Taxonomy, phylogeny and biogeography of francolins

(‘*Francolinus’* spp.)

Aves: Order Galliformes

Family: Phasianidae

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DEDICATION

I dedicate this thesis to my parents who shared the same belief with Robert M. Maciver who once said "…When you educate a man you educate an individual; when you educate a woman you educate a whole family…" Without them, this work would never have begun. To Enos, whose love and support made this journey possible, and to my beloved Uhone whose flexibility and adaptability afforded the completion of this work…

DECLARATION

I hereby declare that the work presented in this thesis is my own, unless otherwise stated. Apart from the guidance received from my supervisors, assistance from all institutions and individuals in this thesis is acknowledged. This thesis has not been previously submitted for the degree at this or any other university and I therefore present it for examination for the degree of PhD.

Signed by candidate

Signature Removed

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Tshifhiwa G. Mandiwana-Neudani	Date

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ABSTRACT

MANDIWANA-NEUDANI, T.G. 2013. Taxonomy, phylogeny and biogeography of francolins (‘*Francolinus’* spp.) Aves: Order Galliformes, Family Phasianidae. PhD thesis, DST/NRF Centre of Excellence at the Percy FitzPatrick Institute of African Ornithology, Department of Biological Sciences, University of Cape Town, Private Bag X3, Rondebosch, 7701, South Africa.

Francolins (*Francolinus* spp.) are small to medium-sized, sedentary, Old World, partridge/quail-like, terrestrial gamebirds (Order Galliformes) that occupy diverse habitats ranging from dry/open/scrubby lowland and montane grasslands, bushveld and savanna/woodland to mesic montane/lowland forests and forest edges. Some francolins have complex distribution patterns and also are morphologically, ecologically and behaviourally diverse. At the start of this research, *Francolinus* Stephens, 1819 was considered a monophyletic galliform genus comprising 41 species (36 African and five Asiatic) divided among eight putatively monophyletic species groups and four taxonomically enigmatic species. However, different taxonomic revisions, especially post Hall’s (1963) classic monograph, challenged the monophyletic status of the genus and that of some of its designated species groups differed markedly in the number of recognized subspecies. Furthermore, there was debate concerning the geographical origin of the genus: Asia versus Africa. Some of the early molecular research on a few exemplar francolin species based on partial mitochondrial Cytochrome-*b* DNA sequences and Restriction Fragment Length Polymorphisms (RFLPs) also challenged the monophyly of the genus and that of some of Hall’s (1963) species groups. These findings suggested that francolins may form at least two distantly related lineages called ‘patryse’ (partridges) and ‘fisante’ (pheasants) by Afrikaans-speaking people. Patryse, or ‘true’ francolins, had been divided into as many as five genera (*Francolinus, Ortygornis, Dendroperdix, Peliperdix, Scleroptila*) and fisante, or spurfowls, all grouped into a single genus, *Pternistis*. Research in this thesis is based on: mitochondrial and nuclear DNA sequences (5554 base pairs), organismal and vocal characters of francolins and spurfowls. Galliform terminal taxa rooted variably on Anseriformes and Megapodes (Chapter 2), *Gallus gallus* and *Bambusicola thoracica* (francolins) and *Coturnix coturnix, Alectoris chukar* (spurfowls) (Chapters 3, 4, 5, 6, 7). The galliform phylogeny (Chapter 2), morphology of syringes (Chapter 3) and the

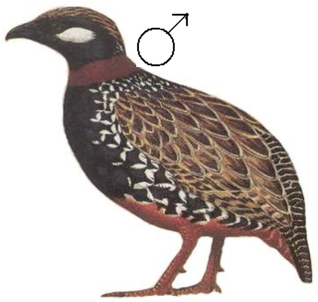
vocalizations of many taxa (Chapter 4) confirm this phylogenetic dichotomy between francolins and spurfowls and the Bayesian reconstruction of molecular divergence date reveal they last shared a common ancestor at c. 33.6 mya. In addition, the taxonomic and phylogenetic outcome of francolins (Chapter 5) and spurfowls (Chapter 6) suggest the need to recognize two additional genera of francolins: *Ortygornis* for the Asian Grey Francolin *'Francolinus' pondicerianus*, Swamp Francolin, *'Francolinus' gularis* (two of four of Hall's taxonomically enigmatic species), and the African Crested Francolin '*Dendroperdix' sephaena;* and *Afrocolinus* gen. nov., for the African Latham's Francolin *'Francolinus' lathami* (another of Hall's taxonomically enigmatic species), which links the basal francolins, *Francolinus* and *Ortygornis* spp. with relatively terminal genera, *Peliperdix* and *Scleroptila*. The 'true' francolins, those related to the nominate species, Black Francolin *Francolinus francolinus*, are monophyletic (having originated at c. 7.6 mya), and sister to junglefowls (*Gallus* spp.) and Bamboo Partridges (*Bambusicola* spp.), and are relatively small and have at most one (generally short) tarsal spur positioned about half-way down the tarsus, give more musical and whistling calls, generally roost on the ground, and have striped and barred rufous dorsal plumage resembling that of quail. Spurfowls which originated at c. 8.7 mya are monophyletic, but are distantly related to francolins. They are sister to the Bush Quail (*Perdicula asiatica*) and the Sand Partridge (*Ammoperdix heyi*) and a range of Palaearctic and African partridges and quails and are relatively large, often have two (generally long) tarsal spurs (the lower of which is positioned about two-thirds down the tarsus), emit raucous grating or cackling advertisement calls (given mainly at dawn/dusk). They have been observed perching in trees and have dark dorsal plumage vermiculated with white or buff. Thus, both francolins and spurfowls appear to have Asian, not African origins. Four of eight of Hall's (1963) groups were recovered and the phylogenetic hypotheses for all four of Hall's taxonomically enigmatic species are offered. The putative taxonomic 'link' species between francolins and spurfowls, the Crested Francolin *Dendroperdix* (now *Ortygornis*) *sephaena*, is shown to consistently group with two of Hall's unplaced Asian species *O. pondicerianus* and *O. gularis.*

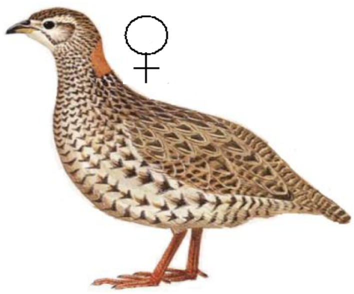
Another important discovery was that one of the unplaced species, the African Nahan's Francolin *Francolinus* (now *Ptilopachus*) *nahani* is not a francolin, but is sister to the African Stone Partridge *Ptilopachus petrosus* (Chapter 2), which in turn, are sister to the New World quails (Odontophoridae).

CHAPTER 1

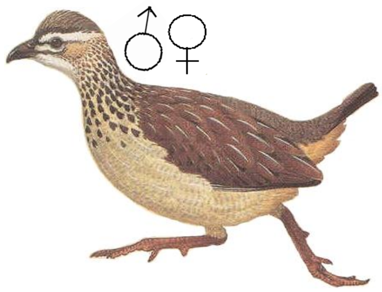
A review of the taxonomy, phylogeny and biogeography of francolins

Quail-like – 'True' Francolins – "patryse"

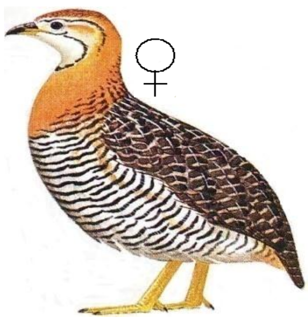




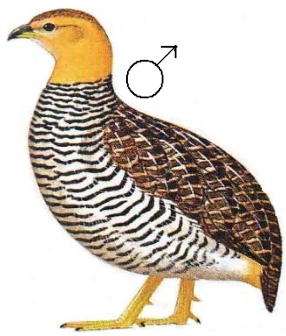
Francolinus francolinus

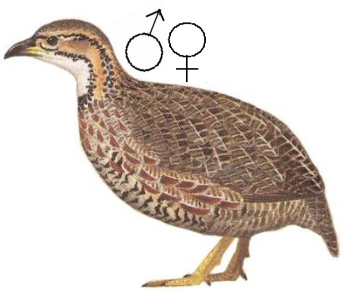


Ortygornis 'Dendroperdix' sephaena



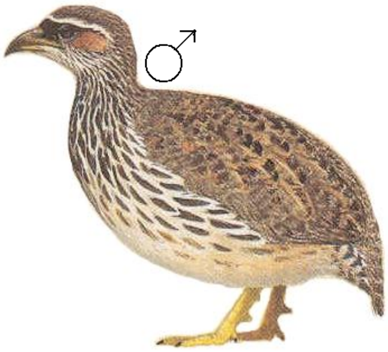
Peliperdix coqui

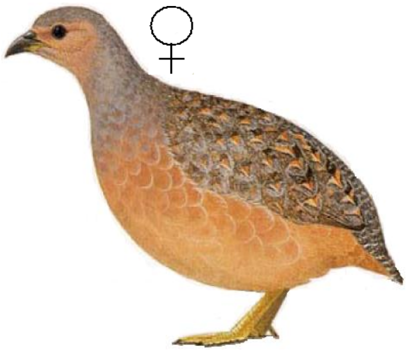




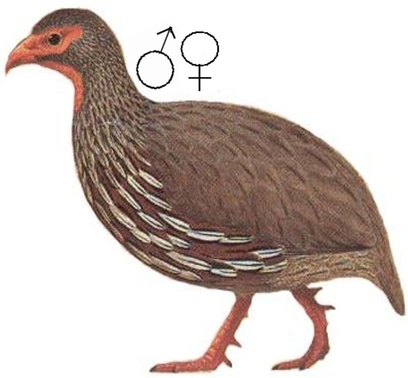
Scleroptila shelleyi

Partridge-like Francolins – Spurfowls – “fisante”



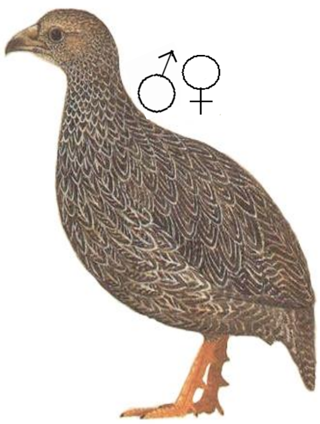


Pternistis hartlaubi

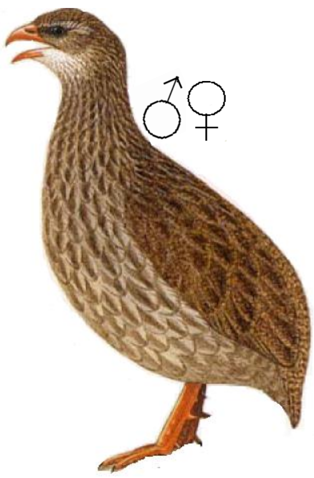


Pternistis afer

Pternistis erckelii



Pternistis capensis



Pternistis squamatus

Nahan's 'Francolin' ***'Acentrortyx' 'Francolinus' nahani***

Introduction – the status quo

Taxonomy - What are francolins?

Francolins (Table 1.1), at the initiation of this research, were classified as small to medium-sized, sedentary, Old World, partridge/quail-like gamebirds adapted to varied, but primarily tropical/sub-tropical, habitats ranging from dry, lowland grassland to montane forests (Hall 1963, Johnsgard 1988, del Hoyo et al. 1994, Madge and McGowan 2002). At the outset of this research, taxonomically, francolins were invariably placed in the Order Galliformes and family Phasianidae. In some more finely partitioned classifications, within the Phasianidae, they were placed in the sub-family Phasianinae (including *Phasianus* and related species) and, with other Old World partridge- and quail-like gamebirds (e.g. *Perdix* and *Coturnix* spp.), in the tribe Perdicini (Chapin 1932, Peters 1934, Wolters 1975-82, Crowe et al. 1986, Johnsgard 1988, Sibley and Monroe 1990, del Hoyo et al. 1994, Madge and McGowan 2002). Although relatively stable at higher taxonomic levels, there remains controversy with respect to the number and limits of subspecies, species and genera of francolins.

A brief respite

The distributions of 36 francolin species are confined to Africa. Those of five further species extend outside of Africa north to the Caspian Sea and east to central Asia and southern China (Johnsgard 1988). Based on the findings of B.P. Hall's (1963) monograph, francolins were (and generally still are) lumped into a single perdicine genus, *Francolinus,* comprising 41 species (del Hoyo et al. 1994). *Francolinus* Stephens, 1819 is currently the most specious genus in the Galliformes (Morony et al.

1975, del Hoyo et al. 1994) and one of the largest genera in the class Aves (Bock and Farrand 1980). However, other taxonomic treatments have partitioned francolins into as many as eight genera (*Francolinus, Pternistis, Peliperdix, Scleroptila, Dendroperdix, Ortygornis*, *Acentrortyx*, and *Chaetopus*) (Roberts 1924, Chapin 1932, Peters 1934, Mackworth-Praed and Grant 1952, 1962, 1970, Hall 1963, Wolters 1975-82, Hockey et al. 2005). Nevertheless, virtually immediately after lumping francolins into a single genus, Hall (1963) hypothesized that all but four *Francolinus* spp. could be assigned to eight putatively monophyletic groups (Table 1.1).

Morphology and behaviour

Francolins, like many perdicine gamebirds, are characterized by having 14 tail feathers that are presumably moulted centrifugally (Johnsgard 1988). Some more partridge-like species of francolins are: relatively large, often have two (generally long) tarsal spurs (positioned about two-thirds down the tarsus), emit raucous grating or cackling advertisement calls (given mainly at dawn/dusk). They have been observed perching in trees or other elevated structures and have dark dorsal plumage vermiculated and/or striped with white or buff (Crowe et al. 1986, Milstein and Wolff 1987, Crowe et al. 1992). Other more quail-like francolins are relatively small, have at most one (generally short) tarsal spur (positioned about half-way down the tarsus), have relatively musical and whistling calls, generally roost on the ground, and have striped and barred rufous dorsal plumage resembling that of quails (*Coturnix* spp.) (Crowe et al. 1986, Milstein and Wolff 1987). This has led the Afrikaans-speaking people to group francolins into two supra-specific groupings; fisante (or pheasants) for the former and patryse (or partridges) for the latter (Milstein and Wolff 1987).

However, the above distinction was difficult to apply to the Crested Francolin, *Dendroperdix sephaena*, since it has attributes of both fisante and patryse. It is relatively small, has quail-like back plumage like patryse, but emits a raucous call, has well-spurred, red tarsi and roosts in trees like many fisante. Thus, it is a 'linking form' that persuaded Hall to lump all 41 species into a single genus *Francolinus*.

The tortuous taxonomic history of francolins

The genus *Francolinus* was first described by Stephens in 1819. Since that time, various taxonomic treatments and revisions have attempted to partition the francolins into two or more genera, a variable numbers of species and a plethora of subspecies (Table 1.2). However, Hall's (1963) monograph still remains the standard reference as far as the classification of francolins is concerned (Johnsgard 1988, Sibley and Monroe 1990, del Hoyo et al. 1994). Table 1.3 attempts to summarize the taxonomic chaos while Table 1.4 outlines the types of characters that have been used in various treatments.

Alternative taxonomic treatments

Roberts (1924), in his checklist of birds of South Africa, recognized six genera of francolins (Table 1.2):

1. ***Pternistis*** Wagler, 1832 -- the species *swainsonii*, *afer, humboldtii* and *castaneiventer* were recognized, the last of which was divided into three subspecies *castaneiventer, notatus* and *krebsi.*
2. ***Chaetopus*** Swainson, 1837 -- *capensis, adspersus* and *natalensis.*
3. ***Peliperdix*** Bonaparte, 1856 -- *hartlaubi*.

4. ***Dendroperdix*** Roberts, 1922 -- *rovuma* (recognized by most avian taxonomists as a subspecies) and *sephaena*.
5. ***Scleroptila*** Blyth, 1849 -- *afra* (= *afra*), *levaillantii*, *shelleyi* and *gariepensis* (= *levaillantoides*).
6. ***Ortygornis*** Reichenbach, 1853 -- *coqui*.

Roberts, in his first edition (1940) of 'The Birds of South Africa' followed the above-mentioned checklist, recognizing the same genera as in Roberts (1924), with just one change in which he erected the genus *Chapinortyx* Roberts, 1928 to distinguish the species *hartlaubi*. The same species as those in the 1924 checklist were retained, but additional subspecies were delineated. Within *Ortygornis coqui*, three subspecies were recognized (*coqui, campbelli, vernayi*); six within *Dendroperdix sephaena* (the nominate *sephaena, zuluensis, zambesiae, chobiensis, mababiensis, thompsoni*); and six within *Scleroptila levaillantoides* (*levaillantoides, gariepensis, ludwigi, pallidior, langi, kalaharica*). In addition to the above species, *Scleroptila jugularis* was delineated within which he recognized one subspecies *cunenensis*; four subspecies were recognized for *Pternistis swainsonii* (*swainsonii, damarensis, chobiensis, gilli*) and two subspecies for *Pternistis afer* (*afer, cunenensis*). A further subspecies *lehmanni*, was recognized for *Pternistis castaneiventer*.

In the 2nd edition of 'Roberts Birds of Southern Africa' (McLachlan and Liversidge 1957), the number of genera recognized was reduced to two (*Francolinus* and *Pternistis*). *Francolinus* was assigned to all partridges and fisante (including *hartlaubi* plus the three subspecies *hartlaubi, bradfieldi, crypticus*) that do not belong to

Hall's Bare-throated Group, whereas *Pternistis* was assigned strictly to the Bare-throated taxa (Table 1.2).

Even though the 1st and the 2nd editions covered the same geographic area, the delineation of taxa continued to vary with the lumping and splitting of previously recognized taxa and the erection of new taxa. This resulted in great inconsistency and instability in the number of taxa recognized. The following taxa were typically recognized: subspecies *coqui, vernayi,* with the addition of *hoeschianus* and the removal of *campbelli* within *F. coqui*; subspecies *mababiensis* and *chobiensis* were synonymized with *F. sephaena*; only five subspecies were recognized within *F. levaillantoides* (*levaillantoides, pallidior, langi, wattii* and *cunenensis* which was considered a subspecies of *S. jugularis*) leaving out *gariepensis, ludwigi, kalaharica;* subspecies *gilli* was synonymized with *swainsonii*; and *notatus, swynnertoni* and *humboldti* were atributed to *P. afer*. The subspecies *lehmanni* was removed from *P. castaneiventer.*

The 3rd and 4th (McLachlan and Liversidge 1970, 1978 respectively) editions were similar to the 2nd edition with regard to the taxa which were recognized. Subspecies *lundazi* was recognized as an additional subspecies of *P. swainsonii,* and *gilli* was re-considered, whereas *chobiensis* was synonymized with *swainsonii*. Subspecies *lehmanni* was re-considered as a valid subspecies of *P. afer*.

The 5th and the 6th editions (Maclean 1985, 1993 respectively) covered the southern African region and recognized the same set of species, the only major difference being that the 5th edition used the genus *Francolinus* for both patryse and fisante and that there was no mention of subspecies with the exception that it is indicated that *rovuma* was considered a subspecies of *D. sephaena*. The 6th edition made use of the genera *Francolinus* and *Pternistis* as in the previous editions and had the same composition of species as in the 4th edition.

The most recent 7th edition of Roberts' Birds of Southern Africa (Hockey et al. 2005), recognized four genera:

1. ***Peliperdix*** -- *coqui* within which they recognized the subspecies *coqui,* which included *campbelii, hoeschianus, lynesi, kasaicus, ruahdae, stuhlmanni, vernayi* and *angolensis.*
2. ***Dendroperdix*** -- *sephaena* comprised of *sephaena* which included the subspecies *zuluensis*, *rovuma* and *zambesiaie* (synonyms of which are *thompsoni*, *chobiensis* and *mababiensis*).
3. ***Scleroptila*** -- *afra*, *levaillantii, shelleyi* within which they recognized subspecies *shelleyi* (synonym *sequestris*) and *canidorsalis*; *levaillantoides* within which they recognized the subspecies *levaillantoides* (synonyms *ludwigi*, *langi* and *kalaharica*)*, jugularis* (synonyms *cunenensis* and *stresemanni*) and *pallidior* (synonym *wattii*).
4. ***Pternistis*** -- *hartlaubi, adspersus* (subspecies - *kalahari* and *mesicus*), *capensis*, *natalensis*, *afer* (subspecies - *afer*, *swynnertoni*, *castaneiventer*) and *swainsonii* (subspecies - *swainsonii* and *lundazi*).

Chapin (1932) divided francolins between two genera *Pternistis* and *Francolinus*:

1. ***Pternistis*** -- included the three species *afer*, *rufopictus* and *swainsonii*

2. ***Francolinus*** -- this genus was assigned to all the other francolins with the exception of *nahani*. *Francolinus nahani* was described by (Dubois, 1905) and moved to *Peliperdix* by van Someren (1926). During the same year, Chapin (1926) suggested *nahani* be placed in a monotypic genus, *Acentrortyx,* as he argued that this perdicine was not congeneric with *Francolinus*.

Peters (1934) recognized 39 species and split the francolins between two genera: *Francolinus* and *Pternistis*. However, he retained the use of the genus *Francolinus* in the broader sense, pending a detailed revision of all the species. Peters' deliniation of *Francolinus* included members of Hall's (1963) Spotted, Montane, Scaly, Vermiculated, Red-winged, Striated and Red-tailed Groups. The genus *Pternistis* was restricted to members of Hall's Bare-throated Group. He recognized '*schlegelii*' as a subspecies of *Francolinus coqui*. Another Peters' 'peculiarity' is that he elevated *Francolinus castaneicollis* '*atrifrons*' to full species status, whereas other authors considered this taxon a subspecies of *castaneicollis*.

Mackworth-Praed and Grant (1952, 1962, 1970) also recognized two genera:

1. ***Pternistis*** -- *rufopictus; leucoscepus* (subspecies *leucoscepus, infuscatus, muhamed-ben-abdullah, kilimensis*)*; swainsonii* (subspecies *swainsonii, damarensis, chobiensis, gilli*), and *afer* (subspecies *afer, cranchii, humboldtii, benguellensis, intercedens, castaneiventer, krebsi, swynnertoni, notatus, lehmanni, cunenensis, loangwae, harterti, nyanzae, leucoparaeus, bohmi, melanogaster, itigi*).

2. ***Francolinus*** -- *sephaena* (subspecies *sephaena, grantii, zambesiae*); *streptophora*; and *rovuma* (which they elevated to species, subspecies *rovuma* and *spilogaster*);

squamatus (subspecies *squamatus, schuetti, doni, maranensis, usambarae, uzungwensis, chyuluensis*); *griseostriatus* and *ahantensis* (subspecies *ahantensis, hopkinsoni*); *nobilis* (subspecies *nobilis, chapini*); *castaneicollis* (subspecies *castaneicollis, gofanus, ogoensis, atrifrons, kaffanus*); *jacksoni* (subspecies *jacksoni, gurae, pollenorum*); *erckelii* (subspecies *erckelii, pentoni*); *swierstrai*; *camerunensis*; *hildebrandti* (subspecies *hildebrandti, altumi, johnstoni*); *harwoodi; bicalcaratus* (subspecies *bicalcaratus, thornei, adamauae, ogilvie-granti, ayesha*); *clappertoni* (subspecies *clappertoni, gedgii, heuglini, cavei, sharpii, konigseggi, nigrosquamatus*); *icterorhynchus* (subspecies *icterorhynchus, emini*); *adspersus; capensis; natalensis* (subspecies *natalensis, neavei*); *hartlaubi* (subspecies *hartlaubi, bradfieldi, crypticus*); *coqui* (subspecies *coqui, angolensis, vernayi, hoeschianus, hubbardi, ruahdae, thikae, maharao, kasaicus, spinetorum*); *schlegelii; albogularis* (subspecies *albogularis, buckleyi, dewittei*); *finschi; levaillantoides* (subspecies *levaillantoides, gariepensis, jugularis, pallidior, ludwigi, langi, cunenensis, kalaharica, wattii*); *levaillantii* (subspecies *levaillantii, kikuyuensis, crawshayi, benguellensis, clayi*); *shelleyi* (subspecies *shelleyi, whytei, theresae, elgonensis, uluensis, macarthuri*); *afer* (= *africanus* = *afra*) and the unplaced *nahani* and *lathami* (subspecies *lathami, schubotzi*).

Mackworth-Praed and Grant (1952, 1962, 1970) demonstrate the taxonomic problems created by their variable use of the name '*afer*' at both the specific and subspecific level: '*afer*' was used in their 1952 publication to refer to Grey-winged Francolin, currently deliniated as *Scleroptila afra* (they described this species' distribution as ranging from the Cape to Ethiopia, but with interruptions) and '*cranchii*' for Red-necked Spurfowl currently *Pternistis afer*. The Red-necked Spurfowl is widely distributed in the lowlands of central and east Africa, from Gabon, western Angola, northwest Namibia, and Zimbabwe to South Africa. However, in 1962 they used '*afer*' for both the Grey-winged Francolin and Red-necked Spurfowl. Currently, the specific name '*afer*' is used for Red-necked Spurfowl *Pternistis afer* whereas '*africanus/afra*' is used for the Grey-winged Francolin *Scleroptila afra*.

Furthermore, within the Grey-winged Francolin (presently considered a South African and Lesotho endemic – Clancey 1986, Sinclair and Ryan 2003), Mackworth-Praed and Grant (1952, 1962, 1970) included several taxa which occur in sub-Saharan Africa. These were *uluensis, lorti, gutturalis, psilolaema, ellenbecki, archeri, friedmanni, marcathuri* and *stantoni*. Other authors (Table 1.2) assigned *uluensis* and *macarthuri* to Shelley's Francolin *F. shelleyi*, and *gutturalis, archeri* and *friedmanni* to the Orange River francolin *F. levaillantoides*. While they considered *psilolaema* a subspecies of Grey-winged Francolin, other authors (Table 1.2) recognized this taxon to be a full species of the Red-winged Group with *ellenbecki* being one of its subspecies.

Wolters (1975-82) proposed the first cladistic system of genera and subgenera for francolins in which he recognized Hall's (1963) 41 species. He recognized six genera:

1. ***Francolinus*** -- this genus included Hall's Spotted taxa *francolinus, pintadeanus, pictus* and her unplaced *gularis,* with *francolinus, pintadeanus, pictus* (except *gularis*) lumped into a subgenus, *Francolinus gularis* was not assigned to any subgenus.
2. ***Pternistis*** -- Hall's Bare-throated *leucoscepus, rufopictus, swainsonii* and *afer* (all placed in the subgenus *Pternistis*) as well as the Montane species *erckelii,*

ochropectus, *castaneicollis*, *jacksoni*, *camerunensis* and *swierstrai* (not placed in any subgenus), the Scaly *squamatus,* g*riseostriatus* and *ahantensis* (no subgenus), *adspersus* and *capensis* (without subgenus). Wolters also assigned *nahani* to genus *Pternistis,* placing it in subgenus *Acentrortyx* following Chapin (1926). Also, placed in the genus *Pternistis* were the Vermiculated *natalensis, hildebrandti, harwoodi, hartlaubi, bicalcaratus, icterorhynchus* and *clappertoni,* all within the subgenus *Chaetopus*.

3. ***Scleroptila*** -- Hall's Red-winged *afra* (= *africanus*)*, finschi, shelleyi, psilolaema, levaillantii* and *levaillantoides.*
4. ***Dendroperdix*** -- Hall's Striated *sephaena* and *streptophora*.
5. ***Peliperdix*** -- Hall's Red-tailed *albogularis, schlegelii, coqui* and the unplaced *lathami.*
6. ***Ortygornis*** -- this genus was assigned to the unplaced *pondicerianus*.

Crowe and Crowe (1985) questioned, but did not refute, the monophyletic status of the genus *Francolinus* as defined in Hall (1963). However, they retained this genus for all the species and suggested a system of subgenera as follows: subgenus '*Francolinus*' included the Spotted species *francolinus, pictus, pintadeanus;* '*Ortygornis*' was assigned to the unplaced *pondicerianus*; '*Scleroptila*' for all the Red-winged species *finschi, levaillantii, afra, psilolaema, shelleyi,* and *levaillantoides* that also incorporated one species from Hall's Striated Group *streptophora*; '*Peliperdix*' for the unplaced *lathami*; '*Dendroperdix*' for the Striated *sephaena*; '*Pternistis*' for the Bare-throated *afer, swainsonii, leucoscepus* and *rufopictus;* and the subgenus '*Acentrortyx*' for *nahani*. Within the subgenus *Peliperdix,* they assigned only *lathami*.

No subgenera were assigned to *coqui, albogularis, schlegelii, gularis, griseostriatus, ahantensis, squamatus, adspersus, hildebrandti, natalensis, hartlaubi, capensis, castaneicollis, jacksoni, erckelii, ochropectus, nobilis, camerunensis, swierstrai, harwoodi, icterorhynchus, clappertoni* and *bicalcaratus*.

Crowe and Crowe (1985) also modified Hall's (1963) classification, by suggesting that *F. streptophora* should be moved from the Striated to the Red-winged Group based on the cladistic analysis of organismal characters. They further maintained that the two Montane Group species *F. camerunensis* and *F. swierstrai* form a second superspecies (= a set of species with ranges that do not overlap) within the Montane Group. However, they supported Hall's suspicion that *lathami* has affinities with members of the Red-tailed Group whereas *nahani* was thought to have affinities with members of the Scaly Group.

Milstein and Wolff (1987) adopted Wolters' (1975-82) classification system in their work on the southern African francolins; they formally recognized the genus '*Pternistis*' which included the Bare-throated species *swainsonii* and *afer,* and the Vermiculated *adspersus, capensis* and *natalensis*. They assigned the genus '*Scleroptila*' to the Red-winged *afra, shelleyi, levaillantoides,* and *levaillantii* whereas '*Peliperdix*' and '*Dendroperdix'* were assigned to a Red-tailed species *coqui* and the Striated species *sephaena,* respectively.

Despite all this taxonomic debate, Crowe et al. (1986) and Sibley and Monroe (1990) recognized only one genus '*Francolinus*' with 41 species within it. They recognized subspecies *francolinus*, *arabistanicus*, *henrici*, *asiae*, *melanonotus* within *F. francolinus*; *pallidus, pictus, watsoni* within *F. pictus*; *phayrei, pintadeanus* within *F. pintadeanus*; *pondicerianus, mecranensis, interpositus* within *F. pondicerianus*. *Francolinus gularis* was recognized as a monotypic species. *Francolinus lathami* consisted of two subspecies, *lathami* and *schubotzi*. Four subspecies were recognized within *F. coqui* (*spinetorum, maharao, hubbardi*, *coqui*) with *thikae* being included in *maharao*; *buckleyi* in *spinetorum*; *angolensis, campbelli, ruahdae, lynesi, vernayi, hoeschianus* and *kasaicus* were all included in the nominate *coqui*.

Three subspecies *albogularis, buckleyi* and *dewittei* were recognized within *F. albogularis*. *Francolinus schlegelii, F. streptophora, F. afra, F. finschi* and *F. nahani* were recognized as monotypic species. Two subspecies, *kikuyuensis* and *levaillantii* were recognized within *F. levaillantii*; subspecies *shelleyi* (which included *uluensis, canidorsalis, sequestris)* and *whytei* were recognized within *F. shelleyi*; *psilolaema* (which included *ellenbecki*) and *elgonensis* (included *theresae*) within *F. psilolaema*; *gutturalis, lorti* (which included *archeri*), *jugularis* (which included *cunenensis*), *levaillantoides* (which included *pallidior, kalaharica*) within *F. levaillantoides; sephaena, rovuma, spilogaster*, *zambesiae* and *grantii* were recognized within *F. sephaena*. *Francolinus squamatus, F. ahantensis, F. griseostriatus, F. hartlaubi, F, icterorhynchus, F. clappertoni, F. harwoodi, F. adspersus, F. capensis, F. natalensis, F. hildebrandti*, *F. leucoscepus, F. rufopictus* were all recognized as monotypic species. The two subspecies *ayesha* and *bicalcaratus* were recognized for *F. bicalcaratus.*

Francolinus swierstrai, F. camerunensis, F. nobilis, F. jacksoni, F. ochropectus, F. erckelii were recognized as monotypic species. Two subspecies were recognized within *F. castaneicollis*, *castaneicollis* (which included *bottegi, ogoensis, kaffanus,* *gofanus*) and *atrifrons*; *lundazi* and *swainsonii* (included *damarensis, chobiensis, gilli)* within *F. swainsonii; harterti, afer, cranchii* (*intercedens*), *leucoparaeus, melanogaster* (included *loangwae), swynnertoni* and *castaneiventer* (included *notatus, lehmanni*) were recognized within *F. afer*.

Crowe et al. (1992) again challenged the status of monophyly of *Francolinus* and proposed a system of genera and subgenera. Genus '*Francolinus*' included the Spotted *pictus, francolinus, pintadeanus* and were all placed in the subgenus *Francolinus*; the unplaced *pondicerianus* was then placed in the subgenus *Ortygornis* and *gularis* in the subgenus *Limnocolinus* (nov.). Genus '*Peliperdix'* included the Red-tailed *coqui, albogularis* and *schlegelii,* and the unplaced *lathami*, were all placed in the subgenus *Peliperdix*; the Striated species *sephaena* was assigned to subgenus *Dendroperdix,* but placed in genus *Peliperdix*. Genus '*Scleroptila'* included the Striated species *streptophora* and the Red-winged *finschi, levaillantii, afra, psilolaema, shelleyi,* and *levaillantoides*.

The genus '*Pternistis'* included *nahani* which was placed in the subgenus *Acentrortyx*; the Vermiculated *hartlaubi* was placed in subgenus *Chapinortyx*; the other Vermiculated species such as *bicalcaratus, icterorhynchus, clappertoni* and *harwoodi* were placed in subgenus *Chaetopus*; the balance of the Vermiculated Group, *adspersus, capensis, natalensis, hildebrandti* were placed in subgenus *Notocolinus* (nov.); the Scaly *squamatus, ahantensis,* and *griseostriatus* were placed in subgenus *Squamatocolinus*; the Bare-throated *leucoscepus, rufopictus, afer, swainsonii* in subgenus *Pternistis*; the Montane *jacksoni, nobilis, camerunensis, swierstrai, castaneicollis, erckelii, ochropectus* were all placed in subgenus *Oreocolinus* (nov.).

Despite the newly proposed taxonomic classification, del Hoyo et al. (1994) followed Hall's (1963) classification system and adopted the genus *Francolinus* (*sensu lato*) for all the species, but did not comment on its monophyly. del Hoyo's species and subspecies delineations were similar to those in Crowe et al. (1986) with the exception that no subspecies were attributed to *castaneiventer*.

Dickinson (2003) did not deviate much from Crowe et al. (1986) with regard to genera, species and subspecies that were recognized. He attributed 41 species to the genus genus *Francolinus*. Within *F. francolinus*, subspecies *francolinus* (which included *billypayni), arabistanicus, bogdanovi* (included *festinus*), *henrici, asiae* (including *parkerae*), *melanonotus* were recognized; *pallidus, pictus, watsoni* were delineated within *F. pictus*; *phayrei, pintadeanus* within *F. pintadeanus*; *pondicerianus* (included *ceylonensis*), *mecranensis, interpositus* (included *prepositus*) within *F. pondicerianus*. *Francolinus gularis* (which included *ridibundus*) and *F. lathami* were recognized as monotypic species. Four subspecies were recognized within *F. coqui* (*spinetorum, maharao, hubbardi, coqui*) with *thikae* being included in *maharao*; *angolensis, campbelli, ruahdae, lynesi, vernayi, bourqoii, hoeschianus* and *kasaicus* were all included in the nominate *coqui*. The taxa *albogularis, buckleyi, dewittei* (included *meinertzhageni*) were recognized within *F. albogularis; F. schlegelii* (included *confusus*); *F. streptophora; F. afra* (which included *proximus*)*; F. finsch; F. griseostriatus* and *F. nahani* were recognized as monotypic species.

Three subspecies *kikuyuensis* (which included *benguellensis, clayi), crawshayi*, and *levaillantii* were recognized within *F. levaillantii*; subspecies *shelleyi* (which included *uluensis, canidorsalis, sequestris)* and *whytei* within *F. shelleyi*; *psilolaema* (which included *ellenbecki*) and *elgonensis* (included *theresae*) within *F. psilolaema*; *gutturalis* (included *eritreae*), *archeri* (included *friedmanni, stantoni*), *lorti, jugularis* (included *cunenensis, stresemanni*), *pallidior* (included *wattii)* and *levaillantoides* (included *kalaharicus)* within *F. levaillantoides; sephaena* (included *zuluensis), rovuma, spilogaster* (included *somaliensis*), *zambesiae* (included *thompsoni)* and *grantii* were recognized within *F. sephaena*; *squamatus* (included *whytei*), *schuetti* (included *tetraoninus*), *zappeyi, maranensis* (included *chyuluensis*), *usambarae, uzungwensis* and *doni* within *F. squamatus*; *hopkinsoni* and *ahantensis* were recognized within *F. ahantensis*; *F. hartlaubi* was represented by three subspecies (*hartlaubi, bradfieldi, crypticus*); *altumi, hildebrandti* (included *helleri, fischeri*), *johnstoni* (included *grotei*) within *F. hildebrandti; natalensis* (included *thamnobium*) and *neavei* within *F. natalensis; ayesha, bicalcaratus* (which included *adamauae*), *thornei* and *ogilviegranti* (included *molunduensis*) within *F. bicalcaratus; clappertoni, sharpii, heuglini, konigseggi, gedgii* (included *cavei*) and *nigrosquamatus* (included *testis*) within *F. clappertoni; F. harwoodi; F. capensis; F. swierstrai; F. camerunensi; F. nobilis* (included *chapini*)*; F. jacksoni* (included *pollenorum*)*; F. ochropectus; F. erckelii; F. rufopictus* and *F. leucoscepus* were recognized as monotypic species. Two subspecies were recognized within *F. adspersus*, *adspersus* (included *kalahari*) and *mesicus*; *castaneicollis* (included *bottegi, gofanus*), *ogoensis, kaffanus* (included *patrizii*) and *atrifrons* within *F. castaneicollis; lundazi* and *swainsonii* (included *damarensis, gilli*) within *F. swainsonii; harterti, afer* (included *chio, palliditectus*), *cranchii* (*boehmi, punctulatus, benguellensis, intercedens, nyanzae, itigi*), *leucoparaeus, melanogaster* (included *loangwae, aylwinae, tertius*) *swynnertoni* and *castaneiventer* (included *notatus*) were recognized within *F. afer*.

Phylogenetics

Hall (1963) presented the first phylogenetic hypothesis for francolins (Fig. 1.1). Bloomer and Crowe (1998) provided the first DNA-based evidence (Fig. 1.2) to suggest a lack of monophyly for *Francolinus* as circumscribed by Hall, but offered no taxonomic recommendations. However, their molecular phylogeny provided support for splitting the francolins into what is today referred as two distinct clades, the 'francolins' and 'spurfowls'.

Highlights of some key taxonomic disagreements:

- It is clear that taxonomic confusion exists, not just among taxonomists, but also between taxonomists and gamebird enthusiasts and hunters. Mackworth-Praed and Grant (1952, 1962, 1970) in all their reviews, split francolins into what they called 'francolins' and 'spurfowls'. They assigned the genus *Pternistis* to the spurfowl taxa belonging to Hall's (1963) Bare-throated Group, and the genus *Francolinus* to all African francolins including the balance of the spurfowl groups identified in Hall's monograph (Table 1.1). The results of Bloomer and Crowe (1998) led to the split of francolins into two major lineages (Fig. 1.2) which they called the quail-francolin (or partridges)' and partridge-francolin (or pheasants) clades. The common names francolin and spurfowl will be used hereafter, since Bloomer and Crowe (1998) found them to be evolutionarily distantly-related from each other.

- The evolutionary affinities of the Crested Francolin *Ortygornis sephaena* have been debated given its possession of features that are found in both francolins and spurfowls. Hall (1963) considered this species to be a 'linking form' and as a consequence placed all 41 species into a single genus *Francolinus*.

- Confusion has surrounded the number of genera recognized among francolins and spurfowls. The earlier revisions (Roberts 1924, 1940) included seven genera (*Pternistis, Chaetopus*, *Peliperdix, Chapinortyx, Dendroperdix, Scleroptila, Ortygornis*), which were reduced to either two (*Francolinus* and *Pternistis*) in Chapin (1932), Peters (1934), Mackworth-Praed and Grant (1952), McLachlan and Liversidge (1957), Mackworth-Praed and Grant (1962), Mackworth-Praed and Grant (1970), McLachlan and Liversidge (1970) or just one genus *Francolinus* (Crowe and Crowe 1985, Maclean 1985, Crowe et al. 1986, Maclean 1993) in several later revisions (Table 1.3). More recently, Crowe et al. (1992) suggested that some earlier genera were indeed valid (*Francolinus, Dendroperdix, Peliperdix, Scleroptila* and *Pternistis*). It should be noted that based on Crowe et al. (2006) and the results emanating from this study, the number of genera recognized within ‘francolins’ might see an increase, but are expected to remain stable beyond the completion of this study.

- The lack of stability and consistency in the subspecies recognized and several revisions of the species complexes, even when similar evidence and geographic areas were covered, has clearly demonstrated the profound difficulties with respect to using morphological characters to delineate taxa.

- *Francolinus nahani* has remained something of an enigma among francolins/spurfowl with a great deal of uncertainty pertaining to its phylogenetic placement. Van Someren (1926) proposed the genus *Peliperdix* for this species, and Chapin (1926) had during the same year proposed to move *nahani* to the genus *Acentrortyx*. Chapin argued that this partridge was not congeneric with the type species of the genus of francolins *Francolinus francolinus*. However, subsequent revisions placed this species back in the genus *Francolinus* (Peters 1934, Hall 1963, Mackworth-Praed and Grant 1970). Wolters (1975-82) and Crowe et al. (1992) placed *nahani* within the genus *Pternistis* in subgenus *Acentrortyx*. Most recently *nahani* has been moved from *Francolinus* to '*Ptilopachus*', a clade of two taxa, the other being the Stone Partridge *Ptilopachus petrosus* which intriguingly forms the sister clade to New World quails Odontophoridae (Crowe et al. 2006, Cohen et al. 2012).

The genus *Francolinus* - African or Asian in origin?

The geographical origin of the genus '*Francolinus*' has remained controversial (Hall 1963, Crowe and Crowe 1985). Two hypotheses are postulated. The first based on the suggestion that the genus *Francolinus* shares its closest affinities with other Palaearctic and Asian genera. Hall (1963) strongly argued for the genus to be of Asian origin with its age being traced back to the Oligocene +-25-35. She further alluded to reduced competition as being the driving factor for the speciation of francolins in Africa. Although Crowe and Crowe (1985) concurred with Hall that the ancestor was quail-like, they hypothesized an African origin for the genus, with Asia being colonized by a nomadic or migratory ancestor that diversified and became sedentary. The reported age of the divergence francolins from Old World quail *Coturnix* spp. was traced to the Pliocene (approx. 4.5-5 mya) using Shields and Wilson's (1987) calibration of 2% divergence per million years (Crowe 1992). Bloomer and Crowe (1998) recovered a divergence date between the quail versus the partridge-like lineages at 5 and 8 mya, whereas the transversion rate from suggested a divergence time of 3-6 mya using the using Shields and Wilson's (1987) conventional calibration of 2% per million years implemented on mitochondrial Cytochrome-*b* data. They believe that the minimum divergence estimates appear to be corroborated by the availability of well-differentiated francolin fossils (Crested Francolin *Ortygornis sephaena*; Crowe 1992). However, as hinted at (although not actually calculated) in Crowe et al. (2006), the divergence of francolins and spurfowl may be considerably older.

Conclusions

The taxonomic review detailed above demonstrates that the confusion over the number of genera and terminal taxa of francolins and spurfowls is profound and that what is needed are characters from a range of sources that can provide solid and objective explanations for every taxonomic decision that is taken. This is especially important given the enormous morphological variation observed within certain species complexes, which has generated considerable debate with respect to the delimitation of species and subspecies. Defensible and robust analytical methods and approaches also need to be adopted to enable objective conclusions to be drawn.

The major aims of this study

On the basis of the confusion/disagreement/hypotheses outlined above regarding: (1) debate on the monophyly of the genus '*Francolinus*', (2) the monophyly and evolutionary relationships of, and within the different species-groups suggested by Hall (1963), (3) the instability/inconsistency of the number of terminal taxa (species, subspecies and genera) recognized, and (4) the dispute on where the *Francolinus* clade first diversified – Africa or Asia - this study aimed at achieving the following:

1. To undertake a general review of the taxonomy of ‘francolins’ (taking views largely – but not exclusively – of Mackworth-Praed and Grant (1952, 1962, 1970) and Hall 1963 as alternative hypotheses) **[Chapter 1]**.
2. To contrast alternative hypotheses concerning the monophyly of the genus ‘*Francolinus*’ (e.g. Hall 1963 versus Bloomer and Crowe 1998) and to further explore DNA-based, vocalization and behavioural evidence in order to test the phylogenetic affinities of the Stone Partridge *Ptilopachus petrosus* and Nahan’s Francolin *Francolinus nahani* as suggested in Crowe et al. (2006) [**Chapter 2]**.
3. To investigate if there are any syringeal features (anatomical) that can be used to further our understanding of the phylogenetic relationships among francolins and spurfowls **[Chapter 3]**.
4. To test the validity of the francolin-spurfowl taxonomic dichotomy based on vocal characters **[Chapter 4]**.
5. To test Hall’s (1963) hypotheses on the monophyly of the suggested eight species groups within her circumscription of the the genus *Francolinus*, and thereby provide a modern systematic revision of the terminal taxa and genera of francolins and spurfowls **[Chapter 5 & 6]**.
6. To describe and explore patterns of distribution of francolins and spurfowls, using Hall’s (1963) monograph as a null hypothesis **[Chapter 7]**.

Tables and Figures

Table 1.1. List of francolin and spurfowl species and their designated species groups recognized by Hall (1963). English and specific names are as proposed in the IOC list (Gill and Donsker 2013) and the generic classification follows Crowe et al. (2006) and Mandiwana-Neudani, this thesis. Genus *Francolinus* Stephens, 1819, *Peliperdix* Bonaparte, 1856, *Scleroptila* Blyth, 1849, *Dendroperdix* Roberts, 1922, *Ortygornis* Reichenbach, 1852, *Pternistis* Wagler, 1832, *Chaetopus* Swainson, 1837, *Afrocolinus* gen. nov. Mandiwana-Neudani, this thesis. Taxon authority citation with a year in parentheses indicates that either the specific or the subspecific epithet was originally published in another genus by the first author, but moved to the present genus by the second revising author.

Species group	English name	Scientific name
1. Spotted	Black Francolin	*Francolinus francolinus* (Linnaeus, 1766)
	Painted Francolin	*F. pictus* (Jardine & Selby, 1828)
	Chinese Francolin	*F. pintadeanus* (Scopoli, 1786)
2. Bare-throated	Red-necked Spurfowl	*Pternistis afer* (Müller, 1776)
	Swainson's Spurfowl	*P. swainsonii* (Smith, 1836)
	Yellow-necked Spurfowl	*P. leucoscepus* (Gray, 1867)
	Grey-breasted Spurfowl	*P. rufopictus* Reichenow, 1887
3. Montane	Erckel's Spurfowl	*P. erckelii* (Rüppell, 1835)
	Djibouti Spurfowl	*P. ochropectus* (Dorst & Jouanin, 1952)
	Chestnut-naped Spurfowl	*P. castaneicollis* Salvadori, 1888
	Jackson's Spurfowl	*P. jacksoni* O. Grant, 1891
	Handsome Spurfowl	*P. nobilis* Reichenow, 1908
	Mount Cameroon Spurfowl	*P. camerunensis* Alexander, 1909
	Swierstra's Spurfowl	*P. swierstrai* (Roberts, 1929)
4. Scaly	Ahanta Spurfowl	*P. ahantensis* Temminck, 1854
	Scaly Spurfowl	*P. squamatus* Cassin, 1857
	Grey-striped Spurfowl	*P. griseostriatus* O. Grant, 1890
5. Vermiculated	Double-spurred Spurfowl	*P. bicalcaratus* (Linnaeus, 1766)
	Heuglin's Spurfowl	*P. icterorhynchus* Heuglin, 1863
	Clapperton's Spurfowl	*P. clappertoni* (Children & Vigors, 1826)
	Hildebrandt's Spurfowl	*P. hildebrandti* Cabanis, 1878
	Natal Spurfowl	*P. natalensis* Smith, 1833

Species group	English name	Scientific name
	Hartlaub's Spurfowl	*P. hartlaubi* Bocage, 1869
	Harwood's Spurfowl	*P. harwoodi* Blundell & Lovat, 1899
	Red-billed Spurfowl	*P. adspersus* Waterhouse, 1838
	Cape Spurfowl	*P. capensis* (Gmelin, 1789)
6. Striated	Crested Francolin	*Ortygornis sephaena* (Smith, 1836)
	Ring-necked Francolin	*Scleroptila streptophora* O. Grant, 1891
7. Red-winged	Shelley's Francolin	*Scleroptila shelleyi* O. Grant, 1890
	Grey-winged Francolin	*S. afra* (Latham, 1790)
	Orange River Francolin	*S. levaillantoides* Smith, 1836
	Red-winged Francolin	*S. levaillantii* (Valenciennes, 1825)
	Finsch's Francolin	*S. finschi* Bocage, 1881
	Moorland Francolin	*S. psilolaema* Gray, 1867
8. Red-tailed	Coqui Francolin	*Peliperdix coqui* (Smith, 1836)
	White-throated Francolin	*P. albogularis* Hartlaub, 1854
	Schlegel's Francolin	*P. schlegelii* Heuglin, 1863
Unplaced species		
	Latham's Francolin	*Afrocolinus lathami* Hartlaub, 1854
	Swamp Francolin	*Ortygornis gularis* (Temminck, 1815)
	Grey Francolin	*O. pondicerianus* (Gmelin, 1789)
	Nahan's Francolin	*Francolinus 'Ptilopachus' nahani* (Dubois, 1905)

Table 1.2. Summary of the taxonomic designations from selected revisions pertaining to francolins, detailed according to putative super-species group, genera, species and subspecies. Fran - Genus *Francolinus* Stephens, 1819, Peli - *Peliperdix* Bonaparte, 1856, Scler - *Scleroptila* Blyth, 1849, Dend - *Dendroperdix* Roberts, 1922, Orty - *Ortygornis* Reichenbach, 1852, Pter - *Pternistis* Wagler 1832, Chae - *Chaetopus* Swainson, 1837, *Afrocolinus* gen. nov. (this thesis).

n/a denotes taxa not investigated (i.e. either falling outside the geographic region covered or taxa not being of interest), **+** denotes taxa recognized, - denotes taxa not recognized, **~** denotes taxa lumped/synonymized with others.

Putative genera - ~8, Putative species - ~41, Putative subspecies - ~164.

Taxon authority citation with a year in parentheses indicates that either the specific or the subspecific epithet was originally published in another genus by the first author, but moved to the present genus by the second revising author.

Putative species and subspecies	Roberts (1924)	Hockey et al. (2005)	Peters (1934)	Mack-worth-Praed & Grant (1952,62,70)	Hall (1963)	Wolters (1975-82)	Mandiwana-Neudani (this study)
Genera							
Spotted Group	***n/a***	***n/a***	***Fran***	***n/a***	***Fran***	***Fran***	***Fran***
Species							
francolinus							
subspecies							
francolinus (Linnaeus, 1766)	n/a	n/a	+	n/a	+	+	+
arabistanicus Zarudny & Härms, 1913	n/a	n/a	+	n/a	+	-	n/a
bogdanovi Zarudny, 1906	n/a	n/a	+	n/a	-	-	n/a
henrici Bonaparte, 1856	n/a	n/a	+	n/a	+	-	n/a
asiae Bonaparte, 1856	n/a	n/a	+	n/a	+	+	n/a
melanotus Hume, 1888	n/a	n/a	+	n/a	+	+	n/a
pictus							
pictus (Jardine & Selby, 1828)	n/a	n/a	+	n/a	+	+	+
pallidus (Gray, 1831)	n/a	n/a	+	n/a	+	-	n/a
watsoni Legge, 1880	n/a	n/a	-	n/a	+	-	n/a
pintadeanus							
pintadeanus (Scopoli, 1786)	n/a	n/a	+	n/a	+	+	+
phayrei (Blyth, 1843)	n/a	n/a	+	n/a	+	+	n/a

Putative species and subspecies	Roberts (1924)	Hockey et al. (2005)	Peters (1934)	Mack-worth-Praed & Grant (1952,62,70)	Hall (1963)	Wolters (1975-82)	Mandiwana-Neudani (this study)
				Genera			
Striated Group	***Dend***	***Dend***	***Fran***	***Fran***	***Fran***	***Dend***	***Orty/Scler***
sephaena							
sephaena (Smith, 1836)	+	+	+	+	+	+	+
spilogaster Salvadori, 1888	n/a	n/a	+	+	+	+	+
somaliensis Grant & Praed, 1934	n/a	n/a	-	-	-	-	~
schoanus Heuglin, 1873	n/a	n/a	+	-	-	-	~
jubaensis Zedlitz, 1913	n/a	n/a	+	-	-	-	~
grantii Hartlaub, 1866	n/a	n/a	+	+	+	+	+
rovuma Gray, 1867	+	+	+	+	+	+	+
zambesiae Praed, 1920	+	+	+	+	+	-	~
chobiensis Roberts, 1932	+	~	+	-	-	-	~
thompsoni Roberts, 1924	+	~	~	-	-	-	~
zuluensis Roberts, 1924	+	~	~	-	-	-	~
mababiensis Roberts, 1932	-	~	~	-	-	-	~
streptophora							
streptophora O. Grant, 1891	n/a	n/a	+	+	+	+	+
Red-tailed Group	***Orty***	***Peli***	***Fran***	***Fran***	***Fran***	***Peli***	***Peli***
coqui							
coqui (Smith, 1836)	+	+	+	+	+	+	+
spinetorum Bates, 1928	n/a	n/a	+	+	+	+	+
buckleyi Peters, 1934	n/a	n/a	+	+	-	-	~
maharao Sclater, 1927	n/a	n/a	+	+	+	-	+
ruahdae Someren, 1926	n/a	~	+	+	+	-	+
hubbardi O. Grant, 1895	n/a	-	+	+	+	-	+
angolensis Rothschild, 1902	n/a	~	+	+	+	-	~
lynesi Sclater, 1932	n/a	~	+	-	-	-	~
vernayi (Roberts, 1932)	n/a	~	+	+	+	-	+
campbelli (Roberts, 1928)	-	~	+	-	-	-	~
thikae Grant & Praed, 1934	n/a	n/a	-	+	+	-	~
kasaicus White, 1945	n/a	~	-	+	+	-	+
hoeschianus Stresemann, 1937	n/a	~	-	+	+	-	~
stuhlmanni Reichenow, 1889	n/a	~	~	-	-	-	+
schlegelii							
schlegelii Heuglin, 1863	n/a	n/a	+	+	+	+	+
albogularis							
albogularis Hartlaub, 1854	n/a	n/a	+	+	+	+	+
buckleyi O. Grant, 1892	n/a	n/a	-	+	+	+	+
dewittei Chapin, 1937	n/a	n/a	-	+	+	+	+
meinertzhageni White, 1944	n/a	n/a	-	+	+	+	~
gambagae (Praed, 1920)	n/a	n/a	+	-	-	-	~

Putative species and subspecies	Roberts (1924)	Hockey et al. (2005)	Peters (1934)	Mack-worth-Praed & Grant (1952,62,70)	Hall (1963)	Wolters (1975-82)	Mandiwana-Neudani (this study)
				Genera			
Red-winged Group	***Scler***	***Scler***	***Fran***	***Fran***	***Fran***	***Scler***	***Scler***
psilolaema							
psilolaema Gray, 1867	n/a	n/a	+	+	+	+	+
ellenbecki Erlanger, 1905	n/a	n/a	+	+	~	+	+
elgonensis O. Grant, 1891	n/a	n/a	+	+	~	+	~
theresae Meinertzhagen, 1937	n/a	n/a	-	+	~	+	+
shelleyi							
shelleyi O. Grant, 1890	+	+	+	+	+	+	+
uluensis O. Grant, 1892	n/a	n/a	+	+	+	-	+
whytei Neumann, 1908	n/a	-	+	+	+	-	+
macarthuri Someren, 1938	n/a	n/a	-	+	~	-	~
trothae Reichenow, 1901	n/a	n/a	+	-	-	-	~
sequestris Clancey, 1960	-	~	-	-	-	-	~
canidorsalis (Lawson, 1963)	-	~	-	-	-	-	~
afra							
afra (Latham, 1790)	+	+	+	+	+	+	+
levaillantoides							
levaillantoides Smith, 1836	+	+	+	+	+	+	+
kalaharica Roberts, 1932	n/a	~	~	+	+	-	~
pallidior Neumann, 1908	n/a	+	+	+	+	-	+
langi Roberts, 1932	n/a	~	+	+	-	-	~
wattii Macdonald, 1953	n/a	~	-	+	-	-	~
jugularis Büttikorfer, 1889	n/a	+	+	+	+	+	+
cunenensis Roberts, 1932	n/a	~	~	+	-	-	~
stresemanni Hoesch & Niethammer, 1940	n/a	~	-	-	-	-	~
gutturalis (Rüppell, 1835)	n/a	n/a	+	+	+	+	+
lorti Sharpe, 1897	n/a	n/a	+	+	+	+	~
archeri Sclater, 1927	n/a	n/a	+	+	+	+	~
ludwigi Neumann, 1920	+	~	+	-	-	-	~
levaillantii							
levaillantii (Valenciennes, 1825)	+	+	+	+	+	+	+
kikuyuensis O. Grant, 1897	n/a	n/a	+	+	+	-	+
crawshayi O. Grant, 1896	n/a	-	+	+	+	-	+
benguellensis Neumann, 1908	n/a	-	+	+	-	-	~
clayi White, 1944	n/a	-	-	+	-	-	~
finschi							
finschi Bocage, 1881	n/a	n/a	+	+	+	+	+

Putative species and subspecies	Roberts (1924)	Hockey et al. (2005)	Peters (1934)	Mack-worth-Praed & Grant (1952,62,70)	Hall (1963)	Wolters (1975-82)	Mandiwana-Neudani (this study)
			Genera				
Vermiculated Group	***Chae/Peli***	***Pter***	***Fran***	***Fran***	***Fran***	***Pter***	***Pter***
hartlaubi							
hartlaubi Bocage, 1869	+	+	+	+	+	+	+
crypticus Stresemann, 1939	n/a	-	-	+	~	-	~
bradfieldi (Roberts, 1928)	n/a	-	+	+	~	-	~
ovambensis (Roberts, 1928)	n/a	-	+	-	-	-	~
adspersus							
adspersus Waterhouse, 1838	+	+	+	+	+	+	+
kalahari de Schauensee, 1931	-	~	+	-	-	-	~
mesicus Clancey, 1996	-	+	-	-	-	-	~
capensis							
capensis (Gmelin, 1789)	+	+	+	+	+	+	+
natalensis							
natalensis Smith, 1833	+	+	+	+	+	+	+
neavei Praed, 1920	-	-	+	+	+	-	~
hildebrandti							
hildebrandti Cabanis, 1878	n/a	n/a	+	+	+	+	+
altumi Fischer & Reichenow, 1884	n/a	n/a	+	+	+	+	~
helleri Mearns, 1915	n/a	n/a	+	-	-	-	~
fischeri Reichenow, 1887	n/a	n/a	+	-	-	-	+
johnstoni Shelley, 1894	n/a	n/a	+	+	+	+	~
grotei Reichenow, 1919	n/a	n/a	+	-	-	-	~
bicalcaratus							
bicalcaratus (Linnaeus, 1766)	n/a	n/a	+	+	+	+	+
ogilvie-grantii Bannerman, 1922	n/a	n/a	+	+	+	-	~
ayesha Hartert, 1917	n/a	n/a	+	-	+	-	~
adamauae Neumann, 1915	n/a	n/a	+	+	+	-	+
thornei Ogilvie-Grant, 1902	n/a	n/a	+	+	+	-	~
icterorhynchus							
icterorhynchus Heuglin, 1863	n/a	n/a	+	+	+	+	+
dybowski Oustalet, 1892	n/a	n/a	+	-	+	+	~
ugandensis Neumann, 1907	n/a	n/a	+	-	-	-	~
emini Neumann, 1907	n/a	n/a	~	+	-	-	~
clappertoni							
clappertoni (Children & Vigors, 1826)	n/a	n/a	+	+	+	+	+
sharpii Ogilvie-Grant, 1892	n/a	n/a	+	+	+	+	+

Putative species and subspecies	Roberts (1924)	Hockey et al. (2005)	Peters (1934)	Mack-worth-Praed & Grant (1952,62,70)	Hall (1963)	Wolters (1975-82)	Mandiwana-Neudani (this study)
			Genera				
Vermiculated Group	***Chae/Peli***	***Pter***	***Fran***	***Fran***	***Fran***	***Pter***	***Pter***
heuglini Neumann, 1907	n/a	n/a	+	+	+	-	~
gedgii Ogilvie-Grant, 1891	n/a	n/a	+	+	+	-	~
nigrosquamatus Neumann, 1902	n/a	n/a	+	+	+	-	~
konigseggi Madarasz, 1914	n/a	n/a	~	+	+	-	~
testis Neumann, 1928	n/a	n/a	+	-	-	-	~
cavei Macdonald, 1940	n/a	n/a	-	+	-	-	~
harwoodi							
harwoodi Blundell & Lovat, 1899	n/a	n/a	+	+	+	+	+
Montane Group	***n/a***	***n/a***	***Fran***	***Fran***	***Fran***	***Pter***	***Pter***
erckelii							
erckelii (Rüppell, 1835)	n/a	n/a	+	+	+	+	+
pentoni Praed,1920	n/a	n/a	+	+	+	-	~
nobilis							
nobilis Reichenow, 1908	n/a	n/a	+	+	+	+	+
chapini Grant & Praed, 1934	n/a	n/a	-	+	+	-	~
camerunensis							
camerunensis Alexander, 1909	n/a	n/a	+	+	+	+	+
swierstrai							
swierstrai (Roberts, 1929)	n/a	n/a	+	+	+	+	+
castaneicollis							
castaneicollis Salvadori, 1888	n/a	n/a	+	+	+	+	+
bottegi Salvadori, 1898	n/a	n/a	+	-	-	-	~
gofanus Neumann, 1904	n/a	n/a	+	+	-	-	~
ogoensis Praed, 1920	n/a	n/a	+	+	+	-	~
kaffanus Grant & Praed 1934	n/a	n/a	-	+	+	-	~
atrifrons (Conover, 1930)	n/a	n/a	+	+	+	+	+
ochropectus							
ochropectus (Dorst & Jouanin, 1952)	n/a	n/a	-	-	+	+	+
jacksoni							
jacksoni O. Grant, 1891	n/a	n/a	+	+	+	+	+
pollenorum Meinertzhagen, 1937	n/a	n/a	-	+	+	-	~
gurae Bowen, 1931	n/a	n/a	+	-	-	-	~

Putative species and subspecies	Roberts (1924)	Hockey et al. (2005)	Peters (1934)	Mack-worth-Praed & Grant (1952,62,70)	Hall (1963)	Wolters (1975-82)	Mandiwana-Neudani (this study)
			Genera				
Scaly Group	***n/a***	***n/a***	***Fran***	***Fran***	***Fran***	***Pter***	***Pter***
squamatus							
squamatus Cassin, 1857	n/a	n/a	+	+	+	+	+
maranensis Mearns, 1910	n/a	n/a	+	+	+	-	~
schuetti Cabanis, 1880	n/a	n/a	+	+	+	+	+
usambarae Conover, 1928	n/a	n/a	+	+	+	+	~
uzungwensis Bangs & Loveridge, 1931	n/a	n/a	+	+	+	-	~
doni Benson, 1939	n/a	n/a	-	+	+	-	~
zappeyi Mearns, 1911	n/a	n/a	+	-	-	-	~
tetraoninus Blundell & Lovat, 1899	n/a	n/a	+	-	-	-	~
chyuluensis Someren, 1939	n/a	n/a	-	+	-	-	~
ahantensis							
ahantensis Temminck, 1854	n/a	n/a	+	+	+	+	+
hopkinsoni Bannerman, 1934	n/a	n/a	-	+	+	-	~
griseostriatus							
griseostriatus O. Grant, 1890	n/a	n/a	+	+	+	+	+
Bare-throated Group	***Pter***	***Pter***	***Pter***	***Pter***	***Fran***	***Pter***	***Pter***
afer							
afer (Müller, 1776)	+	+	+	+	+	+	+
harterti Reichenow, 1909	n/a	n/a	+	+	+	-	~
nyanzae Conover, 1929	n/a	n/a	+	+	-	-	~
böhmi Reichenow, 1885	n/a	n/a	+	+	-	-	~
intercedens Reichenow, 1909	n/a	n/a	+	+	+	-	~
itigi (Bowen, 1930)	n/a	n/a	+	+	-	-	~
cranchii (Leach & Koenig, 1818)	n/a	n/a	+	+	+	+	+
punctulatus (Gray, 1834)	n/a	n/a	+	-	-	-	~
benguellensis Bocage, 1893	n/a	n/a	+	+	-	-	~
leucoparaeus (Fischer & Reichenow, 1884)	n/a	n/a	+	+	+	-	~
humboldtii (Peters, 1854	+	~	+	+	+	-	+
swynnertoni Sclater, 1921	n/a	+	+	+	+	-	~
castaneiventer Gunning & Roberts, 1911	+	+	+	+	+	+	~
melanogaster Neumann, 1898	n/a	n/a	~	+	+	+	~
loangwae Grant & Praed, 1934	n/a	n/a	-	+	+	-	~
lehmanni Roberts, 1931	-	~	~	+	+	-	~
notatus Roberts, 1924	+	~	-	+	+	+	~
krebsi Neumann, 1920	+	~	~	+	-	-	~
cunenensis Roberts, 1932	n/a	~	~	+	-	-	~
cooperi Roberts, 1947	-	~	-	-	-	-	~

Putative species and subspecies	Roberts (1924)	Hockey et al. (2005)	Peters (1934)	Mack-worth-Praed & Grant (1952,62,70)	Hall (1963)	Wolters (1975-82)	Mandiwana-Neudani (this study)
			Genera				
Bare-throated Group	***Pter***	***Pter***	***Pter***	***Pter***	***Fran***	***Pter***	***Pter***
swainsonii							
swainsonii (Smith, 1836)	+	+	+	+	+	+	+
lundazi White, 1947	n/a	+	-	-	~	-	~
gilli Roberts, 1932	n/a	~	~	+	~	-	~
damarensis Roberts, 1932	n/a	~	~	+	~	-	~
chobiensis Roberts, 1932	n/a	~	~	+	-	-	~
rufopictus							
rufopictus Reichenow, 1887	n/a	n/a	+	+	+	+	+
leucoscepus							
leucoscepus (Gray, 1867)	n/a	n/a	+	+	+	+	+
infuscatus Cabanis, 1868	n/a	n/a	+	+	~	-	+
holtemülleri Erlanger, 1904	n/a	n/a	+	-	-	-	~
keniensis Mearns, 1911	n/a	n/a	+	-	-	-	~
kilimensis Mearns, 1911	n/a	n/a	~	+	-	-	~
tokora Stoneham, 1930	n/a	n/a	+	-	-	-	~
muh.-ben-abdul. Erlanger, 1904	n/a	n/a	+	+	-	-	~
Unplaced taxa							
pondicerianus Hall (1963:167) speculates affinities with *sephaena* and/or *coqui*							
pondicerianus (Gmelin, 1789)	n/a	n/a	+	n/a	+	+	+
mecranensis Zarudny & Härms, 1913	n/a	n/a	+	n/a	+	-	n/a
interpositus Hartert, 1917	n/a	n/a	+	n/a	+	-	n/a
ceylonensis Whistler, 1941	n/a	n/a	-	n/a	+	-	n/a
gularis Hall (1963:167-168) *"*comparable in size and general proportions to the largest member of *F. francolinus"* isolated from other francolins" …. "divergence over a long period"							
gularis (Temminck, 1815)	n/a	n/a	+	n/a	+	+	+
nahani Hall (1963:166-167) speculates affinities with *squamatus* and other 'Scaly' francolins							
nahani (Dubois, 1905)	n/a	n/a	+	+	+	+	-
lathami Hall (1963:165-166) speculates affinities with *coqui* and other 'Red-tailed' francolins							
lathami Hartlaub, 1854	n/a	n/a	+	+	+	+	+
schubotzi Reichenow, 1912	n/a	n/a	+	+	+	-	+

A new genus *Afrocolinus* gen. nov. is recognized for *lathami* Hartlaub, 1854 in this study.

Table 1.3. Summary of the number of putative genera, species and subspecies outlined in Table 1.2.

	Taxonomic category			
Author/s	Geographic area covered	Putative genera	Putative species	Putative subspecies
Roberts (1924)	South Africa	6	11	20
Peters (1934)	Asia & Africa	2	39	119
Mackworth-Praed & Grant (1952, 62, 70)	Africa	2	34	113
Hall (1963)	Asia & Africa	1	41	101
Wolters (1975-82	Asia & Africa	5	41	56
Crowe et al. (1986)	Asia & Africa	1	41	50
del Hoyo et al. (1994)	Asia & Africa	1	41	50
Dickinson (2003)	Asia & Africa	1	41	85
Hockey et al. (2005)	Southern Africa	4	11	17
Mandiwana-Neudani (this thesis)	Asia & Africa	8	40	54

Table 1.4. Summary of characters used by authors to justify their positions on the classification of francolins.

Authors	Characters used
Roberts (1924)/Hockey et al. (2005)	Plumage, calls, size, bare skin on throat, distribution range†, breeding information
Chapin (1932)	Habitat type, distribution range†, morphology
Peters (1934)	Breeding information, distribution range†
Mackworth-Praed & Grant (1952, 1962, 1970)	Morphology, geographic distribution†, habits, nest and eggs, breeding information, calls
Hall (1963)	Plumage, size, sexual dimorphism, extent of bare skin, colour of bill and legs, spurs, field habits, vocalizations, chicks, eggs
Wolters (1975-82)	Distribution range†
Crowe and Crowe (1985)	Skeletal and integument characters, vocalizations, ethological and ecological information
Crowe et al. (1986)	Morphology, field characters, voice, habitat and food preferences, breeding habits
Milstein and Wolff (1987)	Calls of adults and chicks, incubation periods, spur development, natal down, hybridization, general behaviour (whether a particular species is a squatter or runner)
Sibley and Monroe (1990)	Habitat preferences, hybridization information, distribution range†
Crowe et al. (1992)	Mitochondrial DNA Restriction Fragment Length Polymorphisms, morpho-behavioural characters
del Hoyo et al. (1994)	Feeding habit, habitat preferences, breeding, distribution range†, morphology
Bloomer and Crowe (1998)	Mitochondrial Cytochrome *b* sequence characters, morpho-behavioural characters
Dickinson (2003)	Primarily results from published molecular DNA phylogenies, also follow Peters (1934)

† indicates that the distribution ranges of taxa were not presented as point localities instead as roughly defined ranges.

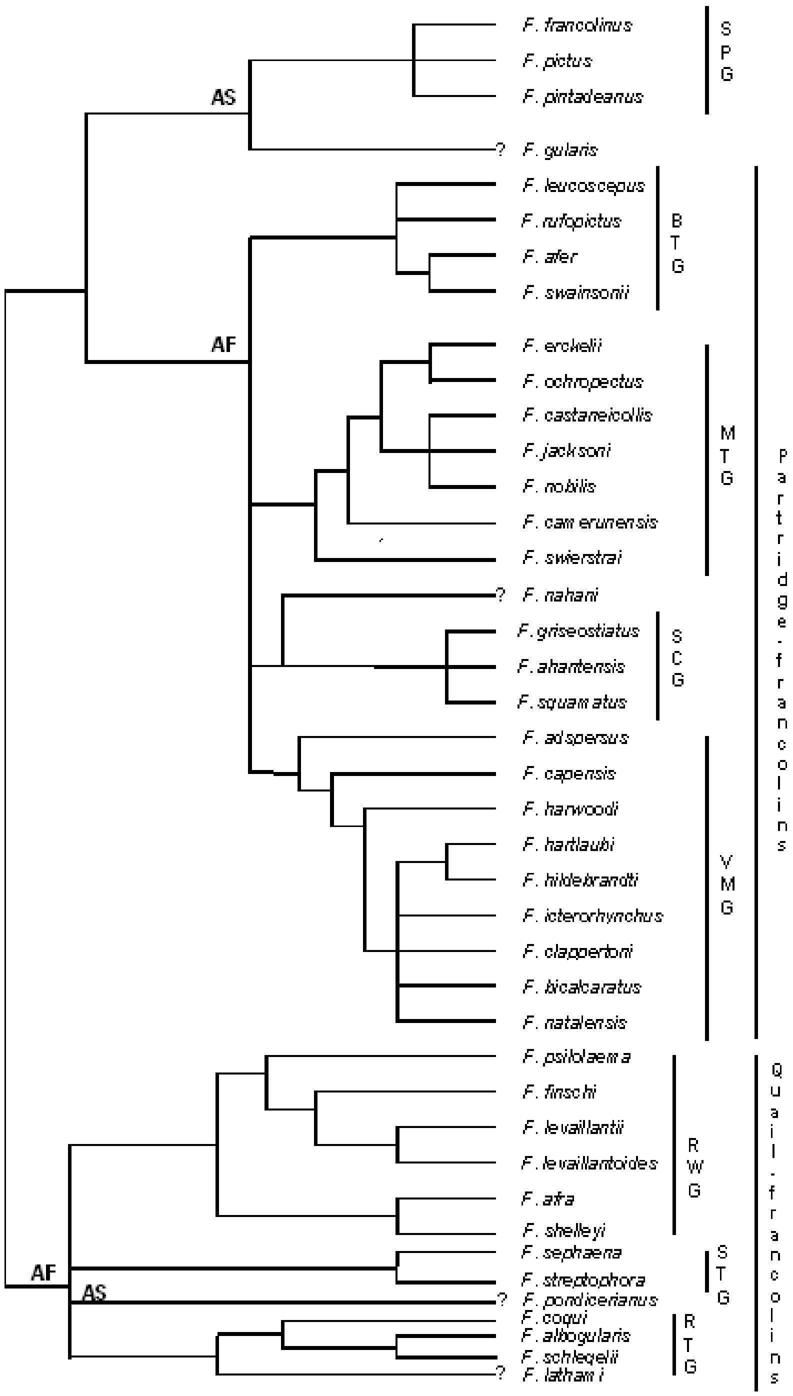


Figure 1.1. The re-drawn hypothetical cladogram of francolins according to Hall (1963). The partridge-quail francolin dichotomy follows Milstein and Wolff (1987). The acronyms used on the tree abbreviate the following: SPG stands for Spotted Group, BTG - Bare-throated Group, MTG - Montane Group, SCG - Scaly Group, VMG - Vermiculated Group, RWG - Red-winged Group, STG - Striated Group and RTG abbreviates Red-tailed Group. AS stands for Asia and AF - Africa.

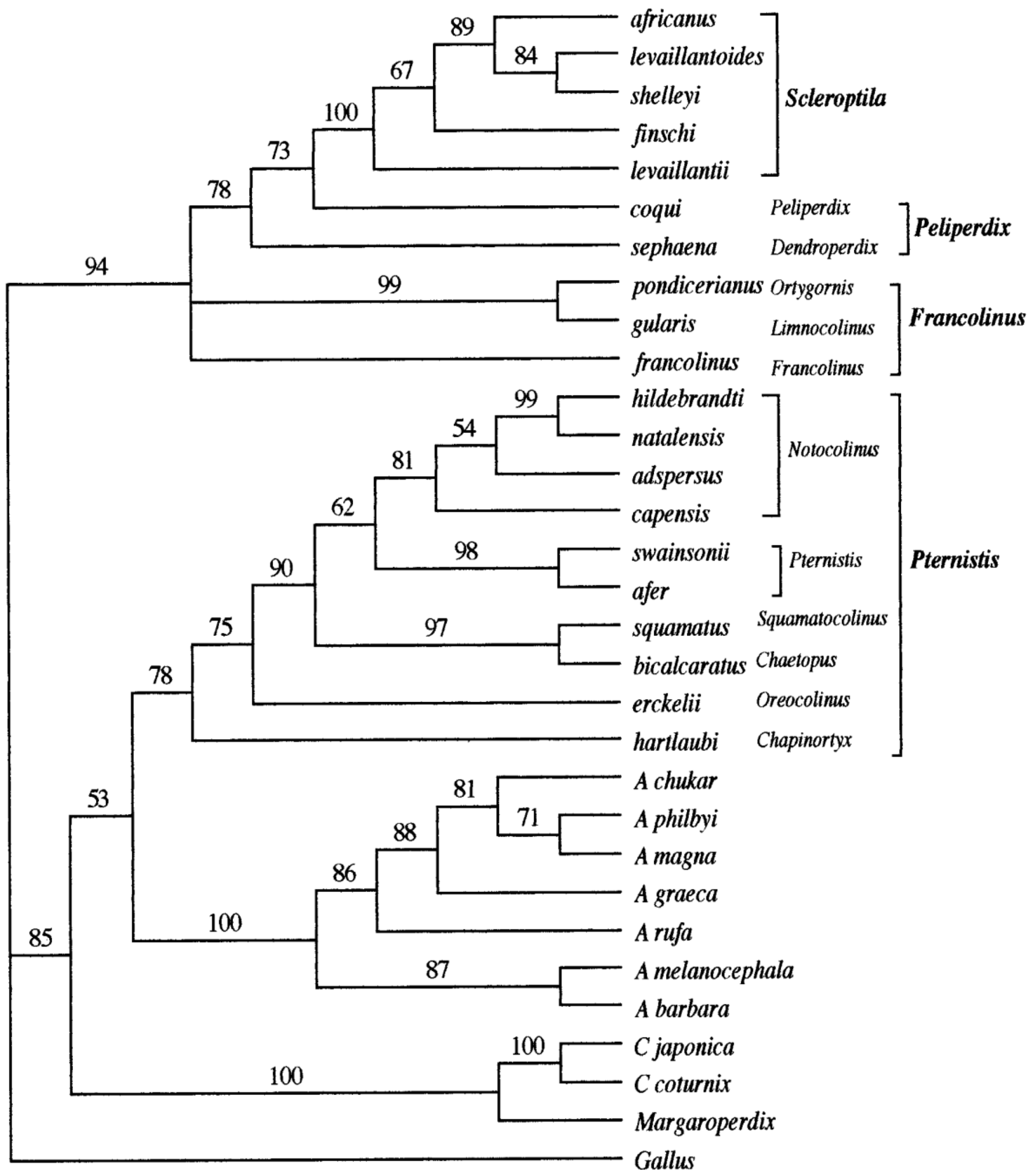


Figure 1.2. The francolin phylogeny based on combined analysis of 200 Cytochrome-*b* and 25 morphobehavioral characters (adopted from Bloomer and Crowe 1998). Bootstrap support values are indicated at nodes.

CHAPTER 2

Phylogenetics of evolutionarily enigmatic terrestrial gamebirds (Aves: Galliformes) with special regard to '*Francolinus*' spp.

Part of the information presented in this chapter is derived from Crowe et al. (2006) and Cohen et al. (2012) (both of which I am a co-author), where I contributed in a primary capacity with regard to content and molecular DNA sequence data on francolins (*Francolinus*, *Ortygornis*, *Afrocolinus*, *Peliperdix* and *Scleroptila* spp.) and spurfowls (*Pternistis*). I was also involved at all levels with respect to the preparation of these manuscripts.

Abstract

The ultimate goal of the cladistic analysis of any putative taxonomic group is to demonstrate (or refute) its monophyly decisively. If the former proves to be the case, the next task is to identify well-resolved and supported monophyletic assemblages within it. Until Crowe et al. (2006), these goals had not been achieved for the terrestrial gamebirds (Aves: Galliformes), a geographically widespread assemblage that harbours some of the most economically important bird species and a spectrum of biologically and geographically diverse taxa that have been used as models for studying broad-scale physiological, ecological, evolutionary and biogeographical phenomena. However, some authors, e.g., Eo et al. (2009), Shen et al. (2010), still maintain that this goal

remains unattained. In particular, the lack of a well-resolved hypothesis concerning phylogenetic relationships within the crown Galliformes, and especially phasianine galliforms (pheasants, partridges, 'francolins', quails, grouse, turkeys and peafowls), hinders interpretation of their morphological and ecological evolution and their utility as biogeographical indicators needed for conservation and management initiatives. In this chapter, four mitochondrial and three nuclear markers were sequenced for a selection of galliform species (and not genera, are terminals as in previous studies). Further evidence in terms of the large number of francolin and spurfowl species analyzed, mitochondrial and nuclear DNA characters (and new evidence particularly from vocalizations and behaviour of particularly *F. nahani*) was explored in the context of the phylogenetic affinities suggested by Crowe et al. (2006) with the goal of producing a robust phylogenetic hypothesis for Africa's diverse Galliform lineages, and in particular francolins *sensu lato*.

Results from this study rejects the traditional classification of galliform families, and instead supports the recognition of only five families, which are the: Megapodiidae, Cracidae, Numididae, Odontophoridae and Phasianidae. Members of the two traditionally recognized families, the Meleagrididae (turkeys) and Tetraonidae (grouse and allies), were nested within the Phasianidae. Regarding the focal taxa, Nahan's Francolin *F. nahani* is not a francolin but a partridge sister to the Stone Partridge *P. petrosus*, and they diverged c. 9.6 mya. Their relationship is strongly supported and contradicting all other published treatments of the galliformes. The two form a basal clade relative to 'true' francolins and spurfowls suggesting that they represent a relictual group sister to the New World quails (Odontophoridae), and are only distantly related to the other Old World galliforms. This study also confirms earlier studies in demonstrating that francolins and spurfowls are not each other's closest relatives as suggested by Hall (1963). The genus *Francolinus* comprises at least two distantly related lineages (excluding *F. nahani*), the partridge-like spurfowls, which are related to quails (e.g. *Coturnix, Excalfactoria, Margaroperdix, Perdicula* and *Ammoperdix* spp.) and certain Old World partridges (e.g. *Tetraogallus* and *Alectoris* spp.), and the quail-like francolins (*Dendroperdix*, *Peliperdix* and *Scleroptila* spp.), which are related to the 'true' Asian francolins (*Francolinus* spp.), chickens (*Gallus* spp.), and other Old World partridges (*Bambusicola* spp.). The estimated divergence date between the *Gallus/Bambusicola/*francolins and the *Coturnix/Alectoris/*spurfowls clade is recovered at c. 33.6 mya.

Introduction

Prior to 2006, there was no consensus on the phylogenetic relationships of, or within, the Galliformes, except that the Galliformes were monophyletic (a view initially challenged by Prager and Wilson 1976, Jolles et al. 1976, 1979). The sister-group relationship between Galliformes and Anseriformes (ducks, geese and screamers) in the avian tree of life is very strongly supported (Hackett et al. 2008), although relationships among the lineages within Galliformes still remain controversial (Wang et al. 2013).

The number of supra-generic monophyletic assemblages within Galliformes has varied greatly. Adopting an extreme 'splitters' viewpoint (Verheyen 1956, Johnsgard 1973, 1986, 1988, 1999), eight groupings with associated core biogeographical affinities have been identified: Megapodiidae (Australasia - megapodes, scrubfowl, brush-turkeys), Cracidae (Neotropics - curassows, guans and chachalacas), Numididae (Afrotropics – guineafowls), Phasiani(n/d)ae (Afro/Asiotropical - pheasants, junglefowls - chickens, peafowls, and peacock- and argus-pheasants), Perdicinae (Palaearctic and Afro/Asiotropical - partridges, francolins and Old World quails), Meleagridi(n/d)ae (Nearctic – turkeys), Tetraoni(n/d)ae (Holarctic – grouse) and Odontophori(n/d)ae (Neotropical and Nearctic - New World quails).

With respect to these groupings (reviewed by Johnsgard 1973, 1986, 1988, 1999 and Sibley and Ahlquist 1985, 1990), there is general agreement that the megapodes and cracids are cladistically basal (and probably sister-taxa – Wetmore 1960, Sibley and Ahlquist 1990), followed by the guineafowls (Cracraft 1981, Crowe 1988) or New World quails (Sibley and Ahlquist 1990, Kornegay et al. 1993) as sister to the remaining phasianine assemblages. Within phasianine galliforms, it is traditionally accepted that the turkeys and grouse form monophyletic clades, with Sibley and

Ahlquist (1990) speculating that they are each other's closest relatives. This leaves the Phasiani(n/d)ae and Perdicinae for which several authors have suggested that their constituent taxa are polyphyletic (e.g. Bloomer and Crowe 1998).

The Afrotropics harbour 49 species of galliform gamebirds, occurring in virtually all habitats across the continent largely south of the Sahara (Crowe et al. 1986, del Hoyo et al. 1994). Crowe et al. (2006) demonstrated decisively (see also Milstein and Wolf 1987, Crowe et al. 1992, Bloomer and Crowe 1998), that Africa's largest gamebird genus (currently 36 spp.), *Francolinus* Stephens, 1819 (*sensu* Hall 1963) comprises at least two distantly related African radiations. The partridge-like spurfowls (*Pternistis*, 24 spp.) are related to quail (e.g. *Coturnix, Excalfactoria, Margaroperdix, Perdicula* and *Ammoperdix* spp.) and certain Old World partridges (e.g. *Tetraogallus* and *Alectoris* spp.). The quail-like francolins (*Dendroperdix*, *Peliperdix* and *Scleroptila*, 12 spp.) are related to 'true' Asian francolins (*Francolinus,* five spp.), junglefowls (*Gallus*) and other Old World partridges (*Bambusicola*). The remaining African galliforms comprise the Old World quails (*Coturnix* and *Excalfactoria*, three spp.), the endemic guineafowls (Numididae, six spp.) and four species with putative Indo-Malaysian affinities: the Congo Peafowl *Afropavo congensis*, the Stone Partridge *Ptilopachus petrosus,* and the Udzungwa and Rubeho Forest Partridges *Xenoperdix udzungwensis* and *X. obscurata* (Dinesen et al. 1994, Johnsgard 1988, Madge and McGowan 2002, Bowie and Fjeldså 2005, Crowe et al. 2006). All of these African taxa were thought to have their nearest phylogenetic relatives elsewhere in the Old World (Sibley and Ahlquist 1990). Thus, it was surprising when Crowe et al. (2006) suggested that the Stone Partridge *Ptilopachus petrosus* and Nahan's Francolin *Francolinus* *nahani* were sister-species, and that this clade (the Ptilopachinae, Bowie et al. 2013) was sister to the New World Quails (Odontophoridae).

Based on an analysis of 158 ingroup taxa representing 65 genera and all putative suprageneric galliform taxa rooted on representatives of the Anseriformes, Crowe et al. (2006) (including myself as a junior author) offered a novel, generally well-resolved and well-supported, phylogenetic hypothesis for the Galliformes (Fig. 2.1). Characters analyzed included 102 morpho-behavioural attributes (Dyke et al. 2003) and 4452 nucleic acid base pairs (bp) from four mitochondrial markers (Cytochrome-*b*, ND2, 12S and control region) and a single nuclear marker, ovomucoid intron G. At the generic level, parsimony-based cladistic analysis of the concatenated character data set yielded a single, completely resolved, supra-generic cladogram, often with high values of nodal jackknife support (Fig. 2.1), which suggested the need for a revised classification for the phasianine galliforms.

A brief review of the major galliform results of Crowe et al. (2006)

The megapodes are monophyletic (clade 1 in Fig. 3.1) and cladistically basal within a monophyletic Galliformes. The next clade comprises the monophyletic cracids (clade 2), followed by the relatively basal guineafowls (clade 3), and not the New World quails (clade 4), both of which are monophyletic and in turn sister to the balance of the phasianids. The New World quails are basal within the remaining phasianids, but include an African sister clade formed by the monotypic stone partridge *Ptilopachus petrosus* and Hall's (1963) previously phylogenetically enigmatic Nahan's 'Francolin' ('*Francolinus*/*Acentrortyx' nahani*) (clade 4). Within the remainder of phasianids, the grouse and 'true' (i.e. wattled) pheasants were the only demonstrably monophyletic supra-generic traditionally recognized clades; Phasianids including the remainder of the Phasianinae and Perdicinae (especially the latter) are polyphyletic; basal among these phasianids is a novel clade comprised of Afro/Asian 'partridges' (*Xenoperdix, Rollulus* and *Arborophila* spp. - clade 5), with the remaining Phasianinae and Perdicinae taxa sundered phylogenetically into five clades which are: the Old World quails (*Coturnix* and *Excalfactoria* spp.) including the monotypic Madagascar 'partridge' *Margaroperdix madagarensis*), some Old World partridges (e.g. *Alectoris*, *Tetraogallus, Ammoperdix* and *Perdicula* spp.), and some 'francolins' (*Pternistis* spp. which are commonly known as spurfowls) (clade 6); the junglefowls (*Gallus* spp.), *Bambusicola* partridges and 'true' (= quail-like) francolins (*Francolinus*, *Dendroperdix*, *Peliperdix* and *Scleroptila* spp.) (clade 7); the Afro-Asian peafowls *sensu lato* including the Argus Pheasant (*Argusianus* and *Rheinardia* spp.) the Congo Peacock (*Afropavo congensis*), and the peacock-pheasants (*Polyplectron* spp.) (clade 8); the turkeys (*Meleagris* spp.) and 'the' partridges (*Perdix* spp.) as sister-species (with relatively weak jackknife support) and sister to the grouse (e.g. *Tetrao*, *Bonasa* and *Tympanuchus* spp.) (clade 9); and the 'true' pheasants (*Phasianus*, *Catreus*, *Syrmaticus*, *Chrysolophus, Lophura* and *Crossoptilon* spp.) that exclude the peacock-pheasants and junglefowls, but that include (with no jackknife nodal support) the somewhat partridge-like taxa *Ithaginis, Lophophorus, Pucrasia* and *Tragopan* spp. (clade 10).

A brief review of Galliform studies published since Crowe et al. (2006)

Since the publication of Crowe et al. (2006) several further manuscripts have been published that have bearing on its conclusions. They, and their key findings, are as follows: Cox et al. (2007) analyzed eight nuclear and three mitochondrial markers for

16 ingroup galliform taxa (rooted on megapodes), and produced a maximum likelihood cladogram that was consistent with the finding that the guineafowls and not the New World Quails are basal phasianoids, i.e. confirming Crowe et al. (2006).

Analysis of 20 ingroup galliforms (rooted on Anseriformes) for 25 retroposed elements (large insertions of nuclear DNA commonly called 'jumping genes') by Kriegs et al. (2007), recovered a cladogram that was consistent with that in Crowe (2006) except in the placement of 'the' partridge, *Perdix perdix*. Rather than being sister to the turkey (*Meleagris gallopavo*), it was placed as sister to the *Chrysolophus* pheasants, leaving the turkey as sister to grouse. However, the methods and criteria used to generate this cladogram were not stated. Subsequent correspondence with the authors revealed that parsimony as implemented in PAUP*10b (Swofford 2002) and that the IRREV.UP option had been used to generate their preferred tree. This strategy assumes an 'all-plesiomorphic' outgroup and prevented the retroposed elements from being lost (reversing to absent) once they appear in a clade. Although this may be a reasonable assumption for retroposed elements, an unconstrained analysis with TNT (Goloboff et al. 2008) using an all-zero outgroup did not resolve the placement of either the partridge or turkey beyond grouping them in a polytomy with grouse and pheasants.

Kimball and Braun's (2008) model-based analysis of four nuclear introns and two mitochondrial coding regions for 41 ingroup taxa rooted on megapodes also recovered a cladogram largely congruent with that in Crowe et al. (2006) except that the turkey was placed as sister to grouse, and the partridges were placed as sister to the true pheasants, while the pavonines emerged paraphyletic. Eo et al. (2009) conducted a supertree analysis (Gatesy et al. 2002, Bininda-Edmonds et al. 2004) of available GenBank data with the resulting topology also being highly congruent with that of

Crowe et al. (2006). Model-based phylogenetic analysis (Shen et al. 2010) of complete mitochondrial genomes of 34 galliform taxa placed turkeys with grouse, the partridges with true pheasants and the pavonines as polyphyletic. This dataset also placed the New World quails as basal to guineafowls. Finally, a paper recently published by Wang et al. (2013) represents the most comphrehensively sampled (in terms of number of characters) molecular phylogeny to date. Their results refuted the traditional consideration of seven families and strongly supported the recognition of five major families within galliformes in the evolutionary sequence: Megapodiidae, Cracidae, Numididae, Odontophoridae and Phasianidae. This is similar to the findings in Crowe et al. (2006). The study also strongly supported the hypothesis that the deepest divergence within extant galliforms is between the Megapodes and all the other galliforms species, with the next divergence corresponding to that between Cracids and Phasianoidea. Similarly, as with Crowe et al. (2006), the turkeys (traditionally classified in Meleagrididae) and the grouse and ptarmigan (Tetraonidae) were nested within Phasianidae, hence this finding rejects the hypothesis that the turkeys and grouse form independent families.

