# PARALLEL RADIATIONS IN THE PRIMARY CLADES OF BIRDS

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*Abstract.*—Knowledge of avian phylogeny is prerequisite to understanding the circumstances and timing of the diversification of birds and the evolution of morphological, behavioral, and life-history traits. Recent molecular datasets have helped to elucidate the three most basal clades in the tree of living birds, but relationships among neoavian orders (the vast majority of birds) remain frustratingly vexing. Here, we examine intron 7 of the β-fibrinogen gene in the most taxonomically inclusive survey of DNA sequences of nonpasserine bird families and orders to date. These data suggest that Neoaves consist of two sister clades with ecological parallelisms comparable to those found between marsupial and placental mammals. Some members of the putative respective clades have long been recognized as examples of convergent evolution, but it was not appreciated that they might be parts of diverse parallel radiations. In contrast, some traditional orders of birds are suggested by these data to be polyphyletic, with representative families in both radiations.

*Key words.*—β-fibrinogen, convergence, Coronaves, Metaves, Neoaves, parallelism, systematics.

Convergence, parallelism, and reversal, all forms of homoplasy, abound in biological evolution, providing some of the most striking evidence for Darwin's theory of natural selection: "For animals, belonging to two most distinct lines of descent, may readily become adapted to similar conditions, and thus assume a close external resemblance" (Darwin 1859, p. 427). Textbook examples include reduced leaf morphologies and succulence in desert-dwelling cacti and euphorbs; gall-forming and leaf-mining in hymenopteran, lepidopteran, dipteran, and coleopteran insects; and the independent evolution of a wide variety of strikingly similar ecological strategies and morphologies in Australian marsupials and placental mammals, including burrowing, gliding, myrmecophagy, carnivory, and grazing (e.g., Springer et al. 1997; Futuyma 1998). We expect that distantly related lineages widely separated by geography may evolve along parallel lines, independently adapting to similar ecological roles with similar solutions in behavior and morphology: "That phenomenon of convergent evolution is specially striking in the cases of parallel continental adaptive radiation" (Simpson 1953, p. 20). Inasmuch as the higher taxa of birds and mammals are hypothesized to have evolved over the same approximate timeframe (late Cretaceous–early Tertiary; Hedges et al. 1996; Cooper and Penny 1997) and thus should have been subject to similar biogeographical constraints, we might predict some similarity in patterns of evolutionary diversification and convergent adaptive radiation. While hypotheses of convergence have been postulated for isolated avian lineages, it is interesting that no broad patterns of continental convergent evolution have been documented at superordinal levels in birds.

In many cases, convergent similarities are readily recognized by comparison with the distribution of other morphological, life-history, behavioral, biogeographic, and molecular features. However, Eisenberg emphasized "repeated trends towards convergent niche occupancy," particularly among eutherians, and particularly with respect to feeding specializations: "Adaptation for different strategies has profound consequences in terms of social organization, home

range size, and population density" (Eisenberg 1981, p. 210). So, at times independent derivation is not readily recognizable, and the interpretation of the character as consistent with derivation from a common ancestor (i.e., homology) or as independently attained (through whatever form of homoplasy), rests critically on an underlying phylogenetic hypothesis. In birds, various questions in evolutionary biology have been addressed in the context of phylogeny ranging from the evolution of genome size and hypothesized correlation with metabolic rate (Waltari and Edwards 2002) to the evolution of developmental life-history strategies (altricial-precocial spectrum; Starck and Ricklefs 1998). Such studies have come to rely primarily on the comprehensive phylogeny of Sibley and Ahlquist (1990) based on DNA × DNA hybridization, despite concerns of its methodological limitations and experimental shortcomings. Independent assessments of this phylogeny would be welcomed.

We present molecular evidence for a radically new perspective of avian relationships. Currently, living birds (Neornithes) are divisible into the monophyletic superorders Palaeognathae and Neognathae. Palaeognathae include tinamous and the large flightless ratites. Neognathae include all others. Fowl and waterfowl (Galloanserae) represent the earliest divergence among neognaths. The ease with which these relations have been independently verified by a variety of genetic loci and methods (e.g., Sibley and Ahlquist 1990; Groth and Barrowclough 1999; van Tuinen et al. 2000; Zusi and Livezey 2000; Cracraft 2001; Sorenson et al. 2003; Chubb 2004) suggests protracted divergences among their members. Superordinal relationships among the remaining monophyletic clade, Neoaves, are virtually unknown (Cracraft and Clarke 2001; Sorenson et al. 2003). The few relationships that have been suggested generally have been between potential paired sister taxa rather than large groups of taxa. The difficulty of teasing apart basal clades within Neoaves suggests an explosive radiation, perhaps in the earliest Cenozoic where their fossil record reliably begins (Bleiweiss 1998; Groth and Barrowclough 1999; Feduccia 2003; Poe and Chubb 2004). Explosive radiations present special
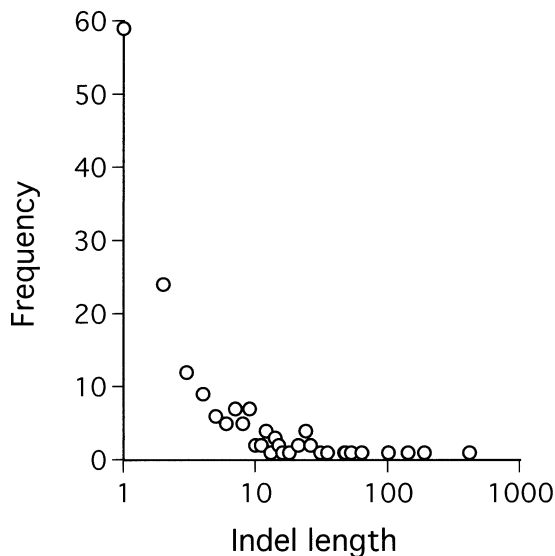
difficulties in phylogeny reconstruction because short inter-nodes are documented by relatively few synapomorphies. Ancient explosive radiations are even more troublesome because phylogenetic signal may be overwritten along long branches emanating from short internodes.

Intron 7 of the nuclear encoded β-fibrinogen gene (FGB-int7) has been used successfully in investigations of avian phylogeny at the familial and ordinal levels (Prychitko and Moore 1997, 2003; Johnson and Clayton 2000; Pereira et al. 2002). A number of desirable properties suggests this locus is appropriate for inferring higher level avian taxonomy. Rates of nucleotide substitution are low relative to commonly used mitochondrial genes and less variant across sites, so saturation (i.e., multiple substitutions at a single position potentially obscuring phylogenetic signal) should be less problematic. Substitutions are also relatively more homogeneous among character states, again resulting in reduced homoplasy compared to genes with highly biased base composition (Prychitko and Moore 1997).

A particularly striking feature of FGB-int7 evolution is the occurrence of numerous insertions and deletions (collectively "indels"). Invoking gaps is necessary to achieve homologous alignment of primary length-variable sequences. This practice produces primary hypotheses of nucleotide- and gap-positional homology that are subsequently tested by phylogenetic analysis (Phillips et al. 2000; Simmons 2004). Despite the fact that there is an element of informed subjectivity in the selection of alignment parameters (e.g., gap penalties), numerous studies have suggested nevertheless that inference of homology of indel characters may be less ambiguous than assessing correspondence of individual nucleotides (nts) in regions of sequence length variation because indel characters exist in a greater character state space (by length and position), where the frequency of any particular state is inversely proportional to its length (Fig. 1; Lloyd and Calder 1991; Lutzoni et al. 2000; Simmons et al. 2001). The ease with which homology of indels is recognized depends on the rates at which indels occur, the distribution of their sizes, and the rates of nucleotide evolution in the flanking sequences, with the homology of singleton gaps generally less certain than that of long gaps.

