

Suprageneric relationships of galliform birds (Aves, Galliformes): a cladistic analysis of morphological characters

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Of the basal clades of extant birds (Neornithes) the 'landfowl' or galliforms (Aves, Galliformes) are the most speciose. Cladistic analysis of more than 100 morphological characters coded at the generic level for most putative galliform genera confirms that the megapodes ('mound builders'; Megapodiidae) are the most basal clade within the order. They are followed successively by the curassows, guans and chachalacas (Cracidae), which comprise the sister-group to all other extant Galliformes (i.e. Phasianoidea). Within this large 'phasianoid' clade, analyses suggest that the guineafowl (Numididae) are the most basal taxon, although monophyly of this 'family' is not strictly supported on the basis of the morphological characters employed. An additional major clade within the phasianoid Galliformes is recovered by this analysis, comprising the traditional groupings of New World quails (Odontophoridae) and Old World quails ('Perdicini'), yet only monophyly of the former is supported unambiguously by morphological characters. Relationships within the remainder of the phasianoid taxa, including the grouse (Tetraonidae), turkeys (i.e. *Meleagris/Agriocharus* spp.) as well as other 'pavonine' galliforms (i.e. peafowl; *Pavo*, *Afropavo*, *Rheinardia*, *Argusianus* and *Polyplectron* spp.) remain largely unresolved on the basis of morphological characters, yet monophyly of the major subdivisions is supported here. Although there are a number of important differences, especially with regard to relationships within the nonquail phasianoids, the results of this morphological phylogenetic (cladistic) analysis are broadly congruent both with traditional classifications and existing molecular hypotheses of galliform phylogenetic relationships. © 2003 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2003, 137, 227–244.

ADDITIONAL KEYWORDS: Galliformes – Aves – bird – cladistics – phylogenetics – morphology – systematics – landfowl.

INTRODUCTION

ORDER GALLIFORMES

The living birds classified within the order Galliformes form a large and cosmopolitan group comprising more than 250 species within some 70 genera (Monroe & Sibley, 1990) that are found on almost all continents across the globe (del Hoyo, Elliott &

Sargatal, 1994). The order contains a number of very familiar taxa, such as pheasants, grouse, Old World quails, partridges, and guineafowls (Numididae), as well as a number of somewhat less well known birds including the 'mound-building' megapodes, the scrubfowl and brush-turkeys (Megapodiidae), as well as the guans, chachalacas and curassows (Cracidae; Delacour & Amadon, 1973), and New World quails (Odontophoridae). Even though the history of galliform classification was reviewed extensively by Sibley & Ahlquist (1990), it is worth noting that from the inception of avian taxonomy (e.g. Linnaeus, 1758; Huxley, 1867; Garrod, 1874; Fürbringer, 1888; Sharpe,

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1891; Gadow, 1893; Beddard, 1898) these birds have consistently been grouped together (yet the composition of families within the order has varied; see Sibley & Ahlquist, 1990). Overall, avian anatomists have considered Galliformes to be an osteologically uniform group (e.g. Lowe, 1938; Verheyen, 1956; Delacour, 1977), although much debate has focused on the question of whether the enigmatic hoatzin (*Opisthocomus hoazin*) should also be classified within the order (e.g. Fürbringer, 1888; Seebohm, 1890; Gadow, 1893; Shufeldt, 1904; Sibley & Ahlquist, 1973, 1990; Cracraft, 1981; Mindell *et al.*, 1997; Hughes & Baker, 1999; Hughes, 2000).

From the results of their now classic DNA-hybridization study, Sibley & Ahlquist (1990) recognized two distinct lineages within their superorder Gallomorphae (equivalent to the 'traditional' order Galliformes of most earlier workers), Craciformes and Galliformes (Fig. 1A). Representing a departure from the majority of older avian classifications, Sibley & Ahlquist (1990) removed Megapodiidae and Cracidae as a separate clade distinct from the remaining 'phasianoid' taxa (Fig. 1A). Most older classifications, albeit not couched within a strictly phylogenetic context, had at least implied a sequence of derivation for these birds within a single, distinct grouping (e.g. Verheyen, 1956, 1961; Johnsgard, 1973, 1986; Fig. 1B).

Order Galliformes generally has been considered to be one of the more basal clades of modern birds (= Neornithes *sensu* Cracraft, 1986). Current classifications (e.g. del Hoyo *et al.*, 1994) suggest that the order comprises at least five distinct families, namely Megapodiidae (megapodes and relatives), Numididae (guineafowl), Phasianidae (pheasants and relatives), Odontophoridae (New World quails), and Cracidae (curassows and relatives; Wetmore, 1960; Cracraft, 1981; Sibley & Ahlquist, 1990). Most often, Galliformes ('landfowl') have been placed within a basal neornithine clade along with the Anseriformes ('waterfowl') that has been termed Galloanserinae or Galloanserimorphae (dependant on implied rank; e.g. Cracraft, 1988; Dzerzhinsky, 1995; Livezey, 1997; Groth & Barrowclough, 1999; see Zusi & Livezey, 2000 for further commentaries; see also Ericson, 1996, 1997 for an alternative view).

AIMS

Existing phylogenetic studies of Galliformes have been limited to the consideration of molecular and behavioural evidence (reviewed by Sibley & Ahlquist, 1990; see below), or to smaller subsets of taxa within the order (e.g. Crowe, 1978; Crowe & Crowe, 1985; Gutiérrez, Barrowclough & Groth, 2000; see below). Here, for the first time, we present a comprehensive review of the morphological (primarily osteological)

character evidence that supports the major phylogenetic subdivisions within this large avian order on the basis of cladistic analysis. The application of phylogenetic (cladistic) analysis utilizing characters drawn from morphology has been relatively little practised within avian systematics (e.g. Cracraft, 1986; Livezey, 1986, 1997, 1998a,b; Ericson, 1997; Siegel-Causey, 1997; Hughes, 2000), and clearly represents an area for much work in the future (Livezey & Zusi, 2001).

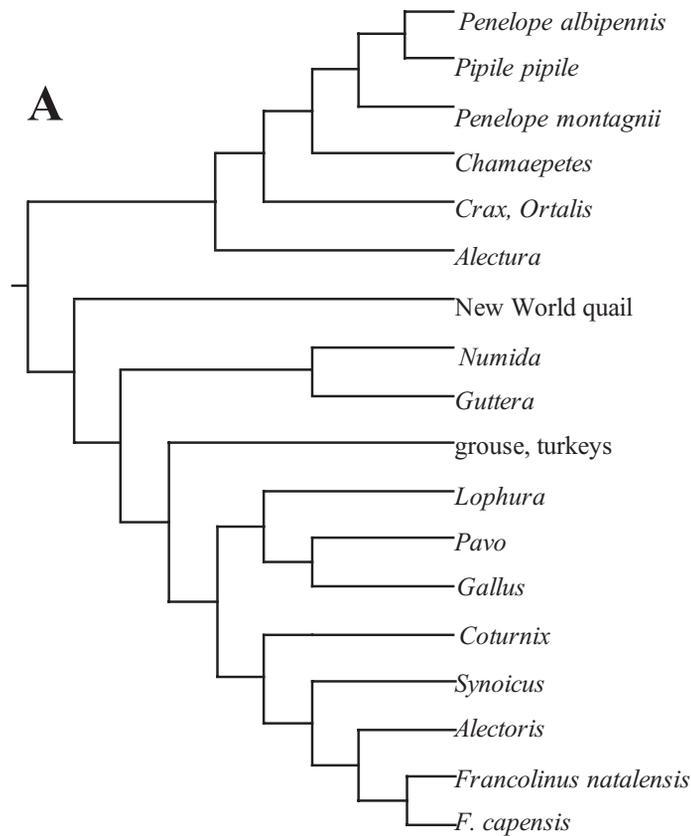
MATERIAL AND METHODS

SPECIMENS AND RELATED DATA

Our anatomical comparisons of extant Galliformes are founded at the generic-level and were based primarily on the series of study skeletons held in the collections of the Department of Ornithology at the American Museum of Natural History, New York (AMNH; see Appendix 3 for specimen numbers), supplemented by additional specimens held in the Division of Birds at the Field Museum of Natural History, Chicago (FMNH), and the Division of Birds at the United States National Museum, Washington D.C. (USNM). Our usage of anatomical terminology follows Baumel & Witmer (1993), with some modifications to English after Howard (1929). Since at this stage the aim of our work is not to present a revised phylogenetic classification for galliform birds (Wiley, 1981), all references to traditional taxonomic groups (including taxon names) follow the standard checklists of Johnsgard (1986), Monroe & Sibley (1990) and del Hoyo *et al.* (1994). We coded representative skeletal material of 58 extant genera of Galliformes (Appendix 3), including (at least on the basis of existing classifications) three genera of megapodes (Megapodiidae), five cracids (Cracidae), four guineafowl (Numididae), seven New World quails (Odontophoridae), two turkeys (Meleagrididae), six grouse (Tetraonidae), and 31 phasianid taxa (including Old World quails, peafowl, tragopans, pheasants, partridges and allies).

CHARACTERS

All of the osteological characters defined and used here are distinct morphological features that were considered, on the basis of our comparisons of skeletal specimens, to be divisible into two (or more) states across the taxa examined (Appendix 1). Multiple specimens (where available) of genera were examined in order to evaluate character variation within terminals. Some of the characters employed were partitioned into a number of states considered to represent points along a continuum of morphological variation, as previously identified by other workers on the basis of morphometric studies (Crowe *et al.*, 1992).



