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Evolutionary differentiation in the Neotropical montane region: Molecular phylogenetics and phylogeography of *Buarremon* brush-finches (Aves, Emberizidae)

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Abstract

Studies on Neotropical phylogeography have largely focused on lowland organisms. Because lowland and highland biotas have different histories and are likely affected by different processes influencing population differentiation, understanding Neotropical diversification requires detailed studies on montane taxa. We present the most comprehensive analysis of population differentiation conducted so far on a widespread group of Neotropical montane organisms, focusing on the evolutionary relationships and phylogeography of *Buarremon* brush-finches (Aves: Emberizidae) in montane areas from Mexico through Argentina. Sequences of mitochondrial and nuclear genes demonstrate that *Buarremon* is not monophyletic with respect to *Arremon* and *Lysurus*. Genetic structure revealed by mtDNA is strong in both *B. brunneinucha* and *B. torquatus*. Gene genealogies and nucleotide diversity indicate that *B. brunneinucha* originated in Mexico and later expanded to South America, where it followed one colonization route through the east, and one through the west of the continent. Differentiation among populations of *B. torquatus* was substantial, reaching 8% uncorrected sequence divergence within South America. Relationships among major lineages of *B. torquatus* were not fully resolved owing to rapid differentiation, but the occurrence of closely related taxa in distant locations suggests a complex history of diversification. Some Colombian populations of *B. brunneinucha* have affinities with populations from Venezuela and the East Andean slope of Ecuador and Peru, and others with those from the Pacific slope of Ecuador. Moreover, five divergent lineages of *B. torquatus* occur within Colombia, highlighting the importance of dense sampling in northwest South America for studies on diversification of widespread Neotropical lineages.

Keywords: Andes; Biogeography; Central American highlands; Comparative phylogeography; Colombia; Neotropical birds; Speciation

1. Introduction

The recent development of comprehensive phylogeographic studies of various groups of organisms has led to important insights on the history of diversification in the Neotropical region that improve our understanding of the genetic structure of populations, the timing of population differentiation, the relationships among areas of endemism, and the role of features of the landscape such as rivers, mountains, or geological arcs as barriers to gene flow (reviewed by Moritz et al., 2000; see also Aleixo, 2004; Cheviron et al., 2005; Dick et al., 2003, 2004; Marks et al., 2002; Ribas and Miyaki, 2006; Ribas et al., 2006; Weigt et al., 2005). Much of this work, however, has focused on lineages occurring in the Neotropical lowlands.

A recent review of avian molecular phylogenies has highlighted apparent differences in the history of diversification between lowland and highland Neotropical regions

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(Weir, 2006). In contrast to lowland areas, where fauna-wide diversification rates appeared to be highest in the late Miocene and to have decreased towards the present, rates of species production in highland areas appeared to increase substantially following the onset of Pleistocene glacial cycles. Therefore, Weir (2006) concluded that lineages occurring in lowland and highland regions were likely affected differently by Pleistocene climatic fluctuations and other recent events. Although some of the results of this analysis may be compromised by the influence of taxonomic practice (i.e. lowland lineages are likely undersplit by taxonomists in comparison to highland lineages; Bates and Demos, 2001; see also Chek et al., 2003), they imply that generalizations concerning population differentiation in the lowlands (e.g. strong genetic structuring and Pre-Pleistocene population differentiation in birds) may not reflect the extent and timing of population differentiation in montane areas. Indeed, different types of historical events influence differentiation in highland and lowland populations. For example, because many Neotropical montane bird species extend over broad latitudinal expanses within narrow elevational ranges along the Andes (Graves, 1985, 1988), their populations are susceptible to fragmentation resulting from local extinctions, particularly when climate change reduces suitable habitat (Graves, 1988). Accordingly, we expect montane species to exhibit strong genetic structure along a latitudinal axis, a hypothesis that remains untested. Likewise, low passes and inter-mountain valleys should present strong barriers to genetic exchange for high-elevation species, but empirical evidence documenting these genetic effects is largely lacking for Neotropical organisms (see Bowie et al., 2006 for an example from Africa). In addition, although some studies have identified montane areas of endemism (e.g. Cracraft, 1985), phylogenetic and phylogeographic studies addressing relationships among areas over broad scales are scarce. In sum, because few comprehensive phylogeographic studies of Neotropical montane taxa have been conducted, and because most of those available have focused on relatively narrow geographic regions, our current understanding of historical diversification in the Neotropical highlands is incomplete.

In this study, we present a detailed assessment of evolutionary relationships and patterns of genetic differentiation in *Buarremon* brush-finches (Aves, Passeriformes, Emberizidae). Because taxa in this group are widely distributed in montane areas of the New World from Mexico through Argentina, a thorough analysis of population differentiation in *Buarremon* represents an important step in understanding diversification in the Neotropical highlands.

The genus *Buarremon* includes three species: *B. torquatus*, which ranges from central Costa Rica to northern Argentina, *B. brunneinucha*, occurring from central Mexico to southern Peru, and *B. virenticeps*, endemic to western and central Mexico (American Ornithologists' Union, 1998; Remsen et al., 2006). Both *B. torquatus* and *B. brunneinucha* were originally described in the genus *Embernagra*, but they were placed in *Buarremon* by Bonaparte (1850), who, without a clear rationale, erected the genus including these two taxa and several other species of emberizines, most of which are now placed in the genus *Atlapetes*. *Buarremon virenticeps* was described a few years later, also by Bonaparte (1855). Based on similarities in bill shape, Hellmayr (1938) merged *Buarremon* with *Atlapetes*, a treatment followed without question by all subsequent authors until mtDNA and allozyme evidence indicated that *Buarremon* (i.e. *B. brunneinucha* and *B. torquatus*) and *Atlapetes* are not each other's closest relatives (Hackett, 1992). This prompted the resurrection of *Buarremon* for *brunneinucha*, *torquatus*, and *virenticeps*, now widely accepted (Remsen and Graves, 1995; American Ornithologists' Union, 1998; Remsen et al., 2006). Ongoing studies with broad taxon sampling support this rearrangement, and suggest that together with the genera *Arremon* and *Lysurus*, the three species of *Buarremon* form one of six major clades within the Emberizidae (J. Klicka et al., unpubl. data). However, relationships among these three genera are uncertain, and the long-held assumption of the monophyly of *Buarremon* has not been rigorously tested.

At a lower level, relationships among *Buarremon* taxa are not well established. Based on the morphological similarity between juvenile *B. torquatus* and adult *B. virenticeps*, Paynter (1970) considered these taxa to be conspecific, but later regarded them as distinct sister species (Paynter, 1978), which has been the more common position of systematists notwithstanding the lack of a phylogenetic appraisal. Species delimitation has been contentious within what is currently treated as *B. torquatus* (Remsen and Graves, 1995). Different authors have argued this taxon may comprise as many as three species, yet there is disagreement over how these should be circumscribed, partly as a result of the phenotypic diversity of the group, which consists of 14 subspecies among which plumage characters vary rather chaotically, with no clear correspondence between geographic proximity and phenotypic similarity (Chapman, 1923; Paynter, 1978). There has also been some discussion regarding species limits in *B. brunneinucha*, with some authors favoring the treatment of the Mexican subspecies *apertus* as a separate species (Navarro-Sigüenza and Peterson, 2004).

Here, we first reconstruct phylogenetic relationships among *Buarremon* and related genera, among species of *Buarremon*, and among lineages of each species occurring in different regions based on sequences of mitochondrial and nuclear genes. Guided by this framework, we use mtDNA data to examine the relationships of population lineages in more detail, to describe the geographic distribution of genetic variation, and to assess the extent of migration between populations separated by potential barriers to gene flow. To our knowledge, this study represents the most comprehensive analysis of population genetic differentiation conducted for a widespread group of Neotropical montane organisms. In addition to furthering our general understanding of the history of diversification in the tropical and subtropical mountains of Central and South America, our results provide a framework for forthcoming

studies on the evolution of phenotypic diversity, species limits, and the role of interspecific interactions in the origin of elevational distributions in *Buarremon* and allies (Cadena, 2006, 2007).

2. Materials and methods

2.1. Taxon and geographic sampling

We followed different taxon sampling and DNA sequencing strategies to reconstruct evolutionary relationships and to examine patterns of population differentiation at various hierarchical levels. We generated sequence data for 238 samples, including 138 individuals representing eight of the nine subspecies of *B. brunneinucha*, 78 representing 13 of the 14 subspecies of *B. torquatus*, eight *B. virenticeps*, and one for each of four species of *Arremon*, the two species of *Lysurus*, and outgroups in the genera *Atlapetes, Pezopetes, Pselliophorus*, *Pipilo, Ammodramus, Junco, Zonotrichia*, and *Melospiza* (Fig. 1, Appendix A). Outgroup selection was guided by analyses based on sequences of multiple genes for nearly all genera in the Emberizidae (J. Klicka et al., unpubl. data).

To obtain a general overview of relationships of major groups and a detailed picture of patterns of differentiation in *Buarremon*, we sequenced the second subunit of the NADH dehydrogenase mitochondrial gene (ND2) for all samples of all taxa. Based on preliminary analyses, we selected a few individuals from each major lineage of *B. torquatus* and *B. brunneinucha* for more data-intensive analyses. For this subset, and for all individuals of other taxa, we sequenced the cytochrome *b* (cyt *b*), ATP-synthase 6 (ATPase 6), and ATP-synthase 8 (ATPase 8) mitochondrial genes in addition to ND2. In addition, for a subset of these, we sequenced fragments of introns of two nuclear genes linked to the *Z* chromosome: intron 10 of aconitase 1 (ACO1) and intron 3 of muscle-specific kinase (MUSK). In sum, we used three data sets for analyses: (1) 1026 bp of ND2 for 238 individuals, (2) 2871 bp of ND2, cyt *b*, ATPase 6, and ATPase 8 for 43 individuals, and (3) 4208 bp of ND2, cyt *b*, ATPase 6, ATPase 8, ACO1, and MUSK for 22 individuals. All sequences were submitted to GenBank (accession numbers not yet available).

2.2. Laboratory procedures

We extracted DNA from liver or pectoral muscle tissues, blood samples, feathers, or skin from specimens using the DNeasy Tissue Kit (Qiagen). We amplified the ND2 gene for most individuals using combinations of primers L5216, H5766, L5758, and H6313 (Sorenson et al., 1999). Whenever possible, the whole gene (1041 bp) was amplified as a single fragment to reduce the likelihood of amplifying nuclear pseudogenes, but this was not always feasible because some samples were degraded. To work with samples yielding low-quality DNA, we designed six internal primers that allowed us to amplify and sequence fragments of 300–350 bp (Table 1). For amplification and sequencing of cyt *b*, we employed primers L14996, H15646, L15413, and H16064 (Sorenson et al., 1999), for ATPase6 and ATPase8 primers CO2GQL and CO3HMH (G. Seutin and E. Bermingham, http://nmg.si.edu/bermlab/bermlab.htm), and for ACO1 and MUSK unpublished primers designed by F.K. Barker.

PCRs consisted of an initial denaturation at 94 °C for 2 min, followed by 35 cycles of denaturation at 94 °C for 45 s, annealing at 52 °C for 30 s and extension at 72 °C for 60 s, finishing with an extension at 72 °C for 10 min. Constituents were: 1–2 μl of DNA extract, 0.625U of *Taq* polymerase (Promega), 10 mM Tris–HCl (pH 9.0), 50 mM KCl, 1.5 mM $MgCl_2$, 0.48 μM of each primer, and 80 μM dNTP's, in a total volume of 25 μl. For poor-quality extracts that could not be amplified as indicated above, reactions used HotStar Taq DNA polymerase (Qiagen) with the concentration of constituents and PCR protocol suggested by the manufacturer. When amplifications yielded a single product of the expected size, we purified them using the QiaQuick PCR Kit (Qiagen). If multiple products were obtained, we excised the appropriate bands from agarose gels and purified them using a Gel Extraction Kit (Qiagen). Clean products were used as templates for sequencing both forward and reverse DNA strands employing the same primers used for amplification and the Big Dye Terminator kit (ABI). Products were treated with ethanol and sodium acetate to remove unincorporated dyes, and run on ABI 377 or 3730XL automated sequencers.

2.3. Alignment and exploration of sequence data

We assembled and edited chromatograms in the program SeqMan (DNAstar), and aligned sequences manually. All mitochondrial sequences lacked conflict between complementary light and heavy strands, their base composition and patterns of substitution were typical of protein-coding mtDNA (most substitutions were transitions at third codon positions), and indels and stop or nonsense codons were lacking, suggesting they were in fact of mitochondrial origin and not nuclear pseudogenes. Insertions and deletions in nuclear sequences were rare, which allowed us to align them manually in straightforward fashion.

The incongruence length difference test (Farris et al., 1995) implemented in PAUP* version 4.0b10 (Swofford, 2002) did not reveal any significant conflict in the phylogenetic signal of different genes or data partitions (mitochondrial *vs.* nuclear genes). Thus, we conducted analyses combining sequences of all genes in single matrices, but also analyzed partitions independently to assess the support for relationships afforded by different character sets.

