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# Going to Extremes: Contrasting Rates of Diversification in a Recent Radiation of New World Passerine Birds

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*Abstract*.—Recent analyses suggest that a few major shifts in diversification rate may be enough to explain most of the disparity in diversity among vertebrate lineages. At least one significant increase in diversification rate appears to have occurred within the birds; however, several nested lineages within birds have been identified as hyperdiverse by different studies. A clade containing the finches and relatives (within the avian order Passeriformes), including a large radiation endemic to the New World that comprises ~8% of all bird species, may be the true driver of this rate increase. Understanding the patterns and processes of diversification of this diverse lineage may go a long way toward explaining the apparently rapid diversification rates of both passerines and of birds as a whole. We present the first multilocus phylogenetic analyses of this endemic New World radiation of finch relatives that include sampling of all recognized genera, a relaxed molecular clock analysis of its divergence history, and an analysis of its broad-scale diversification patterns. These analyses recovered 5 major lineages traditionally recognized as avian families, but identified an additional 10 relatively ancient lineages worthy of recognition at the family level. Time-calibrated diversification analyses suggested that at least 3 of the 15 family-level lineages were significantly species poor given the entire group's background diversification rate, whereas at least one—the tanagers of family Thraupidae—appeared significantly more diverse. Lack of an age–diversity relationship within this clade suggests that, due to rapid initial speciation, it may have experienced density-dependent ecological limits on its overall diversity. [Concatenation; concordance; congruence; diversification; gene tree; New World; Passeriformes.]

Unraveling the factors that influence diversification remains one of the fundamental goals of evolutionary biology (Dial and Marzluff 1989; Purvis et al. 1995; Mittelbach et al. 2007; Ricklefs 2007b; Donoghue 2008; Rabosky 2009a). Many paradigmatic studies of the interplay between adaptation and speciation have focused on examples of adaptive radiation that are particularly dramatic because they have arisen in restricted geographic settings, such as African Rift lake cichlids (Kornfield and Smith 2000; Kocher 2004), Hawaiian archipelago silverswords (Carlquist et al. 2003), and Darwin's finches of the Galapagos (Grant and Grant 2003). Most diversification does not occur in isolated island or lacustrine environments, but rather in more complex continental or oceanic milieux; however, the sometimes much older radiations in these more geographically and ecologically complex settings can be more difficult to recognize. With the advent of molecular phylogenetic methods, identification of continental—and especially of older—radiations has become possible (Givnish and Sytsma 2000; Schluter 2000) because these methods can both identify monophyletic groups and provide a temporal context for their origin and pace of diversification (e.g., Madsen et al. 2001; Rabosky and Lovette 2008; Verboom et al. 2009; Claramunt 2010; Derryberry et al. 2011).

One of the most conspicuous patterns of biodiversity is that some groups of organisms are highly diverse, whereas others of equivalent age are represented by only a few species. A recent survey of extant vertebrate diversity identified a handful of major radiations and "living fossils" that may explain much of this disparity in lineage species numbers (Alfaro et al. 2009). This study identified the Neoaves, or non-ratite birds, as one particularly diverse radiation. However, tests of uniform among-lineage diversification are subject to a "trickle down" effect, where more inclusive clades may seem to exhibit overall nonuniform diversification rates, when closer investigation reveals that the change in diversification is restricted to a more recently derived group within the larger clade (Purvis et al. 1995). Thus, Alfaro et al. (2009) noted that the pattern they observed in Neoaves might actually be attributed to the diversity of passerine birds (order Passeriformes), a single avian order that comprises over half of extant avian species diversity (Raikow and Bledsoe 2000).

In fact, studies more closely focused on avian diversity have identified the oscine passerines (a subclade of passerines comprising nearly half of avian diversity) as a significantly diverse radiation (Nee et al. 1992), as judged against the diversity of other similarly aged avian clades. Even more precisely, studies of passerine diversity alone have identified a few passerine lineages that are more species rich than expected (Ricklefs 2003). The most extreme example of high within-passerine diversity is a clade comprising the traditional families Fringillidae

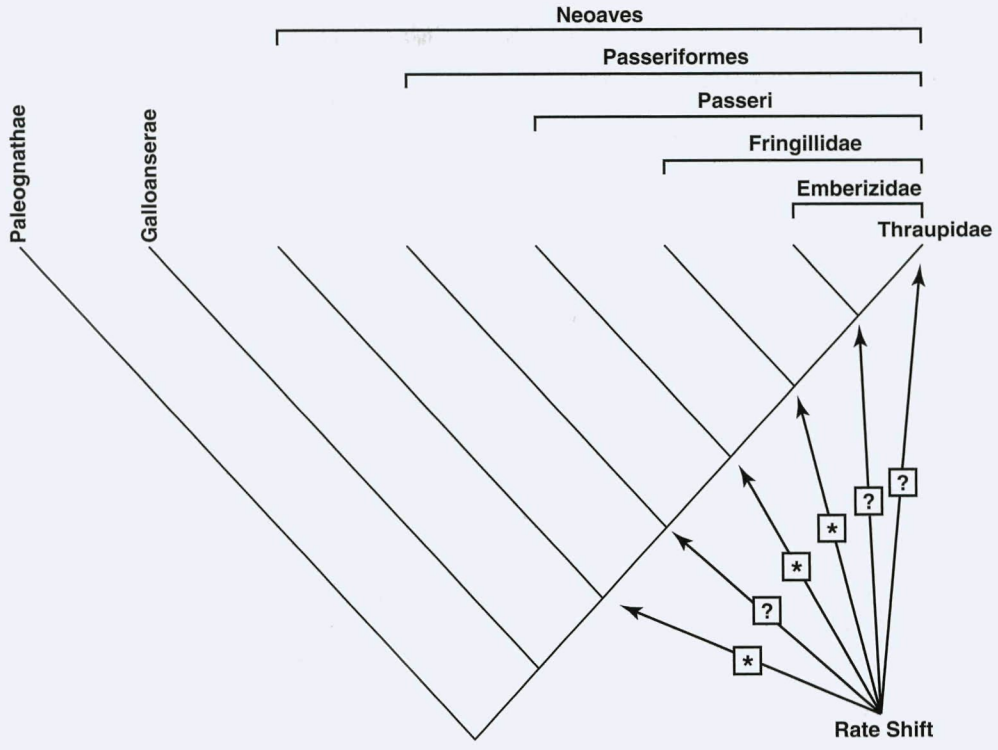


FIGURE 1. The "trickle down" effect on determination of avian diversity patterns. Studies have identified various nodes (labeled with asterisks), including the Neoaves (Alfaro et al. 2009), the Passeri (Nee et al. 1992), and the Fringillidae (Ricklefs 2003) as significantly more diverse than expected relative to different background rates. Additionally, the tanagers (Thraupini) have been found more diverse than null expectation (Ricklefs 2003), though not significantly so (see text).

(canaries, finches, Hawaiian honeycreepers, and allies); Cardinalidae (cardinals and allies); Emberizidae (sparrows, buntings, and longspurs); Icteridae (blackbirds, meadowlarks, and allies), Parulidae (New World warblers); and Thraupidae (tanagers and allies; Ricklefs 2003). This assemblage includes 2 classic cases of adaptive radiation, the Hawaiian honeycreepers (in the Fringillidae) and the Darwin's finches (in the Thraupidae). Even within this group, Ricklefs (2003) found that the Thraupidae were more diverse than expected, although diversity of this lineage did not approach statistical significance. However, that analysis may have been hampered by noncomparability of lineages (Barker 2011), and the incompletely sampled and inaccurate (see below) phylogenetic hypothesis upon which it was based. Thus, although there is evidence of significant shifts in diversification rate within birds as great as any observed among vertebrates, the precise phylogenetic locations—let alone the causes—of these shifts have been difficult to ascertain (Fig. 1). Resolving relationships within and among these diverse lineages is the critical first step toward a better understanding of their differences in diversity.

Although the evolutionary histories of exemplary island radiations of passerines have been studied in great detail (reviewed in Grant and Grant 2003; Pratt 2005), equivalently comprehensive analyses of their continental relatives are still largely lacking. In particular, the Cardinalidae, Emberizidae, Icteridae, Parulidae, and Thraupidae have long been recognized as a monophyletic group termed the New World 9-primaried oscines (= subfamily Emberizinae of Monroe and Sibley 1993). This is an extremely ecologically and morphologically diverse assemblage comprising ~8% of extant avian species diversity, 15% of all passerine species, and 17% of New World bird species. Birds in this group occur in all terrestrial New World biomes and have adaptations to feed on resources ranging from insects, to seeds, fruits, and nectar. The morphological diversity that makes this group such a dramatic example of adaptive radiation has also contributed to its long history of taxonomic difficulties. For instance, a variety of seed-eating finch-like forms (including Darwin's finches) were traditionally considered closely related to the New World sparrows (Emberizidae), but more recent analyses (Bledsoe 1988; Sibley and Ahlquist 1990; Yuri and Mindell 2002; Burns et al. 2002) strongly support their relationship with the primarily frugivorous tanagers. Perhaps more tellingly, until the mid-20th century, a single family (Coerebidae) comprised 11 nectarivorous genera from throughout the Neotropics (Hellmayr 1935). Based on detailed analysis of their jaw musculature, these taxa were subsequently split between the Parulidae and Thraupidae (Beecher 1951), and more recent data suggest that they nearly all represent independent origins of nectarivory within the Thraupidae (Burns 1997; Burns et al. 2003). These are but 2 examples of the problems posed by complex patterns of morphological

evolution in this group. Many molecular phylogenetic studies have addressed aspects of the relationships among these families (Bledsoe 1988; Sibley and Ahlquist 1990; Burns 1997; Klicka et al. 2000; Grapputo et al. 2001; Burns et al. 2002; Lovette and Bermingham 2002; Yuri and Mindell 2002; Klein et al. 2004; Klicka et al. 2007), but there has been no comprehensive analysis of all of the relevant lineages using consistent taxon and gene sampling.

Here, we report phylogenetic analyses including at least one representative of every genus traditionally classified in the 5 families of the New World 9-primaried oscines (204 taxa in total). Phylogenetic analyses of these data provide for the first time a comprehensive phylogenetic and temporal framework for interpreting the diversity of the group. Our corresponding analyses of lineage diversity patterns suggest significant heterogeneity among lineages, both corroborating previous analyses and suggesting novel patterns.

## Materials and Methods

### *Taxon and Character Sampling*

We sampled exemplars from every recognized genus (following Dickinson 2003) of the traditional families Cardinalidae, Emberizidae, Icteridae, Parulidae, and Thraupidae. Although not an exhaustive sample of such cases, we did include multiple representatives of genera that appear paraphyletic based on our own or previously published analyses with more extensive taxon sampling (e.g. *Parula* and *Pipilo*; DaCosta et al. 2009; Lovette et al. 2010), as well as exemplars of a number of genera not recognized by current taxonomy (including *Leistes*, *Gymnostinops*, *Pseudodacnis*, and *Diglossopis*) for a total of 204 sampled taxa (Supplementary Table S1; available on Dryad, doi:10.5061/dryad.52565). As immediate outgroups, we selected members of the family Fringillidae (the sister clade to the New World group; Barker et al. 2002; Ericson and Johansson 2003; Johansson et al. 2008), including the former tanager genera *Euphonia* and *Chlorophonia*, 2 Hawaiian honeycreepers (*Oreomystis* and *Paroreomyza*), *Fringilla*, and *Carduelis* (Supplementary Table S1). In addition, we included 2 members of the more distant family Motacillidae (*Motacilla* and *Anthus*), thought to be sister to the Fringillidae/Emberizidae clade (see above references), and rooted all analyses with these taxa. The complete sample comprised 213 taxa. Of these, 14 were not available to us as frozen tissue (Supplementary Table S1) and were sampled as toe pad clippings obtained from round skins.

We assembled several data sets with varying taxon and gene sampling in order to address relationships within this group. First, for all taxa, we obtained sequences from the mitochondrial genome. For tissue-extracted genomic DNA, we sequenced the entire cytochrome *b* and ND2 genes, as many sequences were already available from previous studies on these groups. For the 14 DNAs extracted from museum skins, we obtained complete (or nearly so) cytochrome *b* in all cases but one (*Leucopeza semperi*) for which we obtained ND2 instead. From all taxa for which we had high-quality genomic DNA, we also targeted 1 nuclear protein-coding locus and 3 introns: recombination activating gene 1 (RAG1), myoglobin intron 2 (MB-I2), β-fibrinogen intron 5 (FGB-I5), and aconitase 1 intron 9 (ACO1-I9).

