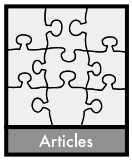

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A molecular systematic revision of two historically problematic songbird clades: *Aimophila* and *Pipilo*

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The emberizid genera *Aimophila* and *Pipilo* represent longstanding taxonomic conundrums. Each is comprised of sub-clades whose members appear to share diagnostic morphological and behavioral characters; however, relationships among sub-clades within each of these genera remain unclear, and numerous authors have suggested that either one or both of these genera may be polyphyletic. We addressed this taxonomic problem by sequencing and analyzing complete mitochondrial cytochrome-*b* and NADH dehydrogenase subunit 2 genes for all members of *Aimophila* and *Pipilo* along with 33 species representing 17 additional emberizid genera. Our maximum likelihood and Bayesian analyses indicate that both *Aimophila* and *Pipilo* are polyphyletic. *Aimophila* is divided into a minimum of three distinct groups. The forms *notosticta, ruficeps*, and *rufescens* are part of a well-supported clade that includes all members of *Melozone* and some members of *Pipilo*. *Aimophila quinquestriata* is placed within *Amphispiza*, and the remaining members of *Aimophila* are placed within a clade that includes all members of *Arremonops* and some members of *Ammodramus*. Within *Pipilo*, the ''rufous-sided'' and ''brown'' towhee groups do not form sister groups. Rather, the former are most closely related to the tropical genus *Atlapetes* whereas the latter are placed nearest *Melozone* and some *Aimophila*. Our analyses reject traditional taxonomic arrangements for both genera, and we present suggestions for a revised taxonomy for all members of *Aimophila* and *Pipilo*. These results provide further evidence of discordance among phylogenetic hypotheses based on morphological and molecular characters for groups of birds with generally conserved morphology.

The genus *Aimophila* contains 13 (Sibley and Monroe 1990), or 14 (AOU 1998) species that represent a morphologically diverse group of sparrows that have been considered by many to constitute an ''unnatural assemblage'' (Ridgway 1901, Dickey and van Rossem 1938, Storer 1955). The most rigorous systematic study of the genus was done by Wolf (1977), who analyzed an array of morphological, behavioral, and ecological characters. His analyses split the genus into three ''species groups'' that he did not believe to be closely related (Fig. 1). He addressed the need for further investigation of closely related species and genera, and hypothesized that ''each group may well be related to different genera''. Since Wolf's study few molecular analyses have addressed relationships of members of *Aimophila*. Some *Aimophila* species have been included in higher-level analyses (Yuri and Mindell 2002, Carson and Spicer 2003), although, sampling of the genus was too sparse to address relationships among most species. Carson and Spicer's (2003) work (using three *Aimophila* species) did indicate a polyphyletic *Aimophila* and deep divergences between species.

The genus *Pipilo* contains eight species (Sibley and Monroe 1990, AOU 1998) of medium-sized emberizids commonly referred to as towhees. Several researchers (Davis 1951, Sibley 1955, Marshall 1960, Marshall 1964, Sibley and Sibley 1964) split it into two major groups: the ''brown'' towhees (*aberti*, *albicollis*, *crissalis*, and *fuscus*), and the ''rufous-sided'' towhees (*chlorurus*, *erythrophthalmus*, *maculatus*, and *ocai*). The genus has been the subject of numerous molecular studies, with markers including allozymes (Zink 1988), mitochondrial DNA (mtDNA) restriction length fragment polymorphisms (Zink and Dittmann 1991), and mtDNA sequence (Dodge et al. 1995, Zink et al. 1998). These studies had varying results due to differences in sampling and phylogenetic signal, but collectively form the systematic hypothesis presented in Fig. 1. Importantly, none of the molecular studies included all of the current members of *Pipilo*, and none included more than one or two potential outgroup taxa. The most recent of these works (Zink et al. 1998) indicated the possibility that *Melozone kieneri* may be embedded within *Pipilo* (Parkes 1957), reinforcing the need for a more comprehensive phylogenetic survey.

We used mtDNA sequence data to re-evaluate the systematics of these enigmatic emberizid genera. Key to

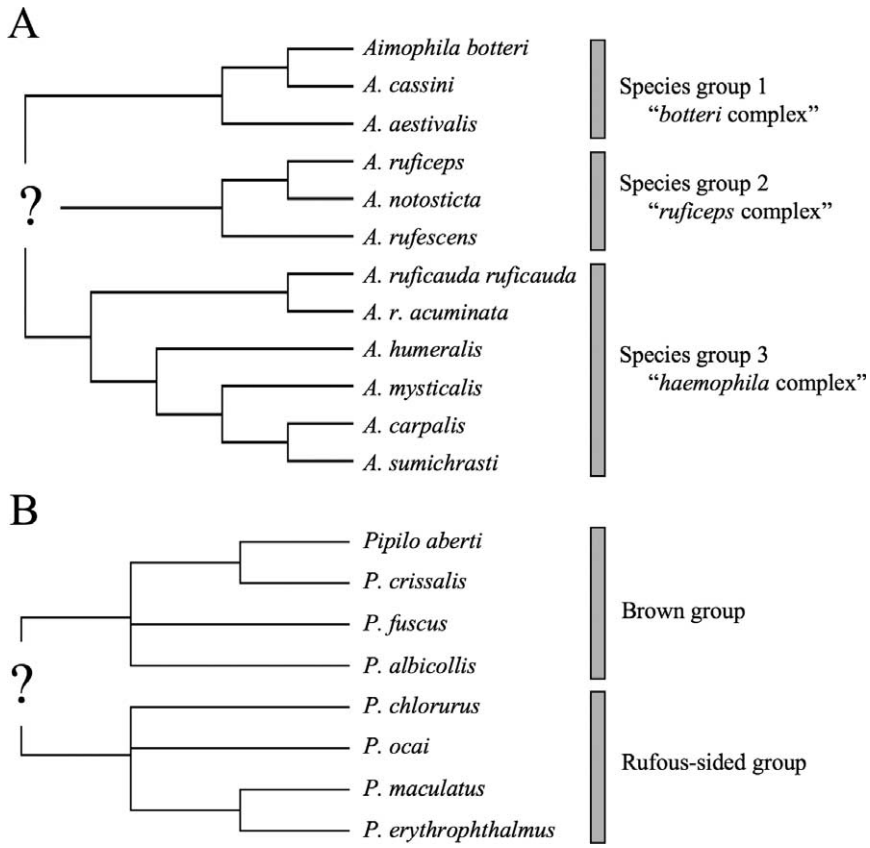

Figure 1. Prevailing phylogenetic hypotheses for two emberizid genera. A) *Aimophila* relationships according to Wolf (1977), his group names in parentheses. Wolf placed a fourth ''group'', *Amphispiza quinquestriata*, outside of this assemblage. B) *Pipilo* relationships according to previous molecular assessments of the genus.

