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First Guyana records, natural history and systematics of the White-naped Seedeater *Dolospingus fringilloides*

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We report the first records of the White-naped Seedeater *Dolospingus fringilloides* for Guyana, provide new information on its natural history and plumage sequences, and clarify its systematic relationships based on DNA sequence data. *Dolospingus* is a rare and patchily distributed endemic of white-sand scrub of the Guianan shield region. Phylogenetic analyses of a broad sampling of emberizine cytochrome *b* sequences identified a 'seed finch' clade consisting of the genera *Sporophila*, *Oryzoborus* and *Dolospingus* with 100% bootstrap support. More intensive maximum-likelihood (ML) and Bayesian analyses conducted with a reduced data set indicated strong support for the same 'seed finch' clade, but could not distinguish the three genera. In the optimal ML trees, *Dolospingus* and *Oryzoborus* were nested within *Sporophila*, and the two *Oryzoborus* sequences did not cluster together. However, resolution within the seed-finch clade was weak, so the possibility that all three genera are monophyletic cannot be excluded on the basis of the available molecular data. Thus, whether to group these genera on the basis of genetic similarity or retain them on the basis of diagnostic bill and skull differences will remain a matter of preference until a more fully resolved phylogeny of the seed-finch clade is achieved.

The White-naped Seedeater *Dolospingus fringilloides* is a poorly known species that has been recorded from only a handful of widely scattered localities in white-sand scrub of the upper Orinoco–Negro drainage in northern South America (Fig. 1; Hilty & Brown 1986, Ridgely & Tudor 1989, Newman 2000, Hilty 2002). Very little has been published on the natural history of this enigmatic species, and no new information has been brought to light on its taxonomy since Hellmayr (1938) confirmed that *Oryzoborus fringilloides* and *Dolospingus nuchalis* represented the same taxon. Here we provide details on the first Guyana records of *Dolospingus*, report new information on its natural history and plumage sequences, and explore its systematic relationships.

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GUYANA RECORDS, NATURAL HISTORY AND SPECIMEN DATA

We obtained the first records of *Dolospingus* for Guyana on 17 August 1998, when N. Rice, B. Schmidt, M.B.R., M.J.B. and C.M.M. found the species to be fairly common in an isolated savanna, known as Gunn's Strip (01°39′N, 58°37′W), on the west bank of the upper Essequibo River in extreme southern Guyana (Fig. 1). About 125 km to the northwest, on 6 April 2000, M.B.R. observed and heard a single adult male singing briefly at the edge of white-sand forest scrub at the southern end of the Rupununi savanna (02°12′N, 59°22′W; Robbins *et al.* 2004). These new localities are not totally surprising given that Andrew Whittaker discovered the species *c.* 150 km north of Manaus, Brazil (about 400 km south of our Guyana localities), on 23 August 1995 (Kirwan 1996). The Guyana records extended the range *c.* 800–900 km to the east of known localities in Amazonas, Venezuela

