Molecular Phylogenetics and Evolution 75 (2014) 41–77

Contents lists available at ScienceDirect

Molecular Phylogenetics and Evolution

journal homepage: www.elsevier.com/locate/ympev

Phylogenetics and diversification of tanagers (Passeriformes: Thraupidae), the largest radiation of Neotropical songbirds

Kevin J. Burns [a,*], Allison J. Shultz [a,b], Pascal O. Title [a,c], Nicholas A. Mason [a,d], F. Keith Barker [e], John Klicka [f], Scott M. Lanyon [e], Irby J. Lovette [d]

[a] Department of Biology, San Diego State University, 5500 Campanile Drive, San Diego, CA 92182, USA
[b] Department of Organismic and Evolutionary Biology, Harvard University, 26 Oxford Street, Cambridge, MA 02138, USA
[c] Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI 48109, USA
[d] Fuller Evolutionary Biology Program, Cornell Lab of Ornithology, Cornell University, 159 Sapsucker Woods Road, Ithaca, NY 14850, USA
[e] Department of Ecology, Evolution and Behavior, Bell Museum of Natural History, University of Minnesota, 100 Ecology Building, 1987 Upper Buford Circle, St. Paul, MN 55108, USA
[f] Barrick Museum of Natural History, University of Nevada, Las Vegas, NV 89154, USA

ARTICLE INFO

Article history:
Received 1 November 2013
Revised 5 February 2014
Accepted 12 February 2014
Available online 26 February 2014

Keywords:
Tanager
Thraupidae
Diversification
Darwin's finches
Emberizidae
Sporophila

ABSTRACT

Thraupidae is the second largest family of birds and represents about 4% of all avian species and 12% of the Neotropical avifauna. Species in this family display a wide range of plumage colors and patterns, foraging behaviors, vocalizations, ecotypes, and habitat preferences. The lack of a complete phylogeny for tanagers has hindered the study of this evolutionary diversity. Here, we present a comprehensive, species-level phylogeny for tanagers using six molecular markers. Our analyses identified 13 major clades of tanagers that we designate as subfamilies. In addition, two species are recognized as distinct branches on the tanager tree. Our topologies disagree in many places with previous estimates of relationships within tanagers, and many long-recognized genera are not monophyletic in our analyses. Our trees identify several cases of convergent evolution in plumage ornaments and bill morphology, and two cases of social mimicry. The phylogeny produced by this study provides a robust framework for studying macroevolutionary patterns and character evolution. We use our new phylogeny to study diversification processes, and find that tanagers show a background model of exponentially declining diversification rates. Thus, the evolution of tanagers began with an initial burst of diversification followed by a rate slowdown. In addition to this background model, two later, clade-specific rate shifts are supported, one increase for Darwin's finches and another increase for some species of *Sporophila*. The rate of diversification within these two groups is exceptional, even when compared to the overall rapid rate of diversification found within tanagers. This study provides the first robust assessment of diversification rates for the Darwin's finches in the context of the larger group within which they evolved.

1. Introduction

The tanagers (Passeriformes: Thraupidae) represent a major continental radiation, making up an important component of the Neotropical fauna. Species in this clade display a range of plumage colors and patterns, behaviors, morphologies, and ecotypes, and no single physical characteristic defines the group well. This trait diversity displayed among tanagers approaches that seen across the entire radiation of passerine birds, but within tanagers, this evolution has happened on reduced temporal and spatial scales. Because of the extensive character variation seen among tanager species, Thraupidae has been long recognized as a problematic clade (e.g., Sclater, 1886; Storer, 1969), with little agreement on its limits. Storer (1970) provided the classic, pre-molecular classification of tanagers that best exemplifies the traditional view; in this classification, the tanagers include 242 mostly colorful, fruit-eating birds, and this representation was followed in many subsequent treatments of tanagers (e.g., Burns, 1997; Howard and Moore, 1991; Isler and Isler, 1999). With the advent of molecular data, ideas about what constitutes Thraupidae began to shift. For example, DNA hybridization studies (Bledsoe, 1988; Sibley and Ahlquist, 1990) indicated that many finch-billed New World sparrows (Emberizidae) from the Neotropics belong to the tanager clade. Over two decades of additional genetic work (e.g., Burns, 1997; Burns et al., 2003; Lougheed et al., 2000; Weir et al., 2009; Yuri and Mindell, 2002) have made further progress towards

---

* Corresponding author.
E-mail address: kburns@mail.sdsu.edu (K.J. Burns).

http://dx.doi.org/10.1016/j.ympev.2014.02.006

defining a monophyletic Thraupidae. However, these studies have mostly explored relationships within different subgroups of tanagers or contained only sparse taxonomic sampling. Recently, Barker et al. (2013) provided the first comprehensive sampling of tanagers and their potential relatives and produced a robust phylogeny that defined a monophyletic Thraupidae. Barker et al. (2013) included six molecular markers and sampled every genus of tanager and every genus of potential tanager relative in the New World, 9-primaried oscine group, representing about 8% of avian species. These data were subjected to maximum likelihood, Bayesian, and species tree analyses, and all of these analyses consistently defined a monophyletic Thraupidae, with strong support. Combining Barker et al.'s (2013) genus-level sampling with current species-level taxonomies (Clements et al., 2013; Remsen et al., 2013) indicates that there are 371 species within Thraupidae. Thus, our newly reconstituted Thraupidae now includes roughly 4% of all avian species and is the second largest avian family, exceeded only by the New World flycatchers in family Tyrannidae (Clements et al., 2013).

This new view of tanagers indicates the group is even more diverse than previously appreciated. Species now included in Thraupidae were formerly spread across multiple avian families and represent a range of feeding morphologies, plumages, vocal abilities, and habitat preferences. For example, tanagers include such divergent taxa as the Darwin's finches (Burns et al., 2002), nectar-feeding honeycreepers (Burns et al., 2003), multicolored cloud-forest species (Sedano and Burns, 2010), and high altitude (>3000 m) specialists (Campagna et al., 2011). Plumage colors and patterns encompass the full range seen within passerines, including many species with ultraviolet coloration (Burns and Shultz, 2012). With the exception of a few species that occur on islands in the South Atlantic (Ryan et al., 2013), tanagers can now be considered an endemic, Neotropical radiation and represent roughly 12% of avian species in the region. As now defined, Thraupidae is ecologically diverse and found from northern Mexico through South America, at elevations ranging from coastlines to Andean highlands. Tanagers occur in 20 of the 22 zoogeographic regions and 27 of the 29 terrestrial habitats of the Neotropics (Parker et al., 1996), inhabiting a range of environments from dense tropical rainforest to high altitude grasslands. Nearly every foraging niche is represented in this new Thraupidae, including thick-billed granivores, thin-billed nectar feeders, aerial insect foragers, foliage gleaners, bark probers, and frugivores. Although this diversity has historically caused taxonomic confusion, it is precisely this physical, behavioral, and ecological disparity that makes tanagers an important group to study from an evolutionary perspective.

The first step towards fully understanding this diversity is to develop a robust phylogeny for the group. Although Barker et al. (2013) were able to define a monophyletic clade of tanagers, their sampling included only one representative per genus. Thus, they were unable to explore relationships within tanagers in detail. In this paper, we expand on Barker et al. (2013) and present the most comprehensive phylogenetic tree of tanagers to date, including 353 of the 371 species. Barker et al. (2013) showed that diversification rates of tanagers were 40% higher than their close relatives and an order of magnitude greater than vertebrates as a whole. Thus, we also use our tree to investigate how diversification has proceeded within this remarkable group.

2. Materials and methods

2.1. Taxon sampling

We used the genus-level phylogeny of Barker et al. (2013) and the species-level taxonomy of Clements et al. (2013) to guide our taxonomic sampling. There are 371 species in Clements et al. (2013) that belong to genera included within Barker et al.'s Thraupidae, and we included 353 (95%) of these in our study (Tables 1 and 2). The 18 species we were not able to sample are *Conothraupis mesoleuca*, *Dacnis berlepschi*, *Embernagra longicauda*, *Incaspiza laeta*, *Incaspiza watkinsi*, *Nemosia rourei*, *Paroaria nigrogenis*, *Poospiza lateralis*, *Sicalis mendozae*, *Sporophila americana*, *S. ardesiaca*, *S. bouvronides*, *S. murallae*, *S. nigrorufa*, *S. bouvreuil*, *Tangara cabanisi*, *T. peruviana*, and *Thraupis glaucocolpa*. We also included two individuals that represent subspecific taxa in Clements et al. (2013), *Sicalis luteoventris* and *Poospiza whitii*. Clements et al. (2013) treats these as subspecies of *S. luteola* and *P. nigrorufa*, respectively. These species were included because, at the time our study was initiated, they were considered full species. Cardinalidae, the cardinal-grosbeaks, is the sister taxon to tanagers (Barker et al., 2013). Thus, we included four representatives of this clade to root our trees: *Cardinalis cardinalis*, *Piranga ludoviciana*, *Pheucticus tibialis*, and *Passerina ciris* (Tables 1 and 2).

2.2. Character sampling

Data for six different molecular markers were used to infer evolutionary relationships among the Thraupidae. We included data from two mtDNA gene regions, cytochrome *b* (cyt *b*) and nicotinamide adenine dehydrogenase subunit 2 (ND2), both of which have been useful in resolving relationships among tanagers (e.g., Sedano and Burns, 2010; Mauck and Burns, 2009). In addition, we sequenced four nuclear loci. These include a protein coding gene, recombination activating gene 1 (RAG1), and three introns: the ninth intron of the sex-linked aconitase 1 (ACO1-I9), myoglobin intron 2 (MB-I2), and β-fibrinogen intron 5 (FGB-I5). These nuclear makers have been useful in resolving relationships at deeper levels within birds (e.g., Barker et al., 2004, 2013). MtDNA was obtained for all species (Table 1). For nuclear markers, we targeted at least one species per genus and included multiple species when non-monophyly of that genus was either known or suspected (Table 2). DNA isolation, amplification, and sequencing followed standard protocols (Mauck and Burns, 2009; Sedano and Burns, 2010; Barker et al., 2013). Protein-coding sequences were aligned manually, and intron sequences were aligned using default settings of Clustal X (Larkin, 2007) with slight adjustments made by hand. Tables 1 and 2 report GenBank numbers for all sequences used in this study. Most sequences are either original to this study or from recent studies by ourselves; however, some sequences came from past studies by others (Bellemain et al., 2008; Campagna et al., 2011; Hackett, 1996; Lougheed et al., 2000; Petren et al., 2005; Sato et al., 1999, 2001; Tonnis et al., 2005; Yuri and Mindell, 2002).

2.3. Phylogenetic analyses

We inferred phylogenies using both maximum likelihood (ML) and Bayesian approaches. ML methods were implemented using RAxML v7.3.1 (Stamatakis, 2006; Stamatakis et al., 2008) on the XSEDE computing cluster, accessed via the CIPRES Science Gateway v3.1 (Miller et al., 2010). Phylogenies were inferred for each individual gene using ML methods. Each analysis of an intron (ACO1-I9, FGB-I5, or MB-I2) used a single partition, while each coding region (cyt *b*, ND2, or RAG1) analysis was partitioned by codon position. RAxML applies a GTR + Γ model to each partition, so model testing was not performed for the ML reconstructions. The most likely tree was computed simultaneously with 100 bootstrap replicates for each gene using the rapid bootstrap technique (Stamatakis et al., 2008). Additional analyses were performed with the concatenated dataset containing all genes and taxa. The dataset was partitioned by gene and codon position when applicable for coding regions, resulting in 12 partitions. The most likely tree

Table 1
Species names, voucher numbers, localities, and GenBank accession numbers of mtDNA sequences for all species included in the study.

	Voucher/Sample Number[a]	Locality	Cyt *b*	ND2
Ingroup species				
Acanthidops bairdi	LSUMZ B16267	Costa Rica: San Jose, Cerro de la Muerte, Pan American Highway, km 113	AF489878	EU647924
Anisognathus igniventris	FMNH 430092	Peru: Cuzco, Paucartambo: Pillahuata	EU647961	EU648006
Anisognathus lacrymosus	IAvH 1755	Colombia: Caldas, Neira, La Cristalina, Finca La Estrella, Cuenca Alta del Rio Tapias	EU647963	EU648007
Anisognathus melanogenys	IAvH 478	Colombia: Magdalena, Santa Marta, San Lorenzo, Sierra Nevada de Santa Marta	EU647965	EU648009
Anisognathus notabilis	ICN 32717	Colombia: Narino, Barbacoas	EU647966	EU648010
Anisognathus somptuosus	LSUMZ B566	Peru: Puno, Abra de Maruncunca, 10 km SW San Juan del Oro	AY383090	EU648011
Bangsia arcaei	USNM B01412	Panama	EU647968	EU648013
Bangsia aureocincta	CVA-UV 6463	Colombia: Valle, El Cairo, Alto Galapagos	EU647969	EU648014
Bangsia edwardsi	CVA-UV 6461	Colombia: Narino, 700 msnm ruta hacia Tumaco	EU647971	–
Bangsia edwardsi 2	CVA-UV 6460	Colombia: Narino, 700 msnm ruta hacia Tumaco	–	EU648015
Bangsia melanochlamys	ICN 31136	Colombia: Antioquia, Yarumal, Alto Ventanas, Corcovado	EU647972	EU648018
Bangsia rothschildi	ANSP 2382	Ecuador: Esmeraldas, 20 km NNW of Alto Tambo	EU647973	EU648017
Buthraupis montana	FMNH 433843	Peru: Cuzco, Paucartambo, La Esperanza, 39 km (road) NE Paucartambo, 2850 m	EU647978	EU648022
Buthraupis wetmorei	LSUMZ B337	Peru: Cajamarca, Cerro Chinguela, 5 km NE Sapalache	EU647980	EU648027
Calochaetes coccineus	LSUMZ B6134	Ecuador: Morona Santiago, W slope de Cutucci Yapitya	AY383092	EU648028
Camarhynchus heliobates	Isabela12	Ecuador: Galapagos, Isabela	AY700042	–
Camarhynchus pallidus	DBF31	not provided; see Sato et al. (2001)	AF108792	–
Camarhynchus parvulus	DCB97	not provided; see Sato et al. (2001)	AF108796	–
Camarhynchus pauper	DB101	not provided; see Sato et al. (2001)	AF108794	–
Camarhynchus psittacula	DBQ111	not provided; see Sato et al. (2001)	AF108799	–
Catamblyrhynchus diadema	FMNH 433908	Peru: Cuzco, Paucartambo, La Esperanza, 39 km (road) NE Paucartambo	JN810051	–
Catamblyrhynchus diadema 2	LSUMZ B338	Peru	–	AF447271
Catamenia analis	MACN Or-ct-5118	Argentina: 8 km W Villa Ventana, Buenos Aires	JN417908	–
Catamenia analis 2	ZMUC 116225	Peru: Apurimac, 7 km S Cotaruse	–	JN810431
Catamenia homochroa	LSUMZ B426	Peru: Dept. Piura; Cruz Blanca; 33 rd km SW Huancabamba	JN810052	JN810432
Catamenia inornata	MBM 6465	Argentina: Tucuman	EF529989	EF529875
Certhidea fusca	GenovesaM64	Ecuador: Genovesa, Galapagos	AY672065	–
Certhidea olivacea	Fernandina100	Ecuador: Fernandina, Galápagos	AY672047	–
Charitospiza eucosma	LSUMZ B15356	Bolivia: Santa Cruz, Serrania de Huanchaca, 45 km E Florida	JN810053	JN810433
Chlorochrysa calliparaea	LSUMZ B8103	Peru: Pasco, Playa Pampo, 8 k NW Cushi on trail to Chaglla	AY383095	EU648029
Chlorochrysa nitidissima	IAvH 2105	Colombia: Antioquia, Municipio de Amalfi, Vereda Salasar, Finca Bodega Vieja	EU647981	EU648030
Chlorochrysa phoenicotis	LSUMZ B34873	Ecuador: Pichincha, 30 km Santo Domingo de los Colorados	AY383094	EU648031
Chlorophanes spiza	LSUMZ B2838	Peru: Loreto, 1 km N Rio Napo, 157 km by river NNE Iquitos	AF006215	JN810434
Chlorornis riefferii	LSUMZ B1859	Peru: Pasco, Chumbre de Ollon, about 12 km E Oxapampa	AY383093	EU648032
Chrysothlypis chrysomelas	LSUMZ B2189	Panama: Darien, about 6 km NW Cana	AF006220	JN810435
Chrysothlypis salmoni	LSUMZ B11822	Ecuador: Esmeraldas, El Placer	JN810054	JN810436
Cissopis leverianus	LSUMZ B1143	Bolivia: La Paz, Rio Beni, ca. 20 km by river N Puerto Linares	AY383096	EU648033
Cnemoscopus rubrirostris	LSUMZ B5624	Peru: Amazonas, 30 km by road E Florida on road to Rioja	AF006222	JN810437
Cnemathraupis aureodorsalis	LSUMZ B3564	Peru: Huanuco, base of bosque Zapatagocha above NE Acomayo	EU647974	EU648019
Cnemathraupis eximia	LSUMZ B327	Peru: Cajamarca, Cerro Chinguela, 5 km NE Sapalache	EU647975	EU648020
Coereba flaveola	STRI ABCFA2	Bahamas: Abaco Island	AF382993	AF383109
Compsospiza baeri	MBM 6457	Argentina: Tucuman	EF529986	EF529872
Compsospiza garleppi	LSUMZ B106745	Bolivia: Cochabamba Department	JN810055	JN810438
Compsothraupis loricata	LACM 45470	Brazil: Goias, Ilha do Bananal	JN810056	–
Conirostrum albifrons	LSUMZ B1965	Peru	AF447365	AF447273
Conirostrum bicolor	STRI TRCBC1	Trinidad and Tobago: St. George County	AF383025	AF383141
Conirostrum cinereum	LSUMZ B8300	Peru: Pasco, Millpo, E Tambo de Vacas on Pozuzo-Chaglla trail	JN810057	JN810439
Conirostrum ferrugineiventre	FMNH 391984	Peru: Cuzco, Urubamba, Pumahuanca	JN810058	JN810440
Conirostrum leucogenys	LSUMZ B2271	Panama: Darien, about 6 km NW Cana	JN810059	JN810441
Conirostrum margaritae	LSUMZ B7293	Peru: Loreto, Amazonas I. Pasto 80 km NE Iquitos 80 m	EU647892	EU647925
Conirostrum rufum	FMNH 258531	Colombia: Cundinamarca, Paramo de Guasca	JN810060	–
Conirostrum sitticolor	ANSP 185901	Ecuador: Carchi Province	AF383000	AF383116

(*continued on next page*)

Table 1 (*continued*)

	Voucher/Sample Number[a]	Locality	Cyt *b*	ND2
Conirostrum speciosum	FMNH 334602	Bolivia: Santa Cruz, Chiquitos, San Jose-San Ignacio Rd, km 69	AY190168	JN810442
Conirostrum tamarugense	LSUMZ B103857	Peru: Arequipa, ca. 20 road km E Chiguata	JN810061	JN810443
Conothraupis speculigera	LSUMZ B5127	Peru: Lambayeque, Las Pampas, km 885 Pan-American Hwy, 11 road km from Olmos	AF006223	JN810444
Coryphaspiza melanotis	LSUMZ B6826	Bolivia: Beni, 3 k SW San Borja	JN810062	JN810445
Coryphospingus cucullatus	FMNH 334587	Bolivia: Santa Cruz, Chiquitos, Purubi, 30 km S San Jose de Chiquitos	FJ799869	–
Coryphospingus cucullatus 2	UMMZ 235435	Captive bird	–	AF447274
Coryphospingus pileatus	FMNH 392719	Brazil: Sergripe, Caninde do Sao Francisco, Curituba, Fazenda Brejo	FJ799870	JN810446
Creurgops dentatus	LSUMZ B580	Peru: Puno, Abra de Maruncunca, 10 km SW San Juan del Oro	FJ799871	JN810447
Creurgops verticalis	LSUMZ B7974	Peru: Pasco, Playa Pampa, 8 km NW Cushi on trail to Chaglla	FJ799872	JN810448
Cyanerpes caeruleus	LSUMZ B14737	Bolivia: Santa Cruz, Serriana de Huanchaca, 25 km SE Catarata Arco Iris	AF006225	JN810449
Cyanerpes cyaneus	FMNH 427305	Brazil: Alagoas	FJ799873	JN810450
Cyanerpes lucidus	USNM B01322	Panama	JN810063	JN810451
Cyanerpes nitidus	FMNH 390048	Brazil: Rondonia, Cachoeeira Nazare, W bank Rio Jiparana	AY190167	JN810452
Cyanicterus cyanicterus	USNM B10923	Guyana	JN810064	JN810453
Cypsnagra hirundinacea	LSUMZ B15290	Bolivia: Santa Cruz, Velasco, Pre Parque Nacional Noel Kempff Mercado, 30 km E Aserradero Moira	AF006226	JN810454
Dacnis albiventris	LSUMZ B28123	Peru: Loreto Department	JN810065	JN810455
Dacnis cayana	LSUMZ B15077	Bolivia: Santa Cruz, Velasco, 13 km SW Piso Firme	AF006227	JN810456
Dacnis flaviventer	FMNH 323898	Peru: Madre de Dios, Hacienda Amazonia	JN810066	JN810457
Dacnis hartlaubi	AMNH 181785	Colombia	JN810067	–
Dacnis lineata	FMNH 391223	Bolivia: El Beni, Hacienda Los Angeles, 10 km E Riberalta	JN810068	JN810458
Dacnis nigripes	FMNH 395733	Brazil: Sao Paulo, Salesopolis, Boraceia Biological Station	JN810069	–
Dacnis venusta	LSUMZ B26588	Panama: Colon, 17 km by road NW Gamboa, Rio Agua Salud	FJ799874	JN810459
Dacnis viguieri	UMMZ 152521	Colombia: Choco, Rio Jurado	JN810070	–
Diglossa albilatera	AMNH DOT 5023	Venezuela: Aragua, km 40 on El Junquito/Col. Tovar Road	EU647893	EU647926
Diglossa baritula	FMNH 393877	Mexico: Jalisco, Las Joyas, Sierra de Manantlan	EU647894	EU647927
Diglossa brunneiventris	AMNH DOT 2892	Bolivia: La Paz Department, Prov. Franz Tamayo, Parque Nacional Apolobamba	EU647896	EU647928
Diglossa caerulescens	AMNH DOT 5022	Venezuela: Aragua, km 40 on El Junquito/Col. Tovar road	EU647908	EU647941
Diglossa carbonaria	LSUMZ B106752	Bolivia: Cochabamba Department	EU647897	EU647930
Diglossa cyanea	FMNH 430124	Peru: Cuzco, Paucartambo, Pillahuata	EU647909	EU647942
Diglossa duidae	AMNH DOT 9754	Venezuela: Amazonas, Cerro Yutaje	EU647898	EU647931
Diglossa glauca	FMNH 430121	Peru: Cuzco, Paucartambo: San Pedro, 1480 m	EU647910	EU647943
Diglossa gloriosa	AMNH 824762	Venezuela: Merida, Laguna Negra	JN810071	–
Diglossa gloriosissima	IAvH BT7531	Colombia: Antioquia, Ciudad Bolivar, Farallones, del Citara	EU647900	EU647932
Diglossa humeralis	USNM B3015	Ecuador	EU647901	EU647933
Diglossa indigotica	IAvH BT7532	Colombia: Antioquia, Yarumal, Alto de Ventanas, Vereda El Rosario-Corcovado, Finca Villa Nueva	EU647911	EU647944
Diglossa lafresnayii	LSUMZ B351	Peru: Cajamarca, Cerro Chinguela, 5 km NE Sapalache	AF006229	EU647934
Diglossa major	FMNH 339722	Venezuela: Bolivar, Santa Elena Hwy, km 122	AF290155	AF290118
Diglossa mystacalis	FMNH 433931	Peru: Cuzco, Paucartambo, La Esperanza, 39 km (road) NE Paucartambo	EU647903	EU647936
Diglossa plumbea	AMNH DOT 3646	Costa Rica: San Jose, Cerro de la Muerte	EU647904	EU647937
Diglossa sittoides	LSUMZ B22814	Bolivia: La Paz, B. Saavedra, 83 km by road E Charazani, Cerro Asunta Pata	EU647905	EU647938
Diglossa venezuelensis	COP 81247	Venezuela: Anzoategui, Serranía del Turimiquire, Cerro La Launa (El Guamal)	EU647907	EU647940
Diuca diuca	MBM 6477	Argentina: Tucuman	EF529984	EF529870
Diuca speculifera	LSUMZ B22574	Bolivia: La Paz, Zongo Valley, 7 km by road N of summit	JN810072	JN810460
Dolospingus fringilloides	USNM B11981	Guyana	JN810073	JN810461
Donacospiza albifrons	KU 3316	Paraguay: Misiones, 5 km NW Yabebyry, Estancia Santa Ana	JN810074	JN810462
Dubusia castaneoventris	LSUMZ B3607	Peru: Huanuco, Quebrada Shugush, 30 km on Huanuco-La Union Rd	AY383097	EU648034
Dubusia taeniata	LSUMZ B7710	Peru: Huanuco, Unchog Pass NNW Acomayo 3450 m	AY383098	EU648035
Emberizoides duidae	USNM 605984	Venezuela: Amazonas, Mount Duida, elevation	JN810075	–
Emberizoides herbicola	MBM 3721	Argentina: Corrientes	EF529974	EF529860
Emberizoides ypiranganus	UWBM 70773	Argentina: Provincia de Corrientes, Corrientes, 55 km S, 5 km E, along Route 103	JN810076	JN810463
Embernagra platensis	FMNH 396034	Bolivia	EU647912	EU647945
Eucometis penicillata	LSUMZ B6551	Bolivia: Santa Cruz, Rio Quizer	FJ799875	JN810464
Euneornis campestris	FMNH 331119	Jamaica: Portland, Hollywell Park	AF489885	EU648036

Table 1 (*continued*)

	Voucher/Sample Number[a]	Locality	Cyt *b*	ND2
Geospiza conirostris	DBF81	not provided; see Sato et al. (2001)	AF108769	–
Geospiza difficilis	D12	not provided; see Sato et al. (2001)	AF108787	–
Geospiza fortis	DCB56	not provided; see Sato et al. (2001)	AF108772	–
Geospiza fortis 2	UMMZ 224890	Ecuador: Galápagos Islands	–	AF447282
Geospiza fuliginosa	DBQ61	not provided; see Sato et al. (2001)	AF108786	–
Geospiza magnirostris	DBQ11	not provided; see Sato et al. (2001)	AF108777	–
Geospiza scandens	DB26	not provided; see Sato et al. (2001)	AF108779	–
Gubernatrix cristata	LSUMZ B51254	Argentina: Corrientes	JN810077	–
Gubernatrix cristata 2	MACN 68379	Argentina: Prov. Buenos Aires; Salinera Universal, Salina de Piedra, Cardenal Cagliero, Partido de Patagones	–	JN810465
Haplospiza rustica	FMNH 433797	Peru: Cuzco, Paucartambo, La Esperanza, 39 km (road) NE Paucartambo, 2900 m	EU647913	EU647946
Haplospiza unicolor	FMNH 5186	Brazil: Sao Paulo	AF290156	AF290119
Hemispingus atropileus	LSUMZ B1889	Peru: Pasco, Chumbre de Ollon, about 12 km E Oxapampa	AF006234	AF383135
Hemispingus calophrys	LSUMZ B547	Peru: Puno, Valcon, 5 km NNW Quiaca	JN810078	JN810466
Hemispingus frontalis	LSUMZ B1766	Peru: Pasco Department	AF383020	AF383136
Hemispingus goeringi	USNM 263922	Venezuela: Culata	JN810079	–
Hemispingus melanotis	FMNH 430079	Peru: Cuzco, Paucartambo: San Pedro	EU647914	EU647947
Hemispingus parodii	FMNH 316432	Peru: Cuzco, Abra Malaga, below, on road to Quillabamba	JN810080	–
Hemispingus reyi	ANSP 162616	Venezuela: Paramo Zumbador	JN810081	–
Hemispingus rufosuperciliaris	LSUMZ B3566	Peru: Huanuco, base of bosque Zapatagocha above NE Acomayo	JN810082	JN810467
Hemispingus superciliaris	FMNH 433858	Peru: Cuzco, Paucartambo, La Esperanza, 39 km (road) NE Paucartambo	JN810083	JN810468
Hemispingus trifasciatus	FMNH 398459	Peru: Cuzco, Paucartambo, Puesto de Vigilancia Acjanaco	JN810084	–
Hemispingus verticalis	LSUMZ B320	Peru: Cajamarca, Cerro Chingueal, 5 km NE Sapalache	JN810085	JN810469
Hemispingus xanthophthalmus	LSUMZ B8223	Peru: Pasco, Millpo, E Tambo de Vacas on Pozuzo-Chaglla trail	JN810086	JN810470
Hemithraupis flavicollis	LSUMZ B5102	Peru: Loreto, S Rio Amazonas, ca. 10 km SSW mouth Rio Napo on E bank Quebrada Vainilla	AF006235	EU647948
Hemithraupis guira	FMNH 427239	Brazil: Alagoas, Ibateouara, Envenho Ceimba, Usina Serra Grande	JN810087	JN810471
Hemithraupis ruficapilla	FMNH 395477	Brazil: Sao Paulo, Boracia	JN810088	–
Heterospingus rubrifrons	LSUMZ B28691	Panama: Colon, Achitoe road at Rio Providencia	JN810089	JN810472
Heterospingus xanthopygius	LSUMZ B2324	Panama: Darien, Cana on E slope Cerro Pirre	EU647915	EU647949
Idiopsar brachyurus	LSUMZ B22571	Bolivia: La Paz, Zongo Valley, 7 km by road N of summit	EU647916	EU647950
Incaspiza ortizi	LSUMZ B10382	Peru: Cajamarca, above Limon Pampa between Calenda and Balsan	JN810090	JN810473
Incaspiza personata	FMNH 299930	Peru: Ancash, Huaylas, Quebrada Rurinura	JN810091	–
Incaspiza pulchra	LSUMZ B10387	Peru: Ancash, just out of Huaylash toward Sucre	JN810092	JN810474
Iridophanes pulcherrimus	MVZ 169712	Peru: Dept. Cajamarca, 1 mi N San Jose de Lourdes, Cordillera del Condor	AY190169	JN810475
Iridosornis analis	LSUMZ B1706	Peru: Pasco, Santa Cruz, about 9 km SSE Oxapampa	AY383099	EU648037
Iridosornis jelskii	FMNH 430099	Peru: Cuzco, Paucartambo: Pillahuata	JN810093	EU648038
Iridosornis porphyrocephalus	CVA-UV 6454	Colombia: Alto Ventanas, Yarumal, Antioquia	EU647983	EU648039
Iridosornis reinhardti	LSUMZ B3538	Peru: Huanuco, Unchog, pass between Churrrubamba and Hola Paty, NNW Acomayo	EU647985	EU648041
Iridosornis rufivertex	LSUMZ B371	Peru: Dept. Cajamarca; Cerro Chinguela, 5 km NE Sapalache	JN810094	JN810476
Lanio aurantius	MBM 8738	Honduras: Depto. Atlantida, La Ceiba, 9.7 km SW Rio Quebrada	FJ799877	JN810477
Lanio fulvus	LSUMZ B2694	Peru: Loreto, 1 km N Rio Napo, 157 km by river NNE Iquitos	EU647917	EU647951
Lanio leucothorax	STRI JTW572	Panama: Cocle, El Cope National Park	FJ799879	JN810478
Lanio versicolor	LSUMZ B1014	Bolivia: La Paz, Rio Beni, ca. 20 km by river N Puerto Linares	FJ799878	JN810479
Lophospingus griseocristatus	FMNH 334558	Bolivia: Cochabamba, Cochabamba-Oruro Rd, km 29	EU647987	EU648043
Lophospingus pusillus	MBM 6491	Argentina: Tucuman	EF529992	EF529878
Loxigilla barbadensis	STRI BA-LNO17	Barbados: Apes Hill	HQ153056	HQ153075
Loxigilla noctis	STRI DO-LNO3	Dominica: Springfield	HQ153057	HQ153076
Loxigilla portoricensis	LSUMZ B11351	Puerto Rico: Cabo Rojo, Boqueron, Penones de Melones, 1 km WNW intersection routes 301 and 303	AF489886	EU648044
Loxigilla violacea	AMNH 25433	Dominican Republic: Independencia	AF489887	HQ153077
Loxipasser anoxanthus	FMNH 331107	Jamaica: Surrey, Portland, Hollywell Park	AF489888	EU648045
Melanodera melanodera	FMNH 120780	Argentina: Tierra del Fuego, San Sebastian	JN810095	–
Melanodera xanthogramma	AMNH DOT 12115	Argentina: Departamento Bariloche, Rio Negro	EU647918	EU647952

(*continued on next page*)

Table 1 (*continued*)