this endeavor is taxon sampling. In addition to sampling all currently recognized *Aimophila* and *Pipilo* species, we analyzed a wider array of outgroup taxa than any other molecular systematic study of these genera. Such thorough taxonomic sampling should provide a more robust molecular phylogenetic assessment of *Aimophila* and *Pipilo* monophyly, relationships among the members of each genus, and their placement among other emberizids.

Materials and methods

Sampling

All members of *Aimophila* (including the South American species *stolzmani* and *strigiceps* not included in Wolf's monograph), *Pipilo*, and *Melozone* are included in our analyses. One sample per species was included, with the exception of *A. ruficeps*, where two well- differentiated subspecies (*A. r. ruficeps* and *A. r. acuminata*) were included following Wolf (1977). Additional representatives of the Emberizidae were then selected to increase the robustness of phylogenetic reconstructions, and to allow the monophyly of these genera to be more rigorously tested. Using the taxonomy of the American Ornithologists' Union (AOU 1998), and Sibley and Monroe (1990) as a reference, we included an additional 33 species from 17 other Emberizidae genera in the analysis. Lastly, samples from the families Icteridae (n = 5) and Parulidae (n = 4) were used as outgroups (Klicka et al. 2000). In total, 64 individuals representing 63 species and 28 genera were sampled for this study (Table 1).

Laboratory protocols

We extracted total genomic DNA from all samples using a DNeasy Tissue Kit (Qiagen Inc.). The manufacturer's protocol was used for fresh tissue and recent toepad samples, and a modified protocol (Nishiguchi et al. 2002) was used for older (20+ years) toepad samples. We then used a polymerase chain reaction (PCR) to amplify the mtDNA genes cytochrome-*b* (cyt-*b*) and NADH dehydrogenase subunit 2 (ND2). Cyt-*b* was amplified with the flanking primers L14764 and H4A (Harshman 1996), and in some cases with the internal primers LCBA (Klicka et al. 1999) and H15299 (Kocher et al. 1989). ND2 was amplified with the flanking primers L5215 and H6313 (Johnson and Sorenson 1998), or HTrpC (Smithsonian Tropical Research Institute), and in some cases with the internal primers L5758 and H5766 (Johnson and Sorenson 1998). Amplifications were done in 12.5 µl reactions under conditions described in a previous study (Klicka et al. 2005), with variations in temperatures and cycle lengths for some older samples. Products were purified using a Qiaquick PCR Purification Kit (Qiagen Inc.), or the enzyme ExoSAP-IT (USB Corp.) following the manufacturer's protocols. We prepared 20 µl sequencing reactions

Table 1. Museum source and localities of specimens used in phylogenetic reconstructions. Taxonomy following the AOU (1998).

