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Defining a monophyletic Cardinalini: A molecular perspective

John Klicka [a,*], Kevin Burns [b], Garth M. Spellman [a,1]

[a] Barrick Museum of Natural History, Box 454012, University of Nevada Las Vegas, 4505 Maryland, Parkway, Las Vegas, NV 89154-4012, USA
[b] Department of Biology, San Diego State University, San Diego, CA 92182-4614, USA

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Abstract

Within the New World nine-primaried oscine assemblage, feeding morphology and behavior have long been used as a guideline for assigning membership to subgroups. For example, birds with stout, conical bills capable of crushing heavy seeds have generally been placed within the tribe Cardinalini (cardinal-grosbeaks). Many workers have tried to characterize this group more definitively, using a variety of morphological characters; however, the characters used often conflicted with one another. Previous molecular studies addressing the monophyly of Cardinalini have had only limited sampling within the group. In this study, we analyze mtDNA sequence data from all genera and 34 of the 42 Cardinalini species (*sensu* [Sibley, C.G., Monroe, B.L., 1990. Distribution and Taxonomy of the Birds of the World, Yale University Press, New Haven, CT]) to address the monophyly of the group and to reconstruct the most complete phylogeny of this tribe published to date. We found strong support for a redefined Cardinalini that now includes some members previously placed within Thraupini (tanagers; the genera *Piranga*, *Habia*, *Chlorothraupis*, and *Amaurospiza*) and some members previously placed within the Parulini (wood-warblers; the genus *Granatellus*). In addition, some genera traditionally considered members of the Cardinalini are shown to have affinities with other groups (the genera *Porphyrospiza*, *Parkerthraustes*, and *Saltator*). Our redefined Cardinalini contains 48 species, six more than are listed in Sibley and Monroe's (1990) taxonomy of the group. Within the nine-primaried oscine assemblage, the Cardinalini are more closely related to the Thraupini (tanagers) than they are to the Emberizini (sparrows), Parulini (wood-warblers), or Icterini (blackbirds), consistently forming a monophyletic group with Thraupini across all analyses. The reconfigured Cardinalini is comprised of five well-supported, major clades: (1) a "masked" clade (*Piranga*, *Cardinalis*, *Caryothraustes*, *Periporphyrus*, and *Rhodothraupis*), (2) a "blue" clade (*Amaurospiza*, *Cyanocompsa*, *Cyanoloxia*, *Passerina*, and *Spiza*), (3) a clade containing the genera *Habia* and *Chlorothraupis*, (4) a clade containing all species of *Granatellus*, and (5) a clade containing only species of *Pheucticus*. Diversification of these five lineages from one another occurred relatively rapidly during the mid-Pliocene, around 5 or 8 million years ago. Each of these major clades includes both North and South American species; thus, a complex biogeographic history is inferred for the group.
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1. Introduction

The New World nine-primaried oscines represent a massive New World songbird radiation that includes 823 species organized into 200 genera (*fide* Sibley and Monroe, 1990). These have historically been divided into five assemblages. A prominent modern avian taxonomy (Sibley and Monroe, 1990; which we follow throughout this manuscript) recognizes each of the five as a tribe within the subfamily Emberizinae (Sibley and Monroe, 1990). These include the Icterini (blackbirds and allies), Parulini (wood-warblers), Emberizini (sparrows) Thraupini (tanagers) and Cardinalini (cardinals and grosbeaks). Relationships among these five tribes have long been the subject of debate among taxonomists (reviewed in Sibley and Ahlquist, 1990; Klicka et al., 2000). Comparative studies of external morphology (e.g. Ridgway, 1901, 1902), jaw

* Corresponding author. Fax: +1 702 895 3094.
E-mail address: klicka@unlv.nevada.edu (J. Klicka).
[1] Present address: CCBR/Westcore, Black Hills State University, 1200 University Street, Unit 9053, Spearfish, SD 57799-9053, USA.

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musculature (Beecher, 1953), pelvic musculature and serology (Stallcup, 1954), cranial and palatal characters (Tordoff, 1954a) and appendicular myology (Raikow, 1978) have yielded only a handful of characters (Mayr and Amadon, 1951; Sibley, 1970; Feduccia, 1996) with which to define among-tribe relationships, and many of these are inconsistent with one another (Bledsoe, 1988). As a result, morphological analyses have led to an array of conflicting taxonomies with little consensus on relationships among tribes.

These same studies did somewhat better in assigning taxa to tribes. The Icterini and Parulini, possessing distinctive bill morphologies, were most easily defined in traditional taxonomies which emphasized different feeding specializations. Membership in the tribe Cardinalini has traditionally been characterized by the possession of a large, stout, conical bill; however, some putative representatives of the Emberizini and the Thraupini also possess similar bills. Overlapping bill morphologies has led to relatively arbitrary boundary distinctions between these tribes (Sclater, 1886; Ridgway, 1902; Tordoff, 1954a). The lack of diagnostic cranial (or post-cranial) characters has compelled some authors (e.g. Steadman and McKitrick, 1982) to conclude that the Cardinalini is an artificial group whose members are referable to either the Thraupini or Emberizini. It has been understood for some time (e.g. Mayr and Amadon, 1951: 13) that "the bill is the most plastic of all organs of the bird" and bill shape "has been used with too much confidence... as a reliable basis for classification" (see also Tordoff, 1954a and recent review by Remsen, 2003). Nevertheless, with no alternative informative characters available, the proper placement of "finch-billed" birds has remained controversial.

Molecular studies have begun to provide some taxonomic clarity with respect to these birds. For example, the DNA hybridization studies of Sibley and Ahlquist (1990) placed within the Thraupini, a suite of finch-billed taxa that had been historically classified as Emberizins. Subsequent works (Klicka et al., 2000; Yuri and Mindell, 2002) have lent credibility to the notion that the nine-primaried oscines are comprised of five distinct clades, each corresponding to one of the traditional nine-primaried oscine tribes, although taxonomic sampling was minimal in these studies. Molecular data not only suggest that the Cardinalini does represent a distinct songbird lineage, but also that it is paraphyletic in its current configuration. A molecular study of thraupin relationships (Burns, 1997) noted that several traditional tanager genera, *Piranga*, *Habia*, and *Chlorothraupis*, form a clade outside of the main Thraupini assemblage. Later studies (Klicka et al., 2000; Yuri and Mindell, 2002) suggested that *Piranga* (and by association *Habia* and *Chlorothraupis*) is embedded within the Cardinalini. Similarly, Lovette and Bermingham (2002) found that the putative warbler genus *Granatellus* lies well outside the Parulini clade, and appears to be most closely related to members of the Cardinalini. This finding is significant given that the three species of *Granatellus* all possess the thin bill type typically associated with an insectivorous diet.

Species currently considered to be cardinalin, are highly variable with respect to plumage coloration, song, body size, geographic distribution, and degree of sexual dimorphism. To study the evolution of these and other characters, strong support for the monophyly of this group is needed as well as a well-resolved phylogeny of the species within this group. Such a phylogeny is not yet available. Previous systematic studies of the Cardinalini include a phenetic analysis of skeletal and plumage characters (Hellack and Schnell, 1977) and an allozyme and morphometric study (Tamplin et al., 1993). The morphometric analyses of both of these studies produced similar classifications that were more consistent with some available linear classifications (Hellmayr, 1938; Sibley and Monroe, 1990) than with others (Payter, 1970). This result is unsurprising given that the same (or similar) characters were used to infer relationships in all of these taxonomies. Tamplin et al.'s (1993) allozyme study yielded a phenogram that was "fundamentally similar" to Hellack and Schnell (1977) "best phenetic classification", although it included only 13 cardinalin taxa and lacked nearly one half of all cardinalin genera. More recently, DNA studies have investigated cardinalin relationships; however, these studies have also sampled relatively few members of this group (Bledsoe, 1988; Sibley and Ahlquist, 1990; Klicka et al., 2000; Yuri and Mindell, 2002) and none have included representatives of all genera (*Piranga*, *Habia*, *Chlorothraupis*, and *Granatellus*) suggested by recent molecular taxonomy to now belong within Cardinalini.

In the current study, we analyze mtDNA sequences of most species of cardinal-grosbeaks in an effort to address three main goals: (1) define membership within the Cardinalini, (2) define placement of the Cardinalini within the overall nine-primaried oscine assemblage, and (3) determine relationships among the genera and species that comprise the Cardinalini. To establish a monophyletic Cardinalini, we sampled broadly from across the nine-primaried oscine assemblage, using previous molecular studies as a guide in our taxon sampling. Importantly, we included a large number of finch-billed species from the other Emberizine tribes because of the prominence of bill size as a taxonomic character in previous classifications.

2. Materials and methods

2.1. Taxon selection and outgroups

Satisfying our first goal (above) required sampling from all known clades within the "New World nine-primaried oscines". Using Sibley and Monroes' (1990) Family Fringillidae as a starting point, we compiled sequence data for 175 songbird taxa (see Appendix A). These included eight genera (10 spp.) from the Fringillinae (finches) and 102 genera from the Emberizinae. Generic level representation among the five constituent tribes of the latter is

characterized as follows: 11 Emberizini (sparrows, 19 spp.), 13 Icterini (blackbirds, 13 spp.), nine Parulini (warblers, 9 spp.), 46 Thraupini (tanagers, 63 spp.) and 17 Cardinalini (cardinal-grosbeaks, 48 spp.). Sampling for the latter included 34 of the 42 species listed in Sibley and Monroe's (1990) Cardinalini along with 14 species (representing the genera *Piranga*, *Habia*, *Chlorothraupis*, and *Granatellus*) that recent molecular studies suggest belong within this tribe. Eight additional songbird genera (12 spp.) of less certain taxonomic affinity were also included. These have been identified in previous studies as genera that belong somewhere within the nine-primaried oscine clade but not conveniently into one of the five existing songbird tribes. The family Passeridae is considered sister to the Fringillidae and from this group a single outgroup taxon was chosen, *Montifringilla davidiana*. For each taxon, cyt-*b* (cytochrome *b*) and ND2 (NADH dehydrogenase subunit 2) sequence were obtained either from genbank or from direct sequencing (see below). All taxa used, museum (or collector) voucher numbers, and collecting localities (when known) are listed in Appendix A.

