

# Morphological and molecular support for nonmonophyly of the Galloanserae

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## ABSTRACT

This paper discusses morphological and molecular data bearing on the earliest evolution of the Neornithes. Phylogenetic analyses of basal neornithine groups frequently result in poorly resolved trees, most likely caused by rapid branching events in the Cretaceous and early Tertiary. Although data that efficiently resolve the earliest history of modern birds are few, a consensus opinion about their basal phylogeny has emerged in recent years. Two major splits within Neornithes are postulated. The first occurs when the palaeognathous birds branch off from the rest (the Neognathae), and the second when the Anseriformes and Galliformes split from all other neognaths. Morphological data presented by Livezey (1997) supporting this second dichotomy are combined with additional data from Ericson (1997) and re-analyzed. In addition, a new data set consisting of nucleotide sequences from the nuclear, single-copy gene *c-myc* is analyzed separately and in combination with the morphological data. Neither analyses support the suggested anseriform–galliform relationship. Instead, the Anseriformes group with the Ciconiiformes, Phoenicopteriformes and Charadriiformes, that is, a clade of wading birds.

## KEYWORDS

Neornithes, Palaeognathae, Neognathae, Anseriformes, Galliformes, phylogeny, skeletal morphology, nucleotide sequences, *c-myc*.

## Introduction

Considering that birds are an unusually well-studied group of animals, surprisingly little is known about the earliest evolution of the Neornithes. As used here, the taxon Neornithes includes the most recent common ancestor of all living birds, and all its descendants (*sensu* Chiappe 1995). Precisely when the neornithines evolved is much disputed (Feduccia 1995), but at least molecular data suggests a radiation that started well back into the Cretaceous (Hedges *et al.* 1996; Cooper and Penny 1997). It is commonly assumed that the Neornithes experienced a very early dichotomy into a palaeognath and a neognath clade (Figure 1). Among living birds

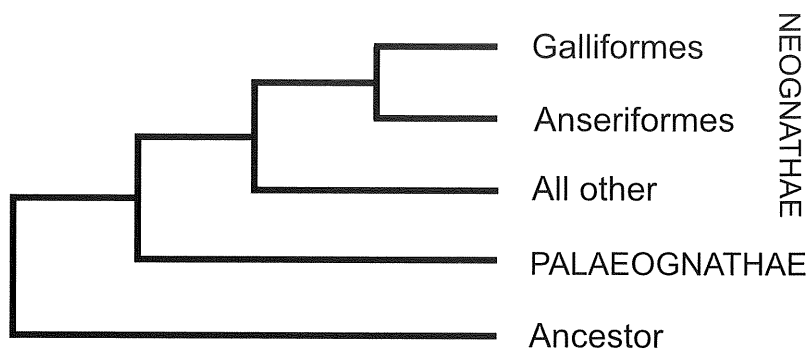


FIGURE 1. The “conventional wisdom” of phylogenetic relationships among major lineages of the Neornithes. The palaeognaths are considered as the first group to branch off from the rest. So far, however, molecular and morphological data does not unambiguously favor this hypothesis. The dichotomy between the anseriform–galliform clade and the other neognaths is supported by some data sets, but contradicted by others.

the Palaeognathae includes the ratites and tinamous, while all other birds form the Neognathae (Huxley 1867). Although it has been questioned, the hypothesis of monophyly of the Palaeognathae seems to be well supported by morphology (e.g., Bock 1963; Bock and Bühler 1990; Kurochkin 1995), and molecular data (e.g., Prager et al. 1976; Lee et al. 1997). A basal position of the palaeognaths within the Neornithes is normally taken for granted although the fossil record is almost silent on this point (compare Olson 1985; Chiappe 1995). Recently, phylogenetic analyses based on molecular sequences obtained from the mitochondrial genome has challenged this view by suggesting the order Passeriformes to be basal sister to all other living neornithines (Härlid et al. 1997, 1998; Mindell et al. 1997).

Within the Neognathae many avian systematists regard the anseriforms and the galliforms as sister taxa, forming the sister group to all other neognaths (Cracraft 1988; Cracraft and Mindell 1989; Weber 1993; Dzerzhinsky 1995). Also the dichotomy between the anseriforms–galliforms in contrast to all other neognathous birds has been questioned (e.g., Olson and Feduccia 1980; Ericson 1996, 1997). Interordinal relationships in birds are poorly understood, however, and the number of phylogenetic hypotheses concerning these relations, based on cladistic principles, are few and sometimes contradictory. An obvious example is the simultaneous publication of two papers that arrived at drastically different conclusions regarding the phylogenetic relationships of anseriform birds, despite both being based on morphology and including more or less a similar set of taxa (Ericson 1997; Livezey 1997). In Ericson’s study the anseriforms group with the orders Ciconiiformes and Charadriiformes (Figure 2A), while Livezey found the anseriforms to be sister to the Galliformes (Figure 2B). Both phylogenetic hypotheses received a rather high bootstrap support.