B

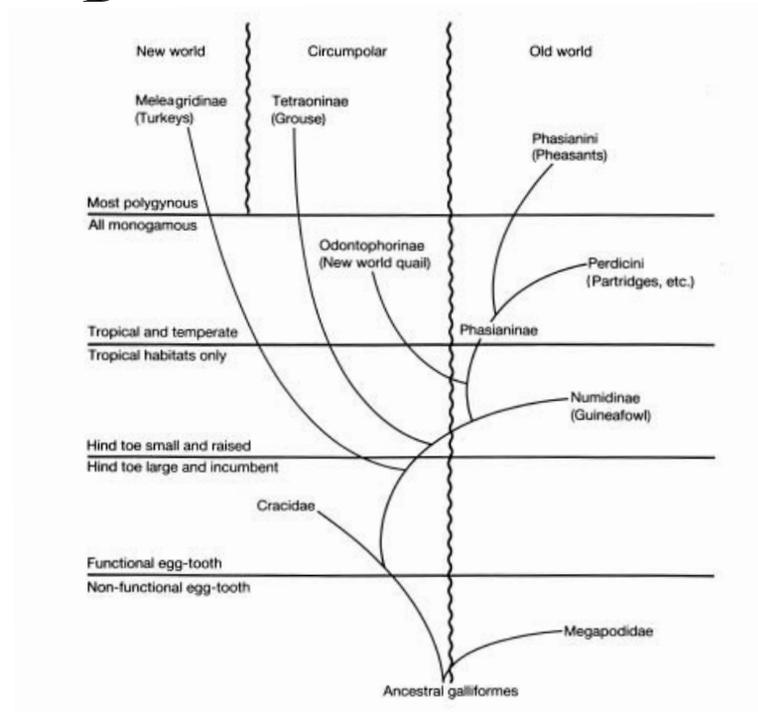


Figure 1. Two previous hypotheses for the internal relationships of Galliformes: A, Sibley & Ahlquist (1990: fig. 357). B, Johnsgard (1986: fig. 3; reproduced with permission, Oxford University Press).

OUTGROUPS AND PHYLOGENETIC ANALYSES

The order Galliformes has long been considered to be 'natural' and thus an uncontroversially monophyletic taxon (reviewed by Sibley & Ahlquist, 1990). The placement of this order close to the base of the neornithine radiation has been corroborated on the basis of both molecular and morphological evidence (Livezey & Zusi, 2001). Since Galliformes have often been placed together with Anseriformes (waterfowl) within a clade termed the Galloanserae (see above) we considered the polarity of our characters through comparison with a number of extant anseriform taxa. The morphology of these birds is highly variable (e.g. Livezey, 1986, 1997), hence taxa considered to be more basal phylogenetically within this particular order (i.e. the screamers *Anhima* and *Chauna* as well as the magpie-goose *Anseranas*) were utilized as outgroups for this study. As we will discuss below, true ducks (Anatidae) are too derived within Anseriformes to be informative for character polarity within Galliformes (Livezey, 1986, 1997, 1998a). Despite this, two anatid taxa were initially coded for formulated characters and are included in the matrix presented here (Appendix 2).

METHOD OF ANALYSIS

Results are based on parsimony analysis of 102 characters of which the vast majority (89) are osteological. A further set of relevant characters related to feathering and adult behaviour were also employed (13; see Discussion). As is standard in phylogenetic studies, characters unique to individual terminal taxa (i.e. autapomorphies) were included within analyses, even though they are uninformative with respect to overall relationships, as they contribute to estimations of total taxon divergence (e.g. Omland, 1997; Livezey, 1998b). Multistate characters were ordered for the purposes of this analysis.

We derived phylogenetic trees using the general optimality criterion of parsimony and PAUP version 4.06b for Macintosh (Swofford, 1998). As a result of the large number of taxa and characters employed, searches were limited by use of the heuristic algorithm (Swofford, 1998; branch-swapping on 1000 addition sequence replicates). Information common to sets of most parsimonious trees (MPTs) was summarized using strict component consensus representations; degrees of support for internal nodes were assessed using both simple counts of hypothesized character changes and the technique of character bootstrapping (e.g. Felsenstein, 1985; Hillis, 1995). Total tree length (L) and consistency index (CI, following the removal of uninformative characters) were also calculated using PAUP.

PHYLOGENETIC RESULTS

RELATIONSHIPS WITHIN GALLIFORMES

Phylogenetic analysis of the complete data-set (61 terminal taxa [not including the two members of the Anatidae included in the matrix, *Anas* and *Dendrocygna*]; 102 characters; Appendix 2) using parsimony resulted in the production of 1700 trees, each 612 steps in length (Fig. 2). Based on these trees and their strict component consensus representation (Fig. 3), the following groupings are supported by the analysis:

- (1) Galliformes are a monophyletic group with respect to Anseriformes.
- (2) A monophyletic Megapodiidae (e.g. *Macrocephalon*, *Alectura*, *Megapodius*) is the sister-group to all other Galliformes.
- (3) A monophyletic Cracidae (e.g. *Ortalis*, *Penelope*, *Aburria*, *Crax*, *Nothocrax*) is the sister-group to the 'phasianoids' (to the exclusion of the Megapodiidae).
- (4) All other phasianoid Galliformes form a monophyletic group with respect to the two, more basal clades Megapodiidae and Cracidae.
- (5) The traditional grouping of guineafowl (Numididae) is the most basal taxon within the phasianoid Galliformes, although monophyly of these birds is not strictly supported on the basis of the morphological characters employed.
- (6) New and Old World quails (i.e. *Magaroperdix*, *Perdix*, *Coturnix*) form a monophyletic group with respect to other phasianoid taxa.
- (7) The remaining Galliformes (including grouse, partridges, pheasants, turkeys, peafowl, tragopans and francolins) comprise a number of smaller clades that are successive sister-taxa with respect to the quails (Figs 2, 3).

All of these groupings are well supported on the basis of both the morphological character evidence and relevant support statistics.

CHARACTER SUPPORT FOR GROUPINGS

In their comprehensive review of the history of galliform classification, Sibley & Ahlquist (1990) listed only a few osteological features purportedly characteristic to this order of birds, including the presence of two deep incisurae in the sternum, a double-headed quadrate, holorhinal nares, and 16 cervical vertebrae. However, none of these characters have been tested thus far for synapomorphy at this level, and at least two (double-headed quadrate and holorhinal nares) are seen in a derived condition much deeper within the phylogeny of Aves (e.g. Chiappe, 1996, 2002). In our review of the literature related to galliform osteology, we found few characters that had been previ-

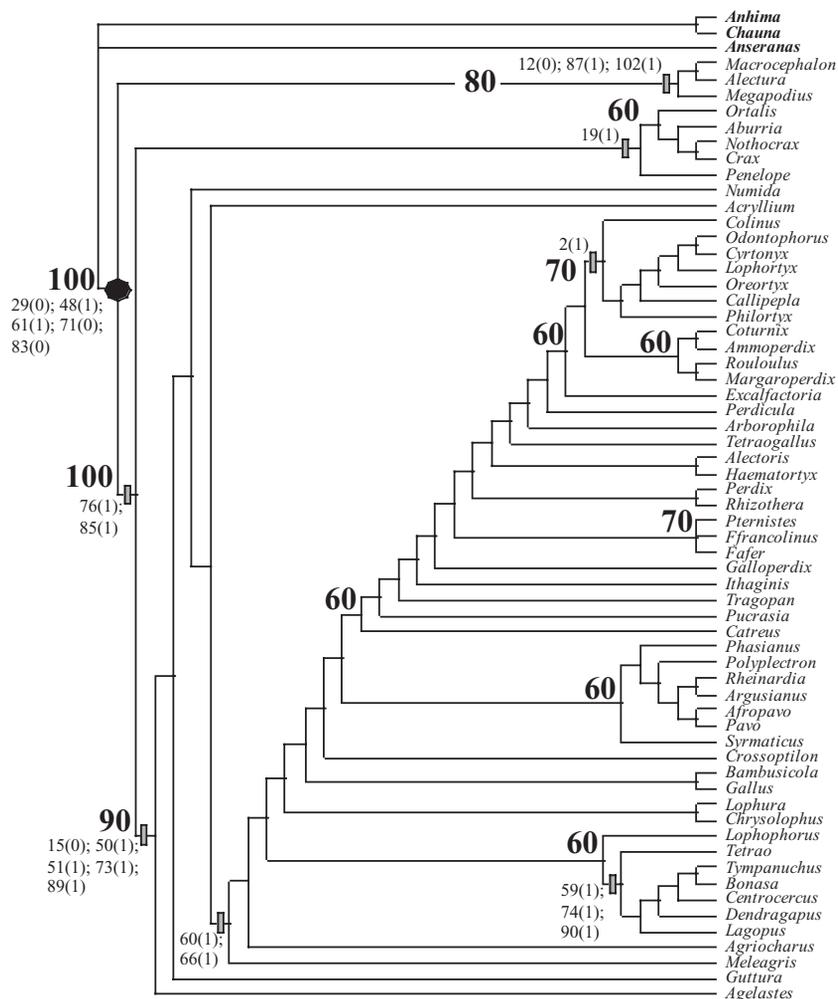


Figure 2. One of the 1700 MPTs (612 steps in length; CI = 0.179) recovered by parsimony analysis of the complete data-set for Galliformes (Appendix 2). Characters having a consistency index of 1 in this tree are given across internal nodes (see text for details); filled circle denotes Galliformes. Taxa of Anseriformes used as outgroups are in bold; bootstrap support values for important nodes are given in bold.

ously proposed as synapomorphic for the order (see e.g. Holman, 1964; Cracraft, 1981; Mayr, 2000; Dyke & Gulas, 2002). To date, the majority of the phylogenetic work pertaining to these birds has either focused on the relationship *between* Galliformes and Anseriformes (e.g. Cracraft, 1988; Dzerzhinsky, 1995; Ericson, 1997; Livezey, 1997; Zusi & Livezey, 2000), or has been concentrated *within* specific subsets of taxa (e.g. Beebe, 1914; , 1918–22; Hudson *et al.*, Lanzillotti & Edwards, 1959, 1966; Holman, 1961; Hudson & Lanzillotti, 1964; Delacour, 1977; Crowe, 1978; Crowe & Crowe, 1985; Sibley & Ahlquist, 1990; McGowan & Panchen, 1994; Akishinomiya *et al.*, 1995; Randi, 1996; Kimball, Braun & Ligon, 1997; Kimball *et al.*, 1999; Scott, 1997; Bloomer & Crowe, 1998; Hennache, Randi & Lucchini, 1998; Gutiérrez, Barrowclough &

Groth, 2000; Randi *et al.*, 2001). Previous noteworthy topologies depicting the ingroup relationships of Galliformes include Johnsgard (1986) and Sibley & Ahlquist (1990; Fig. 1).