Results from analysis of this expanded data set (nine-primaried oscines, referred to hereafter as the "oscine" data set) were used to identify all putative members of the ingroup and to suggest appropriate outgroups for this reduced (hereafter referred to as the "Cardinalini) data set. This smaller data set was used to analyze ingroup relationships with a reduced amount of homoplasy, which should lead to more robust phylogenetic estimates. Homoplasy should be minimized by using an outgroup composed of the taxa that are most closely related to, but not a part of, the ingroup (Smith, 1994; Wheeler, 1990). Although the expanded analysis could not unambiguously identify the sister clade to the Cardinalini, it did identify several reasonable outgroup choices. These included representatives from: (1) Emberizini–Parulini–Icterini (sparrows, warblers, and blackbirds); (2) Thraupini (tanagers); (3) *Saltator*; and (4) *Mitrospingus*. In order to examine the effect of alternative outgroup choices on phylogenetic reconstruction of the Cardinalini, we performed a full series of analyses (see below) using each of these to independently root our topologies.

2.2. Laboratory protocols

Total genomic DNA was extracted from tissue samples (heart, pectoral muscle, or liver) using a Dneasy (Qiagen, Valencia, CA) tissue extraction kit and the manufacturer's protocol. Sequence fragments were amplified via polymerase chain reaction (PCR) using primers L14764 (Sorenson et al., 1999) and H4A (Harshman, 1996) for the cyt-*b* gene; whereas, the ND2 gene was sequenced with primers L5215 (Hackett, 1996) and H6313 (Johnson and Sorenson, 1998). All fragments were amplified in 12.5 μl reactions under the following conditions: denaturation at 94 °C followed by 40 cycles of 94 °C for 30 s, 54 °C for 45 s, and 72 °C for 2 min. This was followed by a 10 min extension at 72 °C and a 4 °C soak. Products were purified using either a Qiaquick PCR purification kit (Qiagen, Valencia, CA) or ExoSAP-IT (USB Corporation, Cambridge, MA) treatment. Standard, 20 μl sequencing reactions were performed using 0.5 μl of BigDye (Applied Biosystems, Foster City, CA) and 20–40 ng of purified and concentrated PCR product. Products of these reactions were purified using a magnetic bead clean-up procedure (Clean-Seq, Agencourt Biosciences, Beverly, MA) and run on an ABI 3100-*Avant* (Applied Biosystems) automated sequencer. Complete, complementary strands of each gene were unambiguously aligned using Sequencher 4.2 (GeneCodes Corporation, Ann Arbor, MI). The veracity of the sequence data was supported in several ways. Both light and heavy strands were sequenced for all PCR fragments and no gaps, insertions, or deletions were apparent in the aligned sequence. All data were translated (using MEGA2 version 3.01, Kumar et al., 2004) without problem into amino acid form. The resulting data set includes complete sequence for both the cyt-*b* gene (1143 bp) and ND2 (1041 bp) genes for a total of 2184 bp of concatenated data.

2.3. Phylogenetic protocols

Phylogenetic analyses were preceded by data exploration. Using PAUP 4.0b10 (Swofford, 2002), we constructed uncorrected genetic (*P*) distance matrices using both inter- and intrageneric pairwise comparisons for both data sets. Once clades were defined, uncorrected among-clade *P* distances were determined using MEGA2 (Kumar et al., 2004). The relatively high genetic distances recovered for the oscine data set suggested potential problems due to homoplasy. We investigated this possibility by plotting pairwise comparisons of corrected (Kimura 2-parameter [K2-P; (Kimura, 1980)] and GTR + I + Γ [see below]) and uncorrected distances for each codon position for both genes. The evolutionary dynamics of each gene and gene partition (codon position) were examined using both the oscine and the cardinalin data sets. PAUP 4.0b10 (Swofford, 2002) was used to generate several parameters for examination, including: Ts/Tv (transition/transversion ratio), relative rates of evolution, percent nucleotide composition, and the gamma-shape parameter (α). For each data set, a series of χ^2 tests of homogeneity was conducted on each gene and gene partition using only informative data. Such tests are useful in detecting potential nucleotide composition bias. For each gene partition, we also plotted the relative proportions of each nucleotide for each taxon (e.g. C vs. T, A vs. G). Outliers in such plots may indicate taxa that are problematic with respect to nucleotide composition biases.

Phylogenetic analyses were performed using maximum likelihood (ML), maximum parsimony (MP), and Bayesian approaches. Because homoplasy was evident in both data sets, weighted parsimony analyses were conducted with transitions downweighted relative to transversions using empirical Ts/Tv ratios (as determined by PAUP 4.0b10,

Swofford, 2002). For both data sets under this weighting scheme, transitions were downweighted by 1/3 for cyt-*b* and by 1/6 for ND2. Independent heuristic MP searches (20 replicate random stepwise additions) were conducted and support for individual nodes was assessed using MP heuristic bootstrap with 500 pseudoreplicates, each with 10 random addition sequence replicates.

ML methods are better able to accommodate the complexities of the DNA sequence evolution process than MP (reviewed in Huelsenbeck and Crandall, 1997); and, they have been shown to outperform MP under a variety of simulated conditions (Huelsenbeck, 1995; Swofford et al., 2001). For these reasons, we decided *a priori* to consider our likelihood topologies our best estimates of phylogenetic relationships. Modeltest 3.04 (Posada and Crandall, 1998) and the Akaike Information Criterion (AIC) were used (see Posada and Buckley, 2004) to determine the most appropriate model of sequence evolution for ML analyses. The best fit for each gene partition and for the combined (cyt-*b* and ND2) data set was the $GTR + I + \Gamma$ model. The large size of our oscine data set required that we use the successive approximations approach of Swofford et al. (2001) to obtain ML estimates of phylogeny using PAUP*. Parameters were re-optimized and a new search started whenever a week passed with no improvement in likelihood score (see Klicka et al., 2005 for details of this procedure). After three such iterations, the tree obtained after 2 weeks with no change in likelihood score was accepted as our "best" phylogenetic hypothesis. This process was repeated twice, converging on the same topology in both cases. A ML analysis of the Cardinalini data set was able to run to completion on PAUP*, provided a neighbor-joining topology was used as a starting tree. This process was repeated three times, with all runs converging on the same topology. Shimodaira and Hasegawa (1999) tests (with the RELL approximation) were used to compare our phylogenetic reconstructions with alternative phylogenetic hypotheses. Shimodaira–Hasegawa (SH) tests are one-sided, non-parametric tests appropriate for testing topologies chosen *a posteriori* although they are known to be conservative due to minimization of type I error (Goldman et al., 2000; Shimodaira, 2002).

For another approach using likelihood, we implemented two relatively new "fast likelihood" programs, PHYML (Guindon and Gascuel, 2003) and TREEFINDER (Jobb, 2005). An advantage of both of these methods is that fewer iterations are required to reach an optimum, resulting in a drastic reduction in required computer time. The $GTR + I + \Gamma$ model of nucleotide evolution was used and both programs were allowed to estimate parameters, re-optimizing regularly as tree scores improved. Non-parametric bootstrap (×100) results obtained using these methods were compared with MP bootstrap values and Bayesian posterior probabilities.

Bayesian inference (Rannala and Yang, 1996) was used primarily as a means of assessing support for nodes obtained via other (ML, MP) tree-building methods. The program MRBAYES version 3.1.2 (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003) was implemented and the $GTR + I + \Gamma$ model of sequence evolution was once again assumed. Specific nucleotide substitution model parameters were left undefined and estimated as part of the analysis. All Bayesian analyses were initiated from random starting trees. Four Markov chain Monte Carlo chains were run for three million generations and sampled every 100 generations, yielding 30,000 trees. The first one million generations (=10,000 trees) were discarded to ensure that stationarity had been reached. To ensure that the Markov chain was sampling from the posterior distribution, this procedure was repeated. Because both runs converged on similar distributions, all trees (excluding those sampled before "burn-in") were combined yielding a total of 40,000 topologies from which a 50% majority rule consensus tree was constructed. Nodes having posterior probability values of 95% or greater on this tree were deemed significantly supported (after Huelsenbeck and Ronquist, 2001).

ML analyses performed in PAUP* necessarily require a single model of sequence evolution. The use of a single model with data comprised of differently evolving subsets (such as cyt-*b* and ND2) may result in significant systematic error, misleading the phylogenetic analysis (e.g. Brandley et al., 2005; Leaché and Reeder, 2002). The use of more complex, partitioned models is known to improve the resolution of nodes deeper in the tree and is considered more effective at estimating phylogeny when homoplasy levels are high (Brandley et al., 2005; Castoe et al., 2005, 2006). Unlike PAUP*, MrBayes can readily accommodate "mixed models" of nucleotide evolution. To test whether the use of such models can improve resolution within the Cardinalini, we compare the results of partitioned vs. unpartitioned Bayesian analyses. For the Cardinalini (ingroup) data set, we partitioned either by gene or by gene-specific codon position and used Modeltest 3.04 (Posada and Crandall, 1998) and the AIC to assign independent models of evolution to various portions of the data set. Bayesian analyses were run for each uniquely partitioned data set using the same protocol described above.

3. Results

3.1. Sequence characteristics

For the larger, oscine data set, the ND2 gene was more variable (approximately 25%) than cyt-*b* (Table 1). Of the 2281 bp of combined sequence, 1222 (53.6%) sites were variable and of these, 1092 were phylogenetically informative. Overall, more than 98% of third position sites varied including all ND2 third positions. As expected, multiple substitutions (homoplasy) at these sites were reflected in plots of third position transition distances vs. corrected sequence divergences for both data sets (not shown). Within the Cardinalini, uncorrected inter-clade distances for cyt-*b* are relatively high (Table 2) ranging from 8.7%

Table 1
Overall and codon position-specific dynamics of the cytochrome-*b* and ND2 genes

Position	Number of sites	Variable sites	Phylogen. informative	Relative rate	% *A*	% *C*	% *G*	% *T*	χ^2	Ts/Tv	α
Cytochrome *b*											
All	1143	568	503	3.0	27.5	34.9	13.1	24.4	$P = 1.0000$	4.2	0.337
		438	*343*	*6.3*	*27.6*	*34.5*	*13.1*	*24.8*	$P = 1.0000$	*5.5*	*0.020*
1st	381	134	108	2.1	25.3	29.9	23.4	21.4	$P = 1.0000$	4.9	0.244
		85	*63*	*3.7*	*25.6*	*29.9*	*23.2*	*21.4*	$P = 1.0000$	*5.5*	*0.121*
2nd	381	64	31	1.0	20.5	25.3	12.8	41.5	$P = 1.0000$	6.7	0.119
		23	*11*	*1.0*	*20.6*	*25.4*	*12.6*	*41.5*	$P = 1.0000$	*4.7*	*0.016*
3rd	381	370	364	5.8	36.8	49.6	3.2	10.4	$P = 0.3440$	9.6	0 .765
		330	*269*	*14.3*	*36.8*	*48.3*	*3.5*	*11.5*	$P = 0.9993$	*9.1*	*1.041*
ND2											
All	1038	654	589	3.8	29.5	35.4	10.8	24.4	$P = 1.0000$	9.1	0.405
		515	*436*	*8.2*	*29.2*	*35.2*	*10.8*	*24.8*	$P = 1.0000$	*9.9*	*0.250*
1st	346	203	175	3.5	35.7	30.0	16.6	17.8	$P = 1.0000$	7.9	0.311
		131	*98*	*6.3*	*35.7*	*30.2*	*16.6*	*17.5*	$P = 1.0000$	*7.4*	*0.214*
2nd	346	105	68	1.8	16.7	34.2	9.7	39.4	$P = 1.0000$	12.1	0.211
		49	*24*	*2.3*	*16.6*	*34.6*	*9.7*	*39.2*	$P = 1.0000$	*4.7*	*0.002*
3rd	346	346	346	6.0	36.0	41.8	6.2	16.0	$P = 0.0003$	12.7	1.524
		335	*314*	*16.0*	*35.4*	*40.8*	*6.2*	*17.6*	$P = 0.95123$	*13.0*	*2.244*

Upper values were calculated using all taxa and those below (in italics) with only ingroup (Cardinalid) taxa. Mean base composition is averaged over all sequences with PAUP*. Transition–transversion ratio (Ts/Tv) values are the average number of changes reconstructed on one of three shortest, weighted MP topologies. Ts/Tv and α values were estimated simultaneously for each partition.

