

Comparative phylogeography of short-tailed bats (*Carollia*: Phyllostomidae)

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Abstract

This is the first study of comparative phylogeography involving closely related species of Neotropical bats of the family Phyllostomidae. We compared patterns of geographical variation within the five species of fruit-eating bats currently recognized in the genus *Carollia* using the complete mitochondrial cytochrome-*b* gene. Our results suggest that the combined effect of the uplift of the Andes and the Panamanian land bridge has been as important for bats as for terrestrial mammals in shaping present-day biodiversity in the New World tropics. Species in this genus can be arranged in two highly supported clades, with a deep subdivision within each that corresponds well to differences across the Andes. We found three congruent phylogeographical patterns across species in this genus. First, the closer relationship between samples from western Ecuador and those from Central America, compared with populations east of the Andes in *C. brevicauda*, *C. castanea* and *C. perspicillata*. Second, the likelihood of a similar timing in South America for the arrival and diversification of *C. brevicauda* and *C. perspicillata* from their Central America ancestors. Third, the expansion of *C. perspicillata* and *C. sowelli* into northwestern Central America in the relatively recent past. Using a molecular clock, with rates ranging from 2.3 to 5% per 10⁶ years, diversification within *Carollia* would have occurred over the last 1–4.5 Myr. These estimates agree well with the last rise of the Northern Andes and the Panama isthmus.

Keywords: *Carollia*, comparative phylogeography, cytochrome-*b*, dispersal

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Introduction

Faunistic exchanges between North and South America have played a key role in determining the current mammalian composition of the tropical fauna of the New World (Wallace 1876; Simpson 1980; Reig 1984). Comparative phylogeography has the potential to incorporate information about common historical and geographical components among and within species (Avise *et al.* 1987; Bermingham & Moritz 1998; Avise 2000; Arbogast & Kenagy 2001). Thus, we are able to gain a more detailed understanding of patterns of variation in codistributed groups. Phylogeographical studies of Neotropical mammals have concentrated on nonvolant, small animals such as

marsupials (Patton *et al.* 1996b; Mustrangi & Patton 1997; Da Silva & Patton 1998; Patton & Da Silva 1998; Costa 2002), echimyid (Da Silva & Patton 1993, 1998; Patton *et al.* 1994; Lara *et al.* 1996) and sigmodontine rodents (Smith & Patton 1991; Patton & Smith 1992; Patton *et al.* 1996a; Da Silva & Patton 1998; Patton & Da Silva 1998; Costa 2002). Even though bats are an important element of Neotropical mammalian fauna, few studies have focused on phylogeographical variation within this group. Zoogeographical descriptions of Neotropical bat distributions (Koopman 1976, 1978, 1982) proposed closer affinities between bat fauna from the western slope of the Andes of northern Peru and Central America than between other bats from South America east of the Andes. Birds, the other extant group of flying vertebrates, appear to show a similar pattern (Cracraft & Prum 1988; Bates *et al.* 1998, 1999; Marks *et al.* 2002).

Patterson *et al.* (1992) studied a species of Phyllostomid bat endemic to the western slope of the Andes in northern

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Peru (*Artibeus fraterculus*), and proposed two alternative scenarios for the biogeographical origin of the highly endemic fauna of this region. In both cases, the Andes played a central role as a barrier to gene flow. They concluded that either the fauna west of the Andes was the product of a vicariant event associated with Andean orogeny, or alternatively, this species was the product of migration along the Pacific from Central America. In a first attempt to understand the general patterns of phylogeographical variation in phyllostomid bats in the New World tropics, Ditchfield & Burns (1998) analysed levels of genetic variation within and between populations of birds and bats. Later, Ditchfield (2000) focused on the patterns of phylogeographical variation in four species of Neotropical bats (*Artibeus lituratus*, *Carollia perspicillata*, *Glossophaga soricina* and *Sturnira lilium*) and compared them with previous work done on rodents and marsupials (Smith & Patton 1991; Patton & Smith 1992; Da Silva & Patton 1993, 1998; Patton *et al.* 1994, 1996a,b; Lara *et al.* 1996; Mustrangi & Patton 1997). He concentrated on the Atlantic versant of South America, north of 30°S, with only limited samples coming from either the Pacific versant of the Andes or Central America. The two studies found that both volant groups presented a similar pattern, with lower levels of intraspecific variation than nonvolant groups (marsupials and rodents), and showed that over the Atlantic versant of the Andes nonvolant mammals exhibit a higher degree of

geographically defined genetic divergence than do bats. Ditchfield (2000) presented additional data for 13 species, which were found to follow the same trend reported for the four species that were sampled more intensively. However, elucidation of the role of the Andes as a barrier to gene flow and the issue of the origin of the bat fauna of the western slope of the Andes remained open.

Short-tailed bats of the genus *Carollia* are an appropriate choice to compare the patterns of variation of codistributed, closely related species because they are, for the most part, widely distributed (Fleming 1988) in the New World tropics (Fig. 1). Interspecific variation within the genus at the morphological and genetic level has been relatively well studied (see Pine 1972; McLellan 1984; Owen *et al.* 1984; Lim & Engstrom 1998; Wright *et al.* 1999). Also, there are detailed altitudinal records from the Peruvian Andes (Patterson *et al.* 1996; Solari *et al.* 2001) and samples of the three South American species found on both sides of the Andes are available. Based on the mitochondrial cytochrome-*b*, Wright *et al.* (1999) found strong support for the monophyly of the genus and for resolving phylogenetic relationships among species (Fig. 2). Three of the species in the genus can be collected on both sides of the South American Andes, allowing us to test models of diversification across the Andes. Given the ability to fly, we would expect dispersal to play a stronger role than vicariance in shaping bat phylogeographical patterns of variation. An event of the magnitude