	Voucher/Sample Number[a]	Locality	Cyt *b*	ND2
Melanospiza richardsoni	Meri-CMB95	Saint Lucia	AF310043	–
Melanospiza richardsoni 2	SL-MRI2	Saint Lucia	–	EF567909
Melopyrrha nigra	Not provided, see Lougheed et al. (2000)	Cuba: Cayo Coco	AY005219	–
Melopyrrha nigra 2	FMNH 342954	captive bird	–	EU648046
Nemosia pileata	LSUMZ B7295	Peru: Loreto, Amazonas I. Pasto 80 km NE Iquitos 80 m	AF006241	JN810480
Neothraupis fasciata	LSUMZ B13914	Bolivia: Santa Cruz, Serrania de Huanchaca, 45 km E Florida	AY383100	EU648047
Nephelornis oneilli	LSUMZ B8402	Peru: Pasco, Millpo, E Tambo de vacas on Pozuzo-Chaglla trail	AF006243	JN810481
Nesospiza acunhae	ITU35	Inaccessible Island, Tristan da Cunha	JN810096	JN810482
Nesospiza wilkinsi	NW5	Nightingale Island, Tristan da Cunha	DQ886520	–
Nesospiza wilkinsi 2	NW17	Nightingale Island, Tristan da Cunha	–	JN810483
Orchesticus abeillei	FMNH 267940	Brazil: Sao Paulo, Boa Vista, Rio Ipiranga	JN810097	–
Oreomanes fraseri	LSUMZ B2069	Peru: Lima, ca. 13 road km W Milloc	AF006244	EU647953
Oryzoborus angolensis	Oran-CMB241	Ecuador: Santo Domingo	AF310055	–
Oryzoborus angolensis 2	FMNH 433798	Peru: Madre de Dios, Moskitania, 13.4 km NNW Atalaya, I bank Alto Madre de Dios	–	JN810484
Oryzoborus atrirostris	ZMUC 123039	Ecuador: Pastaza, N Canelos	JN810098	JN810485
Oryzoborus crassirostris	FMNH 339668	Venezuela: Sucre, Guraunos, 14 km SSE	AF489890	JN810486
Oryzoborus funereus	MBM 8980	Honduras: Atlantida	EF529963	EF529851
Oryzoborus maximiliani	LSUMZ B11908	Ecuador: Esmeraldas, El Placer	EU647919	EU647954
Oryzoborus nuttingi	AMNH 787330	Costa Rica: Guanacaste, Laguna Arenal, Tronadora	JN810099	–
Parkerthraustes humeralis	LSUMZ B9328	Boliva: Pando	EF530024	EF529917
Paroaria baeri	FMNH 356584	Brazil: Mato Grosso; Sao Domingos, Rio das Mortes	JN810100	–
Paroaria capitata	UWBM jag1837	Argentina: Corrientes	EF529977	EF529863
Paroaria coronata	FMNH 394390	Bolivia	EU647990	EU648049
Paroaria dominicana	FMNH 392736	Brazil: Sergripe, Caninde do Sao Francisco, Curituba, Fazenda Porto Belo	EF529994	EF529880
Paroaria gularis	FMNH 323625	Peru: Madre de Dios, Hacienda Amazonia	EU647989	EU648050
Phrygilus alaudinus	MBM 6470	Argentina: Tucuman	EF529981	EF529867
Phrygilus atriceps	MBM 5307	Argentina: Jujuy	EF529982	EF529868
Phrygilus carbonarius	AMNH DOT 10373	Argentina: Neuquen, Departamento Anelo, Sierra Auca Mahuida	JN810101	JN810487
Phrygilus dorsalis	MBM 6476	Argentina: Tucuman	EF529983	EF529869
Phrygilus erythronotus	LSUMZ B103892	Peru: Tacna, Tacna-Llave Rd, ca. 57 km NE Tarata	JN810102	JN810488
Phrygilus fruticeti	MBM 5412	Argentina: Jujuy, Tilcara, 18 km S	JN810103	JN810489
Phrygilus gayi	MBM 6475	Argentina: Tucuman, Amaicha del Valle 12 km S, 12 km E	JN810104	JN810490
Phrygilus patagonicus	MACN 42511	Argentina: El Bolson, Rio Negro	JN810105	JN810491
Phrygilus plebejus	MBM 5310	Argentina: Jujuy	EF529979	EF529865
Phrygilus punensis	LSUMZ B61455	Peru: Apurimac, SE Abancay, Lloccahuani	JN417901	–
Phrygilus unicolor	MBM 6471	Argentina: Tucuman	EF529980	EF529866
Piezorina cinerea	LSUMZ B5169	Peru: Lambayeque, Las Pampas, km 885 Pan-American Hwy, 11 road km from Olmos	JN810106	JN810492
Pinaroloxias inornata	DBT131	Not provided; see Sato et al. (2001)	AF108790	–
Pipraeidea bonariensis	FMNH 433891	Peru: Cuzco, Paucartambo, La Esperanza, 39 km (road) NE Paucartambo	EU647997	EU648100
Pipraeidea melanonota	LSUMZ B12070	Ecuador: Pichincha, Mindo	AY383101	EU648051
Platyspiza crassirostris	DBT72	Not provided; see Sato et al. (2001)	AF108802	–
Poospiza alticola	ZMUC 0665	Peru: Ancash	AY005198	–
Poospiza alticola 2	ZMUC 116453	Peru: Ancash, C. Blanc, Andavite, Rurichinc.	–	JN810493
Poospiza boliviana	LSUMZ B1198	Bolivia: La Paz Department	AY005201	JN810494
Poospiza cabanisi	CUMV 50679	Uruguay: Artigas, Arroyo Mandiyu	EU647920	EU647955
Poospiza caesar	ZMUC 0667	Peru: Andamarca, Ayacucho	AY005202	–
Poospiza cinerea	USNM B05912	Argentina	FJ799880	JN810495
Poospiza erythrophrys	MBM 5491	Argentina: Salta	EF529987	EF529873
Poospiza hispaniolensis	LSUMZ B5205	Peru	AY005205	–
Poospiza hispaniolensis 2	LSUMZ B24977	captive, Louisiana, Baton Rouge, C. Gordon Barney Aviary, captive	–	JN810496
Poospiza hypochondria	MBM 5302	Argentina: Salta	EF529985	EF529871

Table 1 (*continued*)

	Voucher/Sample Number[a]	Locality	Cyt *b*	ND2
Poospiza melanoleuca	Not provided, see Lougheed et al. (2000)	Argentina: Quimili, Santiago del Estero	AY005208	–
Poospiza melanoleuca 2	MBM 5316	Argentina: Salta, J.V. Gonzalez, 14 km NE	–	JN810497
Poospiza nigrorufa	AMNH DOT 9907	Argentina: Buenos Aires, Partido Magdallena	JN810107	JN810498
Poospiza ornata	Not provided, see Lougheed et al. (2000)	Argentina: Amanao, Catamarca	AY005213	–
Poospiza ornata 2	AMNH DOT 9515	locality unknown	–	JN810499
Poospiza rubecula	FMNH 299931	Peru: Ancash, Quitacocha, Huaylas	JN810108	–
Poospiza thoracica	LACM 29015	Brazil: Rio de Janeiro, Itatiaia	JN810109	–
Poospiza torquata	KU 2838	Paraguay: Presidente Hayes, Campo Largo, 5 km S	JN810110	–
Poospiza torquata 2	MBM 6455	Argentina: Tucuman	–	EF529877
Poospiza whitii	LSUMZ B6573	Bolivia: Santa Cruz, 2.5 km N Tambo	JN810111	JN810500
Porphyrospiza caerulescens	LSUMZ B13860	Bolivia: Santa Cruz	EF529978	EF529864
Pyrrhocoma ruficeps	MVZ 165617	Paraguay: Dept. Itapu, El Tirol, 19.5 km by road NNE Encarnacion	AF006249	–
Pyrrhocoma ruficeps 2	KU 91447	Paraguay: Itapua, San Rafael National Park; Parabel	–	JN810501
Ramphocelus bresilius	Not provided, see Hackett (1996)	captive birds	U15724	–
Ramphocelus carbo	LSUMZ B4988	Peru: Loreto; S Río Amazonas, ~10 km SSW Río Napo on E bank Quebrada Vainilla	U15723	–
Ramphocelus carbo 2	FMNH 430084	Peru: Cuzco, Paucartambo: San Pedro	–	JN810502
Ramphocelus costaricensis	LSUMZ B16144	Costa Rica: Prov. Puntarenas; 2 km SE Dominical	U15720	U15711
Ramphocelus dimidiatus	LSUMZ B16559	Panama: Panama Province, Old Gamboa Road-golf course, 4 km NW of Paraiso	FJ799881	JN810503
Ramphocelus flammigerus	USNM B01238	Panama: Punta Alegre, Peninsula Veliente	FJ799882	–
Ramphocelus flammigerus 2	USNM 607943	Panama: Bocas Del Toro	–	JN810504
Ramphocelus melanogaster	LSUMZ B44693	Peru: Dept. San Martin; ~33 km NE Florida	FJ799883	JN810505
Ramphocelus nigrogularis	LSUMZ B2850	Peru: Dpto. Loreto; 1 km N Río Napo, 157 km by river NNE Iquitos	U15721	–
Ramphocelus nigrogularis 2	FMNH 323781	Peru: Madre de Dios, Hacienda Amazonia	–	JN810506
Ramphocelus passerinii	MBM 8627	Honduras: Atlantida	EF529965	EF529853
Ramphocelus sanguinolentus	FMNH 343376	Mexico: Veracruz, El Bastonal, 3 km S, 3 km E, Sierra de Santa Martha	U15718	JN810507
Rhodospingus cruentus	LSUMZ B5184	Peru: Lambayeque, Las Pampas, km 885 Pan-American Hwy, 11 road km from Olmos	FJ799884	JN810508
Rowettia goughensis	GB18	Gough Island	JN810112	JN810509
Saltator albicollis	STRI ccSAL1	Trinidad and Tobago: Chacachacare Island	AF383107	AF281023
Saltator atriceps	FMNH 343357	Mexico: Veracruz	EF530019	EF529912
Saltator atricollis	LSUMZ B15381	Bolivia: Santa Cruz	EF530021	EF529914
Saltator atripennis	ANSP 3491	Ecuador: Azuay	JN810113	JN810510
Saltator aurantiirostris	UWBM 54506	Argentina: Tucuman	EF530017	EF529910
Saltator cinctus	LSUMZ B6233	Ecuador: Prov. Morona-Santiago	JN810114	JN810511
Saltator coerulescens	UWBM gav817	Argentina: Corrientes	EF530013	EF529906
Saltator fuliginosus	MACN P1674	Brazil: Sao Paulo Fazenda Barreiro Rico	JN810115	JN810512
Saltator grossus	LSUMZ B16063	Costa Rica: Herredia	EF530018	EF529911
Saltator maxillosus	FMNH 311035	Brazil: Rio de Janeiro; Parque Nacional do Itatiaia	JN810116	–
Saltator maximus	FMNH 433810	Peru: Cuzco, Paucartambo, Consuelo, 15.9 km SW Pilcopata	JN810117	–
Saltator maximus 2	ZMUC 123036	Ecuador	–	JN810513
Saltator nigriceps	LSUMZ B183	Peru: Piura	EF530016	EF529909
Saltator orenocensis	COP FL2-04//2259	Venezuela: Falcon, Carretara Coro-Curimagua	JN810118	JN810514
Saltator rufiventris	LSUMZ B106750	Bolivia: Cochabamba	EF530025	EF529918
Saltator similis	UWBM 70491	Argentina: Provincia de Corrientes, Corrientes, Manuel Derqui	JN810119	JN810515
Saltator striatipectus	LSUMZ B449	Peru: Lambayeque	JN810120	JN810516
Saltatricula multicolor	MVZ 179401	captive bird	AF489892	–
Saltatricula multicolor 2	MBM 5447	Argentina: Salta	–	EF529913
Schistochlamys melanopis	LSUMZ B9669	Bolivia: Pando, Nicholas Suarez, 12 km by road S of Cojiba, 8 km W on road to Mucden	AY383102	EU648052
Schistochlamys ruficapillus	FMNH 344774	Brazil: Goias, Goiania	EU647991	–
Sericossypha albocristata	LSUMZ B5630	Peru: Amazonas, 30 km by road E Florida on road to Rioja	AF006251	JN810517
Sicalis auriventris	MACN 35187	Argentina: Los Molles, Mendoza	JN810121	–
Sicalis citrina	LSUMZ B15400	Bolivia: Santa Cruz, Serrania De Huanchaca, 45 km E Florida	JN810122	JN810518

(*continued on next page*)

Table 1 (*continued*)

	Voucher/Sample Number[a]	Locality	Cyt *b*	ND2
Sicalis columbiana	FMNH 391601	Brazil: Amapa, Tartatugalzinho, Fazenda Sao Bento	JN810123	JN810519
Sicalis flaveola	UWBM 70184	Argentina: Provincia de Corrientes, Corrientes, Manuel Derqui	JN810124	JN810520
Sicalis lebruni	MACN 52328	Argentina: Chubut, Punta Tombo	JN810125	–
Sicalis lutea	FMNH 391932	Peru: Ayacucho, Ocana	EU647921	EU647956
Sicalis luteiventris	MACN 68470	Argentina: Prov. Buenos Aires; Lago Parque La Salada, Pedro Luro	JN810126	JN810521
Sicalis luteocephala	ZMUC 116483	Bolivia: Cochabamba, Cerro Kehuinal	JN810127	JN810522
Sicalis luteola	FMNH 389274	Brazil: Roraima, Fazenda Santa Cecilia, E Bank Rio Branco, across from boa Vista	AF489893	EU647957
Sicalis olivascens	MBM 5435	Argentina: Jujuy	EF529988	EF529874
Sicalis raimondii	FMNH 287878	Peru: Ayacucho, Ocana	JN810128	–
Sicalis taczanowskii	LSUMZ B5244	Peru: Lambayeque, Las Pampas, km 885 Pan-American Hwy, 11 road km from Olmos	JN810129	JN810523
Sicalis uropygialis	ZMUC 116495	Peru: Junin, 3 km S of Ondores	–	JN810524
Sporophila albogularis	FMNH 392743	Brazil: Alagoas, Piranhas, Fazenda Bela Vista	JN810130	JN810525
Sporophila caerulescens	FMNH 334570	Bolivia: Santa Cruz, Chiquitos, Purubi, 30 km S San Jose de Chiquitos	JN810132	JN810527
Sporophila castaneiventris	FMNH 433815	Peru: Madre de Dios, Moskitania, 13.4 km NNW Atalaya, I bank Alto Madre de Dios, 480 m	JN810133	JN810528
Sporophila cinnamomea	MACN 52373	Argentina: Prov. Entre Rios; Arroyo Barú	JN810134	–
Sporophila collaris	FMNH 334564	Bolivia: El Beni, Laguna Suarez, 5 km SW Trinidad	JN810135	JN810529
Sporophila corvina	STRI GMS2200	Panama: Chiriqui, N of Bahia de Charco Azul, 3 km W of Divala	JN810136	JN810530
Sporophila falcirostris	MACN 39080	Argentina: Prov. Misiones; Arroyo Urugua-i, km. 40	JN810137	–
Sporophila frontalis	LACM 27909	Brazil: Rio de Janiero, Terezopolis	JN810138	–
Sporophila hypochroma	LSUMZ B15265	Bolivia: Santa Cruz, Velasco, Pre Parque Nacional Noel Kempff Mercado, 30 km E Aserradero Moira	JN810139	JN810531
Sporophila hypoxantha	FMNH 334574	Bolivia: Santa Cruz, Chiquitos, San Jose-San Ignacio Rd, km 69	JN810140	JN810532
Sporophila intermedia	FMNH 389269	Brazil: Roraima, Fazenda Santa Cecilia, E Bank Rio Branco, across from boa Vista	EU647922	EU647958
Sporophila leucoptera	FMNH 334573	Bolivia: El Beni, Laguna Suarez, 5 km SW Trinidad	JN810141	JN810533
Sporophila lineola	FMNH 390057	Brazil: Rondonia, Cachoeeira Nazare, W bank Rio jiparana	JN810142	JN810534
Sporophila luctuosa	FMNH 433818	Peru: Madre de Dios, Moskitania, 13.4 km NNW Atalaya, I bank Alto Madre de Dios, 480 m	JN810143	JN810535
Sporophila melanogaster	AMNH 315888	Brazil: Paccaria, Rio Grande do Sul	JN810144	–
Sporophila minuta	FMNH 389270	Brazil: Roraima, Fazenda Santa Cecilia, E Bank Rio Branco, across from boa Vista	JN810145	JN810536
Sporophila nigricollis	Spni-CB191	Ecuador: Santo Domingo	AF310053	–
Sporophila nigricollis 2	FMNH 427217	Brazil: Alagoas, Ibateouara, Envenho Ceimba, Usina Serra Grande	–	JN810537
Sporophila palustris	KU 3689	Paraguay: Itapua, San Rafael National Park, San Pedro Mi,	JN810146	JN810538
Sporophila peruviana	LSUMZ B5243	Peru: Lambayeque, Las Pampas, km 885 Pan-American Hwy, 11 road km from Olmos	JN810147	JN810539
Sporophila pileata	UWBM 70800	Argentina: Provincia de Missiones, Posadas, 25 km E, Estancia San Juan	JN810131	JN810526
Sporophila plumbea	FMNH 389271	Brazil: Roraima, Fazenda Santa Cecilia, E Bank Rio Branco, across from boa Vista	JN810148	JN810540
Sporophila ruficollis	FMNH 334582	Bolivia: Santa Cruz, Chiquitos, Purubi, 30 km s San Jose de Chiquitos	AF489896	–
Sporophila ruficollis 2	FMNH 334583	Bolivia: Santa Cruz, Chiquitos, Purubi, 30 km s San Jose de Chiquitos	–	JN810541
Sporophila schistacea	LSUMZ B22584	Bolivia: La Paz Dept., Prov. B. Saavedra	EF529976	EF529862
Sporophila simplex	LSUMZ B33437	Peru: Cajamarca, Las Juntas, junction of Rios Tabacomasand Chinchipe	JN810149	JN810542
Sporophila telasco	LSUMZ B32935	Peru: Cajamarca, Las Juntas, junction of Rios Tabacomasand Chinchipe	JN810150	JN810543
Sporophila torqueola	MBM 8476	Honduras: Depto. Atlantida, La Ceiba, 15 km W	JN810151	JN810544
Stephanophorus diadematus	AMNH DOT 9915	Argentina: Buenos Aires, Partido Escobar	EU647992	EU648053
Tachyphonus coronatus	AMNH DOT 2452	Argentina: Misiones Departamento San Ignacio, near border Parque Prov. Urugua-I, CA 1 KM W. Park Headquarters Ruta Prov. 19	FJ799885	JN810545
Tachyphonus cristatus	LSUMZ B9548	Bolivia: Pando, Nicholas Suarez, 12 km by road S of Cojiba, 8 km W on road to Mucden	FJ799888	JN810546
Tachyphonus delatrii	LSUMZ B11710	Ecuador: Esmeraldas, El Placer	FJ799890	JN810547
Tachyphonus luctuosus	LSUMZ B2279	Panama: Darien, Cana on E slope Cerro Pirre	FJ799891	JN810548
Tachyphonus phoenicius	AMNH DOT 4797	Venezuela: Bolivar, Cerro Guanay	FJ799893	JN810549
Tachyphonus rufiventer	LSUMZ B3629	Peru: Loreto, S bank Rio Maranon, along Rio Samiria, Est. Biol. Pithecia, Base Tacsha Cocha	FJ799895	JN810550
Tachyphonus rufus	LSUMZ B6668	Bolivia: Santa Cruz, Rio Tucavaca	FJ799896	JN810551
Tachyphonus surinamus	LSUMZ B4795	Peru: Loreto, S Rio Amazonas, ca. 10 km SSW Rio Napo	EU647923	EU647959
Tangara argyrofenges	ANSP 4482	Ecuador: Zamora-Chinchipe, Panguri, ca. 12 km NE San Francisco del Vergel	AY383104	JN810552
Tangara arthus	LSUMZ B22591	Bolivia: La Paz, B. Saavedra, 83 km by road E Charazani, Cerro Asunta Pata	AY383106	EU648055
Tangara callophrys	LSUMZ B34961	Ecuador: Napo, ca. 20 km SSW Loreto	AY383107	EU648056
Tangara cayana	LSUMZ B15414	Bolivia: Santa Cruz, Serrania De Huanchaca, 45 km E Florida	AY383108	JN810553
Tangara chilensis	MVZ 169699	Peru: Dept. Cajamarca, 1 mi N San Jose de Lourdes, Cordillera del Condor	AY383110	EU648058

Table 1 (*continued*)

	Voucher/Sample Number[a]	Locality	Cyt *b*	ND2
Tangara chrysotis	LSUMZ B34927	Ecuador: Napo, ca. 40 km NNE Tena	AY383111	EU648059
Tangara cucullata	STRI SV-TCU2	St. Vincent: Cumberland Valley	AY383113	EU648060
Tangara cyanicollis	LSUMZ B15352	Bolivia: Santa Cruz, Serrania De Huanchaca, 45 km E Florida	AY383115	EU648061
Tangara cyanocephala	FMNH 427278	Brazil: Pernambuco, Taquaritinga	AY383117	–
Tangara cyanocephala 2	FMNH 427279	Brazil: Pernambuco, Taquaritinga	–	EU648062
Tangara cyanoptera	LSUMZ B7436	Venezuela: Amazonas, Cerro de la Neblina Camp VII	AY383116	EU648063
Tangara cyanotis	LSUMZ B22708	Bolivia: La Paz, B. Saavedra, 83 km by road E Charazani, Cerro Asunta Pata	AY383119	EU648064
Tangara cyanoventris	FMNH 311036	Brazil: Rio de Janeiro, Itatiaia, Fazenda de Serra	JN810152	–
Tangara desmaresti	FMNH 395478	Brazil: Sao Paulo, Boracia	AY383120	EU648065
Tangara dowii	LSUMZ B16020	Costa Rica: Herredia, 4 km SE Virgen del Socorro	AY383121	EU648066
Tangara fastuosa	FMNH 427276	Brazil: Alagoas, Ibateouara, Envenho Ceimba, Usina Serra Grande	AY383123	EU648067
Tangara florida	LSUMZ B34982	Ecuador: Esmeraldas, 2 km W Alto Tambo	AY383122	EU648068
Tangara fucosa	LSUMZ B1398	Panama: Darien, ca. 9 km NW Cana on slopes Cerro Pirre	AY383125	EU648069
Tangara guttata	LSUMZ B2190	Panama: Darien, about 6 km NW Cana	AY383126	EU648070
Tangara gyrola	LSUMZ B22850	Bolivia: La Paz, B. Saavedra, 83 km by road E Charazani, Cerro Asunta Pata	AY383131	EU648071
Tangara heinei	LSUMZ B34896	Ecuador: Pichincha, 5 km S Nanegalito	AY383132	EU648072
Tangara icterocephala	LSUMZ B16032	Costa Rica: Herredia, 4 km SE Virgen del Socorro	AY383133	EU648073
Tangara inornata	LSUMZ B28766	Panama: Colon, Achiote Road, ca. 2 km bridge at Rio Providencia	AY383134	EU648074
Tangara johannae	LSUMZ B29956	Ecuador: Imbabura, ca. 20 km N Pedro Vicente Maldonado	AY383135	EU648075
Tangara labradorides	LSUMZ B32686	Peru: Cajamarca, Quebrada Las Palmas, ca. 13 km WSW Chontali	AY383136	EU648076
Tangara larvata	LSUMZ B34909	Ecuador: Pichincha, 15 km N Pedro Vicente Maldonado	AY383138	EU648077
Tangara lavinia	LSUMZ B34987	Ecuador: Esmeraldas, 30 km SE San Lorenzo	AY383139	EU648078
Tangara mexicana	LSUMZ B18465	Bolivia: Santa Cruz, Velasco, Parque Nacional Noel Keonpff Mercado 86 km ESE of Florida	AY383140	EU648079
Tangara meyerdeschauenseei	LSUMZ B43111	Peru: Dept. Puno, 9.5 km N of Sándia	AY383142	EU648080
Tangara nigrocincta	LSUMZ B9758	Bolivia: Pando, Nicholas Suarez, 12 km by road S of Cojiba, 8 km W on road to Mucden	AY383143	EU648081
Tangara nigroviridis	LSUMZ B1627	Peru: Pasco, Santa Cruz, about 9 km SSE Oxapampa	AY383144	EU648082
Tangara palmeri	LSUMZ B11999	Ecuador: Esmeraldas, El Placer	AY383146	EU648083
Tangara parzudakii	LSUMZ B30007	Ecuador: Esmeraldas, ca. 2.7 km E Alto Tambo	AY383147	EU648084
Tangara phillipsi	AMNH 821010	Peru: Dept. Huanuco, Cerros del Sira	JN810153	–
Tangara preciosa	CUMV 50646	Uruguay: Cerro Largo, Rio Yaguaron	EU647994	EU648085
Tangara punctata	LSUMZ B34931	Ecuador: Napo, ca. 40 Km NNE Tena	AY383148	–
Tangara punctata 2	LSUMZ B35552	Brazil: Fazenda Morelandia, 8 km N de Santa barbara, do Para	–	EU648087
Tangara ruficervix	LSUMZ B8190	Peru: Pasco, Playa Pampa, ca. 8 km NW Cushi on trail to Chaglla	AY383150	EU648088
Tangara rufigenis	UMMZ 134758	Venezuela: Aragua, Rancho Grande, Lat	JN810154	–
Tangara rufigula	LSUMZ B11930	Ecuador: Esmeraldas, El Placer	AY383152	EU648089
Tangara schrankii	LSUMZ B34932	Ecuador: Napo, 20 km SSW Loreto	AY383153	EU648090
Tangara seledon	LSUMZ B16942	Brazil: Sao Paulo, Salesopolis, E.B. Boraceia	AY383154	EU648091
Tangara varia	LSUMZ B28010	Peru: Loreto, ca. 77 km WNW Contaman	AY383155	EU648092
Tangara vassorii	LSUMZ B1711	Peru: Pasco, Santa Cruz, about 9 km SSE Oxapampa	AY383156	EU648093
Tangara velia	FMNH 390060	Brazil: Rondonia, Cachoeeira Nazare, W bank Rio jiparana	AY383158	EU648094
Tangara viridicollis	LSUMZ B8090	Peru: Pasco, Playa Pampa, ca. 8 km NW Cushi on trail to Chaglla	AY383159	EU648095
Tangara vitriolina	LSUMZ B34921	Ecuador: Pichincha, Tumbaco, Avenal, Buena Ezperanza	AY383160	EU648096
Tangara xanthocephala	LSUMZ B34922	Ecuador: Pichincha, 5 km SE Baeza	AY383161	EU648097
Tangara xanthogastra	LSUMZ B34934	Ecuador: Napo, 20 km SSW Loreto	AY383162	EU648098
Tersina viridis	LSUMZ B9680	Bolivia: Pando, Nicholas Suarez, 12 km by road S of Cojiba, 8 km W on road to Mucden	AF006255	–
Tersina viridis 2	LSUMZ B14819	Bolivia	–	AF447309
Thlypopsis fulviceps	AMNH 785875	Venezuela: Zulia, Cerro Pejochaina, Perija	JN810155	–
Thlypopsis inornata	MVZ 178272	Peru: Depto. Cajamarca, 1 mi N San José de Lourdes, Cordillera del Condor	JN810156	JN810554
Thlypopsis ornata	LSUMZ B8075	Peru: Pasco, Playa Pampa, 8 km NW Cushi on trail to Chaglla	JN810157	JN810555
Thlypopsis pectoralis	LSUMZ B3608	Peru: Huanuco, Quebrada Shugush, 30 km on Huanuco-La Union Rd	JN810158	JN810556
Thlypopsis ruficeps	FMNH 430081	Peru: Cuzco, Paucartambo: San Pedro, 2460 m	JN810159	JN810557
Thlypopsis sordida	LSUMZ B7260	Peru: Loreto, Amazonas I. Pasto 80 km NE Iquitos 80 m	AF006256	JN810558
Thraupis abbas	MBM 7056	Honduras: Depto. Copan, Copan Ruinas, 10 km ENE	EU647996	EU648099

(*continued on next page*)

Table 1 (*continued*)

	Voucher/Sample Number[a]	Locality	Cyt *b*	ND2
Thraupis cyanocephala	FMNH 433897	Peru: Cuzco, Paucartambo, La Esperanza, 39 km (road) NE Paucartambo, 2850 m	EU647998	EU648101
Thraupis cyanoptera	FMNH 395473	Brazil: Sao Paulo, Boracia	EU647999	EU648102
Thraupis episcopus	FMNH 433904	Peru: Madre de Dios, Moskitania, 13.4 km NNW Atalaya, I bank Alto Madre de Dios, 480 m	EU648000	EU648103
Thraupis ornata	FMNH 395474	Brazil: Sao Paulo, Boracia	EU648001	EU648104
Thraupis palmarum	FMNH 427254	Brazil: Alagoas, Ibateouara, Envenho Ceimba, Usina Serra Grande	EU648002	EU648105
Thraupis sayaca	FMNH 334600	Bolivia: El Beni, Trinidad, 10 km SW	EU648003	EU648106
Tiaris bicolor	MVZ 179402	captive bird	AF489899	–
Tiaris bicolor 2	BMNH JK95001	Bahamas: Long Island	–	AF290115
Tiaris canorus	STRI BH-TCN1	Bahamas: Gape's Backyard	HQ153058	HQ153078
Tiaris fuliginosus	LSUMZ B12612	Bolivia: Santa Cruz, Velasco, 50 km ESE of Florida, Arroyo del Encanto	AF489900	EU648107
Tiaris obscurus	STRI BO-TOB22763	Bolivia: Departmento La Paz; Prov. B. Saavedra; Cerro Asunta Pata	HQ153059	HQ153081
Tiaris olivaceus	AMNH 25429	Dominican Republic: Independencia, Parque Nacional Sierra de Baoruco, El Aceitillar, Alcoa Rd.	AF489901	–
Tiaris olivaceus 2	UMMZ 233813	Dominican Republic: Independencia, Parque Nacional Sierra de Baoruco, El Aceitillar, Alcoa Rd.	–	AF447310
Trichothraupis melanops	AMNH DOT 2464	Argentina: Misiones Departamento San Ignacio about 20 km SE San Ignacio	FJ799899	JN810559
Urothraupis stolzmanni	ZMUC 120310	Ecuador: Tungurahua, C Llanganates	JN810160	JN810560
Volatinia jacarina	FMNH 394403	Bolivia	AF489903	AF290113
Wetmorethraupis sterrhopteron	FMNH 275691	Peru: Amazonas	EU648004	–
Xenodacnis parina	LSUMZ B7760	Ecuador: Azuay, 1 km W CJS Nacional de Recreacion, near MGR	AF006257	EU647960
Xenospingus concolor	LSUMZ B5263	Peru: Dept. Ica; 0.5 km E km 235 Pan-American Hwy	JN810161	JN810561
Outgroup species				
Pheucticus tibialis	LSUMZ B16050	Costa Rica: Heredia Province	JX569837	JX569838
Piranga ludoviciana	BMNH jk94-105	USA: Montana, Missoula Co.	EF529998	AF290109
Cardinalis cardinalis	BMNH X7320	USA: Minnesota	EF530007	EF529902
Passerina ciris	LSUMZ B5694	USA: Louisiana, Cameron Parish	AF301459	EF529883

[a] Museum abbreviations: AMNH, American Museum of Natural History; ANSP, Academy of Natural Sciences, Philadelphia; BMNH, University of Minnesota, Bell Museum of Natural History; COP, Colección Ornitológica Phelps; CUMV, Cornell University Museum of Vertebrates; CVA-UV, Universidad del Valle, Colombia; FMNH, Field Museum of Natural History; IAvH, Instituto de Investigación de recursos Biológicos Alexander von Humboldt; ICN, Instituto de Ciencias Naturales, Universidad Nacional de Colombia; KU, University of Kansas Natural History Museum; LACM, Natural History Museum of Los Angeles County; LSUMZ, Louisiana State University Museum of Natural Science Collection of Genetic Resources; MACN, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"; MBM, University of Nevada Las Vegas, Barrick Museum of Natural History; MVZ, Museum of Vertebrate Zoology, University of California, Berkeley; STRI, Smithsonian Tropical Research Institute; UMMZ, University of Michigan Museum of Zoology; USNM, National Museum of Natural History (Smithsonian Institution); UWBM, University of Washington, Burke Museum; ZMUC, Zoological Museum, University of Copenhagen.

was computed simultaneously with 1000 bootstrap replicates, and run independently several times.

We conducted Bayesian analyses using BEAST v1.7.1 (Drummond et al., 2012) to produce an ultrametric tree. We analyzed the concatenated dataset containing all genes and taxa, partitioned as in the maximum likelihood analyses. We unlinked rate heterogeneity, base frequencies, and substitution rates across partitions. Models of evolution for each partition were inferred using jModelTest (Posada, 2008). Models were selected for the gene partitions using the AIC criterion (Akaike, 1973), and for each codon partition using the AICc, corrected for small sample size (Sugiura, 1978). In cases where the unimplemented TVM or TrN models were selected, we substituted the more general GTR model. All partitions used the GTR + I + G model except for ND2 codon 3, RAG1 codon 3, ACO1-I9, FGB-I5, and MB-I2 partitions, which used the GTR + G model, and the RAG1 codon 2 partition, which used the HKY + I + G model. We used a Yule speciation model for tree shape, and an uncorrelated log-normal relaxed clock model with unlinked estimated rates across all partitions except for cyt *b* (Drummond et al., 2006). We linked rates across the three cyt *b* partitions, and used a substitution rate of 0.0105 mean substitutions per million years along each branch (Weir and Schluter, 2008). We used automatic optimization on MCMC operators, and ran analyses for a total of 200 million generations across four independent runs sampling every 5000 generations. We used Tracer v1.5 (Rambaut and Drummond, 2007) to assess convergence across independent runs and examine effective sample size values for all parameters. We also assessed convergence of the topology and clade stability using the online program Are We There Yet (Nylander et al., 2008). We discarded the first 20 million generations and 4000 trees for each run as a conservative burn-in, and combined both log and trees files using the program LogCombiner v1.7.1 (Drummond et al., 2012). We produced a maximum clade credibility tree using the BEAST program TreeAnnotator v1.7.1 (Drummond et al., 2012).

2.4. Diversification analyses

We compared the fit of five models of diversification for the entire clade (Thraupidae) and for each subfamily of tanagers with more than five species, as implemented in the R packages laser v2.3 (Rabosky, 2006) and TreePar v2.5 (Etienne et al., 2012). These models are: (1) a pure-birth model, which is a 1-parameter rate-constant model with no extinction (PB; Yule, 1924) (2) a birth–death model, which is a 2-parameter rate-constant model that infers speciation and extinction (BD; Kendall, 1948; Nee et al., 1994), (3) a 2-parameter rate-variable exponential-variant diversity-dependent model that assumes no extinction (DDX – E; Nee et al., 1992; Rabosky, 2006), (4) a 2-parameter rate-variable logistic-variant diversity-dependent model that assumes no extinction (DDL – E; Nee et al., 1992; Rabosky, 2006), and (5) a 3-parameter rate-variable diversity-dependent model which does estimate the rate of extinction (DDL + E; Etienne et al., 2012). For each clade, AIC_c scores were used to distinguish which model of diversification fit best. Models were considered to have a difference of fit if the difference in AIC_c scores was two or greater (Burnham and Anderson, 2002). In addition, we created a lineage-through-time plot to get a more intuitive sense of tanager diversification. We also estimated the gamma statistic (Pybus and Harvey, 2000), which is a measure of rate constancy of lineage accumulation through time. The effect of incomplete taxon sampling on gamma statistic estimates was accounted for using the "mccr" test with 10,000 simulation replicates, and the test was run over 1000 trees randomly selected from the post-burn-in posterior distribution of the BEAST analysis.

We also modeled diversification by treating the phylogeny as having been shaped by a mixture of macroevolutionary processes, using a novel Bayesian approach called BAMM (Bayesian Analysis of Macroevolutionary Mixtures, Rabosky et al., 2013; Rabosky and Matute, 2013; Rabosky, 2014). The model fits multiple diversification processes to various subtrees in the phylogeny, and uses reversible jump Markov Chain Monte Carlo to explore potential model space until the combination of processes with the highest likelihood is found. Shifts in diversification are detected automatically, with no *a priori* designations, and can occur at nodes or along branches, where the number of such shifts is assumed to follow a compound Poisson distribution. Importantly, rate constancy in diversification is not assumed, and therefore the phylogeny can be found to include any combination of constant-rate and rate-variable diversification models. We ran BAMM for fifty million generations, allowing for time-heterogeneous speciation rates, but holding extinction rates as time-constant. We accounted for incomplete taxon sampling analytically by supplying numbers of missing species per subfamily.