To assess the possibility of substitutional saturation of mtDNA sequences, we plotted pairwise comparisons of uncorrected *p*-distances based on different substitution types (transitions, transversions) as a function of maximum-likelihood distances estimated under a best-fit model of nucleotide substitution. Plots indicated saturation for

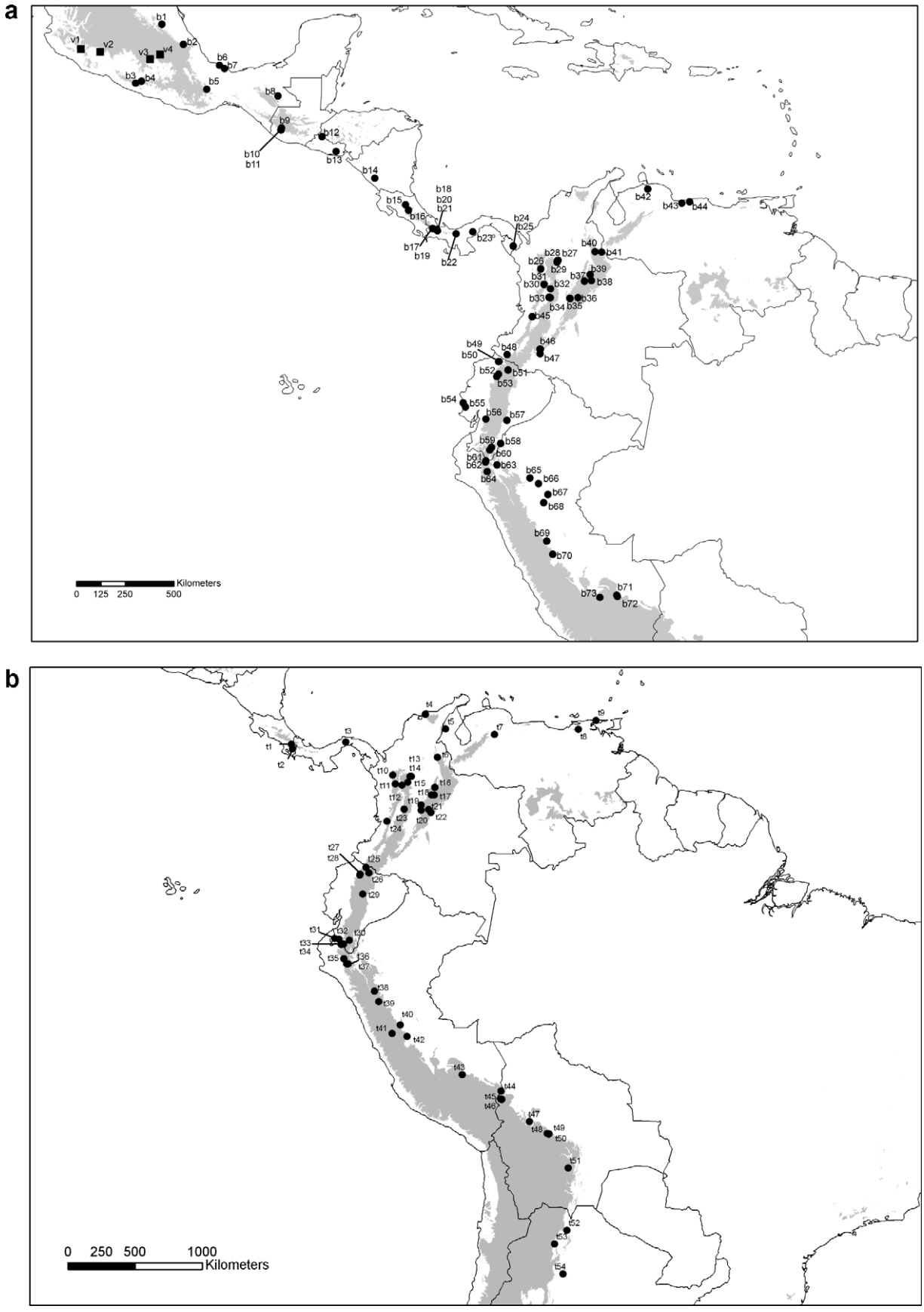

Fig. 1. Geographic distribution of samples of *Buarremon brunneinucha* and *B. virenticeps* (a) and *B. torquatus* (b) included in phylogenetic and phylogeographic analyses. Localities are numbered by species following the locality codes indicated in Appendix A. Areas above 1000 m are shown in grey.

Table 1
Primers designed for PCR amplification of fragments of the ND2 gene from degraded DNA samples

Primer	Sequence (5′–3′)
L5541	GCAGTAGCAATAAAACTYGGAYTAG
H5570	TTCTGGGAATCAGAAGTGGAAT
L5755	ARACACAAATCCGAAAAATCYTAG
H5830	GTTRAGGAGAGTGAGTTTRGGGT
L5937	ACATGAAGCAAAGYYCCA
H6090	AARAAYAGGCTTAGTAGTGAGAGGAG

Primers are named according to their position in the chicken (*Gallus gallus*) mitochondrial genome, and on whether they are located on the light (L) or heavy (H) strand.

transitions in the third position of codons in cyt *b* and the ATPase genes above model-corrected distances of ca. 0.10. We assessed the effect of saturation on phylogenetic inference by employing different character weighting schemes in parsimony analyses (see below).

2.4. Phylogenetic analyses

We conducted maximum likelihood, Bayesian, and maximum parsimony analyses to resolve relationships among *Buarremon* and related genera and among species and major lineages of *Buarremon* based on the multigene mitochondrial and mitochondrial-nuclear data sets. For maximum likelihood analyses we implemented the GTR+I+G model of nucleotide substitution, which was selected as the best fit to all of the data sets according to the Akaike Information Criterion (AIC) in ModelTest version 3.7 (Posada and Crandall, 1998). We conducted heuristic searches under the maximum-likelihood criterion in PAUP*, each consisting of 10 replicates with random taxon addition and tree-bisection reconnection (TBR) branch swapping. We assessed support for nodes under maximum likelihood via bootstrap resampling (200 and 500 pseudoreplicates for the mitochondrial and nuclear-mitochondrial data sets, respectively). We conducted Bayesian analyses using MrBayes version 3.0 (Ronquist and Huelsenbeck, 2003; Altekar et al., 2004) only for the four-gene mitochondrial and combined mitochondrial-nuclear data sets. To ensure proper examination of tree and parameter space, we employed Metropolis-coupled Markov Chain Monte Carlo (MCMC) sampling with one cold and three heated chains run for 25 million generations. To further ensure that results did not depend on starting conditions, we conducted four independent analyses initiated from random trees on each data set. Results of each run were examined for convergence by plotting posterior probabilities of clades as a function of generation number using AWTY (Wilgenbusch et al., 2004); convergence across runs was evaluated by examining the standard deviation of split frequencies and by plotting the correlation of clade frequencies obtained in different analyses in AWTY. We did not observe changes in the posterior probabilities of clades after ca. 5 million generations of sampling in any run; thus, we conservatively discarded the first 10 million generations of each run as the burn-in. Indicating convergence to the posterior distributions, results of independent runs were remarkably similar to each other, so we combined them and constructed a majority rule consensus of 60,000 trees for each data set (trees sampled every 1000 generations were saved). For parsimony analyses, we employed heuristic searches with TBR branch swapping and 100 random stepwise addition replicates in PAUP*, and assessed support with 1000 bootstrap replicates. To explore the effect of saturation on the outcome of parsimony reconstructions, we examined bootstrap support for clades in analyses in which transitions in third codon positions of cyt *b* and ATPase 6 and 8 were excluded or downweighted with respect to other substitution types by factors of 2, 5, and 20.

We reconstructed genealogical relationships among ND2 haplotypes in *Buarremon* using maximum likelihood and maximum parsimony. Separate analyses were conducted for (1) *B. brunneinucha* and *B. virenticeps*, which were shown to be closely related taxa by the comprehensive multigene analyses and (2), the *B. torquatus* complex. Based on the AIC, we selected the GTR+I+G model of nucleotide substitution as the best fit to both data sets and implemented it in maximum-likelihood analyses as described above. Parsimony analyses were similar to those described for the multigene data set, except that the number of trees retained per random addition replicate was set to 100.

2.5. Assessment of statistical conflict between taxonomy and phylogeny

Some relationships revealed by phylogenetic analyses are contrary to those implied by traditional classifications. To assess the significance of these conflicts, we first determined whether observed topologies were statistically more likely than hypotheses of relationships implied by current taxonomy. We calculated the likelihood of constraint trees in which genera were forced to be monophyletic and contrasted these likelihoods with those of the unconstrained maximum-likelihood trees using Shimodaira–Hasegawa (S–H) tests with RELL optimization and 1000 bootstrap replicates. This test evaluates the null hypothesis that all the tested topologies are equally good explanations of the data (Shimodaira and Hasegawa, 1999). From a Bayesian perspective, the posterior probability of a node indicates the probability that the relationships indicated by the node are correct, conditional on the data and the model of nucleotide substitution (Huelsenbeck and Rannala, 2004). Thus, we also determined the posterior probabilities of clades defined by taxonomy that were not recovered in the majority rule consensus of the MCMC samples by excluding from the samples all trees that did not include these clades and determining the proportion represented by the remaining trees.

2.6. Population genetic analyses in Buarremon

Guided by gene genealogies, we used the program DNAsp (Rozas et al., 2003) to calculate nucleotide diversity (Nei, 1987) for selected clades and for populations

occurring in distinct geographic regions. Nucleotide diversity is reduced in areas that have been more recently colonized (reviewed by Zink, 2002), which allowed us to make inferences about the directionality of range expansions. We also used DNAsp to calculate Tajima's (1989) *D* to assess whether departure from neutrality could compromise the use of mtDNA data to make inferences about population history.

To estimate gene flow between selected pairs of populations, we used the coalescent method implemented in MDIV (Nielsen and Wakeley, 2001), focusing on populations of *B. brunneinucha* occurring in lower Central America and South America, where our sampling was most complete. Specific pairs of populations were selected based on the existence of potential barriers to gene flow and patterns observed in genealogies, which seemed to suggest isolation between some of them. The coalescent approach allowed us to estimate gene flow between populations independently of the uncertainty in the reconstruction of genealogies. MDIV uses MCMC sampling to obtain joint estimates of migration rates and divergence times between pairs of populations assuming no further population subdivision and selective neutrality (Nielsen and Wakeley, 2001). Each run consisted of 5,000,000 generations employing the HKY substitution model (Palsbøll et al., 2004), of which the first 500,000 were discarded as burn-in. Based on estimates obtained in preliminary runs, we set the maximum values for the scaled migration rates and divergence times in all analyses to 10 and 5, respectively. To assess convergence, we conducted each analysis three times starting from different random seeds.

3. Results

3.1. Phylogenetics—mitochondrial data

Mitochondrial data support the monophyly of *Arremon* and *Lysurus*, but suggest that *Buarremon* is not monophyletic (Fig. 2). Results obtained using different methods of phylogenetic inference were congruent with each other except for a few nodes that were not strongly supported in any analysis. All analyses placed *Arremon* as sister to *B. torquatus*, a result strongly supported by Bayesian analyses (0.96 posterior probability), but less so by maximum-likelihood (64% bootstrap), or parsimony (53% bootstrap). In all analyses, *B. brunneinucha* appeared closest to *Lysurus*, but this was never strongly supported. Inferences from parsimony bootstrap analyses in which transitions at third codon positions in cyt *b* and the ATPase genes were excluded or downweighted (not shown) were generally consistent with the unweighted analysis. Support for relationships among genera, whose recovery could have been obscured by saturation, was low, as in the unweighted analysis.

In contrast with traditional hypotheses, *B. virenticeps* is more closely allied (100% maximum-likelihood and maximum parsimony bootstrap and 1.00 posterior probability) to *B. brunneinucha* than it is to *B. torquatus*. Moreover, some reconstructions suggested *B. brunneinucha* may be paraphyletic with respect to *B. virenticeps*, a result strongly supported in Bayesian and maximum likelihood analyses, in which a posterior probability of 0.99 and bootstrap value of 78% was obtained for a clade formed by *B. virenticeps* and a representative of the nominate subspecies of *B. brunneinucha*, to the exclusion of other Mexican and Central and South American populations of the latter.

Support for the monophyly of the *B. torquatus* complex was strong in all analyses (100% bootstrap and 1.00 posterior probability). Within the complex, a well-supported basal division separates the Central American taxon *costaricensis* from the rest of the group. Within the latter clade, relationships among major groups (several of which were well-supported) could not be resolved with certainty owing to the collapse in a polytomy of long branches connected by short internodes. Relationships within this group are discussed in detail below based on more comprehensive sampling of populations.

3.2. Phylogenetics—nuclear data

Considering only *Buarremon*, *Arremon*, and *Lysurus*, only 54 and 48 variable characters were observed in ACO1 and MUSK, respectively, of which only 27 and 26 were parsimony-informative. Therefore, the number of characters supporting relationships inferred from nuclear data (Fig. 3) was small, so results should be viewed with care (the unexpected position of *Melospiza* in the MUSK tree immediately calls for caution). Despite their limited information content, both nuclear genes recovered with good support some relationships also obtained with the mitochondrial data (Fig. 3). These include the monophyly of *B. torquatus*, *Arremon*, and *Lysurus*, and the close relationship of *B. virenticeps* and Mexican *B. brunneinucha*. However, the two introns offered contrasting information regarding relationships among genera: whereas inferences from MUSK were consistent with the mitochondrial data in placing *B. torquatus* and *Arremon* as sister clades, ACO1 recovered a clade that included all *Buarremon* and *Lysurus*, with moderate support for *Arremon* as its sister group.

3.3. Phylogenetics—combined data

The topology obtained from combined analyses including mitochondrial and nuclear sequences (Fig. 4) is entirely consistent with mitochondrial trees, which reflects the much higher information content in the mitochondrial data. However, although informative substitutions in nuclear sequences were limited, when analyzed in combination with mitochondrial data they increased support for some relationships. These include the sister relationship of *B. torquatus* and *Arremon* (posterior probability of 1.00, 80% maximum-likelihood bootstrap and 68% parsimony bootstrap) and the relationship of *B. brunneinucha-B. virenticeps* to *Lysurus*, which increased to 0.94 posterior probability,

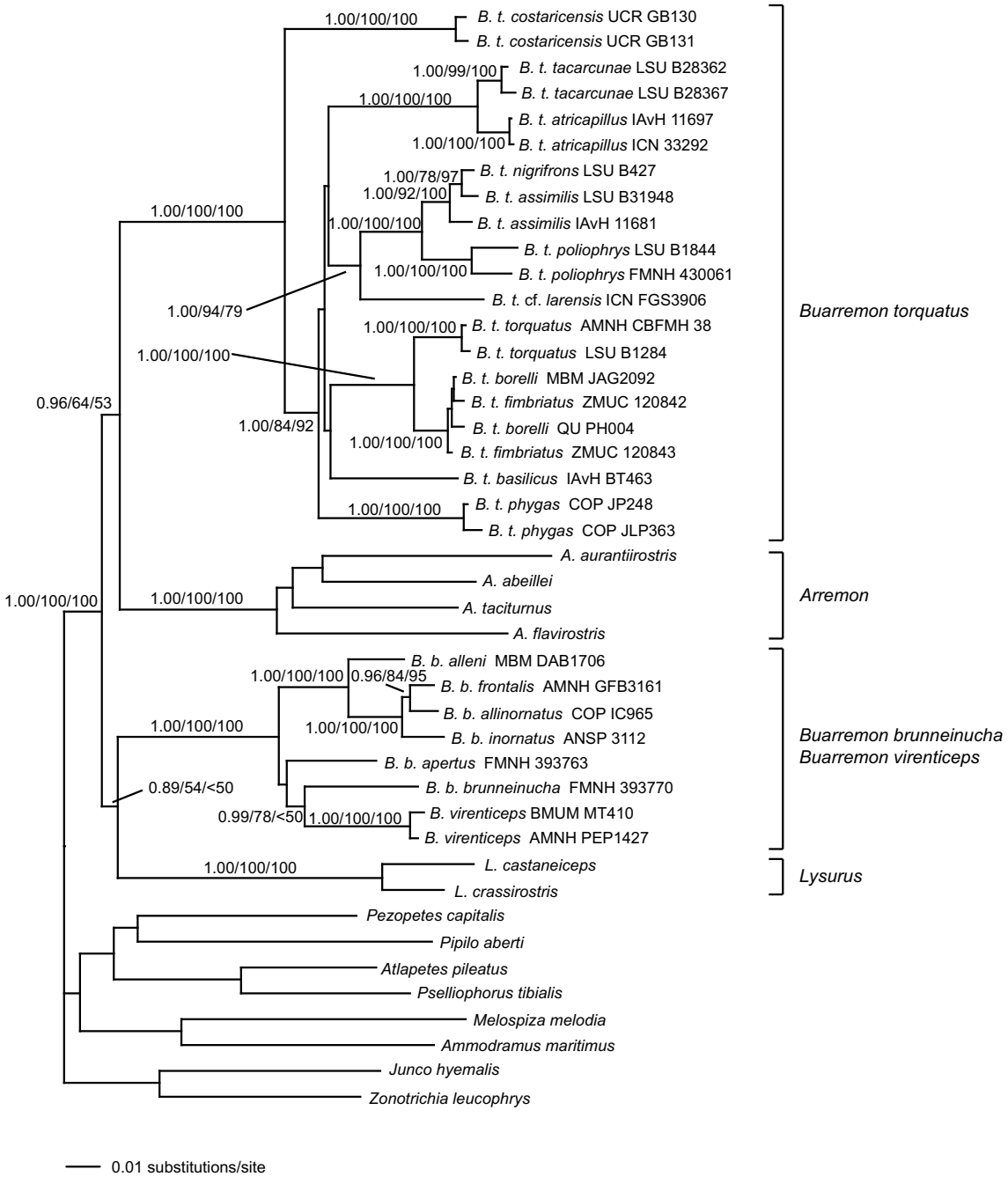

Fig. 2. Phylogenetic hypothesis for relationships of 43 individuals of *Buarremon*, *Lysurus*, *Arremon*, and outgroup taxa based on combined analyses of 2871 aligned base pairs of four mitochondrial genes. The phylogram shown is the maximum-likelihood tree. Numbers on branches indicate Bayesian posterior probabilities and bootstrap values obtained under maximum-likelihood and maximum parsimony, respectively. Support values for relationships of taxa in the outgroup are not shown.

though bootstrap support remained low (61% in maximum-likelihood and less than 50% in parsimony).

