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The historical biogeography of terrestrial gamebirds (Aves: Galliformes)

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Abstract

Whilst the phylogenetic relations of gamebirds are now well understood, there is a great lack of consensus on their biogeographical relationships. It has been suggested that the basal galliform clades, namely the megapodes from Australasia and the cracids from South and Central America, have their origins in the northern hemisphere and have colonised the southern hemisphere more recently. Those in favour of a Northern Hemisphere origin suggest that stem galliforms originated only after the Cretaceous-Tertiary mass extinction event. On the contrary, it has been hypothesized that the ancestors of megapodes and cracids were present in Australasia and South America from the time of the break-up of Gondwana in the Cretaceous. Debate on this subject continues with recent publications supporting both a northern and southern origin for the basal megapodes. All literature on the biogeographical relationships of gamebirds has been based on putative galliform fossils and pure speculation. No quantitative biogeographical analysis has been undertaken on any galliform taxon. The recent publication of a well resolved and strongly supported phylogeny for gamebirds coupled with the availability of comprehensive distribution data for virtually all terminal taxa, allows a comprehensive analysis of the biogeographical history of the Galliformes. However, cladistic biogeographical methods that are currently employed to infer biogeographical histories are particularly unsuited for gamebird research. Gamebird taxa have varied dispersal abilities and numerous species have widespread and sympatric distributions. These factors all degrade biogeographical signature in a cladistic analyses. In this study I adopt a novel approach that is largely free of the limitations of cladistic biogeography. Vicariance biogeography aims to resolve the historical sequence of vicariance events and is concerned only with the geographic positions of observed disjunctions in the distribution of taxa. This study represents the first quantitative attempt to elucidate the historical biogeography of gamebirds and aims to resolve the long standing controversy concerning the centres of origin of the basal gamebird families. Results inferred from analysis using this novel approach are in agreement with a southern hemisphere origin for the megapodes whilst evidence for the southern origin of the cracids is ambiguously supported. The vicariance approach suggests that the megapodes were present in Australasia from the time of the break-up of Gondwana and probably originated in the Cretaceous. Although VIP hints at a southern origin for the cracids, the biogeographical origin of this group remains unresolved.

Chapter 1

Inferring the biogeographical history of terrestrial gamebirds (Aves: Galliformes) using a novel approach: The direct analysis of vicariance

Gamebirds and their systematics

Terrestrial gamebirds (Aves: Galliformes) are a speciose and cosmopolitan order of birds that occur on all the world's continents, with the exception of Antarctica. Within continents, they are represented in all habitat types bar the most barren deserts and areas perpetually covered by ice (Figure 1.). Applying the relatively conservative Biological Species Concept (Mayr 1942), there are at present 281 recognized species of gamebirds within the order Galliformes divided among 81 genera (Sibley and Monroe 1990; del Hoyo *et al.* 1994). They are currently assigned to seven families (Sibley and Ahlquist 1985, 1990; del Hoyo *et al.* 1994) however a revised classification following comprehensive phylogenetic analysis by Crowe *et al.* (2006) suggested that the number of families be reduced to five.

Gamebirds are well known due to their long and extensive relationship with humans. They play important roles in local economies, cultures and sport and have affected man more profoundly than any other group of birds (Madge and McGowan 2002). The domesticated chicken (*Gallus gallus domesticus*) and numerous other species provide an important source of protein across the globe. Pheasants (Phasianidae), especially, have been sought for the beauty of male plumages, with several species being introduced into captivity in Europe during the 18th and 19th centuries (Johnsgard 1999). The brown eared-pheasant (*Crossoptilon auritum*) has long been a symbol of bravery in China. Feathers of the male were used as battle adornments by generals during the Qing Dynasty (Madge and McGowan 2002).

The common generic name of birds belonging to the order Galliformes (gamebirds) derives from the fact that many species are shot for sport (Johnsgard 1999). The efforts of early hunter-naturalists made available greater knowledge on the life histories and distributions of these species than for many other birds that share their habitats. Aristotle, considered by some to be the world's first scientist (Clegg 2003), carried out the first ever „scientific“ ornithological studies on gamebirds in 350BC (Kember 1971). He used observations on the development of chickens to provide insight into how life begins. The close relationship between gamebirds and humans implies that knowledge of the gamebirds is considerably greater than knowledge of any other bird taxa. Galliforms remain one of the most comprehensively studied orders of birds and there exists comprehensive literature on the distribution of virtually all species and well-marked subspecies (Table 2.).



Figure 1: Distribution map of the order Galliformes.

The phylogenetic relationships amongst the galliforms have long been subject to investigation (Crowe *et al.* 2006). Pre-molecular classifications attempted to establish the major groupings within the galliforms and varied greatly in their interpretations. Sibley (1960) suggested that only two families warrant recognition whilst Hudson *et al.* (1959, 1966), Wetmore (1960) and Hudson and Lanzillotti (1964) split the galliforms into two superfamilies and six families. Megapodes (Megapodiidae) and cracids (Cracidae) were grouped into the superfamily Cracoidea whilst the second superfamily Phasianoidea was divided into four families.

Cladistic interpretations of morphological and behavioural (M/B) characters by Cracraft (1981, 1988) and Crowe (1988) suggested that the cracids were sister to the balance of the phasianoides rather than to the megapodes. More extensive research on M/B characters by Brom and Brom (1992) and Dyke *et al.* (2003) supported this hypothesis. Although these M/B assessments generally agreed on the monophyly of the order Galliformes, they were characterised by poor resolution within phasianoid clades. This was due to the remarkable osteological uniformity of the “higher” galliforms, especially phasianids (Crowe *et al.* 2006).

Numerous suprageneric phylogenetic investigations covering different subsets of the galliforms have been undertaken using molecular data (Crowe *et al.* 2006). None of these studies sampled species from all of the current suprageneric taxa listed in Table 1. Additionally, they sampled inadequate numbers of exemplars for these clades and few employed logical outgroups to root their cladograms (Crowe *et al.* 2006). Some early molecular studies even challenged the monophyly of the gamebirds. Jolles *et al.* (1976, 1979) and Prager and Wilson (1976) suggested that

dabbling ducks of the order Anseriformes (ducks and geese) are more closely related to the balance of gamebirds than are the cracids. As with M/B research, many molecular studies have produced poorly resolved cladograms or produced clade nodes with low support (del Hoyo *et al.* 1994; Kimball *et al.* 1999; Lucchini and Randi 1999; Bush and Strobeck 2003; Pereira and Baker 2006).

In a landmark paper, Crowe *et al.* (2006) put to rest most disagreements on the phylogenetic relationships of gamebird taxa. This study took into consideration all suprageneric gamebird taxa and firmly established the monophyly of the galliforms. It included 159 gamebird taxa from 65 genera and was based on 102 morpho-behavioral (M/B) attributes and 4452 nucleic acid base pairs from three mitochondrial markers and one nuclear marker. One major limitation of this study was that it had a strong bias towards mtDNA, which is maternally inherited as a single linkage group. A more recent phylogenetic analysis by Crowe *et al.* (unpublished data) is utilised in this study (Figure 2.). This more inclusive phylogenetic revision incorporated 224 species from 75 genera, representing 80% of all gamebird taxa. It was performed using 120 morpho-behavioral (M/B) attributes, 62 173 nucleic acid base pairs from 13 mitochondrial and 42 nuclear markers (Crowe *et al.* unpublished data).

No biogeographical analysis can be undertaken without an inclusive, well resolved and strongly supported phylogenetic analysis. Most galliform clades are now fully resolved with strong nodal support (Figure 3.), the exceptions being the chachalacas (*Ortalis* spp.) and the grouse (Tetraoninae). Although the phylogenetic relations of gamebirds are now well understood, there is a “great lack of consensus” on the biogeographical relationships of these birds (Jones *et al.* 1995; Crowe *et al.* 2006). No quantitative biogeographical analysis has been undertaken on any galliform taxon. All literature on the biogeographical relationships of gamebirds has been based on putative galliform fossils and pure speculation (Crowe *et al.* 2006). Literature on the biogeographical relationships of gamebirds (Crowe *et al.* 2006) is summarized below with the main debate revolving around the centre of origin of the basal galliform families.

Centre of origin: north or south?

There exists much controversy concerning the position and timing of the origin of the basal galliform families (Jones *et al.* 1995; Crowe *et al.* 2006). It has been suggested that the megapodes (Megapodiidae) reached Australia from the north via Asia and that the cracids (Cracidae) had their centre of origin in tropical North America and colonised South America more recently (Vuilleumier 1965, Delacour and Amadon 1973, Olson 1980, 1985; Mayr and Weidig 2004). On the contrary, it has been hypothesised that the ancestors of megapodes and cracids were present in Australasia and South America from the time of the break-up of Gondwana (Darlington 1957; Crowe and Short 1992; Cracraft 2001 and Dyke *et al.* 2003; Crowe *et al.* 2006)

Those in favour of a Northern Hemisphere origin suggest that stem galliforms originated only after the Cretaceous-Tertiary (K/T) mass extinction event. These authors propose that the megapodes probably reached Australia from the north by the Miocene (Mayr and Weidig 2004) or possibly earlier in the Tertiary (Mayr 1944). This is supported by Northern hemisphere fossils from the Eocene and Oligocene of three extinct galliform families with about 30 genera and 60 species (Mouher-Chauviré 1992). Additionally, putative stem group Eocene galliform (Mayr and Weidig 2004) and Oligocene cracid fossils have been discovered in North America (Tordoff and Macdonald 1957). Vuilleumier (1965) argues that the present distribution of cracids in the Americas and their degree of morphological divergence and isolation suggest that their presence in South America is of more recent origin, probably post-Pliocene or even mid-Pleistocene. To date, no galliform fossils have been found in South America whilst fossil findings in Australia have been limited to Pleistocene deposits (Jones *et al.* 1995).

Darlington (1957) and Cracraft (1973) were of the opinion that the cracid fossils show more resemblance to Phasianidae. They proposed a Gondwana origin for the galliforms and suggested that the cracids and megapodes were derived from ancestors which were present in Australasia and South America from the time of the break-up of Gondwana in the Cretaceous. Cracraft (1973) suggests that this theory most parsimoniously explains the present distribution patterns of these basal galliform families. Further reassessment of these fossils by Crowe and Short (1992) and Dyke (2003) suggest the alleged cracid fossils were in fact, not cracids at all, and that the fossil *Gallinuloides* (Mayr and Weidig 2004) is a basal member of the ‚phasianoid‘ assemblage within the galliforms and not basal within the order as previously interpreted.

Moreover, phylogenetic analyses calibrated with molecular clocks (Cracraft 2001 and Dyke *et al.* 2003) and newly discovered Eocene fossils from North America (Gulas-Wroblewski and Wroblewski 2003) and Europe (Lindow and Dyke 2007) suggest a Southern Hemisphere origin for gamebirds prior to the K/T mass extinction. The long-standing controversy surrounding the question of whether living bird lineages emerged before or after the K/T event was finally resolved with the discovery of a late Cretaceous fossil in Antarctica (Clarke *et al.* 2005). Phylogenetic analysis supported by histological data suggest that this fossil is part of the Anseriformes (Clarke *et al.* 2005), which are sister to the Galliformes (Sibley and Ahlquist 1990; Groth and Barrowclough 1999; Cracraft and Clarke 2001). Using the ages of the above-mentioned fossil galliforms as anchor points, Tuinen and Dyke (2004) and Pereira and Baker (2006) produced molecular clock phylogenies that suggest gamebirds originated on Gondwana and that the basal gamebirds originated in the Cretaceous. Nevertheless, debate on this subject continues with recent publications supporting both a northern (Mayr and Weidig 2004) and southern origin for the basal megapodes (Crowe *et al.* 2006).

A short history of biogeographical analysis

Biogeography is the study of the geographic distribution of taxa and their attributes in space and time (Hausdorf and Hennig 2007). It is a peculiar discipline because it occupies an intermediate area between geography, geology and biology, being practiced by palaeontologists, anthropologists, systematists, ecologists and geographers, among others (Nelson 1985). For this reason biogeography is interdisciplinary and lacks the conceptual unity of other sciences (Morrone 2009).

The questions posed by modern biogeographers were already present in prescientific writings. The concepts of centers of origin and dispersal may be recognized in the biblical accounts of the Garden of Eden and Noah's Ark (Morrone 2009). Carl Linnaeus inaugurated classical biogeography and provided an explanation of the geographic distribution of living beings in accordance with the book of Genesis (Morrone 2009). He predicted the location of the Garden of Eden to be on a tropical island south of the equator. Although this may now seem far fetched, Linnaeus put forward two fundamental biogeographic ideas: a small centre where species appear and their movement to other areas (Morrone 2009).

In "The Origin of Species", Charles Darwin (1859) wrote two chapters on biogeography (Morrone 2009). Whereas Darwin is considered to be the father of evolutionary theory, his counterpart, Alfred Russel Wallace, is considered by several authors to be the father of biogeography (George 1964, Brown and Lomolino 1998, Riddle 2005). Whilst carrying out extensive fieldwork in the Malay Archipelago, Wallace (1863) identified perhaps the most famous biogeographical boundary line. This break, now referred to as the Wallace Line, divides the Indonesian Archipelago into two distinct parts, one in which the fauna closely related to that of Australia is common, and one in which the fauna is largely of Asian origin (Camerini 1993).

Despite Wallace identifying this famous biogeographical disjunction and numerous others, he and other early biogeographers speculated the biogeographical history of various taxa based on non-quantitative procedures. Numerous quantitative procedures to biogeographical analysis have since been formulated, the most prominent being phylogenetic biogeography by Hennig (1950), panbiogeography by Croizat (1958, 1964) and cladistic biogeography by Nelson and Platnick (1981). The cladistic approach has dominated biogeographical analyses over the past three decades and no fewer than 14 cladistic biogeographic methods have been proposed (Morrone 2009). Brooks parsimony analysis (BPA) (Wiley 1987), dispersal-vicariance analyses (DIVA) (Ronquist 1997) and dispersal-extinction-cladogenesis (DEC) (Ree and Smith 2008) are all based on the cladistic approach, have all been implemented into easily accessible software, and are the most widely used methods for inferring biogeographic histories.

Problems with the cladistic approach

Cladistic biogeography assumes a correspondence between the phylogenetic relationships of taxa and the relationships between areas they inhabit (Nelson and Platnick 1980, 1981). It utilises information on the cladistic relationships between taxa and their biogeographical distribution to form hypothesis on the relationships between areas (Morrone 2009). If several taxa show the same pattern then such congruence is translated as evidence of common history (Crisci and Morrone 1992; Ronquist 1997). As a result of this line of thinking, quantification in historical biogeography has usually been based on the search for a single branching relationship amongst areas of endemism (Ronquist 1997). Cladistic biogeography is therefore based on a protocol that is in many ways very similar to phylogenetic systematics (Kluge 1988). As phylogenetic analysis reconstructs the relationships of taxa, biogeographical analysis has been used to reconstruct the relationship of areas (Hovenkamp 1997). However, Linder (2001) has illustrated that the diverse methods utilised to define areas of endemism have produced widely different interpretations in biogeographical analyses. In two landmark papers, Hovenkamp (1997; 2001) highlights numerous problems with this cladistic approach to inferring biogeographical history.

Firstly, areas are not taxa (Hovenkamp 1997). The assumption of an analogy between taxa and areas “presupposes the existence of areas of endemism” that do not necessarily exist (Hovenkamp 1997). Software commonly used to implement the cladistic approach to biogeographical analysis (e.g. DIVA and DEC) are all based on predefined areas. The initial delimitation of these areas is subjective and statistical packages are very sensitive to small differences in area definition (Arias and Goloboff, submitted). The notion of defining areas where evolutionary radiations have taken place before carrying out biogeographical analysis is counter intuitive and does not follow the rules of basic scientific procedure. These areas of endemism ought to be the subject of investigation rather than assumed *a priori* (Hovenkamp 1997). Areas, unlike organisms, rarely have a unique hierarchical history (Ronquist 1997). Evolutionary theory predicts and explains the existence of taxa and their hierarchical relationships (Hovenkamp 1997). There is no corresponding biogeographical theory that predicts the existence of areas of endemism that are characterized by taxa (Hovenkamp 1997). Dispersal barriers have different effects on different species and may appear and disappear over time (Ronquist 1997). For this reason, taxa rarely share the same distribution, let alone groups of taxa (Hovenkamp 1997).

Secondly, areas do not evolve as taxa do (Hovenkamp 1997). The evolution of taxa is usually divergent with full hybridization of species a rare process. When hybridization does occur, it only takes place at or below the species level. Conversely, the evolution of areas is seldom exclusively divergent. In many cases, formerly isolated areas come together and the mixing of biota results in reticulation (Ronquist 1997). An archetypal example of this is the collision of India with

Eurasia in the mid Eocene (Rowley 1996). India and the remainder of Eurasia have certainly not maintained separate identities, and are characterised by a mixture of both regions fauna and flora. Reticulation is a real phenomenon that cannot be represented in the form of a branching diagram (Hovenkamp 1997).

Thirdly, taxa cannot be treated in the same manner in biogeographical analyses as characters are used in phylogenetic analyses (Hovenkamp 1997). In phylogenetic analyses, when several taxa share the same character, synapomorphic similarity can be discerned from homoplastic similarity by congruence with other characters (Hovenkamp 1997). In biogeographical analysis, similarity in the taxonomic makeup of different areas may result from horizontal transmission rather than shared “inheritance” (Sober 1988). The principle difference between taxa in biogeographical analyses and characters in taxon analyses is the considerably greater vagility of taxa compared to characters (Hovenkamp 1997). Characters of taxa are considerably more restricted to the taxon from which they originated and all its direct descendants. Conversely, taxa that are used as characters for areas may move freely between areas. They are constrained only by current barriers, rather than the historical origin of the areas they inhabit. Barriers that are currently formidable may disappear and taxa may disperse into new areas (Hovenkamp 1997).

The handling of dispersal and extinction has caused severe problems in the development of an analytical protocol for cladistic biogeography (Ronquist 1997). The assumption of a single branching pattern for numerous groups of taxa is flawed as dispersal barriers appear and disappear throughout evolutionary history and may have affected dissimilar taxa differently (Ronquist 1997). The loss of species due to extinction reduces the degree of biogeographic congruence recoverable between clades. The dispersal ability of the five families of gamebirds varies greatly (Olson 1980) and the spread of humans out of Africa to other parts of the globe has especially impacted the basal gamebird families (Delacour and Amadon 1973; Jones *et al.* 1995). For this reason, cladistic methods of biogeographical analysis are particularly inappropriate when it comes inferring the biogeographical history of gamebirds.

Olson (1980) suggests that megapodes are excellent overwater dispersers whilst the Phasianidae are poor at crossing water barriers. This is evident in the distribution of these taxa, with the present distribution of megapodes (22 extant species) extending from Australia into Indonesia, to Indian Ocean islands as far north as Nicobar and to Pacific Ocean islands as far east as Niuafo’ou (Kingdom of Tonga) (Jones *et al.* 1995). Conversely, only six of 138 phasianid species have managed to traverse Wallace’s line, including four small migratory quails (*Coturnix* spp.) and two species of *Gallus* that may have been introduced east of the line by humans (Olson 1980). Rampant dispersal by certain taxa, the megapodes in the case of this study, will result in failure to uncover a common branching pattern using cladistic approaches to biogeographical analyses.

Several factors have made gamebirds particularly susceptible to extinction as humans spread out of Africa and colonised other continents. Gamebirds and their eggs provide a rich source of protein for any predator moving into a new habitat. Their often colourful plumage is highly sought after for clothing and traditional ceremonies. Gamebirds are also generally larger than other birds and are consequently less agile. Lastly, the fact that they are ground nesting and ground feeding birds makes them more accessible to predators. These factors have made the galliforms especially susceptible to extinction following human (and other predator) colonisation of new areas. This is evidenced by the fact that megapode fossils have often been found in Holocene deposits on numerous Pacific Islands where they are no longer present, often in association with human remains (Jones *et al.* 1995). Extinctions or “missing taxa” in a cladistic analysis result in the failure to identify common branching patterns amongst taxa.

Finally, cladistic biogeography treats all widespread and sympatric distributions as problematical (Hovenkamp 2001). Widespread taxa often have distributions that extend across the initially predefined areas of endemism that degrade the biogeographic signature that this approach can pick up. There are numerous gamebirds with widespread distributions, particularly within the phasianine genera *Coturnix* and *Lagopus*. Additionally, the excellent dispersal by some galliform clades has resulted in extensive colonisation of new habitats, often followed by speciation and subsequent return dispersal to ancestral areas. Extensive sympatry is evident amongst many closely related gamebird taxa (Jones *et al.* 1995), with up to 17 gamebird species occupying any particular habitat. Cladistic biogeographical analysis carried out on gamebirds would become bogged down in discussions about these widespread and sympatric species, attempting to extract information on past vicariance events where no evidence has survived. Evidence for a vicariance event is lost once a species disperses across the barrier involved in its vicariant origin (Hovenkamp 1997).

Vicariance biogeography

The original goal of historical biogeography was expressed by Rosen (1978): “If the causal explanation of cladogenesis is sought in the interpretations of Earth History, then one would hope to discover a sequence of vicariance events that correspond in relative age with the relative position of taxa in a cladistic sequence and in geographic position with the geographic disjunctions between taxa”. However, all biogeographical methods devised since then have departed from this original aim (Hovenkamp 2001).