Ksepka (2009) and a range of other fossil-related publications

Ksepka's (2009) parsimony analysis of an expanded and revised matrix of 120 organismal characters combined with sequences from four mitochondrial markers (control region, 12S rDNA, CYT*B*, and ND2) and a nuclear ovomucoid intron G for 56 ingroup species rooted on Anseriforms and a *Tinamus* sp. (Tinamiformes), produced a cladogram largely congruent with the one presented in Crowe et al. (2006). However, the major point of criticism presented by Ksepka (2009) is the phylogenetic placement of a key Eocene fossil, *Gallinuloides wyomingensis* (+/-54 mya old) from North America. He maintains that, *contra* Crowe et al. (2006), it is better placed at the stem (and not in the crown) of the galliform cladogram. Furthermore, there are several other fossil-based studies (Mlikovsky 1989, Stidham 2008, Elanowski and Stidham 2011, Mourer-Chauvire et al. 2011) that have challenged the divergence times ascribed to clades in Crowe et al. (2006).

This chapter

In this chapter, the focal taxa are francolins *sensu lato*. They are small to medium-sized, sedentary, Old World, partridge/quail-like gamebirds which occur in varied habitats, from dry, lowland grassland to montane forests (Hall 1963, Johnsgard 1988, del Hoyo et al. 1994, Madge and McGowan 2002). Taxonomically, francolins were invariably placed in the family Phasianidae. In some more finely partitioned classifications, within the Phasianidae, they are placed in the sub-family Phasianinae (including *Phasianus* and related species), and together with other Old World partridge- and quail-like gamebirds (e.g. *Perdix* and *Coturnix* spp.), in the tribe Perdicini (Chapin 1932, Peters 1934, Wolters 1975-82, Crowe et al. 1986, Johnsgard 1988, Sibley and Monroe 1990, del Hoyo et al. 1994, Madge and McGowan 2002). Controversy has centered on the status of monophyly of the genus *Francolinus sensu* Hall (1963) and debate over the geographic origin of the genus '*Francolinus'*, for which two contrasting hypotheses have been postulated (Hall 1963, Crowe and Crowe 1985). Based on the notion that the genus *Francolinus* shares its closest affinities with other Palaearctic and Asian genera, Hall (1963) strongly argued for the genus to be of Asian origin with its age being traced back to the Oligocene +/- 25-35. Although Crowe and Crowe (1985) concurred with Hall that the ancestor was quail-like, they hypothesized an African origin for the genus, with Asia being colonized by a nomadic or migratory ancestor that diversified and became sedentary.

The enigmatic Stone Partridge occurs on rocky outcrops in the arid habitats of the northern savanna belt including the Sahel south of the Sahara, from Gambia to Ethiopia, and south to Cameroon and northern Kenya (Crowe et al. 1986). It was described initially as a *Tetrao* by Gmelin (1789), but was subsequently placed into a monotypic genus *Ptilopachus* by Swainson (1837). Nahan's Francolin in contrast, is a highly-localized species associated with core areas of primary forests of the eastern equatorial lowlands of the Democratic Republic of the Congo and Uganda (Crowe et al. 1986, Sande et al. 2009). This taxon was first placed by Dubois (1905) in the genus *Francolinus*, but subsequently moved by Chapin (1926) into a monotypic genus, *Acentrortyx*. Hall (1963) placed it back into *Francolinus* because she doubted the value of characters used to split it from *Francolinus*. Furthermore, she linked it tentatively to members of her putatively monophyletic 'Scaly Group' of spurfowls (Ahanta Francolin *Pternistis ahantensis*, Scaly Francolin *P. squamatus* and Grey-striped Francolin *P. griseostriatus*; all previously placed into *Francolinus* by Hall) on the basis of bare-part colouration and plumage characteristics. In a morphometric analysis based on osteological features, Crowe and Crowe (1985) also placed *F. nahani* near members of Hall's Scaly Group, closest to *P. ahantensis*. In a further reworking of the francolins, Crowe et al. (1992) placed *F. nahani* in a resurrected monotypic subgenus, *Acentrortyx*, within the African spurfowl genus *Pternistis*, although speculating that it might represent a phylogenetically relictual taxon, unrelated to other African galliforms.

In this chapter, further evidence in terms of the large number of francolin and spurfowl species analyzed, mitochondrial and nuclear DNA (and new evidence from vocalizations and behaviour of particularly *F. nahani*) is explored in the context of the phylogenetic affinities suggested by Crowe et al. (2006) with the goal of producing a robust phylogenetic hypothesis for Africa's diverse Galliform lineages, and in particular francolins *sensu lato*.

Materials and methods

Collection of data

Taxon sampling

The taxon sampling was based on that of Crowe et al. (2006), with a number of important changes. In order to increase the confidence that no taxa had been overlooked, all additional African ‘francolin’ species (e.g. several additional *Pternistis* spp.) as well as additional species of Asian and New World galliforms were sequenced for this study and further sequences were obtained from GenBank (Table 2.1). A sample of *Ptilopachus petrosus* was obtained from Ghana, and three samples of *F. nahani* were obtained from Budongo Forest, Uganda.

Molecular approach

Four mitochondrial (mtDNA) markers and three nuclear (nucDNA) markers, which occur on distinct chromosomes and thus provide independent estimates of phylogeny, were used in this study. The mitochondrial markers (Cytochrome-*b* – CYT*B*, NADH Dehydrogenase Subunit 2 - ND2, 12S Ribosomal DNA - 12S, and Control Region - CR), and nuclear markers (Ovomucoid intron G – OVOG, Transforming Growth Factor

Beta 2 intron 5 – TGFB, and GAPDH intron 11 - GAPDH) were investigated since these markers have helped to resolve the phylogenetic status of other galliform genera and species (Armstrong et al. 2001, Dimcheff et al. 2000, 2002, Crowe et al. 2006, Hackett et al. 2008).

Laboratory techniques

Total genomic DNA was extracted from blood, heart and liver tissue using the DNeasy animal tissue protocol provided with the DNeasy tissue kit (Qiagen). The initial CYT*B* primers amplified 1337 base pairs (Table 3.2). Due to the length of this region, an internal primer (Table 2.2) was also used in sequencing this region. The initial CYT*B* primer pair did not amplify Grey-striped Spurfowl *Pternistis griseostriatus* and Yellow-necked Spurfowl *P. leucoscepus*, thus further galliform specific primers were also used (Table 2.2).

Double stranded DNA templates were amplified by polymerase chain reaction (PCR) using 0.75 units of BIOTAQ™ DNA polymerase (Bioline) in 30 µl reactions. Reactions also contained 1 x NH_4 buffer, 2.5 mM $MgCl_2$, each dNTP at 0.1 mM, each primer at 0.3 µM, and 3 µl of extracted DNA was used as template. The thermal profile used comprised an initial denaturation step at 94°C for two minutes, followed by 30 cycles of 94°C for one minute, 52°C for one minute and 72°C for two minutes, with a final extension step of 72°C for seven minutes.

PCR-amplified products were cleaned from solution or gel using the GFX™ PCR DNA and gel band purification kit (Amersham Biosciences) prior to cycle-sequencing with the ABI PRISM Big Dye™ Terminator v3.1 cycle-sequencing Ready Reaction Kit (Applied Biosystems). Sequencing products were resolved on an ABI

PRISM 3100 Genetic Analyser. Sequences were assembled and checked for incorrect base calling and the presence of stop codons using SeqMan II (LaserGene systems software, DNAstar, Inc.). Consensus sequences were aligned using Clustal and adjusted manually in MegAlign (LaserGene systems software, DNAstar, Inc.).

Analyses of data

Phylogenetic analyses

Three methods of phylogenetic analysis with different optimality criteria were employed to generate phylogenetic hypotheses: Bayesian inference (BI), maximum likelihood (ML) and parsimony. In all analyses, indels and ambiguous character states were considered as 'missing' and all characters were treated as non-additive. Parsimony-based phylogenetic analyses were conducted using TNT (Tree analysis using New Technology - Goloboff et al. 2008). In TNT, the search strategy employed was the ‘traditional’ search option. When multiple, equally parsimonious cladograms persisted, a strict consensus cladogram was constructed. The extent to which each non-terminal node is supported by different character partitions was determined by using the ‘jackknife’ resampling strategy with: 1000 replicates, TBR branch-swapping, five random additions of taxa per replicate with the deletion of 36% of the characters per jackknife replicate (Farris et al. 1996, Källersjö et al. 1998).

Since gene regions can evolve under different models of evolution, it has been argued that a partioned, mixed-model approach should be used when concatenating these different datasets in a model-based phylogenetic analysis (Ronquist and Huelsenbeck 2003, Nylander et al. 2004). Mixed-model Bayesian analyses were undertaken in MrBayes v3.1.2 (Huelsenbeck and Ronquist 2001, Ronquist and

Huelsenbeck 2003). Substitution models for each locus were determined in PAUP*4b10 (Swofford 2002) with Modeltest 3.06 (Posada and Crandall 1998), using the Akaike Information Criterion (Akaike 1973, Posada and Buckley 2004). Mixed-model analyses allowed different parameters (base frequencies, rate matrix or transition/transversion ratio, shape parameter, proportion of invariable sites) to vary between the partitions (gene regions and codon positions) (Nylander et al. 2004). Four Metropolis-coupled MCMC chains (one cold and three heated) were run for 10 million generations with trees sampled every 100 generations. A Dirichlet distribution was assumed for estimation of the base frequency parameters and an uninformative (flat) prior was used for the topology. The 'burn-in' period (discarded cycles before the chains had reached stationarity) varied per analysis but was typically 500 000 generations (5000 trees); posterior probabilities (PP) were estimated from the remaining generations. Each Bayesian analysis was run twice (random starting point for each run). The log-likelihood values and posterior probabilities were checked using Tracer v1.4.1 (Rambaut and Drummond 2007) to confirm that the chains had reached stationarity. The potential scale reduction factor was confirmed to approach 1.0 (for all parameters) and the average deviation of split frequencies converged towards zero.

Mixed-model maximum likelihood analyses were performed using the Randomised Axelerated Maximum Likelihood algorithm for High Performance Computing (RAxML) v7.0.4 (Stamatakis 2006, Stamatakis et al. 2008) as implemented on the CIPRES portal. Mixed-model RAxML analyses make use of a GTR+Γ+I model partitioned by gene or codon postion. The following analyses were run: mixed-model mtDNA (one model for each codon position, and also as a single data partition); a mixed-model analysis of the nuclear DNA genes, partitioned by each of the four gene regions, and a mixed-model analysis of the combined mtDNA and nuclear DNA datasets. Support at nodes was assessed with 100 non-parametric bootstrap (BS) pseudoreplicates. The use of different methodological approaches (optimality criteria) facilitated the identification of method-based incongruence.

Divergence date estimation

The previous and most comprehensive dating analysis of Galliformes was conducted by Crowe et al. (2006), which made use of the Eocene fossils *Gallinuloides wyomingensis* (Green River Formation) and *Amitabha urbsinterdictensis* (Bridger Formation) as calibration points. Further preparation and re-examination of *Amitabha* resulted in this fossil being removed from Galliformes and it is now placed in the Rallidae (Ksepka 2009). Further, Ksepka (2009) argues that *Gallinuloides* is best placed at the stem and not within the crown of the galliform phylogeny, as previously suggested by Crowe et al. (2006). If Ksepka (2009) is correct, this would suggest that previous estimates of divergence dates among galliform lineages have been overestimated. As a consequence, a new dating analysis was conducted using BEAST v. 1.6.2 (Drummond and Rambaut 2007), omitting both *Gallinuloides* and *Amitabha* and instead calibrated via the use of three additional fossil calibration points: (1) a fossil of a Crested Francolin *Dendroperdix sephaena* at 4.5-5.0 mya as a minimum date for the age of the true Francolins (Crowe 1992), (2) a basal date for the Tetraoninae (Grouse and allies) of 27-29 mya (Crowe and Short 1992), and (3) a basal date for *Polyplectron* (Peacock-Pheasants) of 34-36 mya (Olson 1974, modified by T.M. Crowe unpubl. data). An uncorrelated lognormal clock was used with the same data partitions and nucleotide substitution models as described for the Bayesian analyses above. The analysis was run for 80 million generations with tree sampling taking place every 2000 generations. Convergence was determined as described above for the Bayesian phylogenetic analyses.

Field observations of behaviour and vocalizations of P. petrosus and F. nahani

Behavioural observations and vocalizations were recorded in the field: *F. nahani* was observed in the Budongo (1.714°N, 31.543°E) and Mabira (0.399°N, 33.049°E) forests, Uganda, in 1999, 2002, 2008 and 2009 by Callan Cohen; *P. petrosus* was observed near Mora (11.083°N, 14.114°E) and Benoue National Park (8.116°N, 13.679°E) in Northern Cameroon in 2002, 2004 and 2010, and near Bandiagara (14.359°N, 3.584°E), central Mali, in 2006, also by Callan Cohen. Sound recordings were made using a strongly-directional Sennheiser ME-67 microphone with a K6 power module. The recordings were made onto various media including a Fostex FR-LE-2 solid-state recorder, a Sony RH1 minidisc recorder in uncompressed format, and an Edirol R-09HR. These were supplemented by further vocalizations of *F. nahani* from Brian Finch (unpubl. data) and from Chappuis (2000).

Vocal analyses

Calls of *P. petrosus* and *F. nahani* were compared aurally to all available African galliform species on Gibbon (1995) and Chappuis (2000), supplemented by additional calls from the British Library Sound Archive and Macaulay Library of Natural Sounds. In addition, sonograms were made from typical advertisement calls (heard most often at dawn and dusk) for *P. petrosus* and *F. nahani* and compared with those of putative sister taxa (spurfowls - *Pternistis* spp. and francolins - *Scleroptila* spp.) and other

African galliforms. Sonograms were generated in Raven Lite (Version 1.0, Cornell Laboratory of Ornithology).

Results

Phylogenetic analyses

The parsimony tree adopted from Crowe et al. (2006) is presented in this chapter (Fig. 2.1) since it yielded a single, well-resolved, supra-generic cladogram, often with high values of nodal jackknife (JK) support (Fig. 2.1). A combination of all seven sequenced markers resulted in 5554 base pairs, involving 84 taxa, from which the Bayesian inference (BI) and maximum likelihood (ML) analyses were generated (Fig. 2.2 and 2.3).

In comparing the BI (Fig. 2.2) and ML (Fig. 2.3) topologies generated with that of Crowe et al.'s (2006) parsimony tree (Fig. 2.1: based on combined mtDNA, nucDNA and organismal characters) all analyses recovered five major lineages of galliforms and not seven families as traditionally circumscribed. The sequence of divergence of these families is such that the Megapodiidae diverged first, followed in sequence by the Cracidae, Numididae, Odontophoridae and Phasianidae. Members of the two traditionally recognized families, the Meleagrididae (turkeys) and Tetraonidae (grouse and allies), are nested within the Phasianidae with 1.0 posterior probability (PP) and 86% ML bootstrap (BS) support, contrary to the findings in parsimony analysis where the turkeys (*Meleagris* spp.) and ‘the’ partridges (*Perdix* spp.) are sister (with relatively weak 71% JK), and in turn sister to the grouse (e.g. *Tetrao, Bonasa* and *Tympanuchus* spp.) (clade 9) with a lack of JK support.

The nodal support among the five prominent families (Megapodiidae, Cracidae, Numididae, Odontophoridae and Phasianidae) is 1.0 PP, whereas ML analyses recovered 100% BS support for the node between Cracids and Guineafowls, Guineafowls and Odontophorids and 91% between Odontophorids and Phasianids with no support between the basal Megapodes and Cracids. The parsimony topology recovered 100% JK support between Megapodes and Cracids, Guineafowls and Odontophorids, 98% between Cracids and Guineafowls and 91% between Odontophorids and Phasianids. The phylogenetically enigmatic phasianines remain *Ithaginis*, *Tragopan*, *Pucrasia*, *Meleagris,* and *Perdix* spp. (Table 2.3).

With regard to the francolins and spurfowls, the parsimony, BI and ML topologies reject monophyly of the genus *Francolinus* decisively (Fig. 2.1, 2.2, 2.3) in support of francolins *sensu lato* comprising two distantly related species assemblages. Spurfowls (*Pternistis* spp.) form a strongly supported monophyletic lineage with 1.0 PP and 100% BS but interestingly a lack of JK support in parsimony. Lack of support in parsimony could be attributed to among other things, fewer spurfowl species having been included in the analysis, specific differences underlying the analytical principles for the three phylogenetic inference methods, and analyses based on genetic markers representing loci evolving at different rates. On the other hand, francolins (*Francolinus, Dendroperdix, Peliperdix, Scleroptila* spp.) are monophyletic with a PP of 0.99 and BS of 78% respectively, but also with a lack of JK support in parsimony. This could be for the same reasons as highlighted above. However, there is consensus among all three phylogenetic methods in revealing that the closest evolutionary relatives of spurfowls are Old World quails (*Coturnix* spp.), the monotypic Madagascar 'partridge' *Margaroperdix* sp., Old World partridges such as *Alectoris* spp., *Tetraogallus* spp., *Ammoperdix* spp. and *Perdicula* spp. In contrast, francolins are most closely related to the chickens (*Gallus* spp.) and Bamboo partridges (*Bambusicola* spp.)

One other major revelation regards what was traditionally considered a francolin that is, Nahan's Francolin *Francolinus nahani*. All three inference methods strongly refute this in support of Nahan's Francolin being sister to the Stone Partridge *Ptilopachus petrosus* with 1.0 PP and 100% BS (Fig. 2.4, see also Cohen et al. 2012). Also these results demonstrate strong support that the 'duo' form a sister relationship with representatives of the New World Odontophorid quails, *Callipepla*, *Colinus*, *Oreortyx* and *Cyrtonyx* spp. with 1.0 PP and 100% ML BS (Fig. 2.2, 2.3, respectively), 100% JK (Fig. 2.4) and 98 JK (Fig. 2.1).

Analyses of data partitions

Mitochondrial versus nuclear DNA analyses

The combined mt- and nucDNA BI topologies are similar to that of the mt- and nucDNA ML topologies, and as such only the mt- and nucDNA ML trees with branch-lengths are presented. The combined mtDNA ML (Fig. 2.5) and BI analyses recovered similar topologies to that of the combined total evidence BI (Fig. 2.2) and ML (Fig. 2.2) DNA analyses, supporting the five major galliform families in the same sequence of evolution, although with slighly less support at several nodes. In both mtDNA BI and ML (Fig. 2.5) analyses, there is further support for the split of francolins into francolins and spurfowls, and strong support for the phylogenetic placement of Nahan's Francolin and *P. petrosus* as sister species. Further, both spurfowl and francolin taxa were recovered as distinct monophyletic assemblages in the BI and ML mtDNA analyses; these results are consistent among each of the data partitions (Table 2.4).

Both the combined nucDNA BI and ML (Fig. 2.6) analyses appear to have been influenced by missing data for some taxa. For instance, one Cracid species (*Crax* spp.) is nested in the Megapodes and the placement of *Rollulus rouloul* is uncertain. Another difference is that even though the PPs are generally high at the deeper nodes in the BI analyses, there is poor nodal support (less than 50% BP) in the ML tree coupled with very short branch-lengths. The branch between Numididae and Odontophoridade is unresolved.

However, despite some uncertanty at the base of the phylogeny for nucDNA in the BI and ML analyses, the phylogenetic resolution of the focal taxa, that is francolins and spurfowls and also Nahan's Francolin largely remain the same with the exception that the francolins are recovered as monophyletic in both the nucDNA BI and ML (Fig. 2.6) trees. Otherwise, the francolin-spurfowl dichotomy is maintained with spurfowls being monophyletic (1.0 PP, 100% BS) and the relationship between Nahan's Francolin and *P. petrosus* is strongly supported (1.0 PP, 100% BS). Further, the sister relationship between Nahan's Francolin and *P. petrosus* and the New World quails is maintained with 1.0 PP and 99% BS.

Divergence times

The molecular divergence dates (Fig. 2.7) of the deeper nodes point to the oldest split being between the Cracids/Megapodes and the rest of the galliform species and could have happened at around 65.0 mya (HPD 53.5-79.8). The Megapodes and Cracids diverged from each other at c. 56.8 mya (HPD 42.9-72.4), the Numididae at 46.5 mya (HPD 42.1-51.8) and the Odontophorids and Phasianids diverged at c. 44.5 mya (HPD 40.6-49.2).

The estimated date for the timing of the split between *P. petrosus* and *F. nahani* was 9.6 mya (95% HPD 5.8-14.1), and 37.4 mya (95% HPD 31.8-43.1) for the divergence between this clade and the New World Quails. The estimated divergence date between the *Gallus/Bambusicola/*francolins and the *Coturnix/Alectoris/*spurfowls clade is recovered at c. 33.6 mya (HPD 29.8-37.1) with the split between *Gallus/Bambusicola* and francolins at around 10.7 mya (HPD 8.4-13.7) and *Coturnix/Alectoris* and spurfowls at c. 23.1 mya (HPD 20.7-30.0). Interestingly, the time to most recent common ancestor of extant spurfowls is around 8.7 mya (HPD 7.4-10.4) and that for francolins slightly younger at c. 7.6 mya (HPD 7.0-8.3). Whether this could be correlated to habitats in which spurfowls and francolins thrive is a difficult question to answer.

Vocal and behavioural comparison between *F. nahani* and *P. petrosus*

The calls of *P. petrosus* (Fig. 2.8a) and *F. nahani* (Fig. 2.8b) are strikingly similar and differ from those of other francolins and spurfowls both sonographically and aurally: the exemplars presented here are from the widely available Chappuis (2000). They consist of a long series of whistles that increase in volume and are often joined by additional birds calling near the end of the sequence. The structure of the whistle begins with a short lead in tone between 1-1.5 kHz, followed by a double-peaked whistle with high and low frequency values of 1.5 and 2.5 kHz respectively, and associated harmonics (Fig. 2.8c-e). Interspecific variation based on our additional recordings is limited and influenced largely by the number of group members calling simultaneously. These calls differ qualitatively to a large degree from any other African galliform. Thus, it is not possible to identify homologous call units to enable direct comparison among

Galliform lineages. No other African galliform examined has a similar whistle structure. In particular, these calls strongly contrast with typical spurfowl calls of the putative relatives of *F. nahani*, which consist of slurred, almost grating, raucous calls that do not very much in frequency (Fig. 2.8c-e; from Chappuis 2000).

Behavioural observations (substantiated by photographs and extensive field observations) indicate that both *P. petrosus* (Fig. 2.9a) and *F. nahani* (Fig. 2.9b) hold their tails in a distinctive, bantam-like cocked position.

Discussion

Phylogenetic relationships

In general the phylogenetic results for this study, including the family status within galliformes, are similar to those reported by Crowe et al. (2006), with the exception that here species, and not genera, are terminals. With respect to the focal taxa, the supported sister relationship between *F. nahani* and *P. petrosus* contradicts all other published treatments of the Galliformes (e.g. Hall 1963, Crowe et al. 1985, 1986, 1992, Johnsgard 1988, del Hoyo et al. 1994, Madge and McGowan 2002). Furthermore, the basal position of this clade relative to 'true' francolins and spurfowls suggests that they represent a relictual group sister to the New World quails (Odontophoridae), and are only distantly related to the other Old World galliforms. Intriguingly, both species occupy habitats - dense primary forest understorey and rocky outcrops - that have been suggested by Kingdon (1989) as having a higher than expected proportion of relictual species.

Further, the present study confirms the results of Crowe and Bloomer (1998) and Crowe et al. (2006) in suggesting that francolins and spurfowls are not each other's closest relatives as suggested by Hall (1963). The genus *Francolinus* comprises at least two distantly related lineages (excluding *F. nahani*, see above). The partridge-like spurfowls, which are related to quails (e.g. *Coturnix*, *Excalfactoria*, *Margaroperdix*, *Perdicula* and *Ammoperdix* spp.) and certain Old World partridges (e.g. *Tetraogallus* and *Alectoris* spp.), and the quail-like francolins (*Dendroperdix*, *Peliperdix* and *Scleroptila* spp.), which are related to the 'true' Asian francolins (*Francolinus* spp.), chickens (*Gallus* spp.), and other Old World partridges (*Bambusicola* spp.).

Morphological, behavioural and vocal similarities between *F. nahani* and *P. petrosus*

Morphological similarities shared by *F. nahani* and *P. petrosus*, include: small size, red bare skin around the eye, lack of spurs and the lack of sexual dimorphism (Hall 1963, Johnsgard 1988, Madge and McGowan 2002). Although it is well known that *Ptilopachus* has a long, vaulted and regularly cocked tail (Johnsgard 1988, del Hoyo et al. 1994, Madge and McGowan 2002), the same condition in *F. nahani* is less well known, because of its rarity and dense forest habitat (Stevenson and Fanshawe 2002). Hence, most bird artists have depicted the shape of the bird as that of a typical francolin or spurfowl (see illustrations in Crowe et al. 1986, del Hoyo et al. 1994, Sinclair and Ryan 2003). Only one relatively recent publication (Stevenson and Fanshawe 2002) has depicted the posture of this species correctly. This posture is illustrated (Fig. 2.9) based on two photographs of *F. nahani* in natural habitat (in Budongo and Mabira Forests, Uganda) and one *P. petrosus* taken in Cameroon. *Dendroperdix sephaena* is the only other African galliform known to cock its tail (Madge and McGowan 2002), but it is not closely related to these species (Crowe et al. 2006).

The biology of *F. nahani* is very poorly known (Crowe et al. 1986, Sande et al. 2009), and its voice has only been described relatively recently (Chappuis 2000, Stevenson and Fanshawe 2002), thus hampering the correct taxonomic placement of this species. The calls of both *F. nahani* and *P. petrosus* are a series of whistles increasing in volume, and are strikingly similar (see Fig. 2.8). Chappuis (2000), in a booklet accompanying his CD set, noted this similarity, as did Brian Finch, who worked on the voice section of Stevenson and Fanshawe (2002). Furthermore, our field observations attest that both species live in small, family groups and have interactive calling.

Given the long divergence time between these two species (5-13 mya), it is interesting that the nature of the calls have been so well conserved. The group duetting may indicate a strong social cohesiveness function and the calls could be subject to stabilizing selection in this regard (Payne 1971). Another matter to consider is the exact nature of the habitat of these species. Whereas *Ptilopachus* is found in the arid zone, it does inhabit dense bush growth among large boulders, a challenging environment for the broadcast of sounds, with many obstacles, similar to the dense forest understorey inhabited by *F. nahani*. Indeed, given the likely Miocene divergence between these species, it is most likely that their common ancestor inhabited forest habitats (Fjeldså and Bowie 2008). The open savannas and arid land lineages of mammals only seem to have radiated later, in the Plio-Pleistocene when dry habitat became much more widespread in Africa (e.g. deMenocal 2004). The plumage of these similar birds seems to have been very well conserved, and besides aspects of colouration that presumably relate to camouflage (*F. nahani* is darker above, whereas *P. petrosus* is somewhat paler), there has been remarkably little divergence.

Historical biogeography

As expected the omission of the fossil *Gallinuloides wyomingensis* did result in the recovery of younger divergence times. For example, Crowe et al. (2006) estimated that the stem *Ptilopachus* plus Odontophoridae clade to have diverged at 55.5 mya (95% HPD 50.1-65.9) whereas our analyses based on three ingroup fossils recovered this node at 37.4 (95% HPD 31.7-43.0). Overall, these results are in agreement with the view of Ksepka (2009), that although stem galliformes likely existed in the Cretaceous (i.e. pre 65 mya), the divergence of crown-group lineages remains inconclusive.

Our estimated divergence between *Ptilopachus* and the New World quails occurred around the middle of the Eocene period (55.8-33.9 mya). The Eocene was a remarkable period in earth history, with high temperatures and precipitation, in essentially an ice-free world (Eberle and Greenwood 2012, Harrington et al. 2012). Connections existed between Africa and Europe, and Europe and North America via Greenland, although by about 40 mya, the time of our inferred *Ptilopachus*-New World quail split, it seems unlikely that this landbridge was still open (Scotese 2001). However, Eocene and Oligocene fossils have been discovered from France that are most similar to New World quails (Crowe and Short 1992, Crowe et al. 2006, see Mourer-Chauvire 1992 for another view) suggesting that Europe likely played an important part in the biotic exchange between African and North American lineages. Should the 'Greenland landbridge' have been closed, an alternate connection may have been via Asia to North America along the Bering Strait. Given the relatively sedentary habitats of both *Ptilopachus* and New World quails, it seems highly unlikely that direct dispersal between African and the New World occurred, as for example inferred for some lineages of birds such as Thrushes (*Turdus* spp., Voelker et al. 2009). In summary, although difficult to infer without additional fossil evidence, it seems likely that one of the above mentioned landbridges played an important role in shaping the biogeographic origins of both the African and New World members of the Odontophoridae. At 5-13 mya the super-African rainforest was likely still expansive (Fjeldså and Bowie 2008) which may suggest that *P. petrosus* either secondary invaded its present arid and rocky habitat, or that it was more geographically restricted in the past, and that *F. nahani* likely occupies the ancestral habitat of these taxa. Interestingly many of the extant New World Quails are more open habitat associated (de Hoyo et al. 1994), with closer habitat affinities to *P. petrosus* than *F. nahani*.

The relative divergence time between *Gallus/Bambusicola/*francolins and the *Coturnix/Alectoris/*spurfowls clade is recovered at c. 33.6 mya whereas the split between *Gallus/Bambusicola* and francolins and *Coturnix/Alectoris* and spurfowls was recovered at around 10.7 and 23.1 mya respectively. Thus the diversification of, francolins in Africa happened much more recently. Further, the divergence times among the lineages in each of the major clades seem to have occurred consistently over roughly the same period and given that the spurfowls evolved at around 8.7 mya and the francolins c. 7.6 mya, this indicates that spurfowls are a little older than the francolins. Most spurfowl species occur in forests and along forest edges, with only a few species occurring in distinctive habitats such as the rocky hills preferred by *P. hartlaubi* and semi-wooded grasslands preferred by members of the Bare-throated species complex. Francolins on the other hand occur in different types of grasslands including, montane, wooded and scrubby grassland, with the exception of one species, *Francolinus lathami*, which is a forest specialist.

Taxonomic recommendations

On the basis of the close genetic relationship between *F. nahani* and *P. petrosus*, as well as their shared behavioural and vocal characters, we recommend that *F. nahani* be moved to the genus *Ptilopachus* Swainson (on the basis of priority). We recommend the placement of *Ptilopachus* in the Odontophoridae to emphasize its sister relationship to this New World family of galliform birds. *Ptilopachus* should be placed first in the sequence of genera of the Odontophoridae.

With regard to the spurfowls and francolins, this study supports assignment of the genus *Pternistis* to all spurfowl taxa. However, there seems to be a dire need to revise the taxonomic status of francolins in particular, the distinct forest species *F. lathami*, one of Hall's phylogenetically enigmatic species, as well as the other two enigmatic species, the Asian *F. gularis* and *F. pondicerianus,* which emerged as sister species to the enigmatic African *Dendroperdix sephaena*. This will form the focus of a later chapter in this thesis.

Conclusions

After several studies focusing on improving our understanding of the galliform phylogeny, it is frustrating that relationships within the Phasianidae, in particular, the position of the turkeys and grouse and allies, remains unresolved. However, this study clearly demonstrates the support for the five families considered in modern galliform classification thereby rejecting the recognition of the seven traditionally recognized families (including Meleagrididae and Tetraonidae) in the order outlined in Crowe et al. (2006) and Wang et al. (2013). As Wang et al. 2013 concluded "additional data collection will be necessary to resolve the remaining uncertainties within Galliformes", they also consider the challenges that remain to be resolve within the galliform phylogeny, to be aggravated by for example, the use of group names such as ”pheasants” and “partridges” which do not imply common descent. It would be safe to conclude that the traditionally known francolins represent at least two distantly related lineages with *F. nahani* being pulled to the base of the galliform tree to go with *P. petrosus*. Thus, *F. nahani* is not a francolin as traditionally considered but a partridge related to the New World quails.

Tables and Figures

Table 2.1. GenBank accession numbers of the samples analyzed in this study.

Genus	Species	Sample no.	Locality	CYT*B*	ND2	CR	12S	OVOG	TGFB	GAPDH
Acryllium	*vulturinum*	–	–	AF536742	AF536745	–	AF536739	DQ832070	–	–
Afropavo	*congensis*	–	–	AF013760	DQ768253	DQ834507	–	AF170991	–	–
Alectoris	*chukar*	–	–	L083781	DQ768273	DQ834525	–	AF170987	FR694121	FR694070
Alectoris	*graeca*	–	–	Z487724	–	DQ834524	–	–	–	–
Alectoris	*rufa*	–	–	Z487754	–	DQ834523	–	AF170988	–	–
Alectura	*lathami*	–	–	NC007227	AY274051	DQ834465	AY274004	DQ832069	EU737326	–
Arborophila	*javanica*	–	–	AM236890	DG093804	–	DQ832097	DQ832074	–	–
Arborophila	*torqueola*	–	–	AM236889	–	DQ834475	–	–	–	–
Bambusicola	*thoracica*	–	–	EU165706	AF222538	DQ834513	EU165706	AF170978	–	–
Bonasa	*umbellus*	–	–	AF230167	AF222541	DQ834476	U83740	–	–	–
Callipepla	*californica*	–	–	AB120131	AF028773	DQ834473	–	–	Submitted	Submitted
Callipepla	*gambelii*	–	–	L083821	AF028761	DQ834472	–	–	–	–
Catreus	*wallichii*	–	–	AF028792	DQ768254	DQ834499	–	AF170980	–	–
Chrysolophus	*amherstiae*	–	–	AB120130	–	–	DQ832102	–	–	–
Chrysolophus	*pictus*	–	–	AF028793	DQ768255	DQ834497	–	–	–	–
Colinus	*cristatus*	–	–	–	–	–	–	–	EU737357	–
Colinus	*virginianus*	–	–	EU372675	AF222545	DQ834469	AF222576	–	–	Submitted
Coturnix	*coturnix*	–	–	L083771	X57246	DQ834529	X57245	–	Submitted	EU737363
Coturnix	*japonica*	–	–	NC003408	NC003408	–	NC003408	–	–	–
Crax	*alector*	–	–	AY141921	–	–	–	–	Submitted	–
Crax	*rubra*	–	–	AY956378	AY274050	AY145307	AY274003	–	–	–
Crossoptilon	*crossoptilon*	–	–	AF028794	DQ768256	DQ834500	–	AF170981	–	
Cyrtonyx	*montezumae*	–	–	AF068192	AF028779	DQ834467	–	AF170976	–	–
Dendroperdix	*sephaena*	TMC9	Marico, SA	FR694140	DQ768274	DQ834515	FR691559	DQ832083	FR694111	FR694102
Falcipennis	*canadensis*	–	–	AF170992	AF222548	DQ834478	AF222577	AF170986	–	–
Francolinus	*francolinus*	AMNH DOT8023	India	AF013762		FR691376	–	–	–	–
Francolinus	*gularis*	U90649	India	U906497	–	–	–	–	–	–
Francolinus	*lathami*	AM236893	Cameroon	AM236893	DQ768257	FR691377	FR691546	DQ832082	FR694113	FR694080
Francolinus	*pictus*	AMNH 776813	India	FR694142	–	–	–	–	–	–
Francolinus	*pondicerianus*	AMNH DOT8050	India	FR691632	DQ768279	–	FR691547	DQ832081	FR694114	FR694081
Gallus	*gallus*	–	–	L083761	AB086102	DQ834510	NC001323	AF170979	FR694110	FR694078
Gallus	*varius*	–	–	AB044988	AF222551	–	–	–	–	–
Guttera	*pucherani*	–	–	AM236882	–	–	–	–	–	–
Ithaginis	*cruentus*	–	–	AF068193	DQ768258	DQ834487	–	DQ832076	–	–
Leipoa	*ocellata*	–	–	AM236879	AF394619	–	AF222586	–	–	–
Lophophorus	*impejanus*	–	–	AF028796	DQ768259	DQ834486	DQ832098	DQ832075	–	–
Lophura	*nycthemera*	–	–	L083801	DQ768261	DQ834498	–	–	–	–
Margaroperdix	*madagarensis*	–	–	U906407	–	DQ834528	–	–	–	–
Megapodius	*eremita*	–	–	AF082065	AY274052	–	AY274005	–	–	–
Meleagris	*gallopavo*	–	–	L083811	AF222556	DQ834485	U83741	AF170984	–	–
Numida	*meleagris*	–	–	L083831	NC006382	DQ834466	AF222587	AF170975	EU737410	FR694071
Oreortyx	*pictus*	–	–	AF252860	AF028782	DQ834468	–	AF170977	Submitted	Submitted
Ortalis	*vetula*	–	–	L083841	AF394614	–	–	AF170974	–	–
Pauxi	*pauxi*	–	–	AF068190	AY140750	AF165439	AF165449	AF170973	–	–
Pavo	*cristatus*	–	–	L083791	AF394612	DQ834508	AY722396	AF170990	–	–
Peliperdix	*coqui*	PFIAO 45	Settlers, SA	AM236895	DQ768278	FR691379	FR691549	DQ832084	FR694115	FR694082
Perdix	*perdix*	–	–	AF028791	AF222560	DQ834484	AF222590	AF170982	–	–
Phasianus	*colchicus*	–	–	AY368060	AF222561	DQ834495	U837426	–	–	–
Polyplectron	*bicalcaratum*	–	–	AF534564	DQ768263	DQ834503	–	AF331959	–	–
Polyplectron	*emphanum*	–	–	AF330062	DQ768265	DQ834504	–	AF331955	–	–

Genus	Species	Sample no.	Locality	CYT*B*	ND2	CR	12S	OVOG	TGFB	GAPDH
Pternistis	*adspersus*	PFIAO 206A	–	AM236910	DQ768276	DQ834535	DQ832113	DQ832095	FR694122	FR694087
Pternistis	*afer*	PFIAO 108	Watervalboven, SA	AM236908	DQ768281	DQ834533	DQ832111	DQ832092	FR694123	FR694088
Pternistis	*bicalcaratus*	TM 14682	Gold Coast, Hinterland	U906377	FR691578	FR691370	FR691551	FR691690	FR694103	FR694089
Pternistis	*camerunensis*	TMC 42	Mount Cameroon	FR694142	FR691577	FR691382	FR691552	FR691694	FR694124	FR694090
Pternistis	*capensis*	PFIAO 229	Kakamas, SA	AM236909	DQ768282	DQ834534	DQ832112	DQ832093	FR694125	FR694091
Pternistis	*castaneicollis*	GB	–	AM236903	–	–	–	–	–	–
Pternistis	*clappertoni*	AMNH 541305	Takoukout, Cameroon	FR691602	FR691576	FR691383	FR716655	FR691693	FR694126	FR694092
Pternistis	*erckelii*	AMNH DOT11039	Ethiopia	U906387	–	–	–	–	–	–
Pternistis	*griseostriatus*	AMNH 541411	Ndalla Tanda	AM236905	DQ768284	FR691384	FR691554	DQ832089	FR694128	FR694094
Pternistis	*hartlaubi*	TMC 121	Namibia	U906397	FR691572		FR691555	FR691692	FR694129	FR694095
Pternistis	*hildebrandti*	GB	–	U906317	–	–	–	–	–	–
Pternistis	*icterorhynchus*	AMNH 156922	Fanadji	FR691601	–	–	–	–	–	–
Pternistis	*jacksoni*	AMNH26192	East slope, Mt Kenya	FR691594	–	–	–	–	–	–
Pternistis	*leucoscepus*	PFIAO 109	Kenya	AM236906	FR691387	FR691556	DQ832090	FR694131	FR694097	FR694097
Pternistis	*natalensis*	TMC 120	Marico River, SA	AM236911	DQ834536	FR691557	DQ832094	FR694132	FR694098	FR694098
Pternistis	*nobilis*	AMNH1759	West Ruwenzori	FR691592	–	–	–	–	–	–
Pternistis	*ochropectus*	FNHM 1971-1072	Djibouti	FR691590	–	–	–	–	–	–
Pternistis	*rufopictus*	AMNH 202503	Gagayo, Muranza	FR691588	–	–	–	–	–	–
Pternistis	*squamatus*	AMNH 541409	Nr York Pass, Sierra Leone	AM236904	DQ768286	DQ834531	DQ832109	DQ832088	FR694133	FR694099
Pternistis	*swainsonii*	TMC 40	Marico River, SA	AM236907	DQ768287	DQ834532	DQ832110	DQ832091	FR694134	FR694100
Pternistis	*swierstrai*	TMC 67	Angola	FR691593	–	–	–	–	–	–
Ptilopachus	*nahani*	–	Budongo forest, Uganda	AM236885	DQ768288	FR691374	FR691545	DQ832071	FR694107	FR694075
Ptilopachus	*petrosus*	–	Ghana	AM236886	DQ768289	FR691375	FR691544	DQ832072	FR694108	FR694076
Pucrasia	*macrolopha*	–	–	AF028800	DQ768269	DQ834490	–	AF170983	–	–
Rollulus	*rouloul*	–	–	AM236888	–	–	–	–	Submitted	–
Scleroptila	*afra*	PFIAO 59	Eastern Cape, SA	AM236897	AF222550	DQ834517	AF222581	DQ832086	FR694116	FR694083
Scleroptila	*finschi*	AMNH 308887	Angola	AM236896	DQ768290	–	–	–	–	–
Scleroptila	*levaillantii*	TM 78622	Sterkspruit, SA	AM236913	DQ768291	DQ834516	DQ832106	DQ832085	FR694117	FR694084
Scleroptila	*levaillantoides*	TMC 12	Petrus steyn, SA	AM236900	DQ768292	DQ834519	DQ832108	–	FR694118	FR694085
Scleroptila	*psilolaema*	BM 80 1 1 1066	Kenya	FR691614	–	–	–	–	–	–
Scleroptila	*shelleyi*	PFIAO 47	Ayton farm, SA	AM236898	DQ768295	DQ834518	DQ832107	DQ832087	FR694119	FR694101
Scleroptila	*streptophora*	TMC11	Cameroon	FR691617	FR691573	FR691380	FR691550	–	FR694120	FR694086
Syrmaticus	*ellioti*	–	–	–	DQ768270	–	–	–	–	–
Syrmaticus	*humiae*	–	–	AF534706	–	DQ834491	DQ832099	DQ832077	–	–
Tetrao	*urogallus*	–	–	AB120132	AF222565	DQ834480	AF222594	–	–	–
Tragopan	*temminckii*	–	–	AF229838	AF222566	DQ834488	AF222595	–	–	–
Tympanuchus	*phasianellus*	–	–	AF068191	AF222569	DQ834483	AF222598	AF170985	–	–
Xenoperdix	*udzungwensis*	–	–	AM236887	DG093800	DQ834474	DQ832096	DQ832073	–	–

Table 2.2. DNA markers sequenced and primers used for PCR amplifications and sequencing of preserved tissue.

Primer name	Primer sequence (5'to 3')	Reference
All Galliformes (General primers)		
Cytochrome *b*		
L14578	cta gga atc atc cta gcc cta ga	J.G. Groth (pers. comm.)
MH15364	act cta cta ggg ttt ggc c	P. Beresford (pers. comm.)
ML15347	atc aca aac cta ttc tc	P. Beresford (pers. comm.)
H15915	aac gca gtc atc tcc ggt tta caa gac	Edwards & Wilson (1990)
Control region		
PHDL	agg act acg gct tga aaa gc	Fumihito et al. (1995)
PH-H521	tta tgt gct tga ccg agg aac cag	E.A. Scott (pers. comm.)
PH-L400	att tat tga tcg tcc acc tca cg	E.A. Scott (pers. comm.)
PHDH	cat ctt ggc atc ttc agt gcc	Fumihito et al. (1995)
12S rRNA		
L1267	aaa gca tgg cac tga ag(atc) tg	Moum et al. (1994)
H2294	gtg cac ctt ccg gta cac ttac c	O. Haddrath (S. Pereira pers. comm.)
NADH dehydrogenase subunit 2 (ND2)		
L5216	gcc cat acc ccr aaa atg	Sorenson et al. (1999)
H6313	ctc tta ttt aag gct ttg aag gc	Sorenson et al. (1999)
Ovomucoid G		
OVO-G Forward	caa gac ata cgg caa caa rtg	Armstrong et al. (2001)
OVO-G Reverse	ggc tta aag tga gag tcc crt t	Armstrong et al. (2001)
GAPDH intron-11		
GapdL890	acc ttt aat gcg ggt gct ggc att gc	Friesen et al. (1997)
GapdH950	cat caa gtc cac aac acg gtt gct gta	Friesen et al. (1997)
Transforming Growth Factor Beta2 intron-5		
TGFb2-5F	ttg tta ccc tcc tac aga ctt gag tc	Primmer et al. (2002)
TGFb2-6R	gac gca ggc agc aat tat cc	Primmer et al. (2002)
Cytochrome *b* Spurfowl-specific primers		
L14851 (General)	cct act tag gat cat tcg ccc t	Kornegay et al. (1993)
Pt-H195	ttt cgr cat gtg tgg gta cgg ag	R. Moyle & T. Mandiwana-Neudani
Pt-H194	cat gtr tgg gct acg gag g	R. Bowie
MH15145	aag aat gag gcg cca ttt gc	P. Beresford
Pt-L143	gcc tca tta ccc aaa tcc tca c	R. Moyle & T. Mandiwana-Neudani
Pt-H361	gtg gct att agt gtg agg ag	R. Moyle & T. Mandiwana-Neudani
Pt-L330	tat act atg gct cct acc tgt ac	R. Bowie
Pt-H645	ggg tgg aat ggg att ttg tca gag	R. Moyle & T. Mandiwana-Neudani
Pt-L633	ggc tca aac aac cca cta ggc	R. Moyle & T. Mandiwana-Neudani
Pt-H901	agg aag ggg att agg agt agg at	R. Moyle & T. Mandiwana-Neudani

Primer name	Primer sequence (5'to 3')	Reference
Cytochrome *b*		
Spurfowl-specific primers		
L2-2312	cat tcc acg aat cag gct c	R. Bowie
H15696	aat agg aag tat cat tcg ggt ttg atg	Edwards et al. (1991)
Pt-L851alt	cct att tgc cta cgc cat cct ac	R. Bowie
Pt-H1050	gat gct gtt tgg ccg atg	R. Bowie
Pt-L961	cga acc ata aca ttc cca c	R. Moyle & T. Mandiwana-Neudani
Pt-L961alt	ctc atc cta ctc cta atc ccc	R. Bowie
HB20 (General)	ttg gtt cac aag acc aat gtt	J. Feinstein (pers. comm.)

Table 2.3. Cladistic placement of phylogenetically enigmatic phasianine galliforms in concatenated analyses.

	Source of data	*F. nahani*	*Meleagris*	*Ithaginis*	*Tragopan*	*Pucrasia*	*Perdix*
Parsimony	Concatenated organismal, mt & nucDNA	sister to NWQ	sister to Tetraonini	sister to *Pucrasia*	sister to *Tetraophasis* + *Lophophorus*	sister to *Ithaginis*	sister to true pheasants
Bayesian inference	mt & nucDNA	sister to *P. petrosus*	sister to Tetraonini	sister to large Phasianine assemblage	sister to *Lophophorus*	sister to *Perdix* + true pheasants	sister to true pheasants
	mtDNA	sister to *P. petrosus*	sister to Tetraonini	sister to large Phasianine assemblage	sister to *Lophophorus*	sister to *Perdix* + true pheasants	sister to true pheasants
	nucDNA	sister to *P. petrosus*	sister to Tetraonini	sister to large Phasianine assemblage	_	polytomous with assemblage of Phasianine spp.	polytomous with assemblage of Phasianine spp.
Maximum likelihood	mt & nucDNA	sister to *P. petrosus*	sister to Tetraonini	sister to large Phasianine assemblage	sister to true pheaseants	sister to true pheasants	_
	mtDNA	sister to *P. petrosus*	sister to Tetraonini	sister to large Phasianine assemblage	sister to true pheasants	sister to true pheasants	sister to true pheasants
	nucDNA	sister to *P. petrosus*	sister to *Lophophorus*	paraphyletic with large Phasianine assemblage	_	paraphyletic with large Phasianine Assemblage	paraphyletic with large Phasianine assemblage

Table 2.4. Support for the relationship of *Ptilopachus petrosus* and *Francolinus nahani* from different data partitions, + indicates supported branch; U - unresolved (Adopted from Cohen et al. 2012).

	Bayesian Inference		Maximum Likelihood		Parsimony								
Clade	mtDNA	nucDNA	mtDNA	nucDNA	mtDNA	nucDNA	CYTB	CR	ND2	12S	OVOG	TGFB2	GAPDH
Odontophoridae sister to *P. petrosus* & *F. nahani*	1.0	1.0	100	100	+	+	+	+	+	+	+	+	+
P. petrosus* sister to *F. nahani	1.0	1.0	100	100	+	+	+	+	+	+	+	+	U

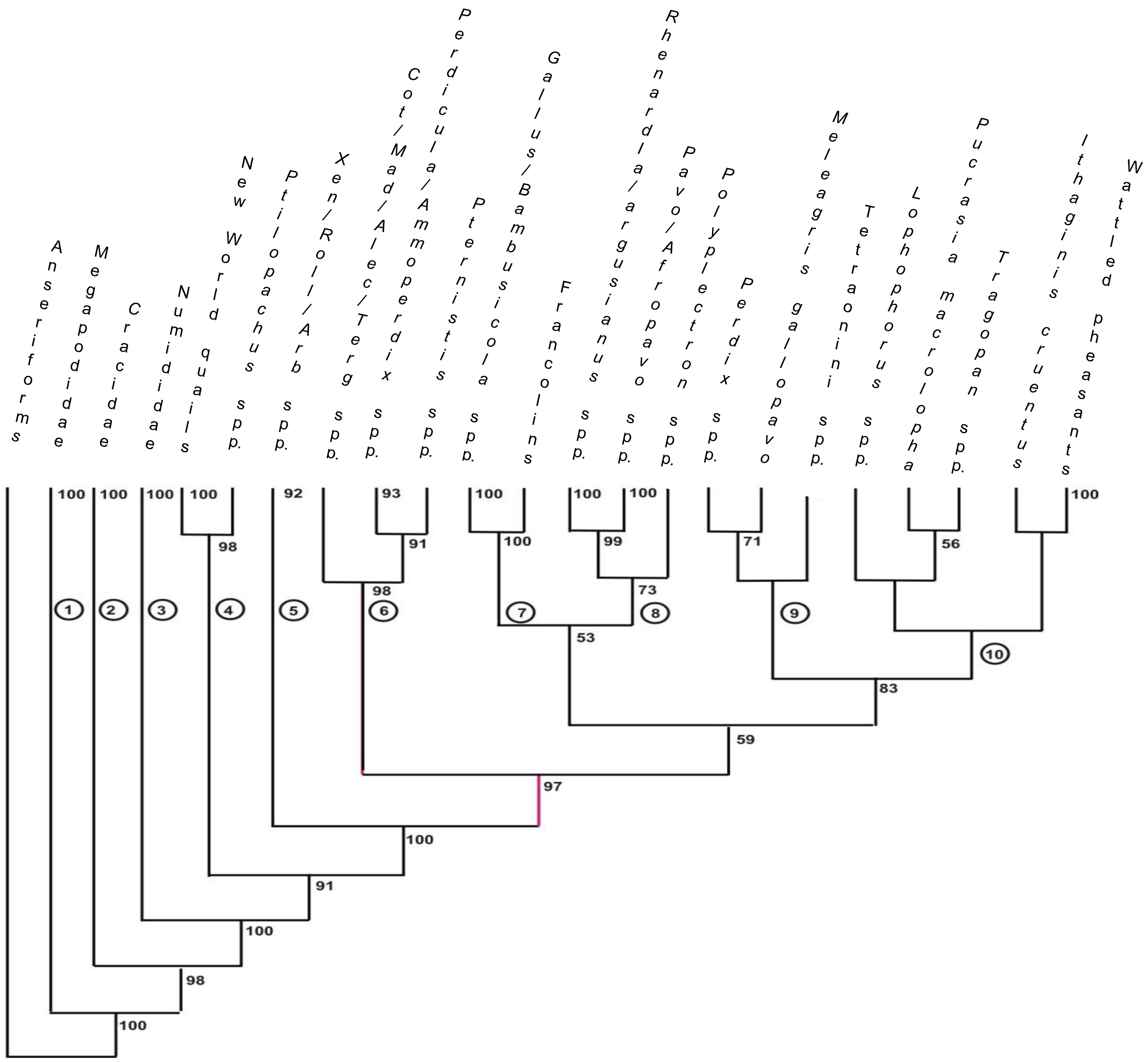


Figure 2.1. Summary of the single strict consensus parsimony cladogram recovered for the Galliformes by Crowe et al. (2006). Anseriforms, Megapodiidae, Cracidae, Guineafowls Numididae, New World quails *sensu stricto* Odontophorines, *Ptilopachus* spp., XEN/ROLL/ARB (*Xenoperdix* + *Rollulus* + *Arborophila* spp.), COT/MAD/ALEC/TETG (*Coturnix* + *Excalfactoria* + *Margaroperdix* + *Alectoris* + *Tetraogallus* spp.), *Perdicula* + *Ammoperdix* spp., Spurfowls *Pternistis* spp., *Gallus* + *Bambusicola* spp., Francolins *Francolinus*, *Ortygornis*, *Afrocolinus*, *Peliperdix*, *Scleroptila* spp., *Rhenardia* + *Argusianus* spp., *Pavo* + *Afropavo* spp., *Polyplectron* spp., *Perdix* spp., Turkey *Meleagris gallopavo*, Grouse *Tetraonini* spp., *Lophophorus* spp., *Pucrasia macrolopha*, *Tragopan* spp., *Ithaginis cruentus*, Wattled – Phesants (*Phasianus*, *Lophura*, *Syrmaticus*, *Catreus*, *Crossoptilon Chrysolophus* spp. Numbers at nodes are jackknife support values. See text for meaning of circled numbers (1-10) on clades.

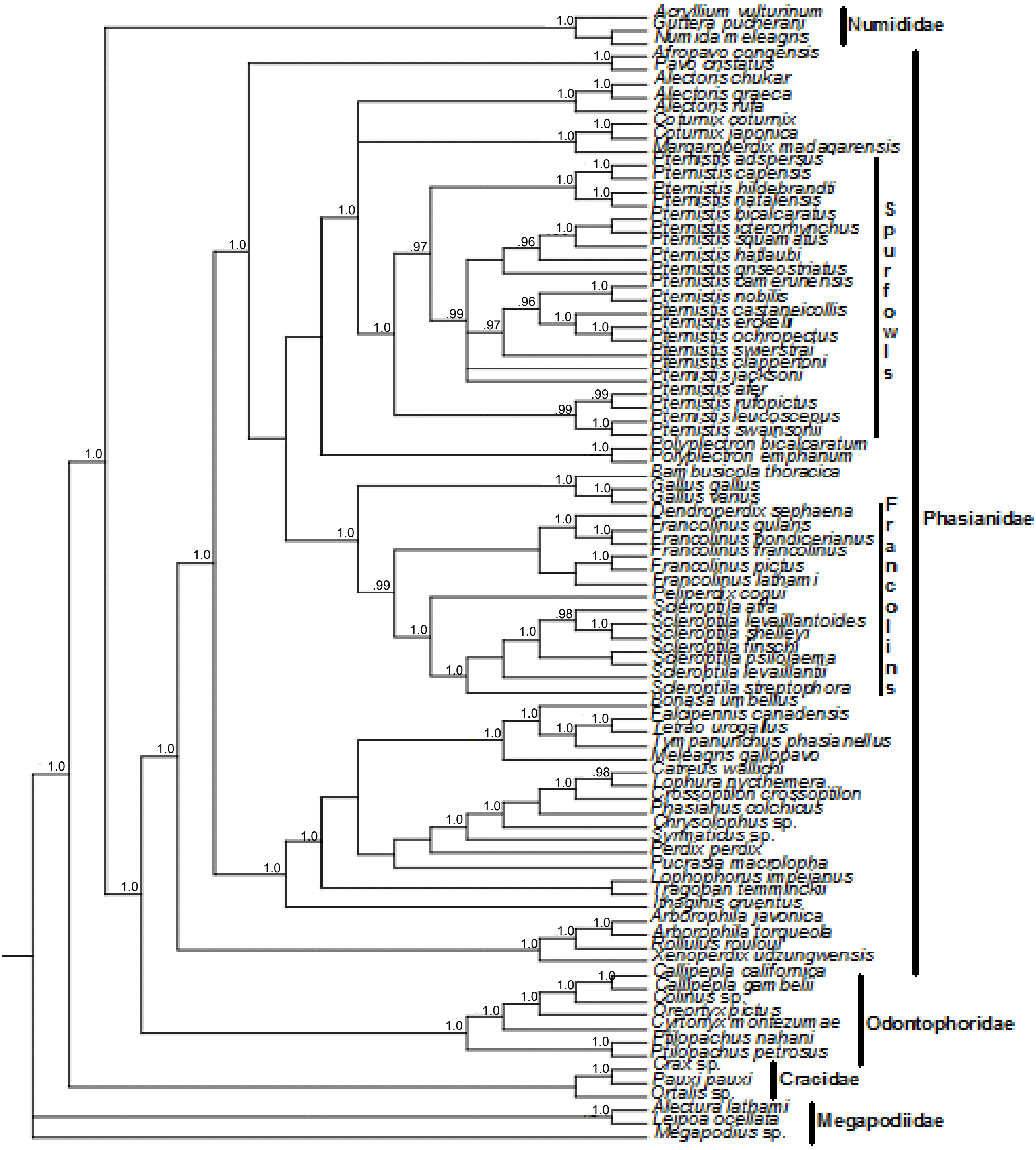


Figure 2.2. The 50% Bayesian majority-rule consensus tree generated from the combined four mitochondrial (Cytochrome-*b* – CYT*B*, NADH Dehydrogenase Subunit 2 - ND2, 12S Ribosomal DNA - 12S, Control Region - CR) and three nuclear (Ovomucoid intron G – OVOG, Transforming Growth Factor Beta 2 intron 5 – TGFB, GAPDH intron 11 - GAPDH) DNA markers. Numbers associated with nodes represent posterior probability values (≥ 0.95 are shown).

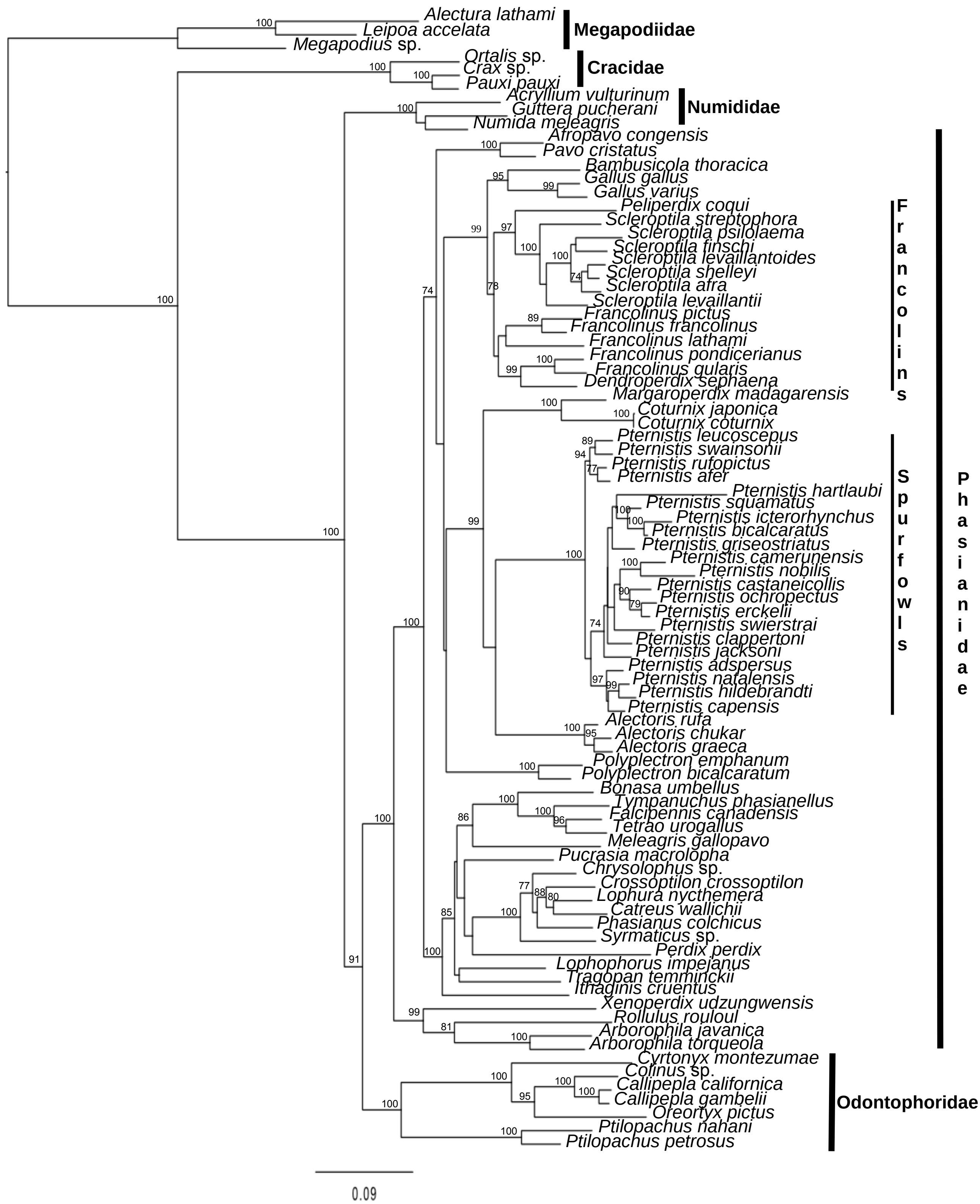


Figure 2.3. Maximum likelihood tree obtained from combined four mitochondrial (Cytochrome-*b* – CYT*B*, NADH Dehydrogenase Subunit 2 - ND2, 12S Ribosomal DNA - 12S, Control Region - CR) and three nuclear (Ovomucoid intron G – OVOG, Transforming Growth Factor Beta 2 intron 5 – TGFB, GAPDH intron 11 - GAPDH) DNA markers. Numbers associated with nodes are bootstrap support values (only ≥ 70% are shown).

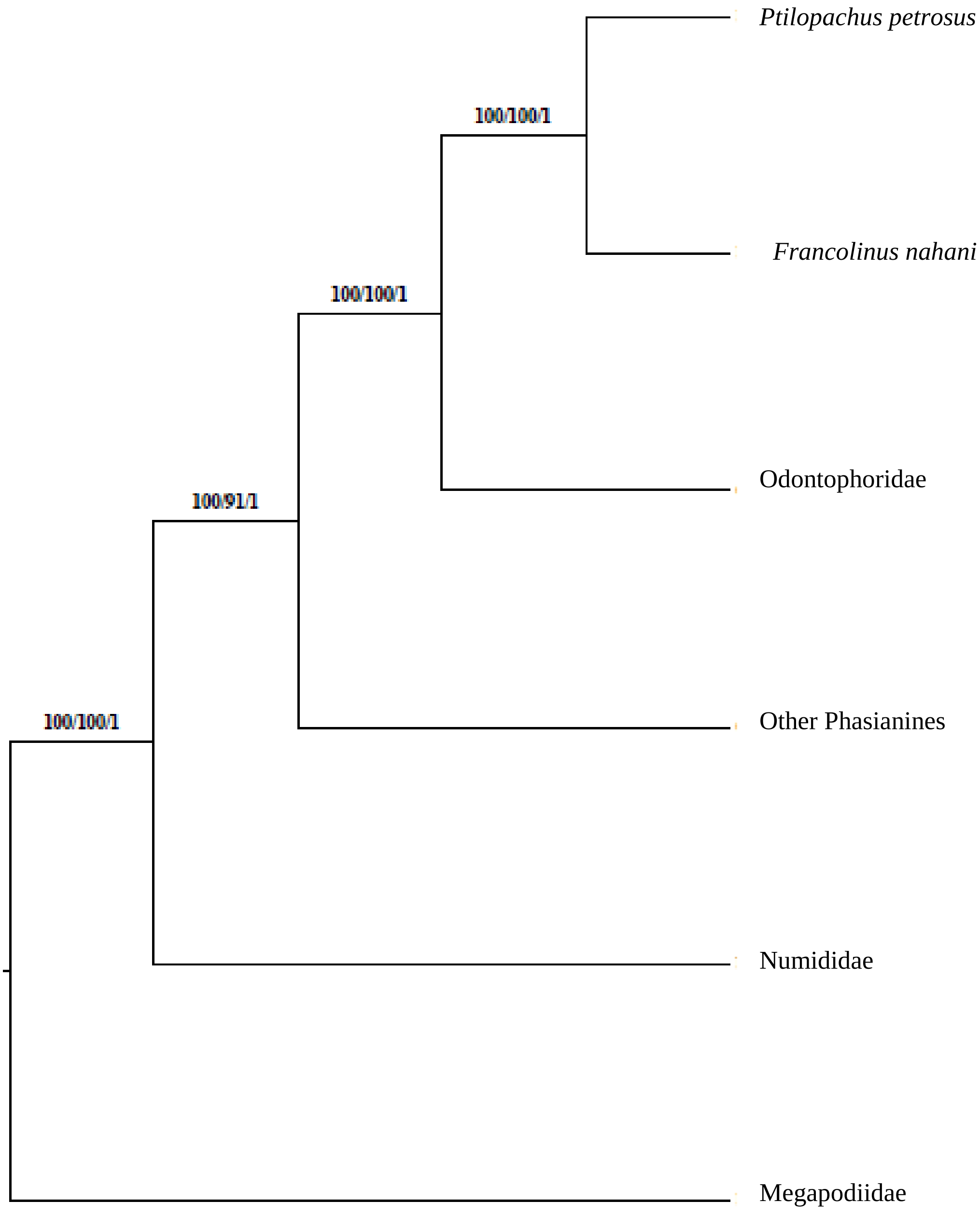


Figure 2.4. Parsimony cladogram for *Ptilopachus petrosus* and *Francolinus nahani*. Numbers at nodes are parsimony jackknife/maximum likelihood bootstrap/Bayesian probability values.

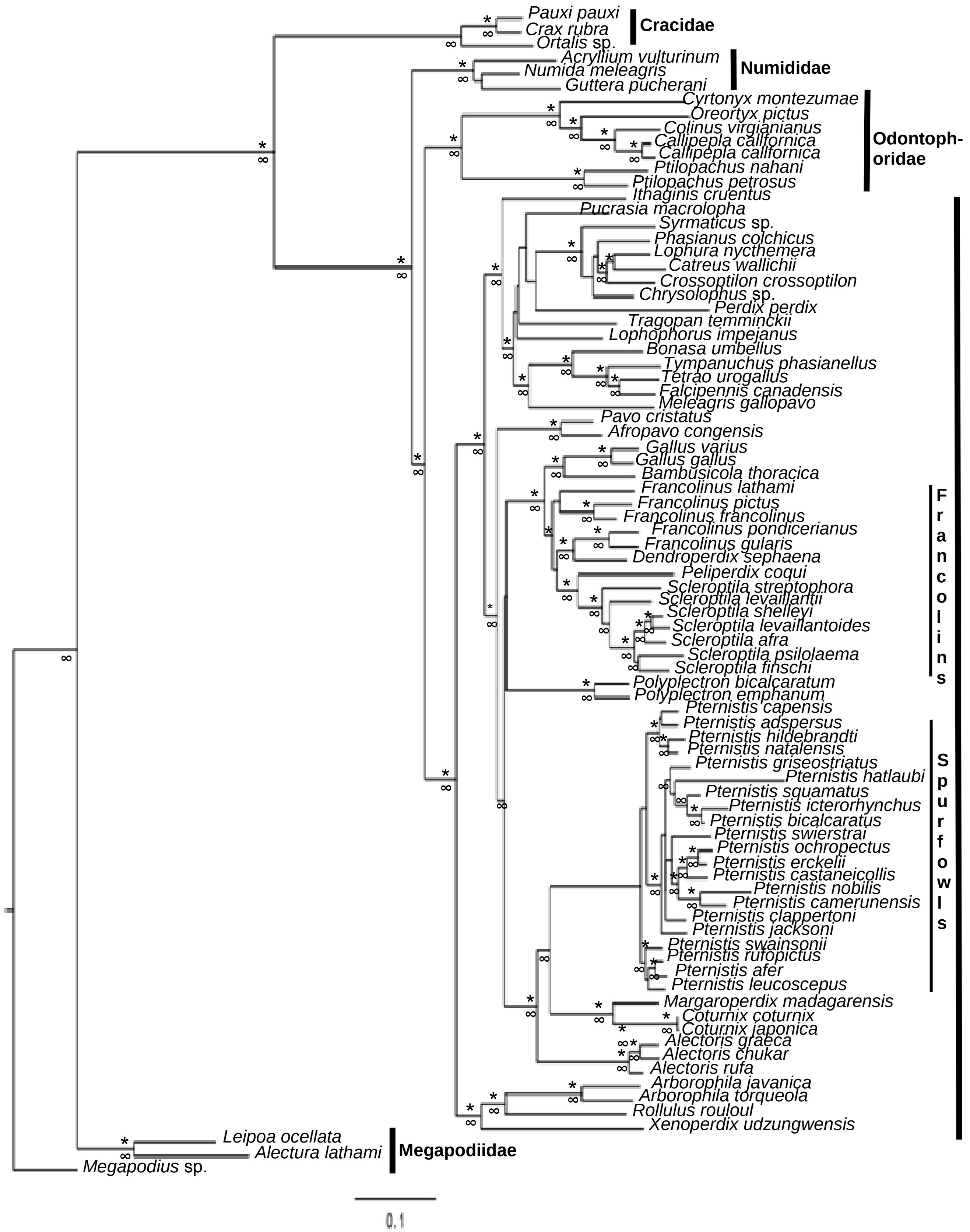


Figure 2.5. Maximum likelihood tree obtained from combined four mitochondrial (Cytochrome-*b* – CYT*B*, NADH Dehydrogenase Subunit 2 - ND2, 12S Ribosomal DNA - 12S, Control Region - CR) DNA markers. Symbols above branches (*) represent bootstrap support values (only ≥ 70% are presented) and symbols below branches (∞) represent the Bayesian posterior probabilities (only ≥ 0.95 are presented) extracted from the 50% majority-rule consensus tree.

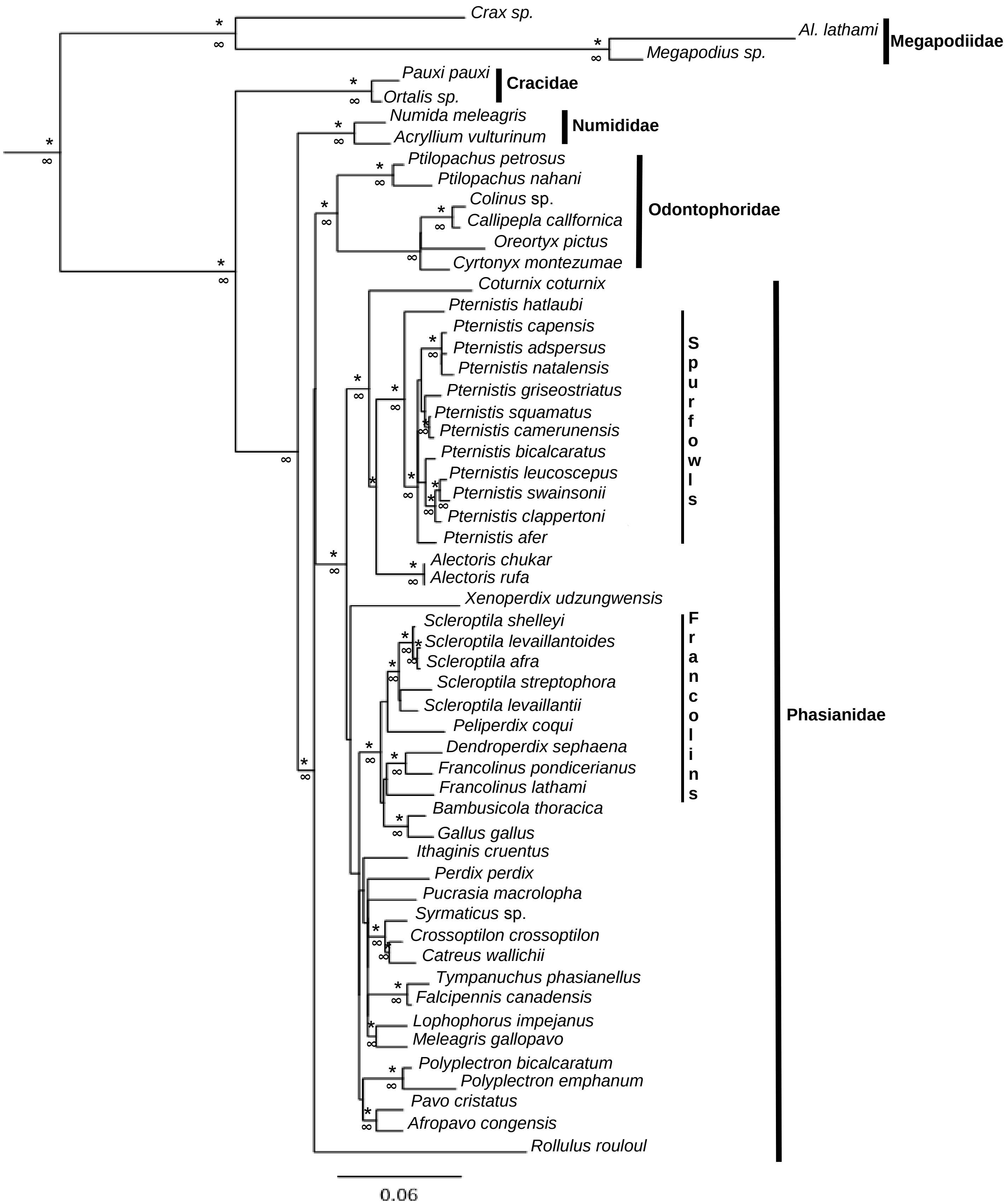


Figure 2.6. Maximum likelihood tree obtained from combined three nuclear (Ovomucoid intron G – OVOG, Transforming Growth Factor Beta 2 intron 5 – TGFB, GAPDH intron 11 - GAPDH) DNA markers. Symbols above branches (*) represent boostrap support values (only ≥ 70% are presented) and symbols below branches (∞) represent the Bayesian posterior probabilities (only ≥ 0.95 are presented as extracted from the 50% majority-rule consensus tree.

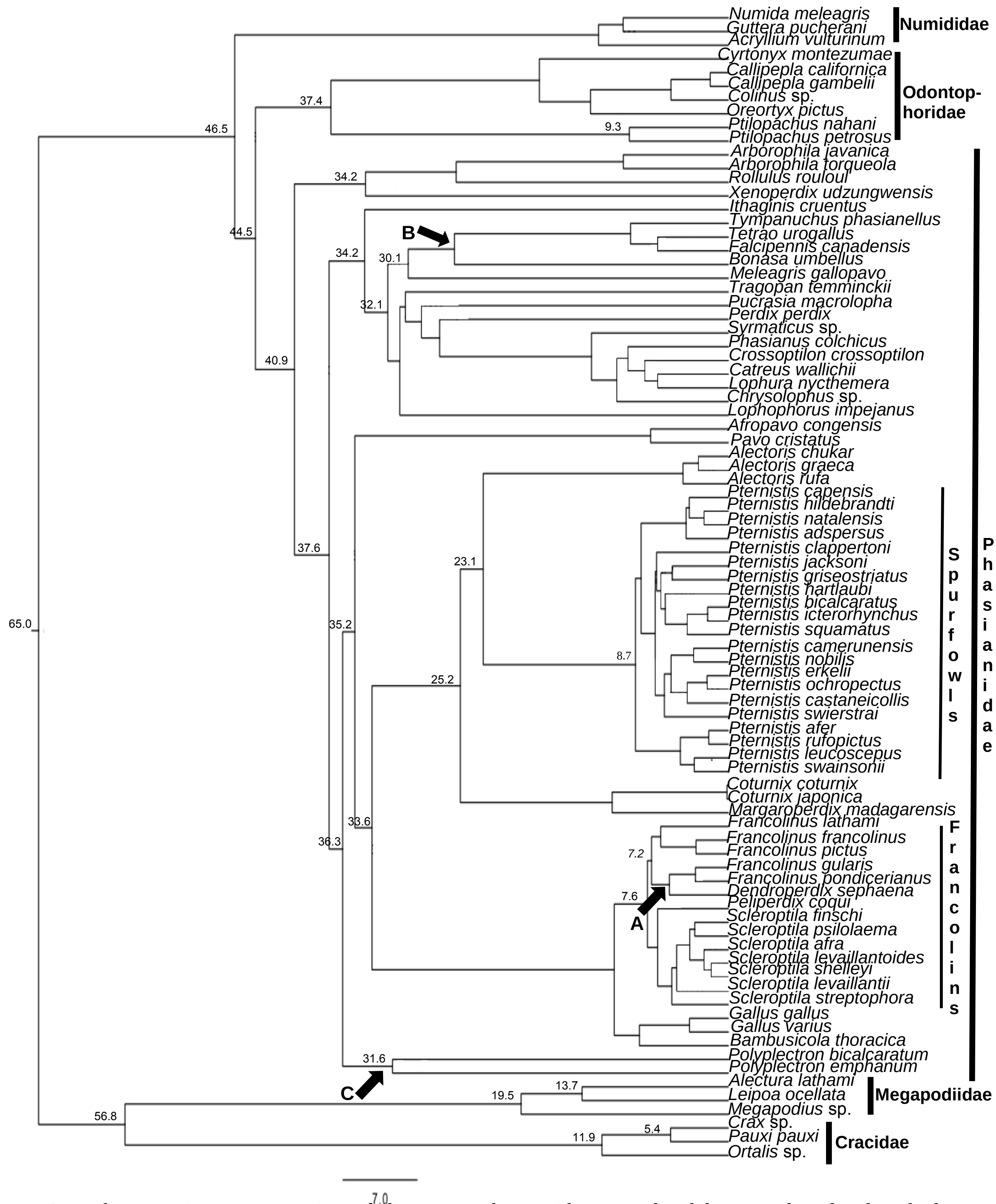


Figure 2.7. The Bayesian reconstruction of divergence dates with uncorrelated lognormal molecular clock. Numbers (only at critical nodes) at nodes are divergence dates estimated with three calibration points, (A) a fossil of Crested Francolin *Dendroperdix sephaena* at 4.5-5.0 mya (Crowe 1992), (B) a basal date for the Tetraoninae (Grouse and allies) of 27-29 mya (Crowe and Short 1992), and (C) a basal date for *Polyplectron* (Peacock-Pheasants) of 34-36 mya (Olson 1974, modified by T. M. Crowe unpubl. data).

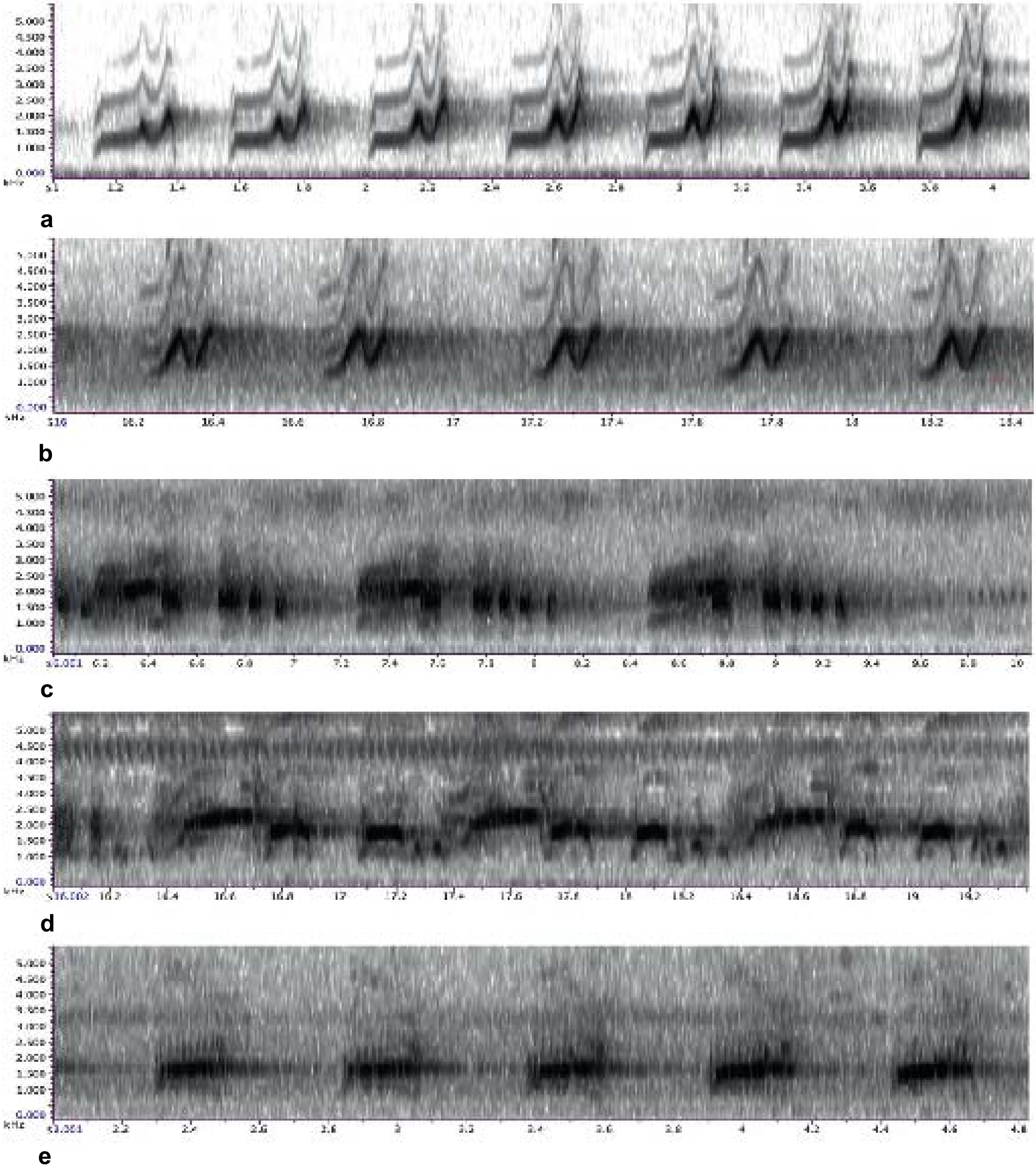


Figure 2.8. Sonograms of the call of (a) Stone Partridge *Ptilopachus petrosus*, (b) Nahan's Francolin *Francolinus nahani*, (c) Scaly Francolin *Pternistis squamatus,* (d) Ahanta Francolin *Pternistis ahantensis* and (e) Red-necked Spurfowl *Pternistis afer*. Frequency (kHz) on the vertical axis with time (seconds) on the horizontal axis.

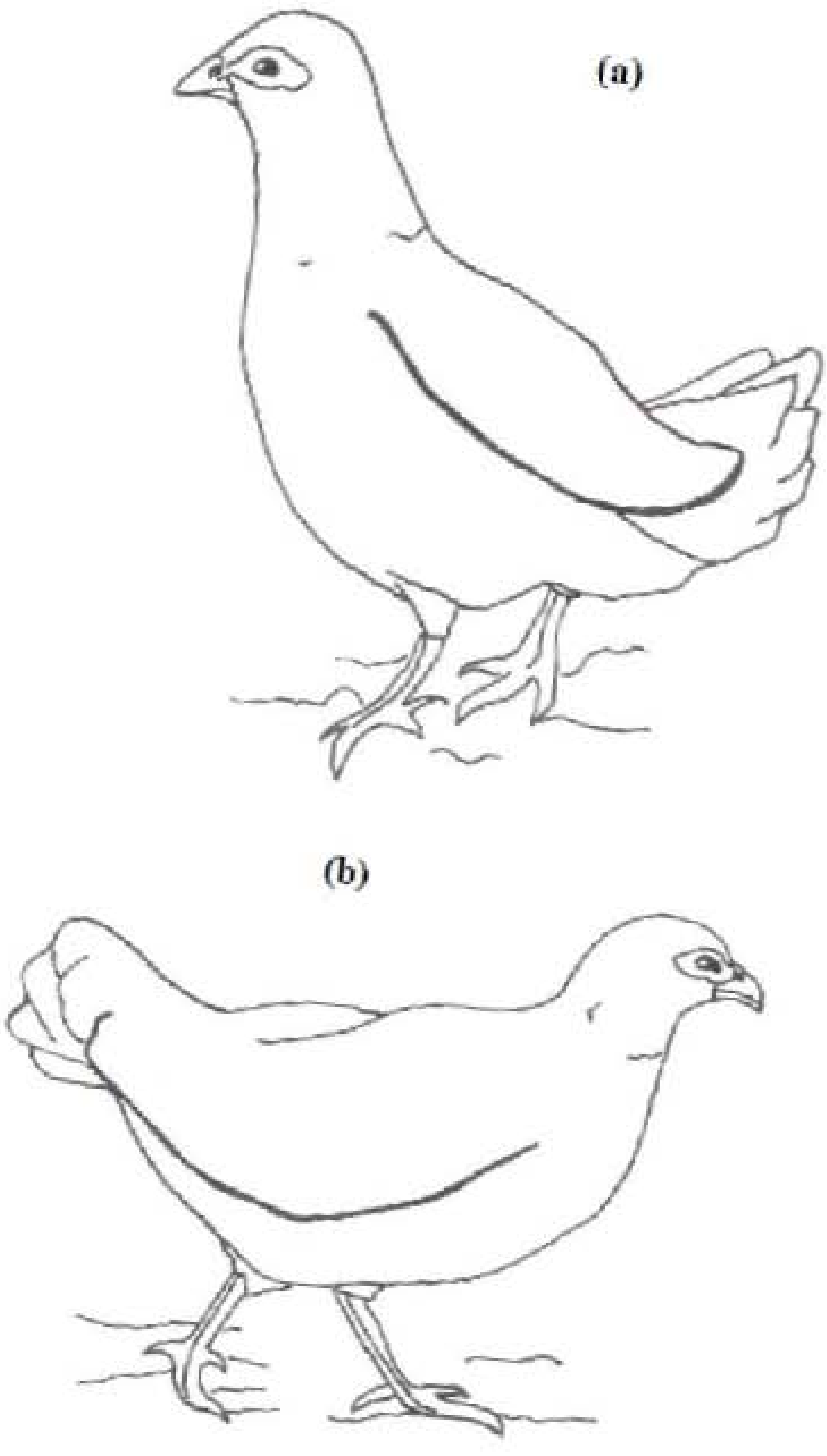


Figure 2.9. Line drawing to show the posture of (a) *Ptilopachus petrosus* and (b) *Francolinus nahani*, after photographs by Callan Cohen, Ron Hoff and Nik Borro.

CHAPTER 3

A study of gross morphological and histological syringeal features of true francolins (Galliformes: *Francolinus*, *Ortygornis*, *Afrocolinus*, *Peliperdix* and *Scleroptila* spp.) and spurfowls (*Pternistis* spp.) in a phylogenetic context

Abstract

Modern taxonomies of francolins recognize 41 congeneric species, forming the largest genus of terrestrial gamebirds (Galliformes). Recent molecular, ecological and behavioural studies challenge this view, suggesting that they comprise two unrelated, monophyletic groups. There are 'true' francolins (*Francolinus, Ortygornis, Afrocolinus*, *Peliperdix* and *Scleroptila* spp.) that are relatively small, ground-roosting birds (with the exception of *Ortygornis sephaena* which roosts in trees), and spurfowls (*Pternistis* spp.) that are large birds that can roost in trees.

This study explores gross morphological and histological syringeal anatomy of francolins, spurfowls and their respective sister taxa to test whether differences are concordant with a molecular-based hypothesis. Differences found were the presence of a shield- versus diamond-shaped tympanum among francolins and spurfowls, respectively. The first bronchial half rings are mineralized among francolins except in *O. sephaena*, whereas almost no mineral deposition was observed among spurfowls.

Histologically, francolins have a small, rounded pessulus (except in *O. sephaena,* which has a rounded, larger pessulus) in contrast to the larger pessulus observed among spurfowls, which is rounded and triangular in *Pternistis capensis* and *P. natalensis.* Both gross and histological similarities within, and differences between, francolin and spurfowl syringes support this division. However, *O. sephaena* shows intermediate features between francolins and spurfowls.

Introduction

Syringeal characters in taxonomy and systematic studies

The syrinx or avian voice box is located in the base of the neck, at the junction of the trachea and bronchi (Ames 1971, Lewis 1983, Seller 1983, Gill 1990). It can be formed from either the tracheal or bronchial tissues, or both. Myers (1917) categorized three types of syrinx based on its location relative to the trachea and the bronchi: 'syrinx trachealis' if it is found at the lower end of the trachea, 'syrinx bronchialis' in the case where the syrinx is located below the bifurcation, and 'syrinx trachea-bronchialis' when the syrinx is located at a position that includes both the lower end of the trachea and the upper parts of the bronchi.

The syringeal structure of songbirds (Passeriformes) has been widely compared with that of non-songbirds (Frank et al. 2006), with passerine birds known to produce complex vocalizations as opposed to the relatively simple vocalizations given by many non-passerine birds. Whether the complexity of the vocalizations is dependent on the number or the complexity of the syringeal components is a question that requires detailed functional investigation of each part. This is because certain non-passerine species, e.g. cockatiels *Nymphicus hollandicus*, which are known to have only three pairs of syringeal muscles and two pairs of tracheal muscles (Larsen and Goller 2002), can mimic many types of sound (Tsukahara et al. 2008). The presence or absence of certain components of the syringes or their musculature, contribute largely to voice production, and has been found to play a significant role in the classification of birds. This is supported by evidence in studies of the syringes of the Red jungle-fowl (Chicken) *Gallus gallus*, the male Mallard Duck *Anas platyrhynchos* and the Greater

Sage-Grouse *Centrocercus urophasianus* (Myers 1917, Frank et al. 2006, Krakauer et al. 2009, respectively).

The syrinx is anatomically complex and interspecifically diverse even in species that lack special structures. Syringeal morphology has been found to be informative in many systematic studies on passerine birds, e.g. Tyrannidae (Lanyon 1986, Prum and Lanyon 1989, Mobley and Prum 1995), Pipridae (Prum 1992) and Furnariidae (Zimmer et al. 2008), as well as in non-passerines, e.g. Anatidae (Delacour and Mayr 1945, Humphrey 1955, Johnsgard 1961, Livezey 1986), Charadriiformes (Brown and Ward 1990), Falconidae (Griffiths 1994a, 1994b) and Psitacidae (Gaban-Lima and Höfling 2006). As an example of the utility of syringeal characters in non-passerines, Livezey (1986) in his phylogenetic analysis of Anseriformes studied tracheal characters and found several important synapomorphies with which to deliniate clades.

Because the demonstrated utility of syringeal characters in studies of phylogenetic relationships among non-passeriform taxa and in the spirit of using multiple lines of evidence to test hypotheses of monophyly (Templeton 1989, Farais et al. 2000, Pruett and Winker 2010), this study explored the gross anatomy and histology of francolin and spurfowl syringes, and the concordance of this feature with phylogenetic relationships supported in previous studies on this group (Crowe and Crowe 1985, Milstein and Wolff 1987, Crowe et al. 1992, Bloomer and Crowe 1998, Crowe et al. 2006, Cohen et al. 2012, Chapter 2).

This is, to my knowledge, the first truly comparative paper of syringeal morphology in francolins and spurfowls. Data on a number of lesser-known species in a group that tends to be dominated by data from a few domesticated or managed north-temperate species is presented

Taxonomy, distribution, ecology and morphology

Based on traditional morphological research, the 41 currently recognized species of francolins are placed within a single genus *Francolinus* Stephens, 1819 within the order Galliformes and family Phasianidae (Hall 1963). They are distributed throughout sub-Saharan Africa (with an isolated population of one species *Pternistis bicalcaratus* occurring in Morocco), the Middle East and Asia (Johnsgard 1988, Madge and McGowan 2002), and are adapted to a variety of habitats, comprised primarily of tropical and unforested vegetation types (McGowan 1994). All francolins have 14 tail feathers and most species are sexually monomorphic in plumage, with males having single- or double-spurred tarsi (Hall 1963, Johnsgard 1988).