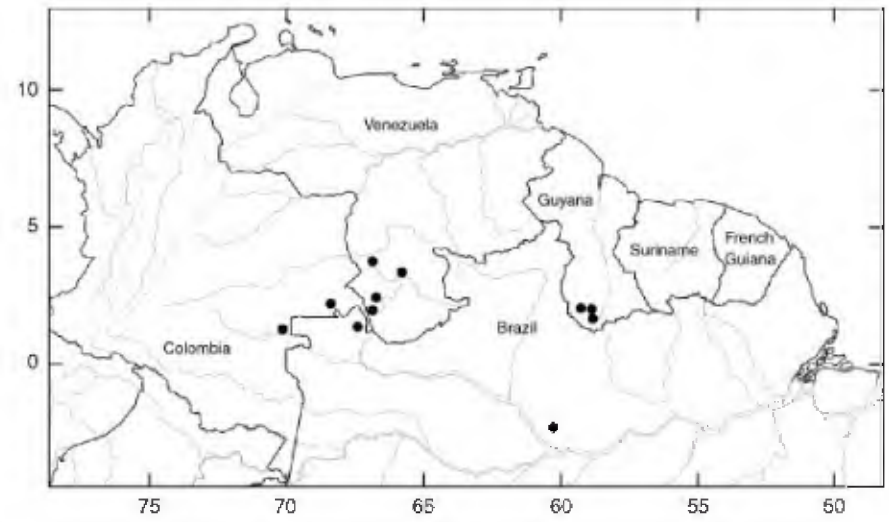

Figure 1. Map of northern South America showing all known localities for *Dolospingus fringilloides* (see text for sources).

and the Rio Xié, upper Rio Negro drainage, Brazil (Ridgely & Tudor 1989, Hilty 2002).

During August 1998, males persistently sang relatively loud and far-carrying songs from exposed perches, *c.* 2–4 m above the ground, in scattered patches of low-stature scrub in savanna and white-sand forest edge (M.B.R. recordings; MLNS 107149–56). A few males' territories were in recently burned areas at the forest edge. Males sang for up to several minutes from the same perch before moving to another perch or pursuing conspecifics. At least ten territorial males were found in *c.* 12 km^2 that we surveyed. From the air, it was apparent that suitable habitat covered a much larger area. All of four adult male specimens collected in August 1998 had enlarged testes, 5 × 5–7 × 6 mm, and a female specimen had a fully ossified skull with a 4 × 2-mm bursa of Fabricius, on the basis of which, we suspect that she was several months old.

M.J.B., C.M.M. and B. Schmidt returned to this area in late February and early March 1999 and found adult and younger males consistently singing over a broader area than was surveyed 6 months earlier. During that period adult males had testes enlarged to the same degree as males taken the previous August. A female that was collected on 4 March was noted as 'laying' with an ovary mass of 16 × 11 mm. One immature male (USNM 625733), which was virtually indistinguishable in plumage from adult females, had a 4 × 3-mm bursa with only a 10% ossified cranium. Two other immature males (USNM 625732, 625731), with partially ossified skulls (40 and 60%, respectively) and 3 × 3-mm bursae, were moulting from pre-basic to first basic plumages. Overall, both these males were darker brown in plumage than adult females. These males had black centres to the crown feathers, black mottling on the face and chin, and an indistinct brown band across the upper chest with some black feathers. The lower breast and abdomen were whitish with a tinge of buffy brown to some feather tips. Both also had the white wing speculum and white wing bars of the definitive adult male plumage. USNM 625732 had recently moulted all remiges except for secondaries 5 and 6. USNM 625731 had primaries 8, 5 and 3 and the three outer pairs of rectrices in moult. Studies of marked individuals are needed to ascertain how many moult stages are necessary to obtain the definitive plumage.

On 17 November 1999, D.W.F. and D. deFreitas obtained video of a male and three females feeding on mistletoe fruit on a small, rocky island near the mouth of the Kassikaityu River (01°50.5′N, 58°33.7′W). The following day at Gunn's Strip they observed two males and a female. Males were heard singing at the latter site on 19 November 2001 and 6 November 2002. On 28–29 April 2001, D.W.F. and others found the Gunn's savanna partially flooded and no *Dolospingus* were encountered.

From the above behavioural observations coupled with specimen data it appears that *Dolospingus* may breed from the end of the rainy season (August) to the end of the dry season (April), but more information is needed to confirm that this is the case.

The habitat in which we encountered *Dolospingus* conforms to what has been reported elsewhere (Hilty & Brown 1986, Ridgely & Tudor 1989, Newman

2000, Hilty 2002). The species seems to be restricted to white-sand scrub in savannas and forest clearings. In much of the known range of *Dolospingus* this habitat is patchy and is often surrounded by hundreds of kilometres of rain forest. The observation by D.W.F. and others of birds on river islands may offer insight into how this species moves across a large matrix of forest-dominated habitat to find pockets of appropriate habitat. *Dolospingus* is now known from extreme eastern Colombia across southern Venezuela east to southern Guyana and northern Brazil (Fig. 1). Investigations of isolated savanna/woodland in northern Brazil will probably fill in some of the apparent gaps depicted in Figure 1.

