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The phylogenetics, taxonomy and biogeography of African arid zone terrestrial birds: the bustards (Otididae), sandgrouse (Pteroclidae), coursers (Glareolidae) and Stone Partridge (*Ptilopachus*)

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Declaration:

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Partridge (*Ptilopachus*)

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Dedication

To my parents, Mark and Alice, whose encouragement for me to follow my interests from an early age made starting this PhD possible, and to Deirdre, whose continual support has made completing it a reality.

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Abstract

Almost all studies of African avian biogeography have focused on forest taxa, and while a few recently-published phylogenies have included arid-zone radiations, no study has examined the phylogenies of multiple families of African arid-zone taxa to evaluate shared biogeographic patterns. In particular, one of the dominant paradigms in African arid-zone biogeography is the ‘arid corridor’ hypothesis. A corridor of arid vegetation is hypothesised to have linked the south-west (Karoo-Namib) and north-east (Kenya-Somalia) arid zones under a drier African climate scenario, and allowed the movement of arid-zone taxa between these zones before a moister climate closed off this link. A central question in this dissertation can be framed as: Is there any evidence to suggest that the ‘arid corridor’ has had an influence on the speciation of arid-zone non-passenger birds? The phylogenetics and biogeography of the following four groups of unrelated terrestrial non-passenger birds, that have endemics in both the south-west and north-east arid-zone lowlands (and Sahel), and which also encompass taxa with differing habitat tolerances, mobility and life-history traits, were examined: the bustards (Otididae), sandgrouse (Pteroclidae), coursers (Glareolidae) and Stone Partridge (*Ptilopachus*). Another aim of this research is to use insights from the evolutionary relationships of these families to assess the current state of their taxonomy, as well as to assess character evolution and other life history attributes (including evolution of their mating systems).

The bustards (Otididae) are large, terrestrial birds of open habitats that occur across the deserts and steppes of the Old World, with 22 of the 27 species occurring in Africa. Both the taxonomy and the deeper level phylogenetic relationships within the bustards are disputed and a recent molecular phylogeny proposed a controversial new set of generic relationships but was poorly sampled with relation to African taxa. The bustards show a fascinating variety of sexual size dimorphism, mating systems (from lek polygyny to monogamy) and striking advertisement displays. The 16 species of sandgrouse (family Pteroclidae) are dove-like, ground-dwelling birds widely distributed across the arid areas of Africa, central Asia and southern Europe. Their camouflaged upperpart plumage contrasts with striking species-specific markings on the head and underparts of the males. To date, no morphological or molecular phylogeny has been undertaken to investigate the numerous generic treatments of this family or hypotheses of morphological and behavioural character evolution. The

coursers (*Cursorius*, *Rhinoptilus* and *Smutsornis*) are a group of plover-like waders, with long legs, short, decurved bills and cryptic plumage, that are found in arid habitats from Africa to India. They are traditionally grouped in the subfamily Cursoriinae whereas the remainder of the Glareolidae belong to the pratincole genera (*Glareola* and *Stiltia*), which are diurnal, long-winged aerial feeders often associated with water, and are grouped in the Glareolinae. To date, no morphological or molecular phylogeny has been undertaken to investigate the monophyly of these subfamilies or the numerous generic treatments of the Glareolidae. *Ptilopachus petrosus* is an arid-zone gamebird (Galliformes) which is distributed in arid hilly country across the Sahel and recent, DNA-based phylogenetic research suggests its closest relative is *Francolinus nahani* that occurs in the deep forests of Uganda and the eastern Democratic Republic of Congo. This study investigates this hypothesis in greater detail using additional DNA evidence and the behaviour and vocalisations of these enigmatic, African phasianine galliforms. The *Ptilopachus* study offers an example to test an arid-zone taxon with an hypothesised sister in the central African forest zone.

To assess the phylogenetics of these groups using a multi-faceted approach, data from both morphological-behavioural characters, and mitochondrial and nuclear DNA, were analysed separately and in combination using three methods of phylogenetic analysis with different optimality criteria: parsimony, Bayesian inference and maximum likelihood. All species were sampled in the morphological-behavioural analyses, resulting in 62, 41, and 47 phylogenetically-informative characters in the Otididae, Pteroclidae and Glareolidae, respectively. In the molecular analyses, the Otididae were the most comprehensively sampled with all 27 species sampled for 5341 bp of nucleotide data, while 13/16 species of Pteroclidae (representing at least one member of each proposed genus) were sampled for 3326 bp, and 10/17 species of Glareolidae (including representatives of all five proposed genera, at least one member of each “superspecies”, and all six species of African-breeding coursers) were sampled for 2627 bp. A total of 5554 bp was analysed in the *Ptilopachus* study.

Despite the relatively large numbers of molecular characters sampled, basal resolution is generally weak across the phylogenies recovered. This is in contrast to the well-supported terminal groupings, which often comprise the currently-recognised genera (especially in the case of the morphological-behavioural analyses), with a few

important exceptions. In the Otididae, *Ardeotis* renders *Neotis* paraphyletic (although more data are required), and *Afrotis* is recovered as sister to **Clade Blue Eupodotis**, rendering *Eupodotis* paraphyletic. The suggestion that *E. rueppellii* is basal to the Otididae is rejected. In the Pteroclidae, most of the proposed generic classifications are not monophyletic, including the current delimitation of *Pterocles*. Further samples are required to improve basal resolution and clarify the placement of *P. alchata* and *P. burchelli*. In the Glareolidae, the mitochondrial and nuclear DNA data, and the combined DNA and morphological-behavioural evidence, support topologies that would render the Cursoriinae paraphyletic, which would make the division of the Glareolidae into currently-recognised subfamilies indefensible. Morphologically, *Stiltia* has characters intermediate between a courser and a pratincole, but results strongly support its placement within *Glareola* and it is not an evolutionary link between the two subfamilies. In the *Ptilopachus* analysis, there is overwhelming support for the sister relationship between *Ptilopachus petrosus* and *Francolinus nahani* and they, in turn, are the distantly related sister taxon of the New World quails (Odontophoridae), and are not related to any other Old World galliform. Detailed taxonomic recommendations are made for all these groups.

In the Otididae, the evolution of polygyny, aerial display, sexual size dimorphism and co-operative breeding is examined in the context of the phylogeny. Monogamous behaviour need only have evolved once in *Eupodotis*, followed by a striking reversal to polygyny in *Afrotis*. In the Pteroclidae, plumage colouration characters are the most homoplasious, whereas structural characters of the wing and tail are more reliable indicators of relationship (although 14 tail feathers and long central tail feathers has evolved more than once). The dusk-drinking behavioural adaptation is highly conserved. Among the Glareolidae, the habitats occupied, foraging level, activity time and migratory behaviour seem to be highly conserved within clades, suggesting there are high evolutionary costs to changing from these relatively specialist niches. The colouration of the bare parts, upperparts and underparts are especially homoplasious. The behaviour and vocalisations of *Ptilopachus petrosus* and *Francolinus nahani* are remarkably well-conserved despite striking habitat differences.

An biogeographic assessment of the clades recovered by the phylogenetic analyses in all four families, including a vicariance analysis, resulted in eight common distribution patterns being detailed. The primary pattern that has led to the suggestion

of the ‘arid corridor’ hypothesis in birds was tested: the presence of putative sister taxa on either side of the presumed corridor. Of all the putative species pairs separated by the ‘arid corridor’ described in the literature, 7/10 of them were supported as sisters with high support. However, as this could also be due to long-distance dispersal, the clade structure of the families as a whole was investigated. Close examination of the clades supported the notion that the ‘arid corridor’ has had an important influence on speciation in these families as almost all the clades that contain Afrotropical species ($n = 10$) show endemic representatives in the south-west and north-east arid zones. It is more parsimonious to suggest that this number of shared connections between these two disjunct arid zones in so many clades is more results from a shared historical event/s, rather than many independent, isolated dispersal events. The hypothesis of an ‘arid corridor’ can be further investigated using the nomadism/migration of the species involved and in the Otididae and Glareolidae, the strongest ‘arid corridor’ pattern is shown in three clades which are sedentary residents not prone to movements. This provides further support for an ‘arid corridor’ link between the areas and suggests that this phenomenon might have had a significant influence on the speciation of arid-zone birds. In contrast to this, *Eupodotis* and *Afrotis* also offer examples of diversification across ecological gradients within the south-west arid zone, which also seems to have been a driver of speciation in Africa’s arid zones.

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CHAPTER 1

Introduction to African arid zone biogeography, study taxa and scope of dissertation

The aim of this research is to use a multi-faceted (morphological/ behavioural/ mitochondrial and nuclear DNA) approach to investigate the phylogenetics, taxonomy and biogeography of three families of African arid zone terrestrial birds, the bustards (Otididae), sandgrouse (Pteroclidae), coursers (Glareolidae) and the Stone Partridge (*Ptilopachus*). This detailed examination of their evolutionary history will in some cases also allow the assessment of character evolution and other life history attributes (including evolution of their mating systems).

Arid zone biogeography of Africa with particular reference to the ‘arid corridor’ hypothesis

The Sahara Desert (Figs 1.1, 1.8) dominates the northern reaches of the African continent. At nine million km², it is the world’s largest desert and is part of a large, broadly connected desert system that stretches from West Africa’s Atlantic coastline via the Middle East to the Sind of India (Goudie, 2003). This broad desert zone shares many faunal components and forms the Saharo-Sindian region, which in turn forms the southern edge of the Palearctic faunal realm (Firouz, 2005), and northern boundary for most sub-Saharan taxa. The biogeographical affinities of the Saharan

bird fauna have been summarised by Moreau (1966). The vastness of the Sahara makes it difficult to generalise its climatic history, although evidence from windblown sand and fossils (see Schuster et al., 2006), and phylogeographic studies of reptiles (Amer and Kumazawa, 2005; Carranza et al., 2008) and mammals (Iyengar et al., 2007; Nicolas et al., 2009) suggest that large arid areas have existed in the Sahara since at least the Late Miocene/Early Pliocene and the vegetation has fluctuated during wet and dry Pleistocene cycles associated with high-latitude glaciations.

All of Africa to the south of the Sahara comprises the Afrotropical (previously known as the Ethiopian) zoogeographic region and it is the arid zone biogeography of this region that this is the focus of this study. The vegetation of the Afrotropical region has been well-summarised by White (1983) and a satellite image and simplified vegetation map are presented here as [Figs 1.1](#) and [1.2](#). There are two disjunct arid zones in this Afrotropical Region. The first is the south-west arid zone, centred on the Karoo-Namib and encompassing large parts of South Africa, Namibia, Botswana and southern Angola ([Figs 1.1, 1.2](#); Cowling et al., 1997). The second, the north-east arid zone, is centred on the Horn of Africa and includes most of Somalia, southern Ethiopia, Kenya and northern Tanzania ([Figs 1.1, 1.2](#); White, 1983). Each arid zone comprises a catena of arid habitats, which differ in terms of vegetation structure and extent of aridity (Kingdon, 1989; Cowling et al., 1997). In the south-west zone, the most extreme arid habitats are those of the Namib desert ([Figs 1.9 - 1.11](#)) along the west coast, and parts of the Karoo semi-desert to its south ([Figs 1.12, 1.13](#)); as one progresses inland, the rainfall increases and a dry *Acacia/Commiphora* woodland occurs on the eastern fringes of the Namib ([Fig. 1.11](#)) and into the Kalahari ([Fig.](#)

1.14), whereas to the south, the Karoo intergrades eastwards into more mesic open grassland habitats (Fig. 1.15; Cowling et al., 1997). In the north-east arid zone, the most extreme deserts occur on the arid plains close to the northern coast (Figs 1.16, 1.17) and in central Kenya; these areas are bordered with less extreme *Acacia/Commiphora* woodlands (Fig. 1.18) and bushland that extend southwards (White, 1983; Kingdon, 1989). These disjunct arid zones are separate by a broad zone in central Africa of tropical forests (Figs 1.19, 1.20) and miombo woodlands (Figs 1.1, 1.2), although mopane woodland (Fig. 1.21) does occur in the major river valleys (White, 1983). The pattern - of an extremely arid desert bordered by xeric acacia savannas - is repeated in North and West Africa. Here, the Sahara desert is bordered along its southern edge, extending from the Atlantic Ocean to the Red Sea coastline, by a large zone of arid acacia savanna known as the Sahel (Figs 1.1, 1.2, 1.22, 1.23). The Sahel is isolated from similar habitats by the Sahara to the north and the moist Guinea-Congolian woodlands to the south (White, 1983). In the east, it adjoins the north-east arid zone and, although these zones appear contiguous on large-scale maps (e.g. Fig. 1.2), the Sahel is largely isolated from the north-east arid zone by the Ethiopian highlands and the complex of vegetation types surrounding this topographically diverse area (White, 1983). This isolation is shown mostly clearly in Fig. 1.3.

Almost all studies of African avian biogeography have focused on forest taxa and have evaluated Pliocene-Pleistocene climate fluctuations, forest refugia and the interaction between montane and lowland forest bird communities (see recent reviews by Fjeldså and Bowie, 2008, and Voelker et al., 2010). There is an increasing body of evidence that suggests that Africa was extensively forested until the Late Tertiary,

when increasing aridification of the continent resulted in an expansion of grassland and arid habitats (Hamilton and Taylor, 1991; Morley, 2000; Plana, 2004; Feakins et al., 2005; Maslin and Christensen 2007). Using the most complete set of long-term paleoclimatic data (5 million years of aeolian dust deposits from sea cores from both West and East Africa), de Menocal (1995; 2004) argues that a significant period of aridification was initiated with the onset of high-latitude glacial cycles. In particular, he found that three major changes in the periodicity of these alternating wetter and drier cycles (from glacial maxima every 19-23 kyr, to 41 kyr, to 100 kyr; kyr = thousands of years) resulted in three especially arid periods centred around 2.8, 1.7 and 1.0 Mya (Million years ago), and correlated these arid periods with an increase in arid-adapted species in the African mammal fossil record. These aridification maxima have been linked to developments in hominid and bovid evolution (Vrba, 1985, Partridge et al., 1995; Vrba, 1999; Templeton, 2002; Maslin and Christensen 2007). The exact timing of arid peaks has been questioned by Trauth et al. (2009), although the broad pattern is still consistent. Sepulchre et al. (2006) and Maslin and Christensen (2007) have also emphasised the effect of African tectonic uplift on aridification over this period.

African biogeographers have long noticed that many fauna and flora are currently distributed in both the north-east and south-west arid zone, but not in the intervening area of unsuitable habitat. This has led to the conclusion that a zone of similar habitats, an ‘arid corridor’, must have linked these areas in the past, and this ‘arid corridor’ has been suggested to account for the disjunct distribution of arid-adapted taxa (Balinsky, 1962; Van Zinderen Bakker, 1969; Verdcourt, 1969; Werger, 1978; Kingdon, 1989; Vernon, 1999), specifically plants (de Winter, 1971; Goldblatt, 1978;

Hilton-Taylor, 1987; Thulin, 1994; Thulin and Johansson, 1996; Jurgens, 1997), mammals (Coe and Skinner, 1993; Turpie and Crowe, 1994), frogs (Poynton, 1995), butterflies (Carcasson, 1964) and birds (Austin Roberts, 1936, in Van Zinderen Bakker, 1969; Moreau, 1952, 1963, 1966; Hall, 1963, Winterbottom, 1967, Hall and Moreau, 1970; Crowe and Crowe, 1982; Crowe and Kemp, 1986; Clancey, 1986, Crowe, 1990, Crowe et al., 1992).

Although there were initially some early botanical researchers who believed this pattern could have been caused by long-distance dispersal, the emergence of vicariance biogeography theory and the fact that many of the disjunct plant taxa have poor dispersal mechanisms has led to the complete acceptance of the ‘arid corridor’ hypothesis in the published literature since the 1970s (Van Zinderen Bakker, 1969; Verdcourt, 1969; Hilton-Taylor, 1987). Winterbottom (1967) also describes Moreau’s initial skepticism of the hypothesis, although there is an increasing trend for Moreau to place greater emphasis on the putative physical link between the two arid zones (Moreau, 1963, 1966; Hall and Moreau, 1970).

This corridor of arid vegetation is hypothesised to have linked the south-west and north-east arid zones under a drier African climate scenario, and has been specifically mapped by Balinsky (Fig. 1.3; 1962) and Winterbottom (Fig. 1.4; 1967). It is postulated to have linked the arid zones via Zambia and central Tanzania where arid conditions would be predisposed to develop in the rain shadows of mountains and valleys, including areas where mopane woodland occurs today (Balinsky, 1962). Balinsky (1962) based his map on current climatic data, and links these areas via his map of Africa showing the zone that currently has less than 10 mm of rain per month

in three consecutive months of the year. So, in effect, there is already a corridor of sorts, although its highly seasonal nature has allowed the development of woodland vegetation and thus it is not suitable year-round for arid-adapted open-country species.

It has been argued that the ‘arid corridor’ could have opened and closed in a cyclical nature (such as in response to high-latitude glaciation events, Hilton-Taylor, 1987) on the basis that many taxonomic levels are rendered disjunct, for example, a disjunct family or genus might indicate an earlier link, while a disjunct species a more recent link (Balinsky, 1962; Verdcourt, 1969; Winterbottom, 1967). Some authors argue for an ancient desert link (Verdcourt, 1969, Lovett and Friis, 1996); others emphasise more recent savanna links between arid zones via the corridor (Winterbottom, 1967; Coe and Skinner, 1993; Barnes, 2007).

Phylogenetic studies using morphological and DNA characters have revolutionised our understanding of how species are related to each other, and when interpreted in a historical biogeographic framework (see Nelson and Platnick, 1981; Donoghue and Moore, 2003; Linder 2005), are able to provide insight into biogeographical hypotheses. Recent studies on African arid-adapted mammals (*Xerus*, Herron et al., 2005) and plants (*Senecio*, Coleman et al., 2005; *Zygophyllum*, Bellstedt et al., 2007) have argued that their patterns of distribution are consistent with the ‘arid corridor’ hypothesis, although the former two studies only postulate one crossing of the corridor.

The only avian phylogenetic studies that have included endemics from either the south-west or north-east arid zone are listed below, and all species examined belong to the avian order Passeriformes. Beresford et al. (2005) examined the paleoendemics of the south-west arid region only and concluded that this region has had a long history of aridity. Voelker (1999a, 1999b) examined the genus *Anthus* and found two species pairs of woodland and open country birds that have a distribution concordant with the arid corridor. Similarly, Outlaw et al. (2007, *Monticola*, and 2010, “chats” including *Cercomela*) found a pattern that could be explained by the presence of an ‘arid corridor’, although the general biogeographical applicability of these groups is complicated by their reliance on rocky habitats, and an Afromontane link, respectively. The most comprehensive study that examined endemics of the south-west and north-east arid zones is undoubtedly the study of larks (Alaudidae) of Barnes (2007) who found limited evidence of an ‘arid corridor’, and suggested that this corridor was more likely to be affecting the distribution of arid woodland species.

Biogeographic approach and choice of study taxa

The evaluation of the ‘arid corridor’ hypothesis should include phylogenetic analysis of groups with many endemic taxa to both the south-west and north-east zones, as species that are endemic to one or both of the zones are more likely to provide biogeographical insight than widespread species. The primary pattern that has led to the suggestion of an ‘arid corridor’ in birds is the presence of putative sister taxa on either side of the presumed corridor (Winterbottom, 1967; Hall and Moreau, 1970; Kingdon, 1989; Vernon, 1999). By evaluating the phylogenies of taxa that have diversified in arid regions, one can test whether these species pairs are sister or

whether their putative relationships have been confounded by convergence in appearance due to similar selective pressure operating in similar habitats. A list of these species and subspecies in the Otididae, Pteroclidae and Glareolidae is presented in [Table 1.1](#).

The second way to evaluate the ‘arid corridor’ hypothesis is to investigate the relationships of clades in arid zone bird families where there are members endemic to one or both arid zones. If the ‘arid corridor’ was very ancient, or if there had never been a corridor and lineages shared by the regions could be explained by long-distance dispersal, one would expect closely-related species to occur alongside each other in the same arid zone, with occasional dispersal to the opposite zone. The alternative scenario, if taxa have occurred across a past band of ‘arid corridor’ habitat stretching across the continent, then one would expect sister taxa to be currently isolated on either side of the continent due to allopatric speciation. Another possible scenario, if there was never a link or only an ancient link, is that the arid-adapted endemics are derived from adjacent forest and woodland species, and this can be examined by reconstructing the ancestral habitat of the clades in question.

Biogeographic questions are often framed as an attempt to distinguish between patterns of dispersal and vicariance (Ball, 1975). Dispersal is expected to produce a random pattern of colonisation, which it has been argued is impossible to test (Nelson and Platnick, 1981). In contrast, a vicariance event (such as the uplift of a mountain range or a rainforest bisecting a desert area) is expected to split the ranges of many taxa simultaneously and it has been argued that such events can be detected by searching for concordance in the area cladograms of multiple lineages (Linder, 2005).

However, it is important to distinguish true congruence, when the taxa and areas share the same history (Cracraft, 1988), from “pseudocongruence” (Cunningham and Collins, 1994; Voelker, 1999; Donoghue and Moore, 2003), which occurs when cyclical processes (such as periodicity of glacial cycles) result in an area characterised by multiple historical events. Evaluation of the ‘arid corridor’ hypothesis is likely to suffer from this confounding effect, as there is evidence that suggests that climate changes in Africa have been highly cyclical in nature (de Menocal, 1995, 2004; Maslin and Christensen 2007). For example, if an ‘arid corridor’ linked the two arid zones at different times, different lineages might have utilised the intervening area in different periods, although these taxa may still exhibit concordant area cladograms.

Molecular ‘clocks’ have proved very informative in assessing problems of bird biogeography in Africa (see Fjeldså and Bowie, 2008, and Voelker et al., 2010) and the molecular clock approach could be used to date these sister-taxon divergences to determine if they are concordant between lineages and cluster around the dates of extreme aridity proposed by de Menocal (1995, 2004) above (Klicka and Zink, 1997). However, calibrating the clock can be problematic (few phylogenetically-placed fossils are known for African avian assemblages) and the time divergence estimates can be confounded by rate variation between lineages (see Fjeldså and Bowie, 2008).

Another factor is that an aridification of Africa might have led to the expansion of the arid zones, but these might not have always or ever become completely linked. However, the distance between them might have been reduced and this might have allowed increased random short-distance dispersal events. This would have allowed the successful colonisation of the opposite area, and this ‘partial arid corridor’ might

create congruent area cladograms between taxa. One way to evaluate this would be to examine the habitat tolerance and vagility of the species on the area cladograms.

For the reasons described above, the primary concern when evaluating the ‘arid corridor’ hypothesis is not to attempt to distinguish between short-distance dispersal and vicariance, but rather to examine patterns of speciation in the context of historical biogeography. Thus, a central question in this dissertation can be framed as: Is there any evidence to suggest that the ‘arid corridor’ has had an influence on the speciation of arid zone non-passerine birds?

I have chosen to examine this pattern in several groups of unrelated terrestrial non-passerine birds that have endemics in both the south-west and north-east arid zone lowlands, and which also encompass taxa with differing habitat tolerances, mobility and life-history traits. I suggest that lowland species without specific topographic habitat requirements would act as a better test of the ‘arid corridor’ hypothesis, as species associated with topographically complex areas might be buffered against climate change by refugia in these areas (see Fjeldså and Bowie, 2008; Voelker et al. 2010).

The groups I have chosen for this study are the bustards (Otididae), sandgrouse (Pteroclidae) and coursers (Glareolidae). The relationships of the arid-zone stone partridge (*Ptilopachus*, Galliformes) are also examined. These groups have primarily diversified in Africa’s arid zones (Johnsgard, 1991; Collar, 1996; Maclean, 1996; de Juana, 1997) and meet the criteria described above, and have been suggested as good

indicators of arid zone biogeography (Snow, 1978; Kingdon, 1989; Vernon, 1999; Cohen, 2000; Barnes, 2007).

Current state of systematic and taxonomic knowledge of study taxa

The current state of the systematics of each of the study groups is summarised in separate sections below and is also highlighted in the introduction to each chapter. Most of the groups contain controversial relationships that are treated differently in the literature by various authors (see [Tables 1.2 – 1.4](#)). There has been limited molecular examination of many bustard species, and this has only created further controversy (Pitra et al., 2002; Broders et al., 2003). Additionally, the sandgrouse and coursers have not been examined using molecular methods. It will thus be necessary to undertake a full systematic reassessment of the proposed study groups in order to evaluate their biogeographical relationships with confidence. A second major theme of this dissertation (other than testing the ‘arid corridor’ hypothesis) will thus be to examine each family in turn and assess their systematic relationships, especially where they have relevance to African biogeography.

Life history evolution in study taxa

The aim is to create a robust phylogeny of each group and this will allow the evolution of life history traits to be interpreted in the context of the phylogenies. In particular, the families selected offer a wide variety of strategies which can be examined in terms of niche conservatism (Wiens and Graham, 2005). A wide variety

of life history traits will be examined that will provide insight into habitat use, activity times, movements, and behavioural ecology; these are summarised in [Table 1.5](#) for each group. These traits and the interpretation of their evolution are discussed in more detail in each family chapter.

Methodological approach

The advent of robust analytical methods in conjunction with the use of DNA sequence data has revolutionised the understanding of avian systematic relationships, including those in Africa (Fjeldså and Bowie, 2008). This combination has been critical in untangling synapomorphies from the homoplasious characters that result from evolutionary convergence, and which can confound understanding of the evolutionary history and biogeography of birds. Whereas some studies have highlighted the plasticity of morphological characters, which can be misleading for the interpretation of evolutionary history (e.g. Hackett et al., 2008), others (e.g. Crowe et al., 2006) have shown that the addition of morphological and behavioural characters to the DNA data can increase the resolution of, and confidence in, phylogenetic hypotheses erected. It is especially important to analyse these characters in an as objective a way as possible, as many of the previous treatments of these families have favoured particular conspicuous characters, often those present in the breeding plumages of adult males, on which to base taxonomic conclusions (e.g. Collar, 1996; Maclean, 1996).

For these reasons, I intend to take the following into account:

1. to use data from multiple, independent lines of evidence, which will include not only morphological and behavioural data, but also DNA data from both the mitochondrial and nuclear genomes (Moore, 1995), and
2. to analyse these data in an objective way, using accepted phylogenetic methods.

A multi-faceted approach will be used to evaluate the relationships among selected groups of Africa's arid zone non-passerine terrestrial bird taxa. Morphological, behavioural and multilocus molecular data will be analysed using three methods of phylogenetic analysis with different optimality criteria (Holder and Lewis, 2003): parsimony (MP), Bayesian inference (BI) and Maximum Likelihood (ML), as used in recent hypotheses of avian phylogenies (e.g. Crowe et al., 2006; Fuchs et al., 2006; Voelker et al., 2007; Irestedt et al., 2008; Fuchs et al., 2008; Melo and Fuchs, 2008; Fuchs et al., 2009; Jónsson et al., 2008, 2009). For the DNA analyses, the following will be analysed: three mitochondrial markers: cytochrome-b (cytb), NADH Dehydrogenase subunit 2 (ND2), Control Region II (CtrII) and five nuclear markers: Beta-Fibrinogen intron-5 (Fib5), Transforming Growth Factor, Beta 2 intron-5 (TGFB), Glyceraldehyde-3-phosphate Dehydrogenase (G3PDH) intron 11 (GAPDH), Ornithine Decarboxylase introns 6 & 7 with the intervening exon 7 (ODC) and, an intron-exon crossing fragment of the Chromo-helicase-DNA binding gene (CHD1Z).

Introduction to the biogeography, diversity and taxonomy of the bustards (Otididae)

The bustards (Otididae) are large, terrestrial birds of open habitats that occur across the deserts and steppes of the Old World (Johnsgard, 1991; Collar, 1996). They are a predominantly African group with 22 of the 27 species occurring in Africa (Gill and Wright, 2006). Because their distribution mirrors that of open, mostly arid areas, and 12 species are endemic to disjunct areas in south-west and north-east Africa, they are an ideal candidate group for examining the arid zone biogeography of Africa ([Figs 1.5, 1.6](#)).

As a group, the bustards form a highly distinctive monophyletic assemblage that is well-differentiated from other avian families, resulting in their placement in an exclusive infraorder in the Gruiformes (Sibley and Monroe, 1990; Collar, 1996; Livezey, 1998). In the largest avian molecular analysis to date, Hackett et al. (2008) place the bustards as a sister group to a clade that include core Gruiformes (cranes, rails, finfoots, trumpeters and limpkin) and the Cuculiformes (bootstrap = 68%). Both the taxonomy and the deeper level systematic relationships within the bustards have been disputed. In the last three decades, a range of different generic classifications of the Otididae have been published (Osborne et al., 1984; Urban et al., 1986; Johnsgard, 1991; Collar, 1996; see [Table 1.2](#)). A recent molecular phylogeny, based largely on 444 base pairs of the cytochrome *b* gene, proposed a controversial new set of generic relationships (Pitra et al., 2002), but was relatively poorly sampled with regard to African taxa. A further study by Broders et al. (2003), who also examined the cytochrome *b* gene of a small subset of bustard species, focused on the Eurasian taxa.

In Table 1.1, it can be seen that five bustard genera are distributed across the arid zone disjunction. *Eupodotis* has four species in southern Africa (centred on the south-west arid zone), one widespread species (*E. senegalensis*; Figs 1.25, 1.25), and one restricted to Somalia (*E. humilis*; Fig. 1.26) in the north-west arid zone (Fig. 1.5; Collar, 1996; Gill and Watkins, 2006). There is fine scale habitat differentiation between the four southern African *Eupodotis*, from extreme desert (*E. rueppellii*; Fig. 1.27) in the north-west, semi-desert Karoo vegetation (*E. vigorsii*; Fig. 1.28) to more mesic open grasslands (*E. caerulescens*; Fig. 1.29) and savanna (*E. barrowii*; Fig. 1.30) in the central parts of the subregion (Allan, 2005). The two *Afrotis* (*A. afraoides*, Fig. 1.31, and *A. afra*, Fig. 1.32) species are exclusively southern African, and are found in the arid-zone grasslands of the summer-rainfall region and the shrublands of the winter-rainfall region respectively (Crowe et al., 1994). *Lophotis* has a habitat preference for arid woodland zones, the most closed habitat occupied by any of the bustards (Collar, 1996). The three species (*L. ruficrista*, Fig. 1.33, *L. gindiana*, Fig. 1.34, and *L. savilei*) are disjunctly distributed in the south-west arid zone, north-east arid zone and the Sahel respectively (Fig. 1.6). *Neotis* also shows a three-way disjunction between the south-west arid zone (*N. ludwigii*; Fig. 1.35), north-east arid zone (*N. heuglinii*; Fig. 1.36) and the Sahel (*N. nuba*; Fig. 1.37); however, these species are unlike the resident, woodland-dwelling *Lophotis* but are nomads of more extreme desert habitats (Collar, 1996). An exception is *N. denhami* (Fig. 1.38), which occurs widely in sub-Saharan Africa in more mesic, grassy habitats, such as upland grasslands and extensive river floodplains. *Lissotis melanogaster* (Fig. 1.39) shares this distribution, but prefers the edge of savannah habitats, whereas *L. hartlaubii* (Fig. 1.40) is restricted to grasslands of the north-east

arid zone. *Ardeotis kori* has distinctive subspecies (Figs 1.41, 1.42) on either side of the proposed arid corridor, which have been treated as separate species in the past (e.g. Mackworth-Praed and Grant, 1952) and also have a conspicuous difference in the “beard” of displaying males (unpublished data together with T. Osborne and S. Hallager) and on closer investigation might be considered separate species, although this is not examined in the context of this thesis. *Ardeotis arabs* (Fig. 1.43) ranges from Ethiopia westwards through the Sahel (and marginally into the extreme western coastal plain of the Middle East; Johnsgard, 1991).

Two further species of *Ardeotis* are distributed further afield in Asia: *A. nigriceps* of India and *A. australis* of Australia and New Guinea (Johnsgard, 1991). The floricans, *Sypheotides indica* (India) and *Houbaropsis bengalensis* (India to South-East Asia), also share a southern Asian distribution. *Otis tarda* and *Tetrax tetrax* are widely distributed across the Palearctic region, ranging from western Europe across to central Asia, and also occur in North Africa. *Chlamydotis undulata* ranges from the Canary Islands across the northern Sahara, whereas *Chlamydotis macqueenii* ranges from the Middle East to central Asia, with populations migrating between those areas (Collar, 1996).

Introduction to the biogeography, diversity and taxonomy of the sandgrouse (Pteroclidae)

The sandgrouse (family Pteroclidae) form a small family of 16 species widely distributed across the arid areas of Africa, central Asia and southern Europe (Johnsgard, 1991; de Juana, 1997). They are dove-like, ground-dwelling birds that

feed almost exclusively on seeds. Their upperpart plumage makes them superbly camouflaged on desert substrata, although the males also have striking species-specific plumage markings on their underparts and heads, which are used in display. Sandgrouse show many morphological adaptations to their harsh environment and are most famous for the absorbent belly feathers of the males, which they soak in water for the chicks on daily commuting flights to water sources (de Juana, 1997).

The systematic position of Pteroclidae has been intensely debated, and they have been allied to the Galliformes, Columbiformes, Charadriiformes and even placed in their own order (see summaries in Sibley and Alquist, 1972; Fjeldså, 1976; Johnsgard, 1986; de Juana, 1997). The hypothesis based on the largest dataset is that proposed by Hackett et al. (2008), which places them as sister to the Columbiformes + Mesites (Mesitornithidae), but without strong support.

The species-level taxonomy has been uncontroversial in recent years and all authors recognise 16 species (Maclean and Fry, 1986; Johnsgard, 1991; de Juana, 1997). The number of genera recognised is more controversial and ranges from 2 to 4 (see [Table 1.3](#)), with a further seven subgenera proposed (Wolters, 1974). The genera *Pterocles* and *Syrrhaptes* are the currently accepted genera since Elliot (1878).

All of the numerous assessments of the number of genera in the family ([Table 1.3](#)) are based on morphological characters only, and some place special emphasis on male plumage characters that are used in display, and which might well be riddled with homoplasy. No previous studies analyse these characters in any objective way.

Three groups of sandgrouse span the arid zone disjunction (Table 1.1). The enigmatic *P. gutturalis* (Fig. 1.44) is typically a species of grasslands both on highland plateaux and floodplains, and has an endemic subspecies on the fringes of each arid zone (*gutturalis* in the south-west and *saturatior* from northern Zambia northwards). *Pterocles namaqua* (Fig. 1.45) is a south-west desert and semi-desert endemic which has been suggested as the closest relative of *P. exustus* (Fig. 1.46; Maclean and Fry, 1986), a species of the north-east desert and semi-desert zone that also extends widely from the Sahel to India. The putative subgenus *Nyctiperdix* also has northern and southern representatives, and these species occur in arid woodlands on the fringes of the deserts. *Pterocles bicinctus* (Fig. 1.47) is a south-west zone endemic, whereas *P. quadricinctus* occurs in the north-east zone and across the Sahel, with *P. lichtensteinii* occurring in the north-east zone, across the Sahel, and through the Middle East into India. *Pterocles indicus* is endemic to India. *Pterocles decoratus* (Fig. 1.48), sometimes allied to the subgenus *Nyctiperdix* members above, is a north-east arid zone endemic.

A number of sandgrouse taxa, in addition to those mentioned above, have distributions that essentially mirror the southern arid border of the Palearctic region. These include *P. coronatus* and *P. senegallus* which inhabit desert regions from the Sahara eastwards to India, and *P. alchata* and *P. orientalis*, which also span the same longitudinal range but occur in more mesic habitats to the north of the previous two species. Further north, the two species in the genus *Syrrhaptes* (*S. paradoxus* and *S. tibetanus*) are endemic to the cold deserts of central Asia (centered on the Tibetan plateau but also extending further north, east and west). *Pterocles personatus* (Fig. 1.49) is an enigmatic Madagascan endemic, and *P. burchelli* is an enigmatic south-

west arid zone endemic.

Introduction to the biogeography, diversity and taxonomy of the coursers (Glareolidae)

The coursers (*Cursorius*, *Rhinoptilus* and *Smutsornis*) form a group of plover-like waders, with long legs, short, decurved bills and cryptic plumage, that are found in arid habitats from Africa to India (Maclean, 1996). Four of the nine species are nocturnal (Maclean, 1996). They are traditionally grouped in the subfamily Cursoriinae (Gray, 1840) together with *Pluvianus* (Egyptian Plover), whereas the pratincole genera, which are diurnal, long-winged aerial feeders often associated with water, *Glareola* and *Stiltia*, are grouped in the Glareolinae (Brehm, 1831). Together these two subfamilies comprise the Glareolidae (Brehm, 1831), which is placed in the Charadriiformes.

Much molecular systematic work has been undertaken on the Charadriiformes in an attempt to resolve the controversial relationships in this order (Ericson et al., 2003; Paton et al., 2003; Paton and Baker, 2006; Baker et al., 2007). It has now been confidently shown that *Pluvianus* is not related to the rest of the Glareolidae, but is more accurately placed in the Charadrii, whereas the Glareolidae have been shown to fall within the Lari (Baker et al., 2007). This latter study included a single exemplar from *Glareola*, *Stiltia*, *Cursorius* and *Rhinoptilus* and showed these to form a monophyletic assemblage, sister to the remaining Lari (Baker et al., 2007). Ericson et al. (2003) also showed *Cursorius* and *Rhinoptilus* to comprise a monophyletic clade

in a large analysis of the Charadriiformes, but *Glareola* was not included in that study.

Interestingly, although this was not mentioned by Baker et al. (2007), their data do not show the two coursers, *Cursorius* and *Rhinoptilus* as sister taxa. Rather, *Cursorius* is placed as sister to the *Glareola* + *Stiltia* clade, and is sister to this *Rhinoptilus* clade. This would suggest that the subfamily Cursoriinae is paraphyletic. However, because only one exemplar of each genus was used, this result should perhaps be treated with caution.

At the generic level, between one (*Cursorius*) and three genera (*Cursorius*, *Rhinoptilus* and *Smutsornis*) are recognised in recent treatments (detailed in [Table 1.4](#)) and the validity of these genera needs to be determined. The only controversial issue in species-level taxonomy has been the placement of the *littoralis*/ *somalensis* taxa which are variously grouped with either *C. cursor* or *C. rufus* or allocated full species status (detailed in [Table 1.4](#); see also Pearson and Ash, 1996). All authors recognise either 16 or 17 species in the Glareolidae (summarised in [Table 1.4](#)). All of the numerous assessments of the number of genera and species in the family ([Table 1.4](#)) are based on morphological characters only and no previous studies analyse these characters in any objective way.

Two groups of coursers have endemic representatives in the south-west and north-east arid zones. *Rhinoptilus* (*Smutornis*) *africanus* ([Figs 1.50, 1.51](#)) has four endemic subspecies in the south-west zone and three endemic subspecies in the north-east zone. The south-west desert endemic *Cursorius rufus* ([Fig. 1.52](#)) has a north-east

desert endemic equivalent *C. somalensis* (Fig. 1.53; see above for discussion on the specific status of this taxon). These in turn are related to the more widespread desert species *C. cursor*, a migratory taxon that extends from the western Sahara across to the Indian deserts. *Cursorius temminckii* (Fig. 1.54) occurs in woodland habitats and is able to utilise them as it is highly nomadic (and might even have migratory populations) and moves into recently burnt and trampled areas where there is open habitat (Maclean, 1996). The Indian *C. coromandelicus* is often proposed as a sister-species to *C. temminckii* (e.g. Snow, 1978).

Members of *Rhinoptilus* prefer arid woodlands and so occur on the fringes of the arid zones, although they still avoid the forests and moist woodlands of central Africa. In central Africa, they are largely restricted to the arid woodlands of the rain shadows and river valleys where the tree *Colophospermum mopane* predominates (Fig. 1.21). Indeed, the distribution of *R. cinctus* mirrors this band of arid woodland in central Africa (Fig. 1.7) that has been proposed by Balinsky (1962) and Winterbottom (1967) as the most likely region through which the ‘arid corridor’ linked the north-east and south-west arid zones (Figs 1.3, 1.4). *Rhinoptilus chalcopterus* (Fig. 1.55), is widely distributed in the arid woodlands of Africa and is similar in plumage to the critically endangered *R. bitorquatus* which is restricted to a small region of dry woodland in India (Maclean, 1996).

The relationships of the arid zone *Ptilopachus* (Galliformes) and its implications for African biogeography

Ptilopachus petrosus (Fig. 1.56) is an arid-zone gamebird (Galliformes) which is distributed in arid hilly country across the Sahel (Fig. 1.23) from Senegal across to north-western Kenya. Recent, DNA-based phylogenetic research (Crowe et al., 2006) suggests its closest relative is *Francolinus nahani* (Fig. 1.57), a rare, relatively-recently rediscovered francolin that occurs in the deep forests of Uganda (Fig. 1.20) and the eastern Democratic Republic of Congo. This study investigates this hypothesis in greater detail using additional DNA evidence and the behaviour and vocalisations of these enigmatic, African phasianine galliforms. The *Ptilopachus* study offers an example to test an arid-zone taxon with a sister in the central African forest zone, unlike the pattern shown by the Otididae, Pteroclidae and Glareolidae.

Table 1.1: Putative sister-species and subspecies pairs in Otididae, Pierocidae and Glareolidae with disjunct distributions on either side of the 'arid corridor'.

Taxon	South-west	North-east	Reference
Otididae			
<i>Ardeotis kori</i>	<i>kori</i>	<i>struthiunculus</i>	Snow, 1978
<i>Neotis ludwigii</i>		<i>heuglinii</i>	Kingdon, 1989
<i>Lophotis ruficrista</i>		<i>gindiana</i>	Snow, 1978
<i>Eupodotis vigorsii</i>	<i>vigorsii</i>	<i>rueppellii</i>	Snow, 1978
<i>Eupodotis barrowii</i>		<i>humilis</i>	Snow, 1978
Pteroclidae			
<i>Pterocles namaqua</i>		<i>exustus</i>	Snow, 1978
<i>Pterocles bicinctus</i>		<i>quadricinctus</i>	Snow, 1978
<i>Pterocles gutturalis</i>	<i>gutturalis</i>	<i>saturator</i>	Snow, 1978
Glareolidae			
<i> Cursorius rufus</i>		<i>somalensis</i>	Pearson & Ash, 1995
<i>Rhinoptilus africanus</i>	5 subspecies (incl. <i>africanus</i> & <i>sharpei</i>)	3 subspecies (incl. <i>gracilis</i>)	Maclean & Urban, 1986

Table 1.2: Family Otididae generic treatments. Genera not currently recognised are in bold and parentheses indicate that the species was only recognised as a subspecies.

Taxa	Scaler, 1924	Peters, 1934	Roberts, 1940	Dementiev and Gladkov, 1951	Mackworth-Praed and Grant, 1952, 1962, 1970	Snow, 1978	Osborne et al., 1984	Collar et al., 1986	Sibley and Monroe, 1990	Johnsgard, 1991	Collar, 1996	Gill and Wright, 2006
<i>Otis tarda</i>	/	<i>Otis</i>	/	<i>Otis</i>	/	<i>Otis</i>	<i>Otis</i>	<i>Otis</i>	<i>Otis</i>	<i>Otis</i>	<i>Otis</i>	<i>Otis</i>
<i>Chlamydotis undulata</i>	/	<i>Chlamydotis</i>	/	<i>Otis</i>	<i>Chlamydotis</i>	<i>Chlamydotis</i>	<i>Chlamydotis</i>	<i>Chlamydotis</i>	<i>Chlamydotis</i>	<i>Chlamydotis</i>	<i>Chlamydotis</i>	<i>Chlamydotis</i>
<i>Chlamydotis macqueenii</i>	/	(<i>Chlamydotis</i>)	/	(<i>Otis</i>)	(<i>Chlamydotis</i>)	(<i>Chlamydotis</i>)	(<i>Chlamydotis</i>)	(<i>Chlamydotis</i>)	(<i>Chlamydotis</i>)	(<i>Chlamydotis</i>)	(<i>Chlamydotis</i>)	<i>Chlamydotis</i>
<i>Tetrapetra tetrapetra</i>	/	<i>Tetrapetra</i>	/	<i>Otis</i>	/	/	<i>Tetrapetra</i>	<i>Tetrapetra</i>	<i>Tetrapetra</i>	<i>Tetrapetra</i>	<i>Tetrapetra</i>	<i>Tetrapetra</i>
<i>Ardeotis arabs</i>	<i>Choriotis</i>	<i>Choriotis</i>	/	/	<i>Ardeotis</i>	<i>Otis</i>	<i>Ardeotis</i>	<i>Ardeotis</i>	<i>Ardeotis</i>	<i>Ardeotis</i>	<i>Ardeotis</i>	<i>Ardeotis</i>
<i>Ardeotis kori</i>	<i>Choriotis</i>	<i>Choriotis</i>	<i>Choriotis</i>	/	<i>Ardeotis</i>	<i>Otis</i>	<i>Ardeotis</i>	<i>Ardeotis</i>	<i>Ardeotis</i>	<i>Ardeotis</i>	<i>Ardeotis</i>	<i>Ardeotis</i>
<i>Ardeotis nigricollis</i>	<i>Choriotis</i>	<i>Choriotis</i>	/	/	/	<i>Otis</i>	<i>Ardeotis</i>	<i>Ardeotis</i>	<i>Ardeotis</i>	<i>Ardeotis</i>	<i>Ardeotis</i>	<i>Ardeotis</i>
<i>Ardeotis australis</i>	<i>Choriotis</i>	<i>Choriotis</i>	/	/	/	<i>Otis</i>	<i>Ardeotis</i>	<i>Ardeotis</i>	<i>Ardeotis</i>	<i>Ardeotis</i>	<i>Ardeotis</i>	<i>Ardeotis</i>
<i>Neotis ludwigii</i>	<i>Neotis</i>	<i>Neotis</i>	<i>Neotis</i>	/	<i>Neotis</i>	<i>Neotis</i>	<i>Neotis</i>	<i>Neotis</i>	<i>Neotis</i>	<i>Neotis</i>	<i>Neotis</i>	<i>Neotis</i>
<i>Neotis denhami</i>	<i>Neotis</i>	<i>Neotis</i>	<i>Neotis</i>	/	<i>Neotis</i>	<i>Neotis</i>	<i>Neotis</i>	<i>Neotis</i>	<i>Neotis</i>	<i>Neotis</i>	<i>Neotis</i>	<i>Neotis</i>
<i>Neotis heuglinii</i>	<i>Neotis</i>	<i>Neotis</i>	/	/	<i>Neotis</i>	<i>Neotis</i>	<i>Neotis</i>	<i>Neotis</i>	<i>Neotis</i>	<i>Neotis</i>	<i>Neotis</i>	<i>Neotis</i>
<i>Neotis nuba</i>	<i>Neotis</i>	<i>Neotis</i>	/	/	<i>Neotis</i>	<i>Neotis</i>	<i>Neotis</i>	<i>Neotis</i>	<i>Neotis</i>	<i>Neotis</i>	<i>Neotis</i>	<i>Neotis</i>
<i>Lissotis melanogaster</i>	<i>Lissotis</i>	<i>Lissotis</i>	<i>Lissotis</i>	/	<i>Lissotis</i>	<i>Eupodotis</i>	<i>Eupodotis</i>	<i>Lissotis</i>	<i>Eupodotis</i>	<i>Eupodotis</i>	<i>Lissotis</i>	<i>Lissotis</i>
<i>Lissotis hartlaubii</i>	<i>Lissotis</i>	<i>Lissotis</i>	/	/	<i>Lissotis</i>	<i>Eupodotis</i>	<i>Eupodotis</i>	<i>Lissotis</i>	<i>Eupodotis</i>	<i>Eupodotis</i>	<i>Lissotis</i>	<i>Lissotis</i>
<i>Afrrotis afra</i>	<i>Afrrotis</i>	<i>Afrrotis</i>	<i>Afrrotis</i>	/	<i>Afrrotis</i>	<i>Eupodotis</i>	<i>Eupodotis</i>	<i>Afrrotis</i>	<i>Eupodotis</i>	<i>Eupodotis</i>	<i>Afrrotis</i>	<i>Afrrotis</i>
<i>Afrrotis afraoides</i>	(<i>Afrrotis</i>)	(<i>Afrrotis</i>)	<i>Afrrotis</i>	/	(<i>Afrrotis</i>)	(<i>Eupodotis</i>)	(<i>Eupodotis</i>)	(<i>Afrrotis</i>)	(<i>Eupodotis</i>)	(<i>Eupodotis</i>)	<i>Afrrotis</i>	<i>Afrrotis</i>
<i>Eupodotis senegalensis</i>	<i>Eupodotis</i>	<i>Eupodotis</i>	/	/	<i>Eupodotis</i>	<i>Eupodotis</i>	<i>Eupodotis</i>	<i>Eupodotis</i>	<i>Eupodotis</i>	<i>Eupodotis</i>	<i>Eupodotis</i>	<i>Eupodotis</i>
<i>Eupodotis barbatus</i>	<i>Eupodotis</i>	(<i>Eupodotis</i>)	<i>Eupodotis</i>	/	<i>Eupodotis</i>	(<i>Eupodotis</i>)	(<i>Eupodotis</i>)	(<i>Eupodotis</i>)	(<i>Eupodotis</i>)	(<i>Eupodotis</i>)	(<i>Eupodotis</i>)	<i>Eupodotis</i>
<i>Eupodotis caerulescens</i>	<i>Eupodotis</i>	<i>Eupodotis</i>	<i>Eupodotis</i>	/	<i>Eupodotis</i>	<i>Eupodotis</i>	<i>Eupodotis</i>	<i>Eupodotis</i>	<i>Eupodotis</i>	<i>Eupodotis</i>	<i>Eupodotis</i>	<i>Eupodotis</i>
<i>Eupodotis vigorsii</i>	<i>Heterotetrax</i>	<i>Eupodotis</i>	<i>Eupodotis</i>	/	<i>Heterotetrax</i>	<i>Eupodotis</i>	<i>Eupodotis</i>	<i>Eupodotis</i>	<i>Eupodotis</i>	<i>Eupodotis</i>	<i>Eupodotis</i>	<i>Eupodotis</i>
<i>Eupodotis rueppellii</i>	(<i>Heterotetrax</i>)	<i>Eupodotis</i>	<i>Eupodotis</i>	/	<i>Heterotetrax</i>	<i>Eupodotis</i>	<i>Eupodotis</i>	<i>Eupodotis</i>	<i>Eupodotis</i>	<i>Eupodotis</i>	<i>Eupodotis</i>	<i>Eupodotis</i>
<i>Eupodotis humilis</i>	<i>Heterotetrax</i>	<i>Eupodotis</i>	/	/	<i>Heterotetrax</i>	<i>Eupodotis</i>	<i>Eupodotis</i>	<i>Eupodotis</i>	<i>Eupodotis</i>	<i>Eupodotis</i>	<i>Eupodotis</i>	<i>Eupodotis</i>
<i>Lophotis savilei</i>	<i>Lophotis</i>	<i>Lophotis</i>	/	/	(<i>Lophotis</i>)	(<i>Eupodotis</i>)	(<i>Eupodotis</i>)	<i>Lophotis</i>	(<i>Eupodotis</i>)	(<i>Eupodotis</i>)	<i>Lophotis</i>	<i>Lophotis</i>
<i>Lophotis gindiana</i>	<i>Lophotis</i>	<i>Lophotis</i>	/	/	(<i>Lophotis</i>)	(<i>Eupodotis</i>)	(<i>Eupodotis</i>)	<i>Lophotis</i>	(<i>Eupodotis</i>)	(<i>Eupodotis</i>)	<i>Lophotis</i>	<i>Lophotis</i>
<i>Lophotis ruficrista</i>	<i>Lophotis</i>	<i>Lophotis</i>	<i>Lophotis</i>	/	<i>Lophotis</i>	<i>Eupodotis</i>	<i>Eupodotis</i>	<i>Lophotis</i>	<i>Eupodotis</i>	<i>Eupodotis</i>	<i>Lophotis</i>	<i>Lophotis</i>
<i>Houbaropsis bengalensis</i>	/	<i>Houbaropsis</i>	/	/	/	<i>Eupodotis</i>	<i>Houbaropsis</i>	<i>Houbaropsis</i>	<i>Eupodotis</i>	<i>Eupodotis</i>	<i>Houbaropsis</i>	<i>Houbaropsis</i>
<i>Sypheotides indica</i>	/	<i>Sypheotides</i>	/	/	/	<i>Eupodotis</i>	<i>Sypheotides</i>	<i>Sypheotides</i>	<i>Eupodotis</i>	<i>Eupodotis</i>	<i>Sypheotides</i>	<i>Sypheotides</i>

Table 1.3: Family Pteroclidae generic treatments. Genera not currently recognised are in bold.

Taxa	Elliot, 1878	Ogilvie-Grant, 1893	Roberts, 1922	Sclater, 1922, 1924	Bowen, 1927	Peters, 1934	Roberts, 1940	Mackworth-Praed and Grant, 1952, 1962, 1970	Wolters, 1974	Maclean, 1984	Snow, 1978; Johnsgard, 1991; Maclean and Fry, 1986; de Juana, 1997
<i>S. tibetanus</i>	<i>Syrrhaptes</i>	<i>Syrrhaptes</i>	n/a	n/a	<i>Syrrhaptes</i>	<i>Syrrhaptes</i>	n/a	n/a	<i>Syrrhaptes (Syrrhaptes)</i>	<i>Syrrhaptes Group2</i>	<i>Syrrhaptes</i>
<i>S. paradoxus</i>	<i>Syrrhaptes</i>	<i>Syrrhaptes</i>	n/a	n/a	<i>Syrrhaptes</i>	<i>Syrrhaptes</i>	n/a	n/a	<i>Syrrhaptes (Syrrhaptes)</i>	<i>Syrrhaptes Group2</i>	<i>Syrrhaptes</i>
<i>P. orientalis</i>	<i>Pterocles</i>	<i>Pterocles</i>	n/a	n/a	<i>Pterocles</i>	<i>Pterocles</i>	n/a	n/a	<i>Syrrhaptes (Eremialector)</i>	<i>Pterocles Group3</i>	<i>Pterocles</i>
<i>P. namaqua</i>	<i>Pterocles</i>	<i>Pteroclurus</i>	n/a	<i>Pterocles</i>	<i>Pterocles</i>	<i>Pterocles</i>	<i>Pterocles</i>	<i>Nyctiperdix (Namapterocles)</i>	<i>Pterocles Group1</i>	<i>Pterocles</i>	
<i>P. exustus</i>	<i>Pterocles</i>	<i>Pteroclurus</i>	n/a	<i>Pterocles</i>	<i>Pterocles</i>	<i>Pterocles</i>	n/a	<i>Pterocles</i>	<i>Nyctiperdix (Namapterocles)</i>	<i>Pterocles Group1</i>	<i>Pterocles</i>
<i>P. senegallus</i>	<i>Pterocles</i>	<i>Pteroclurus</i>	n/a	<i>Pterocles</i>	<i>Pterocles</i>	<i>Pterocles</i>	n/a	<i>Pterocles</i>	<i>Nyctiperdix (Parapterocles)</i>	<i>Pterocles Group1</i>	<i>Pterocles</i>
<i>P. alchata</i>	<i>Pterocles</i>	<i>Pteroclurus</i>	n/a	<i>Pterocles</i>	<i>Pterocles</i>	<i>Pterocles</i>	n/a	n/a	<i>Pterocles</i>	<i>Pterocles Group1</i>	<i>Pterocles</i>
<i>P. gutturalis</i>	<i>Pterocles</i>	<i>Pterocles</i>	n/a	<i>Eremialector</i>	<i>Pterocles</i>	<i>Pterocles</i>	<i>Ganga</i>	<i>Eremialector</i>	<i>Syrrhaptes (Eremialector)</i>	<i>Pterocles Group6</i>	<i>Pterocles</i>
<i>P. coronatus</i>	<i>Pterocles</i>	<i>Pterocles</i>	n/a	<i>Eremialector</i>	<i>Pterocles</i>	<i>Pterocles</i>	n/a	<i>Eremialector</i>	<i>Nyctiperdix (Macleanornis)</i>	<i>Pterocles Group4</i>	<i>Pterocles</i>
<i>P. personatus</i>	<i>Pterocles</i>	<i>Pterocles</i>	n/a	<i>Eremialector</i>	<i>Pterocles</i>	<i>Pterocles</i>	n/a	n/a	<i>Nyctiperdix (Nyctiperdix)</i>	<i>Pterocles Group4</i>	<i>Pterocles</i>
<i>P. decoratus</i>	<i>Pterocles</i>	<i>Pterocles</i>	n/a	<i>Eremialector</i>	<i>Dilophilus</i>	<i>Pterocles</i>	n/a	<i>Eremialector</i>	<i>Nyctiperdix (Nyctiperdix)</i>	<i>Pterocles Group4</i>	<i>Pterocles</i>
<i>P. lichtensteinii</i>	<i>Pterocles</i>	<i>Pterocles</i>	<i>Nyctiperdix</i>	<i>Eremialector</i>	<i>Dilophilus</i>	<i>Pterocles</i>	n/a	<i>Eremialector</i>	<i>Nyctiperdix (Nyctiperdix)</i>	<i>Pterocles Group5</i>	<i>Pterocles</i>
<i>P. indicus</i>	<i>Pterocles</i>	<i>Pterocles</i>	<i>Nyctiperdix</i>	<i>Eremialector</i>	<i>Dilophilus</i>	<i>Pterocles</i>	n/a	n/a	<i>Nyctiperdix (Nyctiperdix)</i>	<i>Pterocles Group5</i>	<i>Pterocles</i>
<i>P. quadricinctus</i>	<i>Pterocles</i>	<i>Pterocles</i>	<i>Nyctiperdix</i>	<i>Eremialector</i>	<i>Dilophilus</i>	<i>Pterocles</i>	n/a	<i>Eremialector</i>	<i>Nyctiperdix (Nyctiperdix)</i>	<i>Pterocles Group5</i>	<i>Pterocles</i>
<i>P. bicinctus</i>	<i>Pterocles</i>	<i>Pterocles</i>	<i>Nyctiperdix</i>	<i>Eremialector</i>	<i>Dilophilus</i>	<i>Pterocles</i>	<i>Nyctiperdix</i>	<i>Eremialector</i>	<i>Nyctiperdix (Dilophilus)</i>	<i>Pterocles Group5</i>	<i>Pterocles</i>
<i>P. burchelli</i>	n/a	n/a	<i>Calopterocles</i>	<i>Eremialector</i>	<i>Pterocles</i>	<i>Pterocles</i>	<i>Calopterocles</i>	<i>Eremialector</i>	<i>Calopterocles</i>	<i>Pterocles Group7</i>	<i>Pterocles</i>

Table 1.4: Family Glareolidae generic treatments. Genera not currently recognised are in bold.

Taxa	Sclater, 1924	Peters, 1934	Roberts, 1940	Mackworth-Praed and Grant, 1952, 1962, 1970	Snow, 1978	Brosset, 1986	Hayman et al., 1986	Sibley and Monroe, 1990	Maclean, 1996	Gill and Wright, 2006-8
<i>Cursorius cursor</i>	<i>Cursorius</i>	<i>Cursorius</i>	/	<i>Cursorius</i>	<i>Cursorius</i>	<i>Cursorius</i>	<i>Cursorius</i>	<i>Cursorius</i>	<i>Cursorius</i>	<i>Cursorius</i>
<i>Cursorius somalensis</i>	with <i>cursor</i>	with <i>cursor</i>	/	with <i>cursor</i>	with <i>cursor</i>	with <i>cursor</i>	with <i>rufus</i>	with <i>cursor</i>	<i>Cursorius</i>	<i>Cursorius</i>
<i>Cursorius rufus</i>	<i>Cursorius</i>	<i>Cursorius</i>	<i>Cursorius</i>	<i>Cursorius</i>	<i>Cursorius</i>	<i>Cursorius</i>	<i>Cursorius</i>	<i>Cursorius</i>	<i>Cursorius</i>	<i>Cursorius</i>
<i>Cursorius temminckii</i>	<i>Cursorius</i>	<i>Cursorius</i>	<i>Cursorius</i>	<i>Cursorius</i>	<i>Cursorius</i>	<i>Cursorius</i>	<i>Cursorius</i>	<i>Cursorius</i>	<i>Cursorius</i>	<i>Cursorius</i>
<i>Cursorius coromandelicus</i>	/	<i>Cursorius</i>	/	/	<i>Cursorius</i>	<i>Cursorius</i>	<i>Cursorius</i>	<i>Cursorius</i>	<i>Cursorius</i>	<i>Cursorius</i>
<i>Rhinoptilus (Smutsornis) africanus</i>	<i>Rhinoptilus</i>	<i>Rhinoptilus</i>	<i>Smutsornis</i>	<i>Hemerodromus</i>	<i>Cursorius</i>	<i>Cursorius</i>	<i>Rhinoptilus</i>	<i>Smutsornis</i>	<i>Rhinoptilus</i>	<i>Rhinoptilus</i>
<i>Rhinoptilus cinctus</i>	<i>Rhinoptilus</i>	<i>Rhinoptilus</i>	<i>Hemerodromus</i>	<i>Hemerodromus</i>	<i>Cursorius</i>	<i>Cursorius</i>	<i>Rhinoptilus</i>	<i>Rhinoptilus</i>	<i>Rhinoptilus</i>	<i>Rhinoptilus</i>
<i>Rhinoptilus chalcopterus</i>	<i>Rhinoptilus</i>	<i>Rhinoptilus</i>	<i>Rhinoptilus</i>	<i>Rhinoptilus</i>	<i>Cursorius</i>	<i>Cursorius</i>	<i>Rhinoptilus</i>	<i>Rhinoptilus</i>	<i>Rhinoptilus</i>	<i>Rhinoptilus</i>
<i>Rhinoptilus bitorquatus</i>	<i>Rhinoptilus</i>	<i>Rhinoptilus</i>	/	/	<i>Cursorius</i>	<i>Cursorius</i>	<i>Rhinoptilus</i>	<i>Rhinoptilus</i>	<i>Rhinoptilus</i>	<i>Rhinoptilus</i>
<i>Stiltia isabella</i>	/	<i>Stiltia</i>	/	/	/	/	<i>Stiltia</i>	<i>Stiltia</i>	<i>Stiltia</i>	<i>Stiltia</i>
<i>Glareola pratincola</i>	<i>Glareola</i>	<i>Glareola</i>	<i>Glareola</i>	<i>Glareola</i>	<i>Glareola</i>	<i>Glareola</i>	<i>Glareola</i>	<i>Glareola</i>	<i>Glareola</i>	<i>Glareola</i>
<i>Glareola maldivarum</i>	/	<i>Glareola</i>	/	/	<i>Glareola</i>	/	<i>Glareola</i>	<i>Glareola</i>	<i>Glareola</i>	<i>Glareola</i>
<i>Glareola nordmanni</i>	<i>Glareola</i>	<i>Glareola</i>	<i>Glareola</i>	<i>Glareola</i>	<i>Glareola</i>	<i>Glareola</i>	<i>Glareola</i>	<i>Glareola</i>	<i>Glareola</i>	<i>Glareola</i>
<i>Glareola ocularis</i>	<i>Glareola</i>	<i>Glareola</i>	/	<i>Glareola</i>	<i>Glareola</i>	<i>Glareola</i>	<i>Glareola</i>	<i>Glareola</i>	<i>Glareola</i>	<i>Glareola</i>
<i>Glareola nuchalis</i>	<i>Galachrysa</i>	<i>Glareola</i>	<i>Galachrysa</i>	<i>Galachrysa</i>	<i>Glareola</i>	<i>Glareola</i>	<i>Glareola</i>	<i>Glareola</i>	<i>Glareola</i>	<i>Glareola</i>
<i>Glareola cinerea</i>	<i>Galachrysa</i>	<i>Galachrysa</i>	/	<i>Galachrysa</i>	<i>Glareola</i>	<i>Glareola</i>	<i>Glareola</i>	<i>Glareola</i>	<i>Glareola</i>	<i>Glareola</i>
<i>Glareola lactea</i>	/	<i>Galachrysa</i>	/	/	<i>Glareola</i>	/	<i>Glareola</i>	<i>Glareola</i>	<i>Glareola</i>	<i>Glareola</i>

Table 1.5: Life history strategy information, including habitat and displays, for each group per category. Three broad morphological characters are also presented. More details are presented in each chapter.

		Otididae	Pteroclidae	Glareolidae	<i>Ptilopachus</i>
Habitat	Desert	1	1	1	
	Grassland	1	1	1	
	Arid Savannah	1	1	1	1
	Forest				1
Feeding mode	Terrestrial	1	1	1	1
	Aerial			1	
Migrant	Long-distance	1		1	
	Nomadic	1	1		
	Sedentary	1	1	1	1
Gregarious	Flocking	1	1	1	
	Group-living	1			1
Sexual Size Dimorphism (SSD)	Significant SSD	1			
	Reversed SSD	1			
Moult	Non-breeding plumage	1	1	1	
	Single plumage type	1	1	1	1
Display	Aerial	1	1	1	
	Terrestrial	1	1	1	1
Lekking	Present	1			
Leg length	Long	1		1	Intermediate
	Short		1	1	Intermediate
Hallux	Present		1	1	1
	Absent	1		1	
Wing length and shape	Long and pointed		1	1	
	Short and rounded	1	1	1	1

Figure legends Ch. 1

Fig. 1.1: A satellite image of the African continent (NASA) depicting broad zones of aridity and an arrow indicating the approximate location of an hypothesised arid corridor. Contemporary regions (delineated more clearly in Fig. 2) are identified by letters as follows:

- A: Sahel
- B: North-east arid zone
- C: South-west arid zone
- D: Sahara desert
- E: Ethiopian highlands
- F: Congo basin forests
- G: Moist woodlands
- M: Madagascar

Fig. 1.2: Simplified vegetation types of sub-Saharan Africa from Kingdom (1989). Colours have been added to highlight the desert, semi desert and arid savanna habitats that comprise the south-west, north-east and Sahel arid zones.

Fig. 1.3: Balinsky's (1962) map of Africa based on contemporary climatic data showing the zone that currently has less than 10 mm of rain per month in three consecutive months of the year.

Fig. 1.4: Winterbottom's (1967) map of Africa showing the hypothesised arid corridor linking the south-west and north-east arid zones.

Fig. 1.5: Distribution of the genus *Eupodotis*, excluding *E. senegalensis* and *E. barrowi*, with some overlap in central South Africa between *E. vigorsii* and *E. caerulescens* (redrawn from Vernon, 1999).

Fig. 1.6: Distribution of the genus *Lophotis* (redrawn from Johnsgard, 1986).

Fig. 1.7: Distribution of *Rhinoptilus cinctus* (redrawn from Maclean and Urban, 1986).

Fig. 1.8: Sahara desert from the air, near Timbuktu in central Mali. Exploration of this area by vehicle revealed *Ardeotis arabs* and *Cursorius cursor*. (© Callan Cohen).

Fig. 1.9: Namib desert plains near the Brandberg in central Namibia. *Eupodotis rueppellii* and *Cursorius rufus* were recorded here; *Neotis ludwigii*, *Rhinoptilus africanus* and *Pterocles namaqua* were recorded in an adjacent, grassier area. (© Callan Cohen).

Fig. 1.10: Stony plains of the Namib desert near Sossusvlei in southern Namibia; the white legs in the bottom left betray the presence of *Cursorius rufus*; *Eupodotis rueppellii* was also recorded here. (© Callan Cohen).

Fig. 1.11: Plains on the eastern edge of the Namib desert at Spitzkoppe in central Namibia showing good *Stipagrostis* grass cover after rain and *Acacia* trees in the

drainage lines; *Eupodotis rueppellii*, *Neotis ludwigii*, *Rhinoptilus africanus* and *Pterocles namaqua* were recorded here. (© Callan Cohen).

Fig. 1.12: Karoo plains of the Tanqua Karoo south of Calvinia, South Africa; *Eupodotis vigorsii*, *Neotis ludwigii*, *Cursorius rufus*, *Rhinoptilus africanus* and *Pterocles namaqua* were recorded in this area. (© Callan Cohen).

Fig. 1.13: Karoo plains in Namaqualand near Vanrhynsdorp, South Africa, in spring; *Eupodotis vigorsii*, *Neotis ludwigii* and *Pterocles namaqua* were recorded in this area. (© Callan Cohen).

Fig. 1.14: Arid savanna of the southern Kalahari near Kimberley, South Africa, with grassy plains alternating with *Acacia* trees; *Pterocles namaqua*, *Afrortis afraoides* and *Lophotis ruficrista* were recorded in this area, with *Ardeotis k. kori* and *Pterocles burchelli* occurring in similar habitat to the north. (© Callan Cohen).

Fig. 1.15: High-altitude grasslands in winter near Wakkerstroom, South Africa; *Eupodotis caerulescens* and *Neotis denhami* were recorded here. (© Callan Cohen).

Fig. 1.16: Arid plains on the Red Sea of the north-east arid zone near Tadjoura, Djibouti (© Callan Cohen).

Fig. 1.17: Arid shrublands near Burco, Somaliland, northern region of Somalia. Remarkably, two north-east arid zone endemic bustards are visible in this photograph: *Neotis heuglinii* on the left and a camouflaged *Eupodotis humilis* in the centre. *Cursorius somalensis* and *Pterocles exustus* were recorded nearby. (© Callan Cohen).

Fig. 1.18: Arid *Acacia* savanna after good rains in the central Serengeti, northern Tanzania. *Ardeotis k. struthiunculus*, *Eupodotis senegalensis*, *Lissotis hartlaubi* and *Pterocles gutturalis* were all recorded in this area. (© Callan Cohen).

Fig. 1.19: Lowland rainforest near Salonga National Park in the central Democratic Republic of the Congo (© Callan Cohen).

Fig. 1.20: Lowland rainforest at Budongo in western Uganda; *Francolinus nahani* was recorded here. (© Callan Cohen).

Fig. 1.21: Mopane woodland (the visible trees are all *Colophospermum mopane*) in eastern Etosha National Park, Namibia. A male *Lophotis ruficrista* (with a black belly) is visible on a mound in the bottom left of the photograph; *Rhinoptilus chalcopterus* and *Pterocles bicinctus* were also recorded here. (© Callan Cohen).

Fig. 1.22: Open plains and arid woodlands of the Sahel, near Waza National Park, northern Cameroon; *Ardeotis arabs*, *Eupodotis senegalensis*, *Rhinoptilus chalcopterus* and *Pterocles quadricinctus* were recorded here. *Lophotis savilei* occurs scarcely here too. The haziness in the photograph is caused by the dust-bearing Saharan wind, the Harmattan. (© Callan Cohen).

Fig. 1.23: Arid rocky hillsides in the Sahel, near Mora, northern Cameroon; *Ptilopachus petrosus* was recorded here. (© Callan Cohen).

Fig. 1.24: *Eupodotis senegalensis*, Serengeti, northern Tanzania (© Callan Cohen).

Fig. 1.25: *Eupodotis senegalensis*, Wajaale, north-west Somaliland, Somalia (© Callan Cohen).

Fig. 1.26: *Eupodotis humilis*, near Burco, central Somaliland, Somalia (© Callan Cohen).

Fig. 1.27: *Eupodotis rueppellii*, near Sossusvlei, southern Namibia (© Callan Cohen).

Fig. 1.28: *Eupodotis vigorsii*, Tanqua Karoo south of Calvinia, South Africa (© Callan Cohen).

Fig. 1.29: *Eupodotis caerulescens*, near Wakkerstroom, South Africa (© Callan Cohen).

Fig. 1.30: *Eupodotis barrowii*, near Wakkerstroom, South Africa (© Callan Cohen).

Fig. 1.31: *Afrotis afraoides*, Etosha National Park, northern Namibia (© Callan Cohen).

Fig. 1.32: *Afrotis afra*, West Coast National Park, Langebaan, South Africa (© Callan Cohen).

Fig. 1.33: *Lophotis ruficrista*, near Windhoek, central Namibia (© Callan Cohen).

Fig. 1.34: *Lophotis gindiana*, south of Saylac, northern Somaliland, Somalia (© Callan Cohen).

Fig. 1.35: *Neotis ludwigii*, near Solitaire, southern Namibia (© Callan Cohen).

Fig. 1.36: *Neotis heuglinii*, near Burco, central Somaliland, Somalia (© Callan Cohen).

Fig. 1.37: *Neotis nuba*, photographed at the American Museum of Natural History, New York (© Callan Cohen).

Fig. 1.38: *Neotis denhami*, near Masindi, western Uganda (© Callan Cohen).

Fig. 1.39: *Lissotis melanogaster*, Serengeti, northern Tanzania (© Callan Cohen).

Fig. 1.40: *Lissotis hartlaubi*, Serengeti, northern Tanzania (© Callan Cohen).

Fig. 1.41: *Ardeotis k. struthiunculus*, Ngorongoro, northern Tanzania (© Callan Cohen).

Fig. 1.42: *Ardeotis k. kori*, Etosha National Park, northern Namibia (© Callan Cohen).

Fig. 1.43: *Ardeotis arabs*, Awash National Park, eastern Ethiopia (© Callan Cohen).

Fig. 1.44: *Pterocles gutturalis*, Serengeti, northern Tanzania (© Callan Cohen).

Fig. 1.45: *Pterocles namaqua*, near Kimberley, South Africa; captured in a mist-net when coming to drink at water, sampled and released. (© Callan Cohen).

Fig. 1.46: *Pterocles exustus*, south of Saylac, northern Somaliland, Somalia (© Callan Cohen).

Fig. 1.47: *Pterocles bicinctus*, Hobatere, northern Namibia (© Callan Cohen).

Fig. 1.48: *Pterocles decoratus*, Tarangire, northern Tanzania (© Callan Cohen).

Fig. 1.49: *Pterocles personatus*, near Toliara, southern Madagascar (© Callan Cohen).

Fig. 1.50: *Rhinoptilus africanus*, Serengeti, northern Tanzania (© Callan Cohen).

Fig. 1.51: *Rhinoptilus africanus*, Etosha, northern Namibia (© Callan Cohen).

Fig. 1.52: *Cursorius rufus*, near Brandvlei, South Africa (© Callan Cohen).

Fig. 1.53: *Cursorius somalensis*, near Bohootleh, southern Somaliland, Somalia (© Callan Cohen).

Fig. 1.54: *Cursorius temminckii*, Etosha, northern Namibia (© Callan Cohen).

Fig. 1.55: *Rhinoptilus chalcopterus*, Hobatere, northern Namibia (© Callan Cohen).

Fig. 1.56: *Ptilopachus petrosus*, dashing between a gap in the rocks, near Mora, northern Cameroon (© Callan Cohen).

Fig. 1.57: *Francolinus nahani*, turning away and to the left, Mabira Forest, central Uganda (© Callan Cohen).