3. Results

3.1. Sequence characteristics and gene properties

The genes varied in their size, number of variable sites, and number of parsimony informative sites. For each marker, these data are as follows: cyt *b* (1143, 589, 519), ND2 (1041, 677, 612), RAG1 (2891, 813, 385), MB-I2 (730, 357, 164), ACO1-I9 (1104, 705, 383), and FGB-I5 (586, 338, 168). Average uncorrected sequence divergences for all pairwise comparisons for each marker were as follows: cyt *b* (10.5%), ND2 (15.8%), RAG1 (1.30%), MB-I2 (2.17%), ACO1-I9 (3.48%), and FGB-I5 (2.33%). As expected, the different markers varied in their ability to resolve relationships among the species (Supplementary Figs. 1–6). Between the two mtDNA markers, ND2 recovered more nodes with $\geqslant$70% ML bootstrap support than cyt *b* (57% of nodes for ND2 vs. 46% for cyt *b*). Among nuclear markers, the protein-coding gene RAG1 and the sex-linked ACO1-I9 recovered more strongly supported nodes than the other markers. For both RAG1 and ACO1-I9, 46% of all possible nodes were strongly supported, whereas the MB-12 gene tree recovered 24% and the FGB-I5 gene tree recovered only 17%.

3.2. Phylogenetic analyses

In general, the ML and Bayesian concatenated trees had similar topologies (Figs. 1–6). A few nodes were recovered with strong support in only one of the two analyses; however, none of these nodes strongly conflicted with those of the other analyses. Both analyses recovered a monophyletic Thraupidae with strong support (1.0 PP [posterior probability]; 100% bootstrap). Thraupidae was also recovered in all of the individual gene trees except FB-I5 (Supplementary Figs. 1–6). Within Thraupidae, 70% of the nodes were strongly supported in the concatenated Bayesian analyses (PP $\geqslant$ 0.95), and 66% of nodes were strongly supported in the concatenated ML analyses (bootstrap $\geqslant$ 70%). Nodes with weaker support include some of the early nodes in the tree and nodes defining relationships among some recent species that are only weakly differentiated from each other (e.g., species within *Geospiza*, *Camarhynchus*, and *Sporophila*).

Our analyses revealed 13 strongly-supported nodes relatively early in the tree that define novel subgroups of tanagers (Fig. 1) that we designate as subfamilies. These clades are the deepest nodes in the tree that are supported by either PP $\geqslant$ 0.95 or bootstrap $\geqslant$ 70%. All are recovered in both Bayesian and ML topologies,

Table 2
Species names, voucher numbers, localities, and GenBank accession numbers of nuclear sequences included in the study.

Species	Voucher/Sample Number[1]	Locality	FGB-I5	MB-I2	Rag 1	ACO1-I9
Ingroup species						
Acanthidops bairdi	LSUMZ B16267	Costa Rica: San Jose, Cerro de la Muerte, Pan American Highway, km 113	JN810162	JN810297	JN810562	JN809918
Anisognathus somptuosus	LSUMZ B566	Peru: Puno, Abra de Maruncunca, 10 km SW San Juan del Oro	JN810163	JN810298	JN810563	JN809919
Bangsia arcaei	USNM B01412	Panama	JN810164	JN810299	JN810564	JN809920
Buthraupis wetmorei	LSUMZ B337	Peru: Cajamarca, Cerro Chinguela, 5 km NE Sapalache	JN810166	JN810301	JN810566	JN809922
Calochaetes coccineus	LSUMZ B6134	Ecuador: Morona Santiago, W slope de Cutucci Yapitya	JN810167	JN810302	JN810567	JN809923
Cnemathraupis eximia	LSUMZ B365	Peru: Cajamarca, Cerro Chinguela, 5 km NE Sapalache	JN810165	JN810300	JN810565	JN809921
Catamblyrhynchus diadema	FMNH 433908	Peru: Cuzco, Paucartambo, La Esperanza, 39 km (road) NE Paucartambo, 2850 m	JN810169	JN810304	JN810569	JN809925
Catamenia homochroa	LSUMZ B426	Peru: Dept. Piura; Cruz Blanca; 33 rd km SW Huancabamba	JN810170	JN810305	JN810570	JN809926
Charitospiza eucosma	LSUMZ B15356	Bolivia: Santa Cruz, Serrania de Huanchaca, 45 km E Florida	JN810171	JN810306	JN810571	JN809927
Chlorochrysa calliparaea	LSUMZ B8103	Peru: Pasco, Playa Pampo, 8 k NW Cushi on trail to Chaglla	JN810172	JN810307	JN810572	JN809928
Chlorochrysa phoenicotis	LSUMZ B34873	Ecuador: Pichincha, 30 km Santo Domingo de los Colorados	JN810173	JN810308	JN810573	JN809929
Chlorophanes spiza	LSUMZ B2838	Peru: Loreto, 1 km N Rio Napo, 157 km by river NNE Iquitos	JN810174	JN810309	JN810574	JN809930
Chlorornis riefferii	LSUMZ B1859	Peru: Pasco, Chumbre de Ollon, about 12 km E Oxapampa	JN810175	JN810310	JN810575	JN809931
Chrysothlypis chrysomelas	LSUMZ B2189	Panama: Darien, about 6 km NW Cana	JN810176	JN810311	JN810576	JN809932
Cissopis leverianus	LSUMZ B1143	Bolivia: La Paz, Rio Beni, ca. 20 km by river N Puerto Linares	JN810177	JN810312	JN810577	JN809933
Cnemoscopus rubrirostris	LSUMZ B5624	Peru: Amazonas, 30 km by road E Florida on road to Rioja	JN810178	JN810313	JN810578	JN809934
Coereba flaveola	FMNH 397158	West Indies: Bahamas, Great Abaco, Little Harbour Lighthouse, 3.75 km SSW, Cay Road	HQ153061	HQ153068	HQ153083	HQ153049
Conirostrum ferrugineiventre	FMNH 391984	Peru: Cuzco, Urubamba, Pumahuanca	JN810179	JN810314	JN810579	JN809935
Conirostrum margaritae	LSUMZ B7293	Peru: Loreto, Amazonas I. Pasto 80 km NE Iquitos 80 m	JN810180	JN810315	JN810580	JN809936
Conothraupis speculigera	LSUMZ B5127	Peru: Lambayeque, Las Pampas, km 885 Pan-American Hwy, 11 road km from Olmos	JN810181	JN810316	JN810581	JN809937
Coryphaspiza melanotis	LSUMZ B6826	Bolivia: Beni, 3 k SW San Borja	JN810182	JN810317	JN810582	JN809938
Coryphospingus cucullatus	FMNH 334587	Bolivia: Santa Cruz, Chiquitos, Purubi, 30 km S San Jose de Chiquitos	JN810183	JN810318	JN810583	JN809939
Creurgops dentatus	LSUMZ B580	Peru: Puno, Abra de Maruncunca, 10 km SW San Juan del Oro	JN810184	JN810319	JN810584	JN809940
Creurgops verticalis	LSUMZ B7974	Peru: Pasco, Playa Pampa, 8 km NW Cushi on trail to Chaglla	JN810185	JN810320	JN810585	JN809941
Cyanerpes cyaneus	FMNH 427305	Brazil: Alagoas	JN810186	JN810321	JN810586	JN809942
Cyanicterus cyanicterus	USNM B10923	Guyana	JN810187	JN810322	JN810587	JN809943
Cypsnagra hirundinacea	LSUMZ B15290	Bolivia: Santa Cruz, Velasco, Pre Parque Nacional Noel Kempff Mercado, 30 km E Aserradero Moira	JN810188	JN810323	JN810588	JN809944
Dacnis cayana	LSUMZ B15077	Bolivia: Santa Cruz, Velasco, 13 km SW Piso Firme	JN810189	JN810324	JN810589	JN809945
Diglossa lafresnayii	LSUMZ B351	Peru: Cajamarca, Cerro Chinguela, 5 km NE Sapalache	JN810191	JN810326	JN810591	JN809947
Diglossa cyanea	FMNH 430124	Peru: Cuzco, Paucartambo, Pillahuata	JN810192	JN810327	JN810592	JN809948
Diuca diuca	AMNH DOT 9942	Argentina, Rio Negro, Departamento Norquinco	None	JN810328	JN810593	JN809949
Diuca speculifera	LSUMZ B22574	Bolivia: La Paz, Zongo Valley, 7 km by road N of summit	JN810193	JN810329	JN810594	JN809950
Dolospingus fringilloides	USNM B11981	Guyana	JN810194	JN810330	JN810595	JN809951
Donacospiza albifrons	KU 3316	Paraguay: Misiones, 5 km NW Yabebyry, Estancia Santa Ana	JN810195	JN810331	JN810596	JN809952
Dubusia castaneoventris	LSUMZ B3607	Peru: Huanuco, Quebrada Shugush, 30 km on Huanuco-La Union Rd	JN810190	JN810325	JN810590	JN809946
Dubusia taeniata	LSUMZ B7710	Peru: Huanuco, Unchog Pass NNW Acomayo 3450 m	JN810196	JN810332	JN810597	JN809953
Emberizoides herbicola	FMNH 395725	Brazil: Roraima, Fazenda Santa Cecilia, E bank Rio Branco, opposite Boa Vista	JN810197	JN810333	JN810598	JN809954
Embernagra platensis	FMNH 396034	Bolivia	JN810198	JN810334	JN810599	JN809955
Eucometis penicillata	LSUMZ B6551	Bolivia: Santa Cruz, Rio Quizer	JN810199	JN810335	JN810600	JN809956
Euneornis campestris	FMNH 331119	Jamaica: Portland, Hollywell Park	HQ153062	HQ153069	HQ153084	HQ153050
Gubernatrix cristata	MACN 68379	Argentina: Prov. Buenos Aires; Salinera Universal, Salina de Piedra, Cardenal Cagliero, Partido de Patagones	JN810200	JN810336	JN810601	JN809957
Haplospiza rustica	FMNH 433797	Peru: Cuzco, Paucartambo, La Esperanza, 39 km (road) NE Paucartambo	JN810201	JN810337	JN810602	JN809958
Haplospiza unicolor	FMNH 395462	Brazil: Sao Paulo, Boracia	JN810202	None	None	None
Hemispingus atropileus	LSUMZ B1889	Peru: Pasco, Chumbre de Ollon, about 12 km E Oxapampa	JN810203	JN810338	JN810603	JN809959
Hemispingus melanotis	FMNH 430079	Peru: Cuzco, Paucartambo: San Pedro	JN810204	JN810339	JN810604	JN809960
Hemispingus rufosuperciliaris	LSUMZ B3566	Peru: Huanuco, base of bosque Zapatagocha above NE Acomayo	JN810205	JN810340	JN810605	JN809961
Hemispingus superciliaris	FMNH 433858	Peru: Cuzco, Paucartambo, La Esperanza, 39 km (road) NE Paucartambo	JN810206	JN810341	JN810606	JN809962
Hemispingus verticalis	LSUMZ B320	Peru: Cajamarca, Cerro Chingueal, 5 km NE Sapalache	JN810207	JN810342	JN810607	JN809963
Hemithraupis flavicollis	LSUMZ B5102	Peru: Loreto, S Rio Amazonas, ca. 10 km SSW mouth Rio Napo on E bank Quebrada Vainilla	JN810208	JN810343	JN810608	JN809964
Heterospingus xanthopygius	LSUMZ B2324	Panama: Darien, Cana on E slope Cerro Pirre	JN810209	JN810344	JN810609	JN809965
Idiopsar brachyurus	LSUMZ B22571	Bolivia: La Paz, Zongo Valley, 7 km by road N of summit	JN810210	JN810345	JN810610	JN809966
Incaspiza ortizi	LSUMZ B10382	Peru: Cajamarca, above Limon Pampa between Calenda and Balsan	JN810211	JN810346	JN810611	JN809967
Incaspiza pulchra	LSUMZ B10387	Peru: Ancash, just out of Huaylash toward Sucre	JN810212	JN810347	JN810612	JN809968
Iridophanes pulcherrimus	MVZ 169712	Peru: Dept. Cajamarca, 1 mi N San Jose de Lourdes, Cordillera del Condor	JN810213	JN810348	JN810613	JN809969
Iridosornis analis	LSUMZ B1706	Peru: Pasco, Santa Cruz, about 9 km SSE Oxapampa	JN810214	JN810349	JN810614	JN809970
Iridosornis jelskii	FMNH 430099	Peru: Cuzco, Paucartambo: Pillahuata, 2460 m	JN810215	JN810350	JN810615	JN809971
Lanio fulvus	LSUMZ B2694	Peru: Loreto, 1 km N Rio Napo, 157 km by river NNE Iquitos	JN810216	JN810351	JN810616	JN809972
Lophospingus griseocristatus	FMNH 334558	Bolivia: Cochabamba, Cochabamba-Oruro Rd, km 29	JN810217	JN810352	JN810617	JN809973
Loxigilla violacea	AMNH 25433	Dominican Republic: Independencia	HQ153063	HQ153070	HQ153085	HQ153051
Loxigilla portoricensis	PR-LPO26	Puerto Rico	EF567717	None	None	None

Table 2 (*continued*)

Species	Voucher/Sample Number[1]	Locality	FGB-I5	MB-I2	Rag 1	ACO1-I9
Loxipasser anoxanthus	FMNH 33107	Jamaica: Surrey, Portland, Hollywell Park	HQ153064	HQ153071	HQ153086	HQ153052
Melanodera xanthogramma	AMNH DOT 12115	Argentina: Departamento Bariloche, Rio Negro	JN810218	JN810353	JN810618	JN809974
Melanospiza richardsoni	SL-MRI2	St. Lucia	EF567721	None	EF567526	None
Melopyrrha nigra	FMNH 342954	captive bird	HQ153065	HQ153072	HQ153087	HQ153053
Nemosia pileata	LSUMZ B7295	Peru: Loreto, Amazonas I. Pasto 80 km NE Iquitos 80 m	JN810219	JN810354	JN810619	JN809975
Neothraupis fasciata	LSUMZ B13914	Bolivia: Santa Cruz, Serrania de Huanchaca, 45 km E Florida	JN810220	JN810355	JN810620	JN809976
Nephelornis oneilli	LSUMZ B8402	Peru: Pasco, Millpo, E Tambo de vacas on Pozuzo-Chaglla trail	JN810221	JN810356	JN810621	JN809977
Nesospiza acunhae	ITU35	Inaccessible Island, Tristan da Cunha	JN810222	JN810357	JN810622	JN809978
Oreomanes fraseri	LSUMZ B2069	Peru: Lima, ca. 13 road km W Milloc	JN810223	JN810358	JN810623	JN809979
Oryzoborus angolensis	FMNH 433798	Peru: Madre de Dios, Moskitania, 13.4 km NNW Atalaya, I bank Alto Madre de Dios	JN810224	JN810359	JN810624	JN809980
Oryzoborus crassirostris	FMNH 339668	Venezuela: Sucre, Guraunos, 14 km SSE	None	JN810360	None	JN809981
Parkerthraustes humeralis	LSUMZ B9328	Boliva: Pando	JN810168	JN810303	JN810568	JN809924
Paroaria capitata	UWBM JAG-1837	Argentina: Corrientes	JN810225	JN810361	JN810625	JN809982
Paroaria coronata	FMNH 394390	Bolivia	JN810226	JN810362	JN810626	JN809983
Paroaria dominicana	FMNH 392736	Brazil: Sergripe, Caninde do Sao Francisco, Curituba, Fazenda Porto Belo	JN810227	JN810363	JN810627	JN809984
Paroaria gularis	FMNH 323625	Peru: Madre de Dios, Hacienda Amazonia	JN810228	JN810364	JN810628	JN809985
Phrygilus carbonarius	AMNH DOT 10373	Argentina: Neuquen, Departamento Anelo, Sierra Auca Mahuida	JN810229	JN810365	JN810629	JN809986
Phrygilus dorsalis	LSUMZ B17176	Argentina	JN810230	JN810366	JN810630	JN809987
Phrygilus erythronotus	LSUMZ B103892	Peru: Tacna, Tacna-Llave Rd, ca. 57 km NE Tarata	JN810231	JN810367	JN810631	JN809988
Phrygilus fruticeti	MBM 5412	Argentina: Jujuy, Tilcara, 18 km S	JN810232	JN810368	JN810632	JN809989
Phrygilus gayi	MBM 6475	Argentina: Tucuman, Amaicha del Valle 12 km S, 12 km E	JN810233	JN810369	JN810633	JN809990
Piezorina cinerea	LSUMZ B5169	Peru: Lambayeque, Las Pampas, km 885 Pan-American Hwy, 11 road km from Olmos	JN810234	JN810370	JN810634	JN809991
Pipraeidea melanonota	LSUMZ B12070	Ecuador: Pichincha, Mindo	JN810235	JN810371	JN810635	JN809992
Poospiza alticola	ZMUC 116453	Peru: Ancash, C. Blanc, Andavite, Rurichinc.	JN810236	JN810372	JN810636	JN809993
Poospiza hispaniolensis	LSUMZ 24977	captive bird	None	JN810373	JN810637	JN809994
Poospiza hypochondria	MBM 6482	Argentina. Tucuman	JN810238	JN810374	JN810638	JN809995
Poospiza cabanisi	CUMV 50661	Uruguay: Cerro Largo; Rio Yaguaron	JN810237	JN810375	JN810639	JN809996
Poospiza melanoleuca	MBM 5316	Argentina: Salta, J.V. Gonzalez, 14 km NE	JN810239	JN810376	JN810640	JN809997
Poospiza ornata	AMNH DOT 9515	locality unknown	JN810240	JN810377	JN810641	JN809998
Poospiza torquata	KU 2838	Paraguay: Presidente Hayes, Campo Largo, 5 km S	JN810241	JN810378	JN810642	JN809999
Poospiza whitii	LSUMZ B6573	Bolivia: Santa Cruz, 2.5 km N Tambo	JN810242	JN810379	JN810643	JN810000
Porphyrospiza caerulescens	LSUMZ B13862	Bolivia: Santa Cruz; Serrania de Huanchaca, 45 km E Florida	JN810243	JN810380	JN810644	JN810001
Pyrrhocoma ruficeps	MVZ 165617	Paraguay: Dept. Itapu, El Tirol, 19.5 km by road NNE Encarnacion	JN810244	JN810381	JN810645	JN810002
Ramphocelus carbo	FMNH 430084	Peru: Cuzco, Paucartambo: San Pedro	JN810245	JN810382	JN810646	JN810003
Ramphocelus passerinii	MBM 4358	Nicaragua, La Luz near Wani on Rio Uli	JN810246	None	None	None
Ramphocelus sanguinolentus	FMNH 343376	Mexico: Veracruz, El Bastonal, 3 km S, 3 km E, Sierra de Santa Martha	JN810247	JN810383	JN810647	JN810004
Rhodospingus cruentus	LSUMZ B5184	Peru: Lambayeque, Las Pampas, km 885 Pan-American Hwy, 11 road km from Olmos	JN810248	JN810384	JN810648	JN810005
Rowettia goughensis	GB18	Gough Island	JN810249	JN810385	JN810649	JN810006
Saltator atriceps	FMNH 343357	Mexico: Veracruz	JN810250	JN810386	JN810650	JN810007
Saltator atricollis	LSUMZ B15381	Bolivia: Santa Cruz	JN810251	JN810387	JN810651	JN810008
Saltator atripennis	ANSP 3491	Ecuador: Azuay	JN810252	JN810388	JN810652	JN810009
Saltator aurantiirostris	UWBM 54506	Argentina: Tucuman	JN810253	JN810389	JN810653	JN810010
Saltator cinctus	LSUMZ B6233	Ecuador: Prov. Morona-Santiago	JN810254	JN810390	JN810654	JN810011
Saltator coerulescens	UWBM GAV817	Argentina: Corrientes	JN810255	JN810391	JN810655	JN810012
Saltator grossus	LSUMZ B16063	Costa Rica: Herredia	JN810256	JN810392	JN810656	JN810013
Saltator maximus	FMNH 433810	Peru: Cuzco, Paucartambo, Consuelo, 15.9 km SW Pilcopata	JN810257	JN810393	JN810657	JN810014
Saltator nigriceps	LSUMZ B183	Peru: Piura	JN810258	JN810394	JN810658	JN810015
Saltator rufiventris	LSUMZ B106750	Bolivia: Cochabamba	JN810259	JN810395	JN810659	JN810016
Saltator similis	UWBM 70491	Argentina: Provincia de Corrientes, Corrientes, Manuel Derqui	JN810260	JN810396	JN810660	JN810017
Saltator striatipectus	LSUMZ B449	Peru: Lambayeque	JN810261	JN810397	JN810661	JN810018
Saltatricula multicolor	MVZ 179401	Luis F. Baptista aviary	JN810262	JN810398	JN810662	JN810019
Schistochlamys melanopis	LSUMZ B9669	Bolivia: Pando, Nicholas Suarez, 12 km by road S of Cojiba, 8 km W on road to Mucden	JN810263	JN810399	JN810663	JN810020
Sericossypha albocristata	LSUMZ B5630	Peru: Amazonas, 30 km by road E Florida on road to Rioja	JN810264	JN810400	JN810664	JN810021
Sicalis citrina	LSUMZ B15400	Bolivia: Santa Cruz, Serrania De Huanchaca, 45 km E Florida	JN810265	JN810401	JN810665	None
Sicalis luteola	FMNH 389274	Brazil: Roraima, Fazenda Santa Cecilia, E Bank Rio Branco, across from boa Vista	JN810266	JN810402	JN810666	JN810022
Sporophila albogularis	FMNH 392743	Brazil: Alagoas, Piranhas, Fazenda Bela Vista	JN810267	JN810403	JN810667	JN810023
Sporophila lineola	FMNH 390057	Brazil: Rondonia, Cachoeeira Nazare, W bank Rio jiparana	JN810268	JN810404	JN810668	JN810024
Stephanophorus diadematus	AMNH 9915	Argentina: Buenos Aires, Partido Escobar	JN810269	JN810405	JN810669	JN810025
Tachyphonus coronatus	AMNH DOT2452	Argentina: Misiones Departamento San Ignacio, near border Parque Prov. Urugua-I, CA 1 KM W. Park Headquarters Ruta Prov. 19, Latitude 25 51 S Longitude 054 10 W	JN810270	JN810406	JN810670	JN810026
Tachyphonus cristatus	LSUMZ B9548	Bolivia: Pando, Nicholas Suarez, 12 km by road S of Cojiba, 8 km W on road to Mucden	JN810271	JN810407	JN810671	JN810027
Tachyphonus delatrii	LSUMZ B11710	Ecuador: Esmeraldas, El Placer	JN810272	JN810408	JN810672	JN810028
Tachyphonus luctuosus	LSUMZ B2279	Panama: Darien, Cana on E slope Cerro Pirre	JN810273	None	None	None
Tachyphonus rufiventer	LSUMZ B3629	Peru: Loreto, S bank Rio Maranon, along Rio Samiria, Est. Biol. Pithecia, Base Tacsha Cocha	JN810274	JN810409	JN810673	JN810029

(*continued on next page*)

Table 2 (*continued*)

Species	Voucher/Sample Number[1]	Locality	FGB-I5	MB-I2	Rag 1	ACO1-I9
Tachyphonus surinamus	LSUMZ B4795	Peru: Loreto, S Rio Amazonas, ca. 10 km SSW Rio Napo	JN810275	JN810410	JN810674	JN810030
Tangara cayana	LSUMZ B15414	Bolivia: Santa Cruz, Serrania De Huanchaca, 45 km E Florida	JN810276	JN810411	JN810675	JN810031
Tangara cyanocephala	FMNH 427278	Brazil: Pernambuco, Taquaritinga	JN810277	JN810412	JN810676	JN810032
Tangara gyrola	LSUMZ B22850	Bolivia: La Paz, B. Saavedra, 83 km by road E Charazani, Cerro Asunta Pata	JN810278	None	None	None
Tangara preciosa	CUMV 50646	Uruguay: Cerro Largo, Rio Yaguaron	JN810279	JN810413	JN810677	JN810033
Tangara punctata	LSUMZ B34931	Ecuador: Napo, ca. 40 Km NNE Tena	JN810280	JN810414	JN810678	JN810034
Tangara vassorii	LSUMZ B1711	Peru: Pasco, Santa Cruz, about 9 km SSE Oxapampa	None	JN810415	JN810679	JN810035
Tangara rufigula	LSUMZ B11930	Ecuador: Esmeraldas, El Placer	JN810281	None	None	None
Tersina viridis	LSUMZ B9680	Bolivia: Pando, Nicholas Suarez, 12 km by road S of Cojiba, 8 km W on road to Mucden	JN810282	JN810416	JN810680	JN810036
Thlypopsis ornata	LSUMZ B8075	Peru: Pasco, Playa Pampa, 8 km NW Cushi on trail to Chaglla	JN810283	JN810417	JN810681	JN810037
Thlypopsis sordida	LSUMZ B7260	Peru: Loreto, Amazonas I. Pasto 80 km NE Iquitos 80 m	JN810284	JN810418	JN810682	JN810038
Thraupis bonariensis	FMNH 433891	Peru: Cuzco, Paucartambo, La Esperanza, 39 km (road) NE Paucartambo	JN810285	JN810419	JN810683	JN810039
Thraupis cyanocephala	FMNH 433897	Peru: Cuzco, Paucartambo, La Esperanza, 39 km (road) NE Paucartambo, 2850 m	JN810286	JN810420	JN810684	JN810040
Thraupis palmarum	FMNH 427254	Brazil: Alagoas, Ibateouara, Envenho Ceimba, Usina Serra Grande	JN810287	JN810421	JN810685	JN810041
Tiaris bicolor	MVZ 179402	captive bird	HQ153066	HQ153073	HQ153088	HQ153054
Tiaris olivaceus	AMNH 25429	Dominican Republic: Independencia, Parque Nacional Sierra de Baoruco, El Aceitillar, Alcoa Rd.	HQ153067	HQ153074	HQ153089	HQ153055
Trichothraupis melanops	UWBM 70274	Argentina: Prov. Misiones; Posadas, 45 km N, 80 km E	JN810288	JN810422	JN810686	JN810042
Urothraupis stolzmanni	ZMUC 120310	Ecuador: Tungurahua, C Llanganates	JN810289	JN810423	None	JN810043
Volatinia jacarina	FMNH 392749	Brazil, Alagoas, Piranhas, Fazenda Mecejana	JN810290	JN810424	JN810687	JN810044
Xenodacnis parina	LSUMZ B7760	Ecuador: Azuay, 1 km W CJS Nacional de Recreacion, near MGR	JN810291	JN810425	JN810688	JN810045
Xenospingus concolor	LSUMZ B5263	Peru: Dept. Ica; 0.5 km E km 235 Pan-American Hwy	JN810292	JN810426	JN810689	JN810046
Outgroup species						
Pheucticus tibialis	LSUMZ B16050	Costa Rica: Heredia Province	JN810293	JN810427	JN810690	JN810047
Passerina ciris	LSUMZ B5694	USA: Louisiana, Cameron Parish	JN810294	JN810428	JN810691	JN810048
Piranga ludoviciana	SDSU 2383	USA: California, San Diego Co., Laguna Mts.	JN810295	JN810429	JN810692	JN810049
Cardinalis cardinalis	BMNH X7320	USA: Minnesota	JN810296	JN810430	JN810693	JN810050

[a] Museum abbreviations: AMNH, American Museum of Natural History; ANSP, Academy of Natural Sciences, Philadelphia; BMNH, University of Minnesota, Bell Museum of Natural History; CUMV, Cornell University Museum of Vertebrates; FMNH, Field Museum of Natural History; KU, University of Kansas Natural History Museum; LSUMZ, Louisiana State University Museum of Natural Science Collection of Genetic Resources; MACN, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"; MBM, University of Nevada Las Vegas, Barrick Museum of Natural History; MVZ, Museum of Vertebrate Zoology, University of California, Berkeley; SDSU, San Diego State University Museum of Biodiversity; USNM, National Museum of Natural History (Smithsonian Institution); UWBM, University of Washington, Burke Museum; ZMUC, Zoological Museum, University of Copenhagen.

and most are also strongly supported by both. In addition, all but one of these subfamilies have significant support (⩾0.95 PP) in the species-tree analyses of Barker et al. (2013). Only two species (*Catamblyrhynchus diadema* and *Charitospiza eucosma*) did not cluster into one of these clades. Because of the distinctiveness of these two lineages, we place each into subfamilies as well. Although we identified these 15 major groups, we did not find strong support for relationships among them (Figs. 1–6).

Thraupidae now represents species that traditionally have belonged to four different avian families or subfamilies outside of Thraupidae (Paynter and Storer, 1970; Figs. 2–6): Catamblyrhynchinae (the Plushcap), Emberizinae (New World sparrows), Parulidae (New World warblers), and Cardinalinae (cardinal-grosbeaks). In most cases, these representatives of other groups do not cluster in a single place on our phylogenies. For example, the Emberizidae species that Sibley and Monroe (1990) transferred to the tanagers can be found in 10 of our 15 subfamilies (Figs. 2–6). Within Thraupidae, many traditional genera are not monophyletic in our phylogenies. Clements et al. (2013) currently recognizes 92 genera of tanagers. Of these, 43 are monotypic, indicating the historical difficulty in classifying tanagers. Of the remaining 49 genera, 17 are not monophyletic in our phylogenies (Figs. 2–6). These include well-known genera such as *Tangara*, *Sporophila*, and *Thraupis*. In fact, only three traditional genera that include more than six species are monophyletic in our phylogenies. In some cases (e.g., *Saltator*, *Diuca*, *Phrygilus*), species in a genus are found in multiple subfamilies of tanagers indicating that major revision at the genus level is warranted for the group.

Our genetic data revealed seven groups of species that are only weakly differentiated from their close relatives compared to other species of tanagers. These include (1) *Geospiza*, (2) *Camarhynchus*, (3) some species of *Sporophila*, (4) members of the *Diglossa carbonaria* superspecies complex (*D. carbonaria*, *D. brunneiventris*, *D. humeralis*, and *D. gloriosa*), (5) *Nesospiza*, (6) *Idiopsar brachyurus*/*Diuca speculifera*, and (7) *Tangara phillipsi*/*T. argyrofenges*/*T. heinei*. Some of these have been previously identified (e.g., Campagna et al., 2012; Mauck and Burns, 2009; Ryan et al., 2007; Sato et al., 1999), but others are shown for the first time as having little genetic divergence. All represent cases of plumage or morphological divergence accompanied by little genetic change, and some are identified as having an exceptional rate of speciation in our diversification analyses.

3.3. Diversification analyses

For the entire clade (Thraupidae), we found that the DDX model had the best fit (Table 3). We were not able to fit the DDL + E due to computational limitations given the large number of species. The lineage-through-time plot showed a clear departure from the straight line expected under a constant-rate diversification scenario (Fig. 1). The gamma statistic and associated *p*-value (Table 3) indicate a significant slowdown in species accumulation through time. For seven of the ten tanager subfamilies tested, we found the best fit model to be a diversity-dependent model, although the specific model varied (Table 3). For the remaining three subfamilies, one (Hemithraupinae) had

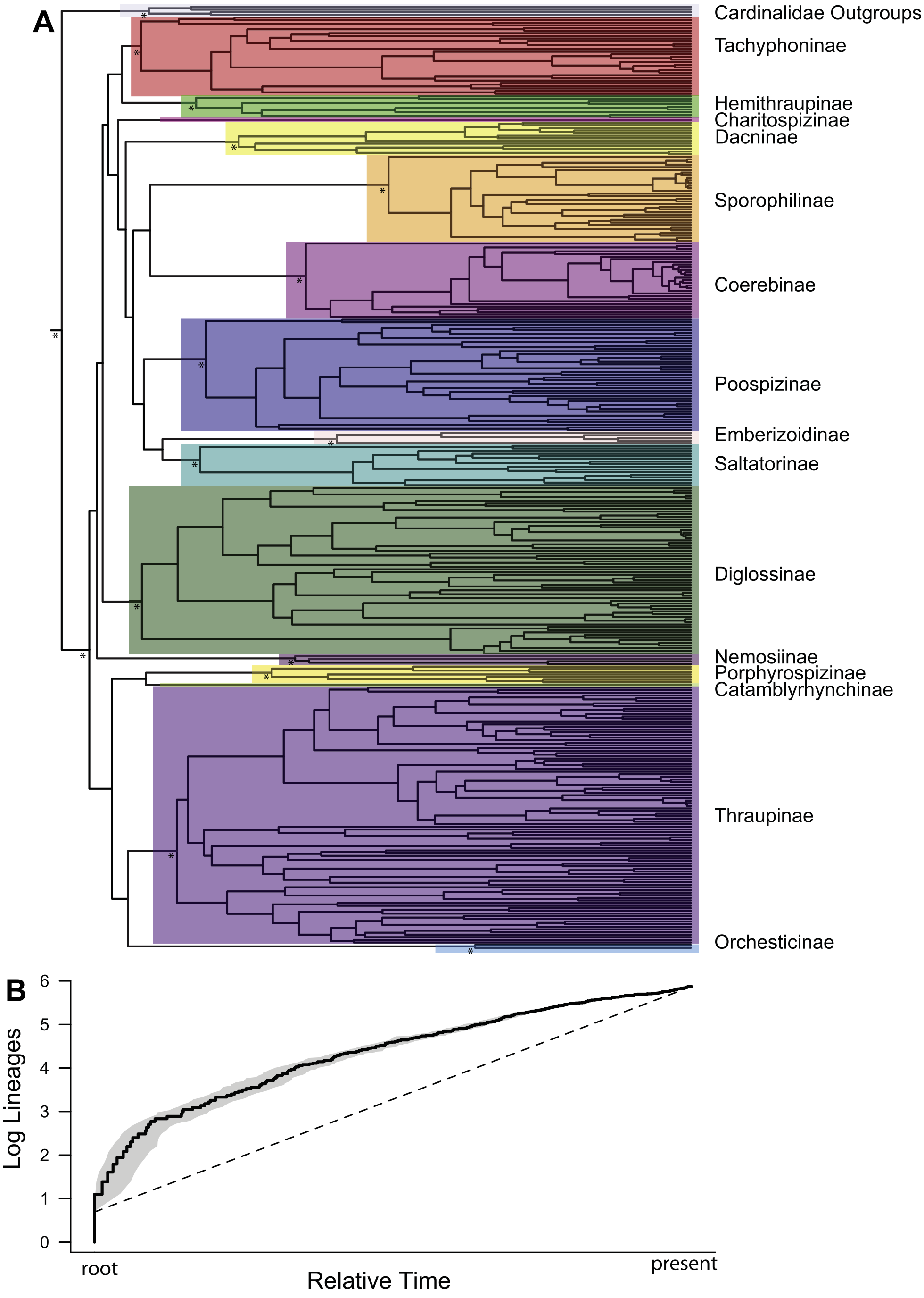

Fig. 1. (A) The maximum clade credibility tree derived from the posterior of the BEAST analysis. Colored boxes highlight subfamilies, with names provided on the right. Nodes at the subfamily level or older with PP ⩾ 0.95 and/or a bootstrap value ⩾70 from the RAxML analysis are designated by an asterisk. (B) A lineage through time plot for the species in Thraupidae. The dashed line is the expectation for constant-rate diversification. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

no difference in fit between the PB, DDL-E and DDX models (Table 3). Sporophilinae and Coerebinae best fit constant-rate models (Table 3). Gamma statistic results largely corroborated the model-fitting results; diversity-dependent model subfamilies have a significantly negative gamma statistic (Table 3), and constant-rate model subfamilies have non-significant, positive gamma statistics (Table 3). The exceptions are Hemithraupinae and Porphyrospizinae, with non-significant, negative gamma statistics, likely due to the small numbers of species in each clade and low statistical power.

