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Patterns of diversification in two species of short-tailed bats (*Carollia* Gray, 1838): the effects of historical fragmentation of Brazilian rainforests

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The small-sized frugivorous bat *Carollia perspicillata* is an understory specialist and occurs in a wide range of lowland habitats, tending to be more common in tropical dry or moist forests of South and Central America. Its sister species, *Carollia brevicauda*, occurs almost exclusively in the Amazon rainforest. A recent phylogeographic study proposed a hypothesis of origin and subsequent diversification for *C. perspicillata* along the Atlantic coastal forest of Brazil. Additionally, it also found two allopatric clades for *C. brevicauda* separated by the Amazon Basin. We used cytochrome *b* gene sequences and a more extensive sampling to test hypotheses related to the origin and diversification of *C. perspicillata* plus *C. brevicauda* clade in South America. The results obtained indicate that there are two sympatric evolutionary lineages within each species. In *C. perspicillata*, one lineage is limited to the Southern Atlantic Forest, whereas the other is widely distributed. Coalescent analysis points to a simultaneous origin for *C. perspicillata* and *C. brevicauda*, although no place for the diversification of each species can be firmly suggested. The phylogeographic pattern shown by *C. perspicillata* is also congruent with the Pleistocene refugia hypothesis as a likely vicariant phenomenon shaping the present distribution of its intraspecific lineages.

ADDITIONAL KEYWORDS: *Carollia brevicauda* – *Carollia perspicillata* – cytochrome *b* – most recent common ancestor – mtDNA – Neotropical biogeography – phylogeography – Pleistocene.

INTRODUCTION

In the last four decades, biodiversity researchers worldwide have proposed different models and mechanisms to explain the gigantic and unique species richness of the Neotropical rainforests, including the Amazon and the Brazilian Atlantic Forest biomes. Consequently, various hypotheses have been established: the refuge hypothesis (Haffer, 1969), the riverine barrier hypothesis (Patton & da Silva, 1998), and the Amazon lagoon hypothesis (Marroig & Cerqueira, 1997), amongst many others. However, the alternative hypotheses underlying the rich

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Neotropical biodiversity are still vigorously debated, as well as the relative contribution of different factors and mechanisms.

The field of phylogeography, which comprises comparisons of phylogenetic relationships and geographic ranges among intraspecific evolutionary lineages and species, has provided a better understanding of Neotropical biogeography, as well as the identification of areas of endemism. Phylogeographic studies that focus on Neotropical vertebrate species have been important for testing these current biogeographic models, and provide empirical evidence that corroborates or refuse biogeographical hypotheses.

Lessa, Cook & Patton (2003) predicted that refuges caused by pleistocenic climatic fluctuations would have caused bottlenecks and subsequent demographic expansion in endemic mammals, leaving a detectable pattern in surviving populations. However, it was shown that these predictions could only be applied for high latitude populations, and not for the Amazonian ones. The Atlantic forest is also known once to have been a fragmented biome with patches of drier areas (Lichte & Behling, 1999). In a recent study, Carnaval & Moritz (2008) provided a model for the spatial range of the Brazilian Atlantic forest, under three climatic scenarios, and investigated whether the location of the forest refugia recognized by their model was consistent with the current patterns of endemism and phylogeographic data. A high congruence was found between the models and pollen records. They predicted the existence of a large and stable forest refuge in the state of Bahia, in the northeast of Brazil, and smaller refuges located along the Brazilian coast: one area north of the Paraiba river (called Pernambuco refuge) and possibly many small patches south of the Doce river. The historical instability regarding the coastal areas south of the Doce river, as predicted by Carnaval & Moritz (2008), agrees with recent phylogeographic data described for many taxa (Costa *et al*., 2000; Costa, 2003; Pellegrino *et al*., 2005; Grazziotin *et al*., 2006; Cabanne, Santos & Miyaki, 2007; Martins *et al*., 2007).

Although there are many phylogeographic studies on Neotropical mammals, only recently have bats become more represented in this literature. Bats are small mammals with an ability of powered flight that provides them a large capacity for long-distance dispersal compared to the low vagility shown by nonflying mammals. Consequently, bats may show markedly different phylogeographic patterns for their haplotype lineages compared to rodents and marsupials (Ditchfield, 2000).

A general phylogeographic pattern observed in Neotropical bats was described by Ditchfield (2000), who analyzed 17 species, using a 400-bp segment of the mitochondrial cytochrome *b* gene (cyt *b*). In general, this work revealed very low (or none) levels of phylogeographic structure in some species of bats. However, a number of factors such as feeding habits, roost site fidelity, colony structure, and dispersal patterns can influence the distribution of genealogical lineages and many studies have shown that a phylogeographic structure exists in bats (Larsen *et al*., 2007; Martins *et al*., 2007; Porter *et al*., 2007; Redondo *et al*., 2008; Velazco & Patterson, 2008). Although the majority of studies investigated the molecular systematics of genera, they revealed a cryptic diversity for some taxa such as *Artibeus obscurus*, *Artibeus jamaicensis* (Larsen *et al*., 2007; Redondo *et al*., 2008), *Micronycteris megalotis*, *Micronycteris microtis* (Porter *et al*., 2007) and *Platyrrhinus helleri* (Velazco & Patterson, 2008).

The short-tailed fruit bat *Carollia perspicillata* Linnaeus (1758) is a widely distributed species, ranging from Mexico to northern Argentina, including Paraguay and Brazil (Pine, 1972), being the most abundant and the most widespread member of its genus (Fleming, 1988). This small-sized frugivorous bat is an understory generalist that can also be found in open areas (Fleming, 1988). Although it occurs in a wide range of lowland habitats, it tends to be more common in tropical dry or moist forests than in tropical wet forests. *Carollia perspicillata* is an important seed disperser, especially for pioneer plants, such as *Vismia*, *Solanum*, and *Piper*, feeding preferably from the latter (Fleming, 1988; Charles-Dominique, 1991). Because of its higher abundance in secondary than in pristine forests, *C. perspicillata* is considered an indicator of habitat disturbance when occurring in elevated frequency (Medellin, Equihua & Amin, 2000). Also, because of its wide geographic distribution, abundance and foraging behaviour, *C. perspicillata* is a good candidate for testing the effects of forest fragmentation on the spatial distribution of lineages.