However, relatively recent morphological, eco-ethological and molecular studies of francolins (Crowe and Crowe 1985, Milstein and Wolff 1987, Crowe et al. 1992, Bloomer and Crowe 1998, Crowe et al. 2006, Chapter 2) have suggested that they form two distantly related lineages: the 'true' francolins and spurfowls (Fig. 3.1). 'True' francolins (allocated to five genera: *Francolinus*, *Ortygornis* (details for taxonomic designation are in Chapter 5), *Afrocolinus* gen. nov. (details for taxonomic designation are in Chapter 5), *Peliperdix* and *Scleroptila*) are relatively small, ground-roosting birds with striped and barred rufous dorsal plumage resembling that of quails *Coturnix* spp., with only males possessing relatively small tarsal spurs. Spurfowls are placed within a single genus *Pternistis* and are generally larger, often roost in trees, and have dark dorsal plumage usually vermiculated with white or buff, and both sexes usually have spurred (often two) tarsi that are much longer in males. Furthermore, spurfowls generally emit atonal, raucous, grating advertisement calls (given at dawn and dusk), whereas francolins have more tonal, often whistling, calls (Milstein and Wolff 1987).

This distinction between the two assemblages becomes blurred owing to *O. sephaena*, the Creasted Francolin which, like other francolins, has quail-like plumage but, like spurfowls has long tarsal spurs, roosts in trees and has an advertisement call with both grating and tonal elements (Milstein and Wolff 1987). It was on the basis of this 'linking form' that Hall (1963) decided to place all 41 species into a single genus, *Francolinus*, which DNA-based data no longer supports (Fig. 3.1). In this context, the aim of this study was to examine the gross morphological and histological anatomical structure of the syringes of selected francolins, spurfowls and their putative sister taxa, as well as to determine whether there are any syringeal characters that could be taxonomically and phylogenetically informative in investigating the proposed diphyletic status of the 'true' francolins and spurfowls.

Materials and methods

Syringeal sampling (gross morphology and anatomy)

Syringes were examined from species that are representative of francolins and spurfowls and those that are from their closest extant relatives (Table 3.1): Common Quail *Coturnix coturnix* and Chukar Partridge *Alectoris chukar* (sister to the spurfowls), *G. gallus* (sister to the francolins), and Helmeted Guineafowl *Numida meleagris*, a distant relative to chickens, quails, partridges, francolins and spurfowls (Chapter 2).

It is appropriate at this point to highlight some of the differences between the syringes of male and female birds. As explained by Frank et al. (2007), the syrinx of male and female birds may have morphological differences that in turn could alter the properties of the voices of each sex. However, Appel (1929) did not find differences between the syringes of males and females in his research on the chicken *Gallus gallus*, a galliform he studied intensively, even in ovariectomised females. Syringes from immature birds were avoided in order to ensure that differences found between syringes were not because of age differences between individuals. As Hogg (1982) described for Galliformes, mineralisation begins well before maturity is reached and virtually achieves its final extent during the growing period, so all adult birds are considered to have a fully developed syrinx. Of course, it would be ideal to confirm our observations by analysing more individuals of each of the species and in particular a developmental sequence of one or more taxa, but this comparative material is at present not available. Thus, the difficulty of acquiring multiple syringeal samples (represented by male and female individuals of a particular species) and the inability to physically sex some of the specimens were major constraints.

Analyses

All syringes examined for gross morphological and anatomical purposes were dissected from frozen whole bird specimens with the exception of three syringes that were dissected from alcohol-preserved whole specimens provided by the Ditsong National Museum of Natural History, South Africa. The syringes were immersed in 70% ethanol until such time that they were processed.

Gross syrynx morphology

The double-staining protocol in Cannell (1988) for the clearing and staining procedures of the syringes was followed. Ossified tissues stained red with Alizarin red, cartilaginous tissues stained blue with Alcian blue, and muscles stained brownish in Lugol solution. Cleared and stained syringes were examined using a Leica S8APO stereomicroscope and the LAS EZ version 1.7.0 software. Syringes of large birds such as *Gallus gallus, Numida meleagris, Pternistis capensis, P. swainsonii* and *P. natalensis* were stained for a few additional days relative to those excised from the smaller francolins.

Histology

For the tissue-sectioning procedure, the syringes were transferred from 70% ethanol to 10% buffered formalin overnight and then taken through a series of 70%, 90% and absolute ethanol washes before being cleared in xylene (1 h in each solution). They were then embedded in paraffin wax and longitudinal sections of 5 μm thickness were cut. Two stains were used, haematoxylin and eosin (Bancroft and Gamble 2002) for more general biological examination, and a more specialised multiple stain, orcein-picroindigocarmine (Steven et al. 2000). The orcein-picroindigocarmine stain is appropriate for staining bird syringes since it has the potential to differentiate tissues and their components.

Tissue sections were stained with orcein, indigocarmine and picric acid following the Steven et al. (2000) protocol. The sections were deparaffinised and placed in distilled water, stained with orcein solution for 45 min at room temperature and rinsed in distilled water. Sections were then differentiated in 96% ethyl alcohol (two times) for 30 s each, rinsed in distilled water and stained with picroindigocarmine solution for 30 min. Slides were drained and differentiated in 70% ethyl alcohol for 2 min and finally mounted with Entellan and examined using a Nikon Stereoscopic Zoom microscope (NIS-Elements version 2.10). The sectioning of tissues was more difficult for the larger birds examined and this was a contributing factor in the distortion of those sections. Finally, even though the staining of whole syringes and the sectioning of samples of larger syringes was challenging, most of the stained syringes and sections were intact and clear with the exceptions of Figure 3.5d and 3.6f.

Results

Syringeal gross morphology

The basic structure of the syringeal morphology (Fig. 3.2) of a typical francolin/spurfowl is characterised by cartilaginous rings (which stained blue with Alcian blue), a very distinctive mineralized tympanum (which stained red with Alizarin red) and muscles (which stained brownish in Lugol solution). All the species analysed have a typical 'tracheobronchialis' type of syrinx (Fig. 3.3-3.5), which means that both the tracheal and the bronchial tissues are involved in the formation of the syrinx and thus possibly in shaping the structure of their vocalizations.

Two significant gross morphological differences between true francolins and spurfowls were observed. Firstly, unlike their putative sister taxon *G. gallus*, which has a mineralized triangular-shaped tympanum (Fig 3.4a), francolins (Fig. 3.4b–f) and *N. meleagris* (Fig. 3.3) have a shield-like calcified tympanum clearly visible from the ventral perspective (Fig. 3.3). *Numida meleagris*, *G. gallus* and francolins show extensive mineral deposition in the tympanum in both ventral and dorsal views but Coqui Francolin *Peliperdix coqui* and Red-winged Francolin *Scleroptila levaillantii* (Fig. 3.4c and d, respectively) show reduced mineral deposition on the dorsal side compared with the ventral side.

In spurfowls, as in their putative sister taxa *A. chukar* and *C. coturnix* (Fig. 3.5a and b, respectively), the tympanum is diamond-shaped with the degree of calcification not as extensive as in francolins and relatives (Fig. 3.5c–e). Secondly, on the ventral side, the first bronchial half rings are well mineralized in *G. gallus* (Fig. 3.4a) and francolins (Fig. 3.4c, d and f), but not so in *O. sephaena* (Fig. 3.4b), spurfowls (Fig. 3.5c–e) and their relatives, *A. chukar* and *C. coturnix* (Fig. 3.5a and b). A further observation is that some species such as *S. levaillantoides*, *G. gallus* and *N. meleagris* show mineral deposition in some tracheal rings.

Histology

The histological structure of the syringes of francolins, spurfowls and their near relatives are generally similar, with only a few small differences observed (Fig. 3.6). The pessulus, which is present in all the species examined (Fig. 3.6a–h), varies considerably in size and shape. It is generally small and rounded in the two true francolins, i.e. *S. levaillantii* and Grey-winged Francolin *S. afra*, and *N. meleagris* (Fig. 3.6a, b and h, respectively) (Table 3.3). The pessulus is large and also rounded in *O. sephaena* (Fig. 3.6c) and in spurfowls even though it is almost triangular in Natal Spurfowl *Pternistis natalensis* (Fig. 3.6f) and *C. coturnix* (Fig. 3.6g). It is markedly large and triangular in *G. gallus* (Fig. 3.6d, see also Myers 1917).

A distinctive interclavicular air sac, which is bound by the internal tympaniform membrane, is found in the two francolins (*S. levaillantii* and *S. afra),* Cape Spurfowl *Pternistis capensis*, *C. coturnix* and *N. meleagris* (Fig. 3.6a, b, e, g and h, respectively) and is absent in *O. sephaena* and *G. gallus* (Fig. 3.6c and d, respectively), while its presence could not be determined in *P. natalensis* (Fig. 3.6f). It was observed that the inner wall of the interclavicular air sac and sometimes the medial bronchial wall are lined with a layer of connective tissue that differs in thickness. Connective tissue fills spaces and provides support to organs. The francolins *S. levaillantii* and *S. afra* (Fig. 3.6a and b) and their relative *G. gallus* (Fig 3.6d) have thin connective tissue lining the walls of the membranes that tends to be moderate in *P. natalensis*, *C. coturnix* and *N. meleagris* (Fig 3.6f, g and h, respectively). *Numida meleagris* has connective lining that runs along the medial bronchial walls. *Pternistis capensis* (Fig 3.6e), as in *O. sephaena* (Fig 3.6c), has a large amount of connective tissue that is restricted to the far corners of the internal tympaniform membrane. This tissue pushes against the internal tympaniform membrane forcing it to expand and hence results in the narrowing of the surrounding airway. The external tympaniform membrane, which is found in all the species examined, differs remarkably in length. This structure is extremely long in *G. gallus* (Fig. 3.6d) and much shorter in the other species (Fig. 3.6a–c and e–h).

Discussion

Although a limited number of species were sampled, there are some marked structural differences in the syrinx that distinguish francolins from spurfowls. The gross morphology of the syrinx is generally consistent and supports the split of francolins and spurfowls into two independent clades. The shape of the tympanum places *O. sephaena* decisively with other francolins. However, *O. sephaena*, as in the two spurfowls *P. capensis* and *P. natalensis* and their evolutionary relatives *C. coturnix* and *A. chukar*, shows no mineral deposition in their first bronchial half rings with *P. swainsonii* showing short first bronchial half rings with very little mineralization. Thus, the aspect of mineral deposition is not fully consistent among francolins and spurfowls. Our observation on the degree of mineralisation in tracheal rings of *S. levaillantoides*, *G. Gallus* and *N. meleagris* could not at this stage translate to any coherent conclusion apart from the fact that a similar observation was made by Hogg (1982), thought this could have to do with conferring rigidity in the tracheal rings, which is an adaptation to vocalization.

With regard to the histology of the syringes, the features that separate francolins from spurfowls are based on the size of the pessulus. There is variation in the shape of the pessulus, the presence/absence of the defined interclavicular air sac and the amount of connective tissue such that differences are observed even between the two spurfowl species. However, the amount of connective tissue puts species with tonal and whistling calls together (*S. levaillantii* and *S. afra*), separated from those that have atonal, raucous and grating calls (*P. capensis, P. natalensis* and *O. sephaena*). This feature could be related to differences in sounds between them, given that whistle-like sounds could be generated by shearing forces as a column of air is forced through a narrow aperture (see Gaunt et al. 1982), and the connective tissue could exert pressure to modify the lumen of the syrinx, which could be considered the column through which air passes, generating the sound. At first glance, this explanation would be contrary to what we would expect, given that spurfowls have thick connective tissue that would narrow their syrinx, but they have raucous calls. However, we know the syrinx is only one component in a vocal system (Gaunt et al. 1982) and other factors may be modulating the final sound we hear.

Conclusions

A number of gross morphological and histological features were identified as differentiating francolins from spurfowls (though with *O. sephaena* being a possible exception). What emerged as an area for future research was investigation into the role of each part of the syrinx in shaping francolin and spurfowl vocalizations, as well as the need to include other galliform species in addition to the sampled francolin and spurfowl taxa. This will require a reasonable number of individuals to be sampled per species, such that any presence or absence of intra- or inter-specific variation can be determined. Finally, it could be concluded that the outcome of this work points to the distinction between francolin and spurfowl assemblages with *O. sephaena* (as indicated in Hall 1963) still presenting some difficulties owing to its possession of characteristic features that are typical of both francolins and spurfowls.

Tables and Figures

Table 3.1. List of species for which syrinxes were analyzed.

Gross morphology					Histology			
Common name	Scientific name	Sample name[1]	Sex[2]	Age	Scientific name	Sample Name[1]	Sex[2]	Age
Grey-winged Francolin	*Scleroptila afra*	TMC67	M	Adult	*S. afra*	TMC01	F	Adult
Orange River Francolin	*S. levaillantoides*	TMC65	F	Adult				
Red-winged Francolin	*S. levaillantii*	TMC60	F	Adult	*S. levaillantii*	TMC15	F	Adult
Crested Francolin	*Ortygornis sephaena*	TM78245	M	Adult	*O. sephaena*	TMC13	M	Adult
Coqui Francolin	*Peliperdix coqui*	TM75627	F	Adult				
Cape Spurfowl	*Pternistis capensis*	TMC70	M	Adult	*P. capensis*	TMC07	M	Adult
Swainson's Spurfowl	*P. swainsonii*	TMC48	M	Adult				
Natal Spurfowl	*P. natalensis*	TM60042	?	Adult	*P. natalensis*	TMC20	M	Adult
Common Quail	*Coturnix coturnix*	TMC50	F	Adult	*C. coturnix*	TMC14	F	Adult
Chukar Partridge	*Alectoris chukar*	TM74489	?	?				
Helmeted Guineafowl	*Numida meleagris*	TMC45	M	Adult	*N. meleagris*	TMC17	F	Adult
Chicken/Red Jungle Fowl	*Gallus gallus*	TMC30	?	Adult	*G. gallus*	TMC02	?	Adult

[1]TM, Transvaal Museum; TMC, Timothy M Crowe (Percy FitzPatrick Institute of African Ornithology, (University of Cape Town).
[2]? = Unknown.

Table 3.2. Comparison of gross morphological features of the syringes.

Taxon	Tympanum shape	Bronchial half ring 1 mineralization	Tracheal ring mineralization
S. afra	Shield-like	Mineralized	Non-mineralized
S. levaillantoides	Shield-like	Mineralized	Mineralized
S. levaillantii	Shield-like	Mineralized	Non-mineralized
O. sephaena	Shield-like	Non-mineralized	Non-mineralized
P. coqui	Shield-like	Mineralized	Non-mineralized
P. capensis	Diamond	Non-mineralized	Non-mineralized
P. swainsonii	Diamond	Mineralized	Non-mineralized
P. natalensis	Diamond	Non-mineralized	Non-mineralized
C. coturnix	Diamond	Non-mineralized	Non-mineralized
A. chukar	Diamond	Non-mineralized	Non-mineralized
N. meleagris	Shield-like	Mineralized	Mineralized
G. gallus	Triangular	Mineralized	Mineralized

Table 3.3. Comparison of the histological features of syringes.

Taxon	Pessulus shape & size	Interclavicular air sac	Amount of connective tissue	External tympaniform membrane
S. afra	Rounded, small	Bound by internal tympaniform membrane	Thin	Shorter
S. levaillantii	Rounded, small	Bound by internal tympaniform membrane	Thin	Shorter
O. sephaena	Rounded, larger	Absent	Thick	Shorter
P. capensis	Rounded, larger	Bound by internal tympaniform membrane	Thick	Shorter
P. natalensis	Triangular, larger	?	Moderate	Shorter
C. coturnix	Triangular, larger	Bound by internal tympaniform membrane	Thin	Shorter
N. meleagris	Rounded, small	Bound by internal tympaniform membrane	Thin	Shorter
G. gallus	Triangular, larger	Absent	Thin	Long

? = Presence or absence of feature cannot be determined from distorted tissue section.

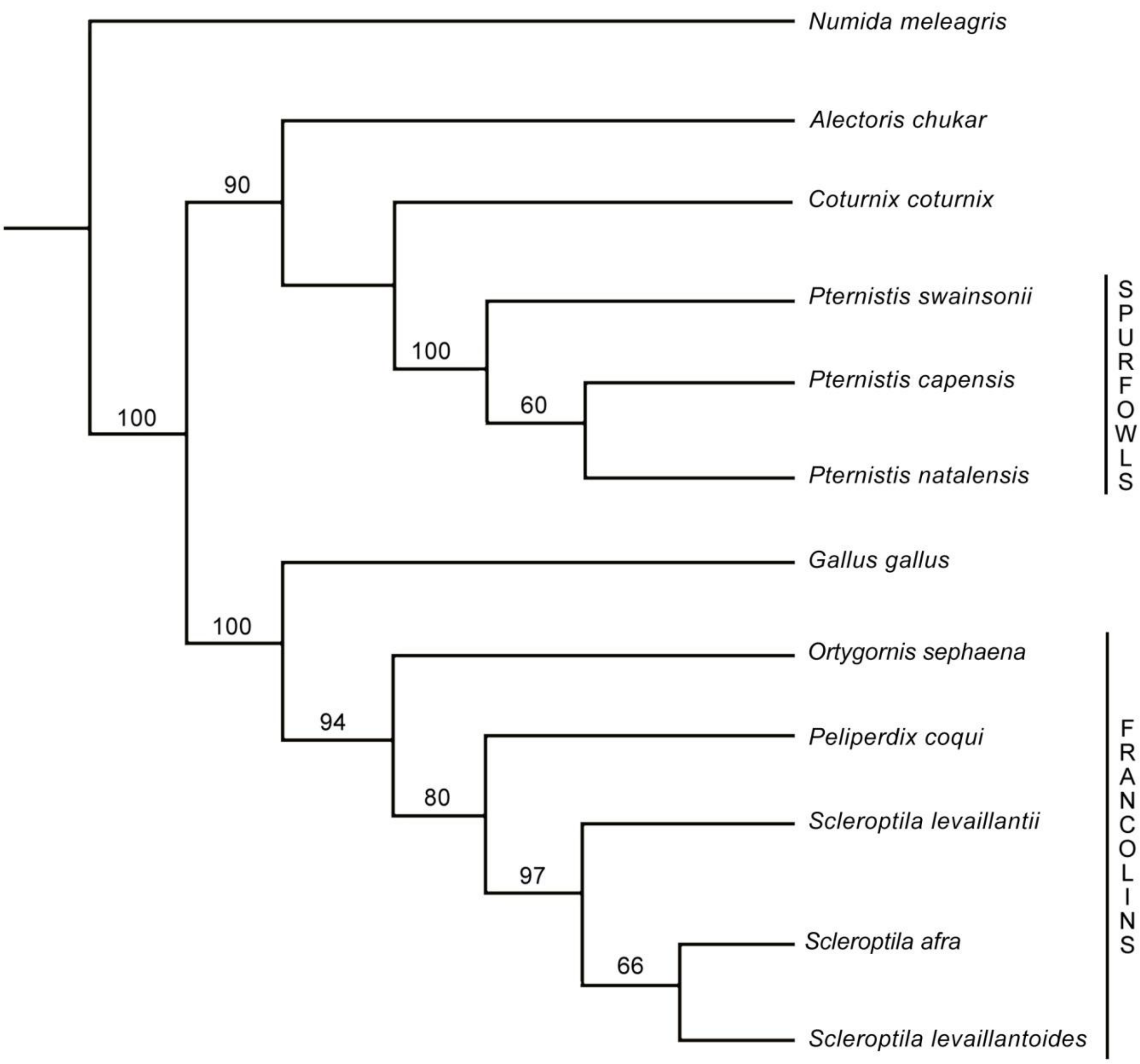


Figure 3.1. Strict consensus cladogram for some 'true' francolins (*Ortygornis*, *Peliperdix* and *Scleroptila* spp.) and spurfowls (*Pternistis* spp.) modified from Crowe et al. (2006). Numbers at nodes are jackknife support values.

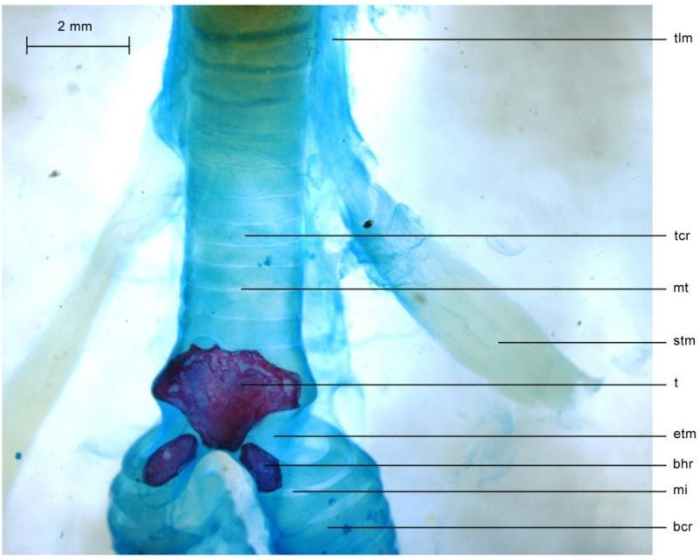
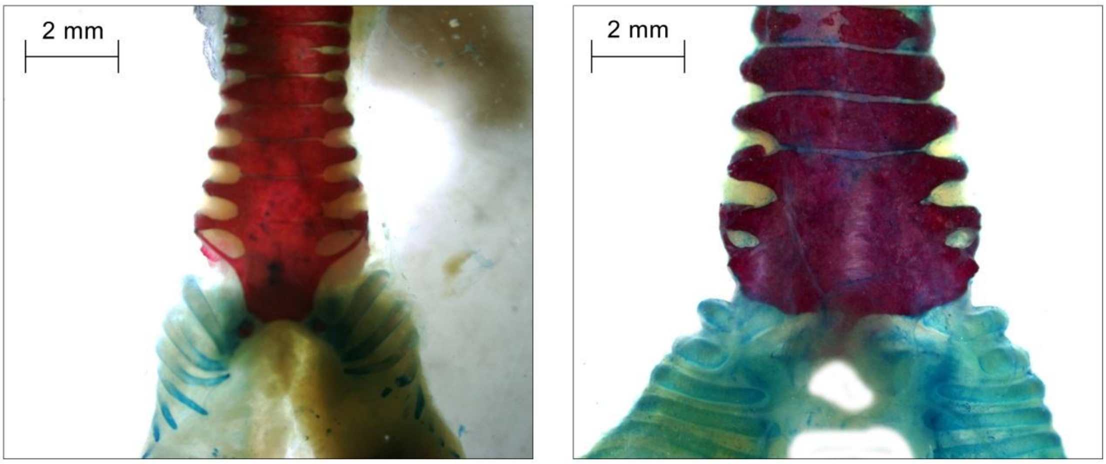


Figure 3.2. Example of a ventral view of the syrinx of a typical Coqui Francolin *Peliperdix coqui* with illustrations of the various parts. Labels: tracheo-lateralis muscle (tlm), tracheal cartilaginous ring (tcr), membrana-trachealis (mt), sterno-trachealis muscle (stm), tympanum (t), external tympaniform membrane (etm), bronchial half ring 1 (bhr1), membrane-interanularis (mi), bronchus cartilaginous ring (bcr). Red colour - mineralized cartilage, blue - cartilage, transparent light brown - muscle.



Numida meleagris (ventral)   *N. meleagris* (dorsal)

Figure 3.3. Ventral (V) and dorsal (D) views o f the syrinx of Helmeted Guineafowl *Numida meleagris*. Red colour - mineralized cartilage, blue - cartilage, transparent light brown - muscle.

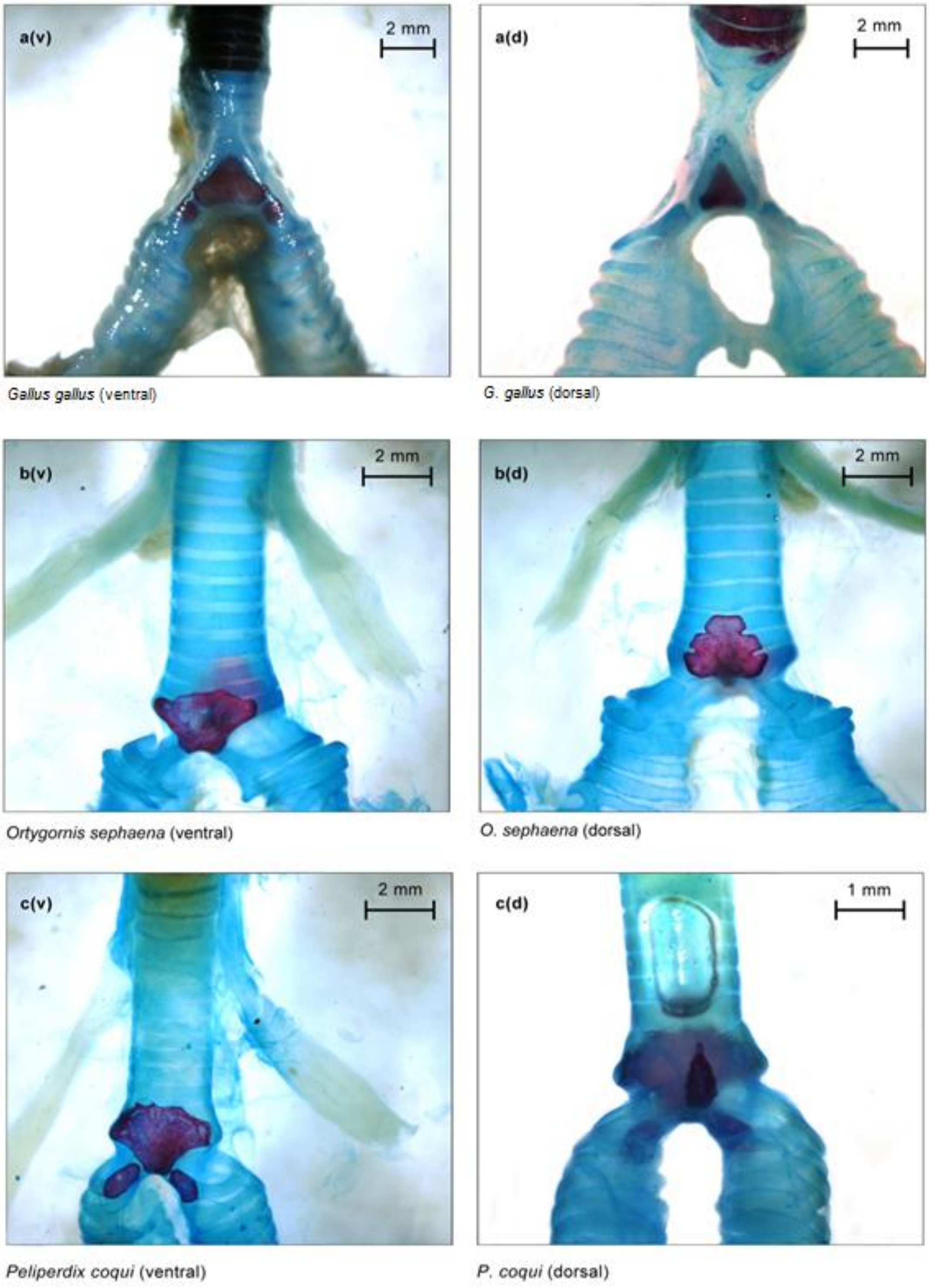


Figure 3.4. Ventral (V) and dorsal (D) views of the syringes of: a. *Gallus gallus*, b. *Ortygornis sephaena*, c. *Peliperdix coqui*, d. *Scleroptila levaillantii*, e. Orange River Francolin *S. levaillantoides* and f. *S. afra*. Red colour - mineralized cartilage, blue - cartilage, transparent light brown - muscle.

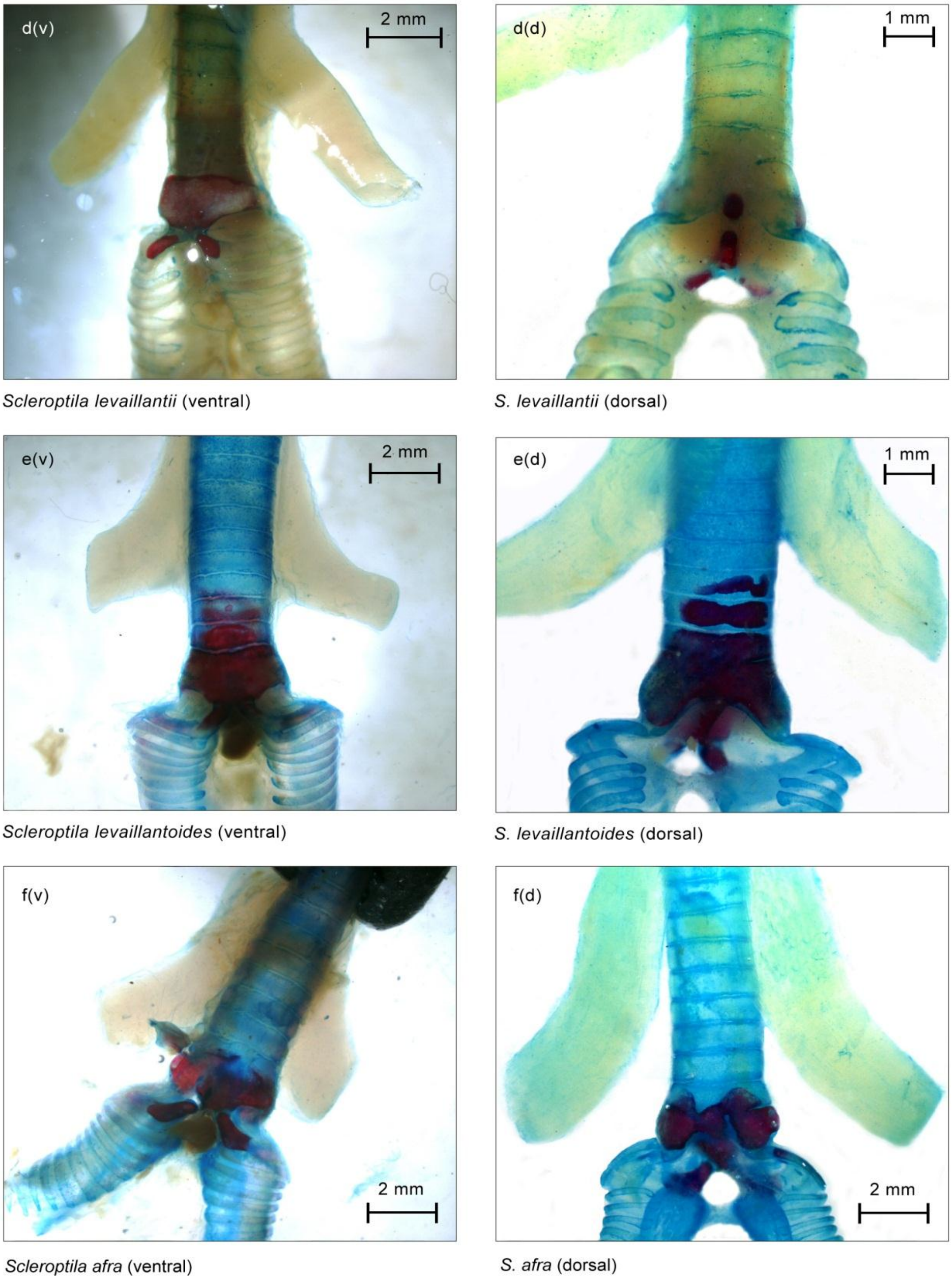


Figure 3.4 (concl.). Ventral (V) and dorsal (D) views of the syringes of: a. *Gallus domesticus*, b. *Ortygornis sephaena*, c. *Peliperdix coqui*, d. *Scleroptila levaillantii*, e. Orange River Francolin *S. levaillantoides* and f. *S. afra*. Red colour - mineralized cartilage, blue - cartilage, transparent light brown - muscle.

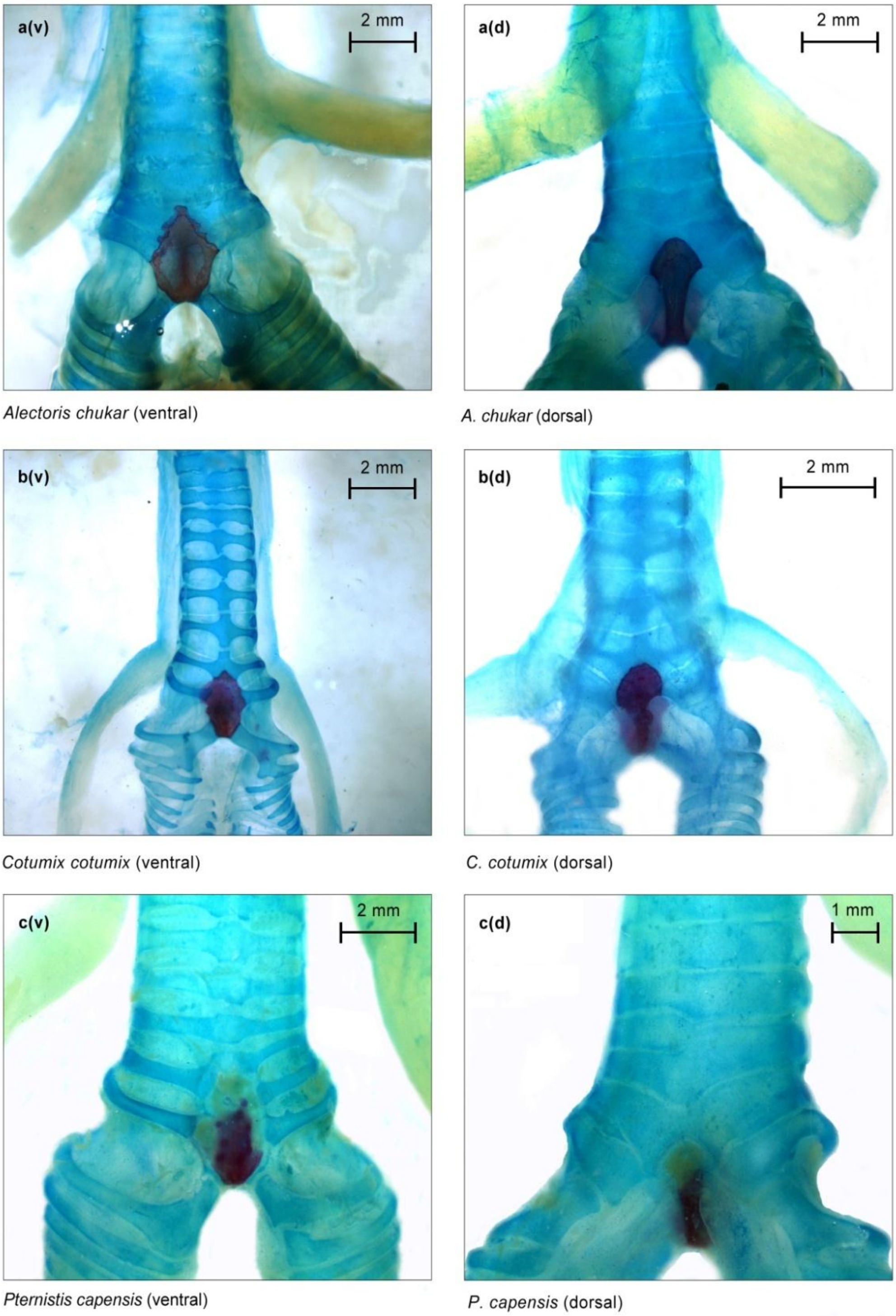


Figure 3.5. Ventral (V) and dorsal (D) views of the syringes of: a. *Alectoris chukar*, b. *Coturnix coturnix*, c. *Pternistis natalensis*, d. *P. capensis*, e. Swainson's Spurfowl *P. swainsonii*. Red colour - mineralized cartilage, blue - cartilage, transparent light brown - muscle.

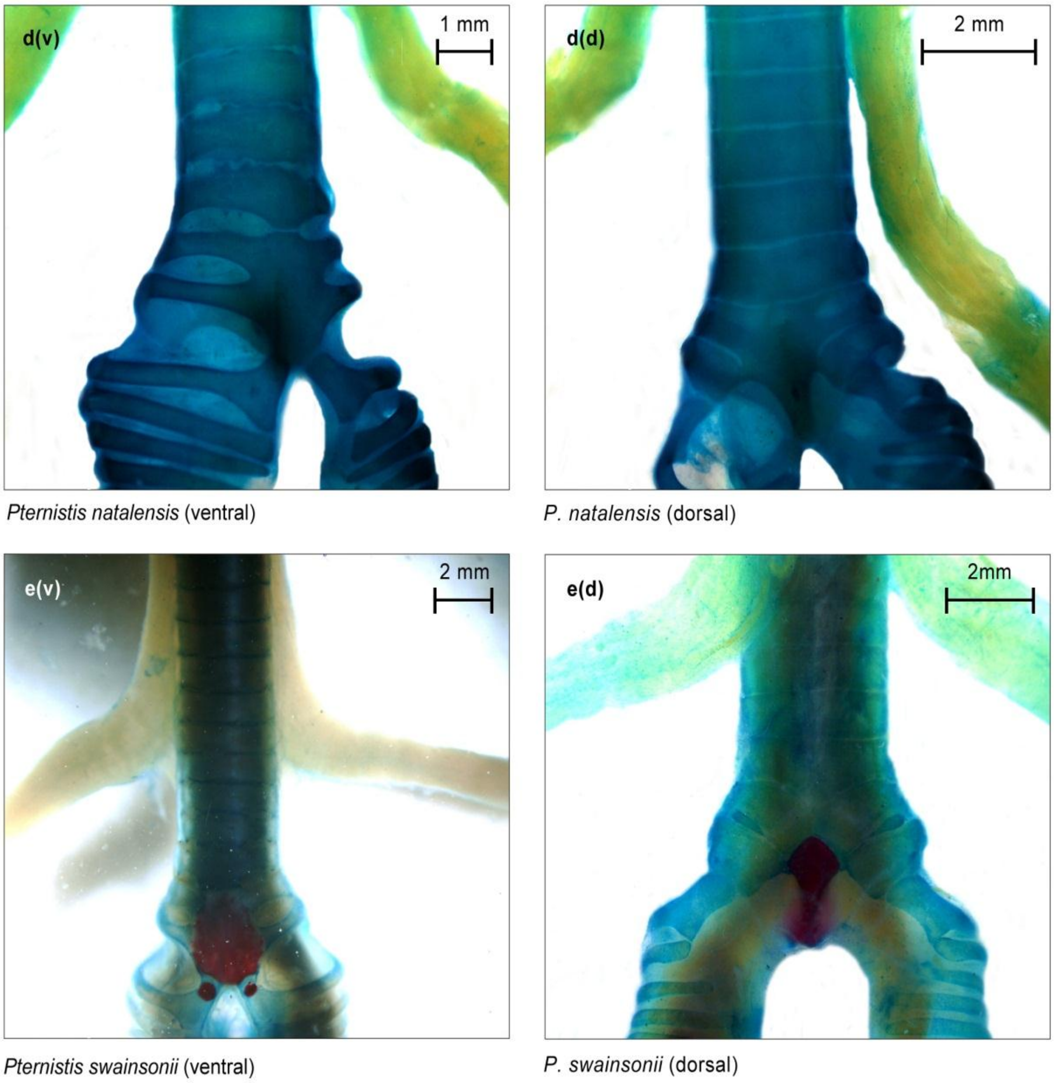
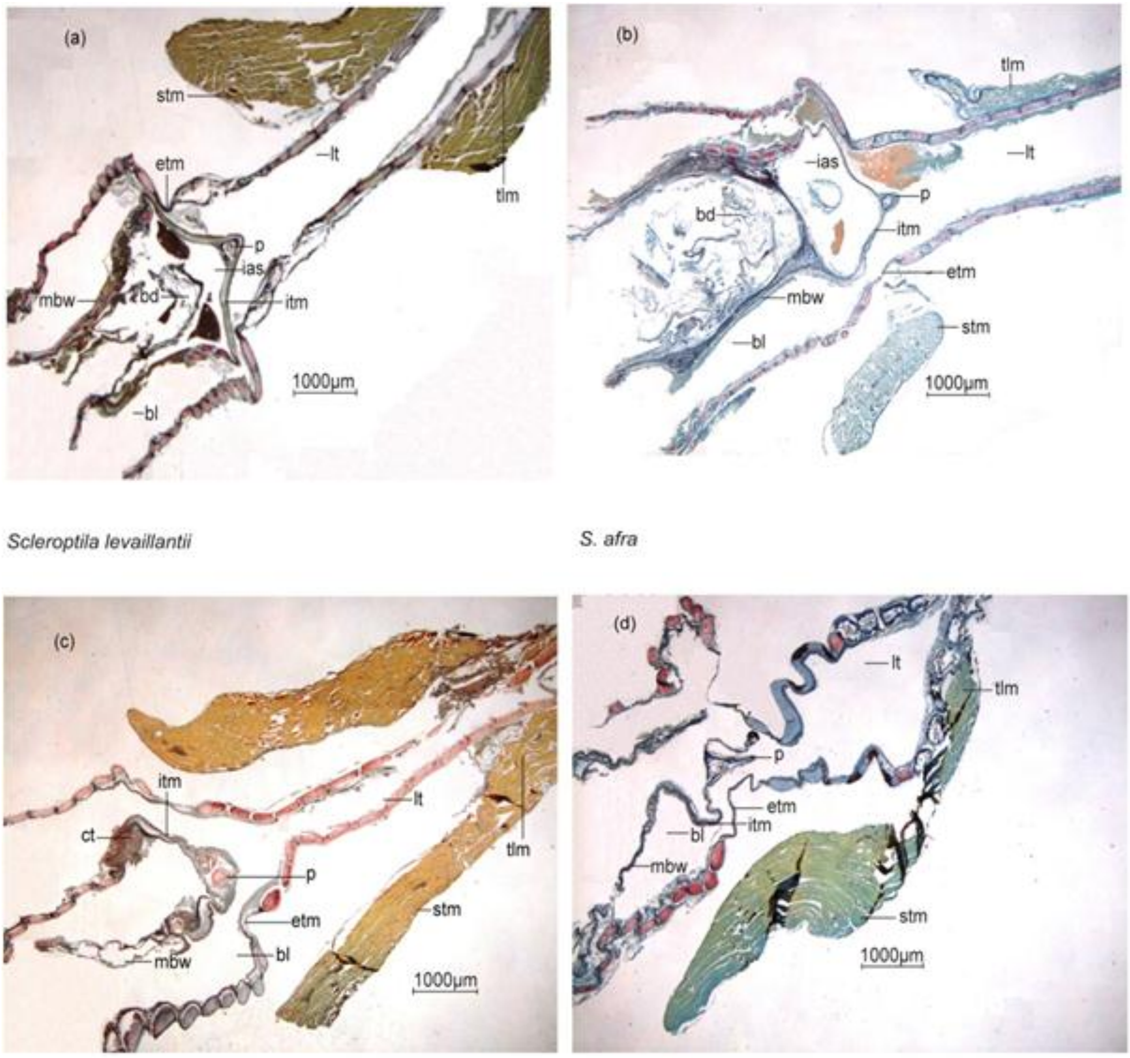


Figure 3.5 (concl.). Ventral (V) and dorsal (D) views of the syringes of: a. *Alectoris chukar*, b. *Coturnix coturnix*, c. *Pternistis natalensis*, d. *P. capensis*, e. Swainson's Spurfowl *P. swainsonii*. Red colour - mineralized cartilage, blue - cartilage, transparent light brown - muscle.



Scleroptila levaillantii *S. afra*

Ortygornis sephaena *Gallus gallus*

Figure 3.6. Histological structure of the syringes of francolins (*a. S. levaillantii*, b. *S. afra* and c. *O. sephaena*), d. Chicken *G. gallus*, spurfowls (e. *P. capensis* and f. *P. natalensis*), g. Common Quail *C. coturnix* and h. Helmeted Guineafowl *N. meleagris*. References: tracheo-lateralis muscle (tlm), lumen of trachea (lt), interclavicular air sac (ias), connective tissue (ct), pessulus (p), internal tympaniform membrane (itm), external tympaniform membrane (etm), medial bronchial wall (mbw), bronchiodesmus (bd), bronchial lumen (bl), sterno-trachealis muscle (stm).

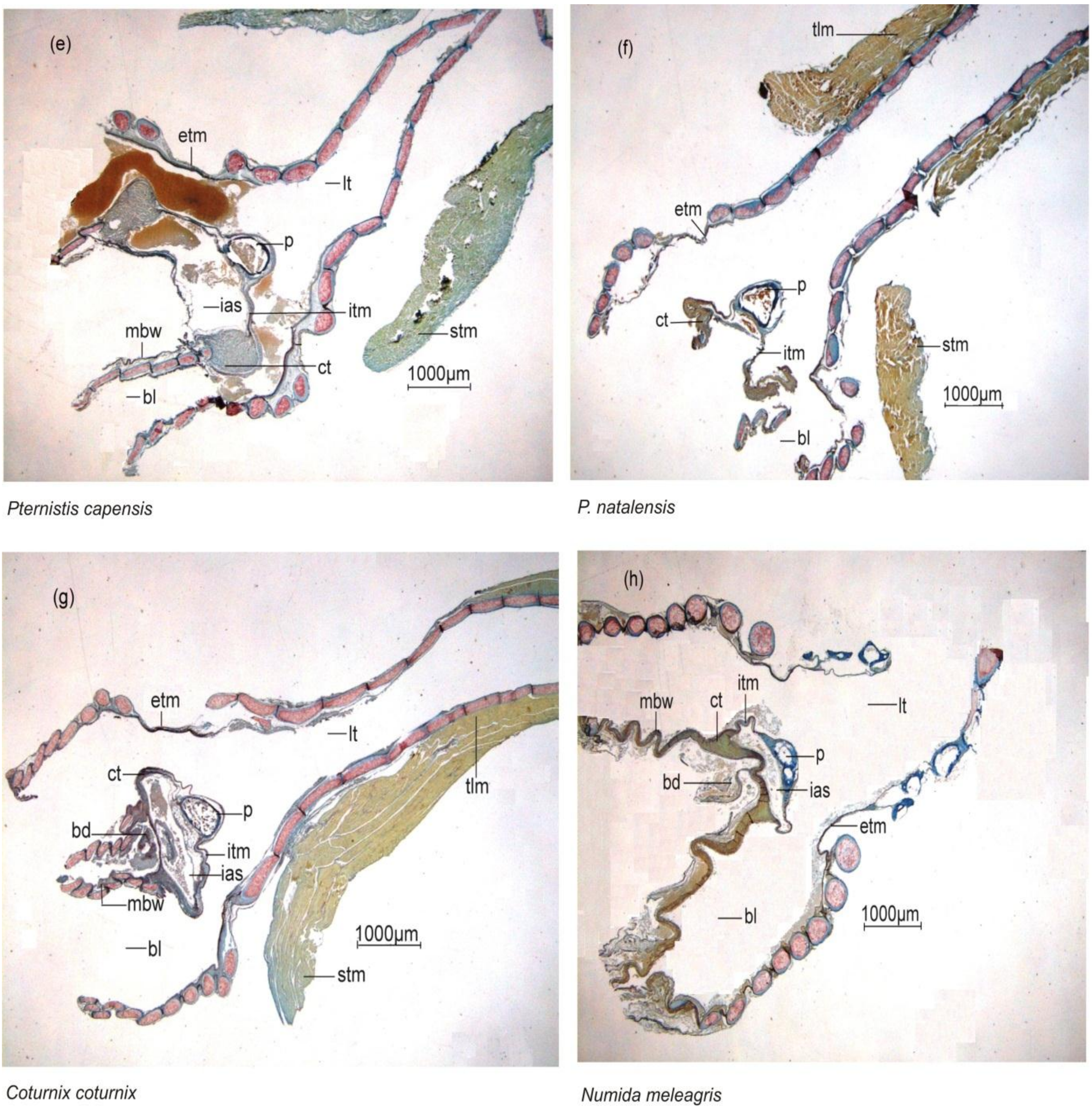


Figure 3.6 (concl.). Histological structure of the syringes of francolins (*a. S. levaillantii*, b. *S. afra* and c. *O. sephaena*), d. Chicken *G. gallus*, spurfowls (e. *P. capensis* and f. *P. natalensis*), g. Common Quail *C. coturnix* and h. helmeted guineafowl *N. meleagris*. Labels: tracheo-lateralis muscle (tlm), lumen of trachea (lt), interclavicular air sac (ias), connective tissue (ct), pessulus (p), internal tympaniform membrane (itm), external tympaniform membrane (etm), medial bronchial wall (mbw), bronchiodesmus (bd), bronchial lumen (bl), sterno-trachealis muscle (stm).

CHAPTER 4

Taxonomic and phylogenetic utility of variation in advertising calls of francolins and spurfowls (Galliformes: Phasianidae)

Abstract

Systematists have not often made use of avian vocalizations to assess the taxonomic rank of birds, or to infer their phylogenetic relationships. The likely reasons for this stem from the perceived inability to distinguish genetic and ecological components of variation in vocalizations, the difficulty in detecting homology across taxa, as well as the diverse selection pressures acting on vocal characters which may make such characters particularly prone to convergent evolution. In this study, we scored and analysed DNA and vocal characters of two delineated assemblages of gamebirds, francolins and spurfowls. Our phylogenetic results suggest that short strophes evolved from longer strophes among taxa within the genera *Scleroptila* and *Peliperdix.* More generally, our results corroborate the francolin-spurfowl dichotomy, with francolin calls generally being long and tonal, containing a series of discrete elements that have detectable harmonics. In contrast, most spurfowls render short, atonal calls with elements that generally have no harmonics, although they may contain discrete elements. Phylogenetically, *Ortygornis sephaena* is placed decisively with 'true' francolins and its closest relatives are the two phylogenetically enigmatic Asian

francolins, the Grey Francolin *Ortygornis pondicerianus* and Swamp Francolin *O. gularis*.

Introduction

Vocalizations are a means of communication and are often of special significance in the social behaviour of animals, and birds in particular. Many birds rely on acoustic signals to convey information to each other over long distances, in dense cover, and at night (Marler 1969, Gill 1990). Systematists have not often made use of vocalizations to assess the taxonomic rank of birds, or to infer their phylogenetic relationships. Possible reasons for this may stem from the perceived inability to distinguish genetic and ecological components of vocalizations (McCracken and Sheldon 1997), as well as the difficulty in detecting homology across taxa (Lanyon 1969). Further, McCracken and Sheldon (1997) maintain that the diverse selection pressures acting on vocal characters may make such characters particularly prone to convergent evolution. For example, species that live in dense vegetation tend to have vocalizations with lower frequencies and narrower frequency ranges than those that inhabit open habitats (Morton 1975). This is because longer wavelengths propagate energy more efficiently through vegetation than shorter wavelengths, which attenuate due to the scattering effects of the vegetation. In addition, several bird species from diverse clades have repertoires of many distinct song types, whereas others have just one simple and stereotyped song or call (Price and Lanyon 2002, Lei et al. 2005), and some species learn the songs of other species, often making it difficult to distinguish homologous components from learned songs (Lei et al. 2005). Other confounding factors include the possibility that parts of the song may change in response to different seasons (Lei et al. 2005, Aubrecht and Holzer 2000, Frank et al. 2007), as well as morphological constraints of the syrinx (McCracken and Sheldon 1997). Finally, bird song usually plays a strong role in mate recognition, and is thus under strong sexual selection, and thereby adapted to the environment in which signalling is taking place (Price and Lanyon 2002). Despite the above caveats, over the past two decades, authors have started to place greater emphasis on exploring the systematic utility of vocal character variation (Enggist-Düblin and Birkhead 1992, Alström 2001, Price and Lanyon 2002, Päckert et al. 2003, Lei et al. 2005, Farnsworth and Lovette 2008).

Non-singing gamebirds such as francolins belonging to the genera *Francolinus* Stephens, 1819, *Ortygornis* Reichenbach, 1852 (see Chapter 5 for details in taxonomic designations), *Afrocolinus* gen. nov. (Mandiwana-Neudani, this thesis) (see Chapter 5 for details in taxonomic designations), *Peliperdix* Bonaparte, 1856 and *Scleroptila* Blyth, 1849, as well as spurfowls *Pternistis* Wagler, 1832, are known to have a few stereotyped call types making up their repertoires (van Niekerk 2010). Furthermore, francolins and spurfowls appear to not be able to learn the calls of other related species (Milstein and Wolff 1987). Here we explore the taxonomic and phylogenetic utility of francolin and spurfowl 'advertisement' calls, that is those calls usually heard at dawn and dusk, primarily during the breeding season.

Systematics

Genus Francolinus Stephens, 1819

Hall's (1963) monograph of 'francolins' *sensu lato* placed 41 traditionally recognized species into a single genus *Francolinus*, with 37 species partitioned into eight putative monophyletic groups of related species and four unplaced species (Hall 1963, Table 1.1). Seven groups have representatives in Africa south of the Sahara, and one group is confined to the Middle East and Asia. The current phylogenetic treatment divides francolins into two distantly related groups of phasianine Galliforms: 'francolins' (shared among genera *Francolinus*, *Ortygornis, Afrocolinus*, *Scleroptila*, *Peliperdix*) and 'spurfowls', all classified in one genus *Pternistis* (Milstein and Wolff 1987, Crowe et al. 1992, Crowe et al. 2006, Mandiwana-Neudani, this thesis). Among attributes that distinguish francolins from spurfowls, is the difference in the acoustic properties of their advertising calls. Aurally, most spurfowl species have raucous grating or cackling calls whereas francolins tend to have more musical and whistling calls (Crowe et al. 1986, Milstein and Wolff 1987, Crowe et al. 1992). Furthermore, spurfowls can perch in trees or other elevated structures and have scaly or striped underpart plumage, whereas francolins roost on the ground and generally have barred, blotched or uniform underparts and quail-like back plumage. However, the above distinction does not apply well to the Crested Francolin *O. sephaena* because it has attributes of both francolins and spurfowls. It is relatively small, but emits a somewhat raucous call and roosts in trees like many spurfowls. Thus, it is the 'linking form' that persuaded Hall (1963) to include all 41 species into a single genus *Francolinus.*

In this study, auditory, visual and quantitative descriptions of the advertising calls of francolins and spurfowls are analysed in order to assess their phylogenetic utility, investigate the validity of the francolin-spurfowl dichotomy and to assess variation between putative related species.

Materials and methods

Collection of data

Call sampling

The calls were sourced from various institutional sound libraries and published collections of recordings (Table 4.1), although many were unfortunately of poor quality.

Sonograms posted online at Xeno-canto [http://www.xeno-canto.org/] were also examined, but were also mostly of poor quality. Frank et al. (2007) highlighted that the syrinx of male and female birds may differ morphologically, which could in turn determine the properties of their voices. However, given the difficulty in gathering multiple vocalizations (for male and female individuals of a particular species), lack of precise knowledge about the habitat from which the sourced call recordings were collected, and often lack of knowledge as to whether the recorder actually saw the bird in close proximity or not, we decided to analyse only the best quality calls and as a consequence we were not always able to account for sex and/or the specific habitat the bird was recorded in for all taxa.

Phylogenetic sampling

Molecular characters

Twenty terminal taxa of francolins (including two outgroups - *Gallus gallus* and *Bambusicola thoracica*) and 24 spurfowl taxa (with two outgroups - *Coturnix coturnix* and *Alectoris chukar*) were sequenced for the mitochondrial Cytochrome-*b* gene (CYT*B* - 1143 base pairs- bp; Table 4.2). In contrast to the earlier work of Crowe et al. (1992) and Bloomer and Crowe (1998), which focused on relatively few species, almost all traditionally recognized species were included in our sampling. Total genomic DNA was extracted from tissue using the animal tissue protocol provided with the DNeasy tissue kit (Qiagen). Primers used in sequencing CYT*B* gene for fresh tissues and from museum toe-pads are detailed in Table 4.3. Double stranded DNA templates were amplified by polymerase chain reaction (PCR) using 0.75 units of BIOTAQ^{TM} DNA polymerase (Bioline) in 30 µl reactions. Reactions also contained 1 x NH_4 buffer, 2.5

mM $MgCl_2$, each dNTP at 0.1 mM and each primer at 0.3 µM, as well as 3 µl of template DNA. The thermal profile used comprised an initial denaturation step at 94°C for two minutes, followed by 30 cycles of 94°C for one minute, 52°C for one minute and 72°C for two minutes, with a final extension step of 72°C for seven minutes.

PCR-amplified products were cleaned from solution or gel using the GFX™ PCR DNA and gel band purification kit (Amersham Biosciences) prior to cycle-sequencing with the ABI PRISM Big Dye™ Terminator v3.1 cycle-sequencing Ready Reaction Kit (Applied Biosystems). Sequencing products were resolved on an ABI PRISM 3100 Genetic Analyser.

Vocal characters

Twenty terminal taxa of francolins (including two outgroups - *Gallus gallus* and *Bambusicola thoracica*) and 24 spurfowl taxa (with two outgroups - *Coturnix coturnix* and *Alectoris chukar*) were sampled and character matrices of vocal characters for the francolins (Table 4.4.) and the spurfowls (Table 4.5) were generated. All calls (in wave format) were analysed using a Linux-based software package 'ANA' (Jean-Pierre Richard, Unpublished version). Multiple recordings of the calls of most species were analysed to examine intraspecific variation and also to assess the quality of the calls for each species. The terminology used hereafter is: strophe, element and pause (following Alström et al. 2008) (Fig. 4.1). A 'strophe' is a call that may be repeated multiple times in sequence and is comprised of elements that are defined as parts within a strophe separated by a pause of duration of at least 0.01s. A 'pause' is an interval between the elements of a strophe. Strophe duration was measured from the start of the first element to the end of the last element on oscillograms and not on sonograms, in order to maximise accuracy.

Sonograms with different acoustic properties were produced. The strophe variables: strophe length; number of elements in a strophe; number of introductory elements in a strophe; nature of the strophe in terms of whether it contains a harmonic or trill; raucousness of advertisement; presence and absence of a warbling ending to the strophe; whether the strophe is a simple musical advertisement, short complex musical advertisement call, or a long complex musical call; whether the inter-element pause exists and is distinct or indistinct; the presence or absence of a cackle-trill ending; the presence or absence of ‘ka-waak/ko-rak' component; whether the pitch of the strophe ascends or descends as it progresses; and whether the strophe is antiphonal or not; were scored from the francolins and spurfowls vocal recordings of suitable quality (Table 4.4, 4.5).

Analyses of data

The generated nucleotide sequences were edited and assembled in the Staden Package (Staden et al. 2003) and aligned using MAFFT (Katoh et al. 2009). All CYT*B* gene sequences were checked for stop codons and insertions or deletions. Two phylogenetic inference methods with different optimality criteria were employed to generate phylogenetic hypotheses: Parsimony was used to construct phylogenetic trees for both CYT*B* and the vocal data matrices, and a maximum likelihood (ML) approach was used in analysing the CYT*B* data set. The francolin data matrices were rooted on *Gallus gallus* and *Bambusicola thoracica* and the spurfowl matrices were rooted with *Coturnix coturnix* and *Alectoris chukar* (see Crowe et al. 2006). Parsimony-based phylogenetic analyses were conducted using PAUP* ver. 4.0b10 (Swofford 2002) under a full heuristic search with all characters unordered and with equal weight, starting tree(s) obtained via stepwise addition; tree-bisection-reconnection branch-swapping, and 1000 random addition replicates (Maddison 1991). When multiple, equally parsimonious cladograms were recovered, a strict consensus cladogram was constructed. The extent to which each non-terminal node is supported by different character partitions was determined by using the bootstrap (BS) (Felsenstein 1985) resampling with 1000 pseudoreplicates, and five random addition replicates of taxa per bootstrap pseudoreplicate.

Mixed-model maximum likelihood analyses were performed using the Randomised Axelerated Maximum Likelihood algorithm for High Performance Computing (RAxML) v7.0.4 (Stamatakis 2006, Stamatakis et al. 2008) implemented on the CIPRES portal. Mixed-model RAxML analyses make use of a GTR+Γ+I model partitioned by gene or codon position. The following analyses were run: mixed-model mtDNA (one model for each codon position, and also as a single data partition). Support at nodes was assessed with 100 non-parametric bootstrap (BS) pseudoreplicates. PAUP* was used to determine three measures of phylogenetic signal by estimating: the consistency index, the retention index and the scaled retention index. This enabled us to directly compare the phylogenetic signal inherent to the mtDNA and vocal character matrices.

Results

Calls

Both structural and temporal characteristics distinguish the calls of francolins and spurfowls, as well as among assemblages of taxa within them. Structural characteristics involve: strophe duration, the number of elements per strophe, and use of harmonics, trills and cackles. Temporal attributes include the sequence of elements and the relative length of the pauses between them.

Francolins

***Francolinus*:** The three members of the Spotted Francolin complex, *F. francolinus*, *F. pictus* and *F. pintadeanus* are characterised by having similarly structured strophes which are 2.0 s, 2.11 s and 1.62 s long, respectively. These strophes are comprised of distinctive elements: seven elements in *F. francolinus*, and five in both *F. pintadeanus* and *F. pictus* (Appendix 4.1). The strophe of *F. francolinus* is relatively tonal with the second element being higher-pitched. The first three elements of the strophe of *F. pintadeanus* are tonal with the second and third elements ending in trills. The third element is remarkably protracted whereas the fourth and fifth elements are fully trilled. *Francolinus pictus* has a less tonal strophe with very fuzzy trilling elements.

These taxa also differ in that *F. francolinus* and *F. pictus* both have one introductory element followed by a series of further elements, whereas *F. pintadeanus* has two introductory elements. The pause between the introductory element/s and the subsequent elements is relatively long in *F. pictus* (0.58 s), 0.43 s in *F. francolinus* and 0.24 s in *F. pintadeanus*. Another difference is seen in the shape of the harmonics, which is rising in *F. pintadeanus*, but comprises a mainly overslurred fundamental frequency in *F. francolinus*. The tonal part in the first element of *F. pictus* is also overslurred.

Ortygornis*: *Ortygornis sephaena has a complicated strophe, which sounds like a 'hybrid' between a francolin and spurfowl strophe to the ear (Appendix 4.1). The advertisement strophe of *O. sephaena* is a high-pitched, squealing cooperative duet led by a male and followed by a female (Little and Crowe 2000, van Niekerk 2010), and is thought to be used in claiming a territory (van Niekerk 2010). Its strophe sounds similar to that of the two Asian francolins, *O. pondicerianus* and *O. gularis*. The global structure of the sonograms of these species looks similar despite the difference in the duration of the strophes. *Ortygornis pondicerianus* and *O. gularis* are among the four species that Hall (1963) did not place decisively in one of her eight species groups.

The duration of the strophes of *O. sephaena* is much shorter (0.55 s) compared to that of the Kenyan *O. grantii* (0.74 s). The strophes of *O. sephaena* and *O. grantii* have four elements, one introductory element followed by three complex elements. There is interspecific variation that relates to the second element, which has two parts that are fused in *O. grantii* but encompasses a distinctive pause in *O. sephaena*. The first component of the second element has harmonics descending in shape in *O. sephaena* and almost linear in *O. grantii*, and trilling parts. The third element has complex variation, with the two parts either fused or separated. The fourth element is quite faint and has an overslurred harmonic-like structure.

Thus, *O. sephaena*, *O. grantii*, *O. gularis* and *O. pondicerianus* have one introductory element followed by a pause, and thereafter two to three additional complex elements. The third element is almost broken into two components with descending harmonics. *Ortygornis gularis* has strophe duration of 0.70 s, which, approaches that of *O. grantii* (0.74 s), with *O. pondicerianus* having the shortest duration (0.46 s) compared to *O. sephaena* and *O. gularis*. There is a much longer pause (0.32 s) between the first and the last sets of elements in *O. gularis* when compared to the other taxa: 0.14 s in *O. grantii,* 0.12 in *O. sephaena,* and 0.09 s in *O. pondicerianus.*

Peliperdix**:** All the *Peliperdix* spp. (also including *A. lathami*) have strophes with an introductory element followed by a pause and then another five to seven elements that trail away in volume, and have tonal and trilling parts. The global structure of the sonograms remains similar despite differences in strophe duration, and the number and structure of elements. The strophes of *Peliperdix* spp. (Appendix 4.1) are relatively high pitched, harsh and tinny (Crowe et al. 1986) to the ear. *Afrocolinus lathami* being an exclusively forest species, has a low frequency 'cooing' strophe which suits the type of habitat it thrives in, but has the basic elemental structure similar to that of the *Peliperdix* spp.

The major difference among the strophes of *Peliperdix* spp. is in their duration. The strophe of *Peliperdix albogularis* is short (1.0 s) consisting of six tonal elements with relatively stable harmonics with some parts of the elements trilled. The strophe of *P. schlegelii* is a little longer (1.89 s) and consists of seven elements, with element E1 more tonal and has clearly defined rising harmonics, element E2 is fully trilled, and the last four element (E 3-7) start with an overslurred component followed by trilling parts. The strophe of *P. coqui* (1.95 s) has eight elements, which can be split into two parts. The first part has stable harmonics followed by the second component which comprises trilling and descending harmonics. The strophe of *A. lathami* (1.89 s) is made up of eight very distinctive elements with E1 being more tonal followed by E 2-8 which begin with tonal parts and end in trills. There is also a remarkable difference in the duration of the pause between E1 and the rest of the elements in the strophes. The inter-element pause (which narrows as the strophe progresses) is 0.10 s long in *P. albogularis,* 0.37 s in *P. schlegelii,* 0.11 s in *A. lathami,* and somewhat longer than that in *P. coqui* (0.25 s). There is a general decreasing trend in the duration of the inter-element pause in strophes within the group. Thus, the strophes of the *Peliperdix* species represent a stepped cline moving from the South African *P. coqui* to the Central African *P. schlegelii*, to the West African *P. albogularis*.

***Scleroptila*:** Unlike the Red-tailed *Peliperdix* francolins, which have harsh short duration strophes, members of the Red-winged Group have whistling strophes. Four species (*S. levaillantoides*, *S. finschi*, *S. shelleyi* and *S. gutturalis*) have strophes similar in structure (four elements) that may be rendered "I'll drink YER-BEER" (Newman 2002) and differ primarily in strophe and pause duration (Appendix 4.1). The strophe of *S. levaillantoides* (0.53 s) is the shortest, with those of *S. finschi* (0.71 s), *S. gutturalis* (0.79 s), and *S. shelleyi,* (0.89 s), respectively increasing in duration. The remaining three species have strophes of much longer duration, (*S. afra* - 2.0 s, *S. levaillantii* - 2.11 s, and *S. streptophora* - 2.22 s) and seven to ten elements (Appendix 4.1).

The typical advertisement strophe of *S. levaillantoides*, *S. gutturalis*, *S. finschi* and *S. shelleyi* (also reported by Madge and McGowan 2002, Hockey et al. 2005 excluding *S. gutturalis*) are similar in that they have four complex elements with the first two elements introducing the strophes. Strophes of *Scleroptila finschi* have harmonics of complex shapes. The element following the two introductory elements is very complex and does not have markedly definable third and fourth elements as in *S. levaillantoides* and *S. shelleyi*. The first two elements of *S. levaillantoides* have rising harmonics, which descend in the second component of E2, E3 is trilled, whereas E4 begins with trilling parts and ends with descending harmonics. The overall strophe structure of *S. shelleyi* is similar with some minor variation in the structure of E3 and E4.

Scleroptila streptophora, *S. levaillantii* and *S. afra* have longer strophes with several elements. *Scleroptila streptophora* has a dove-like cooing strophe, which is very tonal and has one introductory element followed by six additional elements. All the elements have well-defined harmonics, which are stable in the first three elements and descend in the fourth and fifth elements. The fourth through to the seventh elements make a warbling sound. *Scleroptila levaillantii* has a strophe (with overslurred harmonics) which is introduced by seven elements followed by three elements (E 8-10) which make a warbling sound, whereas the strophe of *S. afra* (with overslurred harmonics) is introduced by six elements followed by two elements (E 7 and 8), but includes no warbles. There is a difference in the duration of the pause between the introductory elements and the subsequent elements, which is quite long in *S. streptophora* (0.46 s), and shorter in the other taxa: 0.27 s in *S. shelleyi*, 0.21 s in *S. afra,* 0.18 s in *S. finschi*, 0.12 s in *S. levaillantii*, and 0.10 s in *S. levaillantoides*.

Spurfowls - *Pternistis* species

All four Bare-throated species have a basic atonal ‘ka-waak’ advertisement strophe (0.75 s for *P. swainsonii*, 0.36 s – *P. afer*, 0.57 s – *P. rufopictus* and *P. leucoscepus*) (Appendix 4.1) sounding higher-pitched and more guttural in *P. swainsonii* and lower-pitched and more nasal to the ear in *P. afer*. Furthermore, the strophes of *P. leucoscepus* and *P. rufopictus* are both high-pitched, with an element of screeching and more protracted trilling second elements.

The strophes of *P. swainsonii, P. afer, P. leucoscepus* and *P. rufopictus* are differentiated into two elements, which can be characterised as trills and are separated by a fuzzy pause (except in *P. swainsonii*). The first element is more tonal in *P. swainsonii* and trills in the other species, whereas E2 is completely trilled in *P. swainsonii, P. leucoscepus* and *P. rufopictus* (exceptionally starting with a slower trill and ending with a much faster trill). The inter-element pause is well-differentiated in *P. swainsonii* (0.16 s long) in contrast to the fuzzy pause in *P. afer* (0.04 s), *P. rufopictus* (0.08 s) and *P. leucoscepus* (0.09 s). There is a decreasing trend in the duration of elements and the pause between them from the northeast African *P. leucoscepus* through to the east African *P. rufopictus* to the southern African *P. afer*. *Pternistis swainsonii* has a much longer strophe.

Like the Bare-throated spurfowls, the northern Vermiculated species *P. icterorhynchus, P. bicalcaratus, P. clappertoni* and *P. harwoodi,* all give basic 'ka-waak' strophes that differ mainly in the duration over which they are rendered (0.28 s, 0.33 s, 0.64 s and 0.61 s, respectively; Appendix 4.1). The strophes of these species have two trilling elements, which are separated by a fuzzy pause that is 0.06 s, 0.04 s, 0.14 s and 0.08 s long in *P. icterorhynchus, P. bicalcaratus, P. clappertoni,* and *P. harwoodi*, respectively. Among the four species, *P. clappertoni* is the only species in which its strophe shows a much faster and loud trilling part at the beginning of the second element. The southern Vermiculated species, *P. adspersus, P. capensis, P. hartlaubi, P. hildebrandti* and *P. natalensis* give strophes which are extremely divergent from one another, with the only similarity being that *P. capensis* and *P. adspersus* have strophes ending in 'cackle-trills'. The overall structure of the sonograms, the duration of the strophes (2.10 s, 4.43 s, 1.90 s, 0.34 s and 0.62 s, respectively), number of elements (some with components) and the duration of the inter-element pause differ remarkably. *Pternistis adspersus* gives a strophe that is introduced by four elements followed by two 'cackle-trill' elements. *Pternistis capensis* renders the longest strophe within the group which is more tonal consisting of seven elements (the first five elements with increasing volume followed by a low-pitched 'cackle-trill'). The first two elements have two components, followed by two three-component elements, one four-component element and ends in two five-component 'cackle-trilled' elements.

The most complicated strophe is that of Hartlaub's Spurfowl *P. hartlaubi,* which has a complex high-pitched antiphonal strophe often given by the male (Komen 1987; Maclean 1993). This strophe has tonal and less well-defined trilling parts. *Pternistis hildebrandti* in contrast, gives a trilling strophe with six elements that have no clearly defined pause. The advertisement strophe of *P. natalensis* is a high-pitched, four-element strophe characterized by some tonal, slow and fast trilling parts.

Among the members of the Scaly Group, the advertisement strophe of *P. squamatus* is a high-pitched nasal 'ke-rak' which is repeated several times and increases in volume as it progresses (Appendix 4.1). *Pternistis ahantensis* has a much shorter strophe (0.44 s) compared to *P. squamatus* and *P. griseostriatus* (1.09 s and 0.81 s, respectively).

The Montane species, *P. camerunensis* has a relatively tonal strophe with two elements which are almost fused Appendix 4.1), with the first element being higher-pitched relative to the second element. The same bird also gives a slow two-element strophe with both elements descending in pitch and having a clearly defined pause in between. Interestingly, the strophes from two recorded individuals of *P. camerunensis* differed in their duration (0.37 s and 0.67 s, respectively), as well as the duration of the pause between the two elements (0.03 s and 0.18 s, respectively). A second montane species, *P. nobilis*, has an atonal, two-element strophe (0.60 s, which is reminiscent of the 'ka-waak' strophes of members of the Bare-throated species group. The first element has trilling and tonal parts followed by a pause (0.10 s) before a second protracted trilling element. *Pternistis ochropectus* also gives a two-element tonal strophe (0.48 s) with elements descending in pitch as it ends. The two elements were separated by a distinctive pause (0.21 s). What is remarkable about *P. ochropectus* is that based on the recordings analysed, the same individual sometimes switches the sequence of the elements around starting with the lower-pitched second element followed by a higher-pitched first element.

Three species, *P. erckelii*, *P. swierstrai* and *P. castaneicollis,* render strophes, which are much longer (3.80 s, 4.24 s and 2.67 s long, respectively) with a series of elements that build up in intensity and complexity as the strophes progress. The strophe of *P. erckelii* is made up of 17 elements that increase in intensity from the start of E 1-4, with E 5-14 beginning to subside and the last three elements (E 15-17) forming a 'cackle-trill' that further subsides in intensity as it ends. The duration of the inter-element pause ranges from 0.05 s to 0.21 s. The strophe of *P. swierstrai* consists of seven two-component elements that increase in intensity (from E 1-4) and decrease in volume from E 5-7. The last three elements (E 5-7) form a 'cackle-trill', which starts to break away in the fourth element becoming more apparent in the fifth element and so forth. The duration of the inter-element pause increases from 0.14 s to 0.33 s.

The strophe of *P. castaneicollis* is characterized by six elements with the first element having no components and followed by three two-component elements, one three-component element, and ends in one four-component element. The last two elements (E 5-6) again form a ‘cackle-trill’ as in *P. erckelii* and *P. swierstrai*. The strophe of *P. castaneicollis* has variable intensity from the beginning to the end. The first element starts at a low volume and then builds up in volume (E 2-4) and ends fainter with E 5-6 comprising a 'cackle-trill'. There is an increasing trend in the duration of the pause between elements (0.18 s - 0.21 s). It was reported in Madge and McGowan (2002) that *P. jacksoni* gives very loud, high-pitched series of cackles that sound similar to those of *P. squamatus*. The available recording of *P. jacksoni* was unfortunately of poor quality such that no sonogram could be produced. However, to the ear, it appears to give a loud series of cackles.

Phylogeny

Molecular and vocal characters - francolins

The parsimony analysis of the CYT*B* data set with 1143 characters, contained 248 parsimony informative characters (21.7%); a further 110 (9.6%) variable characters were parsimony uninformative. Five trees of 965 steps were recovered. The vocal character matrix, with nine characters, contained nine parsimony informative characters, and recovered 28 equally parsimonious trees of 225 steps.

The CYT*B* parsimony and ML (not shown) trees (Fig. 4.2) recovered three of Hall’s hypothesised monophyletic groups (Spotted - *Francolinus*, Red-tailed - *Peliperdix*, Red-winged - *Scleroptila*). Further, the inclusion of *Dendroperdix streptophora* into the Red-winged Group of francolins (*Scleroptila* spp.) in the CYT*B* trees confirms the findings of Crowe and Crowe (1985) and Crowe et al. (1992). In the parsimony derived vocal tree (Fig. 4.3), the Red-tailed species group together, but with the inclusion of *A. lathami;* however, overall the resulting phylogeny is largely unresolved.

Molecular and vocal characters - spurfowls

The parsimony analysis for the CYT*B* data set with 1143 characters, contained 231 parsimony informative characters (20.2%); a further 155 (13.6%) variable characters were parsimony uninformative. Four trees of 926 steps were recovered. The vocal character matrix, with eight characters, contained seven parsimony informative characters, one parsimony uninformative character, and recovered 17 equally parsimonious trees of 16 steps. The CYT*B* parsimony and ML (not shown) trees (Fig. 4.4), recovered some phylogenetic structure compared to the vocal tree (Fig. 4.5), which largely forms a polytomy. The CYT*B* tree recovered at least one of Hall's hypothesised monophyletic groups, the Bare-throated Group (82% BS value – Fig. 4.4), though *P. hartlaubi* is recovered within the group. Within the Bare-throated Group, *P. rufopictus* and *P. afer* are recovered as sister taxa. The Vermiculated Group is split geographically into a monophyletic clade comprising the southern Vermiculated taxa, whereas the northern Vermiculated taxa are polyphyletic (*P. bicalcaratus, P. clappertoni, P. icterorhynchus, P. harwoodi*). Montane species are primarily distributed towards the base of the *Pternistis* tree, with the exception of *P. jacksoni* which is sister to the montane Angolan endemic *P. swierstrai*, although with poor support. The East African species (*P. erckelii, P. ochropectus, P. castaneicollis*) form a clade, with the montane West and East African taxa *P. camerunensis* and *P. nobilis* forming a sister group basal to the three East African montane species. The Namibian arid savanna endemic *P.*

hartlaubi is recovered as the basal taxon to all spurfowl species in the CYT*B* parsimony tree.

Phylogenetic signal

In comparing three common parsimony metrics for the francolin CYT*B* and vocal data sets, the vocal matrix has less homoplasy but considerably fewer characters: CYT*B* consistency index (CI) of 0.516 compared to 0.818 in the vocal matrix, retention index (RI) of 0.458 compared to 0.897 in vocal matrix, and a rescaled retention index (RC) of 0.236 compared to 0.734 for the vocal matrix. Similarly for the spurfowl CYT*B* data matrix, the CI is 0.521 compared to 0.625 for the vocal matrix, with a RI of 0.457 versus 0.870, and a RC of 0.238 versus 0.543. In summary, there is less homoplasy in the vocal matrices for both francolins and spurfowls than in the CYT*B* data sets, but because of considerably fewer characters there is less phylogenetic resolution.

Discussion

The quantitative and visual structural descriptions of the advertisement calls support the phylogenetic distinction between francolins and spurfowls. Francolins are found to generally give long, tonal strophes (either whistling, or harsh and tinny calls) that comprise a series of distinctive elements that usually have harmonics. Spurfowls are characterised by having generally short (with a few exceptions), atonal and grating strophes, with very few elements and no harmonics.

Within the Red-winged Group (*Scleroptila* spp.), both the CYT*B* and the vocal trees recover the separation of the core-*Scleroptila* clade from *S. streptophora* and *S. levaillantii.* This is generally in accordance with the sonographic presentations (except

S. afra), which break *Scleroptila* into two quite distinct subgroups: (1) species with short, four-element strophes (*S. finschi, S. levaillantoides S. gutturalis* and *S. shelleyi*) and those with long strophes consisting of many more elements (*S. streptophora, S. levaillantii* and *S. afra*), often ending with a warble. It could be that the similarities in the advertisement calls among *Scleroptila* species may be a consequence of sharing common descent, as in contrast to the parsimony CYT*B* phylogeny, the ML-based topology (not shown) places *S. afra* at the base of a clade comprising *S. finschi, S. levaillantoides, S. gutturalis* and *S. shelleyi*. Even though the Red-winged *Scleroptila* species occur in varied habitats at different latitudes, their primary preference is grassland (Johnsgard 1988, Madge and McGowan 2002), which collectively comprises the open lowland grasslands in which *S. levaillantoides, S. gutturalis, S. finschi* thrive, and the open hilly (*S. shelleyi*) and highland grasslands preferred by *S. afra*, *S. psilolaema*, *S. levaillantii,* and *S. streptophora*.

Within the Red-tailed group, *Peliperdix* species, the CYT*B* topology places *P. albogularis* and *P. schlegelii* together, both taxa with fast, short strophes. Basal to these two taxa is *P. coqui* that has a slower and longer strophe. Although the topology based on vocal characters is poorly resolved, it interestingly recovers the enigmatic *Afrocolinus lathami* to be nested inside *Peliperdix*, rather than as a highly distinct lineage, sister to *Francolinus* revealed in the CYT*B* topology (although with limited support). The grouping together of *A. lathami* and *Peliperdix* taxa in the vocal tree could be attributed to it sharing a series of elements (almost eight) forming its strophe that fade as the strophe progresses, as in other *Peliperdix* species, particularly *P. coqui.* The three Red-tailed *Peliperdix* species inhabit open grassland and woodland savannas. *Afrocolinus lathami* remains the only African francolin to be restricted to dense forested habitats (del Hoyo et al. 1994, Madge and McGowan 2002), hence it has a low frequency 'cooing' strophe (versus the high-pitched, broadband strophe in *Peliperdix* spp.), which suits the forested habitat it thrives in. Frequency was not a character we could reliably score, and hence it was not included in the phylogenetic analyses. If it were included, it may well place *A. lathami* outside the *Peliperdix* clade.

The CYT*B* topology suggests that shorter strophes evolved from longer strophes among both *Scleroptila* and *Peliperdix* species. The placement of *Ortygornis* (*Dendroperdix*) *sephaena* has long been a puzzle because of its aberrant life-history and vocal characteristics, that is, roosting in trees and emitting a somewhat raucous call more similar to spurfowls than francolins. The CYT*B* and vocal topologies suggest *O. sephaena* to be sister to the African *O. grantii*, with the DNA data suggesting this clade to be sister to the Asian *O. gularis* and *O. pondicerianus*. *Ortygornis sephaena* may thus represent a 'linking form' between Asian and African francolins. The global structure of the sonograms of *O. sephaena*, *O. grantii, O. gularis* and *O. pondicerianus* look similar despite the difference in the duration of the strophes. These species all have one introductory element followed by a pause, and thereafter two to three additional complex elements. The third element is almost broken into two components in *O. gularis* and *O. pondicerianus.* Aurally, the strophe of *O. sephaena* and *O. grantii* sound similar to that of the two Asian francolins, *O. pondicerianus* and *O. gularis*.

Despite the Spotted *Francolinus* species emerging as monophyletic, they have remarkably variable strophes but share the feature of having similar introductory elements. Differences between species of spurfowls are mainly in strophe duration, the number of elements per strophe, the duration of the pause between the introductory element and the subsequent elements. The Bare-throated species (*P. swainsonii, P. afer,* *P. rufopictus* and *P. leucoscepus*) and perhaps the northern Vermiculated taxa (*P. bicalcaratus, P. icterorhynchus, P. clappertoni* and *P. harwoodi)* have similar sonographic features despite being well-separated in the CYT*B* topology. The Bare-throated species also inhabit similar habitats to members of the Vermiculated Group (*P. hartlaubi, P. capensis, P. natalensis, P. adspersus, P. hildebrandti, P. clappertoni, P. icterorhynchus, P. bicalcaratus, P. harwoodi*), which generally occupy dense bushy thickets and shrubby grasslands (del Hoyo et al. 1994, Madge and McGowan 2002). The vocal topology recovered for spurfowls is almost completely unresolved and hence is of limited phylogenetic utility.

There is strong divergence among the strophes of members of the Montane species complex with just the two northeast African species (*P. erckelii* and *P. castaneicollis*) and perhaps *P. swierstrai* (Angolan endemic) being brought together by having multiple elements (with components) and a 'cackle-trill' that ends their strophes. The relationship between the strophes of *P. camerunensis, P. nobilis* and *P. ochropectus* is uncertain except that they all have two elements that descend in pitch. *Pternistis nobilis*, however, gives a two-element strophe that is reminiscent of those of the Bare-throated species, suggesting that the 'ka-waak' strophe might be the plesiomorphic state within spurfowls. The vocal relationship within the Scaly Group (*P. squamatus, P. griseostriatus, P. ahantensis*) is uncertain and their strophes are highly divergent.

Conclusions

Comparing the outcome of DNA and vocal characters in a phylogenetic context was not an easy task due to the vocal phylogenetic topology being largely unresolved relative to that recovered from the DNA characters, particularly among spurfowls. However, on the basis of the level of phylogenetic signal within each data set (DNA and vocal characters), vocal characters exhibit less homoplasy. Hence, if a sufficient number of characters can be scored relative to the number of taxa being studied, such characters should be of considerable use in reconstructing phylogenies. Spurfowls, unlike francolins are very divergent vocally, morphologically, as well as with respect to habitat preference. There is however, some phylogenetic concordance between DNA and vocal characters of francolins. Perhaps the most useful phylogenetic outcome of this research are the marked differences between the calls of francolins and spurfowls and the decisive placement of the 'linking form' *Ortygornis sephaena* with francolins, in particular with two of Hall's (1963) unplaced taxa, *O. pondicerianus* and *O. gularis.*

Tables and Figures

Table 4.1. List of species for which calls were analysed. BLSA abbreviates British Library Sound Archive, MLNS - Macaulay Library of Natural Sounds.

Taxon name	ID. No.	Supplier	Recorder	Locality
AFRICAN SPURFOWLS				
Bare-throated Group				
Pternistis afer	CD2.5 - 198	Michael Mills	G. Gibbon	Natal
P. swainsonii	CD2.5 - 199	M. Mills	G. Gibbon	Namibia
P. leucoscepus	100205	MLNS	R. Linda	Ethiopia
P. rufopictus	03052 R1C1	BLSA	Cornell	Tanzania
Montane Group				
P. camerunensis	CD5 - 95	Michael Mills	C. Chappuis	Mt. Cameroon
P. ochropectus	cc26744	BLSA	G. Welch	Djibouti
P. nobilis	CD5 - 96	Michael Mills	C. Chappuis	Uganda
P. erckelii	68756 BD10	BLSA	S. Smith	Unknown
P. swierstrai	Unknown	Michael Mills	M. Mills	Angola
P. castaneicollis	100242	MLNS	R. Linda	Ethiopia
P. jacksoni	Unknown	C. Cohen	B. Finch	Kenya
Vermiculated Group				
P. bicalcaratus	216-231	Michael Mills	C. Chappuis	Ivory Coast
P. icterorhynchus	cc1238 BD20	BLSA	C. Bourguignon	Zaire
P. clappertoni	cc1239 BD21	BLSA	C. Chappuis	Nigeria
P. harwoodi	24718 BD1	BLSA	H. Shirihai	Ethiopia
P. hildebrandti	CD5 – 92	Michael Mills	C. Chappuis	Malawi
P. capensis	CD2 - 195	Michael Mills	G. Gibbon	South Africa
P. natalensis	CD2 - 196	Michael Mills	G. Gibbon	South Africa
P. adspersus	61790 BD24	BLSA	D. Watts	Namibia
P. hartlaubi	CD2 - 197	Michael Mills	G. Gibbon	Namibia
Scaly Group				
P. ahantensis	cc24693BD32	BLSA	C. Chappuis	Senegal
P. griseostriatus	103772BD49	BLSA	I. Sinclair	Angola
P. squamatus	CD5 - 89	Michael Mills	C. Chappuis	Gabon
ASIATIC FRANCOLINS				
Spotted Group				
Francolinus pictus	551	MLNS	B. King	Sri Lanka
F. francolinus	86293	MLNS	P. Holt	India
F. pintadeanus	113300 BD42	BLSA	C. Carter	Burma
AFRICAN FRANCOLINS				
Red-winged Group				
Scleroptila finschi	CD5 - 86	Michael Mills	C. Chappuis	Gabon
S. shelleyi	CD2.5 - 191	Michael Mills	G. Gibbon	South Africa
S. afra	CD2.4 - 190	Michael Mills	G. Gibbon	South Africa

Taxon name	ID. No.	Supplier	Recorder	Locality
S. levaillantoides	CD2.5 - 193	Michael Mills	G. Gibbon	Namibia
S. gutturalis	48414 R1C1	BLSA	D. Pearson	Somalia
S. levaillantii	CD2.5 - 192	Michael Mills	G. Gibbon	South Africa
Red-tailed Group				
Peliperdix coqui	CD2 - 188	M. Mills	G. Gibbon	South Africa
P. schlegelii	cc1214 BD22	BLSA	J. Brunel	Chad
P. albogularis	cc1212 BD20	BLSA	C. Chappuis	Senegal
Striated Group				
Ortygornis sephaena	1095	M. Hausberger	M. Hausberger	South Africa
O. grantii	CD5 - 88	Michael Mills	C. Chappuis	Kenya
S. streptophora	CD5 - 84	Michael Mills	C. Chappuis	Cameroon
Unplaced taxa (excluding *Ptilopachus nahani*)				
Afrocolinus lathami	CD5 - 80	Michael Mills	C. Chappuis	Ivory Coast
Ortygornis gularis	65642 BD20	BLSA	P. Holt	Nepal
O. pondicerianus	41433 R1C10	BLSA	P. Holt	Pakistan

4.2. Francolin and spurfowl taxa for which DNA sequences were generated. **Acronyms**. AMNH abbreviates American Museum of Natural History, TM - Transvaal Museum, BM - British Museum - Natural History Museum at Tring, FMNH – Field Museum of Natural History, PFIAO - Percy FitzPatrick Institute of African Ornithology, TMC - Timothy M. Crowe, University of Cape Town, South Africa, '-' – Unknown. Genera are as recorded on specimen label.

Taxa name	Sample no.	Origin	Date collected	GenBank no.
Francolins				
Spotted Group				
F. francolinus	AMNH DOT8023	India	-	AF013762
F. pictus	AMNH 776813	India	-	FR694142
F. pintadeanus	GenBank	China	-	NC011817
Striated Group				
Francolinus sephaena	TMC 9	Marico River, South Africa	2004	FR694140
F. sephaena grantii	BM 1902 1 20 300	Hulul, Ethiopia	1902	FR694144
F. streptophora	TMC 11	Cameroon	2005	FR691617
Red-winged Group				
F. shelleyi	PFIAO 47	Ayton Farm, South Africa	-	AM236898
F. afra	PFIAO 59	Eastern Cape, South Africa	2002	AM236897
F. levaillantoides levaillantoides	TMC 12	Petrus Steyn, South Africa	2002	FR691612
F. l. gutturalis	AMNH 541174	Ethiopia	-	FR691613
F. levaillantii levaillantii	TM 78622	Sterkspruit, South Africa	2005	U90642
F. finschi	AMNH 308887	Angola	1941	FR691607
Red-tailed Group				
F. coqui	PFIAO 45	Settlers, South Africa	-	AM236895
F. schlegelii	BM 1949 30 19	Mboro, Bahr-El-Ghazel, Chad	1949	FR694149
F. albogularis	BM 1929 3 13 1	Farafeni, Gambia	1929	FR694145
Ungrouped species				
F. lathami	GenBank	Cameroon	-	AM236893
F. pondicerianus	AMNH DOT8050	India	-	FR691632
F. gularis	GenBank	India	-	U90649
Spurfowls				
Bare-throated Group				
Francolinus afer	PFIAO 108,	Tudor East, Watervalboven	2004	AM236908
F. swainsonii	TMC 40	Marico River	2004	AM236907
F. rufopictus	AMNH 202503	Gagayo, Muranza	-	FR691588
F. leucoscepus	PFIAO 109	Kenya	2004	AM236906

Taxa name	Sample no.	Origin	Date collected	GenBank no.
Montane Group				
F. erckelii	AMNH 541471	Badaltino, Shoa	-	FR691589
F. ochropectus	FMNH 1971-1072	Djbouti	-	FR691590
F. castaneicollis	GenBank	-	-	AM236903
F. jacksoni	AMNH261929	East slope, Mt. Kenya	-	FR691594
F. nobilis	AMNH1759	West Ruwenzori	-	FR691592
F. camerunensis	TMC 42	Mount Cameroon	-	FR691591
F. swierstrai	AMNH 419126	Angola	-	FR691593
Scaly Group				
F. squamatus	PFIAO 117	-	-	AM236904
F. griseostriatus	AMNH 541411	Ndalla Tanda	-	AM236905
Vermiculated Group				
F. bicalcaratus	TM 14682	Gold Coast, Hinterland	1901	FR691624
F. clappertoni	TMC 68	Cameroon	2005	FR691602
F. icterorhynchus	AMNH 156922	Fanadji	-	FR691601
F. hildebrandti	GenBank	-	-	FR691595
F. natalensis	TMC 120	Marico River, South Africa	2004	AM236911
F. hartlaubi	TMC 121	Namibia	2006	FR691618
F. capensis	PFIAO 229	Kakamas, South Africa	-	AM236909
F. adspersus	PFIAO 206A	-	-	FR691623
F. harwoodi	BM 1927.11.5.18	-	1927	FR691600
Outgroups				
Gallus gallus	-	-	-	L083761
Bambusicola thoracica	-	-	-	EU165706
Alectoris chukar	-	-	-	L083781
Coturnix coturnix	-	-	-	L083771

Table 4.3. DNA markers sequenced and primers used for PCR amplifications and sequencing of preserved tissues.

