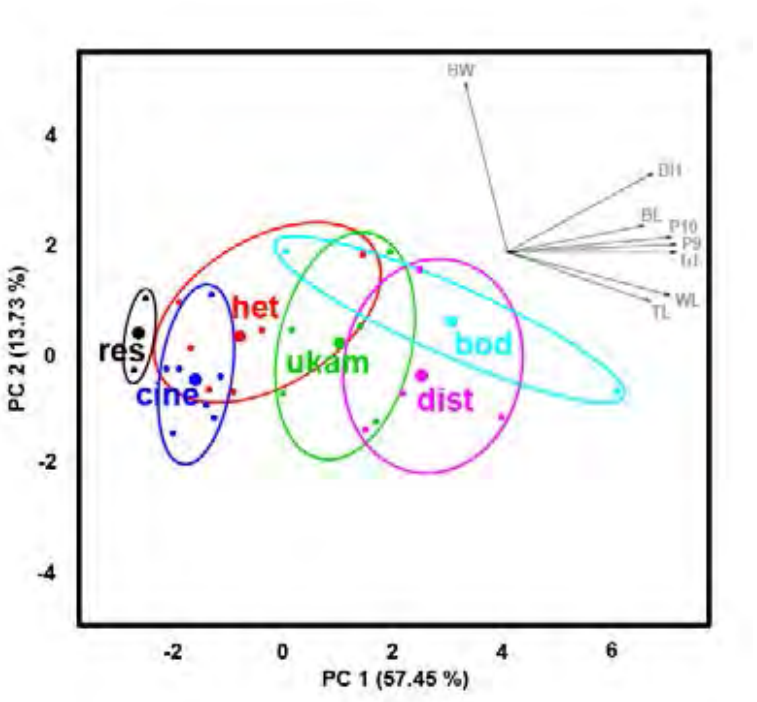


FIGURE 6.5: Principal component analysis of untransformed female *C. restrictus, C. chiniana heterophrys, C. chiniana ukamba, C. bodessa, C. cinereolus* and *C. [lais] distinctus* measurements. Measurements included: BW – bill width; BH – bill height; BL – bill length; P 10 – outermost primary feather; P 9 – primary feather nearest P 10; TrL – tarsus length; WL – wing length and TL – tail length.

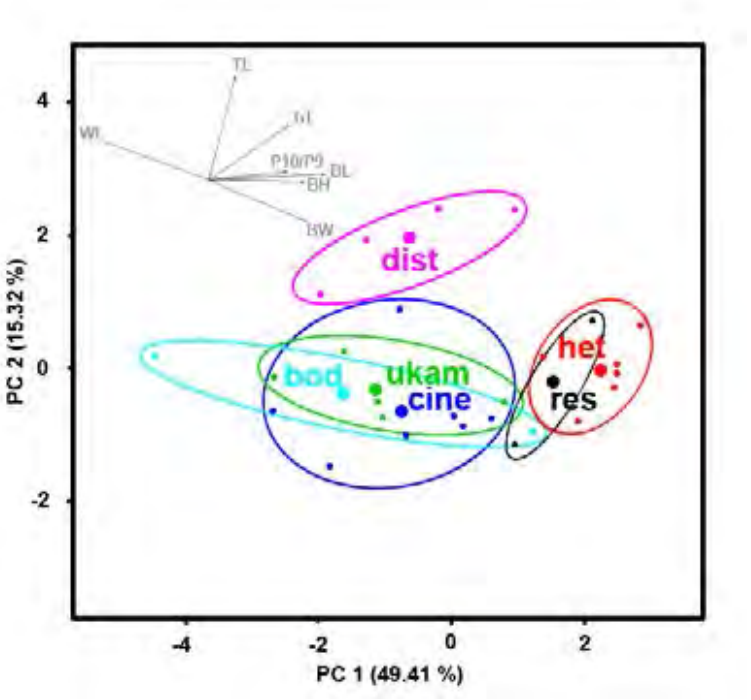


FIGURE 6.6: Principal component analysis of transformed female *C. restrictus, C. chiniana heterophrys, C. chiniana ukamba, C. bodessa, C. cinereolus* and *C. [lais] distinctus* measurements scaled for size. Measurements included: BW – bill width; BH – bill height; BL – bill length; P 10/P 9 – proportion between the two outermost primary feathers; TrL – tarsus length; WL – wing length and TL – tail length.

Bibliography

Adelson, E. H. (1993). Perceptual organization and the judgment of brightness. *Science 262*, 2042–2044.

Adelson, E. H. (2006). Checkershadow illusion. Example. http://web.mit.edu/persci/people/adelson/checkershadow_illusion.html.

Akaike, H. (2006). *Information theory as an extension of the maximum likelihood principle*. Budapest: In: Second International Symposium on Information Theory, Petrov, B.N., Csaki, F. (eds). Akademiai Kiado.

Alpers, D. L., B. J. V. Vuuren, P. Arctander, and T. J. Robinson (2004). Population genetics of the roan antelope (*Hippotragus equinus*) with suggestions for conservation. *Molecular Ecology 13*, 1771–1784.

Amorim, D. S. (1991). Refuge model simulations: testing the theory. *Revista brasileira de entomologia 35*, 803–812.

Anyanzwa, J. (2012). Mumias seeks Sh15b funding for Tarda. The Standard Digital News. 18 July. Published online: http://www.standardmedia.co.ke/business/article/2000062112/mumias-seeks-sh15b-funding-for-tarda [Accessed 31/01/2014].

Badyaev, A. V. and E. S. Leaf (1997). Habitat associations of song characteristics in *Phylloscopus* and *Hippolais* warblers. *Auk 114*(1), 40–46.

Balinsky, B. I. (1962). Patterns of animal distribution on the African continent (summing-up talk). *Annals of the Cape Provincial Museum 2*, 299–310.

Balmford, A., M. J. Lewis, M. de L. Brooke, A. L. R. Thomas, and C. N. Johnson (2000). Experimental analyses of sexual and natural selection on short tails in a polygynous warbler. *Proceedings of the Royal Society of London 267*, 1121–1128.

Bartoli, G., M. Sarnthein, M. Weinelt, H. Erlenkeuser, D. Garbe-Schonberg, and D. W. Lea (2005). Final closure of Panama and the onset of northern hemisphere glaciation. *Earth and Planetary Science Letters 237*, 33–44.

Becker, P. H. (1982). *The coding of species-specific characteristics in bird sounds.* New York: In: *Acoustic Communication in Birds.* Kroodsma D. E., Miller E. H. and Ouellet H. (eds.). Academic Press.

Behrensmeyer, A. K., N. E. Todd, R. Potts, and G. E. McBrinn (1997). Late Pliocene faunal turnover in the Turkana Basin, Kenya and Ethiopia. *Science 278*, 1589–1594.

Benedict, L. and R. C. K. Bowie (2009). Macrogeographical variation in the song of a widely distributed African Warbler. *Biology letters 5*, 484–487.

Benedict, L. and R. C. K. Bowie (2012). Rattling cisticola song features and variability across sub-Saharan Africa. *Journal of Zoology 287*, 96–103.

Benson, C. W. and M. P. S. Irwin (1964). Some additions and corrections to 'a check list of birds of Northern Rhodesia'. *Occasional Papers of the National Museum of southern Rhodesia 27B*, 106–127.

Beresford, P. (2002). *Molecular systematics and biogeography of certain Guineo-Congolian passerines.* Ph. D. thesis, The City University of New York.

Beresford, P. (2003). Molecular systematics of *Alethe*, *Sheppardia* and some other African robins (Muscicapoidea). *Ostrich 74*, 58–73.

Beresford, P. and J. Cracraft (1999). Speciation of African forest robins (*Stiphrornis*): species limits, phylogenetic relationships, and molecular biogeography. *American Museum Novitates 3270*, 1–22.

Berns, R. S. (2000). *Billmeyer and Saltzman's Principles of Color Technology. 3rd edition.* New York: John Wiley.

BirdLife (2014). Species factsheet: *Cisticola restrictus.* http://www.birdlife.org [Accessed 02/02/2014].

Bélanger-Gulick, J. (2013). Canada and the global land rush. Canadian Food Security Policy Group. Unpublished report: http://www.ccic.ca/_files/en/working_groups/2013-08-21_canada_and_the_global_land_rush_fspg_april_2013.pdf [Accessed 02/02/2014].

Bobe, R. and A. K. Behrensmeyer (2004). The expansion of grassland ecosystems in Africa in relation to mammalian evolution and the origin of the genus *Homo*. *Palaeogeography, Palaeoclimatology, Palaeoecology 207*, 399–420.

Bobe, R., A. K. Behrensmeyer, and R. E. Chapman (2002). Faunal change, environmental variability and late Pliocene hominin evolution. *Journal of human evolution 42*, 475–497.

Bonnefille, R. (1983). Evidence for a cooler and drier climate in the ethiopian uplands towards 2.5 myr ago. *Nature 303*, 487–491.

Borncoraglio, G. and N. Saino (2007). Habitat structure and the evolution of bird song: a meta-analysis of the evidence for the acoustic adaptation hypothesis. *Functional Ecology 21*, 134–142.

Boscarol, M. (2008). Deltae. http://www.boscarol.com/.

Bowie, R. C. K., J. Fjeldså, S. J. Hackett, and T. M. Crowe (2004a). Molecular evolution in space and though time: mtDNA phylogeography of the Olive Sunbird (*Nectarinia olivacea/obscura*) throughout continental Africa. *Molecular Phylogenetics and Evolution 33*, 56–76.

Bowie, R. C. K., J. Fjeldså, S. J. Hackett, and T. M. Crowe (2004b). Systematics and biogeography of Double-collared sunbirds of the eastern arc mountains, Tanzania. *Auk 121*, 660–681.

Broadley, D. G. and F. P. D. Cotterill (2004). The reptiles of southeast katange, and overlooked 'hot spot'. *African Journal of Herpetology 53*, 35–61.

Brouat, C., C. Tatard, K. Ba, J.-F. Cosson, G. Dobigny, E. Fichet-Calvet, L. Granjon, E. Lecompte, A. Loiseau, K. Mouline, S. Piry, and J.-M. Duplantier (2009). Phylogeography of the Guinea multimammate mouse (mastomys erythroleucus): a case study for Sahelian species in west Africa. *Journal of Biogeography 36*(12), 2237–2250.

Brown, D. M., R. A. Brenneman, K. P. Koepfli, J. P. Pollinger, B. Mila, N. J. Georgiadis, E. E. Louis, G. F. Grether, D. K. Jacobs, and R. K. Wayne (2007). Extensive population genetic structure in the giraffe. *BMC Biology 5*, 57.

Brown, K. S., J. R. G. Turner, and P. M. Shepard (1974). Quaternary forest refugia in tropical america: Evidence from race formation in *Heliconius* butterflies. *Proceedings of the Royal Society of London 187*, 369–378.

Bures, S., P. Dvornik, and G.-P. Saetre (2002). Brief report hybridization and apparent hybridization between meadow pipit (*Anthus pratensis*) and water pipit (*A. spinoletta*). *Hereditas 136*, 254–256.

Butchart, S. H. M. and J. P. Bird (2010). Data deficient birds on the IUCN red list: What don't we know and why does it matter? *Biological Conservation 143*(1), 239–247.

Carlson, A. (1986). Group territoriality in the Rattling Cisticola, *Cisticola chiniana*. *Oikos 47*, 181–189.

Catchpole, C. K. and P. B. J. Slater (1995). *How song develops.* Great Britain: In: *Bird Song*. Cambridge University Press.

Cerling, T. E. (1992). Development of grasslands, savannas in East Africa during the Neogene. *Palaeogeography, Palaeoclimatology, Palaeoecology 97*, 231–247.

Cerling, T. E., J. R. Bowman, and J. R. O'Neil (1998). An isotopic study of a fluvial-lacustrine sequence: The Plio-Pleistocene koobi fora sequence, East Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology 63*, 335–356.

Chapin, J. P. (1932). The birds of the Belgian Congo, part i. *Bulletin of the American Museum of Natural History 65*.

Chappuis, C. and C. Erard (1991). A new cisticola from west-central Africa. *Bulletin of the British Ornithologists' Club 111*, 59–70.

Chittenden, H., D. Allan, and I. Weiersbye (2012). *Roberts Geographic Variation of Southern African Birds*. Cape Town: The Trustees of the John Voelcker Bird Book Fund.

CHROMiX (2006). Colorthink version 2.1.2. http://www.chromix.com/.

Chubb, C., G. Sperling, and J. A. Solomon (1989). Texture interactions determine perceived contrast. *Proceedings of the National Academy of Science U S A 86*, 9631–9635.

CIE (1986). *Colorimetry*. Bureau Central, Vienna: French Commission international de l'éclairage, CIE publication 15.2.

Ciuri, S. (2014). Mumias seeks financier for Sh34bn Tana plant. Business Daily. 20 January. Published online: http://www.businessdailyafrica.com/Corporate-News/Mumias-seeks-financier-for-Sh34bn-Tana-plant/-/539550/2153352/-/ciord0/-/index.html [Accessed: 31/01/2014].

Clarke, K. R. and R. N. Gorley (2006). PRIMER: User manual/tutorial. version 6. PRIMER-E, Plymouth. http://www.primer-e.com/.

Cotterill, F. P. D. (2004). Drainage evolution in south-central Africa and vicariant speciation in swamp-dwelling weaver birds and swamp flycatcher. *The Honeyguide 50*, 7–25.

Cotterill, F. P. D. (2005). The upemba lechwe: an antelope new to science emphasizes the conservation importance of katanga, democratic republic of congo. *Journal of Zoology (London) 265*, 113–132.

Cotterill, F. P. D. and S. A. Goodier (2008). Dna clocks for dating landforms. *Quest 2*, 19–21.

Couvreur, T. L. P., M. S. M. Chatrou, M. Sosef, and J. M. Richardson (2008). Molecular phylogenetics reveal multiple tertiary vicariance origins of the African rain forest trees. *BMC Biology 6*, 54.

Crowe, T. M. and A. A. Crowe (1982). Patterns of distribution, diversity and endemism in Afrotropical birds. *Journal of Zoology (London) 198*, 417–442.

Cybulskaa, I., T. Chaturvedia, G. P. Brudeckia, Z. Kádárb, A. S. Meyerb, R. M. Baldwina, and M. H. Thomsena (2014). Chemical characterization and hydrothermal pretreatment of *Salicornia bigelovii* straw for enhanced enzymatic hydrolysis and bioethanol potential. *Bioresource Technology 153*, 165–172.

Dart, R. A. (1925). *Australopithecus africanus*: The man ape of South Africa. *Nature 115*, 195–199.

Darwin, C. R. (1958). *The Autobiography of Charles Darwin.* London, U.K.: Barlow, N. (ed.). Collins.

del Hoyo, J., A. Elliott, and D. Christie (2006). *Handbook of the Birds of the World. Volume 11: Old World flycatchers to Old World warblers.* Barcelona: Lynx Edicions.

deMenocal, P. B. (1995). Plio-pleistocene African climate. *Science 270*, 53–59.

deMenocal, P. B. (2004). African climate change and faunal evolution during the Pliocene-Pleistocene. *Earth and Planetary Science Letters 220*, 3–24.

Deprins, J. P. (2009). From dryland to greenland. Miti. Published online: http://betterglobe.com/Scripts/tiny_mce/plugins/filemanager/files/pdf/miti/miti_1.pdf [Accessed: 31/01/2014].

Derryberry, E. P., N. Seddon, S. Claramunt, J. A. Tobais, A. Baker, A. Aleixo, and R. T. Brumfield (2001). Correlated evolution of beak morphology and song in the neotropical Woodcreeper radiation. *Evolution 66*(9), 2784–2797.

Diamond, A. W. and A. C. Hamilton (1980). The distribution of forest passerine birds and Quaternary climatic change in Africa. *Journal of Zoology (London) 191*, 379–402.

Donges, J. F., R. V. Donner, M. H. Trauth, N. Marwan, H.-J. Schellnhuber, and J. Kurths (2011). Nonlinear detection of paleoclimate-variability transitions possibly related to human evolution. *PNAS Early Edition*, 1–6.

Dowsett, R. J. and F. Dowsett-Lemaire (1980). The systematic status of some Zambian birds. *Gerfaut 10*, 151–199.

Drummond, A. J., M. A. Suchard, D. Xie, and A. Rambaut (2012). Bayesian phylogenetics with beauti and the beast 1.7. *Molecular Biology and Evolution 29*, 1969–1973.

EAWLS (2008). Comments on EIA for the Tana River Delta Integrated Sugar Project. East African Wild Life Society. Unpublished report: http://www.tanariverdelta.org/tana/1090-DSY/version/default/part/AttachmentData/data/Tana%20Delta%20EIA%20Study%20Comments.pdf [Accessed 02/02/2014].

Engels, W. R. (1993). Contributing software to the internet: the amplify program. *Trends in Biochemical Sciences 18*, 448–450.

Farris, J. S., V. A. Albert, M. Kallersjo, D. Lipscomb, and A. G. Kluge (1996). Parsimony jackknifing outperforms neighbor-joining. *Cladistics 12*, 99–124.

Felsenstein, J. (1985). Phylogenies and the comparative method. *American Naturalist 125*, 1–15.

Finlayson, C. (2005). Biogeography and evolution of the genus *Homo*. *Trends in Ecology & Evolution 20*, 457–463.

Fjeldså, J. (1994). Geographical patterns for relict and young species of birds in Africa and South America and implications for conservation priorities. *Biodiversity and Conservation 3*, 207–226.

Fjeldså, J. and R. C. K. Bowie (2008). New perspectives on the origin and diversification of Africa's forest avifauna. *African Journal of Ecology 46*, 235–247.

Fjeldså, J. and J. C. Lovett (1997). Geographical patterns of old and young species in African forest biota: the significance of specific montane areas as evolutionary centres. *Biodiversity and Conservation 6*, 325–346.

Flagstad, O., O. P. Syvertsen, N. C. Stenseth, and K. S. Jakobsen (2001). Environmental changes and rates of evolution: the phylogeographic pattern within the hartebeest complex as related to climatic variation. *Proceedings of the Royal Society of Biological Sciences 268*, 667–677.

Flood, Z. (2013). The bitter taste of biofuels. Think. Qatar Foundation. 16 June. Published online: http://www.qf.org.qa/content/think/g8-special-issue/the-bitter-taste-of-biofuels [Accessed 02/02/2014].

Forbes, E. (1846). On the connexion between the distribution of existing fauna and flora of the british isles, and the geographical changes which have affected their area, especially during the epoch of northern drift. *Memoirs of the Geological Survey of Great Britain 1*, 336–432.

Fox, J. (2005). The r commander: A basic statistics graphical user interface to r. *Journal of Statistical Software 14*(9), 1–42.

Fuchs, J., R. C. K. Bowie, J. Fjeldså, and E. Pasquet (2004). Phylogenetic relationships of the African bush-shrikes and helmet-shrikes (passeriformes: Malaconotidae). *Molecular Phylogenetics and Evolution 33*, 428–439.

Fuchs, J., T. M. Crowe, and R. C. K. Bowie (2011). Phylogeography of the Fiscal shrike (*Lanius collaris*): a novel pattern of genetic structure across the arid zones and savannas of Africa. *Journal of Biogeography 38*, 2210–2222.

Fuchs, J., T. M. Crowe, and R. C. K. Bowie (2012). Phylogeography of the fiscal shrike (*Lanius collaris*): a novel pattern of genetic structure across the arid zones and savannas of Africa. *Journal of Biogeography 38*, 2210–2222.

Gibendi, R. (2014). Kenya seeks Sh148bn China loan to build dam. Daily Nation. 21 January. Published online: http://staging.nationmedia.com/lifestyle/smartcompany/Kenya-seeks-Sh148bn-China-loan-to-build-dam-/-/1226/2153756/-/5p26v4z/-/index.html [Accessed 02/02/2014].

Gilblom, K. (2012). Kenya closes seven more exploration deals. Reuters. 2 July. Published online: http://www.reuters.com/article/2012/07/02/ozabs-kenya-oil-idAFJOE86105T20120702 [Accessed 02/02/2014].

Goloboff, P., J. Farris, and K. Nixon (2003). T.n.t: Tree analysis using new technology. www.zmuc.dk/public/phylogeny.

Goloboff, P. A., C. I. Mattoni, and A. S. Quinteros (2006). Continuous characters analysed as such. *Cladistics 22*, 589–601.

Gower, J. C. (1971). A general coefficient of similarity and some of its properties. *Biometrics 27*, 857–874.

Hackett, S. J. (1993). Phylogenetic and biogeographic relationships in the neotropical genus *Gymnopithys* (formicariidae). *Wilson Bulletin (Wilson Journal of Ornithology) 105*, 301–315.

Haffer, J. (1974). *Avian speciation in Tropical South America.* Cambridge, M.A.: Nuttall Ornithological Club.

Hall, B. P. and R. E. Moreau (1970). *An atlas of speciation in African passerine birds.* London: British Museum (Natural History).

Hamerlynck, O., Q. Luke, T. M. Nyange, S. Duvail, and C. Leuthaud (2012). Range extension, imminent threats and conservation options for two endangered primates:

The Tana River Red Colobus *Procolobus rufomitratus rufomitratus* (peters, 1879) and the Tana River Mangabey *Cercocebus galeritus* (peters, 1879) in the lower Tana floodplain and delta, Kenya. *African Primates 7*(2), 211–217.

Hamilton, A. C. (1976). The significance of patterns of distribution shown by forest plants and animals in tropical Africa for the reconstruction of upper Pleistocene palaeoenvironments: a review. *Palaeoecology of Africa, the Surrounding Islands and Antarctica 9*, 63–97.

Hammer, O., D. A. T. Harper, and P. D. Ryan (2001). PAST: Paleontological statistics software package for education and data analysis. *Palaeontologia Electronica* 4(1): 9 pp. http://nhm2.uio.no/norlex/past/download.html.

Haus, T. (2013). *Phylogeography and impact of hybridization on the evolution of African green monkeys (Chlorocebus Gray, 1870)*. Ph. D. thesis, Georg-August-Universität Göttingen.

Herron, M. D., J. M. Waterman, and C. L. Parkinson (2005). Phylogeny and historical biogeography of African ground squirrels: the role of climate change in the evolution of *Xerus*. *Molecular Ecology 14*, 2773–2788.

Heslewood, M. M., M. S. Elphinstone, S. C. Tidemann, and P. R. Bayerstock (1998). Myoglobin intron variation in the Gouldian Finch *Erythrura gouldiae* assessed by temperature gradient gel electrophoresis. *Electrophoresis 19*, 142–151.

Hewitt, G. M. (1996). Some genetic consequence of ice ages, and their role in divergence and speciation. *Biological Journal of the Linnean Society 58*, 247–276.

Hill, L. (2010). Tiomin agrees to sell Kwale mineral-sands asset. Mining Weekly. Creamer Media. 26 February. Published online: http://www.miningweekly.com/article/tiomin-agrees-to-sell-kwale-mineral-sands-asset-2010-02-26 [Accessed 02/02/2014].

Ho, A. J. D. S. Y. W., M. J. Phillips, and A. Rambaut (2006). Relaxed phylogenetics and dating with confidence. *PLoS Biology 4*, 88.

Hunter, H. S. (1948). Photoelectric color-difference meter. *Journal of the Optical Society of America 38*, 661.

Husson, F., J. Josse, S. Le, and J. Mazet (2013). Factominer: Multivariate exploratory data analysis and data mining with r. version 1.25. http://CRAN.R-project.org/package=FactoMineR.

Hustler, K. (2001). The breeding biology of the Black-Backed Cisticola in North-West Zimbabwe with notes on song and specific status. *Honeyguide 42*(1), 25–36.

Irestedt, M., J. I. Ohlson, D. Zuccon, M. Kallersjo, and P. G. P. Ericson (2006). Nuclear DNA from old collections of avian study skins reveals the evolutionary history of the old world suboscines (aves, passeriformes). *Zoologica Scripta 35*, 567–580.

Irwin, M. (1991). The specific characters of the Slender-tailed Cisticola *Cisticola melanura* (Cabanis). *Bulletin of the British Ornithologist Club 11*, 228–236.

Iyama, M., P. Zante, C. Munster, D. Newman, K. Onchieku, M. Nyambenge, V. Moraa, R. Jamnadass, and J. Albergel (2009). *Jatropha* reality check: A field assessment of the agronomic and economic viability of *Jatropha* and other oilseed crops in kenya. Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ) GmbH, Nairobi, Kenya. Published online: http://www.worldagroforestry.org/downloads/publications/PDFs/B16599.PDF [Accessed 02/02/2014].

Jetz, W., C. Rahbek, and R. K. Colwell (2004). The coincidence of rarity and richness and the potential signature of history in centres of endemism. *Ecology Letters 7*, 1180–1191.

Jorgic, D. (2013). Kenya says Chinese firm wins first tender for Lamu port project. Reuters. 11 April. Published online: http://www.reuters.com/article/2013/04/11/kenya-port-lamu-idUSL5N0CX38D20130411 [Accessed 02/02/2014].

Kang'aru, W. (2008). History runs against Tana sugar project. Daily Nation. 22 July. Published online: http://www.tanariverdelta.org/2148-DSY/version/default/part/AttachmentData/data/Smart%20biz%20article%20on%20Tana%2022072008.pdf [Accessed 02/02/2014].

Kasuku, S. (2012). Lamu Port – South Sudan – Ethiopia Transport (LAPSSET) Corridor Project. Office of the Prime Minister. Unpublished presentation: http://www.cbcglobal.org/images/uploads/library/KIS2012_LAPSSET_Corridor_Silvester_Kasuku.pdf [Accessed 01/02/2014].

Keast, A. (1961). Bird speciation on the Australian continent. *Bulletin of the Museum of Comparative Zoology 123*, 305–495.