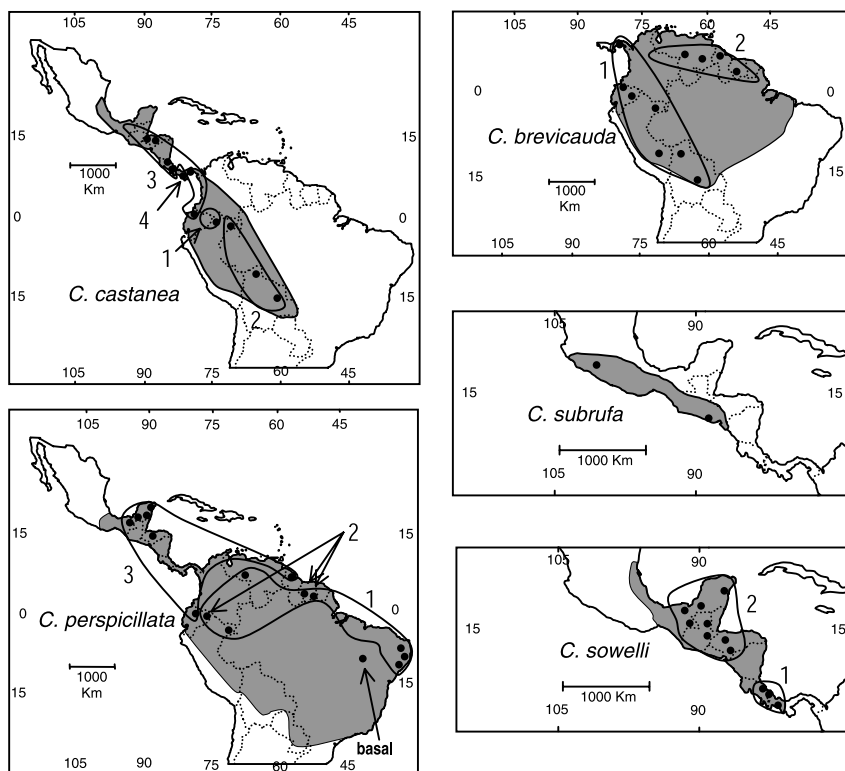


Fig. 1 Geographic distribution of short-tailed bats of the genus *Carollia*, modified from Pine (1972), with phylogroups within each species identified by closed lines. Numbers correspond to the phylogroups defined in the text. In the case of *C. perspicillata*, sampling localities for the basal branch and phylogroup 2 are identified by arrows.

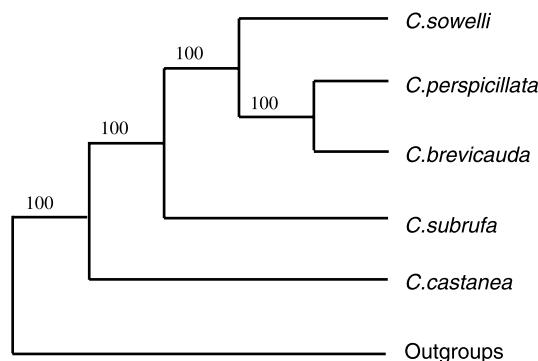


Fig. 2 Phylogenetic relationships among species in the genus *Carollia*, with parsimony bootstrap support values (adapted from Wright *et al.* 1999).

of the elevation of the Andes provides an opportunity to test this view. Had the rise of Andes produced a vicariant episode, we would expect to find similar values of genetic distances in intraspecific comparisons between populations on the two sides of these mountains. As geological reconstructions indicate a date of 2–5 Ma for the latest elevation episode in the Andes of northern South America (Gregory-Wodzicki 2000), we would also expect these divergences to be relatively deep within each of the species. However, shallow nodes would favour recent dispersal as a more plausible explanation, whereas discordances in divergence values among species would suggest the lack of a common history resulting from the elevation of these mountains. Further, phylogeographical variation within each species can potentially reveal the patterns of dispersal in each case.

The purposes of this study were: (i) to explore the patterns of phylogeographical variation in a suite of codistributed species of short-tailed bats of the genus *Carollia*; (ii) attempt a biogeographical reconstruction of speciation in the group; (iii) investigate the processes underlying intra-specific diversification in the genus based on concordance among in phylogeographical structure in codistributed species; and (iv) assess relationships between samples on the western side of the Andes to samples in Middle America and the Amazon basin to shed light on the origin of this fauna.

Materials and methods

Molecular techniques

Genomic DNA was extracted from liver, kidney or muscle tissue preserved by freezing, lysis buffer, or ethanol using either a phenol/PCI protocol (Longmire *et al.* 1997) or an SDS/proteinase K/NaCl extraction and alcohol precipitation protocol (Miller *et al.* 1988; Maniatis *et al.* 1992). The com-

plete mitochondrial cytochrome-*b* gene was amplified and sequenced using the procedures described by Hoffmann & Baker (2001) with the addition of the sequencing primers gini1L (5'-AAAGCCACCCTCACCCGATTC-3'), Phyllo3L (5'-CGAGCATCTATATTCTTTATCTGCC-3') and Uro3L (5'-AGACAAAGCTACCCTCACTCC-3'). DNA sequences were generated using an ABI Prism 310 Genetic Analyser (ABI). Sequences were verified and aligned using SEQUENCHER (v. 3.1.1, Gene Code Corp.).

Data analyses

A total of 67 specimens of *Carollia* were included in this study (GenBank Accession nos AF187017–AF187026 and AF511951–AF512006), in addition to samples of *Glyphonycteris silvestris* used as the outgroup (GenBank Accession no. AY380746). A list of specimens examined and their sampling localities are given in the Appendix.

