

Joel Cracraft
 F. Keith Barker
 Michael Braun
 John Harshman
 Gareth J. Dyke

Julie Feinstein
 Scott Stanley
 Alice Cibois
 Peter Schikler
 Pamela Beresford

Jaime García-Moreno
 Michael D. Sorenson
 Tamaki Yuri
 David P. Mindell

Phylogenetic Relationships among Modern Birds (Neornithes)

Toward an Avian Tree of Life

Modern perceptions of the monophyly of avian higher taxa (modern birds, Neornithes) and their interrelationships are the legacy of systematic work undertaken in the 19th century. Before the introduction of an evolutionary worldview by Charles Darwin in 1859, taxonomists clustered taxa into groups using similarities that reflected a vision of how God might have organized the world at the time of Creation. Such was the case with the Quinerian system of avian classification devised by Macleay (1819–1821) in which groups and subgroups of five were recognized, or of Strickland (1841) or Wallace (1856) in which affinities were graphed as unrooted networks (see O'Hara 1988).

After Darwin, this worldview changed. For those comparative biologists struggling to make sense of Earth's biotic diversity in naturalistic terms, Darwinism provided a framework for organizing similarities and differences hierarchically, as a pattern of ancestry and descent. The search for the Tree of Life was launched, and it did not take long for the structure of avian relationships to be addressed. The first to do so was no less a figure than Thomas Henry Huxley (1867), who produced an important and influential paper on avian classification that was explicitly evolutionary. It was also Huxley who provided the first strong argument that birds were related to dinosaurs (Huxley 1868).

Huxley was particularly influential in England and was read widely across Europe, but the "father of phylogenetics" and phylogenetic "tree-thinking" was clearly Ernst Haeckel. Darwin's conceptual framework had galvanized Haeckel,

and within a few short years after *Origin* and a year before Huxley's seminal paper, he produced the monumental *Generelle Morphologie der Organismen*—the first comprehensive depiction of the Tree of Life (Haeckel 1866). Haeckel's interests were primarily with invertebrates, but one of his students was to have a singular impact on systematic ornithology that lasted more than 125 years.

In 1888 Max Fürbringer published his massive (1751 pages, 30 plates) two-volume tome on the morphology and systematics of birds. Showing his classical training with Haeckel and the comparative anatomist Carl Gegenbaur, Fürbringer meticulously built the first avian Tree of Life—including front and hind views of the tree and cross sections at different levels in time. The vastness of his morphological descriptions and comparisons, and the scope of his vision, established his conception of relationships as the dominant viewpoint within systematic ornithology. All classifications that followed can fairly be said to be variations on Fürbringer's theme. Such was the magnitude of his insights. Indeed, as Stresemann (1959: 270) noted:

On the whole all the avian systems presented in the standard works in this century are similar to each other, since they are all based on Fürbringer and Gadow [who followed Fürbringer's scheme closely and, being fluent in German, was able to read the 1888 tome]. My system of 1934 [Stresemann 1927–1934] does not differ in essence from those which

Wetmore (1951) and Mayr and Amadon (1951) have recommended.

Fürbringer (1888) thus established the framework for virtually all the major higher level taxa in use today, and the fact that subsequent classifications, with relatively minor alterations, adopted his groups entrenched them within ornithology so pervasively that his classificatory scheme has influenced how ornithologists have sampled taxa in systematic studies to the present day.

Despite his monumental achievement in establishing the first comprehensive view of the avian branch of the Tree of Life, avian phylogeny soon became of only passing interest to systematists. Phylogenetic hypotheses—in the sense of taxa being placed on a branching diagram—were largely abandoned until the last several decades of the 20th century. For more than 80 years after Fürbringer the pursuit of an avian Tree of Life was replaced by an interest in tweaking classifications, the most important being those of Wetmore (1930, 1934, 1940, 1951, 1960), Stresemann (1927–1934), Mayr and Amadon (1951), and Storer (1960). Aside from reflecting relationships in terms of overall similarity, these classifications also shaped contemporary views of avian phylogenetics by applying the philosophy of evolutionary classification (Simpson 1961, Mayr 1969), which ranked groups according to how distinct they were morphologically.

What happened to “tree thinking” in systematic ornithology between 1890 and 1970? The first answer to this question was that phylogeny became characterized as the unknown and unknowable. Relationships were considered impossible to recover without fossils and resided solely in the eye of the beholder inasmuch as there was no objective method for determining them. Thus, Stresemann (1959: 270, 277) remarked,

The construction of phylogenetic trees has opened the door to a wave of uninhibited speculation. Everybody may form his own opinion . . . because, as far as birds are concerned, there is virtually no paleontological documentation. . . . Only lucky discoveries of fossils can help us. . . .

A second answer is that phylogeny was eclipsed by a redefinition of systematics, which became more aligned with “population thinking.” This view was ushered in by the rise of the so-called “New Systematics” and the notion that “the population . . . has become the basic taxonomic unit” (Mayr 1942: 7). The functions of the systematist thus became identification, classification (“speculation and theorizing”), and the study of species formation (Mayr 1942: 8–11). Phylogeny became passé [see also Wheeler (1995) for a similar interpretation]. Thus,

The study of phylogenetic trees, of orthogenetic series, and of evolutionary trends comprise a field which was the happy hunting ground of the speculative-minded taxonomist of bygone days. The development of the

“new systematics” has opened up a field which is far more accessible to accurate research and which is more apt to produce tangible and immediate results. (Mayr 1942: 291)

A final answer was that, if phylogeny were essentially unknowable, it would inevitably be decoupled from classification, and the latter would be seen as subjective. The architects of the synthesis clearly understood the power of basing classifications on phylogeny (e.g., Mayr 1942: 280) but in addition to lack of knowledge, “the only intrinsic difficulty of the phylogenetic system consists in the impossibility of representing a ‘phylogenetic tree’ in linear sequence.”

Twenty-seven years later, Stresemann summarized classificatory history to that date in starkly harsh terms:

In view of the continuing absence of trustworthy information on the relationships of the highest categories [taxa] of birds to each other it becomes strictly a matter of convention how to group them into orders. Science ends where comparative morphology, comparative physiology, comparative ethology have failed us after nearly 200 years of effort. The rest is silence. (Stresemann 1959: 277–278)

The silence did not last. A mere four years after this indictment of avian phylogenetics, Wilhelm Meise, whose office was next to that of the founder of phylogenetic systematics, Willi Hennig, published the first explicitly cladistic phylogenetic tree in ornithology, using behavioral characters to group the rare birds (Meise 1963). Avian systematics, like all of systematics, soon became transformed by three events. The first was the introduction of phylogenetic (cladistic) thinking (Hennig 1966) and a quantitative methodology for building trees using those principles (Kluge and Farris 1969; the first quantitative cladistic analysis for birds was included in Payne and Riebel 1976). At the same time, the rise of cladistics logically led to an interest in having classifications represent phylogenetic relationships more explicitly, and that too became a subject of discussion within ornithology (e.g., Cracraft 1972, 1974, 1981). This desire for classifications to reflect phylogeny had its most comprehensive expression in the classification based on DNA–DNA hybridization, a methodology, however, that was largely phenetic (Sibley et al. 1988, Sibley and Ahlquist 1990, Sibley and Monroe 1990).

The second contribution that changed avian systematics was increased use of molecular data of various types. Techniques such as starch-gel electrophoresis, isoelectric-focusing electrophoresis, immunological comparisons of proteins, mitochondrial DNA (mtDNA) RFLP (restriction fragment length polymorphism) analysis, DNA hybridization, and especially mtDNA and nuclear gene sequencing have all been used to infer relationships, from the species-level to that of families and orders. Today, with few exceptions, investigators of avian higher level relationships use DNA sequencing, mostly of mtDNA, but

nuclear gene sequences are now becoming increasingly important.

Finally, not to be forgotten were the continuous innovations in computational and bioinformatic hardware and software over the last three decades that have enabled investigators to collect, store, and analyze increasing amounts of data.

This chapter attempts to summarize what we think we know, and don't know, about avian higher level relationships at this point in time. In the spirit of this volume, the chapter represents a collaboration of independent laboratories actively engaged in understanding higher level relationships, but it by no means involves all those pursuing this problem. Indeed, there is important unpublished morphological and molecular work ongoing that is not included here. Nevertheless, it will be apparent from this synthesis that significant advances are being made, and we can expect the next five years of research to advance measurably our understanding of avian relationships.

Birds Are Dinosaurs

Considerable debate has taken place in recent years over whether birds are phylogenetically linked to maniraptorian dinosaurs, and a small minority of workers have contested this relationship (e.g., Tarsitano and Hecht 1980, Martin 1983, Feduccia 1999, 2002, Olson 2002). In contrast, all researchers who have considered this problem over the last 30 years from a cladistic perspective have supported a theropod relationship for modern birds (Ostrom 1976, Cracraft 1977, 1986, Gauthier 1986, Padian and Chiappe 1998, Chiappe 1995, 2001, Chiappe et al. 1999, Sereno 1999, Norell et al. 2001, Holtz 1994, 2001, Prum 2002, Chiappe and Dyke 2002, Xu et al. 2002), and that hypothesis appears as well corroborated as any in systematics (fig. 27.1).

Having said this, droves of fossils—advanced theropods as well as birds—are being uncovered with increasing regularity, and many of these are providing new insights into character distributions, as well as the tempo of avian evolution. Just 10 years ago, understanding of the early evolution of birds was based on a handful of fossils greatly separated temporally and phylogenetically (e.g., *Archaeopteryx* and a few derived ornithurines). Now, more than 50 individual taxa are known from throughout the Mesozoic (Chiappe and Dyke 2002), and from this new information it is now clear that feathers originated as a series of modifications early in the theropod radiation and that flight is a later innovation (reviewed in Chiappe and Dyke 2002, Xu et al. 2003). Numerous new discoveries of pre-neornithine fossils will undoubtedly provide alternative interpretations to character-state change throughout the line leading to modern birds (for summaries of pre-neornithine relationships, see Chiappe and Dyke 2002).

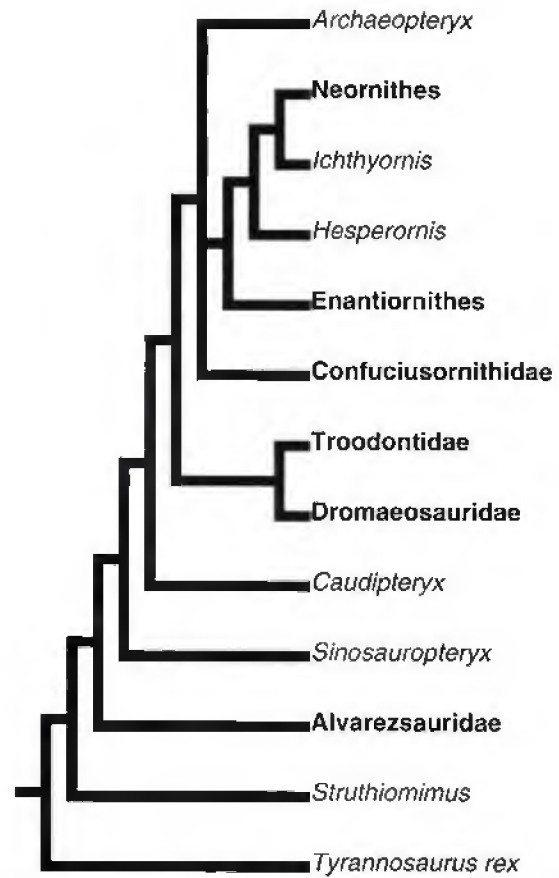


Figure 27.1. Relationships of birds to theropod dinosaurs (after Chiappe and Dyke 2002).