In his classical systematic revision of *Carollia*, Pine (1972) noted that intraspecific variation exists within the species of the genus, although he did not quantify this variation. Pine (1972) treated *C. perspicillata* as polytypic, suggesting the existence of three putative subspecies: *Carollia perspicillata azteca*, *Carollia perspicillata perspicillata*, and *Carollia perspicillata tricolor*. Accordingly, specimens from north and west of the Amazon Basin were assigned to *C. p. azteca* and those from the Amazon Basin and Parana drainage were named *C. p. perspicillata* and *C. p. tricolor*, respectively. In a reanalysis of the specimens, McLellan (1984) did not find a clear distinction among Mexican and Central American populations sampled from South American samples, in correspondence with the North American *C. p. azteca* and the South American *C. p. perspicillata* and *C. p. tricolor*. It was concluded that no subspecies exist on the basis of cranial and mandibular measurements.

The first study presenting the phylogeographic pattern for *C. perspicillata* was performed by Ditchfield (2000), who sampled 54 individuals from Brazil, French Guyana, and Mexico and found two clades (north and south), with a contact zone in the Brazilian northeast. This pattern was attributed to possible forest fragmentation with open areas. Pavan & Ditchfield (2006), using restriction fragment length polymorphism data on a larger sample (65 individuals), also found the contact area described above.The Amazon samples analyzed presented both new haplotypes or shared haplotypes with north-east Atlantic Forest.

Hoffmann & Baker (2003) compared patterns of intraspecific geographical variation within the five species of genus *Carollia* using the complete mitochondrial cyt *b* gene. These authors described the clade that includes *C. perspicillata* and *C. brevicauda* (almost restricted to the Amazon forest) as being the most derived clade in the genus. On the basis of the data obtained, bit without using any time estimation method, they suggested that these two species arrived and diversified in South America at a similar time, as a consequence of an historical event that separated the Atlantic Forest (originating *C. perspicillata*) from the Amazon (*C. brevicauda*). At the intraspecific level, two allopatric clades for *C. brevicauda* were found that were separated by the Amazon Basin: one within the Guyana shield and the other in the Tropical Andes. For *C. perspicillata*, three main clades were described, without any geographic correspondence, and only one basal haplotype in relation to such clades, which corresponded to one sample from Minas Gerais state, Brazil. On the basis on this topology, it was suggested that South America would have been the original area of diversification for the species, probably along the Atlantic coastal forest of Brazil (where the basal haplotype is located).

In accordance with the patterns of the studies described above, the present study uses cyt *b* sequences and a more extensive sampling to test the hypotheses raised by Ditchfield (2000) and Hoffmann & Baker (2003). The study aimed to answer the following questions: (1) Did *C. perspicillata* and *C. brevicauda* originate at a similar time? If so, can we date such an event and correlate it with geological and historical events in South America? (2) Is it possible to infer the original areas of diversification for both species? (3) Does *C. perspicillata* show a phylogeographic pattern with low structure, as suggested by Ditchfield (2000), or does it show a more complex pattern, as suggested by Hoffmann & Baker (2003)?

MATERIAL AND METHODS

Specimens sampled

We analyzed 96 individuals of *C. perspicillata* and *C. brevicauda*. The dataset included the 12 sequences of *C. brevicauda* and the 16 sequences of *C. perspicillata* used by Hoffmann & Baker (2003), available at GenBank, as well as 68 newly-generated sequences in the present study. A total of 80 samples, from 39 localities, including those analyzed by Ditchfield (2000), were used for *C. perspicillata* (Fig. 1B). For *C. brevicauda*, four specimens from two distinct localities were sampled and added to the sequences obtained from GenBank, giving a total of 16 sequences in 13 localities (Fig. 1A). The published sequences of *Carollia castanea*, *Carollia sowelli*, and *Carollia subrufa* deposited at GenBank were also used as outgroups. The individuals and localities sampled in the present study, as well as the institutions where the vouchers are located, are provided in the Appendix (Table A1).

DNA extraction, amplification, and sequencing

DNA was extracted from liver tissue by standard phenol-chloroform-isoamyl-alcohol method (Sambrook & Russel, 2001). The primers and protocols used for the polymerase chain reaction amplification and sequencing of the complete mitochondrial cyt *b* gene were conducted as described previously Redondo *et al*. (2008).

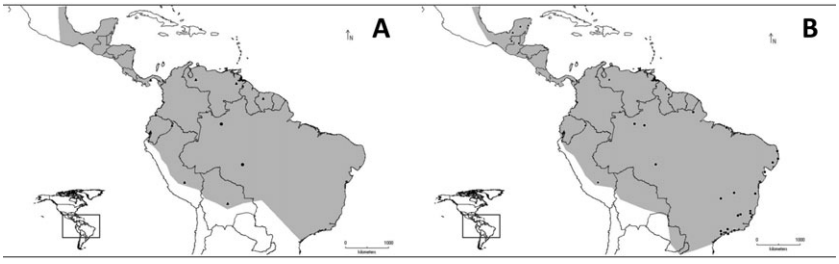


Figure 1. Map showing the geographic ranges of each species (adapted; *sensu* Cloutier & Thomas, 1992; McLellan & Koopman, 2008) with localities sampled for *Carollia brevicauda* (A) (circles) and *Carollia perspicillata* (B) (squares). Triangles in both maps represents samples retrieved from the literature.

Phylogenetic analysis

Three different phylogenetic methods were used: maximum parsimony (MP) and maximum likelihood (ML) were implemented in PAUP*4.0b10 (Swofford, 2002) and a Bayesian method was performed using MrBayes 3.1.2 (Ronquist, Huelsenbeck & van der Mark, 2005). The MP analysis was performed by means of heuristic searches, with 1000 replicates of random addition of taxa and tree–bisection reconnection (TBR). Confidence in the clades was indicated by Bremer decay indices implemented in PRAP (Müller, 2004).

ML analyses used the Hasegawa–Kishino–Yano model of DNA evolution, with heterogeneous rates following a gamma distribution that used the shape parameter $\alpha = 0.8764$ and a proportion of invariant sites I = 0.5640, as indicated by MODELTEST, version 3.1 (Posada & Crandall, 1998). For ML analysis, the search was heuristic, using the TBR algorithm and random addition of taxa. The Bayesian inference was performed using two independent runs of four Markov chains (one cold and three heated), with 3×10^6 generations, sampling every 100 generations. The first 25% of the sampled trees and estimated parameters were burned off to allow the chains to reach stability.

In addition, cyt *b* haplotype networks were also generated using the median-joining algorithm (Bandelt, Forster & Röhl, 1999) implemented in NETWORK software (http://www.fluxus-engineering.com).