Uncorrected pairwise distance comparisons are reported for comparison with other studies, whereas net distances were used in cases where a temporal component was estimated. MODELTEST (Posada & Crandall 1998) was used to select the best fitting model of nucleotide substitution. Based on the likelihood ratio test we selected a GTR model (Rodriguez *et al.* 1990) with among sites rate variation ($\alpha = 1.03$) and a proportion of invariant sites (pinvar = 0.55). Neighbour-joining (NJ; Saitou & Nei 1987), maximum parsimony (MP) and maximum likelihood (ML) searches were implemented in PAUP* v. 4.0b10 (Swofford 1999). NJ and ML searches were carried out under the settings selected in MODELTEST. Parsimony and likelihood heuristic searches were performed using 25 random additions of taxa and the tree bisection–reconnection (TBR) branch-swapping algorithm. In maximum parsimony, all nucleotide changes and codon positions were weighted equally. In addition, we performed a full search using MRBAYES v. 2.01 (Huelsenbeck & Ronquist 2001), setting *Glyphonycteris* as outgroup and running four chains for 2×10^6 generations. After reaching stationarity (5×10^5 generations) trees were saved every 1000 generations and a majority rule consensus of 1500 trees was constructed to estimate posterior probabilities. Bootstrap support (bs; Felsenstein 1985) for the nodes was evaluated using 1000 pseudoreplicates with full heuristic mode in parsimony.

Patterns of phylogeographical variation within *Carollia brevicauda*, *C. castanea*, *C. perspicillata* and *C. sowersi* were explored using a combination of phylogenetic and population genetics tools. Within each species, samples sharing a recent common history and geographical location were pooled together into phylogroups. DNASP v. 3.53 (Rozas & Rozas 1999) was used to obtain estimates of haplotype and nucleotide diversity within each of the groups with more than four samples. Genetic variation was partitioned into within and among phylogroups using an analysis

of molecular variance (AMOVA, Excoffier *et al.* 1992) as implemented by ARLEQUIN v. 2001 (Schneider *et al.* 2001), based on estimates of Φ_{ST} , an analogue to F_{ST} (as calculated by Hudson *et al.* 1992). Two estimates of nucleotide diversity were estimated: the first based on the number of pairwise differences (θ_π), and the second based on the number of segregating sites (θ_s). In order to interpret the estimated values for these two parameters, we computed Tajima's *D*-statistic (Tajima 1989a), which under neutral conditions is expected to have negative values if the population is recovering from a bottleneck (Tajima 1989b). Mismatch distributions, which are histograms of absolute pairwise differences, were explored within each phylogroup. Simulation studies have shown that mismatch distribution are expected to be unimodal in populations expanding from a single source or recovering from a bottleneck (Slatkin & Hudson 1991).

Results

Description of data

A total of 1140 base pairs comprising the entire mitochondrial cytochrome-*b* gene were obtained for each specimen examined. Within *Carollia* 820 positions were invariant and 320 were variable. A summary of the patterns of variation in the genus and within each of the species is presented in Table 1. Haplotype diversity ranged from 0.67 (*C. subrufa*) to 1.0 (*C. brevicauda* and *C. castanea*). Haplotype and nucleotide diversity were lowest in *C. subrufa* (potentially due to the small sample size) and highest in *C. castanea*.

Phylogenetic analyses

NJ, MP, ML and Bayesian analyses (BA) supported the same interspecific relationships presented by Wright *et al.* (1999). In all trees (Figs 2 and 3), *C. castanea* is sister to a clade that included the other four species in the genus. Within this clade, *C. subrufa* was sister to the remainder of the genus. In MP, heuristic searches found 3619 equally parsimonious trees 818 steps long. A strict consensus matches the species phylogeny shown in Fig. 3, with unresolved nodes restricted to the tips. Cytochrome-*b* haplotypes formed monophyletic groups in agreement with species designations with bootstrap support in MP that ranged from 69 to 100% (Fig. 3). The only exception was *C. sowelli*, because haplotypes from this species did not form a monophyletic group under ML or BA, with samples of *C. sowelli* from Costa Rica and Panama as sister to the *C. brevicauda* and *C. perspicillata* clade, and sister to a clade formed by samples of *C. sowelli* samples from Guatemala, Honduras and Mexico. A tree in which we constrained *C. sowelli* to be monophyletic was not significantly different from an unconstrained search in Kishino & Hasegawa (1989) and Shimodaira & Hasegawa (1999) topology tests. Monophyly of *C. brevicauda*, *C. castanea*, *C. perspicillata* and *C. subrufa* was supported by high posterior probabilities in BA (pp \geq 95%).

Intraspecific phylogeography

Levels of variation within *C. brevicauda*, *C. perspicillata*, *C. sowelli* and *C. subrufa* were similar, with average uncorrected intraspecific distances ranging from 1.3 to 2.0% (Table 2),

Table 1 Summary of the variation found in the mitochondrial cytochrome-*b* gene within species in the genus *Carollia*

Species	Number of specimens	Number of haplotypes	Number of Polymorphic sites			AA
			1st position	2nd position	3rd position	
<i>C. brevicauda</i>	13	13	10	2	71	11
<i>C. castanea</i>	17	17	19	3	156	15
<i>C. perspicillata</i>	20	18	9	2	65	7
<i>C. sowelli</i>	14	11	18	5	43	13
<i>C. subrufa</i>	3	2	3	0	16	3
Total	67	61	51	10	259	39