Taxon	Sample source[a]	Collecting locality	Genbank assession no.	
			Cyt-*b*	ND2
Chlorospingus ophthalmicus	MBM (JK99-074)	HON: Copan	FJ547249	FJ547290
Chlorospingus flavigularis	FMNH (430078)	PER: Cuzco	FJ547250	FJ547291
Atlapetes pileatus	MZFC (OVMP227)	MEX: Jalisco	FJ547251	FJ547292
Atlapetes gutturalis	MBM (GAV1374)	HON: Copan	DQ459525	DQ459545
Atlapetes citrinellus	MBM (JAG2001)	ARG: Tucuman	DQ459524	DQ459544
Buarremon brunneinucha	MBM (DAB1706)	NIC: Granada	Cadena et al. 2007	Cadena et al. 2007
Arremon aurantiirostris	MBM (DAB853)	HON: Copan	Cadena et al. 2007	Cadena et al. 2007
Arremon flavirostris	UWBM (DAB853)	ARG: Corrientes	FJ547252	FJ547293
Arremonops rufivirgatus	BMNH (X6828)	USA: Texas	FJ547253	FJ547294
Arremonops chloronotus	KU (KU2031)	MEX: Campeche	FJ547254	FJ547295
Arremonops conirostris	MBM (DAB1049)	NIC: Atlantico Norte	FJ547255	FJ547296
Melozone kieneri	FMNH (343332)	MEX: Jalisco	FJ547256	FJ547297
Melozone biarcuatum	MBM (JK02-032)	GTM: Quetzaltenango	FJ547257	FJ547298
Melozone leucotis	MBM (JK02-053)	GTM: Quetzaltenango	DQ459517	DQ459537
Pipilo chlorurus	MBM (GTT01)	USA: Nevada	FJ547258	FJ547299
Pipilo ocai	FMNH (343329)	MEX: Jalisco	DQ459518	DQ459538
Pipilo maculatus	MBM (JK00-279)	USA: Nevada	FJ547259	FJ547300
Pipilo erythrophthalmus	BMNH (JK94-175)	USA: Minnesota	FJ547260	FJ547301
Pipilo albicollis	MBM (JK06-640)	MEX: Guerrero	FJ547261	FJ547302
Pipilo fuscus	BMNH (RMZ2373)	USA: Arizona	AF290160	AF290123
Pipilo crissalis	MBM (DHB5427)	USA: California	FJ547262	FJ547303
Pipilo aberti	MBM (DHB2352)	USA: Nevada	Cadena et al. 2007	Cadena et al. 2007
Aimophila r. ruficauda	MBM (DAB1680)	NIC: Rivas	FJ547263	FJ547304
Aimophila r. acuminata	CNAV (Po13223)	MEX: Oaxaca	FJ547264	FJ547305
Aimophila humeralis	CNAV (Po11084)	MEX: Morelos	FJ547265	FJ547306
Aimophila mysticalis	MZFC (OVMP773)	MEX: Puebla	FJ547266	FJ547307
Aimophila sumicrasti	CNAV (Po13226)	MEX: Oaxaca	FJ547267	FJ547308
Aimophila carpalis	MZFC (ORRS102)	MEX: Sonora	FJ547268	FJ547309
Aimophila cassini	MVZ (FC20222)	USA: Oklahoma	FJ547269	FJ547310
Aimophila aestivalis	LSUMNS (B-2461)	USA: Louisiana	FJ547270	FJ547311
Aimophila botterii	LSUMNS (B-9880)	USA: Arizona	FJ547271	FJ547312
Aimophila ruficeps	MVZ (FC20115)	USA: Oklahoma	FJ547272	FJ547313
Aimophila rufescens	MBM (DHB3531)	HON: Copan	FJ547273	FJ547314
Aimophila notosticta	CNAV (Po24880)	MEX: Oaxaca	FJ547274	FJ547315
Aimophila quinquestriata	MZFC (ORRS109)	MEX: Sonora	FJ547275	FJ547316
Aimophila stolzmanni	LSUMNS (B-5227)	PER: Lambayeque	FJ547276	FJ547317
Aimophila strigiceps	MBM (DHB2425)	ARG: Salta	FJ547277	FJ547318
Spizella passerina	LSUMNS (B-18047)	CAN: Yukon	FJ547278	FJ547319
Spizella pallida	BMNH (JDW0046)	USA: Minnesota	FJ547279	FJ547320
Amphispiza bilineata	MBM (TKA98)	USA: Nevada	FJ547280	FJ547321
Calamospiza melanocorys	BMNH (JK94-058)	USA: Montana	FJ547281	FJ547322
Passerculus sandwichensis	BMNH (X7320)	USA: Montana	DQ459513	DQ459533
Ammodramus aurifrons	J. Avise lab (DS74)		FJ547282	FJ547323
Ammodramus savannarum	BMNH (JK94-056)	USA: Montana	AF290162	AF290125
Ammodramus leconteii	BMNH (JK94-041)	USA: Minnesota	DQ459512	DQ459532
Ammodramus nelsoni	BMNH (JK97-033)	USA: Minnesota	DQ459522	DQ459542
Ammodramus humeralis	MBM (GAV1018)	ARG: Salta	FJ547283	FJ547324
Passerella iliaca	R. Zink lab (FOSP91)		FJ547284	FJ547325
Melospiza melodia	BMNH (JK94-084)	USA: Montana	DQ459523	DQ459543
Melospiza lincolnii	BMNH (JK97-038)	USA: Minnesota	DQ459515	DQ459535
Zonotrichia capensis	MBM (GAV2345)	GTM: Quetzaltenango	FJ547285	FJ547326
Zonotrichia albicollis	LSUMNS (B-15522)	USA: Louisiana	FJ547286	FJ547327
Junco hyemalis	MBM (GMS087)	USA: Nevada	Cadena et al. 2007	Cadena et al. 2007
Emberiza rustica	UWBM (SVD141)	RUS: Magadanskaya	FJ547287	FJ547328
Melophus lathami	AMNH (JGG1191)	NPL: Kipsung	FJ547288	FJ547329
Outgroup				
Dendroica tigrina			AF256505	AF256493
Protonotaria citrea			FJ547289	FJ547330
Seiurus aurocapillus			AF383007	AF383123
Myioborus miniatus			AF383015	AF383131
Sturnella neglecta			AF290164	AF290127
Molothrus ater			AF290172	AF109958
Icterus bullocki			AF099278	AF099315
Amblycercus holosericeus			AY117723	AY117751
Lampropsar tanagrinus			AF089037	AF109946

[a] Museum sources for specimens used in this study, abbreviations as follows: LSUMNS, Louisiana State University Museum of Natural Science; MZFC, Universidad Nacional Autónoma de México, Museo de Zoologia; MVZ, University of California, Berkeley, Museum of Vertebrate Zoology; CNAV, Universidad Nacional Autónoma de México, La Colleción Nacional de Aves; MBM, Marjorie Barrick Museum of Natural History; BMNH, James Ford Bell Museum of Natural History; FMNH, Field Museum of Natural History; UWBM, University of Washington, Burke Museum of Natural History; KU, University of Kansas Natural History Museum. Those numbers in parentheses represent tissue or collector/preparator numbers instead of study-skin voucher numbers. The *Ammodramus aurifrons* and *Passerella iliaca* samples are from earlier studies of sparrow systematics (Zink and Avise 1990, Zink 1994). Although these authors kindly provided us ultrapurified mtDNA samples for this study, neither was able to furnish the appropriate locality or voucher data at this later date.

using a Big Dye Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems) with 0.5–4 μl of Big Dye and 20–40 ng of purified PCR product. Sequencing reactions were purified using ethanol precipitation or the CleanSEQ (Agencourt Bioscience Corp.) magnetic bead clean-up, and run on an ABI 3100 – *Avant* automated sequencer (Applied Biosystems). We used the program Sequencher v4.6 (Gene Codes Corp.) to unambiguously align complementary strands, check for gaps in the sequences, and translate the nucleotide sequences to check for the absence of stop codons in the open reading frames of the two mtDNA genes.