Intraspecific and coalescent analysis

Diversity patterns of both species were explored using estimates of haplotype and nucleotide diversities, as well as genetic divergences between intraspecific groups. Tajima's *D* neutrality test (Tajima, 1989), using intraspecific genetic variability, was performed to verify population expansions, using the software packages DNAsp, version 4.20 (Rozas *et al.*, 2003) and ARLEQUIN, version 3.1 (Excoffier, Laval & Schneider, 2005).

To test the hypotheses proposed for this group by Hoffmann & Baker (2003), which includes a speciation event along the same time frame for both *C. perspicillata* and *C. brevicauda* involving allopatry, we estimated the time to the most recent common ancestor (T_{MRCA}) for each species and their respective lineages using a Bayesian coalescent approach implemented in BEAST, version 1.5.3 (Drummond & Rambaut, 2007). We used the same evolutionary model calculated above with MODELTEST, leaving the frequencies and parameters estimates as mean priors on the distributions. Tree priors were generated using the coalescent with constant population size and a relaxed clock drawn from an uncorrelated exponential distribution (Drummond *et al.*, 2006); the tree heights priors followed a normal distribution with mean of 0.5 Myr for each species and 1.0 Myr for both species. The prior for the rate of evolution was drawn from a normal distribution with mean of 2.6% per million years as calculated by Hoffmann, Owen & Baker (2003) for phyllostomid bats. The Markov chain Monte Carlo analysis used 40 000 000 generations sampling every 1000 generations; the first 10 000 steps were discarded as burn-in.

RESULTS

Mitochondrial DNA sequence variation

The complete cyt *b* gene (1140 bp) was sequenced in all specimens. Sequences from 65 individuals, each of them presenting a different haplotype, were submitted to GenBank, under accession numbers FJ589651–FJ589715. For *C. perspicillata*, 75 unique haplotypes were identified within the 80 individuals sampled. Among the 1140 aligned sites, 192 nucleotide substitutions were found, of which 148 were transitions and 44 were transversions; there were 172 polymorphic sites. In *C. brevicauda*, each individual had a distinct haplotype. The data set comprised 1140 aligned sites, of which 98 were nucleotide substitutions, 84 were transitions, and 14 were transversions. There were 95 polymorphic positions. The mean intraspecific divergence (*p*-distance) within *C. perspicillata* was 1.8% and 2.1% within *C. brevicauda*.

Evolutionary relationships

All phylogenetic analyses (Bayesian, MP, and ML) yielded similar topologies (Fig. 2, S1). The two species are monophyletic with high bootstrap support values. The genetic distance observed between the intraspecific lineages is similar to that previously described for such species; it remains within the expected range for phyllostomid bats (Bradley & Baker, 2001).

There are two distinct clades in *C. brevicauda*, as previously described (Hoffmann & Baker, 2003). However, the addition of four new samples from Brazil showed the existence of a contact zone between those clades in the locality of Santa Isabel do Rio Negro, AM, located on the left margin of Rio Negro. In this locality, two individuals bearing haplotypes belonging to different clades were sampled (AD 878 and AD 911; Fig. 2). This points to a sympatry of divergent lineages, contrary to the allopatric distribution proposed before; thus, it may be a secondary contact zone. All phylogenetic analyses resulted in the same clades for *C. brevicauda*, with a high bootstrap support.

Table 1. Estimates of time to the most recent common ancestor (T_{MRCA}), and Tajima's neutrality test for *Carollia perspicillata* and *Carollia brevicauda*

	Carollia perspicillata	*Carollia brevicauda*	Both species
T_{MRCA} (Kyr)	688.3	696.7	1036.4
95% CI	[500.01–1049.3]	[500.02–1064.7]	[567.7–1754.2]
Tajima's *D*	–1.50*	–0.94	–

*Significant value ($P < 0.05$); CI = 95% Confidence Interval.

Table 2. Sample sizes (*N*), haplotype numbers (*h*), Tajima's *D* neutrality test with their respective *P*-values, and time to the most recent common ancestor (T_{MRCA}) for both lineages of *Carollia perspicillata* and *Carollia brevicauda*

		N	*H*	Tajima's *D*	*P*	T_{MRCA}
Carollia perspicillata	South-east clade	28	27	–2.35	0.003	235.656
	Widespread clade	52	48	–1.62	0.032	514.734
Carollia brevicauda	Andean clade	11	11	0.02	0.577	321.919
	Guyana clade	5	5	–1.55	0.053	306.256

Carollia perspicillata presents a more complex pattern. There are two main clades for this species: the first clade ($N = 52$) is formed by the bats from all other sampled locations (Widespread clade) and the second clade ($N = 28$) is formed by specimens from south-east Brazil (the South-east clade; Fig. 2). The same topology was found by all phylogenetic methods, with bootstrap support and high Bayesian posterior probabilities. Regarding the subspecies described by Pine (1972), the genetic lineages found here for *C. perspicillata* bear no relationship with them, corroborating the analysis made by McLellan (1984) using morphometric data.