In two contentious papers, Hovenkamp (1997, 2001) proposed a new protocol that aims to resolve the historical sequence of vicariance events rather than the relationship of predefined areas of endemism. This approach (vicariance biogeography) is concerned only with the “geographic positions of observed disjunctions in the distribution of taxa” (Hovenkamp 2001). It is a direct

analysis of vicariance in that it deals only with vicariant events, the “core business of phylogenetic biogeography” (Hovenkamp 1997).

The desired sequence of vicariance events is reconstructed with geographical and historical information (Hovenkamp 1997). Geographical information, the location of the vicariance event, is specified by the area located between the two disjunct distribution ranges. Historical information, the sequential relation of all the vicariance events, is specified by the chronological order of the cladogram nodes.

As with any form of biogeographical analysis, this approach is not without problems. Vicariance biogeography often discards large amounts of information available from cladograms (Hovenkamp 2001). Only distribution patterns that retain evidence for vicariance are utilised. In cases where species have dispersed substantially across barriers involved in their vicariant origin, information about these vicariant events is lost (Hovenkamp 1997). This problem is common to all methods of biogeographical analysis. However, observations that do not constitute evidence are not necessarily discarded, but merely ignored for the time being. At a later stage of the analysis, they may be reconsidered when explanations are sought for the current distribution patterns for individual taxa. It is not possible to extract information about past vicariance events where no information has survived (Hovenkamp 1997). As with other methods of biogeographical analysis, when there has been extensive dispersal and or where sympatry is common in a cladogram, analysis becomes impossible (Hovenkamp 1997).

The advantages posed by using vicariance biogeography over other methods make this approach particularly attractive. It deals with the problems of area evolution by allowing for both reticulate and divergent patterns. It treats all species equally, regardless of the extent of their area, with both endemic and widespread taxa potentially equally informative (Hovenkamp 2001). Widespread species are dealt with by recognising vicariant boundaries regardless of the extension of their ranges in other directions. Widespread species are especially informative when there is little or no overlap in their ranges. Vicariance biogeography does not require predefined “areas of endemism” with all associated problems outlined by Axelius (1991), Morrone (1994), Harold and Mooi (1995) and Hovenkamp (1997). It provides an appropriate method for the reconstruction of biogeographical history based on geographical boundary lines rather than areas that these lines delimit (Hovenkamp 1997). It also allows users to identify those events that have caused “multiple speciation events to occur simultaneously” (Hovenkamp 2001).

Apart from a few missing taxa, the phylogenetic relationships of the Galliformes can be considered as fully resolved. This information, coupled with the comprehensive distribution data for virtually all terminal taxa, allows a comprehensive analysis of the biogeographical history of the Galliformes. Hovenkamp’s ideas and visions have now been formalized in a computer program called VIP (Vicariance Inference Program) (Arias and Goloboff, submitted). The availability of a

biogeographical program that is largely free of the limitations of cladistic approaches makes the prospect of a comprehensive biogeographical analysis even more attractive. This study represents the first quantitative biogeographical analysis of the gamebirds and to resolve the long standing controversy concerning the centres of origin of the basal gamebird families.

Chapter 2

Poultry in motion: The historical biogeography of terrestrial gamebirds (Aves: Galliformes)

Introduction

Gamebirds (Aves: Galliformes) are a cosmopolitan and speciose order of birds. They are represented on all the world's continents, with the exception of Antarctica (Figure 1.). Applying the relatively conservative biological species concept, there are currently 281 recognized species of gamebirds (Table 1.). Gamebirds are very well known, mainly due to their long and extensive relationship with humans. For centuries gamebirds have been highly sought after as a source of protein, for their often colourful plumage and because many species are shot for sport, hence their common generic name (Madge and McGowan 2002). Gamebirds remain one of the most studied orders of birds and there exists comprehensive literature on the distribution of virtually all terminal taxa (Table 2.).

The phylogeny of gamebirds has long been subject to investigation, with numerous suprageneric investigations covering different subsets of the galliforms having been undertaken using both M/B (Sibley 1960; Hudson 1959, 1966; Wetmore 1960; Hudson and Lanzillotti 1964; Cracraft 1981, 1988; Crowe 1988; Brom and Brom 1992; and Dyke *et al.* 2003) and molecular data (Jolles *et al.* 1976, 1979; Prager and Wilson 1976, del Hoyo *et al.* 1994; Kimball *et al.* 1999; Lucchini and Randi 1999; Bush and Strobeck 2003; Pereira and Baker 2006; Crowe *et al.* 2006). In a landmark paper, Crowe *et al.* (2006) put to rest much of the disagreement concerning the phylogenetic relationship of the gamebirds. This study took into consideration 159 species, included all suprageneric taxa and was based on 102 morpho-behavioral (M/B) attributes and 4452 nucleic acid base pairs from three mitochondrial and one nuclear marker. A more recent phylogenetic analysis by Crowe *et al.* (unpublished data) is utilised in this study. This more inclusive phylogenetic revision incorporated 224 species from 75 genera, representing 80% of all gamebird taxa. It was performed using 120 morpho-behavioral (M/B) attributes, 62 173 nucleic acid base pairs from 13 mitochondrial and 42 nuclear markers (Crowe *et al.* unpublished data).

No biogeographical analysis can be undertaken without an inclusive, well resolved and strongly supported phylogenetic analysis. Most galliform clades are now fully resolved with strong nodal support (Figure 2.), the exceptions being the chachalacas (*Ortalis* spp.) and the grouse (Tetraoninae). Despite the existence of this information, no quantitative biogeographical analysis has ever been undertaken on the gamebirds. All literature on the biogeographical relationships of

gamebirds has been based on putative galliform fossils and pure speculation (Crowe *et al.* 2006). This has resulted in much controversy concerning the position and timing of the origin of the basal galliform families.

Those in favour of a northern Hemisphere origin suggest that stem galliforms originated only after the Cretaceous-Tertiary (K/T) mass extinction event (Vuilleumier 1965, Delacour and Amadon 1973, Olson 1980, 1985). Others propose a Gondwana origin for the galliforms and suggest that the cracids and megapodes were derived from ancestors which were present in Australasia and South America from the time of the break-up of Gondwana in the Cretaceous (Darlington 1957; Crowe and Short 1992; Cracraft 2001 and Dyke *et al.* 2003). Nevertheless, the debate continues with recent publications supporting both a northern (Mayr and Weidig 2004) and southern origin for the basal galliforms (Crowe *et al.* 2006).

The cladistic approach to biogeographical analyses has been extensively utilised over the past three decades (Morrone 2009). This method of analysis is based on predefined areas and aims to elucidate a single branching relationship amongst areas of endemism (Ronquist 1997). There are several reasons why this method particularly unsuitable for analysis on the historical biogeography of gamebirds. Some gamebird taxa display a remarkable ability to disperse (e.g. Megapodiidae) whilst others are very poor over-water colonisers (e.g. Phasianidae) (Olson 1980). The reduced agility of galliforms compared to other birds, their often colourful plumage and the fact that they provide a rich source of protein implies that they are been particularly susceptible to extinction following colonisation of their habitat by humans.

Additionally, numerous gamebird species have widespread distributions, extending across numerous continents and the predefined areas of endemism that the cladistic approach requires. Rampant dispersal by some galliform clades has resulted in extensive colonisation of new habitats, often followed by speciation and subsequent return dispersal to ancestral areas. Extensive sympatry is evident amongst closely related gamebird taxa (Jones *et al.* 1995), with up to 17 gamebird species occupying any particular habitat. The cladistic approach treats all widespread and sympatric distributions as problematical (Hovenkamp 2001). Additionally, rampant dispersal and extinction result in failure to uncover a common branching pattern that cladistic approaches aim to elucidate. These factors all degrade biogeographical signature in a cladistic analyses, and such an approach would become bogged down in discussion about widespread species, sympatry and the failure to uncover a single common branching pattern.

For this reason, I have decided to utilise a vicariance approach that was first suggested by Hovenkamp (1997, 2001). Vicariance biogeography aims to resolve the historical sequence of vicariance events rather than the relationship of predefined areas of endemism. It is concerned only with the “geographic positions of observed disjunctions in the distribution of taxa” and deals with the problems of area evolution by allowing for both reticulate and divergent patterns (Hovenkamp 1997).

Table 1: Taxa attributed to the Galliformes by del Hoyo *et al.* (1994) and modified according to a revised classification proposed by Crowe *et al.* 2006. Numbers in parentheses are those of species and genera included in this study.

Scientific names	Common names	Range	No. of species	No. of Genera
Megapodiidae	megapodes, scrubfowl, brush-turkeys	Australasian	19 (15)	7 (7)
Cracidae	cracids: curassows, guans and chachalacas	Neotropical	50 (42)	11 (10)
Numididae	guineafowls	Afrotropical	6 (6)	4 (4)
Odontophoridae	New World quails: quails, wood-quails and bobwhites	Neotropical and Nearctic	32 (13)	9 (6)
Phasianidae	pheasants, junglefowl, peafowl, peacock and argus-pheasants, partridges, francolins, Old World quails, turkeys and grouse	Palaearctic, Nearctic, Holarctic, Afrotropical, Asiotropical	174 (144)	50 (48)

It treats all species equally, regardless of the extent of their area, with both endemic and widespread taxa potentially equally informative.

The availability of a well resolved phylogeny, comprehensive distribution data for virtually all terminal galliform taxa and a new approach to biogeographical analysis that is largely free of the limitations of cladistic biogeography implies that the time is right for a comprehensive analysis of the historical biogeography of the Galliformes. This study represents the first quantitative attempt to elucidate that history and aims to resolve the long standing controversy concerning the centres of origin of the basal gamebird families. The galliform fossil record has provided putative data on the origin of the basal gamebird families that is continually disputed. This study specifically aims to establish whether the direction of dispersal of the basal galliform families has been from north to south or vice versa.

Methods

Taxon sampling

The taxa represented in this study (Appendix 1) include 224 of the 281 currently recognised Galliform species, representing all suprageneric Galliform taxa and 75 of 81 currently recognised genera (Table 2). The selection of outgroups was based on considerable morphological and molecular evidence that demonstrate the Anseriformes to be sister to the Galliformes (Sibley and Ahlquist 1990; Groth and Barrowclough 1999; Cracraft and Clarke 2001; Mayr and Clarke 2003). An additional two species each were selected from the more basal orders Struthioniformes (the ostrich *Struthio camelus* and greater rhea *Rhea americana*) and Tinamiformes (the tinamou's *Tinamus*

major and *Tinamus guttatus*) to root the tree. The Anseriformes exemplars used as outgroups are the two screamers *Anhima cornuta* and *Chauna torquata*, the magpie goose *Anseranas semipalmata*, the muscovy duck *Cairina moschata* and the mallard *Anas platyrhynchos*.

Character sampling

Morpho-behavioral characters

All taxa were scored for a total of 120 morphological and behavioural (M/B) characters, most of which were employed by Dyke et al. (2003). The largest proportion of characters were osteological whilst the remainder related to feathering and adult behaviour. Characters unique to individual terminal taxa were included as they contribute to estimations of total taxon divergence, despite being uninformative with regards to overall relationships (Dyke et al. 2003). Multistate characters were ordered for the purposes of the analysis and in accordance with Dyke et al. (2003).

Molecular characters

Molecular characters include 62–173 nucleic characters from published and unpublished DNA sequences of 13 mitochondrial and 42 nuclear markers (Appendix 2.1). The sources and amounts of DNA sequence data are stipulated in Appendix 2.2.

Phylogenetic analytical approach

Parsimony

A parsimony-based phylogenetic analysis was conducted using TNT Version 1.1 (Goloboff, Farris and Nixon 2008). The search strategy employed was the Rachet Island Hopper option: 1000 iterations per replicate, one tree to hold per iteration and random constraint level 10. Ten equally parsimonious cladograms were produced and a majority rules consensus cladogram was constructed (Figure 2.). The extent to which each non-terminal code is supported by character data was determined by using the “jackknife” option in TNT (Farris et al. 1996) using the following strategy: 1000 replications, branch swapping switched on, random addition of five sequences per replicate and $p = e^{-1}$ (about 37%) of characters deleted per jackknife replicate.

Biogeographical analytical approaches

Spatial analyses of vicariance

Hovenkamp suggests that the identification of barriers separating biotas is more in agreement with the aim of vicariance biogeography than the discovery of relationship between pre-defined areas (Hovenkamp 1997, 2001). Hovenkamp’s ideas have been implemented as the spatial analysis of vicariance, in the program VIP (Vicariance Inference Program) Version 17, available at

<http://www.zmuc.dk/public/phylogeny/vip> (Arias *et al.* submitted). VIP attempts to maximize the identification of distribution disjunctions among sister groups. In VIP, a disjunct distribution is not necessarily caused by a vicariance event; it may have been caused by successful dispersal over a pre-existing barrier (Arias *et al.* submitted). Nevertheless this barrier is effective in maintaining the distributions of sister taxa as separate.

In a spatial analysis of vicariance, the distribution of each node in the cladogram is assigned as the sum of each descendant distribution. When the distributions of a pair of sister taxa are disjunct, this disjunction can be explained in terms of a barrier. Overlap amongst distributions prevents the identification of barriers. VIP aims to maximise identification of the disjunct distributions amongst sister taxa by minimising the pairs of sister nodes that have extensive overlap among their distributions. The spatial analysis of vicariance in VIP does not attempt to give an explanation for speciation at every node, rather it attempts to give a geographical explanation wherever possible (Hovenkamp 1997).

VIP requires historical information in the form of a phylogenetic tree and geographic information in the forms of spatial distributions on the terminals of the tree. The method is implemented on a grid on which taxon distributions are mapped from georeferenced points or shaded distribution maps. Some taxon distributions may potentially blur the vicariant distributions of ancestral nodes. Ignoring these problematic distributions may allow the consideration of nodes that are basal to the node in question as vicariant (Page 1994a, 1994b; Brooks 1990; Arias *et al.* submitted). This elimination of a distribution is accepted if it increases the explanatory power of disjunction in another part of the tree. In order to minimize the number of nodes with removed distributions, an optimality criterion is used that requires the user to provide a cost for distribution eliminations in relation to the cost of non-disjunct sister groups. The sum of both quantities gives the final cost of the reconstruction (Arias *et al.* submitted).

It is often the case that a small degree of overlap in the distribution of two taxa blurs the identification of disjunction (Hovenkamp 1997). When the proportion of overlap against the smaller of the two distributions is below a user defined limit, the distribution may be accepted as vicariant. It is reasonable to assume that although barriers are effective, they are not completely uncrossable (Arias *et al.* submitted). VIP has an option that allows for acknowledgement of lack of complete vicariance by assigning a cost to these nodes that is based on the proportion of overlap (Arias *et al.* submitted).

VIP uses the optimality criterion to identify vicariant nodes within the tree by choosing a set of reconstructions of ancestral distributions (Arias *et al.* submitted). The optimal reconstruction is identified in a heuristic search using a flipping nodes strategy. In each replication, the distribution of each node is removed or reactivated depending on its state and scores are calculated. If a new improved reconstruction with a lower cost is identified, then the process starts again. If this is not the

case then the distribution is restored to its original state and the next node is examined. A replication is completed if no better reconstruction is found after all nodes have been examined. The reconstruction with the lowest cost is the preferred optimal reconstruction. In cases where there are multiple equally optimal reconstructions, a consensus reconstruction may be performed where a vicariant reconstruction is shown only if it is vicariant in all optimal reconstructions and distribution eliminations will only be accepted if the distribution of the node is removed in all reconstructions.

A Voronoi tessellation is used to identify barriers in VIP. Barriers are expressed as lines that form a midpoint separating a set of points (Arias *et al.* submitted). Closer sets of distributions will allow for easier identification of the barrier. For distantly separated points, the location of the barrier created in VIP does not necessarily imply the exact position of the real barrier.

Distribution maps

Accurate distribution maps are a prerequisite of any biogeographical analysis. A concerted effort was made to obtain distribution ranges from the most authoritative and up-to-date sources for all taxa. During an extensive literature and internet search, as many distribution maps as possible were collected for each species. These maps were cross checked for inconsistencies and point data was preferred over shaded distribution maps. When appropriate, more recently published maps were preferred over older records. Recently revised distribution maps are provided for all Galliformes listed as Near Threatened, Vulnerable, Endangered and Critically Endangered by the IUCN (IUCN 2010). This included 75 of the 254 taxa analysed in this study. Distributions maps for the remaining taxa were obtained from a variety of sources listed in Table 2.

Analysis

Taxon distributions in the form of both georeferenced points and shaded distributions were entered onto an equirectangular projection of the world map with a 2° grid projected over it. A 2° grid was considered sufficient to identify vicariance events and was selected to reduce the labour involved in inputting distribution data at finer resolutions. The cost of distribution removal was set to 2 and cost of overlapping distributions was set to 1. The use of these input values ensures that a removal is only tolerated if it finds at least one additional pair of disjunct distributions (pers. com, Arias. Maximum overlap was set to 25% to allow for the identification of disjunction where overlap is minimal. A heuristic search with 10 000 iterations was performed to identify optimal the optimal reconstruction for the data set. A consensus reconstruction was selected as multiple equally optimal reconstructions were produced.

Results

Phylogenetic analysis

The phylogenetic analysis performed in this study took into consideration 14 times as many molecular characters and 15% more M/B characters than the analysis performed in Crowe *et al.* 2006. Consequently, the majority-rules cladogram produced (Figure. 2.) is considerably more resolved and supported than in Crowe *et al.* 2006 (Figure 3.). With the exception of the chachalacas (*Ortalis* spp.) and the grouse (Tetraoninae), all nodes all fully supported.

Biogeographical analysis

The default OR reconstruction (with no node removal) identified 134 disjunctions at a cost of 106. When node removal was allowed, a total of 282 equally optimal reconstructions were obtained at a minimal cost of 97. These optimal reconstructions recognised between 152 and 161 disjunctions amongst sister taxa and required between 9 and 15 nodes to be removed in order to identify these disjunctions. The consensus reconstruction, which is essentially a résumé of all the optimal reconstructions, detected 139 disjunctions and 8 node removals that were consistently identified by all of the 282 equally optimal reconstructions.

Despite the ability of VIP to remove problematic nodes in order to produce more disjunctions amongst sister taxa, small numbers of nodes were removed in optimal reconstructions. The node removal option only resulted in the identification of 8.6 to 13.7% more disjunctions amongst sister taxa.

Table 2: Taxon specific references for distribution maps utilised.

Megapodiidae	Cracidae	Numididae	Odontophoridae	Phasianidae
Jones <i>et al.</i> (1995) IUCN 2010	Delacour and Amadon 1973 CSG 2010 IUCN 2010	Snow 1978 IUCN 2010	Johnsgard 1973, 1986, 1988, 1999 Madge and McGowan 2002 IUCN 2010	Roberts 1924 Mackworth-Praed and Grant 1952, 1962, 1970 Hall 1963 Clancey 1967 Johnsgard 1973, 1986, 1988, 1999 Harrison <i>et al</i> 1997 Madge and McGowan 2002 Hockey <i>et al</i> 2005 IUCN 2010

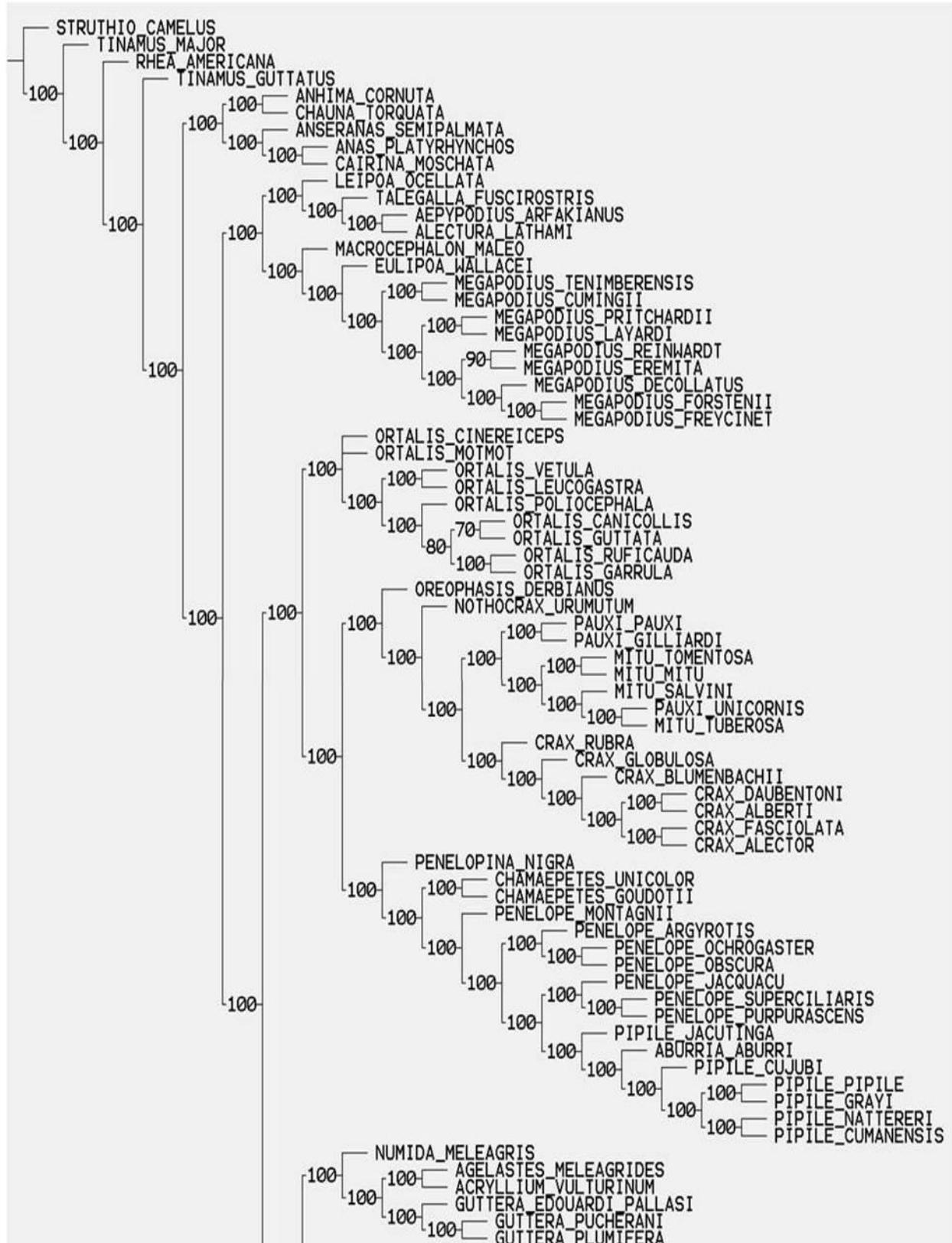


Figure 2. The majority-rules consensus cladogram for the galliforms resulting from the parsimony ratchet analysis of the combined data set. Numbers at nodes are majority rules determinations.

