

Phylogeography of the *Buarremon* brush-finch complex (Aves, Emberizidae) in Mesoamerica

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Abstract

The *Buarremon* brush-finches represent a complex suite of populations distributed in the montane New World Tropics from Mexico south to South America. Traditional taxonomic arrangements have separated populations of this genus into three species, based on plumage variation, although plumage patterns are well known to exhibit homoplasy. We present a first detailed phylogeographic and phylogenetic study, focused on Mesoamerican populations, and signal the existence of strong differentiation among populations with a clear geographic structure. We find well differentiated clades for (1) the Sierra Madre Oriental and Sierra Madre del Sur in Oaxaca, (2) western Mexican populations, including the *B. brunneinucha* populations in the Sierra Madre del Sur and *B. virenticeps*, (3) Sierra Madre Oriental and Sierra de los Tuxtlas, (4) northern Central America, (5) southern Central America, (6) middle Central America, and (7) South America. We demonstrate a lack of concordance with plumage patterns, and argue for several additional species to be recognized in the complex.

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1. Introduction

The genus *Buarremon* comprises a group of Neotropical finches that inhabits humid montane forests from Mexico to Argentina. Merged into *Atlapetes* by Hellmayr (Hellmayr, 1938), but recently recognized again based on molecular systematic studies (García-Moreno and Fjeldså, 1999; Hackett, 1992), they also differ in behavior, distribution, and ecology (Remsen and Graves, 1995). The closest relatives of *Buarremon* are probably *Arremon*, *Pipilo*, and certain *Aimophila*, whereas *Atlapetes sensu stricto* is apparently more closely related to *Junco* and *Chlorospingus* (Yuri and Mindell, 2002).

Distributional patterns within *Buarremon* are also curious. The chestnut-capped *B. brunneinucha* is widespread in montane regions of the Neotropics; the green-capped *B. virenticeps* is endemic to the mountains of west-central Mexico; but the closely similar *B. torquatus* [including *B. atricapillus* (AOU, 1983)] is disjunct, in the mountains of southern Central America and South America. Although *B. virenticeps* and *B. brunneinucha* are largely allopatric, the latter coexists at different degrees of allopatry, parapatry, and sympatry with *B. torquatus* in a complex mosaic (Chapman, 1923; Remsen and Graves, 1995; Ridgely and Gwynne, 1989).

Plumage convergence among this suite of taxa is impressive. Plumage patterns similar to those in *Buarremon* are found in several other tropical finches (e.g., *Arremon* and *Pipilo*). For example, southwestern populations of *Pipilo ocai* (e.g., *P. o. guerrerensis* from the Sierra Madre del Sur) are surprisingly similar in coloration to the sympatric *B. brunneinucha suttoni* (Parkes, 1957; Sibley, 1950); in

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eastern Mexico, the lowland finch *Arremon aurantirostris* is also closely similar.

Buarremon virenticeps is restricted to montane forests of western and central Mexico in the Sierra Madre Occidental and Transvolcanic Belt. It is sometimes considered polytypic (subspecies *virenticeps*, *verecundus*, and *colimae*) (Miller et al., 1957), but more recent treatments suggest that it is monotypic (Dickinson, 2003). This species has often been considered as sister species to or conspecific with *B. torquatus* (AOU, 1983; Remsen and Graves, 1995).

Buarremon brunneinucha is a widespread species distributed from Mexico south to Peru (Chapman, 1923). Parkes (1954, 1957, 1959) and Paynter (1978) made extensive revisions to the taxonomy of this group, analyzing its complex geographic variation (Parkes, 1954). A first molecular study indicated significant genetic subdivision, but did not include enough populations to permit broader conclusions (Peterson et al., 1992). Ten subspecies are generally recognized (Dickinson, 2003), including eight in Mexico and Central America; plumage and size variation is complex and without clear geographic pattern. Three forms (*apertus*, *inornatus*, *allinornatus*), all restricted to isolated mountain ranges, lack the black chest band present in all other populations.

The main habitat of *Buarremon* is humid montane forest, which is highly fragmented owing to the specific conditions of high humidity, high moisture input, and high altitude it requires (Brown and Kappelle, 1995; Foster, 2001; Webster, 1995). In Mexico and Central America, these forests are more fragmented than in South America

(particularly the humid eastern Andean slopes). The fragmented nature of the habitat makes it a center of evolution of remarkable biological diversity (Hernández-Baños et al., 1995), with numerous endemic taxa (Campbell, 1999; Fjeldså and Krabbe, 1990; Gentry, 1995). This rich biodiversity has been explained, among other reasons, as reflecting effects of climatic change in the past (Wijninga, 1995) that allowed alternating periods of isolation and continuity (Gentry, 1995; Graham, 1993; Van der Hammen and Hooghiemstra, 2001), with barriers associated with deep valleys (García-Moreno and Fjeldså, 2000; García-Moreno et al., 2004). Here, we present a mitochondrial DNA-based (mtDNA) assessment of the genetic variation and phylogeographic associations among Mesoamerican *Buarremon* populations, as part of a comprehensive molecular survey of the region's montane avifaunas.

2. Materials and methods

2.1. Taxon sampling and outgroups

We obtained tissue samples from all three *Buarremon* species (Appendix) and relevant outgroups (Fig. 1) via targeted field collections and by tissue grants from other institutions. We used samples of *Atlapetes pileatus*, *A. schistaceus schistaceus*, *A. s. taczanowskii*, *A. rufinucha comptus*, *Junco hyemalis*, *J. phaeonotus*, *Pipilo erythrophthalmus*, and *Calamospiza melanocorys* as outgroups (Yuri and Mindell, 2002). In all, we studied 73 individuals of

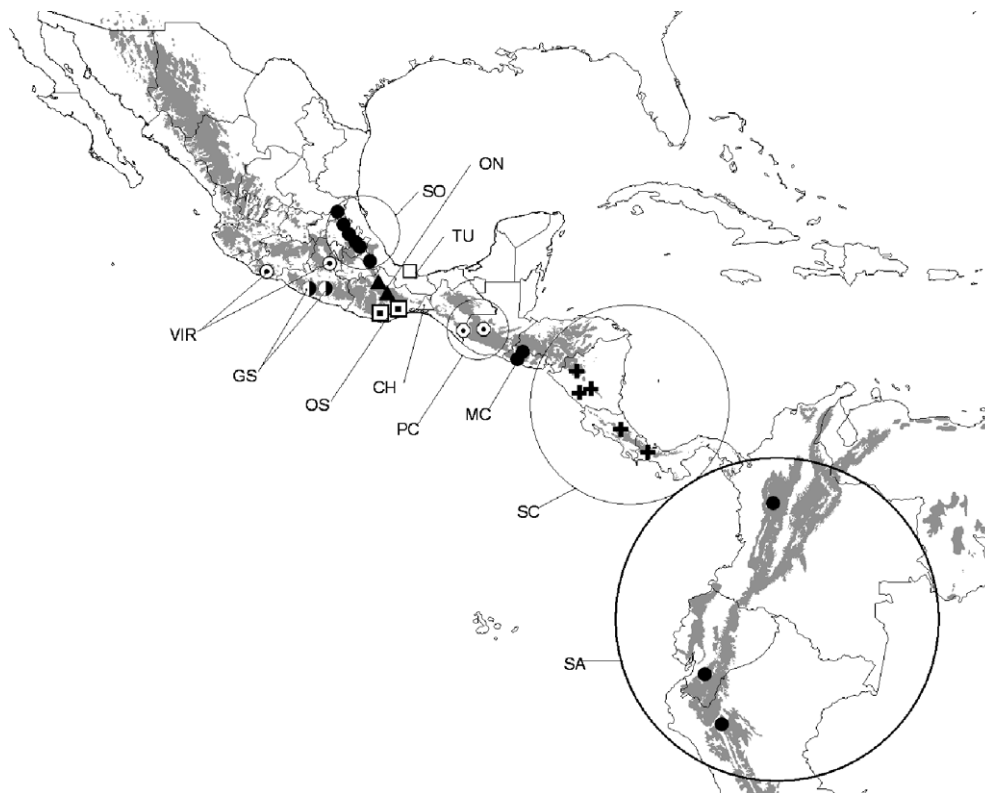


Fig. 1. Summary of population samples included in this study, along with the major clades that resulted from our analyses (circles).