Fig. 1.1

1.32



Fig. 1.2

1.33

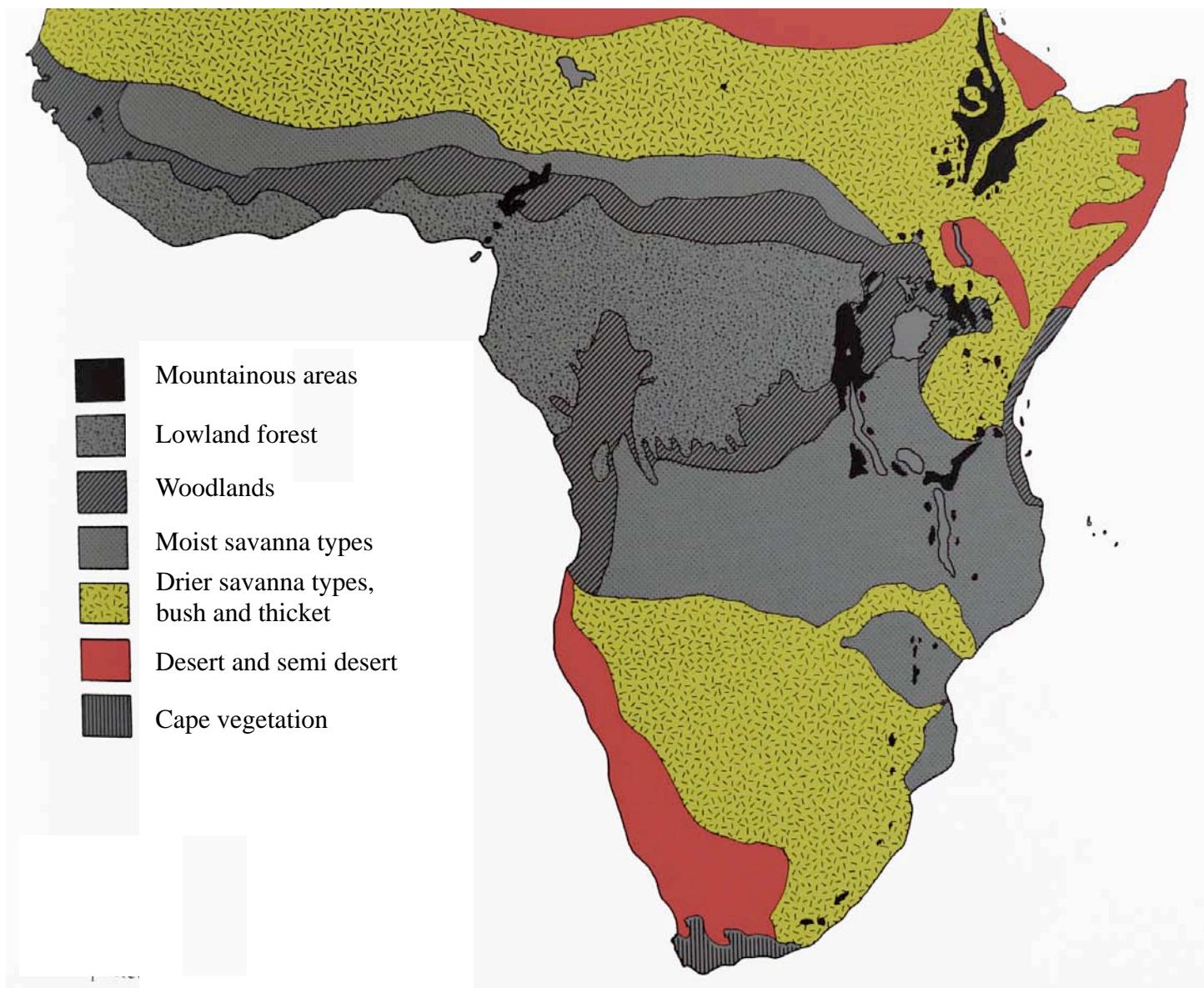


Fig. 1.3

1.34

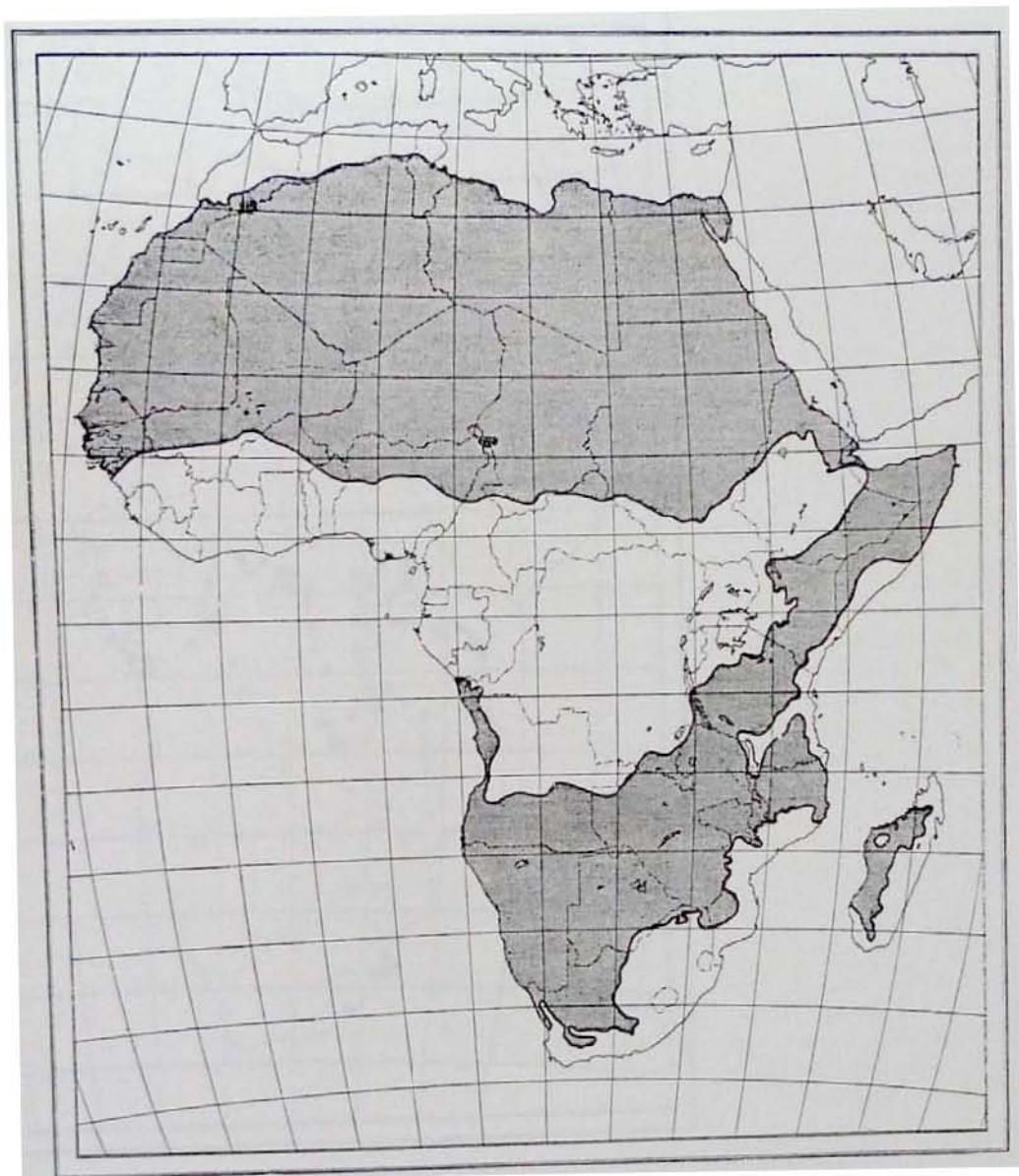


Fig. 1.4

1.35



Fig. 1.5

1.36

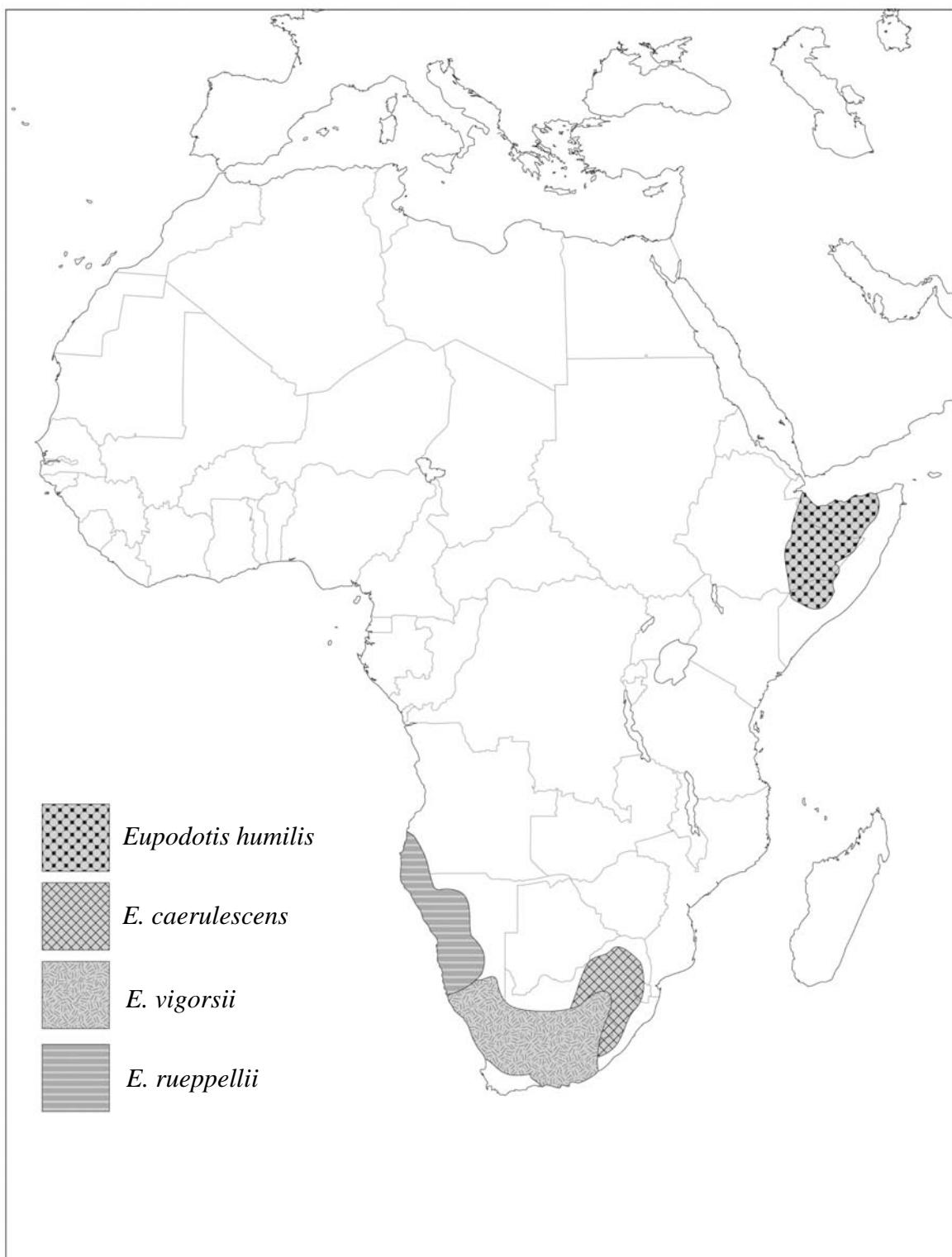


Fig. 1.6

1.37

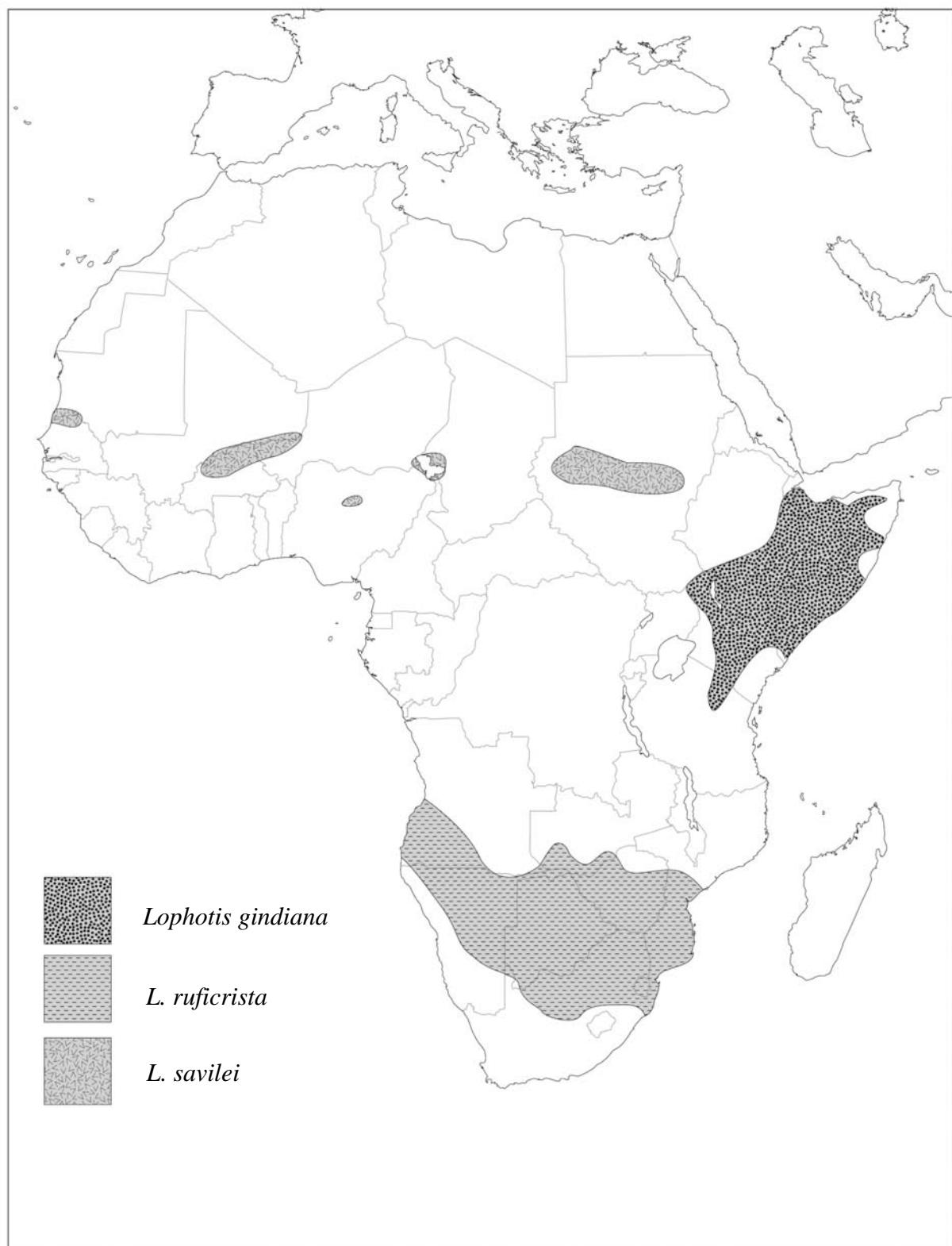


Fig. 1.7

1.38

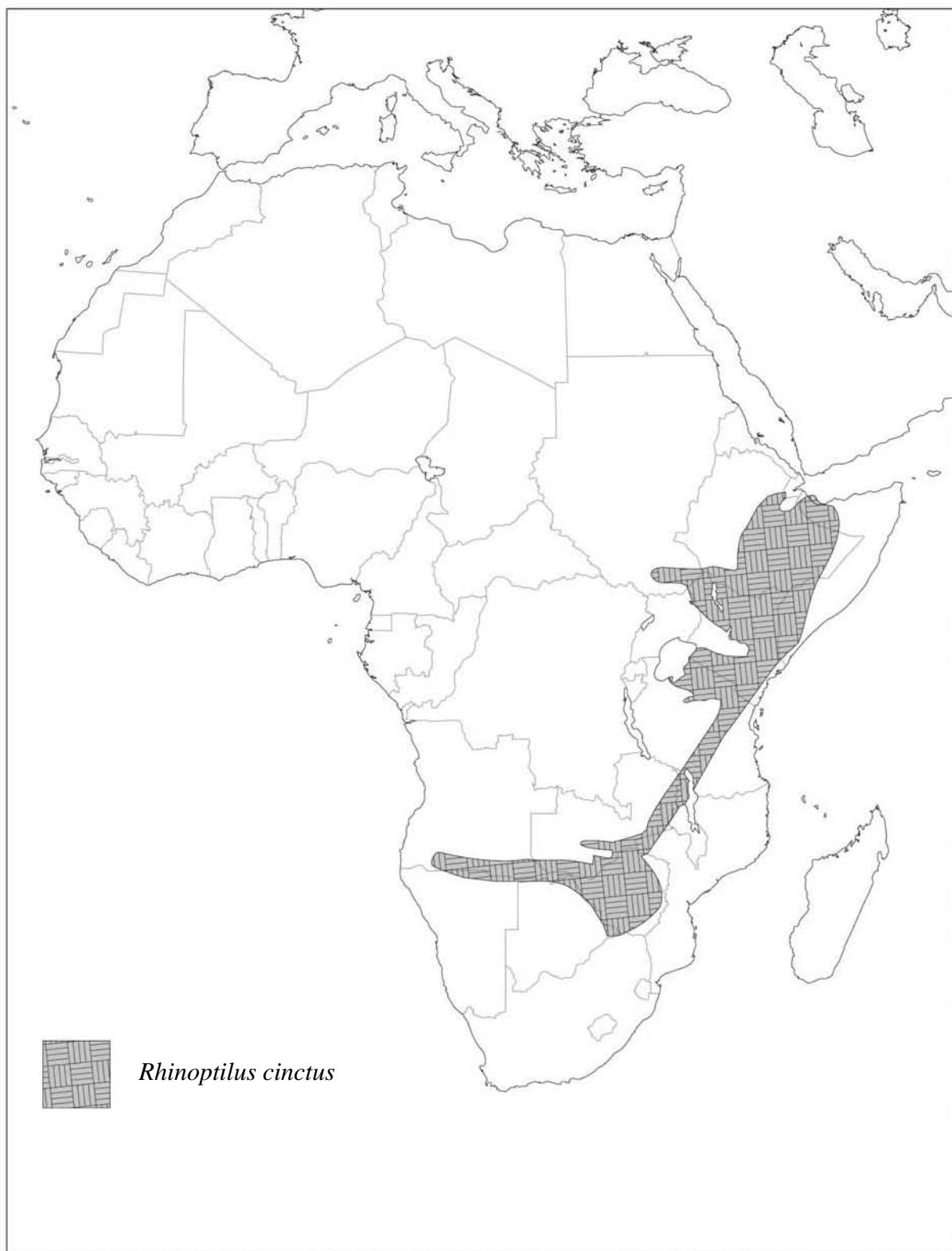


Fig. 1.1

1.32



Fig. 1.2

1.33

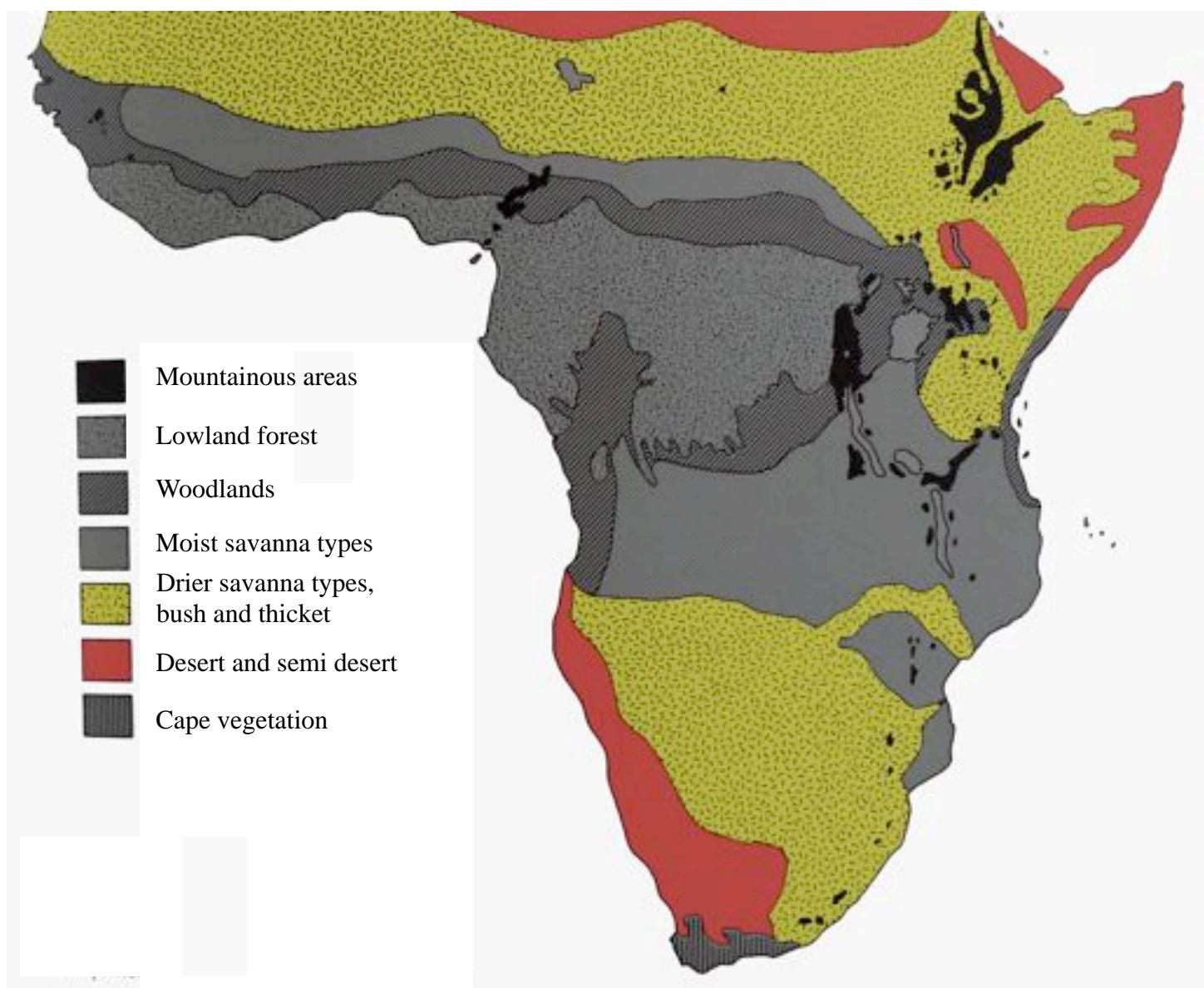


Fig. 1.3

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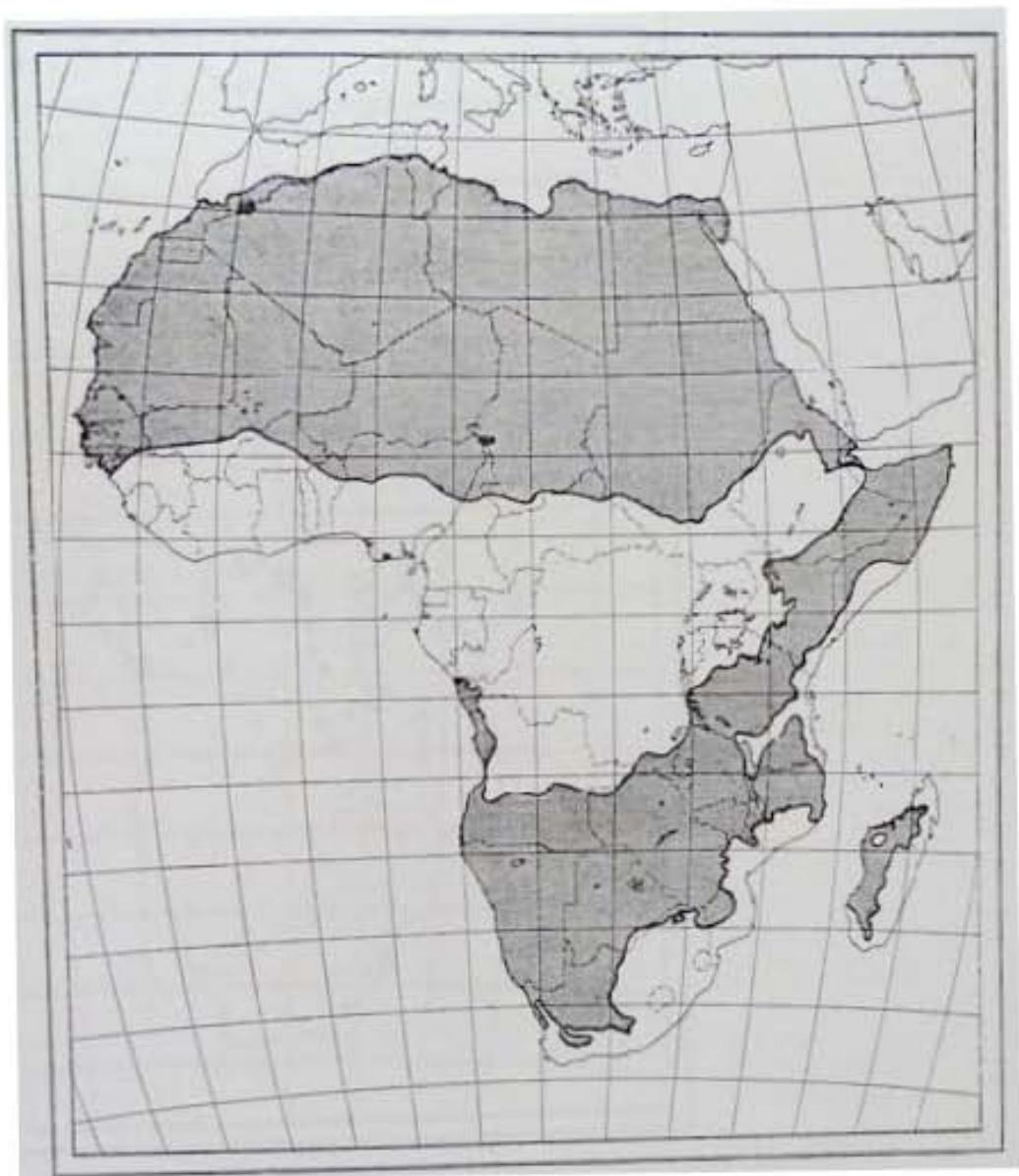


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1.35

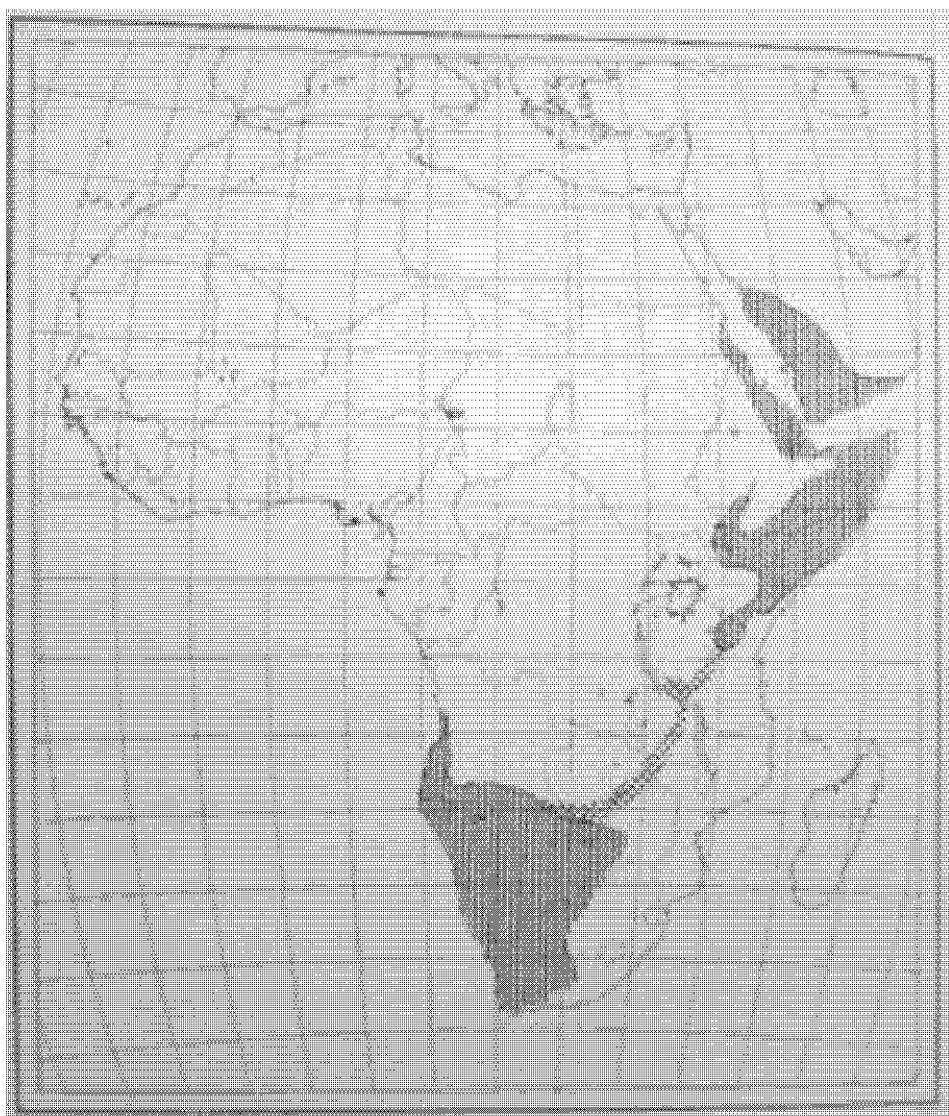


Fig. 1.5

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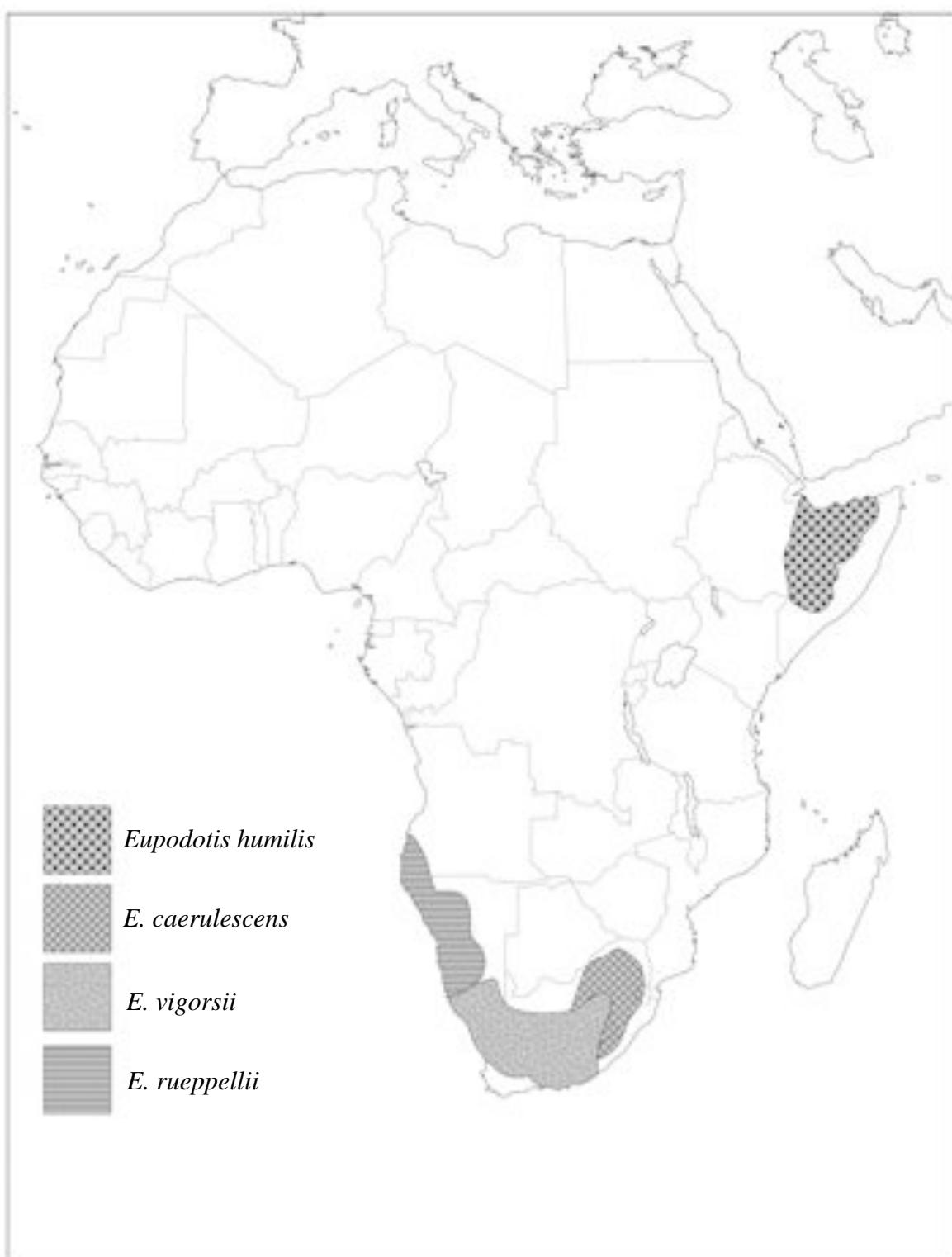


Fig. 1.6

1.37

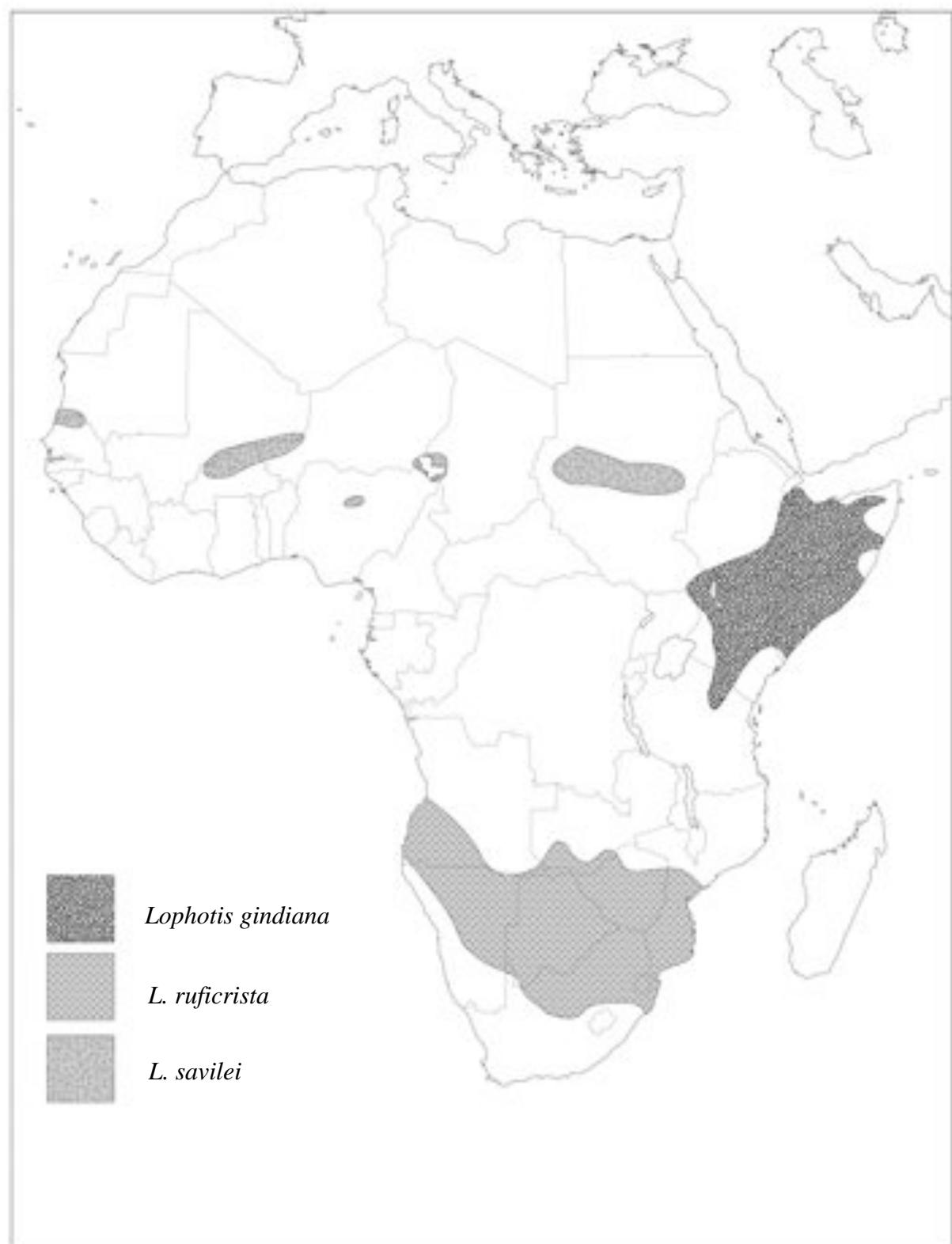


Fig. 1.7

1.38

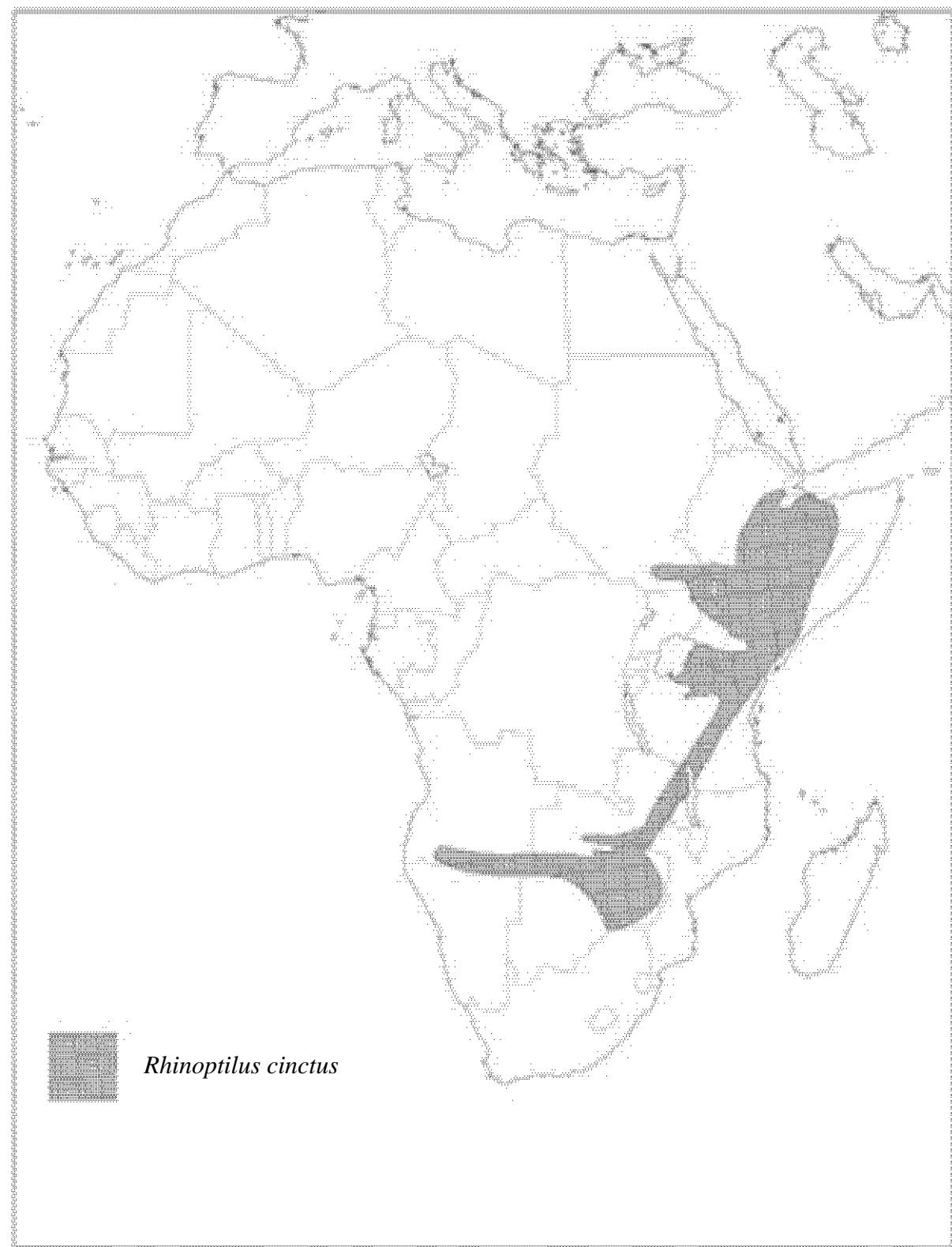


Figure Legends Ch. 2

Fig. 2.1: Hypothesised relationships among the Otididae by Johnsgard (1991) based on morphology, display and distribution.

Fig. 2.2: Parsimony cladogram for concatenated dataset of all morphological-behavioural and multilocus DNA data. Nodes numbers are indication by #. Jackknife support values are presented and are followed by the majority rule if > 50 . The major clades are labelled. The broken line opposite *Lissotis* indicates that although this genus is sometimes included in **Clade Larger bustards**, it is not present in that clade here. Species codes, used throughout this work, are hyphenated, unpunctuated versions, such that *Otis tarda* = *Otis_tarda* and *Ardeotis k. kori* = *Ardeotis_k_kori*. Note *Chlamydotis_u_fuerteventurae* = *Chlamydotis_undulata_fuertaventurae*.

Fig. 2.3: Strict-consensus parsimony cladogram for morphological-behavioural data with jackknife support values < 50 .

Fig. 2.4: Strict consensus parsimony cladogram for DNA data. Bootstrap branch support values > 50 are followed by jackknife values only if these > 50 .

Fig. 2.5: Mixed-model Bayesian analysis of the combined DNA dataset. Support values represent posterior probabilities followed by bootstrap values from the mixed-model Maximum Likelihood analysis.

Fig. 2.6: Strict consensus parsimony cladogram for mtDNA data. Bootstrap branch support values > 50 are presented.

Fig. 2.7: Mixed-model Bayesian analysis of the mtDNA dataset; support values represent posterior probabilities.

Fig. 2.8: Mixed-model Maximum Likelihood analysis of the mtDNA dataset; support values represent bootstrap values.

Fig. 2.9: Strict consensus parsimony cladogram for nuclear DNA data. Bootstrap branch support values > 50 are presented.

Fig. 2.10: Mixed-model Bayesian analysis of the nuclear DNA dataset; support values represent posterior probabilities.

Fig. 2.11: Mixed-model Maximum Likelihood analysis of the nuclear DNA dataset; support values represent bootstrap values.

Fig. 2.12: Strict consensus parsimony cladogram (Fig. 2.2) with selected morphological and behavioural characters mapped.

Fig. 2.13: Live capture and release of *Afrotis afraoides*: the bird was slowly herded by car towards a pre-positioned stretch of net before being flushed into the net. Morphometric measurements are taken. © Callan Cohen.

Fig. 2.14: Live capture and release of *Afrotis afraoides*: blood sample being taken.

Fig. 2.1

2.47

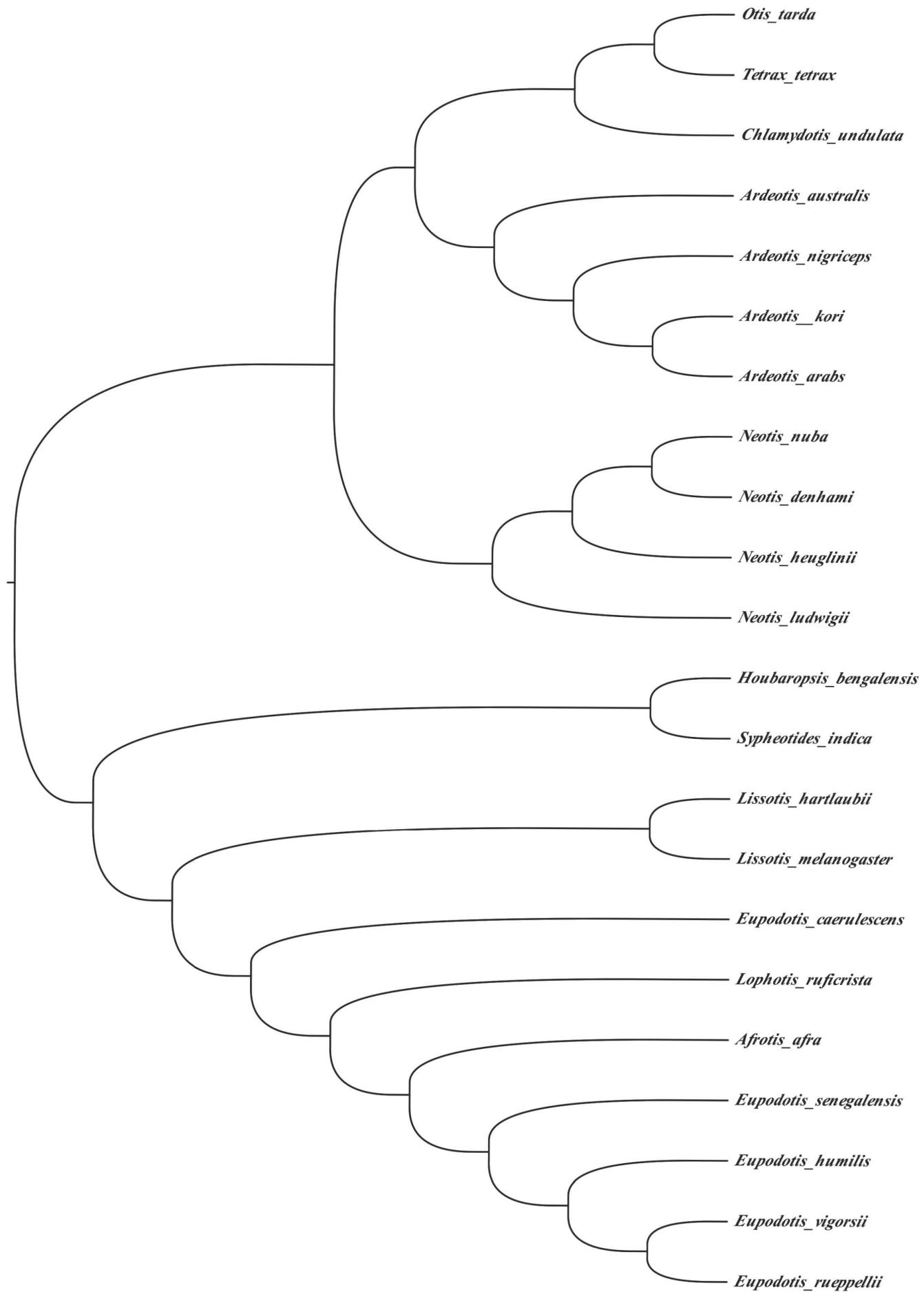


Fig. 2.2

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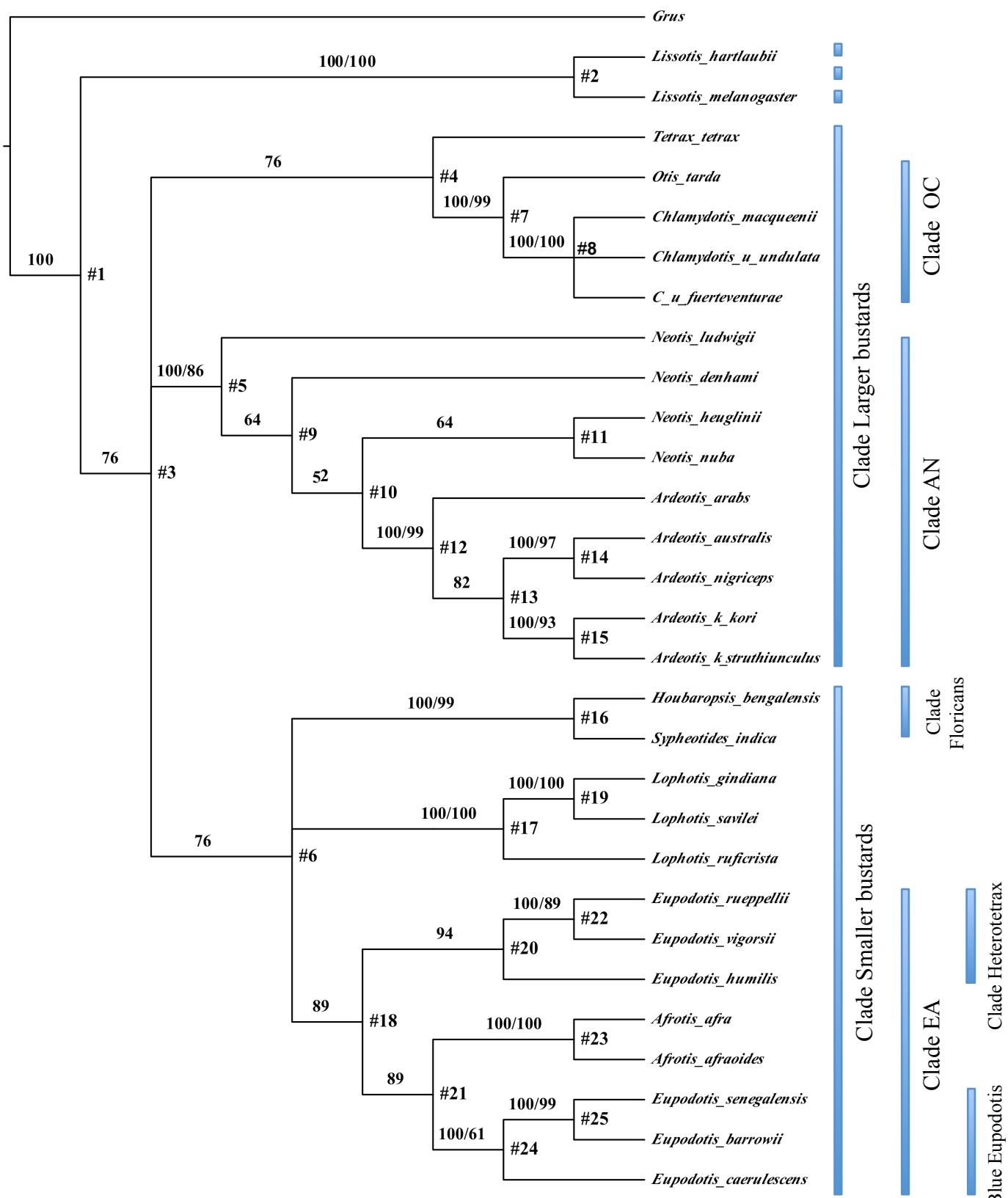


Fig. 2.3

2.49

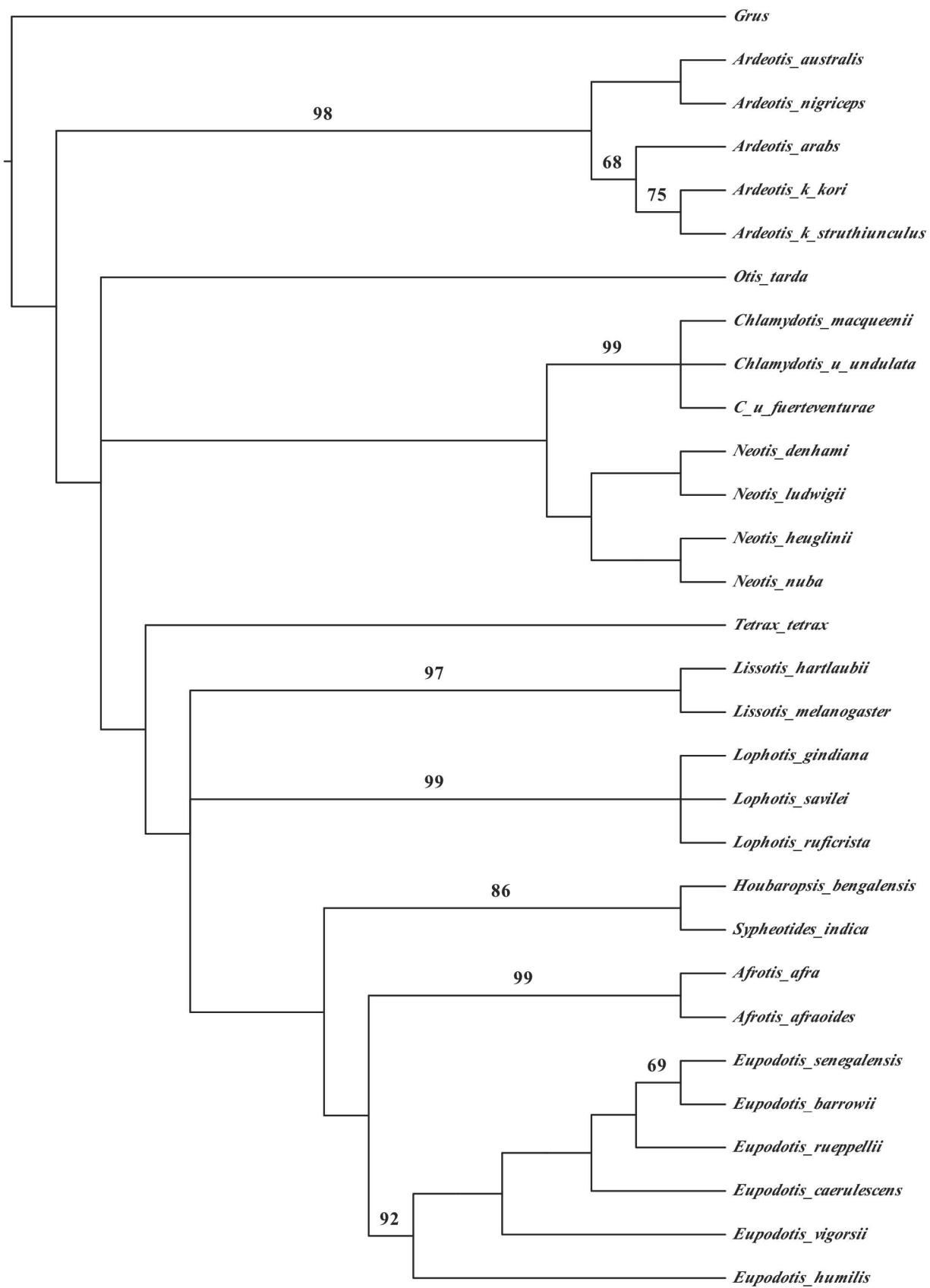


Fig. 2.4

2.50

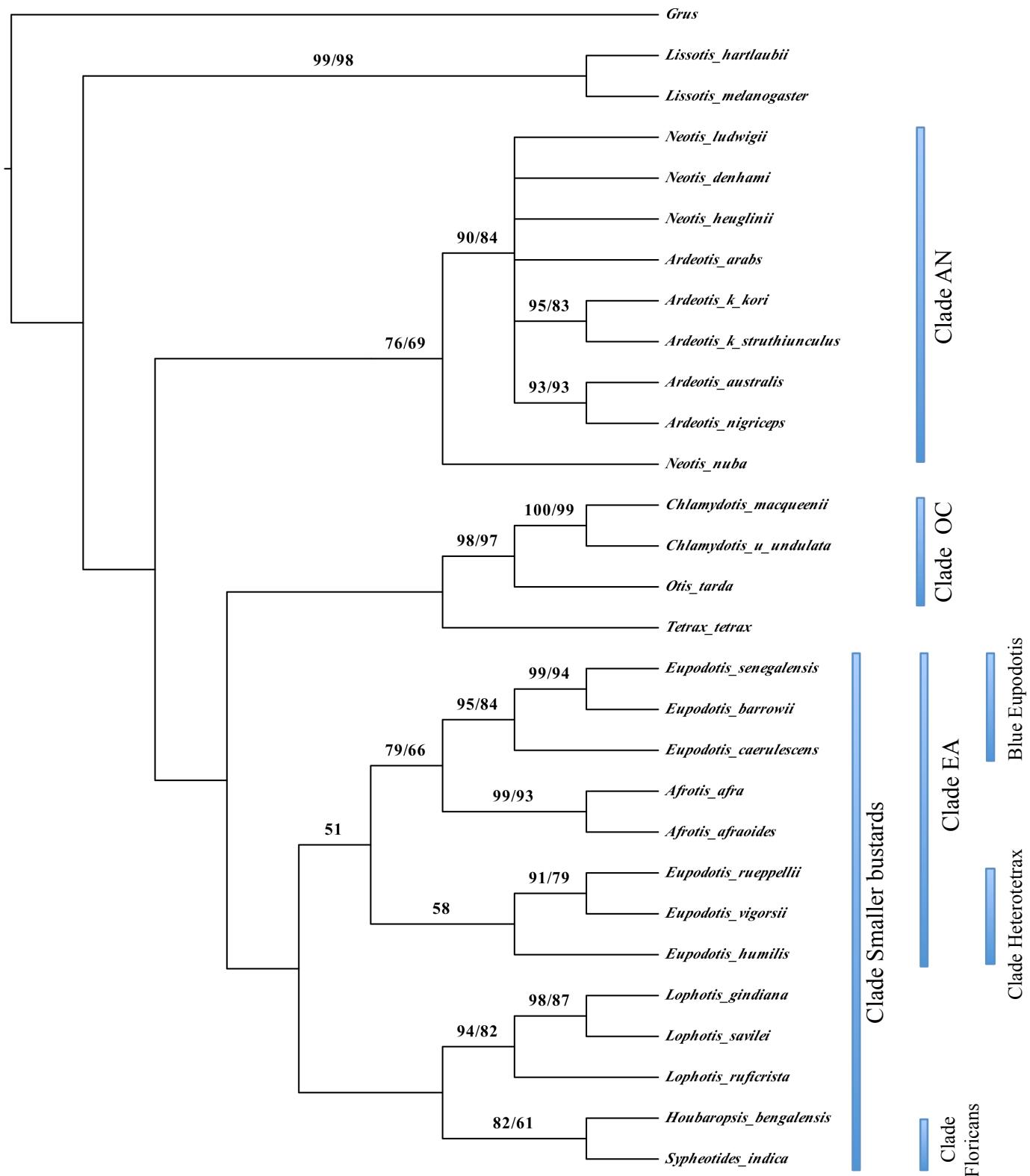


Fig. 2.5

2.51

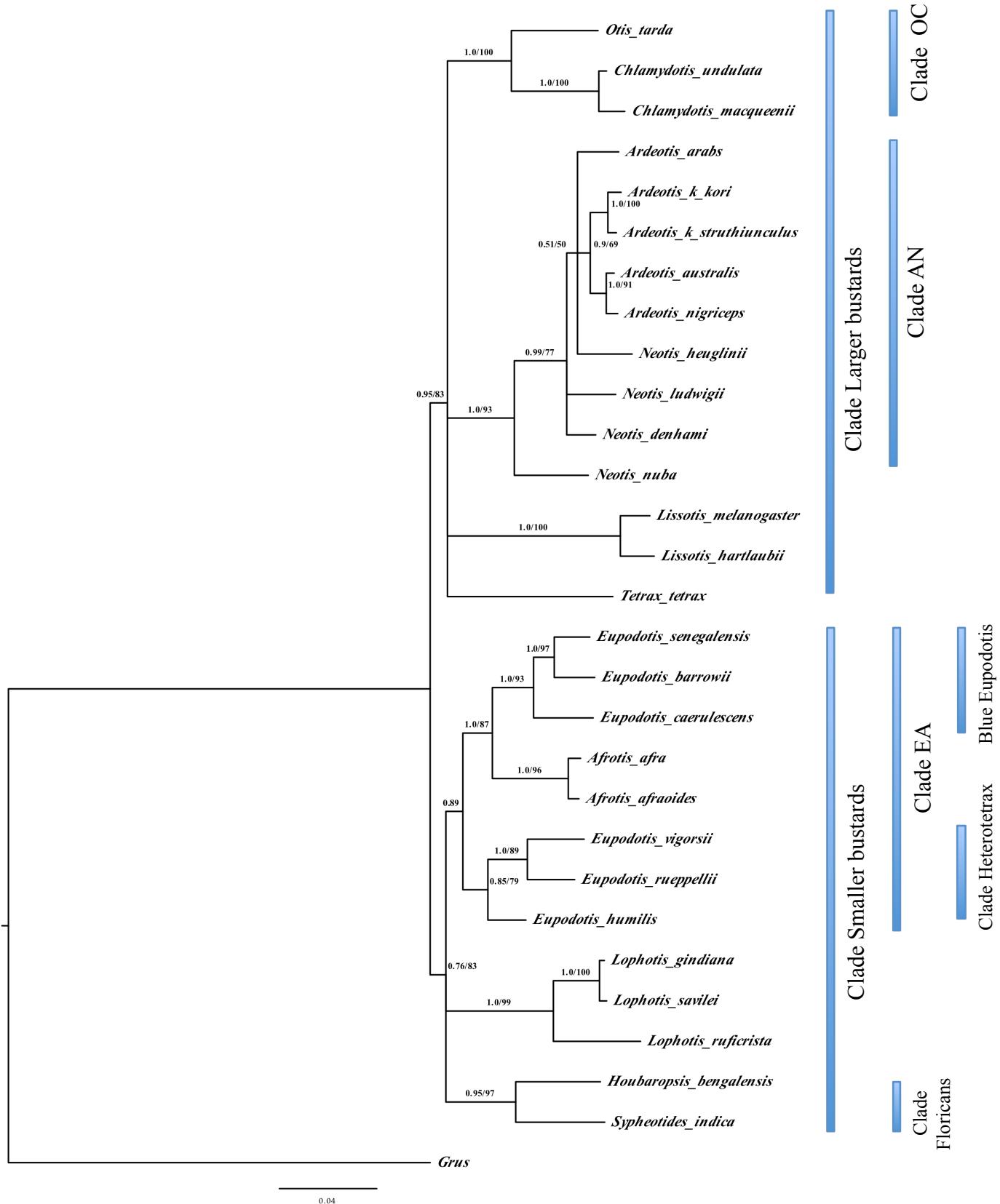


Fig. 2.5 (with larger font support values)

2.52

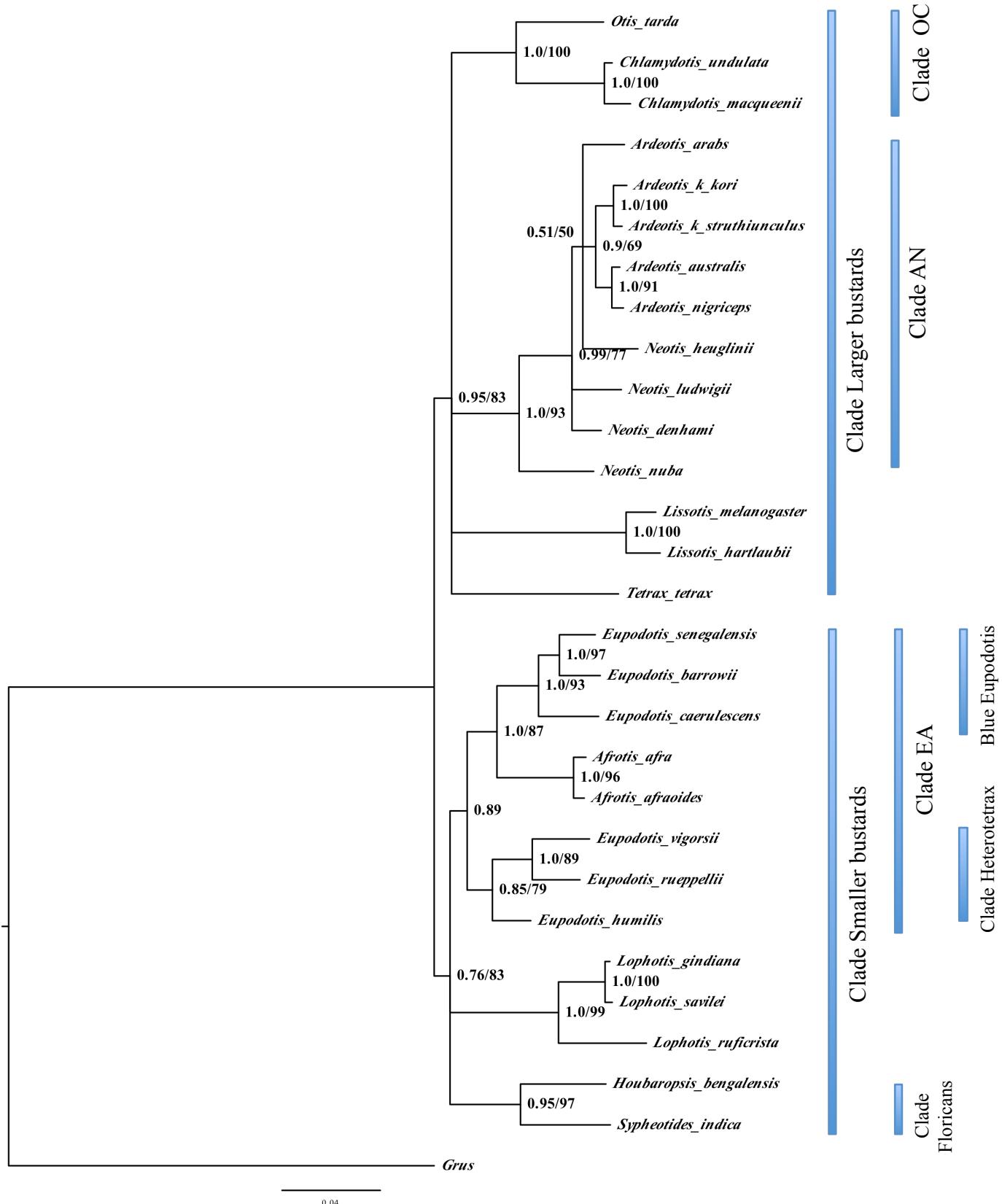


Fig. 2.6

2.53

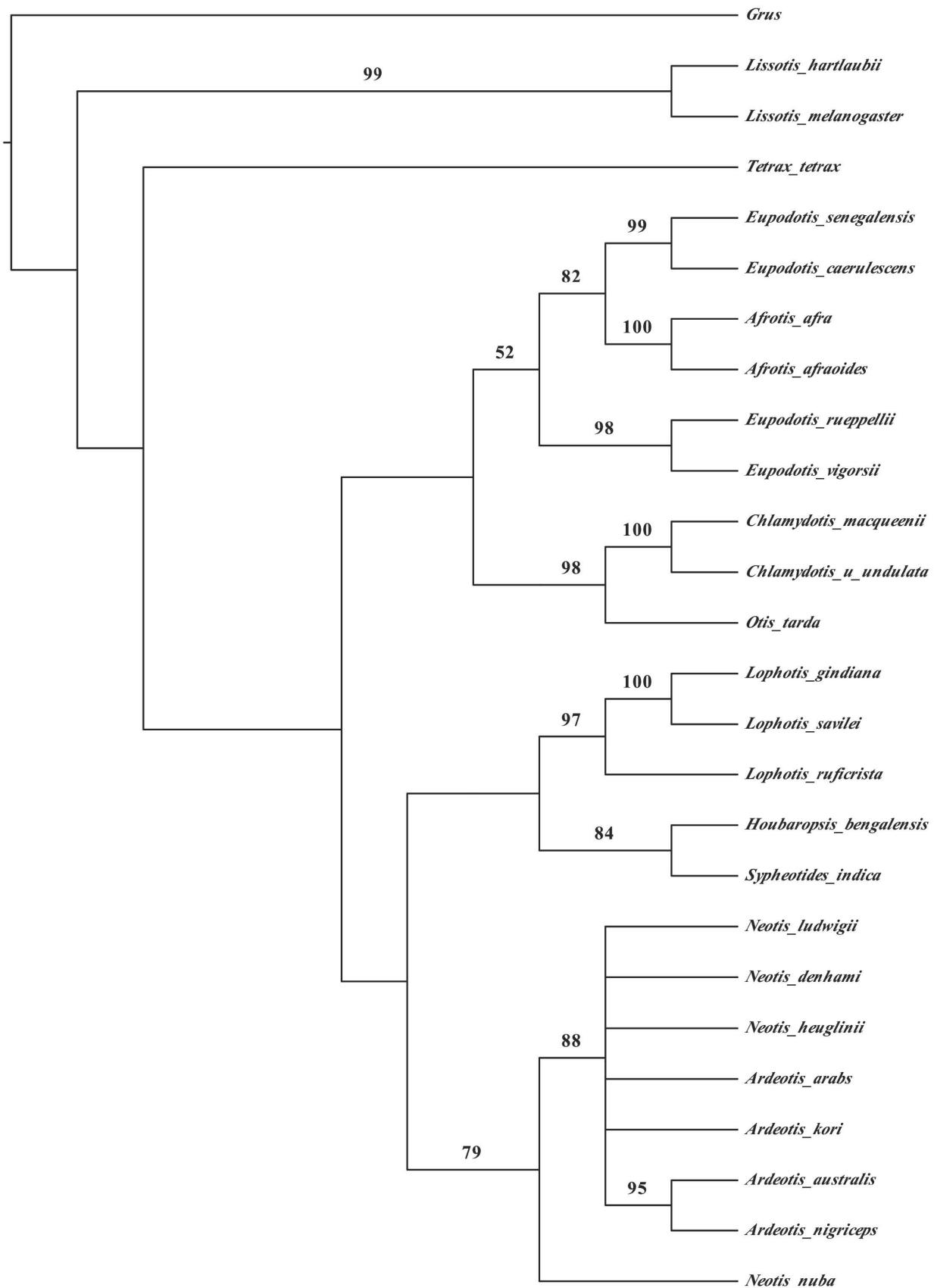


Fig. 2.7

2.54

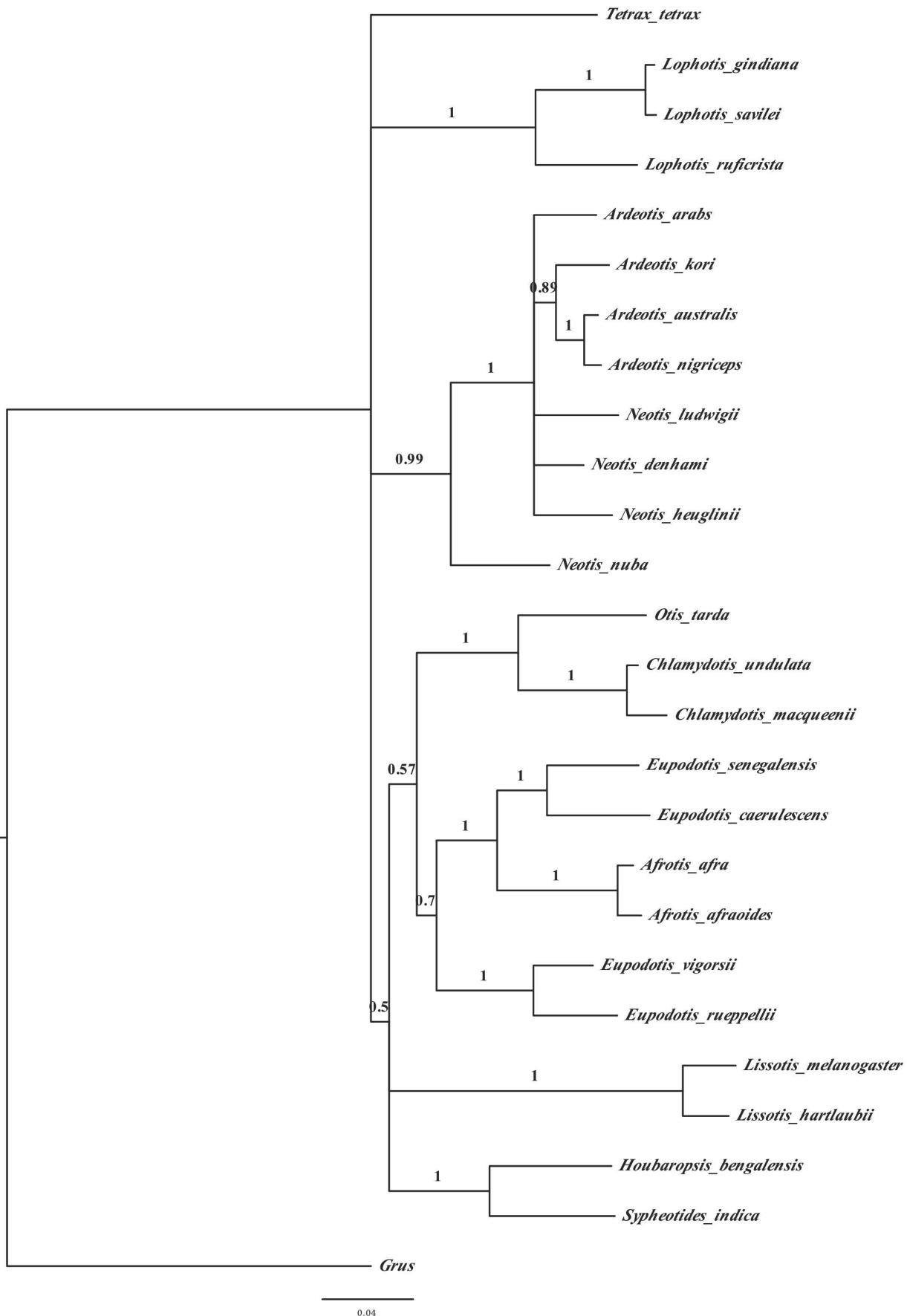


Fig. 2.8

2.55

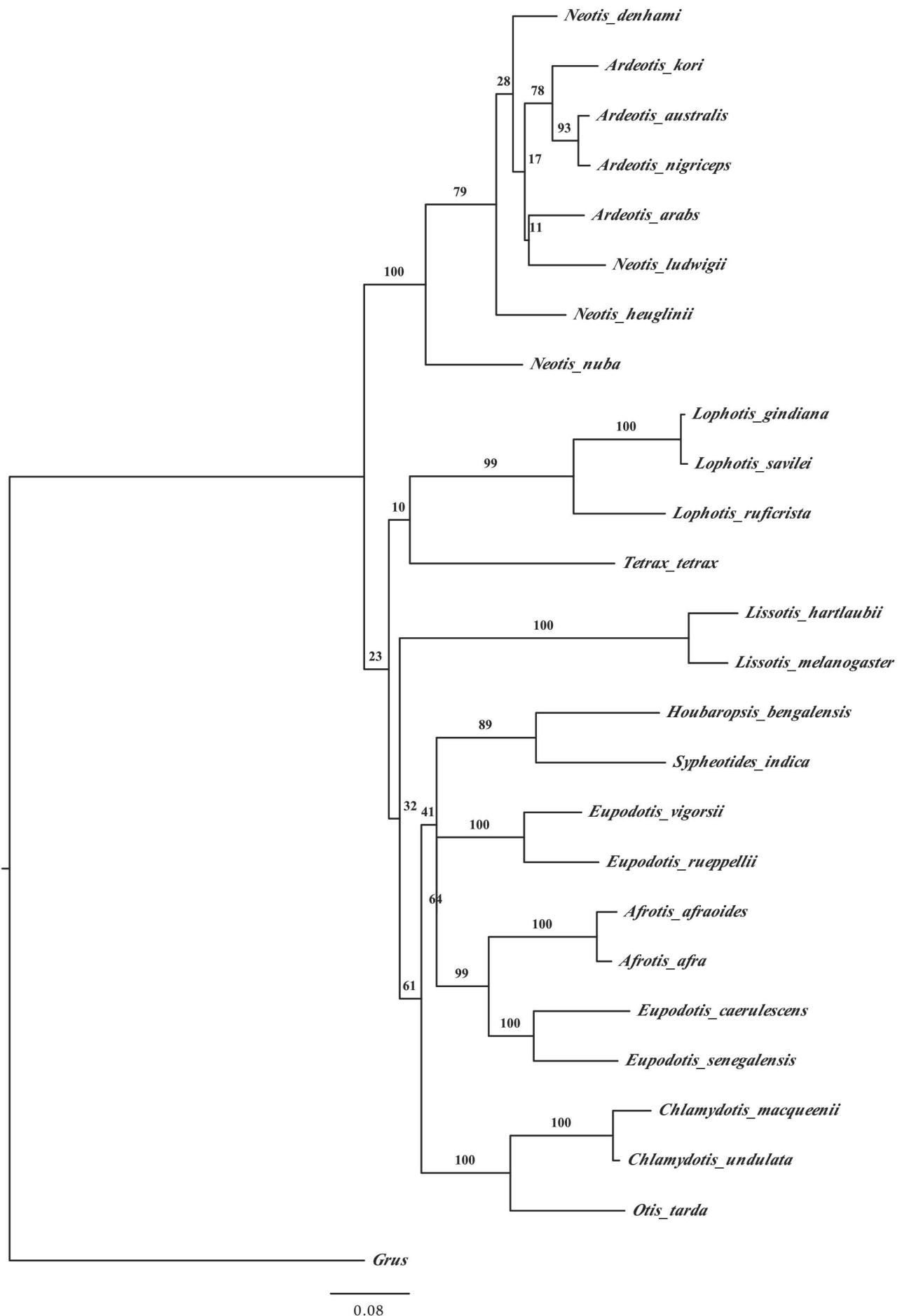


Fig. 2.9

2.56

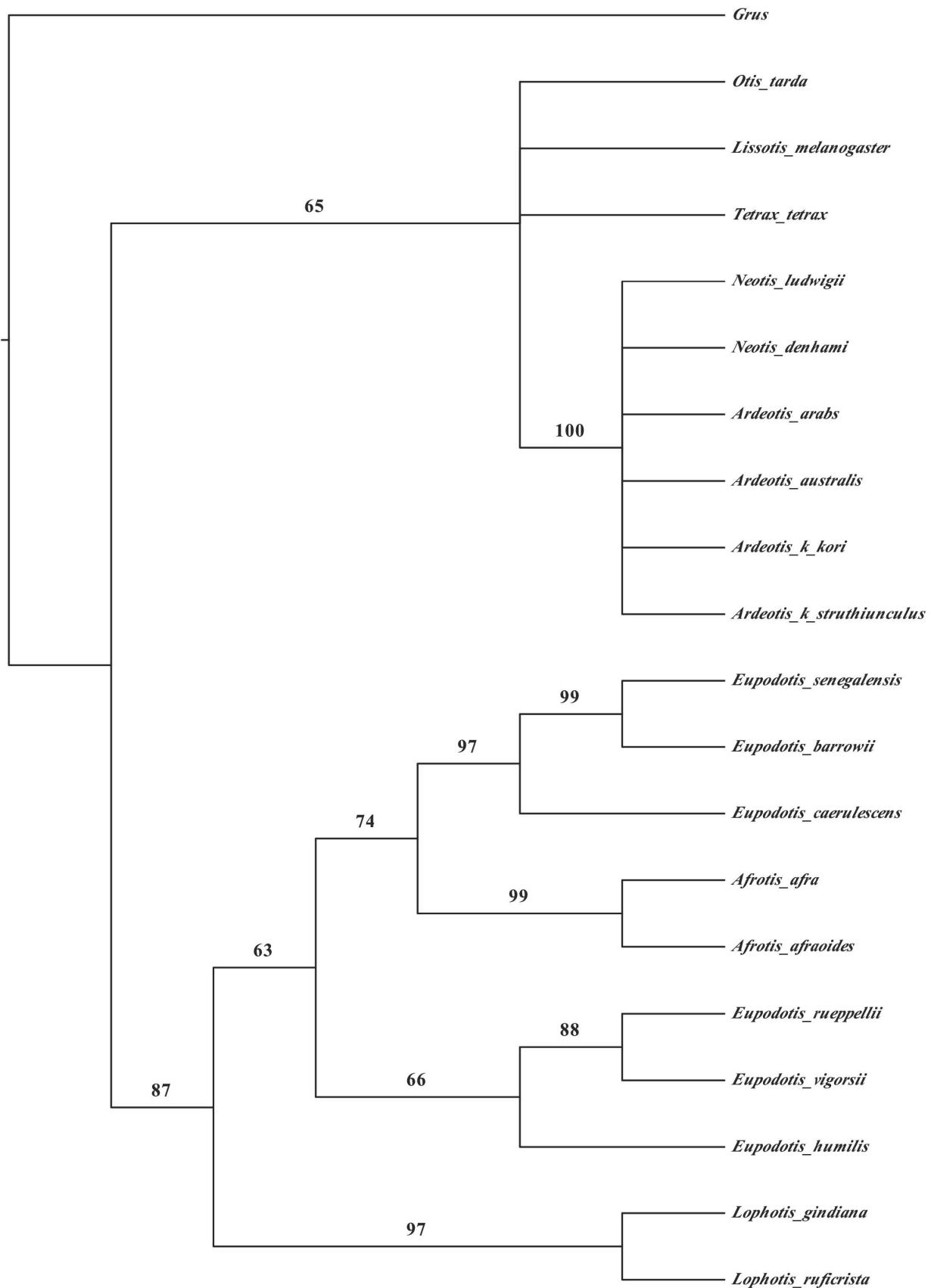


Fig. 2.10

2.57

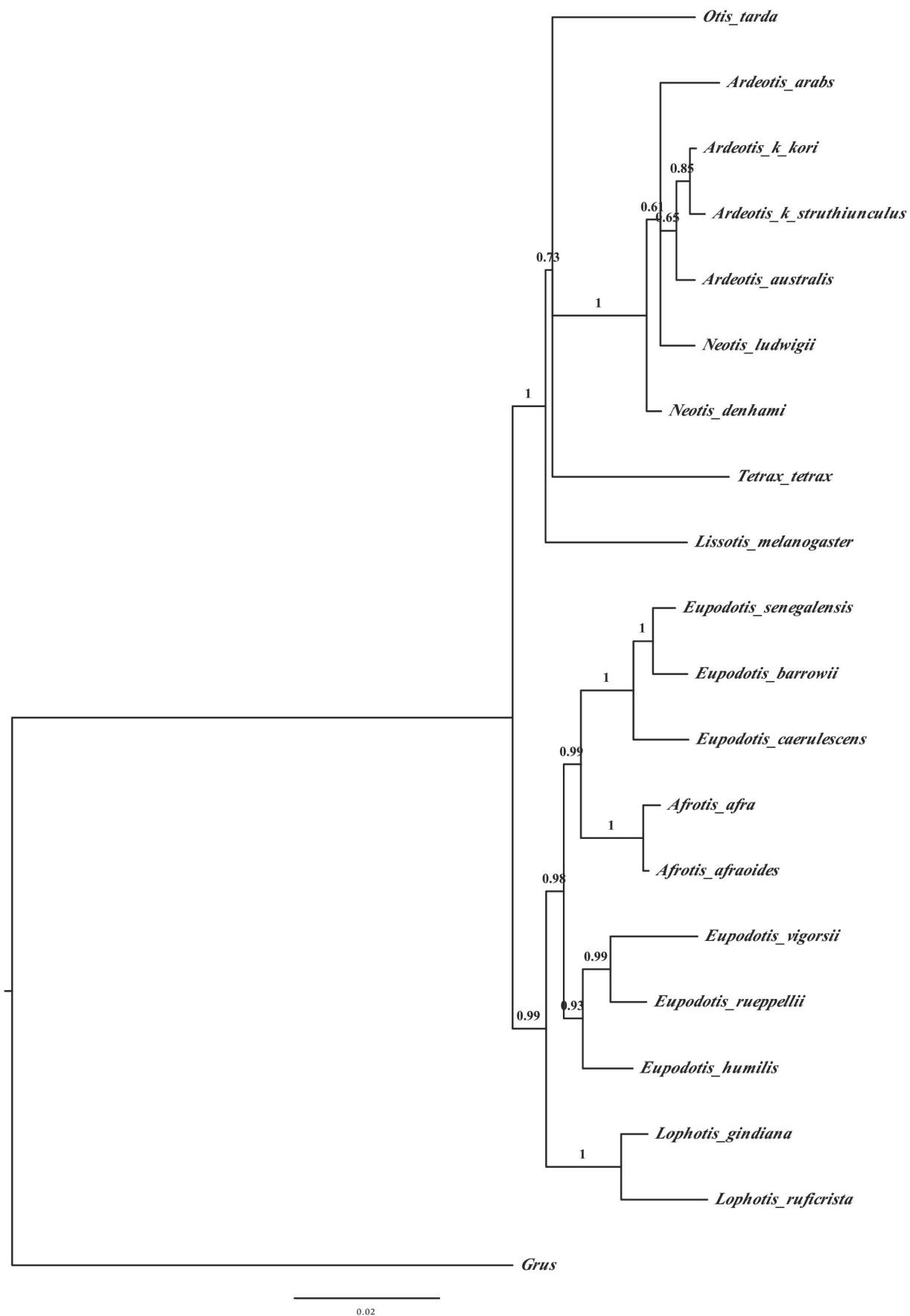


Fig. 2.11

2.58

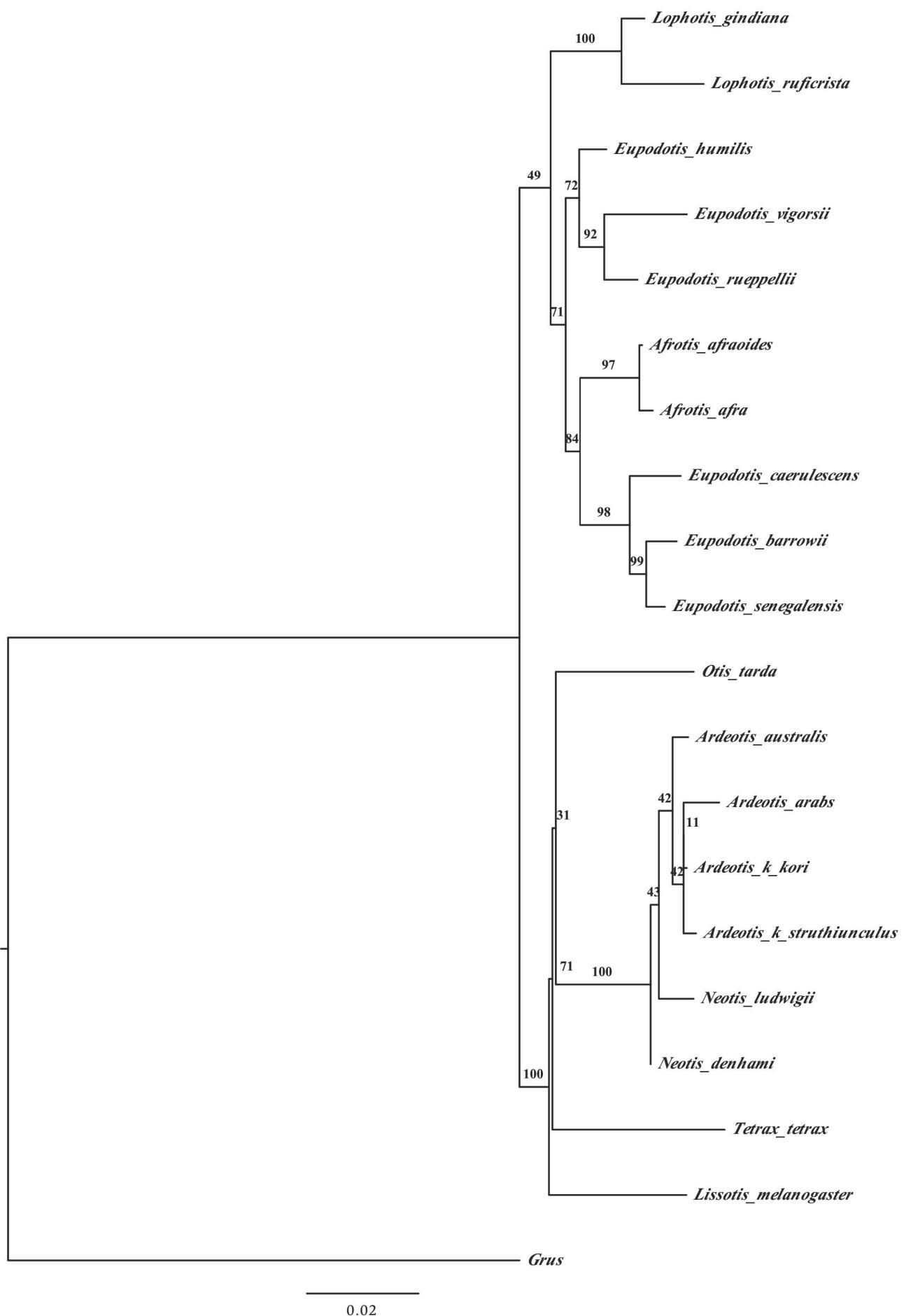
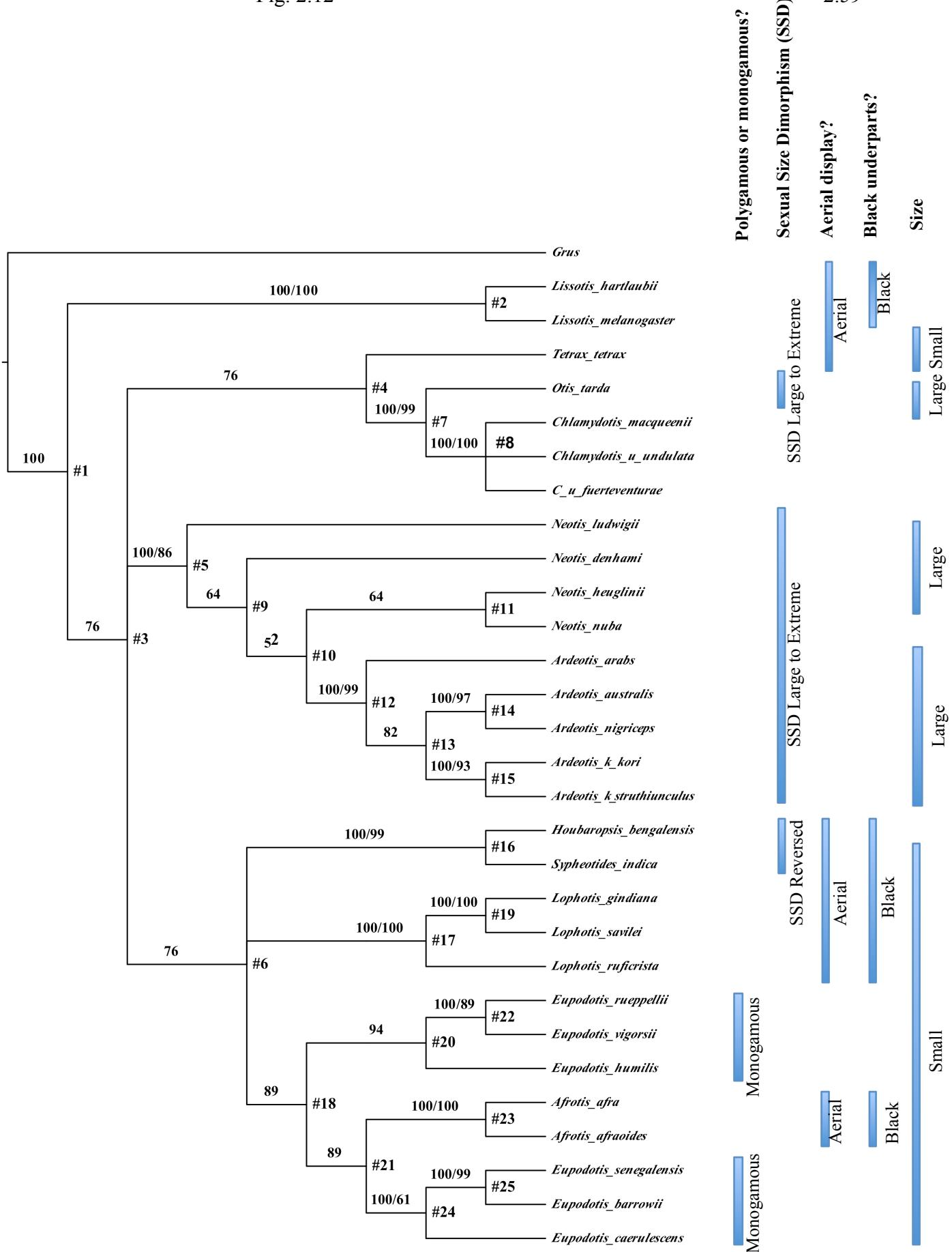


Fig. 2.12

2.59



Appendix Ch. 2

Appendix 2.1: Characters and character states used in morphological-behavioural character matrix for the bustards (Otididae)

All features refer to males in breeding plumage unless otherwise noted. See discussion in the main manuscript for comments. All morphological characters defined as per Hayman et al. (1986).

PLUMAGE CHARACTERS

CREST AND FACIAL ORNAMENTS

1. Crest on hind crown

- 0 Absent or slight
- 1 Less than 100 mm long
- 2 More than 100 mm long

2. Crest on nuchal region

- 0 Absent
- 1 Small
- 2 Large

3. Crest on centre of crown

- 0 Absent or slight
- 1 Present

4. Erectile feathers on facial region

- 0 Absent
- 1 Present

CROWN

5. Crown base colour

- 0 Grey
- 1 Black
- 2 Dark Brown
- 3 Mid Brown
- 4 Pale Brown
- 5 Blue
- 6 White
- 7 Orange

6. Crown patterning

- 0 Unpatterned
- 1 Vermiculated
- 2 Streaked

HEAD REGION

7. Contrasting superciliun

- 0 Absent
- 1 Present

8. Lore colour

- 0 Grey
- 1 Black
- 2 Dark Brown
- 3 Mid Brown
- 4 Pale Brown
- 5 Blue
- 6 White
- 7 Orange
- 8 Naked skin

9. Loral contrast with face

- 0 None
- 1 Above
- 2 Below
- 3 Above and below

10. Moustachial or submoustachial stripe:

- 0 Absent/inconspicuous
- 1 Conspicuous

11. Colour of ear coverts

- 0 Grey
- 1 Black
- 2 Dark Brown
- 3 Mid Brown
- 4 Pale Brown
- 5 Blue
- 6 White
- 7 Orange

12. Pattern on ear coverts

- 0 Unpatterned
- 1 Streaked

13. Contrast of ear coverts with rest of face

- 0 Not contrasting strongly with face
- 1 Contrasting strongly with face: white outlined with black

THROAT

14. Distinct Black throat patch

- 0 Absent
- 1 Present in male only
- 2 Present in male and female

15. Chin colour

- 0 Grey
- 1 Black
- 2 Dark Brown
- 3 Mid Brown
- 4 Pale Brown
- 5 Blue
- 6 White
- 7 Orange

16. Does chin contrast with throat?

- 0 No
- 1 Yes

17. Face black

- 0 No
- 1 Yes, including ear coverts
- 2 Yes, excluding ear coverts

NECK

18. Stripe down front of neck

- 0 Absent
- 1 Present

19. Lateral neck stripe

- 0 Absent
- 1 Present

20. Neck patterning

- 0 Absent
- 1 Finely barred

21. Hind neck base colour

- 0 Grey
- 1 Black
- 2 Dark Brown
- 3 Mid Brown
- 4 Pale Brown
- 5 Blue
- 6 White
- 7 Orange

22. Fore neck base colour

- 0 Grey
- 1 Black
- 2 Dark Brown
- 3 Mid Brown
- 4 Pale Brown
- 5 Blue/blue grey
- 6 White
- 7 Orange

23. Fore neck and hind neck the same colour

- 0 Yes
- 1 No

24. Collar on hindneck or breast

- 0 None
- 1 White Hind neck collar (half moon around back of neck)
- 2 Black Hind neck collar (half moon around back of neck)
- 3 Partial White collar on sides of breast (such as in *Lophotis*)
- 4 Partial Black collar on sides of breast (such as in *Ardeotis*)

BREAST**25. Breast collar**

- 0 None
- 1 Orange collar

26. Breast ground colour:

- 0 Grey
- 1 Black
- 2 Dark Brown
- 3 Mid Brown
- 4 Pale Brown
- 5 Blue
- 6 White
- 7 Orange

BELLY**27. Belly ground colour:**

- 0 White or greyish white to buff
- 1 Black
- 2 Blue

28. Do belly and breast contrast with sides of neck?

- 0 No
- 1 Yes

BACK PLUMAGE

29. Back plumage patterning (gross upperparts pattern):

- 0 Plain
- 1 Coarse horizontal barring (double-barring)
- 2 Finer horizontal barring
- 3 Very finely vermiculated
- 4 Arrow-like streaking
- 5 Broad arrows
- 6 Fine barring on upper back, grading to coarser barring at rear

30. Back plumage ground colour:

- 0 Grey
- 1 Black
- 2 Dark Brown
- 3 Mid Brown
- 4 Pale Brown
- 5 Blue
- 6 White
- 7 Orange

WINGS

31. Do wing coverts contrast with upperpart plumage?

- 0 No
- 1 Slightly
- 2 Strikingly

32. Do the marginal wing coverts contrast strongly with central wing coverts?

- 0 No
- 1 Slightly
- 2 Strikingly

33. Base colour of marginal wing coverts?

- 0 Grey
- 1 Black
- 2 Dark Brown
- 3 Mid Brown
- 4 Pale Brown
- 5 Blue
- 6 White
- 7 Orange

34. Is the pattern of the central wing coverts the same as the back?

- 0 Yes
- 1 Slightly different
- 2 Strikingly different

35. Is there white in the wing coverts?

- 0 No
 1 Yes

36. Pale patch in the primaries (visible in flight)?

- 0 No
 1 Yes, white
 2 Yes, cream
 3 Yes, blue

GENERAL PLUMAGE CHARACTERS

37. Plumage pigment: Presence of blue-grey pigment

- 0 Absent
 1 Present

38. Striking pattern of black and white

- 0 Absent
 1 Black belly and white collar (such as shown by *Lophotis*)
 2 Black head and underparts, white ear patch, collar and wing edge (such as shown by *Afrrotis*)
 3 Black head and underparts, white on wing (such as shown by the floricans)
 4 Black neck and white belly (such as shown by *Tetrax*)

39. Male assumes a non-breeding or first-year plumage

- 0 Yes
 1 No

BARE PARTS

LEGS

40. Leg colour

- 0 pale grey/brown/yellowish
 1 strongly yellow

BILL

41. Bill shape

- 0 Long and slender
 1 Short and thick

42. Bill colour (especially base of lower mandible)

- 0 horn/grey
 1 pink
 2 red
 3 yellow

BEHAVIOUR

CALL

43. Type of call (The nature of the calls are very difficult to transcribe but luckily these call types are so clearly different from each other that there are no cases where there is an ambiguity as to which category a bustard species belongs to.)