We found strong support for multiple diversification rate shifts across the tanager phylogeny (Fig. 7). Although the diversification shift location was not always found on the same branch, we detected a rate shift along one of the branches leading up to the Darwin's Finch radiation in 92% of the post-burn-in posterior distribution of the BAMM results. In the entire post-burn-in posterior distribution, another shift occurred within Sporophilinae. Overall, three processes were found to most likely govern diversification in the tanagers: a background model of exponentially declining speciation rates for the entire tanager phylogeny, with

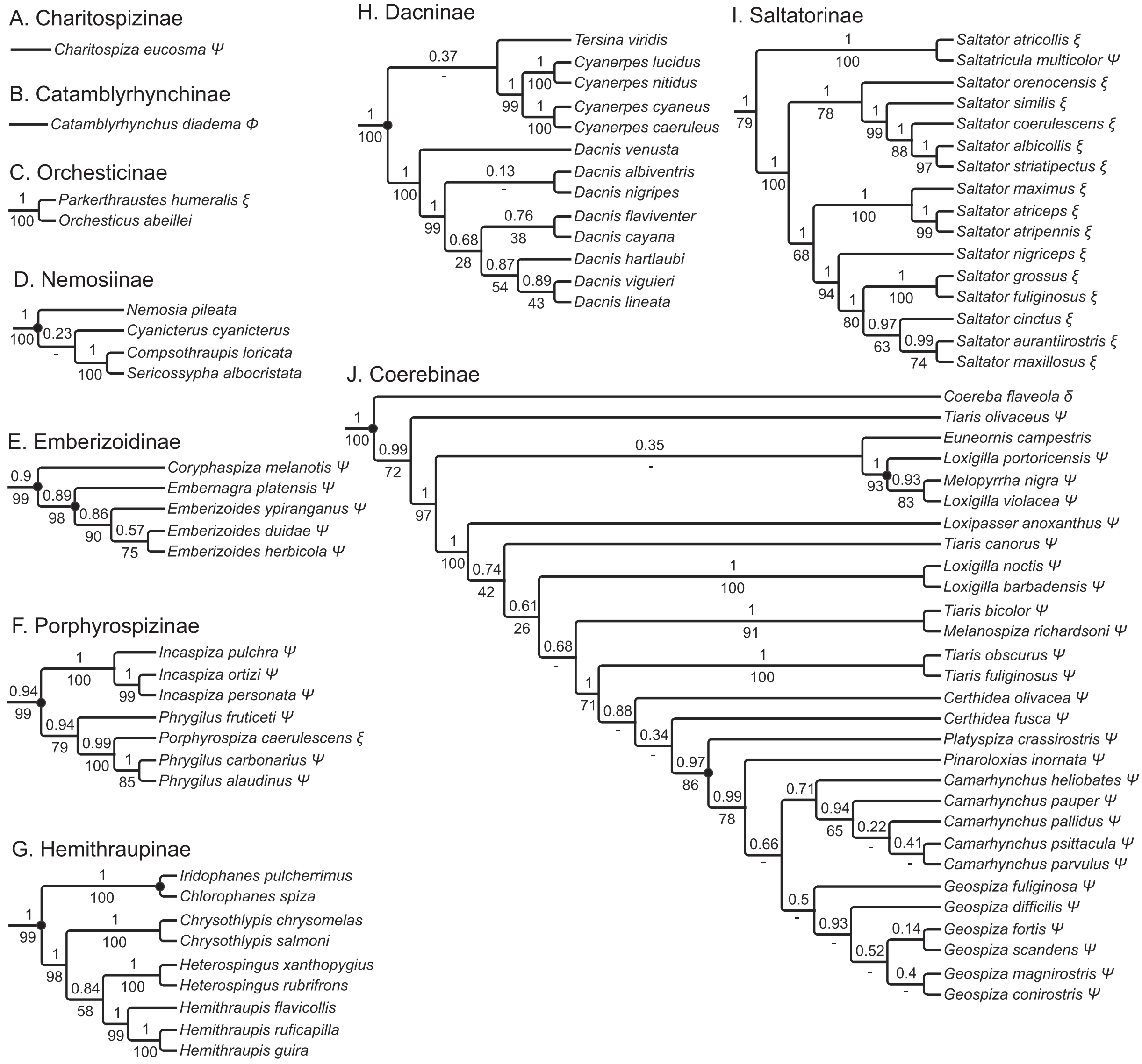

Fig. 2. Results of the concatenated analysis of six genes. The tree structure is derived from the maximum clade credibility tree with arbitrary branch lengths. For each node, the posterior probability from the BEAST analysis is given above the branch leading to that node, and the maximum likelihood value from the RAxML analysis is given below the branch. Nodes that were not present in the most likely RAxML tree are indicated by "–". Closed circles on nodes indicate significant support (PP ⩾ 0.95) estimated in the species tree analysis of Barker et al. (2013); none of the species tree nodes of Barker et al. (2013) conflict with our topology. Taxa previously placed in different families or subfamilies outside of Thraupidae by Paynter and Storer (1970) are indicated by a Greek letter following that species' name as follows: Catamblyrhynchinae, *Φ*; Emberizinae, *Ψ*; Parulidae, *δ*; and Cardinalinae, *ξ*. Species without symbols were placed in Thraupinae by Paynter and Storer (1970). The phylogeny is separated by subfamily, and species within each subfamily are ladderized: (A) Charitospizinae, (B) Catamblyrhynchinae, (C) Orchesticinae, (D) Nemosiinae, (E) Emberizoidinae, (F) Porphyrospizinae, (G) Hemithraupinae, (H) Dacninae, (I) Saltatorinae, (J) Coerebinae.

shifts to a new model of declining speciation rates within Sporophilinae and a model of near constant rate for Darwin's Finches. The initial rate of speciation found for both radiations is over three times the initial speciation rate of the background tanager process of exponential decline in speciation rates.

4. Discussion

4.1. Tanagers as a model for studying character evolution

The lack of a monophyletic Thraupidae has hindered the study of character evolution and diversification in the group. Thus, despite the fact that tanagers encompass a major portion of overall songbird diversity, tanagers are less well known than other better characterized, but smaller, groups of birds such as hummingbirds (335 species) and parrots (345 species). Here, we provide a robust, species-level of phylogeny of tanagers that allows for the study of character evolution in the group. Previous attempts at tanager phylogenies (e.g., Bleiweiss, 2008; Burns, 1997; Fjeldså and Rahbek, 2006; Jetz et al., 2012; Sibley and Ahlquist, 1990; Weir et al., 2009) were missing key taxa, relied on sparse taxon sampling, or assumed genus-level monophyly. Our trees have numerous topological differences when compared to these earlier phylogenies. Therefore, other studies that relied on these earlier phylogenies to make interpretations about biogeography, evolution, behavior, or ecology should be reassessed in light of the new topologies presented here. Now that a monophyletic Thraupidae has been defined and a robust phylogeny provided, analyses of character evolution and biogeography can be pursued. In particular, tanagers appear to be a model system to study convergence. Different bill

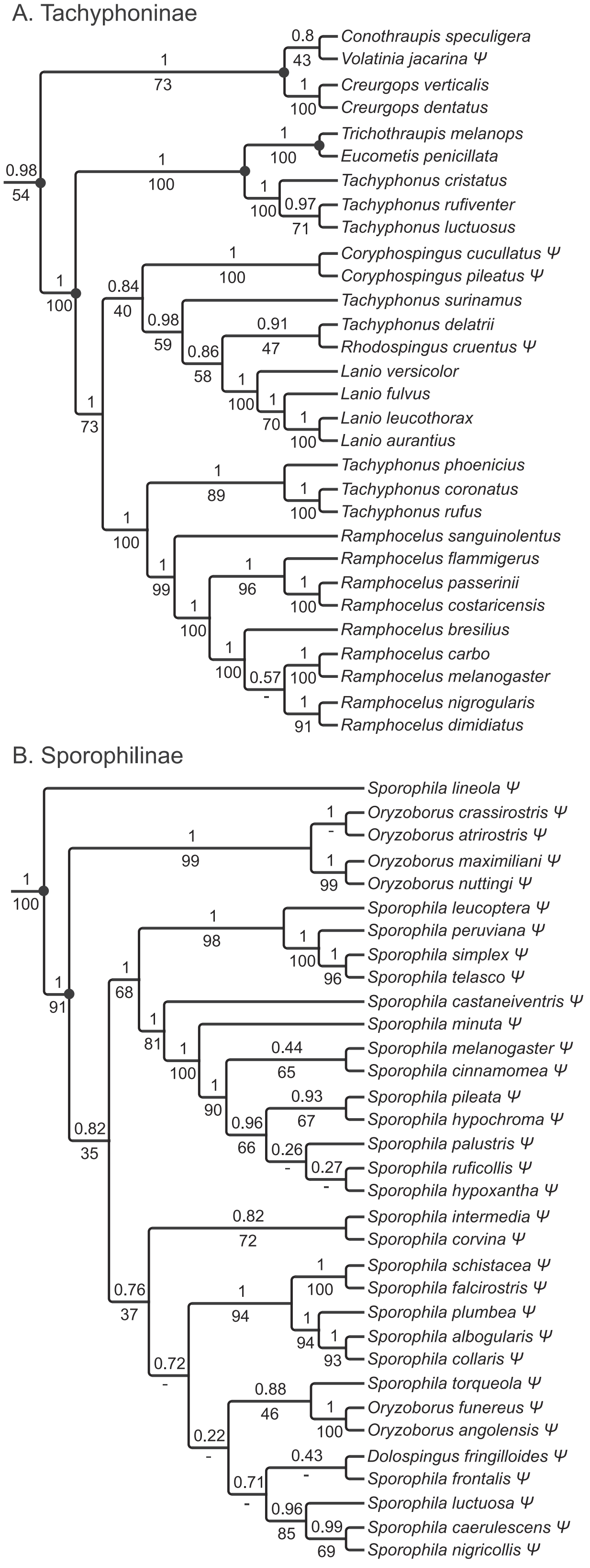

Fig. 3. Results of the concatenated analysis of the six genes for the subfamilies (A) Tachyphoninae and (B) Sporophilinae. Labeling and format as in Fig. 2.

types, foraging strategies, and ecomorphs have evolved repeatedly across the phylogeny. For example, the seed-eating finch-billed species that were previously classified in Emberizidae are spread across our phylogeny, indicating convergence of bill types across the group. In addition, nectar-feeding tanagers (Burns et al., 2003) occur in multiple places across the phylogeny. These and other specific examples are presented below in our discussion of tanager subfamilies (Section 4.3), and more rigorous comparative analyses are ongoing (e.g., Shultz and Burns, 2013).

4.2. Diversification of tanagers

The different approaches that we employed all generally led to the same finding that tanagers underwent an initial rapid burst in diversification, followed by a subsequent slowdown. This corroborates the results of Barker et al. (2013), who showed that Thraupidae exhibited a rate of diversification that was almost 40% higher than the average rate for the 9-primaried oscine clade, to which tanagers belong. Though Phillimore and Price (2008) showed that a negative gamma statistic could result from large clades operating under constant-rate diversification, due to stochasticity in the timing of speciation events, the gamma statistic for tanagers is more negative than any gamma generated in their simulations, lending confidence to a truly diversity-dependent pattern of diversification in tanagers. This pattern is largely paralleled across subfamilies within tanagers, as shown by the best-fitting models and significantly negative gamma statistics (Table 3).

Two subfamilies, however, show increased diversification rates over the background rate. Coerebinae, which includes the Darwin's finches, exhibits an increased rate of diversification with an overall signature of constant-rate diversification. This clade may exhibit a different pattern of diversification from the others due to both extrinsic and intrinsic factors (Rabosky, 2010). One the one hand, increased speciation rates may have been promoted by geographic isolation and ecological release across the Galapagos Islands. On the other, this lineage may exhibit intrinsic evolvability (Burns et al., 2002; Mallarino et al., 2012). Sporophilinae also exhibits a different signature of diversification, with a best-fit constant-rate model when comparing discrete models, and an increase in diversification rate compared to the tanager background rate in the BAMM analysis. Overall, the speciation rate appears to be declining in Sporophilinae. This could be because Sporophilinae is older than the Darwin's finch radiation, and thus may have reached a stage of ecological limits to diversification, whereas the Darwin's finches have not.

Darwin's finches are a classic example of adaptive radiation, and evolution within species in the group is well characterized (Grant, 1999; Grant and Grant, 2008). However, few studies have provided the comparative perspective needed to interpret the phylogenetic context of this adaptive radiation (Burns et al., 2002; Mallarino et al., 2012). In this study, we have quantified the diversification rate of Darwin's Finches in the context of diversification of their closest relatives for the first time. We find that their rate of diversification is exceptional, even when compared to the overall rapid rate of diversification found within tanagers. In addition, we find that the rate of diversification of some seedeaters in *Sporophila* is comparable to that of Darwin's finches. Both lineages are composed of primarily finch-billed forms. Price (2011) suggested that finch-billed lineages might be more prone to higher rates of diversification than other avian ecotypes. Although many other clades of tanagers contain finch-billed species, our finding that the two clades with the highest rates of diversification contain finch-billed forms is consistent with Price's (2011) hypothesis.

With the inclusion of diversification mixture models, we now have much greater ability to investigate the diversification history of large clades. The BAMM approach brings two improvements to existing methods: freedom from designating groups *a priori*, and the ability to treat a large phylogeny as a multi-process phenomenon (Rabosky et al., 2013; Rabosky and Matute, 2013; Rabosky,

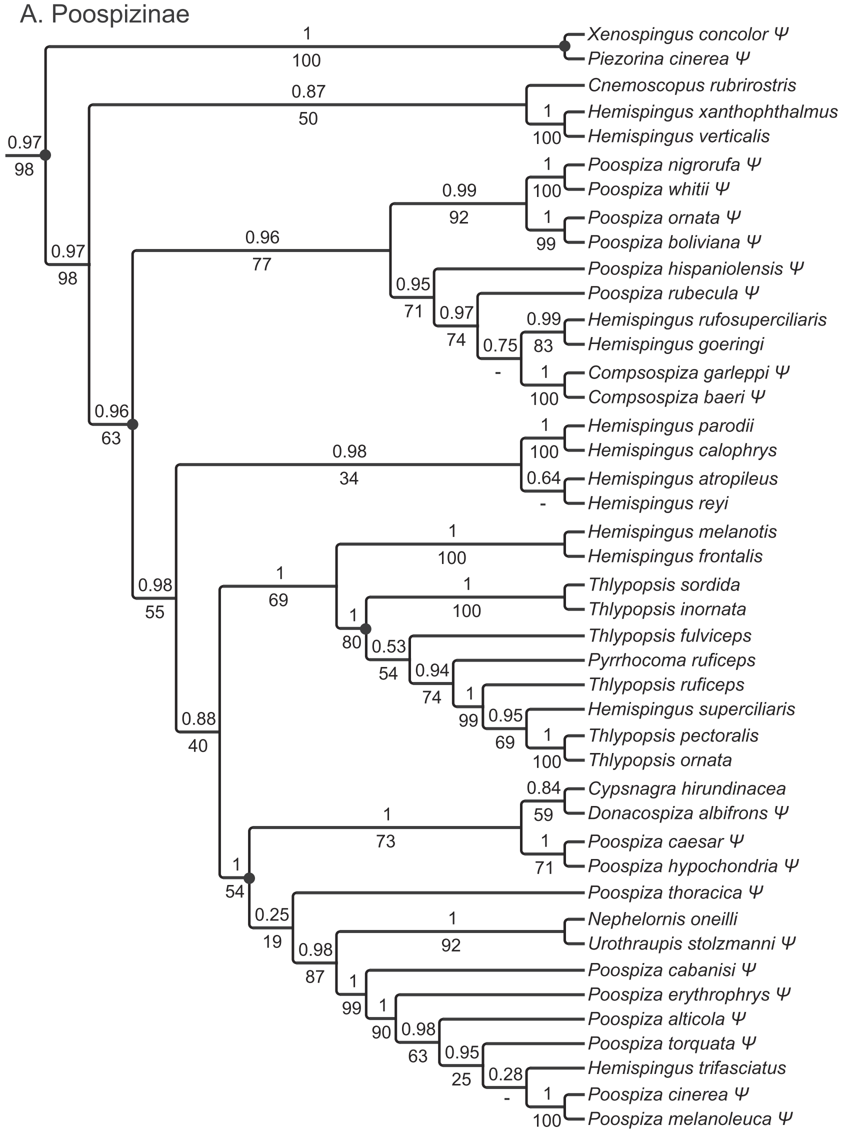

Fig. 4. Results of the concatenated analysis of the six genes for the subfamily Poospizinae. Labeling and format as in Fig. 2.

2014). The similarities between the results of our subfamily model-fitting and BAMM analyses are an excellent example of the first point; Sporophilinae was found to operate under a different diversification process by both approaches. With respect to Coerebinae, model-fit comparison found constant-rate diversification to fit best, but BAMM showed that it is actually a subclade within Coerebinae that is undergoing a different diversification process. The ability to detect different processes within a larger phylogeny was already possible with constant-rate diversification (Alfaro et al., 2009), but BAMM allows for the inclusion of time-varying speciation rates (Rabosky and Matute, 2013; Rabosky, 2014).

4.3. Phylogenetic conclusions and taxonomic recommendations

In this section, we indicate how our phylogenies compare to previous studies of tanager relationships and highlight places where our phylogenies shed light on the evolution of specific characters. Because of the large size of the tanager family, we organize the discussion of these conclusions around a proposed subfamily classification of tanagers. Such a classification is warranted in order to reasonably manage the large size of the group. These subfamilies were identified based on the oldest, strongly supported nodes in our phylogenies (Fig. 1). For each subfamily, we assign the family-group name that was used first for any species in the clade. When no previous name is available, a new name is proposed and a description provided (Appendix A). In one case (Poospizinae), a name was previously used (Wolters, 1975–1982), but a description was not provided. Thus, we provide a description here. Because the relationships among them are unknown, we generally present these subfamilies in order from least to most speciose. Relatively few avian groups have been sampled as comprehensively as the tanagers, and our study revealed the lack of concordance between currently used genus names and phylogeny. Thus, we predict that major generic revisions will be required in other avian groups when they are sampled at the species level. Although a new genus-level classification of tanagers is necessary, proposing new generic names is beyond the scope of this paper but is forthcoming. However, where possible, we propose the use of existing generic names that can reconcile classification with the topologies found in our study.

4.3.1. Catamblyrhynchinae, Ridgway 1901, the Plushcap

This subfamily contains a single species, the Plushcap (*Catamblyrhynchus diadema*), named for its unusual dense, velvety patch

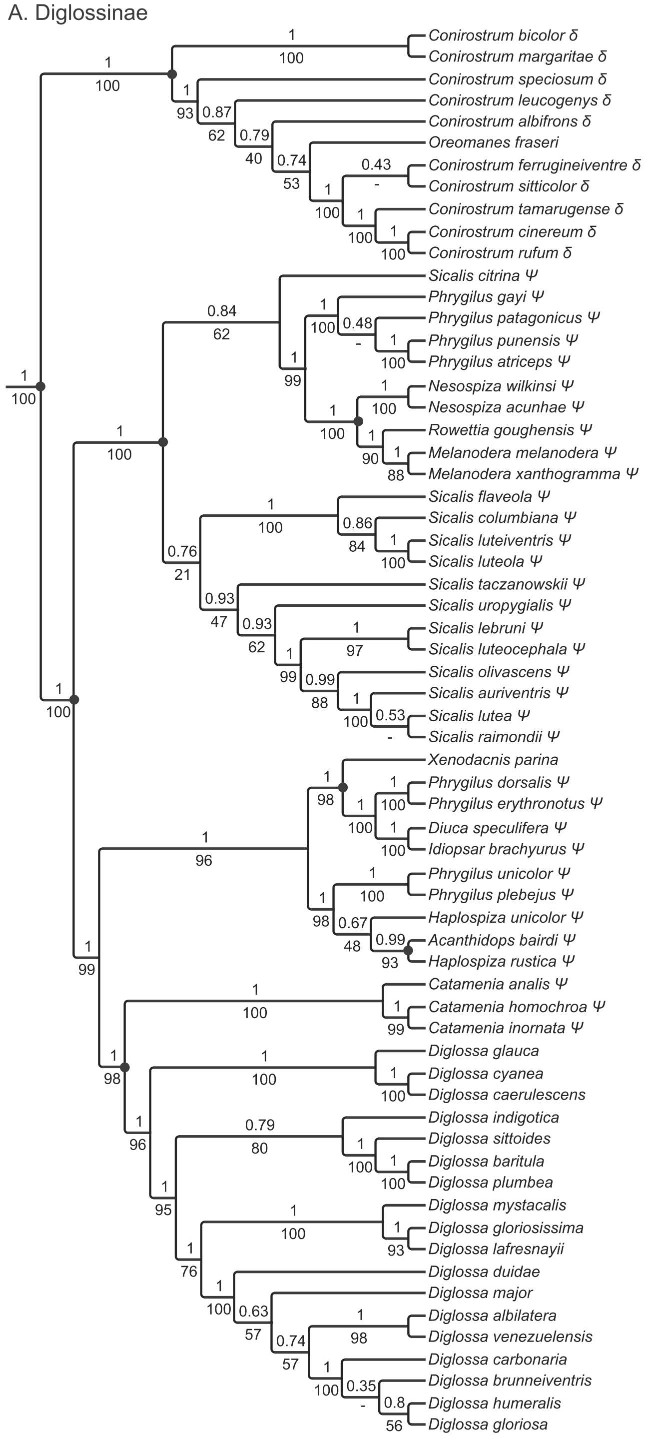

Fig. 5. Results of the concatenated analysis of the six genes for the subfamily Diglossinae. Labeling and format as in Fig. 2.

of bright yellow feathers on its forecrown. Hilty et al. (1979) speculated that these short, dense feathers are less susceptible to feather wear and more resistant to moisture than typical feathers. This may be an adaptation for its specialized feeding mode, in which it uses its thick, stubby bill to probe into dense whorls of *Chusquea* bamboo for its prey items (Hilty et al., 1979). This bill shape is convergent with other bamboo-feeding species in the Old World *Paradoxornis* (Olson, 1986). Because of its unique morphology and behavior, the taxonomic position of the Plushcap has eluded systematists for decades. Sharpe (1888) included it as one of many genera in his large family Fringillidae, which contained other New World sparrows and finches, grosbeaks, buntings, and true finches. Subsequently, Ridgway (1901a) elevated the species to its own family, Catamblyrhynchidae. Later authors continued to consider the Plushcap to represent a monotypic family (e.g., Hellmayr, 1938; Meyer de Schauensee, 1966) or subfamily (Catamblyrhynchinae; e.g., Paynter and Storer, 1970; Ridgely and Tudor, 1989). More recent taxonomies have classified the Plushcap as a species of tanager (e.g., Sibley and Monroe, 1990; Clements et al., 2013), partly based on DNA hybridization studies that show it to be allied to the tanagers (Bledsoe, 1988). The placement of the Plushcap within the tanagers was also indicated by mtDNA sequence data (Yuri and Mindell, 2002) and multi-locus DNA data (Barker et al., 2013). In the present study, we confirm that the Plushcap is a tanager and is distinct from all other tanagers. Although the species was found to be sister to Porphyrospizinae in our BEAST and ML trees (Fig. 1), support was so low (0.74 PP; 26% bootstrap) that this branch should not be treated with any special significance. Furthermore, none of the individual gene trees agree in their placement of *Catamblyrhynchus*, and none provide strong support for a relationship between *Catamblyrhynchus* and other tanager species (Supplementary Figs. 1–6). Thus, *C. diadema* is best thought of as a distinct tanager lineage, and we therefore place it in its own subfamily.

4.3.2. *Charitospizinae, new subfamily; the Coal-crested Finch*

Similar to the Plushcap, our analyses also identified the Coal-crested Finch (*Charitospiza eucosma*) as a distinct lineage with no closely allied extant relatives. This species is endemic to the grasslands of Brazil, has an unusual bimodal breeding season (Diniz et al., 2013), and appears to be a fire-following specialist (Cavalcanti and Alves, 1997; Jaramillo, 2011a). Its plumage colors and patterns are not like those of other tanagers, and both sexes possess a crest, a relatively rare feature in tanagers. Unlike the Plushcap, the Coal-crested Finch has not been previously recognized as distinct above the genus level. Early taxonomies (e.g., Sharpe, 1888) classified it in the same genus as other finches, with Oberholser (1905) being the first to place this species in its own genus. Miller (1928) indicated that *Charitospiza* might be closely related to *Lophospingus* based on similarities in their crests; however, he still argued that other features justified treating *Charitospiza* as generically distinct. Subsequent taxonomies continued to recognize this species as belonging to its own genus (e.g., Clements et al., 2013; Dickinson, 2003; Hellmayr, 1938; Paynter and Storer, 1970; Sibley and Monroe, 1990) but generally considered it to be more closely allied to finches than tanagers. Barker et al.'s (2013) genus-level study showed that this species is a tanager, and our phylogenies confirm this finding. In addition, we show that the Coal-crested Finch is distinct from all other tanagers, and is not closely related to any one species or group of tanager. In particular, there is no evidence for a close relationship between *Lophospingus* and *Charitospiza* as originally suggested by Miller (1928). Thus, the crests of these two species must have evolved convergently. Although our BEAST and ML trees show *Charitospiza* as the sister taxon to a large clade of other tanagers (Fig. 1), the support for this relationship is relatively low (0.85 PP; 23% bootstrap). Furthermore, none of the individual gene trees showed significant support for the placement of *Charitospiza* (Supplementary Figs. 1–6); therefore, we place *C. eucosma* in its own subfamily. This species is likely a relatively old lineage that is as evolutionarily distinct as some larger tanager clades with dozens of species. The Coal-crested Finch is listed as near-threatened due to habitat loss and trapping for the caged-bird trade (Birdlife International, 2013a). Given the importance of preserving evolutionarily distinct taxa, our finding that *Charitospiza* represents an old, distinct lineage argues for prioritizing its conservation.

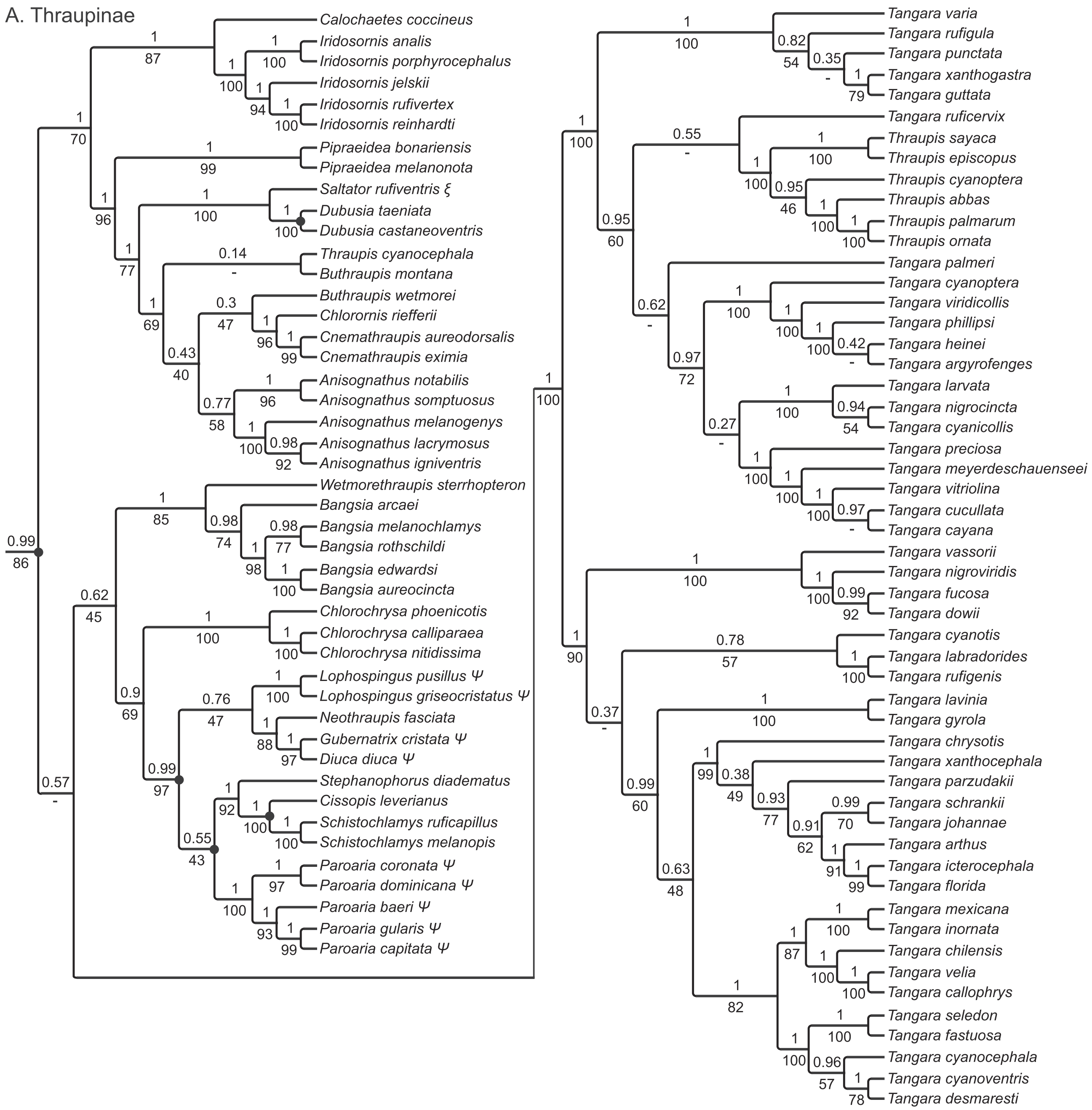

Fig. 6. Results of the concatenated analysis of the six genes for the subfamily Thraupinae. Labeling and format as in Fig. 2.

4.3.3. Orchesticinae, new subfamily; the Grosbeak Tanagers

This subfamily consists of just two species each in its own genus, the Yellow-shouldered Grosbeak (*Parkerthraustes humeralis*) and the Brown Tanager (*Orchesticus abeillei*). Due to the comparatively thick bills of these species, we refer to them as the grosbeak tanagers. Taxonomists have puzzled over the evolutionary affinities of each of these species, and thus they were placed in monotypic genera. *P. humeralis* was originally described as closely related to some species of saltators, and has subsequently been considered closely related to either saltators (e.g., Chapman, 1926) or cardinal-grosbeaks in *Caryothraustes* (e.g., Hellmayr, 1938; Paynter and Storer, 1970; Ridgway, 1901a; Sibley and Monroe, 1990). However, an allozyme study by Demastes and Remsen (1994) showed that it is not closely related to either saltators or grosbeaks; therefore, Remsen (1997) removed the species from *Caryothraustes* and proposed *Parkerthraustes* as a new genus. This recommendation was followed in subsequent taxonomic treatments (Dickinson, 2003; Clements et al., 2013). Klicka et al. (2007) analyzed cyt *b* and ND2 sequences of a variety of tanagers and cardinal-grosbeaks and showed that *Parkerthraustes* belonged with tanagers, not cardinal-grosbeaks. However, Klicka et al. (2007) were not able to identify the closest relative of *Parkerthraustes* within the tanagers. In agreement with Barker et al. (2013), our data show that *Parkerthraustes* forms a strongly supported (1.0 PP; 100% bootstrap) clade with the Brown Tanager, *O. abeillei* (Figs. 1 and 2c). This species is endemic to southeastern Brazil and shares little with *Parkerthraustes* in terms of plumage coloration and pattern. However, the Brown Tanager occurs in close association with *Philydor rufum* (the Buff-fronted Foliage-gleaner), and several studies have provided evidence that the Brown Tanager is a social mimic of this species (Beauchamp and Goodale, 2011; Sazima, 2010; Willis, 1976, 1989). *Philydor rufum* and *O. abeillei* are remarkably

Table 3
Results of diversification analyses for all tanagers, and individual subfamilies with at least nine species. Species richness, the number of missing species in the phylogeny, ΔAICc scores, and gamma statistics for each clade are given. For model selection, the scores from the best-fit models, or models within a value of two are bolded. For the gamma statistic, all significant ($P < 0.05$) tests are bolded.

Clade	Species Richness	# Missing Species	Diversification Model Comparisons (ΔAICc)					Gamma Statistic	
			PB	*BD*	*DDL-E*	*DDX*	*DDL+E*	*Gamma*	*MCCR p-value*
Thraupidae (All Tanagers)	371	16	47.24	52.24	22.97	**0**	N/A	**−5.611**	**0.001**
Subfamily									
Thraupinae	102	4	39.02	41.11	14.73	15.23	**0.00**	**−4.845**	**0.001**
Diglossinae	64	0	4.21	6.35	**1.95**	**0.00**	180.90	**−1.850**	**0.029**
Poospizinae	44	1	7.72	9.93	**0.00**	2.08	307.80	**−2.839**	**0.003**
Sporophilinae	38	5	**0.00**	**1.26**	2.28	2.28	405.67	0.783	0.831
Tachyphoninae	31	1	4.31	6.62	2.24	**0.00**	368.66	**−1.740**	**0.043**
Coerebinae	29	0	**0.00**	**0.05**	2.33	2.20	407.61	1.222	0.897
Saltatorinae	16	0	4.34	7.03	**0.00**	4.61	462.95	**−2.092**	**0.025**
Dacninae	14	1	2.66	5.59	**0.00**	2.14	478.95	**−1.782**	**0.040**
Hemithraupinae	9	0	**0.00**	3.73	**1.96**	**1.16**	502.37	−0.646	0.272
Porphyrospizinae	9	2	2.57	7.57	**0.00**	4.56	524.41	−1.560	0.072

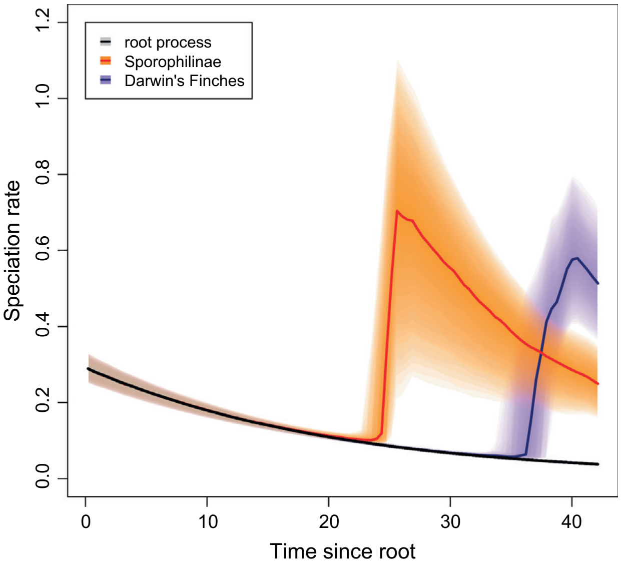

Fig. 7. Diversification models for tanagers. The three diversification processes that describe tanager diversification are plotted separately. The root process is described by a model that governs the entire phylogeny, excluding the Sporophilinae and Coerebinae radiations. For these radiations, the model describing the root process was used to define the speciation rate until the transition to a new diversification model. Results were averaged from 1000 samples from the BAMM posterior distribution of results. The shaded regions represent 25–75% confidence intervals.

similar in plumage; both have overall cinnamon brown plumage, rufous wings, a dark eye line, and a midcrown and nape that are darker than the rest of the head, among other similarities. The two species flock together, with *P. rufum* more common than *O. abeillei*; thus, Willis (1989) hypothesized that *O. abeillei* evolved similar plumage as a means of predator avoidance. The close evolutionary relationship of *Orchesticus* to the differently plumaged *Parkerthraustes* supports this social mimicry hypothesis. Although different in plumage coloration, *Parkerthraustes* and *Orchesticus* are generally similar in overall size, form, bill size, and bill shape. Strong selection acting on plumage color in *Orchesticus* could have masked the shared evolutionary history of *Parkerthraustes* and *Orchesticus*.