3.4. Statistical assessment of *Buarremon* monophyly

According to S–H tests, trees in which the monophyly of *Buarremon* was enforced are not significantly worse explanations of the mitochondrial and combined sequence data than the optimal trees we recovered, in which *Buarremon* was not monophyletic (Table 2). In contrast, not a single tree of the combined total of 120,000 sampled in Bayesian analyses of mitochondrial and combined data showed *B. torquatus*, *B. brunneinucha* and *B. virenticeps* forming a clade, implying that the posterior probability of the monophyly of *Buarremon* is zero.

3.5. Phylogeography of *B. brunneinucha*

We obtained complete ND2 sequences for a total of 135 individuals of *B. brunneinucha* and 8 of *B. virenticeps*, which

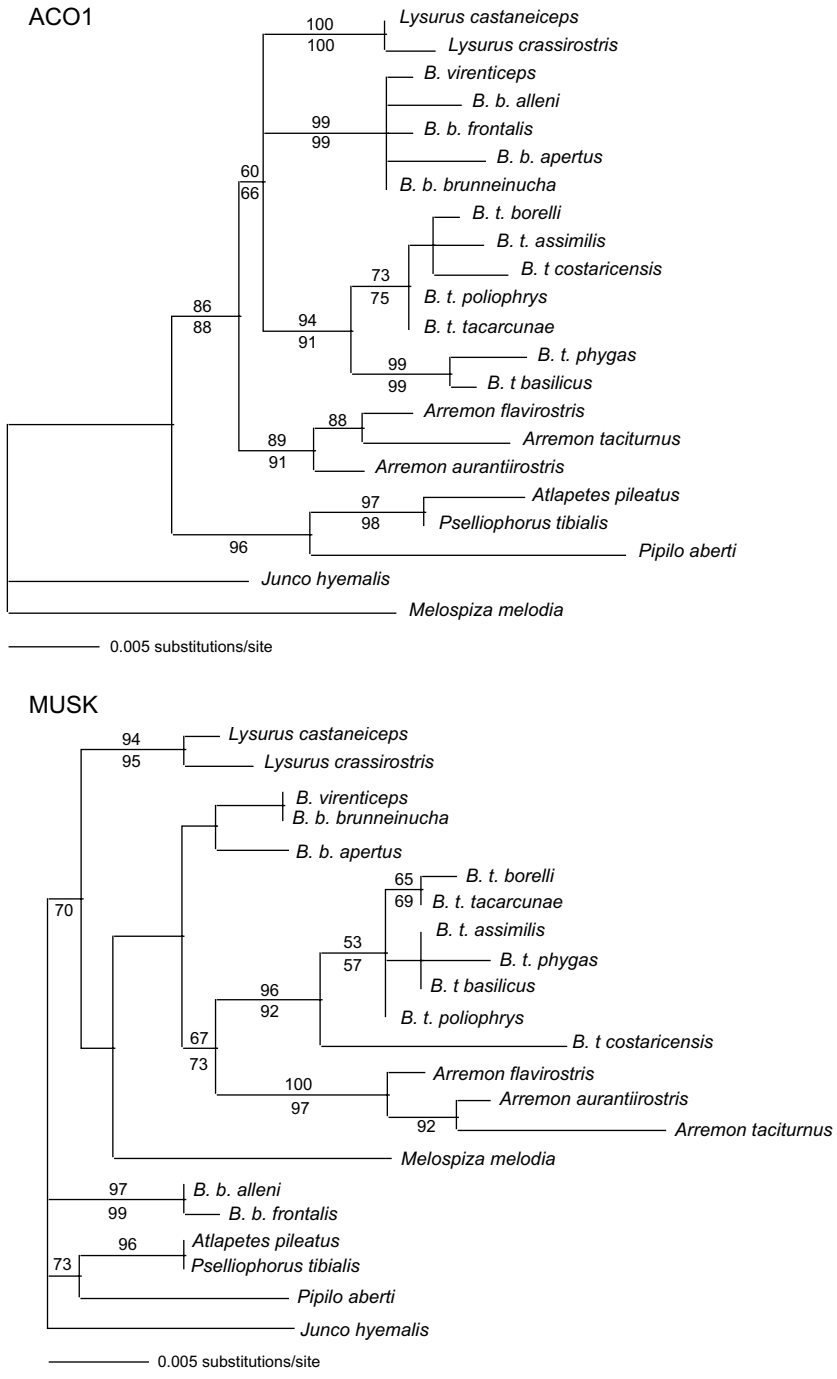

Fig. 3. Phylogenies inferred for 22 individuals using sequences of two nuclear loci, ACO1 (top), and MUSK (bottom). The phylograms shown are the maximum-likelihood trees obtained for each data set. Numbers above and below nodes are bootstrap values obtained under maximum-likelihood and maximum parsimony, respectively, whenever these are greater than 50%.

represented 98 and 6 different haplotypes, respectively. The deep branching structure of the tree depicting genealogical relationships among haplotypes in the *B. brunneinucha–B. virenticeps* clade (Fig. 5) was not well-supported as indicated by low bootstrap values, and by discrepancies in resolution of branching patterns between the maximum-likelihood and maximum parsimony trees (not shown). Despite these discrepancies, reconstructions under both criteria indicated that Mexican populations from west of the Isthmus of Tehuantepec constitute a paraphyletic assemblage composed of several early branching lineages. Due to the lack of support for relationships among deep branches, however, we cannot rule out the hypothesis that lineages from west of Tehuantepec form a clade. Based on this larger sample of individuals, *B. brunneinucha* still appears paraphyletic with respect to *B. virenticeps*, which in turn was recovered as monophyletic. However, support for the paraphyly of *B. brunneinucha* is not compelling based on this data set.

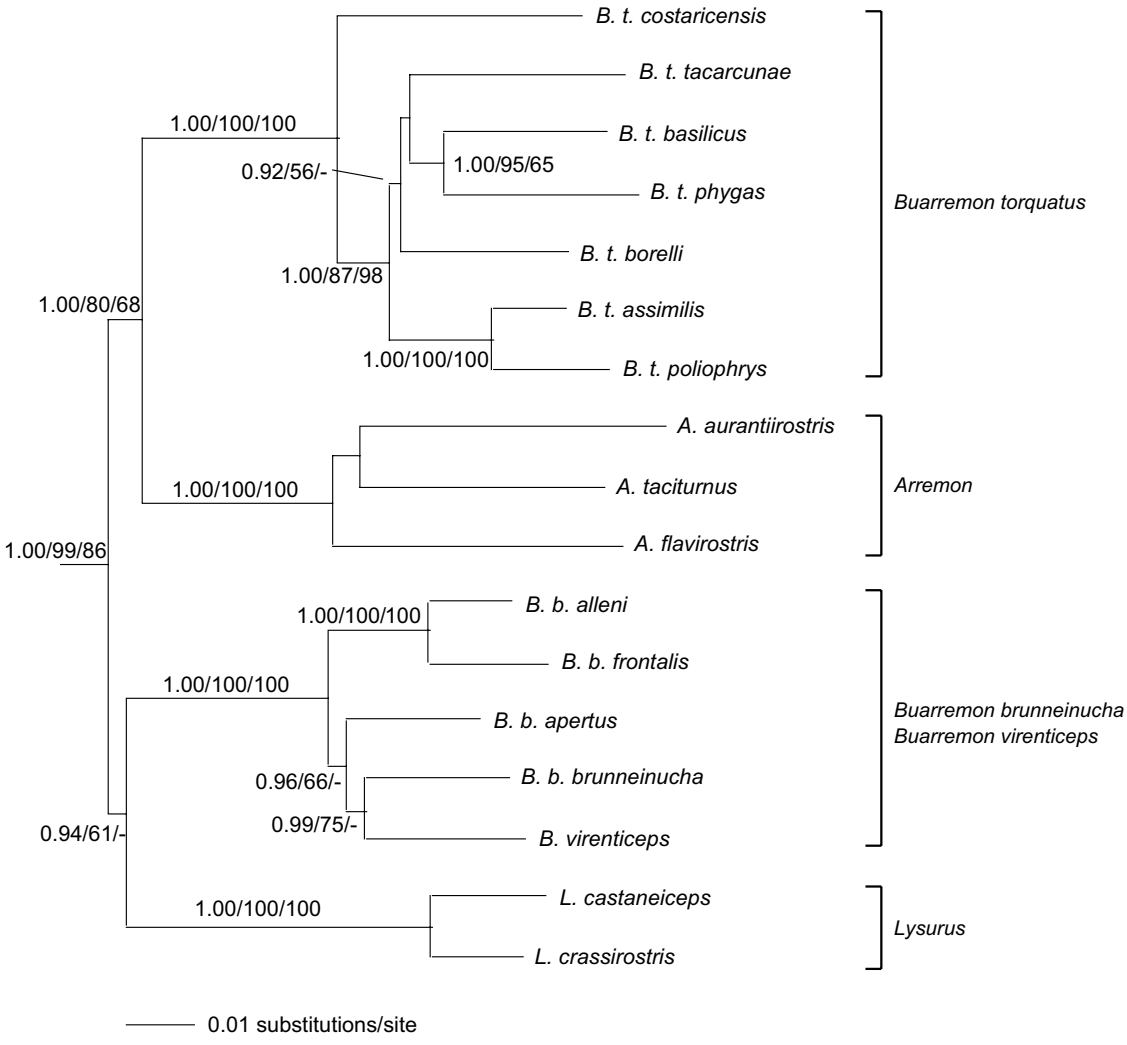

Fig. 4. Phylogenetic hypothesis for relationships of *Buarremon, Lysurus*, and *Arremon* taxa based on combined analyses of 4208 aligned base pairs of four mitochondrial and two nuclear genes. The phylogram shown is the maximum-likelihood tree. Numbers on branches indicate Bayesian posterior probabilities and bootstrap values obtained under maximum-likelihood and maximum parsimony, respectively. Outgroup not shown.

Table 2
Results of Shimodaira–Hasegawa tests comparing the likelihoods of maximum-likelihood estimates of phylogeny obtained for mitochondrial and combined mitochondrial and nuclear data with those of trees recovered in maximum-likelihood analyses in which the monophyly of *Buarremon* was enforced

Data set	ML tree −ln L	Constrained tree −ln L	*p*-value
Mitochondrial (four genes)	19856.741	19861.797	0.216
Mitochondrial–nuclear (six genes)	19217.315	19226.091	0.134

Tests were one-tailed, based on 1000 RELL bootstrap replicates.

Despite the uncertainty in resolving deep branches, all analyses recovered a well-supported "southern" *B. brunneinucha* clade consisting of all samples collected throughout Mesoamerica east of Tehuantepec and South America. Haplotypes from Chiapas, Mexico, are not shown in the tree because the available DNA was degraded, and we could only sequence ca. 300 base pairs; analyses of that fragment unambiguously indicated these populations are closely allied to populations from Guatemala rather than those from Mexico west of Tehuantepec. Relationships among some of the major lineages in the southern *B. brunneinucha* clade were not well-supported, likely a result of rapid population expansion through Central America.