Specimen soft part colours were as follows: all age classes and both sexes had brown or dark brown irides. Adult male bills were 'light blue' or 'greyish-blue' with dark tips. An immature male in female-like plumage had a dark brownish horn-coloured bill. One male in transitional plumage had a grey bill with a black culmen, whereas another transitional-plumaged male had a greyish bill. Both adult and immature females had grey bills. Female tarsi were greyish-black or grey-brown, whereas adult males had grey or dark grey tarsi. Adult and immature males weighed 13.1 g ± 0.7 sd (n = 10) and females 12.3 g ± 0.2 sd (n = 3). All birds had little or only a trace of fat. Stomach contents from five males and one female contained seeds, ranging in size from 2.5 × 2.1 to 3.2 × 2.5 mm.

SYSTEMATICS

Taxonomic background

The female of this species was first described by von Pelzeln (1870), and tentatively placed as '*Oryzoborus (?) fringilloides*'. A year later, Elliot (1871) described an adult male as the species *nuchalis* and created the new genus *Dolospingus*. It was not until Hellmayr (1938) examined a series of recently obtained specimens that it was positively established that *fringilloides* and *nuchalis* represented the same species. Elliot (1871) recognized the similarity in plumage of *Dolospingus* and certain species of *Spermophila* (= *Sporophila*), and stated that 'were it not for its extraordinary bill (it) would seem to find its place most naturally in that genus'. Thus, there was early recognition of a possible relationship of *Dolospingus* to *Sporophila* and *Oryzoborus*. However, although *Sporophila* and *Oryzoborus* have generally been listed next to each other in linear classifications, several genera (*Amaurospiza*, *Melopyrrha*, *Volatinia*) typically are placed between them and *Dolospingus* (e.g. Paynter & Storer 1970, Sibley & Monroe 1990).

Molecular methods

DNA extraction and sequencing

DNA was extracted from tissue samples of *Dolospingus* (USNM 625323, 625324) by a standard proteinase K-phenol/chloroform procedure (Mariaux & Braun 1996) with Phase Lock Gel (Eppendorf) as an aid to phase separation. The cytochrome *b* gene was amplified via polymerase chain reaction (PCR) in 25-μL reactions using Ready-To-Go PCR Beads (Amersham Biosciences). The final reaction conditions were: 200 μM each dNTP, 50 mM KCl, 1.5 mM $MgCl_2$, 10 mM Tris/HCl (pH 9), 0.06 U/μL *Taq* DNA polymerase, 0.6 μM each amplification primer (see Table 1) and 25 ng of template DNA. PCR was performed in a DNA Engine Tetrad thermal cycler (MJ Research) with the following cycling profile: 3 min at 95 °C, followed by 25 cycles of 15 s at 95 °C, 15 s at 55 °C, 30 s at 72 °C, and a final extension phase of 10 min at 72 °C.

The PCR products were purified by precipitation with polyethylene glycol and cycle sequenced completely on both strands, using the primers listed in Table 1, with BigDye v.3.1 chemistry (Applied Biosystems) according to the manufacturer's instructions. BigDye

Table 1. DNA primers used for *Dolospingus*. L14764 and H16060 were used for PCR amplification and sequencing, all others for sequencing only.

Primer	Sequence (5′ to 3′)	Source
L14764	TGRTACAAAAAAATAGGMCCMGAAGG	Sorensen *et al.* (1999)
L14990	CCATCCAACATCTCAGCATGATGAAA	Kocher *et al.* (1989)
L15335	TGRGGCGCTACAGTAATTAC	this study
L15722	CACATCAAACCAGAATGATACTTCCTATT	Helbig and Seibold (1999)
H15549	AGAAGTATGGGTGGAATGGG	this study
H15931	TTGGCCRATAATGATGAATGG	this study
H16060	TTTGGYTTACAAGACCAATG	this study

Terminator v1.1/3.1 sequencing buffer was used to reduce by half the amount of Ready Reaction Premix needed. Reaction products were purified with Sephadex G-50, and sequences were determined on an ABI 3100 capillary DNA sequencer (Applied Biosystems). Consensus sequences were assembled for each individual using Sequencher 4.1.2 (GeneCodes).