Kenya, G. (2007). Government of the Republic of Kenya. kenya vision 2030. Published online: http://theredddesk.org/sites/default/files/vision_2030_brochure__july_2007.pdf [Accessed 02/02/2014].

Kenya, G. (2012a). Government of the Republic of Kenya. Kenya's LAPSSET Corridor mango production investment opportunity. Ministry of Agriculture. Published online: http://growafrica.com/wp/wp-content/uploads/2012/04/Kenya-LAPSSET-Corrido-Mangoes-Business-Case.pdf [Accessed 01/02/2014].

Kenya, G. (2012b). Government of the Republic of Kenya. Kenya's LAPSSET Corridor sugarcane production and processing investment opportunity. Ministry of Agriculture. Published online: http://growafrica.com/wp/wp-content/uploads/2012/04/Kenya-LAPSSET-Corridor-Sugarcane-Business-Case.pdf [Accessed 01/02/2014].

Kenya-Law (1996). Civil Appeal 252 of 1996 commissioner of Lands & another vs. Coastal Aquaculture Ltd. Available online: http://www.kenyalaw.org/caselaw/cases/view/29586/ [Accessed 02/02/2014].

Kenya-Law (2001). Kenya v. Coastal Aquaculture reference no. 3/2001. The Republic of Kenya and The Commissioner of Lands v. Coastasl Acquaculture. Comesa Court of Justice. Available online: http://www.worldcourts.com/comesacj/eng/decisions/2002.04.26_Kenya_v_Coastasl.htm [Accessed 02/02/2014].

Kihara, G. (2011). Mauritian firm to build Sh16.5 bn sugar factory at coast. Business Daily Africa. 5 September. Published online: http://www.businessdailyafrica.com/Corporate-News/Mauritian-firm-to-build-Sh16-5-bn-sugar-factory-at-Coast-/-/539550/1230964/-/r5551nz/-/index.html [Accessed 02/02/2014].

Kingston, J., A. L. Deino, R. K. Edgar, and A. Hill (2007). Astronomically forced climate change in the kenyan rift valley 2.7–2.55 ma: implications for the evolution of early hominin ecosystems. *Journal of Human Evolution 53*.

Kirschel, A. N. G., D. T. Blumstein, R. E. Cohen, W. Buermann, and T. B. Smith (2009). Birdsong tuned to the environment: Green hylia song varies with elevation, tree cover and noise. *Behavioral Ecology 20*(5), 1089–1095.

Kishino, H. and M. Hasegawa (1989). Evaluation of the maximum likelihood estimate of the evolutionary tree topologies from DNA sequence data, and the branching order of the *Hominoidea*. *Journal of Molecular Evolution 29*.

Klicka, J. and R. M. Zink (1997). The importance of recent ice ages in speciation: a failed paradigm. *Science 277*, 1666–1669.

Kroodsma, D. E. (1982). *Learning and the ontogeny of sound signals in birds.* New York: In: *Acoustic Communication in Birds*. Kroodsma D. E., Miller E. H. and Ouellet H. (eds.). Academic Press.

Kroodsma, D. E. (2004). *The diversity and plasticity of birdsong.* San Diego: In: *Nature's Music: The Science of Birdsong*. Marler, P. and Slabbekoorn, H. (eds.). Elsevier.

Laden, G. and R. Wrangham (2005). The rise of the hominids as an adaptive shift in fallback foods: Plant underground storage organs (usos) and australipithican origins. *Journal of Human Evolution 49*(4).

Law, K. (2006). Kenya Law Civil Suit 262 of 2006. mat International Limited v. Tana and Athi Rivers Development Authority. High Court of Kenya at Mombasa. Available online: http://www.kenyalaw.org/caselaw/cases/view/36822/index.php?id=3479 [Accessed 02/02/2014].

Lebrun, D., O. Hamerlynck, S. Duvail, and J. Nyunja (2010). *The importance of flexibility: an analysis of the large-scale Tana Delta irrigation project in Kenya, implemented under an estate system.* IFRA and Hekima College, Nairobi, Kenya.: In: *Shared water, shared opportunities. Hydropolitics in East Africa.* B. Calas & C.A. Mumma Martinon, (eds.).

Lecompte, E., L. Granjon, and C. Denys (2002). The phylogeny of the *Praomys* complex (rodentia: Muridae) and its phylogeographic implications. *Journal of Zoological Systematics and Evolutionary Research 40*, 8–25.

Lerner, H. R. L., M. Mever, H. F. James, M. Hofreiter, and R. C. Fleischer (2011). Multilocus resolution of phylogeny and timescale in the extant adaptive radiation of Hawaiian Honeycreepers. *Current Biology 21*, 1838–1844.

Livingstone, D. A. (1975). Late Quaternary climatic changes in Africa. *Annual Review of Ecology, Evolution, and Systematics 6*, 249–280.

Livingstone, D. A. (1993). *Evolution of African climate.* London, U.K.: In: *Biological Relationships Between Africa and South America.* Goldblatt P. ed. New Haven: Yale University Press, pp. 455-99.

Lorenzen, E. D., R. Heller, and H. R. Siegismund (2012). Comparative phylogeography of African savannah ungulates. *Molecular Ecology 21*, 3656–3670.

Lotto, R. B. (2011). Collection of visual illusions. http://www.lottolab.org/articles/illusionsoflight.asp.

Lou, M. R., G. Cui, and B. Rigg (2001). The development of the cie 2000 colour-difference formula: Ciede2000. *Color Research and Application 26*, 340–350.

Luke, Q., R. Hatfield, and P. Cunneyworth (2005). Rehabilitation of the Tana Delta Irrigation Project, kenya: An environmental assessment. Critical Ecosystem Partnership Fund. Unpublished report: http://www.cepf.net/Documents/Final.TDIP_Environmental_Assessment.pdf [Accessed 02/02/2014].

Lynes, H. (1930). Review of the genus *Cisticola*. *Ibis 12*(6).

Macgregor, D. (2015). History of the development of the East African Rift System: A series of interpreted maps through time. *Journal of African Earth Sciences 101*, 232–252.

Maechler, M., P. Rousseeuw, A. Struyf, M. Hubert, and K. Hornik (2013). cluster: Cluster analysis basics and extensions. version 1.14.4. http://cran.r-project.org/web/packages/cluster/index.html.

Mahler, B. and D. Gil (2009). The evolution of song in the phylloscopus leaf warblers (aves: Sylviidae): a tale of sexual selection, habitat adaptation, and morphological constraints. *Advances in the Study of Behavior 40*, 35–66.

Makutsa, P. (2010). Land grab in Kenya. Eastern Africa Farmers Federation. Available online: http://www.sfoap.net/fileadmin/user_upload/sfoap/KB/docs/Report%20of%20Land%20Grab%20in%20Kenya.pdf [Accessed 02/02/2014].

Marler, P. (1957). Specific distinctiveness in the communication signals of birds. *Behaviour 11*, 13–39.

Masdar (2014). Masdar institute of science and technology: Boeing, united arab emirates partners look to harvest biofuel from desert plants. Press release. Published online: http://www.masdar.ac.ae/media-section/news/item/6277-boeing-united-arab-emirates-partners-look-to-harvest-biofuel-from-desert-plan [Accessed 26/01/2014].

Mayr, E. (1963). *Animal Species and Evolution.* Cambridge, MA.: Harvard University Press.

Mayr, E. and R. J. O'Hara (1986). The biogeographic evidence supporting the Pleistocene Forest Refuge Hypothesis. *Evolution 40*, 55–66.

McCamy, C. S., H. Marcus, and J. G. Davidson (1976). A color-rendition chart. *Journal of Applied Photographic Engineering 3*(2).

Mills, M. S. L., M. Melo, and A. Vax (2011). Black-tailed Cisticola *Cisticola melanurus* in eastern Angola: behavioural notes and the first photographs and sound-recordings. *Bulletin of the African Bird Club 18*(2), 193–198.

Mireri, C. (2010). Tana River Delta (TRD) conservation and development master plan. Nature Kenya. Unpublished report: http://www.avjcf.org/wp-content/uploads/2013/03/Annex_2_Conservation_Master_Plan_and_Action_Plan_for_Tana_River_Delta.pdf [Accessed 02/02/2014].

Mireri, C., K. Onjala, and N. Oguge (2008). The economic valuation of the proposed Tana Integrated Sugar Project (TISP), Kenya. Nature Kenya. Unpublished report: http://www.rspb.org.uk/Images/tana_tcm9-188706.pdf [Accessed 02/02/2014].

Moreau, R. E. (1952). Africa since the Mesozoic: With particular reference to certain biological problems. *Proceedings of the Zoological Society (London) 121*, 869–913.

Morton, E. S. (1975). Ecological sources of selection on avian sounds. *American Naturalist 109*, 17–34.

Muchira, J. (2013). Kenya's Kwale embarks on production this month after two decades of false starts. Mining Weekly. Creamer Media. 27 September. Published online: http://www.miningweekly.com/article/kenyas-kwale-starts-production-this-months-after-two-decades-of-false-starts-2013- [Accessed 02/02/2014].

Munsell, A. H. (1912). A pigment color system and notation. *American Journal of Psychology 23*, 236–244.

Muwanika, V. B., S. Nyakaana, H. R. Siegismund, and P. Arctander (2003). Phylogeography and population structure of the common warthog (*Phacochoerus africanus*) inferred from variation in mitochondrial DNA sequences and microsatellite loci. *Heredity 91*, 361–372.

Mwakio, P. (2013). Kwale sugar processing plant set for commissioning. The Standard Digital News. Published online: http://www.standardmedia.co.ke/business/article/2000097909/kwale-sugar-processing-plant-set-for-commissioning [Accessed 12/12/2013].

Mwaniki, N., D. Mungai, J. Kibwage, P. Mbugua, G. Muchemi, M. Chiuri, R. Abila, W. Ojwang, M. Thande, and T. Thenya (2007). Environmental Impact Assessment study report for the proposed Tana Integrated Sugar Project in Tana River and Lamu districts, Coast Province, Kenya (Land Allocation Reference no. 106796 of 17.1.1995). HVA International and M.A. Consulting. Unpublished report: http://www.tanariverdelta.org/tana/967-DSY/version/default/part/AttachmentData/data/MUMIAS_Tana_EIA_part1.pdf [Accessed 02/02/2014].

Ndoo, V. (2012). Kenya's Tana River Delta designated as newest Ramsar site in Africa. Birdlife International. 18 October. Published online: http://www.birdlife.org/africa/news/kenya%E2%80%99s-tana-river-delta-designated-newest-ramsar-site-africa [Accessed 02/02/2014].

Nenadic, O. and M. Greenacre (2007). Correspondence analysis in r, with two- and three-dimensional graphics: The ca package. *Journal of Statistical Software 20*(3), 1–13.

Nguembock, B., C. Cruaud, and C. Denys (2012). A large evaluation of passerine cisticolids (aves: Passeriformes): More about their phylogeny and diversification. *The Open Ornithology Journal 5*, 42–56.

Nguembock, B., J. Fjeldså, A. Tiller, and E. Pasquet (2007). A phylogeny for the Cisticolidae (Aves: Passeriformes) based on nuclear and mitochondrial DNA sequence data, and a re-interpretation of an unique nest-building specialization. *Molecular Phylogenetics and Evolution 42*, 272–286.

Ng'weno, F. (2008). Brief on tana river delta biodiversity. Tana Delta report. Nature Kenya. Unpublished report:http://www.tanariverdelta.org/1076-DSY/version/default/part/AttachmentData/data/Tana%20Delta%20Biodiversity.pdf [Accessed 02/02/2014].

Nichol, J. E. (1999). Geomorphological evidence and Pleistocene refugia in Africa. *Geographical Journal 165*, 79–89.

Njabo, K. Y., R. C. K. Bowie, and M. D. Sorenson (2008). Phylogeny, biogeography and taxonomy of the African wattle-eyes (Aves: Passeriformes: Platysteiridae). *Molecular Phylogenetics and Evolution 48*, 136–149.

NorthEnergy (2011). Life cycle assessment of refined vegetable oil and biodiesel from *Jatropha* grown in Dakatcha Woodlands of Kenya. Unpublished report: http://www.actionaid.org.uk/sites/default/files/doc_lib/kenyan_jatropha_final_report.pdf [Accessed 01/02/2014].

Nunow, A. (2011). The dynamics of land deals in the Tana Delta, Kenya. Presented at International Conference on Global Land Grabbing. University of Sussex, 6-8 April. Available online: http://www.future-agricultures.org/pp-conference-papers/doc_download/1163-the-dynamics-of-land-deals-in-the-tana-delta-kenya [Accessed 02/02/2014].

O'Brien and C. R. Peters (1999). *Landforms, climate, ecogeographic mosaics, and the potential for hominid diversity in Pliocene Africa.* New York, Oxford: In: *African biogeography, climate change, & human evolution.* Bromage, T.G. Schrenk, F. (eds.). Oxford University Press.

Odhengo, P., P. Matiku, J. Nyangena, K. Wahome, B. Opaa, S. Munguti, G. Koyier, P. Nelson, E. Mnyamwezi, and P. Misati (2012). Tana River

Delta strategic environmental assessment scoping report. Published by the Ministry of Lands, Physical Planning Department, Kenya. Published online: http://www.naturekenya.org/sites/default/files/Tana_River_Delta_Strategic_Environmental_Assessment_Scoping_Report,_2012.pdf [Accessed 02/02/2014].

Odhengo, P., P. Matiku, P. Waweru, D. Guda, T. Kinara, S. Kathike, E. Mnyamwezi, S. Munguti, P. Nelson, and G. Koyier (2012). Tana River Delta land use plan framework. Published by the Ministry of Lands, Physical Planning Department, Kenya. Published online: http://www.naturekenya.org/sites/default/files/Tana_River_Delta_Land_Use_Plan_Framework,_2012.pdf [Accessed 02/02/2014].

Ohlson, J. I., M. Irestedt, J. Fjeldså, and P. G. P. Ericson (2012). Nuclear DNA from a 180-year-old study skin reveals the phylogenetic position of the kinglet *Calyptura cristata* (Passeriformes: Tyrannides). *Ibis 154*, 533–541.

Olsson, U., M. Irestedt, G. Sangster, P. G. P. Ericson, and P. Alstrom (2013). Systematic revision of the avian family Cisticolidae based on a multi-locus phylogeny of all genera. *Molecular Phylogenetics and Evolution 66*, 790–799.

Paradis, E., K. Claude, and K. Strimmer (2004). Ape: analyses of phylogenetics and evolution in r language. *Bioinformatics 20*, 289–290.

Payne, R. B. (1996). *Song traditions in indigo buntings: Origin, improvisation, dispersal, and extinction in cultural evolution.* New York: In: *Ecology and evolution of acoustic communication in birds*. Kroodsma, D.E and Miller, E.H. (eds.). Academic Press.

Plana, V. (2003). Phylogenetic relationships of the Afro-Malagasy members of the large genus *Begonia* inferred from trnL intron sequences. *Systematic Botany 28*, 693–704.

Podos, J. (2001). Correlated evolution of morphology and vocal signal structure in Darwin's finches. *Nature 409*, 185–188.

Posada, D. and K. A. Crandall (1998). Modeltest: testing the model of dna substitution. *Bioinformatics 14*, 817–818.

Potts, R. (1996). Evolution and climate variability. *Science 273*, 922–923.

Potts, R. (1998). Evolution and climate variability. *The Yearbook of Physical Anthropology 41*, 93–136.

Price, J. J. and S. M. Lanyon (2004). Patterns of song evolution and sexual selection in the oropendolas and caciques. *Behavioral Ecology 15*, 485–497.

Price, T. (2008). *Speciation in birds.* Greenwood Village: Roberts & Company Publishers.

Querouil, S., E. Verheyen, M. Dillen, and M. Colyn (2003). Patterns of diversification in two African forest shrews: *Sylvisorex johnstoni* and *Sylvisorex ollula* (soricidae, insectivora) in relation to paleo-environmental changes. *Molecular Phylogenetics and Evolution 28*(1), 24–37.

R-Core-Team (2013). R: A language and environment for statistical computing. version 3.0.1. *R Foundation for Statistical Computing, Vienna, Austria.* http://www.R-project.org/.

Rambaut, A. (2012). Figtree. version 1.4.0. http://tree.bio.ed.ac.uk/software/figtree/.

Rambaut, A. and A. J. Drummond (2009). Tracer. version 1.5. http://beast.bio.ed.ac.uk/Tracer.

Richards, D. G. and R. H. Wiley (1980). Reverberations and amplitude fluctuations in the propagation of sound in a forest: Implications for animal communication. *American Naturalist 115*, 381–399.

Ridgeway, R. (1912). *Color Standards and Color Nomenclature.* Washington D.C.: Ridgeway.

Rohlf, F. J. (2010). tpsdig version 2.16: Digitize coordinates of landmarks and capture outlines and tpsutil version 1.46: Utility program useful when working with tps files. tpstree version 1.21. fit shapes to a hierarchical tree. http://life.bio.sunysb.edu/morph/.

Roy, M. S. (1997). Recent diversification in African greenbuls (Pycnonotidae: *Andropadus*) supports a montane speciation model. *Proceedings of the Royal Society of London B 264*, 1337–1344.

Roy, M. S., R. Sponer, and J. Fjeldså (2000). Molecular systematics and evolutionary history of alalats (genus *Sheppardia*): A pre-Pleistocene radiation in a group of African forest birds. *Molecular Phylogenetics and Evolution 18*, 74–83.

RSPB (2011). UK firm drops controversial African biofuels plan. Royal Society for the Protection of Birds. 21 October. Published online: http://www.rspb.org.uk/news/292988-uk-firm-drops-controversial-african-biofuels-plan [Accessed 01/02/2014].

RSPB (2013). Dakatcha woodland. Royal Society for the Protection of Birds. Available online: http://www.rspb.org.uk/ourwork/casework/details.aspx?id=tcm:9-263030 [Accessed 01/02/2014].

Ryan, M. J. and E. A. Brenowitz (1985). The role of body size, phylogeny, and ambient noise in the evolution of bird song. *American Naturalist 126*(1), 87–100.

Ryan, P. G. (2006). *Cisticolidae*. Barcelona: In: *Handbook of the Birds of the World: Volume 11. Old World flycatchers to Old World warblers*. del Hoyo, J., Elliot, A., Christie, D.A. (eds.). Lynx Edicions.

Seddon, N. (2005). Ecological adaptation and species recognition drives vocal evolution in neotropical suboscine birds. *Evolution 59*(1), 200–215.

Seddon, N., J. A. Tobais, M. Eaton, and A. Odeen (2010). Human vision can provide a valid proxy for avian perception of sexual dichromatism. *Auk 127*, 283–292.

Senut, B., M. Pickford, D. Gommery, P. Mein, K. Cheboi, and Y. Coppens (2001). Development of grasslands, savannas in East Africa during the Neogene. *Comptes Rendus de l'Académie des Sciences Paris IIA 332*, 137–144.

Shimodaira, H. and M. Hasegawa (1999). Multiple comparisons of log-likelihoods with applications to phylogenetic inference. *Molecular Biology and Evolution 16*.

Sibley, C. G. (1996). *Birds of the world*. Thayer Birding.

Sibley, C. G. and J. E. Alquist (1991). Phylogeny and classification of birds: a study in molecular evolution. *Yale University Press, New Haven*.

Sinclair, I. and P. G. Ryan (2003). *Birds of Africa South of the Sahara*. Cape Town: Random House Struik.

Slabbekoorn, H. and T. B. Smith (2002). Bird song, ecology and speciation, philosophical transactions. *Biological Sciences 357*(1420), 493–503.

Slade, R. W., C. Moritz, A. Heideman, and P. T. Hale (1993). Rapid assessment of single-copy nuclear DNA variation in diverse species. *Molecular Ecology 2*, 359–373.

Slater, P. J. B. (1989). Bird song learning: Causes and consequences. *Ethology Ecology & Evolution 1*, 19–46.

Snow, D. W. (1974). *An Atlas of Speciation in African Non-passerine Birds*. London, U.K.: British Museum (Natural History).

Software, S. (2008). MYSTAT is a free, streamlined, student-oriented variation of the systat product. version 12.02.00. Cranes Software International Ltd. http://www.systat.com/.

Solberg, R. (2010). Year 2009 report from Better Globe. Better Globe News. 13 February. Published online: http://www.betterglobe.com/ShowNews.aspx?year=0&newsId=539 [Accessed 03/02/2014].

Solberg, R. (2012). Status and progress in kenya. Better Globe News. 28 September. Published online: http://betterglobe.com/ShowNews.aspx?year=0&newsId=995 [Accessed 03/02/2014].

Solberg, R. (2013a). Better Globe Forestry's work in Africa. Better Globe News. 9 February. Published online: http://betterglobe.com/ShowNews.aspx?newsId=1044 [Accessed 03/02/2014].

Solberg, R. (2013b). News from kenya. Better Globe News. 15 May 2013. Published online: http://betterglobe.com/ShowNews.aspx?newsId=1072 [Accessed 02/02/2014].

Sorenson, M. D., J. C. Ast, D. E. Dimcheff, T. Yuri, and D. P. Mindell (1999). Primers for a pcr-based approach to mitochondrial genome sequencing in birds and other vertebrates. *Molecular Phylogenetics and Evolution 12*, 105–114.

Spottiswoode, C. N. and M. Stevens (2011). How to evade a co-evolving brood parasite: egg discrimination versus egg variability as host defences. *Proceedings of the Royal Society 278*(1724), 3566–3573.

Statsoft (2011). Statistica 10. http://www.statsoft.com/.

Swofford, D. L. (1998). Paup*. phylogenetic analysis using parsimony (* and other methods). version 4. Sunderland, MA, Sinauer.

Taravati, S. (2010). GMTP: Geometric morphometric tools package. version 2.1. http://nhm2.uio.no/norlex/past/download.html.

Tarboton, W. (2001). *Guide to Nests and Eggs of South African Birds*. London: New Holland Publishers.

TARDA (2012). Tarda EOI for partnership for sustainable agri-business development of the Tana Delta Irrigation Project 2012. Published online: http://www.jobsforkenyan.com/tarda-eoi-for-partnership-for-sustainable\-agri-business-development-of-the-tana-delta-irrigation-project-2012/ [Accessed 02/02/2014].

Temper, L. (2010). *Let Them Eat Sugar: Life and Livelihood in Kenya's Tana Delta.* http://www.ceecec.net/wp-content/uploads/2010/02/TANA_DELTA__FINAL.pdf: In: *CEECEC Handbook: Ecological Economics from the Bottom Up.* CEECEC (eds.).

Temper, L. (2013). Who gets the human appropriation of net primary production? biomass distribution & the 'sugar economy' in the Tana Delta, Kenya. The Land Deal Politics Initiative. Available online: http://www.iss.nl/fileadmin/ASSETS/iss/Research_and_projects/Research_networks/LDPI/LDPI_WP_05.pdf [Accessed 01/02/2014].

Temper, L. and J. Martinez-Alier (2012). Mapping successful resistance to the global land-grab: definitions, financial activism and alliances. Presented at the International Conference on Global Land Grabbing II, October 17-19. Cornell University, Ithaca, NY. Available online: http://www.cornell-landproject.org/download/landgrab2012papers/Temper_Alier_LDPI.pdf [Accessed 02/02/2014].

Tolley, K. A., C. R. Tilbury, G. J. Measey, M. Menegon, W. R. Branch, and C. A. Matthee (2011). Ancient forest fragmentation or recent radiation? testing refugial speciation models in chameleons within an African biodiversity hotspot. *Journal of Biogeography 38*, 1748–1760.

Trauth, M. H., J. C. Larrasoana, and M. Mudelsee (2009). Trends, rhythms and events in Plio-Pleistocene African climate. *Quaternary Science Reviews 28*, 399–411.

Trauth, M. H., M. A. Maslin, A. Deino, M. R. Strecker, A. G. N. Bergner, and M. Duhnforth (2007). High- and low-latitude forcing of plio-pleistocene east African climate and human evolution. *Journal of Human Evolution 53*, 475–486.

Trauth, M. H., M. A. Maslin, A. L. Deino, A. Junginger, M. Lesoloyia, E. O. Odada, D. O. Olago, L. A. Olaka, M. R. Strecker, and R. Teidmann (2010). Human evolution in a variable environment: the amplifier lakes of eastern Africa. *Quaternary Science Reviews 29*, 2981–2988.

Traylor, M. A. (1967). A new species of cisticola. *Bulletin of the British Ornithologists Club 87*, 45–48.

Trent, S., J. Williams, C. Thornton, and M. Shanahan (2004). Farming the sea, costing the earth. A report by the Environmental Justice Foundation. Published online: http://ejfoundation.org/sites/default/files/public/farming_the_sea.pdf [Accessed 02/02/2014].

Tubaro, P. L. and E. T. Segura (1995). Geographic, ecological and subspecific variation in the song of the rufous-browed peppershrike (*Cyclarhis gujanensis*). *Condor 97*, 792–803.

Twahir, F. S. (2011). Environmental impact assessment of proposed development of Kurawa saltworks and aquaculture at Ungwana bay, Tana River

District NEMA/pr/5/2/7041. National Environment Management Authority. Kenya. Unpublished report: http://www.nema.go.ke/index.php?option=com_phocadownload&view=category&download=102:eia790saltworks-eiapdf&id=55:eia790-799reports [Accessed 02/02/2014].

Tye, A. (1997). *Sylviidae, Old World warblers.* San Diego: In: *The birds of Africa.* Urban, E. K., Fry, C. K., Keith, S. (eds.). Academic Press.

Urban, K. E., C. H. Fry, and S. K. (eds.) (1997). *The birds of Africa vol. 5.* San Diego: Academic Press).

van Hooft, W. F., A. F. Groen, and H. H. T. Prins (2002). Phylogeography of the African buffalo based on mitochondrial and Y-chromosomal loci: Pleistocene origin and population expansion of the Cape buffalo subspecies. *Molecular Ecology 11*, 267–279.