Primer name	Primer sequence (5'to 3')	Reference
<u>Fresh tissues</u>		
Francolins & Spurfowls (General primers)		
Cytochrome *b*		
L14578	cta gga atc atc cta gcc cta ga	J.G. Groth (pers. comm.)
MH15364	act cta cta ggg ttt ggc c	P. Beresford (pers. comm.)
ML15347	atc aca aac cta ttc tc	P. Beresford (pers. comm.)
H15915	aac gca gtc atc tcc ggt tta caa gac	Edwards & Wilson (1990)
<u>Toe-pads</u>		
Cytochrome *b*		
Spurfowl-specific primers		
L14851 (General)	cct act tag gat cat tcg ccc t	Kornegay et al. (1993)
Pt-H195	ttt cgr cat gtg tgg gta cgg ag	R. Moyle & T. Mandiwana-Neudani
Pt-H194	cat gtr tgg gct acg gag g	R. Bowie
MH15145	aag aat gag gcg cca ttt gc	P. Beresford
Pt-L143	gcc tca tta ccc aaa tcc tca c	R. Moyle & T. Mandiwana-Neudani
Pt-H361	gtg gct att agt gtg agg ag	R. Moyle & T. Mandiwana-Neudani
Pt-L330	tat act atg gct cct acc tgt ac	R. Bowie
Pt-H645	ggg tgg aat ggg att ttg tca gag	R. Moyle & T. Mandiwana-Neudani
Pt-L633	ggc tca aac aac cca cta ggc	R. Moyle & T. Mandiwana-Neudani
Pt-H901	agg aag ggg att agg agt agg at	R. Moyle & T. Mandiwana-Neudani
L2-2312	cat tcc acg aat cag gct c	R. Bowie
H15696	aat agg aag tat cat tcg ggt ttg atg	Edwards et al. (1991)
Pt-L851alt	cct att tgc cta cgc cat cct ac	R. Bowie
Pt-H1050	gat gct gtt tgg ccg atg	R. Bowie
Pt-L961	cga acc ata aca ttc cca c	R. Moyle & T. Mandiwana-Neudani
Pt-L961alt	ctc atc cta ctc cta atc ccc	R. Bowie
HB20 (General)	ttg gtt cac aag acc aat gtt	J. Feinstein (pers. comm.)

Primer name	Primer sequence (5’to 3’)	Reference
Cytochrome *b*		
Francolin-specific primers		
L14851 (General)	cct act tag gat cat tcg ccc t	Kornegay et al. (1993)
Franc-H1	cag cag aca cyt cyc tyg cct tc	R. Bowie
MH15145	aag aat gag gcg cca ttt gc	P. Beresford
Franc-L1	tgc ctc aca acc caa atc ctc ac	R. Bowie
Franc-H2	agg agr agr att act cct gtg ttt cag g	R. Bowie
Franc-L2	gcc tca ttc tty ttc aty tgy atc ttc c	R. Bowie
Franc-H3	ggr tgg aat ggg att ttg tca gag	R. Bowie
Franc-L3	tcatcyractcygacaaaatccc	R. Bowie
Franc-H4	gar rgg gat tag rag gag gat	R. Bowie
Franc-L4	tat tcg cct ayg cya tcc twc gct c	R. Bowie
Franc-H5	gta gga rag kga tgc tat ttg gcc	R. Bowie
Franc-L5	ctc atc ctc ctc cta atc cc	R. Bowie
HB20 (General)	ttg gtt cac aag acc aat gtt	J. Feinstein (pers. comm.)

Table 4.4. Vocal character states scored and used for the phylogenetic analysis of francolins.

1. **Strophe length:** <1.0 s = 1; =1.0 s <2 s = 2; ≥2.0 s = 3
2. **No. of elements in strophe:** <5 = 1; ≥5 = 2
3. **Harmonics:** Absent = 0; Indistinctive = 1; Predominately distinct = 2; Distinct mixed with distinctive trills = 3
4. **Raucous advertisement:** Absent = 0; Type 1 = 1; Type 2 = 2
5. **No. of introductory elements:** one = 1; two = 2; More than two = 3
6. **Strophe warbling ending:** Absent = 0; Present = 1
7. **Simple musical advertisement:** Absent = 0; Slow = 1; Fast = 2; Very fast = 3
8. **Short complex musical advertisement call:** Absent = 0; Slow I'll drink-yer-beer = 1; Fast I'll drink-yer-beer = 2
9. **Long complex musical call:** Absent = 0; Type 1 = 1; Type 2 = 2

A matrix of vocal state scores used for phylogenetic analyses of the francolins.

	Characters								
Taxon	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
Gallus gallus	1	1	2	1	1	0	0	0	0
Bambusicola thoracica	1	1	2	1	1	0	0	0	0
Francolinus francolinus	3	2	2	1	1	0	0	0	0
Francolinus pintadeanus	2	2	3	1	2	0	0	0	0
Francolinus pictus	3	2	1	1	1	0	0	0	0
Afrocolinus lathami	2	2	0	0	1	0	1	0	1
Ortygornis pondicerianus	1	1	2	1	1	0	0	0	0
Ortygornis gularis	1	1	2	1	1	0	0	0	0
Ortygornis grantii	1	1	3	2	1	0	0	0	0
Ortygornis sephaena	1	1	3	2	1	0	0	0	0
Peliperdix albogularis	1	2	2	0	1	0	3	0	1
Peliperdix coqui	2	2	2	0	1	0	1	0	1
Peliperdix schlegelii	2	2	2	0	1	0	2	0	1
Scleroptila afra	3	2	2	0	3	1	0	0	2
Scleroptila finschi	1	1	2	0	2	0	0	1	0
Scleroptila levaillantii	3	2	2	0	3	1	0	0	2
Scleroptila levaillantoides	1	1	2	0	2	0	0	2	0
Scleroptila gutturalis	1	1	2	0	2	0	0	1	0
Scleroptila shelleyi	1	1	2	0	2	0	0	1	0
Scleroptila streptophora	3	2	2	0	1	0	0	0	2

Table 4.5. Vocal characters and states scored and used for phylogenetic analysis of spurfowls.

1. **Strophe length:** <1 s = 1; >1 s =2
2. **No. of elements in strophe:** 2-3 = 1; ≥4 = 2
3. **Strophe type:** Less to no trill = 1; Predominately trilled = 2; Predominately harmonic = 3
4. **Inter-element pause:** Absent/indistinct = 1; Distinctive = 2
5. **Cackle-trill ending:** Absent = 0; Present = 1
6. **Ka-waak/Ko-rak component:** Absent = 0; Present = 1
7. **Strophe pitch:** Stable = 1; Descends as strophe ends = 2; Ascends as strophe ends = 3
8. **Strophe antiphonal?:** No = 0; Yes = 1

A matrix of vocal character used to generate the vocal character phylogeny.

	Characters							
Taxon	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**
Coturnix coturnix	1	1	1	1	0	0	?	0
Alectoris chukar	1	1	1	1	0	0	?	0
Pternistis hartlaubi	2	2	1	2	0	0	1	1
Pternistis camerunensis	1	1	3	2	0	0	1	0
Pternistis nobilis	1	1	2	2	0	1	1	0
Pternistis erckelii	2	2	2	2	1	0	2	0
Pternistis swierstrai	2	2	2	2	1	0	2	0
Pternistis castaneicollis	2	2	2	2	1	0	2	0
Pternistis jacksoni	?	?	?	?	1	0	?	?
Pternistis ochropectus	1	1	3	2	0	0	1	0
Pternistis squamatus	2	1	3	2	0	0	3	0
Pternistis ahantensis	1	1	1	2	0	0	1	0
Pternistis griseostriatus	1	?	1	1	0	0	1	0
Pternistis bicalcaratus	1	1	2	2	0	1	1	0
Pternistis icterorhynchus	1	1	2	1	0	1	1	0
Pternistis clappertoni	1	1	2	1	0	1	1	0
Pternistis harwoodi	1	1	2	1	0	1	1	0
Pternistis hildebrandti	1	1	2	1	0	0	1	0
Pternistis natalensis	1	2	2	2	0	0	1	0
Pternistis adspersus	2	2	2	2	1	0	2	0
Pternistis capensis	2	2	3	2	1	0	3	0
Pternistis leucoscepus	1	1	2	1	0	1	1	0
Pternistis rufopictus	1	1	2	1	0	1	1	0
Pternistis afer	1	1	2	1	0	1	1	0
Pternistis swainsonii	1	1	2	2	0	1	1	0

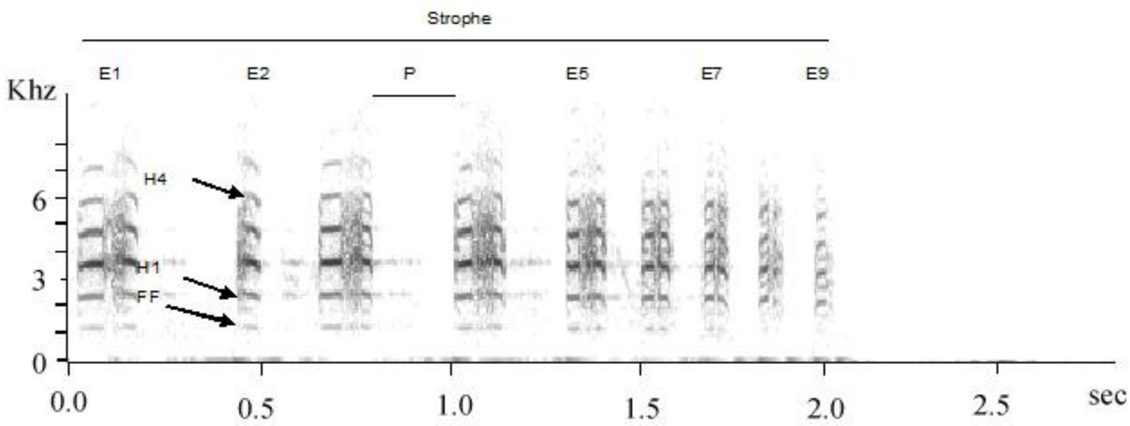


Figure 4.1. Example of a sonogram of a typical francolin, Coqui Francolin *Peliperdix coqui*, illustrating and defining the variables studied: E - element, E1 - element number 1, P - pause, H - harmonic, H1 - harmonic number 1 and FF - fundamental frequency.

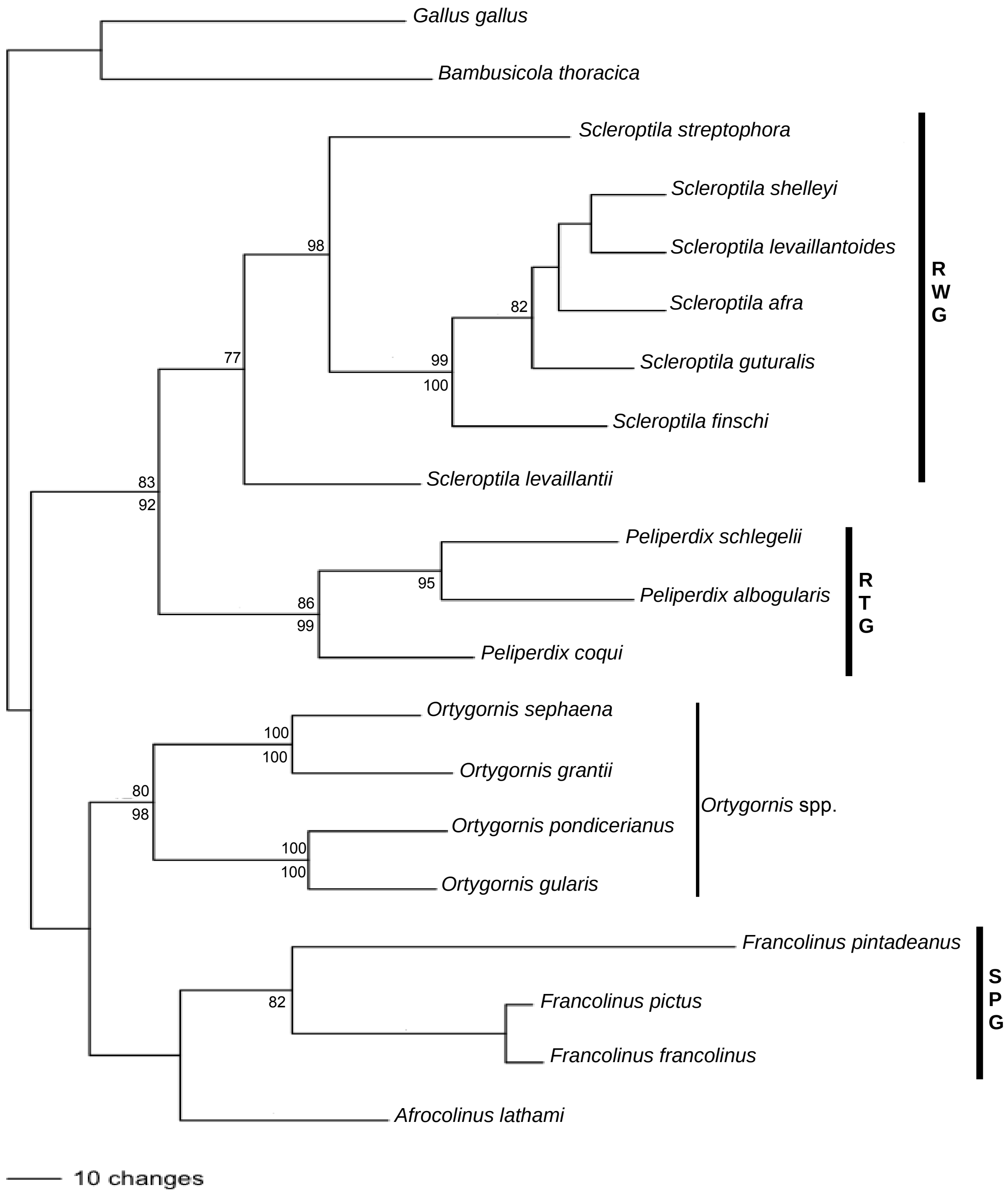


Figure 4.2. A parsimony tree (1 of 5 most parsimonious trees) of francolins obtained from mitochondrial Cytochrome-*b* characters. Numbers above branches represent parsimony boostrap support values and those below branches are maximum likelihood bootstrap support values (only ≥ 70% are presented). RWG stands for Red-winged Group, RTG – Red-tailed Group, SPG – Spotted Group.

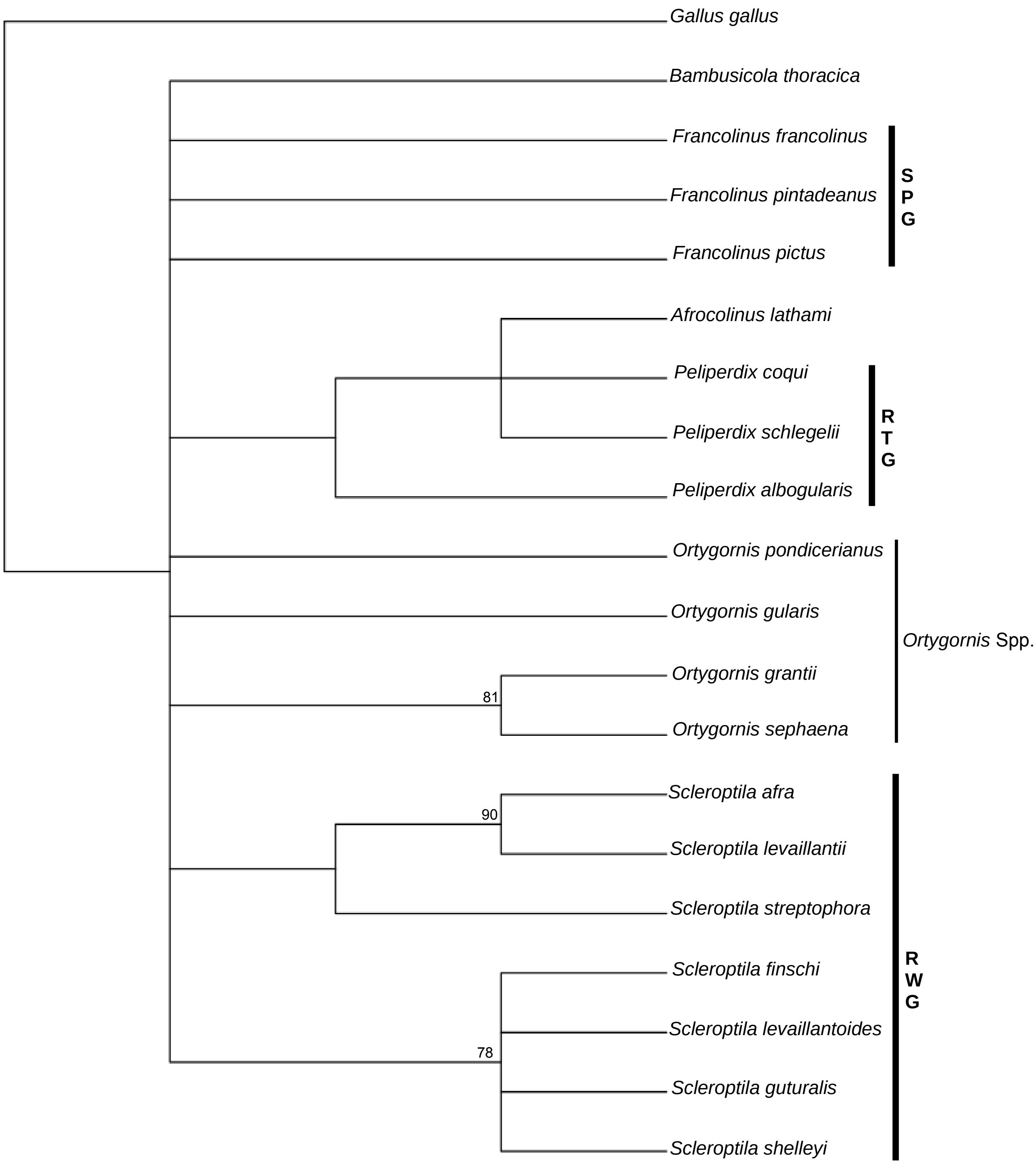


Figure 4.3. The strict consensus parsimony tree of francolins obtained from vocal characters. Numbers above branches represent boostrap support values (only ≥ 70% are presented). RWG stands for Red-winged Group, RTG – Red-tailed Group, SPG – Spotted Group.

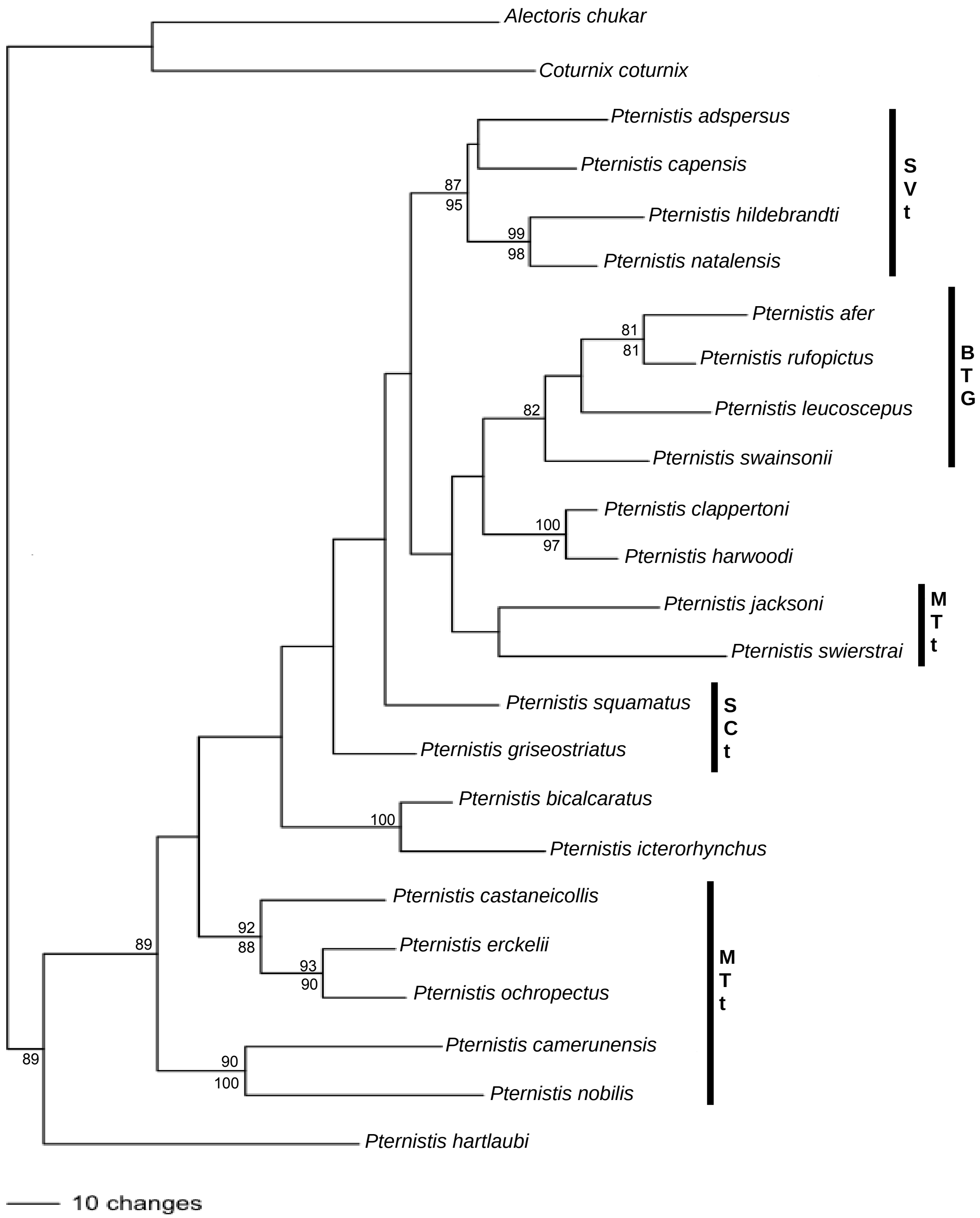


Figure 4.4. A parsimony tree (1 of 4 most parsimonious trees) of spurfowls obtained from mitochondrial Cytochrome-*b* characters. Numbers above branches represent parsimony boostrap support values and numbers below branches represent maximum likelihood boostrap support values (only ≥ 70% are presented). MTt stands for Montane taxa, SCt – Scaly taxa, SVt – Southern Vermiculated taxa and BTG – Bare-throated Group.

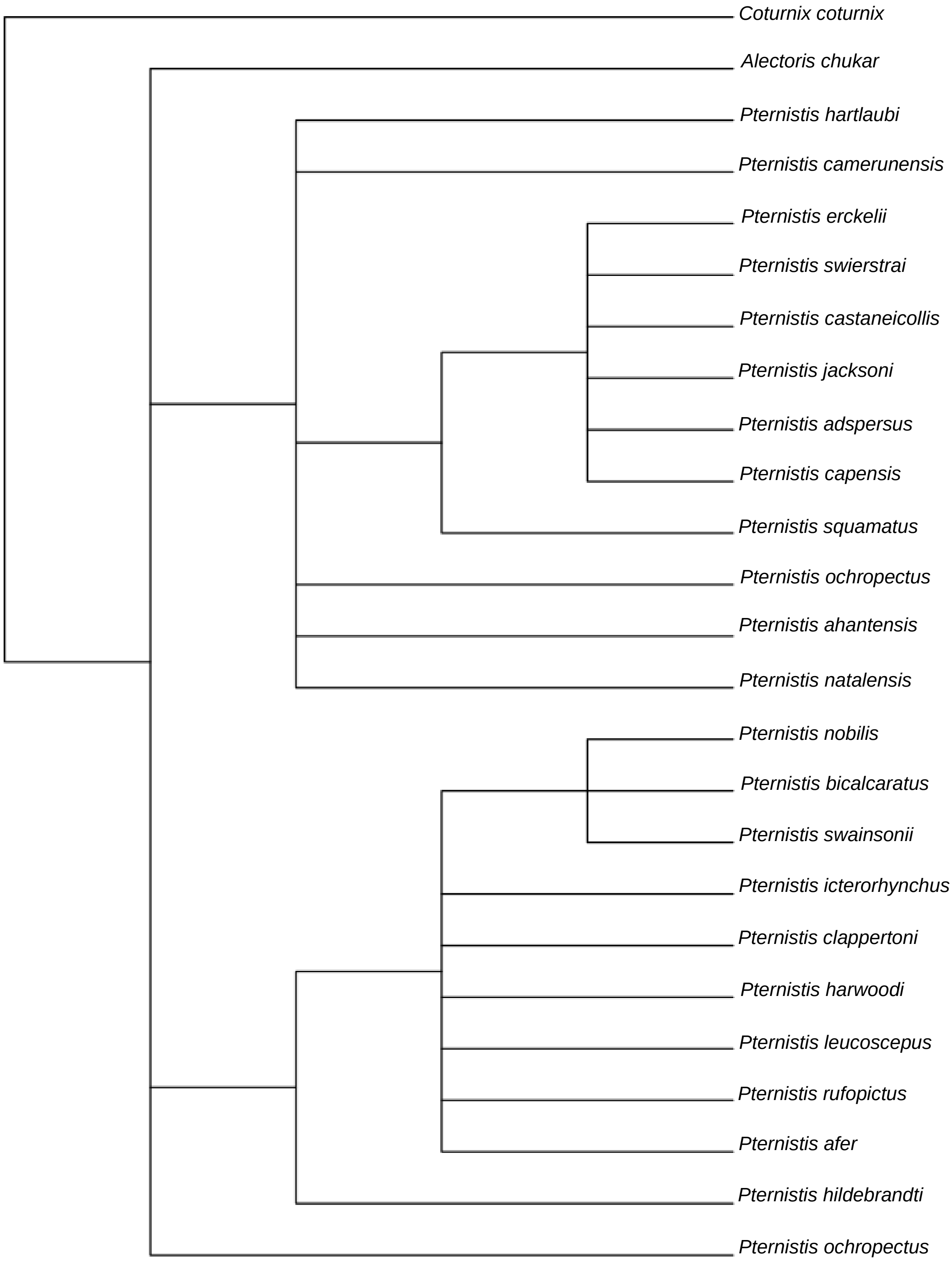
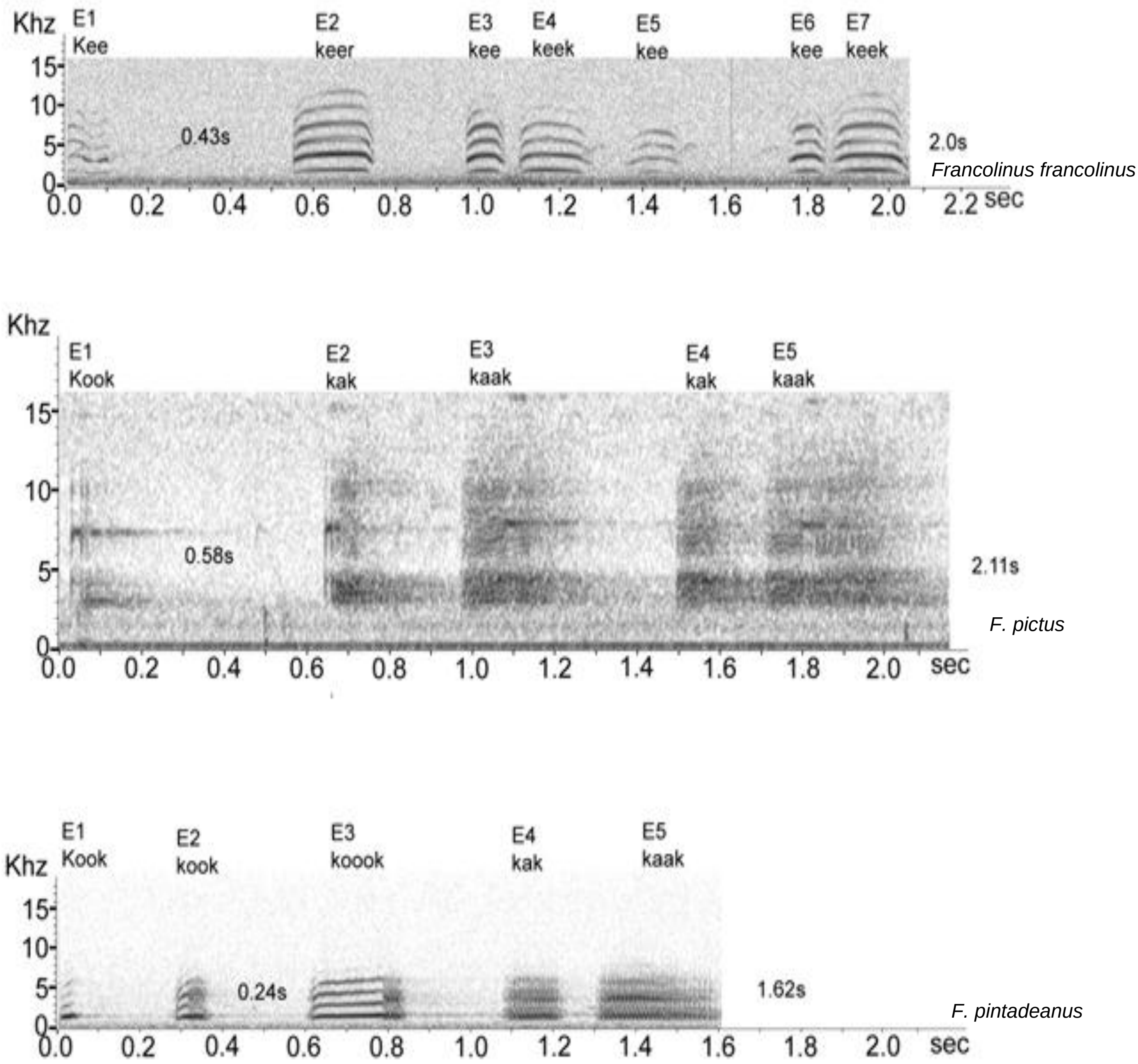
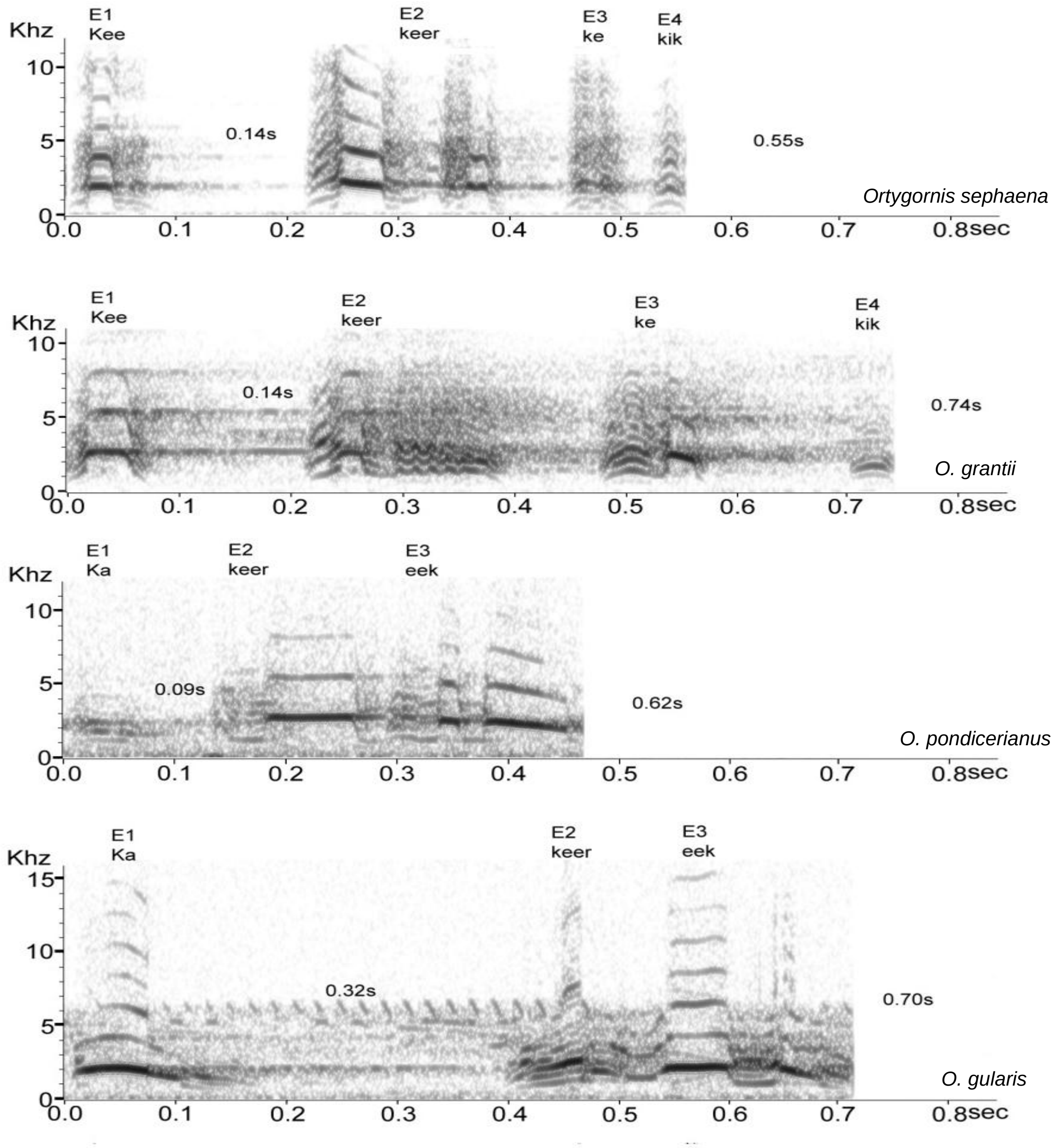


Figure 4.5. The strict consensus parsimony tree of spurfowls obtained from vocal characters. No nodes received bootstrap (i.e. > 50%) support.

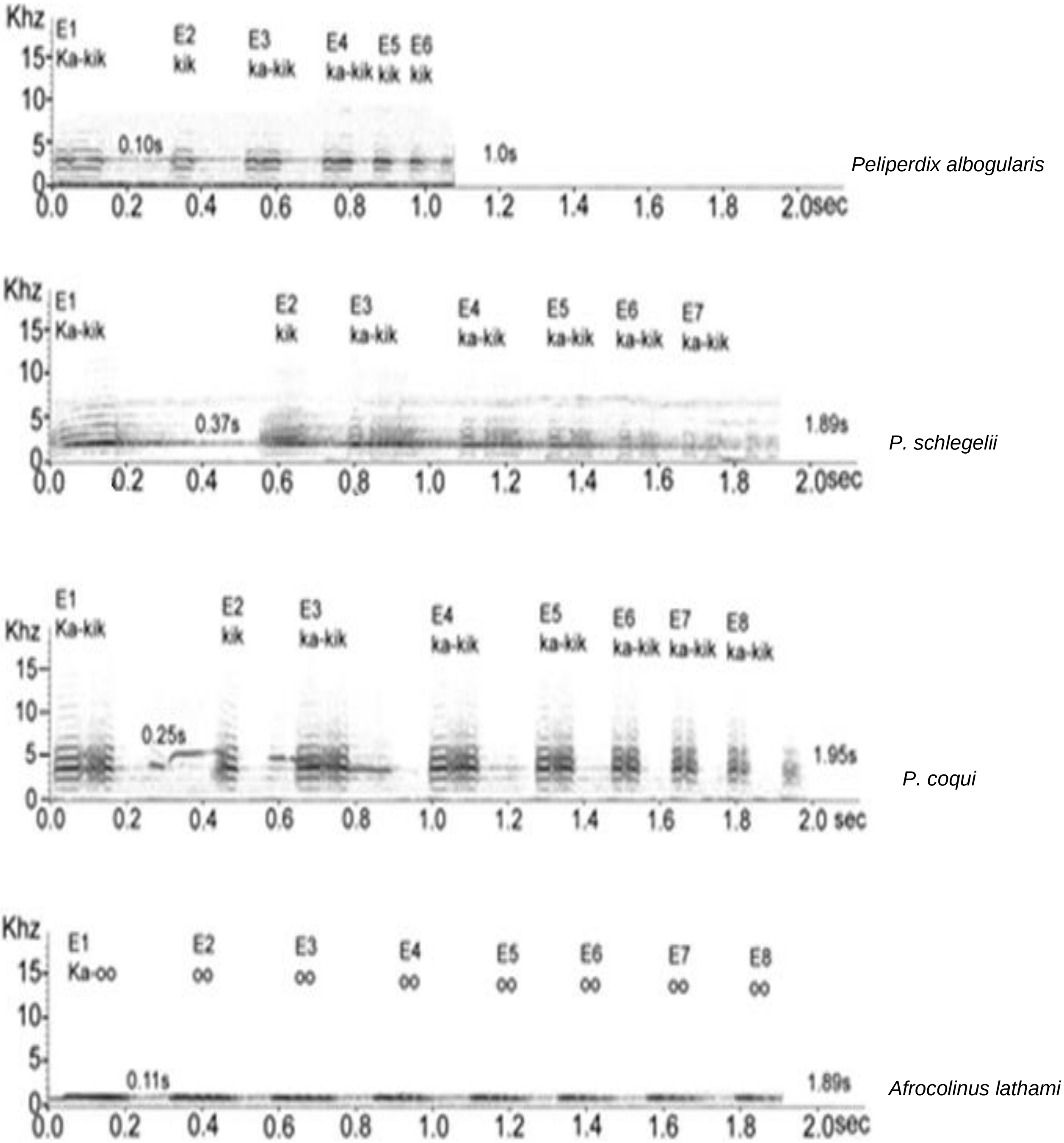
Appendix 1



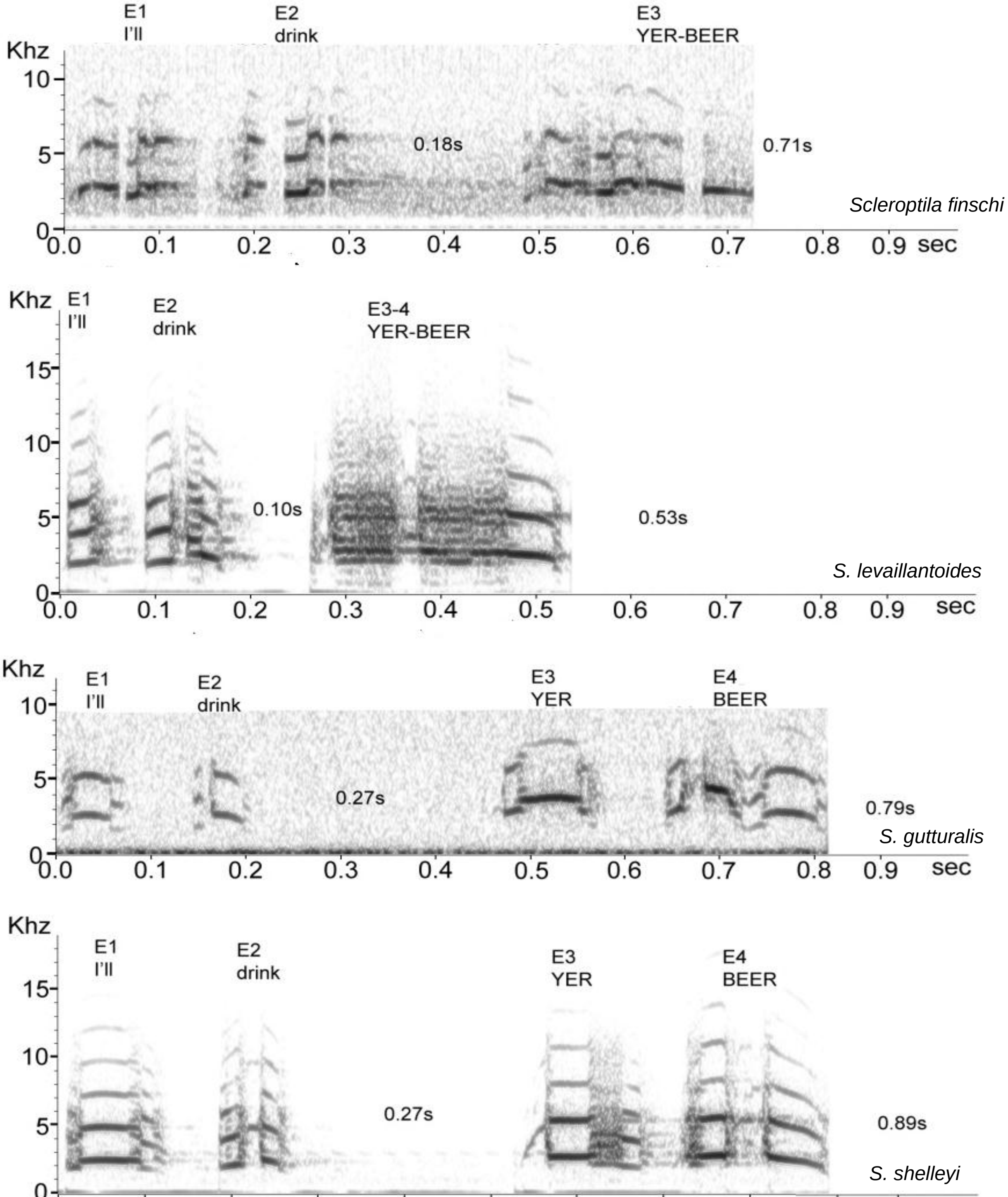
Sonograms of the *Francolinus* species.



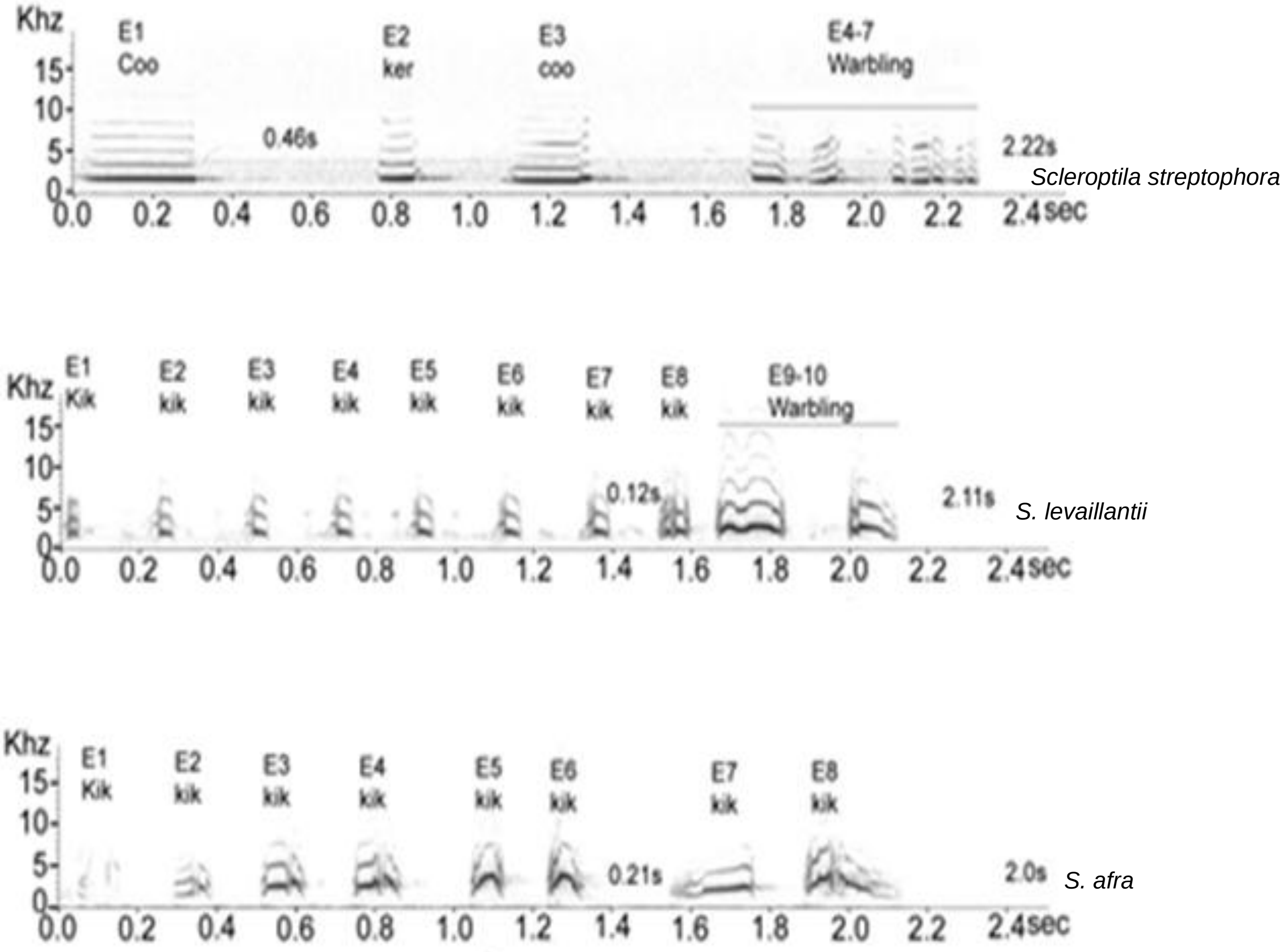
Sonograms of *Ortygornis* species.



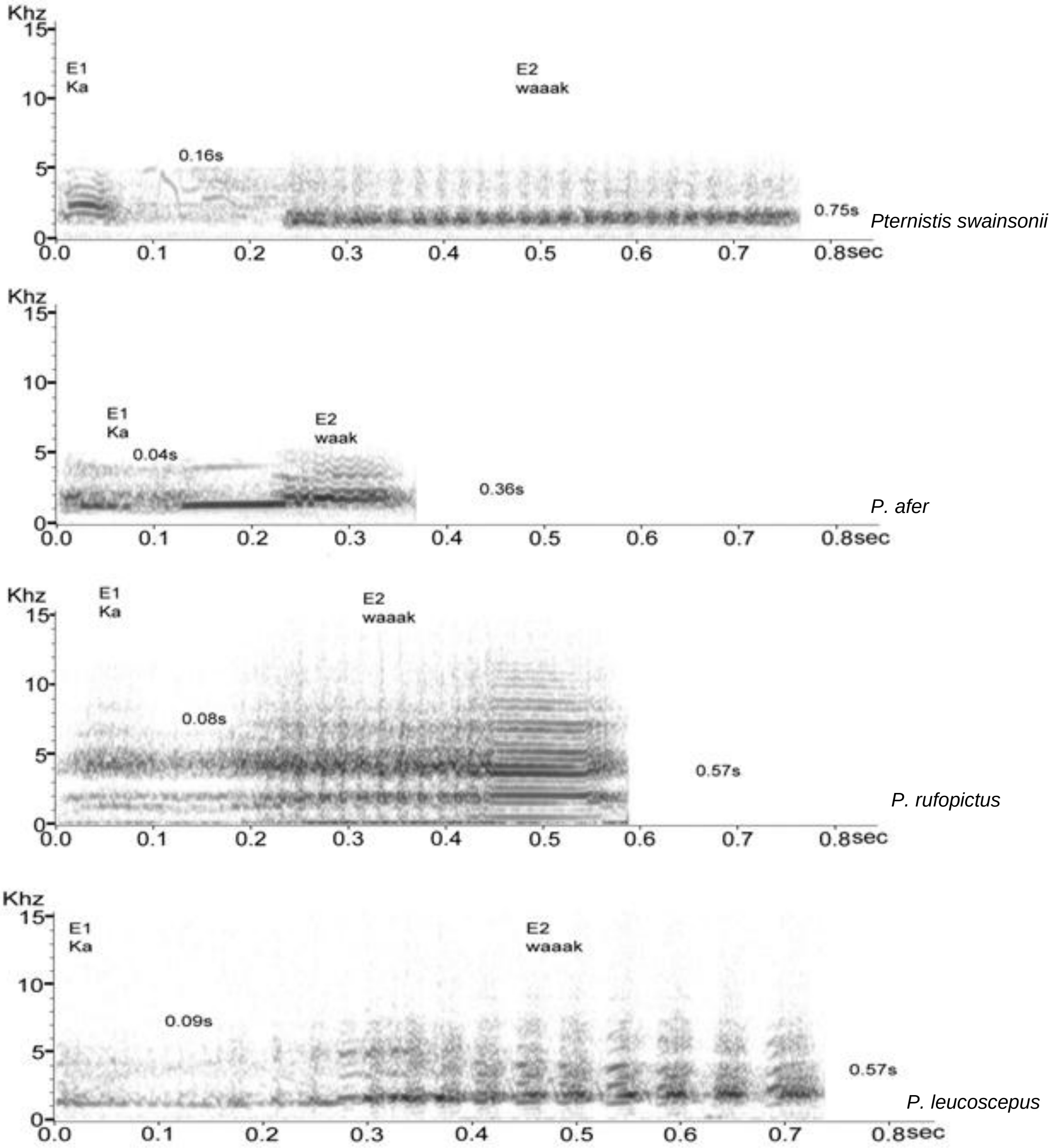
Sonograms of *Peliperdix* species and *Afrocolinus lathami*.



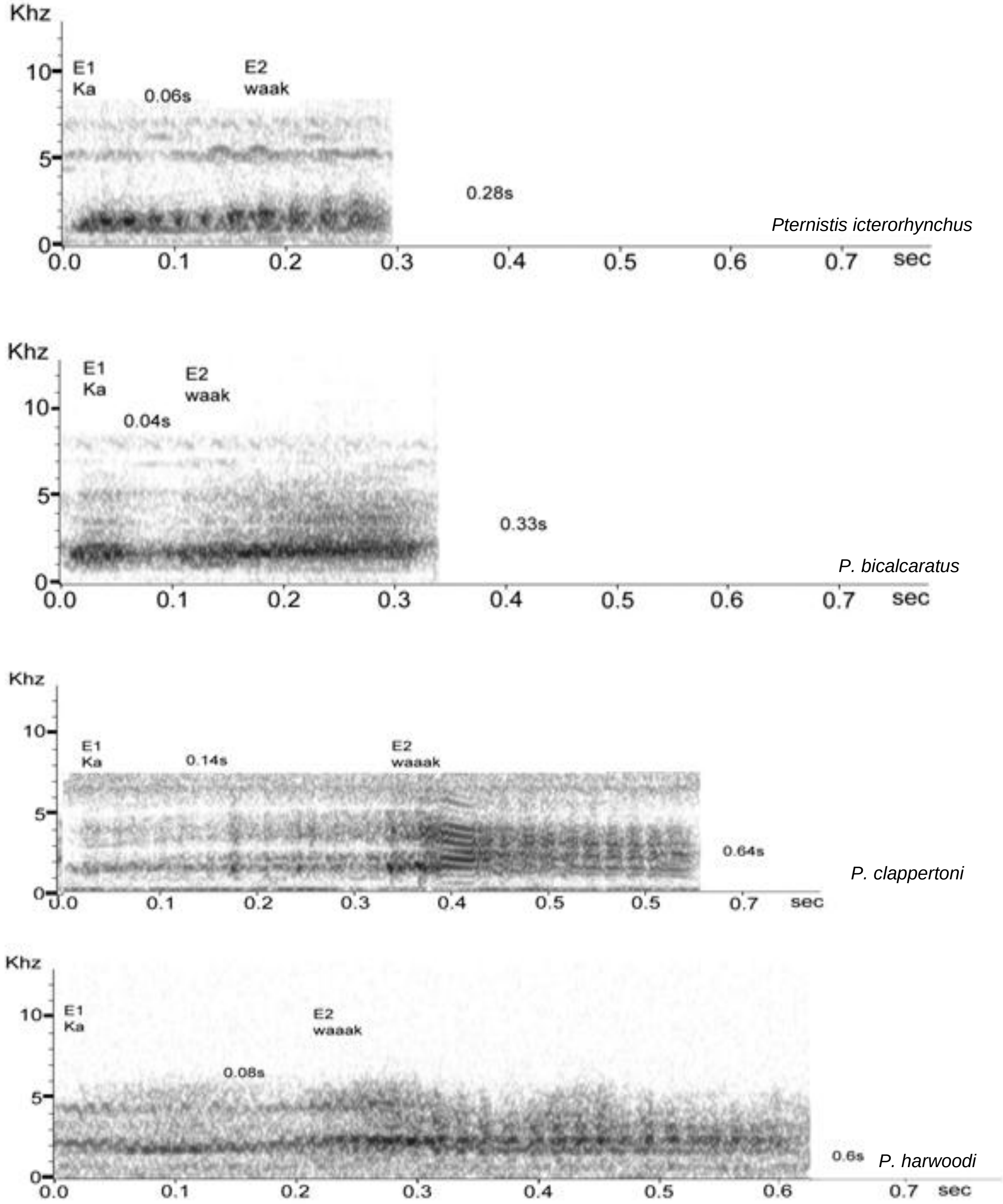
Sonograms of *Scleroptila* species.



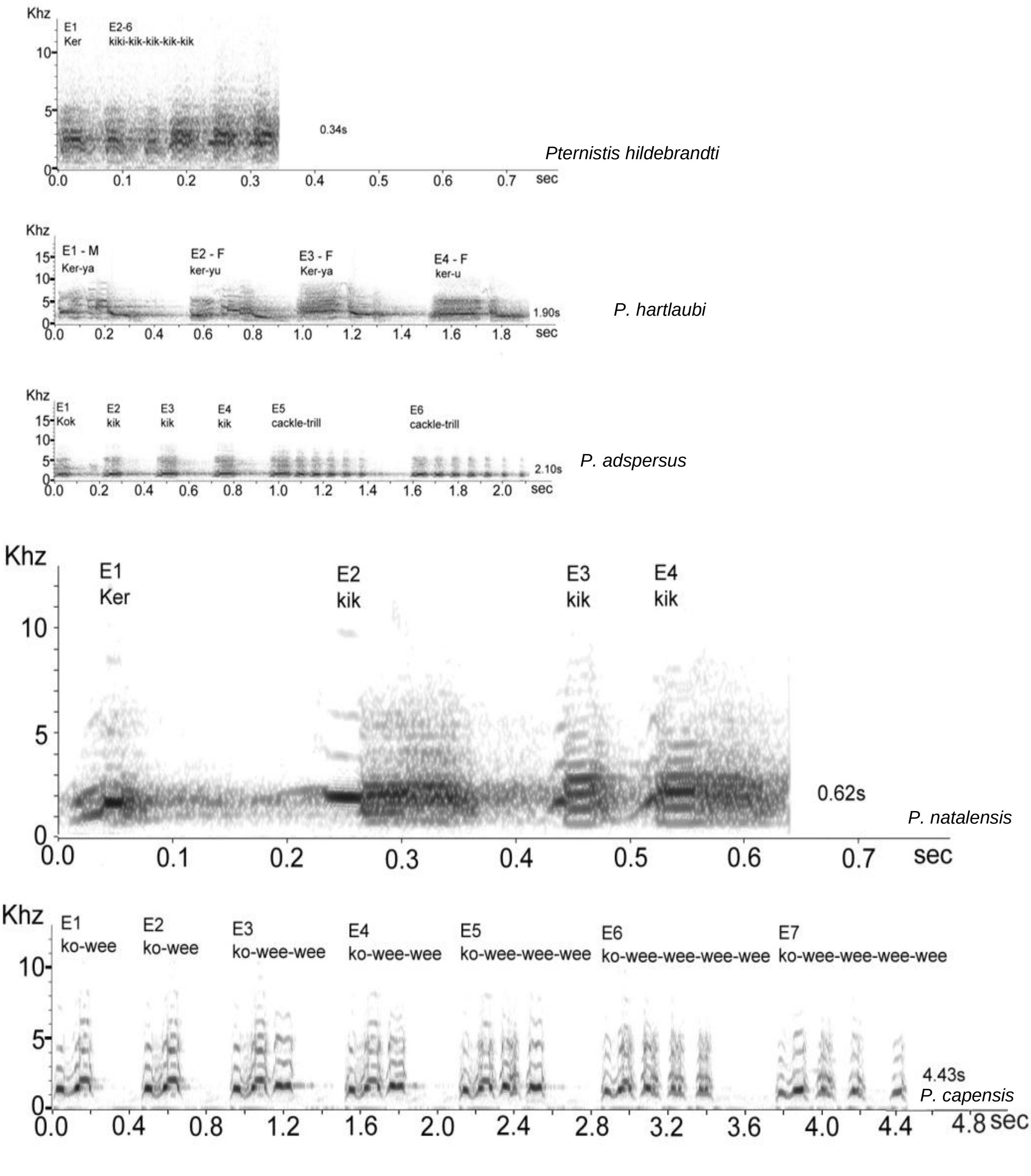
Sonograms of *Scleroptila* species.



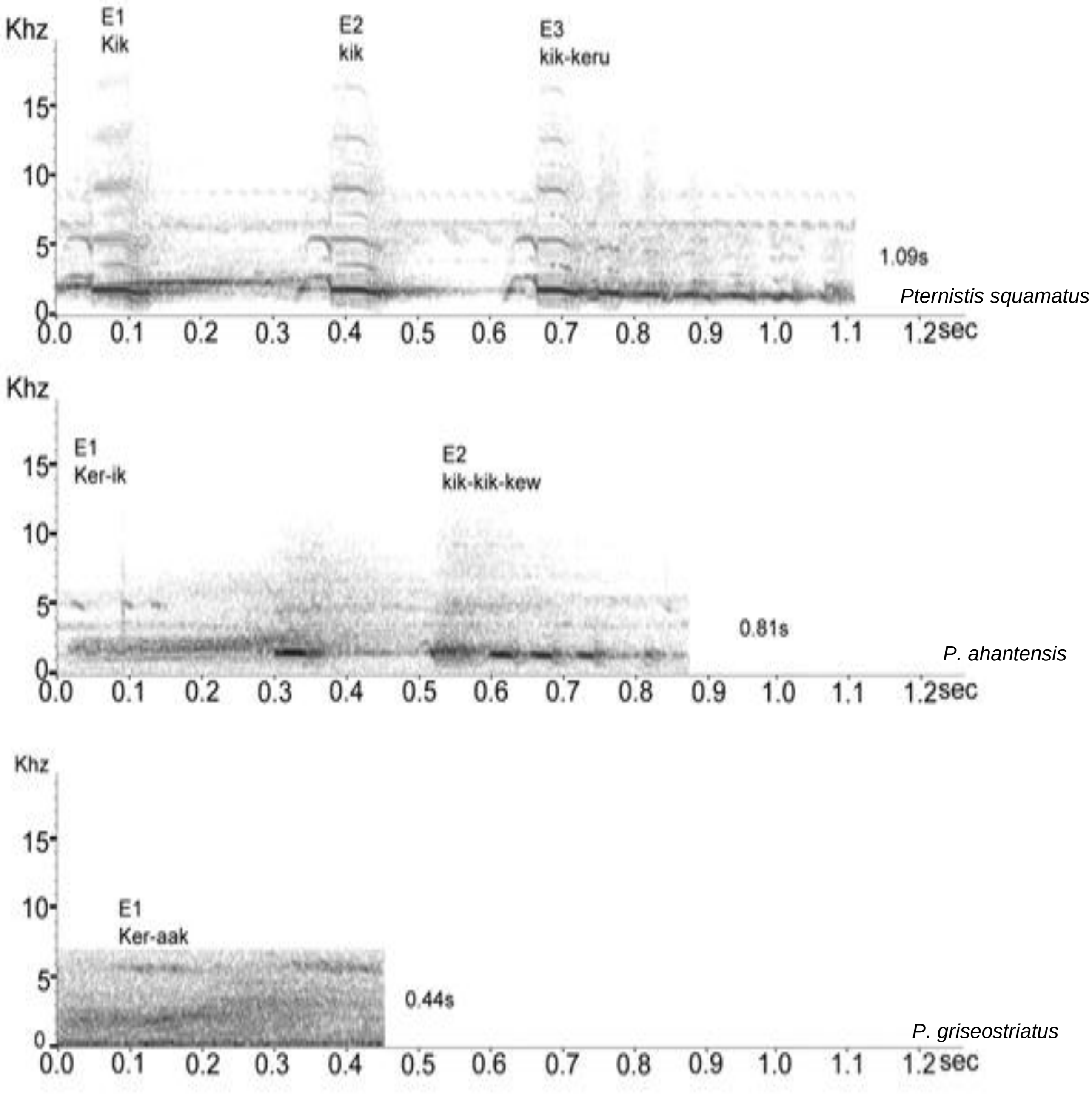
Sonograms of the Bare-throated spurfowls.



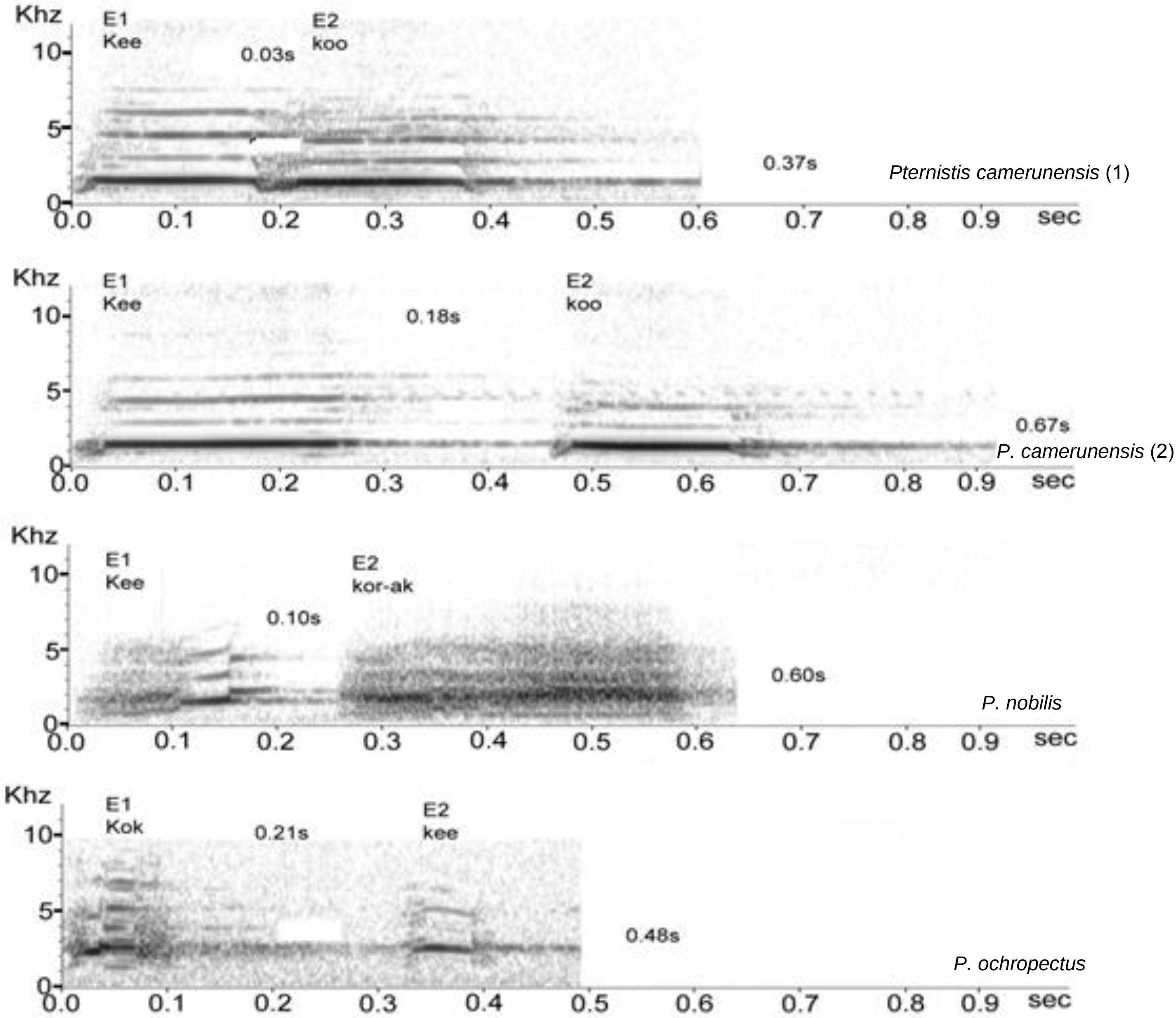
Sonograms of the Vermiculated spurfowls.



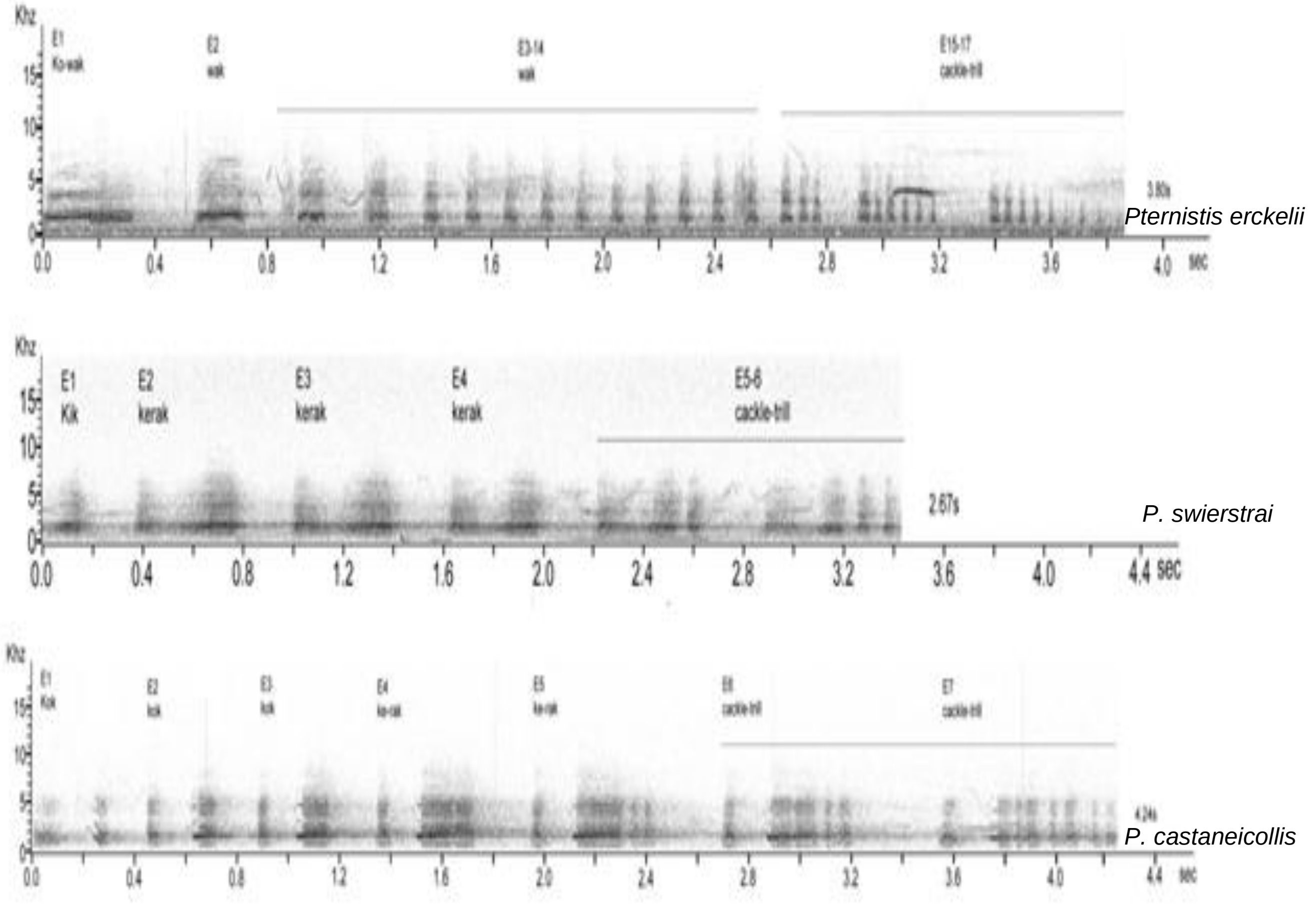
Sonograms of the Vermiculated spurfowls.



Sonograms of the Scaly spurfowls.



Sonograms of the Montane spurfowls.



Sonograms of the Montane spurfowls.

CHAPTER 5

Taxonomy and phylogeny of 'true' francolins

Abstract

The development of a plethora of species and subspecies concepts has had major effects on the delineation of terminal taxa across the Class Aves. The taxonomy and phylogeny of small, quail-like, Afro-Asian phasianine birds now known as 'true' francolins, but traditionally placed in a single genus *Francolinus* Stephens, 1819 with a range of other taxa are revised. The number of taxa that have been recognized as species and, to a larger extent as subspecies among 'true francolins' (*Francolinus, Dendroperdix, Peliperdix* and *Scleroptila* spp.) (*sensu* Crowe et al. 2006) has never been stable. This is due to a lack of objective, evolutionarily relevant species, subspecies and generic circumscription.

This study aimed to establish a classification system of francolins which takes into account the evolutionary relationships among taxa, and which, in turn, could generally bring stability to the number of taxa recognized as valid species, subspecies and genera based on congruent multiple lines of evidence. The model-based Maximum likelihood and parsimony analyses of separate and combined DNA and organismal characters resulted in some putative subspecies being elevated to the species level, others placed into more inclusive entities, and two new genera being established. Most of the phylogenetic hypotheses presented by Hall (1963) were rejected. The genus *Dendroperdix* is replaced by *Ortygornis*. The 'true' francolins are divided among five genera in the following pectinate phylogenetic sequence: *Francolinus / Ortygornis /*

Afrocolinus gen. nov. / *Peliperdix / Scleroptila*. A multi-faceted character approach seems to be a fitting strategy with which to delineate intra-generic relationships in francolins.

Introduction

Despite the challenges and uncertainties that the galliform phylogeny still presents (see Chapter 2), we do know that 'francolins' *sensu lato* do not share common ancestry as traditionally circumscribed. The genus *Francolinus* Stephens, 1819 (*sensu* Hall 1963), is split into two distantly related assemblages: 'francolins', represented by taxa classified in the genera *Francolinus* Stephens, 1819, *Dendroperdix* Roberts, 1922, *Peliperdix* Bonaparte, 1856 and *Scleroptila* Blyth, 1849, and 'spurfowls', with all members being assigned to the genus *Pternistis* Wagler, 1832.

Traditionally, 41 species (Table 1.1.) are assigned to the genus *Francolinus*, 36 occur in sub-Saharan Africa and five in Asia, thus making it the most specious genus in the Galliformes (Morony et al. 1975, del Hoyo et al. 1994) and one of the largest genera in the class Aves (Bock and Farrand 1980). Francolins are placed in the sub-family Phasianinae, and together with other Old World partridge- and quail-like gamebirds (e.g. *Perdix* and *Coturnix* spp.) in the tribe Perdicini (Chapin 1932, Peters 1934, Wolters 1975-82, Crowe et al. 1986, Johnsgard 1988, Sibley and Monroe 1990, del Hoyo et al. 1994, Madge and McGowan 2002). The traditional composition of the genus *Francolinus* has been disputed for over 50 years, with continuing uncertainty regarding the delineation and relationships of taxa within and between constituent species.

Species of francolins and their distribution

The focus in this chapter centres on the 'true' francolins (*Francolinus*, *Dendroperdix, Peliperdix* and *Scleroptila* spp.), that is those taxa assigned to Hall's (1963) species groups (see Table 1.1) with the addition of four species that Hall failed to assign to any of her groups. The species groups are: the Spotted (represented by three Asian species), Striated, Red-tailed and the Red-winged Group (all restricted to Africa). The four species she was unable to assign to a group are two African species, Latham's Francolin *Francolinus lathami* and Nahan's Francolin *Ptilopachus* '*Francolinus*' *nahani*, and two Asian species, Swamp Francolin *Francolinus gularis* and Grey Francolin *Francolinus pondicerianus* (Table 1.1).

Generally, francolins are small to medium sized, quail-like resident birds that can run or fly for short distances when faced with a threat. They are mainly diagnosed by having 14 tail feathers that moult centrifugally. Most species are sexually monomorphic in plumage, with males of most species having single spurred tarsi, with females in only a few cases having relatively smaller spurs (Johnsgard 1988). They represent a morphologically, ecologically and behaviourally diverse group, and have complex distribution patterns (Snow 1978). They occur in diverse habitats of a tropical to sub-tropical nature, with one African species *F. lathami* occurring in forested habitat (excluding *P. nahani*) (Hall 1963, Johnsgard 1988, del Hoyo et al. 1994, Madge and McGowan 2002). Francolins occur at varying altitudes and most of the species assemblages show allopatric distributional patterns among their constituent taxa (Hall 1963).

Species group diversity, distribution and morphology

Spotted Group – Genus Francolinus Stephens, 1819

This Asian group is represented by three recognized species (Table 1.1), the Black Francolin *Francolinus francolinus* (Linnaeus, 1766), Painted Francolin *F. pictus* (Jardine & Selby, 1828) and Chinese Francolin *F. pintadeanus* (Scopoli, 1786). The nominate species of the genus, *F. francolinus*, with its putative subspecies (Table 1.2) occurs from Cyprus to Manipur in northeastern India (Forcina et al. 2012). This species inhabits lowland cultivations, river deltas and lake edges with scrub and reeds (Forcina et al. 2012). *Francolinus pictus* represents the southern counterpart of *F. francolinus*, is distributed from Sri Lanka to north India, where it favours semi-dry undulating grasslands with scrub or cultivation (Forcina et al. 2012). *Francolinus pintadeanus* represents the eastern counterpart of *F. francolinus* (Forcina et al. 2012), inhabiting subtropical or tropical lowland forest from northeastern India, across Myanmar to south eastern China, extending across western and southern Thailand (Forcina et al. 2012).

Striated Group – Genus Dendroperdix Roberts, 1922

This group comprises two species, the polytypic Crested Francolin *Dendroperdix sephaena* (Smith, 1836), and the monotypic Ring-necked Francolin *Dendroperdix streptophora* O. Grant, 1891. The distributional range of *D. sephaena* extends from Somalia through eastern Africa to KwaZulu-Natal in South Africa, and extends westwards across Namibia and southern Angola, where the species inhabits mostly acacia savanna and steppe habitats (Fig. 5.1; Mackworth-Praed and Grant 1952, 1962, 1970, Hall 1963). Several subspecies (Table 1.2) are recognized: in *D. sephaena* there are *sephaena* (Smith, 1836), *spilogaster* Salvadori, 1888, *somaliensis* Grant & Praed, 1934, *schoanus* Heuglin, 1873, *jubaensis* Zedlitz, 1913, *grantii* Hartlaub, 1866, *rovuma* Gray, 1867, *zambesiae* Praed, 1920, *chobiensis* Roberts ,1932, *thompsoni* Roberts, 1924, *zuluensis* Roberts, 1924 and *mababiensis* Roberts, 1932.

Generally, *D. sephaena* is a rich reddish-brown bird with broad white shaft streaks. It has a chestnut collar that is interrupted with white. The patterned feathers of the lower neck are rich dark brown or blackish with broad white centres. This species is slightly dimorphic in that the females unlike the males are slightly vermiculated. The rest of the belly is buff with triangular chestnut markings on the breast, narrow greyish barring on the lower breast and it has an unpatterned belly. This species can be categorized into two distinct types, the "coastal type", which has fine drop-shaped light chestnut streaks on the belly and the "inland type" with no streaks on the belly (Fig. 5.1). *Dendroperdix streptophora* has a markedly disjunct distribution occurring in savanna-grassland in Cameroon in the west, and northern Uganda and northwestern Kenya and Tanganyika in the east (Fig. 5.2). It differs from most of the other Red-winged francolins in having an unpatterned crown, throat colour buff rimmed with rufous, the absence of a gorget, barred breast, blotched and mottled belly, brown (not red) primaries, unpatterned side of the head, and a tiny spur bump.

Red-winged Group – Genus Scleroptila Blyth, 1849

Members of this quail-like plumaged group, Shelley's Francolin *Scleroptila shelleyi* O. Grant, 1890, Grey-winged Francolin *S. afra* (Latham, 1790), Orange River Francolin *S. levaillantoides* Smith, 1836, Red-winged Francolin *S. levaillantii* (Valenciennes, 1825), Finsch's Francolin *S. finschi* Bocage, 1881, Moorland Francolin *S. psilolaema* Gray, 1867 are relatively homogenous in their overall morphology (Hall 1963, Snow 1978) and are distinguished by having red or rufous on their primaries, which is reduced in the Grey-winged Francolin *S. afra*. The distributional range of the group encompasses most of eastern and southern Africa extending from Ethiopia and Eritrea to the Cape, and westwards to Angola and the Congo (Fig. 5.2, 5.3, 5.4). Some species are allopatric (Snow 1978), and others have complex distributions, with species occupying diverse habitats at different altitudes.

Taxonomically, this is Hall's (1963) most contentious group. Several of the species in this complex are polytypic with multiple subspecies as follows: four in *S. psilolaema* (*psilolaema* Gray, 1867, *ellenbecki* Erlanger, 1905, *elgonensis* O. Grant, 1891, *theresae* Meinertzhagen, 1937); seven within *S. shelleyi* (*shelleyi* O. Grant, 1890, *uluensis* O. Grant, 1892, *whytei* Neumann, 1908, *macarthuri* Someren, 1938, *trothae* Reichenow, 1901, *sequestris* Clancey, 1960, *canidorsalis* (Lawson, 1963)); 12 in S. *levaillantoides* (*levaillantoides* Smith, 1836, *kalaharica* Roberts, 1932, *pallidior* Neumann, 1908, *langi* Roberts, 1932, *wattii* Macdonald, 1953, *jugularis* Büttikorfer, 1889, *cunenensis* Roberts, 1932, *stresemanni* Hoesch & Niethammer, 1940, *gutturalis* (Rüppell, 1835), *lorti* Sharpe, 1897, *archeri* Sclater, 1927, *ludwigi* Neumann, 1920); five in *S. levaillantii* (*levaillantii* (Valenciennes, 1825), *kikuyuensis* O. Grant, 1897, *crawshayi* O. Grant, 1896, *benguellensis* Neumann, 1908, *clayi* White, 1944). *Scleroptila finschi* Bocage, 1881 and *S. afra* (Latham, 1790) are monotypic species.

Red-tailed Group – Genus Peliperdix Bonaparte, 1856

The Red-tailed Group is represented by small francolins generally with a wing length of less than 150 mm (Mackworth-Praed and Grant 1952, 1962, 1970). Their distribution range stretches from Senegal to Sudan and from central Kenya west to the central Congo and Angola, and south to the Transvaal and Natal in South Africa (Fig. 5.5). There is an isolated subspecies in the Ethiopian Rift. The three traditionally recognized species are Coqui Francolin *Peliperdix coqui* (Smith, 1836), White-throated Francolin *P. albogularis* Hartlaub, 1854, and Schlegel's Francolin *P. schlegelii* Heuglin, 1863 (Table 1.1), and all are allopatric (Hall 1963, Snow 1978). Members of this group occupy wooded grasslands. All the above taxa generally have a quail-like patterning on the back which is consistent and well-defined, though the basic colour and the colour of the crown varies from brown to rufous in different taxa.

Peliperdix coqui is one of the two African francolins (including *F. lathami*) that exhibits truly marked sexual dimorphism in plumage (Hall 1963). The male birds differ from the females in having the sides of the head and throat ochre or light buff without a black eye stripe or necklace. Females have the sides of the head similar in colour to the males, but the throat is whiter and they have a black necklace and a black eye stripe that continues as a black line down the sides of the head. The breast and lower neck of the male is barred with black, whereas the barring on the breast of the female is overlaid by a pinkish wash and there is no barring on the lower neck.

Peliperdix coqui and *P. albogularis* are the two species in this group that have recognized subspecies (Table 1.2): 14 in *P. coqui* (*coqui* (Smith, 1836), *spinetorum* Bates, 1928, *buckleyi* Peters, 1934, *maharao* Sclater, 1927, *ruahdae* Someren, 1926, *hubbardi* O. Grant, 1895, *angolensis* Rothschild, 1902, *lynesi* Sclater, 1932, *vernayi* (Roberts, 1932), *campbelli* (Roberts, 1928), *thikae* Grant & Praed, 1934, *kasaicus* White, 1945, *hoeschianus* Stresemann, 1937, *stuhlmanni* Reichenow, 1889), and five for *P. albogularis* (*albogularis* Hartlaub, 1854, *buckleyi* O. Grant, 1892, *dewittei* Chapin, 1937, *meinertzhageni* White, 1944, *gambagae* (Praed, 1920)).

The unplaced species of Hall (1963)

The species *Ptilopachus* '*Francolinus*' *nahani*, one of Hall's enigmatic species (others *F. lathami*, *F. gularis* and *F. pondicerianus*) (Table 1.1), is excluded from this chapter on francolins since this species was found not to be a 'francolin', but a 'partridge', with close phylogenetic affinity to the African Stone Partridge *Ptilopachus* *petrosus*, and both these species in turn are the closest extant relatives of the New World quails (see Chapter 2, Cohen et al. 2012, Bowie et al. 2013). Latham's Francolin *F. lathami* is a small francolin with a disjunct distribution and is restricted to forest habitat. Its distribution extends from Sierra Leone to western Uganda and southern Sudan, with two further outlying pockets of occupancy in the Congo (Fig. 5.6). Two subspecies, *lathami* Hartlaub, 1854 and *schubotzi* Reichenow, 1912, are recognized (Table 1.2). *Francolinus pondicerianus* lives on dry plains in semi-desert areas (Forcina et al. 2013) in the Gulf of Oman and on the plains of India. *Francolinus gularis* is patchily distributed between south-western Nepal and extreme north-eastern India (del Hoyo et al. 1994, Forcina et al. 2012), where it is confined to marshes and reeds (Hall 1963) on the plains of the Ganges River.

What do we know about their taxonomy and phylogeny?

Chapter 1 outlines the taxonomic disagreement and confusion that various authors have had with delineating taxa at the subspecific level (Table 1.2), as well as with attempts to assign francolin species to various genera. The classic monograph of Hall (1963) on francolins remains one of the most significant works on any group of African birds. It has significantly enhanced our knowledge and understanding of the taxonomic status of francolins, their evolutionary relationships, current distribution ranges including how species might have spread to their current habitats.

What ignited further investigation of systematic relationships among francolins was Hall's (1963) conclusion that the genus *Francolinus* was monophyletic, and that the 37 species she recognized could be divided among eight putatively monophyletic groups comprising ecologically similar, but largely allo- or parapatric species (Bloomer and

Crowe 1998). The reason Hall (1963) did not recognize distinct genera was because of the difficulties presented by the Crested Francolin *Dendroperdix sephaena* and an atypical *Ptilopachus nahani*. However, she indicated that should generic subdivision be desirable she would have two major groups, one consisting of members that she referred to as belonging to the Spotted Group (Asian francolin group), Bare-throated (African spurfowls), Montane (African spurfowls), Scaly (African spurfowls), Vermiculated Group (African spurfowls) and one of the unplaced Asian francolin *F. gularis*. The second group would be comprised of the Red-winged (francolins), Striated (francolins) and Red-tailed groups (francolins), and two unplaced species *F. pondicerianus* (Asian francolin) and *F. lathami* (African francolin).

Wolters (1975-82) like Roberts (1924) (Table 1.2) recognized the genera: *Francolinus*, *Scleroptila*, *Dendroperdix*, *Peliperdix* and *Ortygornis*. Contrary to Roberts, Peters (1934), and Mackworth-Praed and Grant (1952, 1963, 1970), Wolters assigned the genus *Pternistis* (Table 1.2) to all taxa which are known today as 'spurfowls'. In short, Wolters's system of genera represents what is used today (Table 1.2) with the exception of the genus *Ortygonis,* which he assigned to *F. pondicerianus*. The number of traditionally recognized francolin species ranged widely over time with 17 excluding *P. nahani* (in Peters 1924 - who covered Africa and Asia), 11 excluding *Scleroptila psilolaema* and *P. nahani* (Mackworth-Praed and Grant 1952, 1962, 1970 - Africa only), 17 excluding *P. nahani* (Wolters 1975-82 - Africa and Asia), and 17 excluding *P. nahani* (Hall 1963 - Africa and Asia).

Phylogenetic difficulties have been articulated by Crowe and Crowe (1985), Crowe et al. (1986), Crowe et al. (1992), Bloomer and Crowe (1998), Crowe et al. (2006) and most recently by Forcina et al. (2012), with regard to the monophyletic status of the genus *Francolinus*, and in particular, the status of the different putative monophyletic groups recognized by Hall (1963). It is important to note that different studies used different types of characters (Table 1.4), focussed on different geographic areas of francolin distribution (Table 1.3), and made use of different methods of phylogenetic analysis. Groups that various authors have recovered as monophyletic are the Spotted Group (Crowe and Crowe et al. 1985, Crowe et al. 1992, Forcina et al. 2012), Red-tailed. Group (Crowe and Crowe et al. 1985, Crowe et al. 1992), and the Red-winged Group (Crowe and Crowe et al. 1985, Crowe et al. 1992, Bloomer and Crowe 1998). No study has ever recovered the monophyly of the Striated Group, with Crowe et al. (1986) placing the Ring-necked Francolin *Dendroperdix streptophora* in the Red-winged Group (*Scleroptila*). In most analyses (Crowe and Crowe 1985, Crowe et al. 1992, Bloomer and Crowe 1998, Chapter 2), *F. pondicerianus* and *F. gularis* group with *D. sephaena* and as such it would have been ideal for Forcina et al. (2012) to have included some African francolins to strengthen their findings on the Asian francolins and purported delineation of the Spotted Group as being monophyletic.

On the basis of the chaotic taxonomic status and the phylogenetic uncertainty of francolin taxa (Tables 1.1, 1.2), a formal revision of all francolin taxa is urgently needed.

What is taxonomy and how can we possibly study it?

A review of species and subspecies concepts

Delineating species and/or subspecies boundaries correctly is crucial to the discovery of life's diversity because it determines whether or not we can recognize when different specimens are members of the same cohesive lineage (Dayrat 2005). Many different types of taxonomic characters (morphological, physiological, chemical, behavioural, ecological, molecular, among others) have been used to delineate taxa. In taxonomy, the fundamental components of biodiversity, species and subspecies, are discovered, described, named, and classified. The naming of taxa, in this case francolins, is to some degree of less concern in the present study. However, the classification of these taxa at the species-level and below, presently lacks consensus and therefore there is a need to establish a sound classification system that can best reflect the evolutionary history of francolins.

A number of francolin species are polytypic, being complexes of taxa that exhibit considerable geographical variation in their biological traits and this variation poses serious challenges to classification (Pough 1990). The concept of 'polytypic' species is said to have emerged as a way of simplifying classification by lumping several diverse but difficult to delineate taxa into a single species (Clancey 1957, Maclean 1993). The subspecies concept is one that has been debated for over 100 years with various authors presenting different perspectives on the meaning of 'subspecies'. Many authors interpret subspecies as geographically partitioned variation, which may or may not exhibit intergradation (Winker 2010). Subspecies are often construed as biological entities that provide evidence of adaptation and the early stages of speciation; they are also considered to be important in improving our understanding by alerting us to interesting geographic and behavioural patterns (Cicero 2010).

Cicero (2010), Remsen (2010) and Winker (2010) see subspecies as a meaningful rank, others consider subspecies to be a tool of convenience (Mayr 1982a, FitzPatrick 2010). Zink (2004) calls for the classification and rank names to reflect diagnosable units and hence considers subspecies to be of limited utility. Phillimore et al. (2010) contends that the concept has not been applied appropriately and objectively in that there has to be a sound understanding of the processes that govern the origination and extinction of subspecies. Pruett and Winker (2010) highlighted the importance of using multiple lines of evidence in assessing subspecific status even though they acknowledged the challenge that can arise in cases of discord caused by varying evolutionary rates of character change.

Another complicated issue that continues to challenge biologists is that of developing a species definition of universal application. As Darwin (1859) articulated there is vast vagueness in what naturalists mean by 'species', as a consequence a suite of species concepts have been postulated (reviewed in Mayden 1997, de Queiroz 2007) to date and a consensus is hardly met. de Queiroz (2007) postulated a "Unified Species Concept" which was meant to be a reconciliation of the various species concepts available to date. He defined species as separately evolving metasubspecies lineages or segments (Knowles and Carstens 2007). The properties that were previously treated as necessary properties for species, for example intrinsic reproductive isolation in the case of the Biological Species Concept; occupation of a distinct niche or adaptive zone in the case of the Ecological Species Concept; fixed character state differences in the case of the diagnosable version of the Phylogenetic Species Concept are no longer considered the defining properties of the species category, rather there is a continuum that extends between these alternate definitions of species that may relate to their relative evolutionary age.

Taxonomic determinations made in this chapter

The polytypic nature of several species of francolins is highlighted above and tabulated in Table 1.2. At the end of this chapter, it is expected that some of these taxa will be elevated to species rank, provided they represent distinct phylogenetic and biogeographical eco-evolutionary entities diagnosable in terms of organismal and molecular characters. Other taxa will likely be subsumed into the same terminal taxon if they show relatively little phylogenetic distinctiveness and geographical and/or ecological partitioning. The primary grouping criterion followed in this study is multifaceted consilience in character variation (*sensu* Pruett and Winker 2010), because ultimately one has to draw the taxonomic line somewhere with the goal of finding meaningful evolutionary entities.

Hybridization is known to occur even long after speciation (Mallet 2005, Mallet 2008) and hence is not over-emphasised as a criterion for taxonomic delineation. Thus, in this study, the decision to rank a taxon as a species, is considered if it is morphologically and/or behaviourally diagnosable (as defined above), ≥ 1-2% divergent in unweighted molecular characters, and confined to a specific eco-region. For a particular taxon to be considered a subspecies, it should exhibit relatively little phylogenetic distinctiveness and geographical and/or ecological partitioning, be < 1% divergent in unweighted molecular characters, and be confined to a specific eco-region.

Objectives of the study:

- To review the taxonomic status of the 'true' francolins, with a particular focus on African francolins.
- To re-assess the monophyletic status of the various species groups proposed by Hall (1963).
- To investigate the phylogenetic relationship between Hall's (1963) enigmatic unplaced Asian species *F. pondicerianus* and *F. gularis* , and African species (*F. lathami*) in light of the findings of Cohen et al. (2012) and Forcina et al. (2012).

- To produce a revised classification of African francolins that takes into account the evolutionary relationships among taxa.

Materials and methods

Data collection

Morpho-behavioural characters of francolins

In total, 24 organismal characters reflecting assessment of plumage/integument and colour/pattern (Fig. 5.7), as well as measurements of certain qualitative and quantitative structures (Table 5.1), and several vocal characters extracted from Crowe at al. (1992) and chapter 4, were scored (Table 5.2). Morphometric characters representing bill-length, tarsus- and spur-length were obtained using a Vernier Calliper. A stopped wing-rule and a normal ruler were used to measure wing- and tail-length, respectively. Wing-length was measured with the wing chord flattened and straightened for enhanced accuracy.

Molecular characters

For within-group molecular analyses of ‘true’ francolins, 41 terminal taxa (including two outgroup species) were sampled (Tables 5.3) for the entire mitochondrial Cytochrome-*b* gene (CYT*B* - 1143 base pairs- bp). GenBank accession numbers of taxa sequenced are detailed in Appendix 5.1. Primers used in sequencing molecular markers are listed in Tables 5.4 and 5.5; 67% of DNA samples of francolins sequenced were derived from toe-pads sub-sampled from museum skins.

For the toe-pad samples, instead of sequencing the CYT*B* gene in a single reaction using the available universal primers, multiple sequence fragments (six for each sample) were generated (using primers specifically designed for francolins, Table 5.5) due to the degraded state of the DNA. This meant that 1143 bp for each toe-pad sample would only be recovered by assembling six different PCR-amplified and sequenced fragments.

Maps and mapping of distribution records of investigated taxa

The maps showing the distribution ranges of francolins were produced (Fig. 5.1 – 5.6). This was a challenging task given that the actual point locality data for most taxa were not available. Ranges of all the traditionally recognized species presented in Snow's (1978) atlas were used as the basis for generating range maps (Chapter 5 and 6) because these ranges were produced from the point locality data associated with skins housed in museums. The distribution data in Harrison et al. (1997) were then overlaid on Snow's ranges and this was very helpful in filling in the gaps in the ranges at least of the southern African species. The 2nd step used Hall's (1963) distributions to cover the ranges of both species and subspecies that she recognized.

