Timing and patterns of diversification in the Neotropical bat genus *Pteronotus* (Mormoopidae)

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Ana C. Pavan [a],[*], Gabriel Marroig [b]

[a] *Departamento de Ciências Biológicas, ESALQ/Universidade de São Paulo, 13418-900 Piracicaba, SP, Brazil*
[b] *Departamento de Genética e Biologia Evolutiva, IB/Universidade de São Paulo, 05508-090 São Paulo, SP, Brazil*

ABSTRACT

We investigate the biogeographic processes related to the origin and current patterns of distribution of the extant species of the genus *Pteronotus*. This clade of insectivorous bats is widely distributed in the Neotropical Region and has recently gone through a taxonomic update which increased more than twice its diversity. Using six molecular markers of 15 *Pteronotus* lineages ranging from Mexico to Central Brazil, we reconstruct a time-calibrated tree and infer molecular evolutionary rates for this bat genus. In addition, estimates of range evolution across phylogeny were obtained through statistical model testing among six different biogeographic models. The origin of the genus *Pteronotus* occurred approximately 16 million years ago (Ma), with initial cladogenesis events being evenly distributed across the phylogeny. Divergence between most closely related species is recent, falling in the Pleistocene period less than 2.6 Ma. Mainland lineages present congruent patterns of north versus south continent splitting while insular clades differ in their time of arrival in the Caribbean Islands. Temporal and geographic range estimates for early nodes of *Pteronotus* phylogeny suggest a central role of Neogene tectonic reorganizations of Central America in the group diversification process. Also, South American colonization by *Pteronotus* occurred early in the genus history. Founder-event speciation was an important mode of lineage splitting in *Pteronotus*, with two independent dispersal jumps having occurred to the Greater Antilles. Finally, Pleistocenic sea-level variation and climatic oscillations are possibly associated with divergence between sister-species and recent ages of MRCA for *Pteronotus* species.

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1. Introduction

The order Chiroptera exhibits its highest diversity in the Neotropics and the number of recognized taxa continues to increase as new studies on evolutionary patterns are developed. Despite their high richness, bats were historically not included in early discussions on mammalian biogeography in this region, mainly because of their poor fossil records (Morgan and Czaplewski, 2012). Also, for being the only mammal group with powered flight, bat species usually exhibit high dispersal abilities and large geographic ranges, which made them less attractive for initial historical biogeography investigations (Lim, 2009). This scenario has been changed and bats recently became the focus of many comparative studies on the diversification timescales of neotropical lineages (Dávalos, 2006, 2007; Lim, 2008; Rojas et al., 2012, 2016; Velazco and Patterson, 2013). Given the high number

of endemic but geographically widespread groups in New World, bats offer an excellent opportunity to investigate the role of historical processes in Neotropical biotic diversification.

Mormoopidae is one of six bat families endemic to the New World (Findley, 1993). They represent a group of insectivorous bats ranging from southwestern United States south across Central and South America to Central and Northeastern Brazil, including Greater and Lesser Antilles. Mormoopids occur from humid tropical to semiarid and arid subtropical habitats below 3000 m (Patton and Gardner, 2007). All species are gregarious, roosting exclusively in caves where they form colonies exceeding thousands of individuals (de la Torre and Medellín, 2010; Rocha et al., 2011; Silva-Taboada, 1979). This family comprises two genera, *Pteronotus* (mustached and naked-backed bats) and *Mormoops* (ghost-faced bats), whose taxonomic diversity has being traditionally accepted as eight extant species (Simmons and Conway, 2001; Smith, 1972), many of them being broadly sympatric. Two extinct species, *Mormoops magna* and *Pteronotus pristinus*, have additionally been described from Quaternary cave deposits in Cuba (Silva-Taboada,

1974), and a new genus and species dating to Oligocene remains to be described (Morgan and Czaplewski, 2012).

Biogeographic considerations about the evolutionary history of Mormoopidae were first made by Smith (1972) in his revisionary work based on the distribution of extant lineages. Smith suggested a mormoopid origin either in southern Central America or northern South America and discussed the importance of the Greater Antilles in the evolution of genera *Pteronotus* and *Mormoops*. Later, a new hypothesis based on recent fossil records suggested the origin of Mormoopidae occurred in the Oligocene of North America (i.e. Florida; Morgan and Czaplewski, 2012). The elevated species richness and endemism of this group (both extant and fossil) in the West Indies led the authors to suggest Mormoopidae reached the Antilles early in its evolutionary history and then underwent a long period of autochthonous evolution there.

One single work investigating the biogeographic pattern of Mormoopidae based on molecular data was performed. Dávalos (2006) tested which of the above described hypotheses better explained the inferred phylogenetic relationship within the family. The result supported the origin of Mormoopidae in the north of its current distribution. Higher divergence values between mainland and Antillean lineages than between Central American and northern South American lineages were described, suggesting mormoopids diversified in Mexico, Central America and Greater Antilles before dispersing to South America. Nevertheless, inferences on the geography of diversification of the genus *Pteronotus* were limited due to sampling scarcity or poor analysis performance. Moreover, many diversification events were barely interpreted because a robust phylogenetic hypothesis was not available for evaluating the biogeographic history of the group. Several molecular studies have suggested higher species diversity for the genus *Pteronotus* (Borisenko et al., 2008; Dávalos, 2006; Clare et al., 2011, 2013; Lewis-Oritt et al., 2001; Thoisy et al., 2014). Recently, Pavan and Marroig (2016) investigated the genetic and morphological variation across the complete range of this group. The study presented a new phylogenetic hypothesis and proposed the existence of 16 extant species within the genus. According to this updated phylogeny, *Pteronotus* has more than twice the number of species previously recognized, and many species presumed to occupy large geographic ranges across the continent actually represent complexes of species replaced parapatrically or allopatrically by each other.