Phylogenetic protocols

Phylogenetic analyses were preceded by data exploration. We used PAUP* 4.0b10 (Swofford 2002) to investigate the evolutionary dynamics of each gene and gene partition (i.e. codon position). Parameters examined include: number of variable sites, number of parsimony informative sites, percent nucleotide composition, transition/transversion ratio (Ts/Tv), and gamma shape (Γ). Uncorrected genetic distance matrices were calculated for all samples, and for only the ingroup samples (Emberizidae). Uncorrected genetic distance matrices for the ingroup (concatenated data, not shown) ranged from 0.6% (*Aimophila ruficauda ruficauda – A. r. acuminata*) to 15.6% (*Aimophila sumichrasti – Amphispiza bilineata*). Higher values exceeded the estimated saturation thresholds for both cyt-*b* (Griffiths 1997) and ND2 (Hackett 1996, Johnson and Sorenson 1998) genes. Phylogenetic reconstructions that do not correct for substitution saturation can produce misleading results, particularly due to long-branch attraction (Felsenstein 1978). This problem can be mitigated by assigning greater weight to less homoplastic transversions when performing maximum parsimony (MP) reconstructions, or using an evolutionary model that corrects for saturation effects in maximum likelihood (ML) and Bayesian analyses. We chose *a priori* to rely on ML methodology in our estimation of phylogeny. ML methods are better able to accommodate the complexities of the DNA sequence evolution process than MP (Felsenstein 1978, Huelsenbeck and Hillis 1993, Hillis et al. 1994, Huelsenbeck 1995, Swofford et al. 2001), and have been shown to outperform MP under a variety of simulated conditions (Huelsenbeck 1995, Swofford et al. 2001). Even though the analyzed genes belong to a single linkage group, we executed the incongruence length difference (ILD) test (Farris et al. 1994) to ensure that each gene contained congruent phylogenetic signal. The test consisted of 100 replicates, and did not detect a significant difference between the genes ($P = 0.64$).

MRMODELTEST 2.2 (Nylander 2004) was used to determine the model of molecular evolution for the sequence data. The Akaike Information Criterion option was chosen (Posada and Buckley 2004) and identified the GTR+I+Γ model as the best fit for each individual gene, and both genes combined. PAUP* was used to construct a ML phylogeny using the concatenated dataset and parameter settings determined by MRMODELTEST. ML nodal support was evaluated with 1000 bootstrap replicates using the program Treefinder (Jobb et al. 2004). This program uses a fast sampling algorithm to estimate all parameters while exploring tree space, and its accuracy in phylogeny construction has been demonstrated to equal or exceed other commonly used programs (Jobb et al. 2004). For bootstrap analyses, nodes recovered in 70% or greater of the replicates were considered significantly supported.

We used ML methodology in a Bayesian framework to provide another measure of relationships and nodal support, and to construct phylogenies by partitioning the data by gene region. Both gene partitions were analyzed under the GTR+I+Γ model of evolution, and all parameters were unlinked so that they were independent for each partition (i.e. gene region) in the program MRBAYES 3.1.2 (Ronquist and Huelsenbeck 2003). Analyses were run with random starting trees and four (three heated and one cold) Markov chain Monte Carlo chains. Two runs were performed with 10,000,000 generations and sampling every 1000 generations, resulting in 10,000 topologies per run. Plots of the topology likelihoods as a function of generation number revealed that stationarity was reached well before 100,000 generations, and we conservatively discarded the first 1,000,000 generations (1,000 topologies) as ''burn-in''. Convergence across runs was confirmed by similar clade probabilities and low standard deviations of split frequencies between runs. Therefore, we combined the results from both runs to form a posterior distribution of 18,000 topologies. A 50% majority consensus was constructed from this distribution of topologies, and nodes with a posterior probability of 95% or greater were considered significantly supported.

Hypothesis testing

We tested the monophyly of *Aimophila* and *Pipilo* through topology testing and analysis of the Bayesian posterior distribution. Separate topologies were constructed in MACCLADE 4.03 (Maddison and Maddison 2001), with each constraining one of these genera to be monophyletic. PAUP* was used to construct constrained neighbor-joining topologies for each genus, which were then used with MRMODELTEST to estimate the appropriate model parameters for constructing a ML constrained topology for each genus. Constrained ML topologies were then constructed in PAUP* separately for each genus. Constrained versus unconstrained likelihood scores were compared using the Shimodaira-Hasegawa (S-H; Shimodaira and Hasegawa 1999) and the approximately unbiased (Shimodaira 2002) tests in CONSEL (Shimodaira and Hasegawa 2001). Also, the posterior distribution of the Bayesian analysis (18,000 topologies) was searched for topologies in which either *Aimophila* or *Pipilo* is monophyletic.

Results

Sequence characteristics

The sequences included the complete cyt-*b* (1,143 bp) and ND2 (1,038 bp after removing the stop codon) genes for a total of 2,181 bp. Over the combined sequence, 1,039 bp (47.6%) were variable, and 878 bp (40.3%) were potentially parsimony informative. Nucleotide composition

varied slightly between genes, with an excess of cytosine and a deficiency of guanine nucleotides in both. Nucleotide variability and base composition values were similar to those reported in other studies that used closely related taxa and the same gene regions (Klicka et al. 2000, Klicka and Spellman 2007). The uncorrected rate of evolution for the ND2 gene was 1.3 times faster than cyt-*b*, with third and first codon positions, respectively, more variable than second codon positions for each gene. Chi-square tests of homogeneous base frequencies (not shown) among taxa were not significant for either the cyt-*b* or ND2 genes, any gene codon position, or for both genes combined. Gamma-shape parameter (Γ) values suggest considerable rate variation across genes and codon positions. For example, the Γ estimate at cyt-*b* second positions (0.003) was two orders of magnitude lower than for ND2 third position sites and well outside the range (0.1–0.5) of typical estimates of Γ (Yang 1996).

Phylogenetic analyses

ML and Bayesian methods produced similar phylogenetic hypotheses of relationships among samples, with the few differences among them occurring at poorly supported nodes. Because both methods produced similar topologies, only the ML best estimate of phylogeny in shown here (Fig. 2). ML bootstrap percentages and Bayesian posterior probabilities were generally in agreement in recognizing well-supported nodes (Fig. 2).