Buarremon (2 *B. torquatus*, 4 *B. virenticeps*, 67 *B. brunneinucha*) and 10 outgroup individuals.

2.2. Molecular methods

We extracted DNA from tissue samples using the QIA-GEN DNEasy extraction kit following manufacturer's protocols. We amplified and sequenced a mtDNA fragment comprising the 3' end of the cytochrome oxidase II (26 bp), tRNA-lysine (70 bp), complete ATPase 8 (168 bp) and a 5' end fragment of ATPase 6 (537 bp). Because ATPase 8 and 6 have a 10 bp overlap in different reading frames, the total length of the sequence was 801 bp. We modified several primers from Sorensen et al. (Sorensen et al., 1999) to fit them to our target sequences; amplification was thus conducted using primers L8950 (CCA ACC ACA gCT TCA TrC C), L9368 (gAy AAC CgA TgA ATC ACy AAC), H9442 (Agr ATT Ars gCT CAT TTr TgT C), and H9855 (ACg TAr gCT Tgg ATy ATy gCT ACT gC) [position numbers from the chicken mitochondrial genome (Desjardins and Morais, 1990)]. Amplified products were cleaned by gel filtration using Sephadex G50 columns (Sigma), and sequenced using dye-labelled terminators (BigDye chemistry, Applied Biosystems). Sequencing reaction products were cleaned by gel filtration in the same way as PCR products, and resolved on an ABI 377 automated sequencer. All sequences have been deposited in GenBank under Accession Nos. EU364902–EU364975.

Sequences were aligned and proofread using SeAl v.2.0a11 (Rambaut, 2002); because sequences lacked insertions or deletions, alignment was unambiguous. We corroborated the origin of our sequences by combining at least two of the following: amplifying overlapping gene segments, amplifying or sequencing a region with different primer sets, sequencing both DNA strands, and using multiple individuals of a single species. We found no evidence of numt contamination of our mtDNA sequences (Bensasson et al., 2001; Sorensen and Quinn, 1998; Zhang and Hewitt, 1996), and we obtained congruent sequences that aligned well with sequences of other avian species, suggesting that we had indeed obtained our targeted sequences. Haplotype diversity, nucleotide diversity, and mismatch distributions and raggedness indices were calculated using DNAsp 4.0 (Rozas et al., 2003) and Tajima's *D* test and Fu's test of neutrality (Table 3) were calculated using ARLEQUIN ver. 2000 (Schneider et al., 2000). The distance matrix, base percentages, numbers of transitions (ts) and transversions (tv), and numbers of informative sites were obtained using PAUP* 4.0b10 (Swofford, 2002).

We analyzed general genetic structure of populations via analysis of genetic variance (AMOVA). In particular, we calculated F_{st} values to detect possible geographic genetic structure. Populations were not characterized as subgroups *a priori* (Sgariglia and Burns, 2003); rather, this step was achieved using ARLEQUIN ver. 2.000 (Schneider et al., 2000). We constructed haplotype networks using Network

4.1.1.2 (www.fluxus-engineering.com), using the MJ option (Bandelt et al., 1999).

2.3. Phylogenetic analyses

We conducted phylogenetic analyses of mtDNA sequences using maximum parsimony (MP) and maximum likelihood (ML) criteria. All analyses were performed using PAUP* 4.0b10 (Swofford, 2002) unless otherwise stated. The MP analyses were conducted with a heuristic search using the TBR branch-swapping option, with all positions equally weighted and unordered. Support for each node was obtained from 100 bootstrap replicates (Felsenstein, 1981).

We estimated model parameters for ML searches using ModelTest 3.06 (Posada and Crandall, 1998), which compares goodness-of-fit of models using the hierarchical likelihood ratio test (hLRT) statistic (Huelsenbeck and Rannala, 1997) and the Akaike Information Criterion (AIC). Based on the AIC, the GTR+I+G model of nucleotide substitution was identified as the best fit model, whereas the hLRT identified TrN+I+G as favored model. Analyses were run using both models, but we present only the results of the GTR+I+G analysis, as results were nearly identical. Nodal support was estimated via a 1000 non-parametric bootstrap replicates using 1000 addition replicates, limiting the number of rearrangements in each replicate to 1000.

We also analyzed sequences using a Bayesian inference approach (BI), as implemented in MrBayes 3.0b4 (Huelsenbeck and Ronquist, 2001). Four character partitions were defined, corresponding to COII, tRNA-Lys, ATPase 8, and ATPase 6, allowing for different evolutionary rates in each partition. We made two searches, running four Markov chains for 2.5×10^6 generations and sampling every 1000 generations; chains reached the stationary phase quickly, and we discarded conservatively the first 500 trees as burn-in and computed a consensus tree and posterior probabilities for each node based on the remaining 2000 trees (Huelsenbeck et al., 2002).

We also performed Shimodaira–Hasegawa tests of hypotheses (Shimodaira and Hasegawa, 1999) to assess whether each individual dataset rejected a particular topology, when compared with the ML topology generated by that dataset. For each dataset, we obtained the ML tree using the best-fit model of evolution and estimated parameter values, and used the same data to obtain a ML tree under the constrained topology generated by a different dataset as the null hypothesis. Then, likelihood values of both trees were compared using the Shimodaira–Hasegawa test, as implemented in PAUP* 4.0b10 (Swofford, 2002) (full optimization, 1000 bootstrap replicates).

3. Results

3.1. Ingroup sequence variation

We obtained 73 sequences that represent all *Buarremon* species and outgroups, for a total of 801 base pairs. Of these

bases, 564 were invariant, 237 were variable at some position in the dataset, and 196 were phylogenetically informative. The mean nucleotide composition was 23.5% T, 37% C, 29.9% A, and 9.5% G. Overall, we saw only 16 pairs of identical haplotypes; as such, 50 haplotypes were observed among *Buarremon* populations, with 12 more represented among outgroup taxa. Haplotype diversity was 0.989, and nucleotide diversity was 0.054. As expected, transitions were much more abundant than transversions (Table 1), with twice as many transversions between *B. brunneinucha* and *B. torquatus* (mean = 8.1, range 6–10) or *B. virenticeps* (mean = 9.1, range 7–11) than between *B. brunneinucha* populations (e.g., Guatemala populations vs. other *brunneinucha*: mean = 4.6, range 2–8; Tuxtlas population vs. other *brunneinucha*: mean = 3, range 1–5).

Significant geographic structure was indicated by the AMOVA (Table 2), suggesting that geographic substructuring among *Buarremon* populations is statistically significant and greater than that expected at random. Indeed, more than 30% of the total variation in the overall ingroup dataset is assorted among, rather than within, populations, indicating substantial geographic genetic subdivision of populations.

Maximum likelihood-corrected sequence divergences (Table 1; hereafter ‘genetic distances’) among samples were generally high—for example, distances between Mexican samples and South American samples ranged 4.5–8.2% (average 6.4%), and even higher if *B. virenticeps* was included (average 8%). No clear correlation appears to exist between geographic and genetic distances, as samples from the Tuxtlas region in Mexico are highly divergent from those of the neighboring Sierra Madre Oriental (4.0–4.7%), whereas samples along the Sierra Madre Oriental separated by an equivalent distance are quite similar (e.g., Hidalgo–Puebla: 0–1%); within the Sierra Madre del Sur, Guerrero samples differ from Oaxaca samples by >4% (4.3–5.2%); along the Sierra Madre Oriental, samples from the Zempoaltépetl area of northern Oaxaca differ by >5% from our sample from the Chimalapas area, and by a similar amount from samples taken in Puebla, the neighboring state to the north. In Central America, samples from El Salvador are quite divergent in comparison with others, and samples from the north (Guatemala, southern Chiapas) differ markedly (>3%; 3.1–3.7%) from those from the south (Nicaragua, Costa Rica, Panama). Divergence among *Buarremon brunneinucha* populations in southern Central America appears to be more subtle (highest ML distance 0.8%).