This new taxonomic framework has never been explored using a biogeographic approach and, therefore, a comprehensive and detailed study inferring timing of diversification and ancestral range areas for the genus *Pteronotus* is unprecedented. Also, the current availability of new dating and statistical methods provide a more powerful comparative approach to perform biogeographic analysis (Brown and Lomolino, 2006). We start from this updated taxonomic arrangement to investigate temporal and spatial aspects of the diversification of this bat clade. In addition, the genus *Pteronotus* range across most of the Neotropical region, making it an attractive group for examining diversification patterns at broader scales. Its ecological features, with species occurring in both humid and forested/open and drier areas provide a good model for investigating historical processes acting in the diversification of neotropical bats. Therefore, we inferred the time of the main diversification events within the genus *Pteronotus* and applied a phylogeny-guided model selection procedure to evaluate the relative importance of different historical processes, such as the emergence of the Isthmus of Panama and past sea-level variation, in the origin and current distribution patterns of *Pteronotus* lineages.

2. Materials and methods

2.1. Sampling and molecular dataset

Our study sampling span the geographic range of the genus *Pteronotus* (from Mexico to Central Brazil), including 25 individuals representative of 15 out of the 16 lineages recognized for this group (Pavan and Marroig, 2016). In addition, *Peropteryx kappleri* and *Mormoops megalophylla* were included as outgroups in the dating analysis. Molecular protocols for data acquisition are described in Pavan and Marroig (2016). Sequence data was comprised of six molecular markers: the mitochondrial (mtDNA) genes Cytochrome b (CYTB: 1140 bp) and Cytochrome Oxidase I (COI: 651 bp); a non-coding fragment of the Y-linked gene DEAD-box helicase 3 (DBY: 510 bp); non-coding fragments of the autossomal genes Signal Transducer and Activator of Transcription 5A (STAT5A: 602 bp) and Protein Kinase C 1 (PRKC1: 462 bp), and a coding region of the Recombination Activating Gene 2 (RAG2: 804pb). Information on the voucher specimens with correspondingly localities and GenBank accession numbers is provided in the Supplementary Material (Table S1).

Sequences were assembled and checked for quality using software Geneious v.7.1 (Biomatters). Coding regions (CYTB, COI and RAG2) were aligned by eye, whereas the alignment of intron sequences (STAT5A, PRKC1, DBY) was carried out using the ClustalW tool available in mega 6 (Tamura et al., 2013). The mitochondrial dataset were also submitted to saturation analysis in software dambe5 (Xia, 2013). For autosomal genes analysis, the presence of heterozygous nucleotide positions (SNP) was represented in the dataset as ambiguous IUPAC codes. For the introns PRKC1 and STAT5A, heterozygous individuals for the insertion/deletions (INDELS) of bases were also found, and these samples were represented in the phylogenetic dataset by the longer haplotype of each individual.

2.2. Divergence dating

The package beast v.1.8.0 (Drummond et al., 2012) was used to reconstruct a time-calibrated multilocus phylogeny using one to three individuals from each currently recognized species/genetic lineage in *Pteronotus* and the two outgroups. The complete dataset of 28 individuals and six markers was analysed by partitioning schemes with distinct parameters settings (Table S2), following best-fit models of evolution proposed by partitionfinder v.1.1.0 (Lanfear et al., 2012). Therefore, substitution models were unlinked for all partitions. Clock models of mtDNA partitions were linked to produce only one evolutionary rate, i.e., number of substitutions per site per million years (subst/site/Myr) estimate for the whole mtDNA, and set as unlinked for the remaining markers. Partition trees were linked to generate a single dated phylogeny from all markers. The analysis was set with a Yule speciation tree prior (exponential mean = 0.8) and a lognormal relaxed clock (lognormal mean = 0.05 subst/site/Myr for mtDNA, 0.02 subst/site/Myr for nuclear introns and 0.01 subst/site/Myr for RAG2; standard deviation = 2), to account for lineage-specific rate heterogeneity (Drummond et al., 2006). A calibration point was included in the tree based on the existence of a Mormoopidae fossil specimen dating back to Oligocene, around 31 million years ago [Ma] (Morgan and Czaplewski, 2012). This evidence was integrated into the analysis as an *a priori* specification of the minimum divergence time between *Pteronotus* and *Mormoops*. Two independent runs of 100 million generations sampled every 10,000 steps were performed. Stationarity of runs were checked in tracer v.1.6 (Rambaut et al., 2014) by examining the average standard

deviation of split frequencies (Ronquist et al., 2011). The first 10% of trees and parameters were discarded as burn-in and the remaining samples from the posterior distribution were summarized using TreeAnnotator v.1.8 in the maximum clade credibility tree, which was visualized in FigTree v.1.4.

2.3. Ancestral range estimation

Inferences on the ancestral ranges of the nodes were performed using package BioGeoBEARS (Matzke, 2013), available in R software environment (R Development Core Team, 2013). This package compares different models of range evolution on a phylogeny under the Maximum Likelihood (ML) approach. Three biogeographic models were compared to investigate the cladogenetic pattern of *Pteronotus*: DIVA-like (the likelihood version of the parsimony-based method implemented in Dispersal-Vicariance Analysis; Ronquist, 1997), DEC (Dispersal-Extinction-Cladogenesis; Ree and Smith, 2008) and BayArea-like (the ML equivalent of BayArea program; Landis et al., 2013). These models differ in how they consider dispersal, vicariance and extinction events during cladogenesis process, and therefore allow the exploration of distinct biogeographic scenarios. An additional cladogenetic event can be taken into account in these models' implementation in Bio-GeoBEARS – the founder-event speciation (+J) – which means the new species jumps to a range outside of the ancestral range. This +J implementation is relevant since founder-effect speciation has been shown as a crucial process in several investigated clades, although better measured in insular systems (Matzke, 2014). Therefore, six probabilistic models were tested, the three above described with and without founder-effect. The models were statistically compared by the Akaike Information Criteria (AIC; Burnham and Anderson, 2002), whose values were transformed in Akaike weights (AICwt; Wagenmakers and Farrell, 2004) to allow their direct interpretation as conditional probabilities.