Table 2
Observed inter-clade pairwise genetic distances for Cyt-*b* (below diagonal) and ND2 (above) genes

Clade	1	2	3	4	5	6	7	8	9	10
(1) *Spiza*	[a]	0.1236	0.1336	0.1429	0.1496	0.1565	0.1557	0.1647	0.1564	0.1642
(2) *Passerina*	0.0871	**0.0650**	0.1249	0.1471	0.1484	0.1564	0.1561	0.1617	0.1527	0.1646
(3) *Cyanocompsa* and allies	0.0906	0.0865	**0.0715**	0.1485	0.1474	0.1545	0.1533	0.1637	0.1516	0.1646
(4) *Granatellus*	0.1096	0.1024	0.0982	**0.0773**	0.1479	0.1536	0.1571	0.1638	0.1540	0.1629
(5) *Pheucticus*	0.1076	0.0983	0.0974	0.0979	**0.0531**	0.1443	0.1478	0.1627	0.1442	0.1623
(6) *Piranga*	0.0944	0.0979	0.0898	0.1026	0.0998	**0.0763**	0.1534	0.1529	0.1534	0.1608
(7) *Cardinalis*	0.1056	0.1136	0.1063	0.1126	0.1187	0.1036	**0.0784**	0.1587	0.1503	0.1638
(8) *Caryothraustes* and allies	0.1094	0.1067	0.1011	0.1084	0.1082	0.0961	0.1052	**0.0850**	0.1606	0.1691
(9) *Habia* and *Chlorothraupis*	0.1075	0.1072	0.1011	0.1125	0.1108	0.1045	0.1091	0.1072	**0.0779**	0.1624
(10) *Saltator*	0.1068	0.1072	0.1019	0.1075	0.1080	0.1038	0.1142	0.1074	0.1116	**0.0884**

Those shown in bold on the diagonal reflect mean intra-clade cyt-*b* (only) distances.
All values shown represent uncorrected (*P*) sequence divergence values.
[a] *Spiza* is represented by only a single taxon.

between *Spiza* and *Passerina* to 11.9% between *Pheucticus* and *Cardinalis*, and averaged 10.3% among clades. Intra-clade cyt-*b* comparisons range from 3.0% (*Passerina ciris* vs. *P. versicolor*) to 13.9% (*Habia fuscicauda* vs. *Chlorothraupis carmioli*). Corresponding values from ND2 distances are substantially greater in all comparisons. Nucleotide composition and bias varies only slightly between these two genes (Table 1); both display a deficiency of guanine and an excess of cytosine nucleotides. Base composition biases shown here are similar to those recovered in other avian studies (e.g. Kornegay et al., 1993; Lovette and Bermingham, 2000).

Tests of homogeneity of base frequencies across both data sets (Table 1) were not significant for either gene or for the combined data. When codon partitions were analysed, only ND2 third positions in the expanded data set provided a significant result ($\chi^2_{525} = 643.06$, $P = 0.0003$). Plots of third position purine and pyrimidine content (not shown) identified a possible nucleotide bias with respect to members of several basal lineages. Outliers in such plots included all members of *Calcarius*, some Carduline genera including *Euphonia* and *Carpodacus*, and the outgroup taxon *Montifringilla*. Relative rates of substitution vary between the oscine and Cardinalini data sets. For example, in the expanded data set ND2 third position substitutions are occurring approximately six times as fast as cyt-*b* second position changes, whereas, ND2 third position substitutions in the ingroup are accruing at 16 times the rate of cyt-*b* second positions (Table 1). It is unlikely that these values reflect actual rate differences but rather the apparent "slow down" in the larger (oscine) data set are more likely an artifact of increased homoplasy with increasing taxonomic distance. Collectively, these results suggest that the reduced data set with fewer and more closely related outgroup taxa should provide a more robust phylogenetic hypothesis for the Cardinalini. Not

surprisingly, codon position-specific gamma-shape parameter (α) estimates indicate that among-site rate heterogeneity is likely a problem in our data sets. The problem is most acute when the ingroup (Cardinalini) is examined independently (Table 1) where α values for the overall cyt-*b* gene (0.02), cyt-*b* second positions (0.016), ND2 second (0.002), and third (2.244) positions all lie well outside the range (0.1–0.5, Yang, 1996) typical of gamma-shape parameter estimates.

3.2. Phylogenetic analyses—oscines

Likelihood analysis of the oscine data set recovers core clades corresponding to each of the five songbird tribes within the Emberizinae (Fig. 1A–E). The newly defined Cardinalini now includes all members of *Piranga*, *Habia*, *Chlorothraupis*, *Granatellus* and *Amaurospiza*. Genera traditionally considered Cardinalini that are shown here to have affinities outside of the present clade include *Porphyrospiza*, *Parkerthraustes* and *Saltator*. Topologies in which *Saltator* is constrained to a position within the Cardinalini can be rejected ($P = 0.035$, 0.038) by SH tests; however, a tree in which it is made sister to the Cardinalini cannot ($P = 0.245$). Among-tribe relationships suggested by this tree include an Emberizini–Parulini–Icterini clade and a Thraupini–Cardinalini sister relationship. Weighted MP, ML, and multiple Bayesian analyses yielded the same topologies with respect to these inner nodes. Monophyly of Thraupini and Cardinalini (nodes 1 and 2, Fig. 1) was indicated across all analyses, with high Bayesian posterior probabilities (100%) whether the data were unpartitioned, partitioned by gene, or partitioned by codon position. A Cardinalini clade was also supported by weighted MP analysis (bootstrap frequency = 78%) although the Thraupini clade was not (< 70% support). The Emberizini–Parulini–Icterini clade (node 4, Fig. 1) received 100% Bayesian support across all (partitioned and unpartitioned) analyses and weak support (68%) via weighted parsimony. Although a Cardinalini–Thraupini sister relationship is obtained across all analyses, it is important to note that support was consistently lacking for this node (node 3, Fig. 1). With all unsupported nodes collapsed (tree not shown), we are left with a polytomy in the Emberizinae consisting of three clades, the Cardinalini, the Thraupini, and the Emberizini–Parulini–Icterini assemblage. While the analyses performed do suggest a Cardinalini–Thraupini pairing as most likely, a tree constrained to having an Emberizini–Parulini–Icterini and Cardinalini sister relationship cannot be rejected ($P = 0.647$, SH test), nor can a tree in which the Cardinalini are basal (sister) to the other four tribes of the Emberizinae ($P = 0.495$).

3.3. Phylogenetic analyses—Cardinalini

Our best estimate of relationships within the Cardinalini is shown in Fig. 2, a ML topology rooted with members of their most likely sister group, the Thraupini. Overall, terminal nodes are well supported whereas most interior nodes are not. When poorly supported basal nodes are taken into consideration, the Cardinalini are comprised of five well-resolved lineages of uncertain relationship to one another. According to this tree, a *Spiza–Passerina–*"*Cyanocompsa*" (includes *Amaurozpiza* and *Cyanoloxia*) clade (Fig. 2A) is well supported as is an assemblage comprised of *Piranga*, *Cardinalis*, *Caryothraustes*, *Peripophyrus*, and *Rhodothraupis* (Fig. 2D). *Cyanocompsa*, as presently configured, is paraphyletic with *Amaurospiza* and the monotypic genus *Cyanoloxia* apparently embedded within it. *Habia* (also paraphyletic) along with *Chlorothraupis*, form a well-resolved clade (Fig. 2E) although its affinites within the Cardinalini are uncertain. Similarly, the basal nodes suggesting that *Pheucticus* (Fig. 2C) and *Granatellus* (Fig. 2B) grade into the *Spiza–Passerina–Cyanocompsa* clade are weakly supported casting doubt on their relationships to other constituents of the Cardinalini.

In general, nodes with 95% (or greater) Bayesian posterior probabilities were also well supported (i.e. 70% or greater, see Hillis and Bull, 1993) by MP and ML bootstrap estimates (Fig. 2 and Table 3). Weakly supported nodes remained problematic across all analyses. The use of differing outgroups (Table 3) did result in alternative trees in some cases, however; topology changes always involved these unsupported nodes. For example, a *Passerina–Cyanocompsa–Cyanoloxia–Amaurospiza* clade was not recovered by most analyses when Saltators were used as a root. Instead, a *Spiza–Passerina* sister relationship was indicated. When only supported nodes are considered we are left with a polytomy for this group. Results obtained via various Bayesian partitioning strategies varied slightly. Posterior probabilities increased for three nodes as partitioning schemes became increasingly complex (Table 4). Values at two of these (nodes 3 and 5, Fig. 2) became significant (95% posterior probability) only when the data were partitioned by codon position. An additional two nodes (7 and 14, Fig. 2) lost support as partitioning schemes became more complex.

