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Biogeography and Evolution of Neotropical Small Mammals, with Emphasis on Hystricognath Spiny Rats of the Genus Proechimys (Family Echimyidae)

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Genus *Proechimys* (Family Echimyidae)

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ABSTRACT

Biogeography and Evolution of Neotropical Small Mammals,
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The Neotropical region is the most biologically diverse region on the planet. The region encompasses a variety of ecosystems and has long been the target of researchers interested in patterns of species diversity and distribution. More recently, molecular data have been incorporated into methods for reconstructing the historical relationships among geographical areas and their biotas. Molecular phylogenetics has provided insights into diversification patterns and the influence of Late Cenozoic events on the evolutionary history of the region. Nevertheless, considering the vast extent and complexity of the region, more studies are needed to fully appreciate the patterns of biogeography and the mechanisms that generate and maintain its biodiversity. Therefore, in Chapter 1 I employed molecular methods to reconstruct the phylogenetic relationships of the subfamily Sigmodontinae, which is the most diverse and widespread radiation of Neotropical rodents. I was able to evaluate controversial hypotheses about the paleogeographic scenarios implicated to explain the biogeography of sigmodontines. Advances in sequencing technology and analytical approaches have revolutionized the role of historical biogeography in elucidating the spatial and temporal context of diversification, and the integrative field of phylogeography was fundamental to the development of biogeography at the intraspecific level. However, the potential of phylogeography to unravel diverse historical scenarios in a tractable statistical framework has been largely unexplored for the Neotropics as a whole. In order to integrate more robust hypothesis testing to elucidate the evolutionary history of Amazonia's biota, I devoted Chapter 2 to a review of Amazonian phylogeography that I anticipate will improve the basis for interpreting the patterns and processes of diversification in Amazonia. Chapter 3 is a thorough species account of spiny rats of the genus *Proechimys*, which is poorly known taxonomically despite its diversity and widespread distribution in the Neotropics. This taxonomic revision will benefit researchers interested in using such information with coalescent-based methods of species delimitation aimed at an integrative and stable taxonomy. Lastly, Chapter 4 deals with the phylogeography of *P. roberti*. This species occurs in southeastern Amazonia and the Cerrado of central Brazil. I employed a dense taxon sampling and used coalescent-based methods to demonstrate that rivers and topography have a causal link to the geographic structure of *P. roberti* populations. In my dissertation, I used a combination of molecular genetics tools to provide a better understanding of the biogeography and evolution of some of the most diverse groups of Neotropical mammals. My dissertation interacts in many levels with my future research interests. These present and future efforts hold promise for unraveling the evolutionary history of the Neotropical region and its biota, and will assist in conservation decisions aiming at preserving its unparalleled biodiversity.

Keywords: diversification, coalescent, hypothesis testing, rodents, statistical phylogeography, *Proechimys*, taxonomy, South America, Amazon Basin

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INTRODUCTION

The Neotropics form a vast biogeographic region that includes South and Central America, southern Mexico, the Caribbean and southern Florida (Olson *et al.* 2001). This is the most biologically diverse region on the planet, which shares a large number of biotic groups and encompasses a variety of ecosystems such as deserts, grasslands, scrublands savannas, montane forests, and lowland rainforests. The biodiversity of the Neotropical region has long been the target of scientific investigations that sought to define biogeographic units and their historical relationships based on distribution patterns of the biotic component (Morrone 2001). Molecular data also have been incorporated as a perspective for reconstructing the historical relationships among geographical areas and their biota because they constitute powerful tools for analyzing patterns of species diversity and distribution (Crisci *et al.* 2003). Likewise, combining molecular approaches and biogeography provides a more objective basis for developing conservation strategies (Purvis *et al.* 2005).

The Neotropical region exhibits a regionally complex geological history that involved drastic landscape changes within the relatively recent time-scale of the Neogene (e.g., Duque-Caro 1990; Hoorn *et al.* 2010). For instance, these paleogeographic events which arguably acted as drivers of diversification include the onset of the transcontinental Amazon River and its modern drainage due to an increased Andean uplift (Figueiredo *et al.* 2009), and the completion of the Isthmus of Panama that connected previously isolated biotas in North and South America (Woodburne 2010). Neotectonics (Costa *et al.* 2001; Latrubesse & Rancy 2000) as well as climatic (Zachos *et al.* 2001) and eustatically controlled sea-level (Miller *et al.* 2005) fluctuations during the Late Tertiary–Quaternary also have had an impact on the present-day patterns of species diversity and distribution in the Neotropics (Aleixo & Rossetti 2007;

Antonelli *et al.* 2010; Jaramillo *et al.* 2006; Rossetti *et al.* 2005). Molecular phylogenetics has enabled inferences of divergence dates and ancestral areas from DNA sequence data which provided important insights into the temporal and spatial patterns of diversification and the influence of Late Cenozoic events on the evolutionary history of the Neotropical region (e.g., Antonelli *et al.* 2009; Pinto-Sánchez *et al.* 2012). Similarly, comparative phylogenetics were used to investigate the tempo and mode of biotic evolution related to major paleogeographic events (e.g., Weir *et al.* 2009). Nevertheless, considering the vast extension and complexity of the region, the majority of which is insufficiently surveyed, many more studies are necessary to fully appreciate the patterns of biogeography and the mechanisms that generate and maintain its unparalleled biodiversity.