The genus *Aimophila* did not comprise a monophyletic group in any analysis. The ML topology constrained for monophyly of the genus was statistically inferior ($P < 0.001$) to the unconstrained topology using the S-H and approximately unbiased tests, and no topology in the Bayesian posterior distribution contained a monophyletic *Aimophila*. The species *notosticta*, *ruficeps*, and *rufescens* (the former two recovered as sisters) form a well-defined group that is embedded in a clade comprised of some members of *Pipilo* (see below) and three species of *Melozone*. The species *quinquestriata*, currently classified as *Aimophila* by the AOU (1998), but see Wolf 1977, AOU 1983, Sibley and Monroe 1990), appears instead to belong within the genus *Amphispiza*. The remaining *Aimophila* are included in a well-supported clade that also includes all species of *Arremonops* and some members of *Ammodramus*. The *Ammodramus* species in this clade include the Neotropical migrant taxon *savannarum* and the only two South American representatives of the genus, *humeralis* and *aurifrons*. The phylogenetic placement of the remaining members of *Ammodramus* is discussed elsewhere (Klicka and Spellman 2007). The two South American *Aimophila* species not considered in Wolf (1977), *stolzmani* and *strigiceps*, are sister species, as are the taxa *carpalis* and *sumichrasti*. The remaining *Aimophila* (*aestivalis*, *cassinii*, *botteri*, *humeralis*, *mysticalis*, and *ruficauda*) form a well-supported sub-clade. The basal internode branches in this *Aimophila-Ammodramus* (part)-*Arremonops* clade are relatively short, which makes the support of the basal relationships difficult to assess.

The genus *Pipilo* was not recovered as monophyletic in any analysis. A topology in which *Pipilo* was constrained to be monophyletic was statistically inferior ($P < 0.001$) using the S-H and approximately unbiased tests, and was absent from all trees in the Bayesian posterior distribution. The genus is split into two well-supported clades, which are not sister groups. One clade contains the rufous-sided towhee group (*erythrophthalmus*, *maculatus*, *chlorurus*, and *ocai*), and is most closely related to members of *Atlapetes*. With the exception of a well-supported grouping of *erythrophthalmus* and *maculatus*, the relationships among the lineages of the rufous-sided group are unresolved. The second clade contains the brown towhees (*aberti*, *crissalis*, *albicollis*, and *fuscus*), which are part of an assemblage that also contains the *Aimophila* species *notosticta*, *ruficeps*, and *rufescens*, along with all three species of *Melozone*. The relationships among the brown towhees were not well-supported with the exception of an *aberti-crissalis* sister relationship. *Melozone* does not constitute a clade, and appears to be compromised of three rather disparate and distantly related taxa. Among these, *kieneri* is closely allied with the brown towhees and may best be considered a member of this group.

The ML best estimate of phylogeny contained nodes that were not supported in the ML bootstrap ($\leq$ 70% bootstrap) or Bayesian ($\leq$ 95% posterior probability) analyses. Weakly supported nodes were generally associated with basal relationships among distantly related taxa or short internode branches. Nodes not supported in both the ML bootstrap and Bayesian analyses were collapsed to produce a most "reliable estimate" (Lanyon 1993) of phylogeny (Fig. 3). Although some relationships within *Aimophila* and *Pipilo* could not be described, the resulting topology illustrates the polyphyly of both genera.

Discussion

The emberizid genera *Aimophila* and *Pipilo* have had complex and confusing taxonomic histories, and relationships involving members of these groups remain unresolved to this day. Analyses of presumably neutral mtDNA sequences provide a useful perspective on relationships. Because they were designed to address higher-level taxonomic questions, many published molecular phylogenetic studies on emberizids (Klicka et al. 2000, Yuri and Mindell 2002, Carson and Spicer 2003) have included relatively few taxa, which precludes phylogenetic resolution at the species and genus levels. Here we use a more comprehensive sampling strategy of emberizids to overcome these potential problems and reconstruct an improved emberizid phylogeny (Fig. 3). Relationships suggested by our data differ considerably from those presented in the taxonomies that are in wide use today (Sibley and Monroe 1990, AOU 1998).

Our mtDNA phylogeny of emberizid relationships provides a hypothesis to compare with past and future phylogenetic examinations of the group. Future morphological analyses may discover overlooked or poorly classified characters that are in agreement with the molecular phylogeny presented here (e.g "pair reunion duet" shared by the "*ruficeps* complex" and brown towhee groups?). Future molecular studies could improve on taxonomic and genomic sampling to test our phylogenetic hypothesis. Additional intraspecific sampling may recover non-monophyly or divergent clades within species (Omland et al.