Most individuals of *B. brunneinucha* from western and central Panama from reciprocally monophyletic groups, indicating the existence of a phylogeographic break; individuals from central and eastern Panama are more closely allied to populations occurring in South America. Reciprocal monophyly is not complete, however, owing to the placement of one individual from western Panama in the central clade and of one individual from central Panama in

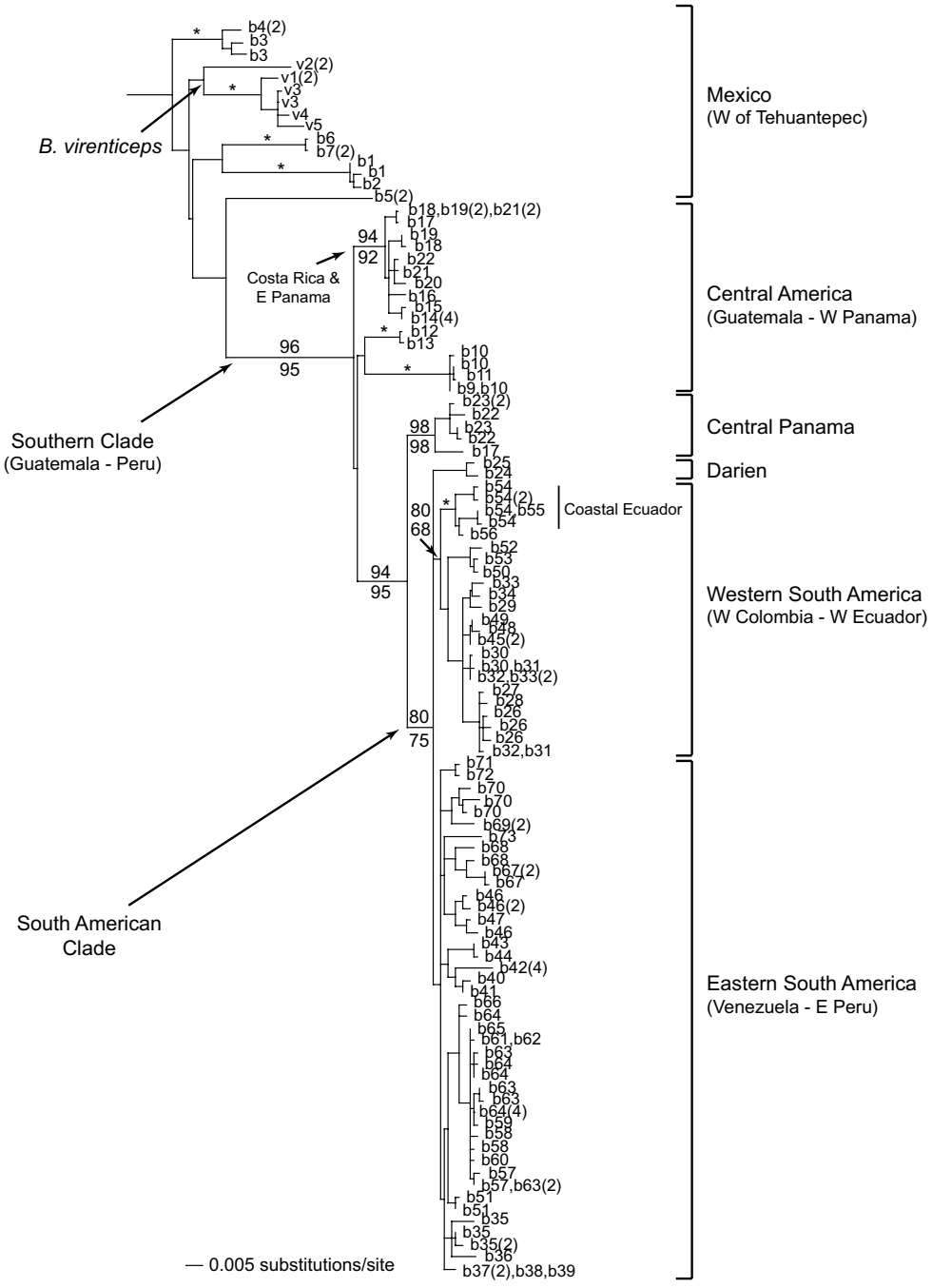

Fig. 5. Maximum-likelihood tree showing relationships among haplotypes of *B. brunneinucha* and *B. virenticeps.* Localities are named as in Fig. 1a and in Appendix A. The number of individuals sharing a given haplotype is indicated in parentheses following each locality, when applicable. Brackets on the right group haplotypes by region, but note that for Mexico and Central America these do not correspond to clades. For selected clades discussed in the text, bootstrap values obtained under maximum-likelihood and maximum parsimony are shown above and below branches, respectively. Other clades receiving high support under both criteria are indicated with asterisks. Support for relationships near terminal branches is not shown for clarity; deep nodes without boostrap values or asterisks were not strongly supported. The tree was rooted with sequences of *Lysurus castaneiceps* and *L. crassirostris* (not shown).

the western clade; these may reflect ongoing gene flow or incomplete lineage sorting in isolated populations (see below).

Further south, another break exists between populations from central Panama and South America (including the Darién region in eastern Panama). The derived position of South American populations with respect to Mexican and Central American lineages suggests that *B. brunneinucha* had a northern origin and expanded its range southward to colonize South America. This hypothesis is further supported by a decline in nucleotide diversity from Mexico south (Table 3).

Within South America, two distinct clades can be identified: one comprises haplotypes from the Cordillera Oriental of Colombia, Venezuela, and the Amazonian slope of the

Table 3
Estimates of nucleotide diversity and its standard deviation calculated for different areas and regions where *B. brunneinucha* occurs, indicating declining genetic diversity from north to south

Region	*n*	Nucleotide diversity ± SD
Mexico (excluding *virenticeps*)	12	0.0459 ± 0.0041
Mexico (including *virenticeps*)	20	0.0445 ± 0.0031
Central America (Guatemala–Panama)	30	0.0249 ± 0.0024
Guatemala–West Panama	24	0.0206 ± 0.0029
Central Panama	6	0.0148 ± 0.0073
South America (East Panama–Peru)	93	0.0168 ± 0.0005
Western Clade	32	0.0134 ± 0.0008
Eastern Clade	59	0.0131 ± 0.0008

Andes of Ecuador and Peru, whereas the other includes haplotypes from the Cordillera Central and Cordillera Occidental of Colombia and the Pacific slope of the Ecuadorian Andes. Within the latter clade, individuals from the Coastal Cordillera of Ecuador (subspecies *inornatus*) form a monophyletic group together with a single individual from the Pacific Andean slope. Ecuadorian populations from the west slope of the Andes do not form a clade with respect to those of Central and Western Colombia. Within the eastern South America clade, geographic structure was limited. The four individuals from the Sierra de San Luis in Venezuela (*allinornatus*) shared a single haplotype, which was most closely allied to other haplotypes from Venezuela.

3.6. Gene flow in B. brunneinucha

Tajima's *D* calculated for several clades and geographic regions where *B. brunneinucha* occurs was never significant ($P > 0.1$ in all cases), indicating variation is consistent with selective neutrality. Coalescent estimates of migration revealed that populations of *B. brunneinucha* separated by lowland areas are genetically isolated to varying degrees (Fig. 6). The most striking pattern is the lack of gene flow between populations occurring in eastern (Cordillera Oriental) and central-western (Cordillera Central and Cordillera Occidental) Colombia: the posterior distribution estimated by MDIV was concentrated at or very near values of zero female migrants per generation. In contrast, the posterior distribution estimated for migration between the Cordillera Central and the Cordillera Occidental of Colombia was essentially flat, with equivalent probabilities extending up to remarkably high levels of migration. Owing to the flat probability distribution, low levels of gene flow cannot be rejected, although it is worth noting that distributions like the one we obtained are typically observed when there is no subdivision between populations (R. Nielsen, pers. comm.). Migration between western and central Panama appears higher than between eastern and central-west Colombia, but still somewhat limited. In western Ecuador, the probability distribution was more evenly spread over values of migration in the range up to ca. 1.5 female migrants per generation between the Coastal Cordillera and the Pacific slope of the Andes. Migration

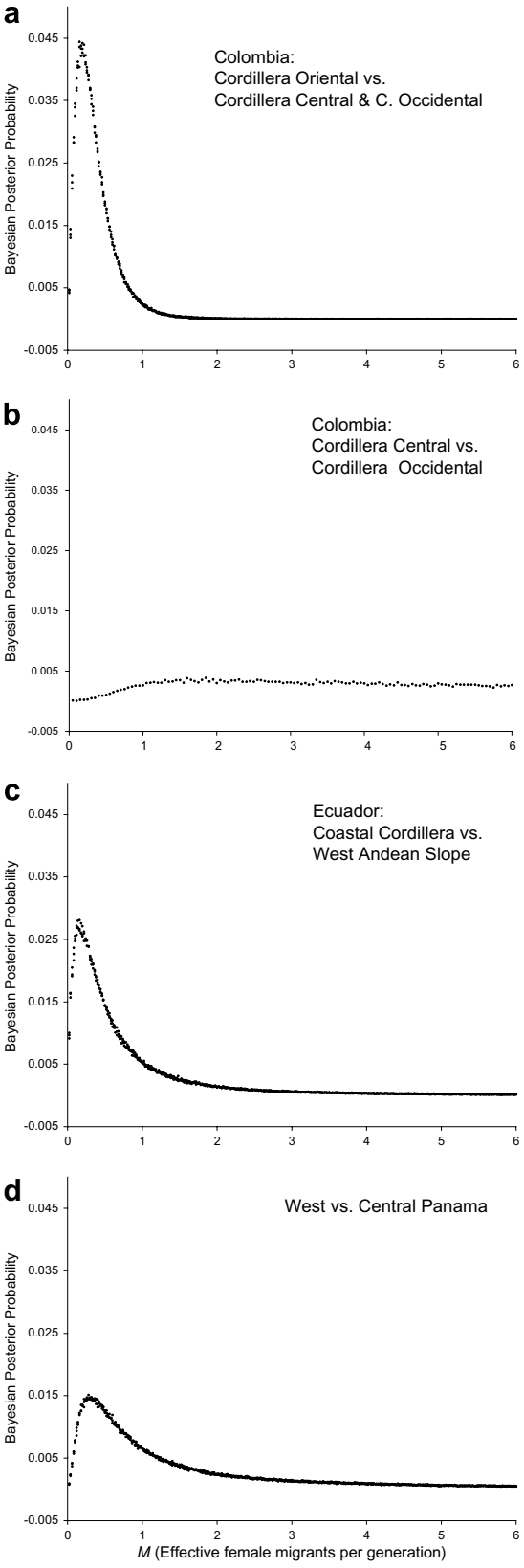

Fig. 6. Posterior probability distributions of estimates of migration between selected pairs of populations of *B. brunneinucha* obtained using coalescent analyses in MDIV. (a) Cordillera Oriental vs. Cordilleras Central and Occidental, Colombia. (b) Cordillera Central vs. Cordillera Occidental, Colombia. (c) Coastal Cordilleras vs. West Andean Slope, Ecuador. (d) West Panama vs. Central Panama.

between the Coastal Cordillera and the Pacific slope of the Andes might be underestimated because we lack sufficient sampling in the southern sector of the latter area.

3.7. Phylogeography of *B. torquatus*

We obtained ND2 sequences for a total of 78 individuals of *B. torquatus*, which represented 68 different haplotypes. Phylogenetic analyses revealed a well-supported basal split between the taxon *costaricensis* of Costa Rica and western Panama, and a clade comprising populations occurring through central and eastern Panama and all of South America (Fig. 7). The Panamanian taxon *tacarcunae* is nested within the clade formed by all South American populations of *B. torquatus*, which suggests its range was likely colonized from South America. The geographic origin of *B. torquatus* as a whole is uncertain, as the sister group of the complex is the genus *Arremon*, which also has both Central and South American members. At any rate, the long branches and distinct clades present within South America indicate that this group has been in that continent for a substantial period of time; uncorrected divergence among South American sequences reaches 8%.

As with the four-gene data set, resolution of relationships among South American lineages of *B. torquatus* was limited, with long branches collapsing in a polytomy. Branches of unresolved affinities correspond to populations occurring in (1) the Sierra Nevada de Santa Marta of Colombia (subspecies *basilicus*), (2) the Serranía de Perijá in the Venezuela-Colombia border (*perijanus*), (3) east Venezuela (*phygas*), (4) extreme southern Peru, Bolivia, and Argentina (*torquatus, fimbriatus*, and *borelli*), (5) high elevation areas of the Colombian Andes, Ecuador, and Peru (*assimilis*, *nigrifrons*, and *poliophrys*) and northeast Colombia and west Venezuela (*larensis*), and (6) mid-elevation areas of the Andes of Colombia and eastern and central Panama (*atricapillus* and *tacarcunae*). Within lineage 4, *borelli* and *fimbriatus* were not reciprocally monophyletic and formed a clade sister to the monophyletic nominate *torquatus.* In lineage 5, *larensis* was sister to the *assimilis–nigrifrons–poliophrys* clade, within which *poliophrys* was sister to the closely allied *assimilis* and *nigrifrons*, which were not reciprocally monophyletic. Note that in contrast to monographic work on *B. torquatus* that treated populations occurring in the northern sector of the Cordillera Oriental of Colombia (Depto. Norte de Santander) as referable to subspecies *perijanus* (Paynter, 1978), here we consider birds from this area as belonging to the taxon *larensis* (formerly thought to occur only in Venezuela) based on their close affinity indicated by mtDNA and similarity in plumage (Cadena, 2006).

4. Discussion

4.1. Phylogenetics

The monophyly of *Buarremon* is dubious. Although support for relationships among major groups of *Buarremon, Arremon*, and *Lysurus* was variable in analyses using different methods (e.g. Bayesian vs. parsimony) and employing different data (mitochondrial vs. nuclear), the most telling fact is that we never recovered a monophyletic *Buarremon* in any analysis of mitochondrial, nuclear, or combined data. Indeed, an exclusive clade formed by *B. torquatus*, *B. brunneinucha*, and *B. virenticeps* was not observed in a single tree of the combined total of 120,000 sampled in Bayesian analyses of mitochondrial and combined data. Thus, conditional on our data and the models employed, the probability that these three taxa form a clade is zero (Huelsenbeck and Rannala, 2004). However, according to S–H tests, the hypothesis of a monophyletic *Buarremon* is not a significantly less likely explanation of the sequence data than the optimal topologies we obtained. This discrepancy in the conclusions reached by Bayesian and maximum-likelihood tests of topologies may be attributable to the tendency for Bayesian analyses to place excessive confidence on relatively short branches owing to how prior probabilities of branch lengths are set (Lewis et al., 2005; Yang and Rannala, 2005), or to the conservative nature of the S–H test (Goldman et al., 2000; Shi et al., 2005). The former possibility appears less likely because branches with high posterior probabilities did not exhibit low maximum-likelihood bootstrap values, which is typical for cases in which high posteriors may be artifactual (Lewis et al., 2005).

Mitochondrial data suggest that *B. torquatus* is more closely related to the genus *Arremon* than to *B. brunneinucha* and *B. virenticeps*, a result consistently recovered in all analyses and supported strongly by Bayesian posterior probability (0.96). However, this result was only moderately to weakly supported by bootstrap values (64% in maximum likelihood and 53% in parsimony). One of the nuclear genes (MUSK) was consistent with this relationship, whereas the other (ACO1) placed *Arremon* outside a clade formed by *Lysurus* and *Buarremon.* The combined analyses of mitochondrial and nuclear data provide strong support for a clade formed by *B. torquatus* and *Arremon*. In retrospect, that *B. torquatus* and *Arremon* may be sister groups is not surprising, because some *Arremon* (e.g. *A. taciturnus*) are strikingly similar in plumage to members of *B. torquatus*. Perhaps the only marked difference between *B. torquatus* and species of *Arremon* is the smaller body size of the latter, which might reflect their occurrence at lower, warmer elevations (Bergmann's ecogeographic "rule"; see Zink and Remsen, 1986). On the other hand, *B. brunneinucha* and *B. virenticeps* may be more closely allied to *Lysurus* than to *B. torquatus*, but support for this relationship in the mitochondrial data set was not compelling, and it was not recovered by any of the nuclear genes. Our findings seemingly contrast with allozyme variation documented by Hackett (1992), who found that *B. brunneinucha* and *B. torquatus* formed a monophyletic group with respect to *Lysurus castaneiceps.* However, her data set lacked representatives of *Arremon*, and bootstrap support for the monophyly of *Buarremon* was not reported.

