

Avian Higher-level Phylogenetics and the Howard and Moore Checklist of Birds

by

Joel Cracraft, F. Keith Barker, and Alice Cibois

Department of Ornithology, American Museum of Natural History
Central Park West at 79th Street, New York, New York 10024

As phylogenetic knowledge has increased over the past 40 years following the introduction of cladistic theory and methodology, systematists have increasingly attempted to make classifications reflect phylogenetic relationships. Given an hypothesis of relationships it is reasonably straight-forward to express those relationships within the context of hierarchical classifications in a number of different ways. Ornithologists have addressed this issue for over 20 years (e.g., Cracraft 1981) ⁽²⁹⁹⁹⁾¹. Without question the best-known attempt at constructing a phylogenetic classification for avian higher taxa was that derived from DNA hybridization distances (Sibley *et al.* 1988; Sibley & Ahlquist 1990; Sibley & Monroe 1990) ^(3025, 2610, 2030). However there are many other examples at lower hierarchical levels within birds (e.g., Livezey's 1998 classification for gruiforms) ⁽³⁰¹⁷⁾.

The present volume — a list of avian species — does not arrange these within a series of hierarchies but instead uses, aside from the Linnean binomial of genus and species, two hierarchical levels, the family and the subfamily. Because knowledge of avian phylogenetic relationships is still clouded with uncertainties, any decision to recognize a complex classificatory hierarchy would have resulted in numerous arbitrary choices. We have attempted to reflect currently accepted hypotheses of relationships to the extent possible within a linear sequence. We have followed a simple set of conventions. First, the list sequentially clusters families in a way that represents what are thought to be groupings of related families; many of these follow traditional orders when compelling alternative evidence is not available. Second, within each of these clusters, subgroups of related families are listed near one another. Finally, within all such groups and subgroups, the presumed basal families are listed first.

This volume is not the place to present an extended discussion about the higher-level relationships of birds. Nevertheless, the present list attempts to incorporate recent evidence on relationships, with the caveat that often the best evidence presently available is only of a single kind — for example, either morphology or molecular. Ideally we would like to have congruence across data sets before concluding that a satisfactory understanding of those relationships has been attained. This is a time of unprecedented activity in avian systematics, with more investigators collecting data than at any time in history. Consequently, understanding of avian relationships is changing rapidly. In discussing the evidence, only that work which is published, or in press, is mentioned. The list errs on the side of conservatism because a list of species, designed in part for a popular audience, is not an appropriate venue for making radical changes. Over the years, and continuing to the present, there have been many calls to dismember traditional orders, but most of these opinions are based on evidence that is still not widely accepted within the systematic community, where ideas about relationships remain contentious.

In the following remarks, not all groupings (orders) will be discussed, either because there is relatively little dispute over relationships or because there has been no new information about relationships published in recent years.

Basal lineages: Palaeognathae, Neognathae, and Galloanserae

The identity of, and relationships among, the three major basal lineages of living birds (Neornithes) have gained increasing support. See literature reviewed in Cracraft & Clarke 2001 ⁽³⁰⁰³⁾; see also Cracraft 1988, 2001 ^(3001, 3002); Groth & Barrowclough 1999 ⁽²⁹⁴⁷⁾; van Tuinen *et al.* 2000 ⁽³⁰³¹⁾; Livezey & Zusi 2001 ⁽³⁰¹⁸⁾; Paton *et al.*, in press ⁽³⁰²¹⁾. These morphological and molecular data support the division of the neornithines into the Palaeognathae (tinamous and ratites) and the Neognathae (all other groups). Within the latter lineage, the Galloanserae (Galliformes and Anseriformes) are the sister-group of all other birds (the Neoaves).

¹ Numbers in brackets such as this refer to the main List of References for the book.

Relationships within the palaeognaths are still very uncertain, as there is conflict among morphological and molecular data, and within the latter the results can differ depending on the data set and the method of analysis (see Lee *et al.* 1997; Haddrath & Baker 2001; Cooper *et al.* 2001) (3013, 3007, 2997). Relationships within the anseriforms, at least at higher taxonomic levels, do not appear to be too controversial (Livezey 1986, 1997) (3015, 3016), and both morphological and molecular data (Cracraft 1981, 1988; Livezey & Zusi 2001; Dimcheff *et al.* 2000) (2999, 3001, 3018, 3004) support at least a tripartite pattern of relationships for galliforms: (Megapodiidae (Cracidae + phasianoids)). Within the phasianoids, the numidids appear to be the sister-group to all others (Cracraft 1981; Dimcheff *et al.* 2000) (2999, 3004).