Step 3 involved the superimposition of Mackworth-Praed and Grant's (1952, 1962, 1970) ranges on Snow's ranges to cover both species and subspecies that these authors recognized. Mackworth-Praed and Grant (1952, 1962, 1970) and Hall (1963) are the two main taxonomic revisions that covered the Africa and Africa and Asia species respectively, contrary to revisions in Roberts (1924), Clancey (1967) and Hockey et al. (2005) that covered smaller geographic areas in which francolins occur. In Step 4 Clancey (1967) and Hockey et al. (2005) were used to account for the distributions ranges of other populations as they recognized them. These two revisions covered the southern African region only. Distribution ranges in steps 2-4 were generally superimposed on Snow's ranges and gaps, which may either translate to the real gaps in distribution or are indicative of under-sampling in the intervening area. It is only with the exception of *Peliperdix schlegelii* where the range is not broken according to Snow since the species is confirmed to have a continuous distribution from eastern Cameroon through to Central African Republic, to the western Bahr-el-Ghazal in Sudan (Mackworth-Praed and Grant 1970, Hall 1963). With regard to the names of studied localities of taxa, old rural names were used to a certain extent when translating them posed difficulty. In order to prepare distribution ranges of taxa to be used in the spatial analysis of vicariance, distribution records were mapped on a continuous basis using a 2x2 degree grid on the world map which was accessed on [http://earthobservatory.nasa.gov/Features/BlueMarble/].

Data analyses

Phylogenetic analyses

The generated nucleotide sequences were edited and assembled in the Staden Package (Staden et al. 2003) and aligned in MAFFT (Katoh et al. 2009). All CYT*B* (coding genes) sequences generated in this study were checked for stop codons before they were analyzed by translating them into amino acids and this was done online at EMBL [http://www.ebi.ac.uk/emboss/transeq/]. Two phylogenetic inference methods with different optimality criteria were employed to generate phylogenetic hypotheses: maximum likelihood (CYT*B*) and parsimony (CYT*B*, organismal, combined CYTB/organismal characters). As suggested by the results of the much larger data set in Chapter 2, all data matrices were rooted on *Gallus gallus* and *Bambusicola thoracica*. For all analyses, characters were treated as non-additive. Parsimony-based phylogenetic analyses were conducted using PAUP ver. 4.0b10 (Swofford 2002). The following settings were effected: full heuristic search with all characters unordered and with equal weight, starting tree(s) obtained via stepwise addition; tree-bisection-reconnection branch-swapping, 1000 random additions of taxa (Maddison 1991), one tree being held at each step during stepwise addition , branches were collapsed (creating polytomies) if the maximum branch-length was zero. When multiple, equally parsimonious cladograms were recovered, a strict consensus cladogram was constructed. The extent to which each non-terminal node is supported by different character partitions was determined by using the bootsrap (BS) (Felsenstein 1985) resampling strategy with 1000 pseudoreplicates, with 5 random additions of taxa per bootstrap pseudoreplicate.

Since different codon positions evolve under different models of evolution, it has been argued that a partitioned, mixed-model approach should be adopted (Ronquist and Huelsenbeck 2003, Nylander et al. 2004). Mixed-model analyses allowed different parameters (base frequencies, rate matrix or transition/transversion ratio, shape parameter, proportion of invariable sites) to vary among the three codon positions.

Mixed-model maximum likelihood analyses were performed using the Randomised Axelerated Maximum Likelihood algorithm for High Performance Computing (RAxML) v7.0.4 (Stamatakis 2006, Stamatakis et al. 2008) as implemented on the CIPRES portal. Mixed-model RAxML analyses make use of a GTR+Γ+I model partitioned by gene or codon postion. Support at nodes was assessed with 100 non-parametric bootstrap (BS) pseudoreplicates. The use of different methodological approaches (optimality criteria) facilitated the identification of method-based incongruence.

Genetic distances

Uncorrected pairwise distances (Table 5.6) were calculated in PAUP ver. 4.0b10 (Swofford 2002) for the CYT*B* data matrix and were converted to percentage sequence divergence.

Results and Discussion

Separate versus combined phylogenetic analyses

The parsimony analysis for the CYT*B* data set (with 1143 bp characters, yielded 315 parsimony informative characters and 110 variable characters that were parsimony uninformative. Four trees of 1356 steps were recovered. The organismal data set comprised 24 characters, 23 of which were parsimony informative, and one that was parsimony uninformative. In total, 390 trees of 104 steps were recovered. The combined CYT*B/*organismal data set comprised 1167 characters of which 334 were parsimony informative and 115 that were variable but parsimony uninformative. In total, 24 trees of 1491 steps were recovered.

The systematics of Hall's species groups and unplaced species

Striated Group and the unplaced Asian species

Traditionally, the Striated Group encompasses two recognized species, a polytypic *Dendroperdix sephaena* and a monotypic species *Dendroperdix streptophora,* and 12 subspecies assigned to *D. sephaena*: *sephaena, spilogaster, somaliensis, schoanus*, *jubaensis*, *grantii*, *rovuma*, *zambesiae*, *chobiensis*, *thompsoni*, *zuluensis* and *mababiensis*.

In comparing the phylogenetic trees (Fig. 5.8, 5.9, 5.10, 5.11), none of these analyses ever recovered the monophyly of the Striated Group as hypothesized by Hall (1963). In all the trees, *D. streptophora* joins the Red-winged Group whereas *D. sephaena* (labelled *Ortygornis* in the trees) is well separated from the Red-Winged Group and remains at the basal parts of the trees. These results confirm earlier suggestions of the distinction of these two taxa (Crowe and Crowe 1985 and Crowe et al. 1992). *Dendroperdix sephaena* (together with *rovuma, grantii*, see below) form a sister relationship in most analyses (Fig. 5.8, 5.9, 5.11, respectively) with the two unplaced Asian species *F. pondicerianus* and *F. gularis*, which in turn emerge as sister species with high support. The organismal tree (Fig. 5.10) does not support the phylogenetic association of *Dendroperdix* taxa with *F. pondicerianus* and *F. gularis*, but instead places *D. sephaena* with other members of the genus *Francolinus. Francolinus gularis* differs from *F. pondicerianus* with 5% sequence divergence (Table 5.6), from *sephaena* with 8%, and there is 9% divergence between *pondicerianus* and *sephaena*. *Francolinus gularis* and *F. pondicerianus* diverged from each other 3.1 mya and both species diverged from *D. sephaena* at 5.5 mya – Fig. 2.7).

Francolinus gularis is quite different in colouration and patterning (with barred back) from the other Asian francolins. The white streaks on the belly strongly contrast with the rufous throat and wings. *Francolinus pondicerianus* is finely patterned with the nominate subspecies *pondicerianus* being the darkest and the least grey and has the greatest amount of chestnut markings. The consistent grouping of *F. pondicerianus* and *F. gularis* with the *Dendroperdix* taxa (Fig. 5.8, 5.9, 5.11, 2.2, 2.3, 2.5, Bloomer and Crowe 1998) refutes the finding in Forcina et al. 2012 that the five Asian species (*F, francolinus, F. pictus, F. pintadeanus, F. pondicerianus, F. gularis*) are monophyletic.

Therefore, it is recommended that *F. pondicerianus* and *F. gularis* be considered congeneric and be placed in the genus *Ortygornis* Reichenbach, 1853 over *Dendroperdix* Roberts, 1922 based on priority, and because *Ortygornis* was once used for *pondicerianus* (Roberts, 1940). Therefore, there will be *Ortygornis pondicerianus* (Gmelin, 1789) and *O. gularis* (Temminck, 1815) (Appendix 5.2).

The *Dendroperdix* taxa form a monophyletic assemblage with *sephaena* being sister to *rovuma* and *grantii* (Fig. 5.8, 5.9, 5.11) with moderate to high support (see rationale below for splitting these taxa from *D. sephaena*). *Rovuma* and *grantii,* are in turn, sister to each with high support in most analyses (Fig. 5.8, 5.9, 5.11, respectively) with the exception of the organismal only dataset (Fig. 5.10), where relationships among these taxa are unresolved. With respect to uncorrected pairwise genetic divergence, *rovuma* differs from *sephaena* by 4%, and *sephaena* differs from *grantii* by 5%, and *rovuma* differs from *grantii* by 4%.

Dendroperdix sephaena can be categorized into two distinct types, the coastal types that have fine drop-shaped light chestnut streaks on the belly and the inland type with no streaks on the belly. *Grantii* has a reduced band of chestnut triangular marks on the breast, narrow greyish somewhat U-shaped streaks on breast and belly with the distal part of the belly being unpatterned. *Rovuma* has a band of chestnut triangular marks being reduced without covering much of the breast, no barring on the belly, has drop-shaped chestnut streaks on the belly and not much distally. In the north, the Ethiopian subspecies *spilogaster* is barred and streaked on the breast with barring being extensive as in *sephaena*. The Somalian subspecies *somaliensis* is like *spilogaster,* but the streaking is not extensive. There is confirmed evidence of hybridization taking place in the north between the southern subspecies *rovuma* and the northern *spilogaster* (Hall

1963, Snow 1978). The distribution range of *rovuma* and *spilogaster* is intercepted by that of *grantii* such that the two streaked subspecies are isolated geographically. It was not possible to fully account for the taxonomic status of *spilogaster* in the absence of genetic information. Given the difference in morphology between *spilogaster* and *rovuma* and the geographic isolation between the two subspecies, *spilogaster* (in the north) and *rovuma* (in the south) both separated by *grantii*, the recommendation is that *rovuma* (once recognized as a species in Roberts 1924) be considered a separate species within which two subspecies *rovuma* and *spilogaster* are recognized. Furthermore, since *grantii*, *jubaensis* and *schoanus* are morphologically inseparable and genetic evidence showed that little genetic distance exists between *grantii* and *jubaensis* and *schoanus*, they are synonymized with *grantii* which is recognized as a full species.

The taxa, *sephaena*, *zambesiae*, *chobiensis*, *zuluensis*, *thompsoni* and *mababiensis* all have buff bellies (with very narrow greyish barring) and a broad band of chestnut triangular markings on the breast and an unpatterned belly. Based on similar morphological attributes and the availability of genetic evidence for some subspecies, *zambesiae*, *chobiensis*, *zuluensis*, *thompsoni* and *mababiensis* should be synonymized with *sephaena.*

Based on the phylogenetic association of the *Dendroperdix* taxa with the Asian species *Ortygornis gularis* and *O. pondicerianus*, it is recommended that the genus *Ortygornis* Reichenbach, 1853 replace *Dendroperdix* Roberts, 1922 based on priority. Therefore, the taxonomic status of the African members of this genus would be: *Ortygornis sephaena* (Smith, 1836), *Ortygornis rovuma* with subspecies *Ortygornis rovuma rovuma* Gray, 1867 and *Ortygornis rovuma spilogaster* Salvadori, 1888 and *Ortygornis grantii* Hartlaubi, 1866 (Appendix 5.2).

The unplaced Francolinus lathami

This is one of Hall's (1963) enigmatic species, that she could not place in any of her groups even though she speculated that it is closest to the Red-tailed francolins (*Peliperdix* spp.) and that morphological similarities between it and the spotted Asian Black Francolin *Francolinus francolinus* are superficial or plesiomorphic. Two putative subspecies, *lathami* and *schubotzi* are recognized.

The underparts of nominate *lathami* are largely black with white spots in the male as opposed to a brown belly colour with white spots in female. Both sexes have a black throat and patterned face (greyish in male and brownish in female). The upperparts are mottled rufous and brown with pronounced white streaks (margined mostly with black) restricted to the lower neck. There is geographical variation in plumage between the nominate subspecies and *schubotzi*. The males of *schubotzi* have the black and white pattern extending down the bulk of the belly continuing to the undertail coverts (Chapin 1932, Hall 1963), where the ground colour still predominates. The females cheeks are more rufous than grey. The species exhibits striking plumage dichromatism and is markedly distinct from any of the African francolins.

The phylogenetic inferences place *F. lathami* near the base of the tree in nearly all the analyses (Fig. 5.8, Fig 5.9, Fig 5.11). The two putative subspecies *lathami* and *schubotzi* are supported as sister taxa in all the analyses with high support. Wolters (1975-82), Crowe and Crowe (1985) and Crowe et al. (1992) supported Hall's (1963) suspicion that *F. lathami* has affinities with members of the Red-tailed Group, with Crowe and Crowe (1985) and Crowe et al. (1992) placing this species in the subgenus *Peliperdix*. In our analyses, only the organismal data matrix places *F. lathami* close to members of the Red-tailed Group (Fig. 4.10). Dating of the molecular characters suggests *Francolinus lathami* and the *Peliperdix* taxa split a long time ago, c. 7.6 mya (Fig. 2.7). The two recognized subspecies, *lathami* and *schubotzi* differ by 1% in sequence divergence (Table 5.6).

Francolinus lathami links the relatively basal Asio-Afrotropical francolins and the quail-like Red-tailed *Peliperdix* and Red-winged *Scleroptila* taxa. On the basis of its distinct phylogenetic placement, morphology, unique forest habitat, geography and large genetic divergence, *lathami* should be recognized in a genus of its own and it should continue to comprise two subspecies *lathami* and *schubotzi*. Therefore, the genus *Francolinus* Stephens, 1819 will be replaced with a newly erected genus *Afrocolinus* gen. nov. *Afrocolinus* is formed from two words, *afro*- meaning African and -*colinus* for 'quail'. The subspecies should be *Afrocolinus lathami lathami* Hartlaub, 1854 and *Afrocolinus lathami schubotzi* Reichenow, 1912 (Appendix 5.2).

Red-tailed group

This group is at represent represented by three species, *Peliperdix coqui*, *P. albogularis* and *P. schlegelii.* Within *P. coqui* there are 14 recognized subspecies: *coqui*, *spinetorum*, *buckleyi*, *maharao*, *ruahdae*, *hubbardi*, *angolensis*, *lynesi*, *vernayi*, *campbelli*, *thikae*, *kasaicus*, *hoeschianus* and *stuhlmanni*, and five subspecies are recognized within *P. albogularis: albogularis*, *buckleyi*, *dewittei*, *meinertzhageni* and *gambagae*. *Peliperdix schlegelii* is at present considered a monotypic species, but was once considered a subspecies of *Peliperdix* '*Francolinus' coqui* (Peters 1934).

The Red-tailed Group is recovered as monophyletic in all analyses (Fig. 5.8, 5.9, 5.10, 5.11) with moderate to high support, with the exception of the organismal analyses where support is lacking. This finding corroborates those of Crowe and Crowe (1985) and Crowe et al. (1992). What stands out within the Red-tailed Group is the split between the *P. schlegelii/P. albogularis* complex and the rest of the *Peliperdix* taxa in all the analyses. *Peliperdix coqui* consists of a number of geographical variants and exhibits sexual dichromatism in plumage (Hall 1963). The various subspecies all have bellies mostly narrowly barred (except *ruahdae* with broader, blacker and more widely-spaced barring), though the degree of barring is variable and the females have a pink wash on their upper belly. Both sexes generally have grey wings, with the exception of *kasaicus* and *vernayi* that have redder, rufous and pinkish wash in the wings, respectively. The colour of the belly varies from being buffish white in *coqui, vernayi, ruahdae, stuhlmanni*, to tawny in *kasaicus*. The degree of barring in *stuhlmanni* is intermediate between that in the nominate *coqui* and *hubbardi* in that the barring is not pronounced especially on the belly. Within *P. coqui*, the various subspecies form a cline in which both sexes of the west African *spinetorum* have unbarred bellies, the east African *hubbardi* has barring on the flanks leaving the centre of the belly unbarred, the east African *maharao* is like the southern African *P. coqui* subspecies in having wholly barred bellies.

Among the recognized subspecies of *P. coqui*, there is a geographical split between the east/west African subspecies (*maharao, hubbardi, spinetorum*) and central/southern African subspecies (*coqui, vernayi, stuhlmanni, kasaicus*) (Fig. 5.8, 5.9, 5.11). However, nodal support for the east/west African clade is only recovered in the ML CYT*B* tree (Fig. 5.8 - 69% BS). What is also supported in the CYT*B* parsimony tree (Fig. 5.10, 4.11) is the sister relationship between *maharao* and *hubbardi* (Fig. 5.9 - 57%, Fig. 5.11, 5% sequence divergence). In the CYT*B* ML tree *maharao* is sister to *spinetorum* with poor BS support (Fig. 5.9), whereas *hubbardi* and *spinetorum* are sister taxa in the organismal tree (55% BS, 6.4% sequence divergence; Fig. 5.10). *Coqui* pairs with *vernayi* in the CYT*B* ML (93% BS, 3% sequence divergence) and CYT*B* parsimony (70% BS) tree, whereas *coqui* pairs with *ruahdae* in both the organismal and CYT*B*/organismal trees (all 64%). *Stuhlmanni* and *kasaicus* are sister taxa in the CYT*B* parsimony tree but with no BS support; they differ by 5% sequence divergence. Their systematic relationship is unresolved in the ML CYT*B* and organismal tree. Overall, the nearest non-*coqui* CYT*B* phylogenetically close and with the least genetic distance to *coqui* is *hubbardi*, differing at 5% sequence divergence.

It is recommended that *lynesi*, *campbelli* and *angolensis* be included in *coqui* based on morphological similarity, phylogenetic affinities and that there exists limited genetic divergence (<1%), and that *vernayi* (Roberts, 1932) be considered a subspecies within *P. coqui* based on their morphological differences (the red wings as opposed to grey wings in nominate *coqui*, as well as the much redder crown as opposed to the less red crown of *coqui*). their phylogenetic affinity and small genetic divergence from *coqui* (3%), It should therefore be recognized as a subspecies *Peliperdix coqui vernayi* (Roberts, 1932). *Hoeschianus* Stresemann, 1937 should be synonymized with *vernayi* based on similar overall morphological appearance and geographic proximity. Specimens of *ruahdae* were not examined directly and as such the morphological description in Mackworth-Praed and Grant, and Hall, was used to classify the Ugandan *ruahdae* and *hoeschianus*. The genetic distance between *ruahdae* (tissue from Rwanda) and the South African nominate *coqui* is 4%. This is not surprising since the two subspecies are morphologically different (*ruahdae* having broad, much black and spaced barring on the belly) and they are geographically isolated. This taxon should therefore be considered a subspecies within *P. coqui* to be named *Peliperdix coqui ruahdae* van Someren, 1926.

Stuhlmanni could be a cryptic taxon that morphologically looks like an intermediate between *coqui* (strongly barred) and *thikae* and *hubbardi* (barring restricted to flanks). The rest of the belly is not strongly barred as in *coqui*, but the barring covers the rest of belly and not just the flanks as in *thikae* and *hubbardi*. *Stuhlmanni* is supported as sister to *kasaicus* in the parsimony CYT*B* and parsimony CYT*B*/organismal tree even though with no BS support and it is very divergent genetically (~5-8%) compared to any other *P. coqui* subspecies. The two subspecies should be considered species and hence *Peliperdix stuhlmanni* Reichenow, 1889. Perhaps *kasaicus*, like *stuhlmanni*, is a cryptic taxon based on the genetic distance, geographic isolation, and phylogenetic placement despite the fact that it has similar morphology to *coqui*. *Kasaicus* should be considered a species based on the geographical isolation with *vernayi* and be named *Peliperdix kasaicus* White, 1945. The western *spinetorum* and east African *maharao* and *hubbardi* form a clade. *Spinetorum* is unarguably evolutionarily distinct, geographically isolated from the rest of *P. coqui* subspecies, genetically different from other subspecies by 6-9%, and both sexes have plain unbarred bellies, but have rufous wings as in *maharao*. It should therefore be considered a species and be named *Peliperdix spinetorum* Bates, 1928.

The isolated Kenyan subspecies *maharao* has its closest phylogenetic association with *hubbardi*. On the other hand, there is considerable genetic divergence (5%). Unlike *hubbardi*, the rest of the belly of *maharao* is barred. On the basis of the remarkable genetic distance, differences on the belly and the isolated distribution, *maharao* should be considered a species and be named *Peliperdix maharao* Sclater 1927.

Thikae and *hubbardi* have a genetic difference of 3%, occur side by side geographically and have the similar belly morphology despite the difference in wing colour (rufous in *thikae* and grey in *hubbardi*). Therefore, *hubbardi* Ogilvie-Grant, 1895 should be recognized as a species and *thikae* Grant and Mackworth-Praed, 1934 must be synonymized with it and be named *Peliperdix hubbardi* Ogilvie-Grant, 1895 (Appendix 5.2).

Peliperdix schlegelii is the sister species to the *P. albogularis* complex and it shares the least sequence difference (1%) with *buckleyi* (Table 5.6). There is no nodal support for the *P. schlegelii/P. albogularis* complex clade in the organismal tree. Within the *P. albogularis* complex, *albogularis* and *buckleyi* are sister taxa (Fig. 5.8, 5.9, 5.11 – 99%, 100%, 100% BS respectively) whereas *albogularis, buckleyi* and *dewittei* are similar in the organismal tree (Fig. 5.10). The taxon *dewittei/* '*meinertzhageni*' forms a sister relationship with *albogularis* (with 5% sequence divergence) and *buckleyi* with high support in the molecular analyses (Fig. 5.8, Fig. 5.9, 5.11). The nearest relative of *buckleyi* is *albogularis* with 1% sequence divergence.

The *Peliperdix albogularis* complex has a disjunct distribution across west and west-central Africa with the nominate subspecies being restricted to Guinean savanna in West Africa between Senegal and Cameroon (Cotterill 2006). *Peliperdix albogularis* resembles *P. c. coqui*, but the quail-type patterning is less well-defined in the females and the shaft streaks and barring are much narrower. The wings are more rufous as in the east Kenyan subspecies of *coqui*. The females (but not the males) also have the black facial pattern and necklace, but both are poorly-defined. Both sexes have a buff throat contrasting with the ochre cheeks. The rest of the underparts of male *albogularis* are quite distinct from any other forms of *coqui,* being chestnut on the upper belly with ochre shaft streaks and richer ochre on the lower belly, lacking any dark barring. The females are barred (to varying degrees) with a faint pinkish wash or rufous on the upper belly similar to the Ethiopian subspecies of *P. c. maharao* and the east Kenyan *P. c. thikae*. The subspecies in which the females are less patterned with narrow barring restricted to the upper belly and flank is in Gambia (*albogularis* – Hall 1963). There is a subspecies that Peters (1934) recognized as *gambagae* (Mackworth-Praed, 1920) from the type locality Gambaga, Gold Coast Colony) which Hall and Serle (1957) synonymized with *buckleyi*. The taxon *dewittei* (including *meinertzhageni*) occurs south of the Congo forest in moist montane grasslands and dambo floodplains (Cotterill 2006) and it is considered common in some parts, even though it was said to not have been collected on the Marungu plateau since 1931 (Dowsett and Prigogine 1974). Birds of both sexes are larger than *albogularis* (wing length ranging from 142 to 147 mm – Mackworth-Praed and Grant, 1970) and more richly coloured than both *albogularis* and *buckleyi* with the female *dewittei* being more heavily barred although this is not as extensive as in *buckleyi*. The eastern Angolan and possibly the northwestern Zambian taxon *meinertzhageni* comprise the darkest birds with heavily barred females. This subspecies is found in montane grassland and it is restricted to the Upper Zambezi floodplains (Cotterill 2006).

The taxon *dewittei* is indisputably morphologically different from the other subspecies recognized within *P. albogularis*, and is divergent genetically. The morphology of *dewittei* (southeastern Congo) resembles that of the Angolan and northwestern Zambian '*meinertzhageni'* (both sexes are large birds with a wing length of 140-147 mm, rich dark-coloured birds, heavily patterned). Unfortunately, *dewittei* could not be sequenced. Geographically, the two subspecies occur in different parts (but occupy similar habitat). Hall (1963) speculated that the northwest Zambian *meinertzhageni* subspecies may be more closely related to the Congo *dewittei* than the Angolan *meinertzhageni* subspecies, this speculation may have been based on the geographical proximity.

Based on morphology, geographical and molecular evidence for the Angolan *meinertzhageni* (in the absence of molecular evidence from northwest *meinertzhageni* subspecies), *meinertzhageni* White 1944 should be moved to species level. It is not possible at this stage to comment on Hall's speculation about the relationship of the north-west Zambia *meinertzhageni* and the Congo *dewittei* subspecies. Despite the absence of molecular evidence for *dewittei* Chapin, 1937, its name has to be given the priority and *meinertzhageni* will be synonymized with it. The name must be *Peliperdix dewittei* Chapin, 1937.

The West African *buckleyi* and *gambagae* are inseparable morphologically and they are almost identical genetically with 0.4% difference. The two subspecies should be merged and form a subspecies with the name *buckleyi* Ogilvie-Grant, 1892 taking priority over *gambagae* (Mackworth-Praed, 1920). The recognized name must be *Peliperdix albogularis buckleyi* Grant, 1892. So, *Peliperdix albogularis* Hartlaub, 1854 will be represented by two subspecies, *Peliperdix albogularis albogularis* Hartlaubi, 1854 and *Peliperdix albogularis buckleyi* Ogilvie-Grant, 1892 (Appendix 5.2).

Another controversial taxon within the Red-tailed Group is *Peliperdix schlegelii*. This taxon was considered a subspecies of *P. coqui* in Chapin (1932) and Peters (1934). Contrary to this, Hall (1963) and Mackworth-Praed and Grant (1970) recognized this taxon as a species. This is a rare bird; its distribution stretches from eastern Cameroon through the Central African Republic to the western Bahr-el-Ghazal in Sudan. The back plumage colouration and patterning of *P. schlegelii* is closer to that of *P. albogularis* than *P. coqui*, though the quail-type patterning is much reduced and the extent of sexual dimorphism is also pronounced. The differences are seen in the male *P. schlegelii*, which has broad buff shaft streaks and some streaks with few transverse blackish brown bars whereas the female is almost unpatterned. The back in both sexes is vinous chestnut with the belly being buff to off-white. The male *P. schlegelii* is similar to southern *P. coqui* subspecies with ochre sides of the head and throat and narrow black and white barring on the upper and lower belly. The female resembles the male on the crown and throat but has the upper belly feathers edged with black, giving a more mottled appearance of simply triangular marks. The flanks are sparsely barred.

The findings demonstrated that *P. schlegelii* is an evolutionarily distinct taxon both morphologically and genetically. It is more closely related to *P. albogularis* than it is to *P. coqui*. Therefore, *P. schlegelii* must be given full specific status and be named *Peliperdix schlegelii* Heuglin, 1863. These findings suggest that Chapin (1932) and Peters (1934) were conservative in considering this taxon a subspecies of *P. coqu* (Appendix 4.2).

Red-winged Group

The Red-winged Group is represented by six species, *Scleroptila shelleyi*, *S. afra*, *S. levaillantoides*, *S. levaillantii*, *S. finschi* and *S. psilolaema*. *Scleroptila afra* and *S. finschi* are monotypic species whereas the balance of the species are polytypic. *Scleroptila shelleyi* comprises seven subspecies (*shelleyi*, *uluensis*, *whytei*, *macarthuri*, *trothae*, *sequestris*, *canidorsalis*); *S. psilolaema* four subspecies (*psilolaema*, *ellenbecki*, *elgonensis*, *theresae*); *S. levaillantii* five subspecies (*levaillantii*, *kikuyuensis*, *crawshayi*, *benguellensis*, *clayi*); *S. levaillantoides* 12 subspecies (*levaillantoides*, *kalaharica*, *pallidior*, *langi*, *wattii*, *jugularis*, *cunenensis*, *stresemanni*, *gutturalis*, *lorti*, *archeri*, *ludwigi*).

The Red-winged Group is monophyletic in all the analyses (Fig. 5.8, 5.9, 5.10, 5.11) with varying levels of support. One further common aspect, is the incorporation of *S. streptophora* as a basal taxon to the group in all the analyses (Fig. 5.8, 5.9, 5.10, 5.11). This finding is consistent with that of Crowe and Crowe (1985) and Crowe et al. (1992). This group presents a very complicated and variable phylogenetic structure with few nodes are consistently supported in most of the analyses: (1) *kikuyuensis* and *crawshayi* and (2) *psilolaema* and *theresae*.

The major taxonomic change relevant to this group has been the shift of the monotypic *Scleroptila streptophora* from the Striated to the Red-winged Group (see above). It has a markedly disjunct distribution occurring in savanna-grassland in Cameroon in the west, and northern Uganda and northwestern Kenya and Tanganyika in the east. It differs from most of the other Red-winged francolins in having an unpatterned crown, throat colour buff rimmed with rufous, the absence of a gorget, barred breast, blotched and mottled belly, brown (not red) primaries, unpatterned side of the head, and tiny spur bump. It differs from *uluensis* and s*helleyi* by 8% sequence divergence.

The monotypic specific status of *S. finschi* has never been disputed. This species is found disjunctly in western Angola and parts of western Congo (Mackworth-Praed and Grant 1962, Hall 1963). It differs from the other Red-winged francolins in lacking black and white patterning on the face and neck and by having the upper belly and the lower end of the lower belly grey. The centre of the belly is buff with chestnut blotching and it is essentially unbarred. The sides of the face and border of the throat are ochre as in *S. levaillantii* but this is less extensive on the hind neck. This species is long-billed like *S. levaillantii*. It shares the least genetic distance with *shelleyi* (5% sequence divergence – Table 4.6).

Scleroptila shelleyi has a buff to white throat, and a distinct black necklace, a moderately developed gorget, blotched and mottled upper belly and a broadly barred lower belly. It occurs in moist, rocky hillsides below 2000 m throughout southeastern Africa from Mozambique in the north to South Africa, and shares the least genetic distance with *gutturalis* (4% sequence divergence). *Gutturalis* was considered by Hall as one of the northeastern subspecies (*lorti* and *friedmanni*, *stantoni*, *eritreae*, *archeri*) attributed to *S. levaillantoides.* It occurs in arid savanna steppe in eastern Ethiopia, Eritrea and northeastern Kenya, and differs from other northern Red-winged francolins in having the lower belly largely unpatterned with bars and throat base freckled, with dark above a well-defined necklace and gorget. It shares the least genetic distance with *uluensis* (3%). *Uluensis* occurs in central Kenya, southern Uganda and northeastern Malawi. It is similar in form and habitat to *S. shelleyi*, but the necklace and gorget are somewhat less distinct and the bill markedly shorter. Some specimens have the throat moderately freckled with black indicating possible hybridization with *gutturalis*. The Malawian taxon *whytei* is very different from *shelleyi* and *uluensis* in having a rufous buff throat and an indistinct necklace. It has a moderately-developed gorget blotched with reddish chestnut distinguishing it from the other *Scleroptila* spp. The belly is buffy white with broad black bars on a background of rufous buff. Its nearest CYT*B* relatives are *finsch*i, *gutturalis* and *psilolaema* at 5% sequence divergence.

Scleroptila afra is endemic to southern Africa generally occurring in montane grasslands above 1800 m. It differs from *uluensis, shelleyi* and *whytei* in having a buff to white throat flecked with black. The reddish colour which is apparent in the wings of other scleroptilids is extremely reduced to absent. The degree of black barring on the buffy belly is very narrow whereas the barring on the underparts of the others is broad. The gorget in *S. afra* is well-defined and eventually grades to the upper belly which forms a band mottled with grey, chestnut and tawny. The former eastern Transvaal province of South Africa subspecies *proximus* (which does not differ genetically from those to the south) is according to Clancey (1967) "similar to *afra*, but darker and more saturated". "On the underside, rather deeper tawny colour to the ground of the lower throat and upper breast, the grey tipping to the feathers more extensive and darker; rest of the underside more yellowish tinged, and chestnut spotting darker and heavier". The nearest relative is *ellenbecki* differing at 2% sequence divergence. *Ellenbecki* is very similar to *afra* in having a buff throat freckled with black, a poorly developed necklace, but differs in having broad black and white barring on the lower belly. It inhabits montane grassland in southern Ethiopia above 2500 m.

Scleroptila psilolaema and *theresae* are typical Red-winged francolins and are similar in appearance in having the most red in their primaries, but *psilolaema* is significantly smaller and shorter billed. Both inhabit montane grassland above 2500 m, the former from southern Ethiopia and the latter from Mt. Kenya and the Aberdares. They differ from *ellenbecki* in having little or no freckling on the throat and have a much more poorly developed necklace and gorget which is replaced by rich chestnut with black indistinct spots. *Scleroptila psilolaema* differs from *theresae* with 2.6% and from *pallidior* at 5% sequence divergence.

Scleroptila levaillantii is endemic to rank highland (1600-2000 m) grasslands of southeastern Africa. It is the largest of the southern African francolins and differs from the other Red-winged francolins in having an ochre collar on the sides of the face and edges of the throat and also inside the black and white facial pattern. Its face is like that of *S. levaillantoides,* but this species has a long bill, it is darker and richer in colour. The black and white patterning of the well-defined necklace (forming a well-developed gorget) extends in a complete collar round the hind neck below the ochre collar and the black and white stripes from above the eye (which in *S. levaillantoides* and *S. shelleyi* run down the side of the face) in the South African *S. levaillantii* subspecies behind the head to join at the back. It also differs from its congeners in having more red on the wings, a longer bill and shorter spurs. It differs from *ellenbecki* at 6.6% sequence divergence.

On the other hand, *S. levaillantoides* is a species endemic to the arid grasslands of northern Namibia, Botswana and central South Africa, occurring at lower altitudes than *shelleyi, levaillantii* and *afra*. It is also smaller than these taxa. It has a moderately developed gorget with the upper belly blotched with buff and reddish brown. The generally paler subspecies *pallidior* is still tentatively placed with *levaillantoides* despite its genetic affinity with *ellenbecki* (9% sequence divergence) and that it is otherwise identical to the nominate subspecies in its overall biology. It shares the least genetic distance with *afra* at 3% sequence divergence. The taxonomic treatment renders S. levaillantoides paraphyletic in molecular tree. *Jugularis* is according to Hall (1963) endemic to southeastern Angola and northwestern Namibia and classified as a subspecies of *S. levaillantoides*. It differs from this taxon in being paler overall and having a well-developed necklace which grades to the breast to form a broad gorget. It differs from *crawshayi* at 4% sequence divergence.

Crawshayi is endemic to northeastern Malawi and western Tanzania and is richer in colour than *levaillantii*, with still more red in the wing, and with more black marking on the belly, whereas *kikuyuensis* (which occurs in Angola and southern Congo – Fig. 5.6) is without the stripe on the hind neck, but otherwise similar to *crawshayi*. Both have similar habitats to *levaillantii*. The nearest relative of *crawshayi* is *afra* which differ at 3% sequence divergence. The nearest relative of *kikuyuensis* is *crawshayi* with 2% sequence divergence.

The taxon *theresae* was considered a subspecies of *S. shelleyi* by Mackworth -Praed and Grant and a synonym of *psilolaema* by Hall (1953). Since it is sister to *psilolaema* here and is 3% divergent from it (as opposed to 6% to *shelleyi*), Hall appears to have been correct. On the other hand, *ellenbecki* was recognized by Mackworth-Praed and Grant as a subspecies of *S. afra*, but synonymized with *psilolaema* by Hall. The genetic difference between *ellenbecki* and *S. afra* is 2%, and 5% between *ellenbecki* and *psilolaema*. Moreover, *S. afra* and *ellenbecki* indeed have morphological affinities, i.e. they have similar underparts with freckled throat and barred bellies. So, in this instance Hall appears to have erred in her decision. One other controversial aspect is the taxonomic status of *psilolaema*. Hall considered this a species, whereas Mackworth-Praed and Grant considered this taxon a subspecies within *S. afra*. Genetically, *psilolaema* differs from *S. afra* by 6% and the two have no apparent phylogenetic affinity.

Within the *Scleroptila levaillantoides*, the genetic distance observed between the three northern subspecies that Hall (1963) attributed to *levaillantoides (lorti, archeri, gutturalis*) is in the range of ~3.1-3.4% to *S. levaillantoides* and ~3-4% to *S. shelleyi*. Among themselves they differ by <2%. These three subspecies are phylogenetically related with *archeri* and *lorti* being sisters (results not shown on the cladogram) and they are in turn sister to *gutturalis*. Since *uluensis* is genetically closest to *guttaralis*, both seem to have been incorrectly placed by Hall and warrant species status.

The southern *jugularis* shares sister relationship with *whytei* in all the analyses (with 77% BS support only in the combined CYT*B*/organismal tree) except in the organismal tree and it differs from the other southern subspecies (*levaillantoides*, *pallidior*), the northern (*gutturalis*) subspecies, as well as *shelleyi* by ~7% sequence divergence. It is closest to the nominate *levaillantoides*, only in the organismal tree but differs by 7% of genetic distance. Despite having a well-developed gorget, *jugularis* has some similarities with *pallidior* in that it has a white to buffy white belly with dark chestnut blotches. *Pallidior* differs by ~3-4% from *levaillantoides*, *gutturalis* and *S. shelleyi*. It has the closest phylogenetic affinities with *S. afra* and *ellenbecki* (though not supported) and the two taxa differ genetically by 2% and 3% respectively. Since *pallidior* has little morphological resemblance to *S. afra* and *ellenbecki* it is still tentatively placed with *levaillantoides*, subject to further phylogeographic study.

Scleroptila levaillantii differs genetically from *kikuyuensis* and *crawshayi* by 9 and 8% respectively, and a 3% difference exists between *kikuyuensis* and *crawshayi*. *Scleroptila shelleyi* remains a valid species including the Natal subspecies *sequestris* Clancey, 1960 and the Inhambane, southern Mozambique subspecies *canidorsalis* (Lawson, 1963). The Malawi subspecies *whytei* should be recognized as a separate species based on the remarkable difference observed in morphology, genetic distance and distinct phylogenetic placement and geographic isolation, and hence be *Scleroptila whytei* Neumann, 1908. The phylogenetic position of *uluensis* does not favour Mackworth-Praed and Grant's classification system, that is, *uluensis* is not phylogenetically related to *S. afra* even though the two are in the same clade in the parsimony CYT*B*/organismal tree. They have a genetic distance of 4%. Despite that the morphological divergence and the geographic isolation of the distribution ranges of the *uluensis* and *S. afra* are difficult to reconcile. Therefore, *uluensis* has to be recognized as an evolutionarily distinct taxon and is upgraded to species *Scleroptila uluensis* (Grant, 1892) with *macarthuri* (van Someren, 1938) being included as a subspecies (Appendix 5.2).

Mackworth-Praed and Grant's classification of *psilolaema* as a subspecies of *S. afra* is probably not correct. The two are phylogenetically and geographically apart, have a genetic difference of 6% and differ morphologically except for the presence of the grey flecks on the throat of *S. afra* and indistinct black spots on the throat of *psilolaema*. Thus, Hall (1963) was probably correct in recognizing *S. psilolaema* as a valid species, *Scleroptila psilolaema* Gray 1867.

The taxonomic status of *theresae* is also uncertain. Mackworth-Praed and Grant considered it a subspecies of *S. shelleyi* whereas Hall included it in *S. psilolaema*. *Theresae* is sister to *psilolaema* and the two differ genetically by 3% (and 6% when compared to *S. shelleyi*). Also, *theresae* is morphologically similar to *psilolaema* and not to *S. shelleyi*. It has rich chestnut in wings and differs from *S. shelleyi* in having some barring on the tips of the primaries and the underparts are rich buff mottled with chestnut and with some less defined brown to black bars. The gorget is poorly-defined and replaced by rich chestnut with black spots and has lighter chestnut throughout the belly. Therefore, *theresae* should be considered a subspecies, *Scleroptila psilolaema theresae* (Meinertzhagen, 1936) with *elgonensis* (Grant, 1891) being synonymized with it. The phylogenetic position of *ellenbecki* and the small genetic divergence between *ellenbecki* and *S. afra* (2%) certainly confirm Mackworth-Praed and Grant's classification system. Hall included *ellenbecki* in *S. psilolaema* (which differ genetically by 5%). Careful examination of the specimens revealed that *S. afra* and *ellenbecki* both have similar underparts with freckled throats and barred bellies. The major difference is that the width of barring on breast and belly is finer in *S. afra* and broader in *ellenbecki.* Furthermore, *ellenbecki* has rich darker chestnut in wings (opposed to grey in *S. afra*) and some barring at the tips of the primaries. It has a poorly-defined gorget (as opposed to a well-developed gorget in *S. afra*) replaced by rich chestnut and has dark chestnut throughout the belly different from the narrow black barring in *S. afra*. In consideration of the similarity in morphology, the small genetic distance and the phylogenetic affinities between *ellenbecki* and *S. afra*, and geographical isolation, it is recommended that *ellenbecki* be considered a species closely related to *S. afra* and hence *Scleroptila ellenbecki* Erlanger, 1905.

Gutturalis should be recognized as a separate taxon, i.e. as a species *Scleroptila gutturalis* (Rüppell, 1835), and *gutturalis* takes priority over *archeri* Sclater, 1927 and *lorti* Sharpe, 1897. *Friedmanni* Grant and Mackworth-Praed, 1934 and *stantoni* (Cave, 1940) should be synonymized with *archeri* and *eritreae* Zedlitz, 1910 with *gutturalis*.

Scleroptila levaillantoides levaillantoides Smith, 1836 remains the valid nominate subspecies with *ludwigi* Neumann, 1920 and *gariepensis* Smith, 1843 being included in it. This subspecies is strongly marked on the upper and lower belly and there exists large genetic difference when compared to *pallidior* (4.2%). *Pallidior* Neumann, 1908, *wattii* Macdonald, 1953, *langi* Roberts, 1932 and *kalaharica* Roberts, 1932 should be considered a single taxon, i.e. subspecies within *S. levaillantoides* based on its morphological attributes (strongly marked on upper belly with a relatively unmarked lower belly) irrespective of its phylogenetic position and the least genetic difference when compared to *S. afra*. *Scleroptila levaillantoides pallidior* Neumann 1908 takes priority over the other names.

From the south, *jugularis* Büttikorfer, 1889 generally looks like the nominate *levaillantoides,* but it is relatively unmarked on the lower belly, posses a well-developed gorget, there is remarkable genetic difference between the two and they are well-supported sister taxa (99%). So, *jugularis* should be recognized as a species, *Scleroptila jugularis* Büttikorfer 1889. This name receives priority over *cunenensis* (Roberts, 1932) and *stresemanni* Hoesch & Niethammer, 1940.

There are marked morphological difference between *levaillantii* and the other subspecies, *kikuyuensis, crawshayi, benguellensis, mulemae* and *clayi*. Generally, differences concern whether a taxon has either rich reddish chestnut colour in the belly feathers, a broken or unbroken ochre collar, rufous band across nape (in *clayi*) and a streak below the eye with less black spotting and some irregular black patches on the belly in *benguellensis*. Among the subspecies for which there are DNA sequence data, the genetic divergence is remarkable between *levaillantii* and the two sister subspecies *kikuyuensis* (9%) and *crawshayi* (8%) even though they appear similar morphologically. The recommendation is that *kikuyuensis* and *crawshayi* be considered as separate taxa taking the status of a species i.e. with *crawshayi* - Ogilvie-Grant 1896 receiving priority over *kikuyuensis* Ogilvie-Grant, 1897 and becoming the nominate subspecies and hence the name *Scleroptila crawshayi crawshayi* Ogilvie-Grant, 1896.

Morphologically *crawshayi* and *kikuyuensis* are similar except that *kikuyuensis* is without the stripe on the hind neck. Thus, *benguellensis* and *mulemae* are similar to *kikuyuensis*. There is no genetic evidence for the recognition of *clayi, benguellensis* and *mulemae* the decision is based on morphological characters and the locality of the taxa. Since *benguellensis* Neumann, 1908, *clayi* White, 1944 and *mulemae* Ogilvie-Grant, 1903 are said to be similar to *kikuyuensis* these subspecies should be synonymized with *crawshayi* due to the geographic proximity and not with *kikuyuensis*. *Kikuyuensis* is isolated from *crawshayi* and has some morphological differences and therefore, it should be considered a subspecies within *S. crawshayi* O. Grant, 1896, and named *Scleroptila crawshayi kikuyuensis* Ogilvie-Grant, 1897.

Scleroptila finschi and *S. streptophora* are the two distinct species with no geographic variation and their species status is not disputed (Appendix 5.2).

Conclusions

This study has attempted to comprehensively revise the systematics of francolins. There is congruence in the topologies resulting from the various analyses, but some discordance in certain areas of the trees, especially within the species groups, remains. What is apparent is that the combined analyses yielded better phylogenetic results. One of the major finding is that the Striated Group is not monophyletic as hypothesised by Hall (1963) whereas the Red-tailed and Red-winged Groups were largely diagnosable. The consistent phylogenetic placement of the two previously unplaced Asian species *Ortygornis pondicerianus* and *O. gularis* as the closest relatives of the African

Ortygornis taxa strongly rejects the monophyletic status of the five Asian francolin species as hypothesized by Forcina et al. (2012). *Francolinus lathami* has distinct evolutionary trajectory, hence it is recommended that it is assigned it own genus *Afrocolinus* gen. nov.

Tables and Figures

Table 5.1. Morpho-behavioural characters and character states scored for phylogenetic analysis of francolins.

1. **Crown patterning:** unpatterned = 0; streaked = 1; mottled = 2
2. **Chestnut collar:** none = 0; chestnut = 1
3. **Upper back patterning:** spotted = 1; streaked = 2; barred or barred and streaked = 3
4. **Back plumage patterning:** streaked = 1; barred = 2; quail-like = 3
5. **Throat base colour:** white-buff = 1; rufous-chestnut = 2; black = 3; buff-rimmed with rufous = 4
6. **Throat flecking/freckling:** none = 0; present = 1
7. **Gorget:** absent = 0; present, but poorly developed = 1; moderately developed = 2; well developed = 3
8. **Breast patterning**: unpatterned = 0; barred = 1; streaked = 2; spotted = 3; blotched/mottled = 4
9. **Belly patterning:** unpatterned = 0; spotted = 1; barred = 2; streaked = 3; blotched/mottled = 4; streaked and barred = 5
10. **Under tail patterning:** unpatterned = 0; barred or barred and blotched = 1
11. **Wing patterning:** unpatterned = 0; blotched = 1
12. **Wing base colour:** greyish brown = 1; greyish brown with some red = 2; moderate to well-developed red = 3
13. **Side of the head patterning:** unpatterned = 0; streaked = 1; striped (eye and/or jaw – progresses to gorget) = 2
14. **Leg colour:** yellow = 1; red, reddish range = 2
15. **Spur number:** none/poorly developed = 0; one = 1
16. **Spur length:** < 1mm = 0; 1-10mm = 1; 11-20mm = 2
17. **Wing length (mm)**: < 140 = 1; < 160 = 2; < 180 = 3
18. **Bill length (mm) / Wing length:** < .15 = 1; < .17 = 2; < .18 = 3; > .18 = 4
19. **Tail length (mm) / Wing length:** < .50 = 1; <.55 = 2; < .60 = 3; > .60 = 4
20. **Sexual plumage dimorphism:** 0 = none; 1 = slight; 2 = marked
21. **Raucous advertisement call:** absent = 0; type 1 = 1; type 2 = 2
22. **Simple musical advertisement call:** 0 = absent; slow = 1; fast = 2; very fast =3
23. **Short complex musical advertisement call:** absent = 0; slow ki-bee-tilli = 1; fast ki-bee-tilli = 2
24. **Long complex musical call:** absent = 0; type 1 = 1; type 2 = 2

Table 5.2. A matrix of organismal character and character state scores used in phylogenetic analysis of francolins.

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
	Character no.																							
Gallus gallus	0	0	2	1	2	0	0	0	0	0	0	1	0	0	1	2	3	1	4	2	1	0	0	0
Bambusicola thoracica	2	0	3	3	2	0	0	2	0	0	0	1	0	0	1	1	2	1	3	0	0	0	0	0
Francolinus francolinus	1	1	1	1	3	0	0	1	2	1	1	1	0	2	1	1	2	2	4	2	1	0	0	0
Francolinus pictus	1	0	1	1	2	0	0	3	1	0	1	1	0	2	1	0	1	2	3	1	1	0	0	0
Francolinus pintadeanus	1	0	1	2	1	0	0	1	2	1	1	1	1	2	1	1	1	4	3	2	1	0	0	0
Ortygornis gularis	0	0	3	2	2	0	0	2	3	0	0	2	0	2	1	1	3	2	4	0	1	1	0	0
Ortygornis pondicerianus	0	0	3	2	1	0	0	1	2	1	0	1	1	2	1	1	1	2	4	0	2	0	0	0
Ortygornis sephaena	1	0	2	3	1	0	0	2	2	0	0	1	1	2	1	2	2	2	4	1	2	0	0	0
Ortygornis grantii	1	0	2	3	1	0	0	2	2	0	0	1	1	2	1	2	2	2	4	1	2	0	0	0
Ortygornis r. rovuma	1	0	2	3	1	0	0	2	3	0	0	1	1	2	1	2	2	2	4	1	2	0	0	0
Ortygornis r. spilogaster	1	0	2	3	1	0	0	2	3	0	0	1	1	2	1	2	2	2	4	1	2	0	0	0
Afrocolinus l. lathami	0	0	2	3	3	0	0	3	1	1	0	1	0	1	1	1	1	1	2	2	0	1	0	0
Afrocolinus l. schubotzi	0	0	2	3	3	0	0	3	1	1	0	1	0	1	1	1	1	1	2	2	0	1	0	0
Peliperdix coqui	2	0	2	3	1	0	1	0	2	1	0	1	2	1	1	1	1	2	3	2	0	1	0	0
Peliperdix kasaicus	2	0	2	3	1	0	1	1	2	1	0	2	2	1	1	1	1	2	3	2	0	1	0	0
Peliperdix maharao	2	0	2	3	1	0	1	1	2	1	0	1	2	1	1	1	1	2	3	2	0	1	0	0
Peliperdix ruandae	2	0	2	3	1	0	1	0	2	1	0	1	2	1	1	1	1	2	3	2	0	1	0	0
Peliperdix stuhlmanni	2	0	2	3	1	0	1	1	2	1	0	1	2	1	1	1	1	2	3	2	0	1	0	0
Peliperdix c. vernayi	2	0	2	3	1	0	1	1	2	1	0	2	2	1	1	1	1	2	3	2	0	1	0	0
Peliperdix hubbardi	2	0	2	3	1	0	1	1	0	0	0	1	2	1	1	1	1	2	3	2	0	1	0	0
Peliperdix spinetorum	2	0	2	3	1	0	2	1	0	0	0	1	0	1	1	1	1	2	3	2	0	1	0	0
Peliperdix albogularis	2	0	2	3	1	0	0	1	2	1	0	2	2	1	1	1	1	2	2	2	0	3	0	0
Peliperdix a. buckleyi	2	0	2	3	1	0	0	1	2	1	0	2	2	1	1	1	1	2	2	2	0	3	0	0
Peliperdix dewittei	2	0	2	3	1	0	0	1	2	1	0	2	2	1	1	1	1	2	2	2	0	3	0	0
Peliperdix schlegelii	2	0	2	3	1	0	0	1	2	1	0	1	0	1	1	1	1	2	2	2	0	2	0	0
Scleroptila streptophora	0	0	3	3	4	0	0	1	4	1	0	1	0	1	0	0	3	3	2	0	0	0	0	2
Scleroptila finschi	2	0	3	3	1	0	0	4	2	1	0	2	0	1	1	1	3	3	2	0	0	0	0	2
Scleroptila levaillantii	1	1	3	3	4	0	3	4	2	1	0	3	2	1	1	1	3	4	2	0	0	0	0	2
Scleroptila c. crawshayi	1	1	3	3	4	0	3	4	2	1	0	3	2	1	1	1	3	4	2	0	0	0	0	2
Scleroptila c. kikuyuensis	1	1	3	3	4	0	3	4	2	1	0	3	2	1	1	1	3	4	2	0	0	0	0	2
Scleroptila levaillantoides	1	0	3	3	1	0	1	4	0	1	0	3	2	1	1	1	3	3	2	0	0	0	2	0
Scleroptila l. pallidior	1	0	3	3	1	0	1	4	0	1	0	3	2	1	1	1	3	3	2	0	0	0	2	0
Scleroptila jugularis	1	0	3	3	1	0	3	4	0	1	0	2	2	1	1	1	3	3	2	0	0	0	2	0
Scleroptila p. psilolaema	1	0	3	3	1	1	2	4	2	1	0	3	2	1	1	1	3	3	2	0	0	0	1	0
Scleroptila p. theresae	1	0	3	3	1	0	2	4	2	1	0	3	2	1	1	1	3	3	2	0	0	0	1	0
Scleroptila afra	1	0	3	3	1	1	3	4	2	1	0	1	2	1	1	1	3	3	2	0	0	0	0	1
Scleroptila ellenbecki	1	0	3	3	1	1	2	4	2	1	0	3	2	1	1	1	3	3	2	0	0	0	1	0
Scleroptila shelleyi	1	0	3	3	1	0	2	4	2	1	0	2	2	1	1	1	3	3	2	0	0	0	1	2
Scleroptila uluensis	1	0	3	3	1	0	2	4	2	1	0	2	2	1	1	1	3	3	2	0	0	0	1	2
Scleroptila gutturalis	1	0	3	3	1	0	2	4	5	1	0	3	2	1	1	1	3	3	2	0	0	0	1	0
Scleroptila whytei	0	0	3	3	2	0	3	4	2	1	0	3	2	1	1	1	3	3	2	0	0	0	1	2

Table 5.3. Francolin taxa for which DNA sequences were generated. **Acronyms**. AMNH - American Museum of Natural History, TM - Transvaal Museum, BM - British Museum, Natural History Museum at Tring, SAM - Iziko Museums of Cape Town (Natural History), PFIAO - Percy FitzPatrick Institute of African Ornithology, TMC - Timothy M. Crowe, University of Cape Town, South Africa, GB - GenBank, '-' - Unknown, Br. muscle - Breast muscle, Pect. muscle - Pectoral muscle. The scientific names below are as recorded on specimen labels.

Taxa name	Sample no.	Origin	Date coll.	Sample type
Spotted Group				
F. francolinus	AMNH DOT8023	India	-	Br. muscle
F. pictus	AMNH 776813	India	-	Toe-pad
F. pintadeanus	GB EU165707	China	-	-
Striated Group				
Francolinus sephaena	TMC 9	Marico River, South Africa	2004	Heart
F. sephaena	TMC 10	South Africa	-	Br. muscle
F. s. rovuma	TM 6410	Zimbiti, Beira, Mozambique	1910	Toe-pad
F. s. grantii	BM 1902 1 20 300	Hulul, Ethiopia	1902	Toe-pad
F. streptophora	TMC 11	Cameroon	2005	Br. muscle
Red-winged Group				
F. psilolaema psilolaema	BM 80 1 1 1066	Kenya	-	-
F. p. theresae	BM 1965 M 2073	Mount Kenya, Kenya	1965	Toe-pad
F. p. ellenbecki	AMNH 68972	Kenya	-	Toe-pad
F. shelleyi	PFIAO 47	Ayton Farm, South Africa	-	Liver
F. s. uluensis	TMC 13	Kenya	-	Br. muscle
F. s. whytei	TM 27245	Mzimba, Malawi	1949	Toe-pad
F. afra	PFIAO 59	Eastern Cape, South Africa	2002	Liver
F. levaillantoides levaillantoides	TMC 12	Petrus Steyn, South Africa	2002	Liver
F. l. pallidior	TM 13217	Quickborn, Namibia	1923	Toe-pad
F. l. kalaharica	SAM 55386	Botswana	-	Toe-pad
F. l. jugularis	SAM 57819	Namibia	-	Toe-pad
F. l. gutturalis	AMNH 541174	Ethiopia	-	Toe-pad
F. l. lorti	AMNH 541185	Somalia	-	Toe-pad
F. l. archeri	AMNH 192573	Ethiopia	-	Toe-pad
F. l. cunenensis	AMNH 542359	Angola	-	Toe-pad
F. levaillantii levaillantii	TM 78622	Sterkspruit, South Africa	2005	Br. muscle
F. l. kikuyuensis	AMNH 406156	Kenya	-	Toe-pad
F. l. crawshayi	TM 23166	Nyika Plateau, Malawi	1940	Toe-pad
F. finschi	AMNH 308887	Angola	1941	Toe-pad
Red-tailed Group				
F. coqui coqui	PFIAO 45	Settlers, South Africa	-	Pect. Muscle
F. c. angolensis	TM 25325	Luluabourg, Dem. Rep. Congo	1939	Toe-pad
F. c. campbelli	BM 1933 7 14 105	Richmond, Natal, South Africa	1933	Toe-pad
F. c. vernayi	TM 17263	Botswana	-	Toe-pad
F. c. lynesi	BM 1953 54 52	Luluaborg, Dem. Rep. Congo	1953	Toe-pad
F. c. ruahdae	TM 52676	Rwinkwaku, Rwanda	-	Toe-pad
F. c. maharao	BM 1956 5 14 85	Mega, Ethiopia	1956	Toe-pad
F. c. hubbardi	AMNH 261916	Kidong Valley, Kenya	-	Toe-pad
F. c. stuhlmanni	TM 23158	Mzimba, Malawi	1934	Toe-pad
F. c. thikae	BM 1963 6 2	Arusha, Tanzania	1963	Toe-pad
F. c. kasaicus	BM 1953 54 49	Luluaborg, Dem. Rep. Congo	1953	Toe-pad
F. c. spinetorum	BM 19339 5 2	Azare banchi, Nigeria	1933	Toe-pad
F. schlegelii	BM 1949 30 19	Mboro, Bahr-El-Ghazel, Chad	1949	Toe-pad
F. albogularis albogularis	BM 1929 3 13 1	Farafeni, Gambia	1929	Toe-pad
F. a. gambagae	BM 1999 9 20 2	Gambaga, Ghana	1999	Toe-pad
F. a. buckleyi	BM 1934 3 16 28	Ejura Ashanti Ghana	1934	Toe-pad

Taxa name	Sample no.	Origin	Date coll.	Sample type
F. a. meinertzhageni	BM 1957 35 13	Luacano, Angola	1957	Toe-pad
Ungrouped taxa				
F. lathami lathami	GB AM236893	Cameroon	-	Blood
F. l. schubotzi	BM 1949 30 17	Benengal Zandi, Sudan	1949	Toe-pad
F. pondicerianus	AMNH DOT8050	India	-	Br. muscle
F. gularis	GB U90649	India	-	-

Table 5.4. DNA markers sequenced and primers used for PCR-amplification and sequencing of preserved francolin tissues.

Primer name	Primer sequence (5'to 3')	Reference
Cytochrome *b*		
L14578	cta gga atc atc cta gcc cta ga	J.G. Groth (pers. comm.)
MH15364	act cta cta ggg ttt ggc c	P. Beresford (pers. comm.)
ML15347	atc aca aac cta ttc tc	P. Beresford (pers. comm.)
H15915	aac gca gtc atc tcc ggt tta caa gac	Edwards & Wilson (1990)

Table 5.5. DNA marker sequenced and primers used for PCR-amplification and sequencing of museum toe-pads for francolins.

Primer name	Primer sequence (5' to 3')	Reference
Cytochrome-*b*		
Francolin-specific primers		
L14851 (General)	cct act tag gat cat tcg ccc t	Kornegay et al. (1993)
Franc-H1	cag cag aca cyt cyc tyg cct tc	R. Bowie
MH15145	aag aat gag gcg cca ttt gc	P. Beresford
Franc-L1	tgcctcacaacccaaatcctcac	R. Bowie
Franc-H2	agg agr agr att act cct gtg ttt cag g	R. Bowie
Franc-L2	gcc tca ttc tty ttc aty tgy atc ttc c	R. Bowie
Franc-H3	ggr tgg aat ggg att ttg tca gag	R. Bowie
Franc-L3	tcatcyractcygacaaaatccc	R. Bowie
Franc-H4	gar rgg gat tag rag gag gat	R. Bowie
Franc-L4	tat tcg cct ayg cya tcc twc gct c	R. Bowie
Franc-H5	gta gga rag kga tgc tat ttg gcc	R. Bowie
Franc-L5	ctc atc ctc ctc cta atc cc	R. Bowie
HB20 (General)	ttg gtt cac aag acc aat gtt	J. Feinstein (pers. comm.)

Table 5.6. The inter- and intraspecific uncorrected 'P' distances calculated from CYT*B.*

Taxon name	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	#	#	41	42	#	44	45	46	47	48	49
1 Francolinus francolinus																																																	
2 Francolinus pintadeanus	11%																																																
3 Ortygornis gularis	9%	12%																																															
4 Afrocolinus lathami	9%	12%	9%																																														
5 Afrocolinus l. schubotzi	10%	12%	9%	1%																																													
6 Francolinus pictus	7%	10%	9%	9%	9%																																												
7 Ortygornis pondicerianus	9%	13%	5%	10%	10%	8%																																											
8 Ortygornis sephaena grantii	10%	14%	9%	10%	11%	9%	9%																																										
9 Ortygornis sephaena (Kenya)	10%	14%	9%	10%	11%	9%	9%	1%																																									
10 Ortygornis s. rovuma	10%	14%	9%	11%	12%	10%	10%	4%	4%																																								
11 Ortygornis sephaena (SA)	9%	13%	8%	9%	10%	11%	9%	5%	5%	6%																																							
12 Ortygornis s. zambesiae	10%	12%	8%	9%	9%	11%	10%	5%	6%	4%	0%																																						
13 Peliperdix albogularis	10%	14%	12%	11%	11%	14%	12%	12%	12%	12%	11%	13%																																					
14 Peliperdix a. buckleyi	11%	14%	12%	11%	11%	14%	12%	12%	12%	12%	11%	12%	1%																																				
15 Peliperdix a. gambagae	11%	13%	12%	11%	11%	14%	12%	12%	12%	12%	11%	12%	2%	0%																																			
16 Peliperdix a. meinertzhageni	11%	14%	11%	10%	11%	10%	11%	11%	12%	12%	11%	10%	5%	5%	6%																																		
17 Peliperdix coqui	10%	13%	10%	10%	11%	10%	11%	11%	11%	11%	10%	8%	8%	8%	9%	8%																																	
18 Peliperdix c. ruahdae (Rwanda)	11%	17%	15%	13%	14%	9%	13%	15%	14%	15%	12%	9%	8%	7%	7%	10%	4%																																
19 Peliperdix coqui (Zambia)	11%	14%	11%	11%	11%	11%	11%	11%	12%	12%	11%	7%	8%	8%	9%	8%	0%	4%																															
20 Peliperdix c. angolensis	11%	14%	11%	11%	11%	11%	12%	12%	12%	12%	11%	8%	8%	8%	9%	8%	0%	4%	0%																														
21 Peliperdix c. campbelii	10%	14%	10%	10%	10%	10%	11%	11%	11%	11%	10%	8%	8%	7%	8%	8%	2%	4%	2%	2%																													
22 Peliperdix hubbardi	10%	13%	11%	10%	10%	9%	11%	11%	11%	12%	11%	10%	8%	8%	9%	8%	5%	5%	5%	5%	6%																												
23 Peliperdix c. kasaicus	10%	11%	10%	10%	10%	10%	11%	9%	10%	10%	11%	10%	9%	9%	7%	8%	7%	2%	8%	8%	6%	9%																											
24 Peliperdix c. lynesi	11%	14%	11%	11%	11%	11%	11%	12%	12%	12%	11%	7%	9%	8%	9%	8%	1%	4%	0%	0%	2%	5%	8%																										
25 Peliperdix c. maharao	10%	13%	11%	10%	11%	9%	11%	12%	12%	13%	12%	11%	10%	10%	10%	9%	6%	11%	6%	6%	8%	5%	9%	6%																									
26 Peliperdix c. spinetorum	11%	14%	11%	11%	11%	10%	11%	11%	12%	12%	10%	11%	9%	9%	9%	10%	8%	7%	8%	8%	8%	6%	10%	8%	7%																								
27 Peliperdix c. stuhlmanni	10%	11%	10%	10%	10%	10%	10%	10%	10%	10%	10%	9%	8%	8%	7%	8%	5%	9%	6%	5%	7%	6%	5%	6%	8%	8%																							
28 Peliperdix c. thikae	10%	12%	10%	10%	11%	9%	11%	10%	11%	12%	10%	10%	9%	8%	9%	8%	6%	9%	6%	6%	6%	3%	7%	6%	5%	7%	7%																						
29 Peliperdix c. vernayi	11%	17%	13%	12%	13%	9%	12%	14%	14%	15%	11%	9%	7%	6%	7%	9%	3%	1%	3%	3%	3%	4%	0%	3%	10%	6%	7%	8%																					
30 Peliperdix schlegelii	10%	13%	10%	10%	10%	8%	11%	10%	11%	12%	10%	9%	8%	8%	7%	8%	9%	8%	9%	9%	8%	8%	7%	9%	9%	8%	8%	9%	8%																				
31 Scleroptila afra	9%	12%	10%	11%	11%	9%	10%	10%	11%	10%	10%	9%	9%	10%	8%	10%	9%	13%	10%	10%	9%	10%	5%	10%	10%	10%	5%	10%	12%	9%																			
32 Scleroptila finschi	10%	13%	10%	11%	11%	9%	10%	11%	11%	11%	11%	10%	11%	11%	10%	10%	10%	13%	10%	11%	10%	10%	8%	10%	11%	10%	8%	10%	12%	11%	6%																		
33 Scleroptila levaillantii	9%	13%	10%	10%	10%	9%	11%	10%	10%	10%	10%	10%	10%	10%	10%	10%	9%	13%	9%	9%	9%	9%	9%	9%	10%	11%	8%	10%	12%	11%	7%	8%																	
34 Scleroptila l. crawshayi	9%	12%	10%	11%	11%	7%	11%	11%	12%	11%	11%	11%	10%	11%	9%	10%	10%	12%	11%	11%	11%	10%	5%	11%	11%	12%	6%	10%	11%	9%	2%	6%	8%																
35 Scleroptila l. kikuyuensis	10%	14%	11%	11%	11%	8%	11%	11%	12%	11%	11%	10%	11%	11%	11%	11%	9%	12%	10%	10%	10%	9%	8%	9%	12%	11%	8%	9%	11%	10%	5%	7%	9%	2%															
36 Scleroptila levaillantoides	10%	12%	11%	11%	10%	8%	11%	11%	11%	11%	11%	8%	10%	10%	9%	10%	9%	11%	10%	10%	9%	9%	7%	10%	10%	10%	6%	10%	10%	9%	3%	5%	8%	5%	5%														
37 Scleroptila l. kalaharica (Botswana)	11%	15%	14%	15%	17%	9%	12%	15%	15%	16%	14%	9%	13%	12%	10%	12%	12%	9%	12%	12%	12%	11%	5%	12%	14%	11%	12%	12%	9%	14%	7%	10%	13%	7%	8%	4%													
38 Scleroptila l. jugularis	10%	13%	11%	11%	11%	9%	10%	9%	8%	11%	6%	9%	10%	11%	12%	12%	12%	11%	12%	12%	11%	11%	12%	12%	12%	12%	11%	10%	11%	12%	8%	10%	10%	8%	4%	7%	5%												
39 Scleroptila l. archeri	9%	11%	9%	10%	9%	4%	9%	10%	11%	11%	10%	9%	10%	9%	8%	9%	9%	11%	9%	10%	9%	9%	5%	10%	10%	9%	6%	9%	10%	8%	4%	6%	7%	5%	5%	3%	6%	7%											
40 Scleroptila l. gutturalis	10%	11%	9%	10%	10%	8%	9%	11%	11%	11%	11%	8%	11%	10%	9%	10%	10%	11%	10%	11%	10%	10%	6%	10%	10%	10%	6%	10%	11%	9%	4%	6%	7%	5%	6%	3%	6%	8%	1%										
41 Scleroptila l. lorti	10%	11%	9%	10%	10%	8%	10%	11%	11%	11%	11%	9%	10%	10%	9%	9%	10%	12%	10%	10%	9%	10%	6%	10%	10%	10%	6%	9%	10%	9%	4%	6%	7%	4%	6%	3%	7%	8%	1%	2%									
42 Scleroptila l. pallidior	9%	12%	10%	11%	11%	8%	11%	11%	11%	11%	10%	9%	9%	9%	9%	10%	9%	12%	9%	9%	9%	10%	5%	9%	11%	10%	6%	10%	11%	10%	2%	7%	7%	3%	4%	4%	7%	8%	4%	4%	4%								
43 Scleroptila psilolaema	10%	12%	10%	11%	10%	10%	11%	11%	11%	11%	11%	10%	11%	11%	11%	11%	11%	14%	12%	12%	12%	11%	9%	12%	11%	10%	9%	11%	13%	11%	6%	6%	8%	6%	7%	6%	9%	9%	5%	5%	6%	5%							
44 Scleroptila p. theresae	11%	12%	10%	10%	10%	10%	10%	11%	11%	11%	11%	10%	11%	11%	11%	11%	11%	13%	11%	11%	11%	10%	9%	11%	10%	10%	8%	11%	12%	11%	6%	6%	8%	7%	8%	6%	9%	9%	6%	6%	6%	7%	3%						
45 Scleroptila p. ellenbecki	10%	13%	10%	12%	12%	9%	11%	10%	11%	10%	10%	9%	10%	10%	10%	11%	10%	12%	10%	10%	10%	10%	8%	10%	10%	11%	7%	9%	12%	11%	2%	5%	7%	3%	5%	3%	5%	7%	4%	4%	3%	3%	5%	6%					
46 Scleroptila shelleyi uluensis	10%	12%	9%	10%	11%	9%	10%	10%	11%	10%	10%	9%	10%	11%	9%	10%	10%	14%	10%	10%	10%	10%	6%	10%	11%	11%	6%	10%	13%	9%	4%	6%	8%	6%	7%	4%	9%	8%	3%	3%	3%	5%	6%	6%	4%				
47 Scleroptila s. whytei	9%	12%	9%	10%	9%	5%	10%	10%	10%	11%	10%	10%	10%	10%	10%	10%	11%	14%	11%	11%	10%	10%	8%	11%	10%	10%	8%	10%	13%	9%	6%	5%	8%	7%	6%	6%	9%	6%	5%	6%	6%	7%	5%	6%	6%	6%			
48 Scleroptila shelleyi (SA)	10%	12%	10%	10%	10%	9%	10%	10%	11%	11%	11%	10%	10%	10%	9%	9%	9%	11%	10%	10%	9%	9%	7%	10%	10%	10%	7%	10%	10%	9%	3%	5%	7%	5%	6%	2%	7%	7%	4%	4%	3%	4%	6%	6%	4%	4%	6%		
49 Scleroptila streptophora	10%	13%	9%	10%	10%	9%	10%	11%	11%	11%	10%	9%	10%	11%	11%	10%	9%	12%	10%	10%	10%	11%	9%	10%	11%	10%	9%	11%	11%	10%	8%	8%	8%	9%	8%	8%	12%	10%	8%	8%	8%	8%	9%	8%	8%	8%	9%	8%	

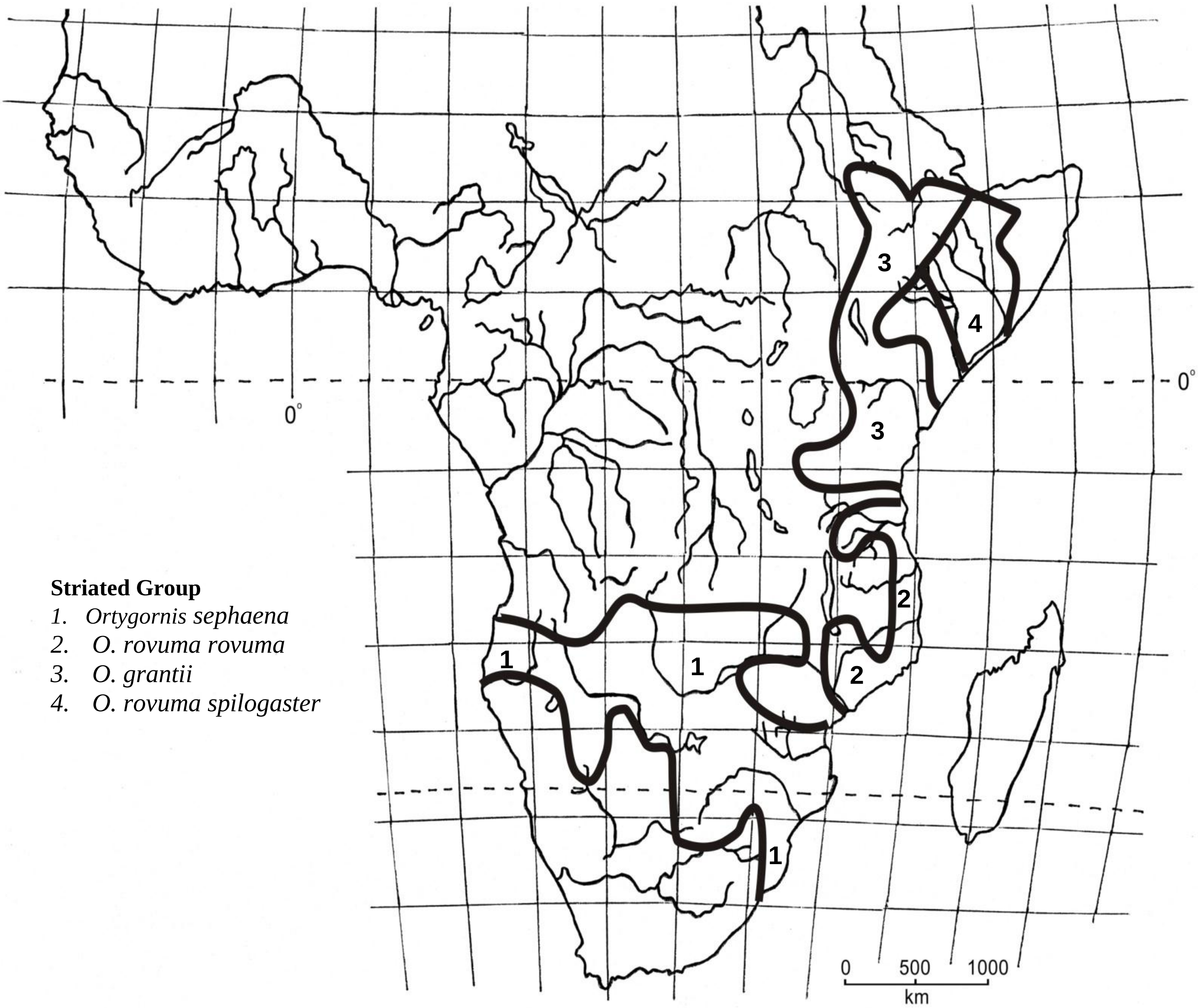


Figure 5.1. Distribution ranges of Hall's Striated Group taxa.

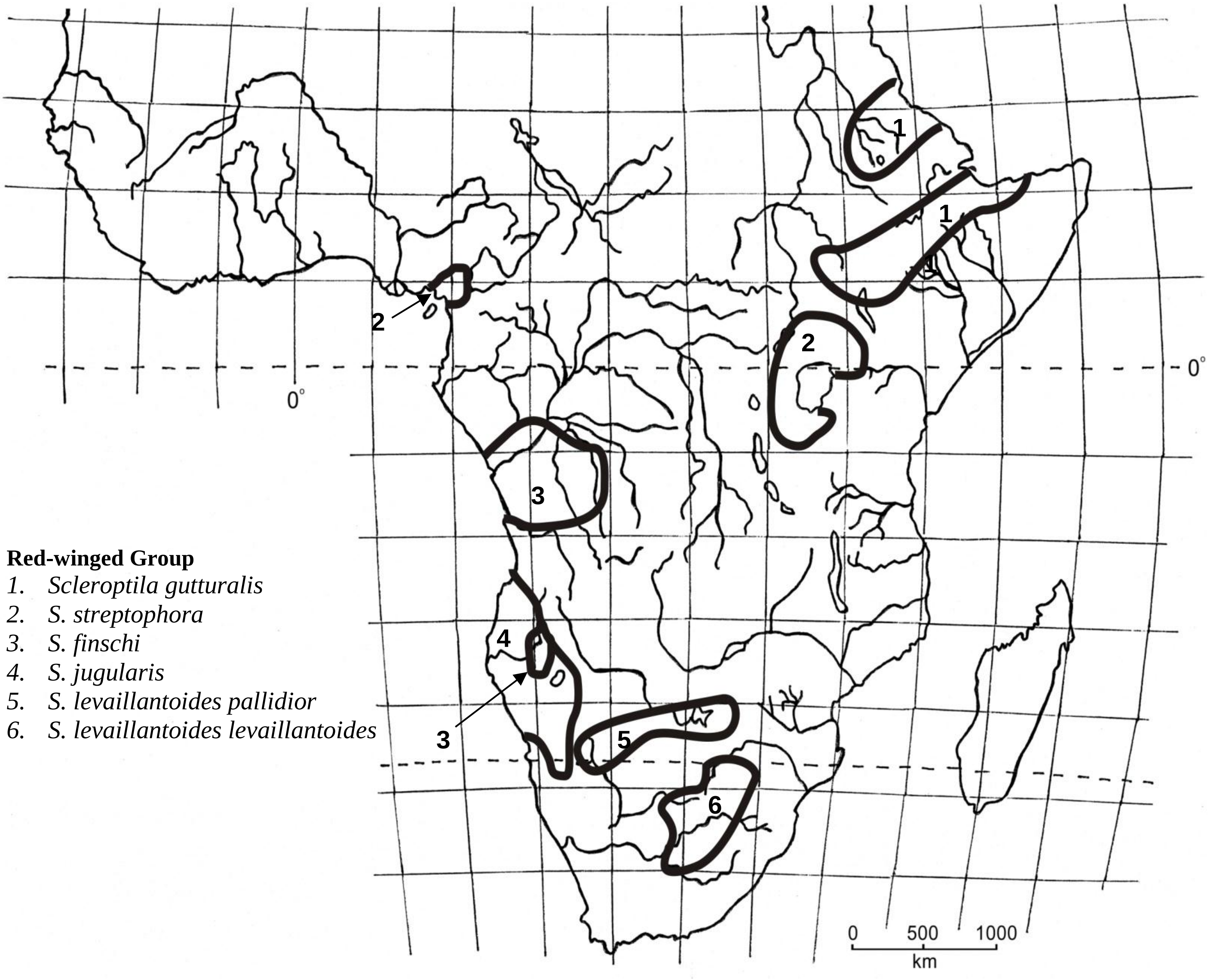


Figure 5.2. Distribution ranges of Hall's Red-winged Group taxa.

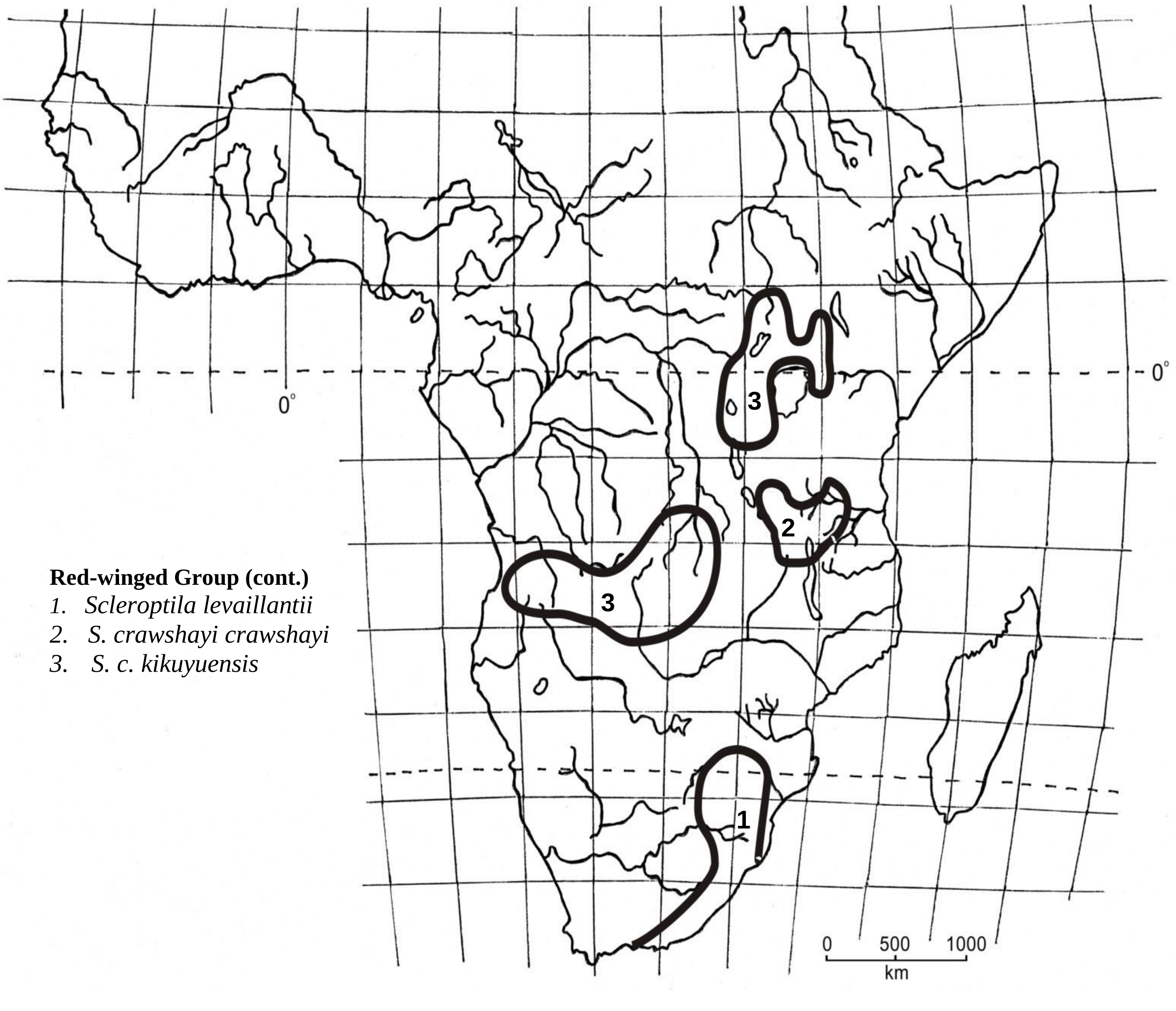


Figure 5.3. Distribution ranges of Hall’s Red-winged Group taxa.

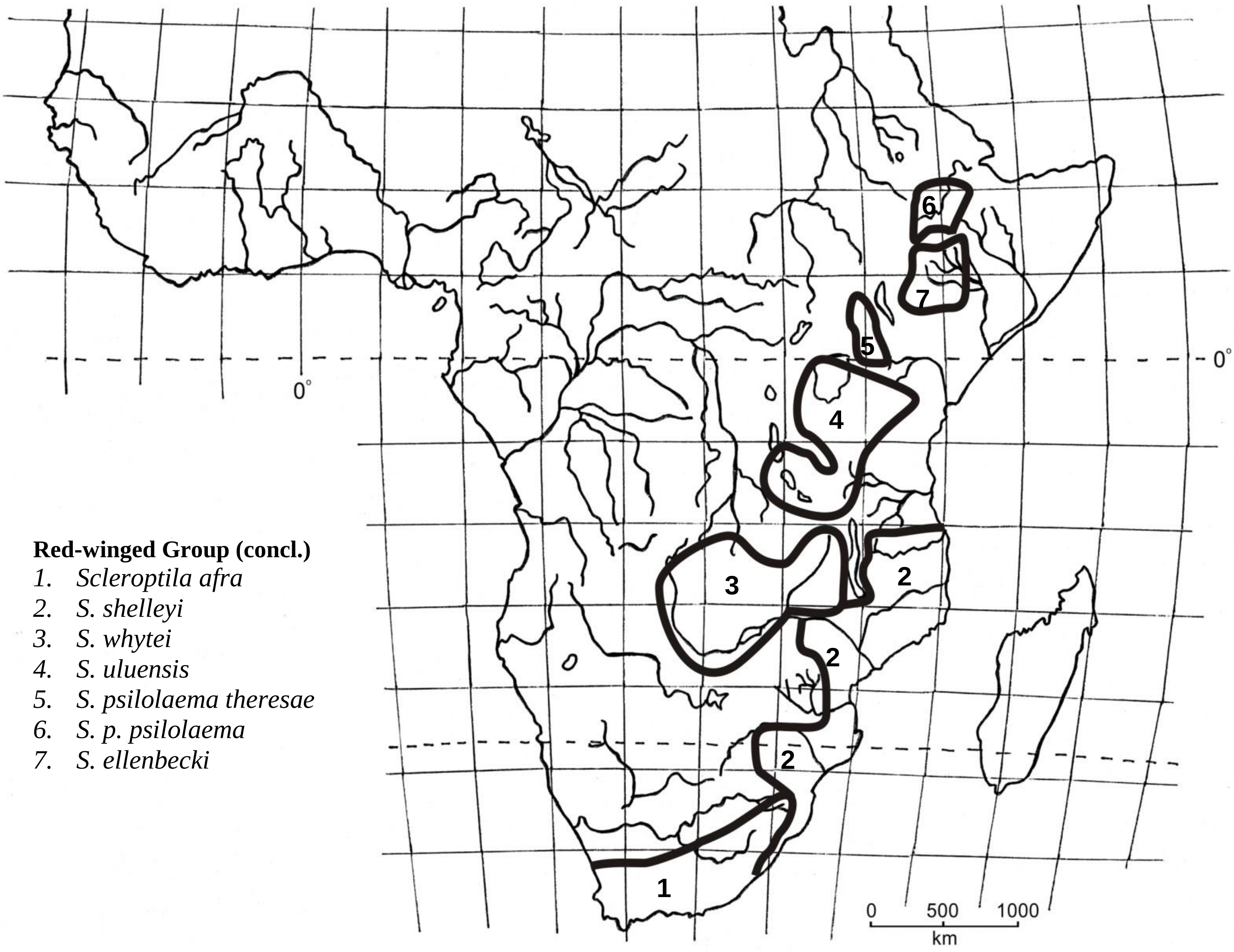


Figure 5.4. Distribution ranges of Hall's Red-winged Group taxa.

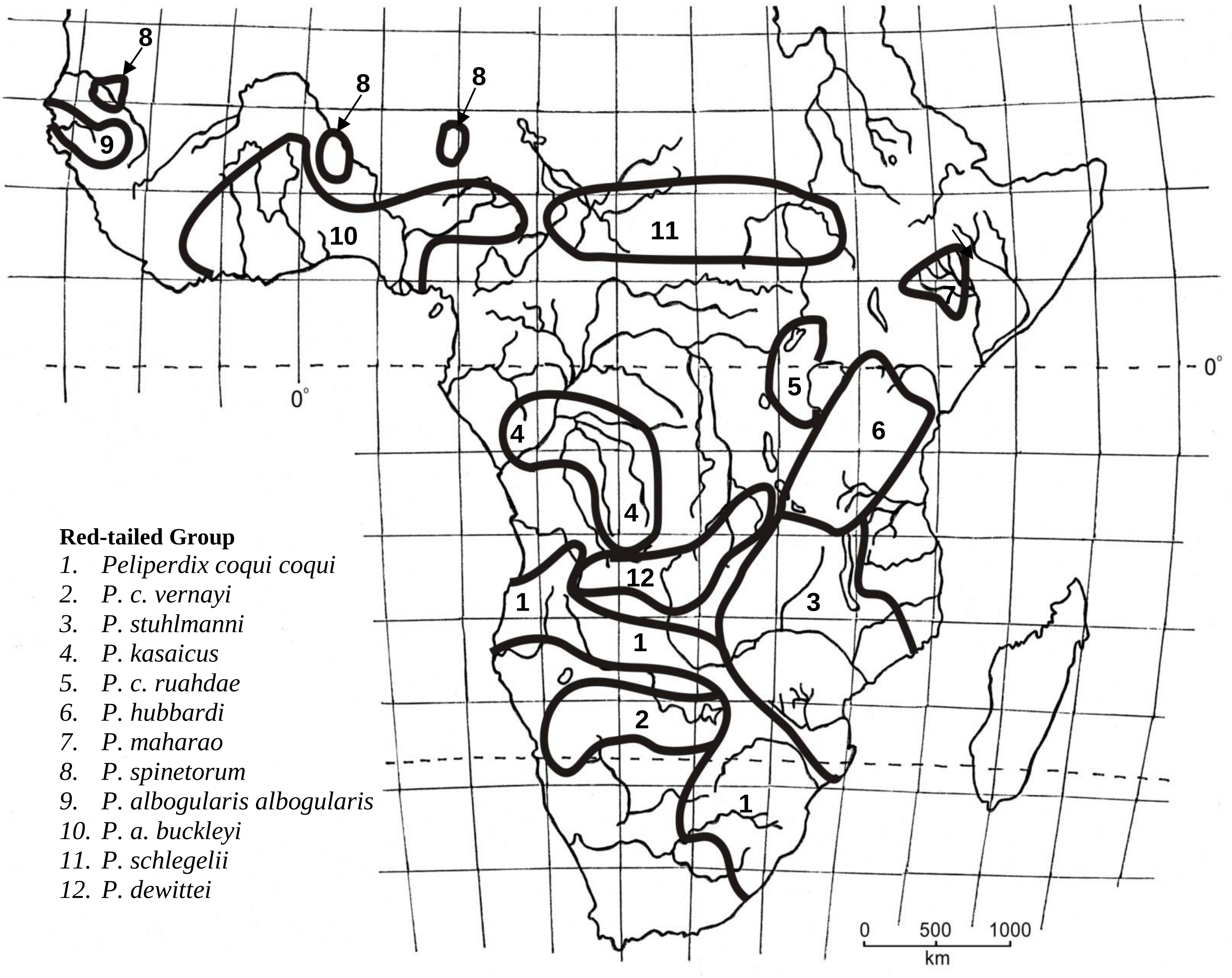
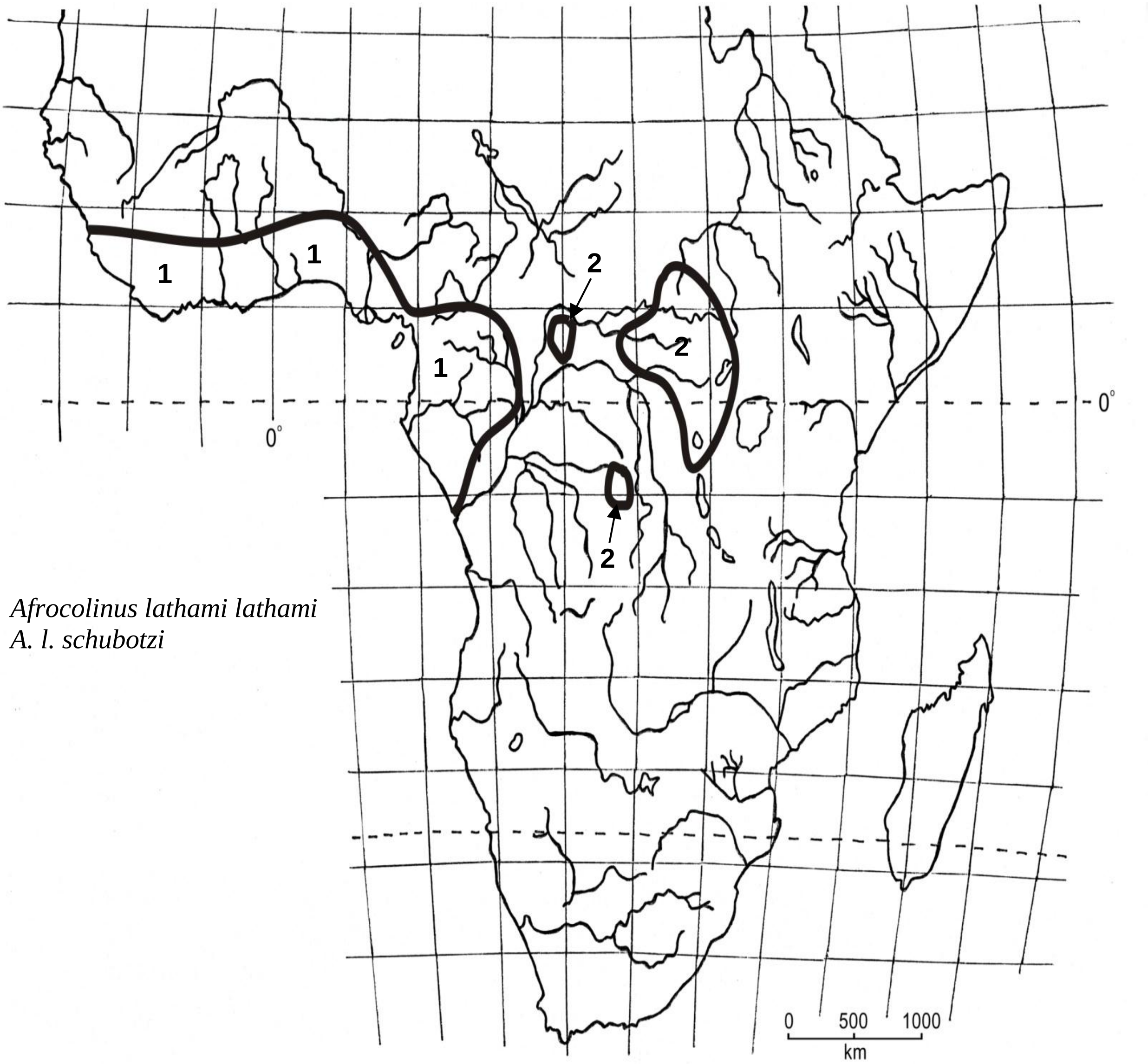


Figure 5.5. Distribution ranges of Hall's Red-tailed Group taxa.



