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Phylogenetics, biogeography and classification of, and character evolution in, gamebirds (Aves: Galliformes): effects of character exclusion, data partitioning and missing data

Timothy M. Crowe[1,2,*], Rauri C. K. Bowie[3], Paulette Bloomer[4], Tshifhiwa G. Mandiwana[1,5], Terry A. J. Hedderson[6], Ettore Randi[7], Sergio L. Pereira[8] and Julia Wakeling[1]

[1]*DST/NRF Center of Excellence in Birds at the Percy FitzPatrick Institute, Department of Zoology, University of Cape Town, Private Bag Rondebosch 7701, South Africa;* [2]*Department of Ornithology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024-5192, USA;* [3]*Department of Botany and Zoology, University of Stellenbosch, Private Bag X1, Matieland 7602, South Africa;* [4]*Department of Genetics, University of Pretoria, Pretoria 0001, South Africa;* [5]*Department of Ornithology, Transvaal Museum, Northern Flagship Institution, PO Box 413, Pretoria 0001, South Africa;* [6]*Department of Botany, University of Cape Town, Private Bag X1, Rondebosch 7701, South Africa;* [7]*Istituto Nazionale per la Fauna Selvatica, Laboratorio di Genetica, Via Cà Fornacetta 9, 40064 Ozzano Emilia (BO), Italy;* [8]*Department of Natural History, Royal Ontario Museum, 100 Queen's Park, Ont., Canada M5S 2C6*

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Abstract

The phylogenetic relationships, biogeography and classification of, and morpho-behavioral (M/B) evolution in, gamebirds (Aves: Galliformes) are investigated. In-group taxa (rooted on representatives of the Anseriformes) include 158 species representing all suprageneric galliform taxa and 65 genera. The characters include 102 M/B attributes and 4452 nucleic acid base pairs from mitochondrial cytochrome *b* (CYT *B*), NADH dehydrogenase subunit 2 (ND2), 12S ribosomal DNA (12S) and control region (CR), and nuclear ovomucoid intron G (OVO-G). Analysis of the combined character data set yielded a single, completely resolved cladogram that had the highest levels of jackknife support, which suggests a need for a revised classification for the phasianine galliforms. Adding 102 M/B characters to the combined CYT *B* and ND2 partitions (2184 characters) decisively overturns the topology suggested by analysis of the two mtDNA partitions alone, refuting the view that M/B characters should be excluded from phylogenetic analyses because of their relatively small number and putative character state ambiguity. Exclusion of the OVO-G partition (with > 70% missing data) from the combined data set had no effect on cladistic structure, but slightly lowered jackknife support at several nodes. Exclusion of third positions of codons in an analysis of a CYT *B* + ND2 partition resulted in a massive loss of resolution and support, and even failed to recover the monophyly of the Galliformes with jackknife support. A combined analysis of putatively less informative, "non-coding" characters (CYT *B*/ND2 third position sites + CR + 12S + OVO-G sequences) yielded a highly resolved consensus cladogram congruent with the combined-evidence cladogram. Traditionally recognized suprageneric galliform taxa emerging in the combined cladogram are: the families Megapodiidae (megapodes), Cracidae (cracids), Numididae (guineafowls), Odontophoridae (New World quails) and Phasianidae (pheasants, pavonines, partridges, quails, francolins, spurfowls and grouse) and the subfamilies Cracinae (curassows, chachalacas and the horned guan), Penelopinae (remaining guans), Pavoninae *sensu lato* (peafowls, peacock pheasants and argus pheasants), Tetraoninae (grouse) and Phasianinae (pheasants minus *Gallus*). The monophyly of some traditional groupings (e.g., the perdicinae: partridges/quails/francolins) is rejected decisively, contrasted by the emergence of other unexpected groupings. The most remarkable phylogenetic results are the placement of endemic African galliforms as sisters to geographically far-distant taxa in Asia and the Americas. Biogeographically, the combined-data cladogram supports the hypothesis that basal lineages of galliforms diverged prior to the Cretaceous/Tertiary (K-T) Event and that the subsequent cladogenesis was influenced by the break-up of Gondwana. The evolution of gamebirds in Africa, Asia and the Americas has a far more complicated historical biogeography than suggested to date. With regard to character evolution: spurs appear to have evolved at least twice within the Galliformes; a relatively large number of tail feathers (≥ 14) at least three times; polygyny at least twice; and sexual dimorphism many times.

*Corresponding author: *E-mail address:* tmcrowe@botzoo.uct.ac.za

Cladistic analysis of taxonomic characters, i.e., features that are effectively invariant within (and variable among) the taxa under study (Nixon and Wheeler, 1990), is central to the inference of phylogenetic relationships among taxa and in developing meaningful systems of classification (Farris, 1983). Cladists who base their research on morphological and behavioral characters have little difficulty in deciding what to do *a priori* with characters. They analyze them, seeking the most parsimonious cladistic hypothesis based on all phylogenetically informative character evidence (Farris, 1983; Kluge, 1989, 2004; Kluge and Wolf, 1993). However, in phylogenetic studies involving nucleic acid characters, especially in analyses of distantly related taxa, some molecular systematists recommend the exclusion, differential weighting or downgrading of some putatively relatively less informative characters to emphasize the contribution of those characters thought to possess stronger phylogenetic signal (Edwards et al., 1991; Irwin et al., 1991; Bull et al., 1993; Kornegay et al., 1993; Swofford et al., 1996; Bowie et al., 2005). For example, at various stages in their study of complete sequences of mitochondrial cytochrome *b* (CYT *B*) from nine exemplar gamebird (chicken-like birds) species within the avian order Galliformes, Kornegay et al. (1993): (1) downgraded DNA sequence data to the amino acids for which they code; (2) excluded third position sites; and (3) downgraded first positions of all leucine codons to generic pyrimidines. The implementation of strategies 2 and 3, in their parsimony analyses, resulted in Kornegay et al. (1993) discarding all but 34 of 254 potentially phylogenetically informative characters. In other studies of similar scope, Edwards et al. (1991) and Cracraft and Helm-Bychowski (1991) employed another tactic, transversion analysis, by downgrading all sites to generic purines and pyrimidines.

Another possible *a priori* treatment of potentially phylogenetically informative data favors dividing molecular and other character data into "process partitions" (e.g., some molecular versus other molecular, or all molecular versus all organismal characters) and subjecting them to independent phylogenetic analysis and screening to determine if they are significantly homogeneous to allow meaningful phylogenetic interpretation as a single, combined data set (Bull et al., 1993; Nixon and Carpenter, 1996). Other systematists (e.g., Swofford, 1991; Lanyon, 1993; Miyamoto and Fitch, 1995) have taken a more severe view and maintain that data sets should not be combined if there is evidence of a lack of topological (= taxonomic) congruence (e.g., due to the effects of hybridization) when they are analyzed separately. More recently, Lecointre and Deleporte (2005) have argued for initial separate analysis of partitions to identify [e.g., through use of the Farris et al.'s (1994) incongruence length difference (ILD) test] "relevant" characters, i.e., those that are congruent between data sets. They then propose to treat incongruent data as missing in a combined analysis of all character partitions. Finally, many molecular systematists (e.g., Avise et al., 1994) conduct analyses using a variety of phylogenetic optimality criteria and then compare the topologies obtained from these different approaches, maintaining that topologies that are resilient to different methods of analysis are relatively more robust than those that vary depending on the method of analysis.

More recently, some molecular systematists have suggested that morphological and behavioral characters should be excluded from primary phylogenetic analyses, and should only be studied within the context of cladograms derived from the analysis of molecular characters only (Scotland et al., 2003). The primary justifications underpinning this suggestion are that the relatively large number of molecular characters will produce cladograms with greater accuracy and precision, and that molecular characters are inherently less "ambiguous" than the generally fewer morpho-behavioral (M/B) characters. In the present study, we investigate the empirical consequences of some of these systematic strategies by analyzing a range of character data partitions for gamebirds (Aves: Galliformes).

Galliformes: taxonomy, classification and phylogeny

Applying the relatively conservative (Cracraft, 1983) Biological Species Concept (Mayr, 1942), there are 281 currently recognized species of gamebirds within the Order Galliformes divided among 81 genera (Sibley and Monroe, 1990; del Hoyo et al., 1994; Hockey et al., 2005). These are currently assigned to seven families (Sibley and Ahlquist, 1985, 1990; del Hoyo et al., 1994; Table 1).

In the last comprehensive premolecular classification of birds of the world, Wetmore (1960) split the Galliformes into two superfamilies: (1) the Cracoidea—including two families, the megapodes (Megapodiidae) and cracids (Cracidae), and (2) the Phasianoidea—including four families, the grouse (Tetraonidae), quails, pheasants, peafowl, partridges and francolins (Phasianidae), guineafowls (Numididae) and turkeys (Meleagrididae). Research by Hudson et al. (1959, 1966) and Hudson and Lanzillotti (1964) based on studies of appendicular musculature supported Wetmore's classification. Based on cladistic interpretations of morphological and behavioral characters, Cracraft (1981, 1988) and Crowe (1988) concluded that the cracids were sister to the balance of the phasianoids and not the megapodes, which they placed as basal within the order. This hypothesis was supported by more extensive M/B research by Brom and Dekker (1992) and Dyke et al. (2003), although the resolution in the latter's cladogram

Table 1
Taxa attributed to the Galliformes by del Hoyo et al. (1994). Numbers in parentheses are those of species and genera investigated in this study

Scientific and common names	Range	No. of species	No. of genera
Megapodiidae megapodes, scrubfowl, brush-turkeys	Australasian	19 (6)	7 (4)
Cracidae cracids: curassows, guans and chachalacas	Neotropical	50 (28)	11 (11)
Numididae guineafowls	Afrotropical	6 (5)	4 (4)
Phasianidae pheasant-like birds	cosmopolitan		
Phasianinae pheasants, junglefowls (= chickens), peafowl and peacock- and argus-pheasants)	Afro/Asiotropical	49 (45)	16 (16)
Perdicinae partridges, francolins and Old World quails	Palaearctic and Afro/Asiotropical	106 (49)	26 (18)
Meleagrididae turkeys	Nearctic	2 (1)	1 (1)
Tetraonidae grouse	Holarctic	17 (17)	7 (7)
Odontophoridae New World quails	Neotropical and Nearctic	32 (7)	9 (4)

(Fig. 1) was poor within the guineafowls and other phasianine suprageneric clades due the remarkable osteological uniformity of "higher" galliforms, especially phasianids (Verheyen, 1956). Nevertheless, the most recent classification/phylogeny of the Galliformes that deals with all suprageneric taxa from both M/B and molecular perspectives (del Hoyo et al., 1994; Table 1) takes Wetmore's (1960) position and places the families Megapodiidae and Cracidae as sister taxa within the suborder Cracini, and groups the balance of the taxa into five families (including the four recognized by Wetmore with the New World quails, Odontophoridae, accorded family status) into a sister suborder, the Phasiani. The phylogenetic status of the families comprising the Phasiani is unresolved in the cladogram presented in del Hoyo et al. (1994). The only phylogenetic resolution within the Phasiani is the partitioning of the Phasianidae into the sister subfamilies Phasianinae (pheasants, junglefowls, peafowls and allies) and Perdicinae (partridges, quails, francolins and spurfowls). Johnsgard (1973, 1986, 1988, 1999) provides a much more fully resolved suprageneric phylogeny (but somewhat different classification) for gamebirds (Fig. 2) based on a subjective evaluation of M/B information within which the still more fully resolved relationships among the megapodes follow those as suggested by Jones et al. (1995); cracids by Delacour and Amadon (1973) and guineafowls by Crowe (1978). Until we present our best-resolved phylogeny and a revised classification based thereon, the terminology given in Fig. 2 will be used.

A range of suprageneric phylogenetic investigations, covering different subsets of the gamebirds, have been undertaken with molecular data (e.g., Sibley and Ahlquist, 1972, 1985, 1990; Ho et al., 1976; Jolles et al., 1976; Helm-Bychowski and Wilson, 1986; Laskowski and Fitch, 1989; Randi et al., 1991; Kornegay et al., 1993; Avise et al., 1994; Sibley, 1994; Mindell et al., 1997; Kimball et al., 1999; Lucchini and Randi, 1999; Dimcheff et al., 2000, 2002; Armstrong et al., 2001; Ericson et al., 2001; Bush and Strobeck, 2003; Dyke et al., 2003; Pereira and Baker, 2006) (Fig. 3a–f). These have, at least in part, been reviewed by Crowe (1988), Sibley and Ahlquist (1990), Sheldon and Bledsoe (1993) and Pereira and Baker (2006). However, few of these studies have sampled species from all of the putative suprageneric taxa listed in Table 1, sampled multiple exemplars for these clades, or employed logical outgroups to root their cladograms. For example, Jolles et al. (1976) analyzed exemplars of only five in-group gamebird genera and used *Homo sapiens* as an outgroup. In fact, only Lucchini and Randi (1999) included more than 30 ingroup gamebird genera in their study, but were unable to include any cracids or a non-galliform outgroup in their research and rooted their cladogram (Fig. 3f) on a megapode. Furthermore, as with the M/B research of Dyke et al. (2003), many of these studies resulted in poorly resolved cladograms and/or clade nodes with low or no nodal support (Fig. 3d–f).

Thus, despite the existence of a relatively large body of potentially useful morphological, behavioral and

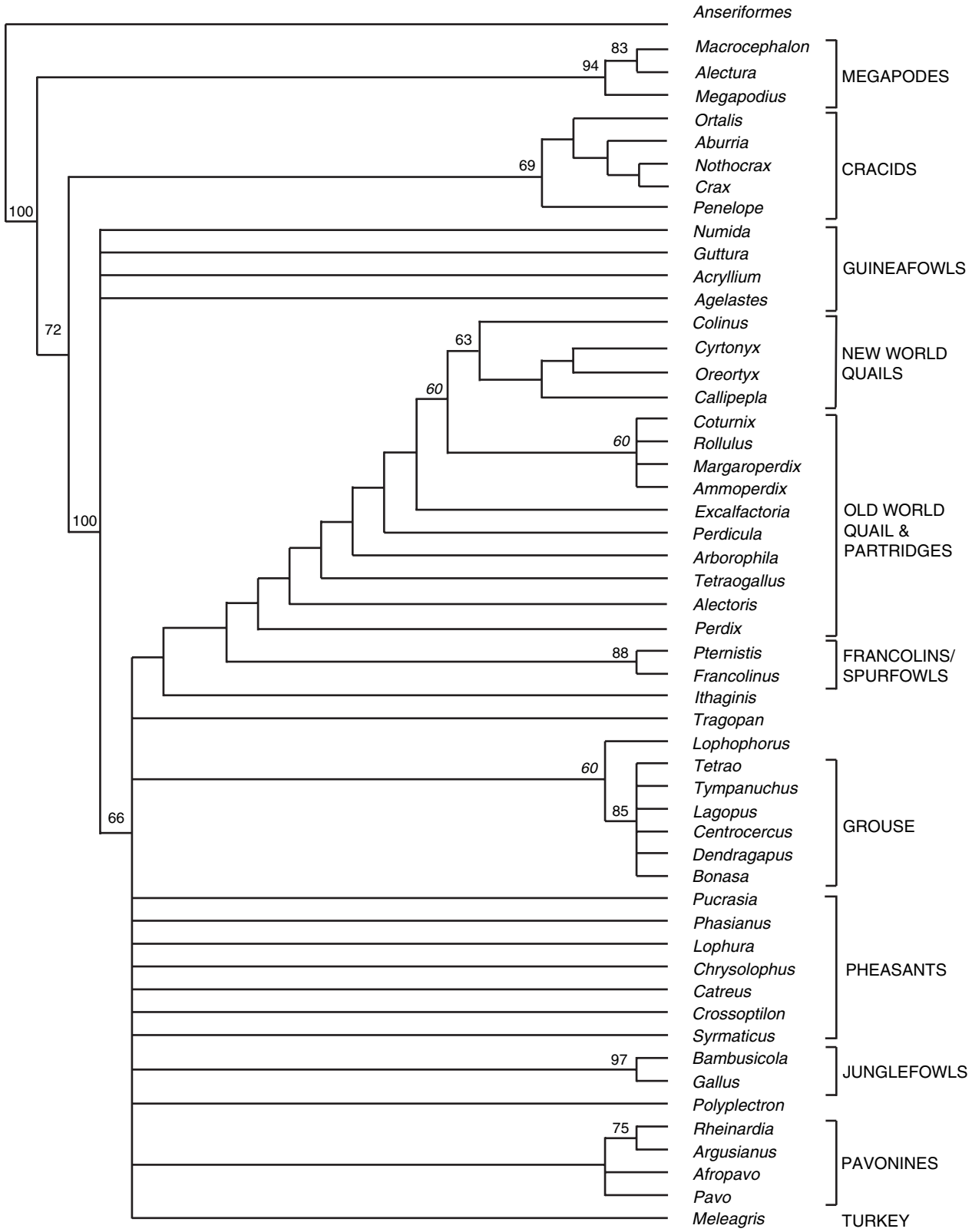

Fig. 1. The strict consensus morpho-behavioral parsimony cladogram from Dyke et al. (2003), including only taxa analyzed in the present study. Numbers above nodes in normal font are jackknife support values from a reanalysis of the data. Those in italics are bootstrap support values found in Dyke et al. (2003), but not in the reanalysis of the data for the taxa analyzed in the present study.

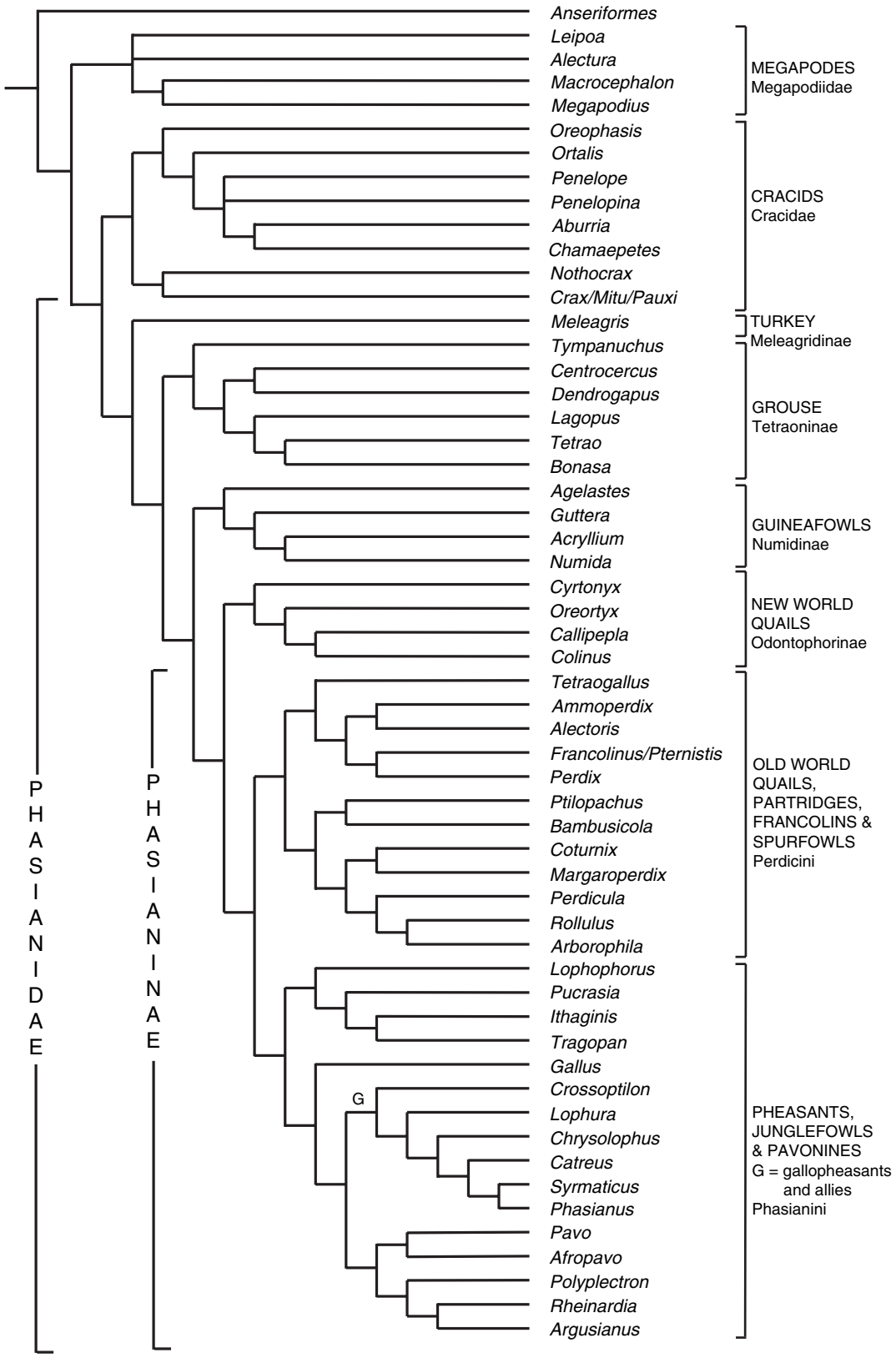

Fig. 2. A "traditional" classification/phylogeny for the galliform genera studied in here adapted from Johnsgard (1973, 1986, 1988, 1999), Jones et al. (1995), Delacour and Amadon (1973) and Crowe (1978).