DNA Hybridization and Beyond

The DNA hybridization work of Sibley and Ahlquist (1990) has had a major impact on avian systematics. Their tree—the so-called “Tapestry” shown in figure 27.2—provided a framework for numerous evolutionary interpretations of avian biology. Avian systematists, however, have long noted shortcomings with the analytical methods and results of Sibley and Ahlquist (Cracraft 1987, Houde 1987, Lanyon 1992, Mindell 1992, Harshman 1994). Moreover, it is obvious that Sibley and Ahlquist, like many others before and after, designed their experiments with significant preconceived assumptions of group monophyly (again, many of which can be traced to Fürbringer 1888).

The spine of the DNA hybridization tree is characterized by a plethora of short internodes, which is consistent with the hypothesis of an early and rapid radiation (discussed more below). The critical issue, however, is that most of the deep internodes on Sibley and Ahlquist's (1990) tree were not based on a rigorous analysis of the data, and in fact the data are generally insufficient to conduct such analyses (Lanyon 1992, Harshman 1994). Relationships implied

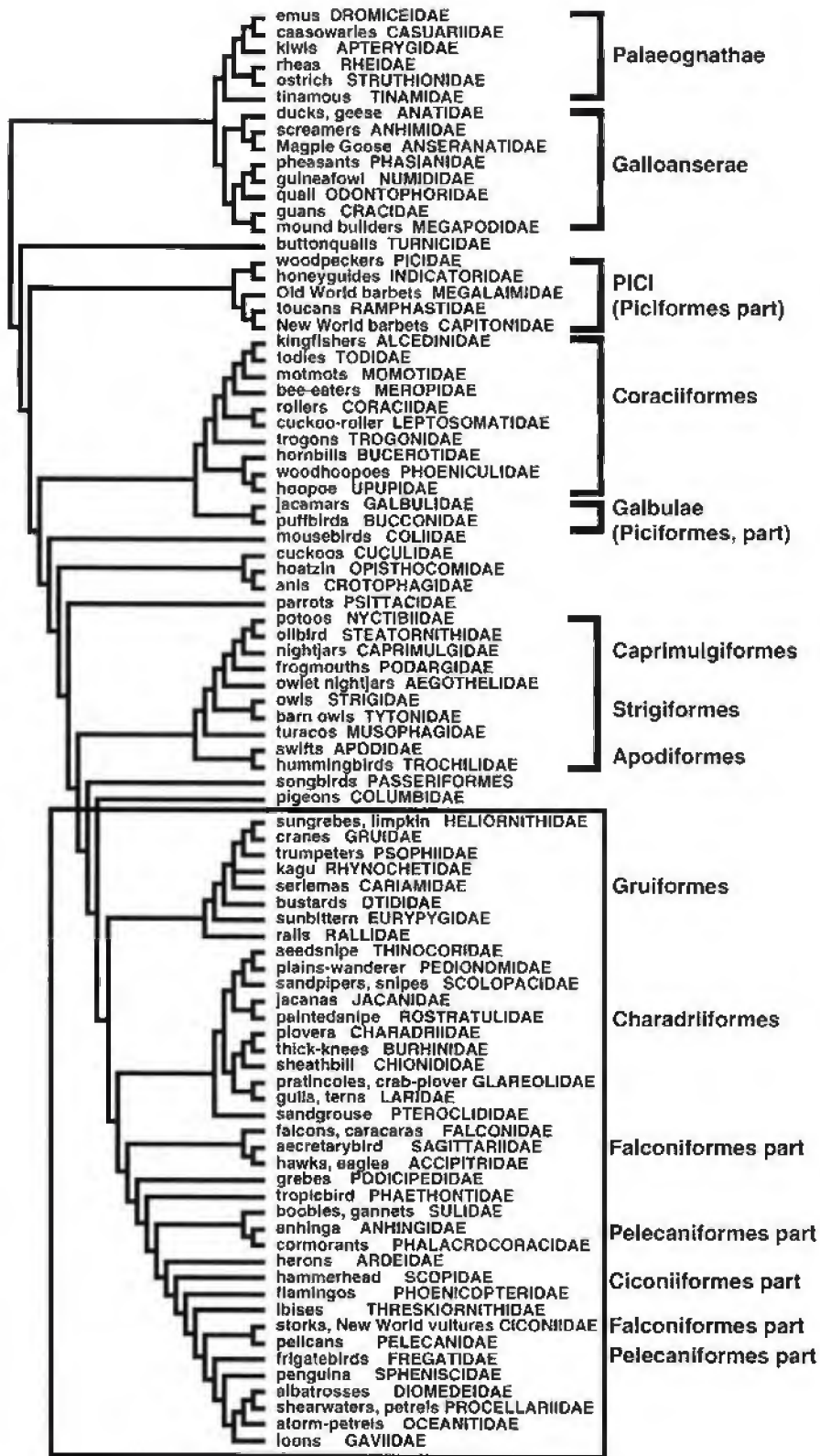


Figure 27.2. The "tapestry" of Sibley and Ahlquist (1990) based on DNA hybridization distances. The tree was constructed by hand from incomplete data matrices. The topology shown here is that of Sibley and Ahlquist (1990), but their classification and nomenclature are modified in some instances to use more familiar names.

by the tree therefore have ambiguous reliability. In addition, because of the manner in which experiments were designed, and possibly because of artifacts due to rate heterogeneity in hybridization distances, instances of incorrect rooting occur across the tree. Thus, although the DNA hybridization data have yielded insight about both novel and previously proposed relationships, they are difficult to interpret and compare with other results except as assertions of relationships.

The tree derived from DNA hybridization data postulated a specific series of relationships among taxa traditionally assigned ordinal rank, as well as among families. It is relevant here to summarize the overall structure of this tree as some of the major groupings it implies will be addressed in subsequent sections of this chapter. Suffice it to say at this point, the emerging morphological and molecular data confirm some of these relationships but not others, both among traditional "orders" but among families as well.

Among its more controversial claims, the DNA hybridization tapestry (fig. 27.2):

1. Recognizes a monophyletic Palaeognathae (ratites and tinamous) and Galloanserae (galliform + anseriform) but unites them, thus placing the neornithine root between them and all other birds: this rooting renders the Neognathae (all birds other than palaeognaths) paraphyletic, a conclusion refuted by substantial data (see below). Oddly, Sibley and Ahlquist (1990) contradicted this in their classification and grouped Galloanserae within their "Neoaves" (equivalent to Neognathae here).
2. Places Turnicidae (buttonquail), Pici (woodpeckers and their allies), and Coraciiformes (kingfishers, rollers, and allies) + Galbulae (traditionally united with the Pici) at the base of the Neoaves.
3. Identifies mousebirds, then cuckoos + Hoatzin, and finally parrots as sequential sister groups to the remaining neognaths.
4. Makes the large songbird (Passeriformes) assemblage the sister group to the remaining neognaths; this latter clade has the pigeons as the sister group of a large, mostly "waterbird," assemblage.
5. Depicts monophyly of Gruiformes (cranes, rails, and allies) and Charadriiformes (shorebirds, gulls, and allies) within the waterbirds: the falconiforms are also monophyletic, except that the New World vultures (Cathartidae) are placed in a family with the storks (Ciconiidae). Within the remainder of the waterbirds, the traditional orders Pelecaniformes (pelicans, gannets, cormorants) and Ciconiiformes (flamingos, storks, herons, ibises) are each rendered paraphyletic and interrelated with groups such as grebes, penguins, loons, and the Procellariiformes (albatrosses, shearwaters).

The Challenge of Resolving Avian Relationships

Initial optimism over the results of DNA hybridization has given way to a realization that understanding the higher level relationships of birds is a complex and difficult scientific problem. There is accumulating evidence that modern birds have had a relatively deep history (Hedges et al. 1996, Cooper and Penny 1997, Waddell et al. 1999, Cracraft 2001, Dyke 2001, Barker et al. 2002, Paton et al. 2002, *contra* Feduccia 1995, 2003) and that internodal distances among these deep lineages are short relative to the terminal branches (Sibley and Ahlquist 1990, Stanley and Cracraft 2002; the evidence is discussed below). To the extent these hypotheses are true, considerable additional data will be required to resolve relationships at the higher levels. This conclusion is supported by the results summarized here.

Although the base of Neoaves is largely unresolved at this time, recent studies are confirming some higher level relationships previously proposed, and others are resolving relationships within groups more satisfactorily than before (the songbird tree discussed below is a good example). At the same time, novel cladistic hypotheses are emerging from the growing body of sequence data (e.g., the proposed connection between grebes and flamingos; van Tuinen et al. 2001). So, even though our ignorance of avian relationships is still substantial, progress is being made, as this review will show.

In addition to summarizing the advances in avian relationships over the past decade (see also Sheldon and Bledsoe 1993, Mindell 1997), the following discussion of neornithine relationships is largely built upon newly completed studies from our various laboratories that emphasize increased taxon and character sampling for both molecular and morphological data. These studies include:

1. An analysis of the *c-myc* oncogene (about 1100 aligned base pairs) for nearly 200 taxa that heavily samples nonpasseriform birds (J. Harshman, M. J. Braun, and C. J. Huddleston, unpubl. obs.)
2. An analysis broadly sampling neornithines that uses 4800 base pairs of mitochondrial sequences in conjunction with 680 base pairs of the *PEPCK* nuclear gene (Sorenson et al. 2003)
3. An analysis of the *RAG-2* [recombination activating protein] nuclear gene for approximately 145 nonpasseriform taxa and a sample of passeriforms (J. Cracraft, P. Schikler, and J. Feinstein, unpubl. obs.)
4. A combined analysis of the *RAG-2* data and a sample of 166 morphological characters for 105 family-level taxa (G. J. Dyke, P. Beresford, and J. Cracraft, unpubl. obs.)
5. A combined analysis of the *c-myc* and *RAG-2* data for 69 taxa, mostly nonpasseriforms (J. Harshman, M. J. Braun, and J. Cracraft, unpubl. obs.)

6. A combined analysis of 74 "waterbird" taxa for 5300 base pairs of mitochondrial and RAG-2 gene sequences (S. Stanley, J. Feinstein, and J. Cracraft, unpubl. obs.)
7. An analysis of 146 passeriform taxa for 4108 base pairs of the RAG-1 and RAG-2 nuclear genes (F. K. Barker, J. F. Feinstein, P. Schikler, A. Cibois, and J. Cracraft, unpubl. obs.)
8. An analysis of 44 nine-primaried passeriforms ("Fringillidae") using 3.2 kilobases of mitochondrial sequence (Yuri and Mindell 2002).