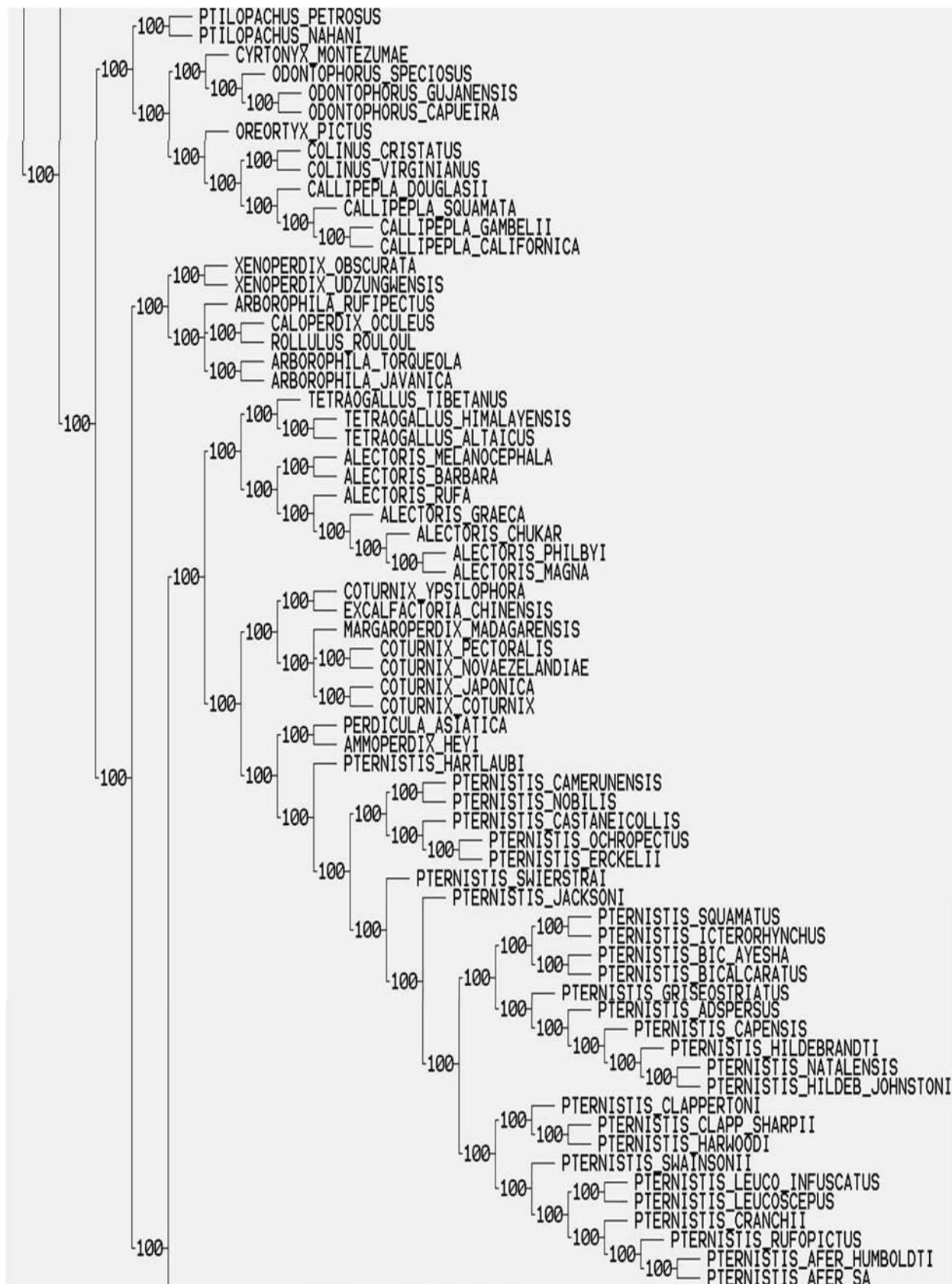


Figure 2. Continued.

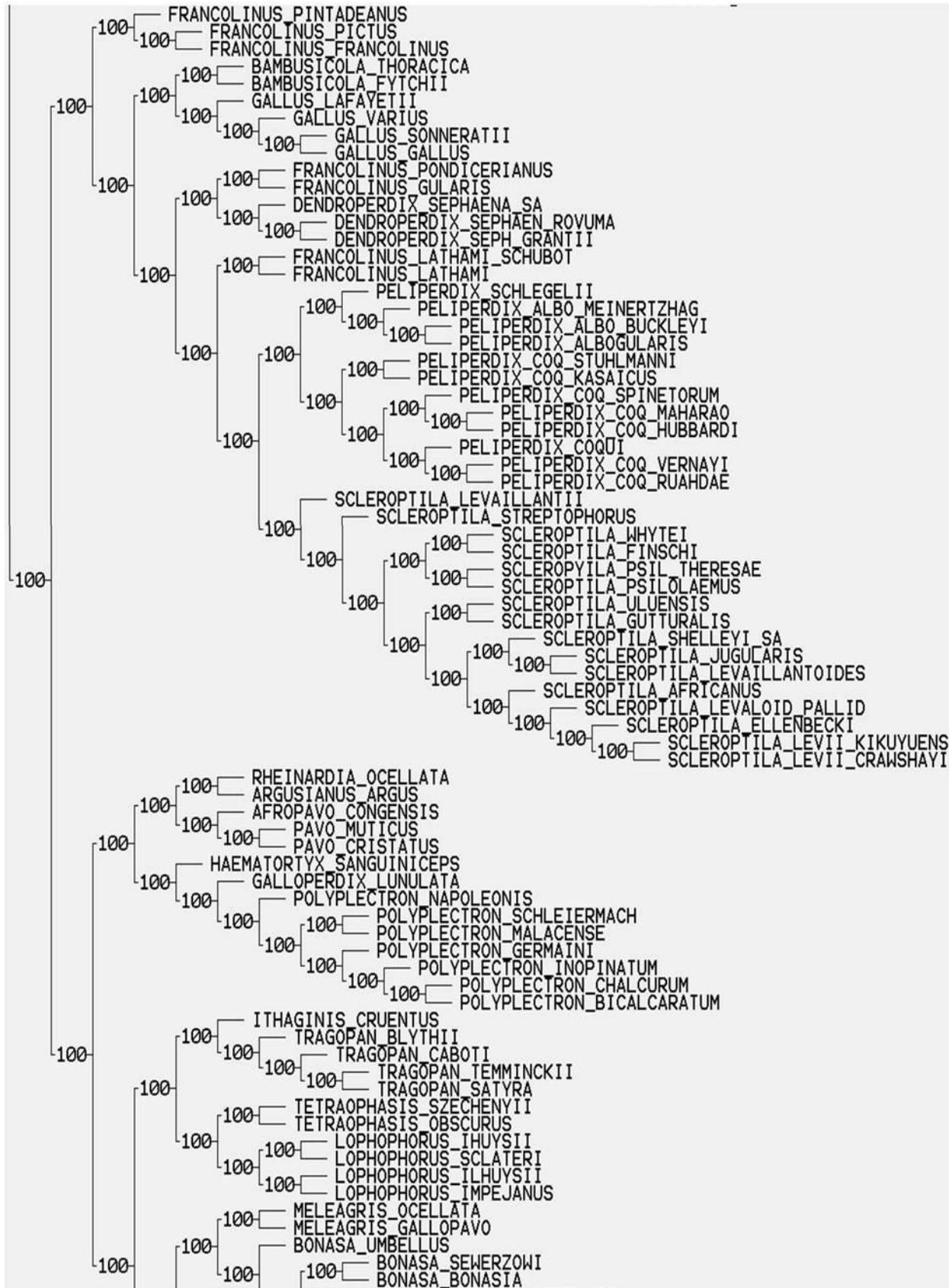


Figure 2. Continued.

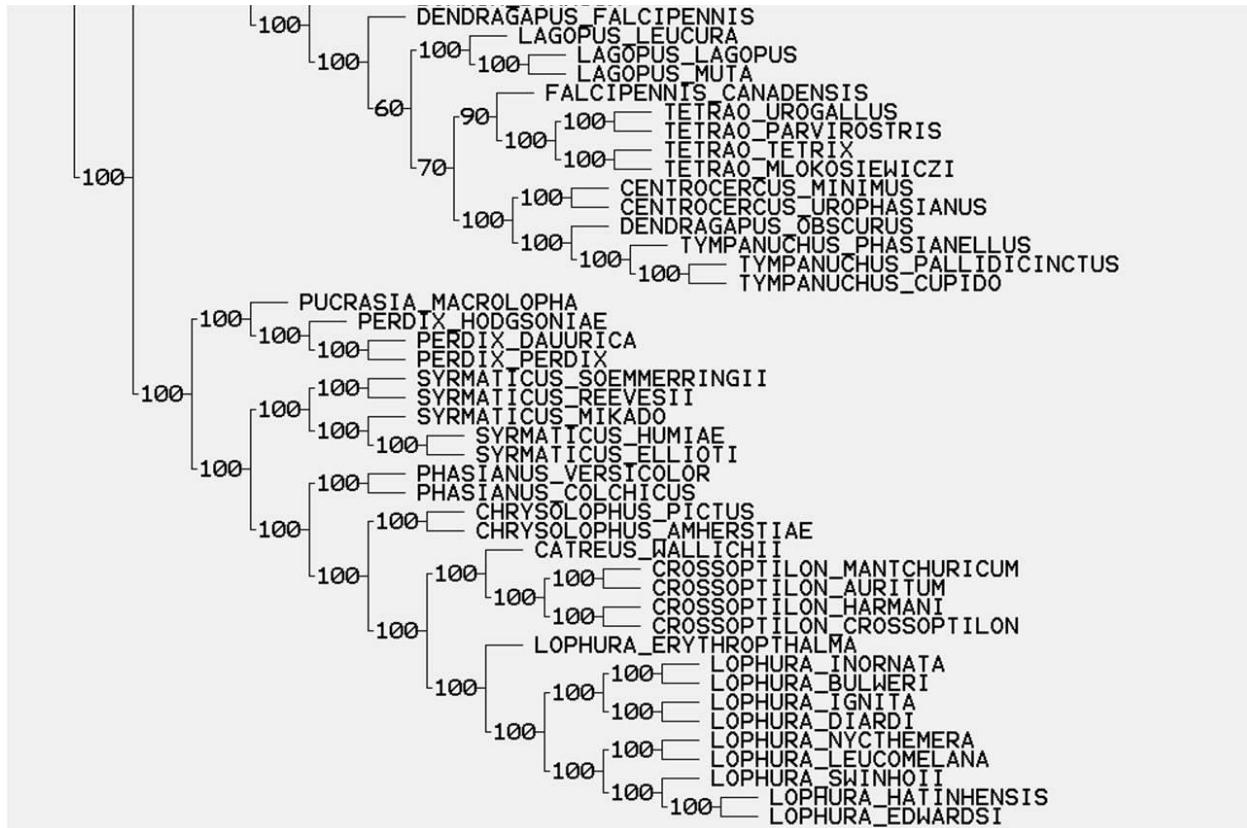


Figure 2. Continued.

Detection of disjunction amongst major galliform groupings

The very first disjunction detected within the galliforms (Fig. 4) is the Wallace line that separates the Megapodes from all other galliform clades. VIP failed to detect further unambiguous disjunctions amongst other major clades. The subsequent split of cracids (Cracidae) from the New World and guineafowls from Africa is ambiguously supported by the data. Evidence for a South America/Africa split was identified in only 30% of all optimal reconstructions (Figure 5.) and when it was supported, different node removals produced different combinations of disjunct distributions. Despite considerable overlap at the Sahel, a split between guineafowls from Africa and the remainder of the galliforms was supported in 71% of reconstructions (Figure 6.). No clear break was detected between New World quails (Odontophoridae) and the phasianids (Phasianidae) and substantial overlap is evident in all reconstructions. Nevertheless, disjunction between these two clades was detected in more than 95% of reconstructions.

Disjunction within the major galliform groupings

A total of 11 disjunctions were identified within the megapode clade and with 79% of nodes displaying vicariance. Considerably less disjunction (59%) was evident for the cracids, with 24 breaks detected. Three of the five nodes within the guineafowl clade demonstrated vicariance whilst the same number of disjunctions were detected for the considerably larger New World quail clade.

The limited disjunction (25%) detected for this clade is most likely as a result of the poor representation of these birds in this study (Table 1). Ninety-six disjunctions were detected for the phasianids, with 67% of nodes displaying vicariance.

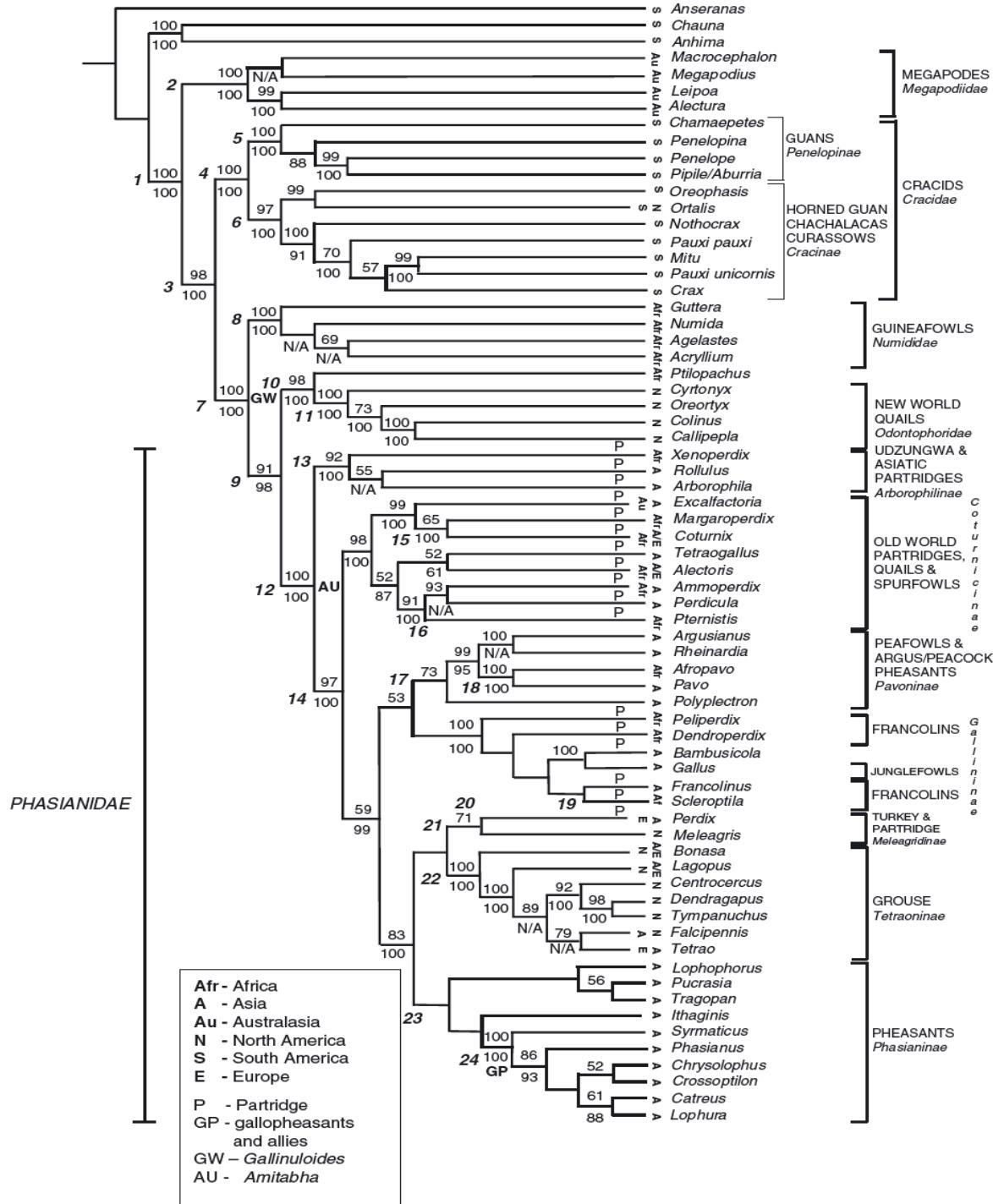


Figure 3. The strict most parsimonious cladogram of gamebird genera resulting from parsimony ratchet analysis from Crowe *et al.* (2006). Numbers in normal text above nodes are jackknife support values. Numbers below are Bayesian posterior probabilities.

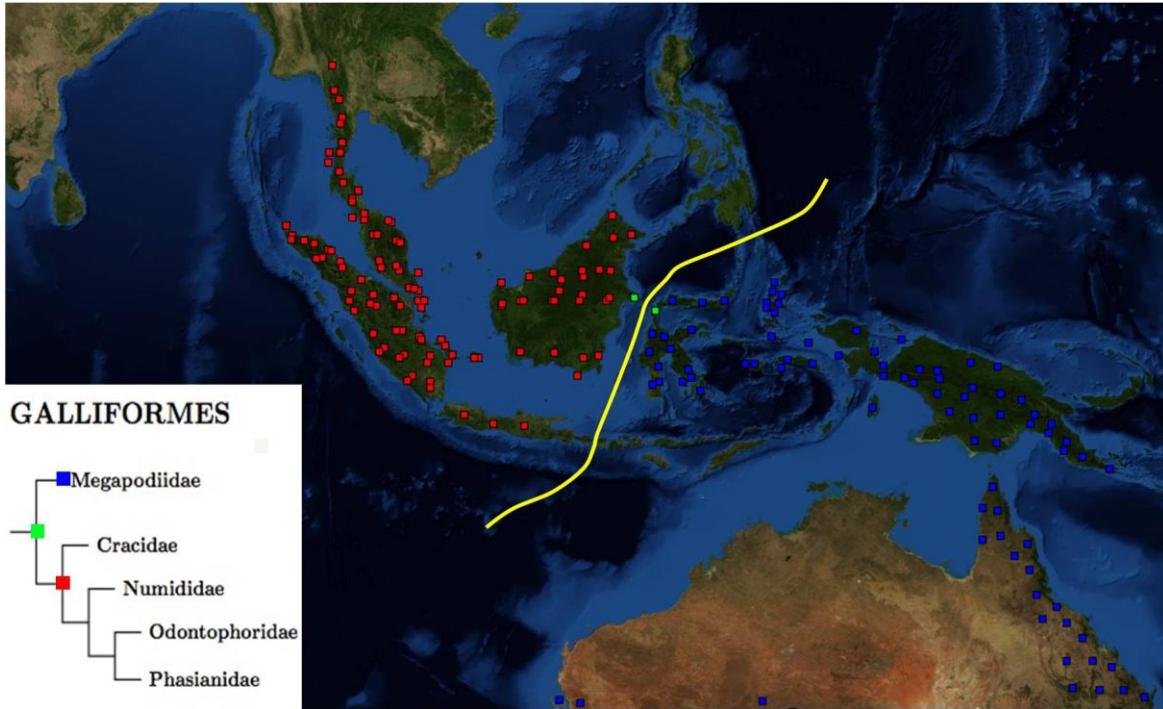


Figure 4. The Wallace Line is identified by VIP as being responsible for the initial disjunction between the megapodes from other gamebird taxa. In a typical VIP map window, the yellow line indicates the barrier detected. Allopatric distributions are displayed using red and blue for each descendant. Overlap between descendants is indicated in green. Without the user defined overlap function in VIP, this clear disjunction would not have been identified.