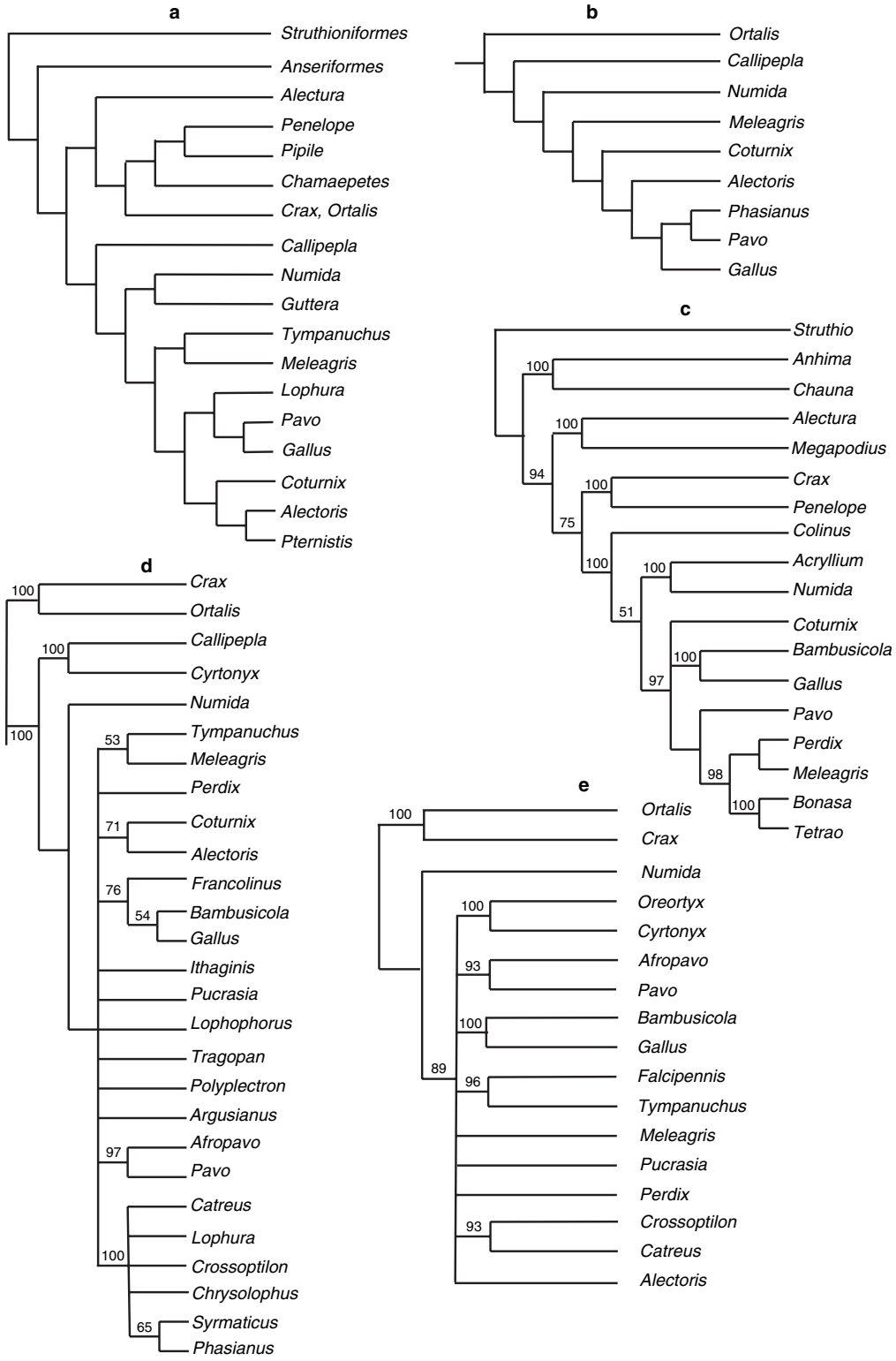

Fig. 3. Cladograms from various molecular phylogenetic analyses of gamebirds, methods of analysis and values for nodal support: (a) DNA–DNA hybridization, distance (Sibley and Ahlquist, 1990); (b) mitochondrial cytochrome *b* sequences, parsimony (Kornegay et al., 1993); (c) mitochondrial cytochrome *b*, 12s rDNA and ND2 sequences, Bayesian, bootstrap (Pereira and Baker, 2006); (d) mitochondrial cytochrome *b* sequences, parsimony, bootstrap (Kimball et al., 1999); (e) nuclear intron ovomucoid G sequences, parsimony, bootstrap (Armstrong et al., 2001); (f) mitochondrial control region, parsimony, jackknife (Lucchini and Randi, 1999).

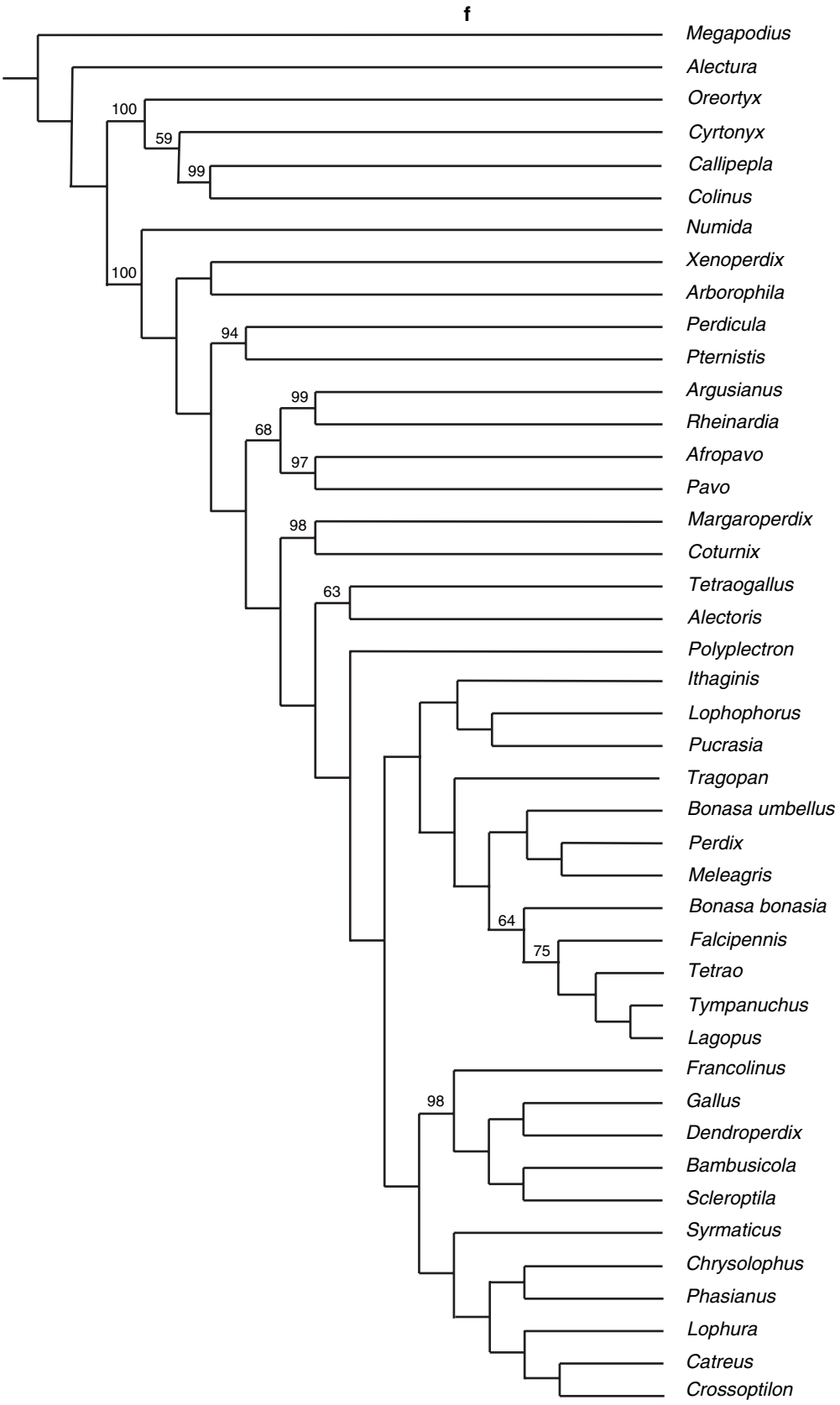

Fig. 3. *Continued.*

molecular information, a well-resolved and supported cladogram adequately representing all putative gamebird suprageneric taxa has not been realized and there remains a lack of consensus on the phylogeny and classification of the group (Figs 1–3). The late Charles Sibley provides examples of extreme positions on classification. At one stage (Sibley, 1960), he suggested that only two families be recognized in a single order, but more recently (Sibley and Monroe, 1990), based on results of DNA–DNA hybridization studies, he maintained that one superorder, two orders, two suborders, two parvorders, two superfamilies and five families warrant recognition.

The phylogenetic status of the gamebirds at the onset of this study may be summarized thus. There is overwhelming morphological and molecular evidence (reviewed by Cracraft and Clarke, 2001; Mayr and Clarke, 2003; Fig. 3a,c) for the status of ducks, geese and screamers (Order Anseriformes) as the sister group of the Galliformes. Ericson (1996) and Ericson et al. (2001) challenged this sister relationship based on morphological and molecular evidence, but reversed this opinion (Ericson et al., 2001) once they became aware of the results of analyses of sequences of RAG-1, a nuclear protein-coding gene, by Groth and Barrowclough (1999). There is also general agreement on the monophyly of the order (Figs 1, 2 and 3a,c), although some studies based on immunological distances (Jolles et al., 1976, 1979; Prager and Wilson, 1976) suggested that *Anas* spp. of anseriforms might be more closely related to the balance of the gamebirds than are the cracids. There is also evidence for the monophyly of: the Megapodiidae (Birks and Edwards, 2002; Figs 1 and 3c), Cracidae (Pereira et al., 2002; Figs 1 and 3a,c); Numidinae (Crowe, 1978; Fig. 3a,c); Odontophorinae (Gutierrez et al., 1983; Figs 1 and 3d–f) and Tetraoninae (Gutierrez et al., 2000; Dimcheff et al., 2002; Drovetski, 2002; Figs 1 and 3c,e); and the basal divergence of megapodes and cracids within the order (Cracraft, 1981, 1988; Crowe, 1988; Garcia-Moreno et al., 2003; Figs 1 and 3a,c). Olson (1980) suggested that the megapodes might be cladistically relatively terminal, closer to the Phasianidae, but provided no cladistic evidence for this hypothesis. Like Wetmore (1960), Laskowski and Fitch (1989) and Sibley and Ahlquist (1990) concluded that megapodes and cracids are sister to one another (Fig. 3a), but this has not been supported by any other M/B or molecular research (e.g., Figs 1 and 3c). All published DNA-based molecular studies to date (except Armstrong et al., 2001; Fig. 3e) place the New World quails phylogenetically basal relative to the guineafowls (Fig. 3a,b,d,f), but generally without nodal support (Fig. 3a–d,f). It has also been suggested that the Phasianini and Perdicini as shown in Fig. 2 might not be monophyletic (Kimball et al., 1999; Fig. 3d; Lucchini and Randi, 1999; Fig. 3f; Bush and Strobeck, 2003; Pereira and Baker, 2006; Fig. 3c), but the cladograms in question generally lack adequate numbers of exemplars, and the clades concerned are poorly resolved and often lack nodal support. The one exception to this is the relatively decisive placement of *Gallus* (grouped with pheasants in Fig. 2) with or near to the bamboo partridges *Bambusicola* spp. (Fumihito et al., 1995; Fig. 3c–f). Furthermore, within the Perdicini *sensu* Fig. 2, Crowe and Crowe (1985), Crowe et al. (1992) and Bloomer and Crowe (1998) presented evidence that questioned, but did not decisively reject, the monophyly of the francolins (*Francolinus sensu* Hall, 1963; Sibley and Monroe, 1990; del Hoyo et al., 1994; Dyke et al., 2003), the largest (41 species) genus within the Galliformes (del Hoyo et al., 1994). Crowe et al. (1992) and Bloomer and Crowe (1998) split *Francolinus* into several genera (analyzed separately here) divided between two major groups, the francolins (*Francolinus*, *Peliperdix*, *Dendroperdix* and *Scleroptila* spp.) and spurfowls (*Pternistis* spp. *sensu* Little and Crowe, 2000). Another novel, but once again tentative, hypothesis that emerges from Fig. 3 is that the gray partridge (*Perdix perdix*), wild turkey (*Meleagris gallopavo*) and grouse (Tetraoninae) might be related cladistically (Fig. 3a,c,d,f).

Biogeography

There is perhaps an even greater lack of consensus on the biogeographical relationships of gamebirds than on their phylogenetic relationships. Based on the presence of putative stem group Eocene galliform and Oligocene cracid fossils in North America (Tordoff and Macdonald, 1957; Mayr and Weidig, 2004) and Eocene and Oligocene fossil megapodes from Europe (Mourer-Chauvire, 1992), Vuilleumier (1965), Delacour and Amadon (1973), Olson (1980) and Mayr and Weidig (2004) hypothesized that these galliform families have their biogeographical origins in the Northern Hemisphere and that stem galliforms originated only after the Cretaceous–Tertiary mass extinction event (65 Ma). Crowe (1978) speculated that guineafowls were derived from a francolin-like ancestor that dispersed from Asia to Africa in the mid-Miocene. However, based on reassessments of the above-mentioned fossils by Crowe and Short (1992) and Dyke (2003), assessments of newly discovered Eocene galliform fossils from North America (Gulas-Wroblewski and Wroblewski, 2003) and Europe (Lindow et al., in review) and on morphological (Cracraft, 1981; Crowe, 1988; Dyke et al., 2003) and molecular clock (Cracraft, 2001; Groth and Barrowclough, 1999) phylogenetic analyses, a Southern Hemisphere origin prior to, or relatively soon after, the Cretaceous–Tertiary event is supported. Moreover, there is now a definite anseriform fossil from the late Cretaceous of

Antarctica (Clarke et al., 2005). Furthermore, research based on analyses of mtDNA sequences by Van Tuinen and Dyke (2004) and Pereira and Baker (2006) using the ages of some of the above-mentioned fossil galliforms as calibration anchorpoints has produced molecular clock phylogenies that also suggest that the gamebirds originated on Gondwana and that the basal megapodes, cracids and, probably, the New World quails originated in the Cretaceous.

Aims and approach

Our aims in this study were to: analyze existing and new information on a range of M/B and molecular characters to infer the suprageneric phylogenetic relationships within the Galliformes; investigate congruence among the M/B and molecular data partitions; evaluate the effects of character exclusion and missing data on cladogram topology and nodal support; offer a phylogenetic classification of the Galliformes; investigate the evolution of M/B characters in galliforms and explore the biogeographical implications of the phylogeny.

Materials and methods

Taxon sampling

Taxa studied herein (Appendix 1) include 158 galliform (of 281 currently recognized) species representing all suprageneric galliform taxa and 65 of 81 genera and multiple representatives of all suprageneric taxa ascribed to the Galliformes (Johnsgard, 1973, 1986, 1988, 1999; Sibley and Monroe, 1990; del Hoyo et al., 1994; Hockey et al., 2005) are included. The choice of outgroups on which to root cladograms is based on the assumption that the Anseriformes (ducks, geese and screamers) are sister to the Galliformes (Sibley and Ahlquist, 1990; Groth and Barrowclough, 1999; Cracraft and Clarke, 2001). The exemplars used as outgroups are the magpie goose *Anseranas semipalmata* and two screamers *Chauna torquata* and *Anhima cornuta*.

Character sampling

Morpho-behavioral characters

The taxa were scored for the 102 M/B characters employed by Dyke et al. (2003). All multistate M/B characters were treated as ordered in accordance with Dyke et al. (2003).

Molecular characters

Molecular characters include published and unpublished DNA sequences of nuclear ovomucoid G intron (OVO-G: $n = 492$ bp including insertions/deletions) and mitochondrial CYT *B* ($n = 1143$ bp), NADH dehydrogenase subunit 2 (ND2: $n = 1041$ bp) gene, 12S rDNA (12S—preferred alignment = 731 bp including insertions/deletions) and the control region (CR: preferred alignment = 1030 bp including insertions/deletions) (Appendix 2).

Laboratory techniques

DNA was extracted from blood, heart or liver tissue using the DNeasy animal tissue protocol provided with the DNeasy tissue kit (Qiagen, Valencia, CA). Primers used for PCR amplification and sequencing of CYT *B*, NADH2 and OVO-G are indicated in Table 2. Galliform-specific primers were designed (Table 2) for *Pternistis griseostriatus* and *P. leucoscepus*, because the initial CYT *B* primer pair (L14578, H16065) did not amplify. All primers are numbered according to the position of the 3′ base of the primer in the complete chicken mitochondrial DNA genome (Desjardins and Morais, 1990).

