

Avian Higher-level Relationships and Classification: Nonpasseriforms

Joel Cracraft

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

Biological classifications are evolving information systems. The information they carry is the hierarchical pattern of evolutionary relationships that has resulted from the unfolding of the great Tree of Life. Knowledge about those relationships keeps being refined and classifications consequently change to accommodate that new understanding. Classifications are generally seen as being less important than the phylogenies on which they are based, and although that will always be the case, classifications are essential frameworks for multiple user-communities just because names and classificatory hierarchies do convey information about levels of relationship. Thus, classifications that mirror the relationships of organisms are of great significance for the general biological community undertaking comparative studies, as well as for audiences who use checklists, field guides, biotic surveys, and other materials that rely on taxonomic names.

In the previous edition of the *Howard & Moore Complete Checklist of the Birds of the World* (Dickinson 2003), an introductory chapter reviewed recent advances in avian phylogenetics (Cracraft et al. 2003). In that edition a decision was made to include only a minimal amount of hierarchical detail in the classification, and thus only the ranks of family, genus, species, and subspecies were used. Since then, understanding about the higher-level relationships of birds has expanded significantly. Data produced from these studies, primarily from molecular systematic analyses, have begun to clarify the relationships among and within the major groups of birds. Therefore, in order to enhance the informativeness of the *Checklist*, this edition expands the use of hierarchical levels to better reflect this growth in knowledge. It is still the case, however, that the phylogenetic placement of many groups remains poorly resolved, hence care has been taken to reflect phylogenetic findings that are well-supported, preferably by large amounts of data or across multiple independent studies.

As was noted in the review in the previous edition, this volume is not the place to debate the science but to summarize emerging consensus about relationships. Although there is considerable debate in the scientific literature over the ability of the Linnaean hierarchy to reflect relationships as organismal phylogenies keep dramatically expanding, it is important to use group-names that are, first, familiar to contemporary systematic ornithology; second, historical names that generally circumscribe clades revealed by new evidence; and third, names that facilitate communication (see Livezey & Zusi, 2007, p. 87). At the same time, stability is not always possible because many traditional group-names (e.g. Ciconiiformes) may apply to groups that are now known to have included families that are not related. In such cases, an effort has been made to apply names in a manner that least disrupts communication about groups, that adheres to the International Code of Zoological Nomenclature (ICZN 1999), and that minimizes the number of new names that have to be introduced to specify hierarchical relationships. There has been considerable debate in zoology and in ornithology on the rules that govern “family-group” names (superfamily down to, but not including, the genus level) (see Bock 1994). Above that level, over the years many ornithologists have used the ordinal-ending “-iformes” but that has not always been the case (see Mayr & Amadon 1951 and Stresemann 1959 for exceptions). The names for taxa ranked above the ordinal-level, in contrast, have not been uniform in ending. We would predict that as relationships become more strongly supported, newly introduced names for clades will become more widely accepted and some of those names (e.g. such as Neoaves) are used here.

Systematic and taxonomic terminology

This chapter discusses phylogenetic relationships and their implications for classification and for the names of groups, therefore it is appropriate to review terminology commonly used within systematic ornithology. In attempting to reconstruct relationships among birds, systematists collect data from species and those data can take the form of morphological (e.g. skeletal or muscular system), or increasingly they extract DNA from tissues, including from museum specimens, and determine their nucleotide sequence. Most of the work discussed here is based on these newer molecular data. Once comparable DNA sequences are gathered for a set of taxa, algorithms are used to analyze the data and build phylogenetic trees. These trees are described by the pattern of branches (lineages) that connect to one another at nodes (internodes) thus signifying a pattern of relationships. Given a specific tree we say that two branches — they may be species or groups of species (e.g. genera, families) — are

sister-groups if they share a more recent common ancestor with each other than either does with a third taxon. Depending on the quality and quantity of data for a particular question, relationships may be fully resolved into two descendant branches (dichotomous) or they may be unresolved with three or more descendant branches from a given node (polytomous). In building trees the algorithms also evaluate statistically the degree to which the data support the relationships specified by each node on the tree. The more data employed in the analysis, the more we expect or hope that support for relationships will increase, although this is not always the case.

Within taxonomy, we say a group is monophyletic if all the members of that named group share a more recent common ancestor with each other than any has to another outside group (e.g. the perching-birds, Passeriformes, are monophyletic). In contrast, a taxonomic group is said to be non-monophyletic or polyphyletic when one or more of its members are related to others outside the group. The classical waterbird orders Pelecaniformes and Ciconiiformes are no longer considered to be monophyletic, consequently this requires changes in classification in order to maintain the principle of recognizing only monophyletic groups.

In this classification widely-used higher-taxon names are maintained as much as possible, especially for names ranked at order level and below. When major changes in relationships require a name to recognize new phylogenetic knowledge, new names are not proposed here. Instead, use is made of pre-existing names from the older literature. Most of these names are applied above the level of superfamily and are not (currently) governed by the International Code of Zoological Nomenclature. Nevertheless, in applying these names, and choosing among alternatives, we have selected the oldest family-group name available, and in order to facilitate the use of this classification, a consistent ending for each rank above the level of superfamily is used. At the same time, this chapter does introduce ranks that will be unfamiliar to some readers, even though many of those ranks are well-known within ornithology (e.g. Sibley & Monroe 1990).

Phylogenetic Relationships and the Checklist Sequence

Translating a complex phylogenetic tree into a linear classification is an inexact science in as much as there are many more hierarchical relationships (groups within groups) than there are Linnaean ranks that can be used to represent them. As a consequence one must adopt various “conventions” within that linear classification (see the suboscine classifications of Moyle *et al.* 2009 and Tello *et al.* 2009 for details). The most important, and often used, convention is that of “phyletic sequencing” in which a linear sequence of taxa *having the same taxonomic rank* is taken to specify a set of phylogenetic relationships, with the first taxon in the sequence interpreted to be the sister-group of all the subsequent taxa *at that same rank*. For example, using this “sequencing convention,” the classification

Order Galliformes

- Family Megapodiidae (megapodes)
- Family Cracidae (guans, curassows)
- Family Numididae (guineafowl)
- Family Odontophoridae (New World quails)
- Family Phasianidae (partridges, pheasants)

would imply that, within the Galliformes, the family Megapodiidae is the sister-group of all four families below it in the list; that Cracidae is the sister-group of Numididae + Odontophoridae + Phasianidae; and that Numididae is the sister-group of Odontophoridae + Phasianidae. Thus, the classification specifies the set of hierarchical relationships: (Megapodiidae (Cracidae (Numididae (Odontophoridae + Phasianidae))))). This example is straightforward because we have strong evidence for the hierarchical relationships of these five families.

There are also many nodes on the avian tree for which there is little or no support, and it is has been difficult for classifications to reflect this ambiguity. This classification therefore introduces another convention: in a list of names *at a given rank*, if those names are preceded by an asterisk (*), then the relationships among those taxa, *at that rank*, are ambiguous or uncertain. Thus the classification

Infraclass Palaeognathae

- Superorder Struthionimorphae
- *Superorder Rheimorphae
- *Superorder Tinamimorphae
- *Superorder Apterygimorphae

implies that the Struthionimorphae (ostriches) are the sister-group of Rheimorphae + Tinamimorphae + Apterygimorphae, but that relationships among the latter three higher taxa are ambiguous given current evidence.