	<i>C. brevicauda</i>	<i>C. perspicillata</i>	<i>C. sowelli</i>	<i>C. subrufa</i>	<i>C. castanea</i>
<i>C. brevicauda</i>	1.98 \pm 0.11				
<i>C. perspicillata</i>	3.67 \pm 0.02	1.46 \pm 0.05			
<i>C. sowelli</i>	4.95 \pm 0.03	4.79 \pm 0.02	1.58 \pm 0.17		
<i>C. subrufa</i>	7.35 \pm 0.05	7.71 \pm 0.04	6.73 \pm 0.05	1.33 \pm 0.14	
<i>C. castanea</i>	12.05 \pm 0.03	11.82 \pm 0.03	11.32 \pm 0.02	11.54 \pm 0.06	5.28 \pm 0.24

Table 2 Inter- and intraspecific pairwise distance comparisons among and within *Carollia brevicauda*, *C. castanea*, *C. perspicillata*, *C. sowelli* and *C. subrufa* using the uncorrected percentage of sequence divergence. Average distance \pm SE expressed as percentage

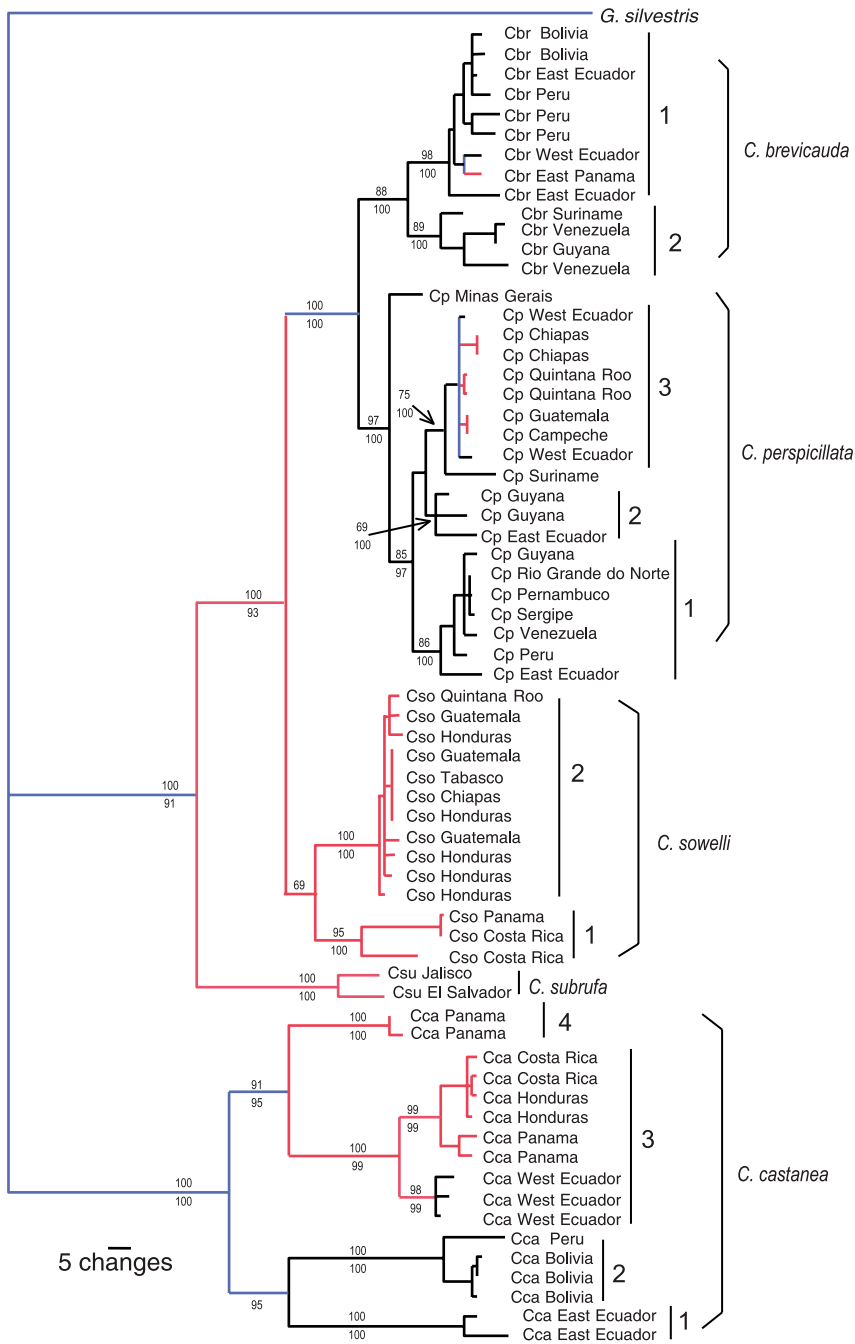


Fig. 3 One of the 3619 most parsimonious trees, with bootstrap support values provided above the corresponding nodes, and posterior probabilities from Bayesian analysis below. Differences among all these trees are restricted to the tips. Vertical bars and their number identify the different phylogroups and colours correspond to present and reconstructed geographical areas. Red corresponds to Central America, black to South America, and blue to the uncertain portions of the tree.

whereas *C. castanea* had higher values of intraspecific variation, with average divergence from all pairwise comparisons of 5.3%, suggesting that more than one species would be lumped under this nominal species. *C. subrufa* was represented by three specimens from the extremes of its distribution, with average pairwise distances of 1.3%.