The ancestral range analysis included two types of data source. The first corresponded to the ultrametric bayesian combined tree generated with beast, which provides the phylogenetic relationships among *Pteronotus* lineages with their respective branch lengths. The second information regards area delimitation of taxa occurrence within the genus, for the elaboration of a presence/absence matrix. Each species was coded as being present or absent in each of ten areas: (1) ME: Mexican west coast, (2) CA: Central America region, (3) JC: Jamaica and Cuba, (4) HI: Hispaniola, (5) PR: Puerto Rico, (6) LA: Lesser Antilles, (7) CC: South America Caribbean coast, (8) AM: Amazon region, (9) CE: Brazilian dry diagonal (Cerrado and Caatinga biomes) and (10) AF: north portion of Brazilian Atlantic Forest, which represents an extension range recently reported for species *P. gymnonotus* and *P. personatus* (Rocha et al., 2011). We identified the biogeographic areas based on distributional patterns of other bat species (Lim, 2008; Velazco and Patterson, 2013) but adapting them to the more geographically structured diversity observed for the genus *Pteronotus* in the Caribbean Islands, Mexican pacific coast and Brazilian Shield (Ibáñez et al., 2000; López-Wilchis et al., 2016; Morgan, 2001; Pavan and Marroig, 2016; Rocha et al., 2011). Species were settled as occurring or not in the aforementioned areas based on the ranges observed for clades in the genus molecular phylogeny (Pavan and Marroig, 2016). We present maps of each species range based on available information of their marginal localities of occurrence as Supplementary data (Fig. S1). We decided to keep Jamaica and Cuba as a single biogeographic unit because, for the current knowledge, both islands harbor the same *Pteronotus* extant species (*P. quadridens*, *P. macleayi* and *P. parnellii*). Also, treating them as separate areas would mean setting an analysis with 11 areas, which would be computationally much more intense and would not result in a better performance of the models. We assigned the same

probability for dispersal between contiguous areas within the continent or in Caribbean Islands, while dispersal events from the continent to a group of islands (Greater or Lesser Antilles) and vice versa were considered less likely. Scenarios with ancestral nodes occupying up to five distinct areas were established, which correspond to the number of areas occupied by *Pteronotus gymnonotus*, the extant evolutionary lineage with the largest geographic range within the genus. The outgroups were removed from the phylogeny used for estimating ancestral ranges, since their long branch lengths in phylogeny would negatively bias the results.

3. Results

3.1. Phylogenetic inference and estimates of evolutionary rates

The alignment used for divergence time analysis included 4172 base pairs with 1345 variable sites and 868 parsimony-informative sites. Dated tree was obtained through the "maximum clade credibility" option, which summarizes the node height and rate statistics on the tree in the posterior sample that has the maximum sum of posterior probabilities on its n - 2 internal nodes [Fig. 1] (Drummond and Rambaut, 2007). Its topology is identical to the phylogenetic pattern found by Pavan and Marroig (2016). The genus *Pteronotus* is composed of four main clades: Clade 1 – *P. fulvus*, *P. davyi* and *P. gymnonotus*; Clade 2 – *P. macleayi* and *P. quadridens*; Clade 3 – *P. personatus* and *P. psilotis*; and Clade 4 – *P. parnellii*, *P. pusillus*, *P. portoricensis*, *P. mexicanus*, *P. mesoamericanus*, *P. fuscus*, *P. rubiginosus* and *Pteronotus* sp1. The phylogenetic structuring within Clade 4 is also congruent with previous results. Clade 4A, composed by Antillean species, is close to Clade 4B, which ranges from Mexico to northern South America, while Clade 4C, exclusively South American, is basal in this group diversification.

Fossil calibration on the phylogeny allowed us to estimate the evolutionary rates for markers included in the study. Table 1 presents the mean rates – the estimated number of substitutions per site across the whole tree divided by the estimated length of the tree in time – for mtDNA, nuclear introns (DBY, STAT5A and PRKC1) and RAG2 gene. Our results point that the substitution rate of mtDNA is at least an order of magnitude higher than the introns, which by turn, present more substitutions per site per million years than RAG2. The substitution rate proposed here for mtDNA falls inside the range of values already proposed by other studies on mammals (between 2.5 and 5%; Hoffmann et al., 2003; Smith and Patton, 1999) but the rate found for RAG2 is higher than previously reported for bats (Martins et al., 2009).