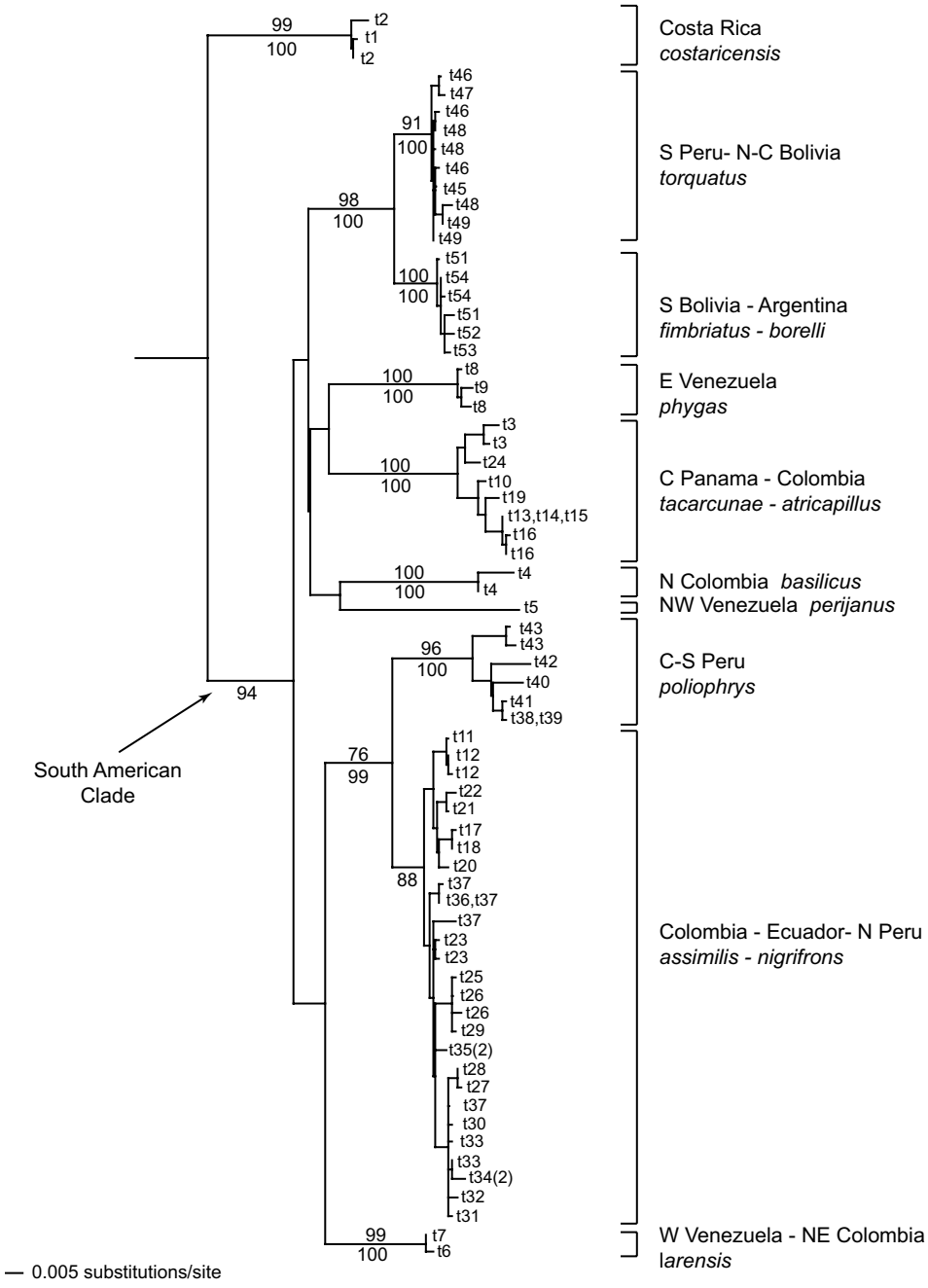

Fig. 7. Maximum-likelihood tree showing relationships among haplotypes of *B. torquatus.* Localities are named as in Fig. 1b and in Appendix A. The number of individuals sharing a given haplotype is indicated in parentheses following each locality, when applicable. Bootstrap values exceeding 70% obtained under maximum-likelihood and maximum parsimony are shown above and below branches, respectively; support values are omitted from terminal branches for clarity. The tree was rooted with sequences of *Arremon aurantiirostris* and *A. taciturnus* (not shown).

In sum, although the monophyly of *Buarremon* cannot be rejected by one statistical test, the evidence points strongly away from *Buarremon* being a monophyletic group. Therefore, we suggest that classification should be revised to be consistent with the recognition of monophyletic supraspecific taxa. Even if the sister relationship between *B. torquatus* and *Arremon* to the exclusion of *B. brunneinucha* and *B. virenticeps* is not supported by additional data, genetic differentiation between the two clades of *Buarremon* is clearly at least as great as the differentiation that exists between *Arremon* and *Lysurus*, and between these and the two *Buarremon* clades. Considering the similarities among all *Buarremon*, *Arremon*, and *Lysurus* taxa in plumage, voices, behavior, and microhabitat, we consider best to treat them all as members of an expanded genus *Arremon* (*Arremon* has priority over *Buarremon* and *Lysurus*; Paynter, 1970). To retain the information conveyed by traditional classification regarding the existence of distinct clades within this genus, *Lysurus* and *Arremon* (*sensu stricto*) could be recognized as subgenera. For consistency,

in the following we continue to refer to the established genus names to avoid confusion.

We found that *B. virenticeps* is not sister to *B. torquatus* as had always been hypothesized based on the close resemblance in plumage of adult *B. virenticeps* and juvenile *B. torquatus* (Paynter, 1978). Rather, *B. virenticeps* is more closely allied to *B. brunneinucha*, a result strongly supported in all analyses, and independently by mitochondrial and nuclear genes. Furthermore, mtDNA suggests that *B. virenticeps* may be nested within *B. brunneinucha*, which would imply a striking decoupling of phenotypic and genetic variation. However, this must be interpreted cautiously because several factors can affect the ability of mitochondrial genealogies to accurately reflect species relationships (Nichols, 2001). At any rate, the close relationship between *B. virenticeps* and *B. brunneinucha* is well-supported, demonstrating that plumage is not a reliable indicator of phylogenetic relationships in *Buarremon*, as documented for the allied genus *Atlapetes* (García-Moreno and Fjeldså, 1999).

4.2. Phylogeography

Variation in mtDNA suggests that *B. brunneinucha* originated in northern Mesoamerica, an area from which populations expanded across Central America and into South America: early branching lineages occur in Mexico, and nucleotide diversity declines markedly from north to south. That populations have had more time to differentiate in the northern sector of the range provides a reasonable explanation for patterns of phenotypic variation: several morphologically distinctive forms of *B. brunneinucha* occur in Mexico and northern Mesoamerica, whereas variation in plumage across lower Central America and South America is limited (Parkes, 1954; Paynter, 1978). Probably as a result of rapid differentiation, relationships among Mexican populations could not be fully resolved, but it is clear that following their rapid divergence these have had a long history of isolation (see also Peterson et al., 1992). Although additional data are necessary to resolve relationships among Mexican lineages, mitochondrial data reveal a marked phylogeographic break within Mexico that separates populations from the western and eastern sides of the Isthmus of Tehuantepec. This pattern is consistent with genetic differentiation in other montane taxa (e.g. Sullivan et al., 2000; Pérez-Emán, 2002; García-Moreno et al., 2004; García-Moreno et al., 2006), highlighting the importance of the low-elevation Isthmus as a barrier to dispersal.

The short internodes separating mitochondrial lineages of *B. brunneinucha* occurring through much of Central America suggests populations expanded rapidly across the region. A similar pattern of rapid north to south expansion across Central America has been documented for *Myioborus miniatus* (Parulidae; Pérez-Emán, 2002). However, assuming that rates of nucleotide substitution are similar in *Buarremon* and *Myioborus*, differentiation across this region does not appear to have occurred concurrently in both groups on the basis of mtDNA distances. Genetic distances among Central American populations of *B. brunneinucha* reach ca. 5%, whereas divergences among populations of *M. miniatus* from the same region only reach ca. 1% (Pérez-Emán, 2002).

Most individuals of *B. brunneinucha* from western and central Panama formed reciprocally monophyletic groups, revealing another phylogeographic break. Isolation of these areas is not complete, however, as coalescent analyses give some support for limited gene flow. From central-southern Costa Rica south, the ranges of *B. brunneinucha* and *B. torquatus* begin to overlap. Although no samples of *B. torquatus* from western Panama were available for this study, populations from Chiriquí Province are referable to the taxon *costaricensis* and thus are probably closest to those from adjacent Costa Rica. Since *costaricensis* is sister to all other members of the *B. torquatus* complex, populations in western and central-eastern Panama are also likely differentiated in this complex. Other phylogeographic studies on montane taxa (e.g. Solórzano et al., 2004) do not have comparable sampling to ours across Panama, and so we cannot determine the generality of this pattern of differentiation. Further analyses of montane species are necessary to better understand the history of diversification across lower Central America, considering the historical complexity of this region revealed by studies on lowland lineages (Bermingham and Martin, 1998; Brumfield and Braun, 2001; Cortés-Ortiz et al., 2003; Dick et al., 2003, 2004; González et al., 2003; Marks et al., 2002; Perdices et al., 2002; Weigt et al., 2005; Witt, 2004).

Divergence between central Panamanian and South American populations of *B. brunneinucha* is relatively modest, with mean uncorrected *p* distances reaching only 2–3%. Therefore, the available estimates of nucleotide substitution rates for avian protein-coding mitochondrial genes (Arbogast et al., 2006; Lovette, 2004a; Pereira and Baker, 2006; Weir, 2006) imply that the colonization of South America by *B. brunneinucha* took place after the completion of the Isthmus of Panama, dated at ca. 3 million years before present (Coates and Obando, 1996). The direction of colonization of *B. torquatus* cannot be established with certainty by polarizing ancestral areas on the phylogeny, but the divergence between Central American (*costaricensis*) and South American populations appears to have occurred earlier than in *B. brunneinucha*. The timing of population divergence in both species is explored in more detail elsewhere using a relaxed molecular clock approach (Cadena, 2007); conclusions of these additional analyses are entirely consistent with those presented here. Although data on other taxa are still limited, studies of avifaunal interchange across the Panamanian land bridge have documented range expansions both north to south (Barker, 2007; Pérez-Emán, 2002, 2005; this study) and south to north (Burns and Naoki, 2004; Hackett, 1995; Witt, 2004), with some of these events occurring prior to the completion of a terrestrial connection (Barker, 2007; Witt, 2004). Genetic distances suggest that colonization of South America by *B. brunneinucha*

may have occurred simultaneously with that of *M. miniatus*, which shows similar levels of divergence across the Isthmus of Panama (Pérez-Emán, 2002), indicating once again that elements of the histories of these co-distributed species appear to have been remarkably congruent. Patterns of geographic variation in plumage are also similar in *B. brunneinucha* and *M. miniatus*, with both species showing minimal variation in South America relative to Middle America. Accumulating similar phylogeographic information for additional taxa will be of great interest to determine whether consistent patterns are observed in multiple lineages; ultimately, this will allow a better understanding of the role of trans-Isthmian colonization events on the historical assembly of communities in North and South America (Ricklefs, 2002).

Although not always strongly supported, distinct western and eastern South American clades of *B. brunneinucha* were recovered in all analyses, and coalescent analyses indicate negligible levels of gene flow between eastern and central-western Colombia. The documentation of these two distinct phylogroups suggests that range expansion by *B. brunneinucha* across South America following its colonization proceeded through two independent routes, one through the west and one through the east of the continent. Members of the two phylogroups probably come close to each other in the Ecuadorian Andes, but they are likely isolated by unsuitable high-elevation habitat. That populations from the Cordillera Oriental of Colombia are genetically isolated from those from the Cordillera Central and Cordillera Occidental represents evidence of the long-suspected effect of the complex geography of the Colombian Andes on patterns of population differentiation, and specifically on the role of the Río Magdalena Valley as a barrier to gene flow for montane organisms. Indeed, of the three pairs of populations among which we documented restricted to moderate migration, the ones occurring in closest geographic proximity to one another are those from eastern and central-western Colombia, where gene flow appears most restricted. Because the elevations of the lowland areas separating these pairs of populations differ little, the more restricted migration in Colombia may reflect the additional barrier to dispersal imposed by the Magdalena. These results are consistent with those of studies showing an effect of lowland areas as barriers to gene flow (Bowie et al., 2006), and of large rivers restricting genetic exchange (Aleixo, 2004; Bates et al., 2004; Cheviron et al., 2005). In contrast, however, populations separated by the Río Cauca Valley (i.e. those occurring in the Cordillera Central and Cordillera Occidental of Colombia) might be connected by high levels of gene flow, although this is not clearly established as a result of the flat posterior probability for the estimate of migration that we observed. The seemingly increased gene flow across the Cauca Valley could be explained by the close proximity of the Cordillera Central and the Cordillera Occidental, by the fact that these mountain ranges are connected at their southern ends, and by the higher elevation of the Cauca Valley in comparison to the Magdalena, which may have allowed for increased connectivity between cordilleras during periods when vegetation zones were displaced downslope (Hooghiemstra and Van der Hammen, 2004). Other studies have documented close affinities between taxa from the Cordillera Central and Cordillera Occidental (see Cuervo et al., 2005), suggesting this pattern may have some generality.

In contrast to signatures of restricted gene flow across some lowland areas in *B. brunneinucha*, differentiation along broad latitudinal expanses of the Andes appears limited in the two South American lineages of *B. brunneinucha* and in the *assimilis–nigrifrons* clade of *B. torquatus*. This lack of structuring with respect to latitude is somewhat surprising, considering that the linear distributions of Andean taxa are thought to be especially prone to fragmentation and subsequent allopatric divergence (Graves, 1988). However, processes of this sort may be responsible for the differentiation between *assimilis–nigrifrons* and *poliophrys*, which despite their relatively close proximity in the Peruvian Andes are reciprocally monophyletic, ca. 4% different in mtDNA, and phenotypically distinct (Cadena, 2006). Another instance of differentiation along the Andes in *B. torquatus* occurs between the clade formed by *larensis, assimilis, nigrifrons*, and *poliophrys* and the one comprising nominate *torquatus, fimbriatus*, and *borelli*. Although members of these clades have been collected within 50 km of one another in southern Peru (Cadena, 2006), mtDNA suggests a long history of isolation, with the minimum uncorrected sequence divergence between the nearly abutting *poliophrys* and *torquatus* being 6.6%. This zone may represent an area of secondary contact. Differentiation along the Andes is also apparent from the recovery of distinct clades in northern-central Bolivia (*torquatus*) and southern Bolivia and Argentina (*fimbriatus* and *borelli*), although we cannot rule out the possibility that these two clades are the extremes of a cline in genetic variation that we did not observe due to sparse sampling (Brumfield, 2005).

The *B. torquatus* complex comprises several relatively old lineages, which according to a rate of nucleotide substitution of 1.6–2% divergence per million years (Lovette, 2004a; Weir, 2006), would appear to have last shared a common ancestor more than 3 million years ago. Even assuming that ND2 evolves at a faster rate (Arbogast et al., 2006), and that available estimates of the rates of molecular evolution for avian mitochondrial genes may not be generally applicable (Pereira and Baker, 2006), the divergence among these lineages appears relatively deep in comparison to levels of divergence observed in earlier studies on other taxa. Regardless of whether these phylogroups represent different species or variants of a single species, these levels of divergence are comparatively high for Neotropical montane birds, many of which diversified within the last million years (Weir, 2006). In fact, the patterns of mtDNA differentiation observed in *B. torquatus* resemble those documented for passerine birds of the Neotropical lowlands (e.g. Bates et al., 1999; Cheviron et al., 2005; Lovette, 2004b; Marks et al., 2002) in terms of the existence of distinct phylogroups

of Pre-Pleistocene age. There are, however, other cases of Pre-Pleistocene differentiation in Andean taxa (e.g. García-Moreno and Fjeldså, 2000; Pérez-Emán, 2005).