4.3.4. Nemosiinae, Bonaparte, 1854; the Flock-dwelling Tanagers

This small subfamily consists of only five species divided among four genera: three are monotypic (*Cyanicterus*, *Sericossypha*, *Compsothraupis*) and one (*Nemosia*) has two species. We sampled all but one (*N. rourei*) of these five species. Species in this group are some of the most spectacular of all tanagers, and these species have some of the most sexually dichromatic plumages (Burns and Shultz, 2012). The group is made up of seemingly disparate taxa whose relationships have puzzled ornithologists for decades. The lack of understanding of their relationships is reflected in the proportion of monotypic genera in the group; however, there are some common plumage themes. Three species (*Sericossypha albocristata*, *Compsothraupis loricata*, and *N. rourei*) have red throats, four species (*S. albocristata*, *Cyanicterus cyanicterus*, *N. rourei*, and *N. pileata*) have bluish plumage, and *S. albocristata* and some individuals of *N. rourei* have white crowns. In addition, most of the species often occur in single-species flocks (Isler and Isler, 1999; Venturini et al., 2005). Prior to molecular studies, a close relationship among all these species was not expected. Burns (1997) and Burns et al. (2003) included *N. pileata and S. albocristata* in phylogenetic analyses of cyt *b* data for tanagers and recovered them as a clade, but support was not strong. Barker et al.'s (2013) genus-level phylogeny found strong support for the monophyly of this group, and our concatenated analyses (Figs. 1 and 2d) also recovered a strongly-supported Nemosiinae (1.0 PP; 100% bootstrap). Most of our individual gene analyses also recovered this clade, with RAG1, cyt *b*, and FGB-I5 all supporting it strongly (Supplementary Figs. 1–6).

S. albocristata and *C. loricata*, have been consistently placed next to each other in most classifications, with some authors (e.g., Meyer de Schauensee, 1966, 1970; Sick, 1993; Zimmer, 1947) considering them congeneric. These two species are among the largest tanagers, and both are more often found in flocks than in pairs. Otherwise, their appearance, behaviors, and geographic distributions are quite different; *S. albocristata* is an Andean species, whereas *C. loricata* is found in the Caatinga of northeastern Brazil. Thus, most authorities (e.g., Clements et al., 2013; Hellmayr, 1936; Sibley and Monroe, 1990) consider the differences between them significant enough to warrant generic separation. In addition, although they have been consistently placed within the tanagers, many authors have noted suspicions that one or both species might belong elsewhere. In particular, the resemblance between *S. albocristata* and the cotingas (e.g., Hellmayr, 1936; Sclater, 1886), and similarities between *C. loricata* and the blackbirds, have been frequently noted (e.g., Gwynne et al., 2010; Ridgely and Tudor, 1989; Zimmer, 1947). Suspicions regarding a connection between *S. albocristata* and the cotingas were largely put to rest by Morony's (1985) study of skeletal anatomy. He established the placement of *S. albocristata* within the nine-primaried oscines, and later molecular studies (Burns, 1997; Burns et al., 2003) cemented its position within Thraupidae. However, the phylogenetic position of *C. loricata* has remained enigmatic. We were able to sequence cyt *b* from a toe pad of this species and our results show a strongly supported sister relationship between *C. loricata* and *S. albocristata*. Thus, despite some authors' expectation that any similarities between the two taxa might be the result of convergence (e.g., Storer, 1970), and suspicions that *C. loricata* might be a blackbird, our study shows that they are closely related tanagers.

Although the relationship between *S. albocristata* and *C. loricata* is well supported (1.0 PP; 100% bootstrap), relationships among the other species in this subfamily are unclear from our analyses (Fig. 2d, Supplementary Figs. 1–6). Other than Barker et al. (2013), no previous study has addressed relationships of *Cyanicterus cyanicterus* using molecular data. This unusual tanager from northern South America is mostly blue and yellow and has a relatively thick, slightly curved bill. Early classifications (Hellmayr, 1935; Sclater, 1886) placed this species near *Piranga*, which is now known to belong to Cardinalidae (Klicka et al., 2007). Later, Storer (1970) moved it to a position adjacent to *Buthraupis* due to similarities in color, pattern, and plumage texture. Subsequent classifications (e.g., Sibley and Monroe, 1990) followed this arrangement. Our molecular data place *C. cyanicterus* firmly in Nemosiinae; however, understanding the relationship of *Cyanicterus* within Nemosiinae will require additional data.

The remaining genus in this subfamily, *Nemosia*, consists of two species: *N. pileata* and the recently rediscovered *N. rourei*. The phylogenetic relationship of *Nemosia* to other tanagers has been unclear. Previous classifications have considered species in present-day *Nemosia* to be closely related to *Hemithraupis*, *Pyrrhocoma*, and *Chrysothlypis* (Hellmayr, 1936; Sclater, 1886; Sibley and Monroe, 1990; Storer, 1970), with some classifications (e.g., Sclater, 1886) considering *Hemithraupis* and *Nemosia* congeneric. However, our phylogenies show that species in these genera are all part of other subfamilies and not closely related to *Nemosia*. We were able to include one *Nemosia* species (*N. pileata*) in our analyses and we confirmed earlier findings based on cyt *b* and partial taxon sampling (Barker et al., 2013; Burns, 1997; Burns et al., 2003) that *Nemosia* is part of Nemosiinae. Although our ML analyses recovered a strongly supported (100% bootstrap) sister relationship between *Nemosia* and the clade containing *Compsothraupis* and *Sericossypha*, this relationship was not recovered in BEAST analyses and was not consistently recovered in single gene analyses (Fig. 2d, Supplementary Figs. 1–6). Thus, with the exception of the sister relationship between *Compsothraupis* and *Sericossypha*, relationships of other species within Nemosiinae remain unclear.

We were unable to include samples of the extremely rare and recently re-discovered *N. rourei* (Bauer et al., 2000; Scott, 1997). However, this species shares similarities with other species in Nemosiinae that lead us to conclude that it belongs in this clade as well. Eye color, plumage colors, and plumage patterns are similar between *N. rourei* and *N. pileata*. Also, *S. cristata*, *C. loricata*, and *N. rourei* have red throats, and the crowns of some individuals of *N. rourei* are white like those of *S. cristata* (as illustrated in Venturini et al., 2005). Venturini et al. (2005) also note apparent similarities in courtship between *N. pileata* and *N. rourei*. Overall, pending further analyses, we recommend retaining *N. rourei* in *Nemosia*.

4.3.5. Hemithraupinae, Sundevall, 1872; the Yellow-and-black Tanagers

This subfamily consists of nine species of mostly slender-billed tanagers placed in five different genera. We sampled all nine species, and our phylogeny is consistent with current genus-level classifications. With the exception of the two species of *Heterospingus*, species in this subfamily have some of the thinnest bills in relation to bill length of all tanagers. In addition, species in this subfamily are some of the most sexually dichromatic of all tanagers (Burns and Shultz, 2012). Yellow and black are predominant plumage colors in the group, although males of *Chrysothlypis salmoni* are bright red, and males of *Chlorophanes spiza* are mostly blue. In addition, most species (those in *Chlorophanes*, *Iridophanes*, and *Hemithraupis*) have dark upper mandibles and yellow lower mandibles. The node uniting Hemithraupinae was strongly supported in our concatenated analyses (Fig. 2g; 1.0 PP; 99% bootstrap), and this clade was also recovered in the genus-level study of Barker et al. (2013). The clade was recovered, though not strongly supported, in earlier analyses that included only cyt *b* and partial taxon sampling (Burns et al., 2003). Previous workers had not suspected a close relationship among all the species in this clade, but some had predicted a close relationship between some of the genera.

Iridophanes pulcherrimus and *Chlorophanes spiza* were previously classified in a family of nectar-feeding honeycreepers (Hellmayr, 1935; Sclater, 1886) that subsequently was shown to be polyphyletic (Burns et al., 2003). These two species form a clade that is sister to the other members of this subfamily. This clade has strong support in our concatenated analyses (1.0 PP: 100% bootstrap), is strongly supported in all but one of our gene trees, and was also supported in the genus-level analyses of Barker et al. (2013). Ridgway (1901b) erected *Iridophanes*, and considered it closely related to other species in our new subfamily such as *Chrysothlypis chrysomelas* and species in *Hemithraupis* (Ridgway, 1902). Among other earlier workers, only Hellmayr (1935) indicated that *Chlorophanes* and *Iridophanes* were likely closely related. He noted similarities in the bill structure (enlarged basal portion of the lower bill) and bill color (yellowish margin of the cutting edge of the lower bill) of both species. Subsequent to Hellmayr (1935), the remarkable similarity in plumage pattern between *Iridophanes* and *Tangara cyanoptera* led Storer (1970) to merge *Iridophanes* into *Tangara*. However, others (e.g., Ridgely and Tudor, 1989) were not comfortable with this merger, noting differences in eye color, bill shape, and bill color; these are characters that *Iridophanes* shares with *Chlorophanes*. After the study of Burns et al. (2003), *Chlorophanes* and *Iridophanes* were typically considered closely related (e.g., Clements et al., 2013; Dickinson, 2003), with Hilty (2011) suggesting the merger of both species into *Chlorophanes*. We suggest keeping the two species in separate genera, mainly to promote taxonomic stability. In addition, our data indicate that each species has been evolving separately for a relatively long period of time (Supplementary Figs. 1–6).

For the remaining three genera in this subfamily (*Heterospingus*, *Hemithraupis*, and *Chrysothlypis*), a close relationship among some of the species was implied in the classifications of earlier workers. Ridgway (1902) classified species from all three genera near each other, Sclater (1886) classified species of *Heterospingus* and *Chrysothlypis* adjacently, and other classifications (Hellmayr, 1936; Sibley and Monroe, 1990) placed *Hemithraupis* and *Chrysothlypis* together. Our phylogenies find strong support (1.0 PP; 98% bootstrap) for a monophyletic group containing all the species in these genera. Our concatenated trees show that *Hemithraupis* is more closely related to *Heterospingus* than it is to *Chrysothlypis*; however, this node was not strongly supported (0.84 PP; 58% bootstrap). Ridgely and Tudor (1989, 2009) suggest that *Hemithraupis* and *Chrysothlypis* could be merged into a single genus. However, merging them into a genus without *Heterospingus* is not supported by our topologies.

Chrysothlypis contains two species, *C. salmoni* and *C. chrysomelas*. Females of these species have similar plumage and are mostly yellow, like other species in this subfamily. However, males of the two species are quite different: *C. salmoni* males are bright red with white bellies, whereas *C. chrysomelas* males are yellow and black. Thus, early classifications separated the two species, with *C. chrysomelas* often placed in the monotypic *Erythrothlypis* (e.g., Hellmayr, 1936). Storer (1970) was the first to merge these two species into the same genus, and subsequent workers have largely followed this placement. More recently, several authors (Hilty, 2011; Ridgely and Greenfield, 2001; Ridgely and Tudor, 2009) have returned to using *Erythrothlypis* for *C. chrysomelas*. Our results show that the two species are not highly divergent (mtDNA uncorrected sequence divergence = 5.6%). In addition, despite radically different male plumages, the two species are similar in female plumage and overall size and shape. Therefore, we advocate the continued use of *Chrysothlypis* for both of these species.

Within *Hemithraupis*, *H. guira* and *H. ruficapilla* are regarded as a superspecies (Sibley and Monroe, 1990) and are known to hybridize in southeastern Brazil (Hilty, 2011; Ridgely and Tudor, 1989). We report the first genetic data for *H. ruficapilla* and show that the two species are more closely related to each other than they are to *H. flavicollis*. Levels of genetic divergence between *H. guira* and *H. ruficapilla* are relatively low (cyt *b* uncorrected difference = 1.2%), but consistent with species-level status for these two taxa. *Heterospingus rubrifrons* and *H. xanthopygius* are also regarded as a superspecies (Sibley and Monroe, 1990), with some classifications considering them conspecific (Storer, 1970; Isler and Isler, 1999). We found that the two species are sister taxa and well differentiated genetically. Uncorrected cyt *b* sequence difference between the two individuals is 2.8% and ND2 pairwise difference is 5.6%; these values are consistent with many other well-differentiated species of tanagers.

4.3.6. Porphyrospizinae, new subfamily; the Yellow-billed Tanagers

This clade consists of nine species; most of these are in genera traditionally considered part of Emberizidae (*Incaspiza*, 5 species; *Phrygilus*, 3 species), and one (*Porphyrospiza*, 1 species) was traditionally placed in Cardinalidae (Fig. 2f). Before Barker et al. (2013), no study had suggested a close relationship among all these species; however, species in this group share some plumage, behavioral, and morphological characters, including yellow-colored bills. Our concatenated phylogeny supports their monophyly (0.94 PP; 99% bootstrap), and three of our gene trees also provide strong support (cyt *b*, ND2, and RAG1).

Within this subfamily, *Incaspiza* consists of five Peruvian endemics that prefer arid scrub habitats. We sampled three of the species and found strong support for their monophyly (1.0 PP; 100% bootstrap). Species status of these has been questioned in previous taxonomies. Both Hellmayr (1938) and Paynter and Storer (1970) considered *I. pulchra* and *I. personata* as conspecific. When Zimmer (1952) described *I. ortizi*, he indicated the possibility that *I. ortizi* and *I. pulchra* might be conspecific, although he argued that there was more evidence that they were separate species. Later, Paynter and Storer (1970) also suggested that *I. ortizi* might also be conspecific with *I. pulchra* and *I. personata*. Sibley and Monroe (1990) treated the three forms as separate species of the same superspecies. Our data support species status for each. Despite similarities in plumage, the three are genetically very distinct, with uncorrected cyt *b* divergence ranging from 7.5% to 9.6%, well above typical values observed within avian species. Ridgely and Tudor (1989) place *I. pulchra*, *I. personata*, and *I. ortizi* in the same group, which they named group A, and the other two species (*I. laeta* and *I. watkinsi*) in a separate group B. Because we were unable to sample members of group B, we cannot confirm the monophyly of these two groups. We found strong support (1.0 PP; 99% bootstrap) for a closer relationship between *I. ortizi* and *I. personata* than between either of these and *I. pulchra*. The additional species within *Incaspiza* need to be sampled before further conclusions can be made about evolution within this group, but we have no reason to suspect that the two species missing from our data set belong outside *Incaspiza*.

Incaspiza is sister to a clade containing the monotypic *Porphyrospiza* and three of the 11 species of *Phrygilus* (*P. alaudinus*, *P. carbonaria*, and *P. fruticeti*). *Phrygilus* is one of the most polytypic tanager genera (Campagna et al., 2011). Although three species belong in Porphyrospizinae, the remaining eight species belong to three distinct clades in the Diglossinae (Section 4.3.14). *Porphyrospiza* was considered a cardinal-grosbeak by Hellmayr (1938); however, based on skull osteology, Tordoff (1954) argued that this species was more closely allied to sparrows that we now consider tanagers. However, Paynter and Storer (1970) disagreed with Tordoff (1954) and continued to place *Porphyrospiza* with the cardinal-grosbeaks, a position followed by many authors (e.g., Sibley and Monroe, 1990). Furthermore, citing plumage similarities between *Porphyrospiza* and *Passerina* buntings (e.g., Allen, 1891), Paynter and Storer (1970) merged *Porphyrospiza* with *Passerina*, a genus of cardinal-grosbeaks. Other authors have argued that these similarities are superficial (Bates et al., 1992; Ridgely and Tudor, 1989), and thus other taxonomies (e.g., Clements et al., 2013; Dickinson, 2003) have removed them from the cardinal-grosbeaks. DNA evidence (Barker et al., 2013; Klicka et al., 2007) clearly shows that *Porphyrospiza* belongs with the tanagers. Our study found that *Porphyrospiza* is embedded within a clade of the three yellow-billed sierra finches (*Phrygilus alaudinus*, *P. carbonaria*, and *P. fruticeti*). These four species have yellow bills and similar, streaked females. Based on morphology, other authors have indicated a close relationship of these three *Phrygilus* (e.g., Fjeldså, 1992; Ridgely and Tudor, 1989). Using molecular data, Klicka et al. (2007) showed a close relationship between *Porphyrospiza* and *P. alaudinus*, Barker et al. (2013) showed a close relationship between *Porphyrospiza* and *P. fruticeti*, and Campagna et al. (2011) found a monophyletic clade containing the three *Phrygilus*. Here, by sampling all species, we found that the three yellow-billed *Phrygilus* are not monophyletic. Instead, our concatenated tree had strong support (0.99 PP; 100% bootstrap) for a clade containing *Porphyrospiza* and two of these *Phrygilus* (*P. alaudinus* and *P. carbonarius*), with *P. fruticeti* as the sister taxon to the clade containing these three species. Because *Phrygilus* is polyphyletic, and the type species of *Phrygilus* (*P. gayi*) belongs in Diglossinae, a new generic taxonomy for these species is necessary. For *P. fruticeti*, we recommend using the available name *Rhopospina* Cabanis 1851 (type = *P. fruticeti*). For *P. alaudinus* and *P. carbonarius*, the name *Corydospiza* Sundevall 1872 (type = *P. alaudinus*) is available.

4.3.7. Dacninae, Sundevall, 1836; the Blue Tanagers

This relatively small clade contains 14 species in three monophyletic genera, *Cyanerpes*, *Dacnis*, and *Tersina*. Of all the subfamilies, Dacninae is the most sexually dichromatic (Burns and Shultz, 2012), with species characterized by a theme of bright blue males and green females. In addition, species in this subfamily have some of the most ultraviolet-reflecting plumage of all tanagers (Burns and Shultz, 2012). Plumage colors of these species are similar not only from a human visual perspective, but also in the shape of their reflectance curves (Barreira et al., 2008; Burns and Shultz, 2012). In contrast to these plumage similarities, species in this clade have dramatic differences in bill shapes and foraging behavior. The Swallow-Tanager, the only species in *Tersina*, has many unique behavioral and morphological characters including a flattened bill that is broad at its base (Isler and Isler, 1999; Lucas, 1895; Schaefer, 1953; Webster, 1988). These characteristics have led the Swallow-Tanager to be described in classifications as a monotypic family (Hellmayr, 1936; Meyer de Schauensee, 1970; Wetmore, 1960), subfamily (Sclater, 1886; Storer, 1970), or tribe (American Ornithologists' Union, 1983). However, subsequent DNA data have confirmed the placement of *Tersina* well within the tanagers (Sibley and Ahlquist, 1990), and more specifically, closely related to species in *Dacnis* and *Cyanerpes* (Burns et al., 2003). Although species in all three genera will feed on fruit and insects, differences in diet are reflected by differences in bill shape. The Swallow-Tanager often sallies from exposed perches, using its unique bill to capture flying insects (Hilty, 2011; Isler and Isler, 1999; Restall et al., 2006). Unlike the Swallow-Tanager, species in *Dacnis* and *Cyanerpes* include nectar in their diet. Species in *Cyanerpes* are nectarivorous (Ridgely and Tudor, 2009), and have narrow, long, decurved bills. Many species of *Dacnis* also feed on nectar (Hilty, 2011). Like species in *Cyanerpes*, the bills of *Dacnis* are also narrow; however, they are overall shorter and more pointed, and the behavior of some species of *Dacnis* is more warbler-like (Restall et al., 2006; Ridgely and Tudor, 2009). This diversity of bill types, which evolved over a relatively short amount of time, highlights one of the major themes of tanager phylogeny: the lability of bill morphology and foraging behavior. The monophyly of this subfamily is strongly supported by our concatenated analyses (1.0 PP; 100% bootstrap) and the topologies of three individual gene trees (Cyt *b*, ND2, and RAG1) (Figs. 1 and 2h; Supplementary Figs. 1–6).

Our phylogenies also clearly identify that each of these three genera is monophyletic; therefore, no changes to the genus-level taxonomy are necessary. However, we did not find strong support for the placement of the three genera with respect to each other. Species-level relationships within *Cyanerpes* and *Dacnis* have not been addressed by previous studies using molecular data. Within *Cyanerpes*, we found two strongly supported clades, one with *C. caeruleus* and *C. cyaneus* and the other with *C. nitidus* and *C. lucidus* (Fig. 2h). This relationship contrasts with the idea that *C. lucidus* and *C. caeruleus* form a superspecies (Sibley and Monroe, 1990) or that they are conspecific (Hellmayr, 1935). Within *Dacnis*, the only strongly supported nodes identify a sister relationships between *D. venusta* and the remaining species. *D. hartlaubi* was originally described by Sclater (1854) as a member of *Dacnis*, but it was subsequently thought to be more similar to species in *Tangara*. Unsure of its relationships, Sclater (1886) placed it in its own monotypic genus, *Pseudodacnis*, which was subsequently used by many authors (e.g., Hellmayr, 1936; Meyer de Schauensee, 1966, 1970). Although Storer (1970) merged *Pseudodacnis* with *Dacnis* based on similar coloration and pattern, not all classifications have followed this recommendation (e.g., Sibley and Monroe, 1990). The results of our study show that this species is embedded well within *Dacnis*, with strong support; therefore, the use of *Pseudodacnis* is no longer warranted. We were not able to sample one species of *Dacnis*, *D. berlepschi*. This species is quite different from other species in the genus, and we regard its placement as uncertain. Superficially its plumage resembles that of *Xenodacnis parina*, which we place in Diglossinae (Section 4.3.14). Storer (1970) also doubted whether *D. berlepschi* was closely related to other species of *Dacnis*, and Wolters (1975–1982) also considered *X. parina* and *D. berlepschi* closely related, placing both within the genus *Xenodacnis*.

4.3.8. Saltatorinae, Bonaparte, 1853; the Saltators

We found a strongly supported clade (1.0 PP; 79% bootstrap) that contained 15 of the 16 species of *Saltator* as well as the sole member of *Saltatricula* (*S. multicolor*) (Figs. 1 and 2i). Saltators have relatively long tails, well developed hindlimbs, and some of the thickest bills of all tanagers. The only species in *Saltator* not found in this clade is *S. rufiventris*, which belongs in Thraupinae (Section 4.3.15). Unlike many subfamilies of tanagers, all nodes within Saltatorinae were strongly supported in either BEAST, ML or both analyses (Fig. 2i). Saltators have long been considered part of Cardinalidae (cardinal-grosbeaks) and, although some workers (e.g., Sushkin, 1924) have suggested they are tanagers, recent classifications have continued to place the saltators with the cardinal-grosbeaks (e.g., Dickinson, 2003; Orenstein, 2011; Sibley and Monroe, 1990). Despite this practice, recent molecular analyses (Barker et al., 2013; Klicka et al., 2007) show they belong with tanagers. Although Klicka et al. (2007) suggested that saltators might represent the sister taxon to the remaining tanagers, more complete character sampling and outgroup sampling (Barker et al., 2013), as well as more complete ingroup sampling (the present study), do not support this hypothesis. Instead, saltators are embedded within tanagers, sister to a clade containing the South American grassland finches and relatives (Emberizoidinae, Section 4.3.9; Fig. 1). Hellack and Schnell (1977) analyzed relationships among saltators using skeletal, external morphological, and color characters, but the species-level relationships of our phylogeny bear little resemblance to those of Hellack and Schnell (1977). In particular, Hellack and Schnell (1977) suggested that *S. aurantiirostris*, *S. atricollis*, and *S. orenocensis* may not belong with the rest of the saltators; however, all three fall within the saltator clade, and none are more closely related to each other than to other saltators. More recently, Klicka et al. (2007) included 11 species of saltators and sampled cyt *b* and ND2. In our study, we included the remaining species and added nuclear genes. Our results agree with those of Klicka et al. (2007), with all the strongly supported nodes of Klicka et al. (2007) recovered in our phylogeny. Klicka et al. (2007) showed that the saltator clade also includes *Saltatricula multicolor*, the Many-colored Chaco Finch. This enigmatic taxon is usually classified in Emberizidae; however, other recent molecular phylogenies had also indicated that it is closely related to tanagers (e.g., Burns et al., 2003). Our results agree with these studies and show that it belongs with saltators and is sister to *Saltator atricollis*. Thus, we recommend merging *Saltatricula* with *Saltator*. Of all the species of *Saltator*, *Saltatricula* is most alike *Saltator atricollis* in plumage. The two species also share a preference for dry habitats and are both restricted to the Central South America zoogeographic region (Parker et al., 1996), with *Saltatricula multicolor* occurring in the dry scrub of the Chaco, and *Saltator atricollis* in the Caatinga and Cerrado scrub (Brewer, 2011; Jaramillo, 2011b; Parker et al., 1996). Both Hellack and Schnell (1977) and Ridgely and Tudor (2009) suggested that *Saltator atricollis* was atypical among saltators. The relationship of this species to *Saltatricula* and the sister relationship of the *Saltatricula*/*Saltator atricollis* clade to other saltators agrees with this assessment. *Saltator grossus* and *S. fuliginosus* were previously considered members of their own genus *Pitylus* (e.g., Ridgely and Tudor, 1989) on the basis of similar morphology and sexual dichromatism. In addition, the two have sometimes been considered members of the same species (Paynter and Storer, 1970) or part of a superspecies (Sibley and Monroe, 1990). Our data show a level of divergence expected between two species, and that the two species form a clade embedded within saltators. Thus, the two species are closely related, but the use of *Pitylus* is not warranted. Additional sets of saltator species have been grouped into subspecies or considered conspecific, and our data set provides genetic evidence to address these hypotheses. *S. similis* and *S. coerulescens* were thought to form a superspecies (Short, 1975; Sibley and Monroe, 1990), but are not sister taxa. Likewise, a superspecies composed of *S. nigriceps*, *S. maxillosus*, and *S. aurantiirostris* (Short, 1975; Sibley and Monroe, 1990) is not supported by our results. *S. nigriceps* and *S. aurantiirostris* were considered conspecific by Hellmayr (1938) and Paynter and Storer (1970), but are only distantly related in our phylogenies. The Lesser Antillean *S. albicollis* was long considered conspecific with continental *S. striatipectus* (Hellmayr, 1938; Paynter and Storer, 1970; Sibley and Monroe, 1990). Both species share similar, streaked plumage. Seutin et al. (1993) showed that populations of these two forms were well-differentiated by mtDNA restriction site variation. In our study, we confirm this finding using sequence data, further justifying their treatment as separate species.

Chaves et al. (2013) produced the most comprehensive molecular phylogeny of saltators to date. Compared to our study, Chaves et al. (2013) had more individuals per species sampled, but fewer genetic markers. The phylogenies of Chaves et al. (2013) are based on ND2 sequences from multiple individuals, as well as some additional cyt *b* sequences from some species. In contrast, our study had mtDNA and nuclear DNA data from most species (Table 1), but we only sampled one individual per species. In general, the findings of the two studies are similar. For example, both studies identified the clade of *Saltatricula multicolor* and *S. atricollis* as sister to the rest of the saltators, and our study recovered the same three main clades (clades A, B, and C) of Chaves et al. (2013). However, Chaves et al. (2013) did not recover a sister taxon relationship between the two streaked saltators (*S. albicollis* and *S. striatipectus*). Instead, they found a sister taxon relationship between *S. albicollis* and *S. similis* and comparatively little genetic divergence between them. Additional study is needed to clarify the relationships among these species.

4.3.9. Emberizoidinae, new subfamily, the Grassland Tanagers

Some of our analyses support a sister relationship between Saltatorinae and Emberizoidinae, a clade containing six species classified into three different genera (*Embernagra*, *Emberizoides*, and *Coryphaspiza*). The Saltatorinae/Emberizoidinae clade is found in both our ML and Bayesian concatenated analyses; however, support was not particularly high (0.89 PP; 69% bootstrap). This clade was also recovered, but with weak support, in our ACO1-I9 and ND2 ML trees (Supplementary Figs. 1–6). Further study with additional data is needed to clarify whether the species in these two subfamilies are more closely related to each other than they are to other tanagers. Nevertheless, similar plumage colors and patterns of the two groups would support their close relationship.

Unlike saltators, which are mostly arboreal, the birds in Emberizoidinae are terrestrial, grassland dwelling birds. All six species were traditionally classified with the New World sparrows, but Sibley and Monroe (1990) considered them tanagers. The monophyly of Emberizoidinae is strongly supported by genus-level analyses (Barker et al., 2013), concatenated analyses (0.90 PP; 99% bootstrap; Figs. 1 and 2i), and separate ML analyses of individual genes (5 genes with greater than 70% support; Supplementary Figs. 1–6). Although the monophyly of this group is strongly supported, prior to Barker et al. (2013) no previous study has considered these species to form a unique clade. The Black-masked Finch (*Coryphaspiza melanotis*), the sole member of its genus, was originally described as a member of *Emberizoides*. The species was later placed in *Coryphaspiza*, and Gray (1870) considered *Coryphaspiza* a subgenus of *Emberizoides*. Sharpe (1888) came close to recognizing the unique relationship of the species in the grassland clade. He placed *Embernagra*, *Coryphaspiza*, and *Emberizoides* in order next to each other in his linear classification; however, he considered *Donacospiza albifrons* a member of *Coryphaspiza*. Later, Hellmayr (1938) considered *D. albifrons* a modified form of *Poospiza*, a result confirmed in our study (see Poospizinae, Section 4.3.13). Although he placed *Coryphaspiza* and *Emberizoides* adjacent to each other in his classification, he placed *Embernagra* elsewhere. In contrast, Paynter and Storer (1970) placed *Embernagra* and *Emberizoides* adjacent to each other, but put *Coryphaspiza* in another part of their classification, together with several other species they considered of uncertain placement. Subsequent classifications have mostly treated the species similarly, with *Coryphaspiza* and *Embernagra*/*Emberizoides* placed apart from each other (e.g., Clements et al., 2013; Dickinson, 2003; Sibley and Monroe, 1990). However, Wolters (1975–1982) placed the three genera together in his linear classification, and Jaramillo (2011c) suggested that aspects of juvenile and adult plumage, tail shape, and song suggest that *Coryphaspiza* may be related to *Embernagra* and *Emberizoides*. Klicka et al. (2007) reported the first phylogeny that contained more than one of these genera and confirmed the close relationships of *Emberizoides* and *Embernagra*. The genus-level DNA study of Barker et al. (2013) identified that *Coryphaspiza* also belongs in this group. With greater character and species sampling, we confirm the monophyly of this novel clade of grassland birds. The identification of all these species as closely related should facilitate the future study of diversification in the South American grasslands. Our data can also address some of the taxonomic issues surrounding species limits in the group. The three species of *Emberizoides* were treated as conspecific for many years (Hellmayr, 1938, Paynter and Storer, 1970). However, Eisenmann and Short (1982) argued that *E. ypiranganus* and *E. duidae* are distinct from *E. herbicola*, and subsequent classifications have followed this recommendation (Clements et al., 2013; Sibley and Monroe, 1990). In addition, Sibley and Monroe (1990) treated *E. herbicola* and *E. duidae* as members of the same superspecies. We include all three species in our phylogeny and show levels of divergence consistent with separate species. We are missing one species of *Embernagra*, *E. longicauda*; however, we feel that this species shows enough similarities to the other *Embernagra* to retain it within this genus.

4.3.10. Coerebinae, d'Orbigny and Lafresnaye, 1838; the Dome-nesting Tanagers

This subfamily includes 29 species in 12 genera, all of which build covered or domed nests with side entrances (Burns et al., 2002). This is an unusual nest construction among birds, and within the tanagers it has only been described among species in this clade and two species of Thraupinae (Freeman and Arango, 2010). In our concatenated analyses, the node uniting Coerebinae is strongly supported (Figs. 1 and 2j; 1.0 PP; 100% bootstrap). In addition, this node is supported in genus-level analyses (Barker et al., 2013), strongly supported in our ACO1-I9, cyt *b*, ND2, and RAG1 gene trees, and also supported, although not strongly, by our MB-I2 gene tree (Supplementary Figs. 1–6). Burns et al. (2002) suggested informally using the name Tholospiza (meaning dome finch) for this group, given their dome-shaped nests. Here, we suggest using Coerebinae to designate the subfamily, given that Coerebinae is the oldest family-group name used for any species in this group. Unfortunately, this name has previously been used to describe a clade of nectar-feeding birds that are now known to be paraphyletic (Burns et al., 2003), and the name is still used in some classifications to refer to a monotypic group containing only the Bananaquit (*Coereba flaveola*). Our subfamily Coerebinae only includes two species (*Euneornis campestris* and *C. flaveola*) that were part of this traditional grouping of Neotropical honeycreepers.

Species in Coerebinae show a variety of bill forms, including nectar-feeders (e.g., *Coereba*, *Euneornis*), seed-eaters (e.g., *Geospiza*, *Loxigilla*, *Tiaris*), and insect foragers (e.g., *Certhidea*). Included within this clade are the Darwin's Finches, a classic example of speciation and adaptive radiation (e.g., Grant, 1999; Grant and Grant, 2008; Lack, 1947). Coerebinae also includes nine species endemic to islands in the Caribbean (*E. campestris*, *Loxigilla portoricensis*, *L. violacea*, *L. noctis*, *L. barbadensis*, *Melopyrrha nigra*, *Loxipasser anoxanthus*, *Tiaris canorus*, and *Melanospiza richardsoni*) and three species in which a large part of the distribution is Caribbean (*C. flaveola*, *T. olivaceus*, *T. bicolor*). The other two non-Darwin's Finch species in Coerebinae (*T. fuliginosa* and *T. obscurus*) are restricted to South America. The number of Caribbean endemics within Coerebinae is unexpected, given the geographic distribution of other tanagers. Other than the Caribbean members of Coerebinae, only a few other tanager species occur on Caribbean islands and only two other tanagers (*Tangara cucullata*, *Saltator albicollis*) are endemic to this area. As was found in previous studies (Burns et al., 2002; Mallarino et al., 2012), our tree indicates that Darwin's finches are embedded within this clade of mostly Caribbean birds, indicating that they are an extension of a radiation that was already occurring among island species in the Caribbean.