3.2. Diversification times in the genus Pteronotus

The rising of Mormoopidae is estimated in the late Oligocene, ca. 32 Ma (95% HPD = 31–36.7 Myr). Divergence time of the Most Recent Common Ancestor (MRCA) of genus *Pteronotus* dates to the middle Miocene, around 16.1 Ma, with a confidence interval (95% HPD) ranging from 12.3 to 20.2 Myr. Diversification events giving rise to the main clades of *Pteronotus* are evenly distributed along the genus phylogeny. The first was the basal split between the ancestor of Clade 4 (subgenus *Phyllodia*) and the branch giving rise to the other *Pteronotus* clades. Splitting between Clade 3 and the ancestor of Clades 1 and 2 also took place early in the genus evolutionary history (~13.9 Ma), followed by the separation of Clades 1 and 2 at 11.3 Ma. Emergence of closely related species started at the late Miocene, around 7.5 Ma, with differentiation between *P. macleayi* and *P. quadridens* within Clade 2, and extended through all Pliocene less than 3 Ma with cladogenesis within Clades 4, 3 and 1. Origin and diversification of most extant
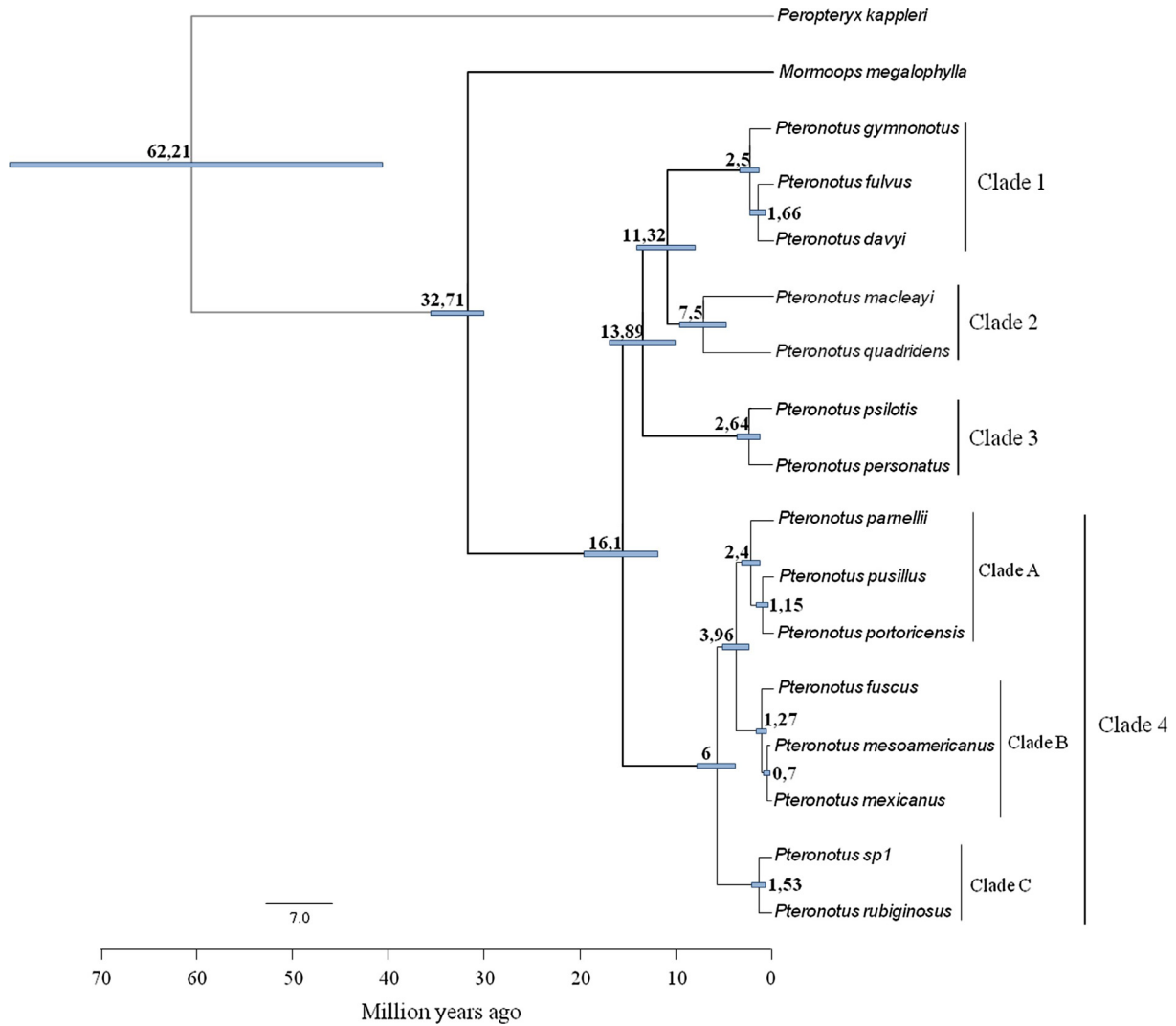
Fig. 1. Maximum clade credibity tree with divergence estimates in the genus *Pteronotus* using fossil calibration. Bars correspond to the 95% High Posterior Density (HPD) time interval of each node. Bayesian Posterior Probabilities (BPP) of all nodes were higher than 0.95.

Table 1
Evolutionary rate statistics for each *loci* investigated in the present study. Values were estimated under the uncorrelated lognormal relaxed molecular clock. HPD = High Posterior Density.

	Loci (units of substitutions per site per million years)				
	mtDNA	DBY	PRKC1	STAT5A	RAG2
Mean	4.5×10^{-2}	6.4×10^{-3}	1.7×10^{-3}	2.9×10^{-3}	8.2×10^{-4}
Median	4.5×10^{-2}	6.2×10^{-3}	1.7×10^{-3}	2.9×10^{-3}	8.1×10^{-4}
Variance	4×10^{-5}	2.5×10^{-6}	6.7×10^{-8}	1.7×10^{-7}	1.6×10^{-8}
95% HPD interval	[0.032–0.057]	[0.0037–0.0094]	[0.0012–0.0022]	[0.0021–0.0037]	[0.0005–0.001]

Pteronotus lineages is recent, occurring during the Pleistocene (Fig. 1 and Table 2).

3.3. Ancestral geographic ranges

Results of the six biogeographic models implemented in BioGeoBEARS are presented in Table 3, which describes Log-likelihood values found for each of them. Comparative statistics show that DIVAj (LnL = −42.27) and DIVA (LnL = −44.07) models best fitted the data, indicating assumptions on geographic range evolution made by dispersal-vicariant method mostly

Table 2
Estimates for the Most Recent Common Ancestor (MRCA) of *Pteronotus* lineages sampled for two or more specimens in the multilocus dating analysis.

Lineage	T_{ACMR} (Myr)
P. gymnonotus	0.297
P. quadridens	0.265
P. psilotis	0.215
P. personatus	0.095
Pteronotus sp1	0.119
P. rubiginosus	0.178
P. mesoamericanus	0.345
P. mexicanus	0.127

Table 3

Log-likelihood values of the six biogeographic models tested in the present study. Models performance was compared through Akaike Information Criterion (AIC) and Akaike weight (AICwt), the last being estimated just between the two better AIC values.