3.2. Haplotype diversity and mismatch distributions

The haplotype network showed considerable diversity and marked differentiation into subgroups (Fig. 2). More importantly, the network structure coincided closely with geographic distributions of samples: the large cluster at the lower left of Fig. 2 corresponds to Mexican samples; intermediate haplotypes are from Central America, and the samples at the upper right are from South America. This impressive

Table 1 Genetic distances (ML-corrected) among different Mesoamerican populations of *B. brunneinucha* (below diagonal), and number of transitions/transversions (above diagonal)

1	TU	—	26/3	26/2	33/1	34/2	35/1	31/2	29/3	33/5	32/5	33/3	33/4	34/3	35/4	32/4	35/8	51/7	
2	SO	0.042	—	4/1	35/4	36/5	37/4	33/5	32/4	33/8	31/8	39/6	37/7	40/6	41/7	42/7	34/11	49/9	
3	SO	0.040	0.006	—	31/3	32/4	33/3	33/4	32/5	33/7	31/7	35/5	33/6	36/5	39/6	40/6	30/10	47/9	
4	ON	0.050	0.061	0.051	—	3/1	12/0	18/1	30/2	33/4	32/4	34/2	32/3	31/2	38/3	33/3	29/7	46/6	
5	ON	0.055	0.065	0.055	0.005	—	0.016	17/2	29/3	32/5	31/5	33/3	31/4	30/3	37/4	30/4	28/8	47/7	
6	OS	0.054	0.064	0.055	0.016	11/1	—	20/1	32/2	38/4	37/4	38/2	36/3	35/2	40/3	35/3	31/7	52/6	
7	OS	0.049	0.067	0.057	0.026	0.026	0.026	—	0.052	0.064	35/5	34/3	38/4	37/3	40/4	37/4	32/8	50/6	
8	GS	0.047	0.055	0.057	0.047	0.048	0.050	32/3	—	0.056	31/6	37/4	34/5	35/4	40/5	37/5	26/7	51/7	
9	CH	0.058	0.066	0.063	0.056	0.057	0.066	36/5	31/6	—	7/2	22/2	22/3	23/3	28/3	31/3	40/11	53/10	
10	PC	0.057	0.062	0.059	0.054	0.054	0.062	0.062	0.056	0.012	—	25/2	21/3	22/2	29/3	32/3	37/11	51/10	
11	MC	0.054	0.073	0.063	0.054	0.054	0.061	0.056	0.063	0.033	0.038	—	14/1	15/0	20/1	21/1	33/9	54/8	
12	SC	0.056	0.071	0.061	0.053	0.053	0.060	0.066	0.060	0.035	0.034	0.020	—	3/1	22/2	21/2	28/10	49/9	
13	SC	0.056	0.076	0.065	0.049	0.053	0.060	0.066	0.060	0.035	0.034	0.020	0.002	—	3/1	22/2	28/10	49/9	
14	SC	0.056	0.075	0.064	0.048	0.049	0.055	0.061	0.060	0.035	0.034	0.020	0.005	0.005	—	23/1	31/9	48/8	
15	SA	0.060	0.080	0.073	0.064	0.065	0.067	0.070	0.072	0.045	0.047	0.029	0.034	0.032	0.032	—	15/0	40/10	54/9
16	SA	0.054	0.082	0.075	0.054	0.051	0.057	0.064	0.066	0.051	0.053	0.030	0.032	0.032	0.020	0.020	—	37/10	53/9
17	VIR	0.070	0.075	0.064	0.057	0.058	0.061	0.063	0.049	0.087	0.081	0.067	0.060	0.064	0.086	0.080	0.080	—	53/12
18	TOR	0.118	0.121	0.115	0.099	0.106	0.114	0.110	0.116	0.131	0.126	0.128	0.118	0.110	0.133	0.129	0.144	0.144	—

Table 2

Summary of results of AMOVA, showing the distribution of genetic variation among groups, populations, and individuals of *Buarremon* brush-finches

Source of variation	df	Sum of squares	Variant components	Percentage of variation
Among groups	4	652.075	5.92678	30.95
Among populations within groups	3	186.513	9.28535	48.49
Within populations	59	232.278	3.93692	20.56
Total	63	1070.866	19.14905	100.00

geographic cohesiveness of haplotypes again indicates significant geographic substructuring in this group.

Raggedness indices can provide indications of recent population expansion—'ragged' distributions support the idea of recent population stability, whereas peaked or single-spiked distributions suggest recent population expansions. In general, raggedness statistics ranged from 0.0262 in southern Central American populations to 0.4533 in northern Central America (Fig. 3). Associated *P*-values for six such distributions, as well as for the entire currently recognized species, were all >0.05 except for Western Mexico ($P = 0.04$); as such, and considering that multiple comparisons were made, the general picture is one of non-significance, indicating little support in general for hypotheses of recent range expansion, possibly excepting some clades like southern Central America and the Sierra

Madre Oriental. Results from Tajima's *D* test and Fu's test of neutrality also support this hypothesis (Table 3).

3.3. Phylogenetic analyses

The haplotype network (Fig. 2), as mentioned above, indicates considerable diversity in the ingroup, with complex relationships that have at least some degree of geographic structure. This network clearly shows both profound differentiation of the ingroup into marked subgroups, and inclusion of *B. virenticeps* among haplotypes of *B. brunneinucha*. We examined the data for fit to models of molecular evolution for selection of the optimal ML approach for tree-fitting. The best-fitting model for our dataset as determined by the AIC criterion (see comments in Section 2) was GTR+G+I, with estimated base frequencies $p_A = 0.3186$, $p_C = 0.3882$, $p_G = 0.0864$, and $p_T = 0.2067$; the substitution model rate matrix had values $R[A-C] = 504.1675$, $R[A-G] = 21297.75$, $R[A-T] = 596.8422$, $R[C-G] = 1498.1027$, $R[C-T] = 9831.332$ and $R[G-T] = 1$; the proportion of invariable sites (I) was 0.6032, and the gamma distribution shape parameter was 1.5914.

ML, BI, and MP analyses including all individuals and characters all converged on the same basic topology (Fig. 4), differing only in small rearrangements of individuals within major clades. In this topology, all individuals pertaining to *B. brunneinucha* and *B. virenticeps* form a strongly supported monophyletic clade (pp 100%, 98% bt). The ML ($-\ln = 3685.0746$), BI, and MP (526 steps, CI = 0.54,

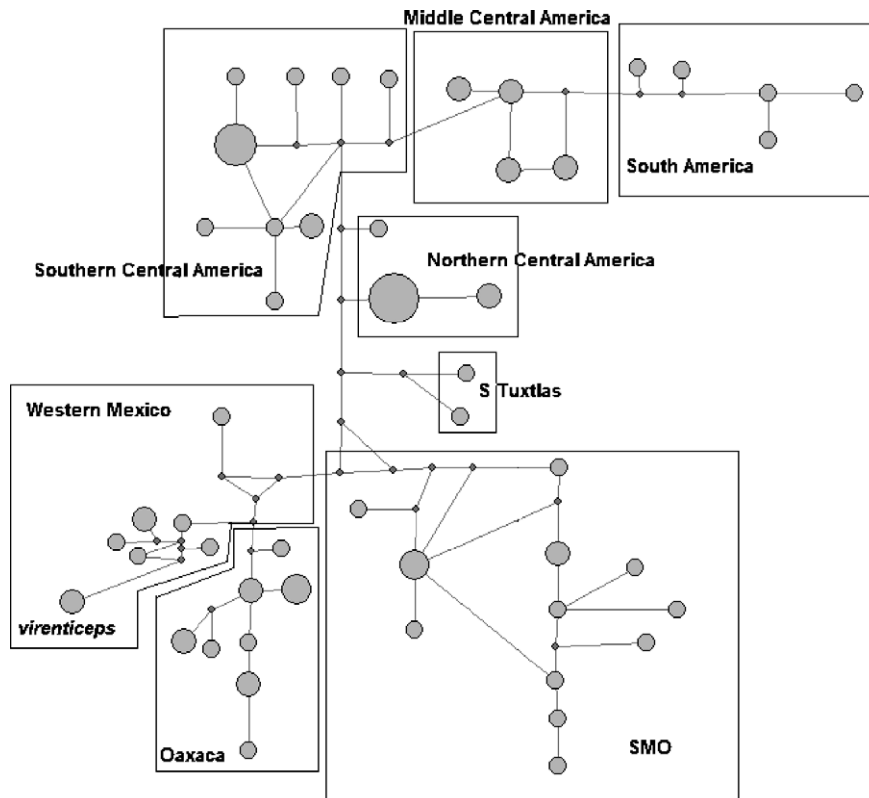


Fig. 2. Haplotype network of the *Buarremon* samples included in this study. Size of each circle indicates the number of individuals having that haplotype.