Recent Advances in Avian Relationships

A current summary of our knowledge among the family-level taxa of birds is shown in the tree in Figure 1, and those relationships are translated to form the classification of Table 1. The framework for Figure 1 is based primarily on the findings of Ericson *et al.* (2006) and Hackett *et al.* (2008), but the results of numerous other studies are incorporated into the classification (other useful reviews of phylogenetic relationships within modern birds include Fain & Houde 2004; Cracraft *et al.* 2004; Brown *et al.* 2008; Mayr 2010a). Because of space limitations, the tree does not include all the group-names ranked above and below the family-level, but they are discussed in the review below and shown in the classification (Table 1).

Class Aves

Subclass Neornithes

Many recent studies that include neornithine outgroups continue to reaffirm the basal splits of birds, namely that the Palaeognathae are the sister-group of the Galloanserae and Neoaves.

Infraclass Palaeognathae

Superorder Struthionimorphae

Order Struthioniformes

Superorder Rheimorphae

Order Rheiformes

Superorder Tinamimorphae

Order Tinamiformes

Superorder Apterygimorphae

Order Apterygiformes

Order Casuariiformes

The past decade has seen confirmation of palaeognath monophyly, but a rather diverse array of opinion has arisen regarding relationships within the group. Indeed, based on their large 19-locus nuclear genome dataset Hackett *et al.* (2008) and Harshman *et al.* (2008) made the most startling proposal that the traditional separation between tinamous and ratites is incorrect and that the “ratites” are paraphyletic, with tinamous embedded within them. Ratite non-monophyly has subsequently been found in morphological (Johnston 2011) and whole mitochondrial datasets (Phillips *et al.* 2010), yet other studies using whole mitochondrial genomes (Haddrath & Baker 2001; Gibb *et al.* 2007) or morphological datasets (Livezey & Zusi 2006, 2007; Bourdon *et al.* 2009) conflict and have supported the traditional ratite versus tinamou dichotomy. The question of ratite monophyly is also tied up with questions about relationships within palaeognaths in that results for both problems vary according to taxon sampling (within birds and whether crocodylians are used as outgroups), and what characters are used (the kind and amount of DNA or morphological data), as well as how those data are analyzed (e.g. Braun & Kimball 2002). The issue is that palaeognath relationships have been difficult to resolve.

Within palaeognaths the dataset of Hackett *et al.* (2008) and Harshman *et al.* (2008) resolved ostrich as sister to other palaeognaths, but there was no satisfactory resolution among rheas, tinamous, and the clade of kiwi and cassowary/emu. The same result is true for whole mitochondrial genomes but in that dataset tinamous cluster strongly with moas (Phillips *et al.* 2010). These results are paralleled in recent morphological studies (Bourdon *et al.* 2009; Johnston 2011) in which rather restricted character sampling yields conflicting results and ambiguous support.

Two new studies (Haddrath and Baker 2012; Smith *et al.* 2012) shed additional light on palaeognath relationships, and at the same time they reinforce the notion that portions of the tree remain difficult to resolve definitively. Both studies generated new data and both combined these new data with those of Harshman *et al.* (2008), Hackett *et al.* (2008), and Phillips *et al.* (2010), hence the results are not entirely independent. All these data argue for ratite non-monophyly, with ostriches being the sister-group of other palaeognaths. Moreover, within the remaining taxa there is agreement that kiwis are sister to cassowaries + emus, and that tinamous are sister to moas. The problem is that sequence data alone are not converging on a clear answer as to how these groups are interrelated and the two studies conflict in that regard. Haddrath & Baker (2012) had Bayesian support for rheas being the sister-group of (or within) the kiwi-cassowary-emu clade, but in a likelihood analysis of all sequence data there was no support for that node (an ambiguous result was also found by Smith *et al.* 2012). Haddrath & Baker (2012) also found two unique derived retroposon insertions linking rheas to kiwis, emus, and cassowaries, and under the assumption that these shared retroposon insertions are very rare events then this could be viewed

as potential support for their tree. Until there is additional evidence to resolve current conflicts, the classification here reflects the continuing uncertainty.

Infraclass Neognathae
Parvclass Galloanseres

Order Anseriformes

Order Galliformes

The Galloanserae are a strongly supported group in all molecular analyses that include representatives of galliforms and anseriforms. The same is true for virtually all morphological data (Cracraft & Clark 2001; Mayr & Clark 2003; Livezey & Zusi 2006, 2007). A recent exception is Bourdon (2005) in which an analysis of the relationships of extinct pseudodontorns (bony-toothed birds; Odontopterygiformes) placed them with the anseriforms but in so doing rendered galliforms as sister to pseudodontorns + anseriforms and Neoaves. The placement of pseudodontorns with anseriforms is a potentially important finding, but Mayr (2011a) has challenged this view and argued instead that they are related to Galloanserae but poorly supported.

The identity of the major groups of galliforms and their overall interrelationships are moderately well established. The group has received extensive attention from investigators using morphological data (Dyke *et al.* 2003, Crowe *et al.* 2006, Ksepka 2009) in which taxon sampling has been large. Molecular studies so far have had more restricted taxon sampling (Pereira & Baker 2006, Kaiser *et al.* 2007, Hackett *et al.* 2008) but, in general, the results are congruent with most morphological analyses at higher taxonomic levels. In these analyses the tree, (Megapodiidae (Cracidae, Phasianoidea), is consistently recovered. It is within the diverse phasianoids that conflicts arise, and at higher levels the main contention is whether New World Quail (Odontophoridae) or guinea fowl (Numididae) are sister to the Phasianidae. The largest dataset (Hackett *et al.* 2008) has strong support for (Megapodiidae (Cracidae (Numididae (Odontophoridae, Phasianidae))). Crowe *et al.* (2006) and Ksepka (2009) undertook analyses of morphological characters as well as of combined morphological and mitochondrial-gene datasets and obtained this same result. There is substantial diversity within Phasianidae that will eventually need finer taxonomic recognition; although some groups are well supported (Kimball & Braun 2008; Kimball *et al.* 2011), some of the basal nodes are not. Sufficient evidence exists to propose seven tribes within Phasianinae.

In contrast to galliforms, there have been relatively few advances in the higher-level systematics of Anseriformes in recent years. Livezey (1986) and Donne-Goussé *et al.* (2002) found the whistling ducks (Dendrocygninae) to be sister to geese and their relatives (Anserinae) plus the true ducks (Anatinae). Gonzalez *et al.* (2009) examined the large-scale relationships of the Anatidae using two mitochondrial genes and also resolved the same relationships. In their study most tribe-level clades were resolved with moderate support but interrelationships among them were generally poor or nonexistent. There are also multiple genera whose relationships are uncertain due to the lack of sampling.