Carollia brevicauda. Intraspecific comparisons within *Carollia brevicauda* ranged from 0.2 to 3.2%. Samples from this species were grouped into two allopatric sister clades (Fig. 3), with high bootstrap support values (bs \geq 89%, pp = 100%) for both. Average pairwise distance between

these two phylogroups was 3.0%. The first phylogroup (labelled 1 in Figs 1 and 3) includes samples from eastern Panama, Ecuador (east and west slope of the Andes), Bolivia and Peru ($N = 11$, average pairwise distance within the group of 1.1%), and the second phylogroup (2 in Figs 1 and 3) includes samples from Guyana, Suriname and Venezuela ($N = 4$, average pairwise distance within the group of 1.1%). Variation within phylogroups accounted for 41% and variation among phylogroups accounted for 59% of the molecular variance. Estimates of Tajima's D were negative in both cases (but not significantly different from 0).

Intraspecific comparisons in *C. perspicillata*, the most widespread species in the genus, ranged from 0 to 2.4%, and averaged 1.5%. We found two haplotypes shared by two individuals in this species, both found in the northern area of Central America. One of was shared by specimens from two localities in Chiapas (Mexico), and the other was shared by a specimen from Campeche, in Mexico, and a specimen from Guatemala. *C. perspicillata* presents a complex phylogeographical pattern. The most basal sample within *C. perspicillata*, was from Minas Gerais in the Atlantic coast of Brazil, followed by three equidistant groups. The first group (1 in Figs 1 and 3) included samples from Brazil, eastern Ecuador, Guyana, Peru and Venezuela ($N = 7$; average pairwise distance of 0.7%); the second (2 in Figs 1 and 3) included samples from eastern Ecuador and Guyana ($N = 3$; average pairwise distance of 1.1%); and the last (3 in Figs 1 and 3) included samples from Suriname, Middle America and western Ecuador ($N = 9$; average pairwise distance of 0.6%). Genetic differences among the four lineages mentioned above accounted for 60% of the variation, and within lineage variation accounted for 40%. Support for each of the three phylogroups was high in BA (pp = 100%), and moderate to high in bootstrap (bs = 86, 69 and 75, respectively). Estimates of D were negative in the case of the first ($N = 7$) and third ($N = 9$) groups (Table 2).

Intraspecific comparisons within *C. sowelli* ranged from 0 to 4.1%, and averaged 1.6%. Samples of this species can be grouped into two highly supported, allopatric phylogroups (bs $\geq 95\%$, pp $\geq 99\%$), with an average pairwise distance between them of 3.6%. A southeastern phylogroup (1 in Figs 1 and 3) comprising samples from Costa Rica and western Panama ($N = 3$, average distance within the group of 1.8%), and a northwestern phylogroup (2 in Figs 1 and 3) that included samples from Honduras, Guatemala and Mexico ($N = 11$, average distance within the group of 0.2%). We found one haplotype shared by four specimens from four different localities (Guatemala, Honduras, and the Mexican states of Tabasco and Chiapas). The within-group component of the AMOVA accounted for 16%, and the among-group component for 84% of the observed molecular variation. Estimates of θ in the northwestern phylogroup yielded negative results for Tajima's D statistic ($P < 0.05$; Table 2).

Pairwise comparisons within *C. castanea* ranged from 0.08 to 8.3%, with an average of 5.3%. Samples from this species can be arranged into four highly supported (bs $\geq 91\%$, pp $\geq 95\%$), genetically quasi-equidistant, geographically distinct groups, with average genetic distance among them of 7.1%. The first group (1 in Figs 1 and 3) includes two representatives from Ecuador east of the Andes (1.1% divergent from each other), the second (2 in Figs 1 and 3) included samples from Bolivia and Peru ($N = 4$, average pairwise distance within the group of 1%), the third (3 in Figs 1 and 3) included samples from western Panama,

Ecuador west of the Andes, Costa Rica and Honduras ($N = 9$, average pairwise distance within the group of 1.5%), and the fourth included two samples from eastern Panama (0.2% distance between them). Estimates of D for the phylogroups 1 (Bolivia and Peru) and 3 (Central America and W Ecuador) were not significantly different from 0 (Table 2). Results from the AMOVA show that the among-phylogroups component accounts for 82.4% of the molecular variance, whereas the within-phylogroups component accounts for the other 17.6%. Genetic distances among these four phylogroups are similar to interspecific comparisons within the *brevicauda*, *perspicillata*, *sowelli*, and *suburufa* clade.

Three of the species: *C. breviscauda*, *C. castanea* and *C. perspicillata* can be found in tropical South America on both sides of the Andes. Genetic distance comparisons between populations on opposite sides of the Andes, in Ecuador, ranged from 1.2% in *C. breviscauda* to 7.8% in *C. castanea* (Table 3), whereas comparisons of populations in Central America with western Ecuador ranged from 0.4% in *C. perspicillata* to 2.7% in *C. castanea*. In all three cases populations from western Ecuador are more closely related to samples in Central America than to populations in eastern Ecuador.

Shared haplotypes among different localities were found only in samples of *C. perspicillata* and *C. sowelli* from the northern portion of Central America (Guatemala, Honduras, and the Mexican states of Campeche, Chiapas and Quintana Roo). Observed mismatch distributions were unimodal for

