Divergence in *Zygodontomys* (Rodentia: Sigmodontinae) and Distribution of Amazonian Savannas

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**Abstract**

Northern South America presents a diverse array of nonforest or savanna-like ecosystems that are patchily distributed. The distribution of these open habitats has been quite dynamic during Quaternary glacial–interglacial cycles; yet, the relevance of climatically driven vicariance events to the diversification of nonforest Amazonian vertebrates remains poorly known. We analyzed karyologic and mitochondrial DNA sequence data of the genus *Zygodontomys*, a small cricetid rodent distributed throughout nonforest habitats of northern Amazonia. Samples analyzed represented 4 Brazilian Amazonian localities and 2 French Guiana localities. Karyologic variation among Amazonian Brazilian *Zygodontomys* populations is high, with, at least, 3 karyomorphotypes. Molecular phylogenetic analyses recovered 3 major clades congruent with known karyotypes, a finding that suggests the existence of 3 species, 2 of which currently undescribed. The French Guiana and Surumã clade, identified as *Zygodontomys brevicuoda microtinus*, is characterized by 2n = 86 and is sister to the clade formed by the 2 undescribed forms. The Rio Negro–Rio Branco form is characterized by 2n = 82, and the Ferreira Gomes–Itapóa form is characterized by 2n = 84. The distribution of the 3 *Zygodontomys* lineages identified is in accordance with the geography of the open vegetation patches in Northern Amazonia, and divergence time estimates relate speciation events to the middle-upper Pleistocene, supporting the prominent role of Quaternary climatically driven vicariance events in the diversification of the genus.

**Key words:** amazonian savanna, phylogeography, *Zygodontomys*

The northern Amazonian region of South America presents a remarkably diverse array of nonforest or savanna-like ecosystems that are patchily distributed from Panama to the Brazilian states of Amapá, Roraima, and Amazonas. In the northern region of the Brazilian Amazon, these enclaves are found intermingled by rainforests or restricted to the highest summits across the Guyanan shield, presenting varying levels of geographic isolation. The distribution of these open habitats has been quite dynamic during the climatic cycles of the Quaternary, with repeated episodes of expansion during glacial periods and retraction on more humid interglacials (Haffer 1969; Vanzolini and Williams 1970; Haffer 2002). Although northern Amazonia has received an increasing attention from paleoecologists and geologists (e.g., Bush et al. 2004; Rosseti et al. 2005; Anhuf et al. 2006), the effects of the climatic cycling on the diversification of its vertebrates are little known. Morphological studies of mammalian genera and species complexes endemic to nonforest Amazonian ecosystems suggest a major differentiation between western and eastern groups of populations (Voss 1991), but no further resolution has been provided within these regions, specially regarding the levels of genetic divergence among populations.

The rodent genus *Zygodontomys*, a member of the tribe Oryzomyini sensu stricto (Voss and Carleton 1993; Steppan 1995; Bonvicino et al. 2003), inhabits open vegetation formations, including anthropogenic ones, in Central America and northern South America (Voss 1991). In Brazil, this species is a typical inhabitant of Amazonian “campinaranas,” a local designation of the grass savanna. The latest
 comprehensive review of the genus *Zygodontomys* considered only 2 species: *Zygodontomys brunneus* and *Zygodontomys brevicauda*, the latter with 3 subspecies. However, karyologic data (Gardner and Patton 1976; Reig et al. 1990) give support for the recognition of other species mentioned throughout this paper. Brazilian populations have not been allocated to any described taxa and were referred to as *Zygodontomys* sp. (Mattevi et al. 2002; Bonvicino et al. 2003).

Whereas the karyotype of *Z. brunneus* remains undescribed, several chromosomal complements have been attributed to *Z. brevicauda* subspecies, with diploid numbers of 84 or 88 and fundamental numbers ranging from 116 to 118 (Gardner and Patton 1976; Perez-Zapata et al. 1984; Reig et al. 1990; Bonvicino et al. 2003). Several chromosomal complements have been associated with *Zygodontomys brevicauda cherriei*, with diploid numbers ranging from 82 to 84 (Gardner and Patton 1976; Voss 1991). However, the actual chromosomal complement of this taxon is the one reported for the Costa Rica population (Gardner and Patton 1976). The karyotype of *Zygodontomys brevicauda microtinus* has not been formally described or illustrated, but Tranier (1976) reported a diploid number of 78 for French Guiana specimens without describing the morphology of the autosomal complement. Other 2 karyotypes have been attributed to this taxon but from localities far from its type locality (Reig et al. 1990; Gardner and Patton 1976).