Therefore, in Chapter 1 I employed molecular phylogenetic methods to reconstruct the relationships among rodents of the subfamily Sigmodontinae, which is the most diverse and widespread radiation of Neotropical mammals. It is well established that sigmodontines originated in North America, however much debate exists about the timing and origin of their diversification, and the number of ancestral lineages involved in the invasion of the South American continent. By using divergence time estimates based on multiple fossil calibrations and ancestral area reconstructions I was able to evaluate competing hypotheses about the historical biogeography of sigmodontines and the paleogeographic scenarios implicated to explain their diversification; in particular, the role of the Great American Biotic Interchange (GABI). In addition, I examined if significant shifts in diversification rates occurred along major sigmodontine lineages using comparative methods. The bridging of the Central American seaway and episodes of low sea level likely facilitated the invasion of South America well before the onset of the GABI. Moreover, the tempo of diversification across most nodes is

comparatively modest considering the Miocene origin of the sigmodontine radiation, except for significant rate increases in two akodontine genera (*Akodon* and *Oxymycterus*). This Chapter will be submitted to the journal *PLOS ONE*.

The growth of molecular-based approaches has been accompanied in recent years by advances in sequencing technology (Brito & Edwards 2009; McCormack *et al.* 2012; Thomson *et al.* 2010) as well as the development of methodological approaches (Corl & Ellegren 2013; Knowles 2004; Liu *et al.* 2009) that explicitly incorporate the stochasticity inherent to the coalescent process while inferring historical relationships above or within the species level. These new analytical tools now accommodate multilocus molecular datasets and can incorporate information from related biological and Earth science disciplines, which have revolutionized the role of historical biogeography in elucidating the spatial and temporal context of diversification (Riddle *et al.* 2008). The integrative field of phylogeography was fundamental to the development of biogeography within the intraspecific venue because of the bridge between phylogenetics and population genetics that allowed evolutionary processes to be considered in a tractable statistical framework (Hickerson *et al.* 2010).

Nevertheless, phylogeographic studies concerned with species-rich regions in the southern hemisphere are as yet underrepresented (Beheregaray 2008). Despite that fact, phylogeography has brought important contributions to understanding the patterns and processes of diversification in various South American ecosystems (Turchetto-Zolet *et al.* 2013). However, the potential of phylogeographical methods to unravel diverse historical scenarios via an explicit hypothesis-driven framework has been largely unexplored for the region as a whole, although there is a growing interest in doing so (e.g., Carnaval *et al.* 2009; Fouquet *et al.* 2012; Torres-Pérez *et al.* 2011; Werneck 2011). Moreover, the intricate geological history of the Neotropical

region necessitates more detailed and multidisciplinary biogeographic investigations that can take advantage of statistical phylogeographic approaches.

In such a context, the link between paleoenvironmental changes in the Amazon Basin, harboring one of the richest biota on Earth, and the evolutionary mechanisms promoting and maintaining its remarkable biodiversity remains elusive despite the fact that several diversification hypotheses have been formulated to explain biogeographic patterns in the region. Therefore, in light of the need to integrate more robust hypothesis testing to elucidate the historical evolution of Amazonia's biota, I devoted Chapter 2 to a review of Amazonian phylogeography focusing on terrestrial vertebrates. I contextualized the paleogeographic settings underpinning the major diversification hypotheses, reviewed each of these hypotheses, and provided expanded predictions. I presented summaries of a number of phylogeographic studies and their geographical focus with respect to areas of endemism as well as their choice of genetic markers and analyses. In addition, I proposed future directions for devising and testing hypotheses and gave an empirical example (using spiny rats as a model) to illustrate how paleoenvironmental data can be incorporated to build alternative biogeographic hypotheses *a priori*. Finally, I discussed the prospects for phylogeographic research in Amazonia and suggest areas for new surveys. I anticipate that this review paper, which is in press in the journal *Organisms Diversity & Evolution,* will improve the basis for interpreting the patterns and processes of Amazonian diversification.

The revolution of biogeography fueled by the expanding role of molecular genetics (Riddle *et al.* 2008) is expected to increase the discovery rate of species that are cryptic and/or inadequately surveyed (e.g. Ceballos & Ehrlich 2009) and the stability of taxonomic assessments owing to a more objective testing of species boundaries (Fujita *et al.* 2012). This is particularly

relevant for Neotropical rainforests, which harbor the greatest amount of undescribed species on the planet (Giam *et al.* 2011). Importantly, the ability to consistently resolve the limits among cryptic species will depend on other types of information available (e.g., morphological and ecological data) (Bickford *et al.* 2007) for an integrative taxonomy that uses new coalescent-based tools (Fujita *et al.* 2012), but also incorporates comparable character-based species names (Bauer *et al.* 2010).

In Chapter 3, a book chapter that I co-author with James L. Patton, an accounts for all species of spiny rats in the genus *Proechimys* are provided. This genus is the most species-rich in the family Echimyidae (infraorder Hystricognathi), primarily inhabiting lowland rainforests (< 2,000 meters in elevation) of Central America and Amazonia, with some species that occur in seasonally dry tropical forests and gallery forests of northern Venezuela and Colombia, southwestern Bolivia and northern Paraguay, and the Cerrado of central Brazil. Despite its diversity and widespread distribution, the genus is taxonomically one of the most poorly known groups of Neotropical mammals. 22 valid species names of *Proechimys* within 10 species groups are recognized, for which detailed diagnoses, dichotomous identification keys, distribution maps as well as remarks on natural history, taxonomy and systematics are also provided. With this taxonomic revision, the stage is set for future studies that will incorporate this information with coalescent-based methods of species delimitation; aiming at an integrative approach that seeks to stabilize the taxonomy of this diverse group via objective testing of hypotheses of evolutionary independence for *Proechimys* species and species groups. This Chapter is in press In: *Mammals of South America, Volume 2*. University of Chicago Press, Chicago.