Parvclass Neoaves

Cracraft *et al.* (2003, 2004) identified the resolution of the major lineages of the Neoaves as the most significant, and difficult, unsolved problem in avian systematics. Subsequent studies have repeatedly confirmed this empirically (Mayr & Clarke 2003; Fain and Houde 2004; Ericson *et al.* 2006; Hackett *et al.* 2008). Although neoavian relationships remain a vexing scientific issue, there is reason for optimism with the introduction of next-generation sequencing and its capability to generate increasingly large amounts of data. Nevertheless, current large multi-locus studies show just how difficult it is to resolve basal avian relationships (Hackett *et al.* 2008; Wang *et al.* 2012). This is exemplified by the maximum likelihood result of Hackett *et al.* (2008, Fig. 3) in which relationships among most neoavian higher taxa are characterized by extremely short internodes.

One basal split within Neoaves was first proposed by Fain & Houde (2004) using a single locus, intron 7 of the β -fibrinogen gene (FBG-int7). Employing a large taxon sample of mostly nonpasseriform higher taxa, they recovered a clade they termed "Metaves" that included the groups Phoenicopteriformes through Opisthocomidae, listed below, and a second clade of all remaining neoavians, which they called "Coronaves." In addition to the FBG-int7 nucleotide data both groups were distinguished on the presence or absence of DNA insertions/deletions (indels). This basal dichotomy was also recovered by Ericson *et al.* (2006) and by Hackett *et al.* (2008; but with *Opisthocomus* in Coronaves instead of Metaves), but as was noted in both studies, the two groups disappear in the absence of FBG sequences. In an independent study Morgan-Richards *et al.* (2008) employed whole mitochondrial genomes plus a small New Zealand-centric taxonomic sample and could not recover the Metaves-Coronaves split; it could be argued, however, that this genomic marker was not a rigorous test of the hypothesis. The Metaves-Coronaves hypothesis is intriguing because a single gene is driving much of the result. Although other gene sets contribute to the association of metavian taxa (Hackett *et al.* 2008), there is virtually no

support among them at this time. Moreover, using FBG sequences alone yields some quite spurious relationships within Metaves and Coronaves (Fain & Houde 2004), as might be expected of any single gene.

The linear classification of Neoaves presented here excludes taxonomic resolution within the perching birds, Passeriformes, and follows the tree shown in Figure 1. The first groups discussed include a series of clades (flamingos and grebes through the hoatzin) whose relationships to other traditional neoavian “orders” are uncertain but they do appear to be more basal and outside several more well-supported branches. Once again, in Figure 1, dichotomous branching indicates relationships for which there is evidence of support, whereas nondichotomous (polytomous) branching indicates uncertainty in relationships; the latter are indicated by asterisks in the classification (Table 1).

Superorder Phoenicopterimorphae
Order Phoenicopteriformes
Order Podicipediformes

van Tuinen *et al.* (2001) were the first authors to argue that molecular data indicate the close relationship of the morphologically disparate grebes (Podicipedidae) and flamingos (Phoenicopteridae). This relationship has been found repeatedly in molecular data (Cracraft *et al.* 2004; Chubb 2004; Ericson *et al.* 2006; Hackett *et al.* 2008; Pratt *et al.* 2009). Analyses based on large taxon- and morphological-character sampling (Livezey & Zusi 2007) find a more traditional solution of placing grebes with loons and flamingos with storks (see also Livezey 2011), but some authors using very restricted sampling have reported presumptive morphological characters uniting grebes + flamingos (Mayr 2004; Manegold 2006).

Because of growing evidence that grebes and flamingos are sister-groups, Sangster (2005a) proposed erecting the higher group-name Mirandornithes, which he formally named and diagnosed. A new superordinal name is not required, however, as Phoenicopterimorphae is available for the two orders, Phoenicopteriformes and Podicipediformes.

Superorder Columbimorphae
Order Columbiformes (Columbidae)
Order Pterocliiformes (Pteroclididae)
Order Mesitornithiformes (Mesitornithidae)

Hackett *et al.*'s (2008) maximum likelihood analysis found weak branch support for Mesitornithidae + Columbidae and these two, in turn, were related to sand-grouse but with poor support. This latter relationship conflicts substantially with morphology: Mayr & Ericson (2004) placed mesites close to cuckoos whereas Livezey & Zusi (2007) had mesites as sister to turnicids, which are strongly associated with charadriiforms (see below). Erickson *et al.* (2006) had strong support for a Columbidae + Pteroclididae, thus current evidence leans, albeit not strongly, towards a monophyletic Columbimorphae.

Relationships within columbids are generally poorly resolved, and it appears that modern clades radiated over a relatively narrow window of time (Pereira *et al.* 2007). This latter study resolved three moderately- to well-supported clades using a large taxon sampling and multiple nuclear and mitochondrial loci. Bock (1994) noted that multiple family-group names have been proposed, and the three major clades recovered by Pereira *et al.* (2007) can be represented by the group-names Columbininae, Peristerinae, and Raphinae. The latter is the oldest available name for clade C of Pereira *et al.* (2007) as a senior synonym of Didinae and is used because the extinct *Raphus* and *Pezophaps* are embedded in this clade (Shapiro *et al.* 2002; Pereira *et al.* 2007).

Superorder Eurypygimorphae
Order Eurypygiformes

The close relationship of the kagu and the sunbittern is strongly supported by morphological (Cracraft 1982; Livezey & Zusi 2007) as well as molecular data (Ericson *et al.* 2006; Hackett *et al.* 2008), but their relationship to other neoavians remains conjectural. Traditionally they have been associated with gruiforms (Livezey 1998; Livezey & Zusi 2007), but molecular evidence provides no support for that and indeed places them deep in the neoavian tree. These taxa are placed in this sequence because Hackett *et al.* (2008) have them very weakly united with nightjars, swifts, and their allies, but this relationship could be spurious.

Superorder Phaethontimorphae
Order Phaethontiformes (Phaethontidae)

Recent molecular studies show that tropicbirds have very distant relationships to pelecaniforms and other waterbird taxa. Rather their affinities, although unresolved at this time, are apparently with one or more of the so-

called “metavian” taxa (Ericson *et al.* 2006; Hackett *et al.* 2008). Morphological data, in contrast, place them with waterbird groups (Livezey & Zusi 2007; Smith 2010).

Superorder Caprimulgimorphae **Order Caprimulgiformes**

It was long been suspected that nightjars and their allies were related to swifts and hummingbirds (e.g. Sibley & Ahlquist 1990), but it was not until morphological data (Mayr 2002) and then molecular *c-myc* sequences (Braun and colleagues in Cracraft *et al.* 2004; Braun & Huddleston 2009) drew attention to a close relationship between aegothelids and apodiforms that the traditional caprimulgiforms were seen to be paraphyletic (summarized in Cracraft *et al.* 2004). The problem turned out to be more complex as some molecular studies based on single genes questioned whether the combined caprimulgiform + apodiform grouping was itself monophyletic (e.g. in Cracraft *et al.* 2004; Barrowclough *et al.* 2006). However, larger datasets (Ericson *et al.* 2006; Hackett *et al.* 2008) support the monophyly of this expanded grouping although relationships within them remain very uncertain and additionally there is conflict between molecules (Hackett *et al.* 2008) and morphology (Livezey & Zusi 2007; Mayr 2010b).