- 0 Gruiform call
- 1 Boom-type (cf. *A. kori*)
- 2 Croak-type (cf. *E. vigorsii*)
- 3 Whistle-type (cf. *Lophotis*)
- 4 Grating type (cf. *Afrotis*)
- 5 Pop-type (cf. *Lissotis*)
- 6 None/poorly developed

44. Is tongue clicked during call?

- 0 No
- 1 Yes

45. Does the call include more than one element?

- 0 No
- 1 Yes

46. Does the call increase in tempo as it proceeds?

- 0 No
- 1 Yes

47. Is the call a duet?

- 0 No
- 1 Yes

48. Regularity of call

- 0 Throughout the year
- 1 Only during breeding
- 2 Mainly during breeding season
- 3 Generally silent
- 0

DISPLAY

49. Type of display

- 0 Ground display, head raised
- 1 Ground display, swelling of oesophagus
- 2 Ground display with running and leaping
- 3 Aerial non-acrobatic display
- 4 Aerial rocket display

50. Is foot stamped during call?

- 0 No
1 Yes

51. Is wing sound used in display?

- 0 No
1 Yes

52. Are throat feathers raised during display?

- 0 No
1 Yes

BREEDING STRATEGY

53. Breeding strategy

- 0 Monogamy
1 Polygynous

TERRITORIALITY

54. Group living

- 0 No
1 Yes

55. Form aggregations when not breeding

- 0 Never or seldom
1 Regularly

SIZE

56. Male wing size:

- 0 Very large (male flattened wing > 550mm)
1 Medium (male flattened wing 350 – 550 mm)
2 Small (male flattened wing < 350mm)

57. Female wing size:

- 0 Very large (female flattened wing > 550mm)
1 Medium (female flattened wing 350 – 550 mm)
2 Small (female flattened wing < 350mm)

SEXUAL DIMORPHISM

58. SD in size (see also Table 2.5):

- 0 Male slightly larger than female
1 Male much larger than female
2 Female larger than male

59. Degree SD in plumage:

- 0 Male slightly different to female
1 Male strikingly different to female

60. Principal sexual differences

- 0 Size
- 1 Head markings
- 2 Neck markings
- 3 Head and neck markings
- 4 Head, neck and belly markings

HABITAT**61. Habitat openness:**

- 0 Open plains without trees, either shrublands or grasslands
- 1 Savannah (with occasional scattered trees)
- 2 Woodland

62. Habitat aridity:

- 0 Mesic
- 1 Arid (rainfall 300-500 mm per annum)
- 2 Hyper arid (rainfall 200-300 mm per annum)

Appendix 2.2: Morphological-behavioural character matrix for the Otididae

Species	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
<i>Otis tarda</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	7	0	1	1	4	2
<i>Ardeotis arabs</i>	1	0	0	0	1	1	1	6	0	0	6	1	0	0	0	0	0	0	0	1	0	0	0	0	0	6	0	1	3	3	2
<i>Ardeotis kori kori</i>	2	0	0	0	1	1	1	6	0	0	6	1	0	0	0	0	0	0	0	1	0	0	0	2	0	6	0	1	3	3	2
<i>Ardeotis kori struthiunculus</i>	2	0	0	0	1	1	1	6	0	0	6	1	0	0	0	0	0	0	0	1	0	0	0	2	0	6	0	1	3	3	2
<i>Ardeotis kori unknown</i>	2	0	0	0	1	1	1	6	0	0	6	1	0	0	0	0	0	0	0	1	0	0	0	2	0	6	0	1	3	3	2
<i>Ardeotis nigriceps</i>	1	0	0	0	1	0	1	6	0	0	6	0	0	0	0	0	0	0	0	1	0	0	0	4	0	6	0	1	3	3	2
<i>Ardeotis australis</i>	1	0	0	0	1	0	1	6	1	0	6	0	0	0	0	0	0	0	0	1	0	0	0	4	0	6	0	1	3	3	2
<i>Chlamydotis u undulata</i>	0	0	1	0	4	1	0	6	0	0	6	0	0	0	0	0	0	0	0	1	0	0	0	0	0	6	0	1	1	4	2
<i>Chlamydotis u fuerteventurae</i>	0	0	1	0	4	1	0	6	0	0	6	0	0	0	0	0	0	0	0	1	0	0	0	0	0	6	0	1	1	4	2
<i>Chlamydotis macqueenii</i>	0	0	1	0	4	1	0	6	0	0	6	0	0	0	0	0	0	0	0	1	0	0	0	0	0	6	0	1	1	4	2
<i>Neotis ludwigii</i>	0	0	0	0	2	0	0	2	0	0	2	0	0	0	2	0	0	0	0	0	7	2	1	0	0	6	0	1	5	2	1
<i>Neotis denhami</i>	0	0	0	0	1	0	1	6	1	0	0	0	0	0	6	0	0	0	0	0	7	0	1	0	0	6	0	1	3	2	2
<i>Neotis heuglinii</i>	0	0	0	0	1	0	0	1	0	0	6	0	0	0	1	0	2	0	0	0	0	0	0	0	1	7	0	1	5	2	1
<i>Neotis nuba</i>	0	0	0	0	7	0	1	1	3	0	0	0	0	2	1	0	0	0	0	5	5	0	0	1	7	0	1	6	4	1	
<i>Eupodotis senegalensis</i>	0	1	0	0	5	0	1	6	1	1	1	0	0	1	6	1	0	0	0	0	5	5	0	0	0	5	0	1	6	4	1
<i>Eupodotis barrowii</i>	0	1	0	0	5	0	1	6	1	0	1	0	0	1	6	1	0	0	0	0	7	5	1	0	0	5	0	1	6	4	1
<i>Eupodotis caerulescens</i>	0	1	0	0	5	0	1	1	3	0	1	0	0	2	1	0	0	0	0	0	5	5	0	0	0	5	2	0	6	3	1
<i>Eupodotis vigorsii</i>	0	1	0	0	2	0	1	2	2	1	3	0	0	2	1	0	0	0	0	0	4	4	0	0	0	3	0	0	6	3	1
<i>Eupodotis rueppellii</i>	0	1	0	0	5	0	1	6	2	1	1	0	0	2	1	0	0	1	0	0	5	5	0	0	0	6	0	1	6	4	1
<i>Eupodotis humilis</i>	0	1	0	0	2	0	1	4	0	0	3	0	0	1	4	1	0	0	0	0	5	4	1	0	0	6	0	1	6	3	1
<i>Lophotis savilei</i>	0	2	0	0	0	0	1	0	0	0	4	0	0	1	4	1	0	0	0	0	7	5	1	3	0	1	1	1	4	4	2
<i>Lophotis gindiana</i>	0	2	0	0	0	0	1	0	0	0	4	0	0	0	4	0	0	1	0	0	7	5	1	3	0	1	1	1	4	4	2
<i>Lophotis ruficrista</i>	0	2	0	0	0	0	1	0	0	0	4	0	0	0	4	0	0	0	0	0	7	5	1	3	0	1	1	1	4	4	2
<i>Afrötis afra</i>	0	1	0	0	6	1	0	1	0	0	6	0	1	0	1	0	2	0	0	0	1	1	0	1	0	1	1	0	2	0	2
<i>Afrötis afraoides</i>	0	1	0	0	6	1	0	1	0	0	6	0	1	0	1	0	2	0	0	0	1	1	0	1	0	1	1	0	2	0	2
<i>Lissotis melanogaster</i>	0	1	0	0	2	2	1	0	0	0	6	0	1	0	0	1	0	1	0	0	3	3	0	0	0	1	1	1	4	3	2
<i>Lissotis hartlaubii</i>	0	1	0	0	2	2	1	0	0	0	6	0	1	0	0	1	0	1	0	0	3	3	0	0	0	1	1	1	4	3	2
<i>Houbaropsis bengalensis</i>	0	0	0	0	1	0	0	1	0	0	1	0	0	0	1	0	1	0	0	0	1	1	0	0	0	1	0	0	4	3	2
<i>Sypheotides indica</i>	0	1	0	1	1	0	0	1	0	0	1	0	0	1	0	1	0	0	0	1	1	0	1	0	1	0	0	4	3	2	
<i>Tetrax tetrax</i>	0	0	0	0	2	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	2	0	6	0	1	3	3	2
OUTGROUP <i>Grus</i>	0	0	0	0	0	0	0	8	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	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

Appendix 2.2: Continued

Species	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62
<i>Otis tarda</i>	2	6	0	1	1	0	0	0	0	1	0	6	0	0	0	0	3	1	1	0	0	1	0	1	0	1	1	0	0	0	
<i>Ardeotis arabs</i>	2	1	0	1	1	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	1	0	0	0	1	1	0	0	1	
<i>Ardeotis kori_kori</i>	2	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	1	0	0	0	0	1	0	0	1	
<i>Ardeotis kori_struthiunculus</i>	2	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	1	0	0	0	0	1	0	0	1	
<i>Ardeotis kori_unknown</i>	2	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	1	0	0	0	0	1	0	0	1	
<i>Ardeotis nigriceps</i>	2	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	1	0	0	0	1	1	0	0	1	
<i>Ardeotis australis</i>	2	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	1	0	0	0	1	1	0	0	1	
<i>Chlamydotis_u_undulata</i>	2	4	1	0	0	0	0	0	0	0	0	6	0	0	0	0	3	0	0	0	0	1	0	1	1	1	1	0	0	2	
<i>Chlamydotis_u_fuerteventurae</i>	2	4	1	0	0	0	0	0	0	0	0	6	0	0	0	0	3	0	0	0	0	1	0	1	1	1	1	0	0	2	
<i>Chlamydotis macqueenii</i>	2	4	1	0	0	0	0	0	0	0	0	6	0	0	0	0	3	0	0	0	0	1	0	1	1	1	1	0	0	2	
<i>Neotis ludwigii</i>	1	2	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0	1	0	1	1	1	1	3	0	2	
<i>Neotis denhami</i>	1	1	2	1	1	0	0	0	0	0	0	6	0	0	0	0	1	1	1	0	0	1	0	1	1	1	0	0	0	0	
<i>Neotis heuglinii</i>	1	1	0	0	1	0	0	0	0	0	0	?	0	?	0	0	?	?	0	0	0	?	0	0	1	1	1	0	2		
<i>Neotis nuba</i>	1	4	1	0	1	1	0	0	0	0	0	?	0	?	0	0	?	?	0	0	0	?	0	0	1	1	0	1	1	1	
<i>Eupodotis senegalensis</i>	1	4	1	0	2	1	0	0	0	0	0	2	0	1	0	1	0	0	0	0	1	0	1	0	2	2	0	1	3	0	
<i>Eupodotis barrowii</i>	1	4	1	0	2	1	0	0	0	0	0	2	0	1	0	1	0	0	0	0	1	0	1	0	2	2	0	1	3	0	
<i>Eupodotis caerulescens</i>	0	3	0	0	3	1	0	0	0	0	0	3	2	0	1	0	1	0	0	0	0	1	0	1	0	2	2	0	0	1	
<i>Eupodotis vigorsii</i>	0	3	0	0	2	0	0	0	0	0	0	2	0	1	0	1	0	0	0	0	1	0	0	2	2	0	0	1	0	2	
<i>Eupodotis rueppellii</i>	0	4	0	0	2	1	0	0	0	0	0	2	0	1	0	1	0	0	0	0	1	0	0	2	2	0	0	3	0	2	
<i>Eupodotis humilis</i>	0	3	0	0	0	1	0	0	0	0	0	2	0	1	0	1	0	0	0	0	1	0	0	2	2	0	1	3	0	2	
<i>Lophotis_savilei</i>	2	6	1	1	0	1	1	0	0	0	0	3	1	1	1	0	2	?	0	0	0	1	0	0	2	2	0	1	2	2	0
<i>Lophotis_gindiana</i>	2	6	1	1	0	1	1	0	0	0	0	3	1	1	1	0	2	4	0	0	0	1	0	0	2	2	0	1	2	2	0
<i>Lophotis_ruficrista</i>	2	6	1	1	0	1	1	0	0	0	0	3	1	1	1	0	2	4	0	0	0	1	0	0	2	2	0	1	2	2	0
<i>Afrötis afra</i>	2	6	0	1	0	0	2	0	1	0	2	4	0	1	0	0	2	3	0	0	1	1	0	0	2	2	0	1	3	0	1
<i>Afrötis afraoides</i>	2	6	0	1	1	0	2	0	1	0	2	4	0	1	0	0	2	3	0	0	1	1	0	0	2	2	0	1	3	0	1
<i>Lissotis melanogaster</i>	2	6	1	1	1	0	0	0	0	0	0	5	0	1	0	0	1	3	0	0	0	1	0	0	2	2	1	1	3	1	0
<i>Lissotis_hartlaubii</i>	2	6	1	1	1	0	0	0	0	0	0	5	0	1	0	0	1	3	0	0	0	1	0	0	2	2	1	1	3	1	0
<i>Houbaropsis bengalensis</i>	0	6	2	1	0	0	3	0	0	0	3	6	0	0	0	0	?	3	0	0	0	1	0	0	2	2	2	1	3	0	0
<i>Syphoetoides indica</i>	0	6	2	1	0	0	3	1	0	0	3	6	0	0	0	0	?	4	0	1	0	1	0	0	2	2	2	1	3	0	0
<i>Tetrax tetrax</i>	2	6	0	1	1	0	4	1	0	1	0	6	0	0	0	0	3	3	0	1	0	1	0	2	2	0	1	3	0	0	
OUTGROUP <i>Grus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62

CHAPTER 2

Phylogenetics of the bustards (Otididae) inferred from morphological, behavioural and multilocus mitochondrial and nuclear DNA data, with comments on the evolution of polygyny, aerial display, sexual size dimorphism and co-operative breeding

Abstract

The bustards (Otididae) are large, terrestrial birds of open habitats that occur across the deserts and steppes of the Old World, with 22 of the 27 species occurring in Africa. Because bustard distributions mirror that of open, mostly arid areas, and 12 species are endemic to disjunct arid zones in south-west and north-east Africa, they are ideal candidates for examining the arid zone biogeography of this continent. Both the taxonomy and the deeper level phylogenetic relationships within the bustards are disputed and a recent molecular phylogeny proposed a controversial new set of generic relationships but was poorly sampled with relation to African taxa. The bustards show a fascinating variety of sexual size dimorphism, mating systems (from lek polygyny to monogamy), and the striking advertisement displays of male bustards are a well-known feature of this group that range from terrestrial strutting with an inflated gular sac and splayed plumage, to conspicuous aerial flights with loud calls. To assess taxonomy, biogeography and character evolution, a multi-faceted approach using morphological-behavioural and molecular characters from all 27 species was

used to evaluate the phylogenetics of the Otididae. The 62 phylogenetically-informative morphological-behavioural characters and 5341 bp of nucleotide data (three mitochondrial markers: cytb, NADH, CtrII; five nuclear markers: Fib5, TGFB, GAPDH, ODC, CHD1Z) were analysed separately and in combination using three methods of phylogenetic analysis with different optimality criteria: parsimony, Bayesian inference and maximum likelihood. The following major clades were generally well-supported in the analyses: 1. **Clade “Larger bustards”** (not always recovered as monophyletic) comprising: **Clade OC** (*Otis* and *Chlamydotis*); **Clade AN** (*Ardeotis* and *Neotis*); *Tetrax*; and sometimes, *Lissotis*; and 2. **Clade “Smaller bustards”** comprising: *Lophotis*; **Clade Floricans** (*Houbaropsis bengalensis* and *Sypheotides indica*); and **Clade EA** with its three subclades: **Clade Heterotetrax** (*Eupodotis humilis*, *E. vigorsii*, *E. rueppellii*); **Clade Blue Eupodotis** (*E. caerulescens*, *E. senegalensis*, *E. barrowii*); and *Afrotis*. Basal resolution is lacking in the trees, but there is strong support for terminal clades comprising the currently-recognised genera, with the exception that *Ardeotis* renders *Neotis* paraphyletic (although more data are required), and *Afrotis* is recovered as sister to **Clade Blue Eupodotis**, rendering *Eupodotis* paraphyletic. The suggestion that *E. rueppellii* is basal to the Otididae is rejected. The evolution of polygyny, aerial display, sexual size dimorphism and co-operative breeding is examined in the context of the phylogeny. Monogamous behaviour need only have evolved once in *Eupodotis*, followed by a striking reversal to polygyny in *Afrotis*.

Introduction

The bustards (Otididae) are large, terrestrial birds of open habitats that occur across the deserts and steppes of the Old World (Collar, 1996). They are a predominantly African group, and of the 27 currently recognised species worldwide, 22 occur in Africa (Johnsgard, 1991; Collar, 1996; Gill and Wright, 2006). Because bustard distributions mirror that of open, mostly arid areas, and 12 species are endemic to disjunct areas in south-western and north-eastern Africa, they are ideal candidates for examining the arid zone biogeography of this continent. As a group, the bustards form a highly distinctive monophyletic assemblage that is well differentiated from other families, resulting in their placement in an exclusive infraorder in the Gruiformes (Sibley and Monroe, 1990; Collar, 1996; Livezey, 1998). In the largest avian molecular analysis to date, Hackett et al. (2008) place the bustards as a sister group to a clade that include core Gruiformes (cranes, rails, finfoots, trumpeters and limpkin) and the Cuculiformes (bootstrap = 68%).

Despite all the ecological and conservation attention directed at certain species of this group, their relationships still remain unclear. Both the taxonomy and the deeper level phylogenetic relationships within the bustards are disputed: in the last three decades, more than five different generic classifications of the Otididae have been published (Osborne et al., 1984; Urban et al., 1986; Johnsgard, 1991; Collar, 1996; see [Table 1.2](#)). A recent molecular phylogeny, based largely on 444 base pairs of the cytochrome-b gene, proposed a controversial new set of generic relationships (Pitra et al., 2002), but was relatively poorly sampled with relation to African taxa. A further

study by Broders et al. (2003), who also examined the cytochrome-b gene of a small subset of bustard species, also focused on the Eurasian taxa.

The bustards show a fascinating variety of mating systems (from lek polygyny to monogamy), and the striking advertisement displays of male bustards are a well-known feature of this group that range from terrestrial strutting with an inflated gular sac and splayed plumage, to conspicuous aerial flights with loud calls (Johnsgard, 1991; Collar, 1996). Bustards display a large range of sexual size dimorphism, and the males of *Otis tarda* (which are up to three times the weight of the females in the breeding season) and *Ardeotis kori*, are the world's heaviest species of bird that are still able to fly (Johnsgard, 1991; Collar, 1996). On the opposite end of the scale, there is reversed sexual dimorphism (with the females larger than the males) in the floricans, *Houbaropsis bengalensis* and *Sypheotides indica* (Johnsgard, 1991). Some species are group-territorial with co-operative breeding (Collar, 1996; Allan, 2005). By examining these in the context of a phylogeny, the evolution of these mating systems and displays can be assessed (Searcy et al., 1999).

I aim to investigate the phylogenetics, taxonomy and evolution of life history of the Otididae with particular reference to the hypotheses phrased as questions below:

1. Is *Eupodotis sensu strictu* (as defined by Collar, 1996) monophyletic (disputed by Pitra et al. 2002 and Broders et al. 2003)?
2. Are the genera in [Table 1.2](#) suggested by Peters (1934), Osborne et al. (1984), Urban et al. (1986), Johnsgard (1991) and Collar (1996), monophyletic?

3. How many times have the monogamous or co-operative breeding life history strategies evolved?
4. What is the role of convergence in the evolution of the striking and varied displays of the bustards?

A multi-faceted approach is used to evaluate the relationships among the Otididae, and morphological, behavioural and multilocus molecular data are analysed using three methods of phylogenetic analysis with different optimality criteria (Holder and Lewis, 2003): parsimony (MP), Bayesian inference (BI) and Maximum Likelihood (ML). In molecular analyses, three mitochondrial markers [cytochrome-b (cytb), NADH dehydrogenase subunit 2 (ND2), Control region II (CtrII)] and five nuclear markers [beta-Fibrinogen intron 5 (Fib5), Transforming Growth Factor Beta 2 intron 5 (TGFB), Glyceraldehyde-3-phosphate dehydrogenase intron 11 (GAPDH), Ornithine Decarboxylase introns 6 & 7 with the intervening exon 7 (ODC) and an intron-exon crossing fragment of the chromo-helicase-DNA binding gene (CHD1Z)] are analysed.

Materials and methods

Taxon sampling

Samples for all 27 described species in the Otididae were obtained for this study. The aim was to get at least two tissue samples from each well-marked subspecies in the family. This is for the following reasons:

1. the second sample for each major taxon acts as check against labelling problems;
2. the use of samples from distinctive subspecies allows one to check that the species is monophyletic and can also offer biogeographic insight;
3. the use of tissue instead of blood reduces the chances of encountering nuclear pseudogenes ('numts', see below).

However, this was not always possible as many of the tissues were not in existing collections and it was simply not possible to collect all species under permit (such as if the species was of conservation concern, or occurred in an area where it is not safe to visit or collect).

Obtaining the tissues was by far the most time-consuming part of the study as relatively few bustards were represented in museum tissue collections. The process of organising field trips, visiting foreign museums and obtaining samples from researchers took years to undertake, but resulted in a large collection of samples from taxa that are notoriously difficult to catch or collect. Tissues were obtained from the following sources:

1. fresh samples of either tissue or blood (stored in either 95% ethanol, or Dimethyl sulfoxide (DMSO) or Ethylene diaminetetraacetic acid (EDTA) solutions respectively) were obtained from museum tissue archives;

2. blood samples, stored in EDTA, were obtained from captive birds in zoological gardens or private collections;
3. fresh tissue or blood samples (stored in either 95% ethanol, or DMSO or EDTA respectively) were obtained from specimens either collected or captured ([Figs 2.12 – 2.13](#)) in the field under permit on field trips;
4. samples were taken, with permission, from the toepad-skin of museum specimens.

Full details of all the samples analysed in this study are in [Table 2.1](#) and fully acknowledged in the Acknowledgements. I was not able to obtain sequence data for many of the toepad samples that I collected, despite attempting the protocol described below at UC Berkeley with internal primers, and only those toepad samples for which extraction and PCR were successful are listed in [Table 2.1](#).

In addition to samples that I collected and sequenced, all the samples analysed by Pitra et al. (2002) and Broders et al. (2003) were downloaded from Genbank for analysis. Thus, both molecular and morphological-behavioural data for all 27 bustard species are analysed in this study ([Table 2.1](#)). I also obtained molecular data for two specimens of both *Ardeotis k. kori* and *Ardeotis k. struthiunculus* as they are disjunctly distributed in the arid zones of south-western and north-eastern Africa respectively.

Outgroup selection

The Otididae form a highly distinctive monophyletic assemblage that is traditionally grouped in the Gruiformes in an exclusive infraorder (Sibley & Monroe, 1990; Collar, 1996; Livezey, 1998). Their position as sister to an enlarged “Gruiformes” is

supported by Hackett et al. (2008) and so I used two genera of Gruidae (cranes) as outgroup taxa (*Anthropoides paradisea* and *Bugeranus carunculatus*).

Morphological-behavioural character matrix

A matrix of 62 morphological and behavioural characters (morphological-behavioural matrix) was prepared that included all species of the Otididae. The characters include the following categories: size, plumage colours and patterns, bare part colouration, sexual dimorphism, behaviour, male display and vocalisations. All characters are described in [Appendix 2.1](#), and the character states for each species are presented in [Appendix 2.2](#). Characters were chosen that appeared to be independent of each other and no attempt was made to select those that were deemed to be phylogenetically informative. Characters that were variable within a species were left off the matrix and missing data were coded as such. Characters that were only applicable to a single species (autoapomorphies) were left off the matrix. Multi-state characters were treated as non-additive.

Morphological characters were assigned to species on the basis of four main sources of information:

1. photographs and notes taken from specimens from the collections - American Museum of Natural History (New York, USA), the Natural History Museum (Tring, UK), the Royal Museum for Central Africa (Tervuren, Belgium), the South African Museum (Ornithology) in Cape Town, the Durban Natural Science Museum, the MacGregor Museum (Kimberley) and the National Museums of Kenya (Ornithology) in Nairobi;

2. published sources of information used to score the species included Collar et al. (1986); Johnsgard (1991; note that the full page colour plates of *Neotis nuba* and *N. heuglinii* are transposed in this reference) and Collar (1996);
3. a database of photographs individually sourced from the internet from birding field trip reports;
4. photographs and specimens collected personally during the field trips.

Morphometric characters were obtained from the museum visits described above, as well as from the bustard morphometrics database compiled by P.D. Goriup and P.E. Osborne (Osborne, 1984).

Sound recordings, to evaluate vocal characters, were made using a 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 and a Sony RH1 minidisc recorder in uncompressed format, and evaluated in Raven Lite (Version 1.0, Cornell Laboratory of Ornithology).

Wing size and breeding system and display characters are as described by Raihani et al. (2005) with some corrections. In particular, the display types of *N. ludwigii*, *N. heuglinii* and *L. hartlaubii* were incorrect (they should be Unknown, Unknown, and Aerial Non-acrobatic respectively) and the means for wing size of *Eupodotis vigorsii* are: Male 334.8 mm (n = 8); Female 329.6 mm (n = 11).

Molecular markers

The following mitochondrial DNA (mtDNA) and nuclear DNA (nDNA) markers were amplified:

Three mitochondrial markers:

Cytochrome-b (cytb),

NADH Dehydrogenase Subunit 2 (ND2),

Control region II (CtrII)

Five nuclear markers:

Beta-Fibrinogen intron 5 (Fib5),

Transforming Growth Factor, Beta 2 intron 5 (TGFB),

Glyceraldehyde-3-phosphate dehydrogenase intron 11 (GAPDH),

Ornithine Decarboxylase introns 6 & 7 with the intervening exon 7 (ODC)

An intron-exon crossing fragment of the chromo-helicase-DNA binding gene (CHD1Z)

The nuclear introns are found on the following chromosomes in the chicken genome:

Chromosome 1: GAPDH; Chromosome 3: TGFB, ODC; Chromosome 4: Fib5 (Fuchs et al., 2009). These markers were investigated as they have helped to resolve a wide range of avian phylogenies (e.g. Fjeldså et al., 2003; Fuchs et al., 2004; Lerner and Mindell, 2005; Crowe et al., 2006; Johansson et al., 2007; Voelker et al., 2007; Hackett et al., 2008; Irestedt et al., 2008; Jónsson et al., 2008, 2009; Fuchs et al., 2009; Gelang et al., 2009).

CtrII and CHD1Z were not sequenced personally but were downloaded from Genbank from the study of Pitra et al. (2002). In addition, most of the cytb sequences were also downloaded from Genbank from Pitra et al. (2002) and Broders et al. (2003). Note

that while Broders et al. (2003) sequenced the full 1143 base pairs for cyt b for 11 species, Pitra et al. (2002) only sequenced a total of 444 base pairs, from two parts of the cyt b gene (15103-345 and 15892-16092, corresponding to the *Vidua chalybeata* complete mtDNA genome AF090341). I had limited success with cyt b and only added 243 base pairs for selected species. A list of ingroup and outgroup taxa for which sequence data were analysed in this study, and information relating to them, are detailed in [Table 2.1](#).

Laboratory techniques: DNA extraction, PCR and sequencing

Total genomic DNA was extracted from blood, pectoral muscle, heart or liver tissue using one of two methods: 1. Quiagen DNeasy animal tissue protocol provided with the DNeasy® tissue kit (Qiagen, Valencia, California); 2. a Cetyl Trimethyl Ammonium Bromide-based protocol (Winnepenninckx et al., 1993) with an overnight Proteinase-K digestion.

Double-stranded DNA templates for the mitochondrial and nuclear loci were amplified by polymerase chain reaction (PCR). I typically used 12 µl reactions with 1-3.5 µl of genomic DNA added. The PCR reactions contained the following: 1.5 mM PCR buffer, 3.0 mM MgCl₂, 0.8mM Bovine Serum Albumin (BSA), 0.25mM of each dNTP, 0.2mM of each primer (but 0.15 for GAPDH and Fib5), and 0.15 units of Taq (Roche). All sets of PCR reactions included a negative control to which no DNA was added. Primers used for amplification and sequencing are listed in [Table 2.2](#).

PCR was mostly performed on a Bio-Rad iCycler (Bio-Rad, Hercules, California) with the following conditions: a hotstart at 94°C for 5 min, an initial denaturation at

94°C for 2 min, followed by 35 cycles of denaturation at 94°C for 30 s, annealing at 53-60 °C (cytb and ND2 at 53°C, Fib5 at 54°C, TGFB and OCD at 58°C, GAPDH 60°C) for 30 s, and extension at 72°C for 80 s (except GAPDH at 60 s), with a final extension at 72°C for 10 min. PCRs were checked (to confirm amplification and fragment sizes) by electrophoresing products on a 1.5% agarose gel stained with ethidium bromide and visualized under UV light. The negative controls were also visualized in this way.

Amplified products were cleaned using a standard Exonuclease I and Shimp Alkaline Phosphatase (Exo/SAP) protocol and then cycle-sequenced using the Big Dye terminator chemistry (version 3.1, ABI, Applied Biosystems). Sequencing was performed in both directions with the primers described in [Table 2.2](#), except that G3P13 was replaced by G3PintL1 (see Fjeldså et al., 2003). Sequencing products were cleaned using Sephadex columns and run on an ABI 3100 DNA analyser.

Laboratory procedure for museum toe pad-skin samples

Toepad-skin samples taken from museum specimens were often over 60 years old and thus the DNA is expected to be highly degraded. Because of this, the regular primers were not able to amplify the specific loci and taxon-specific GAPDH primers were designed ([Table 2.2](#)) that amplified shorter fragments. In addition, AmpliTaq Gold (Applied Biosystems) was used when preparing the PCR reactions for the toe-pads (Nyabo et al., 2008). Contamination from outside sources poses a much higher risk due to the small amounts of DNA remaining in the degraded samples and special precautions were taken. Toe-pad extractions and PCR reaction preparation was performed in a dedicated laboratory with the many precautions described by

Willerslev and Cooper (2005) and Lovette and Rubenstein (2007) implemented in order to reduce the likelihood of contamination.

Assembly of sequences

Sequences were assembled using Sequencer v4.7 (Gene Codes Corp., Ann Arbor, Michigan, USA). Mitochondrial sequences were aligned to the chicken (*Gallus gallus*) (Desjardins and Morais, 1990) and checked for any insertions or deletions. Mitochondrial sequences were also translated into amino acids and checked for the presence of stop codons, as well as for frame shifts that might indicate the amplification of nuclear copies of mitochondrial genes or ‘numts’ (Quinn, 1997; Sorenson and Quinn, 1998).

Alignment of sequences

Sequence alignments were adjusted readily by eye after an initial automatic alignment in Sequencer using the Clustel algorithm. Nuclear sequences were checked carefully for the presence of heterozygous sites as represented by isolated double peaks (single nucleotide polymorphisms) and these were coded using the standard IUPAC codes. The final concatenated alignment, with partitions, is presented as [Appendix 2.3](#).

Base composition

The base composition of gene regions has been shown to affect the outcome of phylogenetic analyses (Collins et al., 1994). The significance of these differences was tested for each gene region in PAUP* using a χ^2 (chi-squared) test (Swofford, 2002).

Phylogenetic analyses and statistical tests

Three methods of phylogenetic analysis with different optimality criteria (Holder and Lewis, 2003) were employed to estimate phylogeny: parsimony (MP), Bayesian inference (BI) and Maximum Likelihood (ML).

Each gene region was first analysed individually using BI and ML. To assess the congruence between trees before combining the data, each tree was assessed visually for conflicting branches that had a high level of support. Branches were considered to be highly supported if they had bootstrap values of >70% (Hillis and Bull, 1993) or posterior probabilities of > 0.95 (Ronquist and Huelsenbeck, 2003).

For the final analyses, concatenated alignments were prepared using the samples described in [Table 2.1](#) in the following partitions which were analysed as follows: 1. all morphological-behavioural data and DNA (MP only), 2. all DNA combined (MP, BI, ML), 3. all mt DNA combined (MP, BI, ML), and 4. all nuclear DNA combined (MP, BI, ML). To save on computing time, only one exemplar for each gene region for each species was chosen for the concatenated alignments, which sometimes included loci from different individuals of the same species ([Table 2.1](#)). Where more than one exemplar of a gene region per species was available, all of these exemplars were analysed in a separate analysis (for each gene region) to check if the species was reciprocally monophyletic and to reduce any potential error from sample mix-ups. Samples from distinctive subspecies were always treated as separate taxa and OTUs in all analyses.

Parsimony-based phylogenetic analyses were conducted using both TNT (Tree analysis using New Technology) (Goloboff *et al.*, 2008a, b) and PAUP*. In TNT, the searching strategy employed was the “new technology 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 character data was determined by using the ‘jackknife’ resampling strategy (Farris *et al.*, 1996; Källersjö *et al.*, 1998) using: 1000 replicates, branch-swapping with five random additions of sequences per replicate, excluding 36% of characters per jackknife replicate. In PAUP* 4.0b10 (Swofford, 2002), parsimony analyses were conducted using a heuristic search with 1000 random addition replicates and tree-bisection-reconnection branch-swapping. All characters were given equal weight and treated as unordered. Clade support was assessed with 500 non-parametric bootstrap replicates (Felsenstein, 1985a).

Because gene regions can evolve under different models of evolution, it has been argued that a partitioned, mixed-model approach should be used when concatenating these different datasets (Ronquist and Huelsenbeck, 2003; Nylander *et al.*, 2004). It is now possible to perform these analyses for BI and ML.

Mixed-model Bayesian analyses were undertaken in Mr Bayes v3.1.2 (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003). Substitution models for each locus were determined in PAUP* with MrModelTest 2.0 (Nylander, 2004) and Modeltest 3.06 (Posada and Crandall, 1998), using the Akaike Information Criterion (Akaike, 1973; Posada and Buckley, 2004) and are presented in [Table 2.3](#). Mixed-model analyses allowed different parameters (base frequencies, rate matrix or

transition/transversion ratio, shape parameter, proportion of invariable sites) to vary (using the *unlink* and *prset* commands) between the partitions (gene regions and codon positions) (Nylander et al., 2004; Johansson et al., 2008; Fuchs et al., 2009).

Four Metropolis-coupled MCMC chains (one cold and three heated) were run for 5 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 by analysis but was typically 500 000 generations (5000 trees); posterior probabilities were estimated from the remaining generations. Each Bayesian analysis was attempted 2-3 times (random, independent runs), but this was not always possible due to the computing time required. The log-likelihood values and posterior probabilities were checked to confirm that the chains had reached stationarity. Checks were made that the Potential Scale Reduction Factor approached 1.0 (for all parameters) and that the average deviation of split frequencies converged towards zero (Fuchs et al., 2009). The program Tracer v1.4.1 (Rambaut and Drummond, 2007) was used for parameter estimates and to help assess whether convergence of the Markov chain had taken place.

Mixed-model Maximum Likelihood analyses were performed using Randomised Axelerated Maximum Likelihood for High Performance Computing (RAxML) v7.0.4 (Stamatakis, 2006; Stamatakis et al., 2008) a programme that has been used in recent avian phylogeny analyses (e.g. Hackett et al., 2008; Johansson et al., 2008; Fuchs et al., 2009; Parra et al., 2009). Mixed-model RAxML analyses uses 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 a single data partition) and then also a mixed-model analysis on the nuclear DNA genes, partitioned by each of the 4 gene regions. Branch support was assessed with 100 non-parametric bootstrap replicates.

Morphological-behavioural character evolution

The evolution of morphological characters and behaviour was assessed by mapping these characters onto the total evidence tree ([Fig. 2.2](#)), as well as into a table with the major clades identified ([Table 2.5](#)).

Results

Species included

This study has gathered together the largest number of bustard samples from different species ever investigated to date: both morphological-behavioural and molecular data were collected from all 27 species of Otididae. All the morphological-behavioural data and the majority of the molecular data were generated for this study (the eight species for which toepad-skin samples failed to amplify were filled in with sequences published on Genbank). The full details of all species included in the study are presented in [Table 2.1](#).

Base composition

Base composition varied among loci ([Table 2.3](#)), with the mitochondrial DNA showing the typical deficiency of Guanine and Thymine relative to Adenine and

Cytosine (e.g. Price and Lanyon, 2002; Kirchman et al., 2004). The χ^2 -test implemented in PAUP* detected no significant base composition biases (see [Table 2.3](#) for *p*-values).

Sequence variation and characteristics

The complete ND2 sequences, with no indels or stop codons, were obtained for the full 1041 bases pairs (bp). It is highly unlikely that any of the mitochondrial sequences were nuclear pseudogenes (Sorenson and Quinn, 1998) because all chromatograms were of good quality and did not contain double-peaks, and all sequences translated into functional amino acids without the presence of internal stop codons. Most of the cyt b (243 – 1143 bp) and all of the CTRII (293 bp) sequences are from Pitra et al. (2002) and Broders et al. (2003). The lengths of the preferred alignments of the nuclear introns are as follows: Fib5, 619 bp; GAPDH, 430 bp; TGFB, 603 bp; ODC 688 bp; CHDZ 524 bp (CHDZ from Pitra et al., 2002). As expected, the nuclear markers were far less variable than the mitochondrial markers (see [Table 2.3](#) for the number and proportion of variable and informative sites).

Evaluation of congruence between the genes

There were no significant branches in conflict for the different gene regions (see [Table 2.4](#) for support values of the major branches recovered in the analyses), and so the data were combined into a large concatenated analysis. The final concatenated DNA alignment was 5341 bp (2477 bp mtDNA and 2864 bp nuclear DNA) with 798 informative characters. The 62 morphological-behavioural characters ([Appendix 2.2](#)) were all phylogenetically informative, bringing the total dataset to 5403 characters.

Phylogenetic inference

Overview of major clades

The analyses broadly identify two major groupings, with a number of sub-groups, within the Otididae. Twenty-five nodes which denote clades are identified on Fig. 2.1 and it is useful to use these as a basis for discussion of the results as a whole. Certain clades that contain either more than one genus, or only part of a genus, were renamed to make them easier to follow in the text. Clades that contain the members of a single genus are referred to by the generic name.

1. Clade 3 (named after the node on Fig. 2.1), hereafter **Clade “Larger bustards”** (not always recovered as monophyletic; not on Fig. 2.2 but see Fig. 2.4), comprising:
 - Clade 7, hereafter **Clade OC**: *Otis* and *Chlamydotis*
 - Clade 5, hereafter **Clade AN**: *Ardeotis* and *Neotis*
 - Tetrax*
 - Clade 2, hereafter *Lissotis* (not part of this clade on Fig 2.2)

2. Clade 6, hereafter **Clade “Smaller bustards”**: often monophyletic, comprising:
 - Clade 17, hereafter *Lophotis*
 - Clade 16, hereafter **Clade Floricans**: *Houbaropsis bengalensis* and *Sypheotides indica* (commonly known as the floricans)
 - Clade 18, hereafter **Clade EA**, with three subclades:
 - Clade 20, hereafter **Clade Heterotetrax**: *Eupodotis humilis*, *E. vigorsii*, *E. rueppellii*
 - Clade 24, hereafter **Clade Blue Eupodotis**: *E. caerulescens*, *E. senegalensis*, *E. barrowii*

-Clade 23, hereafter *Afrotis*.

The levels of support that the different datasets and analyses give these clades are summarised in [Table 2.4](#).

Combined morphological-behavioural and DNA datasets

The most inclusive tree with the largest amount of data is the parsimony analysis that combines all genetic and morphological-behavioural data (30 taxa and 5403 characters). The strict consensus of this, based on 17 trees with a length of 3242, is presented as [Fig. 2.2](#), with jackknife support values. Twenty-five nodes are identified on this tree and it is useful to use these as a basis for discussion of the results as a whole (see above). *Lissotis*, an African genus, is weakly recovered as basal to all the bustards, followed by a trichotomy with **Clade AN**, *Tetrax* sister to **Clade OC**, and **Clade “Smaller bustards”**. Two of the three members of the trichotomy are themselves poorly supported (**Clade AN** is well-supported) and all three are poorly supported at their bases. However, within each major clade, there are many well-supported nodes (all support values in [Table 2.4](#)). **Clade OC** and the monophyly of *Chlamydots* is well-supported. In **Clade AN**, the monophyly of *Ardeotis kori* and sister relationship between *A. australis* and *A. nigriceps* are well-supported. In **Clade “Smaller bustards”**, the following clades are well-supported: the floricans, *Lophotis* (and *L. gindiana* sister to *L. savilei*), **Clade Heterotetra**x, **Clade Blue Eupodotis** and **Afrotis**. **Clade EA**, with **Clade Blue Eupodotis** sister to *Afrotis*, is recovered.

Morphological-behavioural dataset

The strict consensus tree ([Fig. 2.3](#); from four equally parsimonious trees) of the

parsimony analysis reveals that all genera used in this study (after Collar, 1996) are monophyletic, a situation not recovered by the molecular and combined analyses. However, the deeper nodes have little support and if branches of jackknife support of less than 50 are collapsed, the tree collapses to a comb-like structure, with no deeper level structure beyond the recognised genera. High levels of support are shown to the genera *Lissotis*, *Lophotis*, *Eupodotis*, *Ardeotis*, *Chlamydotis*, *Afrotis* and **Clade Floricans**. *Neotis* is no longer monophyletic.

Combined DNA datasets

The Bayesian analysis of the combined genetic data ([Fig 2.5](#)) recovers two major monophyletic clades: **Clade “Smaller bustards”** and **Clade “Larger bustards”**. **Clade “Smaller bustards”** is a trichotomy comprising: **Clade EA**, *Lophotis*, and **Clade Floricans**. **Clade “Larger bustards”** has a polytomy with 4 clades: **Clade OC**, *Lissotis*, *Tetrax*, and **Clade AN**. In **Clade AN**, *Ardeotis* is monophyletic here, with a non-monophyletic *Neotis* as basal to the clade, with *N. nuba* sister to the entire group. A monophyletic *A. kori* is recovered as sister to the *A. australis* and *A. nigriceps* clade. **Clade EA** has **Clade Heterotetrax** as sister to a sister grouping between **Clade Blue Eupodotis** and **Afrotis**. *E. senegalensis* and *E. barrowii* are strongly-supported sisters (PP = 1), as are *E. vigorsii* and *E. rueppellii* (PP = 1). *L. gindiana* is sister to *L. savilei* (PP = 1).

The Maximum Likelihood (ML) analysis also recovers the divide into **Clade “Smaller bustards”** and **Clade “Larger bustards”** (support values are presented in [Fig. 2.5](#)). Within **Clade “Smaller bustards”**, **Clade EA** is supported, and *Lophotis* and **Clade Floricans** are united in a weakly-supported clade (ML BS = 57). The base

of the **Clade “Larger bustards”** is weakly supported and so, like the Bayesian tree, essentially represents a polytomy with *Lissotis*, *Tetrax*, **Clade OC**, and **Clade AN** (the latter clade with *N. nuba* again basal and the others poorly resolved).

In the parsimony analyses ([Fig 2.4](#)), **Clade “Smaller bustards”** is still monophyletic, with the same internal relationships as the ML analysis. Sister to these are *Tetrax* and **Clade OC**, and sister to all of these is **Clade AN**, with *Lissotis* as basal to all the bustards. Applying the jackknifing to collapse branches with JK<50, the tree quickly becomes a polytomy. **Clade “Smaller bustards”** do not remain as a group, and are scattered along the polytomy in the following groups: *Lophotis*, *E. humilis*, *E. vigorsii* sister to *E. rueppellii*, a sister grouping between **Clade Blue Eupodotis** and **Afrotis**, **Clade Floricans** and **Clade AN** (the latter is largely unresolved internally, although *N. nuba* is basal to this group). A similar polytomy exists with the bootstrap tree, but with the important exception that **Clade Heterotetrax** (BS = 58) is recovered and completes **Clade EA** (BS = 51).

Mitochondrial DNA dataset

The Bayesian tree shows a polytomy of five branches ([Fig. 2.7](#)). However, there is little support at the base of a clade that links **Clade EA** with **Clade OC**, and also the trichotomy that links that clade to *Lissotis* and **Clade Floricans**. If those nodes (PP < 0.57) are collapsed, then exactly the same seven main clades were recovered as the parsimony analysis (with branches with BS < 50 collapsed; [Fig. 2.6](#)): **Clade OC**; **Clade AN**, with strong support for a sister relationship between *A. australis* and *A. nigriceps*, and *Neotis nuba* as basal to the clade; **Clade EA**; *Lophotis*; *Lissotis*; **Clade Floricans**; and *Tetrax*. The parsimony majority rule tree does show extra structure,

with *Lissotis* as basal to the bustards, and *Tetrax* as basal to the rest. In the ML analysis ([Fig. 2.8](#)), the basal nodes are so poorly supported that it would be more cautious to think of them as collapsed (ML BS all less than 32). That leaves the major clades as **Clade AN**; *Lophotis*; *Tetrax*; *Lissotis*; and a weakly supported grouping of the following: **Clade Floricans**; **Clade OC**; **Clade EA**.

Nuclear DNA dataset

The nuclear dataset, including parsimony ([Fig. 2.9](#)), Bayesian ([Fig. 2.10](#)), and ML ([Fig. 2.11](#)) analyses, recovers two major monophyletic clades: **Clade “Smaller bustards”** and **Clade “Larger bustards”**, with a relatively high level of support (See [Table 2.4](#)). **Clade “Smaller bustards”** is composed of **Clade EA** sister to *Lophotis*. **Clade “Larger bustards”** has **Clade AN**, *Otis* and *Tetrax* in a polytomy, with *Lissotis* either included here or basal to the clade.

Individual gene datasets

The eight individual gene trees are not presented here but all the nodes, with their support values, are summarised in [Table 2.4](#). Importantly, **Clade “Smaller bustards”** is strongly supported almost throughout, and a high level of support, almost without exception, is given the major clades identified in the first section of the results. Where this support is not given, it is almost always likely because of taxon sampling issues, as not all the gene trees have all the species represented.

Discussion

Relationship between the major clades

This phylogeny identifies a number of well-supported major clades that are discussed under separate subheadings below. The lack of basal resolution in the overall phylogeny obscures confidence in how these clades are related to each other. This is a common phenomenon in avian phylogenies and is believed to result from a rapid radiation, as suggested for Pitra et al. (2002) in their study of the Otididae. This is despite the analysis of a far greater number and variety of characters than in their study. Poor taxon sampling, a huge weakness in the study of Broders et al. (2003), was also not an issue.

Besides the well-supported clades described below, **Clade “Smaller bustards”**, that links **Clade EA**, *Lophotis* and **Clade Floricans**, with a possible sister relationship between the latter two clades, seems to be valid. **Clade “Smaller bustards”** is not recovered by either Pitra et al. (2002) or Broders et al. (2003). It has not specifically been suggested in the literature either, although all its members have in the past been lumped into the genus *Eupodotis*, although this has always also included the current members of *Lissotis* (see [Table 2.5](#)). Johnsgard (1991) suggests that enlarged clade, with the floricans splitting off at the base first, followed by *Lissotis*. **Clade “Smaller bustards”** is not united by any unique morphological or behavioural features, other than being small in size relative to the members of the other bustard clades.

Clade “Larger bustards”, which might be monophyletic, could also have subclades that are recovered as sister to the bustards as a whole. The placement of the

Ardeotis/Neotis clade in the Otididae has proved elusive, with Pitra et al. (2002) suggesting *Lissotis* as the sister whereas Broders et al. (2003) suggest *E. rueppellii* as the sister. The results presented here place it within **Clade “Larger bustards”**, but without a clear sister grouping. *Tetrax* might well be sister to the *Otis* and *Chlamydotis* clade (see below), whereas the placement of *Lissotis* is elusive (Pitra et al., 2002, recover it as sister to the *Ardeotis/Neotis* clade).

The Palearctic genera: Otis, Tetrax and Chlamydotis

The well-supported sister relationship between *Otis* and *Chlamydotis* was suggested by Dementiev and Gladkov (1951), who linked them (and *Tetrax*) in the genus *Otis*, although this has been ignored by subsequent authors (Table 1.2). More recent molecular studies by Pitra et al. (2002), based on 444 base pairs of cytb, and Broders et al. (2003), based on 1143 base pairs of cytb with only 11 taxa sampled, also recovered this relationship. The two genera are not especially close in morphological and molecular analyses, and thus the division into two genera is probably warranted. Both are widely distributed across the Palearctic region and, with *Tetrax*, are the bustards that occur the furthest north, and have the widest latitudinal range of the family (Johnsgard, 1991; Collar, 1996). Johnsgard (1991), like Dementiev and Gladkov (1951), also allied these three Palearctic genera, suggesting a sister relationship between *Otis* and *Tetrax*, which he suggested were in turn related to *Chlamydotis*. Interestingly, *Otis* and *Tetrax* do share a unique short, blunt and broad bill morphology (not dissimilar to that of grouse, *Tetrao*), but this is more likely to reflect a greater reliance of these two species on feeding on vegetable matter (Collar, 1996). In the present study, there is some evidence for a relationship between these genera, as *Tetrax* is recovered as sister to the *Otis* and *Chlamydotis* clade in the

combined analysis of all the morphological-behavioural and DNA characters (majority-rule value of 76% but jackknife < 50) as well as in the parsimony analysis of the combined DNA dataset (but also with jackknife < 50). Pitra et al. (2002) recovered *Tetrax* as sister to *Lophotis*, whereas Broders et al. (2003) recovered it as sister to a clade comprising *Lophotis* and the two floricans (*Houbaropsis* and *Sypheotides*). The present morphological-behavioural dataset suggests *Tetrax* is sister to **Clade “Smaller bustards”**, but almost all the other analyses place it in a polytomy with other member of **Clade “Larger bustards”**, despite its small size.

Ardeotis and *Neotis*

The monophyly of this clade is well-supported and this is also recovered by Pitra et al. (2002) and Broders et al. (2003). Previous authors have also linked these genera, although the smaller *Neotis nuba* has sometimes been suggested to be allied to *Eupodotis* (Collar, 1996; although it has also been linked to *N. denhami* by Snow, 1978). A basal position (sharing a common ancestor with all the other members in this clade and is linked to them in a sister relationship) within this clade for *Neotis nuba* is well-supported by the molecular data. The only dataset that does not support this position for the Sahelian *N. nuba* is the morphological-behavioural dataset, which places it as sister to *N. heuglinii*, another arid land species with an adjacent distribution in north-east Africa. It would have been tempting to speculate that *N. ludwigii*, another desert species from south-western Africa, might have been allied to these previous two species, but there is no evidence for this. The morphological-behavioural dataset recovers both *Neotis* and *Ardeotis* as monophyletic, but this is in contrast to molecular analyses, which recover *Neotis* paraphyletic at the base of this clade). Pitra et al. (2002), also did not recover *Neotis* or *Ardeotis* as monophyletic.

The results presented here strongly support a sister relationship between the Australian *A. australis* and Indian *A. nigriceps* (also recovered by Pitra et al., 2002) which are similar in morphology (the males are typically large *Ardeotis* and share the crisp black cap) and the only members of this clade that do not occur in Africa. The monophyly of the two taxa of Kori Bustard, *A. k. kori* (southern Africa) and *A. k. struthiunculus* (East Africa), was confirmed. These taxa have been treated as separate species in the past (e.g. Mackworth-Praed and Grant, 1952) and also have a conspicuous difference in the “beard” of displaying males (Unpublished data together with T. Osborne and S. Hallager). *Ardeotis kori* is convincingly placed as sister to *A. australis* and *A. nigriceps*, with *A. arabs* a more weakly-supported sister to this group, which results in *Ardeotis* remaining monophyletic. This is in contrast to Pitra et al. (2002) who find *N. heuglinii* as sister to *A. australis* and *A. nigriceps*, although this is not well-supported and is highly unlikely from a morphological perspective. However, the placement of *A. arabs* in a monophyletic *Ardeotis* is weak. This is surprising given the close morphological similarity between *A. arabs* and *A. kori* which has resulted in them being treated as a superspecies (Snow, 1978; Collar, 1996). One of the problems with elucidating the relationships in the *Ardeotis/Neotis* clade is that all the species are large and are thus either very rare or very difficult to capture for sampling. Hence, only relatively short fragments of DNA from toepad-skin of museum specimens were obtained. Broders et al. (2003) did not include *Neotis* in their study so another molecular perspective on the placement of *Neotis* is impossible.

The small black-bellied bustards: Lissotis, Lophotis, Houbaropsis and Sypheotides

It has been suggested that these small black-bellied bustards, together with *Afrotis*,

form a monophyletic group (Collar, 1996), and they have been united in the genus *Eupodotis* by several authors (Snow, 1978; Sibley and Monroe, 1990; Johnsgard, 1991; [Table 1.2](#)).

It has long been recognised that the two southern Asian species (known as “floricans”), *Houbaropsis bengalensis* and *Sypheotides indica*, are sister taxa, although morphological and behavioural differences have led to them being separated in two genera (Johnsgard, 1991; Collar, 1996). Both the morphological and molecular data presented here support this sister relationship with a high degree of support ([Table 2.4](#)). They are placed in the **“Smaller bustards” clade**, and although their exact position is not clear, there is some evidence that they are allied to *Lophotis*. Reverse sexual dimorphism is present in only the floricans, and as they are sister taxa, need only have evolved once.

The results presented here strongly support the monophyly of *Lissotis* (comprising the East African *L. hartlaubii* and the more widespread *L. melanogaster*) which share a unique “popping” call and circling aerial display (Johnsgard, 1991; Collar, 1996; Stevenson and Fanshawe, 2002). They have been most strongly allied to *Lophotis* and *Afrotis* on the basis of morphology (Collar, 1996) but they are more likely linked to the **“Larger bustards” clade**, or perhaps even sister to all the Otididae. Nevertheless, their position is far from clear. Pitra et al. (2002) place *Lissotis* as sister to the *Ardeotis/Neotis* clade, but this is not well-supported.

The support by both morphological-behavioural and molecular data for a monophyletic *Lophotis* is to be expected as the southern African *L. ruficrista*, East

African *L. gindiana* and Sahelian *L. savilei* share a suite of morphological characters, not least being the reddish nuchal crest, and have even been lumped as single species before (e.g. Snow, 1978). These species also share a whistling call that is unique in the Otididae and a tumbling aerial display flight, although this has not been directly observed in the little-studied *L. savilei* (Collar, 1996). *Lophotis* is well-supported in the “**Smaller bustards**” clade, but its position here is not well-supported, although it may be sister to the floricans, which has also been suggested by Pitra et al. (2002). Broders et al. (2003) recovered *Lophotis* as sister to *Tetrax*, but they did not include the floricans in their study.

Eupodotis and *Afrotis*

Perhaps the most significant contribution of this study is clarifying the evolutionary relationships between the genera *Eupodotis* and *Afrotis*. This is especially interesting from a behavioural ecology point of view as *Eupodotis* spp. are the only monogamous members of the Otididae and have a group-living strategy with co-operative breeding, the complete opposite strategy to all other bustards where the male does not assist with breeding (Kemp & Tarboton, 1976; Collar, 1996). While previous morphological treatments (see [Table 1.2](#)) and those presented here have come to the conclusion that they are monophyletic, two published molecular studies (Pitra et al., 2002; Broders et al., 2003) have placed *E. rueppellii* (of **Clade Heterotetra**; see Results) on their trees independently of the other species of *Eupodotis*. Pitra et al. (2002) suggest *E. rueppellii* is sister to the rest of the bustards, with **Clade Blue Eupodotis** (see Results) as sister to *Afrotis*, with this clade in turn sister to *Otis-Chlamydotis*. Broders et al. (2003) suggest that *Afrotis* is sister to the rest of the bustards, with *E. senegalensis* (of **Clade Blue Eupodotis**) sister to the remaining bustards, and *E.*

rueppellii sister to *Ardeotis*. Results presented here suggest that *Eupodotis* and *Afrotis* form a well-supported monophyletic group, which is more parsimonious when considering the unique morphological and behavioural adaptations in *Eupodotis*. However, *Afrotis* renders *Eupodotis* paraphyletic, with *Afrotis* sister to **Clade Blue Eupodotis** (*Eupodotis caerulescens*, *E. senegalensis*, *E. barrowii*), and **Clade Heterotetrax** (*Eupodotis humilis*, *E. vigorsii*, *E. rueppellii*) sister to that grouping. This enlarged clade (**Clade EA**), is a core member of my **Clade “Smaller bustards”** also comprising *Lophotis* and the floricans. The morphological (small bustards with black underparts in the males) and display similarities between the African *Afrotis* and the Asian floricans (*Houbaropsis bengalensis* and *Sypheotides indica*) are due to convergence, as the taxa are not sisters. Johnsgard (1991) suggests a polyphyletic *Eupodotis* with a close *Afrotis* relationship. He suggests that *E. caerulescens* is not allied to the other *Eupodotis*, but rather is sister to the *Eupodotis-Afrotis-Lophotis* clade (Fig. 2.1).

Consilience between the morphological-behavioural and molecular analyses

The morphological-behavioural characters are those on which all the traditional assessments of bustard relationships are based. By including them in this study, it allows not only their critical evaluation within a phylogenetic framework (instead of subjectively deciding which character were more important), but also their comparison with the molecular data. The morphological-behavioural data seem especially poor at providing deeper-level resolution, and the only clades that have jackknife support of > 50 are those that represent currently recognised genera. All the traditional genera are recovered as monophyletic, although *Neotis* is not well-supported, a situation mirrored in the molecular analyses, which additionally split

Eupodotis and possibly *Ardeotis*. A weakness of many of the characters for phylogenetic analysis is that they are probably under strong directional sexual selection (see below) that could obscure the evolutionary relationships. However, most of the genera recognised on morphological evidence are still recovered as monophyletic, in contrast to the situation in many other bird groups (e.g. Fregin et al., 2009; Fuchs et al., 2009; Outlaw et al., 2009).

Morphological character evolution

It is striking how many of the characters that have been considered important for taxonomy are homoplasious, although this often depends on how they are defined, as closer examination often reveals synapomorphies. For example, the presence of a crest is found in many clades ([Appendix 2.2](#)), but only *Ardeotis* shows a hind-crown crest, whereas nuchal crests are found widely in **Clade “Smaller bustards”**. Erectile feathers on the facial region have evolved twice ([Appendix 2.2](#)): once in *Otis* and again in *Syphoetides*, and close examination reveals that different feather tracts are involved.

As has been found in the Pteroclidae (Chapter 3) and Glareolidae (Chapter 4), many of the upperpart patterns and colours, which are no doubt important for camouflage, are homoplasious ([Appendix 2.2](#)). This includes the back pattern and crown streaking, and black and white on the wing coverts, which are also likely important in display ([Appendix 2.2](#)). Collars, head markings and neck stripes are homoplasious, although neck stripes in the front of the neck are only found in **Clade “Smaller bustards”** and side neck stripes only in *Chlamydotis* ([Appendix 2.2](#)). Pale areas in the primaries, only visible in flight, are also apparently homoplasious.

Neotis is definitely the clade with the most morphological diversity, with *N. denhami* (relationship in the clade unclear) sharing many features with *Ardeotis*, and there is a remarkable resemblance between *N. nuba* (basal to the clade) and *Eupodotis*. The distinct black throat patch, presence of a pale blue colour in the plumage, and the minor plumage difference between males and females are features of *N. nuba* that are only otherwise present in *Eupodotis*. This similarity is so marked that one of the specimens of *N. nuba* in the British Natural History Museum was even labeled as *E. barrowii* (Osborne, 1984). *N. nuba* is very poorly known in the wild and the social structure and display are unknown (Collar, 1996). Although it is assumed to be a polygynous lekker like the other members of *Neotis*, the small size and lack of marked plumage dimorphism between the sexes suggest a monogamous life strategy. There are published size differences between the males and females (males are about 17% larger; Johnsgard, 1991; Raihani, 2005) which would suggest polygyny. However, the Bustard Morphometrics Database (Osborne, 1984) suggests that the specimens in the British Natural History Museum, on which these measurements are based, may have been sexed incorrectly. The literature is unclear on the differences between females and juveniles (a reduced throat patch is apparently a feature of both) and so it might just be assumed that the smaller juvenile birds are females. It would be interesting to examine these specimens more closely, and to undertake a field study on the increasingly rare *N. nuba*, which is now in decline across its Sahelian range owing to habitat degradation and hunting (Collar, 1996).

The bare parts of bustards are generally dull-coloured, although a bright bill base is found in many members of **Clade “Smaller bustards”**. The brightest colours are the

bright yellow legs of *Afrotis*, which are dangled conspicuously during the display flight and are likely a display of carotenoids, a signal of male fitness shown in many bird displays (McGraw, 2006). The conspicuous red bill-base of *Afrotis* seems to be caused by flushing the soft tissue with blood as this bright red area immediately became a very pale pink when I handled the *A. afrooides* individual in Fig. 2.13.

The evolution of lekking, aerial display, sexual size dimorphism, sexual plumage dimorphism and co-operative breeding

A test using independent contrasts to control for phylogeny of the evolution of these life history strategies (e.g. Felsenstein, 1985b; Harvey and Pagel, 1991) and character state transitions is limited in the present data set for two reasons. The first is that there is too much uncertainty with regard to the deeper-level relationships between the major clades to hypothesise the character state transitions with confidence. Secondly, although the bustards show a remarkable degree of life history strategy variation for such a small family, there are simply too few species, clades and transitions to produce a statistically significant result for anything but the most basic of correlations. Nonetheless, the inferred relationships among the bustards allow some insights by examining monophyletic groupings.

Polygamy is prevalent in the Otididae, with 21 of 27 species reported to be polygynous, where the male mates with numerous females and plays no role in raising the young (Collar, 1996). Theories for the evolution of polygyny suggest that in situations where resources are plentiful, and the females are able to raise the offspring without male assistance, it benefits male fitness to spend his effort courting more females instead of raising the young (Payne, 1984). An immediate prediction is that

the clades of bustards in the most productive habitats (where abundant food is available to the developing offspring) are likely to be polygamous, although this is difficult to assess because there are no studies that are able to correlate the biome-level productivity with bustard distribution or abundance. Roughly, if one assumes that total annual rainfall can be used as a crude surrogate of habitat productivity (see Cowling et al., 1997), this would place the clades identified in this study into two broad productivity areas. Firstly, *Lissotis*, *Tetrax*, *Otis*, *Neotis denhami*, the floricans, *Lophotis*, *Afrötis* and the **Clade Blue Eupodotis** occur in the higher-rainfall most productive habitats, and of these eight, all are polygynous, with the exception of the monogamous **Clade Blue Eupodotis**. Conversely, the clades that have been identified that occur in the most hyper-arid regions, with 200-300 mm rainfall per annum and potentially non-productive areas, are *Chlamydotis*, *Neotis* (excluding *denhami*, unclear clade relationships make *Neotis* tricky to evaluate) and **Clade Heterotetrax**. These fall into two groups: those that are highly sedentary (**Clade Heterotetrax**) and those that are nomadic or migratory (the remaining). These nomadic or migratory bustards move into areas of high productivity to breed (Collar, 1996; Allan, 2005), and are all polygynous, whereas the highly territorial **Clade Heterotetrax** are site-faithful year-round, invest in territorial defence and are monogamous (Collar, 1996; Allan, 2005).

As far as it is known (information is incomplete for most species), all the polygynous bustards display lekking behaviour, with males displaying in dispersed or “exploded” leks, where males display over a larger area, but still within view of each other (Payne, 1984; Johnsgard, 1991; Collar, 1996; Allan, 2005). Polygynous males are free from the constraint of raising their offspring, and lekking is predicted to increase the

intensity of male-male competition, and to lead to the exaggeration of sexually-selected characters, such as an increase in the size of the males (which tends to lead to sexual size dimorphism) and costly, extravagant displays, with associated sexual plumage dimorphism (Payne, 1984; Andersson, 1984). Indeed, bustards are perhaps best known for their eye-catching displays and large size. These characters are evaluated in terms of the clades recovered in this study.

All of the polygynous clades mentioned above (all the clades with the exception of the monogamous **Clade Heterotetrax** and **Clade Blue Eupodotis**) have elaborate displays that are either 1. aerial or 2. terrestrial (and typically involve an inflation of the neck region to display prominent plumes), whereas the monogamous **Clade Heterotetrax** and **Clade Blue Eupodotis** do not have prominent displays although their heads are lifted while calling, which exposes the black throat ([Fig. 2.12](#), [Table 2.5](#), [Appendix 2](#); Johnsgard, 1991).

The polygynous aerial displayers are members of the following clades identified in this study: *Afrotis*, *Lissotis*, *Tetrax*, *Lophotis* and the floricans ([Fig. 2.12](#), [Table 2.5](#)). It should be noted that the latter two groups, *Lophotis* and the floricans, even though quite divergent, might compose a monophyletic clade, although support is not strong. The **Clade “Smaller bustards”** is more strongly supported as a clade, and so this strategy need not have arisen independently in these lineages ([Fig. 2.12](#)). Assuming a neutral common ancestor, these characters might only have arisen twice: once for *Lophotis* and the floricans, and once in *Afrotis*. It might be interesting to speculate what selective pressures led to the evolution of polygamy in *Afrotis* and how it became so divergent from its sister clade, **Clade Blue Eupodotis**, although there

seems to be no obvious ecological correlate (such as grass cover or bush cover) that differs from the sister clade that can be found in the literature, but a detailed habitat analysis of these species might provide further insight.

The polygynous aerial displayers are all small bustards which are otherwise hidden in their grassy (or woodland in the case of *Lophotis* and to some extent, *Lissotis*) habitats, and their conspicuous aerial displays are often associated with vocalisations that draw attention to them (Johnsgard, 1991). The plumage is highly sexually dimorphic, with the males showing bold black underparts and often white in the wing, features that are conspicuous in flight. Despite this exaggerated sexual plumage dimorphism, which suggests male-male competition (Andersson, 1984), there is only limited sexual size dimorphism, contrary to the prediction mentioned above (Andersson, 1984). Males of *Afrotis*, *Tetrax*, and *Lophotis* are only 1-5% larger than the females, whereas males of both floricans are actually 3-19% smaller than the females ([Table 2.5](#); Osborne, 1989; Collar, 1996; Raihani, 2005). However, these species meet the predictions of the Aerial Agility Hypothesis (Andersson and Norberg, 1981; Raihani, 2005), which suggests that females might actually prefer males with more agile aerial displays, and it seems to have been taken to the extreme in the floricans. Collar (1996) suggests that the agility shown in these aerial displays might be an honest signal of fleeing ability in habitats where the birds can easily be ambushed at close range. The outlier here is *Lissotis*, in which the males are 8-11% larger than the females, although this is not completely unexpected as the males also have a terrestrial component, in addition to the aerial component, to the display (Johnsgard, 1991; Collar, 1996; Stevenson and Fanshawe; 2002).

The second display employed by polygamous males is a terrestrial one, and is only employed in open habitats with long-distance visibility. These monophyletic clades are *Ardeotis/Neotis* and *Otis/Chlamydotis* (which are also hypothesised to be related in the broader **Clade “Larger bustards”**, with *Tetrax* and *Lissotis*, in some of my analyses). Indeed, it is likely that the superficially similar expanded-neck “balloon displays” that are shown by *Otis* and *Ardeotis/Neotis* evolved at least twice; this is supported by the fact that the swelling of the neck is achieved by a gular pouch in *Otis* and an expanded section of the oesophagus in *Ardeotis* (Table 2.5; Johnsgard, 1991). Nonetheless, the expanded neck, with its associated raised plumes, drooped wings and cocked tail grossly enlarges the appearance of these birds and is remarkably similar in these separate clades (Johnsgard, 1991; Collar, 1996). Large size, a prediction of terrestrial lekking, has evolved both in the *Otis/Chlamydotis* clade (*Otis* males are extremely large) and in the *Ardeotis/Neotis* clade (all the members of this clade, except the basal *N. nuba*, are large, and *Ardeotis* have become very large). There is also a seeming increase in sexual size dimorphism in the terrestrial lekking clades, which is consistent with Rensch’s rule that an increase in size is further associated with an exaggerated sexual size dimorphism (Table 2.5; Raihani et al., 2005).

The evolution of monogamy and group living among the monogamous bustards, which also show delayed dispersal and co-operative breeding, is in stark contrast to the promiscuous strategy displayed by the other bustards (Collar, 1996; Allan, 2005). Pitra et al. (2002), by placing *E. rueppellii* at the base of the bustard tree, would hypothesise multiple evolution of the group-living strategy. However, this study suggests that *Eupodotis* is a paraphyletic clade and this strategy only represents one change of strategy in the common ancestor of the group (Fig. 2.12), as it is more

parsimonious that *Afrotis* lost this behaviour, rather than **Clade Blue Eupodotis** developing it for a second time.

Vocal characters, important for signalling either during displays or group cohesion duets, are remarkably well-conserved between the clades ([Appendix 2.2](#)), although *Afrotis* is an exception, as its calls differ strongly from the “frog-like” call of all the other members of **Clade EA** (which are also the only bustards to engage in duetting behaviour, likely important for group cohesion; Payne, 1971). Some of the genera are silent (*Otis-Chlamydota*; Collar, 1996), but most have simple distinctive calls that are closely similar to congeners, such as the “boom” call in *Ardeotis/Neotis*, the whistles in *Lophotis* and the “pop” call in *Lissotis*.

Table 2.1: Samples analysed in this study, with sample source, collection locality, and extraction codes.

The components of the concatenated data sets are detailed, and samples in bold were used in the concatenated genetic analyses.

For each gene region, either the extraction codes (CC = Callan Cohen; ABS = Anna Seles) or Genbank numbers are given. PFIAO = Percy FitzPatrick Institute of African Ornithology.

Taxon	Source of genetic sample (with label annotations)	Genetic sample locality	Morpho-behav. data	Mitochondrial DNA			Nuclear DNA					
				Cytb	ND2	CTRII	Fib5	GAPDH	TGFB	ODC	CHDZ	
<i>Otis tarda</i>	Concatenated from the 3 samples below Callan Cohen (11510/04, 20/05/04, Madrid, OTA) Pitra et al., 2002 Broders et al., 2003	Europe Spain Spain	Yes	AJ511466 CCB1 CCB1	AF372004 AF372041 AJ511466	CCB1 CCB1 CCB1	CCB1 CCB1 CCB1	CCB1 CCB1 CCB1	CCB1 CCB1 CCB1	CCB1 CCB1 CCB1	AF372014 AF372014	
<i>Ardeotis arabs</i>	Concatenated from the 3 samples below Callan Cohen (Toepad, Kenya 99102) Pitra et al., 2002 Broders et al., 2003	Unknown East Africa Unknown	Yes	AJ511432					CCB81 CCB81			
<i>Ardeotis kori kori</i>	Concatenated from the 4 samples below Callan Cohen (10/99, Cohen, Kuruman, AKO1) Callan Cohen (J12909, Namibia, AKO2, Ard kori2) PFIAO (20/05/99, R.Jansen, Roedtan, N.Prov., AKO3) Broders et al., 2003	Southern Africa South Africa Namibia South Africa Namibia	Yes	AJ511439 CCB4 AJ511439	CCB4 CCB4		CCB2 CCB2 CCB3 CCB4	CCB2 CCB2 CCB3 CCB4	CCB2 CCB2 CCB3 CCB4	CCB2 CCB2 CCB3 CCB4		
<i>Ardeotis kori struthiunculus</i>	Callan Cohen (8/99, KEN9905, Chyulu NRFA63, AST, OLD Ard str)	Kenya	Yes									
<i>Ardeotis kori</i>	Pitra et al., 2002	Unknown	Not applic.	AF372022		AF371997						AF372009
<i>Ardeotis nigriceps</i>	Pitra et al., 2002	India	Yes	AF372023								
<i>Ardeotis australis</i>	Concatenated from the 3 samples below Callan Cohen (42915L, AAU1, Ard austr 1) Callan Cohen (42917L, AAU3, Ard austr3)	Australia Australia Australia	Yes	AF372021 CCB6 CCB6 CCB8			CCB6 CCB6 CCB8	CCB6 CCB6 CCB8	CCB6 CCB6 CCB8	CCB6 CCB6 CCB8	CCB6 CCB6 CCB8	
<i>Chlamydota u. undulata</i>	Concatenated from the 2 samples below Pitra et al., 2002	Saudi Arabia	Yes	AJ511448 AF372025		AF371998						AF372010 AF372010
<i>Chlamydota u. fuerteventurae</i>	Broders et al., 2003	Algeria		AJ511448		AF371998						
<i>Chlamydota macqueenii</i>	Broders et al., 2003	Canary Islands	Yes	AJ511463								
<i>Neotis ludwigii</i>	Concatenated from the 2 samples below Callan Cohen (via M.Anderson, Eastern Karoo, NLU, OLD Neo lud)	Asia	Yes	AJ511451								
<i>Neotis denhami</i>	Concatenated from the 3 samples below Callan Cohen (not CCB9; Witsand, NDE1, OLD Neo den)	South Africa South Africa Africa	Yes	AF372039 CCB11 CCB11	AF372037 CCB39 CCB39				CCB11 CCB11	CCB11 CCB11	CCB11 CCB11	
<i>Neotis heuglinii</i>	Pitra et al., 2002	Kenya	Yes	AF372038		AF372003						AF372007
<i>Neotis nuba</i>	Pitra et al., 2002	Sudan	Yes	AF372017								
<i>Eupodotis senegalensis</i>	Concatenated from the 4 samples below Callan Cohen (8/99 KEN9911 Chyulu, NRFA65, ESE1,OLD Eupo sene) Callan Cohen (9/99, KEN9948 Athi, ESE2,OLD Eupo ene)	Kenya Kenya Unknown		AJ511441 CCB17 CCB17 CC18	AF371999 CCB17 CCB17 CC18		CCB17 CCB17 CC18	CCB17 CCB17 CC18	CCB17 CCB17 CC18	CCB17 CCB17 CC18	CCB17 CCB17 CC18	AF372012
<i>Eupodotis barbatus</i>	PFIAO (leg, Ian Little, Eastern South Africa)	West Africa	Yes	AJ511441	AS565 CCB43 CCB19	AF372027	AS565 CCB43 CCB19	AS565 CCB43 CCB19	AS565 CCB43 CCB19	AS565 CCB43 CCB19	AS565 CCB43 CCB19	
<i>Eupodotis caerulescens</i>	Concatenated from the 5 samples below Callan Cohen (BLK 5/11/91, ECA1,OLD Eupo caer) PFIAO (Maselspoort, Bloemfontein 7/00, R.Jansen, ECA2) PFIAO (RSA233) PFIAO (RSA234)	South Africa South Africa South Africa South Africa	Yes	AF372027 CCB19 CCB20 CCB42 CCB43	AF372027 CCB19 CCB20 CCB42 CCB43		CCB19 CCB20 CCB42 CCB43	CCB19 CCB20 CCB42 CCB43	CCB19 CCB20 CCB42 CCB43	CCB19 CCB20 CCB42 CCB43	CCB19 CCB20 CCB42 CCB43	CCB19 CCB20 CCB42 CCB43
<i>Eupodotis vigorsii</i>	PFIAO (RSA234) Pitra et al., 2002 Callan Cohen (Tanqua 12/11/02 (rep2), EVI1, Eupod vigo1) Callan Cohen (Tanqua 12/11/02 (rep2), EVI1, Eupod vigo1) Callan Cohen (Tanqua 12/11/02 (rep1), EVI2, Eupod vigo2)	South Africa South Africa South Africa	Yes	AF372027 CCB31 CCB31 CCB32	CCB31 CCB31 CCB32		CCB31 CCB31 CCB32	CCB31 CCB31 CCB32	CCB31 CCB31 CCB32	CCB31 CCB31 CCB32	CCB31 CCB31 CCB32	

Table 2.1: continued from previous page.

Taxon	Source of genetic sample	Genetic sample locality	Morpho-behav data	Mitochondrial DNA			Nuclear DNA					
				Cytb	ND2	CTRII	Fib5	GAPDH	TGFB	ODC	CHDZ	
<i>Eupodotis rueppellii</i>	Concatenated from the 5 samples below Callan Cohen (624314 Brandberg, ERU1 via Tim Osborne) Callan Cohen (624334 ERU2, via Tim Osborne) Callan Cohen (624315, ERU3, via Tim Osborne) Pitra et al., 2002 Broders et al., 2003	Namibia Namibia Namibia Namibia Namibia Namibia	Yes	AJ511445 CCB28 CCB30 AF372028 AJ511445	CCB28 CCB29 CCB30 AF372000	CCB28 CCB29 CCB30 CCB30	CCB28 CCB29 CCB30 CCB30	CCB28 CCB29 CCB30 CCB30	CCB28 CCB29 CCB30 CCB30	CCB28 CCB29 CCB30 CCB30	AF372011	
<i>Eupodotis humilis</i>	Callan Cohen (KEN99118, NE Somalia, toepad, NMK)	Somalia	Yes	AF372035					CCB89			
<i>Lophotis savilei</i>	Pitra et al., 2002	Unknown	Yes	AF372033	CCB13		CCB13	CCB13	CCB13	CCB13	CCB13	
<i>Lophotis gindiana</i>	Concatenated from the 3 samples below Callan Cohen (8/99, KEN9918 Chyulu WZ190, LGI1, OLD Lop gind) Callan Cohen (8/99, KEN9915 Chyulu WZ236, LGI2) Pitra et al., 2002	East Africa Kenya Kenya		AF372033	CCB12 CCB13		CCB13	CCB13	CCB13	CCB13	CCB13	
<i>Lophotis ruficrista</i>	Concatenated from the 4 samples below Callan Cohen (624341, LRU1, via Tim Osborne) Callan Cohen (KIMB 4/2000, LRU2) Pitra et al., 2002 Broders et al., 2003	Southern Africa Namibia South Africa Unknown Namibia	Yes	AJ511464 AF37203 AF372033 AJ511464	CCB14 CCB14 CCB15	AF372002 AF372002	CCB15	CCB14 CCB14 CCB15	CCB14 CCB14 CCB15	CCB14 CCB14 CCB15	CCB14 CCB14 CCB15	
<i>Afrötis afra</i>	Concatenated from the 4 samples below Callan Cohen (Ceres, AAA1) Callan Cohen (Velddrif, AAA2) PFIAO (RSA239, SL) Pitra et al., 2002	South Africa South Africa South Africa South Africa South Africa	Yes	AF372018 AF372018	CCB40 CCB26 CCB27 CCB40		CCB40 CCB26 CCB27 CCB40	CCB40 CCB26 CCB27 CCB40	CCB40 CCB26 CCB27 CCB40	CCB40 CCB26 CCB27 CCB40	CCB40 CCB26 CCB27 CCB40	
<i>Afrötis afraoides</i>	Concatenated from the 6 samples below Callan Cohen (624338, AA01, via Tim Osborne) Callan Cohen (624353 Etosha, 5/04/04, via Tim Osborne, AAO2) Callan Cohen (624319 Tandala 02, male, AAO3) PFIAO (RSA231, SL) Pitra et al., 2002 Broders et al., 2003	Namibia Namibia Namibia Namibia Namibia Namibia	Yes	AJ511427 AF372019 AJ511427	CCB41 CCB22 CCB23 CCB24 CCB41	AF371996 AF371996	CCB41	CCB41 CCB23 CCB41	CCB41 CCB23 CCB24 CCB41	CCB41 CCB23 CCB24 CCB41	CCB40 CCB26 CCB27 CCB40 CCB40 CCB40	AF372008
<i>Lissotis melanogaster</i>	Concatenated from the 4 samples below Callan Cohen (Durban Nat. Sci. Mus. freezer, Natal, female, LMG1) PFIAO (Kenya, LME, Tim Crowe) Pitra et al., 2002	South Africa Kenya Tanzania	Yes	AF372031 AF372031	CCB37 CCB35 CCB37	AF372001 AF372001	CCB37 CCB35 CCB37	CCB37 CCB35 CCB37	CCB37 CCB35 CCB37	CCB37 CCB35 CCB37	CCB37 CCB35 CCB37	AF372013
<i>Lissotis hartlaubii</i>	Pitra et al., 2002	East Africa	Yes	AF37203								
<i>Houbaropsis bengalensis</i>	Pitra et al., 2002	India	Yes	AF372030								
<i>Syphoetides indica</i>	Pitra et al., 2002	Himalayas	Yes	AF372042								
<i>Tetrapax tetrax</i>	Concatenated from the 4 samples below Callan Cohen (4/04 Toledo, TTE) Pitra et al., 2002 Broders et al., 2003	Spain Spain Spain Spain	Yes	AJ511470 AF37043 AJ511470	CCB25 CCB25	AF372005 AF372005	CCB25 CCB25	CCB25 CCB25	CCB25 CCB25	CCB25 CCB25	CCB25 CCB25	AF372015
<i>Gruidae</i>	Concatenated from the 6 samples below		Yes	EU166997 AF372045 EU166997	CCB38 CCB9 CCB38	AF372006 AF372006	CCB38 CCB9 CCB38	CCB38 CCB9 CCB38	CCB38 CCB9 CCB38	CCB38 CCB9 CCB38	CCB38 CCB9 CCB38	AF372016
<i>Anthropoides paradiseus</i>	Callan Cohen (not 39, CBL Durban Nat. Sci. Mus. freezer)	South Africa										
<i>Grus carunculata</i>	Callan Cohen (CWA, Durban Nat. Sci. Mus. freezer)	South Africa										
<i>Grus grus</i>	Pitra et al., 2002											
<i>Grus antigone</i>	Pitra et al., 2002											
<i>Grus canadensis</i>	Genbank											
<i>Balearica regulorum</i>	Pitra et al., 2002											AF372016

Table 2.2: Primers used for amplification and sequencing of the Otididae.

Gene Region	Primer Name	Primer Sequence	Source
Cytb	L14841	5'-AAAAAGCTTCCATCCAACATCTCAGCATGATGA-AA-3'	Kocher et al., 1989
	H15149	5'-AAACTGCAGCCCCCTCAGAACATGATATTGTCCCTCA-3'	
ND2	L5204	5'-GCTAACAAAGCTATCGGGCCCAT-3'	Cicero and Johnson, 2001
	H6312	5'-CTTATTAAAGGCTTGAAAGGCC-3'	
Fib5	Fib5/FGB	5'-CGCCATACAGAGTATACTGTGACAT-3'	Fuchs et al., 2004; Kimball et al., 2009
	Fib6	5'-GCCATCCTGGCGATTCTGAA-3'	
TGFB	TGFB2.5F	5'-GAAGCGTGCTCTAGATGCTG-3'	Primmer et al., 2002; Kimball et al., 2009
	TGFB2.6R	5'-AGGCAGCAATTATCCTGCAC-3'	
GAPDH	G3P13b	5'-TCCACCTTGATGCGGGTGCTGGCAT-3'	Fjeldså et al., 2003
	G3P14b	5'-AAGTCCACAACACCGGTTGCTGTA-3'	
	G3PintL1	5'-GAACGACCATTGTCAAGCTGGTT-3'	
	GAPDHintFOti	5'- TCTCCTTCRTGATGGGARGGTGG -3'	
ODC	OD6	5'-GACTCAAAGCAGTTGCGTCTCAGTGT-3'	Allen and Omland, 2003
	OD8	5'-ATTGGTGGTGGCTTCCCTGGCTCTGAAGA-3'	

Table 2.3: Data characteristics and estimated model parameters for the datasets (for all the gene regions and concatenated datasets), including length of the alignment, number of variable and informative sites, model selected for the BI analyses, mean of the model parameters, BI likelihood score (arithmetic mean), ML likelihood score and MP tree numbers. The base frequency chi-squared test results are also included. Note that 1143 bp of cyt b is not available for all taxa.

	Total (M-B +DNA)	M-B (Morpho-Behav)	All DNA	Mt DNA	Nuc DNA	Cytb	ND2	CTRII	Fib5	GAPDH	TGFB	ODC	CHDZ
No. of characters													
No. of characters (total)	5403	62	5341	2477	2864	1143	1041	293	619	430	603	688	524
Variable characters	1656	62	1594	953	641	396	447	110	139	125	147	127	103
Proportion variable	0.306	1.000	0.298	0.385	0.224	0.346	0.429	0.375	0.225	0.291	0.244	0.185	0.197
Informative characters	860	62	798	631	167	242	312	77	43	37	37	32	18
Model parameters													
Model Selected	/	/	/	/	/	GTR+I+G	GTR+I+G	GTR+G	TVM+G	GTR+G	GTR	GTR+G	TVM+G
r(A<->C)	/	/	/	/	/	0.018	0.013	0.149	0.095	0.106	0.059	0.086	0.158
r(A<->G)	/	/	/	/	/	0.477	0.662	0.361	0.272	0.247	0.433	0.336	0.232
r(A<->T)	/	/	/	/	/	0.019	0.012	0.141	0.031	0.041	0.038	0.018	0.055
r(C<->G)	/	/	/	/	/	0.005	0.008	0.105	0.131	0.097	0.125	0.169	0.198
r(C<->T)	/	/	/	/	/	0.457	0.267	0.146	0.373	0.407	0.317	0.306	0.308
r(G<->T)	/	/	/	/	/	0.024	0.037	0.099	0.099	0.103	0.028	0.085	0.050
pi(A)	/	/	/	/	/	0.320	0.340	0.196	0.320	0.217	0.251	0.281	0.363
pi(C)	/	/	/	/	/	0.404	0.364	0.298	0.166	0.191	0.212	0.177	0.114
pi(G)	/	/	/	/	/	0.083	0.077	0.172	0.215	0.320	0.218	0.204	0.176
pi(T)	/	/	/	/	/	0.193	0.219	0.335	0.299	0.273	0.319	0.338	0.347
Alpha	/	/	/	/	/	1.383	1.267	0.604	59.551	0.295	0.295	16.323	46.170
Proportion invariable	/	/	/	/	/	0.506	0.450	0.450	0.450	0.450	0.450	0.450	0.450
Base frequency test													
Chi-squared value	/	/	/	/	/	13.268	11.922	6.917	9.860	8.487	2.493	1.629	1.866
Degrees of freedom	/	/	/	/	/	84	84	84	84	84	84	84	84
p	/	/	/	/	/	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
Tree characteristics													
MP No. of trees	17	4	4;4	4	36	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
BI LnL Bayesian	n/a	n/a	-20681.21	-12313.51	-7998.15	-2717.39	-6129.99	-1451.18	-1849.318	-1443.47	-1706.51	-1905.52	-1340.09
RaxML (Max Likelihood)	n/a	n/a	-20630.87	-12288.80	-7944.67	-2681.60	-6093.27	-1435.50	-1792.97	-1481.17	-1731.36	-1851.37	-1323.41

Table 2.4: Resolution and support values of recovered nodes from the concatenated and individual analyses. The node numbers refer to Fig. 2.2, and are also accompanied by a description. Parsimony (MP) support is jackknife for the COMB and M-B analyses, and bootstrap for the others. Posterior probabilities and bootstrap values are given for the Bayesian (BI) and Maximum Likelihood (ML) analyses respectively. Strongly-supported values (JK, BS >= 75; PP >= 0.95) are highlighted in bold. The support values for the previous studies are bootstrap: Pitra et al. (2002) is (MP/Neighbour-joining/ML). Highly supported relationships in bold; COMB = combined M-B and DNA data; M-B = morpho-behavioural; tri = trichotomy; YWL = Yes without *Lophotis*. The first number in the COMB column refers to the majority rule support.