Finally, I dedicated Chapter 4 to examining the phylogeography of *P. roberti*, a taxon that occurs in southeastern Amazonia and the Cerrado of central Brazil. I employed a dense

taxon sampling in terms of both geographic coverage and molecular markers—I designed new primers and novel markers that can be applied to other echimyid and hystricognath rodents. I used coalescent estimates of splitting times and gene flow between populations to examine the influence of major rivers and relief variation on the genetic structuring of *P. roberti*. In addition, I explored the dispersal history of *P. roberti* by applying a spatially explicit Bayesian continuous diffusion model and paleodistribution modeling. I also used a coalescent-based simulation approach to test alternative hypotheses of population structure built using external paleoenvironmental data. I demonstrated that rivers and topography have a causal link to the geographic structure of *P. roberti* populations. For instance, gene flow estimates indicated that rivers act as isolating barriers, whereas variation in relief within interfluves is responsible for isolation with migration. I rejected the hypothesis that more recent (Late Pleistocene) fault reactivation had a significant impact on the population structure of *P. roberti*. Nevertheless, neotectonic events seem to have played an important role in the evolutionary history of these spiny-rats during the Late Tertiary–Quaternary as dispersal routes inferred by the continuous diffusion model tracked the general orientation of fault zones in southeastern Amazonia. According to this model and the paleodistribution modeling, favorable environmental conditions for the establishment of *P. roberti* populations probably existed throughout the Plio-Pleistocene. This Chapter will be submitted to the journal *Molecular Ecology*.

In summary, in my dissertation I investigated the biogeography and evolution of some of the most diverse groups of Neotropical mammals under different hierarchical levels (i.e., above and within species) and using a combination of molecular genetics tools that provided a better understanding of the evolutionary history of these groups. I revisited the Amazonian phylogeography focusing on a hypothesis-driven approach to deal with patterns and processes of

diversification in the Amazon Basin, and the taxonomic status of the genus *Proechimys* also is provided. I developed new primers and novel molecular markers to take advantage of multilocus dataset and coalescent-based parameter estimation to provide a clearer view of the demographic history of *P. roberti* and its relation with the formation history of southeastern Amazon Basin. I expect that my doctoral research will encourage further studies in the Neotropical region interested in, for example, macroevolutionary patterns of trait evolution (e.g., morphological characters and partitioning of ecological resources); integration of geological and GIS-based data (e.g., SRTM imagery) to test biogeographic hypotheses of historical scenarios involved in the Late Tertiary–Quaternary landscape formation; and investigation of adaptive selection in populations diverging with the presence of gene flow (e.g., within interfluves).

More specifically, my dissertation components interact in many levels with my future research directions. During my doctoral studies I secured funding that allowed me to collect additional sequence data which I will use to develop studies of comparative phylogeography to test for simultaneous diversification of two co-distributed spiny rats in the Guiana region (*P. guyannensis* and *P. cuvieri*); coalescent-based species delimitation of the genus *Proechimys* integrated with morphological and karyological data; and comparative phylogenetics to link the evolution of morphological characters and ecological requirements with the phylogeny of *Proechimys*. These present and future efforts have promising perspectives for a collaborative research program engaged in unraveling the history of the Neotropical region and the biogeography and evolution of its biota, and will assist in conservation decisions aiming at preserving its biodiversity.

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CHAPTER 1

In the wake of invasion: tracing the historical biogeography of the South American cricetid radiation (Rodentia, Sigmodontinae)

Manuscript formatted for submission to the journal *PLOS ONE*

Short title: Biogeography of the sigmodontine radiation

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Abstract

The Great American Biotic Interchange (GABI) was triggered by the completion of the Isthmus of Panama (~3.5 Ma) and influenced the composition of modern faunal communities in the Americas. However, the contribution of preceding events has been comparatively less explored, even though waif dispersals are evidenced by early immigrants in the fossil mammal records. The cricetid rodents of the subfamily Sigmodontinae are a classic example of a species-rich South American radiation resulting from an earlier episode of North American invasion. We use a mitochondrial and nuclear dataset and employ divergence time estimation, dispersal-vicariance analysis and phylogenetic comparative methods to provide a temporal and spatial framework for understanding the evolutionary history of this rodent subfamily. We address key aspects about the historical biogeography and diversification of sigmodontine rodents and assess paleogeographic scenarios proposed by early authors based on fossil data. Relaxed-clock time estimates indicate that divergence of the Sigmodontinae begun in the middle–late Miocene (12.3–11.2 Ma), while ancestral distributions support the arrival of a single ancestral lineage in northern South America. The Oryzomyalia diversified between 10.6 and 9.5 Ma, followed by the radiation of main tribes during the late Miocene to early Pliocene. Differentiation of tribes took place initially in eastern South America and multiple dispersals into the Andes promoted further diversification that accounted for the majority of modern genera. A comparatively modest background tempo of diversification across most nodes explains the sigmodontine extant diversity; except for two akodontine genera (*Akodon* and *Oxymycterus*) that more recently experienced increased rate shifts. The bridging of the Central American seaway and episodes of low sea levels likely facilitated the invasion of South America long before the onset of the GABI. Moreover, species richness overall represents what is expected for the sigmodontine radiation given the Miocene origin of this rodent clade.

Keywords

Introduction

The Great American Biotic Interchange (GABI) is one of the major biogeographic events that shaped modern faunal communities in the Americas. It involved significant dispersal episodes of a number of taxa between North and South America [1] that were triggered by the completion of the Isthmus of Panama at around 3.5 million years ago (Ma) [2-4]. The GABI involved mingling of mammals [5,6], birds [7,8], reptiles and amphibians [9,10], arthropods [11,12], and freshwater fishes [13], yet reorganization of faunal assemblages resulting from this biotic upheaval is most strikingly observable in the mammalian fossil record [14]. Overseas dispersals prior to the main pulses of the GABI starting at ~2.7 Ma also had an impact on the composition of terrestrial mammal communities as evidenced in mammal-bearing units of North and South America [15]. The first of these records correspond to ground sloths that arrived in North America ca. 9 Ma [16] and a procyonid carnivore in South America ca. 7.3 Ma [17], or possibly a gomphothere proboscidean in South America ca. 9.5 Ma [18]. However, these dates can serve only as minimum ages for initiation of the exchange of land mammals [19].