In this paper, these two partly contradictory morphological data sets have been pooled. In addition to this new morphological data set, nucleotide sequence data have been obtained from the nuclear, single-copy oncogene *c-myc* gene for a range of taxa that correspond to those included in the morphological data set. Although novel to avian phylogenetics, *c-myc* has proven promising for resolving ancient divergences in vertebrates (Graybeal 1994; Ericson et al. 2000). Phylogenetic analyses are undertaken for the molecular and morphological data, both separately and combined.

Institutional abbreviations used in this paper are: LMS, Laboratory of Molecular Systematics, National Museum of Natural History, Washington, D.C., U.S.A.; LSU, Museum of Natural Science, Louisiana State University, Baton Rouge, Louisiana, U.S.A.; NRM, Swedish Museum of Natural History, Stockholm, Sweden; NCBI, National Center for Biotechnology Information, National Library of Medicine, Bethesda, Maryland, U.S.A.

TABLE 1. List of skeletal characters found to be redundant in the pooled data set based on Ericson (1997) and Livezey (1997). Those marked with an asterisk (\*) have been excluded from the analysis.

Skeletal feature	Character numbers	
	Ericson	Livezey
Fonticulus occipitalis (cranium)	1 *	5
Basipterygoid articulation (cranium)	7 *	7
Ventral surface of processus postorbitalis (cranium)	3 *	8 (state d)
Spatulate bill	15 *	22
Quadratal articulation (mandibula and os quadratum)	18 *	26 * and 51
Cranial kinesis	12 *	36
Anconal surface of crista deltoidea (humerus)	55 *	71
Recessus iliacus (os coxae)	31 *	79
Crista cnemialis cranialis (tibia)	66 *	85

### Material and Methods

The morphological data set consists of the 71 skeletal characters from Ericson (1997), and 96 skeletal, 20 integumental and seven myological characters from Livezey (1997, 1998). The original data sets are largely complementary and only 10 characters were found to be duplicated (Table 1). As these 10 characters were identically coded by the authors, one of the occurrences was excluded. The new, morphological data set thus comprises 184 characters, of which 157 are osteological, 20 are integumental, and seven are myological (see the Appendix).

The molecular data set consists of nucleotide sequences obtained from the nuclear gene *c-myc* for 16 species, representing 13 families (Table 2). The ingroup taxa were chosen to facilitate comparison with the morphological studies of Ericson (1997) and Livezey (1997). Two species of the palaeognathous Tinamidae were used as outgroups. DNA was extracted from tissue or blood specimens using standard techniques of proteinase K/SDS digestion followed by phenol chloroform extraction and ethanol precipitation, or by QIAmp™ DNA extraction kits following manufacturers' recommendations (QIAGEN®). Amplification was performed with primer pairs *mycEX3A* and *RmycEX3A* (CAAGAAGAAGATGAGGAAAT and TTAGCTGCTCAAGTTTGTG, respectively), or *mycEX3D* and *RmycEX3D* (GAAGAAGAACAAGAAGAA-GATG and ACGAGAGTTCCCTTAGCTGCT, respectively). Sequencing was performed using Perkin Elmer Applied BioSystems 373 or 377 automated fluorescent sequencing instruments, and Perkin Elmer Applied BioSystems PRISM terminator cycle sequencing kits with AmpliTaq FS polymerase (either standard rhodamine and BigDye chemistries were employed). Sequence assembly was performed using the program Sequence Navigator (Perkin-Elmer Applied BioSystems). The *c-myc* gene is a rather conservative, protein-coding gene, with extremely few insertions and deletions observed in the Class Aves (Ericson et al. 2000). The alignment of the 498 base pairs obtained thus could be readily performed by eye. The sequences are deposited at the National Center for Biotechnology Information, Maryland, with the Genbank accession numbers AY034411–AY034424 and AF296417.

The molecular and morphological data sets differ somewhat in their taxonomic selections. The molecular data set consists of sequences obtained for the 16 species from 13 families. Morphological data for these 16 species was deduced from Ericson (1997:438, table 1) by assigning them the character states (including polymorphisms) for the family to which they belong. This approach was also taken when adding Livezey's (1997) characters to the data set. However, as Livezey only provided character states at the ordinal level for the Tinamiformes,