Brazilian populations of *Zygodontomys* have, at least, 3 karyotypes reported up to date: the Rio Negro population (Amazonas state) with 2n = 82 and FN = 94; a population from Surumú (Roraima state) with 2n = 86 and FN = 96–98; and a population from Tararugalzinho (Amapá state) with 2n = 84 and FN = 96–98 (Mattevi et al. 2002; Bonvicino et al. 2003). This scenario suggests that the diversity of this genus is underestimated in Brazil, suggesting the existence of several evolutionary lineages.

In this paper, we examine whether the geographic isolation of open vegetation enclaves have influenced population- and species-level diversification in the genus *Zygodontomys* in the northern Brazilian Amazon. Karyomorphotypes and mitochondrial DNA genealogies (23 *Zygodontomys* specimens) are here used to delineate species limits and phylogeographic patterns, which are mapped onto the distribution of open vegetation formations in northern South America, in an attempt to evaluate possible links between the fragmentation of these formations and the speciation events within *Zygodontomys*.

**Materials and Methods**

*Zygodontomys* specimens were collected in 6 Brazilian localities from the states of Amazonas (localities 1 and 2), Roraima (localities 3 and 4), and Amapá (localities 5 and 6, Figure 1), as follows:

1) Igarapé Tucunáre, 00°09′72″N, 63°30′72″W [global positioning system (GPS)], a right-bank affluent of the Rio Caruá in tributaries of the Rio Aracá, a left-bank tributary of the middle Rio Negro, Barcelos: female Museu Nacional (MN) 69027 and male MN 69030;

2) Serra do Aracá, 00°54′05.7″N, 63°26′02.1″W (GPS), near Igarapé da Anta, a right-bank affluent of the Rio Aracá, Barcelos: female MN 69077 and male MN 6907;

3) Parque Nacional do Viruá, Caracará: 1) Serra do Preto (01°48′57″N, 61°07′40″W): females MN 70318 and 70330; males MN 70316, 70329, 70330, 70336, 70337, 70347, 70351, 70352, and 70364; 2) Near Road Perdida, Parque Nacional do Viruá, Caracará, female MN 70400; 3) Rio Branco, Campinho (0°57′34.7″S, 61°09′56.8″W): MN 70581 and 70582; 4) Lavrado Vista Alegre (01°42′18.1″N, 61°08′13.4″W) MN 70742 and 70747; and 5) Castanhál (01°30′34″N, 60°58′41″W) MN 70777;

4) Surumú (4°10′N and 60°30′W): male MN 65549 and female MN 65546; 2n = 86;

5) Fazenda Teimoso, Ferreira Gomes (01°17′N 50°48′W): male AN386 and female AN381; 2n = 84;

6) Fazenda Itapoá, Itapoá (km 380 of AP 156 road, 01°21′N 50°56′W): males AN612 and 615.

The vegetation of all sampled areas, except locality 2, grows on seasonally flooded white sand and is composed of natural grassland around 1-m high and sparse scrub vegetation of up to 3 m in height. Locality 2 is situated at an altitude of 1300 m, in a tabular plateau of the geological formation of Mount Roraima, covered with grassland

![Figure 1. Geographic provenance of samples analyzed in this study. Brazil, Amazonas state, Barcelos: (1) Igarapé Tucunáre and (2) Serra do Aracá; Roraima state: (3) Caracará and (4) Surumú; Amapá state: (5) Fazenda Gomes and (6) Itapoá; French Guiana: (7) Kourou and (8) Macouria. Black areas delimit *campinaranas*, gray area delimits savannas, and spotted area mangrooves as defined by Brazil (1975) and Olson et al. (2001). White squares are localities of *Zygodontomys* brunneus microtinus (2n = 86 and FN = 96–98, Mattevi et al. 2002), white circles are localities of *Zygodontomys* brevicauda cherriei (2n = 82 and FN = 94, this study), black circles are localities of *Zygodontomys* brevicauda microtinus (2n = 86 and FN = 96–98, Mattevi et al. 2002), and black and white circles are localities of sympatry.](image-url)
vegetation intermingled with riparian forest at margins of creeks and depressions.