Relationships among major phylogroups of South American *B. torquatus* are unresolved. Because mitochondrial data recovered deeper and shallower nodes with support, we consider this a hard polytomy resulting from rapid differentiation, similar to those documented in other groups of Neotropical birds (Lovette, 2004b; Pérez-Emán, 2005). The apparently explosive differentiation of *B. torquatus* in South America precludes strong inference about the geographic context of differentiation in the group. It is striking, however, that lineages occurring in the same general area (e.g. *assimilis* and *atricapillus*, which segregate elevationally in the three Colombian cordilleras) are approximately equally divergent from each other as they are from groups occurring in distant locations (e.g. the clade occurring through Bolivia and Argentina). Moreover, although phylogenetic relationships at this level are tentative, lineages separated by thousands of kilometers appear to be each other's closest relatives. If this were correct, then *B. torquatus* would have a complex history of diversification, involving events of vicariance, dispersal, and lineage extinction over broad spatial scales (see also Dingle et al., 2006). Thus, processes of diversification in the Andes may involve complex large-scale processes in addition to the rather simple, small-scale vicariant events that are thought to prevail (García-Moreno and Fjeldså, 2000; Remsen, 1984).

Due to various reasons, researchers working on population genetics, phylogeography, and molecular phylogenetics of Neotropical organisms have largely ignored Colombian populations. Studies on Andean birds have either focused on taxa distributed in the Central and Southern Andes (see García-Moreno and Fjeldså, 2000; Weir, 2006), or have described patterns of differentiation in widespread groups without including material from Colombia (e.g. Dingle et al., 2006; but see Pérez-Emán, 2005; Witt, 2004). Without sampling in Colombia, our analyses would have resulted in a woefully incomplete picture of the history of *Buarremon*, missing the crucial but unexpected affinities of populations of *B. brunneinucha* from the Cordillera Oriental to those of Venezuela and the Amazonian slope of the Andes of Ecuador and Peru, and of populations from the Cordillera Central and Cordillera Occidental to those from the Pacific slope of Ecuador, in addition to the occurrence of five divergent lineages of *B. torquatus* that are not each other's closest relatives within the country. Due to its geographic position at the crossroads between Central and South America and the expected effects of its complex geography on population structure, it comes as no surprise that the results of this study imply that analyses of patterns of differentiation involving detailed sampling in Colombia should be considered essential to understanding the biogeographic history of many Neotropical taxa.

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Appendix A

Information on localities and museum catalogue numbers for samples of *Buarremon* brush-finches included in phylogenetic and phylogeographic analyses

Id	Taxon	Country	Locality	Catalogue No.*	Lat.	Lon.
	Buarremon brunneinucha					
b1	*Buarremon brunneinucha brunneinucha*	Mexico	Hidalgo, 5 km E Tlanchinol	FMNH 394029	21.013	−98.646
b1	*Buarremon brunneinucha brunneinucha*	Mexico	Hidalgo, 5 km E Tlanchinol	FMNH 394035	21.013	−98.646
b2	*Buarremon brunneinucha brunneinucha*	Mexico	Puebla, 2 km W Teziutlán	LSUMZ B44	19.821	−97.379
b3	*Buarremon brunneinucha suttoni*	Mexico	Guerrero, El Iris, Sierra de Atoyac	FMNH 393757	17.504	−100.212
b3	*Buarremon brunneinucha suttoni*	Mexico	Guerrero, El Iris, Sierra de Atoyac	FMNH 394152	17.504	−100.212
b4	*Buarremon brunneinucha suttoni*	Mexico	Guerrero, Carrizal de Bravo, Sierra Madre del Sur	MBM MM 907	17.613	−99.871
b4	*Buarremon brunneinucha suttoni*	Mexico	Guerrero, Carrizal de Bravo, Sierra Madre del Sur	MBM GMS 905	17.613	−99.871
b5	*Buarremon brunneinucha brunneinucha*	Mexico	Oaxaca, Cerro Zempoaltéptl, Totontepec	FMNH 393766	17.133	−95.983
b5**	*Buarremon brunneinucha brunneinucha*	Mexico	Oaxaca, Cerro Zempoaltéptl, Totontepec	FMNH 393770	17.133	−95.983
b6	*Buarremon brunneinucha apertus*	Mexico	Veracruz, Volcan San Martín, 21 km N San Andrés Tuxtla	MBM 4989	18.560	−95.220
b7**	*Buarremon brunneinucha apertus*	Mexico	Veracruz, [Catemaco] El Bastonal, 3 km S, 3 km E, Sierra de Santa Martha	FMNH 393763	18.371	−94.921
b7	*Buarremon brunneinucha apertus*	Mexico	Veracruz, [Catemaco] El Bastonal, 3 km S, 3 km E, Sierra de Santa Martha	FMNH 393870	18.371	−94.921
b8	*Buarremon brunneinucha macrourus*	Mexico	Chiapas, Las Margaritas, approx. 33 mi NE; Finca Patichuiz	WFVZ 1190	16.739	−91.737
b9	*Buarremon brunneinucha macrourus*	Guatemala	Quetzaltenango, Xela, El Baúl	MBM DHB 4405	14.821	−91.521
b10	*Buarremon brunneinucha macrourus*	Guatemala	Quetzaltenango, Santa María de Jesus 5 km SSW, Fca. de Sta. María	MBM DHB 4429	14.713	−91.563
b10	*Buarremon brunneinucha macrourus*	Guatemala	Quetzaltenango, Santa María de Jesus 5 km SSW, Fca. de Sta. María	MBM DHB 4434	14.713	−91.563
b10	*Buarremon brunneinucha macrourus*	Guatemala	Quetzaltenango, Santa María de Jesus 5 km SSW, Fca. de Sta. María	MBM DHB 4440	14.713	−91.563
b11	*Buarremon brunneinucha macrourus*	Guatemala	Quetzaltenango, Santa María de Jesus 2 km E	MBM GAV 2372	14.713	−91.538
b12	*Buarremon brunneinucha alleni*	El Salvador	Chalatenango, Cerro El Pital	KU 5072	14.313	−89.113
b13	*Buarremon brunneinucha alleni*	El Salvador	San Miguel	KU 4903	13.421	−88.279
b14	*Buarremon brunneinucha alleni*	Nicaragua	Nicaragua, Chocoyero, Volcán Mombacho, 48 km SE Managua	MBM DAB 960	11.829	−85.963
b14	*Buarremon brunneinucha alleni*	Nicaragua	Nicaragua, Chocoyero, Volcán Mombacho, 48 km SE Managua	MBM DAB 1751	11.829	−85.963
b14**	*Buarremon brunneinucha alleni*	Nicaragua	Nicaragua, Chocoyero, Volcán Mombacho, 48 km SE Managua	MBM DAB 1706	11.829	−85.963
b14	*Buarremon brunneinucha alleni*	Nicaragua	Nicaragua, Chocoyero, Volcán Mombacho, 48 km SE Managua	MBM DAB 1834	11.829	−85.963
b15	*Buarremon brunneinucha elsae*	Costa Rica	Heredia, Finca La Fortuna, 4 km SE Virgen del Socorro	LSUMZ B16053	10.246	−84.129
b16	*Buarremon brunneinucha elsae*	Costa Rica	Cartago, near Fca. Pizote, Tres Rios, 4.5 km NE	FMNH 393081	9.929	−83.963
b17	*Buarremon brunneinucha elsae*	Panama	Chiriquí, Boquete, Paso de Respingo on Cerro Punta-Boquete trail	LSUMZ B28316	8.838	−82.521
b17	*Buarremon brunneinucha elsae*	Panama	Chiriquí, Boquete, Paso de Respingo on Cerro Punta-Boquete trail	LSUMZ B28322	8.838	−82.521
b18	*Buarremon brunneinucha elsae*	Panama	Chiriquí, Gualaca-Chiriquí Grande Road, at continental divide	USNM B05407	8.763	−82.271
b18	*Buarremon brunneinucha elsae*	Panama	Chiriquí, Gualaca-Chiriquí Grande Road, at continental divide	USNM B05408	8.763	−82.271
b19	*Buarremon brunneinucha elsae*	Panama	Chiriquí, Los Planes, 10 km N Fortuna Field Station	USNM B05300	8.736	−82.273
b19	*Buarremon brunneinucha elsae*	Panama	Chiriquí, Los Planes, 10 km N Fortuna Field Station	USNM B05329	8.736	−82.273
b19	*Buarremon brunneinucha elsae*	Panama	Chiriquí, Los Planes, 10 km N Fortuna Field Station	USNM B05474	8.736	−82.273
b20	*Buarremon brunneinucha elsae*	Panama	Chiriquí, Gualaca, Cordillera Central, 4.3 km by road S Lago Fortuna dam	LSUMZ B26947	8.729	−82.246
b21	*Buarremon brunneinucha elsae*	Panama	Chiriquí, 12.6–23.3 road km N Los Planes, Gualaca-Chiriquí Grande Road	USNM B01436	8.688	−82.229
b21	*Buarremon brunneinucha elsae*	Panama	Chiriquí, 12.6-23.3 road km N Los Planes, Gualaca-Chiriquí Grande Road	USNM B01492	8.688	−82.229
b21	*Buarremon brunneinucha elsae*	Panama	Chiriquí, 12.6–23.3 road km N Los Planes, Gualaca-Chiriquí Grande Road	USNM B01542	8.688	−82.229
b22	*Buarremon brunneinucha elsae*	Panama	Veraguas, Santa Fé 3 km WSW hacia Alto de Piedra Road	MBM JMD 126	8.513	−81.121
b22	*Buarremon brunneinucha elsae*	Panama	Veraguas, Santa Fé 3 km WSW hacia Alto de Piedra Road	MBM JMD 145	8.513	−81.121
b22	*Buarremon brunneinucha elsae*	Panama	Veraguas, Santa Fé 3 km WSW hacia Alto de Piedra Road	MBM JMD 146	8.513	−81.121
b23	*Buarremon brunneinucha elsae*	Panama	Cocle, El Valle, foothills NE of town	MBM JK 04209	8.629	−80.129
b23	*Buarremon brunneinucha elsae*	Panama	Cocle, El Valle, foothills NE of town	MBM JK 04210	8.629	−80.129
b23	*Buarremon brunneinucha elsae*	Panama	Cocle, El Valle, foothills NE of town	MBM JK 04211	8.629	−80.129
b24	*Buarremon brunneinucha frontalis*	Panama	Darién, ca. 9 km NW Cana on slopes of Cerro Pirre	LSUMZ B1371	7.788	−77.721
b25	*Buarremon brunneinucha frontalis*	Panama	Darién, ca. 6 km NW Cana	LSUMZ B2102	7.771	−77.721

(*continued on next page*)

Appendix A (*continued*)