Phylogenetic Relationships among Basal Neornithes

The Base of the Neornithine Tree

In contrast to the considerable uncertainties that exist regarding the higher level relationships among the major avian clades, the base of the neornithine tree now appears to be well corroborated by congruent results from both morphological and molecular data (fig. 27.3; summarized in Cracraft and Clarke 2001, García-Moreno et al. 2003; see below). Thus, modern birds can be divided into two basal clades, Palaeognathae (tinamous and the ratite birds) and Neognathae (all others); Neognathae, in turn, are composed of two sister clades, Galloanserae for the galliform (megapodes, guans, pheasants, and allies) and anseriform (ducks, geese, swans, and allies) birds, and Neoaves for all remaining taxa. This tripartite division of basal neornithines has been recovered using morphological (Livezey 1997a, Livezey and Zusi 2001, Cracraft and Clarke 2001, Mayr and Clarke 2003; see below) and various types of molecular data (Groth and Barrowclough 1999, van Tuinen et al. 2000, García-Moreno and Mindell 2000, García-Moreno et al. 2003, Braun and Kimball 2002, Edwards et al. 2002, Chubb 2004; see also results below). The DNA hybridization tree also recovered this basal structure, but the root, estimated by assuming a molecular clock without an outgroup, was placed incorrectly (fig. 27.2). In contrast, analyses using morphological or nuclear sequences have sought to place the root through outgroup analysis, and their results are consistent in placing it between palaeognaths and neognaths (Cracraft 1986, Groth and Barrowclough 1999, Cracraft and Clarke 2001; see also studies discussed below). Small taxon samples of mitochondrial data have also been particularly prone to placing the presumed fast-evolving passerine birds at the base of the neornithine tree (Härlid and Arnason 1999, Mindell et al. 1997, 1999), but larger taxon samples and analyses using better models of evolution (e.g., Paton et al. 2002) have agreed with the morphological and nuclear sequence analyses. Recent studies of nuclear short sequence motif signatures support the traditional hypothesis (Edwards et al. 2002), and

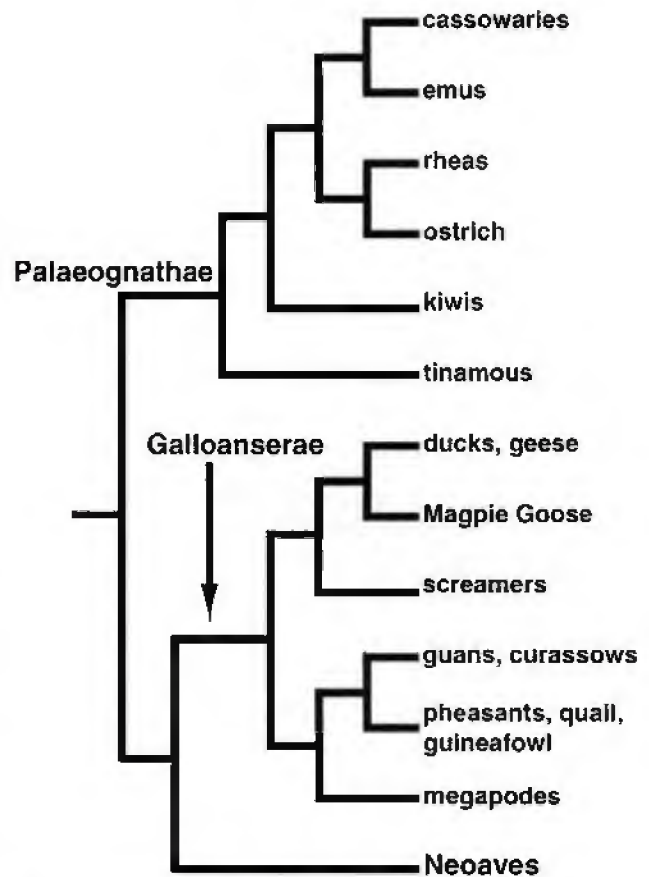


Figure 27.3. The basal relationships of modern birds (Neornithes). Relationships within Palaeognathae are those based on morphology (Lee et al. 1997), which do not agree with results from molecular sequences. See text for further discussion.

it also worth noting that palaeognaths and neognaths are readily distinguished by large homomorphic sex chromosomes in the former and strongly heteromorphic chromosomes in the latter (Ansari et al. 1988, Ogawa et al. 1998).

Palaeognathae

Monophyly of palaeognaths is well corroborated, but relationships within the ratites remain difficult to resolve. The relationships shown in figure 27.3 reflect those indicated by morphology (Cracraft 1974, Lee et al. 1997, Livezey and Zusi 2001), and all the internodes have high branch support. Molecular data, on the other hand, have differed from this view and, in general, data from different loci and methods of analysis have yielded conflicting results. In most of these studies (Lee et al. 1997, Haddrath and Baker 2001, Cooper et al. 2001) the kiwis group with the emu + cassowaries, and the rhea and ostrich diverge independently at the base of the tree. When the extinct New Zealand moas are included in studies using most of the mitochondrial genome (Haddrath and Baker 2001, Cooper et al. 2001), they also tend to be

placed toward the base of the tree. It can be noted that single gene trees often do not recover ratite monophyly with strong support, although these taxa generally group together.

Palaeognaths appear to exhibit molecular rate heterogeneity. Tinamous, in particular, and possibly rheas and ostriches appear to have higher rates of molecular evolution than do kiwis, emus, and cassowaries (Lee et al. 1997, van Tuinen et al. 2000, Haddrath and Baker 2001). Additionally, palaeognath mitochondrial sequences, which have been the primary target of molecular studies, exhibit significant shifts in base composition, which have made phylogenetic interpretations difficult (Haddrath and Baker 2001). Thus, rate artifacts, nonstationarity, the existence of relatively few, deeply divergent species-poor lineages, and short internodal distances among those lineages all play a role in making the resolution of ratite relationships extremely difficult and controversial. Although palaeognath relationships may be solved with additional molecular and morphological data of the traditional kind, the discovery of major character changes in molecular sequences such as indels or gene duplications may also prove to be important.

Galloanserae

Despite occasional debates that galliforms and anseriforms are not sister taxa (Ericson 1996, 1997, Ericson et al. 2001), the predominant conclusion of numerous workers using morphological and/or molecular data is that they are (Livezey 1997a, Groth and Barrowclough 1999, Mindell et al. 1997, 1999, Zusi and Livezey 2000, Livezey and Zusi 2001, Cracraft and Clarke 2001, Mayr and Clarke 2003, Chubb 2004). Molecular studies questioning a monophyletic Galloanserae (e.g., Ericson et al. 2001) have all employed small taxon samples of mtDNA or nuclear DNA, but when samples are increased, or nuclear genes are used, Galloanserae are monophyletic and the sister group of Neoaves (Groth and Barrowclough 1999, García-Moreno and Mindell 2000, van Tuinen et al. 2000, García-Moreno et al. 2003, Chubb 2004; see also J. Harshman, M. J. Braun, and C. J. Huddleston, unpubl. obs.); three indel events in sequences from *c-myc* also support a monophyletic Galloanserae (fig. 27.4). The DNA hybridization tree of Sibley and Ahlquist (1990) recognized Galloanserae, but because the neornithine root was incorrectly placed, Galloanserae was resolved as the sister group of the palaeognaths. With respect to relationships within galliforms, a consistent pattern seems to have emerged (Cracraft 1972, 1981, 1988, Sibley and Ahlquist 1990, fig. 328, Harshman 1994, Dimcheff et al. 2000, 2002, Dyke et al. 2003; see also J. Harshman, M. J. Braun, and C. J. Huddleston, unpubl. obs.): (Megapodiidae (Cracidae (Numididae + Odontophoridae + Phasianidae))). The major questions remain centered around the relative relationships among the guinea fowl (numidids), New World quail (odontophorids), and pheasants (phasianids), as well as the phylogeny within the latter; recent studies suggest that the numidids are out-

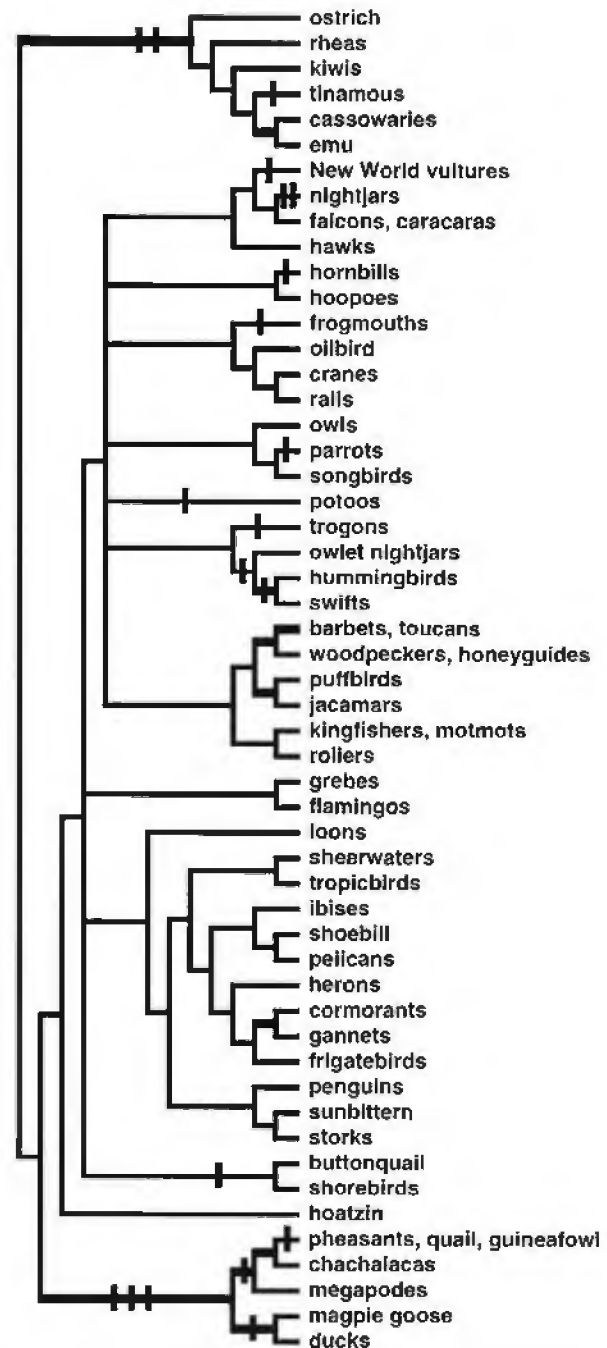


Figure 27.4. Phylogenetic tree based on approximately 1100 bases of the nuclear oncogene *c-myc*, including intron, exon coding, and 3' untranslated region sequence, for 170 taxa (J. Harshman, M. J. Braun, and C. H. Huddleston, unpubl. obs.). The tree shown is an unweighted parsimony majority rule bootstrap tree, plus other compatible branches. Thick branches have 70% or greater bootstrap support; thin branches may have very low support. Vertical tick marks represent phylogenetically informative indels. Most terminal branches represent several species, and all those are strongly supported, although for clarity the branches are not shown as thickened.

side quails and phasianids (Cracraft 1981, Dimcheff et al. 2000, 2002, Dyke et al. 2003).