Model	Number of parameters	LnL	AIC	AICwt
DEC	2	−52.71	109.4	–
DIVA	2	−44.07	92.14	0.31
BAYAREA	2	−77.24	158.5	–
DECj	3	−44.28	94.56	–
DIVAj	3	−42.27	90.54	0.69
BAYAREAj	3	−62.97	131.9	–

satisfy patterns of geographic distribution of *Pteronotus* lineages. Implementation of DIVA model includes two free anagenetic parameters, d (dispersion rate/range expansion) and e (extinction rate/range retraction), and fixed cladogenetic parameters allowing

equal probability of vicariance for all descendant size ranges, but disallowing subset sympatric speciation (Matzke, 2013). The assignment of the free parameter J in the model, specifying weights for jump-dispersal events in the cladogenesis matrix, produced significant improvement of the biogeographic model (AICwt = 0.69 for DIVAj versus 0.31 for DIVA; Table 3). As previously shown for other islands groups (Matzke, 2014), inclusion of the J parameter in the model was important to explain some biogeographic events in the genus *Pteronotus*, such as colonization of Caribbean islands.

The most probable states for the ancestral node ranges for the genus *Pteronotus* were estimated using the DIVAj model (Fig. 2). Geographic range estimates of early nodes in the phylogeny had relatively low probabilities in all biogeographic models (data not shown), demonstrating higher uncertainty of biogeographic inferences. Area combinations displayed with black dashed lines in phylogeny nodes had frequencies smaller than 10% in the
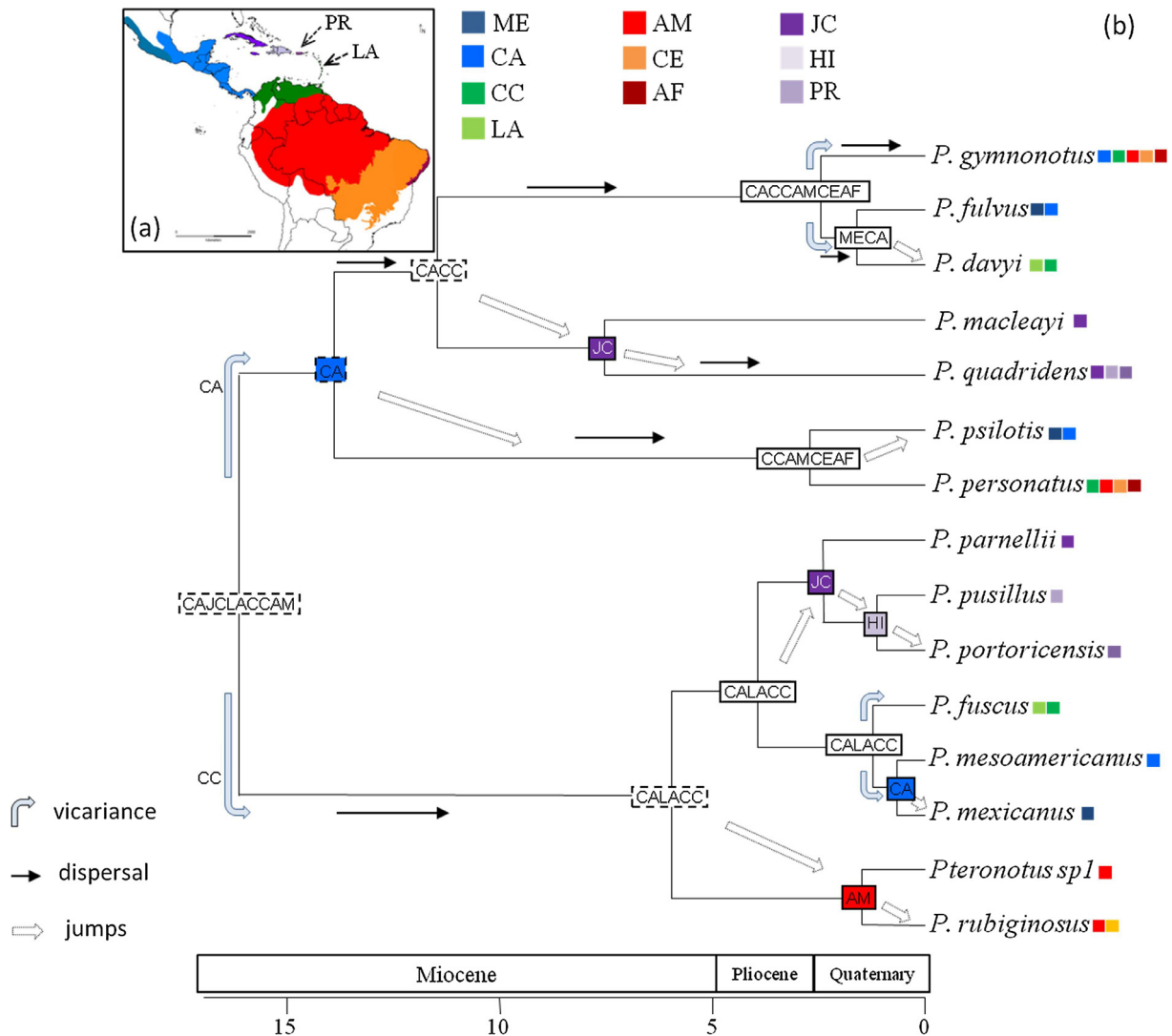

Fig. 2. Geographic range evolution in the genus *Pteronotus*. (a) Current distribution of genus *Pteronotus* (coloured map) with biogeographical areas scored for species presence/absence matrix. ME = Mexico; CA = Central America; CC = Caribean Coast of South America; LA = Lesser Antilles; AM = Amazon; CE = Brazilian Dry Diagonal: Cerrado and Caatinga; AF = Northern Atlantic Forest; JC = Jamaica and Cuba; HI = Hispaniola; PR = Puerto Rico. (b) Geographic range estimates with the highest marginal probabilities for *Pteronotus* ancestral nodes according to DIVAj model. Dashed-line borders indicate area combinations with probabilities smaller than 10% in the model, but still being the most probable state in that node among the 638 possible combinations. Curved arrows represent splits in the ancestral geographic ranges explained by vicariance; many of them were succeeded by anagenetic dispersal/extinction events, as highlighted by the linear black arrows; Dotted-line straight arrows highlight shifts in nodes geographic ranges due to dispersal jumps.

estimates, but that still are the most probable states amongst the 638 possible area combinations. The most probable alternative states of ancestral ranges according to DIVAj model are listed in Table S3.