Double-stranded DNA templates were amplified by the polymerase chain reaction (PCR) using 0.75 units of BIOTAQ DNA polymerase (Bioline, Randolph, MA) in 30 μL reactions. Reactions also contained $1 \times NH_4$ buffer, 2.5 mM $MgCl_2$, each dNTP at 0.1 mM and each

Table 2
Primers used for DNA amplification and sequencing

Gene region	Primer name	Primer sequence	Reference
Cytochrome *b*	L14578	5′-CTAGGAATCATCCTAGCCCTAGA-3′	J.G. Groth pers. comm.
(initial primer pair)	H16065	5′-AACGCAGTCATCTCCGGTTTACAAGAC-3′	Irwin et al. (1991)
(internal)	L15236	5′-TTCCTATACAAAGAAACCTGAAA-3′	Edwards et al. (1991)
(galliform	ML15131	5′-AACGTACAGTACGGCTGACTCAT-3′	P. Beresford pers. comm.
specific)	MH15907	5′-TGTTCTACTGGTTGGCTTCCAAT-3′	
ND2	L5216	5′-GCCCATACCCCRAAAATG-3′	Sorenson et al. (1999)
	H6313	5′-CTCTTATTTAAGGCTTTGAAGGC-3′	
OVO-G	Forward	5′-CAAGACATACGGCAACAARTG-3′	Armstrong et al. (2001)
	Reverse	5′-GGCTTAAAGTGAGAGTCCCRTT-3′	
12S rDNA	L1555	5′-AATCTTGTGCCAGCCACCGCGG-3′	O. Haddrath (S. Pereira, pers.comm.)
	H2241	5′- GTGCACCTTCCGGTACACTTACC-3′	

primer at 0.3 μM. Three microliters of the undiluted and unquantified DNA extraction were used as template. The thermal profile used for all three DNA regions comprised an initial denaturation step at 94 °C for 2 min, followed by 30 cycles of 94 °C for 1 min, 52 °C for 1 min and 72 °C for 2 min, with a final extension step of 72 °C for 7 min. The PCR cycling was performed by a GeneAmp PCR System 2700 (Applied Biosystems, Foster City, CA).

Amplified products were cleaned from solution or gel using the GFX PCR-DNA and gel band purification kit (Amersham Biosciences, Little Chalfont, UK) prior to cycle sequencing with the ABI PRISM Big Dye Terminator V3.1 cycle sequencing Ready Reaction Kit (Applied Biosystems). Sequencing products were resolved on an ABI PRISM 3100 Genetic Analyzer. Sequences were assembled and checked for incorrect base calling and the presence of stop codons using SeqMan II (LaserGene systems software, DNAstar, Inc.) or Sequencher (GeneCodes, Ann Arbor, MI). Consensus sequences were aligned by Clustal X (Thompson et al., 1997) and adjusted manually using MegAlign (LaserGene systems software, DNAstar, Inc., Madison, WI). The alignment of 12S rDNA and control region sequences was done in Clustal X (Thompson et al., 1997) using several different gap opening and gap extension penalties. The preferred alignment, including insertions/deletions for the 12S partition included 731 bp and indels. The aligned control region sequence ($n = 1046$ bp plus indels) was then adjusted manually in regions of hypervariability and length heterogeneity within domains I and III in accordance with Lucchini and Randi (1999).

Analytical approaches: parsimony

Each of the six data partitions (Table 3, M/B, CYT *B*, ND2, 12S, CR, OVO-G) was analyzed independently and as a single combined data set. The DNA-based partitions were also analyzed in combination in contrast to the M/B partition. In order to assess the effects of adding a partition with large amounts of missing data, the combined analysis was run minus the OVO-G partition, which had more than 70% missing data. To assess any potential cladistic variation between M/B and DNA-based data, all DNA partitions were combined and analyzed simultaneously. To determine the relative phylogenetic merits of DNA characters that influence the amino acids produced, the two coding partitions (CYT *B* and ND2) were analyzed in combination stripped of their third codon position bases. Finally, a "non-coding" partition (third positions of CYT *B* and ND2, 12S, CR and OVO-G sequences) was analyzed to explore the utility of characters less constrained by biochemical function in recovering a meaningful cladogram.

All parsimony-based phylogenetic analyses were conducted using Winclada version 0.9.99m24 (BETA) (Nixon, 1992) and Nona Version 2.0 (Goloboff, 1993). The search strategy employed was the default Ratchet Island Hopper option: 200 iterations/rep; one tree to hold/iteration; four characters to sample, amb-poly, and random constraint level 10. When multiple, equally parsimonious cladograms persisted, a strict consensus cladogram was constructed. The extent to which each non-terminal node is supported by character data was determined by using the "jackknife" program XAC (Farris et al., 1996; Källersjö et al., 1998) using the following strategy: 1000 replications, branch swapping switched on, random addition of five sequences per replicate, and $p = e^{-1}$ (about 37%) of the characters deleted per jackknife replicate. We assessed the pair-wise congruence between the various data partitions and between combinations of partitions (e.g., combined DNA partitions versus the M/B partition and nuclear OVO-G partitions versus the combined mitochondrial DNA partitions) with the Winclada implementation of the ILD test (Farris et al., 1994).

Bayesian inference

Model-based analyses were conducted on a truncated data set of 66 taxa that had DNA sequence data for at least three of the five molecular partitions (Appendix 1). Modeltest 3.6 (Posada and Crandall, 1998) was used to determine which model of nucleotide evolution was most appropriate for each of the five data partitions. Under the Akaike Information Criterion variants of the General Time Reversible Model (GTR) were identified as most appropriate for each of the five data partitions.

Table 3
Information on character data partitions

Data set	No. of chars	No. of in-group taxa	% missing cells	No. of informative chars
Morpho-behavioral (M/B)	102	158	<< 1	102
Mitochondrial cytochrome b (CYT B)	1143	158	12	547
Mitochondrial ND2 (ND2)	1041	119	42	594
Mitochondrial control region (CR)	1046	97	53	418
Mitochondrial 12S rDNA (12S)	731	69	61	302
Ovomucoid intron G (OVO-G)	492	52	73	179

MrBayes 3.1 (Ronquist and Huelsenbeck, 2003) was used to undertake the Bayesian approach to phylogenetic inference (BI). Four Metropolis-coupled MCMC chains (one cold and three heated chains) were run simultaneously to optimize efforts to find peaks in tree-space. Initially, two runs each of 2 million generations were implemented under the GTR model of nucleotide substitution, employing a gamma distribution (estimated using four rate categories) and estimation of the proportion of invariable sites implemented (GTR + I + G) to accommodate site-to-site variation in evolutionary rates. A separate set of parameters was estimated for each data partition (i.e., the data partitions were unlinked, Appendix 3). The average standard deviation of the split frequencies was 0.0134. This search strategy was repeated in a single run of 5 million generations. Each run started from a random tree and set of initial parameters. A Dirichlet distribution was assumed for estimation of the base frequency parameters and an uninformative (flat) prior was used for the topology. Trees were sampled every 100 or 250 generations in the 2 million and 5 million generation runs, respectively. This resulted in a sample of 20001 trees for each analysis. A conservative approach was adopted for estimating the number of cycles to discard (the burn-in) and was set as 20% (4001 trees).

Character evolution

Based on information from del Hoyo et al. (1994), the presence of four characters reputed to be under the influence of sexual selection (spurs, a large number of tail feathers, polygynous mating system and sexual plumage/integument dimorphism) (Andersson, 1994) were mapped on to our best resolved cladogram.

Divergences inferred from a galliform relaxed molecular "clock"

Estimation of divergence times requires calibration against fossils of known age. We used the ages of two galliform fossils that have been placed cladistically to calibrate this clock: *Gallinuloides wyomingensis* (54 Ma) and *Amitabha urbsinterdictensis* (50 Ma). Crowe and Short (1992) and Dyke (2003) consider *Gallinuloides* to be a crown-group galliform and the former authors placed it as sister to the phasianines, i.e., New World quails and non-numidine phasianids *sensu* del Hoyo et al. (1994). Based on assessment of 39 of the 102 M/B characters employed in the present study, Dyke (2003) placed *Gallinuloides* at the stem of the Phasianoidea: phasianines plus the guineafowls, Numididae *sensu* del Hoyo et al., 1994). Gulas-Wroblewski and Wroblewski, 2003) place *Amitabha* at the stem of the phasianines. Mayr and Weidig (2004) and Mayr (2005) dispute the placement of *Gallinuloides* and *Amitabha* within the crown Galliformes, and place them as stem-group Galliformes, cladistically basal to all modern galliforms based largely on its possession of a cup-like scapular articulation facet on the coracoid (a plesiomorphic character within neornithines that is also present in Anseriformes). Based on a reassessment of the original *Gallinuloides* fossil specimen and investigations of the second specimen described by Mayr and Weidig (2004) and a new gallinuloid fossil from Lower Eocene deposits in Denmark, Lindow et al. (in review) were able to score *Gallinuloides* for 52 of the 102 M/B characters assessed by Dyke et al. (2003) and reassessed characters that Mayr and Weidig (2004) suggested were coded incorrectly. Parsimony-based cladistic analysis of this new, larger matrix (Lindow et al., in review) once again places *Gallinuloides* with the crown Galliformes and basal to the phasianoids.

The cladogram based on all data combined was the most resolved and best supported and we subsequently accepted this as the best estimate of phylogeny. Therefore we constrained each of the independent data sets to this topology. These analyses were also restricted to the 66 taxa for which the DNA partitions were relatively well-sampled (Appendix 1). The hypothesis of rate constancy was tested for each data set using likelihood ratio tests between rate-constrained and unconstrained trees, and in each case constancy could be rejected ($P < 0.02$).

We estimated ages in three ways. In the first two cases, branch lengths were estimated for each data set under (1) parsimony, and (2) under the likelihood models described for each data set above. In each case, ultrametric trees were produced for each data set using Sanderson's (1997) non-parametric rate smoothing (NPRS) approach as implemented in Tree Edit (Rambaut and Charleston, 1999). The trees were then scaled using the 54 Ma date for the split between guineafowls and other phasianoid birds from megapodes and cracids. Of the possible calibration ages available, we used this split since it is relatively close to the critical nodes that we wished to estimate. Divergence of age estimates from "true ages" tends to increase with distance from the calibration point under most smoothing techniques (e.g., Wikstrom et al., 2001).

In addition, the posterior distribution of divergence times was also approximated under a Bayesian approach (Thorne and Kishino, 2002). For each molecular partition, maximum likelihood estimates of the transition/transversion ratio, nucleotide frequencies and shape parameter of a five-category gamma distribution for among-site rate variation were obtained in PAML 3.14 (Yang, 1997). These estimates were used to obtain a matrix of branch length variance—covariance for each gene, using the ESTBRANCHES program in the MULTIDISTRIBUTE

package (available from J. Thorne, North Carolina State University). These matrices were then integrated to account for each partition's uncertainty in branch length estimates and used to approximate the Bayesian posterior distribution of divergence times in the MULTIDIVTIME program in MULTIDISTRIBUTE. The following priors were set in the MULTIDIVTIME analysis: expected time between the tip and the ingroup root (rttime) = 95.0 Ma, with standard deviation (SD) = 20 Ma based on a molecular time estimate of Pereira and Baker (2006) obtained from mitochondrial DNA sequence data; rate of the root node (rtrate) and its SD = 0.04 substitution per site per unit time, determined as the median of all the tip-to-root branch lengths for each gene divided by rttime; rate of change between ancestral and descendant nodes (brownmean) = 0.105. Because *a priori* information for rtrate and brownmean are largely unknown, the SD was set as the same values to allow a gene to have *a priori* a large variation in rate at the node and rate change over time (Thorne and Kishino, 2002). The analysis was repeated three times, each starting with a randomly selected initial state, to check for convergence of the Markov chain. For each run, the first 5000 cycles of the chain were discarded, and a sample was taken every 1000 cycles to a total of 10 000 samples. Convergence of the Markov chain was assessed by comparing the mean Bayesian posterior distribution of divergence times and their 95% credible interval among the three independent runs, and checking whether the first three figures of the proportion of successful changes for all parameters estimates were similar.

For the Bayesian analysis, data from the fossil record were also used to provide minimum time constraints as follows: stem Phasianines, i.e., New World quails and non-numidine phasianids *sensu* del Hoyo et al. (1994), set at 50 Ma based on the fossil *Amitabha* placed at the stem of the phasianines (Gulas-Wroblewski and Wroblewski, 2003); stem phasianoids at 54 Ma following Crowe and Short (1992), Dyke (2003) and Lindow et al. (in review) that placed *Gallinuloides wyomingensis* (54–55 Ma) as sister to phasianines in a phylogenetic context [*contra* Mayr and Weidig (2004) and Mayr (2005)]; stem cracids and the separation of the clades containing *Gallus* and *Coturnix* were both set to a minimum of 35 Ma as based on *Procrax* (Tordoff and Macdonald, 1957) and *Schaubortix* (Brodkorb, 1964), respectively. Because a maximum time constraint is advisable for at least one node in the tree, and the fossil record does not provide this information for Galliformes, we set a maximum of 123 Ma for the age of crown Galliformes based on the upper limit of the 95% credible interval obtained by Pereira and Baker (2006) using mitochondrial DNA sequences.

Results

Phylogenetic congruence between the character partitions

None of the pair-wise ILD test comparisons between character partitions yielded statistically significant results, suggesting the absence of phylogenetic incongruence between any of the partitions. Furthermore, there were no significant results for the comparisons between the M/B partition and the combined DNA partitions, and between the nuclear DNA partition (OVO-G) and the four mitochondrial partitions (CYT *B*, ND2, CR, 12S) combined.

Phylogenetic analyses: traditional clades

Combined data (COMB)

The analysis of the combined data set (now with our proposed suprageneric taxonomic terminology) yielded the best resolved and a generally well-supported phylogeny (Table 4) with one most parsimonious tree (length = 18 598; CI = 22; RI = 65) which is presented (with genera as terminals) in Fig. 4 annotated with information on jackknife and Bayesian support, classification and biogeography. In this cladogram, the megapodes are basal (with high jackknife support) followed sequentially by the cracids, guineafowls, New World quails and then the balance of phasianine galliforms (all with high jackknife support). Within this phasianine clade, traditionally recognized suprageneric taxa that emerge with support are the pavonines (peafowls + argus pheasants + peacock pheasants = Pavoninae *sensu lato*), grouse (Tetraoninae) and pheasants minus the junglefowls (*Gallus* spp.) (Phasianinae), although the basal portion of the pheasant clade lacks jackknife support.

Bayesian inference of phylogenetic relationships

The resulting tree based on all DNA partitions combined is essentially the same (with very high posterior probability support) at the suprageneric level as the parsimony tree for all partitions combined (Fig. 4), and the nodes are supported by high posterior probabilities (Fig. 4; Table 4 under "All DNA" column). The only differences are within the phasianines. Peacock pheasants (*Polyplectron* spp.) are unresolved within the phasianids and the turkey (*Meleagris*) and gray partridge (*Perdix*) are not sister taxa. The turkey is sister to grouse, and the gray partridge to gallopheasants and allies.

Effects of missing data (COMB minus OVO-G, C-OG)

When the OVO-G partition (with > 70% missing data) is excluded from the combined analysis, there are no topological changes in the cladogram, but nodal support drops for several nodes (Table 4).

Table 4
Resolution of selected nodes (+ = present in strict consensus tree without jackknife support, −= not present) for the Galliformes in Fig. 4 and jackknife branch support values and (for the All DNA analysis only) Bayesian posterior probabilities from analyses of the combined data set (COMB) and various data partitions: combined minus ovomucoid G (C-OG), morpho-behavioral (M/B), cytochrome *b* (CYT *B*), NADH2 (ND2), control region (CR), 12S rDNA (12S), ovomucoid G (OVO-G), all DNA partitions combined (All DNA), cytochrome *b* + ND2 minus 3rd positions (CYT *B* + ND2 no. 3rd pos), cytochrome *b* + ND2 3rd positions + CR + ovomucoid G + 12 rDNA (CYT *B*/ND2 3P + CR, OVO-G, 12S)

Node in Fig. 4	Node no.	COMB	M/B	All DNA	CYT *B*	ND2	CR	12S	OVO-G	C-OG	ND2 CYT *B*+ no. 3P	CYT *B*/ND2 3P + CR, OVO-G, 12S
Galliformes	1	+100	+100	+100 100*	+92	+100	N/A	+91	N/A	+100	+	+86
Megapodes sister to balance	1	+100	+100	+100 100	–	+100	N/A	+	N/A	+100	+	+86
Megapodes monophyletic	2	+100	+94	+100 100	+100	+100	N/A	+100	N/A	+100	+99	+100
Cracids sister to balance	3	+98	+72	+99 100	–	+84	+100	+	+	+100	+100	+83
Cracids monophyletic	4	+100	+69	+100 100	+100	+100	+100	+100	+100	+100	+	+100
Penelopinae monophyletic	5	+100	–	+100 100	+93	+96	UN†	+100	N/A	+100	+	+96
Cracinae monophyletic	6	+97	–	+98 100	+	+93	UN	+	N/A	+100	+	+68
Guineafowls sister to balance	7	+100	+100	+100 100	–	+99	UN	+	–	+100	–	+100
Guineafowls monophyletic	8	+100	UN	+100 100	+100	+100	N/A	+97	+96	+100	+	+100
New World quails sister to balance	9	+91	–	+79 100	–	–	UN	+	–	+86	–	+
Ptilopachus sister to New World quails	10	+98	N/A	+98 100	+71	–	N/A	N/A	+94	+94	–	+59
New World quails monophyletic	11	+100	+63	+100 100	+100	+94	+100	N/A	+100	+100	+71	+100
Xenoperdix clade sister to balance	12	+100	N/A	+99 100	+	–	UN	+	–	+97	–	+
Xenoperdix clade monophyletic	13	+92	N/A	+96 100	+52	+	UN	+92	N/A	+92	–	+
Margaroperdix sister to Coturnix	15	+65	UN	+79 100	+74	N/A	+100	N/A	N/A	+61	–	+85
Pavoninae monophyletic	17	+73	UN	– –	+62	–	–	N/A	PARA‡	+66	–	+
Afropavo sister to Pavo	18	+100	UN	+100 100	+100	+100	+95	N/A	+88	+100	+90	+100
Bambusicola sister to Gallus	19	+100	+97	+78 100	+	+	–	+77	+77	+100	–	+59
Perdix sister to Meleagris	21	+71	–	+79 –	–	+58	+	–	UN	+79	–	+61
Tetraoninae monophyletic	22	+100	+85	+98 100	–	+100	UN	+99	+99	+100	+72	+64
Phasianinae minus Gallus monophyletic	23	+	–	+ –	–	PARA	UN	–	UN	–	–	+
Gallopheasants and allies monophyletic	24	100	UN	+100 100	+99	+100	+95	+	+89	+100	+	+100

*100, Bayesian posterior probability; †UN, unresolved; ‡PARA, paraphyletic.