4. Discussion

4.1. Nine-primaried oscine systematics

The difficulty in sorting out relationships among the Emberizinae tribes is likely due (at least in part) to their relatively recent and rapid diversification (Mayr and Amadon, 1951; Sibley and Ahlquist, 1990; Lovette and Bermingham, 2000). As a result, clades exhibit extremely short internodes (e.g. nodes 1–3, Fig. 1) along with a concomitant paucity of clade-defining molecular characters. In this study, the five "core" tribes of the Emberizinae were recovered (Fig. 1A–E) with significant Bayesian support; although, a handful of taxa (*Calcarius*,

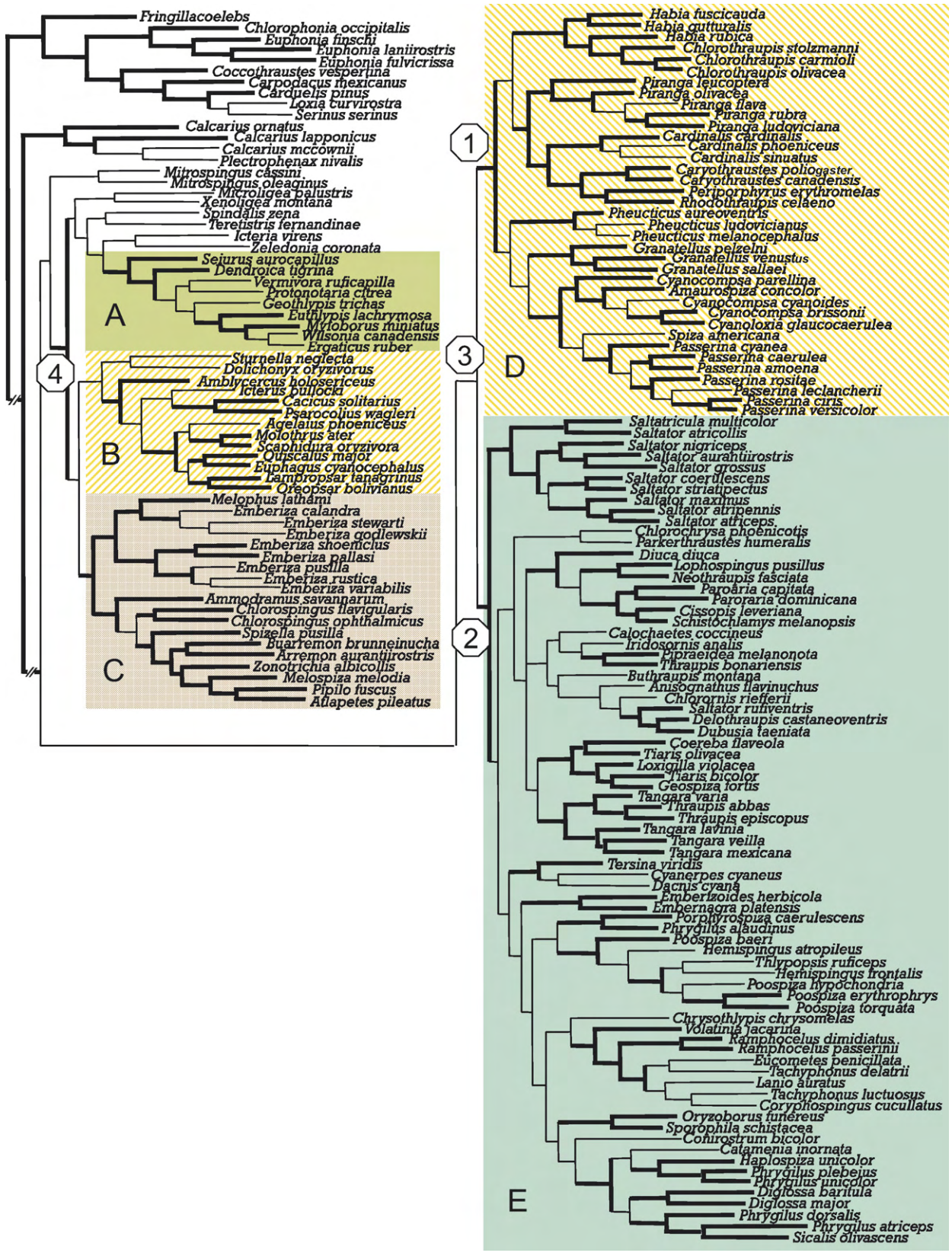

Fig. 1. A maximum likelihood tree depicting relationships among the nine-primaried oscine tribes, according to this study. Because of the size of the data set, a successive approximations approach (see text) of Swofford et al. (2001) was used. Nodes in bold received significant (>95%) support via a Bayesian analysis in which the data were partitioned by gene. Capital letters A–E identify individual songbird tribes; A = Parulini, B = Icterini, C = Emberizini, D = Cardinalini, and E = Thraupini. The numbers shown refer to clades discussed in the text. This tree was rooted with a single outgroup taxon, *Montifringilla davidiana*.

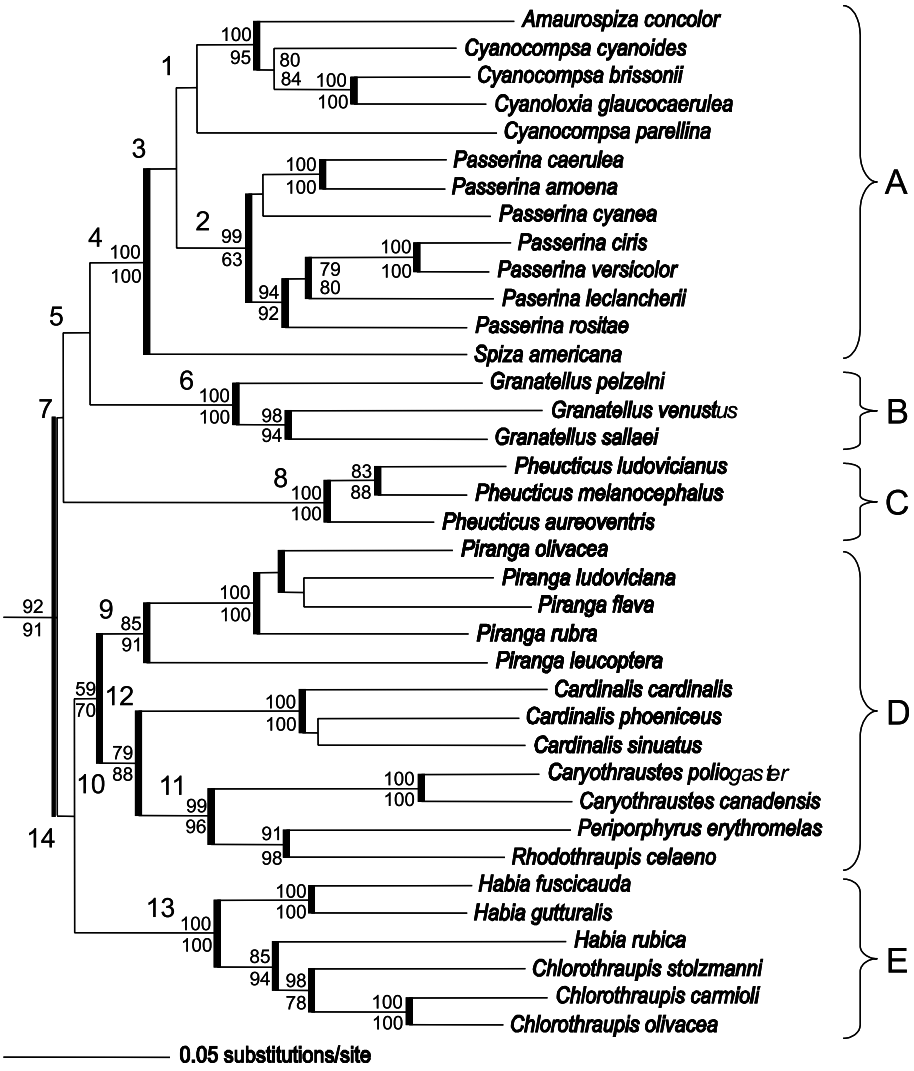

Fig. 2. A maximum likelihood tree (-Ln length = 25, 160.259) obtained using PAUP and a starting (neighbor-joining) tree. The GTR + I + Γ model of sequence evolution was used with parameter settings of $I = 0.499454$ and $\alpha = 1.183944$ (R-matrix available upon request). Branch lengths are scaled to depict relative numbers of changes. A likelihood ratio test for a molecular clock was not significant ($-2\log\Delta = 47.07$, df = 43, $0.5 > P > 0.1$). The small numbers shown above nodes reflect 100 ML bootstrap replicates (obtained using PHYML) and those below reflect 200 replicates using weighted MP. Large numbers in bold identify clades discussed in the text and in Tables 3 and 4. Highlighted nodes (bold vertical lines) have significant (>95%) Bayesian posterior support, when the data were partitioned by gene. The following thraupin taxa were used to root this tree: *Saltator grossus*, *Tangara lavinia*, *Pararoraria capitata*, *Thraupis bonariensis*, *Cyanerpes cyaneus*, *Haplospiza unicolor*, *Lanio auratus*, and *Poospiza hypochondria*. This tree represents our "best" estimate of phylogenetic relationships within the Cardinalini.

Plectrophenax, *Mitrospingus*, *Microligea*, *Xenoligea*, *Spindalis*, *Teretistris*) appear to lie outside of these core tribes (Lovette and Bermingham, 2002; Burns et al., 2003; Klicka et al., 2003). A well-supported Emberizini–Parulini–Icterini clade is evident although relationships among these three groups remains equivocal. This same clade was also recovered in other recent molecular studies (Klicka et al., 2000; Lovette and Bermingham, 2002; Yuri and Mindell, 2002) that have addressed this issue including an early DNA hybridization study (Bledsoe, 1988; but see Sibley and Ahlquist, 1990). The relative placement of the Thraupini and Cardinalini is less clear. Molecular studies by Klicka et al. (2000) and Lovette and Bermingham (2002) suggest that these grade into the Emberizini–Parulini–Icterini assemblage with the Thraupini as sister and the Cardinalini basal to all; however, in these studies both clades were poorly sampled. The more complete sampling in this study and in the work of Yuri and Mindell (2002) suggests instead a Thraupini–Cardinalini sister relationship (across all analyses) with this clade sister to the Emberizini–Parulini–Icterini group. Our arrangement was also recovered in Bledsoe's (1988) phylogeny although the DNA hybridization study of Sibley and Ahlquist (1990) linked the Cardinalini with the Icterini. We stress that strong support for these relationships is lacking in all of these studies. While a Thraupini–Cardinalini sister relationship is our best estimate of evolutionary history, the present data

Table 3
Relative nodal support for select clades as a function of differing outgroup choices and analytical methods (see text)