Relationships among the basal clades of anseriforms are also not too controversial (Livezey 1986, 1997a,; Sibley and Ahlquist 1990: fig. 328 *contra* the "tapestry", Harshman 1994, Ericson 1997, Groth and Barrowclough 1999; for views of relationships within anatids, see Madsen et al. 1988, Livezey 1997b, Donne-Goussé et al. 2002). The screamers (Anhimidae) are the sister group to the magpie goose (Anseranatidae) + ducks, geese, and swans (Anatidae). We note, however, that the resolution of the basal nodes among screamers, magpie goose, and anatids has been difficult and that mitochondrial data sometimes unite the screamers and magpie goose (fig. 27.5), a grouping not suggested by nuclear, morphological, or combined data. The fact that both Livezey (1997a) and Ericson (1997) found the Late Cretaceous-Paleogene fossil *Presbyornis* to be the sister group of Anatidae (see also Kurochkin et al. 2002) is important because it sets the Late Cretaceous as the minimum time of divergence for the anatids and all deeper nodes.

Relationships within Neoaves

Relationships among the neoavian higher taxa have been discussed in a number of studies over the past several decades (e.g., Cracraft 1981, 1988, Sibley and Ahlquist 1990, Ericson 1997, Mindell et al. 1997, 1999, Feduccia 1999, van Tuinen et al. 2000, 2001, among others), and it is clear that relatively little consensus has emerged. The monophyly of many groups that have been accorded the taxonomic rank of "order" such as loons, grebes, penguins, parrots, cuckoos, and the large songbird group (Passeriformes) has not been seriously questioned but that of nearly all other higher taxa has. Thus, it is now broadly accepted that several traditional orders such as pelecaniforms, ciconiiforms, and caprimulgi-forms are nonmonophyletic, whereas the status of others such as gruiforms, coraciiforms, piciforms, and falconiforms remains uncertain in the minds of many workers.

If one had to summarize the current state of knowledge, the most pessimistic view would see the neoavian tree as a "comb," with little or no resolution among most traditional families and orders. Short and poorly supported internodes among major clades of neoavians are characteristic of recent studies using nuclear (Groth and Barrowclough 1999, van Tuinen et al. 2000) or mitochondrial data sets (van Tuinen et al. 2000, 2001, Johnson 2001, Hedges and Sibley 1994, Johansson et al. 2001), and the data sets discussed here also illustrate this point. The trees discussed below will be interpreted within the framework of bootstrap resampling analyses that show sister lineages supported at the 70% level (heavy lines in the figures). Using this approach, relationships among the avian higher taxa can be interpreted as largely unresolved, producing the neoavian comb. Nevertheless, there are emerging similarities in phylogenetic pattern recovered across some of these different studies that suggest some commonality of phylogenetic signal. In these and other published cases, the

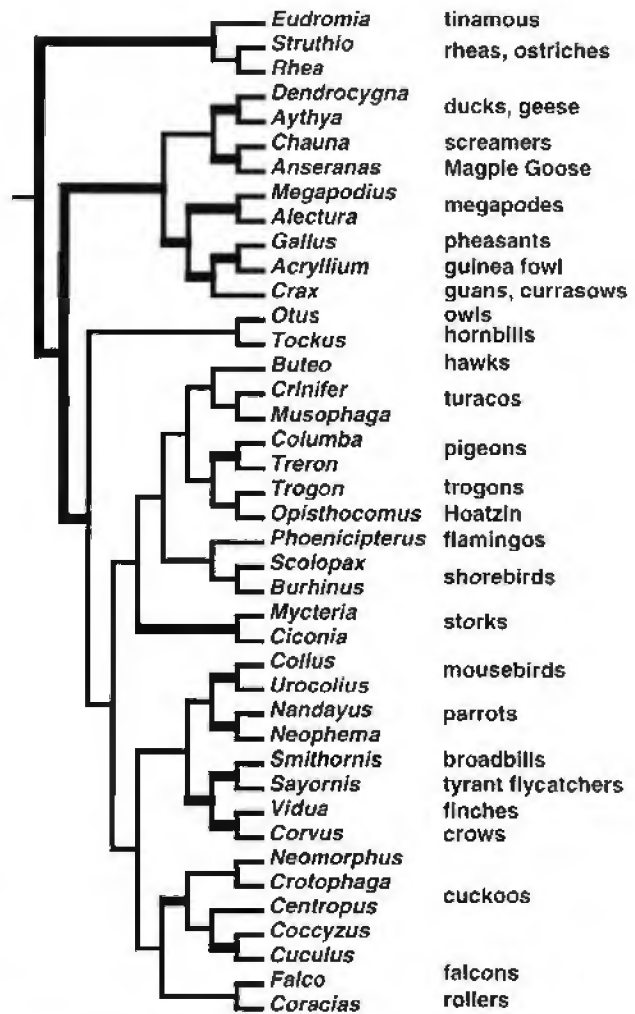


Figure 27.5. A phylogenetic hypothesis for 41 avian taxa based on about 4800 base pairs of mitochondrial sequence and 680 base pairs of PEPCK intron 9 nuclear gene using three paleognaths as the root (Sorenson et al. 2003). Nodes with bootstrap support values of 70% are shown in heavy black, based on maximum likelihood and maximum probability analyses of mitochondrial data and MP analyses of PEPCK intron 9.

primary reason for the neoavian comb is suspected to be insufficient character and/or taxon sampling. As noted above, current evidence suggests that many of these divergences are old and occurred relatively close in time. Thus, we are optimistic that most neoavian relationships will be resolved with additional data (see Discussion, below).

Phylogenetic Relationships among the "Waterbird Assemblage"

Over the years, many authors have suggested that some or all of the waterbird orders, in particular, seabirds (Procellariiformes), penguins (Sphenisciformes), loons (Gaviiformes), grebes (Podicipediformes), storks, herons, flamingos and allies (Ciconiiformes), pelicans, cormorants, and allies (Pele-

caniformes), shorebirds and gulls (Charadriiformes), and cranes, rails, and allies (Gruiformes), are related to one another (see, e.g., Sibley and Ahlquist 1990, Hedges and Sibley 1994, Olson and Feduccia 1980a, 1980b, Cracraft 1988). Some authors have also linked various falconiform families to the waterbird assemblage (Jollie 1976–1977, Rea 1983), including a supposedly close relationship between New World vultures (Cathartidae) and storks (Ligon 1967, Sibley and Ahlquist 1990, Avise et al. 1994; but also see Jollie 1976–1977, Hackett et al. 1995, Helbig and Siebold 1996). As a consequence of these and newer molecular studies, it is now widely thought that several of the large traditional orders of waterbirds may not be monophyletic, and this is especially true of the pelecaniforms and ciconiiforms (Cottam 1957, Sibley and Ahlquist 1990, Hedges and Sibley 1994, Siegel-Causey 1997, van Tuinen et al. 2001).

The supposition that waterbirds are related to one another within neornithines as a whole is not well supported, although the available data are suggestive of a relationship among some of them (see above). Only the DNA hybridization tree of Sibley and Ahlquist (1990) covered all birds, and on their tree (fig. 27.2) the waterbirds and falconiforms are clustered together. Van Tuinen et al. (2001) recently re-evaluated waterbird relationships and compared new DNA hybridization data with results from about 4062 base pairs of mitochondrial and nuclear sequence data for 20 and 19 taxa, respectively. Their most general conclusion was there was relatively little branch support across the spine of the tree, indicating that relationships among waterbirds are still very much uncertain. They did, however, find support for several clades: (1) a grouping of (the shoebill *Balaeniceps* + pelicans) + hammerkop (*Scopus*), and these in turn to ibises and herons, (2) penguins + seabirds (Procellariiformes), and most surprisingly, (3) grebes + flamingos.

Previous studies have had insufficient taxon and character sampling, or both. Even though large taxon samples based on mitochondrial genes (fig. 27.6), or on the *c-myc* and RAG-2 nuclear genes (figs. 27.4, 27.7A), are an improvement on previous work, by themselves or together (fig. 27.8), they are still inadequate to provide strong character support for most clades. Nevertheless, some congruence among these various studies is apparent. The *c-myc* data (fig. 27.4; J. Harshman, M. J. Braun, and C. J. Huddleston, unpubl. obs.), for example, recover (1) (cormorants + gannets) + frigatebirds, (2) (shoebills + pelicans) + ibises, (3) grebes + flamingos, and (4) buttonquails + shorebirds. At the same time, groups such as loons, tropicbirds, penguins, and storks do not show any clear pattern of relationships in the *c-myc* data or the nuclear/mitochondrial tree of van Tuinen et al. (2001). What is clear in the *c-myc* data is that New World vultures and storks are distantly removed from one another; New World vultures were not included in the van Tuinen et al. study. The RAG-2 data (fig. 27.7; J. Cracraft, P. Schikler, and J. Feinstein, unpubl. obs.) also strongly support (1) a pelican/shoebill/hammerkop clade, (2) a cormorant/anhinga/gannet group-

ing, and (3) various clades within traditional charadriiforms and gruiforms. Both *c-myc* and RAG-2 + morphology link frigatebirds to the sulids, phalacrocoracids, and anhingids.

In an attempt to address problems of sparse taxon sampling seen in previous studies, S. Stanley, J. Feinstein, and J. Cracraft (unpubl. obs.) examined 57 waterbird taxa for 5319 base pairs of mitochondrial and nuclear RAG-2 sequences (fig. 27.6). When palaeognaths and Galloanserae are used as outgroups, the root of the waterbird tree was placed on one of the two gruiform lineages, thus suggesting, in agreement with Sibley and Ahlquist (1990) and van Tuinen et al. (2001), that gruiforms are outside the other waterbird taxa, although this is not strongly supported given available data. This larger analysis still provides little resolution for higher level relationships among waterbirds, but it does find support for a grebe + flamingo relationship, monophyly of charadriiforms, and the shoebill + pelicans + hammerkop clade, in agreement with van Tuinen et al. (2001) and the *c-myc* data (fig. 27.4).

The buttonquails (Turnicidae) have traditionally been considered members of the order Gruiformes. Recent molecular analyses, however, now place them decisively with the charadriiforms, and indeed they are the sister-group of the Lari (Paton et al. 2003). The *c-myc* data (fig. 27.4) are consistent with this topology and include a unique indel, uniting turnicids and charadriiforms.

The mitochondrial and RAG-2 data also appear to contain phylogenetic signal for other clades even though they do not have high bootstrap values. Thus, when the data are explored using a variety of methods (e.g., transversion parsimony), the following groups are generally found (fig. 27.6): (1) an expanded "pelecaniform" clade that also includes taxa formerly placed in ciconiiforms (shoebill, hammerkop, ibises, and storks), (2) a grouping of grebes and flamingos with charadriiforms and some falconiforms, and (3) often a monophyletic Falconiformes (although the family Falconidae was not sampled), with no evidence of a relationship between storks and New World vultures. Tropicbirds (phaethontids) and herons (ardeids) represent divergent taxa that have no stable position on the tree. Some of these relationships are also seen in other data sets such as the *c-myc* data (fig. 27.4) and in the mitochondrial data of van Tuinen et al. (2001).