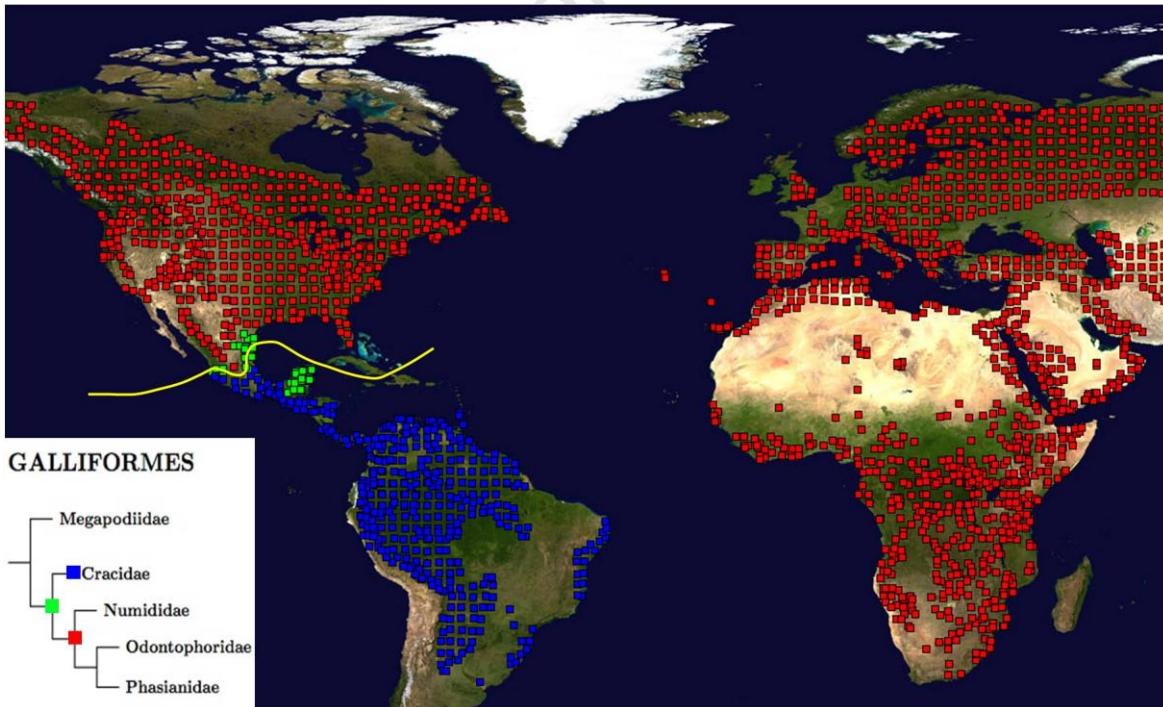


Figure 5. A southern origin for the cracids was supported in only 30% of all optimal reconstructions. When species disperse across barriers involved in their vicariant origin, information about these events is irrecoverably lost.

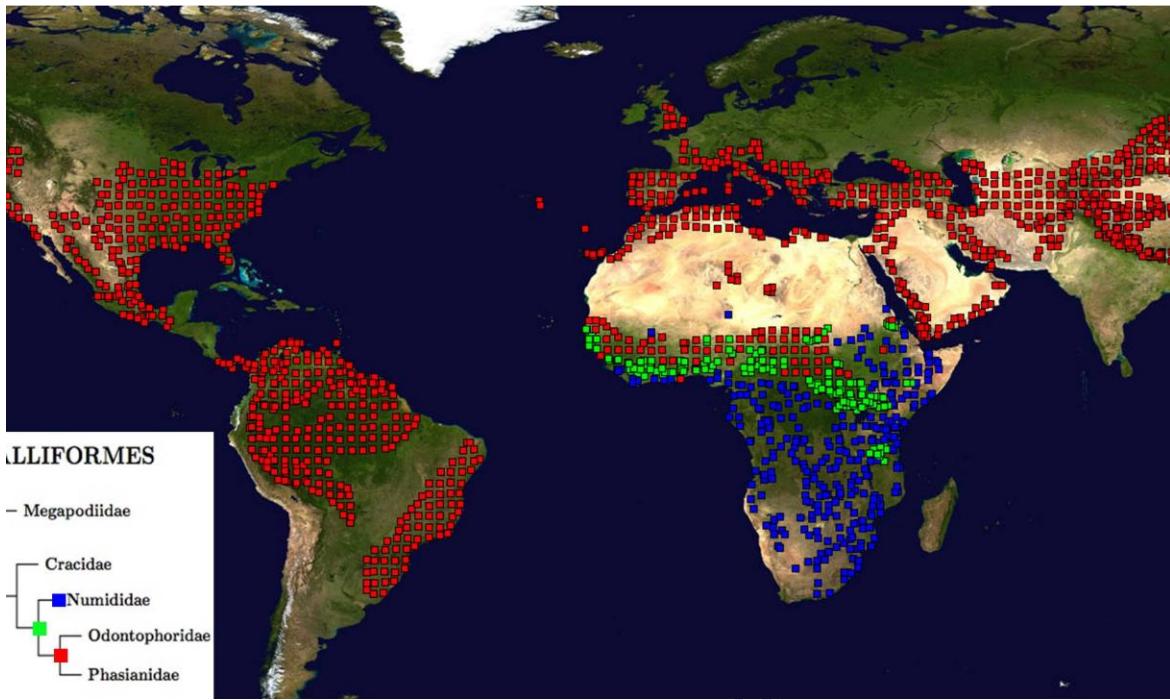


Figure 6. A split between guineafowls and the remainder of galliforms was supported in 71% of reconstructions. The considerable overlap in distributions between guineafowls and other galliforms resulted in the failure of VIP to detect a distinct barrier.

Discussion

Phylogenetics

With the exception of the chachalacas (*Ortalis* spp.) and the grouse (Tetraoninae), all nodes within the majority rules cladogram are fully supported. Apart from these clades and taxa not included in this study, the phylogeny of the galliforms can be considered essentially fully resolved. The weak nodal support and failure to obtain resolution within the chachalacas is most likely due to poor character sampling. Sufficient molecular data has only been collected for two chachalaca species, namely *Ortalis vetula* and *Ortalis canicollis* (Appendix 2.2a-f). The failure to obtain good nodal support with Tetraoninae is perplexing as sufficient molecular data exists for this clade (Appendix 2.2a-f) and radiation within this group does not appear to be recent. Dates of divergence inferred from a galliform relaxed molecular “clock” suggest that the group has been in existence for between 31 to 44 million years (Crowe *et al.* 2006). The use of other markers in future studies may yield greater insights into the evolutionary relationships among the grouse. The phylogenetic analysis performed in this study forms part of another project and will not be discussed further.

Biogeographical origins of the basal clades

Results inferred from analysis in VIP are in agreement with Darlington (1957), Cracraft (2001), Dyke *et al.* (2003) and Crowe *et al.* (2006) who have suggested that the megapodes were present in Australasia from the time of the break-up of Gondwana and probably originated in the Cretaceous. The cladogram produced in the phylogenetic analysis and distribution maps indicate that the basal megapodes all occur within Australia. Additionally, VIP analysis clearly suggests that dispersal to other regions has taken place from south to north.

The subsequent split of cracids (New World) and guineafowls (Africa) is ambiguously supported. This appears to be the effect of the phasianids that are vastly widespread and impair the ability of VIP to identify clear disjunction. Such a result highlights the problems of the intuitive approach of Crowe *et al.* (2006) where this disjunction is taken for granted. Whilst this finding may seem somewhat unencouraging, it is simply not possible to extract information about past vicariance events when no information has survived (Hovenkamp 1997, 2001). These results only partially support the notion of a South American origin for the cracids. Moreover, they are compounded by that fact that phylogenetic analysis and distribution data suggest that many basal cracid species (*Ortalis cinereiceps*, *Oreophasis derbianus* and *Penelopina nigra*) occur in Central America and that most terminal species are located further south. Although VIP hints at a southern origin for the cracids, the biogeographical origin of this group remains unresolved.

Historical biogeography of the megapodes

Rising sea levels during interglacial periods, resulting in the break-up of Meganesia (Australia, Papua New Guinea and Tasmania) (Newton 2003), were most likely responsible for initial speciation within the megapode clade, resulting in much of the generic diversity observed today (*Aepyptodius*, *Talegalla*, *Macrocephalon* and *Eulipoa*). Although estimation of divergence times using a galliform relaxed molecular “clock” suggests that Megapodiidae is a very old family (between 90 and 120MY), much of the diversity within the clade appears to have been generated more recently.

Long distance dispersal has been responsible for producing much of the disjunctions observed between the megapodes. Although it is well known that Megapodes are good over water dispersers (Olson 1980), their dispersal to Indonesian, Melanesian, Micronesian and Polynesian Islands has been greatly assisted by plate tectonics. Meganesia and its associated islands started to approach to islands of the Indian Plate (Borneo, Sumatra, Java etc.) after the K/T extinction event (65 MYA) (Hall 2002). Collision between these two plates took place in the early Miocene (22 MYA) and appears to have enabled megapodes to breach the Wallace line and spread eastwards to Borneo (*Megapodius cumingii*) and northwards to the Philippines (*Megapodius cumingii*), Mariana (*Megapodius laperouse*) and the Andaman Islands (*Megapodius nicobariensis*). This dispersal resulted in isolation of populations and appears to have been followed by allopatric speciation.

The approach of the Melanesian Islands towards Meganesia was initiated later in the Miocene (13 MYA) (Hall 2002) and facilitated the eastward dispersal of the megapodes to Melanesia (*Megapodius eremita*), Vanuatu (*Megapodius layardi*) and Tonga (*Megapodius pritchardii*). The absence of megapodes from islands that lie in-between Australia and the eastern limits of megapode distribution could be explained by extinction following human colonisation of these islands between 2000 and 4000 years ago (Jones *et al.* 1995). This is supported by fossil remains of megapodes that have been discovered on the islands of New Caledonia (*Megapodius molistructor*) (Balouet and Olson 1989), Fiji (*Megapodius* sp.) (Rich and van Tets 1985) and Lifuka (*Megapodius alimentum*) (Steadman 1989).

Analysis in VIP also suggests that, following the colonisation of large island groups (e.g. Moluccas Islands), allopatric speciation amongst widespread ancestors gave rise to species such as *Megapodius forstenii* and *Megapodius freycineti*.

Historical biogeography of the cracids

Riverine barriers have largely been responsible for speciation in the cracids. Distribution data and barriers indicated by analysis in VIP clearly indicate that large South American rivers such as the Amazon, Negro and Madeira rivers constitute boundaries for numerous cracid species (e.g. *Crax globulosa*, *Crax alector* and *Penelope superciliaris*). Hayes and Sewlal 2004 suggest that, although birds could easily traverse these boundaries, large rivers in the Amazon Basin constitute secondary barriers to dispersal. Bird distributions are thought to contract when forests become fragmented during glacial periods. In subsequent interglacial period, distributions then expand until they hit riverine barriers that are now enforced by interspecific competition (Hayes and Sewlal 2004).

Vicariance resulting from the rising of the Andes Mountains (Montgomery *et al.* 2001) has driven much of the recent speciation observed in the cracids. Geological data suggests that the uplift of the northern Andes started in the early Miocene, however this range would only have reached sufficient heights to constitute a barrier to dispersal of birds by the Pliocene (Montgomery *et al.* 2001). The complete lack of resolution observed for the basal chachalacas (Figure. 3) is most likely explained by very recent speciation; with the rise of the Andes separating a once connected population. This vicariant event has contributed to speciation in all three clades within the cracids, with VIP detecting breaks between the chachalacas (*Ortalis cinereiceps* and *Ortalis momot*), the curassows (*Crax rubra* and *Crax rubra*) and the guans (*Penelope purpurascens* and *Penelope superciliaris*). The recent rising of the Andes has additionally created new habitat that has been colonised by the several species of guan (*Chamaepetes goudotii*, *Penelope montagnii* and *Aburria aburri*). The steep environmental gradients created by uplift of the Andes have created diverse habitat zones that have been separately colonised by these species (Delacour and Amadon 1973).

Before the Pliocene closing of the Isthmus of Panama (3.5MYA) (Marshall *et al.* 1979), VIP suggests that there was considerable dispersal by cracids between the North and South American landmasses. Finer analysis of the resulting disjunctions indicates that most basal cracids are found in Central America whilst more terminal taxa are located in South America. These findings are in contradiction with the hypothesis of a southern hemisphere origin for the cracids. However, pre-Andean dispersal events during the warm “Early Eocene Climatic Optimum” (Zachos *et al.* 2001) by basal taxa (*Oreophasis derbianus*, *Penelopina nigra* and *Chamaepetes unicolor*) to montane areas in Central America may be responsible for this pattern. The Amazon was identified as an ecological barrier for cracids that prefer savanna habitat (*Penelope ochrogaster*). In one case, rising sea levels during inter-glacial periods appears to have resulted in the isolation of the island of Trinidad, resulting in allopatric speciation (*Aburria pipile*).

Historical biogeography of the Guineafowl

An African origin for the Guineafowl is ambiguously supported by VIP analysis whilst the suggestion of a mid-Miocene dispersal from Asia (Crowe 1978) to Africa is not supported whatsoever. Phylogenetic analysis and dates of divergence inferred with a calibrated molecular clock (Crowe *et al.* 2006) suggest that the Guineafowl are a relict taxon. However, VIP proposes that recent climate change and the even more recent formation of the Great Rift Valley have contributed to actual forms that are considerably different to the most basal species (*Numida meleagris*). Climatic shifts during Pliocene and Pleistocene glacial and interglacial periods may have resulted in species being isolated in forest refugia (Crowe and Crowe 1982) and consequent allopatric speciation (*Agelastes meleagrides*). The development of the Great Rift Valley in the Pleistocene (Newton 2003) appears to have created a break amongst the most terminal taxa (*Guttera pucherani* and *Guttera plumifera*). Although independent justification is necessary, it appears that ecological speciation in the Guineafowl clade has resulted in a mixture of forest species (*Guttera plumifera*), forest-savanna mosaic species (*Guttera edouardi* and *Guttera pucherani*) and species that reside exclusively in open habitats (*Acryllium vulturinum*).

Historical biogeography of the New World Quails and the Phasianids

Analysis in VIP suggests that New World quails and phasianids have their origins in Africa. As with the more basal galliform clades, their early historical biogeography been influenced by the break-up of Gondwana. In numerous successive phylogenetic splits, a barrier between African and non-African taxa was identified. Moreover, comprehensive phylogenetic analysis firmly places the Guineafowl as basal to these groups. All Guineafowl distributions and disjunctions are located within Africa.

The split between New World Quails and *Ptilopachus* spp. from Africa was first suggested by Crowe *et al.* (2006) and is clearly supported. However, VIP does not provide evidence of a route of dispersal for this event. Date of divergence inferred by Crowe *et al.* 2006 suggest that the split between Guineafowls and New World quails occurred in the late Palaeocene or early Eocene. Although Africa and South America were already well separated by this time, it is plausible that the New World quails may have reached the neotropics by long range dispersal. Pereira and Baker (2006) suggest that this gap may have been traversed by even moderate dispersers. A more likely scenario is that dispersal took place from Africa to North America via the Iberian Peninsula, Britain and across the Atlantic Ocean through Greenland (Crowe *et al.* 2006).

This suggestion is in agreement with the fossil record, earth history and dispersal by other vertebrate groups. Unambiguous gallinuloid fossils have been located in Wyoming (Mayr and Weidig 2004), Nebraska (Crowe and Short 1992), France (Mourer-Chauvire 1992) and Denmark (Lindow and Dyke 2007). Geological data suggests that Europe and North America were connected through a Greenland-Scotland land bridge in the early Eocene (McKenna 1980). This period was additionally characterised by warm temperatures with tropical conditions persisting up to 40° in latitude (Zachos *et al.* 2001; Newton 2003). Considerable dispersal by large terrestrial vertebrates (Gingerich 2003; Rose and Archibald 2005) and plants (Wing *et al.* 2005) into North America has been suggested for this period.

The major split between Africa and southern Asia for the basal phasianids (*Xenoperdix* and *Arborophila*) that was suggested by Crowe *et al.* (2006) is supported by analysis in VIP. This dispersal to Asia is consistent with the Asia-African interchange starting in the late Miocene when a dispersal route opened up due to the junction of Africa and Asia through the Arabian Peninsula (Newton 2003). Dispersal of numerous vertebrate groups during this period was further enhanced by the presence of warm-temperate vegetation on the Arabian Peninsula (Zachos *et al.* 2001).

Barriers detected by VIP and dates of divergence suggested by Crowe *et al.* 2006 suggest that speciation in the true partridges (*Alectoris* spp.) seems to be highly associated with the Zanclean flood in the Miocene (Garcia-Castellanos *et al.* 2009). The barriers detected in VIP and the distributions of these partridges around the Mediterranean coast suggest that speciation in this clade was associated with the filling of the Mediterranean Basin, the opening of Red Sea and the rise of the Alps. The historical biogeography of the francolins (*Pternistis* spp.) and spurfowl (*Scleroptila* spp.) form part of another research project and will not be discussed here.

The break between *Pavo* spp. (Pavioninae) and *Tetrao* spp. (Tetraoninae) could be explained by dispersal over the Himalayas. Inferred dates of divergence (Crowe *et al.* 2006) suggest that vicariance, in the form of the uplift of the Himalayas, is less likely to explain this break. Within the peafowl (*Pavo*) and peacock-pheasant (*Polyplectron*) clade, several disjunctions in Southern Asia can be explained by allopatry due to forest refugia during glacial periods and rising sea level

during interglacials. A dispersal event to Africa, giving rise to *Afropavo* is taken for granted by Crowe *et al.* (2006) whilst analysis in VIP gives only ambiguous support.

The disjunction between the more Tibetan *Tragopan* clade and the more Holarctic *Tetrao* clade, as well as disjunction within these clades, can be explained by glacial refugia. For the remainder of the phasianids, dispersal to the New World (*Falcipennis*) and dispersal to southern Asia (*Lophura*) has resulted in considerable speciation.

Chapter 3

Avenues for future research

Missing taxa

Although this study took into consideration eighty percent of recognized gamebird taxa, a more inclusive analysis will enable greater insights into the historical biogeography of the galliforms. The New World quails were very poorly represented (Table. 2), and interpretation of their historical biogeography was consequently poor. Moreover, species of particular interest with regards to a northern or southern origin for the gamebirds were not represented. No molecular or morphological data is available for the Nicobar Megapode (*Megapodius nicobariensis*). This species resides on Indian Ocean Islands that are distantly removed from all other gamebird taxa. Although classifications based on simple observations suggest that this species is closely related to other terminal megapodes, the phylogenetic placement of this species needs to be established. Should it be found to be basally positioned within the Megapodes, then the southern origin suggested by this analysis can be completely disregarded. If this species is found to be terminal within the megapodes, then this will provide further support for the southern origin of the megapodes.

More characters

Although the phylogeny of the gamebirds is largely resolved, nodal support for the relationships of the grouse (Tetraoninae) is weak and a major polytomy is evident at the base of the chachalaca (*Ortalis*) clade. The low resolution for the chachalacas is most likely explained by very recent speciation and the small number of markers available for these species (Appendix 2.2). Analysis with a greater number of markers may allow for greater resolution and stronger nodal support within this clade. Greater resolution will give critically important insights into the northern or southern hemisphere origin of the cracids. The chachalacas form the basal clade within the cracids. The fact that the phylogenetic relationships of the basal chachalacas are unknown greatly impairs interpretation of the northern or southern origin for the cracids. If future studies reveal that *Ortalis cinereiceps* is the most basal living representative of the cracids, then the spread of chachalacas from north to south is more fully supported. If *Ortalis momot* is found to be more basal, then the spread would appear to be in the other direction.

The low nodal support for the grouse is perplexing as between 8 and 15 markers were analysed for these species. Although the use of different markers is unlikely to improve nodal support, more DNA should be extracted and analysed. The fact that most of these species have widespread and overlapping distributions (Madge and McGowan 2002) suggests that hybridization

may be responsible for the lack of nodal support. Whilst the remaining clades within the galliforms are fully supported (Fig. 2), more than 35% of taxa included in this analysis are represented by less than three molecular markers. The increased availability of markers will contribute to increased confidence in the understanding of the phylogenetic relationships of the galliforms.

Biogeography of the phasianids, the fossil record and distribution data

The phasianids are the most speciose family of gamebirds (Table 2). Their historical biogeography is only briefly investigated in this study and should be the subject of future investigation.

Although distribution data for gamebirds is more comprehensive than in other avian orders, improvement of these records will contribute to improved interpretation of the historical biogeography of the galliforms. Inaccurate and unreliable distribution data often indicates overlap between taxa when in reality there is disjunction. Conversely, these confounding factors may indicate disjunction when there is overlap. This may result in incorrect interpretations of the historical biogeography for gamebirds. Much of the distribution data utilised in this study needs to be updated with improved sampling and greater cohesive effort amongst gamebird researchers. The advent of online GIS databases with reliable distribution data for gamebirds will certainly improve the quality of future systematic and conservation research on the galliforms.

Improved distribution data from less explored and inaccessible portions of Africa, Asia and South America are required. The recent description of two new phasianine species (*Xenoperdix obscurata* and *Xenoperdix udzungwensis*) from remote mountain ranges in Tanzania (Bowie and Fjeldsa 2005) suggests that more species may yet be discovered. These two species have offered indispensable insights into the biogeographical history of the phasianids. Their absence from this analysis would most certainly have resulted in incorrect interpretation of the origin of the phasianines. Areas that are in particular need of sampling include the Amazon and Congo Basins, isolated Pacific Islands, eastern Angola and northern Mozambique.

Future studies on the historical biogeography of the galliforms are likely to be more inclusive, utilise a greater number of molecular markers (and other characters) and will make use of more accurate distribution data. It may however be found that these studies allow for only minor improvements to our current interpretations on the historical biogeography of gamebirds. As Hovenkamp (1997, 2001) suggests, once a species traverses a barrier involved in its vicariant origin, evidence for this vicariant event is lost. More valuable information may come from new fossil findings. The complete lack of cracid fossils in South America and the presence of only Pleistocene megapode fossils in Australasia is perplexing and contradicts the southern origin of gamebirds suggested by this analysis. A concerted effort should be made to improve on the fossil record for galliforms in these regions.

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Appendix 1

Outgroup and gamebird taxa investigated in this research.