According to the DIVAj model, the ancestor of *Pteronotus* inhabited a wide geographic area, ranging from Central America and Jamaica to the Amazon Region. An initial vicariant event split this population in the ancestral lineage of Clade 4 in South America and the ancestral lineage of Clades 1 + 2 + 3 in Central America (both ancestors could not have raised in CA because dispersal-vicariant model does not allow subset sympatric speciation). The ancestral population of Clade 4 later expanded its range into Central America, while ancestor of Clades 1, 2 and 3 diversified and dispersed to South America. In the subsequent cladogenesis event, between Clades 1 and 2, the first dispersal jump to Greater Antilles in the genus evolutionary history took place. The dotted-lined arrows in Fig. 2 highlight the shift in ancestral geographic ranges from Caribbean Coast and Central America to Jamaica and Cuba at Clade 2 ancestor. Diversification events within Clades 3 and 4 also required dispersal jumps, as displayed by the same arrows in the figure. Within Clade 4, both Amazon occupation by the ancestor of Clade 4C and the second colonization event in the Greater Antilles by the ancestor of Clade 4A were presumed to involve shifts in ancestral distributions. A similar scenario is estimated by the DIVA model (Fig. S2), except that occupation of new areas occurred via anagenetic dispersal of ancestral populations instead of through jumps at cladogenesis events.

4. Discussion

4.1. Origin and diversification patterns in the genus Pteronotus

Our time-scale estimates suggest that early cladogenesis events within the genus *Pteronotus* occurred gradually, encompassing a large time range during the evolutionary history of this group. The age of the Most Recent Common Ancestor (MRCA) of genus *Pteronotus* was estimated to be between 12.3 and 20.2 Ma, which is old when compared to divergence of other bat genera (Lim, 2008; Rojas et al., 2016; Velazco and Patterson, 2013). Despite this, the genus *Pteronotus* harbors a relatively small number of species, which are morphologically homogeneous in their skull and external characters (Simmons and Conway, 2001). The lack of phenotypic variation confounded early species designations based solely on morphology, while this genus is characterized by deep genetic divergences among lineages (Pavan and Marroig, 2016). Interestingly, the MRCA of the genus *Pteronotus* lived around 16 Ma, which represents just half of age of the MRCA of Family Mormoopidae, estimated to be at least 32 Myr old. This large interval of ca. 16 Myr between family and genus origins may imply the ancestor of *Pteronotus* underwent a long period of anagenetic evolution or, alternatively, that basal lineages filling this temporal gap became extinct later.

Biogeographic reconstruction of DIVAj model provides a scenario with both vicariant events and dispersal jumps to explain distributional patterns of extant *Pteronotus* lineages. This model proposes a widely distributed ancestor for the genus *Pteronotus*, which does not favor any of the current biogeographic hypotheses on the group origin (Morgan and Czaplewski, 2012; Smith, 1972). It is important to highlight, however, that ancestral range estimates by DIVA model seeks to minimize dispersal-extinction costs (Ronquist, 1997). Thus, it tends to reconstruct wide ancestral ranges at early nodes (which are directly related to the maximum number of areas settled) to explain distributional patterns of phylogeny tips (Lamm and Redelings, 2009; Ree et al., 2005). In spite of this, it seems that founder event speciation was an important mode of lineage splitting in the genus *Pteronotus*, particularly within Clade 4.

4.2. Diversification of mainland lineages

Based on some predictions of relationship among lineages, Dávalos (2006) suggested that mormoopid diversification occurred in the north of its current distribution – Mexico, Central America and Greater Antilles – with subsequent dispersal to the South America, which reinforces the hypothesis of Morgan and Czaplewski (2012). Nevertheless, the molecular phylogeny shown in Fig. 1 strongly supports the subgenus *Phyllodia* (Clade 4) as a basal split within *Pteronotus*. The diversification pattern exhibited by this clade suggests that the ancestor of South American lineages (Clade 4C) diverged earlier than those of Central American and Antillean lineages (Clades 4A and 4B), around 6 Ma. Our results therefore indicate that *Pteronotus* colonized South America early in their evolutionary history, potentially as early as the Miocene. This pattern adds evidences to the biotic dispersal between North and South America before 3.5 million years ago (Bacon et al., 2015; O'Dea et al., 2016).

Pteronotus exhibited initial cladogenic events during the Miocene—a period of known intense geotectonic activity in Lower Central America, with the existence of a volcanic archipelago (Panama Arc) disconnected from Nicaragua and South America by deep marine corridors (Bagley and Johnson, 2014; O'Dea et al., 2016). Although geographically isolated, this Panama Arc underwent uplift during most part of the last 20 Myr, reducing distances for overwater dispersal to South America and the rest of Central America (O'Dea et al., 2016). If our biogeographic estimates are correct in including Central America in the range of most ancestral nodes of mainland lineages (Fig. 2), this geologic event may be related to the early diversification process within the genus. Moreover, the uplift of Panama Arc was interrupted by increased levels in the interoceanic seaways between 9 and 6 Myr (Fig.1 of O'Dea et al., 2016), which is plausible with a period of isolation of Clade 4 ancestor in South America before its cladogenesis. This scenario is more congruent with Smith's (1972) hypothesis of a diversification center in southern Central America or northern South America, at least for the genus *Pteronotus*. It is important to highlight, however, that biogeographic inferences were based on relationships of the extant *Pteronotus* lineages, i.e. fossil records were not taken into account.