Clades	Previous studies		Combined analyses												
	Description of Node	Node No. (Fig. 2.2)	Pitra et al. 2002	Broders et al., 2003	COMB MP	M-B MP	All DNA MP	BI	ML	Mt MP	BI	ML	nuclear MP	BI	ML
Otididae	1														
<i>Lissotis</i> monophyletic	2	99/100/93	n/a	100/100	97	99	1	100	99	1	100	n/a	n/a	n/a	
<i>Lissotis</i> sister to the rest	3				76/		Yes		to Large	Yes		to Small			
Tetrao sister to Clade OC	4				76/		Yes								
Clade AN: <i>Ardeotis/Neotis</i> sister	5	64/86/91	n/a	100/86	98	76	1	93		0.99	100	100	1	100	
Clade Smaller bustards monophyletic	6				76/	YWL	Yes	0.76	83				87	0.99	49
Clade OC: <i>Otis/Chlamydotis</i> sister	7	62/66/73	82	100/99		98	1	100	98	1	100	n/a	n/a	n/a	
<i>Chlamydotis</i> monophyletic	8	99/100/88	100	100/100	99	100	1	100	100	1	100	n/a	n/a	n/a	
Clade AN excluding <i>N. ludwigii</i>	9		n/a		64/			0.51	basal				Yes		basal
Clade AN excluding <i>N. denhami</i>	10		n/a		52/			0.51	basal				Yes	basal	basal
<i>Neotis heuglinii/N. nuba</i> sister	11		n/a		64/								n/a	n/a	n/a
<i>Ardeotis</i> monophyletic	12		n/a	100/99	Yes								Yes		43
Clades 14 and 15 sister	13		n/a	82/			0.9	69		0.89	78	n/a	n/a	n/a	
<i>A. australis/A. nigriceps</i> sister	14	90/89/68	n/a	100/97	Yes	93	1	91	95	1	93	n/a	n/a	n/a	
<i>A. k. kori/A. k. struthiunculus</i> sister	15	n/a	n/a	100/93	75	95	1	100	n/a	n/a	n/a	73	0.85		
Clade Floricans	16	53/68/79	n/a	100/99	86	82	0.95	97	84	1	89	n/a	n/a	n/a	
<i>Lophotis</i> monophyletic	17	99/100/82	n/a	100/100	99	94	1	99	97	1	99	97	1	100	
Clade EA: <i>Eupodotis/Afrotis</i>	18				89/	Yes	51	0.8	89	52	0.7		63	0.98	71
<i>Lophotis gindiana/L. savilei</i> sister	19	98/99/96	n/a	100/100		98	1	100	100	1	100	n/a	n/a	n/a	
Clade Heterotetrao	20	n/a	n/a		94/		58	0.85	79	98	1	100	66	0.93	72
<i>Afrotis/Clade Blue Eupodotis</i> sister	21	51/67/79			89/	79	1	87	82	1	99	97	0.99	84	
<i>Eupodotis rueppellii/E. vigorsii</i>	22	n/a	n/a	100/80		91	1	89	98	1	100	88	0.99	92	
<i>Afrotis</i> monophyletic	23	98/98/91	100	100/100	99	99	1	96	100	1	100	99	1	97	
Clade Blue Eupodotis	24	66/80/88	n/a	100/61		95	1	93	99	1	100	97	1	98	
<i>E. barrowi/E. senegalensis</i> sister	25	n/a	n/a	100/99	70	99	1	97	n/a	n/a	n/a	99	1	99	
<i>N. nuba</i> sister to <i>Ardeotis/Neotis</i>		60/68/92	n/a			90	1	77	88	1	79	n/a	n/a	n/a	
All <i>Eupodotis</i> monophyletic					92										
<i>Neotis</i> monophyletic			n/a		Yes										
Clade Larger bustards monophyletic								0.95	6			65	1	100	
Clade Floricans sister to <i>Lophotis</i>			Yes	n/a					57	Yes		n/a	n/a	n/a	
Clade OC + Clade EA			Yes							Yes	0.57				
<i>Eupodotis rueppellii</i> sister to all			Yes												

Table 2.4: continued from previous page.

CLADES		Individual genes															
Description of Node	Node No. (Fig. 2.1)	mt cytb		mt ND2		mt COHII		nuc fib5		nuc GAPDH		nuc TGFB		nuc ODC		nuc CHDZ	
		BI	ML	BI	ML	BI	ML	BI	ML	BI	ML	BI	ML	BI	ML	BI	ML
Otididae	1																
<i>Lissotis</i> monophyletic	2	1	100	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
<i>Lissotis</i> sister to the rest	3		100											1	100		
Tetrao sister to Clade OC	4		35											n/a			
Clade AN: <i>Ardeotis/Neotis</i> sister	5	1	94	1	100	1	94	0.83	84	1	100	1	100	1	100	1	100
Clade Smaller bustards monophyletic	6							1	100								
Clade OC: <i>Otis/Chlamydotis</i> sister	7	0.95	100	n/a	n/a	1	99	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	0.86	56
<i>Chlamydotis</i> monophyletic	8	1	99	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Clade AN excluding <i>N. ludwigii</i>	9			basal	70	n/a	n/a	n/a	n/a		basal	basal	basal	basal	n/a	n/a	n/a
Clade AN excluding <i>N. denhami</i>	10			basal	100	n/a	n/a	n/a	n/a	basal	basal	n/a	n/a	n/a	n/a	n/a	n/a
<i>Neotis heuglinii/N. nuba</i> sister	11			n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
<i>Ardeotis</i> monophyletic	12			1	100	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Clades 14 and 15 sister	13			n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
<i>A. australis/A. nigriceps</i> sister	14	1	96	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
<i>A. kori/A. k. struthiunculus</i> sister	15	n/a	n/a	1	95	n/a	n/a			0.8		0.98	70	0.99	95	n/a	n/a
Clade Floricans	16	1	98	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
<i>Lophotis</i> monophyletic	17	1	100	1	100	n/a	n/a	1	100	0.76	78	1	100	1	100	n/a	n/a
Clade EA: <i>Eupodotis/Afrötis</i>	18					1	89								14		
<i>Lophotis gindiana/L. savilei</i> sister	19	0.91	98	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Clade Heterotetrao	20	0.84	84	1	100	n/a	n/a	No	No	0.96	79	0.96	69	0.99	73	n/a	n/a
<i>Afrötis</i> /Clade Blue <i>Eupodotis</i> sister	21	1	82	0.99	82	1	98	No	No			No	No	0.93	79	0.97	100
<i>Eupodotis rueppellii/E. vigorsii</i>	22	0.84	84	1	100	n/a	n/a	No	No	1	98	0.96	69	0.99	73	n/a	n/a
<i>Afrötis</i> monophyletic	23	1	99	1	100	n/a	n/a	1	99	1	81	1	98	1	100	n/a	n/a
Clade Blue <i>Eupodotis</i>	24	0.88	56	1	100	n/a	n/a	1	98	0.83	68	1	99	1	98	n/a	n/a
<i>E. barrowi/E. senegalensis</i> sister	25	n/a	n/a	n/a	n/a	n/a	n/a			1	96	0.94	79	0.98	95	n/a	n/a
<i>N. nuba</i> sister to <i>Ardeotis/Neotis</i>		0.92	80	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
All <i>Eupodotis</i> monophyletic						n/a	n/a	n/a	n/a								
<i>Neotis</i> monophyletic																n/a	n/a
Clade Larger bustards monophyletic								1	73	1		n/a	n/a	n/a	n/a		
Clade Floricans sister to <i>Lophotis</i>						n/a	n/a	n/a	n/a		n/a	n/a	n/a	n/a	n/a	n/a	n/a
Clade OC + Clade EA								1	99						13		
<i>Eupodotis rueppellii</i> sister to all																	

Table 2.5: Selected morphological and behavioural characters of species in the Otididae shown in relation to the major clades identified in this study.

Taxa	Clades identified in this study			Breeding strategy	Display	Size	SSD	Black underparts	Habitat	Mobility
	Clade	Subclade	Subclade							
<i>Otis tarda</i>	Clade Larger bustards	Clade OC		Polygyny	Balloon	Large	Extreme		Open	Migrant or nomad
<i>Chlamydotis undulata</i>	Clade Larger bustards	Clade OC		Polygyny	Other	Medium	Medium		Hyper-arid	Migrant or nomad
<i>Chlamydotis macqueenii</i>	Clade Larger bustards	Clade OC		Polygyny	Other	Medium	?		Hyper-arid	Migrant or nomad
<i>Tetrax tetrix</i>	Clade Larger bustards			Polygyny	Aerial	Small	Small		Open	Migrant or nomad
<i>Ardeotis arabs</i>	Clade Larger bustards	Clade AN		Polygyny	Balloon	Large	Very large		Arid	Migrant or nomad
<i>Ardeotis kori</i>	Clade Larger bustards	Clade AN		Polygyny	Balloon	Large	Very large		Arid	Migrant or nomad
<i>Ardeotis nigriceps</i>	Clade Larger bustards	Clade AN		Polygyny	Balloon	Large	Very large		Arid	Migrant or nomad
<i>Ardeotis australis</i>	Clade Larger bustards	Clade AN		Polygyny	Balloon	Large	Very large		Arid	Migrant or nomad
<i>Neotis ludwigii</i>	Clade Larger bustards	Clade AN		Polygyny	Balloon	Large	Large		Hyper-arid	Migrant or nomad
<i>Neotis denhami</i>	Clade Larger bustards	Clade AN		Polygyny	Balloon	Large	Very large		Open	Migrant or nomad
<i>Neotis heuglinii</i>	Clade Larger bustards	Clade AN		?	?	Large	Large		Hyper-arid	Migrant or nomad
<i>Neotis nuba</i>	Clade Larger bustards	Clade AN		?	?	Medium	Large		Hyper-arid	Migrant or nomad
<i>Lissotis melanogaster</i>	Clade Larger bustards	<i>Lissotis</i>		Polygyny	Aerial	Medium	Medium	Black underparts	Open woodlands	Resident
<i>Lissotis hartlaubii</i>	Clade Larger bustards	<i>Lissotis</i>		Polygyny	Aerial	Medium	Medium	Black underparts	Open woodlands	Resident
<i>Afrotis afra</i>	Clade Small bustards	Clade EA	<i>Afrotis</i>	Polygyny	Aerial	Small	Small	Black underparts	Arid	Resident
<i>Afrotis afraoides</i>	Clade Small bustards	Clade EA	<i>Afrotis</i>	Polygyny	Aerial	Small	Small	Black underparts	Arid	Resident
<i>Eupodotis senegalensis</i>	Clade Small bustards	Clade EA	Clade Blue Eupodotis	Monogamy	None	Small	Small		Open	Resident
<i>Eupodotis barrowii</i>	Clade Small bustards	Clade EA	Clade Blue Eupodotis	Monogamy	None	Small	Small		Open	Resident
<i>Eupodotis caerulescens</i>	Clade Small bustards	Clade EA	Clade Blue Eupodotis	Monogamy	None	Small	Small		Open	Resident
<i>Eupodotis vigorsii</i>	Clade Small bustards	Clade EA	Clade Heterotetra	Monogamy	None	Small	Small		Hyper-arid	Resident
<i>Eupodotis rueppellii</i>	Clade Small bustards	Clade EA	Clade Heterotetra	Monogamy	None	Small	Small		Hyper-arid	Resident
<i>Eupodotis humilis</i>	Clade Small bustards	Clade EA	Clade Heterotetra	Monogamy	None	Small	Small		Hyper-arid	Resident
<i>Lophotis savilei</i>	Clade Small bustards	<i>Lophotis</i>		Polygyny	?	Small	Small	Black underparts	Woodlands	Resident
<i>Lophotis gindiana</i>	Clade Small bustards	<i>Lophotis</i>		Polygyny	Aerial	Small	Small	Black underparts	Woodlands	Resident
<i>Lophotis ruficrista</i>	Clade Small bustards	<i>Lophotis</i>		Polygyny	Aerial	Small	Small	Black underparts	Woodlands	Resident
<i>Houbaropsis bengalensis</i>	Clade Small bustards	Clade Floricans		Polygyny	Aerial	Medium	Reversed	Black underparts	Open	Resident
<i>Sypheotides indica</i>	Clade Small bustards	Clade Floricans		Polygyny	Aerial	Small	Reversed	Black underparts	Open	Resident

Key to clade colours

Clade Larger bustards	Clade OC
Clade Larger bustards	Clade AN
Clade Smaller bustards	Clade EA <i>Afrotis</i>
Clade Smaller bustards	Clade EA Clade Blue Eupodotis
Clade Smaller bustards	Clade EA Clade Heterotetra
Clade Smaller bustards	<i>Lophotis</i>
Clade Smaller bustards	Clade Floricans

Characters are explained in Appendix 2.1.

Sexual Size Dimorphism (SSD) is detailed here:

1-5% larger small
 8-11% larger medium
 17-19% larger large
 20-23% larger very large
 29% larger extreme
 3-19% smaller reversed

CHAPTER 3

Phylogenetics of sandgrouse (Pteroclidae) inferred from morphological, behavioural and multilocus mitochondrial and nuclear DNA data

Abstract

The 16 species of sandgrouse (family Pteroclidae) are dove-like, ground-dwelling birds widely distributed across the arid areas of Africa, central Asia and southern Europe. Their camouflaged upperpart plumage contrasts with striking species-specific markings on the head and underparts of the males. To date, no morphological or molecular phylogeny has been undertaken to investigate the numerous generic treatments of this family or hypotheses of morphological and behavioural character evolution. To address these questions, a multi-faceted approach was used to evaluate the phylogenetics of the Pteroclidae. Morphological-behavioural characters were scored for all 16 species based on museum visits, field trips and published literature, and molecular data were obtained for 13 species representing at least one member of each proposed genus. The 41 phylogenetically-informative morphological-behavioural characters and 3326 bp of nucleotide data (one mitochondrial marker: ND2; four nuclear markers: Fib5, TGFB, GAPDH and ODC) were analysed separately and in combination using three methods of phylogenetic analysis with different optimality criteria: parsimony, Bayesian inference and maximum likelihood. Although there is a lack of basal resolution, and *Pterocles alchata* and *P. burchelli*

remain enigmatic, the combined and molecular analyses strongly support the recognition of three major clades: 1. **Clade Nyctiperdix** (*P. decoratus*, *P. bicinctus*, *P. quadricintus*, *P. lichtensteini* and *P. indicus*); 2. **Clade Short-tailed** (*P. personatus*, *P. coronatus* and *P. gutturalis*); and 3. **Clade Long-tailed** (*Syrrhaptes paradoxus* sister to *S. tibetanus*; *P. orientalis*; *P. namaqua* sister to *P. exustus*). The morphological-behavioural analyses result in a relatively poorly-resolved tree and only recover **Clade Nyctiperdix**; *P. namaqua* sister to *P. exustus*; and *S. paradoxus* sister to *S. tibetanus*. Plumage colouration characters are the most homoplasious, whereas structural characters of the wing and tail are more reliable indicators of relationship (although 14 tail feathers and long central tail feathers has evolved more than once). The dusk-drinking behavioural adaptation of **Clade Nyctiperdix** is highly conserved. Most of the proposed generic classifications are not monophyletic, including the current delimitation of *Pterocles*. Further samples are required to improve basal resolution and clarify the placement of *P. alchata* and *P. burchelli*.

Introduction

The sandgrouse (family Pteroclidae) form a small family of 16 species widely distributed across the arid areas of Africa, central Asia and southern Europe (Johnsgard, 1991; de Juana, 1997; Fig. 1.3 in Chapter 1). They are dove-like, ground-dwelling birds that feed almost exclusively on seeds. Their upperpart plumage makes them superbly camouflaged on desert substrata (the cryptic ground colours are enhanced by various upperpart patterns of barring, streaking and spotting), although the males also have striking species-specific plumage markings on their underparts and head that are used in display (which includes black and white banding on the

chest and forehead, prominent throat and cheek colours, contrasting underparts and also brightly-coloured naked skin around the eye). Sandgrouse show many morphological adaptations to their harsh environment and are most famous for the absorbent belly feathers of the males, which they soak in water for the chicks on daily commuting flights to water sources (de Juana, 1997).

The systematic position of Pteroclidae has been intensely debated, and they have been allied to the Galliformes, Columbiformes, Charadriiformes and even placed in their own order (see summaries in Sibley & Alquist, 1972, 1990; Fjeldså, 1976; Johnsgard, 1986; de Juana, 1997). The most comprehensive analysis of avian DNA to date (Hackett et al., 2008), places them as sister to the Columbiformes/ Mesitornithidae clade, with a bootstrap support of 66%.

The species-level taxonomy has been uncontroversial in recent years and all authors recognise 16 species (Maclean, 1986; Johnsgard, 1991; de Juana, 1997). The number of genera recognised is more controversial and ranges from two to four (see [Table 1.3](#) in Chapter 1), with a further seven subgenera proposed (Wolters, 1974). However, *Pterocles* and *Syrrhaptes* are the most commonly accepted genera since Elliot (1878).

All of the numerous assessments of the number of genera in the family ([Table 1.3](#)) are based only on morphological characters, and some authors place special emphasis on male plumage characters that are used in display (e.g. chest and forehead banding, throat colour and length of the central retrices), and which might well be riddled with homoplasy. None analyse the characters in any objective way.

The aims are to evaluate the following hypotheses, phrased as questions:

Generic level (see [Table 1.3](#)):

1. Is the genus *Pterocles* monophyletic and is *Syrrhaptes* derived from *Pterocles* (Maclean, 1984)?
2. Is the subgenus *Nyctiperdix* (Roberts, 1922; Maclean, 1986) including the species *lichtensteinii*, *bicinctus*, *indicus*, *quadricinctus*, monophyletic?
3. Should the species *lichtensteinii*, *bicinctus*, *indicus*, *quadricinctus* and *decoratus* be placed within the genus *Dilophilus*, based on their similar wing-shape and drinking habits (Bowen, 1927)?
4. Is the genus *Eremialector*, comprising the short-tailed *burchelli*, *lichtensteinii*, *bicinctus*, *indicus*, *quadricinctus*, *gutturalis*, *coronatus*, *personatus*, *decoratus*, *orientalis*, monophyletic (Sclater, 1924; Bowen, 1927)?
5. Is the genus *Pteroclurus*, proposed by Olgivie-Grant (1893) and supported by Maclean (1986), for the “pin-tailed” *senegallus*, *alchata*, *exustus* and *namaqua* monophyletic?
6. Are the four genera and seven subgenera proposed by Wolters (1974) monophyletic?

Species-level:

1. Are the species relationships proposed by Johnsgard (1991; [Fig. 3.1](#)) and Maclean (1984; [Fig. 3.2](#)) recovered?
2. Is *P. orientalis* the ancestral species (Maclean, 1984; [Fig. 3.2](#))?
3. Is *P. lichtensteinii* the most primitive member of *Nyctiperdix* (as proposed on the basis of its wide distribution; de Juana 1997)?
4. Are *indicus* and *quadricinctus* sister taxa (Maclean, 1986)?

5. What is the placement of enigmatic *gutturalis* and *burchelli*?
6. Do the black-faced species (*coronatus*, *decoratus* and *personatus*) form a monophyletic clade (Maclean, 1984; de Juana, 1997)?

Morphological character evolution:

1. Is the length of the central tail feathers a less reliable indicator of relationship than the number of retrices and shape of the tail (Bowen, 1927)?
2. What is the reliability of male plumage characters as indicators of relationships?
3. Are long central tail feathers and a black belly are ancestral characters (Maclean, 1984)?

Behavioural character evolution:

Is the timing of drinking in the species daily routine a useful taxonomic character (Bowen, 1927)?

A multi-faceted approach is used to evaluate the relationships among the Pteroclidae. Morphological, behavioural and multilocus molecular data were analysed using three methods of phylogenetic analysis with different optimality criteria (Holder and Lewis, 2003): parsimony (MP), Bayesian inference (BI) and Maximum Likelihood (ML), as used in recent hypotheses of avian phylogenies (e.g. Crowe et al., 2006; Fuchs et al., 2006; Voelker et al., 2007; Irestedt et al., 2008; Fuchs et al., 2008; Melo and Fuchs, 2008; Fuchs et al., 2009; Jønsson et al., 2010).

For the DNA analysis, sequences were obtained for one mitochondrial marker (NADH Dehydrogenase Subunit 2; ND2) and four nuclear markers: Beta-Fibrinogen

intron 5 (Fib5), Transforming Growth Factor Beta 2 intron 5 (TGFB), Glyceraldehyde-3-phosphate Dehydrogenase intron 11 (GAPDH) and Ornithine Decarboxylase introns 6 & 7 with the intervening exon 7 (ODC).

Material and methods

Taxon sampling

Samples for all 16 currently recognised species in the Pteroclidae were obtained for this study. The aim was to get at least two tissue samples from each species in the family. This is for the following reasons: 1. the second sample for each major taxon acts as check against labelling problems; 2. the use of tissue instead of blood reduces the chances of encountering nuclear pseudogenes ('numts', see below). However, this was not always possible as many of the tissues were not in existing collections and it was simply not possible to collect all species under permit (e.g. if the species concerned was of conservation concern, or occurred in an area where it is not safe to visit or collect). At least one sample was obtained for each species in the family, although four of these were specimen toepad-skin samples only, and three of those did not amplify under the protocols attempted below.

Tissues were obtained from the following sources: 1. fresh samples of either tissue or blood (stored in either 95% ethanol, or Dimethyl sulfoxide (DMSO) or Ethylene diaminetetraacetic acid (EDTA) solutions respectively) were obtained from museum tissue archives; 2. blood samples, stored in EDTA, were obtained from captive birds zoological gardens or private collections; 3. fresh tissue or blood samples (stored in

either 95% ethanol, or DMSO or EDTA respectively) were obtained from specimens either collected or captured in the field under permit on field trips; 4. samples were taken, with permission, from the toepad-skin of museum specimens. Full details of all the samples analysed in this study are in [Table 3.1](#) and fully acknowledged in the Acknowledgements. In contrast with the Otididae (see Chapter 2), no sequence data were obtained for the toepad samples, despite attempting the protocol described below at UC Berkeley, and so samples that were not amplified are not listed in [Table 3.1](#).

Outgroup selection

Two genera of columbiforms, *Columba* and *Scardafella* (*C. livia*, *C. leucocephala*, *S. squamata*) were used as outgroups, based on the findings of Hackett et al. (2008), although it should be noted that there is no known strongly-supported sister taxon of the Pteroclidae. *Columba leucocephala* is sometimes placed in the allied genus *Patagioenas* (Gill and Wright, 2006).

Morphological-behavioural character matrix

A matrix of 41 morphological and behavioural characters was prepared that included all species of the Pteroclidae. Morphological characters included plumage of breeding males, as has been done in previous treatments (see [Table 3.1](#)), but also used plumage characters of females, bare part colouration, and structural characters such as the shape of the wing and tail. All characters are described in [Appendix 3.1](#), and the character states for each species are presented in [Appendix 3.2](#). Characters that were only applicable to a single species were not included in the matrix. Multi-state characters were treated as unordered.

Morphological characters were assigned to species on the basis of four main sources of information: 1. photographs and notes taken from specimens in museum collections (including the American Museum of Natural History (New York, USA), the British Natural History Museum (Tring, UK), the Royal Museum for Central Africa (Tervuren, Belgium), the South African Museum (Ornithology) in Cape Town, the Durban Natural Science Museum, the MacGregor Museum (Kimberley) and the National Museums of Kenya (Ornithology) in Nairobi); 2. published sources of information used to score the species included Bowen (1927); Maclean, (1984, 1986); Johnsgard (1991) and de Juana (1997); 3. a database of photographs individually sourced from the internet from birding field trip reports; 4. photographs taken personally during the field trips. Selected errata encountered in the literature are described in [Appendix 3.3](#).

Molecular markers

Mitochondrial DNA (mtDNA) and nuclear DNA markers were chosen to provide independent estimates of phylogeny (Moore 1995; Armstrong et al., 2001). The following markers were amplified:

One mitochondrial marker:

NADH Dehydrogenase Subunit 2 (ND2)

Four nuclear markers:

Beta-Fibrinogen intron 5 (Fib5)

Transforming Growth Factor, Beta 2 intron 5 (TGFB)

Glyceraldehyde-3-phosphate Dehydrogenase (G3PDH) intron 11 (GAPDH)

Ornithine Decarboxylase introns 6 & 7 with the intervening exon 7 (ODC)

The nuclear introns are found on the following chromosomes in the chicken genome:

Chromosome 1: GAPDH; Chromosome 3: TGFB, ODC; Chromosome 4: Fib5 (Fuchs et al., 2009). All Pteroclidae were sequenced for this study, and outgroup sequences were downloaded from Genbank ([Table 3.1](#)).

DNA extraction, PCR and sequencing

Total genomic DNA was extracted from blood, pectoral muscle, heart or liver tissue using one of two methods: 1. Quiagen DNeasy animal tissue protocol provided with the DNeasy® tissue kit (Qiagen, Valencia, California); 2. a Cetyl Trimethyl Ammonium Bromide-based protocol (Winneppenninckx et al., 1993) with an overnight Proteinase-K digestion.

Double-stranded DNA templates for the mitochondrial and nuclear loci were amplified by polymerase chain reaction (PCR). Typically 12 μ l reactions with 1-3.5 μ l of genomic DNA added were employed. The PCR reactions contained the following: 1.5 mM PCR buffer, 3.0 mM MgCl₂, 0.8mM Bovine serum albumin (BSA), 0.25mM of each dNTP, 0.2mM of each primer (but 0.15 for GAPDH and Fib5), and 0.15 units of Taq (Roche). All sets of PCR reactions included a negative control to which no DNA was added. Primers used for amplification and sequencing are detailed in [Table 3.2](#).

PCR was mostly performed on a Bio-Rad iCycler (Bio-Rad, Hercules, California) with the following conditions: a hotstart at 94°C for 5 min, an initial denaturation at 94°C for 2 min, followed by 35 cycles of denaturation at 94°C for 30 s, annealing at 53-60 °C (cytb and ND2 at 53°C, Fib5 at 54°C, TGFB and OCD at 58°C, GAPDH 60°C) for 30 s, and extension at 72°C for 80 s (except GAPDH at 60 s), with a final extension at 72°C for 10 min. PCR products were visualized (to confirm amplification and fragment sizes) by electrophoresing them on a 1.5% agarose gel stained with ethidium bromide under UV light.

Amplified products were cleaned using a standard Exonuclease I and Shrimp Alkaline Phosphatase (Exo/SAP) protocol and then cycle-sequenced using Big Dye terminator chemistry (version 3.1, ABI, Applied Biosystems). Products were sequenced in both directions, with the primers described in [Table 3.2](#), except that G3P13 was replaced with G3PintL1 (see Fjeldså et al., 2003). Sequencing products were cleaned using Sephadex columns and run on an AB3100 DNA analyzer.

Laboratory procedure for museum toepad-skin samples

Toepad-skin samples taken from museum specimens were often over 60 years old and so the DNA was expected to be highly degraded. Because of this, the regular primers were not able to amplify the specific loci and taxon-specific GAPDH primers were designed ([Table 3.2](#)). In addition, AmpliTaq Gold (Applied Biosystems) was used when preparing the PCR reactions for the toepads (Nyabo et al., 2008). Contamination from outside sources poses a much higher risk due to the small amounts of DNA remaining in the degraded samples and special precautions were taken. Toepad-skin extractions and PCR reaction preparation was performed in a

custom-prepared laboratory that was used exclusively for this process with the many precautions described by Willerslev and Cooper (2005) and Lovette and Rubenstein (2007) to reduce the chance of contamination. Toepad extractions were attempted from *S. tibetanus*, *P. coronatus*, *P. senegallus* and *P. indicus*, but were only successful for the latter taxon.

Assembly and alignment of sequences

Sequences were assembled using Sequencer v4.7 (Gene Codes Corp., Ann Arbor, Michigan, USA). Mitochondrial sequences were aligned to the chicken (*Gallus gallus*) (Desjardins and Morais, 1990) and checked for any insertions or deletions. Mitochondrial sequences were also translated into amino acids and checked for the presence of stop codons, as well as for frame shifts that might indicate the amplification of nuclear copies of mitochondrial genes or ‘numts’ (Quinn, 1997; Sorenson and Quinn, 1998).

Sequence alignments were adjusted readily by eye after an initial automatic alignment in Sequencer. Nuclear sequences were checked carefully for the presence of heterozygous sites as represented by isolated double peaks (single nucleotide polymorphisms) and these were coded using the standard IUPAC codes. The final concatenated alignment, with partitions, is presented as [Appendix 3.4](#).

Base composition

The base composition of gene regions has been shown to affect the outcome of phylogenetic analyses (Collins et al., 1994), and so the significance of these

differences was tested for each gene region in PAUP* using a χ^2 (chi-squared) test (Swofford, 2002).

Phylogenetic analyses and statistical tests

Three methods of phylogenetic analysis with different optimality criteria were employed to create estimates of phylogeny: parsimony (MP), Bayesian inference (BI) and Maximum Likelihood (ML). Each gene region was first analysed individually using BI and ML. To assess the congruence between trees before combining the data, each tree was assessed visually for conflicting branches that had a high level of support. Branches were considered to be highly supported if they had bootstrap values of >70% (Hillis and Bull, 1993) or posterior probabilities of > 0.95 (Ronquist and Huelsenbeck, 2003).

For the final analyses, concatenated alignments were prepared using the samples described in [Table 3.1](#) in the following partitions which were analysed as follows: 1. all morphological-behavioural data and DNA (MP only), 2. all DNA combined (MP, BI, ML), 3. all mtDNA combined (MP, BI, ML), and 4. all nuclear DNA combined (MP, BI, ML). To save on computing time, only one exemplar for each gene region for each species was chosen for the concatenated alignments, which sometimes included loci from different individuals of the same species ([Table 3.1](#)). Where more than one exemplar of a gene region per species was available, all of these exemplars were analysed in a separate analysis (for each gene region) to check if the species were reciprocally monophyletic and to reduce any potential error from sample mix-ups. Samples from well-marked subspecies were always treated as separate Operational Taxonomic Units in analyses.

Parsimony-based phylogenetic analyses were conducted using both TNT (Tree analysis using New Technology) (Goloboff et al., 2008a, b) and PAUP*. In TNT, the searching strategy employed was the “new technology 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 character data was determined by using the ‘jackknife’ resampling strategy using: 1000 replications, branch-swapping switched on, five random additions of taxa per replicate, deletion of 36% of characters per jackknife replicate (Farris et al., 1996; Källersjö et al., 1998). In PAUP* 4.0b10 (Swofford, 2002), parsimony analyses were conducted with a heuristic searches with 1000 random addition replicates and tree bisection reconnection branch-swapping. All characters were given equal weight and treated as unordered. Clade support was assessed by 500 non-parametric bootstrap replicates (Felsenstein, 1985a).

Because gene regions can evolve under different models of evolution, it has been argued that a partitioned, mixed-model approach should be used when concatenating these different datasets (Ronquist and Huelsenbeck, 2003; Nylander et al., 2004). It is now possible to perform these analyses for BI and ML.

Mixed-model Bayesian analyses were undertaken in Mr Bayes v3.1.2 (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003). Substitution models for each locus were determined in PAUP* with MrModelTest 2.0 (Nylander, 2004) and Modeltest 3.06 (Posada and Crandall, 1998), using the Akaike Information Criterion (Akaike, 1973; Posada and Buckley, 2004) and are presented in [Table 3.3](#). Mixed-

model analyses allowed different parameters (base frequencies, rate matrix or transition/transversion ratio, shape parameter, proportion of invariable sites) to vary (using the *unlink* and *prset* commands) between the partitions (gene regions and codon positions) (Nylander et al., 2004; Johansson et al., 2008; Fuchs et al., 2009).

Four Metropolis-coupled MCMC chains (one cold and three heated) were run for 5 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 were estimated from the remaining generations. An attempt was made to run each Bayesian analysis 2-3 times (random, independent runs), but this was not always possible due to the computing time required. The log-likelihood values and posterior probabilities were checked to confirm that the chains had reached stationarity. It was also checked that the Potential Scale Reduction Factor approached 1.0 (for all parameters) and that the average deviation of split frequencies converged towards zero (Fuchs et al., 2009). The program Tracer v1.4.1 (Rambaut and Drummond, 2007) was used for parameter estimates.

Mixed-model Maximum Likelihood analyses were performed using Randomised Axelerated Maximum Likelihood for High Performance Computing (RAxML) v7.0.4 (Stamatakis, 2006; Stamatakis et al., 2008), a programme that has been used in recent avian phylogeny analyses (e.g. Johansson et al., 2008; Fuchs et al., 2009; Parra et al., 2009). Mixed-model RAxML analyses use 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 a single data partition); a mixed-model analysis on the nuclear DNA genes, partitioned by each of the four gene regions, and a mixed-model analysis of mt and nuclear DNA combined. Branch support was assessed with 100 non-parametric bootstrap replicates.

Morphological-behavioural character evolution

The evolution of morphological characters and behaviour was assessed by mapping these characters onto the total evidence tree ([Fig. 3.10](#)), as well as into a table with the major clades identified ([Table 3.5](#)).

Results

Species included

Morphological-behavioural data were collected from all 16 species of Pteroclidae. DNA extractions were successful for 13 species representing members of all genera (*P. coronatus*, *P. senegallus* and *S. tibetanus* were not successful). The full details of all species included in the study are presented in [Table 3.1](#).

Base composition

Base composition varied slightly between each locus ([Table 3.3](#)), with the mitochondrial DNA showing the typical deficiency of Guanine and Thymine relative to Adenine and Cytosine (e.g. Kirchman et al., 2004; Price and Lanyon, 2002). The χ^2 test implemented in PAUP* detected no significant base composition biases (see [Table 3.3](#) for p-values).

Sequence variation and characteristics

The complete ND2 sequences (1041 bp) were obtained from 20 individuals of 12 species. It is highly unlikely that any of the mitochondrial sequences were nuclear pseudogenes (Sorenson and Quinn, 1998) because all chromatograms were of good quality and did not contain double-peaks, and all sequences translated into functional amino acids without the presence of internal stop codons. The lengths of the preferred alignments of the nuclear introns are as follows: Fib5, 590 bp; GAPDH, 389 bp; TGFB, 597 bp; ODC, 709 bp. As expected, the nuclear markers were far less variable than the mitochondrial markers (see [Table 3.3](#)). The final DNA concatenated alignment was 3326 bp (1041 bp mtDNA and 2285 bp nuclear DNA) with 559 parsimony informative characters ([Table 3.3](#)).

Evaluation of congruence between the genes

There were no significant branches in conflict for the different gene regions (see [Table 3.4](#) for support values of the major branches recovered in the analyses), and so the data were combined into a large concatenated analysis. The 41 morphological-behavioural characters ([Appendix 3.2](#)) were all phylogenetically informative, bringing the total dataset to 3367 characters.

Phylogenetic inference

Combined morphological-behavioural and DNA datasets

The parsimony analysis of the combined morphological-behavioural (41 characters) and DNA dataset (3326 bp) resulted in one tree with a length of 1950 ([Fig. 3.3](#)). Three well-supported, major clades were recovered, which were consistently recovered in

many of the individual gene analyses ([Table 3.4](#)). These clades are represented on the tree by nodes 1, 8, and 11 respectively and the node support values are presented in [Table 3.4](#). Clade 1 (hereafter known as **Clade Nyctiperdix**) comprises *P. decoratus*, *P. bicinctus*, *P. quadricinctus*, *P. lichtensteini* and *P. indicus*. Clade 8 (hereafter known as **Clade Short-tailed**) comprises *P. personatus*, *P. coronatus* and *P. gutturalis*. Clade 11 (hereafter known as **Clade Long-tailed**) comprises *S. paradoxus*, *S. tibetanus* and *P. orientalis*, and *P. namaqua* and *P. exustus*.

In **Clade Nyctiperdix**, *P. decoratus* is sister to the others (jackknife = 97), which comprise *P. indicus* and *P. lichtensteini* as sisters, with *P. quadricinctus* as sister to them, and *P. bicinctus* sister to this group. **Clade Short-tailed** is not well-supported, although *P. personatus* and *P. coronatus* are given as sisters. **Clade Long-tailed** is comprised of two well-supported clades, **Clade 12** with the two *Syrrhaptes* sister to *P. orientalis*, and **Clade 14** with *P. namaqua* sister to *P. exustus*. *Pterocles senegallus* is sister to Clade 11 while *P. alchata* and *P. burchelli* are weakly supported sisters at the base of the clade that comprises **Clades Short-tailed** and **Long-tailed**.

Morphological-behavioural dataset

The parsimony analysis of the morphological-behavioural dataset resulted in three equally-parsimonious trees and the consensus tree (length = 102) is presented as [Fig. 3.4](#). Only one of the major clades of the combined analysis is recovered, **Clade Nyctiperdix**, which is well-supported (jackknife = 87). *P. decoratus* is again sister to the others, which are linked in a polytomy. **Clade Long-tailed** is not recovered, but its constituent **Clade 14** is supported, while **Clade 12** is not supported, although the two *Syrrhaptes* are recovered as sister (jackknife = 91). *P. orientalis* is sister to *P.*

alchata, with *P. burchelli* now in a basal position to all sandgrouse. **Clade Short-tailed** is not recovered.

Combined DNA datasets

The parsimony (MP; one tree, length = 1840), Bayesian (BI) and Maximum Likelihood (ML) analyses of the combined nuclear and mitochondrial DNA characters also recover the same three major clades (**Nyctiperdix**, **Long-tailed**, **Short-tailed**) as the combined analysis, and also do not provide any deeper level support for the relationships among these clades (Fig. 3.5). **Clade Nyctiperdix** is well supported (PP 1; BS 100; MP: JK 81, BS 89), with the same pattern of internal relationships as the combined morphological-behavioural and DNA dataset. **Clade Short-tailed** is well-supported (PP 1; BS 100; MP: JK 100, BS 100), although *P. coronatus* was not included in the analysis. **Clade Long-tailed** is recovered with high support (PP 1; BS 99; MP: JK 83, BS 85) as are **Clades 12** and **14** (see Fig. 3.5 and Table 3.4). The position of *P. alchata* and *P. burchelli* is not well-supported.

Mitochondrial DNA dataset

All the methods of analysis resulted in the same major relationships as Fig. 3.5, although reduced taxon sampling makes it less informative than the combined DNA tree (Fig. 3.6). **Clade Nyctiperdix** is retrieved, to the exclusion of *P. decoratus*; **Clade Short-tailed** is well-supported; and **Clade Long-tailed** is not well-supported although **Clade 14** is highly supported. The model-based analyses also support a weak sister-relationship between *P. alchata* and *P. burchelli*. Some deeper support is evident, with **Clade Nyctiperdix** as sister to the rest of the family. The Maximum Likelihood analysis was performed both with and without data partitions. An

interesting difference between these two analyses is that the partitioned one seems to give higher terminal support but lower deep node support. The latter analysis recovers the same clades as the Bayesian analysis, which are collapsed in the partitioned analysis.

Nuclear DNA dataset

The combined nuclear dataset analyses (Fig. 3.7) resulted in very high levels of support for the **Clades Nyctiperdix, Short-tailed** and **Long-tailed**, with the same internal relationships as for the combined morphological-behavioural and DNA dataset.

Nuclear Fib5 and TGFB individual datasets

These datasets have reduced taxon sampling but, nonetheless, many common patterns are recovered (Figs 3.8 and 3.9). In particular, **Clade 2 (Clade Nyctiperdix less *P. decoratus*)** and **Clade Long-tailed** (as well as **Clades 12 and 14**) are well-supported. The individual analyses for GAPDH and ODC were not performed owing to a problem with the outgroup samples.

Discussion

Systematics

Determining the relationships among the Pteroclidae with morphological characters alone does not produce a clear result (Snow, 1978; Maclean, 1984; Maclean and Fry, 1986) and has resulted in debate as to which characters are important for classification (Bowen, 1927; Maclean, 1984, 1986). The number of generic treatments of the family since 1878 attests to this (see [Table 1.3](#)). The taxonomy has relied largely on male characteristics that are important in display (Elliot, 1878; Hüe and Etchécopar, 1957; Maclean, 1984; Johnsgard, 1991) and hence are likely to be subject to strong sexual selection that may obscure species relationships.

By performing a cladistic analysis of all the morphological/behavioural characters, the resulting set of relationships should not be influenced by the preference of the researcher. Nonetheless, the cladistic analysis of the morphological-behavioural dataset ([Fig. 3.4](#)) recovered a relatively poorly-resolved tree (the strong influence of natural and sexual selection is likely to result in convergence) with strong support for only two clades (**Clades Nyctiperdix** and **13**). **Clade Nyctiperdix** shares a number of plumage, structure and behavioural characters ([Appendix 3.2](#)), which are discussed below in more detail. The synapomorphies shown by **Clade 13** (*Syrrhaptes*) are likely adaptations to the extreme cold of their mountain deserts. The complete feathering on the legs and feet is for extra insulation, while the fused front toes and lack of a hallux would decrease surface area in contact with the cold substratum.

Total evidence: Although the morphological data by themselves did not produce a fully resolved tree, when combined with the mitochondrial and nuclear DNA data, the resulting tree shows higher branch support for many clades ([Table 3.4](#)), a similar situation to what has been noted in Galliformes (Crowe et al., 2006).

The *first major clade* that is consistently recovered with a high level of support ([Table 3.4](#)) in the analyses is **Clade Nyctiperdix** ([Figs 3.3 – 3.5](#)), comprising *P. decoratus*, *P. bicinctus*, *P. quadricinctus*, *P. lichtensteinii* and *P. indicus*. This group, sometimes with the exclusion of *P. decoratus* (i.e. **Clade 2** of [Fig. 3.3](#)), has been recognised by previous authors. Bowen (1927) suggested that they be allied in the separate genus *Dilophilus*, Maclean (1984) grouped them as his “Group 5”, and again in 1986 linked them in the subgenus *Nyctiperdix* after Roberts (1922) who initially proposed this name. *Pterocles decoratus* has sometimes been excluded from this group because of its black face (Maclean, 1984). Within **Clade Nyctiperdix**, the internal relationships this should be treated as tentative due to the incomplete molecular data available for half the members of this clade. *P. lichtensteinii* is recovered as the sister to *P. indicus* in all the analyses (although only supported by a single base pair), contrary to the assertion by Maclean and Fry (1986) that *P. quadricinctus* and *P. indicus* form a superspecies, and the shared morphological feature of a white central breast band, bordered both above and below by a white band. Also, there is a high level of support that *P. lichtensteinii* is not the ancestral species, as suggested by Maclean (1984) and de Juana (1997) on the basis of its wide distribution. The taxa *P. lichtensteinii*, *P. bicinctus* and *P. indicus* were previously considered conspecific (de Juana 1997), but this would not be a monophyletic group unless *P. quadricinctus* were included.

Clade Nyctiperdix is supported by a suite of morphological characters, including the barred abdomen, prominent chest and forehead banding of the males, and highly cryptic barred plumage of the females. Perhaps more importantly, clade members also share a number of structural differences in the wing and tail shape (Fig. 3.10, Table 3.5, Appendix 3.2). They also share a striking behavioural characteristic. Whereas all the other sandgrouse drink mainly in the early morning (with some occasionally drinking in the late afternoon too), all the members of **Clade Nyctiperdix** drink exclusively after sunset (Table 3.5; Fig 3.10). This seems highly conserved and could be an important adaptation not only to the high day-time temperatures, but also to a reduced predation risk from diurnal predators, such as large falcons (e.g. Lanner Falcon *Falco biarmicus* is an important sandgrouse predator; de Juana, 1997; Lloyd, 2005), during their water commuting flights. The members of this clade also occur in more densely bushed or wooded habitats avoided by all other sandgrouse, and feed in pairs or small groups, only gathering in large numbers after sunset when they drink, but not during the day when feeding like other sandgrouse (Johnsgard, 1991; de Juana, 1997).

The *second major clade* that is well supported is **Clade Short-tailed** comprising *P. gutturalis*, *P. personatus* and *P. coronatus* (the latter with morphological evidence only), a combination that has never before been considered in the literature. Although these three species have a morning drinking peak, they also regularly drink in the late afternoon (Maclean, 1986; Johnsgard, 1991; Morris and Hawkins, 1998; Lloyd, 2005), a feature that is very rare in the remaining sandgrouse, but which is also recorded for *P. namaqua* (Lloyd, 2005; Fig. 3.10). This further suggests that drinking behaviour is phylogenetically informative. This group was not recovered by the

morphological-behavioural analysis, although these three stout-bodied, short-tailed species do have black in the face of the males, which extends both above and below the bill in *P. coronatus* and *P. personatus*. The very high level of support (Table 3.4) for the sister relationship between *P. gutturalis* and *P. personatus* clarifies the relationship of *P. gutturalis* which was previously thought of as highly enigmatic morphologically (Maclean, 1984; Johnsgard, 1991). No sample of *P. coronatus* could be amplified for genetic analysis, so the relationships between these species within **Clade Short-tailed** could not be confirmed. Johnsgard (1991) suggests that the black-faced species, *P. coronatus* and *P. personatus* are related, but also includes *P. decoratus* (also black-faced above and below the bill) as the sister of *P. personatus*, which this study places in **Clade Nyctiperdix** with strong support (Table 3.4).

The *third well-supported major clade* is **Clade Long-tailed** (Figs 3.3 and 3.4), comprising *S. paradoxus*, *S. tibetanus* and *P. orientalis*, a group sister to *P. namaqua* and *P. exustus*, is a novel set of relationships. **Clade 13**, both members of *Syrrhaptes*, have long been recognised as being allied and have traditionally been uncontroversially placed in a separate genus (Johnsgard, 1991; de Juana, 1997). The only other time that *P. orientalis* has been suggested as closely related to *Syrrhaptes* is its placement, together with *P. gutturalis*, in the subgenus *Eremialector* of *Syrrhaptes* by Wolters (1974) (Table 1.3). However, there are a number of morphological features (in the male, orange throat, grey crown, grey breast, narrow chest band, and in both male and female, dark belly) that link *S. paradoxus* and *P. orientalis*. Despite this, *Syrrhaptes* and *P. orientalis* are not recovered as sister in the morphological-behavioural analysis (despite being strongly supported in the DNA data partitions, Table 3.4).

Clade 14, with *P. namaqua* sister to *P. exustus*, has been suggested by Johnsgard (1991). Indeed, Wolters (1974) placed them in the subgenus *Namapterocles* and Maclean (1984) links these two species in his “Group 1”. Although he also included *P. alchata* and *P. senegallus* in this group, these two species could not be placed with any confidence in any of the data partitions. These latter four “pin-tailed” species were placed in the genus *Pteroclurus* by Olgivie-Grant (1893), although it seems unlikely that they are monophyletic as this is not recovered in any of the data partitions.

The most comprehensive hypotheses of the relationships among the Pteroclidae are those proposed by Wolters (1974; through his use of subgenera), Maclean (1984; through the use of a flow chart, [Fig. 3.2](#)), and Johnsgard (1991; with a hand-drawn tree, modified into [Fig. 3.1](#)). It is possible now to critically evaluate these not only with the morphological data analysed in an objective way, but also with the additional molecular data.

Wolters’ (1974) four genera and seven subgenera ([Table 1.3](#)), some of which are described above, are largely not monophyletic, although his greatest insight was perhaps the link between *P. orientalis* and *Syrrhaptes*. Maclean’s (1984) flow chart of evolutionary trends is enticingly detailed and is complete with a description of the character state changes ([Fig. 3.2](#)). His position that *P. orientalis* was the ancestral taxon to all other sandgrouse is not supported by data presented here. His seven subgroups among the Pteroclidae ([Table 1.3](#)) are comprised of three single-species groups of unsure affinities (*P. orientalis*, *P. gutturalis*, *P. burchelli*) and of the

remaining four groups, just two are monophyletic: **Clade 13** of this analysis, and *Syrrhaptes*. The phylogeny proposed by Johnsgard (1991) is also detailed ([Fig. 3.1](#)). There is little support for the placement of *Syrrhaptes* at the base of the sandgrouse tree (Johnsgard, 1991), but Maclean's (1984) suggestion that *Syrrhaptes* is derived from *Pterocles* is supported. Johnsgard does link *P. orientalis* to **Clade 14**, but also includes the other two “pin-tailed” species here (*P. alchata*, *P. senegallus*). He does link **Clade 13** together, but includes *P. decoratus* with *P. personatus*, in turn linked to *P. coronatus* (*P. gutturalis* and *P. burchelli* are again the enigmas).

The genus *Eremialector* (Sclater, 1922; see [Table 1.3](#)), comprising the short-tailed *burchelli*, *lichtensteinii*, *bicinctus*, *indicus*, *quadricinctus*, *gutturalis*, *coronatus*, *personatus*, *decoratus* and *orientalis* is comprised of members of both **Clade 12** and **Clade Short-tailed** and is unlikely to be monophyletic, even though the resolution of the trees presented in [Figs 3.3 - 3.9](#) does not allow determination of the relationship between the major clades with confidence.

Morphological character evolution

The usefulness of particular morphological characters for assessing systematic relationships among the Pteroclidae has been proposed by different taxonomists, although there is rarely agreement on exactly which characters are the most important (discussed above). The interpretation of the character states changes in [Table 3.5](#) and [Fig. 3.10](#) is complicated somewhat by the uncertainty of the relationship between **Clades Nyctiperdix** and **Clade Long-tailed**. Many characters do seem restricted to either **Clade Long-tailed**, **Clade Short-tailed**, both **Clades Short-tailed** and **Long-tailed**, or **Clade Nyctiperdix**. This is especially true of the patterns of black on the

face of the males, the pattern on the tail, and the shape of the tail and wing. The shape of the tail and wing, such as the presence of a long tenth primary and wedge-shaped tail, occurs in all species except **Clade Nyctiperdix** and *P. burchelli* ([Fig. 3.10, Table 3.5](#)). The colouration of the bare parts, upperpart patterning, and underpart banding and colouration seems especially plagued by homoplasious characters. The homoplasious nature of the upperpart colour is to be expected, as the upperparts are highly camouflaged and thus under selection pressure. For example, *P. burchelli* has a uniquely orange ground colour that closely resembles the Kalahari sand substratum to which it is restricted.

Bowen (1927) suggested that the length of the central tail feathers is a less reliable indicator of relationships than the number of retrices and the shape of the tail, although DNA data partitions indicate that these are both relatively reliable indicators of the clades. It appears as if elongated central retrices might have evolved only once (if *P. senegallus* is sister to **Clade Long-tailed** as suggested in [Fig. 3.3](#)) whereas it is less clear if a tail with 14 retrices has evolved once or twice (see [Fig. 3.10, Table 3.5](#)), depending on the placement of *P. burchelli*. These characters are displayed during tail fanning, and in frontal displays (Johnsgard, 1991). Unfortunately, little is known about the displays of sandgrouse (de Juana, 1997) and further research is required to clarify matters. For example, *P. alchata* has been reported to display aerially, and further research is required to determine if this occurs in other species. *Pterocles alchata* has other unique features too: the males and females are both brightly coloured, and the male has a distinct non-breeding plumage (Johnsgard, 1991). Maclean's (1984) idea that the long central tail feathers and black belly are ancestral characters cannot be tested due to a lack of resolution at the bases of the trees.

Unresolved relationships

While results presented here support the recognition of three major clades within the Pteroclidae, they have a few weaknesses. The first is that the placements of *P. alchata* and *P. burchelli* are not well-supported in any of the analyses (but see Fig. 3.7 for *P. burchelli* at the base of **Clades Long-tailed** and **Short-tailed** combined) although it seems highly unlikely that they form part of **Clade Nyctiperdix**). It certainly is tempting to agree with Maclean's (1984) placement of *P. alchata* on the basis of its wing and tail shape (see above). Perhaps the enigmatic *burchelli* does deserve the monotypic genus *Calopterocles* suggested by Roberts (1922)? The differing placement of these two morphological enigmas create uncertainty in the deeper level nodes and thus it is not at present possible to elucidate the ancestral grouping and character states. It is possible that the addition of extra sequence data might clarify their position, but given the strength with which the other clades are recovered, it seems more likely that a rapid radiation early in the history of the sandgrouse has left the relationships among **Clades Nyctiperdix**, **Short-tailed**, **Long-tailed** and the enigmatic *P. alchata* and *P. burchelli* tricky to discern.

Table 3.1: Samples analysed in this study, with sample source, collection locality, and extraction codes.

The components of the concatenated data sets are detailed, and samples in bold were used in the concatenated genetic analyses.

For each gene region, either the extraction codes (CC = Callan Cohen; ABS = Anna Seles) or Genbank numbers are given.

PFIAO = Percy FitzPatrick Institute of African Ornithology; AMNH = American Museum of Natural History; FMNH = Field Museum, Chicago

Taxon	Source of genetic sample (with label annotations)	Genetic sample locality	Morpho- behav. data	MtDNA ND2	Nuclear DNA Fib5	GAPDH	TGFB	ODC
<i>Syrrhaptes tibetanus</i>			Yes					
<i>Syrrhaptes paradoxus</i>	Callan Cohen (Female, RK Number 3) Callan Cohen (Female, RK Number 3) Callan Cohen (Female, RK Number 36)	Unknown	Yes	CCB74	CCB74	CCB74	CCB74	CCB74
<i>Pterocles alchata</i>	CONCATENATED from the two samples below Callan Cohen (Africa male, RK Number 26) Callan Cohen (Dubai male, RK Number 24)	Unknown	Yes	CCB65	CCB65	CCB65	CCB65	CCB64
<i>Pterocles namaqua</i>	PFIAO (Langberg, South Africa, 13Aug91, No. 2) PFIAO (Langberg, South Africa, 13Aug91, No. 2) PFIAO (Langberg, South Africa, 13Aug91, No. 3)	South Africa	Yes	CCB68	CCB68	CCB68	CCB68	CCB68
<i>Pterocles exustus</i>	Callan Cohen (KEN9933, Shaba, Kenya, Sept99) Callan Cohen (KEN9933, Shaba, Kenya, Sept99) PFIAO (Koya, Kenya, 16June05)	Kenya	Yes	CCB62	CCB62	CCB62	CCB62	CCB62
<i>Pterocles senegallus</i>			Yes					
<i>Pterocles orientalis</i>	Callan Cohen (RK, male, Number 35) Callan Cohen (RK, female, Number 33) Callan Cohen (RK, male, Number 35)	Unknown	Yes	CCB78	CCB78	CCB78	CCB78	CCB78
<i>Pterocles gutturalis</i>			Yes					
<i>Pterocles coronatus</i>			Yes					
<i>Pterocles decoratus</i>	Callan Cohen (KEN9959, heart tissue) Callan Cohen (KEN9959, heart tissue) PFIAO (Kenya, 18June05, Koya)	Kenya	Yes	CCB72	CCB72	CCB72	CCB72	CCB72
<i>Pterocles personatus</i>	FMNH438527 FMNH438527 FMNH438530	Madagascar	Yes	ABS571	ABS571	ABS571	ABS571	ABS571
<i>Pterocles lichtensteinii</i>	CONCATENATED from the two samples below Callan Cohen (Africa, male, RK, Number 26) PFIAO (Kenya, Koya, 19June05, Indiv B)	Kenya	Yes	CCB79	CCB80	CCB79	CCB79	CCB79
<i>Pterocles indicus</i>	AMNH63466 (subsp. <i>fasciatus</i>)	India	Yes			CCB94		
<i>Pterocles quadricinctus</i>	Callan Cohen (Mora, Cameroon, March2004, roadkill)	Cameroon	Yes			CCB91	CCB91	CCB91
<i>Pterocles bicinctus</i>	CONCATENATED from the two samples below PFIAO (Langberg, South Africa, Aug91, F1-1, No. 2) PFIAO (Langberg, South Africa, Aug91, F1-1, No. 3)	South Africa	Yes	CCB66	CCB67	CCB67	CCB67	CCB66
<i>Pterocles burchelli</i>	CONCATENATED from the two samples below PFIAO (Langberg, South Africa, 13Aug91, F1-1, No. 2) PFIAO (Langberg, South Africa, 13Aug91, F1-1, No. 1)	South Africa	Yes	CCB70	CCB70	CCB71	CCB70	CCB70
<i>Columba/Scardafella</i>	CONCATENATED from the three samples below		Yes	AY274070	EU739236		EU737359	DQ881727
<i>Columba leucocephala</i>				AY274070				
<i>Columba livia</i>					EU739236		EU737359	
<i>Scardafella squammata</i>								DQ881727

Table 3.2: Primers used for amplification and sequencing of the Pteroclidae.

Gene Region	Primer Name	Primer Sequence	Source
ND2	L5204	5'-GCTAACAAAGCTATCGGGCCCAT-3'	Cicero and Johnson, 2001
	H6312	5'-CTTATTAAAGGCTTGAAAGGCC-3'	
Fib5	Fib5	5'-CGCCATACAGAGTATACTGTGACAT-3'	Fuchs et al., 2004;
	Fib6	5'-GCCATCCTGGCGATTCTGAA-3'	Kimball et al., 2009
TGFB	TGFB2.5F	5'-GAAGCGTGCTCTAGATGCTG-3'	Primmer et al., 2002;
	TGFB2.6R	5'-AGGCAGCAATTATCCTGCAC-3'	Kimball et al., 2009
GAPDH	G3P13b	5'-TCCACCTTGATCGGGTGCTGGCAT-3'	Fjeldså et al., 2003
	G3P14b	5'-AAGTCCACAACACGGTTGCTGTA-3'	
	G3PintL1	5'-GAACGACCATTGTCAAGCTGGTT-3'	
	GAPDHintFPte	5'-TCTRGAGTGTGATTGCTKCTTCCC-3'	Designed for this study
ODC	OD6	5'-GACTCCAAGCAGTTGTCGTCTCAGTGT-3'	Allen and Omland, 2003
	OD8	5'-ATTGGTGGTGGCTTCCCTGGCTCTGAAGA-3'	

Table 3.3: Data characteristics and estimated model parameters for the datasets (for all the gene regions and concatenated datasets), including length of the alignment, number of variable and informative sites, model selected for the BI analyses, mean of the model parameters, BI likelihood score (arithmetic mean), ML likelihood score and MP tree numbers. The base frequency chi-squared test results are also included.

	Total (M-B +DNA)	M-B (Morpho-Behav)	All DNA	Mt DNA	Nuc DNA	ND2	Fib5	GAPDH	TGFB	ODC	
No. of characters											
No. of characters (total)	3367		41	3326	1041	2285	1041	590	389	597	709
Variable characters	1079		41	1038	521	517	521	155	81	155	126
Proportion variable	0.320		1	0.312	0.500	0.226	0.500	0.263	0.208	0.260	0.178
Informative characters	600		41	559	386	173	386	35	33	68	37
Model parameters											
Model selected	/		/	/	/	/	GTR+I+G	HKY	GTR+G	GTR+G	GTR+G
r(A<->C)							0.032	/	0.337	0.080	0.061
r(A<->G)							0.491	/	0.027	0.467	0.320
r(A<->T)							0.032	/	0.129	0.044	0.047
r(C<->G)							0.006	/	0.321	0.126	0.165
r(C<->T)							0.414	/	0.071	0.234	0.301
r(G<->T)							0.025	/	0.414	0.048	0.106
pi(A)							0.332	0.320	0.215	0.245	0.282
pi(C)							0.322	0.167	0.172	0.210	0.178
pi(G)							0.098	0.218	0.338	0.232	0.204
pi(T)							0.248	0.295	0.275	0.314	0.337
Alpha							20.525	/	93.067	0.735	1.163
Proportion invariable							0.505	/	0.444	/	/
Base frequency test											
Chi-squared value							35.6928	6.6636	6.6488	6.092	3.0276
Degrees of freedom							39	39	39	39	39
p							0.62	1	1	1	1
Tree characteristics											
MP No. of trees	1		3	1;1	1	3	as mt DNA	n/a	n/a	n/a	n/a
BI LnL Bayesian	n/a		n/a	-12817.96	-6179.62	-6627.08	-6179.62	-1711.85	n/a	-1950.41	n/a
ML RaxML (Max Likelihood)	n/a		n/a	/	-5736.99	-6542.64	-5736.99	-1695.39	n/a	-1934.40	n/a

Table 3.4: Resolution and support values of recovered nodes from the concatenated and individual analyses. The node numbers refer to Fig. 3.3, and are also accompanied by a description. Parsimony (MP) support is jackknife for the COMB and M-B analyses, and bootstrap for the others. Posterior probabilities and bootstrap values are given for the Bayesian (BI) and Maximum Likelihood (ML) analyses respectively. Strongly-supported values (JK, BS >= 75; PP >= 0.95) are highlighted in bold. The first number in the All DNA column refers to jackknife support.

Highly supported relationships in bold; COMB = combined M-B and DNA data; M-B = morpho-behavioural; tri = trichotomy; U = unpartitioned.

Clades		Combined analyses								Individual genes												
Node description	Node No. (Fig. 3.3)	COMB		M-B		All DNA		Mitochondrial DNA				Nuclear DNA			nuc Fib5			nuc GAPDH				
		MP	MP	MP	MP	BI	ML	MP	BI	ML	ML - U	MP	BI	ML	MP	BI	ML	MP	BI	ML		
<i>Nyctiperdix</i> sister to <i>Pterocles decoratus</i>	1	97	87	81/89	1	100		0.87	82	55		97	1	99						1	99	
<i>Nyctiperdix</i> monophyletic	2	100	99	92/94	1	100		100	1	100		95	1	100	Yes	1	100	Yes	Yes	1	98	
<i>P. quadricinctus</i> sister to 4	3	61		61/81	0.98	100		n/a	n/a	n/a	n/a	81	0.98	80	Yes	1	100	Yes	Yes	1	100	
<i>P. lichtensteinii</i> sister to <i>P. indicus</i>	4	61		63/70	0.98	91		n/a	n/a	n/a	n/a	69	0.97	81	n/a	n/a	n/a	Yes				
<i>P. alchata</i> and <i>P. burchelli</i> basal to non- <i>Nyctiperdix</i>	5	65																				
<i>P. alchata</i> sister to <i>P. burchelli</i>	6	Yes																				
Clade 8 sister to 10/11	7	Yes		89	0.99	100	Yes	0.53				94	0.99	87		tri	tri	Yes	tri	tri		
<i>P. gutturalis</i> sister to 9	8	Yes		100	1	100		99	1			Yes	100	1	100	n/a	n/a	n/a	Yes	Yes	1	100
<i>P. personatus</i> sister to <i>P. coronatus</i>	9	Yes		n/a	n/a	n/a		n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	
<i>P. senegalensis</i> sister to 11	10	Yes		n/a	n/a	n/a		n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	
Clade 12 and 14 sister	11	Yes		83/85	1	99		0.73				94	91	1	100	Yes	0.98	96	Yes	0.9	65	
<i>P. orientalis</i> sister to <i>Syrrhaptes</i>	12	Yes		98/98	1	100		0.91	90			96	100	1		Yes	1	100	Yes	Yes	1	99
<i>Syrrhaptes</i> monophyletic	13	82	91	n/a	n/a	n/a		n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	
<i>P. namaqua</i> sister to <i>P. exustus</i>	14	99	63	100/100	1	100		100	1	93		100	100	1	100	Yes	1	100	Yes	Yes	1	100
<i>P. burchelli</i> sister or in a trichotomy to non- <i>Nyctiperdix</i>		65+ <i>alchata</i>						1	18	Yes	0.91		tri	70	1	99		tri	tri			

Table 3.5: Selected morphological and behavioural characters of species in the Pteroclidae shown in relation to the major clades identified in this study. Characters are described in more detail in Appendix 3.1.

Taxa	Major clades recovered in this study			Morphological and behavioural characters				
	Major clade	Subclade	Subclade	Retrices number	Elongated central retrices	Long 10th primary	Tail wedge-shaped	Dusk drinkers
<i>S. tibetanus</i>	Long-tailed	Clade 12	Clade 13	16	Yes	Yes	Yes	
<i>S. paradoxus</i>	Long-tailed	Clade 12	Clade 13	16	Yes	Yes	Yes	
<i>P. orientalis</i>	Long-tailed	Clade 12		16		Yes	Yes	
<i>P. namaqua</i>	Long-tailed	Clade 14		16	Yes	Yes	Yes	Regular late afternoon
<i>P. exustus</i>	Long-tailed	Clade 14		16	Yes	Yes	Yes	
<i>P. senegallus</i>	Sister to Long-tailed			16	Yes	Yes	Yes	
<i>P. alchata</i>	Uncertain			16	Yes	Yes	Yes	
<i>P. gutturalis</i>	Short-tailed			16		Yes	Yes	Regular late afternoon
<i>P. coronatus</i>	Short-tailed			16		Yes	Yes	Regular late afternoon
<i>P. personatus</i>	Short-tailed			14		Yes	Yes	Regular late afternoon
<i>P. decoratus</i>	Nyctiperdix			16				
<i>P. lichtensteinii</i>	Nyctiperdix			14				Yes
<i>P. indicus</i>	Nyctiperdix			14				Yes
<i>P. quadricinctus</i>	Nyctiperdix			14				Yes
<i>P. bicinctus</i>	Nyctiperdix			14				Yes
<i>P. burchelli</i>	Uncertain			14		Yes	Yes	

Major clade colours:
 Long-tailed
 Short-tailed
 Nyctiperdix

Figure Legends Ch. 3

Fig. 3.1: Hypothesised relationships among the Pteroclidae by Johnsgard (1991) based on morphology and distribution.

Fig. 3.2: Hypothesised relationships among the Pteroclidae by Maclean (1984) based on morphology, behaviour and distribution.

Fig. 3.3: Parsimony cladogram for the concatenated dataset of all morpho-behavioural and multilocus DNA data (3367 characters, one tree, length = 1950). Values depicted directly to the right of the node are as follows:

#Clade Number/ Jackknife support if JK > 50/ Partitions that support the clade
(Key: M = morpho-behavioural characters; D = all DNA partitions; N = nuclear DNA; MT = mitochondrial DNA).

Fig. 3.4: Strict-consensus parsimony cladogram (from 3 trees, length = 102) for morpho-behavioural data, with jackknife support values shown if JK > 50. JK values are depicted directly to the right of the node.

Fig. 3.5: Mixed-model Bayesian analysis of the combined nuclear and mtDNA dataset with the support values of the BI, ML and MP analyses; support values are presented directly to the right of nodes and represent: posterior probabilities (BI)/ bootstrap (ML)/ bootstrap (MP)/ jackknife (MP). Nodes not supported, or supported by BS or JK < 50 are indicated by “-“.

Fig. 3.6: Mixed-model Bayesian analysis of the mtDNA dataset with the support values of the BI, ML and MP analyses; support values are presented directly to the right of nodes and represent: posterior probabilities (BI)/ bootstrap (ML)/ bootstrap (MP). Nodes not supported, or supported by BS < 50 are indicated by “-“.

Fig. 3.7: Mixed-model Maximum Likelihood analysis of the nuclear DNA dataset with the support values of the BI, ML and MP analyses; support values are presented directly to the right of nodes and represent: posterior probabilities (BI)/ bootstrap (ML)/ bootstrap (MP). Nodes not supported indicated by “-“.

Fig. 3.8: Bayesian analysis of the Fib5 DNA dataset with the support values of the BI and ML analyses; support values are presented directly to the right of nodes and represent: posterior probabilities (BI)/ bootstrap (ML). Nodes not supported are indicated by “-“.

Fig. 3.9: Bayesian analysis of the TGFB DNA dataset with the support values of the BI and ML analyses; support values are presented directly to the right of nodes and represent: posterior probabilities (BI)/ bootstrap (ML). Nodes not supported are indicated by “-“.

Fig. 3.10: Strict consensus parsimony cladogram (Fig. 3.3) with selected morphological and behavioural characters mapped.