The Miocene collision between the South American continent and the Panama arc along the southwestern margin of the Caribbean Plate marks the beginning of the uplift of the Central American isthmus [20,21]. Coates et al. [20] interpreted open marine facies of abyssal to lower bathyal depths as part of a precollisional setting, and a regional unconformity as signaling the onset of the collision at 12.8 Ma. Farris et al. [21], on the other hand, proposed that the collision with northwestern South America began at 23–25 Ma on the basis of distinct geochemical changes in arc rocks. Widespread shallowing-upward deposition resulted in complete docking of the Panama volcanic arc with South America by late Miocene, and with continued intraplate deformation the Central American isthmus became extensively emergent [20]. This peninsular

configuration greatly reduced the width and depth of the Central American seaway [22], although interoceanic circulation between Pacific and Caribbean waters through the Atrato strait in northwestern Colombia [3] lasted until the final closure of the Central American isthmus at ~3.5 Ma [4,23].

Paleogeographic models that explain patterns of land mammal dispersal and diversification, as well as the influence and underlying causes associated with tectonics, past vegetation dynamics, and fluctuating climate and sea level have been the target of continued research in the last few decades [e.g., 14,19,24,25-27]. Correlation of land mammal dispersal with chronology of fluctuating sea level is somewhat indefinite and thus difficult to discern [19]. Nevertheless, a number of eustatically-controlled episodes of sea level lowstand since the mid-late Tertiary [28,29] might have facilitated trans-isthmian land mammal movements regardless of the presence of an overland corridor. In addition, paleoclimatic variations produced distinct floral distribution patterns during the late Cenozoic [30,31] that provided differential opportunities for dispersal of land mammal taxa associated with specific plant communities. As a result, the paleogeography of southern Central America presented environmental conditions that would have favored land mammal dispersal prior to complete closure of the Isthmus of Panama [19].

The interchange between land mammals from North and South America involved dispersal dynamics within a generally recognized biotic framework [14]. As a consequence of asymmetrical speciation and extinction rates between northern and southern contingents [6], more than half of the present-day mammalian genera in South America were derived from northern immigrants, contrasted with only 10% of North American genera that have southern ancestry [32]. Therefore, the impacts of pre- and post-isthmian closure dispersal events strongly

influenced the modern composition of South American mammalian fauna [33]. Nevertheless, additional data are necessary to refine historical scenarios at broader resolutions.

In this context, cricetid rodents of the subfamily Sigmodontinae are a classic example of southward invasion followed by a South American radiation. Sigmodontines comprise the second-largest subfamily of muroid rodents in the world and are the most diverse group of Neotropical mammals [34]. Their members possess a range of ecomorphological adaptations to arboreal, terrestrial, fossorial and semi-aquatic life styles, and have successfully occupied a variety of habitats such as tropical and subtropical forests, savannas, grasslands and deserts [35]. The diversification patterns of this impressive mammalian group have been a topic of debate since the early 1950's. Three alternative hypotheses have been advanced to explain the historical biogeography and diversification of the Sigmodontinae, which depart from each other mainly with regard to the timing of arrival in South America and degree of ancestral differentiation.

Based on fossil data, Simpson [36,37] proposed that the sigmodontine invasion took place relatively recently, as part of the GABI. Patterson and Pascual [38], Baskin [39], and Jacobs and Lindsay [40] supported this view by arguing that the majority of sigmodontine ancestral lineages evolved in Central America and southern North America during the late Miocene, because many forms of Miocene and early Pliocene age are presumptively assigned to the Sigmodontinae. This scenario suggests that after the initial *ex situ* differentiation at the generic level an explosive radiation took place once sigmodontines crossed the land bridge and reached the previously isolated South American continent.

On the other hand, Hershkovitz [24,41], Savage [42], and Reig [43-47] postulated that, in order to explain the extraordinary differentiation of the subfamily in South America, an ancestral lineage must have invaded the continent by overseas dispersal well before completion of the

isthmian corridor, during the early–middle Miocene. These authors noted that sigmodontine

fossil records are fragmentary and poorly represented in Miocene strata of North and Central

America, and there is no solid evidence for an alleged *in situ* sigmodontine radiation prior to

southern invasion by an overland route. Hershkovitz and Reig further reasoned that the oldest

fossil remains from Argentina resemble forms of extant genera too advanced to represent the first

invaders, which suggests an older presence of sigmodontines in South America despite an

absence of Miocene records. Moreover, the earliest known fossils at that time [but see 48,49,50]

described by Reig [44] as *Auliscomys formosus* and *Necromys bonapartei*, respectively from the

Montehermosan and lower Chapadmalalan stages, ca. 5–4 Ma and 4–3.5 Ma [after 51],

contradicted Simpson's classic hypothesis given their presence in South America prior to the

Panamanian overland connection.

Marshall [26] advanced a hypothetical model that attempted to reconcile the first known

appearance of sigmodontine and stem members in the fossil records of both North and South

America. According to Marshall, sigmodontines evolved in North America before 7 Ma, and

traveled across Central America by waif dispersal facilitated during a eustatic sea-level drop

between 5 and 7 Ma. Upon settling the new continent, sigmodontines underwent a major

adaptive radiation. He postulated that the northern immigrants were adapted to forest

environments, or that grazing ecomorphs derived from such ancestral lineages would have

inhabited savanna-like ecosystems restricted to northern South America until ~3.5 Ma. By that

time, a glaciation event would have promoted the formation of an open-dry corridor along the

eastern side of the Andes, connecting disjunct savanna woodlands and grasslands located farther

south. Sigmodontines with a grazing ecomorphology then would have spread into southern South

America through this Andean route, and finally reached the Argentinean fossil deposits.