Phylogenetic Relationships among the Owls (Strigiformes), Swifts and Hummingbirds (Apodiformes), and Nightjars and Allies (Caprimulgiformes)

The DNA hybridization tree (fig. 27.2; Sibley and Ahlquist 1990) recognizes a monophyletic Caprimulgiformes that is the sister group of the owls; these two groups, in turn, are the sister group of the turacos (Musophagidae), and finally, all three are the sister clade of the swifts and hummingbirds (Apodiformes). There is now clear evidence that this hypothesis is not correct.

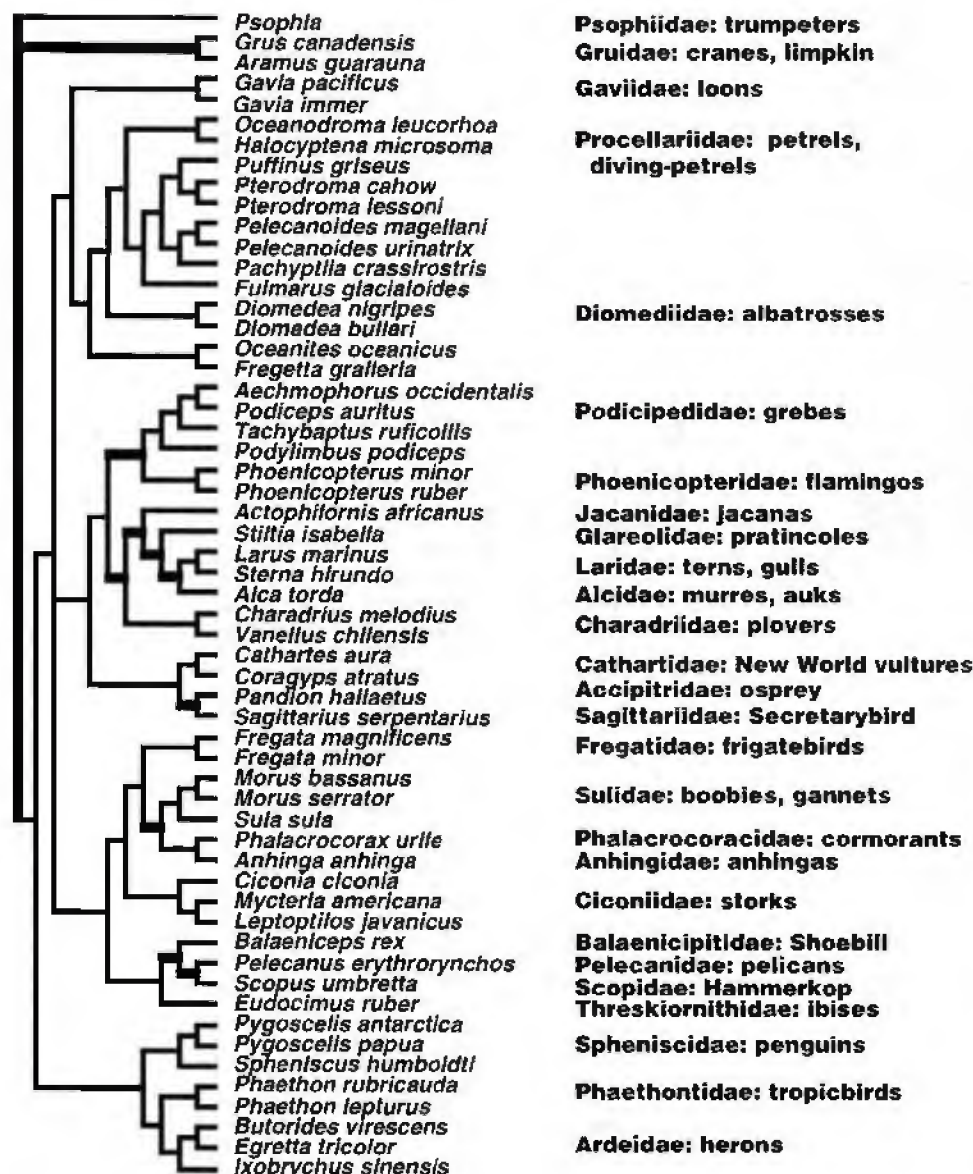


Figure 27.6. A phylogenetic hypothesis for "waterbird" higher taxa using 4164 base pairs of mitochondrial sequence (cytochrome *b*, *COI*, *COII*, *COIII*) and 1155 base pairs of the RAG-2 nuclear gene (transversion weighted) using gruiform taxa as the root (S. Stanley, J. Feinstein, and J. Cracraft, unpubl. obs.). Thick branches represent interfamilial clades supported by bootstrap values greater than 70% (all families had high bootstrap values but are not shown for simplicity).

Both published and unpublished data have recently indicated that caprimuliforms are not monophyletic. Instead of their traditional placement within caprimuliforms, owl-nightjars (Aegothelidae) are most closely related to the swifts and hummingbirds, a hypothesis first recognized in *c-myc* nuclear sequences (Braun and Huddleston 2001; fig. 27.4). This relationship is supported by morphological characters (Mayr 2002) as well as by combined morphological and RAG-2 data (fig. 27.7B) and by combined *c-myc* and RAG-2 data (fig. 27.8). Even with the aegothelids removed from the caprimuliforms there is presently little support for the monophyly of the remaining families. The available molecular data for *c-myc*, RAG-2, or combined *c-myc*/RAG-2 (figs. 27.4, 27.7A, 27.8) do not unite them, nor do combined *c-myc* and RAG-1 fragments (Johansson et al. 2001) or morphology (Mayr 2002). The relationships of owls to various

caprimuliform taxa are also not supported by available sequence data (figs. 27.4, 27.7, 27.8; Johansson et al. 2001, Mindell et al. 1997); however, one subsequent DNA hybridization study has supported this hypothesis, in addition to linking owls, caprimuliforms, and apodiforms (Bleiweiss et al. 1994). Preliminary morphological data also suggest a relationship (Livezey and Zusi 2001).

Phylogenetic Relationships among "Higher Land Birds": Cuculiformes, Coraciiformes, Trogoniformes, Coliiformes, and Piciformes

Few avian relationships are as interesting as those associated with the "higher land bird" question, and it is a problem with important implications for the overall topology of the neornithine tree. Historically, groups such as the piciforms, coraci-

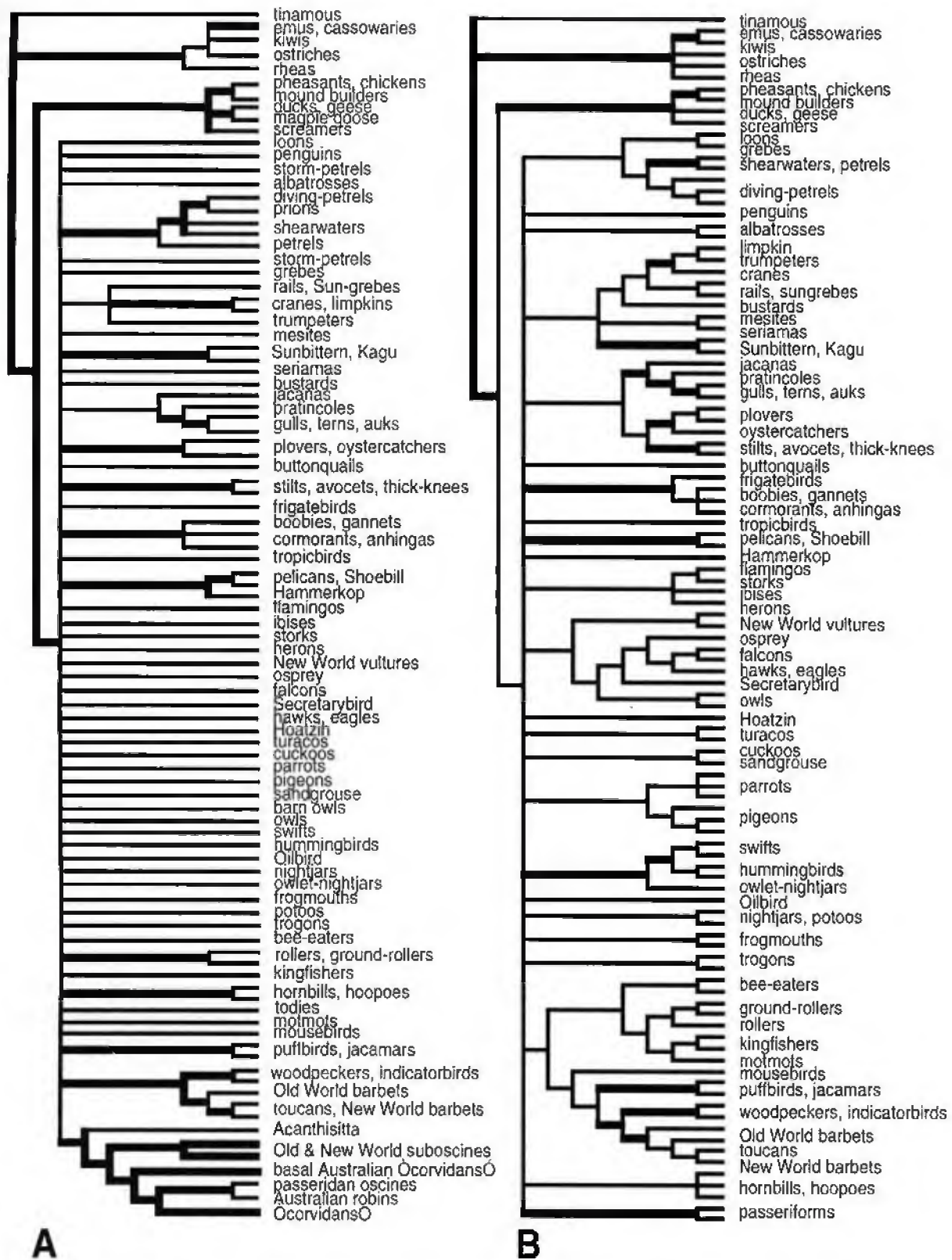
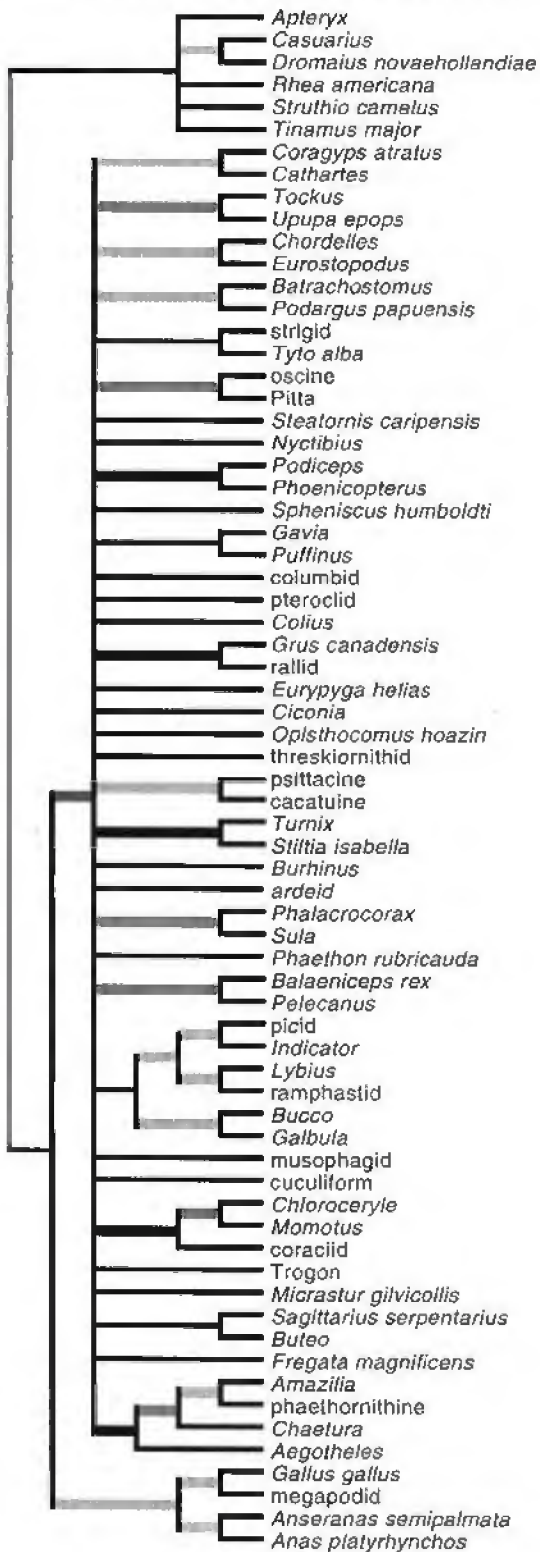