There have been several suggestions about the nomenclature of a combined apodiform + caprimulgiform clade. Sangster (2005b) proposed creating a new name, Daedalornithes, for the swifts, hummingbirds, and owl-nightjars; Mayr (2010a), on the other hand, used the older name Strisores for apodiforms + caprimulgiforms [the use of Strisores for these taxa has a long history: Baird 1858, Cabanis & Heine 1860, Reichenow 1882]. Even though the choice of Strisores is preferable to a new name altogether, both proposed names are unnecessary. First, as noted in Mayr (2010a), Sibley *et al.* (1988) introduced the name Apodimorphae for the aegothelid + apodiform clade. Second, the ordinal name Caprimulgiformes is already available. Thus, to avoid a proliferation of new names, Caprimulgiformes can be used for the expanded clade. The only well-supported subgroup within the caprimulgiforms is the swifts + hummingbirds + owl-nightjars. This clade should be named and Trochiloidea is available. The taxonomy within the apodids follows Päckert *et al.* (2012) but needs much more work.

The hummingbirds have been the subject of a large-scale phylogenetic analysis using two mitochondrial and two nuclear intron genes (McGuire *et al.* 2007). Many traditional clades were well-supported as were most relationships among them. In a subsequent paper McGuire *et al.* (2009) proposed an “informal” taxonomy of hummingbirds based on the phylogeny of McGuire *et al.* (2007). They applied tribe-level endings (-ini) to all major groups but indicated these names should be considered rank-free. Here, a Linnaean approach to classification, along with appropriate endings, is used to represent phylogenetic relationships using phyletic sequencing.

Superorder Opisthocomimorphae **Order Opisthocomiformes**

Little progress has been made on the phylogenetic placement of the hoatzin, merely confirming earlier assessments about its perplexing relationships (Sorenson *et al.* 2003). New molecular data sets place *Opisthocomus* either near the base of “metavian” taxa (Ericson *et al.* 2006) or the base of “coronavian” groups (Hackett *et al.* 2008).

Superorder Cuculimorphae **Order Cuculiformes**

Hackett *et al.* (2008) found weak support for a relationship between cuculiforms and gruiforms and those two with bustards. On the Ericson *et al.* (2006) tree these three were unresolved, but grouped together in the same larger clade with waterbird taxa (Aequornithes, see below), hence for convenience all are placed together in the linear sequence of this classification Hackett *et al.* (2008) included seven species of cuckoos in their study, representing the major lineages. The relationships they recovered were all strongly supported and match those of Sorenson & Payne (2005) who used just two mitochondrial genes. The classification recommended here generally follows that of Sorenson and Payne (2005) except that the closely related Centropodinae and Couinae are united as tribes in a single subfamily. The crotophagines + neomorphines are sister to all other cuckoos, which are split into the Couinae and Cuculinae. The latter is split into the phaenicophaeinines and cuculinines.

Superorder Gruimorphae **Order Gruiformes**

Considerable evidence now indicates that the old concept of Gruiformes is no longer tenable. There is a “core” group to which the ordinal name can apply, and relationships among them are well supported (Ericson *et al.* 2006; Fain *et al.* 2007; Hackett *et al.* 2008). It has become evident that traditional Rallidae are not monophyletic

and that the sarothrurine flufftails are more closely related to the sungrebes (Hackett *et al.* 2008). Thus, the superfamily Ralloidea includes the rails (Rallidae) and their sister-group, the sungrebes (Heliornithidae) + flufftails (Sarothruridae). The sister-group of the Ralloidea is the superfamily Gruoidea. Within that group, the trumpeters (Psophiidae) are sister to the limpkin (Aramidae) and cranes (Gruidae; Krajewski *et al.* 2010).

Superorder Otidimorphae **Order Otidiformes**

The molecular studies of Ericson *et al.* (2006) and Hackett *et al.* (2008) both place the bustards in a weakly-supported clade with the core gruiforms and the cuculiforms. Otitids have traditionally been placed with gruiforms, but current data cannot confirm this and their relationships might be elsewhere.

Superorder Musophagimorphae **Order Musophagiformes**

The relationships of turacos remain problematic, but large molecular data sets are beginning to provide some hints. Both Ericson *et al.* (2006) and Hackett *et al.* (2008) place them within a clade that includes cuckoos, gruiforms, and various waterbird groups. More specifically, the Hackett *et al.* (2008) tree places musophagids as the sister-group to the Aequornithia (see below) but the support is poor.

Cohort Aequornithia

A major achievement of using large amounts of molecular data has been to provide strong evidence for uniting a core group of waterbird taxa (Ericson *et al.* 2006; Hackett *et al.* 2008) that previously had little or no support because of limited taxon and character sampling (for example, see van Tuinen *et al.* 2001; Cracraft *et al.* 2004). The large data set of Hackett *et al.* (2008, their node H) brings together loons, penguins, procellariiforms, and traditional ciconiiforms and pelecaniforms with very strong support. Ericson *et al.* (2006) had found the same grouping but with weak support. Relationships within the clade are also well supported (Fig. 1).

Given the strong support for this node, it seems important for communication that this taxon be named. Mayr (2010a) proposed the term Aequornithes, and that name is adopted and modified here for a taxon of cohort rank.

Superorder Gaviimorphae **Order Gaviiformes**

Gaviidae are strongly resolved as the sister-group of other aequornithines (Hackett *et al.* 2008). Mayr & Clarke (2003) and Livezey & Zusi (2007), like morphologists before them, resolved loons and grebes as sister-groups, although considerable molecular data place grebes well outside the waterbirds and with flamingos (see above). Nevertheless, loon + grebe morphological similarities have been recovered in other studies as well (see Sharpe 1891; Cracraft 1981; Smith 2010).

Superorder Procellariimorphae **Order Sphenisciformes** **Order Procellariiformes**

Penguins and the tube-nosed birds have long been thought to be related and recent morphological and molecular data strongly support this (Livezey & Zusi 2007; Hackett *et al.* 2008). A contrary view was expressed by Mayr (2005), who examined relationships of the extinct diving-birds, the Plotopteridae. On the basis of morphological data he resolved plotopterids as the sister to penguins and then those as the sister to Suloidea, thus placing penguins with traditional pelecaniforms. There appears to be no other evidence for this unusual finding, and it possibly results from poor taxon and character sampling as well as convergence between plotopterids (which have been suggested as being closely related to pelecaniforms) and penguins. Smith (2010) found spheniscids as sister to loons + grebes and those three to phaethontids. The name Procellariimorphae for sphenisciforms and procellariiforms has precedent (Fürbringer 1888; Livezey & Zusi 2007).

In recent years considerable attention has been paid to penguin inter-relationships and the placement of fossil taxa (Gianinni & Bertelli 2004; Baker *et al.* 2006; Ksepka 2006; Clarke *et al.* 2007). These studies have provided an integrative temporal picture of evolutionary and biogeographic change unlike that for any other family.