Phylogenetic analyses offer a robust framework for reconstructing central aspects of the historical biogeography of the GABI [14,32]. Molecular phylogenies constitute a critical component that can shed light on the timing of arrival and patterns of diversification of South American immigrants that otherwise would not be possible due to the fragmentary nature of the mammalian (and other taxa) fossil records. Molecular data and phylogenetic comparative methods have been employed to address key evolutionary questions about the tempo and mode of evolution of several taxa involved in the biotic interchange between North and South America [e.g., 8,9]. Recent meta-analyses of molecular dating studies indicate that plant and animal dispersal across the Isthmus of Panama occurred prior to the complete formation of the land bridge [52]. Previous authors motivated by perspectives from molecular phylogenetics have used divergence time estimates to provide a temporal dimension that is essential for a better understanding the enigmatic evolutionary history of sigmodontine rodents [35,53-55]. These studies pointed to an early sigmodontine diversification. However, conclusions are either based on strict molecular clocks and exclusive mitochondrial datasets [35,53], have a sparse taxon sampling within the Sigmodontinae [54], or make use of limited fossil calibrations in the ingroup [55].

Herein, we expand on the historical biogeography of the subfamily to assess paleogeographic hypotheses proposed by earlier investigators to explain the diversification of sigmodontines with respect to the GABI conundrum. We use a nuclear and mitochondrial DNA sequence dataset to reconstruct the phylogenetic relationships of sigmodontine rodents at the generic and tribal levels and employ methods that estimate divergence times, infer ancestral node geographic distributions, and evaluate significant shifts in diversification rates based on extant species richness. The main goal of our study is to provide a robust temporal and spatial

framework within which the scope for the remarkable radiation of sigmodontines in South America can be clearly defined. To that purpose we utilize a comprehensive taxon sampling, a large set of fossil calibrations under relaxed molecular clocks, a Bayesian approach to dispersal-vicariance analysis of ancestral areas, and phylogenetic comparative methods of diversification rates. We answer key questions regarding the evolutionary history of sigmodontine rodents in the context of the GABI. When did this group arrive in South America? Where did diversification initially take place? How many ancestral lineages participated in the invasion? Are there extant sigmodontine lineages that are more diverse or impoverished than expected by background rates of speciation and extinction?

Materials and Methods

Sampling design

We analyzed samples of 54 sigmodontine genera and a total of 66 extant species. We included genera of all tribes plus two *incertae sedis*: Abrothrichini (5); Akodontini (13); Ichthyomyini (1); Oryzomyini (19); Phyllotini (6); Reithrodontini (1); Sigmodontini (1); Thomasomyini (3); Wiedomyini (1). To assess the placement of Sigmodontinae relative to other Cricetidae subfamilies, we included representatives of the Arvicolinae, Cricetinae, Neotominae and Tylomyinae. In addition, we added members of other muroid families as the most distant outgroups, namely the Calomyscidae, Muridae, Nesomyidae and Spalacidae (GenBank accession numbers are listed in SI Table 1).

We only used samples for which we had sequence data for both protein-coding mitochondrial cytochrome *b* (*cytb*) and nuclear interphotoreceptor retinoid binding protein (*irbp*) genes. Those sequences were complete or mostly complete (≥ 90%) for the majority of samples,

although we also included some pivotal taxa with partial sequences (≥ 60%). Sampling

completeness of over 80% of the focal sigmodontine genera implemented in this study is

expected to avoid the effects of nonrandom sampling design on diversification rates, and possible

biases due to overrepresentation of deep nodes [56]. At the same time, extended sampling of

fast-evolving groups may distort divergence times toward an increased estimation of nodal ages,

especially at deeper nodes [57]. This likely is the case for some species-rich lineages of

sigmodontine rodents, particularly those within the Oryzomyini and Akodontini tribes. There is a

positive association between rates of evolution and species diversity [58] that could explain

anomalies that may arise from biased sampling. Moreover, extended taxon sampling apparently

leads to an overall trend of older divergence time estimates [57]. Hence, we used a single species

for each genus to assemble our dataset, except for those genera 1) representing noteworthy

geographic distributions (*Nesoryzomys* from the Galápagos Islands and *Oryzomys* from southern

United States); 2) from distantly related taxa within the Thomasomyini tribe [59]; 3) or those

which had fossils that provided calibration point for internal nodes (*Oligoryzomys*, *Akodon*,

Scapteromys, *Calomys*, *Sigmodon*).

Laboratory work

DNA extraction, PCR amplifications (thermal profiles and primer combinations), template

purification and cycle-sequencing followed laboratory procedures described in Almeida et al.

[60] and Weksler [61] for *cytb* and *irbp*, respectively.

Phylogenetic inference

Multiple sequence alignments were initially performed with ClustalW [62], and inspected manually to refine coding frame and placement of indels as necessary. Average genetic distances (uncorrected *p*-distance) between major clades were calculated in MEGA 5.1 [63]. We inferred the phylogenetic relationships among sigmodontine rodents and other muroid relatives using a maximum likelihood (ML) framework implemented under the rapid hill-climbing algorithm in the MPI-RAxML version 7 [64]. We calculated the best-scoring ML tree out of 200 randomized maximum parsimony staring trees. Joint branch optimization was performed using two distinct gene partitions under the general time-reversible (GTR) model of nucleotide substitution [65] and among-site rate heterogeneity with four discrete rate categories [66]. *Myospalax aspalax* (Spalacidae) was used as outgroup based on previous muroid molecular systematics studies [54,67]. Node support was assessed through 1,000 nonparametric bootstrap pseudoreplicates [68], and bipartitions values were drawn onto the best-scoring ML tree.