1. *Afrocolinus lathami lathami*
2. *A. l. schubotzi*

Figure 5.6. Distribution of *Afrocolinus lathami*.

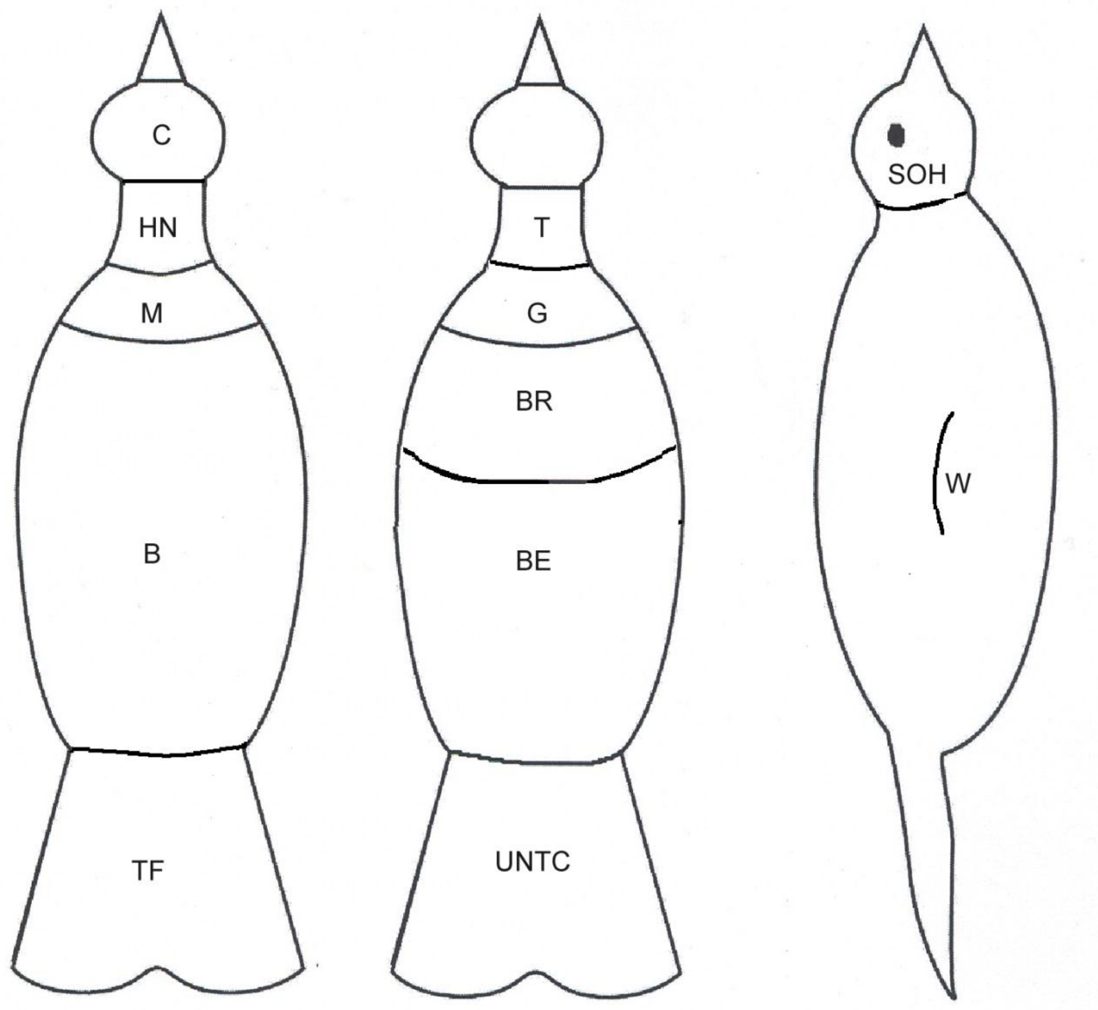


Figure 5.7. Illustration of francolin body partitions scored to generate the plumage character matrix. C - Crown, HN - Hindneck, M - Mantle, B - Back, TF - Tail feathers, T - Throat, G - Gorget, BR - Breast, BE - Belly, UNTC - Undertail coverts, SOH - Side of the head, W - Wing (primaries).

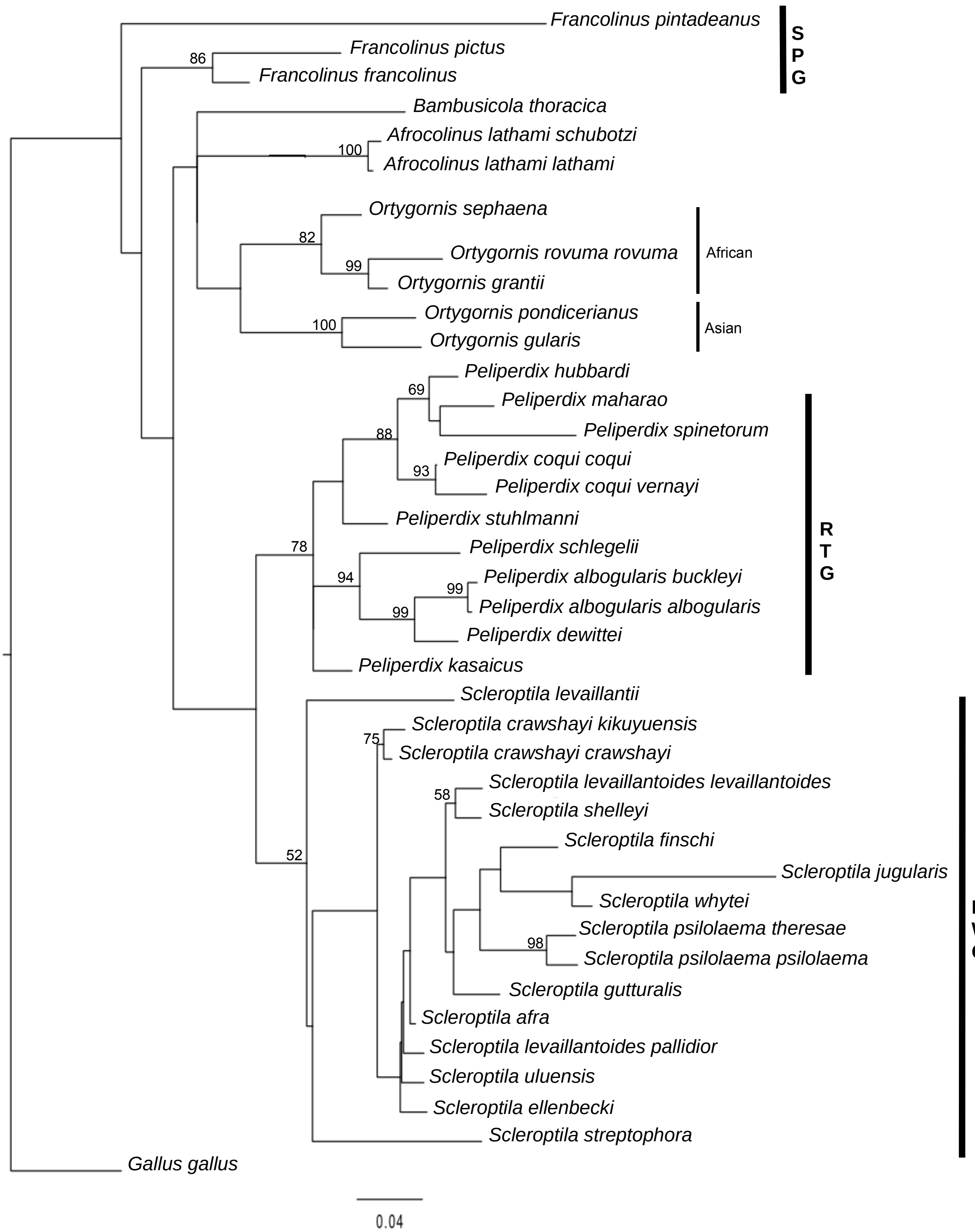


Figure 5.8. Maximum likelihood tree obtained from mitochondrial Cytochrome-*b* characters. Numbers above branches represent boostrap support values (only ≥ 70% are shown). SPG stands for Spotted Group, RTG – Red-tailed Group, RWG – Red-winged Group.

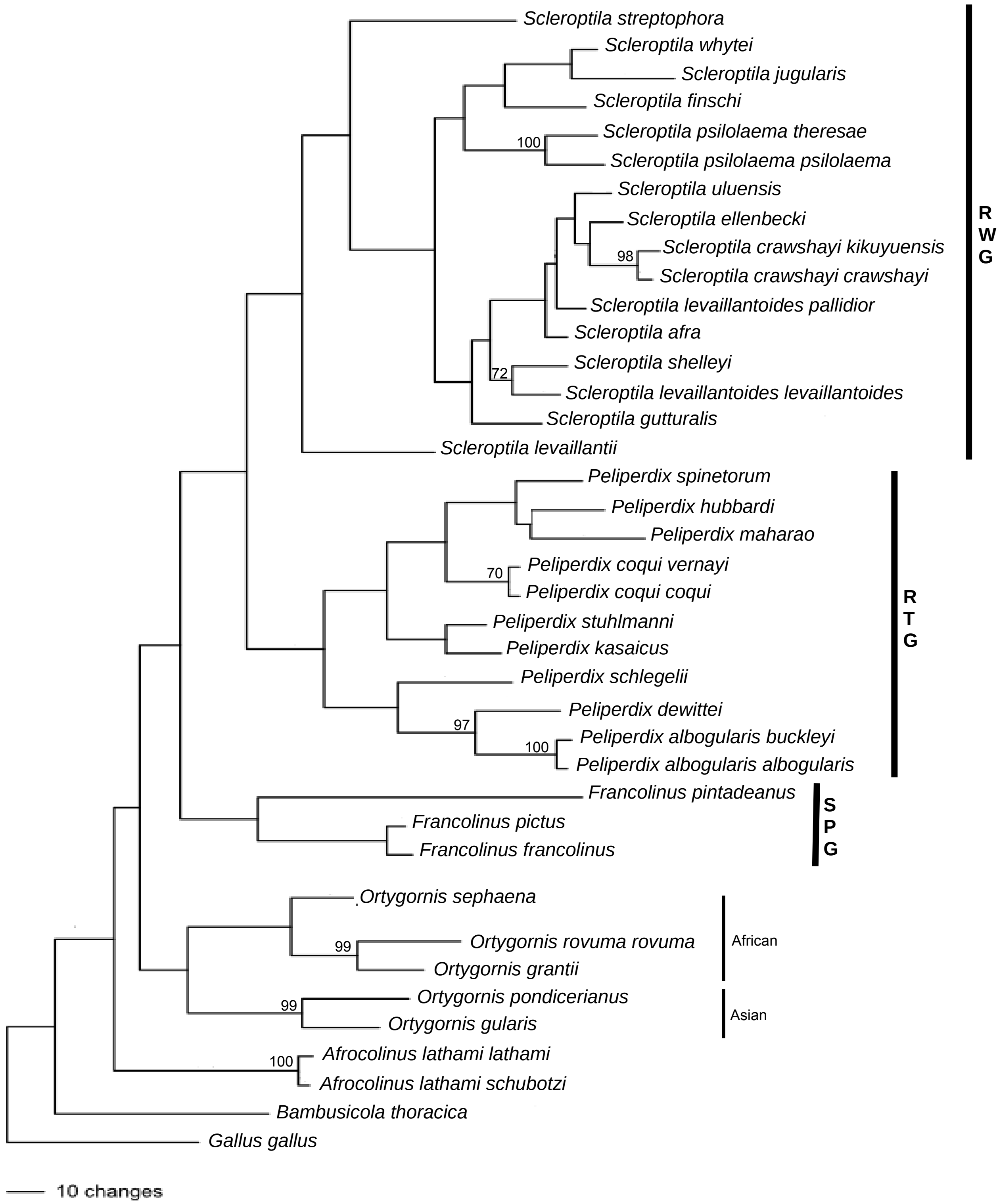


Figure 5.9. A parsimony tree (1 of 4 most parsimonious trees) obtained from mitochondrial Cytochrome-*b* characters. Numbers above branches represent boostrap support values (only ≥ 70% are presented). SPG stands for Spotted Group, RTG – Red-tailed Group, RWG – Red-winged Group.

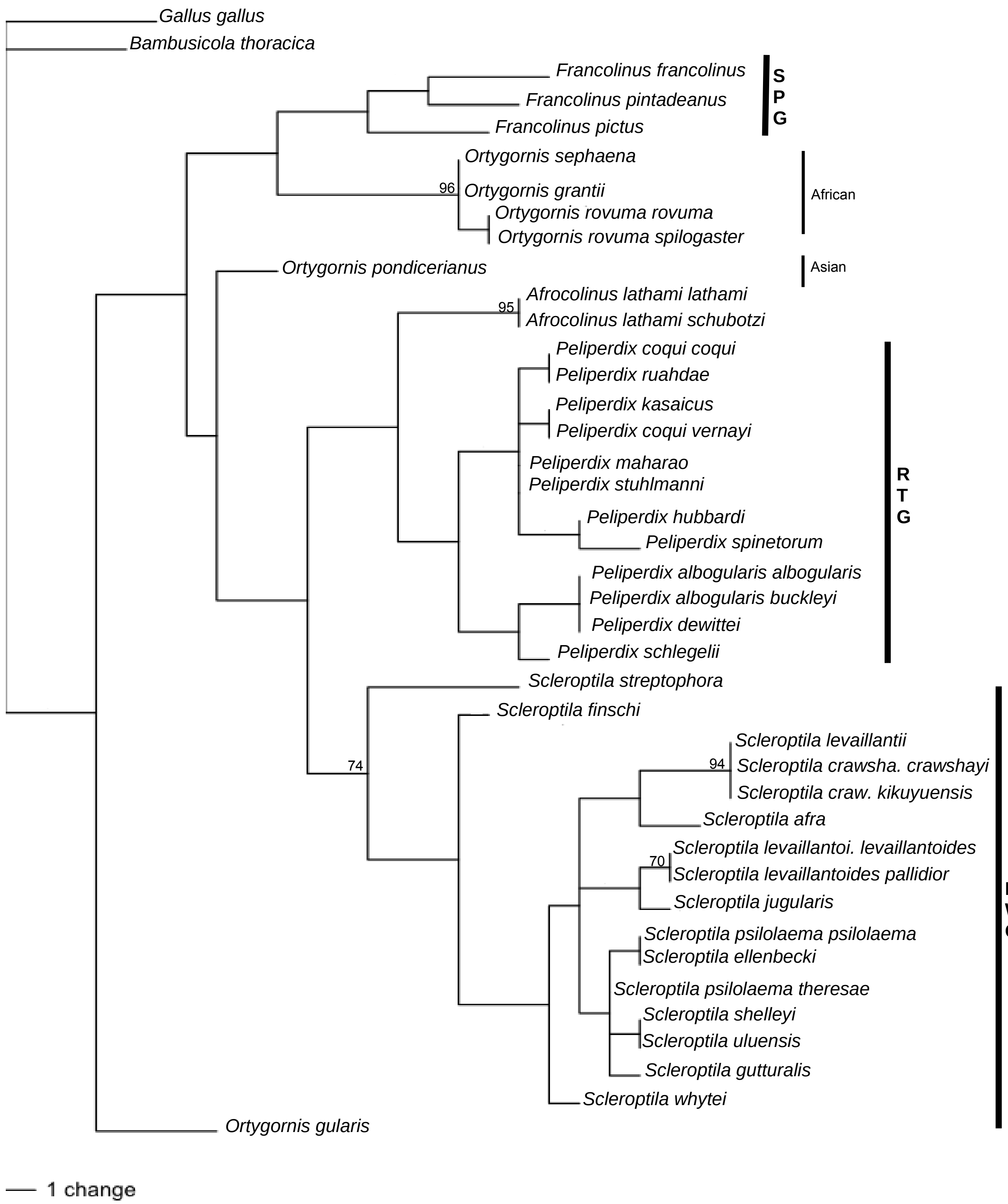


Figure 5.10. A parsimony tree (1 of 397 most parsimonious trees) obtained from organismal characters. Numbers above branches represent bootstrap support values (only ≥ 70% are presented). SPG stands for Spotted Group, RTG – Red-tailed Group, RWG – Red-winged Group.

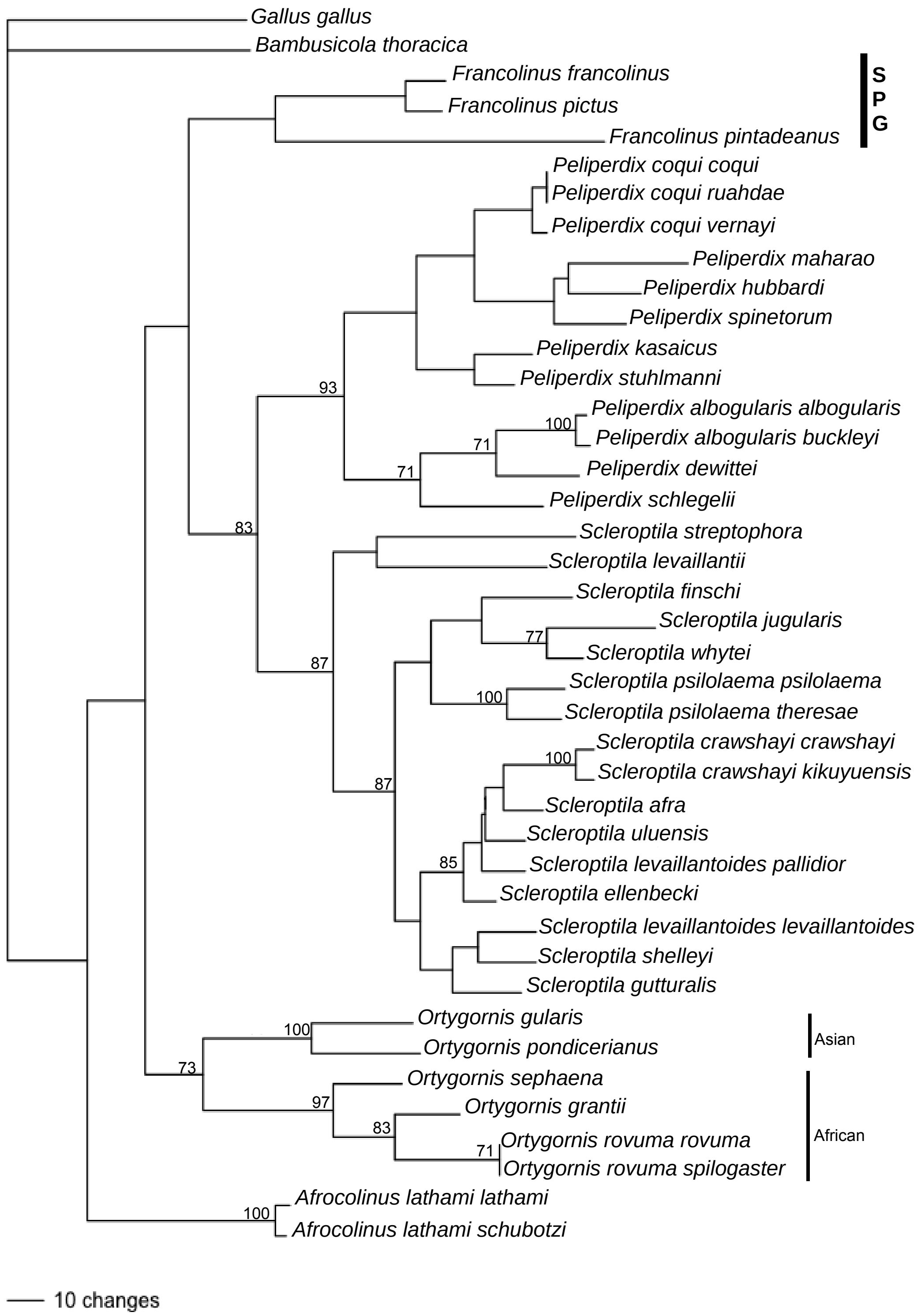


Figure 5.11. A parsimony tree (1 of 24 most parsimonious trees) obtained from combined mitochondrial Cytochrome-*b* and organismal characters. Numbers above branches represent bootstrap support values (only ≥ 70% are presented). SPG stands for Spotted Group, RTG – Red-tailed Group, RWG – Red-winged Group.

Appendix 5.1. List of francolin taxa included in the analysis and the GenBank accession number for CYT*B*.

Taxon	CYT*B* GenBank no.
Francolinus francolinus	AF013762
Francolinus pictus	FR694142
Francolinus pintadeanus	NC011817
Ortygornis pondicerianus	FR691632
Ortygornis gularis	U90649
Afrocolinus lathami lathami	AM236893
Afrocolinus lathami schubotzi	FR694139
Ortygornis grantii	FR694144
Ortygornis sephaena Kenya	FR694141
Ortygornis rovuma rovuma	FR694135
Ortygornis sephaena South Africa	FR694140
Ortygornis sephaena zambesiae	FR694143
Peliperdix albogularis albogularis	FR694145
Peliperdix a. buckleyi	FR694147
Peliperdix a. gambagae	FR694146
Peliperdix a. meinertzhageni	FR694148
Peliperdix coqui coqui	AM236895
Peliperdix coqui angolensis	FR694153
Peliperdix coqui campbelii	FR694156
Peliperdix coqui hubbardi	FR694151
Peliperdix coqui kasaicus	FR694150
Peliperdix coqui lynesi	FR694155
Peliperdix coqui maharao	FR691635
Peliperdix coqui spinetorum	FR694154
Peliperdix coqui stuhlmanni	FR694152
Peliperdix coqui thikae	FR691634
Peliperdix coqui vernayi	FR694157
Peliperdix schlegelii	FR694149
Scleroptila afra	AM236897
Scleroptila finschi	FR691607
Scleroptila levaillantii	U90642
Scleroptila crawshayi crawshayi	FR691605
Scleroptila c. kikuyuensis	FR691606
Scleroptila levaillantoides	FR691612
Scleroptila levaillantoides archeri	FR691610
Scleroptila levaillantoides gutturalis	FR691613
Scleroptila jugularis	FR691608
Scleroptila levaillantoides lorti	FR691611
Scleroptila levaillantoides pallidior	FR691609
Scleroptila psilolaema	FR691614
Scleroptila psilolaema ellenbecki	FR691616
Scleroptila psilolaema theresae	FR691615

Scleroptila uluensis Kenya	FR691620
Scleroptila shelleyi South Africa	AM236898
Scleroptila uluensis	FR691622
Scleroptila whytei	FR691621
Scleroptila streptophora	FR691617

Appendix 5.2. A revised classification of African francolins that is based on evidence presented in this chapter. An asterisk (*) indicates that the taxonomic status of that particular taxon may change when DNA characters become available and are included in the analyses. Species and subspecies authority appear in Table 1.2.

Family: Phasianidae

Sub-family: Phasianinae

Genus: *Francolinus* Stephens, 1819

Francolinus francolinus
Francolinus pintadeanus
Francolinus pictus

Genus: *Ortygornis* Reichenbach, 1853

Ortygornis pondicerianus
Ortygornis gularis
Ortygornis sephaena
Ortygornis rovuma rovuma
Ortygornis rovuma spilogaster *****
Ortygornis grantii

Genus: *Afrocolinus* gen. nov.

Afrocolinus lathami
Afrocolinus lathami schubotzi

Genus: *Peliperdix* Bonaparte, 1856

Peliperdix coqui coqui
Peliperdix coqui vernayi
Peliperdix stuhlmanni
Peliperdix kasaicus
Peliperdix coqui ruahdae
Peliperdix hubbardi
Peliperdix maharao
Peliperdix spinetorum
Peliperdix albogularis albogularis
Peliperdix albogularis buckleyi
Peliperdix schlegelii
Peliperdix dewittei

Genus: *Scleroptila* Blyth, 1849

Scleroptila levaillantoides levaillantoides
Scleroptila levaillantoides pallidior
Scleroptila jugularis
Scleroptila gutturalis
Scleroptila finschi
Scleroptila streptophora
Scleroptila levaillantii
Scleroptila crawshayi crawshayi
Scleroptila crawshayi kikuyuensis

Scleroptila afra
Scleroptila shelleyi
Scleroptila whytei
Scleroptila uluensis
Scleroptila psilolaema psilolaema
Scleroptila psilolaema theresae
Scleroptila ellenbecki

CHAPTER 6

Taxonomy and phylogeny of spurfowls

Abstract

Delimitation of taxa continues to be a challenging exercise in the absence of a universal definition of species and subspecies that can be applied consistently across different groups of study. The spurfowls, members of which share a common evolutionary path (genus *Pternistis* Wagler, 1832, *sensu* Crowe et al. 2006), which are the group of focus in this chapter, are no exception. Over and above the challenges resulting from suspected high levels of hybridization, discordance between organismal and molecular characters, difficulty in determining the genetic threshold when delimiting taxa, and unavailability of fresh samples of many taxa for DNA analyses, this study sought to establish a classification system of spurfowls which takes into account the evolutionary relationships among taxa, with the goal of bringing stability to the taxa recognized as valid species, subspecies and genera, based on congruent multiple lines of evidence. The phylogenetic inference methods, Maximum likelihood and parsimony were performed on separate and combined DNA and organismal characters. The outcome resulted in some subspecies being elevated to the species level with others being placed into more inclusive entities; no generic recommendations are made. Most of the phylogenetic hypotheses presented by Hall (1963) were rejected. Spurfowls are represented by extremely morphologically and vocally divergent taxa. Thus, it is difficult to identify homologuous characters that can be used to investigate their evolutionary relationships. However, a multi-faceted character approach seems to be a

fitting strategy for working out intra-generic relationships within spurfowls. Phylogeographic studies of various species complexes are recommended.

Introduction

What are spurfowls?

The hypothesised monophyly of the genus *Francolinus* Stephens 1819 (*sensu* Hall 1963), was rejected resulting in the split of birds traditionally known as 'francolins' into two lineages, 'true' francolins and spurfowls, that are evolutionary distant (Crowe et al. 2006). Spurfowls are represented by members currently assigned to a single genus *Pternistis* Wagler 1832 (Table 1.1, 1.2). Spurfowls, like francolins are placed in the sub-family Phasianinae, and together with other Old World partridge- and quail-like gamebirds (e.g. *Perdix* and *Coturnix* spp.) are placed in the tribe Perdicini (Chapin 1932, Peters 1934, Wolters 1975-82, Crowe et al. 1986, Johnsgard 1988, Sibley and Monroe 1990, del Hoyo et al. 1994, Madge and McGowan 2002). This assemblage is comprised of 23 traditionally recognized species with their core distribution mainly in sub-Saharan Africa and no species occur in Asia (Hall 1963, Johnsgard 1988). The West African *Pternistis bicalcaratus* is the only species that extends its distribution into Morocco, in North Africa.

Spurfowl species and their distribution

This chapter focuses on spurfowls (*Pternistis* spp.), which Hall (1963) categorized into four putative monophyletic species groups (see Table 1.1), all represented by African species. These are the Bare-throated Group, Montane, Vermiculated, and the Scaly Group. Generally, spurfowls like francolins are (partridge-like) resident birds that can run or fly over short distances when facing a threat. Most species are sexually monochromatic in plumage, but males of most species have a single spur on their tarsus while females in some instances also have relatively smaller spurs (Johnsgard 1988). Members of the different species groups have complex morphology, ecology, behaviour and distribution patterns (Snow 1978) and occur in different habitats primarily of a tropical or sub-tropical nature (Hall 1963, Johnsgard 1988, del Hoyo et al. 1994, Madge and McGowan 2002).

Species group diversity, distribution and morphology

Bare-throated Group

The Bare-throated Group consists of four traditionally recognized species, the Red-necked Spurfowl *Pternistis afer* (Müller, 1776), Swainson's Spurfowl *P. swainsonii* (Smith, 1836), Yellow-necked Spurfowl *P. leucoscepus* (Gray, 1867) and Grey-breasted Spurfowl *P. rufopictus* Reichenow, 1887 (Table 1.1). A number of subspecies are traditionally recognized, 20 in *P. afer* (*afer* (Müller, 1776), *harterti* Reichenow, 1909, *nyanzae* Conover, 1929, *böhmi* Reichenow, 1885, *intercedens* Reichenow, 1909, *itigi* (Bowen, 1930), *cranchii* (Leach & Koenig, 1818), *punctulatus* (Gray, 1834), *benguellensis* Bocage, 1893, *leucoparaeus* (Fischer & Reichenow, 1884), *humboldtii* (Peters, 1854), *swynnertoni* Sclater, 1921, *castaneiventer* Gunning & Roberts, 1911, *melanogaster* Neumann, 1898, *loangwae* Grant & Praed, 1934, *lehmanni* Roberts, 1931, *notatus* Roberts 1924, *krebsi* Neumann, 1920, *cunenensis* Roberts, 1932, *cooperi* Roberts, 1947); five in *P. swainsonii* (*swainsonii* (Smith, 1836)), *lundazi* White, 1947, *gilli* Roberts, 1932, *damarensis* Roberts, 1932, *chobiensis* Roberts, 1932); seven in *P. leucoscepus* (*leucoscepus* (Gray, 1867)), *infuscatus* Cabanis, 1868, *holtemülleri* Erlanger, 1904, *keniensis* Mearns, 1911, *kilimensis* Mearns, 1911, *tokora* Stoneham, 1930, *muhamed-ben-abdullah* Erlanger, 1904) and a monotypic *P. rufopictus* (Table 1.2).

These taxa have widespread distribution in eastern Africa from Eritrea to the Cape Province and extend westward south of the Congo forest to Gabon, Angola and northern Namibia (Hall 1963) (Fig. 6.1, 6.2). They inhabit grasslands with cover of trees and scrubs and they are found near water courses. Members of the Bare-throated Group are large with a body mass ranging from 480 – 960 g (Johnsgard 1988). These birds are distinguished from the other spurfowls by having a patch of bare skin on the throat and round the eye, with the underparts being diagnostic in all four species. The presence of fairly well-developed spurs is a remarkable feature (probably linked to the origin of the group name ‘spurfowls’). The males have a long and strong lower spur with a short blunt upper spur being common in *P. leucoscepus* and *P. rufopictus,* and less common among individuals of *P. afer* and *P. swainsonii.*

The “*afer*” type subspecies have no vermiculation and they are strongly patterned in black, white and grey on the belly and face. The belly of *P. afer* is broadly streaked in white and black, with feathers having black centres and white edges. In short, what characterizes what Hall (1963) refers to as the *cranchii*-type subspecies is that the belly feathers have buff central streak vermiculated with blackish grey and margined with broad chestnut (degree of chestnut colour varies from one subspecies to the other) whereas the *afer*-type subspecies have broad greyish black central streak with buff margins (particularly in the nominate subspecies *afer*) or with thin greyish black central streak separating the long buff parallel streaks margined with black or sometimes maroon. The feathers on the belly of *P. swainsonii* have drop-shaped dark brown shaft streaks which increase in size over the lower belly and flanks. *Pternistis leucoscepus* is the most distinctive member of the group with a yellow bare throat skin and it presents slight variation compared to *P. afer*. The back is diagnosed by white shaft streaks and the underparts are streaked with white and chestnut in a way that each feather has chestnut with narrow white edges and a triangular white patch at the tip, tapering up the shaft. The primaries are said to have a conspicuous patch which according to Hall (1963) is visible during flight. Unlike the other Bare-throated species, *P. rufopictus* has orange pink throat skin, grey with black shaft streaks breast with the belly belly having the narrow central black streak separated from rufous chestnut margins by broad buff to white streaks.

Montane Group

This group consists of seven traditionally species: Erckel's Spurfowl *P. erckelii* (Rüppell, 1835), Djibouti Spurfowl *P. ochropectus* (Dorst & Jouanin, 1952), Chestnut-naped Spurfowl *P. castaneicollis* Salvadori, 1888, Jackson's Spurfowl *P. jacksoni* O. Grant, 1891, Handsome Spurfowl *P. nobilis* Reichenow, 1908, Mount Cameroon Spurfowl *P. camerunensis* Alexander, 1909, Swierstra's Spurfowl *P. swierstrai* (Roberts, 1929) (Table 1.1). The putative subspecies are: two in *P. erckelii (erckelii* (Rüppell, 1835)), *pentoni* Praed, 1920, two in *P. nobilis* (*nobilis* Reichenow, 1908, *chapini* Grant & Praed, 1934); six within *P. castaneicollis* (*castaneicollis* Salvadori, 1888, *bottegi* Salvadori, 1898, *gofanus* Neumann, 1904, *ogoensis* Praed, 1920, *kaffanus* Grant & Praed, 1934, *atrifrons* (Conover, 1930)); three in *P. jacksoni* (*jacksoni* O. Grant, 1891, *pollenorum* Meinertzhagen, 1937, *gurae* Bowen, 1931) (Table 1.2).

In terms of its distribution, the Montane Group is formed of scattered communities in the mountains of north eastern Africa from Eritrea to Mount Kenya, on the eastern Congo border, in the highlands of Angola, and on mount Cameroon (Hall 1963) (Fig. 6.3). Its members are birds which require some trees for cover and roosting and the majority of species are in or near montane evergreen forest. *Pternistis erckelii* is the only member which sometimes wanders into grasslands of the high plateau of northern Ethiopia. The Montane species are said to be the least homogeneous (Snow 1978) of the spurfowl groups morphologically, so much so that, it is impossible to designate any group character other than that the males have the crown, lower back, primaries and tail plain brown or red-brown. In case where the sexes are dichromatic, the lower back and tail are vermiculated.

Hall (1963) acknowledged that variation in some characters follows geographical trends (Meiri and Dayan 2003, James 1970), with the birds of the extreme north eastern parts being the largest and most heavily spurred with dark bills, yellowish legs, no bare skin round the eyes, and with the sexes alike. Birds of the two isolated western subspecies and the one central subspecies are the smallest with a mass that according to Johnsgard (1988) ranges from ~500-600 g in *P. camerunensis* and *P. swierstrai* and 600-890 g in *P. nobilis*. They are the least heavily spurred with red bills and legs, and with the sexes quite unlike (Snow 1978) except for *P. nobilis* that exhibits no sexual dimorphism. The Cameroon species, *P. camerunensis* has an extensive area of red bare skin round the eye.

Generally, the diagnostic characters of the Montane spurfowls are found mainly on the back and to a larger extent on the underparts particularly on the belly in the mid-ventral feathers. The patterning of the belly feathers of *P. castaneicollis*, which has an extensive double-patterning on the back with wing coverts and breast being clearly defined in black and white, with some ochre and chestnut) is generally similar to that in *P. erckelii* and *P. swierstrai* with the feathers being made up of a broad buff central streak which is constricted in the middle and expanded distally into a tear drop distally, margined with rufous. The central buff streak in *P. ochropectus* is margined with greyish black U-shaped streak. The feathers on the belly of *P. camerunensis, P. nobilis* and *P. jacksoni* are uniformly coloured with buff margins in *P. jacksoni* and *P. camerunensis,* and grey margins in *P. nobilis*.

Scaly Group

The Scaly Group comprises three traditionally recognized allopatric species, Ahanta Spurfowl *P. ahantensis* Temminck, 1854, Scaly Spurfowl *P. squamatus* Cassin, 1857 and Grey-striped Spurfowl *P. griseostriatus* O. Grant, 1890 (Table 1.1), with nine putative subspecies recognized within *P. squamatus* (*squamatus* Cassin, 1857, *maranensis* Mearns, 1910, *schuetti* Cabanis, 1880, *usambarae* Conover, 1928, *uzungwensis* Bangs & Loveridge, 1931, *doni* Benson, 1939, *zappeyi* Mearns, 1911, *tetraoninus* Blundell & Lovat, 1899, *chyuluensis* Someren, 1939); two subspecies in *P. ahantensis* (*ahantensis* Temminck, 1854, *hopkinsoni* Bannerman, 1934) being recognized while *Pternistis griseostriatus* is a monotypic species (Table 1.2).

Members of this group are characterized by having scaly underparts and they inhabit the lowland forest in Upper and Lower Guinea, and cultivations and clearings (Hall 1963) (Fig. 6.4). Compared to other spurfowls, these species have very little defining plumage pattern and strong colouration except for *P. ahantensis* which shows some distinct patterning with feathers having paler edges and darker centres. The underparts have some parts that are creamy-buff or brown with the colour and pattern varying in different subspecies, but all have narrow darker edges to breast feathers giving a scaly appearance. There is no marked plumage dimorphism except that the females tend to be more vermiculated than the males.

Pternistis squamatus is not sexually dimorphic but females tend to be less strikingly vermiculated. This species is characterized by having indistinctly vermiculated upperparts with faint U-patterning on the lower neck and the feathers have blackish centres tinged with red-brown. The belly is plain brown with scaly pattern and ill-defined dark shaft streaks margined buff. In *P. ahantensis*, the rest of belly feathers are richly coloured and streaked with dark brown chestnut edged buff while the upperparts are vermiculated with some white U-patterning (indistinct on the back but very distinct on the lower neck). On the other hand, *P. griseostriatus* is the most distinct member of the group in that the lower neck feathers and wing coverts are chestnut and broadly vermiculated. It has plain belly, the breast and flank feathers are chestnut and edged with greyish or creamy buff.

Vermiculated Group

This is the most widespread of all African spurfowl species groups (Fig. 6.5, 6.6, 6.7) consisting of nine traditionally recognized species (Hall 1963). The species are the Double-spurred Spurfowl *P. bicalcaratus* (Linnaeus, 1766), Heuglin's Spurfowl *P. icterorhynchus* Heuglin, 1863, Clapperton's spurfowl *P. clappertoni* (Children & Vigors, 1826), Hildebrandt's Spurfowl *P. hildebrandti* Cabanis, 1878, Natal Spurfowl *P. natalensis* Smith, 1833, Hartlaub's Spurfowl *P. hartlaubi* Bocage, 1869, Harwood's Spurfowl *P. harwoodi* Blundell & Lovat, 1899, Red-billed Spurfowl *P. adspersus* Waterhouse, 1838 and Cape Spurfowl *P. capensis* (Gmelin, 1789) (Table 1.1). The putative subspecies are four within *P. hartlaubi* (*hartlaubi* Bocage, 1869, *crypticus* Stresemann, 1939, *bradfieldi* (Roberts, 1928), *ovambensis* (Roberts, 1928)); three in *P. adspersus* (*adspersus* Waterhouse, 1838, *kalahari* de Schauensee, 1931, *mesicus*

Clancey, 1996); two in *P. natalensis* (*natalensis* Smith 1833, *neavei* Praed, 1920); six subspecies in *P. hildebrandti* (*hildebrandti* Cabanis, 1878, *altumi* Fischer & Reichenow, 1884, *helleri* Mearns, 1915, *fischeri* Reichenow, 1887, *johnstoni* Shelley, 1894, *grotei* Reichenow, 1919); five in *P. bicalcaratus (bicalcaratus* (Linnaeus, 1766), *ogilvie-grantii* Bannerman, 1922, *ayesha* Hartert, 1917, *adamauae* Neumann, 1915, *thornei* Ogilvie-Grant, 1902); four in *P. icterorhynchus* (*icterorhynchus* Heuglin, 1863, *dybowski* Oustalet, 1892, *ugandensis* Neumann, 1907, *emini* Neumann, 1907); eight subspecies in *P. clappertoni* (*clappertoni* (Children & Vigors, 1826), *sharpii* Ogilvie-Grant, 1892, *heuglini* Neumann, 1907, *gedgii* Ogilvie-Grant, 1891, *nigrosquamatus* Neumann, 1902, *konigseggi* Madarasz, 1914, *testis* Neumann, 1928, *cavei* Macdonald, 1940) (Table 1.2). *Pternistis capensis* and *P. harwoodi* are monotypic species.

Members of the group are known to exhibit variation in their ecology, with the northern vermiculated species (*P. bicalcaratus*, *P. icterorhynchus*, *P. clappertoni* and *P. harwoodi*) forming a homogenous assemblage occupying grasslands and savanna habitats (Hall 1963). Within the Vermiculated member species the underparts are diagnostic. *Pternistis bicalcaratus* has buff underparts distinctly and heavily streaked with blackish and chestnut with small arrow-shaped buff marks on most belly feathers. In *P. clappertoni*, the upperparts are greyish brown above with barring in flight feathers. It is buff below with black to brownish marks while the hind and lower neck have U-patterning as in *P. icterorhynchus* whose underparts are buff with dark brown markings. The male *P. harwoodi* that was examined is grey speckled and finely barred with blackish and buff above. The hind and lower neck, sides of face, and throat are speckled with black and white. It has irregular double-V patterning on the belly which tends to be scattered just on the lower extreme of the belly on the buff background. *Pternistis* *hartlaubi* is one of the spurfowls that exhibit striking plumage dimorphism with the difference in the known populations being mainly in the degree of colouration. The male *P. hartlaubi* has buff throat with black streaks which continues to the sides of neck through to the hind neck and to the breast. The belly of male is like the underparts of female which are pale tawny. The underparts of the female are tawny chestnut while males are darker and have broader black streaks on the belly. *Pternistis hildebrandti* shows marked plumage dimorphism with the males of the nominate form *hildebrandti* being greyish brown above with vermiculation, the hind and lower neck streaked black with white margins, the underparts are marked and mottled with black and white almost like in *P. natalensis*. The females have similar backs to the males but they have different underparts which are rusty. In *P. natalensis*, the hind neck mottled black and white, the back is highly vermiculated and it is greyish brown with variable black, whitish and buffish markings. The rest of the belly is buff with the upper belly to mid-belly being heavily patterned in black and buff. The patterning is concentrated on the upper part of the belly with the extreme lower belly having no or few marks. *Pternistis adspersus* is a different looking species with the nominate form *adspersus* consisting of minute vermiculation on the upperparts and with distinct black and white barring on the underparts and variably on the lower neck. It is characterized by having distinctive uniform brown and white double V- or U-patterning on the back and on the belly while the pattern on the throat is reduced to form some irregular black fleckings. The belly patterning also has distinct white shaft streaks.

What do we know about their taxonomy and phylogeny?

Profound taxonomic disagreements and confusion as reflected in Table 1.2 also affect the spurfowls and this disagreement is largely at the subspecies level and to a limited extent at the species level. Hall' (1963) monograph has made a significant contribution (Johnsgard 1988, Sibley and Monroe 1990, del Hoyo et al. 1994) towards the understanding and enhancement of our knowledge about the evolutionary relationships and distribution ranges of these birds. The monophyletic status of genus *Francolinus* as hypothesized in Hall (1963), comprises 37 traditionally recognized species which were divided among the eight putatively monophyletic groups comprising ecologically similar but largely allo- or parapatric species. Even though Hall (1963) did not partition genus *Francolinus*, she suggested that if generic division were necessary, she would have two major groups, one consisting of members that she referred to as belonging to among others, the spurfowls, encompassing members of the Bare-throated, Montane, Scaly, Vermiculated Group. Another group would be represented by the francolins (see Chapter 5).

Contrary to Roberts (1924), Peters (1934) and Mackworth-Praed and Grant (1952, 1962, 1970) and Hall (1963), Wolters (1975-82) is the one who assigned the genus *Pternistis* (Table 1.2) to all taxa which are known as 'spurfowls' today. Peters (1934) recognized the genera *Francolinus* and *Pternistis,* and like Roberts he recognized *Pternistis* for the Bare-throated species only (Table 1.2). Mackworth-Praed and Grant (1952, 1962, 1970) also recognized two genera, *Francolinus* and *Pternistis,* with *Pternistis* being assigned to members of the Bare-throated Group only (Table 1.2).

Phylogenetic difficulties have been articulated by Crowe and Crowe (1985), Crowe et al. (1986), Crowe et al. (1992), Bloomer and Crowe (1998), Crowe et al. (2006) and most recently by Forcina et al. (2012), with regard to the monophyletic status of the genus *Francolinus*, and in particular, the status of the different putative monophyletic groups recognized by Hall (1963). It is important to note that different studies used different types of characters (Table 1.4), focussed on different geographic areas of francolin distribution (Table 1.3), and made use of different methods of phylogenetic analysis. Furthermore, only the Montane Group was once recovered as monophyletic (Crowe and Crowe 1985, Crowe et al. 1992) and the Bare-throated, Vermiculated and the Scaly Groups were either found to be paraphyletic or polyphyletic (Crowe and Crowe 1985, Crowe et al. 1992, Bloomer and Crowe 1998). Based on these results, there is a dear need to test the monophyly of the species groups of spurfowls as delineated by Hall (1963) hypotheses.

What is taxonomy and how can we possibly study it?

Species and subspecies concept review

The species and subspecies concept review is as outlined as it pertains the spurfowls in Chapter 5.

Taxonomic determinations made in this chapter

Most of the spurfowl species are polytypic, encompassing more than one putative subspecies (see Table 1.2). The same criteria as outline in Chapter 5 are used here.

Objectives of the study:

- To review the taxonomic status of spurfowls.
- To re-assess the monophyletic status of the species groups as delineated by Hall (1963).

- To investigate the phylogenetic relationship between taxa within Hall's (1963) putative monophyletic groups.
- To produce a revised classification of spurfowls that takes into account the evolutionary relationships among delineated taxa.

Materials and methods

Data collection

Morpho-behavioural characters of spurfowls

Spurfowls were divided into discrete sections and scored for variation in plumage patterning and colouration (Fig. 5.7). In total, 24 organismal characters reflecting assessment of plumage/integument, colour/pattern, as well as measurements of certain qualitative and quantitative structures (Table 6.1), and several vocal characters extracted from Crowe at al. (1992) and Chapter 4 were scored (Table 6.2). Morphometric characters representing bill-length, tarsus- and spur-length were obtained using a Vernier Calliper. A stopped wing-rule and a normal ruler were used to measure wing- and tail-length, respectively. Wing-length was measured with the wing chord flattened and straightened for maximum accuracy.

Molecular characters

For within-group molecular analyses of spurfowls, 34 terminal taxa (including the two outgroup taxa) were sampled (Tables 6.3) with respect to mitochondrial Cytochrome-*b* (CYT*B* - 1143 base pairs- bp) characters. Primers used in sequencing molecular markers are listed in Table 6.4 and 6.5. The 1143 bp long CYT*B* gene was sequenced for all taxa and Genbank accession numbers are detailed in Appendix 6.1.

72% of DNA samples were toe-pads sub-sampled from museum skins. Due to the degraded state of the DNA, the CYT*B* gene for the toe-pads was sequenced in multiple fragments (six for each sample) using spurfowl-specific primers – Table 6.5).

Maps and mapping of distribution records of investigated taxa

The maps showing the distribution ranges of spurfowls (Fig. 6.1 – 6.7) were produced following the same procedure as outlined in Chapter 5.

Data analyses

Phylogenetic analyses

Two phylogenetic inference methods, parsimony and maximum likelihood with different optimality criteria were employed to generate phylogenetic hypotheses as outlined for francolins in Chapter 5. As suggested by the results in Chapter 2 (Fig. 2.1, 2.2, 2.3, 2.5, 2.6), all the data matrices were rooted on *Alectoris chukar* and *Coturnix coturnix.*

Genetic distances

Uncorrected pairwise distances (Table 6.6) were calculated in PAUP ver. 4.0b10 (Swofford 2002) and were transformed into percentages.

Results and Discussion

Separate versus combined phylogenetic analyses

The parsimony analysis for the CYT*B* data set (with 1143 bp characters, yielded 252 parsimony informative characters, 150 variable characters which are parsimony uninformative and two trees with 995 steps), for the organismal data set (with 33 characters, yielded 33 parsimony informative characters and 397 trees with 192 steps), for combined CYT*B* and organismal data set (with 1176 characters, yielded 283 parsimony informative characters, 148 variable characters which are parsimony uninformative and two trees with 1191 steps).

The systematics of Hall's species groups of spurfowls

Bare-throated Group

The Bare-throated Group consists of four traditionally recognized species, polytypic *Pternistis afer*, *P. swainsonii, P. leucoscepus*, and a monotypic species *P. rufopictus*. *Pternistis afer* is comprised of the following recognized subspecies: (*afer, harterti, nyanzae*, *böhmi*, *intercedens*, *itigi*, *cranchii*, *punctulatus*, *benguellensis*, *leucoparaeus*, *humboldtii*, *swynnertoni*, *castaneiventer*, *melanogaster*, *loangwae*, *lehmanni*, *notatus*, *krebsi*, *cunenensis*, *cooperi*); *P. swainsonii* (*swainsonii, lundazi*, *gilli*, *damarensis*, *chobiensis*); and *P. leucoscepus* (*leucoscepus*, *infuscatus, holtemülleri, keniensis*, *kilimensis, tokora, muhamed-ben-abdullah*) (Table 1.2).

All four of the analyses recovered monophyly of the Bare-throated Group, although with varying levels of support (Fig. 6.8, 6.10, 6.11). *Pternistis nobilis* joins the Bare-throated Group in the organismal tree (Fig. 6.9). These results are consistent with those of Bloomer and Crowe (1998), but contradict those of Crowe and Crowe (1985), Crowe et al. (1992), who suggested the Bare-throated group to be paraphyletic.

Within the Bare-throated Group, there is a split resulting in *P. afer*, *P. rufopictus* and *P. cranchii* grouping together in most analyses with moderate support (Fig. 6.8, 6.10, 6.11). The putative subspecies *afer* and *humboldtii* are sister to each other and they are, in turn sister to *P. rufopictus*, with *P. cranchii* being basal in this clade. *Pternistis rufopictus* is embedded within the *afer* and *cranchii* clade in the combined CYT*B*/organismal, organismal and ML trees, where it is sister to *P. afer*. The southern *P. swainsonii* is sister to the eastern *P. leucoscepus* of which the two subspecies, *P. l. leucoscepus* and *P. l. infuscatus* share a sister relationship.

Pternistis afer complex

This is the most widespread and variable of all the species within the Bare-throated Group and it has an extremely complex distribution (Fig. 6.1). *Pternistis afer* is mainly diagnosed by having red bare throat skin, bill and legs. Hall (1963) maintained that this species forms a complex which could be split into two types with intervening blocks of hybridization, the "*cranchii*" and the "*afer*" type subspecies. The "*cranchii*" subspecies includes all the subspecies of the southern Congo, northern Angola, Northern Zambia, western Tanzania, Uganda and Lake Victoria shores. These are the subspecies characterized by having vermiculated underparts, with sparse chestnut streaks on the belly. *Cranchii* has a black and grey facial pattern and it shares the least genetic distance with *afer* differing at 1% of sequence divergence (Table 6.1).

The "*afer*" subspecies forming the complex have no vermiculation and are strongly patterned in black, white and some grey on the belly and face. In the nominate *afer* subspecies the face is white and the belly is streaked in white and black, with feathers having black centres and white edges. The black and white subspecies have a broken distribution with the nominate subspecies *afer* being restricted to south western Angola along the escarpment and the Cunene basin. The underparts of the Benguella, southern Angola subspecies *benguellensis* has a mix of *afer*- and *cranchii*-type features (black, white and chestnut streaks) due to hybridization between the *afer*- and *cranchii*-type subspecies. Among the South African subspecies, the face is black and the underparts are streaked with black, white and maroon. The bird from north-central Africa (*humboldtii*) (Fig. 6.1) is diagnosed by having white jaw feathers and black belly patch. The feathers on the breast are mainly grey with black shaft streaks that contrast with those of the lower belly which form a black patch and those of the flanks that are streaked black and white. The least genetic distance exists between *humboldtii* and *afer* differing at 2% of sequence divergence. In short, what characterizes Hall's *cranchii*-type subspecies is that the belly feathers have a buff central streak vermiculated with blackish grey and margined with broad chestnut (degree of chestnut colour varies from one subspecies to the other). The belly feather of the *afer*-type subspecies have a broad greyish black central streak with buff margins (particularly in the nominate subspecies *afer*) or with a thin greyish black central streak separating the long buff parallel streaks margined with black or sometimes maroon. In Mozambique, Tanzania and south Kenya the *afer*-type subspecies have very broad black margins and a much narrower central buff to white streak. A range of additional subspecies of intermediate phenotype have been described where these three subspecies are para/sympatric, but they lack the morphological cohesion necessary for recognition.

Generally, the nucleotide sequence divergences do not reveal clear cut differences among the *P. afer* subspecies. Those from the Cunene area of western Angola are 1% sequence divergent from *cranchii,* suggesting close genetic ties between *afer* and *cranchii*, presumably due to hybridization. Indeed, the <1% genetic differences between the subspecies, *nyanzae, böhmi, itigi, intercedens* and *harterti* and *cranchii* indicate that these may be recently diverged lineages. The furthest distance that exists between the *cranchii*-type is that with *humboldtii* at 3%, subsequently followed by 3% to the South African *afer*.

The results point to a split of *P. afer* into what Hall (1963) referred to as the "*afer*-type" and the "*cranchii*-type". The *afer*-type lineage which include the nominate subspecies *afer, castaneiventer/nudicollis, lehmanni, notatus* and *krebsi* and also a group consisting of black and white subspecies that have a black belly patch as in *humboldtii* (including *swynnertoni, melanogaster, leucoparaeus* and *loangwae*). The nominate *afer* is disjunctly distributed from the South African *afer*-type allies. The black and white subspecies have a broken distribution with the nominate *afer* being restricted to the south-western part of Angola along the escarpment and the Cunene basin. The core *cranchii*-type includes *cranchii, nyanzae, harterti, intercedens, itigi* and *böhmi, cunenensis, benguellensis* and *punctulatus*. These subspecies are diagnosed by having vermiculated underparts and sparse chestnut streaks on the belly (chestnut being replaced with maroon in *harterti*, and chestnut and a tinge of black in *punctulatus*). The three subspecies, *böhmi, itigi* and *intercedens* have in addition a mixture of white and black tinge on the belly. The subspecies, *cunenensis* and *benguellensis* are included in the *cranchii*-type because they seem to be intermediate between the *cranchii*- and the *afer*-type subspecies and this is revealed in their morphological attributes, genetic affinities and in how they relate with the other forms. It is recommended that *Pternisti afer* (Müller, 1776) be broken into two subspecies, that is, *Pternistis afer afer* (Müller, 1776) which includes *castaneiventer, nudicollis, lehmanni, notatus* and *krebsi* and another subspecies *Pternistis afer humboldtii* (Peters, 1854) which include *swynnertoni, melanogaster, leucoparaeus* and *loangwae* (Appendix 6.2). There is a geographical break between *P. a. humboldtii* (the black belly patched subspecies) and the south distributed *P. a. afer* which extends to the north of the Limpopo River basin.

Pternistis rufopictus

Pternistis rufopictus is a monotypic species that occurs from the south eastern shores of Lake Victoria to the Wembere in Tanzania along the Acacia belt (Fig. 6.2). Unlike the other Bare-throated species, *P. rufopictus* has orange pink throat skin, grey brown back plumage with dark vermiculation and shaft streaks, and has brown legs. The wing coverts and the feathers on the back are edged with rufous chestnut; the breast is grey with black shaft streaks with the lower belly being richly patterned. The belly feathers have narrow central black streaks separated from rufous chestnut margins by broad buff to white streaks. It is similar to the *cranchii*-type subspecies in western Tanzania except that it has a partial buff to white jaw feathers (as in *humboldtii*), and has no vermiculation. This taxon's distribution range overlaps with that of *P. leucoscepus* in the southern parts of its distribution. The least genetic distance exists between *P. rufopictus* and *cranchii* differing at 2% of sequence divergence. It is an intriguing species that is genetically very different from *P. swainsonii* and *P. leucoscepus* (differing from both at 4%). Its phylogenetic placement (embedded within the *cranchii*/*afer* clade) points to the possibility that it could be a hybrid between the various taxa belonging to the Bare-throated Group. It is the largest species among the Bare-throated members with a mass of 779-964 g (Johnsgard 1988), has orange pink throat skin which could possibly be an indication of a mix between the red throat skin in

P. afer and a yellow throat skin in *P. leucoscepus*. Its morphologically (and the least genetic distance) places it close to the *cranchii*-type subspecies but it is phylogenetically close to the *afer*-type subspecies.

Our results provide new evidence that reveals the possibility of *P. rufopictus* being of hybrid origin. This taxon shows morphological, phylogenetic, genetic affinities and a sympatric distribution with the *cranchii*-type subspecies. Vocally, it sounds very similar to *P. leucoscepus* (details in Chapter 4) except that its call is much faster. Despite the potential of a hybrid origin, morphologically, *Pternistis rufopictus* Reichenow, 1887 still maintains its distinctiveness and has diverged sufficiently from *P. leucoscepus, P. swainsonii* and from some of the *cranchii*-type subspecies to be considered a distinct species.

Pternistis swainsonii complex

Pternistis swainsonii is a polytypic south western African (Fig. 6.2) species diagnosed by having red bare throat skin and black legs. Within *P. swainsonii* the underparts are less diagnostic and the subspecies (*swainsonii, lundazi, gilli, damarensis, chobiensis*) are characterized by having a narrow central greyish black streak separated from greyish chestnut margins by broad buff grey vermiculated streaks. The general colour *swainsonii* is grey brown and lacks the black and white streaking found on the underparts of the nominate subspecies *afer*. The feathers on the belly have drop-shaped dark brown shaft streaks which increase in size over the lower belly and flanks. The differences among *P. swainsonii* subspecies are quantitative rather than qualitative such that there are no remarkable plumage differences. Genetically, the smallest divergence is between *P. swainsonii* and *P. rufopictus* at 4% sequence divergence, although phylogenetic analyses suggest *P. swainsonii* is either the basal member of the Bare-throated Group or sister to *P. leucoscepus*. Therefore, *Pternistis swainsonii* (Smith, 1836) maintains its species status while all the subspecies, *lundazi* White 1947, *gilli* Roberts, 1932, *damarensis* Roberts, 1932 and *chobiensis* Roberts, 1932 are synonymized with it based on priority.

Pternistis leucoscepus complex

This is the most distinctive member of the Bare-throated group comprising the north eastern African (Fig. 6.2) subspecies, *leucoscepus*, *infuscatus*, *holtemülleri*, *keniensis*, *kilimensis, tokora, muhamed-ben-abdullah* with yellow bare throat skin. These subspecies have similar morphological patterns but differ in the amount of white and chestnut in the feathers of the belly. The back plumage among the different subspecies of *P leucoscepus* is diagnosed by white shaft streaks and the underparts are streaked with white and chestnut in a way that each feather has chestnut with narrow white edges and a triangular white patch at the tip, tapering up the shaft. The primaries have a conspicuous white patch which is visible during flight (Hall 1963). The northern subspecies *infuscatus* (differing at 1% sequence divergence from the nominate subspecies) differs from *leucoscepus* in having more chestnut than white on the underparts contrary to the dominant white over chestnut in *leucoscepus.* Genetically, *P. leucoscepus* is close to *P. swainsonii*, differing by 5% sequence divergence.

The morphology and genetic distance point to two subspecies. It is recommended that two subspecies should be recognized: *Pternistis leucoscepus leucoscepus* (Gray, 1867) and *Pternistis l. infuscatus* Cabanis, 1868. The rest of the subspecies (*holtemülleri, keniensis, kilimensis, tokora*, *muhamed-ben-abdullah*) should be synonymized with *P. l. infuscatus* Cabanis, 1868 (Appendix 6.2).

Vermiculated Group

The Vermiculated Group comprises nine traditionally recognized species which are *Pternistis hartlaubi*, *P. bicalcaratus, P. icterorhynchus, P. clappertoni*, *P. hildebrandti*, *P. natalensis*, *P. harwoodi*, *P. adspersus* and *P. capensis*. The putative subspecies are as follows: for *P. hartlaubi* (*hartlaubi*, *crypticus*, *bradfieldi*, *ovambensis*); *P. adspersus* (*adspersus, kalahari*, *mesicus*); *P. natalensis* (*natalensis, neavei*); *P. hildebrandti* (*hildebrandti, altumi*, *helleri*, *fischeri*, *johnstoni*, *grotei*); *P. bicalcaratus (bicalcaratus*), *ogilvie-grantii*, *ayesha*, *adamauae*, *thornei*); *P. icterorhynchus* (*icterorhynchus*, *dybowski*, *ugandensis*, *emini*) and *P. clappertoni* (*clappertoni*, *sharpii*, *heuglini*, *gedgii*, *nigrosquamatus, konigseggi*, *testis*, *cavei*) (Table 1.2).

In comparing all the phylogenetic trees (Fig. 6.8, 6.9, 6.10, 6.11), the position of *P. hartlaubi* is consistently basal to all the other spurfowl taxa in the parsimony trees except in the organismal parsimony tree where it forms a sister relationship with the Montane Group member *P. camerunensis* (Fig. 6.9). In the ML (Fig. 6.11) tree *P. hartlaubi* is embedded within the Montane group with an unresolved branch. These results are in agreement with those in Bloomer and Crowe (1998). Also Crowe et al. (1992) hinted at the uncertain genetic relationships between *P. hartlaubi* and the other spurfowls and found that it was morphometrically the most distinct spurfowl and speculated that this taxon shared morphological similarities to the Old World quails. Bloomer and Crowe (1998) concluded that it represents a very early offshoot from the partridge-francolin lineage.

The other eight species split themselves geographically into the northern (*P. bicalcaratus, P. icterorhynchus, P. clappertoni, P. harwoodi*) and southern (*P. capensis, P. natalensis, P, hildebrandti, P. adspersus*) Vermiculated species in all the trees (Fig. 5.8, 5.9, 5.10, 5.11). The northern Vermiculated clade emerges to be sister to the Bare-throated Group in the combined CYT*B*/organismal (Fig. 6.8) and organismal (Fig. 6.9) tree except in the CYT*B* (Fig. 6.10) tree where it is only members of the *P. clappertoni* complex and *P. harwoodi* that group with the Bare-throated Group while members of the *P. bicalcaratus* complex and *P. icterorhynchus* form a paraphyletic clade at the basal parts of the tree. The northern Vermiculated taxa are paraphyletic in the ML tree. Surprisingly *P. harwoodi* is embedded within *P. clappertoni* complex forming a sister relationship with *P. c. sharpii* with 90% and 99 BS in the combined CYT*B*/organismal (Fig. 6.8), organismal (Fig. 6.9) and CYT*B* (Fig. 6.10) trees. *Pternistis harwoodi* and *P. clappertoni* complex are outliers in the spurfowl clade in the ML tree, The sister relationship between the northern Vemiculated and the Bare-throated clades as consistently recovered in this study, contrasts the finding in Bloomer and Crowe (1998) who found that the southern Vermiculated taxa and not the northern Vermiculated taxa were consistently grouping with each other. This kind of relationship is supported in only one analysis (CYT*B* – Fig. 6.10) in this study even though the Bare-throated clade is part of a large clade which incorporates two species from the northern Vermiculated clade and also the two Montane sister species (*P. jacksoni* and *P. swierstrai*) (CYT*B* – Fig. 6.10). The southern Vermiculated taxa (*P. capensis, P. natalensis, P, hildebrandti, P. adspersus*) form a monophyletic clade only in the combined CYT*B*/organismal (Fig. 5.8), CYT*B* (Fig. 6.10) and Fig. 6.11 tree (64%, 88%, 95% BS respectively). *Pternistis capensis* is an outlier in the southern Vermiculated clade forming a paraphyletic relationship with *P. adspersus*, *P. natalensis* and *P. hildebrandti with P. natalensis* being closely related to the two sister subspecies, *hildebrandti* and *fischeri* (98% BS - CYT*B*/organismal (Fig. 6.8 tree). *Pternistis capensis* emerges as a sister taxon to *P. adspersus* in CYT*B* (Fig. 6.10) and ML (Fig. 6.11) tree, but this relationship received no support. In the organismal (Fig. 6.9) tree, *P. natalensis* is sister to *P. adspersus* but with no nodal support. It is very clear that the Vermiculated Group is polyphyletic just as found in Crowe and Crowe (1985), Crowe et al. (1992) and Bloomer and Crowe (1998). However, the relationships among taxa within the northern Vermiculated clade appear consistent unlike among taxa within the southern Vermiculated clade; the position of *P. hartlaubi* as a basal taxon seems consistent.

Pternistis bicalcaratus complex

Pternistis bicalcaratus is distributed from Senegambia to the Central African Republic, except for one taxon, ayesha, that occurs in isolation in Morocco (Fig. 6.5). All the recognized subspecies of *P. bicalcaratus* are similarly patterned above and below differing in the degree of colouration, patterning, vermiculation and the size of the arrow-shaped buff marks in the centre of the belly feathers. The nominate subspecies *bicalcaratus* is paler with a more rufous crown, vermiculated with V-patterning and slightly rufous on the lower neck. It has buff underparts distinctly and heavily streaked with blackish and chestnut with small arrow-shaped buff marks on most belly feathers. The heavily patterned *ayesha* (from Morocco – not mapped) looks very similar to *bicalcaratus*, but is faintly vermiculated and slightly more rufous on the lower neck, with small arrow-shaped buff marks on belly feathers. The darkest subspecies is *adamauae* (with 2% sequence divergence from *bicalcaratus*) with very little rufous on lower neck, and the underparts are more buff with extremely reduced chestnut and have larger arrow-shaped buff marks in centre of belly feathers. The least genetic distance exists between *bicalcaratus* and *P. icterorhynchus* differing at 3% of sequence divergence. It is apparent that *P. bicalcaratus* represents a cline with regard to the overall colouration of back plumage of the various subspecies and the patterning of plumage on the belly even though these subspecies are not strikingly different. The subspecies *bicalcaratus* is heavily patterned like *thornei* but the two differ in that *bicalcaratus* is less dark compared to *thornei*. *Adamauae* and *Ogilvie-granti* are the darkest subspecies but with less patterning.

The morphological and genetic evidence reveal that *adamauae* is distinct from *bicalcaratus* suggesting that there may be two subspecies within the *P. bicalcaratus* complex. This should be *Pternistis bicalcaratus bicalcaratus* (Linnaeus, 1766) which should include *ayesha, thornei* and *ogilvie-granti* and *Pternistis bicalcaratus adamauae* Neumann, 1915. It is possible that *ogilvie-granti* could well be made a synonym of *P. b. adamauae* but this decision could not be taken in the absence of genetic evidence.

Pternistis clappertoni complex

This species has its distribution range covering Cameroon, Central African Republic, Chad, Eritrea, Ethiopia, Mali, Mauritania, Niger, Nigeria, Sudan, and Uganda (Fig. 6.5). Within *P. clappertoni*, the nominate subspecies *clappertoni* is greyish brown above with barring on the flight feathers. This subspecies is buff below with black to brownish marks. The hind and lower neck have U-patterning as in *P. icterorhynchus.* The subspecies *sharpii* (which differs at 1% sequence divergence *clappertoni*) has marks on the belly which look streakier than those in *clappertoni* in a buffy white background with the breast being similarly V-patterned extending on to the back. The primaries are barred as in the nominate subspecies. It is genetically close to *P. harwoodi* differing at 1% of sequence divergence.

The major plumage differences lie in the colour of the background on the belly and the shape of the marks on the belly. There is very little genetic divergence between the nominate *clappertoni* and *sharpii* and *nigrosquamatus.* Therefore, two subspecies are recognized which are *Pternistis clappertoni clappertoni* (Children & Vigors, 1826) and *P. c. sharpii* Ogilvie-Grant, 1892. *Pternistis c. clappertoni* should include *heuglini*, *gedgii* and *cavei* while *konigseggi*, *nigrosquamatus* and *testis* should be synonymized with *P. c. sharpii*.

Pternistis icterorhynchus complex

Pternistis icterorhynchus is distributed in the Central African Republic, Democratic Republic of the Congo, Sudan, and Uganda (Fig. 6.5). It consists of four putative subspecies, *icterorhynchus*, *dybowski*, *ugandensis* and *emini* mainly diagnosed by having distinct U-patterning on the lower neck and more vermiculation on the back than other vermiculated taxa. The underparts are buff with dark brown markings. It shares the least genetic distance with *bicalcaratus* differing at 3% of sequence divergence. There was no success in sequencing all the subspecies within *P. icterorhynchus*.

Morphologically, there are no striking differences between *icterorhynchus* and *emini* except that *emini* is less patterned on the belly as opposed to *icterorhynchus* which is extensively patterned whereas *ugandensis* has some chestnut on the flanks. In the absence of genetic data, no subspecies are recognized.

Pternistis harwoodi

This is a poorly known species from the Blue Nile gorges (Fig. 6.5), the male bird which was examined is grey speckled and finely barred with blackish and buff above. The hind and lower neck, sides of face, and throat are speckled with black and white. It has irregular double-V patterning on the belly which tends to be scattered just on the lower extreme of the belly on the buff background. Pternistis harwoodi shares the least genetic distance with *sharpii* differing at 1% of sequence divergence.

Phylogenetically, *P. harwoodi* and *sharpii* are sister taxa and also share a sympatric distribution. The two are not similar morphologically except that they are both barely patterned distally on the belly. This is a case where possibily with time morphology and DNA will align. While *Pternistis harwoodi* Blundell & Lovat, 1899 is recognized as a valid species, it could be concluded from the above evidence that *P. harwoodi* could tentatively be a well-marked subspecies of *P. clappertoni* or a linking form through *sharpii*.

Pternistis hildebrandti complex

Pternistis hildebrandti, a species distributed in central and western Kenya, extending south through Tanzania to south eastern Zaire, northeastern Zambia and Malawi (Fig. 6.6), shows marked plumage dimorphism with the males of the nominate subspecies *hildebrandti* being greyish brown above with vermiculation, the hind and lower neck streaked black with white margins, the underparts are marked and mottled with black and white almost like in *P. natalensis*. The females have similar backs to the males but they have different underparts which are rusty. The subspecies *johnstoni* (differing at 1% of sequence divergence) is like *hildebrandti*, but differs in that the female has the nape, hind neck and breast uniform with the rest of the plumage. It shares the least genetic distance with *P. natalensis* differing at 1% of sequence divergence.

The genetic and morphological evidence support a split of *P. hildebrandti* into two subspecies, that is *Pternistis hildebrandti hildebrandti* Cabanis 1878 and *Pternistis hildebrandti fischeri* Reichenow, 1887. The subspecies, *altumi,* 1884 and *helleri* are synonymized with *P. h. hildebrandti,* whereas *johnstoni* and *grotei* are synonymized with *P. h. fischeri*.

Pternistis natalensis complex

Pternistis natalensis is a species complex with the putative subspecies *natalensis* and *neavei* from south eastern Africa (Fig. 6.6). The hind neck is mottled black and white, the back is highly vermiculated and it is greyish brown with variable black, whitish and buffish markings. The rest of the belly is buff with the upper belly to mid-belly being heavily patterned in black and buff. The patterning is concentrated on the upper part of the belly with the extreme lower belly having no or few marks. *Pternistis natalensis* shares the least genetic distance with *P. hildebrandti* differing at 1% of sequence divergence. However, it is particularly close to *altumi*, *fischeri* and *johnstoni* differing at 1%. The morphological similarities between *P. natalensis* and male *P. hildebrandti* could have either been a possibility for *P. natalensis* and *P. hildebrandti* interbreeding in the southeast region or that *P. natalensis* and *P. hildebrandti* could have been the same taxon that got broken up with some changing in appearance but not genetically. Based on the above-mentioned evidence and the absence of genetic data for *neavei* and *thamnobium*, the decision would be to recognize *Pternistis natalensis* Smith 1833 as a species and synonymize *neavei* with it.

Pternistis adspersus complex

Pternistis adspersus consists of three putative subspecies (*adspersus, kalahari, mesicus*) and it is distributed in Namibia and Botswana (Fig. 6.6). It is a very different looking species with the overall plumage dominated by minute vermiculation on the upperparts and with distinct black and white barring on the underparts and variably on the lower neck. This species shares the least genetic distance with *P. capensis* differing at 4% of sequence divergence. The subspecies, *adspersus* and *kalahari* are inseparable morphologically. The specimens of *mesicus* were not examined and no description was provided in the literature in which it was recognized. This study acknowledges that *Pternistis adspersus* Waterhouse 1838 is a valid species, and make no taxonomic decision on the status of other subspecies.

Pternistis capensis

Pternistis capensis is an undisputed monotypic species which is endemic to the southwestern Cape of South Africa (Fig. 6.6). It is the largest vermiculated species (males weighing ~900 g with females being ~600 g – Johnsgard 1988) and is endemic to the south western part of South Africa (the Cape) (Fig. 6.6). It is characterized by having distinctive uniform brown and white double V- or U-patterning on the back and on the belly while the pattern on the throat is reduced to form some irregular black flecking. The belly patterning also has distinct white shaft streaks. This species shares the least genetic distance with *P. adspersus* at 4% sequence divergence.

Pternistis capensis (Gmelin, 1789) is acknowledged as a valid species due to its morphological and genetic differentiation (4-5%) compared to *P. natalensis, P. adspersus* and *P. hildebrandti* and also its phylogenetic position.

Pternistis hartlaubi complex

Pternistis hartlaubi occupies granite and sandstone outcrops surrounded by semi-desert steppe and is confined to northern Namibia and extreme south western Angola (Fig. 6.7). It is comprised of the subspecies, *hartlaubi*, *bradfieldi*, *crypticus* and *ovambensis*. Is one of the spurfowl species that exhibits striking plumage dimorphism with the difference in the subspecies being mainly in the degree of colouration. The male *hartlaubi* has a buff throat with black streaks that continues to the sides of neck through to the hind neck and to the breast. The belly of male birds is like the underparts of the females which is pale tawny. The sides of face and chin and belly of females is pale tawny. It shares the least genetic distance with *P. ochropectus* differing at 9% of sequence divergence.

There is limited genetic and morphological evidence for the separation of *hartlaubi* and *crypticus* and therefore, only one taxon is recognized, *Pternistis hartlaubi* Bocage 1869 and *bradfieldi*, *crypticus* and *ovambensis* are synonymized with it. Nonetheless, *P. hartlaubi* is clearly an ancient African paleoendemic.

The Montane Group

The Montane Group encompasses seven species, *P. erckelii*, *P. ochropectus*, *P. castaneicollis*, *P. jacksoni*, *P. nobilis*, *P. camerunensis* and *P. swierstrai*. The putative subspecies are as follows: within *Pternistis erckelii* (*erckelii*, *pentoni); P. nobilisis* (*nobilis, chapini*); *P. castaneicollis* (*castaneicollis, bottegi*, *gofanus, ogoensis, kaffanus, atrifrons*; *P. jacksoni* (*jacksoni*, *pollenorum*, *gurae*) (Table 1.2).

The Montane Group is polyphyletic in all the analyses (Fig. 6.8, 6.9, 6.10, 6.11) with all the Montane taxa appearing at the base of the tree. This is in contrast with

Crowe and Crowe (1985) and Crowe et al. (1992) wherein the monophyletic status was certain. Despite the Montane Group being polyphyletic, the north eastern species (*P. erckelii, P. ochropectus, P. castaneicollis*) form a monophyletic clade in all the analyses (Fig. 6.8, 6.9, 6.10, 6.11). *Pternistis ochropectus* is consistently sister to *P. erckelii*, and *P. nobilis* is consistently sister to *P. camerunensis*. The phylogenetic position of *Pternistis swierstrai* and *P. jacksoni* is uncertain in all the trees. The evolutionary history of the Montane spurfowls still needs further scrutiny in line with the challenge that this study rejects Hall's (1963) speculation that they form a monophyletic assemblage. Further, she also postulated that *P. swierstrai* and *P. camerunensis* were the first species to be isolated from the ancestral stocks of the other species. This study consistently reveals that *P. camerunensis* and *P. nobilis* were isolated first.

Pternistis ochropectus

This is a monotypic species endemic to the evergreen forest of Djibouti (Fig. 6.3). A closer analysis of the plumage patterning on the belly feathers of *P. ochropectus*, *P. erckelii* and *P. castaneicollis* renders them almost similar. They have a broad buff central streak constricted in the middle and expanded distally into a tear drop, margined by a greyish black U-shaped streak. This species shares the least genetic distance with *P. erckelii* differing at 3% of sequence divergence. This study acknowledges *Pternistis ochropectus* (Dorst & Jouanin, 1952) to be a valid species.

Pternistis jacksoni complex

This is a large species endemic to Kenya (Fig. 6.3) with a body mass ranging from ~1130-1160 g (Johnsgard 1988). It encompasses three subspecies, *jacksoni, pollenorum* and *gurae.* It has a buff throat and greyish lower neck with the proximal part of the lower neck being similarly patterned to the rest of belly. The lower neck feathers are chestnut-coloured edged with buffish to white, but the degree of chestnut and buff and white varies. It shares the least genetic distance with *P. griseostriatus* with which it differs at 5% of sequence divergence.

There is a possibility that there could be two entities (possibly subspecies) within *P. jacksoni* i.e., *jacksoni* and *pollenorum* being one entity and *gurae* being another entity based only on morphology. However, in the absence of molecular evidence for *pollenorum* and *gurae*, our decision is speculation only and hence only *Pternistis jacksoni* O. Grant, 1891 can be acknowledged as a valid species.

Pternistis nobilis complex

This species comprises two putative subspecies, *nobilis* and *chapini* and is distributed in the mountain forests of the eastern Democratic Republic of the Congo, southwest Uganda and borders between Burundi and Rwanda (Fig. 6.3). The head, uppertail coverts and primaries are grey brown. The wing coverts and the lower neck are deep maroon, with light grey scalloping on the lower neck. The throat colour is buff white with the rest of the belly being chestnut with grey edges replacing the broad buff to white edges found in the nominate *jacksoni*. It is genetically close to *P. camerunensis* differing at 7% of sequence divergence.

The morphological difference observed between *nobilis* and *chapini* are quantitative with regard to colouration and hence only one species is recognized in the absence of molecular evidence even though the two subspecies are found on different mountains. *Pternistis nobilis* Reichenow, 1908 remains a valid species and *chapini* should be synonymized with it pending further investigation.

Pternistis erckelii complex

Pternistis erckelii occurs in the Ethiopian massif (Fig. 6.3) and it is the largest spurfowl (males have a maximum mass of ~1590 g, with females having a maximum mass of ~1136 g) (Johnsgard 1988), and is characterized by its black forehead, eye-stripe and chestnut crown. The lower neck is grey like the upper belly, but has greyish brown margins and a thin central buff streak whereas the upper belly feathers have central greyish black streaks. The lower belly feathers consist of a broad buff central streak constricted in the middle and expanded distally into a tear drop, margined with rufous. It shares the least genetic distance with *P. ochropectus* at 3% of sequence divergence.

The specimens of *pentoni* were not available for examination. Irrespective of the quantitative differences presented in literature, the recommendation is that *pentoni* should in the meantime be included in *Pternistis erckelii* (Rüppell, 1835).

Pternistis castaneicollis complex

Pternistis castaneicollis is distributed in Ethiopia, Somalia, and possibly Kenya (Fig. 6.3). The subspecies, *castaneicollis, bottegi, gofanus, ogoensis, kaffanus* and *atrifrons* are recognized within *P. castaneicollis* (Table 1.2). *Pternistis castaneicollis* is generally similar to *P. erckelii* with the belly feathers being made up of a broad buff central streak which is constricted in the middle and expanded distally into a tear drop, margined with rufous. The eastern Ethiopian subspecies have an extensive double-patterning on the back with wing coverts and the upper belly being clearly defined in black and white, with some ochre and chestnut. The subspecies *atrifrons* from southern Ethiopia is quite different from the other subspecies with a lesser degree of colouration and patterning on the belly. The less defined belly patterning is in brown and buff, and the throat and the belly cream instead of white as in other subspecies. Despite its distinct morphology, *atrifrons* was found to have similar voice, habits and environment (Benson 1945) to other subspecies of *P. castaneicollis*. It shares the least genetic distance with *P. camerunensis* differing at 8% of sequence divergence.

The subspecies, *ogoensis*, *bottegi*, *gofanus* and *kaffanus* are morphologically similar to the nominate *castaneicollis*. The southern Ethiopian subspecies, *atrifrons* is the one that is quite distinct in being less coloured and patterned on the belly as well as having the well-defined patterning and rich colour on the back. Despite the similar voice, habit and habitat that *atrifrons* shares with other *P. castaneicollis* subspecies (Hall 1963), it would therefore be crucial to include its DNA in the analysis in order to gain insight into its phylogenetic placement given its distinct morphology. It could be that *atrifrons* is a valid species sister *to P. castaneicollis* Salvadori, 1888 which remains a valid species.

Pternistis camerunensis

This is a monotypic, sexually dimorphic species which is endemic to Mount Cameroon (Fig. 6.3). Its taxonomic status as a monotypic species has never been disputed. The male *P. camerunensis* has the back (strictly excluding the lower neck) and the wings coloured rich dark brown, crown grey brown and the rest of the belly and the lower neck are plain grey with some black feather centres (Hall 1963). The upper- and underparts of the female are mottled and vermiculated with black, dark brown and buff and some off-white U- to V-patterning on belly and U-patterning on the lower neck. It shares the least genetic distance with *P. nobilis* differing at 7% of sequence divergence. *Pternistis camerunensis* Alexander, 1909 is acknowledged as a valid species.

Pternistis swierstrai

This monotypic species is endemic to the patches of evergreen forest in the highlands and along the escarpment of Angola (Fig. 6.3). It is slightly sexually dimorphic in its plumage and it is very different and isolated from the other members of the group. Male and female birds have white eye stripes not found in any other member of the Montane Group. The male breast is black contrasting with the buff throat while the belly consists of broad buff central streaks with blackish margins. The females were not examined and their underparts are according to Hall (1963), buff with irregular black or brown blotches or bars which are concentrated on the upper belly to form a mottled band and are sparse in the centre of the belly. It shares the least genetic distance with *afer* differing at 6% of sequence divergence.

Scaly Group

The Scaly Group comprises three allopatric species, *P. ahantensis*, *P. squamatus*, *P. griseostriatus*, with subspecies, *P. squamatus* (*squamatus, maranensis*, *schuetti*, *usambarae*, *uzungwensis*, *doni*, *zappeyi*, *tetraoninus*, *chyuluensis*) and *P. ahantensis* (*ahantensis*, *hopkinsoni*) being recognized (Table 1.2). The Scaly taxa are paraphyletic, in which case *P. squamatus* and *P. griseostriatus* have close phylogenetic association (Fig. 6.8, 6.10, 6.11). *Squamatus* and *schuetti* appear as sister taxa in some analyses.

(Fig. 6.8, 6.9), and *schuetti* is sister to *P. griseostriatus* others (Fig. 6.10, 6.11). Generally, the phylogenetic relationship of the Scaly Group members is unresolved.

The general finding is that there are no morphological characters that link up the three species within the group except that they all have some degree of scaliness. There is no qualitative break in characters. There is a cline from the west African *P. ahantensis* which has clearly defined patterning through to north, east and central African *P. squamatus* (moderately patterned) and down to southwestern African *P. griseostriatus* which has less defined patterning. *Pternistis griseostriatus* is likely to represent the end of the cline. There is a large genetic jump of 4% between *P. squamatus* and *P. ahantensis* and 5% between *P. squamatus* and *P. griseostriatus*.

Pternistis squamatus complex

Pternistis squamatus, a species distributed in south central Nigeria, south eastern to western Zaire and east to Uganda, south Sudan and south western Ethiopia, then south to east Zaire, north eastern Tanzania and extreme northern Malawi (Fig. 6.4), consists of the following subspecies, *squamatus, maranensis, schuetti, usambarae, uzungwensis, doni*, *zappeyi*, *tetraoninus*, *chyuluensis* (Table 1.2). *Pternistis squamatus* is not sexually dimorphic, although female birds tend to be less strikingly vermiculated. The nominate subspecies *squamatus* is characterized by having indistinctly vermiculated upperparts with faint U-patterning on the lower neck and the feathers have blackish centres tinged with red-brown. The belly is plain brown with a scaly pattern and ill-defined dark shaft streaks margined buff. *Schuetti* (with 1% sequence divergence) differs from *squamatus* in being less vermiculated with the pattern on the lower neck being more clearly defined and with more red-brown at the centre of feathers. The edges of the darker belly feathers have buff edges giving the streaky effect. It shares the least genetic distance with *P. griseostriatus* differing at 3% of sequence divergence. The two subspecies, *schuetti* and *maranensis* have slightly diverged genetically and morphologically from *squamatus* and warrants only subspecies status for the former. The genetic divergence between *schuetti* and *maranensis* is just above 1% and the two subspecies differ in the degree of colouration. Therefore, on the basis of the marked genetic distances and different morphology, two subspecies are recognized within *P. squamatus*, that is, *Pternistis squamatus squamatus* Cassin, 1857 and *Pternistis squamatus schuetti* Cabanis, 1880. *Pternistis s. schuetti* will include *maranensis*, *chyuluensis*, *doni*, *usambarae*, *uzungwensis*, *zappeyi* and *tetraoninus*.

Pternistis ahantensis complex

This species occurs in lowlands of Senegambia to south western Nigeria (Fig. 6.4) and it comprises two putative subspecies, *ahantensis* and *hopkinsoni*. The belly feathers are richly coloured and streaked with dark brown chestnut edged buff while the upperparts are vermiculated with some white U-patterning (indistinct on the back but very distinct on the lower neck). It shares the least genetic distance with *P. squamatus* from which it differs with 4% of sequence divergence. The two subspecies, *ahantensis* and *hopkinsoni* show little morphological differentiation. *Pternistis ahantensis* Temminck, 1854 remains a valid species.

Pternistis griseostriatus

Pternistis griseostriatus is an indistinctive, monotypic species endemic to Angola (Fig. 6.4). The lower neck feathers and wing coverts are chestnut broadly vermiculated as in

P. s. squamatus and *P. a. ahantensis*, but the belly is plain and the upper belly and flank feathers are chestnut and edged with greyish or creamy buff. It shares the least genetic distance with *squamatus* differing at 3% of sequence divergence. This study acknowledges *Pternistis griseostriatus* O. Grant 1890 as a valid species due to its marked genetic distinctiveness (4%) compared to *P. squamatus* and *P. ahantensis*.

Conclusions

The definition of species and subspecies will continue to be contested as more and more data are accumulated, analytical methods continue to be improved and people have freedom to think and present their own views. The good side of this will be that there will be great improvement on how species and subspecies are defined and delimited. The conflict exists between characters from different sources possibly because of hybridization and incomplete lineage sorting and these conditions make taxonomic delineation of spurfowls challenging. Despite the striking diversity within the group, all spurfowls share a single evolutionary path. However, among all of Hall's putative monophyletic species groups, the Bare-throated Group is the only one to be recovered as monophyletic while others remain largely paraphyletic.

The number of species among spurfowls did not increase significantly; *P. afer* is the only species that was split into two *P. afer* and *P. cranchii*. The number of subspecies is reduced (Appendix 6.2). The recommendation is that phylogeographic studies should be conducted for the various species complexes and fresh DNA samples for all the other known subspecies need to be collected and sequenced so that sound taxonomic decisions can be made.

Table and Figures

Table 6.1. Characters and character states scored and used for phylogenetic analysis of spurfowls.

1. **Crown margins:** unmargined = 0, grey = 1, buff = 2, grey brown = 3
2. **Nares:** black = 1, chestnut = 2, grey brown = 3, buff or white =4 buff = 4, white = 5
3. **Hindneck patterning:** unpatterned = 0, mottled = 1, streaked = 2
4. **Hindneck base colour:** grey brown = 1, grey black = 2, grey chestnut = 3 rufous brown = 4, black = 5
5. **Hindneck margins:** unmargined = 0, grey =1, buff = 2, grey brown = 3
6. **Lower neck patterning:** streaked = 1, mottled = 2, barred = 3

7-10. **Back plumage:** absent = 0, streaked = 1 (7), mottled = 1 (8), vermiculated = 1 (9), barred =1 (10)

11-13. multistate **Uppertail coverts**: absent = 0, barred = 1 (11), vermiculated = 1 (12), streaked = 1 (13)

14. **Throat**: feathered = 1, yellow skin = 2, orange = 3, red = 4

15-18. multistate **Undertail coverts**: absent = 0, barred = 1 (15), streaked = 1 (16), vermiculated = 1 (17), mottled = 1 (18)

19. **Bare skin around eye:** none = 0, red = 1, yellow = 2
20. **Leg colour:** yellow = 1, red = 2, orange red = 3, orange = 4, olive green = 5, orange yellow = 6, black = 7
21. **Number of spurs:** one = 1, two = 2
22. **Wing length** (males)**:** <160 mm = 1, <180 mm =2, <200 = 3, >200 =4
23. **Culmen length/wing length:** <.16 = 1, <.20 = 2, >= .20 =3
24. **Tail length/ wing length:** <.54 = 1, >= .54 = 2
25. **Sexual dimorphism** (plumage)**:** absent = 0, present = 1
26. **Sexual dimorphism** (wing length)**:** female >= .9 of male = 0, < .9 = 1
27. **Vocalization strophe duration**: <= 0.3 sec = 1, > 0.3 < 0.6 = 2, > 0.6 = 3
28. **Number of elements:** 1 = 1, 2 = 2, >2 = 3
29. **Inter-element interval:** absent or indistinct = 1, distinct = 2
30. **Cackle-trill:** absent = 0, present = 1

31-32. multistate **Strophe character:** tonal = 0 (31), trill = 1 (32)

33. **'KO-WAAARK' advertisement call:** absent = 0, present = 1

Table 6.2. Organismal character matrix used in phylogenetic analysis. ? indicates information which could not be sourced.