The karyotypes of 4 specimens from Caracarai, Roraima state, listed above are first reported here; those from other locality samples used in the molecular analyses have been previously described (Mattevi et al. 2002; Bonvicino et al. 2003). Karyotyped specimens (2n = 86 and FN = 96–98) from Surumú, Roraima, previously identified as *Zygodontomys* sp. (Mattevi et al. 2002) and here analyzed, are herein referred to as *Z. b. microtinus*. Chromosome preparations were obtained in the field from bone marrow cultures in RPMI 1640 medium supplemented with 20% fetal calf serum, ethidium bromide (5 g/ml), and 10^{-6} M colchicine for 2 h. Estimates of fundamental number were restricted to autosome pairs. Voucher specimens are deposited in the mammal collection of the Museu Nacional (Universidade Federal do Rio de Janeiro) and Museu Paraense Emílio Goeldi (field numbers AN reported above).

DNA of 19 *Zygodontomys* specimens was isolated from livers preserved in 100% ethanol following the procedures of Sambrook et al. (1989). The complete cytochrome *b* gene was amplified with primers L14724 (Irwin et al. 1991) and MVZ14 (Smith and Patton 1993), being sequenced with the polymerase chain reaction primers plus 2 internal primers, MEU1 (5`-ACAACCATAGCAACAGCATTCGT-3`) and MVZ16 (Smith and Patton 1993), in an ABI Prism™ 377 automatic DNA sequence. Sequences were assembled and edited using the ChromasPro software (Technelysium Inc. 2006) and deposited in GenBank (accession numbers EU645578 and EU652749–EU652766). Sequence data gently offered by Dr François Cazetelis from 2 *Z. b. microtinus* specimens from French Guiana (localities 7 and 8 in Figure 1, which are nearer to the type locality of this species) and 2 specimens (GenBank AY029478 and AY029479) from Brazilian state of Amazonas were also included in this study, as well as those of *Hylaeamys megacephalus* (GenBank AF108695), *Neoconoctis albignula* (DQ179858), and *Soliomys serrampelinus* (AF108706), used as outgroups in phylogenetic analyses based on previous phylogenetic hypotheses for the group put forward by Steppan et al. (2004).

Maximum parsimony (MP) analyses were implemented in PAUP 4.0b10 (Swofford 2001) with heuristic searches using the tree bisection reconnection branch-swapping algorithm and starting from 100 random sequences of taxon addition. Confidence intervals for parsimony trees were estimated on the basis of 1000 bootstrap replications (Felsenstein 1985), in which heuristic searches were based on 10 taxon addition sequences. Maximum-likelihood (ML) analyses were carried out using GARLI 0.95 software (Zwickl 2006), which implements a genetic algorithm to rapidly optimize the topology, branch lengths, and model parameters. The most appropriate model of DNA evolution fitting the data was selected using ModelTest 3.7 (Posada and Crandall 1998), and its corresponding estimated parameters were fixed during likelihood tree searches. A likelihood ratio test was performed to evaluate whether the best model differed significantly from a clock-like model. Confidence intervals for trees found under this ML approach were also estimated by bootstrap with 1000 replicates in GARLI 0.95. The topologies generated by different methods were compared through a Shimodaira–Hasegawa (SH) test (Shimodaira and Hasegawa 1999), using full optimization with 1000 bootstrap replicates to generate a null distribution of the likelihood difference statistic.