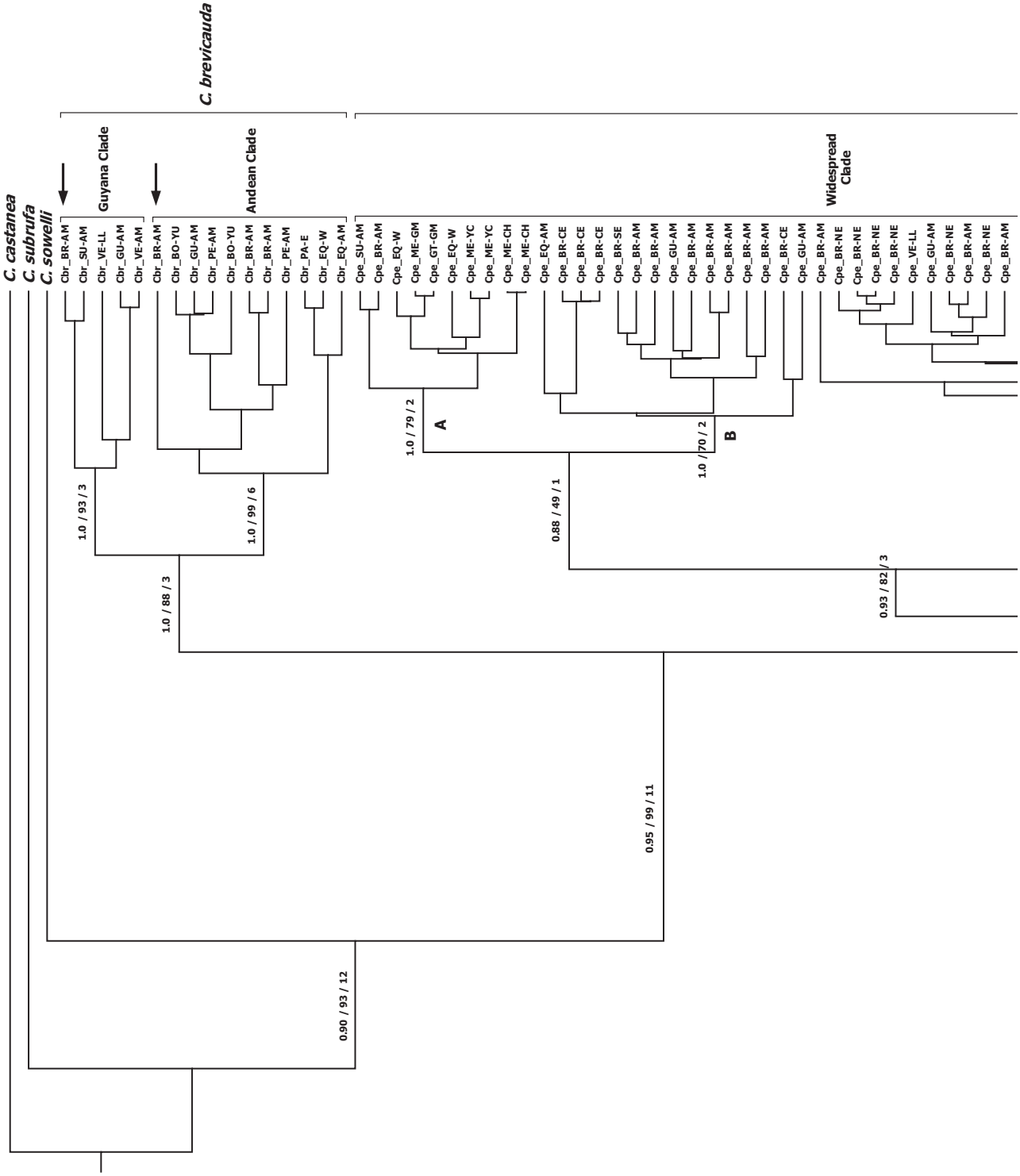
The Widespread clade is further divided into three subgroups (A, B, and C; Fig. 2), which correspond to the same phylogroups found by Hoffmann & Baker (2003), although without any geographic correspondence. High support values for these phylogroups were found only for the Bayesian analysis. The South-east clade contains predominantly individuals from the Brazilian Southern Atlantic Forest with only one exception coming from the Cerrado (MM04). However, some individuals from this region represent cyt *b* haplotypes grouped within the Widespread clade (YL334, AD 444, AD 284). This observation can be explained by incomplete lineage sorting or by contemporary migration. The Widespread clade is composed by individuals coming from all Biomes studied including Northern and Southern Atlantic Forest, the Cerrado, and Amazon. The Bayesian trees showing the detailed phylogenetic relationships between individuals of *C. perspicillata*'s South-east clade and *C. perspicillata*'s General clade are provided in the Appendix (Table A1).

This South-east clade contains the individual AD 371 (MVZ185533) from Caratinga (Minas Gerais, Brazil), which represents the basal haplotype for *C. perspicillata* shown in the previous study (Hoffmann & Baker, 2003). Nevertheless, the present analysis shows a distinct phylogenetic relationship among the lineages of *C. perspicillata* to that presented previously. Alternatively, the haplotype cited above belongs to the sister group of the Widespread clade, which contains the three phylogroups described by Hoffmann & Baker (2003) (Fig. 2; see also Appendix, Table A1), and is not basal to it. Also, we can observe a star-like phylogeny for this clade, which suggests recent population growth (Slatkin & Hudson, 1991). Consequently, based on this sister lineage, the results of the present study do not support the previous hypothesis regarding the origin of *C. perspicillata* in the Southern Atlantic Forest.

The haplotype network (data not shown) has also detected the same pattern of haplotype clustering as depicted in Figure 2, including all clades and subdivisions for both species.

Coalescent analysis and divergence times

Table 1 show coalescent estimates for the T_{MRCA} of each species studied, which are very similar (688 300 years for *C. perspicillata* and 696 700 years for *C. brevicauda*) and the T_{MRCA} for both species, which was approximately 1.036 million years ago, a time coherent with the Pleistocene glacial episodes. The neutrality test result, however, showed distinct values for each species, indicating a history of recent expansion in population size only for *C. perspicillata*.


C. brevicauda
C. castanea
C. subrufa
C. sowelli
Guyana Clade
Andean Clade
Widespread Clade
Cbr_BR-AM
Cbr_SU-AM
Cbr_VE-LL
Cbr_GU-AM
Cbr_VE-AM
Cbr_BR-AM
Cbr_BO-YU
Cbr_GU-AM
Cbr_PE-AM
Cbr_BO-YU
Cbr_BR-AM
Cbr_BR-AM
Cbr_PE-AM
Cbr_PA-E
Cbr_EQ-W
Cbr_EQ-AM
Cpe_SU-AM
Cpe_BR-AM
Cpe_EQ-W
Cpe_ME-GM
Cpe_GT-GM
Cpe_EQ-W
Cpe_ME-YC
Cpe_ME-YC
Cpe_ME-CH
Cpe_ME-CH
Cpe_EQ-AM
Cpe_BR-CE
Cpe_BR-CE
Cpe_BR-CE
Cpe_BR-SE
Cpe_BR-AM
Cpe_BR-AM
Cpe_GU-AM
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Cpe_BR-AM
Cpe_BR-CE
Cpe_GU-AM
Cpe_BR-AM
Cpe_BR-NE
Cpe_BR-NE
Cpe_BR-NE
Cpe_VE-LL
Cpe_GU-AM
Cpe_BR-NE
Cpe_BR-AM
Cpe_BR-NE
Cpe_BR-AM
A
B
1.0 / 93 / 3
1.0 / 99 / 6
1.0 / 79 / 2
1.0 /70 / 2
0.88 / 49 / 1
0.93 / 82 / 3
1.0 / 88 / 3
0.95 / 99 / 11
0.90 / 93 / 12