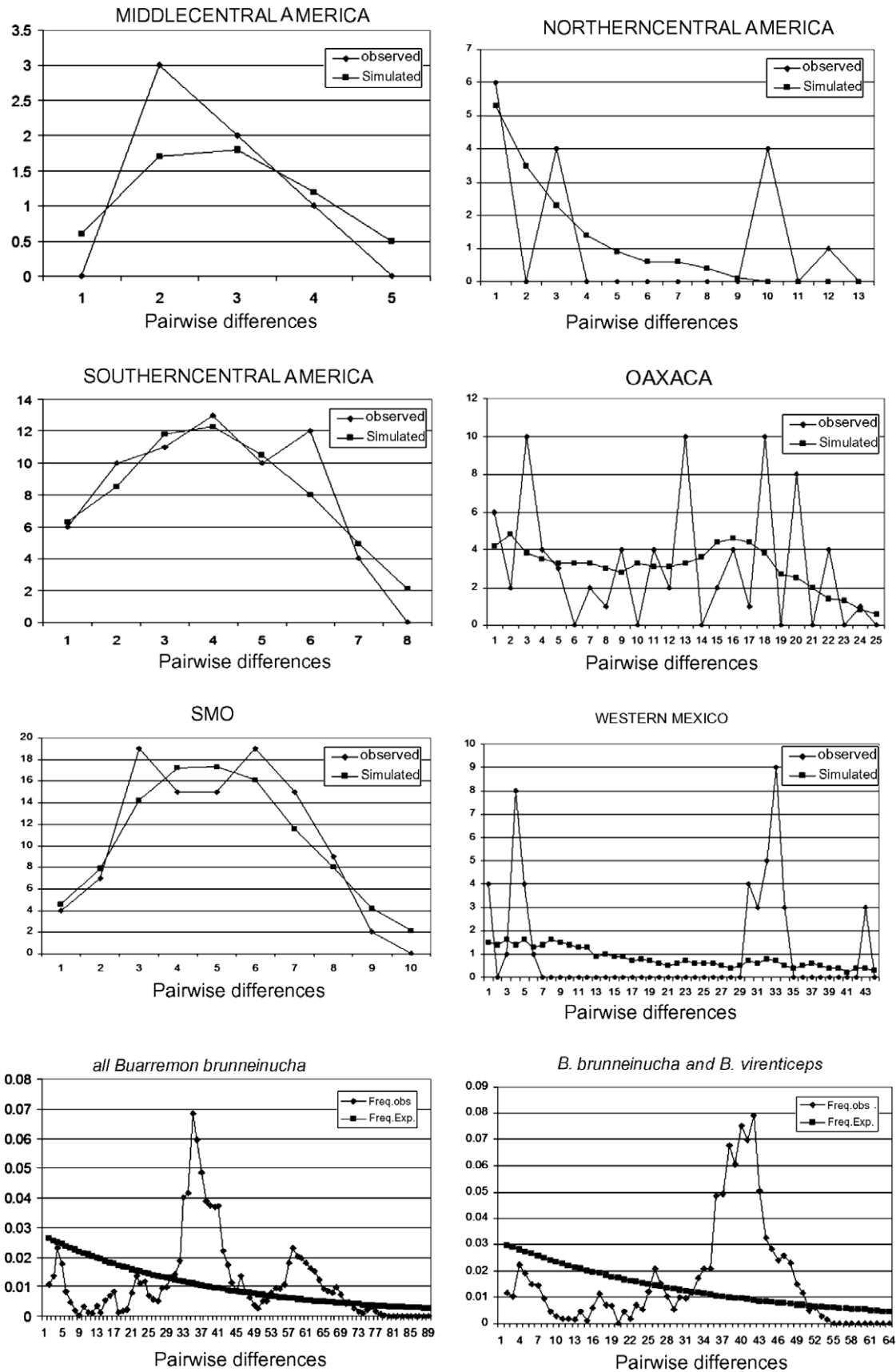


Fig. 3. Raggedness diagrams illustrating mismatch patterns for different *Buarremion* clades. (a) Middle Central America raggedness statistic $r = 0.3333$; (b) northern Central America $r = 0.4533$; (c) southern Central America $r = 0.0262$; (d) Oaxaca $r = 0.1151$; (e) Sierra Madre Oriental (north of Oaxaca) $r = 0.0263$; (f) western Mexico $r = 0.0948$; (g) all *B. brunneinucha* $r = 0.003$; (h) *B. brunneinucha* + *B. virenticeps* $r = 0.0035$.

Table 3
Tajima's *D* and Fu's tests of neutrality

Statistics	South America	Mid-cent America	South-cent America	N-cent America	S Madre Oriental	Sierra Tuxtlas	Western Mexico	Oaxaca	Mean	SD
<i>Tajima's D</i> test										
Sample size	5	4	12	6	15	2	10	13	8.375	4.44234
<i>S</i>	20	3	14	11	14	2	55	32	18.875	16.29753
Π	10.6	1.66667	2.95455	3.66667	3.94286	2	20.46667	10.41026	6.96346	6.08479
Tajima's <i>D</i>	0.77006	0.16766	-1.54738	-1.44477	-0.33398	0	0.25829	0.04197	-0.26102	0.76956
Tajima's <i>D</i> <i>P</i> -value	0.758	0.721	0.058	0.021	0.422	1	0.663	0.578	0.52763	0.32071
<i>Fu's FS</i> test										
No. of alleles (unchecked)	5	4	9	3	12	2	7	8	6.25	3.15238
Theta_pi	10.6	1.66667	2.95455	3.66667	3.94286	2	20.466667	10.41026	6.96346	6.08479
Exp. no. of alleles	4.2605	2.43669	5.21931	3.88411	6.60441	1.66667	8.30872	8.72036	5.1376	2.41695
FS	-0.26142	-2.1811	-4.08099	2.24235	-6.03088	0.69315	2.6597	1.27617	-0.71038	2.91602
FS <i>P</i> -value	0.258	0.022	0.008	0.87	0.002	0.363	0.888	0.706	0.35852	0.35852

HI = 0.4990, RI = 0.8651, RC = 0.4671) trees were not significantly different from each other based on Shimodaira and Hasegawa (Shimodaira and Hasegawa, 1999) tests. This consistent topology has a clear structure, where haplotypes sort out by geography: a clade of Oaxacan haplotypes was most basal in the ingroup, with clades representing eastern (Sierra de los Tuxtlas and Sierra Madre Oriental) and western Mexico clearly defined as one proceeds upward in the phylogeny. A Central American clade (100% posterior probability), where samples from northern Central America (Chiapas, Guatemala) are basal with respect to those of southern Central America (Nicaragua, Costa Rica, Panama) and South America (Colombia, Ecuador). So, in general, basal lineages originated in Mexico, intermediate lineages in Central America, and terminal lineages in South America.

Most nodes received high posterior probabilities ($\geq 95\%$), and bootstrap support ($>70\%$). In BI analyses, three deep nodes received relatively low prior probability support values. (1) The second deepest node within *Buarremon*, separating Western Mexico from the rest of the *Buarremon* (except for Oaxaca), has a PP of 81%. (2) The next node upwards, separating Central American lineages from those of the Sierra Madre Oriental, has a posterior probability of 70%. Finally, (3) the clade uniting samples from El Salvador with those from South America is also somewhat weakly supported (79%).

Compared to the BI analysis, ML recovered the same clades within *Buarremon*; however, several had lower nodal support values. Low bootstrap support was recovered for the node separating Oaxaca from a polytomy of remaining *Buarremon* clades (56%). Within that polytomy, clades from Central and South America received highest support (98%), while members of the Sierra de los Tuxtlas and Sierra Madre Oriental group received a lower value (76%); the western Mexican clade, including *B. virenticeps*, received a relatively low bootstrap support value (51%), but strong (95%) PP support in the BI analysis. Analysis excluding the sample of *B. virenticeps* from Michoacan resulted however on very strong bootstrap

and PP support for both the *B. virenticeps* clade (both 100 %) and the sister relationship between *B. virenticeps* and the *B. brunneinucha* samples from Guerrero (81% and 100%).