Indel characters may complement nucleotide substitutions in phylogenetic reconstruction because of differences in such properties as evolutionary rate and mutational mechanisms (Johnson 2004). Hence, corroboration of otherwise well-supported nodes in a nucleotide tree by multiple large indels lends considerable additional confidence in the phylogenetic hypothesis. Indeed, indel data may be a boon for resolving the topology of early explosive radiations, and such characters are cited as the most compelling evidence for the monophyly of Galloanserae (Groth and Barrowclough 1999; Ericson et al. 2001), Apodiformes (Johansson et al. 2001), seven superfamilial avian clades in a study of *c-myc* oncogene intron and 3′ untranslated region sequence (3′-UTR; Cracraft et al. 2004), an unspecified number of mammalian clades in four noncoding nuclear 3′-UTRs (Murphy et al. 2001), and Afrotherian mammals in a study of breast and ovarian cancer susceptibility gene 1 (BRCA1; Madsen et al. 2001).

While in the process of using FGB-int7 to address the relationships within the order Gruiformes, we were struck that it exhibits fairly high occurrences of indels of potential superordinal phylogenetic informativeness. Prychitko and Moore (2003) and Johnson (2004) independently arrived at a similar conclusion based on a small sample of avian orders coincident with our study. As it became increasingly suspect that our focal taxon is polyphyletic, we were compelled to significantly bolster the number of outgroups examined. Ultimately, we analyzed FGB-int7 sequences of 147 species including representatives of 73 of the 88 Neoavian nonpasserine families (plus eight outgroup and six passerine families, 87 families total) making this the most taxonomically comprehensive survey of nuclear DNA sequences of nonpasserine families to date.

## METHODS

Sequences were downloaded from GenBank (accession numbers AF182648, AF182653, AF182672, AF394330, AY082398, AY082400–AY082410, AY082414–AY082416, AY082418–AY082420, AY082422–AY082425, AY140701–AY140703, AY140711) or amplified from genomic DNA (deposited under accession numbers AY695132–AY695255) using flanking exon primers FIB-BI7U and FIB-BI7L (Prychitko and Moore 1997) and new primer FBE8L2 in exon 8: 5′-TTC TTT GGA GCA CTG TTT TCT TGG ATC-3′. Polymerase chain reaction conditions were as follows: 35 cycles, 94°C denature, 55°C anneal, 72°C extension, 1 min each step. Amplicons were purified by agarose gel electrophoresis and QIA-quick gel extraction kit (Qiagen, Inc., Valencia, CA) according to manufacturer's instructions. Cycle sequencing was performed using the above primers in addition to new internal primers FIBBI7U2: 5′-ATA TGT TTT ATC CCT GCA-3′, and FIBBI7L2: 5′-TAA GCA AAC AGA TCA AC-3′, according to manufacturer's instructions using BigDye v3.1 and read on an ABI 3100 DNA sequencer (Applied Biosystems, Foster City, CA).

Sequences were initially aligned using Se-Al v2.0a11 (Rambaut 1996), and alignment was unambiguous for most

taxa and regions (see supplementary material available online at http: dx.doi.org/10.1554/04-235.1.s1). Furthermore, both authors independently aligned all sequences, and the resulting alignments contained only minor differences that did not affect results of subsequent analyses. Alignments were independently performed using ClustalX (Thompson et al. 1997) and Dialign2 (Morgenstern et al. 1998; Morgenstern 1999) under a variety of gap opening (10–20) and extension (1–10) penalties, and the resulting alignments subjected to parsimony analysis to test the robustness of the main conclusion of this study with respect to alternative alignments. Alignments were also checked for consistency with others published for the same locus (Johnson and Clayton 2000; Pereira et al. 2002; Prychitko and Moore 2003).

Coterminous gaps (i.e., those having identical 5′ and 3′ ends in the alignment) were scored as binary characters by the principle of simple indel coding (Simmons and Ochoterena 2000). Overlapping or nested gaps were scored as missing data. The consistency of indel characters was analyzed both by mapping the characters onto trees obtained from nucleotide characters alone (i.e., treating all gaps as missing data) and by combined analysis of the binary indel character matrix with the nucleotide characters.

Indel characters and some nucleotide data were removed for various analyses. Excluded nucleotide data subsets include: (1) 75 nts in three clusters (i.e., aligned positions 124–139, 1157–1171, and 1877–1917) that appear to represent regions of mononucleotide repeats that had been subject to excessive replication slippage and could not be aligned with confidence for some taxa; (2) approximately 300 nts of raw parrot sequence (i.e., aligned positions 1113–1612) that could not be unambiguously aligned to other birds; and (3) flanking sequences and regions corresponding to four putatively synapomorphic indels of the two primary clades of Neoaves (i.e., aligned positions 124–128, 145–159, 673–693, and 1710–1713). Data subset 3 was removed specifically to address the robustness of the major conclusion of this study in the absence of possible key regions of sequence and indels. All reported results exclude data subsets 1 and 2 and include data subset 3 unless specifically stated otherwise.

Phylogenetic analyses were conducted by equally weighted maximum parsimony (MP), with and without indel characters, using PAUP* 4.0b10 (Swofford 2002) and WinClada 1.00.08 in combination with NONA 2.0 (Goloboff 1999; Nixon 2002). Weighting was considered unnecessary because of the molecular evolutionary properties of this locus mentioned above and because our analyses show no saturation across the entire dataset, including outgroups. For comparison, maximum likelihood (ML) analyses were performed using PHYML 2.1 (Guindon and Gascuel 2003) and neighbor-joining (NJ) using PAUP* 4.0b10. Current model-based phylogenetic methods do not account for insertion-deletion processes, so all gaps in the alignment are treated as missing data. However, these methods may still provide useful comparison to the extent that the missing data does not affect additivity of branch lengths. The best fitting model of evolution for the ML and NJ analyses was chosen by hierarchical likelihood-ratio tests implemented in ModelTest 3.0.6 (Posada and Crandall 1998). Statistical support for the resulting phylogenies was assessed by bootstrapping with either 1000

(MP, NJ) or 500 (ML) replicates (Felsenstein 1985). Posterior probabilities for nodes were calculated using MrBayes (Huelsenbeck and Ronquist 2001) over 1 million Markov generations, running four independent chains and omitting the first 150,000 generations for burn-in after likelihoods had obviously reached stationarity. As a further test of the robustness of the internodes leading to the major lineages, we performed a likelihood-ratio test of branch lengths to determine whether branches were significantly different from zero-length, a procedure recently advocated by Poe and Chubb (2004) in assessing whether short internodes may be indicative of hard polytomies.

## RESULTS

### *Molecular Characterization*

FGB-int7 exhibits a median sequence length of 903 nts (SD = 97.4, range = 308–1158 nts), or 750 to 1000 nts for 90% of all species. Aligned sequence length is 1930 nts (866 parsimony informative [PI] nucleotide sites). This alignment results in an additional 156 coterminous PI indels ranging from 1 to 415 nts in length. Aligned sequence length is 1254 nts when all insertions uniquely derived (autapomorphous) at taxonomic levels of family or lower are omitted. Autapomorphous characters were not excluded from the analysis but they are uninformative and therefore have no effect on the phylogenetic analysis.

Average base composition of FGB-int7 is enriched somewhat in adenine (A) and thymine (T) (64% AT), consistent with previous studies (Prychitko and Moore 1997, 2003; Johnson and Clayton 2000). Frequencies of A and T are approximately equal, as are frequencies of guanine (G) and cytosine (C). A chi-square test using PAUP* shows no significant difference in base composition of nucleotide-variable sites of the taxa sampled. A plot of corrected transition and transversion distances against total distance reveals no asymptotic leveling of either substitution type, even in the pairwise ingroup-outgroup comparisons (data not shown). Prychitko and Moore (2003) reported a slight decline in transition/transversion (ti/tv) ratios with increasing genetic distance. This difference likely can be attributed to differences in taxon sampling or differences in the method of assessing saturation or both. Regardless, their estimate of the instantaneous ti/tv ratio of 1.59 differs little from our ML estimate of 1.8.