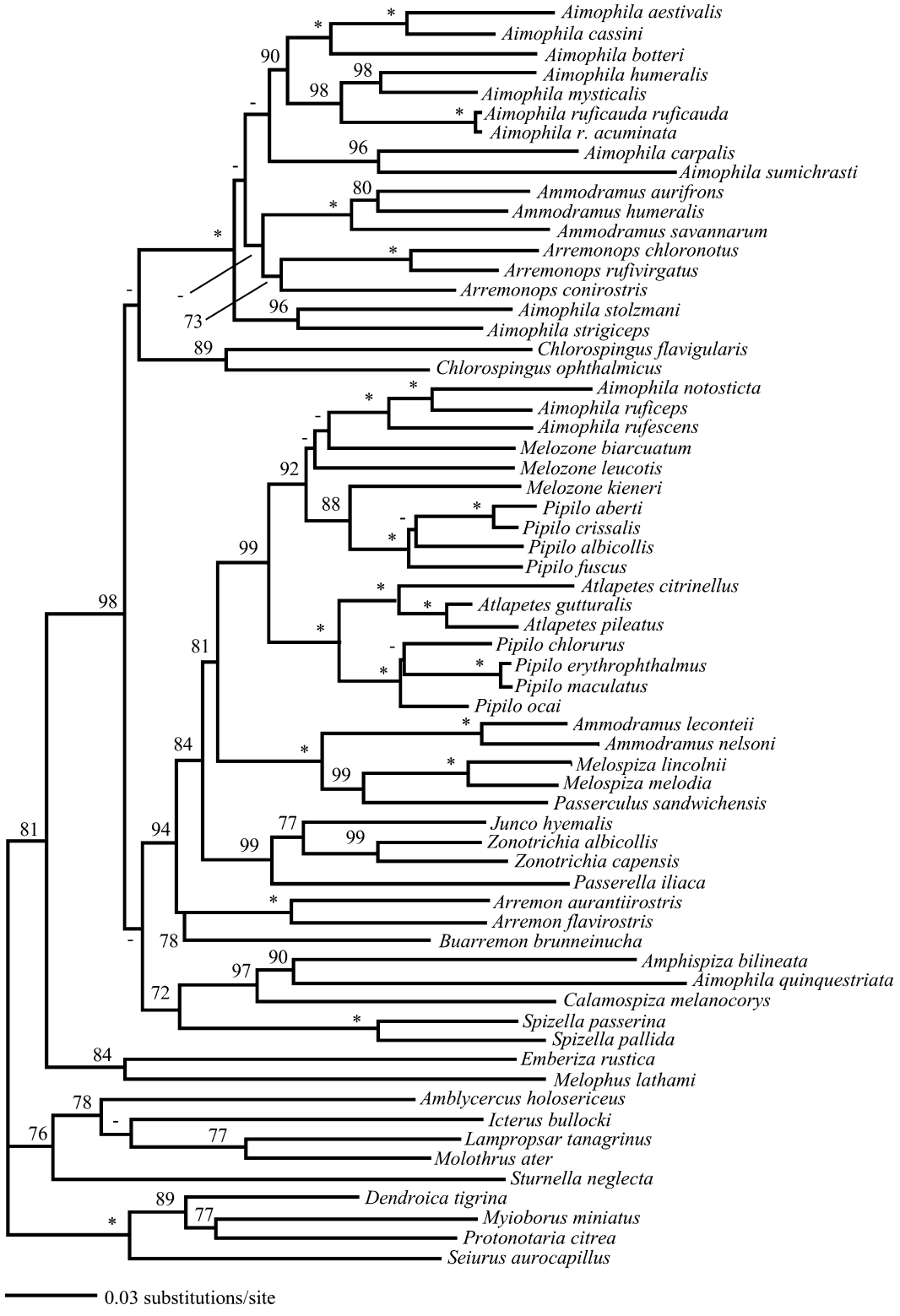

Figure 2. Maximum likelihood topology obtained using the GTR+I+Γ model of sequence evolution (-Ln length = 31,469.23, I = 0.4894, Γ = 1.0816). Nonparametric bootstrap support as determined via likelihood methods are indicated at the nodes. Asterisks are used for values of 100% support, and dashes for values of <70%. The width of vertical lines at nodes identify clades with <95% (thin) or ≥95% (thick) Bayesian posterior support.

1999), and adding other emberizid species may break up long branches and increase resolution (Lecointre et al. 1993). Nuclear DNA data could be used to test if the mtDNA is providing a skewed version of emberizid evolutionary history due to processes such as selection or sex-biased introgression (Ballard and Whitlock 2004). Nuclear DNA data could also increase phylogenetic signal and more confidently describe relationships among species;

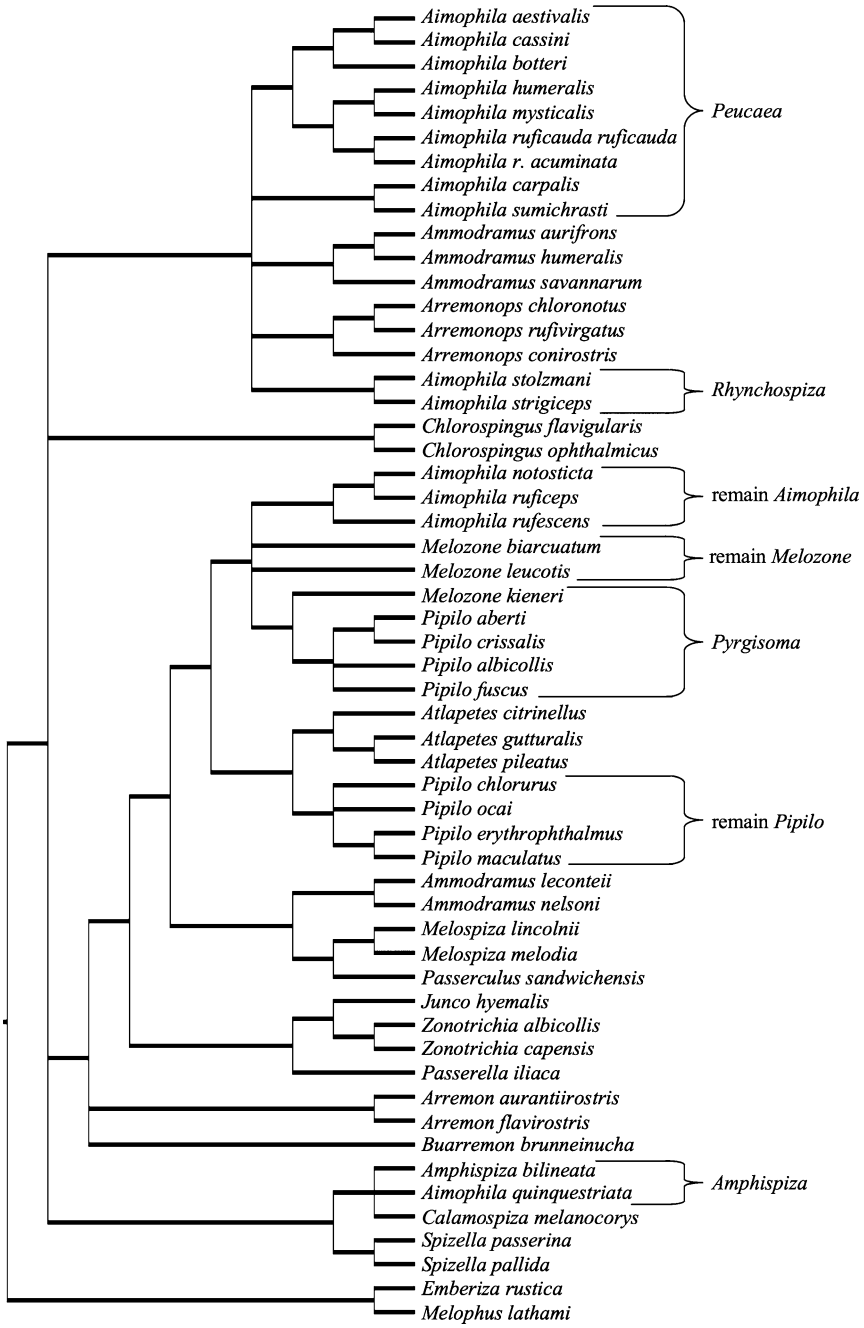

Figure 3. Consensus tree based on ML and Bayesian analyses with all poorly supported nodes collapsed. This tree represents our most "reliable estimate" (Lanyon 1993) of phylogenetic relationships among these emberizids. Brackets and generic names to the right represent taxonomic recommendations.

however, most weakly supported nodes in our phylogeny are associated with short internodes (Fig. 2), and resolution may not increase with the addition of nuclear loci with presumably longer coalescence times (Hoelzer and Melnick 1994).