Id	Taxon	Country	Locality	Catalogue No.*	Lat.	Lon.
b26	*Buarremon brunneinucha frontalis*	Colombia	Antioquia, Páramo de Frontino	ZMUC 134985	6.413	−76.079
b26	*Buarremon brunneinucha frontalis*	Colombia	Antioquia, Páramo de Frontino	ZMUC 134994	6.413	−76.079
b26	*Buarremon brunneinucha frontalis*	Colombia	Antioquia, Páramo de Frontino	ZMUC 134963	6.429	−76.079
b27	*Buarremon brunneinucha frontalis*	Colombia	Antioquia, Amalfi, Vda. Las Animas, Bosque Las Animas	AMC 160	6.929	−75.038
b28	*Buarremon brunneinucha frontalis*	Colombia	Antioquia, Amalfi, Vda. Salazar, Finca Bodega Vieja	IAvH BT-1165	6.902	−75.088
b29	*Buarremon brunneinucha frontalis*	Colombia	Antioquia, Amalfi, Vda. Cajamarca, Fca. Canales	IAvH BT-2137	6.818	−75.104
b30	*Buarremon brunneinucha frontalis*	Colombia	Antioquia, Jardín, Vda. Dojurgo, Finca Las Mercedes	ICN 34716	5.504	−75.871
b30	*Buarremon brunneinucha frontalis*	Colombia	Antioquia, Jardín, Vda. Dojurgo, Finca Las Mercedes	ICN 34717	5.504	−75.871
b31	*Buarremon brunneinucha frontalis*	Colombia	Antioquia, Jardín, La Mesenia	ZMUC 134844	5.496	−75.888
b31	*Buarremon brunneinucha frontalis*	Colombia	Antioquia, Jardín, La Mesenia	ZMUC 134852	5.496	−75.888
b32	*Buarremon brunneinucha frontalis*	Colombia	Caldas, Aranzazu, Vda. El Laurel, Hda. Termopilas	IAvH 11906	5.229	−75.496
b32	*Buarremon brunneinucha frontalis*	Colombia	Caldas, Aranzazu, Vda. El Laurel, Hda. Termopilas	IAvH 11925	5.229	−75.496
b33	*Buarremon brunneinucha frontalis*	Colombia	Risaralda, Pereira, Vda. La Suiza, S.F.F. Otún Quimbaya	IAvH 11691	4.721	−75.579
b33	*Buarremon brunneinucha frontalis*	Colombia	Risaralda, Pereira, Vda. La Suiza, S.F.F. Otún Quimbaya	IAvH 11692	4.721	−75.579
b33	*Buarremon brunneinucha frontalis*	Colombia	Risaralda, Pereira, Vda. La Suiza, S.F.F. Otún Quimbaya	CDC 056	4.721	−75.579
b34	*Buarremon brunneinucha frontalis*	Colombia	Risaralda, Pereira, Parque Ucumarí, La Pastora	IAvH 11693	4.701	−75.504
b35	*Buarremon brunneinucha frontalis*	Colombia	Cundinamarca, Bojacá, Via Bogotá–La Mesa	IAvH 11679	4.663	−74.346
b35	*Buarremon brunneinucha frontalis*	Colombia	Cundinamarca, Bojacá, Via Bogotá–La Mesa	IAvH 11686	4.654	−74.329
b35	*Buarremon brunneinucha frontalis*	Colombia	Cundinamarca, Bojacá, Via Bogotá–La Mesa	CDC 010	4.654	−74.329
b35	*Buarremon brunneinucha frontalis*	Colombia	Cundinamarca, Bojacá, Via Bogotá–La Mesa	CDC 011	4.654	−74.329
b36	*Buarremon brunneinucha frontalis*	Colombia	Cundinamarca, Parque Nacional Chingaza, Río Blanco	IAvH 12676	4.696	−73.854
b37	*Buarremon brunneinucha frontalis*	Colombia	Boyacá, Mpio. Villa de Leyva, S.F.F. Iguaque	IAvH 11661	5.685	−73.470
b37	*Buarremon brunneinucha frontalis*	Colombia	Boyacá, Mpio. Villa de Leyva, S.F.F. Iguaque	IAvH 11667	5.696	−73.471
b38	*Buarremon brunneinucha frontalis*	Colombia	Boyacá, alrededores de S.F.F. Iguaque	IAvH 12562	5.729	−73.054
b39	*Buarremon brunneinucha frontalis*	Colombia	Santander, Encino, Reserva Cachalú	IAvH 11690	6.071	−73.129
b40	*Buarremon brunneinucha frontalis*	Colombia	Norte de Santander, Mpio de Cucutilla, Vda. Carrizal, Sector Sisavita	IAvH 12104	7.446	−72.838
b41	*Buarremon brunneinucha frontalis*	Colombia	Norte de Santander, PNN Tamá. Sector Orocué	IAvH 10650	7.429	−72.446
b42	*Buarremon brunneinucha allinornatus*	Venezuela	Falcón, Sierra de San Luis, Cerro Galicia	COP IC 963	11.180	−69.704
b42*	*Buarremon brunneinucha allinornatus*	Venezuela	Falcón, Sierra de San Luis, Cerro Galicia	COP IC 965	11.180	−69.704
b42	*Buarremon brunneinucha allinornatus*	Venezuela	Falcón, Sierra de San Luis, Cerro Galicia	COP IC 981	11.180	−69.704
b42	*Buarremon brunneinucha allinornatus*	Venezuela	Falcón, Sierra de San Luis, Cerro Galicia	COP IC 991	11.180	−69.704
b43	*Buarremon brunneinucha frontalis*	Venezuela	Aragua, Paso Portachuelo, Rancho Grande, PN Henry Pitier	COP IC 742	10.346	−67.671
b44**	*Buarremon brunneinucha frontalis*	Venezuela	Aragua, km 40 on El Junquito/Col. Tovar Road	AMNH GFB3161	10.421	−67.213
b45	*Buarremon brunneinucha frontalis*	Colombia	Valle del Cauca, La Cumbre, Chicoral	IAvH 12455	3.568	−76.588
b45	*Buarremon brunneinucha frontalis*	Colombia	Valle del Cauca, La Cumbre, Chicoral	IAvH 12461	3.568	−76.588
b46	*Buarremon brunneinucha frontalis*	Colombia	Huila, sendero entre Centro de Visitantes Andaqui y Cueva de los Guácharos	IAvH 11738	1.629	−76.121
b46	*Buarremon brunneinucha frontalis*	Colombia	Huila, sendero entre Centro de Visitantes Andaqui y Cueva de los Guácharos	IAvH 11769	1.629	−76.121
b46	*Buarremon brunneinucha frontalis*	Colombia	Huila, sendero entre Centro de Visitantes Andaqui y Cueva de los Guácharos	IAvH 11806	1.629	−76.121
b46	*Buarremon brunneinucha frontalis*	Colombia	Huila, Cueva de los Guácharos, Puente Nuevo, cuenca del Río Suaza	IAvH 11790	1.629	−76.096
b47	*Buarremon brunneinucha frontalis*	Colombia	Caquetá. Mpio. San José de Fragua. Vda. La Esmeralda, Alto Río Yurayaco	IAvH 11406	1.346	−76.113
b48	*Buarremon brunneinucha frontalis*	Colombia	Nariño, Altaquer, Río Ñambí	JCDC 01	1.300	−78.083
b49	*Buarremon brunneinucha frontalis*	Ecuador	Esmeraldas, El Placer	LSUMZ B11931	0.879	−78.596
b50	*Buarremon brunneinucha frontalis*	Ecuador	Esmeraldas, ca. 2 km E Alto Tambo	LSUMZ B30013	0.883	−78.555
b51	*Buarremon brunneinucha frontalis*	Ecuador	Napo, Río Maspa Chico	ZMUC 120268	0.371	−78.029
b51	*Buarremon brunneinucha frontalis*	Ecuador	Napo, Río Maspa Chico	ZMUC 120271	0.371	−78.029
b52	*Buarremon brunneinucha frontalis*	Ecuador	Pichincha, Maquipucuna	ZMUC 121333	0.129	−78.596
b53	*Buarremon brunneinucha frontalis*	Ecuador	Bellavista Cloud Forest Reserve (ca. 60 km NW Quito)	DB 309	−0.011	−78.705
b54	*Buarremon brunneinucha inornatus*	Ecuador	Manabí, Cerro San Sebastián, PN Machalilla	ANSP 2945	−1.584	−80.689
b54	*Buarremon brunneinucha inornatus*	Ecuador	Manabí, Cerro San Sebastián, PN Machalilla	ANSP 2953	−1.584	−80.689

b54*	*Buarremon brunneinucha inornatus*	Ecuador	Manabí, Cerro San Sebastián, PN Machalilla	ANSP 3112	−1.584	−80.689
b54	*Buarremon brunneinucha inornatus*	Ecuador	Manabí, Cerro San Sebastián, PN Machalilla	ANSP 3149	−1.584	−80.689
b54	*Buarremon brunneinucha inornatus*	Ecuador	Manabí, Cerro San Sebastián, PN Machalilla	ANSP 3384	−1.584	−80.689
b54	*Buarremon brunneinucha inornatus*	Ecuador	Manabi, Cerro San Sebastián, PN Machalilla	DB 289	−1.584	−80.689
b54	*Buarremon brunneinucha inornatus*	Ecuador	Manabi, Cerro San Sebastián, PN Machalilla	DB 450	−1.584	−80.689
b55	*Buarremon brunneinucha inornatus*	Ecuador	Guayas, Loma Alta, Cerro La Torre, 35 km S PN Machalilla	DB 525	−1.829	−80.563
b56	*Buarremon brunneinucha inornatus*	Ecuador	Azuay, Manta Real, ca. 6 km S Zhucay (near Naranjal)	ANSP 3529	−2.554	−79.346
b57	*Buarremon brunneinucha frontalis*	Ecuador	Morona-Santiago, Cordillera de Cutucú, trail Logrono to Yaupi-Yapitya	LSUMZ B6124	−2.629	−78.096
b57	*Buarremon brunneinucha frontalis*	Ecuador	Morona-Santiago, Cordillera de Cutucú, trail Logrono to Yaupi-Yapitya	LSUMZ B6126	−2.629	−78.096
b58	*Buarremon brunneinucha frontalis*	Ecuador	Zamora-Chinchipe, below Chinapinza	ZMUC 116150	−4.001	−78.472
b58	*Buarremon brunneinucha frontalis*	Ecuador	Zamora-Chinchipe, below Chinapinza	ZMUC 116151	−4.001	−78.472
b59	*Buarremon brunneinucha frontalis*	Ecuador	Zamora-Chinchipe, S Romerillos	ZMUC 119146	−4.238	−79.013
b60	*Buarremon brunneinucha frontalis*	Ecuador	Zamora-Chinchipe, Cerro Toledo	ZMUC 122261	−4.384	−79.122
b61	*Buarremon brunneinucha frontalis*	Peru	Cajamarca, Machete on Sapalache-Carmen trail	LSUMZ B224	−5.050	−79.350
b62	*Buarremon brunneinucha frontalis*	Peru	Cajamarca, E slope Cerro Chinguela, 8 km NE Sapalache	LSUMZ B316	−5.113	−79.371
b63	*Buarremon brunneinucha frontalis*	Peru	Cajamarca, Nuevo Perú, 16 km NE junction Ríos Tabacomas and Chinchipe	LSUMZ B33491	−5.285	−78.685
b63	*Buarremon brunneinucha frontalis*	Peru	Cajamarca, Nuevo Perú, 16 km NE junction Ríos Tabacomas and Chinchipe	LSUMZ B33497	−5.285	−78.685
b63	*Buarremon brunneinucha frontalis*	Peru	Cajamarca, Nuevo Perú, 16 km NE junction Ríos Tabacomas and Chinchipe	LSUMZ B33667	−5.285	−78.685
b63	*Buarremon brunneinucha frontalis*	Peru	Cajamarca, Nuevo Perú, 16 km NE junction Ríos Tabacomas and Chinchipe	LSUMZ B33725	−5.285	−78.685
b63	*Buarremon brunneinucha frontalis*	Peru	Cajamarca, Nuevo Perú, 16 km NE junction Ríos Tabacomas and Chinchipe	LSUMZ B33400	−5.285	−78.685
b64	*Buarremon brunneinucha frontalis*	Peru	Cajamarca, Quebrada Lanchal, ca. 8 km ESE Sallique	LSUMZ B31704	−5.688	−79.272
b64	*Buarremon brunneinucha frontalis*	Peru	Cajamarca, Quebrada Lanchal, ca. 8 km ESE Sallique	LSUMZ B31855	−5.688	−79.272
b64	*Buarremon brunneinucha frontalis*	Peru	Cajamarca, Quebrada Lanchal, ca. 8 km ESE Sallique	LSUMZ B31944	−5.688	−79.272
b64	*Buarremon brunneinucha frontalis*	Peru	Cajamarca, Quebrada Lanchal, ca. 8 km ESE Sallique	LSUMZ B31987	−5.688	−79.272
b64	*Buarremon brunneinucha frontalis*	Peru	Cajamarca, Quebrada Lanchal, ca. 8 km ESE Sallique	LSUMZ B32207	−5.688	−79.272
b64	*Buarremon brunneinucha frontalis*	Peru	Cajamarca, Quebrada Lanchal, ca. 8 km ESE Sallique	LSUMZ B32349	−5.688	−79.272
b64	*Buarremon brunneinucha frontalis*	Peru	Cajamarca, Quebrada Lanchal, ca. 8 km ESE Sallique	LSUMZ B32532	−5.688	−79.272
b65	*Buarremon brunneinucha frontalis*	Peru	San Martín, 15 km by trail NE Jirillo on trail to Balsapuerto	LSUMZ B5541	−6.071	−76.721
b66	*Buarremon brunneinucha frontalis*	Peru	San Martín, 20 km by road NE Tarapoto on road to Yurimaguas	LSUMZ B5462	−6.396	−76.213
b67	*Buarremon brunneinucha frontalis*	Peru	Loreto, 77 km WNW Contamana	LSUMZ B27755	−7.054	−75.654
b67	*Buarremon brunneinucha frontalis*	Peru	Loreto, 77 km WNW Contamana	LSUMZ B27816	−7.054	−75.654
b67	*Buarremon brunneinucha frontalis*	Peru	Loreto, 77 km WNW Contamana	LSUMZ B27856	−7.054	−75.654
b68	*Buarremon brunneinucha frontalis*	Peru	Loreto, ca. 86 km SE Juanjui on E bank upper Río Pauya	LSUMZ B39863	−7.538	−75.904
b68	*Buarremon brunneinucha frontalis*	Peru	Loreto, ca. 86 km SE Juanjui on E bank upper Río Pauya	LSUMZ B40009	−7.538	−75.904
b69	*Buarremon brunneinucha frontalis*	Peru	Pasco, Playa Pampa, ca. 8 km NW Cushi on trail to Chaglla	LSUMZ B7990	−9.829	−75.721
b69	*Buarremon brunneinucha frontalis*	Peru	Pasco, Playa Pampa, ca. 8 km NW Cushi on trail to Chaglla	LSUMZ B8095	−9.829	−75.721
b70	*Buarremon brunneinucha frontalis*	Peru	Pasco, Santa Cruz, ca. 9 km SSE Oxapampa	LSUMZ B1626	−10.621	−75.363
b70	*Buarremon brunneinucha frontalis*	Peru	Pasco, Santa Cruz, ca. 9 km SSE Oxapampa	LSUMZ B1645	−10.621	−75.363
b70	*Buarremon brunneinucha frontalis*	Peru	Pasco, Santa Cruz, ca. 9 km SSE Oxapampa	LSUMZ B1688	−10.621	−75.363
b71	*Buarremon brunneinucha frontalis*	Peru	Cusco, Paucartambo, San Pedro	FMNH 430059	−13.056	−71.548
b72	*Buarremon brunneinucha frontalis*	Peru	Cusco, Paucartambo, Suecia, km 138.5 on Cusco-Shintuya Highway	FMNH 398360	−13.129	−71.504
b73	*Buarremon brunneinucha frontalis*	Peru	Cusco, Machu Picchu, Intipata ruins	MUSM 24327	−13.188	−72.546
	Buarremon virenticeps					
v1	*Buarremon virenticeps*	Mexico	Jalisco, Puerto Los Mazos, Sierra de Manantlán	FMNH 343338	19.538	−103.479
v1	*Buarremon virenticeps*	Mexico	Jalisco, Puerto Los Mazos, Sierra de Manantlán	FMNH 343351	19.538	−103.479
v2	*Buarremon virenticeps*	Mexico	Michoacán, 3 km N Zirimondiro, Pico de Tancítaro	FMNH 394040	19.371	−102.334
v2	*Buarremon virenticeps*	Mexico	Michoacán, 3 km N Zirimondiro, Pico de Tancítaro	FMNH 394041	19.371	−102.334
v2	*Buarremon virenticeps*	Mexico	Michoacán, 3 km N Zirimondiro, Pico de Tancítaro	FMNH 394043	19.371	−102.334

(*continued on next page*)

Appendix A (*continued*)