### *Phylogeny*

Figure 2 summarizes the results of the phylogenetic analyses. This topology is a strict consensus of 262 most parsimonious trees based on the nucleotide sequence data alone, but bootstrap support shown includes indel characters. The ensemble consistency index (CI) = 0.37 and retention index (RI) = 0.59 for the nucleotide dataset. The indel data strongly support the phylogenetic reconstruction based on nucleotide sequence with remarkably little homoplasy; far less homoplasy than the nucleotide characters themselves. Indel characters plotted onto the nucleotide tree yield an ensemble CI = 0.7 and RI = 0.87, similar to that found by Johnson (2004). Of the 156 PI indels, 106 uniquely identified the same mono-

phyletic clades as the nucleotide analysis at all taxonomic levels from the genus to subclass (CI = 1.0). Most of these are traditionally recognized taxa. Multiple independent indel events document the monophyly of individual clades in some cases, with most or all members consistently sharing the same indels. The CI of indels as a function of length is shown in Figure 3. Indel consistency is positively related to indel length, and large indels (≥24 nts) exhibit universally perfect consistency with the nucleotide tree.

There is broad congruence between the FGB-int7 phylogeny and gene trees of other loci both at shallow and deep levels of divergence, suggesting that this locus is phylogenetically informative at a wide range of taxonomic levels. Our results at the deepest level of bird phylogeny are perfectly congruent with all other datasets that have been deemed appropriate for addressing higher-level issues in avian systematics. The basal clade of neognathous birds, Galloanserae, is supported as monophyletic by 100% of MP and ML bootstrap replicates, 100% Bayesian posterior probability, and eight synapomorphic indels. The next branch on the avian tree, Neoaves, is supported by 81% bootstrap and 83% Bayesian posterior probability (nucleotide characters only), and three indels and 89% bootstrap with indels included. These results document that the FGB-int7 locus and indels are phylogenetically informative at deep levels of divergence in birds.

Our results at shallow levels of bird phylogeny also agree in many respects with previous studies. For example, the phylogeny of Charadriiformes, including the supposed ''gruiform'' hemipodes and paraphyly of plovers, is perfectly congruent with results from sequences of the recombination activating gene (RAG-1) and intron 2 of myoglobin (Ericson et al. 2003a; Paton et al. 2003). A core of Gruiformes is monophyletic, as is a core of Falconiformes and a core of Pelecaniformes, although the namesake falcons and pelicans are not resolved within them. The monophyly of pelicans, shoebill, and hammerkop is congruent with results from molecular and morphological data (van Tuinen et al. 2001; Mayr 2003), as is the sister relationship of hornbills and trogons (Mayr et al. 2003). The congruence of these results to those of other studies both above and below Neoaves adds to our confidence in the phylogenetic signal of FGB-int7.

Within Neoaves, the first dichotomous branch defines two large monophyletic clades, each comprised of ostensibly unrelated orders. One of these we herein define as the cohort ''Metaves'' (meaning ''between- or near-birds'') and the other ''Coronaves'' (''crown-birds''). MP and ML bootstrap values support the monophyly of Metaves at 73% and 58% and Coronaves at 58% and 62% when analyzed using only nucleotide characters. MP and NJ bootstrap values are 85% and 82% for Metaves and 60% and 52% for Coronaves when indel characters are included in the analysis. Bayesian posterior probabilities are 95% for Metaves (99% excluding hoa-
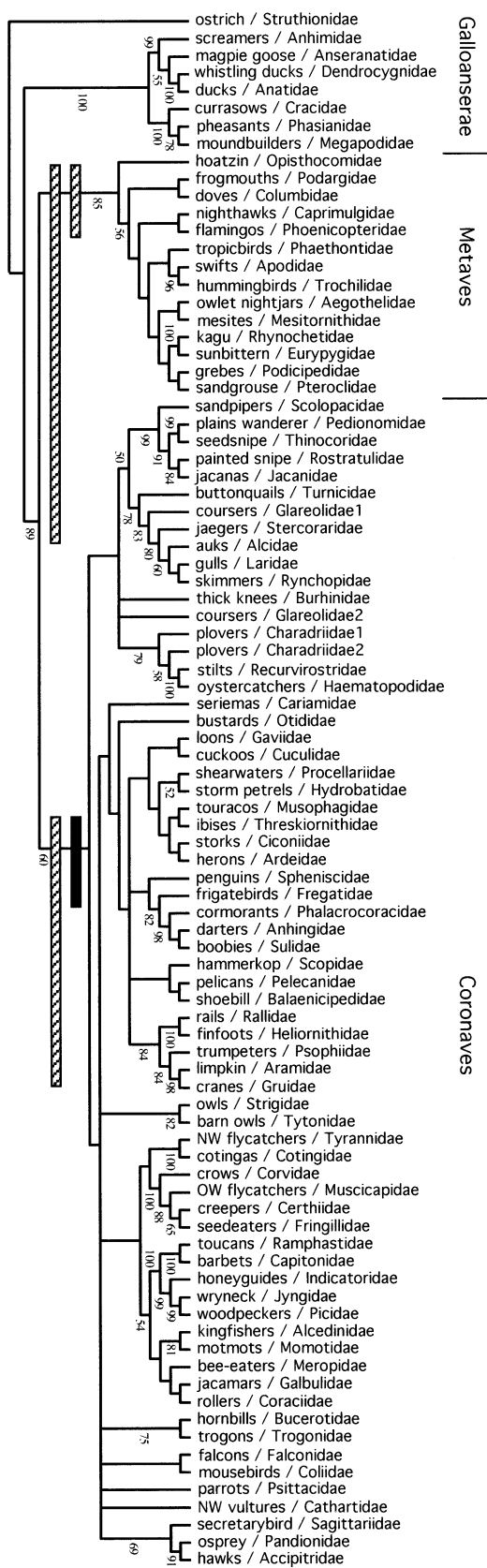
FIG. 2. Phylogenetic reconstruction of Neognathae based on FGB-int7 sequence, strict consensus of 262 equally parsimonious trees (1000 random additions), rooted to ostrich (Palaeognathae). Nu-

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     0.143     1
     0.167        1
     0.200                                   1
 C   0.250        2
 I   0.333     7     1
     0.500    12  8 3 1 1 1 1 1     1 1       1           1
     0.667
     1.000    39 13 8 7 5 4 6 4 6 1 1 1 1 3 1 1   1       1       3   2           1     1 1     1     1     1     1     1
     --------------------------------------------------------------------------------------------------------------------
     length    1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1...46 47...52...63...143...190...415
                                 1                   2                   3

                                           length
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Fig. 3. Number of indels plotted by length and consistency index.

tzin) and 83% for Coronaves using only nucleotide characters. A likelihood-ratio test shows that the branches to Metaves and Coronaves are significantly different from zero at the $P < 0.001$ level.

Others (Prychitko and Moore 2003; Johnson 2004) reported that manual alignment of FGB-int7 sequences is straightforward, and we agree notwithstanding 75 nts of apparent replication slippage and about 300 nts of parrot sequence that were removed before analysis (character subsets 1 and 2). Nonetheless, Metaves and Coronaves are recovered as strictly monophyletic by analysis of alternative alignments produced using ClustalX at a variety of gap and extension penalties, and by Dialign2. This is significant because the latter two methods employ fundamentally different methods for performing alignment. ClustalX uses the Needleman and Wunsch progressive alignment algorithm, initially building a guide tree from pairwise similarities, and then uses that tree to construct a multiple alignment. In both steps, the quality of the alignment is assessed by using specific gap opening, gap extension, and nucleotide mismatch penalties. Dialign2 avoids potential biases of specific gap penalties and assumed topologies, instead employing a nucleotide-string search algorithm. Metaves and Coronaves are recovered as monophyletic even under alignment parameters that give obviously unreasonable alignments. Thus, the signal is insensitive to different interpretations of alignment and the phylogenetic result is robust. Ultimately, one can force an alignment that is utter nonsense. In the most extreme cases we tested various coronavian lineages become unresolved, but we find no evidence that our alignment has either biased the results or obscured any other underlying phylogenetic signal.

