# MOLECULAR PHYLOGENETICS OF THE NEOTROPICAL SEEDEATERS AND SEED-FINCHES (*SPOROPHILA, ORYZOBORUS, DOLOSPINGUS*)

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**Resumen. – Filogenéticas moleculares de los semilleros Neotropicales (*Sporophila, Oryzoborus, Dolospingus).* –** Las relaciones filogenéticas de gran parte de los paseriformes Oscines de nueve primarias aún no están resueltas. Los semilleros Neotropicales, que están conformados por especies de los géneros estrechamente relacionados *Sporophila, Oryzoborus* y *Dolospingus*, representan un desafió taxonómico desde su descripción inicial. En este estudio construimos una filogenia molecular para evaluar la monofilia de estos tres géneros y comprender las relaciones entre especies. Nuestro análisis filogenético, que utilizó 2814 bp del DNA mitocondrial, indicó que *Sporophila* es parafilético en relación a *Oryzoborus* y *Dolospingus*. Nosotros estudiamos 33 de las 39 especies actualmente reconocidas, lo que permitió dividir a los semilleros Neotropicales en nueve grupos bien soportados. Nuestros resultados indicaron que los agrupamientos previos basados en el plumaje de los machos no representan grupos monofiléticos. Es mas, los resultados denotaron también que existe gran convergencia en los patrones básicos de plumaje de los machos de los semilleros Neotropicales (p.ej., gris, y negro con blanco). De acuerdo con calibraciones de las tasas de mutación del gen citocromo b, se estimó que el ancestro común del grupo estudiado habría existido hace aproximadamente 9.5 millones de años.

**Abstract. –** The phylogenetic relationships within and among many groups of nine-primaried oscines are yet to be resolved. The Neotropical seedeaters and seed-finches of the closely-related genera *Sporophila*, *Oryzoborus*, and *Dolospingus* have puzzled avian taxonomists since their initial description. Here, we reconstruct a molecular phylogeny of these three genera to evaluate their reciprocal monophyly and gain insight into species-level relationships within the group. Our phylogenetic analysis, based on 2184 bp of mitochondrial DNA, reveals that *Sporophila* is paraphyletic with respect to *Oryzoborus* and the monotypic *Dolospingus*. We included 33 out of 39 currently recognized species in our phylogenetic estimate and describe nine groups within the Neotropical seedeaters and seed-finches based on strongly supported nodes. We found that previous groupings based on male plumage do not represent monophyletic groupings. Rather, there is widespread convergence in basic plumage patterning (i.e., gray, black-and-white) among males of Neotropical seedeaters and seed-finches. Based on known mutation rates of the cyt *b* region of the mitochondrial genome, we estimate the timing of the most recent common ancestor of this group to have occurred approximately 9.5 million years ago. *Accepted 3 June 2013.*

**Key words:** *Dolospingus, Oryzoborus, Sporophila,* molecular phylogenetics, seedeaters, seed-finches.

## INTRODUCTION

The nine-primaried oscines of the New World have presented avian systematists with a vexing taxonomic puzzle for centuries. The relationships within and among major groups have been repeatedly debated in light of new information and differing perspectives (e.g., Ridgway 1902, Hellmayr 1938, Mayr 1955, Paynter 1970, Sibley & Ahlquist 1990). With the advance of molecular data and phylogenetic analyses, many previously equivocal evolutionary relationships have now been resolved resulting in many taxonomic reclassifications. For instance, molecular analyses (e.g., Bledsoe 1988, Sibley & Monroe 1990, Burns *et al.* 2002, Klicka *et al.* 2007) demonstrate that many species of Neotropical finches previously classified in Emberizidae are actually tanagers (Thraupidae). Additionally, many of these genera of Neotropical finches have been found to be paraphyletic, such as *Tiaris* (Burns *et al.* 2002) and *Poospiza* (Lougheed *et al.* 2000, Shultz & Burns 2013). Despite recent advances, the phylogenetic affinities within and among many "tanager-finch" genera remain largely unresolved.

The genus *Sporophila* (seedeaters) is one of the most speciose genera of tanagers, and together with *Oryzoborus* and *Dolospingus* forms a widespread group of small, granivorous birds comprised of 39 species (Clements *et al.* 2011, Remsen *et al.* 2012). Together, these three genera exist from the southern tip of Texas to southern South America and share an affinity for open and semi-open habitats (Meyer de Schauensee 1952). Males of this group are typically colorful with bold, melanin-based patterning and are frequently sought after by the pet trade for their melodious vocal displays (Ridgely & Tudor 1989, Collar *et al.* 1992, BirdLife International 2012). Contrastingly, females are notably drab and some taxa have few, if any, interspecific differences from a human visual perspective

(Benites *et al.* 2011). Most taxonomic classifications of this assemblage have been organized according to male plumage coloration and patterning (Meyer de Schauensee 1970, Ridgely & Tudor 1989, Stiles 1996). However, the group's taxonomy has been particularly volatile since its initial description (Hellmayr 1938, Meyer de Schauensee 1952, Burns *et al.* 2002). More recent taxonomic revisions have relied heavily on vocal variation among populations and species to assert species limits (Areta & Repenning 2011a, Areta *et al.* 2011).

As has long been suspected, molecular phylogenies have confirmed that *Sporophila* forms a monophyletic group with the closely related genera *Oryzoborus* and *Dolospingus* (Lijtmaer *et al.* 2004, Robbins *et al.* 2005). Within *Sporophila*, a group known colloquially as the "capuchinos" has garnered additional attention as an exceptionally recent and rapidly-diversifying continental radiation with little to no interspecific differences among commonly used molecular markers (Campagna *et al.* 2009; Areta & Repenning 2011a, 2011b; Areta *et al.* 2011, Campagna *et al.* 2011). Despite this recent attention, a comprehensive phylogeny of the entire seedeater and seed-finch group is still lacking. This paucity of a complete phylogeny has encumbered any comparative studies of ecology, morphology, behavior, and lineage diversification of this interesting group of birds.