Figure 27.7. (A) A phylogenetic hypothesis for neoavian taxa using 1152 base pairs of the *RAG-2* exon. (B) A phylogenetic tree based on 1152 base pairs of the *RAG-2* exon and 166 morphological characters. Analyses are all unweighted parsimony. Thick branches have greater than 70% bootstrap support. Data from J. Cracraft, P. Schikler, J. Feinstein, P. Beresford, and G. J. Dyke (unpubl. obs.).

strong support from:

- combined data and both data sets
- combined data only
- combined data and one separate data set



iforms, passeriforms, caprimuliforms, and cuculiforms have been associated with one another in various classifications (e.g., Huxley 1867, Garrod 1874, Fürbringer 1888) and have been loosely called “higher land birds” (e.g., Olson 1985, Feduccia 1999, Johansson et al. 2001). Here we discuss the relationships within and among the coraciiform and piciform birds, their placement on the neornithine tree, and their relationships to the passeriforms.

Although the cuculiforms, coraciiforms, and piciforms have long been seen as “higher” neornithines and often closely related to passeriforms, this view was turned upside down by the DNA hybridization tree (Sibley and Ahlquist 1990), which postulated that all three groups were at the base of the neoavian tree (fig. 27.2). One of the two traditional groups of piciforms, Pici, was placed near the base of the neoavian tree adjacent to the turacids, whereas the other, the jacamars and puffbirds (Galbulae), was placed as the sister group to a monophyletic “Coraciae,” including traditional coraciiforms and trogons. The passeriforms were placed as the sister group to the entire waterbird assemblage but were not found to have any close relationship with either piciform or coraciiform taxa.

At present, none of these relationships can be confirmed or refuted. Available nuclear sequence data for RAG-1 (Groth and Barrowclough 1999) as well as the *c-myc* and RAG-2 data (figs. 27.4, 27.7) cannot resolve the base of Neoaves, indicating that the placement of these (or other) groups within neornithines remains an open question. Recent morphological and molecular studies, however, are identifying some well-supported clades within these groups. The two major clades of the piciforms, Pici and Galbulae, are each strongly monophyletic in all studies (see figs. 27.4, 27.7A,B, 27.8; Johansson et al. 2001), and evidence increasingly indicates that they are sister taxa. Some data, including RAG-2 (fig. 27.7A) and fragments of *c-myc* and RAG-1 (Johansson et al. 2001), cannot resolve this issue, but a monophyletic Piciformes is supported by morphology (Cracraft and Simpson 1981, Swierczewski and Raikow 1981, Raikow and Cracraft 1983, Mayr et al.

Figure 27.8. Phylogenetic hypothesis from combined *c-myc* and RAG-2 data for 69 taxa, analyzed by unweighted parsimony. Branches with bootstrap support greater than 50% are shown. Thick branches have greater than 70% bootstrap support. To maximize the taxon overlap between data sets, equivalent species were combined, and this is reflected in the name given to the terminal node; for example, *Gallus gallus* was sequenced for both genes, but two different species were sequenced from *Aegotheles*, and species were sequenced from two different genera of megapodes. Data from J. Harshman, M. J. Braun, and J. Cracraft (unpubl. obs.).

2003), longer *c-myc* sequences (fig. 27.4), *RAG-2* + morphology (fig. 27.7B), combined *c-myc/RAG-2* data (fig. 27.8), and by other nuclear sequences (Johansson and Ericson 2003). Within Pici, it is now clear that the barbets are paraphyletic and that some or all of the New World taxa are more closely related to toucans (Burton 1984, Sibley and Ahlquist 1990, Lanyon and Hall 1994, Prum 1988, Barker and Lanyon 2000, Moyle 2004) than to other barbets; interrelationships within the barbet and toucan clade still need additional work.

DNA hybridization data were interpreted as supporting a monophyletic coraciiforms (Sibley and Ahlquist 1990). Although recent DNA sequences are insufficient to test coraciiform monophyly, they do show support for groups of families traditionally placed within coraciiforms. There is now congruent support, for example, for the monophyly of (1) hornbills + hoopoes/woodhoopoes (figs. 27.4, 27.7A,B, 27.8; Johansson et al. 2001), (2) motmots + todies (Johansson et al. 2001), and (3) kingfishers + motmots (figs. 27.4A, 27.7B, 27.8; Johansson et al. 2001), and support for (4) the kingfisher/motmot clade with the rollers (figs. 27.4, 27.7B, 27.8; Johansson et al. 2001).

Although they are clearly monophyletic (Hughes and Baker 1999), the relationships of the cuckoos are very uncertain, with no clear pattern across different studies. The distinctive Hoatzin (*Opisthocomus hoazin*) has been variously placed with galliforms (Cracraft 1981), cuculiforms (Sibley and Ahlquist 1990, Mindell et al. 1997), or turacos (Hughes and Baker 1999), yet there is no firm support in the *c-myc* (fig. 27.4), mitochondrial and *PEPCK* data (fig. 27.5), or in those from *RAG-2* and morphology (fig. 27.7B; see also Livezey and Zusi 2001) for any of these hypotheses. A relationship to galliforms at least can be rejected: hoatzins are clearly members of Neoaves, not Galloanserae (figs. 27.4, 27.5, 27.7A,B, 27.8; see also Sorenson et al. 2003).

Trogon and mousebirds are each so unique morphologically that they have been placed in their own order, but both have been allied to coraciiform and/or piciform birds by many authors (for reviews, see Sibley and Ahlquist 1990, Espinosa de los Monteros 2000). In recent years trogons have generally been associated with various coraciiforms on the strength of stapes morphology (Feduccia 1975), myology (Maurer and Raikow 1981), and osteology (Livezey and Zusi 2001). Mousebird relationships have been more difficult to ascertain, and no clear picture has emerged. In the mitochondrial-*PEPCK* data mousebirds group with parrots (fig. 27.5), whereas the *RAG-2* gene is uninformative. The study of Espinosa de los Monteros (2000) linked mousebirds with trogons and then that clade with parrots. The problem is that all these groups are old, divergent taxa with relatively little intrataxon diversity. Much more data will be needed to resolve their relationships.

Phylogenetic Relationships within the Perching Birds (Passeriformes)

The perching birds, order Passeriformes, comprise almost 60% of the extant species of birds. The monophyly of pas-

seriforms has long been accepted and is strongly supported by a variety of studies, including those using morphological or molecular data (Feduccia 1974, 1975, Raikow 1982, 1987; see also figs. 27.4, 27.5, 27.7, 27.8). Our current understanding of their basal relationships and biogeographic distributions strongly suggests that the group is old, with an origin probably more than 79 million years ago, well before the Cretaceous–Tertiary extinction 65 million years ago (e.g., Paton et al. 2002) and on a late-stage Gondwana (Cracraft 2001, Barker et al. 2002, Ericson et al. 2002). Recent molecular work using nuclear genes (Barker et al. 2002, Ericson et al. 2002) supports the hypothesis that the New Zealand wrens (Acanthisittidae) are the sister group to the remainder of the passerines, and that the latter clade can be divided into two sister lineages, the suboscines (Tyranni) and the oscines (Passeri). Resolving relationships within the suboscines and oscines has been complex, not only because of the huge diversity (about 1200 and 4600 species, respectively) but also because many of the traditional families are neither monophyletic nor related as depicted in Sibley and Ahlquist's (1990) tree. Nuclear gene sequences, however, are beginning to clarify phylogenetic patterns within this large group. The results presented here summarize some ongoing studies of the passerines, primarily using two nuclear genes (*RAG-1* and *RAG-2*; F. K. Barker, J. F. Feinstein, P. Schikler, A. Cibois, and J. Cracraft, unpubl. obs.) with dense taxon sampling, and represent the most comprehensive analysis of passeriform relationships to date (4126 aligned positions for 146 taxa).

The DNA hybridization data were interpreted by Sibley and Ahlquist (1990) as showing a division between suboscine and oscine passerines with the New Zealand wrens being the sister group to the remaining suboscines. Within the oscines, there were two sister clades, Corvida, which consisted of all Australian endemics and groups related to crows (the so-called "corvine assemblage"), and Passerida for all remaining taxa. The phylogenetic hypothesis shown in figure 27.9A, which is based on nuclear gene data (F. K. Barker, J. F. Feinstein, P. Schikler, A. Cibois, and J. Cracraft, unpubl. obs.), depicts a substantially different view of passeriform history. Thus, although the subdivision into suboscines and oscines is corroborated, the New Zealand wrens are the sister group of all other passerines. In addition, numerous taxa of the Australian "corvidans" are complexly paraphyletic relative to the passeridans and a core "Corvoidea."