Metaves and Coronaves are broadly distinguished by four indels: a five-base deletion in Coronaves, a 15-base deletion in Coronaves plus *Syrrhaptes* (one of two genera of sandgrouse, both studied), a 21-base deletion in Coronaves plus ostrich or insertion in Metaves plus Galloanserae, and a four-base deletion in Metaves plus bustards (for list of all vernacular and Latin family names see Fig. 2). Less than perfect consistency of these indels demonstrate that they are not evolving in a perfectly correlated fashion. In other words, their change on the metavian and coronavian branches are legitimately treated as independent evolutionary events and characters. While some exhibit homoplasy in the form of a single character state reversal, they are nevertheless considerably less homoplastic than the average of nucleotide characters. It should be noted that our coding of these gaps as

homoplasious is conservative. Some alternative alignments achieved using ClustalX and Dialign2 recover no homoplasy for the 15- and 21-nt deletions (i.e., the 15-base deletion in *Syrrhaptes* and 21-base deletion in ostrich are not coterminous with Coronaves). Furthermore, Johnson (2004) found that the consistency of indels in FGB-int7 is quite high (CI = 0.91) compared to nucleotides alone (CI = 0.30) despite the observation that deletions outnumbered insertions 6:1. Thus, collectively these four indels lend support to the nucleotide tree. ML analysis excluding these regions of the alignment (nucleotide data subset 3, see Methods) still recover Metaves and Coronaves as monophyletic, although with reduced bootstrap support, 71% and 39%, respectively. In other words, the neoavian dichotomy is obtained even when these regions of homology to the metavian- and coronavian-specific indels are completely removed from the dataset. We emphasize that the phylogenetic result does not depend on either the gaps or the regions of DNA sequence in the vicinity of the gaps, only the level of support it receives.

Based on these results, at least five of the traditionally recognized orders of birds (Wetmore 1960) include convergent members of both Metaves and Coronaves (Figs. 4, 5). Pelecaniformes include the metavian tropicbirds, while the remaining families are within Coronaves. Metavian Gruiformes include mesites, kagu, and sunbittern, while the others represent several different clades among Coronaves. Flamingos, sandgrouse, and hoatzin have been included in the orders Ciconiiformes, Charadriiformes, and Cuculiformes, respectively; but these families are Metaves, whereas the orders are otherwise Coronaves.

Most metavian interfamilial relationships (i.e., the exact topology of branching within Metaves) receive no bootstrap support, are not corroborated by indels, and are not advocated here as being necessarily correct. Hoatzin is sister to all other Metaves, and separated from them with MP and ML bootstrap support of 63% and 68% (no indels), and a posterior probability of 99%. The sister relationship of kagu and sunbittern receive 100% bootstrap support, as does the sistership of hummingbirds and swifts (MP only, ML = 93%) and the monophyly of all confamilials studied. Oilbird (Steatornithidae) is omitted from Figure 2 because we obtained only a partial sequence (missing 779 of 1930 aligned positions), but it groups it within Metaves along with other Caprimulgiformes, in which it is traditionally included, and it exhibits all four Metaves-specific indels.
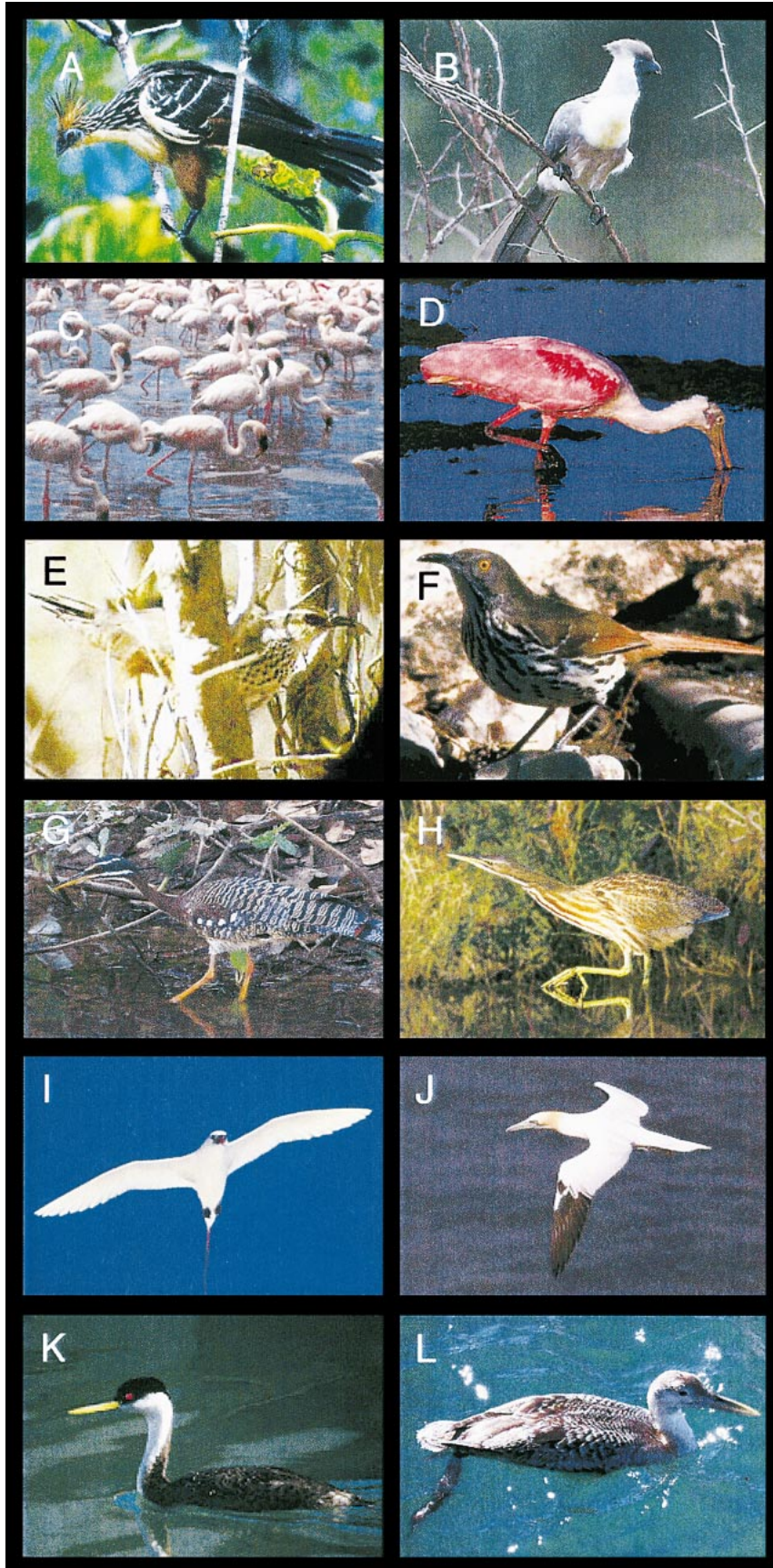
## DISCUSSION

### *Morphology*

Molecular data have significantly broadened the views of phylogeny beyond that which morphological studies previously had deemed plausible. The monophyly of Dahlgren's expanded order Capparales among angiosperms or the superorder Afrotheria among mammals were unthinkable merely a decade ago (Rodman et al. 1996; Madsen et al. 2001; Murphy et al. 2001). Perhaps it should be expected that the renewed interest in avian molecular phylogenetics would reveal similar surprises. Phylogenetic reconstruction of FGB-int7 suggests that Neoaves, comprising the vast majority of birds, are divisible into two superordinal clades, Metaves and Coronaves. If this gene phylogeny accurately represents organismal phylogeny, then the two clades exhibit broad patterns of convergent morphological evolution that have obfuscated their true phylogenetic relationships for nearly two centuries. Many isolated instances of convergent evolution have long been recognized between members of the respective putative clades, but it was never appreciated that these examples of convergence might represent broad patterns of parallelism between two sister groups. Still others were never recognized as convergent and thought instead to be related. That traditional characters would not clearly distinguish homology from homoplasy in the long hegemony of comparative anatomy in avian taxonomy is not surprising; but, morphology has had a strong influence on the selection of taxa to be compared even in recent DNA studies. Thus, few DNA studies have sampled sufficiently widely across Aves to lend alternative insights beyond morphology. Most importantly, the FGB-int7 results appear sufficient to document that at least five of the traditionally recognized orders of birds are polyphyletic (see Phylogenetic Accuracy below). Members of these orders are disparately separated in well-supported clades, regardless of whether Metaves and Coronaves prove to be strictly monophyletic, as suggested by FGB-int7.

