

**PHYLOGEOGRAPHY OF A POLYMORPHIC SOUTHERN  
AFRICAN ENDEMIC SPECIES, THE SOUTHERN BOUBOU  
*LANIARIUS FERRUGINEUS* (GMELIN, 1788)**

by

**DIKOBÉ KAREN MOLEPO**



RESEARCH DISSERTATION

Submitted in fulfilment for the degree of

**MASTER OF SCIENCE**

in

**ZOOLOGY**

in the

**SCHOOL OF MOLECULAR AND LIFE SCIENCES  
FACULTY OF SCIENCE AND AGRICULTURE**

at the

**UNIVERSITY OF LIMPOPO**

**SUPERVISOR: DR TG MANDIWANA-NEUDANI**

**CO-SUPERVISOR: DR J FUCHS**

(Muséum National d'Histoire Naturelle, Paris, France)

**CO-SUPERVISOR: PROF RCK BOWIE**

(University of California, Berkeley, California, USA)

**2019**



Southern Boubou *Laniarius ferrugineus*

(Courtesy: Bowie *et al.* 2005)

## **DEDICATION**

I DEDICATE THIS DISSERTATION TO MY PARENTS MR AND MRS (LEGOHU AND MASEMOLA MOLEPO) WHOSE LOVE CARRIED ME THROUGH EVERY PHASE OF MY STUDY. WITHOUT THEM THIS WORK WOULD NEVER HAVE STARTED. TO MY SON PEAKANYO WHO UNKNOWINGLY GAVE ME COURAGE AND A REASON TO SEE THROUGH THIS STUDY.

## DECLARATION

I declare that the work presented in this dissertation titled: **PHYLOGEOGRAPHY OF A POLYMORPHIC SOUTHERN AFRICAN ENDEMIC SPECIES, THE SOUTHERN BOUBOU *LANIARIUS FERRUGINEUS* (GMELIN, 1788)** reflects my work in design and in execution. All the referenced information contained herein has been duly acknowledged. This work has not previously been submitted by me for examination at this or any other university. I therefore present this dissertation for the examination for the degree of Master of Science in Zoology at the University of Limpopo.

Dikobe Karen Molepo

.....

**Full name**



.....

**Signature**

██████████

.....

**Student number**

11 April 2019

.....

**Date**

## ACKNOWLEDGEMENTS

First, I give praise to the Lord who provided me with the strength to complete my study; all this was possible through him. I am indebted to the various institutions and people who contributed to the success of this study. Firstly, I am grateful to my supervisors (**Dr Tshifhiwa G Mandiwana-Neudani** - University of Limpopo; **Dr Jérôme Fuchs** - Muséum National d'Histoire Naturelle, Paris, France and **Prof Rauri CK Bowie** - University of California, Berkeley, California, USA) for their trust in offering me this research project, their consistent professional guidance, encouragement and financial support. In addition, they demonstrated patience throughout all the stages of the study including the production of this dissertation.

The support I received from the directors of national and international museums and the curators of various ornithological collections was immense, allowing me access to their bird study skin collections. They are: **Mr David Allan** (Director - Durban Natural Science Museum); **Dr Phil Whittington** (Head of Department - East London Museum); **Mr Greg Davies** (former Curator - Ditsong National Museum of Natural History); **Ms Denise Hamerton** (Curator - Iziko Museums of Cape Town, Natural History); **Dr Jérôme Fuchs** (Professor and Curator - Muséum National d'Histoire Naturelle, Paris, France); **Prof Rauri Bowie** (Professor and Curator - Museum of Vertebrate Zoology, University of California, Berkeley, California, USA); **Drs Shannon Hackett** and **John Bates** (Associate Curators - Field Museum of Natural History, Chicago, USA); **Ms Viola Makanzana** (Curator - Natural History Museum of Zimbabwe, Bulawayo, Zimbabwe), **Drs Helen James** and **Gary Graves** (Curators - Smithsonian National Museum of Natural History).

A large number of DNA samples analysed in this study were provided by my co-supervisors (**Dr Jérôme Fuchs** - Muséum National d'Histoire Naturelle, Paris, France and **Prof Rauri Bowie** - Museum of Vertebrate Zoology, University of California, Berkeley, California, USA). The gaps in DNA sampling were filled with toe pad snips sub-sampled from the study skins housed at Durban Natural Science Museum with the permission of the Director, **Mr David Allan**.

All the DNA samples were analysed in a molecular laboratory at the Muséum National d'Histoire Naturelle, Paris, France under the guidance of **Dr Jérôme Fuchs** and **Céline Bonillo** was my second stop. **Drs Sean Marr** (former Postdoctoral fellow

– Biodiversity Department, University of Limpopo) and **Selaelo A Ramoelo** (Council for Scientific and Industrial Research - CSIR) are thanked for their assistance with statistical analyses and mapping, respectively.

This research project would not have materialised if it were not for the funds provided by **National Research Foundation** (NRF) to pay for my study and my visit to Muséum National d’Histoire Naturelle in France where I carried out DNA sequencing. The Department of Biodiversity and the University of Limpopo are also thanked for supporting and funding to in undertaking my trips to some natural history museums in South Africa and trips to attend project-related workshops and to present work at national conferences. The South African DST, NRF in partnership with the US NSF, Howard University funded my trip to present research at the international Women in Science, Technology, Engineering and Mathematics (STEM) conference at Howard University, Washington DC, USA.

I have no words to repay what my family did for me. My parents (**Mr Legohu G. Molepo** and **Mrs Masemola N Molepo**) are the reason for my accomplishment. My son, **Peakanyo Molepo** has always been the source of my strength. I cannot forget my life partner **Mr Morongwa G. Mohubedu** for his love and support. I am truly grateful to the love and generosity of my brother and sister-in-law (**Mr Mokgatla D** and **Mrs Maleopeng R. Molepo**, respectively and my nieces (**Dikobe Jnr. Mokgadi, Kobela and Legohu Jnr**). Lastly, I am thankful to all my friends for their encouragement.

Without the assistance and support from all the institutions and people, this work would never have seen the light.

## **GENERAL ABSTRACT**

It cannot be overemphasised that birds, which form a group of animals that are conspicuous in many habitats, occur worldwide, and are ecologically diverse and better known than any other vertebrate groups. Some species present no geographical variation while others exhibit complex geographic variation rendering them polytypic. The Southern Boubou *Laniarius ferrugineus* (Gmelin, 1788) is a polymorphic and highly vocal resident species endemic to Southern Africa. It overlaps with the Tropical Boubou *Laniarius aethiopicus* in the extreme north of South Africa. The taxonomic circumscription presents six subspecies of *L. ferrugineus* which vary in size and plumage colourations. Although *L. ferrugineus* is of least concern (LC), its wide distribution range calls for its precise taxonomic delineation and our knowledge of its genetic structure hence the need to investigate the status and level of morphological, genetic and vocal differentiation in this species complex. Morphological, genetic and song variation were analysed from museum study skins, DNA sequences spanning one coding mitochondrial gene and three non-coding nuclear introns generated from modern and ancient samples and songs from various sound libraries respectively. While morphometric analyses and Bayesian phylogenetic inference recovered two major lineages in *L. ferrugineus*: 1) *L. f. ferrugineus* / *L. f. pondoensis* / *L. f. natalensis* (southern clade) and 2) *L. f. transvaalensis* / *L. f. tongensis* / *L. f. savensis* (northern clade), *L. f. transvaalensis* overlapped between the two lineages in MDS and Box and whisker plots. The 95% parsimony ATP6 network similarly revealed two distinct lineages with the population demographic histories of the two clades showing expansion. The divergence between the two lineages occurred approximately 1.5 million years ago during the Pleistocene epoch. *Laniarius ferrugineus pondoensis* is the most distinctly dark morph. The moist habitat of *L. f. pondoensis* could be having an effect on plumage while there is no genetic basis for the difference in plumage colouration. Almost all *L. ferrugineus* subspecies render a tonal song duet made up of 'bou' and 'whistle' elements with the significant difference being observed in maximum peak frequency. *Laniarius ferrugineus* (Gmelin, 1788) should at best be split into two species, one representing members of the southern clade to be named *Laniarius ferrugineus* (Gmelin, 1788) and another species representing members of the northern clade

named *Laniarius transvaalensis* Roberts, 1922 based on the Principle of Priority. The current study expanded our knowledge base as far as ornithology is concerned and shed light on the phylogeographic patterns of the Southern Boubou *Laniarius ferrugineus* (Gmelin, 1788). The findings significantly contributed to our understanding of the evolutionary processes governing the geographical variation in *Laniarius ferrugineus* complex and the findings could possibly be extrapolated to other species. It was critical that the taxonomic affinities of *L. ferrugineus* were investigated due to its extensive distribution range for better management and conservation. Future work should further unravel the less differentiation within the south and north lineages with additional songs being analysed to understand the song pattern across the range.



# TABLE OF CONTENTS

ACKNOWLEDGEMENTS .....	i
GENERAL ABSTRACT .....	iii
TABLE OF CONTENTS .....	v
LIST OF FIGURES, TABLES AND APPENDICES .....	vii
CHAPTER 1 .....	1
General Introduction.	
1.1 The subspecies category .....	1
1.2 Family and genera taxonomic history .....	2
1.3 The study species .....	4
1.3.1 Morphology and distribution .....	4
1.3.2 Taxonomic boundaries .....	5
1.3.3. Study area .....	6
1.4 The field of Phylogeography .....	6
1.4.1 Approaches to phylogeography .....	7
1.4.2 Evidence – morphology, molecules and vocalisations .....	8
1.5. Purpose of the current study .....	11
1.5.1 Study aim .....	11
1.5.2 Study objectives .....	11
1.5.3 Research questions .....	11
1.6 Relevance of the study .....	12
CHAPTER 2 .....	15
The morphometric and morphological analysis of the Southern Boubou <i>Laniarius ferrugineus</i> species complex.	
2.1 Introduction .....	15
2.1.1 The focal taxon .....	18
2.1.2 Mapping of species distribution records .....	19
2.1.3 Aim .....	20
2.1.4 Objectives .....	20
2.1.5 Research questions .....	20
2.2 Materials and methods .....	21
2.2.1 Data collection .....	21
2.2.1.1 <i>Bird specimens examined and morphology</i> .....	21
2.2.1.2 <i>Spatial distribution map</i> .....	22

2.2.2 Data analyses	23
2.2.2.1 Morphometric and plumage analysis	23
2.2.2.2 Spatial distribution map	24
2.3 Results	24
2.3.1 Morphometry – multivariate and univariate methods	24
2.3.1.1 Multi - dimensional scaling (MDS)	24
2.3.1.2 Similarities in percentages (SIMPER)	25
2.3.1.3 Box-and-whisker plots	25
2.3.2 Plumage	25
2.3.3 Distribution maps	26
2.4 Discussion	27
2.4.1 Morphometry	27
2.4.2 Assessment of plumage	28
2.4.2.1 Group 1: <i>L. f. ferrugineus</i> , <i>L. f. natalensis</i> and <i>L. f. pondoensis</i>	28
2.4.2.2 Group 2: <i>L. f. tongensis</i> and <i>L. f. savensis</i>	29
2.4.2.3 Overlapping subspecies: <i>L. f. transvaalensis</i>	29
2.4.3 Spatial map	29
2.5 Conclusion	30
APPENDICES	40
Appendix 2.1.	40
Appendix 2.2.	50
CHAPTER 3	66
The phylogeographic structure of the Southern Boubou <i>Laniarius ferrugineus</i> : a molecular perspective.	
3.1 Introduction	66
3.1.1 Aim	70
3.1.2 Objectives	70
3.1.3 Research questions	70
3.2 Materials and methods	71
3.2.1 Data collection	71
3.2.1.1 Taxon sampling	71
3.2.1.2 Laboratory techniques: DNA extraction, PCR amplification and sequencing	71
3.2.2 Data analyses	73
3.2.2.1 Phasing of nuclear alleles	73
3.2.2.2 Population genetic analysis and demographic history	73
3.2.2.3 Phylogenetic reconstruction	74
3.2.2.4 Estimating the divergence times	75
3.3 Results	76

3.3.1 Phylogenetic relationships-----	76
3.3.1.1. <i>Mitochondrial DNA - ATP6</i> -----	76
3.3.1.2 <i>Nuclear DNA - FGB5, MUSK and TGFB2</i> -----	77
3.3.2 Mitochondrial and nuclear DNA - population demographic histories and phylogenetic networks-----	78
3.3.3 Divergence time-----	79
3.4 Discussion -----	79
3.5 Conclusion -----	81
APPENDICES-----	96
Appendix 3.1. A proposed revised classification of the Southern Boubou <i>Laniarius ferrugineus</i> .-----	96
Appendix 3.2.-----	97
CHAPTER 4 -----	100
Assessing patterns of variation in vocalisations of the Southern Boubou <i>Laniarius ferrugineus</i> (Gmelin, 1788).	
4.1 Introduction-----	100
4.1.1 Factors affecting vocalisations-----	103
4.1.2 Study species-----	105
4.1.3 Vocal components employed in previous studies-----	105
4.1.4 Aim -----	106
4.1.5 Objectives-----	106
4.1.6 Research questions -----	106
4.2 Materials and methods-----	106
4.2.1 Data collection-----	106
4.2.1.1 <i>Assembling sound recordings</i> -----	106
4.2.2 Data analyses -----	107
4.2.2.1 <i>Song strophe duets spectrograms</i> -----	107
4.2.2.2 <i>Statistical analysis of song strophes duets</i> -----	107
4.3 Results -----	108
4.3.1 General description of <i>Laniarius ferrugineus</i> song strophe duets --	108
4.3.2 Song strophe duets of various subspecies -----	108
4.3.3 Statistical outcomes-----	109
4.4 Discussion -----	109
4.5 Conclusion -----	110
CHAPTER 5 -----	115
General Discussion-----	115
REFERENCES-----	119

## LIST OF FIGURES, TABLES AND APPENDICES

LIST OF FIGURES		
Item	Caption	Page
<b>Figure 1.1</b>	Distribution map of <i>Laniarius ferrugineus</i> (Southern African Bird Atlas Project 2 - SABAP2, accessed November 2017).	<b>13</b>
<b>Figure 1.2</b>	Plates showing recognised subspecies of <i>Laniarius ferrugineus</i> (Bowie <i>et al.</i> 2005).	<b>14</b>

<b>Figure 2.1</b>	Multi – Dimensional Scaling (MDS) plot of combined males and females of all the recognised subspecies excluding the two variables (total head length and total body length).	<b>31</b>
<b>Figure 2.2</b>	Multi – Dimensional Scaling (MDS) plot of females of all the subspecies excluding the two variables (total head length and total body length).	<b>32</b>
<b>Figure 2.3</b>	Multi – Dimensional Scaling (MDS) plot of males of all the subspecies excluding the two variables (total head length and total body length).	<b>32</b>
<b>Figure 2.4</b>	Multi – Dimensional Scaling (MDS) plot of combined males and females of all subspecies based on all the variables.	<b>33</b>
<b>Figure 2.5</b>	Multi – Dimensional Scaling (MDS) plot of females of all subspecies based on all variables.	<b>33</b>
<b>Figure 2.6</b>	Multi – Dimensional Scaling (MDS) plot of males of all subspecies based on all variables.	<b>34</b>
<b>Figure 2.7</b>	Box-and-whisker plots of combined male and female birds of all the subspecies and all the explored variables.	<b>35</b>
<b>Figure 2.8</b>	Ventral plumage of male birds representing the recognised subspecies (from left to right - <i>Laniarius ferrugineus ferrugineus</i> , <i>L. f. natalensis</i> , <i>L. f. pondoensis</i> , <i>L. f. transvaalensis</i> , <i>L. f. tongensis</i> , <i>L. f. savensis</i> ).	<b>36</b>
<b>Figure 2.9</b>	Ventral plumage of female birds representing the recognised subspecies (from left to right - <i>Laniarius ferrugineus ferrugineus</i> , <i>L.</i>	<b>37</b>

	<i>f. natalensis</i> , <i>L. f. pondoensis</i> , <i>L. f. transvaalensis</i> , <i>L. f. tongensis</i> , <i>L. f. savensis</i> ).	
<b>Figure 2.10</b>	Southern African Bird Atlasing Project 2 (SABAP2) distribution map of <i>Laniarius ferrugineus</i> (Accessed November 2017).	<b>38</b>
<b>Figure 2.11</b>	Distribution map of <i>Laniarius ferrugineus</i> generated from all geo-referenced records excluding those from the Natural History Museum of Zimbabwe (NHMZ).	<b>38</b>
<b>Figure 2.12</b>	Distribution map of <i>Laniarius ferrugineus</i> generated from all geo-referenced data of all records including the Natural History Museum of Zimbabwe (NHMZ).	<b>39</b>

<b>Figure 3.1a</b>	Bayesian phylogenetic tree based on all individuals sampled generated from mitochondrial ATP6 gene. The numbers above the branches are the posterior probabilities (only $\geq 0.65$ are shown, colours in deeper branches indicate nothing but colours in shallow branches are a mere indication of the groups).	<b>84</b>
<b>Figure 3.1b</b>	Parsimony network (95% parsimony) based on ATP6 of all individuals sampled with the exclusion of outgroups for graphical purposes. The sizes of the circles are proportional to the haplotype frequencies, lines represent branches, small lines across branches represent number of mutations and the small black circles represent unsampled or extinct haplotypes. Each subspecies is represented by one colour, north of the range: <i>L. f. transvaalensis</i> , <i>L. f. tongensis</i> and <i>L. f. savensis</i> (blue, purple and yellow respectfully) and south of the range: <i>L. f. natalensis</i> , <i>L. f. ferrugineus</i> and <i>L. f. pondoensis</i> (green, dark red and light blue respectfully).	<b>85</b>
<b>Figure 3.2a</b>	Bayesian phylogenetic tree based on unique haplotypes only generated from mitochondrial ATP6 gene. The numbers above the branches are the posterior probabilities (only $\geq 0.65$ are shown, colours in deeper branches indicate nothing but colours in shallow branches are a mere indication of the groups).	<b>86</b>
<b>Figure 3.2b</b>	Parsimony network (95% parsimony) based on ATP6 unique haplotypes with the exclusion of outgroups for graphical purposes.	<b>87</b>

	Lines represent branches, small lines across branches represent number of mutations and the small black circles represent unsampled or extinct haplotypes. Each subspecies is represented by one colour, north of the range: <i>L. f. transvaalensis</i> , <i>L. f. tongensis</i> and <i>L. f. savensis</i> (blue, purple and yellow respectfully) and south of the range: <i>L. f. natalensis</i> , <i>L. f. ferrugineus</i> and <i>L. f. pondoensis</i> (green, dark red and light blue respectfully) that form two distinct clusters.	
<b>Figure 3.3a</b>	Bayesian phylogenetic tree based on unique haplotypes only generated from nuclear FGB5. Numbers above the branches are the posterior probabilities. (only $\geq 0.65$ are shown, colours in deeper branches indicate nothing but colours in shallow branches are just a mere indication of the groups).	<b>88</b>
<b>Figure 3.3b</b>	Parsimony network (95% parsimony) based on FGB5 unique haplotypes with the exclusion of outgroups for graphical purposes. The sizes of the circles are proportional to the haplotype frequencies, lines represent branches, small lines across branches represent number of mutations and the small black circles represent unsampled or extinct haplotypes. Each subspecies is represented by one colour, north of the range: <i>L. f. transvaalensis</i> (blue) and south of the range: <i>L. f. pondoensis</i> (light blue).	<b>89</b>
<b>Figure 3.4a</b>	TGFB2 Bayesian phylogenetic tree based on unique alleles. Numbers above the branches are the posterior probabilities (only $\geq 0.65$ are shown, colours in deeper branches indicate nothing but colours towards the two groups are just a mere indication of the groups).	<b>90</b>
<b>Figure 3.4b</b>	Parsimony network (95% parsimony) based on TGFB2 unique haplotypes with the exclusion of outgroups for graphical purposes. The sizes of the circles are proportional to the haplotype frequencies, lines represent branches and small lines across branches represent number of mutations. Each subspecies is represented by one colour, north of the range: <i>L. f. transvaalensis</i> and <i>L. f. tongensis</i> (blue and oranges respectfully) and south of the range: <i>L. f. natalensis</i> and <i>L. f. ferrugineus</i> (green and dark red respectfully).	<b>91</b>
<b>Figure 3.5a</b>	Bayesian phylogenetic tree based on unique haplotypes generated	<b>92</b>

	from nuclear MUSK. Numbers above the branches are the posterior probabilities (only $\geq 0.65$ are shown, colours in deeper branches indicate nothing but colours towards the two groups are a mere indication of the groups).	
<b>Figure 3.5b</b>	Parsimony network (95% parsimony) based on MUSK unique haplotypes with the exclusion of outgroups for graphical purposes. The sizes of the circles are proportional to the haplotype frequencies, lines represent branches and small lines across branches represent number of mutations. Each subspecies is represented by one colour: <i>L. f. transvaalensis</i> and <i>L. f. tongensis</i> (blue and oranges respectfully) and <i>L. f. natalensis</i> and <i>L. f. pondoensis</i> (green and light blue respectfully).	<b>93</b>
<b>Figure 3.6</b>	Divergence time phylogenetic tree based on unique haplotypes of the ATP6 mitochondrial marker. Values above branches represent estimated divergence times indicated in million years (colours in deeper branches indicate nothing but colours in shallow branches are a mere indication of the groups).	<b>94</b>
<b>Figure 3.7</b>	Distribution map of <i>Laniarius ferrugineus</i> generated in this study showing a possible geographic break (a black line) separating the southern and the northern lineages.	<b>95</b>
<b>Figure 3.8</b>	Distribution map of <i>Laniarius ferrugineus</i> generated from all the individuals sampled for DNA analysis.	<b>95</b>

<b>Figure 4.1</b>	Spectrograms generated from song strophe duets of various <i>Laniarius ferrugineus</i> subspecies.	<b>112</b>
-------------------	--	------------

<b>LIST OF TABLES</b>		
<b>Item</b>	<b>Caption</b>	<b>Page</b>
<b>Table 3.1</b>	Primers sequences used to PCR-amplify and sequence DNA samples (both modern and ancient samples).	<b>82</b>
<b>Table 3.2</b>	Genetic diversity values (N, number of potential alleles; S, number of segregating sites; Hd, Haplotype diversity; Pi, nucleotide	<b>82</b>

	diversity; $\theta$ , Watterson's theta) based on only the ATP6 marker (- represents uncalculated values).	
<b>Table 3.3</b>	Genetic diversity values within <i>Laniarius ferrugineus</i> (N, number of potential alleles; S, number of segregating sites; Hd, Haplotype diversity; Pi, nucleotide diversity; $\theta$ , Watterson's theta) based on the ATP6 marker for the two lineages recovered in the Bayesian Analysis.	<b>83</b>
<b>Table 3.4</b>	Genetic diversity values within <i>Laniarius ferrugineus</i> (N, number of potential alleles; S, number of segregating sites; Hd, Haplotype diversity; Pi, nucleotide diversity; $\theta$ , Watterson's theta) based the nuclear markers for the ingroup taxa.	<b>83</b>

<b>Table 4.1</b>	List of songs of <i>Laniarius ferrugineus</i> sourced from an online database Xeno-canto and the British Library Sound Archive (BLSA).	<b>110</b>
<b>Table 4.2</b>	Summary of t-test results from song strophe variables and habitat.	<b>111</b>

<b>LIST OF APPENDICES</b>		
<b>Item</b>	<b>Caption</b>	<b>Page</b>
<b>Appendix 2.1</b>	List of individual bird study skins examined for morphometric analyses in this study.	<b>40</b>
<b>Appendix 2.2</b>	List of all records of the geo-referenced data for all individuals examined in this study.	<b>50</b>

<b>Appendix 3.1</b>	A revised classification of the Southern Boubou <i>Laniarius ferrugineus</i> .	<b>96</b>
<b>Appendix 3.2</b>	List of samples (103) sequenced in this study. Abbreviations: MVZ, Museum of Vertebrate Zoology, Berkeley; MNHN, Muséum National d'Histoire, Naturelle, Paris and DNSM, Durban Natural Science Museum, Durban.	<b>97</b>



# **CHAPTER 1**

## **General Introduction**

Birds are conspicuous in many habitats, occur worldwide and are ecologically diverse (Whelan *et al.* 2015). Many species of birds are polymorphic, exhibiting geographic variation across their distribution range, often reflected by the recognition of several subspecies. By understanding and valuing bird services and disservices through careful natural history research, we can better assess the environmental consequences of bird declines and extinctions. These consequences can be communicated to the public and policy makers, thereby increasing support for the conservation of birds and their habitats (Whelan *et al.* 2015). The increasing worldwide destruction and disturbance of natural ecosystems, including through climate change, are precipitating catastrophic extinctions of species (Brook *et al.* 2006). For several biogeographic realms (e.g. Africa, Indian, Indoneasia) the number of bird species remains underestimated because much of the cryptic diversity remains poorly described and efforts to catalogue and explain biodiversity need to be prioritised. The protection of biodiversity and ecosystems is of great importance to human society and should be incorporated more directly into public policy, development plans, and daily life (Lovins *et al.* 1999; Whelan *et al.* 2010; Hackett 2011; Kareiva *et al.* 2011).

### **1.1 The subspecies category**

The taxonomic category of subspecies is assigned to distinct sub-populations of the same species and there have been a number of changes in the classification of bird species and subspecies approved by the committee on classification and nomenclature, the International Ornithologists' Union World Bird list (Gill & Donsker 2017). Geographic or allopatric speciation is a process that typically involves the subdivision of a large and widely distributed parent population (species) into two or more populations (Ratti 1980). Certain populations are said to be at intermediate stages of speciation or have special morphological characteristics (Mayr 1951; Mayr 1987; Stebbins 1971). The sub-populations are often isolated and divergence may

result in differences in one or several factors: colour pattern, size and structure, song/call, feeding habits, habitat selection and behaviour (Ratti 1980). These or other divergence factors may function as isolating mechanisms that could prevent widespread interbreeding when and if the populations expand or overlap. Consequently, most bird populations that undergo geographic speciation likely evolve through a period when they would be recognised a subspecies (Ratti 1980).

The recognition of objectively diagnosable taxa from populations that are not morphologically diagnosable but may represent distinct lineages or evolutionarily significant units (ESUs), is essential for the generation of defensible taxonomic hypotheses that are necessary for all forms of evolutionary and comparative biology and for effective biodiversity conservation (Oatley *et al.* 2011). Ornithologists have spent considerable effort refining and debating subspecies concepts (Wiens 1982) and avian subspecies debates have been motivated by examples of genetic population structure that differed from morphology-based subspecies delineations (Zink 1989; Ball & Avise 1992; Zink *et al.* 2000; Zink 2004). Some ornithologists argue that historic classifications may not accurately reflect phylogeny because morphological differences do not always have a phylogenetic basis (Zink 2004). Others debate whether the subspecies concept has intrinsic value to avian classification (Smith & White 1956; Barrowclough 1982; Wiens 1982; Zink 2004).

The use of modern statistical analyses to assess the congruence and conflict among gross organismal (e.g. behaviour and ecology), morphometric (discrete and continuous characters) and molecular data has changed the face of taxonomy irrevocably (Oatley *et al.* 2011). Such data contribute new knowledge and provide insight into our understanding of the evolutionary processes underpinning the origin and maintenance of geographical variation within and among species, processes that have conservation and taxonomic implications.

## **1.2 Family and genera taxonomic history**

The relationships among several Old World groups popularly called “shrikes” have always been problematic due to taxonomic and systematic challenges. According to Fry (2009), the bush-shrikes, an African radiation, were classified within the family Laniidae, and thought to share close affinities with the true shrikes (mainly genus

*Lanius*) and of various other genera characterised by having a hook-tipped and toothed “bill”. The Laniidae is a poorly defined assemblage that is only supported by the presence of two adaptive characters, a hooked bill and the reduced state of the *Musculus flexor perforates digiti muscle* (Raikow *et al.* 1980). The first rationale for regarding the bush-shrikes as composing a family of their own, distinct from the Laniids, was made by W.P. Pycraft in 1907, but avian systematics remained conservative in their outlook for many decades thereafter (Fry 2009). In 1971, the family Malaconotidae was formally erected by the authors of ‘*The Birds of Zambia*’, by C.W. Benson and colleagues, for the genera *Malaconotanus* / *Chlorophoneus*, *Tchagra*, *Dryoscopus*, *Nilaus*, “perhaps *Larnioturdus*” and *Laniarius* (Fry 2009). The family is characterised by its plumage colours and patterns, loud vocalisations, neat nests, small clutches, woodland habitats, gleaning habits and absence of prey storing larders (Fry 2009). Presently, the family Malaconotidae consists of eight genera: *Malaconotus*, *Chlorophoneus*, *Telophorus*, *Bocagia*, *Tchagra*, *Dryoscopus*, *Laniarius* and *Nilaus* listed in the International Ornithologists’ Congress (IOC) World Bird List version 7.3 (Gill & Donsker 2017). The family consists of 49 species of which 21 belong to the genus *Laniarius* and within the genus the species *Laniarius ferrugineus* consists of six (6) putative subspecies (Gill & Donsker 2017).

The generic name *Laniarius*, given by L.J.P. Vieillot in 1816, is Latin for ‘butcher-like’ and refers to the rapacious habits of birds in this genus (Harris & Arnott 1988). The genus *Laniarius* (Boubous and Gonoleks) constitutes a fascinating group of African bush-shrikes rather uniform by size and shape but with strikingly different combinations of plumage colours and patterns (N’Guembock *et al.* 2008). *Laniarius* was considered to have been comprised of 16 species that are uniform in shape and properties (Fuchs *et al.* 2004) and (Hall & Moreau 1970) recognised three species-assemblages that differed primarily in their plumage colouration and secondarily in their habitat selection. The first of these comprises all black Boubous, which mainly occupy forest, the second lineage, the pied Boubou mostly of scrub thickets and dense riparian bush, and third lineage the Crimson Boubous which occupies a range of habitats from thorn bush to papyrus swamps (N’Guembock *et al.* 2008). All species within the genus *Laniarius* are endemic to Africa and the genus is the largest within the bush-shrike radiation (Dickinson *et al.* 2003). Although the classification of species and subspecies has been relatively stable, it was never been supported by a

clear character analysis hence Hall (1954) and Hall & Moreau (1970) characterised representatives of the proposed *Laniarius ferrugineus* superspecies (*L. ferrugineus*, *L. aethiopicus*, *L. turatti* and *L. bicolor*) by the contrasting plumage, black with white to pinkish or buffy underparts. Hall and Moreau (1970) tried to group species of *Laniarius* on the basis of a set of external characters and ecology.

### 1.3 The study species

#### 1.3.1 Morphology and distribution

The Southern Boubou *Laniarius ferrugineus* (Gmelin, JF, 1788) is the species of focus in this study. The name Boubou is derived from 'le Boubou', Francois Le Vaillant's onomatopoeic rendering of one of its calls (Harris & Arnott 1988). Its specific name *ferrugineus* is Latin for 'rust coloured' and describes the colour of the underparts. Previously, it was thought that this species extended throughout sub-Saharan Africa as a subspecies of the Tropical Boubou *L. aethiopicus* together with Swamp Boubou *L. bicolor*, which are now considered separate species (Harris & Arnott 1988; N'Guembock *et al.* 2008; Gill & Donsker 2017). Little is known about *L. ferrugineus*, despite its common occurrence in the sub-region. *Laniarius ferrugineus* is a plump bush-shrike that skulks about in thick vegetation and is usually difficult to see, except when it exposes itself while giving its loud ringing calls (Harris & Arnott 1988). Given its broad distribution range in a variety of habitats and largely non-migratory behaviour, it is not surprising that this species displays extensive geographical variation, especially in size and plumage features. It is a sexually dichromatic species and can be distinguished in the field by its head mantle that is black in the male and more slate-coloured in the female, who is generally also duller (Harris & Arnott 1988; Harris & Franklin 2000; Chittenden *et al.* 2016).

*Laniarius ferrugineus* is a widely distributed species that is a common breeding resident endemic to southern Africa; it is highly vocal and can often be heard duetting although it is generally a shy bird that creeps about in a horizontal posture in thick bushes (Mackworth-Praed & Grant 1963; Harris & Arnott 1988; Chittenden *et al.* 2016). It is also a highly polymorphic species that overlaps with *L. aethiopicus* in the extreme north of South Africa (Sinclair & Ryan 2003) with its distribution extending into southern Mozambique, down the coast to Kwa-Zulu Natal, eastern and western Cape, south eastern Zimbabwe, Botswana and eastern Swaziland (SABAP2, accessed 2017) (Fig. 1.2). *Laniarius ferrugineus* and *L.*

*aethiopicus* superficially look alike (Chittenden *et al.* 2016) and this may cause confusion among ornithologists and bird enthusiasts. A buffy belly and distinctive call help separate *L. ferrugineus* from *L. aethiopicus* and the nature of overlap between the two species in Limpopo River Valley and southern Mozambique is poorly understood (Chittenden *et al.* 2016). However, Fry (2009) highlighted that *L. ferrugineus* and *L. aethiopicus* meet in the Limpopo river valley (N South Africa and S Mozambique) and because their races are very similar they may hybridise and intergrade. Along the Runde River (SE Zimbabwe); however, subspecies *L. f. savensis* overlaps with the widespread *L. a. limpopoensis* without interbreeding (Fry 2009).

The species (*L. ferrugineus*) requires dense bush (vegetation) and shrubs, favouring tangled coastal and riverine thickets of trees, shrubs and creepers, often along drainage lines, rocky outcrops, alien tree plantations and suburban gardens (Sinclair & Ryan 2003; Chittenden *et al.* 2016). It is a monogamous summer breeder that exhibits territorial behaviour (Mackworth-Praed & Grant 1963; Harris & Arnott 1988; Fry 2009) and is characterised by having black upperparts with a prominent wing-stripe and white underparts with varying degree of an ochre colouration (McGowan 1994; Bowie *et al.* 2005).

### 1.3.2 Taxonomic boundaries

The current taxonomy recognises *L. ferrugineus* as a polytypic species (consisting of two or more subspecies), which shows geographical variation that has confounded taxonomy. The six recognised subspecies are: *L. f. ferrugineus* (Gmelin, 1788) [s Western Cape Province, s South Africa]; *L. f. natalensis* Roberts, 1922 [w and s Kwa-Zulu Natal to sw Eastern Cape Province (e and se South Africa)]; *L. f. pondoensis* Roberts, 1922 [ne Eastern Cape Province (se South Africa)]; *L. f. transvaalensis* Roberts, 1922 (se Botswana, n South Africa and Swaziland); *L. f. tongensis* Roberts, 1931 (s Mozambique and e South Africa) and *L. f. savensis* da Rosa Pinto, 1963 (se Zimbabwe and s Mozambique) (Fig. 2.4, plate a - f). They vary slightly in size and plumage colouration, which could be the result of both latitudinal (Bergman's rule) or ecological (Gloger's rule) factors. Hence, it is currently unknown if the plumage differences among these subspecies are in fact clinal or represent sharp transitions across ecological zones.

### 1.3.3. Study area

The study covered Southern Africa in which this widely distributed species Southern Boubou *Laniarius ferrugineus*, a common breeding resident endemic to the region occurs. Southern Africa is the southernmost region of the African continent which consists of a number of independent countries including South Africa, Zimbabwe and Mozambique, in which the focal species occurs. *Laniarius ferrugineus* is highly polymorphic and overlaps with the Tropical Boubou *L. aethiopicus* in the extreme north of South Africa (Sinclair & Ryan 2003) with its distribution extending into southern Mozambique, down the coast to Kwa-Zulu Natal, eastern and western Cape, south eastern Zimbabwe, Botswana and eastern Swaziland (SABAP2, accessed 2017).

## 1.4 The field of Phylogeography

Phylogeography is the study of the spatial arrangement of genealogical lineages, especially within and among conspecific populations and closely related species (Avice 2000). Systematics is defined as the science of classifying organisms and the determination of identities and inter-relationships at the species level, and of evolutionary relationships above the species level. It is important because it is the primary language for communicating information about the biodiversity of the planet (Mayr 1991; Wheeler 1995; Schuh 2000). Phylogeographic perspectives have transformed aspects of systematics, population biology, genetics, biogeography, ecology and biodiversity conservation (Avice *et al.* 2016). A question on how geographically structured variation among populations and species arise has been central in phylogeography (Kearns *et al.* 2009). Further, divergence within and between species, birds in particular, is seen to be most commonly attributed to differentiation in allopatry, typically following the vicariance of populations on either side of biogeographic barriers (Avice 2000; Barraclough & Vogler 2000).

The development of phylogeography as a field has not been without challenges. However, it is on record that phylogeography does not exist in isolation and has either direct or indirect links with other fields such as systematics, population genetics, conservation, biogeography, climate change and others. During this time when future climate changes are said to likely affect species ranges, the distribution of biodiversity and the evolutionary history it holds (Thuiller *et al.* 2011),

the discovery of phylogeographic lineages within species could motivate and justify a reconsideration of strategies for conserving intra-specific diversity (Crandall *et al.* 2000). Speciation is not always accompanied by morphological change, the true number of biological species is likely to be greater than the current tally of nominal species, most of which are delineated on purely morphological grounds and for this reason this study explores other components of evidence such as genetics, vocalisation and morphology. Multilocus analyses of phylogeography and population history is a powerful tool for understanding the geographic structure of species over time and space, origin and dispersal (Lee & Edwards 2008). Understanding the geographical lineages and the underlying processes generating these patterns has been of great interest to evolutionary biologists (Lee & Edwards 2008). Phylogeography focuses on these distributions within and among closely related species (Avice *et al.* 1987; Arbogast & Kenagy 2001), combining both spatial and phylogenetic components, and thereby contributing to the study of micro- and macroevolution along with fields such as systematics and palaeontology (Avice *et al.* 1987; Avice 1998; Avice 2000; Hewitt 2001).

#### 1.4.1 Approaches to phylogeography

Since the advent of Polymerase Chain Reaction (PCR), the use of DNA sequence variation to reconstruct phylogeographic histories has accelerated the development of the field, relying heavily in its first two decades on mitochondrial DNA (mtDNA). Mitochondrial DNA has proved to be powerful for genealogical and evolutionary studies of animal populations (Zhang & Hewitt 2003) although it has some limitations. Some of the advantages of mtDNA includes its high mutation rate, small effective population size (compared with autosomal nuclear DNA - nuDNA), haploidy, and its putative lack of recombination, although reports of mitochondrial recombination have become more common (Hagelberg *et al.* 2000; Pakendorf & Stoneking 2005; Tsaousis *et al.* 2005). One of the challenge of mtDNA is that all loci are linked so non-independent and so it only represents the maternal line, it can obscure the patterns of male-biased gene flow. One of major issue that has been the centre of phylogeography involves the utility of mitochondrial DNA (mtDNA) and nuclear DNA (nuDNA) markers. The results based solely on mtDNA can be different from those recovered from analyses using nuDNA (Wahlberg *et al.* 2009), a phenomenon known as mito-nuclear discordance (Tóth *et al.* 2017). Thus, mtDNA

may not exhibit genealogical patterns that are representative of the entire population history, especially when there is a sex bias in fitness or dispersal behaviour (Hare 2001). Nuclear DNA markers on the other hand have an advantage of providing genealogical patterns that are representative of the entire population history because they are biparentally inherited unlike mtDNA that is maternally inherited (Hare 2001).

#### 1.4.2 Evidence – morphology, molecules and vocalisations

Bird species have characteristic sizes, shapes, colours and songs, as well as ecological niches and geographical ranges. Different species may interact ecologically, but may not freely exchange genes or novel genetic-based adaptations. Morphological, molecular and vocal approaches each have advantages for systematic, phylogenetic and phylogeographic reconstruction. Morphological techniques are applicable to an enormous range of museum and fossil material, and a large portion of the earth's organisms will continue to be studied primarily or exclusively from morphological information (Hillis 1987). On the other hand, the potential of molecular data set is extensive and when fully utilised, should provide a detailed record of the history of life. Another advantage is that historical samples can be used in molecular studies. For example, a complete horse genome was sequenced from a bone dating back to around 700 000 years ago and this shed light on the equine evolution and dramatically extends the known limit of DNA survival (Craig *et al.* 2013). Studies that combine the two approaches (morphological and molecular) can maximise both information content and usefulness (Hillis 1987). Furthermore, vocalisations consequently provide potentially informative characters for systematics (Parker *et al.* 1995; Kratter & Parker 1997; Zimmer 2002; Remsen 2003) and comparative studies. The three forms of evidence (morphology, molecules and vocalisations) are not immune to the challenges experienced when employed in the context of understanding the evolutionary history of taxa.

Reconstruction of the evolutionary history of birds requires the analysis of specific traits called characters that are shared as a result of common ancestry. Conserved characters are those that do not easily change in the course of ecological adaptation, and are of the greatest value because they retain clues from the ancestors. Wahlberg and Nylin (2003) maintained that morphological data are still crucial to our understanding of the relationships of extant organisms. For example,



colouration traits expressed in animals have proven essential components to understand the nature of selection, sexual selection in particular; only in just over a decade have scientists appreciated the importance of gaining a systematic understanding of both function and evolution of colouration and the mechanisms that underpin it (Hill & McGraw 2006). Birds in particular, due to their colourful display and the role of their colour signals in fitness differentials, have traditionally been employed as prime model systems to understand the cause and the implications of colour evolution.

Behaviour, vocalisations, and proteins yield clues to evolutionary relationships among some birds, so does plumage patterns. However, a constant challenge to accurate reconstruction of the history of lineages is the possibility of convergence between unrelated species, which is prevalent in both external appearance and specific attributes.

The greatest advantage of molecular data is the large extent of the data set. Because all inheritable information is encoded in the DNA, the set of morphological data with a genetic basis is a small subset on molecular information. The maximum number of independent characters available for analyses is limited by the number of nucleotide pairs in its and organisms genome. Advances in DNA sequencing technology have resulted in tremendous increase in the DNA sequence database, which typical represent the largest set of characters for systematic analysis. Among the most rapidly evolving DNA sequences are those found in the mitochondria of eukaryotes (mtDNA) (Avisé & Lansman 1983; Brown 1983). Studies of the mitochondrial DNA have been useful for studying population phylogeny within species (Avisé *et al.* 1979; Cann *et al.* 1987) as well as for recovering phylogenies of closely related complexes of organisms (Brown & Wright 1979; Templeton 1983).

Because genes evolve at different rates from ribosomal RNA genes to mitochondrial DNA, this makes it possible to address virtually any level of phylogenetic question by choosing the correct molecular loci. In addition to the coding regions, some gene arrays contain a diversity of transcribed and non-transcribed spacers that provide a record of evolutionary history from very recent to ancient times (Hillis & Davis 1986, 1987). A major obstacle to increased use of molecular techniques is the cost relative to the cost for collection of morphological data. Morphological approaches has advantages over molecular approaches in systematics due to the greater applicability to the extensive collections of preserved

specimens in museums (Hillis 1987). Although some molecular information can be obtained from traditionally preserved specimens (Ranker & Werth 1986; Thorpe & Giddings 1981), the majority of the molecular techniques require fresh or cryopreserved material (Dessauer *et al.* 1984) although this is starting to change. The study of palaeontology is nearly limited to morphological analysis and has always been primarily a morphological endeavour (Hillis 1987) and the ability to incorporate relevant information from fossils is the great advantage of morphological analyses. Neither molecular nor morphological methods are limited by phylogenetic scale in their application. However, few morphological characters are shared among major groups of organisms.

Vocalisations have mainly been of use to help resolve the taxonomy of closely related allopatric taxa and to infer relationships, both within and between genera. Vocalization data have been crucial to the discovery of several new species (Alström & Ranft 2003). Avian sound archives are crucial to the advancement of such studies but many more recordings are needed and their quality must be high. It is important that the circumstances of recordings be documented, furthermore the identity of vocalising birds needs to be firm, and a fuller system of cooperation between sound archives is required (Alström & Ranft 2003). Acoustic signals have been of great use in a wide range of birds, in the discovery of new species, the assessment of taxonomic rank of allopatric taxa under the biological species concept (Mayr 1942) and phylogenetic analyses (Mandiwana-Neudani *et al.* 2014). The use of vocalisations in systematics is relatively cheap and has a number of advantages nevertheless sounds alone should not be used in making taxonomic decisions. However, it can be a first pointer to the field ornithologist to gather additional evidence such as further morphological, DNA or behavioural data, and these data can then be used in conjunction in taxonomic revisions.

There are challenges in using vocalisations of oscines versus suboscine birds and some studies of suboscine cerebral structure indicate that members of this group seem to lack the brain control centres which are responsible for controlling feedback learning mechanisms in oscines (Brenowitz & Kroodsma 1996). Many oscine passerines therefore have the capacity of developing microgeographic variations of song called dialects (Kroodsma 1994) and many experimental studies have shown that there is a strong correlation between these variations and the

presence of learning ability within the group (Thorpe 1958; Nottebohm 1972; Kroodsma 1981; Lanyon 1979; Weary *et al.* 1990). As a result, the dialects within the oscines are thought to be a cultural phenomenon (Raposo & Höfling 2003). However, suboscine songs are said to be less conservative than morphological features at the species level and thus more informative in detecting recently divergent species (Raposo & Höfling 2003).

## 1.5. Purpose of the current study

### 1.5.1 Study aim

The aim of this study was to determine the phylogeographic patterns of the Southern Boubou, *Laniarius ferrugineus* in an attempt to investigate the level of morphological, genetic, and vocal differentiation in this species.

### 1.5.2 Study objectives

The objectives of this study set out to satisfy the above aim were to:

- i) investigate if *L. ferrugineus* represents a single species or a species complex
- ii) determine the level of genetic and morphological differentiation in *L. ferrugineus* throughout its distribution range.
- iii) compare the evolutionary units of *L. ferrugineus* delineated in this study with the current taxonomic circumscription.
- iv) estimate the divergence times between the recovered phylogeographic lineages within the *L. ferrugineus* complex.
- v) compare the distribution map generated in this study with the ones published in the literature.
- vi) produce a comprehensive description of the songs of the *L. ferrugineus* subspecies.
- vii) investigate whether the song structure is diagnostic of the entities in *L. ferrugineus*.
- viii) determine the relationship between song variables of *L. ferrugineus* and habitat.

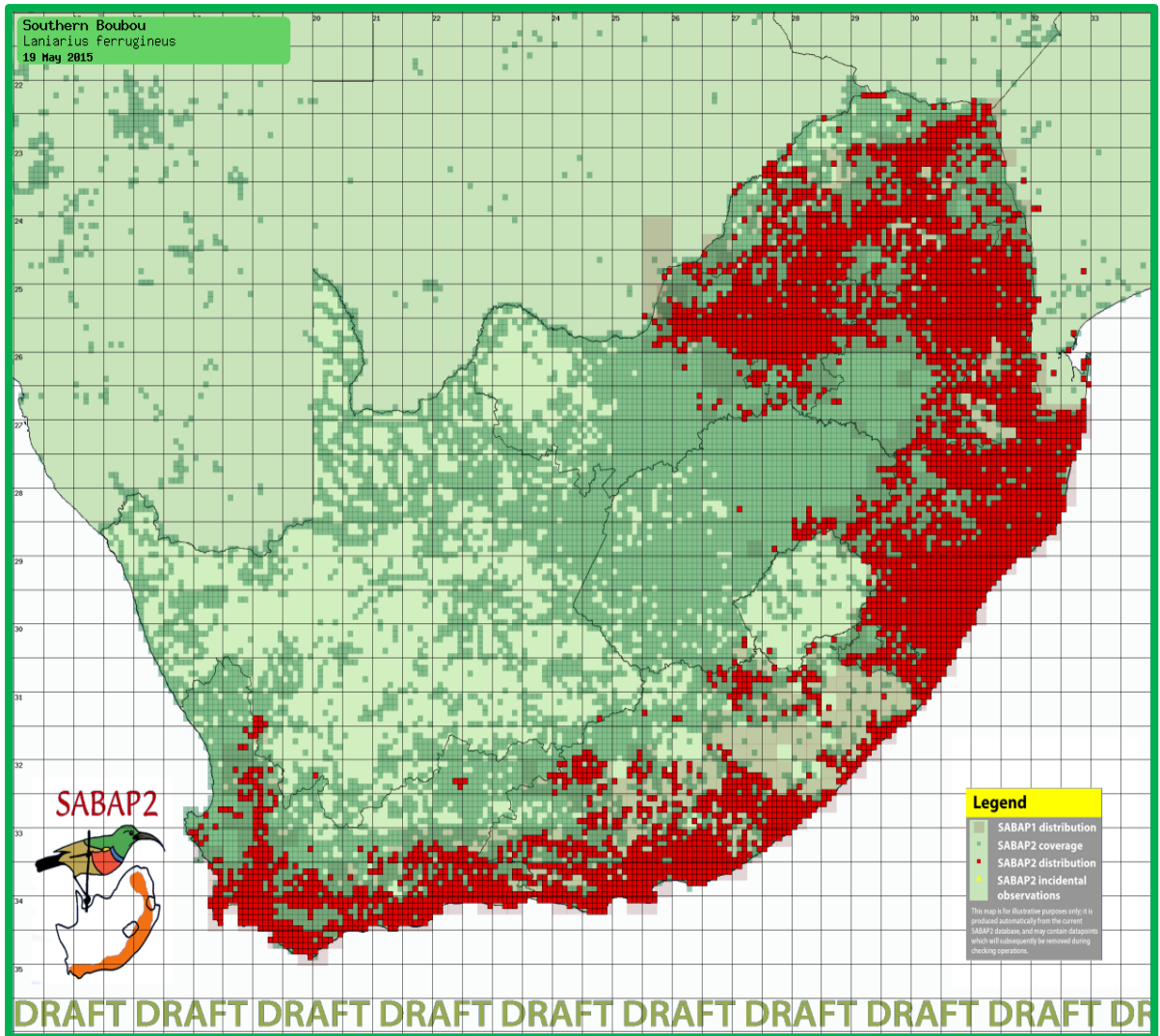
### 1.5.3 Study research questions

- i) Is *Laniarius ferrugineus* a single species or a complex?

- ii) What is the extent and the level of morphological, genetic and song differentiation in *L. ferrugineus* throughout its distribution range?
- iii) What is the estimated divergence time between the lineages?
- iv) How do the evolutionary units of *L. ferrugineus* delineated in this study compare with the current taxonomic circumscription?
- v) How does the spatial map of *L. ferrugineus* subspecies generated in this study compare with the one in literature?

### **1.6 Relevance of the study**

The current study should expand our knowledge base as far as ornithology is concerned and shed light on the phylogeographic patterns of the Southern Boubou *Laniarius ferrugineus* (Gmelin, 1788). The findings should significantly contribute to our understanding of the evolutionary processes governing the geographical variation in *Laniarius ferrugineus* complex. Although *L. ferrugineus* is of least concern (LC), its wide distribution range calls for its precise taxonomic delineation for better management and conservation.



**Figure 1.1.** Distribution map of *Laniarius ferrugineus* (Southern African Bird Atlasing Project 2 - SABAP 2, accessed November 2017).



a) *L. f. ferrugineus*



b) *L. f. pondoensis*



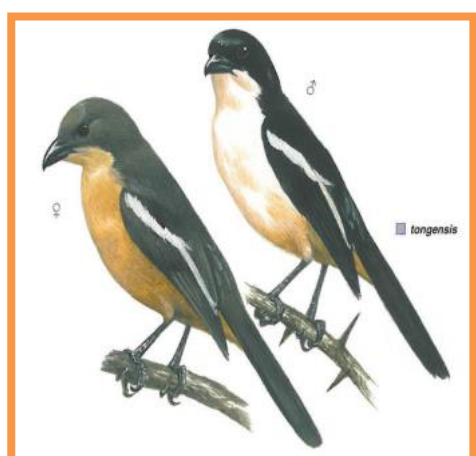
c) *L. f. natalensis*



d) *L. f. transvaalensis*



e) *L. f. savensis*



f) *L. f. tongensis*

**Figure 1.2.** Plates showing recognised subspecies of *Laniarius ferrugineus* (Bowie *et al.* 2005).

## CHAPTER 2

---

---

# The morphometric and morphological analysis of the Southern Boubou *Laniarius ferrugineus* species complex

### 2.1 Introduction

Many bird species show widespread geographic variation phenotypically and in their vocalisations. Others present no geographical variation while some exhibit a complex geographic variation that renders them polytypic in nature. Body size is one of the most important traits affecting the physiology and ecology of animals (Lomolino & Perault 2007; Kingsolver & Huey 2008). Intraspecific geographic variation in body size is assumed to reflect adaptation to local environmental conditions (Mayr 1956; Yom-Tov & Geffen 2011). Bergmann's rule (Bergmann 1847), which postulates that individuals from cooler regions tend to be larger than congeners from warmer regions, is commonly invoked to explain such variation in both homeotherms (McNab 1971; Lin *et al.* 2008; Martinez *et al.* 2013) and ectotherms (Ashton 2002; Pincheira-Donoso *et al.* 2008; Jaffe *et al.* 2016). This rule has been corroborated by data on numerous bird and mammal species in the past. However; a few notable exceptions have been documented (reviewed by Ashton 2002; Meiri & Dayan 2003). Syntheses of overall patterns of geographic variation produced "Gloger's rule" (Gloger 1833), the tendency for populations from more humid areas to be more heavily pigmented than conspecific populations from less humid areas and what could be called "Mayr's rule" the association between geographic isolation and increasingly marked phenotypic differentiation (Remsen 1984).

Traditionally, scientists have relied on morphology to understand intraspecific variations of different organisms and this is still crucial for understanding the relationships between and within species (Wahlberg & Nylin 2003), despite published views to the contrary. For example, Poisot *et al.* (2011) hinted that describing new species solely on the basis of their morphology is often not straightforward, and especially so for small-bodied organisms that display few

morphological features on which to rely. Furthermore, Zhang (2016) stated that phylogenetic trees reconstructed from molecular sequences are often considered more reliable than those reconstructed from morphological characters, in part because convergent evolution, which confounds phylogenetic reconstruction, is believed to be rarer for molecular sequences than for morphological characters. Another great advantage of using molecular data is the extent of the data set, which is molecular sequences provides many more characters than morphological characters (Hillis 1987). Morphological studies; however, have many advantages. Incorporation of morphological characters enables application to an enormous range of museum and fossil materials and a large portion of the Earth's organisms will continue to be studied primarily or exclusively from morphological information (Hillis 1987).

Morphology is a branch of biology that deals with the form and structure of organisms and the structural features. It is also used when identifying, naming, describing and in the classification of organisms. It refers to the physical appearance, for example: size, shape, colour, texture and location or position of a feature on an organism. Many organisms are subdivided into morphologically and genetically distinct groups, which can be recognised as subspecies (Largiader *et al.* 1994), distinguished based on noticeable morphological criteria such as plumage patterns (Hewitt 1988). The beautiful and varied colours of bird plumage have long captured the imagination of researchers (Jessica *et al.* 2008) and have been used in evolutionary studies. Museum bird study skins are used widely to assess these plumage colours (Schmitz-Ornés 2006) and to study the evolution of colour traits and sexual dichromatism in birds (Owens & Hartley 1998). These specimens are valuable for studies of plumage colour, though feather colour may fade over time and not accurately reflect the colours of live birds. However, Jessica *et al.* (2008) provide strong support for the use of museum specimens to examine colouration in birds, provided that the specimens were collected relatively recently, that is 50-100 years ago.

There are different methods used in the assessment of plumage colouration in ornithological studies including the use of colour charts, visual evaluation and spectrophotometric analysis. According to Jessica *et al.* (2008), certain methods may be better suited to a particular study depending on the questions addressed and the



specific colours examined. They found that human visual estimate of dichromatism were similar to the spectrophotometric estimates of dichromatism in the bird-visible range, however human visual estimates of dichromatism did not predict the extent of UV dichromatism. It is also possible that certain types of feather colours differ in their susceptibility to fading.

Morphological characters of birds reflect their adaptive evolution and ecological requirements and are also relevant to phylogenetic relationships within a group of related species (Shao *et al.* 2016). These characters are frequently used to investigate adaptive radiations, such as bill shape adapting to different food sources in Darwin's finches (Grant 1986) and the extremely diverse bill morphology of the Hawaiian honey creepers (Lerner *et al.* 2011). This is as a result of morphological divergence, which enables related organisms to avoid competition and exploit available niches, playing an important role in adaptive radiation (Schluter 2000; Jönsson *et al.* 2012). The shapes of the features of a bird and its body size are related to its behaviour (migratory habits, flight mode, habitat use and foraging) as well as sexual selection (Burns *et al.* 2002; Kaboli *et al.* 2007). Also the bird's bill/beak is considered relevant to song structure / vocalisation, foraging modes, food types and parental care (Forstmeier *et al.* 2001; Badyaev *et al.* 2008; Kulemeyer *et al.* 2009). There is observed association between morphology and habitat and this is a central theme in evolutionary biology, because it reflects the way organisms adapt to their surrounding environment (Kaliontzopoulou *et al.* 2010).

Morphometrics is the quantitative description, analysis and interpretation of the shapes and shape variation in biology and this is also a fundamental area of research. There are many biometric measurements that can be taken but many of these are unnecessary or redundant (de Beer *et al.* 2001). Measurements should be restricted to those that are important for the particular species and these vary from species to species (de Beer *et al.* 2001). Techniques of description and comparison of shapes of structures are needed in any systematic study that is based on the morphology of the organism (Rohlf 1990). The length of the wing, bill, tarsus, head and tail have a long tradition of being the fundamental taxonomic measurements of birds and these may be of value in separating races of the same species and also distinguishing sexes (de Beer *et al.* 2001). The two variables (total body length and total head length) have long been contentious, as the measurements of such

variables are believed to be less accurate when compared to other variables (de Beer *et al.* 2001). Body size is also considered to be important for evolutionary and ecological studies (Alatalo *et al.* 1986), bird skins were also closely examined for this purpose.

### 2.1.1 The focal taxon

*Laniarius ferrugineus* (Gmelin, 1788), a species of bird commonly known as the Southern Boubou, is a highly polymorphic and slightly dichromatic species generally characterised by black (male) and grey (female) upperparts with a white wing-stripe duller or creamy white in females (Harris & Arnott 1988; Bowie *et al.* 2005; Fry 2009; Chittenden *et al.* 2016). The underparts differ significantly between sexes with the males generally having a white throat and breast merging to ochreous on the flanks and belly, whereas the females have more extensively ochreous underparts giving an overall duller appearance (Harris & Arnott 1988; Bowie *et al.* 2005; Fry 2009; Chittenden *et al.* 2016). It is a small to medium-sized passerine bird (around 21-23 cm and 59 g) (Fry 2009; Chittenden *et al.* 2016), which is widely distributed in South Africa (mainly across the east and south-western biomes), extending into southern Mozambique, south-eastern Zimbabwe, Botswana and eastern Swaziland (Fry 2009). It is one of the 49 species of the genus *Laniarius* (Fig. 1.1) (Gill & Donsker 2017). It is a species that prefers dense mesic woodlands, leafy bushes, riverine thickets, and edges of forests, stands of proteas, dense scrub and garden habitat (Fry 2009; Chittenden *et al.* 2016). *Laniarius ferrugineus* is a monogamous summer breeder that exhibits territorial behaviour (Mackworth-Praed & Grant 1963; Harris & Arnott 1988). In northern South Africa the species breeds between August and May (mainly Oct – Dec), in Kwa-Zulu Natal it breeds between September and December (mainly Oct – Nov), in the Western Cape (between August and March) and between October and December (Fry 2009) in Mozambique.