The suboscine taxon sample is small, but these nuclear data are able to resolve a number of the major clades with strong support (fig. 27.9B). New World and Old World clades are sister groups (Irestedt et al. 2001, Barker et al. 2002). Within the Old World group, the data strongly support the pittas as being the sister group of the paraphyletic broadbills and the Malagasy asities (see also Prum 1993). The New World suboscines are divisible into two large clades. The first includes nearly 550 species of New World flycatchers, manakins, and cotingas; although this clade is strongly sup-

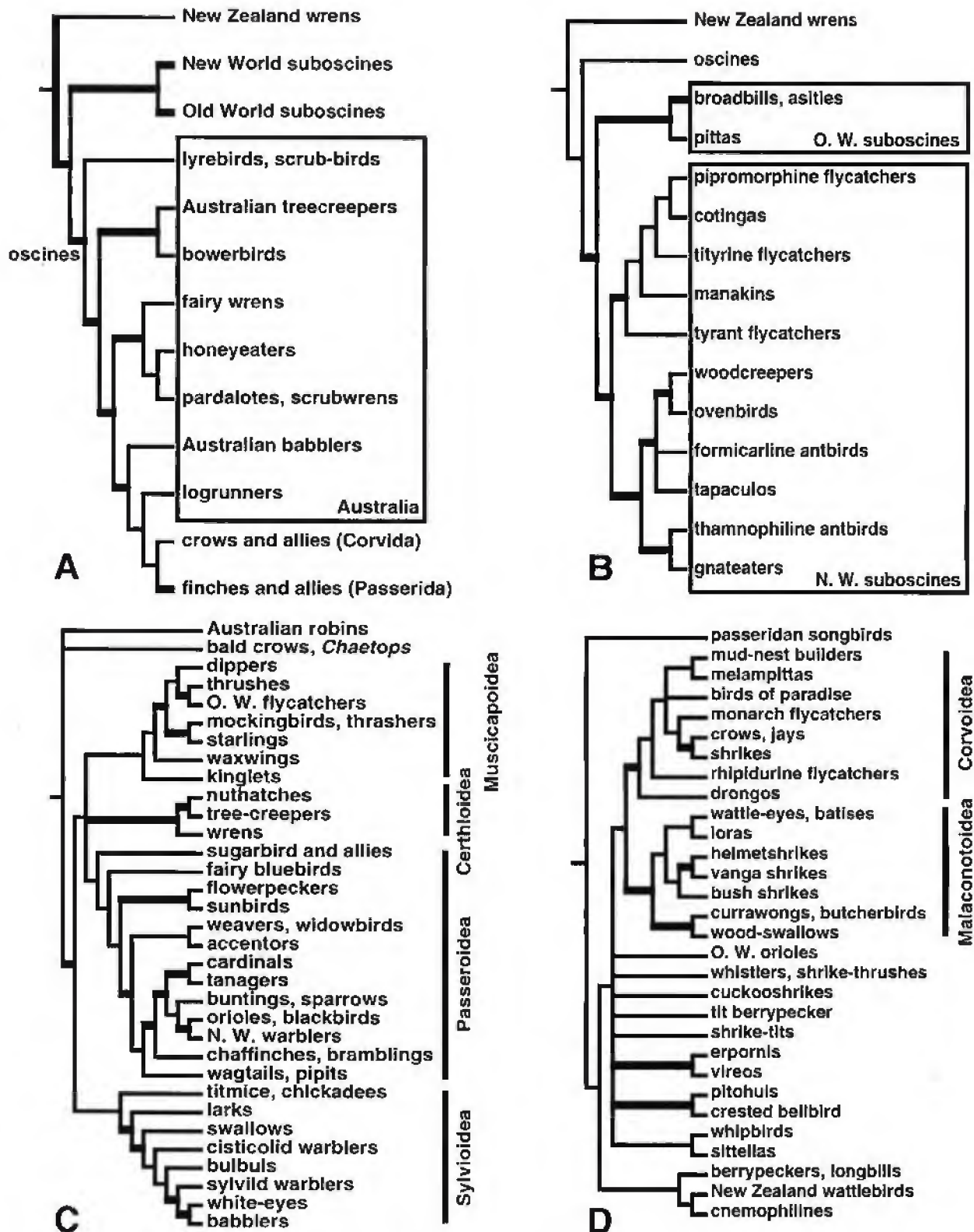


Figure 27.9. Phylogenetic analyses from an analysis of 146 passeriform taxa for 4126 base pairs of RAG-1 and RAG-2 exons using maximum parsimony. (A) Relationships among the basal lineages. (B) Relationships among the suboscine passeriforms. (C) Relationships among the passeridan songbirds. (D) Relationships among the basal oscines and corvidan songbirds. Data from F. K. Barker, J. F. Feinstein, P. Schikler, A. Cibois, and J. Cracraft (unpubl. obs.).

ported, relationships within the group are still uncertain (see also Johansson et al. 2002). The remaining 560 species of New World suboscines are split into the thamnophiline antbirds and their sister clade, the formicarinine antbirds and the ovenbirds and woodcreepers. The most thorough study of New World suboscine relationships to date is that of Irestedt et al. (2002), which examined more than 3000 base pairs of nuclear and mitochondrial sequences for 32 ingroup taxa of woodcreepers, ovenbirds, and antbirds; our results are congruent with those reported in their study.

As noted, the oscines, or songbirds, have been subdivided into two large assemblages, the Corvida and Passerida, based on inferences from DNA hybridization. This simple partition has been shown to be incorrect (Barker et al. 2002, Ericson et al. 2002), but we are now able to tell a much more interesting story because of a larger taxon sample. No fewer than five distinctive Australian "corvidan" clades are sequential sister groups to the core corvid and passeridan clades (Barker et al. 2002; see also F. K. Barker, J. F. Feinstein, P. Schikler, A. Cibois, and J. Cracraft, unpubl. obs.): the lyrebirds (Menuridae), the bowerbirds and Australian treecreepers (Ptilonorhynchoidea), the diverse meliphagoid assemblage, the pomotostomine babbler, and the orthonychid logrunners (fig. 27.9A). This phylogenetic pattern firmly anchors the origin of the oscines in East Gondwana.

But the story of corvidan paraphyly is not yet exhausted. The passeridan clade has three basal clades (fig. 27.9C), one of which is the Australian robins (Eopsaltridae), included by DNA hybridization data within the corvidans. A second clade is the peculiar African genus *Picathartes*, the bald crows or rock-fowl, also placed toward the base of the passerines by hybridization data (see Sibley and Ahlquist 1990: 625–626), and its sister taxon, the rock-jumpers (*Chaetops*). Finally, there are the core passeridans (Ericson et al. 2000, Barker et al. 2002; see also F. K. Barker, J. F. Feinstein, P. Schikler, A. Cibois, and J. Cracraft, unpubl. obs.). It is not clear from the available data whether the *Picathartes* + *Chaetops* clade or the eopsaltrids is the sister group of the core passeridans, although present data suggest the robins are more closely related.

The basal relationships of the core passeridans are still unclear. There are four moderately well-defined clades within the group (fig. 27.9C; see also Ericson and Johansson 2003). The first, Sylvioidea, includes groups such as the titmice and chickadees, larks, bulbuls, Old World warblers, white-eyes, babbler, and swallows. The second, here termed Certhioidea, consists of the wrens, nuthatches, and treecreepers. The third is a very large group, Passeroidea, that includes various Old World taxa basally—the fairy bluebirds, sunbirds, flowerpeckers, sparrows, wagtails, and pipits—and the huge (almost 1000 species) so-called nine-primaried oscine assemblage (Fringillidae of Monroe and Sibley 1993), most of which are New World (Emberizinae: buntings, wood warblers, tanagers, cardinals, and the orioles and blackbirds; for recent discussions of relationships, see Groth 1998, Klicka et al.

2000, Lovette and Bermingham 2002, Yuri and Mindell 2002). The last group of core passeridans is Muscicapoidea, which encompasses the kinglets, waxwings, starlings, thrashers and mockingbirds, and the large thrush and Old World flycatcher clade of some 450 species.

With the elimination of the early "corvidan" clades discussed above (fig. 27.9A), the remainder of Sibley and Ahlquist's "Corvida" do appear to form a monophyletic assemblage, although it is not well supported at this time, and we restrict the name "Corvida" to this clade (fig. 27.9D). Although relationships among family-level taxa within this complex cannot be completely resolved with *RAG-1* and *RAG-2* sequences, these data do identify several well-defined clades, and they partition relationships more satisfactorily than previous work.

Two of the corvidan clades are well supported. The first we term here Corvoidea, which include the crows and jays (Corvidae) and their sister group, the true shrikes (Laniidae), the monarch and rhipidurine flycatchers, drongos, mud-nest builders (Struthidea, *Corcorax*), the two species of *Melampitta*, and the birds of paradise (Paradisaeidae). The second well-supported lineage of the corvidans we term Malaconotoidea. This "shrike-like" assemblage is comprised of the African bush-shrikes (Malaconotidae), the helmet shrikes (*Prionops*), *Batis*, the Asian ioras (Aegithinidae), and the vanga shrikes (Vangidae) of Madagascar. Also included in this clade are the woodswallows (Artamidae) and their sister group the Australian magpies and currawongs (Cracticidae).

All other corvidans appear to be basal to the corvids and malaconotoids but are, on present evidence, unresolved relative to these two clades. Most of these groups, including the pachycephalids, oriolids, campephagids, daphoenosittids, falcunculids, and other assorted genera are mostly Australasian in distribution, and presumably in origin. Also included in this melange are the vireos and their Asian sister group, *Erpornis zantholeuca*.

Outside of all these corvidan groups is a clade comprising some ancient corvidans that appear to be related: the New Zealand wattlebirds (Callaeatidae), the cnemophilines (formally placed in the birds of paradise), and the berrypeckers (Melanocharitidae). The basal position of these groups relative to the remaining Corvida provides persuasive evidence that the group as a whole had its origin in Australia (and perhaps adjacent Antarctica), further tying the origins of the oscine radiation to this landmass.

Discussion

Where We Are

To judge from the large numbers of papers reviewed above, research on the higher level relationships of birds has made significant progress over the last decade, yet it is obvious from the results of these studies that compelling evidence for re-

relationships among most major clades of Neoaves is still lacking. Nevertheless, a function of this chapter is to serve as a benchmark of our current understanding of avian relationships, and one way expressing this progress is to propose a summary hypothesis that attempts to reflect the improvements in our knowledge of avian relationships, even though the underlying evidence may be imperfect. Different investigators, including the authors of this chapter, will disagree about what constitutes sufficient evidence for supporting the monophyly of a clade, and most would no doubt prefer to see a tree that is based on all avian higher taxa and a very large data set of molecular and morphological characters numbering in the tens of thousands. That ideal is 5–10 years away, however, yet it is still useful to examine how far have we come over the last decade.

Figure 27.10 depicts a summary phylogenetic hypothesis for the avian higher taxa. It represents an estimate of avian history at this point in time and is admittedly speculative in a number of places that we note below; it represents, moreover, a compromise among the authors. We therefore have no illusions that all of these relationships will stand the test of time and evidence, but a number will. The thick lines are meant to identify clades in which relatively strong evidence for their monophyly has been discovered in one or more individual studies. The thin lines depict clades that have been recovered in various studies, even though the evidence for these individual hypotheses may be weak. Congruence across studies suggests that with more data, many of these clades will gain increased support.

As already noted, the base of the neornithine tree is no longer particularly controversial, with palaeognaths and then Galloanserae being successive sister groups to Neoaves. Relationships within ratites are unsettled, however, because of conflict among the molecular data and with the morphological evidence.