Outgroup:	Emberizini–Parulini–Icterini				Thraupini				*Saltator*				*Mitrospingus*			
Analytical method:	MP	Bayes	Phyml	TF	MP	Bayes	Phyml	TF	MP	Bayes	Phyml	TF	MP	Bayes	Phyml	TF
Passerina & "*Cyanocompsa*" [3]	58	54	—	—	60	85	<50	52	<50	—	—	—	63	90	—	55
Passerina–"*Cyanocompsa*" & *Spiza* [4]	96	100	100	100	96	100	100	98	96	100	100	100	97	100	99	100
Pheucticus & *Granatellus*	75	—	<50	<50	59	—	—	—	63	72	52	—	81	—	53	<50
Lineages A, B, and C [7]	—	92	<50	<50	—	73	<50	<50	—	53	<50	—	—	77	<50	—
Lineages D and E [14]	—	94	<50	<50	—	69	<50	<50	—	89	<50	51	—	59	—	—
Habia & *Chlorothraupis* [13]	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100
"Masked" clade [10]	77	100	70	86	88	100	79	70	78	100	79	72	80	100	71	73
"Masked" clade & *Piranga* [12]	63	100	65	63	70	100	59	73	56	95	58	64	64	100	60	<50

Designated lineages and nodes (in brackets) refer to Fig. 2.
Dashed lines indicate nodes absent from a particular analysis. Numerical clade designations (in brackets) refer to nodes shown in Fig. 2. Parsimony (MP) and likelihood (PHYML, Treefinder) values shown each reflect 100 non-parametric bootstrap replications. Bayesian values reflect posterior probabilities. All MP values were obtained via weighted (Tv × 3 for cyt-*b*, Tv × 6 for ND2) analyses. The GTR + I + Γ model of sequence evolution was assumed for all ML and Bayesian analyses. Outgroup composition: Emberizini–Parulini–Icterini = *Zonotrichia albicollis*, *Ammodramus savannarum*, *Geothlypis trichas*, *Seirus aurocapillus*, *Amblycercus holosericeus*, *Euphagus cyanocephalus*; Thraupini = *Saltator grossus*, *Tangara lavinia*, *Paroraria capitata*, *Thraupis bonariensis*, *Cyanerpes cyaneus*, *Haplospiza unicolor*, *Lanio auratus*, *Poospiza hypochondria*; *Saltator* = *Saltator grossus*, *Saltator aurantiirostris*, *Saltator nigriceps*, *Saltator striatipectus*, *Saltator coerulescens*, *Saltator maximus*, *Saltator atripennis*, *Saltator atriceps*, *Saltator atricollis*, *Saltatricula multicolor*; *Mitrospingus* = *Mitrospingus cassinii*, *Mitrospingus oleagineus*.

set cannot rule out alternatives including: Cardinalini sister to Emberizini–Parulini–Icterini; Cardinalini sister to Thraupini–Emberizini–Parulini–Icterini; or, Cardinalini as a subclade (i.e. embedded within) of the Thraupini. In the most current songbird classification available, Sibley and Monroe list 413 species in 104 putative tanager genera in their tribe Thraupini. Although we sampled extensively, this study includes only 74 of these species (49 genera). Including additional thraupin taxa will almost certainly improve resolution and determine which (if any) of these alternatives is a better hypothesis. Nevertheless, in terms of taxon sampling, the present study is the most comprehensive to date and we suggest that the relationships indicated should be used as the working hypothesis for this group.

4.2. Cardinalini systematics

Despite being unable to place the Cardinalini clade with certainty, we have identified a well-supported Cardinalini clade (Fig. 2) that differs in several ways from any historic or modern taxonomy of the group. The genera *Piranga*, *Habia*, *Chlorothraupis*, *Granatellus*, and *Amaurospiza* are clearly members of the newly defined Cardinalini; whereas, historically cardinalin taxa that are shown to have affinities outside of the present clade include the monotypic forms *Porphyrospiza* and *Parkerthraustes*, along with all members of the genus *Saltator*.

4.2.1. The "masked" clade

Although long considered one of the "classic tanagers" (Ridgely and Tudor, 1989), a series of molecular studies (Burns, 1997; Klicka et al., 2000; Yuri and Mindell, 2002) has indicated that *Piranga* is not a member of the Thraupini but more likely belongs among the Cardinalini. Our topology indicates that *Piranga* is likely sister (Fig. 2D) to a well-resolved clade comprised of *Cardinalis*, *Caryothraustes*, *Peripophyrus*, and *Rhodothraupis*. These genera can be characterized as being brightly colored (red, orange, or yellow carotenoid pigments) and sexually dichromatic. The latter is a trait that was apparently lost along the branch leading to *Caryothraustes*, the only members of this clade with similar plumages for both sexes. Another prominent morphological feature within this clade is the presence of a black "mask" around the bill and eyes. Among the *Caryothraustes*, *Peripophyrus*, and *Rhodothraupis* taxa, both sexes possess this feature. It occurs only in males of *Cardinalis* and is red, instead of black, in *phoeniceus* and *sinuatus*. Within *Piranga*, only the forms *leucoptera*, *erythrocephala*, and *rubriceps* exhibit a mask, although it is much reduced in size. According to Burns (1998, his Fig. 4), these three form a well-supported clade that diverged early in the history of this genus, suggesting that the "mask" character may have been lost by the ancestor of the remaining members of *Piranga*. Although our sampling of this

Table 4
Bayesian posterior support values for select nodes (in brackets, see Fig. 2) using alternative partitioning strategies

Node:	No partition	By gene	By codon
Bayesian partitioning scheme			
Cyanocompsa and allies (*Cyanocompsa–Amaurospiza–Cyanoloxia*) [1]	62	68	71
Passerina monophyly [2]	100	100	100
Passerina plus "*Cyanocompsa*" [3]	84	92	97
Lineage A (*Passerina*–"*Cyanocompsa*"–*Spiza*) [4]	100	100	100
Granatellus sister to lineage A [5]	80	92	95
Granatellus monophyly [6]	100	100	100
Pheucticus sister to *Granatellus* plus lineage A [7]	73	68	65
Pheucticus monophyly [8]	100	100	100
Piranga monophyly [9]	100	100	100
Caryothraustes–Periphorphyrus–Rhodothraupis plus *Cardinalis* [10]	100	100	100
Caryothraustes–Periphorphyrus–Rhodothraupis [11]	100	100	100
Lineage D (node 10 above, plus *Piranga*) [12]	100	100	100
Lineage E (*Habia* plus *Chlorothraupis*) [13]	100	100	100
Lineages D plus E [14]	69	56	—

genus is limited, the topology (Fig. 2) is consistent with this interpretation. Our data indicate that the widely separated, monotypic forms *Periporphyrus* (NE South America) and *Rhodothraupis* (NE Mexico) are sister taxa, a pairing that makes sense given their plumage similarities (extensive black masks, red males, and yellow females). These in turn are clearly sister to both representatives of *Caryothraustes*, and collectively, this group is sister to *Cardinalis*. The only unresolved node in the "masked" clade appears within the completely sampled genus *Cardinalis* despite the fact that *cardinalis* and *sinuatus* (traditionally considered sister taxa) occur in North America and *phoeniceus* along the arid coast of Venezuela.

4.2.2. Habia and Chlorothraupis

In Burns's (1997) work on the molecular systematics of the Thraupini, *the genera Piranga*, *Habia* and *Chlorothraupis* grouped consistently near the base of his topology. Thus, it is not surprising that the latter two are now shown to belong within the Cardinalini along with *Piranga*. Together, they form a well-supported clade (Fig. 2E) and one of the five unresolved Cardinalini lineages. Morphological similarities suggest that its placement as sister to the clade just discussed (Fig. 2D) is probable; however, support for this relationship is lacking and inconsistent across analyses. Our results indicate that the current configuration of *Habia* is polyphyletic, with *Habia rubica* more closely related to members of the genus *Chlorothraupis*. Although our sampling of this clade is lacking two putative members of *Habia*, the tree indicates an abrupt shift in both plumage coloration and degree of dichromatism on the branch of the *Chlorothraupis* ancestor. *Habia* males (including *rubica*) are mostly red and females reddish- or yellowish brown. Sexes are morphologically similar in *Chlorothraupis*, with both displaying yellowish green or olive plumage throughout.

4.2.3. Pheucticus and Granatellus

With their conical, crushing bills, members of the genus *Pheucticus* have long been considered part of the tribe currently recognized as the Cardinalini. *Granatellus*, however, is an unlikely candidate for the group due to their more narrow and insectivorous bill. It has traditionally been considered a member of the Parulini (e.g. Ridgway, 1902; Sibley and Monroe, 1990), although many workers considered it an aberrant and likely misplaced member of that group (e.g. Lowery and Monroe, 1968). This skepticism was justified by a recent molecular systematic assessment of the Parulini (Lovette and Bermingham, 2002) in which *Granatellus* appeared to be more closely allied to members of the Cardinalini, a finding supported here. The placements of both *Granatellus* and *Pheucticus* within the Cardinalini are unresolved in our analyses with each originating early on in the tribe's history. All members of both of these clades are sexually dichromatic with males displaying bright carotenoid pigments in their plumage; but, unlike most other members of the Cardinalini, these are heavily melanistic with mostly black backs and flight feathers. The similarities between *Pheucticus ludovicianus* and the three members of *Granatellus* in both plumage pattern and color are striking, and given their systematic affinities, unlikely to be due to convergence. Whether these similarities are indicative of a close (sister?) relationship between these two genera or simply represent retained ancestral characters, requires a more thorough analysis. Our hypothesis of *Granatellus* (complete sampling, 3 species) relationships indicates a deep history for this group, with the South American endemic *pelzelni* sister to a pair of endemic Mexican forms, *venustus* (Pacific lowlands) and *sallaei* (Caribbean lowlands).

4.2.4. The "blue" clade

That the genera *Cyanocompsa*, *Amaurospiza*, *Cyanoloxia*, *Passerina*, and *Spiza* form a clade is unequivocal (Fig. 2A), according to our data. The close relationship

between members of *Passerina* and *Cyanocompsa* was known from an earlier study (Klicka et al., 2001) although *Amaurospiza* and the monotypic *Cyanoloxia* were not a part of this work. Our topology indicates that the latter two appear to be embedded within *Cyanocompsa*, rendering this genus paraphyletic. On morphological grounds, this is not particularly surprising. Males for all members of this clade may be characterized as having blue or blue-black plumage while all females are typically brown or reddish-brown. Despite having a cardinalin-like bill and plumage similarities, *Amaurospiza* is presently classified among the Thraupini (as one of the "tanager-finches"). It had previously been placed among the Emberizini, but has never been placed among the Cardinalini (but see Payter, 1970). Our tree (Fig. 2) is consistent with a *Passerina–Cyanocompsa* (and allies) sister relationship (Klicka et al., 2001) although this node (Fig. 2, node 3) lacks support and the exact placement of *C. parellina* remains equivocal. Relationships among *Passerina* taxa are nearly identical to those recovered in a previous molecular phylogeny (Klicka et al., 2001), differing only in the relative position of *cyanea*. We note that the placement of *cyanea* was not supported in either work. Like all members of the *Cyanocompsa* clade, all male *Passerina* also display at least some blue (presumably structural) pigmentation in their plumage. A subclade within *Passerina* (*ciris*, *versicolor*, *leclancherii*, and *rositae*) also display the bright, carotenoid pigmentation that is conspicuous in the other (Fig. 2, Clades B, C, D, E) cardinalin clades. Like *Cyanocompsa*, females in this assemblage are comparatively drab with a muted plumage of olives or browns. Considered by many workers to be an aberrant cardinalin genus (e.g. Tordoff, 1954b), the monotypic form *Spiza* is without doubt a part of this assemblage, branching off early in the group's history. From a morphological perspective, *Spiza* is an unlikely member, possessing a smaller, more sparrow-like bill and lacking entirely any blue coloration. The results of an allozyme study by Tamplin et al. (1993) concluded that *Spiza* was the sister to all cardinalins examined; whereas, a detailed morphometric analysis did link *Spiza* with *Passerina* (Hellack and Schnell, 1977). Our study indicates a clear affinity with both *Passerina* and *Cyanocompsa* (Fig. 2) although more data are required to sort out the basal relationships within this clade. At present, we are left with a four-way polytomy when unsupported nodes are collapsed.