Fig. 3.1

3.34

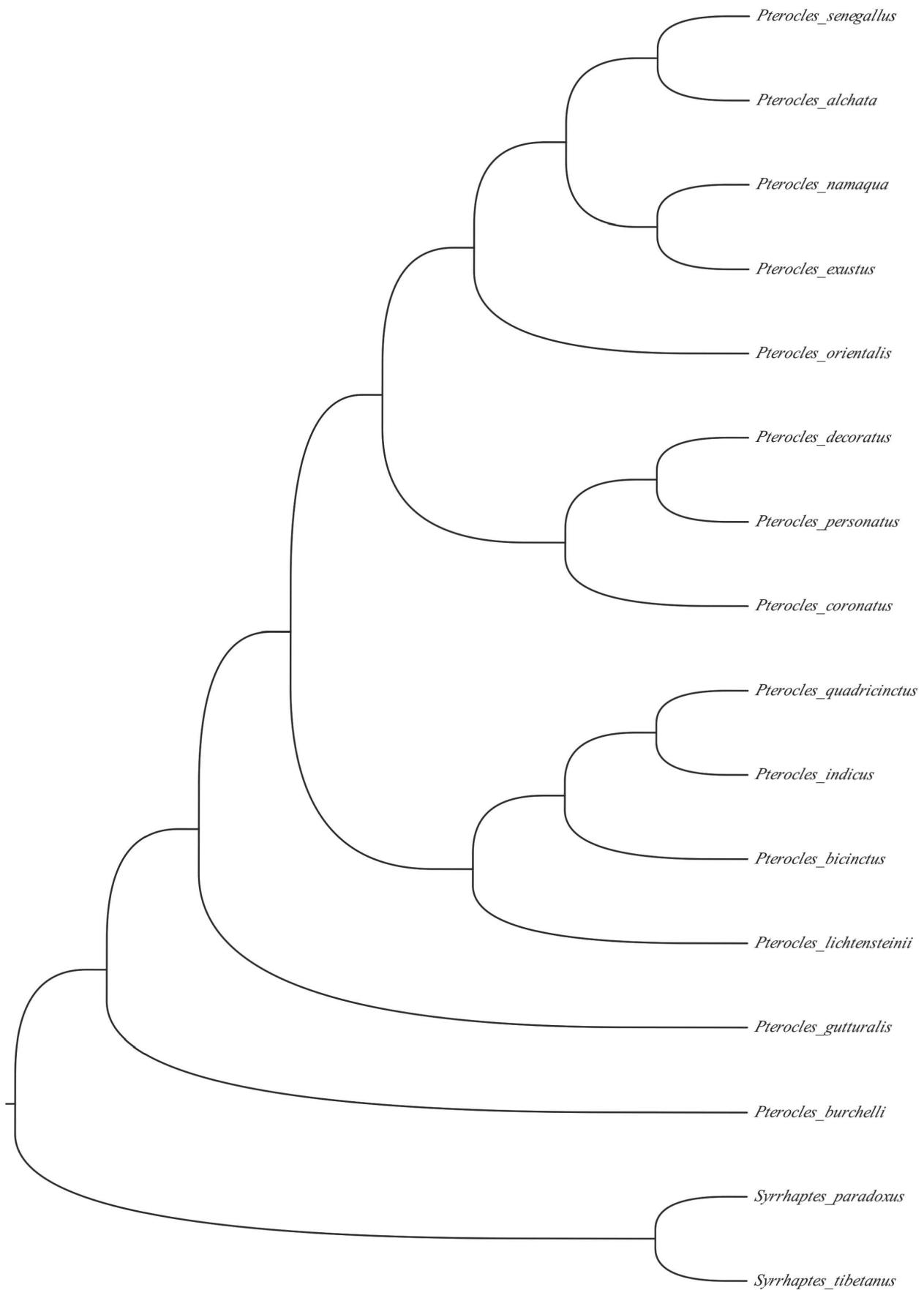


Fig. 3.2

EVOLUTIONARY TRENDS IN THE SANDGROUSE

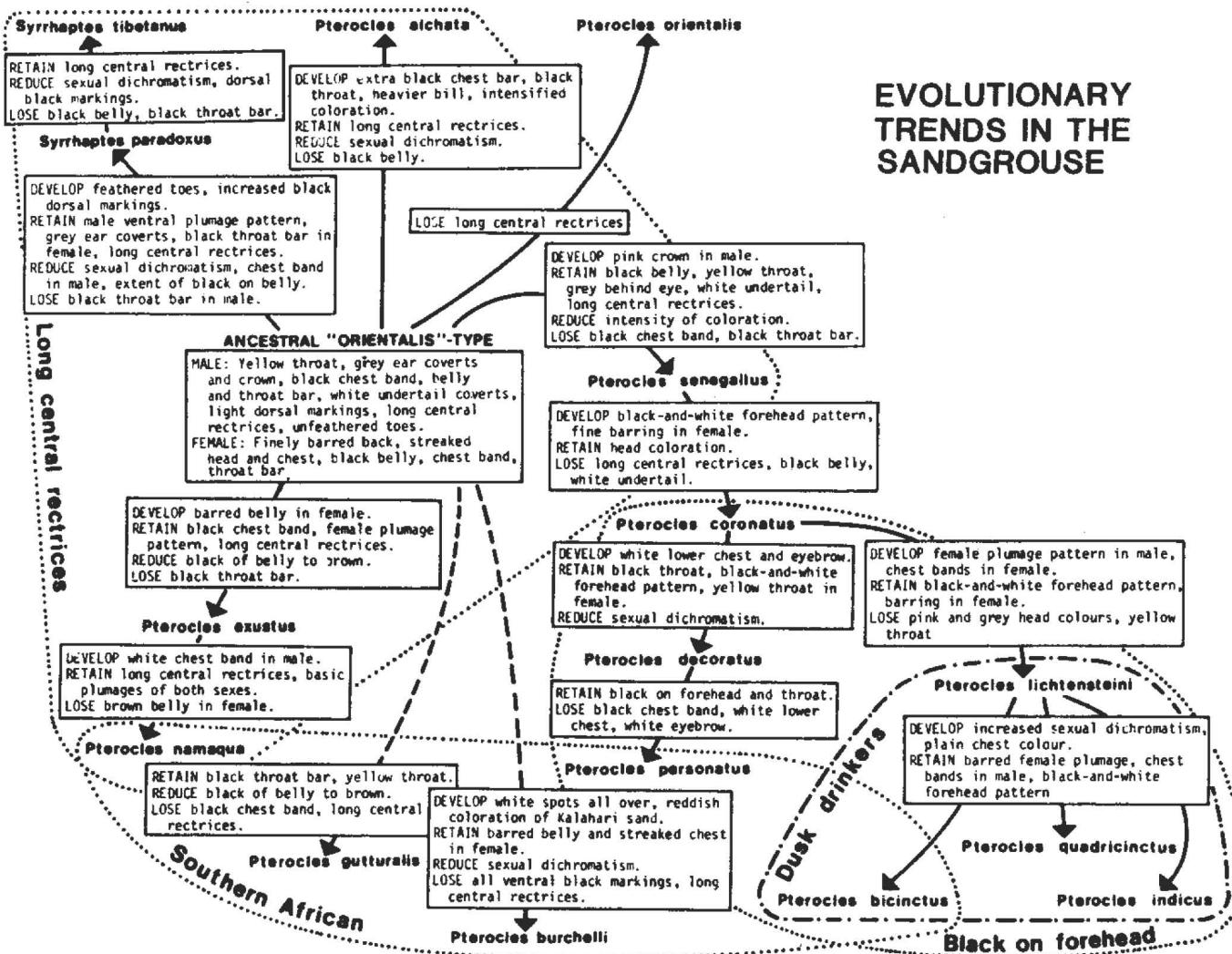


Fig. 3.3

3.36

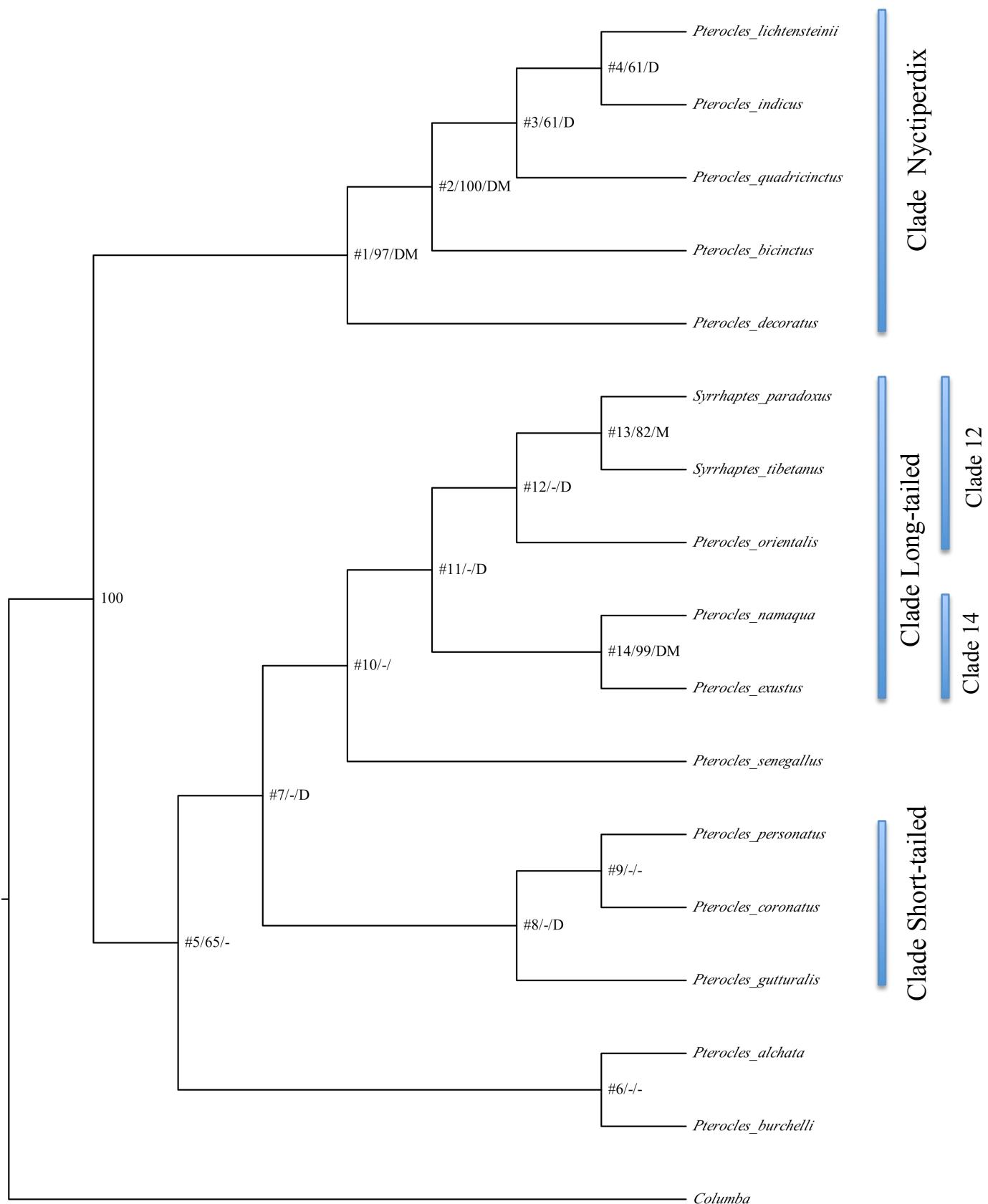


Fig. 3.4

3.37

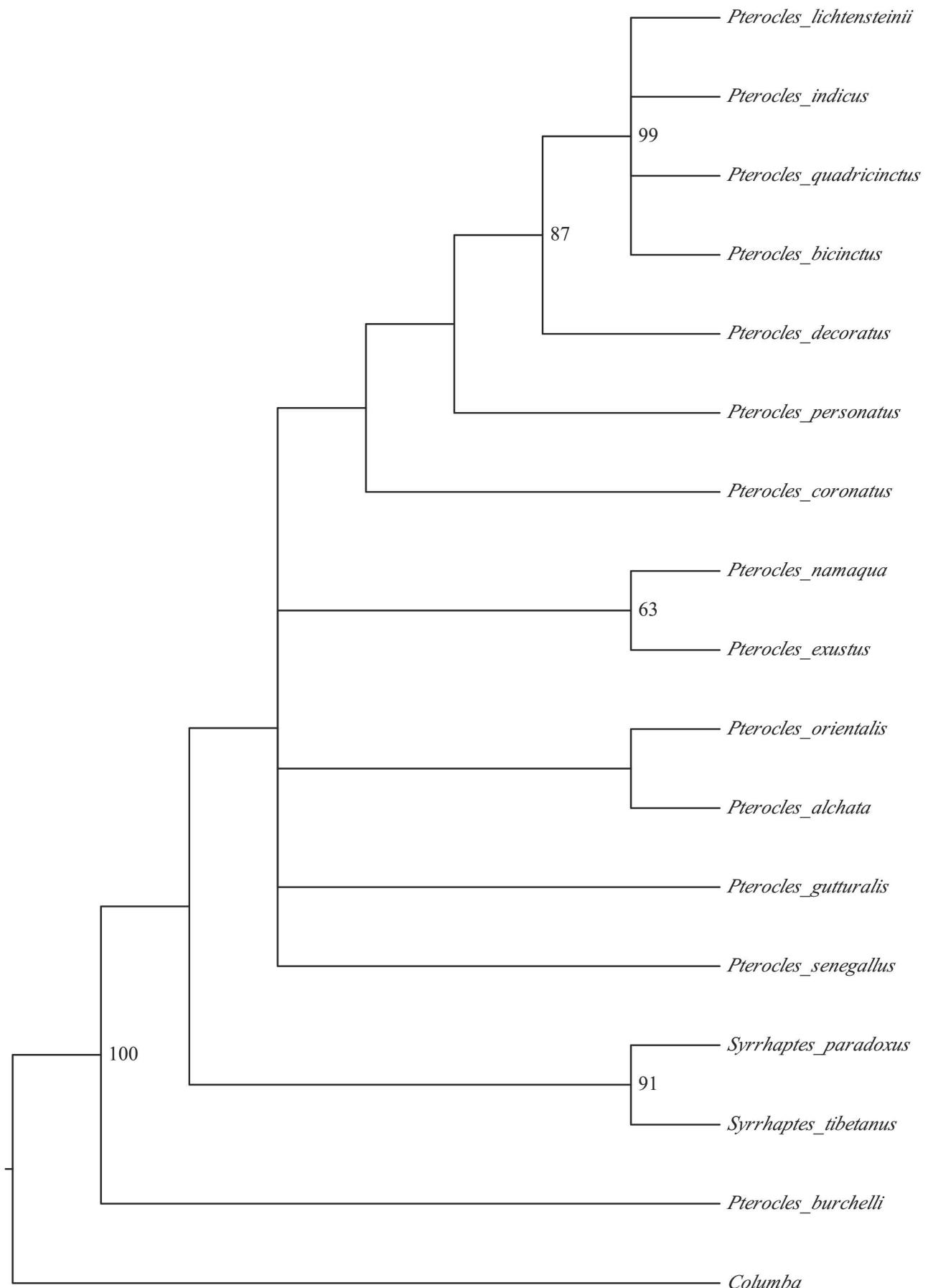


Fig. 3.5

3.38

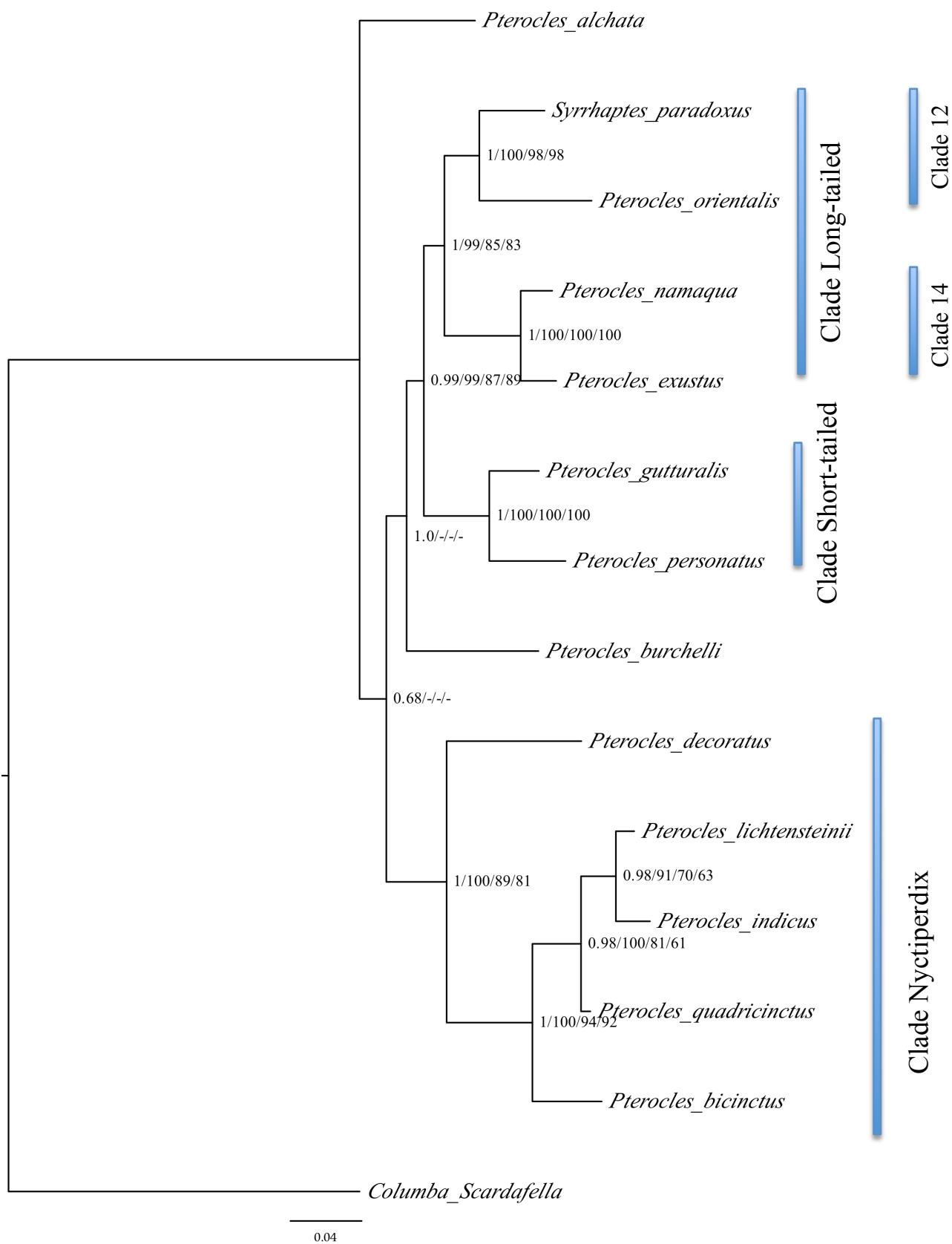


Fig. 3.6

3.39

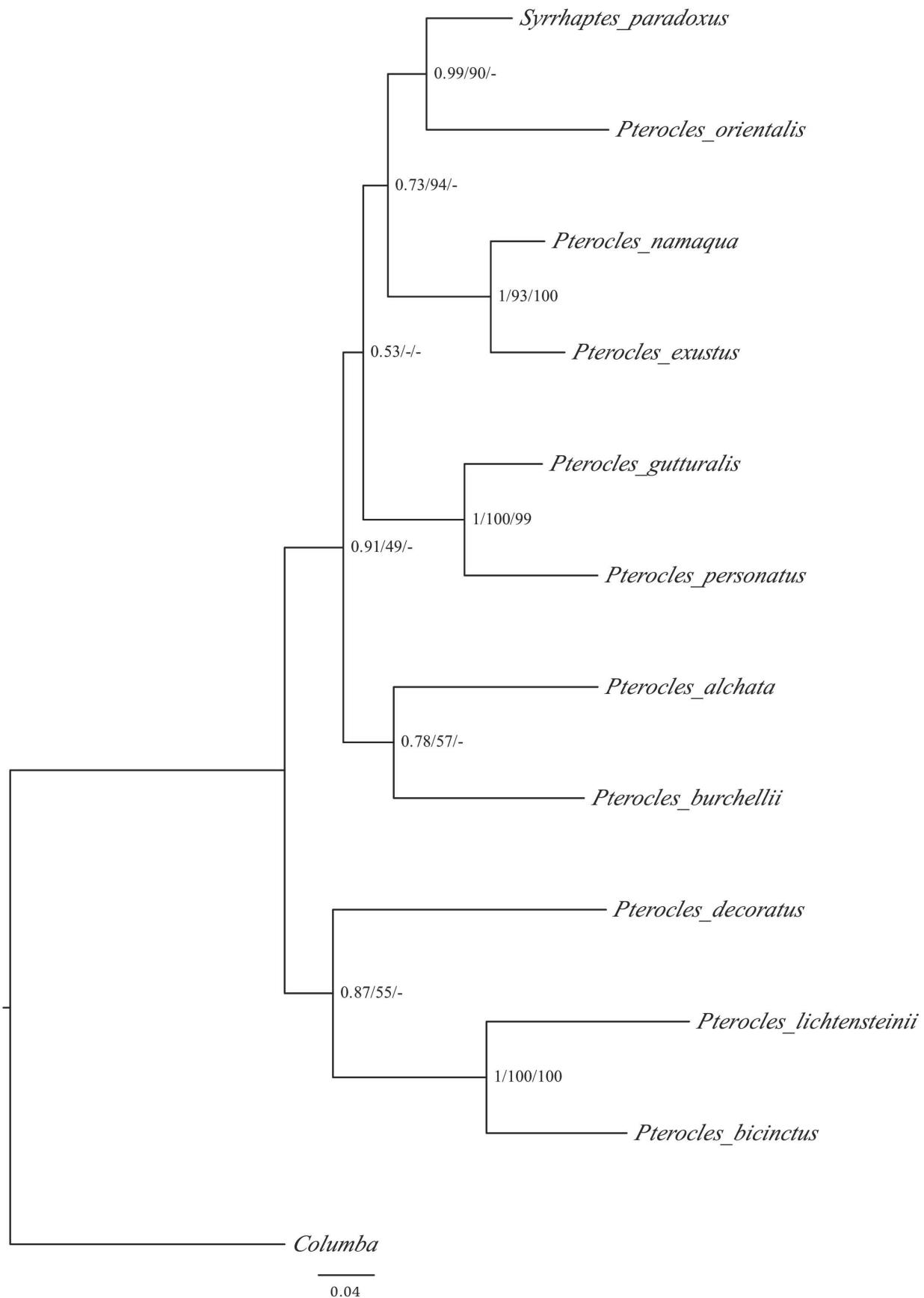


Fig. 3.7

3.40

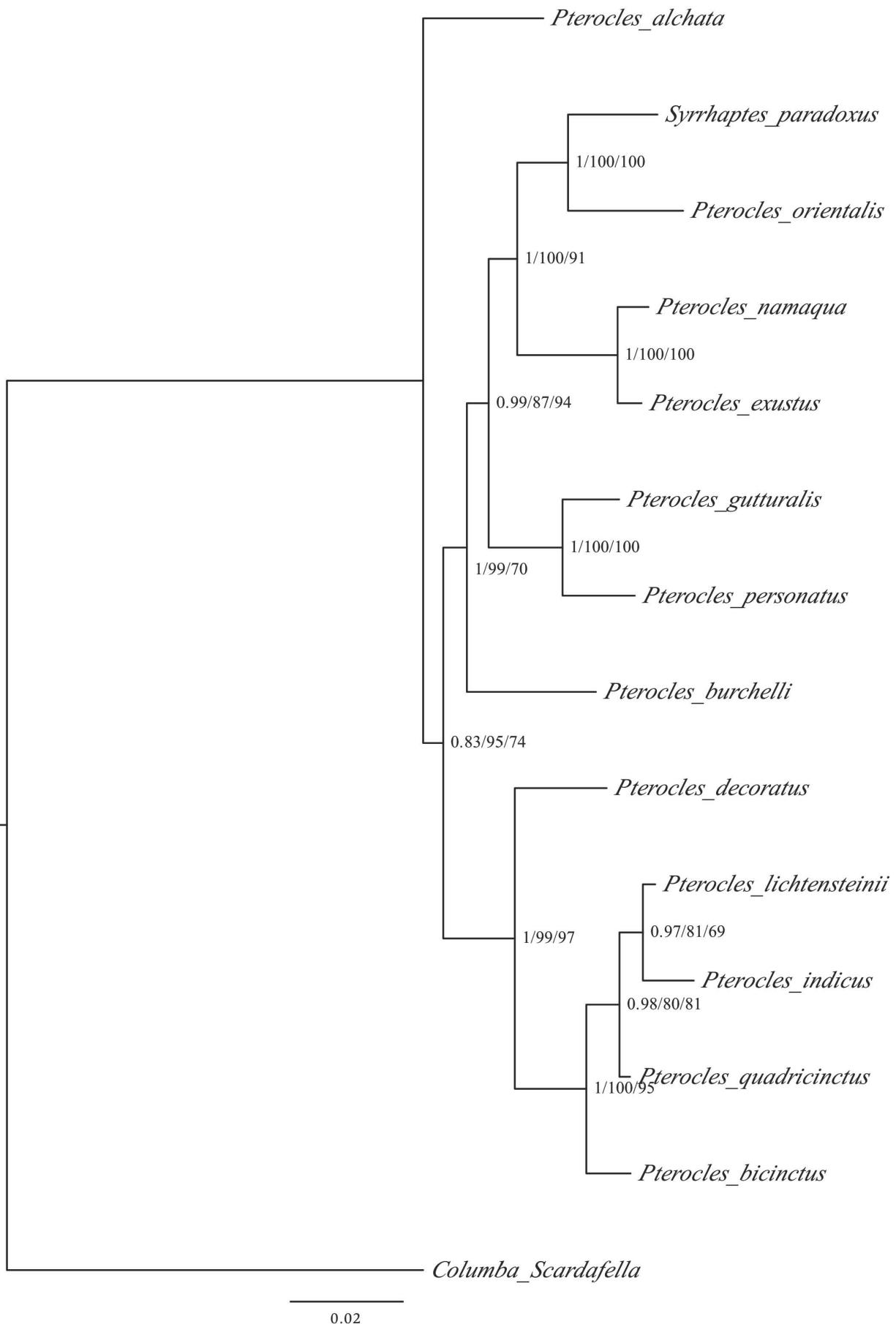


Fig. 3.8

3.41

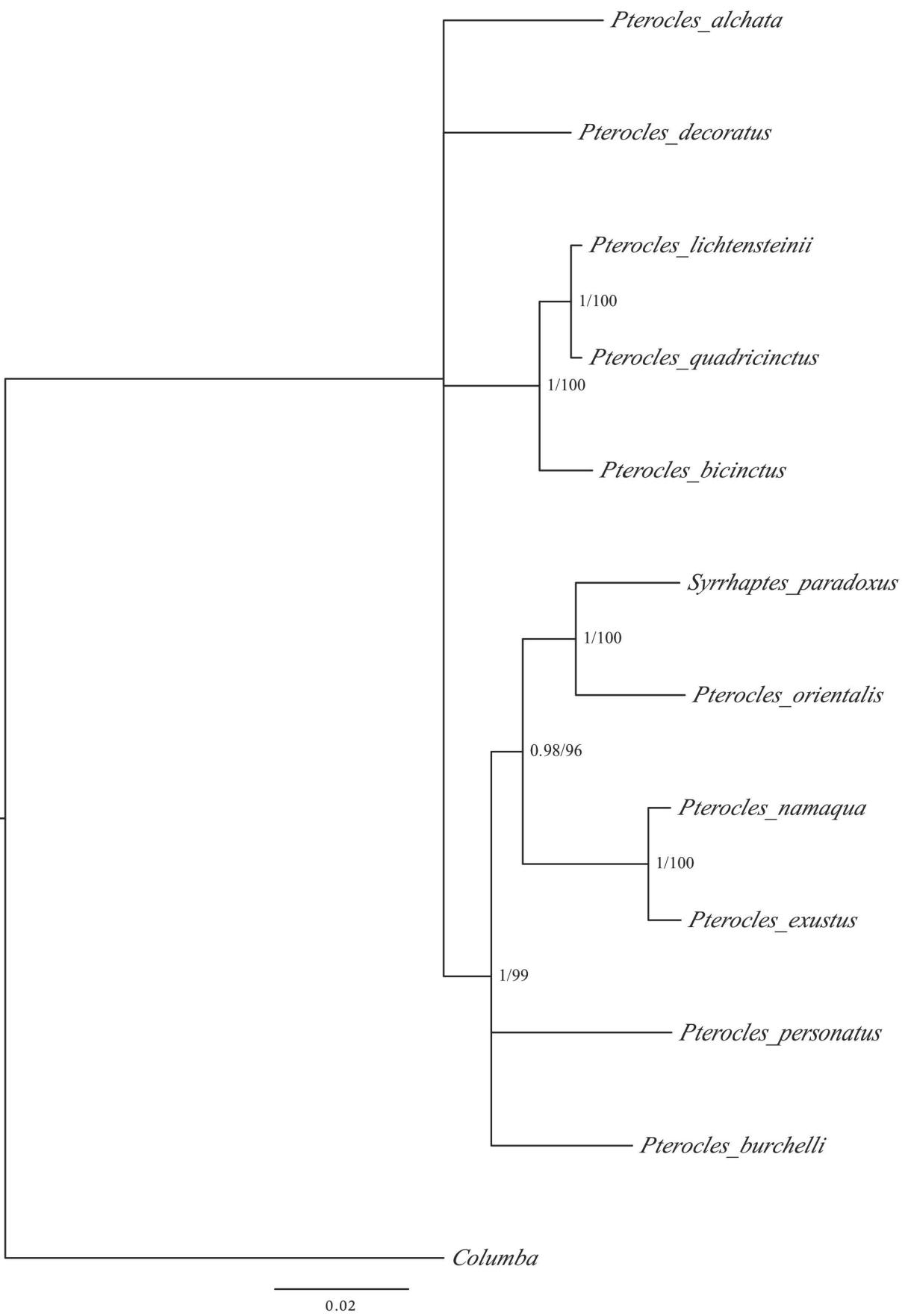


Fig. 3.9

3.42

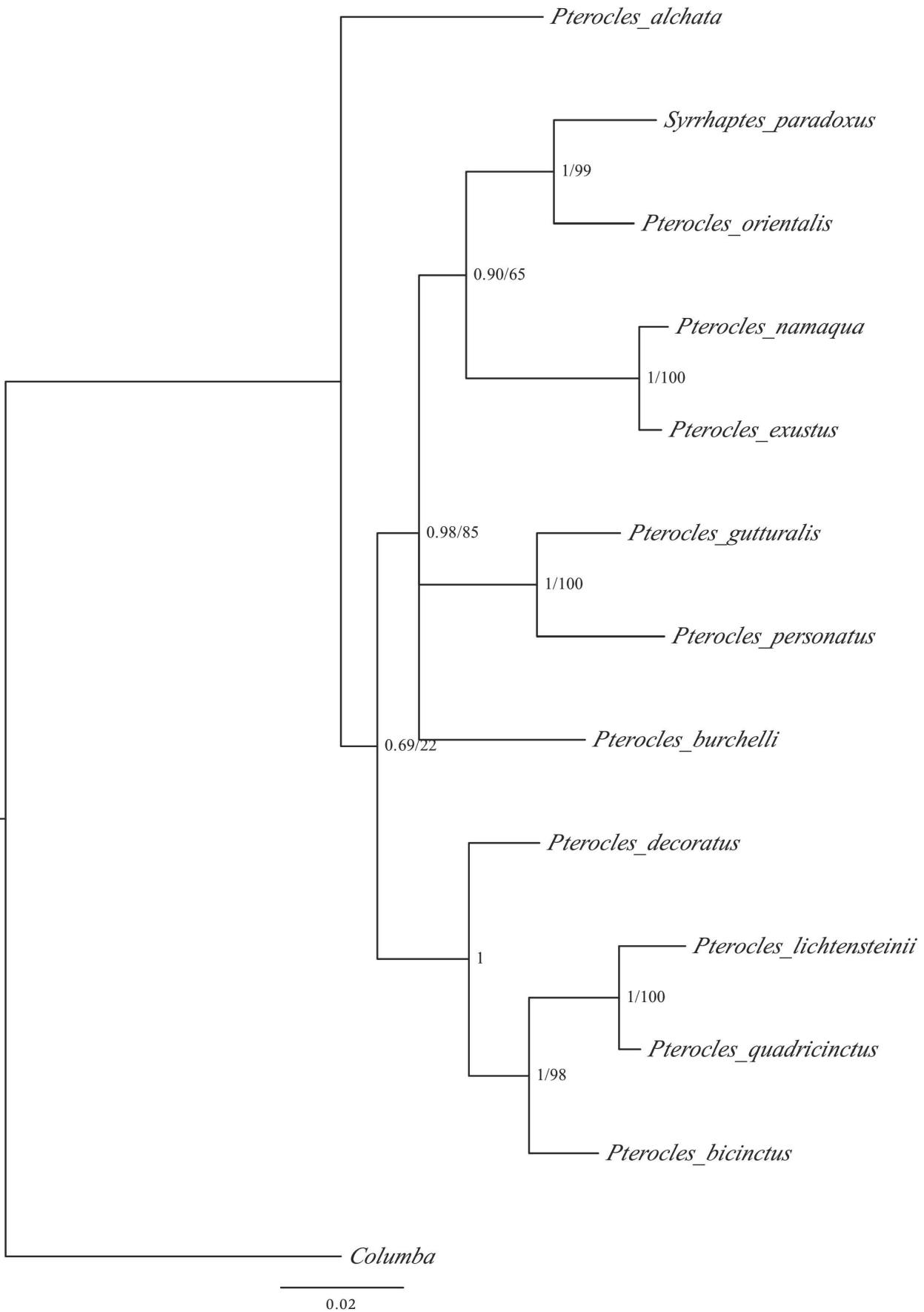
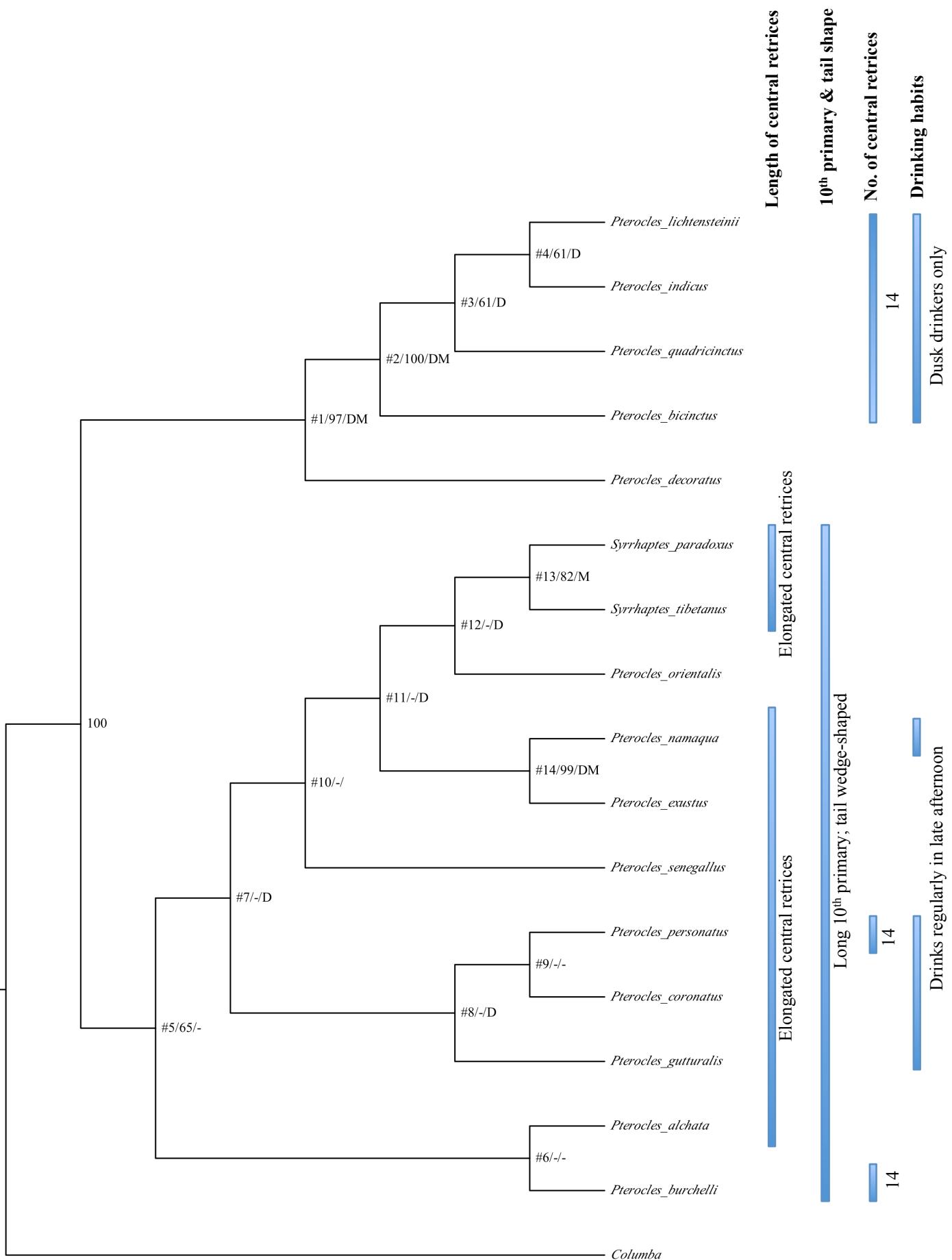


Fig. 3.10

3.43



Appendix Ch. 3

Appendix 3.1: Characters and character states used in morphological-behavioural character matrix for the sandgrouse (Pteroclidae)

All features refer to males in breeding plumage unless otherwise noted. See discussion in the main manuscript for comments. All morphological characters defined as per Hayman et al. (1986).

PLUMAGE CHARACTERS

HEAD

1. Black patch on the forehead feathers

- 0 Absent
- 1 Present

2. White on the forehead feathers

- 0 Absent
- 1 Present

3. Is the forehead white with a black bar through the centre?

- 0 No
- 1 Yes

4. Is the chin and or throat black?

- 0 No
- 1 Yes

5. Are the throat and the forehead both black, i.e. is there a black pattern both above and below the bill?

- 0 No
- 1 Yes

6. Are the sides of the face washed yellow, orange or grey?

- 0 No
- 1 Yes

7. Distinct eye-stripe present either in front of or behind the eye

- 0 Absent
- 1 Present

BARE PARTS COLOURATION

8. Colour of the bill

- 0 Grey
- 1 Orange

9. Colour of the bare patch around the eye and eye-ring

0 Grey/blue-grey or pale grey

1 Yellow

10. Size of the eye-ring and bare-patch around the eye

0 Eye-ring only

1 Bare patch surrounding the eye ring

UNDERPARTS**11. Sharp division of colour between breast and belly**

0 No

1 Yes

12. Belly colour

0 White

1 Black

2 Chestnut

3 Black and white

4 Orange

13. Belly pattern

0 Unbarred

1 Barred

14. Distinct contrast of throat with breast

0 No

1 Yes

15. Does the male have a throat/upperchest band?

0 Absent

1 Present

16. Does the female have a throat/upperchest band?

0 Absent

1 Present

17. Are there one or more distinct bands on the breast/belly border?

0 Absent

1 Present

18. Number of distinct black bands on the breast and belly

0 None

1 One

2 Two

19. Number of white bands on the breast and belly

0 None

1 One

2 Two

20. Breast barred in the female?

- 0 No
1 Yes

21. Breast streaked in the female?

- 0 No
1 Yes

22. Belly barred in the female?

- 0 No
1 Yes

23. Is the vent barred in the male?

- 0 No
1 Yes

24. Colour of underwing coverts

- 0 Pale white to buff-brown
1 Strikingly dark

UPPERPARTS

25. Rump pattern

- 0 Plain (or spotted)
1 Heavily and densely barred

26. Back and mantle pattern

- 0 Plain (or spotted)
1 Heavily and densely barred

27. Wing covert patterns

- 0 Unmarked or some black spots
1 Horizontal black bars
2 Broad pale tips
3 Small white tips

28. Scapular patterns

- 0 Unmarked or some black spots
1 Horizontal black bars
2 Broad pale tips
3 Small white tips

TAIL PATTERN

29. Banding of retrices

- 0 Weak or with pale bands broader than dark ones
1 Black banding equal or wider than pale banding

30. Colour of central retrices

- 0 As the adjacent feathers
- 1 Contrasting with the adjacent feathers

STRUCTURAL CHARACTERS**TAIL AND WING SHAPE****31. Presence of two highly elongated central retrices**

- 0 Absent
- 1 Present

32. Number of retrices

- 0 16
- 1 14

33. Individual retrices pointed or rounded/almost square-ended (see Bowen, 1927)?

- 0 Rounded
- 1 Pointed

34. Tail shape (when spread out) rounded or wedge-shaped (see Bowen, 1927)?

- 0 Rounded
- 1 Wedge-shaped

35. Primary shape (see Bowen, 1927)

- 0 Inner primaries rounded; only out ones pointed
- 1 All primaries acutely pointed
- 2 Intermediate

36. Wing and primary proportion (see Bowen, 1927)

- 0 Broad winged, first (inner) primary about 2/3 the length of the wing
- 1 Long-winged, first (inner) primary about 1/2 the length of the wing

37. Tenth primary distinctly longer than the others (see Bowen, 1927)

- 0 No
- 1 Yes

FOOT MORPHOLOGY**38. Feathering on the rear of the tarsometatarsus and toes**

- 0 Not present
- 1 Feet and toes completely feathered

39. Presence of hallux (the 4th, rear toe)

- 0 Present
- 1 Absent

40. Fusion of the three front toes

- 0 Not fused
- 1 Fused on the undersides

BEHAVIOURAL CHARACTERS

41. Daily drinking times

- 0 During the day (mainly in the first few hours of daylight)
- 1 Crepuscular or nocturnal

Appendix 3.2: Morphological-behavioural character matrix for the Pteroclidae

Species	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
<i>Syrrhaptes tibetanus</i>	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	1	1
<i>Syrrhaptes paradoxus</i>	0	0	0	0	0	1	0	0	0	0	1	3	0	1	0	1	1	0	0	0	0	0	0	0	1
<i>Pterocles orientalis</i>	0	0	0	1	0	1	0	0	0	0	1	1	0	1	0	1	1	1	1	0	1	0	0	0	0
<i>Pterocles namaqua</i>	0	0	0	0	0	1	0	0	1	0	1	2	0	1	0	0	1	1	1	0	1	1	0	1	0
<i>Pterocles exustus</i>	0	0	0	0	0	1	0	0	1	0	1	2	0	1	0	0	1	1	0	0	1	1	0	1	0
<i>Pterocles senegallus</i>	0	0	0	0	0	1	0	0	0	0	1	3	0	1	0	0	0	0	0	0	1	0	0	0	0
<i>Pterocles alchata</i>	0	0	0	1	0	1	1	0	0	1	1	0	0	1	1	1	1	2	0	0	0	0	0	0	1
<i>Pterocles gutturalis</i>	0	0	0	0	0	1	1	0	0	0	1	2	0	1	1	0	0	0	0	0	1	1	0	0	0
<i>Pterocles coronatus</i>	1	1	0	1	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Pterocles personatus</i>	1	0	0	1	1	1	0	0	1	0	1	3	1	1	0	0	0	0	0	0	0	1	1	1	1
<i>Pterocles decoratus</i>	1	1	0	1	1	1	0	1	1	0	1	1	0	1	0	0	1	2	1	1	0	0	0	0	1
<i>Pterocles bicinctus</i>	1	1	1	0	0	0	0	1	1	1	1	3	1	0	0	0	1	1	1	1	0	1	1	0	1
<i>Pterocles quadricinctus</i>	1	1	1	0	0	0	0	1	1	1	1	3	1	0	0	0	1	2	1	1	0	1	1	0	1
<i>Pterocles indicus</i>	1	1	1	0	0	0	0	1	1	1	1	3	1	0	0	0	1	2	1	1	0	1	1	0	1
<i>Pterocles lichtensteinii</i>	1	1	1	0	0	0	0	1	1	1	1	3	1	0	0	0	1	2	0	1	0	1	1	0	1
<i>Pterocles burchelli</i>	0	0	0	0	0	1	0	0	1	1	0	4	0	1	0	0	0	0	0	0	0	0	0	0	0
OUTGROUP: <i>Columba livia</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	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

Appendix 3.2: Continued

Species	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41
<i>Syrrhaptes tibetanus</i>	1	0	0	0	1	1	0	1	1	1	1	1	1	1	1	0
<i>Syrrhaptes paradoxus</i>	1	0	0	0	1	1	0	1	1	1	1	1	1	1	1	0
<i>Pterocles orientalis</i>	0	2	2	0	1	0	0	1	1	1	1	1	0	0	0	0
<i>Pterocles namaqua</i>	0	2	2	0	1	1	0	1	1	1	1	1	0	0	0	0
<i>Pterocles exustus</i>	0	1	1	0	1	1	0	1	1	1	1	1	0	0	0	0
<i>Pterocles senegallus</i>	0	2	2	0	1	1	0	1	1	1	1	1	0	0	0	0
<i>Pterocles alchata</i>	0	1	2	0	1	1	0	1	1	1	1	1	0	0	0	0
<i>Pterocles gutturalis</i>	0	2	2	0	1	0	0	1	1	1	1	1	0	0	0	0
<i>Pterocles coronatus</i>	0	2	2	0	1	0	0	1	1	1	1	1	0	0	0	0
<i>Pterocles personatus</i>	0	1	2	0	1	0	1	1	1	2	0	1	0	0	0	0
<i>Pterocles decoratus</i>	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pterocles bicinctus</i>	1	3	3	1	0	0	1	0	0	0	0	0	0	0	0	1
<i>Pterocles quadricinctus</i>	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	1
<i>Pterocles indicus</i>	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	1
<i>Pterocles lichtensteinii</i>	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	1
<i>Pterocles burchelli</i>	0	3	3	0	1	0	1	?	1	1	1	1	0	0	0	0
OUTGROUP: <i>Columba livia</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41

CHAPTER 4

Phylogenetics of the coursers and pratincoles (Glareolidae) inferred from morphological, behavioural and multilocus mitochondrial and nuclear DNA data with comments on the placement of the enigmatic genus *Stiltia*

Abstract

The coursers (*Cursorius*, *Rhinoptilus* and *Smutsornis*) are a group of plover-like waders, with long legs, short, decurved bills and cryptic plumage, that are found in arid habitats from Africa to India. They are traditionally grouped in the subfamily Cursoriinae whereas the remainder of the Glareolidae belong to the pratincole genera (*Glareola* and *Stiltia*), which are diurnal, long-winged aerial feeders often associated with water, and are grouped in the Glareolinae. To date, no morphological or molecular phylogeny has been undertaken to investigate the monophyly of these subfamilies or the numerous generic treatments of the Glareolidae. The Glareolidae also present an opportunity to evaluate the evolution of characters associated with different behavioural strategies and habitat selection (species occur both in arid habitats and are associated with water, four of the species are nocturnal and there has been a divergence between a cursorial ground-feeding lifestyle and an aerial foraging strategy). To address these questions, a multi-faceted approach was used to evaluate

the phylogenetics of the Glareolidae. Morphological-behavioural characters were scored for all 17 species based on museum visits, field trips and published literature, and molecular data were obtained for 10 species including representatives of all five proposed genera in the Glareolidae, at least one member of each “superspecies”, and all six species of African-breeding coursers. The 47 phylogenetically-informative morphological-behavioural characters and 2627 bp of nucleotide data (one mitochondrial marker: ND2; three nuclear markers: Fib5, TGFB and GAPDH) were analysed separately and in combination using three methods of phylogenetic analysis with different optimality criteria: parsimony, Bayesian inference and maximum likelihood. The following clades were strongly supported in all analyses: 1. **Clade Cursorius** (all members of the genus *Cursorius*); 2. **Clade Rhinoptilus** (all members of the genera *Rhinoptilus* and monotypic *Smutsornis*); and 3. **Clade Glareola** (all members of the genera *Glareola* and *Stiltia*). Only the morphological-behavioural analysis recovers **Clade Rhinoptilus** sister to **Clade Cursorius** (i.e. Cursoriinae monophyletic) which would make the division of the Glareolidae into currently-recognised subfamilies defensible. In contrast, the mitochondrial and nuclear DNA data, and the combined DNA and morphological-behavioural evidence, support topologies that would render the Cursoriinae paraphyletic, although the base of the trees are weakly resolved. Morphologically, *Stiltia* has characters intermediate between a courser and a pratincole, but results strongly support its placement within *Glareola* and it is not an evolutionary link between the two subfamilies. Among the Glareolidae, the habitats occupied, foraging level, activity time and migratory behaviour seem to be highly conserved within clades, suggesting there are high evolutionary costs to changing from these relatively specialist niches. The colouration of the bare parts, upperparts and underparts are especially homoplasious.

Introduction

The coursers (*Cursorius*, *Rhinoptilus* and *Smutsornis*) are a group of plover-like waders, with long legs, short, decurved bills and cryptic plumage, that are found in arid habitats from Africa to India (Maclean, 1996). Four of the nine species are nocturnal (Maclean, 1996). They are traditionally grouped in the subfamily Cursoriinae (Gray, 1840) together with *Pluvianus* (Egyptian Plover), whereas the pratincole genera (*Glareola* and *Stiltia*) which are diurnal, long-winged aerial feeders often associated with water, are grouped in the Glareolinae (Brehm, 1831). Together these two subfamilies comprise the Glareolidae (Brehm, 1831), which is placed in the Charadriiformes (Maclean, 1996).

Much molecular work has been undertaken in an attempt to resolve the controversial relationships among members of the Charadriiformes (Ericson et al., 2003; Paton et al., 2003; Paton and Baker, 2006; Baker et al., 2007; Fain and Houde, 2007; Hackett et al., 2008). The use of DNA datasets and phylogenetic analyses have confidently shown that *Pluvianus* is not related to the rest of the Glareolidae, but is more accurately placed in the suborder Charadrii (plovers, stilts and allies), with the Glareolidae falling within the suborder Lari (gulls, terns, skuas, alcids and allies). Baker et al. (2007) included a single exemplar from *Glareola*, *Stiltia*, *Cursorius* and *Rhinoptilus* and showed these to form a monophyletic clade (posterior probability = 1.0), sister to the remaining Lari. Ericson et al. (2003) also demonstrated that *Cursorius* and *Rhinoptilus* comprise a monophyletic clade (posterior probability = 1.0) in a large analysis of the Charadriiformes, but *Glareola* was not included in that study.

Interestingly, although this was not mentioned by Baker et al. (2007), their data show the two coursers, *Cursorius* and *Rhinoptilus* are not placed as sisters. Rather *Cursorius* is placed as sister to the *Glareola* + *Stiltia* clade, and this clade is sister to *Rhinoptilus*. This would suggest that the subfamily Cursoriinae as presently recognised is not monophyletic. However, because only one exemplar of each genus was used, this result should perhaps be treated with caution.

Between one (*Cursorius*) and three genera (*Cursorius*, *Rhinoptilus* and *Smutsornis*) are recognised by recent treatments ([Table 1.4](#)). The only controversial issue in species-level taxonomy within the traditionally defined Glareolidae has been the placement of the *C. littoralis*/ *C. somalensis* taxa which are variously grouped with either *C. cursor* or *C. rufus* or allocated full species status ([Table 1.4](#); see also Pearson and Ash, 1996). All authors recognise either 16 or 17 species in the Glareolidae ([Table 1.4](#)). All of the numerous assessments of the number of genera and species in the family ([Table 1.4](#)) have made use of only morphological characters and, to date, no cladistic analyses have been conducted in order to analyse morphological characters in an objective way.

A further taxonomic category that has been important in the courser literature has been the use of the concept of “superspecies”. Amadon (1966) incorporated Mayr’s (1931) ideas in his summary of the “superspecies” concept, which he maintained is “a monophyletic group of allopatric or nearly allopatric taxa that are known or believed to have evolved to the species level.” Snow (1978) and Maclean (1996) have suggested detailed “superspecies” hypotheses for the Glareolidae ([Table 4.2](#)).

The following sub-family, generic and species-level relationships questions/hypotheses will be addressed:

1. Is the Cursoriinae monophyletic?
2. Are the currently recognised genera (*Cursorius*, *Rhinoptilus* and *Smutsornis*) monophyletic?
3. Is the proposed genus *Hemerodromus* for *R. africanus* and *R. cinctus* valid?
4. Are the superspecies outlined in [Table 4.2](#) monophyletic?
5. Is *R. chalcopterus* the most primitive species as suggested by Maclean (1996) or is *R. africanus* the most primitive form as suggested by its mallophagan feather-lice (Timmerman, 1952)?
6. Is the genus *Stiltia* a link between the coursers and pratincole as suggested by Maclean (1996)?

The Glareolidae also present an opportunity to evaluate the evolution of characters associated with different behavioural strategies and habitat selection. Species occur both in arid habitats and associated with water, four of the species are nocturnal and there has been a divergence between a cursorial ground-feeding lifestyle and an aerial foraging strategy. A robust phylogeny would allow the evolution of these strategies and the characters associated with them to be evaluated.

A multi-faceted approach was used to evaluate the relationships among members of the Glareolidae. Morphological, behavioural and multilocus molecular data were analysed using three methods of phylogenetic analysis with different optimality criteria (Holder and Lewis, 2003): parsimony (MP), Bayesian inference (BI) and

Maximum Likelihood (ML). For the DNA analysis, one mitochondrial marker (NADH Dehydrogenase subunit 2; ND2) and three nuclear markers: beta-Fibrinogen introns-5 (Fib5), Transforming Growth Factor Beta 2 intron-5 (TGFB) and Glyceraldehyde-3-phosphate Dehydrogenase intron 11 (GAPDH), were sequenced.

Materials and Methods

Taxon sampling

The initial emphasis was to sample all African courser species to gain insights into their biogeography and relationships. The objective was to get at least two tissue samples from each distinctive subspecies in the Cursoriinae, using a *Glareola* species as an outgroup. This is for the following reasons: 1. the second sample for each major taxon acts as check against labelling problems; 2. the use of samples from distinctive subspecies allows one to check that the species is monophyletic; 3. the use of tissue instead of blood reduces the chances of encountering nuclear pseudogenes ('numts', see below). Unfortunately, this was not always possible as many of the tissues were not in existing collections and it was simply not possible to collect all species under permit (such as if the species was of conservation concern, or occurred in an area where it is not safe to visit or collect). However, once it became apparent that the Cursoriinae might not be monophyletic, *Glareola nuchalis* was included as part of the ingroup, and sequences from *Stiltia* and two further species of *Glareola* were added from Genbank. This study now includes all six species of African-breeding coursers and representatives of all five proposed genera in the Glareolidae ([Table 4.1](#)). Two species for which there are presently no molecular data available are hypothesised to

be close relatives of ingroup taxa (see [Table 1.4](#) and [4.2](#)), described as members of possible “superspecies” by Snow (1978) and Maclean (1996). Morphological-behavioural data for all 17 described species in the Glareolidae were obtained for this study ([Table 4.1](#)). Molecular data were also obtained for three subspecies of the courser *R. africanus* as it is disjunctly distributed in the deserts of north-eastern and south-western Africa.

Fresh samples of either tissue or blood (stored in either 95% ethanol, or Dimethyl sulfoxide (DMSO) or Ethylene diaminetetraacetic acid (EDTA) solutions respectively) were obtained from museum tissue archives (FMNH) or from specimens either collected or captured in the field ([Figs 4.10 – 4.12](#)) under permit on field trips. Full details of all the samples analysed in this study are in [Table 4.1](#) and fully acknowledged in the Acknowledgements. In contrast with the Otididae (see [Chapter 2](#)), it was not possible to obtain any sequence data for any of the toepad samples from the American Museum of Natural History for the missing two coursers, despite attempting the protocol described in [Chapter 2](#) at UC Berkeley; samples that were not amplified are not listed in [Table 4.1](#).

Outgroup selection

It has now been demonstrated decisively that *Pluvianus* should not be placed in the Glareolidae, but within the Charadrii, whereas the Glareolidae have been shown to fall within the Lari (Baker et al., 2007). This placement of Glareolidae in the Lari is also supported by Sibley and Ahlquist (1990) and Ericson et al. (2003), leading to the choice of *Larus* (*L. delawarensis* and *L. marinus*) as the outgroup taxa for this study.

Morphological-behavioural character matrix

A matrix of 47 morphological and behavioural characters (morphological-behavioural matrix) was prepared that included all species of the Glareolidae. Morphological characters included plumage of breeding males, as has been done in previous treatments (see [Table 4.1](#)), but also used plumage characters of females, bare part colouration, and structural characters such as the shape of the wing and tail. All characters are described in [Appendix 4.1](#), and the character states for each species are presented in [Appendix 4.2](#). Characters that were only applicable to a single species (autapomorphic) were not included in the matrix. Multi-state characters were treated as unordered.

Morphological and behavioural characters were assigned to species on the basis of these sources of information: 1. published sources of information used to score the species included Hayman et al. (1986), Maclean and Urban (1986), Maclean (1996) and Hockey et al. (2005); 2. a database of photographs individually sourced from the internet from birding field trip reports; 3. photographs taken personally during field trips.

Molecular markers

The following mitochondrial DNA (mtDNA) and nuclear DNA markers were amplified:

One mitochondrial marker:

NADH Dehydrogenase subunit 2 (ND2)

Three nuclear markers:

Beta-Fibrinogen introns-5 (Fib5)

Transforming Growth Factor Beta 2 intron-5 (TGFB)

Glyceraldehyde-3-phosphate Dehydrogenase intron 11 (GAPDH)

The nuclear introns are found on the following chromosomes in the chicken genome:

Chromosome 1: GAPDH; Chromosome 3: TGFB, ODC; Chromosome 4: Fib5 (Fuchs et al., 2009).

Laboratory techniques: extraction, PCR and sequencing

Total genomic DNA was extracted from blood, pectoral muscle, heart and liver tissue using the following two methods: 1. Quiagen DNeasy animal tissue protocol provided with the DNeasy® tissue kit (Qiagen, Valencia, California); 2. Cetyl Trimethyl Ammonium Bromide-based protocol (Winnepenninckx et al., 1993) with an overnight Proteinase-K digestion.

Double-stranded DNA templates for the mitochondrial and nuclear loci were amplified by polymerase chain reaction (PCR). I typically used 12 µl reactions with 1-3.5 µl of genomic DNA added. The PCR reactions contained the following: 1.5 mM PCR buffer, 3.0 mM MgCl₂, 0.8 mM Bovine Serum Albumin (BSA), 0.25 mM of each dNTP, 0.2 mM of each primer (but 0.15 mM for GAPDH and Fib5), and 0.15 units of Taq (Roche). All sets of PCR-amplifications included a negative control to which no DNA was added. Primers used for PCR-amplification and DNA sequencing are listed in [Table 4.3](#).

Thermal cycling was mostly performed on a Bio-Rad iCycler (Bio-Rad, Hercules, California) with the following conditions: a hotstart at 94°C for 2 min, followed by 35 cycles of denaturation at 94°C for 30 s, annealing at 53-60 °C (cytb and ND2 at 53°C, Fib5 at 54°C, TGFB at 58°C, GAPDH at 60°C) for 30 s, and extension at 72°C for 80 s (except GAPDH for 60 s), with a final extension at 72°C for 10 min. PCR products were visualized (to confirm amplification and fragment sizes) by running them on a 1.5% agarose TAE gel, stained with ethidium bromide and visualized under UV light. The negative controls were also visualized in this way.

Amplified products were cleaned using a standard Exonuclease I and Shimp Alkaline Phophatase (Exo/SAP) protocol and then cycle-sequenced using the Big Dye terminator chemistry (version 3.1, AB - Applied Biosystems). Sequencing was performed in both directions with the primers described in [Table 4.3](#), with the exception that G3P13 was replaced by G3PintL1 (see Fjeldså et al., 2003) as the forward primer for GAPDH. Sequencing products were cleaned using Sephadex columns and processed on an AB 3100 DNA sequencer.

Assembly of sequences and alignment

Sequences were assembled using Sequencer v4.7 (Gene Codes Corp., Ann Arbor, Michigan, USA). Mitochondrial sequences were aligned to the chicken (*Gallus gallus*) (Desjardins and Morais, 1990) and checked for any insertions or deletions. Mitochondrial sequences were also translated into amino acids and checked for the presence of stop codons, as well as for frame shifts that might indicate the amplification of nuclear copies of mitochondrial genes or ‘numts’ (Quinn, 1997;

Sorenson and Quinn, 1998). No double peaks were noted in any mtDNA chromatograms.

Sequence alignments were adjusted readily by eye after an initial automatic alignment in Sequencer using the Clustal algorithm. Nuclear sequences were checked carefully for the presence of heterozygous sites as represented by isolated double peaks (single nucleotide polymorphisms) and these were coded using the standard IUPAC codes. The final concatenated alignment, with partitions, is presented as [Appendix 4.3](#).

Base composition

The base composition of gene regions has been shown to affect the outcome of phylogenetic analyses (Collins et al., 1994) and so the significance of these differences was tested for each gene region in PAUP* using a χ^2 (chi-squared) test (Swofford, 2002).

Phylogenetic analyses and statistical tests

Three methods of phylogenetic analysis with different optimality criteria (Holder and Lewis, 2003) were employed to generate estimates of phylogeny: parsimony (MP), Bayesian inference (BI) and Maximum Likelihood (ML).

Each gene region was first analysed individually using BI and ML. To assess the congruence between trees before combining the data, each tree was assessed visually for conflicting branches that had a high level of support. Branches were considered to be highly supported if they had bootstrap values of > 70% (Hillis and Bull, 1993) or posterior probabilities of > 0.95 (Ronquist and Huelsenbeck, 2003).

For the final analyses, concatenated alignments were prepared using the samples described in [Table 4.1](#) which were analysed as follows: 1. all morphological-behavioural data and DNA (MP only), 2. all DNA combined (MP, BI, ML), 3. all mtDNA combined (MP, BI, ML), and 4. all nuclear DNA combined (MP, BI, ML). To save on computing time, only one exemplar for each gene region for each species was chosen for the concatenated alignments, which sometimes included loci from different individuals of the same species ([Table 4.1](#)). Where more than one exemplar of a gene region per species was available, all of these individuals were included in individual gene analyses. Samples from well-marked subspecies were always treated as separate taxa in all phylogenetic analyses.

Parsimony-based phylogenetic analyses were conducted using both TNT (Tree analysis using New Technology; Goloboff *et al.* 2008a, b) and PAUP*. In TNT, the searching strategy employed was the “new technology 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 character data was determined by using the ‘jackknife’ resampling strategy using: 1000 replications, branch-swapping , random addition of five sequences per replicate and, with the exclusion of 36% of the characters per jackknife replicate (Farris *et al.*, 1996; Källersjö *et al.*, 1998). In PAUP* 4.0b10 (Swofford, 2002), parsimony analyses were conducted using heuristic searches with 1000 random addition replicates and tree-bisection-reconnection branch-swapping. All characters were given equal weight and treated as unordered. Clade support was assessed by running 500 nonparametric bootstrap replicates (Felsenstein, 1985a).

Because gene regions can evolve under different models of evolution, it has been argued that a partitioned, mixed-model approach should be used when concatenating these different datasets (Ronquist and Huelsenbeck, 2003; Nylander et al., 2004). It is now possible to perform these analyses for BI and ML. Mixed-model Bayesian analyses were undertaken in Mr Bayes v3.1.2 (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003). Substitution models for each locus were determined in PAUP* with MrModelTest 2.0 (Nylander, 2004) and Modeltest 3.06 (Posada and Crandall, 1998), using the Akaike Information Criterion (Akaike, 1973; Posada and Buckley, 2004) and are presented in [Table 4.4](#).

Mixed-model analyses allowed different parameters (base frequencies, rate matrix or transition/transversion ratio, shape parameter, proportion of invariable sites) to vary (using the *unlink* and *prset* commands) between the partitions (gene regions and mtDNA codon positions) (Nylander et al., 2004; Johansson et al., 2008; Fuchs et al., 2009). Four Metropolis-coupled MCMC chains (one cold and three heated) were run for 5 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 were estimated from the remaining generations. An attempt was made to run each Bayesian analysis 2-3 times (random, independent runs), but this not always possible due to computing time required. The log-likelihood values and posterior probabilities were checked to confirm that the chains had reached stationarity. It was also checked that the Potential

Scale Reduction Factor approached 1.0 (for all parameters) and that the average deviation of split frequencies converged towards zero (Fuchs et al., 2009). The program Tracer v1.4.1 (Rambaut and Drummond, 2007) was used for parameter estimates.

Mixed-model Maximum Likelihood analyses were performed using the Randomised Axelerated Maximum Likelihood for High Performance Computing algorithm (RAxML) v7.0.4 (Stamatakis, 2006; Stamatakis et al., 2008). Mixed-model RAxML analyses use 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 a single data partition) and then also a mixed-model analysis on the nuclear DNA genes, partitioned by each of the four gene regions, and a mixed-model analysis of mt and nuclear DNA combined. Branch support was assessed with 100 nonparametric bootstrap replicates.

Morphological-behavioural character evolution

The evolution of morphological characters and behaviour was assessed by mapping these characters onto the total evidence tree ([Fig. 4.9](#)), as well as into a table with the major clades identified ([Table 4.6](#)).

Results

Base composition

Base composition varied slightly among loci ([Table 4.4](#)), with the mitochondrial DNA showing the typical deficiency of Guanine and Thymine relative to Adenine and Cytosine (e.g. Kirchman et al., 2004; Price and Lanyon, 2002). The χ^2 test implemented in PAUP* detected no significant base composition biases (see [Table 4.4](#) for p-values).

Sequence variation and characteristics

ND2 sequences were obtained for the full 1041 bases pairs (bp) of the gene. It is highly unlikely that any of the mitochondrial sequences were nuclear pseudogenes (Sorenson and Quinn, 1998) because all chromatograms were of good quality and did not contain double-peaks, and all sequences translated into functional amino acids without the presence of internal stop codons. The lengths of the preferred alignments of the nuclear introns are as follows: Fib5 - 562 bp; GAPDH - 438 bp; TGFB - 586 bp. As expected, the nuclear markers were far less variable than the mitochondrial markers (see [Table 4.4](#)). The final concatenated DNA alignment was 2627 bp (1041 bp mtDNA and 1586 bp nuclear DNA) with 405 parsimony informative characters ([Table 4.4](#)).

Evaluation of congruence between the genes

There were no significant branches in conflict for the different gene regions (see [Table 4.5](#) for support values of the major branches recovered in the analyses); thus the data were combined into a large concatenated analysis. The 47 morphological-

behavioural characters ([Appendix 4.2](#)) were all phylogenetically informative, bringing the total dataset to 2674 characters.

Phylogenetic inference

Combined morphological-behavioural and DNA datasets

The parsimony analysis of the combined morphological-behavioural and DNA dataset resulted in six trees with a length of 1320 ([Fig. 4.1](#)). Three well-supported, major clades were recovered, which were also consistently recovered in many of the other individual analyses (see below). These clades are represented on the tree ([Fig. 4.1](#)) by nodes 1, 2, and 3 respectively and the node support values are presented in [Table 4.5](#). Clade 1, hereafter referred to as **Clade Cursorius**, which is supported by a jackknife value of 100%, comprises all members of the genus *Cursorius* as recognised by Gill and Wright (2006): *C. cursor*, *C. rufus*, *C. somalensis*, *C. temminckii* and *C. coromandelicus*. Clade 2, hereafter referred to as **Clade Rhinoptilus**, which is supported by a jackknife value of 98, comprises all members of the genus *Rhinoptilus* as recognised by Gill and Wright (2006): *R. africanus*, *R. cinctus*, *R. chalcopterus* and *R. bitorquatus*. Clade 3, hereafter referred to as **Clade Glareola**, which is supported by a jackknife value of 92, comprises all members of the genus *Glareola* and *Stiltia* as recognised by Gill and Wright (2006): *G. pratincola*, *G. maldivarum*, *G. nordmanni*, *G. ocularis*, *G. nuchalis*, *G. cinerea*, *G. lactea* and *S. isabella*.

In **Clade Cursorius**, *C. temminckii* and *C. coromandelicus* are sister, with *C. rufus* sister to them, and the base of the clade is an unresolved polytomy with the previously mentioned species and *C. cursor* and *C. somalensis*. Note that the placement of *C. coromandelicus* and *C. rufus* is based on morphological-behavioural data only. **Clade**

Rhinoptilus comprises two groupings, **Clade 7** and **Clade 9**. **Clade 7** includes the three subspecies of *R. africanus* sampled, with *R. a. africanus* and *R. a. sharpei* sisters. **Clade 9** includes *R. chalcopterus* sister to *R. bitorquatus*, and these two species are in turn sister to *R. cinctus*. **Clade Glareola** comprises a polytomy with 1. *G. cinerea*; 2. *G. lactea*; 3. **Clade 11** (*G. ocularis* sister to *G. nuchalis*); 4. **Clade 12**. **Clade 12** comprises *G. pratincola* sister to *G. maldivarum*, and these sister to *G. nordmanni* (these three species together form **Clade 13**). The remaining member of **Clade 12** is the monotypic *Stiltia*, in a basal position with a high (JK = 90) level of support.

Relationships between the three major clades are supported (Fig. 4.1), with **Clade Rhinoptilus** sister to **Clade Glareola** (jackknife = 80), and **Clade Cursorius** at the base (jackknife = 100).

Morphological-behavioural dataset

The parsimony analysis of the morphological-behavioural dataset resulted in two equally-parsimonious trees and the consensus tree is presented as Fig. 4.2. All three major clades are again recovered with high jackknife support (Table 4.5), although here **Clade Glareola** is basal with **Clade Rhinoptilus** sister to **Clade Cursorius** (jackknife = 74). All *Cursorius* form an unresolved polytomy suggesting that many of the morpho-behavioural characters are homoplasious in this group. In **Clade Rhinoptilus**, when unsupported nodes are collapsed (jackknife < 50) three groups emerge: 1. *R. cinctus*; 2. *R. chalcopterus* sister to *R. bitorquatus*; 3. *R. africanus* with three subspecies united in a polytomy. **Clade Glareola** comprises two groups: **Clade 12** as above, with *Stiltia* basal and *G. pratincola* sister to *G. maldivarum*; and **Clade**

11 (*G. ocularis* and *G. nuchalis*) sister to *G. cinerea* and *G. lactea*. This latter group is not well-supported, neither is the base of **Clade Glareola**.

Combined DNA datasets

The Bayesian analysis of the combined nuclear and mitochondrial DNA characters are presented as Fig. 4.3 and as the topologies suggested by the different analyses are almost identical, the support values for the ML and MP analyses are also depicted on this figure. Despite the fact that fewer taxa are included than in Fig 4.1 as molecular data were not available for all species, the same three major groups are recovered, with high levels of jackknife, bootstrap and posterior probability support (Table 4.5). The different analyses, however, suggest different relationships between the main clade with differing levels of support (Table 4.5). The parsimony analysis suggests **Clade Cursorius** is basal, with **Clade Rhinoptilus** sister to **Clade Glareola** (JK = 76, BS = 74), whereas the model-based analyses suggest **Clade Rhinoptilus** is basal, with **Clade Cursorius** sister to **Clade Glareola** (PP = 0.93, ML BS < 50).

The internal relationships in the major clades are all identical between the different analyses (with one exception in the internal relationships of **Clade Rhinoptilus**, see below). In **Clade Cursorius**, *C. temminckii* and *C. rufus* are sisters (PP = 0.99, ML BS = 99, JK = 54, BS = 54). **Clade Rhinoptilus** comprises the slightly impoverished **Clades 7 and 9**. **Clade 9** includes *R. chalcopterus* sister to *R. cinctus* (PP = 0.91, JK = 71, BS = 66). An exception to this is shown in the ML tree, which groups *R. chalcopterus* with *R. africanus*, although this is poorly supported (ML BS = < 50). **Clade Glareola** comprises *G. nuchalis* sister to **Clade 12**, which comprises *G.*

pratincola sister to *G. maldivarum*, and these taxa are sister to the monotypic *Stiltia* (PP = 0.78, ML BS = 85, JK = 54, BS = 58).

Mitochondrial DNA dataset

The relationships within each of the major clades are identical to those recovered for the combined DNA analysis, but the relationships among the major clades are less clear, with only the MP analyses supporting **Clade Rhinoptilus** sister to **Clade Glareola** (BS = 86; see [Fig. 4.4](#)).

Nuclear DNA dataset

A reduced number of taxa and informative characters resulted in very poorly resolved trees ([Fig. 4.5](#)). **Clade Cursorius** and *R. africanus* are consistently recovered as monophyletic in all trees, and the only basal resolution is shown by the ML tree for a sister relationship between **Clade Glareola** and **Clade Cursorius** (ML BS = 86).

Nuclear Fib5, GAPDH and TGFB individual datasets

These datasets (see [Figs 4.6 – 4.8](#)) have reduced taxon sampling but nonetheless many common patterns are recovered. In particular, analyses of both the Fib5 and TGFB datasets recover a sister relationship between **Clade Glareola** and **Clade Cursorius**. The Fib5 trees show a sister relationship between *C. somalensis* and *C. temmincki* (PP = 0.94; ML BS = 67), which is not recovered anywhere else.

Discussion

Combining data

The combined morphological-behavioural and DNA analysis has the most strongly supported branches in all of the analyses (Table 4.5), a pattern that is shared by Crowe et al. (2006) in galliforms. The different datasets, while not able to clearly resolve the basal relationships of the three major clades, strongly support each other by recognising the same major and most of the internal clade relationships (Table 4.5). The three major clades recovered in this study correspond broadly with the currently recognised genera within the Glareolidae (Gill and Wright, 2006). Each of the major clades are outlined in more detail below.

The monophyly of the Cursoriinae

The relationship between these clades in the Glareolidae has implications for the division of the family into two subfamilies, with Cursoriinae (“the coursers”) traditionally comprising members of **Clade Cursorius** and **Clade Rhinoptilus** and Glareolinae (“the pratincoles”) comprising members of **Clade Glareola** (Maclean, 1996). This traditional approach is based on selective morphological characters alone (Maclean, 1996). Indeed, it is only the analysis of the morphological-behavioural character matrix that recovers the pattern of **Clade Rhinoptilus** sister to **Clade Cursorius** (jackknife = 74), which would make the division of the Glareolidae into these subfamilies defensible. In contrast, the mitochondrial and nuclear DNA data, and the combined DNA and morphological-behavioural evidence, support topologies that would render the Cursoriinae paraphyletic. Firstly, the combined evidence suggests **Clade Rhinoptilus** is sister to **Clade Glareola** (jackknife = 80), which is

also supported by the parsimony analyses of the DNA and mtDNA data ($JK = 76$, $BS = 74$; $BS = 86$; respectively). The pattern recovered by Baker et al. (2007), who used one exemplar species from each genus, with **Clade Cursorius** sister to **Clade Glareola** (posterior probability = 1.0 in Baker et al., 2007), is recovered by both the Bayesian and ML analyses of the combined DNA data but without support ($PP = 0.93$, $ML\ BS < 50$). A similar result is obtained with some of the nuclear data analyses (see [Table 4.5](#)). Hence, even though there is not a well-supported sister clade to the pratincoles (it is either the “rhinoptiline” or the “cursorinine” coursers), it seems highly unlikely that the Cursoriinae are monophyletic.

Clade Cursorius (Cursorius)

Clade Cursorius recovers the members of the genus *Cursorius* as circumscribed by Sclater (1924), Maclean (1996) and Gill and Wright (2006). The larger circumscription of *Cursorius* to include all the coursers and thus also members of **Clade Rhinoptilus** below (e.g. Snow, 1978; Maclean and Urban, 1986; see [Table 1.4](#)) may not be monophyletic.

The sister relationship recovered between *C. temminckii* and *C. coromandelicus* is supported by Snow (1978) and Maclean (1996) who regard these two species as members of a “superspecies” (see [Table 4.2](#)). Although these two species are quite different in size, they share a number of plumage features, such as the orange crown and dark belly patch, which are unique in *Cursorius*. Curiously, the plumage pattern of these species is highly similar to the unrelated *Vanellus gregarius* (Charadrii; Charadriiformes; Hayman et al., 1986), which may be due to convergence as both taxa occur in similar open habitats. Remarkably, *V. gregarius* even shares the white

rump and black lores of *C. coromandelicus*. *Cursorius temminckii* and *C. coromandelicus* occur in a slightly different habitat to other members of the Cursoniinae, preferring open areas (regularly burnt grasslands) often not far from wooded areas, in strong contrast to the open desert habitats favoured by the other members of *Cursorius* (Hayman et al., 1986; Maclean, 1996). This species-pair also shares an unusual African-Indian biogeography with members of *Otis*, *Glareola*, *Rhinoptilus* and *Pterocles* (see [Chapter 6](#)). The remaining species of *Cursorius*, which share the grey rear crown and plain underparts are all species of open desert, and are often linked together as one “superspecies” (Snow, 1978; Maclean, 1996). It is therefore surprising that *C. rufus* should be consistently recovered as sister to the *C. coromandelicus*-*C. temminckii* clade. *Cursorius somalensis*, which is variously treated as a subspecies of both *C. rufus* and *C. cursor* ([Table 1.4](#)), is not recovered as sister to either of these taxa and this probably indicates that it warrants species status, although further sampling would be required to validate this finding.

Clade Rhinoptilus (Rhinoptilus and Smutsornis)

The sister relationship recovered between *R. chalcopterus* and *R. bitorquatus*, which are similar morphologically, is also supported by Snow (1978) who links these in a “superspecies” ([Table 4.2](#)). There is a striking difference in abundance between these two species. *Rhinoptilus bitorquatus* is one of the rarest birds in the world, having been sighted only a handful of times and thought extinct for much of the 20th century (Hayman et al., 1986). It occupies the densest woodland habitat of any courser, and is only known from a small area in India (Maclean, 1996). *Rhinoptilus chalcopterus* is also a species of dry woodlands, but is widespread in Africa and moves extensively in response to rain fronts (Maclean and Urban, 1986; Hockey et al., 2005). These two

species are, in turn, sister to *R. cinctus*, which also occurs in dry woodland habitats as opposed to the open plains and low shrublands occupied by *R. africanus* (Maclean, 1996), the only other member of **Clade Rhinoptilus**. *Rhinoptilus africanus* and *R. cinctus* are not likely to be sister, and thus the genus *Hemerodromus* (Heuglin, 1863) is not monophyletic. They are linked by the disruptive colouration on their upperparts as both have streaked crowns and scaled feather patterns on their backs, characters lacking in all other glareolids. This plumage is probably adaptive for camouflage, especially in the open-country *R. africanus*, as these nocturnal species roost on the ground during the day (Maclean, 1996). The plumage development is also likely to be neotonous as other glareolids only show upperpart scaling in the juveniles (Hayman et al., 1986), which one would expect to require increased camouflage as they crouch to escape predators instead of running or flying away like the adults (Maclean, 1996). The basal position of *R. africanus* is consistent with the placement of its mallophagan feather-lice (Timmerman, 1952, although assessing the “primitive” nature of the feather-lice themselves is very subjective) and conflicts with Maclean’s (1996) suggestion that *R. chalcopterus* is the most “primitive”. Although it was beyond the scope of this research to evaluate the taxonomy of the different subspecies of *R. africanus*, the very slight genetic differences and subtle colour variations between the three subspecies included does not suggest that any of them are potential cryptic species.

Clade Glareola (Glareola and Stiltia)

The three clades recovered for the members of *Glareola* (excluding *Stiltia*; see below) correspond to the three “superspecies” suggested by Snow (1978) as described in [Table 4.2](#). *Glareola cinerea* and *G. lactea* are small, pale-plumaged species that occur

on sandy river banks in Africa and India respectively. These taxa are recovered in the morphological-behavioural analysis as sister to *G. ocularis* and *G. nuchalis*, medium-sized, dark-plumaged species that have a white sub-ocular line and occur on rocky islands in rivers. Previously, these riverine species, excluding *G. ocularis* and sometimes *G. nuchalis*, have been allied in the genus *Galachrysia* (Maclean, 1996). Since DNA data were only available for one species (*G. nuchalis*), future studies should examine DNA of these species to clearly elucidate these relationships.

The remaining species in *Glareola*, are long-winged and the most migratory of all species in the family (Maclean, 1996). They are united by Maclean (1996) as a “superspecies”, although the inclusion of *G. nordmanni* (as it widely overlaps in distribution with *G. pratincola*) has been questioned (Snow, 1978). The sister taxa *G. pratincola* and *G. maldivarum*, share the rufous underwing covers that are used as an important taxonomic character in the family (Hayman et al., 1986). These three species also all have a distinct non-breeding plumage, a trait shared with *Stiltia*.

The aberrant Stiltia

In morphology, *Stiltia isabella* appears intermediate in form between a courser and a pratincole, and it has been suggested to be an evolutionary link between these two groups, sometimes even being accorded its own subfamily, Stiltiinae (Maclean, 1996). It has the long legs and long neck of a courser, but the very long outer primaries typical of a pratincole, and it feeds on its large insect prey both on the ground and aerially (Maclean, 1996; Fig 4.9). Indeed, *Stiltia* is widely regarded as an enigmatic taxon, and the young have the unique habit of hiding in subterranean mammal burrows when threatened at their nest sites in the Australian outback

(Maclean, 1996). The analyses here clearly place *Stiltia* as nested within the pratincoles, which suggest that the long legs and neck are secondary adaptations to terrestrial feeding. It seems Vieillot was correct when he placed the species into the genus *Glareola* when he described it in 1816. It is interesting that *Stiltia* is placed in the same position by both the DNA and morphological-behavioural characters, which suggests that it is not new molecular data that renders *Glareola* non-monophyletic, but rather the cladistic framework which does not place undue emphasis on certain morphological characters, such as leg length, which is an example of convergence in this case.

Behavioural and morphological character evolution

Although the results clearly support the recognition of three major clades within the Glareolidae, the uncertainty in resolving the deeper level nodes makes it difficult to elucidate the ancestral grouping and resulting character states. It is possible that the addition of more sequence data might clarify their position, but given the strength with which the three major clades are recovered, it seems more likely that a rapid radiation (hard polytomy) occurred early in the evolution of the Glareolidae which has left the relationships among the major clades to discern with confidence. There have not been many character state reversals within the major clades. The habitats occupied, foraging level, activity time and migratory behaviour seem to be highly conserved within clades, suggesting there are high evolutionary costs to changing from these relatively specialist niches (Fig. 4.9; Table 4.6). The Glareolidae occupy relatively extreme niches (deserts and ephemeral river habitats) where relatively few other bird families have diversified (Maclean, 1996).

Many of the characters described in [Table 4.6](#) and [Appendix 4.2](#) are correlated with the clades and are thus phylogenetically informative synapomorphies. For example, the large eyes of *Rhinoptilus* are a likely adaptation to their nocturnal behaviour, as are the scaled upperparts for day-roosting, although this seems to have been lost in *R. chalcopterus* and *R. bitorquatus*, which are found in denser woodlands where camouflage might be less important.

The colouration of the bare parts, upperparts and underparts seems especially homoplasious, and not correlated with clades, with the exception of the central breast banding. The homoplasious nature of the upperpart colour is to be expected, as the upperparts are highly camouflaged and thus under selection pressure. For example, many of the *Cursorius* have upperpart colours which match the substratum to which they are restricted (Maclean, 1996). The underwing coverts, nuchal patches and head markings are presumably used in breeding displays, and thus under strong sexual selection, but very little is known about these displays (Maclean, 1996).

Long-distance migratory behaviour is usually associated with long, pointed wings (which results in reduced energy consumption on long flights; Winkler and Leisler, 1992), and aerial feeding also seems associated with long, pointed wings and a forked tail. In the Glareolidae, it is not possible to reconstruct the order of these changes, as aerial prey is typically highly seasonal, and so the long wings might have arisen either to hunt the prey or to move large distance between seasonal prey sources. An interesting case is *Stiltia*, which feeds on both aerial and terrestrial insects. It has long wings (but it is also a short-distant migrant; Maclean, 1996) typical of pratincoles, but also has long legs and neck like coursers, which given the phylogeny recovered,

suggests that the courser-like features are secondarily derived ([Fig. 4.9](#)).

Further research

The placement of some of the taxa in this study is based solely on morphological-behavioural data (where DNA data were not available) and future research should endeavour to obtain samples and sequences for these species to increase the number of characters on which to base the phylogenetic hypotheses.

Table 4.1: Samples analysed in this study, with sample source, collection locality, and extraction codes.

The components of the concatenated data sets are detailed, and samples in bold were used in the concatenated genetic analyses.

For each gene region, either the extraction codes (CC = Callan Cohen; ABS = Anna Seles) or Genbank numbers are given.

Taxon	Source of genetic sample (where a genetic sample was not obtained the superspecies is given per Snow, 1978; Maclean, 1996)	Genetic sample locality	Morpho-behav. data	Extraction codes and Genbank numbers			
				ND2	Fib5	GAPDH	TGFB
<i>Cursorius cursor</i>	<i>Superspecies with C. rufus</i>		Yes				
<i>Cursorius somalensis</i>	Callan Cohen (COHENKEN99, Shaba)	Kenya	Yes	ABS566	ABS566	ABS566	ABS566
<i>Cursorius rufus</i>	CONCATENATED from the two samples below: Callan Cohen (Danielskuil, 15Jan2000) Callan Cohen (Hobatere, Namibia, 4H0926)	South Africa South Africa Namibia	Yes Yes Yes	CCB60	CCB60	CCB60	CCB60
<i>Cursorius temminckii</i>	CONCATENATED from the two samples below: Callan Cohen (Hobatere, Namibia, 10March05, BE30453) Genbank: DQ385090	Namibia	Yes	DQ385090	CCB58 CCB58	CCB58	CCB58
<i>Cursorius coromandelicus</i>	<i>Superspecies with C. temminckii</i>		Yes				
<i>Rhinoptilus (Smutsornis) a. africanus</i>	Callan Cohen (Kimberley, Apr2000)	South Africa	Yes	CCB55	CCB55	CCB55	CCB55
<i>Rhinoptilus (Smutsornis) a. sharpei</i>	Callan Cohen (Halali, Etosha, Namibia, 5Apr05, roadkill)	Namibia	Yes	CCB56	CCB56	CCB56	CCB56
<i>Rhinoptilus (Smutsornis) a. gracilis</i>	Callan Cohen (Chyulu, Kenya, Aug99, NRFA48, KEN9922)	Kenya	Yes			CCB57	
<i>Rhinoptilus cinctus</i>	Callan Cohen (Zambia, via Claire Spottiwoode)	Zambia	Yes	ABS567	ABS567		ABS567
<i>Rhinoptilus chalcopterus</i>	Callan Cohen (Hobatere, Namibia, 4Apr04, 4H09003)	Namibia	Yes	CCB53	CCB53	CCB53	
<i>Rhinoptilus bitorquatus</i>	<i>Superspecies with R. chalcopterus</i>		Yes				
<i>Stiltia isabella</i>	Genbank: EF373268		Yes	EF373268			
<i>Glareola pratincola</i>	Genbank: EU372681		Yes	EU372681			
<i>Glareola maldivarum</i>	Genbank: EF373241		Yes	EF373241			
<i>Glareola nordmanni</i>	<i>Superspecies with G. pratincola and G. maldivarum</i>		Yes				
<i>Glareola ocularis</i>	<i>Superspecies with G. nuchalis</i>		Yes				
<i>Glareola nuchalis</i>	FM429394 (Field Museum, Chicago)	Central African Republic	Yes	ABS573	ABS573	ABS573	ABS573
<i>Glareola cinerea</i>	<i>Superspecies with G. lactea</i>		Yes				
<i>Glareola lactea</i>	<i>Superspecies with G. cinerea</i>		Yes				
<i>Larus</i>	CONCATENATED from the two samples below:		Yes	AY631363	EU739270	FM209966	EU737395
<i>Larus delawarensis</i>	Genbank: AY631363			AY631363			
<i>Larus marinus</i>	Genbank: multiple			EU739270			
				FM209966			
				EU737395			

Table 4.2: Superspecies recognised in the Glareolidae by Snow (1978) and Maclean (1996) showing those represented in this study.

TAXON	SUPERSPECIES SUGGESTED BY SNOW, 1978 AND MACLEAN, 1996	EVIDENCE USED IN THIS STUDY:	
		DNA EVIDENCE	MORPHOLOGICAL/BEHAVIOURAL EVIDENCE
<i>Cursorius cursor</i>	Superspecies 1		YES
<i>Cursorius somalensis</i>	Superspecies 1	DNA	YES
<i>Cursorius rufus</i>	Superspecies 1	DNA	YES
<i>Cursorius temminckii</i>	Superspecies 2 (sometimes with 1)	DNA	YES
<i>Cursorius coromandelicus</i>	Superspecies 2 (sometimes with 1)		YES
<i>Rhinoptilus (Smutsornis) africanus</i>		DNA	YES
<i>Rhinoptilus cinctus</i>		DNA	YES
<i>Rhinoptilus chalcopterus</i>	Superspecies 3	DNA	YES
<i>Rhinoptilus bitorquatus</i>	Superspecies 3		YES
<i>Stiltia isabella</i>		DNA	YES
<i>Glareola pratincola</i>	Superspecies 4	DNA	YES
<i>Glareola maldivarum</i>	Superspecies 4	DNA	YES
<i>Glareola nordmanni</i>	Superspecies 4		YES
<i>Glareola ocularis</i>	Superspecies 5		YES
<i>Glareola nuchalis</i>	Superspecies 5	DNA	YES
<i>Glareola cinerea</i>	Superspecies 6		YES
<i>Glareola lactea</i>	Superspecies 6		YES

Table 4.3: Primers used for amplification and sequencing of the Glareolidae.

Gene Region	Primer Name	Primer Sequence	Source
ND2	L5204	5'-GCTAACAAAGCTATCGGGCCCAT-3'	Cicero and Johnson, 2001
	H6312	5'-CTTATTAAAGGCTTGAGGCC-3'	
Fib5	Fib5	5'-CGCCATACAGAGTATACTGTGACAT-3'	Fuchs et al., 2004;
	Fib6	5'-GCCATCCTGGCGATTCTGAA-3'	Kimball et al., 2009
TGFB	TGFB2.5F	5'-GAAGCGTGCTCTAGATGCTG-3'	Primmer et al., 2002;
	TGFB2.6R	5'-AGGCAGCAATTATCCTGCAC-3'	Kimball et al., 2009
GAPDH	G3P13b	5'-TCCACCTTGATGCGGGTGCTGGCAT-3'	Fjeldså et al., 2003
	G3P14b	5'-AAGTCCACAACACCGGTTGCTGTA-3'	
	G3PintL1	5'-GAACGACCATTTGTCAAGCTGGTT-3'	

Table 4.4: Data characteristics and estimated model parameters for the datasets (for all the gene regions and concatenated datasets), including length of the alignment, number of variable and informative sites, model selected for the BI analyses, mean of the model parameters, BI likelihood score (arithmetic mean), ML likelihood score and MP tree numbers. The base frequency chi-squared test results are also included.

	Total (M-B +DNA)	M-B (Morpho-Behav)	All DNA	Mt DNA	Nuc DNA	ND2	Fib5	GAPDH	TGFB	
No. of characters										
No. of characters (total)	2674		47	2627	1041	1586	1041	562	438	586
Variable characters	779		47	732	436	296	436	104	97	95
Proportion variable	0.291		1	0.279	0.419	0.187	0.419	0.185	0.221	0.162
Informative characters	452		47	405	297	108	297	38	31	39
Model parameters										
Model selected	/		/	/	/	/	GTR+I+G	HKY+G	HKY	GTR
r(A<->C)	/		/	/	/	/	0.021	0.114	0.095	0.096
r(A<->G)	/		/	/	/	/	0.609	0.316	0.241	0.452
r(A<->T)	/		/	/	/	/	0.024	0.051	0.071	0.040
r(C<->G)	/		/	/	/	/	0.020	0.092	0.082	0.118
r(C<->T)	/		/	/	/	/	0.288	0.346	0.415	0.227
r(G<->T)	/		/	/	/	/	0.038	0.082	0.095	0.067
pi(A)	/		/	/	/	/	0.347	0.325	0.215	0.250
pi(C)	/		/	/	/	/	0.355	0.159	0.178	0.213
pi(G)	/		/	/	/	/	0.080	0.199	0.340	0.230
pi(T)	/		/	/	/	/	0.217	0.318	0.267	0.308
Alpha	/		/	/	/	/	1.459	68.714	97.667	97.667
Proportion invariable	/		/	/	/	/	0.461	n/a	n/a	n/a
Base frequency test										
Chi-squared value	/		/	/	/	/	9.8716	2.78556	1.3868	2.7238
Degrees of freedom	/		/	/	/	/	33	27	18	21
p	/		/	/	/	/	1	1	1	1
Tree characteristics										
MP No. of trees	6		2	1;1	1	3 as mt DNA	n/a	n/a	n/a	
BI LnL Bayesian	n/a		n/a	-8905.14	-4941.10	-3940.82	-4941.10	-1447.31	-1123.40	-1394.52
ML RaxML (Max Likelihood)	n/a		n/a	-8866.40	-4928.53	-3925.76	-4928.53	-1432.24	-1112.70	-1382.34

Table 4.5: Resolution and support values of recovered nodes from the concatenated and individual analyses. The node numbers refer to Fig. 4.1, and are also accompanied by a description. Parsimony (MP) support is jackknife for the COMB and M-B analyses, and bootstrap for the others. Posterior probabilities and bootstrap values are given for the Bayesian (BI) and Maximum Likelihood (ML) analyses respectively. Strongly-supported values (JK, BS >= 75; PP >= 0.95) are highlighted in bold. The first number in the All DNA column refers to jackknife support.

Highly supported relationships in bold; COMB = combined M-B and DNA data; M-B = morpho-behavioural; tri = trichotomy.

Node description	Node No.	COMB		M/B MP	All DNA			All mitochondrial			All nuclear			Fib5			GAPDH			TGFB			
		MP	MP		MP	BI	ML	MP	BI	ML	MP	BI	ML	MP	BI	ML	MP	BI	ML	MP	BI	ML	
<i>Cursorius</i> monophyletic	1	100	100	00/100	1	100		100	1	100	100	0.58	100	Yes	1	100	n/a	n/a	n/a	1	100		
<i>Rhinoptilus</i> monophyletic	2	98	91	76/75	1	100		70	1	99			39							0.52	83		
<i>Pratincoles</i> monophyletic	3	80	90	81/82	1	100		81	1	100	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	
<i>Rhinoptilus</i> sister to Pratincoles	4	80		76/74				86	tri													0.68	100
<i>Cursorius</i> sister to Pratincoles					0.94	4			tri	7	Yes		85	0.57	85								
<i>Rhinoptilus</i> and <i>Cursorius</i> sister				74																			
<i>Cursorius temmincki</i> sister to <i>C. coromandelicus</i>	5	70		n/a	n/a	n/a		n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	
<i>Cursorius rufus</i> sister to 5	6	51		54/54	0.99	99		Yes	0.87	84	55	0.67	67				n/a	n/a	n/a	Yes	0.92	96	
<i>Cursorius rufus</i> sister to <i>C. somalensis</i>																	n/a	n/a	n/a				
<i>Rhinoptilus africanus</i> monophyletic	7	99	71	99/100	1	100		100	1	100	100	98	100			1	100	Yes	1	100	1	100	
<i>Rhinoptilus a. africanus</i> sister to <i>R. a. sharpei</i>	8	88		n/a	1	n/a		100	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	0.99	100	n/a	n/a	n/a	
<i>Rhinoptilus cintus</i> sister to Clade 10	9	80	No	71/66	0.91			65	0.73	37			64	Yes		48	n/a	n/a	n/a	n/a	n/a	n/a	
<i>Rhinoptilus chalcopterus</i> sister to <i>R. bitorquatus</i>	10	78	84	n/a	n/a	n/a		n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	
<i>Glareola ocularis</i> sister to <i>G. nuchalis</i>	11	89	87	n/a	n/a	n/a		n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	
<i>Glareola cinerea</i> sister to <i>G. lactea</i>				55	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	
<i>Stiltia</i> sister to Clade 13	12	90	92	54/58	0.78	85		59	0.75	42	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	
<i>Glareola nordmanni</i> sister to Clade 14	13	87	85	99/100	1	100		100	1	100	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	
<i>Glareola pratincola</i> sister to <i>G. maldivarum</i>	14	60	56	99/100	1	100		100	1	100	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	

Table 4.6: Selected morphological and behavioural characters of species in the Glareolidae shown in relation to the major clades identified in this study.

Taxa	Clades recovered in this study		Behavioural characters			Migrant	Gregarious	Morphological characters					No hallux	Bill length	Long-wings & forked tail
	Clade	Subclade	Nocturnal	Feeding mode	Habitat			Upperpart scaling	Upperchest band	Bold eye-stripe	Leg length				
<i>Cursorius cursor</i>	1 <i>Cursorius</i>			Cursorial	Desert	Yes				Present	Long	Absent	Long		
<i>Cursorius somalensis</i>	1 <i>Cursorius</i>			Cursorial	Desert					Present	Long	Absent	Long		
<i>Cursorius rufus</i>	1 <i>Cursorius</i>			Cursorial	Desert					Present	Long	Absent	Long		
<i>Cursorius temminckii</i>	1 <i>Cursorius</i>	Clade 5		Cursorial	Open areas in woodland	Some popns				Present	Long	Absent	Long		
<i>Cursorius coromandelicus</i>	1 <i>Cursorius</i>	Clade 5		Cursorial	Open areas in woodland					Present	Long	Absent	Long		
<i>Rhinoptilus (Smutsornis) africanus</i>	2 <i>Rhinoptilus</i>		Yes	Cursorial	Desert		Present	Present	Present	Present	Long	Absent	Short		
<i>Rhinoptilus cinctus</i>	2 <i>Rhinoptilus</i>	Clade 9	Yes	Cursorial	Dry woodland		Present	Present	Present	Present	Long	Absent	Short		
<i>Rhinoptilus chalcopterus</i>	2 <i>Rhinoptilus</i>	Clade 9	Yes	Cursorial	Dry woodland	With rains	Present	Present	Present	Present	Long	Absent	Short		
<i>Rhinoptilus bitorquatus</i>	2 <i>Rhinoptilus</i>	Clade 9	Yes	Cursorial	Dry woodland		Present	Present	Present	Present	Long	Absent	Short		
<i>Stiltia isabella</i>	3 <i>Glareola</i>	Clade 12		Cursorial and aerial	Often near water	Yes	Yes				Long		Short, wide gape	Present	
<i>Glareola pratincola</i>	3 <i>Glareola</i>	Clade 12		Aerial	Often near water	Yes	Yes	Present			Medium		Short, wide gape	Present	
<i>Glareola maldivarum</i>	3 <i>Glareola</i>	Clade 12		Aerial	Often near water	Yes	Yes	Present			Medium		Short, wide gape	Present	
<i>Glareola nordmanni</i>	3 <i>Glareola</i>	Clade 12		Aerial	Often near water	Yes	Yes	Present			Medium		Short, wide gape	Present	
<i>Glareola ocularis</i>	3 <i>Glareola</i>			Aerial	Rivers - rocky	Yes	Yes				Short		Short, wide gape	Present	
<i>Glareola nuchalis</i>	3 <i>Glareola</i>			Aerial	Rivers - rocky	Yes	Yes				Short		Short, wide gape	Present	
<i>Glareola cinerea</i>	3 <i>Glareola</i>			Aerial	Rivers - sandy		Yes				Short		Short, wide gape	Present	
<i>Glareola lactea</i>	3 <i>Glareola</i>			Aerial	Rivers - sandy		Yes				Short		Short, wide gape	Present	

Key to clade colours	
1 <i>Cursorius</i>	Clade 5
2 <i>Rhinoptilus</i>	Clade 9
3 <i>Glareola</i>	Clade 12

Figure Legends Ch. 4

Fig. 4.1: Strict consensus parsimony cladogram for concatenated dataset of all morpho-behavioural and multilocus DNA data (2674 characters, 6 trees, L = 1320). Values depicted directly to the right of the node are as follows:
#Clade Number/ Jackknife support/ Partitions that support the clade (Key: M = morpho-behavioural characters; D = all DNA partitions; N = ND2; F = Fib5; T = TGFB; G = GAPDH).

Fig. 4.2: Strict-consensus parsimony cladogram (from 2 trees) for morpho-behavioural data, with jackknife support values shown if JK>50. JK values are depicted directly to the right of the node (except in the *Rhinoptilus africanus* trichotomy where it would overlap with the taxon line; in this case, the value is moved downwards slightly).

Fig. 4.3: Mixed-model Bayesian analysis of the combined nuclear and mtDNA dataset with the support values of the BI, ML and MP analyses; support values are presented directly to the right of nodes and represent: posterior probabilities (BI)/ bootstrap (ML)/ jackknife (MP)/ bootstrap (MP). Nodes not supported, or supported by BS or JK < 50 are indicated by “-“.

Fig. 4.4: Mixed-model Bayesian analysis of the mtDNA dataset with the support values of the BI, ML and MP analyses; support values are presented directly to the right of nodes and represent: posterior probabilities (BI)/ bootstrap (ML)/ bootstrap (MP). Nodes not supported, or supported by BS < 50 are indicated by “-“.

Fig. 4.5: Mixed-model Maximum Likelihood analysis of the nuclear DNA dataset with the support values of the BI, ML and MP analyses; support values are presented directly to the right of nodes and represent: posterior probabilities (BI)/ bootstrap (ML)/ bootstrap (MP). Nodes not supported indicated by “-“.

Fig. 4.6: Bayesian analysis of the Fib5 DNA dataset with the support values of the BI and ML analyses; support values are presented directly to the right of nodes and represent: posterior probabilities (BI)/ bootstrap (ML). Nodes not supported are indicated by “-“.

Fig. 4.7: Bayesian analysis of the GAPDH DNA dataset with the support values of the BI and ML analyses; support values are presented directly to the right of nodes (except in *Rhinoptilus-Cursorius* trichotomy where it would overlap with the taxon line; in this case, the value is moved downwards slightly) and represent: posterior probabilities (BI)/ bootstrap (ML). Nodes not supported are indicated by “-“.

Fig. 4.8: Bayesian analysis of the TGFB DNA dataset with the support values of the BI and ML analyses; support values are presented directly to the right of nodes and represent: posterior probabilities (BI)/ bootstrap (ML). Nodes not supported are indicated by “-“.

Fig. 4.9: Strict consensus parsimony cladogram (Fig. 4.1) with selected morphological and behavioural characters mapped.

Fig. 4.10: Live capture and release of *Rhinoptilus chalcopterus*: individual located by vehicle, and then mesmerised by spotlight before being caught in a hoop-net. © Callan Cohen.

Fig. 4.11: Live capture and release of *Rhinoptilus chalcopterus*: individual being banded to ensure it is recognised if recaptured. © Callan Cohen.

Fig. 4.12: Live capture and release of *Rhinoptilus chalcopterus*: all birds are photographed. In this case the spread wing reveals the seldom-seen coppery-bronze primary wing tips after which the species is named. © Callan Cohen.