Our phylogenies are largely concordant with previously published studies investigating relationships among these species. In particular, Mallarino et al. (2012) presented a phylogeny using a similar data set to that presented here. Thus, we do not describe in detail the relationships or taxonomic history of species in this clade. However, our phylogenies (Figs. 1 and 2j), as well as those presented in previous studies (Burns et al., 2002; Mallarino et al., 2012; Petren et al., 2005), indicate that several genera are paraphyletic and need taxonomic revision. For example, as in Petren et al. (2005), we found that the two species of *Certhidea* do not form a monophyletic clade, with *C. fusca* more closely related to the rest of the Darwin's Finches than it is to *C. olivacea*. However, this relationship was not strongly supported in our data set. If additional data continue to uphold paraphyly, retaining *Certhidea* for both of these species would be misleading. Thus, a new generic name will be needed for *C. fusca* to reflect accurately the relationship of these species to other birds. For *Tiaris* and *Loxigilla*, we found strong support for lack of monophyly. *Melopyrrha nigra* is embedded within a clade that contains two of the four species of *Loxigilla*, and this clade has strong support (1.0 PP; 93% bootstrap). We recommend merging these species into *Melopyrrha* (type species = *M. nigra*), and retaining *Loxigilla* (type species = *L. noctis*) for the other two species of *Loxigilla*, *L. noctis* and *L. barbadensis*, which form a strongly supported clade elsewhere in the tree. The five species of *Tiaris* occur in four different parts of the tree. The type species, *T. olivacea*, is the sister taxon to all species in Coerebinae except for *C. flaveola* (1.0 PP; 97% bootstrap). Because *T. olivacea* is the type species for the genus, *Tiaris* can be retained for *T. olivacea*. *Tiaris bicolor* is the sister to *Melanospiza richardsoni*. This relationship has strong support (1.0 PP; 91% bootstrap); thus, we recommend merging *T. bicolor* into *Melanospiza*. *T. canorus* is not closely related to the other species of *Tiaris*; we recommend using the available name *Phonipara* Gray 1850 (type = *T. canorus*) for this species. The two remaining species of *Tiaris* (*T. fuliginosa* and *T. obscurus*) are sister species in another part of the tree. We are not aware of an available name for these species; therefore, a new generic name will be required under the classification scheme described above.

For *Geospiza* and *Camarhynchus*, we only included cyt *b* from one individual for each species. Because these species do not sort into monophyletic groups based on their cyt *b* sequence (Petren et al., 2005; Sato et al., 1999), we caution that the branching order in the trees presented here (Fig. 2j; Supplementary Fig. 1) should not be taken to indicate relationships of those species. Furthermore, Zink (2002) presented an analysis that clouds the species status of forms within *Geospiza* and within *Camarhynchus*. Genomic data from multiple individuals of each putative species are likely needed to fully understand evolutionary patterns and species-level relationships within *Geospiza* and *Camarhynchus*.

4.3.11. Tachyphoninae, Bonaparte, 1853; the Ornamented Tanagers

This clade contains 31 species that are mostly distributed in the Neotropical lowlands (Fig. 3a). The majority of species in this group have long been considered tanagers; however, *Volatinia jacarina*, *Rhodospingus cruentus*, and the two species of *Coryphospingus* have traditionally been considered New World sparrows (Paynter and Storer, 1970). There are 10 genera in this clade, with most species belonging to either *Tachyphonus* (8 species) or *Ramphocelus* (9 species). Both Tachyphoninae and Ramphocelinae have been used as subfamily names in the past to describe some of the species in this clade. Both of these names were used in the same publication; we act as first revisers in selecting Tachyphoninae Bonaparte, 1853 to take precedence over Ramphocelinae Bonaparte, 1853 as the name of this subfamily. Most species in Tachyphoninae have social ornaments such as crests, enlarged lower mandibles, brightly colored carotenoid patches, white plumage patches, and partially concealed feather patches on the crown. Thus, we suggest a common name of 'ornamented tanagers' for describing this group. The presence of these plumage and bill ornaments and their associated displays (Isler and Isler, 1999; Moynihan, 1962, 1966; Willis, 1985), as well as the marked sexual dichromatism of most species, suggest that sexual selection is strong in this group. Identifying this group as a novel clade should facilitate the study of these features and their associated behaviors.

Tachyphoninae is strongly supported in our concatenated BEAST (0.98 PP) and species tree analyses (Barker et al., 2013). Although Tachyphoninae is monophyletic in our ML tree, our bootstrap analysis recovered this clade in only 54% of replicates. There are two subclades within Tachyphoninae, which are both strongly supported in Bayesian and ML analyses (Fig. 3a) as well as genus-level analyses (Barker et al., 2013). This basal split involves a small clade (1.0 PP; 73% bootstrap) containing species in *Conothraupis*, *Volatinia*, and *Creurgops* and a large clade (1.0 PP; 100% bootstrap) that was termed the 'lowland clade' by Burns and Racicot (2009).

Within the smaller clade, the two species of *Creurgops* are sister to each other with strong support, as found in previous studies. A close relationship between *Creurgops* and either *Volatinia* or *Conothraupis* has not been previously suggested. However, previous linear classifications (e.g., Hellmayr, 1936; Sclater, 1886; Storer, 1970) have arranged *Creurgops* near other genera of Tachyphoninae (e.g., *Lanio*, *Tachyphonus*, *Eucometis*, *Trichothraupis*). The presence of elongated head feathers (i.e., a crest) in *Creurgops verticalis* also supports the placement of *Creurgops* within Tachyphoninae. Within Tachyphoninae, 13 of the 31 species have crests. Otherwise, crests are relatively rare in tanagers and are found only in Charitospizinae (Section 4.3.2) and a few species of Thraupinae (Section 4.3.15).

In both ML and Bayesian analyses, *Creurgops* is sister to a clade containing *Conothraupis speculigera* and *Volatinia jacarina*. Bledsoe (1988) was the first to show that *V. jacarina*, the sole member of *Volatinia*, was a tanager based on DNA hybridization data. Subsequent sequencing studies have confirmed this finding. However, the placement of *Volatinia* within tanagers has remained unsettled, with the species most often considered closely related to *Sporophila* (Clark, 1986; Paynter and Storer, 1970; Sibley and Monroe, 1990) or the Darwin's finches (Steadman, 1982). Previous mtDNA analyses that included some tanagers (Burns et al., 2003; Weir et al., 2009) recovered *Volatinia* as the sister to *Conothraupis speculigera*, and we confirm that finding in the present study using more species and genes. The placement of *Volatinia* within the broader Tachyphoninae agrees with similarities in plumage and overall appearance. Many other species in Tachyphoninae have mostly bluish black plumage like *Volatinia*, and *Volatinia* is reminiscent of a small version of *Tachyphonus*. *Volatinia* also has white underwing coverts, a character it shares with *C. speculigera* and some species of *Tachyphonus*.

The phylogenetic position of *Conothraupis* in relation to the tanagers has been unclear, with most linear classifications including it near the beginning of tanagers alongside genera of uncertain relationships. Storer (1960) remarked on the similarities of *Conothraupis* with seedeaters, especially *Sporophila luctuosa*. He considered its relationship to other species undetermined, but most likely close to *Schistochlamys* and *Neothraupis*. *Conothraupis* includes two species, but we were only able to sample *C. speculigera*. In our phylogenies, *C. speculigera* is clearly part of Tachyphoninae, and this position is also supported by several morphological features. Males have glossy blue-black plumage that is similar to species in *Tachyphonus*, *Ramphocelus*, and *Volatinia*. The female plumage of *C. speculigera* is largely yellow or olive, similar to that of *Lanio*, *Eucometis*, and females of some species of *Tachyphonus* and *Ramphocelus*. Furthermore, like many other members of Tachyphoninae, adult male *C. speculigera* have elongated head feathers that form a crest. In *C. speculigera*, the crest is rudimentary (Bond, 1951) and when raised by the male during singing bouts

(Ingels, 2007), an otherwise concealed white patch (Lebbin, 2005, 2006; Witt, 2005) is exposed.

Despite these similarities to Tachyphoninae, the overall plumage color and pattern of *C. speculigera* is very similar to a distantly related species, *Sporophila luctuosa* (Storer, 1960; Witt, 2005). These similarities include black upperparts, white underparts, and a white wing speculum. Witt (2005) demonstrated that these similarities were likely the result of interspecific visual mimicry between these two species. Our study provides the phylogenetic evidence needed to support this hypothesis; these two species are distantly related to each other in our trees (Fig. 3a and b). Thus, we confirm two cases of interspecific mimicry in tanagers, *C. speculigera*/*S. luctuosa* as well as *Orchesticus*/*Philydor rufum* in Orchesticinae (Section 4.3.3).

We were unable to sample the other species of *Conothraupis*, *C. mesoleuca*, previously known from only a single specimen but recently rediscovered (Buzzetti and Carlos, 2005). Based on observations of newly-discovered individuals, Candia-Gallardo et al. (2010) argue that this species might be closely related to the White-naped Seedeater (*Dolospingus fringilloides*), which belongs to Sporophilinae (Section 4.3.12) in our phylogeny. Similarities between the two species include voice (Ridgely and Tudor, 2009), female plumage, bill color and shape, and morphological measurements (Candia-Gallardo et al., 2010). However, Candia-Gallardo et al. (2010) also report that the call notes of *C. mesoleuca* are similar to those of the sympatric *Ramphocelus carbo*, which our trees show belongs to Tachyphoninae. Thus, genetic studies are needed to clarify the relationship of *C. mesoleuca* to other tanagers.

The remaining species in Tachyphoninae form a clade of mostly lowland tanagers. The phylogenetic relationships of these species were studied by Burns and Racicot (2009) using ND2 and cyt *b* sequences. Because Burns and Racicot (2009) discuss the taxonomic history of these species, we do not discuss it here. The additional data included in the current study produced largely congruent results, with most nodes receiving increased posterior probabilities and maximum likelihood support. However, Clade “B” of Burns and Racicot (2009) was not recovered in our study. Instead, some of the species in this clade (*Coryphospingus*, *Rhodospingus*, *Lanio*, and *Tachyphonus delatrii*) are more closely related to a clade containing *T. phoenicius*, *T. rufus*, *T. coronatus*, and species in *Ramphocelus* than they are to other members of this group. Thus, the suggestion by Burns and Racicot (2009) to merge these species into a broad genus *Lanio* is not supported by current results. Burns and Racicot (2009) suggested several alternatives to reconcile the generic taxonomy with the phylogeny. Of those proposed, we recommend retaining *Tachyphonus* (type species = *T. rufus*) for the clade containing *T. phoenicius*, *T. coronatus*, and *T. rufus*, and using three new generic names, one for *T. delatrii*, one for *T. surinamus* and one for the clade containing for *T. cristatus*, *T. rufiventer*, and *T. luctuosus*. The current usage of the remaining generic names in Tachyphoninae can be retained.

4.3.12. Sporophilinae Ridgway, 1901; the Seedeaters

This clade contains 39 species that are currently classified into three genera. The 32 species that we included in this study form a monophyletic group with strong support (Figs. 1 and 3b; 1.0 PP; 100% bootstrap). Our cyt *b*, ND2, ACO1-I9, and MBI2, RAG1 gene trees also strongly supported the monophyly of this group (Supplementary Figs. 1–6), as do genus-level analyses (Barker et al., 2013). Although this clade has historically been included within the New World sparrows (Paynter and Storer, 1970), here we demonstrate conclusively that it is part of the tanagers. Most of the species within this subfamily are part of *Sporophila*, whose name reflects their granivorous diet. Six additional species are included in *Oryzoborus*, and *Dolospingus* is monotypic. Seedeaters and seed-finches in these genera are small bodied with conical bills and melanin-based plumage, and are widespread from southern Texas to southern Argentina.

Mason and Burns (2013) recently studied phylogenetic relationships within this group. The relationships inferred here are largely congruent with the phylogeny presented by Mason and Burns (2013), which was based solely on ND2 and cyt *b*. Because Mason and Burns (2013) discussed the taxonomic history of this subfamily, we do not repeat that information here. Our data recapitulate the findings of Mason and Burns (2013) that *Sporophila* is paraphyletic as currently described, with *Dolospingus* and *Oryzoborus* embedded within *Sporophila*. We follow their suggestion in recommending that these three genera be lumped into a monophyletic, broadly-defined *Sporophila*.

Between the current study and Mason and Burns (2013), no nodes show strongly supported conflict. However, there are some differences in topology and taxonomic sampling. We did not include *S. bouvreuil*, which was included in Mason and Burns (2013). Also, the present study included *S. frontalis*, which was excluded from Mason and Burns (2013). The inclusion of this species resulted in a topological difference. In our Bayesian trees, we inferred a sister relationship between *S. frontalis* and *Dolospingus fringilloides*, whereas Mason and Burns (2013) found a strongly supported sister relationship between *D. fringilloides* and a clade containing *S. luctuosa*, *S. caerulescens*, and *S. nigricollis* (1.0 PP).

Another difference between the present study and Mason and Burns (2013) is in the placement of *Oryzoborus funereus* and *O. angolensis* with respect to the other species in *Oryzoborus*. Mason and Burns (2013) inferred a strongly supported clade containing all six *Oryzoborus* species. Our cyt *b* and ND2 gene trees also recovered a strongly supported *Oryzoborus* (Supplementary Figs. 1 and 2). In contrast, our concatenated analyses (Fig. 3b) rendered *Oryzoborus* polyphyletic, wherein *O. crassirostris*, *O. atrirostris*, *O. maximiliani*, and *O. nuttingi* form a clade that is distantly related to *O. funereus* and *O. angolensis*. However, none of the nodes separating these two clades were strongly supported. The lack of monophyly in our concatenated analyses appears to be driven by ACO1-I9. We sampled two species of *Oryzoborus* for this gene, *O. angolensis* and *O. crassirostris*, and these two species appear in different parts of this gene tree (Supplementary Fig. 3). However, relatively few taxa within this subfamily were sampled for ACO1-I9 or other nuclear genes; thus, sparse taxon sampling could be driving the polyphyletic arrangement. Because these species share morphological as well as mtDNA characters, we consider *Oryzoborus* to represent a monophyletic lineage unless additional data from other nuclear genes also demonstrate non-monophyly.

4.3.13. Poospizinae, Wolters, 1980; the Warbler Tanagers

This large clade contains 44 species currently classified into 12 genera. The node uniting Poospizinae was strongly supported in our concatenated analyses (0.97 PP; 98% bootstrap; Fig. 4), as well as the generic-level trees of Barker et al. (2013). The cyt *b* and ND2 gene trees also strongly supported this clade (Supplementary Figs. 1 and 2). About half the species have historically been classified with the tanagers, and the remaining species with New World sparrows, including all members of *Poospiza*, *Compsospiza*, *Xenospingus*, *Piezorina*, *Urothraupis*, and *Donacospiza*. Our analyses show that all of these species are tanagers.

The subfamily is dominated by two relatively large genera (*Poospiza* and *Hemispingus*); most other genera are monotypic. Species in *Poospiza* are commonly referred to as warbling-finches due to their melodious songs. *Cypsnagra hirundinacea*, some species of *Hemispingus*, and some species of *Thlypopsis* are known for their complex vocal displays, often given as duets, trios, or in larger groups (Hilty, 2011). Species in *Hemispingus* are morphologically and behaviorally similar to, and often confused with, wood-warblers in *Basileuterus* (Hilty, 2011; Isler and Isler, 1999).

Although species in *Hemispingus* vary in bill size, many species of this and other genera in the subfamily (e.g., *Thlypopsis*, *Nephelornis*, *Urothraupis*, *Cnemoscopus*) have relatively thin, warbler-like bills. Thus, the name 'warbler tanagers' provides a convenient way to refer to this diverse group, considering the warbling songs of some species and the warbler-like morphology of others.

The data sets of the current study and Shultz and Burns (2013) are largely the same; therefore, topological relationship within Poospizinae presented in the current paper are largely concordant with those presented in Shultz and Burns (2013). Support is very similar between the two studies, and no strongly supported nodes conflict. There are only three topological differences between Bayesian trees presented in Shultz and Burns (2013) and those of the current paper. These changes involve the positions of *Hemispingus reyi*, *Poospiza thoracica*, and *P. torquata*. Of these topological changes, only the change in position of *P. torquata* results in a significant change in support values. In the analyses presented here, the position of *P. torquata* results in an increase in support from 0.49 to 0.95 PP for the clade containing *P. torquata*, *H. trifasciatus*, *P. melanoleuca*, and *P. cinerea*.

Shultz and Burns (2013) discussed the taxonomic history of species in this subfamily; thus, that information is not repeated here. However, we note that our topology will require extensive generic revision within the group. In particular, the large genera *Hemispingus* and *Poospiza* are polyphyletic with respect to each other; therefore, for the classification to be consistent with strongly-supported monophyletic lineages, several new genera will need to be named. In other cases, previously used generic names can be resurrected to accommodate our topology. For example, *Pseudospingus* Berlepsch and Stolzmann, 1896 (type = *H. xanthophthalmus*) is available for the clade containing *Hemispingus verticalis* and *H. xanthophthalmus*. Similarly, *Sphenops* Sclater, 1862 (type = *H. frontalis*) is available for *H. frontalis* and *H. melanotis*, *Orospingus* Riley, 1922 (type = *H. goeringi*) is available for *H. goeringi* and *H. rufosuperciliaris*, and *Poospizopis* Berlepsch, 1893 (type = *Poospiza caesar*) is available for *P. hypochondria* and *P. caesar*. *Microspingus* Taczanowski, 1874 (type species = *Hemispingus trifasciatus*) is available for the large clade containing *H. trifasciatus*, *Poospiza cabanisi*, *P. erythrophrys*, *P. alticola*, *P. torquata*, *P. melanoleuca*, and *P. cinerea*. We were unable to include a sample of *P. lateralis*. *P. cabanisi* was recently split from *P. lateralis* (Assis et al., 2007); thus, the two species are likely related, and we would place both in *Microspingus*. We recommend using the name *Thlypopsis* Cabanis, 1851 for the clade containing all species of *Thlypopsis*, *Pyrrhocoma ruficeps*, and *H. superciliaris* (all three genera date to 1851). Under the above described classification scenario, *Poospiza* would be retained for the clade containing *P. boliviana*, *P. ornata*, and *P. whitii/nigrorufa*, and *Compsospiza* would be retained for *C. baeri* and *C. garleppi*. In addition, the monotypic *Piezorina*, *Xenospingus*, *Cnemoscopus*, *Donacospiza*, *Cypsnagra*, *Urothraupis*, and *Nephelornis* would be retained; however, *Hemispingus* would no longer be used. If all of the above taxonomic recommendations are followed, new genera will be needed for *P. hispaniolensis*, for *P. rubecula*, for the clade containing *H. reyi*, *H. atropileus*, *H. calophrys*, and *H. parodii*, and for *P. thoracica*. An alternative classification scheme could involve lumping species into larger genera; however, to be consistent with strongly-supported nodes, these genera would be morphologically diverse.

4.3.14. Diglossinae, Sclater, 1875, the Highland Tanagers

With 64 species and 14 genera, this clade is one of the largest and most morphologically diverse tanager subfamilies. Diglossinae, as defined in this paper, has not previously been recognized as a clade because no prior study has comprehensively sampled the tanagers. However, some earlier studies that sampled fewer species (Barker et al., 2013; Burns et al., 2002, 2003; Campagna et al., 2011; Yuri and Mindell, 2002) have recovered aspects of this clade. Here, we found strong support in our concatenated phylogenies (1.0 PP; 100% bootstrap; Figs. 1 and 5) for a clade containing *Conirostrum*, *Oreomanes*, *Sicalis*, *Catamenia*, *Diglossa*, *Idiopsar*, *Xenodacnis*, *Haplospiza*, *Acanthidops*, *Nesospiza*, *Rowettia*, *Melanodera*, one of the two species of *Diuca*, and eight of the 11 species of *Phrygilus*. A few of these species were historically considered tanagers (species in *Oreomanes* and *Diglossa*); however, most were traditionally considered members of Parulidae (*Conirostrum*) or Emberizidae (the remaining genera) (Fig. 5; Lowery and Monroe, 1968; Paynter and Storer, 1970). Even among the tanagers, the bill morphologies and feeding behaviors of species in Diglossinae are particularly diverse. There are nectar feeders (*Diglossa*), finch-billed seed-eaters (e.g., *Nesospiza*, *Sicalis*, *Catamenia*, *Haplospiza*), a bark gleaner (*Oreomanes*), arthropod feeders (*Conirostrum*), a bamboo specialist (*Acanthidops*), an aphid and nectar feeder (*Xenodacnis*), and a boulder field specialist (*Idiopsar*). Although some species occur only in the lowlands, over 80% have their center of abundance at 900 m or higher, and over 75% occur above 2500 m (Parker et al., 1996). Thus, we recommend the name "highland tanagers" to describe this group.

The genus *Phrygilus* is one of the most polyphyletic in our tanager phylogeny, with members appearing in four distinct clades, three of which are in Diglossinae. Previous workers (e.g., Fjeldså, 1992; Lowe, 1923) have appreciated the heterogeneous nature of *Phrygilus*, and Campagna et al. (2011) were the first to demonstrate polyphyly across the group using molecular characters. In general, our results are concordant with those of Campagna et al. (2011), who sampled fewer species of tanagers, but found the same four distinct *Phrygilus* clades. These four clades have also been identified on the basis of plumage differences (Ridgely and Tudor, 1989) and agree to some extent with skeletal differences (Webster and Webster, 1999). For convenience, we refer to these groups as the "gray sierra-finches" (*P. unicolor*, *P. plebejus*), the "yellow-billed sierra-finches" (*P. alaudinus*, *P. fruticeti*, *P. carbonarius*), the "hooded sierra finches" (*P. atriceps*, *P. gayi*, *P. punensis*, *P. patagonicus*), and the "gray and white sierra-finches" (*P. dorsalis*, *P. erythronotus*). The yellow-billed Sierra finches were discussed earlier (Porphyrospizinae, Section 4.3.6). The other three sierra-finch clades belong within Diglossinae, but are not closely related to each other within Diglossinae. In the following paragraphs, we discuss relationships of these three clades in the context of their nearest relatives. Overall, our results with regard to species-level relationships of *Phrygilus* are consistent with those of Campagna et al. (2011), to the extent that the two studies sampled taxa in common. However, our more complete sampling does allow us to identify with confidence the closest relatives to each of these clades.

Within Diglossinae, the clade containing the conebills *Conirostrum* and *Oreomanes* is sister to all remaining species (1.0 PP; 100% bootstrap). *Conirostrum* itself has been classified in a variety of different groups including warblers (e.g., Howard and Moore, 1991; Lowery and Monroe, 1968), tanagers (e.g., American Ornithologists' Union, 1998; Sibley and Monroe, 1990), and honeycreepers (e.g., Hellmayr, 1935). The warbler-like bills of all *Conirostrum* and nectar-feeding habits of some species (Hilty, 2011; Vogt, 2006) have contributed to this taxonomic confusion. However, all modern molecular studies have placed *Conirostrum* within the tanagers (e.g., Barker et al., 2013; Burns et al., 2003; Campagna et al., 2011; Lovette and Bermingham, 2002; Yuri and Mindell, 2002). The Giant Conebill (*Oreomanes fraseri*) has had a similar taxonomic history, and has been shuffled among warblers, tanagers, and honeycreepers by various taxonomists. *Oreomanes fraseri* is a *Polylepis* specialist that has a larger, more rounded body shape than conebills in the genus *Conirostrum*, and closely resembles nuthatches in its morphology, tree-climbing, and bark-probing behaviors (Mason and Burns, 2010; Vuilleumier, 1984). *Oreomanes* was often placed adjacent to *Conirostrum* in early linear arrangements (Hellmayr, 1935; Sclater, 1886), implying a close relationship between these two genera, and Sclater (1886) and Ridgway (1902) specifically noted the similarity between them. In particular, Sclater (1886) called *Oreomanes* "an exaggerated form of *Conirostrum*"; however, other later arrangements (Howard and Moore, 1991; Lowery and Monroe, 1968; Storer, 1970) did not consider these taxa to be closely related. This discrepancy was likely due to a study of Coerebidae by Beecher (1951) that placed *Conirostrum* with the warblers and *Oreomanes* with the tanagers. Similarities between *Oreomanes* and *Diglossa*, another member of our Diglossinae, have also been recognized (George, 1964; Sclater, 1860; Storer, 1970). Schulenberg (1985) described a hybrid between *Oreomanes* and *C. ferrugineiventre*. Based on this hybrid and similarities in plumage color, plumage pattern, and body shape, Schulenberg (1985) provided the most detailed argument for a close relationship between *Oreomanes* and *Conirostrum*. He proposed two alternative possibilities: either *Oreomanes* and *Conirostrum* are sister taxa, or *Conirostrum* is paraphyletic with *Oreomanes* being more closely related to some Andean species of *Conirostrum*. Fjeldså (1992) suggested a sister relationship between *Oreomanes* and *C. ferrugineiventre* based on similar coloration and shared behavior of feeding on *Polylepis* trunks. Molecular phylogenetic analyses have confirmed that *Oreomanes* is a tanager (Burns, 1997; Burns et al., 2003), and confirmed a close relationship between *Oreomanes* and *Conirostrum* (Barker et al., 2013; Burns et al., 2003; Campagna et al., 2011; Lovette and Bermingham, 2002; Yuri and Mindell, 2002). Burns et al. (2003) sequenced cyt *b* from a broad sampling of tanagers, Neotropical finches, and species previously considered part of Coerebidae, and they found that *Oreomanes* was most closely related to the two species of *Conirostrum* (*C. bicolor* and *C. speciosum*) included in their study. Similarly, Campagna et al. (2011) sampled cyt *b* from five species of *Conirostrum* and also found that *Conirostrum* was paraphyletic with respect to *Oreomanes*. In the present study, we include all species of *Conirostrum* and confirm both the monophyly of *Conirostrum* + *Oreomanes* (1.0 PP; 100% bootstrap) and the paraphyly of *Conirostrum* with respect to *Oreomanes*. These results are supported by separate gene analyses (Supplementary Figs. 1–6). Our findings agree with the prediction of Schulenberg (1985) that *Oreomanes* is closely related to a clade of mostly Andean *Conirostrum*. Although *O. fraseri* and *C. ferrugineiventre* have hybridized, we did not find that these two species were sister taxa. Instead, *O. fraseri* is sister to a clade of five species of *Conirostrum* (referred to as Group A in Ridgely and Tudor (1989)), one of which is *C. ferrugineiventre*. Thus, *Oreomanes* is a specialized *Conirostrum*, and the morphological and behavioral differences of *Oreomanes* are best interpreted as recently evolved adaptations. Given that the position of *Oreomanes* renders *Conirostrum* paraphyletic, we recommend merging *Oreomanes* with *Conirostrum*, which has taxonomic priority.

Within *Conirostrum*, species are generally divided into two groups based on differences in habitat preference (e.g., Ridgely and Tudor, 2009). The four species of lowland conebills (*C. bicolor*, *C. margaritae*, *C. leucogenys*, *C. speciosum*) have historically been placed in *Ateleodacnis* (e.g., Hellmayr, 1935) and the six species of highland conebills (*C. sitticolor*, *C. cinereum*, *C. tamarugense*, *C. ferrugineiventre*, *C. rufum*, and *C. albifrons*) are considered to be members of true *Conirostrum*. However, Zimmer (1942) was unable to find morphological characters to justify this separation. Our phylogenies also do not support a monophyletic lowland clade. Instead, two of the lowland species (*C. leucogenys* and *C. speciosum*) are more closely related to highland species than to the other lowland species (*C. margaritae* and *C. bicolor*). Support for this relationship is high (1.0 PP; 93% bootstrap). Thus, the use of *Ateleodacnis* to recognize a clade of lowland conebills is not warranted. However, the highland species, together with *Oreomanes*, do form a clade with respect to the lowland species. This topology suggests that the highland distribution of these conebills was derived from a lowland ancestor.

In our phylogenies, the earliest split within *Conirostrum* is between a clade containing *C. margaritae* and *C. bicolor* and a clade containing the remaining species. These two clades are well differentiated genetically from each other and each is strongly supported. This early division within *Conirostrum* was also recovered in the phylogenies of Campagna et al. (2011), who sampled fewer species than in our study. This division corresponds with habitat differences; *C. bicolor* and *C. margaritae* inhabit riverine forests, specializing on river islands.

The Tamarugo Conebill (*C. tamarugense*) is a relatively recently described species (Johnson and Millie, 1972), classified as vulnerable by the IUCN (BirdLife International, 2013b). The species has a very limited distribution in southwestern Peru and northern Chile. Little has been written on its potential relationships, but Mayr and Vuilleumier (1983) considered this species closely related to *C. rufum* and *C. ferrugineiventre*, and Fjeldså (1992) considered it to be sister to *C. cinereum*. We report the first genetic data for this species and show that it is well differentiated from the other species of *Conirostrum* and its sister taxon is a clade containing *C. rufum* and *C. cinereum*.

Conirostrum is sister to a large clade composed of the remaining Diglossinae. This clade can be further divided into two strongly supported main clades. One of these clades contains the yellow finches (*Sicalis*), the two species of bridled finches (*Melanodera*), three species of tanagers that occur on islands in the South Atlantic (*Rowettia*, *Nesospiza*), and the hooded Sierra-finches (*Phrygilus*). All species in this clade have yellow in their plumage, thus we refer to them as the "yellow clade" below. The other clade contains the flowerpiercers (*Diglossa*), four species of sierra-finches (*Phrygilus*), the Slaty and Uniform Finches (*Haplospiza*), the Peg-billed Finch (*Acanthidops*), the White-winged Diuca Finch (*Diuca speculifera*), the Short-tailed Finch (*Idiopsar*) and the Tit-like Dacnis (*Xenodacnis*). All of these species have gray and/or blue in their plumage, thus we refer to them as the "gray/blue clade" below. Both are strongly supported in our analyses (1.0 PP for both clades; 100% bootstrap for yellow clade, 99% for gray/blue clade).

Within the "yellow clade", the largest genus is *Sicalis* with 12 species. Commonly known as yellow finches, these ground-feeding birds are found mostly in open habitats at both high and low elevations. Like other finch-billed tanagers, species in *Sicalis* were not considered tanagers until relatively recently. Sharpe (1888) divided species in this genus into two groups, with some placed in *Pseudochloris* near other emberizids and other species in *Sycalis* (i.e., *Sicalis*) near old world cardueline finches such as *Serinus* (currently considered Fringillidae). However, Ridgway (1901a) correctly felt that the species classified as *Sicalis* by Sharpe (1888) were closely related to those in *Pseudochloris*. Ridgway (1901a) was also correct in placing *Sicalis* with other Neotropical emberizines (such as *Acanthidops* and *Haplospiza*). The position of *Sicalis* in Hellmayr's (1938) classification reverts somewhat to that of Sharpe's (1888) in that he placed the genus near species now considered Fringillidae. Meyer de Schauensee (1966), following Tordoff (1954), considered *Sicalis* to belong with emberizine finches, and subsequent classifications (e.g., Paynter and Storer, 1970) followed this arrangement. DNA analyses, however, have shown that finches in *Sicalis*, like many other Neotropical Emberizidae, are tanagers (Barker et al., 2013; Bledsoe, 1988; Burns et al., 2002, 2003; Campagna et al., 2011; Klicka et al., 2007).

In our concatenated ML and BEAST analyses, *Sicalis* is not monophyletic, with *S. citrina* more closely related to species in the "yellow clade" than to other species in *Sicalis*. However, support for this relationship is not strong (0.84 PP; 62% bootstrap). In addition, none of the individual gene phylogenies provides strong support either for or against a monophyletic *Sicalis* (Supplementary Figs. 1–6). Given the lack of strong support for the position of *S. citrina*, additional data are needed to clarify the monophyly of *Sicalis*. Until then, despite the position of *S. citrina* in our concatenated phylogeny, we recommend that *Sicalis* be maintained for all species in the genus, given their morphological and behavioral similarities.

Our data can be used to address several preexisting hypotheses about both relationships within *Sicalis* and relative distinctiveness of particular taxa. Our phylogenies agree in topology with respect to the four species of *Sicalis* (*S. flaveola*, *S. luteola*, *S. luteocephala*, *S. olivascens*) also sampled in the molecular phylogenetic analyses of Campagna et al. (2011). *S. taczanowskii* has a much thicker bill than other species of *Sicalis* and has therefore sometimes been classified in its own genus, *Gnathospiza* (e.g., Hellmayr, 1938; Meyer de Schauensee, 1966). In our trees, S. *taczanowskii* is embedded within the phylogeny of *Sicalis* with strong support; therefore, there is no justification for the use of *Gnathospiza*, and the large bill of this species is best interpreted as yet another case within tanagers of rapid bill evolution. Ridgely and Tudor (1989) divided *Sicalis* into two groups ("Group A" and "Group B") that mostly corresponded to Sharpe's *Sicalis* and *Pseudochloris*. Group A species occur in the arid Pacific slope or are widespread in the lowlands; species in this group include *S. taczanowskii*, *S. flaveola*, *S. columbiana*, *S. citrina*, *S. luteola*, and *S. raimondii*. Group B species are found in the Andes and/or Patagonia and include *S. uropygialis*, *S. luteocephala*, *S. lutea*, *S. olivascens*, *S. auriventris*, and *S. lebruni*. With the exception of *S. citrina*, Sharpe's (1888) *Pseudochloris* correspond to Ridgely and Tudor's (1989) Group B. None of these proposed groupings are monophyletic in our phylogenies. However, Ridgely and Tudor's Group B is monophyletic if *S. raimondii* is included within Group B rather than Group A. Similarly, with the exception of *S. citrina* and *S. raimondii*, *Pseudochloris* would be monophyletic. *Sicalis columbiana* and *S. flaveola* have red facial feathers but are not each other's closest relatives, with *S. columbiana* more closely related to the clade containing *S. luteola* and *S. luteiventris*. This topological position suggests either red plumage has evolved twice within *Sicalis* or that red plumage was lost in the lineage leading to *S. luteola*/*S. luteiventris*.

Species limits within *Sicalis* have shifted throughout the classification history of the group, with many forms considered species or subspecies by different taxonomists. For example, Sibley and Monroe (1990) consider *S. luteiventris* a valid species; however, Clements et al. (2013) consider it a subspecies of *S. luteola*. Because we had genetic material of *S. luteiventris*, we included it in our analyses. Levels of uncorrected mtDNA sequence divergence between these two taxa average 0.61%, similar to values seen within other species of tanagers. Our phylogeny shows little agreement with regards to previous ideas about superspecies, further emphasizing the prior lack of understanding of species limits and species-level relationships in this group. For example, *S. olivascens* and *S. lebruni* are considered a superspecies by Sibley and Monroe (1990) and subspecies of the same species by Paynter and Storer (1970); however, these species are only distantly related to each other in our phylogeny. Likewise, *S. luteola*/*S. luteiventris* and *S. raimondii* form another superspecies (Sibley and Monroe, 1990), and *S. raimondii* was long considered a subspecies of *S. luteola* (Ridgely and Tudor, 1989). However, *S. raimondii* is more closely related to two species found allopatrically further south in the Andes, *S. lutea* and *S. auriventris*. We were unable to include samples of *S. mendozae*, a species recently split from *S. olivascens* (Areta et al., 2012). Based on plumage, structural features, and voice, Areta et al. (2012) consider this species most closely related to *S. lebruni*.