The monophyly of procellariiforms is hardly in doubt, but relationships among the higher taxa have been. Molecular data conflict: Ericson *et al.* (2006) have the diomedids as sister to the remaining procellariiforms with strong support, whereas Hackett *et al.* (2008) have oceanitids as sister with strong support, a similar result to that found with mitochondrial data (Cracraft *et al.* 2004). The morphological data of Livezey & Zusi (2007), in contrast,

placed *Diomedea* within the procellariids and had *Pelecanoides* as the sister to the remaining taxa. In Smith's (2010) morphological analysis, on the other hand, diomedeids were sister to procellariids and the two, in turn were sister to hydrobatids. Both the Ericson *et al.* and Hackett *et al.* trees support a close relationship of *Pelecanoides* and traditional procellariid taxa, but relationships within that large group are uncertain due to poor character and taxon sampling, and thus recognition of higher taxa would be premature (e.g. Penhallurick & Wink 2004). The sequence here follows Cracraft *et al.* (2004) and Hackett *et al.* (2008).

Superorder Pelecanimorphae

Order Pelecaniformes

It has been known for some time that the traditional Pelecaniformes and Ciconiiformes are not monophyletic and that their taxa are complexly interrelated to each other and to other taxa (Sibley & Ahlquist 1990; van Tuinen *et al.* 2001; Cracraft *et al.* 2004; Brown *et al.* 2008). Of the recent studies, only the large character-sampling of Hackett *et al.* (2008) has been able to provide substantial clarification of this phylogenetic problem and in their multi-gene phylogeny relationships are moderately to well-resolved. Their results call for a new taxonomy. The best solution is to unite all these taxa into a single order, the Pelecaniformes, which is the sister-group to the Procellariimorphae (Procellariiformes + Sphenisciformes) (Fig. 1).

The storks (Ciconiidae) are strongly supported as the sister-group of all other pelecaniforms (Hackett *et al.* 2008). These latter taxa can be divided into three clades, here given superfamily designation: ((Pelecanoidea + Ardeoidea) Suloidea) (Fig. 1).

The Ericson *et al.* (2006) and Hackett *et al.* (2008) trees resolve three clades within the Pelecanoidea that are recognized here as families: the (Pelecanidae (Scopidae + Balaenicipitidae)). Morphological data fail to bring these latter two families together or with pelicans [Mayr (2003) with small taxon sampling; Livezey & Zusi (2007) and Smith (2010) with large taxon sampling].

Hérons and ibises (Ardeoidea) are placed together on molecular trees (Ericson *et al.* 2006; Hackett *et al.* 2008) but not on morphological trees (Mayr & Clarke 2003; Livezey & Zusi 2007) or only weakly so (Smith 2010). A strongly-supported clade is the Suloidea (Ericson *et al.* 2006; Hackett *et al.* 2008). Morphology also resolves this group, but pelicans are often imbedded within them and/or phaethontids are found to be their sister-group (Cracraft 1985; Mayr & Clark 2003; Livezey & Zusi 2007; Smith 2010). In all these studies the sister relationship between fregatids and the sulids + (phalacrocoracids + anhingids) is found.

Cohort Charadrii, *incertae sedis*

Relationships of charadriiforms to other Neoaves are uncertain. Ericson *et al.* (2006) placed them unresolved with other "coronavian" taxa including the large monophyletic assemblages Aequornithia and Coracornithia (see below). Hackett *et al.* (2008) had them closer to the latter group of higher land birds. They are tentatively placed in their own cohort *incertae sedis* until their relationships to other major clades are clarified.

Superorder Charadriimorphae

Order Charadriiformes

Relationships within the charadriiforms have received substantial study in recent years and their interrelationships are now well resolved by molecular data (Paton *et al.* 2003; Ericson *et al.* 2003; Paton & Baker 2006; Fain & Houde 2007; Baker *et al.* 2007; Hackett *et al.* 2008), although morphological data are substantially incongruent (Livezey & Zusi 2007; Livezey 2009, 2010; Mayr 2011b). The classificatory arrangement proposed here follows Paton *et al.* (2003), which had broad taxonomic coverage for the nuclear RAG-1 gene, as well as the analyses of Ericson *et al.* (2003), Paton & Baker (2006), Baker *et al.* (2007), and Hackett *et al.* (2008), all of which were more restricted in taxonomic scope but are nevertheless congruent with Paton *et al.* (2003). Charadriiformes can be partitioned into three suborders, Charadrii, Scolopaci, and Lari, with the first being the sister of the other two.

There are two major clades in the Charadrii. The burhinids and chionids are united and are the sister-group to all other Charadrii (Fig. 1). Within this latter group, the charadriids are the sister to Haematopodidae + Recurvirostridae. Previous studies (Ericson *et al.* 2003; Baker *et al.* 2007) recovered a nonmonophyletic Charadriidae in that *Pluvialis* was found to be sister to oystercatchers and stilts or to them and other plovers. Recently, using species-tree approaches, Baker *et al.* (2012) have argued that this anomalous position of *Pluvialis* is an example of incomplete lineage sorting (ILS) and that the plovers are in fact monophyletic. This result makes sense for a number of reasons, and is followed here. Yet, this interpretation was based only on five genera of plovers and five closely related outgroups. Thus, left unexplored is whether this somewhat controversial analytical approach would have contradicted other charadriiform relationships revealed in previous studies.

The second large clade within the Charadriiformes is the diverse Scolopaci. It has two core lineages (Ericson *et al.* 2003; Paton *et al.* 2003; Baker *et al.* 2007; Hackett *et al.* 2008; Gibson & Baker 2012; Fig. 1). The first, the parvorder Jacanida, includes the plains-wanderer and the seedsnipes (Pedionomidae + Thinocoridae), which are the sister-group of the painted-snipes and jacanas (Rostratulidae + Jacanidae). The second lineage, the parvorder Scolopacida, includes a single family, the Scolopacidae. Monophyly of the scolopacid subfamilies and their interrelationships has broad support (Paton *et al.* 2003; Ericson *et al.* 2003; Baker *et al.* 2007; Gibson & Baker 2012; Fig. 1).

One of the more surprising systematic discoveries this past decade was the finding (Paton *et al.* 2003; Ericson *et al.* 2006; Baker *et al.* 2007; Fain & Houde 2007; Hackett *et al.* 2008) that turnicids are the sister-group of the other Lari (Parvorder Larida), a relationship supported by independent datasets. Within the remainder of the Larida there are three main clades: the Glareoloidea, Alcoidea, and Laroidea, with the Glareoidea being sister to the other two (Fig. 1).

The Glareoloidea are comprised of two families, the crab-plover (Dromadidae) and the pratincoles and cursors (Glareolidae). In recent studies their sister-group relationship has been marginally (Pareia & Baker 2010) or strongly supported (Hackett *et al.* 2008). The second major lineage within Larida is the Alcoidea, which includes the stercorariids and the alcids. Finally, the Laroidea contains the terns, skimmers, and gulls. Interestingly, however, with large taxon-sampling Baker *et al.* (2007) found that *Gygis* is the sister-group of these three groups, and *Anous* the sister of all four.

Cohort Coracornithia

One of the most well-supported nodes on the Ericson *et al.* (2006; their node 2) and Hackett *et al.* (2008; their node F) trees identified a clade including accipitriforms, strigiforms, traditional coraciiforms and piciforms, as well as a group comprising cariamids, falconids, psittaciforms, and passeriforms. This large clade can be called Coracornithia because it is a relatively close match in content to the Coracornithes proposed long ago by Fürbringer (1888). In his classificatory system, there were some differences from that identified by these more recent studies: he placed psittaciforms next to (but not within) his Coracornithes as an “intermediate” taxon; he included caprimulgiforms (discussed above), which are resolved elsewhere on the tree (Fig. 1); and he excluded accipitriforms.