Striking examples of convergent evolution abound between members of Metaves and Coronaves in nearly every conceivable adaptive zone, from the pelagic to the arboreal to the terrestrial realms. Convergent forms include hoatzin and touracos as large crested zygodactyl arboreal herbivores and also in the use of wing claws for climbing by nestlings (Fig. 4A, B); flamingos and spoonbills as wading filter feeders, colonial breeders, in pink coloration, and in display (Fig. 4C, D); monias and thrashers in plumage and ground-litter foraging behavior (Fig. 4E, F); sunbittern and bitterns as cryptic, stealthy piscivorous waders (Fig. 4G, H); tropicbirds and boobies as pelagic soaring plunge divers (Fig. 4I, J); grebes and loons as countershaded foot-propelled divers with high wing loading (Fig. 4K, L); hummingbirds and sunbirds as nectivores with iridescent plumage (Fig. 5A, B); swifts and swallows as dark aerial insectivores (Fig. 5C, D); frogmouths and owls as cryptic nocturnal predators (Fig. 5E, F); sandgrouse and seedsnipes as terrestrial granivores (Fig. 5G, H); and kagu and hammerkop in dance display (Fig. 5I, J). Both groups further include colonial breeders, polyandrous species, and lekking species. Early on, and in some cases even recently, many of these convergent forms were erroneously believed to be one another's closest relatives, for example, seedsnipe and sandgrouse (Bonaparte 1853; Lowe 1923; Verheyen 1958), loons and grebes (Beddard 1898; Cracraft 1982), swallows and swifts (Huxley 1867; Parker 1875; Shufeldt 1889; Lowe 1939), sunbirds and hummingbirds (Linnaeus 1758), flamingos and spoonbills (Gadow 1877; Wetmore 1960), mesites and passerines (Sundeval 1872), hoatzin and touracos (Nitzsch 1840; Verheyen 1956), and sunbittern and herons (Nitzsch 1840; Olson 1979). These and others are now widely acknowledged in textbooks as classic examples of convergence (e.g., Austin 1961; Faaborg 1988; Feduccia 1996), but it was not appreciated that they might be parts of parallel radiations. Still others were not previously recognized as convergent and remain classified in polyphyletic orders of similar ecotypes, for example, tropicbirds within Pelecaniformes (Wetmore 1960); hoatzin within Cuculiformes (Sibley and Ahlquist 1990); flamingos next to spoonbills within Ciconiiformes (Sibley and Ahlquist 1990); and kagu, sunbittern, and mesites in Gruiformes (Livezey 1997).

A comparison to mammals is illustrative. Convergent radiations have occurred at several taxonomic levels within mammals. For example, among Theria, both marsupials and placentals include fossorial, gliding, myrmecophagous, carnivorous, and grazing forms (Scally et al. 2001). Aquatic, ungulate-like, insectivore-like, and myrmecophagous forms also have evolved independently in Afrotherian and Laurasiatherian placentals (Madsen et al. 2001). The former were easily distinguished by their outwardly conspicuous differences in reproductive biology, but the latter remained obscure until the application of molecular systematics. It is not clear which, if any, radiation of mammals is directly analogous to Neoaves by constraints of common biogeography, but the ages of Neoaves and Theria are hypothesized to be similar (Hedges et al. 1996). An analogy may be drawn within Neoaves, based on taxonomic diversity and numbers of convergences, that Metaves are to marsupials (Metatheria) as Coronaves are to placentals (Eutheria). Both pairs of clades include a wide diversity of forms (Metatheria: 272 species in 19 families, and Eutheria: 4354 species in 115 families, per Wilson and Reeder [1993]; Metaves: 896 species in 19 families, and Coronaves 9171 species in 109 families, per Sibley and Monroe [1992]), exhibiting numerous and broad patterns of convergence or parallelism. The degree and number of examples of convergence between Metaves and Coronaves is at least as extensive as that between marsupials and placentals—the result being the inability to recognize that some of these birds are convergent rather than related until now. It should not be at all surprising that the radiations of birds and mammals experienced similar effects in light of the similarities in age and continental biogeography they are alleged to share (Hedges et al. 1996; Cooper and Penny 1997; Cracraft 2001; Ericson et al. 2002; Barker et al. 2002; Paton et al. 2003).

What is surprising is that morphological evidence in support of relationships between some Metaves had been reported as early as the 19th century (Table 1). Apparently, the big picture had not come to light previously simply because no single study was sufficiently comprehensive in the sampling of families. Metaves and Coronaves have each undergone such wholesale divergence that any traces of diagnostic morphological synapomorphies that may have once distin-

guished respective members of the groups as a whole have been all but lost. Perhaps the one thing that Metaves have most in common is having been characterized by taxonomists as problematic, especially sandgrouse, hoatzin, mesites, flamingos, and tropicbirds. Each at times has been placed in its own order (reviewed by Austin 1961; Sibley and Ahlquist 1990; Mindell et al. 1997; Hughes and Baker 1999; Ericson et al. 2003a; Sorenson et al. 2003). Thus, FGB-int7 offers a unifying explanation for several historically persistent, particularly pernicious, and seemingly unrelated problems in avian taxonomy.

While there appear to be no morphological characters that unambiguously distinguish Metaves from Coronaves, the retrospective light of the FGB-int7 results elucidates a handful of unusual traits shared by at least a few Metaves, which may (or may not) represent clades within Metaves. Many exhibit specialized foreguts. Flamingos, doves, sandgrouse, and hummingbirds are capable of drawing water through the bill by movement of the tongue or larynx or both rather than scooping with the bill (Austin 1961; VanTyne and Berger 1971; Zweers et al. 1981; Ewald and Williams 1982; Zweers 1982). Flamingos and doves are unique in feeding their nestlings an esophageal secretion of ''milk.'' The esophageal crop of the hoatzin has been modified into a rumen, from which adults feed their young. Kagu, doves, and mesites are documented as having a nasal operculum and it appears that some other Metaves do as well. The uropygial gland is either small or absent in doves, mesites, and frogmouths. The clavicles are reduced in mesites and many doves (Van Tyne and Berger 1971). Sunbittern, kagu, and mesites are all noted for possessing powderdown feathers in tracts (Beddard 1898).

### Biogeography

Such parallelism as exhibited by marsupials and placentals or Afrotheria and Laurasiatheria on the one hand or as inferred for Metaves and Coronaves on the other suggests radiations separate from one another, either geographically or temporally or both. The first criterion for recognizing the origin of a clade in a geographic area is the sistership of two or more taxa that are endemic to that area (Cracraft 2001). Metaves meet that criterion.

Eight of the 19 known families of Metaves are currently endemic to southern landmasses, while another eight are predominantly southern taxa and two to four of these are conspicuously absent from the fossil record in the Northern Hemisphere until the Miocene (Olson 1989; but see Peters 1987). With the notable exceptions of hummingbirds and doves, most families of Metaves are highly diverged yet extremely low in species diversity, suggesting that they could be the last survivors of ancient radiations. Knowing that var-

ious DNA sequence studies advocate Cretaceous divergences among birds (Hedges et al. 1996; Cooper and Penny 1997; van Tuinen and Hedges 2001; Ericson et al. 2003b), we might be tempted to surmise that Metaves were Gondwanan in origin. In fact, the evidence is equivocal.