Furthermore, recent molecular phylogenies have cast doubt on the monophyly of *Sporophila* and *Oryzoborus* (Lijtmaer *et al.* 2004, Robbins *et al.* 2005). The probable paraphyly of *Sporophila*, as well as similarities in morphology and plumage (Olson 1981a, 1981b), have led many authors to suggest lumping *Oryzoborus* and *Dolospingus* into a broadly-defined, monophyletic *Sporophila* (Sato *et al.* 2001, Burns *et al.* 2002, Lijtmaer *et al.* 2004). However, these previous studies did not sample enough species of both *Oryzoborus* and *Sporophila* to definitively demonstrate

*Sporophila* paraphyly. Here, we provide the most comprehensive species-level taxonomic sampling of the group to date and use mtDNA to construct a phylogenetic hypothesis in order to (1) evaluate the reciprocal monophyly of *Sporophila* and *Oryzoborus*, (2) place *Dolospingus* in the seedeater and seedfinch radiation, and (3) examine the validity of merging these three genera into a single monophyletic genus.

METHODS

*Taxonomic sampling.* We sampled 33 of the 39 currently recognized species (Clements *et al.* 2011, Remsen *et al.* 2012) within the genera *Sporophila*, *Oryzoborus*, and *Dolospingus* (Appendix 1). We were not able to secure samples of *S. americana*, *S. ardesiaca*, *S. bouvronides*, *S. frontalis*, *S. murallae*, or *S. nigrorufa*. Within tanagers, the closest living relative to the seedeaters is unknown (Klicka *et al.* 2007, Barker *et al.* 2013). Thus, we included 21 species from 18 genera representing each of the major clades of tanagers (*Anisognathus, Conirostrum, Creurgops, Cyanerpes, Dacnis, Diglossa, Hemispingus, Hemithraupis, Lanio, Loxigilla, Poospiza, Sicalis, Stephanophorus, Tachyphonus, Tangara, Tiaris,* and *Xenodacnis*). We used the Rose-breasted Grosbeak (*Pheucticus ludovicianus*) to root the relationships of all tanagers.

*Lab procedures.* Nicotinamide dehydrogenase 2 (ND2) and cytochrome *b* (cyt *b*) were used to reconstruct relationships. These mitochondrial markers were selected due to their extensive use and previous success in inferring relationships within other clades of closely related tanagers (Garcia-Moreno *et al.* 2001, Burns & Naoki 2004, Lijtmaer *et al.* 2004, Burns & Racicot 2009, Mauck & Burns 2009, Sedano & Burns 2010). For most species, we sequenced a single individual for both gene regions. However, for three species (*S. nigricollis, S. ruficollis and O. angolensis*), different individuals were sampled for ND2 and cyt *b*. Sampling different individuals for different markers likely did not influence our phylogenetic inference. However, if different populations that are currently recognized as a single species are actually members of distantly related clades, then this practice could negatively influence our ability to infer the true underlying topology. DNA extractions were performed either with the QIAmp DNA Minikit (Qiagen, Valencia, California) or using a 5% Chelex solution (Walsh *et al.* 1991). Reactions were performed in 10-μL capillary tubes and generally involved 40 amplification cycles in a hot-air thermocycler (3 s at 94°C, < 1s at 43–50°C, 30 s at 71°C). Agarose plugs were taken and diluted in 250 μL of water. Plugs were then melted and 3 μL of this solution was reamplified in a 40-μL total reaction volume. Typical re-amplification involved 41 cycles (12 s at 94°C, 4 s at 52°C, and 26 s at 71°C). The final product of polymerase chain reaction was purified using either Exonuclease I and Shrimp Alkaline phosphatase or a GeneClean Kit. The product was then cycle sequenced (96°C for 1 min, 96°C for 30 s, 50°C for 15 s, 60°C for 4 m – 28 cycles) using BigDye terminator reaction mix (Applied Biosystems, Foster City, California). Samples were cleaned using a Sephadex bead column before being sequenced either with a ABI 3100 or ABI 377 DNA sequencer (Applied Biosystems). SEQUENCHER (Gene Codes, Ann Arbor, Michigan) was used to reverse-complement opposing directions, to align different fragments from the same individual, and to translate complete sequences into amino acids. In order to preclude nuclear copies, both heavy and light strands were sequenced, overlapping fragments of cyt *b* and ND 2 were used, the amino acid translation was scanned for stop codons or gaps, and we compared levels of sequence divergence separately for the three cyt *b* fragments as well as the two ND2 fragments.

Most sequences are new to this study (Appendix 1) but some additional sequences (particularly those of the outgroups) were obtained from previously published work (Burns 1998, Klicka *et al.* 2000, Sato *et al.* 2001, Burns *et al.* 2002, Lovette & Bermingham 2002, Burns & Naoki 2004, Klicka *et al.* 2007, Burns & Racicot 2009, Mauck & Burns 2009, Sedano & Burns 2010).

*Phylogenetic inference.* Phylogenetic inference was performed using maximum-likelihood (ML) and Bayesian methods. ML analyses were run using RAxML v7.2.8 (Stamatakis 2006, Stamatakis *et al.* 2008) on the CIPRES v3.1 portal (Miller *et al.* 2010) under the assumed GTR+Gamma model. Multiple runs were performed and each run resulted in an identical topology. The data set was also bootstrapped for 1000 replicates to assess the strength of support for each clade. The resulting trees from the bootstrap replicates were used to construct a 50% majority-rule consensus tree.

Bayesian analyses were run using MrBayes v3.1.2 (Huelsenbeck & Ronquist 2001, Ronquist & Huelsenbeck 2003) on the CIPRES v3.1 portal (Miller *et al.* 2010) with data partitioned by gene region and codon. The appropriate models of evolution for each codon position of both ND2 and cyt *b* were determined using jModelTest v0.1.1 (Posada 2008). Two independent runs of both partitioned and unpartitioned data were run for 20 million generations and sampled every 1000 generations. To examine the possibility of generic-level reciprocal monophyly, we also used MrBayes 3.1.2 (Ronquist & Huelsenbeck 2003) to compare the log-likelihood scores of phylogenetic inference with both *Sporophila* and *Oryzoborus* constrained to be monophyletic to an unconstrained topology using Bayes factors.