The overall tree supported by all three methods of analysis includes nine clades (Fig. 4), with major features as follows. First, *Buarremon torquatus* and *B. virenticeps*, frequently considered conspecific, are widely separated on the tree—*B. torquatus* is placed basally, and indeed is not linked to the ingroup by any character, whereas *B. virenticeps* is well within the ingroup tree, placed as sister to *B. brunneinucha* populations from the Sierra Madre del Sur in Guerrero, Mexico. Shimodaira–Hasegawa tests rejected the monophyly of *B. torquatus* + *B. virenticeps* ($P < 0.05$), and also a monophyletic *B. brunneinucha* as a better overall solution ($P < 0.05$). It is thus clear that grouping the two stripe-headed taxa as a monophyletic lineage is a significantly worse solution to the data available.

The basal group in the ingroup is composed of populations from Oaxaca, in southern Mexico, which curiously includes populations from both the Sierra Madre del Sur (specifically the Sierra de Yucuñacua in southwestern Oaxaca) and populations of the Sierra Madre Oriental. Next most basal on the tree is a clade composed of *B. brunneinucha* populations from the Sierra Madre del Sur of Guerrero and *B. virenticeps*; Shimodaira–Hasegawa tests rejected the monophyly of the Sierra Madre del Sur populations ($P < 0.05$).

The interiormost clade of the *Buarremon* tree is composed of two main groups. The first links well-differentiated populations from the Sierra de los Tuxtlas (Veracruz, Mexico) with those of the northern Sierra Madre Oriental (north of Oaxaca). No particular structure that coincides with geographic patterns is observable among the numerous samples in the latter group.

The final group is complex, with perhaps four well-differentiated subgroups. Basal are the populations of the Chimalapas of eastern Oaxaca and those of the volcanoes of the Pacific slope of Chiapas (Mexico) and Guatemala. Next is

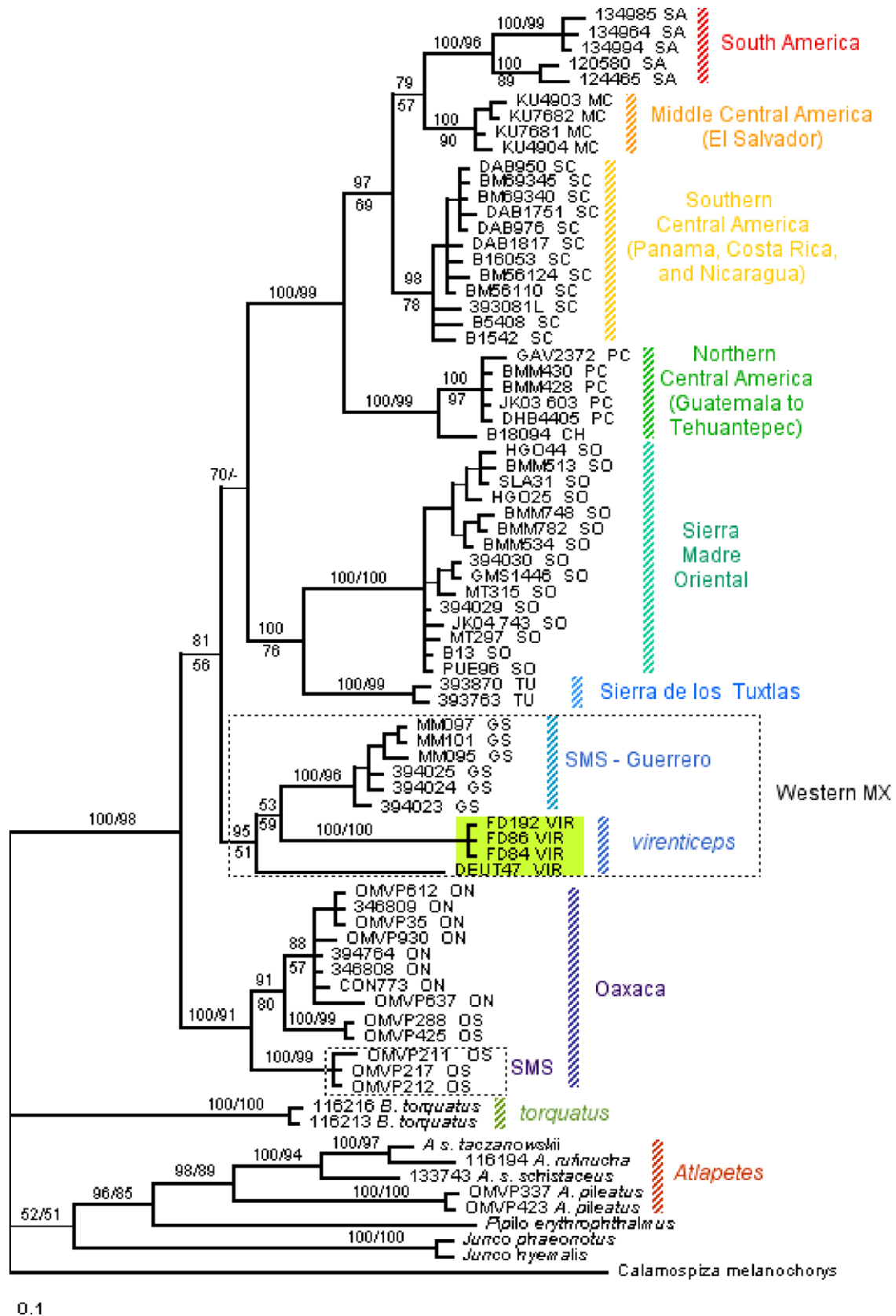


Fig. 4. Phylogenetic tree showing results of Bayesian analyses of mitochondrial DNA sequences of *Buarremon* and related species. Figures next to the nodes indicate posterior probabilities (above) and bootstrap support (below). Other phylogenetic methods yielded trees with topologies consistent with the one depicted (see text for details). Two-letter codes next to the sample numbers refers to the main groups discussed in the text; localities are listed in Appendix.

a broad assemblage from southern Central America (Panamá, Costa Rica, Nicaragua). Finally, sister to the southern Central American clade are a pair of groups: one composed of samples from El Salvador, and the other including all South American samples studied.

4. Discussion

Detailed study of mtDNA sequences of Mesoamerican *Buarremon brunneinucha* populations revealed extreme levels of genetic differentiation. These results agree with previous studies (Peterson et al., 1992), which identified strong differentiation among Mexican populations based on 29 allozyme loci. The diverse phylogenetic reconstruction approaches used herein converged on a single basic solution: seven well-differentiated clades in Mesoamerica, with a clear hierarchical pattern of relationships, and segregated from one another along clear geographic boundaries. Each of these clades has apparently been isolated genetically from all others for significant periods of time, at least as is reflected by substantial genetic distances. The raggedness indices and tests of neutrality indicated little support for hypotheses of recent population expansion as a general tendency in the history of *Buarremon* populations.

4.1. Phylogeny and geography of differentiation

The phylogeny obtained from our different analyses of sequences of mtDNA sequences indicates the existence of seven well-differentiated clades. These nodes defining these groups are well supported as evidenced by high posterior probabilities (BI) and bootstrap support (ML), and show considerable geographic coherence (Fig. 4). However, looking at relationships among these groups, several points merit further discussion. First, we failed to corroborate the monophyly of *Buarremon*. Instead we found a clade containing *brunneinucha* + *virenticeps*, to the exclusion of *torquatus*. All three current *Buarremon* are distant and distinct from *Atlapetes* (García-Moreno et al., unpublished results), with which they were previously combined. Our results suggest that these early taxonomic arrangements were based on phenotypic features that have little to do evolutionarily with phylogenetic history.

Of particular relevance is the monophyly—or lack thereof—of the currently recognized species in the genus (AOU, 1998). Indeed, we found that the *B. torquatus*–*B. virenticeps* ‘superspecies’ (AOU, 1983; Remsen and Graves, 1995) is artificial, with *B. torquatus* falling outside of the *Buarremon* clade entirely, but the near-identical *B. virenticeps* lying well within the clade. Indeed, the latter form falls as sister to the western Mexican forms of *B. brunneinucha*, confirming the well-known biogeographic relationship between the Transvolcanic Belt of central Mexico and the Sierra Madre del Sur of southwestern Mexico. The correct placement of *B. torquatus* falls beyond the scope of this work, and this relationship is explored elsewhere (García-Moreno et al., unpublished results).