This is a resident species with limited local movements and has a diverse set of songs / calls with regular duetting by pairs, exhibiting a loud ringing antiphonal duet which may be initiated by either sex (Chittenden *et al.* 2016). *Laniarius ferrugineus* belongs in the order Passeriformes that is classified into two major suborders, the suboscines and the oscines (Sibley & Ahlquist 1990; Barker *et al.* 2004). Biogeographic analyses of passerine birds demonstrate that oscines are

dominant in Europe, Asia, North America, Africa and Australia, whereas suboscines are dominant in South America. *Laniarius ferrugineus* is an oscine (Fry 2009) which has a diverse set of songs with regular duetting by pairs, exhibiting a loud ringing antiphonal duet which may be initiated by either sex (Chittenden *et al.* 2017) and this is attributed to the oscines having the best control of their syringeal muscles and they produce a wide range of songs and other vocalisations.

The current taxonomic circumscription recognises six subspecies within *L. ferrugineus*, hence it is a polytypic species that shows remarkable geographical variation across its distribution range (Harris & Franklin 2000). The different subspecies are: *L. f. ferrugineus* (Gmelin, 1788); *L. f. natalensis* Roberts, 1922; *L. f. pondoensis* Roberts, 1922; *L. f. transvaalensis* Roberts, 1922; *L. f. tongensis* Roberts, 1922; *L. f. savensis* Rosa pinto, 1963. These subspecies vary in size for example, *L. f. savensis* and *L. f. tongensis* are generally smaller than the other subspecies, they also differ in the extent of their ochreous colourations where *L. f. pondoensis* appears to be the darkest morph with a large degree of ochreous colourations, even more so on the females (Bowie *et al.* 2005) (Fig. 1.2). Generally, these subspecies vary in size and plumage colouration, which could be the results of both latitudinal (Bergman's rule) or ecological (Gloger's rule) factors (Gloger 1833; Bergmann 1847). It is currently unknown if the plumage differences among the subspecies is in fact clinal or represents a sharp transition across ecological zones. According to Bickford *et al.* (2006), the polytypic nature of a species may pose a serious classification challenge and this could have implications for conservation planning and management of populations, our understanding of the evolutionary theory and biogeography. Therefore, it is imperative that the geographic variation of *L. ferrugineus* complex is understood.

### 2.1.2 Mapping of species distribution records

Mapping is when spatial locations of real-world features are mapped and the spatial relationships among them visualised. Mapping of geo-referenced records is important and a Geographic Information System (GIS) lets us visualise, question, analyse and interpret data to understand relationships, patterns and trends. Geospatial data can be analysed to determine: the location of features, where the most or the least of some feature exists and the density of some features in a given

space. Specimen-label records are of critical importance for biodiversity research and conservation, and this can be used to estimate species diversity, to direct future collecting to areas that are under-sampled or likely to be rich in new species (Myers *et al.* 2000). The geographic information system benefits organisations of all sizes and in almost every industry including science (e.g. Biodiversity studies, Taxonomy, Biogeography, Systematics). For example, the International Convention on Biological Diversity (CBD) has highlighted the importance of conserving biodiversity in light of climate change, changing environments and a growing human population (Convention on Biological Diversity 2011). This will rely on sound estimates of the geographic mapping and quantification of biodiversity (Shapcott *et al.* 2015).

### 2.1.3 Aim

The aim in this chapter was to study variation in the morphology of the various subspecies in order to assess the degree of differentiation within *L. ferrugineus*.

### 2.1.4 Objectives

The objectives were to:

- i) investigate if there are any morphologically-defined entities or groupings within *L. ferrugineus*
- ii) determine the level of morphological differentiation within *L. ferrugineus* and identify variables that contribute to the differentiation.
- iii) compare the distribution map generated in this study with the ones published in literature.

### 2.1.5 Research questions

- i) Are there any possible discernible entities or groups within *L. ferrugineus*?
- ii) To what extent are *L. ferrugineus* subspecies morphologically differentiated and what variables define them?
- iii) How does the distribution of *L. ferrugineus* generated in this study compare to the one in literature?

## 2.2 Materials and methods

### 2.2.1 Data collection

#### 2.2.1.1 *Bird specimens examined and morphology*

Museum bird study skin collections were the core source of information in this chapter. Study skins representing the six putative subspecies recognised in *L. ferrugineus* were examined with an endeavour to cover the species' distribution range. These spanned collections housed in five national natural history museums in South Africa (Ditsong National Museum of Natural History – DNMNH, East London Museum - ELM, Durban Natural Science Museum - DNSM, Iziko Museums of South Africa, Natural History – SAM) and one international natural history museum (Muséum National d'Histoire Naturelle – MNHN, Paris, France). Morphological data were collected based on mensural variables and plumage from 404 adult individual skins from these various collections (Appendix 2.1). In this study, only adult specimens were studied and this decision was influenced by several factors. For example, juvenile males are similar to adult females (Fry 2009) and juveniles are difficult to sex such that males may falsely be misidentified as females. Another reason was that because of the expected small size of juveniles or immature birds, some specimens can be mistakenly considered as one of the smaller-sized se Zimbabwe and s Mozambique distributed subspecies, *L. f. savensis*. This may result in the overall misrepresentation of some variables (plumage colouration and body size) and therefore may provide false results.

*Morphometric procedure and plumage assessment* - morphometric measurements of eight variables were taken from the individual birds following the guidelines in the SAFRING manual (de Beer *et al.* 2001). It is advantageous if similar guidelines are used to afford consistency and reliability of the results. The variables considered were: bill length (measured from angle in front of skull to the tip of the culmen), bill depth (from edge of the lower mandible to the proximal edge of the nostrils) and bill width (measured at the point where the exposed culmen begins). Another variable was wing length (which was measured from the carpal joint to the tip of the longest primary feather); tarsus length (from the notch of the inter-tarsal joint to the lowest edge at the last complete scale before the toe diverge) and tail length which was measured with a tail rule starting between the rectrices and the undertail coverts until

it came to a stop at the root of the central pair of tail feathers). In spite of the controversy associated with measurements of total body length, this variable was measured with a stopped wing rule starting from the head to longest tail feather/s – birds were measured with their back down on the stopped rule. Total head length was also measured from the back of the bird's head to the beak point. Total body and total head length were measured despite being criticised for inaccuracy that may result from poorly prepared skins e.g. stretched body or bent head. The lengths of the wing, bill, tarsus, head and tail have a long tradition of being the fundamental taxonomic measurements of birds (de Beer *et al.* 2001). Furthermore, because body size is considered to be important for evolutionary and ecological studies (Alatalo *et al.* 1986), the skins were also closely examined for this purpose.

Swiss Measy clock dial callipers - 150 mm, of an accuracy of 0.1 mm were used to measure the bill (length, width, depth) and tarsus length and a 150 mm stopped metal wing rule was used measure the wing length and a 150 mm unstopped tail rule was used to measure the tail length as described in de Beer *et al.* (2001). The SAFRING bird-ringing manual was followed according to the standardised or specified techniques used for measuring all the parameters. Damaged skins were not measured e.g. study skins with broken tarsi, bill and wings, skins with bent heads or missing heads and all skins that are missing some features such as tarsi.

With regard to plumage, in a comparative fashion, a closer assessment of plumage was done visually for all the 404 individual skins. Comparisons were also made with published information.

#### *2.2.1.2 Spatial distribution map*

It was necessary that instead of relying on the distribution maps (both point locality and range maps) in the literature, a point locality distribution map was produced from the records of all specimens examined in this study. This was critical to finding out if a map generated from this study could be a good representative of species distribution maps in the literature. The point locality map from this study was generated from geo-referenced data of all records of skins housed in various museums. Records of all captured and released birds (from which blood samples were taken) were also included. All geo-referenced data were obtained from

specimens housed in all the listed museums. In addition, geo-referenced data associated with specimens housed at the Field Museum of Natural History (FMNH) collection, Smithsonian National Museum of Natural History (NMNH) and the Natural History Museum of Zimbabwe (NHMZ) collections were assembled. For this section of this chapter, all records of adult and juvenile birds were considered and summed to a total of 675 records.

*Mapping of records of specimens examined* – most records already included geo-referenced information of individual birds and these were obtained from the databases of the above-mentioned natural history museums while this was lacking for some records of localities of specimens. In this case, Google Earth was used to access geo-referenced information not available for other localities of examined specimens. GPS coordinates which were not in decimal degrees were converted to decimal degrees and the conversion was performed using either the formulae [Minutes/60+Seconds/3600=Degrees] or [www.onlineconversion.com](http://www.onlineconversion.com). The spatial distribution maps were generated based on the geo-referenced data assembled.

## 2.2.2 Data analyses

### 2.2.2.1 Morphometric and plumage analysis

Prior to all the statistical analyses being run, it was necessary that the dataset with original measurements be log-transformed ( $\text{Log}_{10}$ ) in order to normalise the distributions (Kaboli 2007). Both inferential multivariate and descriptive univariate methods were used in the analyses of morphometric data. The multivariate methods were Multi-Dimensional Scaling (MDS) and Similarities in Percentages (SIMPER), both implemented in Primer V6 (Clarke & Gorley 2006) as well as Primer V6 (Clarke & Warwick 2001), respectively. A univariate, Box-and-whisker plots method was implemented in Tinn-R (R Core Development Team 2015).

The MDS analysis generates graphical diagrams that visually display the variation among groups and SIMPER determines the variables contributing to the similarity within the group and dissimilarity among the groups. The Box-and-Whisker plots were used to analyse each variable against all the other variables in the study and also to display diagrams that show similarities and differences of the different groups based on each of the variables in a comparative manner. For comparative

purposes, all the analyses were performed for separate datasets partitioned by sex. A combined dataset consisting of both male and female birds was also analysed in order to investigate whether or not the results are influenced by gender in relation to the variables and also to be able to compare within and between sexes. Based on the controversy concerning the consideration of the use of total body length and total head length in morphometric analysis, two data sets (one including all eight and the other excluding the two variables, total body length and total head length) were analysed.

Plumage colouration of skins was closely assessed by visual examination and judgement was based on published literature. Some species of birds are known to fade plumage colour over time while shelved in museum environments therefore there is a need to venture into spectrophotometric analysis, this was anticipated in order to employ a more advanced method for plumage analysis. Unfortunately, attempts made to contact institutions and individuals to help with this endeavour were unsuccessful.

#### *2.2.2.2 Spatial distribution map*

The GPS coordinates were imported into QGIS version 2.12. Lyon (QGIS Development Team 2009) and two distribution maps were generated using the southern African base map. One map was generated based on all records excluding those from the Natural History Museum of Zimbabwe and another map was generated from all records from the Natural History Museum of Zimbabwe. All records that were found to be outliers were identified, checked and corrected for errors which may have occurred during the data capturing process.

### **2.3 Results**

#### 2.3.1 Morphometry – multivariate and univariate methods

##### *2.3.1.1 Multi - dimensional scaling (MDS)*

The MDS results across all datasets were consistent (Figs. 2.1 – 2.6). Two major groups emerged within *L. ferrugineus*, the southern group consisted of: *L. f. ferrugineus*, *L. f. natalensis* and *L. f. pondoensis*, with the other group (northern) includes: *L. f. tongensis* and *L. f. savensis* with *L. f. transvaalensis*, with some



overlap between the two main groups (Figs. 2.1 – 2.6). The MDS plots indicated that the major groups were recovered when all variables were analysed, as well as with a more restrictive set of variables in which total body length and total head length were omitted (Figs. 2.1 - 2.3).

#### 2.3.1.2 Similarities in percentages (SIMPER)

Two sets of data were analysed in SIMPER, a combined data set and one which excluded two variables (total body length and total head length) for the same reason as indicated under 2.3.1.1. For the analysis that included all variables, total body length was the variable that contributed a higher percentage towards the dissimilarities among most of the subspecies (21.6% – 32.4%) with the exception of *L. f. savensis* and *L. f. tongensis* that were primarily separated on bill width (23.1%). Total body length accounted for the dissimilarities between sexes when the two subspecies (*L. f. savensis* and *L. f. tongensis*) were excluded.

The SIMPER analyses for the dataset that excluded total body length and total head length indicates that tail length (21.1% - 34.4%) and bill width (22.1% – 32.5%) contribute the highest percentage towards dissimilarity among subspecies. Furthermore, tail length (23.7%) was found to be the variable that contributes most towards the dissimilarities between sexes.

#### 2.3.1.3 Box-and-whisker plots

The findings from the univariate method, Box and Whisker plots generally reveal separation between two groups (Fig. 2.7). One group consists of: *L. f. ferrugineus* / *L. f. natalensis* / *L. f. pondoensis* and the other comprises of *L. f. savensis* and *L. f. tongensis* with *L. f. transvaalensis* consistently overlapping between the two groups. Variables were analysed separately against the different subspecies and of all the three variables (bill depth, tarsus length, total body length) appear to separate subspecies into the two main groupings.

#### 2.3.2 Plumage

Strong sexual dimorphism was generally observed for all six subspecies based on size and there was also marked sexual dichromatism. Dorsal colouration in males is mainly black and females are predominantly grey. There is also strong sexual dichromatism subject to the ventral side as observed for *L. f. ferrugineus*, *L. f.*

*natalensis* and *L. f. pondoensis*, becoming reduced in *L. f. savensis* and *L. f. tongensis* and almost absent for *L. f. transvaalensis*.

The dorsal grey colouration in females is tinged with ochre whereas males generally exhibit black colouration and this is in agreement with what was reported in the literature (Harris & Arnot 1988; Harris & Franklin 2000). Males appear to have white and a buff-to-white coloured wing stripe and females have the same colouration except that they have a tinge of ochre on the stripe evident especially in *L. f. pondoensis* (Mackworth-Praed & Grant 1963). The throat colouration in males is white and this was seen to be more apparent in *L. f. natalensis* males and the rest of the subspecies have a buff white throat and to some extent the buff is tinged with the ochreous colour. The throat of females appears to be buff or cream white tinged with ochre. The male breast was white, buff or cream white tinged with ochre and this was largely observed in *L. f. transvaalensis* with the females having a dark ochreous colouration predominantly seen in *L. f. pondoensis*. However, females of other subspecies had a buff or cream white breast colouration tinged with a bit of ochre.

The belly colouration of males was found to be buff or cream white with reduced ochre tinge as seen in *L. f. tongensis*; the rest of the subspecies (males) mainly exhibited the ochre colouration. Females on the other hand, exhibited a dark ochre colouration of the belly particularly *L. f. pondoensis* and the rest (females) were buff or cream shaded with the ochre. The flank of males had buff or cream tinged with a bit of the ochre chiefly seen in *L. f. tongensis* and the rest (males) had ochre flanks. Among females there was dominant dark ochreous colouration observed primarily in *L. f. pondoensis* and the rest were buff or cream white with a shade of ochre. White patches or windows were observed towards the tips of the inner uppertail coverts in both sexes but were much more prominent among the males and this was observed in all six subspecies.

### 2.3.3 Distribution maps

The map generated in this study (excluding NHMZ records) was similar to the Southern African Bird Atlasing Project 2 (SABAP2) map except that it showed subspecies boundaries, overlaps in distribution ranges, and showed a fair coverage of *L. f. savensis* (Figs. 2.10, 2.11 respectively). It should be noted that the SABAP2 distribution maps were based on validated observation records (Chittenden *et al.*

2016). There was distribution range shift which was observed when comparing SABAP2 and the map generated from this study. There was a slight range shift inland in parts where this species was known to occur. There seemed to be limited to the distribution range of the subspecies (*L. f. savensis*) at the extreme southern parts towards the centre of Mozambique. Furthermore, a distribution map generated from combined datasets including records from Natural History Museum of Zimbabwe skin collection (Fig. 2.12) was surprising in that the distribution range of *L. ferrugineus* spreads evenly throughout Zimbabwe while none of the maps in literature reflects this extensive distribution coverage in Zimbabwe. This raises some questions and there is a need to verify the specimen labels.

## 2.4 Discussion

### 2.4.1 Morphometry

The MDS and the Box-and-whisker plots based on full and reduced datasets consistently revealed two major groupings with one subspecies, *L. f. transvaalensis* overlapping the two groups. The two groups were represented by *L. f. ferrugineus*, *L. f. pondoensis* and *L. f. natalensis* whereas the other group was represented by *L. f. tongensis* and *L. f. savensis*, while *L. f. transvaalensis* overlapped the two groups. The two groups (southern and northern) occupied different habitats, the southern group generally occurred in dense scrub to coastal forest, occupied by *L. f. ferrugineus*, *L. f. natalensis* and *L. f. pondoensis*, whereas the northern group occupied habitats such as savanna, temperate grassland and forest occupied by *L. f. transvaalensis*, *L. f. tongensis* and *L. f. savensis*. The area that formed a geographic break between the two groups included the southern African Maputaland-Pondoland-Albany region, an area that harbours high species plant richness (Rebeiro *et al.* 2014). SIMPER revealed that total body length mainly contributed towards the variation among the subspecies and when total body length and total head length were excluded in the analysis, tail length and bill width contributed more towards the variation. Furthermore, tail length contributed more towards the differences between males and females. In full regard of the controversy about total body and head length, we considered the findings when the two variables were excluded to be valid and as a result bill width and tail length were the primary variables that account for

the differences observed among *L. ferrugineus* subspecies and between the sexes, respectfully.

#### 2.4.2 Assessment of plumage

Apart from determining the differences in plumage colouration among the subspecies, we also aimed to assess the plumage variation between males and females in each of the subspecies. The method (visual examination) used was suitable according to Jessica *et al.* (2008) as the study only addressed the plumage colouration question of which the colours examined are not associated with UV colours. According to Jessica *et al.* (2008), it was suggested that there was no effect of specimen age on rust, blue, or black plumage colours but other colours showed variable effects of age including white which has significantly less susceptibility to fading. The *L. ferrugineus* complex was characterised by black, grey, rufous/rust/ochre and white plumage which are considered to be less susceptibility to fading as a result of specimen age (Jessica *et al.* 2008). Therefore, it seemed that it was ideal to use museum study skins to examine the plumage colouration of the subspecies being studied.

All the study skins could evidently be grouped as follows based on plumage colouration:

##### 2.4.2.1 Group 1: *L. f. ferrugineus*, *L. f. natalensis* and *L. f. pondoensis*

Subspecies in this group had marked sexual dichromatism, the males had a black colouration on the dorsal side while the females exhibited a grey colour. Ventrally, males had a white to buff or cream white colouration on the throat (tinged with ochre only in juvenile birds) and chest, the rust or ochre colour occurred on the belly and flanks. In contrast females generally had buff or cream white throat, chest tinged with ochre, belly with a greater degree of the ochreous colouration and the flanks had a strong ochre colour. The males and females had white wing-stripes except for *L. f. pondoensis* males and females that had a buff white wing-stripe and a buff white wing-stripe with a darker shade of the ochreous colour, respectively. There was also white patches on the inner tail coverts in both sexes although they were more prominent in males. There was a robust size dimorphism between the males and females of these subspecies with the males being larger than the females. In this

group *L. f. pondoensis* was generally seen to be the darkest morph and the females had more vigorous ochre colour on the belly and flanks.

#### 2.4.2.2 Group 2: *L. f. tongensis* and *L. f. savensis*

The subspecies *L. f. tongensis* and *L. f. savensis* were generally small in size compared to the other four. They were also similar in that the males had black upperparts and the females had grey upperparts and *L. f. tongensis* females had a tinge of the ochre colour. The underparts were different between sexes although not entirely and this resulted in weak sexual dichromatism in the two subspecies. The males had a white throat, buff breast slightly tinged with ochre while the belly and flank are ochreous although not to a large degree. The females had a buff throat and buff breast tinged with a bit of ochre and there was a slightly stronger ochreous colouration of the belly and flanks. Both males and females had a white-wing stripe and white patches at the tips of the inner tail coverts. Generally, the males were larger than the females meaning like the northern group there was strong sexual dimorphism.

#### 2.4.2.3 Overlapping subspecies: *L. f. transvaalensis*

The males of *L. f. transvaalensis* had black upperparts while the females had a grey colouration on the underparts. The subspecies exhibited a buff or cream white throat with a tinge of ochre, a buff white colouration tinged with a greater degree of ochre on the breast, the chest and belly were very ochreous particularly around the vent and flanks. Females of this subspecies were similar to the males in that both had a cream or buff white throat that had a tinge of ochre, while the breast and belly were buff with more ochreous colouration; the vent and flanks had a stronger degree of ochreous colour. Both had a white wing-stripe and white patches on the inner coverts at the tips of the tail feathers. Females were generally smaller than males and this implied the presence of size dimorphism.

#### 2.4.3 Spatial map

This study revealed certain highlights in relation to the generated species' distribution maps of subspecies boundaries, overlaps in distribution ranges among subspecies and a fair coverage of *L. f. savensis* despite the small sample size of some subspecies (*L. f. savensis* and *L. f. tongensis*). Based on the distribution map

generated (all records except NHMZ) there is evident change in the distribution ranges that is, a range shift to the interior of South Africa and reduction in the range in the southern parts of Mozambique. Although the distribution map generated from all records (including NHMZ) still needs to be reviewed before making conclusions, the current distribution map based on all assembled geo-referenced data is questionable. The custodian of SABAP2 is the University of Cape Town's Animal Demographic Unit (ADU) which has recently expanded its coverage from southern Africa, further into central and extreme northern parts of Botswana, Namibia and Mozambique (<http://sabap2.adu.org.za/>) but does not cover Zimbabwe. It could be possible that some of the NHMZ specimens may have been mislabelled. The actual examination of skins could assist in answering some of these questions.

## 2.5 Conclusion

The findings in this chapter demonstrated the possibility of two groups in *L. ferrugineus* highlighted in the morphometric results. The groups were represented by *L. f. ferrugineus* / *L. f. pondoensis* / *L. f. natalensis* (the southern group) and *L. f. tongensis* / *L. f. savensis* (the northern group). *Laniarius ferrugineus transvaalensis* consistently overlapped these two main groups.

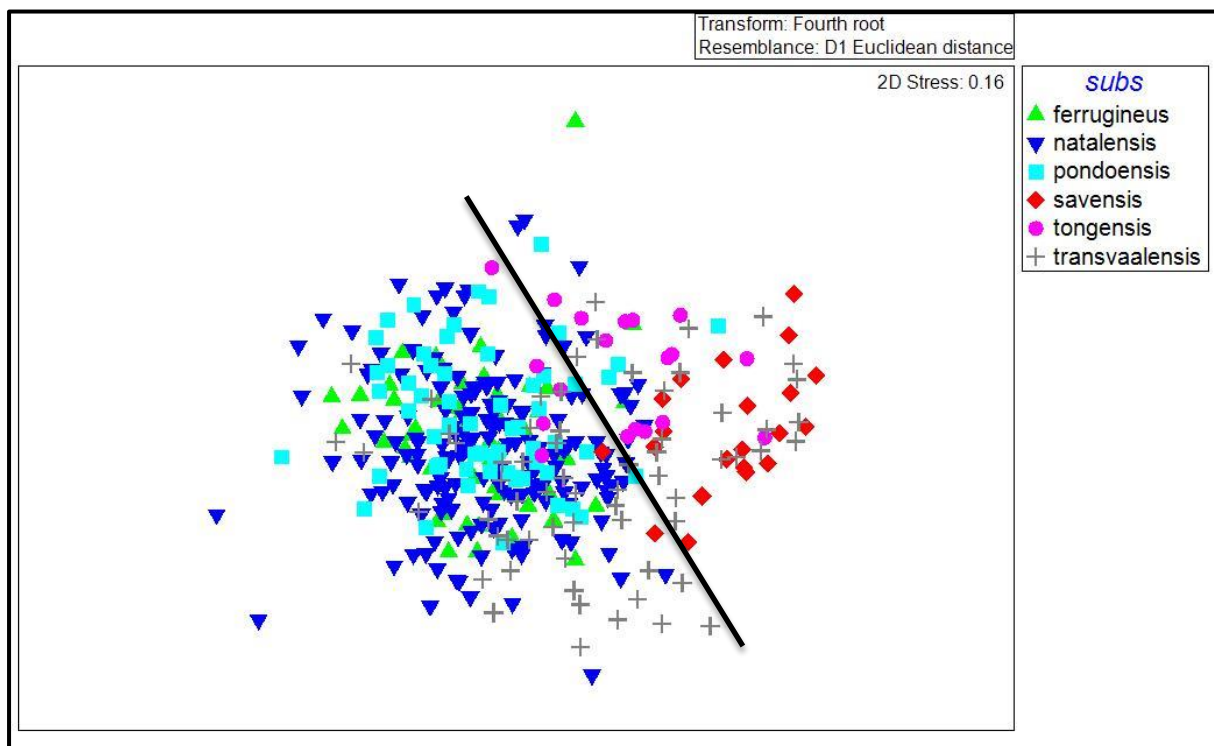
With regard to plumage, the observations made confirm that *L. f. pondoensis* is the darkest morph and this could be due to this subspecies inhabiting a unique forested habitat that forms part of the highly species-rich Maputaland – Pondoland - Albany Hotspot (Mittermeier *et al.* 2004). Despite its dark plumage, *L. f. pondoensis* still grouped with the other southern subspecies (*L. f. ferrugineus* and *L. f. natalensis*). The distribution map (one excluding the records from NHMZ) showed that there were changes in the distribution range of *L. ferrugineus* which seemed to have expanded towards the inner parts of South Africa and also contracted at the extreme southern part of Mozambique and this could be attributable to a number of factors, including habitat loss and climate change. The expansion of the range towards the interior compared to the depicted ranges in literature could be a real expansion or a result of increased sampling effort in these areas over modern times as part of southern Africa's bird atlas projects.

The morphometric study was crucial as it revealed the pattern within *L. ferrugineus* and this definitely formed a basis for the subsequent chapters in this thesis. These findings could benefit from the population genetic study in order to

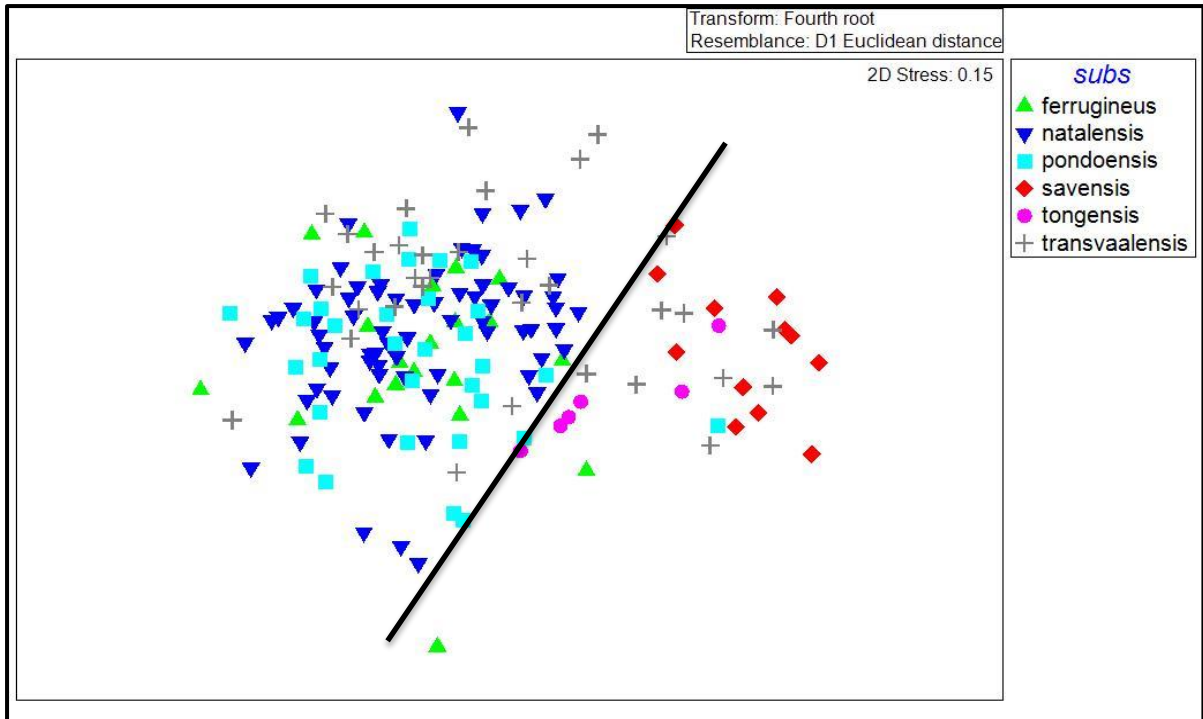
investigate the deeper phylogeographic patterns within this species and possibly investigate the phylogenetic position of the subspecies and the consistently overlapping taxon, *L. f. transvaalensis*.

At the onset of this research, one wondered what the dark plumage colouration in *L. f. pondoensis* meant. It seemed that this was as a result of the taxon inhabiting the forest habitat. Therefore, there was a need to perform the spectrophotometric analysis of plumage and it was recommended that the genetic analysis of all the subspecies be performed in order to gain further understanding of the phylogenetic position of the subspecies and the genetic diversity within *L. ferrugineus*. It was also recommended that the fine-scale analysis of the habitats where *L. ferrugineus* occurs be performed in order to understand the role played by habitat.

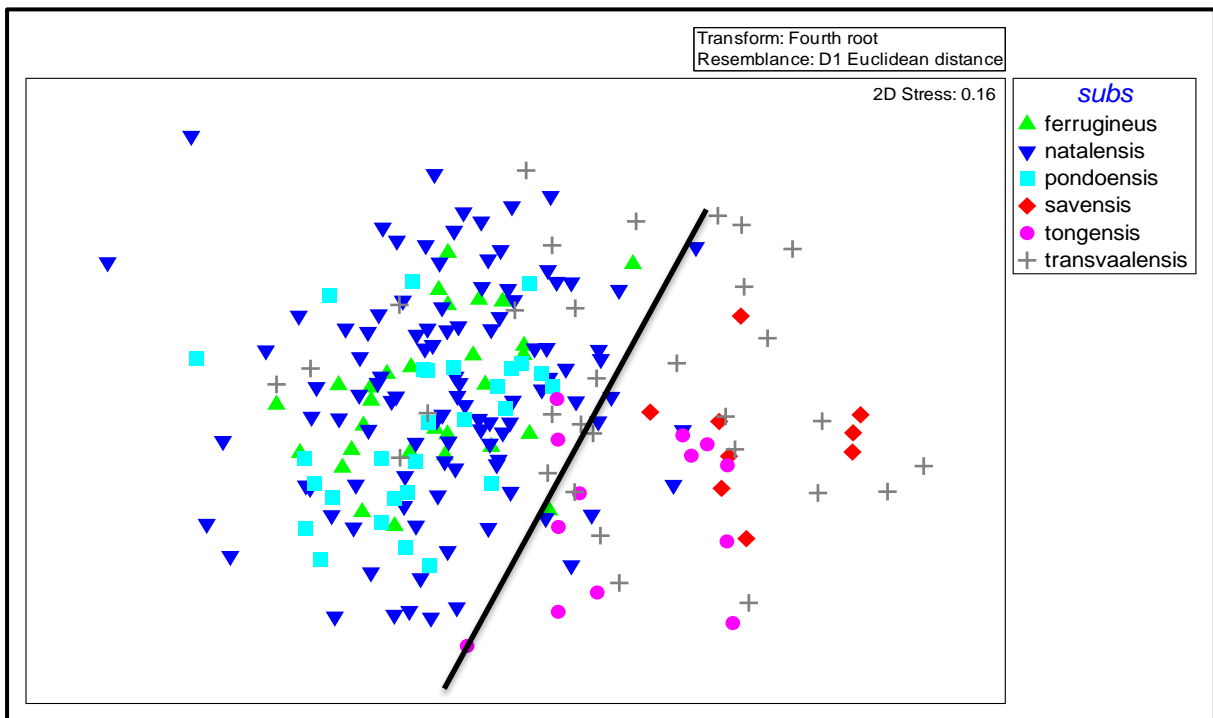
The expansion of the range map when *L. ferrugineus* study skin records from NHMZ collection were included raises some concerns. It is critical that the validity of these records be checked so that the distribution gaps of *L. ferrugineus* can be filled.



**Figure 2.1.** Multi – Dimensional Scaling (MDS) plot of combined males and females of all the *Lanarius ferrugineus* recognised subspecies excluding the two variables (total head length and total body length).

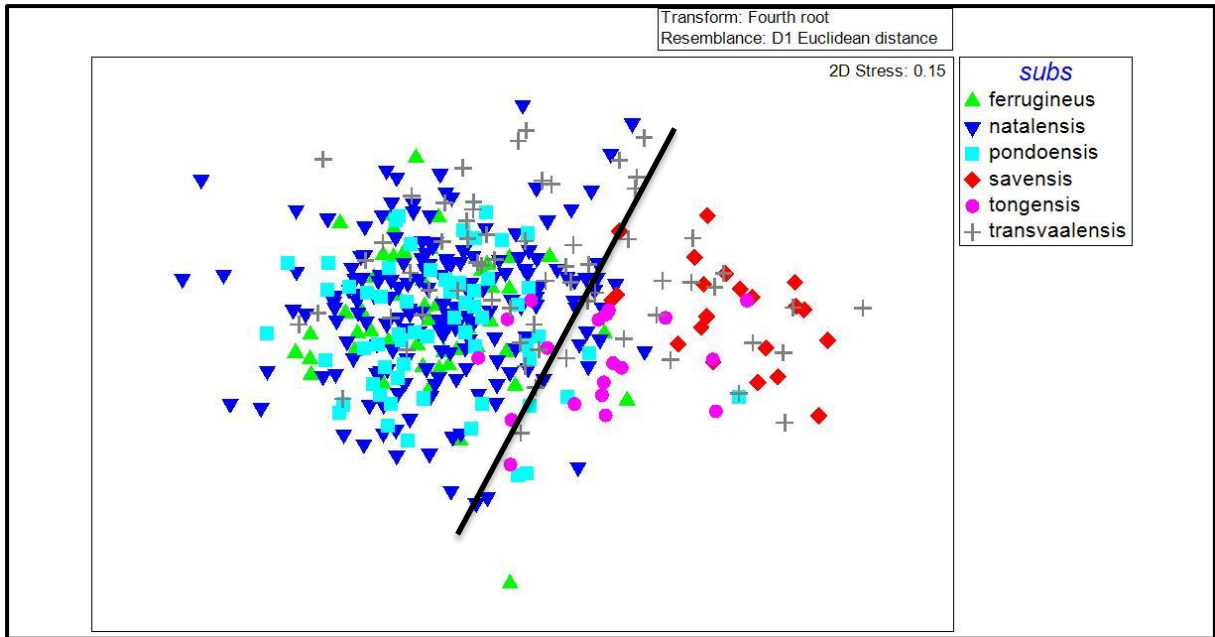


**Figure 2.2.** Multi – Dimensional Scaling (MDS) plot of females of all the *Laniarius ferrugineus* subspecies excluding the two variables (total head length and total body length).

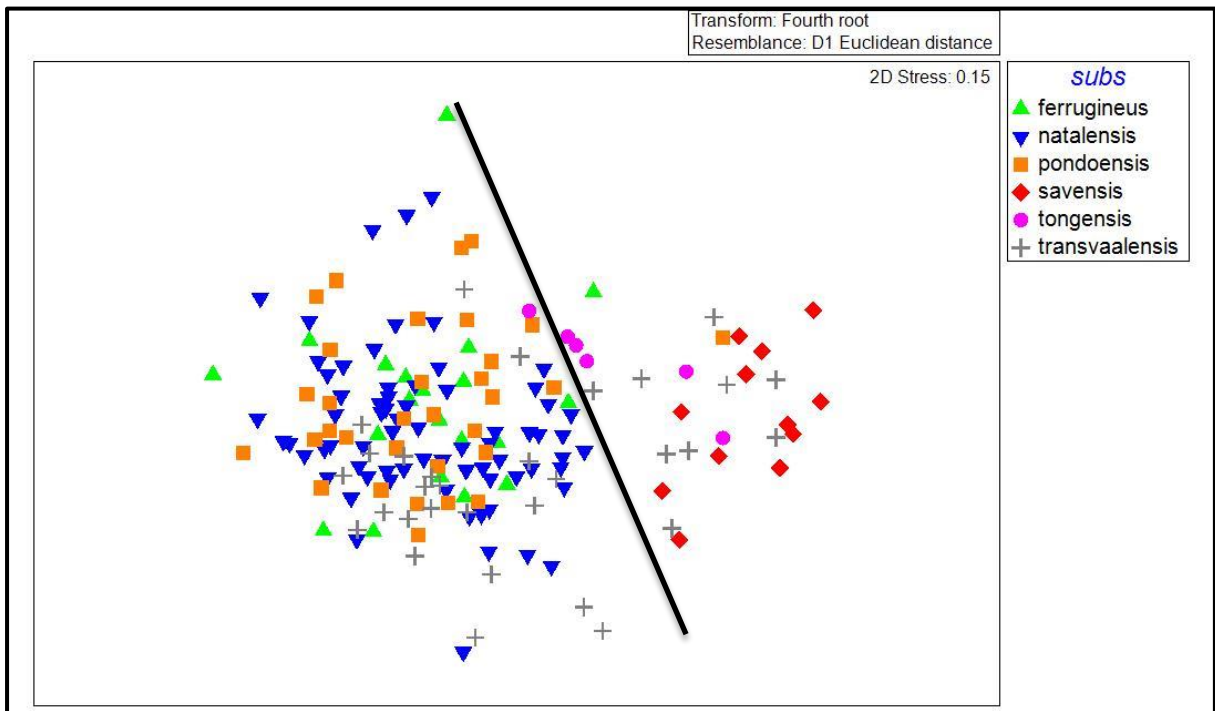


**Figure 2.3.** Multi – Dimensional Scaling (MDS) plot of males of all the *Laniarius ferrugineus* subspecies excluding the two variables (total head length and total body length).

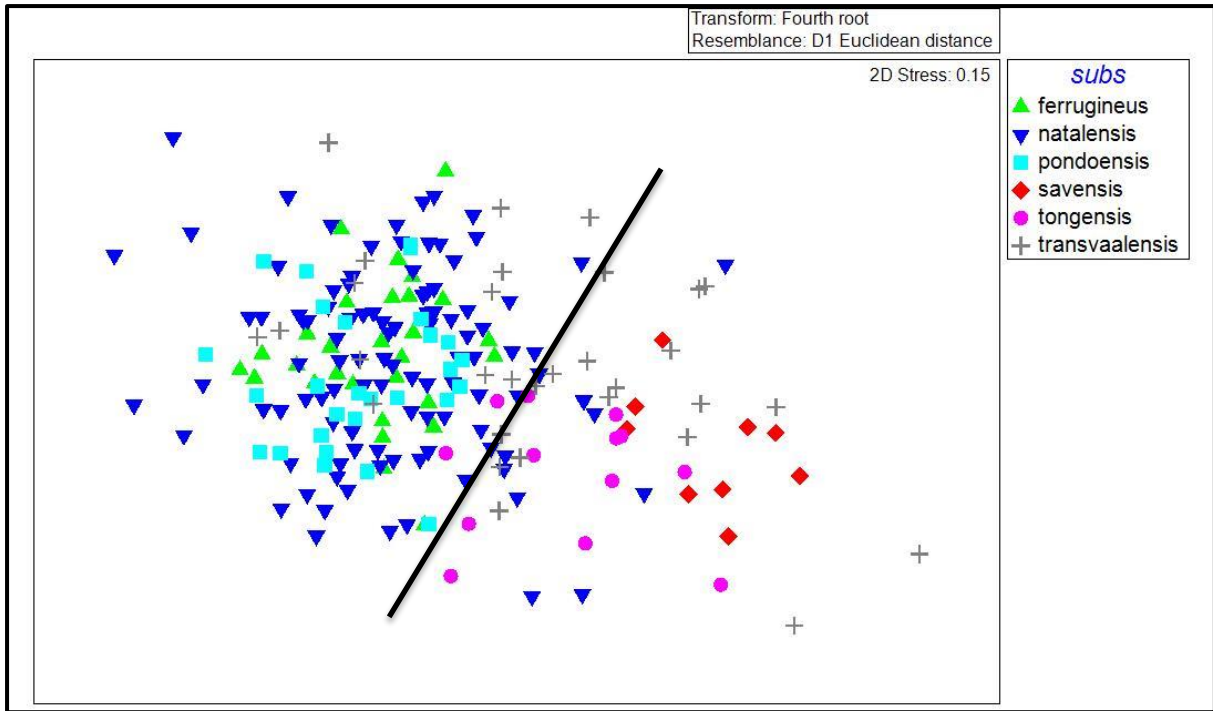




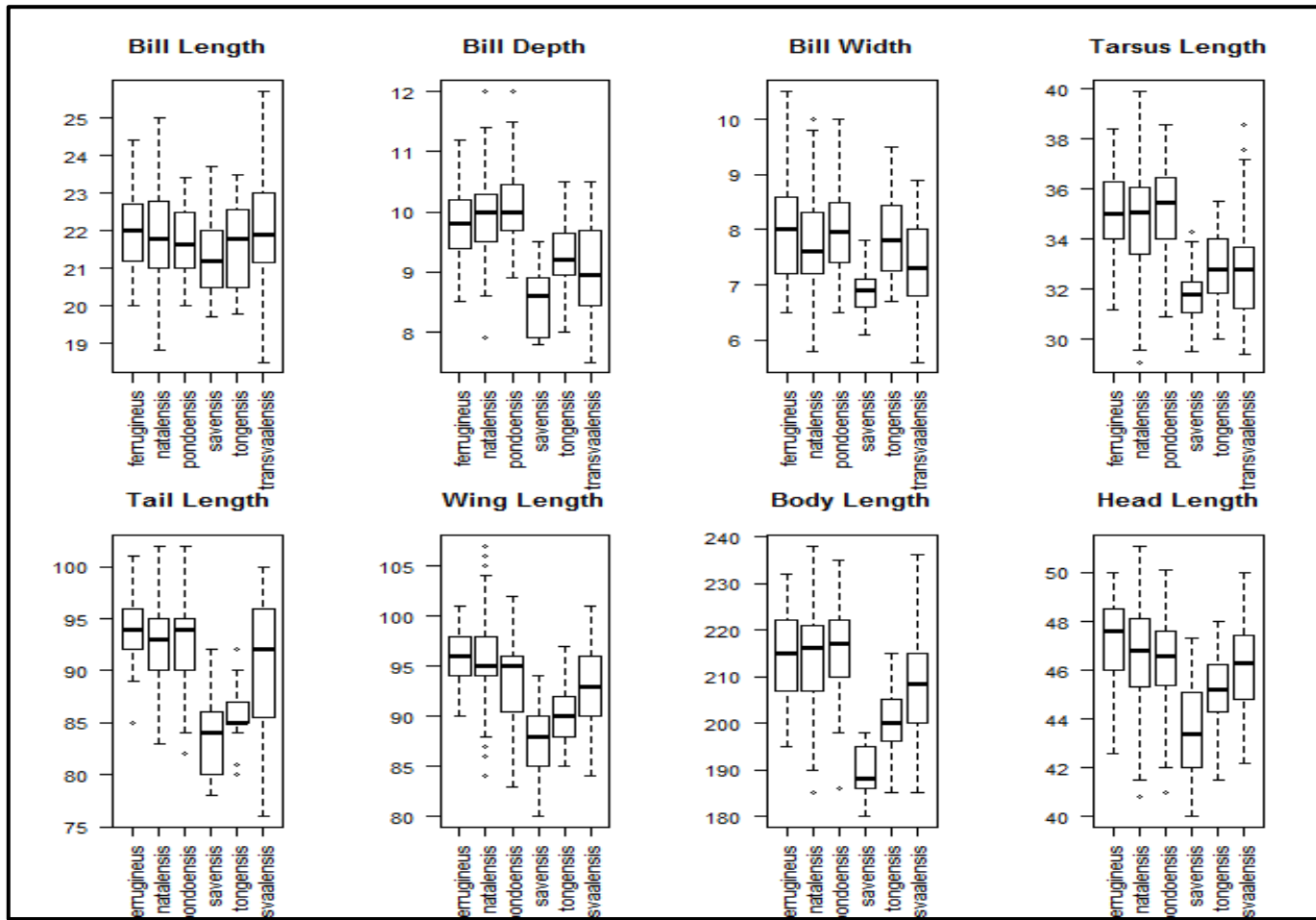
**Figure 2.4.** Multi – Dimensional Scaling (MDS) plot of combined males and females of all subspecies of *Laniarius ferrugineus* based on all the variables.



**Figure 2.5.** Multi – Dimensional Scaling (MDS) plot of females of all subspecies of *Laniarius ferrugineus* based on all variables.



**Figure 2.6.** Multi – Dimensional Scaling (MDS) plot of males of all subspecies of *Laniarius ferrugineus* based on all variables.



**Figure 2.7.** Box-and-whisker plots of combined male and female birds of all the *Laniarius ferrugineus* subspecies and all the explored variables.

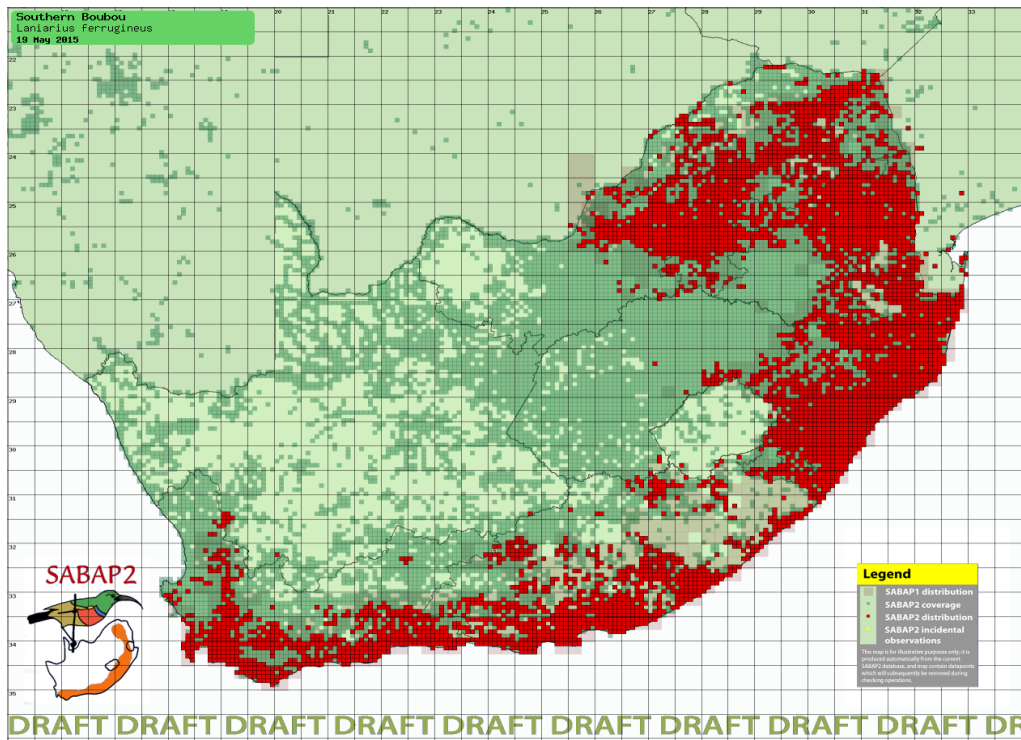


**Figure 2.8.** Ventral plumage of male birds representing the recognised subspecies of *Laniarius ferrugineus* (from left to right - *Laniarius ferrugineus ferrugineus*, *L. f. natalensis*, *L. f. pondoensis*, *L. f. transvaalensis*, *L. f. tongensis*, *L. f. savensis*) [Photo by David Allan].

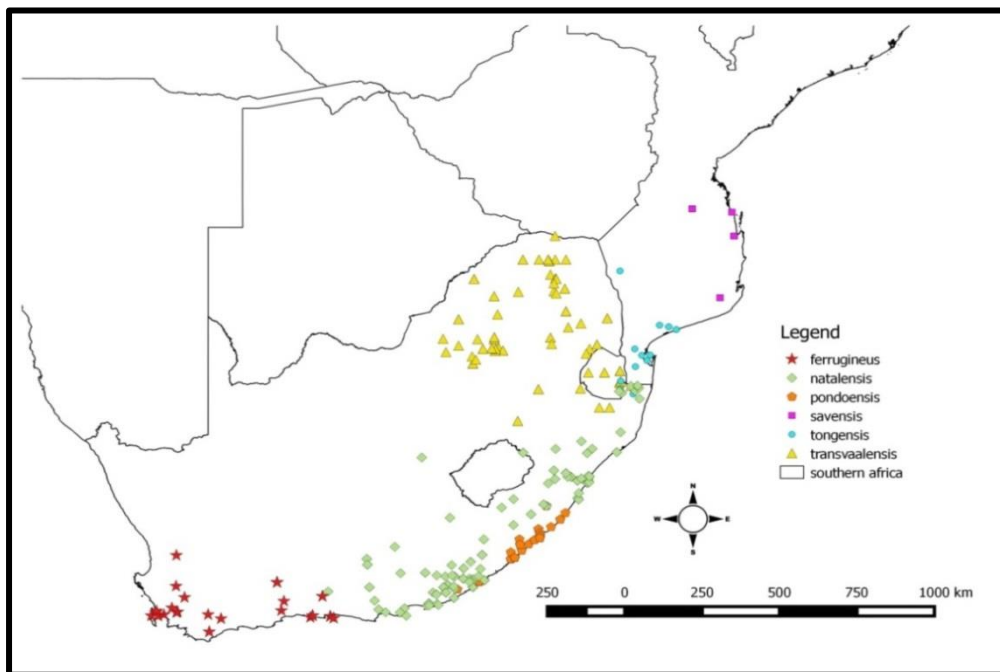




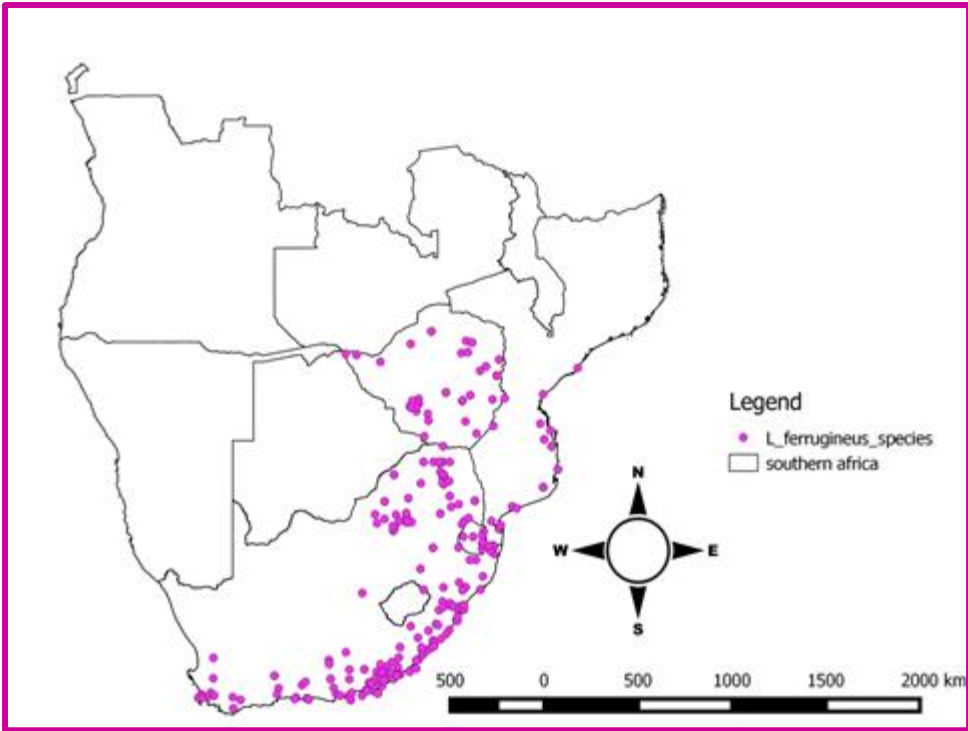
**Figure 2.9.** Ventral plumage of female birds representing the recognised subspecies of *Laniarius ferrugineus* (from left to right - *Laniarius ferrugineus ferrugineus*, *L. f. natalensis*, *L. f. pondoensis*, *L. f. transvaalensis*, *L. f. tongensis*, *L. f. savensis*) [Photo by David Allan].



**Figure 2.10.** Southern African Bird Atlasing Project 2 (SABAP2) distribution map of *Laniarius ferrugineus* (accessed November 2017).



**Figure 2.11.** Distribution map of *Laniarius ferrugineus* generated from all georeferenced records excluding those from the Natural History Museum of Zimbabwe (NHMZ).



**Figure 2.12.** Distribution map of *Laniarius ferrugineus* generated from all geo-referenced data of all records including the Natural History Museum of Zimbabwe (NHMZ).