Struthioniformes	
<i>Struthio camelus</i>	ostrich
<i>Rhea americana</i>	greater rhea
Tinamiformes	
<i>Tinamus major</i>	great tinamou
<i>Tinamus guttatus</i>	white-throated tinamou
Anseriformes	
<i>Anseranas semipalmata</i>	magpie goose
<i>Chauna torquata</i>	southern screamer
<i>Anhima cornuta</i>	horned screamer
<i>Cairina moschata</i>	muscovy duck
<i>Anas platyrhynchos</i>	mallard
Galliformes	
Megapodiidae	
<i>Leipoa ocellata</i>	malleefowl
<i>Talegalla fuscirostris</i>	black-billed talegalla
<i>Aepypodius arfakianus</i>	wattled brush-turkey
<i>Alectura lathami</i>	Australian brush-turkey
<i>Macrocephalon maleo</i>	maleo
<i>Eulipoa wallacei</i>	Moluccan megapode
<i>Megapodius tenimberensis</i>	Tunimbar megapode
<i>Megapodius cumingii</i>	Philippine megapode
<i>Megapodius pritchardii</i>	Polynesian megapode
<i>Megapodius layardi</i>	Vanuatu megapode
<i>Megapodius reinwardt</i>	orange-footed scrubfowl
<i>Megapodius eremita</i>	Melanesian scrubfowl
<i>Megapodius decollatus</i>	New Guinea megapode
<i>Megapodius forstenii</i>	Forsten's megapode
<i>Megapodius freycinet</i>	dusky scrubfowl
Cracidae	
<i>Ortalis cinereiceps</i>	grey-headed chachalaca
<i>Ortalis motmot</i>	little chachalaca
<i>Ortalis vetula</i>	plain chachalaca
<i>Ortalis leucogastra</i>	white-bellied chachalaca
<i>Ortalis poliocephala</i>	west Mexican chachalaca
<i>Ortalis canicollis</i>	chaco chachalaca
<i>Ortalis guttata</i>	speckled chachalaca
<i>Ortalis ruficauda</i>	rufous-vented chachalaca
<i>Ortalis garrula</i>	chestnut-winged chachalaca
<i>Oreophasis derbianus</i>	horned guan
<i>Nothocrax urumutum</i>	nocturnal curassow
<i>Pauxi pauxi</i>	northern helmeted curassow
<i>Pauxi gilliardi</i>	northern helmeted curassow
<i>Mitu tomentosa</i>	crestless curassow
<i>Mitu mitu</i>	Alagoas curassow
<i>Mitu salvini</i>	Salvin's curassow
<i>Pauxi unicornis</i>	horned curassow
<i>Mitu tuberosa</i>	razor-billed curassow
<i>Crax rubra</i>	great curassow
<i>Crax globulosa</i>	wattled curassow
<i>Crax blumenbachii</i>	red-billed curassow

<i>Crax daubentoni</i>	yellow-knobbed curassow
<i>Crax alberti</i>	blue-billed curassow
<i>Crax fasciolata</i>	bare-faced curassow
<i>Crax alector</i>	black curassow
<i>Penelopina nigra</i>	highland guan
<i>Chamaepetes unicolor</i>	black guan
<i>Chamaepetes goudotii</i>	sickle-winged guan
<i>Penelope montagnii</i>	Andean guan
<i>Penelope argyrotis</i>	band-tailed guan
<i>Penelope ochrogaster</i>	chestnut-bellied guan
<i>Penelope obscura</i>	dusky-legged guan
<i>Penelope jacquacu</i>	Spix's guan
<i>Penelope superciliaris</i>	rusty-margined guan
<i>Penelope purpurascens</i>	crested guan
<i>Pipile jacutinga</i>	black-fronted piping-guan
<i>Aburria aburri</i>	wattled guan
<i>Pipile cujubi</i>	red-throated piping-guan
<i>Pipile pipile</i>	Trinidad piping-guan
<i>Pipile grayi</i>	gray's piping-guan
<i>Pipile nattereri</i>	red-throated piping-guan
<i>Pipile curumanensis</i>	blue-throated piping-guan
Numididae	
<i>Numida meleagris</i>	helmeted guineafowl
<i>Agelastes meleagrides</i>	white-breasted guineafowl
<i>Acryllium vulturinum</i>	vulturine guineafowl
<i>Guttera edouardi</i>	southern crested guineafowl
<i>Guttera pucherani</i>	northern crested guineafowl
<i>Guttera plumifera</i>	plumed guineafowl
Odontophoridae	
<i>Ptilopachus petrosus</i>	stone partridge
<i>Ptilopachus nahani</i>	Nahan's francolin
<i>Cyrtonyx montezumae</i>	Montezuma quail
<i>Odontophorus speciosus</i>	rufous-breasted wood-quail
<i>Odontophorus gujanensis</i>	marbled wood-quail
<i>Odontophorus capueira</i>	spot-winged wood-quail
<i>Oreortyx pictus</i>	mountain quail
<i>Colinus cristatus</i>	crested bobwhite
<i>Colinus virginianus</i>	northern bobwhite
<i>Callipepla douglasii</i>	elegant quail
<i>Callipepla squamata</i>	scaled quail
<i>Callipepla gambelii</i>	Gambel's quail
<i>Callipepla californica</i>	California quail
Phasianidae	
<i>Xenoperdix obscurata</i>	Rubeho forest partridge
<i>Xenoperdix udzungwensis</i>	Udzunga partridge
<i>Arborophila rufipectus</i>	Sichuan hill-partridge
<i>Caloperdix oculeus</i>	Ferruginous partridge
<i>Rollulus rouloul</i>	crested partridge
<i>Arborophila torqueola</i>	necklaced hill-partridge
<i>Arborophila javanica</i>	Javan hill-partridge
<i>Tetraogallus tibetanus</i>	Tibetan snowcock
<i>Tetraogallus himalayensis</i>	Himalayan snowcock
<i>Tetraogallus altaicus</i>	Altai snowcock
<i>Alectoris melanocephala</i>	Arabian partridge
<i>Alectoris barbara</i>	Barbary partridge
<i>Alectoris rufa</i>	red-legged partridge

<i>Alectoris graeca</i>	rock partridge
<i>Alectoris chukar</i>	chukar
<i>Alectoris philbyi</i>	Philby's partridge
<i>Alectoris magna</i>	Przevalski's partridge
<i>Coturnix ypsiloniphora</i>	brown quail
<i>Excalfactoria chinensis</i>	king quail
<i>Coturnix pectoralis</i>	stubble quail
<i>Coturnix novaezelandiae</i>	New Zealand quail
<i>Margaroperdix madagarensis</i>	Madagascar partridge
<i>Coturnix japonica</i>	Japanese quail
<i>Coturnix coturnix</i>	common quail
<i>Perdicula asiatica</i>	jungle Bush-quail
<i>Ammoperdix heyi</i>	sand partridge
<i>Pternistis hartlaubi hartlaubi</i>	Hartlaub's francolin
<i>Pternistis camerunensis</i>	Mount Cameroon francolin
<i>Pternistis nobilis</i>	handsome francolin
<i>Pternistis castaneicollis castaneicollis</i>	chesnut-naped francolin
<i>Pternistis ochropectus</i>	Djibouti francolin
<i>Pternistis erckelii</i>	Erckel's francolin
<i>Pternistis swierstrai</i>	Swierstra's francolin
<i>Pternistis jacksoni</i>	Jackson's francolin
<i>Pternistis squamatus squamatus</i>	scaly francolin
<i>Pternistis icterorhynchus</i>	Heuglin's francolin
<i>Pternistis bicalcaratus ayesha</i>	double-spurred francolin
<i>Pternistis bicalcaratus bicalcaratus</i>	double-spurred francolin
<i>Pternistis griseostriatus</i>	grey-striped francolin
<i>Pternistis adspersus</i>	red-billed francolin
<i>Pternistis capensis</i>	Cape francolin
<i>Pternistis hildebrandti hildebrandti</i>	Hildebrandt's francolin
<i>Pternistis natalensis</i>	Natal francolin
<i>Pternistis clappertoni clappertoni</i>	Clapperton's francolin
<i>Pternistis hildebrandti johnstoni</i>	Hildebrandt's francolin
<i>Pternistis clappertoni sharpii</i>	Clapperton's francolin
<i>Pternistis harwoodi</i>	Harwood's francolin
<i>Pternistis leucoscepus infuscatus</i>	yellow-necked francolin
<i>Pternistis swainsonii swainsonii</i>	Swainson's francolin
<i>Pternistis leucoscepus leucoscepus</i>	yellow-necked francolin
<i>Pternistis cranchii cranchii</i>	bare-throated francolin
<i>Pternistis rufopictus</i>	grey-breasted francolin
<i>Pternistis afer humboldti</i>	red-necked francolin
<i>Pternistis afer SA</i>	red-necked francolin
<i>Francolinus pintadeanus</i>	Chinese francolin
<i>Francolinus pictus</i>	painted francolin
<i>Francolinus francolinus</i>	black francolin
<i>Bambusicola thoracica</i>	Chinese bamboo partridge
<i>Bambusicola fytchii</i>	mountain bamboo partridge
<i>Gallus lafayettei</i>	Sri Lanka junglefowl
<i>Gallus varius</i>	green junglefowl
<i>Gallus sonneratii</i>	grey junglefowl
<i>Gallus gallus</i>	red junglefowl
<i>Francolinus pondicerianus</i>	grey francolin
<i>Francolinus gularis</i>	swamp francolin
<i>Dendroperdix sephaena SA</i>	crested francolin
<i>Dendroperdix sephaena rovuma</i>	crested francolin
<i>Dendroperdix sephaena grantii</i>	crested francolin
<i>Francolinus lathami schubotzi</i>	forest francolin

<i>Francolinus lathami</i>	forest francolin
<i>Peliperdix schlegelii</i>	Schlegel's francolin
<i>Peliperdix albogularis meinertzhageni</i>	white-throated francolin
<i>Peliperdix albogularis buckleyi</i>	white-throated francolin
<i>Peliperdix albogularis albogularis</i>	white-throated francolin
<i>Peliperdix coqui stuhlmanni</i>	Coqui francolin
<i>Peliperdix coqui kasaicus</i>	Coqui francolin
<i>Peliperdix coqui hubbardi</i>	Coqui francolin
<i>Peliperdix coqui maharao</i>	Coqui francolin
<i>Peliperdix coqui spinetorum</i>	Coqui francolin
<i>Peliperdix coqui coqui</i>	Coqui francolin
<i>Peliperdix coqui vernayi</i>	Coqui francolin
<i>Peliperdix coqui ruahdae</i>	Coqui francolin
<i>Scleroptila streptophorus</i>	ring-necked francolin
<i>Scleroptila levaillantii</i>	redwing francolin
<i>Scleroptila finschi</i>	Finsch's francolin
<i>Scleroptila whytei</i>	Shelley's francolin
<i>Scleroptila psilolaemus theresae</i>	moorland francolin
<i>Scleroptila psilolaemus</i>	moorland francolin
<i>Scleroptila uluensis</i>	Shelley's francolin
<i>Scleroptila gutturalis</i>	Orange River francolin
<i>Scleroptila shelleyi SA</i>	Shelley's francolin
<i>Scleroptila jugularis</i>	Orange River francolin
<i>Scleroptila levaillantoides</i>	Orange River francolin
<i>Scleroptila africanus</i>	greywing francolin
<i>Scleroptila levaillantoides pallidior</i>	Orange River francolin
<i>Scleroptila ellenbecki</i>	moorland francolin
<i>Scleroptila levaillantii kikuyuensis</i>	redwing francolin
<i>Scleroptila levaillantii crawshayi</i>	redwing francolin
<i>Rheinardia ocellata</i>	crested argus
<i>Argusianus argus</i>	great argus
<i>Afropavo congensis</i>	Congo peafowl
<i>Pavo muticus</i>	green peafowl
<i>Pavo cristatus</i>	Indian peafowl
<i>Haematortyx sanguiniceps</i>	crimson-headed partridge
<i>Galloperdix lunulata</i>	painted spurfowl
<i>Polyplectron napoleonis</i>	Palwan peacock-pheasant
<i>Polyplectron schleiermachi</i>	Bornean peacock-pheasant
<i>Polyplectron malacense</i>	Malayan peacock-pheasant
<i>Polyplectron germaini</i>	Germain's peacock-pheasant
<i>Polyplectron inopinatum</i>	mountain peacock-pheasant
<i>Polyplectron chalcurum</i>	Sumatran peacock-pheasant
<i>Polyplectron bicalcaratum</i>	grey peacock-pheasant
<i>Ithaginus cruentus</i>	blood pheasant
<i>Tragopan blythii</i>	Blyth's tragopan
<i>Tragopan caboti</i>	Cabot's tragopan
<i>Tragopan temminckii</i>	Temminck's tragopan
<i>Tragopan satyra</i>	Satyr tragopan
<i>Tetraophasis szechenyii</i>	Szechenyi's monal-partridge
<i>Tetraophasis obscurus</i>	Verreaux's monal-partridge
<i>Lophophorus ihuysii</i>	Chinese monal
<i>Lophophorus sclateri</i>	Sclater's monal
<i>Lophophorus impejanus</i>	Himalayan monal
<i>Meleagris ocellata</i>	ocellated turkey
<i>Meleagris gallopavo</i>	wild turkey
<i>Bonasa umbellus</i>	ruffed grouse

<i>Bonasa sewerzowi</i>	Severtzov's grouse
<i>Bonasa bonasia</i>	hazel grouse
<i>Lagopus leucura</i>	white-tailed ptarmigan
<i>Lagopus lagopus</i>	willow ptarmigan
<i>Lagopus muta</i>	rock ptarmigan
<i>Dendragapus falcipennis</i>	Siberian spruce grouse
<i>Falcipennis canadensis</i>	American spruce grouse
<i>Tetrao urogallus</i>	western capercaillie
<i>Tetrao parvirostris</i>	black-billed capercaillie
<i>Tetrao tetrix</i>	black grouse
<i>Tetrao mlokosiewiczi</i>	Caucasian grouse
<i>Centrocercus minimus</i>	Gunnison grouse
<i>Centrocercus urophasianus</i>	sage grouse
<i>Dendragapus obscurus</i>	dusky grouse
<i>Tympanuchus phasianellus</i>	sharp-tailed grouse
<i>Tympanuchus pallidicinctus</i>	lesser Prairie chicken
<i>Tympanuchus cupido</i>	greater Prairie chicken
<i>Pucrasia macrolopha</i>	koklass
<i>Perdix hodgsoniae</i>	Tibetan partridge
<i>Perdix daurica</i>	Daurian partridge
<i>Perdix perdix</i>	grey partridge
<i>Syrmaticus soemmerringi</i>	copper pheasant
<i>Syrmaticus reevesii</i>	Reeves's pheasant
<i>Syrmaticus mikado</i>	Mikado pheasant
<i>Syrmaticus humiae</i>	Hume's pheasant
<i>Syrmaticus ellioti</i>	Elliot's pheasant
<i>Phasianus versicolor</i>	green pheasant
<i>Phasianus colchicus</i>	common pheasant
<i>Chrysolophus pictus</i>	golden pheasant
<i>Chrysolophus amherstiae</i>	Lady Amherst's pheasant
<i>Catreus wallichii</i>	cheer pheasant
<i>Crossoptilon mantchuricum</i>	brown eared- pheasant
<i>Crossoptilon auritum</i>	blue eared – pheasant
<i>Crossoptilon harmani</i>	Tibetan eared - pheasant
<i>Crossoptilon crossoptilon</i>	white eared - pheasant
<i>Lophura erythrophthalma</i>	crestless fireback
<i>Lophura inornata</i>	Salvadori's fireback
<i>Lophura bulweri</i>	Bulwer's pheasant
<i>Lophura ignita</i>	crested fireback
<i>Lophura diardi</i>	Siamese pheasant
<i>Lophura nycthemera</i>	silver pheasant
<i>Lophura swinhoii</i>	Kalij pheasant
<i>Lophura hatinhensis</i>	Swinhoe's pheasant
<i>Lophura edwardsi</i>	Vietnamese pheasant

Appendix 2.1

Acronyms and full names of molecular markers for which DNA sequences were analyzed in this study

Acronym	Full name
12S	12S ribosomal RNA
16S	16S ribosomal RNA
COI	cytochrome oxidase subunit I
COII	cytochrome oxidase subunit II
COIII	cytochrome oxidase subunit III
CR	D-loop
CYTb	cytochrome b (cytb) gene
ND1	NADH dehydrogenase subunit 1
ND2	NADH dehydrogenase subunit 2
ND3	NADH dehydrogenase subunit 3
ND4	NADH dehydrogenase subunit 4
ND5	NADH dehydrogenase subunit 5
ND6	NADH dehydrogenase subunit 6
AG3	aggrecan gene
AGC1	AGC1-like sequence
AGRP	agouti-related protein mRNA
ALDOB_exon	aldolase B fructose-bisphosphate (ALDOB) gene
ALDOB_UTR	aldolase B fructose-bisphosphate (ALDOB) gene, 3' UTR
ASW	avian sex-specific W-linked protein gene
BDNF	brain-derived neurotrophic factor gene
BFIB/Beta-fib	beta-fibrinogen (beta-fib) gene
CALB / Calbindin	calbindin gene
CLTC	clathrin heavy chain gene
C-MOS	c-mos (c-mos) gene
CRYAA_exon	crystallin alpha A gene, exons
CRYAA_intron2	crystallin alpha A (CRYAA) gene, intron 2
CRYAA_UTR	crystallin alpha A (CRYAA) gene, 3' UTR
DCoH	dimerization cofactor of hepatocyte nuclear factor 1 gene
EEF2_exon	eukaryotic translation elongation factor 2 gene
EEF2_UTR	eukaryotic translation elongation factor 2 (EEF2) gene, 3' UTR
EGR1	early growth response 1 gene
FGB	fibrinogen beta chain gene
G3PDH	glyceraldehyde-3-phosphate dehydrogenase gene
GH1	growth hormone 1 gene
HMGN2_exon	nonhistone chromosomal protein HMG-17 gene, exons
HMGN2_UTR	nonhistone chromosomal protein HMG-17 gene, 3' UTR
IRF2	interferon regulatory factor 2 gene
MB	myoglobin gene
MC1R	melanocortin-1 receptor gene
MUSK	muscle skeletal receptor tyrosine kinase gene
MYC	v-myc myelocytomatosis viral oncogene-like protein gene

NGF	nerve growth factor beta polypeptide gene
NTF3	neurotrophin 3 gene
OVO-G	ovomucoid gene, intron G
PCBD1	pterin-4 alpha-carbinolamine dehydratase gene
RAG1	recombination activating protein gene
RAG2	recombination activating protein gene
RDP1 EX	isolate cons.mfr. rhodopsin gene, exons
RDP1 INT	isolate cons.mfr. rhodopsin gene, intron
RHO	rhodopsin gene
TGFB2	transforming growth factor beta 2 gene
TPM1	tropomyosin 1 alpha gene
TYR	tyrosinase (TYR) gene
TYRP1	tyrosinase related protein 1 gene
DCT/TYRP2	dopachrome tautomerase/tyrosinase related protein 2 gene
WPG	WPG pseudogene

Appendix 2.2a

GenBank numbers and the amounts of DNA sequence data used for 9 of the 13 mitochondrial utilised in the phylogenetic analysis. (- = no sequence). Refer to Appendix 2.1 for the full names of the molecular markers. Numbers in parenthesis indicate the number of markers used for that particular taxon in the final analysis.