Basal relationships

On the basis of our analyses, monophyly of Galliformes (i.e. Megapodiidae, Cracidae and phasianoids; Figs 2, 3) is supported by three unique synapomorphies (with respect to the relevant anseriform outgroups): presence of double, and open, incisurae laterales on the sternum (character 48; Fig. 4A, B); incisura capitis of proximal humerus enclosed from crus dorsale fossa by a distinct ridge (character 61; see also Mayr, 2000; Fig. 4C, D); and trochlea metatarsalia III of tarsometatarsus distinctly asymmetric (char-

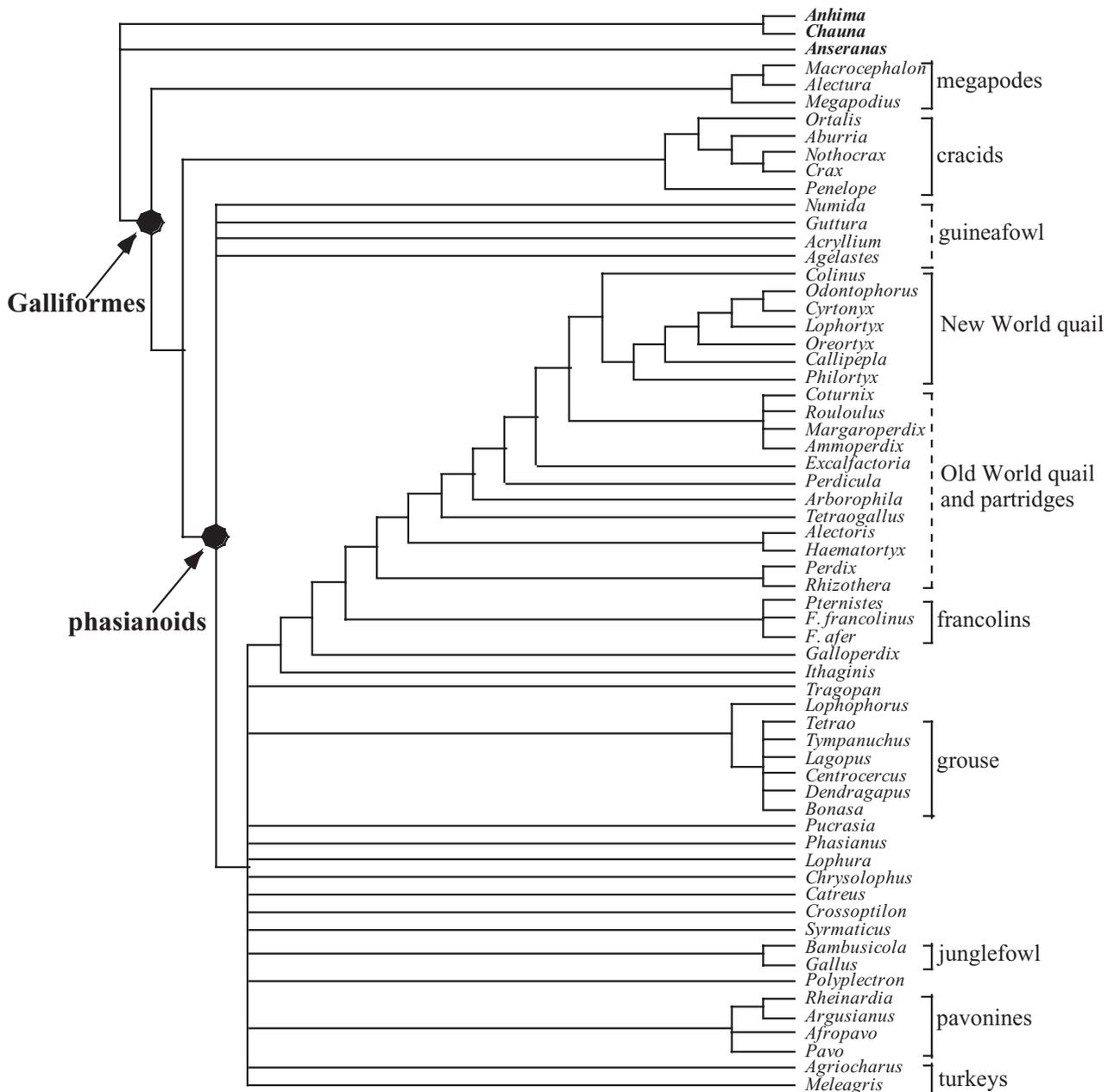


Figure 3. Strict consensus representation of 1700 MPTs recovered by parsimony analysis of the complete data-set for Galliformes (Appendix 2). Taxa of Anseriformes used as outgroups are in bold.

acter 83; see also Mayr, 2000; Dyke & Gulas, 2002; Fig. 4E, F).

The monophyly of the three megapodid taxa included within our analyses (Figs 2, 3) is supported by derived states for two characters: presence of super-elongated toes relative to the length of the tarsometatarsus (character 87) and incubation by use of external means (as opposed to by one, or both, parents, as is the case in all the other 'fowl-like' birds; del Hoyo, Elliott & Sargatal, 1994; character 102).

Two unambiguously optimized characters support monophyly of Cracidae and phasianoids to the exclusion of the basal Megapodiidae (Figs 2, 3): presence of a quadruple scar on the proximolateral surface of the proximal femur (character 76; see also Olson, 1974), and all three trochlea of tarsometatarsus close together (as opposed to being splayed laterally, as is the condition in Megapodiidae and Anseriformes; character 85). We find support for the monophyly of Cracidae (Figs 2, 3) due to the presence of an interme-

diate state for character 19: processus postorbitalis approaching, but not completely fused with, the orbit. In addition, these birds have long, deep and markedly recurved rostra (as is seen in the much more derived New World quails; character 1), and possess an angled extension that projects from the distal end of the processus lateralis of the coracoid (also seen uniquely in the blood pheasant *Ithaginis*; character 46).

The remainder of Galliformes (i.e. the phasianoids; Phasianoidea depending on author) that were considered in this analysis form a monophyletic group (Figs 2, 3), corroborated on the basis of five characters: caudal end of palatines indented in ventral view (character 15); little (or no) pneumaticity of the sternal plate (character 50); processus craniolateralis angled at 45° with respect to carina sternum (character 51, state 1; Fig. 5A, B); transverse processes of sacral vertebrae short, not reaching the level of the ilium (character 73); and hallux raised (character 89).

Relationships within phasianoid Galliformes

Based on a summary of relationships depicted by the strict consensus of the 1700 MPTs (Fig. 3) and examination of all of these trees, our analysis places the traditional guineafowl grouping Numididae (i.e. *Numida*, *Acryllium*, *Agelastes*, *Guttera*), as a series of paraphyletic taxa at the base of the phasianoids (Figs 2, 3). Although these endemic African birds most often have been placed together within a single family (e.g. Johnsgard, 1986; del Hoyo *et al.*, 1994), at this stage we are unable to find any morphological characters to unambiguously support the monophyly of this group. Apart from these taxa, the remainder of relationships within the phasianoids can be summarized by division of the group into a number of clades (Fig. 3). The larg-

est grouping supported by the analysis comprises the Old and New World Quails (i.e. *Perdicini* and *Odontophoridae*, respectively), and the francolins (e.g. *Pternistis*, *Francolinus*; Figs 2, 3).