### *Molecular Methods*

Total genomic DNA was extracted from tissue samples using the Qiagen DNA Mini Kit (Qiagen, Valencia, CA, USA) following the manufacturer's instructions. The procedure for toe pad specimens was modified by the addition of 30 μL 1% dithiothreitol (Gold Biotechnology, St Louis, MO, USA) during tissue lysis, and final elution in 50 μL rather than 200. All DNA extraction and polymerase chain reaction (PCR) setup for toe pad samples were done in another laboratory and building where avian molecular work did not otherwise occur. Amplification of cytochrome *b*, ND2, RAG1, and ACO1-I9 was as previously described (Barker et al. 2002, 2008). Amplification of MB-I2 was generally direct, using primers Myo2/Myo3f (Heslewood et al. 1998), though occasional specimens required an initial amplification using Myo2/Myo3 (Slade et al. 1993), followed by nested PCR using Myo2/Myo3f. The remaining introns were amplified directly using exon priming: FGB-I5 with primers Fib5/Fib6 and ACO1-I9 with ACO1-I9F/ACO1-I9R (Kimball et al. 2009). Reaction conditions for all introns were as described previously for ACO1-I9 (Barker et al. 2008). Amplification of cytochrome *b* or ND2 from museum skin samples targeted 5 (Barker et al. 2008) or more (Lovette et al. 2010) overlapping fragments, respectively. Successful reactions were digested enzymatically in preparation for sequencing (Werle et al. 1994). All cycle sequencing was performed using both external primers for each fragment, using BigDye v3.1 terminator chemistry (Applied Biosystems, Foster City, CA, USA), electrophoresed on an ABI 3730xl sequencer. Contig alignment was performed using Sequencher v4.8. Heterozygous positions were identified by quality scores and visual inspection of electropherogram data. Where length heterozygotes were amplified, the longer allele was determined by sequence subtraction (Flot et al. 2006) or cloning.

### *Separate and Concatenated Phylogenetic Analyses*

Data from the protein-coding genes were aligned manually, whereas sequences from the introns were initially aligned using ClustalX (Thompson et al. 1994; using default parameters), with subsequent modification by hand. These alignments were concatenated for subsequent analyses. Individual gene regions were examined for stationarity using taxon-by-taxon goodness-of-fit tests, correcting for multiple comparisons (Gruber et al. 2007). Three data

matrices were analyzed: (1) including only those taxa with at least 3 nuclear loci sampled in addition to mtDNA (the **core taxa** matrix; $S=199$ taxa, and $L=7701$ bases); (2) including all sampled taxa, with missing data for the nuclear loci of those taxa sampled from skin specimens (**complete taxa**; $S=213$, and $L=7701$); and (3) including only taxa for which all loci were sampled (**complete character**; $S=191$, and $L=7701$). For clarity, reference to these matrices (**core taxa**, **complete taxa**, and **complete character**) is made in boldface type.

A series of a priori partitions were defined as each sequenced gene or gene region. Prior to any combined analysis, each a priori partition was analyzed separately in order to identify potential regions of conflict. Although the 2 mitochondrial regions should share the same underlying genealogy, they may have different evolutionary dynamics; thus, these regions were treated as separate partitions for model fitting but not for topology estimation. Best-fit models for each gene region were estimated using ModelTest v3.7 (Posada and Crandall 1998), according to the Akaike Information Criterion (AIC) for each model as calculated on an initial tree obtained by equally weighted parsimony. Subsequent to model selection, each genealogically distinct partition was analyzed separately using maximum likelihood (ML; RAxML v7.0.4; Stamatakis 2006a, 2006b) and Bayesian (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003; Altekar et al. 2004) methods. For ML analyses, multiple runs were performed for each gene, starting from random trees and parameter values, and using the default population and mutation parameters. Tree searches were performed using the GTRCAT model with the default number of categories (25). Support for relationships was assessed by the nonparametric bootstrap (200 replicates; Felsenstein 1985). For Bayesian analyses, 2 runs ($1\times10^7$ generations each) of 4 Metropolis-coupled Markov chains each were performed using the best-fit model as chosen by AIC (or the next-most parameter-rich option, if not implemented in MrBayes), with the default heating parameter and prior distributions. Posterior parameter distributions were examined for convergence and adequate sampling using Tracer v1.5 (Rambaut and Drummond 2007). Posterior tree distributions were examined for intrachain convergence using AWTY (Nylander et al. 2004), and for interchain convergence by comparison of estimated nodal posterior probabilities. All trees were investigated for strongly supported conflicting hypotheses of relationship, operationally defined as incompatible bipartitions found in >75% of bootstrap replicates or 95% of posterior samples from separate analyses of 2 data sets. Node-by-node comparisons were made by extraction of bootstrap percentages and estimated Bayesian posterior probabilities for all nodes recovered in individual gene region analyses, and representing these graphically for all nodes in specific target trees (e.g., the combined ML tree).

Subsequent to separate analyses, the 2 concatenated (**core taxa** and **complete taxa**) matrices were analyzed using ML and Bayesian methods. In ML analyses, a priori partitions corresponding to each gene region were recognized, and branch lengths were estimated under a proportional model. In Bayesian analyses, partitions were analyzed under the models implemented in MrBayes most closely matching their optimal AIC models, with unlinked parameters, and branch lengths constrained to proportionality. As above, support for relationships under ML was assessed by the nonparametric bootstrap, and for Bayesian analyses, 2 runs ($1\times10^7$ generations each) of 4 Metropolis-coupled Markov chains each were performed.

### *Congruence and Concordance Analyses*

As discussed above, we have assessed congruence among individual gene partitions on a node-by-node basis, comparing bootstrap and posterior probability values across a target tree. In addition to this, we inferred combined-data trees using Bayesian concordance analysis (BCA) (Ané et al. 2007), as implemented in BUCKy v.1.3.2 (Larget et al. 2010). This approach takes distributions of trees (e.g., Markov Chain Monte Carlo [MCMC] samples) from multiple loci and estimates a combined-evidence tree from reweighting of genealogies based on among-gene concordance. Associated with this tree are nodal concordance factors that scale from 0 to 1, with fractional values representing the approximate proportion of individual partitions supporting a given node. We performed this analysis using gene tree posterior distributions from the Bayesian analyses described above, pruning taxa missing in one or more gene data sets ($S=8$) from all gene trees. In addition to input trees, BUCKy requires an a priori discordance parameter $\alpha$ with $\alpha=0$ indicating no expected discordance, and $\alpha=\infty$ indicating complete independence. We ran analyses using $\alpha=0.1$ and $\alpha=1$, corresponding to either 1–2 or 1–5 possible distinct gene trees, and compared results from these analyses both in terms of the concordance tree and nodal concordance values.

### *Estimation of Species Tree, Relative, and Absolute Timing of Lineage Divergence*

Although congruence and concordance among individual loci give a qualitative sense of support for inferred relationships, these measures do not incorporate the effects of variance in effective population size across the genome (e.g., due to relative ploidy levels of mtDNA, sex-linked, and autosomal loci). In addition, it is well established that under some conditions, consensus will be positively misleading (Degnan and Rosenberg 2006; Rosenberg and Tao 2008). For these reasons, we also performed species tree analysis of our **complete character** matrix. A variety of heuristic and full-likelihood methods are available for species tree estimation (Liu 2008; Kubatko et al. 2009; Liu et al. 2009a;

Heled and Drummond 2010; Liu et al. 2010), but we chose the method implemented in *BEAST (Drummond and Rambaut 2007; Heled and Drummond 2010) for 3 primary reasons. First, preliminary analyses of our data suggested that support for some relationships only appeared in combined analysis—that is, individually estimated gene trees (especially for the mtDNA) failed to yield support for nodes that appeared with strong support in concatenation (see "Results" section). This "emergent" signal would not be detected by heuristic methods that depend on gene tree summation (Liu et al. 2009a; Kubatko et al. 2009; Liu et al. 2010). Second, of methods explicitly estimating alignment likelihood on gene trees as well as gene tree likelihoods given a species tree, *BEAST was the only one that yielded repeatable results in reasonable timeframes (e.g., on the order of weeks). Finally, this implementation allows explicit temporal constraints to be incorporated directly into the analysis, which provides an absolute timescale for inferred divergence times.

We analyzed the **complete character** data set partitioned by gene, using gene-specific models as selected above (or the next most complex alternative, if not implemented in BEAST). Gene tree topologies for the 2 mitochondrial genes were linked, but all other loci treated as independent, and ploidy levels assigned based on linkage of the corresponding loci in the *Taeniopygia* genome (although we note that we found no cases of heterozygosity in sequences of females from our single sex-linked locus, ACO1-I9). All loci except mtDNA ($P < 0.001$) conformed to a molecular clock ($P \geqslant 0.8$; likelihood ratio tests on locus-specific trees; Felsenstein 1981), so to reduce the dimensionality of our MCMC run, we enforced a molecular clock for all loci except mtDNA, for which we modeled rate change as an uncorrelated lognormal process (with an exponential prior [$\mu = 0.1$] on its standard deviation; Drummond et al. 2006). For the species tree, we set a Yule prior with a piecewise linear, constant root demographic function. We estimated absolute timing of divergence events using 2 different constraints: (1) the divergence of the Hawaiian honeycreepers *Oreomystis* and *Paroreomyza* at 5.1 Ma (Fleischer et al. 1998), implemented as a uniform prior of [5.1, 0] and (2) an external calibration of the Fringillidae/New World 9-primaried oscine divergence at 20–22 Ma based on the biogeography of basal passerine divergences (Barker et al. 2004), implemented as a normal prior with mean of 21 Ma with standard deviation of 3.9 (the larger of 2 bootstrap standard error estimates from Barker et al. 2004). For both calibrated and uncalibrated analyses, we ran multiple Markov chains for $2 \times 10^7$ generations to assess among-run variance in topology and parameter values and to approximate time to convergence. A final production run was set to $5 \times 10^8$ generations. To minimize file sizes and reduce autocorrelation, chains were thinned to $10^{-4}$. The results were analyzed for convergence and adequate sampling using Tracer and AWTY and maximum clade-credibility trees constructed.

*Analysis of Diversity Patterns*

Recently, much discussion has focused on interpretation of diversity patterns with respect to speciation and extinction rates (Magallón and Sanderson 2001; McPeek and Brown 2007; Ricklefs 2007a; Rabosky 2009b). In particular, both the generality and interpretation of the expected relationship between clade diversity and time have been called into question (Rabosky 2009a, 2009b, 2010). Early in a radiation, it is expected that lineages freely diversify, with little constraint due to competitive interactions, yielding a positive relationship between clade age and clade diversity within the lineage. Due to ecological constraints, it might be expected that over evolutionary timescales lineages will "saturate" the geographic regions in which they occur, erasing the relationship between clade size and clade age (Rabosky 2009a). Thus, we might expect a positive relationship for recent radiations, and a nonexistent one for older groups. Both patterns have been found using molecular data for various taxa (reviewed in Rabosky 2009b), but given the relative youth and extreme diversity of the New World 9-primaried oscines (Ricklefs 2003; Barker et al. 2004), we might expect the former pattern for this group.

In order to assess this relationship, we plotted clade diversity versus age for the major groups of the New World clade corresponding to traditional families, as well as for the remaining monophyletic groups on the tree. We interpreted this diversity pattern relative to a uniform birth–death process with varying levels of extinction, and a net diversification rate estimated from New World crown-clade age and diversity, following Magallón and Sanderson (2001), using functions in GEIGER (Harmon et al. 2008). We note that although we have time calibrated the phylogeny inferred here, the absolute clade ages are not essential to interpreting diversity patterns in the group, only the relative ages. Thus, our analysis of the relationships between clade diversity and clade age depends only on reasonably accurate modeling of shifts in molecular evolutionary rates across lineages within the study group, not on the accuracy of our calibrations *per se*. Given that our nuclear data fit a molecular clock, and that the mitochondrial data show relatively little rate heterogeneity (standard deviation of relaxed clock rates $\sigma = 0.175$), it seems reasonable that relative branching times are well estimated.

In addition to this analysis, we looked for significant shifts in diversification rate across our inferred tree by fitting a piecewise diversification model. As implemented in the R package turboMEDUSA (Harmon et al. 2011), shift points are sequentially added to the tree such that small-sample AIC is minimized at each step (up to a set number or a threshold value of $\Delta AIC_c$), then sequentially removed likewise, until additional removals fail to decrease the AIC below a given threshold. We applied this method (using default threshold values) to our maximum clade credibility species tree from *BEAST analyses (see above), as

well as to a set of 100 trees from the species tree posterior distribution. These trees were pruned to terminals of certain monophyly (essentially at what we are recognizing as the family level; see "Discussion" section and "Appendix"), and species diversity assigned to the terminals using standard taxonomic sources (e.g., Dickinson 2003).

## Results

### *Data Characteristics*

We obtained sequence data from every genus of New World 9-primaried oscine. In a few cases (8 of 199 samples), we were unable to obtain one nuclear gene from DNA derived from frozen tissues, but the **core taxa** matrix is >99% complete. As noted above, an additional 14 taxa were added to our analysis based on partial mtDNA sequences obtained from museum toe pad samples. Due to the relatively small number of taxa sampled in this way, even this matrix is >95% complete. As expected given the diverse regions targeted, the data vary considerably in their characteristics and evolutionary dynamics (Table 1). In particular, the 3 protein-coding regions require more complex models (GTR+I+G) than the 3 introns (GTR+G or TVM+G); the mtDNA genes differ significantly from the nuclear genes in base composition (lower guanine frequency) and evolutionary rate (an order of magnitude higher: mean ML tree length for mtDNA genes is 23.5; mean tree length for nuclear genes is 1.9); and the nuclear-coding gene evolves less rapidly (tree length of 1.1) than the introns (mean tree length is 2.3), presumably due to purifying selection on its nonsynonymous sites.