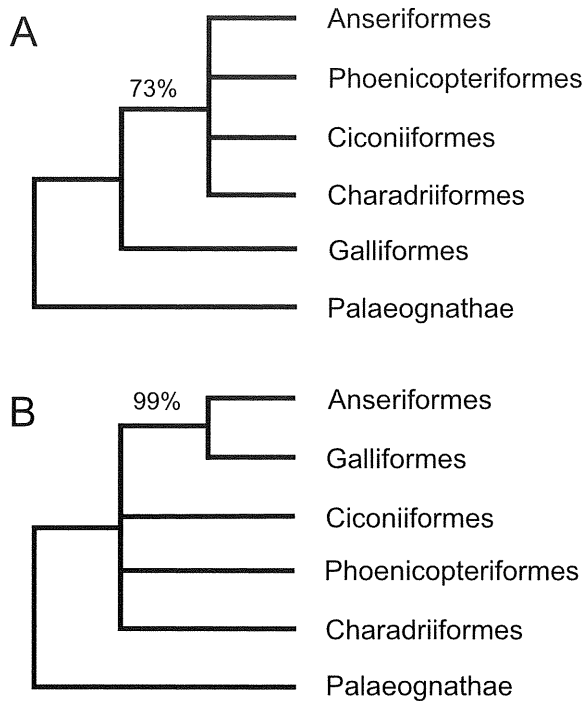


FIGURE 2. Two hypotheses of basal neognath relationships **A**, Ericson (1997, re-analyzed); **B**, Livezey (1997:376, fig.1 simplified). Both analyses are based on morphology (mainly skeletal) and the ingroup includes a similar set of taxa (palaeognathous birds were used as outgroups). Nevertheless, they arrive at utterly different conclusions regarding the closest affinities of the Anseriformes. As the two data sets are largely complementary they were pooled here into a new set of characters.

Ciconiiformes, Galliformes and Charadriiformes, the different species belonging to each of these orders were assigned identical character states.

Parsimony analyses were performed in PAUP\*, v. 4.0b2 (Swofford 1998). Taxa in which two or more states have been observed were interpreted as polymorphic. All searches were performed under the branch-and-bound option in PAUP\* and the estimated bootstrap support values are based on at least 100 replications. Only values above 50% are indicated in the bootstrap trees. Decay indices (Bremer 1988, 1994) were calculated with TreeRot, v. 2a (Sorenson 1999). The consistency index (c.i.), excluding parsimony uninformative characters, and the retention index (r.i.) are given as an indication on how well the data fit the estimated phylogeny.

The paleognathous family Tinamidae was used as outgroup in all analyses. For morphology the rationale for this is the assumed sister group relation between paleognaths and neognaths (see Introduction above). Also, morphological comparisons with the closest nonavian taxon, the Crocodylia, is often impossible because of the many specializations both in crocodiles and birds. Although no complete crocodylian *c-myc* sequence was available to include in the publication, trials with adding a partial alligator sequence to the analysis showed it to attach to the phylogeny on the branch between the tinamous and the neognaths (unpublished data).

## Results and Discussion

With the character types and transformation series coded as in the original publications (all Ericson's characters unordered, and Livezey's ordered according to his "standard ordering" type set), one most parsimonious tree (321 steps, c.i. = 0.61, r.i. = 0.73) was found in the phylogenetic analysis of the expanded, morphological data set (Figure 3). Monophyly of the in-

TABLE 2. Specimens for which the nuclear gene *c-myc* have been sequenced.

Order	Family	Species	Source
Tinamiformes	Tinamidae	<i>Tinamus major</i>	T. J. Parsons
Tinamiformes	Tinamidae	<i>Crypturellus tataupa</i>	NRM 947248
Ciconiiformes	Ardeidae	<i>Tigrisoma lineatum</i>	LMS B 1212
Ciconiiformes	Scopidae	<i>Scopus umbretta</i>	LSU B-16327
Ciconiiformes	Threskiornithidae	<i>Harpiprion caerulescens</i>	NRM 937350
Phoenicopteriformes	Phoenicopteridae	<i>Phoenicopterus chilensis</i>	NRM P5
Anseriformes	Anhimidae	<i>Chauna torquata</i>	T. J. Parsons
Anseriformes	Anseranatidae	<i>Anseranas semipalmata</i>	LSU B-20700
Anseriformes	Anatidae	<i>Amazonetta brasiliensis</i>	NRM 937401
Anseriformes	Anatidae	<i>Branta canadensis</i>	T.J. Parsons
Galliformes	Megapodiidae	<i>Alectura lathami</i>	LSU B-20851
Galliformes	Cracidae	<i>Ortalis canicollis</i>	NRM 937180
Galliformes	Phasianidae	<i>Phasianus colchius</i>	T. J. Parsons
Galliformes	Phasianidae	<i>Gallus gallus</i>	NCBI, Genbank J00889
Charadriiformes	Thinocoridae	<i>Thinocorus orbignyianus</i>	LSU B-1205
Charadriiformes	Scolopacidae	<i>Tringa flavipes</i>	NRM 937392

group was ascertained with a bootstrap support of 100%. Within the ingroup the galliforms are the sister taxon to the other neognaths. The other clade of anseriforms, ciconiiforms and charadriiforms obtained a bootstrap support of 68%. The bootstrap support for this node increased to 85% when applying a character coding regime in which all characters were treated as unordered.