Neoaves

Although the interrelationships of the basal lineages of the neornithes have been clarified in recent years, we have no firm idea how the basal relationships of the Neoaves might be resolved and this constitutes a major unsolved problem for avian systematics. Sibley & Ahlquist (1990) (2610) placed the Pici at the base of their DNA hybridization tree, but their evidence was hardly persuasive and that result has not emerged from any other study. Resolving the basal lineages of the Neoaves is likely to be a very difficult problem that probably will require considerable data to solve.

Sphenisciformes, Gaviiformes, Procellariiformes

The interrelationships of penguins, loons, and procellariiform seabirds are still not established convincingly. However, various authors using morphological (Cracraft 1988; Livezey & Zusi 2001) (3001, 3018) or molecular data (Sibley & Ahlquist 1990; van Tuinen *et al.* 2001) (2610, 3030) have them clustering together or near one another, with penguins and procellariiforms generally being sister-taxa.

Podicipediformes, Phoenicopteriformes, Ciconiiformes

It has become fashionable in recent years to dismember the traditional Ciconiiformes (e.g., Sibley & Ahlquist 1990) (2610). It now seems there may be at least a core group of taxa that are related, including ciconiids, threskiornithids, and ardeids (van Tuinen *et al.* 2001; Livezey & Zusi 2001) (3030, 3018). However, other former ciconiiforms (*Balaeniceps* and *Scopus*) appear closer to pelecaniforms (see below). Surprising recent molecular analyses place flamingos with grebes (van Tuinen *et al.* 2001) (3030), and a preliminary analysis of cranial characters only (Livezey & Zusi 2001) (3018) put these two in the vicinity of one another.

Pelecaniformes

Like the ciconiiforms, the pelecaniforms have also been the subject of exuberant claims of paraphyly (Sibley & Ahlquist 1990; Hedges & Sibley 1994) (2610, 3008), yet the idea that they are not related was never adequately supported by the data. Morphological (Cracraft 1985; Livezey & Zusi 2001) (3000, 3018) and behavioral (van Tets 1965; Kennedy *et al.* 1996) (3029, 3011) analyses found characters uniting them, but this was often dismissed as convergence (Hedges & Sibley 1994) (3008). These conflicts and confusion over pelecaniform relationships may have been magnified by the traditional exclusion of the Shoebill (*Balaeniceps*) and the Hamerkop (*Scopus*) from the pelecaniforms (e.g., Cracraft 1988) (3001) and their placement in ciconiiforms (but see Cottam 1957 (2998), for an exception). And yet mounting evidence suggests they belong near pelecanids (e.g., van Tuinen *et al.* 2001; see also Livezey & Zusi 2001) (3030, 3018). Phaethontids and fregatids have been problem groups for molecular analysis because both, especially tropicbirds, are relatively long-branch taxa; see, for example, the data of van Tuinen *et al.* 2001 (3030), for *Phaethon*. This, combined with the fact they are fairly ancient lineages, may be the reason for their questionable position on some trees (Sibley & Ahlquist 1990; Hedges & Sibley 1994) (2610, 3008). Although additional study is clearly needed, it would not be surprising to see most, perhaps all, traditional pelecaniforms reunited in an expanded clade that includes the Shoebill and Hamerkop.

Falconiformes

Much ado has also been made of the nonmonophyly of the falconiforms (Ligon 1967; Sibley & Ahlquist 1990; Avise *et al.* 1994) (3014, 2610, 2994). This has mostly concerned the placement of the cathartids with respect to storks, although the evidence supporting the various alternative hypotheses has not been very compelling. The weight of the morphological evidence, at least, argues for falconiform monophyly (Cracraft 1981; Griffiths 1994; Livezey & Zusi 2001) (2999, 3006, 3018). Previous ideas (Cracraft 1988) (3001) that owls and falconiforms might be related seem incorrect.

Gruiformes

This list follows the detailed morphological analysis of Livezey (1998) (3017), although a broader comparison

of cranial characters alone (Livezey & Zusi 2001) ⁽³⁰¹⁸⁾ did not result in gruiform monophyly. The placement of the otidids is particularly uncertain.

Charadriiformes

Current evidence supports the hypothesis that virtually all the groups traditionally included in the charadriiforms comprise a monophyletic lineage (Sibley & Ahlquist 1990; Livezey & Zusi 2001) ^(2610, 3018), the major uncertainty being the turnicids (see for example Rotthowe & Starck 1998) ⁽³⁰²³⁾. Moreover, charadriiforms do not represent the primitive neornithine morphotype (see Paton *et al.* in press) ⁽³⁰²¹⁾.