Bayesian analyses were performed using Markov chain Monte Carlo (MCMC) sampling as implemented in BEAST 1.4.8 [69]. We employed the GTR+Γ_4 model of nucleotide substitution and gene-specific unlinked models. Uniform interval priors were assumed for all parameters except base composition, for which we assumed a Dirichlet prior. We performed four independent runs of 25 million generations with each sampling for trees and parameters every 5,000 generations. The first 5 million generations were discarded as burn-in, and the remaining trees were used to estimate posterior probabilities for each node. All analyses were checked for convergence by plotting the log-likelihood values against generation time for each run, using Tracer 1.4 [70]. All posterior parameter estimates were checked for effective sample sizes (ESS) above 200.

Divergence time estimation

We tested for a molecular clock-like behavior of our dataset via a likelihood ratio test (LRT)

using MEGA 5.1 [63]. Because the presence of a global molecular clock was rejected (see

Results), we used two different and frequently used Bayesian relaxed-clock approaches [71] for

estimation of sigmodontine divergence times.

The method implemented by the program Multidivtime derives a probabilistic model that

describes autocorrelated changes in the evolutionary rate among lineages over time [72]. It

allows multiple calibration windows and the use of multilocus data with partitioned models,

while providing confidence intervals for rate and time estimates. We used the tree topology

obtained from RAxML and estimated branch lengths under the F84 model in the program

estbranches (distributed with the software package). We ran the Markov chain for ten million

generations sampling at every 2,000[th] step, and with a burn-in of one million cycles. We set the

expected number of time units between the tip and ingroup root to 2.7, and its standard deviation

to 0.5. These somewhat are arbitrary values referring to 27 ± 5 Ma (Oligocene), which is in

between the age of the first Miocene forms assigned to modern Cricetidae subfamilies [73-75]

and the putative stem Cricetidae from Late Eocene [76]. Moreover, this date is similar to a

previous age estimate for the appearance of Cricetidae [54]. The mean and standard deviation of

the prior distribution for the rate at root node were given by the average median of the distance

between the tip and ingroup root, calculated for each gene in TreeStat 1.1 [77], divided by the

time unit.

We further estimated divergence times using a relaxed-clock framework in BEAST (see

Phylogenetic inference section above for parameter settings) that allow for evolutionary rates to

vary along the tree branches under a uncorrelated lognormal relaxed-clock model [78]. We used

a combination of exponential and uniform prior distributions to calibrate the nodes of the sigmodontine phylogeny. To avoid potential pitfalls during divergence time estimations associated with the number and distribution of time constrains among nodes [79], we used a total of 15 fossil calibrations on the nodes indicated in Figure 1. These nodes represented multiple shallow (younger) and deep (older) calibrations, as well two upper- and 13 lower-limit ages, including fossils within crown lineages whenever possible. Moreover, we calibrated only well-supported nodes for those fossils which we had supporting evidence from the literature of their clade membership and taxonomic status. We assessed consistency of fossil calibrations using a jackknife approach in which Multidivtime pseudoreplicates were performed removing each calibration point at a time. Detailed information regarding fossil calibrations used in this study is available at the Supporting Information online material (Table S2).

Dispersal-vicariance analysis

We investigated the biogeographic history of the major sigmodontine clades using Bayes-DIVA [80], which is a Bayesian approach to dispersal-vicariance analysis (DIVA). In the latter method, ancestral areas are reconstructed onto the nodes of a user-defined phylogeny based on a parsimony criterion, which minimizes the number of dispersal and extinction events and assumes that speciation results from vicariance of widespread species [81]. Although DIVA does not rely on *a priori* assumptions about area relationships, there is uncertainty associated with the phylogenetic inference that is ignored since ancestral distributions are reconstructed onto a single phylogenetic hypothesis (i.e., tree topology). In addition, optimization of ancestral areas may be ambiguous due to multiple equally parsimonious distributions of ancestral nodes.

In Bayes-DIVA, standard dispersal-vicariance analyses are performed with several phylogenetic trees obtained from a posterior distribution of trees inferred via Bayesian approximation. Potentially different ancestral distributions reconstructed by DIVA runs may account for alternative biogeographic scenarios that are averaged by the posterior probability of each tree [80]. Bayesian phylogenetic inferences were implemented in MrBayes [82] using partitioned models of nucleotide substitution (GTR+Γ) and estimated model parameters. We performed two independent runs of 20 million generations each and sampling at every $10,000^{th}$ step using an MCMC procedure. The first 500 samples of each run were discarded as burn-in. A Perl script (made available by JAA Nylander) was used for the batch implementation of DIVA on all 3,000 phylogenetic trees, with *maxarea* = 2 or 3, alternatively. We used a Perl script written by FC Almeida to parse DIVA outputs for the nodes of the phylogeny. We considered the geographic distributions of genera among ten major areas, namely: Afrotropical, Palearctic, Nearctic, Central America, Eastern South America, Northern Andes, Central Andes, Southern Andes, Amazonia, and Galapagos Islands.

Phylogenetic comparative analyses

All phylogenetic comparative analyses were based on the dated chronogram comprised of 66 sigmodontine terminal taxa obtained from BEAST. We explored the tempo of increase in species richness as a function of speciation and extinction within the Sigmodontinae by plotting the number of lineages through time (i.e., lineages-through-time plot: LTT) observed on the topology. We also used MEDUSA comparative algorithm [83] to investigate if sigmodontine extant diversity could be explained by background rates of speciation and extinction, or if any significant shifts in diversification rates occurred along major lineages. MEDUSA integrates

taxonomic richness data in a stepwise approach to fit probabilistic models with subsequently complex rates for the entire phylogenetic backbone tree, and then uses the corrected Akaike information criterion (AICc) [84] to contrast and choose the best-fitting rate shift model. We fitted both birth-and-death and pure-birth (Yule) models and the AICc threshold was calculated automatically using the threshold selection function. We generated the richness dataset with the number of species for each genus, which was compiled from Musser and Carleton [34] and amended with new species descriptions from the literature. In addition, the 66-taxa tree was pruned down to 55 tips representing unique sigmodontine genera, except for the paraphyletic genus *Necromys* that for the purpose of the analysis we opted to designate as two distinct lineages including either lowland or highland species [sensu 85]. We performed comparative diversification analyses with R 2.15.2 [86] using packages 'geiger' [87], 'medusa' [83], 'ape' [88], 'picante' [89], and 'laser' [90].