Placed within this large clade, consensus results suggest that the most basal quail genus is *Perdicula* (Figs 2, 3), although this is not well supported by results of the bootstrap analysis. Monophyly of this

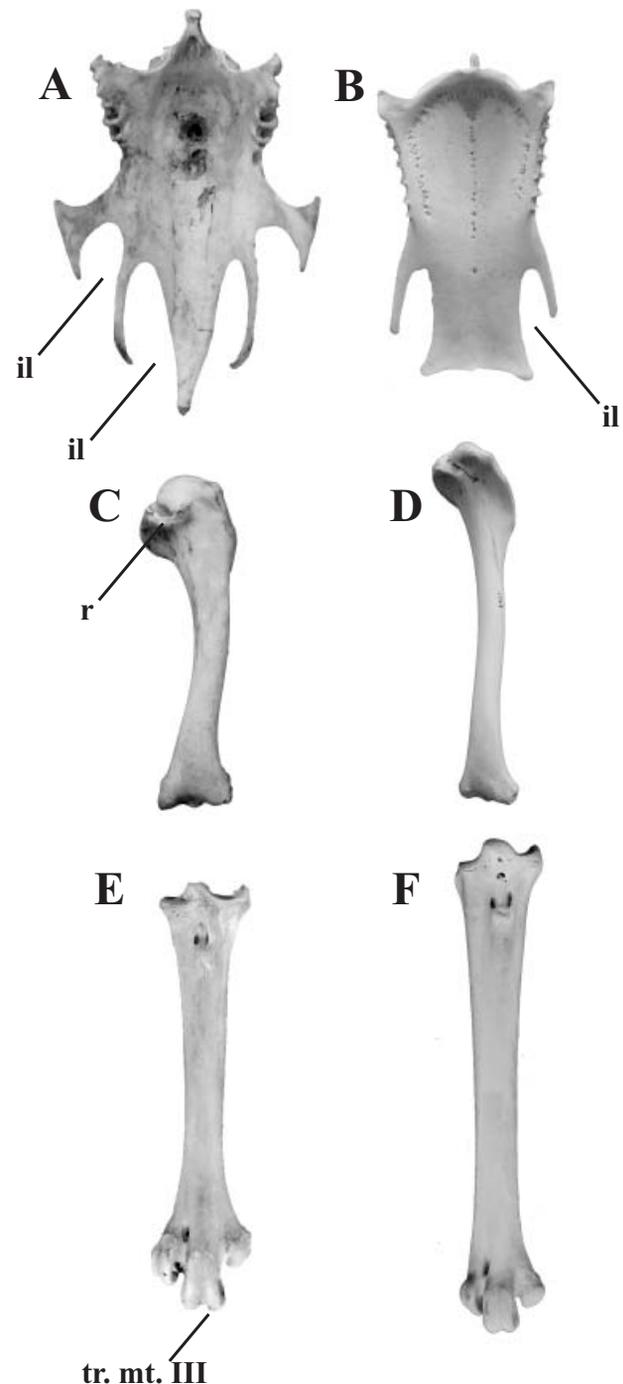


Figure 4. Some characters supporting the monophyly of Galliformes with respect to Anseriformes (Figs 2, 3). Incisurae laterales of sternum (character 48): A, sternum of *Aburria pipile* (Galliformes, Cracidae) in ventral view; B, sternum of *Cairina moschata* (Anseriformes, Anatidae) in ventral views; incisura capitis of proximal humerus enclosed from crus dorsale fossa by a distinct ridge (character 61): C, left humerus of *Aburria pipile* (Galliformes, Cracidae) in caudal view; D, left humerus of *Chauna chavaria* (Anseriformes, Anhimidae) in caudal view; trochlea metatarsal III distinctly asymmetric (character 83): E, right tarsometatarsus of *Lagopus mutus* (Galliformes, Tetraonidae) in dorsal view; F, right tarsometatarsus of *Chauna torquata* (Anseriformes, Anhimidae) in dorsal view. *Abbreviations:* il, incisura laterale; r, ridge between incisura capitis and crus dorsale fossae of proximal humerus (caudal view); tr. mt. III, trochlea metatarsalia III (figure not to scale).

taxon along with the other Old World and New World quails is supported by a single character: secondary fossa pneumaticum on proximal humerus well-developed (Fig. 6; character 56, state 3; Holman, 1964). Parsimony analysis of available morphological data suggests that the Old World quails ('Perdicini') form a series of successively more derived sister-taxa with respect to a monophyletic New World quail grouping (Figs 2, 3). Monophyly of this latter group (Odontophoridae; e.g. *Odontophorus*, *Colinus*, *Cyrtonyx*, *Lophortyx*, *Oreortyx*, *Callipepla*, *Philortyx*) is supported by a single unambiguously derived character: presence of serrations on the cutting edge of the lower mandible (the tomium of Holman, 1961; charac-

ter 2). A reversal to the primitive state in character 41 (i.e. sulcus articularis humeralis located on dorsal surface) with respect to Old World quails lends additional support to the monophyly of this clade.

Other than this large, and well-resolved, clade which includes the quail and francolins (Figs 2, 3), little further high-level resolution is achieved by this analysis within the phasianoids. The remaining taxa, including grouse, junglefowl, pavoines, turkeys and the majority of the pheasants, are unresolved in the strict consensus tree (Fig. 3). One of the best-supported nodes on the basis of characters within these remaining phasianoid Galliformes is the lineage that comprises the grouse (Tetraonidae; i.e. *Dendrago-*

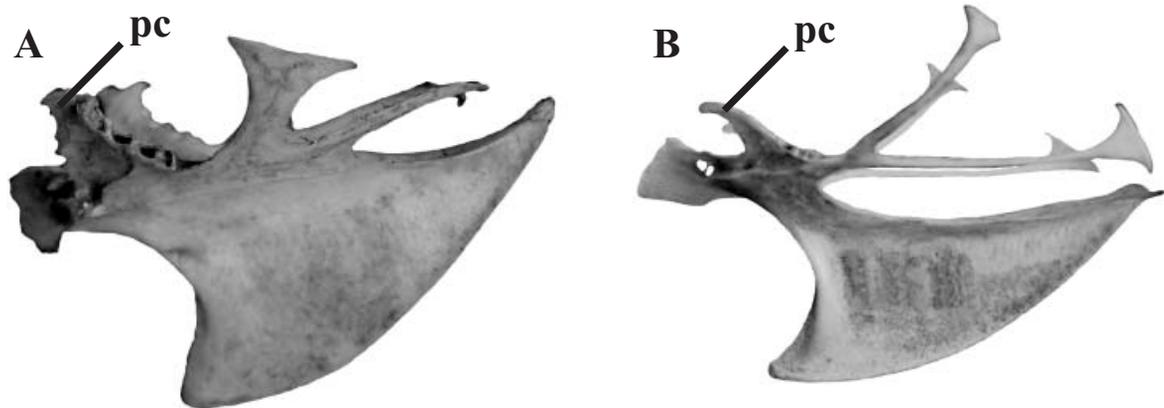


Figure 5. One of the characters supporting the monophyly of the phasianoid Galliformes – processus craniolateralis angled at 45° with respect to carina sternum (character 51): A, sternum of *Aburria pipile* (Cracidae) in left lateral view; B, sternum of *Lagopus lagopus* (Tetraonidae) in left lateral view. *Abbreviation:* pc, processus craniolateralis (figure not to scale).

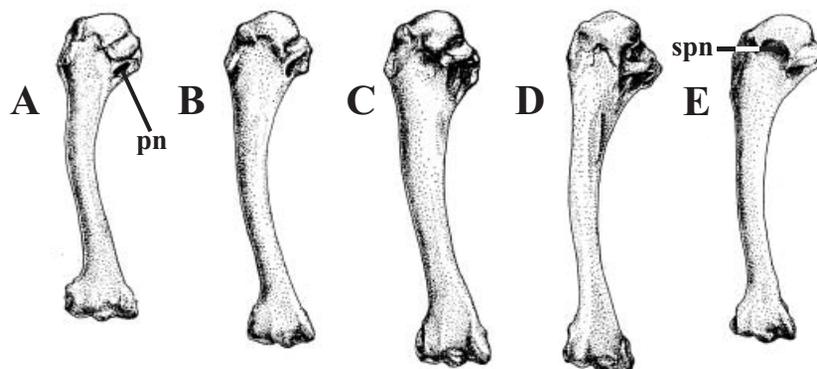


Figure 6. Character supporting the monophyly of quails – secondary fossa pneumaticum on proximal end of humerus well developed (character 56). Caudal views of humeri: A, *Crax globulosa*; B, *Numida meleagris*; C, *Meleagris gallopavo*; D, *Phasianus colchicus*; E, *Colinus virginianus*. Not to scale – this figure reproduced from Holman (1964: Plate 2) with permission of the Florida Academy of Sciences. *Abbreviations:* pn, fossa pneumaticum; spn, second well-developed fossa pneumaticum.

pus, *Lagopus*, *Tetrao*, *Bonasa*, *Centrocercus*, *Tympanuchus*), although this result is not reflected clearly by bootstrap analysis. This clade is supported by three unambiguously derived characters: distal end of condylus ventralis of humerus greatly extended distally (character 59); ischium shallow and wide, relative to the width of the synsacrum (character 74); and tarsus partially feathered (character 90). In addition, the condition of a number of other characters (with respect to other, closely related, phasianoid taxa) also corroborates the monophyly of this group: distal margin of the processus lateralis of coracoid pointed (character 43; reversal to the primitive state when compared to all other Galliformes, with the exception of *Chrysolophus*) and pectineal process of the pelvis projected as a small point (character 68; also seen in the distantly related New World quails). With respect to the closely related grouse, pheasants and partridges, monophyly of the two genera of turkeys (i.e. *Agriocharus*, *Meleagris*; Meleagrididae) is supported in 60% of the MPTs on the basis of their naked heads (character 101).

In our analyses, little further resolution was achieved within the generalized pheasants and partridges. While a clade comprising the 'pavonine phasianoids' (i.e. peafowl, argus and allies; *Argusianus*, *Afropavo*, *Pavo*, *Rheinardia*) was recovered (Fig. 3), the majority of the remaining taxa (e.g. *Pucrasia*, *Phasianus*, *Catreus*) occur within an unresolved polytomy at this level (Figs 2, 3).

DISCUSSION

Through the use of 102 morphological characters, including 89 based on osteology, we present the first cladistic analysis of representative genera of all putative supra-generic taxa attributed to the Galliformes. Although our analyses are not entirely comprehensive even at the level of individual genera, our aim is to provide a morphological framework for further systematic work on these birds. Future research must involve exploration of the extensive fossil record of Galliformes (e.g. Brodkorb, 1964; Olson, 1985; Mayr, 2000; Dyke & Gulas, 2002; Hope, 2002) within a cladistic context. Despite almost two centuries of morphological work, the formulation of characters and analysis of avian relationships within a phylogenetic (cladistic) context is still rarely practised, even with respect to extant taxa. Although the fossil record of Galliformes is often cited, especially in connection with 'molecular clock' age-estimates for the divergence of Neornithes (Hedges *et al.*, 1996; Cooper & Penny, 1997), none of these fossil remains have yet been evaluated within a phylogenetic context for the extant taxa.