Superorder Accipitriformae **Order Accipitriformes**

After many years of uncertainty about the higher-level relationships among raptors, the last ten years of research have brought some clarity. That falcons are not related to traditional accipitriforms but rather to passeriforms and psittaciforms is now well-supported by available data (see below). There is still a question about whether New World vultures are related to other accipitriforms and this remains a difficult problem (Ericson *et al.* 2006). The Hackett *et al.* (2008) data set does resolve a monophyletic accipitriforms with cathartids as sister to the others, yet support remains low even with a large number of loci. Nevertheless, this is the best hypothesis at this time. Within the core accipitriforms, all data support the secretary-bird as being sister to the osprey + remaining accipitrids.

Within the accipitrids there is extensive taxonomic diversity. Two recent studies have brought significant resolution to the relationships within this radiation. Thus, the results of Lerner & Mindell (2005), using two mitochondrial genes and a single nuclear intron, and Griffiths *et al.* (2007), employing the *RAG-1* nuclear gene, are significantly congruent with each other and provide a solid framework for the phylogenetic structure within the group. The classification proposed here relies heavily on their results, particularly the classificatory scheme of Griffiths *et al.* (2007), although the ranks adopted here differ.

Superorder Strigimorphae **Order Strigiformes**

The two families of the strigiforms are supported as members of the Coracornithia (Ericson *et al.* 2006; Hackett *et al.* 2008). Hackett *et al.* (2008) unite strigiforms with colliiforms but with no support. Relationships within owls have been relatively poorly studied. Higher-level relationships have been examined by Wink *et al.* (2009) using partial sequences of the nuclear *RAG-1* and mitochondrial cytochrome *b* genes. Most of the major groups were well-supported, and those groups are recognized in this classification.

Superorder Coraciiformae **Order Coliiformes**

The large dataset of Hackett *et al.* (2008) resolves coliiids as the poorly supported sister-group of the strigiforms and *Leptosomus* as the sister of a higher landbird clade (their node D) that includes traditional coraciiforms and piciforms. On the Ericson *et al.* (2006) tree coliiids are strongly supported as being clustered (their node 3) with the higher landbirds, not with the strigiforms. The leptosomatids are outside this group.

Present evidence, including morphology (Livezey & Zusi 1997) and molecules (Ericson *et al.* 2006; Wang *et al.* 2012), suggests that coliiids are in the Coraciimorphae and near the base of that tree.

Order Leptosomatiformes

The leptosomatids are moderately-well supported on the Hackett *et al.* (2008) tree as the sister-group of the trogons, hornbills, core coraciiforms, and piciforms (Fig. 1). Although molecular data resolve these relationships well, morphology has been unable to do so (Mayr & Clarke 2003; Livezey & Zusi 2007). Relationships within these clades are moderately well understood (Fig. 1; Ericson *et al.* 2006; Hackett *et al.* 2008).

Order Trogoniformes

Order Bucerotiformes

Trogons are now supported as the sister-group of bucerotids, core coraciiforms, and piciforms. There are four major clades within trogons, but relationships among them are still ambiguous (Moyle 2005). Within the Bucerotiformes, the Bucerotidae are sister to Upupidae + Phoeniculidae.

Order Piciformes

The large-scale relationships of piciform birds have been established by many studies, with the Galbuli (Galbulidae + Bucconidae) being the sister-group of the Pici. The Pici are themselves separable into the Picoidea (Indicatoridae + Picidae) and their sister, the Ramphastidae, including the barbets and toucans. Relationships within the Ramphastidae, however, are still uncertain, mostly due to insufficient character-sampling (Barker & Lanyon 2000; Moyle 2004). These studies provide strong evidence for three lineages of New World taxa: the barbets proper *Capito* + *Eubucco*, *Semnornis*, and the toucans proper. In studies with admittedly poor sampling, *Semnornis* may be related to those barbets or to the toucans. In all these analyses, there are two independent clades of Old World barbets, the Megalaiminae and Lybiinae.

Order Coraciiformes

The revised relationships of higher land birds discussed here call for a redefinition of the traditional order Coraciiformes. This restricted order now contains three major groups.

The bee-eaters, Meropoidea (Meropidae), are ambiguously the sister-group of the rollers Coracioidea (Coraciidae + Brachypteraciidae) and the kingfishers and allies, the Alcedinoidea (Ericson *et al.* 2006; Hackett *et al.* 2008). Within the Alcedinoidea, the Todidae are sister to Momotidae + Alcedinidae. The latter family has three subfamilies (Moyle 2006): (Alcedininae (Cerylinae + Halcyoninae)).

Superorder Passerimorphae

This clade includes cariamids, falconids, psittacids, and passeriforms (Fig. 1). The clade formed by the last three taxa is the equivalent of node B, and the latter two of node A, on the Hackett *et al.* (2008) tree. The latter study found cariamids as the sister-group of the other three with low to moderate support. All four groups are in an unresolved, but highly supported, polytomy on the Ericson *et al.* (2006) tree. Wang *et al.* (2012) collected sequence data for 30 new nuclear loci for 28 taxa included in the Hackett *et al.* (2008) dataset. The combined data set for these two studies resulted in 59 kilobases of sequence data for the 28 taxa, and likelihood analysis yielded the Hackett *et al.* (2008) tree with moderate to high support for the position of cariamids. The relationships of all four taxa (Cariamidae (Falconidae (Psittaciformes + Passeriformes))) were also supported by an analysis of 51 retroposon markers (Suh *et al.* 2011) but the taxonomic scope of that study was limited. Suh *et al.* (2011) proposed the name of Psittacopasserae for parrots and passerines and Eufalconimorphae for falcons, parrots, and passerines. The former name is descriptive, and the node is clearly an important one to name. The latter name, however, is not descriptive and implies there is a group of "false falcons" in contrast to "true falcons." The large group is here called the Passerimorphae in agreement with the superordinal suffix used throughout this classification.

Order Psittaciformes (Psittacidae)

Parrots have been the subject of important phylogenetic studies in recent years, and their taxonomic treatment here follows Wright *et al.* (2008), Schweizer *et al.* (2011), Schirtzinger *et al.* (2012), and especially for nomenclature, Joseph *et al.* (2012). Wright *et al.* (2008) and Schweitzer *et al.* (2011) used independent data sets [with Schirtzinger *et al.* (2012) overlapping significantly but not entirely with Wright *et al.* (2008)] and all three results exhibit substantial congruence at higher taxonomic levels. Still, many nodes remain poorly supported on all three trees. Other investigations that provide more phylogenetic detail for genera within some major parrot groups include Tavares *et al.* (2006) for arines and Joseph *et al.* (2011) for platycercines. With minor differences in ranking, the classification and nomenclature adopted here follow Joseph *et al.* (2012) and conservatively reflect our current state of phylogenetic knowledge.

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Table 1. A higher-level classification of nonpasserine birds (asterisks identify taxa whose relationships are uncertain at that hierarchical rank, see text for explanation).