Musophagiformes, Cuculiformes, *Opisthocomus*

These three groups are listed together merely for want of a better alternative. They may very well prove unrelated. Hughes & Baker (1999) ⁽²⁶³³⁾ proposed that *Opisthocomus* is closer to musophagids than cuculids, but their study effectively included only these three taxa and so is inconclusive. Livezey & Zusi (2001) ⁽³⁰¹⁸⁾, using cranial characters, placed *Opisthocomus* with core gruiform taxa, thus suggesting a novel arrangement. Based on a small amount of nuclear data, Johansson *et al.* (2001) ⁽³⁰¹⁰⁾ found that cuculids and musophagids were distant from one another. Veron & Winney (2000) ⁽²²⁷⁷⁾ examined relationships within turacos using partial cytochrome *b* sequences, but their comparisons to cuckoos and the Hoatzin were also inconclusive because of restricted taxon sampling.

Caprimulgiformes, Apodiformes, Strigiformes

DNA hybridization distances placed these three groups in a clade (Sibley & Ahlquist 1990; Bleiweiss *et al.* 1994) ^(2610, 2996), and that arrangement is also supported by cranial morphological characters (Livezey & Zusi 2001) ⁽³⁰¹⁸⁾. The monophyly of swifts and hummingbirds is strongly supported (Cracraft 1988) ⁽³⁰⁰¹⁾; however, given that caprimulgiform taxa do not often group together on molecular trees (Johansson *et al.* 2001) ⁽³⁰¹⁰⁾, and are not clustered by Livezey & Zusi's data (2001) ⁽³⁰¹⁸⁾, questions remain about their monophyly.

Coraciiformes, Coliiformes, Trogoniformes, Galbulae

Most recent work suggests that these four groups are related in some way or another, often in association with the Pici and/or the Passeriformes (Espinosa de los Monteros 2000; Johansson *et al.* 2001) ^(2799, 3010). However the data are insufficient to resolve their relationships clearly. The coraciiforms, as traditionally constituted, are apparently separable into at least two major groups that may or may not be related (Johansson *et al.* 2001) ⁽³⁰¹⁰⁾. One includes the alcedinids, momotids, todids, and the three groups of rollers, the leptosomatids, coraciids, and brachypteraciids (Kirchman *et al.* 2001) ⁽³⁰¹²⁾; the second, bucerotids and upupids. Groups such as trogonids, coliids, Galbulae, Pici, and possibly passeriforms are probably related to these coraciiform lineages, but the topology is unclear. At present, it is difficult to say what the molecular data mean, since most studies have had restricted taxon and character samples. Finally, even morphology breaks up the coraciiforms (Livezey & Zusi 2001) ⁽³⁰¹⁸⁾. Clearly, much work is needed.

Pici

Relationships among the Pici now seem moderately well established. Picids and indicatorids are sister-taxa, and they, in turn, are related to barbets and toucans (Simpson & Cracraft 1981; Swiercewski & Raikow 1981) ^(3027, 3028). It is now apparent, however, that barbets are seriously paraphyletic. New World taxa are nonmonophyletic and some, but not all, are related to toucans, and to make matters more complicated, Old World barbets are also paraphyletic, with some probably being more closely related to the New World taxa (Prum 1988; Barker & Lanyon 2000) ^(2797, 2928). The position of the Galbulae is still a question, but molecular data, none of which is entirely adequate at present, associate them most often with various coraciiform taxa (see above).

Passeriformes: basal relationships and major lineages

The monophyly of passeriforms is firmly established (Raikow 1982) ⁽³⁰²²⁾ and considerable evidence supports a basal division into two large monophyletic groups, the suboscines and oscines (e.g., see review in Sibley & Ahlquist 1990; Barker *et al.* 2002) ^(2610, 2995). A major question has always been the position of the New Zealand wrens (Acanthisittidae). Using sequences from the nuclear genes RAG-1 and *c-mos*, Barker *et al.* (2002) ⁽²⁹⁹⁵⁾ found strong support for a sister-group relationship between acanthisittids and all other passeriforms; using a smaller data set of partial RAG-1 and *c-myc* sequences, a similar conclusion was reached by Ericson *et al.* (2002) ⁽³⁰⁰⁵⁾.

Suboscines

The suboscines are divisible into two monophyletic groups: (a) the Old World pittids and eurylaimids-philipittids (Prum 1993, Barker *et al.* 2002) (2313, 2995), and possibly the South American genus *Sapayoa* (Sibley & Ahlquist 1990) (2610), and (b) the New World Tyranni. The latter clade is a diverse assemblage whose systematic relationships are not well resolved, but molecular evidence (Sibley & Ahlquist 1990; Irestedt *et al.* 2001; Barker *et al.* 2002) (2610, 3009, 2995) supports of a sister-group relationship of piprids, cotingids, and tyrannids, on the one hand, and furnariids, dendrocolaptids, formicariids, thamnophilids, rhinocryptids, and conopophagids, on the other.