## APPENDICES

**Appendix 2.1.** List of individual bird study skins examined for morphometric analyses performed in this study.

Taxon name	Museum no.	Country	Province	Locality	Age	Bill length (mm)	Bill length (mm)	Bill depth (mm)	Wing length (mm)	Tail length (mm)	Tarsus length (mm)	Total body length (mm)	Total head length (mm)
<i>Laniarius ferrugineus ferrugineus</i>	MNHN ZO 1839-9907	South Africa	western Cape	Cape Town	Adult	22.6	8.2	9.6	95	87	35.7	215	49.7
<i>Laniarius ferrugineus ferrugineus</i>	MNHN ZO 1839-9908	South Africa	Limpopo	Ntafufu river	Adult	22.5	9	10.3	90	95	33.6	200	46.3
<i>Laniarius ferrugineus ferrugineus</i>	DM 26080	South Africa	Eastern Cape	Patensie, Ferndale	Adult	22.1	7.2	8.9	95	34	33.6	205	49.3
<i>Laniarius ferrugineus ferrugineus</i>	DM 26081	South Africa	Eastern Cape	Patensie, Ferndale	Adult	22.2	7.1	9.6	96	80	36.2	195	47.8
<i>Laniarius ferrugineus ferrugineus</i>	DM 7321	South Africa	Eastern Cape	Fish River Mouth	Adult	22.6	7.5	8.9	99	92	35.8	206	48.6
<i>Laniarius ferrugineus ferrugineus</i>	DM 7322	South Africa	Eastern Cape	Fish River Mouth	Adult	22.8	7.4	8.8	100	95	35.8	215	47.8
<i>Laniarius ferrugineus ferrugineus</i>	DM 7324	South Africa	Eastern Cape	Fish River Mouth	Adult	22.9	8.4	9.4	98	98	34.4	215	48.4
<i>Laniarius ferrugineus ferrugineus</i>	DM 7325	South Africa	Eastern Cape	Fish River Mouth	Adult	20.8	6.5	9.4	93	92	33.3	205	45.5
<i>Laniarius ferrugineus ferrugineus</i>	DM 7326	South Africa	Eastern Cape	Fish River Mouth	Adult	20.3	7.3	9.1	91	85	34.9	199	44.3
<i>Laniarius ferrugineus ferrugineus</i>	DM 7327	South Africa	Eastern Cape	Committees Drift, Albany	Adult	22	7.1	9.3	99	101	35.8	219	47.3
<i>Laniarius ferrugineus ferrugineus</i>	DM 7328	South Africa	Eastern Cape	Committees Drift, Albany	Adult	21.8	7.1	9.7	101	95	37.6	215	48
<i>Laniarius ferrugineus ferrugineus</i>	DM 7329	South Africa	Eastern Cape	Committees Drift, Albany	Adult	22.6	7.6	8.8	98	92	36.3	205	47.5
<i>Laniarius ferrugineus ferrugineus</i>	DM 7330	South Africa	Eastern Cape	Committees Drift, Albany	Adult	20.8	7.1	9.7	97	95	33.1	210	45.6
<i>Laniarius ferrugineus ferrugineus</i>	DM 7331	South Africa	Western Cape	Clanwilliam, Pakhuis	Adult	23	8.7	9.8	95	94	36.2	220	48.3
<i>Laniarius ferrugineus ferrugineus</i>	ELM 1020	South Africa	Eastern Cape	Breakfast Vlei dist	Adult	22	8.9	10.6	90	96	35	210	46.8
<i>Laniarius ferrugineus ferrugineus</i>	ELM 11555	South Africa	Western Cape	Nature's valley dist	Adult	22	9	9.2	95	94	34.6	212	44.6
<i>Laniarius ferrugineus ferrugineus</i>	ELM 11559	South Africa	Western Cape	Nature's valley dist	Adult	23.1	8.9	9.9	97	95	37.5	220	48.8
<i>Laniarius ferrugineus ferrugineus</i>	ELM 11566	South Africa	Western Cape	Nature's valley dist	Adult	21.2	8.2	10.5	100	96	38	215	46.6
<i>Laniarius ferrugineus ferrugineus</i>	ELM 11583	South Africa	Western Cape	Knysna dist	Adult	21.3	8.5	9.5	92	90	34	207	44.9
<i>Laniarius ferrugineus ferrugineus</i>	ELM 11587	South Africa	Western Cape	Knysna dist	Adult	22.1	7.5	9.5	90	91	36.5	218	45.5
<i>Laniarius ferrugineus ferrugineus</i>	ELM 11631	South Africa	Western Cape	Knysna dist	Adult	24.4	9.1	10.4	97	98	37.8	215	50
<i>Laniarius ferrugineus ferrugineus</i>	ELM 11810	South Africa	Western Cape	Tsholweni e-dist	Adult	21	8	9	94	95	36.2	205	46
<i>Laniarius ferrugineus ferrugineus</i>	ELM 11822	South Africa	Western Cape	Tsholweni e-dist	Adult	22.2	7.9	9.7	93	96	33.9	220	43.8
<i>Laniarius ferrugineus ferrugineus</i>	ELM 11862	South Africa	Western Cape	Tsholweni e-dist	Adult	23.1	8.9	10.8	95	98	37.6	230	49
<i>Laniarius ferrugineus ferrugineus</i>	ELM 11875	South Africa	Western Cape	Tsholweni e-dist	Adult	22.5	7.7	10.1	92	92	33.7	225	47.6
<i>Laniarius ferrugineus ferrugineus</i>	ELM 11876	South Africa	Western Cape	Tsholweni e-dist	Adult	22	7.4	10.2	100	93	35	215	49.2
<i>Laniarius ferrugineus ferrugineus</i>	ELM 11877	South Africa	Western Cape	Tsholweni e-dist	Adult	22.7	8.7	10	96	94	33.4	218	42.6
<i>Laniarius ferrugineus ferrugineus</i>	ELM 12576	South Africa	Eastern Cape	Goodhope	Adult	21.1	8.8	9.6	101	95	34.8	225	49
<i>Laniarius ferrugineus ferrugineus</i>	ELM 18248	South Africa	Western Cape	Pakhuis Pass dist	Adult	23.6	7	10	96	98	35	232	50



Taxon name	Museum no.	Country	Province	Locality	Age	Bill length (mm)	Bill length (mm)	Bill depth (mm)	Wing length (mm)	Tail length (mm)	Tarsus length (mm)	Total body length (mm)	Total head length (mm)
<i>Laniarius ferrugineus ferrugineus</i>	ELM 3719	South Africa	Western Cape	Georgida	Adult	22	8	10.2	98	90	36.7	207	50
<i>Laniarius ferrugineus ferrugineus</i>	ELM 3720	South Africa	Western Cape	Georgida	Adult	21	7	10	95	89	34.1	202	47.6
<i>Laniarius ferrugineus ferrugineus</i>	ELM 5437	South Africa	Western Cape	Knysna dist	Adult	22	8.4	10.5	92	100	33.7	212	45.8
<i>Laniarius ferrugineus ferrugineus</i>	ELM 5450	South Africa	Western Cape	Knysna dist	Adult	22.7	7	10.2	100	95	36.7	219	48.1
<i>Laniarius ferrugineus ferrugineus</i>	MNHN 176	South Africa	Western Cape	Cape Town	Adult	21.8	8.1	10.8	91	85	34.4	256	49.9
<i>Laniarius ferrugineus ferrugineus</i>	SAM 20122	South Africa	Western Cape	Cape Town	Adult	24.1	8.6	10.2	96	90	38.4	200	46.2
<i>Laniarius ferrugineus ferrugineus</i>	SAM 20624	South Africa	Free States	Lindesthof, Bloemfontein	Adult	25	8.3	9.5	94	95	32	220	48
<i>Laniarius ferrugineus ferrugineus</i>	SAM 53845	South Africa	Western Cape	Eerste river	Adult	21.8	9.2	10.4	100	100	36.1	223	48.1
<i>Laniarius ferrugineus ferrugineus</i>	SAM 58449	South Africa	Western Cape	Kirstenbosch	Adult	21.8	10.5	8.5	80	90	34.4	215	45.7
<i>Laniarius ferrugineus ferrugineus</i>	TM 10966	South Africa	Western Cape	Cape Town	Adult	22.8	8	11.2	97	97	35	222	47.7
<i>Laniarius ferrugineus ferrugineus</i>	TM 17202	South Africa	Eastern Cape	Grahamstown	Adult	22.7	8	10.4	100	96	36.7	200	46.6
<i>Laniarius ferrugineus ferrugineus</i>	TM 17203	South Africa	Eastern Cape	Grahamstown	Adult	20.1	8.4	10.2	92	93	35.5	198	46.5
<i>Laniarius ferrugineus ferrugineus</i>	TM 2330	South Africa	Western Cape	Knysna	Adult	23.1	8.8	10.7	96	94	37.7	232	48.1
<i>Laniarius ferrugineus ferrugineus</i>	TM 24549	South Africa	Western Cape	LaMatte, Cape town	Adult	20	8	9.6	90	91	35	217	46.2
<i>Laniarius ferrugineus ferrugineus</i>	TM 24550	South Africa	Western Cape	LaMatte, Cape town	Adult	20.8	8.2	10.1	96	92	33.6	220	47.6
<i>Laniarius ferrugineus ferrugineus</i>	TM 24552	South Africa	Western Cape	Knysna	Adult	21	8	10.2	94	95	36.3	231	43.5
<i>Laniarius ferrugineus ferrugineus</i>	TM 24553	South Africa	Western Cape	Cape Town	Adult	23.7	8.8	10.3	94	89	34	225	48.6
<i>Laniarius ferrugineus ferrugineus</i>	TM 24554	South Africa	Western Cape	Cape Town	Adult	20.3	6.9	9.7	94	90	35.5	210	46.3
<i>Laniarius ferrugineus ferrugineus</i>	TM 24561	South Africa	Western Cape	Cape Town	Adult	21.1	7.5	10.5	96	94	34.2	230	48.5
<i>Laniarius ferrugineus ferrugineus</i>	TM 3426	South Africa	Western Cape	Albany, c.c	Adult	21.7	6.8	8.9	97	96	31.2	232	47.9
<i>Laniarius ferrugineus ferrugineus</i>	TM 43994	South Africa	Kwa-Zulu Natal	Maritzburg, Natal	Adult	21.6	8.5	9.9	95	90	34.6	215	44.6
<i>Laniarius ferrugineus ferrugineus</i>	TM 5574	South Africa	Western Cape	Knysna, c.c	Adult	22.2	7.1	9.3	94	100	33.6	227	48.8
<i>Laniarius ferrugineus ferrugineus</i>	TM 80647	South Africa	Western Cape	Mossel Bay dist, Western Cape	Adult	22.5	6.8	9.3	95	95	32.8	224	48.9
<i>Laniarius ferrugineus natalensis</i>	MNHN ZO 2000-1688	South Africa	Kwa-Zulu Natal	Natal	Adult	23.9	8	9	94	95	36.1	225	48
<i>Laniarius ferrugineus natalensis</i>	MNHN ZO 2015-431	South Africa	Eastern Cape	Doodsklip Camp, Baviaanskloof Nature Reserve	Adult	22.1	7.1	9.9	92	87	34.4	197	47.8
<i>Laniarius ferrugineus natalensis</i>	MNHN ZO 2015-432	South Africa	Eastern Cape	close to Research Center, Great Fish Nature Reserve	Adult	24.4	7.2	10.5	98	96	38	190	58.8
<i>Laniarius ferrugineus natalensis</i>	MNHN ZO 2015-433	South Africa	Eastern Cape	close to Research Center, Great Fish Nature Reserve	Adult	23	7.2	9	94	92	34.6	215	47.5
<i>Laniarius ferrugineus natalensis</i>	MNHN ZO 2015-434	South Africa	Eastern Cape	Fort Fordyce, close to Mpofu Nature Reserve	Adult	22	5.8	9	90	87	36.2	195	47
<i>Laniarius ferrugineus natalensis</i>	MNHN ZO 2015-430	South Africa	Eastern Cape	Hunter's Lodge, 12 kms from Kenton on Sea towards Alexandria on R72, Cacadu District	Adult	21.7	7.1	10.2	98	85	35.5	198	46.8
<i>Laniarius ferrugineus natalensis</i>	MNHN ZO 2015-435	South Africa	Eastern Cape	Shamwari Game Reserve, 10 kms SE of Paterson, Cacadu District	Adult	22.9	7.5	10	97	56	36	211	47.8
<i>Laniarius ferrugineus natalensis</i>	MNHN ZO 2015-436	South Africa	Eastern Cape	Shamwari Game Reserve, 10 kms SE of Paterson, Cacadu District	Adult	22	7.1	9.1	96	95	38.1	220	50
<i>Laniarius ferrugineus natalensis</i>	DM 15929	South Africa	Kwa-Zulu Natal	Durban, Umhlanga Rocks	Adult	21.5	7.1	9.3	92	86	32.1	204	46.8
<i>Laniarius ferrugineus natalensis</i>	DM 16308	South Africa	Kwa-Zulu Natal	Durban, Shongweni Dam	Adult	22.9	7.4	10.1	90	94	33.4	204	49
<i>Laniarius ferrugineus natalensis</i>	DM 16309	South Africa	Kwa-Zulu Natal	Durban, Shongweni Dam	Adult	23.6	7.2	10.2	97	90	33.1	205	49

Taxon name	Museum no.	Country	Province	Locality	Age	Bill length (mm)	Bill length (mm)	Bill depth (mm)	Wing length (mm)	Tail length (mm)	Tarsus length (mm)	Total body length (mm)	Total head length (mm)
<i>Laniarius ferrugineus natalensis</i>	DM 17597	South Africa	Kwa-Zulu Natal	Durban, Umhlanga River	Adult	21.1	6.7	9.7	91	90	33.1	195	49.1
<i>Laniarius ferrugineus natalensis</i>	DM 18379	South Africa	Kwa-Zulu Natal	Durban, Umhlanga River	Adult	21.3	7.3	8.6	93	89	33.8	195	47.7
<i>Laniarius ferrugineus natalensis</i>	DM 18675	South Africa	Kwa-Zulu Natal	Durban, Umhlanga River	Adult	22.5	7.8	9.8	96	90	36.7	213	47.5
<i>Laniarius ferrugineus natalensis</i>	DM 18803	South Africa	Eastern Cape	Stutterheim, Bolo Bridge	Adult	21.5	7	8.9	98	94	35.7	201	44.8
<i>Laniarius ferrugineus natalensis</i>	DM 18804	South Africa	Eastern Cape	Stutterheim, Bolo Bridge	Adult	21.4	7.3	9.7	106	96	35.4	222	48.2
<i>Laniarius ferrugineus natalensis</i>	DM 18805	South Africa	Eastern Cape	Stutterheim, Bolo Bridge	Adult	18.8	6.7	9	98	100	29.6	212	43.8
<i>Laniarius ferrugineus natalensis</i>	DM 18806	South Africa	Eastern Cape	Stutterheim, Bolo Bridge	Adult	21.5	7.1	9.5	101	95	34.1	210	46.9
<i>Laniarius ferrugineus natalensis</i>	DM 18808	South Africa	Eastern Cape	King William's Town	Adult	22.3	7.2	9.2	106	95	35.8	220	47.1
<i>Laniarius ferrugineus natalensis</i>	DM 18809	South Africa	Eastern Cape	King William's Town	Adult	19.1	7.1	9.4	95	90	33.3	215	45.8
<i>Laniarius ferrugineus natalensis</i>	DM 18814	South Africa	Eastern Cape	King William's Town	Adult	20.8	5.8	9.7	95	90	34.8	210	47.3
<i>Laniarius ferrugineus natalensis</i>	DM 18815	South Africa	Eastern Cape	King William's Town	Adult	21	6.4	10.2	102	100	36.2	215	46.8
<i>Laniarius ferrugineus natalensis</i>	DM 18816	South Africa	Eastern Cape	King William's Town	Adult	21	7.5	9	100	97	34	218	46.2
<i>Laniarius ferrugineus natalensis</i>	DM 18817	South Africa	Eastern Cape	King William's Town	Adult	22.7	6.6	8.9	94	92	32.4	210	47.6
<i>Laniarius ferrugineus natalensis</i>	DM 18818	South Africa	Eastern Cape	King William's Town	Adult	24.4	6.6	9.4	100	98	35.1	218	51.1
<i>Laniarius ferrugineus natalensis</i>	DM 18819	South Africa	Eastern Cape	King William's Town	Adult	22.7	7.1	9.1	105	97	34.5	215	47.2
<i>Laniarius ferrugineus natalensis</i>	DM 18820	South Africa	Eastern Cape	King William's Town	Adult	22.5	7.4	9.4	101	96	36.8	210	47.8
<i>Laniarius ferrugineus natalensis</i>	DM 18821	South Africa	Eastern Cape	King William's Town	Adult	21	7.3	8.7	101	97	35.5	213	49.3
<i>Laniarius ferrugineus natalensis</i>	DM 19016	South Africa	Kwa-Zulu Natal	Durban, Shongweni Dam	Adult	20.3	7	10.1	93	95	34.2	210	45.5
<i>Laniarius ferrugineus natalensis</i>	DM 19571	South Africa	Kwa-Zulu Natal	Nkandhla Forest	Adult	20	7.2	9.7	97	87	31.4	197	43.8
<i>Laniarius ferrugineus natalensis</i>	DM 19572	South Africa	Kwa-Zulu Natal	Ngoye Forest	Adult	22.6	7.4	9.4	90	92	33.3	209	44.56
<i>Laniarius ferrugineus natalensis</i>	DM 19574	South Africa	Kwa-Zulu Natal	Ngoye Forest	Adult	24.1	7.1	10.2	95	95	36.8	207	47.8
<i>Laniarius ferrugineus natalensis</i>	DM 19575	South Africa	Kwa-Zulu Natal	Qudeni Forest	Adult	20.5	7.6	9.8	97	92	29.1	201	48.6
<i>Laniarius ferrugineus natalensis</i>	DM 21162	South Africa	Kwa-Zulu Natal	Pietermaritzburg	Adult	22.9	7	8.8	90	91	32.3	200	43.9
<i>Laniarius ferrugineus natalensis</i>	DM 21370	South Africa	Kwa-Zulu Natal	Durban, Umhlanga River	Adult	20.5	7.9	9.6	90	88	31	209	41.5
<i>Laniarius ferrugineus natalensis</i>	DM 23192	South Africa	Kwa-Zulu Natal	Durban, Shongweni Dam	Adult	22.8	7.9	10.3	100	87	35	203	46.7
<i>Laniarius ferrugineus natalensis</i>	DM 28148	South Africa	Kwa-Zulu Natal	Manderston	Adult	20.6	7.1	9.7	86	90	32.2	200	47
<i>Laniarius ferrugineus natalensis</i>	DM 30216	South Africa	Kwa-Zulu Natal	Manderston	Adult	22.1	6.7	9.6	95	89	36.5	196	43.9
<i>Laniarius ferrugineus natalensis</i>	DM 33573	South Africa	Kwa-Zulu Natal	Umkomaas	Adult	23.2	7.8	9.5	95	90	35.5	215	49.3
<i>Laniarius ferrugineus natalensis</i>	DM 33574	South Africa	Kwa-Zulu Natal	Margate	Adult	21	6.7	10	95	90	32.9	208	46.7
<i>Laniarius ferrugineus natalensis</i>	DM 33894	South Africa	Kwa-Zulu Natal	Durban area	Adult	22.2	7.5	9.1	99	96	35.1	204	48.5
<i>Laniarius ferrugineus natalensis</i>	DM 33895	South Africa	Kwa-Zulu Natal	Durban	Adult	21.6	7.2	8.7	95	90	32.5	200	46.4
<i>Laniarius ferrugineus natalensis</i>	DM 33896	South Africa	Kwa-Zulu Natal	Durban	Adult	20	7.5	9.3	90	84	33.8	207	45.5
<i>Laniarius ferrugineus natalensis</i>	DM 37385	South Africa	Kwa-Zulu Natal	Durban, Bluff, Wentworth forest	Adult	20.4	7.8	9.8	93	90	33	191	44.9
<i>Laniarius ferrugineus natalensis</i>	DM 37395	South Africa	Kwa-Zulu Natal	Durban, Bluff, Wentworth forest	Adult	22	7.1	10.5	95	98	31.6	180	47.9
<i>Laniarius ferrugineus natalensis</i>	DM 37397	South Africa	Kwa-Zulu Natal	Durban, Bluff, Wentworth forest	Adult	21.4	7.1	9.3	93	83	35.7	190	48.1
<i>Laniarius ferrugineus natalensis</i>	DM 37398	South Africa	Kwa-Zulu Natal	Durban, Bluff, Wentworth forest	Adult	22.9	8.1	11	91	93	35.7	185	46
<i>Laniarius ferrugineus natalensis</i>	DM 37400	South Africa	Kwa-Zulu Natal	Durban, Bluff, Wentworth forest	Adult	21.7	7.2	9.1	92	93	34.5	200	47.8
<i>Laniarius ferrugineus natalensis</i>	DM 5854	South Africa	Kwa-Zulu Natal	Pietermaritzburg, Table Mountain	Adult	22.4	6.9	9.4	98	89	33.7	205	46
<i>Laniarius ferrugineus natalensis</i>	DM 5855	South Africa	Kwa-Zulu Natal	Pietermaritzburg, Table Mountain	Adult	23	7	9.7	98	91	34.7	217	48.6
<i>Laniarius ferrugineus natalensis</i>	DM 5856	South Africa	Kwa-Zulu Natal	Pietermaritzburg, Table Mountain	Adult	21.2	6.2	7.9	95	92	32.5	206	45.5
<i>Laniarius ferrugineus natalensis</i>	DM 5858	South Africa	Kwa-Zulu Natal	Pietermaritzburg, Table Mountain	Adult	23.5	7.6	10.5	94	94	33.1	206	45.2

Taxon name	Museum no.	Country	Province	Locality	Age	Bill length (mm)	Bill length (mm)	Bill depth (mm)	Wing length (mm)	Tail length (mm)	Tarsus length (mm)	Total body length (mm)	Total head length (mm)
<i>Laniarius ferrugineus natalensis</i>	DM 5860	South Africa	Kwa-Zulu Natal	Weza-Ingeli Forest	Adult	21.5	7.7	9.9	100	91	36.5	205	48
<i>Laniarius ferrugineus natalensis</i>	DM 7348	South Africa	Kwa-Zulu Natal	Durban, Reunion Rocks	Adult	21.2	7.2	9.1	97	87	35.7	204	48.5
<i>Laniarius ferrugineus natalensis</i>	DM 7351	South Africa	Kwa-Zulu Natal	Camperdown, Near	Adult	22.3	7.1	9.1	98	97	38.4	217	47.8
<i>Laniarius ferrugineus natalensis</i>	DM 7352	South Africa	Kwa-Zulu Natal	Durban, Shongweni Dam	Adult	22.6	6.4	10.1	98	91	36.1	211	45.1
<i>Laniarius ferrugineus natalensis</i>	DM 7353	South Africa	Kwa-Zulu Natal	Durban, Shongweni Dam	Adult	201.3	6.9	8.9	94	91	32.7	212	44.7
<i>Laniarius ferrugineus natalensis</i>	DM 7357	South Africa	Kwa-Zulu Natal	Pietermaritzburg, Near	Adult	21	7.9	10.2	99	90	34.5	218	45.5
<i>Laniarius ferrugineus natalensis</i>	DM 7360	South Africa	Kwa-Zulu Natal	Scottburgh, Mpambanyoni River	Adult	20.9	8	10.2	95	90	33.5	218	46.3
<i>Laniarius ferrugineus natalensis</i>	DM 7361	South Africa	Kwa-Zulu Natal	Scottburgh, Mpambanyoni River	Adult	22.1	8.5	10.3	98	90	35	210	47.9
<i>Laniarius ferrugineus natalensis</i>	DM 7365	South Africa	Kwa-Zulu Natal	Durban, Reunion Rocks	Adult	21.5	7.2	8.6	92	92	32.1	204	47.2
<i>Laniarius ferrugineus natalensis</i>	DM 7366	South Africa	Kwa-Zulu Natal	Pietermaritzburg, Table Mountain	Adult	22.5	8.4	10	90	90	32.6	220	45.6
<i>Laniarius ferrugineus natalensis</i>	ELM 10022	South Africa	Eastern Cape	Gonubie dist	Adult	21.7	8.4	10	96	100	35.1	228	49.5
<i>Laniarius ferrugineus natalensis</i>	ELM 10578	South Africa	Eastern Cape	Alexandria dist	Adult	23	8.6	9.5	100	95	35.5	230	48.1
<i>Laniarius ferrugineus natalensis</i>	ELM 10590	South Africa	Eastern Cape	Alexandria dist	Adult	22.5	8	21.9	95	90	35.5	232	48.5
<i>Laniarius ferrugineus natalensis</i>	ELM 10626	South Africa	Eastern Cape	Alexandria dist	Adult	23.4	8	9.8	97	94	35	230	50.1
<i>Laniarius ferrugineus natalensis</i>	ELM 10627	South Africa	Eastern Cape	Alexandria dist	Adult	23	8.4	10	93	90	35.8	225	46
<i>Laniarius ferrugineus natalensis</i>	ELM 10646	South Africa	Eastern Cape	Alexandria dist	Adult	22.9	7.2	10	84	91	35.8	230	46.6
<i>Laniarius ferrugineus natalensis</i>	ELM 1091	South Africa	Eastern Cape	Loerie dist	Adult	23	7.5	10.5	100	90	36.1	218	49.8
<i>Laniarius ferrugineus natalensis</i>	ELM 11049	South Africa	Eastern Cape	Debe Nek dist	Adult	21.8	8.4	9.8	95	90	37	225	47.7
<i>Laniarius ferrugineus natalensis</i>	ELM 11152	South Africa	Eastern Cape	Debe Nek dist	Adult	22.8	8	9.4	100	98	37.9	232	50.5
<i>Laniarius ferrugineus natalensis</i>	ELM 11180	South Africa	Eastern Cape	Bolo dist	Adult	19.8	9.5	10	100	87	30.6	216	43.1
<i>Laniarius ferrugineus natalensis</i>	ELM 11192	South Africa	Eastern Cape	Bolo dist	Adult	21	9	9.8	103	95	35	230	48.5
<i>Laniarius ferrugineus natalensis</i>	ELM 11246	South Africa	Eastern Cape	Bolo dist	Adult	21.7	7.5	10.6	95	97	37.7	209	48.1
<i>Laniarius ferrugineus natalensis</i>	ELM 11678	South Africa	Western Cape	Knysna dist	Adult	24.8	7.7	11	95	98	35	215	48.7
<i>Laniarius ferrugineus natalensis</i>	ELM 11925	South Africa	Eastern Cape	Willowmore dist	Adult	21	7.5	9.5	92	90	31.4	200	44.5
<i>Laniarius ferrugineus natalensis</i>	ELM 12262	South Africa	Eastern Cape	Port St. Johns dist	Adult	21.4	7.5	10.5	95	90	35.5	215	43
<i>Laniarius ferrugineus natalensis</i>	ELM 12263	South Africa	Eastern Cape	Port St. Johns dist	Adult	23	7.5	11	100	95	34.4	222	45.3
<i>Laniarius ferrugineus natalensis</i>	ELM 12287	South Africa	Eastern Cape	Needs Camp	Adult	24.5	8	10.5	97	94	39	215	47.5
<i>Laniarius ferrugineus natalensis</i>	ELM 12289	South Africa	Eastern Cape	Needs Camp	Adult	22	7.5	9.7	98	95	33.6	210	44.6
<i>Laniarius ferrugineus natalensis</i>	ELM 12304	South Africa	Eastern Cape	Needs Camp	Adult	20.7	9	10.5	100	85	36.5	220	48.5
<i>Laniarius ferrugineus natalensis</i>	ELM 12306	South Africa	Eastern Cape	Needs Camp	Adult	23	7.3	10	104	102	35	225	48.7
<i>Laniarius ferrugineus natalensis</i>	ELM 12354	South Africa	Kwa-Zulu Natal	Durban dist	Adult	23.4	8	10.3	88	92	36.1	205	45
<i>Laniarius ferrugineus natalensis</i>	ELM 12355	South Africa	Kwa-Zulu Natal	Shongweni dist	Adult	19	7	10.5	94	90	33.5	203	43.9
<i>Laniarius ferrugineus natalensis</i>	ELM 1236	South Africa	Eastern Cape	Kidds Beach dist	Adult	21.5	7.7	9.9	95	92	34.1	220	47.1
<i>Laniarius ferrugineus natalensis</i>	ELM 1237	South Africa	Eastern Cape	Kidds Beach dist	Adult	21.5	9.2	9.7	96	88	35.9	215	47.6
<i>Laniarius ferrugineus natalensis</i>	ELM 12545	South Africa	Eastern Cape	Adelaide dist	Adult	21	7.8	9	96	96	35.8	220	44.2
<i>Laniarius ferrugineus natalensis</i>	ELM 12547	South Africa	Eastern Cape	Adelaide dist	Adult	21.4	7	9.9	100	94	35	221	44.6
<i>Laniarius ferrugineus natalensis</i>	ELM 12918	South Africa	Eastern Cape	P.E. dist	Adult	22.9	9	11	100	7	39.9	229	46
<i>Laniarius ferrugineus natalensis</i>	ELM 13116	South Africa	Eastern Cape	Gonubie dist	Adult	21	8.4	10.3	97	92	32.7	216	46
<i>Laniarius ferrugineus natalensis</i>	ELM 13150	South Africa	Eastern Cape	Kidds Beach dist	Adult	22	8	10	95	95	35.8	225	44.6
<i>Laniarius ferrugineus natalensis</i>	ELM 13179	South Africa	Eastern Cape	East London dist	Adult	23	7.2	10.7	98	96	35	228	44.5
<i>Laniarius ferrugineus natalensis</i>	ELM 13209	South Africa	Eastern Cape	Gonubie dist	Adult	23	9.5	11.4	104	105	31	230	45
<i>Laniarius ferrugineus natalensis</i>	ELM 13364	South Africa	Eastern Cape	Alexandria dist	Adult	23	9.2	11	90	92	36	220	42

Taxon name	Museum no.	Country	Province	Locality	Age	Bill length (mm)	Bill length (mm)	Bill depth (mm)	Wing length (mm)	Tail length (mm)	Tarsus length (mm)	Total body length (mm)	Total head length (mm)
<i>Laniarius ferrugineus natalensis</i>	ELM 13364	South Africa	Eastern Cape	Alexandria dist	Adult	22	8.4	10.4	96	96	37.7	220	45
<i>Laniarius ferrugineus natalensis</i>	ELM 13365	South Africa	Eastern Cape	Alexandria dist	Adult	22.2	8	10.8	94	90	36	218	42.7
<i>Laniarius ferrugineus natalensis</i>	ELM 13366	South Africa	Eastern Cape	P.E. dist	Adult	22.9	8.4	10	95	96	34	222	40.8
<i>Laniarius ferrugineus natalensis</i>	ELM 13754	South Africa	Eastern Cape	Kidds Beach dist	Adult	23	8	10.2	98	97	37.4	228	49
<i>Laniarius ferrugineus natalensis</i>	ELM 13925	South Africa	Eastern Cape	The Haven dist	Adult	22.2	8	9.6	100	95	38.9	220	47.8
<i>Laniarius ferrugineus natalensis</i>	ELM 13934	South Africa	Eastern Cape	The Haven dist	Adult	21.8	8.5	9.7	93	92	34.5	213	44.3
<i>Laniarius ferrugineus natalensis</i>	ELM 13937	South Africa	Eastern Cape	The Haven dist	Adult	20.8	7.5	9.4	86	93	35.5	217	43.4
<i>Laniarius ferrugineus natalensis</i>	ELM 13938	South Africa	Eastern Cape	The Haven dist	Adult	22.2	9.1	10.6	87	90	36.5	210	46.9
<i>Laniarius ferrugineus natalensis</i>	ELM 14061	South Africa	Eastern Cape	Graaff-Reinett dist	Adult	22	8	9.5	93	95	35.5	221	47
<i>Laniarius ferrugineus natalensis</i>	ELM 14074	South Africa	Eastern Cape	Graaff-Reinett dist	Adult	23.3	7.3	10.6	97	96	36	219	49.7
<i>Laniarius ferrugineus natalensis</i>	ELM 14076	South Africa	Eastern Cape	Graaff-Reinett dist	Adult	22.1	88	10.5	100	96	36.5	205	48.6
<i>Laniarius ferrugineus natalensis</i>	ELM 14174	South Africa	Eastern Cape	Gonubie dist	Adult	23.5	7	10	96	93	34.5	222	46.4
<i>Laniarius ferrugineus natalensis</i>	ELM 14235	South Africa	Eastern Cape	Peddie dist	Adult	22	7.4	0.8	98	95	33.2	222	47.1
<i>Laniarius ferrugineus natalensis</i>	ELM 14434	South Africa	Eastern Cape	Mt Fletcher dist	Adult	22	7.1	10.8	100	95	33	215	48.5
<i>Laniarius ferrugineus natalensis</i>	ELM 14463	South Africa	Eastern Cape	Matatiela dist	Adult	22.1	8.8	10	107	110	32	233	44.8
<i>Laniarius ferrugineus natalensis</i>	ELM 14545	South Africa	Eastern Cape	Cockscomb dist	Adult	23	8.8	10	95	93	38.6	216	48
<i>Laniarius ferrugineus natalensis</i>	ELM 14607	South Africa	Eastern Cape	The Haven dist	Adult	22.8	9.8	9.5	95	90	33.5	208	46.6
<i>Laniarius ferrugineus natalensis</i>	ELM 14917	South Africa	Eastern Cape	The Haven dist	Adult	20	8.3	11	95	92	36.2	209	48.6
<i>Laniarius ferrugineus natalensis</i>	ELM 16295	South Africa	Eastern Cape	East London dist	Adult	22.5	7.5	9.3	93	95	31.1	212	46.5
<i>Laniarius ferrugineus natalensis</i>	ELM 17483	South Africa	Eastern Cape	Thornpark	Adult	20	8	10	90	93	32	208	45.5
<i>Laniarius ferrugineus natalensis</i>	ELM 1786	South Africa	Eastern Cape	Breakfast Vlei dist	Adult	22.5	8.2	9.9	96	92	36.6	218	49.2
<i>Laniarius ferrugineus natalensis</i>	ELM 1788	South Africa	Eastern Cape	Kidds Beach dist	Adult	27	9	10.8	96	94	36.6	226	50.3
<i>Laniarius ferrugineus natalensis</i>	ELM 18231	South Africa	Eastern Cape	Somerset East	Adult	24	9.2	10.2	95	80	34.7	210	48.6
<i>Laniarius ferrugineus natalensis</i>	ELM 18232	South Africa	Eastern Cape	P.E. dist	Adult	20.4	7.1	10.5	100	85	35.8	218	44.7
<i>Laniarius ferrugineus natalensis</i>	ELM 18233	South Africa	Eastern Cape	P.E. dist	Adult	22.1	8.1	9.2	97	93	36.4	222	46.3
<i>Laniarius ferrugineus natalensis</i>	ELM 18234	South Africa	Eastern Cape	P.E. dist	Adult	22.2	7.5	10.5	100	100	34.5	222	48.9
<i>Laniarius ferrugineus natalensis</i>	ELM 18235	South Africa	Eastern Cape	P.E. dist	Adult	21.4	7.5	12	90	91	37.5	220	46.5
<i>Laniarius ferrugineus natalensis</i>	ELM 18236	South Africa	Eastern Cape	P.E. dist	Adult	21	8.3	9.7	95	93	34	224	41.8
<i>Laniarius ferrugineus natalensis</i>	ELM 18237	South Africa	Eastern Cape	Cape Recife	Adult	23.8	9	10.2	92	95	34	218	45
<i>Laniarius ferrugineus natalensis</i>	ELM 18238	South Africa	Eastern Cape	Alexander Forest	Adult	22.9	8	10.2	92	88	35.5	200	45
<i>Laniarius ferrugineus natalensis</i>	ELM 18239	South Africa	Eastern Cape	Kenton	Adult	23.6	7	10.1	98	88	34	223	46.9
<i>Laniarius ferrugineus natalensis</i>	ELM 18241	South Africa	Eastern Cape	Pirie Mosion	Adult	20	7.5	10.1	100	94	37.2	217	47.2
<i>Laniarius ferrugineus natalensis</i>	ELM 18242	South Africa	Eastern Cape	Debe Nek dist	Adult	21	7	10	94	96	38	218	48.4
<i>Laniarius ferrugineus natalensis</i>	ELM 18243	South Africa	Eastern Cape	KWT dist	Adult	21.9	7	9.4	92	95	34.8	22	47.9
<i>Laniarius ferrugineus natalensis</i>	ELM 18247	South Africa	Eastern Cape	Fort Jackson	Adult	21.7	8.9	10.1	96	86	38	220	45.7
<i>Laniarius ferrugineus natalensis</i>	ELM 1849	South Africa	Eastern Cape	Kidds Beach dist	Adult	21	7.2	9.8	101	102	36	238	46.5
<i>Laniarius ferrugineus natalensis</i>	ELM 2068	South Africa	Eastern Cape	Kidds Beach dist	Adult	21.8	9	10.6	93	94	36	220	47
<i>Laniarius ferrugineus natalensis</i>	ELM 2629	South Africa	Eastern Cape	Breakfast Vlei dist	Adult	20.6	7.5	11	92	85	36	215	44.5
<i>Laniarius ferrugineus natalensis</i>	ELM 2863	South Africa	Eastern Cape	Ncera	Adult	21	7.8	10.2	93	95	33.4	218	42.6
<i>Laniarius ferrugineus natalensis</i>	ELM 2913	South Africa	Eastern Cape	Committees	Adult	20.5	8.1	10.4	95	92	38	205	47.3
<i>Laniarius ferrugineus natalensis</i>	ELM 3016	South Africa	Eastern Cape	Committees	Adult	22.5	7.8	9.6	96	102	36.5	223	48.5
<i>Laniarius ferrugineus natalensis</i>	ELM 3075	South Africa	Eastern Cape	Kwelera	Adult	20	8.3	9.6	91	95	35.5	216	45.3
<i>Laniarius ferrugineus natalensis</i>	ELM 3139	South Africa	Eastern Cape	Committees	Adult	24.5	9	10	96	92	38	212	47

Taxon name	Museum no.	Country	Province	Locality	Age	Bill length (mm)	Bill length (mm)	Bill depth (mm)	Wing length (mm)	Tail length (mm)	Tarsus length (mm)	Total body length (mm)	Total head length (mm)
<i>Laniarius ferrugineus natalensis</i>	ELM 3160	South Africa	Eastern Cape	Committees	Adult	23	8.2	10.7	97	98	36.6	215	49
<i>Laniarius ferrugineus natalensis</i>	ELM 3161	South Africa	Eastern Cape	Committees	Adult	20.3	7.6	9.8	100	95	36.5	216	48
<i>Laniarius ferrugineus natalensis</i>	ELM 3634	South Africa	Eastern Cape	Committees	Adult	21.1	8	10.5	95	95	35.2	213	44.6
<i>Laniarius ferrugineus natalensis</i>	ELM 3635	South Africa	Eastern Cape	Committees	Adult	21.7	7.1	10.2	102	100	32.2	221	46.2
<i>Laniarius ferrugineus natalensis</i>	ELM 3652	South Africa	Eastern Cape	Committees	Adult	21	8.5	9.9	102	98	37.8	220	45.7
<i>Laniarius ferrugineus natalensis</i>	ELM 3671	South Africa	Eastern Cape	Committees	Adult	20.7	8	9.7	87	88	36.1	204	45.5
<i>Laniarius ferrugineus natalensis</i>	ELM 3680	South Africa	Eastern Cape	Committees	Adult	21.2	7.5	10	95	90	37.5	204	46.6
<i>Laniarius ferrugineus natalensis</i>	ELM 4608	South Africa	Eastern Cape	Kei Bridge	Adult	19.5	7.7	10.8	94	100	36.8	213	47.5
<i>Laniarius ferrugineus natalensis</i>	ELM 4732	South Africa	Eastern Cape	Needs Camp	Adult	23.7	9.4	10.6	96	96	35.5	221	48.4
<i>Laniarius ferrugineus natalensis</i>	ELM 4798	South Africa	Eastern Cape	Committees	Adult	20.7	8.5	10	97	97	33.4	227	48.5
<i>Laniarius ferrugineus natalensis</i>	ELM 4799	South Africa	Eastern Cape	Committees	Adult	20	7	10.5	95	92	35	201	45.6
<i>Laniarius ferrugineus natalensis</i>	ELM 4829	South Africa	Eastern Cape	Committees	Adult	21	7.5	9.8	96	95	34.6	220	49.7
<i>Laniarius ferrugineus natalensis</i>	ELM 4873	South Africa	Eastern Cape	Alexandria dist	Adult	21.4	7.5	10.5	100	95	36	215	50.2
<i>Laniarius ferrugineus natalensis</i>	ELM 7193	South Africa	Eastern Cape	Komga dist	Adult	20.4	8.7	10.5	105	97	36.5	225	48.5
<i>Laniarius ferrugineus natalensis</i>	ELM 7468	South Africa	Eastern Cape	Cambria dist	Adult	20	7.7	9.6	95	86	31	205	43.8
<i>Laniarius ferrugineus natalensis</i>	ELM 7521	South Africa	Eastern Cape	Alexandria dist	Adult	22.1	9	11.2	95	95	37.7	223	49.7
<i>Laniarius ferrugineus natalensis</i>	ELM 7584	South Africa	Eastern Cape	Fort Pato	Adult	21.6	8.4	9.7	95	94	37.3	220	46.5
<i>Laniarius ferrugineus natalensis</i>	ELM 7585	South Africa	Eastern Cape	Fort Pato	Adult	21.8	7.4	10.3	92	90	36	221	47
<i>Laniarius ferrugineus natalensis</i>	ELM 7637	South Africa	Gauteng	Ferndale	Adult	22.1	7.5	9.4	95	90	35.4	221	44.5
<i>Laniarius ferrugineus natalensis</i>	ELM 7695	South Africa	Eastern Cape	Debe Nek dist	Adult	23	8.5	10	100	95	35.7	230	57.5
<i>Laniarius ferrugineus natalensis</i>	ELM 8022	South Africa	Eastern Cape	Kleinpoort	Adult	22	7	9.4	90	95	36	220	44.4
<i>Laniarius ferrugineus natalensis</i>	ELM 8908	South Africa	Eastern Cape	Fort Pato	Adult	23.5	8	10	97	92	36.4	225	45.5
<i>Laniarius ferrugineus natalensis</i>	SAM 14605	South Africa	Eastern Cape	Glen Grey	Adult	22	8.5	10	90	80	36	228	46.5
<i>Laniarius ferrugineus natalensis</i>	TM 12407	South Africa	Kwa-Zulu Natal	Kilgobbin, Dargle	Adult	21.8	7.3	9.6	95	93	33.4	224	46.6
<i>Laniarius ferrugineus natalensis</i>	TM 17092	South Africa	Eastern Cape	Kleinpoort, Grahamstown	Adult	23	7.9	10.5	95	95	34	203	47.7
<i>Laniarius ferrugineus natalensis</i>	TM 1943	South Africa	Eastern Cape	Grahamstown, C.C	Adult	21.8	6.4	9.4	102	98	33.2	215	48.7
<i>Laniarius ferrugineus natalensis</i>	TM 3060	Swaziland	Swaziland	Swaziland	Adult	23.9	7.2	9.6	100	92	32.3	211	49.4
<i>Laniarius ferrugineus natalensis</i>	TM 31844	South Africa	Gauteng	Uithorns	Adult	22.5	7.9	8.7	90	95	31.3	227	46.8
<i>Laniarius ferrugineus natalensis</i>	TM 3366	South Africa	Western Cape	Zuurberg, Cape Colony	Adult	20.2	7.2	11	101	91	33.8	185	46
<i>Laniarius ferrugineus natalensis</i>	TM 3765	South Africa	Eastern Cape	Grahamstown, C.C	Adult	20.7	6.8	8.9	96	96	33.1	207	46.3
<i>Laniarius ferrugineus natalensis</i>	TM 39030	South Africa	Mpumalanga	Piet Retief, Transvaal	Adult	20.8	8.2	9.8	95	90	35.1	200	46.1
<i>Laniarius ferrugineus natalensis</i>	TM 41580	South Africa	Kwa-Zulu Natal	Donnybrook, Polela	Adult	21.1	10	10.8	97	95	35.8	219	43.7
<i>Laniarius ferrugineus natalensis</i>	TM 41585	South Africa	Kwa-Zulu Natal	Pietermaritzburg	Adult	20.6	9.4	10.3	94	95	35.5	223	43.7
<i>Laniarius ferrugineus natalensis</i>	TM 41587	South Africa	Kwa-Zulu Natal	Mt. Edgcombe, Natal	Adult	23	6.9	9.4	100	95	32.8	225	48.1
<i>Laniarius ferrugineus natalensis</i>	TM 41597	South Africa	Kwa-Zulu Natal	Maritzburg, Natal	Adult	21.4	6.6	9.4	100	91	32.6	225	46.8
<i>Laniarius ferrugineus natalensis</i>	TM 41598	South Africa	Kwa-Zulu Natal	Maritzburg, Natal	Adult	21.6	8.1	10.2	95	92	36.4	220	46.4
<i>Laniarius ferrugineus natalensis</i>	TM 43997	South Africa	Kwa-Zulu Natal	Umgeni river	Adult	23	9.5	10.2	87	95	37.5	221	46.6
<i>Laniarius ferrugineus natalensis</i>	TM 44001	South Africa	Kwa-Zulu Natal	R.Umgeni river, Natal	Adult	22.7	7.6	9.5	96	92	33.2	213	47.3
<i>Laniarius ferrugineus natalensis</i>	TM 44001	South Africa	Kwa-Zulu Natal	R.Umgeni river, Natal	Adult	21.1	7.5	9.5	95	91	32.8	214	48.5
<i>Laniarius ferrugineus natalensis</i>	TM 5566	South Africa	Eastern Cape	Grahamstown	Adult	22.1	8.1	9.9	100	95	35	230	47.5
<i>Laniarius ferrugineus natalensis</i>	TM 5572	South Africa	Eastern Cape	Grahamstown	Adult	20	9.5	12	96	96	35.9	238	48.4
<i>Laniarius ferrugineus natalensis</i>	TM 60361	South Africa	Kwa-Zulu Natal	Cathedral peak forestry, Natal	Adult	20.2	7.4	10.3	95	97	36.1	205	47.3
<i>Laniarius ferrugineus natalensis</i>	TM 6072	South Africa	Eastern Cape	Grahamstown	Adult	21.9	8.4	9.5	95	98	33.8	225	48.9

Taxon name	Museum no.	Country	Province	Locality	Age	Bill length (mm)	Bill length (mm)	Bill depth (mm)	Wing length (mm)	Tail length (mm)	Tarsus length (mm)	Total body length (mm)	Total head length (mm)
<i>Laniarius ferrugineus pondoensis</i>	MNHN ZO 1981-81	South Africa	Limpopo	Ntafufu river	Adult	25,5	9,1	10,5	90	88	37,8	208	48,8
<i>Laniarius ferrugineus pondoensis</i>	MNHN ZO 1981-83	South Africa	Limpopo	Ntafufu river	Adult	23	8,4	9,6	87	75	34,3	190	47,4
<i>Laniarius ferrugineus pondoensis</i>	MNHN ZO 1981-84	South Africa	Limpopo	Ntafufu river	Adult	22,2	8	10,2	88	85	33	201	45,5
<i>Laniarius ferrugineus pondoensis</i>	MNHN ZO 1981-85	South Africa	Limpopo	Ntafufu river	Adult	23,4	7,8	10,7	88	95	33,2	190	46,1
<i>Laniarius ferrugineus pondoensis</i>	DM 7332	South Africa	Eastern Cape	Mutafufu River, Sea View, Near River Mouth	Adult	22,8	7,8	9,8	98	96	36,7	226	48,4
<i>Laniarius ferrugineus pondoensis</i>	DM 7333	South Africa	Eastern Cape	Mutafufu River, Sea View, Near River Mouth	Adult	22,3	7,5	9,4	94	94	36,5	210	46,9
<i>Laniarius ferrugineus pondoensis</i>	DM 7335	South Africa	Eastern Cape	Mutafufu River, Sea View, Near River Mouth	Adult	23,1	9,5	10,4	96	95	35	215	47,3
<i>Laniarius ferrugineus pondoensis</i>	DM 7336	South Africa	Eastern Cape	Mutafufu River, Sea View, Near River Mouth	Adult	21,8	7,4	10	95	96	34,8	215	43,9
<i>Laniarius ferrugineus pondoensis</i>	DM 7337	South Africa	Eastern Cape	Mutafufu River, Sea View, Near River Mouth	Adult	22,5	7,3	9,5	91	91	34,4	205	47,9
<i>Laniarius ferrugineus pondoensis</i>	DM 7339	South Africa	Eastern Cape	Embotyi, Lusikisiki	Adult	21,4	7,2	9,9	96	94	34,1	219	46,7
<i>Laniarius ferrugineus pondoensis</i>	DM 7342	South Africa	Eastern Cape	Port St Johns	Adult	22,3	7,3	9,8	96	94	34,4	210	45,3
<i>Laniarius ferrugineus pondoensis</i>	DM 7343	South Africa	Eastern Cape	Port St Johns	Adult	20,7	8	10	90	88	30,9	200	44,8
<i>Laniarius ferrugineus pondoensis</i>	DM 7344	South Africa	Eastern Cape	Port St Johns	Adult	21,4	7	10	93	93	33,5	203	44,9
<i>Laniarius ferrugineus pondoensis</i>	ELM 10223	South Africa	Eastern Cape	Dwesa dist	Adult	20	9	10,5	96	97	36,4	228	45,7
<i>Laniarius ferrugineus pondoensis</i>	ELM 10255	South Africa	Eastern Cape	Dwesa dist	Adult	22	7,6	10	96	97	35,5	235	50,1
<i>Laniarius ferrugineus pondoensis</i>	ELM 10282	South Africa	Eastern Cape	Dwesa dist	Adult	21,7	10	9,8	96	93	36,5	225	46,5
<i>Laniarius ferrugineus pondoensis</i>	ELM 10283	South Africa	Eastern Cape	Dwesa dist	Adult	20,5	7	10,3	94	91	35,8	228	44
<i>Laniarius ferrugineus pondoensis</i>	ELM 10284	South Africa	Eastern Cape	Dwesa dist	Adult	21	7	9,7	90	91	33,4	228	45,4
<i>Laniarius ferrugineus pondoensis</i>	ELM 10347	South Africa	Eastern Cape	Nthlonzana	Adult	20,8	7,8	10,5	90	95	34,7	224	45,5
<i>Laniarius ferrugineus pondoensis</i>	ELM 11242	South Africa	Eastern Cape	Bolo dist	Adult	22	9,5	10	90	88	36	220	49,3
<i>Laniarius ferrugineus pondoensis</i>	ELM 12256	South Africa	Eastern Cape	Port St. Johns dist	Adult	20,7	9	10	94	90	37,6	215	46
<i>Laniarius ferrugineus pondoensis</i>	ELM 12257	South Africa	Eastern Cape	Port St. Johns dist	Adult	21,1	9,8	9,7	93	92	37,2	217	47,2
<i>Laniarius ferrugineus pondoensis</i>	ELM 12258	South Africa	Eastern Cape	Port St. Johns dist	Adult	23	8,6	10,5	90	94	37,6	200	45,4
<i>Laniarius ferrugineus pondoensis</i>	ELM 12259	South Africa	Eastern Cape	Port St. Johns dist	Adult	22,8	7,5	10	88	93	35	200	45,9
<i>Laniarius ferrugineus pondoensis</i>	ELM 12260	South Africa	Eastern Cape	Port St. Johns dist	Adult	23,4	8	10,1	90	90	37,4	210	42,7
<i>Laniarius ferrugineus pondoensis</i>	ELM 12261	South Africa	Eastern Cape	Port St. Johns dist	Adult	21	8,9	10,9	86	84	35,5	210	44
<i>Laniarius ferrugineus pondoensis</i>	ELM 12292	South Africa	Eastern Cape	Needs Camp	Adult	20	8,4	9,3	98	95	36	220	44
<i>Laniarius ferrugineus pondoensis</i>	ELM 12432	South Africa	Kwa-Zulu Natal	Mkambati dist	Adult	23	8	11,4	90	90	37	222	47,5
<i>Laniarius ferrugineus pondoensis</i>	ELM 13028	South Africa	Eastern Cape	East London dist	Adult	21,5	7,2	9,7	98	92	31,5	220	42
<i>Laniarius ferrugineus pondoensis</i>	ELM 13030	South Africa	Eastern Cape	East London dist	Adult	20,6	8	9,5	90	84	33	222	43,9
<i>Laniarius ferrugineus pondoensis</i>	ELM 13256	South Africa	Eastern Cape	Tombo mission museum	Adult	21,7	8	9,5	93	100	34	220	50
<i>Laniarius ferrugineus pondoensis</i>	ELM 13318	South Africa	Kwa-Zulu Natal	Port Edward dist	Adult	22,7	7,5	10,5	92	95	34	208	47
<i>Laniarius ferrugineus pondoensis</i>	ELM 13361	South Africa	Kwa-Zulu Natal	Port Edward dist	Adult	21,4	9	10,4	96	94	37	215	44,6
<i>Laniarius ferrugineus pondoensis</i>	ELM 14626	South Africa	Eastern Cape	Hluleka dist	Adult	21,5	7	10,2	93	95	34,8	206	48,4
<i>Laniarius ferrugineus pondoensis</i>	ELM 14627	South Africa	Eastern Cape	Hluleka dist	Adult	22,1	8,6	9,6	90	85	34,6	198	45,4
<i>Laniarius ferrugineus pondoensis</i>	ELM 15050	South Africa	Eastern Cape	Port St. Johns dist	Adult	20,4	8,4	10,4	95	94	35,9	218	48,5
<i>Laniarius ferrugineus pondoensis</i>	ELM 1768	South Africa	Eastern Cape	Breakfast Vlei dist	Adult	20,3	7,4	9,9	96	90	36,4	210	46,5
<i>Laniarius ferrugineus pondoensis</i>	ELM 18244	South Africa	Eastern Cape	Port St. Johns dist	Adult	22,8	7,5	9,7	90	86	35,4	208	46,8
<i>Laniarius ferrugineus pondoensis</i>	ELM 18245	South Africa	Eastern Cape	Port St. Johns dist	Adult	23	8,2	10,5	96	94	35	214	44,5
<i>Laniarius ferrugineus pondoensis</i>	ELM 18246	South Africa	Eastern Cape	Port St. Johns dist	Adult	21,5	7,6	10,5	90	89	35,5	215	46,8

Taxon name	Museum no.	Country	Province	Locality	Age	Bill length (mm)	Bill length (mm)	Bill depth (mm)	Wing length (mm)	Tail length (mm)	Tarsus length (mm)	Total body length (mm)	Total head length (mm)
<i>Laniarius ferrugineus pondoensis</i>	ELM 1879	South Africa	Eastern Cape	Cambridge dist	Adult	21.5	8	9.4	94	97	35.5	223	46.4
<i>Laniarius ferrugineus pondoensis</i>	ELM 320	South Africa	Eastern Cape	East London dist	Adult	22	9.5	10.3	96	96	36.7	210	47
<i>Laniarius ferrugineus pondoensis</i>	ELM 321	South Africa	Eastern Cape	East London dist	Adult	22.5	8.1	12	96	90	38	217	49.7
<i>Laniarius ferrugineus pondoensis</i>	ELM 3253	South Africa	Eastern Cape	Committees	Adult	21	8.8	9.8	85	96	35.6	205	41
<i>Laniarius ferrugineus pondoensis</i>	ELM 4607	South Africa	Eastern Cape	Kei Bridge	Adult	20.5	8.7	11.5	102	102	37.3	212	49.5
<i>Laniarius ferrugineus pondoensis</i>	ELM 7113	South Africa	Eastern Cape	Cambridge dist	Adult	21.5	9	10.2	95	92	35.9	218	47.4
<i>Laniarius ferrugineus pondoensis</i>	ELM 7436	South Africa	Eastern Cape	Cambria dist	Adult	22.2	7.8	10.2	100	98	38.6	223	49.4
<i>Laniarius ferrugineus pondoensis</i>	ELM 7567	South Africa	Eastern Cape	Alexandria dist	Adult	21.7	9.1	10.1	100	90	35	220	47.3
<i>Laniarius ferrugineus pondoensis</i>	ELM 8878	South Africa	Eastern Cape	Black Rock	Adult	22	8.2	11	95	93	37.4	225	47
<i>Laniarius ferrugineus pondoensis</i>	ELM 9820	South Africa	Eastern Cape	Black Rock	Adult	23	8	10.5	100	95	33.8	230	45.8
<i>Laniarius ferrugineus pondoensis</i>	TM 0	South Africa	Eastern Cape	Port St Johns, W.Pondoland	Adult	21.3	6.8	8.9	94	94	33.7	220	46.8
<i>Laniarius ferrugineus pondoensis</i>	TM 10967	South Africa	Western Cape	Cape Town	Adult	20.6	8.2	9.4	95	93	34	217	45.7
<i>Laniarius ferrugineus pondoensis</i>	TM 18413	South Africa	Kwa-Zulu Natal	Kloof, Natal	Adult	21.8	7.4	11	96	91	36	207	47.6
<i>Laniarius ferrugineus pondoensis</i>	TM 18510	South Africa	Kwa-Zulu Natal	Zululand	Adult	21.1	7.9	9.2	83	82	31.3	186	43.4
<i>Laniarius ferrugineus pondoensis</i>	TM 18627	South Africa	Kwa-Zulu Natal	Kloof, Natal	Adult	21.5	7.2	10.1	100	100	36	215	42.5
<i>Laniarius ferrugineus pondoensis</i>	TM 3763	South Africa	Eastern Cape	Ngqeleni dist, W.Pondoland	Adult	21.6	7.9	9.9	95	96	34.6	230	46.4
<i>Laniarius ferrugineus pondoensis</i>	TM 41582	South Africa	Kwa-Zulu Natal	Cape natal border	Adult	22.7	7.5	11	100	101	37	233	47.5
<i>Laniarius ferrugineus pondoensis</i>	TM 4370	South Africa	Eastern Cape	Port St John's dist	Adult	22.7	7.6	9.7	96	94	32.3	222	48.1
<i>Laniarius ferrugineus pondoensis</i>	TM 4371	South Africa	Eastern Cape	Port St Johns, W.Pondoland	Adult	21	6.5	9.6	93	87	32.7	218	47.6
<i>Laniarius ferrugineus pondoensis</i>	TM 4373	South Africa	Eastern Cape	Pondoland	Adult	23	8.3	9.7	93	87	33.6	202	47.8
<i>Laniarius ferrugineus pondoensis</i>	TM 43995	South Africa	Kwa-Zulu Natal	Ngele (Weza) forest	Adult	22.8	6.9	9.5	101	95	33.8	225	48.9
<i>Laniarius ferrugineus pondoensis</i>	TM 5403	South Africa	Eastern Cape	Port St John's, Pondoland	Adult	21.9	7.5	9.7	97	91	32.8	217	48.4
<i>Laniarius ferrugineus pondoensis</i>	TM 5406	South Africa	Eastern Cape	Port St John's, Nor Pondoland	Adult	21.4	6.8	8.9	93	95	32.9	215	45.5
<i>Laniarius ferrugineus pondoensis</i>	TM 8142	South Africa	Eastern Cape	Port St John's	Adult	21	8.2	11.2	95	96	36.3	220	45.7
<i>Laniarius ferrugineus savensis</i>	DM 19770	Mozambique	Inhambane	Mapinhane	Adult	21	7	8.8	83	82	29.5	180	41.4
<i>Laniarius ferrugineus savensis</i>	DM 19771	Mozambique	Inhambane	Mapinhane	Adult	21.8	7	8.7	82	80	29.6	198	42.4
<i>Laniarius ferrugineus savensis</i>	DM 19772	Mozambique	Inhambane	Mapinhane	Adult	21	6.6	8.2	88	85	31.9	190	40.8
<i>Laniarius ferrugineus savensis</i>	DM 19775	Mozambique	Inhambane	Mapinhane	Adult	21.1	7.8	8.6	87	84	32.3	186	42.9
<i>Laniarius ferrugineus savensis</i>	DM 19776	Mozambique	Inhambane	Mapinhane	Adult	22.1	6.1	9.5	92	90	31.3	198	45.5
<i>Laniarius ferrugineus savensis</i>	DM 19777	Mozambique	Inhambane	Panda	Adult	21.1	6.5	9.3	88	80	31.8	195	44.5
<i>Laniarius ferrugineus savensis</i>	DM 19778	Mozambique	Inhambane	Panda	Adult	23.7	6.9	9.5	90	83	33.9	188	45.6
<i>Laniarius ferrugineus savensis</i>	DM 19780	Mozambique	Inhambane	Panda	Adult	20.1	7.6	8.5	85	78	30.7	188	43.6
<i>Laniarius ferrugineus savensis</i>	DM 19784	Mozambique	Inhambane	Massinga	Adult	22.9	6.9	8.6	90	86	34.3	198	47.3
<i>Laniarius ferrugineus savensis</i>	DM 19786	Mozambique	Inhambane	Massinga	Adult	20.5	7.6	8.9	80	78	32	180	45.1
<i>Laniarius ferrugineus savensis</i>	DM 26861	Mozambique	Inhambane	Vila Franca do Save	Adult	19.7	6.4	8.6	94	90	30.5	189	41.9
<i>Laniarius ferrugineus savensis</i>	DM 26862	Mozambique	Inhambane	Rumbacaca	Adult	21.9	6.6	7.9	89	84	31.5	189	45.7
<i>Laniarius ferrugineus savensis</i>	DM 26863	Mozambique	Inhambane	Rumbacaca	Adult	22	7.1	8.9	90	90	33.7	195	43.4
<i>Laniarius ferrugineus savensis</i>	DM 26864	Mozambique	Inhambane	Rumbacaca	Adult	21.2	6.9	7.8	86	86	32.1	187	42.1
<i>Laniarius ferrugineus savensis</i>	DM 26866	Mozambique	Inhambane	Rumbacaca	Adult	21.7	6.8	7.9	83	83	30.5	184	43.1
<i>Laniarius ferrugineus savensis</i>	DM 26867	Mozambique	Inhambane	Rumbacaca	Adult	19.7	6.8	8.8	86	92	31.1	190	44.3
<i>Laniarius ferrugineus savensis</i>	DM 26868	Mozambique	Inhambane	Rumbacaca	Adult	20.2	6.3	8.5	85	85	31.4	182	42
<i>Laniarius ferrugineus savensis</i>	DM 26869	Mozambique	Inhambane	Vilanculos	Adult	22.4	7.7	7.9	90	88	33.5	184	46.1
<i>Laniarius ferrugineus savensis</i>	DM 26870	Mozambique	Inhambane	Vilanculos	Adult	20.5	7.1	8.9	88	79	33.9	188	40