The result from the analysis of the pooled morphological data set agrees with that of Ericson (1997). Thus, despite the inclusion of all known osteological characters regarded as evidence of such a relationship (compare Bock 1970; Dzerzhinsky 1982, 1995; Cracraft 1988; Cracraft and Mindell 1989; Weber 1993), the anseriform–galliform clade obtained by Livezey (1997) based on a subset of the characters used here, is not supported. All those characters were entered in the analysis as synapomorphies for the Galliformes and Anseriformes, but the resulting phylogeny suggests them to be due to parallelisms or reversals. However, the homologies of several of these skeletal features also need to be ascertained (Ericson 1996).

In the molecular part of the study the phylogenetic analysis of the *c-myc* sequences results in seven most parsimonious trees (183 steps, c.i. = 0.57, r.i. = 0.70). The strict consensus tree calculated from these seven trees contains a dichotomy of the Neognathae between the Galliformes and the other neognaths (Figure 4). However, this node has a low bootstrap support (55%). The order Galliformes (four species from three families) has a bootstrap support of 100%, the Anseriformes (four species from three families) one of 62%, and the Ciconiiformes (three species from three families; the flamingos were placed in a separate order) one of 70%. Obviously, the often suggested sister group relationship of anseriform and galliform birds received no support from the *c-myc* sequence data. Instead, the topology of the tree supports the results from the analysis of pooled morphological data set above (Figure 3).

The molecular and morphological data sets above were combined and analyzed together. The analysis of the data set (now comprising 682 characters, 184 morphological and 498 molecular; 203 of these were parsimony informative), yielded one most parsimonious tree (434 steps, c.i. = 0.66, r.i. = 0.81). The ingroup has a bootstrap support of 100% with a decay value of 36. Like in the analyses of morphology and molecular data taken separately, the neognaths are divided into two groups with galliforms being the sister group to the rest. This node has a

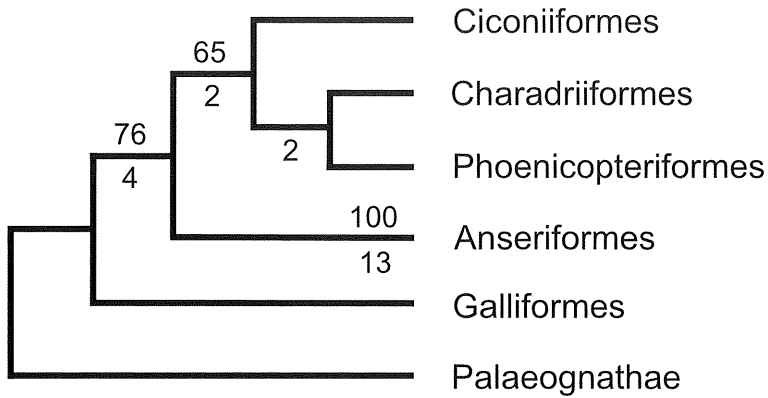


FIGURE 3. The single most parsimonious tree (321 steps long, c.i. = 0.61, r.i. = 0.73) calculated from the pooled morphological data set in the Appendix (184 characters, of which 114 are parsimony informative). The tree is simplified in that the order Anseriformes is represented by four species in the analysis. Bootstrap support values are given above the nodes and decay indices below.

bootstrap support of 88% (decay value of 7). The four taxa of anseriforms and galliforms, respectively, form monophyletic groups with 100% bootstrap supports. Also, the clades of representatives of the Ciconiiformes (*Harpiprion*, *Scopus* and *Tigrisoma*) and Charadriiformes (*Tringa* and *Thinocorus*) receive high bootstrap supports (97% and 99%, respectively).

The phylogenetic analyses of the morphological and molecular data sets here, combined or separately, do not support the often suggested sister group relationship between anseriform and galliform birds. For example, applying a topological constraint to enforce monophyly of the anseriforms and galliforms in the analysis of the combined data set results in a most parsimonious tree that is seven steps longer than otherwise. Instead, the data suggests a closer affinity of anseriforms with the ciconiiforms and charadriiforms.