4.2.5. Excluded taxa

The exclusion of the monotypic forms *Porphyrospiza* and *Parkerthraustes* from the Cardinalini is not surprising. *Porphyrospiza* plumage is nearly identical to that of *Passerina cyanea* although instead of a robust, seed-crushing bill, the bill of this species is relatively thin and light-colored. Although long placed among the Cardinalini (Hellmayr, 1938; Payter, 1970; Sibley and Monroe, 1990) some have suggested that it belongs elsewhere based on osteological (Tordoff, 1954a) and behavioral (Ridgely and Tudor, 1989) evidence. Our topology (Fig. 1) places it deep within the Thraupini, sister (with support) to *Phrygilus alaudinus*. Allozyme data (Tamplin et al., 1993; Demastes and Remsen, 1994) and behavioral observations (Tamplin et al. and references therein) led to the recent splitting of the genus *Parkerthraustes* (monotypic, formerly *Caryothraustes humeralis*) from *Caryothraustes* (Remsen, 1997). The results of Tamplin et al. (1993) suggested that this form was not a member of the Cardinalini, although it has been retained within the tribe. Our tree indicates that *Parkerthraustes* is a member of the Thraupini but affinities within that clade remain undetermined (Fig. 1). The genus *Saltator* has long been entrenched within the Cardinalini (e.g. Ridgway, 1901) but here, they occupy a basal position within the Thraupini (Fig. 1). However, our data cannot rule out the hypothesis that they are a sister clade to the Cardinalini. It is noteworthy that Sushkin (1924) considered *Saltator* "a thick-billed" tanager, while others (e.g. Mayr and Amadon, 1951; Tordoff, 1954a) thought they provided a "transition" between the Cardinalini and the Thraupini. Although *Saltator* is not the focus of this paper, we note that the genus does appear to be polyphyletic. Among the sampled *Saltator* taxa (Fig. 1) only *rufiventris* is not a member of the group; it is instead more closely aligned with representatives of the genera *Delothraupis* and *Dubusia*. In addition, the putative "tanager-finch" *Saltatricula multicolor* appears to belong among the Saltators, pairing with *S. atricollis* in all analyses.

4.3. The Cardinalini radiation

The short internodes and lack of resolution near the base of the tree (Fig. 2) are likely the consequence of a rapid radiation event in which the ancestors of each of the five Cardinalini lineages (Fig. 3) diverged from one another during a relatively brief interval of time. This event is reflected in the similarities of among-lineage genetic distances (cyt-*b* only, uncorrected) that range from 9.8% (*Pheucticus–Granatellus*) to 11.2% (*Habia* & *Chlorothraupis–Granatellus*), averaging 10.5% (SE = 0.006, matrix not shown). Evolution within the Cardinalini clade is clock-like (Fig. 2, legend) allowing for direct inferences to be made regarding relative diversification times. Application of the often used 2%/MY rate of cyt-*b* sequence evolution to our uncorrected distances suggests that the cardinalin radiation occurred approximately five million years ago, during the mid to late Pliocene. However, the uncritical application of this "molecular clock" calibration has rightly been questioned (see Lovette, 2004; Garcia-Moreno, 2004; Pereira and Baker, 2006).

Paramount among the factors known to affect "clock" calibrations are: (1) variation in rates of sequence change between lineages; (2) variation in rates of change between different genetic markers; (3) uncertainties associated with calibration points; (4) poorly fitting models of sequence

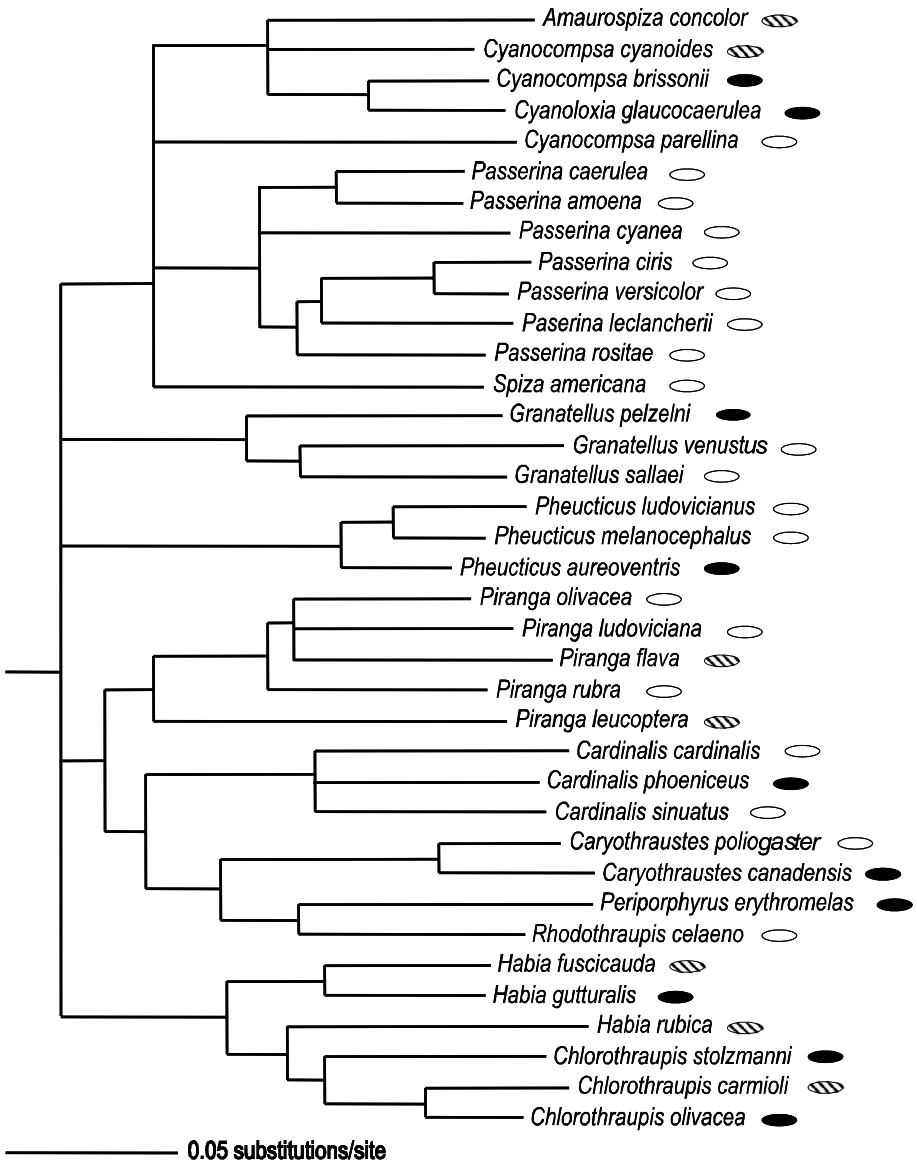

Fig. 3. Our most "reliable" estimate (after Lanyon, 1993) of phylogenetic relationships among members of the redefined Cardinalini. All unsupported and conflicting nodes have been collapsed. Taxa restricted to either North or South America are indicated by open and closed ovals, respectively. For those taxa distributed on both continents, ovals are striped.

evolution (see thorough reviews by Arbogast et al., 2002; Broham and Penny, 2003 on this topic).

We can account for most of these problems by using the data of Fleischer et al. (1998). Cardinalins, like the honeycreepers (tribe Carduelini) studied by these authors, are songbirds with similar body sizes, generation times, and presumably metabolic rates, all factors assumed to influence mutation rates (Martin and Palumbi, 1993; Gillooly et al., 2005). Fleischer et al. (1998) data consisted of 675 bp of cyt-*b* data and according to the AIC of Modeltest 3.04 (Posada and Crandall, 1998), the GTR + I + Γ model of sequence evolution was the best fit to these data. Fleischer et al. used the well documented emergence times of three different islands in the Hawaiian archipelago with ages of 0.43 MY (Hawaii), 1.6 MY (Maui) and 3.7 MY (Oahu) as calibration points. Using these calibration times, their GTR + I + Γ corrected data yield rate estimates of 2.18%/MY, 1.8%/MY, and 1.99%/MY, respectively, or approximately 2%/MY on average. Our Cardinalini cyt-*b* data, when trimmed to 675 bp and corrected (also GTR + I + Γ) yielded among-lineage divergences ranging from 14.25% (*Pheucticus–Granatellus)* to 17.78% (*Habia* & *Chlorothraupis–Granatellus*) and averaged 16.2%. According to this analysis, the cardinalin radiation occurred around 8 million years ago. Collectively, our divergence time estimates (5MYA, 8MYA) suggest a Pliocene origin for the Cardinalini radiation, and likely for the entire nine-primaried oscine clade. Whether the Cardinalini radiation began in North or South America is unclear. With basal

relationships unknown and several important taxa missing from the dataset, a thorough biogeographic analysis is beyond the scope of this work. We note, however that each of the five lineages in the Cardinalini have both North and South American representation (Fig. 3), suggesting a dynamic and complex biogeographic history for the group. Future analyses should include all available species and multiple exemplars for broadly distributed taxa, particularly those which occur in both North and South America.