We also inferred a time-calibrated phylogeny using BEAST v1.7.2 (Drummond *et al.* 2012) under an uncorrelated log-normal model (Drummond *et al.* 2006). We unlinked rate heterogeneity, base frequencies, and substitution models across partitions. We employed a Yule prior for tree-shape and used a relaxed log-normal molecular clock with the substitution rate reported by Weir & Schluter (2008) of 2.1% (0.0105 mean substitutions per million years along each branch) for the cyt *b* partition. We allowed the substitution rate for ND2 to vary with a uniform prior. To optimize MCMC operators, we ran incrementally longer chains and altered the scale-factors as suggested by the BEAST output. Once scale-factors stabilized, we ran analyses for a total of 110 million generations across five independent runs. We used Tracer v1.5 (Drummond & Rambaut 2007) to confirm convergence among replicate analyses and to ensure that all parameters met threshold effective sample size values ($> 200$). We also used the online program AWTY to assess topological convergence with the "compare" function (Wilgenbusch *et al.* 2004). After identifying and discarding the burn-in, converged runs were combined and subsequently used to estimate divergence times, posterior distributions of topologies, and the maximum clade credibility (MCC) tree.

## RESULTS

*Sequence characteristics.* We found no indels, premature stop-codons or reading frame shifts in our sequences. Upon establishing homology and aligning our sequences, the concatenated data set contained 2184 bp. 1533 bp remained constant, 166 characters were parsimony-uninformative and 485 characters were synapomorphic.

Using a chi-square test, we detected no departure from homogeneity of base frequencies for any codon position in either gene ($P > 0.05$ for all). A partition homogeneity test detected no significant differences in phyloge-

netic signal among the trees reconstructed from individual genes (*P* = 0.67). Including outgroups, Nei's *p* distance of cyt *b* had a mean value of 10.0% (range: 0–14.7%) and 14.2% for ND2 (0–22.1%). Mean uncorrected sequence divergence within the seedeaters was 6.5% for cyt *b* (0–9.7%) and 8.8% for ND2 (0–12.0%). Within the southern capuchinos group, mean divergence was 0.4% for cytb (0–1.0%) and 0.2% for ND2 (0–0.4%).

*Phylogenetic inference.* Neotropical seedeaters and seed-finches (*Sporophila*, *Dolospingus*, and *Oryzoborus*) form a monophyletic group (100 bootstrap (BS), 1.0 posterior probability (PP) within Thraupidae (100 BS, 1.0 PP). However, the closest relative to the seedeater clade remains unclear, as no other group of tanagers received noteworthy support as sister to the seedeaters and seed-finches. Phylogenies inferred with RAxML and BEAST were congruent in topology but differed slightly in branch lengths and node support (Fig. 1). A simultaneous estimation of topology and divergence times in a Bayesian framework using the program BEAST produced a phylogenetic estimate for the seedeaters with generally good resolution and high nodal support (69% of nodes with *PP* = 0.95; Fig. 2). The age of the most recent common ancestor of all ingroup taxa was estimated at 9.5 million years ago based on our relaxed molecular clock (Fig. 2).

Within the clade containing seedeaters and seed-finches, we inferred a sister relationship between *S. lineola* and all remaining ingroup taxa (1.0 PP). We also inferred a monophyletic *Oryzoborus* that is well supported as nested within *Sporophila* (1.0 PP). Additionally, we were able to place the monotypic *Dolospingus* as sister to a clade containing *S. luctuosa, S. nigricollis,* and *S. caerulescens* (1.0 PP*)*. Furthermore, a MrBayes run with *Sporophila* and *Oryzoborus* constrained to be mono-

phyletic performed decisively worse than one where topology was unconstrained (2ln [Bayes Factor] = 18.9). Thus, the genus *Sporophila* is paraphyletic as currently defined (Fig. 1). The implications of the relationships inferred here with respect to previous studies and the current taxonomy are discussed below.

DISCUSSION

Based on our extensive taxonomic sampling at the species level, we were able to infer the most comprehensive molecular phylogeny of the Neotropical seedeaters and seed-finches to date. However, we note that our sampling strategy is limited to a single individual from each currently recognized species that we sampled. Because many species considered here exhibit extensive geographic variation, future work should focus on expanding the phylogenetic hypothesis presented here to include multiple independently evolving loci and multiple individuals per species. The taxonomy of this group has historically been dictated by male plumage patterning (Meyer de Schauensee 1952, Ridgely & Tudor 1989, Stiles 1996) with color groups such as 'gray,' 'black-and- white,' or 'chestnut-colored.' Of the seven groups based on plumage patterning and bill coloration described by Ridgely & Tudor (1989), we recovered only one as monophyletic (Group G; capuchinos). Subsequently, there is a high level of convergence in basic plumage patterning and bill coloration among males of *Sporophila*, such that many of the lineages identified here contain representatives of two or all of the 'gray,' 'black-and-white,' or 'chestnut' groups (Fig. 2). Here, we have identified nine groups within the seedeaters based on strongly supported nodes in our phylogeny. Below, we discuss the implications of these groupings with respect to previous studies
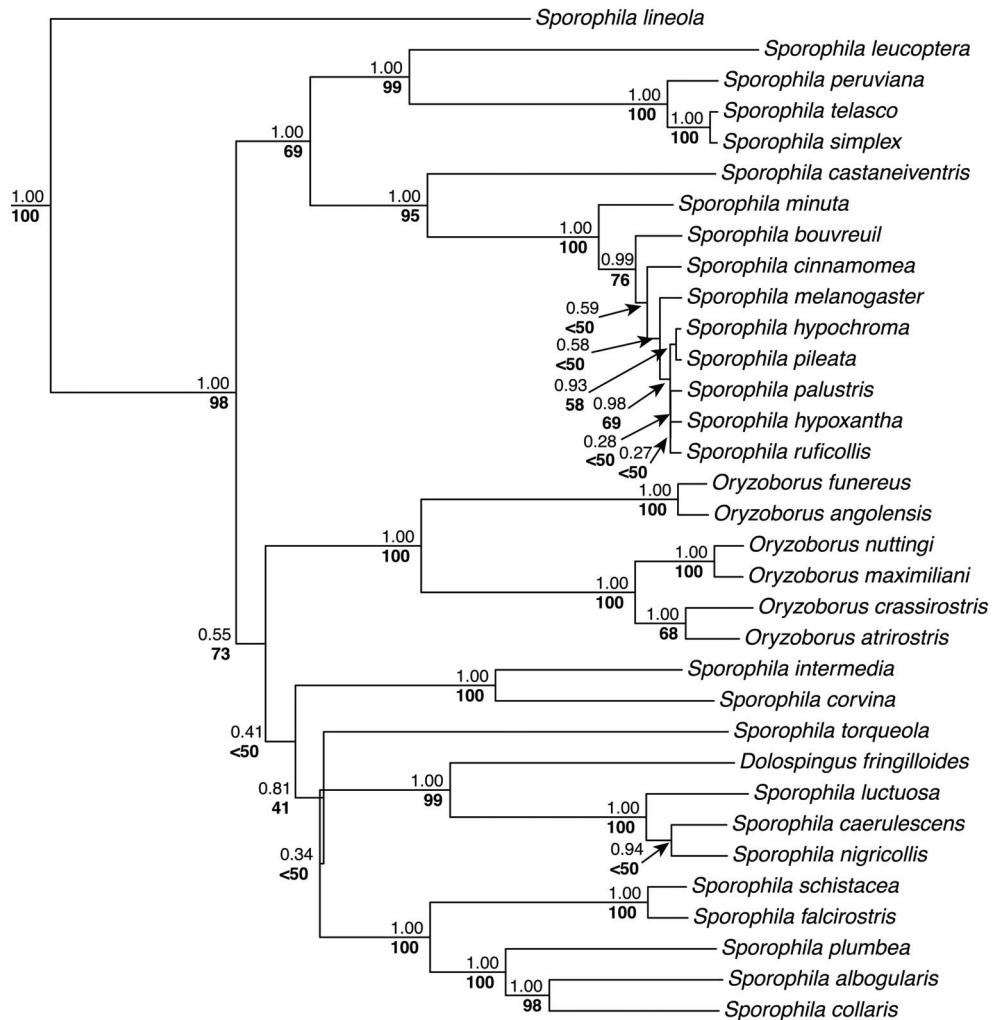
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FIG. 1. Maximum clade credibility tree of Neotropical seedeaters and seed-finches inferred using BEAST with posterior probabilities above each node and bootstrap support values below each node. Phylogeny is rooted with 21 species from 18 genera representing each of the major clades of tanagers.