Vanzolini, P. E. and E. E. Williams (1970). South american anoles: The geographic differentiation and evolution of the *Anolis chrysolepis* species group (sauria: Iguanidae). *Arquivos de Zoologia Sao Paulo 19.*

Voelker, G., R. C. K. Bowie, B. Wilson, and C. Anderson (2012). Phylogenetic relationships and speciation patterns in an African savanna dwelling bird genus (*Myrmecocichla*). *Biological Journal of the Linnean Society 106*, 180–190.

Voelker, G., R. K. Outlaw, and R. C. K. Bowie (2010). Pliocene forest dynamics as a primary driver of African bird speciation. *Global Ecology and Biogeography 19*, 111–121.

Voje, K. L., C. Hemp, O. Flagstad, G.-P. Saetre, and N. C. Stenseth (2009). Climatic change as an engine for speciation in flightless Orthoptera species inhabiting African mountains. *Molecular Ecology 18*(1), 93–108.

Vrba, E. S. (1985). *Ecological and adaptive changes associated with early hominid evolution.* New York, NY: In: *Ancestors: The Hard Evidence.* Delson, E. (ed.), A.R. Liss.

Vrba, E. S. (1995). *The fossil record of African antelopes (Mammalia, Bovidae) in relation to human evolution and paleoclimate.* New Haven: In: *Paleoclimate and Evolution With Emphasis on Human Origins.* Vrba, E., Denton, G., Burckle, L., and Partridge, T. (eds.). Yale University Press.

Vrba, E. S. (2000). *Major features of Neogene mammalian evolution in Africa.* Oxford: In: *The Cenozoic of Southern Africa.* Partridge, T.C., Maud, R. R. (eds.). Oxford University Press.

Wiley, R. H. (1991). Associations of song properties with habitats for territorial oscine birds of eastern north america. *American Naturalist 138*, 973–993.

Wiley, R. H. and D. G. Richards (1982). *Adaptations for acoustic communication in birds: Sound transmission and signal detection.* New York: In: *Acoustic Communication in Birds*. Kroodsma D. E., Miller E. H. and Ouellet H. (eds.). Academic Press.

Wolters, H. E. (1982). *Die Vogelarten der Erde - Eine systematische Liste mit Verbreitungsangaben sowie deutschen und englischen Namen.* Berlin: Parey.

Appendix A

Historical sequence of species and subspecies descriptions.

TABLE A.1: Historical sequence of species and subspecies descriptions, with original and current classification following Ryan (2006). Those descriptions left blank are not currently accepted as valid taxa.

Date	*Original genus*	*species*	*subspecies*	*Current genus*	*species*	*subspecies*
1810	*Sylvia*	*juncidis*		*Cisticola*	*juncidis*	*juncidis*
1817	*Sylvia*	*textrix*		*Cisticola*	*textrix*	*textrix*
1817	*Sylvia*	*fulvicapilla*		*Cisticola*	*fulvicapilla*	*fulvicapilla*
1820	*Sylvia*	*cisticola*		*Cisticola*	*juncidis*	*cisticola*
1823	*Malurus*	*galactotes*		*Cisticola*	*galactotes*	*galactotes*
1827	*Malurus*	*exilis*		*Cisticola*	*exilis*	*exilis*
1830	*Malurus*	*ruficeps*		*Cisticola*	*ruficeps*	*ruficeps*
1831	*Prinia*	*cursitans*		*Cisticola*	*juncidis*	*cursitans*
1838	*Cisticola*	*schoenicola*				
1840	*Sylvia*	*erythrogenis*				
1840	*Sylvia*	*lugubris*		*Cisticola*	*lugubris*	
1842	*Drymoica*	*levaillantii*				
1842	*Drymoica*	*terrestris*		*Cisticola*	*juncidis*	*terrestris*
1842	*Malurus*	*tinniens*		*Cisticola*	*tinniens*	*tinniens*
1843	*Drymoica*	*aberrans*		*Cisticola*	*aberrans*	*aberrans*
1843	*Drymoica*	*cherina*		*Cisticola*	*cherina*	
1843	*Drymoica*	*chiniana*		*Cisticola*	*chiniana*	*chiniana*
1843	*Cisticola*	*lateralis*		*Cisticola*	*lateralis*	*lateralis*
1843	*Drymoica*	*natalensis*		*Cisticola*	*natalensis*	*natalensis*
1843	*Drymoica*	*rufa*		*Cisticola*	*rufus*	
1843	*Drymoica*	*ruficapilla*		*Cisticola*	*fulvicapilla*	*ruficapilla*
1843	*Drymoica*	*strangei*		*Cisticola*	*natalensis*	*strangei*
1843	*Drymoica*	*subruficapilla*		*Cisticola*	*subruficapilla*	*subruficapilla*
1843	*Drymoica*	*uropygialis*		*Cisticola*	*juncidis*	*uropygialis*
1844	*Prinia*	*subhemalayana*				
1845	*Cisticola*	*campestris*		*Cisticola*	*chiniana*	*campestris*
1845	*Drymoica*	*robusta*		*Cisticola*	*robustus*	*robustus*
1847	*Cisticola*	*isura*				

Continued on next page

Table A.1 – *Continued from previous page*

Date	*Original genus*	*species*	*subspecies*	*Current genus*	*species*	*subspecies*
1847	*Cisticola*	*lineocapilla*		*Cisticola*	*exilis*	*lineocapilla*
1848	*Cysticola*	*magna*				
1848	*Drymoica*	*stangeri*				
1850	*Salicaria*	*brunneiceps*		*Cisticola*	*juncidis*	*brunniceps*
1850	*Drymoica*	*chloris*				
1850	*Drymoica*	*curvirostris*				
1850	*Drymoica*	*fulvescens*		*Cisticola*	*ruficeps*	*scotoptera*
1850	*Drymoica*	*fulvifrons*				
1850	*Drymoica*	*obscura*				
1850	*Drymoica*	*procerula*				
1850	*Drymoica*	*scotoptera*				
1850	*Drymoica*	*smithi*				
1851	*Cisticola*	*erythrocephala*		*Cisticola*	*exilis*	*erythrocephalus*
1851	*Cisticola*	*omalura*		*Cisticola*	*juncidis*	*omalurus*
1852	*Drymoica*	*fortirostris*				
1855	*Drymoeca*	*anonyma*		*Cisticola*	*anonymus*	
1856	*Sylvia*	*arquata*				
1856	*Drymoeca*	*bisonura*				
1857	*Drymoeca*	*erythrops*		*Cisticola*	*erythrops*	*erythrops*
1857	*Drymoeca*	*naevia*				
1859	*Calamanthella*	*tinnabulans*		*Cisticola*	*juncidis*	*tinnabulans*
1859	*Calamanthella*	*volitans*		*Cisticola*	*exilis*	*volitans*
1861	*Drymoica*	*madagascariensis*				
1862	*Cisticola*	*brunnescens*		*Cisticola*	*brunnescens*	*brunnescens*
1862	*Drymoeca*	*flaveola*				
1862	*Cisticola*	*semitorques*				
1863	*Cisticola*	*tytleri*		*Cisticola*	*exilis*	*tytleri*
1863	*Cisticola*	*ayresii*		*Cisticola*	*ayresii*	*ayresii*
1863	*Cisticola*	*europaea*				
1863	*Cisticola*	*fuscicapilla*		*Cisticola*	*juncidis*	*fuscicapilla*
1863	*Cisticola*	*rustica*		*Cisticola*	*exilis*	*rusticus*
1864	*Cisticola*	*ferruginea*		*Cisticola*	*troglodytes*	*ferrugineus*
1864	*Drymoica*	*troglodytes*		*Cisticola*	*troglodytes*	*troglodytes*
1864	*Drymoeca*	*valida*				
1866	*Hemipteryx*	*immaculata*				
1866	*Cisticola*	*semirufa*				
1867	*Drymoeca*	*cinerascens*				
1868	*Cisticola*	*haematocephala*		*Cisticola*	*haematocephala*	
1868	*Cisticola*	*isodactyla*		*Cisticola*	*galactotes*	*isodactylus*
1868	*Cisticola*	*melanocephala*				
1868	*Cisticola*	*procera*		*Cisticola*	*chiniana*	*procerus*
1869	*Drymoeca*	*antinorii*		*Cisticola*	*lateralis*	*antinorii*
1869	*Drymoeca*	*marginalis*		*Cisticola*	*marginatus*	*marginatus*
1869	*Cisticola*	*cantans*		*Cisticola*	*cantans*	*cantans*
1869	*Cisticola*	*clamans*				
1869	*Drymoeca*	*concolor*		*Cisticola*	*cantans*	*concolor*
1869	*Drymoeca*	*cordofana*				
1869	*Drymoeca*	*eximia*		*Cisticola*	*eximius*	*eximius*
1869	*Hemipteryx*	*habessinica*				
1869	*Hemipteryx*	*iodopyga*				
1869	*Cisticola*	*jodoptera*				
1869	*Drymoeca*	*laticauda*				

Continued on next page

Table A.1 – *Continued from previous page*

Date	*Original genus*	*species*	*subspecies*	*Current genus*	*species*	*subspecies*
1869	*Drymoeca*	*leucopyga*				
1869	*Drymoeca*	*malzaci*				
1869	*Drymoeca*	*marginata*				
1869	*Hemipteryx*	*oligura*				
1869	*Drymoeca*	*pachyrhyncha*				
1869	*Cisticola*	*rufifrons*				
1869	*Drymoeca*	*simplex*		*Cisticola*	*chiniana*	*simplex*
1869	*Drymoica*	*stulta*				
1869	*Drymoeca*	*virgata*				
1870	*Drymoeca*	*brachyptera*		*Cisticola*	*brachypterus*	*brachypterus*
1870	*Cisticola*	*delicatula*				
1870	*Drymoica*	*elegans*		*Cisticola*	*tinniens*	*elegans*
1870	*Drymoica*	*lais*		*Cisticola*	*lais*	*lais*
1870	*Drymoica*	*rufilata*		*Cisticola*	*rufilatus*	*rufilatus*
1870	*Drymoeca*	*swanzii*		*Cisticola*	*cantans*	*swanzii*
1871	*Cisticola*	*ruficollis*				
1872	*Cisticola*	*grayi*				
1872	*Cisticola*	*semirufa*		*Cisticola*	*exilis*	*semirufus*
1872	*Drymoeca*	*schwanzi*				
1874	*Cisticola*	*munipurensis*				
1875	*Cisticola*	*amphilecta*		*Cisticola*	*marginatus*	*amphilectus*
1875	*Cisticola*	*celebensis*				
1875	*Melocichla*	*pyrrhops*				
1876	*Cisticola*	*landanae*				
1877	*Drymoica*	*angolensis*		*Cisticola*	*robustus*	*angolensis*
1877	*Cisticola*	*subcinnamomea*				
1880	*Drymoica*	*modesta*		*Cisticola*	*lateralis*	*modestus*
1881	*Cisticola*	*hypoxantha*		*Cisticola*	*brachypterus*	*hypoxanthus*
1881	*Drymoeca*	*haesitata*		*Cisticola*	*haesitatus*	
1881	*Cisticola*	*incana*				
1882	*Drymoica*	*holubi*		*Cisticola*	*natalensis*	*holubii*
1882	*Cisticola*	*ladoensis*				
1882	*Dryodromas*	*melanura*		*Cisticola*	*melanurus*	
1884	*Cisticola*	*nana*		*Cisticola*	*nana*	
1887	*Cisticola*	*dispar*		*Cisticola*	*fulvicapilla*	*dispar*
1888	*Cisticola*	*cinereola*		*Cisticola*	*cinereolus*	*cinereolus*
1889	*Cisticola*	*hunteri*		*Cisticola*	*hunteri*	
1891	*Cisticola*	*angusticauda*		*Cisticola*	*angusticauda*	
1891	*Cisticola*	*fischeri*		*Cisticola*	*chiniana*	*fischeri*
1892	*Cisticola*	*chubbi*		*Cisticola*	*chubbi*	*chubbi*
1892	*Cisticola*	*emini*		*Cisticola*	*aberrans*	*emini*
1893	*Cisticola*	*discolor*		*Cisticola*	*chubbi*	*discolor*
1893	*Cisticola*	*nuchalis*		*Cisticola*	*robustus*	*nuchalis*
1895	*Cisticola*	*dodsoni*				
1895	*Cisticola*	*somalica*				
1896	*Cisticola*	*hindii*		*Cisticola*	*brunnescens*	*hindii*
1896	*Cisticola*	*slatini*				
1897	*Cisticola*	*nigriloris*		*Cisticola*	*nigriloris*	
1899	*Cisticola*	*alticola*				
1899	*Cisticola*	*muelleri*		*Cisticola*	*fulvicapilla*	*muelleri*
1900	*Cisticola*	*ambigua*				
1900	*Cisticola*	*lovati*				

Continued on next page

Table A.1 – *Continued from previous page*

Date	*Original genus*	*species*	*subspecies*	*Current genus*	*species*	*subspecies*
1900	*Cisticola*	*priniodes*				
1900	*Cisticola*	*aridula*	*aridula*	*Cisticola*	*aridulus*	*aridulus*
1901	*Cisticola*	*ambigua*				
1901	*Cisticola*	*cisticola*	*annae*			
1901	*Cisticola*	*lavendulae*		*Cisticola*	*aridulus*	*lavendulae*
1901	*Cisticola*	*neumanni*				
1903	*Cisticola*	*angusticauda*				
1904	*Cisticola*	*ruficapilla*				
1904	*Cisticola*	*cinnamomea*		*Cisticola*	*cinnamomeus*	*cinnamomeus*
1904	*Cisticola*	*erythrogenys*	*djamdjamensis*			
1904	*Cisticola*	*humilis*		*Cisticola*	*chiniana*	*humilis*
1904	*Cisticola*	*katonae*		*Cisticola*	*brachypterus*	*katonae*
1904	*Cisticola*	*sylvia*		*Cisticola*	*erythrops*	*sylvia*
1905	*Cisticola*	*argentea*		*Cisticola*	*natalensis*	*argenteus*
1905	*Cisticola*	*harrisoni*				
1905	*Cisticola*	*robusta*	*massaica*			
1905	*Cisticola*	*cisticola*	*mauritanica*			
1905	*Cisticola*	*lugubris*	*nyansae*	*Cisticola*	*marginatus*	*nyansae*
1905	*Cisticola*	*pictipennis*		*Cisticola*	*cantans*	*pictipennis*
1905	*Cisticola*	*schillingsi*		*Cisticola*	*cinereolus*	*schillingsi*
1905	*Cisticola*	*semifasciata*		*Cisticola*	*lais*	*semifasciatus*
1905	*Cisticola*	*lugubris*	*suahelica*	*Cisticola*	*marginatus*	*suahelicus*
1906	*Cisticola*	*robusta*	*ambigua*			
1906	*Cisticola*	*lugubris*	*amphilecta*			
1906	*Cisticola*	*robusta*	*angolensis*			
1906	*Cisticola*	*ansorgei*		*Cisticola*	*rufilatus*	*ansorgei*
1906	*Cisticola*	*heterophrys*		*Cisticola*	*chiniana*	*heterophrys*
1906	*Cisticola*	*natalensis*	*inexpectata*	*Cisticola*	*natalensis*	*inexpectatus*
1906	*Cisticola*	*robusta*	*schraderi*	*Cisticola*	*robustus*	*schraderi*
1907	*Cisticola*	*butleri*				
1907	*Cisticola*	*isabellina*		*Cisticola*	*brachypterus*	*isabellinus*
1907	*Cisticola*	*petrophila*		*Cisticola*	*aberrans*	*petrophilus*
1907	*Cisticola*	*stoehri*				
1907	*Cisticola*	*wellsi*				
1908	*Cisticola*	*rufopileata*				
1908	*Cisticola*	*rufopileata*				
1908	*Cisticola*	*belli*		*Cisticola*	*cantans*	*belli*
1908	*Cisticola*	*simplicissima*				
1908	*Cisticola*	*ugandae*				
1908	*Cisticola*	*woosnami*		*Cisticola*	*woosnami*	*woosnami*
1909	*Dryodromas*	*pearsoni*				
1909	*Cisticola*	*pretoriae*				
1909	*Cisticola*	*carruthersi*		*Cisticola*	*carruthersi*	
1909	*Cisticola*	*cinnamomeiceps*				
1909	*Cisticola*	*difficilis*				
1909	*Hemipteryx*	*minuta*				
1909	*Cisticola*	*pretoriae*				
1909	*Cisticola*	*zedlitzi*		*Cisticola*	*brachypterus*	*zedlitzi*
1910	*Cisticola*	*adamauae*		*Cisticola*	*cantans*	*adamauae*
1910	*Cisticola*	*adametzi*		*Cisticola*	*chubbi*	*adametzi*
1910	*Cisticola*	*wellsi*				
1910	*Cisticola*	*camerunensis*				

Continued on next page

Table A.1 – *Continued from previous page*

Date	*Original genus*	*species*	*subspecies*	*Current genus*	*species*	*subspecies*
1910	*Cisticola*	*floweri*				
1910	*Cisticola*	*garuensis*				
1910	*Cisticola*	*kalahari*		*Cisticola*	*aridulus*	*kalahari*
1911	*Cisticola*	*aequitorialis*				
1911	*Cisticola*	*alleni*				
1911	*Cisticola*	*borea*				
1911	*Cisticola*	*strangei*	*kapitensis*			
1911	*Cisticola*	*priniodes*	*kilimensis*			
1911	*Cisticola*	*pusilla*				
1911	*Cisticola*	*hypoxantha*	*reichenowi*	*Cisticola*	*brachypterus*	*reichenowi*
1911	*Cisticola*	*sudanica*				
1911	*Cisticola*	*vulpina*				
1912	*Cisticola*	*exilis*	*parryi*	*Cisticola*	*exilis*	*alexandrae*
1912	*Cisticola*	*exilis*	*tormenti*			
1912	*Cisticola*	*rufopileata*				
1912	*Cisticola*	*ruficapilla*	*bororensis*			
1912	*Cisticola*	*kmumkei*				
1912	*Cisticola*	*exilis*	*melvillensis*			
1912	*Cisticola*	*exilis*	*mixta*			
1912	*Cisticola*	*robusta*	*tana*			
1913	*Cisticola*	*robusta*	*abaya*			
1913	*Cisticola*	*elgonensis*				
1913	*Cisticola*	*subruficapilla*	*bodessa*	*Cisticola*	*bodessa*	*bodessa*
1913	*Hemipteryx*	*egregia*		*Cisticola*	*cinnamomeus*	*egregia*
1913	*Cisticola*	*elgonensis*				
1913	*Cisticola*	*subruficapilla*	*fricki*	*Cisticola*	*chiniana*	*fricki*
1913	*Cisticola*	*cisticola*	*jordansi*			
1913	*Hemipteryx*	*major*		*Cisticola*	*textrix*	*major*
1913	*Cisticola*	*aberrans*	*minor*	*Cisticola*	*aberrans*	*minor*
1913	*Cisticola*	*monticola*		*Cisticola*	*lais*	*monticola*
1913	*Cisticola*	*schusteri*				
1913	*Cisticola*	*priniodes*	*wambuguensis*			
1914	*Cisticola*	*mystica*				
1914	*Cisticola*	*nilotica*		*Cisticola*	*erythrops*	*niloticus*
1914	*Cisticola*	*exilis*	*normani*	*Cisticola*	*juncidis*	*normani*
1914	*Cisticola*	*blanfordi*	*sobatensis*			
1915	*Cisticola*	*rufopileata*				
1915	*Cisticola*	*exilis*	*equicaudata*	*Cisticola*	*exilis*	*equicaudatus*
1916	*Cisticola*	*strangei*	*argentea*			
1916	*Cisticola*	*deserticolor*				
1916	*Cisticola*	*frater*		*Cisticola*	*chiniana*	*frater*
1916	*Cisticola*	*munzneri*		*Cisticola*	*cantans*	*muenzneri*
1916	*Cisticola*	*pyrrhomitra*		*Cisticola*	*erythrops*	*pyrrhomitra*
1916	*Cisticola*	*soror*				
1917	*Cisticola*	*cisticola*	*arabica*			
1918	*Cisticola*	*erythrops*	*roseires*			
1918	*Cisticola*	*erythrops*	*zwaiensis*			
1919	*Dryodromas*	*fulvicapilla*	*silberbaueri*	*Cisticola*	*fulvicapilla*	*silberbauer*
1920	*Cisticola*	*nuchalis*	*sclateri*			
1920	*Cisticola*	*angusticauda*				
1920	*Cisticola*	*subruficapilla*	*ansorgei*			
1920	*Cisticola*	*harterti*				

Continued on next page

Table A.1 – *Continued from previous page*

Date	*Original genus*	*species*	*subspecies*	*Current genus*	*species*	*subspecies*
1920	*Cisticola*	*cisticola*	*neurotica*	*Cisticola*	*juncidis*	*neuroticus*
1920	*Cisticola*	*tinniens*	*perpulla*	*Cisticola*	*tinniens*	*perpullus*
1920	*Cisticola*	*nuchalis*	*sclateri*			
1921	*Cisticola*	*rufopileata*	*rufopileata*			
1922	*Cisticola*	*exilis*	*alexandrae*			
1922	*Cisticola*	*rufa*				
1922	*Cisticola*	*lateralis*	*ugandensis*			
1922	*Cisticola*	*cisticola*	*berberae*			
1922	*Cisticola*	*exilis*	*diminuta*	*Cisticola*	*exilis*	*diminutus*
1922	*Cisticola*	*exilis*	*exaggerata*			
1922	*Cisticola*	*carruthersi*	*kavirondensis*			
1922	*Cisticola*	*terrestris*	*mauensis*	*Cisticola*	*ayresii*	*mauensis*
1922	*Cisticola*	*terrestris*	*nakuruensis*	*Cisticola*	*brunnescens*	*nakuruensis*
1922	*Cisticola*	*tinniens*	*oreophila*	*Cisticola*	*tinniens*	*oreophilus*
1922	*Cisticola*	*teitensis*				
1922	*Cisticola*	*lateralis*	*ugandensis*			
1923	*Cisticola*	*cisticola*	*djadja*			
1923	*Cisticola*	*tinniens*	*subrufescens*			
1924	*Drymodyta*	*aberrans*	*aberrans*			
1924	*Cisticola*	*ruficapilla*	*adamuauae*			
1924	*Cisticola*	*discolor*				
1924	*Cisticola*	*rufopileata*				
1924	*Cisticola*	*juncidis*	*intermedia*			
1926	*Cisticola*	*exilis*	*courtoisi*	*Cisticola*	*exilis*	*courtoisi*
1926	*Cisticola*	*ayresii*	*lynesi*	*Cisticola*	*brunnescens*	*lynesi*
1926	*Cisticola*	*robusta*	*santae*	*Cisticola*	*robustus*	*santae*
1927	*Cisticola*	*concolor*	*pictipennis*			
1927	*Cisticola*	*rufopileata*	*rufopileata*			
1928	*Cisticola*	*robusta*	*omo*	*Cisticola*	*robustus*	*omo*
1930	*Cisticola*	*juncidis*	*malaya*	*Cisticola*	*juncidis*	*malaya*
1930	*Cisticola*	*robusta*	*aberdare*	*Cisticola*	*aberdare*	
1930	*Cisticola*	*brachptera*	*ankole*	*Cisticola*	*brachypterus*	*ankole*
1930	*Cisticola*	*bulliens*		*Cisticola*	*bulliens*	*bulliens*
1930	*Cisticola*	*distincta*		*Cisticola*	*lais*	*distinctus*
1930	*Cisticola*	*ayresii*	*entebbe*	*Cisticola*	*ayresii*	*entebbe*
1930	*Cisticola*	*fortis*		*Cisticola*	*chiniana*	*fortis*
1930	*Cisticola*	*ruficeps*	*guinea*	*Cisticola*	*guinea*	
1930	*Cisticola*	*natalensis*	*huambo*	*Cisticola*	*natalensis*	*huambo*
1930	*Cisticola*	*subruficapilla*	*jamesi*	*Cisticola*	*subruficapilla*	*jamesi*
1930	*Cisticola*	*natalensis*	*katanga*	*Cisticola*	*natalensis*	*katanga*
1930	*Cisticola*	*brachyptera*	*kericho*	*Cisticola*	*brachypterus*	*kericho*
1930	*Cisticola*	*erythrops*	*lepe*	*Cisticola*	*erythrops*	*lepe*
1930	*Cisticola*	*brachyptera*	*loanda*	*Cisticola*	*brachypterus*	*loanda*
1930	*Cisticola*	*aridula*	*lobito*	*Cisticola*	*aridulus*	*lobito*
1930	*Cisticola*	*woosnami*	*lufira*	*Cisticola*	*woosnami*	*lufira*
1930	*Cisticola*	*lais*	*maculata*	*Cisticola*	*lais*	*maculatus*
1930	*Cisticola*	*lais*	*mashona*	*Cisticola*	*lais*	*mashona*
1930	*Cisticola*	*ruficeps*	*mongalla*	*Cisticola*	*ruficeps*	*mongalla*
1930	*Cisticola*	*erythrops*	*nyasa*	*Cisticola*	*erythrops*	*nyasa*
1930	*Cisticola*	*aberrans*	*nyika*	*Cisticola*	*aberrans*	*nyika*
1930	*Cisticola*	*eximia*	*occidens*	*Cisticola*	*eximius*	*occidens*
1930	*Cisticola*	*juncidis*	*perrenia*	*Cisticola*	*juncidis*	*perennius*