Taxon name	Museum no.	Country	Province	Locality	Age	Bill length (mm)	Bill length (mm)	Bill depth (mm)	Wing length (mm)	Tail length (mm)	Tarsus length (mm)	Total body length (mm)	Total head length (mm)
<i>Laniarius ferrugineus savensis</i>	DM 26871	Mozambique	Inhambane	Vilanculos	Adult	21.8	6.7	7.9	89	80	31.8	187	40.1
<i>Laniarius ferrugineus savensis</i>	DM 7372	Mozambique	Inhambane	Panda	Adult	22.9	7	7.8	87	86	31.2	195	44
<i>Laniarius ferrugineus tongensis</i>	MNHN ZO-1968-1629	South Africa	Western Cape	Cape Town	Adult	20.8	8.3	8.6	80	87	32.4	188	43.7
<i>Laniarius ferrugineus tongensis</i>	MNHN ZO 1969-2778	South Africa	Swaziland	Mzenene River (near Balegane)	Adult	22.5	8.2	10.1	90	90	34.4	193	42.6
<i>Laniarius ferrugineus tongensis</i>	DM 7368	Mozambique	Maputo	Bela Vista	Adult	20.8	7.1	9.1	92	86	33	200	43
<i>Laniarius ferrugineus tongensis</i>	DM 7369	Mozambique	Maputo	Bela Vista	Adult	21.6	7.6	8.4	90	88	32.8	199	44.8
<i>Laniarius ferrugineus tongensis</i>	DM 7373	Mozambique	Inhambane	Panda	Adult	22.6	7.4	9.6	92	80	32.4	204	45.9
<i>Laniarius ferrugineus tongensis</i>	DM 7374	Mozambique	Inhambane	Panda	Adult	20.5	7.1	8.9	92	85	33.3	192	42
<i>Laniarius ferrugineus tongensis</i>	DM 7377	Mozambique	Maputo	Vila Luiza	Adult	19.8	6.7	8.2	86	84	31.4	193	41.5
<i>Laniarius ferrugineus tongensis</i>	DM 7378	Swaziland	Swaziland	Nsoko, Lubuli	Adult	22.8	6.8	9.5	88	85	33	210	43.4
<i>Laniarius ferrugineus tongensis</i>	TM 15296	South Africa	Kwa-Zulu Natal	Manaba	Adult	23.5	8.5	8.9	88	85	32.2	209	44.7
<i>Laniarius ferrugineus tongensis</i>	TM 18509	South Africa	Kwa-Zulu Natal	Ndumu	Adult	23	8.4	9.6	87	85	34.4	193	46.8
<i>Laniarius ferrugineus tongensis</i>	TM 19128	South Africa	Kwa-Zulu Natal	Ingwavuma river	Adult	21.8	8	10.5	95	86	30	197	45.2
<i>Laniarius ferrugineus tongensis</i>	TM 19130	South Africa	Kwa-Zulu Natal	Ingwavuma river	Adult	22	7.3	9.6	93	92	34	200	46.5
<i>Laniarius ferrugineus tongensis</i>	TM 21947	South Africa	Swaziland	Swaziland	Adult	20	8.5	9.7	97	92	31.5	215	45.2
<i>Laniarius ferrugineus tongensis</i>	TM 21948	South Africa	Swaziland	Swaziland	Adult	20.5	7.8	9.2	90	81	32.4	204	44.6
<i>Laniarius ferrugineus tongensis</i>	TM 21949	South Africa	Swaziland	Swaziland	Adult	22	8.3	9	90	90	34	201	45.8
<i>Laniarius ferrugineus tongensis</i>	TM 41581	South Africa	Eastern Cape	Shimula's Pont, Pongola River	Adult	20.2	7.2	9.2	85	80	31.5	195	44.1
<i>Laniarius ferrugineus tongensis</i>	TM 41586	South Africa	Kwa-Zulu Natal	Ingwavuma Lebombo Mts	Adult	22.5	7.4	9.7	91	90	35.5	206	48
<i>Laniarius ferrugineus tongensis</i>	TM 41588	South Africa	Eastern Cape	Shimula's Pont, Pongola River	Adult	22.7	9.5	10.4	91	85	35	201	47
<i>Laniarius ferrugineus tongensis</i>	TM 41594	South Africa	Kwa-Zulu Natal	Ingwavuma Lebombo Mts	Adult	21	8.4	9.9	87	85	31.5	200	46
<i>Laniarius ferrugineus tongensis</i>	TM 41950	South Africa	Kwa-Zulu Natal	Tongaland	Adult	20	8.6	8	88	86	32.6	185	44.5
<i>Laniarius ferrugineus tongensis</i>	TM 80695	South Africa	Mpumalanga	SA, Mpumalanga, Nelspruit	Adult	22	9.2	9.1	92	85	34	210	47.4
<i>Laniarius ferrugineus transvaalensis</i>	DM 15424	Swaziland	Swaziland	Stegi, Mlaula Estates	Adult	19.2	7	8.5	85	80	31	198	42.2
<i>Laniarius ferrugineus transvaalensis</i>	MNHN 2013-262	South Africa	Limpopo	Ben Lavin Nature Reserve (Long wall dam)	Adult	23.5	8.8	9.4	81	90	35.5	185	45.5
<i>Laniarius ferrugineus transvaalensis</i>	DM 15425	Swaziland	Swaziland	Stegi, Mlaula Estates	Adult	20.2	5.6	8.9	98	88	35.4	200	45
<i>Laniarius ferrugineus transvaalensis</i>	DM 15427	Swaziland	Swaziland	Stegi	Adult	19.6	7.4	8.6	90	76	33.1	194	43
<i>Laniarius ferrugineus transvaalensis</i>	DM 25366	South Africa	Northern	Northam	Adult	23.5	7.5	9.5	97	88	35.5	200	50
<i>Laniarius ferrugineus transvaalensis</i>	DM 25368	South Africa	Northern	Northam	Adult	21.7	6.1	8.1	98	99	33.3	205	48.3
<i>Laniarius ferrugineus transvaalensis</i>	DM 25648	South Africa	North-West	Swartruggens, Blokkloof	Adult	23.3	6.9	8.8	97	99	34.2	210	45.5
<i>Laniarius ferrugineus transvaalensis</i>	DM 27988	South Africa	North-West	Swartruggens, Elands River	Adult	22.6	6.5	8.9	93	85	33.8	205	46.9
<i>Laniarius ferrugineus transvaalensis</i>	DM 30059	South Africa	Limpopo	Louis Trichardt, Entabeni Forest	Adult	21.2	6.8	8.2	91	99	30.6	193	46.2
<i>Laniarius ferrugineus transvaalensis</i>	DM 7381	South Africa	Mpumalanga	Newington, Malamala	Adult	22.3	6.5	8.3	93	89	31.1	199	45.7
<i>Laniarius ferrugineus transvaalensis</i>	DM 7382	South Africa	Mpumalanga	Newington, Malamala	Adult	21.8	8	9.8	90	88	33.6	205	44
<i>Laniarius ferrugineus transvaalensis</i>	DM 7383	South Africa	Mpumalanga	Newington, Malamala	Adult	20	6.7	8.6	85	84	30.5	170	43.5
<i>Laniarius ferrugineus transvaalensis</i>	DM 7385	South Africa	Mpumalanga	Newington, Malamala	Adult	19.6	6.7	8.2	84	83	30.8	185	43.4
<i>Laniarius ferrugineus transvaalensis</i>	DM 7386	South Africa	Mpumalanga	Newington, Malamala	Adult	21.2	7.2	8.2	93	86	33.3	207	44.1
<i>Laniarius ferrugineus transvaalensis</i>	DM 7387	Swaziland	Swaziland	Nsoko, Lubuli	Adult	22.1	7.3	8.8	87	84	34.3	199	47.4
<i>Laniarius ferrugineus transvaalensis</i>	DM 7388	Swaziland	Swaziland	Nsoko, Lubuli	Adult	20.9	6.1	8.2	94	93	30.6	100	44.4
<i>Laniarius ferrugineus transvaalensis</i>	DM 7389	Swaziland	Swaziland	Nsoko, Lubuli	Adult	21.2	5.7	7.8	97	91	31.2	205	42.9
<i>Laniarius ferrugineus transvaalensis</i>	DM 7390	Swaziland	Swaziland	Big Bend, Mcandatshe near	Adult	18.5	7	9.5	97	96	31.2	205	46.4



Taxon name	Museum no.	Country	Province	Locality	Age	Bill length (mm)	Bill length (mm)	Bill depth (mm)	Wing length (mm)	Tail length (mm)	Tarsus length (mm)	Total body length (mm)	Total head length (mm)
<i>Laniarius ferrugineus transvaalensis</i>	DM 7391	Swaziland	Swaziland	Big Bend, Mcandatshe near	Adult	22.3	6.4	8.5	88	84	32.8	100	45.1
<i>Laniarius ferrugineus transvaalensis</i>	DM 7392	Swaziland	Swaziland	Stegi	Adult	21.3	6.8	8.5	86	85	29.4	195	44.5
<i>Laniarius ferrugineus transvaalensis</i>	DM 7393	South Africa	Kwa-Zulu Natal	Magut	Adult	20.6	6.8	9.4	95	96	33.1	216	44.3
<i>Laniarius ferrugineus transvaalensis</i>	ELM 4762	South Africa	Gauteng	Ferndale	Adult	21	8.3	10.2	100	98	38.6	223	49.4
<i>Laniarius ferrugineus transvaalensis</i>	ELM 7261	South Africa	Gauteng	Ferndale	Adult	22.7	8.9	10.2	101	100	37.6	225	48
<i>Laniarius ferrugineus transvaalensis</i>	ELM 7337	South Africa	Gauteng	Ferndale	Adult	23.1	8.5	9.8	93	95	37.2	215	47.2
<i>Laniarius ferrugineus transvaalensis</i>	TM 10660	South Africa	North West	Borchhoek	Adult	22.2	6.4	8.9	87	84	31	195	45.6
<i>Laniarius ferrugineus transvaalensis</i>	TM 11405	South Africa	Gauteng	Pretoria	Adult	20.7	8	10	95	95	31.6	215	47.1
<i>Laniarius ferrugineus transvaalensis</i>	TM 120165	South Africa	Limpopo	Luis Trichart	Adult	23	7.7	9.5	92	92	32.4	212	47.7
<i>Laniarius ferrugineus transvaalensis</i>	TM 12600	South Africa	Limpopo	Mokeetsi	Adult	21.8	8	10.1	95	87	33.4	203	48.1
<i>Laniarius ferrugineus transvaalensis</i>	TM 12669	South Africa	Limpopo	Leydsdorp	Adult	21.8	6.5	8.3	91	78	31.1	199	46.6
<i>Laniarius ferrugineus transvaalensis</i>	TM 13070	South Africa	Gauteng	Pretoria	Adult	23.1	7.2	10.3	90	95	31.3	225	45
<i>Laniarius ferrugineus transvaalensis</i>	TM 13071	South Africa	Gauteng	PTA	Adult	23.9	7.6	10	95	100	31.1	220	44.5
<i>Laniarius ferrugineus transvaalensis</i>	TM 13460	South Africa	Limpopo	Moorddrift	Adult	22.8	8.1	9.2	100	100	34.8	223	45.5
<i>Laniarius ferrugineus transvaalensis</i>	TM 13461	South Africa	Limpopo	Moorddrift	Adult	23.2	8.1	8.5	90	86	33	209	45.5
<i>Laniarius ferrugineus transvaalensis</i>	TM 13462	South Africa	Limpopo	Moorddrift	Adult	25.2	6.5	8.2	93	95	32.8	210	49.2
<i>Laniarius ferrugineus transvaalensis</i>	TM 13785	South Africa	Mpumalanga	Acornhoek, pilgrim's rest	Adult	22.9	8.2	10.2	96	95	35.4	223	47
<i>Laniarius ferrugineus transvaalensis</i>	TM 13873	South Africa	Gauteng	Scheumanberg	Adult	21.3	7.3	9.4	97	96	33.4	211	44.1
<i>Laniarius ferrugineus transvaalensis</i>	TM 16592	South Africa	Gauteng	Hamankraal	Adult	23	8.3	10	96	96	33.9	215	46.5
<i>Laniarius ferrugineus transvaalensis</i>	TM 17866	South Africa	Limpopo	Mokeetsi, Northern TVL	Adult	24.1	6.4	8.2	90	93	34.3	210	47.1
<i>Laniarius ferrugineus transvaalensis</i>	TM 19131	South Africa	Kwa-Zulu Natal	Ndumu	Adult	22.1	7.8	7.5	85	82	30.7	186	45
<i>Laniarius ferrugineus transvaalensis</i>	TM 19599	South Africa	Limpopo	Mokeetsi Transvaal	Adult	21.2	7.3	8.5	87	89	32.5	208	46
<i>Laniarius ferrugineus transvaalensis</i>	TM 20164	South Africa	Limpopo	Luis Trichart	Adult	21.4	6.8	9.7	93	90	31	205	45
<i>Laniarius ferrugineus transvaalensis</i>	TM 20166	South Africa	Limpopo	Luis Trichart	Adult	20.6	7	8.4	87	83	32.5	205	44.3
<i>Laniarius ferrugineus transvaalensis</i>	TM 20169	South Africa	Limpopo	Soutpansberg	Adult	22.8	6.8	8.4	93	92	32.3	204	44.8
<i>Laniarius ferrugineus transvaalensis</i>	TM 21950	South Africa	Swaziland	Swaziland	Adult	20	8	8.5	90	84	32	195	42.7
<i>Laniarius ferrugineus transvaalensis</i>	TM 26182	South Africa	Gauteng	Wonderboom, Hamaanskraal	Adult	21.6	8.1	9	96	99	32.8	227	45.8
<i>Laniarius ferrugineus transvaalensis</i>	TM 27593	South Africa	Gauteng	Hamankraal	Adult	21.6	7.6	8.2	92	94	32	212	47.4
<i>Laniarius ferrugineus transvaalensis</i>	TM 29296	South Africa	Limpopo	Blouberg, Northern TVL	Adult	21.4	6.5	8.4	99	96	32.8	220	48.4
<i>Laniarius ferrugineus transvaalensis</i>	TM 29297	South Africa	Limpopo	Blouberg, Northern TVL	Adult	23.1	7.1	9.4	95	93	33.1	213	48.5
<i>Laniarius ferrugineus transvaalensis</i>	TM 29298	South Africa	Limpopo	NTVL, Blouberg	Adult	21.5	8	10.5	95	85	31.8	210	46
<i>Laniarius ferrugineus transvaalensis</i>	TM 29304	South Africa	Limpopo	NTVL, Blouberg	Adult	19.1	8.1	10.1	9.2	86	32.8	212	45.5
<i>Laniarius ferrugineus transvaalensis</i>	TM 31577	Swaziland	Gauteng	Hornsnek, Magaliesburg	Adult	22.1	7.5	9	96	100	33.4	215	47
<i>Laniarius ferrugineus transvaalensis</i>	TM 31603	Swaziland	Swaziland	Bossig, Swaziland	Adult	21.1	7	8.5	90	90	34	204	47
<i>Laniarius ferrugineus transvaalensis</i>	TM 3364	South Africa	Gauteng	PTA	Adult	23.3	7.5	8.4	90	91	30	186	47.5
<i>Laniarius ferrugineus transvaalensis</i>	TM 3766	South Africa	Gauteng	Hennops River	Adult	22.9	7	8.7	98	95	31.6	216	48.4
<i>Laniarius ferrugineus transvaalensis</i>	TM 41579	South Africa	Limpopo	Transvaal	Adult	25.7	8.8	10.5	95	94	37.1	214	48.9
<i>Laniarius ferrugineus transvaalensis</i>	TM 5402	South Africa	Limpopo	Doornboom, Groot Spelonken	Adult	23.3	7.3	9.5	95	91	32.2	200	47.3
<i>Laniarius ferrugineus transvaalensis</i>	TM 5405	South Africa	Limpopo	Moorddrift	Adult	23.6	7.5	10	93	96	33.4	224	46.8
<i>Laniarius ferrugineus transvaalensis</i>	TM 5410	South Africa	Limpopo	Moorddrift	Adult	23	7.8	9.7	96	94	33.3	220	47.8
<i>Laniarius ferrugineus transvaalensis</i>	TM 5573	South Africa	Gauteng	Hennops River	Adult	21.7	8	9.1	100	100	30.1	236	48.3
<i>Laniarius ferrugineus transvaalensis</i>	TM 5575	South Africa	Western Cape	Sand drif	Adult	20.5	8.5	9.7	90	82	34.6	218	44.8
<i>Laniarius ferrugineus transvaalensis</i>	TM 6591	South Africa	Gauteng	Hamankraal	Adult	23	8.1	8.5	94	92	33.8	207	48

Taxon name	Museum no.	Country	Province	Locality	Age	Bill length (mm)	Bill length (mm)	Bill depth (mm)	Wing length (mm)	Tail length (mm)	Tarsus length (mm)	Total body length (mm)	Total head length (mm)
<i>Laniarius ferrugineus transvaalensis</i>	TM 80593	South Africa	Limpopo	Limpopo, Maluma Boerdery	Adult	22	7.7	9	95	100	32.5	210	47
<i>Laniarius ferrugineus transvaalensis</i>	TM 80667	South Africa	Limpopo	Limpopo, Soutpansberg	Adult	21	7.6	9.7	86	80	32.9	175	43.4
<i>Laniarius ferrugineus transvaalensis</i>	TM 8777	South Africa	Gauteng	Pretoria	Adult	23.3	7	9.7	93	92	32	215	46.4

## Appendix 2.2. List of all records of the geo-referenced data for all individuals examined in this study.

Taxon name	Country	Province	Locality	GPS Coordinates	Latitude	Longitude
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Western cape	Georgida	33°26'00"S, 23°19'00"E	-33,433	23,317
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Western cape	Georgida	33°26'00"S, 23°19'00"E	-33,433	23,317
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Western cape	Knysna dist	34°02'08"S, 23°02'56"E	-34,055	23,544
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Western cape	Knysna dist	34°02'08"S, 23°02'56"E	-34,055	23,544
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Western cape	Knysna dist	34°02'08"S, 23°02'56"E	-34,055	23,544
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Western cape	Knysna dist	34°02'08"S, 23°02'56"E	-34,055	23,544
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Western cape	Knysna dist	34°02'08"S, 23°02'56"E	-34,055	23,544
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Western cape	Knysna dist	34°02'08"S, 23°02'56"E	-34,055	23,544
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Western cape	Knysna dist	34°02'08"S, 23°02'56"E	-34,055	23,544
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Western cape	Nature's valley dist	33°58'50"S, 23°33'33"E	-34,106	23,642
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Western cape	Nature's valley dist	33°58'50"S, 23°33'33"E	-34,106	23,642
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Western cape	Pakhuis Pass dist	32°08'10.5396"S, 19°00'28.6200"E	-32,162	19,08
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Western cape	Tsholweni e-dist	33°S, 22°E	-33	22
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Western cape	Tsholweni e-dist	33°S, 22°E	-33	22
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Western cape	Tsholweni e-dist	33°S, 22°E	-33	22
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Western cape	Tsholweni e-dist	33°S, 22°E	-33	22
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Western cape	Tsholweni e-dist	33°S, 22°E	-33	22
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Western Cape	Albany, c.c	33°18'49.81"S, 26°31'20.98"E	-33,3138	26,522
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Western Cape	Blodschap, Private Nature reserve, SKM	34° S, 20° E	-34	34
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Western Cape	Bontebok park	34°07'30.00"S, 20°22'30.00"E	-34,125	20,375
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Western Cape	Braedasdork, CP	34° 32' 0" S, 20° 2' 0" E	-34,533	20,033
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Western Cape	Braedasdork, CP	34° 32' 0" S, 20° 2' 0" E	-34,533	20,033
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Western Cape	Braedasdork, CP	34° 32' 0" S, 20° 2' 0" E	-34,533	20,033
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Western Cape	Buffels Bay, Knysna Cape Province	34° 5' 0" S, 22° 58' 0" E	-34,083	22,967
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Western Cape	Cape Town	33° 56'S, 18° 29'E	-33,933	18,483
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Western Cape	Cape Town	33° 56'S, 18° 29'E	-33,933	18,483
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Western Cape	Cape Town	33° 56'S, 18° 29'E	-33,933	18,483
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Western Cape	Cape Town	33° 56'S, 18° 29'E	-33,933	18,483
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Western Cape	Cape Town	33° 56'S, 18° 29'E	-33,933	18,483
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Western Cape	Cape town	33°56'S, 18°29'E	-33,933	18,483
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Western Cape	Clanwilliam, Pakhuis	32°07'00"S, 19°01'00"E	-33,117	19,07

Taxon name	Country	Province	Locality	GPS Coordinates	Latitude	Longitude
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Eastern cape	Committees Drift	33°14'05"S, 26°25'29"E	-33,316	26,9
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Eastern Cape	Committees Drift, Albany	33°14'05"S, 26°25'29"E	-33,316	26,9
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Eastern Cape	Committees Drift, Albany	33°14'05"S, 26°25'29"E	-33,316	26,9
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Eastern Cape	Committees Drift, Albany	33°14'05"S, 26°25'29"E	-33,316	26,9
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Eastern Cape	Committees Drift, Albany	33°14'05"S, 26°25'29"E	-33,316	26,9
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Western Cape	Eerste river	34°00'S, 18°43'E	-34	18,717
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Eastern Cape	Fish River Mouth	33°29'S, 27°8'00"E	-33,483	27,133
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Eastern Cape	Fish River Mouth	33°29'S, 27°8'00"E	-33,483	27,133
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Eastern Cape	Fish River Mouth	33°29'S, 27°8'00"E	-33,483	27,133
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Eastern Cape	Fish River Mouth	33°29'S, 27°8'00"E	-33,483	27,133
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Cape Prov	Fort Beaufort	32°47'00"S, 26°38'00"E	-32,783	26,633
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Western Cape	French Hoek	33°55'00"S, 19°07'00"E	-33,917	19,117
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Eastern Cape	Grahamstown	33°22'30.00"S, 26°37'30.00"E	-33,375	26,625
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Eastern Cape	Grahamstown	33°22'30.00"S, 26°37'30.00"E	-33,375	26,625
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Eastern Cape	Grahamstown	33°22'30.00"S, 26°37'30.00"E	-33,375	26,625
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Eastern Cape	Grahamstown	33°22'30.00"S, 26°37'30.00"E	-33,375	26,625
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Western Cape	Haut Bay, Cape town	34°02'S, 18°21'E	-34,033	18,35
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Western Cape	Kirstenbosch	33°59'22"S, 18°25'49"E	-34,044	18,553
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Eastern Cape	Kleinpoort, Grahamstown	32°19'49"S, 24°52'32"E	-32,453	24,622
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Western Cape	Knysna	34°02'00"S, 23°02'00"E	-34,033	23,033
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Western Cape	Knysna	34°02'00"S, 23°02'00"E	-34,033	23,033
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Western Cape	Knysna	34°02'00"S, 23°02'00"E	-34,033	23,033
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Western Cape	Knysna	34°02'00"S, 23°02'00"E	-34,033	23,033
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Western cape	Knysna District	34°02'08"S, 23°02'56"E	-34,055	23,544
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Western Cape	Knysna, c.c	34°02'08"S, 23°02'56"E	-34,055	23,544
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Western Cape	La Motte, Cape town	33°56'00"S, 19°05'00"E	-33,933	19,083
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Western Cape	La Motte, Cape town	33°56'00"S, 19°05'00"E	-33,933	19,083
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Western Cape	Mossel Bay dist, Western Cape	33°52'30.00"S, 22°07'30.00"E	-33,875	22,125
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Western Cape	Nature's Valley	33°58'50"S, 23°33'33"E	-34,106	23,642
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Western Cape	Oudtshoorn	33°35'00"S, 22°12'00"E	-33,583	22,2
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Western Cape	Paarl Lormarins	33°43'27"S, 18°57'21"E	-33,792	18,95
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Eastern Cape	Patensie, Ferndale	33°45'32"S, 24°48'53"E	-33,839	24,947
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Eastern Cape	Patensie, Ferndale	33°45'32"S, 24°48'53"E	-33,839	24,947
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Limpopo	Pulala, Waterberg dist, Transvaal	24° 42' S, 28° 24' E	-24,7	28,4
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Western Cape	Sand drift	33°53'00"S, 18°30'00"E	-33,883	18,5
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Western Cape	The point, Knysna, c.c	34°02'00"S, 23°02'00"E	-34,033	23,033
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Western Cape	The point, Knysna, c.c	34°02'00"S, 23°02'00"E	-34,033	23,033
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Western Cape	Zuurberg, Cape Colony	33°40'06"S, 19°15'48"E	-33,933	19,24
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Western Cape	Goudini Spa	33°40'06"S, 19°15'48"E	-33,5	19,24
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Western Cape	Bontebok NP	34°07'30.00"S, 20°22'30.00"E	-34,0778	20,4539
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Western Cape	Bontebok NP	33°29'18.24"S, 22°32'6.36"E	-34,0778	20,4539
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Western Cape	Le Roux Voorsorg, De Rust	34°07'30.00"S, 20°22'30.00"E	-33,6	22,5333

Taxon name	Country	Province	Locality	GPS Coordinates	Latitude	Longitude
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Western Cape	Beaverlac	32°54'28"S, 19°4'1.9"E	-32,8869	19,0828
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Western Cape	Good Hope	32°45'20.7828"S, 27°43'47.9352"E	-32,808	27,85
<i>Laniarius ferrugineus ferrugineus</i>	South Africa	Western Cape	Good Hope	32°45'20.7828"S, 27°43'47.9352"E	-32,808	27,85
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Adelaide dist	32°42'S, 26°18'E	-32,7	26,3
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Adelaide dist	32°42'S, 26°18'E	-32,7	26,3
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Adelaide District	32°42'S, 26°18'E	-32,7	26,3
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Alexander Forest	33°43'S, 26°21'E	-33,717	26,35
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Alexandria dist	33°39.2'S, 26°24.5'E	-33,653	26,408
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Alexandria dist	33°39.2'S, 26°24.5'E	-33,653	26,408
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Alexandria dist	33°39.2'S, 26°24.5'E	-33,653	26,408
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Alexandria dist	33°39.2'S, 26°24.5'E	-33,653	26,408
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Alexandria dist	33°39.2'S, 26°24.5'E	-33,653	26,408
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Alexandria dist	33°39.2'S, 26°24.5'E	-33,653	26,408
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Alexandria dist	33°39.2'S, 26°24.5'E	-33,653	26,408
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Alexandria dist	33°39.2'S, 26°24.5'E	-33,653	26,408
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Alexandria District	33°39.2'S, 26°24.5'E	-33,653	26,408
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Alexandria District	33°39.2'S, 26°24.5'E	-33,653	26,408
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern Cape	Alexandria Forest, Cape Province	33°43'0" S, 26°25'0" E	-33,717	26,417
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Berlin District	32°53'00"S, 27°35'00"E	-32,883	27,583
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Bluff	29°55'S, 31°00'E	-29,917	31
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Bolo dist	32°22'00"S, 27°37'00"E	-32,367	27,617
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Bolo dist	32°22'00"S, 27°37'00"E	-32,367	27,617
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Bolo dist	32°22'00"S, 27°37'00"E	-32,367	27,617
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Bolo dist	32°22'00"S, 27°37'00"E	-32,367	27,617
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Breakfast Vlei dist	33°05'00"S, 26°57'00"E	-33,833	26,95
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Breakfast Vlei dist	33°05'00"S, 26°57'00"E	-33,833	26,95
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Breakfast Vlei dist	33°05'00"S, 26°57'00"E	-33,833	26,95
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Breakfast Vlei dist	33°05'00"S, 26°57'00"E	-33,833	26,95
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Breakfast Vlei District	33°05'00"S, 26°57'00"E	-33,833	26,95
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Cambria dist	33°40'00"S, 24°34'00"E	-33,15	24,683
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Cambria dist	33°40'00"S, 24°34'00"E	-33,15	24,683
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Cambria District	33°40'00"S, 24°34'00"E	-33,15	24,683
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Camperdown	29°44'S, 30°32'E	-29,733	30,533
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Camperdown	29°44'S, 30°32'E	-29,733	30,533
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Cape natal border	30°20'32"S, 28°48'22"E	-31,223	28,861
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Cape Recife	34°01'43"S, 25°42'02"E	-34,136	25,65
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Cathedral peak forestry, Natal	28°55'24"S, 29°08'02"E	-28,984	29,139
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Cathedral peak forestry, Natal	28°55'24"S, 29°08'02"E	-28,984	29,139
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Cathedral peak forestry, Natal	28°55'24"S, 29°08'02"E	-28,984	29,139
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Christmas Rock	33°12'00"S, 27°38'00"E	-33,2	27,15

Taxon name	Country	Province	Locality	GPS Coordinates	Latitude	Longitude
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Cockscomb dist	33°34'00"S, 24°40'59"E	-33,567	24,831
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern Cape	Coega River near Port Elizabeth	33°48'00"S, 25°42'00"E	-33,8	25,7
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Committees	33°09'00" S, 26°50'00"E	-33,15	26,833
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Committees	33°09'00" S, 26°50'00"E	-33,15	26,833
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Committees	33°09'00" S, 26°50'00"E	-33,15	26,833
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	committees	33°09'00" S, 26°50'00"E	-33,15	26,833
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	committees	33°09'00" S, 26°50'00"E	-33,15	26,833
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Committees	33°09'00" S, 26°50'00"E	-33,15	26,833
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Committees	33°09'00" S, 26°50'00"E	-33,15	26,833
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Committees	33°09'00" S, 26°50'00"E	-33,15	26,833
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Committees	33°09'00" S, 26°50'00"E	-33,15	26,833
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Committees	33°09'00" S, 26°50'00"E	-33,15	26,833
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Committees	33°09'00" S, 26°50'00"E	-33,15	26,833
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Committees	33°09'00" S, 26°50'00"E	-33,15	26,833
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Debe Nek dist	32°49'00"S, 27°09'00"E	-32,817	27,15
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Debe Nek dist	32°49'00"S, 27°09'00"E	-32,817	27,15
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Debe Nek dist	32°49'00"S, 27°09'00"E	-32,817	27,15
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Debe Nek dist	32°49'00"S, 27°09'00"E	-32,817	27,15
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Debe Nek dist	32°49'00"S, 27°09'00"E	-32,817	27,15
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Debe Nek District	32°49'00"S, 27°09'00"E	-32,817	27,15
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Debe Nek District	32°49'00"S, 27°09'00"E	-32,817	27,15
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Debe Nek District	32°49'00"S, 27°09'00"E	-32,817	27,15
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Debe Nek District	32°49'00"S, 27°09'00"E	-32,817	27,15
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Debe Nek District	32°49'00"S, 27°09'00"E	-32,817	27,15
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Debe Nek District	32°49'00"S, 27°09'00"E	-32,817	27,15
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Donnybrook, Polela	29°56'00"S, 29°52'00"E	-29,933	29,867
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Durban	29°51'28.35"S, 31°01'39.29"E	-29,8579	31,028
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Durban	29°51'28.35"S, 31°01'39.29"E	-29,8579	31,028
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Durban	29°51'28.35"S, 31°01'39.29"E	-29,8579	31,028
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Durban area	29°51'28.35"S, 31°01'39.29"E	-29,8579	31,028
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Durban dist	29°51'28.35"S, 31°01'39.29"E	-29,8579	31,028
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Durban, Bluff	29°55' S, 31°00'E	-29,917	31
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Durban, Bluff, Wentworth forest	29°55' S, 31°00'E	-29,917	31
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Durban, Bluff, Wentworth forest	29°55' S, 31°00'E	-29,917	31
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Durban, Bluff, Wentworth forest	29°55' S, 31°00'E	-29,917	31
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Durban, Bluff, Wentworth forest	29°55' S, 31°00'E	-29,917	31
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Durban, Bluff, Wentworth forest	29°55' S, 31°00'E	-29,917	31
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Durban, Bluff, Wentworth forest	29°55' S, 31°00'E	-29,917	31
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Durban, Bluff, Wentworth forest	29°55' S, 31°00'E	-29,917	31
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Durban, Kloof	29°47' S, 30°50'E	-29,783	30,833
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Durban, Reunion Rocks	29°43'00"S, 31°04'00"E	-29,717	31,067
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Durban, Reunion Rocks	29°43'00"S, 31°04'00"E	-29,717	31,067
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Durban, Shongweni	29°51'0" S, 30°43'0"E	-29,85	30,716
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Durban, Shongweni Dam	29°51'0" S, 30°43'0"E	-29,85	30,717

Taxon name	Country	Province	Locality	GPS Coordinates	Latitude	Longitude
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Durban, Shongweni Dam	29°51'0"S, 30°43'0"E	-29,85	30,717
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Durban, Shongweni Dam	29°51'0"S, 30°43'0"E	-29,85	30,717
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Durban, Shongweni Dam	29°51'00"S, 30°43'00"E	-29,85	30,717
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Durban, Shongweni Dam	29°51'0"S, 30°43'0"E	-29,85	30,717
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Durban, Shongweni Dam	29°51'00"S, 30°43'00"E	-29,85	30,717
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Durban, Umhlanga River	29°51'00"S, 30°43'00"E	-29,85	30,716
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Durban, Umhlanga River	29°51'00"S, 30°43'00"E	-29,85	30,716
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Durban, Umhlanga River	29°51'00"S, 30°43'00"E	-29,85	30,716
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Durban, Umhlanga River	29°51'00"S, 30°43'00"E	-29,85	30,716
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Durban, Umhlanga River	29°51'00"S, 30°43'00"E	-29,85	30,716
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Durban, Umhlanga River	29°51'00"S, 30°43'00"E	-29,85	30,716
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Durban, Umhlanga Rocks	29°44'S, 30°32'E	-29,733	30,533
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Durban, Umhlanga Rocks	29°44'S, 30°32'E	-29,733	30,533
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Fish River Station	31°54'00"S, 25°25'00"E	-31,9	25,417
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Fort Jackson	32°54'00"S, 27°42'00"E	-32,9	27,7
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern Cape	Fort Pato	32°59'00"S, 27°39'00"E	-32,983	27,65
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Fort Pato	32°59'00"S, 27°39'00"E	-32,983	27,65
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Fort Pato	32°59'00"S, 27°39'00"E	-32,983	27,65
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Fort Pato	32°59'00"S, 27°39'00"E	-32,983	27,65
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern Cape	Glen Grey	31°00"S, 27°01'00"E	-31	31,017
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Gonubie dist	32°56'00"S, 28°01'00"E	-32,933	28,017
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Gonubie dist	32°56'00"S, 28°01'00"E	-32,933	28,017
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Gonubie dist	32°56'00"S, 28°01'00"E	-32,933	28,017
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Gonubie dist	32°56'00"S, 28°01'00"E	-32,933	28,017
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Goodhope	32°45'20.7828"S, 27°43'47.9352"E	-32,808	27,85
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Goodhope Estate, 9.3 km W Boston	29° 41' 42"S, 29° 55' 54.012"E	-29,8	30,067
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Goodhope Estate, 9.3 km W Boston	29° 41' 42"S, 29° 55' 54.012"E	-29,8	30,067
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Graaff-Reinett dist	32°15'08"S, 24°32'26"E	-32,272	24,605
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Graaff-Reinett dist	32°15'08"S, 24°32'26"E	-32,272	24,605
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Graaff-Reinett dist	32°15'08"S, 24°32'26"E	-32,272	24,605
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern Cape	Grahamstown	33°22'30.00"S, 26°37'30.00"E	-33,375	26,625
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern Cape	Grahamstown	33°22'30.00"S, 26°37'30.00"E	-33,375	26,625
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern Cape	Grahamstown	33°22'30.00"S, 26°37'30.00"E	-33,375	26,625
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern Cape	Grahamstown	33°22'30.00"S, 26°37'30.00"E	-33,375	26,625
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern Cape	Grahamstown, C.C	33°22'30.00"S, 26°37'30.00"E	-33,375	26,625
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern Cape	Grahamstown, C.C	33°22'30.00"S, 26°37'30.00"E	-33,375	26,625
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern Cape	Happy Valley, Port Elizabeth	32° 28' 0" S, 27° 4' 0" E	-32,467	27,067
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Ingwavuma Lebombo Mts	26°15'00"S, 32°00'00"E	-26,25	32
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Ingwavuma Lebombo Mts	26°15'00"S, 32°00'00"E	-26,25	32
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Ingwavuma Lebombo Mts	26°15'00"S, 32°00'00"E	-26,25	32
<i>Laniarius ferrugineus natalensis</i>	South Africa	Swaziland	Ingwavuma river	26°57'42"S, 32°17'39"E	-27,067	32,391
<i>Laniarius ferrugineus natalensis</i>	South Africa	Swaziland	Ingwavuma river	26°57'42"S, 32°17'39"E	-27,067	32,391

Taxon name	Country	Province	Locality	GPS Coordinates	Latitude	Longitude
<i>Laniarius ferrugineus natalensis</i>	South Africa	Swaziland	Ingwavuma river	26°57'42"S, 32°17'39"E	-27,067	32,391
<i>Laniarius ferrugineus natalensis</i>	South Africa	Swaziland	Ingwavuma river	26°57'42"S, 32°17'39"E	-27,067	32,391
<i>Laniarius ferrugineus natalensis</i>	South Africa	Swaziland	Ingwavuma river	26°57'42"S, 32°17'39"E	-27,067	32,391
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Kei Bridge	32°31'00"S, 27°58'00"E	-32,15	27,95
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Kei Bridge	32°31'00"S, 27°58'00"E	-32,15	27,95
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Kei Bridge	32°31'00"S, 27°58'00"E	-32,15	27,95
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Kei Bridge	32°31'00"S, 27°58'00"E	-32,15	27,95
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Kenton	33°40'00"S, 26°39'00"E	-33,667	26,65
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern Cape	Kenton-on-Sea	33°42'00"S, 26°41'00"E	-33,7	26,683
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Kidds Beach dist	33°09'00"S, 27°41'00"E	-33,15	27,683
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Kidds Beach dist	33°09'00"S, 27°41'00"E	-33,15	27,683
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Kidds Beach dist	33°09'00"S, 27°41'00"E	-33,15	27,683
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Kidds Beach dist	33°09'00"S, 27°41'00"E	-33,15	27,683
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Kidds Beach dist	33°09'00"S, 27°41'00"E	-33,15	27,683
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Kidds Beach dist	33°09'00"S, 27°41'00"E	-33,15	27,683
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Kidds Beach dist	33°09'00"S, 27°41'00"E	-33,15	27,683
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Kidds Beach dist	33°09'00"S, 27°41'00"E	-33,15	27,683
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Kidd's Beach District	33°09'00"S, 27°41'00"E	-33,15	27,683
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Kilgobbin, Dargle	29° 32' 00" S, 30° 02' 00" E	-29,533	30,033
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Kilgobbin, Dargle	29°32'00"S, 30°02'00"E	-29,533	30,033
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern Cape	King William's Town	32°53'00"S, 27°24'00"E	-32,883	27,4
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern Cape	King William's Town	32°53'00"S, 27°24'00"E	-32,883	27,4
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern Cape	King William's Town	32°53'00"S, 27°24'00"E	-32,883	27,4
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern Cape	King William's Town	32°53'00"S, 27°24'00"E	-32,883	27,4
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern Cape	King William's Town	32°53'00"S, 27°24'00"E	-32,883	27,4
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern Cape	King William's Town	32°53'00"S, 27°24'00"E	-32,883	27,4
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern Cape	King William's Town	32°53'00"S, 27°24'00"E	-32,883	27,4
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern Cape	King William's Town	32°53'00"S, 27°24'00"E	-32,883	27,4
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern Cape	King William's Town	32°53'00"S, 27°24'00"E	-32,883	27,4
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern Cape	King William's Town	32°53'00"S, 27°24'00"E	-32,883	27,4
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern Cape	King William's Town	32°53'00"S, 27°24'00"E	-32,883	27,4
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern Cape	King William's Town	32°53'00"S, 27°24'00"E	-32,883	27,4
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern Cape	King William's Town	32°53'00"S, 27°24'00"E	-32,883	27,4
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Kleinpoort	32°19'49"S, 24°52'32"E	-32,453	24,622
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern Cape	Kleinpoort, Grahamstown	32°19'49"S, 24°52'32"E	-32,453	24,622
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Klipfontein, Transvaal	24°08'56.37S, 28°19'24.74"E	-24,133	28,3
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Kloof, Natal	29°47'0"S, 30°50'0"E	-29,783	30,833
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Komga dist	32°35'00"S, 27°54'00"E	-32,583	27,9
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Kwelera	32°48'05" S, 27°88'00"E	-32,814	28,467
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	KWT dist	32°53' S, 27°24'E	-32,883	27,4
<i>Laniarius ferrugineus natalensis</i>	South Africa	Free States	Lindesthof, Bloemfontein	29°08'00"S, 26°12'00"E	-29,133	26,2
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Loerie dist	33°52'21.75"S, 25°01'47.82"E	-33,927	25,15
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Manaba	27°17'10.61"S, 32°25'36.12"E	-27,312	32,517
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Manderston	29°44'00"S, 30°26'00"E	-29,733	30,433
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Maputaland	26°59'S, 32°30'E	-26,983	32,5

Taxon name	Country	Province	Locality	GPS Coordinates	Latitude	Longitude
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Maritzburg, Natal	29°37'00"S, 30°23'00"E	-29,617	30,383
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Maritzburg, Natal	29°37'00"S, 30°23'00"E	-29,617	30,383
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Maritzburg, Natal	29°37'00"S, 30°23'00"E	-29,617	30,383
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Maritzburg, Natal	29°37'00"S, 30°23'00"E	-29,617	30,383
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Maritzburg, Natal	29°37'00"S, 30°23'00"E	-29,617	30,383
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Matatiela dist	33°20'32" S, 28°48'22"E	-33,422	28,861
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Mt Fletcher dist	30°41'00"S, 28°31'00"E	-30,683	28,517
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Mt. Edgcombe, Natal	29°42'00"S, 31°02'00"E	-29,7	31,033
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Natal	29°S, 31°E	-29	31
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Natal	29°S, 31°E	-29	31
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Natal	29°S, 31°E	-29	31
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Ncera	32°49'00"S, 26°53'00"E	-32,817	26,883
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Ndumu, Zululand	26°55'00"S, 32°16'00"E	-26,917	32,267
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Needs Camp	32°59'00"S, 27°35'00"E	-32,983	27,583
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Needs Camp	32°59'00"S, 27°35'00"E	-32,983	27,583
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Needs Camp	32°59'00"S, 27°35'00"E	-32,983	27,583
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Needs Camp	32°59'00"S, 27°35'00"E	-32,983	27,583
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Needs Camp	32°59'00"S, 27°35'00"E	-32,983	27,583
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Needs Camp	32°59'00"S, 27°35'00"E	-32,983	27,583
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Ngele (Weza) forest	30°36'12.1"S, 29°39'59.2"E	-30,634	29,814
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Ngoye Forest	28°50'48"S, 31°43'50"E	-28,966	31,856
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Ngoye Forest	28°50'48"S, 31°43'50"E	-28,966	31,856
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Ngoye Forest	28°50'48"S, 31°43'50"E	-28,966	31,856
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Nkandhla Forest	28°43'51.3"S, 31°79.6"E	-28,86	31,144
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Nkandhla Forest	28°43'51.3"S, 31°79.6"E	-28,86	31,144
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	P.E. dist	33°55'57.50"S, 25°34'11.82"E	-33,9326	25,57
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	P.E. dist	33°55'57.50"S, 25°34'11.82"E	-33,9326	25,57
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	P.E. dist	33°55'57.50"S, 25°34'11.82"E	-33,9326	25,57
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	P.E. dist	33°55'57.50"S, 25°34'11.82"E	-33,9326	25,57
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	P.E. dist	33°55'57.50"S, 25°34'11.82"E	-33,9326	25,57
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	P.E. dist	33°55'57.50"S, 25°34'11.82"E	-33,9326	25,57
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	P.E. dist	33°55'57.50"S, 25°34'11.82"E	-33,9326	25,57
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Peddle dist	33°07'30.00"S, 27°07'30.00"E	-33,125	27,125
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Pennington	30°23'S, 30°42'E	-30,383	30,7
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Pennington	30°23'S, 30°42'E	-30,383	30,7
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Pennington	30°23'S, 30°42'E	-30,383	30,7
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Pietermaritzburg	29°37'00"S, 30°23'00"E	-29,617	30,383
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Pietermaritzburg	29°37'00"S, 30°23'00"E	-29,617	30,383
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Pietermaritzburg	29°37'00"S, 30°23'00"E	-29,617	30,383
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Pietermaritzburg, Bisley	29°39'00"S, 30°23'00"E	-29,65	30,383
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Pietermaritzburg, Table Mountain	29°37'S, 36°23'E	-29,617	36,383
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Pietermaritzburg, Table Mountain	29°37'S, 36°23'E	-29,617	36,383
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Pietermaritzburg, Table Mountain	29°37'S, 36°23'E	-29,617	36,383
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Pietermaritzburg, Table Mountain	29°37'S, 36°23'E	-29,617	36,383



Taxon name	Country	Province	Locality	GPS Coordinates	Latitude	Longitude
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Pietermaritzburg, Table Mountain	29°37'S, 36°23'E	-29,617	36,383
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Pietermaritzburg, Table Mountain	29°37'S, 36°23'E	-29,617	36,383
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Pietermaritzburg, Table Mountain	29°37'S, 36°23'E	-29,617	36,383
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Pirie Mission	32°47'00" S, 27°05'00"E	-32,783	27,083
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern Cape	Port Elizabeth	33°55'57"S, 25°34'11.82"E	-34,075	25,6
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern Cape	Port Elizabeth	33°55'57"S, 25°34'11.82"E	-34,075	25,6
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Qudeni Forest	28°38'00"S, 30°50'00"E	-28,633	30,833
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	R.Umgeni river, Natal	29°48'36"S, 31°02'08"E	-29,9	31,055
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	R.Umgeni river, Natal	29°48'36"S, 31°02'08"E	-29,9	31,055
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Red Hill Coast	29°47'0.24"S, 31°01'23.88" E	-29,784	31,683
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Scottburgh, Mpambanyoni River	30°16'60"S, 30°45'00"E	-30,434	30,75
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Scottburgh, Mpambanyoni River	30°16'60"S, 30°45'00"E	-30,434	30,75
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Scottburgh, Mpambanyoni River	30°16'60"S, 30°45'00"E	-30,434	30,75
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Shimula's Pont, Pongola River	26°51'21"S, 32°20'47"E	-26,908	32,461
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Shongweni dist	29°51'S, 30°43'E	-29,85	30,717
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Somerset East	32°43'0"S, 25°35'0"E	-32,717	25,583
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Stanmore Farm, on Pongola River	27°21'23.76"S, 31°50'33.15" E	-27,083	31,925
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern Cape	Stutterheim, Bolo Bridge	32°34'00"S, 27°25'00"E	-32,5667	27,417
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern Cape	Stutterheim, Bolo Bridge	32°34'00"S, 27°25'00"E	-32,5667	27,417
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern Cape	Stutterheim, Bolo Bridge	32°34'00"S, 27°25'00"E	-32,5667	27,417
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern Cape	Stutterheim, Bolo Bridge	32°34'00"S, 27°25'00"E	-32,5667	27,417
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern Cape	Stutterheim, Bolo Bridge	32°34'00"S, 27°25'00"E	-32,5667	27,417
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	The Haven dist	32°14'00"S, 28°54'00"E	-32,233	28,9
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	The Haven dist	32°14'00"S, 28°54'00"E	-32,233	28,9
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	The Haven dist	32°14'00"S, 28°54'00"E	-32,233	28,9
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	The Haven dist	32°14'00"S, 28°54'00"E	-32,233	28,9
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	The Haven dist	32°14'00"S, 28°54'00"E	-32,233	28,9
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	The Haven dist	32°14'00"S, 28°54'00"E	-32,233	28,9
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Thornpark	32°55'00"S, 27°38'00"E	-32,917	27,633
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Umgeni river	29°48'36"S, 31°02'08"E	-29,9	31,055
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Umgeni river	29°48'36"S, 31°02'08"E	-29,9	31,055
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Umgeni river	29°48'36"S, 31°02'08"E	-29,9	31,055
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Umgeni river	29°48'36"S, 31°02'08"E	-29,9	31,055
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Umkomaas	30°14'04.54"S, 30°45'25.36"E	-30,2346	30,757
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	weenen Thorns	28° 52.00'S, 30° 05.00'E	-28,8667	30,083
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Weza-Ingeli Forest	30°35'S, 29°44' E	-30,583	29,733
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Weza-Ingeli Forest	30°35'S, 29°44'E	-30,583	29,733
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	White Umfolozi	28°21'00"S, 31°58'00" E	-28,35	31,967
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern cape	Willowmore dist	33°17'S, 23°29'E	-33,283	23,483
<i>Laniarius ferrugineus natalensis</i>	South Africa	Western Cape	Zuurberg	33°22'00"S, 26°11'00"E	-33,933	26,183
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern Cape	Stead Farm, 20 kms off Tarkastdt	32°1'0"S, 26°16'0"E	-32.0394	26.2933
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern Cape	Stead Farm, 20 kms off Tarkastdt	32°1'0"S, 26°16'0"E	-32.0394	26.2933
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern Cape	Stead Farm, 20 kms off Tarkastdt	32°1'0"S, 26°16'0"E	-32.0394	26.2933

Taxon name	Country	Province	Locality	GPS Coordinates	Latitude	Longitude
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern Cape	Stead Farm, 20 kms off Tarkastdt	32°1'0"S, 26°16'0"E	-32.0394	26.2933
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern Cape	close to Research Center, Great Fish NR	33°3'55"S, 26°49'13"E	-33.0654	26,8204
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern Cape	close to Research Center, Great Fish NR	33°3'55"S, 26°49'13"E	-33,0654	26,8204
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern Cape	close to Research Center, Great Fish NR	33°3'55"S, 26°49'13"E	-33,0654	26,8204
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern Cape	close to Research Center, Great Fish NR	33°3'55"S, 26°49'13"E	-33,0654	26,8204
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern Cape	close to Research Center, Great Fish NR	33°3'55"S, 26°49'13"E	-33,0654	26,8204
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern Cape	close to Research Center, Great Fish NR	33°3'55"S, 26°49'13"E	-33,0654	26,8204
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern Cape	close to Research Center, Great Fish NR	33°3'55"S, 26°49'13"E	-33,0654	26,8204
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern Cape	Doodsklip Camp, Baviaanskloof Nature Reserve	33°29'26"S, 23°38'06"E	-33,6588	24,43164
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern Cape	Doodsklip Camp, Baviaanskloof NR, Cacadu District	33°29'26"S, 23°38'06"E	-33,6588	24,43165
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern Cape	Fort Fordyce, close to Mpopu Nature Reserve	32°41'3"S, 26°29'45"E	-32,6666	26,4833
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern Cape	Fort Fordyce, close to Mpopu Nature Reserve	32°41'3"S, 26°29'45"E	-32,6666	26,4833
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern Cape	Fort Fordyce, close to Mpopu Nature Reserve	32°41'3"S, 26°29'45"E	-32,6666	26,4833
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern Cape	Fort Fordyce, close to Mpopu Nature Reserve	32°41'3"S, 26°29'45"E	-32,6666	26,4833
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern Cape	Fort Fordyce, close to Mpopu NR, Amathole District	32°41'3"S, 26°29'45"E	-32,6666	26,4833
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern Cape	Hunter's Lodge, Cacadu District	33°56'39"S, 25°54'48"E	-33,6273	26,5083
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern Cape	Shamwari Game Reserve, Cacadu District	33°28'40"S, 26°2'10"E	-33,4929	26,0637
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern Cape	Shamwari Game Reserve, Cacadu District	33°28'40"S, 26°2'10"E	-33,4929	26,0637
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern Cape	Shamwari Game Reserve, Cacadu District	33°28'40"S, 26°2'10"E	-33,4929	26,0637
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern Cape	Shamwari Game Reserve, Cacadu District	33°28'40"S, 26°2'10"E	-33,4929	26,0637
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern Cape	Tent site, Shamwari Game Reserve, Cacadu District	33°28'40"S, 26°2'10"E	-33,5068	26,0246
<i>Laniarius ferrugineus natalensis</i>	South Africa	Kwa-Zulu Natal	Natal	29°S, 31°E	-29	31
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern Cape	Mpopu Nature Reserve	32°37'48"S, 23°38'06"E	-32,601	26,5746
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern Cape	Shamwari Game Reserve	33°28'40"S, 26°2'10"E	-33,4929	26,0637
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern Cape	Shamwari Game Reserve	33°28'40"S, 26°2'10"E	-33,4929	26,0637
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern Cape	Great Fish nature reserve	33°3'55"S, 26°49'13"E	-33,0654	26,8204
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern Cape	Dooringkloof bush camp, Baviaanskloof NR	33°29'26"S, 23°38'06"E	-33,65	24,3833
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern Cape	Great Fish nature reserve	33°3'55"S, 26°49'13"E	-33,0654	26,8204
<i>Laniarius ferrugineus natalensis</i>	South Africa	Eastern Cape	Hunter's Lodge	33°56'39"S, 25°54'48"E	-33,6273	26,5083
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern cape	Black Rock	32°01'00"S, 29°06'00"E	-32,017	29,1
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern cape	Black Rock	32°01'00"S, 29°06'00"E	-32,017	29,1
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern cape	Cambridge dist	32°58'00"S, 27°53'00"E	-32,967	27,883
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern cape	Cambridge dist	32°58'00"S, 27°53'00"E	-32,967	27,883
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Kwa-Zulu Natal	Durban, Reunion Rocks	29°43'00"S, 31°4'00"E	-29,717	31,067
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern cape	Dwesa dist	32°17'0" S, 28°47'0"E	-32,283	28,783
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern cape	Dwesa dist	32°17'0" S, 28°47'0"E	-32,283	28,783
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern cape	Dwesa dist	32°17'0" S, 28°47'0"E	-32,283	28,783
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern cape	Dwesa dist	32°17'0" S, 28°47'0"E	-32,283	28,783
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern cape	Dwesa dist	32°17'0" S, 28°47'0"E	-32,283	28,783
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern cape	East London dist	32°59'S, 27°52'E	-32,983	27,867
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern cape	East London dist	32°59'S, 27°52'E	-32,983	27,867
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern cape	East London dist	32°59'S, 27°52'E	-32,983	27,867
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern cape	East London dist	32°59'S, 27°52'E	-32,983	27,867
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern cape	East London dist	32°59'S, 27°52'E	-32,983	27,867

Taxon name	Country	Province	Locality	GPS Coordinates	Latitude	Longitude
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern cape	East London dist	32°59'S, 27°52'E	-32,983	27,867
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern cape	East London dist	32°59'S, 27°52'E	-32,983	27,867
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern cape	East London District	32°59'S, 27°52'E	-32,983	27,867
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern cape	East London District	32°59'S, 27°52'E	-32,983	27,867
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	Embotyi, Lusikisiki	31°21'00"S, 29°35'00"E	-31,35	29,583
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	Embotyi, Lusikisiki	31°21'00"S, 29°35'00"E	-31,35	29,583
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	Embotyi, Lusikisiki	31°21'00"S, 29°35'00"E	-31,35	29,583
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern cape	Engcobo District	31°40'00"S, 28°00'00"E	-31,667	28
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern cape	Engcobo District	31°40'00"S, 28°00'00"E	-31,667	28
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern cape	Hluleka dist	31°49'00"S, 29°18'00"E	-31,817	29,3
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern cape	Hluleka dist	31°49'00"S, 29°18'00"E	-31,817	29,3
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern cape	Lusikisiki District	31° 21'43"S, 29°34'23"E	-31,469	29,631
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Kwa-Zulu Natal	Margate	30°51'00"S, 30°22'00"E	-30,85	30,367
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Kwa-Zulu Natal	Mkambati dist	31°17'00"S, 29°57'00"E	-31,283	29,95
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern cape	Mout Ayliff	30°48'33" S, 29°22'01"E	-30,892	29,37
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Cape Prov	Mt Ayliff	30°48'33" S, 29°22'01"E	-30,892	29,37
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	Mutafufu River, Sea View, Near River Mouth	31°33'00"S, 29°38'00"E	-31,55	29,633
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	Mutafufu River, Sea View, Near River Mouth	31°33'00"S, 29°38'00"E	-31,55	29,633
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	Mutafufu River, Sea View, Near River Mouth	31°33'00"S, 29°38'00"E	-31,55	29,633
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	Mutafufu River, Sea View, Near River Mouth	31°33'00"S, 29°38'00"E	-31,55	29,633
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	Mutafufu River, Sea View, Near River Mouth	31°33'00"S, 29°38'00"E	-31,55	29,633
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	Mutafufu River, Sea View, Near River Mouth	31°33'00"S, 29°38'00"E	-31,55	29,633
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Kwa-Zulu Natal	Ngele (Weza) forest	30°36'12.1"S, 29°39'59.2"E	-30,634	29,814
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	Nggeleni	31°40'00"S, 29°02'00"E	-31,667	29,033
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	Ngqeleni dist, W.Pondoland	31° 50' S, 29° 3' E	-31,8333	29,05
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	Ngqeleni dist, W.Pondoland	31° 50' S, 29° 3' E	-31,8333	29,05
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern cape	Nthlonzana	32°40'00"S, 28°47'00"E	-32,667	28,783
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	Pondoland	31°37'30.00"S, 29°37'30.00"E	-31,625	29,625
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Kwa-Zulu Natal	Port Edward dist	31°03'00"S, 30°13'00"E	-31,05	30,217
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Kwa-Zulu Natal	Port Edward dist	31°03'00"S, 30°13'00"E	-31,05	30,217
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	Port S.t John's	31°37'30.00"S, 29°37'30.00"E	-31,625	29,625
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	Port S.t John's	31°37'30.00"S, 29°37'30.00"E	-31,625	29,625
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	Port S.t John's	31°37'30.00"S, 29°37'30.00"E	-31,625	29,625
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	Port S.t John's	31°37'30.00"S, 29°37'30.00"E	-31,625	29,625
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	Port St John	31°37'30.00"S, 29°37'30.00"E	-31,625	29,625
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	Port St John	31°37'30.00"S, 29°37'30.00"E	-31,625	29,625
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	Port St Johns	31°37'30.00"S, 29°37'30.00"E	-31,625	29,625
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	Port St Johns	31°37'30.00"S, 29°37'30.00"E	-31,625	29,625
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	Port St Johns	31°37'30.00"S, 29°37'30.00"E	-31,625	29,625
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	Port St Johns	31°37'30.00"S, 29°37'30.00"E	-31,625	29,625
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	Port St Johns	31°37'30.00"S, 29°37'30.00"E	-31,625	29,625
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	Port St Johns	31°37'30.00"S, 29°37'30.00"E	-31,625	29,625
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	Port St Johns	31°37'30.00"S, 29°37'30.00"E	-31,625	29,625
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	Port St John's	31°37'30.00"S, 29°37'30.00"E	-31,625	29,625
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	Port St John's	31°37'30.00"S, 29°37'30.00"E	-31,625	29,625
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	Port St John's	31°37'30.00"S, 29°37'30.00"E	-31,625	29,625
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	Port St John's	31°37'30.00"S, 29°37'30.00"E	-31,625	29,625
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	Port St John's	31°37'30.00"S, 29°37'30.00"E	-31,625	29,625
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	Port St John's	31°37'30.00"S, 29°37'30.00"E	-31,625	29,625
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	Port St John's	31°37'30.00"S, 29°37'30.00"E	-31,625	29,625