Results

Sequence data

We analyzed a dataset consisted of 88 sequences from all sigmodontine tribes and major muroid clades. Aligned sequences were 1,140 and 1,236 bases long, respectively, for the mitochondrial *cytb* and nuclear *irbp* genes. The concatenated sequence data of 2,376 nucleotides contained a total of 1,262 variable sites and 1,002 parsimony informative sites. *cytb* partition contributed 646 variable and 572 parsimony informative positions, whereas *irbp* contributed 616 variable and 430 parsimony informative positions. Average pairwise sequence divergence (uncorrected *p* distance) based on *cytb* data ranged from 17 to 26% between tribes or *incertae sedis* genera. Mean sequence distance between Oryzomyalia and Sigmodontalia was 20% and varied from 20

to 24% between Sigmodontinae and other cricetid subfamilies. For *irbp*, average pairwise sequence distance ranged from 3 to 7% between tribes or *incertae sedis* genera. Mean sequence divergence between Oryzomyalia and Sigmodontalia was 6% and varied from 7 to 9% between Sigmodontinae and other cricetid subfamilies.

Phylogenetic relationships

The subfamily Sigmodontinae was recovered as a well-supported monophyletic clade in both maximum likelihood and Bayesian phylogenetic inferences with a bootstrap value (BS) of 100% and posterior probability (PP) equal to 1.00, respectively (Figs. S1 and S2). Two major subclades within the Sigmodontinae also were recovered with high nodal support in the analyses (BS = 100%; PP = 1.00): (1) Oryzomyalia, which is the most diverse and widespread clade within the subfamily and that includes the most recent common ancestor (MRCA) of sigmodontines and all of its descendants, except for the tribes Sigmodontini and Ichthyomyini [sensu 54]; and (2) Sigmodontalia (new taxon), herein defined as the clade forming a sister-group relationship with Oryzomyalia and that is comprised of the MRCA of the tribes Sigmodontini and Ichthyomyini and all of its descendants.

Basal relationships within Oryzomyalia are poorly resolved, as also demonstrated by previous molecular phylogenetic analyses that produced similar results albeit having somewhat different sampling designs [35,54,55,61,67,91,92]. The tribes Abrothrichini, Akodontini, Oryzomyini and Phyllotini were consistently recovered as well-supported monophyletic clades (BS ≥ 94%; PP = 1.00), but the monophyly of Thomasomyini [sensu 93] was recovered only in the ML inference and with little nodal support (BS = 46%) (Fig. S1)

Seven genera including *Reithrodon*, *Wiedomys* and five others regarded as *incertae sedis* (Table 1) have ambiguous phylogenetic placements and negligible support values. However, *Euneomys* and *Irenomys* were recovered as sister taxa in both inferences with high nodal support (BS = 94%; PP = 1.00), and comprise a clade that corresponds to the new tribe termed herein as Euneomyini. This clade in turn forms a sister-group relationship with *Juliomys* in both inferences, but with low to moderate support (BS = 34%; PP = 0.93); its association with the Euneomyini should be corroborated with further analyses using additional nuclear loci and morphology-based characters. The subfamilies Sigmodontinae and Tylomyinae were recovered as a sister-group in the phylogenetic analyses with moderate levels of support (BS = 65%; PP = 0.95). The Neotominae was placed in a clade basal to all the Cricetidae, but this arrangement is well supported only in the Bayesian inference (BS = 62%; PP = 0.99). Basal relationships between the Sigmodontinae and the cricetid subfamilies Arvicolinae, Cricetinae and Neotominae are poorly resolved overall; a phylogenetic signal that is in agreement with previous results from a dataset of four other nuclear genes [54].

Divergence time estimates

The clock-like phylogenetic evolution of sigmodontines and additional muroid rodents was statically rejected in favor of a relaxed one (LR = 2(29664 – 29525), df = 86, $P \leq 0.0001$). Hence, we estimated divergence dates fitting the assumption of a relaxed molecular clock that allows substitution rates to vary across the branches of the phylogeny. Distribution of the rank correlation for rate change between the pair of genes and the *P*-value approximated in the Multidivtime program could not reject the null hypothesis that *cytb* and *irbp* change rates independently (r = – 0.16; P = 0.77).

In general, divergence dates estimated in Multidivtime are older and confidence intervals are broader than those estimated in BEAST (Table 1; see also Fig. S2). These time differences tend to increase at the deeper nodes mainly towards the lower limit of confidence intervals. There is a 3.6-Ma difference between BEAST and Multidivtime age estimates for the split between cricetids and murids. For cricetid subfamilies (excluding sigmodontines) dates of divergence are 2.2- to 2.7-Ma different, but for nodes within the Sigmodontinae time differences amount to less than 1.5 Ma. Moreover, confidence intervals show broad consensus with credibility overlap above 70% for major sigmodontine nodes (Table 1), except for the Akodontini and Abrothrichini (with 50% and 46% credibility overlap, respectively). We attribute this relative lack of overlap to topological differences between the maximum likelihood phylogeny reconstructed in RAxML and used as input in Multidivtime analysis versus the Bayesian phylogeny inferred jointly in BEAST analysis.