and identify any natural history traits that the included taxa share.

*The white-cheeked, black-and-white seedeaters.* We inferred a sister relationship between *S. lineola* and the remaining seedeaters and seed-finches (Clade I; Fig. 2). Neither *S. lineola*, nor the presumed close relative *S. bouvronides*, have

been included in any previous molecular phylogenies. The status of these two taxa has been controversial for decades (Meyer de Schauensee 1952). Certain authorities have treated them as a single species citing gradation in the extent of white on the crown and black barring in the chest among museum specimens (e.g., Sclater 1871, Hellmayr 1938,
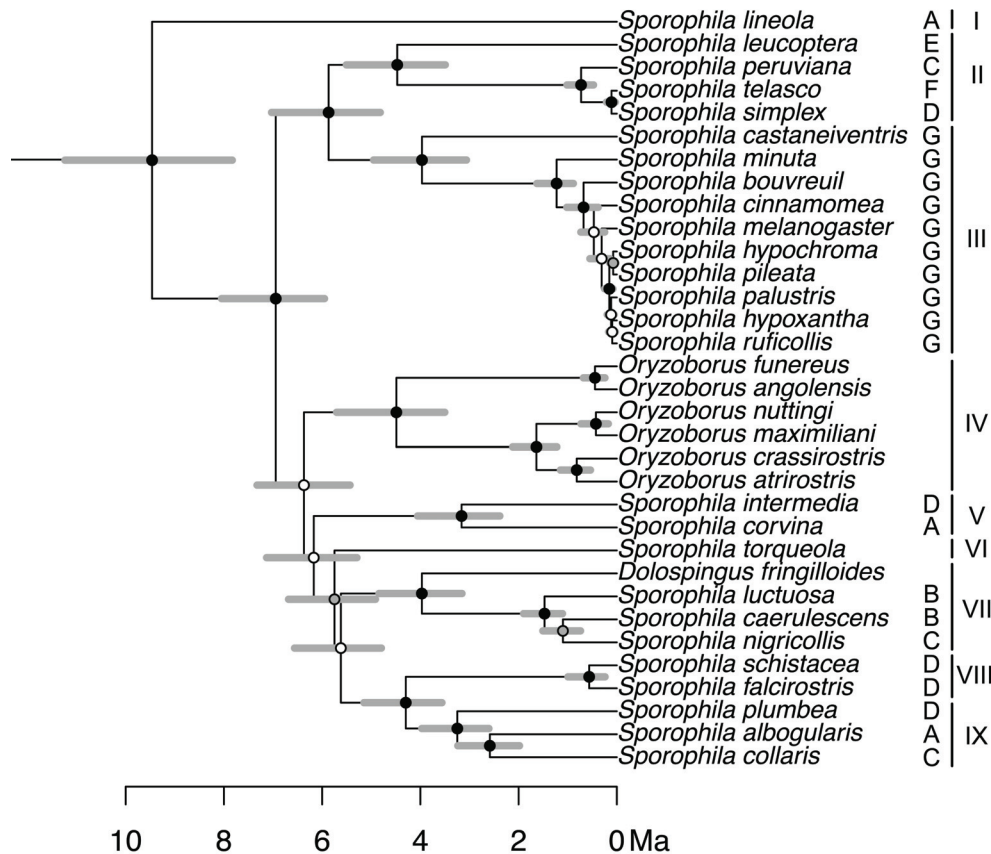
FIG. 2. Time-calibrated maximum clade credibility tree inferred using a relaxed molecular clock with BEAST. Relative levels of node support are represented by white ($PP < 0.75$), grey ($0.75 = PP < 0.95$) and black node colors ($PP = 0.95$). Time scale is in million of years, while node bars represent 95% confidence intervals for divergence timings. Roman letters represent groupings proposed by Ridgely & Tudor (1989), while roman numerals indicate strongly supported clades inferred in this study. Note that Ridgely & Tudor (1989) did not consider species that occur outside of South America (i.e., *S. torqueola*), *Oryzoborus*, or *Dolospingus* in their treatment of the seedeaters and seed-finches.