The newly determined sequences (GenBank accession nos. AY705434–5) contained a full-length open reading frame for cytochrome *b* of 1143 bp and had sequence characteristics (e.g. base composition, substitution patterns) consistent with a mitochondrial DNA origin. The two *Dolospingus* individuals differed by just three substitutions. Two were synonymous third-position transitions; the third was a third-position transversion that predicts a leucine to phenylalanine replacement at amino acid site 373, seven residues from the carboxy terminus.

Phylogenetic analysis

Cytochrome *b* sequences of selected emberizines (taxonomy and nomenclature follow Sibley & Monroe 1990) were downloaded from GenBank and aligned with *Dolospingus* to construct a 50-taxon data set. Sequences included in this data set (and their GenBank accession nos.) were *Anisognathus somptuosus* AF006211, *Atlapetes rufinucha* AF310061, *Catamenia inornata* AF310049, *Chlorospingus pileatus* AF006218, *Chlorothraupis carmioli* AF006219, *Coryphospingus cucullatus* AY005221, *Cyanocompsa brissonii* AF301461, *Cyanocompsa cyanoides* AF301462, *Cyanocompsa parellina* AF301460, *Embernagra platensis* AY005220, *Euphonia fulvicrissa* AF383014, *Euphonia finschi* AF290143, *Euphonia laniirostris* AF006232, *Euphonia musica* AF310067, *Geospiza fortis* AF447369, AF108773, AF108772 and AF108771, *Haplospiza unicolor* AF290156, *Loxigilla portoricensis* AF489886, *Loxipasser anoxanthus* AF489888, *Melanospiza richardsoni* AF310043, *Melopyrrha nigra* AY005219, *Mitrospingus cassinii* AF006240, *Neothraupis fasciata* AF006242, *Oryzoborus angolensis* AF310055, *Oryzoborus crassirostris* AF489890, *Passerina ciris* AF301459, *Phrygilus alaudinus* AY005218, *Piranga ludoviciana* AY124545, *Poospiza hispaniolensis* AF310052, *Saltator striatipectus* AF383107, *Saltatricula multicolor* AY005217, *Sicalis luteola* AF489893, *Spindalis zena* AF383018, *Sporophila americana* AF310054, *Sporophila collaris* AF489895, *Sporophila castaneiventris* AF310056, *Sporophila nigricollis* AF310053, *Sporophila plumbea* AY115409, *Sporophila ruficollis* AF489896, *Sporophila schistacea* AF290149, *Tangara seledon* AY228083, *Tiaris fuliginosa* AF489900, *Tiaris olivacea* AF489901 and AF447375, and *Volatinia jacarina* AF310046 and AF290150. All sequences were aligned using Clustal W (Thompson *et al.* 1994) and no internal gaps were required. Sequences varied in length from 849 to 1143 bp.