Current ranges of *Pteronotus* species vary considerably across the phylogeny, from species exhibiting a continental-scale distribution, such as *P. gymnonotus*, to species exhibiting more restricted ranges, like those within Clade 4, which includes island-specific lineages. In general, mainland species from distinct clades have equivalent geographic ranges or overlap broadly, while close species within clades replace each other in geography para- or allopatrically. Regardless of the species extent, a similar pattern of north × south continent split comes out for the mainland *Pteronotus*: *P. fulvus* × *P. davyi* in Clade 1, *P. psilotis* × *P. personatus* in Clade 3 and *P. mesoamericanus* × *P. fuscus* in Clade 4. According to Smith (1972), the contact zone between *P. fulvus* × *P. davyi* and *P. psilotis* × *P. personatus* is located in Nicaragua and Costa Rica, but our data could not exactly place the geographic limits for these lineages in Central America, since molecular sampling was not available for this region (Pavan and Marroig, 2016). Regarding Clade 4, it is known that the geographic range of *P. mesoamericanus* extends south to Panamá, while *P. fuscus* is distributed in Venezuela and Lesser Antilles islands; to which of these lineages the individuals from Colombia belong to is still an open question. Diversification between sister species all occurred less than 2.6 Ma (Fig. 1) and are potentially related to sea-level fluctuations bearing isolated

habitats in Lower Central America during Pleistocene (Bagley and Johnson, 2014).

4.3. Greater Antilles colonization

According to Morgan and Czaplewski (2012), overwater dispersal ability was probably one of the factors promoting diversification in Neotropical bat fauna. Tectonic movements caused the rising of temporary land bridges which facilitated dispersal events from Central and northern South America to the Caribbean Islands (Griffiths and Klingener, 1988). Our results suggest the occurrence of two independent dispersal jumps from the American continent to the Greater Antilles in the evolutionary history of the genus *Pteronotus*. The first one took place around 11 Ma, when the ancestor of Clade 2 reached the islands (via Jamaica or Cuba) and then diversified, giving rise to the Antillean species *P. quadridens* and *P. macleayi*. As proposed previously (Morgan and Czaplewski, 2012; Smith, 1972), this dispersal event has occurred early in *Pteronotus* evolutionary history. The second event, more recently, was responsible for the origin of the insular lineages in the subgenus *Phyllodia* (Clade 4) in Pliocene, around 3.9 Ma.

Several hypotheses have been proposed to explain how mainland fauna colonized the Greater Antilles, including arguments favoring vicariance (Iturralde-Vinent and MacPhee, 1999; Rosen, 1975) or overwater dispersal (Hedges, 1982, 2001; Koopman, 1958). According to data presented by such studies, vicariant models involving the presence of land bridges or archipelagos (Proto-Antilles and GAARlandia) could explain islands colonization by mainland fauna until the Oligocene (Griffiths and Klingener, 1988), though not the more recent diversification patterns emerging in late Neogene and Quaternary periods. By the middle Miocene (∼16 Myr), these small islands acting as stepping stones for fauna movement from the American continent to the Caribbean plate islands were already widely separated (Iturralde-Vinent and MacPhee, 1999). After this, significant decrease in islands geographic isolation has only occurred during the Quaternary glaciations, although physical connection has never existed again (Griffiths and Klingener, 1988). Therefore, estimated times for the MRCA and divergence dates among *Pteronotus* lineages currently occupying the Greater Antilles suggest overwater dispersal was the single mechanism responsible for the group distributional pattern (Morgan and Woods, 1986).

Two independent dispersal routes are currently used to explain bats distributional patterns in the Greater Antilles. The first one points to initial colonization through Cuba or Jamaica, from mainland populations in Mexico/Florida or Central America, respectively (Koopman, 1989; Morgan, 2001; Smith, 1972); the second suggests source populations from South America, throughout the Lesser Antilles, reaching Puerto Rico earlier than the remaining Greater Antillean islands (Baker and Genoways, 1978). Our results support Caribbean islands colonization by *Pteronotus* via Jamaica/ Cuba. Intraspecific mitochondrial data from Clade 2 (*P. macleayi* and *P. quadridens)* show that Jamaican and Cuban haplotypes diverged earlier within this group (Fig. S3). For *P. quadridens*, which presents a wide range in the Greater Antilles, all Jamaican haplotypes are sister to one clade including Cuban haplotypes and another clade comprising samples from Hispaniola and Puerto Rico, suggesting Jamaica was the first island colonized by its ancestor. Within Clade 4 (subgenus *Phyllodia*), the species *P. parnellii*, distributed in Jamaica, also diverged earlier in the insular clade, being sister to a clade composed by the species *P. pusillus* and *P. portoricensis*, respectively from Hispaniola and Puerto Rico (Fig. 1). The MRCA of the insular clade within *Phyllodia* (clade 4A), dating to 2.4 Ma, coincides with climatic fluctuations characterizing the late Neogene/Quaternary boundary (Bagley and Johnson, 2014). Decreasing sea levels of 100–150 m during this

time exposed land areas and may have facilitated dispersal of this group ancestor from Yucatán or Florida Peninsula to Cuba or, alternatively, from Nicaragua plateau to Jamaica (Griffiths and Klingener, 1988). Additional data clarifying the phylogenetic position of Cuban specimens in the subgenus *Phyllodia* is therefore necessary to ascertain the ancestral dispersal route of this group into the Greater Antilles. The existence of an independent lineage for Cuba basal to *P. parnellii* from Jamaica, allied to the abundant fossil record at this region (Morgan and Woods, 1986) and the two described mormoopid fossil species *P. pristinus* e *M. magna* (Silva-Taboada, 1974), would support the hypothesis of a mainland ancestor in the Yucatán or Florida Peninsula and corroborate the important role of Cuba in the colonization and diversification of subgenus *Phyllodia* in the Greater Antilles. On the other hand, retention of *P. parnellii* from Jamaica as the basal lineage in the insular clade would support the dispersal model via Jamaica, as seems to be the case of *P. quadridens*.