Aimophila

This genus has long been considered an unnatural assemblage of species (Ridgway 1901, Dickey and van Rossem 1938, Storer 1955, Paynter and Storer 1970). The lack of definitive taxonomic characters made these previous authors reluctant to offer new classifications. Davis (1951) suggested that "the ground dwelling [emberizids] should be studied from all standpoints of their biology before generic realignment", a view later echoed by Storer (1955) and Marshall (1964). This task was attempted by Wolf (1977), culminating in his excellent monograph on species relationships in *Aimophila*. Despite his monumental efforts, Wolf also discovered a paucity of useful characters with which to clarify relationships. Ultimately, he found that the few characters that do vary consistently across taxa correlated with adaptations to particular habitat types. On this basis, Wolf recognized within *Aimophila* four "groups of species that might be thought of as evolutionary units" (Wolf

1977, pp.1), which included: 1) "*botterii* complex" defined by dull plumage, yellow patch at bend of wing, and courtship displays with a flight song. 2) "*ruficeps* complex" defined by cryptic plumage, primary songs, and distribution in pine-oak habitats. 3) "*haemophila* complex" defined by bright plumage, additional (pre-nuptial) molt, and a unique "chatter-duet" call. 4) "*Aimophila quinquestriata",*which Wolf concluded was not more closely related to *Aimophila* than to certain other emberizids.

Because specimens and relevant natural history information were not available, the South American forms of *Aimophila* (*strigiceps, stolzmani*) were not examined as part of his study. Wolf (op cit., pp. 208) concluded by claiming that the groups that he defined "are probably not as closely related to each other as some earlier authors thought". Despite his extraordinary efforts, Wolf's *Aimophila* groupings differed little from those identified earlier by Storer (1955) and are less predictive than those of Ridgway (1901, pp. 232) who identified "five more or less well-defined groups" within the genus.

The results of our molecular analyses are in general agreement with Wolf's (1977) and Storer's (1955) hypotheses concerning groupings within *Aimophila*, and reflect exactly the five groups put forth by Ridgway (1901). Our data also suggest where each group is placed within the overall emberizid assemblage, a task these earlier workers were unable to accomplish. Our topology (Fig. 2) recovers the "*botterii* complex" (*botterii*, *aestivalis, cassiniii*) as a well-supported clade that is embedded within a larger assemblage that also includes all members of the "*haemophila* complex" (*ruficauda, r. acuminata*, *sumichrasti, carpalis, mysticalis, humeralis*), the two South American taxa (*strigiceps, stolzmani*), all sampled species of *Arremonops*, and a subset of the genus *Ammodramus*. Although this large (combined) clade is well supported, relationships among its constituent lineages are poorly resolved and when unsupported nodes are collapsed a five-way polytomy results (Fig. 3). We do, however, find support for subclades within the "*haemophila complex".* Morphological clues had suggested both the *sumichrasti-carpalis* (Ridgway 1901, Wolf 1977) and the *mysticalis-humeralis-ruficauda* (Ridgway 1901) groupings recovered here. According to our analyses, the latter is sister to the "*botterii* complex". We are unaware of any earlier taxonomy that had suggested this arrangement. At the time of Wolf's work, the South American forms *strigiceps* and *stolzmani* were placed in different genera (*Aimophila* and *Rhynchospiza*, respectively), due mainly to the much larger bill size of the latter (Storer 1955). These taxa are sisters in our analyses although their precise placement within this *Aimophila-Ammodramus-Arremonops* assemblage remains obscure. Our topology (Fig. 2) also recovers Wolf's (1977) "*ruficeps* complex" (*ruficeps, rufescens, notosticta*). Members of this clade have affinities well apart from their *Aimophila* congeners, and are placed here with *Melozone* and some *Pipilo*. Although this clade is well supported, we are unable to identify with certainty the sister lineage of this complex. Similarities between *rufescens* and some *Pipilo* species in the "pair reunion duet" and display (see Marshall 1964) led Wolf (1977, pp. 200) to suggest that the "*ruficeps* complex" was "most closely related to the brown towhees of the genus *Pipilo",* a conclusion that our data are unable to reject.

We suggest the following taxonomic revisions to describe the evolutionary history of *Aimophila* captured in our phylogeny. The genus *Aimophila* was erected to include *A. rufescens* and *A.* (now *Oriturus*) *superciliosa* (Swainson 1937), and *rufescens* was later designated the type member of the genus (Gray 1840). Therefore, this name should remain with *rufescens* and the other two members of the "*ruficeps* complex", *ruficeps* and *notosticta*. New generic placements are then required for those *Aimophila* taxa in the *botterii* and *haemophila* "complexes". Although not strongly supported across all analyses, our best estimate of phylogeny (Fig. 2), indicates that these two groups form a clade. For taxonomic clarity, and until the evidence suggests otherwise, all members of this assemblage would best be considered constituents of a single genus. The available genus *Peucaea* has taxonomic priority. It was erected by Audubon (1839) to include *Fringilla bachmanii* (*Aimophila aestivalis*) and *Fringilla lincolnii* (*Melospiza lincolnii*), and later expanded to include taxa from both *Aimophila* complexes (Baird 1858, Sclater and Salvin 1868, Coues 1884). Later, the AOU (1910) redefined it to include only the three species in the "*botterii* complex". Our data are equivocal on the placement of the South American species pair, *strigiceps* and *stolzmani*. Although their taxonomic placement is uncertain (Fig. 3), this lineage appears to have diverged from all other taxa early in this clade's history. Due to this long and independent history, we suggest placing them in the resurrected genus *Rhynchospiza* (Ridgway 1898, type = *Haemophila stolzmanni* Taczanowski). Our results indicate that the form *quinquestriata*, historically shuffled between the genera *Aimophila* (e.g. Ridgway 1901, Paynter and Storer 1970, AOU 1998) and *Amphispiza* (Sharpe 1888, AOU 1983, Sibley and Monroe 1990), should properly be placed within the latter.