Continued on next page

Table A.1 – *Continued from previous page*

Date	*Original genus*	*species*	*subspecies*	*Current genus*	*species*	*subspecies*
1930	*Cisticola*	*pipiens*		*Cisticola*	*pipiens*	*pipiens*
1930	*Cisticola*	*aridula*	*tanganyika*	*Cisticola*	*aridulus*	*tanganyika*
1930	*Cisticola*	*natalensis*	*tonga*	*Cisticola*	*natalensis*	*tonga*
1930	*Cisticola*	*brunnescens*	*wambera*	*Cisticola*	*brunnescens*	*wambera*
1930	*Cisticola*	*galactotes*	*zalingei*	*Cisticola*	*marginatus*	*zalingei*
1930	*Cisticola*	*semifasciata*	*ukamba*	*Cisticola*	*chiniana*	*ukamba*
1930	*Cisticola*	*fischeri*	*victoria*	*Cisticola*	*chiniana*	*victoria*
1930	*Cisticola*	*aberrans*	*admiralis*	*Cisticola*	*aberrans*	*admiralis*
1930	*Cisticola*	*subruficapilla*	*namaqua*	*Cisticola*	*subruficapilla*	*namaqua*
1930	*Cisticola*	*hunteri*	*masaba*			
1930	*Cisticola*	*lais*	*gaza*			
1930	*Cisticola*	*juncidis*	*mcgregori*			
1931	*Cisticola*	*emini*	*bailunduensis*	*Cisticola*	*aberrans*	*bailunduensis*
1931	*Cisticola*	*lais*	*namba*	*Cisticola*	*lais*	*namba*
1931	*Cisticola*	*textrix*	*bulubulu*	*Cisticola*	*textrix*	*bulubulu*
1931	*Cisticola*	*eximia*	*winneba*	*Cisticola*	*eximius*	*winneba*
1931	*Cisticola*	*dambo*	*dambo*	*Cisticola*	*dambo*	*dambo*
1931	*Cisticola*	*ayresii*	*gabun*	*Cisticola*	*ayresii*	*gabun*
1932	*Cisticola*	*chubbi*	*marungensis*	*Cisticola*	*chubbi*	*marungensis*
1932	*Cisticola*	*juncidis*	*okinavae*			
1932	*Cisticola*	*textrix*	*marleyi*	*Cisticola*	*textrix*	*marleyi*
1933	*Cisticola*	*emini*	*lurio*	*Cisticola*	*aberrans*	*lurio*
1933	*Cisticola*	*chiniana*	*mocuba*			
1933	*Cisticola*	*aberrans*	*njombe*	*Cisticola*	*njombe*	*njombe*
1933	*Cisticola*	*galactotes*	*luapula*	*Cisticola*	*luapula*	
1933	*Cisticola*	*robusta*	*awemba*	*Cisticola*	*robustus*	*awemba*
1934	*Cisticola*	*natalensis*	*matengorum*			
1934	*Cisticola*	*exilis*	*pilionatus*	*Cisticola*	*exilis*	*polionotus*
1936	*Cisticola*	*pipiens*	*congo*	*Cisticola*	*pipiens*	*congo*
1936	*Cisticola*	*fulvicapilla*	*lembombo*	*Cisticola*	*fulvicapilla*	*lebombo*
1936	*Cisticola*	*juncidis*	*salimalii*	*Cisticola*	*juncidis*	*salimalii*
1936	*Cisticola*	*dambo*	*kasai*	*Cisticola*	*dambo*	*kasai*
1937	*Cisticola*	*subruficapilla*	*windhoekensis*	*Cisticola*	*subruficapilla*	*windhoekensis*
1937	*Cisticola*	*subruficapilla*	*karasensis*	*Cisticola*	*subruficapilla*	*karasensis*
1938	*Cisticola*	*juncidis*	*constans*	*Cisticola*	*juncidis*	*constans*
1938	*Cisticola*	*brunnescens*	*midgongo*	*Cisticola*	*cinnamomeus*	*midcongo*
1938	*Cisticola*	*ayresii*	*imatong*	*Cisticola*	*ayresii*	*imatong*
1941	*Cisticola*	*lais*	*nyikae*			
1943	*Cisticola*	*natalensis*	*littoralis*			
1944	*Cisticola*	*chiniana*	*emendatus*	*Cisticola*	*chiniana*	*emendatus*
1945	*Cisticola*	*lais*	*mariae*	*Cisticola*	*njombe*	*mariae*
1947	*Cisticola*	*hunteri*	*hypernephala*			
1947	*Cisticola*	*tinniens*	*shiwae*	*Cisticola*	*tinniens*	*shiwae*
1947	*Cisticola*	*aridula*	*perplexa*	*Cisticola*	*aridulus*	*perplexus*
1952	*Cisticola*	*tinniens*	*dyleffi*	*Cisticola*	*tinniens*	*dyleffi*
1953	*Cisticola*	*lateralis*	*vincenti*			
1953	*Cisticola*	*juncidis*	*leanyeri*	*Cisticola*	*juncidis*	*leanyeri*
1954	*Cisticola*	*galactotes*	*schoutedeni*			
1955	*Cisticola*	*fulvicapilla*	*hallae*	*Cisticola*	*fulvicapilla*	*hallae*
1955	*Cisticola*	*aridula*	*caligina*	*Cisticola*	*aridulus*	*caliginus*
1956	*Cisticola*	*chiniana*	*smithersi*	*Cisticola*	*chiniana*	*smithersi*
1957	*Cisticola*	*ayresii*	*itombwensis*	*Cisticola*	*ayresii*	*itombwensis*

Continued on next page

Table A.1 – *Continued from previous page*

Date	***Original genus***	***species***	***subspecies***	***Current genus***	***species***	***subspecies***
1960	*Cisticola*	*textrix*	*anselli*	*Cisticola*	*textrix*	*anselli*
1964	*Cisticola*	*chiniana*	*bensoni*	*Cisticola*	*chiniana*	*bensoni*
1966	*Cisticola*	*lais*	*oreobates*	*Cisticola*	*lais*	*oreobates*
1966	*Cisticola*	*brachyptera*	*tenebricosa*			
1966	*Cisticola*	*aridula*	*traylori*	*Cisticola*	*aridulus*	*traylori*
1967	*Cisticola*	*chiniana*	*huilensis*			
1967	*Cisticola*	*restrictus*		*Cisticola*	*restrictus*	
1967	*Cisticola*	*subruficapilla*	*newtoni*	*Cisticola*	*subruficapilla*	*newtoni*
1967	*Cisticola*	*galactotes*	*grisea*			
1969	*Cisticola*	*galactotes*	*stagnans*			
1969	*Cisticola*	*pipiens*	*arundicola*	*Cisticola*	*pipiens*	*arundicola*
1971	*Cisticola*	*fulvicapilla*	*dexter*	*Cisticola*	*fulvicapilla*	*dexter*
1971	*Cisticola*	*juncidis*	*nigrostriata*	*Cisticola*	*juncidis*	*nigrostriatus*
1973	*Cisticola*	*rufilatus*	*vicinior*	*Cisticola*	*rufilatus*	*vicinior*
1973	*Cisticola*	*brunnescens*	*mbangensis*	*Cisticola*	*brunnescens*	*mbangensis*
1974	*Cisticola*	*bodessa*	*kaffensis*	*Cisticola*	*bodessa*	*kaffensis*
1978	*Cisticola*	*erythrops*	*arcana*			
1978	*Cisticola*	*erythrops*	*elusa*			
1979	*Cisticola*	*juncidis*	*laveryi*	*Cisticola*	*juncidis*	*laveryi*
1982	*Cisticola*	*lais*	*oreodytes*			
1983	*Cisticola*	*fulvicapilla*	*dumicola*	*Cisticola*	*fulvicapilla*	*dumicola*
1984	*Cisticola*	*rufilatus*	*venestulus*			
1984	*Cisticola*	*subruficapilla*	*euroa*			
1984	*Cisticola*	*aridula*	*eremica*	*Cisticola*	*aridulus*	*eremicus*
1987	*Cisticola*	*chiniana*	*mbeya*	*Cisticola*	*chiniana*	*mbeya*
1987	*Cisticola*	*chiniana*	*keithi*	*Cisticola*	*chiniana*	*keithi*
1991	*Cisticola*	*dorsti*				
1992	*Cisticola*	*chiniana*	*vulpiniceps*			
1992	*Cisticola*	*taciturnus*				
1992	*Cisticola*	*bulliens*	*septentrionalis*	*Cisticola*	*bulliens*	*septentrionalis*
1994	*Cisticola*	*natalensis*	*vigilax*			
1999	*Cisticola*	*tinniens*	*brookei*			

Appendix B

Lynes' linear classification.

TABLE B.1: Lynes (1930) linear relationship showing nine of his groups; those taxa that he did not include in groups are placed near where Lynes suggested that they might best fit.

Group	Taxa included
Juncidis group	Zitting Cisticola (*Cisticola juncidis: C. j. juncidis, C. j. cisticola, C. j. neurotica, C. j. cursitans, C. j. omalura, C. j. malaya, C. j. fuscicapilla, C. j. tinnabulans, C. j. brunneiceps, C. j. normani, C. j. uropygialis, C. j. perennia, C. j. terrestris*) Madagascar Cisticola (*C. cherina*) Socotra Cisticola (*C. haesitata*) Desert Cisticola (*C. aridula: C. a. aridula, C. a. lavendulae, C. a. tanganyika, C. a. lobito, C. a. kalahari*)
Textrix group	Cloud Cisticola (*C. textrix: C. t. textrix, C. t. mystica*) Wing-snapping Cisticola (*C. ayresii: C. a. ayresii, C. a. mauensis, C. a. entebbe*) Pectoral-patch Cisticola (*C. brunnescens: C. b. brunnescens, C. b. wambera, C. b. nakuruensis, C. b. hindii, C. b. lynesi, C. b. cinnamomea, C. b. egregia*) Black-backed Cisticola (*C. eximia: C. e. eximia, C. e. occidens*)
Unplaced	Golden-headed Cisticola (*C. exilis: C. e. exilis, C. e. diminuta, C. e. lineocapilla, C. e. alexandrae, C. e. rustica, C. e. equicaudata, C. e. erythrocephala, C. e. tytleri, C. e. volitans*)

Continued on next page

Table B.1 – *Continued from previous page*

Group	**Taxa included**
Unplaced	Red-pate Cisticola (*C. ruficeps: C. r. ruficeps, C. r. scotoptera, C. r. mongalla, C. r. guinea*)
Unplaced	Tiny Cisticola (*C. nana*)
Subruficapilla group	Grey-backed Cisticola (*C. subruficapilla: C. s. subruficapilla, C. s. namaqua, C. s. jamesi*) Wailing Cisticola (*C. lais: C. l. lais, C. l. maculata, C. l. monticola, C. l. mashona, C. l. semifasciata*) Tinkling Cisticola (*C. rufilata: C. r. rufilata, C. r. ansorgei*) 'Spangled Fantail' (*C. distincta*)
Unplaced	Levaillant's Cisticola (*C. tinniens: C. t. tinniens, C. t. perpulla, C. t. oreophila*)
Unplaced	Ashy Cisticola (*C. cinereola: C. c. cinereola, C. c.shillingsi*)
Unplaced	Rattling Cisticola, (*C. chiniana: C. c. chiniana, C. c. campestris, C. c. frater, C. c. procera, C. c. heterophrys, C. c. fischeri, C. c. victoria, C. c. ukamba, C. c. humilis, C. c. bodessa, C. c. simplex*)
Lateralis group	Whistling Cisticola (*C. lateralis: C. l. lateralis, C. l. antinorii, C. l. modesta*) Trilling Cisticola (*C. woosnami: C. w. woosnami, C. w. schusteri, C. w. lufira*) Chattering Cisticola (*C. anonyma*) Rock-loving Cisticola (*C. emini: C. e. emini, C. e. teitensis, C. e. petrophila*) Bubbling Cisticola (*C. bulliens*) Sturdy Cisticola (*C. fortis*)
Nigriloris group	Black-lored Cisticola (*C. nigriloris*) Brown-backed Cisticola (*C. discolor: C. d. discolor, C. d. adametzi*) Chubb's Cisticola (*C. chubbi*) Hunter's Cisticola (*C. hunteri: C. h. hunteri, C. h. prinioides, C. h. masaba*)

Continued on next page

Table B.1 – *Continued from previous page*

Group	**Taxa included**
Cantans & erythrops pair	Singing Cisticola (*C. cantans: C. c. cantans, C. c. concolor, C. c. swanzii, C. c. adamauae, C. c. belli, C. c. pictipennis, C. c. munzneri*) Red-faced Cisticola (*C. erythrops: C. e. erythrops, C. e. pyrrhomitra, C. e. nilotica, C. e. sylvia, C. e. nyasa, C. e. lepe*)
Galactotes group	Rufous-winged Cisticola (*C. galactotes: C. g. galactotes, C. g. lugubris, C. g. marginata, C. g. zalingei, C. g. amphilecta, C. g. nyanzae, C. g. haematocephala, C. g. suahelica*) Chirping Cisticola (*C. pipiens*) Carruther's Cisticola (*C. carruthersi*)
Robusta & natalensis pair	Stout Cisticola (*C. robusta: C. r. robusta, C. r. schraderi, C. r. omo, C. r. ambigua, C. r. aberdare, C. r. nuchalis, C. r. angolensis, C. r. santae*) Croaking Cisticola (*C. natalensis: C. n. natalensis, C. n. huambo, C. n. katanga, C. n. strangei, C. n. inexpectata, C. n. tonga, C. n. argentea, C. n. kapitensis, C. n. valida*).
Brachyptera group	Short-winged Cisticola (*C. brachyptera: C. b. brachyptera, C. b. hypoxantha, C. b. zedlitzi, C. b. katonae, C. b. reichenowi, C. b. kericho, C. b. ankole, C. b. isabellina, C. b. loanda*) Rufous Cisticola (*C. rufa*) Foxy Cisticola (*C. troglodytes: C. t. troglodytes, C. t. ferruginea*) Neddicky (*C. fulvicapilla: C. f. fulvicapilla, C. f. silberbaueri, C. f. ruficapilla, C. f. muelleri, C. f. dispar*)
Unplaced	Lazy Cisticola (C. aberrans: C. a. aberrans, C. a. minor, C. a. nyika)

Appendix C

Characters captured from Lynes' review.

TABLE C.1: Table of characters and scores captured from Lynes (1930). Locations mentioned in the text are labelled in Figure 2.2. Characters marked with an asterisk (*) were omitted from multiple correspondence analyses.

Character	Score
1 Wing length	(1) <50 mm, very small; (2) 50–60 mm, small; (3) 60–70 mm, medium; (4) >70 mm, large.
2 Breeding tail proportion of wing length	(1) 1/3 shorter; (2) 1/4 shorter; (3) 1/6 shorter; (4) sub-equal; (5) equal; (6) longer.
3 Leg strength	(1) weak; (2) slender; (3) average; (4) strong; (5) very strong.
4 Sexual dimorphism	(1) <10%, small; (2) 10–20%, moderate; (3) >20%, great.
5 P10/P9	(1) 40–50%; (2) 50–60%; (3) 60–70%; (4) >70%.
6 Bill length	(1) short; (2) medium; (3) long.
7 Bill strength	(1) very fine; (2) weak; (3) medium; (4) strong.
8 Bill curve	(1) straight; (2) lightly curved; (3) moderately curved; (4) curved.
9 Head-top colour	(1) dull sepia; (2) medium sepia; (3) dark sepia; (4) light rust brown; (5) medium rust brown; (6) dark rust brown;(7) light yellow; (8) medium yellow; (9) dark yellow; (A) light orange; (B) medium orange; (C) light red; (D) medium red; (E) dark red; (F) medium black; (G) dark black.

Continued on next page

Table C.1 – *Continued from previous page*

Character	Score
10 Head-top mottling	(0) absent; (1) slight; (2) moderate; (3) heavy.
11 Head-top darkness of mottles	(1) faint; (2) light; (3) medium; (4) dark.*
12 Head-top cresting	(0) absent; (1) small; (2) large.
13 Forehead	(0) as head-top; (1) different colour; (2) more mottled.
14 Nape	(0) plain; (1) light marking; (2) heavy marking.
15 Back contrast with head	(0) no contrast; (1) slight contrast; (2) moderate contrast; (3) conspicuous contrast; (4) very conspicuous contrast; (5) exaggerated.
16 Back mottling	(0) plain; (1) faintly mottled; (2) moderately mottled; (3) boldly mottled; (4) heavily mottled; (5) extremely mottled.
17 Back feather centre	(1) brown; (2) sepia; (3) grey; (4) black; (5) plain.
18 Back feather centre size	(0) none; (1) narrow; (2) broad.
19 Back feather border colour	(1) light sepia; (2) medium sepia; (3) dark sepia; (4) light buff; (5) medium buff; (6) dark buff; (7) light grey; (8) medium grey; (9) light black; (A) medium black; (B) dark black; (C) light brown; (D) medium brown; (E) dark brown; (F) light olive; (G) medium olive; (H) dark olive.
20 Hind neck colour	(1) light sepia; (2) medium sepia; (3) dark sepia; (4) light rust brown; (5) medium rust brown; (6) dark rust brown; (7) light brown; (7) medium brown; (8) light yellow; (9) medium yellow; (A) dark orange; (B) light red; (C) medium red; (D) dark red; (E) medium black; (F) dark black.
21 Hind neck 'collarette'	(0) none; (1) slight collarette; (2) strong collarette.
22 Hind neck mottling	(0) none; (1) almost plain; (2) lightly mottled; (3) strongly mottled.
23 Rump conspicuousness	(0) inconspicuous; (1) slightly conspicuous; (2) conspicuous; (3) very conspicuous.

Continued on next page

Table C.1 – *Continued from previous page*

Character	Score
24 Rump colour	(1) dull sepia; (2) medium sepia; (3) dark sepia; (4) light rust brown; (5) medium rust brown; (6) dark rust brown; (7) light brown; (8) medium brown; (9) dark brown; (A) light auburn; (B) medium auburn; (C) dark auburn; (D) light yellow; (E) light red; (F) medium red; (G) dark red; (H) light black; (I) medium black.
25 Rump mottling	(0) absent; (1) slight mottling; (2) heavy mottling.
26 Upper tail coverts mottling	(0) absent; (1) mottled.
27 Colour below (base ventral colouration)	(0) bright white; (1) white; (2) shady white; (3) light brown; (4) medium brown; (5) dark brown; (6) light rusty buff; (7) rusty buff; (8) dark rusty buff.
28 Colour below wash (tint over ventral surface)	(0) light brown; (1) medium brown; (2) dark brown; (3) light rusty buff; (4) rusty buff; (5) dark rusty buff; (6) light red; (7) red; (8) dark red; (9) light smokey grey; (A) smokey grey; (B) dark smokey grey.
29 Underside spotting	(0) plain; (1) spotted.
30 Chin colour	(0) tinted; (1) white.
31 Throat colour	(0) tinted; (1) white.
32 Belly colour	(0) tinted; (1) white.
33 Breast colour	(1) ochreous; (2) rusty buff; (3) brown; (4) cream; (5) light smoke grey; (6) dark smoke grey.
34 Side colour	(1) light buff; (2) buff; (3) strong buff; (4) light brown; (5) brown; (6) dark brown; (7) light grey; (8) smokey grey; (9) dark grey.
35 Side markings	(0) none; (1) spotted.
36 Flank colour	(1) light rusty buff; (2) rusty buff; (3) dark rusty buff; (4) snuff; (5) brown; (6) light grey; (7) grey; (8) dark grey.
37 Flank striping	(0) none; (1) striped.
38 Thighs wash	(0) same as underside; (1) light rust brown; (2) rust brown; (3) bright rust brown; (4) dark rusty buff; (5) light rust red; (6) rust red; (7) grey; (8) cream.

Continued on next page

Table C.1 – *Continued from previous page*

Character	Score
39 Pectoral patch	(0) none; (1) slight; (2) small; (3) conspicuous; (4) large.
40 Lores	(0) whitish; (1) white; (2) rusty buff; (3) red; (4) black.
41 Face freckling	(0) absent; (1) slightly freckled; (2) heavily freckled.
42 Supraloral colour	(0) absent; (1) present.
43 Subloral spot	(0) absent; (1) slight; (2) small; (3) conspicuous; (4) large.
44 Eyebrow size	(0) absent; (1) slight; (2) well defined; (3) large.
45 Eyebrow colour	(1) whitish; (2) rusty white; (3) red.*
46 Ear coverts colour	(0) none; (1) whitish; (2) brown; (3) black; (4) red.
47 Ear coverts shading	(0) no shading; (1) shading.
48 Wing contrast with dorsal surface	(0) no contrast; (1) moderate; (2) conspicuous.
49 Wing edging	(0) none; (1) slight; (2) conspicuous.
50 Tertials	(0) no borders; (1) borders.
51 Tail pattern above	(0) plain; (1) slight patterning; (2) bold spotted fan.
52 Tail pattern below	(0) plain; (1) slight patterning; (2) bold spotted fan.
53 Tail tips	(0) none; (1) whitish; (2) rust; (3) grey; (4) variable.
54 Tail edging	(0) none; (1) white; (2) brown; (3) rusty; (4) red.
55 Tail subterminal spot	(0) none; (1) slight; (2) bold; (3) variable.
56 Tail mirrors colour	(0) none; (1) cinnamon; (2) white; (3) variable.
57 Iris colour	(1) brown; (2) hazel; (3) grey.
58 Leg colour	(1) flesh; (2) dark flesh; (3) pinkish buff; (4) brown.
59 Mandible	(1) grey; (2) blackish; (3) black; (4) sepia.
60 Culmen colour	(1) grey; (2) sepia; (3) black.
61 Male summer palate colour	(1) grey; (2) black.*
62 Female difference	(0) same as male; (1) different pattern; (2) different colour; (3) both.
63 Winter male colour above	(0) same as summer; (1) buff; (2) light rusty buff; (3) dark buff; (4) sandy; (5) light grey; (6) grey; (7) black; (8) deep black; (9) light red; (A) warmer red; (B) bright red; (C) dull brown; (D) warm brown; (E) wood brown; (F) dark brown.*

Continued on next page

Table C.1 – *Continued from previous page*

Character	Score
64 Winter male above pattern	(0) same as summer; (1) plainer; (2) slightly streaked; (3) streaked; (4) heavily streaked; (5) mottled.*
65 Winter male head top	(0) same as summer; (1) more streaking; (2) darker colour; (3) lighter colour; (4) plainer.*
66 Winter male tail coverts	(0) same as summer; (1) plainer; (2) different colours; (3) darker tints.*
67 Winter male rump	(0) same as summer; (1) different.*
68 Winter male subloral spot	(0) same as summer; (1) different.*
69 Winter male hind neck	(0) same as summer; (1) different.*
70 Winter male collarette	(0) same as summer; (1) different.*
71 Winter male eyebrow	(0) same as summer; (1) smaller; (2) larger.*
72 Winter eyebrow colour	(0) same as summer; (1) white; (2) rust; (3) buff; (4) red.*
73 Winter male wing edging	(0) same as summer; (1) different.*
74 Winter male tail mirrors	(0) same as summer; (1) different.*
75 Winter tail pattern above	(0) same as summer; (1) plain; (2) slight spots; (3) bold spotted fan; (4) different tint.*
76 Winter tail pattern below	(0) same as summer; (1) larger markings; (2) smaller markings.*
77 Winter tail retrices	(0) same as summer; (1) different.*
78 Winter colour below	(0) same as summer; (1) less suffused; (2) more suffused; (3) heavily suffused.*
79 Winter bill colour	(0) same as summer; (1) lighter.*
80 Winter palate	(0) same as summer; (1) flesh.*
81 Winter tail edging	(0) same as summer; (1) different.*
82 Mid-toe and claw	(1) 13–15 mm; (2) 16–18 mm; (3) 19–21 mm; (4) 22–24 mm.
83 Egg colour	(1) white; (2) green; (3) turquoise; (4) red; (5) variable.*
84 Egg pattern	(1) fine speckles; (2) well marked; (3) thick spots; (4) heavily marked; (5) variable.*
85 Egg clutch	(1) small; (2) medium; (3) large.*

Continued on next page

Table C.1 – *Continued from previous page*

Character	**Score**
86 Habitat	(1) grass; (2) scrub; (3) savanna woodland; (4) woodland; (5) marsh.
87 Display	(1) perched; (2) perched or low; (3) low; (4) moderate height; (5) high; (6) variable.
88 Wing snap	(0) absent; (1) present; (2) variable.
89 Nest	(1) ball; (2) soda-bottle; (3) tailored ball; (4) deep cup; (5) elliptical ball.
90 Difference of winter tail length	(0) no difference; (1) 0–5%; (2) 6–10%; (3) 11–15%; (4) 16–20%; (5) 21–25%; (6) 26–30%; (7) 31–35%; (8) 36–40%; (9) 41–45%.*
91 Molt	(0) regular; (1) perennial summer; (2) perennial winter; (3) variable; (4) perennial intermediate.
92 Shape of outermost primary feather	(0) acute; (1) narrow blade; (2) blade; (3) scimitar; (4) broad blade.

Appendix D

Colour illusions: the same colours appear different depending on their context and the shades of the colours surrounding them.

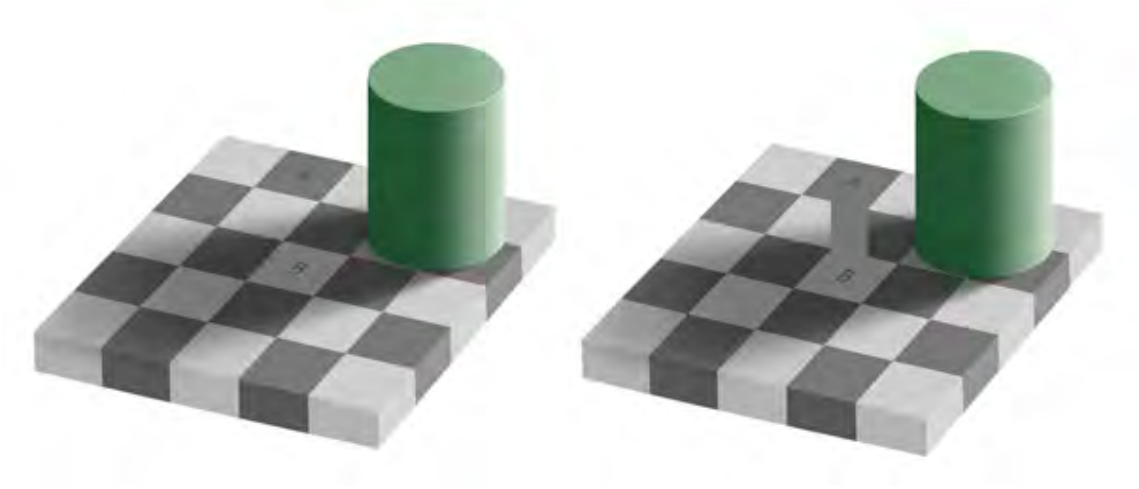


FIGURE D.1: The 'Checker Shadow Illusion' that exposes biases in human perception of colour and shades where blocks labelled A and B appear to be different colours but are actually identical. From Adelson (2006).