The yellow clade also includes the four species of sierra-finches that make of up the hooded sierra-finch clade (*Phrygilus gayi*, *P. atriceps*, *P. punensis*, and *P. patagonicus*). These species share similar plumage patterns and colors (Ridgely and Tudor, 1989) and have been considered a superspecies by some authorities (Sibley and Monroe, 1990). In agreement with Campagna et al. (2011), we found strong support for a clade containing these species in our concatenated BEAST and ML analyses (1.0 PP; 100% bootstrap).

Species limits in the hooded sierra-finch group have fluctuated throughout their taxonomic history, with successive authorities variously classifying the different forms as subspecies or species. Sharpe (1888) considered *P. patagonicus* synonymous with *P. gayi*, but considered *P. atriceps*, *P. gayi*, and *P. punensis* as specifically distinct. Hellmayr (1932, 1938) argued that *P. patagonicus* was a valid species, but considered the other three hooded sierra-finches part of *P. gayi*. Both Meyer de Schauensee (1966) and Paynter and Storer (1970) split *P. atriceps* from *P. gayi* because the two species co-occur in Chile without interbreeding (Philippi, 1942), but continued to keep *P. punensis* as a subspecies of *P. gayi*. Based on Vuilleumier (1967), Ridgely and Tudor (1989) split *P. punensis* from *P. atriceps*. Subsequent taxonomic treatments (e.g., Sibley and Monroe, 1990; Clements et al., 2013) followed Ridgely and Tudor's (1989) treatment and recognized four valid species of hooded sierra-finches. Hybridization among taxa has contributed to some of this taxonomic confusion; *P. gayi* is known to hybridize with both *P. atriceps* (Marín et al., 1989) and *P. patagonicus* (Vuilleumier, 1991). Vuilleumier (1991) hypothesized a sister taxon relationship between *P. patagonicus* and *P. gayi*, with their speciation associated with a habitat shift. Molecular phylogenetic data support the current taxonomy of the four species. In our study, we found these taxa to be genetically distinct from each other. Furthermore, Campagna et al. (2011) sampled multiple individuals of each species and found each to form a well differentiated clade whose monophyly was strongly supported. Nevertheless, species limits within the group are complex, including at least one population of *P. gayi* that perhaps belongs in *P. patagonicus* (Jaramillo, 2011d); thus, further intraspecific sampling within this group would help clarify species limits. Although current species limits agree with molecular phylogenetic data, relationships of the four species to each other do not necessarily agree with hybridization patterns or the previous taxonomies described above. Our concatenated tree agrees in topology with the concatenated tree of Campagna et al. (2011), with *P. atriceps* and *P. punensis* as sister taxa. Campagna et al. (2011) also found that *P. gayi* is more closely related to the *P. atriceps*/*P. punensis* clade than to *P. patagonicus*. However, we were not able to recover strong support for placement of *P. gayi* and *P. patagonicus* with respect to the *P. atriceps*/*P. punensis* clade. Our ML analyses recovered the same topology as Campagna et al. (2011), but without strong support (56% bootstrap). In contrast, our BEAST analyses show *P. patagonicus* as sister to the *P. atriceps*/*P. punensis* clade, albeit with weak support (0.48 PP). *Phrygilus* is polyphyletic, and the type species (*P. gayi*) is a member of the hooded sierra-finch clade. Thus, we recommend retaining the genus name *Phrygilus* for these four species.

The hooded sierra-finch clade is sister to a clade containing the two bridled finches (*Melanodera*) of southern South America and the only tanagers found outside Mexico, Central, or South America (*Nesospiza*, *Rowettia*). The two species of *Nesospiza* and the one species of *Rowettia* are found on islands in the South Atlantic Ocean. The Nightingale Finch (*N. acunhae*) and Wilkin's Finch (*N. wilkinsi*) occur in the Tristan da Cunha archipelago and the Gough Island Finch (*R. goughensis*) occurs on Gough Island. Tristan da Cunha is about halfway between the southern tips of South America and Africa, with Gough Island 350 km southeast of the Tristan group (Ryan, 2007). Relationships among these species were reported in Ryan et al. (2013) using some of the same data as reported in the current study, and the results of these two studies are concordant. The topologies of both studies imply two colonization events by tanagers of these South Atlantic islands. Ryan et al. (2013) discussed the taxonomic implications of phylogenetic relationships in this part of the tree.

Within the gray/blue clade, the largest genus is *Diglossa*. The 18 species in *Diglossa* are known as flowerpiercers, and they have adaptations that allow them to obtain floral nectar without pollination. These adaptations include a specialized hook at the tip of the maxilla used to hold the corolla of a tubular flower while the sharp lower mandible is used to pierce the flower base (Skutch, 1954). Mauck and Burns (2009) studied relationships among the flowerpiercers using cyt *b* and ND2. The current study used these data as well as additional nuclear sequences. The taxonomic history of the group was described in Mauck and Burns (2009) and is not repeated here. The topological relationships found in the current study are largely congruent with those of Mauck and Burns (2009); therefore, relationships among these taxa are also not described in detail here. As in Mauck and Burns (2009), we found a rapid radiation of the four species in the *carbonaria* superspecies. Our concatenated BEAST tree differs in one place from the trees of Mauck and Burns (2009). The Tepui species, *D. major* and *D. duidae*, were weakly supported as monophyletic in Mauck and Burns (2009); in the current study, we do not recover an exclusive clade containing *D. duidae* and *D. major*. Instead, weak support is found for a clade containing *D. major* and six other species of *Diglossa*. Our results agree with those of Mauck and Burns (2009) in that recognition of *Diglossopis* is not warranted, given the position of *D. indigotica*. Mauck and Burns (2009) were unable to identify the sister group to *Diglossa*, although they did identify a large clade containing *Diglossa* as well as *Acanthidops*, *Catamenia*, *Conirostrum*, *Haplospiza*, *Idiopsar*, *Melanodera*, *Oreomanes*, *Phrygilus*, *Sicalis*, and *Xenodacnis*. This clade is consistent with our Diglossinae and aspects of this clade were also recovered in Burns et al. (2003). With the more extensive sampling of the current study, we were able to identify *Catamenia* as the sister to *Diglossa*, with strong support (1.0 PP; 98% bootstrap).

Catamenia consists of three species of Andean birds commonly known as seedeaters: the Paramo Seedeater (*C. homochroa*), the Plain-colored Seedeater (*C. inornata*), and the Band-tailed Seedeater (*C. analis*). The sister relationship between *Catamenia* and *Diglossa* is notable for a couple of reasons. The bill shapes of *Diglossa* and *Catamenia* are very different; the three species of *Catamenia* have conical, seed-eating bills whereas *Diglossa* flowerpiercers have longer, thinner bills specialized for nectar feeding. Although the bill shapes are different, at least one species of *Catamenia* (*C. analis*) has been observed stealing nectar from flowers, similar to *Diglossa* (Wester and Claßen-Bockhoff, 2006). This observation suggests a deeper evolutionary origin for this behavior than previously recognized.

Like other seed-eating Neotropical tanagers, *Catamenia* was typically classified in families of other seed-eating birds (e.g., Sharpe, 1888; Hellmayr, 1938; Paynter and Storer, 1970). However, Sibley and Monroe (1990) classified it with tanagers, and subsequent DNA phylogenies have confirmed this (e.g., Barker et al., 2013; Burns et al., 2002, 2003; Campagna et al., 2011; Klicka et al., 2007). Most pre-molecular classifications have considered *Catamenia* to be related to *Sporophila*, either placing species of *Catamenia* within *Sporophila* (e.g., Sharpe, 1888) or adjacent to *Sporophila* (e.g., Hellmayr, 1938; Paynter and Storer, 1970). Our phylogenies show that despite their shared seed-eating habits, *Catamenia* and *Sporophila* are not closely related. In contrast to most classifications, Ridgely and Tudor (1989) considered *Catamenia* near *Idiopsar*, *Phrygilus*, *Diuca*, and *Melanodera*. This arrangement more closely matches our phylogenies. Some of the analyses of Burns et al. (2003) placed *Catamenia* and *Diglossa* as sister taxa, although support for this relationship was not strong (<60%). The increased data and character sampling of the current study increased support for this relationship and confirms that these two genera are each other's closest relatives. Within *Catamenia*, we found that *C. inornata* and *C. homochroa* are more closely related to each other than they are to *C. analis*. This agrees with shared plumage coloration and plumage molt sequences of these two species (Dickerman, 1986; Fjeldså, 1992).

The *Catamenia*/*Diglossa* clade is most closely related to a clade of 10 species that includes *Xenodacnis parina*, the gray and white sierra-finches (*Phrygilus erythronotus* and *P. dorsalis*), *Idiopsar brachyurus*, *Diuca speculifera*, the gray sierra-finches (*P. plebejus* and *P. unicolor*), the two species of *Haplospiza*, and *Acanthidops bairdi*. Monophyly of this clade was strongly supported (1.0 PP; 96% bootstrap). The Tit-like Dacnis, *X. parina*, has many unusual features; therefore, it has been classified in its own genus with an uncertain taxonomic position (Fjeldså, 1992; George, 1964; Zimmer, 1942). Some of the unique features of this high elevation species include bright blue plumage of males, marked sexual dichromatism, and a relatively small bill given overall body size. Earlier taxonomies (e.g., Hellmayr, 1936; Sclater, 1886) considered it part of the Neotropical honeycreeper family Coerebidae. This family has subsequently been dissolved (Burns et al., 2003), and DNA phylogenies indicate that this species belongs with the tanagers (Barker et al., 2013; Burns et al., 2003). Burns et al. (2003) had less complete taxon sampling than the present study and showed strong support that *Xenodacnis* was closely related to species in *Catamenia*, *Diglossa*, *Haplospiza*, and *Acanthidops*, with some evidence for *Sicalis*, *Oreomanes*, and *Conirostrum* being included in this clade as well. Results of the current study are consistent with these findings with respect to species sampled in common between the two studies. Although the bright blue coloration of males is similar to some species of *Diglossa* (Fjeldså, 1992), our trees show that *Xenodacnis* is embedded within a clade of mostly gray-plumaged birds (some *Phrygilus*, *Idiopsar*, *D. speculifera*, *Haplospiza*, and *Acanthidops*).

Among these species, *Xenodacnis* is most closely related to a clade containing *I. brachyurus*, *D. speculifera*, and the two species of gray and white sierra-finches (*P. erythronotus* and *P. dorsalis*). Campagna et al. (2011) did not sample *D. speculifera*, but otherwise also identified a strongly supported clade containing *I. brachyurus*, *P. erythronotus*, and *P. dorsalis*. Our analyses are the first to identify an exclusive clade containing these four species; however, Fjeldså (1992) noted plumage and distribution similarities that these species share. All species inhabit high arid puna or very high altitudes in the puna and they share the plumage synapomorphies of white throat and white mottling below the eye (Fjeldså, 1992). In contrast, the other species of *Diuca*, *D. diuca*, is found at lower elevations in semi-open habitat. Voice differences and locomotion differences also suggest that the two *Diuca* species are not closely related (Jaramillo, 2011e). Our phylogenies are congruent with these differences and show the two *Diuca* species are distantly related, with *D. speculifera* belonging to Diglossinae and *D. diuca* belonging to Thraupinae (Section 4.3.15).

In our phylogenies, the closest relative to *D. speculifera* is the Short-tailed Finch (*I. brachyurus*), also known as the Andean Boulder-finch (Lloyd et al., 2005), a relatively large bodied finch with a sharply-pointed bill that occurs in the high elevation Andean grasslands. The bill shape of *Idiopsar* is quite different from that *D. speculifera*; however, the species occur in the same habitat, have similar call notes (Fjeldså and Krabbe, 1990; Ridgely and Tudor, 2009), share similar posture, and have similar foraging behaviors (Lloyd, 2009). Levels of pairwise sequence divergence between these two species are remarkably low. We found no differences in the nuclear genes sequenced and levels of uncorrected mtDNA sequence divergence (0.42%) are similar to what is seen within other species of tanagers. Given this low level of sequence variation, we sequenced multiple individuals of each species (data not shown) and confirmed this result. These data suggest either recent hybridization between the two species, or rapid evolution of morphological characters. More research is needed to distinguish between these scenarios.

The *D. speculifera*/*Idiopsar* clade is most closely related to the two gray and white sierra-finches, *P. erythronotus* and *P. dorsalis*. These two species are both high altitude specialists with nearly allopatric distributions (Ridgely and Tudor, 1989). They were considered a superspecies by Sibley and Monroe (1990) and are known to interbreed (Fjeldså and Krabbe, 1990), suggesting only one species is involved. Our genetic results confirm the close relationship of these two species, and Campagna et al. (2011) sampled multiple individuals of each and recovered reciprocal monophyly, as expected for taxa representing well-differentiated species.

Because *Phrygilus* and *Diuca* are polyphyletic, a new generic taxonomy is needed for the four tanagers in this part of our phylogeny. The type species of *Phrygilus*, *P. gayi*, belongs to the hooded sierra-finch clade described above. Thus, we recommend merging these four species into *Diuca* Reichenbach 1850 (type = *D. speculifera*), which has taxonomic priority over *Idiopsar* Cassin 1866 (type = *I. brachyurus*). Merging these species has some precedent in the literature. Paynter and Storer (1970) noted that *Diuca* was possibly congeneric with *Idiopsar*, and Wolters (1975–1980) included all four in *Diuca*. Alternatively, both *Diuca* and *Idiopsar* could be retained as monotypic genera, but a new genus name would be needed for *P. erythronotus* and *P. dorsalis*.

The *Xenodacnis* – *Idiopsar* clade is most closely related to a clade containing *Acanthidops bairdi*, the two species of *Haplospiza*, and the two species of gray sierra-finches (*Phrygilus plebejus* and *P. unicolor*). The clade uniting these species has strong support in our molecular phylogenies (1.0 PP; 98% bootstrap) and earlier workers suspected a close relationship among these species based on other characters. For example, the two *Phrygilus* species share streaked female plumage with one other (Fjeldså, 1992), as well as plumage and structural similarities with *Haplospiza* (Jaramillo, 2011f, 2011g). In addition, a close relationship between *Acanthidops* and *Haplospiza* has long been suspected (e.g., Ridgway, 1901a) based on similarities in plumage and other characters. Paynter and Storer (1970) suggested that *Acanthidops* and *Haplospiza* were "offshoots" of *Phrygilus*. Although there are morphological similarities among these five species, *Acanthidops* and the two *Haplospiza* species are found in association with bamboo, while the *Phrygilus* species in this clade are found in high-elevation, open habitats.

Haplospiza and *Acanthidops* have been classified in alternative ways throughout their taxonomic history. Sibley and Monroe (1990) treated the two species of *Haplospiza* as a superspecies, and Paynter and Storer (1970) suggested that these two as well as *Acanthidops* might be conspecific. In contrast, the two *Haplospiza* species have been considered members of separate genera (e.g., Hellmayr, 1938; Sharpe, 1888), with *H. rustica* placed in *Spodiornis*. We sampled both species of *Haplospiza* for FGB-I5, cyt *b*, and ND2 (Supplementary Figs. 1–6); *Haplospiza* did not form an exclusive monophyletic group in any of these gene trees. Our BEAST tree using the concatenated data shows that *H. rustica* was more closely related to *Acanthidops* than to *H. unicolor*, with strong support (0.99 PP; 93% bootstrap). Thus, we do not recommend retaining *Haplospiza* as currently used. Instead, *Spodiornis* Sclater 1866 (type = *H. rustica*) is an available name that can be used for *H. rustica*. *Haplospiza* can be retained for *H. unicolor*, and *Acanthidops* can be retained for *A. bairdi*. This approach emphasizes the distinctive upturned and pointed bill of *Acanthidops*. Alternatively, all three species could be merged into *Haplospiza*, which has priority over *Acanthidops*. However, there is not strong support for such a clade and we recommend that each species has its own genus. Because of *Phrygilus* polyphyly, a name other than *Phrygilus* is needed for the two gray sierra finches (*P. plebejus* and *P. unicolor*). We suggest using the available generic name *Geospizopsis* Bonaparte 1856, which has *unicolor* as the designated type species.

4.3.15. Thraupinae, Cabanis, 1847; the Core Tanagers

With 102 species and 22 genera, Thraupinae is the largest tanager subfamily. It contains many of the species typically associated with the tanagers; therefore, we follow the recommendation of Burns and Naoki (2004) and use the name 'core tanagers' to describe this group. However, there are also nine species in this clade traditionally associated with the New World sparrows, and one is associated with the cardinal-grosbeaks (Fig. 6). We found strong support for monophyly of Thraupinae in our concatenated analyses (0.99 PP; 86% bootstrap); monophyly was also supported in the genus-level analyses of Barker et al. (2013). Many core tanager species were included in two prior phylogenetic studies. Burns and Naoki (2004) studied relationships among species in *Tangara* using cyt *b* and partial ND2 sequences. Sedano and Burns (2010) expanded this study to include 34 additional species in the core tanager clade and complete ND2 sequences. In the present study, we included five additional species and four additional genetic markers. In general, our results are similar to those reported by Sedano and Burns (2010). None of the nodes that were strongly supported in Sedano and Burns (2010) conflict with those reported in our BEAST and ML trees (Fig. 6). However, support for many nodes increased in our more complete data set. Because the previous studies (Burns and Naoki, 2004; Sedano and Burns, 2010) discussed relationships among these taxa, we do not discuss them in detail here. However, we report the first genetic data for several additional species and comment on their relationships below.

Within *Tangara*, two additional species were included in the present study, *T. rufigenis*, a rare species endemic to Venezuela, and *T. phillipsi*, a relatively recently described species (Graves and Weske, 1987). Prior to Burns and Naoki (2004) and Sedano and Burns (2010), Isler and Isler (1999) provided the most comprehensive, recent treatment of *Tangara*. Isler and Isler (1999) classified species in the genus into 13 species groups based on range, physical appearance, behaviors, and ecology. Isler and Isler (1999) placed *T. rufigenis* into species group 7 along with *T. lavinia* and *T. gyrola*. However, they considered this placement tentative, and suggested that an alternative placement in group 9 (*T. ruficervix*, *T. labradorides*, and *T. cyanotis*) might be more accurate. Our results indicate that *T. rufigenis* belongs in a clade with *T. labradorides* and *T. cyanotis*; thus, *T. rufigenis* is more closely related to some of the species in Isler and Isler's group 9 than to any other *Tangara*. *T. ruficervix*, the other member of Isler and Isler's species group 9, is only distantly related to these species. Sedano and Burns (2010) also identified a close relationship between *T. labradorides* and *T. cyanotis*, but did not sample *T. rufigenis*. Here, we show that *T. rufigenis* belongs in this clade as well and is the closest living relative to *T. labradorides* (1.0 PP; 100% bootstrap). The close relationship of *T. labradorides*, *T. cyanotis*, and *T. rufigenis* was anticipated by some workers before Isler and Isler (1999). When *T. rufigenis* was originally described, Sclater (1856) indicated it was most similar to *T. labradorides*. Although Sclater's later classification (Sclater, 1886) did not place these species near each other, Hellmayr (1935) placed *T. rufigenis*, *T. cyanotis*, and *T. labradorides* all near each other. Later classifications (e.g., Dickinson, 2003; Sibley and Monroe, 1990; Storer, 1970) included *T. ruficervix* with these species, which is not supported by the findings of our study.

Tangara phillipsi is one of the most recently described tanagers (Graves and Weske, 1987) and is only found on the slopes of Cerros del Sira, Peru. On the basis of plumage, Graves and Weske (1987) argued that the species was part of a monophyletic "black-capped" species complex that also included *T. heinei*, *T. argyrofenges*, and *T. viridicollis*. In addition, they suggested *T. cyanoptera* was closely related to the species in this group. Isler and Isler (1999) later included all of these in their species group 12. Graves and Weske (1987) argued that *T. phillipsi* was most closely related to *T. heinei*, and that *T. phillipsi* and *T. heinei* formed a superspecies. Subsequent classifications (e.g., Sibley and Monroe, 1990) have also treated *T. phillipsi* as specifically distinct and part of a species group with *T. heinei*. More recently, Vuilleumier et al. (1992) questioned the species status of *T. phillipsi* and argued that *T. phillipsi* was better treated as a subspecies of *T. heinei*. Ridgely and Tudor (2009) disagreed with Vuilleumier et al. (1992), citing the disjunct distribution of the two species and plumage differences. *T. heinei* is geographically isolated from *T. phillipsi* and occurs in the mountains of Venezuela, Colombia, and Ecuador. Prior to the current study, molecular phylogenetic analyses (Burns and Naoki, 2004; Sedano and Burns, 2010) included all these species except *T. phillipsi* and identified a strongly supported monophyletic clade consisting of *T. heinei*, *T. argyrofenges*, *T. viridicollis*, and *T. cyanoptera*. However, *T. argyrofenges* was only weakly differentiated genetically from *T. heinei*. The present study reports the first genetic data for *T. phillipsi* and shows that this species belongs in this clade as well, as anticipated by Graves and Weske (1987). However, we did not find strong support for the placement of *T. heinei*, *T. argyrofenges*, and *T. phillipsi* with respect to each other. All three are genetically very similar, although they each have unique plumage patterns and colors. Levels of uncorrected cyt *b* sequence divergence among these species averages 0.34% (0.29–0.44%), similar to that seen within species of other tanagers. However, levels of sequence variation can be affected by factors such as time since the cessation of gene flow, different rates of sequence evolution, population size, and past history of bottlenecks. Thus, if molecular data are to be used to assess species status, detailed phylogeographic studies involving numerous individuals across the range of a species are needed. Regardless of species status, our data indicate that these taxa have undergone rapid plumage evolution in the face of little genetic change.

In addition to *T. rufigenis* and *T. phillipsi*, the current study provides sequence data for three additional species of core tanagers that were not included in Sedano and Burns (2010): *Gubernatrix cristata*, *Saltator rufiventris*, and *Paroaria baeri*. *G. cristata*, the Yellow Cardinal, has had a complicated taxonomic history, having been classified at various times with cardinal-grosbeaks (e.g., Hellmayr, 1938; Ridgely and Tudor, 2009) or New World sparrows (e.g., Dickinson, 2003; Paynter and Storer, 1970; Rising, 2011; Sibley and Monroe, 1990; Webster and Webster, 1999). Tordoff's (1954) morphological study showed this species was not a cardinal; therefore, most recent classifications have placed *Gubernatrix* with the New World sparrows. Within this group, *Gubernatrix* is typically placed adjacent to the genus *Paroaria* and other Neotropical genera. Although Sibley and Monroe (1990) transferred many of these Neotropical sparrows to the tanagers, they kept *Gubernatrix* and *Paroaria* with the New World sparrows. Campagna et al. (2011) provided the first molecular phylogenetic analysis that included *Gubernatrix*. They analyzed 694 base pairs of COI and found that *G. cristata* was most closely related to *Diuca diuca* among the 39 species of tanagers included in their phylogeny. Although based on only a small fragment of DNA and only a relatively few number of species, this finding is confirmed by both Barker et al.'s (2013) genus-level sampling and the comprehensive species-level sampling of the current study. We found strong support (1.0 PP; 97% bootstrap) for a sister relationship between *G. cristata* and *D. diuca*, which share a southern South American distribution and have hybridized in nature (Bertonatti and Guerra, 1997). Together, the clade containing *G. cristata* and *D. diuca* is most closely related to *Neothraupis fasciata* (1.0 PP; 88% bootstrap), a species long considered a tanager (e.g., Hellmayr, 1935). Similarities between *Neothraupis* and *Diuca* are reflected in the taxonomic history of *N. fasciata*, which was previously classified in *Diuca* or *Diucopsis* (= 'Diuca-faced'). Although *Diuca diuca* and *D. speculifera* were once considered to be part of the same superspecies (Paynter and Storer, 1970), they are not closely related (see Diglossinae, Section 4.3.14 for *D. speculifera*). *D. speculifera* is the type species of *Diuca*; therefore, for *D. diuca*, we recommend using the available name *Hedyglossa* Reichenback 1851 (type = *D. diuca*).

Our broad taxonomic sampling allowed us to identify cases, such as we found with *Diuca*, where species are only distantly related to their traditional congeners. Similarly, *Saltator rufiventris* belongs to Thraupinae in our phylogenies and is only distantly related to other members of *Saltator* (Saltatorinae, Section 4.3.8). Within the core tanager tree, we found strong support (1.0 PP; 100% bootstrap) for a clade containing *S. rufiventris* and the two species of *Dubusia*. This result agrees with earlier studies (Klicka et al., 2007; Barker et al., 2013) that included some of the data analyzed here. The close relationship of *S. rufiventris* and *Dubusia* agrees with similarities in habitats and elevational distribution of these three species. All species are Andean, with a center of abundance in the upper-montane elevational zone (Parker et al., 1996). Aspects of bill shape and plumage also make *S. rufiventris* a better fit with *Dubusia* than with the other saltators. Because the phylogenetic position of *S. rufiventris* renders *Saltator* paraphyletic, either *Saltator rufiventris* should be merged with *Dubusia* or a new genus name is needed for *S. rufiventris*.

We included an additional species of *Paroaria* (*P. baeri*) that was not included in Sedano and Burns (2010) and found strong support (1.0 PP; 93% bootstrap) for this species being sister to the clade containing *P. gularis* and *P. capitata*. The close relationship of these taxa is consistent with their treatment as a superspecies by Sibley and Monroe (1990). In addition, other authors have considered *P. baeri* a subspecies of *P. gularis*, and *P. baeri* and *P. gularis* have hybridized (Lopes and Gonzaga, 2013). Dávalos and Porzecanski (2009) recently studied species limits in the genus *Paroaria* and included a molecular phylogenetic analysis of cyt *b* sequences from multiple individuals of each species. For the species sampled in common, our phylogeny is largely congruent with that of Dávalos and Porzecanski (2009). Differences include the most basal split within *Paroaria*. Dávalos and Porzecanski (2009) found *P. coronata* to be the sister taxon to all other *Paroaria*, whereas we found a clade containing *P. coronata* and *P. dominicana* to be sister to the remaining species of *Paroaria* sampled. Although we found strong support for a sister relationship between *P. dominicana* and *P. coronata*, Dávalos and Porzecanski (2009) found weak support for a sister relationship between *P. dominicana* and *P. nigrogenis*, a species we did not sample. Differences between the trees of our study and those of Dávalos and Porzecanski (2009) are likely due to differences in sampling, with Dávalos and Porzecanski (2009) including more individuals and taxa and our study including more loci and more outgroups.

In addition to *P. nigrogenis*, we are only missing three other species of core tanagers: *Tangara peruviana*, *T. cabanisi*, and *Thraupis glaucocolpa*. *Tangara peruviana* is very similar in plumage to *T. preciosa*; thus it is likely the sister species of *T. preciosa*. *T. cabanisi* is likely closely related to *T. palmeri* based on similarities in plumage, size, habitat preference, and vocalizations (Hilty and Simon, 1977; Isler and Isler, 1999). *Thraupis glaucocolpa* was previously considered a subspecies of *T. sayaca* (e.g., Hellmayr, 1936; Storer, 1970); thus, these two species are likely sister taxa.

Sedano and Burns (2010) made several taxonomic recommendations for the core tanagers that are supported by the additional data presented here. Specifically, we recommend merging several species of *Thraupis* (*Thraupis episcopus*, *T. sayaca*, *T. glaucocolpa*, *T. cyanoptera*, *T. palmarum*, *T. ornata*, and *T. abbas*) with *Tangara*.

This change is necessary to preserve the monophyly of *Tangara*, a well-known and widely used generic name. Because the name of *Thraupis ornata* will change to *Tangara ornata*, we agree with the recommendation of Sedano and Burns (2010) that the available junior synonym *Tangara argentea* Lafresnaye 1943 be used for the species currently known as *Tangara ornata*. The other species of *Thraupis*, *T. cyanocephala*, is not closely related to the other species in the genus; thus, a new generic name is necessary. No close relatives of *T. cyanocephala* were identified by our phylogenies; therefore, we recommend using the available generic name *Sporathraupis* Ridgway 1898 (type = *T. cyanocephala*) for this species. The two species of *Buthraupis*, *B. montana* and *B. wetmorei*, are not closely related to each other, and our phylogenies did not identify close relatives of either. Thus, we recommend retaining *Buthraupis* for the type species, *B. montana*, and using the available name *Tephrophilus* Moore 1934 (type = *B. wetmorei*) for *B. wetmorei*. The monophyly of *Anisognathus* was equivocal in Sedano and Burns (2010). In the present study, we recovered a monophyletic *Anisognathus*, but support for this clade was only moderate (0.77; 58% bootstrap). Nonetheless, because *Anisognathus* is monophyletic, and because of morphological similarities of these species, we recommend retaining the current species composition of *Anisognathus*.

4.4. Conclusion

The phylogeny presented here has greatly strengthened our understanding of evolutionary relationships and patterns of diversification within Thraupidae. Moreover, this phylogeny sets the stage for studies of trait evolution in a comparative framework. Interspecific studies of various phenotypic traits in tanagers, such as bill morphology, vocal and plumage characters, and ecological niches, have the potential to reveal macroevolutionary patterns, such as correlated evolution and trait-dependent diversification. Using this phylogeny, future studies will shed light on the evolutionary processes that underlie speciation and the accumulation of phenotypic diversity in the largest radiation of Neotropical songbirds.

Acknowledgments

We thank the scientific collectors, collection managers, staff, and curators at the following institutions for providing the tissues used in this study: American Museum of Natural History; Academy of Natural Sciences, Philadelphia; University of Minnesota, Bell Museum of Natural History; Colección Ornitológica Phelps; Cornell University Museum of Vertebrates; Universidad del Valle, Colombia; Field Museum of Natural History; Instituto de Investigación de recursos Biológicos Alexander von Humboldt; Instituto de Ciencias Naturales, Universidad Nacional de Colombia; University of Kansas Natural History Museum; Natural History Museum of Los Angeles County; Louisiana State University Museum of Natural Science Collection of Genetic Resources; Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"; University of Nevada Las Vegas, Barrick Museum of Natural History; Museum of Vertebrate Zoology, University of California, Berkeley; San Diego State University Museum of Biodiversity, Smithsonian Tropical Research Institute; University of Michigan Museum of Zoology; National Museum of Natural History (Smithsonian Institution); University of Washington, Burke Museum; and Zoological Museum, University of Copenhagen. We thank W. Mauck, R. Sedano, R. Keith, M. Alexander, and T. Shepherd for assistance with lab work. E. Dickinson and L. Christidis provided taxonomic advice. For advice on diversification analyses, we thank D. Rabosky. For suggestions on the manuscript, we thank C. Krajewski and two anonymous reviewers. Some of the photos in the graphical abstract were provided by M. Alexander and L. Calvert. This research was supported by the National Geographic Society (KJB) and the National Science Foundation (IBN-0217817 and DEB-0315416 to KJB; DEB-0315218 to IJL; DEB-0315469 to JK; and DEB-0316092 to SML and FKB). AJS was supported by a National Science Foundation Graduate Research Fellowship (2008074713).

Appendix A. New subfamilies

Subfamily Charitospizinae (*new subfamily*); Type genus: *Charitospiza*; Diagnosis: containing a single species, this subfamily is diagnosed by the species characters of *Charitospiza eucosma* Oberholser 1925; Genus: *Charitospiza*.

Subfamily Orchesticinae (*new subfamily*); Type genus: *Orchesticus*; Diagnosis: these two genera are united by a red iris and relatively thick and swollen bill with a hook on the upper mandible. *Orchesticus* has a dark eyeline, and the dark area around the eye in *Parkerthraustes* also includes the lores and ear coverts. We do not know any other morphological characters that unite these genera. Therefore, we also provide 31 unreversed molecular synapomorphies from the cyt *b* gene. These include (numbered by their position in the gene alignment): C243G, T252C, C264T, C307A, C318T, A346G, C348A, A474C, C501A, A504C, C558A, G565C, C591T, T640C, C756A, C768T, C795T, A879C, C888T, C897T, A900C, C903A, A913C, C914T, C957T, C960T, C1074A, C1095T, T1115C, C1117T, and A1122G. Cladistically, we define this subfamily as the descendants of the common ancestor of *Orchesticus abeillei* and *Parkerthraustes humeralis*. Genera: *Orchesticus* and *Parkerthraustes*.

Subfamily Porphyrospizinae *(new subfamily)*; Type genus: *Porphyrospiza*; Diagnosis: members of this subfamily are united by the presence of a bright yellow bill and dark lores in males. Additionally, we have identified 24 unreversed molecular synapomorphies across five genes: cyt *b*: C615A and A729C; ND2: C32T, A39G, C81T, C300A, A484G, C549T, G574A, T715C, C736T, C843A, T924C, T951C, C1033A and T1035C; ACO1: C476T and A768G; MBI2: T190C; and RAG1: G426A, T622C, C1018T and A1870G. Cladistically, we define this subfamily as the descendants of the common ancestor of *Incaspiza pulchra* and *Phrygilus alaudinus*. Genera: *Incaspiza*, *Phrygilus*, and *Porphyrospiza*.

Subfamily Emberizoidinae (*new subfamily*); Type genus: *Emberizoides*; Diagnosis: Species of these three genera share a dark brown iris, green wing feathers, a yellow lower mandible, and a dark culmen. Additionally, we have identified 53 unreversed molecular synapomorphies across five genes: cyt *b*: T161C and C174A; ND2: A39G, C63T, A118G, A277G, C278T, C292T, C366T, C396T, C460T, C477T, A484G, C549T, C606A, G640A, A703G, A722G, G724A, C747T, C762T, C793T, G826A, A844C, C850A, C902T, G948C, C969T, T992C, G993A and C1033A; ACO1: C56T, C74T, T290C, T550G and T825C; Fgbi5: G549A; Mbi2: G32A, G110A, T141A, T190C, G501T and T555C; and RAG1: T253C, T457C, T622C, C1018T, C1198T, T1603C, T1889C, A1984G, T2060C and T2347C. Cladistically, we define this subfamily as the descendants of the common ancestor of *Coryphaspiza melanotis* and *Emberizoides herbicola*. Genera: *Coryphaspiza*, *Emberizoides*, and *Embernagra*.

Subfamily Poospizinae (*new description*); Type genus: *Poospiza*; Diagnosis: We do not know any morphological characters that unite this diverse group. Instead, we have identified seven unreversed molecular synapomorphies across four genes: ND2: C1003A; ACO1: A768G; MBI2: G110A and T190C; and RAG1: T253C, C568G and A1984G. Cladistically, we define this subfamily as the descendants of the common ancestor of *Xenospingus concolor* and *Poospiza melanoleuca*. Genera: *Cnemoscopus*, *Compsospiza*, *Cypsnagra*, *Donacospiza*, *Hemispingus*, *Nephelornis*, *Piezorina*, *Poospiza*, *Pyrrhocoma*, *Thlypopsis*, *Urothraupis*, *Xenospingus*.

Appendix B. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ympev.2014.02.006.

References

Akaike, H., 1973. Information theory and an extension of the maximum likelihood principle. In: Petrov, B.N., Csaki, F. (Eds.), Second International Symposium on Information Theory. Akademiai Kiado, Budapest, pp. 267–281.

Alfaro, M.E., Santini, F., Brock, C., Alamillo, H., Dornburg, A., Rabosky, D.L., Carnevale, G., Harmon, L.J., 2009. Nine exceptional radiations plus high turnover explain species diversity in jawed vertebrates. Proc. Natl. Acad. Sci. USA 106, 13410–13414.