### Acknowledgments

P. E. greatly acknowledges the invitation from Jacques Gauthier and the Peabody Museum of Natural History, Yale University, to present this paper at the symposium in honor of John Ostrom. Bradley C. Livezey and an anonymous reviewer commented on an earlier draft of the manuscript. Tissue samples have kindly been put at our disposal by the Swedish Museum of Natural History, Smithsonian Institution and Louisiana State University (through Donna L. Dittmann, J. Van Remsen and Frederick H. Sheldon). Other samples used here were collected in Paraguay as part of the collaboration between the Museo Nacional de Historia Natural del Paraguay, San Lorenzo, and the Swedish Museum of Natural History. The Direccion de Parques Nacional y Vida Silvestre, Asuncion, kindly issued necessary collecting and export permits. This project has received funding from the Magnus Bergvalls Stiftelse, Olle och Signhild Engkvists Stiftelser, and the Swedish Natural Science Research Council (grant no. B-AA/BU 01913-304). The opinions and assertions contained herein are solely those of the authors and are not to be construed as official or as views of the U.S. Department of Defense or the U.S. Department of the Army.

### Addendum

After this manuscript was submitted, Groth and Barrowclough (1999) published a phylogeny of major lineages of birds based on nucleotide sequence data. By obtaining long sequences from a nuclear, protein-coding gene (RAG-1), the authors produced what we believe to be the most robust estimate of basal divergencies in birds yet. The data strongly supports a sister group relationship between an anseriform–galliform clade and all other neognaths. This result is at odds

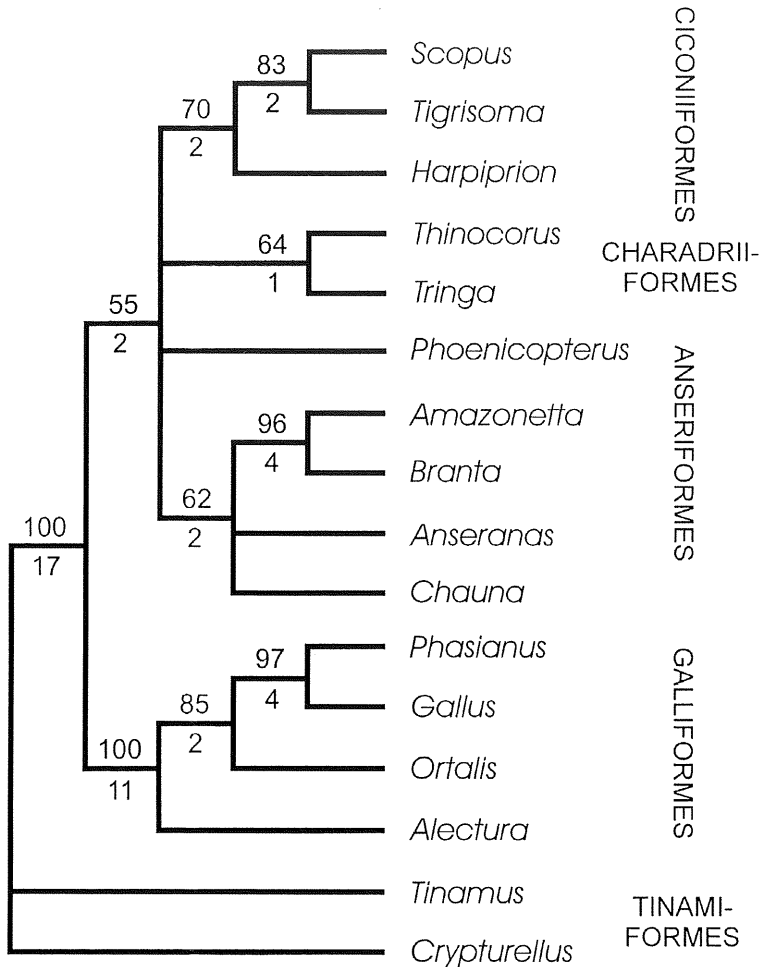


FIGURE 4. Parsimony analysis of nucleotide sequences obtained from the nuclear *c-myc* gene. Strict consensus tree calculated from the six shortest trees (183 steps, c.i. = 0.57, r.i. = 0.70). Bootstrap support values are given above the nodes and decay indices below.

with the phylogenetic estimates presented here, based on the pooled morphological data sets and the nucleotide sequences obtained from the nuclear *c-myc* gene. Although the results based on the RAG-1 gene represents but one gene tree, which does not necessarily correspond to the species tree (Takahata 1989), in our opinion this phylogenetic estimate is based on the best quality data so far.

The discrepancies between the results based on the RAG-1 gene, and those presented above based on morphology and *c-myc*, are puzzling. For molecular data, differences in mutation rates between two genes could explain differences between phylogenetic estimates. A study of passerine birds (Irestedt et al. 2001) proved *c-myc* to be moderately slower than RAG-1. This, in combination with the rather short sequence length of *c-myc* (498 base pairs), might, for purely stochastic reasons, lead to inaccurate estimates of the true species tree. Sequencing of additional taxa and longer portions of *c-myc* hopefully will provide further insights into this.