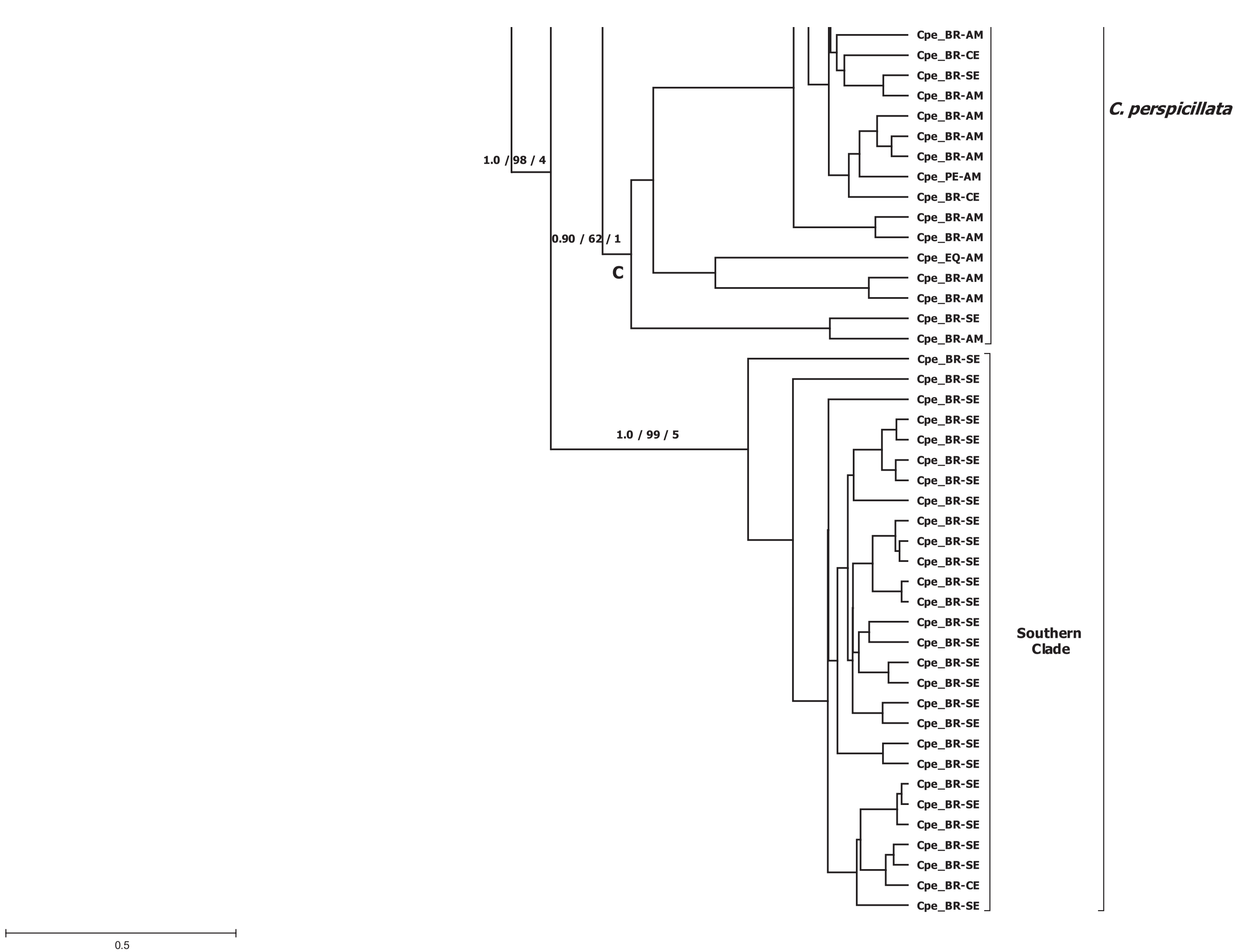

Figure 2. General topology showing the intraspecific lineages of *Carollia perspicillata* and *Carollia brevicauda*, with three different phylogenetic support methods: Bayesian posterior probabilities/ML bootstrap/Bremer decay index. Black arrows show *C. brevicauda* haplotypes sampled in the same location but belonging to different clades. Cbr, *Carollia brevicauda*; Cpe, *Carollia perspicillata*; BO, Bolivia; BR, Brazil; EQ, Equador; GT, Guatemala; GU, Guyana; ME, Mexico; PA, Panama; PE, Peru; SU, Suriname; VE, Venezuela; AM, Amazonia; CE, Serrado; NE, North-East Atlantic Forest; SE, South-East Atlantic Forest; CE, Cerrado; CH, Chiapas; GM, Golfo de Mexico; LL, Llanos; YC, Yucatán; YU, Yungas; E, East; W, West. (*sensu* Morrone, 2001).

For *C. perspicillata*, T_{MRCA} differed significantly between clades, indicating a more recent diversification (235 700 years ago) for the South-east clade than for the General clade (514 700 years; Table 2). These results suggest a more recent colonization time of the Southern Atlantic Forest, where the South-east clade appears almost exclusively. Tajima's *D*-test showed significant negative values in both groups. However, the comparison of Tajima's neutrality tests between these groups showed a greater value for the South-east clade. This difference is also highlighted by a mismatch distribution analysis (data not show). The T_{MRCA} estimates for the lineages of *C. brevicauda* were more similar, being approximately 306 300 and 321 900 years for the Guyana and Andean clades, respectively. However, Tajima's test was only significant in the latter case (Table 2).

DISCUSSION

Origin of *C. perspicillata* and *C. brevicauda*

The results of the coalescent analysis, as described for the T_{MRCA}, showed a similar time of origin for both *C. perspicillata* and *C. brevicauda* during the Pleistocene, as hypothesized by Hoffmann & Baker (2003). However, it is known that a non-neutral model of population growth influences the T_{MRCA} estimate, meaning that values found by this method can be underestimated in cases where the population analyzed has gone through a bottleneck (Wakeley, 2008). Because the neutrality tests suggest that *C. perspicillata* experienced an abrupt population growth in the recent past, it is probable that the estimate of the T_{MRCA} estimated represents the time of this demographic event. This means that the T_{MRCA} of *C. perspicillata* must have been earlier, although we were unable to infer how many years before. We consider, however, that the difference between the T_{MRCA} in both species is minimal, and this result allows us to suggest that they originated almost simultaneously following vicariant events in the Amazon during the Pleistocene. As a test, a simple parsimony area analysis using the locations of the haplotypes indicated in Figure 2 shows that the common ancestor of both *C. perspicillata* and *C. brevicauda* maps to Amazon Region. Therefore, it is very likely that the same historical process is responsible for the patterns described for both species.