One pair of Metaves whose divergence has been vigorously attributed to the vicariance of Gondwana is sunbittern and kagu. The sistership of these monotypic families is perhaps the best documented of all interfamilial relationships among Metaves (Houde et al. 1997). This, together with their respective endemism to South America and New Caledonia and the near flightlessness of the kagu, has been cited as evidence that the two diverged from one another in Gondwana (Cracraft 2001). Yet, molecular and fossil data present an equally plausible alternative to this scenario. We have not attempted to date their divergences with either molecular clock or other methods, but the FGB-int7 distance of sunbittern-kagu is roughly equivalent to those between genera in the sandpiper family. The similarity of root-to-tip path lengths for these taxa also suggests an approximate correspondence in lineage-specific rates of evolution. Sandpiper divergence times have been estimated at 35 million years ago based on RAG-1 sequences (Paton et al. 2003). The sunbittern-kagu divergence may be inferred to possibly be this young as well, since evolutionary rates for these two genes across lineages appear to be correlated (M. G. Fain and P. Houde, unpubl. obs.). If so, then this suggests a recent divergence of sunbittern-kagu consistent with dispersal prior to the Oligocene disappearance of cosmopolitan tropical forests (Wolfe 1992; Zachos et al. 2001). Furthermore, if the early Eocene fossil *Messelornis* from Germany and Wyoming is sister to sunbittern, as alleged (Hesse 1988, 1992; Livezey 1998), then the sunbittern-kagu clade had a pantropical distribution through the Northern Hemisphere long after the breakup of Gondwana. There are several avian families with modern pantropical distributions in which the closest relationships exist between Asian and South American members of each rather than with African members (Houde et al. 1995; Espinosa de los Monteros 1998; Whittingham et al. 2000). Similar distributions among plants are suggested to represent dispersal in the late Paleogene, rather than vicariance of western Gondwana as originally hypothesized (Davis et al. 2002; Manchester and Chen 2002).

The modern endemism of bird families in southern continents or islands is not evidence that they originated there or never existed elsewhere. Many families currently restricted to southern landmasses are described as occurring as fossils in Europe and North America during the globally warmer Paleogene (Mourer-Chauviré 1982; Olson 1989), including members of or sisters to eight metavian families (Andrews 1899; Mourer-Chauviré 1982, 1992; Peters 1985; Mayr 1999,

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FIG. 4. Examples of convergence between Metaves and Coronaves. Left column Metaves, right column Coronaves. (A, B) arboreal zygodactyl herbivores; (C, D) wading filter feeders; (E, F) ground litter foragers; (G, H) stealth piscivorous waders; (I, J) pelagic piscivorous plunge divers; (K, L) piscivorous foot-propelled divers; (A) hoatzin (Opisthocomidae, © D. L'Hoste); (B) touraco (Musophagidae, © P. Young); (C) flamingos (Phoenicopteridae, © L. Blumrosen); (D) spoonbill (Threskiornithidae, © P. Wallack); (E) monias (Mesitornithidae, © D. Roberson); (F) thrasher (Mimidae, © G. Jameson); (G) sunbittern (Eurypygidae, © S. Woolley); (H) bittern (Ardeidae, © A. J. Hand); (I) tropicbird (Phaethontidae, © D. Coggshall, USFWS); (J) gannet (Sulidae, © N. Blake); (K) grebe (Podicipedidae, © S. Robinson); (L) loon (Gaviidae, © B. Miller).
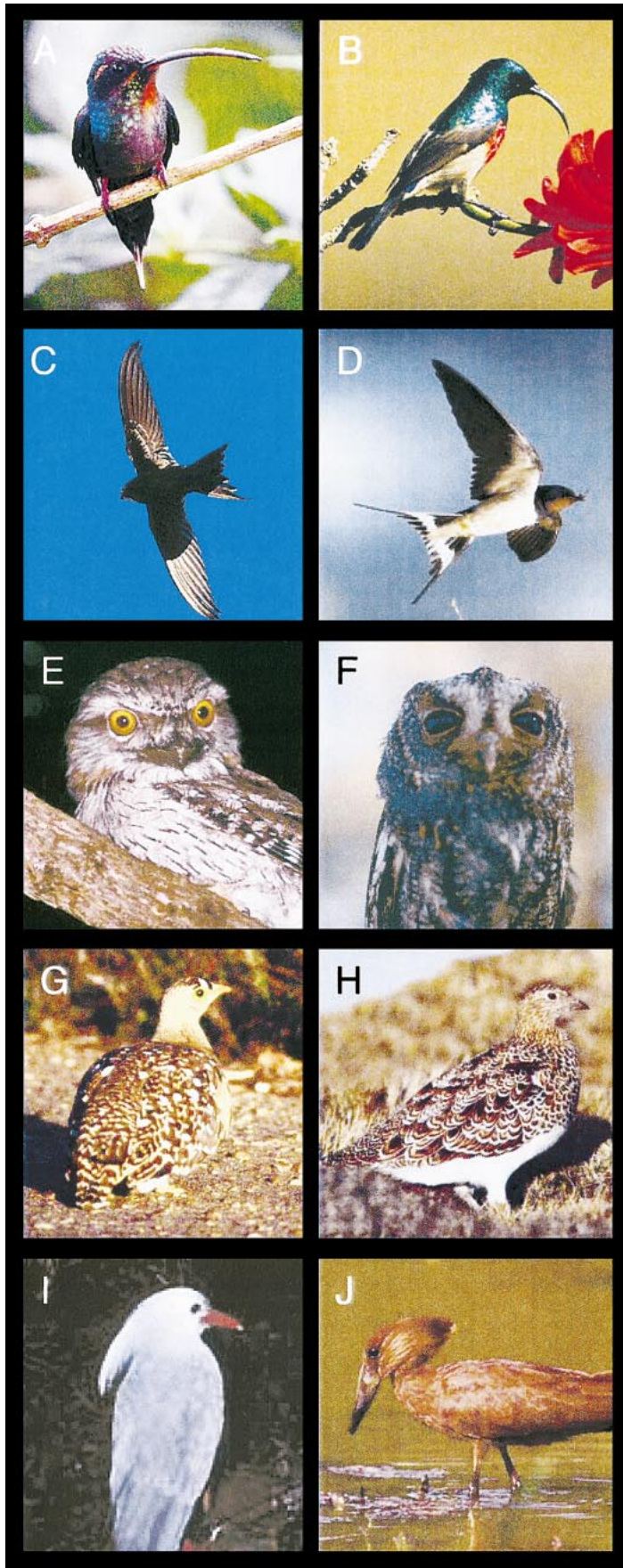
2004; Mayr and Peters 1999). Any tropical groups present in the north during the Tertiary necessarily either became isolated in tropical forest refugia of the Southern Hemisphere due to worldwide cooling trends beginning in the Oligocene or became extinct.

### Phylogenetic Accuracy

Empirically, the single-copy nuclear FGB-int7 locus appears to be more valuable than any others yet examined in recovering superordinal groups of Neoaves based on bootstrap values of nucleotide analyses both with and without indel characters, based on posterior probabilities, and because of significantly positive branch lengths to Metaves and Coronaves. Roughly half of the internal nodes in Figure 2 (90 terminals) are supported by bootstrap levels $\geq 50\%$, and 18 internal nodes are supported $\geq 95\%$. Bootstrap values for terminal OTUs (i.e., families) are not shown in Figure 2, but 28 of 30 families for which we studied multiple species are supported $\geq 99\%$. The deep phylogenetic utility of this locus probably owes to its high percentage of PI sites without saturation (Prychitko and Moore 2003). FGB-int7 nucleotide characters alone recover the Metaves/Coronaves node; indels lend support to the overall phylogenetic signal in this dataset with remarkably little homoplasy but are not essential for its recovery.

No single locus is a panacea for reconstructing phylogeny. The best yardstick for the historical accuracy of phylogenetic reconstructions is concordance between phylogenies derived from independent and well-supported datasets. We advocate only those nodes that are statistically supported by bootstrap and that enjoy some level of support from other datasets. Novel relationships that are neither statistically robust nor corroborated by other datasets may simply reflect errors in recovery of the gene phylogeny, whether due to vagaries of the evolutionary process in specific lineages, incorrect assumptions of the inference methods used, or some combination of the two (e.g., Nei 1991; Huelsenbeck and Hillis 1993).