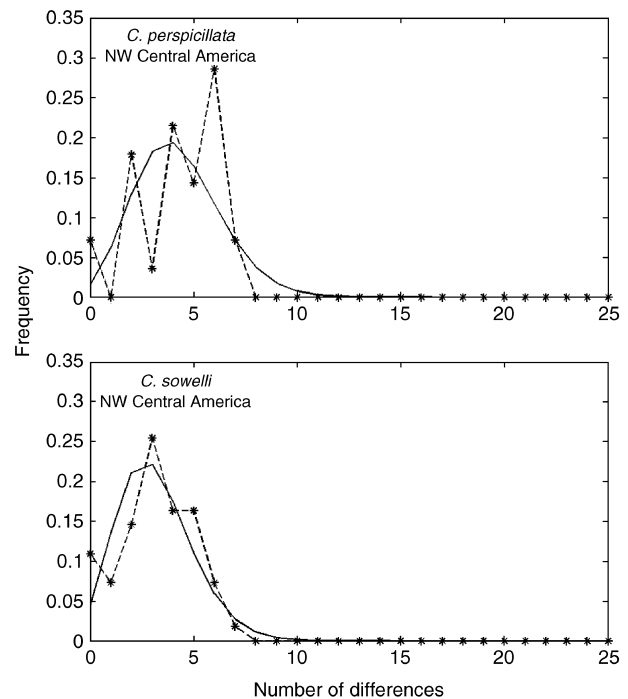


Fig. 4 Expected (solid) and observed (dashed) mismatch distributions among haplotypes of the northwestern phylogroup of *Carollia perspicillata* (upper) and *C. sowelli* (lower) under a model of population growth.

	<i>N</i>	Haplotypes	θ_π	θ_s	Tajima's <i>D</i>
<i>Carollia brevicauda</i>					
Phylogroup 1	4	4	0.0137	0.0139	-0.09896 (NS)
Phylogroup 2	9	9	0.0110	0.0149	-1.31336 (NS)
<i>Carollia castanea</i>					
Phylogroup 1	2	2	0.0114	0.0114	NA
Phylogroup 2	4	4	0.0095	0.0100	-0.5566 (NS)
Phylogroup 3	9	9	0.0153	0.0142	0.3761 (NS)
Phylogroup 4	2	2	0.0263	0.0263	NA
<i>Carollia perspicillata</i>					
Minas Gerais, Brazil	1	1	NA	NA	NA
Phylogroup 1	7	7	0.0071	0.0093	-1.34646 (NS)
Phylogroup 2	3	3	0.0111	0.0111	NA
Phylogroup 3	9	7	0.0061	0.0084	-1.36622 (NS)
<i>Carollia sowelli</i>					
SE Middle America	3	3	0.0175	0.0175	NA
NW Middle America	11	8	0.0028	0.0048	-1.8759 (<i>P</i> < 0.05)

Table 3 Estimates of genetic diversity within the different phylogroups in *Carollia brevicauda*, *C. castanea*, *C. perspicillata* and *C. sowelli*. θ_π and θ_s are estimates of nucleotide diversity per site

populations from this region in these two species (Fig. 4). McDonald and Kreitman neutrality tests (McDonald & Kreitman 1991) did not detect deviations from neutral expectations when comparing changes in the cytochrome-*b* in these groups against their conspecific counterparts.

Discussion

Two geological episodes have been hypothesized as central in determining the present-day faunal composition of the New World tropics: the rise of the Andes and the establishment of the Panama isthmus. The uplift of the Andes generated environmental heterogeneity by fragmenting habitat and creating new habitats, whereas the Panamanian land bridge opened up a pathway, increasing the possibilities for dispersal. The role of these phenomena has been well studied for terrestrial mammals (Wallace 1876; Simpson 1980; Reig 1984; Marshall 1988), although the case of bats has remained poorly understood because of the lack of fossil material. Further, forest expansions throughout the Pleistocene are also likely to have played a strong role in the diversification of phyllostomid bats. Molecular methods and comparative phylogeography provide a means to gain insight into the influence of these geological events on the geographical patterns of variation among and within species of bats.

Previous phylogeographical studies (i.e. Costa 2002; Da Silva & Patton 1993, 1998; Patton *et al.* 1994, 1996a,b; Lara *et al.* 1996; Mustrangi & Patton 1997; Patton & Da Silva 1998; Ditchfield 2000) of Neotropical mammals have documented differing patterns or degrees of geographical differentiation between bats and nonvolant small mammals (rodents and marsupials). These studies agree on assigning a central role to the uplifting of the Andes in shaping

patterns of genetic variation, as this resulted in greater environmental heterogeneity and created effective barriers to dispersal. This phenomenon is central to the discussion of the areas of original diversification of sigmodontine rodents presented by Reig (1984, 1986), who tied taxonomic diversity in this group of rodents with geological changes in the Andean region. In bat biogeography, a role for the uplifting of the Andes as a source of genetic isolation and the possibility of a vicariant event has been proposed in the particular cases of *Artibeus* (Patterson *et al.* 1992; Van Den Bussche *et al.* 1998) and *Glossophaga soricina* (Hoffmann & Baker 2001).

In the case of *Carollia*, the deepest divergence within the genus gave rise to what is currently recognized as *Carollia castanea* in one clade, and to the remaining four species in the other (Fig. 2). There is inconclusive evidence associated with the geographical location of the split between *C. castanea* and the *C. brevicauda*, *C. perspicillata*, *C. sowelli* and *C. subrufa* clade. More significantly, there is no indication that the rise of the Andes was related to this split, given that both clades are quite widely distributed on both sides of the Andes. Within these two clades, in turn, there is a major break that can be associated to exchanges between Central and South America, and that geographically correspond loosely to the Andean mountains. The deepest branching event within *C. castanea* separates samples across the Andes, with phylogroups 1 and 2 restricted to the Amazonian region of South America, and phylogroups 3 and 4 to Central America and the Pacific slope of the coast of South America. In the clade that includes *C. brevicauda*, *C. perspicillata*, *C. sowelli* and *C. subrufa*, this divergence corresponds to the separation between the *C. brevicauda* and *C. perspicillata* clade and *C. sowelli*. The genetic signatures of the hypothesized exchanges are

relatively deep nodes, which are probably posterior to the uplift of the Panama isthmus.