Phylogenetic analyses were performed with PAUP* 4.0b10 (Swofford 2003). Neighbour-joining analysis (NJ; Saitou & Nei 1987) used uncorrected pairwise sequence divergence values (p distances) and 1000 bootstrap pseudoreplicate data sets. Maximum parsimony tree searches were conducted with all characters equally weighted, ten random addition heuristic searches with TBR branch-swapping per data set and 1000 bootstrap pseudoreplicate data sets. For maximum likelihood (ML) analysis, models of evolution and rate heterogeneity parameters were evaluated using methodologies described in the ModelTest version 3.06 package (Posada & Crandall 1998). First, an NJ tree was produced via PAUP* using Jukes–Cantor distances. Parameters were then calculated for 56 nested models of sequence evolution on the NJ tree and the models evaluated with ModelTest using the Akaike information criterion (AIC) and the successive approximations approach suggested by Swofford *et al.* (1996). In this case, the general time reversible with invariant sites and gamma distribution model (GTR + I + Γ) was selected, allowing for unequal base frequencies, unequal mutation rates and among-site rate variation. This model was then applied to heuristic ML tree searches performed with PAUP*. The original data were analysed with TBR branch-swapping and ten random addition searches. One hundred bootstrap pseudoreplicate data sets were analysed also, with TBR branch-swapping and one random addition search per data set. Bayesian phylogenetic analysis was performed using MrBayes 3.0b4 (Huelsenbeck & Ronquist 2001) and a GTR + I + Γ model. Four Markov chains were run for 5 million generations each. Topology and model parameters were sampled every 100th generation and used to determine the posterior probabilities of clades and estimates of model parameters. The first 10 000 samples were discarded to allow for burn-in to the target distributions; default settings were used for all other options.

RESULTS AND DISCUSSION

Phylogenetic analyses

Several recent studies have examined emberizine phylogeny using DNA sequence data from the

Table 2. Genetic divergence of cytochrome *b* sequences. Mean uncorrected sequence divergence (p) of *Dolospingus* vs. various groups of emberizids and *Euphonia* from Figure 2.

Taxa compared	*n*	Mean p (range)	Variable sites	Aligned sites
Dolospingus vs. *Dolospingus*	1	0.003	3	1143
Within seed-finch clade	36	0.061 (0.046–0.078)	176	894–1143
Seed finch clade vs. Outgroup emberizids	55	0.102 (0.087–0.115)	268	849–1143
Emberizids vs. *Euphonia*	14	0.151 (0.138–0.158)	314	849–1143

cytochrome *b* gene (Klicka *et al.* 2001, Sato *et al.* 2001, Burns *et al.* 2002, Yuri & Mindell 2002). These studies provide a framework of emberizine relationships and a resource to help place enigmatic taxa such as *Dolospingus*. We first compared the *Dolospingus* sequences to a broad selection of emberizines, concentrating on genera with heavier, finch-like bills in Sibley and Monroe's (1990) Thraupini (see Methods). Neighbour-joining and maximum parsimony analyses of this 50-taxon data set identified a 'seed finch' clade consisting of the genera *Sporophila*, *Oryzoborus* and *Dolospingus* with 100% bootstrap support in both cases (trees not shown). A close relationship between *Sporophila* and *Oryzoborus* cytochrome *b* sequences has previously been found by Sato *et al.* (2001) and Burns *et al.* (2002) based on the same data used here. Uncorrected pairwise sequence divergence values within this clade ranged from 4.6 to 7.8%, while distances to other thraupines were higher, averaging around 10% (Table 2). Divergence values to the outgroup *Euphonia* were higher still, ranging from 13.8 to 15.8%.

We next performed ML and Bayesian analyses on a reduced data set to minimize the computation time required. This data set consisted of the 'seed finch' clade plus six outgroup taxa. Two optimal trees were recovered in the ML analysis (Fig. 2). Both ML bootstrapping and Bayesian posterior probability indicated strong support for the same seed-finch clade consisting of *Sporophila*, *Oryzoborus* and *Dolospingus*, but could not distinguish the three genera (Fig. 2). In the optimal ML trees, *Dolospingus* was nested within *Sporophila*, and the two *Oryzoborus* sequences did not cluster together. However, there was only one well-supported supraspecific node within the seed-finch clade, *S. castaneiventris* plus *S. ruficollis*. These two species share chestnut underparts in the adult male plumage, a character defining species group G of Ridgely and Tudor (1989). Thus, it is equally reasonable to think of relationships within the seed-finch clade as a largely unresolved polytomy based on the current cytochrome *b* evidence.