### *Separate Phylogenetic Analyses and Inferring Patterns of Congruence and Conflict*

We analyzed each of 5 gene regions separately prior to concatenated analysis in order to determine the resolving power of individual gene regions, as well as the occurrence of conflict among estimates of phylogeny from each region. In order to evaluate congruence, we pruned trees obtained for each region to include a core set of completely sampled taxa, corresponding to the **complete character** matrix ($S=191$). The resolving power of individual gene regions along with patterns of conflict and congruence using 2 inference methods (ML and Bayesian) are summarized in Table 2. In general, the number of bipartitions resolved at a given level of support was correlated with the number of variable characters in a gene region, such that ~2 kb of mtDNA data outperformed ~3 kb of RAG1 (1280 vs. 1059 variable sites), whereas both outperformed the shorter introns (428–799 variable sites). However, the ACO1-I9 data yielded equivalent or better resolution than the larger RAG1 data set for both types of analysis. In ML analyses, at a given support level, ACO1-I9 yielded higher resolution per base pair than any other region sampled, whereas in Bayesian analyses, MB-I2 performed slightly better. At the levels of support reported here, no gene region resolved more than 101 out of the 188 bipartitions possible given 191 terminals (54%). Thus, no single region sampled appears adequate to fully resolve relationships among these taxa.

We evaluated congruence among regions in both positive and negative senses and found that congruence was better predicted by locus ploidy than by resolving power. Specifically, we tabulated pairwise bipartition conflicts as well as shared supported bipartitions for given analyses (ML and Bayesian) and multiple levels of support (75% and 90% bootstrap, and 0.95 estimated posterior probability). Although these absolute numbers are of interest, they are better evaluated relative to the overall resolving power of the gene regions being compared. Therefore, we also scaled these numbers by the number of bipartitions retained in a semistrict (combinable component) consensus of bipartitions from all gene regions (Table 2). In all cases, the gene region providing the second lowest resolving power (MB-I2) yielded the fewest conflicts in pairwise comparisons with other regions. However, in 2 out of 3 comparisons, the minimum number of conflicts was not with the most poorly resolved region (FGB-I5), but rather with the highly informative ACO1-I9. Among the regions with better resolving power (mtDNA, RAG1, and ACO1-I9), the lowest levels of conflict were fairly uniform, but tended to be lower in comparisons with RAG1, which was only slightly less informative than ACO1-I9. The data on positive congruence are perhaps more interesting. In all 3 comparisons, mtDNA and ACO1-I9 shared more supported bipartitions (both absolutely and as a proportion of total nonconflicting bipartitions) than any other pair of gene regions. Estimates of positive congruence between RAG1 and ACO1-I9 and between RAG1 and mtDNA were generally the next highest, followed by comparisons with the other introns. This overall pattern fits with expectations of congruence based on the effective population sizes of these markers, which should scale approximately: mtDNA$\ll$ACO1-I9$<$RAG1$<$FGB-I5$\approx$MB-I2. This is because mtDNA is maternally inherited, ACO1-I9 is Z-linked, and of the remaining 3 autosomal genes, RAG1 is protein coding and therefore directly subject to the diversity-reducing effects of positive and purifying selection.

### *Concatenated Analyses*

In addition to the separate analyses summarized above, we analyzed 2 concatenated data sets, the **complete taxa** ($S=213$) and **core taxa** ($S=199$) matrices. For the sake of brevity and simplicity, we present these results, as well as the contribution of individual gene regions to specific phylogenetic hypotheses, in the context of a single inferred tree topology: the best ML tree estimated for the more comprehensive **complete taxa** matrix (Figs. 2–7). Analyses of the

TABLE 1. Characteristics of gene regions sampled in this study

| | Gene region | | | | | |
|---|---|---|---|---|---|---|
| | CYTB | ND2 | RAG1 | ACO1-I9 | FGB-I5 | MB-I2 |
| # Characters | 1143 | 1041 | 2893 | 1136 | 611 | 749 |
| % Variable | 51.7 | 66.2 | 36.6 | 70.3 | 70.0 | 59.4 |
| % Informative | 44.2 | 58.4 | 20.2 | 44.5 | 41.4 | 32.9 |
| AIC Model | GTR+I+G | GTR+I+G | GTR+I+G | GTR+G | TVM+G | TVM+G |
| Tree length | 22.87288 | 24.11908 | 1.12150 | 2.69560 | 2.16200 | 1.58548 |
| $\pi_A$ | 0.413 (1.00) | 0.339 (1.00) | 0.332 (1.00) | 0.279 (1.00) | 0.297 (1.00) | 0.302 (1.00) |
| $\pi_C$ | 0.397 (1.00) | 0.379 (1.00) | 0.192 (1.00) | 0.167 (1.00) | 0.176 (1.00) | 0.208 (1.00) |
| $\pi_G$ | 0.086 (1.00) | 0.086 (1.00) | 0.232 (1.00) | 0.184 (1.00) | 0.206 (1.00) | 0.209 (1.00) |
| $\pi_T$ | 0.105 (1.00) | 0.196 (1.00) | 0.244 (1.00) | 0.370 (1.00) | 0.321 (1.00) | 0.280 (1.00) |
| $\kappa$ | NA (0.00) | 8.618 (0.00) | 3.299 (0.00) | 1.824 (0.00) | 1.811 (0.00) | 2.297 (0.00) |
| $r_{AC}$ | 0.252 (1.00) | 0.445 (1.00) | 1.502 (1.00) | 0.921 (1.00) | 1.108 (1.00) | 1.064 (1.00) |
| $r_{AG}$ | 4.183 (1.00) | 15.800 (1.00) | 5.473 (1.00) | 4.209 (1.00) | 3.997 (0.28) | 4.782 (0.30) |
| $r_{AT}$ | 1.172 (1.00) | 0.571 (1.00) | 0.970 (1.00) | 0.521 (1.00) | 0.781 (1.00) | 0.739 (1.00) |
| $r_{CG}$ | 0.115 (1.00) | 0.226 (1.00) | 1.762 (1.00) | 1.365 (1.00) | 1.607 (1.00) | 1.604 (1.00) |
| $r_{CT}$ | 12.865 (1.00) | 7.776 (1.00) | 12.724 (1.00) | 2.596 (1.00) | 3.821 (0.28) | 5.132 (0.30) |
| $p_i$ (I) | NA (0.00) | NA (0.00) | NA (0.00) | NA (0.00) | 0.113 (0.00) | 0.221 (0.00) |
| $\alpha$ (G) | NA (0.00) | NA (0.00) | 0.338 (0.00) | 2.460 (0.73) | 2.830 (0.70) | 1.343 (0.73) |
| $p_i$ (IG) | 0.451 (1.00) | 0.323 (1.00) | 0.437 (1.00) | 0.000 (0.27) | 0.022 (0.30) | 0.000 (0.27) |
| $\alpha$ (IG) | 0.511 (1.00) | 0.667 (1.00) | 0.861 (1.00) | 2.460 (0.27) | 3.189 (0.30) | 1.343 (0.27) |

The number of characters in each region, the percentage of variable and informative characters, the best-fit model selected using the AIC, tree lengths (in number of substitutions per site across the entire sample of taxa) and the model-averaged parameter estimates for models of DNA sequence evolution with associated importance values (as estimated using ModelTest v3.7; Posada and Crandall 1998).

TABLE 2. Congruence and conflict of inferred bipartitions among data sets

| | | Data set | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Support level | Data set | mtDNA | RAG1 | ACO1-I9 | FGB-I5 | MB-I2 | Concatenated | #Conflicts | #Resolved (/variable base) |
| 90% ML | mtDNA | – | 1 (0.012) | 4 (0.044) | 2 (0.028) | 0 (0.000) | 1 (0.006) | 8 | 67 (0.052) |
| | RAG1 | 26 (0.302) | – | 1 (0.015) | 1 (0.019) | 0 (0.000) | 0 (0.000) | 3 | 45 (0.043) |
| | ACO1-I9 | 31 (0.369) | 25 (0.368) | – | 1 (0.018) | 0 (0.000) | 0 (0.000) | 6 | 48 (0.060) |
| | FGB-I5 | 13 (0.181) | 9 (0.167) | 10 (0.179) | – | 0 (0.000) | 0 (0.000) | 4 | 18 (0.042) |
| | MB-I2 | 15 (0.208) | 15 (0.300) | 15 (0.283) | 7 (0.226) | – | 0 (0.000) | 0 | 20 (0.045) |
| | Concatenated | 54 (0.320) | 41 (0.256) | 43 (0.267) | 14 (0.088) | 18 (0.114) | – | 1 | 156 (0.039) |
| 75% ML | mtDNA | – | 7 (0.058) | 14 (0.113) | 9 (0.089) | 4 (0.041) | 6 (0.032) | 40 | 89 (0.070) |
| | RAG1 | 37 (0.308) | – | 6 (0.058) | 6 (0.070) | 6 (0.071) | 8 (0.043) | 33 | 68 (0.064) |
| | ACO1-I9 | 42 (0.365) | 33 (0.320) | – | 7 (0.082) | 1 (0.012) | 3 (0.016) | 31 | 68 (0.086) |
| | FGB-I5 | 23 (0.228) | 17 (0.198) | 18 (0.212) | – | 3 (0.054) | 7 (0.039) | 32 | 35 (0.082) |
| | MB-I2 | 26 (0.265) | 19 (0.226) | 20 (0.241) | 14 (0.250) | – | 3 (0.017) | 17 | 35 (0.079) |
| | Concatenated | 75 (0.403) | 53 (0.283) | 56 (0.304) | 27 (0.150) | 28 (0.156) | – | 27 | 172 (0.043) |
| 95% Bayesian | mtDNA | – | 20 (0.146) | 20 (0.141) | 11 (0.092) | 10 (0.084) | 13 (0.082) | 74 | 101 (0.079) |
| | RAG1 | 38 (0.277) | – | 13 (0.113) | 17 (0.170) | 14 (0.140) | 14 (0.091) | 78 | 74 (0.070) |
| | ACO1-I9 | 46 (0.348) | 36 (0.313) | – | 12 (0.119) | 5 (0.051) | 14 (0.092) | 64 | 77 (0.097) |
| | FGB-I5 | 26 (0.218) | 18 (0.180) | 20 (0.198) | – | 9 (0.117) | 15 (0.099) | 64 | 44 (0.103) |
| | MB-I2 | 31 (0.261) | 23 (0.230) | 27 (0.273) | 16 (0.208) | – | 8 (0.053) | 46 | 49 (0.110) |
| | Concatenated | 81 (0.513) | 58 (0.377) | 63 (0.414) | 30 (0.197) | 37 (0.247) | – | 64 | 138 (0.034) |

The numbers of conflicting (above the diagonal) and congruent (below the diagonal) bipartitions of the **complete character** matrix (i.e. no missing data; $S = 191$) for 5 data sets, at 3 levels of support from 2 analysis types (90 and 75% bootstrap under ML, and 95% Bayesian estimated posterior probability). Each conflict and congruence number is also shown scaled by the number of bipartitions retained in a semistrict consensus of trees from the 2 data sets being compared (in parenthesis). In addition, for each data set the total number of conflicting bipartitions (# Conflicts) and the total number of bipartitions supported at a given criterion level (# Resolved; also scaled by number of variable bases, in parenthesis), are given. Note: because bipartitions can conflict with multiple data sets and multiple bipartitions in those data sets, these numbers can exceed the number of resolved nodes for a given data set and support level.