Pinto 1944, Meyer de Schauensee 1952). Others have considered them separate species (e.g., Phelps & Phelps 1950, Meyer de Schauensee 1951, Schwartz 1975, Clements *et al.* 2011). A comprehensive molecular study would greatly improve our understanding of the validity and history of these two taxa.

*The parrot-billed seedeaters.* We uncovered a strongly-supported clade containing four spe-

cies that share a distinctly curved maxilla and a mostly trans-Andean distribution: *S. leucoptera*, *S. peruviana*, *S. telasco*, and *S. simplex* (Clade II; Fig. 2). However, it should be noted that other taxa outside of this clade have converged on a similar bill shape, such as *S. intermedia*. With the exception of *S. telasco*, the remaining three species occur together in most linear classifications (e.g., Clements *et al.* 2011). Within this clade, the widespread *S.*

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*leucoptera* is sister to the remaining species, all of which occur west of the Andes. Future studies should focus on increased sampling of geographically isolated subspecies within *S. leucoptera* to provide a comprehensive picture of evolutionary relationships within this clade. The sister taxon to this clade is the capuchinos (1.0 PP), which together suggests a recent cis- to trans-Andean colonization event leading to the diversification of *S. peruviana, S. telasco,* and *S. simplex* throughout the arid coastal lowlands west of the Andes from southwest Columbia to northernmost Chile.

The Parrot-billed Seedeater (*S. peruviana*) has a large, thick bill, as its common name implies. A relationship between *S. peruviana* and *S. simplex* was hypothesized by Meyer de Schauensee (1952) based on similarities in dorsal coloration and the curvature of the upper mandible, which is also approximated, albeit smaller in scale, by *S. leucoptera*. Furthermore, *S. peruviana and S. simplex* usually follow *S. leucoptera* in modern linear classifications (e.g., Clements *et al.* 2011). However, we inferred a sister relationship between *S. peruviana* and a clade containing *S. simplex* and *S. telasco* (1.0 PP).

The position of *S. telasco* within the seedeaters has been historically troublesome. While this taxon occurs adjacent to the capuchinos in most linear classifications (e.g., Hellmayr 1938, Meyer de Schauensee 1952, Clements *et al.* 2011), we inferred *S. simplex* as its sister taxon with strong support (1.0 PP). Although the chestnut-colored throat of *S. telasco* is unique within the trans-Andean seedeaters, this taxon does share a similar geographic distribution and bill shape with *S. simplex* and *S. peruviana*, with which it forms a monophyletic group.

*The capuchinos.* The capuchinos represent the only group described by Ridgely & Tudor (1989) to exhibit monophyly (Clade III; Fig. 2). The capuchino radiation is often split into two groups: the northern capuchinos (*S. castaneiventris* and *S. minuta*) and the southern capuchinos (S. *hypoxantha, S. ruficollis, S. palustris, S. hypochroma, S. cinnamomea, S. melanogaster, S. nigrorufa, S. bouvreuil,* and *S. pileata*), which occur north and south of the Amazon River, respectively. Although Lijtmaer *et al.* (2004) inferred monophyly among northern capuchinos, more recent studies (i.e., Campagna *et al.* 2009, Campagna *et al.* 2011) have revealed paraphyly between these two groups. In agreement with the increased taxonomic sampling of Campagna *et al.* (2011), we inferred a paraphyletic grouping of the northern capuchinos with respect to the southern capuchinos. More specifically, *S. castaneiventris* is sister to all remaining capuchinos and *S. minuta* is sister to the southern capuchinos, which form a strongly supported clade. The rare *S. nigro-rufa* was not sampled in this study. However, a COI sequence of this taxon was included by Campagna *et al.* (2011), wherein *S. nigrorufa* formed a monophyletic group with the remaining capuchinos. We note that our sample of *S. pileata* represents a taxon that was recently split from *S. bouveril* based on diagnostic differences in male plumage that lack intergradation in sympatry (Machado & Silveira 2010, 2011; Remsen *et al.* 2012). Interestingly, these two taxa are not recovered as sister species and forthcoming data appear to confirm that they are not each other's closest relatives (Campagna pers. comm.).

Within the southern capuchinos, we found no relationships that were strongly supported by both BEAST and RAxML inference methods (Fig. 2). Given the lack of multiple individuals in our taxonomic sampling strategy and the rampant paraphyly observed within southern capuchino species (Campagna *et al.* 2011), we are hesitant to draw any conclusions regarding relationships in this rapidly diversifying radiation. Whether the southern capuchinos are the products of

an on-going bout of rapid speciation or are members of a hybrid swarm will require further investigation.

*The seed-finches.* We inferred a well-supported clade containing all six of the currently recognized species within the genus *Oryzoborus*, which is nested within *Sporophila* (Clade IV; Fig. 2). Within *Oryzoborus*, *O. funereus,* and *O. angolensis* are sister species and have a known contact zone in northern Colombia (Olson 1981a). The clade containing *O. funereus* and *O. angolensis* is sister to a clade containing the remaining four *Oryzoborus* species. Among these species, *O. nuttingi* and *O. maximiliani* form a clade sister to *O. crassirostris* and *O. atrirostris*. We note that our sample of *O. maximiliani* is from a small population in the Esmeraldas province of northwest Ecuador, where it seldom comes into contact with the phenotypically similar *O. crassirostris*. The two taxa are well differentiated on our phylogeny and are separated by their respective sister species, reflecting the taxonomic splits of *O. nuttingi* from *O. maximiliani* (Stiles 1984) and of *O. atrirostris* from *O. crassirostris* (Sclater & Salvin 1878) based on differences in bill size and coloration.

*The variable seedeater complex.* In addition to the capuchinos, another intriguing, recent radiation exists within *Sporophila*. The "variable-seedeater" complex consists of four currently recognized species (*S. corvina*, *S. intermedia*, *S. americana*, and *S. murallae*), which form a "superspecies" with little overlap among their geographic distributions throughout Central America and northern South America (cf. Haffer 1986, Stiles 1996). *S. intermedia* was not considered part of this group until hybridization with *S. corvina* was described by Stiles (1996). We inferred a monophyletic group containing *S. corvina* and *S. intermedia*, thereby confirming the inclusion of *S. intermedia* in this "superspecies" group (Clade V; Fig. 2).

Unfortunately, due to a lack of samples of *S. murallae* and *S. americana*, we are unable to further elaborate on any relationships within this complex.