Taxon name	Country	Province	Locality	GPS Coordinates	Latitude	Longitude
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	Port St John's dist	31°37'30.00"S, 29°37'30.00"E	-31,625	29,625
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	Port St John's, Nor Pondoland	31°37'30.00"S, 29°37'30.00"E	-31,625	29,625
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	Port St John's, Pondoland	31°37'30.00"S, 29°37'30.00"E	-31,625	29,625
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	Port St Johns, W.Pondoland	31°37'30.00"S, 29°37'30.00"E	-31,625	29,625
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	Port St Johns, W.Pondoland	31°37'30.00"S, 29°37'30.00"E	-31,625	29,625
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern cape	Port St. Johns dist	31°37'30.00"S, 29°37'30.00"E	-31,625	29,625
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern cape	Port St. Johns dist	31°37'30.00"S, 29°37'30.00"E	-31,625	29,625
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern cape	Port St. Johns dist	31°37'30.00"S, 29°37'30.00"E	-31,625	29,625
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern cape	Port St. Johns dist	31°37'30.00"S, 29°37'30.00"E	-31,625	29,625
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern cape	Port St. Johns dist	31°37'30.00"S, 29°37'30.00"E	-31,625	29,625
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern cape	Port St. Johns dist	31°37'30.00"S, 29°37'30.00"E	-31,625	29,625
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern cape	Port St. Johns dist	31°37'30.00"S, 29°37'30.00"E	-31,625	29,625
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern cape	Port St. Johns dist	31°37'30.00"S, 29°37'30.00"E	-31,625	29,625
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern cape	Port St. Johns dist	31°37'30.00"S, 29°37'30.00"E	-31,625	29,625
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern cape	Port St. Johns dist	31°37'30.00"S, 29°37'30.00"E	-31,625	29,625
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern cape	Port St. Johns dist	31°37'30.00"S, 29°37'30.00"E	-31,625	29,625
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	Shimula's Pont, Pongola River	26°51'21"S, 32°20'47"E	-26,908	32,461
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	Shimula's Pont, Pongola River	26°51'21"S, 32°20'47"E	-26,908	32,461
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern cape	Tombo Mission District	31°37'25.45"S, 29°23'30.57"E	-31,688	30,233
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	Tombo mission museum	31°37'25.45"S, 29°23'30.57"E	-31,688	30,233
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	W. Pondoland	31°37'30.00"S, 29°37'30.00"E	-31,625	29,625
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern cape	Wooldridge	33°13'00"S, 27°14'00"E	-33,217	27,233
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	Cape St Francis	34° 12'22" S, 24° 49' 48" E	-34.0089	25.3556
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	Cape St Francis	34° 12'22" S, 24° 49' 48" E	-34.0089	25.3556
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	Kasouga	33° 38'53" S, 26° 44' 10" E	-33.6483	26.7711
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	Kasouga	33° 38'53" S, 26° 44' 10" E	-33.6483	26.7711
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	Kasouga	33° 38'53" S, 26° 44' 10" E	-33.6483	26.7711
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	Kasouga	33° 38'53" S, 26° 44' 10" E	-33.6483	26.7711
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	Kasouga	33° 38'53" S, 26° 44' 10" E	-33.6483	26.7711
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	Kasouga	33° 38'53" S, 26° 44' 10" E	-33.6483	26.7711
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	Kasouga	33° 38'53" S, 26° 44' 10" E	-33.6483	26.7711
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	Kasouga	33° 38'53" S, 26° 44' 10" E	-33.6483	26.7711
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	Kasouga	33° 38'53" S, 26° 44' 10" E	-33.6483	26.7711
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	Morgans Bay	32° 42'11" S, 28° 20' 9" E	-32.6881	28.4308
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	Morgans Bay	32° 42'11" S, 28° 20' 9" E	-32.6881	28.4308
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	Morgans Bay	32° 42'11" S, 28° 20' 9" E	-32.6881	28.4308
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	10 kms Port St Johns	31°37'30.00"S, 29°37'30.00"E	-31.6056	29.55
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	10 kms Port St Johns	31°37'30.00"S, 29°37'30.00"E	-31.6056	29.55
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	10 kms Port St Johns	31°37'30.00"S, 29°37'30.00"E	-31.6056	29.55
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Kwa-Zulu Natal	Pennington and Umdoni Golf	30° 22'58" S, 30° 41' 31" E	-30.3092	30.7508

Taxon name	Country	Province	Locality	GPS Coordinates	Latitude	Longitude
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Kwa-Zulu Natal	Pennington and Umdoni Golf	30° 22'58" S, 30° 41' 31" E	-30.3092	30.7508
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Kwa-Zulu Natal	Pennington and Umdoni Golf	30° 22'58" S, 30° 41' 31" E	-30.3092	30.7508
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	Mbotye	31° 27'43" S, 29° 44' 6" E	-32.0808	29.0642
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	Morgans Bay	32° 42'11" S, 28° 20' 9" E	-32.6881	28.4308
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	Kleine Monde, close to Kasouga	33° 32'8.66" S, 27° 2' 46.20" E	-33.648	27.0461
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Kwa-Zulu Natal	Lorraine Estates, Uzumbe	30° 29'5.3" S, 30° 17' 50" E	-30.5833	30.5
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	Ntafufu river (near port st john)	31°33'00"S, 29°38'00"E	-31,5	29,6333
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	Ntafufu river (near port st john)	31°33'00"S, 29°38'00"E	-31,5	29,6333
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern Cape	Ntafufu river (near port st john)	31°33'00"S, 29°38'00"E	-31,5	29,6333
<i>Laniarius ferrugineus pondoensis</i>	South Africa	Eastern cape	Ntafufu river (near port st john)	31°33'00"S, 29°38'00"E	-31,5	29,6333
<i>Laniarius ferrugineus savensis</i>	Mozambique	Inhambane	Mapinhane	22° 16' 2" S, 35° 6' 58" E	-22,273	35,261
<i>Laniarius ferrugineus savensis</i>	Mozambique	Inhambane	Mapinhane	22° 16' 2" S, 35° 6' 58" E	-22,273	35,261
<i>Laniarius ferrugineus savensis</i>	Mozambique	Inhambane	Mapinhane	22° 16' 2" S, 35° 6' 58" E	-22,273	35,261
<i>Laniarius ferrugineus savensis</i>	Mozambique	Inhambane	Mapinhane	22° 16' 2" S, 35° 6' 58" E	-22,273	35,261
<i>Laniarius ferrugineus savensis</i>	Mozambique	Inhambane	Mapinhane	22° 16' 2" S, 35° 6' 58" E	-22,273	35,261
<i>Laniarius ferrugineus savensis</i>	Mozambique	Inhambane	Mapinhane, Vilanculos	22°16'02"S, 35°06'58"E	-22,273	35,261
<i>Laniarius ferrugineus savensis</i>	Mozambique	Inhambane	Mapinhane, Vilanculos	22°16'02"S, 35°06'58"E	-22,273	35,261
<i>Laniarius ferrugineus savensis</i>	Mozambique	Inhambane	Massinga	23° 21'01.0"S, 35°28'33.9"E	-22,273	35,261
<i>Laniarius ferrugineus savensis</i>	Mozambique	Inhambane	Massinga	23° 21'01.0"S, 35°28'33.9"E	-22,273	35,261
<i>Laniarius ferrugineus savensis</i>	Mozambique	Inhambane	Massinga	23° 21'01.0"S, 35°28'33.9"E	-22,273	35,261
<i>Laniarius ferrugineus savensis</i>	Zimbabwe	Manicaland	Murambi, Mutare	18°58'S, 32°38'E	-18,967	32,633
<i>Laniarius ferrugineus savensis</i>	Mozambique	Inhambane	Panda	24° 3' 48" S, 34° 43' 49" E	-24,183	34,853
<i>Laniarius ferrugineus savensis</i>	Mozambique	Inhambane	Panda	24° 3' 48" S, 34° 43' 49" E	-24,183	34,853
<i>Laniarius ferrugineus savensis</i>	Mozambique	Inhambane	Panda	24° 3' 48" S, 34° 43' 49" E	-24,183	34,853
<i>Laniarius ferrugineus savensis</i>	Mozambique	Inhambane	Panda	24° 3' 48" S, 34° 43' 49" E	-24,183	34,853
<i>Laniarius ferrugineus savensis</i>	Mozambique	Inhambane	Panda	24° 3' 48" S, 34° 43' 49" E	-24,183	34,853
<i>Laniarius ferrugineus savensis</i>	Mozambique	Inhambane	Panda	24° 3' 48" S, 34° 43' 49" E	-24,183	34,853
<i>Laniarius ferrugineus savensis</i>	Mozambique	Inhambane	Panda	24° 3' 48" S, 34° 43' 49" E	-24,183	34,853
<i>Laniarius ferrugineus savensis</i>	Mozambique	Inhambane	Panda	24° 3' 48" S, 34° 43' 49" E	-24,183	34,853
<i>Laniarius ferrugineus savensis</i>	Mozambique	Inhambane	Rumbacaca	21° 48' 53" S, 34° 54' 01" E	-24,183	34,853
<i>Laniarius ferrugineus savensis</i>	Mozambique	Inhambane	Rumbacaca	21° 48' 53" S, 34° 54' 01" E	-24,183	34,853
<i>Laniarius ferrugineus savensis</i>	Mozambique	Inhambane	Rumbacaca	21° 48' 53" S, 34° 54' 01" E	-24,183	34,853
<i>Laniarius ferrugineus savensis</i>	Mozambique	Inhambane	Rumbacaca	21° 48' 53" S, 34° 54' 01" E	-24,183	34,853
<i>Laniarius ferrugineus savensis</i>	Mozambique	Inhambane	Rumbacaca	21° 48' 53" S, 34° 54' 01" E	-24,183	34,853
<i>Laniarius ferrugineus savensis</i>	Mozambique	Inhambane	Rumbacaca	21° 48' 53" S, 34° 54' 01" E	-24,183	34,853
<i>Laniarius ferrugineus savensis</i>	Mozambique	Inhambane	Rumbacaca	21° 48' 53" S, 34° 54' 01" E	-24,183	34,853
<i>Laniarius ferrugineus savensis</i>	Mozambique	Inhambane	Rumbacaca	21° 48' 53" S, 34° 54' 01" E	-24,183	34,853
<i>Laniarius ferrugineus savensis</i>	Mozambique	Inhambane	Vila Franca do Save, 10 km S of	21° 8' 29" S, 34° 33' 59" E	-22,273	35,261
<i>Laniarius ferrugineus savensis</i>	Mozambique	Inhambane	Vilanculos	21° 40' 0" S, 35° 30' 0" E	-21,214	34,714
<i>Laniarius ferrugineus savensis</i>	Mozambique	Inhambane	Vilanculos	21° 40' 0" S, 35° 30' 0" E	-24,947	34,903
<i>Laniarius ferrugineus savensis</i>	Mozambique	Inhambane	Vilanculos	21° 40' 0" S, 35° 30' 0" E	-24,947	34,903
<i>Laniarius ferrugineus tongensis</i>	Mozambique	Maputo	Bela Vista	26° 20' 34" S, 32° 40' 25" E	-26,128	32,737
<i>Laniarius ferrugineus tongensis</i>	Mozambique	Maputo	Bela Vista	26° 20' 34" S, 32° 40' 25" E	-26,128	32,737
<i>Laniarius ferrugineus tongensis</i>	Mozambique	Maputo	Bela Vista	26° 20' 34" S, 32° 40' 25" E	-26,128	32,737
<i>Laniarius ferrugineus tongensis</i>	Mozambique	Maputo	Chimonzo	24° 56' 54" S, 33° 17' 30" E	-25,083	33,366
<i>Laniarius ferrugineus tongensis</i>	Mozambique	Maputo	Chimonzo	24° 56' 54" S, 33° 17' 30" E	-25,083	33,366

Taxon name	Country	Province	Locality	GPS Coordinates	Latitude	Longitude
<i>Laniarius ferrugineus tongensis</i>	Mozambique	Maputo	Chimonzo, Macia	24° 56' 54" S, 33° 17' 30" E	-25,083	33,366
<i>Laniarius ferrugineus tongensis</i>	Mozambique	Inhambane	Inhassoro Coastal, P.E.A	21°32'S, 35°12'E	-21,533	35,2
<i>Laniarius ferrugineus tongensis</i>	Mozambique	Inhambane	Inhassoro Coastal, P.E.A	21°32'S, 35°12'E	-21,533	35,2
<i>Laniarius ferrugineus tongensis</i>	Swaziland	Swaziland	Lubuli	27°01'00"S, 31°54'00"E	-27,017	29,583
<i>Laniarius ferrugineus tongensis</i>	Mozambique	Maputo	Maputo, Bela Vista	26° 20' 34" S, 32° 40' 25" E	-26,128	32,737
<i>Laniarius ferrugineus tongensis</i>	Mozambique	Maputo	Maputo, Bela Vista	26° 20' 34" S, 32° 40' 25" E	-26,128	32,737
<i>Laniarius ferrugineus tongensis</i>	Mozambique	Inhambane	Maputo, Mozambique	23° 21'01.0"S, 35°28'33.9"E	-23,353	35,561
<i>Laniarius ferrugineus tongensis</i>	Mozambique	Inhambane	Massinga	23° 21'01.0"S, 35°28'33.9"E	-23,353	35,561
<i>Laniarius ferrugineus tongensis</i>	Mozambique	Inhambane	Massinga, Macia	26° 18' 58" S, 32° 22' 11" E	-23,353	35,561
<i>Laniarius ferrugineus tongensis</i>	Mozambique	Inhambane	Massinga, Macia	26° 18' 58" S, 32° 22' 11" E	-23,353	35,561
<i>Laniarius ferrugineus tongensis</i>	Mozambique	Inhambane	Massinga, Mozambique	23° 21'01.0"S, 35°28'33.9"E	-22,273	35,261
<i>Laniarius ferrugineus tongensis</i>	Swaziland	Swaziland	Nsoko, Lubuli	27°01'00"S, 31°54'00"E	-27,017	29,583
<i>Laniarius ferrugineus tongensis</i>	Swaziland	Swaziland	Nsoko, Lubuli	27°01'00"S, 31°54'00"E	-27,017	29,583
<i>Laniarius ferrugineus tongensis</i>	Mozambique	Inhambane	Panda	24° 3' 48" S, 34° 43' 49" E	-24,183	34,853
<i>Laniarius ferrugineus tongensis</i>	Mozambique	Inhambane	Panda	24° 3' 48" S, 34° 43' 49" E	-24,183	34,853
<i>Laniarius ferrugineus tongensis</i>	South Africa	Swaziland	Ranches Ltd	26°46'00"S, 31°56'14"E	-26,767	31,972
<i>Laniarius ferrugineus tongensis</i>	South Africa	Swaziland	Ranches Ltd	26°46'00"S, 31°56'14"E	-26,767	31,972
<i>Laniarius ferrugineus tongensis</i>	South Africa	Swaziland	Ranches Ltd	26°46'00"S, 31°56'14"E	-26,767	31,972
<i>Laniarius ferrugineus tongensis</i>	South Africa	Kwa-Zulu Natal	Tongaland ,Kangazeni Pan	27°10'00"S, 32°20'00"E	-27,167	32,333
<i>Laniarius ferrugineus tongensis</i>	Mozambique	Maputo	Vila Luiza	25° 44' 13" S, 32° 40' 35" E	-25,769	32,38
<i>Laniarius ferrugineus tongensis</i>	South Africa	Mpumalanga	Komatipoort	25° 26' S, 31° 57' E	-25,4333	31,9667
<i>Laniarius ferrugineus tongensis</i>	South Africa	Kwa-Zulu Natal	St Lucia	28°22'59"S, 32°25'01" E	-28,3833	32,5667
<i>Laniarius ferrugineus tongensis</i>	South Africa	Kwa-Zulu Natal	Kosi Bay		-26,95	32,8333
<i>Laniarius ferrugineus tongensis</i>	Swaziland	Swaziland	Mzenene River (near Balegane)	26°06'00"S, 31°34'00" E	-26,1	31,566
<i>Laniarius ferrugineus tongensis</i>	Mozambique	Sofala	Muanza	18°53'29.99"S, 34°47'20.39" E	-18,897	34,793
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Limpopo	Maluma Boerdery, Soutpansberg	23°00'00"S, 29°52'00" E	-23	29,867
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Mpumalanga	Acornhoek, pilgrim's rest	24°54'28"S, 30°45'24"E	-24,978	30,817
<i>Laniarius ferrugineus transvaalensis</i>	Swaziland	Swaziland	Balegane, near, Komati River	25°48'57.46"S, 32°43'38.89"E	-25,96	32,825
<i>Laniarius ferrugineus transvaalensis</i>	Swaziland	Swaziland	Balegane, near, Komati River	25°48'57.46"S, 32°43'38.89"E	-25,96	32,825
<i>Laniarius ferrugineus transvaalensis</i>	Swaziland	Swaziland	Balegane, near, Komati River	25°48'57.46"S, 32°43'38.89"E	-25,96	32,825
<i>Laniarius ferrugineus transvaalensis</i>	Swaziland	Swaziland	Big Bend, Mcandatshe near	26°49'S, 31°56'E	-26,817	31,933
<i>Laniarius ferrugineus transvaalensis</i>	Swaziland	Swaziland	Big Bend, Mcandatshe near	26°49'S, 31°56'E	-26,817	31,933
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Limpopo	Blouberg, Northern TVL	23°00'00"S, 29°08'00"E	-23	29,133
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Limpopo	Blouberg, Northern TVL	23°00'00"S, 29°08'00"E	-23	29,133
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	North west	Borchhoek	27°35'00"S, 31°21'00"E	-27,583	31,35
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Swaziland	Bossig, Swaziland	26° 30' S, 31° 30' E	-26,5	31,5
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Swaziland	Bossig, Swaziland	26° 30' S, 31° 30' E	-26,5	31,5
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Mpumalanga	Daisy Kopje, Barbeton	25°46'S, 31°04'E	-25,767	31,067
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Limpopo	Doornboom, Groot Spelonken	25°25'00"S, 29°56'00" E	-25,417	29,933
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Limpopo	Elim, Soutpansberg	23°00'00"S, 29°52'00"E	-23	29,6
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Limpopo	Entambeni forest reserve	23°00'00"S, 30°14'00"E	-23	30,072
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Limpopo	Farm Malta	24°06'00"S, 30°23'00"E	-24,6	30,383
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Limpopo	Farm Malta	24°06'00"S, 30°23'00"E	-24,6	30,383
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Gauteng	Ferndale	26°04'56"S, 27°58'57"E	-26,222	27,683

Taxon name	Country	Province	Locality	GPS Coordinates	Latitude	Longitude
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Gauteng	Ferndale	26°04'56"S, 27°58'57"E	-26,222	27,683
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Gauteng	Ferndale	26°04'56"S, 27°58'57"E	-26,222	27,683
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Gauteng	Ferndale	26°04'56"S, 27°58'57"E	-26,222	27,683
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Gauteng	Ferndale	26°04'56"S, 27°58'57"E	-26,222	27,683
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Gauteng	Gauteng, PTA, brummeria	25°44'44"S, 28°16'59"E	-25,733	28,43
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Limpopo	Groot spelonken	25°25'00"S, 29°56'00" E	-25,417	29,933
<i>Laniarius Ferrugineus transvaalensis</i>	South Africa	Limpopo	Grootspelonken	23°28'00"S, 29°56'00" E	-23,467	29,933
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Gauteng	Hamanskraal	25°24'02"S, 28°17'08"E	-25,406	28,305
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Gauteng	Hamanskraal	25°24'02"S, 28°17'08"E	-25,406	28,305
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Gauteng	Hamanskraal	25°24'02"S, 28°17'08"E	-25,406	28,305
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Gauteng	Harmanskraal, Transvaal	25° 24' 27" S, 28° 17' 8" E	-25,475	28,305
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Gauteng	Harmanskraal, Transvaal	25° 24' 27" S, 28° 17' 8" E	-25,475	28,305
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Gauteng	Hennops River	25°49'12.69"S, 28°06'14.58"	-25,8202	28,554
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Gauteng	Hennops River	25°49'12.69"S, 28°06'14.58"E	-25,8202	28,554
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Gauteng	Hillcrest, Pretoria	25°45'30.13"S, 28°14'33.97"E	-25,834	28,324
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Gauteng	Hornsnek, magaliesburg	26°00'00"S, 27°32'45"E	-26	27,658
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Swaziland	Indlovodwalile	26° 30' S, 31° 30' E	-26,5	31,033
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Limpopo	Klipfontein, Waterburg	24°08'56.37S, 28°19'24.74"E	-24,133	28,3
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Limpopo	Kloof, Natal	29°47'0"S, 30°50'0"E	-29,783	30,833
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	North west	Koster	25°52'00"S, 26°54'00"E	-25,867	26,9
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Limpopo	Leydsdorp	23°59'00"S, 30°32'00"E	-23,983	30,033
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Limpopo	Limpopo river	25°10'S, 33°35'E	-25,167	33,583
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Limpopo	Limpopo river, TVL	25°10'S, 33°35'E	-25,167	33,583
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Limpopo	Limpopo, Soutpansberg	23°00'00"S, 29°52'00" E	-23	29,867
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Limpopo	Louis Trichardt, Entabeni Forest	23°00'00"S, 30°13'60"E	-23	30,384
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Mpumalanga	Louws Creek, Barbeton	25°38'00"S, 31°17'00"E	-25,633	31,283
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Mpumalanga	Louws Creek, Barbeton	25°38'00"S, 31°17'00"E	-25,633	31,283
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Mpumalanga	Louws Creek, Barbeton	25°38'00"S, 31°17'00"E	-25,633	31,283
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Limpopo	Luis Trichart	23°03'00"S, 29°54'00" E	-23,05	29,9
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Limpopo	Luis Trichart	23°03'00"S, 29°54'00" E	-23,05	29,9
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Limpopo	Luis Trichart	23°03'00"S, 29°54'00" E	-23,05	29,9
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Mpumalanga	Lydenburg	25°06'00"S, 30°27'00"E	-25,1	30,45
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Kwa-Zulu Natal	Magut	27°35'00"S, 31°39'00"E	-27,583	31,65
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Limpopo	Malala, Transvaal	22°16'00"S, 30°04'00"E	-22,267	30,067
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Limpopo	Malta farm, near Ofcolaco	24°06'00"S, 30°23'00"E	-24,6	30,383
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Limpopo	Malta farm, near Ofcolaco	24°06'00"S, 30°23'00"E	-24,6	30,383
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Limpopo	Manetsi river, transvaal, SOUTPANSBERG	23°00'00"S, 29°52'00"E	-23	29,867
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Limpopo	Mapagone, transvaal	24°S, 29°E	-24	29
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Limpopo	Messina on Limpopo river, TVL	25°10'S, 33°35'E	-25,167	33,583
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Limpopo	Mokeetsi	23°35'00"S, 30°05'00"E	-23,583	30,083
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Limpopo	Mokeetsi	23°35'00"S, 30°05'00"E	-23,583	30,083
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Limpopo	Mokeetsi Transvaal	23°35'00"S, 30°05'00"E	-23,583	30,083
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Limpopo	Mokeetsi, Northern TVL	23°35'00"S, 30°05'00"E	-23,583	30,083
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Limpopo	Mooketsi	23°36'00"S, 30°06'00"E	-23,6	30,1

Taxon name	Country	Province	Locality	GPS Coordinates	Latitude	Longitude
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Limpopo	Mooketsi	23°36'00"S, 30°06'00"E	-23,6	30,1
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Limpopo	Moorddrift	23°36'00"S, 27°43'00"E	-23,6	27,717
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Limpopo	Moorddrift	23°36'00"S, 27°43'00"E	-23,6	27,717
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Limpopo	Moorddrift	23°36'00"S, 27°43'00"E	-23,6	27,717
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Limpopo	Moorddrift	23°36'00"S, 27°43'00"E	-23,6	27,717
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Limpopo	Moorddrift	23°36'00"S, 27°43'00"E	-23,6	27,717
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Kwa-Zulu Natal	Ndumu	26°55'00"S, 32°16'00"E	-26,917	32,267
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Kwa-Zulu Natal	Ndumu	26°55'00"S, 32°16'00"E	-26,917	32,267
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Mpumalanga	Newington, Malamala	24°49'00"S, 31°35'00"E	-24,817	31,583
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Mpumalanga	Newington, Malamala	24°49'00"S, 31°35'00"E	-24,817	31,583
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Mpumalanga	Newington, Malamala	24°49'00"S, 31°35'00"E	-24,817	31,583
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Mpumalanga	Newington, Malamala	24°49'00"S, 31°35'00"E	-24,817	31,583
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Mpumalanga	Newington, Malamala	24°49'00"S, 31°35'00"E	-24,817	31,583
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Mpumalanga	Newington, Malamala	24°49'00"S, 31°35'00"E	-24,817	31,583
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Limpopo	Northam	24°51'00"S, 27°16'00"E	-24,85	27,267
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Limpopo	Northam	24°51'00"S, 27°16'00"E	-24,85	27,267
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Limpopo	Northam	24°51'00"S, 27°16'00"E	-24,85	27,267
<i>Laniarius ferrugineus transvaalensis</i>	Swaziland	Swaziland	Nsoko, Lubuli	27°01'00"S, 29°35'00"E	-27,017	29,583
<i>Laniarius ferrugineus transvaalensis</i>	Swaziland	Swaziland	Nsoko, Lubuli	27°01'00"S, 29°35'00"E	-27,017	29,583
<i>Laniarius ferrugineus transvaalensis</i>	Swaziland	Swaziland	Nsoko, Lubuli	27°01'00"S, 29°35'00"E	-27,017	29,583
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Limpopo	NTVL, Blouberg	23°07'00"S, 28°59'00"E	-28	28,983
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Limpopo	NTVL, Blouberg	23°07'00"S, 28°59'00"E	-28	28,983
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Mpumalanga	Piet Retief, Transvaal	27°00'00"S, 30°48'00"E	-27	30,8
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Gauteng	Pretoria	25°42'25"S, 28°13'46" E	-25,77	28,345
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Gauteng	Pretoria	25°42'25"S, 28°13'46" E	-25,77	28,345
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Gauteng	Pretoria	25°42'25"S, 28°13'46" E	-25,77	28,345
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Gauteng	Pretoria	25°42'25"S, 28°13'46" E	-25,77	28,345
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Gauteng	Pretoria	25°42'25"S, 28°13'46" E	-25,77	28,345
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Gauteng	Pretoria, Hamanskraal	25°24'02"S, 28°17'08"E	-25,406	28,305
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Gauteng	Pretoria, Hamanskraal	25°24'02"S, 28°17'08"E	-25,406	28,305
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Gauteng	PTA	25°42'25"S, 28°13'46" E	-25,75	28,233
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Gauteng	PTA	25°42'25"S, 28°13'46" E	-25,75	28,233
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Gauteng	PTA,	25°42'25"S, 28°13'46" E	-25,75	28,233
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Swaziland	Ranches Ltd	26°46'00"S, 31°56'14"E	-26,767	31,972
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	North West	Rustenburg	25°40'S, 27°16'E	-25,666	27,267
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Mpumalanga	SA, Mpumalanga, Nelspruit	25°28'00"S, 30°58'00"E	-25,917	30,967
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Gauteng	Schurverberg	25° 46' 14.70" S , 27° 54' 27.04"E	-25,767	27,975
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Gauteng	Schurverberg	25°46'14.70"S , 27°54'27.04"E	-25,767	27,975
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Limpopo	Seraia Forest Station, Wolkberg	24°03'S, 30°06'E	-24,05	30,1
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Limpopo	Soutpansberg	23°00'00"S, 29°52'00"E	-23	29,867
<i>Laniarius ferrugineus transvaalensis</i>	Swaziland	Swaziland	Stegi	26°27'S, 31°57'E	-26,45	31,95
<i>Laniarius ferrugineus transvaalensis</i>	Swaziland	Swaziland	Stegi	26°27'S, 31°57'E	-26,45	31,95
<i>Laniarius ferrugineus transvaalensis</i>	Swaziland	Swaziland	Stegi	26°27'S, 31°57'E	-26,45	31,95
<i>Laniarius ferrugineus transvaalensis</i>	Swaziland	Swaziland	Stegi	26°27'S, 31°57'E	-26,45	31,95



Taxon name	Country	Province	Locality	GPS Coordinates	Latitude	Longitude
<i>Laniarius ferrugineus transvaalensis</i>	Swaziland	Swaziland	Stegi	26°27'S, 31°57'E	-26,45	31,95
<i>Laniarius ferrugineus transvaalensis</i>	Swaziland	Swaziland	Stegi, Mlaula Estates	26°27'S, 31°57'E	-26,45	31,95
<i>Laniarius ferrugineus transvaalensis</i>	Swaziland	Swaziland	Stegi, Mlaula Estates	26°27'S, 31°57'E	-26,45	31,95
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	North-West	Swartruggens, Blokkloof	25°28'00"S, 26°49'00"E	-25,467	27,817
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	North-West	Swartruggens, Elands River	25°27'1"S, 26°45'24"E	-25,453	26,817
<i>Laniarius Ferrugineus transvaalensis</i>	South Africa	Limpopo	Thabina river	23°54'00"S, 30°21'00" E	-23,9	30,35
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Limpopo	Thabina River	23°54'00"S, 30°21'00"E	-23,9	30,35
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Gauteng	Uitkoms, krugerdsdorp	26°6'S, 27°46'E	-26,1	27,767
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Gauteng	Wonderboom, Hamaanskraal	25°24'02"S, 28°17'08"E	-25,406	28,305
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Limpopo	Woodbush Forest	23°44'00"S, 30°02'00"E	-23,733	30,033
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Mpumalanga	Worcester mine, Baberton	31°37'30.00"S, 29°37'30.00"E	-31,9	29,7
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Kwa-Zulu Natal	EcoPark Newcastle	27°42'49.83"S, 29°59'49.83"E	-27.7722	30.01
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	North West	Wonderhoek Farm, 3 km from Ottoshoop	25°48'00"S, 25°58'00"E	-25,7291	25.97475
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Limpopo	Schoemendaal EEC	23°05'09"S, 29°46'12"E	-23.0189	29.7244
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Limpopo	Schoemendaal EEC	23°05'09"S, 29°46'12"E	-23.0189	29.7244
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Limpopo	Schoemendaal EEC	23°05'09"S, 29°46'12"E	-23.0189	29.7244
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Kwa-Zulu Natal	Nkandela Forest	28°43'51"S, 31°07'9.99"E	-28,7232	31.13045
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Kwa-Zulu Natal	Entumeni Forest	28°53'00"S, 31°53'00"E	-28,8867	31,37727
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Limpopo	Schoemendaal EEC	23°05'09"S, 29°46'12"E	-23.0189	29.7244
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Limpopo	Schoemendaal EEC	23°05'09"S, 29°46'12"E	-23.0189	29.7244
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Limpopo	Naboomspruit-Entabeni*Bream Dam	24°03'00"S, 28°43'00"E	-24.2386	28.7003
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Limpopo	Nylstroom - Olienhoutstraat 47	24°04'00"S, 28°24'00"E	-24.7	28.3833
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Mpumalanga	Rockabye, Hazyview	25°02'35"S, 31°07'45"E	-25.0167	31.0333
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Limpopo	Blouberg NR	22°58'59.88"S, 29°08'59.99"E	-22.9833	29.15
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Mpumalanga	Rockabye, Hazyview	25°02'35"S, 31°07'45"E	-25.0167	31.0333
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Limpopo	Blouberg NR	22°58'59.88"S, 29°08'59.99"E	-23.0019	29.0639
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Limpopo	Ben Lavin Nature Reserve, Longwall Dam	23°08'31"S, 29°58'5"E	-23,1419	29,9891
<i>Laniarius ferrugineus transvaalensis</i>	South Africa	Limpopo	Ben Lavin Nature Reserve (Long wall dam)	23°08'31"S, 29°58'5"E	-23,1419	29,9891

## **CHAPTER 3**

### **The phylogeographic structure of the Southern Boubou *Laniarius ferrugineus*: a molecular perspective**

#### **3.1 Introduction**

Phylogeography is the study of spatial arrangement of genealogical lineages, especially within and among conspecific populations and closely related species (Avice 2000). Phylogeographic perspectives have transformed aspects of population biology, biogeography, systematics, ecology, genetics, and biodiversity conservation (Avice *et al.* 2016). A central issue in phylogeography and evolutionary biology is how geographically structured variation among populations and species arise (Kearns *et al.* 2009). Further to this, divergence within and between bird species is most commonly attributed to differentiation in allopatry, typically following the vicariance of populations on either side of biogeographic barriers (Avice 2000; Barraclough & Vogler 2000). The achievements in this field were reached due to the development of phylogeographical approaches that combine information on intraspecific differentiation with that of the geographical distribution of mitochondrial DNA haplotypes (Avice 2000; Hundertmark *et al.* 2001) and nuclear DNA (Tavares *et al.* 2016; Tóth *et al.* 2016; Zhou *et al.* 2017).

One of the major issues at the centre of phylogeography involves the use of mitochondrial DNA (mtDNA) versus nuclear DNA (nuDNA) markers. Mitochondrial DNA has proved to be powerful for genealogical and evolutionary studies of animal populations (Zhang & Hewitt 2003). The small size, high copy number, lack of recombination and high mutation rate (compared to the nuclear genes) of the mitochondrial DNA have greatly facilitated the investigation of complex genetic ancestries and phylogeographic patterns (e.g. Avice *et al.* 1987; Birky 2001; Slate & Gemmell 2004). The use of mtDNA has limitations; one is that the results based solely on mtDNA could be very different from those inferred from nuDNA (Wahlberg *et al.* 2009), a phenomenon known as mito-nuclear discordance (Larmuseau *et al.*

2010). The most frequent explanations of mito-nuclear discordance are incomplete lineage sorting, adaptive introgression of mtDNA, demographic disparities and hybrid zone movement (Toews & Brelsford 2012). Incomplete lineage sorting occurs when genetic drift has not had enough time to bring individual gene loci to fixation and/or reciprocal monophyly before subsequent divergence (Lee *et al.* 2011).

The effective population size of mtDNA is also only a fourth of that of nuclear autosomal sequences and mtDNA lineages have a much faster lineage sorting rate and higher allele extinction rate (Zhang & Hewitt 2003). Furthermore, there is also the existence of pseudogenes in avian genomes; however, there are methods and techniques to reduce the interference of mtDNA pseudogenes in sample preparation and data analysis (Zhang & Hewitt 1996; Bensasson *et al.* 2001). Despite all these limitations, mtDNA still remains highly informative in phylogenetic and phylogeographic studies and is still widely used (Kearns *et al.* 2009; Fuchs *et al.* 2008; N'Guembock *et al.* 2008; Oleinik *et al.* 2010; Corrales *et al.* 2014; Fuchs *et al.* 2017).

Nuclear DNA markers have an advantage of providing genealogical patterns that are representative of the entire population history because they are biparentally inherited (Hare 2001). The inclusion of nuDNA markers in evolutionary and population-genetic studies is necessary for a better understanding of evolutionary processes that have occurred, and thereby extend the ability to infer the past (Zhang & Hewitt 2003; Cabanne *et al.* 2008). Nuclear DNA polymorphisms that exist widely in eukaryotic organisms provide virtually unlimited opportunities for studying the mechanisms of evolution. However, nuDNA markers could involve analytical complications, recombination, selection (non-neutrality), heterozygosity, and limited divergence (Zhang & Hewitt 2003). Although challenges still exist, recent progress in genomic studies and molecular biology technologies (Zhang & Hewitt 2003; Yang & Rannala 2014), and an increase in the statistical rigor/power (Liu *et al.* 2009; Kubatko *et al.* 2009; Hickerson *et al.* 2010; Ence & Carstens 2011) provide a basis for nuDNA analyses to be widely applicable (Zhang & Hewitt 2003).

The use of nuclear markers together with mitochondrial DNA improves the power of phylogenetic and phylogeographic hypothesis testing significantly and

highlights the limitations of studies that used only mitochondrial DNA markers (Tóth *et al.* 2016). Furthermore, several studies have demonstrated that increasing the number of loci has a critical effect on the accuracy of the parameter estimates, although in some cases increasing the number of individuals or the number of sites per sequence read (i.e. more variable loci) is also important (Poe & Swofford 1999; Maddison & Knowles 2006; Hime *et al.* 2016).

The rise of phylogeography as a field has not been without challenges. Phylogeography does not exist in isolation and has either direct or indirect links with other fields such as conservation, systematics, biogeography, population genetics, climate change etc. During this time when future climate changes are said to likely affect species ranges, the distribution of biodiversity and the evolutionary history it holds (Thuiller *et al.* 2011), the discovery of phylogeographic lineages within species could motivate and justify a reconsideration of strategies for conserving intra-specific diversity (Crandall *et al.* 2000). Empirical evidence suggests that ongoing species distribution range shifts in response to changing climate are occurring globally (Parmesan & Yohe 2003). D'Amen and colleagues (2012) discovered the importance of information about intra-specific diversity/subspecific units, which when not distinguished in niche modelling lead to failure to identify potential risks of climate change to lineages.

There are a number of studies that highlight the phylogeographic approach and how it is helpful in the investigation of intra-specific genetic diversity. For example, Oatley *et al.* (2011) used uni- and multi-variate statistical approaches to re-investigate the morphological characteristics (morphometric and plumage colouration) used in the past taxonomic studies to propose nine putative southern African white-eyes (*Zosterops*) described at that time as subspecies and four evolutionary significant units emerged from this. Furthermore, as a result of geographical, discriminatory, multifaceted analyses they suggest that four taxa warrant species status. Another example was seen in Mynhardt *et al.* (2015) where they investigated the phylogeography of a morphologically cryptic golden mole assemblage from south-eastern Africa. It was discovered that the mole (*Amblysomus hottentotus*) comprised of several distinct lineages and some had restricted geographic ranges and thus worthy of conservation attention.

In this chapter, the phylogeographic structure of the highly polymorphic and slightly dichromatic passerine species *Laniarius ferrugineus* (Gmelin, 1788), Southern Boubou was investigated. The current taxonomic circumscription places *L. ferrugineus* in the family Malaconotidae - Passeriformes (N'Guembock *et al.* 2008). This species is distributed widely in South Africa extending into southern Mozambique, down the coast to Kwa-Zulu Natal, Eastern and Western Cape, south-eastern Zimbabwe, Botswana and eastern Swaziland (SABAP 2, accessed October 2017). The Southern Boubou is an inconspicuous species that occurs in thick bush and can often be heard duetting; it is a monogamous summer breeder (August-March, mainly September-November) that exhibits territorial behaviour (Mackworth-Praed & Grant 1963; Harris & Arnott 1988; Chittenden *et al.* 2016). *Laniarius ferrugineus* is a resident species, endemic to southern Africa and overlaps in the extreme north of South Africa (McGowan 1994) with the more widespread Tropical Boubou *L. aethiopicus* (Gmelin, 1788). The eastern and southern African populations of *L. aethiopicus* were recently found to be more closely related to *L. ferrugineus* than to its supposed conspecific populations from west and central Africa (N'Guembock *et al.* 2008).

Currently, *L. ferrugineus* is recognised as a polytypic species that shows geographical variation. The recognised subspecies are: *L. f. ferrugineus* (Gmelin, 1788); *L. f. natalensis* Roberts, 1922; *L. f. pondoensis* Roberts, 1922; *L. f. transvaalensis* Roberts, 1922; *L. f. tongensis* Roberts, 1931 and *L. f. savensis* da Rosa Pinto, 1963, which vary slightly in size and plumage colouration. It is unknown if these could be the results of both latitudinal (Bergman's rule) or ecological (Gloger's rule) factors and also if plumage differences among the subspecies is clinal or represents a sharp transition across ecological zones. South Africa is a biodiverse country with three major zones, namely the winter rainfall region of western, south western and southern Cape, the bimodal rainfall region of the Eastern Cape and the strong summer seasonally of the central Highveld and Kwa-zulu Natal ([www.dwaf.gov.za](http://www.dwaf.gov.za), accessed November 2017).

On the other hand, there are many other species complexes of birds where geographic variation is remarkable (Ashton 2002; Kearns *et al.* 2009; Chittenden *et al.* 2012; Scordato & Safran 2014) there happens to be challenges in classifying these taxa and understanding of their evolutionary relationships as well as

determining their level of genetic diversity and divergence times. Likewise, *L. ferrugineus* is not immune to these classification challenges. Despite the traditional way of relying on morphology and patterns of distribution to understand intra-specific variation and its origin, not much is known about the genetic structure within *L. ferrugineus*. This work is to our knowledge the first phylogeographic study of this southern African endemic species (Southern Boubou) hence the significance of this study.

### 3.1.1 Aim

The aim in this chapter was to investigate the degree of genetic differentiation within the *Laniarius ferrugineus* species complex

### 3.1.2 Objectives

The objectives were to:

- i) investigate whether *L. ferrugineus* represents a single species or a species complex.
- ii) determine the level of genetic differentiation within *L. ferrugineus* across its distribution range.
- iii) compare the evolutionary units of *L. ferrugineus* delineated in this study with the current circumscription of subspecies.
- iv) estimate the divergence times between the recovered phylogeographic lineages within *L. ferrugineus*.

### 3.1.3 Research questions

- i) Does *L. ferrugineus* represent a single species or a complex?
- ii) What is the level of genetic differentiation within *L. ferrugineus* across its distribution range?
- iii) How do the evolutionary units of *L. ferrugineus* delineated in this study compare with the current taxonomic circumscription?
- iv) What is the estimated time divergence between the recovered phylogeographic lineages within *L. ferrugineus*?

## 3.2 Materials and methods

### 3.2.1 Data collection

#### 3.2.1.1 Taxon sampling

Individual birds were sampled in order to cover the distribution range of *L. ferrugineus*; samples consisted of recently collected tissues (blood, liver) and historical (museum dry toe-pad snips) samples, highlighting the need for continued and reasonable scientific collecting (Rocha *et al.* 2014). The toe-pad snips were sub-sampled from the skin collection housed at the South African's Durban Museum of Natural Sciences (DMNS) and Muséum National d'Histoire Naturelle (MNHN) in Paris, France. Efforts were made to cover the distribution of the species in question and the historical samples were considered the last option solely to fill gaps. This was to make sure that the number of individuals sampled was a fair representation of each of the putative subspecies (Table 3.1). All outgroup sequences used were sequenced for this study and this includes the proximate outgroup taxa Ethiopian Boubou, *L. aethiopicus mossambicus*; Tropical Boubou, *L. aethiopicus*; East Coast Boubou, *L. subclateus* and the most distant outgroup Crimson-breasted Gonolek, *L. atrococcineus* (Appendix 3.2).

#### 3.2.1.2 Laboratory techniques: DNA extraction, PCR amplification and sequencing

Genomic DNA from both modern and historical samples was extracted using the QIAampDNA and QIAamp DNA blood mini kits following the manufacture's protocol. Extracted samples were taken through the Polymerase Chain Reaction (PCR). Four molecular markers were sequenced including one mitochondrial protein coding gene (ATP6 – ATP Synthase subunit 6) and three nuclear introns (autosomal FGB5 – Beta fibrinogen intron-5; TGFB2 – Transforming growth factor beta2 intron-5; Z linked MUSK – Muscle associated receptor tyrosine kinase).

The choice of four markers was informed by the outcomes in a number of studies that maintain that a single locus would offer low precision for estimating parameters such as population divergence time (Edwards & Beerli 2000; Hudson & Turelli 2003), and consequently multilocus investigations are desirable for understanding the geographic structure and the population divergence (Schaal *et al.* 1998; Hewitt 2001). Mitochondrial ATP6 was chosen mainly due to the numerous comparative data that was available from other lineages (N'Guembock *et al.* 2008;

Fuchs *et al.* 2011; Oatley *et al.* 2011; Fuchs *et al.* 2017). Sequencing multilocus nuDNA markers could elucidate a number of independent genealogies and be appropriate for phylogeographic studies based on demographic parameters and also including hypotheses testing (Knowles 2009).

Based on the knowledge that museum toe-pads typically yield low volumes, of DNA that is mostly degraded, and hence are more susceptible to contamination than for fresh samples, internal ATP6 primers were designed specifically for *L. ferrugineus* (Table 3.1). Both forward and reverse primers were used to sequence the various markers (Table 3.1).

For the modern samples, individuals were sexed through standard PCR conditions (Fridolfsson & Ellegren 1999) using primers shown in (Table 3.1) and this was done only when sex was not noted by the collector. This assisted in the investigation of the sex ratio of the birds from which the DNA samples were obtained.

For PCR amplification a master mix of a total of approximately 20  $\mu$ l was prepared for each of the samples. This master mix included 2.0  $\mu$ l of template DNA (adjusted depending on the strength of genomic DNA) and approximately 18.0  $\mu$ l of the PCR cocktail which consisted of several reagents namely: 14.3  $\mu$ l of sterile water, 2.0  $\mu$ l - PCR buffer, 0.8  $\mu$ l - Bovine Serum Albumin (BSA), 0.5 – 1.0  $\mu$ l - MgCl<sub>2</sub> [Magnesium chloride], 0.4  $\mu$ l - Deoxynucleotide Triphosphate (dNTPs), 0.25  $\mu$ l of forward and 0.25  $\mu$ l of reverse primers and 0.15  $\mu$ l of Platinum Taq (Qiagen). Further to this, for the historical samples extracted, a number of overlapping PCR-amplifications were performed for the fragments of only the ATP6 this was done using specific primers (Table 3.1).

The PCR-amplification protocol included an initial denaturation at 94°C for 7 min and this is the first stage (denaturing stage), followed by 35 cycles at annealing temperature of 56°C for 30 s (annealing stage) and terminated by a final elongation step at 72°C for 15 min (extension stage) and this was done for all the markers. Sequences from historical specimens were obtained by performing several overlapping PCR-amplifications (200-350 bp) using primers that were designed specifically for this study (Table 3.1) and the PCR-amplification conditions slightly varied for the historical samples in that an initial denaturation at 94°C for 7 min



(denaturing stage), followed by 40 cycles at annealing temperature of 56°C 30 s and 72°C 30s (annealing stage) and terminated by a final elongation step at 72°C for 15 minutes (extension stage).

The PCR amplifications were checked using gel electrophoresis which was prepared using 1.5% agarose gel and 240 ml TAE buffer (Tris-Acetate-EDTA) mixed with Ethidium bromide that enabled the visualisation of DNA bands; to determine the size of the amplified fragments, a ladder (MXIV) was added. The gels were viewed under an Ultra-Violet (Vilber Lourmat) to check if the amplification was successful and positively amplified PCR products were purified using EXOSAP (Exonuclease I and Shrimp Alkaline Phosphatase). The exonuclease I degraded any excess primer from the original PCR while the SAP de-phosphorylated degraded any dNTPs from the original PCR. The DNA sequencing was done at Eurofins Laboratories and at the molecular laboratory at Muséum National d'Histoire Naturelle (MNHN). Sequence assembly, contig editing and mutation detection was done in CodonCode Aligner program (CodonCode Corporation, <http://www.codoncode.com/aligner>).

### 3.2.2 Data analyses

#### 3.2.2.1 Phasing of nuclear alleles

PHASE V2.1.1 (Stephens *et al.* 2001) implemented in DNAsp 5.0 (Librado & Rozas 2009) was used to infer the alleles for each nuclear locus (FGB5, TGFB2, MUSK) due to its known low false-positive (a low rate of confidently inferring haplotype pairs that are incorrect) (Garrick *et al.* 2010). During phasing more than two runs were performed and the results were compared across the runs. The output of the final phase run was considered the best estimate of the alleles and used for subsequent analyses.

#### 3.2.2.2 Population genetic analysis and demographic history

Population demographic parameters including haplotype diversity ( $H_d$ ) and nucleotide diversity ( $\pi$ ) were estimated in DNAsp 5.0 (Librado & Rozas 2009) for each subspecies, ingroup taxa, outgroup taxa recovered in the Bayesian trees of taxa (Table 3.2) represented by all four markers. These analyses were performed on two ATP6 datasets, one containing all generated sequences and the other containing only the unique haplotypes. Statistical parsimony TCS networks were inferred using the algorithm described by Clement *et al.* (2000) with a 95%

connection limit for each of the four loci but visualised in POPART (Leigh & Bryant 2015).

### 3.2.2.3 Phylogenetic reconstruction

Phylogenetic reconstruction of trees was carried out using the Bayesian inference method based on alleles (nuDNA and mtDNA) and unique haplotypes and this was implemented in MRBAYES 3.2 (Ronquist *et al.* 2012). The nst=mixed option was set such that model uncertainty was taken into account during the phylogenetic reconstruction, rate variation was incorporated using gamma settings and all trees were rooted with the outgroup: *L. atrococcineus*. Four Metropolis-coupled MCMC chains were run for five million generations with trees and parameters sampled every 100 iterations. The 500 000 burn-in was used and the GTR model was estimated for each data set. I considered the two runs to have converged when the standard deviation of split frequencies reached <0.01.

The species phylogenetic trees were reconstructed using the coalescent-based model implemented in BEAST v1.8.4 (Rambaut *et al.* 2007). All primary lineages were included although some taxa could not be sequenced for some loci (nuclear loci for historical samples). The substitution model was selected using jmodeltest 2.1.6 (Guindon & Gascuel 2003; Posada 2008) under the Akaike Information Criterion – AIC (Akaike 1973). Each of the loci has their own substitution rate and a Yule process was used for the tree prior. A normal prior distribution was used for ATP6 (0.026 s/s/l/myr; 95% HPD: 0.021-0.031 s/s/l/myr) and TGFB2 (0.0017 s/s/l/myr; 95% HPD: 0.0013–0.0022 s/s/l/myr) as proposed by Lerner *et al.* (2011). The rates for the other nuclear loci (FGB5 and MUSK) were estimated in relation to ATP6 and TGFB2. The length of the MCMC was set to five million for two runs, with trees and parameters sampled every 100 iterations. The first 2.5 million iterations were discarded as burnin period.

Tracer v1.6 (Rambaut & Drummond 2007) was used to ensure that the effective sample size for all Bayesian analyses of the underlying posterior distribution was large enough (>200) for a meaningful estimation of parameters. The trees were viewed in FigTree v1.4.3 (Rambaut 2016).

#### 3.2.2.4 Estimating the divergence times

The times to the most recent common ancestor (TMRCA) among *Laniarius* haplotypes were estimated using BEAST v1.8.4 (Rambaut *et al.* 2007). A substitution model for the ATP6 unique haplotypes was selected in jmodeltest 2.1.6 (Guindon & Gascuel 2003; Posada *et al.* 2012) under the Akaike Information Criterion – AIC (Akaike 1973), and the corrected one - AICc (Sugira 1978; Hurvich & Tsai 1989). Divergence times were only estimated for the ATP6 data file due to unavailability of DNA sequences for most taxa in the three nuclear markers.

The use of different model selection strategies may lead to the selection of different models of evolution (Posada & Crandall 2001) and model choice affects all aspects of phylogenetic analysis. For example, estimates of phylogeny, substitution rates, bootstrap values, posterior probabilities, or tests of the molecular clock are clearly influenced by the model of evolution used in the analysis (Tamura 1994; Yang *et al.* 1995; Kesley *et al.* 1999; Zhang 1999; Buckley 2002; Buckley & Cunningham 2002; Pupko *et al.* 2002; Buckley *et al.* 2001). In this study the Bayesian Information Criterion – BIC (Schwarz 1978) and Akaike Information Criterion - AIC (Akaike 1973) approaches were used because according to Posada & Buckley (2004) they present several important advantages over the hierarchical likelihood ratio tests (hLRTs) for model selection.

These approaches are able to simultaneously compare multiple nested or non-nested models (Chamberlain 1890), account for model selection uncertainty and allow for model-averaged inference. The models TIM2 + G and TrN + G were selected under the (AIC, AICc) and the BIC Bayesian Information Criterion respectively and when setting the substitution model in Bayesian Evolutionary Analysis Utility (BEAUti); the GTR model was selected as it is closest to the selected models implemented in BEAST. It is also understood that if an invalid evolutionary model is implemented the analysis will be negatively affected and aspects such as underparameterisation can lead to inflated estimates of the posterior probability values while overparameterisation leads to non-identifiable parameter distribution and also slows down the analysis. The analysis was performed with a strict molecular clock model enforced with a Yule tree prior.

Inferring divergence time within species is a challenge because the internal fossil calibration is not always available. Although it is a limiting factor there are ways to overcome this problem. In this study two substitution rates were used together with their associated uncertainties to calibrate the trees. These new substitution rates for ATP6 (0.026 s/s/l/myr; 95% HPD: 0.021-0.031 s/s/l/myr) and TGFB2 (0.0017 s/s/l/myr; 95% HPD: 0.0013–0.0022 s/s/l/myr) were proposed by Lerner *et al.* (2011) using complete mtDNA genomes and nuclear regions from honeycreepers, respectively (Passeriformes, Drepanididae). The calibration points were based on the age of volcanic islands of the Hawaiian Archipelago and the rates for the other nuclear loci (FGB5 and MUSK) were estimated in relation to TGFB2. The length of the MCMC was set to five million in BEAST and TreeAnnotator (Rambaut *et al.* 2007) was used to summarise a sample of plausible trees to the best supported one, the tree was annotated with the mean ages of all the nodes and then finally viewed in FigTree v1.4.3 (Rambaut 2016).

### 3.3 Results

#### 3.3.1 Phylogenetic relationships

##### 3.3.1.1. Mitochondrial DNA - ATP6

Forty eight unique haplotypes were obtained for the ingroup taxa representing the six recognised subspecies: *L. f. ferrugineus*, *L. f. natalensis*, *L. f. pondoensis*, *L. f. transvaalensis*, *L. f. tongensis* and *L. f. savensis*, and then five outgroup taxa (*L. aethiopicus mossambicus*, *L. aethiopicus subclateus* and *L. atrococcineus*) were sequenced (Table 3.2). The phylogeny recovered two distinct reciprocally monophyletic lineages within *L. ferrugineus* (Fig. 3.2a). The two lineages were represented by 1) *L. f. ferrugineus* / *L. f. pondoensis* / *L. f. natalensis* (southern clade) and 2) *L. f. transvaalensis* / *L. f. tongensis* / *L. f. savensis* (northern clade) which are strongly supported with a posterior probability (PP) value of 1.0. The full ATP 6 phylogeny yielded similar results (Fig. 3.1a). The northern clade was recovered to be sister to the proximate outgroup taxa representing the Tropical Boubou *L. aethiopicus* in support of the findings in N'Guembock *et al.* (2008).

### 3.3.1.2 Nuclear DNA - FGB5, MUSK and TGFB2

Each nuclear marker sequenced in this study recovered different number of sequences and this is as a result of the success and failure of the sequencing of some samples. Eighty-four sequences were obtained for the FGB5 marker, 74 for MUSK, and 78 for the TGFB2, but only the unique haplotypes of the four loci were analysed. Generally, the topologies of the phylogenies of the three nuclear loci were poorly resolved with only a few nodes receiving strong support unlike what was observed in the both the ATP6 phylogenies.

The FGB5 phylogeny (Fig 3.3a) recovered two monophyletic groups, the one group consisted of (*L. f. tongensis* and *L. f. transvaalensis*) and the two outgroup taxa: *L. a. mossambicus* and *L. atrococcineus* are basal to the grouping. Another grouping consisted of *L. f. pondoensis* and *L. f. transvaalensis* supported by a PP of 1.0. The TGFB2 phylogeny (Fig 3.4a) also recovered two monophyletic groups, one consisted of almost all the ingroup taxa including *L. f. natalensis*, *L. f. ferrugineus*, *L. f. transvaalensis*, *L. f. pondoensis* and *L. f. tongensis* (PP = 0.88) and the other comprised largely of the proximate outgroup taxa (PP = 0.52), with the exception of one ingroup taxon *L. f. transvaalensis*. Surprisingly, one of the proximate ingroup taxon *L. a. mossambicus* was basal to the two monophyletic groups with a PP of 1.0. The phylogeny recovered by MUSK (Fig 3.5a) revealed a monophyletic group which consisted of all the ingroup taxa that was, *L. f. natalensis*, *L. f. transvaalensis*, *L. f. tongensis* and *L. f. pondoensis* (PP = 0.99) and this group being sister to the proximate taxon *L. aethiopicus* with a PP of 1.0.

Comparatively, the clear differentiation of *L. ferrugineus* into the southern and northern populations observed in both the ATP6 phylogenies (Figs. 3.1a, 3.1b, respectively) was not recovered in the three nuclear phylogenies and this could be attributed to the unavailability of DNA sequences for some of the individual samples in these markers. However, what was common across the nuclear phylogenies is that the ingroup taxa consistently clustered together and that *L. aethiopicus* consistently emerged a sister to *L. ferrugineus*.

### 3.3.2 Mitochondrial and nuclear DNA - population demographic histories and phylogenetic networks

The two primary lineages of the Southern boubou, northern and southern were found to vary with respect to nucleotide diversity and there were also slight differences in other population demographic parameters which were estimated from the ATP6 full data set (polymorphic sites, number of haplotypes and haplotype diversity) (Table 3.3). To detect departures from a neutral Wright-Fisher's model, Fu's  $F_s$  neutrality test implemented in DNAsp 5.0 was used (Fu 1997; Librado & Rozas 2009). Assuming selective neutrality, significant negative values of  $F_s$  indicate population growth while significant positive values are a signature of either genetic subdivision or population contraction and Watterson's  $\theta$  describes the genetic diversity within a population.

With regard to the nuclear data sets (Figs 3.3a, 3.4a, 3.5a), there were no major variations in the nucleotide diversity and other population demographic parameters (polymorphic sites, number of haplotypes and haplotype diversity) which were estimated for *L. ferrugineus* complex (Table 3.4).

When comparing the population demographic histories of the mitochondrial marker versus the nuclear markers of the Southern Boubou, there were differences in the nucleotide diversity. The possibility of population expansion as estimated from the nuclear loci was in support of what resulted from the mitochondrial estimation of population parameters. In comparing the population demographic histories of the northern and the southern clades, they differed in the nuclear diversity, haplotype diversity and all the other parameters estimated (Table 3.4). Although with different values of Fu's test and Watterson's  $\theta$ , both clades seemed to be undergoing expansion, the different values could mean different rate of expansion and contraction for the two populations.

The 95% parsimony network based on both ATP6 datasets revealed two well-differentiated haplotype lineages within *L. ferrugineus* (Fig. 3.1b & 3.2b). One group consisted of the northern taxa (*L. f. transvaalensis*, *L. f. tongensis* and *L. f. savensis*) and the other group represented the southern taxa (*L. f. ferrugineus*, *L. f. natalensis* and *L. f. pondoensis*) and this was in agreement with the outcomes in the Bayesian

phylogeny (Fig 3.2a). There were thirty-one mutations that occurred between the northern and southern lineages.

The 95% parsimony networks based on the nuclear introns did not consistently separate a north or southern lineages for *L. ferrugineus* (Figs. 3.3b, 3.4b & 3.5b), rather taxa were mixed across the network, a result expected when taxa have diverged recently.

### 3.3.3 Divergence time

With regard to the ingroup taxa based on only ATP6 unique haplotype dataset, the time analysis revealed that the major split within the *L. ferrugineus* occurred between the south and the north lineages at approximately 1.5 million years ago (mya) (95% HPD: Highest Posterior Density 1.04 – 1.92; Fig. 3.6), which was during the Pleistocene epoch. The divergence between *L. ferrugineus* and the proximate outgroup taxa (*L. aethiopicus mossambicus*, *L. aethiopicus* and *L. subclateus*) occurred approximately 1.8 mya (95% HPD: 1.31 – 2.32) while the earliest divergence occurred between the ingroup lineage (*L. ferrugineus*) and the relatively distant outgroup species *L. atrococcineus* (approx. 4 mya – Pliocene epoch). The shallow divergence was observed within the proximate outgroup (*L. a. mossambicus*, *L. aethiopicus*, *L. subclateus*), a species found to share a sister relationship with *L. ferrugineus* (N'Guembock *et al.* 2008).

## 3.4 Discussion

Phylogeography enables the investigation of fundamental links between population processes and regional patterns of diversity and biogeography (Avice 2000; Hedrick 2001). It has become standard practice to include geographical information with population genetic data to explain patterns over a spatial scale. There are a number of African studies that have investigated the phylogeography of different species [e.g. frogs – Clawed frog (*Xenopus laevis*) and Clicking stream frog (*Strongylopus grayii*), chameleons – Dwarf chameleons (Bradypodion), birds - Fiscal shrike (*Lanius collaris*), mammals – Rock hyrax (*Procavia capensis*) and Golden moles (Chrysochloridae)] (Evans *et al.* 2004; Tolley *et al.* 2004; Tolley *et al.* 2010; Fuchs *et al.* 2011; Mynhardt *et al.* 2015; Maswanganye *et al.* 2017).