Class Aves

Subclass **Neornithes**

Infraclass **Palaeognathae**

- Superorder Struthionimorphae
 - Order Struthioniformes
 - Family Struthionidae
- *Superorder Rheimorphae
 - Order Rheiformes
 - Family Rheidae
- *Superorder Tinamimorphae
 - Order Tinamiformes
 - Family Tinamidae
- *Superorder Apterygimorphae
 - Order Apterygiformes
 - Family Apterygidae
 - Order Casuariiformes
 - Family Casuariidae
 - Subfamily Casuariinae
 - Subfamily Dromaiinae

Infraclass **Neognathae**

Parvclass **Galloanseres**

- Order Anseriformes
 - Family Anhimidae
 - Family Anseranatidae
 - Family Anatidae
 - Subfamily Dendrocygninae
 - *Subfamily Oxyurinae
 - *Subfamily Anserinae
 - Tribe Malacorhynchini
 - Tribe Cereopseinae
 - Tribe Cygnini
 - Tribe Anserini
 - *Subfamily Anatinae
 - *Tribe Mergini
 - *Tribe Tadornini
 - *Tribe Aythyini
 - *Tribe Anatini
- Order Galliformes
 - Family Megapodiidae
 - Family Cracidae
 - Family Numididae
 - Family Odontophoridae
 - Family Phasianidae
 - Subfamily Rollulinae
 - Subfamily Phasianinae
 - *Tribe Pavonini
 - *Tribe Polyplectronini
 - *Tribe Coturnicini
 - *Tribe Gallini
 - *Tribe Lophophorini
 - *Tribe Phasianini
 - *Tribe Tetraonini

Parvclass **Neoaves**

- *Superorder Phoenicopterimorphae
 - Order Phoenicopteriformes
 - Family Phoenicopteridae
 - Family Podicipedidae
- *Superorder Columbimorphae
 - *Order Columbiformes
 - Family Columbidae
 - Subfamily Columbinae
 - Subfamily Peristerinae
 - Subfamily Raphinae
 - *Order Pterocliiformes
 - Family Pteroclididae
 - *Order Mesitornithiformes
 - Family Mesitornithidae
- *Superorder Eurypygimorphae
 - Order Eurypygiformes
 - Family Eurypygidae
 - Family Rhynochetidae
- *Superorder Phaethontimorphae
 - Order Phaethontiformes
 - Family Phaethontidae
- *Superorder Caprimulgimorphae
 - Order Caprimulgiformes
 - Family Steatornithidae
 - Family Podargidae
 - Family Nyctibiidae
 - Family Caprimulgidae
 - Subfamily Eurostopodinae
 - Subfamily Caprimulginae
 - Superfamily Trochiloidea
 - Family Aegothelidae
 - Family Apodidae
 - Subfamily Hemiprocninae
 - Subfamily Cypseloidinae
 - Subfamily Apodinae
 - Tribe Cypseloidini
 - Tribe Chaeturini
 - Tribe Collocaliini
 - Tribe Apodini
 - Family Trochilidae
 - Subfamily Florisuginae
 - Subfamily Phaethornithinae
 - Subfamily Polytminae
 - Subfamily Lesbiinae
 - Subfamily Patagoninae
 - Subfamily Trochilinae
 - Tribe Trochilini
 - Tribe Lampornithini
 - Tribe Mellisugini
- *Superorder Opisthocomimorphae
 - Order Opisthocomiformes
 - Family Opisthocomidae
- *Superorder Cuculimorphae
 - Order Cuculiformes
 - Family Cuculidae
 - Subfamily Crotophaginae

- Tribe Crotophagini
 - Tribe Neomorphini
 - Subfamily Centropodinae
 - Tribe Couini
 - Tribe Centropodini
 - Subfamily Cuculinae
 - Tribe Phaenicophaeini
 - Tribe Cuculini
 - *Superorder Gruimorphae
 - Order Gruiformes
 - Superfamily Ralloidea
 - Family Rallidae
 - Subfamily Himantornithidae
 - Subfamily Rallinae
 - Family Sarothruridae
 - Family Heliornithidae
 - Superfamily Gruoidea
 - Family Psophiidae
 - Family Aramidae
 - Family Gruidae
 - Subfamily Balearicinae
 - Subfamily Gruinae
 - *Superorder Otidimorphae
 - Order Otidiformes
 - Family Otididae
 - *Superorder Musophagimorphae
 - Order Musophagiformes
 - Family Musophagidae
- Cohort **Aequornithia**
- Superorder Gaviimorphae
 - Order Gaviiformes
 - Family Gaviidae
 - Superorder Procellariimorphae
 - Order Sphenisciformes
 - Family Spheniscidae
 - Order Procellariiformes
 - Family Oceanitidae
 - Family Diomedeidae
 - Family Hydrobatidae
 - Family Procellariidae
 - Superorder Pelecanimorphae
 - Order Pelecaniformes
 - Suborder Ciconii
 - Superfamily Ciconioidea
 - Family Ciconiidae
 - Suborder Pelecani
 - Superfamily Pelecanoidea
 - Family Pelecanidae
 - Family Scopidae
 - Family Balaenicipitidae
 - Superfamily Ardeoidea
 - Family Ardeidae
 - Family Threskiornithidae
 - Superfamily Suloidea
 - Family Fregatidae
 - Family Sulidae

Family Phalacrocoracidae
Family Anhingidae

Cohort **Charadrii**, *incertae sedis*

*Superorder Charadriimorphae

Order Charadriiformes

Suborder Charadrii

Parvorder Chionida

Superfamily Chionoidea

Family Burhinidae

Family Chionidae

Subfamily Chioninae

Subfamily Pluvianellinae

Parvorder Charadriida

Superfamily Pluvianoidea

Family Pluvianidae

Superfamily Haematopodoidea

Family Haematopodidae

Subfamily Haematopodinae

Subfamily Ibidorhynchinae

Family Recurvirostridae

Subfamily Recurvirostrinae

Subfamily Himantopodinae

Superfamily Charadrioidea

Family Charadriidae

Subfamily Pluvialinae

Subfamily Charadriinae

Subfamily Vanellinae

Suborder Scolopaci

Parvorder Jacanida

Superfamily Thincoroidea

Family Pedionomidae

Family Thinocoridae

Superfamily Jacanoidea

Family Rostratulidae

Family Jacanidae

Parvorder Scolopacida

Superfamily Scolopacoidea

Family Scolopacidae

Subfamily Numininae

Subfamily Limosinae

Subfamily Calidrinae

Tribe Arenariini

Tribe Calidrini

Subfamily Scolopacinae

Tribe Limnodromini

Tribe Scolopacini

Subfamily Tringinae

Tribe Tringini

Tribe Phalaropodini

Suborder Lari

Parvorder Turnicida

Family Turnicidae

Parvorder Larida

Superfamily Glareoloidea

Family Dromadidae

Family Glareolidae

Subfamily Glareolinae
 Subfamily Cursoriinae
 Superfamily Alcoidea
 Family Alcidae
 Family Stercorariidae
 Superfamily Laroidea
 Family Laridae
 Subfamily Anoinae
 Subfamily Gyginae
 Subfamily Rynchopinae
 Subfamily Larinae
 Subfamily Sterninae