Cytochrome b

The resulting strict consensus cladogram (Fig. 5) differs markedly from those generated by previous analyses of CYT *B* sequences (Kornegay et al., 1993; Avise et al., 1994; Kimball et al., 1999) and analyses of most of the other DNA partitions and the combined data set (Table 4). The cracids and megapodes remain basal, but contrary to previous CYT *B*-based studies the cracids are basal (with jackknife nodal support) relative to the megapodes. Furthermore, as in Sibley and Ahlquist's (1985, 1990) DNA–DNA hybridization study and the Kornegay et al. (1993) CYT *B*-based study, the

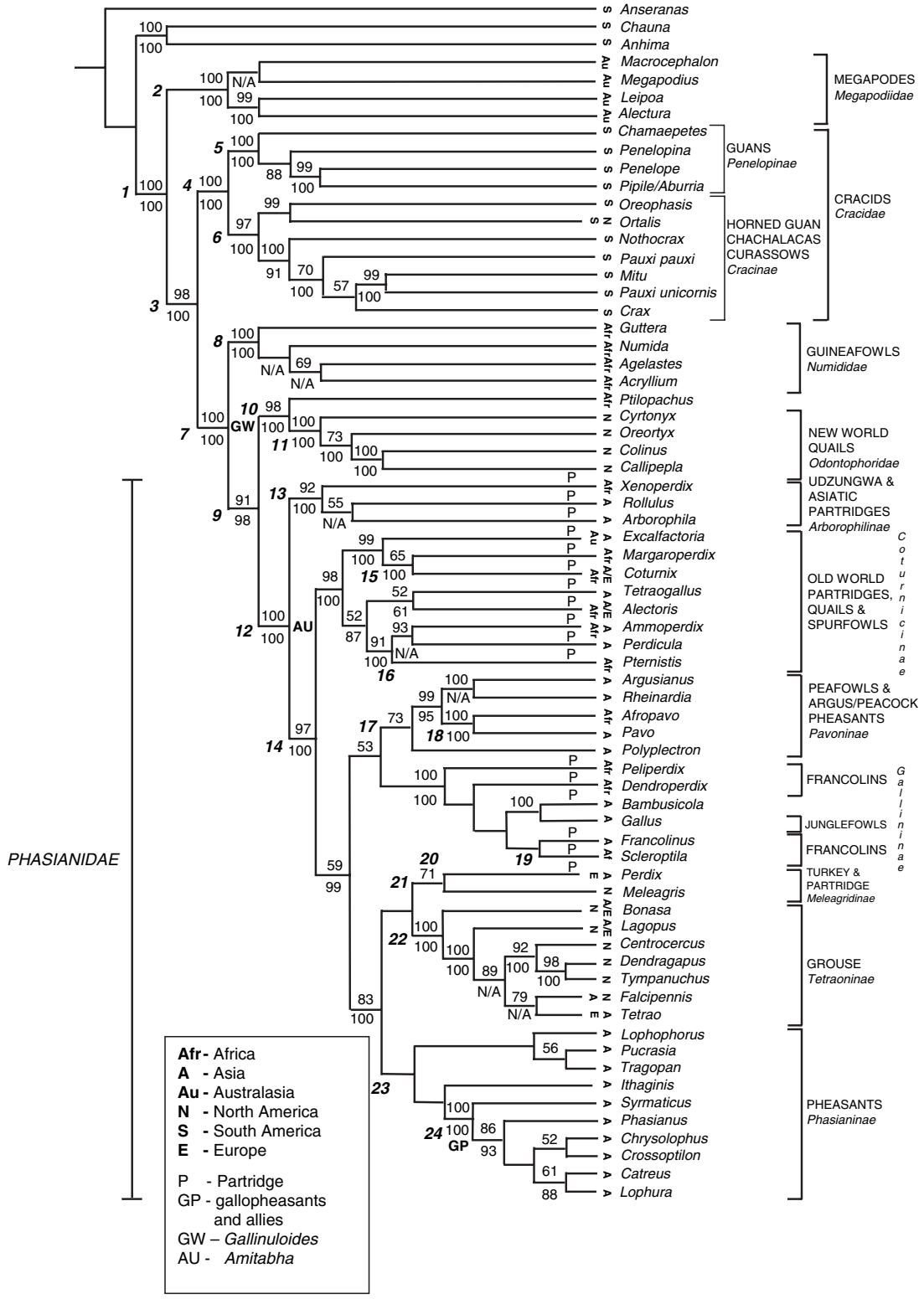

Fig. 4. The single most parsimonious cladogram of gamebird genera resulting from the parsimony ratchet analysis of the combined data set with biogeographical regions of occurrence. Numbers in bold italics at nodes indicate nodes mentioned in Table 4 and depicted in Fig. 10. Numbers in normal text above nodes are jackknife support values. Numbers below are Bayesian posterior probabilities. GW and AU indicate the placement of fossils, *Gallinuloides wyomingensis* (54 Ma) and *Amitabha urbsinterdictensis* (50 Ma), used as calibrations in the molecular clock analyses. Scientific names are those from our proposed revised classification.

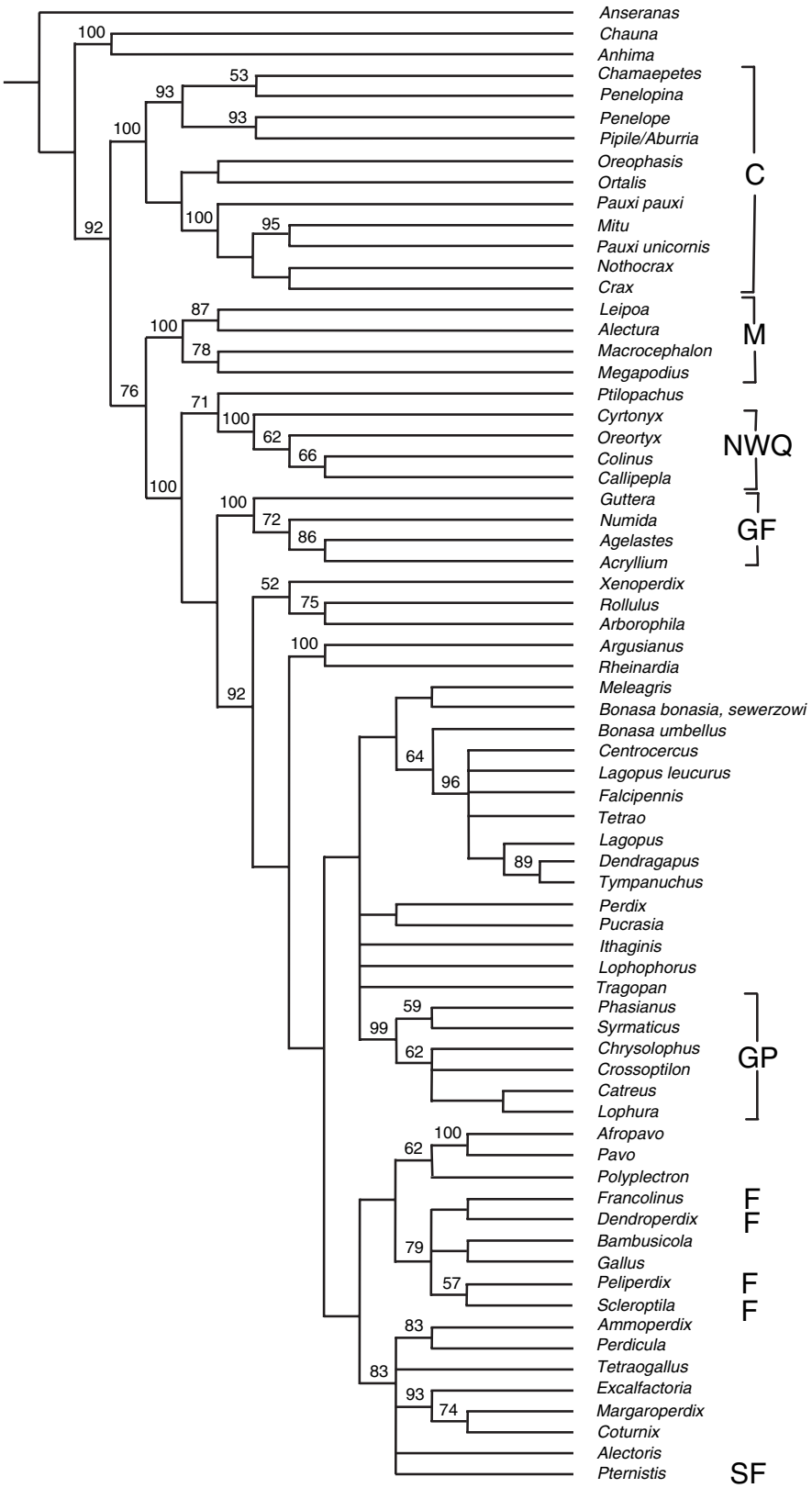

Fig. 5. The strict consensus cladogram for the cytochrome *b* character partition with jackknife nodal support values. C = cracids, M = megapodes, NWQ = New World quails, GF = guineafowls, GP = gallopheasants and allies, F = francolins, and SF = spurfowls.

New World quails are basal (but without support) relative to the guineafowls. The balance of the phasianines follows, with support. Within this phasianine clade, no currently recognized suprageneric grouping is recovered in total with support. Even the normally well supported grouse (Table 4). In fact, *Bonasa bonasia* and *B. sewerzowi* cease to link with *Bonasa umbellus*, but are sister to the turkey *Meleagris*. Within the Phasianinae, the gallopheasants and allies are recovered with support. The francolins and spurfowls are not monophyletic. All spurfowls form a monophyletic assemblage within the genus *Pternistis*, but the francolins are polyphyletic.

NADH2 (ND2)

The strict consensus ND2 cladogram (Fig. 6) parallels that of the combined analysis, but the jackknife support for the New World quails as being terminal relative to the guineafowls is low (54) (Table 4). The megapodes, cracids, guineafowls and New World quails are recovered with support. Within the phasianine clade only the grouse are recovered in total with support (Table 4). The pheasants (minus *Gallus*) form a paraphyletic assemblage, with only the gallopheasants and allies grouped as monophyletic with support.

Control region (CR)

The strict consensus CR cladogram (Fig. 7) places the cracids basal to the phasianoids with jackknife nodal support. The next most basal assemblage is an unresolved, unsupported polytomy comprising *Numida*, *Xenoperdix*, *Arborophila* and the New World quails that is basal to the balance of the phasianines. Within the phasianine clade, none of the traditional clades are recovered, although subsets of the pavonines, grouse and pheasants, e.g., gallopheasants and allies form monophyletic assemblages with support. Once again, the grouse do not form a monophyletic group, with *Bonasa umbellus* now in an unresolved position.

12S rDNA (12S)

The strict consensus 12S cladogram (Fig. 8) has topological similarities with both the CYT *B* and COMB cladograms. As in the COMB cladogram, the megapodes are basal relative to the cracids, but without jackknife nodal support. Also as in the cladogram for the combined data (Fig. 4), the guineafowls are basal relative to the New World quails, but also without support. Within the phasianines, only the grouse emerge with support (Table 4).

Ovomucoid G (OVO-G)

The OVO-G strict consensus cladogram (Fig. 9) differs markedly from that of Armstrong et al. (2001; Fig. 3e) and those generated for the other partitions. Rooted on a megapode, it places the two cracids as basal relative to the remaining exemplars, but without jackknife support. Then *Xenoperdix* (two species of small partridges from three Eastern Arc mountains in Tanzania — Dinesen et al., 1994; Bowie and Fjeldså, 2005), emerges (without support) as basal to the balance of the gamebirds. The only traditional groupings recovered with support in the remainder of the cladogram are the guineafowls and New World quails (that are now sister taxa without support), grouse and the francolins *sensu strictu*.

All DNA partitions combined

The ALL-DNA cladogram parallels that for the combined data (Table 4; Fig. 4) exactly, except that it does not recover the pavonines *in toto* as a single clade, but rather as a paraphyletic assemblage.

CYT B + ND2 minus third position nucleotides (CYT *B* + ND2 no. 3P)

This composite "coding" partition cladogram is the least resolved and worst supported of all (Table 4). It even fails to recover the gamebirds as a monophyletic group with support. In the strict consensus cladogram, the megapodes are monophyletic (with support) and basal (without support) followed by the cracids (without support). Indeed, the monophyly of the normally cladistically resilient cracids also fails to have jackknife support. The remaining taxa form a massive polytomy (Table 4) within which the only suprageneric groups emerging are the guineafowls, New World quails, grouse and gallopheasants and allies, generally without support.

*"Non-coding" data (CYT B/*ND2 3 P + CR, OVO-G, 12S)

Contrary to the view that third positions and noncoding DNA are not useful in recovering deep basal lineages, analysis of the combined CYT *B/*ND2 third position + CR + 12S + OVO-G partitions recovers a strict consensus cladogram remarkably congruent with that produced by analysis of all partitions combined (Table 4).

Traditional groups sundered

The demise of the Perdicinae (partridges/quails/francolins) and francolins sensu lato

The only traditional groups of gamebirds traditionally presumed monophyletic (Fig. 2) that are not recovered in the combined partition analysis are the Perdicinae and francolins *sensu lato* (P and francolins and *Pternistis* in Fig. 4). In Figs 5–9, some partridges and the Old World quails form a paraphyletic assemblage, linking with spurfowls (*Pternistis* spp.).

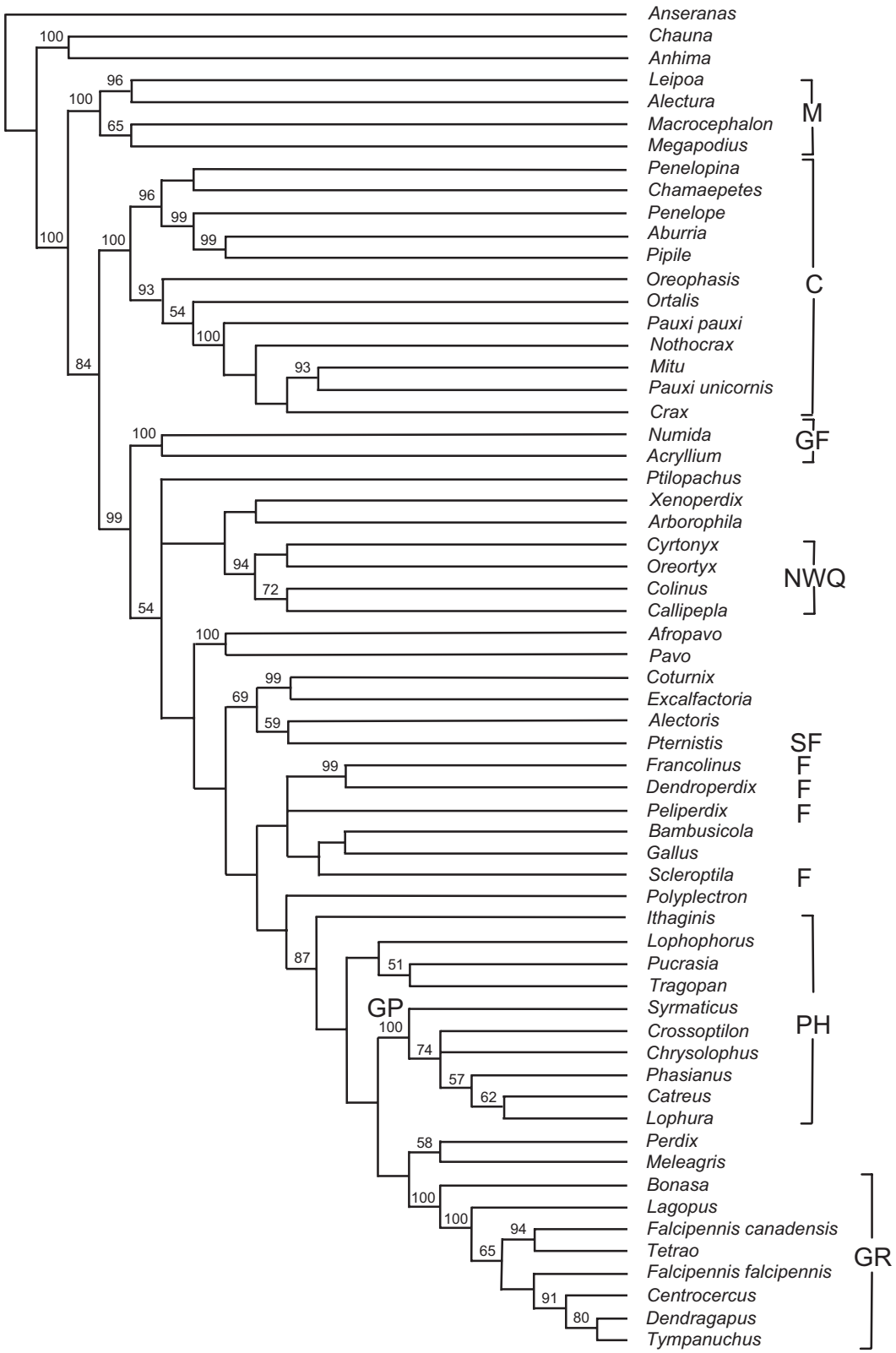

Fig. 6. The strict consensus cladogram for the NADH2 character partition with jackknife nodal support values. M = megapodes, C = cracids, GF = guineafowls, NWQ = New World quails, SF = spurfowls, F = francolins, PH = pheasants, GP = gallopheasants and allies, and GR = grouse.

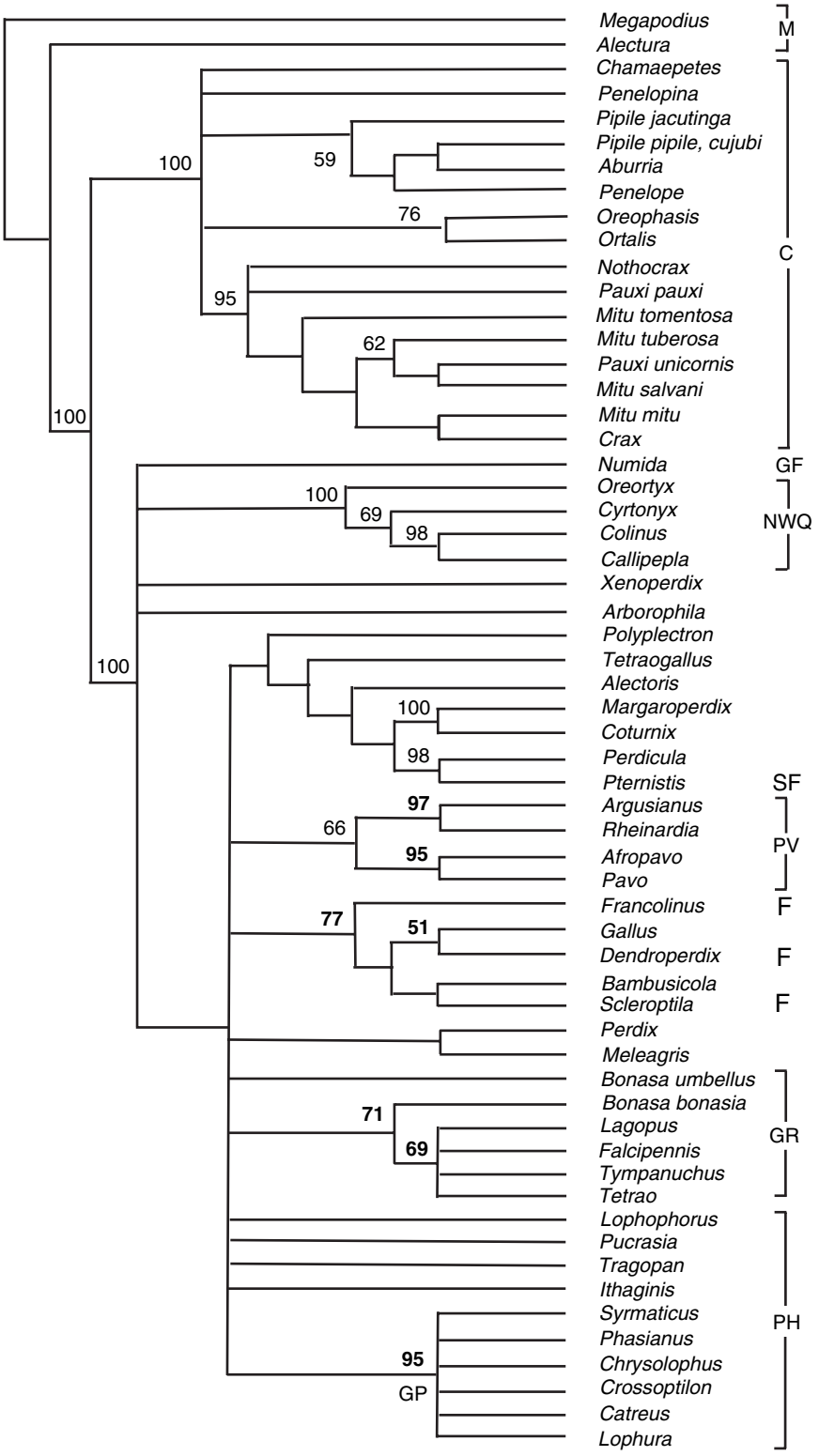

Fig. 7. The strict consensus cladogram for the control region character partition with jackknife nodal support values. M = megapodes, C = cracids, GF = guineafowl, NWQ = New World quails, SF = spurfowls, PV = pavonines, F = francolins, GR = grouse, GP = gallopheasants and allies, and PH = pheasants.