4.4. Taxonomic implications

A close relationship between members of the *Passerina–Cyanocompsa* complex has long been recognized. In the most widely used of the "pre-molecular" taxonomies, Payter (1970) merged *Passerina*, *Cyanocompsa*, and *Cyanoloxia* into *Passerina* and commented that *Amaurospiza* also was "close to or conspecific with, *Passerina*," although he kept this genus among a group now recognized as the tanager-finches (Thraupini). In our topology (Fig. 2), this complex is divided into two clades, although the exact position of *Cyanocompsa parellina* remains unresolved. Nevertheless, *Cyanocompsa* as shown is paraphyletic with respect to both *Cyanoloxia* and *Amaurospiza*. We favor a taxonomy that recognizes two clades within this group, *Passerina*, as presently recognized, and a revised *Cyanocompsa*. The genus *Cyanoloxia* (Bonaparte, 1850, Consp. Gen. Av., 1 (2), p. 503) has priority over *Cyanocompsa* and *Amaurospiza* (both Cabanis, 1861; J.F. Ornith, 9, pp. 3–4); thus, we recommend that these latter two genera be merged into *Cyanoloxia*. The sister to the *Passerina–Cyanocompsa* complex is the monotypic form *Spiza*. Because of its distinctive morphology and behaviors, and its systematic position outside of the core clade, we suggest that it is best retained as monotypic.

The genera *Caryothraustes* (Reichenbach, 1850, Av. Syst. Nat., pl. 78), *Periporphyrus* (Reichenbach, 1850, Av. Syst. Nat., pl. 77), and *Rhodothraupis* (Ridgway, 1898, Auk. 15, p. 226), form a well-supported clade that is also distinct morphologically. We favor the elimination of two monotypic forms by merging of these genera into a single genus containing four species. Although *Caryothraustes* and *Periporphyrus* were described at the same time, we suggest that the more widely distributed (and better known?) *Caryothraustes* be taken as the name of this merged group. As an alternative, *Rhodothraupis* could be merged into *Periporphyrus*, leaving this expanded genus as sister to a retained *Caryothraustes*.

According to our topology, the genus *Habia* (although sampling is not complete) as presently configured is polyphyletic as *H. rubica* is sister to the *Chlorothraupis* (complete sampling) assemblage. Although this problem could be solved by merging *rubica* into *Chlorothraupis*, such a solution is confounded by morphology. All members of *Habia* are similarly plumaged with reddish males and yellowish-brown females whereas all members of *Chlorothraupis* lack this high degree of sexual dichromatism, with a uniformly drab, olive coloration. To eliminate confusion, we prefer the merging of these two genera into a single genus (eight species). In this case *Habia* (Blyth, 1840, *in* Cuvier's Animal Kingdom, p.184) would have taxonomic precedence over *Chorothraupis* (Salvin and Goodman, 1883, Biol. Cent. Amer. Aves, 1, p. 297).

5. Conclusion

In order to assess the taxonomic validity of the tribe Cardinalini, we have presented the taxonomically most complete study of New world nine-primaried oscines done to date. A monophyletic Cardinalini is identified, although it differs from that described by Sibley and Monroe (1990). Theirs is comprised of 42 species organized into 13 genera while the reconfigured Cardinalini of this study contains 15 genera and, despite the "loss" of the speciose genus *Saltator* (14 spp.), now consists of 48 species. The data suggest a Cardinalini–Thraupini sister relationship. Although strong support for this relationship was lacking, this result has been consistently obtained across analyses (this study) and across taxonomic studies (e.g. Yuri and Mindell, 2002).

The species now included in the Cardinalini are a varied and heterogeneous assemblage with respect to many traits. As noted earlier, they vary with respect to plumage coloration and degree of sexual dichromatism. Within the group, both song and size (see Klicka et al., 2001) are variable, as are geographic distributions. It is appropriate to study the evolution of such characters by mapping them onto a well-resolved phylogenetic tree. Unfortunately, this study was unable to identify with certainty the sister group to the Cardinalini and within the clade we are left with five lineages of yet uncertain relationship to one another. Proper study of cardinalin character evolution awaits further analyses that include additional sequence markers and complete taxon sampling.

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Appendix A

Taxa used in this study with specimen source and locality information

Taxon[a]	Specimen source[b,c]	Collecting locality
Outgroup		
Montifringilla davidiana	UWBM 57838 (bks3926)	Mongolia: Tov Aymag
Fringillinae (finches)		
Fringilla coelebs	LSUMNH 13466 [AF447368, AF447281]	Germany
Coccothraustes vespertina	BMNH (af1007)	U.S.: Minnesota
Carduelis pinus	BMNH (X7293) [AF29015]	U.S.: Minnesota
Carpodacus mexicanus	UMMZ 224950 [AF447364, AF447300]	U.S.: Michigan
*Serinus serinus**	UMMZ 233806 [L76263, AF447305]	Captive stock
*Loxia curvirostra**	UMMZ 227667 [AF171657, AF447290]	U.S.: Michigan
Euphonia fulvicrissa	STRI (paEFUL102) [AF383014, AF383130]	Panama: Panama
*Euphonia laniirostris**	[AF006232, AF447280]	
Euphonia finschi	FMNH 389276 (5166) [AF290106]	Brazil: Roraima
Chlorophonia occipitalis	MBM 4349 (dab1277)	Nicaragua: Matagalpa
Emberizini (sparrows)		
Zonotrichia albicollis	WTSP22a (RM Zink)	
Pipilo fuscus	BRTO2373 (RM Zink) [AF290123]	U.S.: Arizona
Atlapetes pileatus	MBM 13996 (jk04-056)	Mexico: Guerrero
Melospiza melodia	BMNH (jk94-84)	U.S.: Montana
Buarremon brunneinucha	MBM 4600 (dab1706)	Nicaragua: Managua
Arremon aurantiirostris	MBM 7856 (jk00-053)	Honduras: Copan
Spizella pusilla	BMNH (jk96-014)	U.S.: Minnesota
Ammodramus savannarum	BMNH (jk954-56) [AF290125]	U.S.: Montana
Chlorospingus flavigularis	FMNH430078	Peru: Cuzco
Chlorospingus ophthalmicus	MBM 7094 (jk99-74)	Honduras: Atlantida
Melophus lathami	AMNH (jgg1191)	Nepal: Kipsung
Emberiza stewarti	FMNH 347945	Pakistan: NW Frontier
Emberiza godlewskii	UWBM 57948 (dab2221)	Mongolia: Omngovi Aymag
Emberiza calandra	UWBM 61357 (svd1604)	Russia: Khabarovskiy Kray
Emberiza variabilis	UWBM 46944 (bks1013)	Russia: Sakhalinskaya Oblast
Emberiza schoeniclus	UWBM 49230 (bks1624)	Russia: Moscovskaya Oblast
Emberiza rustica	UWBM 52657(svd141)	Russia: Magadanskaya Oblast
Emberiza pusilla	UWBM 44474 (sar6107)	Russia: Magadanskaya Oblast
Emberiza pallasi	UWBM 47188 (sar6412)	Russia: Khabarovskiy Kray
Icterini (blackbirds)		
Icterus bullocki	BMNH (jk95-095)	U.S.: Oregon
Cacicus solitarius	FMNH 324089 [AY117719, AY117747]	Peru: Madre de Dios
Psarocolius wagleri	LSUMNH (mjb126) [AF472369, AF472394]	
Agelaius phoeniceus	FMNH 341893 [AF290173, AF290134]	U.S.: Louisiana
Molothrus ater	BMNH (JK96-016)	U.S.: Minnesota
Scaphidura oryzivora	FMNH 324097 [AF089060, AF109960]	
Quiscalus major	FMNH 341918 [AF290171, AF109953]	U.S.: Louisiana
Euphagus cyanocephalus	FMNH 341985 [AF089024, AF109951]	
Lampropsar tanagrinus	LSUMNH 125586 [AF089037, AF109946]	
Oreopsar bolivianus	FMNH 334687 [AF089046, AF109940]	
Amblycercus holosericeus	KU 2075 [AY117723, AY117751]	
Dolichonyx oryzivorus	UMMZ 234583 [AF447367, AF447326]	U.S.: Michigan
Sturnella neglecta	BMNH (jk95-088)	U.S.: Oregon

(*continued on next page*)

Appendix A (*continued*)

Taxon[a]	Specimen source[b,c]	Collecting locality
Parulini (warblers)		
Geothlypis trichas	BMNH (jk92-119) [AF290135]	U.S.: Oregon
Dendroica tigrina	STRI (jadt11) [AF256505, AF256493]	Jamaica: St. Elizabeth
Vermivora ruficapilla	UWBM (csw5040) [AF256510, AF256501]	U.S.: Washington
Protonotaria citrea	BMNH (X7389)	U.S.: Minnesota
Seiurus aurocapillus	STRI (jaSAU1) [AF383007, AF383123]	Jamaica: Westmoreland
Wilsonia canadensis	ANSP 184471 [AF383016, AF383132]	Panama: Panama
Myioborus miniatus	LSUMNH (B-26421) [AF383015, AF383131]	Panama: Chiriqui
Ergaticus ruber	FMNH (bmm169) [AF383101, AF383125]	Mexico: Michoacan
Euthlypis lachrymosa	FMNH (bmm252) [AF383009, AF383125]	Mexico: Oaxaca
Thraupini (tanagers)		
Chrysothlypis chrysomelas	MBM 15584 (gms1096)	Panama: Cocle
Phrygilus unicolor	MBM 6471 (jag2074)	Argentina: Tucuman
Phrygilus atriceps	MBM 5307 (dhb2414)	Argentina: Jujuy
Phrygilus dorsalis	MBM 6476 (jag2075)	Argentina: Tucuman
Phrygilus plebejus	MBM 5310 (dhb2441)	Argentina: Jujuy
Phrygilus alaudinus	MBM 6470 (jag1890)	Argentina: Tucuman
Thlypopsis ruficeps	MBM 6577 (b8245)	Argentina: Tucuman
Hemispingus frontalis	LSUMNH (B-1766) [AF38020, AF383136]	Peru: Pasco
Hemispingus atropileus	LSUMNH (B-18890) [AF383019, AF383135]	Peru: Pasco
Poospiza hypochondria	MBM 5302 (dhb2367)	Argentina: Salta
Poospiza erythrophrys	MBM 5491 (jag2101)	Argentina: Salta
Poospiza torquata	MBM 6455 (jag 2010)	Argentina: Tucuman
Poospiza baeri	MBM 6457 (jag1901)	Argentina: Tucuman
Diglossa baritula	MBM 13911 (jk04-386)	Mexico: Guerrero
Diglossa major	FMNH 339722 [AF290118]	Venezuela: Bolivar
Haplospiza unicolor	FMNH (5186) [AF290118]	Brazil: Sao Paulo
Catamenia inornata	MBM 6465 (jag2014)	Argentina: Tucuman
Sicalis olivascens	MBM 5435 (gav993)	Argentina: Jujuy
Conirostrum bicolor	STRI (trCBCL1) [AF38025, AF383141]	Trinidad(?)
Eucometes penicillata	MBM 14831 (jk04-299)	Panama: Colon
Tachyphonus luctuosus	MBM 8846 (jk01-051)	Honduras: Atlantida
Tachyphonus delatrii	MBM 15562 (jk04-262)	Panama: Cocle
Lanio auratus	MBM 8966 (dhb3785)	Honduras: Atlantida
Coryphospingus cucullatus	MBM 6485 (jag2050)	Argentina: Tucuman
Ramphocelus passerinii	MBM 8627 (jk01-031)	Honduras: Atlantida
Ramphocelus dimidiatus	MBM 14837 (gms1173)	Panama: Colon
Oryzoborus funereus	MBM 8980 (gav2044)	Honduras: Atlantida
Volatinia jacarina	FMNH (ank228) [AF290113]	Bolivia: Santa Cruz
Sporophila schistacea	LSUMNH (B-22584) [AF290112]	Bolivia: La Paz
Saltatricula multicolor	MBM 5447 (gav1009)	Argentina: Salta
Embernagra platensis	MBM 5512 (jag2154)	Argentina: Salta
Emberizoides herbicola	MBM 3721	Argentina: Corrientes
Dacnis cyana	MBM 16116 (mjm1170)	Panama: Panama
Cyanerpes cyaneus	MBM 7803(jk00-080)	Honduras: Copan
Tersina viridis[*]	LSUMNH (B-14819) [AF006255, AF447309]	Bolivia
Thraupis abbas	MBM 8671 (gms094)	Honduras: Atlantida
Thraupis episcopus	MBM 7057 (jk99-31)	Honduras: Copan
Thraupis bonariensis	LSUMNH (B-3587) [AY383103, AY383176]	Peru: Huanuco
Tangara veilla	FMNH (1886)	
Tangara mexicana[*]	UMMZ 233276	
Tangara varia	LSUMNH (B-28010)	Peru: Loreto