Id	Taxon	Country	Locality	Catalogue No.*	Lat.	Lon.
v3	*Buarremon virenticeps*	Mexico	Ocuilón-Cuernavaca Hwy, km 14	FMNH 394044	18.938	−99.354
v3	*Buarremon virenticeps*	Mexico	Ocuilón-Cuernavaca Hwy, km 14	FMNH 395825	18.938	−99.354
v4**	*Buarremon virenticeps*	Mexico	Mexico, 2 km E San Rafael, hacia Cañada de los Diamantes, Iztaccihuatl	AMNH PEP 1427	19.209	−98.758
v5*	*Buarremon virenticeps*	Mexico	Mexico, undetermined locality	BMUM MT410	—	—
	Buarremon torquatus					
t1	*Buarremon torquatus costaricensis*	Costa Rica	Puntarenas, Potrero Grande, 12 km NE; Finca Los Helechales	WFVZ 26697	9.096	−83.063
t2**	*Buarremon torquatus costaricensis*	Costa Rica	Puntarenas, Coto Brus, Estación Biológica Las Cruces	UCR GB 130	8.786	−82.973
t2*	*Buarremon torquatus costaricensis*	Costa Rica	Puntarenas, Coto Brus, Estación Biológica Las Cruces	UCR GB 131	8.786	−82.973
t3**	*Buarremon torquatus tacarcunae*	Panama	Panama, NW slope Cerro Jefe	LSUMZ B28362	9.254	−79.413
t3*	*Buarremon torquatus tacarcunae*	Panama	Panama, NW slope Cerro Jefe	LSUMZ B28367	9.254	−79.413
t4**	*Buarremon torquatus basilicus*	Colombia	Magdalena, Sierra Nevada de Santa Marta, Estación San Lorenzo	IAvH BT-463	11.104	−74.063
t4	*Buarremon torquatus basilicus*	Colombia	Magdalena, Sierra Nevada de Santa Marta, Estación San Lorenzo	ICN 23517	11.104	−74.063
t5	*Buarremon torquatus perijanus*	Venezuela	Zulia, Sierra del Perijá, Barranquilla Ranchería Julián	COP 58258	10.121	−72.713
t6*	*Buarremon torquatus* cf *larensis*	Colombia	Norte de Santander, Agua de la Virgen	ICN FGS 3906	8.229	−73.254
t7	*Buarremon torquatus larensis*	Venezuela	Lara, 40 km S Cabudare	COP 72251	9.746	−69.429
t8	*Buarremon torquatus phygas*	Venezuela	Sucre, Piedra de Moler, San Antonio, Serranía del Turimiquire	COP JLP 358	10.103	−63.815
t8*	*Buarremon torquatus phygas*	Venezuela	Sucre, Piedra de Moler, San Antonio, Serranía del Turimiquire	COP JLP 363	10.103	−63.815
t9**	*Buarremon torquatus phygas*	Venezuela	Sucre, PN Península de Paria, Subida al Cerro Humo desde Las Melenas	COP JLP 248	10.704	−62.629
t10	*Buarremon torquatus atricapillus*	Colombia	Antioquia, Dabeiba, Río Amparradó, campamento Pantano Ingeominas	ICN 27218	7.017	−76.267
t11	*Buarremon torquatus assimilis*	Colombia	Antioquia, Páramo de Frontino	ZMUC 134956	6.429	−76.079
t11	*Buarremon torquatus assimilis*	Colombia	Antioquia, Páramo de Frontino	ZMUC 134979	6.429	−76.079
t12	*Buarremon torquatus assimilis*	Colombia	Antioquia, Bello, Cgto. San Félix, Cuchilla de Las Baldías, "Las Antenas"	IAvH 11698	6.338	−75.654
t12	*Buarremon torquatus assimilis*	Colombia	Antioquia, Bello, Cgto. San Félix, Cuchilla de Las Baldías, "Las Antenas"	IAvH 11700	6.338	−75.654
t13	*Buarremon torquatus atricapillus*	Colombia	Antioquia, Amalfi, Vda. Salazar, Finca Bodega Vieja	ICN AMC 658	6.929	−75.096
t14	*Buarremon torquatus atricapillus*	Colombia	Antioquia, Amalfi, Vda. Las Animas, Bosque La Escuela	ICN AMC 634	6.929	−75.004
t15*	*Buarremon torquatus atricapillus*	Colombia	Antioquia, Mpio. Don Matías, Estación Pradera	IAvH 11697	6.529	−75.263
t16	*Buarremon torquatus atricapillus*	Colombia	Santander, Suaita, 3 km ENE San José de Suaita	ICN 33290	6.188	−73.429
t16*	*Buarremon torquatus atricapillus*	Colombia	Santander, Suaita, 3 km ENE San José de Suaita	ICN 33292	6.188	−73.429
t17	*Buarremon torquatus assimilis*	Colombia	Boyacá, Santuario de Fauna y Flora de Iguaque	IAvH 12207	5.696	−73.471
t18	*Buarremon torquatus assimilis*	Colombia	Boyaca, Sutamarchán, Serranía de Merchan	IAvH 12271	5.679	−73.663
t19	*Buarremon torquatus atricapillus*	Colombia	Cundinamarca, La Vega, Finca El Encanto	ICN 16248	5.000	−74.350
t20**	*Buarremon torquatus assimilis*	Colombia	Cundinamarca, Bojacá, Via Bogotá–La Mesa	IAvH 11681	4.663	−74.346
t21	*Buarremon torquatus assimilis*	Colombia	Cundinamarca, Parque Nacional Chingaza, Río Blanco	IAvH 12680	4.696	−73.854
t22	*Buarremon torquatus assimilis*	Colombia	Meta, Parque Nacional Chingaza, San José	IAvH 12632	4.494	−73.693
t23	*Buarremon torquatus assimilis*	Colombia	Risaralda, Parque Regional Ucumarí, Camino Peña Bonita a Peñas Blancas	IAvH 11695	4.718	−75.488
t23	*Buarremon torquatus assimilis*	Colombia	Risaralda, Parque Regional Ucumarí, Camino Peña Bonita a Peñas Blancas	IAvH 11696	4.718	−75.488
t24	*Buarremon torquatus atricapillus*	Colombia	Valle del Cauca, Río Bravo, Embalse Río Calima	ICN 28442	3.921	−76.646
t25	*Buarremon torquatus assimilis*	Ecuador	Carchi, W slope, near road Maldonado-Tulcán along Río La Plata	ANSP 631	0.804	−78.054
t26	*Buarremon torquatus assimilis*	Ecuador	Carchi, ca. 3 km SE Impueran, Cerro Mongus	ANSP 3955	0.438	−77.854
t26	*Buarremon torquatus assimilis*	Ecuador	Carchi, ca. 3 km SE Impueran, Cerro Mongus	ANSP 4001	0.438	−77.854
t27	*Buarremon torquatus assimilis*	Ecuador	Imbabura, Apuela road	ZMUC 116213	0.346	−78.438
t28	*Buarremon torquatus assimilis*	Ecuador	Imbabura, Loma Taminanga	ZMUC 116216	0.271	−78.471
t29	*Buarremon torquatus assimilis*	Ecuador	Napo, Río Azul	ZMUC 122189	−0.979	−78.271
t30	*Buarremon torquatus nigrifrons*	Ecuador	Loja, Cajanuma	ZMUC 121538	−4.101	−79.172
t31	*Buarremon torquatus nigrifrons*	Ecuador	Loja, 10 km E El Limo	ANSP 5164	−3.988	−80.163
t32	*Buarremon torquatus nigrifrons*	Ecuador	Loja, Celica Mts.	ZMUC 116214	−4.029	−79.879
t33	*Buarremon torquatus nigrifrons*	Ecuador	Loja, Utuana	ZMUC 116219	−4.371	−79.721
t33	*Buarremon torquatus nigrifrons*	Ecuador	Loja, Utuana	ZMUC 116220	−4.371	−79.721

t34	*Buarremon torquatus nigrifrons*	Ecuador	Loja, 1 km SE Carimanga	ZMUC 116217	−4.354	−79.563
t34	*Buarremon torquatus nigrifrons*	Ecuador	Loja, 1 km SE Carimanga	ZMUC 116218	−4.354	−79.563
t35	*Buarremon torquatus nigrifrons*	Peru	Piura, Cruz Blanca, 33 rd km SW Huancabamba	LSUMZ B405	−5.338	−79.546
t35*	*Buarremon torquatus nigrifrons*	Peru	Piura, Cruz Blanca, 33 rd km SW Huancabamba	LSUMZ B427	−5.338	−79.546
t36	*Buarremon torquatus assimilis*	Peru	Cajamarca, El Espino	LSUMZ B31669	−5.688	−79.338
t37*	*Buarremon torquatus assimilis*	Peru	Cajamarca, Quebrada Lanchal, ca. 8 km ESE Sallique	LSUMZ B31948	−5.688	−79.254
t37	*Buarremon torquatus assimilis*	Peru	Cajamarca, Quebrada Lanchal, ca. 8 km ESE Sallique	LSUMZ B31970	−5.688	−79.254
t37	*Buarremon torquatus assimilis*	Peru	Cajamarca, Quebrada Lanchal, ca. 8 km ESE Sallique	LSUMZ B32429	−5.688	−79.254
t37	*Buarremon torquatus assimilis*	Peru	Cajamarca, Quebrada Lanchal, ca. 8 km ESE Sallique	LSUMZ B32460	−5.688	−79.254
t38	*Buarremon torquatus poliophrys*	Peru	San Martín, Puerta del Monte, 30 km NE Los Alisos	LSUMZ B51279	−7.538	−77.479
t39	*Buarremon torquatus poliophrys*	Peru	La Libertad, Masua, E Tayabamba, on trail to Ongon	LSUMZ B51355	−8.221	−77.196
t40	*Buarremon torquatus poliophrys*	Peru	Pasco, Playa Pampa, ca. 8 km NW Cushi on trail to Chaglla	LSUMZ B8129	−9.796	−75.746
t41	*Buarremon torquatus poliophrys*	Peru	Pasco, Millpo, E Tambo de Vacas on Pozuzo-Chaglla Trail	LSUMZ B8240	−10.371	−76.304
t42*	*Buarremon torquatus poliophrys*	Peru	Pasco, Cumbre de Ollón, ca. 12 km E Oxapampa	LSUMZ B1844	−10.579	−75.296
t43	*Buarremon torquatus poliophrys*	Peru	Cusco, Paucartambo, Pillahuata	FMNH 430060	−13.164	−71.595
t43*	*Buarremon torquatus poliophrys*	Peru	Cusco, Paucartambo, Pillahuata	FMNH 430061	−13.164	−71.595
t44	*Buarremon torquatus torquatus*	Peru	Puno, Abra de Maruncunca, 10 km SW San Juan del Oro	LSUMZ B51275	−14.246	−69.004
t45*	*Buarremon torquatus torquatus*	Bolivia	La Paz, Piara, near Pelechuco	AMNH CBF 38	−14.787	−69.019
t46	*Buarremon torquatus torquatus*	Bolivia	Franz Tamayo, Parque Nacional Apolobamba	AMNH CJV 379	−14.821	−68.952
t46	*Buarremon torquatus torquatus*	Bolivia	Franz Tamayo, Parque Nacional Apolobamba	AMNH CJV 384	−14.821	−68.952
t46	*Buarremon torquatus torquatus*	Bolivia	Franz Tamayo, Parque Nacional Apolobamba	AMNH OMZ 102	−14.821	−68.952
t46	*Buarremon torquatus torquatus*	Bolivia	Franz Tamayo, Parque Nacional Apolobamba	AMNH OMZ 129	−14.821	−68.952
t47*	*Buarremon torquatus torquatus*	Bolivia	La Paz, ca. 1 km S Chuspipata	LSUMZ B1284	−16.296	−67.084
t48	*Buarremon torquatus torquatus*	Bolivia	Cochabamba, Tablas Montes, Tunari	ZMUC 122899	−17.104	−65.888
t48	*Buarremon torquatus torquatus*	Bolivia	Cochabamba, Tablas Montes, Tunari	ZMUC 122904	−17.104	−65.888
t48	*Buarremon torquatus torquatus*	Bolivia	Cochabamba, Tablas Montes, Tunari	ZMUC 122925	−17.104	−65.888
t49	*Buarremon torquatus torquatus*	Bolivia	Cochabamba, Chapare, San Onofre, ca. 43 km W Villa Tunari	LSUMZ B38932	−17.138	−65.785
t49	*Buarremon torquatus torquatus*	Bolivia	Cochabamba, Chapare, San Onofre, ca. 43 km W Villa Tunari	LSUMZ B39032	−17.138	−65.785
t50	*Buarremon torquatus torquatus*	Bolivia	Cochabamba, Villa Tunari	UWBM RIS 114	−17.163	−65.796
t51*	*Buarremon torquatus fimbriatus*	Bolivia	Chuquisaca, 7 km N Sopachuy	ZMUC 120842	−19.438	−64.479
t51*	*Buarremon torquatus fimbriatus*	Bolivia	Chuquisaca, 7 km N Sopachuy	ZMUC 120843	−19.438	−64.479
t52	*Buarremon torquatus borelli*	Argentina	Jujuy, Yuto	WFVZ 37050	−23.638	−64.571
t53**	*Buarremon torquatus borelli*	Argentina	Salta, 30 km N, 5 km E Salta	MBM 5489	−24.554	−65.404
t54	*Buarremon torquatus borelli*	Argentina	Tucumán, Rio Tajamar, a few kilometers from Taruca towards Río Nio	PH 003 (1992)	−26.574	−64.834
t54*	*Buarremon torquatus borelli*	Argentina	Tucumán, Rio Tajamar, a few kilometers from Taruca towards Río Nio	PH 004 (1992)	−26.574	−64.834
	Arremon					
	Arremon aurantiirostris	Honduras	Copán	MBM 7856	—	—
	Arremon taciturnus	Brazil	Pará	FMNH 391609	—	—
	Arremon flavirostris	Paraguay	Alto Paraguay	KU 143	—	—
	Arremon abeillei	Ecuador	Loja	ANSP 5224	—	—
	Lysurus					
	Lysurus castaneiceps	Ecuador	Morona-Santiago	LSUMZ B6029		
	Lysurus crassirostris	Panama	Chiriquí	LSUMZ B26437		
	Outgroups					
	Pezopetes capitalis	Costa Rica	San José	LSUMZ 12632	—	—
	Atlapetes pileatus	Mexico	Jalisco	MBM 12967	—	—
	Pselliophorus tibialis	Costa Rica	San José	LSUMZ B9941	—	—
	Pipilo aberti	USA	Nevada	MBM 5270	—	—

(*continued on next page*)

Appendix A (*continued*)

Id	Taxon	Country	Locality	Catalogue No.*	Lat.	Lon.
	Junco hyemalis	USA	Nevada	MBM 8554	—	—
	Melospiza melodia	USA	Montana	BMUM JK 94-84	—	—
	Zonotrichia leucophrys	USA	Minnesotta	BMUM JDW 0054	—	—
	Ammodramus maritimus	USA	Locality unknown	JA JDW0054	—	—

* Acronyms, AMNH (American Museum of Natural History); ANSP (Academy of Natural Sciences of Philadelphia); BMUM (Bell Museum of Natural History; University of Minnesota); COP (Colección Ornitológica Phelps); FMNH (Field Museum of Natural History); IAvH (Instituto Alexander von Humboldt); ICN (Instituto de Ciencias Naturales; Universidad Nacional de Colombia); KU (University of Kansas Natural History Museum); JA (John Avise); LSUMZ (Louisiana State University Museum of Natural Science); MBM (Marjorie Barrick Musem, University of Nevada-Las Vegas); MUSM (Museo de la Universidad de San Marcos); UCR (Universidad de Costa Rica); USNM (United States National Museum, Smithsonian Institution); UWBM (University of Washington Burke Museum); WFVZ (Western Foundation of Vertebrate Zoology); ZMUC (Zoological Museum, University of Copenhagen).

** Collections of blood or feather samples, AMC (Andrés M. Cuervo); CDC (Carlos Daniel Cadena); DB (Dusti Becker, University of New Mexico); JCDC (Juan Carlos de las Casas); PH (Paul Handford—Steven Lougheed; Queens University).

The ID field indicates localities as shown in Figs. 1, 5, and 7. Sequences of the ND2 gene were obtained for all samples; samples with an asterisk after the ID were included in analyses of ND2, cyt *b*, ATPase 6 and ATPase 8; those with two asterisks were included in analyses of the four mitochondrial genes and the ACO1 and MUSK nuclear introns.

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