*The northern seedeaters.* We were unable to confidently place the White-collared Seedeater (*S. torqueola*), within any of the eight other clades identified here (VI; Fig. 2). This taxon is the northernmost representative of the seedeaters and seed-finches and has not been included in any previous phylogenetic estimates of the group. It was also not considered in Ridgely & Tudor (1989), as these authors only included South American taxa. Some authorities consider this taxon as two species citing non-overlapping geographic distributions as well as differences in wing bars and the extent of cinnamon plumage on the belly and rump among subspecies (Ridgway 1902, Binford 1990). Based on plumage patterning, Eitniear (1997) considered *S. torqueola* to be related to the "variable seedeater" complex. Although we did not recover this relationship, there are no strongly supported nodes separating these taxa, therefore, the possibility of a monophyletic group containing *S. torqueola* and the "variable seedeater" complex persists.

*The gray-billed seedeaters.* We recovered a monophyletic group containing *Dolospingus fringilloides*, *S. nigricollis*, *S. caerulescens*, and *S. luctuosa* (Clade VII; Fig. 2). These taxa are united by predominantly gray bill coloration (but see geographic variation in the bill color of *S. caerulescens*) and typically possess black-and-white plumage patterning (but see the yellow undersides of *S. nigricollis*). This group likely includes the unsampled and poorly-known *S. ardesiaca*, whose taxonomic validity is uncertain but is likely closely related to *S. nigricollis*, from which it was split (Ouellet 1992). Additionally, the little-known and taxonomically contentious *S. melanops* (Hellmayr 1938, Pinto 1944, Ridgely & Tudor 1989, Clements *et al.*

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2011) is also thought to be closely related to *S. nigricollis*. Additional work is required to assess the validity and evolutionary relationships of these enigmatic taxa.

As had long been suspected based on morphological evidence, Robbins *et al.* (2005) confirmed that *Sporophila*, *Oryzoborus*, and the monotypic *Dolospingus* form a monophyletic group. However, Robbins *et al.* (2005) were unable to comment on the placement of *Dolospingus* within the radiation due to sparse taxonomic sampling. We found that within the gray-billed seedeater group, *D. fringilloides* is sister to the remaining taxa. Among the remaining three species, our Bayesian analyses recovered a sister relationship between *S. luctuosa* and a clade containing *S. nigricollis* and *S. caerulescens* (0.94 *PP*). However, this relationship was not recovered by our RAxML analyses (< 50 BS). Males of *S. nigricollis* and *S. caerulescens* are also united by similarities in vocalizations (Mason and Burns unpubl.) and the lack of a prominent small-white speculum that is otherwise widespread among *Sporophila* seedeaters; however, there is variation in the prominence of the speculum among individuals of both species.

*The bamboo specialists.* We recovered a monophyletic group containing the widespread *S. schistacea* and the geographically restricted *S. falcirostris* (Clade VIII; Fig. 2). Together with *S. frontalis*, these three taxa occur together at the beginning of most linear classifications of *Sporophila* (Meyer de Schauensee 1952, Clements 2011) and share a strong affinity for bamboo strands (Ridgely & Tudor 1989). Unfortunately, we lack samples of the little-known *S. frontalis* and are therefore unable to comment on any phylogenetic affinities within this group. However, similarities in ecology and morphology between *S. falcirostris* and *S. schistacea* provide support for a sister relationship between these two taxa (Parker 1982, Areta *et al.* 2013). On a deeper phyloge-

netic level, our phylogenetic estimate places the bamboo specialists as sister to a clade containing *S. plumbea*, *S. collaris*, and *S. albogularis*.

*The white-throated seedeaters.* We inferred a novel clade containing *S. collaris*, *S. plumbea,* and *S. albogularis*, which are united by the presence of a white throat patch (Clade IX; Fig. 2). These taxa are not adjacent in any linear classifications of the seedeaters, demonstrating the wide array of plumage patterns exhibited by males of these taxa. *S. collaris* and *S. albogularis* both possess a distinct black collar and also have similar facial patterns. *S. collaris* is colorful with rusty tones appearing on the nape and belly, whereas *S. albogularis* has entirely black and white plumage. However, it should be noted that *S. collaris* exhibits extensive geographic variation wherein some subspecies lack any rusty coloration (Ridgely & Tudor 1989). In contrast, *S. plumbea* is gray overall with very little patterning, save for a white throat and belly. However, *S. plumbea* exhibits geographic variation in plumage wherein the white chin and throat patch vary in size and are even absent in certain populations (Areta, pers. comm.). Thus, it is difficult to identify a phenotypic character that unites *S. plumbea* with the remaining species in this clade.

*Suggested taxonomic revisions.* Given the topology of our phylogeny and our inclusion of the type species of *Sporophila* (*S. falcirostris*, Temminck 1820), we recommend a taxonomic revision wherein *Dolospingus* and *Oryzoborus* are merged into a broadly-defined *Sporophila*, which has taxonomic priority among the three genera (Cabanis 1844, 1851; Elliot 1871). While certain authors have indicated that bill size and shape (Stiles 1996), in addition to certain skeletal characters (Webster & Webster 1999), distinguish *Oryzoborus* and *Dolospingus* from *Sporophila*, we recommend recognizing the genetic similarity among spe-

cies in these genera revealed by the phylogeny. Bill characters are known to be labile (Remsen 2003), and thus we prefer using the genetic data over bill size and shape for making taxonomic recommendations. This revision has been supported by previous authors based on similarities between *Sporophila* and *Oryzoborus* in morphology and plumage (Olson 1981a, 1981b) as well as the presence of intergeneric hybrids (Sick 1963).

While some taxonomists might be uncomfortable with the generic-level diversity in bill sizes if these three genera are merged, we note that *Sporophila* currently includes *S. peruviana*, which has a bill shape and size that is reminiscent of the *Oryzoborus* seed-finches. Additionally, *S. falcirostris, S. schistaceae*, and *S. frontalis* all possess large lower-mandibles that are unique within *Sporophila* and may represent special adaptations for feeding on bamboo seeds (Areta *et al.* 2009). Thus, *Sporophila* is already diverse in bill size and shape as currently defined. Furthermore, other granivorous nine-primaried oscine genera, such as *Geospiza* (Bowman 1961) and *Passerina* (Klicka *et al.* 2001), express a comparable level of diversity in bill size among species.