Marker Taxon no. bases	12S 118754	16S 59 2258	COI 84 1203	COII 45 687	COIII 54 184	CR 155 1032	CYTB 279 1143	ND1 35 976	ND2 170 1041
<i>Struthio camelus</i> (30)	NC002785	NC002785	NC002785	NC002785	NC002785		NC002785	NC002785	NC002785
<i>Rhea americana</i> (30)	NC000846	NC000846	NC000846	NC000846	NC000846		NC000846	NC000846	NC000846
<i>Tinamus major/guttatus</i> (16)	NC002781	NC002781	NC002781	NC002781	NC002781		NC002781	NC002781	NC002781
<i>Anhima cornuta</i> (11)	NC005933	NC005933	NC005933	NC005933	NC005933		NC005933	NC005933	NC005933
<i>Chauna torquata</i> (30)	NC009684	NC009684	NC009684	NC009684	NC009684		NC009684	NC009684	NC009684
<i>Anseranas semipalmata</i> (30)	NC010965	NC010965	NC010965	NC010965	NC010965		NC010965	NC010965	NC010965
<i>Anas platyrhynchos</i> (31)	U83728		AY140729	AY140731	AY140733		AY140735		AY140737
<i>Cairina moschata</i> (13)	AY140700		AY140730	AY140732	AY140734		AY140736	AY274053	AY140738
<i>Leipoa ocellata</i> (18)									AF394617
<i>Talegalla fuscirostris</i> (2)	NC002227	NC002227	NC002227	NC007227	NC002227	NC002227	NC007227	NC007227	NC007227
<i>Aepyornis arfakianus</i> (6)									AF394623
<i>Alectura lathami</i> (39)	AF222586						AM236879		AF394619
<i>Macrocephalon maleo</i> (3)							AM236881		AF394621
<i>Eulipoa wallacei</i> (2)									AF394624
<i>Megapodius tenimberensis</i> (3)									AF394625
<i>Megapodius cumingii</i> (1)	AY274005						AF082065	AY274052	AY274052
<i>Megapodius pritchardii</i> (2)									AF394630
<i>Megapodius layardi</i> (16)						DQ834464	AM236880		AF394631
<i>Megapodius reinwardt</i> (13)	AY952761						AY952696		AF394635
<i>Megapodius eremita</i> (25)									AF394636
<i>Megapodius decollatus</i> (1)	AF165441	AF165453	AF165489	AF165501	AF165477		AF165465		AF140739
<i>Megapodius forstenii</i> (1)									AF394637
<i>Megapodius freycinet</i> (5)									AF394620
<i>Ornithodoros cinereiceps</i> (3)	AF165442	AF165454	AF165490	AF165502	AF165480	AF165430	AF165466		AY140740
<i>Ornithodoros motmot</i> (1)	AF165443	AF165455	AF165491	AF165503	AF165481	AF165434	AF165467		AY140741
<i>Ornithodoros vetula</i> (14)							AY659796		
<i>Ornithodoros leucogastra</i> (1)			AY141910		AY141900	AY145304	AY659794		AY141930
<i>Ornithodoros poliocephala</i> (1)			AY141911		AY141901	AY145315	AY141921		AY141931
<i>Ornithodoros canicollis</i> (14)	AF165444	AF165456	AF165492	AF165504	AF165482	AF165438	AY659791		AY140747
<i>Ornithodoros guttata</i> (3)			AY141912		AY141902	AY145305	AY141922		AY141932
<i>Ornithodoros ruficauda</i> (1)							AF106496		
<i>Ornithodoros garrula</i> (1)			AY141913		AY141903	AY145306	AY141923		AY141933
<i>Oreophasis derbianus</i> (13)			AY141914		AY141904	AY145316	AY141924		AY141934
<i>Nothocrax urumutum</i> (14)	AY274003		AY141915		AY141905	AY145307	AY956378	AY274050	AY141935
<i>Pauxi pauxi</i> (15)							AF106499		
<i>Pauxi gilliardi</i> (1)			AY141916		AY141906	AY145308	AY141926		AY141936
<i>Mitu tomentosa</i> (6)	NC002785	NC002785	NC002785	NC002785	NC002785		NC002785	NC002785	NC002785
<i>Mitu mitu</i> (6)	NC000846	NC000846	NC000846	NC000846	NC000846		NC000846	NC000846	NC000846
<i>Mitu salvani</i> (6)			AY141917		AY141907	AY145309	AY141927		AY141937
<i>Pauxi unicornis</i> (6)			AY141919		AY141909	AY145317	AY141929		AY141939
<i>Mitu tuberosa</i> (14)	AF165445	AF165457	EU525439	AF165505	AF165483	AF165437	AF165469		AY140748
<i>Crax rubra</i> (23)	AY274003		AY141915		AY141905	AY145307	AY956378	AY274050	AY141935

Appendix 2.2a (continued)

Marker Taxon no. bases	12S 118754	16S 59 2258	COI 84 1203	COII 45 687	COIII 54 184	CR 155 1032	CYTB 279 1143	ND1 35 976	ND2 170 1041
<i>Crax globulosa</i> (6)			AY141914		AY141904	AY145316	AY141924		AY141934
<i>Crax blumenbachii</i> (14)	AF165444	AF165456	AF165492	AF165504	AF165482	AF165438	AY659791		AY140747
<i>Crax daubentoni</i> (6)			AY141912		AY141902	AY145305	AY141922		AY141932
<i>Crax alberti</i> (6)			AY141910		AY141900	AY145304	AY659794		AY141930
<i>Crax fasciolata</i> (6)			AY141913		AY141903	AY145306	AY141923		AY141933
<i>Crax alector</i> (31)			AY141911		AY141901	AY145315	AY141921		AY141931
<i>Penelopina nigra</i> (15)	AF165451	AF165463	AF165499	AF165511	AF165487	AF165433	AF165475		AY140743
<i>Chamaepetes unicolor</i> (1)							AY659796		
<i>Chamaepetes goudotii</i> (14)	AF165443	AF165455	AF165491	AF165503	AF165481	AF165434	AF165467		AY140741
<i>Penelope montagnii</i> (1)							AY659802		
<i>Penelope argyrotis</i> (1)							AY659803		
<i>Penelope ochrogaster</i> (3)						AY145311	AY367101		AY367089
<i>Penelope obscura</i> (14)	AF165450	AF165462	AF165498	AF165510	AF165486	AF165432	AF165474		AY140742
<i>Penelope jacquacu</i> (2)						AY145318	AY659801		
<i>Penelope superciliaris</i> (3)						AY145313	AY367102		AY367090
<i>Penelope purpurascens</i> (3)						AY145312	AY659800		AY367091
<i>Pipile jacutinga</i> (14)	AF165452	AF165464	AF165500	AF165512	AF165488	AF165431	AF165476		AY140744
<i>Aburria aburri</i> (14)	AF165442	AF165454	AF165490	AF165502	AF165480	AF165430	AF165466		AY140740
<i>Pipile cujubi</i> (3)						AY145314	AY367104		AY367092
<i>Pipile pipile</i> (3)						AY145320	AY367106		AY367094
<i>Pipile grayi</i> (2)							AY659797		
<i>Pipile nattereri</i> (1)							AY354490		
<i>Pipile cumanensis</i> (3)						AY145319	AY367105		AY367093
<i>Numida meleagris</i> (49)	NC006382	NC006382	NC006382	NC006382	NC006382	DQ834466	L08383	NC006382	NC006382
<i>Agelastes meleagrides</i> (1)							AM236884		
<i>Acryllium vulturinum</i> (12)	AF536739						AF536742	AF536745	AF536745
<i>Guttera edouardi</i> (1)							Unpub.		
<i>Guttera pucherani</i> (18)	AY952763						AM236882		AY952747
<i>Guttera plumifera</i> (1)							AM236883		
<i>Ptilopachus petrosus</i> (6)	FR691544					FR691375	AM236886		AM236886
<i>Ptilopachus nahani</i> (6)	FR691545					FR691374	AM236885		AM236885
<i>Cyrtonyx montezumae</i> (19)	AY952764					DQ834467	AF068192		AF068192
<i>Odontophorus speciosus</i> (6)	FR691561					FR691373	FR694138		FR694138
<i>Odontophorus gujanensis</i> (6)	FR691562					FR691372	FR694137		FR694137
<i>Odontophorus capueira</i> (6)	FR691563					FR691371	FR694136		FR694136
<i>Oreortyx pictus</i> (20)	AY952765		DQ433856			DQ834468	AF252860		AF252860
<i>Colinus cristatus</i> (20)	AF222575								AF222544
<i>Colinus virginianus</i> (15)	AF222576		DQ433524			DQ834469	EU372675	EU166949	EU166949
<i>Callipepla douglasii</i> (3)						DQ834470	AF028750		AF028750
<i>Callipepla squamata</i> (4)			DQ432806			DQ834471	AF028753		AF028753
<i>Callipepla gambelii</i> (8)	DQ485791	DQ485829	DQ433416			DQ834472	L08382		AF028761
<i>Callipepla californica</i> (6)			FJ027272			DQ834473	AB120131		AB120131
<i>Xenoperdix obscurata</i> (1)									SEQQQ
<i>Xenoperdix udzungwensis</i> (5)	DQ832096					DQ834474	AM236887		AM236887
<i>Arborophila rufipectus</i> (13)	NC012453	NC012453	NC012453	NC012453	NC012453	NC012453	NC012453	NC012453	DQ093800
<i>Caloperdix oculeus</i> (1)							EF620768		EF620768

Appendix 2.2a (continued)

Marker Taxon no. bases	12S 118754	16S 59 2258	COI 84 1203	COII 45 687	COIII 54 184	CR 155 1032	CYTB 279 1143	ND1 35 976	ND2 170 1041
<i>Rollulus rouloul</i> (28)							AM236888		
<i>Arborophila torqueola</i> (2)						DQ834475	AM236889		
<i>Arborophila javanica</i> (6)		DQ832097				Unpub.	AM236880		DQ093804
<i>Tetraogallus tibetanus</i> (3)						GQ343551	EU839456		EU845747
<i>Tetraogallus himalayensis</i> (3)						DQ834520	AY678108		EU845750
<i>Tetraogallus altaicus</i> (2)				GQ482760			AY563127		
<i>Alectoris melanocephala</i> (2)						DQ834521	Z48773		
<i>Alectoris barbara</i> (3)	AM944502					DQ834522	Z48771		
<i>Alectoris rufa</i> (14)	FN675611					DQ834523	Z48775		
<i>Alectoris graeca</i> (2)						DQ834524	Z48772		
<i>Alectoris chukar</i> (17)	FR691558	FJ465186	GQ481315			DQ834525	L08378		DQ768273
<i>Alectoris philbyi</i> (3)						DQ834526	Z48774		
<i>Alectoris magna</i> (3)						DQ834527	Z48776		EU845744
<i>Coturnix ypsilophora</i> (5)	AF222574		GQ150384				GQ150393		AF222543
<i>Excalfactoria chinensis</i> (14)	NC004575	NC004575	NC004575	NC004575	NC004575	NC004575	NC004575	NC004575	NC004575
<i>Coturnix pectoralis</i> (3)			GQ150379				GQ150389		
<i>Coturnix novaezelandiae</i> (2)			GQ150381				GQ150391		
<i>Margaroperdix madagarensis</i> (2)						DQ834528	U90640		
<i>Coturnix japonica</i> (29)	NC003408	NC003408	GQ481652	NC003408	NC003408	NC003408	NC003408	NC003408	NC003408
<i>Coturnix coturnix</i> (33)	X57245	AF302070	GQ481648			DQ834529	L08377		EU845745
<i>Perdicula asiatica</i> (2)						DQ834530	AM236902		
<i>Ammoperdix heyi</i> (1)							AM236901		
<i>Pternistis hartlaubi hartlaubi</i> (6)	FR691555					FR716656	FR691618		FR691572
<i>Pternistis camerunensis</i> (6)	FR691552					FR691382	FR691591		FR691577
<i>Pternistis nobilis</i> (1)							FR691592		
<i>Pternistis castaneicollis castaneicollis</i> (1)							AM236903		
<i>Pternistis ochropectus</i> (1)							FR691590		
<i>Pternistis erckelii</i> (5)	FR691553						FR691589		FR691575
<i>Pternistis swierstrai</i> (1)							FR691593		
<i>Pternistis jacksoni</i> (1)							FR691594		
<i>Pternistis squamatus squamatus</i> (6)	DQ832109					FR691388	AM236904		DQ768286
<i>Pternistis icterorhynchus</i> (1)							FR691601		
<i>Pternistis bicalcaratus ayesha</i> (1)							FR691625		
<i>Pternistis bicalcaratus bicalcaratus</i> (6)	FR691551								
<i>Pternistis griseostriatus</i> (6)	FR691554					FR691370	FR691624		FR691578
<i>Pternistis adspersus</i> (6)	DQ832113					FR691384	AM236905		DQ768284
<i>Pternistis capensis</i> (6)	DQ832112					FR691381	FR691623		DQ768276
<i>Pternistis hildebrandti hildebrandti</i> (5)						DQ834534	AM236909		DQ768282
<i>Pternistis natalensis</i> (6)	FR691557					FR691385	FR691595		
<i>Pternistis clappertoni clappertoni</i> (6)	FR716655					DQ834536	AM236911		DQ768285
<i>Pternistis hildebrandti johnstoni</i> (1)						FR691383	FR691602		FR691576
<i>Pternistis clappertoni sharpii</i> (1)							FR691596		
<i>Pternistis harwoodi</i> (1)							FR691603		
<i>Pternistis leucoscepus infuscatus</i> (1)							FR691600		
<i>Pternistis swainsonii swainsonii</i> (9)	DQ832110						FR691587		
<i>Pternistis leucoscepus leucoscepus</i> (6)	FR691556					DQ834532	AM236907		DQ768287
							FR691387	AM236906	DQ768283

Appendix 2.2a (continued)

Marker Taxon no. bases	12S 118754	16S 59 2258	COI 84 1203	COII 45 687	COIII 54 184	CR 155 1032	CYTB 279 1143	ND1 35 976	ND2 170 1041
<i>Pternistis cranchii cranchii</i> (1)							FR694164		
<i>Pternistis rufopictus</i> (1)							FR691588		
<i>Pternistis afer humboldti</i> (1)							FR694168		
<i>Pternistis afer</i> SA (6)	DQ832111					DQ834533	AM236908		DQ768280
<i>Francolinus pintadeanus</i> (12)	NC011817	NC011817	NC011817	NC011817	NC011817	NC011817		NC011817	EU165707
<i>Francolinus pictus</i> (1)							FR694142		
<i>Francolinus francolinus</i> (6)	FR691548	DQ868944				FR691376	AF013762		FR691585
<i>Bambusicola thoracica</i> (16)	EU165706	EU165706	EU165706	EU165706	EU165706	DQ834513	EU165706	EU165706	EU165706
<i>Bambusicola fytchii</i> (2)						EU240214	AM236891		
<i>Gallus lafayettei</i> (16)	NC007239	NC007239	NC007239	AP003325	NC007239	DQ834512	NC007239	NC007239	NC007239
<i>Gallus varius</i> (16)	NC007238	NC007238	NC007238	NC007238	NC007238	NC007238	NC007238	NC007238	NC007238
<i>Gallus sonneratii</i> (25)	NC007240	NC007240	NC007240	NC007240	NC007240	DQ834511	NC007240	NC007240	NC007240
<i>Gallus gallus</i> (52)	NC007236	NC007236	NC007236	NC007236	NC007236	NC007236	L08376	NC007236	NC007236
<i>Francolinus pondicerianus</i> (13)	FR691547			EF527259		FR691378	FR691632		DQ768279
<i>Francolinus gularis</i> (1)							U90649		
<i>Dendropix sephaena</i> SA (6)	FR691559					DQ834515	FR694140		DQ768274
<i>Dendropix sephaena rovuma</i> (1)							FR694135		
<i>Dendropix sephaena grantii</i> (1)							FR694144		
<i>Francolinus lathami schubotzi</i> (1)							FR694139		
<i>Francolinus lathami</i> (6)	FR691546					FR691377	AM236893		DQ768257
<i>Peliperdix schlegelii</i> (1)							FR694149		
<i>Peliperdix albogularis meinertzhageni</i> (1)							FR694148		
<i>Peliperdix albogularis buckleyi</i> (1)							FR694147		
<i>Peliperdix albogularis albogularis</i> (1)							FR694145		
<i>Peliperdix coqui stuhlmanni</i> (1)							FR694152		
<i>Peliperdix coqui kasaicus</i> (1)							FR694150		
<i>Peliperdix coqui hubbardi</i> (1)							FR694151		
<i>Peliperdix coqui maharao</i> (1)							FR691635		
<i>Peliperdix coqui spinetorum</i> (1)							FR694154		
<i>Peliperdix coqui coqui</i> (6)	FR691549					FR691379	AM236895		DQ768278
<i>Peliperdix coqui vernayi</i> (1)							FR694157		
<i>Peliperdix coqui ruahdae</i> (1)							Unpub.		
<i>Scleroptila streptophorus</i> (6)	FR691550					FR691380	FR691617		FR691573
<i>Scleroptila levaillantii</i> (12)	DQ832106					DQ834516	U90642		DQ768291
<i>Scleroptila finschi</i> (2)							FR691607		DQ768290
<i>Scleroptila whytei</i> (2)							FR691621		
<i>Scleroptila psilolaemus theresae</i> (1)							FR691615		
<i>Scleroptila psilolaemus</i> (1)							FR691614		
<i>Scleroptila uluensis</i> (1)							FR691622		
<i>Scleroptila gutturalis</i> (1)							FR691613		
<i>Scleroptila shelleyi</i> SA (6)	DQ832107					DQ834518	AM236898		DQ768295
<i>Scleroptila jugularis</i> (1)							FR691608		
<i>Scleroptila levaillantoides</i> (1)	DQ832108					DQ834519	FR691612		DQ768292
<i>Scleroptila africanus</i> (9)	AF222581					DQ834517	AM236897		AF222550
<i>Scleroptila levaillantoides pallidior</i> (1)							FR691609		
<i>Scleroptila ellenbecki</i> (1)							FR691616		

Appendix 2.2a (continued)

Marker Taxon no. bases	12S 118754	16S 59 2258	COI 84 1203	COII 45 687	COIII 54 184	CR 155 1032	CYTB 279 1143	ND1 35 976	ND2 170 1041
<i>Scleroptila levaillantii kikuyuensis</i> (1)							FR691606		
<i>Scleroptila levaillantii crawshayi</i> (2)							FR691605		
<i>Rheinardia ocellata</i> (2)						DQ834506	AF330060		
<i>Argusianus argus</i> (15)						DQ834505	AF013761		
<i>Afropavo congensis</i> (20)						DQ834507	AF013760		DQ768253
<i>Pavo muticus</i> (21)	NC012897	NC012897	NC012897	NC012897	NC012897	NC012897	AF01376	NC012897	NC012897
<i>Pavo cristatus</i> (21)	AY722396					DQ834508	L083793		AF394612
<i>Haematoxylum sanguiniceps</i> (6)	FR691560					EU036221	EU036222		FR691581
<i>Galloperdix lunulata</i> (1)							EF620766		
<i>Polyplectron napoleonis</i> (19)						DQ834504	AF330062		EF569481
<i>Polyplectron schleiermach</i> (2)							EU005562		
<i>Polyplectron malacense</i> (11)						AJ295260	AF330065		DQ768268
<i>Polyplectron germaini</i> (6)						AJ295257	AF330063		DQ768266
<i>Polyplectron inopinatum</i> (11)						AJ295258	AF330064		DQ768267
<i>Polyplectron chalcurum</i> (6)						AJ295256	AF330061		DQ768264
<i>Polyplectron bicalcaratum</i> (16)	NC012900	NC012900	NC012900	NC012900	NC012900	NC012900	AF534564	NC012900	DQ768263
<i>Ithaginis cruentus</i> (6)						DQ834487	AF068193		DQ768258
<i>Tragopan blythii</i> (5)							AF200722		DQ768272
<i>Tragopan caboti</i> (13)	NC013619	NC013619	NC013619	NC013619	NC013619	NC013619	NC013619	NC013619	NC013619
<i>Tragopan temminckii</i> (13)	AF222595					DQ834488	AF229838		AF222566
<i>Tragopan satyra</i> (25)						DQ834489	AF534555		
<i>Tetraphasis szechenyii</i> (14)	FJ799728	FJ799728	FJ799728	FJ799728	FJ799728	FJ799728	EU049324	FJ799728	EU845759
<i>Tetraphasis obscurus</i> (3)							EU839482		EU845758
<i>Lophophorus ihuysii</i> (14)	GQ871234	GQ871234	GQ871234	GQ871234	GQ871234	GQ871234	GQ871234	GQ871234	GQ871234
<i>Lophophorus sclateri</i> (2)						AY376860	AY265310		
<i>Lophophorus impejanus</i> (13)	DQ832098					DQ834486	AF028796		DQ768259
<i>Meleagris ocellata</i> (1)						AF487120			
<i>Meleagris gallopavo</i> (36)	NC010195	NC010195	NC010195	NC010195	NC010195	DQ834485	L08381	NC010195	NC010195
<i>Bonasa umbellus</i> (11)	U83740	AF230131	DQ434343			DQ834476	AF230167		AF222541
<i>Bonasa sewerzowi</i> (9)	AF222572	AF230130				SEQQ	AF230166		AF222540
<i>Bonasa bonasia</i> (11)	AF222571	AF230129	GQ481397			DQ834477	AF230165		AF222539
<i>Lagopus leucura</i> (9)	AF222584	AF230135	DQ433717				AF230171		AF222553
<i>Lagopus lagopus</i> (15)	AF222583	AF230134	DQ433712			DQ834482	AF230170		AF222552
<i>Lagopus muta</i> (11)	AF222585	AF230136	GQ482003			DQ834481	AY156346		AF222554
<i>Dendragapus falcipennis</i> (8)	AF222578	AF230133					AF230169		AF222547
<i>Falco sparverius</i> (13)	AF222579	AF230132	GQ375607			DQ834478	AF170992		AF222548
<i>Tetrao urogallus</i> (15)	AF222565	DQ916156	GQ482772			DQ834480	AB120132		AF222565
<i>Tetrao parvirostris</i> (10)	AF222592	AF230139	GQ482764			AF532462	AF230175		AF222563
<i>Tetrao tetrix</i> (15)	AF222593	AF230138	GQ482768			DQ834479	E5571183		AF222564
<i>Tetrao mlokosiewiczi</i> (9)	AF222562	AF230137				AF532461	AF230173		AF222562
<i>Centrocercus minimus</i> (3)			DQ432832			AF532435			
<i>Centrocercus urophasianus</i> (10)	AF222573	AF230141	DQ432834			AF532424	AF230177		AF222542
<i>Dendragapus obscurus</i> (11)	AF222580	AF230142	DQ433565			SEQQ	AF230178		AF222549
<i>Tympanuchus phasianellus</i> (13)	AF222598	AF230145	DQ434204			DQ834483	AF068191		AF222569
<i>Tympanuchus pallidicinctus</i> (10)	AF222597	AF230145	DQ434202			AF532434	AF230180		AF222568
<i>Tympanuchus cupido</i> (10)	AF222596	AF230143	AY666333			AF532432	AF230179		AF222567

Appendix 2.2a (continued)

Marker Taxon no. bases	12S 118754	16S 59 2258	COI 84 1203	COII 45 687	COIII 54 184	CR 155 1032	CYTB 279 1143	ND1 35 976	ND2 170 1041
<i>Pucrasia macrolopha</i> (7)						DQ834490	AF028800		DQ768269
<i>Perdix hodgsoniae</i> (2)							EU839472		EU845766
<i>Perdix dauurica</i> (7)	AF222589		GQ482330				EU839469		AF222559
<i>Perdix perdix</i> (25)	AF222590		DQ433069			DQ834484	AF028791		AF222560
<i>Syrmaticus soemmerringi</i> (13)	NC010767	NC010767	NC010767	NC010767	NC010767	NC010767	NC010767	NC010767	NC010767
<i>Syrmaticus reevesii</i> (28)	NC010770	NC010770	NC010770	NC010770	NC010770	NC010770	AY368059	NC010770	DQ768271
<i>Syrmaticus mikado</i> (6)	DQ832101					DQ834494	AY368056		DQ768294
<i>Syrmaticus humiae</i> (14)	NC010774	NC010774	NC010774	NC010774	NC010774	NC010774	AF534706	NC010774	DQ768293
<i>Syrmaticus ellioti</i> (16)	NC010771	NC010771	NC010771	NC010771	NC010771	NC010771	AB164624	NC010771	DQ768270
<i>Phasianus versicolor</i> (13)	NC010778	NC010778	NC010778	NC010778	NC010778	NC010778	AY368058	NC010778	NC010778
<i>Phasianus colchicus</i> (28)	U83742		GQ482363			DQ834495	AY368060		AF222561
<i>Chrysolophus pictus</i> (15)						DQ834497	AF028793		DQ768255
<i>Chrysolophus amherstiae</i> (15)	DQ832102					AY368067	AB120130		DQ768277
<i>Catreus wallichii</i> (20)						DQ834499	AF028792		DQ768254
<i>Crossoptilon mantchuricum</i> (7)						DQ834502	AF534553		
<i>Crossoptilon auritum</i> (3)						DQ834501	AF534552		EU845771
<i>Crossoptilon harmani</i> (2)						AY373521	AY343524		
<i>Crossoptilon crossoptilon</i> (11)						DQ834500	AF028794		DQ768256
<i>Lophura erythrophthalma</i> (2)						SEQ	AF314639		
<i>Lophura ignota</i> (6)						AJ300152	AF314642		DQ768260
<i>Lophura bulweri</i> (2)						AJ300146	AF314637		
<i>Lophura ignita</i> (14)	NC010781	NC010781	NC010781	NC010781	NC010781	NC010781	AF314641	NC010781	NC010781
<i>Lophura diardi</i> (7)						AJ300147	AF028797		
<i>Lophura nycthemera</i> (30)	NC012895	NC012895	NC012895	NC012895	NC012895	NC012895	L08380	NC012895	DQ768261
<i>Lophura leucomelana</i> (2)						AJ300153	AF314643		
<i>Lophura swinhoii</i> (11)						AJ300155	AF534558		DQ768262
<i>Lophura hatinhensis</i> (2)						AJ300150	AF314640		
<i>Lophura edwardsi</i> (7)						AJ300148	AF534557		

Appendix 2.2b

GenBank numbers and the amounts of DNA sequence data used for the 4 of the 13 mitochondrial (ND3 to ND6) and 5 of the 42 nuclear markers utilised in the phylogenetic analysis. (- = no sequence). Refer to Appendix 2.1 for the full names of the molecular markers. Numbers in parenthesis indicate the number of markers used for that particular taxon.