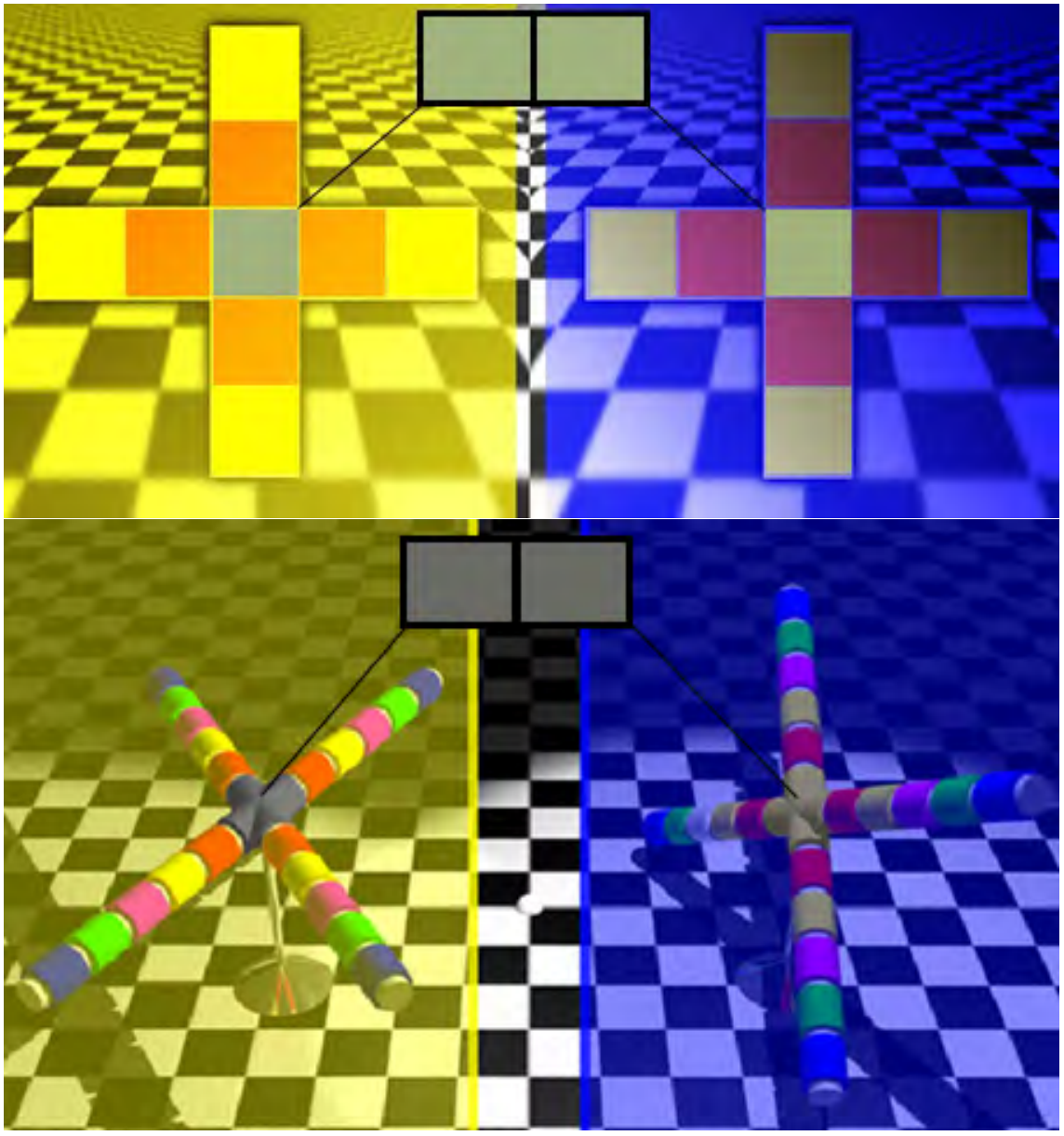


FIGURE D.2: Human perception of colour is also influenced by their context, centre colours appear blueish-green in images on the left, and yellowish in images on the right, but are identical in reality (see Lotto (2011)). Methods employed in this study attempt to avoid these perception issues.

Appendix E

Pixelation and the advantage of averaging.

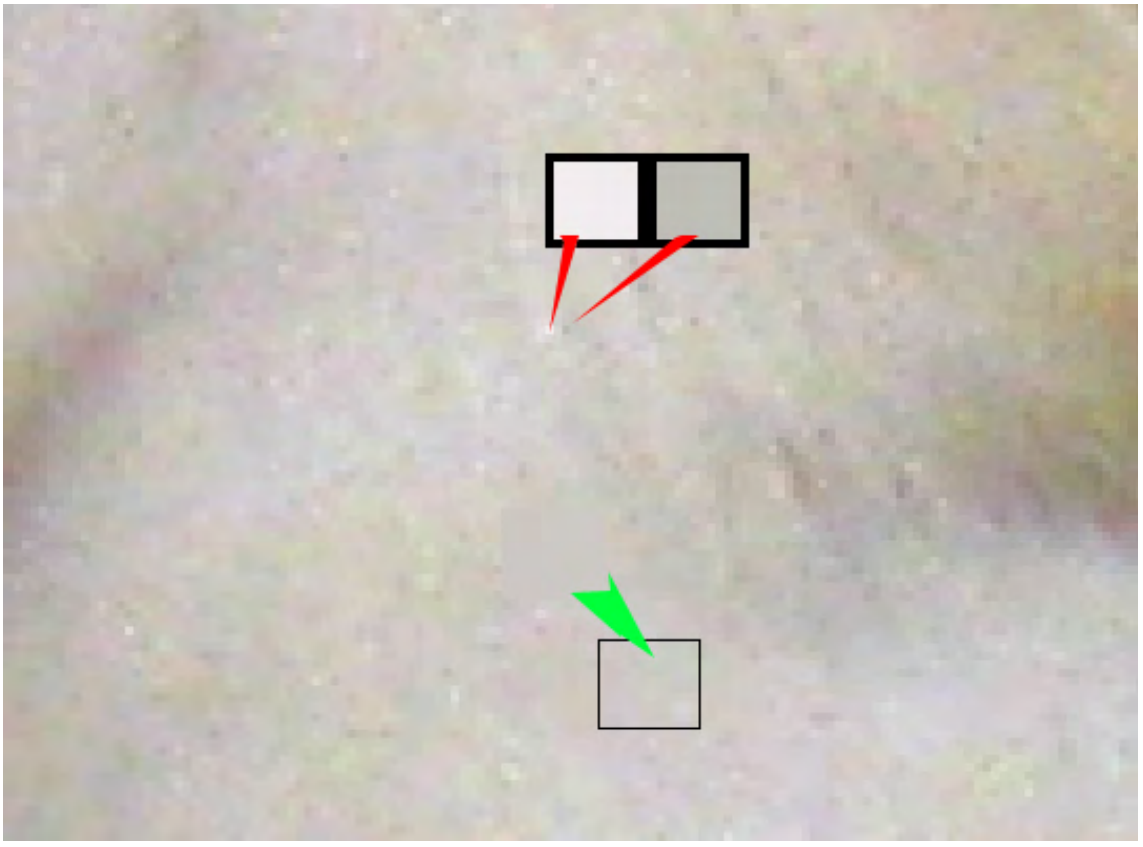


FIGURE E.1: A close-up of digital image demonstrating that two pixels close together can have different colours, an average blur produces a colour that better represents the true colour of the area of interest than either of the pixels alone.

Appendix F

Plumage colour character score delineation.

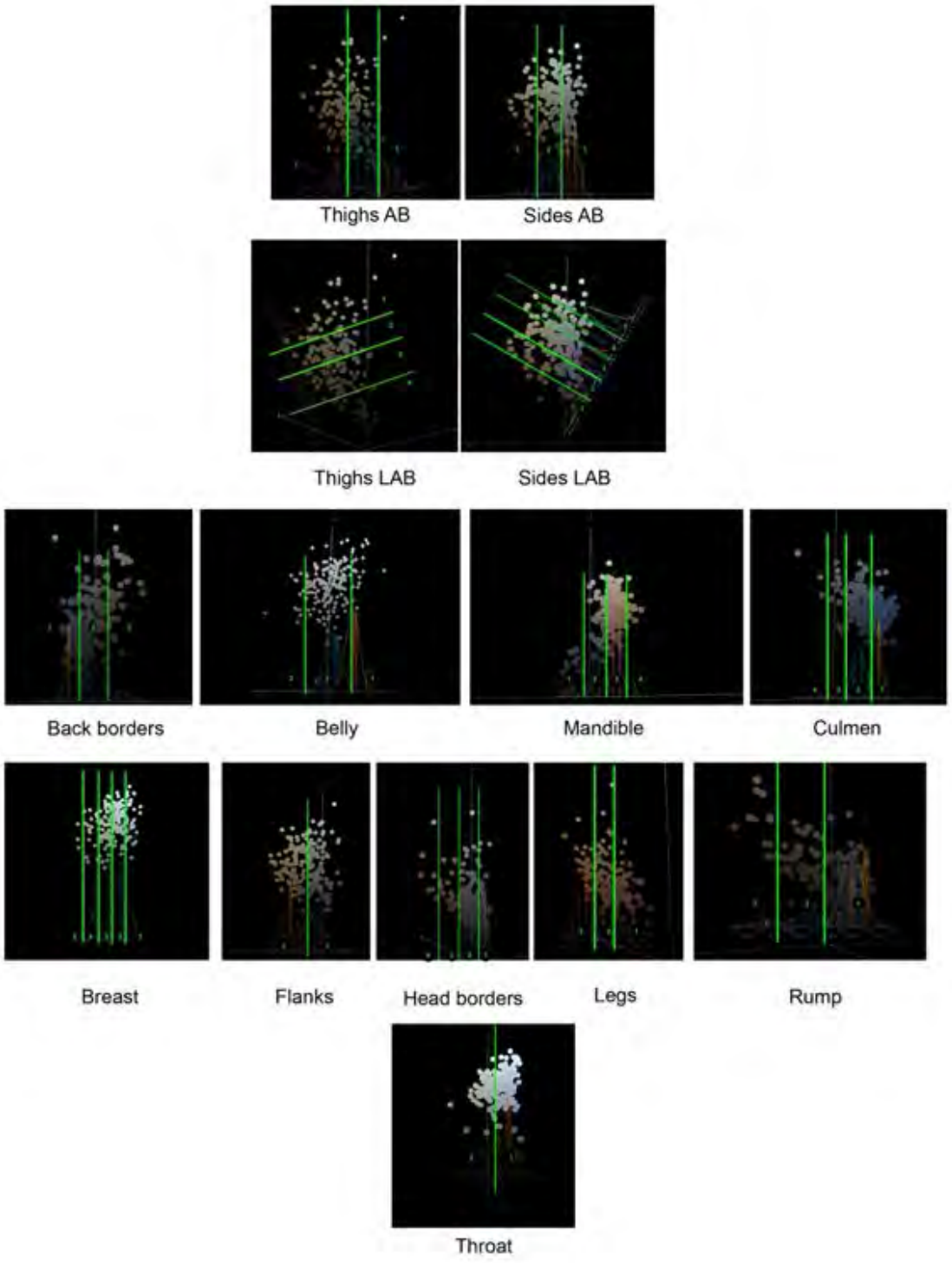


FIGURE F.1: Coding of colour values for each character. The first four graphs demonstrate the difference between using AB and using LAB values, with AB clustering by chromaticity and LAB by luminosity. The remaining graphs indicate how plumage characters were scored using the AB method.

Appendix G

Table of measurements and characters captured and scored using the AB method.

TABLE G.1: Table of measurements and characters captured and scored using the AB method (AB scored data). Locations mentioned in the text are labelled in Figure 2.3 and 2.4; colour descriptions follow Ridgeway (1912).

Character	Score
1 Bill length	Divided by Wing length.
2 Bill width	Divided by Wing length.
3 Bill height	Divided by Wing length.
4 P10/P9	The proportion of the two outermost primary feathers.
5 Tarsus length	Divided by Wing length.
6 Tail length	Divided by Wing length.
7 Primary width 2	Width of outermost primary feather at 25% of its length.
8 Primary width 3	Width of outermost primary feather at 50% of its length.
9 Primary width 4	Width of outermost primary feather at 75% of its length.
10 Primary length 5	Distance from the tip of the outermost primary feather to the point of maximum width.
11 Sexual dimorphism	Calculated using Wing length of males and females.
12 Wing length	The total Wing length.

Continued on next page

Table G.1 – *Continued from previous page*

Character	Score
13 Back borders	(1) Light Sepia (38 4 17); (2) Clove Brown (29 3 8); (3) Chaetura Drab (15 1 1).
14 Belly	(1) Buffy Brown (52 7 28); (2) Light Drab (61 2 17); (3) Smoke Grey (67 0 9).
15 Bill below	(1) Dark Greyish Olive (22 3 2); (2) Citrine Drab (52 4 23).
16 Bill top	(1) Sorgham Brown (41 10 13); (2) Dark Venaceous Drab (32 5 1); (3) Castor Grey (25 1 -6).
17 Breast	(1) Clear Green-blue Grey (65 2 -12); (2) Light Gull-grey (75 -2 -6); (3) Pale Drab-grey (71 -1 2); (4) Light Greyish-olive; (5) Citrine Drab (55 4 24).
18 Chin	(1) Citrine Drab (54 5 22); (2) Light Drab (63 3 16); (3) Smoke Grey (69 1 9); (4) Pale Smoke Grey (78 0 4).
19 Flanks	(1) Dark Buffy Brown (44 7 27); (2) Drab (49 2 18); (3) Deep Greyish Olive (36 1 7).
20 Head borders	(1) Saccardo's umber (41 11 28); (2) Olive Brown (36 9 18); (3) Deep Olive (33 5 11); (4) Clove Brown (23 4 5); (5) Chaetura Drab (15 2 0).
21 Legs	(1) Tawny Olive (56 10 41); (2) Snuff Brown (39 14 34); (3) Brussels Brown (29 15 26); (4) Dark Natal Brown (21 15 18).
22 Rump	(1) Olive Brown (31 10 24); (2) Warm Sepia (22 7 15); (3) Clove Brown (18 4 8); (4) Blackish Brown (11 0 1).
23 Sides	(1) Buffy Brown (46 8 30); (2) Citrine Drab (51 4 26); (3) Drab (56 2 18); (4) Light Greyish Olive (51 1 11); (5) Mouse Grey (41 0 4).
24 Thighs	(1) Buffy Brown (46 7 30); (2) Olive Brown (38 7 21); (3) Light Sepia (27 5 14); (4) Dark Clove Brown (15 3 6).
25 Throat	(1) Dark Olive Buff (71 2 14); (2) Pale Smoke Grey (74 0 6).
26 Head-stripe contrast	(1) dE <= 12.2025; (2) dE = 12.2025 to 21.515; (3) dE = 21.515 to 30.8275; (4) dE => 30.8275.

Continued on next page

Table G.1 – *Continued from previous page*

Character	Score
27 Back-stripes contrast	(1) dE <= 12.2439; (2) dE = 12.2439 to 22.3329; (3) dE = 22.3329 to 32.4219; (4) dE = 32.4219 to 42.511; (5) dE > 42.511.
28 Head to back contrast	(1) dE <= 8.065; (2) dE = 8.065 to 15.48; (3) dE = 15.48 to 22.895; (4) dE > 22.895.
29 Rump to back contrast	(1) dE <= 7.6525; (2) dE = 7.6525 to 14.705; (3) dE = 14.705 to 21.7575; (4) dE >21.7575.
30 Sides to belly contrast	(1) dE <= 14.3333; (2) dE = 14.3333 to 27.9267; (3) dE > 27.9267.
31 Back to belly contrast	(1) dE <= 23.82; (2) dE = 23.82 to 41.72; (3) dE = 41.72 to 59.62; (4) dE > 59.62.
32 Pectoral patch	(0) absent; (1) slight; (2) small; (3) conspicuous; (4) large.
33 Lores	(0) whitish; (1) white; (2) rusty buff; (3) red; (4) black.
34 Face freckling	(0) absent; (1) slightly freckled; (2) heavily freckled.
35 Subloral spot	(0) absent; (1) slight; (2) small; (3) conspicuous; (4) large.
36 Eyebrow size	(0) absent; (1) slight; (2) well defined; (3) large.
37 Wing contrast with dorsal surface	(0) no contrast; (1) moderate; (2) conspicuous.
38 Wing edging	(0) none; (1) slight; (2) conspicuous.
39 Tertials	(0) no borders; (1) borders.
40 Tail pattern above	(0) plain; (1) slight patterning; (2) bold spotted fan.
41 Tail pattern below	(0) plain; (1) slight patterning; (2) bold spotted fan.
42 Tail tips	(0) none; (1) whitish; (2) rust; (3) grey; (4) variable.
43 Tail edgings	(0) none; (1) white; (2) brown; (3) rusty; (4) red.
44 Subterminal spot	(0) none; (1) slight; (2) bold; (3) variable.
45 Mid-toe and claw	(0) 13–15 mm; (1) 16–18 mm; (2) 19–21 mm; (3) 22–24 mm.
46 Egg colour	(0) white; (1) green; (2) turqiouse; (3) red; (4) variable.
47 Egg patterning	(0) fine speckles; (1) well marked; (2) thick spots; (3) heavily marked; (4) variable.
48 Egg clutch	(0) small; (1) medium; (2) large.

Continued on next page

Table G.1 – *Continued from previous page*

Character	**Score**
49 Habitat	(1) grass; (2) scrub; (3) savanna woodland; (4) woodland; (5) marsh.
50 Display	(1) perched; (2) perched or low; (3) low; (4) moderate height; (5) high; (6) variable.
51 Wing snap	(0) absent; (1) present; (2) variable.
52 Nest	(1) ball; (2) soda-bottle; (3) tailored ball; (4) deep cup; (5) elliptical ball.
53 Difference winter tail	(0) no difference; (1) 0–5%; (2) 6–10%; (3) 11–15%; (4) 16–20%; (5) 21–25%; (6) 26–30%; (7) 31-35%; (8) 36–40%; (9) 41–45%.
54 Molt	(1) regular; (2) perennial summer; (3) perennial winter; (4) variable; (5) perennial intermediate.

Appendix H

Multiple Factor Analysis of subspecies.

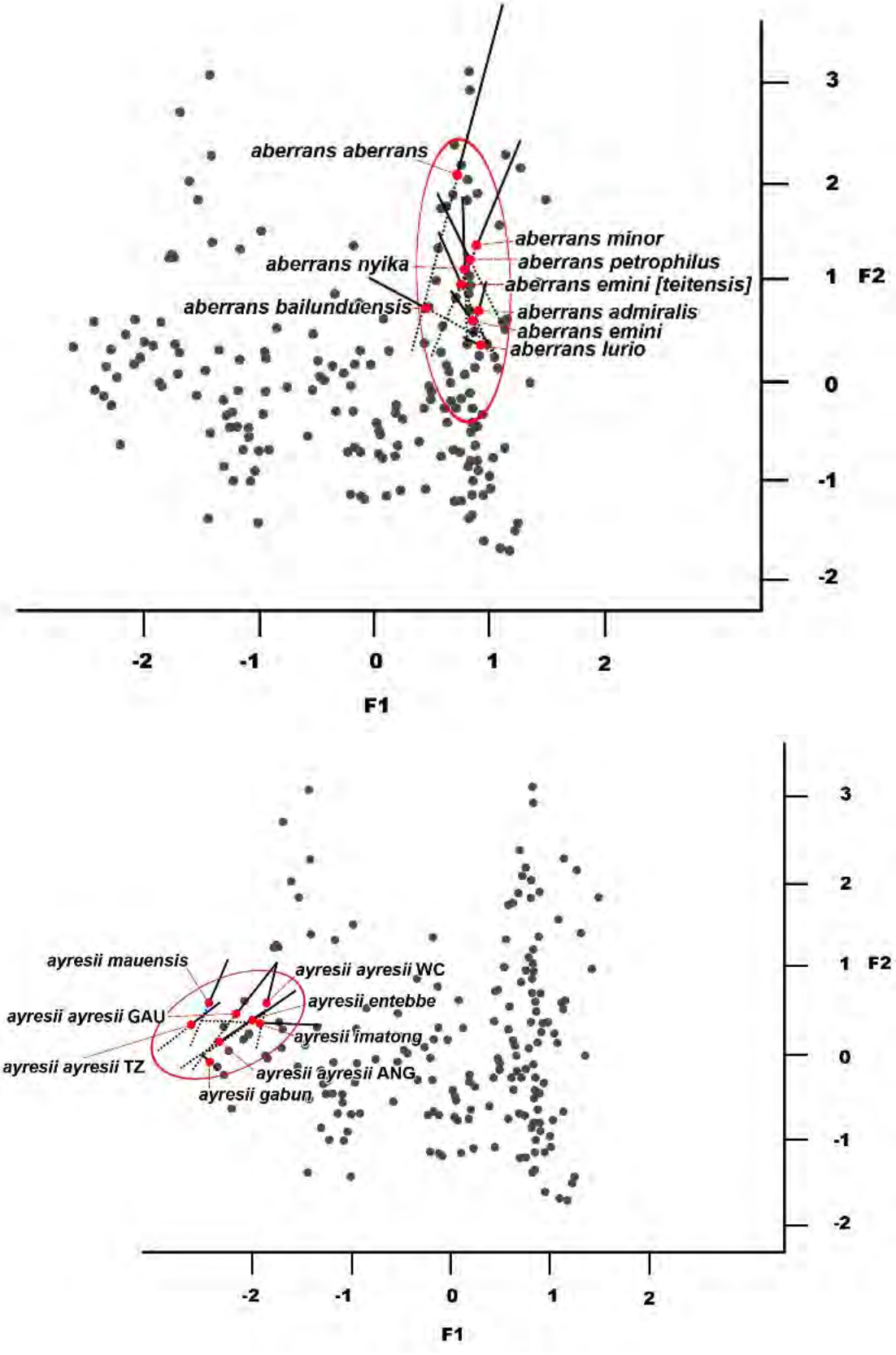
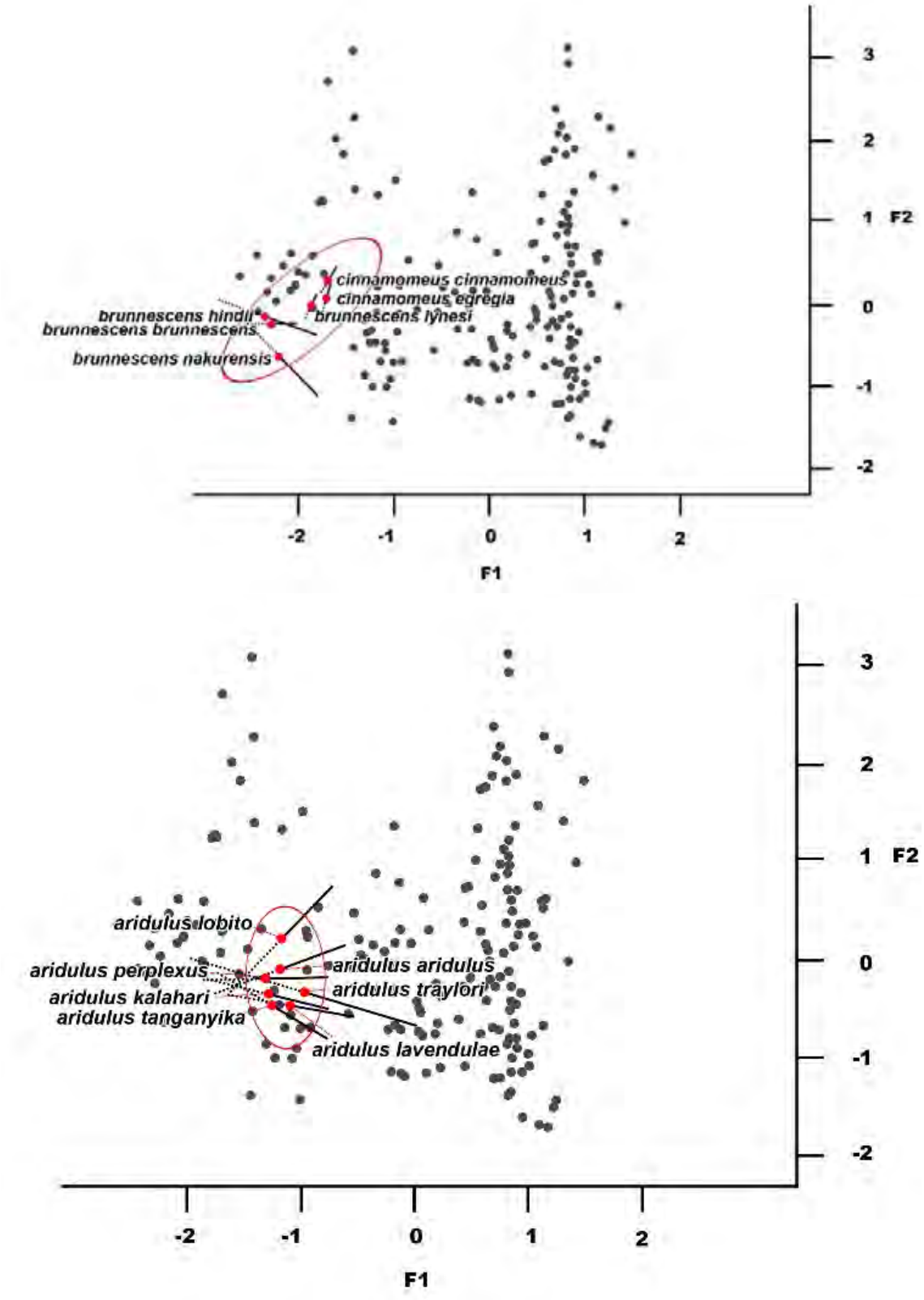
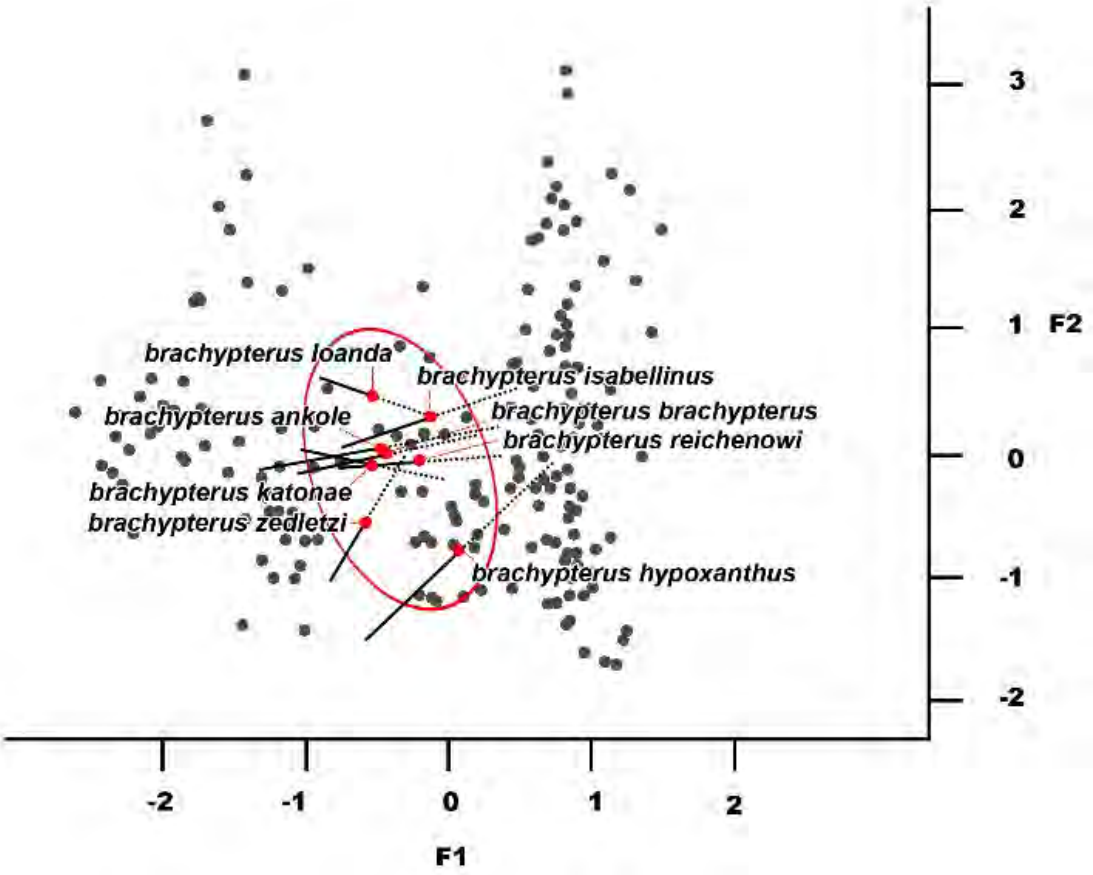