Phylogeographic pattern of each species

Carollia brevicauda presents two main evolutionary lineages, the first including individuals from the Guyana shield and the second covering localities from Panama to the Bolivian and Brazilian Amazon. These lineages are sympatric, at least in part of their geographic ranges. They present a contact zone in the Brazilian state of Amazonas, where two individuals from the same locality had haplotypes from different lineages. The results of the coalescent analysis revealed a T_{MRCA} that was slightly older for the Andean clade than for the Guyana clade. At the same time, the marginally significant neutrality test suggests a possible event of demographic expansion just in the Guyana lineage. These differences, however, can be attributed to the reduced sampling. An increase of individuals analyzed in the Guyana clade could result in a different scenario because it is known that a low number of samples (less than ten) may influence the estimates based on the coalescent process (Wakeley, 2008). Although we have a limited sampling for *C. brevicauda*, considering both the results and the species distribution of the present study, it is tempting to assume an equatorial origin for *C. brevicauda*, somewhere in the Amazon. Furthermore, a vicariant event later in the Pleistocene maybe likely the cause of the two divergent clades observed, with a contemporary secondary contact zone appearing in central Amazon.

For *C. perspicillata*, two main evolutionary lineages were found. Individuals from Bahia to Paraná states, on the Brazilian South Atlantic Forest, comprise the first. The second and geographically more widespread lineage is distributed along the Brazilian North Atlantic Forest, the Cerrado, and the Amazon, as well as in other biomes of South and Central America. Coalescent analysis points to different times for the diversification process of each lineage, as indicated by the estimates of T_{MRCA}, with the South-east clade probably diversifying more recently. It is important to highlight that these lineages found for *C. perspicillata* bear no relationship to the subspecies described by Pine (1972), corroborating the results of McLellan (1984) using morphometric data. However, given the phylogeographic and demographic patterns reported in the present study, we were able to infer a different scenario for the origin and diversification for both species. By contrast to Hoffmann & Baker (2003), the results obtained in the present study for *C. perspicillata* are compatible with an Amazonian origin because populations in this region present a higher diversity and more lineages from different clades. The Northern Atlantic Forest and the Amazon exchange a considerable amount of haplotypes and the Cerrado region appears to permeate all clades. This pattern is coherent with a scenario where the Cerrado has a significant input of migrants from the Amazon, and the Northern Atlantic forest has been colonized by individuals from the surrounding biomes, independently of the Southern Atlantic forest populations (South-east clade). Furthermore, the demographic

analysis of the South-east clade indicates a recent bottleneck and founder effect followed by rapid population expansion in the Southern Atlantic Forest biome.

Diversification of *C. perspicillata* in the Brazilian Atlantic Forest

Numerous studies recognize the Atlantic Forest as a composite area, with biome subdivisions first recognized in amphibians (Muller, 1973; Lynch, 1979), reptiles (Vanzolini, 1988), and birds (Cracraft & Prum, 1988) using parsimony analysis of endemicity. Recent phylogeographic studies in different vertebrate groups have also pointed to a latitudinal differentiation in this biome. Costa (2003) described such patterns for three species of nonflying small mammals, recognizing northern and southern components for the genera *Rhipidomys*, *Micoureus*, and *Metachirus*. Grazziotin *et al*. (2006) found the same division on the Atlantic Forest for the lancehead pitviper *Bothrops jararaca*, describing a long history of constant population size followed by a recent expansion estimated to have occurred in the Pleistocene approximately 0.1 Mya ago. Another study by Lara & Patton (2000) found a similar pattern for rats of the genus *Trinomys* with two clades occurring on the coast and in the interior plateau of Brazil, respectively. We found this same pattern of latitudinal differentiation within the Brazilian Atlantic Forest for *C. perspicillata*, with southern and northern groups.

The fact that *C. perspicillata* has a mitochondrial clade that corresponds to south-east Brazil was shown by Ditchfield (2000) on a smaller scale. Martins *et al*. (2007) also found a monophyletic mitochondrial clade in south-east Brazil that bears a significant negative value of Tajima's *D* that is congruent with a scenario of recent expansion. It was suggested that Pleistocenic fluctuations would have limited the Atlantic forest to the steep humid slopes in this region, meaning that only very small fragments of forest remained in this period. That would have caused a drastic reduction in the effective number of forest-dwelling species and a subsequent expansion when the conditions changed. A similar scenario was described for a southern phylogroup of *B. jararaca* (Grazziotin *et al*., 2006).

However, *C. perspicillata* presents a slightly different pattern to the ones obtained for the previously studied species. Although the finding of a recent population expansion in south-east Brazil agrees with a recent occupation of this biome, the phylogenetic trees and phylogeographic network (data not shown) depicts separate colonization events between northern and southern parts of the Atlantic Forest. Thus, we hypothesize that another historical process could have been responsible for this scenario. Although past climatic oscillations must have contributed to forest fragmentation and vicariance as a result of the Pleistocenic refugia in the Atlantic Forest, there were also corridor patches of savannas formed between the Amazon and Atlantic Forest in interglacial periods; these events could have generated distinct lineages in forest-dwelling animals such as the understory dwelling *C. perspicillata*.

Moreover, the pattern found in *C. perspicillata* also coincides with that found of *Trinomys* (Lara & Patton, 2000) with respect to the types of vegetation and current humidity gradients: one clade from which the samples' geographic distribution coincides with the geographic range of forested, more humid areas in south-east Brazil, whereas another clade has samples from the interior plateau, characterized by savanna-like habitats. The coalescent time estimates also corroborate the idea that *C. perspicillata*'s phylogeographic pattern was shaped by the same historical climatic events that shaped the distribution of other species in the same area. All of the estimates of time fall within the Pleistocene epoch (0.01–1.8 Mya).

In the present study, we describe a detailed phylogeographic pattern confirming that the species comprises two major clades along its distribution range. We also found that the latitudinal division between these lineages appears to coincide with that described for other groups of vertebrates. Because *C. perspicillata* is an understory specialist, past forest fragmentation could have played a major role in shaping the contemporary distribution of genetic lineages.