Fig. 4.1

4.36

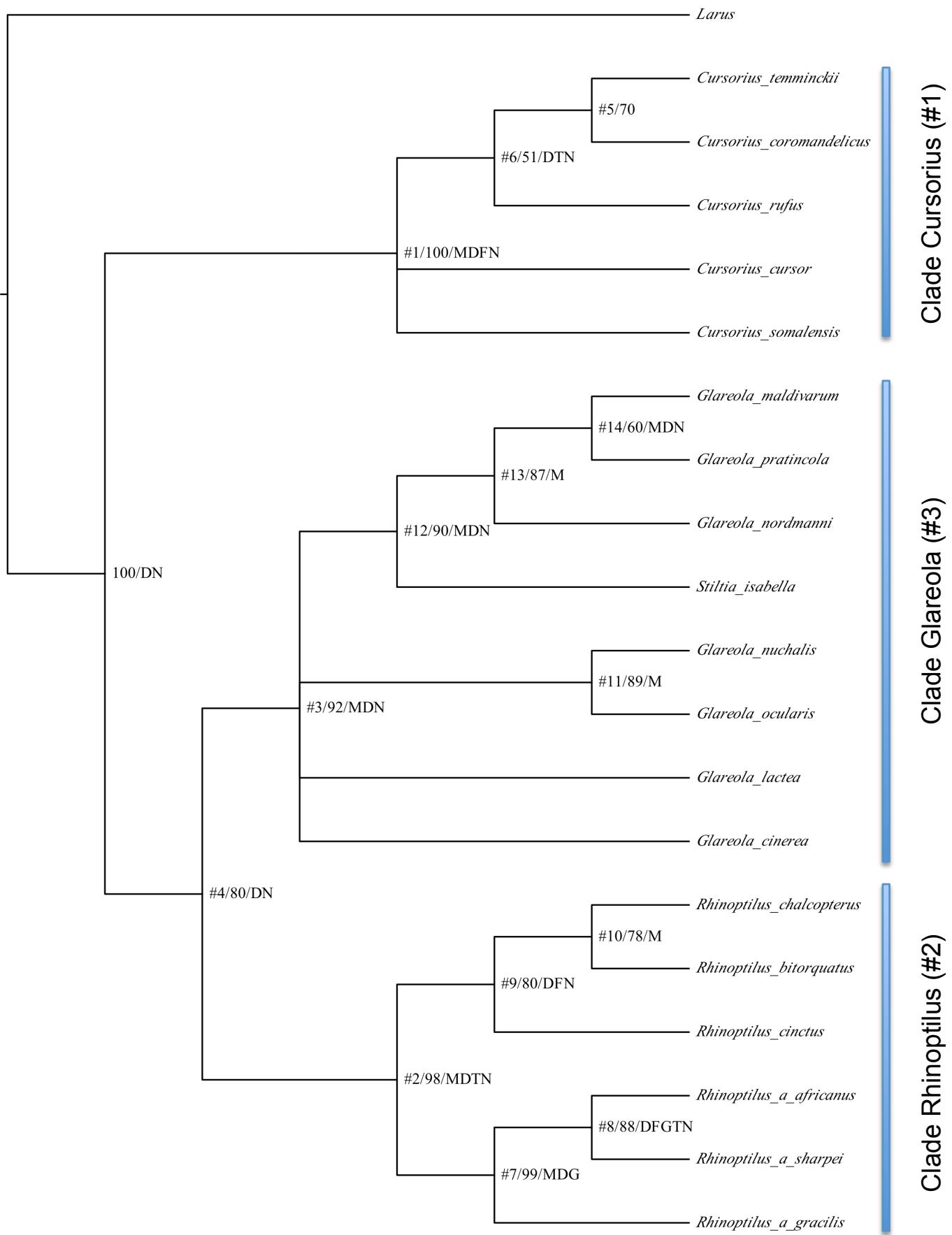


Fig. 4.2

4.37

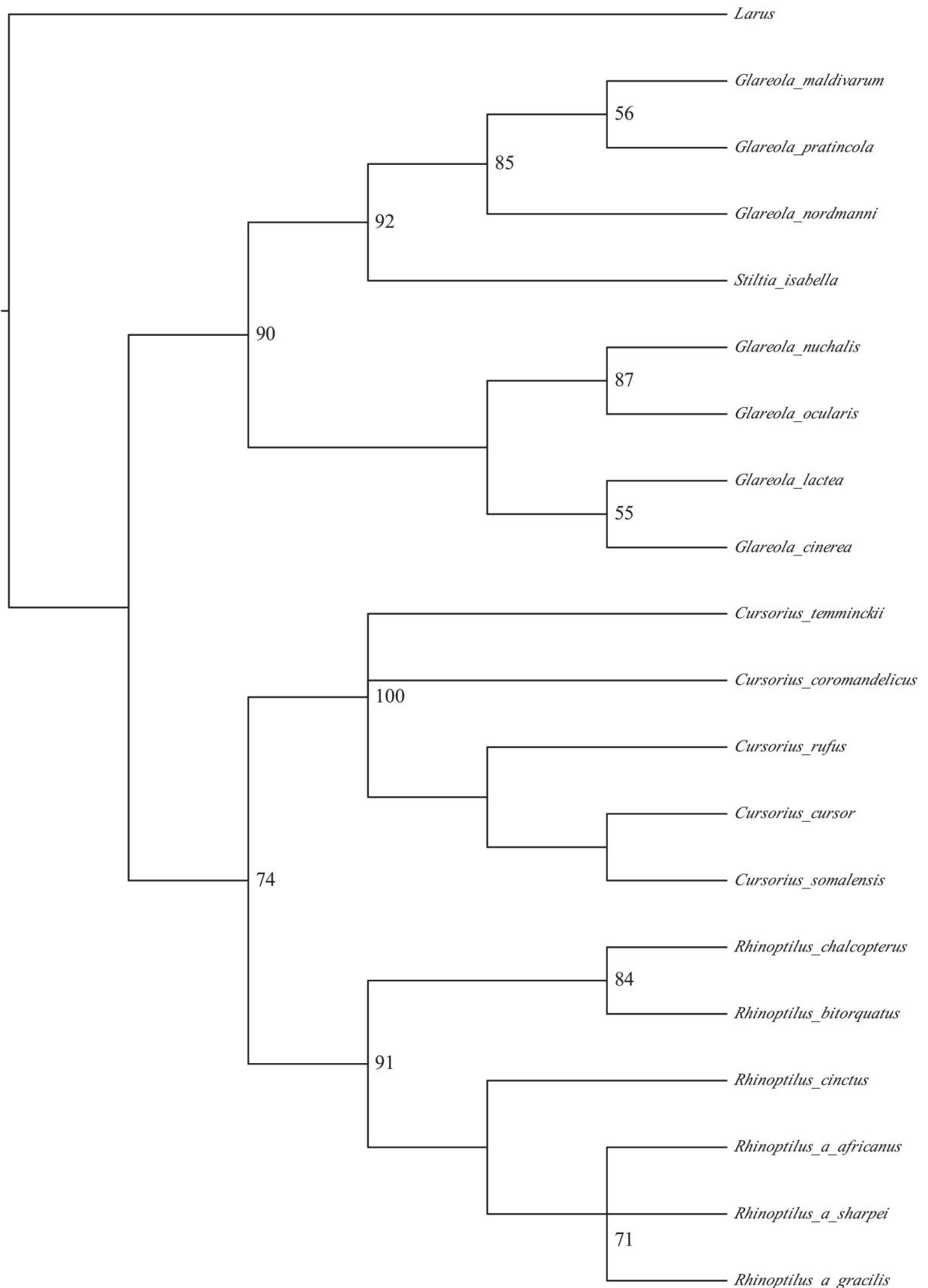


Fig. 4.3

4.38

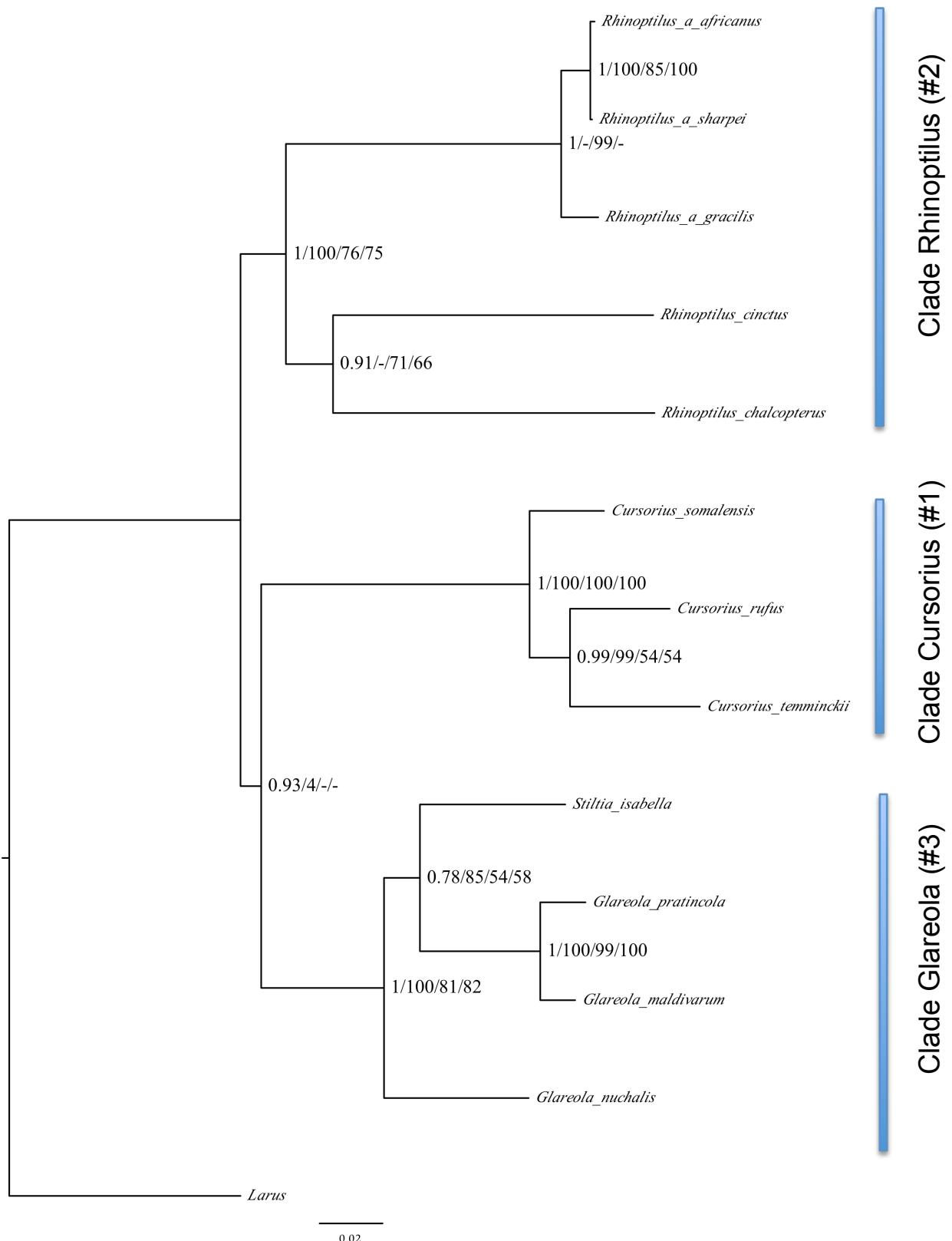


Fig. 4.4

4.39

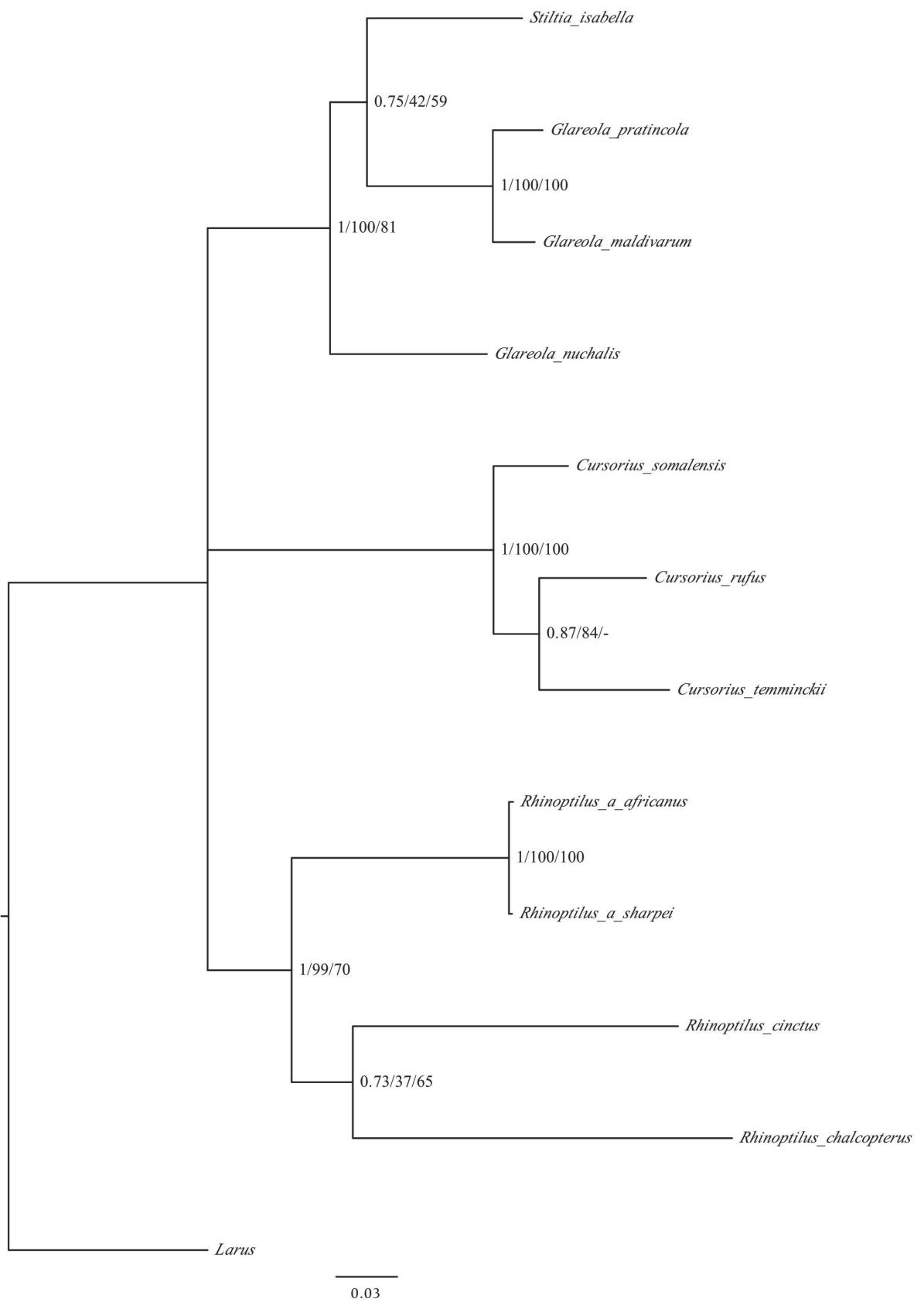


Fig. 4.5

4.40

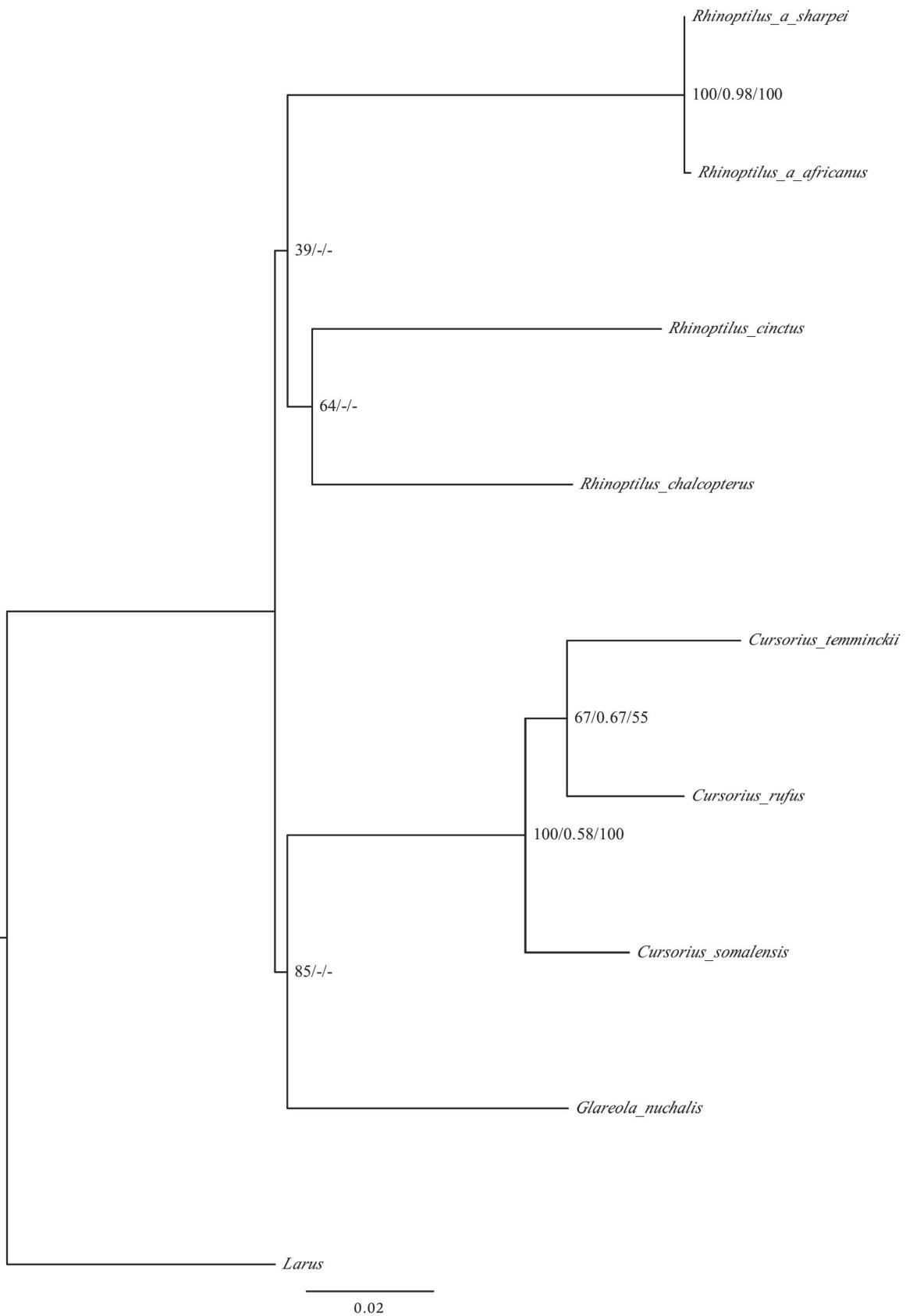


Fig. 4.6

4.41

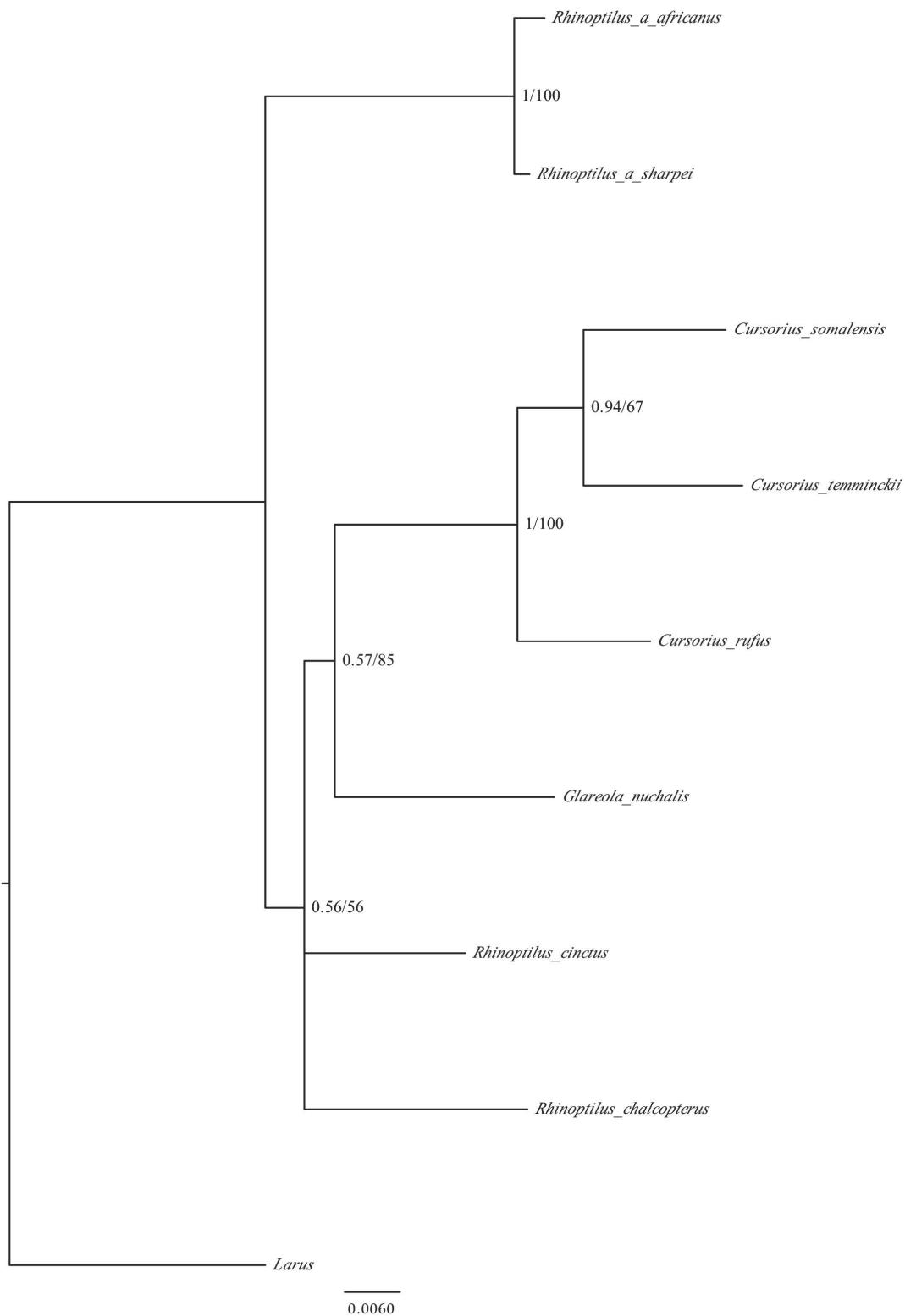


Fig. 4.7

4.42

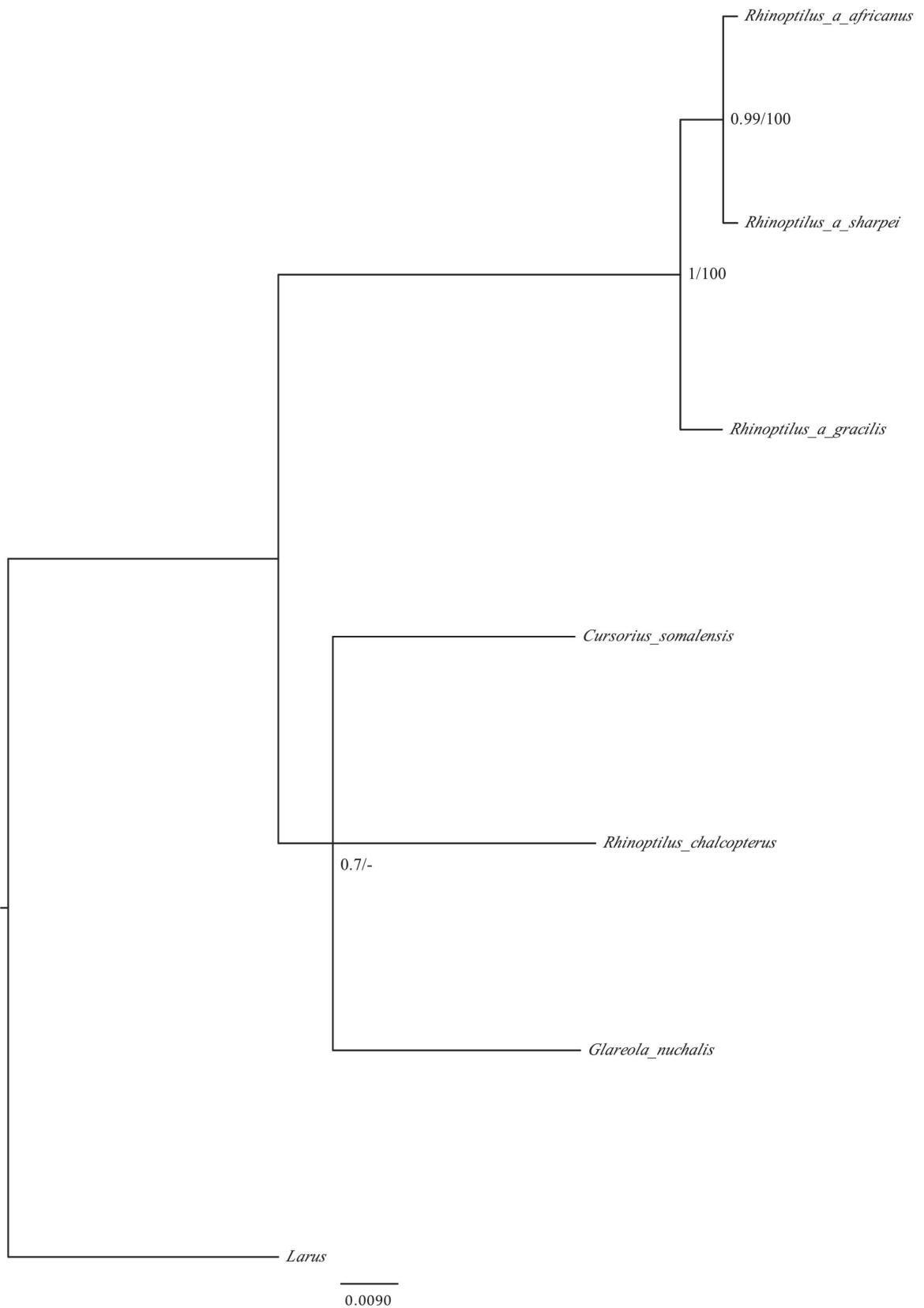


Fig. 4.8

4.43

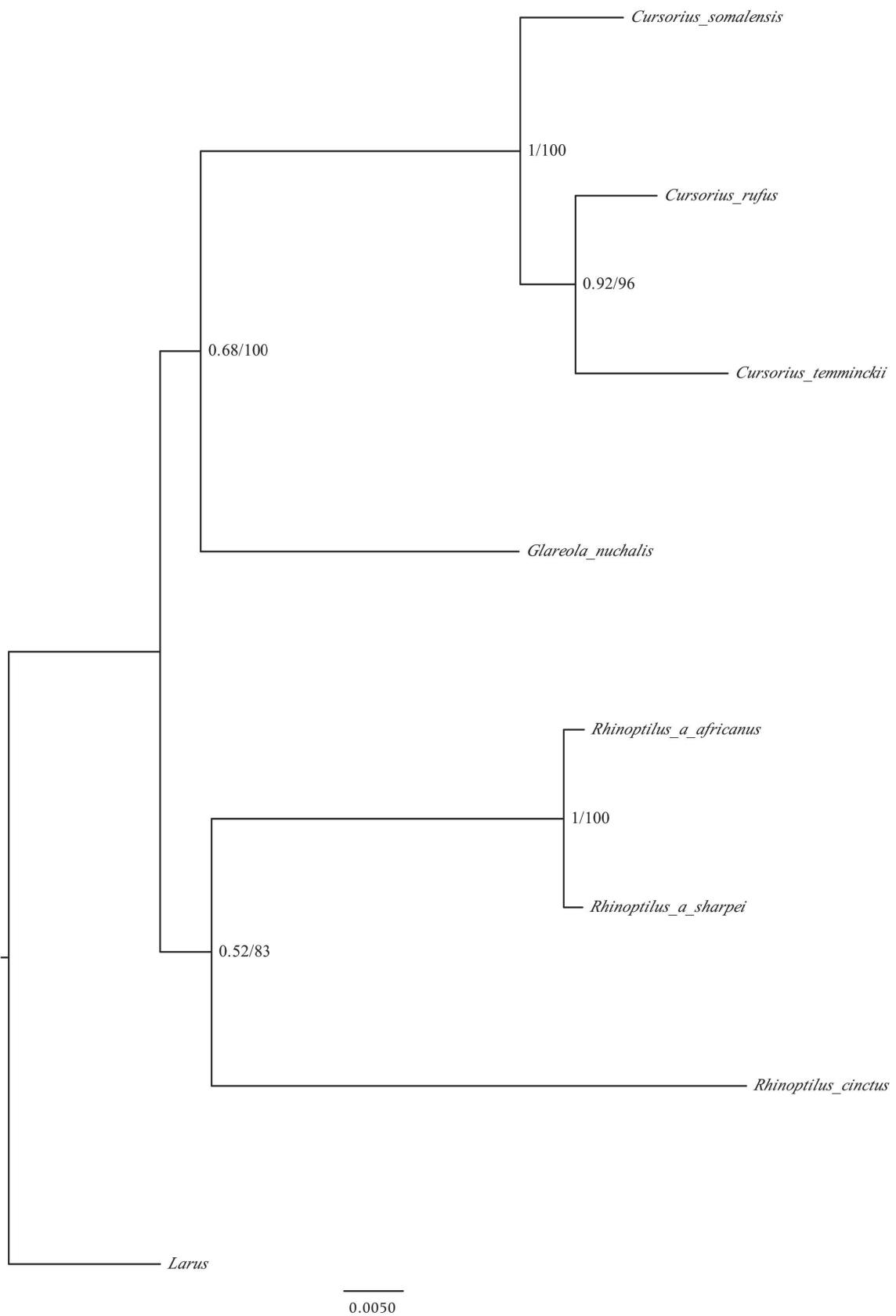
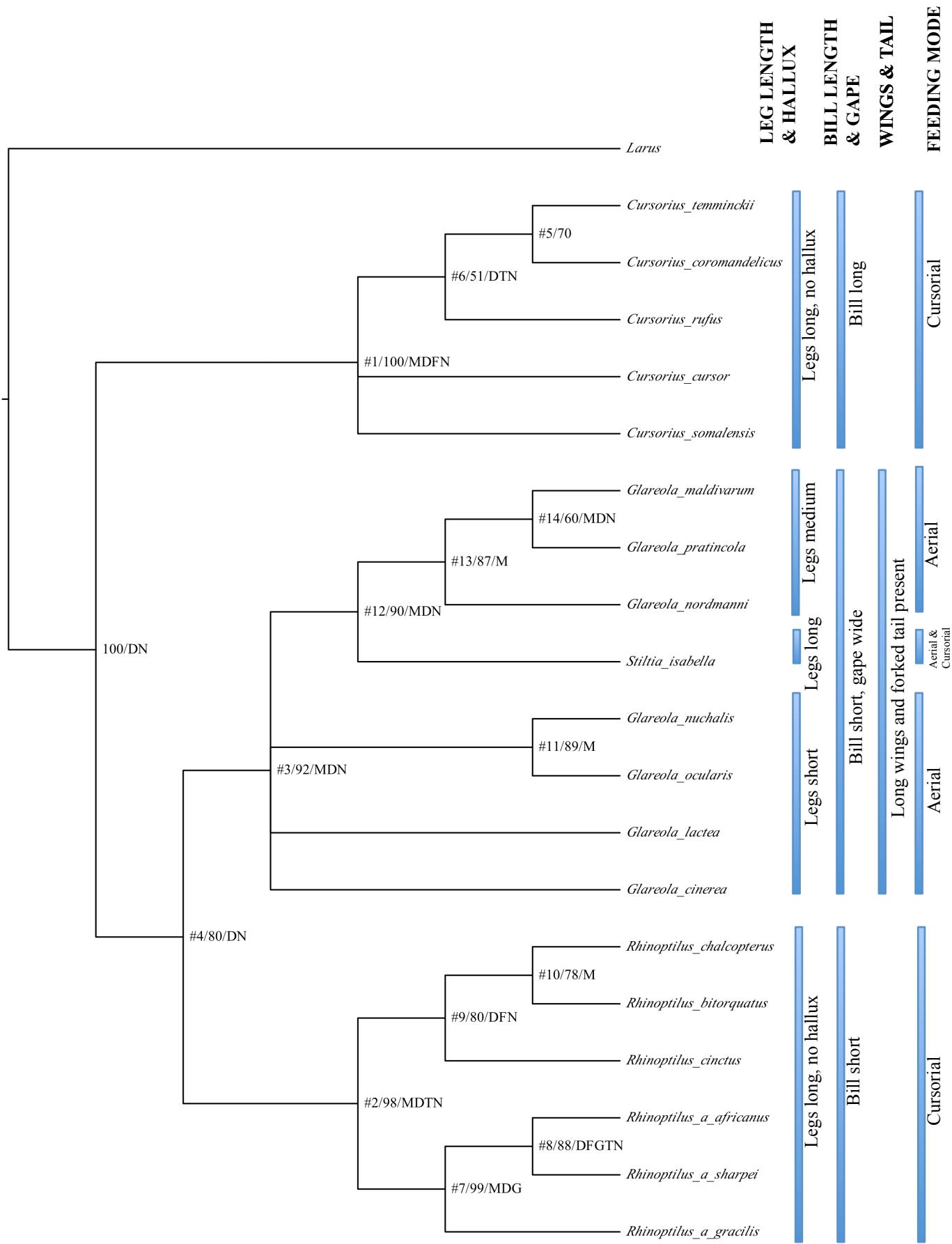


Fig. 4.9

4.44



Appendix Ch. 4

Appendix 4.1: Characters and character states used in morphological-behavioural character matrix for the Glareolidae

All morphological characters defined as per Hayman et al. (1986).

PLUMAGE CHARACTERS

HEAD

1. Colour of lores

- 0 Pale
- 1 Dark

2. Is there a white supercilium that extends behind the eye?

- 0 Absent
- 1 Present

3. Do the supercilia join on the rear of the crown?

- 0 No
- 1 Yes

4. Do the supercilia and eye-stripes bend *sharply* downwards on the rear of the crown?

- 0 No
- 1 Yes

5. Is a black eye-stripe present?

- 0 Absent
- 1 Present

6. Is the nape contrastingly dark with the rear of the crown?

- 0 No
- 1 Yes

7. Are the ear coverts contrastingly dark?

- 0 No
- 1 Yes

8. Is the crown relatively uniform in colour?

- 0 Yes
- 1 No, sharp contrast in colour between front and rear

9. Crown pattern

- 0 Unstreaked
- 1 Streaked

10. Ground colour of the crown

- 0 Black (outgroup only)
- 1 Orange-brown
- 2 Orange-brown with a grey rear
- 3 Mid to pale brown
- 4 Dark brown
- 5 Pale grey

11. Are there any moustachial or sub-moustachial stripes present?

- 0 Absent
- 1 Present

UNDERPARTS**12. Is there a contrastingly dark patch on the belly?**

- 0 Absent
- 1 Present

13. Belly colour

- 0 White/buff
- 1 Rufous/orange-brown (with or without a dark brown patch)

14. Is there a throat/upperchest band?

- 0 Absent
- 1 Present

15. Is there a central breast band?

- 0 Absent
- 1 Present

16. Colour of underwing coverts

- 0 Pale white to buff-brown
- 1 Strikingly dark
- 2 Dark rufous-orange

17. Pattern on primary underwing coverts

- 0 Uniform
- 1 Black feathers tips contrasting with the white on primary underwing coverts

18. Trailing edge to underwing

- 0 None or white
- 1 Black trailing edge to underwing caused by black tips to white secondary feathers

UPPERPARTS (including the wing and tail)**19. Mantle and back feathers plain or edged with pale (scaled)**

- 0 Plain
- 1 Scaled

20. Upper-wing covert feathers plain or edged with pale (scaled)

- 0 Plain
- 1 Scaled

21. Ground colour of mantle

- 0 Black or grey
- 1 Rufous to orange brown
- 2 Mid-brown
- 3 Dark brown

22. Pattern on upperwing coverts

- 0 Outer greater upperwing coverts uniform with wing
- 1 Outer greater upperwing coverts white or edged white
- 2 Outer greater upperwing coverts edged buff

23. Presence of white uppertail coverts?

- 0 Absent
- 1 Present

24. White trailing edge to the secondaries?

- 0 Absent
- 1 Present

STRUCTURAL CHARACTERS**TAIL, HEAD AND WING SHAPE****25. Tail shape**

- 0 Outer retrices similar in length to central retrices creating a rounded tail shape
- 1 Outer retrices distinctly longer than central retrices creating forked tail in flight

26. Presence of highly-elongated outer retrices

- 0 Absent
- 1 Outer retrices almost twice as long as others

27. Wing and primary proportion

- 0 Broad winged, first (inner) primary about 2/3 the length of the wing
- 1 Long-winged, first (inner) primary about 1/2 the length of the wing

28. Relative size of the eye

- 0 Similar in proportions to other similar ground-dwelling birds
- 1 Staringly large in proportion to the side of the face

29. Bill shape

- 0 Short
- 1 Long and down-curved

30. Head Shape

- 0 Steep forehead
- 1 Attenuated in the front, resulting in a shallow forehead

LEG AND FOOT MORPHOLOGY

31. Length of legs

- 0 Proportion and length of tarsus not unlike *Larus*
- 1 Elongated tarsus, similar in proportion to *Vanellus*
- 2 Tarsus even shorter in proportion than *Larus*

32. Presence of hallux (the 4th, rear toe)

- 0 Present
- 1 Absent

BARE PART COLORATION

33. Colour of the bill base

- 0 Reddish or yellowish
- 1 Dark

34. Colour of legs

- 0 Yellow or red
- 1 Pale grey to white
- 2 Dark

BEHAVIOURAL CHARACTERS

35. Habitat

- 0 Associated with all water habitats
- 1 Associated strongly with rivers
- 2 Restricted to open, arid areas
- 3 Found in open patches in dry woodlands

36. Feeding habits

- 0 Ground feeder
- 1 Aerial feeder
- 2 Both

37. Primarily nocturnal or diurnal?

- 0 Diurnal
- 1 Nocturnal
- 2 Diurnal but strongly crepuscular

38. Calls frequently when feeding

- 0 Yes
- 1 No, calls very infrequently

ADDITIONAL CHARACTERS

39. Is there a white eye-stripe that extends under the eye?

0 Absent

1 Present

40. Is there an eye-stripe that joins behind the head?

0 Absent

1 Present

41. Is an orange nuchal patch present?

0 Absent

1 Present in at least one subspecies

42. Presence of a cream/buff throat patch, bordered in a solid black line?

0 Absent

1 Present

43. White in tail feathers (retrices)

0 Limited, mainly on the outer feathers

1 Extensive, on many of the feather bases as well

44. Is the species largely restricted to breeding in rocky islands in rivers?

0 No

1 Yes

45. Do the tertials extend to the end of the tail?

0 Yes

1 No, the tail extends significantly further

46. Is there a distinct non-breeding plumage?

0 Absent

1 Present

47. Sharp, piercing feeding calls

0 Absent

1 Present

Appendix 4.2: Morphological-behavioural character matrix for the Glareolidae

Species	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
<i>Cursorius_cursor</i>	0	1	1	1	1	1	0	1	0	2	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0
<i>Cursorius_somalensis</i>	0	1	1	1	1	1	0	1	0	2	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0
<i>Cursorius_rufus</i>	0	1	1	1	1	1	0	1	0	2	0	1	1	0	0	1	0	0	0	0	1	0	0	1	0
<i>Cursorius_temmincki</i>	0	1	1	1	1	1	0	0	0	1	0	1	1	0	0	1	0	0	0	0	1	0	0	0	0
<i>Cursorius_coromandelicus</i>	1	1	1	1	1	1	0	0	0	1	0	1	1	0	0	1	0	0	0	0	1	0	1	1	0
<i>Rhinoptilus_africanus_africanus</i>	1	0	0	0	1	0	0	0	1	3	0	0	0	1	1	0	1	0	1	1	2	2	1	0	0
<i>Rhinoptilus_africanus_sharpei</i>	1	0	0	0	1	0	0	0	1	3	0	0	0	1	1	0	1	0	1	1	2	2	1	0	0
<i>Rhinoptilus_africanus_gracilis</i>	1	0	0	0	1	0	0	0	1	3	0	0	0	1	1	0	1	0	1	1	2	2	1	0	0
<i>Rhinoptilus_cinctus</i>	0	1	1	0	1	0	0	0	1	3	1	0	0	1	1	0	1	0	1	1	2	2	1	0	0
<i>Rhinoptilus_chalcopterus</i>	1	1	0	0	1	0	1	0	0	3	1	0	0	1	1	0	1	1	0	0	2	1	1	0	0
<i>Rhinoptilus_bitorquatus</i>	0	1	0	0	0	0	1	0	1	3	1	0	0	1	1	0	1	1	0	0	2	1	1	0	0
<i>Stiltia_isabella</i>	1	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	0	0	2	0	1	0	1
<i>Glareola_pratincola</i>	1	0	0	0	0	0	0	0	0	3	0	0	0	1	0	2	0	0	0	0	2	0	1	1	1
<i>Glareola_maldivarum</i>	1	0	0	0	0	0	0	0	0	3	0	0	0	1	0	2	0	0	0	0	2	0	1	0	1
<i>Glareola_nordmanni</i>	1	0	0	0	0	0	0	0	0	3	0	0	0	1	0	1	0	0	0	0	2	0	1	0	1
<i>Glareola_ocularis</i>	1	0	0	0	0	0	0	0	0	4	0	1	1	0	0	2	0	0	0	0	3	0	1	0	1
<i>Glareola_nuchalis</i>	1	0	0	0	0	0	0	0	0	4	0	0	0	0	1	0	0	0	0	0	3	0	1	0	1
<i>Glareola_cinerea</i>	1	0	0	0	1	0	0	0	0	5	0	0	0	0	0	1	1	0	0	0	0	1	0	0	1
<i>Glareola_lactea</i>	1	0	0	0	0	0	0	0	0	5	0	0	0	0	0	1	0	1	0	0	0	0	1	0	1
OUTGROUP <i>Larus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
	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

Appendix 4.2: Continued

Species	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47
<i>Cursorius_cursor</i>	0	0	0	1	1	1	1	1	1	2	0	0	1	0	1	0	0	0	0	0	0	
<i>Cursorius_somalensis</i>	0	0	0	1	1	1	1	1	1	2	0	0	1	0	1	0	0	0	0	0	0	
<i>Cursorius_rufus</i>	0	0	0	1	1	1	1	1	1	2	0	0	1	0	1	0	0	0	0	0	0	
<i>Cursorius_temmincki</i>	0	0	0	1	1	1	1	1	1	3	0	0	1	0	1	0	0	0	0	0	0	
<i>Cursorius_coromandelicus</i>	0	0	0	1	1	1	1	1	1	3	0	0	1	0	1	0	0	0	0	0	0	
<i>Rhinoptilus_africanus_africanus</i>	0	0	1	0	0	1	1	1	1	2	0	1	1	0	0	0	0	0	0	0	0	
<i>Rhinoptilus_africanus_sharpei</i>	0	0	1	0	0	1	1	1	1	2	0	1	1	0	0	0	0	0	0	0	0	
<i>Rhinoptilus_africanus_gracilis</i>	0	0	1	0	0	1	1	1	1	2	0	1	1	0	0	0	0	0	0	0	0	
<i>Rhinoptilus_cinctus</i>	0	0	1	0	0	1	1	0	0	3	0	1	1	0	1	0	0	0	0	0	0	
<i>Rhinoptilus_chalcopterus</i>	0	0	1	0	0	1	1	0	0	3	0	1	1	0	0	0	0	0	0	0	0	
<i>Rhinoptilus_bitorquatus</i>	0	0	1	0	0	1	1	0	0	3	0	1	1	0	0	0	0	0	0	0	0	
<i>Stiltia_isabella</i>	1	1	0	0	1	1	0	0	2	0	2	2	0	0	0	0	0	1	0	1	1	
<i>Glareola_pratincola</i>	1	1	0	0	1	0	0	0	2	0	1	2	0	0	0	0	1	1	0	1	1	
<i>Glareola_maldivarum</i>	1	1	0	0	1	0	0	0	2	0	1	2	0	0	0	0	1	1	0	1	1	
<i>Glareola_nordmanni</i>	1	1	0	0	1	0	0	0	2	0	1	2	0	0	0	0	1	1	0	1	1	
<i>Glareola_ocularis</i>	0	1	0	0	0	2	0	0	1	1	1	2	0	1	0	0	0	1	0	0	1	
<i>Glareola_nuchalis</i>	0	1	0	0	0	2	0	0	0	1	1	2	0	1	1	0	0	1	0	0	1	
<i>Glareola_cinerea</i>	0	1	0	0	0	2	0	0	0	1	1	2	0	0	0	1	0	0	0	0	1	
<i>Glareola_lactea</i>	0	1	0	0	0	2	0	0	2	1	1	2	0	0	0	0	0	1	0	0	0	
OUTGROUP <i>Larus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47

CHAPTER 5

The evolutionary relationships of the arid zone *Ptilopachus* (Galliformes) and implications for African biogeography

Abstract

The monotypic Stone Partridge *Ptilopachus petrosus* (Galliformes: Phasianidae), restricted to arid rocky areas of the Sahel savanna on the southern border of the Sahara Desert, is a taxonomic enigma. It has historically been grouped tentatively with Asian forest partridges (*Galloperdix* and *Bambusicola* spp.). However, recent DNA-based phylogenetic research suggests that its closest relative is Nahan's Francolin *Francolinus nahani*, another taxonomically enigmatic African galliform, and a globally threatened, narrow endemic species associated with the interior of remnant primary forests of the eastern equatorial lowlands of the Democratic Republic of the Congo and Uganda. This hypothesis is investigated in greater detail using additional DNA evidence and information on behaviour and vocalisations. Phylogenetic analyses of the combined sequences from three nuclear and four mitochondrial markers (5554 bases for 84 galliform taxa) overwhelmingly support the sister relationship between *F. nahani* and *P. petrosus*. They, in turn, are the distantly related sister taxon of the New World quails (Odontophoridae), and are not related to any other Old World galliform.

Introduction

The Afrotropics harbour 49 species of galliform gamebirds, occurring in virtually all habitats across the continent south of the Sahara (Crowe et al., 1986; del Hoyo et al., 1994). Crowe et al. (2006) have demonstrated decisively (see also Milstein and Wolf, 1987; Crowe et al., 1992a, b; Bloomer and Crowe, 1998), that Africa's largest (currently 36 spp.) gamebird genus, *Francolinus* (*sensu* Hall, 1963) actually comprises at least two distantly related African radiations. The partridge-like spurfowls (*Pternistis*, 24 spp.) are related to Old World quails (e.g. *Coturnix*, *Excalfactoria*, *Margaroperdix*, *Perdicula* and *Ammoperdix*) and certain Old World partridges (e.g. *Tetraogallus* and *Alectoris*). The quail-like francolins (*Dendroperdix*, *Peliperdix* and *Scleroptila*, 12 spp.) are related to 'true' Asian francolins (*Francolinus* 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 monotypic 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 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, in fact, sister species, which in turn were sister to the New World Quails (Odontophoridae).

The evolutionary enigmatic Stone Partridge occurs on rocky outcrops in the arid habitats of 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 placed subsequently 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). First placed by Dubois (1905) in the genus *Francolinus*, it was 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 Spurfowl *Pternistis ahantensis*, Scaly Spurfowl *P. squamatus* and Grey-striped Spurfowl *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. (1992b) 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 DNA-based evidence and new evidence from vocalisations and behaviour is investigated in the context of the phylogenetic affinities suggested by Crowe et al. (2006) with the goal of producing a robust phylogenetic hypothesis for both of these evolutionarily enigmatic African galliforms.

Material and methods

Taxon sampling

Taxon sampling was based on that of Crowe et al. (2006), with a number of important changes. In order to increase confidence that no taxa had been overlooked, all additional African ‘francolin’ species (e.g. several extra *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 5.1](#) lists the accession numbers of all samples analysed). A sample of *Ptilopachus petrosus* was obtained from Ghana, and three samples of *F. nahani* were obtained from Budongo Forest, Uganda.

Molecular approach and materials

Four mitochondrial (mtDNA) markers and three nuclear DNA 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).

Primers used for PCR-amplification and sequencing are detailed in [Table 5.2](#). The initial *cytb* primers amplified 1337 base pairs. Due to the length of this region, an internal primer (Table 2) was also used in sequencing this region. The initial *cytb* primer pair did not amplify *Pternistis griseostriatus* and Yellow-necked Spurfowl *P. leucoscepus*, thus further galliform specific primers were also used ([Table 5.2](#)).

Double stranded DNA templates were amplified by polymerase chain reaction (PCR) using 0.75 units of BIOTAQTM DNA polymerase (Bioline) in 30 µl reactions. Reactions also contained 1 x NH₄ buffer, 2.5 mM MgCl₂, each dNTP at 0.1 mM and each primer at 0.3 µM. Three 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.

Amplified products were cleaned from solution or gel using the GFXTM PCR DNA and gel band purification kit (Amersham Biosciences), prior to cycle sequencing with the ABI PRISM® Big DyeTM 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, DNAsstar, Inc.). Consensus sequences were aligned using Clustal and adjusted manually in MegAlign (LaserGene systems software, DNAsstar, Inc.).

Phylogenetic analyses

Three methods of phylogenetic analysis with different optimality criteria were employed to generate phylogenetic hypotheses: parsimony (MP), Bayesian inference

(BI) and maximum likelihood (ML). Parsimony-based phylogenetic analyses were conducted using TNT (Tree analysis using New Technology - Goloboff et al., 2008a, b). In TNT, the searching 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 characters per jackknife replicate (Farris et al., 1996; Källersjö et al., 1998).

Because gene regions can evolve under different models of evolution, it has been argued that a partitioned, 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* 4.0b10 (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; Fuchs et al., 2009). 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 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 (Fuchs et al., 2009).

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). Mixed-model RAxML analyses use 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 mtDNA and nuclear DNA combined. Support at nodes was assessed with 100 non-parametric bootstrap pseudoreplicates.

In four genera (*Ortalis*, *Crax*, *Syrmaticus* and *Colinus*) each of the two species per genus had missing loci and so these pairs were combined in the final concatenated analyses (and are thereafter are identified by the genus name only).

Field observations of behaviour and vocalisations

Behavioural observations and vocalisations were recorded in the field: *Francolinus 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; *Ptilopachus 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. 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 vocalisations of *F. nahani* from Brian Finch (unpublished data) and from Chappuis (2000).

Vocal analyses

Calls of *P. petrosus* and *F. nahani* were compared aurally to all available African galliform species on Gibbons (1991) and Chappuis (2000), supplemented by additional calls from the British Library Sound Archive. In addition, sonograms were made of typical advertisement calls (heard most often at dawn and dusk) for *Ptilopachus petrosus* and *F. nahani* and compared with those of putative sister taxa (*Pternistis* spp.) and other African galliforms. Sonograms were generated in Raven Lite (Version 1.0, Cornell Laboratory of Ornithology).

Results

Phylogenetic analyses

Analysis of the combined sequences from all seven markers (5554 bases, 84 taxa; Figs 5.1 – 5.3) strongly confirms the sister relationship between *P. petrosus* and *F. nahani*. The parsimony analysis yielded 10 equally parsimonious trees of 14991 steps and this relationship is supported in the consensus tree with a jackknife (JK) support of 100%. Additionally, this node is supported by each of the individual loci with the exception of GAPDH where the node is unresolved (Table 5.3). The nodal support for the concatenated BI and ML analyses is a posterior probability (PP) of 1 and a bootstrap value (BS) of 100, respectively (Figs 5.1 – 5.3), and this result is consistent among each of the data partitions (Table 5.3). These two taxa, in turn, are sisters to representatives of the New World quails (Odontophoridae) with a high degree of support (MP: JK = 100; BI: PP = 1; ML: BS = 100) in the combined DNA (Figs 5.1 – 5.3), mitochondrial and nuclear DNA analyses (Table 5.3).

Vocal and behavioural comparison

The calls of *P. petrosus* (Fig. 5.4a) and *F. nahani* (Fig. 5.4b) are strikingly similar and differ from those of other francoins and spurfowls; 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 further 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. 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 such a large degree

from any other African galliform that it is not possible to identify homologous call units to compare directly. No other African galliform examined has a similar whistled structure. In particular, these calls are in strong contrast to typical spurfowl calls of the putative relatives of *F. nahani*, which consist of slurred, almost grating, raucous calls that do not vary much in frequency (Figs 5.4c-e; from Chappuis, 2000).

Behavioural observations (substantiated by photographs and extensive field observations) indicate that both *P. petrosus* (Fig. 5.5a) and *F. nahani* (Fig. 5.5b), hold their tails in a distinctive, bantam-like cocked position.

Discussion

The 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, 1992b; 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 grouping sister to New World quails (Odontophoridae), and are only distantly related to 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.

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. 5.5](#)) 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. 5.4](#)). 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, field observations attest that both species live in small, family groups and have interactive calling.

Given the long divergence between these two species (19 mya, see Crowe et al., 2006), it does seem interesting that the nature of the calls has 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; Voelker et al., 2010). 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 for aspects of colouration that presumably relate to camouflage (*F. nahani* is darker above, whereas *P. petrosus* somewhat paler), there has been remarkably little divergence.

Table 5.1: Genbank accession numbers of the samples analysed in this study.

Genus	species	Cytb	ND2	CR	12S	OVOG	TGFB	GAPDH
<i>Acryllium</i>	<i>vulturinum</i>	AF536742	AF536745	—	AF536739	DQ832070	—	—
<i>Afropavo</i>	<i>congensis</i>	AF013760	DQ768253	DQ834507	—	AF170991	—	—
<i>Alectoris</i>	<i>chukar</i>	L083781	DQ768273	DQ834525	—	AF170987	FR694121	FR694070
<i>Alectoris</i>	<i>graeca</i>	Z487724	—	DQ834524	—	—	—	—
<i>Alectoris</i>	<i>rufa</i>	Z487754	—	DQ834523	—	AF170988	—	—
<i>Alectura</i>	<i>lathami</i>	NC007227	AY274051	DQ834465	AY274004	DQ832069	EU737326	—
<i>Arborophila</i>	<i>javanica</i>	AM236890	DG093804	—	DQ832097	DQ832074	—	—
<i>Arborophila</i>	<i>torqueola</i>	AM236889	—	DQ834475	—	—	—	—
<i>Bambusicola</i>	<i>thoracica</i>	EU165706	AF222538	DQ834513	EU165706	AF170978	—	—
<i>Bonasa</i>	<i>umbellus</i>	AF230167	AF222541	DQ834476	U83740	—	—	—
<i>Callipepla</i>	<i>californica</i>	AB120131	AF028773	DQ834473	—	—	Submitted	Submitted
<i>Callipepla</i>	<i>gambelii</i>	L083821	AF028761	DQ834472	—	—	—	—
<i>Catreus</i>	<i>wallachii</i>	AF028792	DQ768254	DQ834499	—	AF170980	—	—
<i>Chrysolophus</i>	<i>amherstiae</i>	AB120130	—	—	DQ832102	—	—	—
<i>Chrysolophus</i>	<i>pictus</i>	AF028793	DQ768255	DQ834497	—	—	—	—
<i>Colinus</i>	<i>cristatus</i>	—	—	—	—	—	EU737357	—
<i>Colinus</i>	<i>virginianus</i>	EU372675	AF222545	DQ834469	AF222576	—	—	Submitted
<i>Coturnix</i>	<i>coturnix</i>	L083771	X57246	DQ834529	X57245	—	Submitted	Submitted
<i>Coturnix</i>	<i>japonica</i>	NC003408	NC003408	—	NC003408	—	—	—
<i>Crax</i>	<i>alector</i>	AY141921	—	—	—	—	Submitted	—
<i>Crax</i>	<i>rubra</i>	AY956378	AY274050	AY145307	AY274003	—	—	—
<i>Crossoptilon</i>	<i>crossoptilon</i>	AF028794	DQ768256	DQ834500	—	AF170981	—	—
<i>Cyrtonyx</i>	<i>montezumae</i>	AF068192	AF028779	DQ834467	—	AF170976	—	—
<i>Dendropidix</i>	<i>sephaena</i>	FR694140	DQ768274	DQ834515	FR691559	DQ832083	FR694111	FR694102
<i>Falcipennis</i>	<i>canadensis</i>	AF170992	AF222548	DQ834478	AF222577	AF170986	—	—
<i>Francolinus</i>	<i>francolinus</i>	AF013762		FR691376	—	—	—	—
<i>Francolinus</i>	<i>gularis</i>	U906497	—	—	—	—	—	—
<i>Francolinus</i>	<i>lathami</i>	AM236893	DQ768257	FR691377	FR691546	DQ832082	FR694113	FR694080
<i>Francolinus</i>	<i>pictus</i>	FR694142	—	—	—	—	—	—
<i>Francolinus</i>	<i>pondicerianus</i>	FR691632	DQ768279	—	FR691547	DQ832081	FR694114	FR694081
<i>Gallus</i>	<i>gallus</i>	L083761	AB086102	DQ834510	NC001323	AF170979	FR694110	FR694078
<i>Gallus</i>	<i>varius</i>	AB044988	AF222551	—	—	—	—	—
<i>Guttera</i>	<i>pucherani</i>	AM236882	—	—	—	—	—	—
<i>Ithaginis</i>	<i>cruentus</i>	AF068193	DQ768258	DQ834487	—	DQ832076	—	—
<i>Leipoa</i>	<i>ocellata</i>	AM236879	AF394619	—	AF222586	—	—	—
<i>Lophophorus</i>	<i>impejanus</i>	AF028796	DQ768259	DQ834486	DQ832098	DQ832075	—	—
<i>Lophura</i>	<i>nycthemera</i>	L083801	DQ768261	DQ834498	—	—	—	—
<i>Margaroperdix</i>	<i>madagarensis</i>	U906407	—	DQ834528	—	—	—	—
<i>Megapodius</i>	<i>eremita</i>	AF082065	AY274052	—	AY274005	—	—	—
<i>Meleagris</i>	<i>gallopavo</i>	L083811	AF222556	DQ834485	U83741	AF170984	—	—
<i>Numida</i>	<i>meleagris</i>	L083831	NC006382	DQ834466	AF222587	AF170975	EU737410	FR694071
<i>Oreortyx</i>	<i>pictus</i>	AF252860	AF028782	DQ834468	—	AF170977	Submitted	Submitted
<i>Ortalis</i>	<i>vetula</i>	L083841	AF394614	—	—	AF170974	—	—
<i>Pauxi</i>	<i>pauxi</i>	AF068190	AY140750	AF165439	AF165449	AF170973	—	—
<i>Pavo</i>	<i>cristatus</i>	L083791	AF394612	DQ834508	AY722396	AF170990	—	—
<i>Peliperdix</i>	<i>coqui</i>	AM236895	DQ768278	FR691379	FR691549	DQ832084	FR694115	FR694082
<i>Perdix</i>	<i>perdix</i>	AF028791	AF222560	DQ834484	AF222590	AF170982	—	—
<i>Phasianus</i>	<i>colchicus</i>	AY368060	AF222561	DQ834495	U837426	—	—	—
<i>Polyplectron</i>	<i>bicalcaratum</i>	AF534564	DQ768263	DQ834503	—	AF331959	—	—
<i>Polyplectron</i>	<i>emphanum</i>	AF330062	DQ768265	DQ834504	—	AF331955	—	—
<i>Pternistis</i>	<i>adspersus</i>	AM236910	DQ768276	DQ834535	DQ832113	DQ832095	FR694122	FR694087
<i>Pternistis</i>	<i>afer</i>	AM236908	DQ768281	DQ834533	DQ832111	DQ832092	FR694123	FR694088
<i>Pternistis</i>	<i>bicalcaratus</i>	U906377	FR691578	FR691370	FR691551	FR691690	FR694103	FR694089
<i>Pternistis</i>	<i>camerunensis</i>	FR694142	FR691577	FR691382	FR691552	FR691694	FR694124	FR694090
<i>Pternistis</i>	<i>capensis</i>	AM236909	DQ768282	DQ834534	DQ832112	DQ832093	FR694125	FR694091
<i>Pternistis</i>	<i>castaneicollis</i>	AM236903	—	—	—	—	—	—
<i>Pternistis</i>	<i>clappertoni</i>	FR691602	FR691576	FR691383	FR716655	FR691693	FR694126	FR694092

Table 5.1: Continued.

Genus	species	Cytb	ND2	CR	12S	OVOG	TGFB	GAPDH
<i>Pternistis</i>	<i>erckelii</i>	U906387	—	—	—	—	—	—
<i>Pternistis</i>	<i>griseostriatus</i>	AM236905	DQ768284	FR691384	FR691554	DQ832089	FR694128	FR694094
<i>Pternistis</i>	<i>hartlaubi</i>	U906397	FR691572		FR691555	FR691692	FR694129	FR694095
<i>Pternistis</i>	<i>hildebrandti</i>	U906317	—	—	—	—	—	—
<i>Pternistis</i>	<i>icterorhynchus</i>	FR691601	—	—	—	—	—	—
<i>Pternistis</i>	<i>jacksoni</i>	FR691594	—	—	—	—	—	—
<i>Pternistis</i>	<i>leucoscepus</i>	AM236906	FR691387	FR691556	DQ832090	FR694131	FR694097	Submitted
<i>Pternistis</i>	<i>natalensis</i>	AM236911	DQ834536	FR691557	DQ832094	FR694132	FR694098	Submitted
<i>Pternistis</i>	<i>nobilis</i>	FR691592	—	—	—	—	—	—
<i>Pternistis</i>	<i>ochropectus</i>	FR691590	—	—	—	—	—	—
<i>Pternistis</i>	<i>rufopictus</i>	FR691588	—	—	—	—	—	—
<i>Pternistis</i>	<i>squamatus</i>	AM236904	DQ768286	DQ834531	DQ832109	DQ832088	FR694133	FR694099
<i>Pternistis</i>	<i>swainsonii</i>	AM236907	DQ768287	DQ834532	DQ832110	DQ832091	FR694134	FR694100
<i>Pternistis</i>	<i>swierstrai</i>	FR691593	—	—	—	—	—	—
<i>Ptilopachus</i>	<i>nahani</i>	AM236885	DQ768288	FR691374	FR691545	DQ832071	FR694107	FR694075
<i>Ptilopachus</i>	<i>petrosus</i>	AM236886	DQ768289	FR691375	FR691544	DQ832072	FR694108	FR694076
<i>Pucrasia</i>	<i>macrolopha</i>	AF028800	DQ768269	DQ834490	—	AF170983	—	—
<i>Rollulus</i>	<i>rouloul</i>	AM236888	—	—	—	—	Submitted	—
<i>Scleroptila</i>	<i>africanus</i>	AM236897	AF222550	DQ834517	AF222581	DQ832086	FR694116	FR694083
<i>Scleroptila</i>	<i>finschi</i>	AM236896	DQ768290	—	—	—	—	—
<i>Scleroptila</i>	<i>levaillantii</i>	AM236913	DQ768291	DQ834516	DQ832106	DQ832085	FR694117	FR694084
<i>Scleroptila</i>	<i>levaillantoides</i>	AM236900	DQ768292	DQ834519	DQ832108	—	FR694118	FR694085
<i>Scleroptila</i>	<i>psilolaemus</i>	FR691614	—	—	—	—	—	—
<i>Scleroptila</i>	<i>shellyi</i>	AM236898	DQ768295	DQ834518	DQ832107	DQ832087	FR694119	FR694101
<i>Scleroptila</i>	<i>streptophorus</i>	FR691617	FR691573	FR691380	FR691550	Submitted	FR694120	FR694086
<i>Syrmaticus</i>	<i>elliotti</i>	—	DQ768270	—	—	—	—	—
<i>Syrmaticus</i>	<i>humiae</i>	AF534706	—	DQ834491	DQ832099	DQ832077	—	—
<i>Tetrao</i>	<i>urogallus</i>	AB120132	AF222565	DQ834480	AF222594	—	—	—
<i>Tragopan</i>	<i>temminckii</i>	AF229838	AF222566	DQ834488	AF222595	—	—	—
<i>Tympanuchus</i>	<i>phasianellus</i>	AF068191	AF222569	DQ834483	AF222598	AF170985	—	—
<i>Xenoperdix</i>	<i>udzungwensis</i>	AM236887	DG093800	DQ834474	DQ832096	DQ832073	—	—

Table 5.2: Primers used for sequencing the fresh material and toepad-skin samples in this study

Gene Region Fresh material	Primer Name	Primer Sequence	Source
(internal) (galliform specific)	L14578	5'-CTAGGAATCATCCCTAGGCCCTAGA-3'	Edwards & Wilson, 1990
	H5915	5'-AACGCAGTCATCTCGGTTTACAAGAC-3'	J. G. Groth, pers. comm.
	L15087	5'-TTCCCTATACAAAGAAACCTGAA-3'	Edwards et al., 1991
	ML15131	5'-AACGTACAGTACGGCTGACTCAT-3'	P. Bererford, pers. comm.
ND2	MH15907	5'-TGTCTCTACTGGTGGCTTCAAT-3'	P. Bererford, pers. comm.
	L5216	5'-GCCCATACCCRAAAATG-3'	Sorenson et al., 1999
Control Region (CR)	PHDL	5'-CCTCTATTAAAGGCTTGAAGGC-3'	Fumihito et al., 1995
	PH-H521	5'-AGGACTACG GCTTGAAAAGC-3'	E.A. Scott, pers. comm.
	PH-L400	5'-TTATGTGCTTGACCCAGGAACACAG-3'	E.A. Scott, pers. comm.
	PHDH	5'-ATTATTGATCGTCCACCTCACG-3'	Fumihito et al., 1995
12S	L1267	5'-AAA GCA TGG CAC TGA AGA TG-3'	Moum et al., 1994
	H2294	5'-GTGCCACCTTCGGTACACTTACCC-3'	O. Haddrath, S. Pereira, pers. comm.
	Forward	5'-CAAGACATA CGGACAACAARTG-3'	Armstrong et al., 2001
	Reverse	5'-GGCTTAAGTGAGAGTCCCRT-3'	
TGF β	TGFB2.5F	5'-GAAGCGTGTCTAGATGCTG-3'	Primmer et al., 2002; Kimball et al., 2009
	TGFB2.6R	5'-AGGCAGCAATTATCCTGAC-3'	
GAPDH	GAPDL890	5'-ACCTTTAATGCGGGTGTGGCATTGCA-3'	Friesen et al., 1997
	GAPDH950	5'-CATCAAGTCCACAAACACGGTGTGCTGA-3'	Friesen et al., 1997
Toepad-skin samples			
Cytb	L14851 (General)	5'-CCTACTTAGGATCATCGCCCT-3'	Kornegay et al., 1993
	Pt-H195	5'-TTICGRCAATGTTGGGTACGGAG-3'	R. Moyle & T. Mandiwana-Neudani
	Pt-L143	5'-GCCTCATTAACCCAAATCCTCAC-3'	R. Moyle & T. Mandiwana-Neudani
	Pt-H361	5'-GTGGCTATTAGTGTGAGGAG-3'	R. Moyle & T. Mandiwana-Neudani
	Pt-L330	5'-TATACTATGGCTTACCTGTAC-3'	R. Moyle & T. Mandiwana-Neudani
	Pt-H645	5'-GGGTGGAAATGGGATTTGTCAAGAG-3'	R. Moyle & T. Mandiwana-Neudani
	Pt-L633	5'-GGCTCAAACAACCCACTAGGC-3'	R. Moyle & T. Mandiwana-Neudani
	Pt-H901	5'-AGGAAGGGGATTAGGAGTAGGAT-3'	R. Moyle & T. Mandiwana-Neudani
	Pt-H1083alt	5'-TAGGAGAAGGATGCTGTTGGC-3'	R. Moyle & T. Mandiwana-Neudani
	Pt-H1050	5'-GATGCTGTGTTGGCCGATG-3'	R. Moyle & T. Mandiwana-Neudani
	Pt-L961	5'-GAAACCATAACATTCCCCAC-3'	R. Moyle & T. Mandiwana-Neudani
	HB20 (General)	5'-TTGGTTACAAGACCAATGTT-3'	J. Feinstein, pers. comm.

Table 5.3: Support for the relationship of *Ptilopachus petrosus* and *Francolinus nahani* from data partitions. + = supported branch; U = unresolved.

Clade	Bayesian Inference:			Maximum Likelihood:			Parsimony:						
	mtdNA	nDNA	mtDNA	nDNA	mtDNA	nDNA	CYTB	CR	ND2	12S	OVOG	TGFB	GAPDH
Odontophoridae sister to <i>P. petrosus</i> and <i>F. nahani</i>	1	1		100	100		+	+	+	+	+	+	U
<i>P. petrosus</i> sister to <i>F. nahani</i>	1	1	100	100	100		+	+	+	+	+	+	+

Figure Legends Ch. 5

Fig. 5.1 Phylogenetic relationships of *Ptilopachus petrosus* and *Francolinus nahani* indicated by a parsimony-based analysis of seven DNA markers (5554 bases, 84 taxa). Numbers along branches represent the following support values: jackknife (MP) / bootstrap (ML) / posterior probability (BI).

Fig. 5.2 Phylogenetic relationships of *Ptilopachus petrosus* and *Francolinus nahani* indicated by Bayesian inference. Numbers opposite nodes represent posterior probabilities.

Fig. 5.3 Phylogenetic relationships of *Ptilopachus petrosus* and *Francolinus nahani* indicated by maximum likelihood analysis. Numbers opposite nodes represent bootstrap values.

Fig. 5.4: Sonograms of the call of (a) Stone Partridge *Ptilopachus petrosus*, (b) Nahan's Francolin *Francolinus nahani*, (c) Scaly Spurfowl *Pternistis squamatus*, (d) Ahanta Spurfowl *Pternistis ahantensis* and (e) Red-necked Spurfowl *Pternistis afer*. Frequency (kHz) on the vertical axis with time (seconds) on the horizontal axis. All exemplars from Chappuis (2000).

Fig. 5.5: Line drawing to show the posture of (a) *Ptilopachus petrosus* and (b) *Francolinus nahani*, after photographs by Ron Hoff, Nik Borrow and Callan Cohen.

Fig. 5.1

5.18

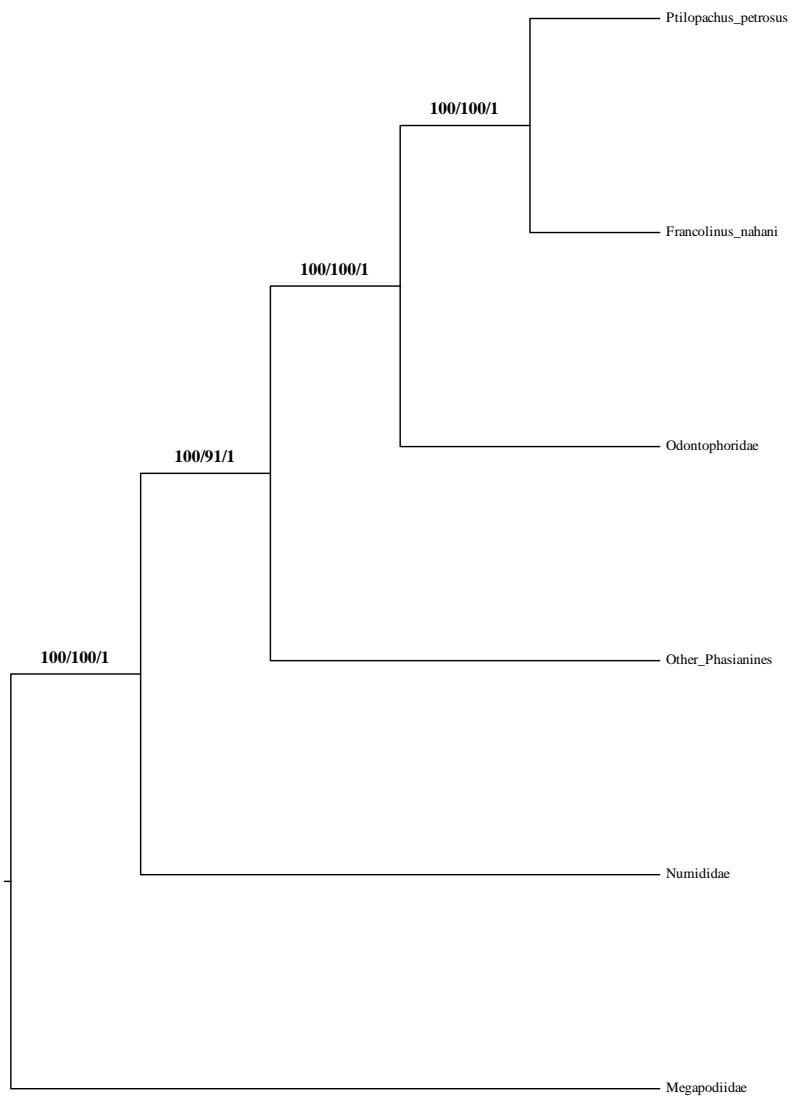


Fig. 5.2

5.19

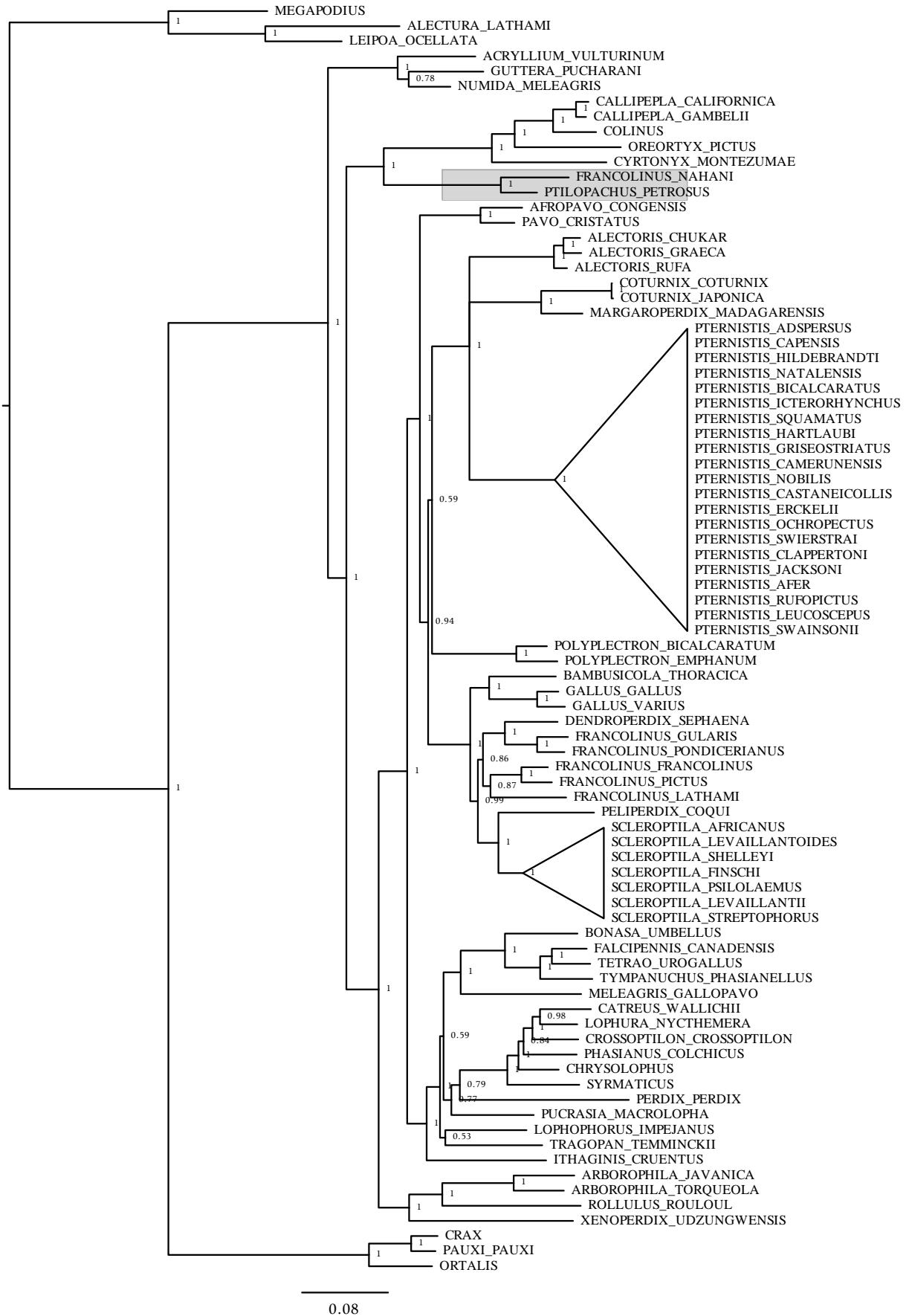


Fig. 5.3

5.20

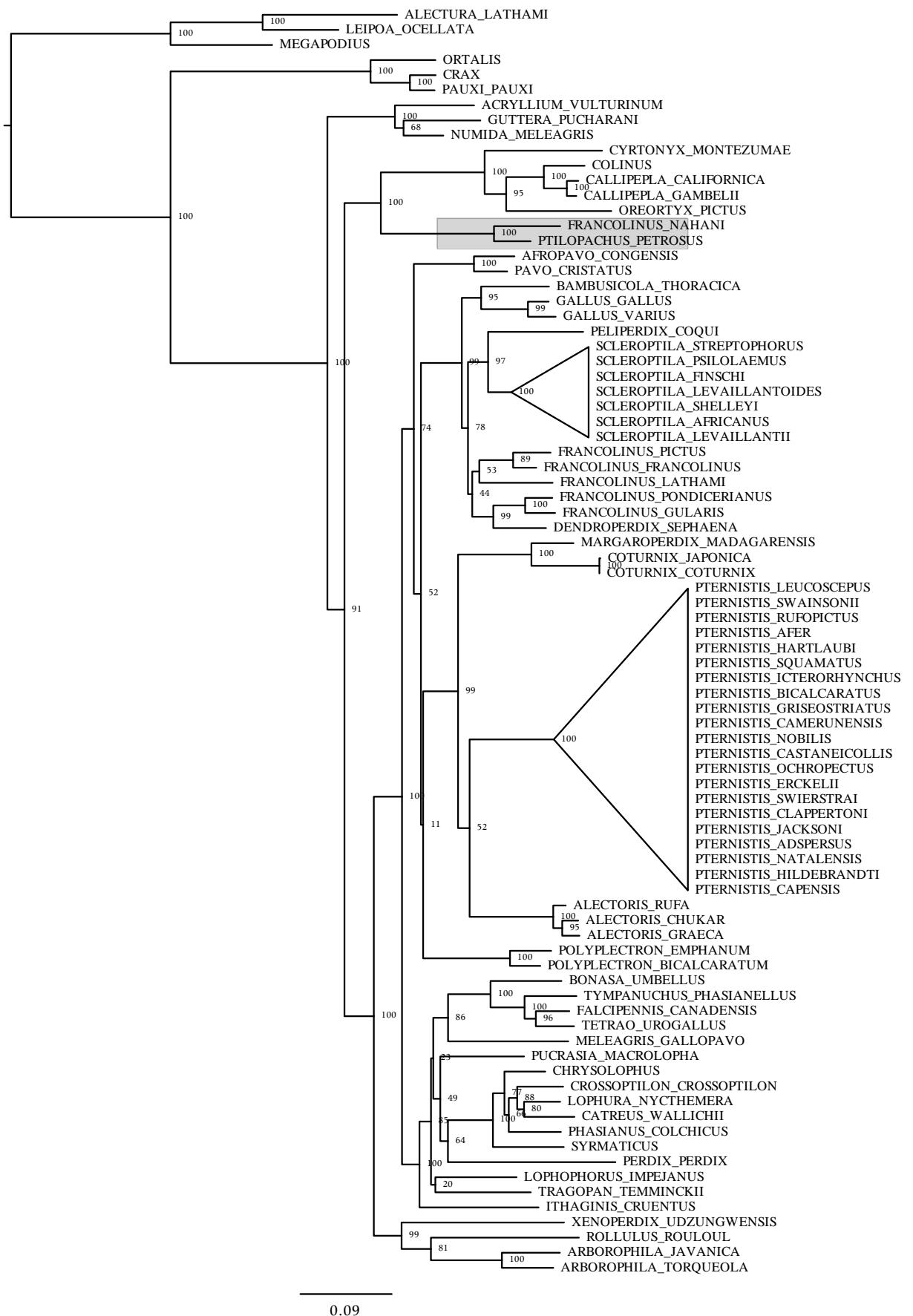


Fig. 5.4

5.21

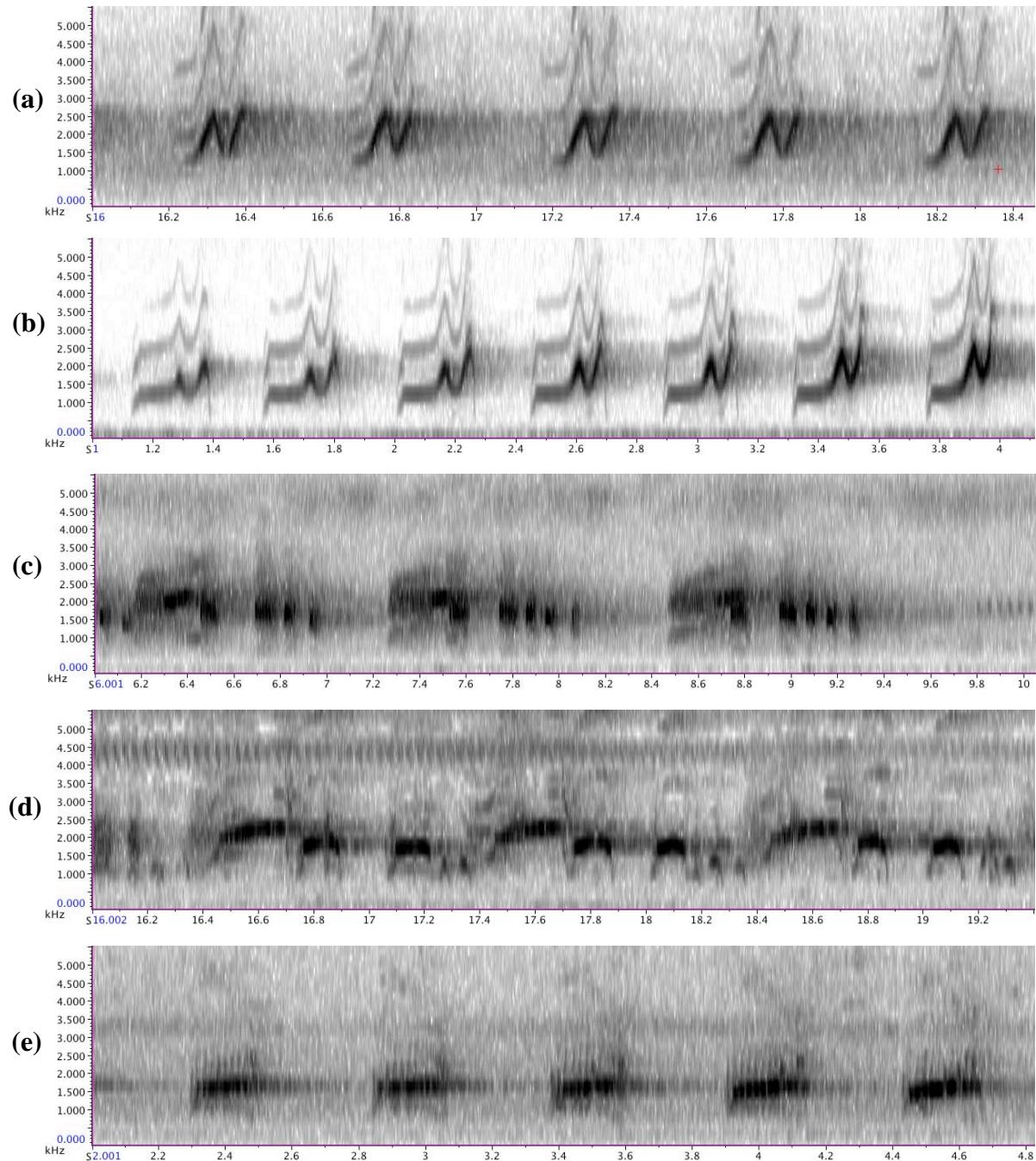
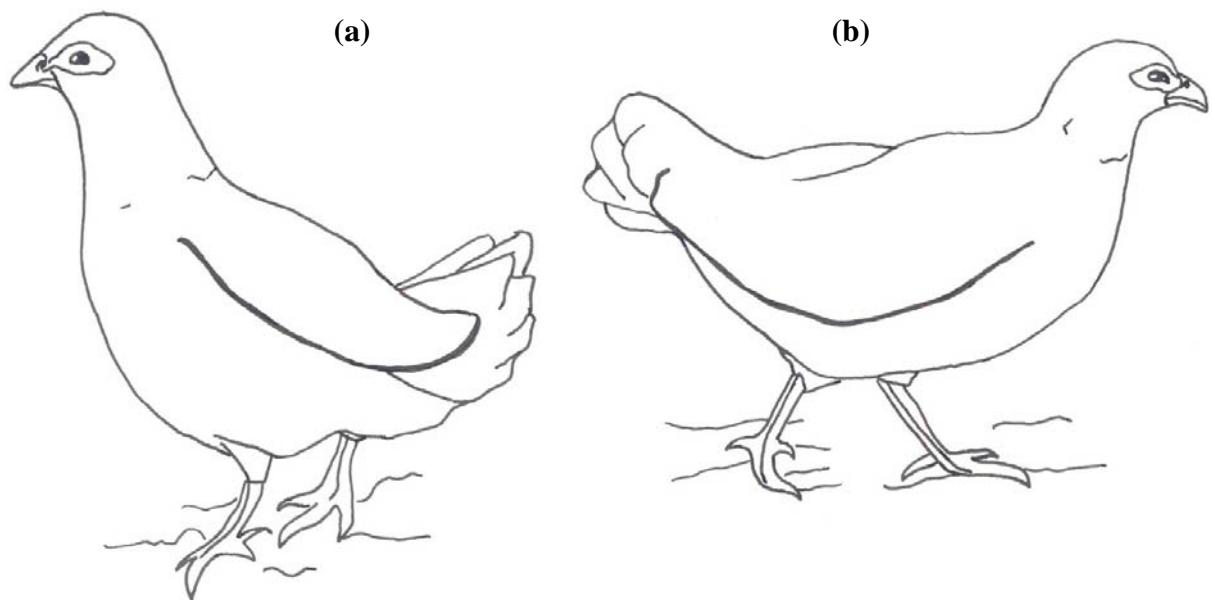


Fig. 5.5

5.22



CHAPTER 6

Synthesis: Biogeography and taxonomy of Africa's arid zone non-passerine terrestrial birds - the bustards (Otididae), sandgrouse (Pteroclidae), coursers (Glareolidae) and Stone Partridge (*Ptilopachus*).

This synthesis discusses the major results of the Chapters 2-5, specifically focusing on the following:

1. The biogeography of Africa's arid zone non-passerine terrestrial birds with special focus on the 'arid corridor' hypothesis.
2. The taxonomy of Africa's arid zone non-passerine terrestrial birds in relation to previous classifications.
3. Life history evolution in the study taxa.
4. Improvements and directions for future research.

1. The biogeography of Africa's arid zone non-passerine terrestrial birds with special focus on the 'arid corridor' hypothesis

Two methods are used to infer biogeographic patterns: 1. clade structure with broad geographical distribution of each taxon mapped onto phylogenies presented in [Figs 6.1 - 6.4](#), and 2. Spatial analysis of vicariance.

Spatial analysis of vicariance

Spatial analysis of vicariance is a method for the analysis of taxon history based on identifying sister nodes with disjunct (allopatric/ vicariant) distributions (Arias et al., subm.). It is based on Hovenkamp's (1997, 2001) ideas on historical biogeography: instead of searching for ancestral areas, it identifies disjunctions between sister groups and thus highlights natural barriers. The method uses observed distributions as data (and thus does not require distributions to be classified into predefined areas; Arias et al., subm.). To implement these across the tree, internal nodes are assigned distributions as the sum of the distributions of the descendant nodes, and barriers will only be detected if these are essentially non-overlapping (although it can be argued that a small amount of overlap is permissible, and an optimality criterion has been developed for cases when a small number of distributions overlap and potentially obscure a biogeographic pattern; Arias et al., subm.). Spatial analysis of vicariance was implemented using the computer program, VIP (Vicariance Inference Program; Arias, 2010). The distribution of each taxon in the phylogenies in [Figs 6.1 – 6.3](#) was mapped onto a world map using a grid of 3 x 3 degrees based on maps in Collar (1996), de Juana (1997) and Maclean (1996). This was then analysed with the phylogenies in [Figs 6.1 – 6.3](#) using a cost for overlapped distributions of 1.00, a cost

for a removal distribution of 2.00, an overlap threshold of less than 25%, and an heuristic search of 100 replications was performed to search for optimal reconstructions. The optimality criterion seeks to find the best compromise between the maximum possible number of disjunct sister nodes and the minimum number of eliminated distributions (Arias et al., subm.), although for the present data, no distributions were eliminated. The barrier recovered for each disjunction was mapped onto a world map using a geometric algorithm (Voronoi tessellation), which is quite effective when the distributions were close together, but becomes least accurate for large gaps between distributions (J. Salvador Arias, in litt.). All the barriers recovered in VIP are mapped as [Figs 6.8 – 6.35](#) and are discussed below, in combination with the insights obtained from clade structure.

Biogeographic patterns

Phylogenetic analyses of the Otididae, Pteroclidae, Glareolidae and *Ptilopachus* (Chapters 2-5) have revealed a number of biogeographic patterns within clades which can be summarised as follows and are discussed in more detail below:

- (i) widespread Palearctic clades with distributions that essentially mirror the southern arid border of the Palearctic region (centered on the southern areas of the Western Palearctic, often including the Saharan region, and the Middle East, eastwards to India, and occasionally further eastwards still)
- (ii) clades restricted to Asia (and Australia)
- (iii) clades with members in both the Afrotropical region and India (sometimes including the Middle East)

- (iv) clades with representatives in both the south-west and north-east arid zones of Africa, sometimes with another clade member in the Sahel
- (v) clades endemic to the south-west arid zone
- (vi) clades occurring in the Sahel and central African forest zone
- (vii) clades with species widespread across the Afrotropical zone
- (viii) clades with species occurring in Madagascar

(i) Widespread Palearctic clades

The Otididae, Pteroclidae, Glareolidae all contain species with a widespread Palearctic distribution (Figs 6.1 - 6.4). In the Otididae, *Otis* and *Chlamydotis* form a well-supported monophyletic clade, with the latter occupying more arid areas to the south of the distribution of *Otis* (Fig. 6.8). Both are widely distributed across the Palearctic region with *Tetrax*, allied to them with moderate support (Fig. 6.1), collectively are the bustards that occur the furthest north, and have the widest latitudinal range of the family (Johnsgard, 1991; Collar, 1996). The biogeography of *Chlamydotis* is complex with both island and migratory forms and is detailed in Gaucher et al. (1996). In Africa, these Palearctic bustard species occur only in the Mediterranean and Saharan regions (Collar, 1996).

In the Pteroclidae, several species share a southern arid Palearctic distribution (e.g. *P. coronatus* and *P. senegallus* which inhabit desert regions from the Sahara eastwards to India, and *P. alchata* and *P. orientalis*, which also span a similar longitudinal range but occur to the north of the previous two species), but are not closely related. The only clade that is exclusively Palearctic is the sister relationship between *P. orientalis* and the two *Syrrhaptes* species (Fig. 6.29; see ii below).