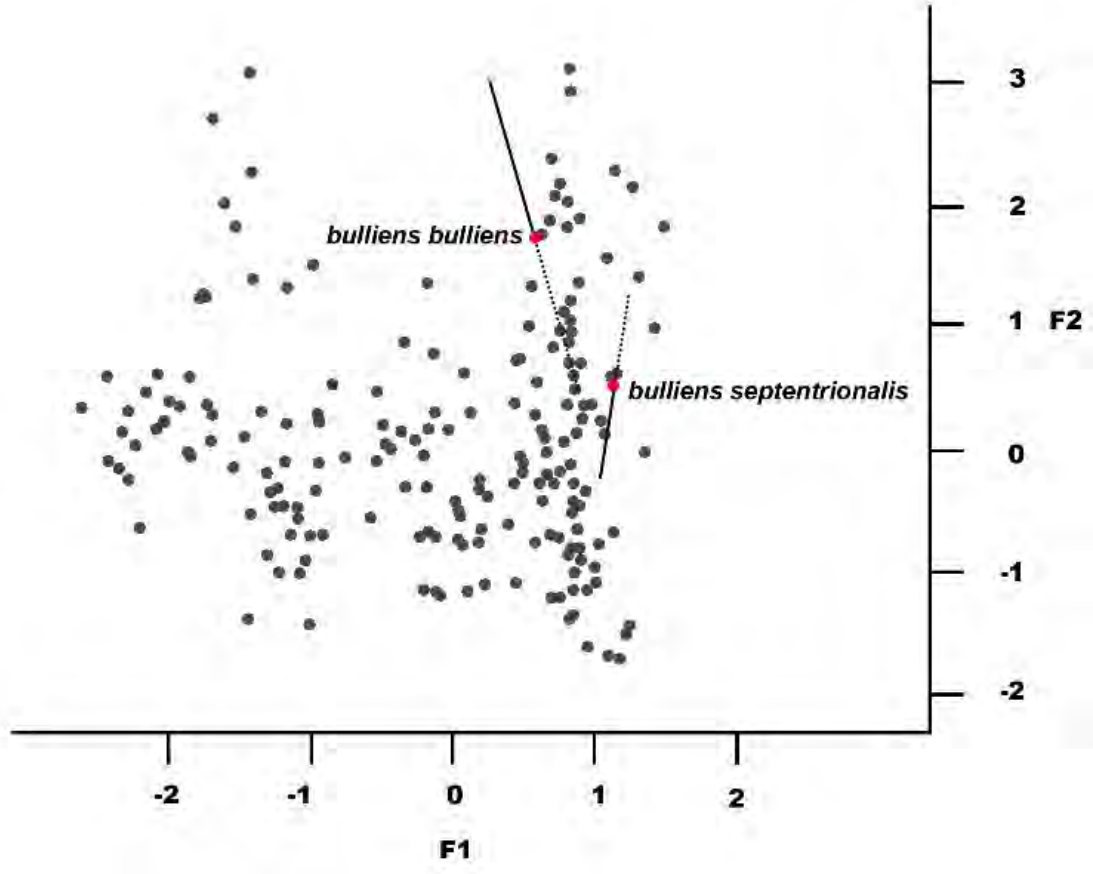
FIGURE H.1: Multiple Factor Analysis of subspecies, axes as in Figure 2.10.