Conclusions

The present work provides a more detailed picture for the origin and diversification of the most derived clade of the genus *Carollia*. According to our phylogenetic and coalescent data, *C. perspicillata* and *C. brevicauda* could have diversified simultaneously, through the same historical event approximately 0.7 Mya. However, the results of the present study obtained with a large sample did not identify basal lineages for either species, a criterion used in a previous report (Hoffmann & Baker, 2003) to suggest areas of origin and diversification for both species. Consequently, if we assume that the sister species *C. perspicillata* and *C. brevicauda* have been both derived from a single speciation event in South America, the most parsimonious place for their common ancestor is likely the Amazon. Furthermore, if we equate the intraspecific phylogenies of both species with their history of origin and diversification, the distribution of lineages and clades as well as the indication of a more recent colonization of the Atlantic

Forest by *C. perspicillata* also indicates an Amazon origin.

The phylogenetic and phylogeographic histories of these two species of *Carollia*, specifically *C. perspicillata*, represent another piece in the puzzle of Neotropical biogeography. However, they corroborate the relative importance of vicariant events during the Pleistocene, such as cycles of contraction and expansion of forested areas, particularly in the Amazon, for the diversification and speciation in South America.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1. Bayesian Phylogenetic tree showing the intraspecific lineages of *C. perspicillata* and *C. brevicauda* and the level of divergence expressed by the size of the branch-lengths.

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APPENDIX

Table 1. List of individuals sampled for the present study

Sample	Institution	Taxon	Locality	GenBank accession number
YL334	UFES	*Carollia perspicillata*	Aguia Branca-ES, Brazil	FJ589655
YL364	UFES	*Carollia perspicillata*	Aguia Branca-ES, Brazil	FJ589656
YL365	UFES	*Carollia perspicillata*	Aguia Branca-ES, Brazil	FJ589657
YL391	UFES	*Carollia perspicillata*	Aguia Branca-ES, Brazil	FJ589658
RF04	UFES	*Carollia perspicillata*	Cariacica-ES, Brazil	FJ589659
RF05	UFES	*Carollia perspicillata*	Cariacica-ES, Brazil	FJ589660
AD200	MZUSP	*Carollia perspicillata*	Una-BA, Brazil	FJ589661
AD199	MZUSP	*Carollia perspicillata*	Una-BA, Brazil	FJ589662
AD217	MZUSP	*Carollia perspicillata*	IlhaBela-SP, Brazil	FJ589663
AD238	MZUSP	*Carollia perspicillata*	IlhaBela-SP, Brazil	FJ589664
AD662	MZUSP	*Carollia perspicillata*	Salesópolis-SP, Brazil	FJ589665
AD244	MZUSP	*Carollia perspicillata*	Ribeirao Grande-SP, Brazil	FJ589666
AD444	MZUSP	*Carollia perspicillata*	Jundiai-SP, Brazil	FJ589667
AD975	MZUSP	*Carollia perspicillata*	Embuguaçu-SP, Brazil	FJ589668
AD765	MZUSP	*Carollia perspicillata*	Mogi das Cruzes-SP, Brazil	FJ589669
AD281	MZUSP	*Carollia perspicillata*	Mangaratiba-RJ, Brazil	FJ589688
AD284	MZUSP	*Carollia perspicillata*	Mangaratiba-RJ, Brazil	FJ589687
AD342	MZUSP	*Carollia perspicillata*	Aracruz-ES, Brazil	FJ589670
AD341	MZUSP	*Carollia perspicillata*	Aracruz-ES, Brazil	FJ589671
AD355	MZUSP	*Carollia perspicillata*	Linhares-ES, Brazil	FJ589672
AD370	MZUSP	*Carollia perspicillata*	Caratinga-MG, Brazil	FJ589673
AD371	MZUSP	*Carollia perspicillata*	Caratinga-MG, Brazil	FJ589674
PERD18	UFMG	*Carollia perspicillata*	Marliéria-MG, Brazil	FJ589675
PERD04	UFMG	*Carollia perspicillata*	Marliéria-MG, Brazil	FJ589676
PERD19	UFMG	*Carollia perspicillata*	Marliéria-MG, Brazil	FJ589677
PERDBH24	UFMG	*Carollia perspicillata*	Marliéria-MG, Brazil	FJ589678
PERDBH29	UFMG	*Carollia perspicillata*	Marliéria-MG, Brazil	FJ589679
PETI39	UFMG	*Carollia perspicillata*	Santa Bárbara-MG, Brazil	FJ589680
PETI07	UFMG	*Carollia perspicillata*	Santa Bárbara-MG, Brazil	FJ589681
PNP11	UFMG	*Carollia perspicillata*	Itacarambi-MG, Brazil	FJ589682
PNPBH46	UFMG	*Carollia perspicillata*	Itacarambi-MG, Brazil	FJ589683
PNPBH43	UFMG	*Carollia perspicillata*	Itacarambi-MG, Brazil	FJ589684
PNPBH45	UFMG	*Carollia perspicillata*	Itacarambi-MG, Brazil	FJ589685
MM04	UFMG	*Carollia perspicillata*	Unaí-MG, Brazil	FJ589686
RZ33	INPA	*Carollia perspicillata*	Barcelos-AM, Brazil	FJ589689
RZ05	INPA	*Carollia perspicillata*	Barcelos-AM, Brazil	FJ589690
RZ28	INPA	*Carollia perspicillata*	Barcelos-AM, Brazil	FJ589691
ARI10	UFMG	*Carollia perspicillata*	Aripuanã-MT, Brazil	FJ589692
ARI22	UFMG	*Carollia perspicillata*	Aripuanã-MT, Brazil	FJ589693
ARI40	UFMG	*Carollia perspicillata*	Aripuanã-MT, Brazil	FJ589694
VCT316	UFMG	*Carollia perspicillata*	São Luis-MA, Brazil	FJ589695
AD122	MZUSP	*Carollia perspicillata*	Tamandaré-PE, Brazil	FJ589696
AD121	MZUSP	*Carollia perspicillata*	Tamandaré-PE, Brazil	FJ589697
AD108	MZUSP	*Carollia perspicillata*	Baia Formosa-RN, Brazil	FJ589698
AD162	MZUSP	*Carollia perspicillata*	Santo Amaro das Brotas-SE, Brazil	FJ589699
AD152	MZUSP	*Carollia perspicillata*	Olinda-PE, Brazil	FJ589700
AD153	MZUSP	*Carollia perspicillata*	Olinda-PE, Brazil	FJ589701
LK14	UFMG	*Carollia perspicillata*	Cândido Mendes-MA, Brazil	FJ589702
LK16	UFMG	*Carollia perspicillata*	Cândido Mendes-MA, Brazil	FJ589703
LK22	UFMG	*Carollia perspicillata*	Cândido Mendes-MA, Brazil	FJ589704
AD802	MZUSP	*Carollia perspicillata*	Santa Isabel do Rio Negro-AM, Brazil	FJ589705