Basal lineages of the oscines

Based on DNA hybridization evidence (Sibley & Ahlquist 1985, 1990) (3026, 2610) it has become widely accepted that oscines can be divided into two monophyletic groups, the Australasian Corvida and the worldwide Passerida. Recent and ongoing studies using nuclear genes are proving this incorrect. The corvidans are paraphyletic: some are at the base of the oscines and others may be more closely related to passeridans than to core corvidans {Barker *et al.* (2002) (2995) using RAG-1 and *c-mos* nuclear sequences; Ericson *et al.* 2002 (3005), using fragments of RAG-1 and *c-myc*}. Barker *et al.* (2002) (2995) placed *Menura* as the sister-group of the remaining oscines, and within the latter group relationships have the structure: ((climacterids + ptilonorhynchids) (meliphagoids + all other oscines)). The core “corvidans” and passeridans are monophyletic, but several other groups, including pomatostomids, orthonychids, and petroicids have ambiguous relationships.

“Corvida”

With the exception of the DNA hybridization data (Sibley & Ahlquist 1990) (2610), taxon sampling across the core corvidans has been insufficient to specify a clear set of relationships among this large assemblage. Currently available sequence data (Cracraft & Feinstein 2000; Barker *et al.* 2002) (2920, 2995) suggest major conflicts with the DNA hybridization results, which is not surprising given the very short internodes indicated by the DNA hybridization phenograms. A major finding of the mitochondrial sequences (and morphology) is that cnemophilines are not paradisaeids but near the base of corvidans (Cracraft & Feinstein 2000) (2920), whereas RAG-1 and *c-mos* sequences remove the melanocharitids from the passeridans and move them to a basal position within corvids (Barker *et al.* 2002) (2995). Two clades strongly supported by the sequence data include (many other groups were not sampled in these studies): (a) *Aegithina*, vangids, artamids, cracticids, and (b) paradisaeids, corvids, laniids, monarchids, dicurids. Groups such as oriolids, vireonids, campephagids, and pachycephalids appear to be more basal within corvids than do these two clades.

Passerida

The passeridans are a very large monophyletic group whose relationships, at least at the higher taxonomic levels, are becoming better understood as DNA sequences accumulate. At the same time, these new studies make it clear that many traditional families are not monophyletic, and that a fuller understanding of passeridan phylogeny will only unfold as more and more of its diversity is sampled genetically.

Both DNA hybridization (Sibley & Ahlquist 1990) (2610) and nuclear gene sequences (Barker *et al.* 2002) (2995) delineate three major clades of passeridans — conveniently termed passeroids, muscipapoids, and sylvioids — yet the placement of a number of “families” in these three groups differs between the two data sets. Many, but not all, of the differences are due to very short internodal distances, especially on the DNA hybridization phenogram, and poor internodal support on the nuclear gene tree because of insufficient data (it will take additional sequence information to provide satisfactory resolution).

The nuclear gene data of Barker *et al.* (2002) (2995) suggest the following sequence of families, beginning with those most basal within the three major clades (again, keeping in mind that not all these family-group names represent monophyletic groups):

Sylvioidea: Bombycillidae + Paridae, Hirundinidae, (Pycnonotidae, Sylviidae, Zosteropidae, Timaliidae), (Aegithalidae, Alaudidae, Cisticolidae)

Muscipapoidea: (Troglodytidae, Sittidae, Certhiidae), (Mimidae+Sturnidae), (Turdidae, Muscipapidae), Cinclidae)

Passeroidea: (Chloropseidae, Dicaeidae, Nectariniidae), (Prunellidae, Ploceidae), (Passeridae, (Motacillidae, (Fringillidae, (Icteridae, Parulidae), (Emberizidae, (Cardinalidae, Thraupidae)

Additionally, the Irenidae and Regulidae represent ancient lineages the relationships of which remain uncertain. Although a number of nodes in the nuclear gene passeridan tree are not well supported — especially within the muscipoids and passeroids — these results are more consistent with the DNA hybridization experiments of Sheldon & Gill (1996) (3024), which were undertaken with stringent analytical procedures, than with those of Sibley & Ahlquist (1990) (2610). Thus, Sheldon & Gill (1996) (3024), unlike Sibley & Ahlquist (1990) (2610), found the alaudids were not passeroids but sylvioids, and troglodytes, sittids, and certhiids went with muscipoids rather than sylvioids.

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