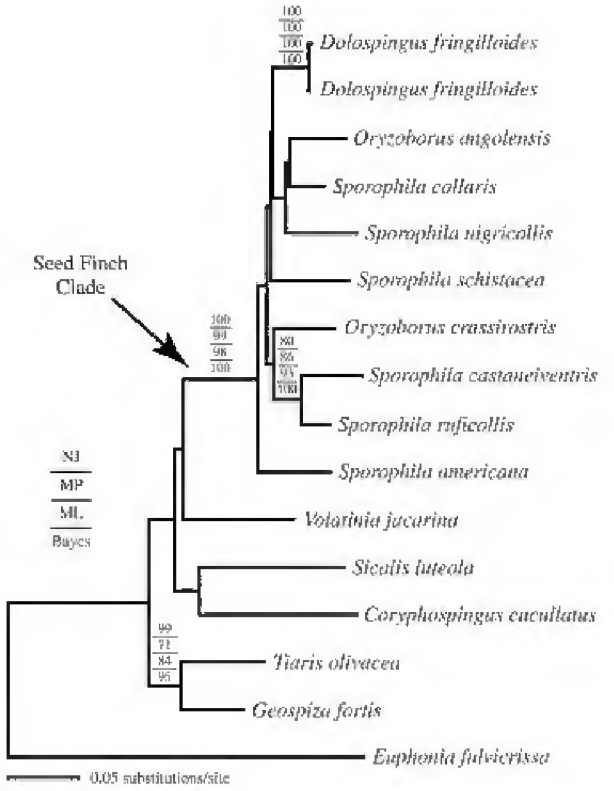

Figure 2. Phylogenetic relationships based on maximum likelihood analysis of cytochrome *b* DNA sequences. The tree shown is one of two optimal topologies found; the other differed only in the placement of *O. crassirostris*. Numbers on branches reflect bootstrap support values for neighbour-joining (NJ), maximum parsimony (MP) and maximum likelihood (ML) analyses and posterior clade probabilities for Bayesian analysis. All other internal branches had support values of less than 50. Previous molecular studies have shown that *Euphonia* is not closely related to other emberizines (McDonald 1988, Burns 1997) and is probably a derived fringilline (Klicka *et al.* 2000, Yuri & Mindell 2002), so it was treated as an outgroup. The parameter values of the GTR + I + Γ model were: base frequencies (A = 0.2785, C = 0.3851, G = 0.1283, T = 0.2081); rate matrix (A–C = 5.0107, A–G = 20.5812, A–T = 2.6914, C–G = 1.0657, C–T = 33.2377, G–T = 1.0000); gamma shape parameter = 1.5437; proportion of invariant sites = 0.6500.

Two other interesting possibilities are suggested by the topology of the optimal ML trees (Fig. 2). First, *S. americana* is basal to other taxa in the seed-finch clade, suggesting that its black and white plumage pattern may be ancestral. A black and white pattern is shared with at least five other species of *Sporophila*

(*corvina*, *murallae*, *luctuosa*, *lineola* and *bouvronides*) and *Dolospingus*. Stiles (1996) showed that *S. intermedia*, with grey adult male plumage, is part of an allospecies complex with *americana*, *corvina* and *murallae*, and suggested that black and white male plumage was ancestral within the complex. Stiles (1996) also pointed out that no member of this complex was known to occupy the Guyana Shield. With the new distributional information, the range of *Dolospingus* fills this void. Whether it might belong to an enlarged species complex of seedeaters with black and white male plumage will require more sequence data and more complete taxon sampling of *Sporophila* to test.

Secondly, *Volatinia* is weakly supported as the sister group of the seed-finch clade in the topology of Figure 2. This is consistent with the possibility suggested by Clark (1986) that five finch genera (*Dolospingus*, *Sporophila*, *Oryzoborus*, *Volatinia* and *Charitospiza*) that share a unique pattern of foot scutellation form a monophyletic group. Again, more data from additional taxa will be required to test this hypothesis adequately.