The studies investigating the phylogeography of the different species in southern Africa mentioned above do not concordance with the geographic break in

their distribution ranges as observed in *L. ferrugineus*. This break is seen in an area within the Greater Maputaland-Pondoland-Albany region of southern Africa which was recently designated a centre of vertebrate endemism (Perera *et al.* 2011). It is observed in the northern parts of Kwa-Zulu Natal, south of Swaziland. The same break was found to be a possible explanation of the morphological differentiation in the Brown scrub-robin (*Cercotrichas signata*) (Rebeiro *et al.* 2014). The Zululand dwarf chameleon (*Bradypodion nemorale*), a species of the southern African dwarf chameleons is thought to occur in this area with its distribution range limited to the northern Kwa-Zulu Natal Province (Tolley *et al.* 2004). Individuals collected in this region formed Separate Operational Taxonomic Units that were highly divergent from all other clades although collected from within the recognised range of *B. nemorale*.

The investigation of the phylogeographic patterns using the genetic evidence of this widely-distributed southern African species, *L. ferrugineus* uncovered the genetic diversity within *L. ferrugineus*, and point to two well-supported major phylogeographic lineages which split the distribution range into south and north populations. The findings in Chapter 2 served as a first pointer and slightly coincide with the genetic outcomes (Chapter 3) even though there the two groups were not fully separated due to the overlapping nature of *L. f. transvaalensis*. The superimposition of the map (Fig. 3.7) generated from this study (Chapter 2) dictated that there could be a geographic break separating the south and north lineages in the northern parts of Kwa-Zulu Natal, south of Swaziland (include places such as Hluhluwe-Umfolozi Game Reserve and St Lucia); this is given the divergence times of all major clades. The current taxonomic recognition of six subspecies (*L. f. ferrugineus*, *L. f. natalensis*, *L. f. pondoensis*, *L. f. transvaalensis*, *L. f. tongensis* and *L. f. savensis*) is refuted by the findings in this chapter, which conclusively showed that there are two major ESUs. It is also worth noting that as in N'Guembock *et al.* (2008), the eastern and southern African populations of *L. aethiopicus* emerged to be more closely related to *L. ferrugineus*.

The south and north lineages of the Southern Boubou occur in different habitats, the south lineage generally occurring in broadly defined fynbos, afro-montane and coastal forest, which cover *L. f. ferrugineus*, *L. f. natalensis* and *L. f.*



*pondoensis* respectively. While the north lineage occupies the broadly defined habitats such as savanna, temperate grassland and temperate forest occupied by *L. f. transvaalensis*, *L. f. tongensis* and *L. f. savensis* respectively.

Clearly, *L. ferrugineus* represents two lineages and there is potential to recognise two species. One species in the south that is, *Laniarius ferrugineus* (Gmelin, 1788) represented by members of the southern clade: *L. f. ferrugineus*; *L. f. natalensis* and *L. f. pondoensis* and another species to be named *Laniarius transvaalensis* Roberts, 1922 in the north based on the Principle of priority. Given that there is less differentiation within the south and the north clade, it is recommended that *Laniarius ferrugineus natalensis* Roberts, 1922 and *Laniarius ferrugineus pondoensis* Roberts, 1922 be synonymised with *L. ferrugineus* (Gmelin, 1788). On the other hand, *L. f. tongensis* Roberts, 1931 and *L. f. savensis* da Rosa Pinto, 1963 should be synonymised with *L. transvaalensis* (Roberts, 1922). This taxonomic status was implicated in light of the revelations brought forth by the genetic and morphological data used and in applying the principle of priority.

The population demographic histories of the northern and southern clades seem to be undergoing expansion although the variation in the values of Fu's test and Watterson's theta could mean that the rate of expansion and contraction for the two populations differ. The 95% parsimony network based on both ATP6 datasets revealed two well-differentiated lineages within *L. ferrugineus* although there was poor resolution based on the nuclear introns. The major split within *L. ferrugineus* occurred between the south and the north lineages at approximately 1.5 million years ago.

### **3.5 Conclusion**

The findings presented in this chapter demonstrate clearly that the six subspecies did not follow the same evolutionary path. In other words, two species should be recognised, one in the south, *Laniarius ferrugineus* (Gmelin, 1788) and another one in the north which should be named *Laniarius transvaalensis* Roberts, 1922 based on priority. However, recommendations are made and additional analyses such as molecular species delimitation, gene flow and also more samples for at least *Laniarius transvaalensis tongensis* and *Laniarius transvaalensis savensis* should be analysed.

**Table 3.1.** Primers sequences used to PCR-amplify and sequence DNA samples in the present study (both modern and historical samples).

Locus	Primers (5'-3')	Reference
ATP6	A8PWL: CCTGAACCTGACCATGAAC	Eberhard & Bermingham (2004)
	CO3: CATGGGCTGGGGTCTACTATGTG	
	450L: AACCAATCAGCCTACTTATCCG	Fuchs & Molepo (unpul)
	27OR: GGTRAAATGTGTATGGTAGTAG	
FGB5	Fib5: CGCCATACAGAGTATACTGTGACAT	Marini & Hackett (2002)
	Fib6: GCCATCCTGGCGATTCTGAA	
TGFB2	TGF5: GAAGCGTGCTCTAGATGCTG	Primmer <i>et al.</i> (2002)
	TGF6: AGGCAGCAATTATCCTGCAC	
MUSK	MUSK13F: CTTCCATGCACTACAATGGGAAA	Kimballa <i>et al.</i> (2009)
	MUSK13R: CTCTGAACATTGTGGATCCTCAA	
SEXING	255OF: GTTACTGATTCGTCTACGAGA	Fridolfsson & Ellegren (1999)
	2718R: ATTGAAATGATCCAGTGCTTG	

\*450L and 270H were primers specifically designed for *Laniarius ferrugineus* historical DNA samples.

**Table 3.2.** Genetic diversity values (N, number of potential alleles; S, number of segregating sites; Hd, Haplotype diversity; Pi, nucleotide diversity;  $\theta$ , Watterson's theta) based on only the ATP6 marker of *Laniarius ferrugineus* (- represents uncalculated values).

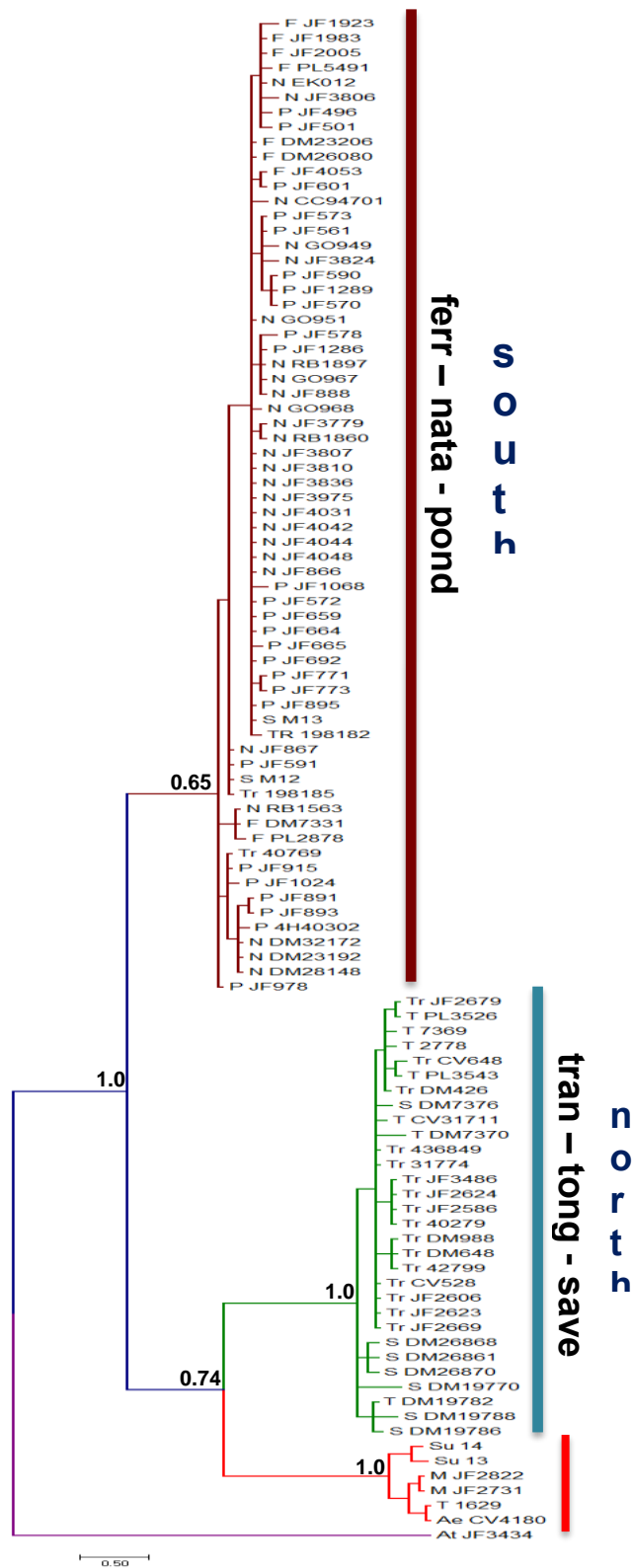
ATP6 (684bp)	S (Segregating sites)	h (No. of haplotypes)	Hd (haplotype diversity)	Pi (Nucleotide diversity)	No. of sequences	Fu (Fu's test)	Watterson's theta ( $\theta$ )
Outgroup taxa	94	5	0.933	0.04825	6	-	0.06019
Ingroup taxa	103	48	0.9416	0.03397	97	-	0.03265
<i>L. f. ferrugineus</i>	13	7	0.944	0.00702	9	-1.544	0.00765
<i>L. f. natalensis</i>	22	12	0.840	0.00474	26	-3.404	0.00843
<i>L. f. pondoensis</i>	22	17	0.951	0.00589	26	-8.542	0.00843
<i>L. f. savensis</i>	52	9	1.00	0.03208	9	-1.390	0.03121
<i>L. f. tongensis</i>	60	8	1.00	0.02381	8	-1.251	0.03383
<i>L. f. transvaalensis</i>	51	9	0.860	0.02043	19	3.578	0.02133
All taxa	143	52	0.953	0.03956	103	-4.731	0.04480

**Table 3.3.** Genetic diversity values within *Laniarius ferrugineus* (N, number of potential alleles; S, number of segregating sites; Hd, Haplotype diversity; Pi, nucleotide diversity;  $\theta$ , Watterson's theta) based on the ATP6 marker for the two lineages recovered in the Bayesian Analysis.

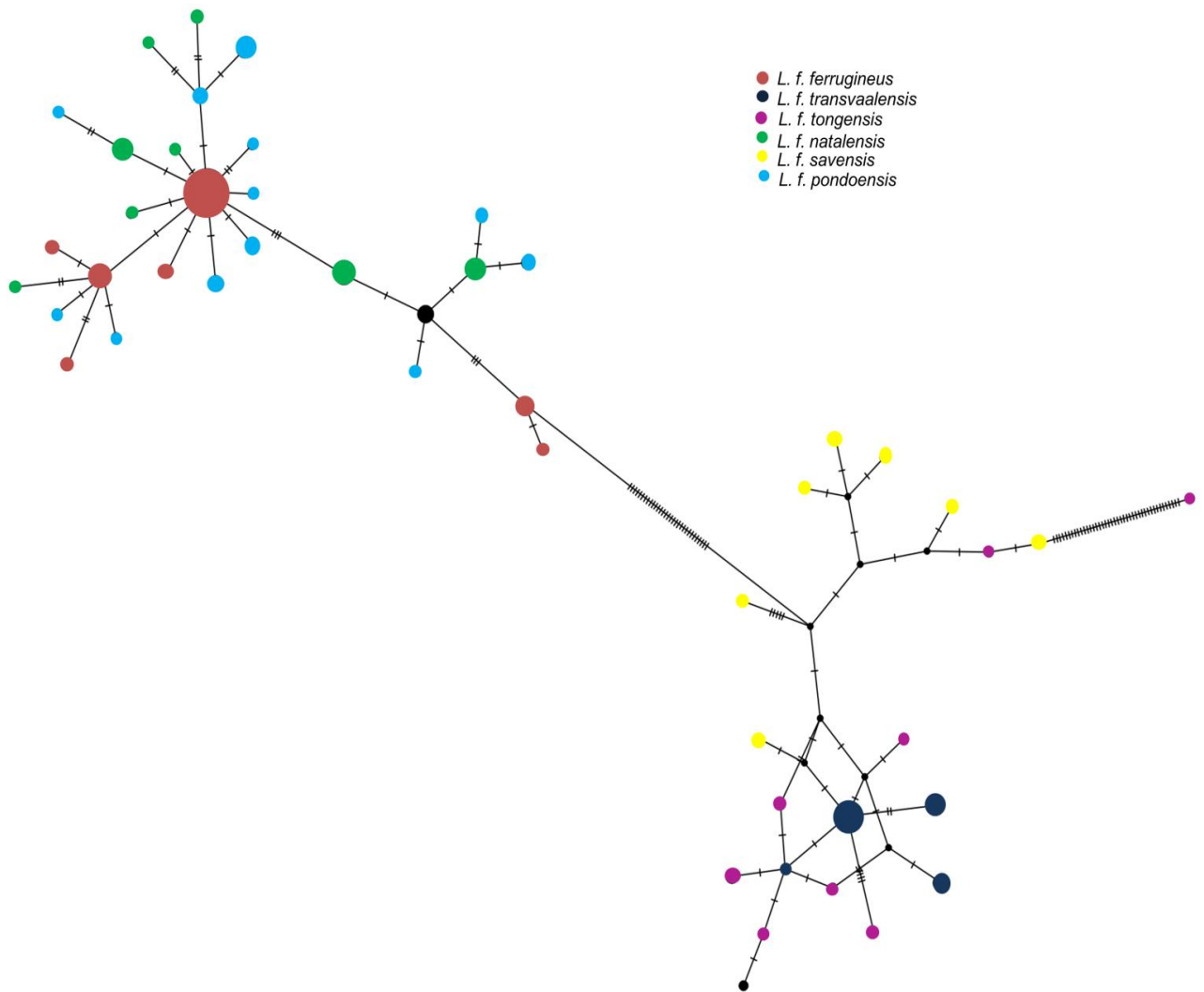
ATP6 (684 bp)	Northern Group	Southern Group
	( <i>L. f. transvaalensis</i> , <i>L. f. tongensis</i> , <i>L. f. savensis</i> )	( <i>L. f. ferrugineus</i> , <i>L. f. natalensis</i> , <i>L. f. pondoensis</i> )
No. of sequences	36	62
S (Polymorphic sites)	83	37
h (No. of haplotypes)	24	28
Hd (Haplotype diversity)	0.959	0.888
Pi (Nucleotide diversity)	0.026	0.005

**Table 3.4.** Genetic diversity values within *Laniarius ferrugineus* (N, number of potential alleles; S, number of segregating sites; Hd, Haplotype diversity; Pi, nucleotide diversity;  $\theta$ , Watterson's theta) based the nuclear markers for the ingroup taxa.

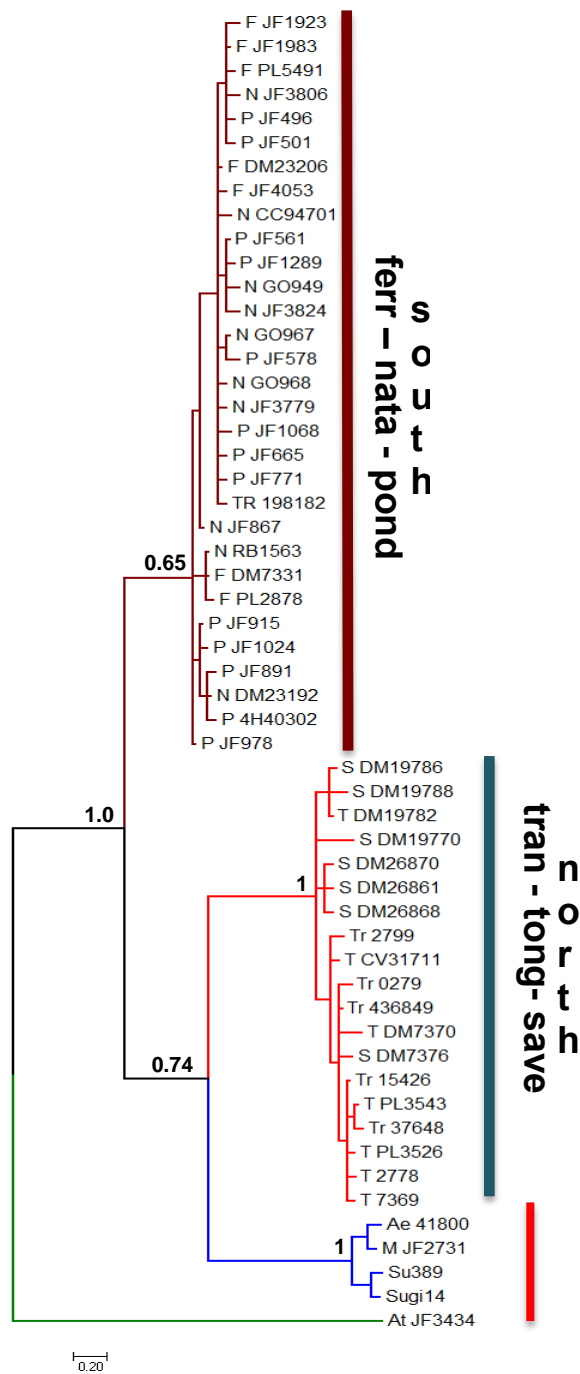
Ingroup taxa	FGB5 (Beta Fibrinogen Intron)	MUSK (Muscle associated receptor tyrosine kinase)	TGFB2 (Transforming growth bet intron)
	564bp	~ 570bp	568bp
S (segregating sites)	23	10	14
h (Number of haplotypes)	14	11	12
Hd (Haplotype diversity)	0,616	0,671	0,622
Pi (Nucleotide diversity)	0,00815	0,00175	0,0017
Fs (Fu & Li's tests)	1,661	-4,584	-5,567
W (Waterson's theta)	0,00723	0,00321	0,00429



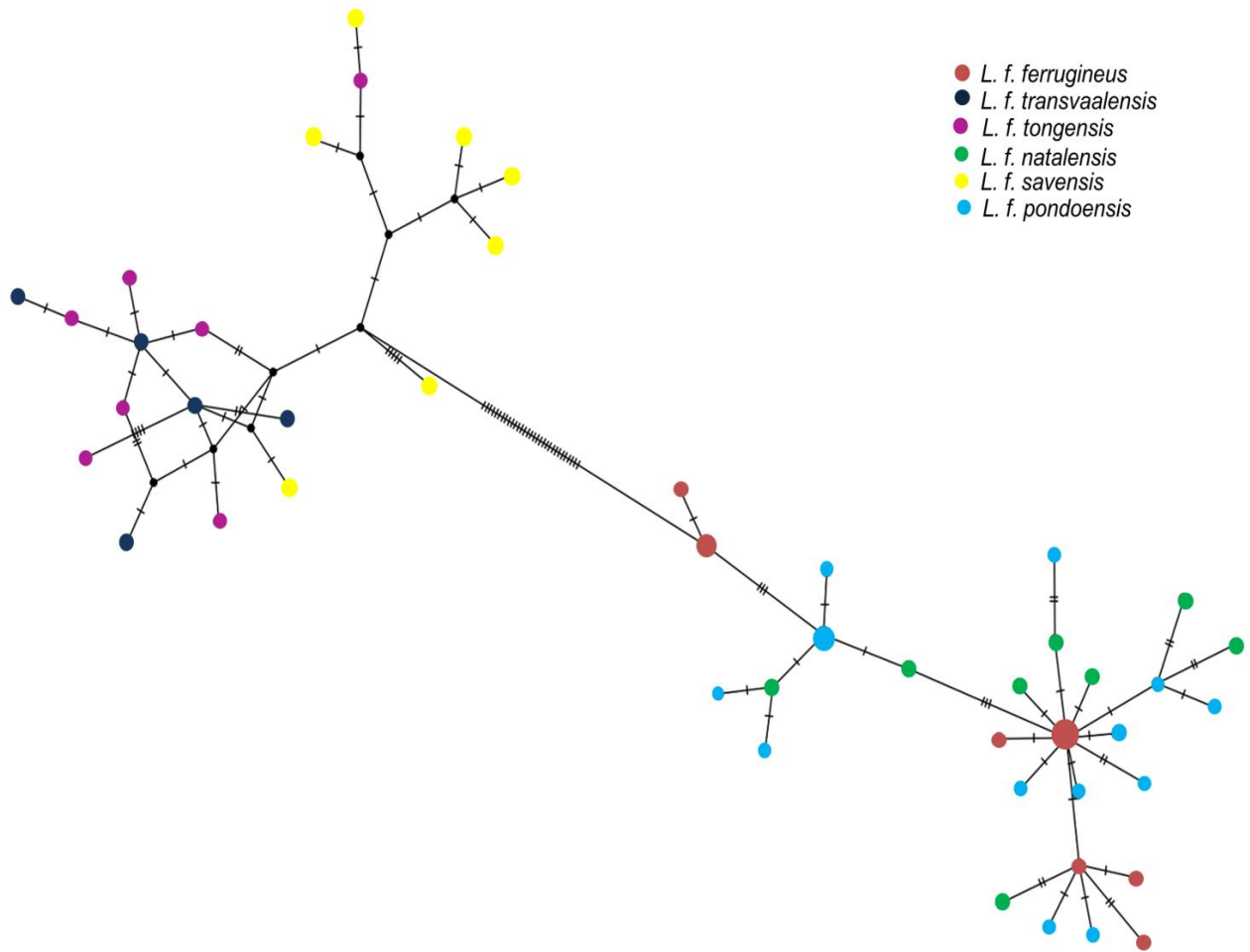
**Figure 3.1a.** Bayesian phylogenetic tree based on all individuals sampled generated from mitochondrial ATP6 gene of *Laniarius ferrugineus*. The numbers above the branches are the posterior probabilities (only  $\geq 0.65$  are shown, colours in deeper branches indicate nothing but colours in shallow branches are a mere indication of the groups).



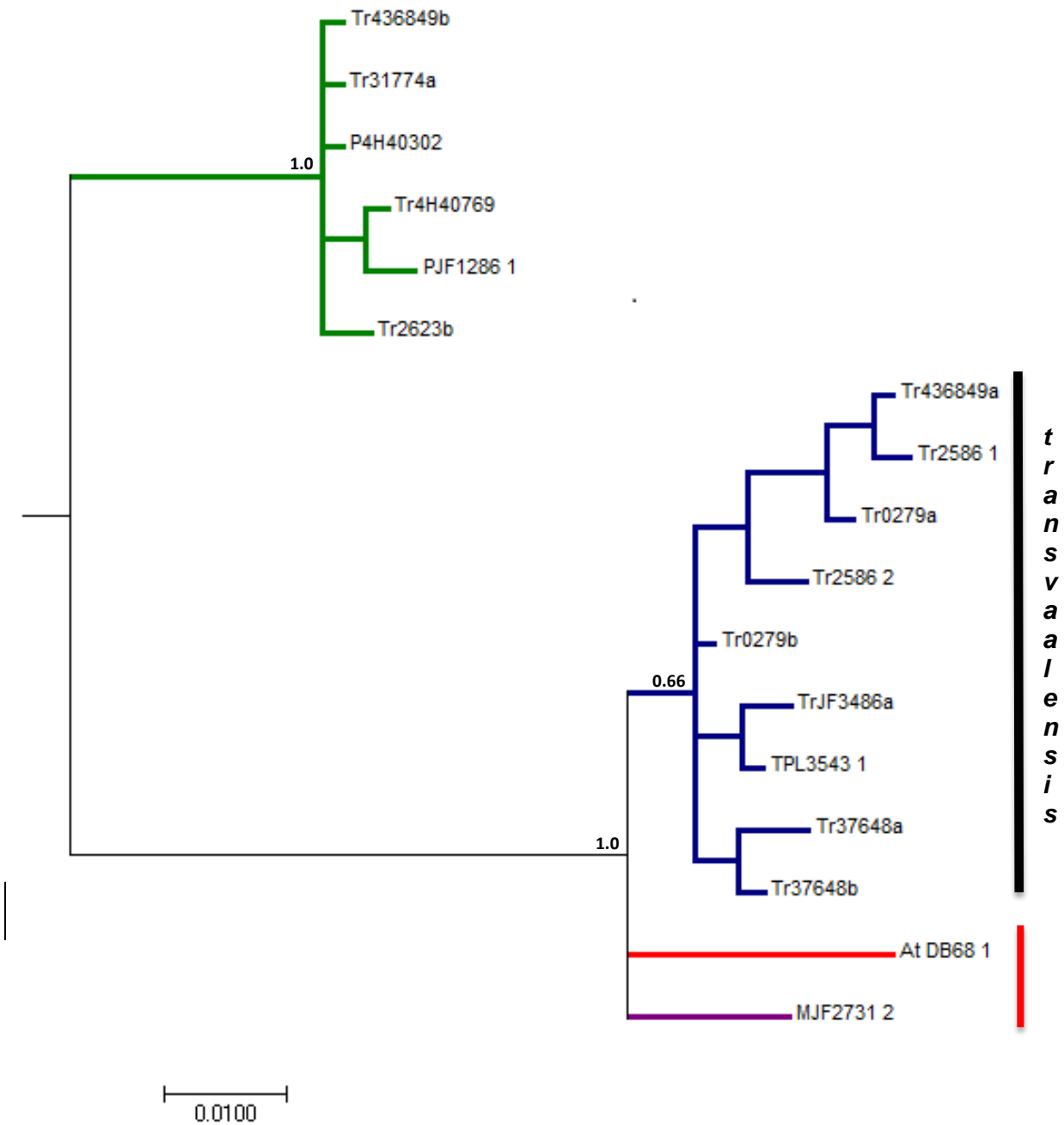
**Figure 3.1b.** Parsimony network (95% parsimony) based on ATP6 of all individuals of *Laniarius ferrugineus* sampled with the exclusion of outgroups for graphical purposes. The sizes of the circles are proportional to the haplotype frequencies, lines represent branches, small lines across branches represent number of mutations and the small black circles represent unsampled or extinct haplotypes. Each subspecies is represented by one colour, north of the range: *L. f. transvaalensis*, *L. f. tongensis* and *L. f. savensis* (blue, purple and yellow respectfully) and south of the range: *L. f. natalensis*, *L. f. ferrugineus* and *L. f. pondoensis* (green, dark red and light blue respectfully).



**Figure 3.2a.** Bayesian phylogenetic tree based on unique haplotypes of *Lanarius ferrugineus* only generated from mitochondrial ATP6 gene. The numbers above the branches are the posterior probabilities (only  $\geq 0.65$  are shown, colours in deeper branches indicate nothing but colours in shallow branches are a mere indication of the groups).

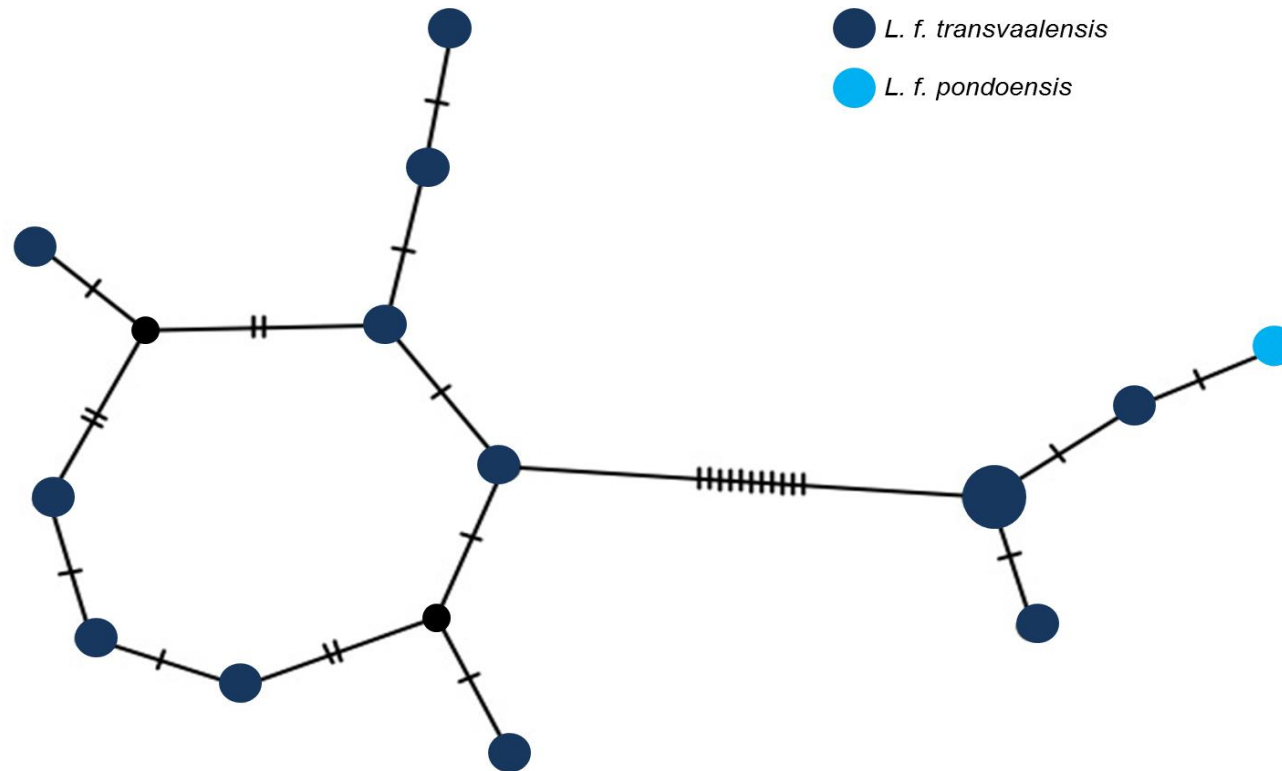


**Figure 3.2b.** Parsimony network (95% parsimony) based on ATP6 unique haplotypes of *Laniarius ferrugineus* with the exclusion of outgroups for graphical purposes. Lines represent branches, small lines across branches represent number of mutations and the small black circles represent unsampled or extinct haplotypes. Each subspecies is represented by one colour, north of the range: *L. f. transvaalensis*, *L. f. tongensis* and *L. f. savensis* (blue, purple and yellow respectively) and south of the range: *L. f. natalensis*, *L. f. ferrugineus* and *L. f. pondoensis* (green, dark red and light blue respectively) that form two distinct clusters.

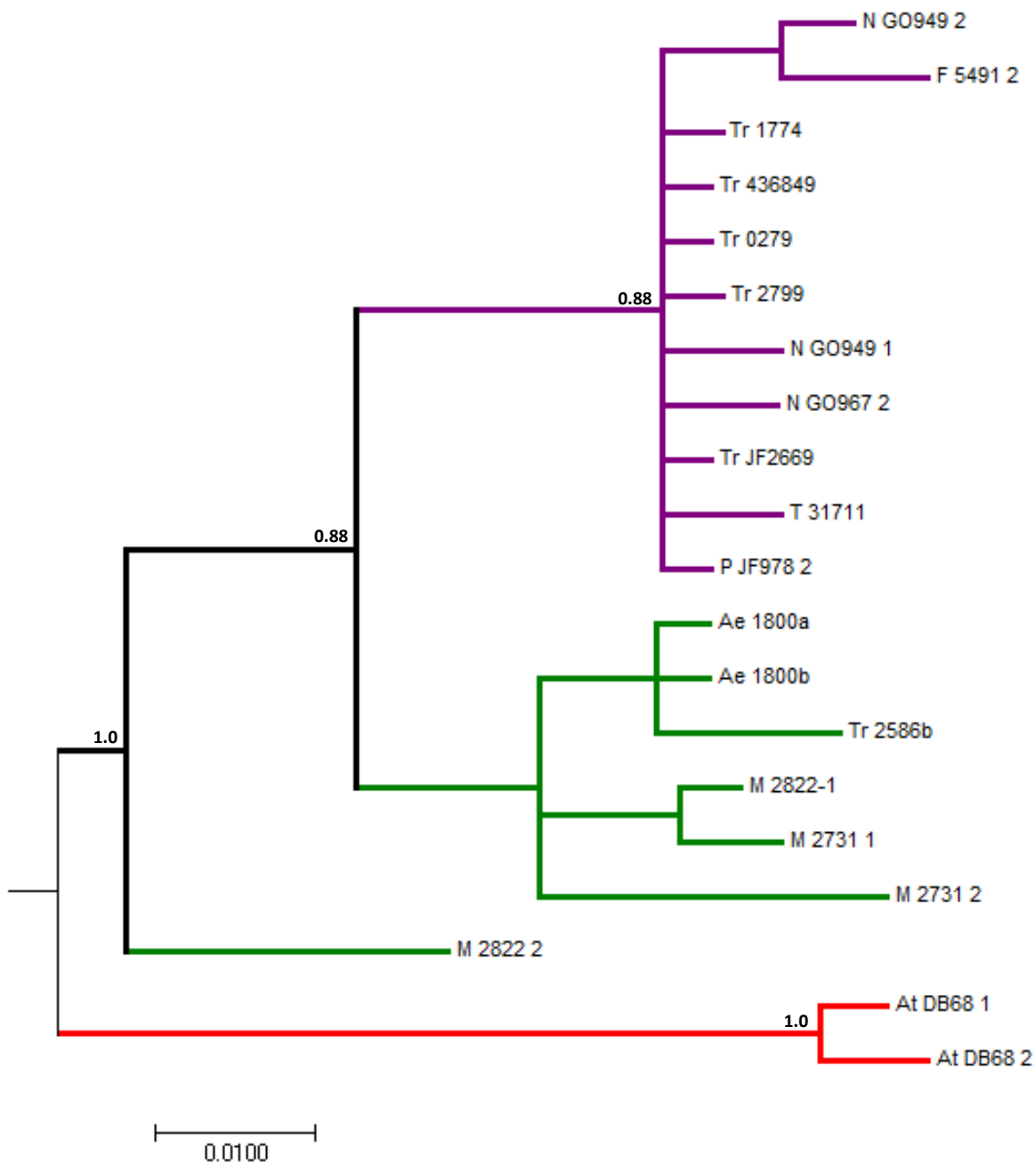


**Figure 3.3a.** Bayesian phylogenetic tree of *Laniarius ferrugineus* based on unique haplotypes only generated from nuclear FGB5. Numbers above the branches are the posterior probabilities. (only  $\geq 0.65$  are shown, colours in deeper branches indicate nothing but colours in shallow branches are a mere indication of the groups).

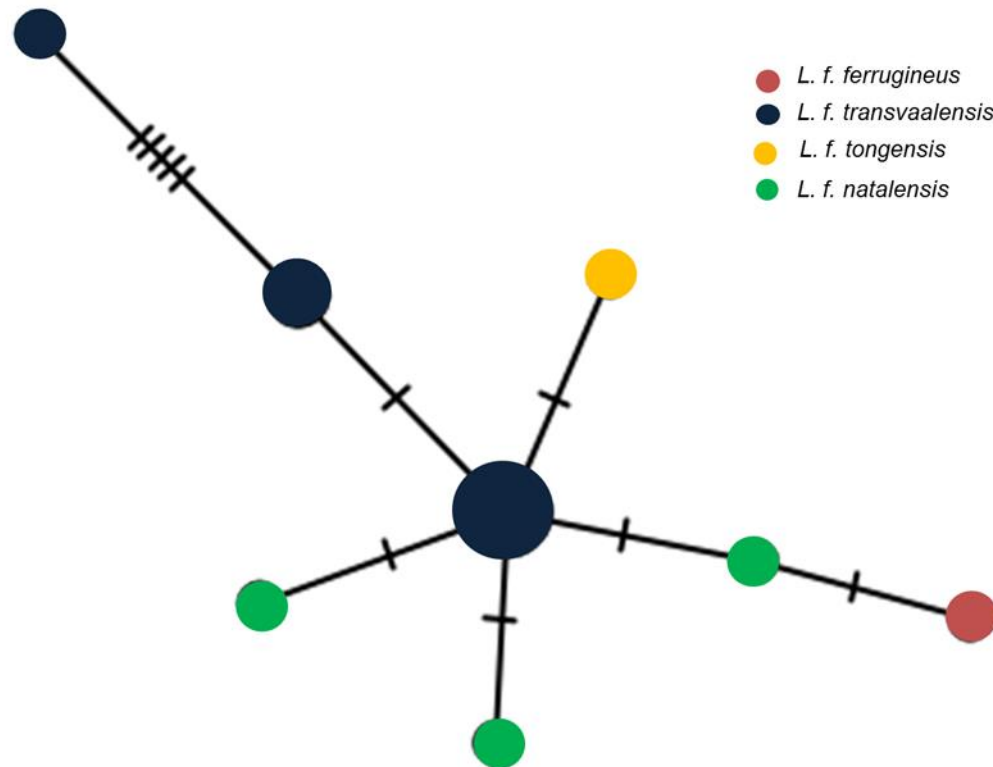




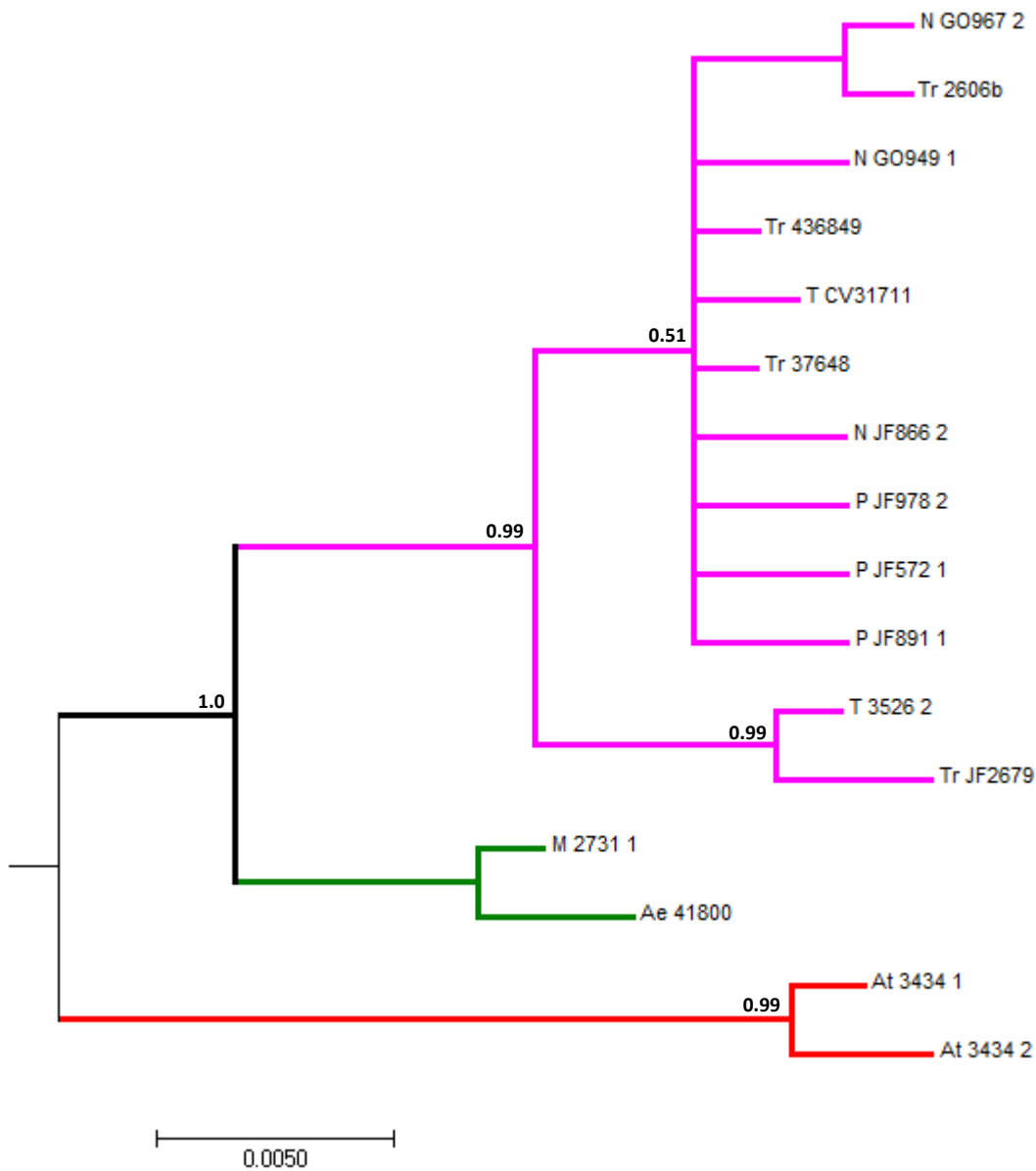
**Figure 3.3b.** Parsimony network (95% parsimony) of *Laniarius ferrugineus* based on FGB5 unique haplotypes with the exclusion of outgroups for graphical purposes. The sizes of the circles are proportional to the haplotype frequencies, lines represent branches, small lines across branches represent number of mutations and the small black circles represent unsampled or extinct haplotypes. Each subspecies is represented by one colour, north of the range: *L. f. transvaalensis* (blue) and south of the range: *L. f. pondoensis* (light blue).



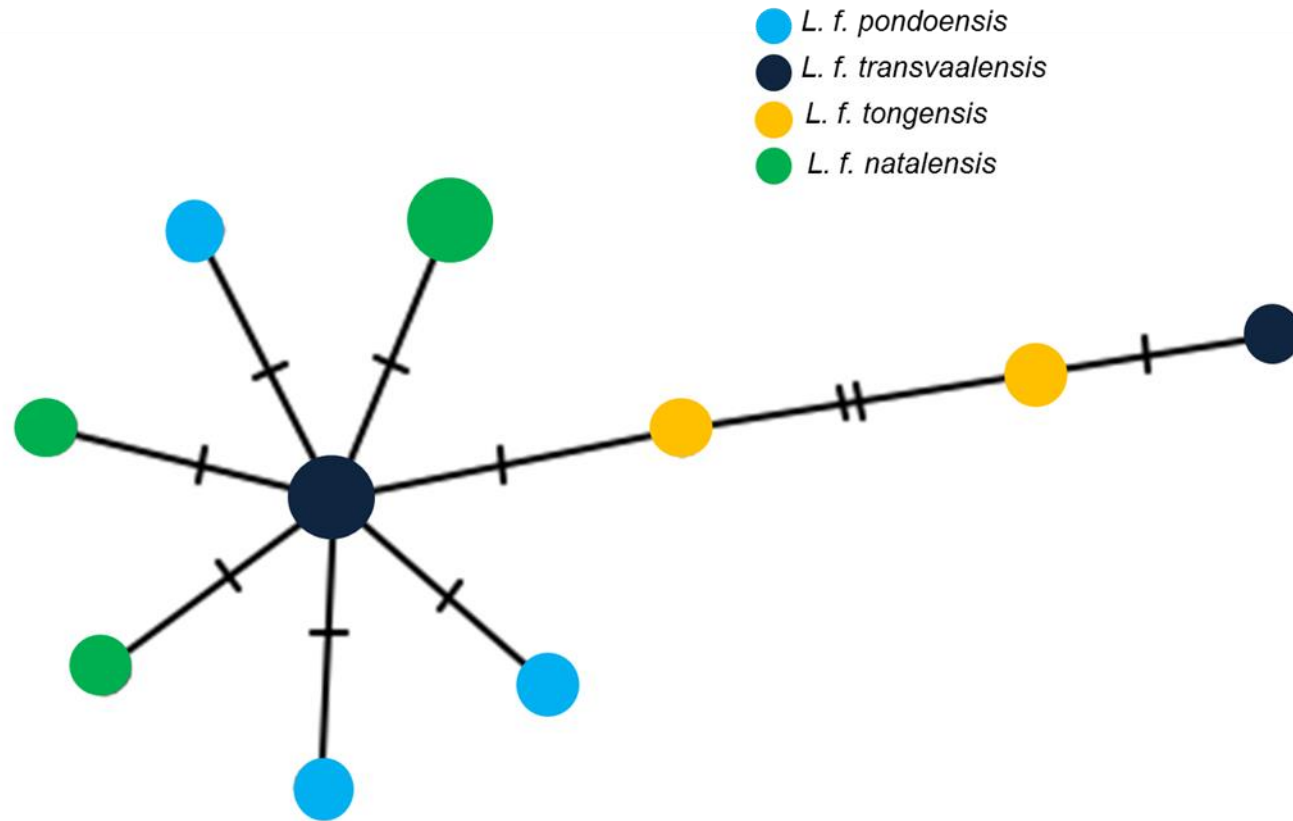
**Figure 3.4a.** TGFB2 Bayesian phylogenetic tree of *Laniarius ferrugineus* based on unique alleles. Numbers above the branches are the posterior probabilities (only  $\geq 0.65$  are shown, colours in deeper branches indicate nothing but colours in shallow branches are a mere indication of the groups).



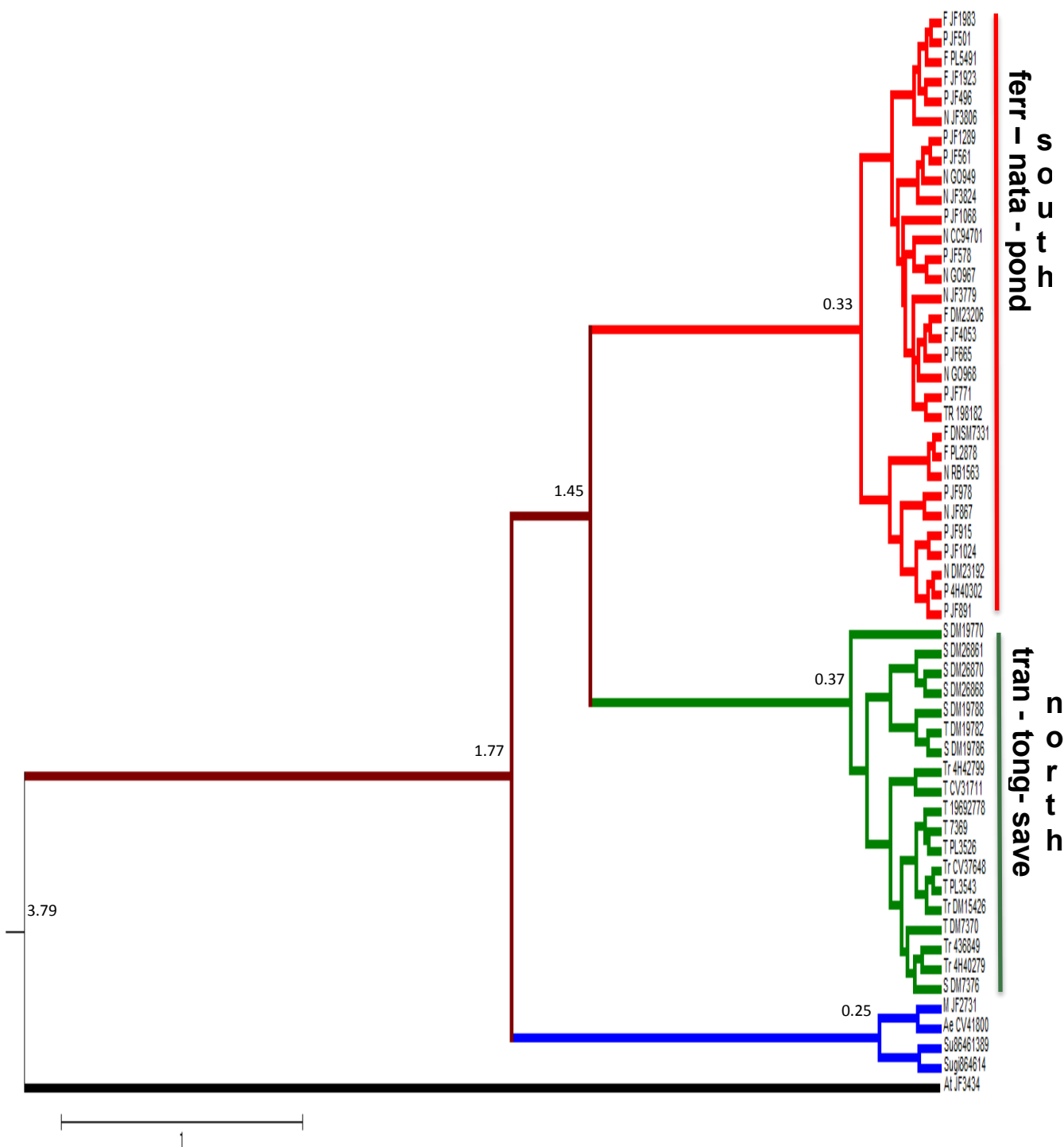
**Figure 3.4b.** Parsimony network (95% parsimony) of *Laniarius ferrugineus* based on TGFB2 unique haplotypes with the exclusion of outgroups for graphical purposes. The sizes of the circles are proportional to the haplotype frequencies, lines represent branches and small lines across branches represent number of mutations. Each subspecies is represented by one colour, north of the range: *L. f. transvaalensis* and *L. f. tongensis* (blue and oranges respectively) and south of the range: *L. f. natalensis* and *L. f. ferrugineus* (green and dark red respectively).



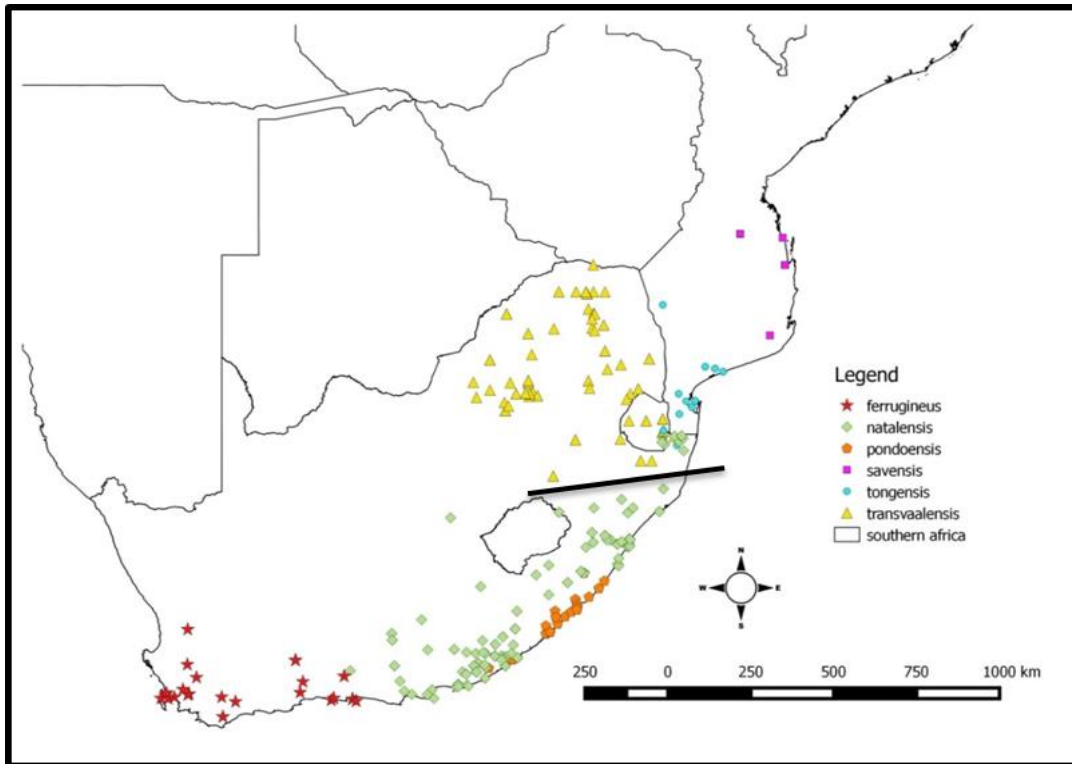
**Figure 3.5a.** Bayesian phylogenetic tree of *Lanarius ferrugineus* based on unique haplotypes generated from nuclear MUSK. Numbers above the branches are the posterior probabilities (only  $\geq 0.65$  are shown, colours in deeper branches indicate nothing but colours in shallow branches are a mere indication of the groups).



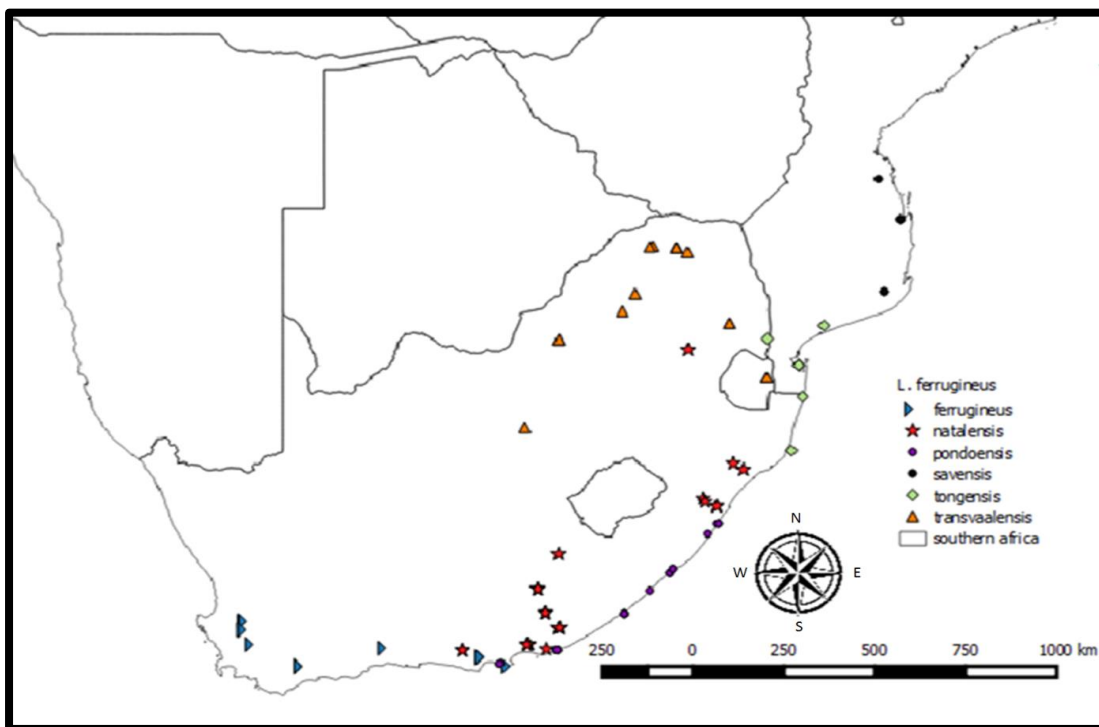
**Figure 3.5b.** Parsimony network (95% parsimony) of *Laniarius ferrugineus* based on MUSK unique haplotypes with the exclusion of outgroups for graphical purposes. The sizes of the circles are proportional to the haplotype frequencies, lines represent branches and small lines across branches represent number of mutations. Each subspecies is represented by one colour: *L. f. transvaalensis* and *L. f. tongensis* (blue and oranges respectively) and *L. f. natalensis* and *L. f. pondoensis* (green and light blue respectively).



**Figure 3.6.** Divergence time phylogenetic tree based on unique haplotypes of the ATP6 mitochondrial marker. Values above branches represent estimated divergence times indicated in million years (colours in deeper branches indicate nothing but colours in shallow branches are a mere indication of the groups).



**Figure 3.7.** Distribution map of *Laniarius ferrugineus* generated in this study showing a possible geographic break (a black line) separating the southern and the northern lineages.



**Figure 3.8.** Distribution map of *Laniarius ferrugineus* generated from all the individuals sampled for DNA analysis.

## **APPENDICES**

**Appendix 3.1.** A proposed revised classification of the Southern Boubou *Laniarius ferrugineus*.

**Family:** Malaconotidae

**Genus:** *Laniarius* Vieillot, 1816

**Species:** *Laniarius ferrugineus* (Gmelin, 1788)  
*Laniarius transvaalensis* (Roberts, 1922)



**Appendix 3.2.** List of samples (103) sequenced in this study (DNA samples). Abbreviations: MVZ, Museum of Vertebrate Zoology, Berkeley; MNHN, Muséum National d'Histoire, Naturelle, Paris and DNSM, Durban Natural Science Museum, Durban.