The diversification history of *Pteronotus* in the Greater Antilles calls attention because of the disparate biogeographic patterns exhibited by Clades 2 and 4 in the region. While diversification process within Clade 4 resulted in divergent lineages for each island despite the recent colonization by its ancestor, species *P. quadridens* and *P. macleayi* (Clade 2) have been in Caribbean for a much longer period, at least 7 Myr, without significant genetic and cranial morphological differences among populations inhabiting distinct islands (Pavan and Marroig, 2016). This contrasting pattern suggests that non-geographic factors may be also playing a role in the speciation process within this genus.

4.4. Species groups differentiation in the Quaternary

The Quaternary is considered the pinnacle of mormoopid diversity, with two additional (extinct) species and several occurrence records of extant species outside their current ranges (Czaplewski and Cartelle, 1998; Morgan and Woods, 1986; Salles et al., 2014; Silva-Taboada, 1974;Velazco et al., 2013). According to our results, splitting between most of *Pteronotus* sister-species took place in the last 2.6 Myr and estimated dates of intraspecific diversification for *Pteronotus* lineages are younger than 0.35 Myr (Fig. 1 and Table 2).

During the Neogene, the Neotropics were characterized by significant palaeogeographic and tectonic reorganizations, leading to the emergence of new routes and barriers to biotic evolution. Differently, the main Quaternary environmental shifts were caused by climatic variation due to successive glacial–interglacial cycles (Rull, 2011). At this time, the Isthmus of Panama had completely emerged, allowing terrestrial fauna interchange between both continents. On the other hand, late Pliocene and Pleistocene in the lower Central America (Costa Rica and Panama) was marked by multiple biogeographic changes, with successive events of sea-level fluctuations affecting spatial and habitat composition at the region. Marine corridors have been formed in lowland areas, which may have limited dispersal of lower Central American populations and probably caused genetic isolation (Bagley and Johnson, 2014). Such events may have promoted divergence between *P. fulvus* and *P. davyi* at 1.6 Ma as well as acted on the diversification of Clade 4B (*P. fuscus*, *P. mesoamericanus* and *P. mexicanus*) around 1.3 Ma. Phylogeographic data of *P. fulvus* from Mexico points to decreased levels of genetic diversity in the higher latitudes of species range and a strong signal of demographic expansion at this region (Guevara-Chumacero et al., 2010), suggesting *P. fulvus* dispersed from south to north in Central America, reaching Mexico later in its evolutionary history.

Pleistocene sea-level fluctuations may also be related to the current biogeographic pattern exhibited by *Pteronotus* species in the Greater Antilles. The close proximity between the islands as a

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result of the lower sea level may have facilitated dispersal followed by speciation in *Phyllodia* insular clade, promoting divergence between *P. pusillus* and *P. portoricensis* around 1.15 Ma. In addition, this same factor can explain low values of intraspecific genetic divergence for *P. quadridens* and *P. macleayi*. Despite their long evolutionary history in the Greater Antilles, these species apparently have maintained gene flow among populations from distinct islands until less than 0.3 Ma. Also, Pleistocene records for *P. macleayi* and *P. quadridens* suggest these species exhibited wider ranges in the past (Morgan, 1989; Velazco et al., 2013).

Likewise, divergence between *P. rubiginosus* and *Pteronotus* sp1 seems to have occurred in the Amazon region around 1.5 Ma (Fig. 2). Several mechanisms promoting speciation in Amazon have been proposed, including geotectonic events, marine incursions, riverine barriers and pleistocenic refugia caused by climatic fluctuations (Antonelli et al., 2009). Similarly to the events in southern Central America, hot-humid sea-level rise cycles during late Pliocene and Pleistocene led to the flooding of the Amazonian lowlands several times in the last 2.5 myr (Marroig and Cerqueira, 1997; Campbell et al., 2006). This Amazon seaway or lagoon could have promoted isolation and differentiation at the highlands of Amazon basin (Fig. 1 of Marroig and Cerqueira, 1997), contributing to the current pattern of distribution of the two South American lineages of *Pteronotus* Clade 4.

The age of MRCA of all *Pteronotus* lineages, particularly those distributed in South America, are relatively young, suggesting one common factor acted over them in this time interval. Mormoopids in fact exhibit small tolerance to lower temperatures (Bonaccorso et al., 1992), and climatic oscillations throughout Quaternary age may have impacted negatively mormoopid populations across their ranges. Pleistocene fossils of mormoopids are known from several islands in West Indies (Morgan and Woods, 1986), suggesting mormoopid species once presented larger ranges than in the present, and population bottlenecks would explain low intraspecific genetic values found for many *Pteronotus* species (data not shown).

In summary, temporal and spatial diversification patterns in the genus *Pteronotus* suggest a complex biogeographic history for this group, requiring distinct models to explain cladogenesis events along the phylogeny. Our results suggest an important role of Central America in the early group diversification process, while Pleistocenic climatic oscillations and sea-level variation seems to be a general factor shaping recent diversity within the genus. Nevertheless, many biogeographic questions can only be addressed with a deeper knowledge on the species ranges and secondary contact zones. Most *Pteronotus* lineages belonging to the same clade seem to replace each other across the geography but some do exhibit geographic overlaps in their current distributions, which makes difficult inferences about their place and mode of speciation. Also, information about ecological preferences and specific environmental requirements that could be used to better recognize speciation process in the genus is scarce. Additional information is therefore necessary for understanding which phenomena may have acted as isolating barriers for this remarkable clade of bats.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ympev.2017.01.017.

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