The conflict between phylogenies calculated from the morphological data sets and those based on the RAG-1 sequences is even more intriguing. The morphological characters analyzed here have been defined and coded to the best ability of ourselves and other workers. If the RAG-

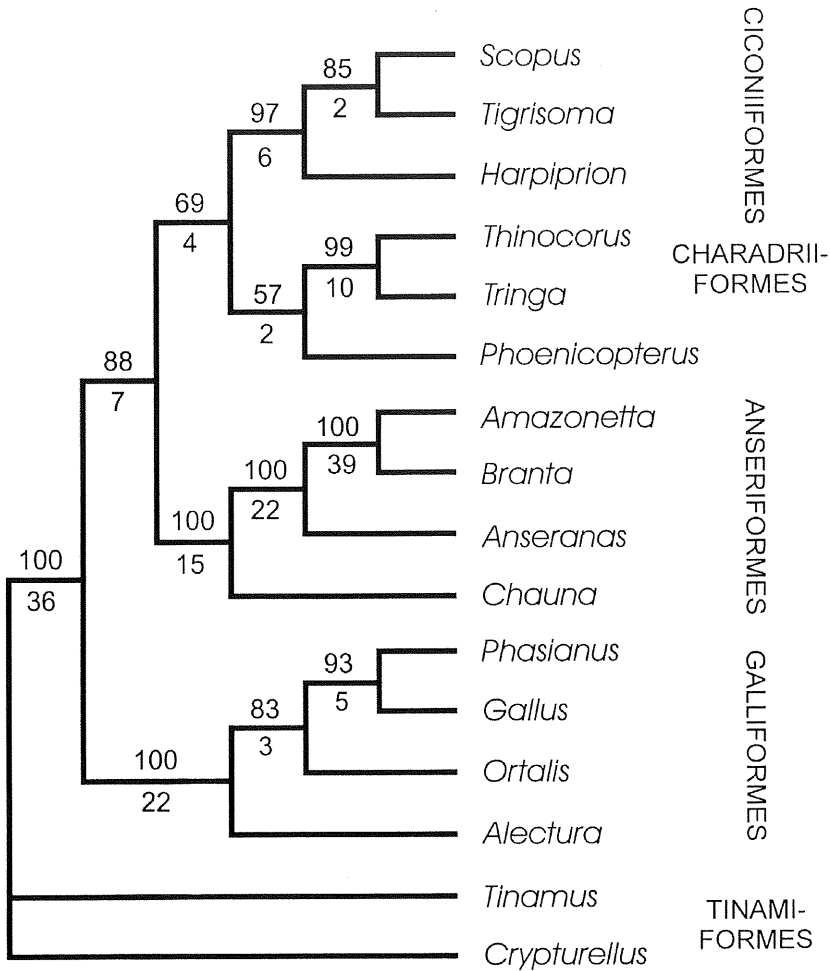


FIGURE 5. The single most parsimonious tree (434 steps long, c.i. = 0.66, r.i. = 0.81) calculated from the combined morphological and molecular data sets. Bootstrap support values are given above the nodes and decay indices below.

If phylogeny is a good estimate of basal divergencies in birds, several of the morphological characters need revision. It is fully clear that the homologies of many characters and character states used here are uncertain (Ericson 1996). Unfortunately, very few embryological studies involving wide taxonomic samples of birds are at hand. Furthermore, although similar morphologies are known to develop convergently or through evolutionary reversals, the extent to which such events occur is virtually unknown. A solid phylogeny based on, for example nucleotide sequence data, on which morphological traits can be mapped, would facilitate investigations to increase our understanding of this and other aspects of character evolution.

## Appendix

The appendix accompanying this paper is also available online at the Yale Peabody Museum website at <http://www.peabody.yale.edu/collections/vp/>.



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## Appendix: Data matrix

Data matrix for the analysis of the pooled morphological data sets of Ericson (1997) and Livezey (1997). Below the character numbers are indicated the numbers in the original data sets. Character descriptions, codings and polarities are as in the original publications.