**complete taxa** and **core taxa** matrices yielded trees that were largely congruent, differing only at nodes receiving low support values (e.g., $<75\%$ bootstrap or $<0.95$ estimated posterior probabilities). By contrast, relationships inferred from individual gene analyses conflicted with these concatenated trees and with trees inferred from other genes (see above). These bipartition-specific patterns of conflict and congruence are

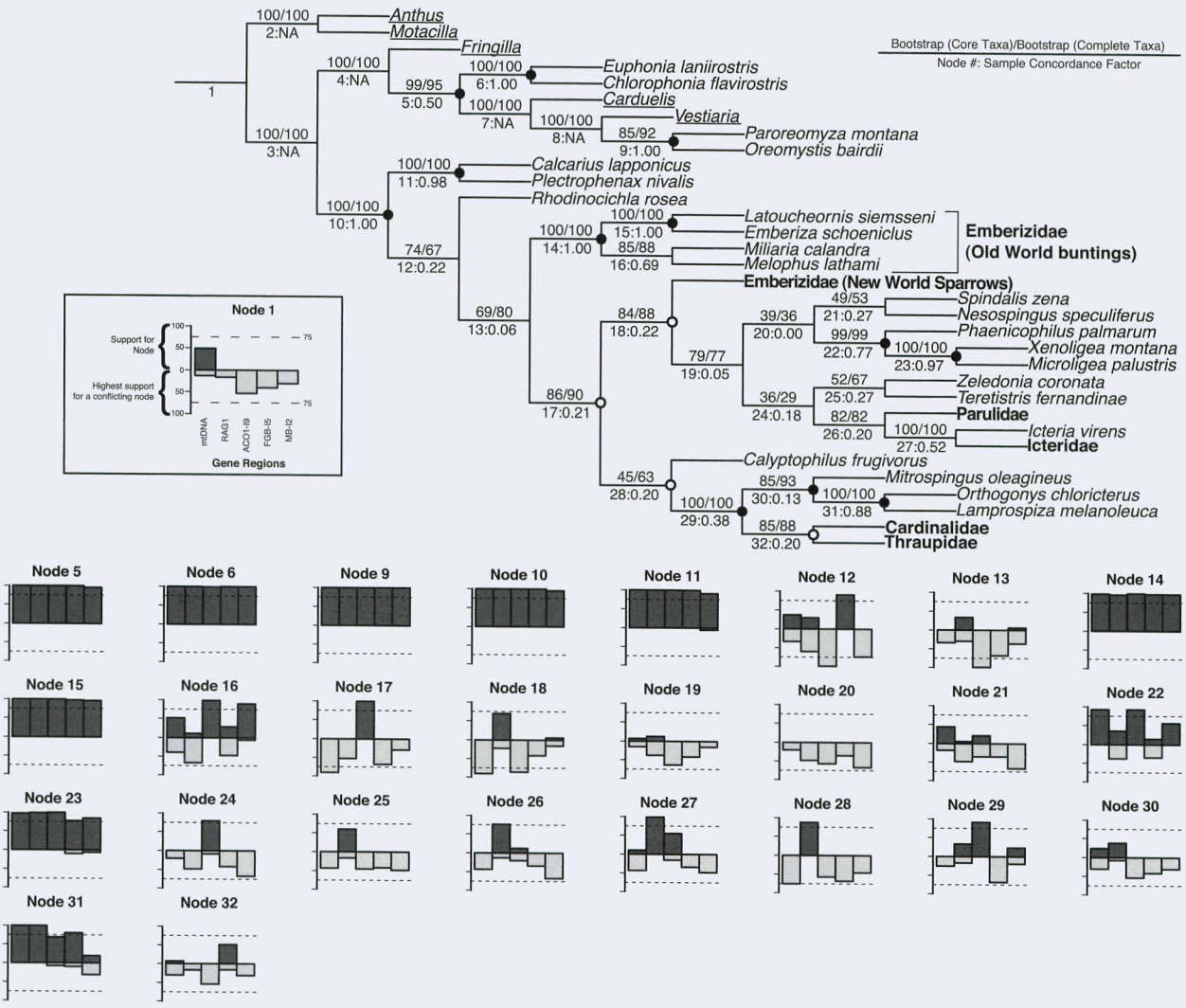


FIGURE 2. Results of concatenated analysis of 6 genes from New World 9-primaried oscines. The topology shown (with arbitrary branch lengths) is a "backbone" derived from partitioned ML analysis of the data: 5 core clades are represented as traditional family names (see Figs. 3–7 for details on relationships within each). Underlined taxa lack at least one nuclear gene. Nodes are labeled with a numeric index, as well as with bootstrap support from analyses of the **core taxa** and **complete taxa** matrices and sample-wide concordance factors from BCA (Ané et al. 2007) of the data (see "Methods" section for description). Closed circles indicate significant support (estimated posterior probability $\geqslant 0.95$) estimated in species tree analysis of the same data, and open circles significant conflict (i.e., a conflicting relationship was found with $\geqslant 0.95$ estimated posterior probability). For each node in this tree, a graph indicates individual gene patterns of support and conflict based on separate gene region analyses (ML bootstrap values are given, but qualitatively similar results were obtained from comparison of estimated Bayesian posterior probabilities, not shown; see inset for interpretation of these graphs). Note that since not all taxa have complete data (e.g., some outgroups and ingroup taxa sampled only for mtDNA), and support/conflict measures and concordance analyses were performed on the **complete character** data set, not all nodes have corresponding graphs.

summarized in Figures 2–7 (for Figs. 3–7, the bipartition-specific patterns of conflict and congruence are shown only for the basal node; for the patterns associated with the remaining nodes, see Supplementary Figs. S1–S4, available from doi: 10.5061/dryad.52565).

As evaluated relative to individual gene regions through analyses of the **complete character** matrix, concatenated analyses yielded much greater resolution (from 138 to 172 of the possible 188 bipartitions, depending on the analysis and support level; Table 2). This difference may suggest that individual gene regions contribute support to partially overlapping sets of bipartitions that combine incrementally. In addition, it is also possible that combining data sets assists in resolving patterns of homoplasy in individual partitions (especially the rapidly evolving mtDNA): the so-called "emergent signal" phenomenon (Barrett et al. 1991; Chippindale and Wiens 1994; Gatesy et al. 1999; Gatesy and Baker 2005). Examination of gene-specific patterns of support and conflict for individual bipartitions suggests incrementalism is at least partly responsible for the higher resolution of the concatenated trees. For instance, although Nodes 26 and 28 in Figure 2 are each strongly supported by only a single gene region (RAG1

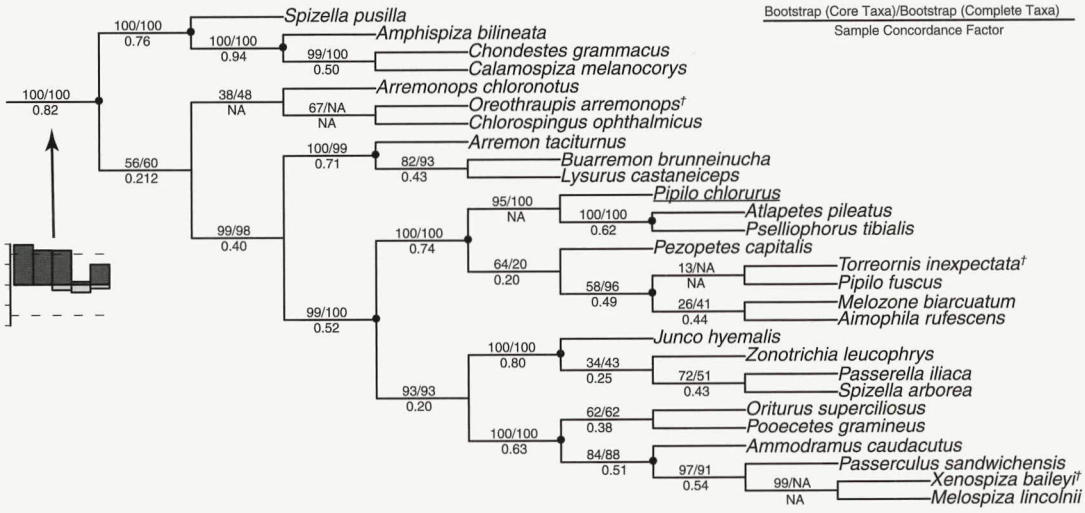


FIGURE 3. Results of concatenated analysis of 6 genes from the New World sparrows (family Emberizidae, in part). Support and conflict for monophyly of this group are shown graphically as in Figure 2. Underlined taxa lack at least one nuclear gene, and daggers next to taxon names indicate only mitochondrial sampling. Individual nodes are labeled with bootstrap support from analyses of the **core taxa** and **complete taxa** matrices (see "Methods" section for description), and with concordance factors from BCA. Circles indicate support and conflict from the species tree analysis, as described in Figure 2.

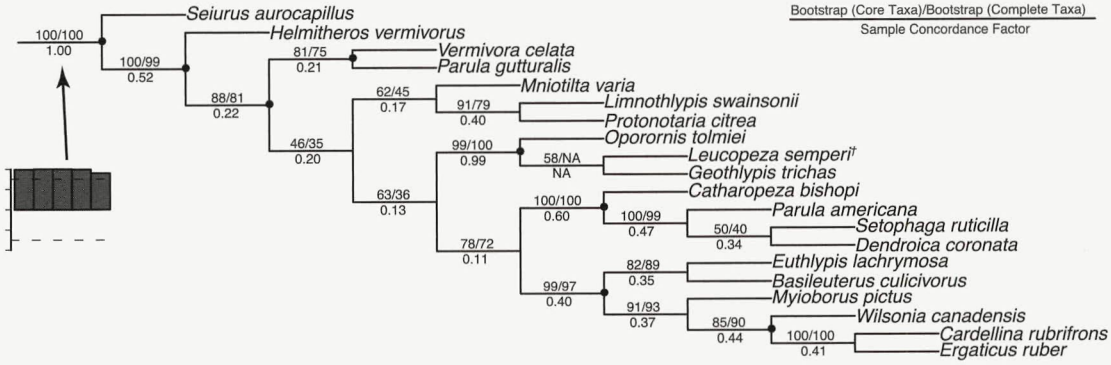


FIGURE 4. Results of concatenated analysis of 6 genes from the warblers (Parulidae). Labeling as in Figure 3.

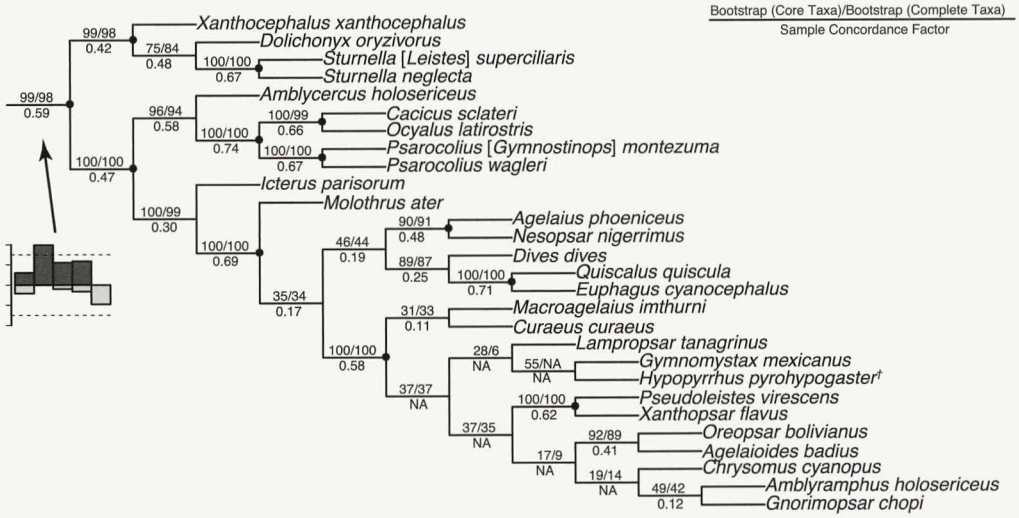


FIGURE 5. Results of concatenated analysis of 6 genes from the blackbirds and allies (Icteridae). Labeling as in Figure 3.

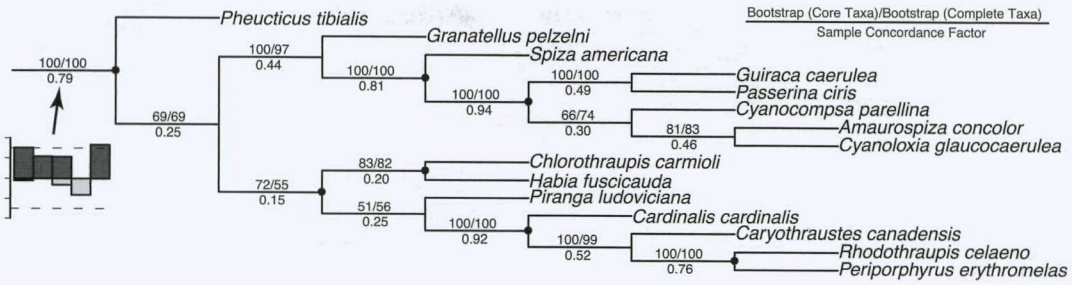


FIGURE 6. Results of concatenated analysis of 6 genes from the cardinals (Cardinalidae). Labeling as in Figure 3.

TABLE 3. Patterns of bipartition-specific support and conflict among-gene regions

| # Regions supporting | # Regions Conflicting | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Concatenated support <75% | | | | Concatenated support ⩾75% | | | |
| | 0 | 1 | 2 | 3 | 0 | 1 | 2 | 3 |
| 0 | 34 | 15 | 1 | 1 | 8 | 3 | 2 | 0 |
| 1 | 7 | 8 | 2 | 0 | 32 | 8 | 1 | 0 |
| 2 | 0 | 1 | 0 | 0 | 21 | 5 | 0 | 0 |
| 3 | 0 | 0 | 0 | 0 | 16 | 2 | 0 | 0 |
| 4 | 0 | 0 | 0 | 0 | 8 | 0 | 0 | 0 |
| 5 | 0 | 0 | 0 | 0 | 13 | 0 | 0 | 0 |

Tabulated are the numbers of bipartitions among 191 taxa in the **complete character** matrix (see text for explanation) in the concatenated-data tree (Figs. 2–7) that are recovered in ⩾75% of bootstrap replicates from 0 to 5 individual gene analyses (# regions supporting), and for which 0–3 individual genes recover ⩾75% bootstrap support for a conflicting bipartition (# regions conflicting). The data are also split by whether or not individual bipartitions are supported in a concatenated analysis of the data (concatenated support ⩾ or <75%). For example, there are 13 bipartitions supported in the concatenated analysis that are recovered with ⩾75% bootstrap by all 5 individual gene regions and contradicted by none.

and ACO1-I9, respectively), both are recovered with strong support in the combined analyses. In fact, there are 32 bipartitions with at least moderate support (⩾75% bootstrap recovery) in the combined analyses that are supported by only a single gene region analysis (Table 3). However, this is not the entire explanation, as we also see evidence of bipartitions that are not supported by any single gene region but are nevertheless strongly supported by the concatenated data. Two such examples are Node 29 in Figure 2, and the basal node of tanagers (Fig. 7); in neither case is there significant support for, or conflict with, these relationships in individual gene analyses, whereas the concatenated analyses yield strong support (85–93% bootstrap recovery). Systematic examination of the concatenated tree yields a total of 8 such cases (Table 3). Thus, it seems clear that both incrementalism and "emergent signal" contribute to the overall greater resolution of the concatenated tree.