Kimura 2 parameters (Kimura 1980) were used to calculate pairwise sequence divergence between cytochrome *b* haplotypes using MEGA 4 (Tamura et al. 2007). In addition to genetic distances, summary statistics of intraspecific molecular diversity were also calculated. The nucleotide diversity (*π*) and the number of polymorphic sites were computed directly from the sequence alignment entered using ARLEQUIN 3.1 (Excoffier et al. 2005). The population diversity parameter θ (θ = N_0μ), representing the product of population size and neutral mutation rate, was estimated using the ML coalescent approach implemented in MIGRATE 2.4.3 (Beerli and Felsenstein 1999; Beerli 1997–2004). We estimated divergence times between sister species using the genealogical approach implemented in the program IMA (Hey and Nielsen 2007). The software employs a Markov chain Monte Carlo procedure to sample across genealogies, generating a marginal distribution of the posterior probabilities for the parameters of an isolation-with-migration model of divergence (Hey and Nielsen 2004). This model assumes that some gene flow may have occurred during the divergence of sister lineages from a common ancestor and thus include parameters of time since divergence scaled by the mutation rate (*i = T/μ*), population genetic diversity of contemporary sister species and their ancestor (*θ_1, θ_2, and θ_0*), and asymmetric migration rates (*m_1* and *m_2*). Our initial runs with the full model parameters readily showed that parameter estimates did not converge or were inconsistent across multiple runs (flat probability distributions), probably because the cytochrome *b* data set did not have enough sample sizes to provide consistent estimates of the large number of parameters of the isolation-with-migration model. Therefore, we simplified the model by excluding the migration parameters and run the analyses under a simpler isolation model, which fitted the data better, providing more consistent and convergent estimates across multiple runs. Furthermore, the geographic isolation of patch of savannah by extensive areas of forested areas reinforces the plausibility of the isolation model. We run 10 Metropolis-coupled Markov chains of 5 million steps each, repeating the analysis multiple times and thoroughly investigating the effects of prior parameter values. We chose the rate of 0.023 substitution per site per million years (My), which was calibrated by Smith and Patton (1993) on the basis of the fossil record for the subfamily Sigmodontinae (the splitting between *Akodon* and *Necromys*), a calibration point phylogenetically closer to *Zygodontomys*.

**Results**

Karyotypic analyses of 9 specimens (females MN 70400 and males MN 70330, MN 70337, MN 70347, MN 70351,
Figure 2. Conventional Giemsa staining of *Zygodontomys* sp.2 (male MN 70352), 2n = 82 and FN = 94, from Parque Nacional do Viruá, Caracaraí, Roraima state, Brazil. Sex chromosomes are depicted to the right, the larger being the X chromosome and the smallest the Y chromosome.

MN 70352, MN 70742, MN 70747, and MN 70777) from Caracaraí showed 2n = 82 and FN = 94 (Figure 2). The autosome complement is composed by 7 pairs of biarmed chromosomes (2 large and 5 varying in size from medium to small) and 33 pairs of acrocentric chromosomes varying in size from medium to small (Figure 2). The X chromosome is a large submetacentric and the Y chromosome is a small chromosome.

The complete cytochrome *b* (1.144 bp) of 17 specimens (16 haplotypes) and 1.026 bp of 3 specimens were here sequenced. Analysis of 20 *Zygodontomys* specimens sequenced here, 2 gently provided by Dr F. Catzflis and 2 from GenBank, showed 430 variable sites, 252 of which were parsimony informative. The MP and ML trees displayed basically the same topology with no statistically significant differences (SH test: ln L difference = 21.31, P = 0.102). The MP analyses recovered 63 equally parsimonious trees of 667 steps (consistency index = 0.7991, retention index = 0.7929), whose consensus differed from the ML only in the lack of resolution within more exclusive clades of haplotypes within localities. Therefore, only the ML tree is shown in Figure 3 portraying the bootstrap nodal support values of both analyses. The selected model fitting the data performed significantly worse when a clock-like pattern of evolution was enforced (A = 24.4186, degrees of freedom = 23, P < 0.005).