Allen, J.A., 1891. On a collection of birds from Chapada, Matto Grosso, Brazil, made by Mr. Herbert H. Smith. Part I-Oscines. Bull. Am. Mus. Nat. Hist. 3, 337–380.

American Ornithologists' Union, 1983. Check-List of North American Birds, sixth ed. American Ornithologists' Union, Washington, DC.

American Ornithologists' Union, 1998. Check-List of North American Birds, seventh ed. American Ornithologists' Union, Washington, DC.

Areta, J.I., Pearman, M., Ábalos, R., 2012. Taxonomy and biogeography of the Monte Yellow-Finch (*Sicalis mendozae*): understanding the endemic avifauna of Argentina's Monte Desert. Condor 114, 654–671.

Assis, C.P., Raposo, M.A., Parrini, R., 2007. Validação de *Poospiza cabanisi* Bonaparte, 1850 (Passeriformes: Emberizidae). Rev. Bras. Ornitol. 15, 103–112.

Barker, F.K., Burns, K.J., Klicka, J., Lanyon, S.M., Lovette, I.J., 2013. Going to extremes: contrasting rates of diversification in a recent radiation of New World passerine birds. Syst. Biol. 62, 298–320.

Barker, F.K., Cibois, A., Schikler, P., Feinstein, J., Cracraft, J., 2004. Phylogeny and diversification of the largest avian radiation. Proc. Natl. Acad. Sci. USA 101, 11040–11045.

Barreira, A.S., Garcia, G., Lijtmaer, D.A., Lougheed, S.C., Tubaro, P.L., 2008. Blue males and green females: sexual dichromatism in the Blue Dacnis (*Dacnis cayana*) and the Swallow Tanager (*Tersina viridis*). Ornitol. Neotrop. 19, 441–450.

Bates, J.M., Parker III, T.A., Capparella, A.P., Davis, T.J., 1992. Observations on the *campo*, *cerrado* and forest avifaunas of eastern Dpto. Santa Cruz, Bolivia, including 21 species new to the country. Bull. Brit. Ornithol. Club 112, 86–98.

Bauer, C., Pacheco, J.F., Venturini, A.C., Whitney, B.M., 2000. Rediscovery of the Cherry-throated Tanager *Nemosia rourei* in southern Espirito Santo, Brazil. Bird Conserv. Int. 10, 97–108.

Beauchamp, G., Goodale, E., 2011. Plumage mimicry in avian mixed-species flocks: more or less than meets the eye? The Auk 128, 487–496.

Beecher, W.J., 1951. Convergence in the Coerebidae. Wilson Bull. 63, 274–287.

Bellemain, E., Bermingham, E., Ricklefs, R., 2008. The dynamic evolutionary history of the bananaquit (*Coereba flaveola*) in the Caribbean revealed by a multigene analysis. BMC Evol. Biol. 8, 240.

Bertonatti, C., Guerra, A. López, 1997. Hibridación entre Cardenal Amarillo (*Gubernatrix cristata*) y Diuca Común (*Diuca diuca*) en estado silvestre, en Argentina. El Hornero 14, 243–246.

BirdLife International, 2013a. Species Factsheet: *Charitospiza eucosma*. <http://www.birdlife.org> (accessed 30.10.13).

BirdLife International, 2013b. Species Factsheet: *Conirostrum tamarugense*. <http://www.birdlife.org> (accessed 12.09.13).

Bleiweiss, R., 2008. Phenotypic integration expressed by carotenoid-bearing plumages of tanager-finches (Thraupini, Emberizinae) across the avian visible spectrum. Biol. J. Linn. Soc. 93, 89–109.

Bledsoe, A.H., 1988. Nuclear DNA evolution and phylogeny of the New World nine-primaried oscines. The Auk 105, 504–515.

Bond, J., 1951. Taxonomic notes on South American birds. The Auk 68, 527–529.

Brewer, D., 2011. Black-throated Saltator *Saltator atricollis*. In: del Hoyo, J., Elliot, A., Christie, D. (Eds.), Handbook of the Birds of the World. Tangers to New World Blackbirds, vol. 16. Lynx Edicions, Barcelona, p. 419.

Burns, K.J., 1997. Molecular systematics of tanagers (Thraupinae): evolution and biogeography of a diverse radiation of Neotropical birds. Mol. Phylogenet. Evol. 8, 334–348.

Burns, K.J., Hackett, S.J., Klein, N.K., 2002. Phylogenetic relationships and morphological diversity in Darwin's finches and their relatives. Evolution 56, 1240–1252.

Burns, K.J., Hackett, S.J., Klein, N.K., 2003. Phylogenetic relationships of Neotropical honeycreepers and the evolution of feeding morphology. J. Avian Biol. 34, 360–370.

Burns, K.J., Naoki, K., 2004. Molecular phylogenetics and biogeography of neotropical tanagers in the genus *Tangara*. Mol. Phylogenet. Evol. 32, 838–854.

Burns, K.J., Racicot, R.A., 2009. Molecular phylogenetics of a clade of lowland tanagers: implications for avian participation in the Great American Interchange. The Auk 126, 635–648.

Burns, K.J., Shultz, A.J., 2012. Widespread cryptic dichromatism and ultraviolet reflectance in the largest radiation of Neotropical songbirds: implications of accounting for avian vision in the study of plumage evolution. The Auk 129, 211–221.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference. Springer, New York.

Buzzetti, D., Carlos, B.A., 2005. A redescoberta do tiê-bicudo (*Conothraupis mesoleuca*) (Berlioz, 1939). Atual. Ornito. 127, 16–17.

Campagna, L., Geale, K., Handford, P., Lijtmaer, D.A., Tubaro, P.L., Lougheed, S.C., 2011. A molecular phylogeny of the Sierra-Finches (*Phrygilus*, Passeriformes): extreme polyphyly in a group of Andean specialists. Mol. Phylogenet. Evol. 61, 521–533.

Campagna, L., Benites, P., Lougheed, S.C., Lijtmaer, D.A., Di Giacomo, A.S., Eaton, M.D., Tubaro, P.L., 2012. Rapid phenotypic evolution during incipient speciation in a continental avian radiation. Proc. Roy. Soc. B 279, 1847–1856.

Candia-Gallardo, C.E., Silveira, L.F.B., Kuniy, A.A., 2010. A new population of the Cone-billed Tanager *Conothraupis mesoleuca*, with information on the biology, behaviour and type locality of the species. Bird Conserv. Int. 20, 149–160.

Cavalcanti, R.B., Alves, M.A.S., 1997. Effects of fire on savanna birds in Central Brazil. Ornitol. Neotrop. 8, 85–87.

Chapman, F.M., 1926. The distribution of bird-life in Ecuador. Bull. Am. Mus. Nat. Hist. 55, 1–784.

Clark, G.A., 1986. Systematic interpretations of foot-scute patterns in Neotropical finches. Wilson Bull. 98, 594–597.

Chaves, J.A., Hidalgo, J.R., Klicka, J., 2013. Biogeography and evolutionary history of the Neotropical genus *Saltator* (Aves: Thraupini). J. Biogeogr.. http://dx.doi.org/10.1111/jbi.12150.

Clements, J.F., Schulenberg, T.S., Iliff, M.J., Sullivan, B.L., Wood, C.L., Roberson, D., 2013. The Clements Checklist of Birds of the World: Version 6.8. <http://www.birds.cornell.edu/clementschecklist/download/> (accessed 04.10.13).

Dávalos, L.M., Porzecanski, A.L., 2009. Accounting for molecular stochasticity in systematic revisions: species limits and phylogeny of *Paroaria*. Mol. Phylogenet. Evol. 53, 234–248.

Demastes, J.W., Remsen, J.V., 1994. The genus *Caryothraustes* (Cardinalinae) is not monophyletic. Wilson Bull. 106, 733–738.

Dickerman, R.W., 1986. Notes on the plumages of the Paramo Seedeater (*Catamenia homochroa*). The Auk 103, 227–230.

Dickinson, E.C., 2003. The Howard and Moore Complete Checklist of the Birds of the World. Princeton University Press, Princeton.

Diniz, P., Ramos, D.M., Chemin, N., 2013. Breeding biology of Coal-crested Finches. Wilson J. Ornithol. 125, 592–599.

Drummond, A.J., Ho, S.Y., Phillips, M.J., Rambaut, A., 2006. Relaxed phylogenetics and dating with confidence. PLoS Biol. 4, e88.

Drummond, A.J., Suchard, M.A., Xie, D., Rambaut, A., 2012. Bayesian phylogenetics with BEAUti and the BEAST 1.7. Mol. Biol. Evol. 29, 1969–1973.

Eisenmann, E., Short, L.L., 1982. Systematics of the avian genus *Emberizoides* (Emberizidae). Am. Mus. Novit. 2740.

Etienne, R.S., Haegeman, B., Stadler, T., Aze, T., Pearson, P.N., Purvis, A., Phillimore, A.B., 2012. Diversity-dependence brings molecular phylogenies closer to agreement with the fossil record. Proc. Roy. Soc. B 279, 1300–1309.

Fjeldså, J., 1992. Biogeographic patterns and evolution of the avifauna of relict high-altitude woodlands of the Andes. Steenstrupia 18, 9–62.

Fjeldså, J., Krabbe, N., 1990. Birds of the High Andes. Zoological Museum, Univ. Copenhagen, Copenhagen.

Fjeldså, J., Rahbek, C., 2006. Diversification of tanagers, a species rich bird group, from lowlands to montane regions of South America. Integr. Comp. Biol. 46, 72–81.

Freeman, B.G., Arango, J.A., 2010. The nest of the Gold-ringed Tanager (*Bangsia aureocincta*), a Colombian endemic. Ornito. Colombiana 9, 71–75.

George, W.G., 1964. Rarely seen songbirds of Peru's high Andes. Nat. Hist. 73, 26–29.

Grant, P.R., 1999. Ecology and Evolution of Darwin's Finches. Princeton University Press, Princeton, New Jersey.

Grant, P.R., Grant, B.R., 2008. How and Why Species Multiply: The Radiation of Darwin's Finches. Princeton University Press, Princeton, New Jersey.

Graves, G.R., Weske, J.S., 1987. *Tangara phillipsi*, a new species of tanager from the Cerros del Sira, eastern Peru. Wilson Bull. 99, 1–6.

Gray, G.R., 1870. Hand-List of Genera and Species of Birds. Taylor and Francis, London.

Gwynne, J.A., Ridgely, R.S., Tudor, G., Argel, M., 2010. Wildlife Conservation Society Birds of Brazil: The Pantanal and Cerrado of Central Brazil. Comstock Pub. Associates, London.

Hackett, S.J., 1996. Molecular phylogenetics and biogeography of tanagers in the genus *Ramphocelus* (Aves). Mol. Phylogenet. Evol. 5, 368–382.

Hellack, J.J., Schnell, G.D., 1977. Phenetic analysis of the subfamily Cardinalinae using external and skeletal characters. Wilson Bull. 89, 130–148.

Hellmayr, C.E., 1932. The birds of Chile. Field Mus. Nat. Hist., Zool. Ser. 19, 1–472.

Hellmayr, C.E., 1935. Catalogue of birds of the Americas and the adjacent islands. Field Mus. Nat. Hist., Zool. Ser. 13 (Pt. 9).

Hellmayr, C.E., 1936. Catalogue of birds of the Americas and the adjacent islands. Field Mus. Nat. Hist. Publ. Zool. Ser. 13 (Pt. 9).

Hellmayr, C.E., 1938. Catalogue of birds of the Americas and the adjacent islands. Field Mus. Nat. Hist. Publ. Zool. Ser. 13 (Pt. 11).

Hilty, S.L., Simon, D., 1977. The Azure-rumped Tanager in Mexico with comparative remarks on the Gray-and-gold Tanager. The Auk 94, 605–606.

Hilty, S.L., Parker III, T.A., Silliman, J., 1979. Observations on Plush-capped Finches in the Andes with a description of the juvenal and immature plumages. Wilson Bull. 91, 145–148.

Hilty, S.L., 2011. Family Thraupidae (Tanagers). In: del Hoyo, J., Elliott, A., Christie, D.A. (Eds.), Handbook of the Birds of the World. Tanagers to New World Blackbirds, vol. 16. Lynx Edicions, Barcelona, pp. 46–329.

Howard, R., Moore, A., 1991. A Complete Checklist of the Birds of the World. Academic Press, London.

Ingels, J., 2007. Additional information on the breeding biology of the Black-and-white Tanager (*Conothraupis speculigera*) in Ecuador. Boletín SAO 17, 98–103.

Isler, M.L., Isler, P.R., 1999. The Tanagers. Smithsonian Institution Press, Washington, DC.

Jaramillo, A., 2011a. Coal-crested Finch *Charitospiza eucosma*. In: del Hoyo, J., Elliott, A., Christie, D.A. (Eds.), Handbook of the Birds of the World. Tanagers to New World Blackbirds, vol. 16. Lynx Edicions, Barcelona, p. 639.

Jaramillo, A., 2011b. Many-colored Chaco Finch *Saltatricula multicolor*. In: del Hoyo, J., Elliott, A., Christie, D.A. (Eds.), Handbook of the Birds of the World. Tanagers to New World Blackbirds, vol. 16. Lynx Edicions, Barcelona, p. 683.

Jaramillo, A., 2011c. Black-masked Finch *Coryphaspiza melanotis*. In: del Hoyo, J., Elliott, A., Christie, D.A. (Eds.), Handbook of the Birds of the World. Tanagers to New World Blackbirds, vol. 16. Lynx Edicions, Barcelona, p. 640.

Jaramillo, A., 2011d. Patagonian Sierra-finch *Phrygilus patagonicus*. In: del Hoyo, J., Elliott, A., Christie, D.A. (Eds.), Handbook of the Birds of the World. Tanagers to New World Blackbirds, vol. 16. Lynx Edicions, Barcelona, pp. 606–607.

Jaramillo, A., 2011e. White-winged Diuca-finch *Diuca speculifera*. In: del Hoyo, J., Elliott, A., Christie, D.A. (Eds.), Handbook of the Birds of the World. Tanagers to New World Blackbirds, vol. 16. Lynx Edicions, Barcelona, p. 616.

Jaramillo, A., 2011f. Ash-breasted Sierra-finch *Phrygilus plebejus*. In: del Hoyo, J., Elliott, A., Christie, D.A. (Eds.), Handbook of the Birds of the World. Tanagers to New World Blackbirds, vol. 16. Lynx Edicions, Barcelona, p. 608.

Jaramillo, A., 2011g. Plumbeous Sierra-finch *Phrygilus unicolor*. In: del Hoyo, J., Elliott, A., Christie, D.A. (Eds.), Handbook of the Birds of the World. Tanagers to New World Blackbirds, vol. 16. Lynx Edicions, Barcelona, p. 608.

Jetz, W., Thomas, G.H., Joy, J.B., Hartmann, K., Mooers, A.O., 2012. The global diversity of birds in space and time. Nature 491, 444–448.

Johnson, A.W., Millie, W.R., 1972. A new species of conebill (*Conirostrum*) from northern Chile. In: Johnson, A.W. (Ed.), Supplement to the Birds of Chile and Adjacent Regions of Argentina, Bolivia, and Peru. Platt Establecimientos Gráficos S.A., Buenos Aires, pp. 3–8

Kendall, D.G., 1948. On the generalized birth-and-death process. Ann. Math. Stat. 19, 1–15.

Klicka, J., Burns, K.J., Spellman, G.M., 2007. Defining a monophyletic Cardinalini: a molecular perspective. Mol. Phylogenet. Evol. 45, 1014–1032.

Lack, D., 1947. Darwin's Finches. Cambridge Univ. Press, London.

Larkin, M.A., 2007. ClustalW and ClustalX version 2.0. Bioinformatics 23, 2947–2948.

Lebbin, D., 2005. Aberrant plumage in a Black-and-white Tanager (*Conothraupis speculigera*). Boletín SAO 15, 100–104.

Lebbin, D., 2006. Correction of "aberrant plumage" in a Black-and-white Tanager (*Conothraupis speculigera*). Boletín SAO 16, 100–101.

Lloyd, H., Walker, B., Aucca Chutas, C., Schmitt, F., 2005. Range extension of Short-tailed Finch *Idiopsar brachyurus* in Perú with notes on its behaviour, plumage and soft-part colouration and nomenclature. Cotinga 23, 48–51.

Lloyd, H., 2009. In: Schulenberg, T.S. (Ed.) Short-tailed Finch (*Idiopsar brachyurus*), Neotropical Birds Online. Cornell Lab of Ornithology, Ithaca, New York (USA). <http://neotropical.birds.cornell.edu/portal/species/overview?p_p_spp=42732> (accessed 4.10.13).

Lopes, L.E., Gonzaga, L.P., 2013. Taxonomy, natural history, and conservation of *Paroaria baeri* (Aves: Thraupidae). Trop. Zool. 26, 87–103.

Lougheed, S.C., Freeland, J.R., Hanford, P., Boag, P.T., 2000. A molecular phylogeny of Warbling-Finches (*Poospiza*) paraphyly in a Neotropical Emberizid genus. Mol. Phylogenet. Evol. 17, 367–378.

Lovette, I.J., Bermingham, E., 2002. What is a Wood-Warbler? Molecular characterization of a monophyletic Parulidae. The Auk 119, 695–714.

Lowe, P.R., 1923. Notes on some land birds of the Tristan da Cunha group collected by the 'Quest' expedition. Ibis 65, 511–528.

Lowery, G.H., Monroe, B.L., 1968. Family Parulidae. In: Paynter, R.A., Jr. (Ed.), Peter's Check-List of Birds of the World, vol. 14. Museum of Comparative Zoology, Cambridge, Massachusetts, pp. 3–93.

Lucas, F.A., 1895. Osteological and pterylographical characters of the Procniatidae. Proc. US Nat. Mus. 18, 505–507.

Mason, N.A., Burns, K.J. 2010. In: Schulenberg, T.S. (Ed.), Giant Conebill (*Oreomanes fraseri*), Neotropical Birds Online. Cornell Lab of Ornithology, Ithaca, New York (USA). <http://neotropical.birds.cornell.edu/portal/species/overview?p_p_spp=589196> (accessed 30.10.13).

Mason, N.A., Burns, K.J., 2013. Molecular phylogenetics of the Neotropical seedeaters and seed-finches (*Sporophila*, *Oryzoborus*, *Dolospingus*). Ornitol. Neotrop. 24, 139–155.

Marín, M., Kiff, L.F., Peña, L., 1989. Notes on Chilean birds, with descriptions of two new subspecies. Bull. Brit. Ornithol. Club 109, 66–82.

Mauck, W.M., Burns, K.J., 2009. Phylogeny, biogeography, and recurrent evolution of divergent bill types in the nectar-stealing flowerpiercers (Thraupini: Diglossa and Diglossopis). Biol. J. Linn. Soc. 98, 14–28.

Mallarino, R., Campàs, O., Fritz, J.A., Burns, K.J., Weeks, O.G., Brenner, M.P., Abzhanov, A., 2012. Closely related bird species demonstrate flexibility between beak morphology and underlying developmental programs. Proc. Natl. Acad. Sci. USA 109, 16222–16227.

Mayr, E., Vuilleumier, F., 1983. New species of birds described from 1966 to 1975. J. Ornithol. 124, 217–232.

Meyer De Schauensee, R., 1966. The Species of Birds of South America and Their Distribution. Livingston Publishing Co., Narberth, Pennsylvania.

Meyer De Schauensee, R., 1970. A Guide to the Birds of South America. Livingston Publishing Co., Wynnewood, Pennsylvania.

Miller, M.A., Pfeiffer, W., Schwartz, T., 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In: Proceedings of the Gateway Computing Environments Workshop (GCE), 14 November, 2010, New Orleans, LA, pp. 1–8.

Miller, W.De.W., 1928. *Schistospiza* Sharpe not separable from *Lophospingus* Cabanis. The Auk 45, 380–381.

Moynihan, M., 1962. Display patterns of tropical American "nine-primaried" songbirds II. Some species of *Ramphocelus*. The Auk 79, 655–686.

Moynihan, M., 1966. Display patterns of tropical American "nine-primaried" songbirds. IV. The Yellow-rumped Tanager. Smith. Misc. Coll. 149 (5).

Morony Jr, J.J., 1985. Systematic relations of *Sericossypha albocristata* (Thraupinae). Ornithol. Monogr. 36, 382–389.

Nee, S., May, R.M., Harvey, P.H., 1994. The reconstructed evolutionary process. Phil. Trans. Roy. Soc. B 344, 305–311.

Nee, S., Mooers, A., Harvey, P.H., 1992. Tempo and mode of evolution revealed from molecular phylogenies. Proc. Natl. Acad. Sci. USA 89, 8322–8326.

Nylander, J.A.A., Wilgenbusch, J.C., Warren, D.L., Swofford, D.L., 2008. AWTY (are we there yet?): a system for graphical exploration of MCMC convergence in Bayesian phylogenetics. Bioinformatics 24, 58–583.

Oberholser, H.C., 1905. Notes on the nomenclature of certain genera of birds. Smith. Misc. Coll. 48, 59–68.

Olson, S.L., 1986. *Catamblyrhynchus* and *Paradoxornis*: an unremarked instance of convergence in bill morphology for feeding on bamboo. Bull. Brit. Ornithol. Club 106, 161–163.

Orenstein, R.I., 2011. Family Cardinalidae (Cardinals). In: del Hoyo, J., Elliott, A., Christie, D.A. (Eds.), Handbook of the Birds of the World. Tanagers to New World Blackbirds. Lynx Edicions, Barcelona, pp. 330–427.

Parker III, T.A., Stotz, D.F., Fitzpatrick, J.W., 1996. Ecological and distributional databases. In: Stotz, D.F., Fitzpatrick, J.W., Parker, T.A., III, Moskovits, D.K. (Eds.), Neotropical Birds: Ecology and Conservation. Univ. of Chicago Press, Chicago, Illinois, pp. 113–436.

Paynter, R.A., Storer, R.W., 1970. Subfamilies Emberizinae, Catamblyrhynchinae, Cardinalinae, Thraupinae, and Tersininae. In: Paynter Jr., R.A. (Ed.), Check-List of Birds of the World, vol. 13. Museum of Comparative Zoology, Cambridge, MA.

Petren, K., Grant, P.R., Grant, B.R., Keller, L.F., 2005. Comparative landscape genetics and the adaptive radiation of Darwin's finches: the role of peripheral isolation. Mol. Ecol. 14, 2943–2957.

Philippi, B.R.A., 1942. Notas sobre Aves Chilenas. Bol. Mus. Nac. Hist. Nat. Chile 20, 81–89.

Phillimore, A.B., Price, T.D., 2008. Density-dependent cladogenesis in birds. PLoS Biol. 6, 0483–0489.

Posada, D., 2008. JModelTest: phylogenetic model averaging. Mol. Biol. Evol. 25, 1253.

Price, T.D., 2011. Adaptive radiations: there's something about finches. Curr. Biol. 21, R953–R955.

Pybus, O.G., Harvey, P.H., 2000. Testing macro-evolutionary models using incomplete molecular phylogenies. Proc. Roy. Soc. B 267, 2267–2272.

Rabosky, D.L., 2006. LASER: a maximum likelihood toolkit for detecting temporal shifts in diversification rates from molecular phylogenies. Evol. Bioinform. 2, 247–250.

Rabosky, D.L., 2010. Primary controls on species richness in higher taxa. Syst. Biol. 59, 634–645.

Rabosky, D.L., Santini, F., Eastman, J., Smith, S.A., Sidlauskas, B., Chang, J., Alfaro, M.E., 2013. Rates of speciation and morphological evolution are correlated across the largest vertebrate radiation. Nat. Commun. 4, 1–8.

Rabosky, D.L., 2014. Automatic detection of key innovations, rate shifts, and diversity-dependence on phylogenetic trees. *PlosONE* 9:e89543.

Rabosky, D.L., Matute, D.R., 2013. Macroevolutionary speciation rates are decoupled from the evolution of intrinsic reproductive isolation in *Drosophila* and birds. Proc. Natl. Acad. Sci. USA 110, 15354–15359.

Rambaut, A., Drummond, A.J., 2007. Tracer v1.4. <http://beast.bio.ed.ac.uk/Tracer> (accessed 04.10.13).

Remsen Jr, J.V., 1997. A new genus for the Yellow-shouldered Grosbeak. Ornithol. Monogr. 48, 89–90.

Remsen Jr, J.V., Cadena, C.D., Jaramillo, A., Nores, M., Pacheco, J.F., Pérez-Emán, J., Robbins, M.B., Stiles, F.G., Stotz, D.F., Zimmer, K.J., 2013. A Classification of the Bird Species of South America. American Ornithologists' Union. <http://www.museum.lsu.edu/~Remsen/SACCBaseline.html> (accessed 17.09.13).

Restall, R., Rodner, C., Lentino, M., 2006. Birds of Northern South America. Yale University Press, New Haven, Connecticut.

Ridgely, R.S., Tudor, G., 1989. The Birds of South America, The *Oscine Passerines*, vol. 1. Univ. of Texas Press, Austin.

Ridgely, R.S., Tudor, G., 2009. Field Guide to the Songbirds of South America: The Passerines. Univ. of Texas Press, Austin.

Ridgely, R.S., Greenfield, P.J., 2001. The Birds of Ecuador. Cornell Univ. Press, Ithaca.

Ridgway, R., 1901a. The birds of North and Middle America, part I. Bull. US Natl. Mus. 50.

Ridgway, R., 1901b. New birds of the families Tanagridae and Icteridae. Proc. Wash. Acad. Sci. 3, 149–155.

Ridgway, R., 1902. The birds of North and Middle America, part II. Bull. US Natl. Mus. 50.

Rising, J.D., 2011. Family Emberizidae (Buntings and New World Sparrows). In: del Hoyo, J., Elliott, A., Christie, D.A. (Eds.), Handbook of the Birds of the World. Tanagers to New World Blackbirds. Lynx Edicions, Barcelona, pp. 428–683.

Ryan, P.G., 2007. Field Guide to the Animals and Plants of Tristan da Cunha and Gough Island. Pisces Publications, Newbury.

Ryan, P.G., Bloomer, P., Moloney, C.L., Grant, T.J., Delport, W., 2007. Ecological speciation in South Atlantic Finches. Science 315, 1420–1423.

Ryan, P.G., Klicka, L.B., Barker, F.K., Burns, K.J., 2013. The origin of finches on Tristan da Cunha and Gough Island, central South Atlantic Ocean. Mol. Phylogenet. Evol. 69, 299–305.

Sato, A., O'hUigin, C., Figueroa, F., Grant, P.R., Grant, B.R., Tichy, H., Klein, J., 1999. Phylogeny of Darwin's finches as revealed by mtDNA sequences. Proc. Natl. Acad. Sci. USA 96, 5101–5106.

Sato, A., Tichy, H., O'hUigin, C., Grant, P.R., Grant, B.R., Klein, J., 2001. On the origin of Darwin's finches. Mol. Biol. Evol. 18, 299–311.

Sazima, I., 2010. Five instances of bird mimicry suggested for Neotropical birds: a brief reappraisal. Rev. Bras. Ornitol. 18, 328–335.

Schaefer, E., 1953. Contribution to the life history of the Swallow-Tanager. The Auk 70, 403–460.

Schulenberg, T.S., 1985. An intergeneric hybrid conebill (*Conirostrum* x *Oreomanes*) from Peru. Ornithol. Monogr. 36, 390–395.

Sclater, P.L., 1854. On two new species of *Dacnis*, and on the general arrangement on the genus. Proc. Zool. Soc. Lond. 22, 251–252.

Sclater, P.L., 1856. On a new tanager of the genus *Calliste*. Proc. Zool. Soc. Lond. 24, 311.

Sclater, P.L., 1860. List of birds collected by Mr. Fraser in the vicinity of Quito, and during excursions to Pichincha and Chimborazo; with notes and descriptions of new species. Proc. Zool. Soc. Lond. 28, 73–83.

Sclater, P.L., 1886. Catalogue of the Birds in the British Museum, vol. XI. British Museum, London.

Scott, D.A., 1997. A possible re-sighting of the Cherry-throated Tanager *Nemosia rourei* in Espirito Santo, Brazil. Cotinga 7, 61–63.

Sedano, R.E., Burns, K.J., 2010. Are the Northern Andes a species pump for Neotropical birds? Phylogenetics and biogeography of a clade of Neotropical tanagers (Aves: Thraupini). J. Biogeogr. 37, 325–343.

Seutin, G., Brawn, J., Ricklefs, R.E., Bermingham, E., 1993. Genetic divergence among populations of a tropical passerine, the streaked saltator (*Saltator albicollis*). The Auk 110, 117–126.

Sharpe, R.B., 1888. Catalogue of the Birds of the British Museum, vol. XII. British Museum, London.

Short, L.L., 1975. A zoogeographic analysis of the South American chaco avifauna. Bull. Am. Mus. Nat. Hist. 154, 163–352.

Shultz, A.J., Burns, K.J., 2013. Plumage evolution in relation to light environment in a novel clade of Neotropical tanagers. Mol. Phylogenet. Evol. 66, 112–125.

Sick, H., 1993. Birds in Brazil: A Natural History. Princeton University Press, Princeton.

Sibley, C.G., Ahlquist, J.E., 1990. Phylogeny and Classification of Birds. Yale Univ. Press, New Haven.

Sibley, C.G., Monroe, B.L., 1990. Distribution and Taxonomy of the Birds of the World. Yale University Press, New Haven, Connecticut.

Skutch, A.F., 1954. Life histories of Central American birds. In: Pacific Coast Avifauna. Cooper Ornithological Society, Berkeley, California, USA.

Stamatakis, A., 2006. RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. Bioinformatics 22, 2688–2690.

Stamatakis, A., Hoover, P., Rougemont, J., 2008. A rapid bootstrap algorithm for the RAxML web servers. Syst. Biol. 57, 758–771.

Steadman, D., 1982. The origin of Darwin's finches (Fringillidae, Passeriformes). Trans. San Diego Soc. Nat. Hist. 19, 279–296.

Storer, R.W., 1960. Notes on the systematics of the tanager genus *Conothraupis*. The Auk 77, 350–351.

Storer, R.W., 1969. What is a tanager? Living Bird 8, 127–136.

Storer, R.W., 1970. Subfamilies Thraupinae and Tersininae. In: Paynter, R.A., Jr. (Ed.), Check-List of Birds of the World, vol. 13. Museum of Comparative Zoology, Cambridge, MA, pp. 246–409.

Sugiura, N., 1978. Further analysis of the data by Akaike's information criterion and the finite corrections. Commun. Stat. Theory Methods A7, 13–26.

Sushkin, P.P., 1924. On the Fringillidae and allied groups. Bull. Brit. Ornithol. Club 45, 36–39.

Tonnis, B., Grant, P.R., Grant, B.R., Petren, K., 2005. Habitat selection and ecological speciation in Galápagos warbler finches (*Certhidea olivacea* and *Certhidea fusca*). Proc. Roy. Soc. B 272, 819–826.

Tordoff, H.B., 1954. A systematic study of the avian family Fringillidae based on the structure of the skull. Misc. Publ. Mus. of Zool. Univ. Michigan 81.

Venturini, A.C., de Paz, P.R., Kirwan, G.M., 2005. A new locality and records of Cherry-throated Tanager *Nemosia rourei* in Espírito Santo, south-east Brazil, with fresh natural history data for the species. Cotinga 24, 60–70.

Vogt, C.A., 2006. Secondary nectar robbing, a previously unsubstantiated foraging behavior of the Cinereous Conebill (*Conirostrum cinereum*). Ornitol. Neotrop. 17, 613–617.

Vuilleumier, F., 1984. Patchy distribution and systematics of *Oreomanes fraseri* (Aves: Coerebidae) of Andean Polylepis woodlands. Am. Mus. Novit. 2777, 1–17.

Vuilleumier, F., 1967. Speciation in High Andean Birds. Ph.D. Dissertation, Harvard University, 444 pp.

Vuilleumier, F., 1991. A quantitative survey of speciation phenomena in Patagonian birds. Ornitol. Neotrop. 2, 5–28.

Vuilleumier, F., LeCroy, M., Mayr, E., 1992. New species of birds described from 1981 to 1990. Bull. Brit. Orn. Club 122, 267–309.

Webster, J.D., 1988. Skeletons and the genera of tanagers. Proc. Indiana Acad. Sci. 98, 581–593.

Webster, J.D., Webster, J.R., 1999. Skeletons and the genera of sparrows (Emberizinae). The Auk 115, 1054–1074.

Weir, J.T., Bermingham, E., Schluter, D., 2009. The great American biotic interchange in birds. Proc. Natl. Acad. Sci. 106, 21737–21742.

Weir, J.T., Schluter, D., 2008. Calibrating the avian molecular clock. Mol. Ecol. 17, 231–2328.

Wester, P., Claßen-Bockhoff, R., 2006. Hummingbird pollination in *Salvia haenkei* (Lamiaceae) lacking the typical lever mechanism. Plant Syst. Evol. 257, 133–146.

Wetmore, A., 1960. A classification for the birds of the world. Smith. Misc. Coll. 139.

Willis, E.O., 1976. Similarity of a tanager (*Orchesticus abeillei*) and an Ovenbird (*Philydor rufus*): a possible case of mimicry. Ciência e Cultura 28, 1492–1493.

Willis, E.O., 1985. Behavior and systematic status of Gray-headed Tanagers (*Trichothraupis penicillata*, Emberizidae). Naturalia 10, 113–145.

Willis, E.O., 1989. Mimicry in bird flocks of cloud forests in south-eastern Brazil. Rev. Bras. Biol. 49, 615–619.

Witt, C.C., 2005. Syntopic breeding suggests mimicry of the Black-and-white Seedeater (*Sporophila luctuosa*) by the Black-and-white Tanager (*Conothraupis speculigera*). Ornitol. Neotrop. 16, 387–396.

Wolters, H.E., 1975–1982. Die vogelarten der erde, Paul Parey, Hamburg and Berlin.

Yule, G.U., 1924. A mathematical theory of evolution, based on the conclusions of Dr. J. C. Willis, F.R.S. Phil. Trans. Roy. Soc B 213, 21–87.

Yuri, T., Mindell, D.P., 2002. Molecular phylogenetic analysis of Fringillidae, "New World nine-primaried oscines" (Aves: Passeriformes). Mol. Phylogenet. Evol. 23, 229–243.

Zimmer, J.T., 1942. Studies of Peruvian birds, No. 43. Notes on the genera *Dacnis*, *Xenodacnis*, *Coereba*, *Conirostrum*, and *Oreomanes*. Am. Mus. Novit. 1193, 1–16.

Zimmer, J.T., 1947. Studies of Peruvian birds, No. 52. The genera *Sericossypha*, *Chlorospingus*, *Cnemoscopus*, *Hemispingus*, *Conothraupis*, *Chlorornis*, *Lamprospiza*, *Cissopis*, and *Schistochlamys*. Am. Mus. Novit. 1367, 1–26.

Zimmer, J.T., 1952. A new finch from northern Peru. J. Wash. Acad. Sci. 42, 103–104.

Zink, R.M., 2002. A new perspective on the evolutionary history of Darwin's finches. The Auk 119, 864–871.