The phylogenetic relationships of galliform taxa inferred by our morphological cladistic analysis are

broadly congruent both with traditional classifications and the molecular evidence that is available to date. Sibley & Ahlquist (1990: fig. 357) presented an average linkage (UPGMA) tree for Galliformes that agrees in a number of respects with our results. However, areas of conflict within this 'tapestry' include the presence of a monophyletic taxon including the Cracidae and Megapodiidae (the order Craciformes of Sibley & Ahlquist, 1990) as well as a basal position for the New World quail within phasianoids. Our results are congruent with those of Sibley & Ahlquist (1990) in that guineafowl are hypothesized to be basal within the phasianoids (Figs 2, 3). In agreement with traditional considerations of galliform osteology (e.g. Verheyen, 1956; Holman, 1964), and recent, less inclusive, cladistic treatments (Mayr, 2000; Dyke & Gulas, 2002), the recovery of a single clade comprising both Megapodiidae and Cracidae is not supported by a single morphological character. Aside from a number of technical difficulties with the distance-based hybridization methodology adopted by Sibley & Ahlquist (1990: fig. 357) (e.g. Houde, 1987, 1992; O'Hara, 1991; Lanyon, 1992), the taxon-coverage of Galliformes reported in this work is limited. Our analysis recovers a much greater degree of phylogenetic resolution within taxa sampled; broad-scale differences between our topology and that of Sibley & Ahlquist (1990) may be explained by our consideration of a larger number of genera (Figs 2, 3; Appendix 3).

Armstrong, Braun & Kimball (2001) compared the results of a phylogenetic analysis of the avian ovomucoid intron G (OVOG) with those obtained using the mitochondrial cytochrome *b* (*cytb*) for a limited number of galliform taxa and recovered relationships broadly comparable with those reported here (i.e. basal position for cracids, monophyly of the pavonines). Even though trees presented by Armstrong *et al.* (2001) depict relationships among a limit range of taxa, strong conflict is seen with the morphological result with regard to the position of New World quail (Odontophoridae) with respect to other phasianoids (Fig. 3) on the basis of *both* intron and *cytb* data.

This result, a basal position for the New World quails (Odontophoridae) with respect to other Galliformes (i.e. at the base of the phasianoids), has been reported by a number of workers (e.g. Sibley & Ahlquist, 1990 [DNA-hybridization]; Kimball *et al.* 1999; Armstrong *et al.*, 2001 [*cytb* sequences]) on the basis of molecular comparisons. Based on morphological evidence, however, this conclusion may occur as the result of inappropriate outgroup comparisons. New World quails share a number of presumably convergent skeletal features with more derived anseriforms, such as *Anas* and *Dendrocygna* (Anatidae; e.g. lamina basitemporalis medially indented and raised

centrally; dorsal rim of frontal distal to orbit wide; cotyla scapularis of coracoid cup-like and excavated; and crista cnemialis lateralis of tibiotarsus rounded). As discussed above, although we initially coded taxa of Anatidae (Appendix 2), these were not used as outgroups in the final analysis due to this problem. For example, polarizing characters using the derived anatid *Anas* (Livezey, 1986) will force Cracidae and Odontophoridae to move into more basal positions within the phylogeny because of the occurrence of osteological characters presumed to be convergent in these taxa.

It is worth noting that the vast majority of published phasianoid classifications stems from the early work of Beebe (1914, 1918–22), which has remained largely unchallenged. One of the most comprehensive recent treatments of these birds is that synthesized by Johnsgard (1986), who published a ‘dendrogram’ recognizing six distinct groupings of derived phasianoid galliforms: Meleagridinae (turkeys), Tetraoninae (grouse), Numidinae (guineafowl), Odontophoridae (New World quail), Phasianini (pheasants) and Perdiciini (partridges and allies; the latter two being placed within the Phasianinae). As noted above, the results of our analysis show strong support for the presence of the majority of these large clades (i.e. monophyly of grouse, New World quails, turkeys, and the ‘Phasianinae’) albeit nested and consequently ranked differently than implied by Johnsgard (1986). However, our analysis does to some extent support the contention of Johnsgard that the most basal phasianoid lineage comprises the turkeys (his Meleagridinae). As mentioned previously, the morphological evidence suggests that these birds do occur in a clade (albeit unresolved) towards the base of this part of the tree (Fig. 3). Furthermore, we find no support for the presence of a clade of tragopans (i.e. *Pucrasia*, *Tragopan*, *Lophophorus*; Figs 2, 3) as suggested by Johnsgard (1986). The monal *Lophophorus* is instead hypothesized to be the sister-taxon to the clade comprising the grouse (Tetraonidae). *Pucrasia* falls within a large and unresolved polytomy along with the generalized pheasants and partridges, while *Tragopan* and *Ithaginis* are basal within the large clade that contains the grouse, turkeys, pheasants and allies (Fig. 3). However, the presence of a clade comprising the peafowl is supported here on the basis of morphology (as again proposed by Johnsgard, 1986): *Rheinardia*, *Argusianus*, *Afropavo* and *Pavo* consistently are placed together in our analyses (see also Kimball *et al.*, 1997) within the clade that also includes the grouse, turkeys, *Tragopan*, the pheasants and allies (Fig. 3).

Despite earlier contentions to the contrary (Lowe, 1938; Verheyen, 1956; Delacour, 1977), our analyses demonstrate that Galliformes is a morphologically diverse group of birds (at least at the generic level and

below) and that this variation is informative with regard to the phylogenetic relationships of taxa. However, another of the principal conclusions of this study is that, although morphology can be used to resolve the broad-scale phylogenetic relationships of these birds, this type of data will not produce clear resolution above the generic level or indeed within certain groups (the pheasants and partridges, for example). One of the reasons we have not produced a phylogenetic classification for Galliformes is our belief that such an undertaking must be based on all available character information, not just morphology or sequence data.

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APPENDIX 1: CHARACTER DESCRIPTIONS

List of morphological characters employed in the phylogenetic analyses (followed by consistency indices, [CI]; see text for details). All characters treated as ordered.

OSTEOLOGICA

Cranium, maxilla and mandible

1. Rostrum: long, deep, and markedly recurved (0); long, shallow, not markedly recurved (1) [0.50].
2. 'Serrations' on cutting edge of lower mandible ('tomium' of Holman, 1961): absent (0); present (1) [1.00].
3. Processus mandibulae medialis: rounded on distal ends (0); tapered on distal ends (1) [0.25].
4. Tuberculum pseudotemporale: present and projected (0); not well developed (1) [0.50].
5. Dorsal projection of surangular: projecting as rounded or pointed tubercle (0); flattened, or absent (1) [0.33].
6. Pneumatic fossa(e) distal to rostrum mandibulae: present (0); absent (1) [0.33].
7. Lamina basitemporalis: not medially indented (0); medially indented and having no raised central portion (1); medially indented and raised centrally (2) [0.12].
8. Ectethmoid: present (0); reduced, or lost (1) (Cracraft, 1981) [0.16].
9. Width of nasal process of premaxilla between external nares: wide (0); narrow (1) [0.50].
10. Frontals, nasal process of premaxilla divides rostral portion of frontal: present (0); absent (1) [0.11].
11. Frontals at midpoint above orbit: wide (0); narrow (1) [0.20].
12. Cranial end of septum interorbitale bears wide lateral projections: present (0); absent (1) [1.00].
13. Vomer: fused with ossi palatini: present (0); absent (1) [0.08].
14. Ossa palatini, processus pterygoidei: rounded or pointed (0); straight (1) [0.07].
15. Caudal end of palatines, indented in ventral view: present (0); absent (1) [1.00].
16. Lacrimals: project caudally from skull margin into orbit (0); fused to frontal along their total length and hence not projected outwards from skull (1) [0.33].
17. Maxillopalatine shelf (in ventral view): present (0); absent, maxillopalatines widely separated (1) [0.25].
18. Pterygoid: attaches to quadrate level with condylus medialis (ventral view) (0); attaches below level of condylus medialis (1) [0.10].

19. Processus postorbitalis: completely unfused (0); partially fused (1); fused with processus zygomaticus (2) [1.00].
20. Dorsal rim of frontal, distal to orbit: thin, no shelf formed (0); margin wide, sometimes formed into distinct shelf distal to orbit (1) [0.14].
21. Lower part of foramen magnum: flattened at junction with condylus occipitalis (0); rounded, or tapered to junction with condylus occipitalis (1) [0.33].
22. Quadrate, processus orbitalis long and thin: present (0); absent (1) (Mayr, 2000) [0.20].

Vertebrae

23. Lateral fossa pneumaticum on thoracic vertebrae: present (0); absent (1) [0.33].
24. Thoracic centra: approximately as wide as tall (or taller than wide) (0); distinctly wider than tall (1) [0.05].
25. Cervical vertebrae, groove on caudal surface of hypapophysis: present (0); absent (1).
26. Notarium of incorporated vertebrae: four, or less (0); five (1) [0.06].