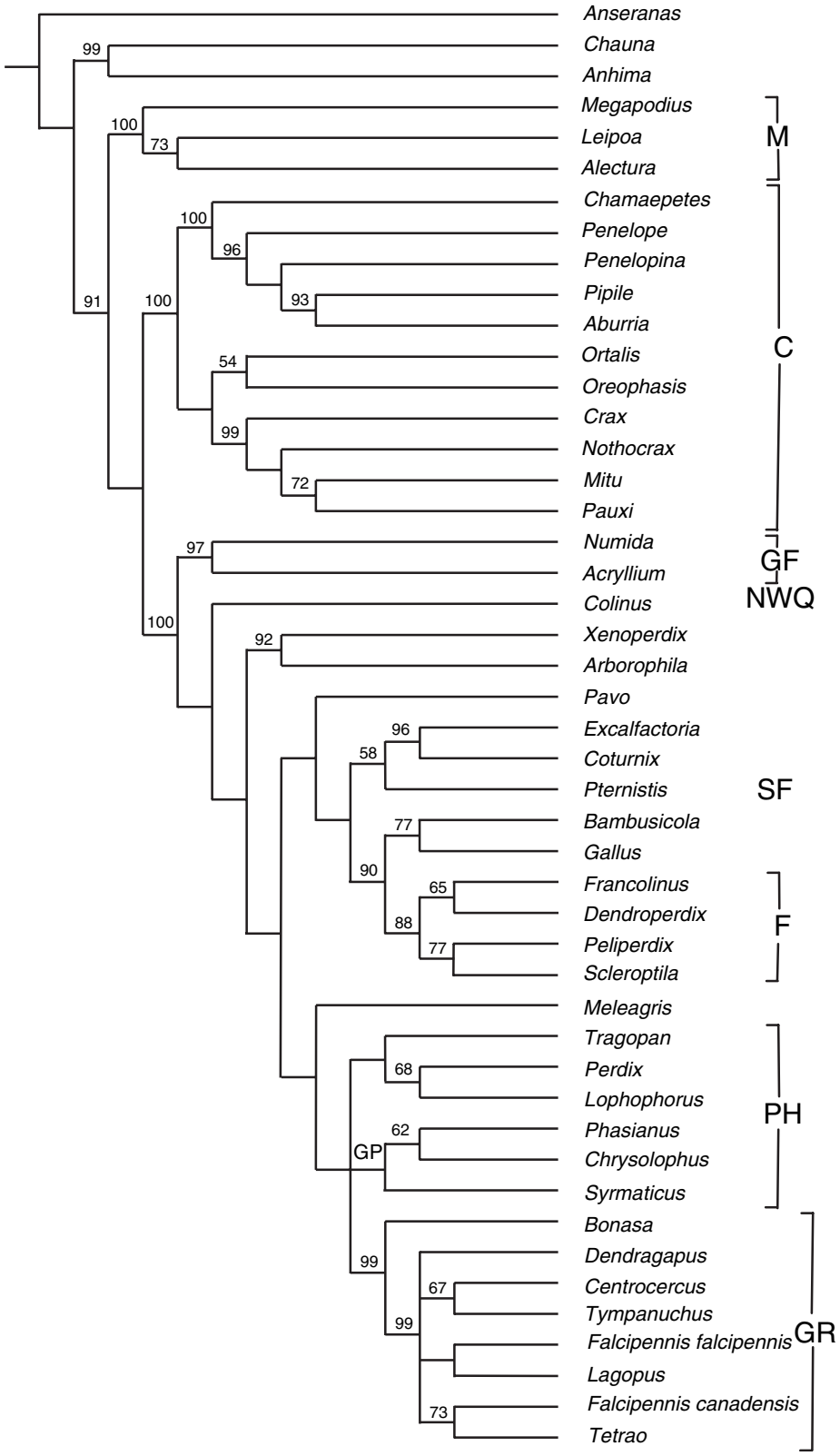

Fig. 8. The strict consensus cladogram for the 12S rDNA character partition with jackknife nodal support values. M = megapodes, C = cracids, GF = guineafowls, NWQ = New World quail, SF = spurfowls, F = francolins, GP = gallopheasants and allies, PH = pheasants, and GR = grouse.

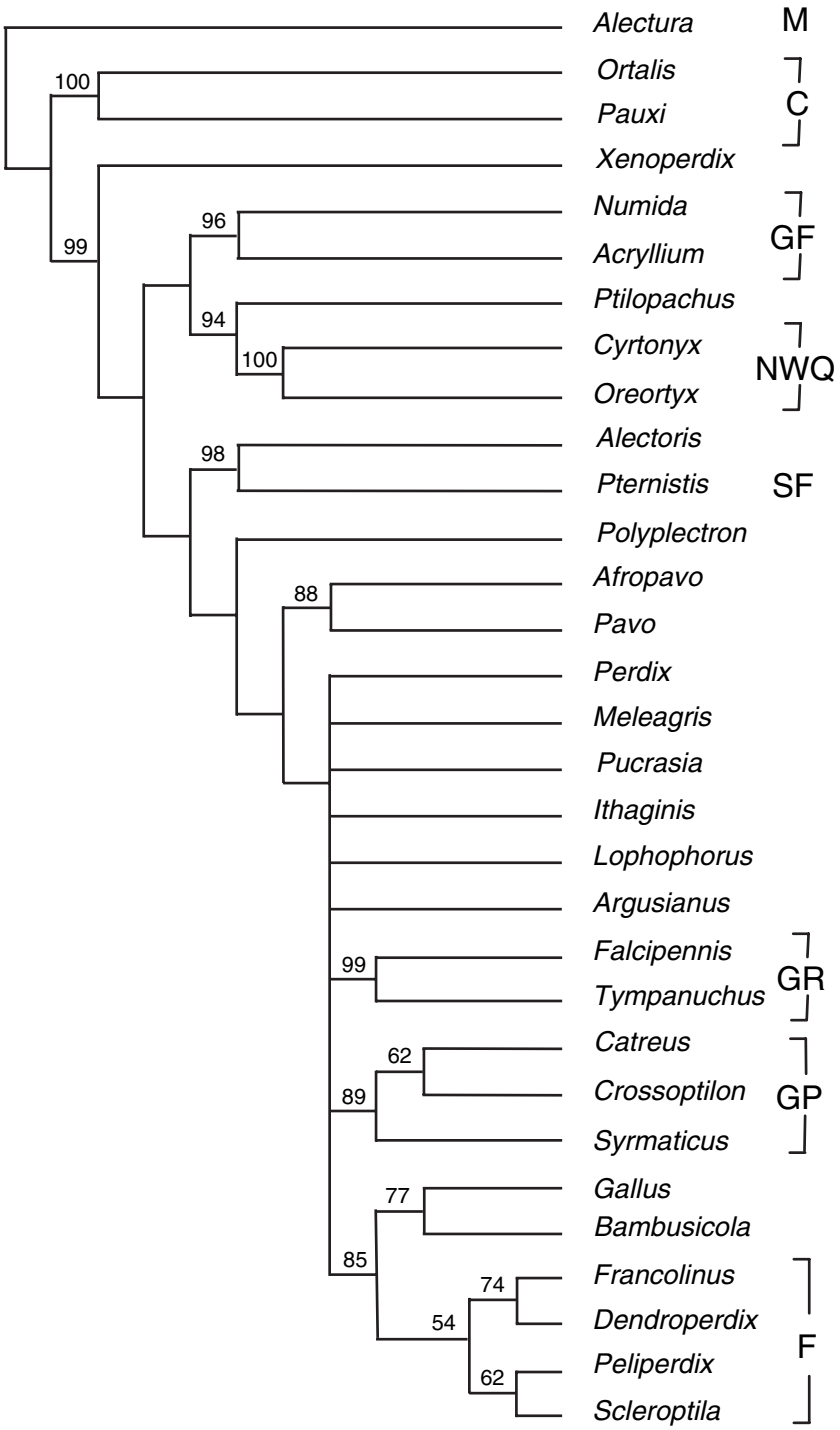

Fig. 9. The strict consensus cladogram for the ovomucoid G character partition with jackknife nodal support values. M = megapode, C = cracids, GF = guineafowls, NWQ = New World quails, SF = spurfowls, GR = grouse, GP = gallopheasants and allies, and F = francolins.

Other partridges (minus *Perdix*) and the francolins (*Francolinus*, *Peliperdix*, *Dendroperdix* and *Scleroptila* spp.) form a monophyletic group with the bamboo partridges (*Bambusicola* spp.) and junglefowls (*Gallus* spp.).

Non-traditional groupings (summarized in Table 4)

Sister group relationship between megapodes and cracids

None of the analyses indicate a sister relationship between the megapodes and cracids (Figs 4–9, Table 4).

The megapodes are generally placed basal within the Galliformes with the cracids branching off next as sister to the balance of galliforms.

Xenoperdix/Rollulus/Arborophila clade sister to balance of phasianine galliforms

This clade appears as sister to the phasianines in the CYT *B* and 12S cladograms (Figs 5 and 8), but only with high jackknife support (100) in the combined cladogram (Fig. 4) and that based on analyses of all DNA partitions combined (99) (Table 4). In the analysis of the ND2 partition (Fig. 6), this clade appears within the *Ptilopachus/*New World quail clade, but without support.

Madagascar partridge (Margaroperdix madagarensis) sister to common quail (*Coturnix coturnix*)

These two taxa are strongly supported as sisters in analyses of both molecular partitions in which they are represented (CYT *B*, Fig. 5; CR, Fig. 7) (Table 4).

Bamboo partridge (Bambusicola) sister to junglefowls (*Gallus*)

This sister relationship was found in the analysis of the M/B (Fig. 1) and CYT *B* and ND2 partitions (Figs 5 and 6, without support), in the 12S (Fig. 8) and OVO-G partitions (Fig. 9) (with support), and in the combined DNA (Fig. 4) and All DNA analyses with support (Table 4).

The gray partridge (Perdix perdix) sister to the wild turkey (*Meleagris gallopavo*)

These taxa are sisters (with support) in the combined cladogram (Fig. 4), and the All DNA and ND2 (Fig. 6) cladograms in the parsimony analyses (Table 4). In the Bayesian analyses, the grey partridge is sister to pheasants and the wild turkey to grouse.

Character evolution

The presence of spurs, ≥14 tail feathers, sexual dimorphism and polygynous mating system in the gamebird genera represented here is shown in Fig. 10.

Inferred dates of divergence

Estimates of the dates of divergence of selected galliform clades are given in Table 5. All of the divergence estimates suggest that the Galliformes, megapodes and cracids diverged prior to the K-T Event. The 95% credible intervals on age estimates from the Bayesian analysis do not exclude the possibility that guineafowls and phasianids also diverged prior to the K-T event. Except for the split of the lineages leading to megapodes and cracids, NPRS and the Bayesian method result in similar estimates of divergence times. The differences observed at the oldest nodes are a reflection of how the fossil age was used in the NPRS and Bayesian methods. The former method uses fossil data as a fixed, minimum age of 54 Ma for Numididae, whereas the latter integrates several fossil data as *a priori* time constraints to obtain estimates of divergence times and assumes *a priori* an age for crown Galliformes around 95 Ma (Pereira and Baker, 2006). Moreover, branch lengths provided by the NPRS methods under parsimony are likely to underestimate the number of substitutions, especially along older branches such those at the origin of megapodes and cracids, and therefore underestimate the age of older divergences.

Discussion

To partition or not to partition?

As none of the pair-wise ILD tests between all partitions (and combinations thereof) and between the M/B partition and that for all DNA-based partitions combined yielded significant results suggesting incongruence, there is no statistically justifiable reason for maintaining the partitions as separate phylogenetic entities. Indeed, the single most parsimonious cladogram for the combined data (Fig. 4) is the most fully resolved one (Table 4) and, with very few exceptions (and almost always only when the M/B and DNA partition data clashed), had the highest nodal jackknife support values (Table 4). Therefore, although analysis of no single partition on its own produces a well-resolved cladogram that recovers suprageneric taxa with high nodal support, they complement one another in the combined analysis cladogram (Fig. 4), which does precisely that, supporting the position that the most powerful cladistic hypothesis is that based on all characters analyzed together (Kluge, 1989; Kluge and Wolf, 1993; Freundenstein et al., 2003; Kluge, 2004).

Character exclusion

Excluding the OVO-G partition (with > 70% missing data) from the combined data partitions had no effect on the cladistic structure, but resulted in slightly lower jackknife support at several nodes (Table 4). So, it appears that, provided that data partitions with missing entries have adequate taxic representation and there is sufficient information for informative characters, they can contribute to cladistic analyses (Kearney and Clarke, 2003; Wiens, 2003, 2005). Furthermore, the utility of separate analysis of characters thought to be phylogenetically more reliable (e.g., first and second positions of DNA codons) is unjustifiable (at least for gamebirds) because it produced the least resolved tree with the lowest (or absent) values of nodal jackknife

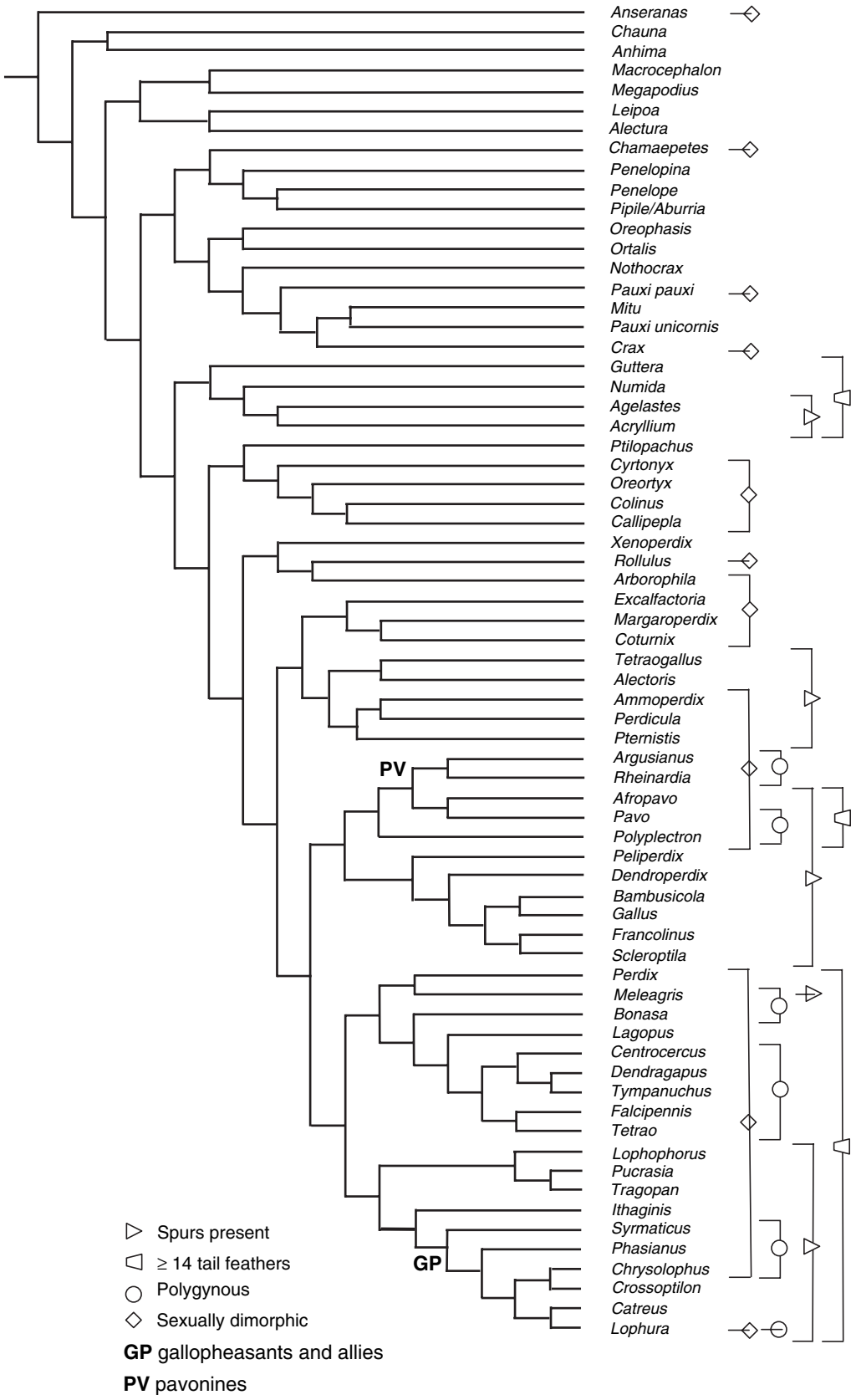

Fig. 10. Putative sexually selected characters mapped on to Fig. 4.