Historical and biogeographic interpretations of the diversification of *Buarremon* present some interesting challenges. First, the basal clade corresponds to the *B. brunneinucha* populations of the Mexican state of Oaxaca (north and west of the Isthmus of Tehuantepec); curiously, though, this clade includes populations from both the north and east (i.e., Sierra Madre Oriental) and those of the Sierra Madre del Sur in the southern part of the state. This result is quite surprising, as studies of other species associated with the same habitats (e.g., *Chlorospingus ophthalmicus*, *Aulacorhynchus prasinus*) (García-Moreno et al., 2004; Peterson et al., 1992) have shown northern populations to be associated phylogenetically with populations of the northern Sierra Madre Oriental and/or the Sierra de los Tuxtlas, whereas the Oaxaca portion of the Sierra Madre del Sur (Sierra de Miahuatlán, Sierra de Yucuñacua) is related to the Sierra Madre del Sur of Guerrero. Nonetheless, the species endemic to the southern sierras of Oaxaca (e.g., *Eupherusa cyanophrys*) at least indicate a long period of significant isolation of these mountains from other ranges.

The remainder of the ingroup consists of a monophyletic clade with intermediate Bayesian branch support, which itself is constituted of two subclades. One of these lineages includes all *Buarremon* populations of western and central Mexico—the Sierra Madre Occidental, Sierra Madre del Sur (in Guerrero), and the Transvolcanic Belt. Although geographically this clade makes a lot of sense, quite unexpected was the placement of all samples of *B. virenticeps* within this clade, placed as sister to the *B. brunneinucha* populations of the Sierra Madre del Sur. It is important to stress that, in spite of its position in the phylogeny, our results do not put into question the validity of *B. virenticeps* as a species, as it is clearly distinguishable from other species by both morphological and genetic characters (Helbig et al., 2002). This arrangement reinforces the point that plumage evolution in this group, as in other related groups (e.g., *Atlapetes*, García-Moreno and Fjeldså, 1999; García-Moreno et al., unpublished results), is quite plastic and very homoplasious, and also coincides with known patterns of faunal similarity (Hernández-Baños et al., 1995).

The other main clade is also coherent geographically, including all traditional *B. brunneinucha* populations of eastern Mexico, Central America, and South America. One subclade links the populations of the Sierra de los Tuxtlas with those of the Sierra Madre Oriental, but only the part of the latter that is north of Oaxaca; this clade thus constitutes the last portion of the genus’ distributional areas north of the Isthmus of Tehuantepec. The remainder of this clade consists of populations of Central and South America: a clade of individuals from the Chimalapas region immediately east of the Isthmus and individuals from Guatemala, a clade from southern Central America (Nicaragua, Costa Rica, Panama), a clade of samples from El Salvador, and a clade of populations from South America. Each of these clades is clearly and well differentiated from each other, although the South American ‘clade’ doubtless includes considerable complexity not represented in our sampling. The strong isolation of pop-

ulations of the Tuxtlas massif is now becoming a repeated pattern in such phylogeographic studies [e.g., *Geotrygon carrikeri* (Peterson, 1993); *Campylopterus curvipennis-excellens* (AOU, 1998); *Chlorospingus ophthalmicus* (García-Moreno et al., 2004)]. The relative isolation and phylogenetic distinctiveness of populations from the northern versus southern portions of the Sierra Madre Oriental is also impressive, given the relative continuity of that mountain range.

The clade that unites all populations south and east of the Isthmus of Tehuantepec is strongly supported by all measures of branch support that we calculated. Within Central America, the analysis revealed three main groups, including (1) samples of populations of the Chimalapas east into Guatemala (although the Chimalapas sample is relatively distinct from the others in this group), (2) the samples that were available to us from El Salvador, and (3) samples from southern Central America. The division between groups (1) and (2), however, is a bit obscure, as distances between the sampling sites are not particularly great. However, the group 1 samples come exclusively from the Pacific slope volcanoes of southern Guatemala, whereas the Salvadoran samples come from the interior highlands. As such, we suspect that group 1 will encompass populations from the Chimalapas south and east along the Pacific coastal ranges (Sierra Madre de Chiapas) and on into the volcanoes of southern Guatemala, whereas group 2 will likely include populations in northern Guatemala and central Honduras as well. Clearly, denser sampling is needed for this situation to be clarified.

Finally, the patterns of similarity and relatedness among the few representatives of South American populations included in this study suggest that similar patterns of differentiation will likely be found there as well. That is, a reasonably marked break is observed between the three Colombian samples and samples from Ecuador and Peru. Given Parkes' (Parkes, 1954) summary of phenotypic variation across the species' range, clearly considerably more samples are needed

to summarize patterns of variation and differentiation in this portion of the range of the complex.

Overall, this pattern of diversification suggests a Mesoamerican origin for this group. Subsequent range expansions took the complex southward across major biogeographic barriers well south into South America. This pattern of origin and diversification likely contrasts with that of the 'other' brush-finches (*Atlapetes*), which has a clear center of diversity in the Andes of South America (Paynter, 1978), although origins do not necessarily coincide with centers of diversity. Subsequent patterns of isolation and independent evolution then led to the overall present diversity within this group.

4.2. Status of the "green-striped morphs"

The supposedly close relationship of *B. virenticeps* and *B. torquatus* has long been assumed and accepted with little doubt, even with the suggestion of conspecificity (AOU, 1983, 1998). Our analyses reveal that these two green-striped *Buarremon* are not closely related, and that their plumage similarity is entirely homoplasious. Indeed, *B. torquatus* is not even necessarily part of our ingroup, as no characters united it to the base of the *Buarremon* tree. Its true affinities will have to await a broader sequence-based survey.

As such, clearly, the idea that the disjunct forms of green-striped *Buarremon* are conspecific is untenable. Indeed, the situation is quite different: once again, what appears to be a broad disjunction turns out to be more complex (Parkes, 1954)—the only disjunctions among Mexican birds that have been analyzed in details that turn out to be real disjunctions among closely related lineages are two hummingbirds (Banks, 1990; Ortíz-Pulido et al., 2002). In the present case, however, the 'disjunction' is between two entities that only seem similar, but in reality have no particular phylogenetic affinities.

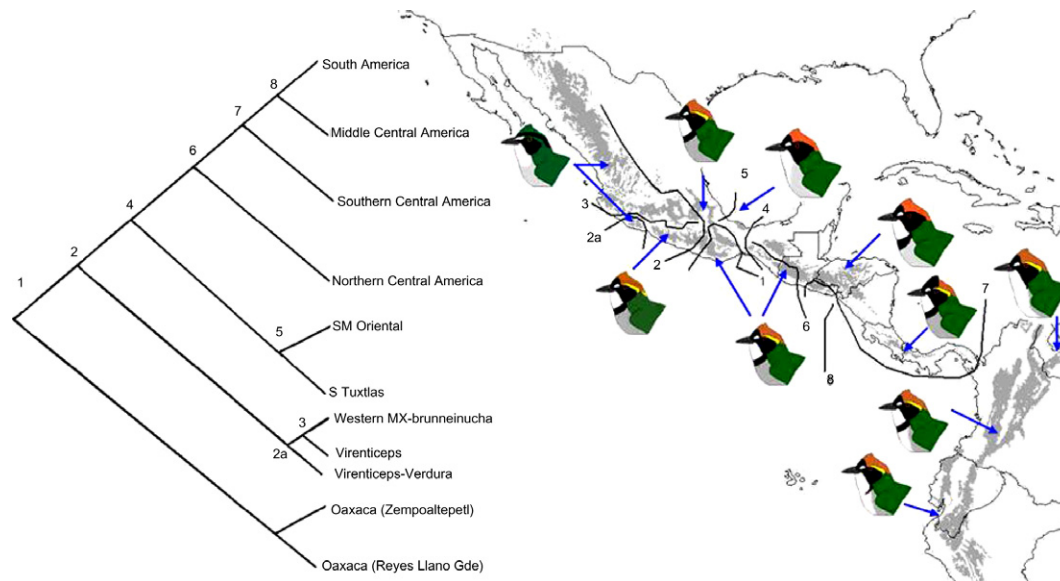


Fig. 5. Relationships among *Buarremon* populations linked to plumage patterns. The detail available in this study focuses on the Mesoamerican portion of the range of the genus. Numbers at the cladogram's nodes depict mapped divergence events.