Postcranial skeleton

27. Furcula: U-shaped (0); V-shaped (1) [0.11].
28. Furcula, scapus clavicularae: widening towards extremitas omalis (0); of uniform thickness towards extremitas omalis (1) [0.07].
29. Furcula, apophysis furculae: pronounced and pointed (0); small or obsolete, not pronounced (1) [1.00].
30. Furcula, dorsal side of corpus scapulae bears distinct tubercle: present (0); absent (1) [0.09].
31. Scapula, distal end tapered: present (0); absent (1) [0.50].
32. Scapula, acromion: hooked (0); flat (1) (Holman, 1964) [0.12].
33. Scapula, facies articularis humeralis: semicircular in outline (0); circular in outline (1) [0.06].
34. Scapula, facies articularis humeralis: parallel to the corpus scapulae (0); acute with respect to corpus (1) [0.16].
35. Scapula, dorsal surface of facies articularis humeralis: excavated by fossa (0); not excavated, fossa absent (1) (Holman, 1964) [0.12].
36. Scapula, fossa between acromion and facies articularis humeralis (scapula): present (0); absent (1) (Holman, 1964) [0.11].
37. Coracoid, cotyla scapularis: shallow, not excavated (0); cup-like, excavated (1) [1.00].
38. Coracoid, processus acroracoides: hooked caudally (0); straighter, not hooked caudally (1) [0.16].

39. Coracoid, distinct fossa pneumaticum on dorsal surface: present (0); absent (1) (Holman, 1964) [0.14].
40. Coracoid, processus procoracoideus: present and projected (0); absent (1) [0.20].
41. Coracoid, sulcus articularis humeralis: located on dorsal surface (0); clearly turned distolaterally (1) [0.06].
42. Coracoid, processus acrocoracoideus, medial view: surface depressed (0); not bearing marked depression (1) [0.25].
43. Coracoid, processus lateralis, caudal margin (medial view): pointed (0); rounded (1) [0.08].
44. Coracoid, processus lateralis, cranial margin (medial view): prominent and upturned (0); rounded (1) [0.08].
45. Coracoid, facies articularis sternalis: distinctly excavated (0); smooth and not excavated (1) [0.09].
46. Coracoid, extension from processus lateralis: projects at angle from caudal end of coracoid (0); no extension (1) [0.05].
47. Sternum, apex carinae: distinctly pointed cranially (0); rounded (1) [0.05].
48. Sternum, incisurae laterali: single, open (0); double, open (1) [1.00].
49. Sternum, foramen pneumaticum on dorsal surface: penetrates corpus sternum (0); does not penetrate corpus sternum (1) [0.12].
50. Sternum, pneumaticity of ventral surface: extensive (0); little or none (1) (Holman, 1964) [1.00].
51. Processus craniolateralis: perpendicular to carina (0); 45 degrees with respect to carina (1); parallel to carina (2) (sternocoracoid process of Holman, 1964) [1.00].
52. Processus craniolateralis: very short (0); short (1); long (2); very long (3) (Crowe *et al.*, 1992) [0.60].
53. Processus craniolateralis: wide (0); narrow (1); very narrow (2) (Crowe *et al.*, 1992) [0.66].
54. Sternum, rostrum sterni, spina interna and spina externa, comparative size: equal (0); interna larger than externa (1) [0.83].
55. Humerus, condylus dorsalis: hooked proximally (0); rounded (1) [0.11].
56. Humerus, secondary fossa pneumaticum on caudal surface: rudimentary or absent (0); poorly developed (1); moderately developed (2); well-developed (3) (Holman, 1964) [0.75].
57. Humerus, processus flexorius: reaches as far dorsally as does condylus ventralis (0); reaches farther than condylus dorsalis (1) [0.20].
58. Humerus, attachment site for musculus supracoracoideus: absent (0); present (1) (Mayr, 2000) [0.50].
59. Humerus, distal extent of condylus ventralis in cranial view: not markedly extended distally (0); markedly protrudes distally (1) [1.00].
60. Humerus, caudal surface, foramen pneumaticum: small (0); large (1) (Holman, 1964) [1.00].
61. Humerus, incisura capitis: open groove (0); enclosed distally from crus dorsale fossa by a ridge (1) (Mayr, 2000) [1.00].
62. Ulna shorter than, or subequal to, humerus (0); ulna longer than humerus (1) [0.14].
63. Ulna, distinct indentation under distal margin of condylus dorsalis: present (0); absent (1) [0.05].
64. Ulna, incisura tendinosa: distinct (0); obsolete (1) [0.06].
65. Carpometacarpus, wide spatium intermetacarpale: absent (0); present (1) (Mayr, 2000) [0.50].
66. Carpometacarpus, processus intermetacarpalis present and overlapping os metacarpale minus: absent (0); present (1) (Holman, 1964) [1.00].
67. Carpometacarpus, processus pisiformis: single (0); divided (1) [0.11].
68. Pelvis, pectineal process: long and projected (0); small point (1) (Holman, 1964) [0.10].
69. Pelvis, cranial margin flared lateral to the margo dorsalis: present (0); absent, unflared (1) [0.50].
70. Pelvis, pubis fused to ischium caudal to the foramen obturatum: for half length of more (0); less (1) [[0.83].
71. Pelvis, two large and depressed foramina located between the anterior iliac crests, lateral to the margo dorsalis (0); foramina small and flat, or absent (1) [1.00].
72. Pelvis, caudal end of ischium: rounded (0); pointed (1) [0.12].
73. Pelvic sacral vertebral transverse processes: long, extending well onto ilium (0); shorter, barely extending onto, or not reaching ilium (1) [1.00].
74. Depth of ischium relative to width of synsacrum: deep (0); shallow and wide (1) [1.00].
75. Facies articularis antitrochanteris: distal pneumatic foramen present on caudal surface (0); absent (1) (Holman, 1964) [0.67].
76. Femur, quadruple scar on proximo-lateral surface of shaft: absent, or two scars at most (0); present (1) (Olson, 1974) [1.00].
77. Femur, fossa poplitea: recessed with pneumatic fossae (0); not deeply recessed (sometimes still having pneumatic fossae) (1) [0.50].
78. Tibiotarsus, trochlea cartilaginosa tibialis: asymmetrical (0); symmetrical (1) [0.08].
79. Tibiotarsus, condyles: of equal size (0); of unequal size (1) [0.20].
80. Tibiotarsus, fibula: extends two-thirds or less the length of tibiotarsus (0); more than two-thirds (1) [0.05].

81. Tibiotarsus, crista cnemialis lateralis: pointed (0); rounded (1) [0.09].
82. Tarsometatarsus, trochlea metatarsi II and IV of similar length (0); trochlea metatarsi II distinctly shorter than IV (1) (Holman, 1964) [0.25].
83. Tarsometatarsus, trochlea metatarsi III: distinctly asymmetric (0); symmetric (1) (Crowe *et al.*, 1992) [1.00].
84. Tarsometatarsus, plantar projection of trochlea metatarsi II: separated from remainder of trochlea by distinct indentation (0); not clearly separated, no indentation (1) [0.14].
85. Tarsometatarsus, trochlea splayed (0); close together (1) [1.00].
86. Tarsometatarsus, spurs absent in males (0); present in males (1) (Holman, 1964) [0.14].
87. Tarsometatarsus, length of toes relative to tarsometatarsus: short (0); long (1) [1.00].
88. Ungulares: bearing distinct sulcus on ventral surface (0); no distinct groove (1) [0.14].
89. Hallux incumbent (0); elevated (1) [1.00].
90. Tarsus: unfeathered (0); at least partially feathered (1) [1.00].
91. Number of tail feathers: less than 16 (0); greater than, or equal to, 16 (1) [0.16].
92. Tail feather moult: irregular or bi-directional (0); centrifugal (1); centripetal (2) (Johnsgard, 1986) [0.50].
93. Tail shape: round (0); wedged or graduated (1); vaulted (2) [0.50].
94. Wing longer than tail (0); shorter than tail (1) [0.33].
95. Spotted/vermiculated body plumage: absent (0); body plumage black spotted with white and having intervening white vermiculations (1) [0.50].
96. Ocelli: absent (0); rudimentary (1); well-developed (2) [0.50].
97. Sexual plumage dimorphism: absent (0); slight (1); marked (2) [0.11].
98. Feathered orbit (0); naked eye-ring (1) [0.14].
99. Average clutch size: greater than, or equal to, four eggs (0); 2–3 eggs (1) (McGowan & Panchen, 1994) [0.25].
100. Monogamous mating system (0); polygynous (1) [0.20].
101. Feathered, or largely feathered, head (0); largely naked head (1); totally naked head (2) [0.25].
102. Incubation system: by one, or both, parents (0); by external means (1) [1.00].

ADDITIONAL CHARACTERS

APPENDIX 2: CHARACTER MATRIX

Matrix of 102 morphological characters utilized in the phylogenetic analysis of Galliformes and relevant outgroups. Characters were coded either '0', '1', '2' or '3'; missing data (including nonapplicable character states) coded '?' (see text for details).

| Taxon | Character | | | | |
|----------------------|------------|------------|------------|------------|------------|
| | 1–10 | 11–20 | 21–30 | 31–40 | 41–50 |
| <i>Anas</i> | 1000112011 | 1111110001 | 0000010111 | 0100110110 | 1000011010 |
| <i>Anseranas</i> | 1011100011 | 1111110001 | 1101010111 | 0100101100 | 0100011010 |
| <i>Dendrocygna</i> | 1001102000 | 1111100001 | 0111010110 | 0100110110 | 0100011010 |
| <i>Chauna</i> | 1001110011 | 0111110000 | 1101110111 | 0110100100 | 0110011010 |
| <i>Anhima</i> | 1000001010 | 0110110100 | 1100010111 | 0110110100 | 0110011010 |
| <i>Macrocephalon</i> | 1000111001 | 0011110000 | 0011000000 | 0001000011 | 1101110110 |
| <i>Alectura</i> | 1000112000 | 0001111000 | 0111101000 | 0001010011 | 1111011110 |
| <i>Megapodius</i> | 1000111001 | 0001111000 | 0010100000 | 0011110001 | 0000010110 |
| <i>Ortalis</i> | 0011100110 | 1110110110 | 0010101001 | 0111010001 | 0001001100 |
| <i>Penelope</i> | 0011100011 | 1110110110 | 0001100000 | 0111010101 | 0001001100 |
| <i>Aburria</i> | 0011100110 | 1111110110 | 0111101001 | 0110000101 | 1101001100 |
| <i>Nothocrax</i> | 0011002110 | 0101110010 | 0010101101 | 0111010001 | 0111001100 |
| <i>Crax</i> | 0011000101 | 0111110110 | 1110101001 | 0101010001 | 1111001100 |
| <i>Numida</i> | 1011002110 | 0101011101 | 0010001100 | 0011110011 | 0000011101 |
| <i>Guttura</i> | 1011000010 | 1101001100 | 0010101100 | 0001110011 | 0010111101 |