Indel characters and nucleotide substitutions evolve at different rates and by different evolutionary processes. The result of this dynamic heterogeneity among data types is that the two sets of characters should not necessarily be expected to be of equal phylogenetic utility. The high degree of consistency of indel characters with the topology inferred from nucleotide substitutions alone is remarkable for FGB-int7. The observed support from indels for well-corroborated nodes both below and above the level of Neoaves, and the robustness of the metavian-coronavian dichotomy to different methods of alignment and removal of key indel regions suggest that this single-locus gene tree may be fairly accurately reconstructed. However, even when the reconstruction of a gene tree is accurate, the resulting topology from any individual gene may differ from the true organismal phylogeny at a particular point in time. Inconsistencies in genealogies of genes and organisms can arise from incomplete lineage sorting or following recombination among nuclear loci of alleles that have experienced different histories in different populations or introgression between hybridizing species. All of these factors are more likely to be problematic when internodes are shorter than coalescence times or when genes are exchanged between closely related taxa (Moore 1995). When a true gene phylogeny disagrees with an organismal phylogeny, it is expected that taxa will not be disparately misplaced and that the taxa affected will be separated from one another by very short internodes. For example, this has been a problem for inferring the phylogenies of species with short internodes such as human-chimp-gorilla (e.g., Ruvolo 1997), and resolution of such problems rely on data from numerous unlinked loci. Short internodes are widely acknowledged to confound attempts to reconstruct basal divergences among neoavian birds (Poe and Chubb 2004), therefore we must address to what degree such effects warrant serious concern in our result.

What would we have to assume regarding the neoavian ancestor for lineage sorting, recombination, or introgression to be factors in either producing structure in the FGB-int7 tree that is misrepresentative of organismal phylogeny or producing structure that did not exist? The ancestral neoavian population would need to be extremely large and panmictic. The internodes to descendant clades would have to be sufficiently short that different *families* within five individual orders could fix metavian and coronavian alleles; yet, the internodes could not be so short as to preclude the vastly different branch lengths from the neoavian ancestor to each of the orders that are actually observed. In other words, the structure observed within these two clades, particularly those among Coronaves that are well supported by bootstrap, would also have to be discounted as representative of phylogenetic history if the metavian lineages are to be placed near their presumed closest (coronavian) relatives. And coincidentally, those families that fixed the metavian alleles would be characterized among their respective orders as historically difficult to classify by morphological criteria.

Theoretical work suggests that it may take upward of $8N_e$ generations to achieve 95% probability of observing reciprocal monophyly at a single locus between two populations, especially among recombining nuclear genes (Hudson and Coyne 2002). A range of $N_e$ from $10^5$ to $10^6$ and a generation time of two years might therefore require internodes of 1.6–16 million years to achieve reciprocal monophyly. Although these estimates are liberally high among modern birds, perhaps internodes among early descendants of the neoavian ancestor were shorter than coalescence times for the vast majority of loci and could cause difficulties for reconstructing

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FIG. 5. Examples of convergence between Metaves and Coronaves. Left column Metaves, right column Coronaves. (A, B) nectivores; (C, D) aerial insectivores; (E, F) nocturnal predators; (G, H) terrestrial granivores; (I, J) ritualized dance display; (A) hummingbird (Trochilidae, © R. Miro); (B) sunbird (Nectariniidae); (C) swift (Apodidae, © W. Tarboton); (D) swallow (Hirundidae, © C. Pitman); (E) frogmouth (Podargidae, © O. Oczko); (F) owl (Strigidae, © G. M. Stoltz, USFWS); (G) sandgrouse (Pteroclidae, © D. Roberson); (H) seedsnipe (Thinocoridae, © A. Villalobos); (I) kagu (Rhynochetidae, © D. Roberson); (J) hammerkop (Scopidae, © G. Mornie).

phylogeny. Such a result would require a truly hard polytomy for more than 20 basal neoavian lineages.

In a study of five gene phylogenies including protein coding and transcribed ribosomal genes, Poe and Chubb (2004) present evidence for a hard lineage-level polytomy of Neoaves. The two criteria they cite for documenting hard lineage-level polytomy are the inability to reject clade branch lengths as different than zero using the likelihood-ratio test and congruence between independent loci. The FGB-int7 phylogeny has significantly positive branch lengths to Metaves and Coronaves and is topologically congruent with other datasets (Tables 1, 2). Poe and Chubb (2004, p. 409) report finding a minimum of two congruent gene-tree trichotomies (zero branch length) among neoavian orders ''even though [they] are unable to identify these relationships by name . . . [because they] are unable to determine which among the many thousands of candidate lineage trees is most appropriate.'' We note that trichotomies in three of the five locus-specific gene trees and the combined-locus gene tree are not incongruent with the significantly positive branches to Metaves and Coronaves in the FGB-int7 tree. This is because the trichotomies are contained entirely within Coronaves (i.e., trogon-cuckoo-coraciiform, and possibly owls, woodpeckers, and passerines), within which we did not test for significance of branch lengths. Whereas Poe and Chubb ''currently favor a hypothesis of lineage-level polytomy for the relationship of some bird orders . . . we eagerly await new data that may falsify this hypothesis'' (2004; p. 414). In particular, they ''recommend continued analysis of other [than nucleotide] characters'' and noted that in contrast to the coding genes they studied, two nuclear introns ''appeared useful for older divergences in birds'' (p. 414). FGB-int7 is one of those introns, and indels provide an alternative to nucleotide characters.

While the aforementioned effects could hamper our ability to distinguish the exact phylogenetic topology near the divergence of two or more closely related lineages, we should also consider the implications if the FGB-int7 topology accurately reflects a basal dichotomy in Neoaves. Over 40% of 53 individual gene trees conflicted with the branching pattern of (gorilla, (chimp, human)), a result that is strongly supported by the combined data (Chen and Li 2001) and widely held to be correct. In the FGB-int7 topology, the likelihood-ratio test indicates significant positive length for the internodes leading to both Metaves and Coronaves. This observation makes the disparate placement of members of numerous traditional taxa less probable. However, these branches are still short and could result in a substantial proportion of loci disagreeing with the species phylogeny. Accurately reconstructing such short internodes may eventually rely on rare molecular characters that are less likely to be overwritten by subsequent evolution; diagnostic large indels have been cited as such characters. Regardless whether other data eventually support strict monophyly of Metaves or Coronaves, the FGB-int7 result is sufficient to strongly imply polyphyly of five traditional orders of birds and hence broad patterns of convergent evolution among them. We are optimistic that, similar to the situation in mammalian systematics a few years ago, sufficient sampling of taxa and loci will result in some resolution of the neoavian ''polytomy.'' This work is a step

toward that goal, and we must next rely on independent estimates from other loci in confirming or contradicting the phylogenetic pattern obtained.

Corroboration of many of the FGB-int7 results in the form of monophyletic groupings of Metaves and Coronaves comes from more taxonomically restrictive analyses of a variety of independent loci (Tables 1, 2). Combined multilocus analysis also lends credibility to the division of Neoaves into Metaves and Coronaves. We performed MP analyses on up to 12.6 kb of concatenated DNA sequences from 11 loci of representatives from 90 families (range = 2.8–12.6 kb aligned sequence, mean = 8.1 kb, median = 8.2 kb, standard deviation = 2.3 kb, 4938 PI sites). We analyzed subsets of taxa separately (e.g., 21 families all represented by >10 kb, 49 families > 8 kb, 69 families > 6 kb, etc.). Although the exact results varied depending on taxa included, all MP trees recovered either Metaves or Coronaves or both as strictly monophyletic (P. Houde and M. G. Fain, unpubl. ms.). Most often, one was recovered as paraphyletic to the other. Whereas only certain of the combined loci yielded bootstrap support for Metaves or Coronaves or both, there was no well-supported conflicting signal present in any of the other loci. This can be inferred both because the FGB-int7 locus comprised only a small fraction of the combined dataset and because no analysis produced bootstrap support for any clade inconsistent with Metaves and Coronaves.