Taxon Names	Institution	Tissue/Voucher number	Locality	Latitude	Longitude	Country	Province	Sex	Sample type
<i>Laniarius aethiopicus</i>	MVZ	CV41800	Moreland	-22.5333	28.6833	South Africa	Limpopo	Female	Blood
<i>Laniarius aethiopicus mossambicus</i>	MNHN	ZO 2011-228	2 km from Nhica de Rovuma, Main Camp site	-10.76	40.2183	Mozambique		Female	Muscle, Liver, Heart
<i>Laniarius aethiopicus mossambicus</i>	MNHN	ZO 2011-216	2 km from Nhica de Rovuma, Main Camp site	-10.76	40.2183	Mozambique		Female	Muscle, Liver, Heart
<i>Laniarius atrococcinus</i>	MNHN	ZO 2013-291	Polokwane Game Reserve, Warthog Picnic Site	-23.99267	29.46695	South Africa	Limpopo	Male	Muscle, Liver, Heart
<i>Laniarius ferrugineus ferrugineus</i>	MVZ	JF1923	Goudini Spa	-33.5	19.25	South Africa	Western Cape	Female	Blood
<i>Laniarius ferrugineus ferrugineus</i>	MVZ	JF1983	Bontebok NP	-34.0778	20.4539	South Africa	Western Cape	Male	Blood
<i>Laniarius ferrugineus ferrugineus</i>	MVZ	JF2005	Bontebok NP	-34.0778	20.4539	South Africa	Western Cape	Male	Blood
<i>Laniarius ferrugineus ferrugineus</i>	MVZ	PL5491	Le Roux Voorsorg, De Rust	-33,6	22,5333	South Africa	Western Cape	Male	Blood
<i>Laniarius ferrugineus ferrugineus</i>	MVZ	PL2878	Beaverlac	-32.8869	19.0828	South Africa	Western Cape	Male	Blood
<i>Laniarius ferrugineus ferrugineus</i>	DMNS	DM7331	Clanwilliam, Pakhuis	-33,117	19,07	South Africa	Western Cape	Male	Blood
<i>Laniarius ferrugineus ferrugineus</i>	DMNS	DM26080	Patensie, Ferndale	-33,839	24,947	South Africa	Eastern Cape	Female	Blood
<i>Laniarius ferrugineus ferrugineus</i>	DMNS	DM23206	Port Elizabeth	-34,075	25,6	South Africa	Eastern Cape	Female	Blood
<i>Laniarius ferrugineus natalensis</i>	MVZ	CC94701	Tasmania, Jamestown	-31.1211	26.8069	South Africa	Eastern Cape	Female	Blood
<i>Laniarius ferrugineus natalensis</i>	MVZ	JF866	Stead Farm, 20 kms off Tarkastdt	-32.0394	26.2933	South Africa	Eastern Cape	Male	Blood
<i>Laniarius ferrugineus natalensis</i>	MVZ	JF867	Stead Farm, 20 kms off Tarkastdt	-32.0394	26.2933	South Africa	Eastern Cape	Female	Blood
<i>Laniarius ferrugineus natalensis</i>	MVZ	JF888	Stead Farm, 20 kms off Tarkastdt	-32.0394	26.2933	South Africa	Eastern Cape	Male	Blood
<i>Laniarius ferrugineus natalensis</i>	MVZ	GO949	close to Research Center, Great Fish Nature Reserve	-33,0654	26,8204	South Africa	Eastern Cape	Female	Blood
<i>Laniarius ferrugineus natalensis</i>	MVZ	GO951	close to Research Center, Great Fish Nature Reserve	-33,0654	26,8204	South Africa	Eastern Cape	Female	Blood
<i>Laniarius ferrugineus natalensis</i>	MNHN	JF3806	close to Research Center, Great Fish Nature Reserve	-33,0654	26,8204	South Africa	Eastern Cape	Male	Blood
<i>Laniarius ferrugineus natalensis</i>	MNHN	JF3807	close to Research Center, Great Fish Nature Reserve	-33,0654	26,8204	South Africa	Eastern Cape	Male	Muscle, Liver, Heart
<i>Laniarius ferrugineus natalensis</i>	MNHN	JF3810	close to Research Center, Great Fish Nature Reserve	-33,0654	26,8204	South Africa	Eastern Cape	Female	Muscle, Liver, Heart
<i>Laniarius ferrugineus natalensis</i>	MNHN	JF3824	close to Research Center, Great Fish Nature Reserve	-33,0654	26,8204	South Africa	Eastern Cape	Male	Blood
<i>Laniarius ferrugineus natalensis</i>	MNHN	JF3779	Doodsklip Camp, Baviaanskloof Nature Reserve	-32,6666	26,4833	South Africa	Eastern Cape	Female	Muscle, Liver, Heart
<i>Laniarius ferrugineus natalensis</i>	MVZ	RCKB1860	Doodsklip Camp, Baviaanskloof Nature Reserve, Cacadu District	-33,6588	24,43165	South Africa	Eastern Cape	Male	Skin
<i>Laniarius ferrugineus natalensis</i>	MNHN	JF3836	Fort Fordyce, close to Mpofo Nature Reserve	-32,6666	26,4833	South Africa	Eastern Cape	Female	Muscle, Liver, Heart
<i>Laniarius ferrugineus natalensis</i>	MVZ	GO967	Fort Fordyce, close to Mpofo Nature Reserve	-32,6666	26,4833	South Africa	Eastern Cape	Male	Blood
<i>Laniarius ferrugineus natalensis</i>	MVZ	GO968	Fort Fordyce, close to Mpofo Nature Reserve	-32,6666	26,4833	South Africa	Eastern Cape	Male	Muscle, liver
<i>Laniarius ferrugineus natalensis</i>	MVZ	EK12	Fort Fordyce, close to Mpofo Nature Reserve	-32,6666	26,4833	South Africa	Eastern Cape	Female	Muscle, liver
<i>Laniarius ferrugineus natalensis</i>	MVZ	RCKB1897	Fort Fordyce, close to Mpofo Nature Reserve, Amathole District	-32,6666	26,4833	South Africa	Eastern Cape	Male	Blood
<i>Laniarius ferrugineus natalensis</i>	MNHN	JF3975	Hunter's Lodge, 12 kms from Kenton on Sea towards Alexandria on R72, Cacadu District	-33,62734	26,50834	South Africa	Eastern Cape	Female	Muscle, Liver, Heart
<i>Laniarius ferrugineus natalensis</i>	MNHN	JF4031	Shamwari Game Reserve, 10 kms SE of Paterson, Cacadu District	-33.4929	26.06365	South Africa	Eastern Cape	Male	Muscle, Liver, Heart
<i>Laniarius ferrugineus natalensis</i>	MNHN	JF4042	Shamwari Game Reserve, 10 kms SE of Paterson, Cacadu District	-33.4929	26.06365	South Africa	Eastern Cape	Female	Blood
<i>Laniarius ferrugineus natalensis</i>	MNHN	JF4044	Shamwari Game Reserve, 10 kms SE of Paterson, Cacadu District	-33.4929	26.06365	South Africa	Eastern Cape	Male	Blood
<i>Laniarius ferrugineus natalensis</i>	MNHN	JF4048b	Shamwari Game Reserve, 10 kms SE of Paterson, Cacadu District	-33.4929	26.06365	South Africa	Eastern Cape	Male	Muscle, Liver, Heart
<i>Laniarius ferrugineus natalensis</i>	MNHN	JF4053	Tent site, Shamwari Game Reserve, 10 kms SE of Paterson, Cacadu District	-33.50682	26.02464	South Africa	Eastern Cape	Female	Blood

Taxon Names	Institution	Tissue/Voucher number	Locality	Latitude	Longitude	Country	Province	Sex	Sample type
<i>Laniarius ferrugineus natalensis</i>	DMNS	DM28148	Pietermaritzburg, Bisley	-29,65	30,383	South Africa	Kwazulu Natal	Female	Blood
<i>Laniarius ferrugineus natalensis</i>	DMNS	DM32172	Durban, Shongweni	-29,85	30,716	South Africa	Kwazulu Natal	Male	Blood
<i>Laniarius ferrugineus natalensis</i>	DMNS	DM23192	Durban, Shongweni Dam	-29,85	30,717	South Africa	Kwazulu Natal	Male	Blood
<i>Laniarius ferrugineus pondoensis</i>	MVZ	JF561	Kasouga	-33.6483	26.7711	South Africa	Eastern Cape	Male	Blood
<i>Laniarius ferrugineus pondoensis</i>	MVZ	JF570	Kasouga	-33.6483	26.7711	South Africa	Eastern Cape	Male	Blood
<i>Laniarius ferrugineus pondoensis</i>	MVZ	JF572	Kasouga	-33.6483	26.7711	South Africa	Eastern Cape	Female	Blood
<i>Laniarius ferrugineus pondoensis</i>	MVZ	JF573	Kasouga	-33.6483	26.7711	South Africa	Eastern Cape	Female	Blood
<i>Laniarius ferrugineus pondoensis</i>	MVZ	JF578	Kasouga	-33.6483	26.7711	South Africa	Eastern Cape	Male	Blood
<i>Laniarius ferrugineus pondoensis</i>	MVZ	JF590	Kasouga	-33.6483	26.7711	South Africa	Eastern Cape	Female	Blood
<i>Laniarius ferrugineus pondoensis</i>	MVZ	JF591	Kasouga	-33.6483	26.7711	South Africa	Eastern Cape	Male	Blood
<i>Laniarius ferrugineus pondoensis</i>	MVZ	JF601	Kasouga	-33.6483	26.7711	South Africa	Eastern Cape	Male	Blood
<i>Laniarius ferrugineus pondoensis</i>	MVZ	JF659	Kasouga	-33.6483	26.7711	South Africa	Eastern Cape	Female	Blood
<i>Laniarius ferrugineus pondoensis</i>	MVZ	JF664	Kasouga	-33.6483	26.7711	South Africa	Eastern Cape	Female	Blood
<i>Laniarius ferrugineus pondoensis</i>	MVZ	JF665	Kasouga	-33.6483	26.7711	South Africa	Eastern Cape	Male	Blood
<i>Laniarius ferrugineus pondoensis</i>	MVZ	JF692	Morgans Bay	-32.6881	28.4308	South Africa	Eastern Cape	Female	Blood
<i>Laniarius ferrugineus pondoensis</i>	MVZ	JF771	Morgans Bay	-32.6881	28.4308	South Africa	Eastern Cape	Male	Blood
<i>Laniarius ferrugineus pondoensis</i>	MVZ	JF773	Morgans Bay	-32.6881	28.4308	South Africa	Eastern Cape	Female	Blood
<i>Laniarius ferrugineus pondoensis</i>	MVZ	JF891	10 kms Port St Johns	-31.6056	29.55	South Africa	Eastern Cape	Female	Blood
<i>Laniarius ferrugineus pondoensis</i>	MVZ	JF893	10 kms Port St Johns	-31.6056	29.55	South Africa	Eastern Cape	Male	Blood
<i>Laniarius ferrugineus pondoensis</i>	MVZ	JF895	10 kms Port St Johns	-31.6056	29.55	South Africa	Eastern Cape	Male	Blood
<i>Laniarius ferrugineus pondoensis</i>	MVZ	JF915	Pennington and Umdoni Golf	-30.3092	30.7508	South Africa	KwaZulu Natal	Female	Blood
<i>Laniarius ferrugineus pondoensis</i>	MVZ	JF978	Pennington and Umdoni Golf	-30.3092	30.7508	South Africa	KwaZulu Natal	Male	Blood
<i>Laniarius ferrugineus pondoensis</i>	MVZ	JF1024	Pennington and Umdoni Golf	-30.3092	30.7508	South Africa	KwaZulu Natal	Male	Blood
<i>Laniarius ferrugineus pondoensis</i>	MVZ	JF1068	Mbotye	-32.0808	29.0642	South Africa	Eastern Cape	Female	Blood
<i>Laniarius ferrugineus pondoensis</i>	MVZ	JF1286	Morgans Bay	-32.6881	28.4308	South Africa	Eastern Cape	Male	Blood
<i>Laniarius ferrugineus pondoensis</i>	MVZ	JF1289	Kleine Monde, close to Kasouga	-33.648	26.7711	South Africa	Eastern Cape	Female	Blood
<i>Laniarius ferrugineus pondoensis</i>	MVZ	4H40302	Lorraine Estates, Uzumbe	-30.5833	30.5	South Africa	KwaZulu Natal	Male	Blood
<i>Laniarius ferrugineus pondoensis</i>	MNHN	ZO 1981-82	Ntafufu river (near port st john)	-31,5	29,6333	South Africa	Eastern Cape	Female	Blood
<i>Laniarius ferrugineus pondoensis</i>	MNHN	ZO 1981-85	Ntafufu river (near port st john)	-31,5	29,6333	South Africa	Eastern Cape	Male	Blood
<i>Laniarius ferrugineus savensis</i>	DMNS	DM26870	Vilanculos	-21,214	34,714	Mozambique	Inhambane	Female	Blood
<i>Laniarius ferrugineus savensis</i>	DMNS	DM19786	Massinga	-22,273	35,261	Mozambique	Inhambane	Female	Blood
<i>Laniarius ferrugineus savensis</i>	DMNS	DM19788	Massinga	-22,273	35,261	Mozambique	Inhambane	Male	Blood
<i>Laniarius ferrugineus savensis</i>	DMNS	DM26861	Vila Franca do Save, 10 km S of	-22,273	35,261	Mozambique	Inhambane	Female	Blood
<i>Laniarius ferrugineus savensis</i>	DMNS	DM26868	Rumbacaca	-24,183	34,853	Mozambique	Inhambane	Female	Blood
<i>Laniarius ferrugineus savensis</i>	DMNS	DM7376	Panda	-24,183	34,853	Mozambique	Inhambane	Female	Blood
<i>Laniarius ferrugineus savensis</i>	DMNS	DM19770	Mapinhane	-22,273	35,261	Mozambique	Inhambane	Female	Blood
<i>Laniarius ferrugineus savensis</i>	MNHN	MNHN ZO 1981-80							Blood
<i>Laniarius ferrugineus savensis</i>	MNHN	MNHN ZO 1981-80							Blood
<i>Laniarius ferrugineus tongensis</i>	MVZ	CV31711	Komatiepoort	-25.4333	31.9667	South Africa	Mpumalanga	Male	Blood
<i>Laniarius ferrugineus tongensis</i>	MVZ	PL3526	St Lucia	-28,38333	32,5667	South Africa	Kwazulu Natal	Male	Blood
<i>Laniarius ferrugineus tongensis</i>	MVZ	PL3543	Kosi Bay	-26,95	32,8333	South Africa	Kwazulu Natal	Female	Blood
<i>Laniarius ferrugineus tongensis</i>	DMNS	DM19782	Chimonzo	-25,083	33,366	Mozambique	Maputo	Female	Blood
<i>Laniarius ferrugineus tongensis</i>	DMNS	DM7370	Bela Vista	-26,128	32,737	Mozambique	Maputo	Male	Blood

Taxon Names	Institution	Tissue/Voucher number	Locality	Latitude	Longitude	Country	Province	Sex	Sample type
<i>Laniarius ferrugineus tongensis</i>	DMNS	DM7369	Bela Vista	-26,128	32,737	Mozambique	Maputo	Male	Blood
<i>Laniarius ferrugineus tongensis</i>	MNHN	MNHN ZO 1969-2778	Mzenene River (near Balegane)	26.1	31.566	Swaziland		Male	Blood
<i>Laniarius ferrugineus tongensis</i>	MNHN	MNHN ZO 1968-1629	Muanza	-18,897	34,793	Mozambique	Sofala	Female	Blood
<i>Laniarius ferrugineus transvaalensis</i>	MVZ	JF2586	Wonderhoek Farm, 3 km from Ottoshoop	25.72906	25.97475	South Africa	North West	Female	Muscle, Liver, Heart
<i>Laniarius ferrugineus transvaalensis</i>	MVZ	JF2606	Schoemendaal EEC	-23.0189	29.7244	South Africa	Limpopo	Male	Blood
<i>Laniarius ferrugineus transvaalensis</i>	MVZ	JF2623	Schoemendaal EEC	-23.0189	29.7244	South Africa	Limpopo	Male	Blood
<i>Laniarius ferrugineus transvaalensis</i>	MVZ	JF2624	Schoemendaal EEC	-23.0189	29.7244	South Africa	Limpopo	Female	Blood
<i>Laniarius ferrugineus transvaalensis</i>	MVZ	JF2669	Nkandela Forest	28.723188	31.13045	South Africa	Kwazulu Natal	Female	Blood
<i>Laniarius ferrugineus transvaalensis</i>	MVZ	JF2679	Entumeni Forest	-28,88671	31,37727	South Africa	Kwazulu Natal	Female	Blood
<i>Laniarius ferrugineus transvaalensis</i>	MVZ	4H20279	Schoemendaal EEC	-23.0189	29.7244	South Africa	Limpopo	Female	Blood
<i>Laniarius ferrugineus transvaalensis</i>	MVZ	4A42799	Naboomspruit-Entabeni*Bream Dam	-24.2386	28.7003	South Africa	Limpopo	Male	Blood
<i>Laniarius ferrugineus transvaalensis</i>	MVZ	436849	Nylstroom - Olienhoutstraat 47	-24.7	28.3833	South Africa	Limpopo	Male	Blood
<i>Laniarius ferrugineus transvaalensis</i>	MVZ	CV37648	Rockabye, Hazyview	-25.0167	31.0333	South Africa	Mpumalanga	Male	Blood
<i>Laniarius ferrugineus transvaalensis</i>	MVZ	CV31528	Rockabye, Hazyview	-25.0167	31.0333	South Africa	Mpumalanga	Female	Blood
<i>Laniarius ferrugineus transvaalensis</i>	MVZ	4H31774	Blouberg NR	-23.0019	29.0639	South Africa	Limpopo	Male	Blood
<i>Laniarius ferrugineus transvaalensis</i>	MNHN	JF3486	Ben Lavin Nature Reserve, Longwall Dam	-23,1419	29,9891	South Africa	Limpopo	Male	Muscle, Liver, Heart
<i>Laniarius ferrugineus transvaalensis</i>	DMNS	DM27988	Swartruggens, Elands River	-25,453	26,817	South Africa	North West	Female	Blood
<i>Laniarius ferrugineus transvaalensis</i>	DMNS	DM15426	Stegi	-26,45	31,95	Swaziland		Female	Blood
<i>Laniarius ferrugineus transvaalensis</i>	DMNS	DM25648	Swartruggens, Blokkloof	-25,453	26,817	South Africa	North West	Male	Blood
<i>Laniarius ferrugineus transvaalensis</i>	MVZ	4H40769	EcoPark Newcastle	-27.7722	30.01	South Africa	Kwazulu Natal	Female	Blood
<i>Laniarius subclateus</i>	GenBank	gi86461389							Blood
<i>Laniarius subclateus</i>	GenBank	gi86461407							Blood

## **CHAPTER 4**

---

---

### **Assessing patterns of variation in vocalisations of the Southern Boubou *Laniarius ferrugineus* (Gmelin, 1788)**

#### **4.1 Introduction**

Many birds use acoustic signals to communicate their species and individual identity, fighting ability, physical condition, and/or motivational intent (Bradbury & Vehrencamp 1998) as well as mate choice (Kroodsma & Miller 1982; Catchpole & Slater 1995). This information can be conveyed over long distances, in dense cover, and at night (Marler 1969; Gill 1990). Sexual selection commonly referred to as mate choice or mate attraction is hypothesised to have led to the evolution of bird vocalisations and experiments suggest that the quality of the vocalisations may be a good indicator of fitness (Read & Weary 1990). Avian vocalisation is traditionally divided into calls and songs but there is however no clear cut distinction between the two (Bonnievie & Craig 2018) with the term 'song' being reserved for loud and sustained vocalisations delivered seasonally by males in possession of breeding or courting territory. Songs are primarily loud and complex consisting mainly of syllables, phrases and trills (Gill 2007). On the other hand, calls tend to be shorter and simply structured such that the context in which they are delivered, the identity of the calling individual and the response elicited from conspecifics suggest the information conveyed and the function of the call. Overall, both songs and calls can be rendered either by a single individual bird, or the involvement of a male and a female bird that is, through simple duetting (simple answering of partners) or antiphonally (highly synchronised songs or calls that alternate between male and female) (Thorpe 1972).

Several aspects of animal behaviour such as mate choice or attraction, kin recognition, territorial defence and parent-offspring communication involve acoustic signals (Kroodsma & Miller 1982; Catchpole & Slater 1995). Vocalisations consequently could provide potentially informative characters for systematic (Parker

*et al.* 1995; Zimmer 2002; Remsen 2003; Mandiwana-Neudani *et al.* 2014) and comparative studies and this could depend on species, that is song versus calls, passerines versus non-passerines and whether they are oscines or suboscines. Vocalisations have also mainly been of use in the ranking of closely related allopatric taxa especially under the biological species concept (Mayr 1942), discovery of several new species (Alström & Ranft 2003, Cohen *et al.* 2012) and inference of relationships (Mandiwana-Neudani *et al.* 2014), both within and between genera. To some extent field ornithologists are often able to predict taxonomic relationships on the basis of voice alone and population biologists have used vocalisations to study the evolution of populations and species groups (Kroodsma 1977; Gill 1990; Payne 1983; Catchpole 1983). However, in the contrary, vocalisations alone may not be used for phylogenetic studies. This is due to the fact that although it has a number of advantages there is difficulty in separating genetic and ecological components of vocalisations.

This has discouraged biologists, avian systematists in particular, from using vocal characters to investigate phylogenetic and ecological history (McCracken & Sheldon 1997). This has been largely as a consequence of the difficulty of detecting homology across taxa (Lanyon 1969). The physical, ecological, behavioural, and morphological forces that cause vocal characters to be similar by convergent evolution or by chance and thus limiting their usefulness for inferring phylogeny make systematic studies of avian vocalisations particularly difficult. This is simply homoplasy and can potentially affect all types of phylogenetic characters. With these areas of use of vocalisations, it is critical that multiple sound recordings of high quality are considered and that the circumstances of recordings need to be documented, identity of vocalising birds needs to be firm, and a full system of cooperation between sound archives is required (Alström & Ranft 2003). Authors such as McCracken and Sheldon (1997) have conceded that recovering phylogenetic signal should be possible by careful analysis of vocal characters in taxa that have either calls or simple songs that are not learned and whose habitat distributions are well-understood.

Regardless of the difficulties mentioned, vocalisations can definitely be a first pointer to the field ornithologist to further gather additional evidence such as morphological; DNA or behavioural data, and these data can then be used in conjunction in taxonomic research. Examples of work where authors have explored

the utility of vocalisations in phylogenetic context include (Alström 2001; Price & Lanyon 2002; Päckert *et al.* 2003; Lei *et al.* 2005; Farnsworth & Lovette 2008; Mandiwana-Neudani *et al.* 2014). The physical environment and other ecological factors play important roles in shaping vocalisations of most species, so that distantly related populations occupying similar habitats may possess vocalisations more similar than those of closely related populations in different habitats (Nottebohm 1975; Hunter 1979). For example, vocalisations of species that live in dense vegetation generally tend to have lower frequencies and narrower frequency ranges than those of species that inhabit open areas. This is because longer wavelengths propagate energy more efficiently through vegetation than shorter wavelengths, which attenuate due to the scattering effects of leaves and branches (Chappius 1971; Morton 1975; Wiley & Richards 1982). This is one of the factors that results in many bird species showing widespread geographic variation in their vocalisations.

The acoustic structure of avian vocalisations can vary across either a limited or broad geographic range (Mager III 2007). Macrogeographic variation, or variation in signal structure between populations that experience reduced gene flow or transmission of cultural traditions, has long been of interest among scientists, particularly to those interested in biological evolution of song dialects (Mundinger 1982; Catchpole & Slater 1995). Song dialects within the oscines are thought to be a cultural phenomenon (Raposo & Höfling 2003) that results from many oscine passerines having the capacity of developing microgeographic variations of song (Kroodsma 1994) and many experimental studies have shown that there is a strong correlation between these variations and the presence of learning ability within the group (Kroodsma 1981; Lein 1978; Weary *et al.* 1990). There is much research of macrogeographic variability in bird vocalisations however this has been restricted to oscines, and has focused mainly on regional differences in syllable repertoires (Mundinger 1982). This might be due to the challenges that exist in using vocalisations in oscines versus suboscine birds. Some studies of suboscine cerebral structure indicate that members of this group seem to lack the brain control centres which are responsible for controlling feedback learning mechanisms in oscines (Brenowitz & Kroodsma 1996) and suboscine songs are thought to be less conservative than morphological features at the species level and thus more informative in detecting recently divergent species (Raposo & Höfling 2003).

#### 4.1.1 Factors affecting vocalisations

Habitat structure has been considered the main factor shaping particularly, the evolution of bird song acoustics (Shy 1983; Boncoraglio & Saino 2007) and several avian studies have shown that interspecific differences in song structure can be partially explained by the characteristics of the habitat used by each species (Morton 1975; Kopuchian *et al.* 2004). Many species of birds show significant variation in vocal traits over their geographical ranges, often in the form of local dialects that may cause complete turnover in song type within only a few miles (Marler & Tamura 1962). Across very large geographical scales most bird species show songs with substantial regional variation that is often attributed to learning and the success of local dialects through sexual selection (Podos & Warren 2007). By contrast, a few species show very little variation in song over enormous distances (Martens 1996). Song similarity across ranges is to be expected if song functions primarily as a species-recognition signal, but such a signal could also be produced by species with dialects if all individuals retain just one or a few common song characteristics (Price 2008). This balance between variation and stability in song traits presents an interesting evolutionary puzzle and few studies have examined song diversity across very large geographical scales in species where song may be an important species recognition signal.

The effect of anthropogenic noise on avian vocalisations mostly in cities puts severe constraints on vocal communication by interfering with the detection of acoustic signals (Nemeth *et al.* 2013). Some studies show that city birds sing higher frequency songs than their conspecifics in non-urban habitats (Slabbekoorn & Peet 2003; Nemeth & Brumm 2009; Mockford & Marshall 2009; Potvin *et al.* 2011). Changes in atmospheric pressure are also known to affect avian songs (Nowicki 1987; Catchpole & Slater 1995) and this phenomenon was well-demonstrated in the Rufous-collared sparrow (*Zonotrichia capensis*) where there was gradual reduction in the song length with increasing altitude (Nottebohm 1975). Further to this, vocalisations of this species also showed some correlation with the availability of food and with temperature (Raposo & Höfling 2003). The transmission properties of acoustic signals can also change with the time of day (Henwood & Fabrick 1979; Dabelsteen & Mathevon 2002). Diurnal fluctuation can also often be observed in the levels of ambient noise, which is another important constraint on acoustic communication (Brumm & Slabbekoorn 2005). The influence of environmental

factors in sound producing mechanisms is well-established in poikilothermic animals (e.g frogs, snakes) (Gerhardt 1978; Duellman & Trueb 1994) and this should not be overlooked in avian studies. Avian vocalisations are said to also vary depending on the season (Blumenrath & Dabelsteen 2004) and are influenced by the state of seasonal development of the sex hormone. For example, some songs are expected to be of abundance in certain seasons but do not differ in structure from season to season.

Body size is another important trait which affects the physiology and ecology of animals (Lomolino & Perault 2007; Kingsolver & Huey 2008). It is considered a key sexually selected trait. According to Hall *et al.* (2013), body size constraints on low-frequency vocalisations could be more widespread than is currently recognised. Potvin (2013) found larger body-sized Whites-eyes birds (genus *Zosterops*) to have lower frequency vocalisations while Mager III *et al.* (2007) found smaller-bodied Common loons (*Gavia immer*) to have higher frequency yodels. However, sometimes body size–vocalisation frequency allometry is negatively correlated depending on whether the phylogeny is taken into account or not. For example, Laiolo & Rolando (2003) found that frequency also decreased with decreasing body size in corvid species (oscine passerines containing crows, ravens, magpie) when phylogeny is taken into account, but the relationship was weaker than that resulting from a phylogeny-free analysis. In contrast, Greenewalt (1968) highlights that there is no strict correlation between the size of a bird and the frequency it produces.

Experiments also suggest that parasites and diseases may directly affect song characteristics such as song rate, which thereby act as reliable indicator of health (Garamszegi *et al.* 2004; Redpath *et al.* 2000). On the other hand, song repertoire also appears to indicate fitness in some species (Reid *et al.* 2005; Møller *et al.* 2005) and this highlights that the general health of the bird also greatly affects its vocalisation. Differences between the syrinxes of male and female birds could determine the properties of bird vocalisation. The musculature of the syrinxes contributes largely to voice production and has been found to play a significant role in the classification of birds (Myers 1917; Frank *et al.* 2007; Krakauer *et al.* 2009). For example, in passerine birds there are two main suborders, oscines and suboscines which are mainly separated by the derived, complex anatomy of the



syrinx in oscines (Forbes 1882; Ames 1971) and the unique, bulbous columella in suboscines (Feduccia 1975).

#### 4.1.2 Study species

In this chapter the focus was on the highly secretive and sedentary passerine species, the Southern Boubou *Laniarius ferrugineus* (Gmelin, 1788) which is endemic to southern Africa (Bowie *et al.* 2005). Taxonomically, this species is polytypic in nature consisting of six currently recognised subspecies: *L. f. ferrugineus*; *L. f. natalensis*; *L. f. pondoensis*; *L. f. transvaalensis*; *L. f. tongensis* and *L. f. savensis* (see Fig 1.2 a - f).

#### 4.1.3 Vocal components employed in previous studies

There are a number of vocal components that are investigated to separate taxa especially when external morphological differences are few (Tietze *et al.* 2008) although this remains a challenge in that; there exists difficulty in detecting homology across taxa (Lanyon 1969). This has discouraged particularly, avian systematists from using vocal characters to investigate phylogenetic relationships (McCracken & Sheldon 1997). This leaves vocalisations of birds being mostly used in verbal descriptive or comparative studies. Similarly, the research on vocalisations of *L. ferrugineus* in previous studies was mostly descriptive (Mackworth-Praed & Grant 1963; Harris & Arnott 1988; Fry 2009; Merkle 2010).

These studies do not compare or differentiate the songs within the species but only report on the type of songs rendered by *L. ferrugineus* without focusing on geographic variation of this species. Reports on the songs of *L. ferrugineus* are however important in differentiating songs between species within *Laniarius* (Boubous) as they give some taxonomic light. Based on the fact that *L. ferrugineus* shows extensive phenotypic variation and thrive in forested and dense scrubs habitats, that is closed and open respectively, it is therefore important to study the song variation across large geographical scales in species where song may be an important recognition signal.

#### 4.1.4 Aim

The aim was to produce a comprehensive description of the songs of *Laniarius ferrugineus* subspecies and to investigate the relationship between song variables and habitat.

#### 4.1.5 Objectives

The objectives were to:

- i) describe the songs of recognised *L. ferrugineus* subspecies.
- ii) investigate whether the song structure is diagnostic of the entities in *L. ferrugineus*.
- iii) determine the relationship between songs and habitats

#### 4.1.6 Research questions

- i) How are the songs of *L. ferrugineus* subspecies structured?
- ii) Is the song structure diagnostic of the entities within *L. ferrugineus*?
- iii) What is the relationship between the songs of the subspecies and the habitats where they occur?

## 4.2 Materials and methods

### 4.2.1 Data collection

#### 4.2.1.1 Assembling sound recordings

The archived sound recordings existing in various libraries and online databases were the core source of *L. ferrugineus* vocalisations analysed in this study. Bird song recordings representing only five subspecies (Table 4.1) were sourced from the British Library Sound Archive (BLSA) and an online database Xeno-canto ([www.xeno-canto.org](http://www.xeno-canto.org)). None of the recordings were made in this study and therefore, information about sex and whether the bird recorded was seen or not was not available. Unfortunately, there were no song recordings for *L. f. savensis*. Songs that were analysed in this study and were defined as loud and sustained vocalisations delivered seasonally by males in possession of breeding or courting territory (Gill 2007). In this study, a song consists of strophe(s), single phrases usually consisting of elements separated by intervals (Weier 2018) and they are repeated a few times.

## 4.2.2 Data analyses

### 4.2.2.1 Song strophe duets spectrograms

Original song recordings of good quality were imported into GoldWave Inc. v5.70 (GoldWave Inc 1993) for trimming of target parts. Only song strophe duets were analysed in this study. The number of song duets assembled for the five subspecies were as follows: *L. f. ferrugineus* (n=7), *L. f. pondoensis* (n=4), *L. f. natalensis* (n=1), *L. f. transvaalensis* (n=1) and *L. f. tongensis* (n=3) [Table 4.1]. The selected strophes were analysed using the analytical software Avisoft-SASLab Pro (McGregor 1995), an advanced windows application used to investigate animal acoustic communication. To generate spectrograms for all the strophe duets, spectrogram parameters were set as follows with regard to frequency resolution: a fast Fourier transform (FFT) of 256, frame size (75%) and Blackman window. Temporal resolution was set to an overlap of 75%. In keeping with the standard practice, an element was defined as a single trace on a spectrogram. The following temporal spectrogram parameter measurements were analysed: strophe duration, number of elements, duration of an individual elements in the strophe, inter-element interval or temporal spacing between elements (only between a 'bou' element preceding a 'whistle' element or vice versa), and with regard to spectrum-based parameters the following strophe parameters were analysed: maximum peak frequency (frequency of greatest power), maximum frequency, minimum frequency, fundamental frequency and frequency bandwidth (computed as maximum frequency minus the minimum frequency) (Table 4.1). The terminology used in this study follows Cardoso (2010) and Luttrell and Lohr (2018) (see annotated Fig. 4.1). All the strophe variables were also categorised according to habitat, either forest (closed) or dense scrubs (open).

### 4.2.2.2 Statistical analysis of song strophes duets

All the dataset measurements were log-transformed ( $\text{Log}_{10}$ ) prior to the analysis to normalise the distributions (Kaboli 2007). The relationship between variables was investigated by comparing the mean of the dependent variables (strophe variables) between two groups within the independent variable (habitat) using *t-test* ( $p < 0.05$ ) performed at 95% confidence level. This was run in SPSS ver. 25.0 (IBM Corp. 2017).

## 4.3 Results

### 4.3.1 General description of *Laniarius ferrugineus* song strophe duets

Generally, the typical song strophe of *L. ferrugineus* is commonly a “*bou-bou*” / “*bou-bou-bou*” (and less frequently a “*bou*”) that is mostly rendered in the form of a duet by male and female birds (Fig. 4.1). A song strophe duet becomes a combination of *bou-bou/bou-bou-bou/bou* and a whistle that may be given in no particular order. However, one individual (either male or female) may still render a song in the absence of a response that is, either a *bou-bou/bou-bou-bou/bou* or a whistle. The strophes of the different subspecies slightly vary aurally and visually.

### 4.3.2 Song strophe duets of various subspecies

*Laniarius ferrugineus tongensis* - among individual songs of *L. f. tongensis*, all versions of strophe duets were gained in different order that is, a combination of a mostly high-pitched whistle (1 500 – 2 400 Hz) accompanied or preceded by a low-pitched *bou/bou-bou/bou-bou-bou*. This means that the strophe duets had the number of elements in the range of two to four while the strophe duration ranges from 1.0 - 1.1 s. The interval between a whistle and either a preceding or subsequent *bou* ranged from 0.02 to 0.03 s.

*Laniarius ferrugineus ferrugineus* - among individual songs of *L. f. ferrugineus*, all the song strophe variants were recovered in different order forming a combination of a mostly high-pitched whistle (2 400 – 3 700 Hz) accompanied or preceded by a low-pitched *bou/bou-bou/bou-bou-bou*. This means that the song duets have the number of elements in the range of two to four while the strophe duration ranges from 0.9 - 1.1 s. The interval between a whistle and either a preceding or subsequent *bou* ranged from 0.05 to 0.2 s. This taxon was the only one that gives tonal/musical and harsh (BD24 and BD25) whistle which gets really protracted (almost 0.7 s long) compared to other subspecies.

*Laniarius ferrugineus pondoensis* – for this taxon, four strophe duets were gained. Similarly, all versions were presented in different order that is, a combination of a mostly high-pitched whistle (1 500 – 2 400 Hz) accompanied or preceded by a low-pitched *bou/bou-bou/bou-bou-bou*. This means that the strophe duets have two to four elements and song duration ranging from 0.35 - 1.1 s. The interval between a

whistle and either a preceding or subsequent *bou* ranged from 0.01 to 0.16 s. Sometimes whistle element was split into two parts (e.g. BD9).

*Laniarius ferrugineus natalensis* – only one song strophe duet was recovered for this taxon, starting with a high-pitched whistle (2 400 Hz) succeeded by two low-pitched *bou* elements. The strophe consisted of three elements, song duration of 0.78 s and an interval between a whistle and either a subsequent *bou* element of 0.37 s

*Laniarius ferrugineus transvaalensis* – for this taxon one song strophe duet was recovered, starting with a high-pitched whistled element (2 000 Hz) succeeded by one low-pitched and protracted *bou* element (0.8 s long) and an interval between a whistle and a succeeding element of 0.03 s.

#### 4.3.3 Statistical outcomes

The findings were such that there was no statistical significant difference between the means of all but one song strophe variable (strophe maximum peak frequency) and those of habitats (Table 4.2). This means that the significant differences were found as it pertained to strophe maximum peak frequency between the forested birds, *L. f. pondoensis* and the other taxa that thrive in open dense scrubs (*L. f. ferrugineus*, *L. f. transvaalensis*, *L. f. tongensis*, *L. f. natalensis*). The song strophe duets were similar across all the subspecies in that the maximum peak frequency is invested largely in the ‘whistle’ elements.

#### 4.4 Discussion

All *L. ferrugineus* subspecies generally gave a tonal song strophe duet that was made up of ‘*bou*’ and ‘whistle’ elements with the exception of some individuals of *L. f. ferrugineus* that tend to render a protracted harsh whistle. Despite this and the fact that the strophes differed in the maximum peak frequency of the stophe duets, maximum peak frequency was generally invested in the whistle element that could be single, partially or completely split. With regard to the generality about the association of song frequency and open versus closed habits where species that inhabit closed habitat such as forest are known to use lower frequencies and narrower bandwidth than those that thrive in more open habitat, this study failed to

support this generality. Some studies have recorded the similar findings where a study of the Rufous-collared sparrow (*Zonotrichia capensis*) showed the opposite pattern, with higher frequency and broader bandwidth associated with more closed and mesic environments (Nottebohm 1975, Handford & Loughheed 1991).

#### 4.5 Conclusion

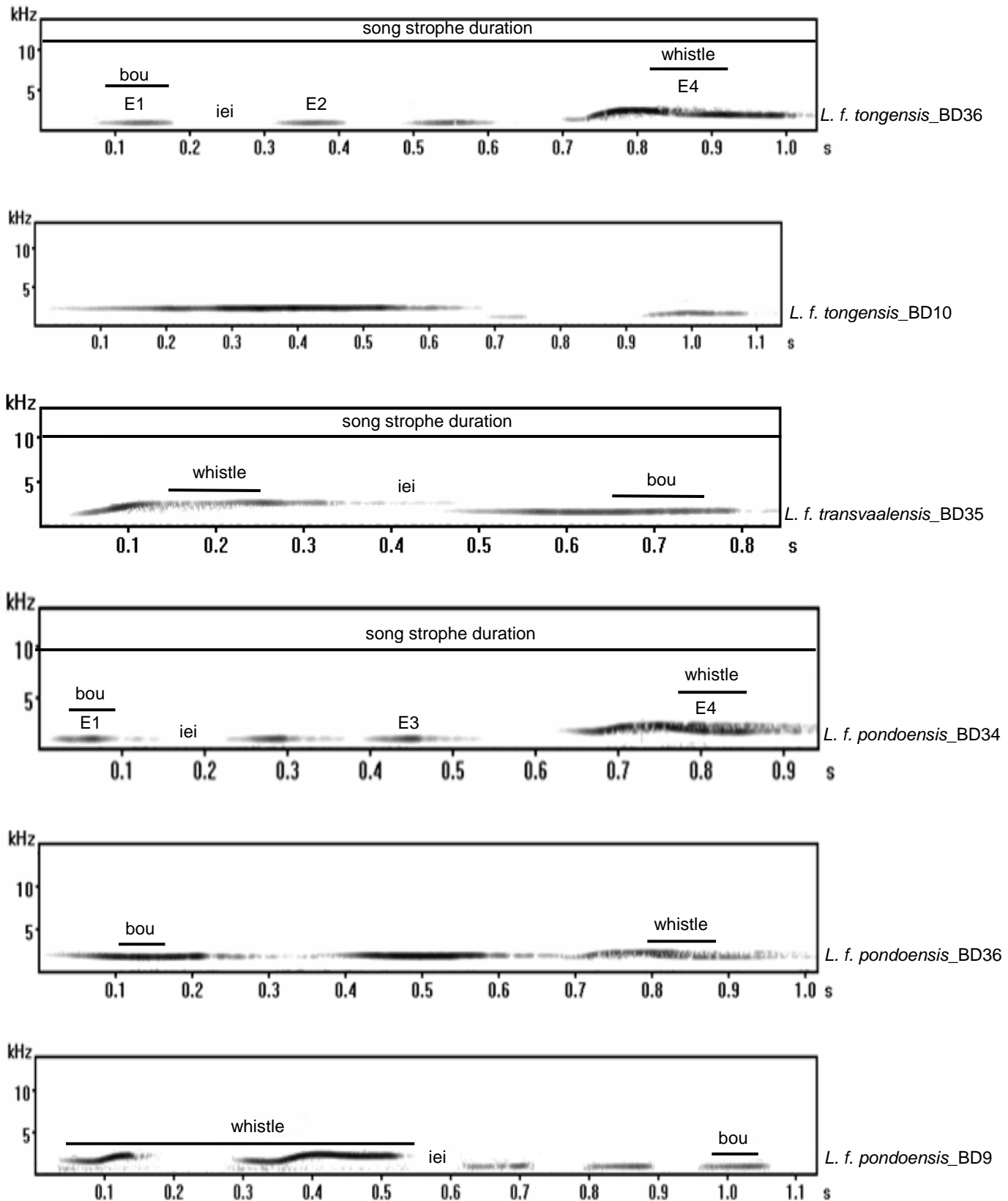
Slight geographic variation in the song strophe duets of *L. ferrugineus* is seen visually on the spectrograms and it is also evident in strophe duets aurally. The findings in this chapter call for recommended future work to use *L. ferrugineus* as a candidate to comprehensively study the association of song structure and habitat given its occurrence in different habitats, forested (closed) versus dense scrubs (open) habitats.

**Table 4.1.** List of songs of *Laniarius ferrugineus* sourced from an online database Xeno-canto and the British Library Sound Archive (BLSA).

<b>Subspecies</b>	<b>Number of calls analysed</b>	<b>Source of songs</b>
<i>Laniarius ferrugineus ferrugineus</i>	7	BLSA, Xeno-canto
<i>Laniarius ferrugineus pondoensis</i>	3	BLSA, Xeno-canto
<i>Laniarius ferrugineus natalensis</i>	1	BLSA, Xeno-canto
<i>Laniarius ferrugineus transvaalensis</i>	1	BLSA, Xeno-canto
<i>Laniarius ferrugineus savensis</i>	0	-
<i>Laniarius ferrugineus tongensis</i>	2	BLSA

**Table 4.2.** Summary of t-test results from song strophe variables and habitat of *Laniarius ferrugineus*.

Independent Samples Test										
		Levene's Test for Equality of Variances		t-test for Equality of Means						
		F	Sig.	t	df	Sig. (2-tailed)	Mean Difference	Std. Error Difference	95% Confidence Interval of the Difference	
									Lower	Upper
interval between <i>bou</i> & whistle element(s) in song strophe	Equal variances assumed	0.198	0.664	-1.267	13	0.227	-0.04341	0.03426	-0.11743	0.03061
	Equal variances not assumed			-1.133	4.488	0.314	-0.04341	0.0383	-0.14534	0.05852
song strophe max peak frequency (Hz)	Equal variances assumed	0.031	0.863	2.561	13	0.024	602.273	235.19	94.176	1110.37
	Equal variances not assumed			3.048	7.868	0.016	602.273	197.574	145.329	1059.217
song strophe fundamental(Hz)	Equal variances assumed	0.42	0.528	1.055	13	0.311	293.182	277.847	-307.071	893.435
	Equal variances not assumed			1.358	9.668	0.205	293.182	215.922	-190.174	776.537
song strophe min frequency(Hz)	Equal variances assumed	2.503	0.138	-0.141	13	0.89	-43.182	306.566	-705.476	619.113
	Equal variances not assumed			-0.168	7.947	0.871	-43.182	256.523	-635.407	549.043
song strophe max frequency(Hz)	Equal variances assumed	0.57	0.464	0.98	13	0.345	420.455	428.898	-506.124	1347.033
	Equal variances not assumed			1.301	10.49	0.221	420.455	323.138	-295.024	1135.933
song strophe bandwidth(Hz)	Equal variances assumed	0.318	0.583	0.921	13	0.374	563.636	612.061	-758.641	1885.914
	Equal variances not assumed			1.036	6.845	0.336	563.636	544.216	-729.143	1856.415
song strophe duration(s)	Equal variances assumed	5.399	0.037	1.407	13	0.183	0.16091	0.1144	-0.08624	0.40806
	Equal variances not assumed			0.944	3.342	0.408	0.16091	0.1704	-0.35134	0.67315



**Figure 4.1.** Spectrograms generated from song strophe duets of various *Laniarius ferrugineus* subspecies.



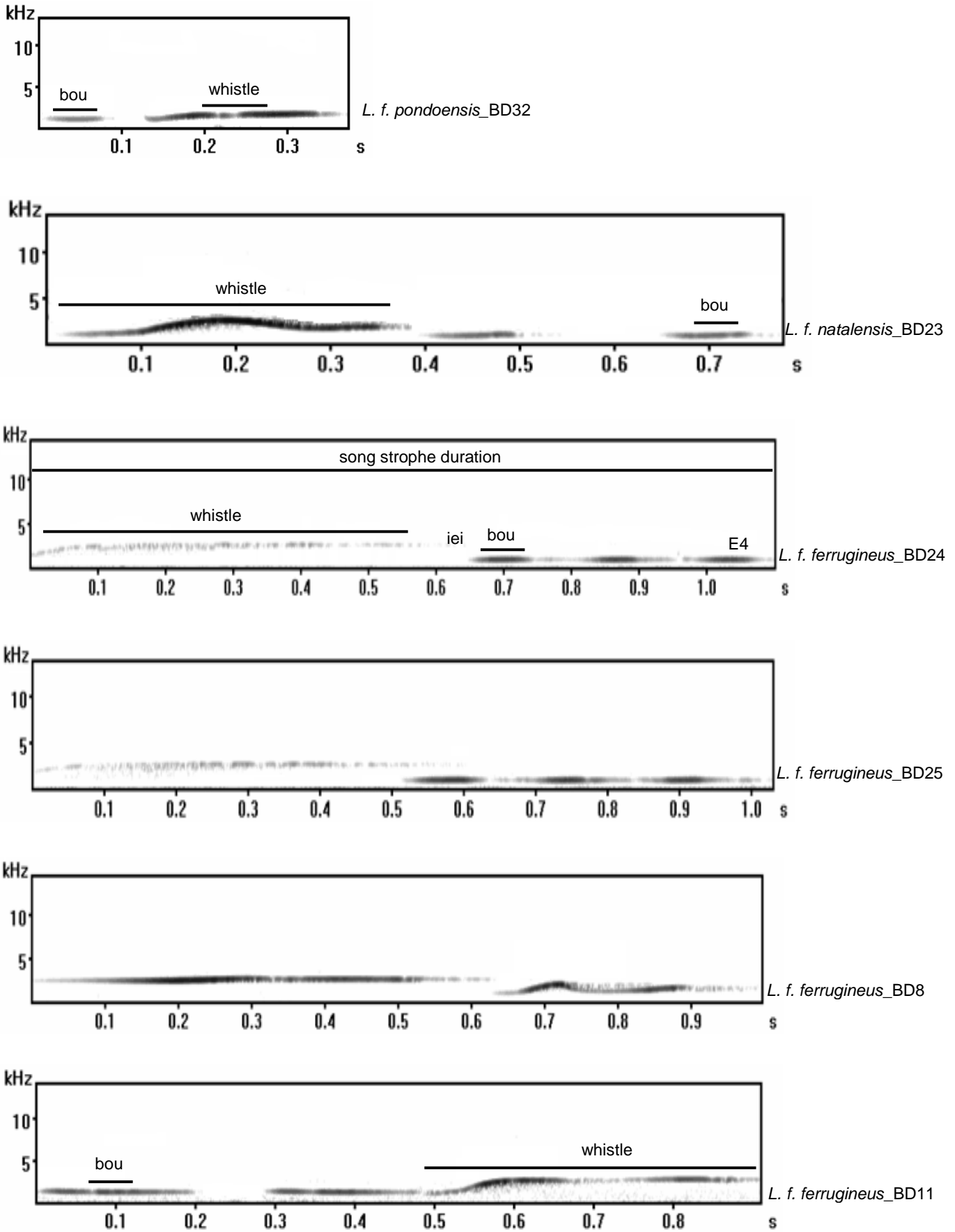
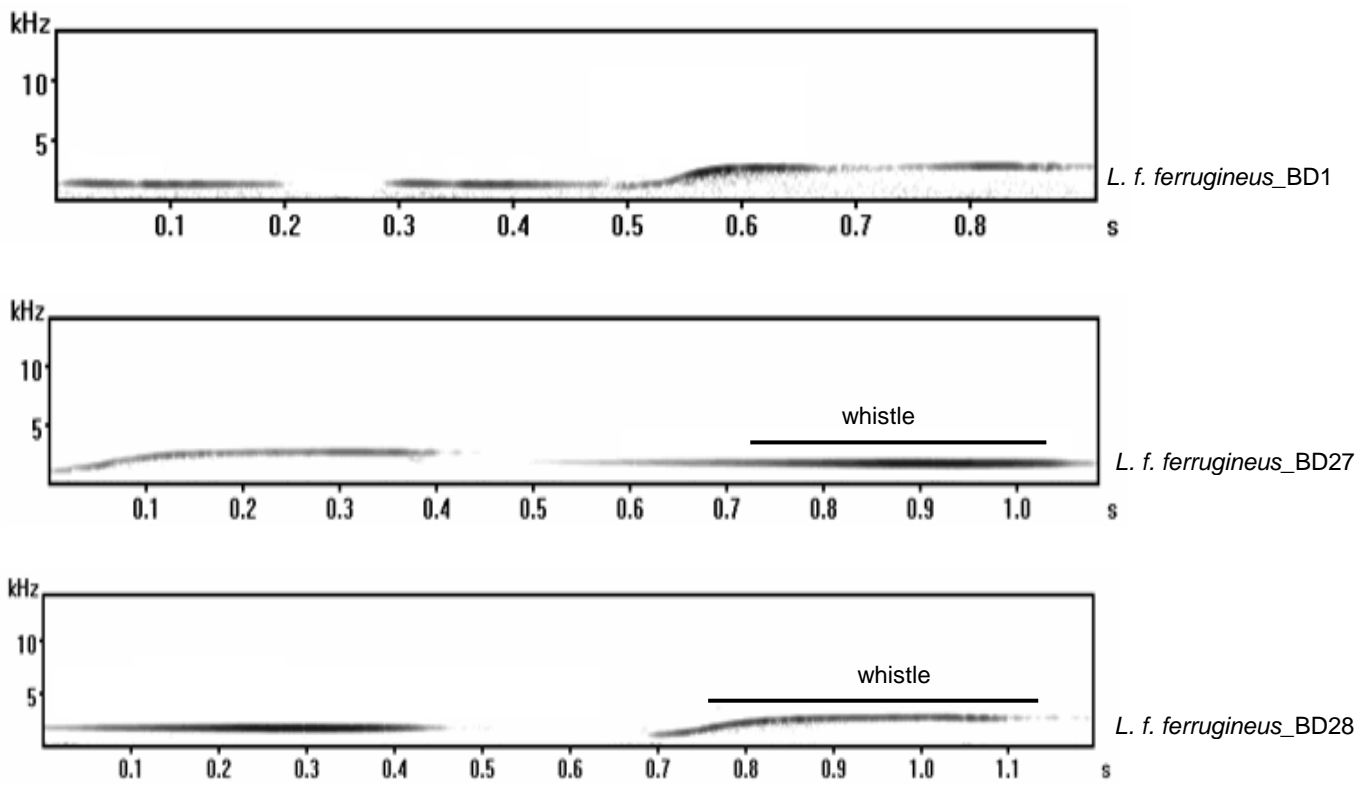


Figure 4.1. Continued



**Figure 4.1.** Ends.

## **CHAPTER 5**

### **General Discussion**

At the onset of this study, this research was set out to address the following study questions:

- i) Is *Laniarius ferrugineus* a single species or a complex? [CHAPTER 2 & 3]
- ii) What is the extent and the level of morphological, genetic and song differentiation in *L. ferrugineus* throughout its distribution range? [CHAPTER 2, 3 & 4]
- iii) What is the estimated divergence time between the lineages? [CHAPTER 3]
- iv) How do the evolutionary units of *L. ferrugineus* delineated in this study compare with the current taxonomic circumscription? [CHAPTER 3]
- v) How does the spatial map of *L. ferrugineus* subspecies generated in this study compare with the one in literature? [CHAPTER 2]

The findings presented in this study refuted and challenged the status quo with regard to our knowledge of this southern African endemic species and our understanding of the phylogenetic relationship within *L. ferrugineus* complex. Several authors including Harris & Franklin (2000) and Bowie *et al.* (2005) recognised *L. ferrugineus* as a polytypic species consisting of six putative subspecies (*L. f. ferrugineus*, *L. f. natalensis*, *L. f. pondoensis*, *L. f. transvaalensis*; *L. f. tongensis*; *L. f. savensis*). However, on the basis of the morphometric and mitochondrial and nuclear DNA analyses, *L. ferrugineus* had sufficiently diverged. These kind of findings are seen in a number of phylogeographic studies of different animal groups including birds (Fuchs *et al.* 2017), which highlights the diversification across major biogeographic breaks in the African Shining-Square tailed Drongos complex (Dicruridae). The consistent pattern emerged where *L. ferrugineus* consistently showed the deep phylogeographic divergence into the southern and northern phylogeographic lineages with strong nodal support in the phylogenetic analyses. The southern lineage included the nominate subspecies *L. f. ferrugineus*, *L. f. natalensis* and *L. f. pondoensis* whereas the northern lineage comprises of *L. f.*

*transvaalensis*, *L. f. tongensis* and *L. f. savensis*. The recent divergence time between the two lineages was estimated to have occurred at approximately 1.5 million years ago (mya) (95% HPD: Highest Posterior Density 1.04 – 1.92) during the Pleistocene epoch. This showed that *L. ferrugineus* is continuing to differentiate.

When the recovered phylogeographic patterns of *L. ferrugineus* was superimposed onto the distribution map generated in this study (Chapter 3, Fig. 3.7), there seemed to be a geographic break in the northern parts of Kwa-Zulu Natal, south of Swaziland. However, it was not yet known as to what could be going on in the area where the break exists. The same break was found to be a possible explanation of the morphological differentiation in the Brown scrub-robin (*Cercotrichas signata*) (Rebeiro *et al.* 2014). Taking into account the need to sample intensively, perhaps there is a need to study other taxa in this area so that a coherent conclusion could be drawn.

With regard to plumage analysis, the forest inhabitant *L. f. pondoensis* stood out from the other subspecies by being the darkest morph. Ornithologists had questioned whether this subspecies could not be distinct enough to be considered a separate species. However, the morphometric and molecular analyses place *L. f. pondoensis* together with the nominate *L. f. ferrugineus* and also *L. f. natalensis*. The dark colouration could be a result of the effect of thriving in the forest.

Despite that the vocal component of the study is data limited, inability to determine the sex of the birds in duets, unavailability of song recordings for *L. f. savensis* as well as availability of few individual songs for *L. f. natalensis* and *L. f. transvaalensis*, the findings revealed the song is a duet comprised of a 'bou' and whistle element which can be rendered in any order. The significant difference between songs and habitats was found with respect to maximum peak frequency which is invested in the whistle element across the songs of the various subspecies. However, the findings in this chapter have failed to support the general hypothesis about the relationship between the song structure and habitat type (Nicholls & Goldizen 2006). This was not the first study to recover the opposite pattern.

The existing distribution maps in literature and the distribution map generated from this study showed the similar range of the study species *L. ferrugineus* but the difference is the extent of coverage.

Therefore, on the basis of the evidence presented above and in spite of the fact that some nuclear amplification was unsuccessful, the less distinct morphometric groupings, the well-supported molecular phylogeographic structures recovered are sufficient to allow the following recommendations to be made:

Instead of recognising six subspecies as belonging to *L. ferrugineus*, it is recommended that *L. ferrugineus* be split into two species that is, one species representing members of the southern clade: *L. f. ferrugineus* (Gmelin, 1788); *L. f. natalensis* Roberts, 1922 and *L. f. pondoensis* Roberts, 1922. Another species representing members of the northern clade: *L. f. transvaalensis* Roberts, 1922; *L. f. tongensis* Roberts, 1931 and *L. f. savensis* da Rosa Pinto, 1963. Therefore, following the principle of priority, the species in the south should be named *Laniarius ferrugineus* (Gmelin, 1788) with *L. f. natalensis* and *L. f. pondoensis* being synonymised with it (Appendix 5.1). The northern species should on the basis of priority be named *Laniarius transvaalensis* Roberts, 1922 with *L. f. tongensis* and *L. f. savensis* being synonymised with it (Appendix 3.1).

Undoubtedly, the findings from molecular data analyses and to some degree the morphometric data, are consistent and clearly support the two south and north lineages. There is; however, less differentiation within each of these major lineages. These could be attributed to unavailability of nuclear DNA sequences for some samples. This factor should be considered for future work so that resolution could be attained within the south and north lineages. A detailed analysis of plumage colouration of these birds is recommended and the spectrophotometric and genetic analysis could be better suited for this particular analysis. With regard to vocalisations, it will be important to make well-documented recordings across *L. ferrugineus* range so that comprehensive analysis of songs and the relationship with habitat can be conducted. Based on its occurrence in both open (dense scrubs) and closed (forest) habitats, this species could be a good candidate to comprehensively test the generality of the hypothesis about the association of habitats and song structure.

The study encountered few limitations including a small number of song recordings of the Southern Boubou. Having multiple song recordings for each of the subspecies would have been a great advantage, as this would have resulted in a comprehensive understanding of the song of the species. Although efforts were made to cover the distribution range of the species with regards to the DNA samples, including using historical samples (museum toe pads) to fill gaps, there were few *L. f. savensis* and *L. f. tongensis*. Some of these subspecies would need to be analysed in the future to understand the differentiation within each of the major lineages recovered. There were also few records of *L. f. savensis* and *L. f. tongensis* when mapping the distribution of the species as a result of fewer spatial records of the two subspecies as compared to the other subspecies.