Marker Taxon no. bases	ND3 33 352	ND4 50 1327	ND5 56 1811	ND6 31 522	AG3 20 861	AGC1 33 590	AGR P 36 1591	ALDOB EX 22 3010	ALDOB UT 23 353
<i>Struthio camelus</i> (30)	NC002785	NC002785	NC002785	NC002785				EU737782	
<i>Rhea americana</i> (30)	NC000846	NC000846	NC000846	NC000846				EU737781	
<i>Tinamus major/guttatus</i> (16)	NC002781	NC002781	NC002781	NC002781				EU737783	
<i>Anhima cornuta</i> (11)			AY140751						
<i>Chauna torquata</i> (30)			AY140752					EU737817	
<i>Anseranas semipalmata</i> (30)	NC005933	NC005933	NC005933	NC005933				EU737797	
<i>Anas platyrhynchos</i> (31)	NC009684	NC009684	NC009684	NC009684			AY635903	EU737784	
<i>Cairina moschata</i> (13)	NC010965	NC010965	NC010965	NC010965				EU737817	
<i>Leipoa ocellata</i> (18)						AF246136			FJ881767
<i>Talegalla fuscirostris</i> (2)									
<i>Aepyornis arfakianus</i> (6)									
<i>Alectura lathami</i> (39)	NC007227	NC002227	NC002227	NC002227				EU737793	
<i>Macrocephalon maleo</i> (3)									
<i>Eulipoa wallacei</i> (2)									
<i>Megapodius tenimberensis</i> (3)									
<i>Megapodius cumingii</i> (1)									
<i>Megapodius pritchardii</i> (2)									
<i>Megapodius layardi</i> (16)									FJ881768
<i>Megapodius reinwardt</i> (13)			AY140753						
<i>Megapodius eremita</i> (25)			AF082065					EU737862	
<i>Megapodius decollatus</i> (1)									
<i>Megapodius forstenii</i> (1)									
<i>Megapodius freycinet</i> (5)									
<i>Ornithodoros cinereiceps</i> (3)						AF215972			
<i>Ornithodoros motmot</i> (1)									
<i>Ornithodoros vetula</i> (14)									FJ881782
<i>Ornithodoros leucogastra</i> (1)									
<i>Ornithodoros poliocephala</i> (1)									
<i>Ornithodoros canicollis</i> (14)		AY141954	AY140760						
<i>Ornithodoros guttata</i> (3)									
<i>Ornithodoros ruficauda</i> (1)									
<i>Ornithodoros garrula</i> (1)									
<i>Oreophasis derbianus</i> (13)				AY140759					
<i>Nothocrax urumutum</i> (14)		AY141953	AY140763						
<i>Pauxi pauxi</i> (15)		AY141955	AY140764						
<i>Pauxi gilliardi</i> (1)									
<i>Mitu tomentosa</i> (6)		AY141951	AY141968						
<i>Mitu mitu</i> (6)		AY141949	AY141966						
<i>Mitu salvani</i> (6)		AY141950	AY141967						
<i>Pauxi unicornis</i> (6)		AY141956	AY141969						
<i>Mitu tuberosa</i> (14)		AY141952	AY140762						
<i>Crax rubra</i> (23)		AY141948	AY141965						FJ881774

Appendix 2.2b (continued)

Appendix 2.2b (continued)

Appendix 2.2b (continued)

Appendix 2.2b (continued)

Marker Taxon no. bases	ND3 33 352	ND4 50 1327	ND5 56 1811	ND6 31 522	AG3 20 861	AGC1 33 590	AGRP 36 1591	ALDOB EX 22 3010	ALDOB UT 23 353
<i>Scleroptila levaillantii kikuyuensis</i> (1)									
<i>Scleroptila levaillantii crawshayi</i> (2)									
<i>Rheinardia ocellata</i> (2)									
<i>Argusianus argus</i> (15)							EF571222	FJ881836	FJ881770
<i>Afropavo congensis</i> (20)							EF571221	FJ881835	FJ881769
<i>Pavo muticus</i> (21)	NC012897	NC012897	NC012897	NC012897					
<i>Pavo cristatus</i> (21)							EF571196		
<i>Haematoptyx sanguiniceps</i> (6)							EF571200		FJ881783
<i>Galloperdix lunulata</i> (1)									
<i>Polypelectron napoleonis</i> (19)							EF571198	FJ881840	FJ881784
<i>Polypelectron schleiermach</i> (2)									
<i>Polypelectron malacense</i> (11)							EF571195		
<i>Polypelectron germaini</i> (6)									
<i>Polypelectron inopinatum</i> (11)							EF571197		
<i>Polypelectron chalcurum</i> (6)									
<i>Polypelectron bicalcaratum</i> (16)	NC012900	NC012900	NC012900	NC012900					
<i>Ithaginis cruentus</i> (6)									
<i>Tragopan blythii</i> (5)									
<i>Tragopan caboti</i> (13)	NC013619	NC013619	NC013619	NC013619					
<i>Tragopan temminckii</i> (13)									
<i>Tragopan satyra</i> (25)							AF532365		
<i>Tetraphasis szechenyii</i> (14)	FJ799728	FJ799728	FJ799728	FJ799728					
<i>Tetraphasis obscurus</i> (3)									
<i>Lophophorus ihuysii</i> (14)	GQ871234	GQ871234	GQ871234	GQ871234					
<i>Lophophorus sclateri</i> (2)									
<i>Lophophorus impejanus</i> (13)							EF571207		
<i>Meleagris ocellata</i> (1)									
<i>Meleagris gallopavo</i> (36)	NC010195	NC010195	NC010195	NC010195	AF532366	AF215943	EF571202		FJ881779
<i>Bonasa umbellus</i> (11)	AF076344			AF532369	AF215966				AF076344
<i>Bonasa sewerzowi</i> (9)					AF532374		AF215965		
<i>Bonasa bonasia</i> (11)					AF532372		AF215964		
<i>Lagopus leucura</i> (9)					AF532390		AF215953		
<i>Lagopus lagopus</i> (15)					AF532392		AF215952	EF571206	
<i>Lagopus muta</i> (11)					AF532395		AF215954		
<i>Dendragapus falcipennis</i> (8)					AF532401		AF246135		
<i>Falcipennis canadensis</i> (13)					AF532399		AF215946		
<i>Tetrao urogallus</i> (15)					AF532411		AF215963	EF571189	
<i>Tetrao parvirostris</i> (10)					AF532408		AF215970		
<i>Tetrao tetrix</i> (15)					AF532403		AF215962	EF571203	
<i>Tetrao mlokosiewiczi</i> (9)					AF532405		AF215958		
<i>Centrocercus minimus</i> (3)					AF532377				
<i>Centrocercus urophasianus</i> (10)					AF532376		AF215967		
<i>Dendragapus obscurus</i> (11)					AF532381		AF215947		
<i>Tympanuchus phasianellus</i> (13)					AF532388		AF246136		
<i>Tympanuchus pallidicinctus</i> (10)					AF532386		AF215961		
<i>Tympanuchus cupido</i> (10)					AF532384		AF215959		

Appendix 2.2b (continued)

Marker Taxon no. bases	ND3 33 352	ND4 50 1327	ND5 56 1811	ND6 31 522	AG3 20 861	AGC1 33 590	AGRP 36 1591	ALDOB EX 22 3010	ALDOB UT 23 353
<i>Pucrasia macrolopha</i> (7)									
<i>Perdix hodgsoniae</i> (2)									
<i>Perdix dauurica</i> (7)									
<i>Perdix perdix</i> (25)									
<i>Syrmaticus soemmerringi</i> (13)	NC010767	NC010767	NC010767	NC010767			AF215956		
<i>Syrmaticus reevesii</i> (28)	NC010770	NC010770	NC010770	NC010770			AF215957	EF571194	FJ881841
<i>Syrmaticus mikado</i> (6)									FJ881786
<i>Syrmaticus humiae</i> (14)	NC010774	NC010774	NC010774	NC010774					
<i>Syrmaticus ellioti</i> (16)	NC010771	NC010771	NC010771	NC010771					
<i>Phasianus versicolor</i> (13)	NC010778	NC010778	NC010778	NC010778					
<i>Phasianus colchicus</i> (28)	AF076366							EF571199	
<i>Chrysolophus pictus</i> (15)								FJ881838	
<i>Chrysolophus amherstiae</i> (15)								FJ881772	
<i>Catreus wallichii</i> (20)								EF571213	
<i>Crossoptilon mantchuricum</i> (7)								FJ881837	
<i>Crossoptilon auritum</i> (3)								EF571214	
<i>Crossoptilon harmani</i> (2)									FJ881771
<i>Crossoptilon crossoptilon</i> (11)									
<i>Lophura erythrophthalma</i> (2)								EF571217	
<i>Lophura inornata</i> (6)									
<i>Lophura bulweri</i> (2)									
<i>Lophura ignita</i> (14)	NC010781	NC010781	NC010781	NC010781					
<i>Lophura diardi</i> (7)								EF571209	
<i>Lophura nycthemera</i> (30)	NC012895	NC012895	NC012895	NC012895			EF571205	FJ881839	
<i>Lophura leucomelana</i> (2)									FJ881778
<i>Lophura swinhoii</i> (11)								EF571204	
<i>Lophura hatinhensis</i> (2)									
<i>Lophura edwardsi</i> (7)								EF571208	

Appendix 2.2c

GenBank numbers and the amounts of DNA sequence data used for 9 of the 42 nuclear markers utilised in the phylogenetic analysis. (- = no sequence). Refer to Appendix 2.1 for the full names of the molecular markers. Numbers in parenthesis indicate the number of markers used for that particular taxon.

Marker Taxon no. bases	ASW 21 854	BDNF 13 660	BFIB 56 1829	CALB 16 524	CLTC 132 233	C-MOS 18 586	CRYAA EX 131 319	CRYAA IN 221 124	CRYAA UT 23 753
<i>Struthio camelus</i> (30)		EU737943			EU302743		EU737629		
<i>Rhea americana</i> (30)		EU737942			EU302738		EU737628		
<i>Tinamus major/guttatus</i> (16)							EU737630		
<i>Anhima cornuta</i> (11)			AY140701			AY140715			
<i>Chauna torquata</i> (30)		EU737980	AY140702		EU738133	AY140716	EU737665		
<i>Anseranas semipalmata</i> (30)		EU737959			EU738115		EU737644		
<i>Anas platyrhynchos</i> (31)		EU737945			EU738108		EU737631		
<i>Cairina moschata</i> (13)									
<i>Leipoa ocellata</i> (18)			AY952648	AY952680				FJ881712	FJ881812
<i>Talegalla fuscirostris</i> (2)									
<i>Aepyornis arfakianus</i> (6)									
<i>Alectura lathami</i> (39)		EU737955	AY952647	AY952679	EU738113		EU737640		
<i>Macrocephalon maleo</i> (3)									
<i>Eulipoa wallacei</i> (2)									
<i>Megapodius tenimberensis</i> (3)									
<i>Megapodius cumingii</i> (1)									
<i>Megapodius pritchardii</i> (2)									
<i>Megapodius layardi</i> (16)			AY952649	AY952681				FJ881713	FJ881813
<i>Megapodius reinwardt</i> (13)			AY140703			AY140717			
<i>Megapodius eremita</i> (25)		EU738029			EU738169		EU737709		
<i>Megapodius decollatus</i> (1)									
<i>Megapodius forstenii</i> (1)									
<i>Megapodius freycinet</i> (5)									
<i>Ornithodoros cinereiceps</i> (3)									
<i>Ornithodoros motmot</i> (1)								FJ881727	FJ881827
<i>Ornithodoros vetula</i> (14)			AY952651	AY952683					
<i>Ornithodoros leucogastra</i> (1)									
<i>Ornithodoros poliocephala</i> (1)									
<i>Ornithodoros canicollis</i> (14)			AY140710			AY140724			
<i>Ornithodoros guttata</i> (3)									
<i>Ornithodoros ruficauda</i> (1)									
<i>Ornithodoros garrula</i> (1)									
<i>Oreophasis derbianus</i> (13)			AY140709			AY140723			
<i>Nothocrax urumutum</i> (14)			AY140713			AY140727			
<i>Pauxi pauxi</i> (15)			AY140714			AY140728			
<i>Pauxi gilliardi</i> (1)									
<i>Mitu tomentosa</i> (6)									
<i>Mitu mitu</i> (6)									
<i>Mitu salvani</i> (6)									
<i>Pauxi unicornis</i> (6)									
<i>Mitu tuberosa</i> (14)			AY140712			AY140726			
<i>Crax rubra</i> (23)			AY952650	AY952682				FJ881719	FJ881819

Appendix 2.2c (continued)

Marker Taxon no. bases	ASW 21 854	BDNF 13 660	BFIB 56 1829	CALB 16 524	CLTC 132 233	C-MOS 18 586	CRYAA EX 131 319	CRYAA IN 221 124	CRYAA UT 23 753
<i>Crax globulosa</i> (6)									
<i>Crax blumenbachii</i> (14)					AY140711				AY140725
<i>Crax daubentoni</i> (6)									
<i>Crax alberti</i> (6)									
<i>Crax fasciolata</i> (6)									
<i>Crax alector</i> (31)									
<i>Penelopina nigra</i> (15)									
<i>Chamaepetes unicolor</i> (1)									
<i>Chamaepetes goudotii</i> (14)									
<i>Penelope montagnii</i> (1)									
<i>Penelope argyrotis</i> (1)									
<i>Penelope ochrogaster</i> (3)									
<i>Penelope obscura</i> (14)									
<i>Penelope jacquacu</i> (2)									
<i>Penelope superciliaris</i> (3)									
<i>Penelope purpurascens</i> (3)									
<i>Pipile jacutinga</i> (14)									
<i>Aburria aburri</i> (14)									
<i>Pipile cujubi</i> (3)									
<i>Pipile pipile</i> (3)									
<i>Pipile grayi</i> (2)									
<i>Pipile nattereri</i> (1)									
<i>Pipile cumanensis</i> (3)									
<i>Numida meleagris</i> (49)									
<i>Agelastes meleagrides</i> (1)									
<i>Acryllium vulturinum</i> (12)									
<i>Guttera edouardi</i> (1)									
<i>Guttera pucherani</i> (18)									
<i>Guttera plumifera</i> (1)									
<i>Ptilopachus petrosus</i> (6)									
<i>Ptilopachus nahani</i> (6)									
<i>Cyrtonyx montezumae</i> (19)									
<i>Odontophorus speciosus</i> (6)									
<i>Odontophorus gujanensis</i> (6)									
<i>Odontophorus capueira</i> (6)									
<i>Oreortyx pictus</i> (20)									
<i>Colinus cristatus</i> (20)									
<i>Colinus virginianus</i> (15)									
<i>Callipepla douglasii</i> (3)									
<i>Callipepla squamata</i> (4)									
<i>Callipepla gambelii</i> (8)									
<i>Callipepla californica</i> (6)									
<i>Xenoperdix obscurata</i> (1)									
<i>Xenoperdix udzungwensis</i> (5)									
<i>Arborophila rufipectus</i> (13)									
<i>Caloperdix oculeus</i> (1)					DQ494145				

Appendix 2.2c (continued)

Appendix 2.2c (continued)

Appendix 2.2c (continued)

Appendix 2.2c (continued)

Appendix 2.2d

GenBank numbers and the amounts of DNA sequence data used for 9 of the 42 nuclear markers utilised in the phylogenetic analysis. (- = no sequence). Refer to Appendix 2.1 for the full names of the molecular markers. Numbers in parenthesis indicate the number of markers used for that particular taxon.