	Character no.																																
Taxon	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**
Pternistis hartlaubi	0	1	1	1	0	1	1	1	0	0	1	1	0	1	1	0	0	0	0	1	2	1	3	2	1	0	3	3	2	0	1	1	0
Pternistis camerunensis	0	1	1	2	0	2	0	1	1	0	1	1	0	1	1	0	0	0	1	2	2	2	1	1	1	0	2	2	2	0	1	0	0
Pternistis nobilis	0	1	1	2	0	1	1	0	0	0	0	0	0	1	0	0	0	0	1	2	2	3	1	1	0	0	2	2	2	0	1	1	1
Pternistis erckelii	0	2	1	3	0	1	0	0	1	0	0	0	0	1	0	1	1	0	0	2	2	4	1	2	0	1	3	3	2	1	0	1	0
Pternistis swierstrai	0	1	0	5	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	2	2	3	2	2	1	0	3	3	2	1	0	1	0
Pternistis castaneicollis	0	1	0	3	0	1	1	0	1	0	0	0	0	1	0	1	0	0	1	2	2	4	1	2	0	1	3	3	2	1	0	1	0
Pternistis c. atrifrons	0	1	2	1	2	1	1	0	1	0	0	0	0	1	0	1	0	0	1	2	2	4	1	2	0	1	3	3	2	1	0	1	0
Pternistis ochropectus	0	2	1	3	0	1	0	0	1	0	0	0	0	1	0	1	1	0	0	2	2	4	1	2	0	1	2	2	2	0	1	0	0
Pternistis jacksoni	0	1	0	3	0	1	1	0	1	0	0	0	0	1	0	1	0	0	0	2	2	4	1	2	0	0	?	?	?	?	?	?	0
Pternistis squamatus	0	3	0	1	0	2	0	1	1	0	1	1	0	1	0	0	0	1	0	3	2	2	1	2	0	0	3	3	2	0	1	1	0
Pternistis s. schuetti	0	3	1	1	0	2	0	1	1	0	1	1	0	1	0	1	0	0	0	3	2	2	1	2	0	0	3	3	2	0	1	1	0
Pternistis ahantensis	0	4	0	1	0	1	1	0	1	0	0	1	0	1	0	1	1	0	0	4	2	2	1	2	0	0	2	2	2	0	1	1	0
Pternistis griseostriatus	0	3	0	1	0	1	1	0	1	1	1	0	0	1	0	0	0	0	0	3	1	1	1	2	0	0	3	1	1	0	0	1	0
Pternistis b. bicalcaratus	0	1	1	4	0	1	1	0	1	0	1	1	0	1	0	1	0	0	0	5	2	2	2	1	0	0	1	2	1	0	0	1	0
Pternistis b. ayesha	0	1	1	4	0	1	1	0	1	0	1	1	0	1	0	1	0	0	0	5	2	2	2	1	0	0	1	2	1	0	0	1	0
Pternistis b. adamauae	0	1	1	2	0	2	1	0	1	0	1	1	0	1	0	1	0	0	0	5	2	2	2	1	0	0	1	2	1	0	0	1	0
Pternistis icterorhynchus	0	1	1	2	0	1	0	0	1	1	1	1	0	1	1	0	0	0	2	6	2	2	2	1	0	0	1	2	1	0	0	1	0
Pternistis clappertoni	0	1	1	4	0	1	1	0	0	0	1	1	0	1	0	1	0	0	1	2	2	2	2	1	0	0	2	2	1	0	0	1	0
Pternistis c. sharpii	0	1	0	1	0	1	1	0	0	0	1	1	0	1	0	1	0	0	1	2	2	2	2	1	0	0	2	2	1	0	0	1	0
Pternistis harwoodi	0	1	1	4	0	1	1	0	0	0	1	1	0	1	0	1	0	0	1	2	2	2	2	2	?	1	2	2	1	0	0	1	0
Pternistis h. hildebrandti	1	1	2	2	1	1	0	0	1	1	1	1	0	1	1	0	1	0	0	2	2	2	1	2	1	0	1	3	2	0	0	1	0
Pternistis h. fischeri	1	1	2	2	1	1	0	0	1	1	1	1	0	1	1	0	1	0	0	2	2	2	1	2	1	0	1	3	2	0	0	1	0
Pternistis natalensis	0	3	0	1	0	1	0	0	1	1	1	1	0	1	1	0	0	0	0	2	1	2	1	2	0	0	2	3	2	0	1	1	0
Pternistis adspersus	0	1	0	2	0	3	0	0	0	1	1	0	0	1	1	0	0	0	2	2	1	2	1	2	0	0	3	3	2	1	1	1	0
Pternistis capensis	2	3	2	1	2	1	1	0	0	0	1	0	0	1	0	1	0	0	0	2	2	4	1	2	0	0	3	3	2	0	1	0	0
Pternistis leucoscepus	3	4	2	1	3	1	1	0	1	0	1	1	0	2	0	0	1	0	1	7	2	3	2	1	0	0	3	2	2	0	0	1	1
Pternistis l. infuscatus	0	1	2	1	0	1	0	0	1	0	1	1	0	2	0	0	1	0	1	7	2	3	2	1	0	0	3	2	2	0	0	1	1
Pternistis rufopictus	0	3	0	1	0	1	1	0	1	0	0	1	1	3	0	1	0	0	1	7	2	4	2	1	0	0	2	2	2	0	0	1	1
Pternistis afer afer	3	5	2	1	0	1	1	0	0	0	0	0	0	4	0	1	0	0	1	2	2	3	2	1	0	0	2	2	2	0	1	1	1
Pternistis cranchii	0	1	0	1	0	1	1	0	1	0	0	1	0	4	0	1	1	0	1	2	2	3	2	1	0	0	2	2	2	0	1	1	1
Pternistis afer humboldtii	3	4	2	1	3	1	1	0	0	0	0	0	0	4	0	0	0	0	1	2	2	3	2	1	0	0	2	2	2	0	1	1	1
Pternistis swainsonii	3	3	2	1	3	1	1	0	1	0	0	1	1	4	1	0	1	0	1	7	1	3	2	1	0	0	3	2	2	0	1	1	1

Table 6.3. Taxa for which DNA sequences were generated. AMNH stands for American Museum of Natural History, FHHM = Franch Natural Histiry Museum, TM = Transvaal Museum, BM = British Museum - Natural History Museum at Tring, SAM = Iziko Museums of Cape Town (Natural History), PFIAO = Percy FitzPatrick Institute of African Ornithology, TMC = Timothy M. Crowe, University of Cape Town, South Africa, GB = GenBank, '-' = Unknown, Br. muscle = Breast muscle, Pect. muscle = Pectoral muscle. The specific and susubpecific epithets are as recorded on specimen label.

Taxa name	Sample No.	Origin	Date coll.	Sample type
Bare-throated Group				
P. afer	PFIAO 108,	Tudor East, Watervalboven	2004	Liver
P. afer benguellensis	AMNH 267682	Mombola	-	Toe-pad
P. afer harterti	AMNH 541485	Russisi River	-	Toe-pad
P. afer nudicollis	BM 1903.10.14.91	E. Transvaal	1903	Toe-pad
P. afer böhmi	BM 1932.5.10.214	S. Tanganyika	1932	Toe-pad
P. afer cunenensis	TM 28584	Cunene River	1957	Toe-pad
P. humboldtii swynnertoni	TM 20341	Selindu, Mabsettler	1935	Toe-pad
P. cranchii cranchii	BM 1953.54.56	Mwinilunga, N. Rhodesia	1953	Toe-pad
P. cranchii itigi	AMNH 202502	Poona Singida	-	Toe-pad
P. cranchii intercedens	AMNH 416180	Tukuyu	-	Toe-pad
P. cranchii nyanzae	AMNH211906	Buhumbiro	-	Toe-pad
P. swainsonii	TMC 40	Marico River	2004	Liver
P. s. lundazi	SAM 2055756a	Deka	1969	Toe-pad
P. s. chobiensis	SAM 2003501	Victoria falls	1904	Toe-pad
P. rufopictus	AMNH 202503	Gagayo, Muranza	-	Toe-pad
P. leucoscepus	PFIAO 109	Kenya-	2004	Heart
P. l. infuscatus	AMNH 419169	Tana River, Kenya colony	-	Toe-pad
P. l. muhamed-ben-abdullah	AMNH 541581	-	-	Toe-pad
Montane Group				
P. erckelii	AMNH 541471	Badaltino, Shoa	-	Toe-pad
P. erckelii	AMNH DOT11039	Ethiopia	-	Liver
P. ochropectus	FMNH 1971-1072	Djbouti	-	Toe-pad
P. castaneicollis	GB	-	-	Toe-pad
P. c. bottegi	AMNH541435	Rafissa, Abyssinia		Toe-pad
P. c. ogoensis	AMNH541426	Lower Sheikh	-	Toe-pad
P. jacksoni	AMNH261929	East slope, Mt. Kenya	-	Toe-pad
P. nobilis	AMNH1759	West Ruwenzori	-	Toe-pad
P. camerunensis	TMC 42	Mount Cameroon	-	Liver
P. swierstrai	AMNH 419126	Angola	-	Toe-pad
P. swierstrai	TMC 67	Angola, 14.49 S 13.23 E	30/06/2010	Blood
Scaly Group				
P. ahantensis	AMNH 541409	Nr York Pass, Sierra Leone	-	Toe-pad
P. squamatus	PFIAO 117	-	-	DNA
P. s. maranensis	AMNH 541407	Kilimanjaro district	-	Toe-pad
P. s. schuetti	AMNH 763912	Tshibati, Dem. Rep. Congo	-	Toe-pad
P. griseostriatus	AMNH 541411	Ndalla Tanda	-	Toe-pad
Vermiculated Group				
P. b. bicalcaratus	TM 14682	Gold Coast, Hinterland	1901	Toe-pad
P. b. ayesha	AMNH 541250	Forest of Mamora	-	Toe-pad
P. b. thornei	AMNH 541280	Kavene District, Sierra Leone	-	Toe-pad
P. b. adamauae	AMNH 704359	Cameroon	-	Toe-pad

Taxa name	Sample No.	Origin	Date coll.	Sample type
Vermiculated Group				
P. clappertoni	AMNH 541305	Takoukout, Camergon	-	Toe-pad
P. clappertoni	TMC 68	Cameroon	2005	Br. muscle
P. c. sharpii	AMNH 541324	Adarte	-	Toe-pad
P. c. nigrosquamatus	AMNH 541341	S. Ethiopia	-	Toe-pad
P. icterorhynchus	AMNH 156922	Fanadji	-	Toe-pad
P. hildebrandti	GB	-	-	Blood
P. h. altumi	AMNH 551345	Gilgil River	-	Toe-pad
P. h. fischeri	AMNH 261945	N. Tanganyika Territory	-	Toe-pad
P. h. johnstoni	AMNH 347277	Mafinga Mt., N. Rhodesia	-	Toe-pad
P. h. helleri	AMNH 207771	Neng	-	Toe-pad
P. natalensis	TMC 120	Marico River, South Africa	2004	Liver
P. hartlaubi	TMC 121	Namibia	2006	Br. muscle
P. h. crypticus	AMNH 703654	Erungo Plateau	-	Toe-pad
P. capensis	PFIAO 229	Kakamas, South Africa	-	Heart
P. adspersus	PFIAO 206A	-	-	Liver
P. harwoodi	BM 1927.11.5.18	-	1927	Toe-pad

Table 6.4. DNA markers sequenced and primers used for PCR amplification and sequencing of preserved tissues.

Primer name	Primer sequence (5'to 3')	Reference
Spurfowls		
Cytochrome *b*		
L14578	cta gga atc atc cta gcc cta ga	J.G. Groth (pers. comm.)
MH15364	act cta cta ggg ttt ggc c	P. Beresford (pers. comm.)
ML15347	atc aca aac cta ttc tc	P. Beresford (pers. comm.)
H15915	aac gca gtc atc tcc ggt tta caa gac	Edwards & Wilson (1990)

Table 6.5. DNA marker sequenced and primers used for DNA amplification and sequencing of museum toe-pads.

Primer name	Primer sequence (5' to 3')	Reference
Cytochrome *b*		
Spurfowl-specific primers		
L14851 (General)	cct act tag gat cat tcg ccc t	Kornegay et al. (1993)
Pt-H195	ttt cgr cat gtg tgg gta cgg ag	R. Moyle & T. Mandiwana-Neudani
Pt-H194	cat gtr tgg gct acg gag g	R. Bowie
MH15145	aag aat gag gcg cca ttt gc	P. Beresford
Pt-L143	gcc tca tta ccc aaa tcc tca c	R. Moyle & T. Mandiwana-Neudani
Pt-H361	gtg gct att agt gtg agg ag	R. Moyle & T. Mandiwana-Neudani
Pt-L330	tat act atg gct cct acc tgt ac	R. Bowie
Pt-H645	ggg tgg aat ggg att ttg tca gag	R. Moyle & T. Mandiwana-Neudani
Pt-L633	ggc tca aac aac cca cta ggc	R. Moyle & T. Mandiwana-Neudani
Pt-H901	agg aag ggg att agg agt agg at	R. Moyle & T. Mandiwana-Neudani
L2-2312	cat tcc acg aat cag gct c	R. Bowie
H15696	aat agg aag tat cat tcg ggt ttg atg	Edwards et al. (1991)
Pt-L851alt	cct att tgc cta cgc cat cct ac	R. Bowie
Pt-H1050	gat gct gtt tgg ccg atg	R. Bowie
Pt-L961	cga acc ata aca ttc cca c	R. Moyle & T. Mandiwana-Neudani
Pt-L961alt	ctc atc cta ctc cta atc ccc	R. Bowie
HB20 (General)	ttg gtt cac aag acc aat gtt	J. Feinstein (pers. comm.)

Table 6.6. The inter- and intraspecific uncorrected 'P' distances calculated from CYT*B* data partition only. Taxon names are as known prior to this study.

Taxon name	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52
1 *Pternistis hartlaubi*																																																				
2 *Pternistis h. crypticus*	0%																																																			
3 *Pternistis camerunensis*	11%	10%																																																	
4 *Pternistis nobilis*	11%	11%	7%																																																
5 *Pternistis castaneicollis*	10%	10%	8%	8%																																															
6 *Pternistis c. bottegi*	10%	10%	8%	8%	0%																																														
7 *Pternistis c. ogoensis*	10%	10%	8%	8%	1%	1%																																													
8 *Pternistis erckelii*	9%	9%	7%	8%	4%	4%	4%																																												
9 *Pternistis ochropectus*	8%	8%	8%	8%	4%	4%	4%	3%																																											
10 *Pternistis swierstrai*	11%	11%	8%	9%	7%	7%	7%	6%	8%																																										
11 *Pternistis jacksoni*	11%	11%	9%	10%	8%	8%	7%	7%	7%	7%																																									
12 *Pternistis ahantensis*	9%	7%	8%	8%	7%	5%	7%	6%	8%	7%	8%																																								
13 *Pternistis squamatus*	10%	10%	8%	9%	7%	7%	6%	7%	7%	7%	6%	4%																																							
14 *Pternistis s. maranensis*	9%	9%	8%	8%	6%	7%	6%	6%	7%	7%	6%	4%	3%																																						
15 *Pternistis s. schuetti*	8%	8%	8%	8%	6%	7%	6%	5%	6%	5%	7%	4%	4%	1%																																					
16 *Pternistis griseostriatus*	10%	10%	8%	9%	6%	6%	6%	6%	6%	7%	5%	5%	4%	4%	3%																																				
17 *Pternistis b. bicalcaratus*	10%	10%	8%	9%	7%	7%	7%	6%	7%	7%	7%	6%	6%	5%	6%	5%																																			
18 *Pternistis b. adamauae*	10%	10%	8%	8%	7%	7%	7%	6%	7%	7%	7%	6%	6%	6%	6%	5%	2%																																		
19 *Pternistis b. ayesha*	11%	10%	8%	9%	7%	7%	7%	7%	7%	7%	7%	6%	6%	6%	7%	5%	1%	1%																																	
20 *Pternistis b. thornei*	11%	10%	8%	9%	7%	7%	7%	7%	7%	7%	7%	6%	6%	6%	7%	5%	1%	1%	1%																																
21 *Pternistis icterorhynchus*	11%	11%	9%	9%	8%	8%	8%	7%	7%	8%	8%	6%	7%	7%	8%	6%	3%	3%	3%	3%																															
22 *Pternistis clappertoni*	9%	9%	8%	9%	6%	6%	6%	5%	6%	6%	5%	6%	5%	5%	5%	4%	5%	6%	6%	6%	6%																														
23 *Pternistis c. nigrosquamatus*	9%	9%	8%	9%	6%	6%	6%	6%	7%	7%	6%	7%	5%	5%	5%	5%	6%	6%	6%	6%	7%	1%																													
24 *Pternistis c. sharpii*	9%	9%	8%	9%	6%	6%	6%	6%	7%	7%	6%	7%	5%	5%	5%	5%	6%	6%	6%	6%	7%	1%	1%																												
25 *Pternistis harwoodi*	9%	9%	8%	9%	6%	6%	6%	6%	7%	7%	6%	7%	5%	5%	5%	5%	6%	6%	6%	6%	7%	1%	1%	1%																											
26 *Pternistis capensis*	10%	10%	8%	9%	6%	7%	7%	7%	7%	6%	6%	8%	5%	5%	5%	4%	6%	6%	6%	6%	7%	5%	5%	5%	5%																										
27 *Pternistis adspersus*	10%	10%	9%	10%	7%	7%	7%	7%	7%	7%	6%	8%	6%	5%	6%	5%	6%	7%	7%	7%	7%	5%	5%	6%	6%	4%																									
28 *Pternistis natalensis*	10%	10%	8%	9%	7%	7%	7%	7%	7%	7%	6%	6%	5%	5%	5%	5%	6%	6%	6%	6%	7%	4%	5%	5%	5%	4%	4%																								
29 *Pternistis hildebrandti*	10%	10%	9%	9%	7%	7%	7%	8%	8%	7%	7%	5%	5%	5%	4%	6%	7%	6%	7%	7%	8%	6%	6%	6%	6%	5%	5%	3%																							
30 *Pternistis h. altumi*	10%	10%	9%	10%	7%	7%	8%	8%	8%	7%	7%	7%	6%	5%	5%	6%	7%	6%	7%	7%	8%	6%	6%	6%	6%	5%	5%	3%	1%																						
31 *Pternistis h. fischeri*	10%	10%	8%	9%	6%	6%	7%	7%	7%	7%	6%	7%	5%	5%	6%	5%	6%	6%	6%	7%	7%	5%	5%	5%	5%	4%	4%	1%	3%	3%																					
32 *Pternistis h. helleri*	9%	9%	9%	8%	7%	8%	7%	7%	7%	6%	7%	7%	6%	4%	4%	6%	6%	6%	6%	7%	7%	5%	6%	6%	6%	4%	4%	2%	2%	1%	3%																				
33 *Pternistis h. johnstoni*	10%	10%	8%	9%	7%	7%	7%	7%	7%	7%	6%	7%	5%	5%	6%	5%	6%	6%	7%	7%	7%	5%	5%	5%	5%	4%	5%	1%	3%	3%	0%	3%																			
34 *Pternistis afer* (Angola)	10%	10%	8%	8%	7%	8%	7%	7%	7%	7%	6%	7%	5%	6%	5%	6%	7%	7%	8%	8%	7%	5%	5%	5%	5%	6%	7%	6%	6%	6%	6%	6%	6%																		
35 *Pternistis afer* (SA)	10%	10%	8%	9%	7%	7%	7%	7%	7%	7%	6%	6%	6%	6%	6%	6%	7%	7%	8%	7%	8%	6%	6%	6%	6%	5%	6%	6%	6%	6%	6%	6%	6%	3%																	
36 *Pternistis a. nudicollis*	9%	9%	8%	9%	6%	7%	6%	6%	7%	8%	7%	6%	6%	5%	5%	6%	7%	7%	7%	7%	8%	5%	5%	5%	5%	6%	6%	6%	6%	6%	6%	6%	6%	3%	3%																
37 *Pternistis a. benguellensis*	9%	9%	8%	8%	6%	6%	6%	6%	6%	7%	6%	7%	5%	5%	5%	6%	6%	7%	7%	7%	7%	5%	5%	4%	5%	5%	6%	5%	5%	5%	5%	5%	5%	1%	3%	2%															
38 *Pternistis a. bohmi*	9%	9%	7%	8%	6%	6%	6%	5%	5%	7%	5%	6%	4%	5%	3%	5%	6%	6%	6%	6%	6%	4%	5%	4%	5%	5%	5%	5%	5%	5%	5%	5%	5%	2%	3%	2%	1%														
39 *Pternistis a. cranchii*	9%	9%	8%	8%	6%	7%	6%	6%	6%	7%	6%	6%	5%	5%	5%	6%	7%	7%	7%	7%	7%	5%	5%	5%	5%	5%	6%	5%	5%	5%	5%	5%	5%	2%	4%	2%	0%	1%													
40 *Pternistis a. cunenensis*	8%	7%	7%	7%	6%	7%	6%	5%	6%	6%	5%	7%	5%	5%	5%	5%	6%	6%	7%	7%	6%	5%	5%	5%	5%	5%	5%	4%	5%	5%	5%	4%	5%	3%	3%	3%	1%	1%	1%												
41 *Pternistis a. harterti*	9%	9%	8%	8%	6%	6%	6%	6%	7%	7%	6%	6%	5%	5%	5%	6%	7%	7%	7%	7%	7%	5%	5%	4%	5%	5%	6%	5%	6%	6%	5%	5%	5%	2%	3%	2%	0%	1%	1%	1%											
42 *Pternistis a. intercedens*	9%	9%	8%	8%	6%	6%	6%	6%	7%	7%	6%	6%	5%	5%	5%	6%	7%	7%	7%	7%	7%	5%	5%	5%	5%	5%	6%	5%	6%	6%	5%	5%	5%	2%	4%	2%	1%	1%	1%	1%	0%										
43 *Pternistis a. itigi*	10%	9%	8%	8%	7%	7%	6%	6%	7%	7%	6%	7%	5%	5%	6%	6%	7%	7%	7%	7%	8%	5%	5%	5%	5%	6%	6%	6%	6%	6%	6%	6%	6%	2%	4%	3%	1%	0%	1%	1%	1%	1%									
44 *Pternistis a. nyanzae*	9%	9%	8%	8%	6%	7%	6%	6%	6%	7%	6%	6%	5%	5%	5%	6%	7%	7%	7%	7%	7%	5%	5%	5%	5%	5%	6%	5%	5%	5%	5%	5%	5%	2%	4%	2%	0%	1%	0%	1%	1%	1%	1%								
45 *Pternistis a. swynnertoni*	10%	9%	9%	9%	7%	7%	7%	7%	7%	8%	7%	7%	6%	6%	6%	7%	7%	7%	8%	7%	8%	6%	6%	6%	6%	6%	6%	6%	6%	6%	6%	6%	6%	3%	4%	1%	2%	2%	3%	3%	2%	2%	3%	3%							
46 *Pternistis rufopictus*	9%	9%	8%	8%	6%	6%	6%	6%	7%	7%	6%	6%	5%	5%	4%	6%	7%	7%	7%	7%	8%	5%	5%	5%	5%	5%	6%	6%	6%	6%	6%	5%	6%	2%	3%	2%	2%	2%	2%	2%	2%	2%	2%	2%	2%						
47 *Pternistis leucoscepus*	10%	10%	9%	9%	7%	7%	7%	7%	7%	8%	7%	7%	6%	6%	6%	6%	7%	7%	7%	7%	8%	5%	5%	5%	5%	6%	7%	6%	6%	7%	6%	6%	6%	4%	6%	5%	4%	4%	4%	4%	4%	4%	4%	4%	5%	4%					
48 *Pternistis l. infuscatus*	9%	9%	8%	9%	7%	7%	7%	6%	7%	7%	6%	6%	5%	6%	5%	6%	6%	7%	7%	7%	7%	5%	5%	5%	5%	6%	6%	6%	6%	6%	6%	5%	6%	5%	6%	5%	4%	4%	4%	4%	4%	4%	4%	4%	5%	4%	1%				
49 *Pternistis l. muh-ben-abdullah*	9%	9%	8%	9%	6%	6%	6%	6%	6%	7%	6%	7%	5%	5%	5%	5%	6%	7%	6%	7%	7%	5%	5%	4%	4%	6%	6%	6%	6%	6%	6%	5%	6%	4%	5%	5%	4%	4%	4%	4%	4%	4%	4%	4%	5%	4%	2%	2%			
50 *Pternistis swainsonii*	10%	9%	7%	9%	6%	6%	6%	6%	6%	7%	6%	8%	6%	5%	5%	6%	7%	7%	7%	7%	7%	5%	5%	5%	5%	6%	6%	6%	6%	6%	6%	6%	6%	5%	5%	4%	4%	4%	4%	5%	4%	4%	4%	4%	5%	4%	5%	4%	4%		
51 *Pternistis s. chobiensis*	11%	11%	9%	11%	8%	8%	8%	8%	8%	9%	6%	7%	8%	8%	7%	7%	8%	8%	9%	8%	9%	7%	8%	7%	7%	7%	8%	7%	9%	8%	7%	9%	7%	8%	7%	7%	7%	7%	7%	7%	7%	7%	7%	7%	7%	7%	7%	8%	7%	5%	
52 *Pternistis s. lundazi*	10%	10%	9%	11%	8%	8%	8%	7%	8%	9%	8%	8%	7%	7%	6%	8%	8%	8%	8%	8%	9%	6%	6%	6%	6%	7%	8%	7%	8%	8%	7%	9%	7%	8%	7%	6%	6%	6%	6%	6%	6%	6%	6%	6%	6%	6%	7%	7%	6%	3%	2%	

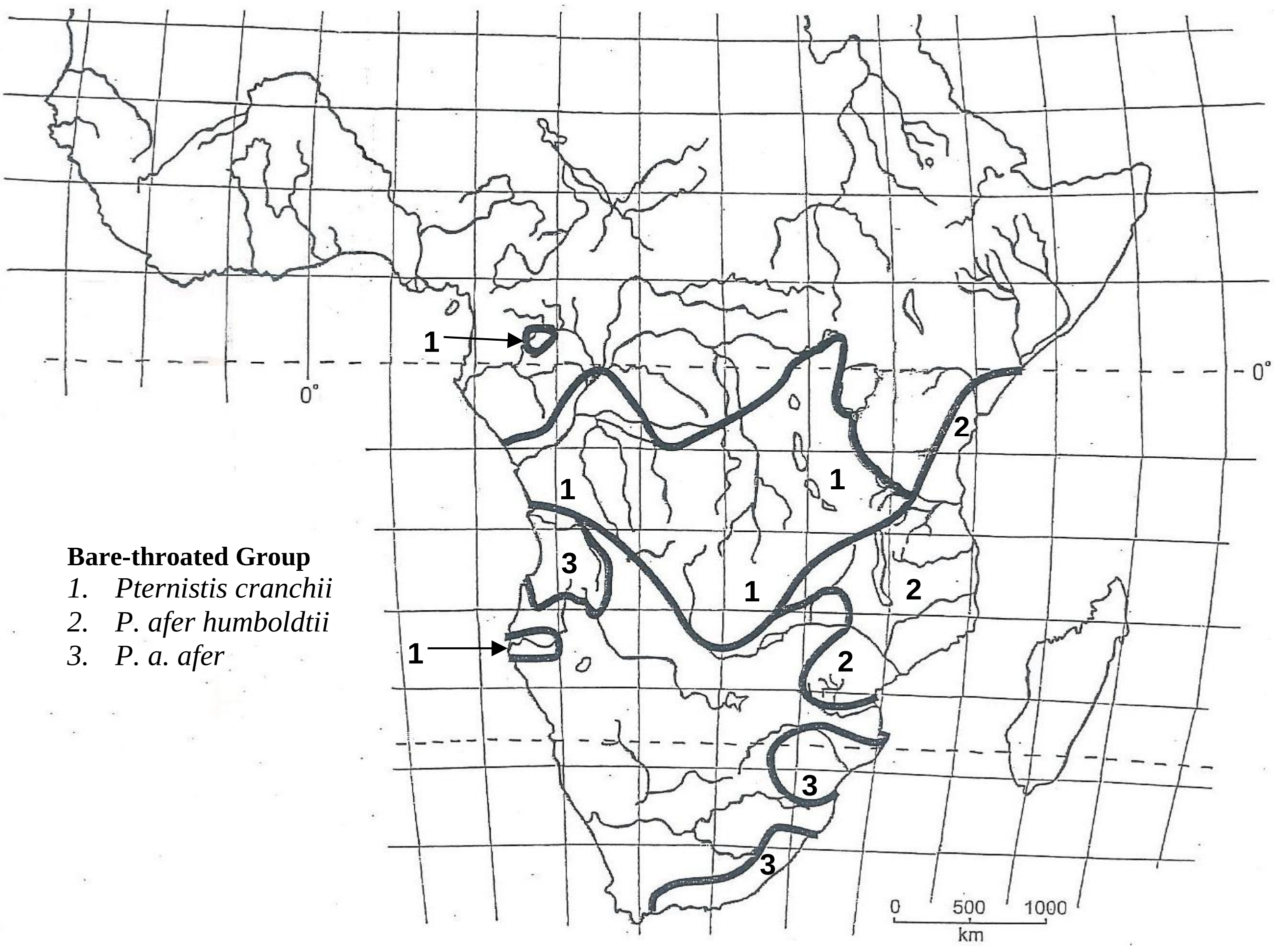


Figure 6.1. Distribution ranges of Hall's Bare-throated Group taxa.

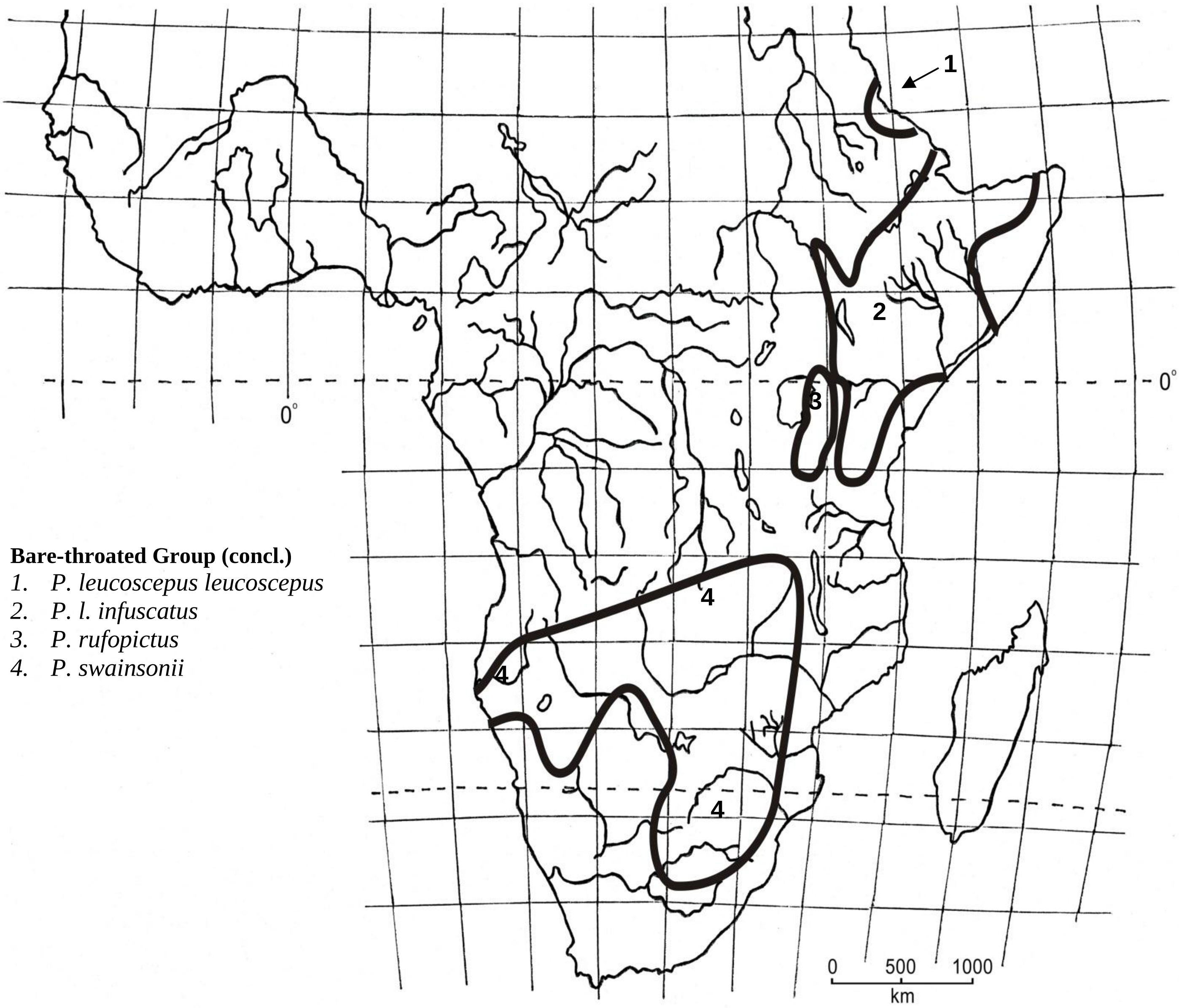


Figure 6.2. Distribution ranges Hall's Bare-throated Group taxa.

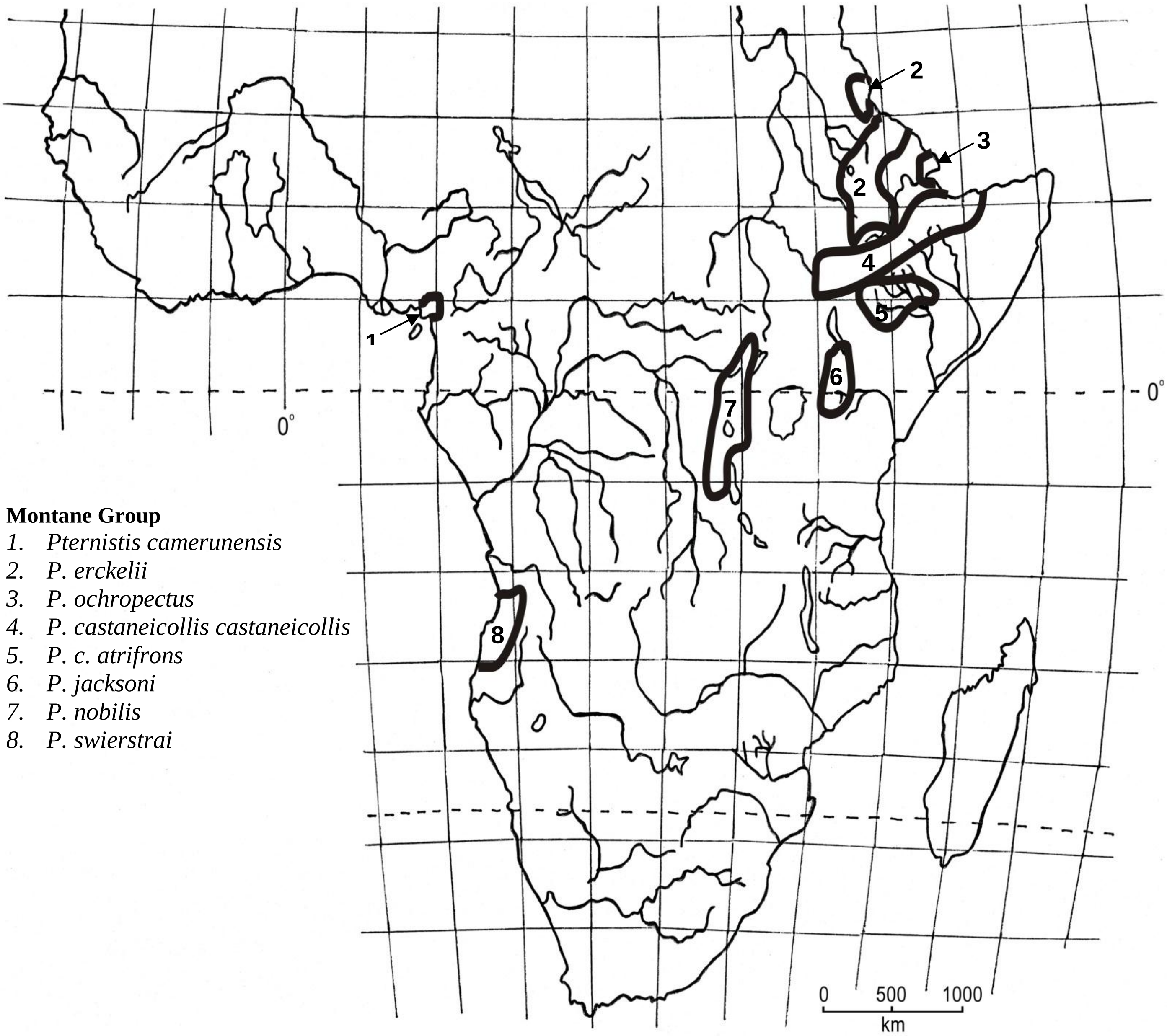


Figure 6.3. Distribution ranges of Hall's Montane Group of spurfowls.

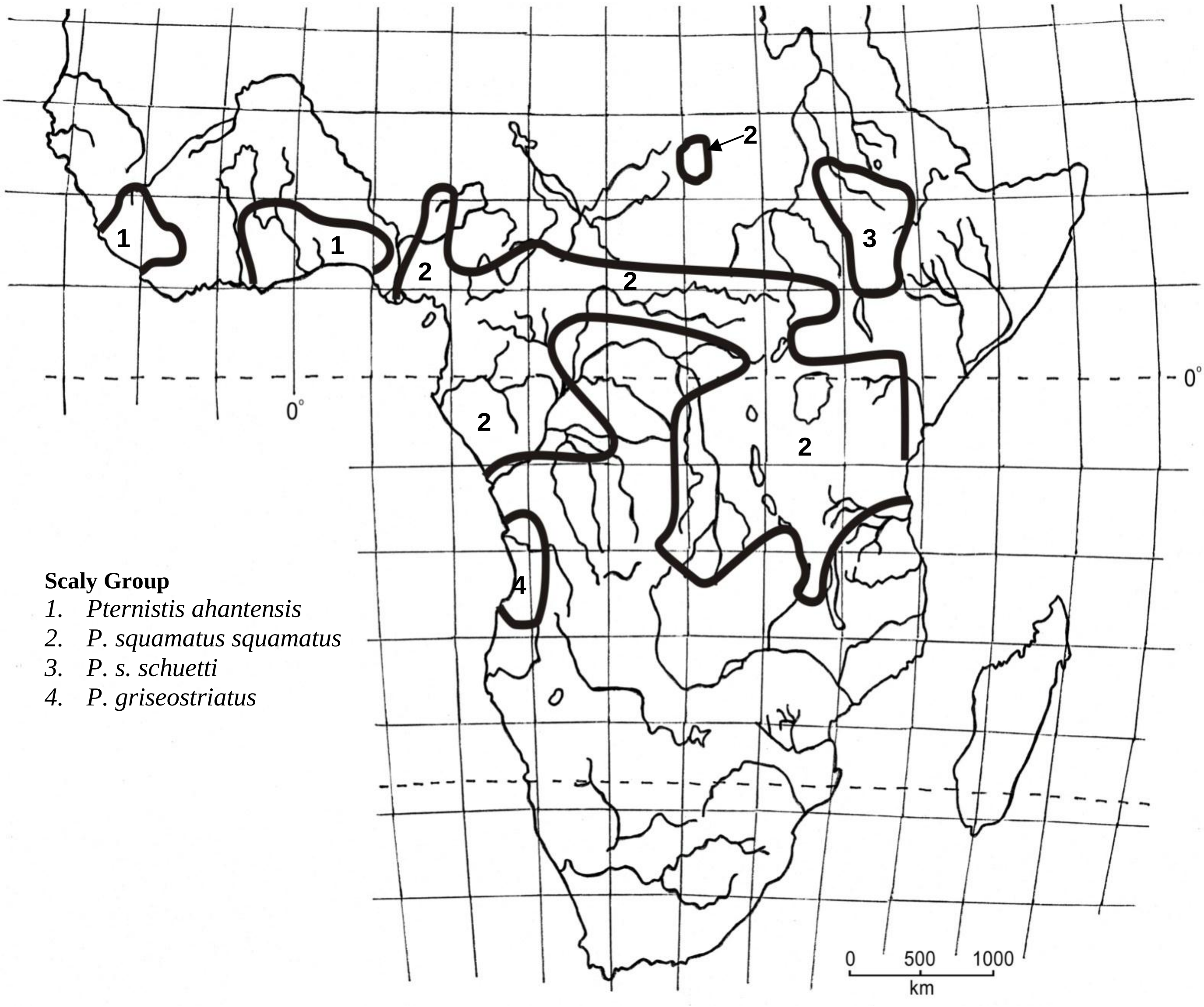


Figure 6.4. Distribution ranges of Hall's Scaly Group taxa.

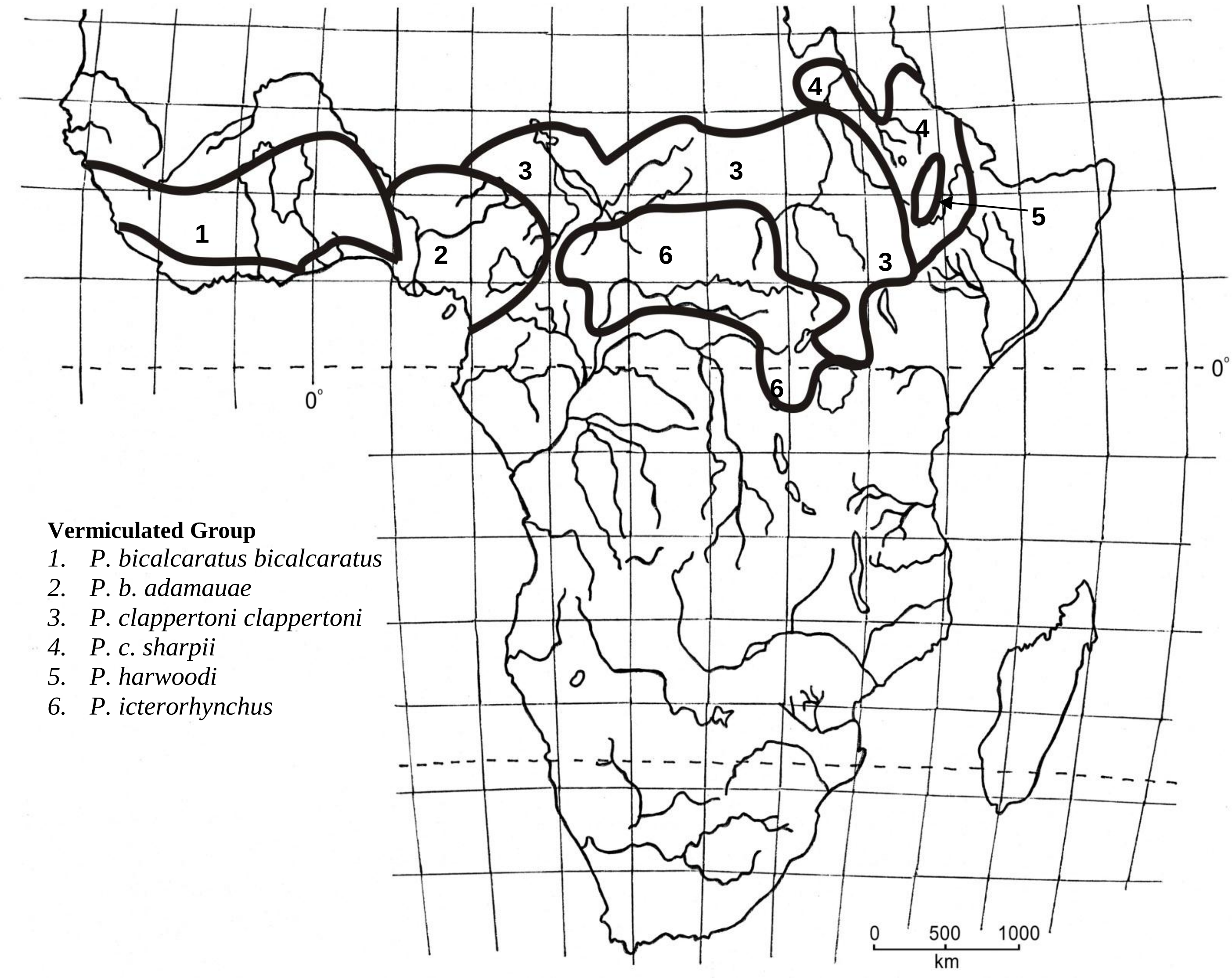


Figure 6.5. Distributional ranges of Hall's Vermiculated Group.

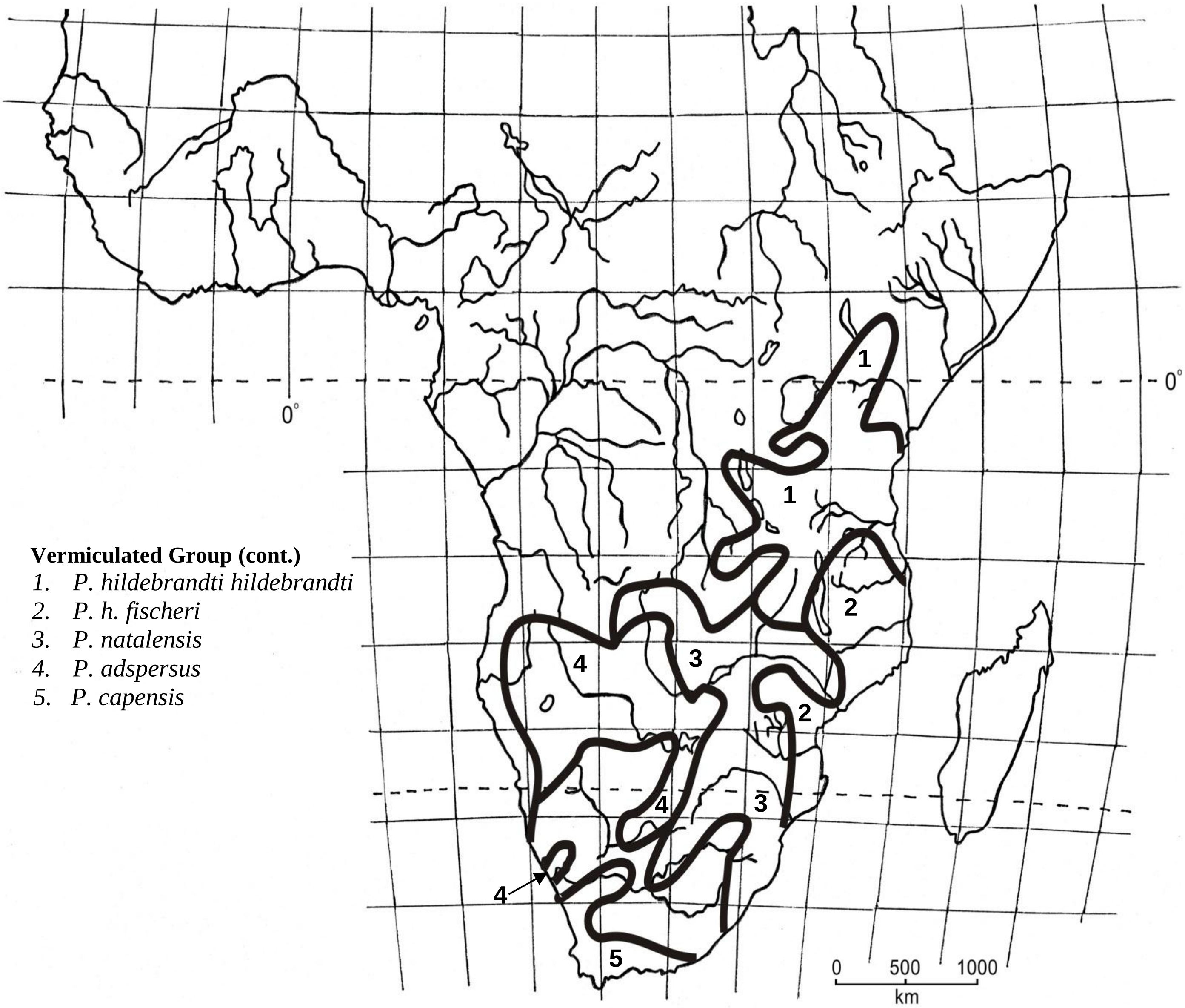
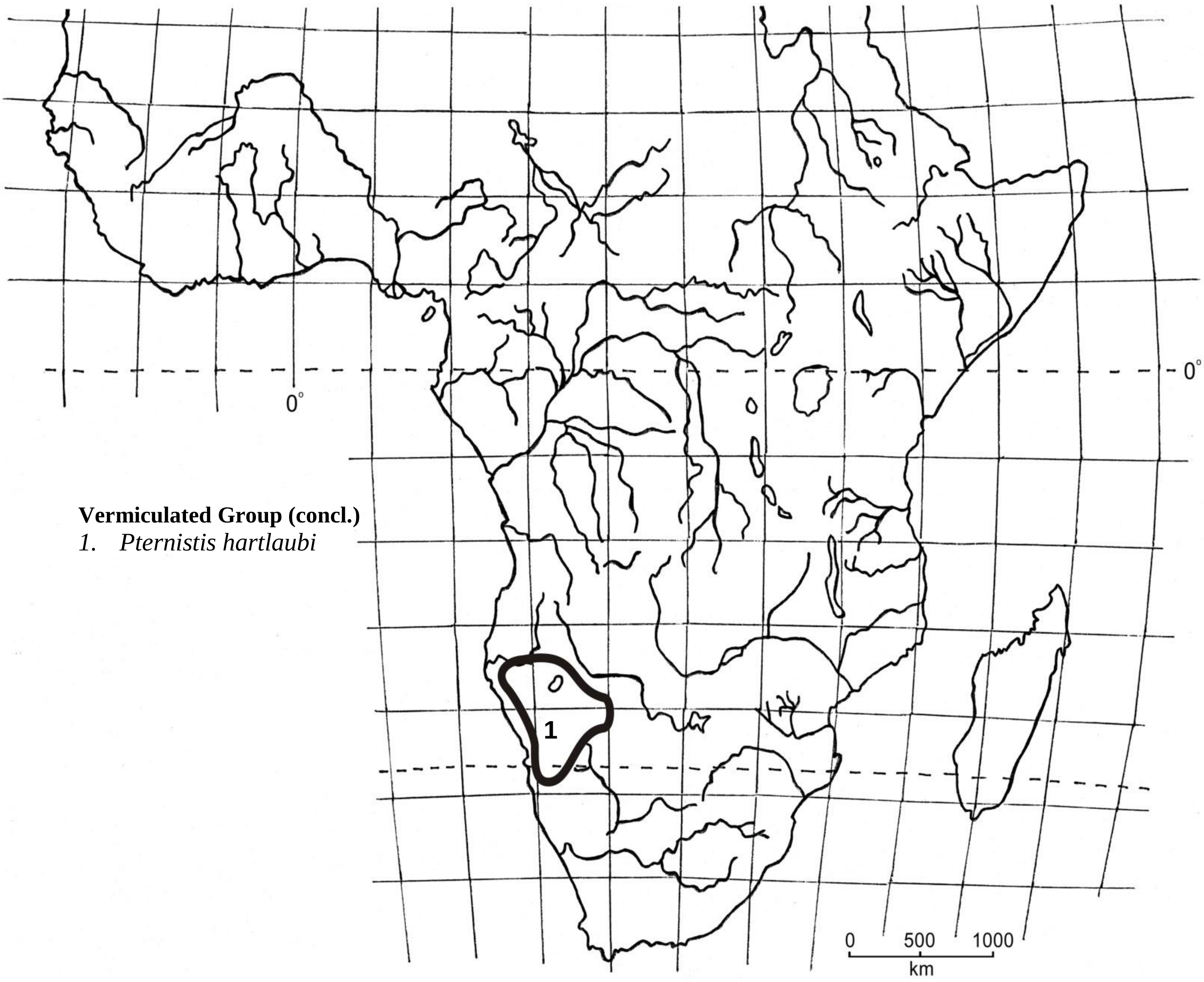


Figure 6.6. Distributional ranges of Hall's (1963) Vermiculated Group.



Vermiculated Group (concl.)
1. Pternistis hartlaubi

Figure 6.7. Distributional ranges of Hall's (1963) Vermiculated Group.

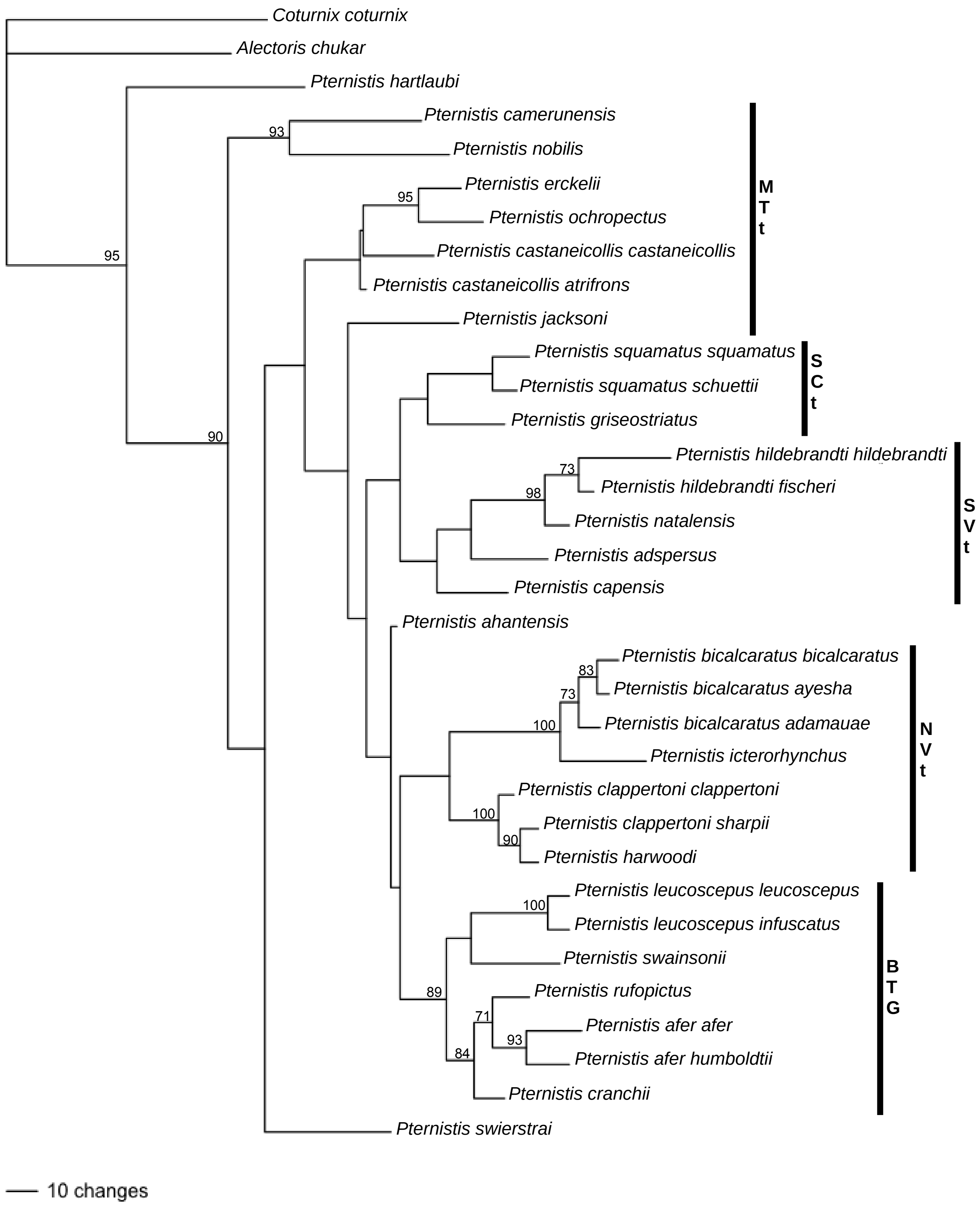


Figure 6.8. A parsimony tree (1 of 2 most parsimonious trees similar to Strict Concensus tree) obtained from combined mitochondrial Cytochrome-*b* and organismal characters. Numbers above branches represent boostrap support values (only ≥ 70% are presented). MTt stands for Montane taxa SCt – Scaly taxa, SVt – Southern Vermiculated taxa, NVt – Northern Vermiculated taxa and BTG – Bare-throated Group.

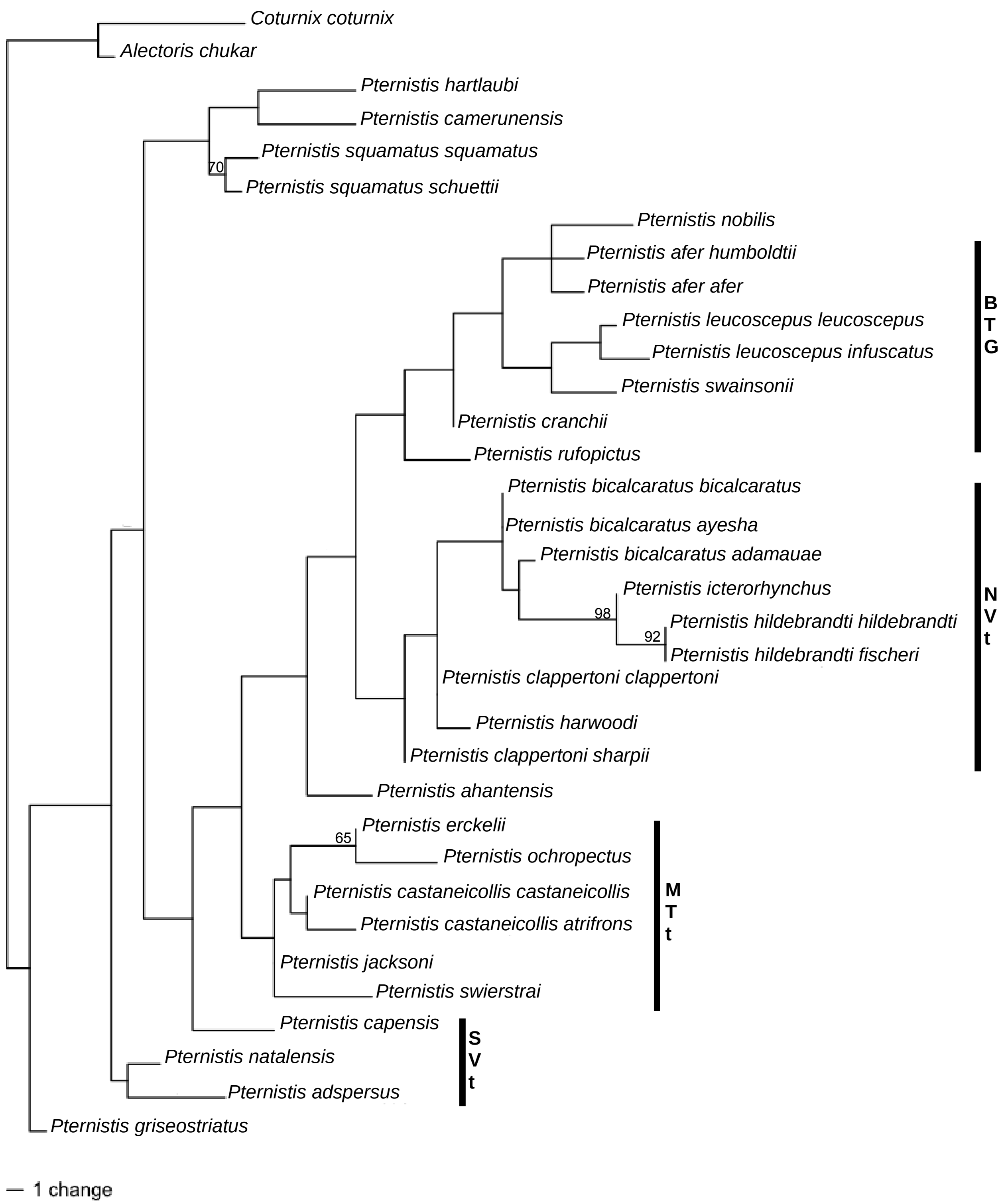


Figure 6.9. A parsimony tree (1 of 397 most parsimonious trees) obtained from organismal characters. Numbers above branches represent boostrap support values (only ≥ 70% are presented). MTt stands for Montane taxa, SCt – Scaly taxa, SVt – Southern Vermiculated taxa, NVt – Northern Vermiculated taxa and BTG – Bare-throated Group.

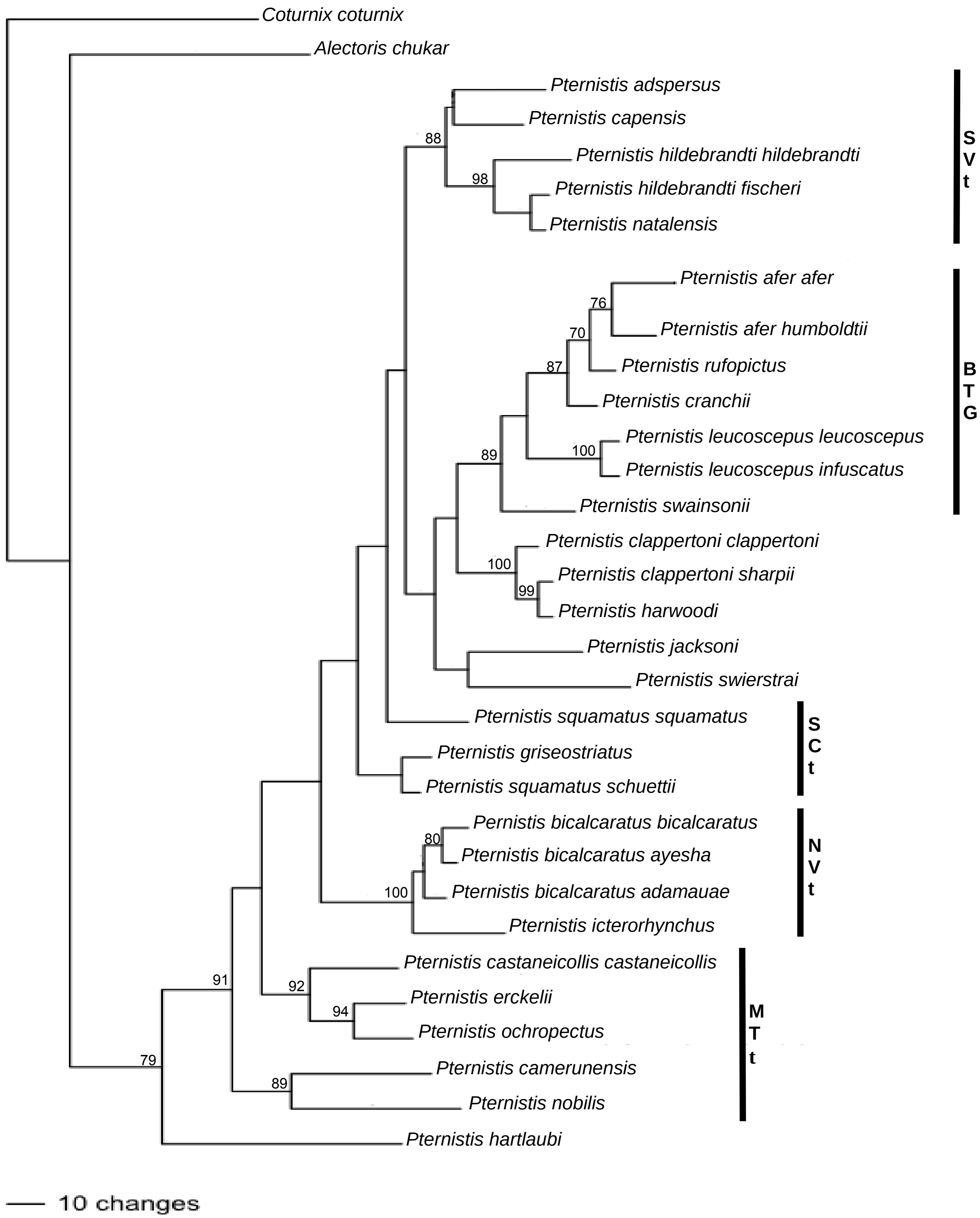


Figure 6.10. A parsimony tree (1 of 2 most parsimonious trees similar to Strict Consensus tree) obtained from combined mitochondrial Cytochrome-*b* and organismal characters. Numbers above branches represent boostrap support values (only ≥ 70% are presented). MTt stands for Montane taxa, SCt – Scaly taxa, SVt – Southern Vermiculated taxa, NVt – Northern Vermiculated taxa and BTG – Bare-throated Group.

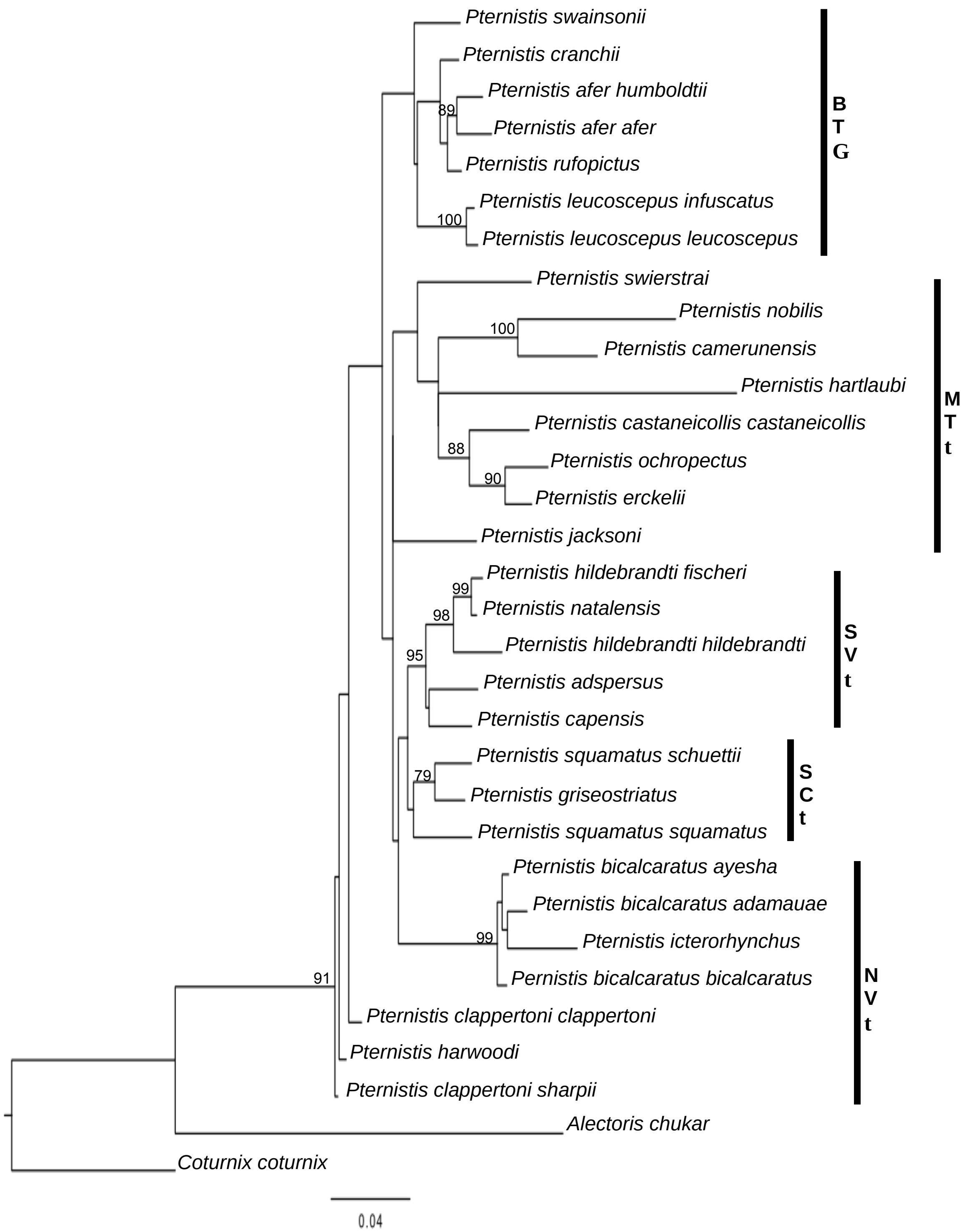


Figure 6.11. Maximum likelihood tree obtained from mitochondrial Cytochrome-*b* characters. Numbers above branches represent boostrap support values (only ≥ 70% are presented). MTt stands for Montane taxa, SCt – Scaly taxa, SVt – Southern Vermiculated taxa, NVt – Northern Vermiculated taxa and BTG – Bare-throated Group.

Appendix 6.1. GenBank accession numbers for taxa sequenced for mitochondrial Cytochrome-*b*.

Taxon	**CYT*B* GenBank no.**
Pternistis hartlaubi hartlaubi	FR691618
Pternistis hartlaubi crypticus	FR691619
Pternistis adspersus	FR691623
Pternistis afer Angola	FR694158
Pternistis afer benguellensis	FR694159
Pternistis afer böhmi	FR694162
Pternistis cranchii cranchii	FR694164
Pternistis afer cunenensis	FR694160
Pternistis afer harterti	FR694161
Pternistis afer intercedens	FR694165
Pternistis afer itigi	FR694166
Pternistis afer nudicollis	FR694163
Pternistis afer nyanzae	FR694167
Pternistis afer South Africa	AM236908
Pternistis afer swynnertoni	FR694168
Pternistis bicalcaratus bicalcaratus	FR691624
Pternistis bicalcaratus adamauae	FR691626
Pternistis bicalcaratus ayesha	FR691625
Pternistis bicalcaratus thornei	FR691627
Pternistis camerunensis	FR691591
Pternistis capensis	AM236909
Pternistis castaneicollis castaneicollis	AM236903
Pternistis castaneicollis bottegi	FR691629
Pternistis castaneicollis ogoensis	FR691628
Pternistis clappertoniclappertoni	FR691602
Pternistis clappertoni nigrosquamatus	FR691604
Pternistis clappertoni sharpii	FR691603
Pternistis erckelii	FR691589
Pternistis griseostriatus	AM236905
Pternistis harwoodi	FR691600
Pternistis hildebrandti hildebrandti	FR691595
Pternistis hildebrandti altumi	FR691597
Pternistis hildebrandti fischeri	FR691598
Pternistis hildebrandti helleri	FR691599
Pternistis hildebrandti johnstoni	FR691596
Pternistis icterorhynchus	FR691601
Pternistis jacksoni	FR691594
Pternistis leucoscepus	AM236906
Pternistis leucoscepus infuscatus	FR691587
Pternistis leucoscepus muhamed-ben-abdullah	FR691586

Taxon	CYT*B* GenBank no.
Pternistis natalensis	AM236911
Pternistis nobilis	FR691592
Pternistis ochropectus	FR691590
Pternistis rufopictus	FR691588
Pternistis squamatus squamatus	AM236904
Pternistis squamatus maranensis	FR691630
Pternistis squamatus schuettii	FR691631
Pternistis swainsonii swainsonii	AM236907
Pternistis swainsonii chobiensis	FR694170
Pternistis swainsonii lundazi	FR694169
Pternistis swierstrai	FR691593

Appendix 6.2. A revised classification of spurfowls which was based on multiple lines of evidence presented in this chapter. The status of taxa with an asterisk (*) might change when DNA sequence data (or with increased number of nucleotide bases) are included in the analyses. Species and subspecies authority appear in Table 1.2.

Family: Phasianidae

Sub-family: Phasianinae

Genus: *Pternistis* Wagler, 1832
Pternistis hartlaubi

Pternistis camerunensis
Pternistis erckelii
Pternistis ochropectus
Pternistis castaneicollis castaneicollis
*Pternistis castaneicollis atrifrons**
Pternistis jacksoni
Pternistis nobilis
Pternistis swierstrai

Pternistis bicalcaratus bicalcaratus
Pternistis bicalcaratus adamauae
Pternistis clappertoni clappertoni
Pternistis clappertoni sharpii
Pternistis harwoodi
Pternistis icterorhynchus
Pternistis hildebrandti hildebrandti
Pternistis hildebrandti fischeri
Pternistis natalensis
Pternistis adspersus
Pternistis capensis

*Pternistis ahantensis ahantensis**
Pternistis squamatus squamatus
Pternistis squamatus schuetti
Pternistis griseostriatus

Pternistis cranchii
Pternistis afer afer
Pternistis afer humboldtii
Pternistis leucoscepus leucoscepus
Pternistis leucoscepus infuscatus
Pternistis rufopictus
Pternistis swainsonii

CHAPTER 7

Historical biogeography of francolins and spurfowls (Galliformes: Phasianidae)

Abstract

The biogeography of francolins has not received much attention since the monograph of Hall (1963). Apart from the dispute about their monophyly, uncertainties in the taxonomic designations and their phylogenetic relationships have generated opposing hypotheses ("out of Asia" or "out of Africa") pertinent to the origin of the genus *Francolinus*. Francolins (*sensu lato*) are galliform birds that occur in Africa, and are mainly restricted to sub-Saharan and the Indian Sub-continent; inhabiting primarily tropical/sub-tropical areas with some species occurring in forested habitats. They were recently split into two distantly related assemblages, francolins and spurfowls (divergence date going back to c. 33.6 mya) which are split among five francolin genera *Francolinus, Ortygornis, Afrocolinus, Peliperdix, Scleroptila* as opposed to the single genus *Pternistis* assigned to all spurfowl taxa.

This chapter seeks to understand the history of the current geographic distribution patterns of francolins and spurfowls in light of their phylogeny and to test the two opposing hypotheses on their origin. A range of organismal and DNA characters were analyzed using parsimony and Bayesian methods. A new biogeographical reconstruction method, spatial analysis of vicariance, was used to detect disjunctions and to infer barriers while the ancestral area and habitat were reconstructed in Mesquite. The colonization of Africa by ancestral species may have

been through dispersal from Asia, which resulted in the formation of disjunct distributions and the somewhat rapid diversification of francolins and spurfowls within Africa.

The Rift Valley system, Lake Chad, Upper Guinea and the Congolian forest, major rivers such as Limpopo, Zambezi, Rovuma, Volta and Rufiji, the Okavango Swamp and Sahara Desert emerged as the major physical breaks that may have created and maintained the distributions observed today and promoted speciation among the African francolins and spurfowls. Sharp diversity gradients in habitat appear to also have played an important ecological role in facilitating diversification among these taxa.

Introduction

General background

Cracraft (1994) argued that a scientific problem that is central to systematists and ecology has been to explain the spatio-temporal patterns of species diversity and attempt to understand why taxa occur in particular areas and not others, as well as how they assembled or spread to those regions. This becomes a difficult exercise to do given that historical biogeography is at best poorly known. Some authors, e.g. de Quieroz (2005), Donoghue and Moore (2003), Lamm and Redelings (2009) argue that the challenge of historical biogeography is to distinguish dispersal and vicariance whereas (Hovenkamp 1997, 2001) argued for the recognition of barriers being an important task in a framework that can examine both inter and intra-continental distributional patterns.

In this chapter the focus is on francolins and spurfowls (Table 1.1), here considered two independent radiations of taxa (Crowe et al. 2006, Chapter 2). These assemblages are francolins, divided among the genera *Francolinus, Ortygornis, Afrocolinus, Peliperdix* and *Scleroptila* (details in Chapter 5) and spurfowls, which are attributed to a single genus *Pternistis* (Crowe et al. 2006, Chapter 6). The closest relatives of each of these independent radiations occur in Asia and Europe: the genera *Gallus, Bambusicola* spp., which are the close relatives of the francolins, and *Coturnix, Margaroperdix, Alectoris, Perdicula, Tetraogallus, Excalfactoria* and *Ammoperdix* spp., which are closely related to the spurfowls.

Habitat preferences of francolins and spurfowls

Francolins and spurfowls have complex distribution patterns (Snow 1978), occurring in different habitats primarily of a tropical/sub-tropical nature, with some species occurring in forested habitats (Hall 1963, Johnsgard 1988, del Hoyo et al. 1994, Madge and McGowan 2002). The three Spotted Middle Eastern-Asian *Francolinus* species, *F. francolinus*, *F. pictus* and *F. pintadeanus*, thrive in thick bush and patches of scrub jungle (Johnsgard 1988). The *Ortygornis* taxa, *O. sephaena* and *O. grantii* occur in scrubby African woodlands with grass habitats. The Asian francolin *O. gularis* is a swamp-dwelling species, whereas Asian *O. pondicerianus* thrives in woodland and bushes. The Red-tailed *Peliperdix* spp. inhabit open grassland and woodland savannas. *Afrocolinus lathami* remains the only African francolin to be restricted to deeply forested habitats (del Hoyo et al. 1994, Madge and McGowan 2002). Although the Red-winged *Scleroptila* spp. occur in varied habitats at different latitudes, they primarily occupy grassland (Johnsgard 1988, Madge and McGowan 2002), which could be open lowland grasslands in which *S. levaillantoides*, *S. gutturalis*, *S. finschi* thrive, or the open hilly (*S. shelleyi*) and highland grasslands preferred by *S. afra, S. psilolaema, S. levaillantii,* and *S. streptophora*.

With regard to the spurfowls, the Bare-throated Group includes four relatively large species, *P. swainsonii* which inhabits thickets and dry savannas, *P. afer* which thrives in thickets, riparian scrub and adjoining grassland and forest edges, *P. leucoscepus* occupies thicket and open savanna scrub areas and adjacent fields, and *P. rufopictus* which occurs in thickets and in Acacia scrub and woodland. Members of the Vermiculated Group (*P. hartlaubi, P. capensis, P. natalensis, P. adspersus, P. hildebrandti, P. clappertoni, P. icterorhynchus, P. bicalcaratus, P. harwoodi*) generally occupy dense bushy thickets and shrubby grasslands (del Hoyo et al. 1994, Madge and McGowan 2002). In contrast to the habitat preferences of the Bare-throated and the Vermiculated spp., members of the Montane Group (*P. camerunensis, P. swierstrai, P.*

nobilis, *P. ochropectus*, *P. jacksoni*, *P. castaneicollis*) inhabit largely montane forest patches and scrubby slopes (Madge and McGowan 2002) with the exception of *P. erckelii* being the only member that ventures into adjacent grasslands. The Scaly Group spp., *P. squamatus*, *P. griseostriatus* and *P. ahantensis* inhabit forest edges with dense undergrowth (Madge and McGowan 2002).

The origin of the genus Francolinus Stephens, 1819

The relationships between francolins with Palaearctic and Asian genera influenced Hall's (1963) hypothesis on the origin of the genus *Francolinus*. Even though Hall (1963) produced commendable work in describing the geographical distribution patterns of francolins, the origin of the genus '*Francolinus*'; however, continued to be highly disputed (Hall 1963, Crowe et al. 1992). Based on the fact that francolins and spurfowls share the closest relationships with Palearctic and Asian genera, Hall (1963) strongly argued for this genus to be of Asian origin and she speculated that its age extended back to the Oligocene 25-35 mya (Hall 1963, Sibley and Alquist 1985). She further maintained that speciation of francolins in Africa was likely promoted by other factors such as reduced competition. In contrast, Crowe and Crowe (1985) and Bloomer and Crowe (1998) argued that the ancestor of francolins was African, inferring that francolins dispersed from Africa to Asia. Despite the difference in opinion about the origin of this lineage, Hall (1963), Crowe and Crowe (1985) and Bloomer and Crowe (1998), all hypothesized that the ancestral francolin (traditionally including spurfowls) was a small, quail-like phasianid based on the observation that the plumage and other integumentary features of immature francolins resemble those of quails (Crowe et al. 1986).

A brief overview of historical biogeographical approaches

One way to investigate the biogeography of taxa is by tracing ancestral patterns i.e., the history of character evolution and also by reconstructing the evolution of geographic ranges of taxa on phylogenetic trees. In addressing the evolution of the distribution patterns of francolins (*sensu lato*), Hall (1963) made a direct comparison of the ranges of species with vegetation types and "tentatively tried to correlate some of the climatic eras postulated with those known" as outlined in the monograph in Appendix 1, on page 173-174. Her attempts to explain the evolution of species involved two assumptions. The first one being that the degree of divergence shown by two isolated populations can be correlated with the length of time spent in isolation and secondly, that the species assemblage present originated in some part or parts of their current range.

Until recently a commonly utilized approach to investigate historical biogeography was that of dispersal-vicariance analysis (Ronquist 1997), which is implemented in the software DIVA (Ronquist 1996). This approach requires one fully-resolved phylogenetic tree and minimizes the number of dispersal and extinction events required to explain the species' distributions by way of optimizing the ancestral areas onto internal nodes of a phylogeny. Jønsson et al. (2010) used what they call a newly developed Bayesian approach to dispersal-vicariance analysis, 'Bayes-diva' (Nylander et al. 2008), which unlike Ronquist's DIVA approach, accounts for phylogenetic uncertainty. Ree and Smith (2008) developed a dispersal-extinction-cladogenesis (DEC) model that reconstructs the evolution of geographic ranges. The DEC model has been criticized for "ignoring vicariance" and assuming that the rate of evolution of geographic ranges occurs independently, an assumption that may not be applicable to some biogeographic inferences.

Spatial analysis of vicariance by Arias et al. (2011) is a new method which is based on the ideas of Hovenkamp (1997, 2001) as implemented in VIP (Arias et al. 2011), which instead of looking at pre-defined areas, uses direct geographic/georeferenced data to detect disjunctions between sister groups and infers barriers associated with them. It uses an optimality criterion framework which maximizes the number of possible pairs of disjunct sister nodes while minimizing the number of eliminated distributions (Arias et al. 2011). This method requires a phylogeny.

In this chapter, the aim was to understand the history of the current geographic distributional patterns of francolins and spurfowls in light of the species groups suggested by Hall (1963), with modifications as outlined in Chapters 5 and 6, in order to detect disjunctions and infer barriers, as well as to resolve the contrasting hypotheses on the origin of the genus *Francolinus sensu lato* outlined by Hall (1963; our of Asia) and Crowe and Crowe (1985; our of Africa), respectively.

Materials and methods

Data collection

Sampling of taxa and characters

Only francolin and spurfowl taxa that were recognized as valid terminal taxa in Chapter 5 (francolins) and Chapter 6 (spurfowls) were analyzed in this chapter.

Maps and mapping of distribution records of investigated taxa

The maps depicting the distribution ranges of francolins and spurfowls were produced as outlined in Chapter 5 and 6.

Ancestral state reconstructions

The multistate matrices for francolins and spurfowls were generated for two traits: area and habitat. The francolin area states were scored as follows: Southern Asia (0), West Africa (1), Southern Africa (2), Central Africa (3) and East Africa (4), whereas those for habitat were: open grasslands (0), scrubby grasslands (1), wooded grasslands (2), Montane grasslands (3) and Forest (4). The states for area and habitat of the spurfowls were coded as Southern Africa (0), West Africa (1), North Africa (2), Central Africa (3) and East Africa (4) and those for habitat were: savanna and arid woodlands (0), mesic woodlands (1), forest/forest edge (FFE) (2), lowland fynbos (3) and macchia (a scrubland vegetation of the Mediterranean region which is composed primarily of leathery, broad-leaved evergreen shrubs).

Spatial analysis of vicariance

In the absence of direct georeferenced distribution data, the distribution ranges of taxa were used to detect disjunctions and infer barriers between sister groups.

Data analyses

Chapter 2 demonstrated that instead of francolins being considered a single evolutionary lineage, they represent two lineages and as a result francolin and spurfowl analyses were conducted separately

Ancestral state reconstructions

To reconstruct the ancestral patterns, a maximum likelihood approach (based on a Bayesian topology) which seeks to find the ancestral states that maximize the probability that the observed states would evolve under a stochastic model of evolution (Schluter et al. 1997, Pagel 1999) was used. What differentiates this approach and makes it a better method in reconstructing ancestral states over the parsimony approach is that it incorporates both topology and branch-lengths. Another advantage of a Bayesian reconstruction is that the marginal probabilities are assigned to nodes and thus the level of confidence can be gained for any assignment. Ancestral area and habitat reconstructions were implemented in Mesquite (Maddison and Maddison 2006) with the idea of tracing the evolution of area and habitat among francolins and spurfowls. Bayesian and parsimony phylogenetic trees were appended to the input files and the analyses were performed under the mk1 model (Lewis 2001).

Spatial analysis of vicariance

Distributional ranges of taxa were analysed and an overlap of up to 25% was accepted as a disjunct distribution. The cost of overlapped (i.e. non-disjunct) distributions was set to the default of 1.00 and the cost for removal of distribution was 2.00, which means that a removal was only accepted if it was found at least in one additional pair of disjunct sister groups. To detect barriers, a simple hill climbing heuristic search was performed starting with a sector of 20 nodes over 1000 iterations during which a "flipping nodes" strategy was used. This procedure is quite effective when the distributions are close together, but it becomes less accurate for distributions placed far away, as it is placed in the line that is equidistant to each point.

Phylogenetic analyses

Bayesian and parsimony methods were used in analysing combined mitochondrial and nuclear DNA data partitions from Chapter 2, 4 to 6, and the combined organismal (Chapter 4, 5 and 6) and DNA data partitions, respectively. The francolin and spurfowl trees were each rooted with the most basal taxon among members of these assemblages, that is, *F. francolinus* for the francolins and *P. hartlaubi* for the spurfowls. Combined organismal and DNA parsimony analyses consisting of 5141 characters of francolins and 5203 characters of spurfowls were performed and these characters were used to build the strict consensus trees (the boldest hypotheses of relationship) implemented in TNT (Tree analysis using New Technology - Goloboff et al. 2008). All characters were equally weighted and treated as non-additive. It must be noted that, in order to reduce the denseness of taxa on the tree, the phylogenetic trees presented only included taxa that are recognized in Chapter 5 and 6. The settings for the analyses followed the option of a full heuristic search with the starting tree(s) being obtained via stepwise addition and random addition of sequences (Maddison 1991) over 1000 replicates. One tree was held at each step during stepwise addition. The tree-bisection-reconnection option was implemented and Farris et al.'s (1996) jackknife measure was used to assess branch support over 1000 pseudoreplicates.

Bayesian analyses of the combined mitochondrial and nuclear DNA characters for francolins (5116 bp) and spurfowls (5170 bp) were implemented in MrBayes 3.1.2 (Ronquist and Heulsenbeck 2003). The francolin and spurfowl Bayesian analyses excluded one taxon each, *O. r. spilogaster* and *P. castaneicollis atrifrons*, respectively due to unavailability of DNA characters. Over and above parsimony analyses, the use of a Bayesian approach was to investigate the influence of mixed models (parameter-rich) on the phylogeny. Modeltest 3.7 (Posada and Crandall 1998) was used to search for the best-fit model for each molecular marker and each codon data partition for CYT*B* and ND2. The parameters for the model considered were those under the Akaike Information Criterion (AIC). The best-fit model of nucleotide substitution suggested for all the data partitions was the GTR+I+G model. These analyses involved two independent runs (with random starting trees) and they proceeded without a molecular clock being imposed upon the rate of sequence evolution.

The Markov Chain Monte Carlo (MCMC) for the spurfowl and francolin data set was run for 3 x 10^6 and 1.5 x 10^6 generations, respectively, sampling every 100^{th} generation using four chains (one cold and three heated). Tracer v 1.5 (Rambaut and Drummond 2007) was used to check the 'burn-in' phase and the state of convergence of the two parallel runs: 300 000 and 150 000 trees from the burn-in phase for the spurfowls and francolins, respectively, were discarded and convergence was attained when the average deviation of split frequencies converged towards zero. Finally, the 50% majority rule consensus of sampled trees (excluding the burn-in) was obtained with posterior probabilities (PPs) appearing above nodes.

Results

Ancestral state reconstructions

Even though the parsimony ancestral area and habitat reconstructions of francolins and spurfowls were performed, the results were used for comparison with those for the Bayesian reconstructions irrespective of the differences inherent in the methodology of these two approaches. The results discussed in subsequent sections are based solely on Bayesian reconstructions.

Francolins – area and habitat

Figure 7.1 and 7.2 respectively show the Bayesian reconstructions through which the ancestral area and habitat among Asian and African francolins were traced. The marginal probabilities are assigned to each node and these are estimated based on the regional and habitat data that were incorporated into the input file and they indicate the confidence that each state can be assigned at a particular node. Figure 7.1 showed mixed results, e.g. some nodes such as 1, 7, 9, 10, 11, 12 have probabilities above 0.90; node 2, 6, 14 were assigned with probabilities between 0.80 and 0.90 and the rest of the nodes showed great uncertainties. The root, node 1, points to southern Asia being the ancestral area that gave rise to all other francolins. Node 3 links the Asian francolins and the rest of Africa, but with very low probabilities (0.52 and 0.36) being assigned to the rest of Africa and Asia, respectively. The immediate link of Asia and Africa is at node 4, which links the Asian *O. gularis/O. pondicerianus* and the African *Ortygornis* clade (Fig. 7.1). The probabilities are very low with the proportions 0.48 and 0.40 pointing to southern Africa and southern Asia respectively as being the ancestral areas. These species possibly evolved in scrubby grassland habitats (probabilities of 0.99).

Afrocolinus lathami is the only West African (and forest endemic) species supported with a probability of 0.99. This species probably made its way to the forest habitat from a scrubby grassland ancestor. The Red-tailed and the Red-winged clade (node 6) are truly southern African clades supported with 0.88 probability of which the probability assigned to their ancestral habitat (Fig. 7.2) is uncertain. Within the Red-tailed Group clade (node 7), members share a most recent common ancestor in southern African (0.99 probability) that likely thrived in wooded grasslands from which these clades diversified in other parts of Africa i.e., two species spread to West Africa (*P.*

albogularis and *P. spinetorum*), one to Central (*P. schlegelii*) and two to East Africa (*P. maharao* and *P. hubbardi*). When these species diversified in different parts of Africa they retained the ancestral preference of wooded habitats with a slight difference being that *P. albogularis* occurred in mesic woodlands, whereas the other three species occurred in arid woodlands.

Seemingly, the most recent common ancestral area of the Red-winged taxa (node 10) was in southern Africa (0.91 probability), although this clade underwent its greatest diversification in East Africa. Most species inhabit open grasslands, three species, with two taxa (*S. psilolaema psilolaema* and *S. ellenbecki*) that went into montane grasslands in East Africa and one species *S. afra* made its way to montane grasslands in southern Africa. *Scleroptila streptophora* spread to the scrubby mesic habitat in Cameroon and around Lake Victoria that differs from that of its former group member *O. sephaena* that mainly occupies arid scrubby grasslands and woodlands. Thus, the Red-winged Group diversified into mesic, arid, and montane grasslands. The Striated members spread from the south to East Africa and the probability assigned to this node is 0.80. *O. grantii* and *O. r. spilogaster* occupy arid scrubby habitat. The nominate *O. r. rovuma* occupies mesic scrub habitat. It seems that, in Africa, francolins diversified out of southern Africa, spreading mainly to the East, then West and *P. schlegelii* (inhabitant of savanna and arid woodlands) evolved in central Africa where it remained isolated. The Red-tailed diverged to occupy both mesic and arid woodland habitats.

Spurfowls – area and habitat

The likelihood reconstruction for area (Fig. 7.3), unlike that for habitat (Fig. 7.4) exhibited ambiguity at several nodes with respect to the ancestral distribution of spurfowl. Although with a low probability of assignment the root node suggests southern Africa as the potential ancestral area. Habitat reconstruction (Fig. 7.4) showed some support (0.64) for tracing all spurfowls back to forest (node 1).

The Bare-throated Group/*P. clappertoni/P. leucoscepus/P. swainsonii* (node 7 which combines node 8 and 9) is assigned with a low probability values with east Africa (0.47) being favoured to be an ancestral area over southern Africa (0.40). With regard to habitat, taxa that thrive in mesic woodlands (*P. rufopictus, P. cranchii, P. a. afer, P. a. humboldtii* and *P. l. leucoscepus, P. l. infuscatus, P. swainsonii*) are reconstructed as occupying savanna and arid woodlands with high probability (0.95; Fig. 9.12). Node 4 joins the Montane Group (forest inhabitants) to *P. clappertoni* (savanna and arid woodland), *P. a. afer* (mesic woodlands), *P. c. sharpii*, *P. harwoodi* and the Bare-throated Group, and is reconstructed to likely have had a forest ancestor with a probability of 0.70. The most recent common ancestor of *P. b. bicalcaratus, P. b. adamauae, P. icterorhynchus, 'ayesha'* has a savanna and arid woodland ancestor (0.87 probability).

In Fig. 7.4, node 10 connects the Scaly Group and the southern Vermiculated clade has the highest probability of 0.72 and this is in support of a forest ancestor, while the most recent common ancestor of the Scaly Group is supported with 0.99 probability to have lived in forest in southern Africa (0.68). The probability of 0.89 supports the southern African origin of the Vermiculated species *P. adspersus, P. capensis, P. hildebrandti,* and *P. natalensis. Pternistis hildebrandti* has its distribution in southern and eastern Africa. Most of the nodes on the ancestral area reconstruction showed great uncertainty in the assignment of marginal probabilities. It is, however, clear that colonization of areas happened more than once with the exception of North Africa where *P. b. ayesha* has an isolated distribution in Morocco in the macchia type of habitat. Areas too were colonized more than once except for the lowland fynbos, a home for *P. capensis.*

Spatial analysis of vicariance

The spatial analysis of vicariance of francolins yielded two reconstructions from which a consensus reconstruction analysis was performed yielding the best score associated with a cost of 9.0, and 320 hits of 1000 iterations. Thirty optimum disjunct sister groups were recovered and these disjunctions are mapped at nodes on the parsimony tree (Fig. 7.5). The spurfowl distribution ranges resulted in one reconstruction with 28 optimum disjunctions (Fig. 7.6) accompanied by a best score with a cost of 6.0 for 471 hits of 1000 iterations.

The history of evolution of distribution ranges

Francolins **-** The phylogenetic results confirmed that the Asian francolins are the most basal of all francolins and the main geographic barriers exist around the Indian sub-continent (Fig. 7.7a-b). The first break being near the Windhya Range of Mountains (Fig. 7.7a), that are located in Rajasthan, south of Delhi, between *F. francolinus* and *F. pictus* (node 1, Fig. 7.5). According to Hall (1963), Rajasthan has no clear natural barrier. Thus, it remains uncertain whether the Windhya Range and possibly the Ganges tributaries should be considered effective physical barriers. The Ganges River in northeast India separates *Francolinus pictus* from *F. pintadeanus* (Fig. 7.7b, node 2 in Fig. 7.5) as well as the Asian/African francolin clade represented by all taxa restricted to the sub-Saharan region.

The Naga Hills in Burma in addition to the Chin Hills and the Manipur Range as alluded to by Hall (1963) act as the possible barriers between *F. pintadeanus* and the Asian+African francolin clade (Fig. 7.7c, node 3 in Fig. 7.5). The disjunction (node 4 in Fig. 7.5) between the clade that includes members of *Ortygornis* and the African clade circumscribed by *A. lathami/Peliperdix/Scleroptila* is associated with a barrier that runs along the Rift Valley system down to the south and in the west meets the Congolian forest, setting itself as the main barrier in the south separating the African *Ortygornis* taxa on the east, from the rest of the African francolins in the west (Fig. 7.7d). Another barrier is set by the Limpopo River in the south separating the African *Ortygornis* clade from specifically *S. levaillantii* and *S. afra* in the area where they overlap (Fig. 7.7d).