Pipilo

The genus *Pipilo* has historically been divided into two groups (e.g. Ridgway 1901), the brown towhees (*crissalis, aberti, fuscus, albicollis*) and rufous-sided towhees (*chlorurus, ocai, maculatus, erythrophthalmus*). Although each of these groups is distinctive, they have long been placed within the same genus under the presumption that they represent sister groups. However, Davis (1951) challenged the monophyly of this genus, and concluded from his own work that the brown towhees are more closely related to members of the genus *Melozone* than they are to their rufous-sided towhee congeners. This view was later supported by a detailed analysis of molts and plumages (Parkes 1957). After examination of vocalizations, Marshall (1964) concluded instead that it was the rufous-sided towhees that are most similar to *Melozone* and that " . . . the brown towhee group is distinct, homogeneous, and has no close relatives" (Marshall 1964, pp. 354). Past molecular assessments of the relationships for this genus (Zink 1988, Zink and Dittmann 1991, Dodge et al. 1995, Zink et al. 1998) were equivocal with respect to the question of *Pipilo* monophyly due to incomplete taxon sampling. Zink et al. (1998) suggested that resolution of this issue would require the addition all *Melozone* species along with additional outgroups. Here, we build upon Zink et al.'s earlier study with the addition of these components.

Our results recover the traditional brown (*fuscatus*, *albicollis*, *aberti*, and *crissalis*) and rufous-sided (*chlorurus*, *ocai*, *maculatus*, and *erythrophthalmus*) towhee groupings, but these groups are highly divergent and not each other's closest relatives (Fig. 3). The brown towhees are embedded within a well-supported clade that also includes some *Aimophila* taxa (discussed above) and all members of *Melozone*. The genus *Melozone* is polyphyletic and none of its three members appear closely related to one another. *Melozone kieneri* is apparently sister to the brown towhee assemblage whereas the other two *Melozone* represent early and independent diversification events within the clade. According to our topology, the rufous-sided towhee group is monophyletic and most closely related to members of the speciose tropical sparrow genus *Atlapetes*.

The study of Zink et al. (1998) was unable to resolve several relationships within *Pipilo*. Using both MP and ML analyses, they identified six topologies that they considered viable phylogenetic hypotheses. The brown towhee group was monophyletic in five out of six trees and they recovered an *aberti-crissalis* sister relationship in all of them. The relative placements of *albicollis, fuscus*, and *M. kieneri* were ambiguous across arrangements. We too obtained strong support for an *aberti-crissalis* relationship and were unable to resolve the placement of *albicollis* and *fuscus*. Zink et al. (1998) suggested that a hard polytomy is present within the brown towhee group, with *albicollis, fuscus*, and the ancestor of *aberti-crissalis* evolving ''essentially contemporaneously''. Our results are consistent with this interpretation, although it is possible that additional data could resolve the polytomy (Maddison 1989). Our tree differs from Zink et al.'s in that we find strong support for *M. kieneri* as sister to the four members of the brown towhee group whereas they did not. Five of six of Zink et al.'s topologies suggested an *ocai-maculatus* (*erythrophthalmus* was not sampled) sister pairing in the rufous-sided group. Our results suggest that *chlorurus* is instead sister to *maculatus-erythrophthalmus*, although strong support for this result was lacking. The strength of the present study is in addressing polyphyly in the genera examined, and correctly placing subsets of taxa within the overall emberizid phylogeny. In several cases however, relationships within these subsets remains equivocal and additional data are required for more complete resolution.

Polyphyly within *Pipilo* requires that it be split into two genera. The type species for this genus is *erythrophthalmus* (*Fringilla erythrophthalmus*; Linnaeus 1758). This generic epithet should then remain with the four members of the rufous-sided group, *erythrophthalmus*, *maculatus, chlorurus*, and *ocai*. The brown towhee group, then, remains in need of a new generic home. Since they are linked with all members of a polyphyletic *Melozone* and the three members of a revised *Aimophila* (above), it is tempting to lump all of these into a single genus. In this case, *Aimophila* (Swainson 1837) would have priority and the genus *Melozone* (Reichenbach 1850) would be taken out of use. However, we favor a taxonomic solution that more closely reflects the relationship of brown towhees and *M. kierneri*, and as an alternative suggest that they be merged into a single genus. The former generic epithet for *kieneri* is *Pyrgisoma* (Bonaparte 1851, *Pyrgisoma kieneri*). This name would have priority and should be resurrected. According to our analyses, the remaining *Melozone* taxa (*biarcuatum*, *leucotis*) are not closely related and may not be sisters. Nevertheless, we suggest they remain placed in *Melozone* until their taxonomic affinities have been more closely studied.

Molecular vs. morphological perspectives

Relationships depicted in our phylogeny differ considerably from those inferred using traditional taxonomic methods, suggesting once again that morphological and behavioral clues alone may not be sufficient to reconstruct relationships at this taxonomic level. In these genera, traditional characters such as size, shape, plumage patterns, vocalizations, and habitat selection do contain phylogenetic signal. For example, Ridgway (1901), Storer (1955) and Wolf (1977) used these same characters to identify *Aimophila* groupings that are well supported by the molecular data. Such characters, however, were insufficient to define relationships among these groups or to establish their taxonomic placement with confidence among other sparrow genera, perhaps due in part to a generally conserved ''bauplan'' among sparrows. Numerous molecular studies on birds (Kennedy et al. 2000, Omland and Lanyon 2000, Burns et al. 2003, Pereira and Baker 2005, Weckstein 2005, Weibel and Moore 2005, Klicka and Spellman 2007, Moyle et al. 2007) have shown that similarities among morphological characters are frequently the result of convergence, and not necessarily indicative of close relationship. The results of this study affirm that phylogeny reconstructions based on morphological and behavioral characters should be interpreted with caution.

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