APPENDIX *Continued*

Sample	Institution	Taxon	Locality	GenBank accession number
AD833	MZUSP	*Carollia perspicillata*	Santa Isabel do Rio Negro-AM, Brazil	FJ589706
AD843	MZUSP	*Carollia perspicillata*	Santa Isabel do Rio Negro-AM, Brazil	FJ589707
AD849	MZUSP	*Carollia perspicillata*	Santa Isabel do Rio Negro-AM, Brazil	FJ589708
AD847	MZUSP	*Carollia perspicillata*	Santa Isabel do Rio Negro-AM, Brazil	FJ589709
AD851	MZUSP	*Carollia perspicillata*	Santa Isabel do Rio Negro-AM, Brazil	FJ589710
AD902	MZUSP	*Carollia perspicillata*	Santa Isabel do Rio Negro-AM, Brazil	FJ589711
AD907	MZUSP	*Carollia perspicillata*	Santa Isabel do Rio Negro-AM, Brazil	FJ589712
AD909	MZUSP	*Carollia perspicillata*	Santa Isabel do Rio Negro-AM, Brazil	FJ589713
AD913	MZUSP	*Carollia perspicillata*	Santa Isabel do Rio Negro-AM, Brazil	FJ589714
MAP482	IEPA	*Carollia perspicillata*	Rio Anacuí-AP, Brazil	FJ589715
AD343*	MZUSP	*Carollia perspicillata*	Aracruz-ES, Brazil	FJ589680
PNPBH37†	UFMG	*Carollia perspicillata*	Itacarambi-MG, Brazil	FJ589682
PNPBH44†	UFMG	*Carollia perspicillata*	Itacarambi-MG, Brazil	FJ589682
ARI01	UFMG	*Carollia brevicauda*	Aripuanã-MT, Brazil	FJ589651
ARI04	UFMG	*Carollia brevicauda*	Aripuanã-MT, Brazil	FJ589652
AD911	MZUSP	*Carollia brevicauda*	Santa Isabel do Rio Negro-AM, Brazil	FJ589653
AD878	MZUSP	*Carollia brevicauda*	Santa Isabel do Rio Negro-AM, Brazil	FJ589654
TK19315	GenBank	*Carollia perspicillata*	Barinas, Barinitas, Venezuela	AF511983
TK86671	GenBank	*Carollia perspicillata*	Berbice District, Dubulay Ranch, GUIANA	AF511978
TK70435	GenBank	*Carollia perspicillata*	Cuzco, La Convencion, PERU	AF187026
FN37084	GenBank	*Carollia perspicillata*	Napo, Parque Nacional Yasuni, EQUADOR	AF511990
FN30973	GenBank	*Carollia perspicillata*	Quintana Roo, Laguna Noh-Bec, MEXICO	AF511987
MDE6004	GenBank	*Carollia perspicillata*	Tulum, MEXICO	AF511986
TK104613	GenBank	*Carollia perspicillata*	Esmeraldas, San Lorenzo, EQUADOR	AF511975
NK8645	GenBank	*Carollia perspicillata*	Chiapas, Agua Azul, MEXICO	AF511985
NK8644	GenBank	*Carollia perspicillata*	Chiapas, Agua Azul, MEXICO	AF511984
FN31809	GenBank	*Carollia perspicillata*	El Peten, Poptun, GUATEMALA	AF511988
FN33206	GenBank	*Carollia perspicillata*	Campeche, Escarcega, MEXICO	AF511989
TK104631	GenBank	*Carollia perspicillata*	Esmeraldas, San Lorenzo, EQUADOR	AF511976
TK17466	GenBank	*Carollia perspicillata*	Nickerie, Kabalebo, SURINAME	AF187025
TK86503	GenBank	*Carollia perspicillata*	Northwest District, Baramita, GUIANA	AF511977
FN37107	GenBank	*Carollia perspicillata*	Napo, Parque Nacional Yasuni, EQUADOR	AF511991
TK86691	GenBank	*Carollia perspicillata*	Berbice District, Dubulay Ranch, GUIANA	AF511979
TK86502	GenBank	*Carollia brevicauda*	Northwest District, Baramita, GUYANA	AF511958
TK19273	GenBank	*Carollia brevicauda*	Bolivar, El Palmar, Venezuela	AF511957
TK19316	GenBank	*Carollia brevicauda*	Barinas, Barinitas, Venezuela	AF511959
TK10218	GenBank	*Carollia brevicauda*	Saramacca, Raleigh Falls, Suriname	AF511955
FN38117	GenBank	*Carollia brevicauda*	Panama, Parque Nacional Altos de Campana, Panama	AF511960
TK104530	GenBank	*Carollia brevicauda*	Esmeraldas, San Lorenzo, Ecuador	AF511953
TK46010	GenBank	*Carollia brevicauda*	Loreto, Aguas Negras, Peru	AF187018
FN37060	GenBank	*Carollia brevicauda*	Napo, Parque Nacional Yasuni, Ecuador	AF511956
NK12171	GenBank	*Carollia brevicauda*	Santa Cruz, Buen Retiro, Bolivia	AF511951
FN37059	GenBank	*Carollia brevicauda*	Napo, Parque Nacional Yasuni, Ecuador	AF511954
NK15417	GenBank	*Carollia brevicauda*	Santa Cruz, Bolivia	AF511952
TK70412	GenBank	*Carollia brevicauda*	Cuzco, La Convencion, Peru	AF187019
FN44027	GenBank	*Carollia sowelli*	Limon, Estacion Biologica Cano Palma, Costa Rica	AF511973
TK19550	GenBank	*Carollia subrufa*	Jalisco, Chamela, Mexico	AF187023
FN37061	GenBank	*Carollia castanea*	Napo, Parque Nacional Yasuni, Ecuador	AF512006

UFES, Universidade Federal do Espírito Santo; MZUSP, Museu de Zoologia da USP; UFMG, Universidade Federal de Minas Gerais; INPA, Instituto de Pesquisas da Amazônia; IEPA, Instituto Estadual de Pesquisas do Amapá.
*Same haplotype of PETI39.
†Same haplotype of PNP11.