## ACKNOWLEDGMENTS

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APPENDIX 1. GenBank accession numbers, museum voucher numbers[1], and localities of taxa used in this study. [1]Acronyms for institutions are as follows: American Museum of Natural History (AMNH), Louisiana State University, Museum of Natural Science (LSUMZ), (The) Field Museum of Natural History (FMNH), University of Washington, Burke Museum (UWBM); Zoological Museum, University of Copenhagen (ZMUC); Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN) Barrick Museum (MBM); National Museum of Natural History, Smithsonian Institution (USNM); Smithsonian Tropical Research Institute (STRI); University of Kansas - Museum of Natural History (KU).

| Taxon name | Source[1]/locality | Accession |
|---|---|---|
| *Anisognathus somptuosus* | LSUMZ B566; Peru: Puno, Abra de Maruncunca, 10 km SW San Juan del Oro | AY383090 (Cyt b); EU648011 (ND2) |
| *Conirostrum margaritae* | LSUMZ B-7293; Peru: Loreto, Amazonas I. Pasto 80 km NE Iquitos 80 m | EU647892 (Cyt b); EU647925 (ND2) |
| *Creurgops dentata* | LSUMZ B-580; Peru: Puno, Abra de Maruncunca, 10 km SW San Juan del Oro | FJ799871 (Cyt b); JN810447 (ND2) |
| *Creurgops verticalis* | LSUMZ B-7974; Peru: Pasco, Playa Pampa, 8 km NW Cushi on trail to Chaglla | FJ799872 (Cyt b); JN810448 (ND2) |
| *Cyanerpes cyaneus* | FMNH 427305; Brazil: Alagoas | FJ799873 (Cyt b); JN810450 (ND2) |
| *Dacnis venusta* | LSUMZ B-26588; Panama: Colon, 17 km by road NW Gamboa, Rio Agua Salud | FJ799874 (Cyt b); JN810459 (ND2) |
| *Diglossa albilatera* | AMNH DOT5023; Venezuela: Aragua, km 40 on El Junquito/Col. Tovar Road | EU647893 (Cyt b); EU647926 (ND2) |
| *Hemispingus atropileus* | LSUMZ B-1889; Peru: Pasco, Chumbre de Ollon, about 12 km E Oxapampa | AF006234 (Cyt b); AF383135 (ND2) |
| *Hemispingus xanthophthalmus* | LSUMZ B-8223; Peru: Pasco, Millpo, E Tambo de Vacas on Pozuzo-Chaglla trail | JN810086 (Cyt b); JN810470 (ND2) |
| *Hemithraupis flavicollis* | LSUMZ B-5102; Peru: Loreto, S Rio Amazonas, ca. 10 km SSW mouth Rio Napo on E bank Quebrada Vainilla | AF006235 (Cyt b); EU647948 (ND2) |
| *Lanio fulvus* | LSUMZ B-2694; Peru: Loreto, 1 km N Rio Napo, 157 km by river NNE Iquitos | EU647917 (Cyt b); EU647951 (ND2) |
| *Loxigilla violacea* | AMNH 25433; Dominican Republic: Independencia | AF489887 (Cyt b); HQ153077 (ND2) |
| *Pheucticus ludovicianus* | MBM X7523; USA: Minnesota, Brown Co. | EF530010 (Cyt b); AF290108 (ND2) |
| *Poospiza cinerea* | USNM B05912; Argentina | FJ799880 (Cyt b); JN810495 (ND2) |
| *Sicalis lutea* | FMNH 391932; Peru: Ancash, Carhuaz, Ishinca, 09°22'49"S, 77°28'08"W | EU647921 (Cyt b); EU647956 (ND2) |
| *Sicalis luteola* | FMNH 389274; Brazil: Roraima, Fazenda Santa Cecilia, E Bank Rio Branco, across from boa Vista | AF489893 (Cyt b); EU647957 (ND2) |
| *Stephanophorus diadematus* | AMNH 9915; Argentina: Buenos Aires, Partido Escobar | EU647992 (Cyt b); EU648053 (ND2) |
| *Tachyphonus surinamus* | LSUMZ B-4795; Peru: Loreto, S Rio Amazonas, ca. 10 km SSW Rio Napo | EU647923 (Cyt b); EU647959 (ND2) |
| *Tangara gyrola* | LSUMZ: B-22850; Bolivia: La Paz, B. Saavedra, 83 km by road E Charazani, Cerro Asunta Pata | AY383131 (Cyt b); EU648071 (ND2) |

APPENDIX 1. Continuation.