4.3. Plumage variation and species limits

Parkes (Parkes, 1954) emphasized the impressive inconsistencies in plumage evolution among populations of *B. brunneinucha*. He turns out to be even more correct than he had imagined—not only do plumage features such as the breast band appear and disappear in different (and unrelated) populations, but even the ‘species’ character of chestnut *versus* green-striped cap has evolved with homoplasy (Fig. 5). Overall, given these unpredictable changes in plumage pattern and coloration, and the lack of appreciable morphological variation, it is clear that molecular characters must be central to any phylogenetically based taxonomic arrangement for this group, as they are for other brush-finches (e.g., *Atlapetes*) (García-Moreno and Fjeldsá, 1999; García-Moreno et al., unpublished results).

Buarremon brunneinucha, in the traditional sense (AOU, 1998), is paraphyletic owing to the inclusion of *B. virenticeps* populations—as such, it is not a natural group, and should not be used to represent a unit of biological diversity (whatever the species concept). To avoid recognition of paraphyletic ‘grades,’ however, serious rearrangements of species limits will be necessary to solve the problems with non-monophyly, and these changes should be made regardless of ideas regarding species concepts. Nevertheless, we believe that several subdivision may be warranted—here, however, questions of species concepts necessarily enter the picture (Navarro and Peterson, 2004; Remsen, 2005). Under the evolutionary species concept (ESC), as well as the phylogenetic species concept (PSC), decisions are clear—the Oaxaca and Sierra Madre del Sur of Guerrero populations each

merit species status, as would populations of Los Tuxtlas, the northern Sierra Madre Oriental, and the Chimalapas-Pacific Coast volcanoes, in view of their striking differentiation and the excellent population sampling available to us. The lineages corresponding to middle Central America, southern Central America, and South America can likely be divided as well, but we are concerned about the density of sampling, particularly for South America; also, we do not have enough samples in Central America to place other, key populations, such as those of the central cordillera of Honduras, in species units confidently. As such, we defer opinions on these populations until further samples become available for genetic studies.

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Appendix

Summary of samples included in this study, with species, Genbank accession number, source (i.e., museum and sample number where sample is deposited), approximate locality of provenance (locality, state or province, and country), and a group label that corresponds roughly to the evolutionary species listed in the Discussion. Note that the single specimen available from the Chimalapas region of southern Mexico is listed separately (group ‘CH’).

Group ^a	Genus	Species	Genbank No.	Tissue	Museum ^b	Locality	State/Province	Country ^c
1 SA	<i>Buarremon</i>	<i>brunneinucha</i>	EU364961	134985	ZMUC	Frontino Camp 1	Antioquia	COL
2 SA	<i>Buarremon</i>	<i>brunneinucha</i>	EU364962	134994	ZMUC	Frontino Camp 1	Antioquia	COL
3 SA	<i>Buarremon</i>	<i>brunneinucha</i>	EU364963	134964	ZMUC	Frontino Camp 1	Antioquia	COL
4 SA	<i>Buarremon</i>	<i>brunneinucha</i>	EU364964	120580	ZMUC	Panguri	Zamore-Chichipe	ECU
5 SA	<i>Buarremon</i>	<i>brunneinucha</i>	EU364965	124465	ZMUC	Hotel Turistas, Cerro Colan	Amazonas	PE
6 MC	<i>Buarremon</i>	<i>brunneinucha</i>	EU364945	KU7681	KU	N slope volcan San Vicente, finca El Carmen	Nuevo Tepetitlan	SL
7 MC	<i>Buarremon</i>	<i>brunneinucha</i>	EU364946	KU4903	KU	Cerro Las Nubes, NE C. Pital	San Ignacio	SL
8 MC	<i>Buarremon</i>	<i>brunneinucha</i>	EU364947	KU7682	KU	N slope volcan San Vicente, finca El Carmen	Nuevo Tepetitlan	SL

(continued on next page)

Appendix (continued)

Group ^a	Genus	Species	Genbank No.	Tissue	Museum ^b	Locality	State/Province	Country ^c
9 MC	<i>Buarremon</i>	<i>brunneinucha</i>	EU364948	KU4904	KU	Cerro Las Nubes, NE C. Pital	San Ignacio	SL
10 SC	<i>Buarremon</i>	<i>brunneinucha</i>	EU364949	DAB950	UNLV		Managua	NIC
11 SC	<i>Buarremon</i>	<i>brunneinucha</i>	EU364950	DAB976	UNLV		Managua	NIC
12 SC	<i>Buarremon</i>	<i>brunneinucha</i>	EU364951	DAB1817	UNLV	Chocoyero, 48 km SE Managua	Managua	NIC
13 SC	<i>Buarremon</i>	<i>brunneinucha</i>	EU364952	DAB1751	UNVL	Chocoyero, 48 km SE Managua	Managua	NIC
14 SC	<i>Buarremon</i>	<i>brunneinucha</i>	EU364953	BM56110	BM	10 km N Matagalpa	Matagalpa	NIC
15 SC	<i>Buarremon</i>	<i>brunneinucha</i>	EU364954	BM56124	BM	10 km N Matagalpa	Matagalpa	NIC
16 SC	<i>Buarremon</i>	<i>brunneinucha</i>	EU364955	BM69340	BM	Mombacho, 10 km S Granada	Granada	NIC
17 SC	<i>Buarremon</i>	<i>brunneinucha</i>	EU364956	BM69345	BM	Mombacho, 10 km S Granada	Granada	NIC
18 SC	<i>Buarremon</i>	<i>brunneinucha</i>	EU364957	393081	FMNH			CR
19 SC	<i>Buarremon</i>	<i>brunneinucha</i>	EU364958	B16053	LSU	Finca La Fortuna	Heredia	CR
20 SC	<i>Buarremon</i>	<i>brunneinucha</i>	EU364959	B1542	LSU		Chiriqui	PAN
21 SC	<i>Buarremon</i>	<i>brunneinucha</i>	EU364960	B5408	LSU		Chiriqui	PAN
22 PC	<i>Buarremon</i>	<i>brunneinucha</i>	EU364940	GAV2372	UNLV	Sta. María de Jesús, 2km E	Quetzaltenango	GUA
23 PC	<i>Buarremon</i>	<i>brunneinucha</i>	EU364941	DHB4405	UNLV	El Baúl, Xela	Quetzaltenango	GUA
24 PC	<i>Buarremon</i>	<i>brunneinucha</i>	EU364942	JK03-603	UNLV	Sta. María de Jesús, 5km SSW; finca de Santa Maria	Quetzaltenango	GUA
25 PC	<i>Buarremon</i>	<i>brunneinucha</i>	EU364943	BMM428	UNAM	Volcan de Tacana	Chiapas	MX
26 PC	<i>Buarremon</i>	<i>brunneinucha</i>	EU364944	BMM430	UNAM	Volcan de Tacana	Chiapas	MX
27 CH	<i>Buarremon</i>	<i>brunneinucha</i>	EU364929	B18094	LSU	Espinazo del Diablo, Chimalapas	Oaxaca	MX
28 SO	<i>Buarremon</i>	<i>brunneinucha</i>	EU364904	HGO-SLP 25	UNAM	Cerro Jarros	Hidalgo	MX
29 SO	<i>Buarremon</i>	<i>brunneinucha</i>	EU364905	HGO-SLP 44	UNAM	Cerro Jarros	Hidalgo	MX
30 SO	<i>Buarremon</i>	<i>brunneinucha</i>	EU364906	SLA31	UNAM	El Coyol	Hidalgo	MX
31 SO	<i>Buarremon</i>	<i>brunneinucha</i>	EU364907	BMM513	UNAM	El Potrero, Tenango	Hidalgo	MX
32 SO	<i>Buarremon</i>	<i>brunneinucha</i>	EU364908	BMM534	UNAM	El Potrero, Tenango	Hidalgo	MX
33 SO	<i>Buarremon</i>	<i>brunneinucha</i>	EU364909	BMM748	UNAM	Tlanchinol	Hidalgo	MX
34 SO	<i>Buarremon</i>	<i>brunneinucha</i>	EU364910	BMM782	UNAM	Tlanchinol	Hidalgo	MX
35 SO	<i>Buarremon</i>	<i>brunneinucha</i>	EU364911	394029	FMNH	Tlanchinol, 5 km E	Hidalgo	MX
36 SO	<i>Buarremon</i>	<i>brunneinucha</i>	EU364912	394030	FMNH	Tlanchinol, 5 km E	Hidalgo	MX
37 SO	<i>Buarremon</i>	<i>brunneinucha</i>	EU364913	PUE96	UNAM	Cuetzalan	Puebla	MX
38 SO	<i>Buarremon</i>	<i>brunneinucha</i>	EU364914	B-13	LSU	Teziutlan, 2 km E	Puebla	MX
39 SO	<i>Buarremon</i>	<i>brunneinucha</i>	EU364915	MT315	UNAM	Teocelo	Veracruz	MX
40 SO	<i>Buarremon</i>	<i>brunneinucha</i>	EU364916	MT297	UNAM	Teocelo	Veracruz	MX
41 SO	<i>Buarremon</i>	<i>brunneinucha</i>	EU364917	GMS1446	UNLV	Zacapoaxtla- Instituto Tecnologico Superior	Puebla	MX
42 SO	<i>Buarremon</i>	<i>brunneinucha</i>	EU364918	JK04-743	UNLV	Zacapoaxtla- Instituto Tecnologico Superior	Puebla	MX
43 TU	<i>Buarremon</i>	<i>brunneinucha</i>	EU364902	393870	FMNH	El Bastonal, Volcan Sta Marta	Veracruz	MX
44 TU	<i>Buarremon</i>	<i>brunneinucha</i>	EU364903	393763	FMNH	El Bastonal, Volcan Sta Marta	Veracruz	MX