Table 5
Evolutionary timescale in millions of years for selected nodes in the combined-data cladogram for the Galliformes (Fig. 4)

Node in Fig. 4	Node no.	Marker and inferred age (Ma)								
		Parsimony/Likelihood					Bayesian			
		CYT B	ND2	12S	CR	OVO-G	COMB	SD	LOWER	UPPER
Origin of Galliformes	1	64.5	68.6	72.1	N/A	N/A	107.9	8.4	91.1	121.8
Stem Megapodiidae		68.7	76.4	79.0	N/A	N/A				
Stem Cracidae	4	57.6	58.1	60.7	64.9	72.6	92.8	7.3	79.2	107.3
		59.9	62.1	67.7	71.5	80.2				
Stem Numididae	8	54.0	54.0	54.0	54.0	54.0	60.2	4.7	53.3	71.3
		54.0	54.0	54.0	54.0	54.0				
Stem *Ptilopachus* + Odontophoridae	10	51.5	49.8	N/A	N/A	47.9	55.5	4.3	50.1	65.9
		52.0	51.4	N/A	N/A	49.6				
Stem Phasianidae	12	50.3	48.0	48.2	50.0	51.8	55.5	4.3	50.1	65.9
		51.0	49.4	51.9	49.0	48.0				
Stem *Xenoperdix* + *Arborophila*	13	46.3	45.1	42.4	47.2	N/A	48.9	4.1	43.0	58.6
		46.8	45.6	49.4	49.4	N/A				
Margaroperdix/ *Coturnix*	15	14.2	N/A	N/A	17.1	N/A	15.0	2.5	10.5	20.6
		17.2	N/A	N/A	18.1	N/A				
Stem *Pternistis*	16	31.0	32.7	29.8	35.1	28.1	32.5	3.3	27.0	40.0
		33.3	35.9	31.7	36.3	29.5				
Stem Pavoninae	17	40.1	39.1	N/A	30.5	33.0	38.6	3.5	32.9	46.9
		41.8	42.5	N/A	32.1	36.6				
Afropavo/*Pavo*	18	17.5	15.4	N/A	18.4	18.0	17.1	2.4	12.7	22.4
		17.0	17.3	N/A	18.9	19.1				
Bambusicola/ *Gallus*	19	23.1	23.6	14.9	16.0	11.9	24.1	2.8	19.3	30.4
		24.9	24.9	15.9	17.6	12.5				
Stem *Scleroptila*	20	17.2	26.6	19.9	19.4	19.6	28.3	3.0	23.3	35.2
		19.4	30.3	24.3	19.6	23.9				
Stem Tetraoninae	22	35.6	32.9	30.3	30.4	26.8	36.2	3.4	30.8	44.1
		37.2	33.0	34.6	30.5	34.6				

CYT *B*, cytochrome *b*; ND2, NADH dehydrogenase subunit 2; 12S, 12 rDNA; CR, control region; OVO-G, intron ovomucoid G; COMB, Bayesian estimate for the combined molecular markers; SD, standard deviation of COMB; LOWER, lower 95% credible interval; UPPER, upper 95% credible interval.

support (Table 4). Indeed, excluding the third positions from the CYT *B*/ND2 combined partitions results in a loss of more than half of the phylogenetically informative characters. Furthermore, separate analysis of all the putatively less informative characters (e.g., DNA third codon positions and non-coding DNA) often excluded from, or downweighted in, molecular phylogenetic analyses produced a well-resolved cladogram remarkably congruent with that produced through analysis of all characters combined (Table 4). Thus, third codon positions and non-coding DNA provide the bulk of informative characters, cladistic structure and support in this study.

The value of morpho-behavioral data

The 102 M/B characters of Dyke et al. (2003) played a pivotal phylogenetic role in this research. This is best illustrated in the guineafowls-versus-New World quails-basal debate. Based on their DNA–DNA hybridization studies Sibley and Ahlquist (1985, 1990) maintain that the New World quails are not crown galliforms most closely related to Old World quails and/or partridges (Crowe, 1988; Dyke et al., 2003), but form a basal taxon (relative to the guineafowls). Analyses based on mtDNA sequences by Kornegay et al. (1993—CYT *B*), Avise et al. (1994—CYT *B*), Kimball et al. (1999—CYT *B*), Lucchini and Randi (1999—CR) and Pereira and Baker (2006—CYT *B*, ND2, 12S rDNA) took a similar position. In contrast, Dimcheff et al. (2002) found the guineafowls to be basal (or sister to) to New World quails, also based on analyses of mtDNA sequences (CYT *B*, ND2). However, with the much larger taxon sampling in our study, the analysis of the CYT *B* partition actually fails to resolve this node with jackknife support (Fig. 5). That for ND2 places the guineafowls basal with high jackknife support (99) (Fig. 6), and that for a combined CYT *B* + ND2 + 12S partition place the guineafowls basal with a support value of 100 (Table 4). Furthermore, adding information from the 102 M/B characters to that of the two coding mtDNA partitions (CYT *B*, ND2 with more than 10 times the number of phylogenetically informative characters — Table 3) also results in a cladogram that strongly supports a basal position for the guineafowls (jackknife nodal support = 100), followed by the New

World quail/*Ptilopachus* clade (support = 79). In the combined cladogram, the support for this node rises to 100 (Fig. 4; Table 4). Indeed, Harshman (1994) had already highlighted the fact that the internode between the New World quails and the guineafowls in Sibley and Ahlquist's (1985, 1990) DNA–DNA hybridization cladograms was extremely short and of debatable decisiveness. Cox et al. (in press) have also reached the same phylogenetic conclusion based on analyses of eight nuclear loci and three mitochondrial regions. Thus, *contra* Scotland et al. (2003), at least for the gamebirds, M/B characters can provide decisive, relatively unambiguous information in cladistic analysis, albeit in this case primarily at the basal nodes of the cladogram. Indeed, much of the phylogenetic ambiguity, at all levels, comes from the molecular characters.

Congruence between the combined-partition and published cladograms

The topology of the combined partition cladogram (Fig. 4) supports the monophyly of all of the Johnsgard's suprageneric clades depicted in Fig. 2 except the Perdicini, which is polyphyletic, and the Phasiani from which the pavonines and *Gallus* are removed. *Gallus* is placed into one of the perdicine subclades with the pavonines placed sister to it. It differs from the M/B cladogram of Dyke et al. (2003; Fig. 1) in that it resolves the relationships of phasianoid gamebirds much more fully and generally with jackknife support. Furthermore, in the M/B cladogram (Fig. 1): the guineafowls are paraphyletic; *Polyplectron* is not placed with the pavonines; the New World quails are sister to Old World quails and partridges and not to the entire phasianine clade; the francolins and spurfowls are mono- and not diphyletic; and the pheasants and perdicines are paraphyletic or unresolved. One interesting congruent result is that *Bambusicola* and *Gallus* are sister taxa in both M/B cladograms *contra* to the traditional placement of *Gallus* with pheasants (Fig. 2).

The combined partition cladogram differs from some, most or all of the relatively taxon-poor DNA-based cladograms (Fig. 3a–f) in that the megapodes and cracids are not sisters and the guineafowls are basal relative to the New World quails. Furthermore, none of the DNA-based cladograms shown in Fig. 3 resolve phasianines decisively with support. In fact, the cladogram for the control region partition (Fig. 7), the molecular partition for which there was a good sampling of phasianoids, has particularly poor resolution and jackknife nodal support.

Relationships within major traditional clades

The phylogenetic relationships within the Megapodiidae in the combined cladogram (Fig. 4) are largely congruent with those found by Birks and Edwards (2002) based on analyses of sequences from rhodopsin, a nuclear gene, and mtDNA, although they found that *Macrocephalon* was sister to *Leipoa* + *Alectura* and not to *Megapodius* (Fig. 3). Those for the cracids are congruent with those suggested by Pereira et al. (2002) (based on analyses of three nuclear genes: RAG-1, RAG-2, c-mos; an intron: Beta-fibrinogen; and seven mtDNA genes: 12S rDNA, CO1, CO2, CO3, CYT *B*, ND2/$tRNA^{Trp}$ and ND5) in that the horned guan and chachalaca shift from the guans *sensu* Delacour and Amadon (1973) to a basal position within the curassow clade. However, the suggested relationships among the genera within these two subfamilies but do not mirror those suggested by Pereira et al. (2002). Relationships within the guineafowls differ from those suggested by Crowe (1978) in that *Agelastes* (and not *Numida*) is sister to *Acryllium*. Those for the four genera of New World quails studied here are completely congruent with those based on distance-based analyses of allozymes (Gutierrez et al., 1983). Those for the grouse are completely congruent with those found by Dimcheff et al. (2000) based on ND2 and 12S sequences and Drovetski (2002) based on the W-linked autosomal locus and CR sequences. Our results for the pheasants differ from those suggested in Fig. 2 in that *Gallus* spp. and the pavonines are place with other taxa. They agree in that they separate *Lophophorus*, *Pucrasia* and *Ithaginis* spp. (but not T*ragopan* spp.) from the gallopheasants and allies.

Traditional groupings sundered (Fig. 4)

The basal positioning (rather than sister relationship) of the megapodes relative to the cracids confirms the findings of Dimcheff et al. (2000, 2002) based on mitochondrial genes; Ericson et al. (2001) based on morphology and the nuclear *c-myc* gene; and Harshman's (1994) reanalysis of the Sibley and Ahlquist (1990) DNA–DNA hybridization data.

Perhaps the most striking cladistic result of this study is the decisive demonstration of the polyphyly of partridges (Perdicinae *sensu* del Hoyo et al., 1994). On reflection, however, this may not be surprising at all, as two of the key "characters" used to distinguish partridges from pheasants, the sexual monomorphism in the integument and the possession of less than 14 tail feathers (Johnsgard, 1973, 1986, 1988, 1999), have arisen (and appear to have been lost) many times in Fig. 10. Indeed, "the" grey partridge *Perdix perdix* (*perdix* is Greek for partridge) like the turkey, grouse and pheasants with which it groups is sexually dimorphic and has > 14 tail feathers (Johnsgard, 1973, 1986, 1988, 1999; del Hoyo et al., 1994). Pheasants (minus *Gallus* and pavonines), on the other hand, *contra* Kimball et al. (1999), Lucchini and Randi (1999) and Bush and

Strobeck (2003) form a monophyletic group in the combined cladogram (Fig. 4).

Another traditional taxon that fails to emerge as monophyletic is the francolins *sensu* Hall (1963), Sibley and Monroe (1990), del Hoyo et al. (1994), and Dyke et al. (2003). At least two distantly related clades are recovered in Fig. 4, one comprising the "true" francolins (= relatives of *F. francolinus*) that includes *Francolinus*, *Dendroperdix*, *Peliperdix* and *Scleroptila* spp., the other comprising the partridge-like spurfowls (*Pternistis* spp.). Indeed, the phenetically aberrant African endemic Nahan's "francolin" *Francolinus nahani* is neither a francolin nor a spurfowl, but is sister to the stone partridge *Ptilopachus petrosus* (Cohen et al., in prep.). *Ptilopachus* spp., in turn, are sister to the New World quails (Fig. 4). This decisively confirms the speculations raised by Crowe and Crowe (1985), Milstein and Wolff (1987), Crowe et al. (1992) and Bloomer and Crowe (1998) that *Francolinus sensu lato* might not be monophyletic.

Character evolution (Fig. 10)

Spurs appear to have evolved at least twice within the Galliformes, once in the guineafowls (*Agelastes* + *Acryllium*) and a second time in the large clade spanning *Tetraogallus* through to *Lophura* spp. This is not surprising as spurs in guineafowls are not homologous to spurs in phasianines. In guineafowls, they develop directly from the tarsometatarsus, whereas in phasianines they develop initially on the hypotarsus and only secondarily attach to the tarsometatarsus (Holman, 1964). Within the large phasianine clade they appear to have been lost secondarily three times: in the argus pheasants (*Argusianus* + *Rheinardia*), grey partridge (*Perdix*) and grouse (*Bonasa* through to *Tetrao*). Davison (1985) has hypothesized that spurs are likely to have evolved first in monogamous species to favor competition between males for resources other than mates. However, research on free-ranging introduced ring-necked pheasants *Phasianus colchicus* by Goransson et al. (1990) suggests that harem females preferred males with longer spurs, but long spurs were not indicative of success in male–male contests. Therefore, although it is tempting to speculate that the loss of these in the above-mentioned taxa is due to a lessening of importance of male–male competition for acquisition of female mates, the only empirical data available do not support such a hypothesis. Nevertheless, it would be instructive to conduct more detailed studies on these aspects of the mating system of vulturine guineafowl *Acryllium vulturinum* (spurred), as those of the helmeted guineafowl *Numida meleagris* (unspurred) are relatively well-understood (Little and Crowe, 2000). The spurless helmeted guineafowl is monogamous and female choice (during a period of several weeks of "dating" in the essential absence of male–male direct competition) plays a major part in the hen's selection of a sexual partner. Similarly, it would also be instructive to determine the relative importance of male–male competition and female choice in the apparently secondarily spurless argus pheasants, grey partridge and grouse *vis-à-vis* their spurred near relatives. Another possible explanation for the loss of spurs in grouse and *Perdix* is that they might be sites of heat loss and therefore a strong disadvantage during the boreal winter on the upland steppes of northern Eurasia.

A large number of tail feathers (≥ 14) appears to have evolved at least three times: in the guineafowls (*Guttera* through to *Acryllium*); in the pavonines (*Afropavo*, *Pavo*, *Polyplectron*, being lost secondarily in the argus pheasants), and in a large clade including: the gray partridge (*Perdix*), turkey (*Meleagris*), grouse (*Bonasa* through to *Tetrao*) and pheasants (*Ithaginis* through to *Lophura*). Polygyny appears to have evolved at least twice: in the pavonines [being lost secondarily *contra* (Johnsgard, 1999) in *Afropavo*] and in the large clade spanning *Perdix/Lophura*, being lost secondarily in *Perdix*, the basal grouse (*Bonasa* through to *Lagopus*), the blood pheasant (*Ithaginis*), koklass (*Pucrasia*), tragopans (*Tragopan*), and eared pheasants (*Crossoptilon*).

Sexual dimorphism is perhaps the most complex of the "adaptive" characters explored here. It seems to have evolved many times: twice in the Cracidae in guans (*Penelopina nigra*) and in the currasows (*Mitu* + *Pauxi* + *Crax*); in the New World quails (*Cyrtonyx* through to *Callipepla*); and several times in the large clade spanning *Xenoperdix–Lophura*.

Once again, as there is very little reliable information on aspects of courtship and mating in gamebirds in the wild (Ridley, 1987; Andersson, 1994; Johnsgard, 1999; Kimball et al., 2001), it is difficult to do more than speculate on the selective forces that influence these putatively adaptive characters. Ridley (1987) is the most recent review of this question. He hypothesized that polygyny was most likely to occur in forest-dwelling pheasants, as it is easier for males to guard females in thicker vegetation. However, these four adaptive characters do seem to have burgeoned in the relatively terminal phasianine clades from *Argusianus* onwards, with several genera, e.g., *Meleagris*, *Pavo* and several of the gallopheasants (especially polygynous species) possessing all four characters. This is consistent with the hypothesis that sexual selection involving improvement of both male competition and attractiveness to females has played a key role in the selection of these attributes (Davison, 1981, 1983, 1985). Nevertheless, as with spurs, a polygynous mating system is probably not an homologous condition, as it can be sequential, harem-based or promiscuous (del Hoyo et al., 1994; Johnsgard, 1999). It also seems that these attributes may be lost secondarily,

e.g., in grouse (Johnsgard, 1973) and gallopheasants (del Hoyo et al., 1994), should the selective advantage no longer apply.

Biogeography of basal clades

The present-day Southern Hemisphere distributions of members of the basal clades of the combined-data gamebird cladogram (Fig. 4) and their inferred dates of divergence (Table 5) indicate that, contrary to the views of some avian paleontologists (e.g., Feduccia, 1999), the duck-gamebird (Galloanserae) clade of modern birds diverged prior to the Cretaceous–Tertiary mass extinction event and that the cladogenesis of the basal gamebird clades (megapodes from Australasia, cracids from South America and guineafowls from Africa) took place in the Southern, not Northern, Hemisphere. Furthermore, if the Bayesian model-based estimates account more effectively for uncertainty in the estimation of branch lengths and heterogeneity in the rate of substitution among sites in different lineages (Pereira and Baker, 2006), the divergence of the guineafowls, New World quails (plus *Ptilopachus* spp.) and phasianids may also have been influenced by the break-up of Gondwana. These findings support those of Cracraft (2001), van Tuinen and Dyke (2004) and Clarke et al. (2005).

Nevertheless, if the split between guineafowls and New World quails occurred at more than 60 Ma, or even closer to the upper estimate for the 95% credible interval, a vicariance event between Africa and South America is not the most likely cause of this cladogenic event, as these two continents were already well separated by that time (Smith et al., 1994). In this case, the most plausible explanation for this event is dispersal from Africa to North America via Iberia, northern Britain, across what is now the Atlantic Ocean through Greenland. Pereira and Baker (2006) hypothesize a dispersal event for the guineafowls in the opposite direction because the New World quails are basal relative to guineafowls in their analyses. However, if the split between guineafowls and New World quails occurred at the upper limits indicated in Table 5, another possible, but perhaps less likely, means for the precursors of New World quails to have reached the neotropics is a dispersal event from Africa to South America. North-western Africa was still relatively close to north-eastern South America in the very Early Tertiary. North-western Africa was still relatively close to north-eastern South America in the very Early Tertiary, and the gap may have been traversed by even moderate dispersers (D. McCarthy, pers. comm.; Mueller et al., 1993).

The timing of an Africa-to-North America dispersal via Europe is in accord with the fossil record since the oldest unambiguous gamebird fossil *Gallinuloides wyomingensis* (Lower Eocene, $\sim$ 55 Ma) found in Wyoming (northern USA) has been placed cladistically at the base of a clade, including the guineafowls and remaining phasianoid gamebirds (Dyke, 2003; Lindow et al., in review), or even as sister to the phasianoids minus the guineafowls (Crowe and Short, 1992). Another fossil gallinuloid, *Archaealectrornis sibleyi* from the Middle to Upper Oligocene of Nebraska ($\sim$ 35 Ma), shows even closer affinities to phasianines (Crowe and Short, 1992). There are also Eocene fossil gallinuloids from France (Mourer-Chauvire, 1988) and Denmark (Lindow et al., in review) and Oligocene fossils from France (*Quercymegapodius* spp.) that are most similar, at least morphometrically, to New World quails (Crowe and Short, 1992; but see Mourer-Chauvire, 1992 for another view).

This scenario is also in accord with Earth history, as the north Atlantic only started opening up along this route at about 55 Ma (Smith et al., 1994) and Europe and North America were connected across the Greenland–Scotland ridge (McKenna, 1980, 1983). Furthermore, around this period, known as the ''Early Eocene Climatic Optimum'', the Earth was much warmer and covered with warm-temperate vegetation (Koch et al., 1992; Prothero, 1994; Blondel and Mourer-Chauvire, 1998; Scotese, 2001; Zachos et al., 2001) and much of Europe and North America (Wing et al., 2005) and Africa (Axelrod and Raven, 1978) was wetter along the suggested dispersal route. This is markedly different from the much more xeric present-day vegetation (e.g., a much wider Sahara desert) and would not have been a major barrier to traversal by largely terrestrial gamebirds. Finally, at $\pm$ 55 Ma there were also major bouts of dispersal into North America by large terrestrial vertebrates (Koch et al., 1992; Gunnell, 1998; Bowen et al., 2002; Gingerich, 2003; Rose and Archibald, 2005) and plants (Wing et al., 2005) involving massive intra- and intercontinental dispersals.

Moving to the other families, the guineafowls have an ancient African origin and are not the result of a mid-Miocene dispersal from Asia (Crowe, 1978) and the balance of the Asian phasianines are derived from a dispersal event from Africa. The converse seems to be the case for African spurfowls (*Pternistis* spp.) and scleroptilid francolins (*Scleroptila* spp.), which appear to have been the results of independent Asia-to-Africa dispersal events (Fig. 4; Table 5).