## REFERENCES

- AKAIKE, H. 1973. Information theory as an extension of the maximum likelihood principle. In: *Second International Symposium on Information Theory*. B.N. PETROV & F. CSAKI (eds.). Akademiai Kiado, Budapest. Pp. 276–281.
- ALATALO, R.V., GUSTAFSSON, L. & LUNDBERG, A. 1986. Interspecific competition and niche changes in tits (*Parus* Spp.) evaluation of nonexperimental data. *The American Naturalist* **127(6)**: 819–834.
- ALSTRÖM, P. & RANFT, R. 2003. The use of sounds in avian systematics and the importance of birds sound archives. *Bulletin of the British Ornithologists' Club* **123**: 114-135.
- ALSTRÖM, P. 2001. *The use of sounds in bird systematics*. Introductory Research Essay No. 2. Uppsala University, Uppsala, Sweden.
- AMES, P.L. 1971. The morphology of the syrinx in passerine birds. *Bulletin of the Peabody Museum of Natural History* **37**: 1–194.
- ARBOGAST, B.S. & KENAGY, G.J. 2001. Comparative phylogeography as an integrative approach to historical biogeography. *Journal of Biogeography* **28**: 819–825.
- ARMENTA, J.K., DUNN, P.O. & WHITTINGHAM, L.A. 2009. Effects of specimen age on plumage color. *The Auk* **125**: 803–808.
- ASHTON, K.G. 2002. Patterns of within-species body size variation of birds: strong evidence for Bergmann's rule. *Global Ecology and Biogeography* **11(6)**: 505–523.
- AVISE, J.C. & LANSMAN, R.A. 1983. Polymorphism of mitochondrial DNA in populations of higher animals. In: *Evolution of genes and proteins*. M. Nei & R.K. Koehn. Sinauer Associates Inc., Sunderland, MA. Pp. 147-164.
- AVISE, J.C. 1998. The history and purview of phylogeography: a personal reflection. *Molecular Ecology* **7**: 371–379.
- AVISE, J.C. 2000. *Phylogeography: the history and formation of species*. Harvard University Press, Cambridge, MA.
- AVISE, J.C., ARNOLD, J., BALL, R.M. Jr., BERMINGHAM, E.T., LAMB, J. NEIGEL, E., REEB, C.A. & SAUNDERS, N.C. 1987. Intraspecific phylogeography: the

- mitochondrial DNA bridge between population genetics and systematics. *Annual review of Ecology and Systematics* **18**: 489–522.
- AVISE, J.C., BOWEN, B.W. & AYALA, F.J. 2016. In light of evolution X: comparative phylogeography. *Proceedings of the National Academy of Sciences* **113**: 7957–7961.
- AVISE, J.C., GIBLIN-DAVIDSON, C., LAERM, J., PATTON, J.C. & LANSMAN, R.A. 1979. Mitochondrial DNA clones and matriarchal phylogeny within and among geographic populations of the pocket gopher, *Geomys pinetis*. *Proceedings of the National Academy of Sciences of the United States of America* **76(12)**: 6694–6698.
- BADYAEV, A.V., YOUNG, R.L., OH, K.P. & ADDISON, C. 2008. Evolution on a local scale: developmental, functional, and genetic bases of divergence in bill form and associated changes in song structure between adjacent habitats. *Evolution* **62(8)**: 1951–64.
- BALL, R.M. Jr., & AVISE, J.C. 1992. Mitochondrial DNA phylogeographic differentiation among avian populations and the evolutionary significance of subspecies. *The Auk* **109**: 626–636.
- BARKER, F.K., CIBOIS, A., SCHIKLER, P., FEINSTEIN, J. & CRACRAFT, J. 2004. Phylogeny and diversification of the largest avian radiation. *Proceedings of the National Academy of Sciences* **101(30)**: 11040-11045.
- BARRACLOUGH, T.G. & VOGLER, A.P. 2000. Detecting the geographical pattern of Speciation from species-level phylogenies. *American Naturalist* **155**: 419–434.
- BARROWCLOUGH, G.F. 1982. Subspecies and predictiveness. *The Auk* **99**: 601–603.
- BENSASSON, D., ZHANG, D-X., HARTL, D.L. & HEWITT, G.M. 2001. Mitochondrial pseudogenes: evolution's misplaced witnesses. *Trends in Ecology and Evolution* **16**: 314–321.
- BERGMANN, C. 1847. Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. *Göttinger Studien, Göttingen* **3**: 595–708.
- BLUMENRATH, S.H. & DABELSTEEN, T. 2004. Degradation of great tit (*Parus major*) song before and after foliation: implications for vocal communication in a deciduous forest. *Behaviour* **141**: 935-958.
- BODE, S.N.S., ADOLFSSON, S., LAMATSCH, D.K., MARTINS, M.J.F., SCHMIT, O., VANDEKERKHOVE, J., MEZQUITA, F., NAMIoTOKO, T., ROSSETTI, G.,



- SCH ÖN I., BUTLIN, R.K. & MARTENS, K. 2009. Exceptional cryptic diversity and multiple origins of parthenogenesis in a freshwater ostracod. *Molecular Phylogenetics and Evolution* **54**: 542–552.
- BONCORAGLIO, G. & SAINO, N. 2007. “Habitat structure and the evolution of bird song: a meta-analysis of the evidence for the acoustic adaptation hypothesis” *Functional Ecology* **21(1)**: 134–142.
- BONNEVIE, B.T. & CRAIG, A.J.F.K. 2018. A song for the South also: defining birdsong in global terms. *Ibis*. doi: 10.1111/ibi.12627.
- BOWIE, R.C.K., OATLEY, T.B., DEAN, W.R.J., SMITH, N., JOHNSON, D.N., VERNON, C.J., BOIX-HINZEN, C., HOCKEY, P.A.R, SIMMONS, R.E. & SPOTTISWOODE, C.N. 2005. Malaconotidae. Pp. 688-721. In HOCKEY, P.A.R, DEAN, W.R.J. & RYAN, P.G. (eds). *Roberts birds of southern Africa VII edition*. The Trustees of the John Voelcker Bird Book Fund, Cape Town. ISBN 0-620-34053-3.
- BRADBURY, J.W., CORTOPASSI, K.A., & CLEMMONS, J. R. 2001. Geographic variation in the contact calls of Orange-fronted parakeets. *The Auk* **118**: 958–972.
- BRADBURY, J.W. & VEHRENCAMP, S.L. 1998. Principles of animal communication. Sinauer Associates, Sunderland, MA.
- BRADBURY, J.W. & VEHRENCAMP, S.L. 1998. *Principles of animal communication*. Sinauer Associates, Sunderland, MA,
- BRENOWITZ, E.A. & KROODSMA, D.E. 1996. Bird song neuroethology. In: *Ecology and evolution of acoustic communication in birds*. D.E. KROODSMA & E.H. MILLER (eds.). Cornell University Press, New York. Pp. 285–304.
- BRETAGNOLLE, V. 1996. Acoustic communication in a group of non-passerine birds, the petrels. In: *Ecology and Evolution of Acoustic Communication in Birds*. D.E. KROODSMA & E.H. MILLER (eds.). Cornell University Press, Ithaca, New York. Pp. 160–178.
- BROOKS, T.M., MITTERMEIER, R.A., DA FONSECA G.A.B., GERLACH, J., HOFFMANN, M., LAMOREUX, J.F., MITTERMEIER, C.G., PILGRIM, J.D. & RODRIGUES, A.S.L. 2006. Global biodiversity conservation priorities. *Science* **313**: 58–61.

- BROWN, W.M. & WRIGHT, J.W. 1979. Mitochondrial DNA analyses and the origin and relative age of parthenogenetic lizards (genus *Cnemidophorus*). *Science* **203**: 247–49.
- BROWN, W.M. 1983. Evolution of animal mitochondrial DNA. *In evolution of Genes and Proteins*. M. NEI & R.K. KOEHN (eds.). Sinauer Associates Inc., Sunderland, MA. Pp. 62–88.
- BRUMM, H. & SLABBEKOORN, H. 2005. Acoustic communication in noise. *Advances in the Study of Behavior* **35**: 151–209.
- BUCKLEY, T.R. & CUNNINGHAM, C.W. 2002. The effects of nucleotide substitution model assumptions on estimates of nonparametric bootstrap support. *Molecular Biology and Evolution* **19**: 394–405.
- BUCKLEY, T.R. 2002. Model misspecification and probabilistic tests of topology: evidence from empirical data sets. *Systematic Biology* **51**: 509–523.
- BUCKLEY, T.R., SIMON, C. & CHAMBERS, G.K. 2001. Exploring among site rate variation models in a maximum likelihood framework using empirical data: the effects of model assumption on estimates of topology, branch lengths, and bootstrap support. *Systematic Biology* **50**: 67–86.
- BURNS, K.J., HACKET, S.J. & KLEIN, N.K. 2002. Phylogenetic relationships and morphological diversity in Darwin's Finches and their relatives. *Evolution* **56**: 1240–1252.
- CABANNE, G.S., D'HORTA, F.M., SARI, H.E.R., SANOS, F.R. & MIYAKI, C.Y. 2008. Nuclear and mitochondrial phylogeography of the Atlantic forest endemic *Xiphorhynchus fuscus* (Aves: Dendrocolaptidae): biogeography and systematics implications. *Molecular Phylogenetics and Evolution* **49**: 760–773.
- CANN, R.L., STONEKING, M. & WILSON, A.C. 1987. Mitochondrial DNA and human evolution. *Nature* **325**: 31–36.
- CARDOSO, G.C. 2010. Loudness of birdsong is related to the body size, syntax and phonology of passerine species. *Journal of Evolutionary Biology* **23**: 212–219.
- CARSTENS, B.C. & KNOWLES, L.L. 2007. Estimating species phylogeny from gene-tree probabilities despite incomplete lineage sorting: an example from *Melanoplus* grasshoppers. *Systematic Biology* **56**: 1–12.
- CATCHPOLE, C.K. & SLATER, P.J.B. 1995. Bird song: biological themes and variations. Cambridge University Press, Cambridge, U.K.

- CATCHPOLE, C.K. 1983. Variation in the song of the Great reed warbler *Acrocephalus arundinaceus* in relation to mate attraction and territorial defence. *Animal Behaviour* **31**: 1217–1225.
- CHAPPUIS, C. 1971. Un exemple de l'influence du milieu sur les émissions vocales des oiseaux: révolution de chants en forêt équatoriale. *Revue d'Écologie, la Terre et la Vie* **25**:183–202.
- CHITTENDEN, H., ALLAN, D. & WEIERSBYE, I. 2012. *Roberts – Geographic variation of Southern African Birds*. The Trustees of the John Voelcker Bird Book Fund, Cape Town.
- CHITTENDEN, H., DAVIES, G. & WEIERSBYE, I. 2016. *Roberts Bird Guide*. 2<sup>nd</sup> ed. Jacana Media, Cape Town.
- CLARKE, K.R. & GORLEY, R.N. 2006. *PRIMER v6: User manual/tutorial*, PRIMER-E. Plymouth, UK. Pp. 192.
- CLARKE, K.R. & WARWICK, R.M. 2001. Change in marine communities: *an approach to statistical analysis and interpretation*. 2nd ed. PRIMER-E: Plymouth Marine Laboratory. Plymouth, UK. Pp. 190.
- CLEMENT, M., POSADA, D. & CRANDALL, K.A. 2000. TCS: a computer program to estimate gene genealogies. *Molecular Ecology* **9**: 1657–1659.
- COHEN, C., WAKELING, J.L., MANDIWANA-NEUDANI, T.G. & BOWIE, R.C.K. Phylogenetic affinities of evolutionary enigmatic African Galliformes: The Stone Partridge *Ptilopachus petrosus* and Nahan's Francolin *Francolinus nahani*, and support for their sister relationship with New World quails. *Ibis* **154(4)**: 768–780.
- CORRALES, C., PAVLOVSKA, M. & HÖGLUND, J. 2014. Phylogeography and subspecies status of Black Grouse. *Journal of Ornithology* **155**: 13-25.
- CRANDALL, K.A., BININDA-EMONDS, O.R.P., MACE, G.M. & WAYNE, R.K. 2000. Considering evolutionary processes in conservation biology. *Trends in Ecology and Evolution* **15**: 290–295.
- D'AMEN, M., ZIMMERMANN, N.E. & PEARMAN, P.B. 2013. Conservation of phylogeographic lineages under climate change. *Global Ecology and Biogeography* **22**: 93–104.
- DABELSTEEN, T. & MATHEVON, N. 2002. Why do songbirds sing intensively at dawn? A test of the acoustic transmission hypothesis. *Acta Ethologica* **4**: 65-72.
- DE BEER, S.J., LOCKWOOD, G.M., RAIJMAKERS, J.H.F.A., RAIJMAKERS, J.M.H., SCOTT, W.A., OSCHADLEUS, H.D. & UNDERHILL, L.G. (eds.). 2001.

- SAFRING Bird Ringing Manual, ADU Guide 5. Avian Demographi Unit, University of Cape Town, Cape Town.
- DEPARTMENT OF WATER AFFAIRS. South Africa. <http://www.dwa.gov.za>, accessed November 2017.
- DESSAUER, H.C., HAFNER, M.S., & LAWRENCE, K.S. 1984. Collection of Frozen Tissues: value, management, field and laboratory procedures, and directory of existing collections. *Association of Information Systems. Collections*, University of Kansas, Lawrence. Pp. 74.
- DICKINSON, E.C. 2003. The Howard and Moore Complete Checklist of the Birds of the World. 3<sup>rd</sup> ed. Princeton University Press, Princeton, New Jersey.
- DUELLMAN, W.E. & TRUEB, L. 1994. Biology of Amphibians. The Johns Hopkins University Press, Baltimore. Pp. 670.
- EBERHARD, J.R. & BERMINGHAM, E. 2004. Phylogeny and biogeography of the *Amazona ochrocephala* (Aves: Psittacidae) complex. *Auk* **121**: 318-32.
- EDWARDS, S.V. & BEERLI, P. 2000. Gene divergence, population divergence, and the variance in the coalescence time in phylogeographic studies. *Evolution* **54**: 1839–1854.
- EDWARDS, S.V. & BEERLI, P. 2000. Perspective: gene divergence, population divergence, and the variance in coalescence time in phylogeography studies. *Evolution* **54**: 1839–1854.
- ENCE, D.D. & CARSTENS, B.C. 2011. SpedeSTEM: a rapid and accurate method for species delimitation. *Molecular Ecology Resources* **11**: 473–480.
- EVANS, B.J., KELLEY, D.B., TINSLEY, R.C., MELNICK, D.J., & CANNATELLA, D.C. 2004. A mitochondrial DNA phylogeny of African clawed frogs: phylogeography and implications for polyploid evolution. *Molecular Phylogenetics and Evolution* **33**: 197–213.
- FARNSWORTH, A. & LOVETTE, I.J. 2008. Phylogenetic and ecological effects on interspecific variation in structurally simple avian vocalizations. *Biological Journal of the Linnean Society* **94**: 155–173.
- FEDUCCIA, A. 1975. Morphology of the bony stapes in the Menuridae and Acanthisittidae: evidence for oscine affinities. *The Wilson Bulletin* **87(3)**: 418–420.
- FORBES, W.A. Contribution to the anatomy of passerine birds. Part 6. On *Xenicus* and *Achantisitta* as types of a new family (Xenicidae) of Mesomyodian Passers

- from New Zealand. *Proceedings of the Zoological Society London* **1882**: 569–571.
- FORSTMEIER, W., LEISLER, B. & KEMPENAERS, B. 2001. Bill morphology reflects female independence from male parental help. *Proceedings of the Royal Society B* **268(1476)**: 1583–1588.
- FRANK, T., PROBST, A., K€ONIG, H.E. & WALTER, I. 2007. The syrinx of the male mallard (*Anas platyrhynchos*): special anatomical features. *Anatomia Histologia Embryologia* **36**: 121–126.
- FRIDOLFSSON, A-K. & ELLEGREN, H.1999. A simple and universal method for molecular sexing of non-ratite birds. *Journal of Avian Biology* **30**: 116–121.
- FRY, C.H. 2009. Family Malaconotidae (Bush-shrikes). Vol. 14. In: *Handbook of the Birds of the World*. J. Del HOYO, A. ELLIOT & D.A. CHRISTIE. Bushrikes to old World Sparrows. Lynx Editions, Barcelona. Pp. 50–122.
- FU, Y.X. 1997. Statistical tests of neutrality of mutations against population growth, hitchhiking and back-ground selection. *Genetics* **147**: 915–925.
- FUCHS, J., BOWIE, R.C.K., FJELDSÅ, J., PASQUET, E. 2004. Phylogenetic relationships of the African bush-shrikes and helmet-shrikes (Passeriformes: Malaconotidae). *Molecular Phylogenetics and Evolution* **33**: 428–430.
- FUCHS, J., CROWE, T.M. & BOWIE, R.C.K. 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., FJELDSÅ, J. & BOWIE, R.C.K. 2017. Diversification across major biogeographic breaks in the African Shining/Square-tailed Drongos complex (Passeriformes: Dicuridae). *Zoologica Scripta* **46**: 27–41.
- FUCHS, J., FJELDSÅ, J. & BOWIE, R.C.K., 2011. Diversification across an altitudinal gradient in the Tiny Greenbul (*Phyllastrephus debilis*) from the Eastern Arc Mountains of Africa. *BMC Evolutionary Biology* **11(1)**: 117.
- FUCHS, J., PONS, J-M., ERICSON, P.G.P., BONILLO, C., COULOUX, A. & PASQUET, E. 2008. Molecular support for a rapid cladogenesis of the woodpecker clade Malarpicini, with further insights into the genus *Picus* (Piciformes: Picinae). *Molecular phylogenetics and Evolution* **48**: 34–46.
- GARAMSZEGI, L.Z., MØLLER, A.P. TÖRÖK, J., MICHL, G., PÉTER PÉCZELY, P. & RICHARD, M. 2004. "Immune challenge mediates vocal communication in a passerine bird: an experiment". *Behavioral Ecology* **15(1)**: 148–157.

- GARRICK, R.C., SUNNUCK, P. & DYERS, R.J. 2010. Nuclear gene phylogeography using PHASE: dealing with unresolved genotypes, lost alleles, and systematic bias in parameter estimation. *BMC Evolutionary Biology* **10**:118.
- GERHARDT, H.C. 1978. Temperature coupling in the vocal communication system of the gray treefrog, *Hyla versicolor*. *Science* **199**: 992-994.
- GILL, F. & DONSKER, D. (eds.). 2017. IOC World Bird List (v 7.3). Available at <http://www.worldbirdnames.org/>.
- GILL, F.B. 1990. *Ornithology*. 2<sup>nd</sup> ed. W.H. Freeman and Company, New York.
- GILL, F.B. 2007. *Ornithology*. 3rd ed. W.H. Freeman, New York.
- GLOGER, C. L. 1833. Das Abändern der Vögel durch Einfluss des Klimas. Breslau, Germany.
- GUINDON, S. & GASCUEL, O. 2003. A simple, fast and accurate algorithm to estimate large phylogenies by maximum likelihood. *Systematic Biology* **52**: 696–704.
- HACKETT, S.C. 2011. *Environmental and natural resource economics: theory, policy, and the sustainable society*. 4th ed. M.E, Sharpe Armonk, NY.
- HAGELBERG, E., GOLDMAN, N., LIÓ, P., WHELAN, S., SCHIEFENHÖVEL, W., CLEGG, J.B. & BOWDEN, D.K. 2000. Evidence for mitochondrial DNA recombination in a human population of island Melanesia: correction. *Proceedings of the Royal Society B* **267**: 1595–1596.
- HALL, B.P. & MOREAU, R.E. 1970. *An atlas of speciation in African passerine birds*. Trustees of the British Museum, London.
- HALL, B.P. 1954. A review of the Boubou Shrike *Laniarius ferrugineus*. *Ibis* **96**: 343–355.
- HALL, M.L., KINGMA, S.A. & PETERS, A. 2013. Male songbird indicates body size with low-pitched advertising songs. *PLOS One* **8(2)**: e56717.
- HANDFORD, P., & LOUGHEED, S.C. 1991. Variation in duration and frequency characters in the song of the Rufous-collared Sparrow, *Zonotrichia capensis*, with respect to habitat, trill dialects and body size. *Condor* **93**: 644–658.
- HARE, M.P. 2001. Prospects for nuclear gene Phylogeography. *Trends in Ecology & Evolution* **16**: 12.
- HARRIS, T. & ARNOTT, G. 1988. *Shrikes of Southern Africa*. Struik Winchester, Cape Town.

- HARRIS, T. & FRANKLIN, K. 2000. *Shrikes and bush-shrikes*. Princeton University Press, Princeton, NJ.
- HEDRICK, P.W. 2001. Conservation genetics: where are we now? *Trends in Ecology and Evolution* **16**: 629–636.
- HELED, J. & DRUMMOND, A.J. 2010. Bayesian inference of species trees from multilocus data. *Molecular Biology and Evolution* **27**: 570–580.
- HENWOOD, K. & FABRICK, A. 1979. "A Quantitative Analysis of the Dawn Chorus: Temporal Selection for Communicatory Optimization" *The American Naturalist* **114(2)**: 260–274.
- HEWITT, G.M. 2001. Speciation, hybrid zones and phylogeography – or seeing gene in space and time. *Molecular Ecology* **10**: 537–549.
- HEWITT, G.M. 1988. Hybrid zones – natural laboratories for evolutionary studies. *Trends in Ecology and Evolution* **3**: 158–167.
- HEWITT, J. 1927. Further descriptions of reptiles and batrachians from South Africa. *Records of the Albany Museum* **3**: 371–415.
- HICKERSON, M.J., CARSTENS, B.C., CAVENDER-BARES, J., CRANDALL, K.A., GRAHAM, C.H., JOHNSON, J.B., RISSLER, L., VICTORIANO, P.F. & YODER, A.D. 2010. Phylogeography's past, present, and future: 10 years after Avise, 2000. *Molecular Phylogenetics and Evolution* **54(1)**: 291–301
- HILL, G & MCGRAW, K. 2006. *Bird coloration, Volume I: mechanisms and measurements*. Harvard University Press, Cambridge, MA, USA.
- HILL, G.E. 2006. Environmental Regulation of Ornamental Coloration. In: *Bird Coloration*. Vol i. pp. 507–755. (eds) G.E. HILL & K.J. MCGRAW. Harvard University Press, Massachusetts, USA.
- HILLIS, D.M. & DAVIS, S.K. 1986. Evolution of ribosomal DNA: Fifty million years of recorded history in the frog genus *Rana*. *Evolution* **40**: 1275–1288.
- HILLIS, D.M. & DAVIS, S.K. 1987. Evolution of the 28S ribosomal RNA gene in anurans: Region of variability and their phylogenetic implications. *Molecular Biology and Evolution* **4**: 117–25.
- HILLIS, D.M. 1987. Molecular versus morphological Approaches to systematics. *Annual Review of Ecology and Systematics* **18**: 23–42.
- HIME, P.M., HOTALING, S., GREWELLE, R.E., O'NEILL, E.M., VOSS, S.R., SHAFFER, H.B. & WEISROCK, D.W. 2016. The influence of locus number and

- information content on species delimitation: an empirical test case in an endangered Mexican salamander. *Molecular Ecology* **25(23)**: 5959–5974.
- HUDSON, R.R. & TURELLI, M. 2003. Stochasticity overrules *the* "three-times rule": genetic drift, genetic draft, *and* coalescence times *for* nuclear loci versus mitochondrial DNA. *Evolution* **57(1)**: 182–190.
- HUNTER, M.L. & KREBS, J.R. 1979. Geographical variation in the song of the Great Tit (*Parus major*) in relation to ecological factors. *Journal of Animal Ecology* **48**: 759–785.
- HURVICH, C.M. & TSAI, C-L. 1989. Regression and time series model selection in small samples. *Biometrika* **76**: 297–307.
- HUSON, D.H. & BRYANT, D. 2006. Application of phylogenetic networks in evolutionary studies. *Molecular Biology and Evolution* **23**: 254–26.
- IBM Corp. Released 2017. *IBM SPSS Statistics for windows*, Version 25.0. Armonk, IBM Corp., New York.
- JAFFE, A.L., CAMPBELL-STATON, S.C. & LOSOS, J.B. 2016. Geographical variation in morphology and its environmental correlates in a widespread North American lizard, *Anolis carolinensis* (Squamata: Dactyloidae). *Biological Journal of the Linnean Society* **117**: 760–74.
- JØNSSON, K.A., FABRE, P.H., FRITZ, S.A., ETIENNE, R.S., RICKLEFS, R.E. & JORGENSEN, T.B. 2012. Ecological and evolutionary determinants for the adaptive radiation of the Madagascan vangas. *Proceedings of the National Academy of Sciences of the United States of America* **109(17)**: 6620–6625.
- KABOLI, M., ALIABADIAN, M., GUILLAUMET, A., ROSELAAR, C.S. & PRODON, R. 2007. Ecomorphology of the wheaters (genus *Oenanthe*). *Ibis* **149**: 792–805.
- KALIONTZOPOULOU, A., CARRETERO, M.A. & LLORENTE, G.A. 2010. Intraspecific ecomorphological variation: linear and geometric morphometrics reveal habitat-related patterns within *Podarcis bocagei* wall lizards. *Journal of Evolutionary Biology* **23**: 1234–1244.
- KAREIVA, P., TALLIS, H., RICKETTS, T.H., DAILY, G.C. & POLASKY, S. 2011. *Natural Capital: Theory and Practice of Mapping Ecosystem Services*. 1st edn. Oxford Univ Press; New York.
- KIMBALL, R.T., BRAUNA, E.L., BARKERB, F.K., BOWIEC, R.C.K., BRAUNF, M.J., CHOJNOWSKIA, J.L., HACKETTC, S.J., HANA, K-L., HARSHMANC, J., HEIMER-TORRESA, V., HOLZNAGELF, W., HUDDLESTONF, C.J., MARKSI,



- B.D., MIGLIAJ, K.J., MOOREJ, W.S., REDDYC, S., SHELDONI, F.H., SMITHA, J.V., WITTI, C.C. & YURIA, T. 2009. A well-tested set of primers to amplify regions spread across the avian genome. *Molecular Phylogenetics and Evolution* **50**: 654–660.
- KEARNS, A.M., JOSEPH, L., EDWARDS, S.V. & DOUBLE, M.C. 2009. Inferring the phylogeography and evolutionary history of the splendid fairy-wren *Malurus splendens* from mitochondrial DNA and spectrophotometry. *Journal of Avian Biology* **40**: 7–17.
- KELSEY, C.R., CRANDALL, K.A. & VOEVODIN, A.F. 1999. Different models, different trees: The geographic origin of PTLV-I. *Molecular Phylogenetics and Evolution* **13**: 336–347.
- KINGSOLVER, J.G & HUEY, R.B. 2008. Size, temperature, and fitness: three rule. *Evolutionary Ecology Research* **10**: 251–268.
- KNOWLES, L.L. & CARSTENS, B.C. 2007. Delimiting species without monophyletic gene trees. *Systematic Biology* **56**: 887–895.
- KNOWLES, L.L. 2009. Statistical phylogeography. *Annual Review of Ecology, Evolution and Systematics* **40**: 593–612.
- KOPUCHIAN, C., LIJMAER, D.A., TUBARO, P.L. & HANDFORD, P. 2004. Temporal stability and change in a microgeographical pattern of song variation in the Rufous-collared sparrow. *Animal behaviour* **68 (3)**: 551–559.
- KRAKAUER, A., TYRRELL, M., LEHMANN, K. & PATRICELLI, G. 2009. Vocal and anatomical evidence for a two voiced system in the greater sage-grouse (*Centrocercus urophasianus*). *Journal of Experimental biology* **212(Pt 22)**: 3719–3727.
- KRATTER, A.W. & PARKER, T.A. 1997. Relationship of two bamboo-specialized foliage-gleaners: *Automolus dorsalis* and *Anabazenops fuscus* (Furnariidae). In: *Studies in Neotropical ornithology honouring Ted Parker*. Pp. 383-397 (ed) J.V REMSEN. *Ornithological Monograph* 48.
- KROODSMA, D.E. & MILLER, E. 1982. *Acoustic Communication in Birds*, Vol. 2. Academic Press, New York.
- KROODSMA, D.E. & MILLER, E.H. 1982. *Acoustic communication in birds*. Academic Press, New York. LINHART, P., SLABBEKOORN, H. & FUCHS, R. (Eds) 2012. The communicative significance of song length in territorial chiffchaffs. *Behavioral Ecology* **23**: 1338–1347.

- KROODSMA, D.E. 1977. A re-evaluation of song development in the Song Sparrow. *Animal Behaviour* **25**: 390–399.
- KROODSMA, D.E. 1981. Geographical variation and functions of song types in warblers (Parulidae). *The Auk* **98**: 743–751.
- KROODSMA, D.E. 1994. Song variation within and among populations of Red-winged Blackbirds. *Wilson Bulletin* **106**: 156–162.
- KROODSMA, D.E. 1996. Ecology of passerine song development. In: *Ecology and evolution of acoustic communication in birds*. D.E. KROODSMA & E.H.MILLER (eds.). Cornell University Press, Ithaca, NY, USA. Pp. 3–19.
- KROODSMA, E.D. 1977. Correlates of Song Organization Among North American Wrens. *The American Naturalist* **111**: 995–1008.
- KUBATKO, L.S., CARSTENS, B.C. & KNOWLES, L.L. 2009. STEM: species tree estimation using maximum likelihood for gene trees under coalescence. *Bioinformatics* **25**: 971–973.
- KULEMEYER, C., ASBAHR, K., GUNZ, P., FRAHNERT, S. & BAIRLEIN, F. 2009. Functional morphology and integration of corvid skulls - a 3D geometric morphometric approach. *Frontiers in Zoology* **6**: 2.
- LAILOLO, P. & ROLANDO, A. 2003. Comparative analysis of the rattle calls in *Corvus* and *Nucifraga*: the effect of body size, bill size, and phylogeny. *The Condor* **105**: 139–144.
- LANYON, W.E. 1969 Vocal characters and avian systematics. In: *Bird vocalizations: their relation to current problems in biology and psychology*. R.A HINDE (ed.). Cambridge University Press, London. Pp. 291–310.
- LANYON, W.E. 1979. Development of song in the Wood Thrush (*Hylocichla mustelina*), with notes on a technique for passerines from the egg. *American Museum Novitates* **2666**: 1–27.
- LARMUSEAU, M.H.D., RAEYMAEKERS, J.A.M., HELLEMANS, B., VAN HOUDT J.K.J. & VOLCKAERT, F.A.M. 2010. Mito-nuclear discordance in the degree of population differentiation in a Marine goby. *Heredity* **105**: 532–542.
- LEE, J.Y. & EDWARDS, S.V. 2008. Divergence across Australia's Carpentarian barrier: statistical phylogeography of the red-backed fairy wren (*Malurus melanocephalus*). *Evolution* **62**: 3117–34.

- LEE, J.Y., JOSEPH, L. & EDWARDS, S.V. 2012. A Species Tree for the Australo-Papuan Fairy-wren and Allies (Aves: Muluridae). *Systematic Biology* **61(2)**: 253–271.
- LEI, F.M., WANG, A.Z., WANG, G. & YIN, Z.H. 2005. Vocalizations of Red-necked snow finch, *Pyrgilauda ruficollis* on the Tibetan plateau, China – a syllable taxonomic signal? *Folia Zoologica* **54**: 135–146.
- LEIGH, J.W. & BRYANT, D. 2015. POPART: full-feature software for haplotype network construction. *Methods in Ecology and Evolution* **6**: 1110–1116.
- LEIN, M.R. 1978. Song variation in a population of Chestnut-sided warblers (*Dendroica pensylvanica*): its nature and suggested significance. *Canadian Journal of Zoology* **56**: 1266–1283.
- LERNER, H.R.L., MEYER, M., JAMES, H.F., HOFREITER, M. & FLEISCHER, R.C. 2011. Multilocus resolution of phylogeny and timescale in the extant adaptive radiation of Hawaiian Honeycreepers. *Current Biology* **21**: 1838–1844.
- LIBRADO, P., & ROZAS, J. 2009. DnaSP v5: a software for comprehensive analysis of DNA polymorphism data. *Bioinformatics* **25**: 1451–1452.
- LIN, G., CI, H., ZHANG, T. & SU, J. 2008. Conformity to Bergmann's rule in the plateau pika (*Ochotona curzoniae* Hodgson, 1857) on the Qinghai-Tibetan plateau. *Acta Zoologica Academiae Scientiarum Hungaricae* **54**: 411–418.
- LIU, L., YU, L., KUBATKO, L., PEARL, D.K. & EDWARDS, S.V. 2009. Coalescent methods for estimating multilocus phylogenetic trees. *Molecular Biology and Evolution* **53**: 320–328.
- LOMOLINO, M.V. & PERAULT, D.R. 2007. Body size variation of mammals in fragmented, Temperate Rainforest. *Conservation Biology* **21(4)**: 1059–1069.
- LOVINS, A.B., LOVINS, L.H. & HAWKEN, P. 1999. A road map for natural capitalism. *Harvard Business Review* **77**: 145–158.
- LUTTRELL, S.A.M. & LOHR, B. 2018. Geographic variation in song structure, likelihood, and call song associations across subspecies boundaries, migratory patterns, and habitat types in Marsh Wren (*Cistothorus palustris*). *The Auk* **135(1)**: 127–151.
- LYNCH, M. 2007. *The Origins of Genome Architecture*. Sinauer Associates Inc., Sunderland, MA.
- MACKWORTH-PRAED, C.W. & GRANT, C.H.B. 1962. *Birds of the Southern third of Africa: African handbook of birds Vol. 2*. Longmans Publishers, London.

- MADDISON, W.P. & KNOWLES, L.L. 2006. Inferring phylogeny despite incomplete lineage sorting. *Systematic Biology* **55**: 21–30.
- MAGER, J.N. III, WALCOTT, C. & PIPER, W.H. 2007. Male common loons, *Gavia immer*, communicate body mass and condition through dominant frequencies of territorial yodel. *Animal Behaviour* **73**: 683–690.
- MANDIWANA-NEUDANI, T.G, BOWIE, R.C.K., HAUBERGER, M., HENRY, L. & CROWE, T.M. 2014. Taxonomic and phylogenetic utility of variation in advertising calls of francolins and spurfowls (Galliformes: Phasianidae). *African Zoology* **49(1)**: 54–82.
- MARLER, P. & TAMURA, M. 1962. "Song dialects in three populations of the white-crowned sparrow". *The Condor* **64(5)**: 368–377.
- MARLER, P. 1969. Tonal quality of bird sounds. In: *Bird vocalizations: their relation to current problems in Biology and Psychology*. R.A. HINDE (ed.). Cambridge University Press, London. Pp. 5–18.
- MARTENS, J. 1996. Vocalizations and speciation of palearctic birds. In: *Ecology and evolution of acoustic communication in birds*. D.E. KROODSMA & E.H. MILLER (eds.). Cornell University Press, Ithaca, NY, USA. Pp. 221–240.
- MARTINEZ, P.A, MARTI, D.A., MOLINA, W.F. & BIDAU, C.J. 2013. Bergmann's rule across the Equator: a case study in *Cerdocyon thous* (Canidae). *Journal of Animal Ecology* **82**: 997–1008.
- MASWANGANYE, K.A., CUNNINGHAM, M.J., BENNETT, N.C., CHIMIMBA, C.T. & BLOOMER, P. 2017. Life on the rocks: Multilocus Phylogeography of the rock hyrax (*Procavia capensis*) from southern Africa. *Molecular Phylogenetics and Evolution* **14**: 49–62.
- MAYR, E. 1942. *Systematics and the origin of species from the viewpoint of a Zoologist*. Columbia University Press, New York, NY, USA.
- MAYR, E. 1951. Speciation in birds. *Proceedings of the 10<sup>th</sup> International Ornithological Congress* **10**: 91–131.
- MAYR, E. 1956. Geographical character gradients and climatic adaptation. *Evolution* **10(1)**: 105–108.
- MAYR, E. 1987. The ontological status of species. *Biology and Philosophy* **2**: 145–166.
- MAYR, E. 1991. Principles of systematic zoology. 2<sup>nd</sup> ed. McGraw-Hill, Singapore.

- MCCRACKEN, K.G & SHELDON, F.H. 1997. Avian vocalizations and phylogenetic signal. *Proceedings of the National Academy of Sciences of the United States of America* **94**: 3833–3836.
- MCGOWAN, P.J.K. 1994. Family PHASIANIDAE (Pheasants and Partridges). In: *Handbook of the Birds of the World*. Vol. 2. J. DEL HOYO, A. ELLIOTT & J. SARGATAL (eds.). Lynx Edicions, Barcelona. Pp. 434–552.
- MCGREGOR, P. K. 1995. Nottingham University and Jo Holland, University of Copenhagen. *Review in Animal Behaviour* **50**: 10.
- MCNAB, B.K. 1971. On the Ecological Significance of Bergmann's Rule. *Ecology* **52(5)**: 845–854.
- MEIRI, S. & DAYAN, T. 2003. On the validity of Bergmann's rule. *Journal of Biogeography* **30**: 331–351.
- MERKLE, T.F.C. 2010. Vocalisation of the Southern Boubou in the Eastern Cape, South Africa. *Ostrich* **81(1)**: 77–79.
- MILÁ, B., GIRMAN, D.J., KIMURA, M. & SMITH, T.B. 2000. Genetic evidence for the effect of a postglacial population expansion on the phylogeography of a North American songbird. *Proceedings of the Royal Society of London. Proceedings of the Royal Society of London* **267**: 1033–1040.
- MILLAR, C. D. & LAMBERT, D. 2013. Ancient DNA: towards a million-year-old genome. *Nature* **499(7456)**.
- MITTERMEIER, R.A., ROBLES-GI, L P., HOFFMANN, M., PILGRIM, J., BROOKS, T., MITTERMEIER, C.G., LAMOREUX, J.D.A. & FONSECA, G.A.B (eds.). 2004. Hotspots revisited: Earth's biologically richest and most endangered terrestrial ecoregions. CEMEX, Mexico City.
- MOCKFORD, E.J. & MARSHALL, R.C. 2009. Effects of urban noise on song and response behaviour in great tits. *Proceedings of the Royal Society B* **276**: 2979–2985.
- MØLLER, A.P., ERRITZØE, J. & GARAMSZEGI, L.Z. 2005. "Covariation between brain size and immunity in birds: implications for brain size evolution". *Journal of Evolutionary Biology* **18(1)**: 223–237.
- MONAGHAN, M.T., WILD, R., ELLIOT, M., FUJISAWA, T., BALKE, M., INWARD, D.J.G., LEES, D.C., RANAIVOSOLO, R., EGGLETON, P., BARRACLOUGH, T.G. & VOGLER, A.P. 2009. Accelerated species inventory on Madagascar

- using coalescent-based models of species delineation. *Systematic Biology* **58**: 298–311.
- MORTON, E.S. 1975. Ecological sources of selection on avian sounds. *American Naturalist* **109**: 17–34.
- MORTON, E.S. 1975. Ecological sources of selection on avian sounds. *The American Naturalist* **109**: 17–34.
- MUNDINGER P.C. 1982. Microgeographic and macrogeographic variation in the acquired vocalizations of birds. In: *Acoustic Communication in Birds*. Vol. 2. D.E. KROODSMA & E.H. MILLER (eds.). Academic Press: London, UK. Pp.147–208.
- MYNHARD, T.S., MAREE, S., PELSER, I., BENNETT, N.C., BRONNER, G.N., WILSON, J.W. & BLOOMER, P. 2015. Phylogeography of a Morphologically Cryptic Golden Mole Assemblage from South-Eastern Africa. *PLOS One* **10(12)**: e0144995.
- N'GUEMBOCK, B., FJELDSA, J., COULOUX, A. & PASQUET, E. 2008. Phylogeny of *Laniarius*: molecular data reveal *L. liberates* synonymous with *L. erlangeri* and “plumage coloration” as unreliable morphological characters for defining species groups. *Molecular Phylogenetics and Evolution* **48**: 39.
- NEMETH, E. & BRUMM, H. 2009. Blackbirds sing higher-pitched songs in cities: adaptation to habitat acoustics or side-effect of urbanization? *Animal Behaviour* **78**: 637–641.
- NEMETH, E., PIERETTI, N., ZOLLINGER, S.A., GEBERZAHN, N., PARTECKE, J., MIRANDA, A.C. & BRUMM, H. 2013. Bird song and anthropogenic noise: vocal constraints may explain why birds sing higher-frequency songs in cities. *Proceedings of the Royal Society B* **280**: 1471–2954.
- NICHOLLS, J.A. & GOLDIZEN, A.W. 2006. Habitat type and density influence vocal signal design in satin bowerbirds. *Journal of Animal Ecology* **75**: 549–558.
- NOTTEBOHM, F. 1972. The origin of vocal learning. *American Naturalist* **106**: 116–140.
- NOTTEBOHM, F. 1975. Continental patterns of song variability in *Zonotrichia capensis*: some possible ecological correlates. *The American Naturalist* **109**: 605–624.
- NOWICKI, S. 1987. Vocal-tract resonances in oscine bird sound production: Evidence from birdsongs in a helium atmosphere. *Nature* **325**: 53–55.

- OATLEY, G., BOWIE, R.C.K. & CROWE, T.M. 2011. The use of subspecies in the systematics of southern African white-eyes: historical entities or eco-geographic variants. *Journal of Zoology* **284**: 21–30.
- OLEINIK, A.G., SKURIKHINA, L.A. & CHUKOVA, E.I. 2010. Phylogeography of Southern Asian Dolly Varden Char *Salvelinus malma krascheninnikovi*: genealogical analysis of mitochondrial DNA. *Russian Journal of Genetics* **46**: 226–238.
- OWENS, I.P.F. & HARTLEY, I.R. 1998. Sexual dimorphism in birds: Why are they so many different forms of dimorphism? *Proceedings of the Royal Society* **265**: 397–407.
- PÄCKERT, M., MARTENS, J., KOSUCH, J., NAZARENKO, A.A. & VEIN, M. 2003. Phylogenetic signal in the song of the crests and kinglets (Aves: *Regulus*). *Evolution* **57**: 616–629.
- PAKENDORF, B. & STONEKING, M. 2005. Mitochondrial DNA and Human Evolution. *Annual Review of Genomics and Human Genetics* **6**: 165–183.
- PARKER, T.A. III, SCHULENBERG, T.S., KESSLER, M. & WUST, W.H. 1995. Natural history and conservation of the endemic avifauna in north-west Peru. *Bird Conservation International* **5**: 201–231.
- PARMESAN, C. & YOHE, G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**: 37–42.
- PAYNE, R.B. 1983. Bird songs, sexual selection and female mating strategies, In: *Social Behavior of Female Vertebrates*. S.K. WASSER (ed.). Academic Press, New York. Pp. 55–91.
- PERERA, S., RATNAYAKE-PERERA, D. & PROCHEŞ, Ş. 2011. Vertebrate distributions indicate a greater Maputaland-Pondoland-Albany region of endemism. *South African Journal of Science* **107**: 49–63.
- PINCHEIRA-DONOSO, D., HODGSON, D.J. & TREGENZA, T. 2008. The evolution of body size under environmental gradients in ectotherms: why should Bergmann's rule apply to lizards? *BMC Evolutionary Biology* **8**: 68.
- PODOS J. & WARREN, P.S. 2007. The evolution of geographic variation in birdsong. *Advances in the Study of Behavior* **37**: 403–458.
- POE, S. & SWOFFORD, D.L. 1999. Taxon sampling revisited. *Nature* **398**: 299–300.

- POISOT, T., VERNEAU, O. & DESDEVISES, Y. 2011. Morphological and Molecular Evolution Are Not Linked in *Lamellodiscus* (Plathyhelminthes, Monogenea). *PLOS One* **6(10)**: e26252.
- PONS, J., BARRACLOUGH, T.G., GOMEZ-ZURITA, J., CARDOSO, A., DURAN, D.P., HAZELL, S., KAMOUN, S., SUMLIN, W.D. & VOGLER, A.P. 2006. Sequence-based species delimitation for the DNA taxonomy of undescribed insects. *Systematic Biology* **55**: 595–609.
- POSADA, D. & BUCKLEY, T.R. 2004. Model selection and model averaging in phylogenetics: advantages of Akaike information criterion and Bayesian approaches over likelihood ratio tests. *Systematic Biology* **53**: 793–808.
- POSADA, D. & CRANDALL, K.A. 2001. Selecting the best-fit model of nucleotide substitution. *Systematic Biology* **50**: 580–601.
- POSADA, D. 2008. jModelTest: Phylogenetic model averaging. *Molecular Biology and Evolution* **25(7)**: 1253–1256.
- POTVIN, D.A. 2013. Larger body size on islands affects silvereye *Zosterops lateralis* song and call frequency. *Journal of Avian Biology* **44**: 221–225.
- POTVIN, D.A., PARRIS, K.M. & MULDER, R.A. 2011. Geographically pervasive effects of urban noise on frequency and syllable rate of songs and calls in silver-eyes (*Zosterops lateralis*). *Proceedings of the Royal Society B* **278**: 2464–2469.
- PRICE, J.J. & LANYON, S.M. 2002. RECONSTRUCTING THE EVOLUTION OF COMPLEX BIRD SONG IN THE OROPENDOLAS. *Evolution* **56(7)**: 1514–1529.
- PRICE, T. 2008. Speciation in birds Greenwood Village, CO: Roberts and Company.
- PUPKO, T., HUCHON, D., CAO, Y., OKADA, N. & HASEGAWA, M. 2002. Combining multiple data sets in a likelihood analysis: Which models are the best? *Molecular Biology and Evolution* **19**: 2294–2307.
- R CORE DEVELOPMENT TEAM. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Australia. URL <http://www.R-project.org>.
- RAIKOW, R.J., POLUMBO, P.J. & BORECKY, S.R. 1980. Appendicular myology and relationships of the Shrikes (Aves: Passeriformes: Laniidae). *Annals of the Carnegie Museum, Carnegie Museum of Natural History* **49**: 131–152.



- RAMBAUT, A. & DRUMMOND, A.J. 2007. *Tracer v1.4* [Internet]. Available from <http://www.beast.bio.ed.ac.uk/Tracer>, accessed 20 November 2017
- RAMBAUT, A. & DRUMMOND, A.J. 2007. *Tracer v1.4: MCMC trace analyses tool*. Available from <http://beast.bio.ed.ac.uk/Tracer>, accessed 20 November 2017.
- RAMBAUT, A. 2012. *FigTree v1.4.3*. Available from [<http://tree.bio.ed.ac.uk/software/tracer/>].
- RANKER, T. & WERTH, C.R. 1986. Active enzymes from herbarium specimens: Electrophoresis as an afterthought. *American Fern Journal* **76**: 102–113.
- RAPOSO, M. & HÖFLING, E. 2003. Overestimation of vocal characters in Suboscine taxonomy (Aves: Passeriformes: Tyranni): causes and implications. *Lundiana* **4**: 35–42.
- RAPOSO, M.A. & HÖFLING, E. 2003. Overestimation of vocal characters in suboscine taxonomy (Aves: Passeriformes: Tyranni): causes and implications. *Lundiana* **4(1)**: 35–42.
- RATTI, T.J. 1980. The classification of avian species and subspecies. *American Birds* **1980**: 860–866.
- READ, A.F. & WEARY, D.M. 1990. Sexual selection and the evolution of bird song: a test of the Hamilton-Zuk hypothesis. *Behavioral Ecology and Sociobiology* **26**: 47–56.
- REDPATH, S. M., APPLEBY, B.M. & PETTY, S.J. 2000. "Do male hoots betray parasite loads in Tawny Owls?" *Journal of Avian Biology* **31(4)**: 457–462
- REID, J.M.P., ARCESE, A.L., CASSIDY, E.V., HIEBERT, S.M., SMITH, J.N., STODDARD, P., MARR, B. & KELLER, L.F. 2005. Fitness correlates of song repertoires size in free living song sparrow (*Melospiza melodia*). *The American naturalist* **165(3)**: 299–310.
- REID, N.M. & CARSTENS, B.C. 2012. Phylogenetic estimation error can decrease the accuracy of species delimitation: a Bayesian implementation of the general mixed Yule-coalescent model. *BMC Evolutionary Biology* **12(1)**: 196.
- REMSEN, J.V. 2003. Family Furnariidae (ovenbirds). In: *Handbook of the birds of the World, Broadbills to Tapaculos*. Vol. 8: J. DEL HOYO, A. ELLIOTT & D.A. CHRISTIE (eds.). Lynx Edicions, Barcelona, Spain. Pp. 162–357.
- RIBEIRO, Â.M., LLOYD, P., DEAN, W.R.J., BROWN, M. & BOWIE, R.C.K. 2014. The ecological and geographic context of morphological and genetic divergence in an understorey-dwelling bird. *PLOS One* **9(2)**: e85903.

- RICHARDS, D.G. & WILEY, R.H. 1980. Reverberations and amplitude fluctuations in the propagation of sound in a forest. Implications for animal communication. *American Naturalist* **115**: 381–399.
- ROCHA, LUIZ & ALEIXO, ALEXANDRE & ALLEN, G & ALMEDA, FRANK & BALDWIN, CAROLE & BARCLAY, MAXWELL & BATES, JOHN & BAUER, A & BENZONI, FRANCESCA & BERNIS, CHELSEA & BERUMEN, MICHAEL & BLACKBURN, DAVID & BLUM, STAN & BOLAÑOS, F & BOWIE, RAURI & BRITZ, R & BROWN, RAFAEL & CADENA, CARLOS & CARPENTER, K & WITT, CHRISTOPHER. 2014. Specimen collection: an essential tool. *Science* **344**: 814–815.
- ROHLF, F.J. 1990. Fitting curves to outlines. In: *Proceedings of the Michigan morphometrics workshop*. Special Publication No. 2. F.J. ROHLF & F.L. BOOKSTEIN (eds.). University of Michigan Museum of Zoology, Ann Arbor. Pp. 167–177.
- ROHLF, F.J. 1990. Morphometrics. *Annual review of ecology and systematics* **21**: 299–316.
- RONQUIST, F., TESLENKO, M., VAN DER MARK, P., AYRES, D.L., DARLING, A., HÖHNA, S., LARGET, B., LIU, L., SUCHARD, M.A. & HUELSENBECK, J.P. 2012. MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* **61(3)**: 539–542.
- SCHAAL, B.A., HAYWORTH, D.A., OLSEN, K.M., RAUSCHER, J.T. & SMITH, W.A. 1998. Phylogeographic studies in plants: problems and prospects. *Molecular Ecology* **7**: 465–474.
- SCHLUTER, D. 2000. Ecological character displacement in adaptive radiation. *The American Naturalist* **156**: S4–S16.
- SCHMITZ-ORNÉS, A. 2006. Using colour spectral data in studies of geographic variation and taxonomy of birds: Examples with two hummingbird genera, *Anthracothorax* and *Eulampis*. *Journal of Ornithology* **147**: 495–503.
- SCHUH, T. 2000. *Biological systematics: principles and applications*. Cornell University Press. Ithaca, NY, USA. Pp. 3–44.
- SCHWARZ, G. 1978. Estimating the dimension of a model. *The Annals of Statistics* **6**: 461–464.

- SCORDATO, E.S.C., SYMES, L.B., MENDELSON, T.C. & SAFRAN, R.J. 2014. The role of ecology in speciation by sexual selection: a systematic empirical review. *Journal of Heredity* **105(Special Issue)**: 782–794.
- SHAO, S., QUAN, Q., CAI, T., SONG, G., QU, Y. & LEI, F. 2016. Evolution of body morphology and beak shape revealed by a morphometric analysis of 14 Paridae species. *Frontiers in Zoology* **13**: 30.
- SHY, E. 1983. The relation of geographical variation in song to habitat characteristics and body size in North American Tanagers (Thraupinae: *Piranga*). *Behavioral Ecology and Sociobiology* **12**: 71–76.
- SIBLEY, C.G. & AHLQUIST, J.E. 1990. “Phylogeny and Classification of Birds”, Yale University Press, New Haven, CT.
- SINCLAIR, I. & RYAN, P. 2003. *Birds of Africa South of the Sahara*. Struik publishers, Cape Town.
- SLABBEKOORN, H. & PEET, M. 2003. Birds sing at a higher pitch in urban noise. *Nature* **424**: 267.
- SLATE, J. & GEMMELL, N.J. 2004. Eve ‘n’ Steve: recombination of human mitochondrial DNA. *Trends in Ecology & Evolution* **19**: 561–563.
- SMITH, H.M. & WHITE, F.N. 1956. A case for the trinomen. *Systematic Zoology* **5**: 183–190.
- SOUTHERN AFRICAN BIRD ATLASING PROJECT 1 & 2 (SAPAB 1 & 2).  
[Accessed 03 February 2017].
- STEBBINS, G.L. 1971. *Process of organic evolution*. Prentice-Hall, New Jersey. Pp. 193.
- STEPHENS, M., NICHOLAS, J.N. & PETER, D. 2001. A new statistical method for haplotype reconstruction from population data. *American Journal of Human Genetics* **68**: 978–89.
- SUGIURA, N. 1978. Further analysis of the data by Akaike’s information criterion and the finite corrections. *Communications in Statistics, Theory and Methods* **A7**: 13–26.
- TAMURA, K. 1994. Model selection in the estimation of the number of nucleotide substitutions. *Molecular Biology and Evolution* **11**: 154–157.
- TEMPLETON, A.R. 1983. Phylogenetic inference from restriction endonuclease cleavage site maps with particular reference to the evolution of, man and the apes. *Evolution* **37**: 221–290.

- THORPE, R.S. & GIDDINGS, M.R. 1981. A novel biochemical systematic technique for herpetology based on epidermal keratin. *Experientia* **37**: 700–702.
- THORPE, W.H. 1972. Duetting and antiphonal song in birds, its extent and significance. *Behaviour* **18 (Sup.)**: 1–197.
- THORPE, W.H. & BRILL, L.E.J. 1972. Duetting and antiphonal song in birds: Its extent and significance song and call frequency. *Journal of Avian biology* **44**: 221–225.
- THORPE, W.H. 1958. The learning of song patterns by birds, with especial reference to the song of the chaffinch *Fringilla coelebs*. *Ibis* **100(4)**: 535–520.
- THUILLER, W., LAVERGNE, S., ROQUET, C., BOULANGEAT, I. & ARAÚJO, M.B. 2011. Consequences of climate change on the Tree of Life Europe. *Nature* **448**: 550–552.
- TIETZE, D.T., MARTENS, J., SUN, Y-H, PÄCKERT, M. 2008. Evolutionary history of treecreeper vocalisations (Aves: Certhia). *Organisms, Diversity & Evolution* **8**: 305–324.
- TOEWS, D.P.L. & BRELFOORD, A. 2012. The biography of mitochondrial and nuclear discordance in animals. *Molecular Ecology* **21**: 3907–3930.
- TOLLEY, K.A., TILBURY, C.R., BRANCH, W.R., & MATTHEE, C.A. 2004. Phylogenetics of the southern African dwarf chameleons, *Bradypodion* (Squamata: Chameleonidae). *Molecular Phylogenetics and Evolution* **30(2)**: 354–365.
- TOLLEY, K.A., BRAAE, A. & CUNNINGHAM, M. 2010. Phylogeography of the Clicking Stream Frog *Strongylopus grayii* (Anura, Pyxicephalidae) reveals cryptic divergence across climatic zones in an abundant and widespread taxon. *African Journal of Herpetology* **59(1)**: 17–32.
- TÓTH, J.P., VARGA, Z., VEROVNIK, R., WAHLBERG, N., VÁRADI, A. & JUDIT BERECSKI, J. 2017. Mito-nuclear discordance helps to reveal the phylogeographic patterns of *Melitaea ornata* (Lepidoptera: Nymphalidae). *Biological Journal of the Linnean Society* **121(2)**: 267–281.
- TSAOUSIS, A.D., MARTIN, D.P., LADOUKAKIS, E.D., POSADA, D. & ZOUROS, E. 2005. Widespread recombination in published animal mtDNA sequences. *Molecular Biology and Evolution* **22**: 925–933.

- WAHLBERG, N. & NYLIN, S. 2003. Morphology versus molecules: resolution of the position of *Nymphalis*, *Polygonia* and related genera (Lepidoptera: Nymphalidae). *Cladistics* **19**: 213–223.
- WAHLBERG, N., WEINGARTNER, E., WARREN, A.D. & NYLIN, S. 2009. Timing conflict between mitochondrial and nuclear genes is species relationships of *Polygonia* butterflies (Nymphalidae: Nymphalini). *BMC Evolutionary Biology* **9**: 9.
- WEARY, D.M., NORRIS, K.J. & FALLS, J.B. 1990. Song features birds use to identify individuals. *The Auk* **107**: 623–625.
- WEARY, J.W., NORRIS, K.J. & FALLS, J.B. 1990. Song feature use to identify individuals. *The Auk* **107**: 623–625.
- WEIER, J.T. 2018. Description of the song of the Nilgiri Thrush (*Zoothera [aurea] neilgherriensis*) and song differentiation across the *Zoothera dauma* species complex. *Avian Research* **9**: 28. <https://doi.org/10.1186/s40657-018-0121-x>.
- WHEELER, Q.D. 1995. Systematics, the scientific basis for inventories of biodiversity. *Biodiversity and Conservation* **4**: 476–489.
- WHELAN, C.J., SEKERCIOGLU, C.H. & WENNY, D.G. 2015. Why birds matter: From Economic Ornithology to Ecosystem Services. *Journal of Ornithology* **156**: 227–238.
- WHELAN, C.J., WENNY, D.G. & MARQUIS, R.J. 2010. Policy implications of ecosystem services provided by birds. *Synesis* **1**: 11–20.
- WIENS J.A. 1982. Forum: Avian subspecies in the 1980's. *The Auk* **99**: 593.
- WILEY, R.H. & RICHARDS, D.G. 1982. Adaptations for acoustic communication in birds: sound propagation and signal detection. In: *Acoustic Communication in Birds*. Vol. 1. D.E. KROODSMA & E.H. MILLER (eds.). Academic Press, New York. Pp. 131–181.
- YANG, Z. & RANNALA, B. 2014. Unguided species delimitation using DNA sequence data from multiple loci. *Molecular Biology and Evolution* **31**: 3125–3135.
- YANG, Z., GOLDMAN, N. & FRIDAY, A. 1995. Maximum likelihood trees from DNA sequences: A peculiar statistical estimation problem. *Systematic Biology* **44**: 384–399.

- YASSIN, A., AM'ED'EGNATO, C., CRUAUD, C. & VEUILLE, M. 2009. Molecular taxonomy and species delimitation in *Andean Schistocerca* (Orthoptera: Acrididae). *Molecular Phylogenetics and Evolution* **53**: 404–411.
- YOM-TOV, Y. & GEFFEN, E. 2011. Recent spatial and temporal changes in body size of terrestrial vertebrates: probable causes and pitfalls. *Biological Reviews* **86**: 531–41.
- ZEFFER, A., JOHANSSON, L. & MARMEBRO, Å. 2003. Functional correlation between habitat use and leg in birds (Aves). *Biological Journal of the Linnean Society* **79**: 461–484.
- ZHANG, D-X. & HEWITT, G.M. 1996. Nuclear integrations: Challenges for mitochondrial DNA markers. *Trends in Ecology and Evolution* **11**: 247–251.
- ZHANG, D-X. & HEWITT, G.M. 1996. Use of DNA markers in population genetics and ecological studies of the desert locust (*Schistocerca gregaria*). In: *The ecology of agricultural pests: biochemical approaches*. W.O.C. SYMONDSON & J.E. LIDDELL (eds.). Chapman & Hall, London. Pp. 213–230.
- ZHANG, D-X. & HEWITT, G.M. 2003. Nuclear DNA analyses in genetic studies of populations: practise, problems and prospects. *Molecular Ecology* **12**: 563–584.
- ZHANG, D-X. & HEWITT, G.M. 2003. State key laboratory of integrated management of pest insects. Nuclear DNA analyses in genetic studies of populations: practice, problems and prospects. *Molecular Ecology* **12**: 563–584.
- ZHANG, J. 1999. Performance of likelihood ratio tests of evolutionary hypotheses under inadequate substitution models. *Molecular Biology and Evolution* **16**: 868–875.
- ZHANG, X., KHALIDI, O., KIM, S.Y., WANG, R. SCHULTZ, V., CRESS, B.F., KOFFAS, M.A.G. & LINHARDT, R.J. 2016. Synthesis and biological evolution of 5,7-dihydroxyflavanone derivatives as antimicrobial agents. *Bioorganic & Medical Chemistry Letters* **26(13)**: 3089–3092.
- ZHOU, W., BARRETT, S.C., LI, H.D., WU, Z.K., WANG, X.J., WANG, H. & LI, D.Z. 2017. Phylogeographic insights on the evolutionary breakdown of heterostyly. *The New Phytologist* **214**: 1368–1380.
- ZIMMER, K. J. 2002. Species limits in olive-backed foliage-gleaners (*Automolus*; Furnariidae). *Wilson Bulletin* **114**: 20–37.

- ZINK, G. 1989. Morphologie du français medieval. Presses Universitaires de France, Paris. Pp 48–49.
- ZINK, R.M. 2004. The role of subspecies in obscuring avian biological diversity and misleading conservation policy. *Proceedings of the Royal Society of London* **271**: 561–564.
- ZINK, R.M., BARROWCLOUGH, G.F., ATWOOD, J. L. & BLACKWELL-RAGO, R. C. 2000. Genetics, taxonomy and conservation of the threatened California Gnatcatcher. *Conservation Biology* **14**: 1394–1405.