In the Glareolidae, only a single species of the subfamily Cursoriinae (coursers), *C. cursor*, has a wide Palearctic distribution. The Glareolinae (pratincoles) are closely tied ecologically to wetland habitats and do not share the arid zone distribution of the Cursoriinae (Maclean, 1996) and were included in this study largely to ensure correct placement of the members of the Cursoriinae. Three species of Glareolinae (*G. maldivarum*, *G. pratincola* and *G. nordmanni*) that form a clade show a widespread Palearctic distribution and all undergo regular migrations to more southerly areas; the former two of these species are distributed disjunctly (Fig. 6.35; Maclean, 1996).

(ii) clades restricted to Asia (and Australia)

In the Otididae, the two floricans, *Sypheotides indica* (India) and *Houbaropsis bengalensis* (India to South-east Asia) share a southern Asian distribution, and this study confirms their sister-relationship (Fig. 6.15). This clade is also the only non-African subclade of **Clade Smaller Bustards**. However, its relationship to the other subclades in **Clade Smaller Bustards** is not resolved (Fig. 6.1), hampering further interpretation. Thus, it remains uncertain whether the common ancestor of the floricans dispersed out of Africa to diversify in southern Asia, or vice-versa.

The results presented here strongly support a sister relationship between the Australian *A. australis* and Indian *A. nigriceps* and these are the only members of the *Ardeotis-Neotis* clade that do not occur in Africa (Figs 6.1, 6.11 and 6.13). As all the basal species of the *Ardeotis-Neotis* clade (all *Neotis* and *A. arabs*) share an Afrotropical distribution (although *A. arabs* ranges marginally into the Saharan region), this would suggest an African origin to this clade and an eastwards expansion

into Asia by *A. australis* and *A. nigriceps* (see Figs 6.11 and 6.12; passerine examples include *Anthus*, Voelker, 1999, and *Monticola*, Outlaw et al., 2007).

In the Pteroclidae, the two species in the genus *Syrrhaptes* (*S. paradoxus* and *S. tibetanus*) are supported as sister taxa (Fig. 6.30). They are endemic to the cold deserts of central Asia (centered on the Tibetan Plateau, but also extend further north, east and west), and are sister to the western Palearctic *P. orientalis*; this clade is thus wholly restricted to the Palearctic (see above; Fig. 6.2).

The aberrant *Stiltia*, confined to Australia and southern Asia, is decisively shown to be sister to the widespread Palearctic *Glareola* clade mentioned above and is not an intermediate form between the Glareolinae and Cursoriinae.

(iii) clades with members in both the Afrotropical region and India (sometimes including the Middle East)

In the Otididae, as mentioned above, **Clade Smaller bustards** and the *Ardeotis-Neotis* clade (**Clade AN**, Fig. 6.1) are both primarily composed of species from the Afrotropics, with at least one species occurring in India in each clade (*Sypheotides indica* and *A. nigriceps* respectively). The Indian species are, in turn, sister to another species that ranges further east and south, to South-East Asia and Australia (*H. bengalensis* and *A. australis*, respectively). It seems likely these clades once ranged through the Middle East during a time when there was suitable grassland habitat was present (Moreau, 1952; Vrba, 1985). Data here do not give sufficient resolution to assess the ancestral biogeographic pattern in **Clade Smaller bustards**, but in the *Ardeotis* clade, there has most likely been an eastwards expansion (see above).

Pteroclidae are more tolerant of extreme aridity and have the most extensive contemporary Middle Eastern distribution of all the species studied here (Johnsgard, 1991; Maclean, 1996). All three of the major sandgrouse clades identified in this study (**Clades Short-tailed, Long-tailed** and **Nyctiperdix**) have representatives in the Afrotropics and India (Fig. 6.2) and all have at least one species that occurs in the Middle East. In **Clade Long-tailed**, **Clade 14** in particular comprises the south-west desert endemic *P. namaqua* sister to *P. exustus*, a species of the north-east desert and semi-desert zone that also extends widely from the Sahel to India (but which is largely absent from the Middle East, occurring only in pockets in the less extreme coastal areas; Fig. 6.28; de Juana, 1997). **Clade Short-tailed** comprises three species: *P. coronatus* which inhabits extreme desert regions from the Sahara through the Middle East to the western deserts of India (Johnsgard, 1991); *P. gutturalis* endemic to the Afrotropics; and *P. personatus* of Madagascar (Fig. 6.24). The three most basal members of **Clade Nyctiperdix** (*P. bicinctus*, *P. quadricinctus* and *P. decoratus*) are Afrotropical endemics, whereas their sister clade (*P. indicus* and *P. lichtensteinii*) have an Indian distribution. *P. indicus* is endemic to India, whereas *P. lichtensteinii* ranges more widely through the Sahara, less extreme parts of the Middle East, and marginally in the north-east arid zone of Africa (Figs 6.21 – 6.23; de Juana, 1997). The clade structure thus suggests an eastwards expansion into Asia from Africa, as in *Ardeotis* (see above).

This study revealed that the Glareolidae have two species pairs that occur only in the Afrotropics and India, and not in the intervening area. *Cursorius temminckii* occurs in open areas in woodland habitats throughout Africa and is sister to the Indian *C.*

coromandelicus (Figs 6.3 and 6.31). The other members of the *Cursorius* clade are distributed in both Africa and the Palearctic and it is not possible to deduce the ancestral area with confidence. However, the sister taxon to the *Cursorius temminckii* (Africa) - *C. coromandelicus* (India) clade, *C. rufus*, is an African endemic, suggesting an African origin of the clade comprising these three species (Fig. 6.3). *Rhinoptilus chalcopterus* is widely distributed in the arid woodlands of Africa and is found to be sister to the localised Indian endemic *R. bitorquatus* (Fig. 6.3 and 6.32). All the basal members of *Rhinoptilus* (indeed, all species of *Rhinoptilus* except *R. bitorquatus*) are endemic to Africa, and it also seems most likely that this genus expanded eastwards into Asia. In the pratincoles (**Clade Glareola**), it has been suggested that the African *G. cinerea* is sister to the Indian *G. lactea* (Maclean, 1996), both of which occur on the sandbars of large rivers (Maclean, 1996), and this is supported by morphological evidence (Fig. 4.2), but is unresolved in the total evidence tree due to the lack of molecular data from either species (Fig. 6.3).

(iv) clades with representatives in both the south-west and north-east arid zones of Africa, sometimes with another clade member in the Sahel

This is the characteristic distribution pattern that led to the initial speculation of the ‘arid corridor’ (see Chapter 1) and is well-illustrated in the Otididae by the strongly-supported **Clade Heterotetrax** (Figs 1.5, 6.1 and 6.17). The sisters *E. rueppellii* and *E. vigorsii* are endemic to the south-west arid zone and have diversified across a habitat gradient, with the former replacing the latter in the more arid areas of the Namib (Fig. 6.18; Vernon, 1995). These are, in turn, sister to the north-east endemic *E. humilis* of Somalia and the Ogaden of Ethiopia (Fig. 6.17). **Clade Blue Eupodotis**

has also diversified across a habitat gradient in South Africa, with *E. caerulescens* in the mesic open grasslands and *E. barrowii* in the adjacent lower-lying savannas (Allan, 2005). The sister to *E. barrowii*, *E. senegalensis*, occurs in arid and open patches across Africa, and has subspecies in both the north-east arid zone and the Sahel (Fig. 6.20; Collar, 1986). The *Lophotis* clade also shows this classic distribution pattern, and the three species (*L. ruficrista*, *L. gindiana* and *L. savilei*) are disjunctly distributed in the south-west arid zone, north-east arid zone and the Sahel respectively (Figs 1.6, 6.1 and 6.16). Because these *Lophotis* species show a habitat preference for arid woodland zones, their distributions fringe the edges of the arid zones and are thus closer geographically than those of **Clade Heterotetra**. Although the desert nomads *Neotis* (excluding *N. denhami*) also show a three-way disjunction between the south-west arid zone (*N. ludwigii*), north-east arid zone (*N. heuglinii*) and the Sahel (*N. nuba*), data here (e.g. Fig. 2.5) show that these species do not form a monophyletic clade as suggested by Kingdon (1989). *Neotis nuba* is weakly recovered as sister to *N. heuglinii* in Figs 6.1 and 6.10, but this relationship does not hold in any of the molecular analyses (Fig 2.5). *Ardeotis kori* has a distinctive subspecies on either side of the proposed arid corridor, which have been treated as separate species in the past (e.g. Mackworth-Praed and Grant, 1952), and is thus another clade exhibiting this disjunction (Fig 6.14).

Three clades of sandgrouse are confirmed that span the arid zone disjunction (Fig. 6.1). *Pterocles namaqua* is a south-west desert and semi-desert endemic which is a strongly-supported sister of *P. exustus*, a species of the north-east desert and semi-desert zone (that also extends widely from the Sahel to India; Maclean, 1996; Fig 6.28). The enigmatic *P. gutturalis* is typically a species of open grasslands and has an

endemic subspecies on the fringes of each arid zone (*gutturalis* in the south-west and *saturatior* from northern Zambia northwards; Maclean, 1996). **Clade Nyctiperdix** (members of which typically occur in arid woodlands on the fringes of the deserts, although *P. lichtensteinii* can also occupy more arid habitats; Maclean, 1996) also has northern and southern representatives on the fringes of the arid zones (Fig. 6.2). *Pterocles bicinctus* is a south-west zone endemic, which is sister to the clade comprising *P. quadricinctus* (north-east arid zone and across the Sahel), *P. lichtensteinii* (north-east zone, across the Sahel, and through the Middle East into India), and *P. indicus* (India) as shown in Fig. 6.21. *Pterocles decoratus*, is sister to the clade of *P. bicinctus* and its sisters mentioned above, and is a north-east arid zone endemic (Fig. 6.2).

Two groups of coursers are confirmed to have endemic representatives in the south-west and north-east arid zones, *Cursorius* and *Rhinoptilus africanus* (Fig. 6.3). The two south-west arid endemic subspecies of *Rhinoptilus africanus* are sister to the north-east arid subspecies (Figs 6.3 and 6.33). It would be interesting to speculate that the south-west desert endemic *Cursorius rufus* is sister to the north-east desert endemic equivalent *C. somalensis*. However, this is not recovered here but is included in a polytomy among the desert *Cursorius* (Fig. 6.3). More data might resolve the exact relationships among these species.

(v) clades endemic to the south-west arid zone

The two *Afrotis* (*A. afraoides* and *A. afra*) species are exclusively southern African, and are found in the arid zone in grasslands of the summer-rainfall region and the shrublands of the winter-rainfall region respectively (Crowe et al., 1994; Allan, 2005).

Similar examples of speciation across fine-scale arid zone ecological boundaries in southern Africa, such as in *Afrotis*, **Clade Heterotetrax** (Fig. 6.18) and **Clade Blue Eupodotis**, have also been noted for other south-west arid zone taxa, for example larks Alaudidae (Barnes, 2007), rock-thrushes *Monticola* (Outlaw et al., 2007; Zuccon and Ericson, 2010), chats *Cercomela* (Outlaw et al., 2010) and non-avian taxa such as the lizards *Cordylus* (Vernon, 1995) and ground squirrels *Xerus* (Herron et al., 2005), but these show finer scale differentiation than shown by the Otididae. *P. burchelli* is an enigmatic south-west arid zone endemic of the red Kalahari sands (Maclean, 1996).

(vi) clade occurring in the Sahel and central African forest zone

This remarkable biogeographic pattern is shown by *Ptilopachus petrosus* and *Francolinus nahani* and is the only known example of an African arid zone taxon with a sister species in the Central African forest zone (Fig. 6.4). It is in strong contrast to the Otididae, Pteroclidae and Glareolidae also studied here (Figs 6.1 - 6.3). Whereas *Ptilopachus* is distributed in the arid zone, it does inhabit dense bush growth among large boulders, a habitat more similar to the dense forest understorey inhabited by *F. nahani* than to the open plains inhabited by the majority of the Otididae, Pteroclidae and Glareolidae. Indeed, given the likely Miocene divergence between these species following the molecular clock approach of Crowe et al. (2006), it is most likely that their common ancestor inhabited the widespread forest habitats of that period (Fjeldså and Bowie, 2008; Voelker et al., 2010).

(vii) species widespread across the Afrotropical zone

No clades in the Otididae are comprised of widespread Afrotropical species, although

three clades each contain one widespread species. The open country *Neotis denhami* (**Clade Larger bustards**), *Eupodotis senegalensis* (**Clade Smaller bustards**) and *Lissotis melanogaster* all range through grassy habitats across Africa (Collar, 1996). Each of these species are, in turn, related to more localised species (*E. senegalensis* to a south-west endemic, *E. barrowii*; *L. melanogaster* to a north-east endemic, *L. hartlaubii*). The exact position of *N. denhami* is not determined conclusively and this might be an exception (Fig. 6.1).

Pterocles gutturalis has a wide distribution in the fringes of the south-west and north-east arid zones, although different subspecies inhabit the northern and southern parts of its range (see above). *Rhinoptilus cinctus* and *R. chalcopterus* prefer arid woodlands and so occur on the fringes of the arid zones and in suitable habitat in the areas in between the arid zones (Maclean, 1997).

(viii) species occurring in Madagascar

In the Pteroclidae, *Pterocles personatus* is a Madagascan endemic within **Clade Short-tailed** (Figs 6.24 and 6.25). It is recovered as sister to *P. coronatus*, although with limited support (Fig. 6.2), and so its sister species cannot be confirmed. It would be interesting to resolve this clade to provide another perspective on the avian colonisation of Madagascar; see Fuchs et al. (2008), Melo and Fuchs (2008) and Warren et al. (2010) and references therein, for recent examples of non-passerine colonisations of Madagascar. In the Glareolidae, *Glareola nuchalis* is recovered as sister to the Madagascan *G. ocularis* (Fig. 6.3). The latter species is a breeding endemic to Madagascar, but migrates to the East African coast in the austral winter; both species breed on rocky islands in large rivers (Maclean, 1996). Interestingly, the

VIP analysis suggests the Rift Valley as the barrier and not the Mozambique Channel; this is due to the wintering movements of *G. ocularis* to the East Africa coast ([Fig. 6.34](#)).

Evidence for the ‘arid corridor’ hypothesis

Is there any evidence to suggest that the ‘arid corridor’ has had an influence on the speciation of arid zone birds?

First, the primary pattern that has led to the suggestion of the ‘arid corridor’ hypothesis in birds was tested: the presence of putative sister taxa on either side of the presumed corridor (Winterbottom, 1967; Hall and Moreau, 1970; Kingdon, 1989; Vernon, 1999). Of all the putative species pairs separated by the ‘arid corridor’ mentioned in [Table 1.1](#), the majority of them were supported as sisters with high support ([Table 6.1](#); [Figs 6.1 – 6.4](#); see text for section iv above).

However, the presence of a few sister-species pairs on either side of the corridor could also be due to long-distance dispersal of species between the north-east and south-west arid zones, without the presence of a corridor. In order to evaluate this, the clade structure of the families as a whole was investigated. If there had never been an ‘arid corridor’ and lineages shared by the regions could be explained by long-distance dispersal, one might expect closely-related sister species to occur alongside each other in the same arid zone, with occasional dispersal to the opposite zone. The alternative scenario, if taxa have occurred across a past band of ‘arid corridor’ habitat stretching across the continent, then one would expect many sister taxa to be currently isolated on either side of the continent due to allopatric speciation. Close examination of the

clades in Figs 6.1 – 6.3 as well as Figs 6.14, 6.16, 6.17, 6.21, 6.28 and 6.33 suggests that the ‘arid corridor’ has had an important influence on speciation in these families as almost all the clades with Afro-tropical species show representatives in both the south-west and north-east arid zones (Otididae: **Clade AN**, *Ardeotis kori* subspecies, *Lophotis*, **Clade Heterotetrax**, **Clade Blue Eupodotis**; Pteroclidae: **Clade Nyctiperdix**, **Clade 14**, *Pterocles gutturalis* subspecies; Glareolidae: **Clade Cursorius**, *Rhinoptilus africanus* subspecies). It is more parsimonious to suggest that this number of shared connections between these two disjunct arid zones in so many clades (congruence, or perhaps “pseudocongruence”, see below) is more likely to suggest a shared historical event, rather than many isolated dispersal events. This shared historical event is postulated to be the ‘arid corridor’ link between the south-west and north-east arid zones.

Results here do not allow the determination between congruence or pseudocongruence (Cunningham and Collins, 1994; Donoghue and Moore, 2003, Voelker, 1999); in other words, whether the shared pattern between the clades results from a single occurrence of the ‘arid corridor’ or whether this corridor has existed (opened and closed) a number of times in the past. This latter scenario has been suggested on the basis that many taxonomic levels are rendered disjunct, for example, a disjunct family or genus might indicate an earlier link while a disjunct species a more recent link (Balinsky, 1962; Verdcourt, 1969; Winterbottom, 1967), and also from evidence that suggests that climate changes in Africa have been highly cyclical in nature (de Menocal, 1995, 2004; Maslin and Christensen 2007). Another factor is that the aridification of Africa might have led to the expansion of the arid zones, but these might not have always or ever become completely linked. However, the

distance between them might have been reduced and this might have allowed increased random short-distance dispersal events to successfully colonise the opposite area, and this might create congruent area cladograms between taxa. This could be described as a ‘partial arid corridor’.

The hypothesis of an ‘arid corridor’ can be further investigated using the vagility of the species involved (e.g. Barnes, 2007). In [Figs 6.4 - 6.7](#), the mobility of the taxa onto the phylogenies obtained has been mapped. This allows the evaluation of whether species pairs across the disjunction are those that are most sedentary (suggesting vicariance: an ‘arid corridor’) or most mobile (suggesting long-distance dispersal). In the Otididae, the strongest ‘arid corridor’ pattern is shown by *Lophotis* and **Clade Heterotetrax** ([Fig 6.5](#)), which are sedentary residents not prone to nomadism or migration. This provides further evidence for an ‘arid corridor’ link between the areas and suggests that this phenomenon might have had a significant influence on the speciation of arid zone birds. However, as discussed in section (v) above, speciation across ecological gradients within the south-west arid zone, also seems to have been an important driver of speciation (Vernon, 1999; Barnes, 2007; Outlaw et al. 2007).

The Pteroclidae are highly dependent on regular access to drinking water and all species are prone to nomadic or migratory movements (Johnsgard, 1991; du Juana, 1997), similar to *Eremopterix* larks (Barnes, 2007). Even though many sandgrouse species are described in de Juana (1997) as “sedentary”, further reading of the detailed species accounts in Johnsgard (1991), Maclean and Fry (1986) and de Juana (1997) reveal that all species are documented to undertake migrations or sporadic

movements, and no sandgrouse species could be described as a sedentary resident. There were three species for which little information was available on their movements and might be more sedentary than the others, *Pterocles bicinctus*, *P. decoratus* and *P. personatus*, but this could not be ascertained with certainty. *P. namaqua* and *P. exustus* show an ‘arid corridor’ disjunction but this might be due to a long distance dispersal event in these mobile species.

The only clade in the Glareolidae which shows the classic ‘arid corridor’ distribution is *Rhinoptilus africanus*, and it is one of the few coursers that can be described as sedentary (Fig. 6.7). This adds further support to the Otididae examples described above as evidence for the existence of an ‘arid-corridor’ linking the south-western and north-eastern arid-zones of Africa in the past.

The nature of the habitats in the arid zone also provides insight as each arid zone is bordered by a gradient of less arid woodland habitats. Taxa found in these zones are closer in proximity to each other than those restricted to hyper-arid desert areas, which are further apart in distance (Fig. 1.2). This is illustrated by the geographic distance between species in desert **Clade Heterotetrax** species (Figs 1.5 and 6.17) versus those in arid woodland *Lophotis* (Figs 1.6 and 6.16). Disjunct desert species pairs are thus more likely to have resulted from vicariance, as the sisters are further apart geographically than those found in woodlands which might have a greater probability for long-distance dispersal due to their closer proximity. Barnes (2007) suggests that these arid savanna links are the most significant ‘arid corridor’ pattern shown in larks (e.g. *Calendulauda africanoides* versus *C. alopex*). Whereas these arid savanna links seem to be important for *Lophotis* (Fig. 6.16) and *Ardeotis kori*

subspecies ([Fig. 6.14](#)) in the Otididae, and **Clade Nyctiperdix** in the Pteroclidae ([Fig. 6.21](#)), there is also a strong pattern in the families investigated here for disjunct true desert species ([Figs 6.5 - 6.7](#)): **Clade Heterotetra**x (Otididae; [Fig. 6.17](#)), **Clade 14** (*Pterocles namaqua* versus *P. exustus*; Pteroclidae; [Fig. 6.28](#)) and *Rhinoptilus africanus* subspecies (Glareolidae; [Fig. 6.33](#)).

Another possible scenario, if there was never an ‘arid corridor’ between Africa’s deserts, is that the arid-adapted endemics are derived from adjacent forest and moist woodland species. This is not the case for the Otididae, Pteroclidae or Glareolidae, as the habitat type seems very well conserved within clades and basal species, indeed almost all species, are arid-adapted ([Figs 6.5 - 6.7](#)). This is not the case for *Ptilopachus* ([Fig. 6.4](#)), where intriguingly a forest species is sister to an arid-zone Sahelian species.

There is a biogeographic link between the north-east arid zone and the Sahel. In the Otididae, different subspecies of *Eupodotis senegalensis* occur in these areas (Collar, 1996), and two sister-species occur across this disjunction: *Lophotis gindiana* and *L. savilei*, and *Neotis heuglinii* and *N. nuba* ([Figs 6.1, 6.16](#) and [6.10](#)). Two species of sandgrouse occur in both these areas, but not further south (*P. exustus* and *P. quadricinctus*; de Juana, 1997). Interestingly, Ostrich *Struthio camelus* shows a closer link between south-west and north-east taxa, but a large difference occurring between the north-east and Sahelian populations, although this is complicated by a second highly-divergent north-east taxon (Freitag and Robinson, 1993; Robinson and Matthee, 1999; Miller et al., 2010).

2. The taxonomy of Africa's arid zone non-passerine terrestrial birds

In this dissertation, morphological, behavioural and molecular data are used to infer the relationships and taxonomy of bird in four African bird families. It is important to include morphological characters (unlike in many current systematic studies which are solely molecular-based), as it is these characters on which all the traditional assessments of taxonomy are based. By including them in this study, it allows the critical evaluation of them in a phylogenetic framework, instead of subjectively deciding which characters are the more important for inferring taxonomy, such as has been the case in many studies, e.g. Bowen (1927), Maclean (1984) and Johnsgard (1991).

Nonetheless, the morphological-behavioural analyses ([Figs 2.3, 3.4, 4.2](#)) bear a strong resemblance to the traditionally accepted taxonomy ([Tables 1.2 - 1.4](#)), with almost all genera and subfamilies being recovered as monophyletic. Exceptions to this are the placement of the enigmatic *Pterocles burchelli* at the base of the Pteroclidae tree which renders *Pterocles* polyphyletic ([Fig. 3.4](#)) and, in the Glareolidae, the nested nature of *Stiltia* within *Glareola* ([Fig. 4.2](#)). Including morphological-behavioural characters also allows the comparison of these analyses directly to analyses of the molecular characters, as well as to combine them to provide the most complete dataset possible (see Crowe et al., 2006). The molecular data not only confirm the non-monophyly of *Pterocles* and *Glareola*, but the Otididae genera *Eupodotis* and *Neotis*, and the Glareolidae subfamily Cursoriinae, are also shown to be not monophyletic. The molecular data also strongly support the sister relationship between *Francolinus nahani* and *Ptilopachus petrosus*, which is supported by

behavioural characters. Based on the results of these analyses, taxonomic recommendations are detailed below.

Otididae

Results are largely concordant with the taxonomy of the bustards as proposed by Collar (1996), with differences only in the treatment of *Eupodotis* and possibly *Neotis*. It should be emphasised that the previous broad use of *Eupodotis* to include all the smaller African (and sometimes Asian) bustards (e.g. Snow, 1978; Collar et al., 1986; Sibley and Monroe, 1990; Johnsgard, 1991) is misleading, as this assemblage is not a single, monophyletic lineage.

The results allow for more than one classification scheme for the Otididae, depending on how one argues the generic limitations in the case of 1. *Neotis*, and 2. the number of small genera which show large morphological diversity but which are placed together in monophyletic clades. Two classification schemes are proposed below, A (split) and B (lumped), both of which are defensible.

1. The treatment of *Ardeotis* and *Neotis* has not been fully resolved due to a limited amount of molecular material sequenced from museum specimens, and further data may help to clarify their relationships. Although it seems that *Ardeotis* is monophyletic, results show that it renders *Neotis* paraphyletic and it might thus be cautious to subsume the members of *Neotis* into *Ardeotis*, which has priority. However, this treatment cannot be recommend until this clade has been examined in more detail, and so the *status quo* should remain until such data are available. It might also be argued that because a previous study has also failed to recover a monophyletic

Neotis (Pitra et al., 2002), that *Neotis* be subsumed, and this is proposed in Classification Scheme B.

2. The Otididae contain a high proportion of monotypic genera, and genera with only two species, which some may argue should be subsumed into larger, more inclusive genera. These genera delimit an extraordinary amount of morphological, behavioural and genetic diversity which argues for retaining them, even if they are not very speciose. However, in Classification Scheme B below, those small genera have been lumped that form well-supported monophyletic clades with other genera.

Classification Scheme A: Family Otididae

Otis (Linnaeus 1758)

Otis tarda

Chlamydotis (Lesson 1839)

Chlamydotis undulata

C. macqueenii

Tetrax (T. Forster 1817)

Tetrax tetrax

Ardeotis (Le Mahout 1853)*Ardeotis arabs**A. kori**A. nigriceps**A. australis****Neotis*** (Sharpe 1893) (Should possibly be subsumed into *Ardeotis*; see below)*Neotis ludwigii**N. denhami**N. heuglinii**N. nuba****Lissotis*** (Reichenbach 1848)*Lissotis melanogaster**L. hartlaubii****Afrotis*** (G.R. Gray 1855)*Afrotis afra**A. afraoides****Eupodotis*** (Lesson 1839)*Eupodotis senegalensis* (type species, Vieillot 1820)*E. barrowii* (further study to clarify the specific status of *barrowii* is recommended)*E. caerulescens*

Heterotetrax (Sharpe 1894)*Heterotetrax vigorsii* (type species, A. Smith 1831)*H. rueppellii**H. humilis****Lophotis*** (Reichenbach 1848)*Lophotis savilei**L. gindiana**L. ruficrista****Houbaropsis*** (Sharpe 1893)*Houbaropsis bengalensis****Syphoetides*** (Lesson 1839)*Syphoetides indica***Classification Scheme B: Family Otididae*****Otis*** (Linnaeus 1758)*Otis tarda**O. undulata**O. macqueenii****Tetrax*** (T. Forster 1817)*Tetrax tetrax*

Ardeotis (Le Mahout 1853)*Ardeotis arabs**A. kori**A. nigriceps**A. australis**A. ludwigii**A. denhami**A. heuglinii**A. nuba****Lissotis*** (Reichenbach 1848)*Lissotis melanogaster**L. hartlaubii****Eupodotis*** (Lesson 1839)*Eupodotis senegalensis* (type species, Vieillot 1820)*E. barrowii* (further study to clarify the specific status of *barrowii* is recommended)*E. caerulescens**E. afra**E. afraoides**E. vigorsii* (type species, A. Smith 1831)*E. rueppellii**E. humilis*

Lophotis* (Reichenbach 1848)L. savilei**L. gindiana**L. ruficrista****Syphoetides* (Lesson 1839)***Syphoetides indica**S. bengalensis***Pteroclidae**

The two *Syrrhaptes* species are considered sister-taxa only by a suite of morphological characters as no DNA sample could be amplified for *S. tibetanus*, but there seems no reason to doubt the close relationship between these two central Asian species. The genus *Pterocles* is not recovered as monophyletic in any of the analyses, as it is rendered paraphyletic by *Syrrhaptes*. One solution to ensure that the genera in Pteroclidae retain monophyly is to subsume all the species into one genus. *Syrrhaptes* (Illiger 1811) predates *Pterocles* (Temminck 1815) and so all species would need to be transferred to *Syrrhaptes*, as presented in Classification Scheme A, below:

Classification Scheme A: Family Pteroclidae***Syrrhaptes* (Illiger 1811)***S. paradoxus**S. tibetanus*

S. orientalis

S. namaqua

S. exustus

S. gutturalis

S. personatus

S. coronatus

S. decoratus

S. bicinctus

S. quadricinctus

S. lichtensteinii

S. indicus

S. alchata

S. burchelli

However, containing all the members of a family in a single genus provides no information on their relationships. Another approach would be to tentatively group species identified in this study's three well-supported clades into the following genera:

Classification Scheme B: Family Pteroclidae

***Syrrhaptes* (Illiger 1811) (Clade 11)**

S. paradoxus

S. tibetanus

S. orientalis

S. namaqua

S. exustus

***Pterocles* (Temminck 1815) (Clade 8)**

P. gutturalis

P. personatus

P. coronatus

***Nyctiperdix* (Roberts 1922) (Clade 2)**

N. decoratus

N. bicinctus

N. quadricinctus

N. lichtensteinii

N. indicus

Uncertain:

alchata

burchelli

The reason that this approach is not currently defensible is that placement of *alchata* and *burchelli* is uncertain. A more conservative approach, suggested by the combined data tree (Fig. 6.2) is the split between **Clade Nyctiperdix** and the others, which might result in a treatment as follows:

Classification Scheme C: Family Pteroclidae

Syrrhaptes (Illiger 1811)

S. paradoxus

S. tibetanus

S. orientalis

S. namaqua

S. exustus

S. gutturalis

S. personatus

S. coronatus

S. alchata

S. burchelli

Pterocles (Temminck 1815) (Clade Nyctiperdix)

P. decoratus

P. bicinctus

P. quadricinctus

P. lichtensteini

P. indicus

In this case, *Pterocles* (Temminck 1815) predates *Nyctiperdix* (Roberts 1922). The recommendation is to further investigate the position of *alchata* and *burchelli* before revising the taxonomy of this family, and if no further clarification resolves the

placement of the major clades, I would then recommend using Classification Scheme C.

Glareolidae

The subfamilies Cursoriinae and Glareolinae (with the inclusion of the monotypic Stiltiinae) are not monophyletic and should be dropped from the taxonomy of this family. *Cursorius* (Latham 1790) should be limited to those species in the monophyletic **Clade Cursorius**. The taxa *somalensis* and *littoralis* should be treated as a full species, *C. somalensis*, as they are neither sister to *C. rufus* nor *C. cursor* (more data are required to clarify this position). Members of **Clade Rhinoptilus** should be included in *Rhinoptilus* (Strickland 1852), and while there is no strong objection to *R. africanus* being included in the monotypic *Smutsornis* (Roberts 1922), this does not add much useful information on the structure of the family. The differences between the subspecies of *R. africanus* could be investigated further, although the preliminary data in this study indicate that there are not significant differences between them and they are perhaps best retained as subspecies pending further research. The pratincoles require further data to test their relationships. Provisionally, *Stiltia* (Gray 1855) should be dropped as it renders *Glareola* (Brisson 1760) polyphyletic. Further research might strongly support a division between the four “river pratincoles” and the others, in which case the “river pratincoles” might merit generic status - *Galachrysa*. The following treatment is recommended:

Family Glareolidae***Cursorius* (Latham 1790)**

Cursorius cursor

C. somalensis

C. rufus

C. temminckii

C. coromandelicus

***Rhinoptilus* (Strickland 1852)**

Rhinoptilus africanus

R. cinctus

R. chalcopterus

R. bitorquatus

***Glareola* (Brisson 1760)**

Glareola isabella

G. pratincola

G. maldivarum

G. nordmanni

G. ocularis

G. nuchalis

G. cinerea

G. lactea

Phasianidae/ Odontophoridae

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

Family Odontophoridae

***Ptilopachus* (Swainson 1837)**

Ptilopachus petrosus

P. nahani

3. Life history evolution in study taxa

The evolution of a wide variety of life history traits, habitat use, activity times, movements, and behavioural ecology are investigated for each family and these are interpreted in detail in [Chapters 2-5](#). A general problem in assessing character evolution has been the lack of support at the bases of the trees, making it impossible to assess the ancestral states with any certainty.

4. Improvements and future research

The most disappointing aspect of these analyses have been the lack of basal resolution of the trees and this has weakened the taxonomic, systematic and biogeographic interpretation of the results. This might be due to rapid radiation of the clades involved (Pitra et al., 2002; Hackett et al., 2008), especially in the well-sampled Otididae, but it might also be due incomplete taxon and locus sampling. While these analyses represent the most complete morphological-behavioural and molecular sampling of these families to date, there are still important gaps, and genetic material was not available for all species. Thus, the placement of some of the taxa in this study is based solely on morphological-behavioural data (where DNA data was not available) and future research should endeavour to obtain samples and sequences for these species to increase the number of characters on which to base the phylogenetic hypotheses. Ideally, fresh samples for at least two individuals of each species involved would allow a more complete set of genes to be sequenced, which might provide greater phylogenetic resolution. This is especially relevant for the genus *Neotis* (Otididae), for a number of Pteroclidae (see [Table 3.1](#)), and for the Glareolinae of the Glareolidae.

At the species level, further insight into Africa's arid zones might be obtained through phylogeographic study of the following species, which have isolated arid zone subspecies and are controversial taxonomically: *Eupodotis senegalensis* (and *barrowii*), *Ardeotis kori* and *Cursorius somalensis*. In addition, further investigation of the isolated arid zone subspecies of *Rhinoptilus africanus* and *Pterocles gutturalis* might also provide additional insight. Practically, it is very difficult to amass the fresh samples required for analyses of these phylogeographic patterns, although much

progress has been made with *A. kori* (T. Osborne, S. Hallager and C. Cohen, unpublished data).

A molecular clock approach, which would include calculating approximate time divergence estimates for sister-species across the ‘arid corridor’ disjunction, might provide further insight, as concordance of divergence dates may provide time estimates for the existence of such a vicariance event (Klicka and Zink, 1997; Voelker, 1999). However, calibrating the clock is problematic (no phylogenetically-placed fossils are known for the Otididae, Pteroclidae or Glareolidae) and the time divergence estimates can be confounded by rate variation between lineages (see Pereira and Baker, 2006; Fjeldså and Bowie, 2008). For these reasons, this approach has not been followed here.

CHAPTER 6

Synthesis: Biogeography and taxonomy of Africa's arid zone non-passerine terrestrial birds - the bustards (Otididae), sandgrouse (Pteroclidae), coursers (Glareolidae) and Stone Partridge (*Ptilopachus*).

This synthesis discusses the major results of the Chapters 2-5, specifically focusing on the following:

1. The biogeography of Africa's arid zone non-passerine terrestrial birds with special focus on the 'arid corridor' hypothesis.
2. The taxonomy of Africa's arid zone non-passerine terrestrial birds in relation to previous classifications.
3. Life history evolution in the study taxa.
4. Improvements and directions for future research.

1. The biogeography of Africa's arid zone non-passerine terrestrial birds with special focus on the 'arid corridor' hypothesis

Two methods are used to infer biogeographic patterns: 1. clade structure with broad geographical distribution of each taxon mapped onto phylogenies presented in [Figs 6.1 - 6.4](#), and 2. Spatial analysis of vicariance, which is explained in more detail below.

Spatial analysis of vicariance

Spatial analysis of vicariance is a method for the analysis of taxon history based on identifying sister nodes with disjunct (allopatric/ vicariant) distributions (Arias et al., subm.). It is based on Hovenkamp's (1997, 2001) ideas on historical biogeography: instead of searching for ancestral areas, it identifies disjunctions between sister groups and thus highlights natural barriers. The method uses observed distributions as data (and thus does not require distributions to be classified into predefined areas; Arias et al., subm.). To implement these across the tree, internal nodes are assigned distributions as the sum of the distributions of the descendant nodes, and barriers will only be detected if these are essentially non-overlapping (although it can be argued that a small amount of overlap is permissible, and an optimality criterion has been developed for cases when a small number of distributions overlap and potentially obscure a biogeographic pattern; Arias et al., subm.). Spatial analysis of vicariance was implemented using the computer program, VIP (Vicariance Inference Program; Arias, 2010). The distribution of each taxon in the phylogenies in [Figs 6.1 – 6.3](#) was mapped onto a world map using a grid of 3 x 3 degrees based on maps in Collar (1996), de Juana (1997) and Maclean (1996). This was then analysed with the

phylogenies in Figs 6.1 – 6.3 using a cost for overlapped distributions of 1.00, a cost for a removal distribution of 2.00, an overlap threshold of less than 25%, and an heuristic search of 100 replications was performed to search for optimal reconstructions. The optimality criterion seeks to find the best compromise between the maximum possible number of disjunct sister nodes and the minimum number of eliminated distributions (Arias et al., subm.), although for the present data, no distributions were eliminated. The barrier recovered for each disjunction was mapped onto a world map using a geometric algorithm (Voronoi tessellation), which is quite effective when the distributions were close together, but becomes least accurate for large gaps between distributions (J. Salvador Arias, in litt.). All the barriers recovered in VIP are mapped as Figs 6.8 – 6.35 and are discussed below, in combination with the insights obtained from clade structure.

Biogeographic patterns

Phylogenetic analyses of the Otididae, Pteroclidae, Glareolidae and *Ptilopachus* (Chapters 2-5) have revealed a number of biogeographic patterns within clades which can be summarised as follows and are discussed in more detail below:

- (i) widespread Palearctic clades with distributions that essentially mirror the southern arid border of the Palearctic region (centered on the southern areas of the Western Palearctic, often including the Saharan region, and the Middle East, eastwards to India, and occasionally further eastwards still)
- (ii) clades restricted to Asia (and Australia)
- (iii) clades with members in both the Afrotropical region and India (sometimes including the Middle East)

- (iv) clades with representatives in both the south-west and north-east arid zones of Africa, sometimes with another clade member in the Sahel
- (v) clades endemic to the south-west arid zone
- (vi) clades occurring in the Sahel and central African forest zone
- (vii) clades with species widespread across the Afrotropical zone
- (viii) clades with species occurring in Madagascar

(i) Widespread Palearctic clades

The Otididae, Pteroclidae, Glareolidae all contain species with a widespread Palearctic distribution (Figs 6.1 - 6.4). In the Otididae, *Otis* and *Chlamydotis* form a well-supported monophyletic clade, with the latter occupying more arid areas to the south of the distribution of *Otis* (Fig. 6.8). Both are widely distributed across the Palearctic region with *Tetrax*, allied to them with moderate support (Fig. 6.1), collectively are the bustards that occur the furthest north, and have the widest latitudinal range of the family (Johnsgard, 1991; Collar, 1996). The biogeography of *Chlamydotis* is complex with both island and migratory forms and is detailed in Gaucher et al. (1996). In Africa, these Palearctic bustard species occur only in the Mediterranean and Saharan regions (Collar, 1996).

In the Pteroclidae, several species share a southern arid Palearctic distribution (e.g. *P. coronatus* and *P. senegallus* which inhabit desert regions from the Sahara eastwards to India, and *P. alchata* and *P. orientalis*, which also span a similar longitudinal range but occur to the north of the previous two species), but are not closely related. The only clade that is exclusively Palearctic is the sister relationship between *P. orientalis* and the two *Syrrhaptes* species (Fig. 6.29; see ii below).

In the Glareolidae, only a single species of the subfamily Cursoriinae (coursers), *C. cursor*, has a wide Palearctic distribution. The Glareolinae (pratincoles) are closely tied ecologically to wetland habitats and do not share the arid zone distribution of the Cursoriinae (Maclean, 1996) and were included in this study largely to ensure correct placement of the members of the Cursoriinae. Three species of Glareolinae (*G. maldivarum*, *G. pratincola* and *G. nordmanni*) that form a clade show a widespread Palearctic distribution and all undergo regular migrations to more southerly areas; the former two of these species are distributed disjunctly (Fig. 6.35; Maclean, 1996).

(ii) clades restricted to Asia (and Australia)

In the Otididae, the two floricans, *Sypheotides indica* (India) and *Houbaropsis bengalensis* (India to South-east Asia) share a southern Asian distribution, and this study confirms their sister-relationship (Fig. 6.15). This clade is also the only non-African subclade of **Clade Smaller Bustards**. However, its relationship to the other subclades in **Clade Smaller Bustards** is not resolved (Fig. 6.1), hampering further interpretation. Thus, it remains uncertain whether the common ancestor of the floricans dispersed out of Africa to diversify in southern Asia, or vice-versa.

The results presented here strongly support a sister relationship between the Australian *A. australis* and Indian *A. nigriceps* and these are the only members of the *Ardeotis-Neotis* clade that do not occur in Africa (Figs 6.1, 6.11 and 6.13). As all the basal species of the *Ardeotis-Neotis* clade (all *Neotis* and *A. arabs*) share an Afrotropical distribution (although *A. arabs* ranges marginally into the Saharan region), this would suggest an African origin to this clade and an eastwards expansion

into Asia by *A. australis* and *A. nigriceps* (see Figs 6.11 and 6.12; passerine examples include *Anthus*, Voelker, 1999, and *Monticola*, Outlaw et al., 2007).

In the Pteroclidae, the two species in the genus *Syrrhaptes* (*S. paradoxus* and *S. tibetanus*) are supported as sister taxa (Fig. 6.30). They are endemic to the cold deserts of central Asia (centered on the Tibetan Plateau, but also extend further north, east and west), and are sister to the western Palearctic *P. orientalis*; this clade is thus wholly restricted to the Palearctic (see above; Fig. 6.2).

The aberrant *Stiltia*, confined to Australia and southern Asia, is decisively shown to be sister to the widespread Palearctic *Glareola* clade mentioned above and is not an intermediate form between the Glareolinae and Cursoriinae.

(iii) clades with members in both the Afrotropical region and India (sometimes including the Middle East)

In the Otididae, as mentioned above, **Clade Smaller bustards** and the *Ardeotis-Neotis* clade (**Clade AN**, Fig. 6.1) are both primarily composed of species from the Afrotropics, with at least one species occurring in India in each clade (*Sypheotides indica* and *A. nigriceps* respectively). The Indian species are, in turn, sister to another species that ranges further east and south, to South-East Asia and Australia (*H. bengalensis* and *A. australis*, respectively). It seems likely these clades once ranged through the Middle East during a time when there was suitable grassland habitat was present (Moreau, 1952; Vrba, 1985). Data here do not give sufficient resolution to assess the ancestral biogeographic pattern in **Clade Smaller bustards**, but in the *Ardeotis* clade, there has most likely been an eastwards expansion (see above).

Pteroclidae are more tolerant of extreme aridity and have the most extensive contemporary Middle Eastern distribution of all the species studied here (Johnsgard, 1991; Maclean, 1996). All three of the major sandgrouse clades identified in this study (**Clades Short-tailed, Long-tailed** and **Nyctiperdix**) have representatives in the Afrotropics and India (Fig. 6.2) and all have at least one species that occurs in the Middle East. In **Clade Long-tailed**, **Clade 14** in particular comprises the south-west desert endemic *P. namaqua* sister to *P. exustus*, a species of the north-east desert and semi-desert zone that also extends widely from the Sahel to India (but which is largely absent from the Middle East, occurring only in pockets in the less extreme coastal areas; Fig. 6.28; de Juana, 1997). **Clade Short-tailed** comprises three species: *P. coronatus* which inhabits extreme desert regions from the Sahara through the Middle East to the western deserts of India (Johnsgard, 1991); *P. gutturalis* endemic to the Afrotropics; and *P. personatus* of Madagascar (Fig. 6.24). The three most basal members of **Clade Nyctiperdix** (*P. bicinctus*, *P. quadricinctus* and *P. decoratus*) are Afrotropical endemics, whereas their sister clade (*P. indicus* and *P. lichtensteinii*) have an Indian distribution. *P. indicus* is endemic to India, whereas *P. lichtensteinii* ranges more widely through the Sahara, less extreme parts of the Middle East, and marginally in the north-east arid zone of Africa (Figs 6.21 – 6.23; de Juana, 1997). The clade structure thus suggests an eastwards expansion into Asia from Africa, as in *Ardeotis* (see above).

This study revealed that the Glareolidae have two species pairs that occur only in the Afrotropics and India, and not in the intervening area. *Cursorius temminckii* occurs in open areas in woodland habitats throughout Africa and is sister to the Indian *C.*

coromandelicus (Figs 6.3 and 6.31). The other members of the *Cursorius* clade are distributed in both Africa and the Palearctic and it is not possible to deduce the ancestral area with confidence. However, the sister taxon to the *Cursorius temminckii* (Africa) - *C. coromandelicus* (India) clade, *C. rufus*, is an African endemic, suggesting an African origin of the clade comprising these three species (Fig. 6.3). *Rhinoptilus chalcopterus* is widely distributed in the arid woodlands of Africa and is found to be sister to the localised Indian endemic *R. bitorquatus* (Fig. 6.3 and 6.32). All the basal members of *Rhinoptilus* (indeed, all species of *Rhinoptilus* except *R. bitorquatus*) are endemic to Africa, and it also seems most likely that this genus expanded eastwards into Asia. In the pratincoles (**Clade Glareola**), it has been suggested that the African *G. cinerea* is sister to the Indian *G. lactea* (Maclean, 1996), both of which occur on the sandbars of large rivers (Maclean, 1996), and this is supported by morphological evidence (Fig. 4.2), but is unresolved in the total evidence tree due to the lack of molecular data from either species (Fig. 6.3).

(iv) clades with representatives in both the south-west and north-east arid zones of Africa, sometimes with another clade member in the Sahel

This is the characteristic distribution pattern that led to the initial speculation of the ‘arid corridor’ (see Chapter 1) and is well-illustrated in the Otididae by the strongly-supported **Clade Heterotetrax** (Figs 1.5, 6.1 and 6.17). The sisters *E. rueppellii* and *E. vigorsii* are endemic to the south-west arid zone and have diversified across a habitat gradient, with the former replacing the latter in the more arid areas of the Namib (Fig. 6.18; Vernon, 1995). These are, in turn, sister to the north-east endemic *E. humilis* of Somalia and the Ogaden of Ethiopia (Fig. 6.17). **Clade Blue Eupodotis**

has also diversified across a habitat gradient in South Africa, with *E. caerulescens* in the mesic open grasslands and *E. barrowii* in the adjacent lower-lying savannas (Allan, 2005). The sister to *E. barrowii*, *E. senegalensis*, occurs in arid and open patches across Africa, and has subspecies in both the north-east arid zone and the Sahel (Fig. 6.20; Collar et al., 1986). The *Lophotis* clade also shows this classic distribution pattern, and the three species (*L. ruficrista*, *L. gindiana* and *L. savilei*) are disjunctly distributed in the south-west arid zone, north-east arid zone and the Sahel respectively (Figs 1.6, 6.1 and 6.16). Because these *Lophotis* species show a habitat preference for arid woodland zones, their distributions fringe the edges of the arid zones and are thus closer geographically than those of **Clade Heterotetrax**. Although the desert nomads *Neotis* (excluding *N. denhami*) also show a three-way disjunction between the south-west arid zone (*N. ludwigii*), north-east arid zone (*N. heuglinii*) and the Sahel (*N. nuba*), data here (Fig. 6.1) show that these species do not form a monophyletic clade as suggested by Kingdon (1989). *Neotis nuba* is weakly recovered as sister to *N. heuglinii* in Figs 6.1 and 6.10, but this relationship does not hold in any of the molecular analyses (Fig. 2.5). *Ardeotis kori* has a distinctive subspecies on either side of the proposed arid corridor, which have been treated as separate species in the past (e.g. Mackworth-Praed and Grant, 1952), and is thus another clade exhibiting this disjunction (Fig. 6.14).

Three clades of sandgrouse are confirmed that span the arid zone disjunction (Fig. 6.1). *Pterocles namaqua* is a south-west desert and semi-desert endemic which is a strongly-supported sister of *P. exustus*, a species of the north-east desert and semi-desert zone (that also extends widely from the Sahel to India; Maclean, 1996; Fig. 6.28). The enigmatic *P. gutturalis* is typically a species of open grasslands and has an

endemic subspecies on the fringes of each arid zone (*gutturalis* in the south-west and *saturatior* from northern Zambia northwards; Maclean, 1996). **Clade Nyctiperdix** (members of which typically occur in arid woodlands on the fringes of the deserts, although *P. lichtensteinii* can also occupy more arid habitats; Maclean, 1996) also has northern and southern representatives on the fringes of the arid zones (Fig. 6.2). *Pterocles bicinctus* is a south-west zone endemic, which is sister to the clade comprising *P. quadricinctus* (north-east arid zone and across the Sahel), *P. lichtensteinii* (north-east zone, across the Sahel, and through the Middle East into India), and *P. indicus* (India) as shown in Fig. 6.21. *Pterocles decoratus*, is sister to the clade of *P. bicinctus* and its sisters mentioned above, and is a north-east arid zone endemic (Fig. 6.2).

Two groups of coursers are confirmed to have endemic representatives in the south-west and north-east arid zones, *Cursorius* and *Rhinoptilus africanus* (Fig. 6.3). The two south-west arid endemic subspecies of *Rhinoptilus africanus* are sister to the north-east arid subspecies (Figs 6.3 and 6.33). It would be interesting to speculate that the south-west desert endemic *Cursorius rufus* is sister to the north-east desert endemic equivalent *C. somalensis*. However, this is not recovered here but is included in a polytomy among the desert *Cursorius* (Fig. 6.3). More data might resolve the exact relationships among these species.

(v) clades endemic to the south-west arid zone

The two *Afrotis* (*A. afraoides* and *A. afra*) species are exclusively southern African, and are found in the arid zone in grasslands of the summer-rainfall region and the shrublands of the winter-rainfall region respectively (Crowe et al., 1994; Allan, 2005).

Similar examples of speciation across fine-scale arid zone ecological boundaries in southern Africa, such as in *Afrotis*, **Clade Heterotetrax** (Fig. 6.18) and **Clade Blue Eupodotis**, have also been noted for other south-west arid zone taxa, for example larks Alaudidae (Barnes, 2007), rock-thrushes *Monticola* (Outlaw et al., 2007; Zuccon and Ericson, 2010), chats *Cercomela* (Outlaw et al., 2010) and non-avian taxa such as the lizards *Cordylus* (Vernon, 1995) and ground squirrels *Xerus* (Herron et al., 2005), but these show finer scale differentiation than shown by the Otididae. *P. burchelli* is an enigmatic south-west arid zone endemic of the red Kalahari sands (Maclean, 1996).

(vi) clade occurring in the Sahel and central African forest zone

This remarkable biogeographic pattern is shown by *Ptilopachus petrosus* and *Francolinus nahani* and is the only known example of an African arid zone taxon with a sister species in the Central African forest zone (Fig. 6.4). It is in strong contrast to the Otididae, Pteroclidae and Glareolidae also studied here (Figs 6.1 - 6.3). Whereas *Ptilopachus* is distributed in the arid zone, it does inhabit dense bush growth among large boulders, a habitat more similar to the dense forest understorey inhabited by *F. nahani* than to the open plains inhabited by the majority of the Otididae, Pteroclidae and Glareolidae. Indeed, given the likely Miocene divergence between these species following the molecular clock approach of Crowe et al. (2006), it is most likely that their common ancestor inhabited the widespread forest habitats of that period (Fjeldså and Bowie, 2008; Voelker et al., 2010).

(vii) species widespread across the Afrotropical zone

No clades in the Otididae are comprised of widespread Afrotropical species, although

three clades each contain one widespread species. The open country *Neotis denhami* (**Clade Larger bustards**), *Eupodotis senegalensis* (**Clade Smaller bustards**) and *Lissotis melanogaster* all range through grassy habitats across Africa (Collar, 1996). Each of these species are, in turn, related to more localised species (*E. senegalensis* to a south-west endemic, *E. barrowii*; *L. melanogaster* to a north-east endemic, *L. hartlaubii*). The exact position of *N. denhami* is not determined conclusively and this might be an exception (Fig. 6.1).

Pterocles gutturalis has a wide distribution in the fringes of the south-west and north-east arid zones, although different subspecies inhabit the northern and southern parts of its range (see above). *Rhinoptilus cinctus* and *R. chalcopterus* prefer arid woodlands and so occur on the fringes of the arid zones and in suitable habitat in the areas in between the arid zones (Maclean, 1997).

(viii) species occurring in Madagascar

In the Pteroclidae, *Pterocles personatus* is a Madagascan endemic within **Clade Short-tailed** (Figs 6.24 and 6.25). It is recovered as sister to *P. coronatus*, although with limited support (Fig. 6.2), and so its sister species cannot be confirmed. It would be interesting to resolve this clade to provide another perspective on the avian colonisation of Madagascar; see Fuchs et al. (2008), Melo and Fuchs (2008) and Warren et al. (2010) and references therein, for recent examples of non-passerine colonisations of Madagascar. In the Glareolidae, *Glareola nuchalis* is recovered as sister to the Madagascan *G. ocularis* (Fig. 6.3). The latter species is a breeding endemic to Madagascar, but migrates to the East African coast in the austral winter; both species breed on rocky islands in large rivers (Maclean, 1996). Interestingly, the

VIP analysis suggests the Rift Valley as the barrier and not the Mozambique Channel; this is due to the wintering movements of *G. ocularis* to the East Africa coast ([Fig. 6.34](#)).

Evidence for the ‘arid corridor’ hypothesis

Is there any evidence to suggest that the ‘arid corridor’ has had an influence on the speciation of arid zone birds?

First, the primary pattern that has led to the suggestion of the ‘arid corridor’ hypothesis in birds was tested: the presence of putative sister taxa on either side of the presumed corridor (Winterbottom, 1967; Hall and Moreau, 1970; Kingdon, 1989; Vernon, 1999). Of all the putative species pairs separated by the ‘arid corridor’ mentioned in [Table 1.1](#), the majority of them were supported as sisters with high support ([Table 6.1](#); [Figs 6.1 – 6.4](#); see text for section iv above).

However, the presence of a few sister-species pairs on either side of the corridor could also be due to long-distance dispersal of species between the north-east and south-west arid zones, without the presence of a corridor. In order to evaluate this, the clade structure of the families as a whole was investigated. If there had never been an ‘arid corridor’ and lineages shared by the regions could be explained by long-distance dispersal, one might expect closely-related sister species to occur alongside each other in the same arid zone, with occasional dispersal to the opposite zone. The alternative scenario, if taxa have occurred across a past band of ‘arid corridor’ habitat stretching across the continent, then one would expect many sister taxa to be currently isolated on either side of the continent due to allopatric speciation. Close examination of the

clades in Figs 6.1 – 6.3 as well as Figs 6.14, 6.16, 6.17, 6.21, 6.28 and 6.33 suggests that the ‘arid corridor’ has had an important influence on speciation in these families as almost all the clades with Afro-tropical species show representatives in both the south-west and north-east arid zones (Otididae: **Clade AN**, *Ardeotis kori* subspecies, *Lophotis*, **Clade Heterotetrax**, **Clade Blue Eupodotis**; Pteroclidae: **Clade Nyctiperdix**, **Clade 14**, *Pterocles gutturalis* subspecies; Glareolidae: **Clade Cursorius**, *Rhinoptilus africanus* subspecies). It is more parsimonious to suggest that this number of shared connections between these two disjunct arid zones in so many clades (congruence, or perhaps “pseudocongruence”, see below) is more likely to suggest a shared historical event, rather than many isolated dispersal events. This shared historical event is postulated to be the ‘arid corridor’ link between the south-west and north-east arid zones.

Results here do not allow the determination between congruence or pseudocongruence (Cunningham and Collins, 1994; Donoghue and Moore, 2003, Voelker, 1999); in other words, whether the shared pattern between the clades results from a single occurrence of the ‘arid corridor’ or whether this corridor has existed (opened and closed) a number of times in the past. This latter scenario has been suggested on the basis that many taxonomic levels are rendered disjunct, for example, a disjunct family or genus might indicate an earlier link while a disjunct species a more recent link (Balinsky, 1962; Verdcourt, 1969; Winterbottom, 1967), and also from evidence that suggests that climate changes in Africa have been highly cyclical in nature (de Menocal, 1995, 2004; Maslin and Christensen 2007). Another factor is that the aridification of Africa might have led to the expansion of the arid zones, but these might not have always or ever become completely linked. However, the

distance between them might have been reduced and this might have allowed increased random short-distance dispersal events to successfully colonise the opposite area, and this might create congruent area cladograms between taxa. This could be described as a ‘partial arid corridor’.

The hypothesis of an ‘arid corridor’ can be further investigated using the vagility of the species involved (e.g. Barnes, 2007). In [Figs 6.4 - 6.7](#), the mobility of the taxa onto the phylogenies obtained has been mapped. This allows the evaluation of whether species pairs across the disjunction are those that are most sedentary (suggesting vicariance: an ‘arid corridor’) or most mobile (suggesting long-distance dispersal). In the Otididae, the strongest ‘arid corridor’ pattern is shown by *Lophotis* and **Clade Heterotetrax** ([Fig 6.5](#)), which are sedentary residents not prone to nomadism or migration. This provides further evidence for an ‘arid corridor’ link between the areas and suggests that this phenomenon might have had a significant influence on the speciation of arid zone birds. However, as discussed in section (v) above, speciation across ecological gradients within the south-west arid zone also seems to have been an important driver of speciation in *Afrotis*, **Clade Heterotetrax** ([Fig. 6.18](#)) and **Clade Blue Eupodotis**, which is mirrored in other taxa (Vernon, 1999; Barnes, 2007; Outlaw et al. 2007).

The Pteroclidae are highly dependent on regular access to drinking water and all species are prone to nomadic or migratory movements (Johnsgard, 1991; du Juana, 1997), similar to *Eremopterix* larks (Barnes, 2007). Even though many sandgrouse species are described in de Juana (1997) as “sedentary”, further reading of the detailed species accounts in Johnsgard (1991), Maclean and Fry (1986) and de Juana

(1997) reveal that all species are documented to undertake migrations or sporadic movements, and no sandgrouse species could be described as a sedentary resident across their entire distribution. There were three species for which little information was available on their movements and might be more sedentary than the others, *Pterocles bicinctus*, *P. decoratus* and *P. personatus*, but this could not be ascertained with certainty. *P. namaqua* and *P. exustus* show an ‘arid corridor’ disjunction but this might be due to a long distance dispersal event in these mobile species.

The only clade in the Glareolidae which shows the classic ‘arid corridor’ distribution is *Rhinoptilus africanus*, and it is one of the few coursers that can be described as sedentary (Fig. 6.7). This adds further support to the Otididae examples described above as evidence for the existence of an ‘arid-corridor’ linking the south-western and north-eastern arid-zones of Africa in the past.

The nature of the habitats in the arid zone also provides insight as each arid zone is bordered by a gradient of less arid woodland habitats. Taxa found in these zones are closer in proximity to each other than those restricted to hyper-arid desert areas, which are further apart in distance (Fig. 1.2). This is illustrated by the geographic distance between species in desert **Clade Heterotetrax** species (Figs 1.5 and 6.17) versus those in arid woodland *Lophotis* (Figs 1.6 and 6.16). Disjunct desert species pairs are thus more likely to have resulted from vicariance, as the sisters are further apart geographically than those found in woodlands which might have a greater probability for long-distance dispersal due to their closer proximity. Barnes (2007) suggests that these arid savanna links are the most significant ‘arid corridor’ pattern shown in larks (e.g. *Calendulauda africanoides* versus *C. alopex*). Whereas these arid

savanna links seem to be important for *Lophotis* (Fig. 6.16) and *Ardeotis kori* subspecies (Fig. 6.14) in the Otididae, and **Clade Nyctiperdix** in the Pteroclidae (Fig. 6.21), there is also a strong pattern in the families investigated here for disjunct true desert species (Figs 6.5 - 6.7): **Clade Heterotetrax** (Otididae; Fig. 6.17), **Clade 14** (*Pterocles namaqua* versus *P. exustus*; Pteroclidae; Fig. 6.28) and *Rhinoptilus africanus* subspecies (Glareolidae; Fig. 6.33).

Another possible scenario, if there was never an ‘arid corridor’ between Africa’s deserts, is that the arid-adapted endemics are derived from adjacent forest and moist woodland species. However, this is not the case for the Otididae, Pteroclidae or Glareolidae, as the habitat type seems very well conserved within clades and basal species, indeed almost all species, are arid-adapted (Figs 6.5 - 6.7). Also, this is not the case for *Ptilopachus* (Fig. 6.4), where intriguingly a forest species is sister to an arid-zone Sahelian species.

There is a biogeographic link between the north-east arid zone and the Sahel. In the Otididae, different subspecies of *Eupodotis senegalensis* occur in these areas (Collar, 1996), and two sister-species occur across this disjunction: *Lophotis gindiana* and *L. savilei*, and *Neotis heuglinii* and *N. nuba* (Figs 6.1, 6.16 and 6.10). Two species of sandgrouse occur in both these areas, but not further south (*P. exustus* and *P. quadricinctus*; de Juana, 1997). In contrast, Ostrich *Struthio camelus* shows a closer link between south-west and north-east taxa, but a large difference occurring between the north-east and Sahelian populations, although this is complicated by a second highly-divergent north-east taxon (Freitag and Robinson, 1993; Robinson and Matthee, 1999; Miller et al., 2010).

2. The taxonomy of Africa's arid zone non-passerine terrestrial birds

In this dissertation, morphological, behavioural and molecular data are used to infer the relationships and taxonomy of four African bird families. It is important to include morphological characters (unlike in many current systematic studies which are solely molecular-based), as it is these characters on which all the traditional assessments of taxonomy are based. By including them in this study, it allows the critical evaluation of them in a phylogenetic framework, instead of subjectively deciding which characters are the more important for inferring taxonomy, such as has been the case in many studies, e.g. Bowen (1927), Maclean (1984) and Johnsgard (1991).

Nonetheless, the morphological-behavioural analyses ([Figs 2.3, 3.4, 4.2](#)) bear a strong resemblance to the traditionally accepted taxonomy ([Tables 1.2 - 1.4](#)), with almost all genera and subfamilies being recovered as monophyletic. Exceptions to this are the placement of the enigmatic *Pterocles burchelli* at the base of the Pteroclidae tree which renders *Pterocles* polyphyletic ([Fig. 3.4](#)) and, in the Glareolidae, the nested nature of *Stiltia* within *Glareola* ([Fig. 4.2](#)). Including morphological-behavioural characters also allows the comparison of these analyses directly to analyses of the molecular characters, as well as to combine them to provide the most complete dataset possible (see Crowe et al., 2006). The molecular data not only confirm the non-monophyly of *Pterocles* and *Glareola*, but the Otididae genera *Eupodotis* and *Neotis*, and the Glareolidae subfamily Cursoriinae, are also shown to be not monophyletic. The molecular data also strongly support the sister relationship between *Francolinus nahani* and *Ptilopachus petrosus*, which is supported by

behavioural characters. Based on the results of these analyses, taxonomic recommendations are detailed below.

Otididae

Results are largely concordant with the taxonomy of the bustards as proposed by Collar (1996), with differences only in the treatment of *Eupodotis* and possibly *Neotis*. It should be emphasised that the previous broad use of *Eupodotis* to include all the smaller African (and sometimes Asian) bustards (e.g. Snow, 1978; Collar et al., 1986; Sibley and Monroe, 1990; Johnsgard, 1991) is misleading, as this assemblage is not a single, monophyletic lineage.

The results allow for more than one classification scheme for the Otididae, depending on how one argues the generic limitations in the case of 1. *Neotis*, and 2. the number of small genera which show large morphological diversity but which are placed together in monophyletic clades. Two classification schemes are proposed below, A (split) and B (lumped), both of which are defensible.

1. The treatment of *Ardeotis* and *Neotis* has not been fully resolved due to a limited amount of molecular material sequenced from museum specimens, and further data may help to clarify their relationships. Although it seems that *Ardeotis* is monophyletic, results show that it renders *Neotis* paraphyletic and it might thus be cautious to subsume the members of *Neotis* into *Ardeotis*, which has priority. However, this treatment cannot be recommended until this clade has been examined in more detail, and so the *status quo* should remain until such data are available. It might also be argued that because a previous study has also failed to recover a

monophyletic *Neotis* (Pitra et al., 2002), that *Neotis* be subsumed, and this is proposed in Classification Scheme B.

2. The Otididae contain a high proportion of monotypic genera, and genera with only two species, which some may argue should be subsumed into larger, more inclusive genera. These genera delimit an extraordinary amount of morphological, behavioural and genetic diversity which argues for retaining them, even if they are not very speciose. However, in Classification Scheme B below, those small genera have been lumped that form well-supported monophyletic clades with other genera.

Classification Scheme A: Family Otididae

Otis (Linnaeus 1758)

Otis tarda

Chlamydotis (Lesson 1839)

Chlamydotis undulata

C. macqueenii

Tetrax (T. Forster 1817)

Tetrax tetrax

Ardeotis (Le Mahout 1853)*Ardeotis arabs**A. kori**A. nigriceps**A. australis****Neotis*** (Sharpe 1893) (Should possibly be subsumed into *Ardeotis*; see below)*Neotis ludwigii**N. denhami**N. heuglinii**N. nuba****Lissotis*** (Reichenbach 1848)*Lissotis melanogaster**L. hartlaubii****Afrotis*** (G.R. Gray 1855)*Afrotis afra**A. afraoides****Eupodotis*** (Lesson 1839)*Eupodotis senegalensis* (type species, Vieillot 1820)*E. barrowii* (further study to clarify the specific status of *barrowii* is recommended)*E. caerulescens*

Heterotetrax (Sharpe 1894)*Heterotetrax vigorsii* (type species, A. Smith 1831)*H. rueppellii**H. humilis****Lophotis*** (Reichenbach 1848)*Lophotis savilei**L. gindiana**L. ruficrista****Houbaropsis*** (Sharpe 1893)*Houbaropsis bengalensis****Syphoetides*** (Lesson 1839)*Syphoetides indica***Classification Scheme B: Family Otididae*****Otis*** (Linnaeus 1758)*Otis tarda**O. undulata**O. macqueenii****Tetrax*** (T. Forster 1817)*Tetrax tetrax*

Ardeotis (Le Mahout 1853)*Ardeotis arabs**A. kori**A. nigriceps**A. australis**A. ludwigii**A. denhami**A. heuglinii**A. nuba****Lissotis*** (Reichenbach 1848)*Lissotis melanogaster**L. hartlaubii****Eupodotis*** (Lesson 1839)*Eupodotis senegalensis* (type species, Vieillot 1820)*E. barrowii* (further study to clarify the specific status of *barrowii* is recommended)*E. caerulescens**E. afra**E. afraoides**E. vigorsii* (type species, A. Smith 1831)*E. rueppellii**E. humilis*

Lophotis* (Reichenbach 1848)L. savilei**L. gindiana**L. ruficrista****Sypheotides* (Lesson 1839)***Sypheotides indica**S. bengalensis***Pteroclidae**

The two *Syrrhaptes* species are considered sister-taxa only by a suite of morphological characters as no DNA sample could be amplified for *S. tibetanus*, but there seems no reason to doubt the close relationship between these two central Asian species. The genus *Pterocles* is not recovered as monophyletic in any of the analyses, as it is rendered paraphyletic by *Syrrhaptes*. One solution to ensure that the genera in Pteroclidae retain monophyly is to subsume all the species into one genus. *Syrrhaptes* (Illiger 1811) pre-dates *Pterocles* (Temminck 1815) and so all species would need to be transferred to *Syrrhaptes*, as presented in Classification Scheme A, below:

Classification Scheme A: Family Pteroclidae***Syrrhaptes* (Illiger 1811)***S. paradoxus**S. tibetanus*

S. orientalis

S. namaqua

S. exustus

S. gutturalis

S. personatus

S. coronatus

S. decoratus

S. bicinctus

S. quadricinctus

S. lichtensteinii

S. indicus

S. alchata

S. burchelli

However, containing all the members of a family in a single genus provides no information on their relationships. Another approach would be to tentatively group species identified in this study's three well-supported clades into the following genera:

Classification Scheme B: Family Pteroclidae

***Syrrhaptes* (Illiger 1811) (Clade 11)**

S. paradoxus

S. tibetanus

S. orientalis

S. namaqua

S. exustus

***Eremialector* (Sclater 1924) (Clade 8)**

E. gutturalis

E. personatus

E. coronatus

***Pterocles* (Temminck 1815) (Clade 2)**

P. decoratus

P. bicinctus

P. quadricinctus

P. lichtensteinii

P. indicus

Uncertain:

alchata

burchelli

The reason that this approach is not currently defensible is that placement of *alchata* and *burchelli* is uncertain. A more conservative approach, suggested by the combined data tree (Fig. 6.2) is the split between **Clade Nyctiperdix** and the others, which might result in a treatment as follows:

Classification Scheme C: Family Pteroclidae

Syrrhaptes (Illiger 1811)

S. paradoxus

S. tibetanus

S. orientalis

S. namaqua

S. exustus

S. gutturalis

S. personatus

S. coronatus

S. alchata

S. burchelli

Pterocles (Temminck 1815) (Clade Nyctiperdix)

P. decoratus

P. bicinctus

P. quadricinctus

P. lichtensteini

P. indicus

In this case, *Pterocles* (Temminck 1815) pre-dates *Nyctiperdix* (Roberts 1922). The recommendation is to further investigate the position of *alchata* and *burchelli* before revising the taxonomy of this family, and if no further clarification resolves the

placement of the major clades, I would then recommend using Classification Scheme C.

Glareolidae

The subfamilies Cursoriinae and Glareolinae (with the inclusion of the monotypic Stiltiinae) are not monophyletic and should be dropped from the taxonomy of this family. *Cursorius* (Latham 1790) should be limited to those species in the monophyletic **Clade Cursorius**. The taxa *somalensis* and *littoralis* should be treated as a full species, *C. somalensis*, as they are neither sister to *C. rufus* nor *C. cursor* (more data are required to clarify this position). Members of **Clade Rhinoptilus** should be included in *Rhinoptilus* (Strickland 1852), and while there is no strong objection to *R. africanus* being included in the monotypic *Smutsornis* (Roberts 1922), this does not add much useful information on the structure of the family. The differences between the subspecies of *R. africanus* could be investigated further, although the preliminary data in this study indicate that there are not significant differences between them and they are perhaps best retained as subspecies pending further research. The pratincoles require further data to test their relationships. Provisionally, *Stiltia* (Gray 1855) should be dropped as it renders *Glareola* (Brisson 1760) polyphyletic. Further research might strongly support a division between the four “river pratincoles” and the others, in which case the “river pratincoles” might merit generic status - *Galachrysa*. The following treatment is recommended:

Family Glareolidae***Cursorius* (Latham 1790)**

Cursorius cursor

C. somalensis

C. rufus

C. temminckii

C. coromandelicus

***Rhinoptilus* (Strickland 1852)**

Rhinoptilus africanus

R. cinctus

R. chalcopterus

R. bitorquatus

***Glareola* (Brisson 1760)**

Glareola isabella

G. pratincola

G. maldivarum

G. nordmanni

G. ocularis

G. nuchalis

G. cinerea

G. lactea

Phasianidae/ Odontophoridae

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

Family Odontophoridae

***Ptilopachus* (Swainson 1837)**

Ptilopachus petrosus

P. nahani

3. Life history evolution in study taxa

The evolution of a wide variety of life history traits, habitat use, activity times, movements, and behavioural ecology are investigated for each family and these are interpreted in detail in [Chapters 2-5](#). A general problem in assessing character evolution has been the lack of support at the bases of the trees, making it impossible to assess the ancestral states with any certainty.

4. Improvements and future research

The most disappointing aspect of these analyses have been the lack of basal resolution of the trees and this has weakened the taxonomic, systematic and biogeographic interpretation of the results. This might be due to rapid radiation of the clades involved (Pitra et al., 2002; Hackett et al., 2008), especially in the well-sampled Otididae, but it might also be due incomplete taxon and locus sampling. While these analyses represent the most complete morphological-behavioural and molecular sampling of these families to date, there are still important gaps, and genetic material was not available for all species. Thus, the placement of some of the taxa in this study is based solely on morphological-behavioural data (where DNA data was not available) and future research should endeavour to obtain samples and sequences for these species to increase the number of characters on which to base the phylogenetic hypotheses. Ideally, fresh samples for at least two individuals of each species involved would allow a more complete set of genes to be sequenced, which might provide greater phylogenetic resolution. This is especially relevant for the genus *Neotis* (Otididae), for a number of Pteroclidae (see [Table 3.1](#)), and for the Glareolinae of the Glareolidae.

At the species level, further insight into Africa's arid zones might be obtained through phylogeographic study of the following species, which have isolated arid zone subspecies and are controversial taxonomically: *Eupodotis senegalensis* (and *barrowii*), *Ardeotis kori* and *Cursorius somalensis*. In addition, further investigation of the isolated arid zone subspecies of *Rhinoptilus africanus* and *Pterocles gutturalis* might also provide additional insight. Practically, it is very difficult to amass the fresh samples required for analyses of these phylogeographic patterns, although much

progress has been made with *A. kori* (T. Osborne, S. Hallager and C. Cohen, unpublished data).

A molecular clock approach, which would include calculating approximate time divergence estimates for sister-species across the ‘arid corridor’ disjunction, might provide further insight, as concordance of divergence dates may provide time estimates for the existence of such a vicariance event (Klicka and Zink, 1997; Voelker, 1999). However, calibrating the clock is problematic (no phylogenetically-placed fossils are known for the Otididae, Pteroclidae or Glareolidae) and the time divergence estimates can be confounded by rate variation between lineages (see Pereira and Baker, 2006; Fjeldså and Bowie, 2008). For these reasons, this approach has not been followed here.

Table 6.1: Putative sister-species and subspecies pairs with disjunct distributions on either side of the 'arid corridor', together with support values recovered in this study.
 (JK = jackknife; PP = posterior probability; BS = bootstrap)

Taxon	South-west	North-east	Reference	Relationship	JK	PP	BS
Otididae							
<i>Ardeotis kori</i>	<i>kori</i>	<i>struthiunculus</i>	Snow, 1978	Sister	100	1	100
<i>Neotis</i>	<i>ludwigii</i>	<i>heuglinii</i>	Kingdon, 1989	Not sister	-	-	-
<i>Lophotis</i>	<i>ruficrista</i>	<i>gindiana</i>	Snow, 1978	Sister to <i>gindiana-savilei</i>	100	1	99
<i>Eupodotis</i>	<i>vigorsii, rueppellii</i>	<i>humilis</i>	Snow, 1978	Sister	94	1	97
<i>Eupodotis</i>	<i>barrowii</i>	<i>senegalensis</i>	Snow, 1978	Sister	100	0.85	79
Pteroclidae							
<i>Pterocles</i>	<i>namaqua</i>	<i>exustus</i>	Snow, 1978	Sister	99	1	100
<i>Pterocles</i>	<i>bicinctus</i>	<i>quadricinctus</i>	Snow, 1978	Sister to <i>quad.+lichtensteinii+indicus</i>	100	1	100
<i>Pterocles gutturalis</i>	<i>gutturalis</i>	<i>saturator</i>	Snow, 1978	Not tested	-	-	-
Glareolidae							
<i>Cursorius</i>	<i>rufus</i>	<i>somalensis</i>	Pearson & Ash, 1996	Not sister	-	-	-
<i>Rhinoptilus africanus</i>	5 subspecies (incl. <i>africanus</i> & <i>sharpei</i>)	3 subspecies (incl. <i>gracilis</i>)	Maclean & Urban, 1986	Sister	99	1	n/a

Figure Legends Ch. 6

Fig. 6.1: Geographical distribution mapped onto the Otididae clades recovered in Chapter 2. Parsimony cladogram for the concatenated dataset of all morphological-behavioural and multilocus DNA characters. Node numbers are indicated by #. Jackknife support values are presented and are followed by the majority rule if > 50. The major clades are labelled on the right. The broken line opposite *Lissotis* indicates that although this genus is sometimes included in **Clade Larger bustards**, it is not present in that clade in this figure. The distribution of species is colour-coded according to the key; *Ardeotis australis* and *Houbaropsis bengalensis* occur in Australia and southeast Asia respectively.

Fig. 6.2: Geographical distribution mapped onto the Pteroclidae clades recovered in Chapter 3. Parsimony cladogram for the concatenated dataset of all morpho-behavioural and multilocus DNA characters (3367 characters, one tree, length = 1950). Values depicted directly to the right of the node are as follows: #Clade Number/ Jackknife support if JK > 50/ Partitions that support the clade (Key: M = morpho-behavioural characters; D = all DNA partitions; N = nuclear DNA; MT = mitochondrial DNA). The distribution of species is colour-coded according to the key; *Pterocles personatus* is endemic to Madagascar. “India” refers to Indian subcontinent endemic, and *P. exustus* and *P. lichtensteinii* occur more widely than just the north-east arid zone, ranging from the Sahel to India.

Fig. 6.3: Geographical distribution mapped onto the Glareolidae clades recovered in Chapter 4. Strict consensus parsimony cladogram for concatenated dataset of all morpho-behavioural and multilocus DNA data (2674 characters, 6 trees, L = 1320). Values depicted directly to the right of the node are as follows: #Clade Number/ Jackknife support/ Partitions that support the clade (Key: M = morpho-behavioural characters; D = all DNA partitions; N = ND2; F = Fib5; T = TGFB; G = GAPDH). The distribution of species is colour-coded according to the key; *Stiltia isabella* and *Glareola ocularis* occur in Australia and Madagascar respectively.

Fig. 6.4: Geographical distribution, habitat and mobility mapped onto the *Ptilopachus* clade recovered in Chapter 4. Phylogenetic relationships of *Ptilopachus petrosus* and *Francolinus nahani* indicated by a parsimony-based analysis of seven DNA markers (5554 bases, 84 taxa). Numbers along branches represent the following support values: jack-knife (MP) / bootstrap (ML) / posterior probability (BI).

Fig. 6.5: Habitat and mobility mapped onto the Otididae cladogram of Fig. 6.1.

Fig. 6.6: Habitat mapped onto the Pteroclidae cladogram of Fig. 6.2. None of the Pteroclidae are sedentary residents. Species not colour-coded are open country generalists.

Fig. 6.7: Habitat and mobility mapped onto the Glareolidae cladogram of Fig. 6.3.

Figs 6.8 – 6.20: Disjunctions between sister clades of the Otididae recovered by VIP. The colour-coded distributions are for clades or taxa identified in the phylogeny

extracts below each map (based on Fig. 6.1). Green squares indicate areas of overlap. The green line represents a crude estimate of the barrier between clades.

Figs 6.21 – 6.30: Disjunctions between sister clades of the Pteroclidae recovered by VIP. The colour-coded distributions are for clades or taxa identified in the phylogeny extracts below each map (based on Fig. 6.2). Green squares indicate areas of overlap. The green line represents a crude estimate of the barrier between clades.

Figs 6.31 – 6.35: Disjunctions between sister clades of the Glareolidae recovered by VIP. The colour-coded distributions are for clades or taxa identified in the phylogeny extracts below each map (based on Fig. 6.3). Green squares indicate areas of overlap. The green line represents a crude estimate of the barrier between clades.