Historical biogeography of other unexpected sisters (Fig. 4, Table 5)

The sister relationship between *Margaroperdix* and *Coturnix* is easier to explain. First, there are also chick plumage characters that support such a phylogenetic relationship (Frost, 1975). Second, despite the fact that Africa and Madagascar were well separated at 120 Ma (Smith et al., 1994; Sparks and Smith, 2004), there were

mid-Tertiary stepping-stones in the Mozambique channel (McCall, 1997) and it is not difficult to posit an aerial dispersal event at ± 18 Ma (Table 5) given the ability of *Coturnix* spp. to traverse thousands of kilometers during their annual migrations (del Hoyo et al., 1994). The sister relationship between the forest-dwelling African (*Afropavo*) and Indian (*Pavo*) peafowl at 17–19 Ma appears to be the result of an Asia-to-Africa dispersal, and that of Udzungwa (*Xenoperdix*) and Hill (*Arborophila*) partridges at ± 39 Ma (Table 5) may be due to an Africa-to-Asia dispersal through continuous or stepping-stone warm-temperate vegetation that expanded and contracted during the late Eocene or early Oligocene, with *Xenoperdix* being a relictual form now confined to three mountains in Tanzania (Dinesen et al., 1994; Fjeldså and Lovett, 1997; Bowie and Fjeldså, 2005). Such vegetation may have persisted or changed dynamically with fluctuating climate in corridors through the southern Middle East well into the Miocene (Axelrod and Raven, 1978; Dinesen et al., 1994; Scotese, 2001). Indeed, there is fossil evidence that a *Pavo* spp. persisted in Ethiopia as far back as the Early Pliocene (Louchart, 2003). The cladistic topology of Fig. 4 suggests that there was an initial dispersal by the common ancestor of *Xenoperdix* and *Arborophila* from Africa to Asia, and a subsequent dispersal of a pavonine from Asia back to Africa culminating in *Afropavo*. Other African forest birds (e.g., the white-crested tiger heron *Tigriornis leucolophus*, Nkulengu rail *Himantornis hematopus*, gray-throated rail *Canirallus oculeus*, Congo Bay owl *Phodilus prigoginei*, African green broadbill *Pseudocalyptomena graueri*, trogons *Apaloderma* spp., etc.) also have putative sister taxa in the Asiotropical Region (Olson, 1973).

Perhaps the easiest unexpected sister relationship to explain biogeographically is that between the bamboo "partridges" (*Bambusicola* spp.) and junglefowls (*Gallus* spp.) dating back 30 Ma (Table 5). Members of these genera are, in fact, currently essentially parapatrically distributed in south-eastern Asia (del Hoyo et al., 1994).

Conclusions

If one returns to the aims of our research as outlined in the introductory section, the following conclusions can be made.

1 The monophyly of many of the currently recognized suprageneric galliform taxa Megapodiidae (megapodes), Cracidae (cracids), Numididae (guineafowls), Odontophoridae (New World quails), Tetraoninae (grouse), Pavoninae (peafowls *sensu lato*) and Phasianinae (pheasants minus *Gallus*) is confirmed decisively.

2 That of other taxa, e.g., partridges (Perdicinae) and francolins (*Francolinus sensu lato*), is rejected decisively.

3 New World quails are not phylogenetically relatively terminal galliforms related to Old World quails and partridges, but represent a much more basal divergence than traditional classifications have suggested.

4 New World quails are not basal relative to guineafowls as suggested by results of research based on DNA–DNA hybridization and analysis of mtDNA sequences, but are sister to the non-numidine phasianoids.

5 It is phylogenetically more sensible to analyze all character data partitions in combination rather than use a divisive "process"-partition approach as the different partitions in combination complement one another.

6 Discarding M/B and non-coding molecular characters results in massive losses of phylogenetic resolution and nodal support, particularly at deeper nodes within Galliformes.

7 Some "adaptive" characters (e.g., spurs and large number of tail feathers) have relatively uncomplicated evolutionary origins, whereas others (e.g., sexual dimorphism and polygamy) do not.

8 The early cladogenesis in the Galliformes pre-dates the Cretaceous–Tertiary mass extinction event and that basal divergences within the Order were influenced by the break-up of Gondwana.

9 The non-numidine phasianoids have a much more complex historical biogeography than previously thought, with connections between Africa and Europe, North America, South America and Asia.

Classification

A tentative revised classification of the Galliformes consistent with the cladistic structure in Fig. 4 is given below:

Order GALLIFORMES

Family Megapodiidae: scrubfowl (*Megapodius*), brush-turkeys (*Alectura*), mallefowl (*Leipoa*), maleo (*Macrocephalon*)

Family Cracidae

Subfamily Cracinae: horned guan (*Oreophasis*), chachalacas (*Ortalis*), currasows (*Crax*, *Nothocrax*, *Mitu*, *Pauxi*)

Subfamily Penelopinae: remaining guans (*Penelope*, *Penelopina*, *Chamaepetes*, *Pipile*, *Aburria*)

Family Numididae: guineafowls (*Agelastes*, *Acryllium*, *Guttera*, *Numida*)

Family Odontophoridae: New World quails (*Cyrtonyx*, *Oreortyx*, *Colinus*, *Callipepla*) including the stone partridge *Ptilopachus petrosus* and Nahan's "francolin" *Ptilopachus "Francolinus" nahani*

Family Phasianidae

Subfamily Arborophilinae: Udzungwa and Rubeho forest partridges (*Xenoperdix*), hill partridges (*Arborphila*), crested wood-partridge (*Rollulus*)

Subfamily Coturnicinae: Old World quails (*Coturnix*, *Excalfactoria*), Madagascar partridge (*Margaroperdix*), snowcocks (*Tetraogallus*), partridges (*Alectoris*), sand partridge (*Ammoperdix*), bush-quails (*Perdicula*), spurfowls (*Pternistis*)

Subfamily Pavoninae: peafowls (*Afropavo*, *Pavo*), argus pheasants (*Rheinardia*, *Argusianus*), peacock pheasants (*Polyplectron*)

Subfamily Gallininae: bamboo-partridges (*Bambusicola*), junglefowls (*Gallus*), francolins (*Francolinus*, *Dendroperdix*, *Peliperdix*, *Scleroptila*)

Subfamily Meleagridinae: turkey (*Meleagris*), grey partridge (*Perdix*)

Subfamily Tetraoninae: grouse and capercaillie (*Falcipennis*, *Dendragapus*, *Tetrao*, *Bonasa*, *Centrocercus*), ptarmigans (*Lagopus*), prairie-chickens (*Tympanuchus*)

Subfamily Phasianinae: monals (*Lophophorus*), tragopans (*Tragopan*), pheasants (*Phasianus*, *Chrysolophus*, *Lophura*, *Catreus*, *Crossoptilon*)

Future research

Despite that fact that the cladogram for the combined analysis is well resolved, generally with strong nodal support, this situation lessens markedly within the "higher" phasianines from *Argusianus* onwards (Fig. 4). The monophyly of the pavonines to include the peacock pheasants (*Polyplectron* spp.) is clearly dependent on evidence provided by M/B characters. The sister relationship between the turkey (*Meleagris*) and grey partridge (*Perdix*) is also not recovered in the Bayesian analysis (Table 4) and is only recovered with low (58) jackknife support in the cladogram for the ND2 partition (Fig. 6). Finally, the monophyly of the pheasants minus *Gallus* spp. has yet to be established with nodal support using the normally accepted ± 37% of characters deleted per jackknife replicate. If this value is reduced to 20%, the Phasianinae become monophyletic with a support value of 62. Nevertheless, this calls for the exploration for more M/B and molecular evidence, and perhaps a reassessment of the former.

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Appendix 1

Outgroup and gamebird taxa investigated in this research. Those taxa marked with * were used in the Bayesian and molecular clock divergence analyses

Anseriformes	
Anseranas semipalmata	magpie goose
Chauna torquata	southern screamer*
Anhima cornuta	horned screamer*
Galliformes	
Megapodiidae	
Megapodius freycinet	dusky scrubfowl
Megapodius reinwardt	orange-footed scrubfowl
Megapodius eremita	Melanesian scrubfowl*
Leipoa ocellata	malleefowl*
Macrocephalon maleo	maleo
Alectura lathami	Australian brush-turkey*
Cracidae	
Ortalis vetula	plain chachalaca
Ortalis canicollis	chaco chachalaca*
Oreophasis derbianus	horned guan*
Penelope obscura	dusky-legged guan*
Penelope superciliaris	rusty-margined guan
Penelope ochrogaster	chestnut-bellied guan
Penelope purpurascens	crested guan
Penelopina nigra	highland guan*
Pipile jacutinga	black-fronted piping-guan*
Pipile pipile	Trinidad piping-guan
Pipile cumanensis	blue-throated piping-guan
Pipile cujubi	red-throated piping-guan
Aburria aburri	wattled guan*
Crax rubra	great curassow*
Crax alector	black curassow
Crax alberti	blue-bellied curassow
Crax daubentoni	yellow-knobbed curassow
Crax blumenbachii	red-billed curassow*
Crax globulosa	wattled curassow
Crax fasciolata	bare-faced curassow
Mitu tuberosa	razor-billed curassow*

Appendix 1 *Continued*

Mitu mitu	Alagoas curassow
Mitu salvini	Salvin's curassow
Mitu tomentosa	crestless curassow*
Chamaepetes goudotii	sickle-winged guan*
Pauxi pauxi	northern helmeted curassow*
Pauxi unicornis	southern helmeted curassow
Nothocrax urumutum	nocturnal curassow*
Numididae	
Guttera pucherani	crested guineafowl
Guttera plumifera	plumed guineafowl
Numida meleagris	helmeted guineafowl*
Agelastes meleagrides	white-breasted guineafowl
Acryllium vulturinum	vulturine guineafowl*
Odontophoridae	
Cyrtonyx montezumae	Montezuma quail*
Oreortyx pictus	mountain quail*
Callipepla squamata	scaled quail
Callipepla gambelii	Gambel's quail*
Callipepla californica	California quail
Callipepla douglasii	elegant quail
Colinus virginianus	northern bobwhite quail*
Tetraonidae	
Bonasa umbellus	ruffed grouse*
Bonasa bonasia	hazel grouse
Bonasa sewerzowi	Severtsov's grouse
Dendragapus obscurus	blue grouse
Falcipennis canadensis	spruce grouse*
Falcipennis falcipennis	Siberian grouse
Tetrao urogallus	western capercaillie
Tetrao tetrix	eurasian black grouse*
Tetrao parvirostris	black-billed capercaillie
Tetrao mlokosiewiczi	Caucasian black grouse
Centrocercus urophasianus	sage grouse
Lagopus leucurus	white-tailed ptarmigan
Lagopus mutus	rock ptarmigan*
Lagopus lagopus	willow ptarmigan*
Tympanuchus pallidicinctus	lesser prairie-chicken
Tympanuchus cupido	greater prairie-chicken
Tympanuchus phasianellus	sharp-tailed grouse*
Meleagrididae	
Meleagris gallopavo	wild turkey*
Phasianidae	
Phasianinae	
Ithaginis cruentus	blood pheasant*
Lophophorus impejanus	Himalayan monal*
Lophophorus ilhuysii	Chinese monal
Lophophorus sclateri	Sclater's monal
Pucrasia macrolopha	koklass pheasant*
Tragopan temminckii	Temminck's tragopan*
Tragopan satyra	satyr tragopan
Tragopan blythii	Blyth's tragopan
Tragopan caboti	Cabot's tragopan
Syrmaticus humiae	Hume's pheasant
Syrmaticus reevesii	Reeves's pheasant
Syrmaticus ellioti	Elliot's pheasant*
Syrmaticus mikado	Mikado pheasant
Phasianus versicolor	green pheasant
Phasianus colchicus	ring-necked pheasant*
Chrysolophus pictus	golden pheasant*
Chrysolophus amherstiae	Lady Amherst's pheasant

Appendix 1 *Continued*

Lophura nycthemera	silver pheasant*
Lophura diardi	Siamese fireback
Lophura swinhoii	Swinhoe's pheasant
Lophura edwardsi	Edwards's pheasant
Lophura bulweri	Bulwer's pheasant
Lophura erythropthalma	crestless fireback pheasant
Lophura ignita	crested fireback pheasant
Lophura inornata	Salvadori's pheasant
Lophura leucomelanos	Kalij pheasant
Catreus wallichii	cheer pheasant*
Crossoptilon crossoptilon	white eared-pheasant*
Crossoptilon auritum	blue eared-pheasant
Crossoptilon mantchuricum	brown eared-pheasant
Gallus gallus	red junglefowl*
Gallus varius	green junglefowl
Gallus sonnerati	grey junglefowl
Gallus lafayettei	Ceylon junglefowl
Polyplectron biclacaratum	grey peacock-pheasant*
Polyplectron emphanum	Palawan peacock-pheasant*
Polyplectron chalcurum	bronze-tailed peacock-pheasant
Polyplectron germaini	Germain's peacock-pheasant
Polyplectron inopinatum	mountain peacock-pheasant
Polyplectron malacense	Malaysian peacock-pheasant
Argusianus argus	great argus*
Rheinardia ocellata	crested argus
Afropavo congensis	Congo peafowl*
Pavo cristatus	Indian peafowl*
Pavo muticus	green peafowl*
Perdicinae	
Ptilopachus "*Francolinus*" *nahani*	Nahan's francolin*
Ptilopachus petrosus	stone partridge*
Xenoperdix udzungwensis	Udzungwa forest-partridge*
Rollulus rouloul	crested wood-partridge
Arborophila javanica	chestnut-bellied hill-partridge*
Arborophila torqueola	common hill-partridge
Perdix perdix	grey partridge*
Bambusicola thoracica	Chinese bamboo-partridge*
Bambusicola fytchii	mountain bamboo-partridge
Dendroperdix sephaena	South Africa crested francolin*
Dendroperdix sephaena	Kenya crested francolin
Francolinus francolinus	black francolin
Francolinus pondicerianus	grey francolin
Francolinus gularis	swamp francolin
Francolinus lathami	Latham's francolin
Peliperdix coqui	coqui francolin
Scleroptila levaillantii	red-winged francolin*
Scleroptila finschi	Finsch's francolin
Scleroptila levaillantoides	Orange River francolin*
Scleroptila africanus	grey-winged francolin*
Scleroptila shelleyi South Africa	Shelley's francolin*
Scleroptila shelleyi Kenya	Shelley's francolin
Tetraogallus himalayensis	Himalayan snowcock
Tetraogallus tibetanus	Tibetan snowcock
Tetraogallus altaicus	Atai snowcock
Alectoris melanocephala	Arabian partridge
Alectoris barbara	Barbary partridge
Alectoris rufa	red-legged partridge*
Alectoris graeca	rock partridge
Alectoris chukar	chukar partridge*
Alectoris philbyi	Philby's partridge
Alectoris magna	Przevalski's partridge
Margaroperdix madagarensis	Madagascar partridge*
Coturnix japonica	Japanese quail*
Coturnix coturnix	common quail

Appendix 1 *Continued*

Excalfactoria chinensis	Asian blue quail
Ammoperdix heyi	sand partridge
Perdicula asiatica	jungle bush-quail
Pternistis hartlaubi	Hartlaub's spurfowl
Pternistis erckelii	Erckel's spurfowl
Pternistis castaneicollis	chestnut-naped spurfowl
Pternistis bicalcaratus	double-spurred spurfowl
Pternistis griseostriatus	grey-striped spurfowl
Pternistis leucoscepus	yellow-necked spurfowl

Appendix 1 *Continued*

Pternistis squamatus	scaly spurfowl*
Pternistis swainsonii	Swainson's spurfowl
Pternistis afer South Africa	red-necked spurfowl
Pternistis afer Angola	red-necked spurfowl
Pternistis capensis	Cape spurfowl*
Pternistis adspersus	red-billed spurfowl
Pternistis hildebrandti	Hildebrandt's spurfowl
Pternistis natalensis	Natal spurfowl*

Appendix 2

Sources and amounts of DNA sequence data for mitochondrial cytochrome *b*, NADH dehydrogenase subunit 2 (ND2), control region, 12S rDNA (12S) and nuclear ovomucoid G sequences (+ = sequence, –= no sequence). Superscripts on GenBank numbers refer to publications listed below

Taxon	No. bases	CYT *B* GenBank no.		No. bases	ND2 GenBank no.	control* region $n = 1030$ bases	12S $n = 731$ bases	Ovomucoid G† $n = 492$ bases
Anseranas semipalmata	1143	NC00593335		1041	NC005933[35]	–	NC005933[35]	–
Chauna torquata	1143	AY14073621	AY274030[25]	999	AY140738[21]	–	AY140700[21]	–
Anhima cornuta	1002	AY14073521		999	AY140737[21]	–	AY140699[21]	–
Megapodius freycinet	659	AM236880		1041	AF394631[u]	DQ834464	–	–
Megapodius reinwardt	1002	AF16546521		1041	AY140739[21]	–	AF165441[21]	–
Megapodius eremita	1143	AF0820659		1041	AY274052[25]	–	AY274005[25]	–
Leipoa ocellata	1143	AM236879		1041	AF394619[u]	–	AF222586[12]	–
Macrocephalon maleo	1143	AM236881		1041	AF394621[u]	–	–	–
Alectura lathami	1143	NC007227[u]		1041	AY274051[25]	DQ834465	AY274004[25]	DQ832069
Ortalis vetula	1143	L083841		1041	AF394614[u]	–	–	AF170974[14]
Ortalis canicollis	1002	AF16547221		999	AY140746[21]	AF165436[29]	AF165448[21]	–
Oreophasis derbianus	1002	AF16547121		1041	AY140745[21]	AF165435[29]	AF165447[21]	–
Penelope obscura	1002	AF16547421		999	AY140742[21]	AF165432[29]	AF165450[21]	–
Penelope superciliaris	699	AY36710229		441	AY367096[29]	AY145313[29]	–	–
Penelope ochrogaster	699	AY36710129		441	AY367O95[29]	AY145311[29]	–	–
Penelope purpurascens	792	AY354491[u]	AY367103[29]	441	AY367097[29]	AY145312[29]	–	–
Penelopina nigra	1002	AF16547521		999	AY140743[21]	AF165433[29]	AF165451[21]	–
Pipile jacutinga	1002	AF16547621		999	AY140744[21]	AF165431[29]	AF165452[21]	–
Pipile pipile	699	AY36710629		441	AY367100[29]	AY145320[29]	–	–
Pipile cumanensis	699	AY36710529		441	AY367099[29]	AY145319[29]	–	–
Pipile cujubi	699	AY36710429		441	AY367098[29]	AY145314[29]	–	–
Aburria aburria	1002	AF16546621		997	AY140740[21]	AF165430[29]	AF165442[21]	–
Crax rubra	1143	AY14192528 AF106502[10]	AY274029[25]	1041	AY274050[25]	AY145307[29]	AY274003[25] –	–
Crax alector	1143	AY14192128	AF106507[10]	999	AY141931[28]	AY145315[29]	–	–
Crax alberti	1014	AY14192028	AF106498[10]	999	AY141930[28]	AY145304[29]	–	–
Crax daubentoni	1014	AY14192228	AF106500[10]	999	AY141932[28]	AY145305[29]	–	–
Crax blumenbachii	1002	AF16546821		999	AY140747[21]	AF165438[29]	AF165444[21]	–
Crax globulosa	1014	AY14192428	AF106506[10]	999	AY141934[28]	AY145316[29]	–	–
Crax fasciolata	1014	AY354487[u]	AY141923[28]	999	AY141933[28]	AY145306[29]	–	–
Mitu tuberosa	1002	AF16546921		999	AY140748[21]	AF165437[29]	AF165445[21]	–
Mitu mitu	1002	AY14192628	AY098552[24]	999	AY141936[28]	AY145308[29]	–	–
Mitu salvani	1002	AY14192728		999	AY141937[28]	AY145309[29]	–	–
Mitu tomentosa	1002	AY14192828	AY098556[24]	999	AY141938[28]	AY145310[29]	–	–
Chamaepetes goudotii	1002	AF16546721		997	AY140741[21]	AF165434[29]	AF165443[21]	–
Pauxi pauxi	1143	AF06819011		999	AY140750[21]	AF165439[29]	AF165449[21]	AF170973[14]
Pauxi unicornis	1002	AY14192928		999	AY141939[28]	AY145317[29]	–	–
Nothocrax urumutum	1002	AF16547021		999	AY140749[21]	AF165440[29]	AF165446[21]	–
Guttera pucherani	1143	AM236882			–	–	–	–
Guttera plumifera	1143	AM236883			–	–	–	–
Numida meleagris	1143	L083831		1041	NC006382[27]	DQ834466	AF222587[12]	AF170975[14]
Agelastes meleagrides	1143	AM236884			–	–	–	–
Acryllium vulturinum	1143	AF53674223		1041	AF536745[23]	–	AF536739[23]	DQ832070
Cyrtonyx montezumae	1143	AF06819211		303	AF028779[u]	DQ834467	–	AF170976[14]
Oreortyx pictus	1143	AF25286014		301	AF028782[u]	DQ834468	–	AF170977[14]