| Taxon name | Source/locality | Accession |
| --- | --- | --- |
| *Tiaris fuliginosa* | LSUMZ B-12612; Bolivia: Santa Cruz, Velasco, 50 km ESE of Florida, Arroyo del Encanto | AF489900 (Cyt b); EU648107 (ND2) |
| *Xenodacnis parina* | LSUMZ B-7760; Ecuador: Azuay, 1 km W CJS Nacional de Recreacion, near MGR | AF006257 (Cyt b); EU647960 (ND2) |
| *Dolospingus fringilloides* | USNM B11981; Guyana | JN810073 (Cyt b); JN810461 (ND2) |
| *Oryzoborus angolensis 1* | Oran-CMB241 (Sato *et al.* 2001); Ecuador: Santo Domingo | AF310055 (Cyt b); |
| *Oryzoborus angolensis 2* | FM433798; Peru: Madre de Dios, Moskitania, 13.4 km NNW Atalaya, I bank Alto Madre de Dios, 12°46'S, 71°22'59"W | JN810484 (ND2) |
| *Oryzoborus atrirostris* | ZMUC 123039; Ecuador: Pastaza, N Canelos | JN810098 (Cyt b); JN810485 (ND2) |
| *Oryzoborus crassirostris* | FMNH 339668; Venezuela: Sucre, Guraunos, 14 km SSE | AF489890 (Cyt b); JN810486 (ND2) |
| *Oryzoborus funereus* | MBM 8980; Honduras: Atlantida | EF529963 (Cyt b); EF529851 (ND2) |
| *Oryzoborus maximiliani* | LSUMNS B-11908; Ecuador: Esmeraldas, El Placer, 00°52'N, 78°33'W | EU647919 (Cyt b); EU647954 (ND2) |
| *Oryzoborus nuttingi* | AMNH 787330; Costa Rica: Guanacaste, Laguna Arenal, Tronadora | JN810099 (Cyt b); ND2 not sampled |
| *Sporophila albogularis* | FMNH 392743; Brazil: Alagoas, Piranhas, Fazenda Bela Vista | JN810130 (Cyt b); JN810525 (ND2) |
| *Sporophila bouvreuil* | Brazil, Rio de Janiero, Pontal Lagoa Feia | Pending (Cyt b); ND2 not sampled |
| *Sporophila corvina* | STRI GMS2200; Panama: Chiriqui, N of Bahia de Charco Azul, 3 km W of Divala | JN810136 (Cyt b); JN810530 (ND2) |
| *Sporophila caerulescens* | FMNH 334570; Bolivia: Santa Cruz, Chiquitos, Purubi, 30 km S San Jose de Chiquitos | JN810132 (Cyt b); JN810527 (ND2) |
| *Sporophila castaneiventris* | FMNH 433815; Peru: Madre de Dios, Moskitania, 13.4 km NNW Atalaya, I bank Alto Madre de Dios, 480 m; 12°46'S, 71°22'59"W | JN810133 (Cyt b); JN810528 (ND2) |
| *Sporophila cinnamomea* | MACN 52373; Argentina: Prov. Entre Rios; Arroyo Barú | JN810134 (Cyt b); ND2 not sampled |
| *Sporophila collaris* | FMNH 334564; Bolivia: El Beni, Laguna Suarez, 5 km SW Trinidad | JN810135 (Cyt b); JN810529 (ND2) |
| *Sporophila falcirostris* | MACN 39080; Argentina: Prov. Misiones; Arroyo Urugua-i, km. 40 | JN810137 (Cyt b); ND2 not sampled |
| *Sporophila hypochroma* | LSUMZ B-15265; Bolivia: Santa Cruz, Velasco, Pre Parque Nacional Noel Kempff Mercado, 30 km E Aserradero Moira | JN810139 (Cyt b); JN810531 (ND2) |
| *Sporophila hypoxantha* | FMNH 334574; Bolivia: Santa Cruz, Chiquitos, San Jose-San Ignacio Rd, km 69 | JN810140 (Cyt b); JN810532 (ND2) |
| *Sporophila intermedia* | FMNH 389269; Brazil: Roraima, Fazenda Santa Cecilia, E Bank Rio Branco, across from Boa Vista | EU647922 (Cyt b); EU647958 (ND2) |

APPENDIX 1. Continuation.

| Taxon name | Source/locality | Accession |
| --- | --- | --- |
| *Sporophila leucoptera* | FMNH 334573; Bolivia: El Beni, Laguna Suarez, 5 km SW Trinidad | JN810141 (Cyt b); JN810533 (ND2) |
| *Sporophila lineola* | FMNH 390057; Brazil: Rondonia, Cachoeeira Nazare, W bank Rio Jiparana | JN810142 (Cyt b); JN810534 (ND2) |
| *Sporophila luctuosa* | FMNH 433818; Peru: Madre de Dios, Moskitania, 13.4 km NNW Atalaya, I bank Alto Madre de Dios, 480 m; 12°46'S, 71°22'59"W | JN810143 (Cyt b); JN810535 (ND2) |
| *Sporophila melanogaster* | AMNH 315888; Brazil: Paccaria, Rio Grande do Sul | JN810144 (Cyt b); ND2 not sampled |
| *Sporophila minuta* | FMNH 389270; Brazil: Roraima, Fazenda Santa Cecilia, E Bank Rio Branco, across from Boa Vista | JN810145 (Cyt b); JN810536 (ND2) |
| *Sporophila nigricollis 1* | Spni-CB191 (Sato *et al.* 2001); Ecuador: Santo Domingo | AF310053 (Cyt b) |
| *Sporophila nigricollis 2* | FMNH 427217; Brazil: Alagoas, Ibateouara, Envenho Ceimba, Usina Serra Grande | JN810537 (ND2) |
| *Sporophila palustris* | KU 3689; Paraguay: Itapua, San Rafael National Park, San Pedro Mi, Lat -26.52, Long -55.8 | JN810146 (Cyt b); JN810538 (ND2) |
| *Sporophila peruviana* | LSUMZ B-5243; Peru: Lambayeque, Las Pampas, km 885 Pan-American Hwy, 11 road km from Olmos | JN810147 (Cyt b); JN810539 (ND2) |
| *Sporophila pileata* | UWBM 70800; Argentina: Provincia de Missiones, Posadas, 25 km E, Estancia San Juan; 27°24.36'S, 55°37.22'W | JN810131 (Cyt b); JN810526 (ND2) |
| *Sporophila plumbea* | FMNH 389271; Brazil: Roraima, Fazenda Santa Cecilia, E Bank Rio Branco, across from Boa Vista | JN810148 (Cyt b); JN810540 (ND2) |
| *Sporophila ruficollis 1* | FMNH 334582; Bolivia: Santa Cruz, Chiquitos, Purubi, 30 km S San Jose de Chiquitos | AF489896 (Cyt b) |
| *Sporophila ruficollis 2* | FMNH 334583; Bolivia: La Paz Dept., Prov. B. Saavedra | JN810541 (ND2) |
| *Sporophila schistacea* | LSUMZ B-22584; Bolivia: La Paz Dept., Prov. B. Saavedra | EF529976 (Cyt b); EF529862 (ND2) |
| *Sporophila simplex* | LSUMZ B-33437; Peru: Cajamarca, Las Juntas, junction of Rios Tabacomas and Chinchipe; 05°23.0'S, 78°46.3'W | JN810149 (Cyt b); JN810542 (ND2) |
| *Sporophila telasco* | LSUMZ B-32935; Peru: Cajamarca, Las Juntas, junction of Rios Tabacomas and Chinchipe; 05°23.0'S, 78°46.3'W | JN810150 (Cyt b); JN810543 (ND2) |
| *Sporophila torqueola* | MBM 8476; Honduras: Depto. Atlantida, La Ceiba, 15 km W | JN810151 (Cyt b); JN810544 (ND2) |