Appendix A (*continued*)

Taxon[a]	Specimen source[b,c]	Collecting locality
Tangara lavinia	LSUMNH (B-34987)	
Tiaris bicolor	BMNH (jk95-001) [AF290115]	Bahamas: Long Island
Tiaris olivacea	UMMZ 233813 [AF447373, AF447310]	Captive stock
Coereba flaveola	STRI (abCFA2) [AF382999, AF383109]	Bahamas: Abaco
Loxigilla violacea	AMNH 25433 [AF489887, AY383180]	Dominican Republic
Geospiza fortis[*]	UMMZ 224890 [AF108773, AF447282]	Ecuador: Galapagos
Buthraupis montana[*]	[AF006212, AF447264]	Bolivia
Anisognathus flavinuchus	LSUMNH (B-566) [AY383090, AY383164]	Peru: Puno
Calochaetes coccineus	LSUMNH (B-6134) [AY383090, AY383165]	Ecuador: Morona-Santiago
Chlorornis riefferii	LSUMNH (B-1859) [AY383093, AY383166]	Peru: Pasco
Delothraupis castaneoventris	LSUMNH (B-6931) [AY383097, AY383170]	Peru: Huanuco
Dubusia taeniata	LSUMNH (B-7710) [AY383098, AY383171]	Peru: Huanuco
Iridosornis analis	LSUMNH (B-B1706) [AY383099, AY383172]	Peru: Pasco
Neothraupis fasciata	LSUMNH (B-13914) [AY383100, AY383173]	Bolivia: Santa Cruz
Pipraeidea melanonota	LSUMNH (B-12070) [AY383101, AY383174]	Ecuador: Pichincha
Schistochlamys melanopsis	LSUMNH (B-9669) [AY383102, AY383175]	Bolivia: Pando
Paroraria dominicana	FMNH 392736	Brazil: Sergipe
Paroaria capitata	UWBM (jag1837)	Argentina: Corrientes
Lophospingus pusillus	MBM 6491 (jag2058)	Argentina: Tucuman
Diuca diuca	MBM 6477 (jag2005)	Argentina: Tucuman
Chlorochrysa phoenicotis	LSUMNH (B-34873) [AY383094, AY393167]	Ecuador: Pichincha
Cissopis leveriana	LSUMNH (B-1143) [AY383096, AY383169]	Bolivia: La Paz
Porphyrospiza caerulescens	LSUMNH (B-13860)	Bolivia: Santa Cruz
Parkerthraustes humeralis	LSUMNH (B-9328)	Bolivia: Pando
Saltator grossus	LSUMNH (B-16063)	Costa Rica: Heredia
Saltator coerulescens	UWBM (gav817)	Argentina: Corrientes
Saltator striatipectus	STRI (ccSAL1) [AF383107, AF281023]	Trinidad: Chacachacare Isle.
Saltator atripennis	ANSP (3485)	Ecuador: Azuay
Saltator atriceps	FMNH 343357 (4885)	Mexico: Veracruz
Saltator maximus	LSUMMNH (B-15194)	Bolivia: Santa Cruz
Saltator nigriceps	LSUMNH (B-183)	Peru: Piura
Saltator aurantiirostris	UWBM 54506 (gav685)	Argentina: Tucuman
Saltator atricollis	LSUMNH (B-15381)	Bolivia: Santa Cruz
Saltator rufiventris	LSUMNH (B-106750)	Bolivia: Cochabamba
Cardinalini (cardinal-grosbeaks)		
Amaurospiza concolor	MBM (jk02-012)	Guatemala: Retalhuleu
Cyanocompsa brissonii	LSUMNH 153865 (B-18658) [AF301461]	Bolivia: Santa Cruz
Cyanocompsa cyanoides	LSUMNH 137749 (B-12708) [AF301462]	Bolivia: Santa Cruz
Cyanocompsa parellina	UWBM (cwt082) [AF301460]	Mexico: Oaxaca
Cyanoloxia glaucocaerulea	ANSP 10255	Uruguay: Rocha
Passerina caerulea	LSUMNH 154263 (B-20958) [AF301449]	U.S.: Louisiana
Passerina cyanea	BMNH (X7250) [AF301446]	U.S.: Wisconsin
Passerina rositae	UWBM (cwt036) [AF301453]	Mexico: Chiapas
Passerina amoena	BMNH (jk96-030) [AF301450]	U.S.: Oregon
Passerina versicolor	UWBM (cwt095) [AF301457]	Mexico: Coahuila
Passerina ciris	LSUMNH 11711 (B-5694) [AF301459]	U.S.: Louisiana
Passerina leclancherii	UWBM (cwt 034) [AF301454]	Mexico: Chiapas
Spiza americana	BMNH (jk95-047) [AF290110]	U.S.: Texas
Granatellus sallaei	KU 89487 (mbr4475)	Mexico: Campeche
Granatellus venustus	MBM 14068 (jk04-788)	Mexico: Oaxaca
Granatellus pelzelni	LSUMNH (B-18554) [AF382995, AF383111]	Bolivia: Santa Cruz
Pheucticus aureoventris	LSUMNH (B-18866)	Bolivia: Santa Cruz

(*continued on next page*)

Appendix A (*continued*)

Taxon[a]	Specimen source[b,c]	Collecting locality
Pheucticus ludovicianus	BMNH (X7253) [AF290108]	U.S.: Minnesota
Pheucticus melanocephalus	BMNH (jk95-078)	U.S.: Oregon
Piranga ludoviciana	BMNH (jk94-105) [AF290109]	U.S.: Montana
Piranga olivacea	BMNH (X7284)	U.S.: Minnesota
*Piranga rubra**	LSUMNH (B-2364) [AF011779, AF447300]	U.S.: Louisiana
Piranga flava	MBM 8265 (jk00-248)	U.S.: Arizona
Piranga leucoptera	MBM 8664 (dhb3741)	Honduras: Atlantida
Cardinalis phoeniceus	STRI (CPH1) [AF447268]	Venezuela: Guarapo
Cardinalis sinuatus	MBM 14723 (dhb5750)	U.S.: Texas
Cardinalis cardinalis	BMNH (X7320a)	U.S.: Minnesota
Caryothraustes poliogaster	MBM 8986 (jk01-044)	Honduras: Atlantida
Caryothraustes canadensis	LSUMNH (B-1414)	Panama: Darien
Periporphyrus erythromelas	ANSP 187491 (6193)	Guyana: Potaro-Siparuni
Rhodothraupis celaeno	UNAM (X17)	Mexico: Tamaulipas
Habia rubica	MBM 9096 (gms145)	Honduras: Atlantida
Habia fuscicauda	MBM 6631 (gav1363)	Honduras: Copan
Habia gutturalis	PCPR089	Colombia: Antioquia
Chlorothraupis stolzmanni	ANSP (3503)	Ecuador: Azuay
Chlorothraupis carmioli	ANSP (5867)	Ecuador
Chlorothraupis olivacea	ANSP (2006)	Ecuador
Incertae cedis		
Calcarius lapponicus	BMNH (jdw0062) [AF290107]	U.S.: Minnesota
Calcarius ornatus	BMNH (jk94-187)	U.S.: Montana
Calcarius mccownii	BMNH (jk94-74)	U.S.: Montana
Calcarius nivalis	BMNH (af1011)	U.S.: Minnesota
Icteria virens	BMNH (jk95-141) [AF290126]	U.S.: Texas
Zeledonia coronata	LSUMNH (B-19939) [AF382998, AF383114]	Costa Rica: San Jose
Microligea palustris	STRI (rdMPAL1) [AF383021, AF383137]	Dominican Republic
Xenoligea montana	STRI (rdXMOL1) [AF383022, AF383138]	Dominican Republic
Teretistris fernandinae	ANSP (5548) [AF382999, AF383115]	Cuba
Spindalis xena	STRI (prSXE3) [AF383018, AF383134]	Puerto Rico
Mitrospingus cassinii	LSUMNH (B-11802) [AF006240]	
Mitrospingus oleagineus	FMNH 339677	Venezuela: Bolivar

[a] Species with asterisks are represented by more than one individual (chimeric sequences).

[b] Institutional abbreviations are as follows: UWBM, University of Washington, Burke Museum; LSUMNH, Louisiana State University, Museum of Natural History; BMNH, University of Minnesota, Bell Museum of Natural History; UMMZ, University of Michigan Museum of Zoology; STRI, Smithsonian Tropical Research Institute; FMNH, Field museum of Natural History; AMNH, American Museum of Natural History; ANSP, Academy of Natural Sciences, Philadelphia; KU, University of Kansas Natural History Museum; MBM, University of Nevada Las Vegas, Barrick Museum of Natural History.

[c] Tissue accession numbers, field collector numbers, or prep numbers are shown in parentheses. Those sequences obtained from genbank are indicated in brackets.

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