In terms of specific relationships found in single gene and concatenated analyses, we outline several notable results. First, concatenated analyses strongly support the monophyly of each of 5 clades roughly corresponding to traditional notions of New World 9-primaried oscine families: the Emberizidae, Parulidae, Icteridae, Cardinalidae, and Thraupidae. In addition to concatenated support, these lineages derive substantial (i.e. ⩾75% ML bootstrap or ⩾0.95 estimated posterior probability) support from between 0 (Thraupidae) and 5 (Parulidae) genes analyzed separately (Figs. 2–7). Despite this rough correspondence with the traditional taxonomy of these groups, a number of lineages classically associated with one core clade in fact appear to be members of another (e.g., *Oreothraupis* appears to be a sparrow rather than a tanager), including many cases previously reported in phylogenetic surveys that addressed subsets of this overall radiation (e.g. *Piranga* "tanagers" as cardinals; Klicka et al. 2000; Yuri and Mindell 2002; Klicka et al. 2007): these are discussed in more detail below.

Outside of these core lineages, a number of monotypic or low diversity genera fall out as distant relatives. These genera, which have traditionally been associated with the Emberizidae, Thraupidae, or Parulidae, include the North American longspurs and snow and McKay's buntings (*Calcarius* and *Plectrophenax*; hereafter called "longspurs"); the Central and South American endemic *Rhodinocichla*; the Central American montane forest specialist *Zeledonia*; the Caribbean endemic taxa *Spindalis*, *Nesospingus*, *Phaenicophilus*, *Xenoligea*, *Microligea*, *Teretistris*, and *Calyptophilus*; and the primarily South American endemic genera *Mitrospingus*, *Orthogonys*, and *Lamprospiza*. Of these, the sister-group relationship of the last 3 genera to the Thraupidae plus Cardinalidae appears to be strongly supported by concatenated analysis, but only by RAG1 in single gene analyses. In addition a monophyletic Hispaniolan radiation comprising *Phaenicophilus*, *Xenoligea*, and *Microligea* is also well supported (see also Lovette and Bermingham 2002; Klein et al. 2004). Relationships among the remaining taxa vary widely among-gene regions, although concatenated analyses suggest that many of these genera fall into a well-supported grouping that also includes the core Parulidae and Icteridae. Finally, we note that one significant among-region conflict affects the relationships of a core group, as traditional taxonomy places the Old World buntings (*Emberiza*, *Miliaria*, *Melophus*, and *Latoucheornis*) in the Emberizidae along

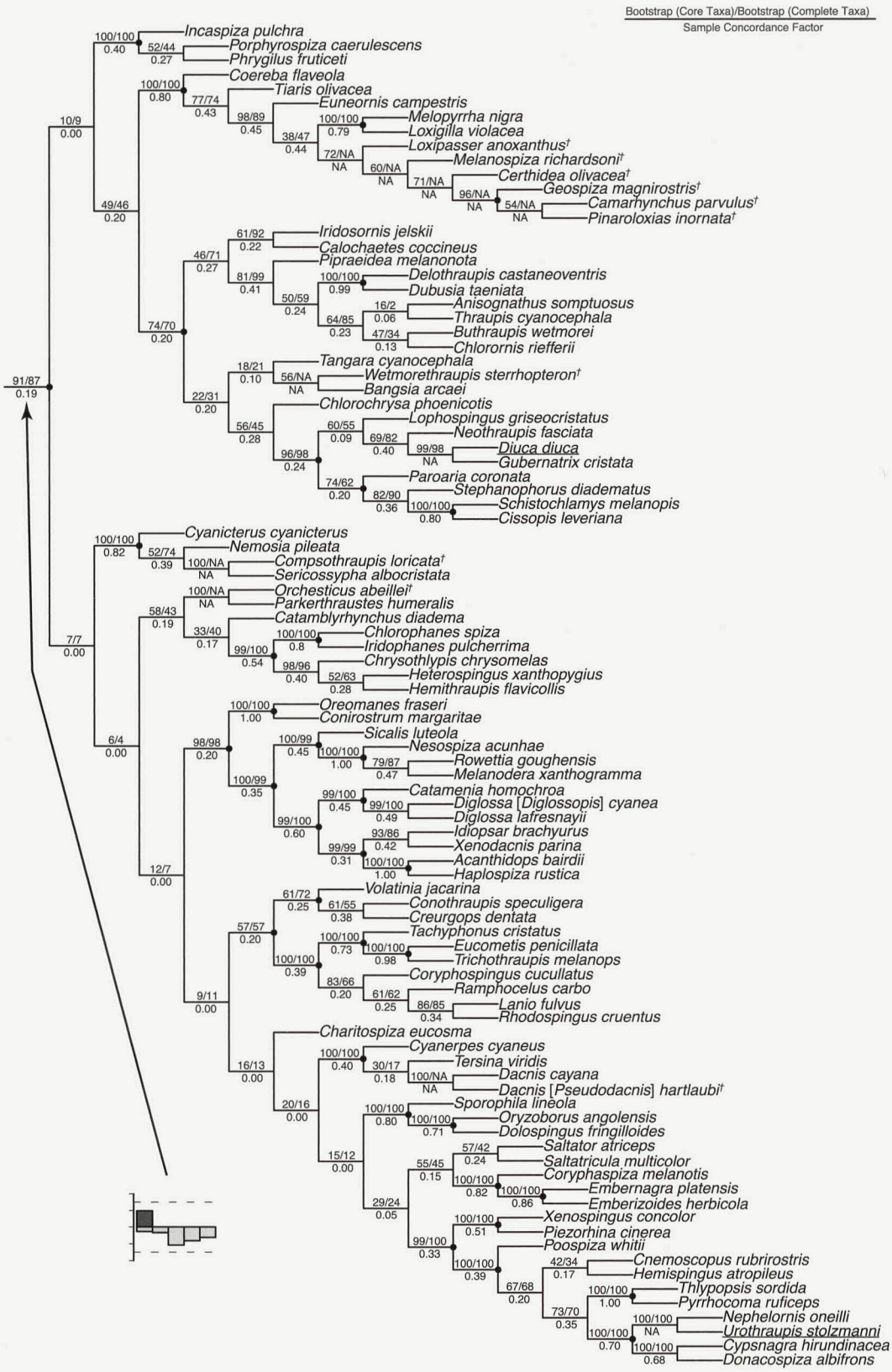


FIGURE 7. Results of concatenated analysis of 6 genes from the tanagers (family Thraupidae). Labeling as in Figure 3.

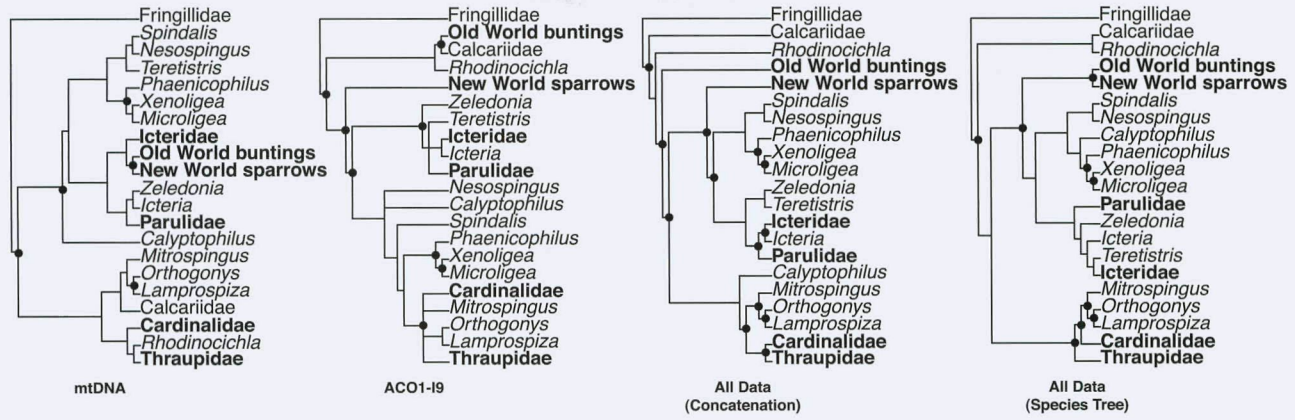


FIGURE 8. Summary of results from selected single-gene, concatenated, and species tree analyses. Shown are 4 "backbone" trees with 8 clades collapsed and highlighted in bold (see Figs. 2–7 for composition). Nodes with $\geqslant 75\%$ bootstrap support or $\geqslant 0.95$ estimated posterior probability are marked with closed circles.

with the New World sparrows. Previous phylogenetic reconstructions based on mtDNA (Klicka et al. 2000; Yuri and Mindell 2002) and the mtDNA results obtained here strongly support this view (Fig. 8). By contrast, 1 of 4 nuclear loci sampled (ACO1-I9) strongly contradicts it, placing the Old World buntings in a clade with the longspurs, and uniting the New World sparrows with all other New World taxa to the exclusion of this bunting/longspur group (Fig. 8). Our concatenated analysis (Figs. 2 and 8) agrees with this latter arrangement, actually nesting the sparrows within an exclusively New World clade. This conflict constitutes the disagreement with perhaps the most profound biogeographic and taxonomic implications in our analysis.

### *Bayesian Concordance Analysis*

In addition to the congruence and concatenation analyses reported above, we also performed BCA, using the trees obtained from primary Bayesian analyses of individual gene regions for the **complete character** matrix. BCA of these trees yielded posterior probabilities of 1 for the occurrence of 5 separate gene trees in the data, regardless of the prior on gene tree number determined by $\alpha$. The primary concordance trees obtained from these analyses were fairly similar to those obtained from concatenated analysis. In particular, the BCA analysis recovered monophyly of the 5 core lineages with concordance factors ranging from 0.19 (Thraupidae) to 1.00 (Parulidae; Figs. 3–7). The concordance trees differed from the concatenated results mainly in their separation of the Icteridae from the Parulidae by several old endemic lineages, and in the relationships among those lineages. The concordance analysis recovered monophyly of Cardinalidae+Thraupidae, as well as a sister-group relationship between these 2 clades and 1 containing *Mitrospingus*, *Orthogonys*, and *Lamprospiza*, as found in the concatenated analysis. This congruence is somewhat surprising given that no single gene region recovered these relationships with appreciable support (see above).

### *Species Tree Analyses*

Three preliminary $2 \times 10^8$ generation runs of BEAST indicated that convergence in terms of model parameters and likelihoods was not reached until $\sim 5 \times 10^7$ generations (not shown). Importantly, these runs also established consistent convergence of clade posterior probabilities, especially with regard to monophyly of the 5 core lineages (Supplementary Fig. S5). The maximum clade-credibility tree reconstructed from the posterior of the $5 \times 10^8$ final run (Supplementary Fig. S3) was consistent with these preliminary runs both in terms of estimated parameters (all of which had effective sample sizes $> 200$ with the majority $> 1000$; results not shown) and clade posterior probabilities. The only remarkable difference between this tree and that obtained via concatenation or concordance was the strong estimated support for monophyly of the traditionally constituted Emberizidae, including both the New World sparrows and the Old World buntings (Fig. 8 and Supplementary Figs. S3 and S4). In fact, only 4 relationships in the estimated species tree strongly conflict with those found by concatenation, all at basal positions within the tree (Fig. 2). Two of these involve conflict over the monophyly of Emberizidae, and the third involves placement of *Calyptophilus*, which species tree analysis places with other Caribbean taxa with strong support. The last conflict involves relationships among the *Mitrospingus* and its allies, the Cardinalidae, and the Thraupidae, where the species tree analysis strongly favors a relationship between the cardinalids and *Mitrospingus* and allies, rather than with the thraupids.