	5					10					15					20					25				
	E2	E4	E5	E6	E8	E9	E10	E11	E13	E14	E16	E17	E19	E20	E21	E22	E23	E24	E25	E26	E27	E28	E29	E30	E32
Tinamiformes	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Charadriiformes	1	0	0	1	1	1	0	0	0	0	1	0	0	0	1	1	0	1	1	0	0	1	0	0	0
Ciconiiformes	0/1	0	0	0/1	2	1	0	0	0/1	0/1	1	0	0	0	1	0	0	0	0/1	0/1	0	0	0	0	0
Phoenicopteriformes	1	1	0	1	2	1	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0
Galliformes	1	0	0	0/1	1	0	0/1	0	0	0	1	0	0/1	0	1	0	0	0	0	0	0	0	1	0/1	0
<i>Anhima</i>	1	0	0	1	2	0	0	0	0	0	1	1	1	0	1	0	1	0	0	1	0	0	0	0	0
<i>Chauna</i>	1	0	0	1	2	0	0	0	0	0	1	1	1	0	1	0	1	0	0	1	0	0	0	0	0
<i>Anseranas</i>	1	0	0	1	2	0	0	1	0	0	1	1	1	1	1	0	0	0	0	1	1	0	0	0	0
Anatidae	1	0	1	1	2	0	0	1	0	0	1	1	1	1	1	0	0	0	0	0	1	0	0	0	0
	30					35					40					45					50				
	E33	E34	E35	E36	E37	E38	E39	E40	E41	E42	E43	E44	E45	E46	E47	E48	E49	E50	E51	E52	E53	E54	E56	E57	E58
Tinamiformes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Charadriiformes	0	1	0	0	1	0	1	2	1	0	1	1	1	0	0	0	0	0	1	0	0	1	0	0	0
Ciconiiformes	0	1	0	0	0	0	1	1/2	1	0	0	0/1	1/2	0/2	0/1	0	0	0	0	0	0	1	0	0	0
Phoenicopteriformes	0	1	0	0	1	0	1	2	1	0	0	1	1	0	0	1	0	0	0	0	0	1	0	0	0
Galliformes	0/1	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0
<i>Anhima</i>	0	0	0	0	1	0	1	2	1	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0
<i>Chauna</i>	0	0	0	0	1	0	1	2	1	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0
<i>Anseranas</i>	0	0	0	0	1	1	1	2	1	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0
Anatidae	0	0	0	0	0	1	1	2	1	0	0	1	1	0	0	1	0	0	0	0	0	1	0	0	0
	55					60					65					70					75				
	E59	E60	E61	E62	E63	E64	E65	E67	E68	E69	E70	E71	L1	L2	L3	L4	L5	L6	L7	L8	L9	L10	L11	L12	L13
Tinamiformes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Charadriiformes	0	1	1	1	0	1	0	0/1	0	0	0	0	0	0	0/1	0	0	0	2/3	0	0/1	0	0	0	0
Ciconiiformes	0	1	1	1	0	1	0	1	0	0	0	0	0/1	0	0/1	0	0	0	3	0	0/1	0	0	0	0
Phoenicopteriformes	0	1	1	1	0	1	0	0	0	0	0	0	1	1	0	0	0	0	3	0	0	0	0	0	0
Galliformes	0	0	0	0	0	0	0	0	0	0	0/1	0	1	0	0	1	0	0	1	1	0	0	0	0/1	0
<i>Anhima</i>	0	1	1	1	0	2	0	0	0	1	0	0	1	0	0	1	1	1	1	2	0	0	1	0	1
<i>Chauna</i>	0	1	1	1	0	2	0	0	0	1	0	0	1	0	0	1	1	1	1	2	0	1	0	0	1
<i>Anseranas</i>	0	1	1	1	0	1	0	0	0	1	0	0	1	1	1	0	2	0	1	3	1	0	0	1	0
Anatidae	0	1	1	1	0	1	0	0	0	1	0	0	1	1	1	0	2	0	1	3	1	0	0	0	0
	80					85					90					95					100				
	L14	L15	L16	L17	L18	L19	L20	L21	L22	L23	L24	L25	L27	L28	L29	L30	L31	L32	L33	L34	L35	L36	L37	L38	L39
Tinamiformes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Charadriiformes	0	0	0	0/1	0	0	0	0	0	0	0	0	0/1	0	0	0/1	0	0	0/1	0	0/1	0/1	0	0	0
Ciconiiformes	0	0	0	0/1	0	0	3	0	0	0	0	0	0	1	0	0	0	0	0/1	0	0/1	0/1	0	2	0
Phoenicopteriformes	2	0	0	0	0	0	2	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	0	2	0
Galliformes	0	0/1	0	0	0	1	1	0	0	0	1	1	0	1	0	0	0	0	0	0	0/1	1	0	0	0
<i>Anhima</i>	0	1	0	0	0	1	2	0	0	0	1	1	0	1	0	0	0	0	0	0	1	1	0	1	1
<i>Chauna</i>	0	1	0	0	0	1	2	0	0	0	1	1	0	1	0	0	0	0	0	0	1	1	0	1	1
<i>Anseranas</i>	0	0	1	1	1	1	2	0	1	1	1	1	1	1	0	1	1	0	1	1	1	1	1	2	1
Anatidae	1	0	1	1	1	1	2	1	1	1	1	1	1	1	0/1	1	1	1	1	1	1	1	1	2	1