(A) *figure H.1 continued*

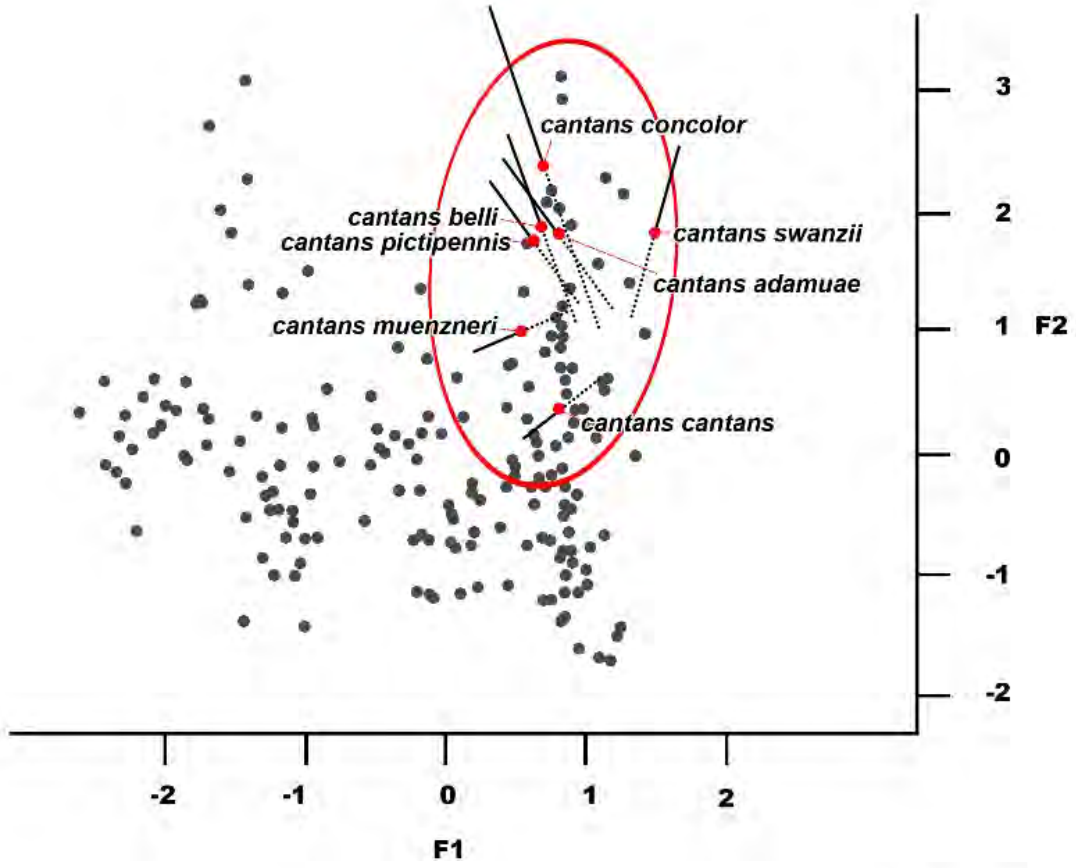


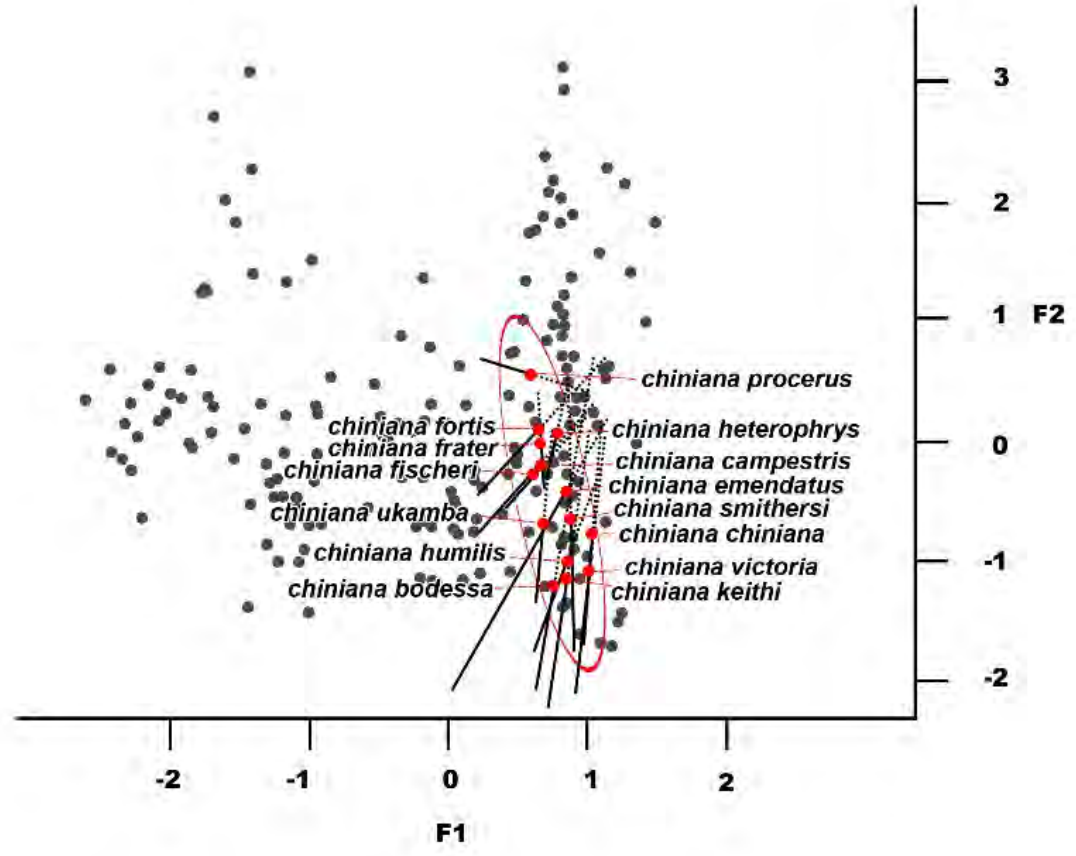
(B) *figure H.1 continued*



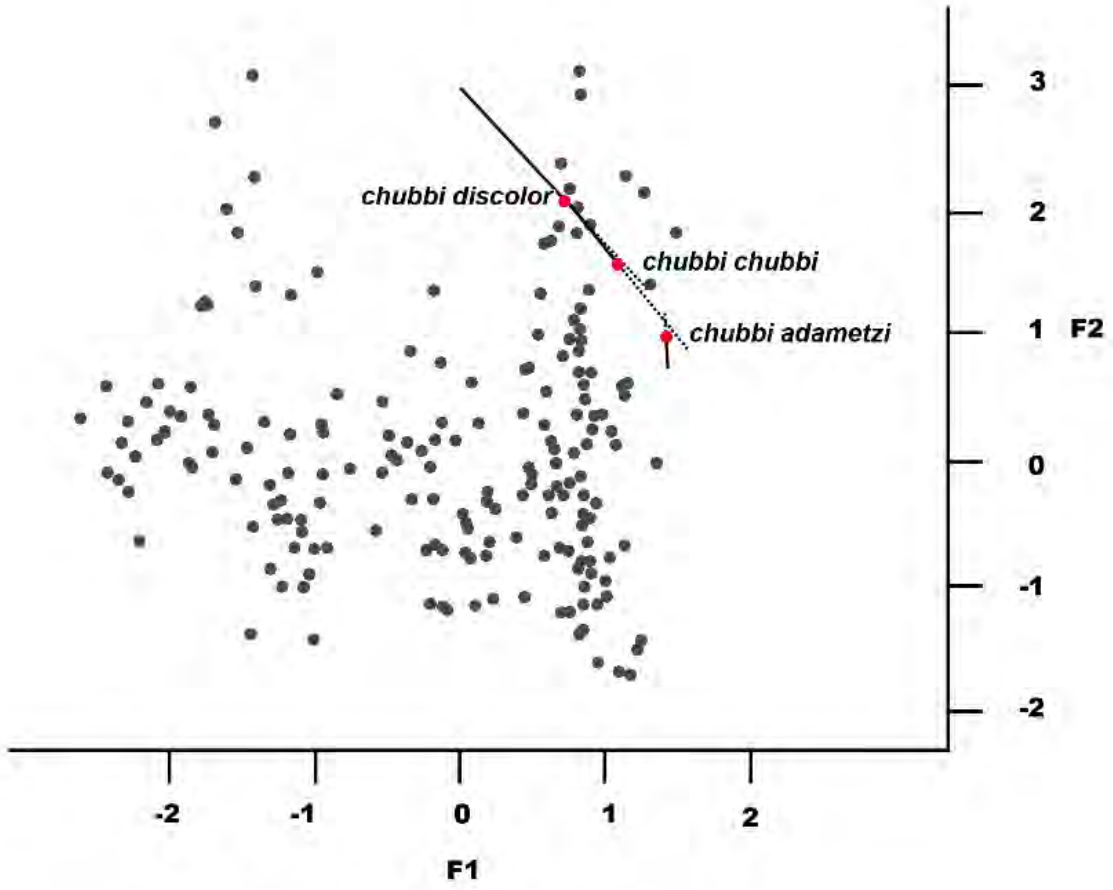


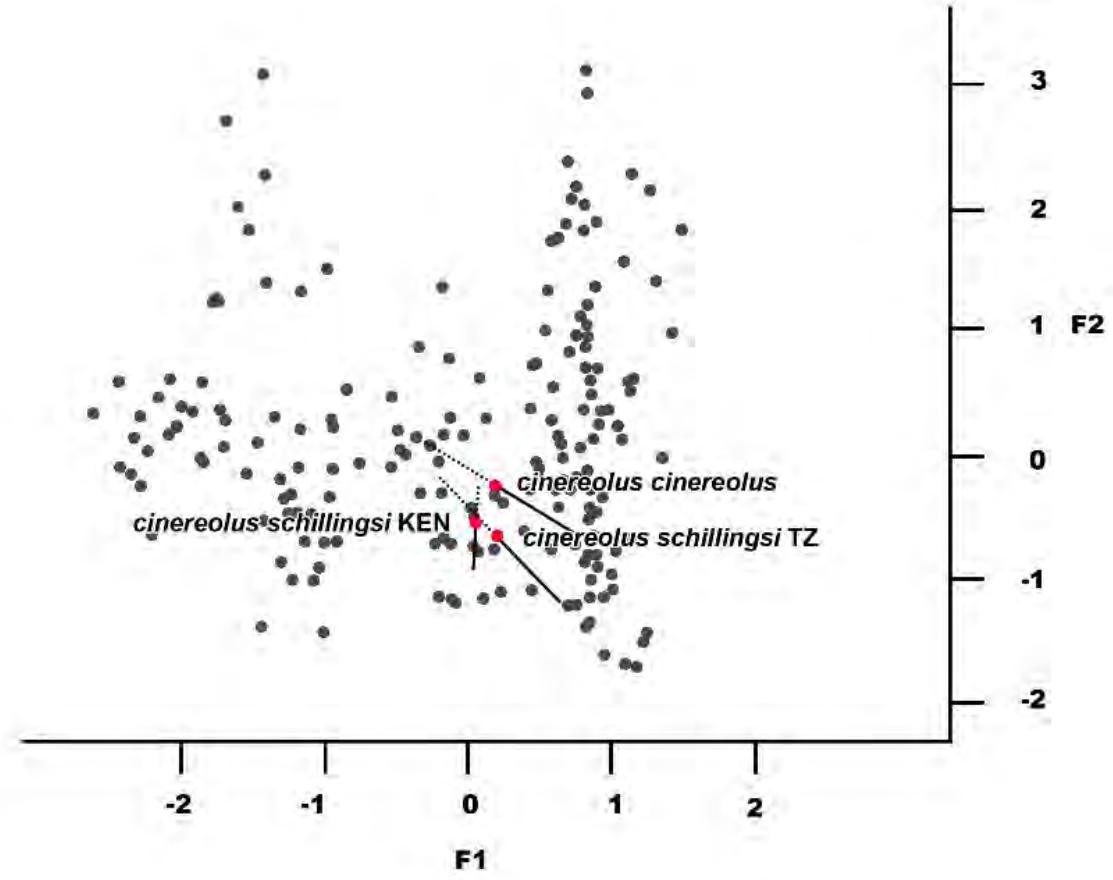
(c) *figure H.1 continued*



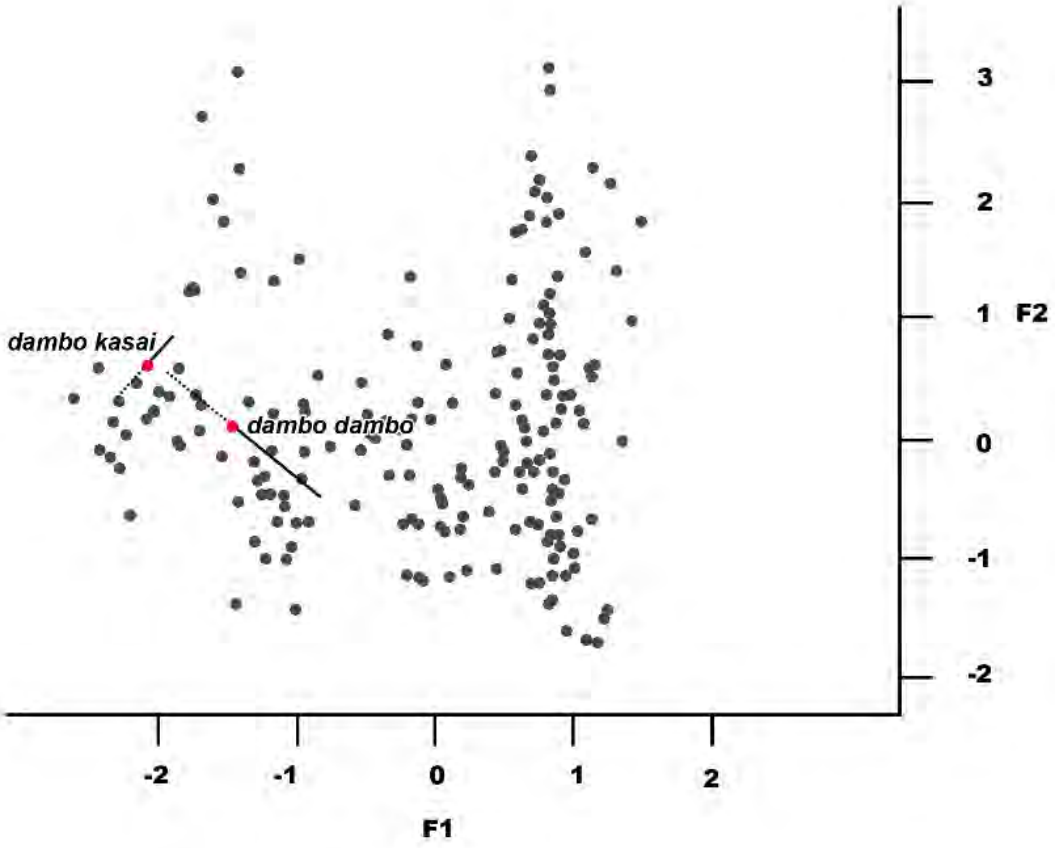


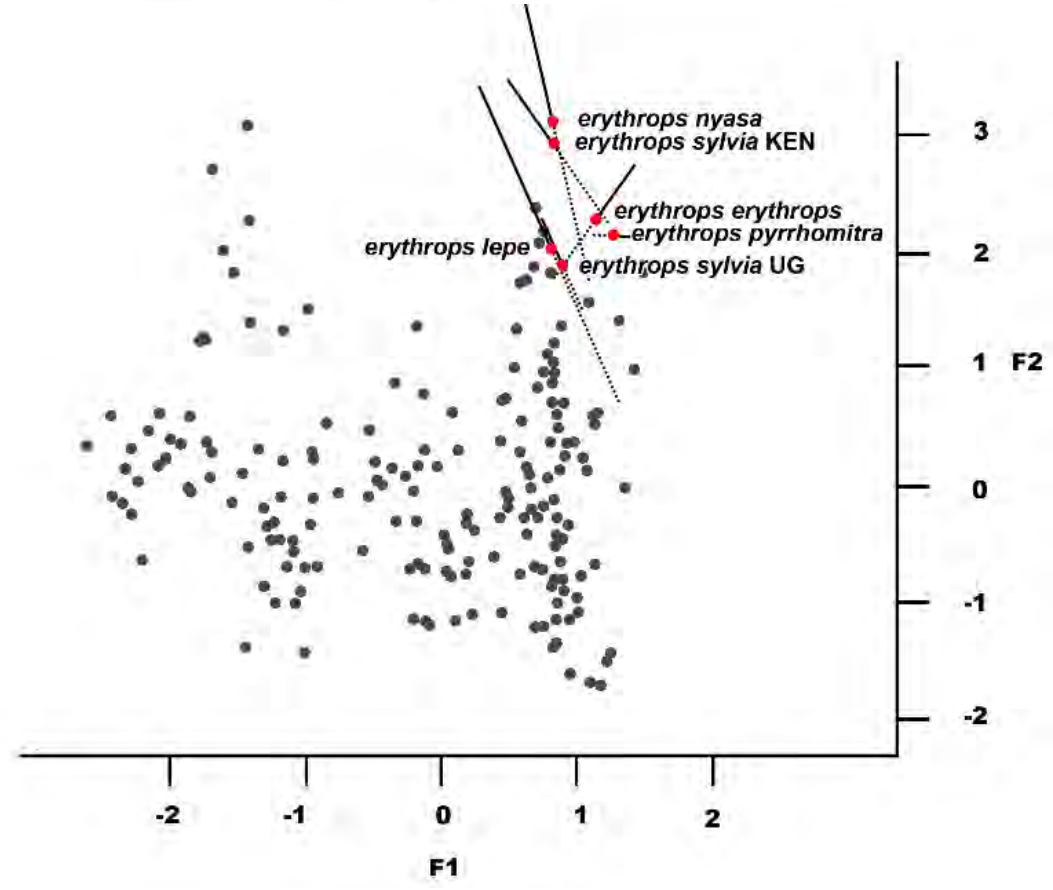
(D) *figure H.1 continued*



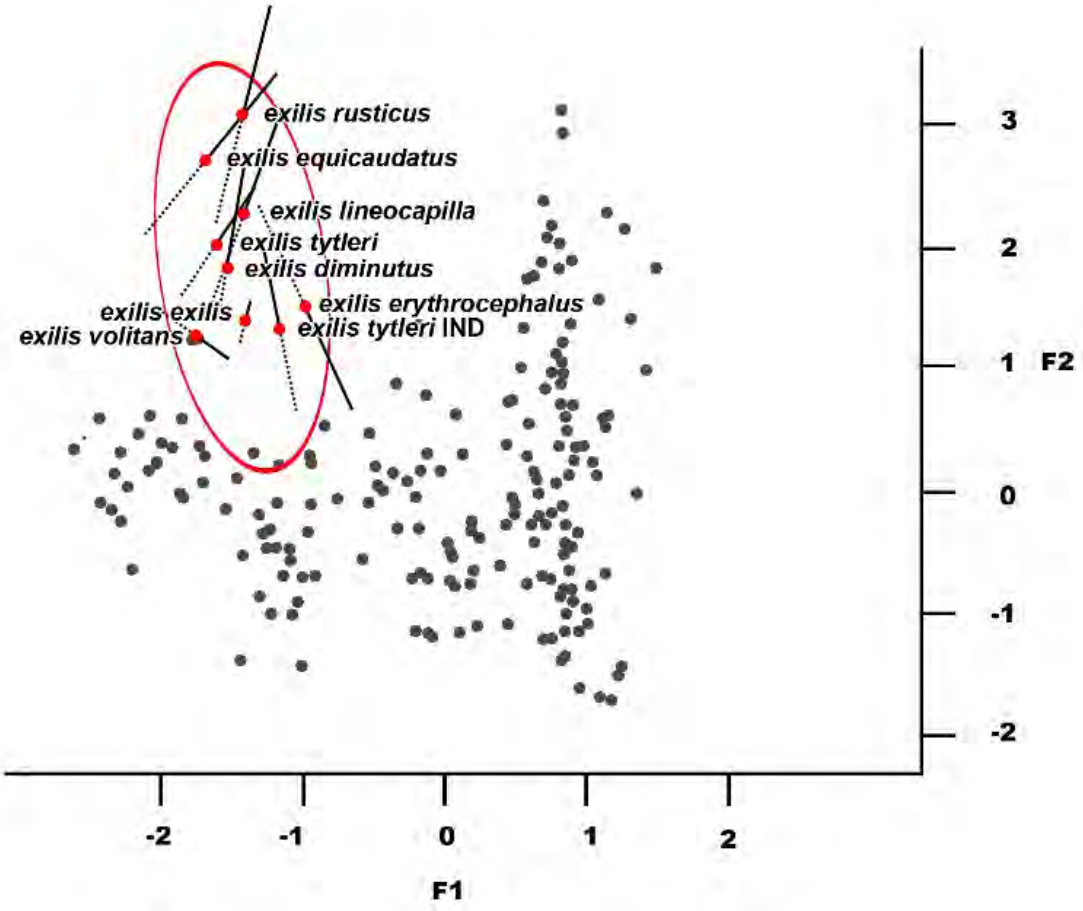


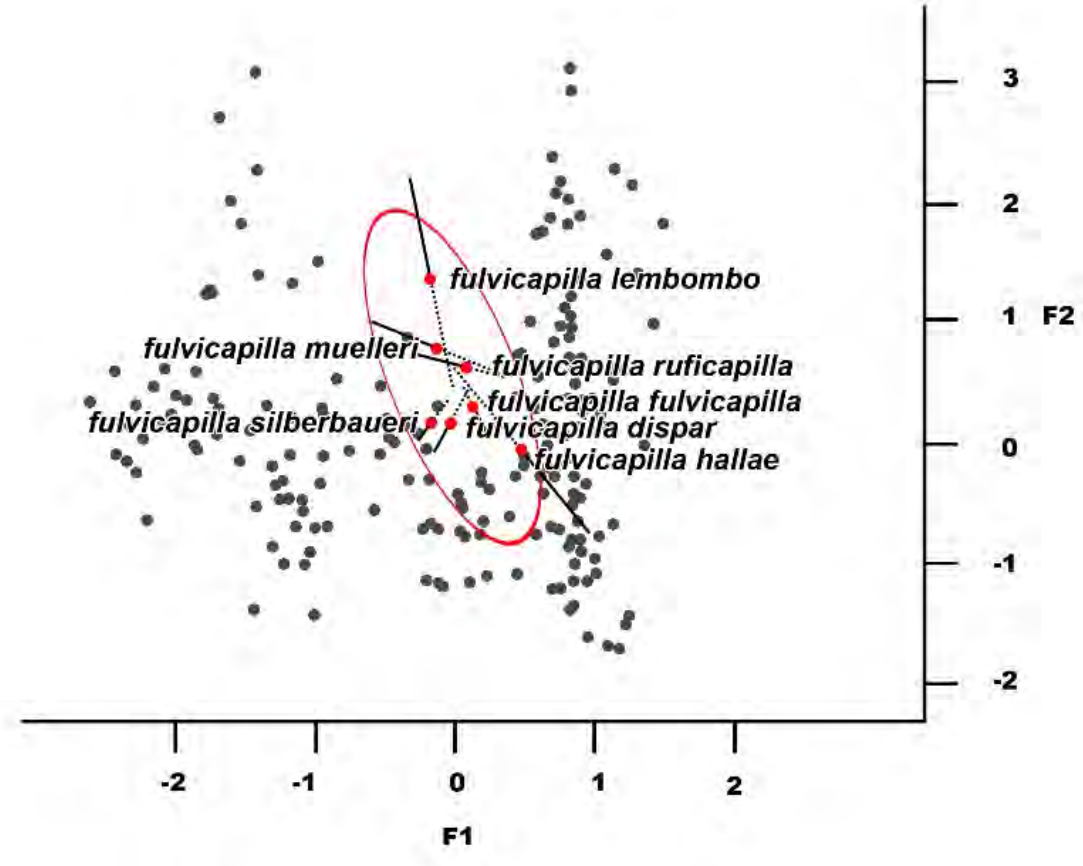
(E) *figure H.1 continued*



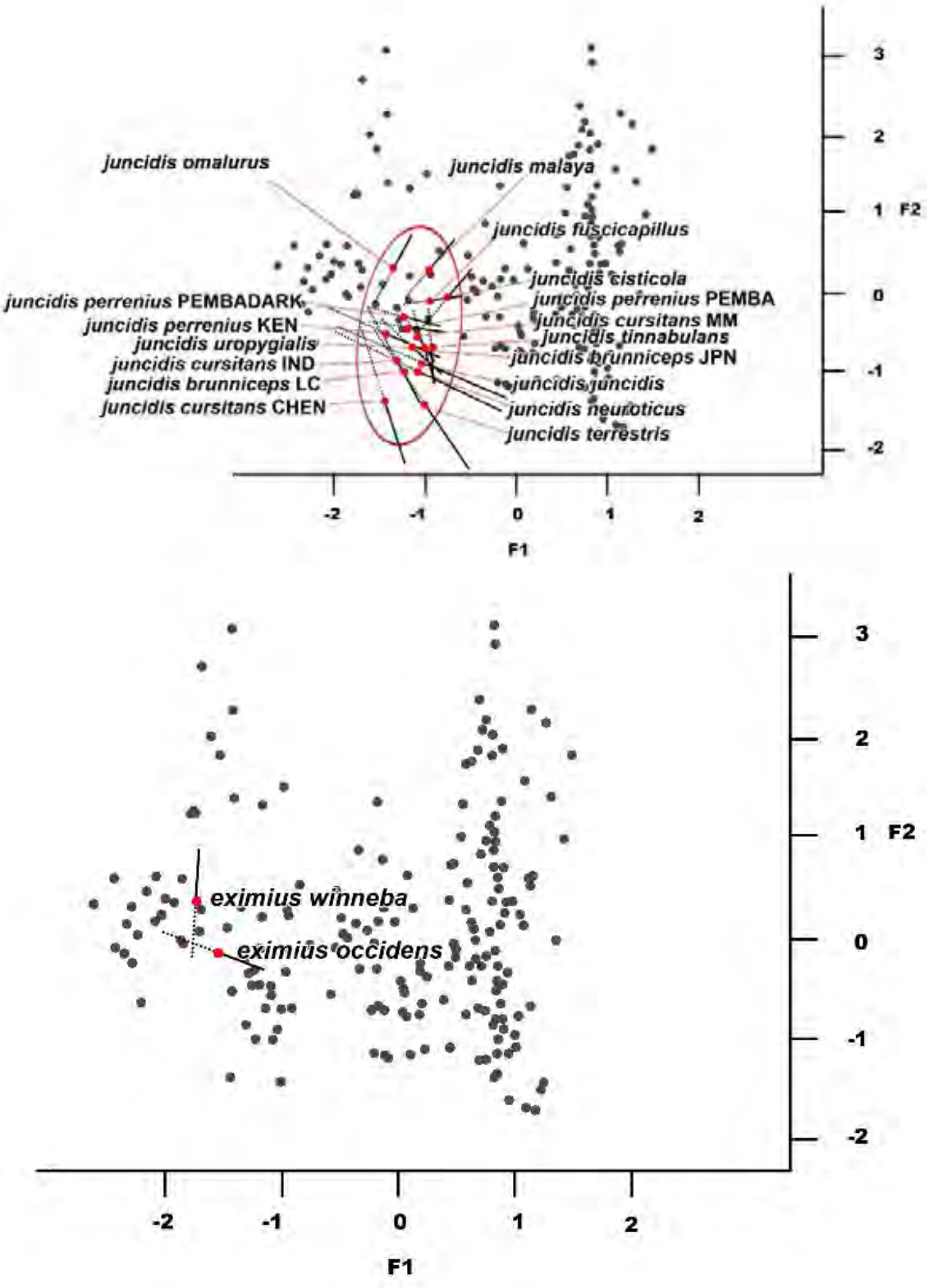


(F) *figure H.1 continued*

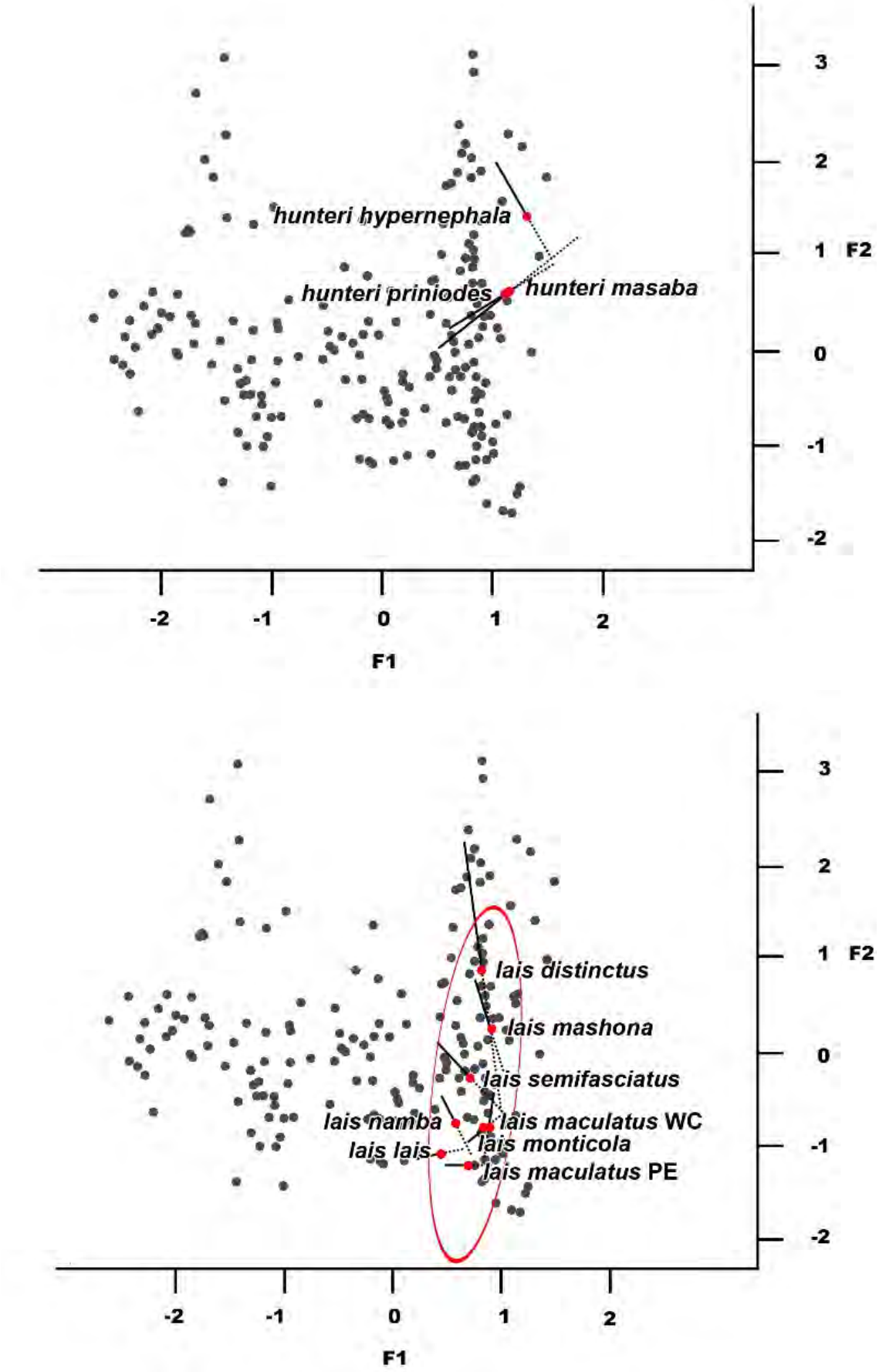




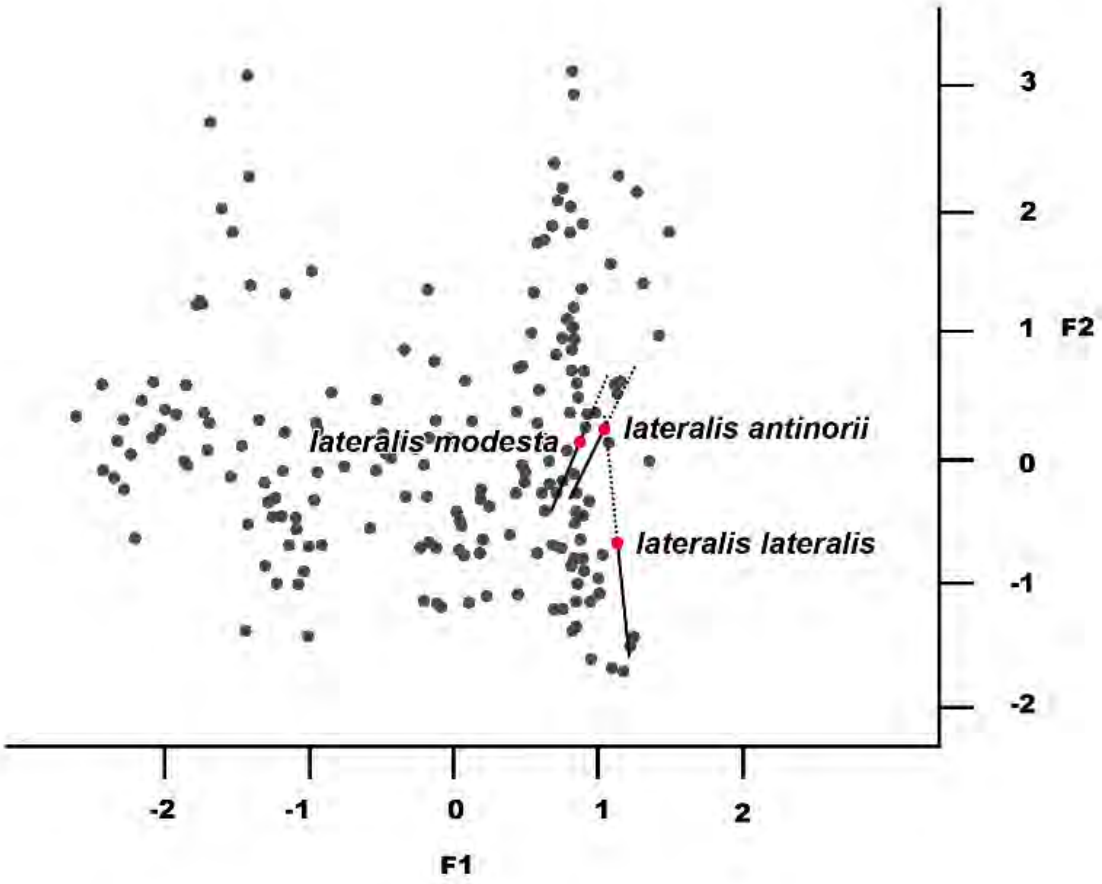
(G) *figure H.1 continued*

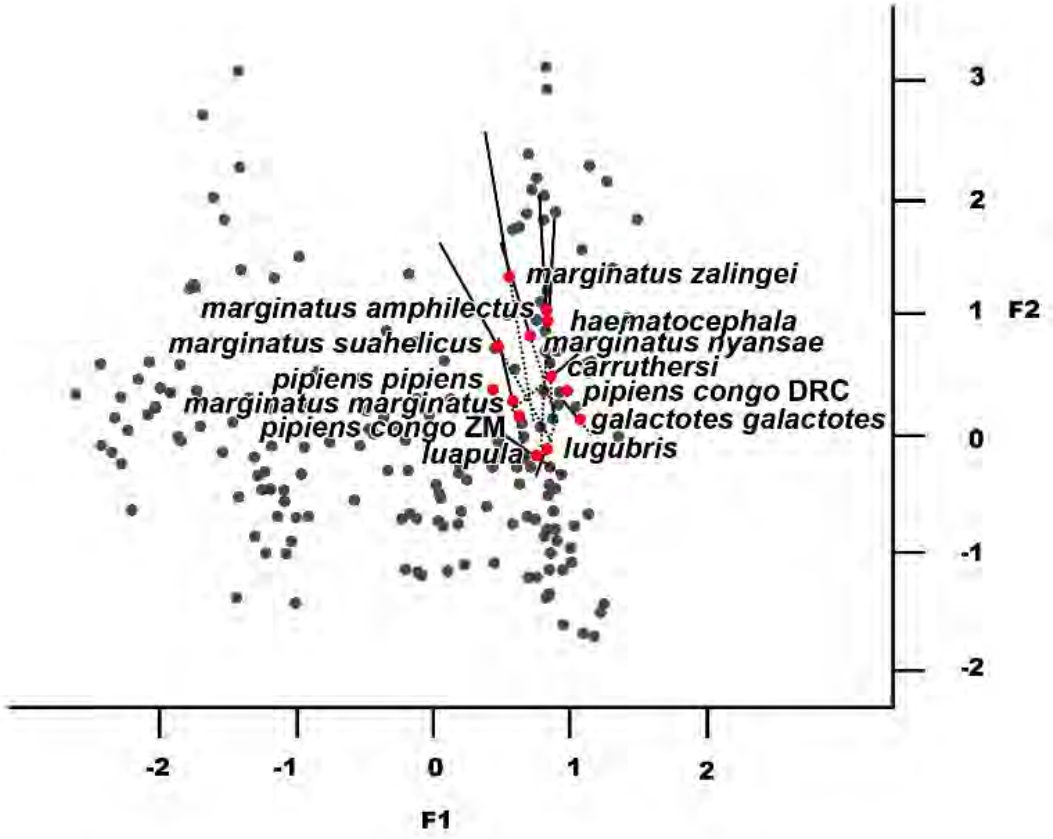


(H) *figure H.1 continued*

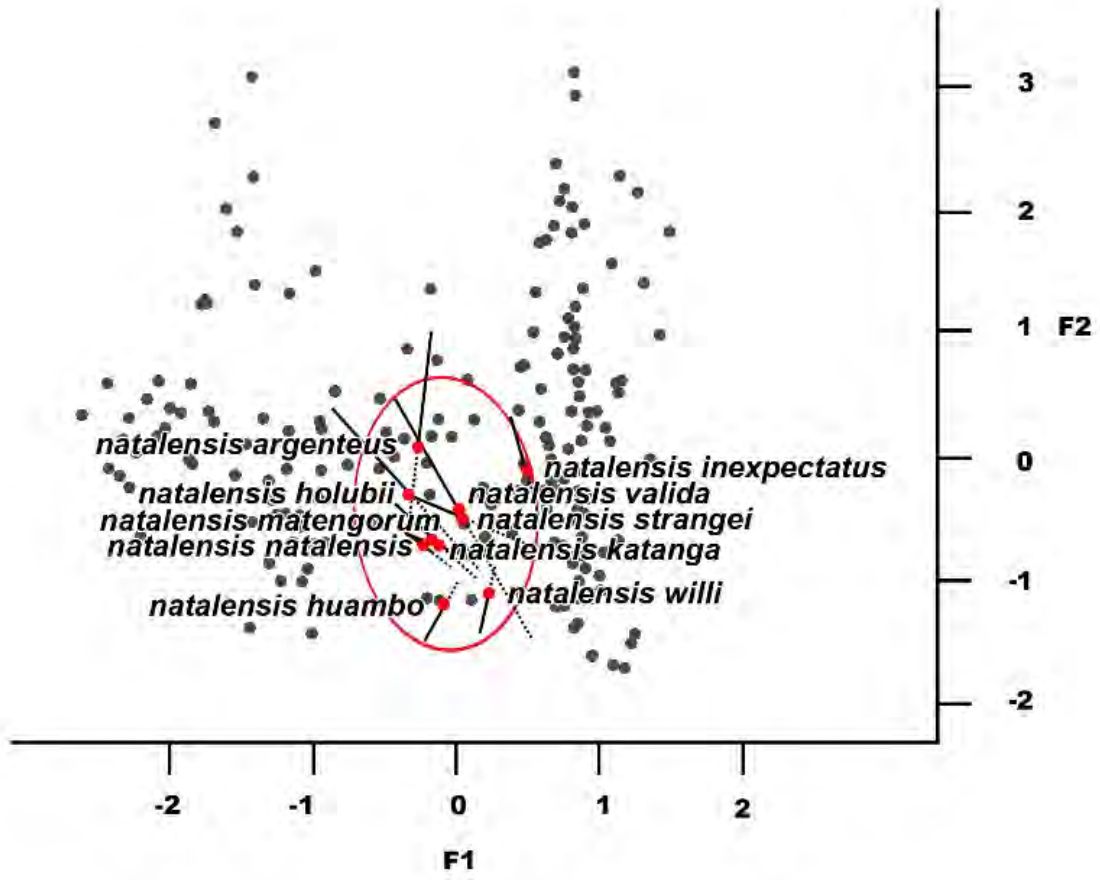


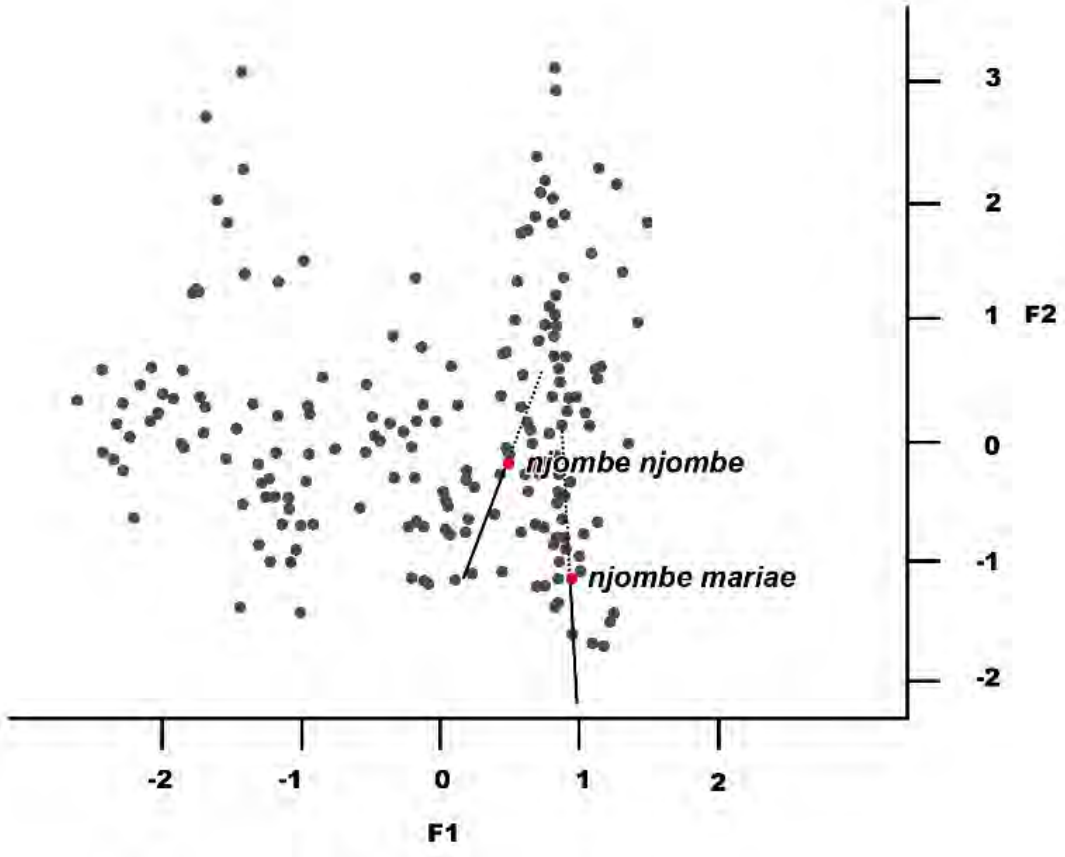
(1) *figure H.1 continued*



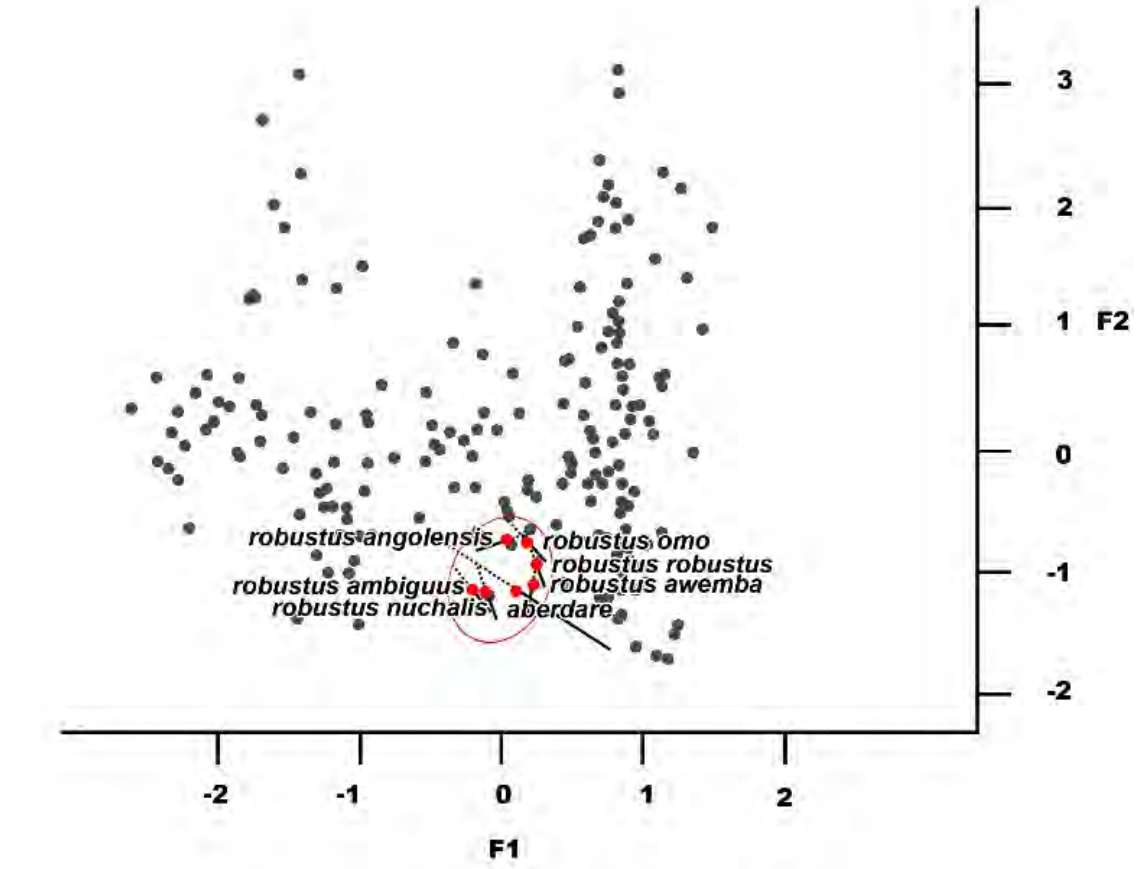


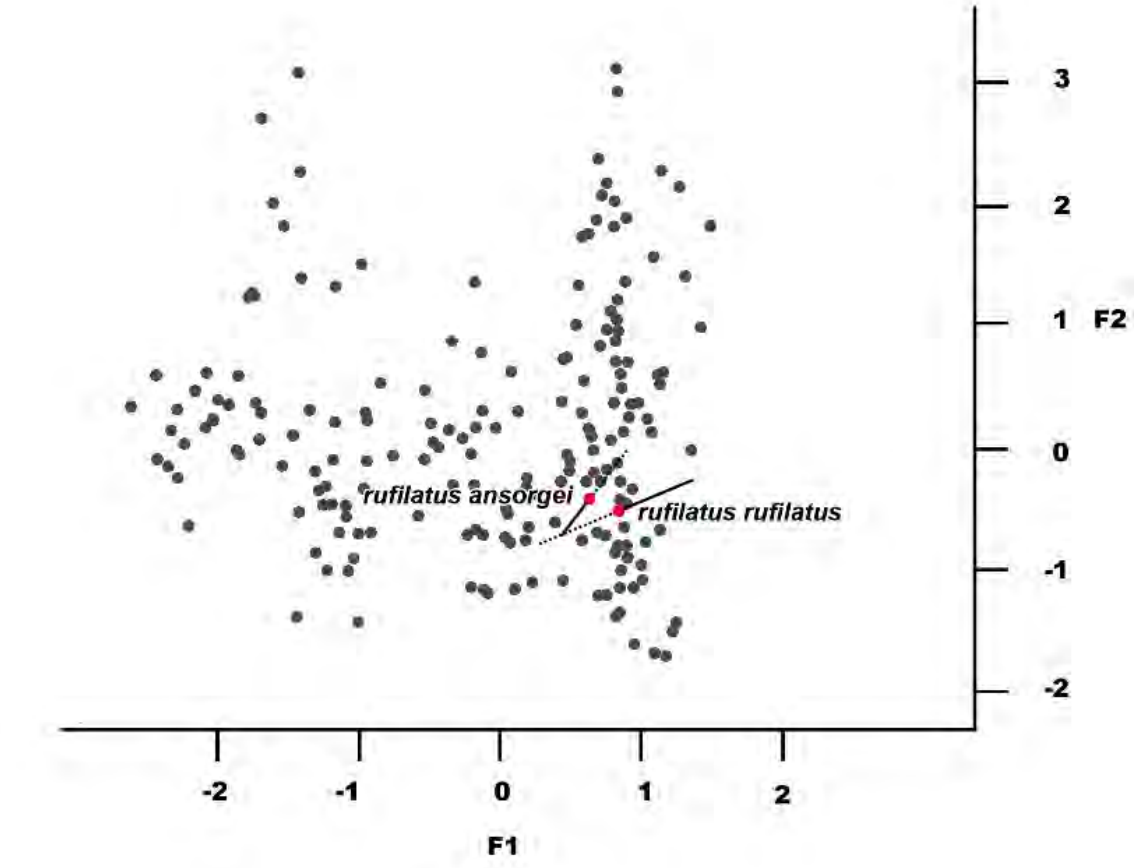
(J) *figure H.1 continued*



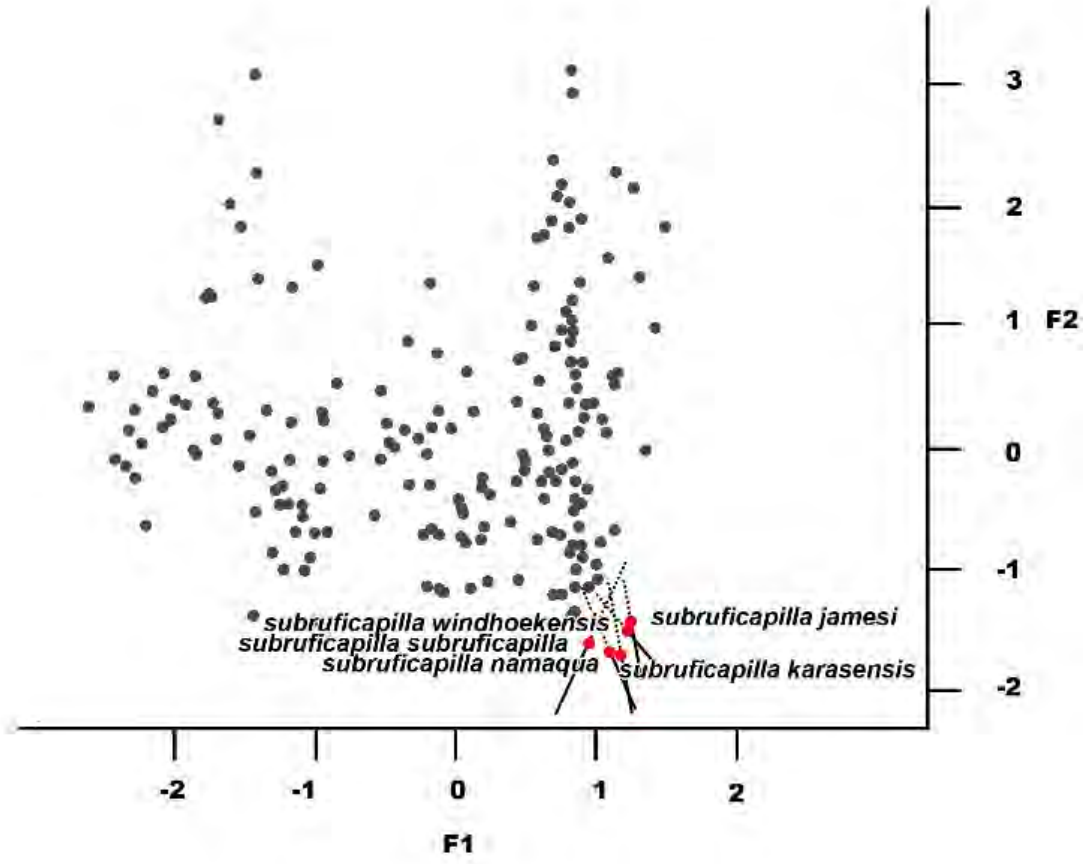


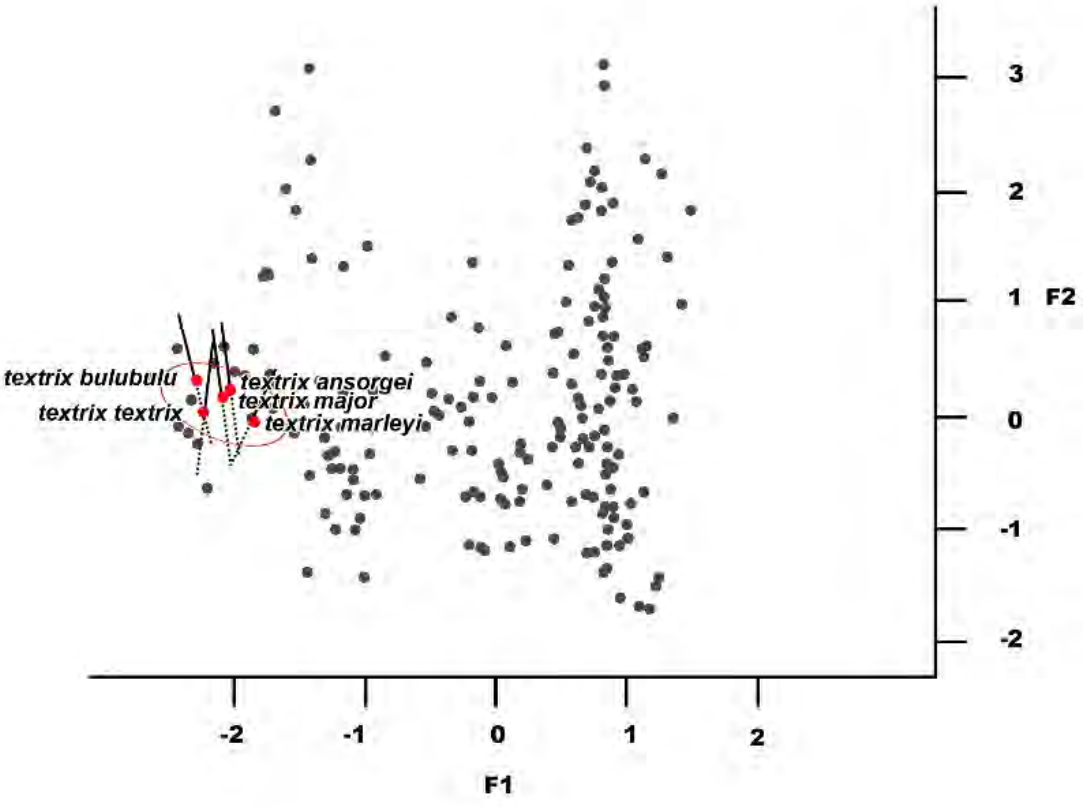
(K) *figure H.1 continued*



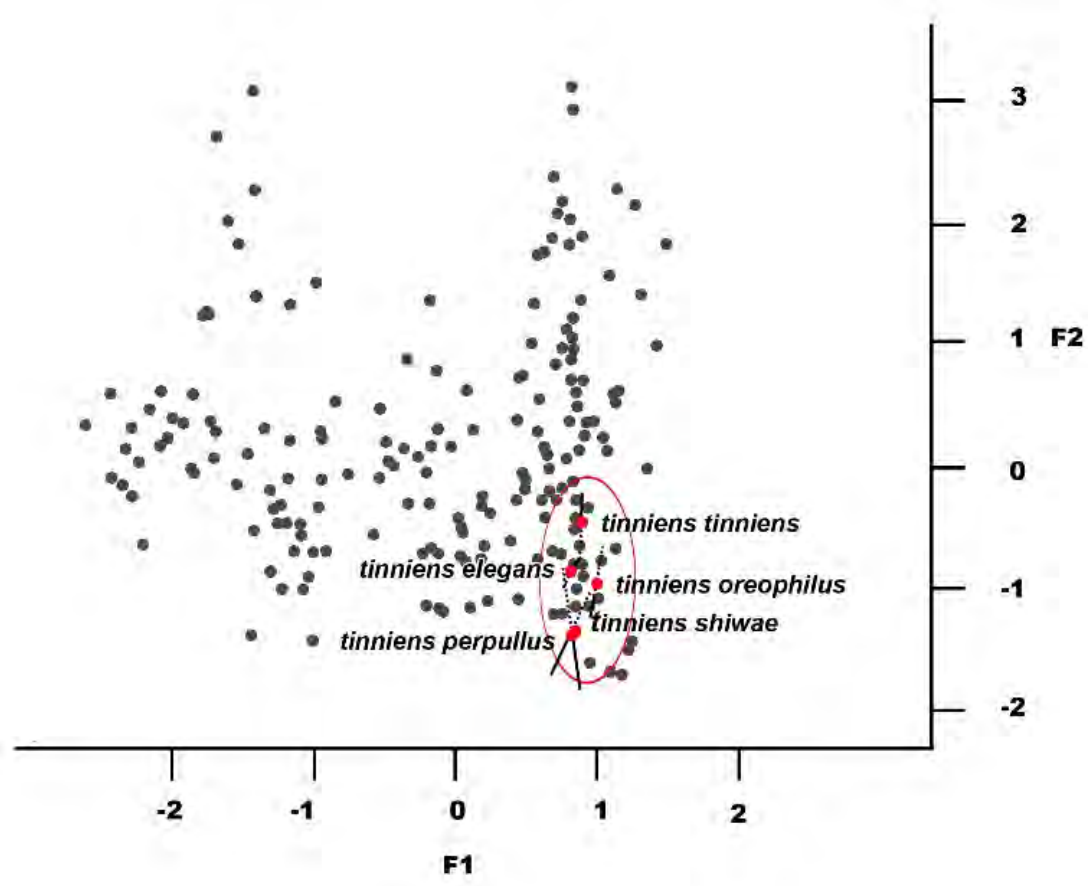


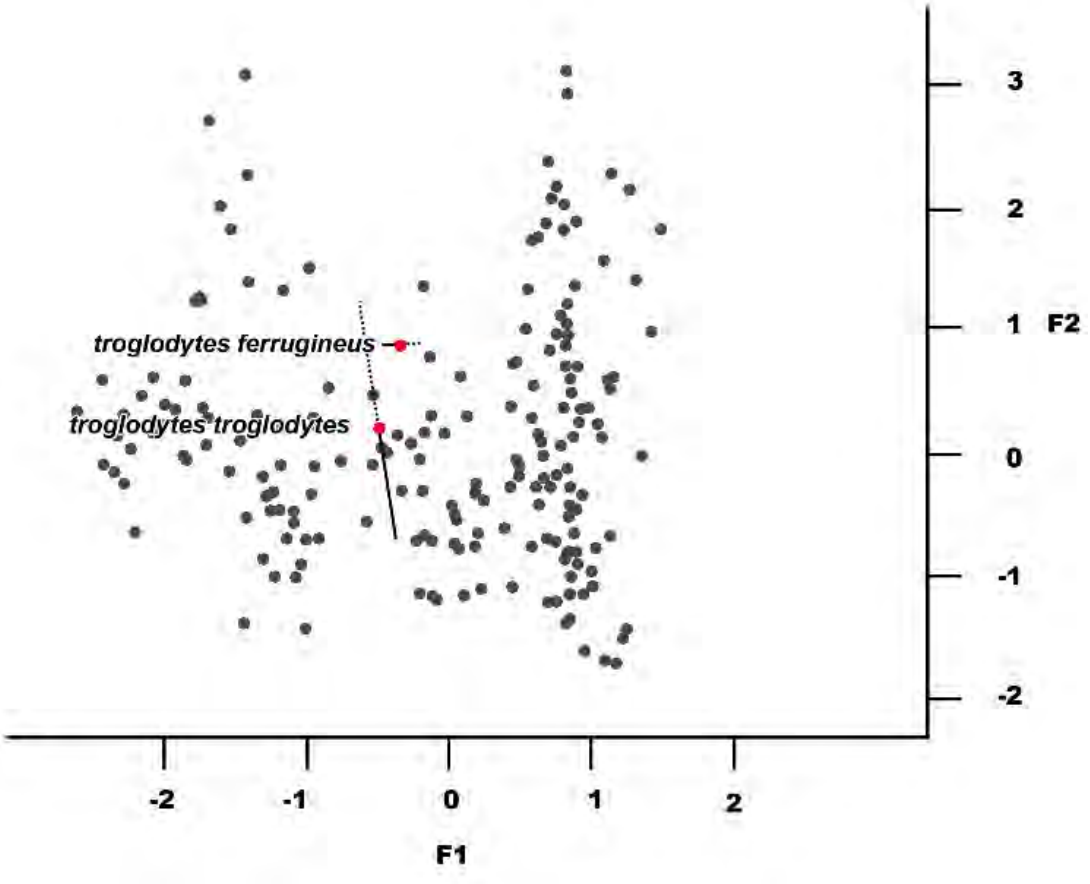
(L) *figure H.1 continued*



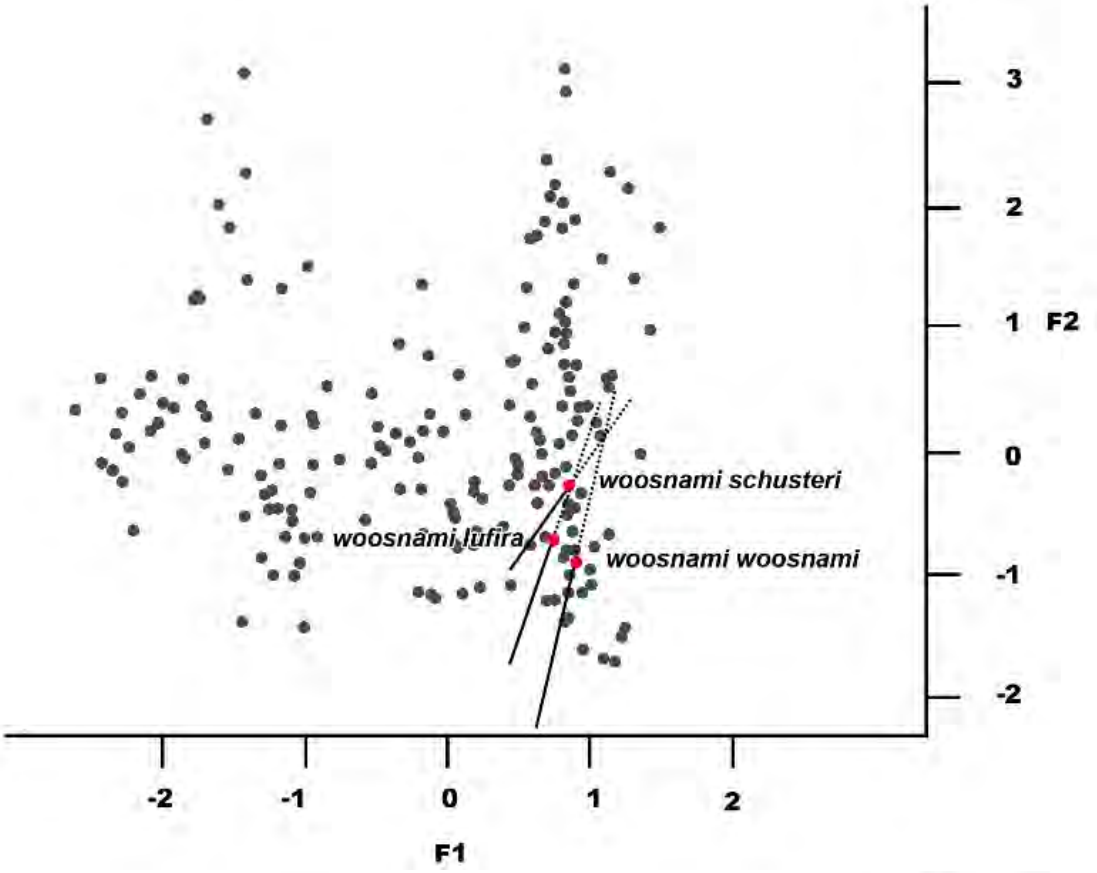


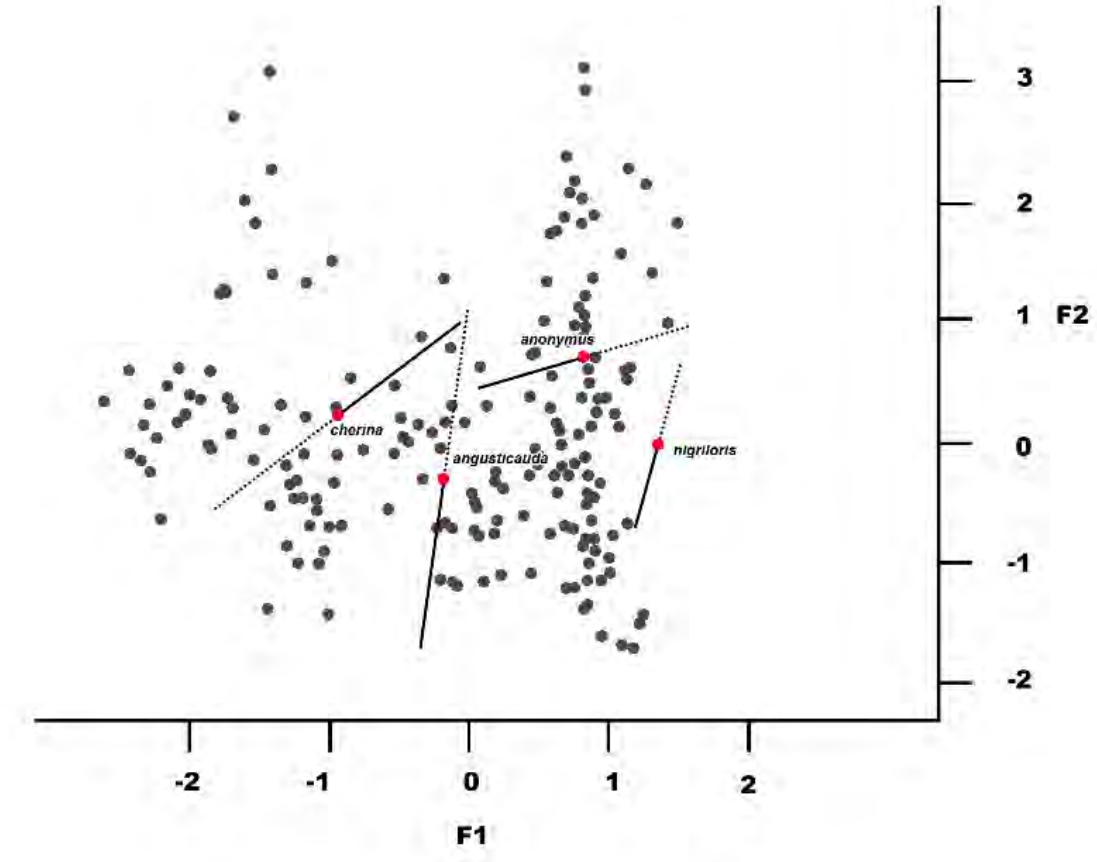
(M) *figure H.1 continued*





(N) *figure H.1 continued*





Appendix I

SUPPLEMENTARY DATA: A compendium of plumage and measurement data used in this study.

Following the tradition set by Lynes, who included numerous colour plates and drawings of specimens in his Review of the genus *Cisticola* (Lynes, 1930), I have collated the data that were used in this study in a series of colour plates that may facilitate the utility of these data outside the context of this study alone. While presented in a familiar style, the intention of this collection is not to take the place of field guides, whose drawings are more lifelike and descriptions more comprehensive, but rather to present the colour and measurement data that were analysed in this study in a way that helps to visualise the variation between samples of very similar-looking birds. The drawings were therefore intentionally