Appendix 2 *Continued*

| Taxon | Character | | | | |
|----------------------|------------|------------|------------|------------|------------|
| | 1-10 | 11-20 | 21-30 | 31-40 | 41-50 |
| <i>Acryllium</i> | 1011002010 | 1101001101 | 0011101000 | 0011110001 | 0011011101 |
| <i>Agelastes</i> | 1011000011 | 1101001101 | 0010001101 | 0011110011 | 0001111101 |
| <i>Colinus</i> | 0111000110 | 1100001021 | 0011001000 | 0011110011 | 0000111111 |
| <i>Odontophorus</i> | 0111000110 | 1110001020 | 0110101001 | 1111110011 | 1000111111 |
| <i>Cyrtonyx</i> | 0111000110 | 1110001020 | 0110101001 | 1111110011 | 1000111111 |
| <i>Philortyx</i> | 0111010111 | 1100001021 | 0111001000 | 1011110011 | 0000111111 |
| <i>Oreortyx</i> | 0111001110 | 1100001021 | 0111001001 | 1111110011 | 1000111111 |
| <i>Lophortyx</i> | 0111001110 | 1110001021 | 0111001001 | 1111110011 | 1000111111 |
| <i>Callipepla</i> | 0111000111 | 1100001021 | 0111001001 | 1111110011 | 0000111111 |
| <i>Coturnix</i> | 1011000110 | 1100001121 | 0011001100 | 1010110110 | 0000111111 |
| <i>Excalfactoria</i> | 1011000110 | 1100001021 | 0011001101 | 1011110011 | 1011111111 |
| <i>Perdicula</i> | 1001000110 | 1111001121 | 0010001101 | 1011110011 | 0000011111 |
| <i>Pternistes</i> | 1011000110 | 1100001121 | 0011101000 | 1011110001 | 0000011111 |
| <i>F.francolinus</i> | 1011000110 | 1100001121 | 0011101000 | 1011110001 | 0000011111 |
| <i>F.afer</i> | 1011000110 | 1100001121 | 0011101000 | 1011110001 | 0000011111 |
| <i>Alectoris</i> | 1011000110 | 1101001121 | 0010001000 | 1011100010 | 0000111111 |
| <i>Tetraogallus</i> | 1011001110 | 1101001121 | 0010101100 | 1001110111 | 1001011111 |
| <i>Rouloulus</i> | 1011000111 | 1110011021 | 0011001000 | 1001010010 | 1001111111 |
| <i>Arborophila</i> | 1011000110 | 1100001120 | 0011001101 | 1001110011 | 0000011111 |
| <i>Margaroperdix</i> | 1011000110 | 1100001021 | 0011001000 | 1011110011 | 1000011101 |
| <i>Ammoperdix</i> | 1011000110 | 1100001121 | 0010101001 | 1001110011 | 0000111111 |
| <i>Galloperdix</i> | 1011000110 | 1100001121 | 0010000000 | 1001010011 | 1000011101 |
| <i>Haematortyx</i> | 1011002110 | 1100001120 | 0010001100 | 1011100011 | 1000111101 |
| <i>Perdix</i> | 1001000110 | 1100001121 | 0010001100 | 1001110001 | 1000011111 |
| <i>Rhizothera</i> | 1001000110 | 1100001121 | 0010001100 | 1001110001 | 1000011111 |
| <i>Ithaginis</i> | 1011000110 | 1101001021 | 0010001000 | 1001110001 | 1001001101 |
| <i>Tragopan</i> | 1011000110 | 1100001121 | 0011101101 | 1001110011 | 0001011101 |
| <i>Lophophorus</i> | 1011001110 | 1101001121 | 0000001001 | 1110100001 | 0010111111 |
| <i>Pucrasia</i> | 1011000110 | 1111001121 | 0010000000 | 1011110001 | 0001111101 |
| <i>Phasianus</i> | 1011001110 | 1100001121 | 1011101000 | 1001110001 | 0000111111 |
| <i>Lophura</i> | 1011000010 | 1100001021 | 0011000000 | 1111110001 | 0011011111 |
| <i>Chrysolophus</i> | 1011000110 | 1100001121 | 0011001100 | 1111000001 | 0001011111 |
| <i>Catreus</i> | 1011002110 | 1100001121 | 0010001001 | 1111110001 | 0001011101 |
| <i>Crossoptilon</i> | 1011002110 | 1111001121 | 0011001100 | 1011110001 | 0011011101 |
| <i>Syrnaticus</i> | 1011000010 | 1100001121 | 0011001000 | 1001100001 | 0011011101 |
| <i>Bambusicola</i> | 1011000010 | 1100001121 | 0011101000 | 1111110011 | 1011011111 |
| <i>Gallus</i> | 1011000010 | 1100001121 | 0011101000 | 1111110011 | 1011011111 |
| <i>Polyplectron</i> | 1011000111 | 1100001121 | 0011000100 | 1001110001 | 1010011111 |
| <i>Rheinardia</i> | 1011000110 | 1111000121 | 0011001000 | 1111000101 | 0001011101 |
| <i>Argusianus</i> | 1011000110 | 1100001121 | 0010000100 | 1111000000 | 0000011101 |
| <i>Afropavo</i> | 1011002110 | 1100001121 | 0010001100 | 1011000001 | 0001011111 |
| <i>Pavo</i> | 1011002110 | 1100001121 | 0011011100 | 1010100001 | 0101011111 |
| <i>Agriocharus</i> | 1011000110 | 0100001021 | 0011101000 | 1111010001 | 0011011111 |
| <i>Meleagris</i> | 1011002110 | 1100001120 | 0011001100 | 1111110001 | 1011011111 |
| <i>Tetrao</i> | 1011000110 | 1110001021 | 0010101000 | 1001100001 | 1000011111 |
| <i>Tympanuchus</i> | 1011000110 | 1100001021 | 0011101000 | 1100100001 | 0000111111 |
| <i>Lagopus</i> | 1011001110 | 1101001121 | 0011101000 | 1111100001 | 1000011111 |
| <i>Centrocercus</i> | 1011000110 | 11100?1021 | 0010100001 | 1101100001 | 0000011111 |
| <i>Dendragapus</i> | 1011000110 | 1100001121 | 0010101000 | 1101100001 | 1000111111 |
| <i>Bonasa</i> | 1011000110 | 1100001021 | 0011001000 | 1111110001 | 0000111111 |