## Appendix, continued.

	105					110					115					120					125				
	L40	L41	L42	L43	L44	L45	L46	L47	L48	L49	L50	L51	L52	L53	L54	L55	L56	L57	L58	L59	L60	L61	L62	L63	L64
Tinamiformes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Charadriiformes	0	1	1	1	1	0	1	2	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0/1	0	0
Ciconiiformes	0	1	1	1	1	0	1	2	0	0	0	0	0	0	0/1	0	0/1	0	0	0	0	0	0/1	0	1
Phoenicopteriformes	0	1	1	1	1	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Galliformes	0	1	0	1	1	0	0	2	0/1	1	0	1	0	0	0/1	0	0	0	0	0	1	1	1	0	1
<i>Anhima</i>	0	1	0	1	1	1	0	1	0	2	0	1	1	1	0	0	1	1	1	0	0	0	0	1	1
<i>Chauna</i>	0	1	0	1	1	1	0	1	0	2	0	1	1	1	0	0	1	1	1	0	0	0	0	1	1
<i>Anseranas</i>	1	1	1	1	1	2	0	1	1	1	1	1	1	1	1	1	1	1	0	1	0	0	0	0	1
Anatidae	1	1	1	1	1	2	0	1	1	1	1	1	1	1	0	1	1	1	0	2	0/1	0	0	0	0/1
	130					135					140					145					150				
	L65	L66	L67	L68	L69	L70	L71	L72	L73	L74	L75	L76	L77	L78	L79	L80	L81	L82	L83	L84	L85	L86	L87	L88	L89
Tinamiformes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Charadriiformes	0	0	1	1	0/1	0	0/1	0	0	0	0/1	0	0	1	0	0	0	1	0	0	0/1	0	0	0/1/2	0
Ciconiiformes	0/1	0/1	1	1	1	0	0/1	0	0	0	0/1	0	0	1	0/1	0/1	0	1	0	0	0	0	0	1/2	0
Phoenicopteriformes	0	0	1	0	0	0	1	0	0	0	1	0	0	1	0	0	1	0	0	0	1	0	0	2	0
Galliformes	0	1	1	1	0/1	0/1	0	0	0	0/1	0	0	0	1	2	0	0	0	0	0	0	0	0	0/1	1
<i>Anhima</i>	1	1	0	1	0	1	1	1	1	0	1	1	1	1	2	1	0	1	0	1	0	1	1	1	0
<i>Chauna</i>	1	1	0	1	0/1	1	1	1	1	0	1	1	1	1	2	1	0	1	0	1	0	1	1	1	0
<i>Anseranas</i>	1	0	1	1	0	1	1	0	0	0	1	0	0	1	1	1	0	1	0	0	1	1	1	1	0
Anatidae	0	0/1	0	0	1	0	0/1	0	0	0	1	0	0	1	0	1	1	1	1	0	1	1	1	0/1	0
	155					160					165					170									
	L90	L91	L92	L93	L94	L95	L96	L97	L98	L99	L100	L101	L102	L103	L104	L105	L106	L107	L108	L109					
Tinamiformes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0					
Charadriiformes	0	0	0	0	0/1	0	0/1	1	0	0	0	0	0/1	0	0	0	0	0	0	0					
Ciconiiformes	0	1	0	0	0	0	1	1	0	0	0	0	0/1	0	0	0	0	0	0	0					
Phoenicopteriformes	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0					
Galliformes	1	1	0	0	0	0	1	0/1	0	0/1	0	0	0/1	0	0	0	0	0	0	0					
<i>Anhima</i>	1	1	0	0	0	1	1	0	1	1	1	0	1	1	0	1	1	0	0	0					
<i>Chauna</i>	1	1	0	0	0	1	1	0	1	1	1	1	1	1	1	0	1	1	0	1					
<i>Anseranas</i>	1	1	0	1	0	1	1	0	0	1	0	0	1	2	0	0	0	0	1	0					
Anatidae	0	0	1	0	1	1	0	1	0	1	0	0	0	2	0	0	0	0	0	0					
	175					180					184														
	L110	L111	L112	L113	L114	L115	L116	L117	L118	L119	L120	L121	L122	L123											
Tinamiformes	0	0	1	2/3	2	0	0	0	0	0	0	0	0/1	0											
Charadriiformes	0	0	0	2	1	0	0	1	1	0	0/1	0	1/2	0											
Ciconiiformes	0	0	0	2	2	0/1/2	0	1	1	0	0	0	2	0											
Phoenicopteriformes	1	0	0	2	2	3	0	1	1	0	0	0	1	0											
Galliformes	0	0/1	0	0/2	0	0/1	0	0	0	0	0	0	2	0											
<i>Anhima</i>	0	0	0	0	0	1	1	0	0	0	0	0	0	0											
<i>Chauna</i>	0	0	0	0/2	0	1	1	0	0	0	0	0	0	0											
<i>Anseranas</i>	0	0/1	0	0/2	0	2	0	0	0	1	0	0	0	0											
Anatidae	0	1	0	0	0	3	0	0	0	1	1	1	0	1											