All analyses consistently recovered the monophyly of *Zygodontomys* (bootstrap 100%, Figure 3), divided into 2 major clades. One clade (bootstrap values 99% and 96%, respectively), here ascribed to *Z. b. microtinus*, consists of haplotypes from French Guiana and Surumú and one haplotype from Itapoá. The second clade (bootstrap values 99% and 78%) is further divided into 2 subgroups, herein referred to as *Zygodontomys* sp.1 and *Zygodontomys* sp.2. *Zygodontomys* sp.1 exclusively includes haplotypes from Amapá state in the localities of Ferreira Gomes and Itapoá, where it is sympatric with *Z. b. microtinus*, as revealed by molecular analyses (bootstrap values of 100% and 99%). *Zygodontomys* sp.2 is formed by Rio Negro and Rio Branco (Caracaraí) haplotypes, which although consistently recovered in MP analysis (bootstrap value 85%) has low nodal support in ML analysis. *Zygodontomys* sp.2 is further structured in 2 geographic

Figure 3. ML topology depicting phylogenetic relationships among cytochrome *b* haplotypes in *Zygodontomys* from northeastern Amazon. The best tree (ln L = −4552.5297) was selected with the following parameters of a general time reversible model: mutation rate matrix 3.6758 (AC), 7.7132 (AG), 2.1494 (AT), 1.1862 (CG), 13.6859 (CT), and 1 (GT); base frequencies $A = 0.3093, C = 0.2944, G = 0.1170$, and $T = 0.2794$; gamma-distributed rates with $\alpha = 0.3771$. Numbers near nodes represent bootstrap support values for groups obtained under parsimony and likelihood analyses, respectively (only values above 50% are shown). BR, Brazil, FG, French Guiana. Symbols refer to Figure 1.
groups, one comprised by Rio Negro haplotypes (bootstrap value 73%) and the other by Caracaraí haplotypes (bootstrap values 92% and 72%). A large concordance is found between karyotypes and mitochondrial clades (Figure 3). Karyotyped specimens with 2n = 82 and FN = 94 grouped in the *Zygodontomys* sp.2 clade, whereas specimens with 2n = 84 and FN = 96–98 grouped in *Zygodontomys* sp.1. *Z. b. microtinus* is also karyologically distinct and characterized by 2n = 86 and FN = 96–98.

Interlineage pairwise genetic divergences vary from 2.4% to 6.7% among the species analyzed. The deepest divergence is presented in comparisons between *Z. b. microtinus* and the Brazilian species (*Zygodontomys* sp.1 and *Zygodontomys* sp.2), varying from 4.3% to 6.7%. *Zygodontomys* sp.1 and *Zygodontomys* sp.2 haplotypes differ by 2.4% to 3.5%. Sympatric individuals of *Z. b. microtinus* and *Zygodontomys* sp.1 at the locality of Itapoaí differ by 5% of sequence. Intraspecific mean genetic distances were 1.7% (0.1–2.5%) for *Z. microtinus* haplotypes, 0.5% (0.4–0.7%) for *Zygodontomys* sp.1, and 1.2% (0.1–2.7%) for *Zygodontomys* sp.2. Despite the limited intraspecific sampling, 26 haplotypes could be identified among the samples, revealing a moderate level of polymorphism within species. The highest levels of molecular diversity were found in *Z. b. microtinus* (π = 0.016, θ = 0.0285) and *Zygodontomys* sp.2 (π = 0.012, θ = 0.0193), which were 2- to 4-fold higher than the polymorphism found in *Zygodontomys* sp.1 (π = 0.005, θ = 0.0065).

**Discussion**

Karyologic variation in Brazilian populations of *Zygodontomys* is high, with, at least, 3 karyomorphotypes reported so far (Mattevi et al. 2002; Bonvicino et al. 2003). The 2n = 82 and FN = 94 karyotype here described for specimens from Caracaraí is similar to that reported for Rio Negro specimens (Bonvicino et al. 2003). This karyotype differs from the other 2 chromosome complements described for Brazilian populations with 2n = 84 and FN = 96–98 for specimens from Ferreira Gomes and 2n = 86 and FN = 96–98 for specimens from Surumú (Mattevi et al. 2002). Moreover, these karyotypes are also different from those described from non-Brazilian populations, strengthening the evolutionary uniqueness of the Brazilian populations.