Cohort Coracornithia

Superorder Accipitrimorphae

Order Accipitriiformes

Family Cathartidae
 Family Sagittariidae
 Family Pandionidae
 Family Accipitridae
 Subfamily Elaninae
 Subfamily Gypaetinae
 Tribe Gypaetini
 Tribe Pernini
 Subfamily Accipitrinae
 Tribe Circaetini
 Tribe Gypini
 Tribe Accipitrini

Superorder Strigimorphae

Order Strigiformes

Family Tytonidae
 Family Strigidae
 Subfamily Ieraglaucinae
 Subfamily Surniinae
 Subfamily Striginae

Superorder Coraciimorphae

Order Coliiformes

Family Coliidae

Order Leptosomatiformes

Family Leptosomidae

Order Trogoniformes

Family Trogonidae

Order Bucerotiformes

Family Bucerotidae
 Family Upupidae
 Family Phoeniculidae

Order Piciformes

Suborder Galbuli

Family Galbulidae
 Family Bucconidae

Suborder Pici

Superfamily Picoidea
 Family Indicatoridae
 Family Picidae
 Subfamily Jygninae
 Subfamily Picumninae
 Subfamily Picinae

- Tribe Nesocitini
- Tribe Hemicircini
- Tribe Picini
- Tribe Campephilini
- Tribe Melanerpini
- Superfamily Ramphastoidea
- Family Ramphastidae
 - Subfamily Megalaiminae
 - Tribe Calorhamphini
 - Tribe Megalaimini
 - Subfamily Semnornithinae
 - Subfamily Rhamphastinae
 - Tribe Capitonini
 - Tribe Rhamphastini
 - Subfamily Lybiinae
 - Tribe Trachyphonini
 - Tribe Lybiini
- Order Coraciiformes
 - Superfamily Meropoidea
 - Family Meropidae
 - Superfamily Coracioidea
 - Family Coraciidae
 - Family Brachypteraciidae
 - Superfamily Alcedinoidea
 - Family Todidae
 - Family Momotidae
 - Family Alcedinidae
 - Subfamily Alcedininae
 - Subfamily Cerylinae
 - Subfamily Halcyoninae
- Superorder Passerimorphae
 - Order Cariamiformes
 - Family Cariamidae
 - Order Falconiformes
 - Family Falconidae
 - Subfamily Herpetotherinae
 - Subfamily Falconinae
 - Tribe Polyborini
 - Tribe Falconini
 - Order Psittaciformes
 - Family Strigopidae
 - Subfamily Strigopinae
 - Subfamily Nestorinae
 - Family Cacatuidae
 - Subfamily Nymphicinae
 - Subfamily Calyptorhynchinae
 - Subfamily Cacatuinae
 - Tribe Microglossini
 - Tribe Cacatuini
 - Family Psittacidae
 - Subfamily Psittacinae
 - Subfamily Arinae
 - Tribe Amoropsittacini
 - Tribe Androglossini
 - Tribe Forpini
 - Tribe Arini
 - Family Psittaculidae
 - Subfamily Psitttrichasinae

Subfamily Psittaculinae

Tribe Micropsittini

Tribe Psittaculini

Subfamily Loriinae

*Tribe Psittacellini

*Tribe Platycercini

*Tribe Loriini

*Tribe Agapornithini

Order Passeriformes

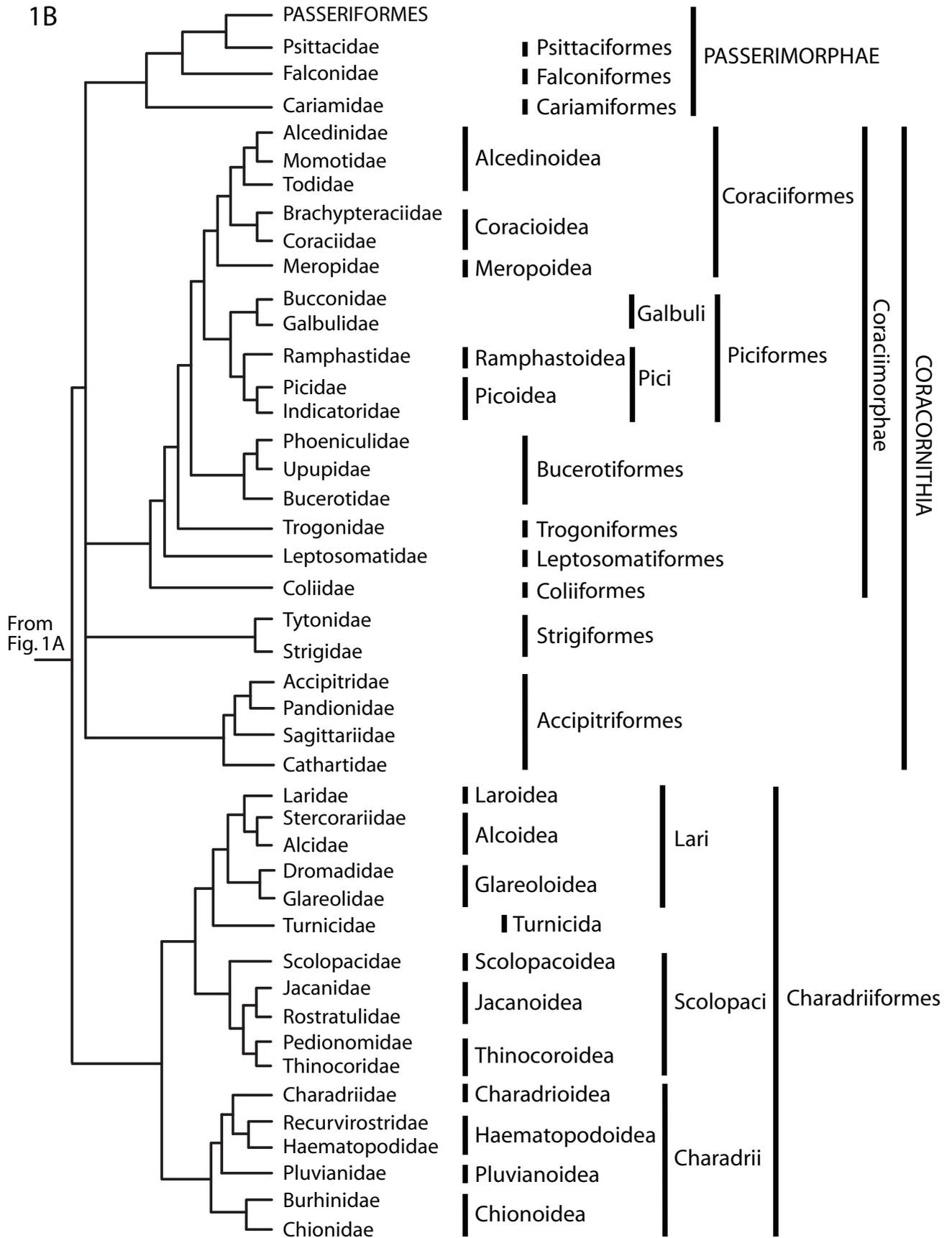


Figure 1B. Phylogenetic tree to family level cohorts Charadriia and Coracornithia. N.B. For Leptosomatidae read Leptosomidae.