reproduced with the same pose so that small differences between specimens can be more easily appreciated, as the reader's eye is not distracted by behavioural poses often found in field guides. While the behaviour of the birds is undoubtedly invaluable in identification of birds in the field, it is not the focus of these descriptions.

The drawings are roughly scaled proportionally to the overall size of the birds, and some care was taken to account for slight differences in tail length, but comparative measurements should not be taken from the drawings but rather from the tables presented. The drawings and descriptions of eggs were not done from personal inspection of egg collections but rather interpreted from images, drawings and descriptions in the literature (Lynes, 1930; Tarboton, 2001; Urban et al., 1997).

Measurements were obtained from specimens housed in the Natural History Museum at Tring (from individuals in breeding plumage) and images were taken from those individuals thought to be a good representation of the taxa and from birds in fresh plumage where possible. A colour bar is included here for the reader to identify any plates which have been incorrectly reproduced through the printing process; the colours and their LAB values are displayed explicitly. The digital version of these drawings should be used over printed versions as the gamut of colours that are able to be reproduced by printing technology is smaller than that available to viewers on a screen. It must be remembered that colours may even appear different depending on the software and screen on which the images are viewed (this is true for all digital images), though colour values will remain the same if measured digitally. The feather outline displayed alongside many of the specimens is the outermost primary feather, P10, the shape presented here represents the consensus shape of multiple shapes captured digitally for each taxon. Distribution maps are reproduced with modifications from Handbook of Birds of the World (Ryan, 2006) with subspecies ranges interpreted from the text. Map points indicate where the specimens used in this study originated.