C. brevicauda and *C. perspicillata* have an almost entirely South American distribution; however, the geographical affinity of the ancestor to these two species is probably Central American in origin. Intraspecific variation within *C. brevicauda* and *C. perspicillata* suggest the timing of their arrival and diversification of South America was similar. *C. brevicauda* is found throughout the Amazonian basin on the Atlantic slope of the Andes and the Choco forest over the Pacific slope of the Andes. The deepest split in this species identifies two highly supported phylogroups, which correspond to the Guianas shield and the western portion of the Amazon basin, respectively. This subdivision could be related to changes in vegetation in the Amazonian basin associated with climatic oscillations during the Pleistocene. The available data would suggest the Amazonian basin as the area of original diversification (AOD *sensu* Reig 1986) for this species. Variation within *C. perspicillata* also suggests a South American area of original diversification, probably along the Atlantic coastal forest of Brazil, and a relatively recent entrance and expansion into Central America. This scenario is supported by the paraphyly of South America samples with respect to samples from Central America, and the negative values of estimates of *D* and lack of resolution within the Central American phylogroup. A possibility suggested by Ditchfield (2000) based on different geographical samples from this species.

C. sowelli and *C. suburufa* are restricted to Central America, which is probably the area of origin of this clade, and the posterior diversification of *C. brevicauda* and *C. perspicillata* appears to be associated with a subsequent invasion of South America. *C. suburufa* is restricted to the Pacific coast of southern Mexico, Guatemala, Honduras and El Salvador, whereas *C. sowelli* is distributed over most Central America. The deeper nodes within the limited samples of *C. sowelli* from the Costa Rican and Panamanian region suggest an older geographical presence in this area, and a later expansion into the northern portion of its range. Thus, speciation between these two taxa could be related to isolation associated with forest expansion and contraction. The taxonomy of the recently described *C. sowelli* (Baker *et al.* 2002) appears to be worthy of further attention in light of divergence between the phylogroups and the lack of support for its monophyly in ML and BA.

C. castanea has the highest level of intraspecific divergence in the genus (Table 2). Genetic divergences among the four phylogroups defined were equal to or greater than any interspecific comparison among the four other species in the genus. It also shows the highest divergence across the Andes in Ecuador, and the deepest split between phylogroups found east of the Andes (7.6%). In addition, in the phylogroup distributed over Central America and western Ecuador there is another deep subdivision that exceeds

most interspecific comparisons within *C. brevicauda*, *C. perspicillata* and *C. sowelli*. The magnitude of the genetic differences in the mitochondrial cytochrome-*b* suggests that *C. castanea* represents multiple biological species (Johns & Avise 1998; Avise & Johns 1999; Avise & Walker 1999; Bradley & Baker 2001), in agreement with previous reports of karyologic variation (Baker 1979; Baker & Bleier 1971; Patton & Gardner 1971).

There is evidence for an additional dispersal event within the *brevicauda*, *perspicillata* *sowelli* and *suburufa* clade, involving the expansion of *C. sowelli* and *C. perspicillata* into northern Central America. This expansion left very similar traces in each species, suggesting a common temporal component. Four features of the patterns of intraspecific variation in samples from this area suggest the timing of the expansion into Guatemala, Honduras and Mexico is recent: (i) it is the only area in which we found shared haplotypes; (ii) there is weak phylogenetic signal to resolve their relationships beyond the bases of the respective phylogroups; (iii) estimates of *D* are negative (Tajima 1989b); and (iv) the agreement between observed mismatch distributions against the ones predicted under the expectations of exponential population growth (Fig. 5). In *C. sowelli* expansion probably occurred from populations in Costa Rica and Panama, whereas in *C. perspicillata* it probably originated in northern South America.

Perhaps the clearest example of the combined role of the Panamanian isthmus and the Andes comes from the phylogeographical relationships of samples from the Pacific slope of South America. In the three species of *Carollia* found over tropical South America, samples from western Ecuador had stronger affinities for Central American samples rather than samples from the Atlantic versant of the Andes in eastern Ecuador (Fig. 3). Moreover, we found an inverse relationship between genetic distances across the Andes and the highest altitude in which *C. brevicauda*, *C. castanea* and *C. perspicillata* have been recorded (Table 4). As the last uplift episode of the northern portion of the Andes is hypothesized to have occurred during the Pliocene between 5 and 2 Mya (Gregory-Wodzicki 2000),

Table 4 Average uncorrected distances of intraspecific comparisons between populations of *Carollia brevicauda*, *C. castanea* and *C. perspicillata* in Ecuador west of the Andes, and eastern Ecuador and Panama in the first two columns. Highest altitudinal record in the Peruvian Andes from Patterson *et al.* (1996) and Solari *et al.* (2001)

Species	W Ecuador vs. Central America	East vs. West Ecuador	Altitude
<i>C. brevicauda</i>	0.60%	1.1%	1700 m
<i>C. castanea</i>	2.66%	7.8%	900 m
<i>C. perspicillata</i>	0.01%	1.8%	1300 m

we would expect relatively deep nodes as its signature. The depth of the nodes leading to representative of *Carollia* present in western Ecuador is therefore more compatible with a dispersal scenario than with a vicariant one, with a probable recent entrance into the Pacific versant of the Andes from tropical Central America.