Marker Taxon no. bases	DCoH 44 579	EEF2-EX 29 2270	EEF2 UTR 16 543	EGR1 131 205	FGB 13 1581	G3PDH 38 438	GH1 125 676	HMGN EX 32 1827	HMGN UT 23 779
<i>Struthio camelus</i> (30)		EU738563		EU738886	EU739350		EF521423	EU739514	
<i>Rhea americana</i> (30)		EU738562		EU738885	EU739349		EF521422	EU739513	
<i>Tinamus major/guttatus</i> (16)		EU738564							
<i>Anhima cornuta</i> (11)									
<i>Chauna torquata</i> (30)		EU738598		EU738921	EU739387		EF521458	EU739536	
<i>Anseranas semipalmata</i> (30)		EU738578		EU738900	EU739366		EF521439	EU739527	
<i>Anas platyrhynchos</i> (31)		EU738565		EU738887	EU739352		EF521425	EU739516	
<i>Cairina moschata</i> (13)									
<i>Leipoa ocellata</i> (18)	AY952699	FJ881843	FJ881696			AY952715		AY952731	FJ881735
<i>Talegalla fuscirostris</i> (2)									
<i>Aepyornis arfakianus</i> (6)									
<i>Alectura lathami</i> (39)	AY952698	EU738574		EU738896	EU739362	AY952714	EF521435	AY952730	
<i>Macrocephalon maleo</i> (3)									
<i>Eulipoa wallacei</i> (2)									
<i>Megapodius tenimberensis</i> (3)									
<i>Megapodius cumingii</i> (1)									
<i>Megapodius pritchardii</i> (2)									
<i>Megapodius layardi</i> (16)	AY952700	FJ881844	FJ881697			AY952716		AY952732	FJ881736
<i>Megapodius reinwardt</i> (13)									
<i>Megapodius eremita</i> (25)		EU738642		EU738970	EU739436		EF521503	EU739552	
<i>Megapodius decollatus</i> (1)									
<i>Megapodius forstenii</i> (1)									
<i>Megapodius freycinet</i> (5)									
<i>Ornithodoros cinereiceps</i> (3)									
<i>Ornithodoros motmot</i> (1)									
<i>Ornithodoros vetula</i> (14)	AY952702	FJ881846	FJ881698			AY952718		AY952734	FJ881750
<i>Ornithodoros leucogastra</i> (1)									
<i>Ornithodoros poliocephala</i> (1)									
<i>Ornithodoros canicollis</i> (14)									
<i>Ornithodoros guttata</i> (3)									
<i>Ornithodoros ruficauda</i> (1)									
<i>Ornithodoros garrula</i> (1)									
<i>Oreophasis derbianus</i> (13)									
<i>Nothocrax urumutum</i> (14)									
<i>Pauxi pauxi</i> (15)									
<i>Pauxi gilliardi</i> (1)									
<i>Mitu tomentosa</i> (6)									
<i>Mitu mitu</i> (6)									
<i>Mitu salvani</i> (6)									
<i>Pauxi unicornis</i> (6)									
<i>Mitu tuberosa</i> (14)									
<i>Crax rubra</i> (23)	AY952701	FJ881845	FJ881699			AY952717		AY952733	FJ881742

Appendix 2.2d (continued)

Appendix 2.2d (continued)

Marker Taxon no. bases	DCoH 44 579	EEF2-EX 29 2270	EEF2 UTR 16 543	EGR1 131 205	FGB 13 1581	G3PDH 38 438	GH1 125 676	HMGN EX 32 1827	HMGN UT 23 779
<i>Rollulus rouloul</i> (28)		EU738688		EU739018	EU739482		EF521549	FJ881765	FJ881755
<i>Arborophila torqueola</i> (2)						DQ093812			
<i>Arborophila javanica</i> (6)									
<i>Tetraogallus tibetanus</i> (3)									
<i>Tetraogallus himalayensis</i> (3)									
<i>Tetraogallus altaicus</i> (2)									
<i>Alectoris melanocephala</i> (2)									
<i>Alectoris barbara</i> (3)									
<i>Alectoris rufa</i> (14)		Unpub.				EF152483			
<i>Alectoris graeca</i> (2)									
<i>Alectoris chukar</i> (17)		Unpub.				FR694070			
<i>Alectoris philbyi</i> (3)									
<i>Alectoris magna</i> (3)									
<i>Coturnix ypsilophora</i> (5)									
<i>Excalfactoria chinensis</i> (14)									
<i>Coturnix pectoralis</i> (3)									
<i>Coturnix novaezelandiae</i> (2)									
<i>Margaroperdix madagarensis</i> (2)									
<i>Coturnix japonica</i> (29)	AY952708					AY952724		AY952740	FJ881741
<i>Coturnix coturnix</i> (33)		EU738609		EU738933	EU739399		EF521468	EU739541	
<i>Perdicula asiatica</i> (2)									
<i>Ammoperdix heyi</i> (1)									
<i>Pternistis hartlaubi hartlaubi</i> (6)				FR694095					
<i>Pternistis camerunensis</i> (6)				FR694090					
<i>Pternistis nobilis</i> (1)									
<i>Pternistis castaneicollis castaneicollis</i> (1)									
<i>Pternistis ochropectus</i> (1)									
<i>Pternistis erckelii</i> (5)				FR694093					
<i>Pternistis swierstrai</i> (1)									
<i>Pternistis jacksoni</i> (1)									
<i>Pternistis squamatus squamatus</i> (6)				FR694099					
<i>Pternistis icterorhynchus</i> (1)									
<i>Pternistis bicalcaratus ayesha</i> (1)									
<i>Pternistis bicalcaratus bicalcaratus</i> (6)				FR694089					
<i>Pternistis griseostriatus</i> (6)				FR694094					
<i>Pternistis adspersus</i> (6)				FR694087					
<i>Pternistis capensis</i> (6)				FR694091					
<i>Pternistis hildebrandti hildebrandti</i> (5)				FR694096					
<i>Pternistis natalensis</i> (6)				FR694098					
<i>Pternistis clappertoni clappertoni</i> (6)				FR694092					
<i>Pternistis hildebrandti johnstoni</i> (1)									
<i>Pternistis clappertoni sharpii</i> (1)									
<i>Pternistis harwoodi</i> (1)									
<i>Pternistis leucoscepus infuscatus</i> (1)									
<i>Pternistis swainsonii swainsonii</i> (9)				FR694100					
<i>Pternistis leucoscepus leucoscepus</i> (6)				FR694097					

Appendix 2.2d (continued)

Appendix 2.2d (continued)

Appendix 2.2d (continued)

Appendix 2.2e

GenBank numbers and the amounts of DNA sequence data used for 9 of the 42 nuclear markers utilised in the phylogenetic analysis. (- = no sequence). Refer to Appendix 2.1 for the full names of the molecular markers. Numbers in parenthesis indicate the number of markers used for that particular taxon.

Marker Taxon no. bases	IRF2 8 645	MB 12 962	MC1R 38 859	MUSK 38 859	MYC 13 1282	NGF 13 750	NTF3 14 731	OVO-G 90 589	PCBD1 28 1296
<i>Struthio camelus</i> (30)		EU739904		EU739749	SEQ	EU740066	EU740230		EU738399
<i>Rhea americana</i> (30)		EU739903		EU739748	EU738234	EU740065	EU740229		EU738398
<i>Tinamus major/guttatus</i> (16)									
<i>Anhima cornuta</i> (11)									
<i>Chauna torquata</i> (30)		EU739939		EU739783	EU738269	EU740102	EU740265		EU738436
<i>Anseranas semipalmata</i> (30)		EU739919		UE739763	SEQ	EU740081	EU740244		EU738415
<i>Anas platyrhynchos</i> (31)		EU739906		EU739751	EU738236	EU740068	EU740232		EU738401
<i>Cairina moschata</i> (13)									
<i>Leipoa ocellata</i> (18)								AY952768	FJ881790
<i>Talegalla fuscirostris</i> (2)									
<i>Aepyornis arfakianus</i> (6)									
<i>Alectura lathami</i> (39)	EU739600	EU739915	EF571042	EU739759	EU738246	EU740077	EU740240	AY952767	EU738411
<i>Macrocephalon maleo</i> (3)									
<i>Eulipoa wallacei</i> (2)									
<i>Megapodius tenimberensis</i> (3)									Unpub.
<i>Megapodius cumingii</i> (1)									
<i>Megapodius pritchardii</i> (2)									
<i>Megapodius layardi</i> (16)									AY952769
<i>Megapodius reinwardt</i> (13)									
<i>Megapodius eremita</i> (25)	EU739671	EU739985		EU739830	EU738316	EU740149	EU740312		EU738483
<i>Megapodius decollatus</i> (1)									
<i>Megapodius forstenii</i> (1)									
<i>Megapodius freycinet</i> (5)									
<i>Ornithodoros cinereiceps</i> (3)									
<i>Ornithodoros motmot</i> (1)									
<i>Ornithodoros vetula</i> (14)								AF170974	FJ881804
<i>Ornithodoros leucogaster</i> (1)									
<i>Ornithodoros poliocephala</i> (1)									
<i>Ornithodoros canicollis</i> (14)									
<i>Ornithodoros guttata</i> (3)									
<i>Ornithodoros ruficauda</i> (1)									
<i>Ornithodoros garrula</i> (1)									
<i>Oreophasis derbianus</i> (13)									
<i>Nothocrax urumutum</i> (14)									
<i>Pauxi pauxi</i> (15)									AF170973
<i>Pauxi gilliardi</i> (1)									
<i>Mitu tomentosa</i> (6)									
<i>Mitu mitu</i> (6)									
<i>Mitu salvani</i> (6)									
<i>Pauxi unicornis</i> (6)									
<i>Mitu tuberosa</i> (14)									
<i>Crax rubra</i> (23)								AY952770	FJ881796

Appendix 2.2e (continued)

Appendix 2.2e (continued)

Appendix 2.2e (continued)

Appendix 2.2e (continued)

Appendix 2.2e (continued)

Marker Taxon no. bases	IRF2 8 645	MB 12 962	MC1R 38 859	MUSK 38 859	MYC 13 1282	NGF 13 750	NTF3 14 731	OVO-G 90 589	PCBD1 28 1296
<i>Pucrasia macrolopha</i> (7)								AF170983	
<i>Perdix hodgsoniae</i> (2)									
<i>Perdix dauurica</i> (7)									
<i>Perdix perdix</i> (25)				EF571013				AF170982	FJ881808
<i>Syrmaticus soemmerringi</i> (13)									
<i>Syrmaticus reevesii</i> (28)				EF571022				DQ307020	FJ881810
<i>Syrmaticus mikado</i> (6)								DQ832079	
<i>Syrmaticus humiae</i> (14)								DQ832077	
<i>Syrmaticus ellioti</i> (16)								DQ832078	
<i>Phasianus versicolor</i> (13)									
<i>Phasianus colchicus</i> (28)				EF571043				AY952774	FJ881807
<i>Chrysolophus pictus</i> (15)								DQ307014	FJ881794
<i>Chrysolophus amherstiae</i> (15)								DQ832080	
<i>Catreus wallichii</i> (20)				EF571015				AF170980	FJ881793
<i>Crossoptilon mantchuricum</i> (7)				EF571031					
<i>Crossoptilon auritum</i> (3)									
<i>Crossoptilon harmani</i> (2)									
<i>Crossoptilon crossoptilon</i> (11)				EF571040				AF170981	
<i>Lophura erythrophthalma</i> (2)									
<i>Lophura inornata</i> (6)								DQ307016	
<i>Lophura bulweri</i> (2)									
<i>Lophura ignita</i> (14)									
<i>Lophura diardi</i> (7)				EF571032					
<i>Lophura nycthemera</i> (30)				EF571035				DQ307017	FJ881800
<i>Lophura leucomelana</i> (2)									
<i>Lophura swinhoii</i> (11)				EF571036				DQ307018	
<i>Lophura hatinhensis</i> (2)									
<i>Lophura edwardsi</i> (7)				EF571034					

Appendix 2.2f

GenBank numbers and the amounts of DNA sequence data used for 11 of the 42 nuclear markers utilised in the phylogenetic analysis. (- = no sequence). Refer to Appendix 2.1 for the full names of the molecular markers. Numbers in parenthesis indicate the number of markers used for that particular taxon.

Marker Taxon no. bases	RAG1 172 855	RAG2 15 926	RDP1 EX 18 958	RDP1 INT 131 032	RHO 252 162	TGFB2 462 717	TPM1 12 477	TYR 35 772	TYRP1 35 267	TYRP2 35 233	WPG 29 331	
<i>Struthio camelus</i> (30)						EU737156	EU737314	EU737483				
<i>Rhea americana</i> (30)						EU737156	EU737313	EU737482				
<i>Tinamus major/guttatus</i> (16)												
<i>Anhima cornuta</i> (11)	AY140765	AY140779										
<i>Chauna torquata</i> (30)	AY140766	AY140780				EU737192	EU737351	EU737512				
<i>Anseranas semipalmata</i> (30)						EU737172	EU737330	EU737497				
<i>Anas platyrhynchos</i> (31)						EU737172	EU737316	EU737485				
<i>Cairina moschata</i> (13)												
<i>Leipoa ocellata</i> (18)						AF394647						
<i>Talegalla fuscirostris</i> (2)						AF394648						
<i>Aepypterus arfakianus</i> (6)						AF394645						
<i>Alectura lathami</i> (39)	AF294687					AF394643	EU737168	EU737326	EU737493	EF571127	EF571093	EF571074
<i>Macrocephalon maleo</i> (3)						AF394649						
<i>Eulipoa wallacei</i> (2)						AF394651						
<i>Megapodius tenimberensis</i> (3)						AF394659						
<i>Megapodius cumingii</i> (1)												
<i>Megapodius pritchardii</i> (2)						AF394658						
<i>Megapodius layardi</i> (16)						AF394657						
<i>Megapodius reinwardt</i> (13)	AY140767	AY140781				AF394655						
<i>Megapodius eremita</i> (25)						AF394653						
<i>Megapodius decollatus</i> (1)												
<i>Megapodius forstenii</i> (1)												
<i>Megapodius freycinet</i> (5)						AF143731						
<i>Ortalis cinereiceps</i> (3)						AF222508						
<i>Ortalis motmot</i> (1)												
<i>Ortalis vetula</i> (14)												
<i>Ortalis leucogastra</i> (1)												
<i>Ortalis poliocephala</i> (1)												
<i>Ortalis canicollis</i> (14)	AY140774	AY140788										
<i>Ortalis guttata</i> (3)												
<i>Ortalis ruficauda</i> (1)												
<i>Ortalis garrula</i> (1)												
<i>Oreophasis derbianus</i> (13)												
<i>Nothocrax urumutum</i> (14)	AY140773	AY140787										
<i>Pauxi pauxi</i> (15)	AY140777	AY140791										
<i>Pauxi gilliardi</i> (1)	AY140778	AY140792										
<i>Mitu tomentosa</i> (6)												
<i>Mitu mitu</i> (6)												
<i>Mitu salvani</i> (6)												
<i>Pauxi unicornis</i> (6)												
<i>Mitu tuberosa</i> (14)	AY140776	AY140790										
<i>Crax rubra</i> (23)						AY952750						

Appendix 2.2f (continued)

Marker Taxon no. bases	RAG1 172 855	RAG2 15 926	RDP1 EX 18 958	RDP1 INT 131 032	RHO 252 162	TGFB2 462 717	TPM1 12 477	TYR 35 772	TYRP1 35 267	TYRP2 35 233	WPG 29 331
<i>Crax globulosa</i> (6)											
<i>Crax blumenbachii</i> (14)	AY140775	AY140789									
<i>Crax daubentoni</i> (6)											
<i>Crax alberti</i> (6)											
<i>Crax fasciolata</i> (6)											
<i>Crax alector</i> (31)											
<i>Penelopina nigra</i> (15)	AY140771	AY140785				EU737204	EU737365	EU737524	EF571142	EF571108	EF571071
<i>Chamaepetes unicolor</i> (1)											
<i>Chamaepetes goudotii</i> (14)	AY140769	AY140783									
<i>Penelope montagnii</i> (1)											
<i>Penelope argyrotis</i> (1)											
<i>Penelope ochrogaster</i> (3)											
<i>Penelope obscura</i> (14)	AY140770	AY140784									
<i>Penelope jacquacu</i> (2)											
<i>Penelope superciliaris</i> (3)											
<i>Penelope purpurascens</i> (3)											
<i>Pipile jacutinga</i> (14)	AY140772	AY140786									
<i>Aburria aburri</i> (14)	AY140768	AY140782									
<i>Pipile cujubi</i> (3)											
<i>Pipile pipile</i> (3)											
<i>Pipile grayi</i> (2)											
<i>Pipile nattereri</i> (1)											
<i>Pipile cumanensis</i> (3)											
<i>Numida meleagris</i> (49)											
<i>Agelastes meleagrides</i> (1)											
<i>Acryllium vulturinum</i> (12)											
<i>Guttera edouardi</i> (1)											
<i>Guttera pucherani</i> (18)											
<i>Guttera plumifera</i> (1)											
<i>Ptilopachus petrosus</i> (6)											
<i>Ptilopachus nahani</i> (6)											
<i>Cyrtonyx montezumae</i> (19)											
<i>Odontophorus speciosus</i> (6)											
<i>Odontophorus gujanensis</i> (6)											
<i>Odontophorus capueira</i> (6)											
<i>Oreortyx pictus</i> (20)											
<i>Colinus cristatus</i> (20)											
<i>Colinus virginianus</i> (15)											
<i>Callipepla douglasii</i> (3)											
<i>Callipepla squamata</i> (4)											
<i>Callipepla gambelii</i> (8)											
<i>Callipepla californica</i> (6)											
<i>Xenoperdix obscurata</i> (1)											
<i>Xenoperdix udzungwensis</i> (5)											
<i>Arborophila rufipectus</i> (13)											
<i>Caloperdix oculeus</i> (1)											

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Appendix 2.2f (continued)

Marker Taxon no. bases	RAG1 172 855	RAG2 15 926	RDP1 EX 18 958	RDP1 INT 131 032	RHO 252 162	TGFB2 462 717	TPM1 12 477	TYR 35 772	TYRP1 35 267	TYRP2 35 233	WPG 29 331
<i>Rollulus rouloul</i> (28)						EU737280	EU737448		EF571117	EF571083	EU571048
<i>Arborophila torqueola</i> (2)											
<i>Arborophila javanica</i> (6)											
<i>Tetraogallus tibetanus</i> (3)											
<i>Tetraogallus himalayensis</i> (3)											
<i>Tetraogallus altaicus</i> (2)											
<i>Alectoris melanocephala</i> (2)											
<i>Alectoris barbara</i> (3)											
<i>Alectoris rufa</i> (14)						FN811363	Unpub.		EF571144	EF571110	EF571073
<i>Alectoris graeca</i> (2)											
<i>Alectoris chukar</i> (17)						AF394641	FN811346		FR694121		
<i>Alectoris philbyi</i> (3)									EF571145	EF571111	EF571075
<i>Alectoris magna</i> (3)											
<i>Coturnix ypsilophora</i> (5)											
<i>Excalfactoria chinensis</i> (14)											
<i>Coturnix pectoralis</i> (3)											
<i>Coturnix novaezealandiae</i> (2)											
<i>Margaroperdix madagarensis</i> (2)											
<i>Coturnix japonica</i> (29)						AY952756		DQ402443		EU046600	
<i>Coturnix coturnix</i> (33)								EU737363		EF571106	
<i>Perdicula asiatica</i> (2)								EU737522		EF571140	
<i>Ammoperdix heyi</i> (1)											
<i>Pternistis hartlaubi</i> <i>hartlaubi</i> (6)								FR694129			
<i>Pternistis camerunensis</i> (6)								FR694124			
<i>Pternistis nobilis</i> (1)											
<i>Pternistis castaneicollis</i> <i>castaneicollis</i> (1)											
<i>Pternistis ochropectus</i> (1)											
<i>Pternistis erckelii</i> (5)											
<i>Pternistis swierstrai</i> (1)											
<i>Pternistis jacksoni</i> (1)											
<i>Pternistis squamatus</i> <i>squamatus</i> (6)								FR694133			
<i>Pternistis icterorhynchus</i> (1)											
<i>Pternistis bicalcaratus</i> <i>ayesha</i> (1)											
<i>Pternistis bicalcaratus</i> <i>bicalcaratus</i> (6)											
<i>Pternistis griseostriatus</i> (6)								FR694103			
<i>Pternistis adspersus</i> (6)								FR694128			
<i>Pternistis capensis</i> (6)								FR694122			
<i>Pternistis hildebrandti</i> <i>hildebrandti</i> (5)								FR694125			
<i>Pternistis natalensis</i> (6)								FR694130			
<i>Pternistis clappertoni</i> <i>clappertoni</i> (6)								FR694132			
<i>Pternistis hildebrandti</i> <i>johnstoni</i> (1)								FR694126			
<i>Pternistis clappertoni</i> <i>sharpii</i> (1)											
<i>Pternistis harwoodi</i> (1)											
<i>Pternistis leucoscepus</i> <i>infuscatus</i> (1)											
<i>Pternistis swainsonii</i> <i>swainsonii</i> (9)								FR694134			
<i>Pternistis leucoscepus</i> <i>leucoscepus</i> (6)								FR694131			AF532470

Appendix 2.2f (continued)

Marker Taxon no. bases	RAG1 172 855	RAG2 15 926	RDP1 EX 18 958	RDP1 IN 131 032	RHO 252 162	TGFB2 462 717	TPM1 12 477	TYR 35 772	TYRP1 35 267	TYRP2 35 233	WPG 29 331
<i>Pternistis cranchii</i> cranchii (1)											
<i>Pternistis rufopictus</i> (1)											
<i>Pternistis afer humboldti</i> (1)											
<i>Pternistis afer</i> SA (6)								FR694123			
<i>Francolinus pintadeanus</i> (12)											
<i>Francolinus pictus</i> (1)											
<i>Francolinus francolinus</i> (6)								FR694112			
<i>Bambusicola thoracica</i> (16)											
<i>Bambusicola fytchii</i> (2)											
<i>Gallus lafayetii</i> (16)											
<i>Gallus varius</i> (16)											
<i>Gallus sonneratii</i> (25)											
<i>Gallus gallus</i> (52)	NM001031188	AY443150		AY952757	Unpub.	FR694110	NM205401	EF571135	EF571101	EF571064	AF532471
<i>Francolinus pondicerianus</i> (13)						FR694114		EF571136	NM205045	AF023471	AF532472
<i>Francolinus gularis</i> (1)									EF571113	EF571065	
<i>Dendroperdix sephaena</i> SA (6)								FR694111			
<i>Dendroperdix sephaena</i> rovuma (1)											
<i>Dendroperdix sephaena</i> grantii (1)											
<i>Francolinus lathami schubotzi</i> (1)											
<i>Francolinus lathami</i> (6)								FR694113			
<i>Peliperdix schlegelii</i> (1)											
<i>Peliperdix albogularis meinertzthalieni</i> (1)											
<i>Peliperdix albogularis buckleyi</i> (1)											
<i>Peliperdix albogularis albogularis</i> (1)											
<i>Peliperdix coqui stuhlmanni</i> (1)											
<i>Peliperdix coqui kasaicus</i> (1)											
<i>Peliperdix coqui hubbardi</i> (1)											
<i>Peliperdix coqui maharao</i> (1)											
<i>Peliperdix coqui spinetorum</i> (1)											
<i>Peliperdix coqui coqui</i> (6)								FR694115			
<i>Peliperdix coqui vernayi</i> (1)											
<i>Peliperdix coqui ruahdae</i> (1)											
<i>Scleroptila streptophorus</i> (6)											
<i>Scleroptila levaillantii</i> (12)									FR694120		
<i>Scleroptila finschi</i> (2)									FR694117		
<i>Scleroptila whytei</i> (2)										EF571137	
<i>Scleroptila psilolaemus theresae</i> (1)										EF571103	
<i>Scleroptila psilolaemus</i> (1)											EF571066
<i>Scleroptila uluensis</i> (1)											
<i>Scleroptila gutturalis</i> (1)											
<i>Scleroptila shelleyi</i> SA (6)											
<i>Scleroptila jugularis</i> (1)											
<i>Scleroptila levaillantoides</i> (1)											
<i>Scleroptila africanus</i> (9)											
<i>Scleroptila levaillantoides pallidior</i> (1)											
<i>Scleroptila ellenbecki</i> (1)											

AF532469

Appendix 2.2f (continued)

Appendix 2.2f (continued)