Appendix 2 *Continued*

Taxon	No. bases	CYT *B* GenBank no.		No. bases	ND2 GenBank no.	control* region $n = 1030$ bases	12S $n = 731$ bases	Ovomucoid G† $n = 492$ bases
Colinus virginianus	912	AF028775[u]	AF028774[u]	1041	AF222545[12]	DQ834469	AF222576[12]	–
Callipepla douglasii	734	AF028750[u]	AF028751[u]	303	AF028752[u]	DQ834470	–	–
Callipepla squamata	1012	AF028753[u] AF028756[u]	AF028754[u]	303	AF028758[u]	DQ834471	– –	–
Callipepla gambelii	1143	L083821		297	AF028761[u]	DQ834472	–	–
Callipepla californica	1143	AB12013130		303	AF028773[u]	DQ834473	–	–
Ptilopachus nahani	1142	AM236885		1039	DQ768288	–	–	DQ832071
Ptilopachus petrosus	1132	AM236886		1039	DQ768289	–	–	DQ832072
Xenoperdix udzungwensis	1143	AM236887		1041	DG09380034	DQ834474	DQ832096	DQ832073
Rollulus rouloul	1140	AM236888			–	–	–	–
Arborophila javanica	1143	AM236889		1041	DG09380434	–	DQ832097	DQ832074
Arborophila torqueola	1143	AM23688t			–	DQ834475	–	–
Bonasa umbellus	1141	AY50967732	AF230167[16]	1041	AF222541[12]	DQ834476	U83740[6]	–
Bonasa bonasia	609	AF23016516		1041	AF222539[12]	DQ834477	AF222571[12]	–
Bonasa sewerzowi	612	AF23016616		1041	AF222540[12]	–	AF222572[12]	–
Dendragapus obscurus	609	AF23017816		1041	AF222549[12]	–	AF222580[12]	–
Falcipennis canadensis	1143	AF170992[u]		1041	AF222548[12]	DQ834478	AF222577[12]	AF170986[14]
Falcipennis falcipennis	609	AF23016916		1041	AF222547[12]	–	AF222578[12]	–
Centrocercus urophasianus	609	AF23017716		1041	AF222542[12]	–	AF222573[12]	–
Tetrao tetrix	609	AF23017416		1041	AF222564[12]	DQ834479	AF222593[12]	–
Tetrao urogallus	1143	AB12013230		1041	AF222565[19]	DQ834480	AF222594[19]	–
Tetrao parvirostris	549	AF23017516		1041	AF222563[12]	–	AF222592[12]	–
Tetrao mlokosiewiczi	561	AF23017316		1041	AF222562[19]	–	AF222591[19]	–
Lagopus leucurus	609	AF23017116		1041	AF222553[12]	–	AF222584[12]	–
Lagopus mutus	1033	AY156346[u]		1041	AF222554[12]	DQ834481	AF222585[12]	–
Lagopus lagopus	609	AF23017016		1041	AF222552[12]	DQ834482	AF222583[12]	–
Tympanuchus pallidicinctus	609	AF23018016		1041	AF222568[12]	–	AF222597[12]	–
Tympanuchus cupido	609	AF23017916		1041	AF222567[12]	–	AF222596[12]	–
Tympanuchus phasianellus	1143	AF06819111		1041	AF222569[12]	DQ834483	AF222598[12]	AF170985[14]
Perdix perdix	1143	AF02879111		1041	AF222560[12]	DQ834484	AF222590[12]	AF170982[14]
Meleagris gallopavo	1143	L083811		1041	AF222556[19]	DQ834485	U83741[6]	AF170984[14]
Lophophorus impejanus	1143	AF02879611		1041	DQ768259	DQ834486	DQ832098	DQ832075
Lophophorus ilhuysii	1143	AY26530926			–	–	AY447956[u]	–
Lophophorus sclateri	1143	AY26531026			–	–	–	–
Ithaginis cruentus	1143	AF06819311		1040	DQ768258	DQ834487	–	DQ832076
Tragopan temminckii	1143	AF22983813		1041	AF222566[19]	DQ834488	AF222595[19]	–
Tragopan satyra	1143	AF53455522			–	DQ834489	–	–
Tragopan blythii	1143	AF20072213		1041	DQ768272	–	–	–
Tragopan caboti	1143	AF53455422			–	–	AB004240[u]	–
Pucrasia macrolopha	1143	AF02880011		1041	DQ768269	DQ834490	–	AF17098314
Syrmaticus humiae	1143	AF534706[u]		1038	DQ768293	DQ834491	DQ832099	DQ832077
Syrmaticus reevesii	1143	AY368059[u]		1041	DQ768271	DQ834492	–	–
Syrmaticus ellioti	1143	AY368061[u]		1041	DQ768270	DQ834493	DQ832100	DQ832078
Syrmaticus mikado	1143	AY368056[u]		1032	DQ768294	DQ834494	DQ832101	DQ832079
Phasianus colchicus	1143	AY368060[u]		1041	AF222561[12]	DQ834495	U83742[6]	–
Phasianus versicolor	1143	AY368058[u]			–	DQ834496	–	–
Chrysolophus pictus	1143	AF02879311		1041	DQ768255	DQ834497		–
Chrysolophus amherstiae	1143	AB12013030		1031	DQ768277	–	DQ832102	DQ832080
Lophura nycthemera	1143	L083801		1041	DQ768261	DQ834498	–	–
Lophura diardi	1143	AF02879711			–	–	–	–
Lophura swinhoii	1143	AF53455822		1041	DQ768262	–	–	–
Lophura edwardsi	1143	AF53455722			–	–	–	–
Lophura bulweri	1143	AF31463718			–	–	–	–
Lophura erythropthalma	1143	AF31463918			–	–	–	–
Lophura ignita	1143	AF31464118			–	–	–	–
Lophura inornata	1143	AF31464218		1041	DQ768260	–	–	–
Lophura leucomelana	1143	AF31464318			–	–	–	–
Catreus wallichii	1143	AF02879211		1041	DQ768254	DQ834499	–	AF17098014
Crossoptilon crossoptilon	1143	AF02879411		1041	DQ768256	DQ834500	–	AF17098114
Crossoptilon auritum	1143	AF53455222			–	DQ834501	–	–

Appendix 2 *Continued*

Taxon	No. bases	CYT *B* GenBank no.		No. bases	ND2 GenBank no.	control* region $n = 1030$ bases	12S $n = 731$ bases	Ovomucoid G† $n = 492$ bases
Crossoptilon mantchuricum	1143	AF53455322			–	DQ834502	–	–
Polyplectron bicalcaratum	1143	AF53456422		1041	DQ768263	DQ834503	–	AF33195915
Polyplectron emphanum	1143	AF33006215		1041	DQ768265	DQ834504	–	AF33195515
Polyplectron chalcurum	1143	AF33006115		1041	DQ768264	–	–	AF33195615
Polyplectron germaini	1143	AF33006315		1041	DQ768266	–	–	AF33196015
Polyplectron inopinatum	1143	AF33006415		1041	DQ768267	–	–	AF33195815
Polyplectron malacense	1143	AF33006515		1041	DQ768268	–	–	AF33195715
Argusianus argus	1143	AF0137615			–	DQ834505	–	AF331954[15]
Rheinardia ocellata	1143	AF33006015			–	DQ834506	–	–
Afropavo congensis	1143	AF0137605		1041	DQ768253	DQ834507	–	AF17099114
Pavo cristatus	1143	L083791		1041	AF394612[u]	DQ834508	AY722396[u]	AF170990[14]
Pavo muticus	1143	AF0137635			–	DQ834509	–	AF170989[14]
Gallus gallus	1143	L083761		1041	AB086102[31]	DQ834510	NC001323[2]	AF170979[14]
Gallus varius	1143	AB044988[u]		1041	AF222551[12]	–	–	–
Gallus sonneratii	1143	AB044989[u]				DQ834511	AP006746[33]	–
Gallus lafayettei	1143	AB044990[u]			–	DQ834512	AP003325[33]	–
Bambusicola thoracica	1143	AF02879011		1041	AF222538[12]	DQ834513	AF222570[12]	AF170978[14]
Bambusicola fytchii	1143	AM236891			–	–	–	–
Francolinus francolinus	1143	AF0137625			–	DQ834514		–
Francolinus pondicerianus	660	U906487		1032	DQ768279	–	DQ832103	DQ832081
Francolinus gularis	660	U906497			–	–	–	–
Francolinus lathami	1143	AM236893		1041	DQ768257	–	–	DQ832082
Dendroperdix sephaena	1143	U906477	AM236894	1040	DQ768274	DQ834515	DQ832104	DQ832083
Peliperdix coqui	785	U906467	AM236895	1040	DQ768278	–	DQ832105	DQ832084
Scleroptila levaillantii	1143	U906427	AM236913	1039	DQ768291	DQ834516	DQ832106	DQ832085
Scleroptila finschi	1095	U906437	AM236896	701	DQ768290	–	–	–
Scleroptila africanus	1143	U906297	AM236897	1041	AF22255012	DQ834517	AF222581[12]	DQ832086
Scleroptila shelleyi	1143	U906457	AM236898	684	DQ768295	DQ834518	DQ832107	DQ832087
Scleroptila levaillantoides	1143	U906447	AM236900	1038	DQ768292	DQ834519	DQ832108	–
Tetraogallus himalayensis	1143	AY678108[u]			–	DQ834520	–	–
Tetraogallus tibetanus	535	AY563133[u]			–	–	–	–
Tetraogallus altaicus	535	AY563127[u]			–	–	–	–
Alectoris melanocephala	1143	Z487734			–	DQ834521	–	–
Alectoris barbara	1143	Z487714			–	DQ834522	–	–
Alectoris rufa	1143	Z487754			–	DQ834523	–	AF170988[14]
Alectoris graeca	1143	Z487724			–	DQ834524	–	–
Alectoris chukar	1143	L083781		1040	DQ768273	DQ834525	–	AF17098714
Alectoris philbyi	1143	Z487744			–	DQ834526	–	–
Alectoris magna	1143	Z487764			–	DQ834527	–	–
Margaroperdix madagarensis	660	U906407			–	DQ834528	–	–
Coturnix coturnix	1143	L083771		1041	X57246[36]	DQ834529	X57245[36]	–
Coturnix japonica	1143	NC00340817		1041	NC003408[17]	–	NC003408[17]	–
Excalfactoria chinensis	1143	NC00457520		1041	NC004575[20]	–	AB073301[20]	–
Ammoperdix heyi	622	AM236901			–	–	–	–
Perdicula asiatica	1143	AY390778[u]	AM236902		–	DQ834530	–	–
Pternistis hartlaubi	660	U906397			–	–	–	–
Pternistis erckelii	660	U906387			–	–	–	–
Pternistis castaneicollis	1143	AM236903			–	–	–	–
Pternistis bicalcaratus	660	U906377			–	–	–	–
Pternistis squamatus	1136	U906367	AM236904	1039	DQ768286	DQ834531	DQ832109	DQ832088
Pternistis griseostriatus	763	AM236905		1040	DQ768284	–	–	DQ832089
Pternistis leucoscepus	1138	AM236906		1034	DQ768283	–	–	DQ832090
Pternistis swainsonii	1142	U906347	AM236907	1039	DQ768287	DQ834532	DQ832110	DQ832091
Pternistis afer	1143	U906357	AM236908	1038	DQ768281	DQ834533	DQ832111	DQ832092
Pternistis capensis	1143	U906327	AM236909	1038	DQ768282	DQ834534	DQ832112	DQ832093
Pternistis adspersus	789	U906337	AM236910	1039	DQ768276	DQ834535	DQ832113	DQ832095
Pternistis hildebrandti	617	U906317			–	–	–	–
Pternistis natalensis	1143	U906307	AM236911	1039	DQ768285	DQ834536	–	DQ832094

*+ from Lucchini and Randi (1999) and Pereira et al. (2004) corresponding to bases 13–169 and 377–1033 in *Gallus gallus* from Desjardins and Morais (1990) GenBank no. NC001323; †
corresponding to bases 1228–1296 in *Gallus gallus* from Desjardins and Morais (1990) GenBank no. NC001323; ‡largely from Armstrong et al. (2001) and Kimball et al. (2001).
References to GenBank no. publications $-^{u}$ = unpublished; [1]Kornegay et al. (1993); [2]Valverde et al. (1994); [3]Liu et al. (1996); [4]Randi (1996); [5]Kimball et al. (1997); [6]Mindell et al. (1997); [7]Bloomer and Crowe (1998); [8]Johnson and Sorenson (1998); [9]Mindell et al. (1998); [10]Joseph et al. (1999); [11]Kimball et al. (1999); [12]Dimcheff et al. (2000); [13]Randi et al. (2000); [14]Armstrong et al. (2001); [15]Kimball et al. (2001); [16]Lucchini et al. (2001); [17]Nishibori et al. (2001); [18]Randi et al. (2001); [19]Dimcheff et al. (2002); [20]Nishibori et al. (2002); [21]Pereira et al. (2002); [22]Bush and Strobeck (2003); [23]Garcia-Moreno et al. (2003); [24]Grau et al. (2003); [25]Sorenson et al. (2003); [26]Zhan and Zhang (2003); [27]Nishibori et al. (2004); [28]Pereira and Baker (2004); [29]Pereira et al. (2004); [30]Shibusawa et al. (2004); [31]Wada et al. (2004); [32]Meece et al. (2005); [33]Nishibori et al. in press); [34]Bowie and Fjeldså (2005), [35]Harrison et al. (2004), [36]Desjardins and Morais (1991).

Appendix 3

Marginal posterior probabilities of the General Time Reversible Model obtained from a 5 million generation Bayesian inference run (burnin = 20% of the posterior distribution or 4000/20000 sampling points). Parameters were obtained for each of the gene regions separately: (1) CYT *B* (2) ND2 (3) OVO-G (4) 12s and (5) CR

			95% Credible Interval		
Parameter	Mean	Variance	Lower	Upper	Median
Rate matrices (General time reversible model of nucleotide evolution)					
r(G↔T){1}	1.00	0.00	1.00	1.00	1.00
r(C↔T){1}	12.2	33.3	6.23	24.4	11.0
r(C↔G){1}	0.89	0.23	0.37	1.96	0.79
r(A↔T){1}	1.27	0.41	0.58	2.67	1.13
r(A↔G){1}	20.4	87.4	10.4	41.1	18.4
r(A↔C){1}	0.36	0.03	0.17	0.75	0.33
r(G↔T){2}	1.00	0.00	1.00	1.00	1.00
r(C↔T){2}	3.99	0.58	2.81	5.66	3.87
r(C↔G){2}	0.48	0.01	0.29	0.75	0.47
r(A↔T){2}	0.32	0.01	0.20	0.51	0.31
r(A↔G){2}	9.18	2.65	6.62	12.7	8.99
r(A↔C){2}	0.18	0.00	0.12	0.27	0.18
r(G↔T){3}	1.00	0.00	1.00	1.00	1.00
r(C↔T){3}	2.55	0.20	1.80	3.53	2.51
r(C↔G){3}	0.71	0.03	0.41	1.13	0.69
r(A↔T){3}	1.10	0.05	0.71	1.61	1.07
r(A↔G){3}	3.43	0.36	2.74	4.74	3.37
r(A↔C){3}	1.17	0.07	0.74	1.74	1.15
r(G↔T){4}	1.00	0.00	1.00	1.00	1.00
r(C↔T){4}	74.1	305.1	38.8	99.0	76.3
r(C↔G){4}	0.96	0.23	0.23	2.10	0.89
r(A↔T){4}	7.22	4.21	3.43	11.2	7.23
r(A↔G){4}	31.7	77.9	15.7	49.5	31.4
r(A↔C){4}	5.96	2.57	2.95	9.00	5.97
r(G↔T){5}	1.00	0.00	1.00	1.00	1.00
r(C↔T){5}	4.51	0.42	3.45	5.94	4.45
r(C↔G){5}	1.02	0.04	0.68	1.47	1.00
r(A↔T){5}	2.08	0.10	1.54	2.80	2.05
r(A↔G){5}	4.33	0.40	0.27	5.76	4.28
r(A↔C){5}	1.56	0.07	1.10	2.16	1.53
State (base) frequencies					
pi(A){1}	0.346	0.000	0.325	0.369	0.347
pi(C){1}	0.448	0.000	0.427	0.467	0.448
pi(G){1}	0.051	0.000	0.046	0.057	0.051
pi(T){1}	0.154	0.000	0.146	0.163	0.154
pi(A){2}	0.350	0.000	0.331	0.371	0.350
pi(C){2}	0.412	0.000	0.393	0.431	0.413
pi(G){2}	0.052	0.000	0.047	0.057	0.052
pi(T){2}	0.185	0.000	0.174	0.196	0.185

Appendix 3 *Continued*

Parameter	Mean	Variance	95% Credible Interval		
			Lower	Upper	Median
pi(A){3}	0.225	0.000	0.199	0.254	0.225
pi(C){3}	0.223	0.000	0.195	0.251	0.222
pi(G){3}	0.226	0.000	0.198	0.256	0.226
pi(T){3}	0.326	0.000	0.294	0.358	0.326
pi(A){4}	0.357	0.000	0.329	0.385	0.357
pi(C){4}	0.327	0.000	0.302	0.352	0.327
pi(G){4}	0.148	0.000	0.127	0.170	0.148
pi(T){4}	0.168	0.000	0.151	0.185	0.167
pi(A){5}	0.263	0.000	0.242	0.286	0.263
pi(C){5}	0.255	0.000	0.234	0.276	0.255
pi(G){5}	0.142	0.000	0.125	0.159	0.142
pi(T){5}	0.338	0.000	0.316	0.362	0.338
Alpha shape parameter of the gamma distribution					
alpha{1}	0.575	0.001	0.512	0.640	0.573
alpha{2}	0.773	0.002	0.692	0.858	0.773
alpha{3}	21.64	158.8	4.948	47.76	18.96
alpha{4}	0.748	0.011	0.543	0.961	0.746
alpha{5}	0.551	0.004	0.440	0.684	0.550
Proportion of invariable sites					
pinvar{1}	0.440	0.000	0.407	0.473	0.440
pinvar{2}	0.326	0.000	0.293	0.359	0.326
pinvar{3}	0.038	0.000	0.001	0.102	0.033
pinvar{4}	0.430	0.000	0.362	0.486	0.432
pinvar{5}	0.160	0.002	0.075	0.236	0.162