Conclusion

Our results are similar to the general pattern described by Ditchfield (2000). *Carollia brevicauda*, *C. perspicillata* and *C. sowelli* present a high percentage of unique haplotypes (ranging from 66 to 100%) and low levels of intraspecific variation. *C. castanea* deserves further study, as the magnitude of divergence among geographical subdivisions are similar to interspecific comparisons among the other four species in the genus, and probably indicate that *C. castanea* represents several biological species. Intraspecific variation within *C. brevicauda* and *C. perspicillata* suggest a diversification in South America at a similar time but along different areas. The observation that the only area where we have found shared haplotypes is among samples of *C. perspicillata* and *C. sowelli* from the northern portion of Central America (Guatemala, Honduras and southern Mexico), in addition to the star-like phylogenies, negative estimates of *D*, and mismatch distributions support an expansion into this area in a geologically recent time.

Our reconstruction of diversification within this genus demonstrates that migration across the Panamanian isthmus has been a strong determinant in bat biogeography, as already shown for terrestrial mammals (Wallace 1876; Simpson 1980; Reig 1984; Marshall 1988). The Andes have also been a strong biogeographical agent in these bats. In agreement with Koopman's views (Koopman 1976, 1978, 1982), variation across the Andes is also congruent in *C. brevicauda*, *C. castanea* and *C. perspicillata*, with a close relationship between western South America and Central America, as in birds and fish (Bates *et al.* 1998, 1999; Cracraft & Prum 1988; Bermingham & Martin 1998; Marks *et al.* 2002). Furthermore, all evidence favours a dispersal scenario into western South America rather than a vicariant one.

In summary, the similarities across species found in the pattern of variation relative to the Ecuadorian Andes in *C. brevicauda*, *C. castanea* and *C. perspicillata*, the similar degree of diversification of *C. brevicauda* and *C. perspicillata* in South America, and of *C. perspicillata* and *C. sowelli* in northern Central America indicate a common historical explanation for the similarities. In the three cases there seems to be a common temporal and geographical component in these dispersal events. Aside from these similarities, each species presents a unique pattern of intraspecific geographical breaks in each species and variation in time and magnitude of divergence. These differences document

that multiple factors (such as, but not limited to, geographical variation, habitat change and karyotypic variation) are required to explain the speciation and genetic differentiation within the morphologically similar monophyletic assemblage referred to *Carollia*. This implies that caution should be exercised when extrapolating cause and effect to the patterns and processes shaping variation among closely related species.

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Appendix

Specimens examined and their geographical localities are given below: TK numbers correspond to samples from the frozen tissue collection at the Natural Science Research Laboratory from Texas Tech University, Lubbock, TX; NK numbers correspond to samples in the Museum of Southwestern Biology, Albuquerque, NM; MVZ numbers correspond to samples from the Museum of Vertebrate Zoology, Berkeley, CA; F and MDE numbers correspond to samples from the Royal Ontario Museum, Ontario, Canada.

Carollia brevicauda

BOLIVIA: Santa Cruz, Buen Retiro NK12171; Santa Cruz NK15417; ECUADOR: Esmeraldas, San Lorenzo TK104530; Napo, Parque Nacional Yasuni F37060; GUYANA: Northwest District, Baramita TK86502; PANAMA: Panama, Parque Nacional Altos de Campana FN38117; PERU: Loreto, Aguas Negras TK46009, TK46010; Cuzco, La Convencion, TK70412, SURINAME: Saramacca, Raleigh Falls TK10218, VENEZUELA: Barinas, Barinitas 19316; Bolivar, El Palmar TK19273.

Carollia castanea

BOLIVIA: Beni, Yucumo NK25385; Cochabamba, Villa Tunaria NK30033; Sajta NK30150, COSTA RICA: Limon, Estacion Biologica Cano Palma F44029; Tortuga Lodge FN44016; ECUADOR: Esmeraldas, San Lorenzo TK104506, TK104508, TK104681; Napo, Parque Nacional Yasuni F37061, F37065, HONDURAS: Comayagua, Cueva de Taulabe TK101378; Atlantida, Lancetilla TK101462; PANAMA:

Chiriqui, Ojo de Agua F38156; Darien, Parque Nacional Darien F38195.

Carollia perspicillata

BRAZIL: Minas Gerais, Municipio de Caratinga MVZ185533; Pernambuco, Municipio Tamandare MVZ185518; Rio Grande do Norte, Municipio Baia Formosa MVZ185806; Sergipe, Municipio Santo Amaro Das Brotas MVZ185813; ECUADOR: Esmeraldas, San Lorenzo TK104613, TK104631; Napo, Parque Nacional Yasuni F37084, F37107; GUATEMALA: El Peten, Poptun F31809; GUYANA: Berbice District, Dubulay Ranch TK86671, TK86691; Northwest District, Baramita TK86503; MEXICO: Campeche, Escarcega F33206; Chiapas, Agua Azul NK8644, NK8645; Quintana Roo, Laguna Noh-Bec F30973; Tulum MDE 6004; PERU: Cuzco, La Convencion, TK70435; SURINAME: Nickerie, Kabalebo TK17466; VENEZUELA: Barinas, Barinitas TK19315.

Carollia sowelli

COSTA RICA: Limon, Estacion Biologica Cano Palma F44027; Tortuga Lodge F44017; GUATEMALA: El Peten, Poptun F31769; Poptun F31805, F31824; HONDURAS: Francisco Morazan, Parque Nacional La Tigra TK101005, TK101010, TK101013; Comayagua, Cueva de Taulabe TK101341, TK101377; MEXICO: Chiapas, Agua Azul NK8641; Quintana Roo, Laguna Noh-Bec F30976; Tabasco, Jonuta F30002; PANAMA: Chiriqui, Ojo de Agua F38140.

Carollia subrufa

EL SALVADOR: Auachapan, El Refugio TK15818; MEXICO: Jalisco, Chamela TK19550, TK19551.