The association of *Zygodontomys* karyotypes to nominal forms in this genus is not clear. Other karyotypes have been attributed to *Z. b. microtinus*, also in Venezuela, 2n = 88 from Isla Guara, isolated from continental populations with 2n = 84, suggesting that each of these karyotypes was fixed rather than polymorphic (Reig et al. 1990). Karyotypes of 2n = 78 (Tranier 1976) and 2n = 84 (Reig et al. 1990) have also been referred to *Z. b. microtinus* in French Guiana. In the same way, more than one chromosome complement have been attributed to *Z. brevicauda*, 2n = 84 for specimens from one locality of Costa Rica (Gardner and Patton 1976), 2n = 82 for specimens from another locality in the same country (Voss 1991), and 2n = 82 and FN = 116 for the Venezuelan population of Misión Tukuko (Bonvicino et al. 2003).

Notwithstanding the above efforts in karyologic sampling, the correct chromosome complement of *Z. brevicauda* is still unknown (Bonvicino et al. 2003). Molecular phylogenetic analyses depicted a perfect match between mitochondrial clades and karyotypes, adding support to the fact that at least 3 evolutionary lineages should be recognized among *Zygodontomys* populations analyzed here. The molecular data also indicated sympathy between *Z. b. microtinus* and *Zygodontomys* sp.1 from Itapoaí, representing direct evidence of species-level distinctiveness of these lineages. However, the possibility of hybrids cannot be discarded, and karyologic and/or nuclear data analyses are needed to confirm this hypothesis. Nevertheless, karyologic differences between *Z. b. microtinus* (2n = 86 and FN = 96–98) and *Zygodontomys* sp.1 (2n = 84 and FN = 96–98) are sufficient for excluding the possibility of fertile hybrids. Deriving one karyotype from another requires one tandem fission (or fusion). This rearrangement is rather drastic and relevant for establishing reproductive barriers due to meiotic abnormalities in hybrids. The 2n = 84 and 2n = 82 lineages refer to 2 apparently undescribed species, in as much as the clade formed by Surumú–French Guiana–Itapoaí is referable to *Z. b. microtinus*, based on the proximity to the type locality of this species, in Suriname.

The distribution of the genus *Zygodontomys* is closely linked to the current distribution of open phytophysiognomies of northern South America (Voss 1991). Detailed paleopalinological information covers only the last 30 000 years (encompassing the last glacial maximum—Flinley 1998; Anhuf et al. 2006), but an expansion–fragmentation cycle of savannas was a recurrent phenomenon during the last 2 My (Bennett 1990), promoting repeated opportunities for geographic isolation and differentiation of populations of *Zygodontomys*. The central question is whether species-level divergence in the genus is a legacy of Quaternary fragmentation episodes or was rather a consequence of previous events in the Tertiary. If speciation in *Zygodontomys* was prompted by climatically driven fragmentations of savannas during warmer and more humid interglacial periods, the divergence between sister species should date back to a specific interglacial period. In order to test this expectation, we estimated the divergence times between sister species pairs following a genealogical–coalescent approach (Hey and Nielsen 2004). According to these estimates, *Zygodontomys* sp.1 and *Zygodontomys* sp.2 diverged from a common ancestor approximately 670 thousand years ago, as given by the highest probability point estimate (Figure 4). This estimate is associated with a wide 90% confidence interval of 633 750 years (348 550–982 300 years) but corroborates the splitting of the Brazilian species at the upper Pleistocene. The split between *Z. b. microtinus* and the common ancestor of the 2 Brazilian species is older, dating approximately 1.16 Million years ago at the mid-Pleistocene (Figure 4b), and is associated with a broader 90% confidence interval of 880 000 years (0.56–1.44 My).

These results do corroborate a Quaternary divergence among the species analyzed, most likely occurring between mid- and upper Pleistocene. However, the broad confidence
intervals associated with divergence estimates do not allow the identification of specific interglacial periods. Recent studies have questioned the influence of Quaternary climatic oscillations on the origin of vertebrate species diversity in Amazonia, dating speciation events to older periods in the Tertiary and relating them to geological rather than climatic changes (e.g., Patton et al. 2000; Bates 2001; Rosseti et al. 2005). These studies, however, are focused on the forest fauna of western Amazonia, a region that has experienced little ecological instability during the glacial–interglacial cycles (Colinvaux et al. 1996; Bush et al. 2004; Anhuf et al. 2006). The scenario for northern Amazonia seems to indicate that Quaternary climatic changes had a major influence in the species-level diversification in the Amazonian campinaranas, probably giving rise to a still overlooked diversity of vertebrates.

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