Fig. 6.1

6.36

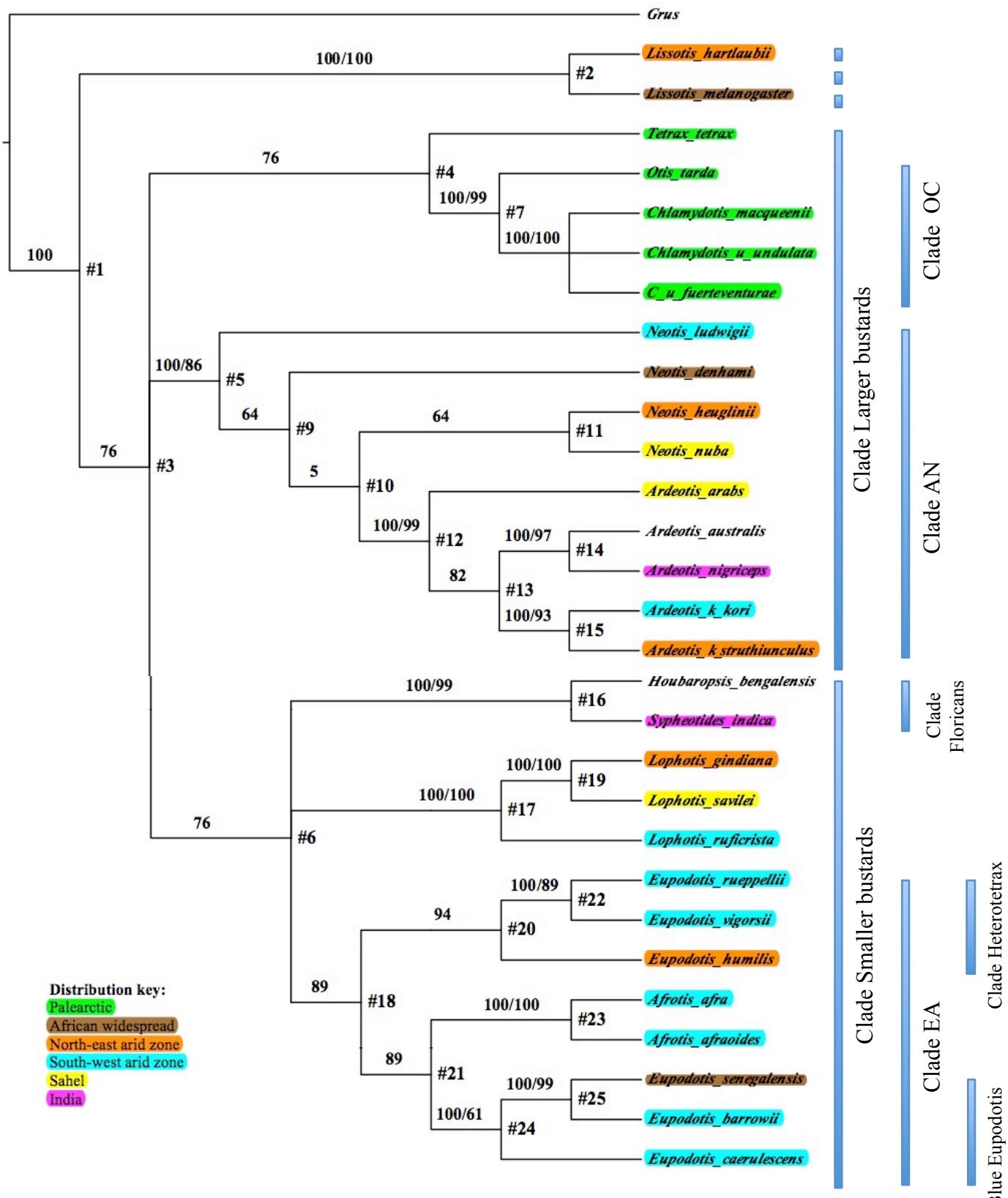


Fig. 6.2

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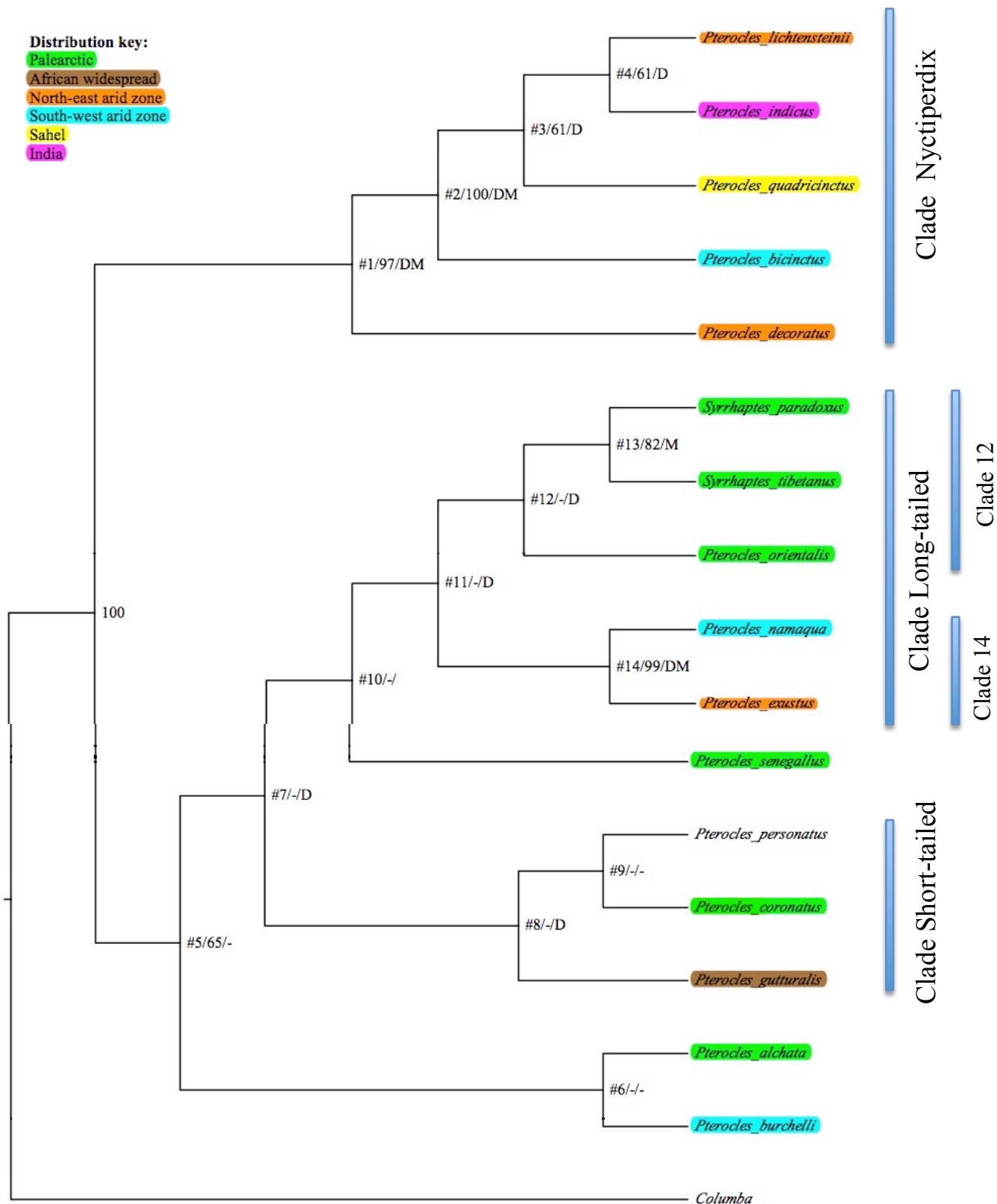


Fig. 6.3

6.38

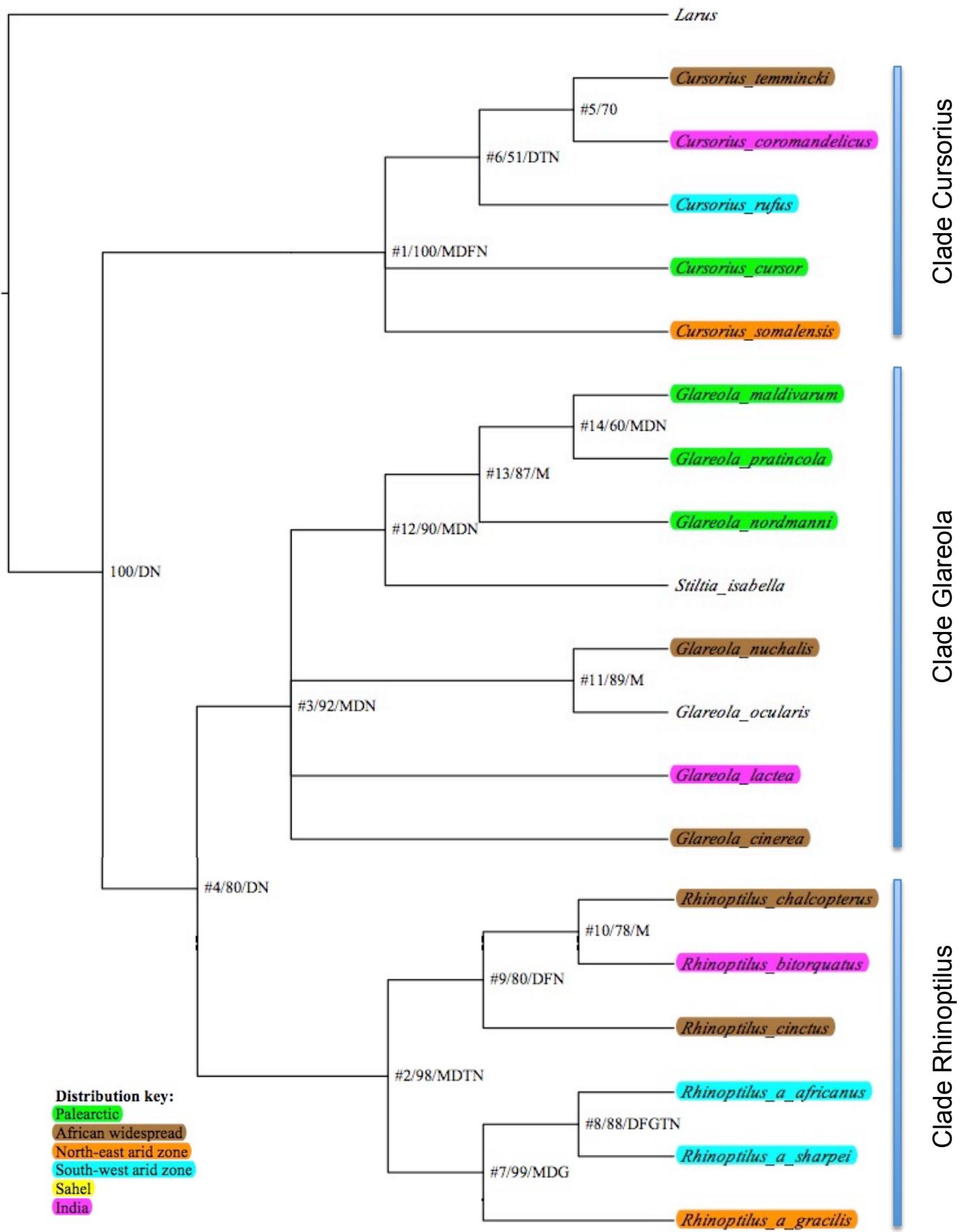


Fig. 6.4

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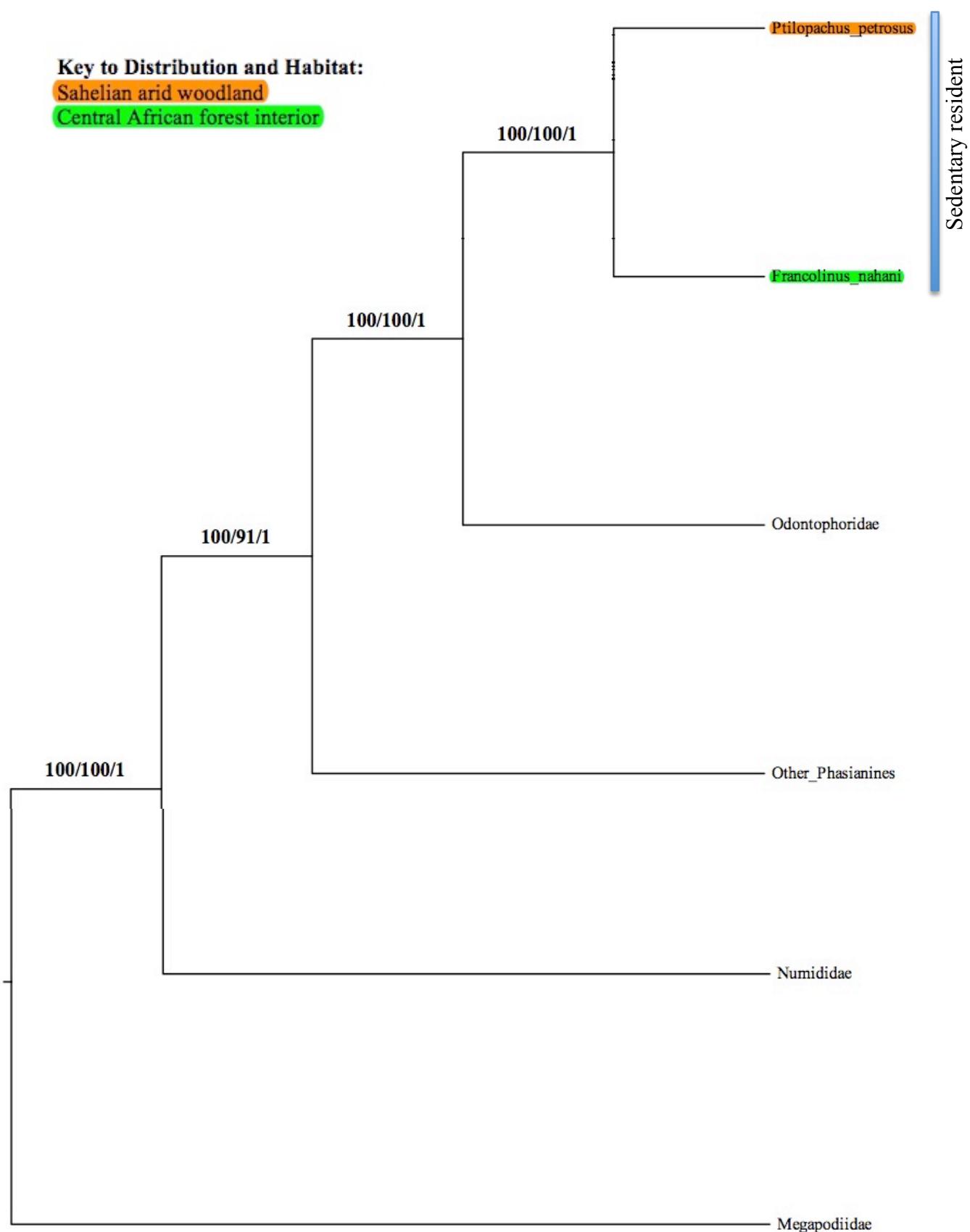


Fig. 6.5

6.40

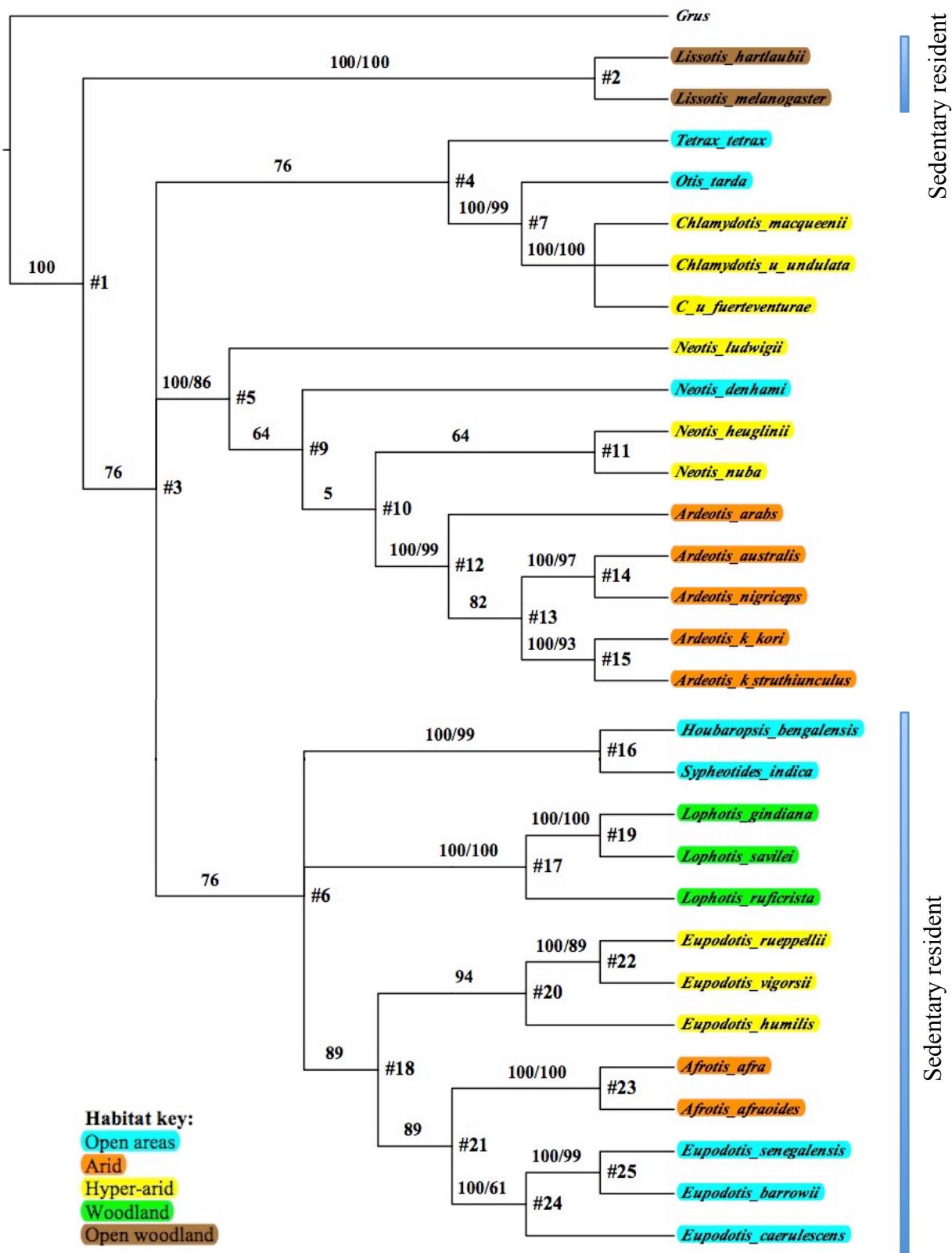


Fig. 6.6

6.41

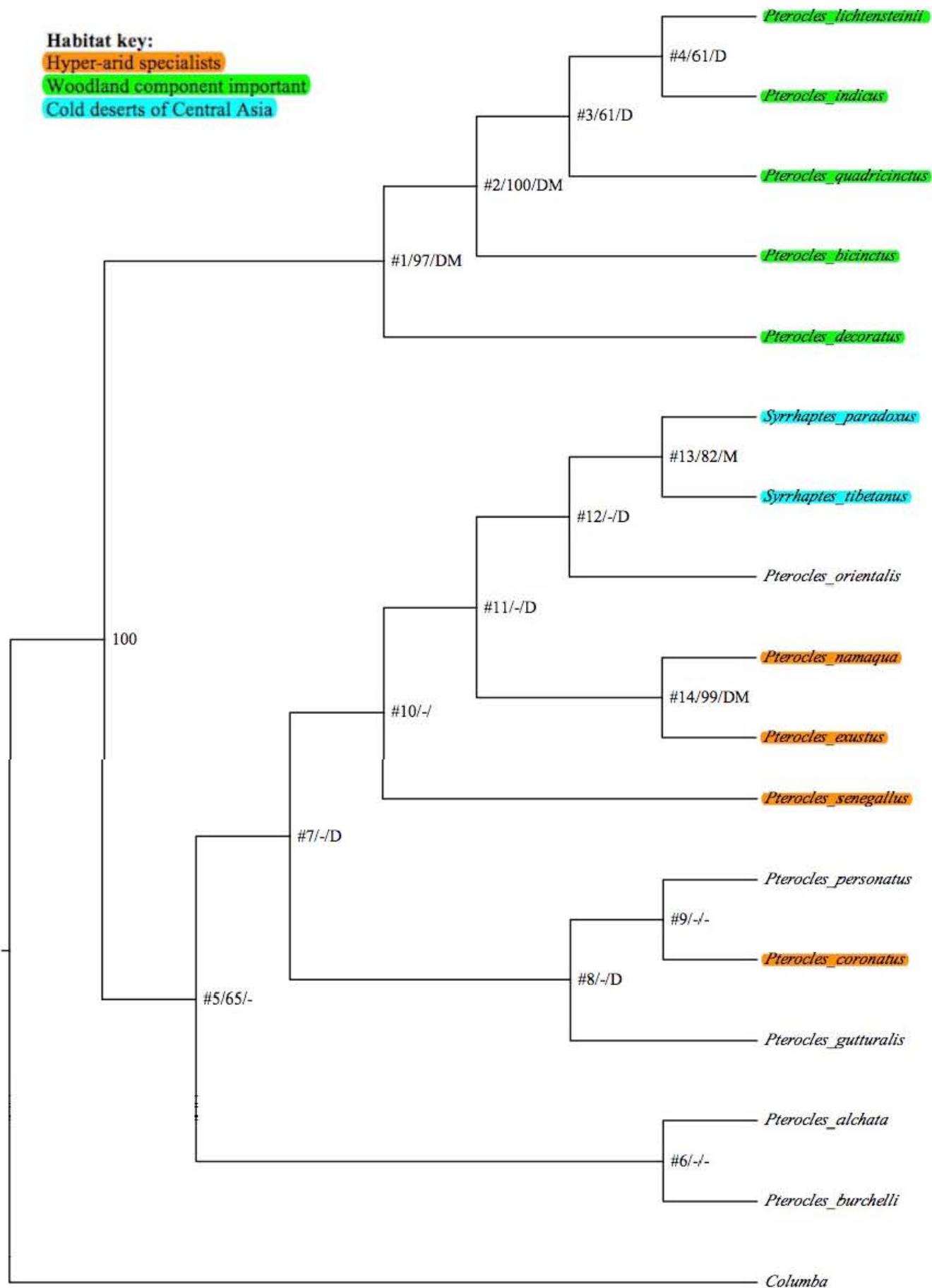


Fig. 6.7

6.42

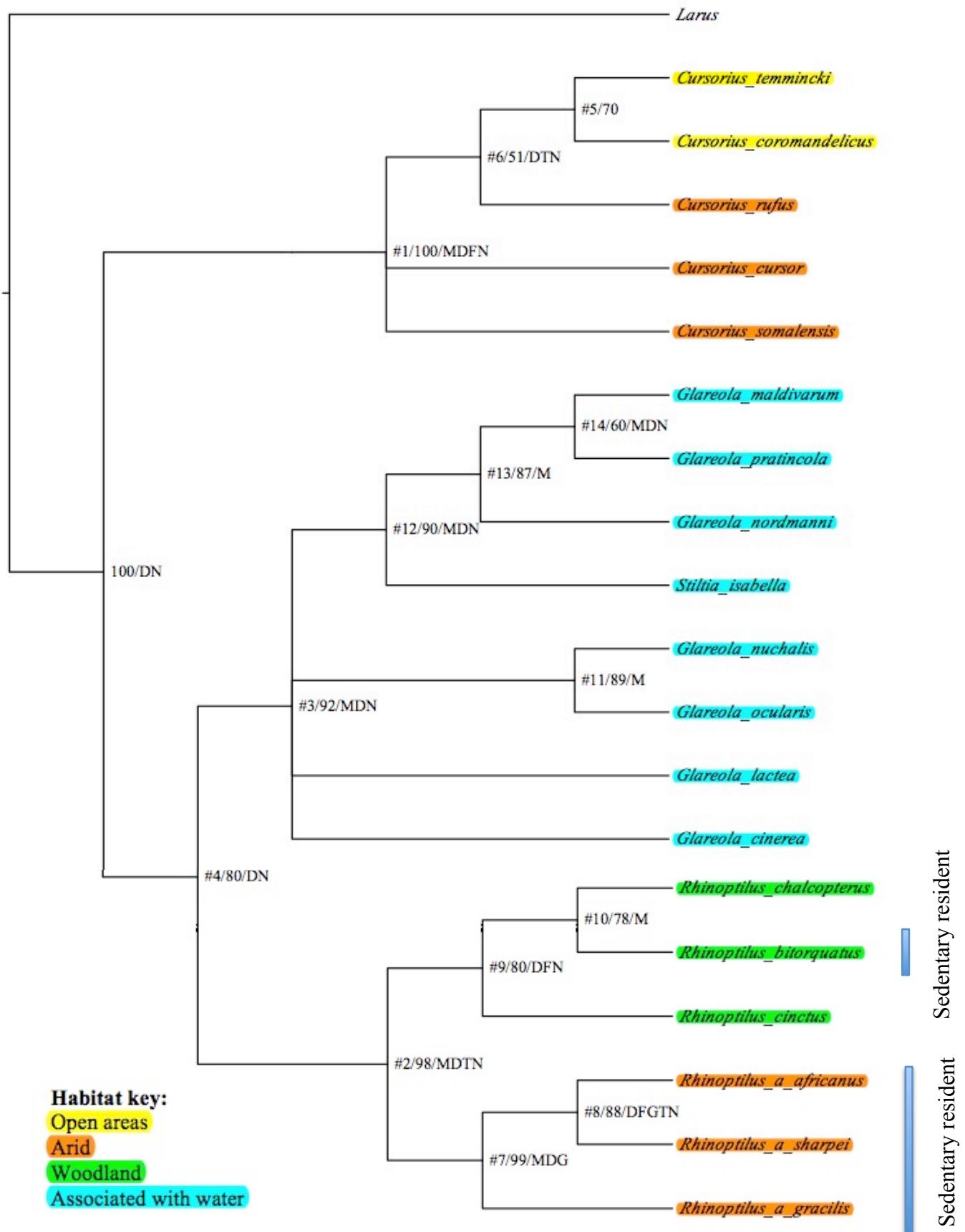


Fig. 6.8

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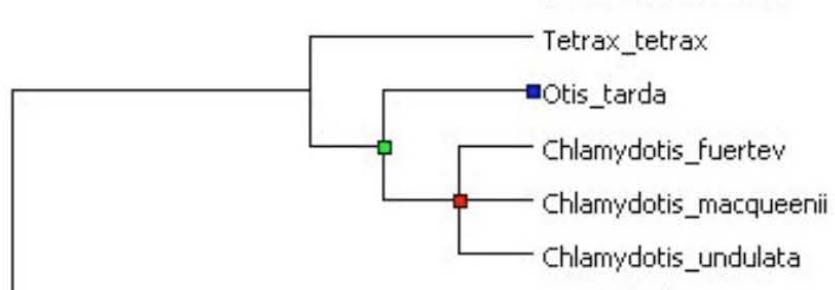
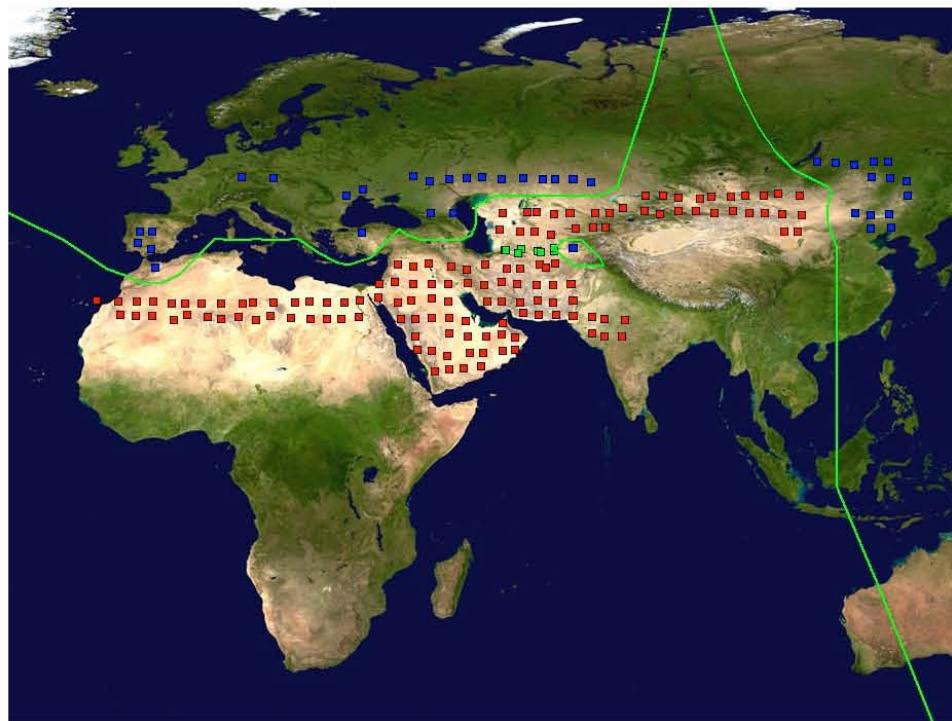


Fig. 6.9

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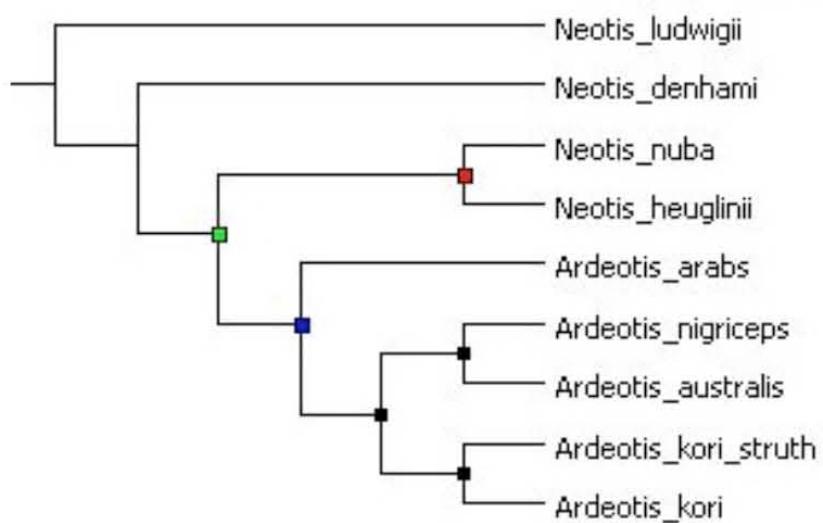
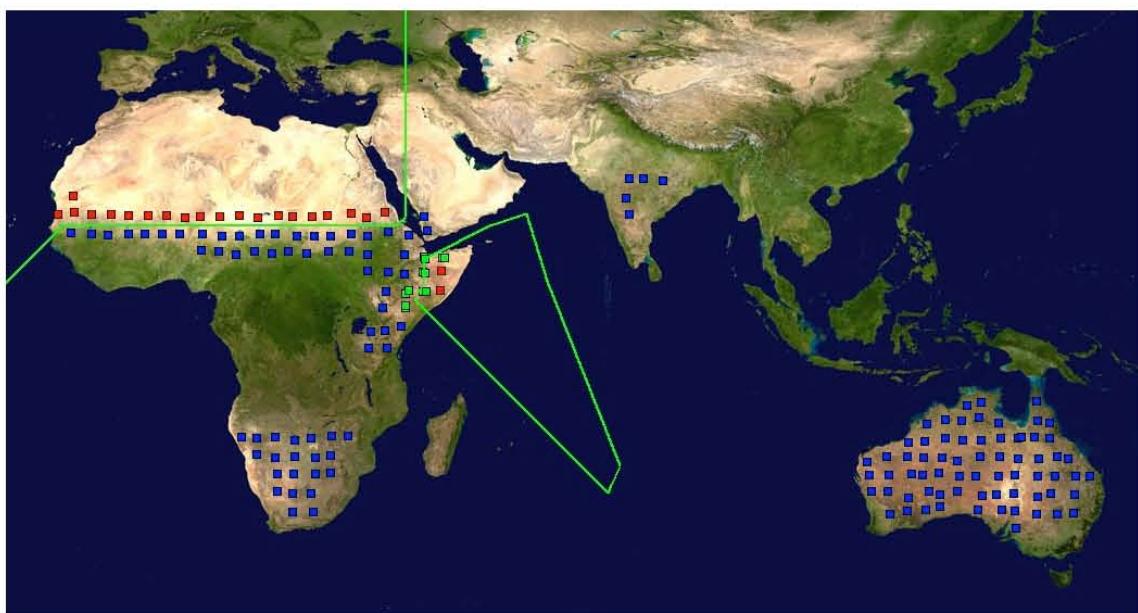


Fig. 6.10

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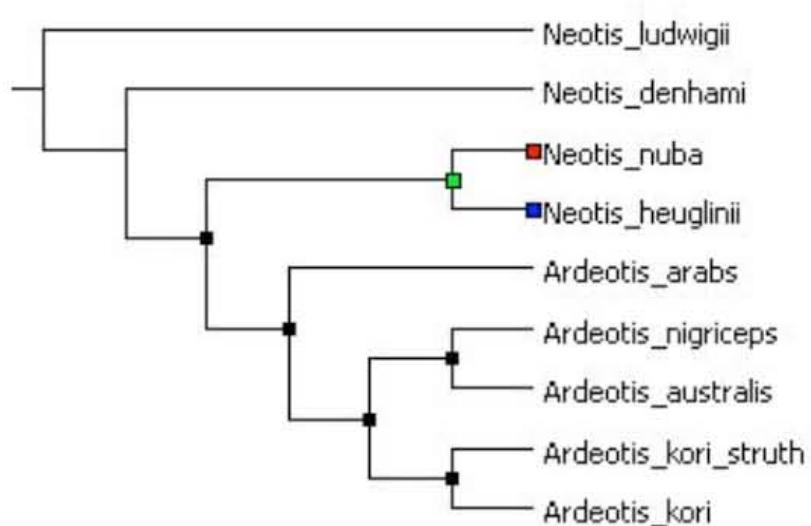


Fig. 6.11

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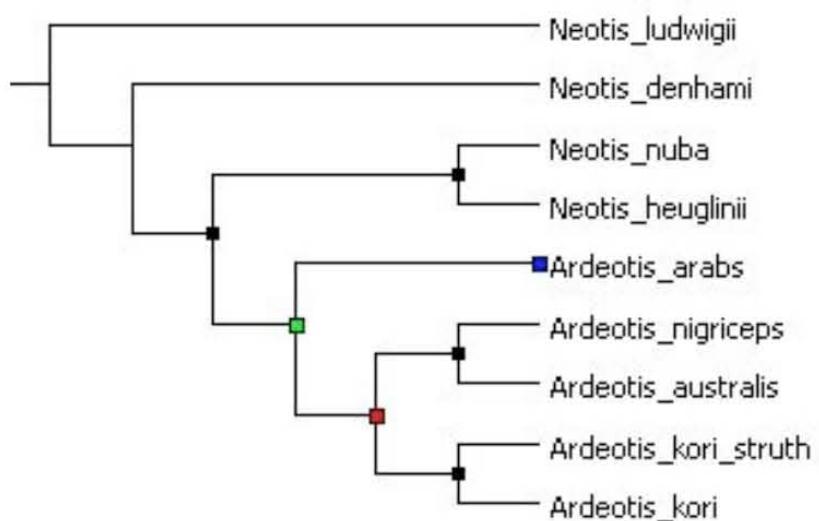


Fig. 6.12

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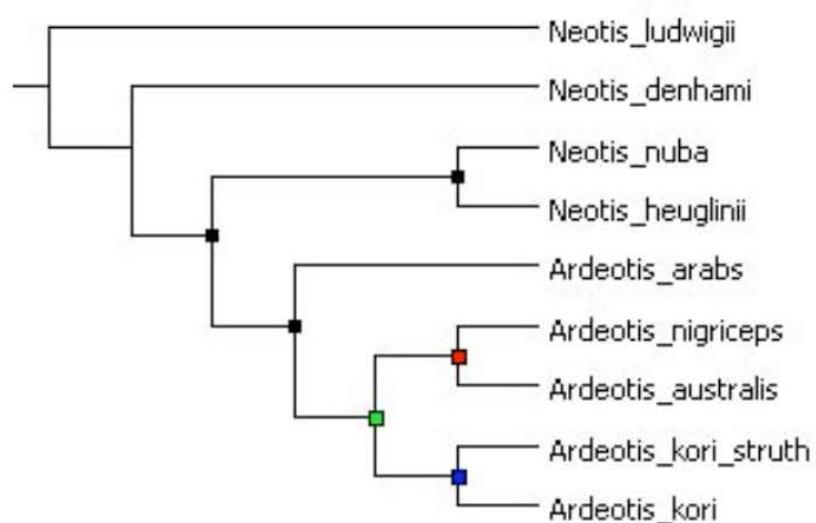


Fig. 6.13

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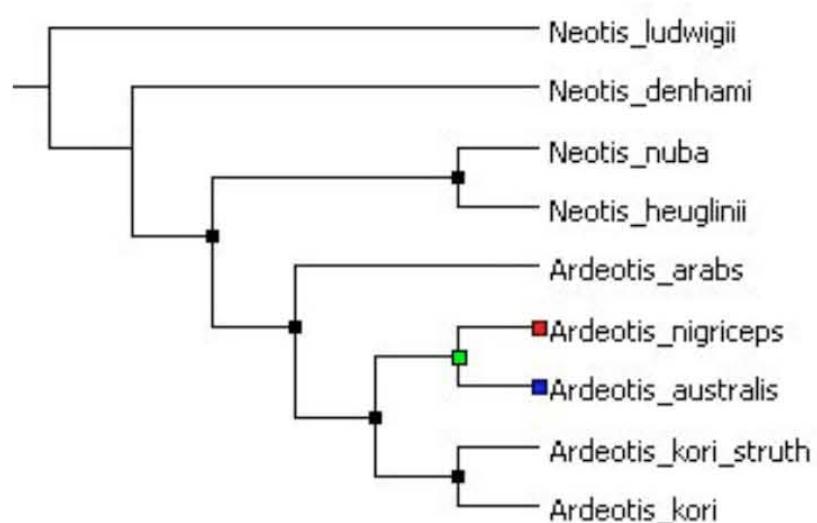


Fig. 6.14

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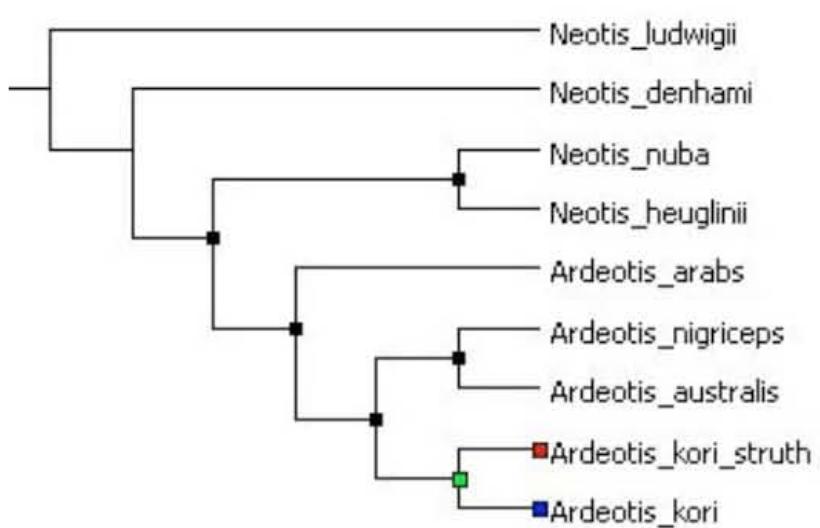


Fig. 6.15

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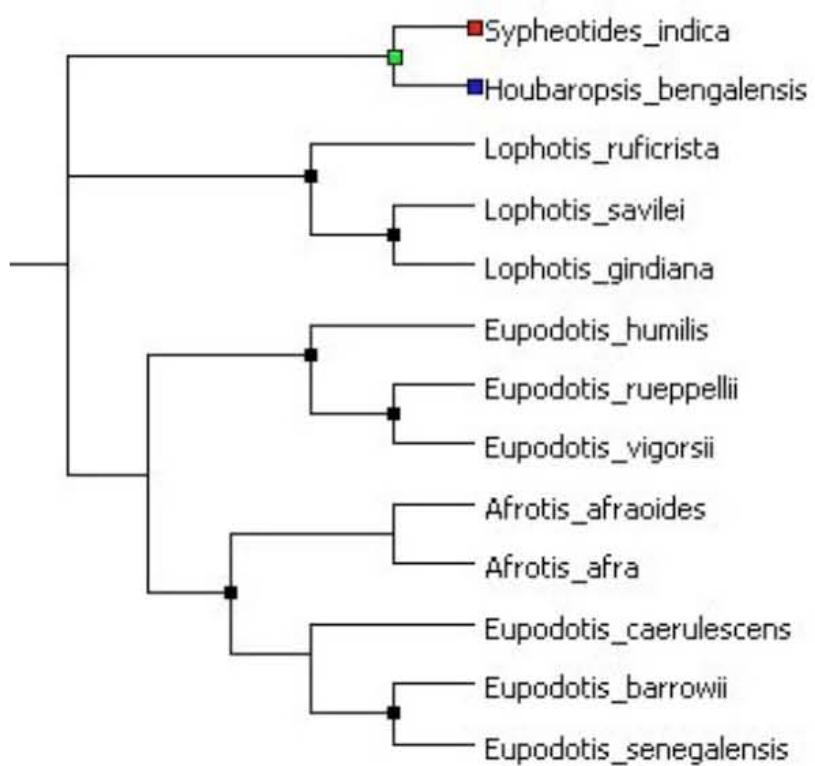


Fig. 6.16

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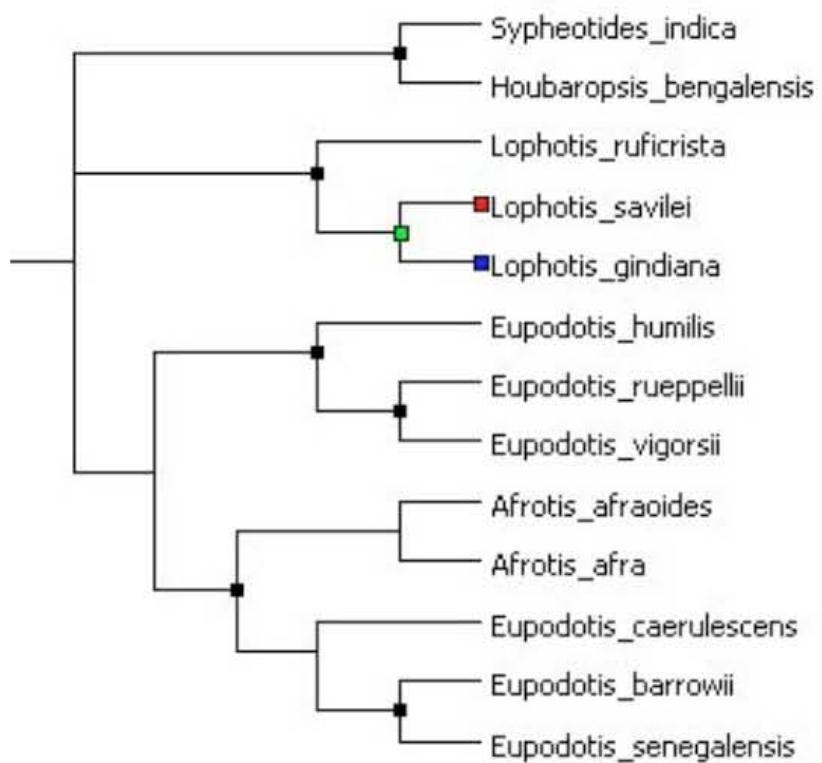
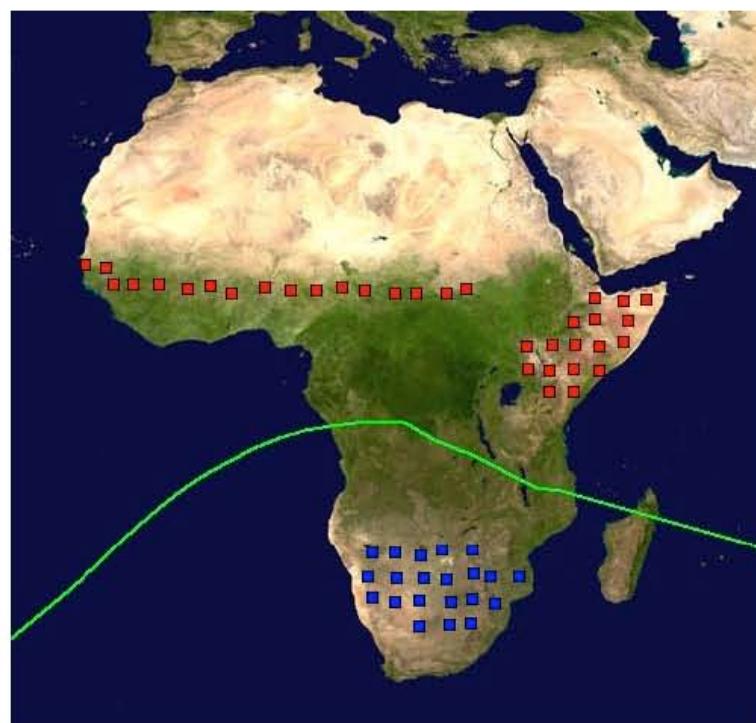


Fig. 6.17

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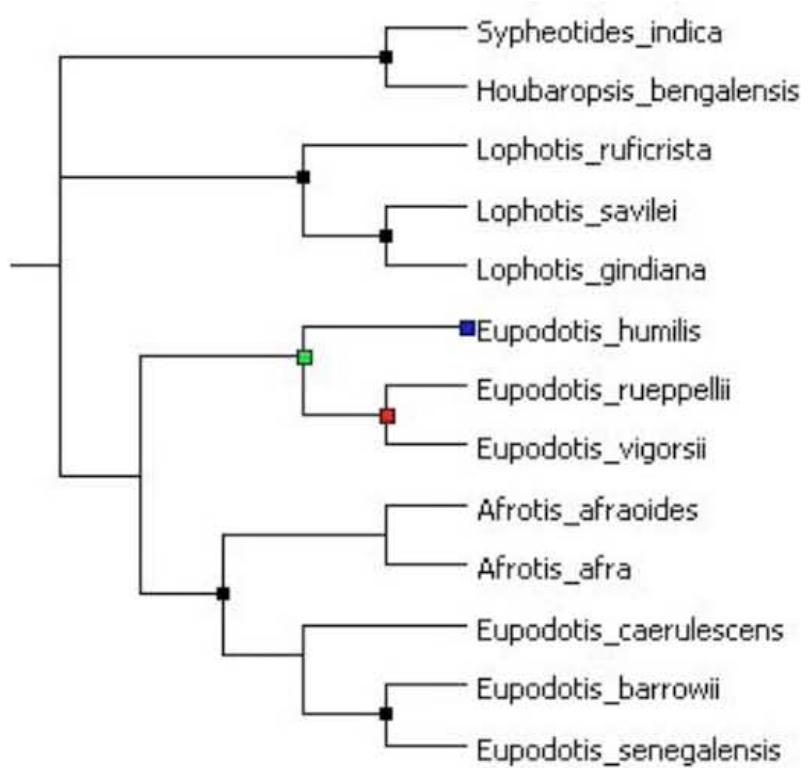


Fig. 6.18

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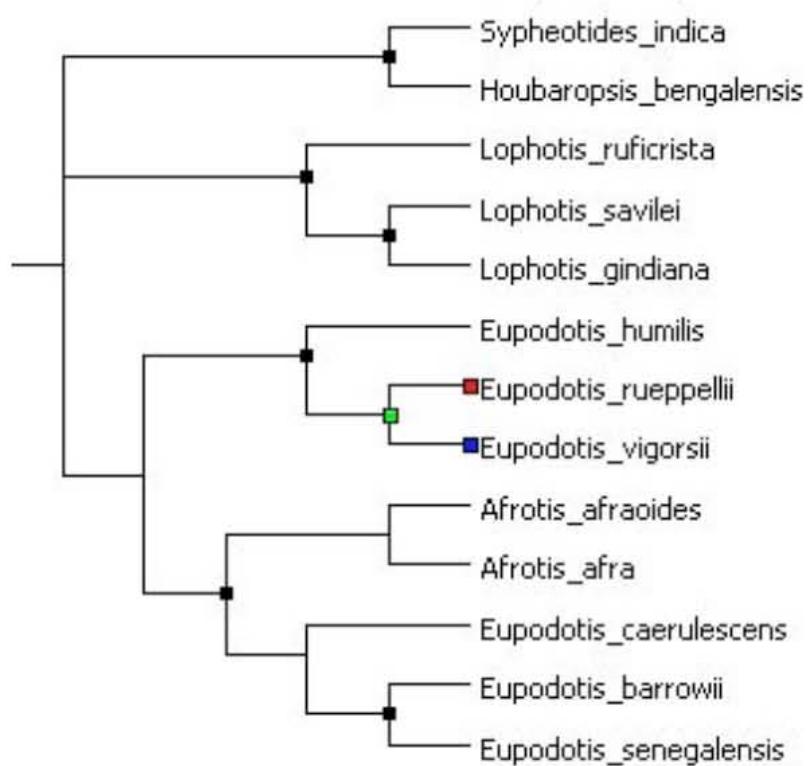


Fig. 6.19

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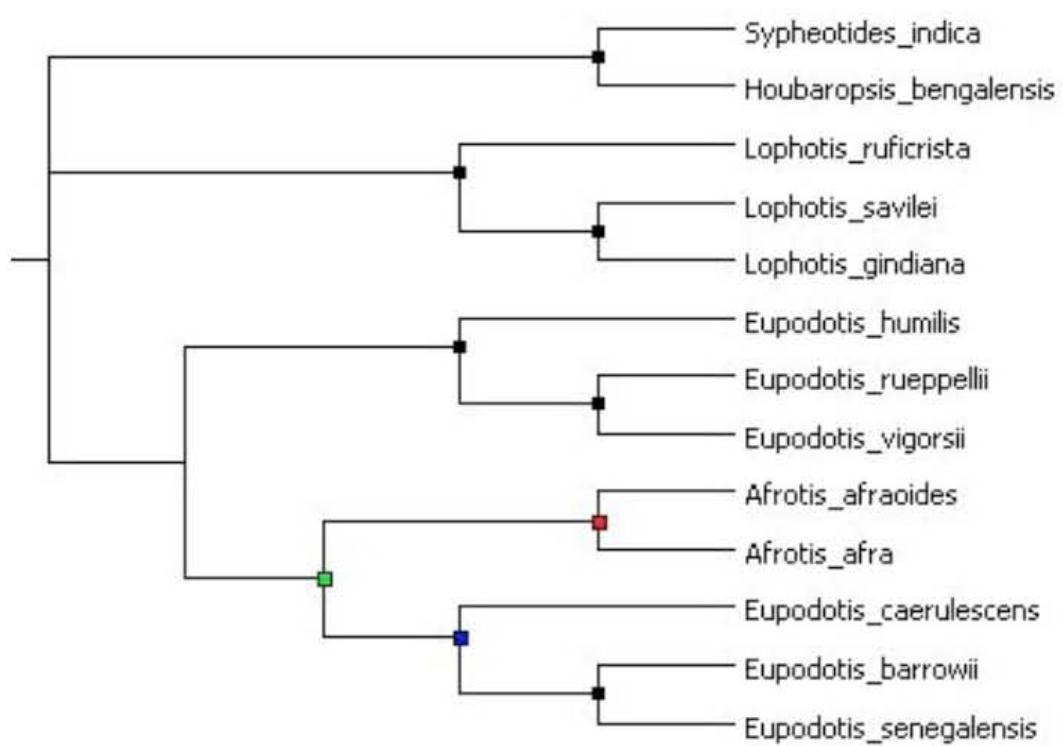
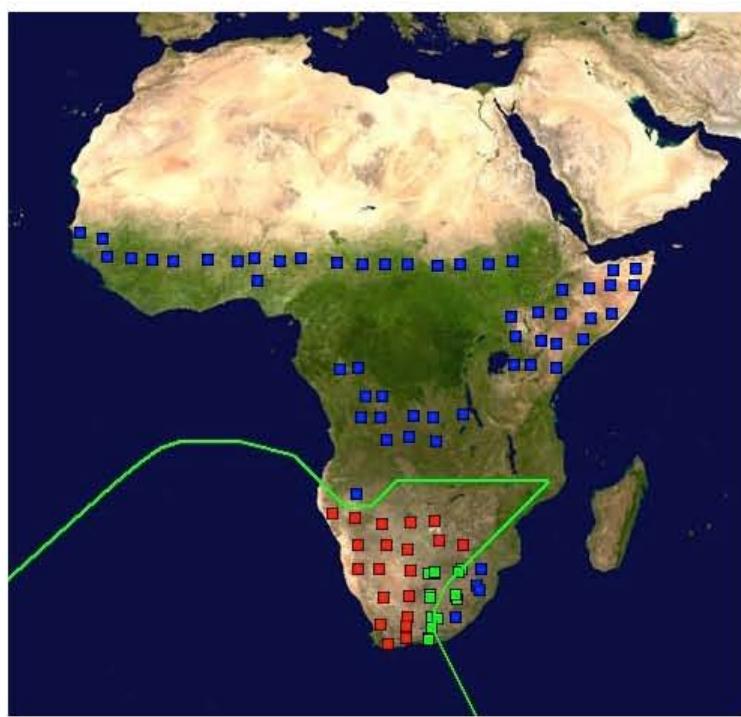


Fig. 6.20

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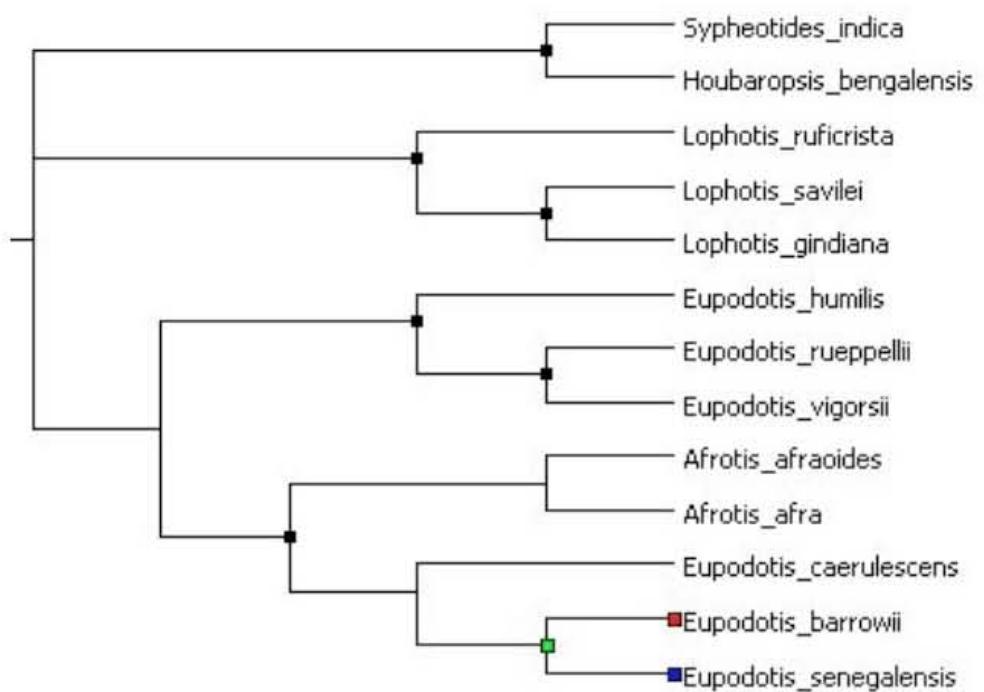


Fig. 6.21

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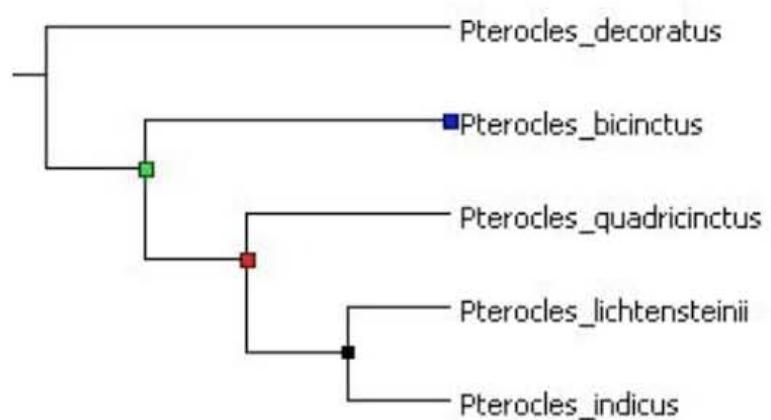
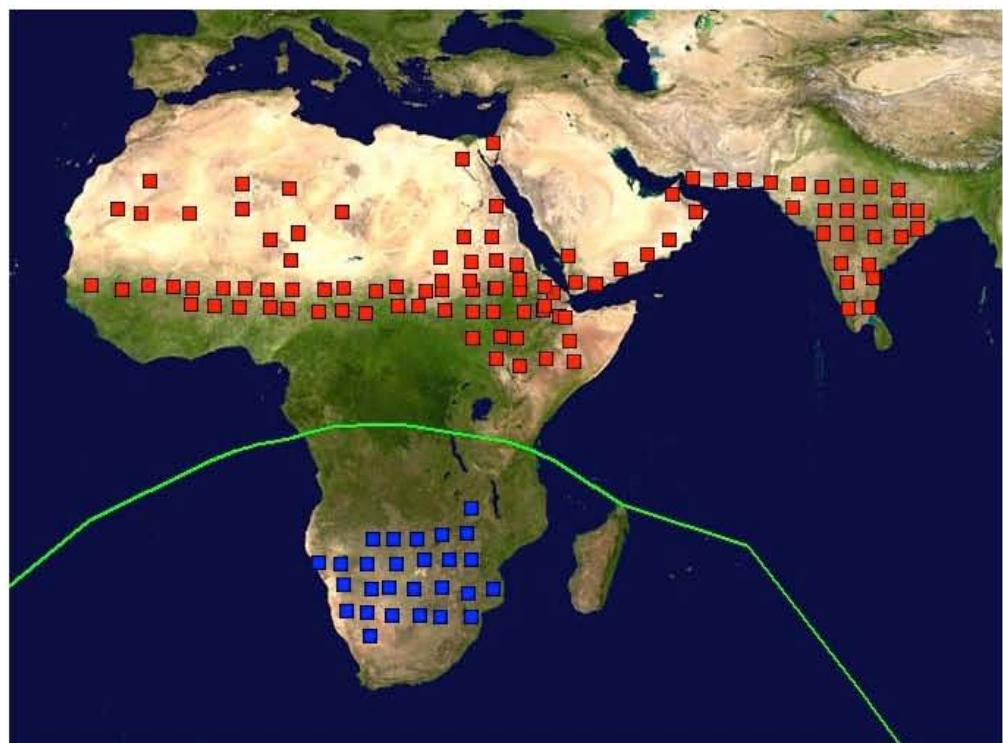


Fig. 6.22

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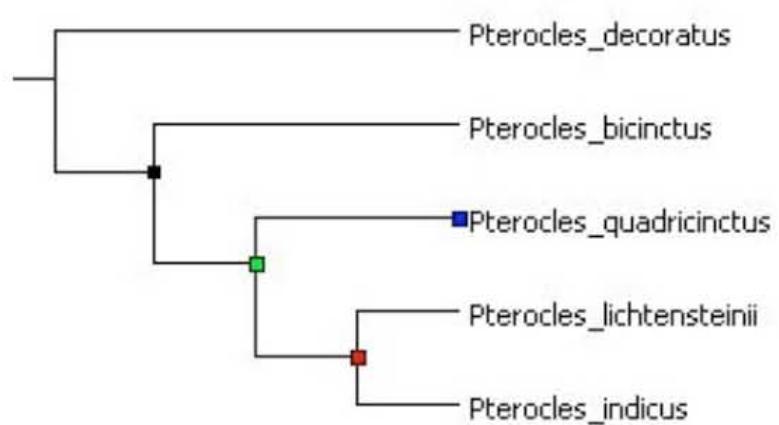
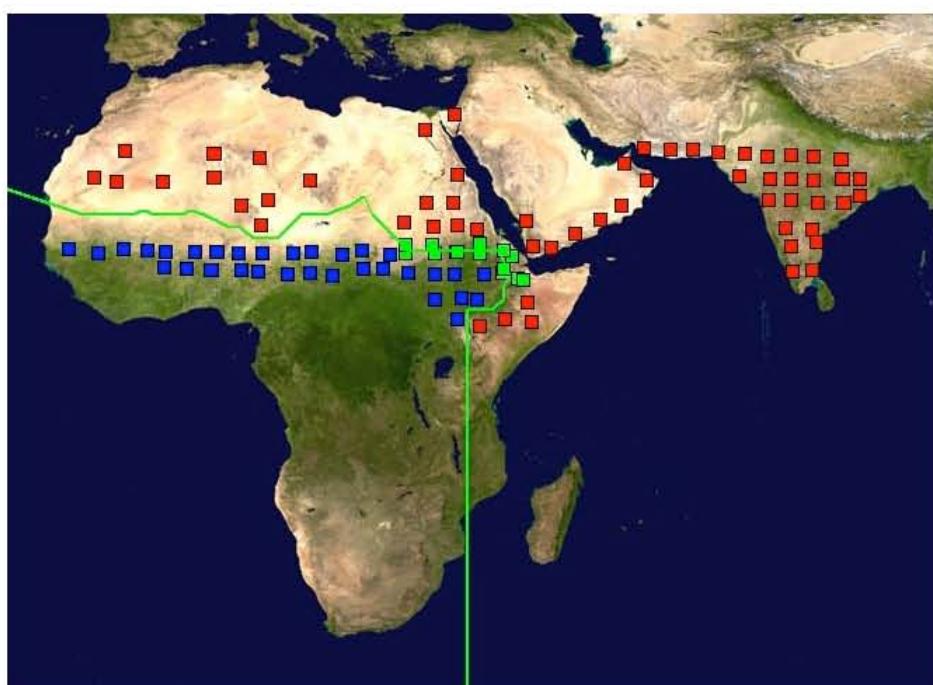


Fig. 6.23

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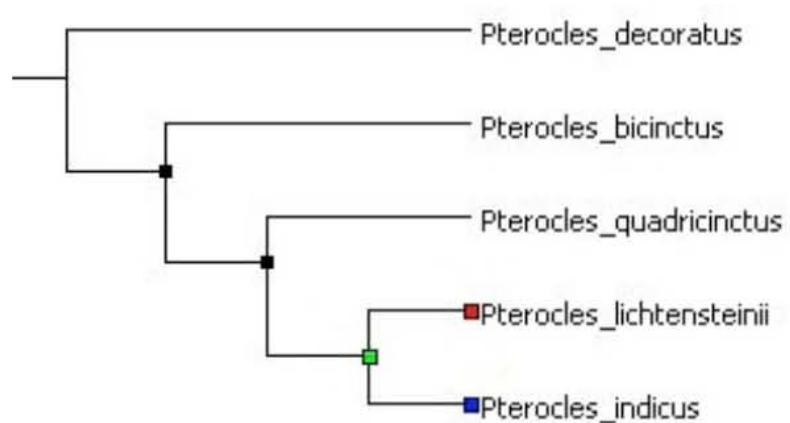
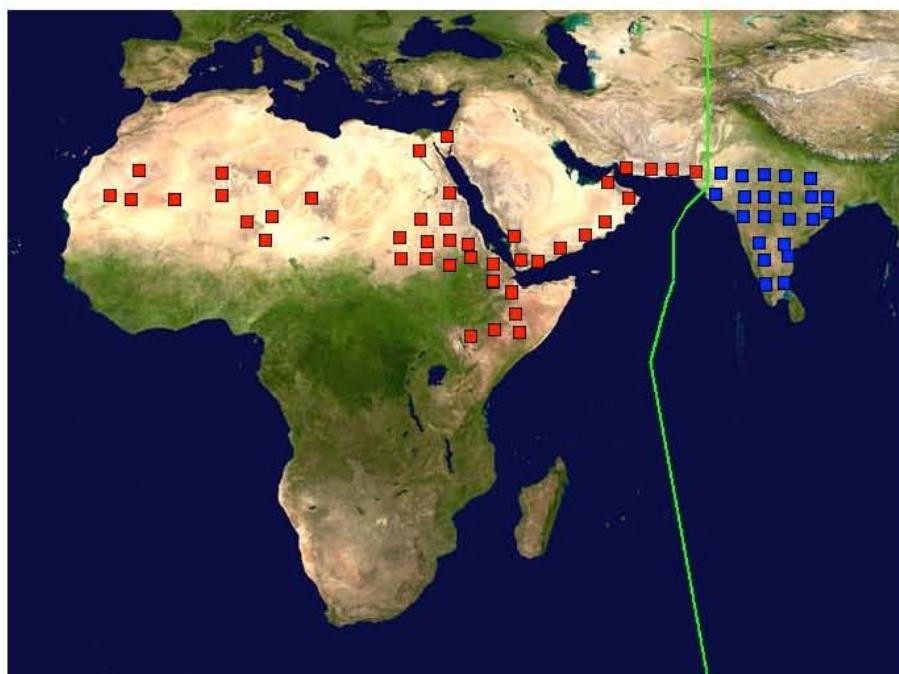


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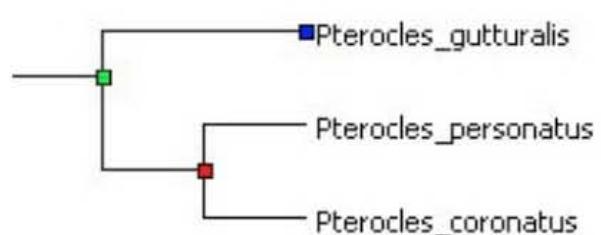
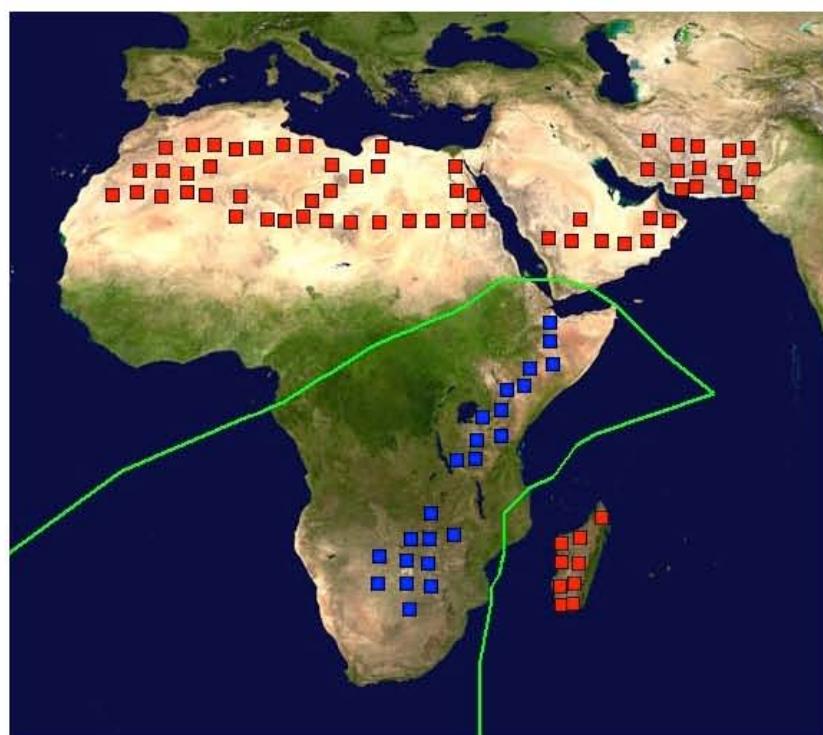


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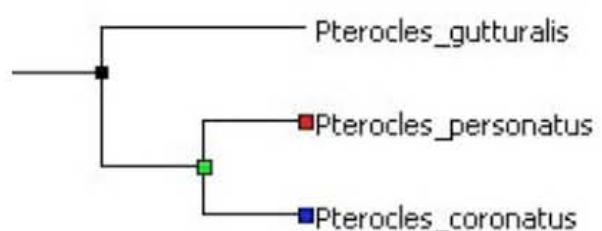


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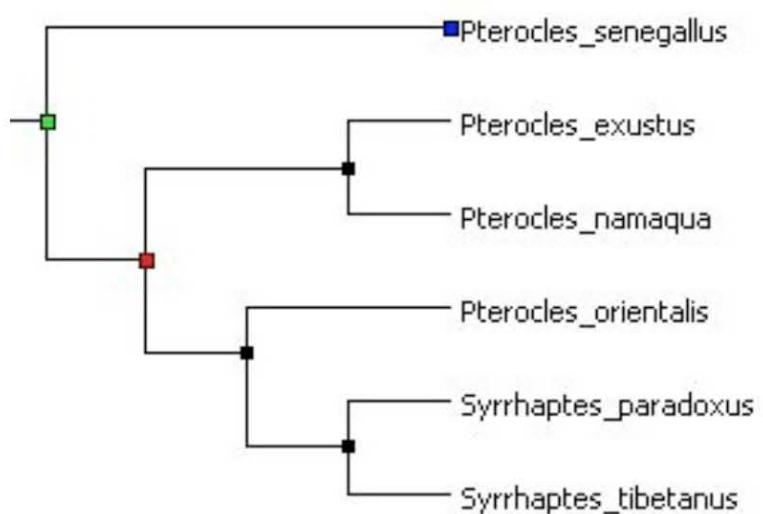
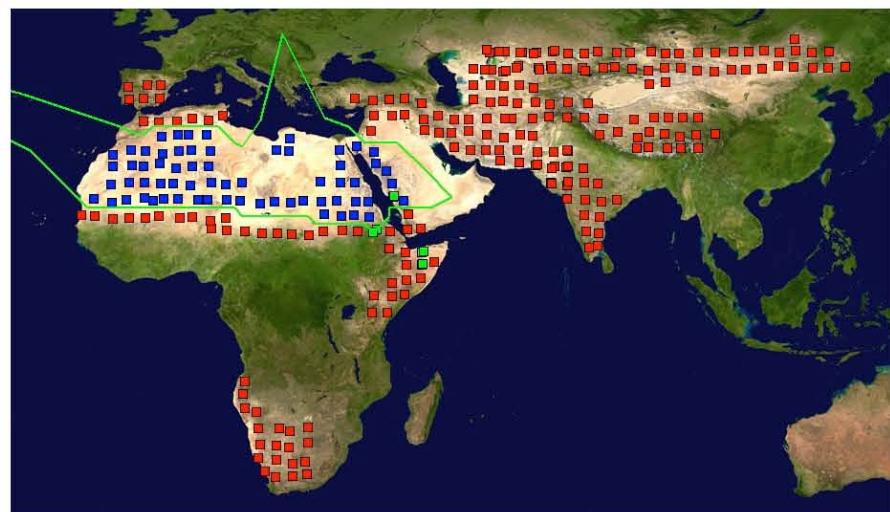


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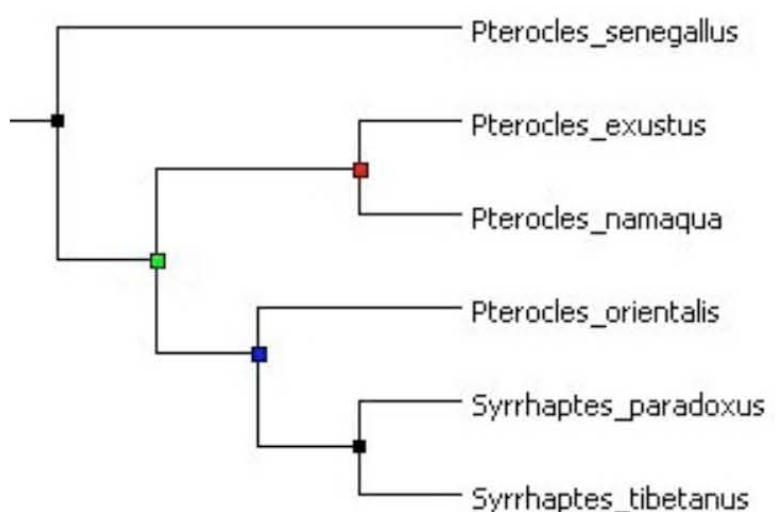
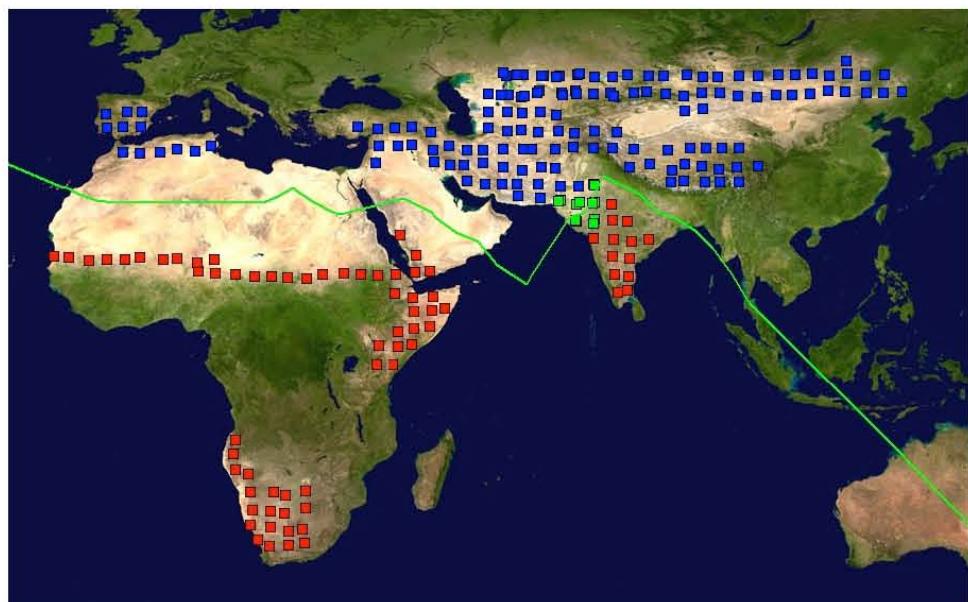


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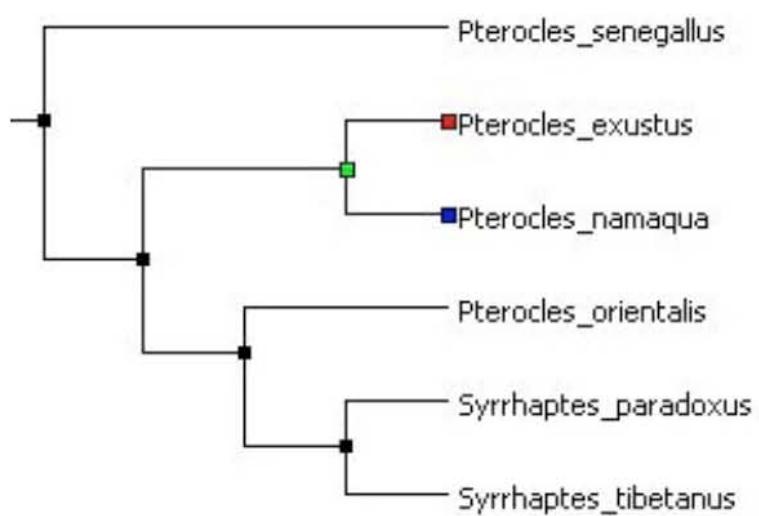


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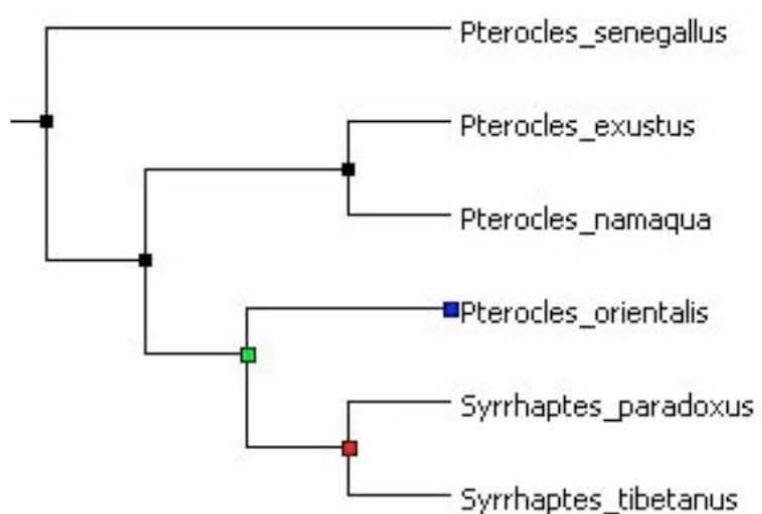
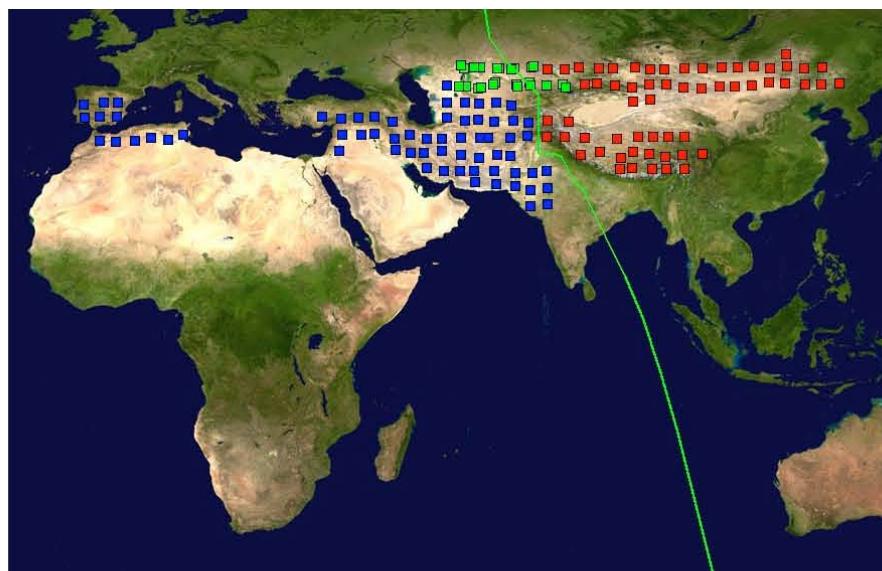


Fig. 6.30

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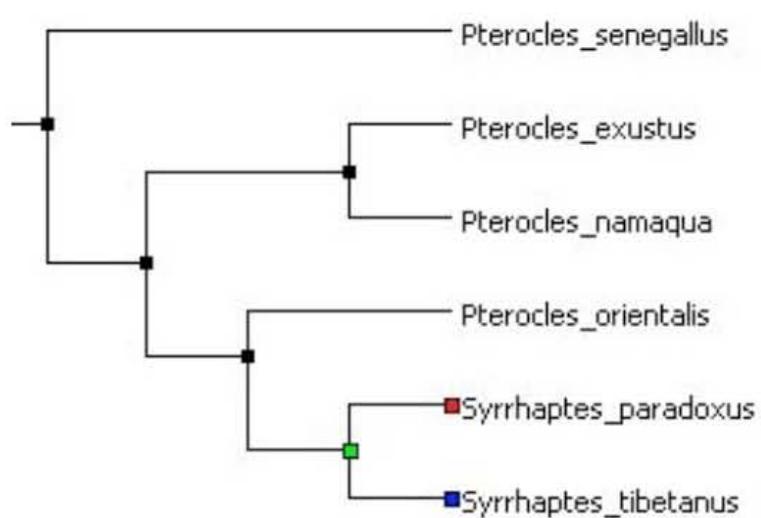
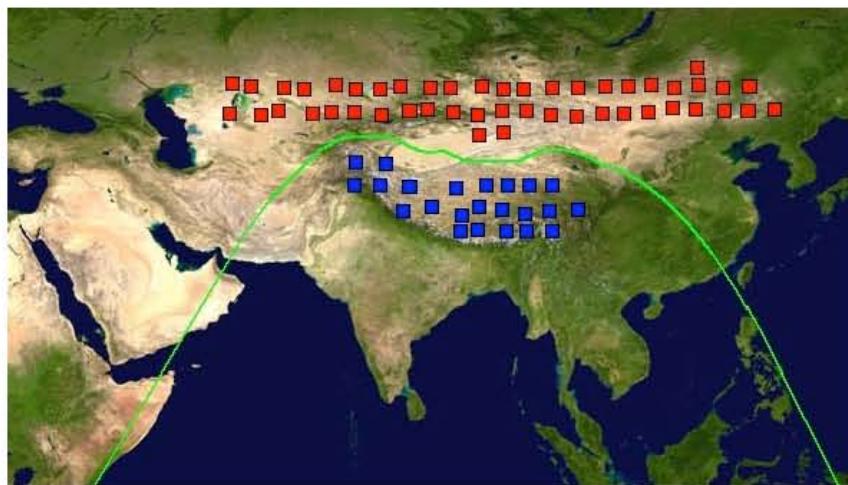


Fig. 6.31

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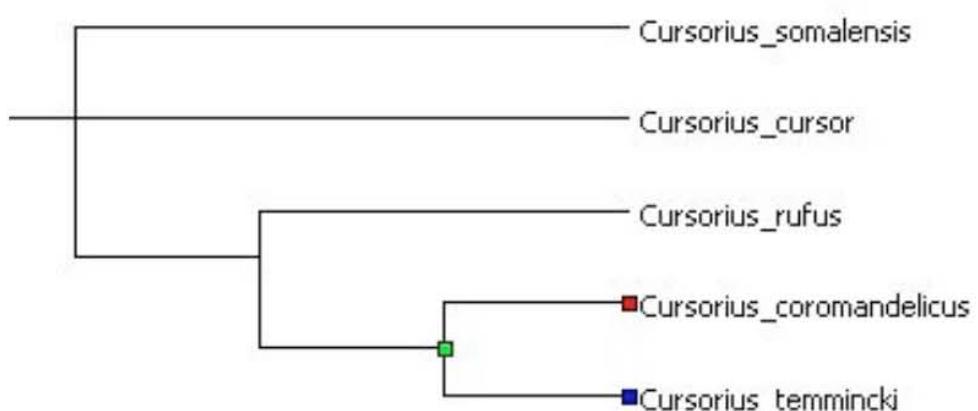
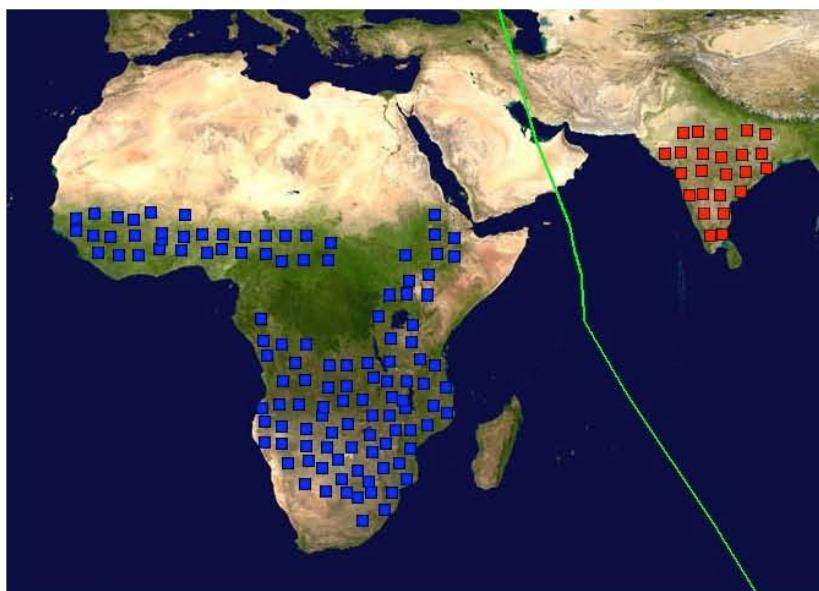


Fig. 6.32

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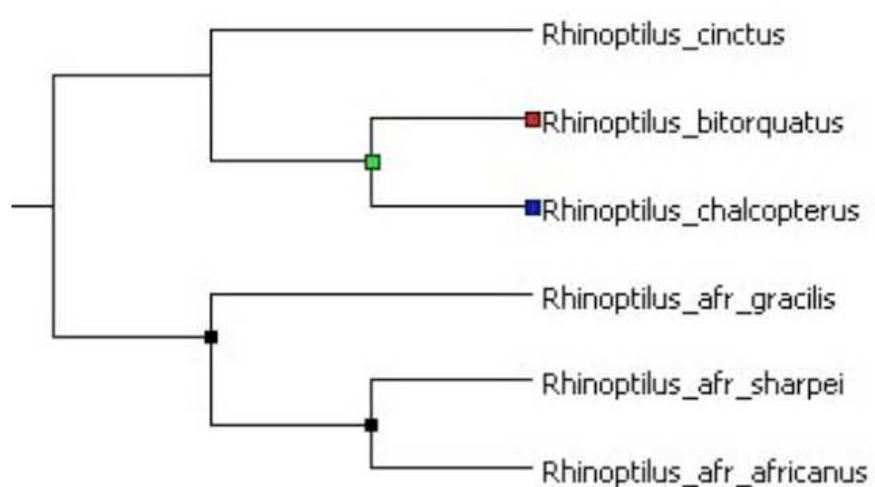
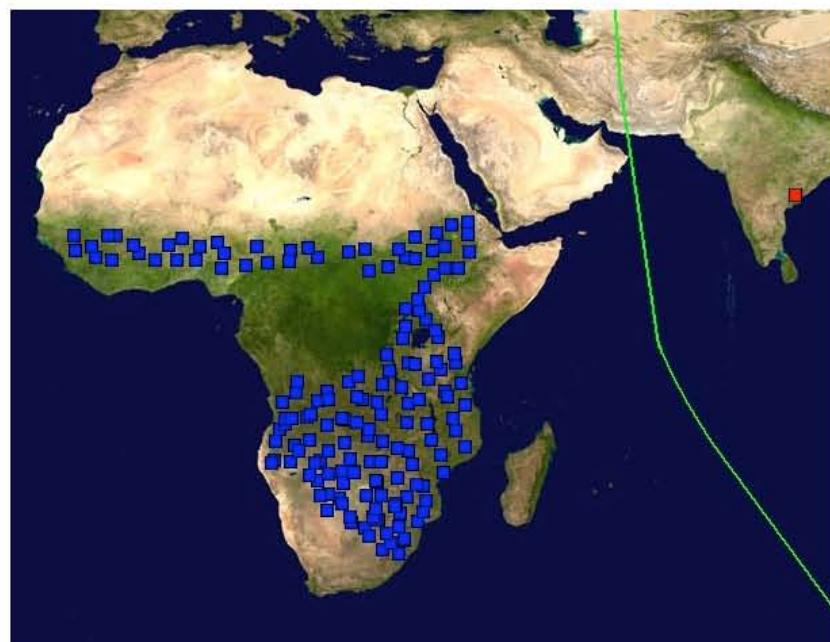


Fig. 6.33

6.68

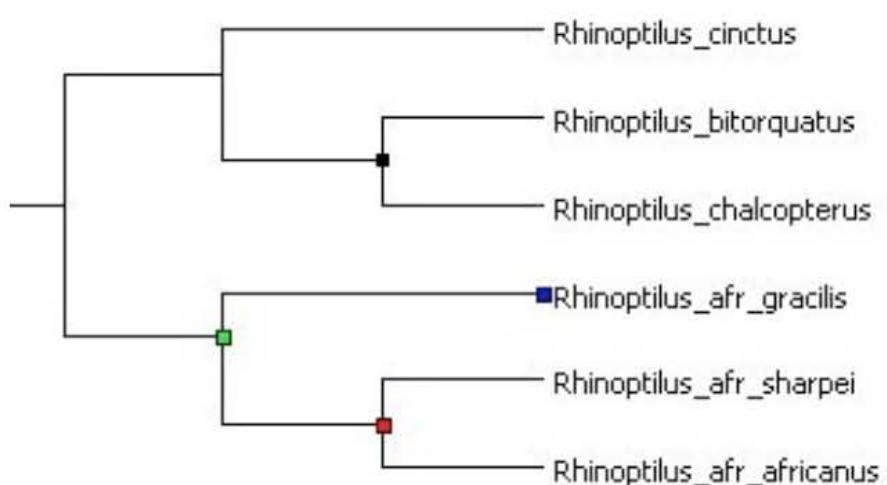
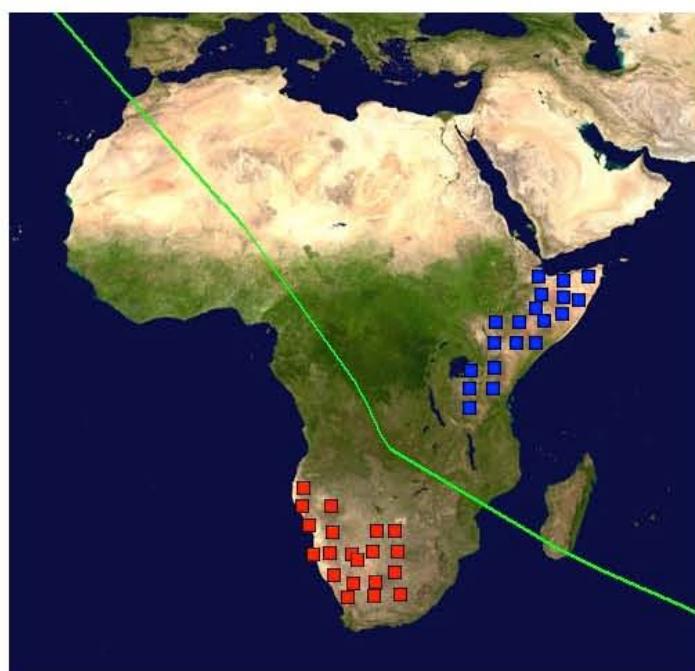


Fig. 6.34

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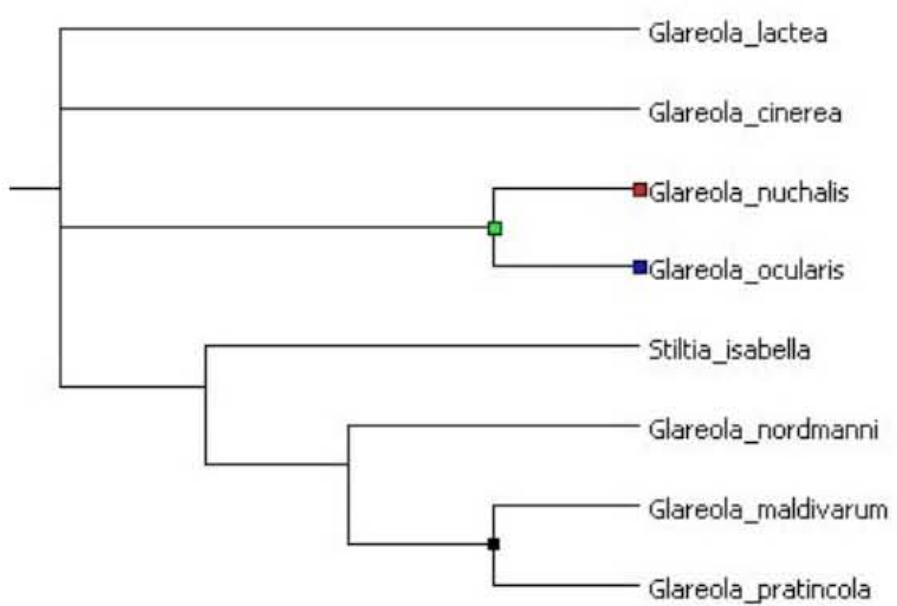
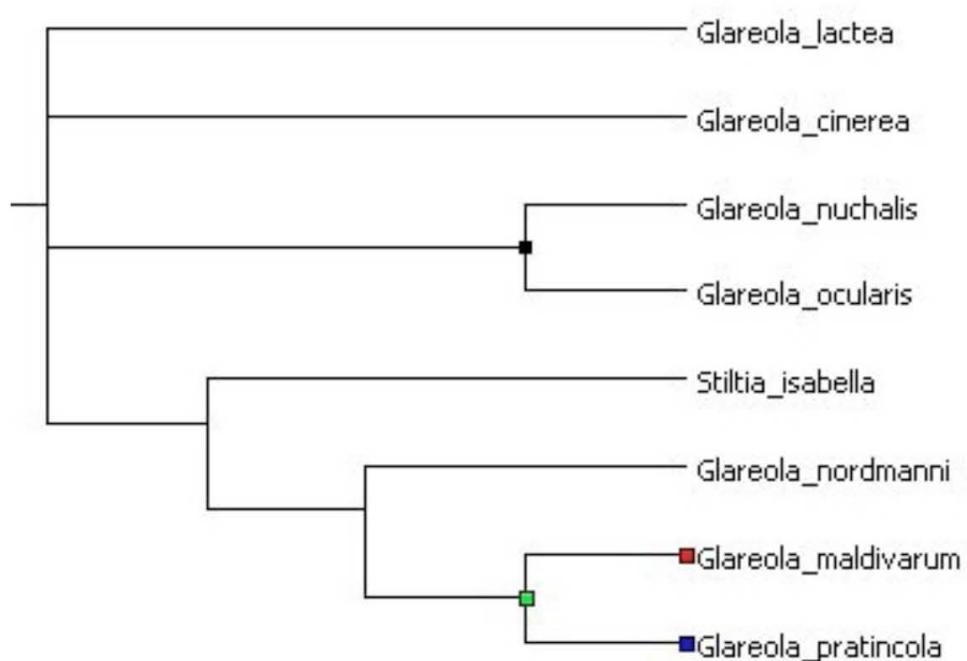
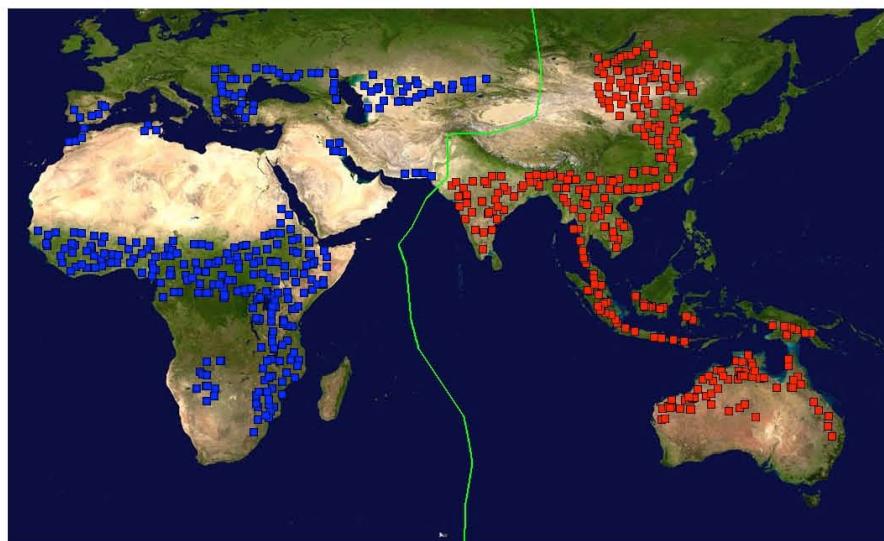


Fig. 6.35

6.70



CHAPTER 7

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