### *Lineage-Specific Diversity Patterns*

BEAST analysis of the **complete character** matrix yielded an absolute time-calibrated tree for the New

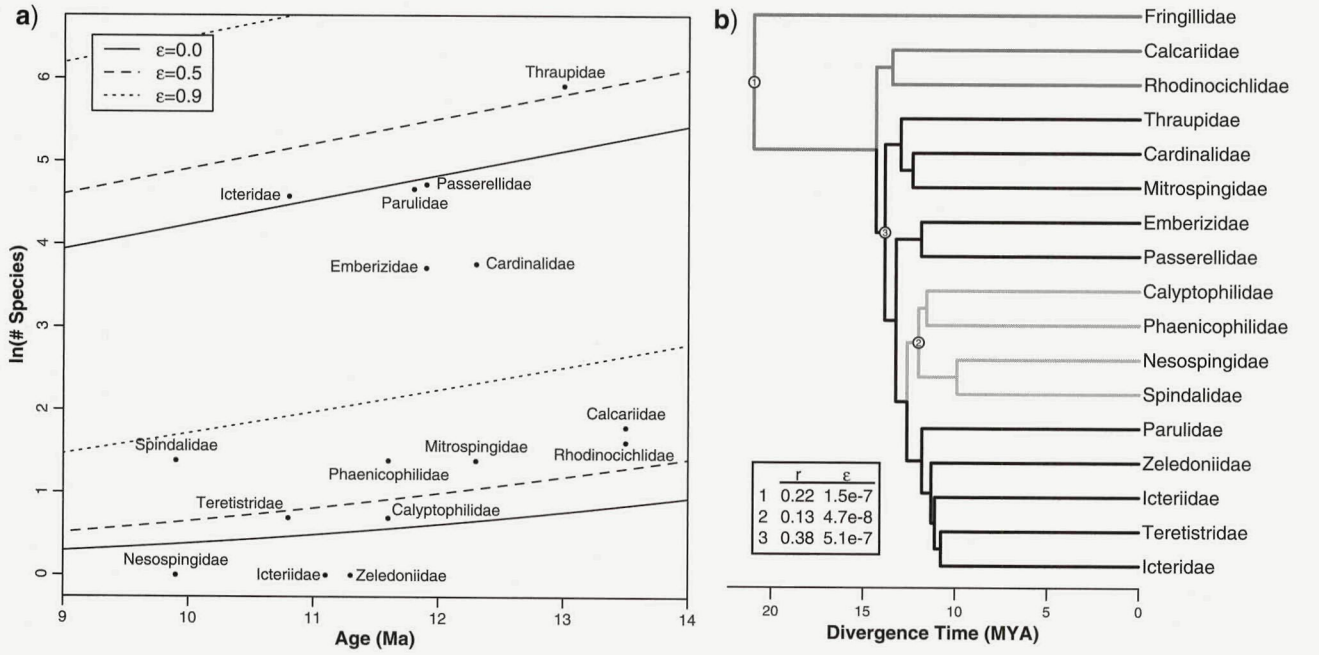


FIGURE 9. Diversification analyses of New World 9-primaried oscines. a) Relationship between clade age and clade diversity. Shown are the 5 core clades, and deeply divergent noncore lineages (Fig. 2; using taxonomy of Appendix), with ages estimated by Bayesian species tree analysis (see "Methods" section), and lineage diversities derived from standard taxonomies (Dickinson 2003). The 95% confidence intervals on lineage diversity given a background diversification rate for the ingroup of $(\ln[765]-\ln[2])/18\ \text{Ma}=0.33/\text{Ma}$, and 3 extinction fractions (0, 0.5, and 0.9) are plotted. b) MEDUSA analysis of clade diversity in the context of basal relationships among major clades. A 3 rate model was selected as the best fit ($-ln[\text{L}]=96.0$, $K=8$), with corresponding net diversification ($r$) and extinction fractions ($\varepsilon$) shown in the inset.

World 9-primaried oscines (Supplementary Fig. S6). We split this tree up into major lineages primarily following traditional taxonomy, extracting the ages and diversities of the 5 core clades, the Old World buntings, the longspurs, and the "old endemic" genera discussed above, treating *Phaenicophilus*, *Xenoligea*, and *Microligea* together as a single clade, and likewise *Mitrospingus*, *Orthogonys*, and *Lamprospiza*. We compared the stem ages and diversities of these groups with expected diversities under a uniform birth–death process with net diversification rate equal to the crown-clade estimate for their summed diversity and crown divergence time, allowing 3 extinction fractions (0.0, 0.5, and 0.9). The most striking pattern observed in this analysis (Fig. 9a) is that as many as 10 lineages appear to have lower diversity than expected under a uniform birth–death process for this group, with at least 5 showing significantly low diversity when some amount of extinction is assumed (the most reasonable scenario for these taxa given the age of the group). Under pure birth, 3 of these lineages (Icteriidae, Nesospingidae, and Zeledoniidae) are significantly less diverse than expected, and with 50% extinction, 2 more (*Teretistris* and *Calyptophilus*) are also significantly species poor. By contrast, only a single lineage—the phenotypically diverse, primarily South American clade Thraupidae—appears to be significantly more diverse than expected, assuming extinction in this clade is $\leqslant 50\%$ (Fig. 9a).

Fitting of piecewise diversification models to the same data using turboMEDUSA yielded an additional perspective on diversification in this group (Fig. 9b). The best-fit model for the maximum clade-credibility tree included 3 rate domains ($\Delta\text{AIC}_c=1.13$ relative to a one rate model): a basal domain covering the outgroup and the longspurs (*Calcarius* and *Plectrophenax*) with an intermediate diversification rate ($r=0.22$), a second domain covering most of the New World clade with approximately twice the basal diversification rate, and a third domain covering a monophyletic group of Caribbean endemics with approximately half the basal rate (inset, Fig. 9b). Extinction rates were estimated to be negligible for this clade; however, the power to estimate an extinction fraction should be very poor with these data, given the degree to which the tree was abstracted. Notably, this result was not representative of the array of diversification histories consistent with our data. Table 4 summarizes the results of repeating this analysis on a sample from the species tree posterior for our data. Two points of note are that no sampled trees favored rate uniformity, and that the result for the clade-credibility tree (one rate increase and one rate decrease) is in the minority, occurring in only 17% of the sample. The most common result obtained (48%) was for no rate increase and one rate decrease. Rate decreases were invariably associated with a clade dominated by Caribbean endemic lineages; whereas rate increases were either for all New World 9-primaried oscines excluding the longspurs and buntings (82%) or for the Thraupidae alone (18%).

TABLE 4. Results of MEDUSA analyses of 100 trees selected randomly from the species tree posterior distribution, categorized by the number of reconstructed rate increases and decreases for each sampled history

| Taxa included | # Rate increases | # Rate decreases | | | Row totals |
|---|---|---|---|---|---|
| | | 0 | 1 | 2 | |
| All Taxa | 0 | 0 | 48 | 26 | 74 |
| | 1 | 9 | 17[a] | 0 | 26 |
| | Column totals | 9 | 65 | 26 | 100 |
| Mainland taxa only | 0 | 0 | 63 | 0 | 63 |
| | 1 | 20[a] | 17 | 0 | 37 |
| | Column totals | 20 | 80 | 0 | 100 |

[a]The results obtained from analysis of the *BEAST maximum clade credibility tree estimate.

## DISCUSSION

### *Consensus, Concatenation, Concordance, and Species Tree Perspectives on New World 9-Primaried Oscine Relationships*

For over 20 years, it has been known that individual gene trees may conflict with one another, and with the true hierarchical relationships among species (the "species tree"), due to the inherent stochasticity of mutation-drift processes (Pamilo and Nei 1988; Doyle 1992; Moore 1995; Degnan and Rosenberg 2009). Although the early history of molecular systematics was dominated by work on a single locus (mtDNA), over the past decade, it has become increasingly common to sample multiple loci, raising the specter of gene-tree species-tree incongruence as an empirical as well as a theoretical problem. This has driven the development of an array of methods that explicitly incorporate stochastic variation in gene genealogies into phylogenetic inference (Liu and Pearl 2007; Kubatko et al. 2009; Liu et al. 2010; reviewed in Liu et al. 2009b). In a recent review, Edwards 2009 called for incorporation of species tree thinking into modern phylogenetic practice. However, empirical progress in this area has to some extent been limited by the computational tools available, especially given the large size (both in terms of genes and taxa) of many recent data sets. For instance, a number of studies have reported inconsistent behavior from MCMC methods for species tree estimation (e.g., BEST; Liu 2008), despite the moderate size of data sets analyzed and sometimes extraordinarily long chains being run (e.g., Cranston et al. 2009; Alström et al. 2011). In part because of this limitation, a number of less computationally intensive alternatives have been developed based on point estimates of multiple gene trees (Kubatko et al. 2009) or heuristic analyses of coalescent time distributions (Liu et al. 2009a). In addition to these coalescent methods, more general congruence analyses that can handle quite large gene trees are also being developed for analysis of posterior distributions of trees from multiple gene regions (Ané et al. 2007; Larget et al. 2010). However, our results suggest that purely gene-tree-based methods may have significant disadvantages relative to full-likelihood methods.

Although consensus and concordance methods are appealing choices for analysis of data sets with large numbers of taxa, our data present difficulties for both. This is primarily because they encompass multiple modes of inheritance and thus ploidy levels. Although we can easily count the number of genes supporting any relationship (a more appropriate measure of support than the number of characters, in a species tree framework; Degnan et al. 2009), the evidential weight of those genes is not equivalent. That is, there is a higher probability of the genealogy of mtDNA and Z-linked genes (such as ACO1-I9) matching the species tree than the genealogies of autosomal genes (FGB-I5, MB-I2, and RAG1). Neither simple consensus nor current implementations of concordance approaches (BCA) can take this into account. Consequently, although each relationship is supported by 2 independent loci, we cannot say that Node 16 (ACO1-I9 and MB-I2) has support equal to Node 22 (mtDNA and ACO1-I9; Fig. 2). More importantly, we cannot accurately adjudicate between conflicting genes differing in ploidy, as seen at Nodes 17 and 28 (Fig. 2). More generally, use of consensus itself can be problematic in species tree estimation, due to the existence of conditions under which it can be positively misleading (Degnan and Rosenberg 2006; but see Huang and Knowles 2009).

For these reasons, species tree estimation methods are preferable for our data. As noted above, such methods fall into 2 categories: those that work with point estimates or posterior distributions of gene trees, and those that work directly with sequence data, jointly estimating gene and species trees. The former are appealing, on the one hand because using modern methods (Stamatakis 2006a; Zwickl 2006; Liu et al. 2009), phylogenetic inference of gene trees can be quite efficient even for large numbers of taxa, and on the other that joint estimation of gene and species trees can be computationally challenging, even for relatively small numbers of taxa (e.g., Cranston et al. 2009; Alström et al. 2011). However, to date no such method explicitly incorporates information on ploidy into species tree estimation, a drawback shared with consensus methods (although not intrinsically). Perhaps more problematically, our data suggest that the robustness of individual gene tree inference may be significantly influenced by other gene trees, through their interaction via the species tree—an effect that cannot occur with summary statistic methods. Notably, monophyly of the Thraupidae is not recovered with strong support in any single gene analysis, although it is strongly supported by both concatenation and species tree inference (Fig. 7). Although not a pervasive phenomenon (we detected only 7 other cases of "emergent" support; Table 3), it proves critical for delineating a major lineage within our group. For these reasons, even though use of full data and likelihood methods is challenging for large data sets and may currently be impossible for the largest data sets, we

suggest that it is critical for appropriate analysis of heterogeneous data such as ours (e.g., those including mitochondrial, sex-linked, and autosomal data).

### *Phylogenetic Relationships among New World 9-Primaried Oscines*

This study provides the first comprehensive generic sampling for a clade comprising ~8% of all birds. Our analyses establish the monophyly of 5 large clades within this monophyletic radiation that roughly correspond to 5 currently recognized families: the Emberizidae, Parulidae, Icteridae, Cardinalidae, and Thraupidae (Figs. 2–7). Exceptions to the monophyly of these groups as they are currently recognized involve either (1) individual genera that appear to be placed in the wrong family-level clade or (2) deeply divergent lineages that fall outside of the major clades, often with poor support for their relative placement, or with conflicting support among-gene regions. We discuss each of these types of conflict in turn.

Among the misplaced taxa, 2 genera of tanagers, *Chlorospingus* and *Oreothraupis*, were strongly supported in this analysis as members of the New World sparrows (Emberizidae). Previous work (Yuri and Mindell 2002; Klicka et al. 2007) had shown that the bush "tanagers" of genus *Chlorospingus* are sparrows. In our study, cytochrome *b* data obtained from a museum skin also supported placement of the "tanager-finch" *Oreothraupis*, a narrowly distributed Andean endemic (sometimes classified within the sparrow genus *Atlapetes* (Storer 1958; Paynter 1970), within the sparrows as well. Conversely, many granivorous, relatively heavy billed taxa that have until recently been classified as sparrows are instead quite clearly tanagers, including the genera *Porphyrospiza, Phrygilus, Melanodera, Haplospiza, Acanthidops, Lophospingus, Donacospiza, Rowettia, Nesospiza, Diuca, Idiopsar, Piezorhina, Xenospingus, Incaspiza, Poospiza, Sicalis, Emberizoides, Embernagra, Volatinia, Sporophila, Oryzoborus, Melopyrrha, Dolospingus, Catamenia, Tiaris, Loxipasser, Loxigilla, Euneornis*, and *Melanospiza*, all 4 genera of Darwin's finches (*Geospiza, Camarhynchus, Certhidea*, and *Pinaroloxias*), *Urothraupis, Charitospiza, Saltatricula, Coryphaspiza, Coryphospingus, Rhodospingus, Gubernatrix*, and *Paroaria*. Following pioneering DNA–DNA hybridization work by Bledsoe (1988) that first suggested some of these relationships, many previous sequence-based studies (Burns 1997; Klicka et al. 2000; Burns et al. 2002; Lovette and Bermingham 2002; Yuri and Mindell 2002; Burns et al. 2003; Klicka et al. 2007) established that one or more of these genera had affinities with tanagers rather than sparrows. Our present sampling allows us to declare this list complete.