Paraphyly of Metaves is a potentially attractive alternate hypothesis to their monophyly because their pattern of FGB-int7 indels appears more primitive (i.e., similar to outgroups) than that of Coronaves and there is no evidence for paraphyly of Coronaves. Even if paraphyletic, Metaves would still require the polyphyly of at least five traditionally recognized orders of birds. However, it is Metaves for which FGB-int7 provides reasonably strong bootstrap support as monophyletic (85%), not to mention synapomorphic indels. While 85% is not ideal support, bootstrap values as low as 70% can equate with as much as 95% confidence depending on tree topology (Hillis and Bull 1993), and bootstrap values are believed to be inversely related to taxon sample size (Bremer et al. 1999). Furthermore, Sanderson and Wojciechowski (2000) documented a decrease in bootstrap support with increasing numbers of taxa. We saw a similar effect, with much higher bootstrap percentages early in the study with few taxa. However, we feel that the stability of Metaves and Coronaves to the larger taxon sample is far more compelling than reporting high bootstraps based on a limited taxon sample.

Sibley and Ahlquist's (1990) phylogeny of birds based on DNA hybridization is the standard by which virtually all new studies are compared both because of its unequalled taxonomic scope and uniformity of method (e.g., Groth and Barrowclough 1999; Cracraft 2001; Johansson et al. 2001; Barker et al. 2002; Ericson et al. 2002; Mayr and Clarke 2003; Mayr et al. 2003; Paton et al. 2003; Chubb 2004; Poe and Chubb 2004). All agree on the most basal clades Neognathae, Galloanserae, and Neoaves, but there is no agreement with DNA hybridization on divisions within Neoaves. The FGB-int7 phylogeny, like those of other loci, bears little resemblance to the DNA hybridization tree because the latter shows no evidence of a large dichotomy of Neoaves (but note the congruence between loci in Table 2). Many members of Me-

TABLE 1. Monophyletic groupings of Metavian families.

| Data | Reference | Hoatzin | Kagu | Sunbittern | Mesites | Doves | Sandgrouse | Tropicbirds | Grebes | Flamingos | Potoos | Frogmouths | Nighthawks | Owlet nightjars | Swifts | Hummingbirds |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| RAG-1 | Paton et al. 2003 | | | | | * | * | | | | | | | | | |
| *c-myc* | Johansson et al. 2001 | | | | | | | | | | | | | | * | * |
| RAG-1, *c-myc* | Johansson et al. 2001 | | | | | | | | | | | * | | | * | |
| RAG-1, myoglobin-int2 | Ericson et al. 2003 | | | | | * | * | | | | | | | | | |
| RAG-1, *cmyc*, myoglobin-int2 | Mayr et al. 2003 | | | | | | | | | | * | * | * | * | * | * |
| G3PDH, 12S, 16SrDNA | van Tuinen et al. 2001 | | * | | | | | | * | * | | | | | | |
| 12SrDNA | Houde et al. 1997 | * | | * | | | | | | | | | | | | |
| 12SrDNA | Mindell et al. 1997 | | | | | | | | | * | | | * | | | |
| PEPCK9, 12S, 16SrDNA, ND1, ND2, COI | Sorenson et al. 2003 | * | | | | * | | | | | | | | | | |
| FGB-int7 | Prychito and Moore 2003 | | | | | * | | | * | | | * | | | | |
| ZENK | Chubb 2004 | | | | | | | | * | * | | | | | * | * |
| DNA hybridization | van Tuinen et al. 2001 | | | | | | | * | * | * | | | | | | |
| Morphology | Huxley 1868 | * | | | | * | | | | | | | | | | |
| | Bartlett 1877 | | | * | * | | | | | | | | | | | |
| | Forbes 1882 | | * | * | * | | | | | | | | | | | |
| | reviewed by Sibley and Ahlquist 1990 | | | | | | | | | | | | | | | |
| | Evans et al. 1996 | | | | * | * | * | | | | | | | | | |
| | Livezey 1998 | | * | * | | * | * | | | | | | | | | |
| | Livezey and Zusi 2001 | | | | | * | | | | | * | * | * | * | * | * |
| | Mayr 2002 | | | | | | | | * | | * | * | * | * | * | * |
| | Mayr et al. 2003 | | | | | | | | | | * | * | * | * | * | |
| | Mayr and Clarke 2003 | | | | | * | * | | | * | | | | | | * |

TABLE 2. Monophyletic groupings of Metavian and Coronavian families from DNA sequence data.

| Data | Reference | Total families including outgroups | Metaves monophyletic/ total | Coronaves monophyletic/ total |
|------|-----------|-----------------------------------|----------------------------|-------------------------------|
| 12SrDNA | Houde et al. 1997 | 12 | 2/3* | 8/8 |
| 12SrDNA | Mindell et al. 1997 | 30 | 3/5 | 22/24 |
| 12SrDNA, *cyt*-b | Espinosa de los Monteros 2000 | 17 | 0/2* | 13/13 |
| RAG-1, *c-myc*, myoglobin-int2, morphology | Mayr et al. 2003 | 27 | 6/7* | 15/16 |
| RAG-1 | Paton et al. 2003 | 19 | 2/2 | 15/16 |

* All Metaves recovered as paraphyletic to Coronaves.

taves and Coronaves are juxtaposed in their phylogeny (e.g., swifts/hummingbirds and owls, doves and perching birds, sandgrouse within Charadriiformes, hoatzin within Cuculiformes, and flamingos within Ciconiiformes).

The technique of DNA hybridization is a valuable method for inferring phylogeny, but its resolution is limited to subordinal levels in birds unless internodes are widely spaced. DNA hybridization is further limited in scope by the geometric increase in number of pairwise comparisons that must be made with linearly increasing sample size. Since pairwise comparisons become too numerous to be practical, the choice of taxa to be compared is necessarily guided to some degree by expected relationships. The DNA hybridization phylogeny in truth represents a supertree that was assembled from predominantly nonoverlapping subsets of pairwise comparisons (Ericson et al. 2003b). Not every family was compared with every other; in fact, very few were compared directly, and it is not documented which pairwise comparisons were actually made. Historically contentious issues in avian systematics that were alleged to have been resolved, such as the positions of hoatzin and sandgrouse, apparently were constrained by comparisons only among preexisting candidates of relationships. The relationship of flamingos that was said to be resolved among Ciconiiformes (Sibley and Ahlquist 1990) was subsequently refuted with the same technique but wider taxon sampling (van Tuinen et al. 2001). Several other researchers were unable to replicate Sibley and Ahlquist's data using the same technique and taxa (Sheldon 1987; Sheldon et al. 1992; Houde et al. 1995). Furthermore, because of preconceptions that Gruiformes were monophyletic and that Charadriiformes were their sisters, the DNA hybridization tree (Sibley et al. 1993) was incorrectly rooted using Charadriiformes rather than sunbittern, thus misrepresenting results that actually support the FGB-int7 results herein and introducing a topological error when fitted to the supertree.

## Conclusion

The discovery of parallel radiations of Metaves and Coronaves based on FGB-int7 will hopefully broaden morphological and paleontological inquiry. Just as comparisons among neotaxa in phylogenetic analyses have been guided by preconceptions of relationships, the interpretation of fossils is guided by preconceptions of the relationships of neotaxa. Paleontological interpretation has been successfully guided by and corroborated controversial molecular inquiry in the past, for example, the paraphyletic relationship of artiodactyls to cetaceans (Graur and Higgins 1994; Gingerich et al. 2001) or the relative recency of hominoid divergences (Sarich and Wilson 1967; Pilbeam 1996). It should now be reconsidered whether direct common ancestors ever existed between ecologically convergent metavian and coronavian families that have traditionally been united in polyphyletic orders. On the other hand, seemingly implausible direct common ancestors should be sought between ecologically diverse families, especially within Metaves. Certainly, greater circumspection in interpreting hypotheses of character evolution from DNA hybridization and morphological data is warranted in light of the FGB-int7 results, regardless of whether they eventually are corroborated in every detail. Perhaps most importantly, patterns in biogeography and adaptive radiation both within birds and in comparison to other groups should be reconsidered with reference to these new insights into phylogeny, much as is now being attempted for some mammals (Nikaido et al. 2003).

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