Appendix (continued)

Group ^a	Genus	Species	Genbank No.	Tissue	Museum ^b	Locality	State/Province	Country ^c
45 GS	<i>Buarremon</i>	<i>brunneinucha</i>	EU364931	MM095	UNAM	Carrizal de Bravo	Guerrero	MX
46 GS	<i>Buarremon</i>	<i>brunneinucha</i>	EU364932	MM097	UNAM	Carrizal de Bravo	Guerrero	MX
47 GS	<i>Buarremon</i>	<i>brunneinucha</i>	EU364933	MM101	UNAM	Carrizal de Bravo	Guerrero	MX
48 GS	<i>Buarremon</i>	<i>brunneinucha</i>	EU364934	394025	FMNH	El Iris, S. de Atoyac	Guerrero	MX
49 GS	<i>Buarremon</i>	<i>brunneinucha</i>	EU364935	394023	FMNH	El Iris, S. de Atoyac	Guerrero	MX
50 GS	<i>Buarremon</i>	<i>brunneinucha</i>	EU364936	394024	FMNH	El Iris, S. de Atoyac	Guerrero	MX
51 VIR	<i>Buarremon</i>	<i>brunneinucha</i>	EU364930	DEUT47	UNAM	La Verdura	Michoacan	MX
52 VIR	<i>Buarremon</i>	<i>virenticeps</i>	EU364966	FD192	UNAM	Ocuilan	Mexico	MX
53 VIR	<i>Buarremon</i>	<i>virenticeps</i>	EU364967	FD84	UNAM	Ocuilan	Mexico	MX
54 VIR	<i>Buarremon</i>	<i>virenticeps</i>	EU364968	FD86	UNAM	Ocuilan	Mexico	MX
55 ON	<i>Buarremon</i>	<i>brunneinucha</i>	EU364919	OMVP930	UNAM	Cerro Peña Verde	Oaxaca	MX
56 ON	<i>Buarremon</i>	<i>brunneinucha</i>	EU364922	OMVP637	UNAM	La Clemencia	Oaxaca	MX
57 ON	<i>Buarremon</i>	<i>brunneinucha</i>	EU364923	OMVP612	UNAM	Puerto de la Soledad	Oaxaca	MX
58 ON	<i>Buarremon</i>	<i>brunneinucha</i>	EU364924	CONACyT 773	UNAM	Puerto de la Soledad	Oaxaca	MX
59 ON	<i>Buarremon</i>	<i>brunneinucha</i>	EU364925	OMVP35	UNAM	Puerto de la Soledad	Oaxaca	MX
60 ON	<i>Buarremon</i>	<i>brunneinucha</i>	EU364926	346809	FMNH	Totontepec, C. de Zempoaltepetl	Oaxaca	MX
61 ON	<i>Buarremon</i>	<i>brunneinucha</i>	EU364927	346808	FMNH	Totontepec, C. de Zempoaltepetl	Oaxaca	MX
62 ON	<i>Buarremon</i>	<i>brunneinucha</i>	EU364928	344764	FMNH	Totontepec, C. de Zempoaltepetl	Oaxaca	MX
63 OS	<i>Buarremon</i>	<i>brunneinucha</i>	EU364920	OMVP288	UNAM	Cerro Piedra Larga	Oaxaca	MX
64 OS	<i>Buarremon</i>	<i>brunneinucha</i>	EU364921	OMVP425	UNAM	Cerro Piedra Larga	Oaxaca	MX
65 OS	<i>Buarremon</i>	<i>brunneinucha</i>	EU364937	OMVP211	UNAM	Reyes Llano Grande	Oaxaca	MX
66 OS	<i>Buarremon</i>	<i>brunneinucha</i>	EU364938	OMVP212	UNAM	Reyes Llano Grande	Oaxaca	MX
67 OS	<i>Buarremon</i>	<i>brunneinucha</i>	EU364939	OMVP217	UNAM	Reyes Llano Grande	Oaxaca	MX
68 TOR	<i>Buarremon</i>	<i>torquatus</i>	EU364969	116216	ZMUC	Apuela road	Imbabura	ECU
69 TOR	<i>Buarremon</i>	<i>torquatus</i>	EU364970	116213	ZMUC	Loma Taminanga	Imbabura	ECU
70	<i>Atlapetes</i>	<i>pileatus</i>	EU364971	OMVP337	UNAM	El Aguacata, Cerro Piedra Larga	Oaxaca	MX
71	<i>Atlapetes</i>	<i>pileatus</i>	EU364972	OMVP423	UNAM	El Aguacata, Cerro Piedra Larga	Oaxaca	MX
72	<i>Atlapetes</i>	<i>s. taczanowskii</i>	EU364973		ZMUC		Huanuco- Carpish	PE
73	<i>Atlapetes</i>	<i>s. schistaceus</i>	EU364974	133743	ZMUC	Río Azul	Napo	ECU
74	<i>Atlapetes</i>	<i>rufinucha comptus</i>	EU364975	116194	ZMUC	Celica 1	Loja	ECU
75	<i>Calamospiza</i>	<i>melanocorys</i>	AF447316			Genbank		
76	<i>Junco</i>	<i>hyemalis</i>	AF447338			Genbank		
77	<i>Junco</i>	<i>phaeonotus</i>	AF468825			Genbank		

Note: Partial sequences of four additional specimens (three from Mexico and one from Panama) are not included in the list.

^a Groups: SA – South America; MC – Middle Central America; SC – Southern Central America; PC – Pacific Coast Guatemala and Chiapas; CH – Chimalapas; SO – Sierra Madre Oriental; TU – Sierra de los Tuxtlas; GS –Guerrero(Sierra Madre del Sur); ON – North of Oaxaca (Sierra Madre Oriental); OS – Oaxaca Sur (Sierra Madre del Sur); VIR – Buarremon virenticeps (Sierra Madre Occidental and Transvolcanic belt); TOR – Buarremon torquatus.

^b Museums: UNLV - University of Nevada, Las Vegas; UNAM – Universidad Nacional Autónoma de México; FMNH – Field Museum of Natural History; KU – Kansas University; LSU – Louisiana State University; ZMUC – Zoological Museum, University of Copenhagen.

^c Countries: COL – Colombia; CR – Costa Rica; ECU – Ecuador; GUA – Guatemala; MX – Mexico; NIC – Nicaragua; PAN – Panama; PE – Peru; SV – El Salvador.

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