Previous studies (Lanyon and Omland 1999; Klicka et al. 2000; Lovette and Bermingham 2002) have also clearly delineated the warblers (Parulidae) and blackbirds (Icteridae) and established that lineages sometimes previously thought to be allied to the Parulidae (the conebills *Conirostrum* and *Oreomanes*) are actually tanagers, whereas others (*Granatellus*) are cardinals, as corroborated here. In addition, these previous studies identified a number of highly divergent "warbler" lineages whose placement relative to the core warbler radiation was ambiguous: these are discussed below. The remaining "misplaced" taxa involve the Cardinalidae and Thraupidae. We found 4 traditional tanager genera—*Amaurospiza, Chlorothraupis, Habia*, and *Piranga*—to be members of a strongly supported cardinal clade, corroborating previously published phylogenies based on mtDNA (reviewed in Klicka et al. 2007). Conversely, we found additional support for placement of the genera *Saltator* and *Parkerthraustes* (a monotypic genus recently separated from the cardinalid *Caryothraustes*; Remsen 1997), within the tanagers (Klicka et al. 2007).

The last group of conflicts involve deeply divergent lineages variously allied in traditional taxonomies with the Emberizidae, Thraupidae, and especially the Parulidae (Figs. 2 and 7). Two lineages of sparrow-like birds, the longspurs and snow and McKay's buntings (*Plectrophenax* and *Calcarius*, collectively the "longspurs"), and the Old World buntings (*Emberiza, Miliaria, Melophus*, and *Latoucheornis*) appear only distantly related to the New World sparrows with which they have historically been allied in the Emberizidae. The distinctness of the longspurs has long been recognized in analyses of mtDNA sequence data (Klicka et al. 2000; Yuri and Mindell 2002), such that recent taxonomies (Chesser et al. 2010) recognize this lineage as its own family, the Calcariidae. By contrast, the relationship of the Old World buntings obtained here in the concatenated-data analyses is novel and surprising, as it contradicts analyses of mtDNA data that strongly support their presumed relationship with the New World sparrows (Klicka et al. 2000, 2007). Indeed, this conflict is present in our own data and analyses: mtDNA data and species tree analysis of the combined data strongly support the traditional relationship of these groups, whereas both ACO1-I9 and concatenated and concordance analyses of mtDNA and nuclear data support placement of the buntings outside of an exclusively New World radiation of sparrows, warblers, blackbirds, cardinals, and tanagers (Fig. 8).

These alternative relationships of sparrows and buntings are irreconcilable except by invoking differential lineage sorting or horizontal gene transfer. Ané (2010) suggested a test of the lineage sorting explanation for conflict, by comparison of genome-wide concordance factors for alternative conflicting bipartitions of the taxa in question. This test involves comparison of split concordance factors for the alternative splits not found in the primary concordance tree, relative to their estimated 95% credibility intervals. If the alternative histories have similar concordance factors with overlapping CIs, this is consistent with a lineage sorting explanation. In the case of the Old World buntings, the bipartition in the primary concordance tree supports separation of the buntings and sparrows

(CF = 0.219, 95% CI = [0.007, 0.661]), whereas the best 2 alternative arrangements (the second of which is the traditional arrangement) have similar CFs with broadly overlapping CIs (0.210 [0.007, 0.615] and 0.196 [0.007, 0.602], respectively). Although there is high variance in all of these estimates due to our small sample of loci, this pattern suggests that lineage sorting is a possible explanation for this conflict. This conclusion is corroborated by the fact that our species tree analysis—which explicitly incorporates coalescent variation in gene trees—yields a topology in agreement with the mtDNA tree, which due to ploidy has a higher expectation of matching the species tree. In addition, examination of the estimated ancestral effective population sizes at nodes involved in this conflict indicates that none appear to have unreasonably high estimates, as might be expected if the species tree had been distorted by the effects of horizontal gene transfer (results not shown). More extensive analysis of this problem using larger data sets (in terms of sampled loci) will be necessary to clarify the relationships of these groups; however, in recognition of the uncertainty of their relationship and their biological distinctiveness each from the other, we propose to recognize them as separate families (Appendix).

The other 12 deeply divergent genera are traditionally classified as warblers or tanagers. Of these, one (*Rhodinocichla*) was weakly supported as an early diverging lineage within the New World 9-primaried oscines, 3 (*Mitrospingus*, *Orthogonys*, and *Lamprospiza*) were strongly supported as a sister clade to the cardinals and tanagers, another (*Calyptophilus*) was weakly supported as sister to the previous 3 plus cardinals and tanagers, and the remainder formed a moderately well-supported clade with the Parulidae and Icteridae (Fig. 8). It should be noted, however, that placement of many of these taxa relative to the core lineages (even where strongly supported by concatenation) varies and in some cases, conflicts among gene regions and analytical approaches (e.g., Node 27, Fig. 2). For instance, one of these lineages—the yellow-breasted chat *Icteria virens*—was supported as the sister lineage to the blackbird family Icteridae (Fig. 2); however, this is one case where there were contrasting results between concatenation and species-tree results for our data. Specifically, concatenation strongly supports a sister relationship of *Icteria* and Icteridae, whereas species tree analysis places *Teretistris* in this position, albeit with poor support (Supplementary Figs. S3 and S4). The only truly unambiguous relationship among them is the unity of the Hispaniolan endemics *Phaenicophilus*, *Xenoligea*, and *Microligea*, a result previously obtained using mtDNA data alone (Lovette and Bermingham 2002; Klein et al. 2004). Interestingly, 7 of these deeply divergent genera are Caribbean—primarily Greater Antillean—endemics, suggesting an important role for this region in acting as a dispersal route in the early history of this group, in preserving ancient diversity, or both (see below). In order to preserve ranking of the 5 core lineages as families, as currently recognized, we propose to recognize these divergent lineages as an additional 10 families (Appendix).

### *Dating and Diversification Rates of New World 9-Primaried Oscines*

We have reconstructed a timescale for diversification in this species-rich group. Our species tree analysis of the **complete character** data set calibrated by the basal divergence between the finches (Fringillidae) and our focal clade at 21 Ma (±3.9 standard error) yielded a crown-clade age of 14.3 Ma (15.4–13.6; 95% highest posterior density [HPD] interval). It could be argued that this external calibration is too old, as it is based on assuming a vicariant divergence between the "suboscine" *Acanthisitta* and all other passerine birds (Barker et al. 2004), but there are 2 lines of evidence that it is a reasonable estimate for our group of interest. First, this calibration yielded an estimated divergence time of 1.1 Ma (2.5–0 95% HPD) for the 2 honeycreepers *Oreomystis* and *Paroreomyza*, previously hypothesized to have diverged at a maximum of 5 Ma, based on the history of island formation in the Hawaiian archipelago. Thus, our estimate is significantly *younger* than—but still consistent with—expectations based on the geological record. Second, the per-lineage rate of cytochrome *b* evolution estimated in this analysis was 0.019/Ma (0.011–0.030 95% HPD), almost twice the pairwise rate of ~2%/Ma estimated in previous studies (Garcia-Moreno 2004; Lovette 2004; Weir and Schluter 2008). For these reasons, we suspect the ages reported here may be underestimates, rather than overestimates as expected if our external calibration was grossly in error. It is worth noting that our conclusions about general lineage diversification patterns should be unaffected by the absolute dates of these divergences. Given that our HPD age range for the honeycreepers (our only internal calibration) does not include its upper calibration boundary, dates on our tree are primarily driven by the assumed age of the root. More accurate estimation of this age in the broader context of passerine diversification, as well as incorporation of additional internal constraints (e.g., *trans*-Isthmian dispersal events), should be a priority for future work.

Comparisons of the extant diversity of these groups suggest that they have experienced differing rates of net diversification. First, regression of clade diversity on clade age failed to recover an age–diversity relationship (Fig. 9a). As has been pointed out previously (Rabosky 2009a), a clade age–diversity relationship is only expected during the early stages of a radiation, before ecological constraints have begun to limit net diversity. The fact that we find no relationship between clade diversity and age suggests that diversification of these lineages may have been impacted by ecological limits, as has already been suggested based on species-level analyses of one subset of them, the *Dendroica* warblers (Rabosky and Lovette 2008). Secondly, piecewise diversification models fit the pruned species tree

appreciably better than a uniform-rate model (Table 4 and Fig. 9b). Although results vary depending on the specific tree selected, our analysis indicates a single 2-fold rate increase within the New World 9-primaried oscines (excluding the longspurs), with a subsequent 3-fold decrease in a clade comprising *Calyptophilus*, *Phaenicophilus* and allies, *Nesospingus* and *Spindalis*. Taken together, these results suggest that diversification rates have varied widely among these lineages.

Neither of these analyses can explicitly account for the fact that individual lineages may not have had equal opportunities for diversification. For instance, spatial constraints (e.g., water barriers) may reduce the dispersal and subsequent diversification of some lineages. This is an intriguing possibility, as we found an excess of species-poor family-level clades (Fig. 9a), of which 3 (*Nesospingus*, *Teretistris*, and *Calyptophilus*) are endemic to the Caribbean. An additional 2 Caribbean lineages (*Spindalis* and *Phaenicophilus* and allies) are among the least diverse clades for their age in our sample. Additionally, the piecewise diversification analysis found the lowest diversification rates in a clade of 4 of these same Caribbean endemic genera. Thus, it seems clear that Caribbean lineages have experienced significantly lower diversification rates, most likely due to a combination of the strong spatial constraints of island area, extinction (due to sea-level changes, extreme weather events, or anthropogenic effects), and relatively high dispersal ability (which limits the potential for intra-island differentiation seen in other Caribbean taxa such as anoles; Losos 2009).

That said, removal of island lineages had no significant effect on the age/diversity regression, and in fact changed the estimated relationship to a negative one (not shown). Likewise, a piecewise diversification model fit to the species tree excluding all island lineages was essentially unaffected, showing an ~2-fold rate difference between the outgroup plus the longspurs and buntings and the core New World 9-primaried oscines (not shown). Based on these results, we speculate that ecological factors such as among-lineage competition may have affected diversification of the nonisland members of this clade. Alternatively, these lineages may vary in intrinsic characteristics (e.g., competitive ability, dispersal, and phenotypic lability) that have contributed to differing rates of lineage accumulation. Resolution of these competing explanations will be challenging (e.g., Rabosky 2010), but will be greatly facilitated by forthcoming species-level analyses of these groups.

A striking pattern in recent analyses of global passerine diversity (Ricklefs 2003) is the occurrence of large numbers of relatively species-poor lineages. Although none of the low diversity lineages identified here were similarly identified in previous studies (as they were subsumed within the higher level clades on which they were based), the pattern found here is consistent. For example, Ricklefs (2003) found that species-poor passerine lineages were distributed on islands significantly more often than expected by chance. Subsequent analysis (Ricklefs 2005) further suggested that many species-poor lineages were ecologically specialized, residing at the periphery of passerine morphospace. The island distributions and ecological specialization of many of the species-poor lineages within our focal clade are consistent with trends seen across passerines as a whole. As noted above, 3 of the lineages identified as significantly species poor in this study are essentially Greater Antillean endemics, and another 2 relatively species-poor (not significantly so, unless extinction $>50\%$) lineages are also Caribbean. Of the remaining 2 significantly species-poor lineages, *Zeledonia* is a narrowly distributed montane endemic from Central America, apparently adapted to a semiterrestrial lifestyle (Hunt 1971), whereas *Icteria* has a wide continental distribution and seems more generalist in its habits. We know of nothing particularly noteworthy about the remaining relatively (but not significantly) species-poor lineages with regard to their ecology or distribution, but the life histories of all except the longspurs and snow buntings are quite poorly known.