The barrier between the *O. gularis/O. pondicerianus* clade and the *O. sephaena/grantii/rovuma* clade (node 5 in Fig. 7.5) is quite ambiguous, because in this case the barrier could be any intervening feature, possibilities include the: Arabian Sea, and the large rivers and mountain ranges in Pakistan and Iran (Persia) (Fig. 7.7e). The disjunction that exists within the clade that includes *O. pondicerianus + O. gularis* and *O. sephaena/grantii/rovuma* clade might be an indication of colonization of Africa by the clade ancestor from Asia or a return of the clade ancestor to Asia. In colonizing Africa, the clade ancestor landed itself on the east side of the Rift Valley system thereby inhabiting arid habitats. The *O. pondicerianus/O. gularis/O. sephaena* clade diverged c. 7.2 mya (Chapter 2). The estimated age for the formation of the Rift Valley is c. 6 mya. It could be speculated that the clade ancestor possibly crossed the Rift system diversifying in central and west Africa occurring along the mesic Congolian and Upper Guinea forests.

Within the *O. sephaena/grantii/rovuma* clade, the Zambezi River acts as the major barrier that separates *O. sephaena* (in the south) and the *O. grantii* clade in the north (Fig. 7.7f). The Rufiji River separates the southern African *O. r. rovuma* from *O. grantii* (Fig. 7.7h) whereas the northeastern *O. r. spilogaster* is separated from *O. grantii* by the Ganane Basin and possibly the Ethiopian Rift (Fig. 7.7g). In addition, the difference in habitat, xeric versus mesic scrub, seems to have an influence within the *O. sephaena/grantii/rovuma* clade. The xeric habitats differ in the amount of mean annual rainfall received, ~400-800 mm where *O. sephaena* and *O. grantii* occurs, ~200-400 mm where *O. r. spilogaster* occurs (Clark 1967). The mesic scrubs receive the mean annual rainfall of ~800-1600 mm and this is occupied by *O. r. rovuma*. The mesic versus xeric habitat preference seems to set itself as the possible barrier between the southern *O. r. rovuma* and its northern counterpart *O. r. spilogaster* (Fig. 7.7h). There is a disjunction (node 9 in Fig. 7.5) between the *A. lathami/Peliperdix* and *Scleroptila* clades (Fig. 7.7i). The Congolian and the Upper Guinea forest emerged to be effective breaks between the two clades. While there is no detected barrier to separate *A. lathami* and the *Peliperdix* clade, the west African forest population *A. l. lathami* is set apart from the central *A. l. schubotzi* by the Congo Basin (Fig. 7.7j). Both taxa occur in high rainfall areas of above 3200-4000 mm annually (Clark 1967).

Due to the presence of a disjunction in just one of the reconstructions, there was no barrier detected between node 11 and node 14 in Figure 7.5 which links the *P. schlegelii/P. albogularis* and *P. coqui* clade. Therefore, there are no definitive barriers to infer between *P. schlegelii* and *P. albogularis* (Fig. 7.7k, node 11 in Fig. 7.5), between *P. a. dewittei* and *P. albogularis albogularis/P. a. buckleyi* clade (Fig. 7.7l), node 12 in Fig. 7.5) and also between *P. a. albogularis* and *P. a. buckleyi* (Fig. 7.7m). Both clades occur in habitats that receive similar amounts of annual rainfall (800-1600 mm).

The occurrence of *P. a. dewittei* on montane wooded grasslands south of the Congo forest (Cotterill 2006) could be attributed to the fact that during the time when Africa was wet the forest may have formed a continuous belt from west Africa through to central and down to south central Africa (Clark 1967, Crowe and Crowe 1982). During this time the proto-*albogularis* may have had a continuous distribution along the forest belt. During a dry period (possibly glaciation), forest contracted and formed pockets leaving *P. a. dewittei* being isolated south of the Congo. Morphologically, there are subtle differences between *P. a. albogularis* and *P. a. dewittei* which relate to the size and extent of barring on the underparts. The predicted mean annual rainfall in areas where *P. a. albogularis* and *P. a. dewittei* occur is 100-1400 and 1400-1800 mm, respectively.

Within the clade that includes *P. stuhlmanni/P. kasaicus* and *P. c. coqui/P. c. vernayi/P. c. ruahdae/P. hubbardi/P. maharao/P. spinetorum* (node 14 in Fig. 7.5), the Rovuma River was detected as an effective barrier that exists on the east at least between *P. stuhlmanni/P. hubbardi* and *P. maharao* in the south the Limpopo River for a barrier separating *P. stuhlmanni* from *P. c. coqui/P. c. vernayi* (Fig. 7.7n). *P. kasaicus* is separated from the other taxa in this clade, but there is no definite barrier attributable to this disjunction. *Peliperdix kasaicus* and *P. stuhlmanni* both occur in mesic conditions which differ in areas where the mean annual rainfall is 1000-1400 mm. The mesic woodland *P. c. ruahdae* (800-1600 mm of mean annual rainfall) on the west is separated from *P. hubbardi,* which occurs in much more xeric habitat to the east around Lake Victoria and Lake Tanganyika (400-800 mm of mean annual rainfall) (Fig. 7.7o).

The southern African *P. c. coqui* and *P. c. vernayi* are separated by the Okavango swamp (Fig. 7.7p) with *P. c. ruahdae* and *P. c. vernayi* being separated by the mesic and arid habitat respectively (Fig. 7.7q). The area between the Ethiopian and the East African Rift might possibly be the barrier separating *P. hubbardi* from *P. maharao* in Malawi (400-800 mm of mean annual rainfall), whereas all the remaining taxa occur in arid savanna (including *P. spinetorum* 200-400 mm of mean annual rainfall) (Fig. 7.7r). Habitat separation definitely has an influential role among these disjunctions.

The first divergence within the *Scleroptila* clade led to the separation of *S. streptophora/S. levaillantii* from the rest of the *Scleroptila* taxa (Fig. 7.7s, node 21 in Fig. 7.5). The *Scleroptila* taxa mainly occur in xeric environments. In the south the Limpopo and Zambezi Rivers act as barriers between *S. levaillantii* and the other *Scleroptila* taxa (Fig. 7.7t), whereas northern Lake Tanganyika and the Rufiji River separate the east African *S. streptophora* population from the other *Scleroptila* taxa (Fig. 7.7u). Mesic habitat links the two west and east *S. streptophora* populations that occur on either side of the Congo Basin. It is quite strange that not even habitat links the disjunct west and east African *S. streptophora* populations with those of southern African *S. levaillantii*. *Scleroptila streptophora* has a puzzling distribution being found in grasslands in Cameroon where the annual rainfall reaches ~2600-3200 mm and in east Africa (800-1600 mm) and it was included in the Striated Group together with *O. sephaena* by Hall (1963). From examination of museum skins of the two populations of *S. streptophora,* there were no differences observed. The two species *S. streptophora* and *O. sephaena* are distinct morphologically and at least ecologically (Hall 1963), but the east African population shares almost the same type of habitat with that of *O. sephaena*. *Scleroptila streptophora* occurs in mesic habitat (at an altitude ranging from 1050–1200 m in Cameroon and 600-1800 m in scrub-covered hillsides in east Africa – del Hoyo et al. 1994), whereas *S. levaillantii* is found in xeric to mesic habitats (Fig. 7.7t) at an altitude of 600-2 250 m (Hall 1963, Snow 1978) and the mean annual rainfall of 600-800 mm.

The disjunction between the *S. psilolaema* and *S. uluensis/S. shelleyi* is not associated with any detectable barrier. However, the African Great lakes (Lake Victoria, Lake Tanganyika, Lake Malawi) form a barrier that separate *S. psilolaema* from *S. finschi* (Fig. 7.7v), with *S. finschi* being separated from *S. whytei/S. jugularis* (Fig. 7.7w, node 25 in Fig. 7.5). The African Great lakes appear to be effective barriers between *S. uluesis* and *S. shelleyi* (Fig. 7.7x), whereas *S. gutturalis* and *S. uluensis* are separated by the Ethiopian Rift, with but taxa occurring in xeric grassland habitats (Fig. 7.7y). Among members of the *S. shelleyi/S. levaillantoides* and the *S. ellenbecki* clade, the distribution ranges of *S. shelleyi* and *S. levaillantoides* are maintained by two breaks, Lake Malawi in the north and the Limpopo River in the south (Fig. 7.7z). *Scleroptila shelleyi* and *S. levaillantoides* overlap in the southern part of their ranges and there was no detectable barrier. The mean annual rainfall is the area according to Clark (1967) is 600-800 mm, i.e. in areas where *S. levaillantoides*, *S. shelleyi*, *S. levaillantii* occur and 400-600 mm in areas where *S. afra* occurs. The impact of the African Great Lakes is also observed between *S. c. crawshayi* and *S. c. kikuyuensis* (Fig. 7.7aa, node 30 in Fig. 7.5). The ranges of the taxa that belong to *S. ellenbecki* have no barriers detected among them and they are completely disjunct. The Zambezi and

Limpopo valleys appear to be effective barriers among some of the species and this confirms the findings in Benson et al. (1962).

Spurfowls - the results in Figure 7.8a reveal that the most basal disjunct node (1 in Fig. 7.6) is associated with a barrier that separates the clade comprising *Ammoperdix heyi* from the rest of the African spurfowls. The Red Sea emerges to be the main barrier with some overlap along the Bab al Mandab Mountains that lie between the Red Sea and the Gulf of Aden. The barrier may have resulted from the opening of the Red Sea. The barrier between *A. heyi* and *P. asiatica* (Fig 9.8b, node 2 in Fig. 7.5) could be anything between Saudi Arabia and India with the possible barriers being the Arabian Sea, and the rivers and mountain ranges in Pakistan and Iran.

It is possible that dispersal route may have started in Asia, into Saudi Arabia and subsequently into Africa or *vice versa*. It is somewhat difficult to explain clearly how Africa was colonized by the ancestral-spurfowl, but to some extent it could have been that the ancestral-spurfowl dispersed from Asia along the desert of Saudi Arabian coast and settled in the desert in the south western part of Africa i.e., in Namibia and south western Angola where *P. hartlaubi* occurs (Fig. 7.8c). The ancestral-*hartlaubi* diversified to other parts of Africa from the desert habitat. Whereas *P. hartlaubi* is said to occur in savanna and arid woodlands where the mean annual rainfall is below 100 mm (Clark 1967), it has been observed in boulder-strewn slopes and rocky outcrops (Komen 1987, Sinclair and Ryan 2005). The subsequent Africa spurfowl radiation involved the evolution of the montane lineage that includes species that were confined to the mountain forests. The first break, the African Great Lakes is detected between the clades comprising *P. nobilis* and *P. swierstrai* (node 4 in Fig. 7.6) with habitat acting as another barrier (Fig. 7.8d). *Pternistis nobilis* and *P. camerunensis* inhabit the mesic montane forest occurring on the extreme side of the Congo Basin, whereas the other taxa that they are being compared with in this context are found in arid savannas and they are both separated by the Congo forest (Fig. 7.8e). *Pternistis nobilis* occurs in an area where the mean annual rainfall is ~ 800-1600 mm, whereas *P. camerunensis* is endemic to an area which receives an average of more than 3200 mm of rain annually. The disjunction exists between the Angolan highlands endemic species *P. swierstrai* and the north eastern *P. c. castaneicollis* clade, and this separation is mainly promoted by habitat differences, mesic versus xeric environment, even though they all occur in forests (Fig. 7.8f). The separation seems large such that vegetation alone may not explain the present distribution.

The main barrier between the *P. c. castaneicollis* clade and the other spurfowls (especially *P. jacksoni* as other ranges are removed) is the area that forms part of the Rift Valley system between the Ethiopian and the East African Rift as they are generally found in similar habitat (Fig. 7.8g, node 7 in Fig. 7.6). There is a slight overlap between the clades comprising *P. c. castaneicollis* and *P. ochropectus* along the Ethiopian Rift (Fig. 7.8h). The distribution ranges of *P. c. castaneicollis* and *P. c. atrifrons* are possibly maintained by part of the Ethiopian Rift (Fig. 7.8i). *Pternistis erckelii* and *P. ochropectus* prefer similar habitat, they are montane forest species, with the exception of *P. erckelii,* which sometimes wanders into montane grasslands. Their distribution ranges are also maintained by part of the Ethiopian Rift (Fig. 7.8j).

The disjunction that exists between *P. ahantensis* and *P. icterorhynchus* cannot be explained geographically because the sister groups were removed (Fig. 7.6). Figure 7.8k shows the detected barrier between *P. ahantensis* and *P. griseostriatus* clade (node 12 in

Fig. 7.6) which cuts through east of Lake Victoria, along Lake Tanganyika (where they slightly overlap) separating the two clades into mesic versus somewhat xeric habitat taxa with the Congolian and Upper Guinea forest being effective barrier between the northern and the southern taxa. The Niger River strongly separates *P. ahantensis* which occurs in the far west in the Upper Guinea forest from *P. squamatus* (Fig. 7.8l) which is mainly confined to the Congolian forest while *P. s. squamatus* is separated from *P. s. schuetti* by the area between the Ethiopian and the East African Rift (Fig. 7.8m). *Pternistis griseostriatus* is endemic to Angola and occurs in riverine forest (Sinclair and Ryan 2005). The *P. griseostriatus* clade also include the southern Vermiculated species *P. capensis, P. natalensis, P. hildebrandti* and *P. adspersus* that occur along the arid belt which acts as a barrier between them and *P. griseostriatus* (Fig. 7.8n). In Figure 7.8o, it is apparent that *P. capensis* and *P. natalensis* clades (node 16 in Fig. 7.6) are dissected by the Okavango swamps along the area of slight overlap whereas they are all found in the intervening arid habitats. Between *P. capensis* and *P. adspersus* the Orange River emerges as an effective barrier (Fig. 7.8p) whereas the Zambezi River and Lake Malawi separate *P. hildebradti* from *P. natalensis* (Fig. 7.8q). Lake Malawi also acts as a barrier between *P. h. hildebrandti* and *P. h. fischeri* along the area where they overlap slightly (Fig. 7.8r).

Although some parts of the mesic and arid savannas are covered, the Upper Guinea and the Congolian forest act as a barrier between the clades that include *P. icterorhynchus* and *P. clappertoni/P. leucoscepus* along the area where they overlap (Fig. 7.8s, node 20 in Fig. 7.6) with *P. icterorhynchus* and *P. bicalcaratus* being separated from each other by the Niger River and Lake Chad (Fig. 7.8t). The Volta and Niger River likely both play a role in breaking *P. b. adamauae* from *P. b. bicalcaratus* clade (Fig. 7.8t) with the isolated Moroccan *P. b. ayesha* being strongly separated from *P. b. bicalcaratus* by the Sahara Desert (Fig. 7.8t). The spurfowls occur in almost the rest of the sub-Saharan region with the exception of *P. bicalcaratus* that expanded its range to Morocco in north Africa where *ayesha* occurs (Fig. 7.8a).

Spurfowl typically occur in various montane/lowland habitats as well as xeric/mesic habitats that vary in mean annual rainfall. The Ethiopian Rift may have been effective in maintaining the break between the *P. clappertoni* and *P. leucoscepus* clades (Fig. 7.8u). The eastern branch of the East African Rift and possibly the Rufiji River separate the distribution range into *P. leucoscepus* clade in the north and *P. swainsonii* clade in the south (Fig. 7.8v, node 25 in Fig. 7.6), with *P. l. leucoscepus* and *P. l. infuscatus* being separated by the Ethiopian Rift (Fig. 7.8w). No barrier was detected between the *P. swainsonii* and the *P. rufopictus* clade, whereas *P. cranchii* is separated from *P. rufopictus* by the Rift Valley system in the east and the Congolian forest in the west (Fig. 7.8x).

Pternistis cranchii primarily occurs in mesic woodlands. Habitat seems to be playing a role in maintaining the break between *P. rufopictus* and *P. a. afer* (Fig. 7.8y). According to Hall (1963), they all occur along the acacia belt that is differentiated by different *Acacia* species. *Pternistis rufopictus* occupied largely the mesic part with *P. a. afer* and *P. a. humboldtii* getting into the dry and mesic parts. The Zambezi River strongly separates the two subspecies *P. a. afer* and *P. a. humboldtii* (Fig. 7.8z).

Discussion

Reconstruction of ancestral area and habitat

Francolins and spurfowls

On the basis of the results, it was difficult to determine where the ancestor of francolins could have lived based on the evolution of area, whereas in terms of habitat, it could be concluded that the ancestor of francolins likely evolved in scrubby grassland. Even though the spurfowl area reconstruction had the poorest probabilities assigned to nodes, habitat reconstruction suggests that the ancestral distribution was restricted to forest. However, it was difficult to draw definitive conclusions on the basis of the area and habitat maximum likelihood reconstructions due to uncertainties in nodal probabilities assigned to states among francolins and spurfowls.

The two biogeographic methods, one focusing on 'detecting barriers' and the other one focusing on 'mapping of ancestral areas and habitat' both seek to explain the history of distribution ranges of taxa, but differ in their underlying theoretical applications. Even though both applications made use recovered phylogeny, the ancestral reconstructions seem uncertain when there is poor phylogenetic resolution. In the context of francolins and spurfowls, the spatial analysis of vicariance results provided a much better picture on the history of their distribution patterns.

Spatial analysis of vicariance

Francolins

Some barriers that were detected among the Asian species are geologically and geographically associated with the Indian sub-continent. While it may be possible that *F. francolinus* and *F. pictus* are ecologically separated, the Wandhya Range seems unlikely to be a significant barrier. The Asian species generally have different habitat preferences. *Ortygornis gularis* is confined to marshes and reeds in the plains of the Ganges River, *O. pondicerianus* occurs in the Gulf of Oman in the plains of India, *F. pictus* inhabits the plains of India, whereas *F. pintadeanus* occurs in marshes and hills such as the Naga and Chin and Manipur range.

Francolinus francolinus prefers mountainous areas for example, the Himalayan Mountains in Nepal, and extending to the west reaching Iran and Afghanistan. The results here suggest that habitat type could have been an effective ecological break between these *F. francolinus* and *F. pictus*. The Naga and Chin Hills as well as the higher ranges of Manipur are effective barriers along most of the boundary between *F. francolinus* and *F. pintadeanus* even though the two species might be expected to meet along the coastal strip.

It could be possible that speciation may have started around the India–Eurasia border even though the actual age of this event has always been uncertain. The latest evidence points to c. 40 mya (Bouilhol 2013) while the split between *Gallus/Bambusicola*/francolins and *Coturnix/Alectoris*/spurfowls is at around 33.6 mya which is Oligocene. Plate tectonics may have led to the formation of different topographical features such as the Himalayan Mountains and the Kūhha-ye-zāgros in Iran. At the same time during collision the ancestral species may have been able to disperse into Africa possibly cutting through south eastern Saudi Arabia into Africa. The unfavourable era may have pushed the range of the ancestral species southwards, isolating the ancestral stock of the three species in south western Asia that is where *F. francolinus* currently occurs, southern India (*F. pictus*) and south eastern Asia where *F. pintadeanus* occurs.

The Oligocene to Miocene is said to have marked the start of generalized cooling, with glaciers forming in Antarctica for the first time. The increase in ice sheets led to a fall in sea level while the tropics diminished, giving way to cooler woodlands and grasslands. Diversification of habitat has occurred with *A. lathami* being the only francolin species that is endemic to primary forest. Among the *Scleroptila* taxa, there is a somewhat weaker, but possible retreat of some of the species to montane areas possibly seeking the favourable habitat. Examples of these are the southern African *S. afra*, the east African *S. p. psilolaema, S. p. theresae* and *P. ellenbecki*.

Scleroptila afra and *S. levaillantii* have sympatric distributions, but they are divided altitudinally (del Hoyo et al. 1994, Little and Crowe 2000, Sinclair and Ryan 2005). The *Peliperdix* taxa are all found in arid or mesic wooded savannas. Habitat preference seems to play an influential role among members of the *P. coqui* clade. They all occur along the dry belt differing in the amount of annual rainfall that is received in those areas with the exception of *P. c. kasaicas* and *P. stuhlmanni* which occur in mesic habitats with mean annual rainfall of 800-1600 mm. The Rift Valley system which includes the Great African lakes (Lake Victoria, Lake Tanganyika, Lake Malawi), the Upper Guinea and the Congolian forest, major rivers such as the Limpopo, Zambezi and Rovuma may have played a crucial role in maintaining the distribution ranges of francolins.

The two streaked subspecies, the northern *O. r. spilogaster* (xeric scrubs) and the southern *O. r. rovuma* (mesic scrubs) are separated by habitat types which are characterized by difference in the amount of rainfall received in a year.

Spurfowls

A number of nodes have disjunctions that can be explained by geography and had detectable barriers associated with them. It is possible that the tectonic effect that resulted from the collision of Africa with Asia may have caused the clade ancestor to disperse along the Saudi Arabian coast into Africa moving to the desert in southwest Africa. *Pternistis hartlaubi* is the most basal spurfowl which probably is a paleo-endemic species that occurs in the desert of Namibia and southwestern Angola where the mean annual rainfall is below 100 mm. The India-Saudi Arabia-Africa route and vice versa is quite possible with difficulty arising with regard to understanding how different parts of Africa including different habitats were colonized as the spurfowls diversified within various bushy habitats. However, it seems possible that, in Africa, diversification may have been initiated in southwestern Africa where *P. hartlaubi* occurs and subsequently followed by the radiation into forests of montane areas (Clark 1967). During this dry period the range of forest was reduced leading to montane forest pockets being occupied by the few species that preferred these kinds of habitat. Some species such as *P. squamatus, P. ahantensis and P. griseostriatus* remained in lowland forests, while others remained in other lowland habitats such as mesic and arid bushy and wooded grassland habitats and diversified there. Habitat type is clearly linked to the rainfall amount that each habitat type receives and this clearly separate out parts even within species.

The Rift Valley system is acting as an effective barrier that is maintaining the ranges of most of the spurfowl distributions, for example among the north eastern and east African montane spurfowls, among the Bare-throated taxa *P. leucoscepus/P. swainsonii/P. rufopictus/P. afer,* between *P. clappertoni/P. harwoodi* and the Bare-throated clade, as well as between the *P. squamatus/P. ahantensis* and *P. griseostriatus/*southern Vermiculated species clade. Major rivers such as the Niger, Volta, Zambezi, Orange and Rufiji River have played significant roles as barriers. The Upper Guinea and Congolian forest, Okavango swamp and also the mesic versus arid habitats were found to be effective barriers.

Conclusions

The history of taxa can never be explained with ease because history is generally unknown. The colonization of Africa by the ancestral species may have been through dispersal which resulted in the formation of disjunct distributions and the somewhat rapid diversification of francolins and spurfowls in Africa. Even though francolins and spurfowls evolved at almost the same time that is, during the Miocene francolins (c. 7.6 mya) are slightly younger than spurfowls (c. 8.7 mya). However, the main divergence between these two lineages occurred at around 33.6 mya in the Oligocene and this is probably the initial speciation of genus *Francolinus* around India. The major physical breaks that may have maintained the distributions and at the same time promoted speciation among the African francolins were the Rift Valley system which includes the Great African lakes (Lake Victoria, Lake Tanganyika, Lake Malawi), Lake Chad, the Upper Guinea and the Congolian forest, and major rivers such as Limpopo, Zambezi and Rovuma River. The diversity in habitat for example, xeric/mesic savanna versus mesic savanna, montane and lowland grasslands and forest habitat has also played an important ecological role in facilitating diversification among francolins. Among spurfowls, similar barriers as those among francolins were inferred with the addition of the Niger and Rufiji River, Okavango Swamp and Sahara Desert acting as barriers between some taxa.

In conclusion, the overall possible biogeographic explanation among francolins is that the ancestral species may have dispersed from Asia to Africa and later possibly returned to Asia. If Asian and African species are monophyletic, it could be fitting that during the collision of Asia and Africa some individuals remained in Asia while others remained in Africa resulting in the two groups differentiating with subsequent speciation occurring on both continents. In this case, the Asian *Ortygornis gularis* clade is sister to the *O. sephaena* complex clade and this fits the former explanation.

The direction of dispersal is difficult to determine for the spurfowls. One possible explanation on the origin of the spurfowls is that the ancestor may have dispersed from Asia, into the desert of Saudi Arabia along its coast and then into Africa where it eventually arrived in the desert in south western Africa. Generally, there is support for Hall's (1963) hypothesis on the evolution of the genus *Francolinus* having dispersed from Asia where its related genera occur, as opposed to Crowe and Crowe (1985) and Bloomer and Crowe's (1998) hypothesized African origin of the genus *Francolinus*. Despite that the ancestral area and habitat from the maximum likelihood reconstructions were highly undecided, the spatial analysis of vicariance results at least clearly demonstrated that the ancestral francolin was Asian and they lived in dry and mesic scrubby and wooded grassland habitat.

It is important to note that since the two approaches (spatial analysis of variance, ancestral character reconstructions) are dependent on the phylogeny, poor phylogenetic resolution influences the pattern. In other words, phylogenetic signal plays a core role in the outcome of the analyses and in the absence of well-resolved phylogenies, informed ancestral patterns cannot be traced and the colonization route can hardly be determined. The maximum likelihood ancestral area and habitat reconstruction provided little and decisive insight into the history of the distribution of ranges of francolins and spurfowls, and a genomic approach to data collection may be required to fully resolve spurfowl relationships.

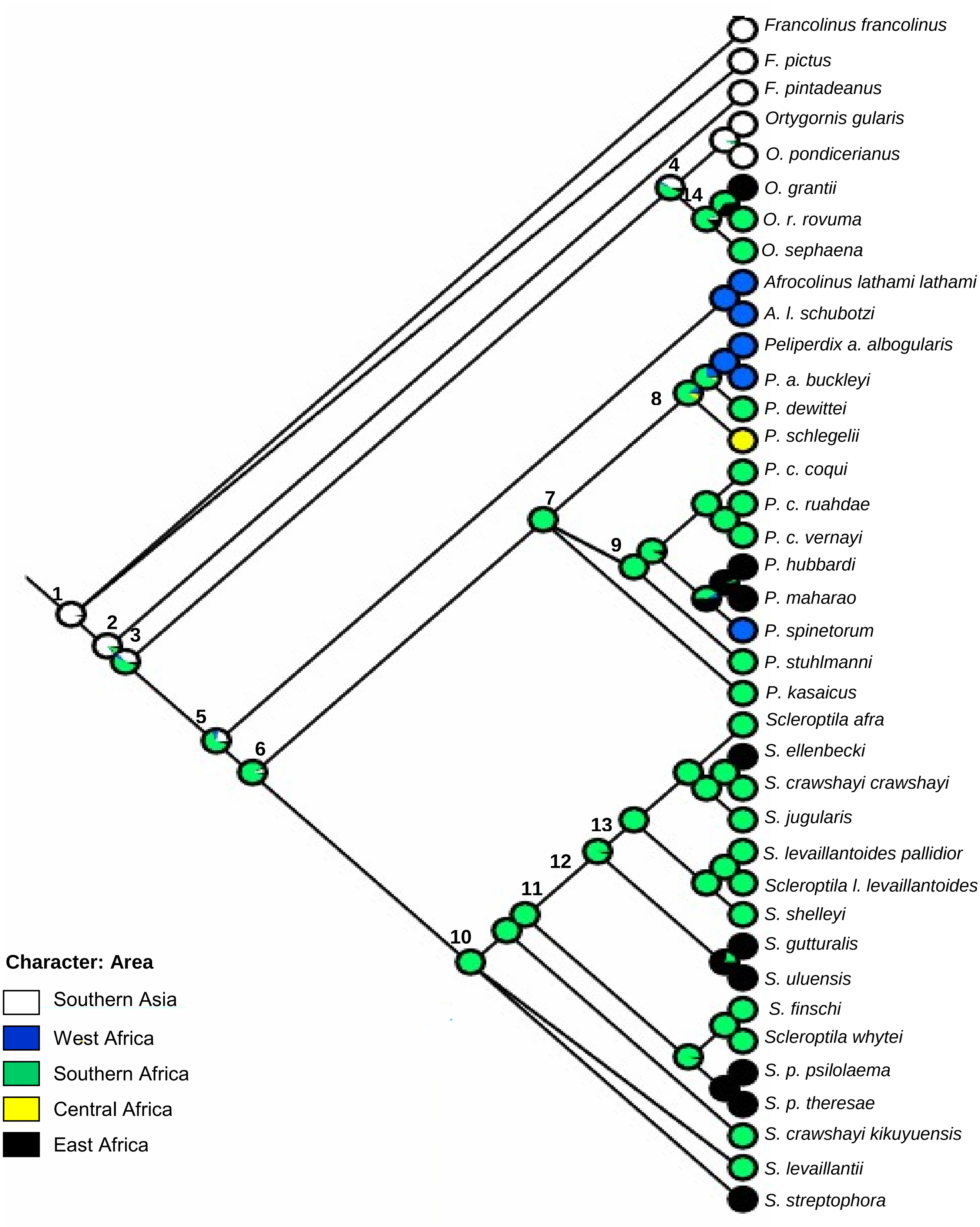


Figure 7.1. The Bayesian reconstruction of ancestral area of francolins inferred from Bayesian topology and branch-lengths. Numbers 1-14 identifies the nodes they are associated with. The marginal probabilities are not mapped on the tree but references to them are in the main text.

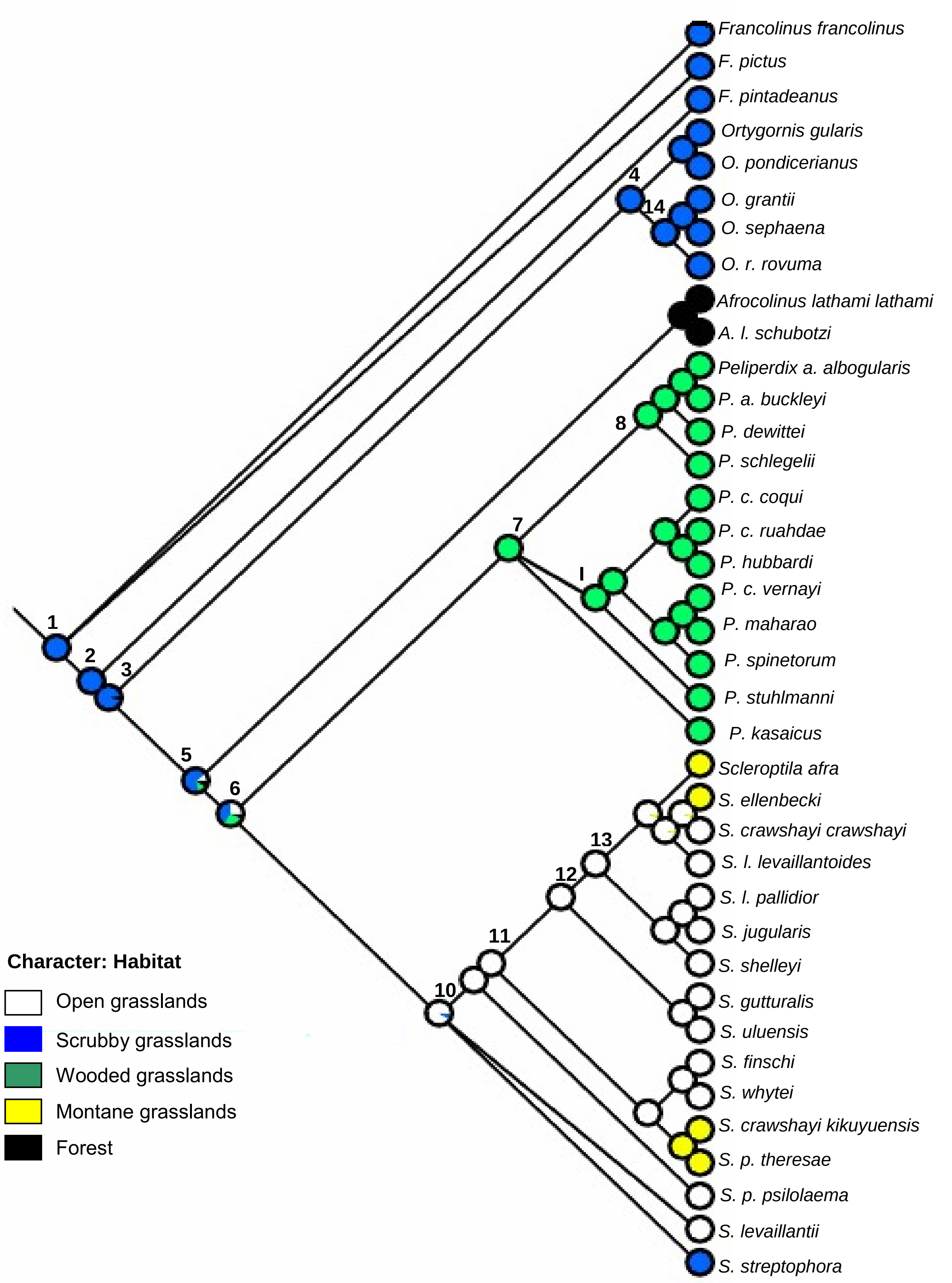


Figure 7.2. The Bayesian reconstruction of ancestral habitat of francolins inferred from Bayesian topology and branch-lengths. Numbers 1-14 identifies the nodes they are associated with. The marginal probabilities are not mapped on the tree but references to them are in the main text.

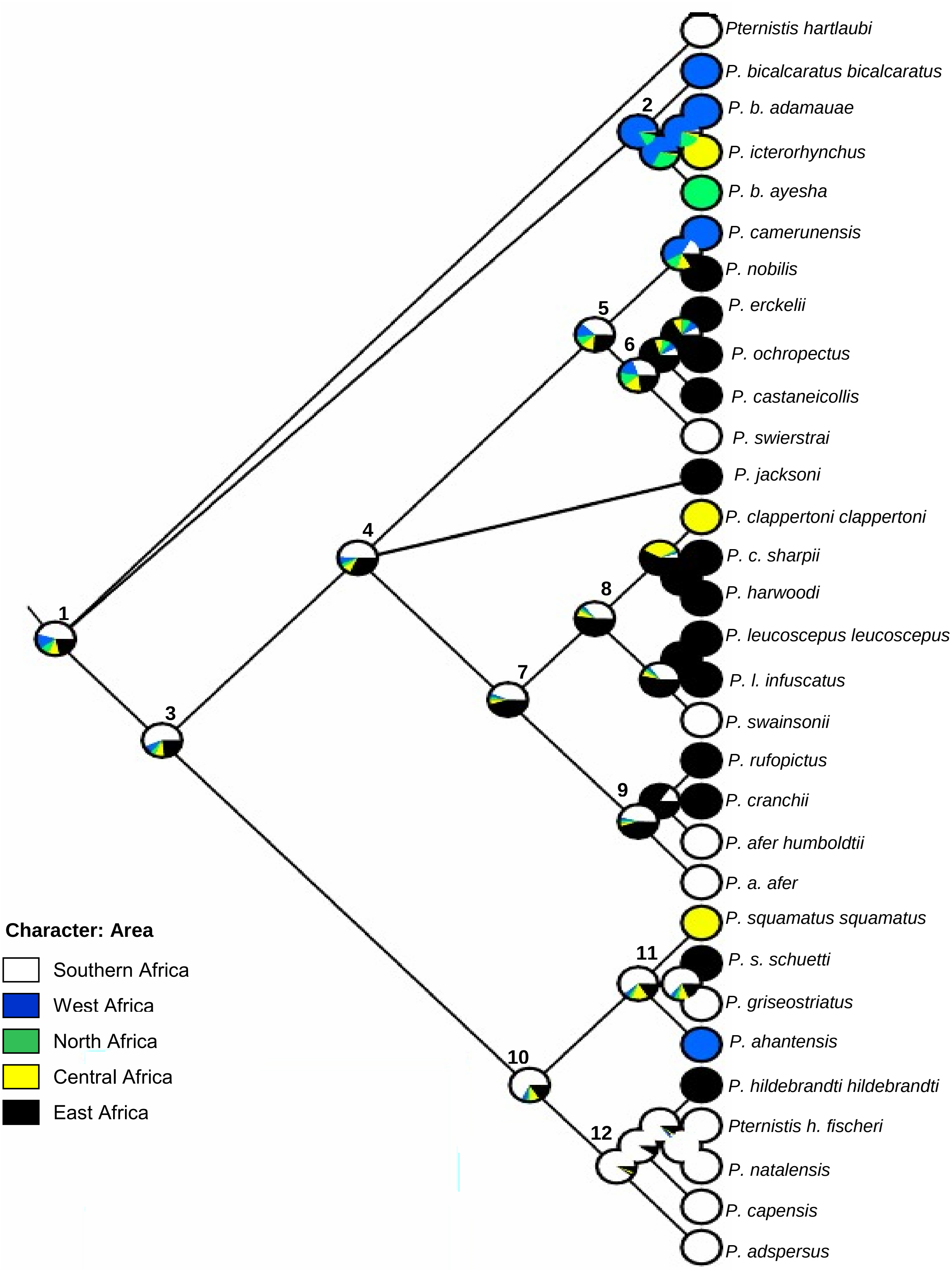


Figure 7.3. The Bayesian reconstruction of ancestral area of spurfowls inferred from Bayesian topology and branch-lengths. Numbers 1-12 identifies the nodes they are associated with. The marginal probabilities are not mapped on the tree but references to them are in the main text.

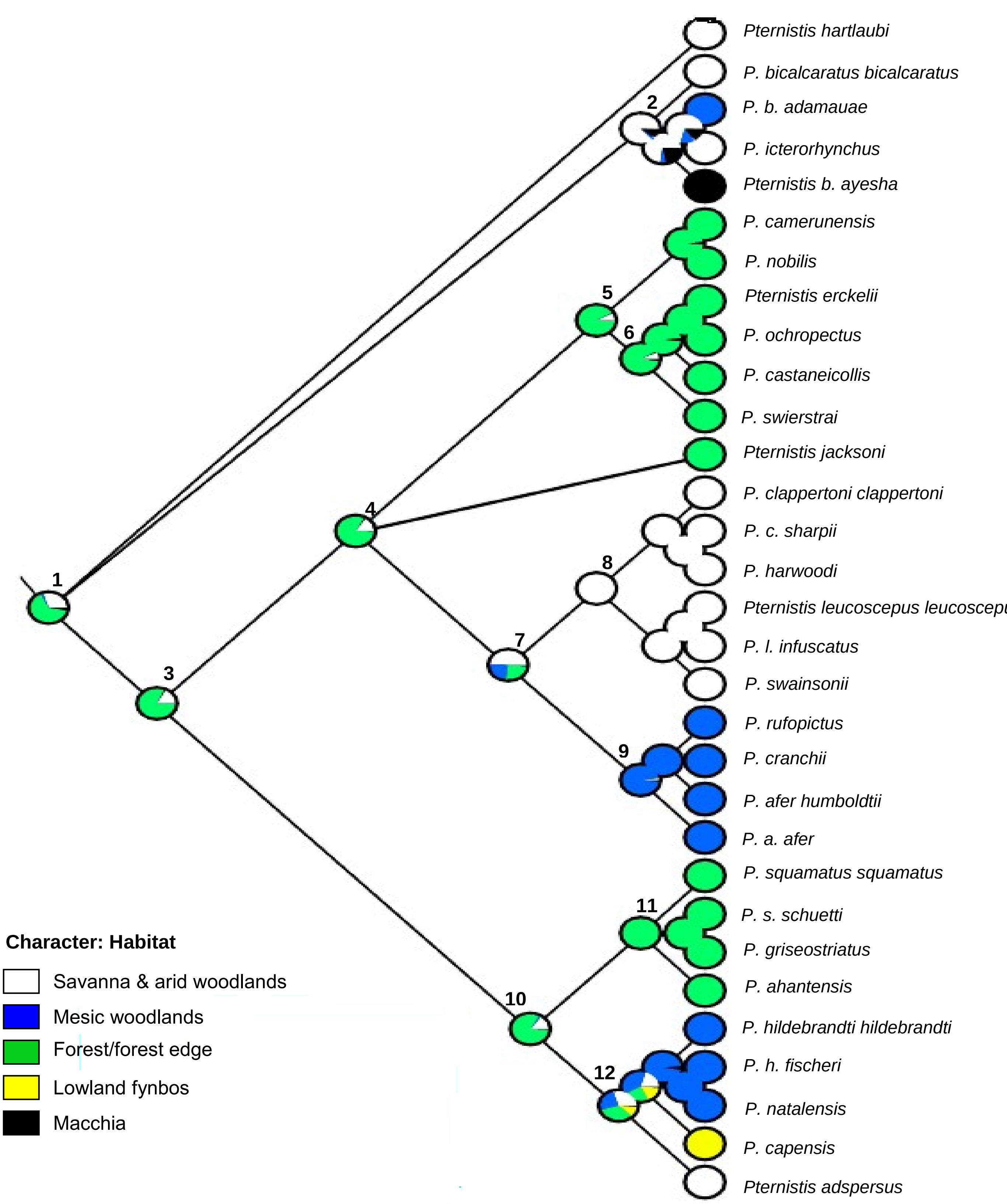


Figure 7.4. The Bayesian reconstruction of ancestral habitat of francolins inferred from Bayesian topology and branch-lengths. Numbers 1-12 identify the nodes they are associated with. The marginal probabilities are not mapped on the tree but references to them are in the main text.

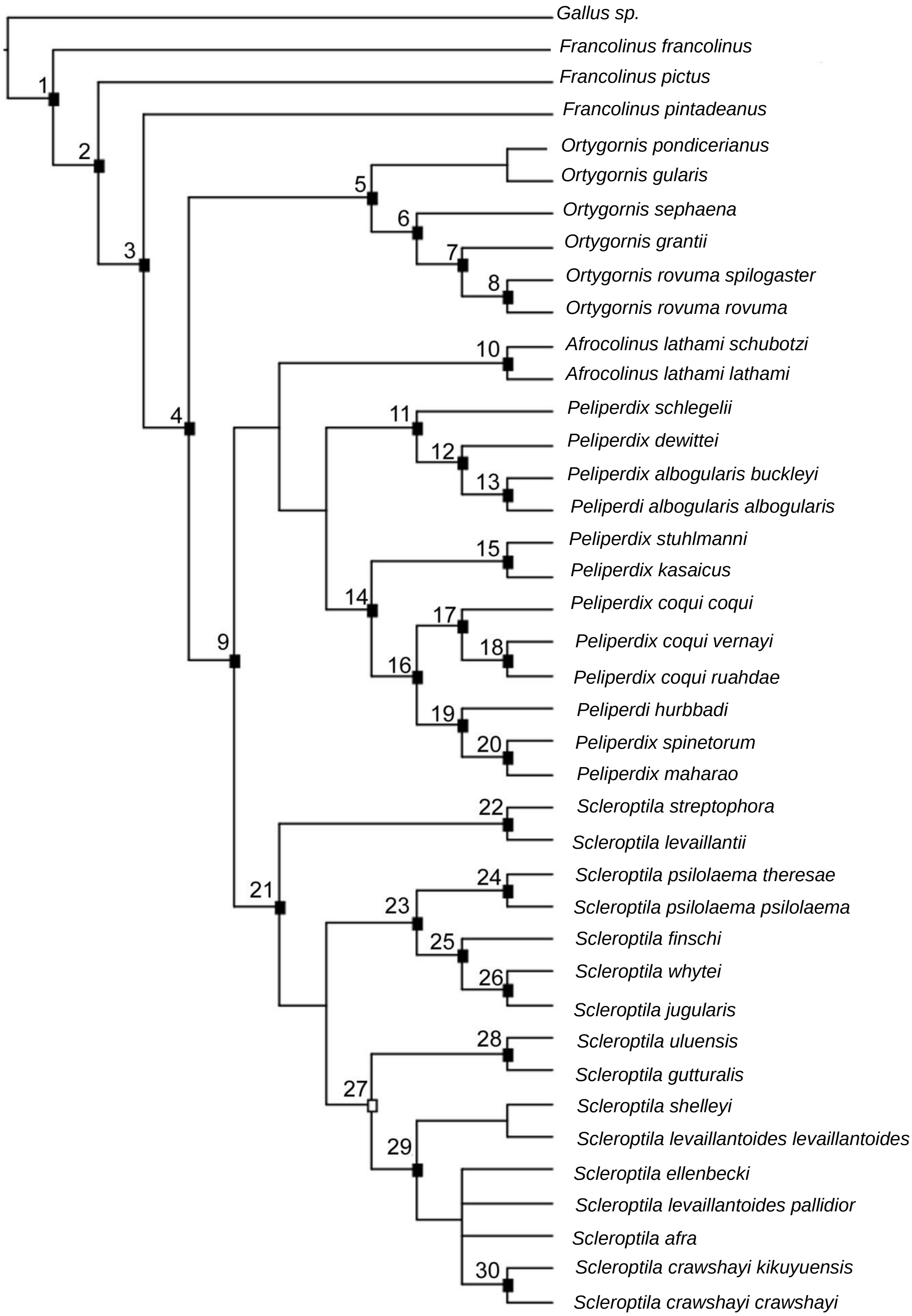


Figure 7.5. The francolin parsimony tree showing disjunct nodes which are associated with barriers (filled black squares) and disjunct nodes indicative of removed distribution (unfilled squares). The unmarked nodes could not be explained geographically due to large overlap in distributions.

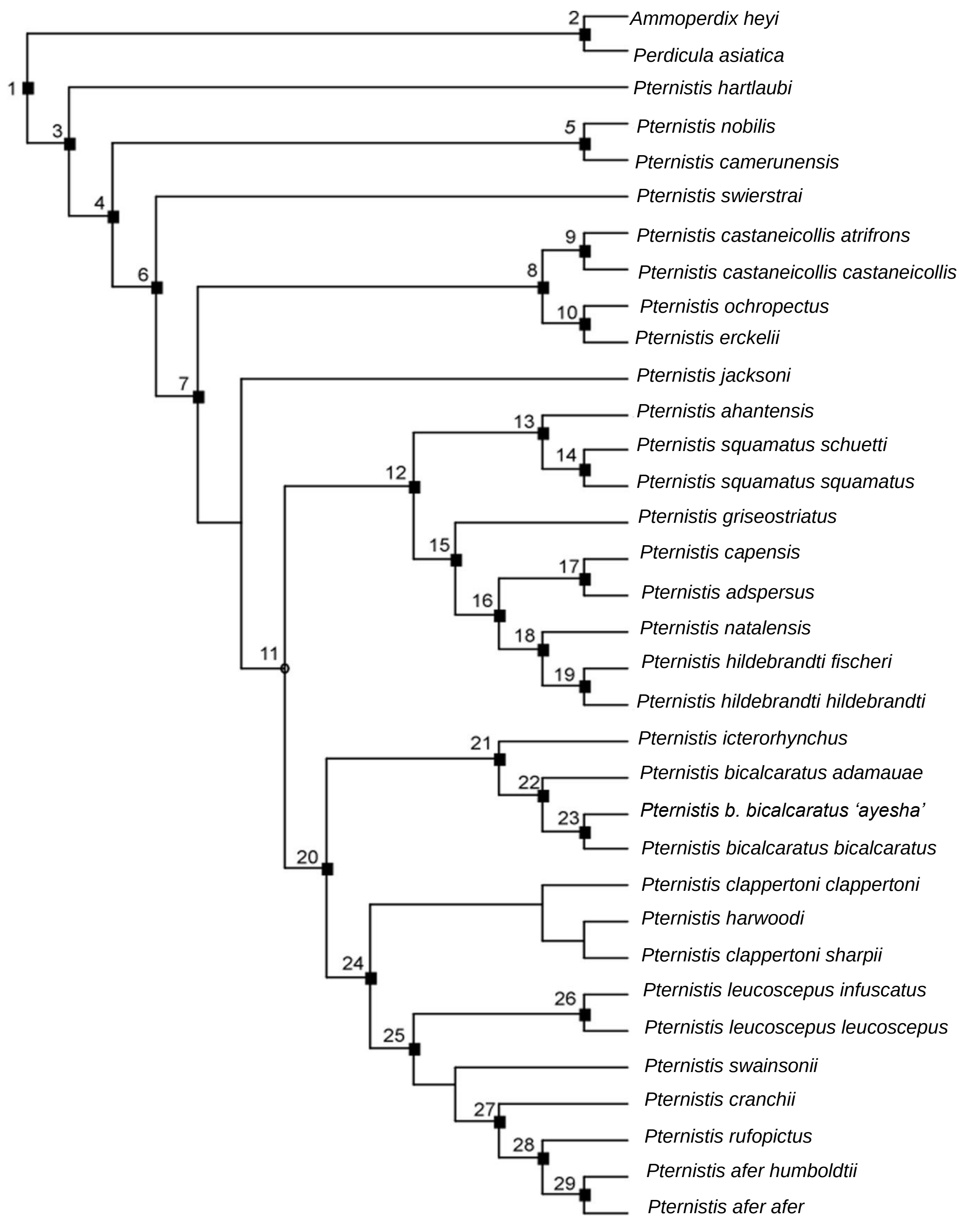


Figure 7.6. The spurfowl parsimony tree showing showing disjunct nodes which are associated with barriers (filled black squares) and disjunct nodes indicative of removed distribution (unfilled squares). The unmarked nodes could not be explained geographically due to large overlap in distributions.

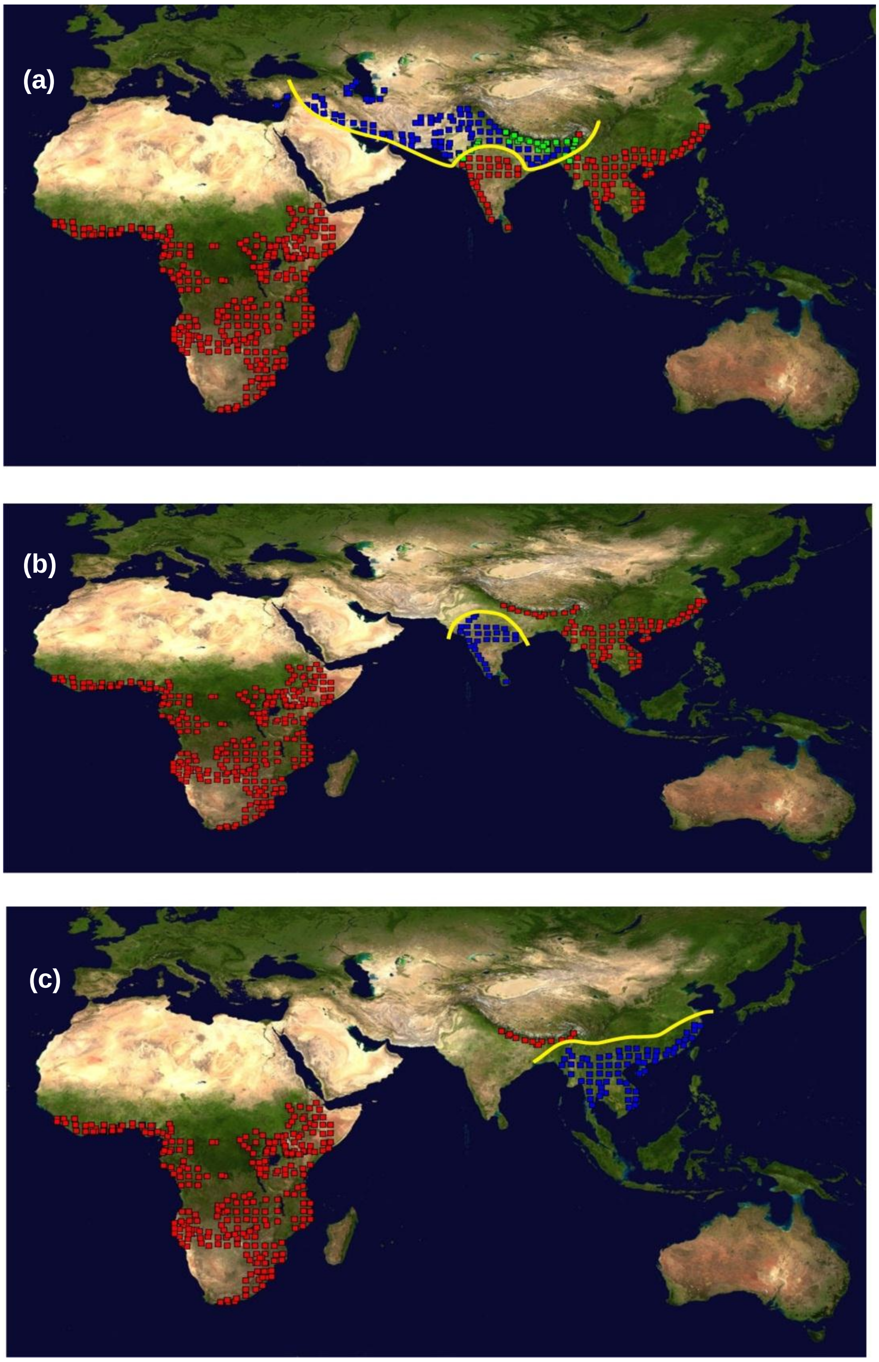


Figure 7.7 (a-aa). The range maps of francolins indicating where barriers lie between each the two circumscribed clades that are being compared. The range in blue is a reference taxon/clade which is compared to the range of the taxon/clade in red. The yellow lines are barriers detected, whereas the red and dark blue lines are connecting lines. Green grids indicate area of overlap of distribution ranges.

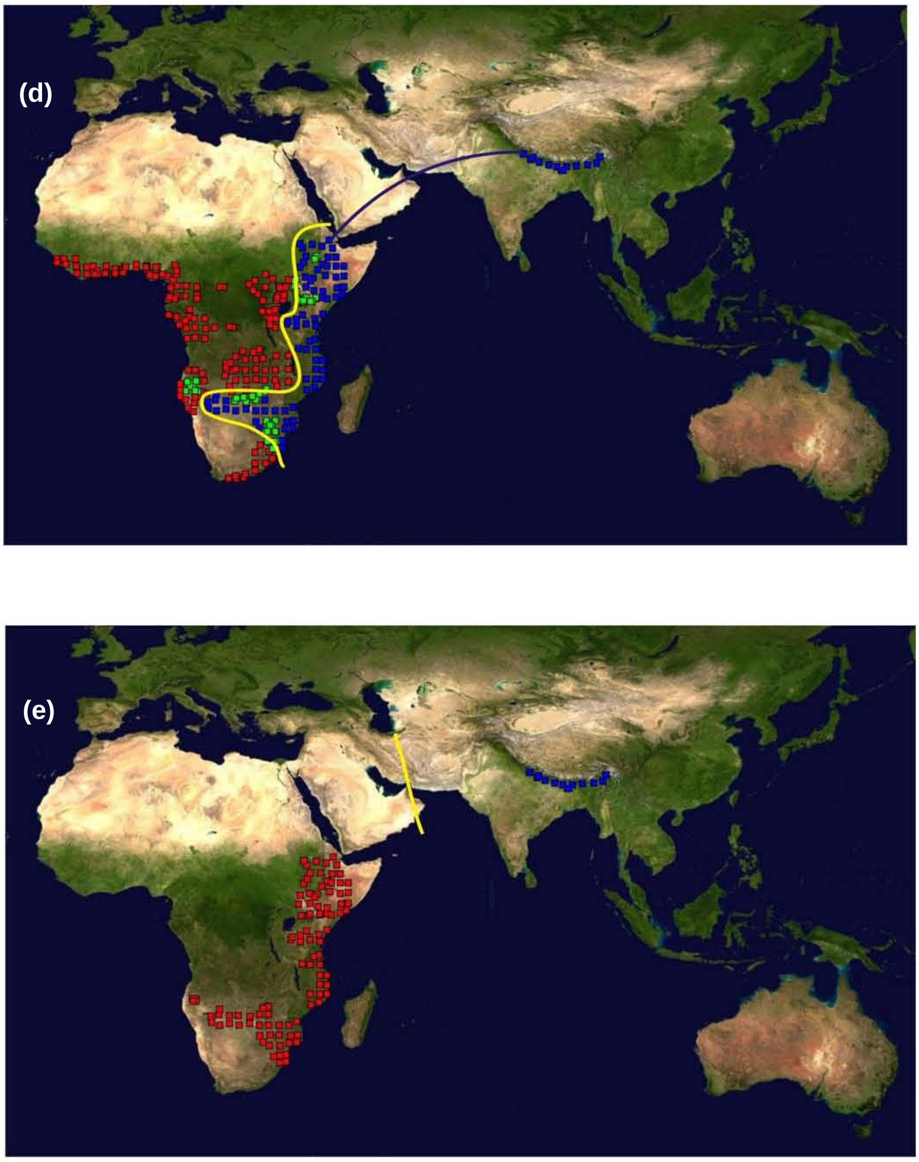


Figure 7.7. (cont.)

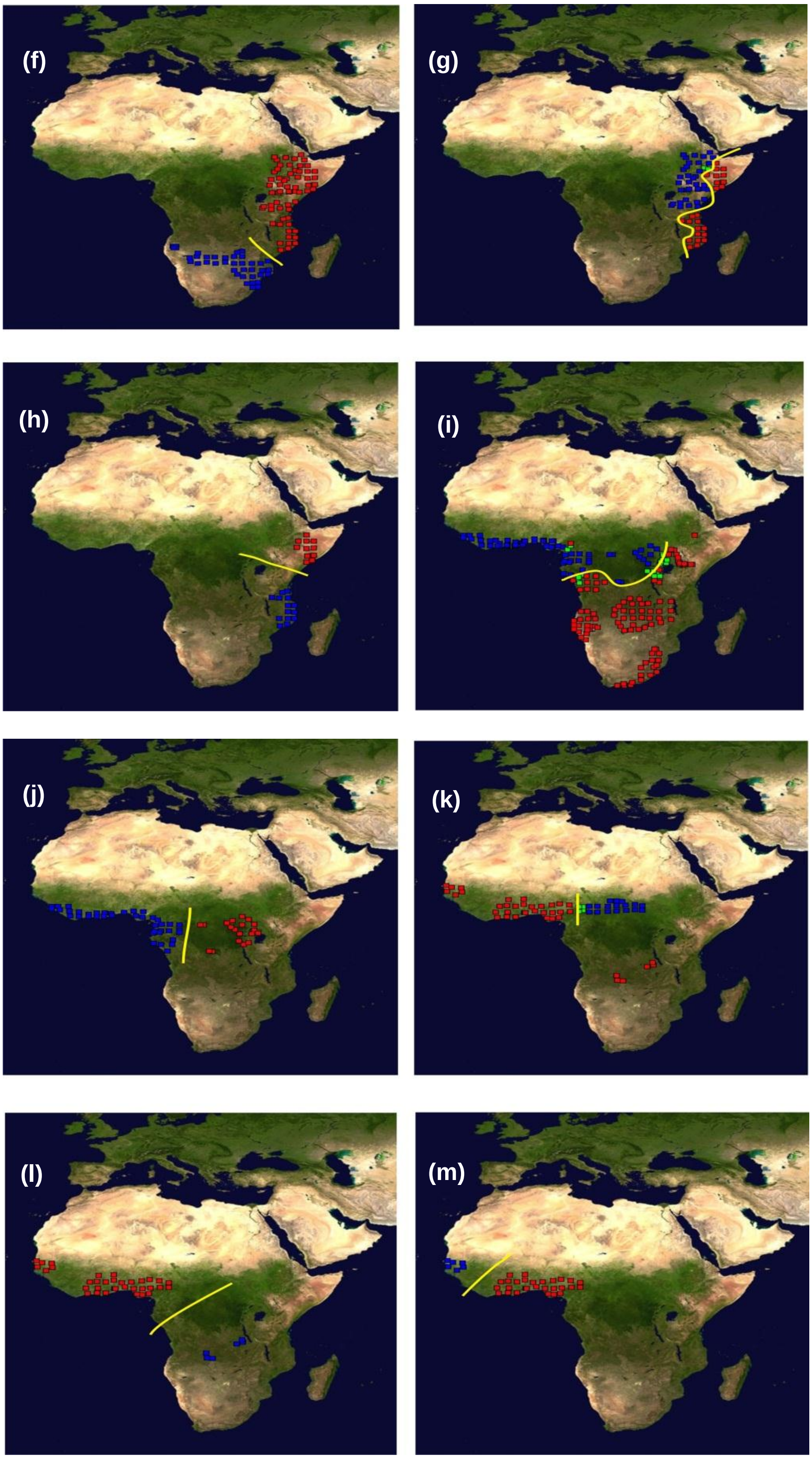


Figure 7.7. (cont.)

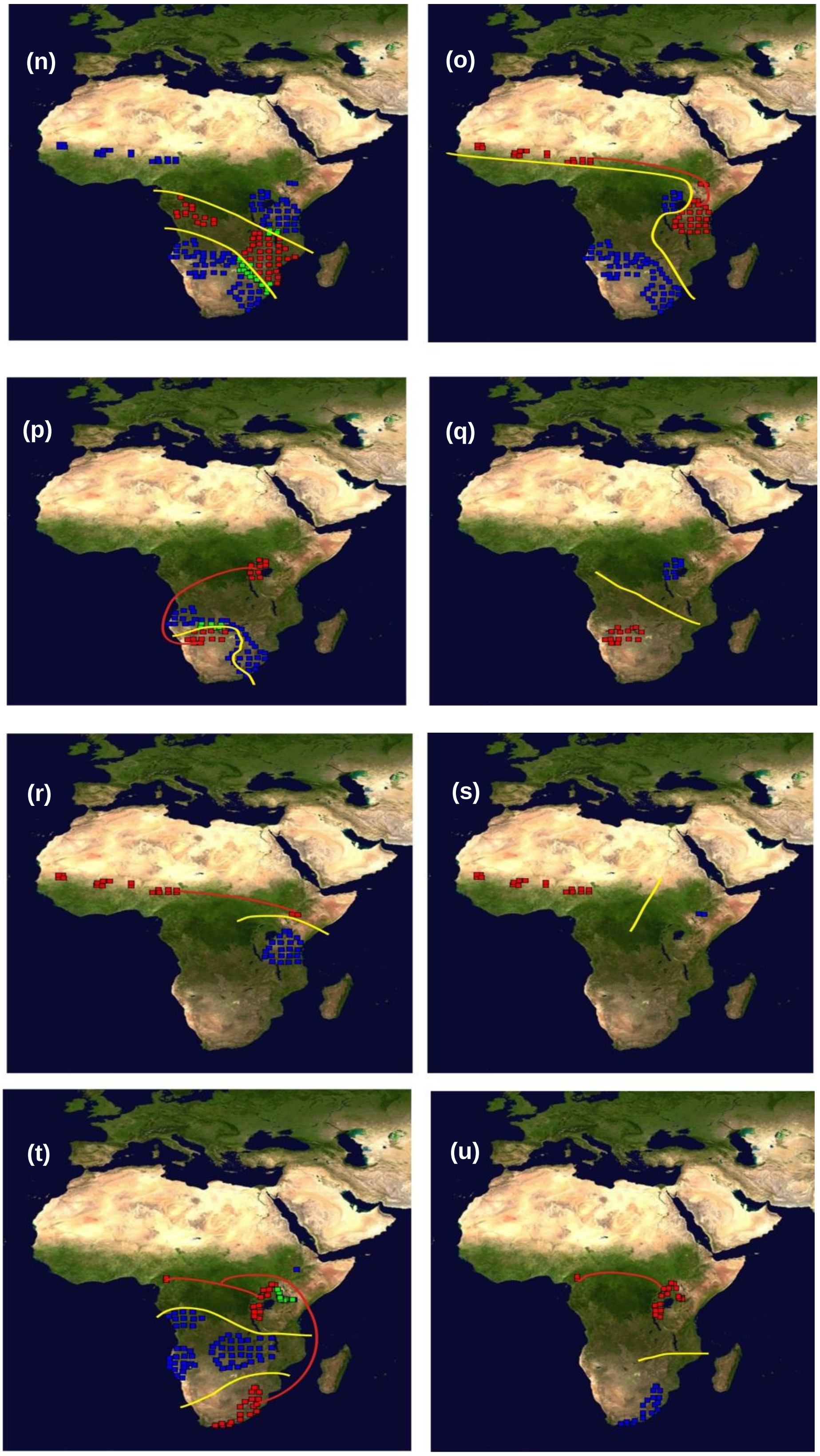


Figure 7.7 (cont.)

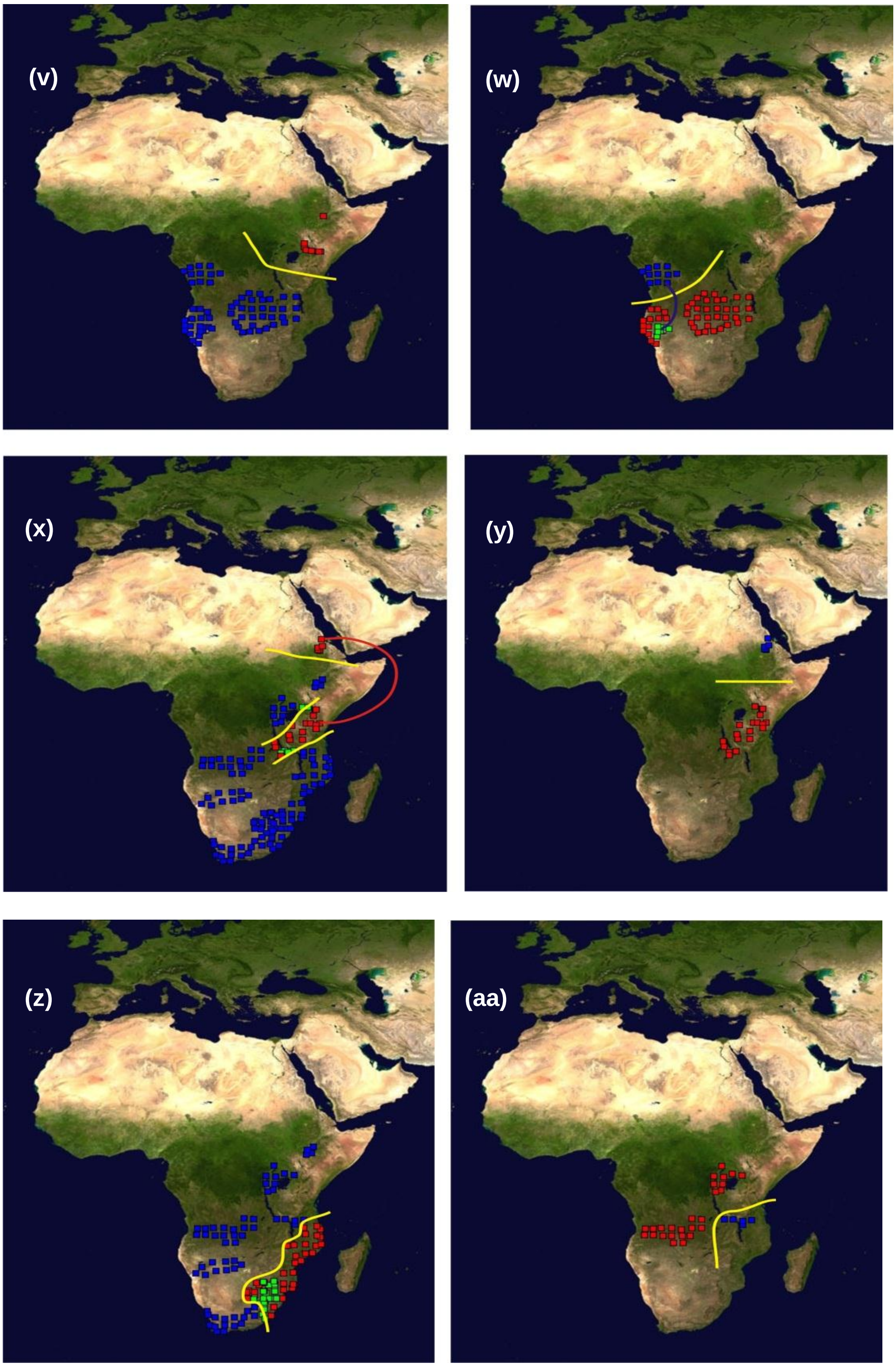
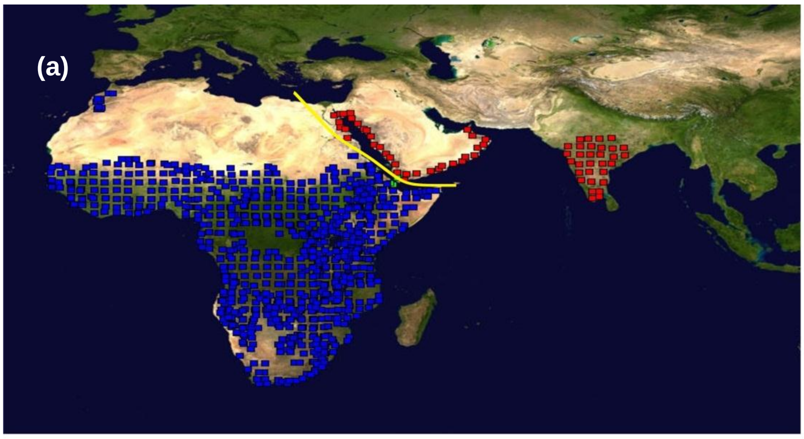


Figure 7.7 (concl.).



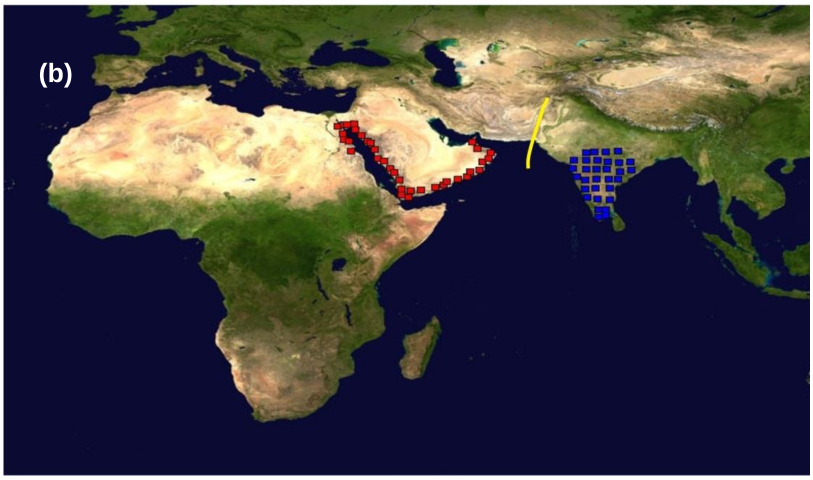


Figure 7.8 (a-z). The range maps of spurfowls indicating where barriers lie between two clades that are being compared. The range in blue is a reference taxon/clade which is compared to the range of the taxon/clade in red. The yellow lines are barriers detected whereas the red and dark blue lines are connecting lines. Green grids indicate areas of overlap of distribution ranges.

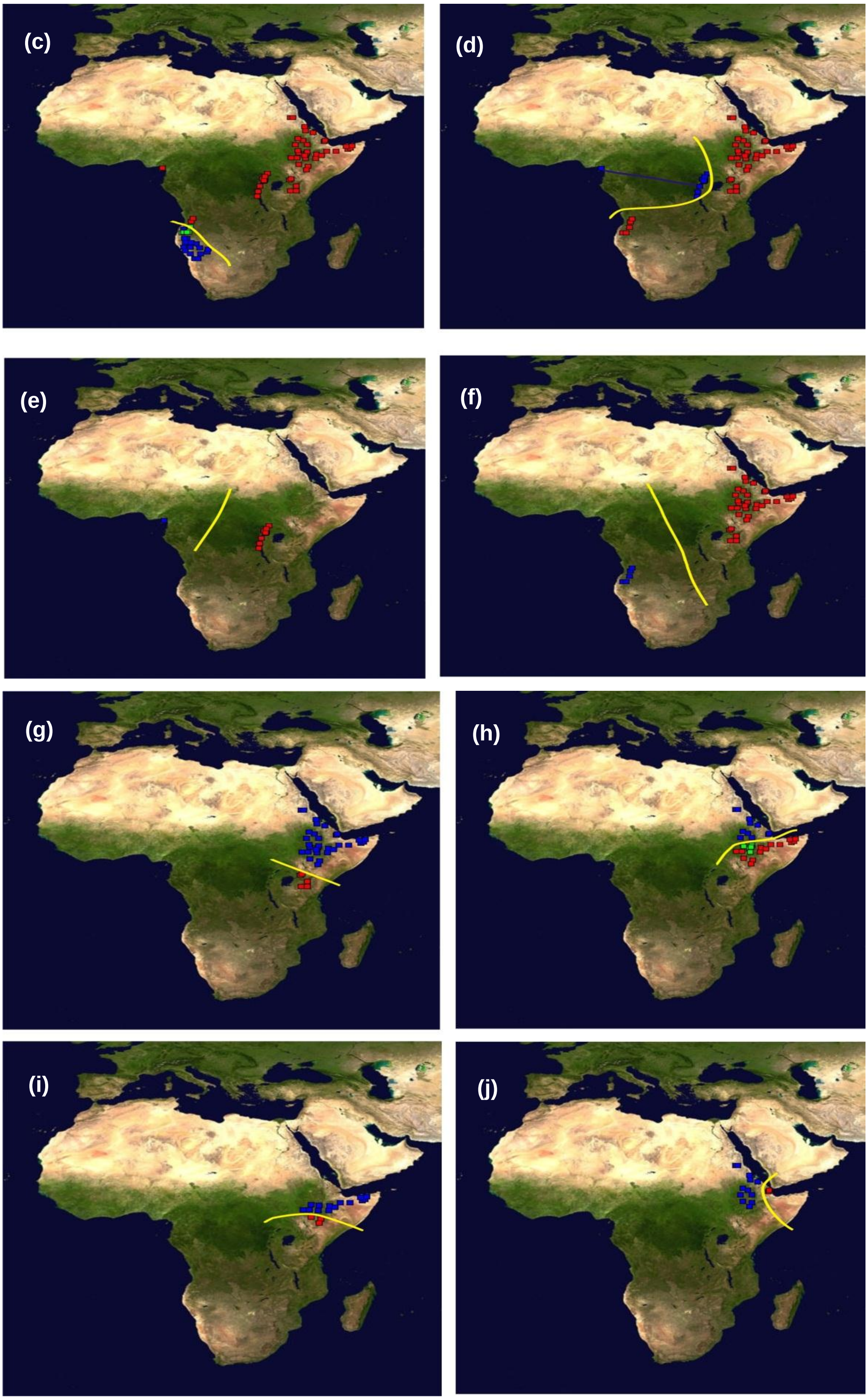


Figure 7.8. cont.

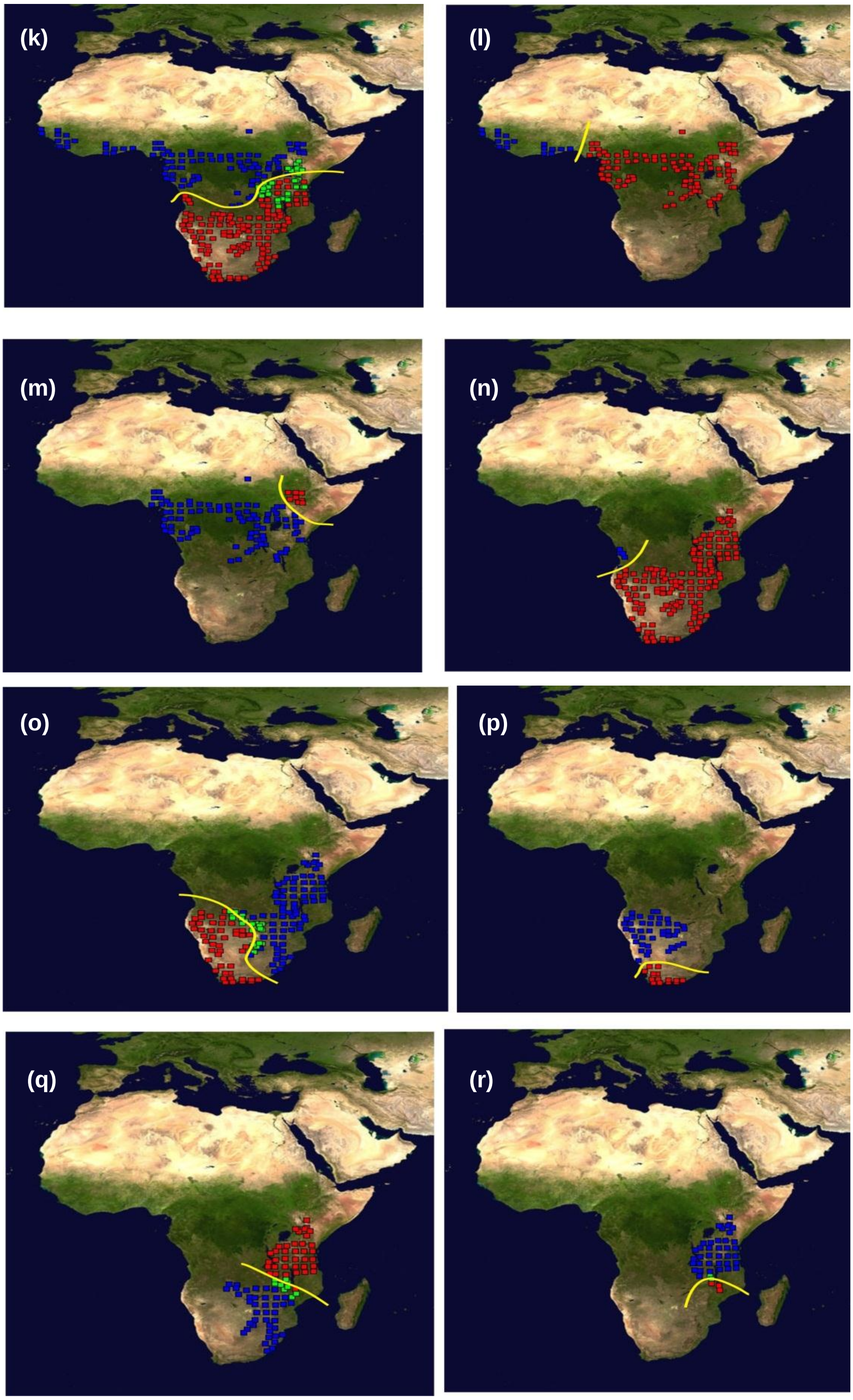


Figure 7.8. cont.

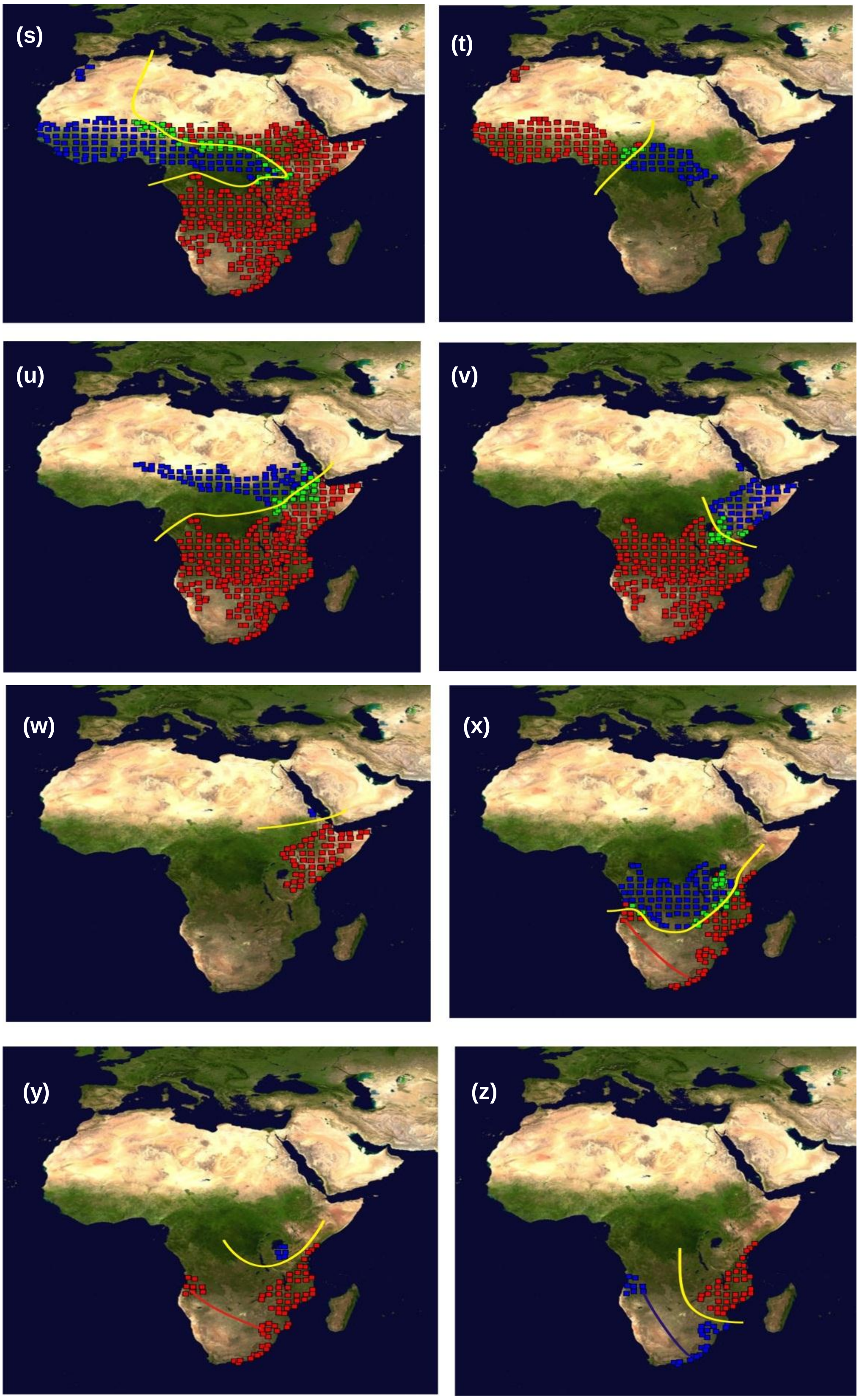


Figure 7.8. concl.

CHAPTER 8

Summary and Synthesis

Aims of this thesis:

1. To undertake a general review of the taxonomy of 'francolins' **[Chapter 1]**.
2. To contrast alternative hypotheses concerning the monophyly of the genus '*Francolinus*' (e.g. Hall 1963 versus Bloomer and Crowe 1998) and to further explore DNA-based, vocalization and behavioural evidence in order to test the phylogenetic affinities of the Stone Partridge *Ptilopachus petrosus* and Nahan's Francolin *Francolinus nahani* as suggested in Crowe et al. (2006) [**Chapter 2]**.
3. To investigate if there are any syringeal features (anatomical) that can be used to further our understanding of phylogenetic relationships among francolin and spurfowl taxa **[Chapter 3]**.
4. To test the validity of the francolin-spurfowl taxonomic dichotomy based on vocal characters **[Chapter 4]**.
5. To test Hall's (1963) hypotheses on the monophyly of the suggested eight species groups within her circumscription of the genus *Francolinus*, and thereby provide a modern systematic revision of the terminal taxa and genera of francolins and spurfowls **[Chapter 5 & 6]**.
6. To describe and explore the patterns of distribution of francolins and spurfowls using Hall's (1963) monograph as a null hypothesis **[Chapter 7]**.

The key findings of this thesis

A general review of the taxonomy of *Francolinus* (*sensu lato*)

There has been persistent confusion regarding the taxonomic status of francolins *sensu lato* since the description of the genus *Francolinus* in the mid-1830s. This is readily demonstrated in the outline of the various taxonomic reviews carried out on the genus (Chapter 1). The confusion centred on the taxonomic and phylogenetic status of the genus, the taxonomic status and the number of valid genera, terminal species and subspecies of francolins, the phylogenetic position of Hall's (1963) putative monophyletic species groups, as well as the phylogenetic position of *Ortygornis sephaena* and Hall's (1963) four unplaced enigmatic species (now *Ptilopachus nahani*, *Afrocolinus lathami*, *Ortygornis pondicerianus*, *Ortygornis gularis*), and finally the origin of the genus *Francolinus* which involves two conflicting hypotheses postulated by Hall (1963) and Crowe and Crowe (1985), respectively.

One of the major motivations for conducting this study was to establish a classification system that accounts for the evolutionary history of francolin and spurfowl taxa. Most species of francolins and spurfowls vary, often strikingly, in morphology, and they form complexes of species that make delimitation of taxa and the endeavour to define species complicated and difficult to achieve. The conclusions drawn from the taxonomic reviews were that taxon and character sampling procedures, types of characters (organismal versus molecules) and analytical methods (quantitative statistical methods versus model-/non-model-based phylogenetic methods) have significantly improved our understanding of the systematics of francolins and spurfowls, that have important implications for designating taxonomic rank: e.g. whether a taxon should be considered a species, subspecies or a synonym. These results in turn have improved our understanding of the biogeography of francolins and spurfowls.

Contrasting ideas:

Monophyly of the genus *Francolinus* (*sensu* Hall 1963) and the species groups

The advent of molecular data has revolutionized the understanding of evolutionary aspects of francolins and spurfowls. One of Hall's major challenges was the difficulty of determining the phylogenetic position of *Ortygornis sephaena* and hence she was forced to place 41 traditionally recognized species in a single genus *Francolinus*. Without the use of discrete molecular data and modern phylogenetic inference methods, as well as the need for excellent taxon sampling, early studies could not decisively reject monophyly of *Francolinus* and had to simply allude to the possibility of francolins forming two major lineages, and hence often opted to retain all species in a single genus *Francolinus.*

This study decisively demonstrates that the genus *Francolinus* is not monophyletic, instead it can be split into two distantly related assemblages (Chapter 2): 'francolins' (partitioned among the genera *Francolinus, Ortygornis, Afrocolinus, Peliperdix, Scleroptila*) and 'spurfowls' (all placed in the genus *Pternistis*). The Bayesian reconstruction for the time of divergence between these two lineages, that is, the *Coturnix/Alectoris*/spurfowls and *Gallus/Bambusicola*/francolins, was recovered at c. 33.6 mya. The estimated evolutionary date for the time-to-most-recent-common-ancestor for francolins and spurfowls was recovered at c. 7.6 and 8.7 mya, respectively.

Monophyly of four (the Red-tailed, Red-winged, Spotted and the Bare-throated Groups) of eight species groups, as delimited by Hall (1963), was recovered. Significantly, this study was able to decisively place the problematic species *O. sephaena* within the 'true' francolins, despite its possession of mixed francolin and spurfowl features. This study also revealed that its closest evolutionary relatives are the two unplaced Asian species *O.*

pondicerianus and *O. gularis*. *Ortygornis sephaena* may well be a derived francolin that emerged early in the history of the genus *Francolinus*.

Another major revelation was that Hall's (1963) difficulty in assigning Nahan's Francolin *Francolinus* '*Ptilopachus' nahani* to any specific species group made sense since this study unequivocally revealed that Nahan's Francolin is not a francolin but a partridge, and sister to the African Stone Partridge *Ptilopachus petrosus* (having diverged c. 9.6 mya - details in Chapter 2), and the duo are in turn, sister to the New World quails. The remaining enigmatic morphological taxon of Hall (1963), *Afrocolinus lathami* was in most analyses, found to represent its own evolutionary trajectory and a new genus name *Afrocolinus* gen. nov. was assigned in Chapter 5.

Further investigation into the phylogenetic affinities of the Stone Partridge *Ptilopachus petrosus* and Nahan's Francolin *Francolinus nahani* (*sensu* Crowe et al. 2006)

Francolinus nahani is a taxonomically enigmatic African galliform restricted to the interior of remnant primary forests of the eastern equatorial lowlands of the Democratic Republic of the Congo and Uganda. This thesis extended the earlier result of Crowe et al. (2006) by confirming that the closest extant relative of *Francolinus nahani* is *Ptilopachus petrosus* with an estimated divergence time at c. 9.6 mya. The two species are in turn most closely related to the New World quails (Odontophoridae) than any other Old World galliform. On the basis of the close phylogenetic relationship between *F. nahani* and *P. petrosus*, and their shared vocal and behavioural characters, this study recommended that *F. nahani* be moved to the genus *Ptilopachus* Swainson, based on name priority, subfamily Ptilopachinae subfam. nov. (Bowie et al. 2013), and family Odontophoridae.

Francolin-spurfowl dichotomy – syryngeal and vocalization perspective

With ever increasing data suggesting a deep divergence between the francolin and spurfowl assemblages, the syringes (Chapter 3) of selected francolins and spurfowls and the calls (Chapter 4) of the various species were analyzed in an effort to further validate the divergence between these two lineages of primarily African galliforms. It was found that there were clear-cut vocal differences between (and among) francolins and spurfowls with francolins generally rendering longer tonal strophes with distinct elements that have detectable harmonics. Spurfowls, in contrast, generally give shorter atonal strophes with elements that generally have no harmonics. The structure of the syringes also supports this distinction, with the shape of the tympanum placing *O. sephaena* decisively with other francolins despite the lack of the mineralized bronchial half rings that are present in other francolins, and the size of the pessulus corroborates the francolin-spurfowl dichotomy. The amount of connective tissue places species with tonal and whistling calls together (*Scleroptila levaillantii* and *S. afra*) to the exclusion of those taxa that have atonal, raucous and grating calls (*Pternistis capensis*, *P. natalensis* and *O. sephaena*).

The validity of terminal taxa - francolins and spurfowls

In Chapter 5 and 6, the focus was to establish an evolutionary-based classification system to enable the identification of those francolin and spurfowl taxa that represent valid species and subspecies, as well as to determine the validity of various proposed generic names. The major disagreement recorded was at the subspecies level, followed by the generic and to some degree at the species level. As outlined in Chapters 5 and 6, this study proposes a tremendous decrease in the number of subspecies traditionally recognized in the earlier reviews (see Chapter 1) with most of these taxa being synonymized (with those deemed valid subspecies) whenever they were found to not represent distinct evolutionary units and fail to meet the criteria as outlined in Chapter 5. In summary, the number of francolin and spurfowl species increased while additional genera were recognized for francolins. Five francolin genera *Francolinus, Ortygornis, Afrocolinus* gen. nov., *Peliperdix* and *Scleroptila* are recognized and all spurfowl species are placed in a single genus *Pternistis*.

A number of traditionally recognized subspecies were elevated to species in this revision, resulting in 31 and 24 species of francolins and spurfowls, respectively. Although some subspecies are morphologically distinct, combined phylogenetic evidence from organismal and DNA characters, together with sequence divergence estimates based on Cytochrome-*b* characters, suggests that these taxa have yet to reach an independent evolutionary trajectory that warrants species status, hence they are synonymized with other taxa. What differentiates the taxonomic approach adopted in this study from those in the previous revisions is that the evolutionary relationships among taxa played a central role.

The history of distributional patterns of francolins and spurfowls and the origin of the genus *Francolinus*

The focus in Chapter 7 was to interpret the current distributional patterns of francolins and spurfowls using historical information. Further, in light of the two alternate hypotheses for the origin of francolins and spurfowl, this study sought to determine the origin of the ancestral francolin and spurfowl. Between the two approaches that were used, the disjunction-detecting and barrier-inferring spatial analysis of vicariance or the ancestral reconstruction of area and habitat, it could be concluded that the spatial analysis of vicariance provided a better picture of the history of distribution patterns of francolins and spurfowls. So, the colonization of Africa by the ancestral species may have been through dispersal which resulted in the formation of disjunct distributions and the somewhat rapid diversification of francolins and spurfowls in Africa. The direction of dispersal might have gone either way, i.e. from Asia to Africa, and vise versa. The sister relationship between the Asian *O. gularis* clade and the *O. sephaena* complex could fit the explanation that, during the collision of Asia and Africa, some individuals may have remained in Asia while others remained in Africa resulting in the two groups differentiating with subsequent speciation occurring on both continents. On the other hand, one other possible explanation on the origin of the spurfowls is that the ancestor may have dispersed from Asia, into the desert of Saudi Arabia along its coast and then into Africa where it eventually arrived in the desert in south western Africa. Generally, there is strong support for Hall's (1963) hypothesis for the evolution of the genus *Francolinus* being of Asian origin.

The Rift Valley system, Lake Chad, Upper Guinea and the Congolian forest, major rivers such as Limpopo, Zambezi, Rovuma and the Volta River were found to be maintaining the distribution patterns and possibly promoting speciation among African francolins. In addition, the Niger and Rufiji River, Okavango swamp and the Sahara desert have maintained the distribution ranges of the spurfowl taxa. Habitat heterogeneity e.g. xeric/mesic savanna versus mesic savanna, montane and lowland grasslands and forest habitat also play an important ecological role in facilitating diversification among francolins. Among spurfowls, similar habitat barriers to those detected among francolins were inferred.

Future prospects

Taxonomy remains a challenging discipline especially in the absence of a universal definition, which can be applied at both the species and subspecies level. The long-standing debate on the definition of species (as well as subspecies) is one that will remain difficult to resolve. The conflict exists between character partitions from different sources possibly due to the high level of hybridization and incomplete lineage sorting and these conditions make taxonomic practice complicated. Thus, there has been profound taxonomic confusion.

Future prospects to specifically focus on the phylogeographic studies of selected species complexes of francolins and spurfowls and also to investigate the nature of hybrid zones, are brought forth. The role of various syringeal features in voice production among francolins and spurfowls should be investigated.

CHAPTER 9

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