Neoavian relationships, on the other hand, are decidedly uncertain, although new information becomes available with each new study. The base of the neoavian tree is a complete unknown, but within Neoaves evidence for relationships among a number of major groups is emerging. There is a suggestion that many of the traditional “waterbird” groups are related, although a monophyletic assemblage that includes all “waterbird” taxa itself is unlikely. Thus, some “waterbird” taxa are definitely related, others probably so, but other nonwaterbird taxa will almost certainly be found to be embedded within waterbirds. It now seems clear that some traditional groups such as Pelecaniformes and Ciconiiformes are not monophyletic, but many of their constituent taxa are related. Thus there is now evidence for a shoebill + pelican + hammerkop clade and for an anhinga + cormorant + gannet + (more marginally) frigatebird clade, and these two clades are probably related to each other, along with ibises, herons, and storks. Tropicbirds (phaethontids) are a real puzzle as this old, long-branch taxon is quite unstable on all trees.

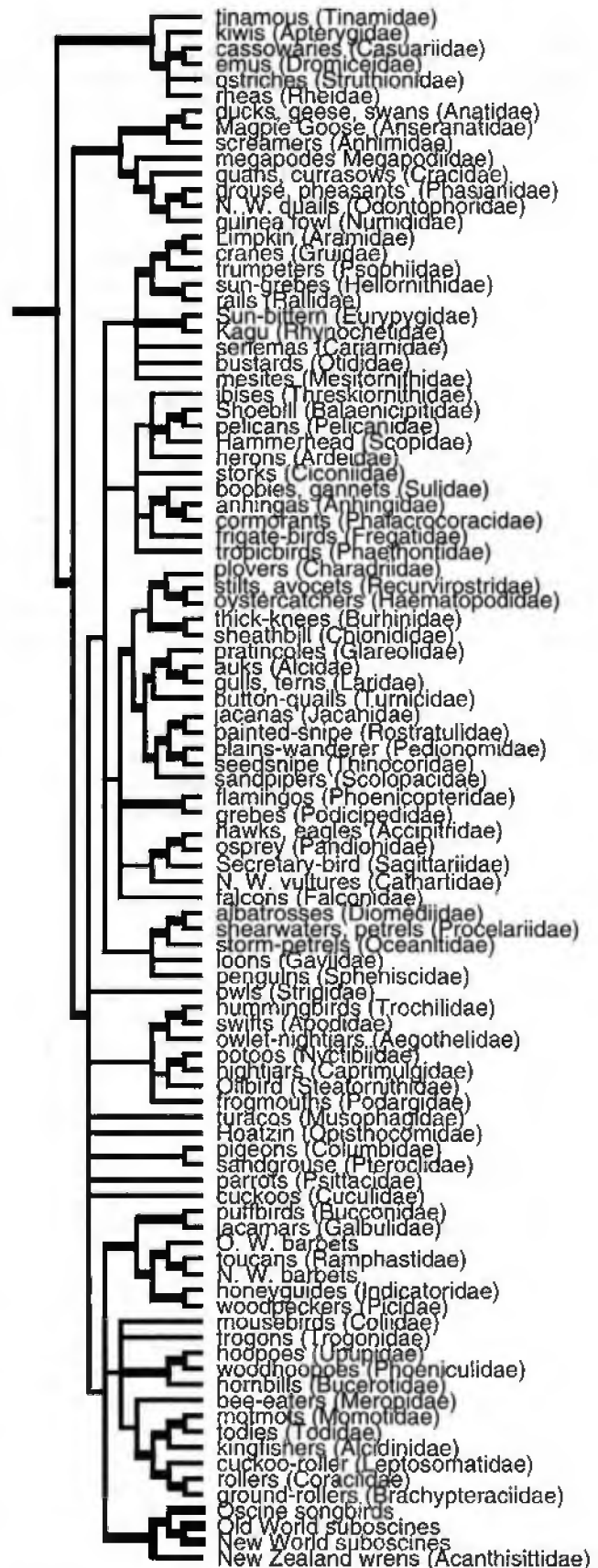


Figure 27.10. Summary hypothesis for avian higher level relationships (see discussion in text).

There is a core group of gruiform taxa with well supported relationships, including rails + sungebes, on the one hand, and cranes + limpkins + trumpeters, on the other. Moreover, the kagu and sunbittern are strongly supported sister taxa. Aside from some morphological character data (e.g., Livezey 1998), there is little current evidence to support monophyly of traditional Gruiformes. This is an old group, with basal divergences almost certainly in the Cretaceous (Cracraft 2001) that cannot be resolved given the character data currently available; yet, there is no firm evidence that any of these groups is related to a nongruiform taxon, so we retain the traditional order.

Ongoing work in various labs is confirming the monophyly of the charadriiforms, including the buttonquails, often placed in gruiforms. Current sequence data (Paton et al. 2003) indicate the relationships shown in figure 27.10. There is also a suggestion in the molecular data presented earlier that charadriiforms are associated with flamingos + grebes, and possibly with some or all of the falconiforms. The latter group consists of three well defined clades (falcons, cathartids, and accipitrids + osprey + secretary bird), but whether these are related to each other is still uncertain. Morphology indicates that they are, but molecular data cannot yet confirm or deny this.

Relationships among the "higher land birds" remain controversial in many cases. Swifts, hummingbirds, and owl-nightjars are monophyletic but their relationships to other taxa traditionally called caprimulgiforms are unsupported; as with gruiforms, we have no clear evidence that any of them are more closely related to other taxa, and so we retain the group. Whether owls cluster with these families is also uncertain. Again, all of these taxa are very old groups and resolution of their relationships will require more data.

The three "orders" Piciformes, Coraciiformes, and Passeriformes may or may not be related to one another, but in many studies subgroups of them are clustered together. More and more data sets are showing a monophyletic piciforms. Passeriforms are strongly monophyletic, and relationships among their basal clades are becoming well understood (see discussion above). Finally, the traditional coraciiforms group into two clades whose relationships to each other are neither supported nor refuted by our data. The relationships of mousebirds and trogons are also still obscure.

In contrast to many of the above groups, there are some highly distinctive taxa such as turacos, parrots, pigeons, the hoatzin, and cuckoos that have been notoriously difficult to associate with other groups using both molecular and morphological data. Deciphering their relationships will require larger amounts of data than are currently available.

Despite the appearance of substantial structure, the hypothesis of figure 27.10 could be interpreted pessimistically by examination of those clades subtended by thin branches—indicating insufficient support—versus those with thick-branched clades we judge to be either moderately or strongly supported. Seen in this way, the tree is mostly a polytomy

and suggests we know very little about avian relationships. Viewed more optimistically, however, the tree is a working hypothesis that suggests progress is being made. Critically, this representation of our state of knowledge contradicts the false notion that the broad picture of avian phylogenetics has been drawn, and only the details remain to be filled (e.g., Mooers and Cotgreave 1994). Given the state of current activity in many laboratories around the world, we predict that in little more than five years a similar figure, whatever its configuration, will have a substantially larger proportion of well-supported clades.

The Future

These are exciting and productive times for avian systematists. We are witnessing the growth of molecular databases, containing sequences from homologous genes across most avian taxa. As recently as 10 years ago the availability of such comprehensive, comparative, discrete character data sets was little more than a dream. Within the next several years large data sets for both molecular and morphological data will be published that span all the major clades of nonpasseriform birds. At the same time, avian systematics is becoming increasingly collaborative with groups of researchers pooling resources and publishing together. These collaborations involve both molecular and morphological data and extend back across time through the incorporation of fossils.

All of these data will soon be publicly available on the Internet as a result of these collaborations, and these data should greatly accelerate avian systematic research. Discrete-character data sets lend themselves to continual growth and addition in a manner entirely absent from the early comprehensive work based on DNA hybridization distances (Sibley and Ahlquist 1990). These data sets will variously confirm, challenge, or overturn earlier hypotheses of avian phylogeny, and this may be expected to continue as both character and taxon sampling increase. We view the continued collection of comparative data as imperative not just for avian systematics, but for elaborating the insight into evolutionary history and processes at multiple hierarchical levels that only phylogeny can provide.

The Challenge

Just how difficult will it be to build a comprehensive avian Tree of Life (ATOL)? Several observations suggest it will be extremely so. First, there are about 20,000 nodes on the extant avian Tree of Life. Fossil taxa only add to that number. Then, there is the challenge presented by the history of birds itself. It is now evident that there have been many episodes of rapid radiation across the neoavian tree, perhaps involving thousands of nodes, and resolving these will require unprecedented access to specimen material (including anatomical preparations and fresh tissues) as well as large character sampling to establish relationships. Gone are the

days when a single person or laboratory might hope to solve the problem of avian relationships. The problem is too difficult and complex for single laboratories in which time and money are limited. The scientific challenge presented by the avian Tree of Life will call for large taxon and character sampling, goals best achieved by a communitywide effort.

There are also conceptual roadblocks. One is the problem of uncertain knowledge. More taxa and characters may not guarantee a "satisfying" answer, by which we mean having resolution of nodes with sufficiently strong branch support that additional data will merely confirm what has already been found. The issue is that more taxa guarantee (some) uncertainty. More taxa are good, of course, but they also means more character data will likely be required to attain strong support for any particular node. Measuring phylogenetic understanding on very large trees such as the avian Tree of Life will also be a complex challenge. Measures of support are ambiguous in their own right, and whatever answer we get depends on the taxon and character sampling—that is, on the available data. Thus, what are the boundaries of a study? How will we know when to stop (because it has been determined we "know" relationships) and move on to an unresolved part of the tree? This is a nontrivial problem, but as we erect a scaffold that identifies strongly supported monophyletic groups, perhaps that will make it easier to circumscribe studies and resolve the tree more finely.

Another conceptual roadblock is the problem of investigator tenacity. It should be straightforward to build the scaffold of the avian Tree of Life. Systematists are doing that now. There will be—and already are—lots of trees that are moderately resolved but still have little satisfactory branch support (remember that the DNA hybridization tree was nearly "fully" resolved). So how much do we, the investigators, really want to know relationships? If the object is to publish more papers, then as more and more taxa are added, and if character sampling does not also increase, more and more nodes are likely to be supported rather poorly, especially across those parts of the tree representing rapid radiations (short internodes). Resolving these nodes with some measure of confidence will require substantial amounts of data (much more than is currently collected in typical studies). In the near future, this may not be an issue as technical innovations allow systematists to gather more data more rapidly. However, many investigators will not necessarily have easy access to these technologies, and it is already becoming apparent that being able to collect large volumes of data (genomes) does not necessarily mean that the data themselves are going to be phylogenetically useful for the problem at hand.

Although many phylogenetic problems in birds, at all taxonomic levels, will be quite difficult to resolve, we must be resolute. Resolving relationships is crucial for answering numerous questions in evolutionary biology, and to the extent that these questions are worth pursuing we should not settle for not knowing phylogeny. One result emerging from

the studies discussed here illustrates this point. Evidence now indicates owllet-nightjars are the sister group of swifts and hummingbirds. Depending on the sister group of this clade, it implies either that adaptation to nocturnal lifestyle arose multiple times in aegothelids and other birds, or that nocturnal habits are primitive and swifts and hummingbirds are secondarily diurnal. Phylogeny thus provides important insight into understanding avian diversification.

Finally, our perspectives on avian evolution will not be—should not be—built on one kind of data. Tree topologies should reflect the most comprehensive description of character evolution over time, which means that all forms of character information—genetic, morphological, behavioral, and so forth—should be incorporated into analyses. They may not only contribute to phylogenetic resolution in their own right, but will give us a richer picture of the history of avian evolution.

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