Given that this study targets a lineage already identified as species rich in higher level analyses (e.g., Ricklefs 2003), it is perhaps more surprising that our analyses identified some lineages as significantly species rich relative to uniform expectations. Our piecewise diversification analysis identified all New World 9-primaried oscines except the longspurs and buntings as having an elevated diversification rate (Fig. 9b) on the maximum clade-credibility tree. However, similar results were only obtained in analyses of a minority of trees sampled from the posterior (Table 4), and many such analyses identified the Thraupidae alone as having an elevated rate (see "Results" section). By contrast, the diversity–age correlation identified both the Icteridae and Thraupidae as significantly diverse in the absence of extinction, and the Thraupidae alone at extinction levels $>50\%$ (Fig. 9a). These results are of particular interest, because in comparisons with similar aged clades of passerines worldwide, the Thraupidae was previously identified as more species rich than expected (Ricklefs 2003). Our crown-clade estimate of diversification rate (without extinction) in this lineage is 0.45 $s \cdot Ma^{-1}$, which is nearly 40% above the average for the 9-primaried oscine clade as a whole. Despite the rather old external calibration used in this study, this high rate is comparable, for example, to rates estimated for Hawaiian silverswords (Baldwin and Sanderson 1998), although lower than estimated rates for some other putative radiations (e.g., salamanders of the *Plethodon glutinosus* group, Kozak et al. 2006; African ice plants, Klak et al. 2004). On the other hand, it is nearly an order of magnitude higher than the pure birth estimate for vertebrates as a whole ($b = 0.059\ s \cdot Ma^{-1}$; Alfaro et al. 2009), and 5 times the estimated net diversification rate for Neoaves ($0.089\ s \cdot Ma^{-1}$). These estimates suggest that diversification of this lineage has made a substantial contribution to the remarkably high overall diversity of the Neoaves.

The Thraupidae comprises a phenotypically diverse array of taxa that occupy nearly all South and Central

American habitats. It includes taxa as divergent as the large-billed, granivorous Darwin's finches (*Geospiza*), specialized nectarivores (*Cyanerpes*), and brilliantly colored high-altitude frugivores (*Buthraupis*). The group not only contains exemplars of each of these ecophenotypes (and more) but also includes multiple independent derivations of each of them (e.g., granivorous *Oryzoborus*, nectarivorous *Coereba*). Furthermore, tanagers have much more diverse plumage coloration patterns than related groups, reflecting the complex imprint of sexual and natural selection in this diverse group. This phenotypic diversity has driven their history of taxonomic confusion, since classical taxonomy was based primarily on external characters of the bill, legs, and plumage, all of which have evolved rapidly and repeatedly among the tanagers. It will be of great interest to more carefully dissect patterns of diversification within this group using phylogenetic reconstructions that are complete at the species level, especially with regard to bill morphologies, plumage evolution, and changes in distribution (e.g., see Mauck and Burns 2009; Sedano and Burns 2010; Burns and Shultz 2012).

## Supplementary Material

Supplementary material, including data files and/or online-only appendices, can be found in the Dryad data repository at http://datadryad.org, doi:10.5061/dryad.52565.

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## Appendix

### *A Taxonomy of New World 9-Primaried Oscines*

The New World 9-primaried oscines are traditionally classified in 5 families, with nothing to associate them with one another except adjacency within the linear order of passerines. Sibley and Monroe (1990), in an attempt to determine rank by genetic divergence, classified these 5 families as tribes within a single subfamily, the Emberizinae, within the family Fringillidae. As discussed in the main text, there is substantial evidence from molecular data for the existence of 5 clades corresponding to the traditional families. However, a number of genera appear to be more distantly related, raising the question of how those groups should be classified, and how the relatedness of all of them to one another should be reflected taxonomically. The sister group to this clade, comprising the chaffinches, goldfinches, honeycreepers, and allies, is currently recognized as a single family, the Fringillidae, by most taxonomies (American Ornithologists' Union 1998; (Dickinson, 2003)). One possible treatment for the group under consideration would be to rank it as a family (the Emberizidae), and to rank lineages within it as subfamilies; however, to do so would overturn more than a century of taxonomic practice. Instead, we have chosen to minimize changes to higher level avian classification and to continue to rank the lineages within this group as families. In addition, as a further effort to maintain stability, we have chosen to continue to recognize the 5 core lineages (Emberizidae, Cardinalidae, Thraupidae, Parulidae, and Icteridae) as families in accordance with universal practice (excepting Sibley and Monroe 1990). Perhaps unfortunately, given the constraint of naming only monophyletic groups, recognizing these 5 families requires that we recognize 11 additional families within this larger radiation. One of these—the Calcariidae—which includes the genera *Calcarius* and *Plectrophenax*, in addition to the recently resurrected genus *Rhynchophanes*, has already been recognized by the AOU (American Ornithologists' Union 1998). Another 5—the Rhodinocichlidae, Zeledoniidae, Teretistridae, Icteriidae and Calyptophilidae—have also been previously recognized (Bock 1994) for their

corresponding genera. Another family-level name, Phaenicophilidae, has previously been applied to that genus alone (Sclater 1886), but we suggest expanding its definition to include *Xenoligea* and *Microligea*. In addition to these previously named groups, we propose the following new family names (see descriptions below): Spindalidae (genus *Spindalis*), Nesospingidae (genus *Nesospingus*), and Mitrospingidae (genera *Mitrospingus*, *Lamprospiza*, and *Orthogonys*). These steps would triple the number of families in this diverse radiation of birds. More importantly, this would give formal recognition to the deep evolutionary history preserved in these unique lineages of birds, especially those in Caribbean habitats, some of which are threatened by habitat fragmentation and loss.

Finally, in addition to the 5 traditional core families and the 9 families listed above, we recommend recognition of a separate family name for the New World sparrows. As discussed previously, although our data strongly support monophyly of the Old World buntings and New World sparrows, they also demonstrate significant conflict over the placement of these groups relative to one another, with mtDNA strongly supporting a monophyletic grouping of the 2, and ACO1-I9 and combined analyses favoring their separation: analyses including additional gene regions will be used to address this conflict in more detail. For the sake of future taxonomic stability, and to recognize real biological differences between the 2 groups, we propose their separation and recognition of both at the family level. Aside from the obvious biogeographic difference (one group is exclusively New World, and the other is Old World with a single species breeding marginally in Alaska), these groups also differ in the frequency of sexual dichromatism (buntings are generally sexually dichromatic, sparrows monochromatic) and have often been seen as more closely allied to the genera *Plectrophenax* and *Calcarius* (Paynter 1970; Patten and Fugate 1998). Restriction of the family name Emberizidae to the Old World buntings (genus *Emberiza* and allies) requires application of another name to the sparrows. Several names for this group are already available, but the oldest is the Passerellidae (Cabanis and Heine 1850; see Bock 1994).

Here, we recognize the primarily New World group of 9-primaried oscines that form a clade sister to the finch family Fringillidae as the superfamily Emberizoidea. We list the families in our currently preferred order, with the genera (as recognized in the taxonomy of Dickinson 2003, with emendations from American Ornithologists' Union (1998) and Lovette et al. (2010)) assigned to each listed (alphabetically with the exception of the Parulidae; ordering within other families will depend on better sampled analyses of relationships in each, combined with standard sequencing conventions), although we recognize that substantial revision of generic limits will be necessary in the near future. Type designations and diagnoses are given for 3 new families, and a diagnosis is given for a fourth family not previously used for 2 of the genera we place within it.

Superfamily **Emberizoidea**

Family **Calcariidae** (Ridgway 1901); Genera: *Calcarius*, *Plectrophenax*, and *Rhynchophanes*.

Family **Rhodinocichlidae** (Ridgway 1902); Genera: *Rhodinocichla*.

Family **Emberizidae** (Vigors 1825b); Genera: *Emberiza*, *Latoucheornis*, *Melophus*, and *Miliaria*.

Family **Passerellidae** (Cabanis and Heine 1850–51); Genera: *Aimophila*, *Ammodramus*, *Amphispiza*, *Arremon*, *Arremonops*, *Atlapetes*, *Calamospiza*, *Chlorospingus*, *Chondestes*, *Junco*, *Lysurus*, *Melospiza*, *Melozone*, *Oreothraupis*, *Oriturus*, *Passerculus*, *Passerella*, *Pezopetes*, *Pipilo*, *Pooecetes*, *Pselliophorus*, *Spizella*, *Torreornis*, *Xenospiza*, and *Zonotrichia*.

Family **Spindalidae** (*new family*); Type genus: *Spindalis*; Diagnosis: containing a single genus, this family is diagnosed by the generic characters of *Spindalis* (Jardine and Selby 1837); Genus: *Spindalis*.

Family **Nesospingidae** (*new family*); Type genus: *Nesospingus*; Diagnosis: containing a single genus, this family is diagnosed by the generic characters of *Nesospingus* (Sclater 1885); Genus: *Nesospingus*.

Family **Phaenicophilidae** (Sclater 1886); Diagnosis: this family was originally erected for the genus *Phaenicophilus* alone. However, the 2 species in this genus share an olive back, wings and tail, gray underparts, and a broken white eye ring with both *Xenoligea* and *Microligea*; Genera: *Phaenicophilus*, *Xenoligea*, and *Microligea*.

Family **Zeledoniidae** (Ridgway 1907); Genus: *Zeledonia*.

Family **Teretistridae** (Baird 1864); Genus: *Teretistris*.

Family **Parulidae** (Wetmore et al. 1947); Genera: *Seiurus*, *Helmitheros*, *Parkesia*, *Vermivora*, *Mniotilta*, *Protonotaria*, *Limnothlypis*, *Oreothlypis*, *Leucopeza*, *Oporornis*, *Geothlypis*, *Catharopeza*, *Setophaga*, *Myiothlypis*, *Basileuterus*, *Cardellina*, and *Myioborus* (see Lovette et al. 2010; Chesser et al. 2010).

Family **Icteriidae** (Baird 1858); Genus: *Icteria*.

Family **Icteridae** (Vigors 1825a); Genera: *Agelaioides*, *Agelaius*, *Agelasticus*, *Amblycercus*, *Amblyramphus*, *Cacicus*, *Chrysomus*, *Curaeus*, *Dives*, *Dolichonyx*, *Euphagus*, *Gnorimopsar*, *Gymnomystax*, *Hypopyrrhus*, *Icterus*, *Lampropsar*, *Macroagelaius*, *Molothrus*, *Nesopsar*, *Ocyalus*, *Oreopsar*, *Psarocolius* (including *Gymnostinops*), *Pseudoleistes*, *Quiscalus*, *Sturnella* (including *Leistes*), and *Xanthocephalus*.

Family **Calyptophilidae** (Ridgway 1907); Genus: *Calyptophilus*.

Family **Mitrospingidae** (*new family*); Type genus: *Mitrospingus*; Diagnosis: we know of no morphological characters that unite these 3 genera of South and southern Central America. In lieu of such characters, we list 13 unreversed molecular synapomorphies of the group, from 4 different genes. These changes include (numbered by their position in each gene alignment) CYTB: A627C, T798C, C801T, and A1074G; ND2: C27T, T195C, C231T, C372A, G637A, C710T, and T968C; ACO1-I9: C977T; and RAG1: A1987G. Cladistically, we define this family as the descendants of the common ancestor of *Mitrospingus cassinii* and *Lamprospiza melanoleuca*; Genera: *Lamprospiza*, *Mitrospingus*, and *Orthogonys*.

Family **Cardinalidae** (Ridgway 1901); Genera: *Amaurospiza*, *Cardinalis*, *Caryothraustes*, *Chlorothraupis*, *Cyanocompsa*, *Cyanoloxia*, *Granatellus*, *Guiraca*, *Habia*, *Passerina*, *Periporphyrus*, *Pheucticus*, *Piranga*, *Rhodothraupis*, and *Spiza*.

Family **Thraupidae** (Cabanis 1847); Genera: *Acanthidops*, *Anisognathus*, *Bangsia*, *Buthraupis*, *Calochaetes*, *Camarhynchus*, *Catamblyrhynchus*, *Catamenia*, *Certhidea*, *Charitospiza*, *Chlorochrysa*, *Chlorophanes*, *Chlorornis*, *Chrysothlypis*, *Cissopis*, *Cnemoscopus*, *Coereba*, *Compsothraupis*, *Conirostrum*, *Conothraupis*, *Coryphaspiza*, *Coryphospingus*, *Creurgops*, *Cyanerpes*, *Cyanicterus*, *Cypsnagra*, *Dacnis* (including *Pseudodacnis*), *Delothraupis*, *Diglossa* (including *Diglossopis*), *Diuca*, *Dolospingus*, *Donacospiza*, *Dubusia*, *Emberizoides*, *Embernagra*, *Eucometis*, *Euneornis*, *Geospiza*, *Gubernatrix*, *Haplospiza*, *Hemispingus*, *Hemithraupis*, *Heterospingus*, *Idiopsar*, *Incaspiza*, *Iridophanes*, *Iridosornis*, *Lanio*, *Lophospingus*, *Loxigilla*, *Loxipasser*, *Melanodera*, *Melanospiza*, *Melopyrrha*, *Nemosia*, *Neothraupis*, *Nephelornis*, *Nesospiza*, *Orchesticus*, *Oreomanes*, *Oryzoborus*, *Parkerthraustes*, *Paroaria*, *Phrygilus*, *Piezorhina*, *Pinaroloxias*, *Pipraeidea*, *Poospiza*, *Porphyrospiza*, *Pyrrhocoma*, *Ramphocelus*, *Rhodospingus*, *Rowettia*, *Saltator*, *Saltatricula*, *Schistochlamys*, *Sericossypha*, *Sicalis*, *Sporophila*, *Stephanophorus*, *Tachyphonus*, *Tangara*, *Tersina*, *Thlypopsis*, *Thraupis*, *Tiaris*, *Trichothraupis*, *Urothraupis*, *Volatinia*, *Wetmorethraupis*, *Xenodacnis*, and *Xenospingus*.

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