Vocalizations

Recognizing that song is apparently learned in most emberizids (Kroodsma & Baylis 1982), we nonetheless compared our recordings of the song of *Dolospingus* with available song recordings of *Oryzoborus* and *Sporophila* (our pers. recordings, Boesman 1999, Mayer 2000) to determine whether this might shed any light on relationships. The song of *Dolospingus* is totally unlike any *Sporophila* and it is quite distinct from the sweet prolonged series of warbled notes of *O. funereus*, *O. angolensis* and apparently *O. nuttingi* (for which we relied on published song descriptions in Stiles & Skutch 1989). The loud, complex and musical song of *Dolospingus* is most similar to that of *Oryzoborus crassirostris* and *O. maximilliani*, but it lacks the trills that are intermixed in *maximilliani*'s song. Nevertheless, the superficial similarities of the song of *Dolospingus* to those of *crassirostris* and *maximilliani* may not reflect any close relationship. The complex, far-carrying song of *Dolospingus* simply may be a reflection of communication in a more enclosed habitat than for the other seedeaters, which are typically in very open areas.

Generic limits

The basal polytomy found in the seed-finch clade and the tight clustering of sequence divergence values in the range 4.6–7.8% suggest that this clade underwent a rapid radiation shortly after its origin. Either or both of the genera *Sporophila* and *Oryzoborus* may be non-monophyletic; they are certainly closely related to each other and to *Dolospingus*. The three form a natural group apparently without other close relatives; the only putatively related genera for which cytochrome *b* sequences are lacking are *Charitospiza* (Clark 1986) and *Amaurospiza* (Paynter & Storer 1970, Webster & Webster 1999), neither of which seems likely to be especially close.

The foregoing suggests the possibility that *Dolospingus*, *Sporophila* and *Oryzoborus* could be merged into a single genus. That course was advocated for *Sporophila* and *Oryzoborus* by Olson (1981a, 1981b) on the basis of similarity in plumage and morphology, and the existence of hybrids between them (Sick 1963). Stiles (1996) argued against grouping on the basis of the unique allometry of *Oryzoborus* bills, but considerable differences in bill structure and ecology exist within other genera of seed-eating finches, e.g. *Geospiza* (Bowman 1961, Grant 1986) and *Passerina* (Klicka *et al.* 2001). Webster and Webster (1999) found that this merger was not indicated by a broad survey of emberizine skeletons. Although their analysis was phenetic, they did describe three features that may prove to be synapomorphies for *Oryzoborus* or *Sporophila*.

J.R. Webster (pers. comm.) examined a putative adult male *Dolospingus* skeleton (CAS 71570), and found that it clustered with *Sporophila* in their correspondence analysis (Webster & Webster 1999). Comparison of that skeleton with our recently collected series of *Dolospingus* demonstrated it to be a misidentified *Sporophila* skeleton. Based on that specimen's coastal locality in Guyana, where *Dolospingus* is not known to occur despite over a century of work (Fig. 1), and the presumed plumage resemblance to *Dolospingus*, we suspect that CAS 71570 is a *Sporophila americana*. Now that authentic *Dolospingus* skeletons are available, a careful morphological analysis of bill/skull evolution in the seed-finch clade would be desirable, especially in the light of a well-resolved molecular phylogeny.

The basal polytomy in the cytochrome *b* tree certainly leaves open the possibility that *Dolospingus*, *Sporophila* and *Oryzoborus* are all reciprocally monophyletic. To achieve a completely dichotomous and strongly supported resolution of this polytomy will require more extensive taxon sampling and more molecular data from both mitochondrial and nuclear genes. At present, it is largely a matter of preference

whether to merge or continue to recognize these genera. Differences in bill structure are diagnostic for all three genera, and probably relate to ecological differences as well. Until a robust phylogeny is available, these differences may be sufficient for many to prefer the status quo, which several recent treatments have maintained (American Ornithologists' Union 1998; Hilty 2002).

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