Appendix 2 *Continued*

| Taxon | Character | | | | |
|-----------------------|------------|------------|------------|------------|--------------|
| | 51-60 | 61-70 | 71-80 | 81-90 | 91-102 |
| <i>Anas</i> | 000?000000 | 0011000111 | 1000001010 | 0111000000 | 000000?0000 |
| <i>Anseranas</i> | 000?000100 | 0011000111 | 1000001110 | 0011000000 | 000000?0000 |
| <i>Dendrocygna</i> | 000?000100 | 0111000001 | 1000101110 | 0111000000 | 000000?0000 |
| <i>Chauna</i> | 000?000000 | 0111000101 | 1000101010 | 1010000000 | 000000010000 |
| <i>Anhima</i> | 000?100000 | 0111101111 | 1000101010 | 1011000100 | 000000?0000 |
| <i>Macrocephalon</i> | 0000001100 | 1101000101 | 0000001111 | 1001001100 | 1?2000000001 |
| <i>Alectura</i> | 0001001100 | 1111001101 | 0000001010 | 1000001100 | 1?2000000011 |
| <i>Megapodius</i> | 0001001100 | 1101100101 | 0000101010 | 1101001000 | 0?0000000001 |
| <i>Ortalis</i> | 0001001100 | 1001100000 | 0000010100 | 0000100000 | 000000001000 |
| <i>Penelope</i> | 0001001100 | 1100101100 | 0000110011 | 1001100000 | 000000101000 |
| <i>Aburria</i> | 0001000100 | 1111100000 | 0000010110 | 0000100100 | 000000101000 |
| <i>Nothocrax</i> | 0001001100 | 1110100001 | 0000010111 | 1000100000 | 000000101000 |
| <i>Crax</i> | 0000000100 | 1111100001 | 0000110110 | 1001100000 | 000000101000 |
| <i>Numida</i> | 1111001100 | 1001100001 | 0110011010 | 0100100110 | 110010000010 |
| <i>Guttura</i> | 1111001100 | 1010100101 | 0110111011 | 1100100010 | 110010000010 |
| <i>Acryllium</i> | 1111001100 | 1011100001 | 0110011011 | 0100110110 | 110010000010 |
| <i>Agelastes</i> | 1110001100 | 1001100101 | 0010111010 | 1100110010 | 010000000010 |
| <i>Colinus</i> | 2320131101 | 1011110100 | 0110111110 | 0100100010 | 010000100000 |
| <i>Odontophorus</i> | 2320131101 | 1011110100 | 0010111011 | 0100100010 | 010000100000 |
| <i>Cyrtonyx</i> | 2320131101 | 1011110100 | 0010111011 | 0100100010 | 010000100000 |
| <i>Philortyx</i> | 2320131101 | 1001110100 | 0110111010 | 0100100010 | 010000?00000 |
| <i>Oreortyx</i> | 2321131101 | 1000110100 | 0110111111 | 1100100110 | 010000?00000 |
| <i>Lophortyx</i> | 2321131101 | 1010110100 | 0010111011 | 0100100010 | 010000?00000 |
| <i>Callipepla</i> | 2321131101 | 1011110100 | 0110111110 | 0100100010 | 010000100000 |
| <i>Coturnix</i> | 2321031101 | 1010110000 | 0010111010 | 1100100010 | 010000100000 |
| <i>Excalfactoria</i> | 2320131101 | 1011110000 | 0110111110 | 1100110010 | 010000100000 |
| <i>Perdicula</i> | 2320031101 | 100111000? | 0110111010 | 0100110010 | 010000100000 |
| <i>Pternistes</i> | 2320121101 | 1001110001 | 0010011011 | 0101110010 | 010000010000 |
| <i>F. francolinus</i> | 2320121101 | 1001110001 | 0010011011 | 0101110010 | 010000010000 |
| <i>F. afer</i> | 2320121101 | 1001110001 | 0010011011 | 0101110010 | 010000010000 |
| <i>Alectoris</i> | 2321121101 | 1011111000 | 0110011110 | 0100110010 | 010000010000 |
| <i>Tetraogallus</i> | 2321121101 | 1001110000 | 0010110110 | 0000110010 | 110000010000 |
| <i>Rouloulus</i> | 2121031101 | 1001110000 | 0010111101 | 0100100010 | 010000110000 |
| <i>Arborophila</i> | 2321131101 | 1001110101 | 0110111110 | 0100110010 | 010000010000 |
| <i>Margaroperdix</i> | 2321031101 | 1010110000 | 0110111111 | 0100100010 | 010000100000 |
| <i>Ammoperdix</i> | 2321031101 | 1000110100 | 0010011110 | 0100100010 | 010000100000 |
| <i>Galloperdix</i> | 2321121101 | 1000111101 | 0110011011 | 1100110010 | 0100001?0000 |
| <i>Haematortyx</i> | 2321131101 | 1101110001 | 0010011111 | 0100110110 | 010000100000 |
| <i>Perdix</i> | 2320121101 | 1001110000 | 0110011111 | 0100110010 | 010000??0000 |
| <i>Rhizothera</i> | 2320121101 | 1001110000 | 0110011111 | 0100110010 | 010000??0000 |
| <i>Ithaginis</i> | 2321021101 | 1011110001 | 0110111010 | 1100110010 | 010000110000 |
| <i>Tragopan</i> | 2321021101 | 1000110000 | 0110111011 | 1100110010 | 110000111000 |
| <i>Lophophorus</i> | 2321120101 | 1001110000 | 0110011011 | 0100110010 | 120000110100 |
| <i>Pucrasia</i> | 2321021101 | 1001110000 | 0110011011 | 1100110010 | 121000100000 |
| <i>Phasianus</i> | 2321121101 | 1011110000 | 0110011110 | 1100110010 | 121100110100 |
| <i>Lophura</i> | 2320021101 | 1101111000 | 0110111010 | 0100110010 | 122100100100 |
| <i>Chrysolophus</i> | 2321021101 | 1000110000 | 0110111010 | 0100110010 | 122100100100 |
| <i>Catreus</i> | 2321021101 | 1010110000 | 0110111110 | 1100110010 | 121100110000 |
| <i>Crossoptilon</i> | 2321121101 | 1001110000 | 0110111011 | 0100110010 | 122100010000 |
| <i>Syrnaticus</i> | 2321121101 | 1000110000 | 0110011010 | 1100110010 | 121100110100 |
| <i>Bambusicola</i> | 2321021101 | 1011110001 | 0110111011 | 1100110010 | 022100110000 |
| <i>Gallus</i> | 2321021101 | 1011110001 | 0110111011 | 1100110010 | 022100110000 |

Appendix 2 *Continued*

| Taxon | Character | | | | |
|---------------------|------------|------------|------------|------------|--------------|
| | 51–60 | 61–70 | 71–80 | 81–90 | 91–102 |
| <i>Polyplectron</i> | 2321121101 | 1010111100 | 0110011111 | 0100110010 | 101101111100 |
| <i>Rheinardia</i> | 2211021101 | 1001111000 | 0110011011 | 1100110010 | 001100111110 |
| <i>Argusianus</i> | 2211021101 | 1111110001 | 0110011000 | 1100110010 | 001101111110 |
| <i>Afropavo</i> | 2210021101 | 1001110001 | 0010111010 | 1100110010 | 1?1001111000 |
| <i>Pavo</i> | 2211021101 | 1011110000 | 0110011011 | 1000110010 | 101001110000 |
| <i>Agriocharus</i> | 2321011101 | 1000110100 | 0110111011 | 0100110010 | 120000100110 |
| <i>Meleagris</i> | 2311011101 | 1001110001 | 0110111010 | 0100110010 | 120000100110 |
| <i>Tetrao</i> | 2321020111 | 1001111100 | 0111011011 | 0101110011 | 120000100100 |
| <i>Tympanuchus</i> | 2121121111 | 1011110000 | 0111011000 | 0100110011 | 120000100100 |
| <i>Lagopus</i> | 2120021111 | 1010110100 | 0111111011 | 0100110011 | 120000000000 |
| <i>Centrocercus</i> | 2121021111 | 1110110?01 | 0111111101 | 0100110011 | 120000100100 |
| <i>Dendragapus</i> | 2121021111 | 1001110100 | 0111111001 | 0100110011 | 120000100100 |
| <i>Bonasa</i> | 2121121111 | 1001110101 | 0111111010 | 0100110011 | 120000000100 |

APPENDIX 3: GENERA OF GALLIFORMS

The following genera of extant Galliformes (and anseriform outgroups) were used for character formulations and coding of the matrix (see Appendix 2). Within Galliformes, taxonomy follows del Hoyo *et al.* (1994).

Anseriformes

Anhimidae: *Chauna chavaria* AMNH 1771; *Chauna torquata* AMNH 10864; *Anhima cornuta* AMNH 4402, 1766. Anseranatidae: *Anseranas semipalmata* AMNH 1772. Anatidae: *Dendrocygna viduata* AMNH 4723; *Anas rubripes* AMNH 10735.

Galliformes

Megapodiidae: *Macrocephalon maleo* AMNH 12013; *Megapodius duperryi* AMNH 1389; *Megapodius freycineti* FMNH 104631 (lacks skull); *Alectura lathami* AMNH 13751; *Cracidae*: *Aburria aburri* AMNH 2625; *Nothocrax urumutum* AMNH 6043; *Crax mitu* AMNH 3815; *Crax alberti* AMNH 1395; *Penelope purpurascens* AMNH 1368; *Ortalis vetula* AMNH 1405. Numididae: *Acryllium vulturinum* AMNH 11341; *Numida meleagris* AMNH 23327, 16090; *Guttera plumifera* AMNH 4258; *Agelastes (Phasidus) niger* AMNH 6051, 4147, 6044. Odontophoridae: *Odontophorus stellatus* FMNH 330229; *Cyrtonyx montezumae* AMNH 3449; *Colinus virginianus* AMNH 2310; *Lophortyx californicus* AMNH 5464; *Philortyx fasciatus* AMNH 4799; *Oreortyx picta* AMNH 1654; *Callipepla squamata* AMNH 18789. Meleagrididae: *Agriocharus (Melea-*

gris) ocellata AMNH 11530, FMNH 338596; *Meleagris gallopavo* AMNH 18704. Tetraonidae: *Dendrogapus franklini* AMNH 21628; *Lagopus lagopus* AMNH 18360; *Tetrao tetrax* AMNH 12844; *Bonasa bonasia* AMNH 19596; *Centrocercus urophasianus* AMNH 60; *Tympanuchus phasianellus* AMNH 23621. Phasianidae: *Pternistis (Francolinus) squamatus* AMNH 4184; *Francolinus francolinus* AMNH 1414, 524; *Francolinus afer* AMNH 5050; *Francolinus pictus* AMNH 2826; *Perdix perdix* FMNH 330903, 365043, 351166; *Galloperdix spadicea* AMNH 1349; *Haematortyx sanguiniceps* AMNH 20893; *Perdicula argoondah (asiatica)* AMNH 1583; *Crossoptilon crossoptilon* AMNH 14677; *Catreus wallichii* AMNH 5194; *Alectoris gracea* AMNH 1584; *Magaroperdix madagarensis (madagasgarensis)* AMNH 523; *Pavo cristatus* AMNH 16428; *Gallus gallus* AMNH 12165; *Afropavo congensis* AMNH 12367; *Rollulus rouloul* AMNH 11571; *Bambusicola thoracica* AMNH 2441, FMNH 105833 (both lack skulls), USNM 611819; *Ithaginis cruentis* AMNH 21986; *Phasianus colchicus* AMNH 20970; *Polyplectron inopinatum* AMNH 22690; *Lophophorus inpejanus* AMNH 1975; *Tetraogallus himalayensis* AMNH 16360; *Syrmaticus soemmerringii* AMNH 11070; *Syrmaticus reevesi* AMNH 3678; *Lophura bulweri* AMNH 10962; *Excalfactoria sinensis* AMNH 3748; *Pucrasia macrolopha* AMNH 17641; *Tragopan satyra* AMNH 1318; *Argusianus argus* AMNH 11094; *Rheinardia ocellata* AMNH 6046; *Chrysolophus amherstiae* AMNH 3439; *Ammoperdix heyi* AMNH 5366; *Arborophila torqueola* AMNH 11006; *Coturnix japonica* AMNH 8585; *Rhizothera longirostris* AMNH 2741.