Divergence time estimates from jackknife analyses indicate that fossil calibrations were consistent across nodes except for age constrains imposed on divergence dates of the Sigmodontini and Peromyscini. In the full set of node calibrations, the tribe Sigmodontini was assigned a maximum date of 4.8 Ma assuming the age of the fossil *Prosigmodon oroscoi*, and the Peromyscini was assigned a minimum age of 11.6 Ma considering the fossil genus *Paronychomys* (Table S2), each of which, when excluded, produced older and younger divergence date estimates, respectively.

The split between Muridae and Cricetidae is dated to the mid-early Miocene between 22.4 and 18.8 Ma. Despite point estimates generated by BEAST and Multidivtime approaches for the split between these two major muroid clades fall at or outside each other's confidence limits, there is some overlap of credibility intervals from uppermost to lowest values that range

from 26.6 to 16.2 Ma. This time period corresponds to a global warming trend that reduced the extent of Antarctic ice-sheets lasting until the late Oligocene (27 to 26 Ma), followed by a warm phase that persisted until the middle Miocene Climatic Optimum (17 to 15 Ma). These divergence dates are similar to a previous study by Steppan et al. [54] in that all age estimates point to a late Oligocene–early Miocene diversification of modern muroid clades.

Divergence of the modern Cricetidae clades began in the early Miocene between 18.7 and 16 Ma (21.7 to 14.3 Ma), and the basal radiation among cricetid subfamilies occurred within a short period of transition to the middle Miocene age (Table 1). The ancestral sigmodontine lineage diverged from its MRCA with the tylomyine clade of Middle American endemics between 16.7 and 14.3 Ma (19.7 to 12.5 Ma), while the MRCA of the Sigmodontinae dated from 12.3 to 11.2 Ma (14.6 to 9.6 Ma). Divergence of Oryzomyalia and Sigmodontalia took place between 10.6 and 9.5 Ma (12.7 to 8.4 Ma) and 9.3 and 8.8 Ma (11.3 to 6.7 Ma), respectively, and radiations of major tribes occurred within the late Miocene to early Pliocene (Table 1).

The tribes Oryzomyini, Akodontini, and Phyllotini, which together comprise the greatest diversity among sigmodontine rodents [> 63%, sensu 94], diversified prior to the early Pliocene, whereas divergence of Euneomyini, Abrothrichini, and Sigmodontini preceded the late Pliocene. In sum, all tribes and genera considered as *incertae sedis*, as well as the majority of sigmodontine lineages at the generic level diverged before the formation of the Panamanian land bridge. Only some of the intrageneric divergence date estimates (*Oryzomys*, *Nesoryzomys*, *Oligoryzomys*, *Abrothrix*, *Akodon*, *Scapteromys*, and *Thomasomys aureus–baeops*), and the split time between a few genera (*Microryzomys–Oreoryzomys*, *Geoxus–Pearsonomys*, *Auliscomys–Loxodontomys*, *Deltamys–*[*Necromys lasiurus–Akodon*], and *Juscelinomys–Oxymycterus*) occurred when an overland connection between the Americas was already in place (i.e., late

Pliocene and earlier). Nevertheless, confidence intervals for the majority of these nodes encompass older times, with a few exceptions (*Geoxus–Pearsonomys*, *Oryzomys*, *Nesoryzomys*, *Oligoryzomys*, *Akodon*, *Scapteromys*, and *T. aureus–baeops*; Fig. 1).

Ancestral area distributions

The Bayes-DIVA analysis using *maxarea* = 2 (results using *maxarea* = 3 are very similar; not shown) suggests that the biogeographic history of sigmodontine rodents and their cricetid ancestors has been punctuated by dispersal events followed by episodes of vicariance. Reconstruction of ancestral ranges indicates that the majority of subfamily crown nodes have a single area of ancestral distribution in either the Nearctic (Neotominae), Palearctic (Arvicolinae and Cricetinae), or Central America (Tylomyinae). The ancestral range of the Sigmodontinae is an exception. Whereas the internode leading to both tylomyines and sigmodontines is distributed essentially in Central America and the ancestral distribution of the subfamily Tylomyinae remains exclusively in that area, the MRCA of the sigmodontines undergoes an additional dispersal into Eastern South America (ESA). From this node, vicariance separates the widespread sigmodontine ancestor into one lineage corresponding to Sigmodontalia with a Central American ancestral distribution, and another clade for Oryzomyalia with ancestral distribution in ESA. The tribes Sigmodontini and Ichthyomyini both have ancestral nodes distributed in Central America.

Ancestral areas within Oryzomyalia crown groups have an Eastern South American distribution, despite poorly resolved relationships at basal nodes. Moreover, among those Oryzomyalia tribes with high nodal support, ancestral distributions are reconstructed as one single geographic area, except for the Oryzomyini and Phyllotini. The MRCA of Oryzomyini

extends its ancestral distribution via dispersal into Amazonia, but a subsequent vicariance event splits the ancestor of *Scolomys* and *Zygodontomys* in Amazonia and remaining oryzomyines in ESA. From this point, most oryzomyine nodes have partial or entire ancestral distributions in ESA, but there is some ambiguity among areas in the Northern Andes, Central America and the Galapagos Islands, for example in the ancestral node of *Euryoryzomys* plus *Transandinomys*, or *Melanomys* plus *Nectomys* and *Nesoryzomys*. The stem node leading to *Oryzomys* and its sister clade with ancestral distribution in ESA and the Nearctic suggests a reinvasion of Central and North America. In fact, episodes of overseas dispersal of South American oryzomyines are relatively recent in time dating from the early Pliocene onwards.

Phyllotini rodents have ancestral nodes with ambiguous area combinations of ESA and the Central and Southern Andes. Diversification of the Akodontini begins in ESA, with one of its two major subclades having ancestral nodes exclusively in ESA, whereas the other subclade has ambiguous ancestral area reconstructions in ESA and the Central Andes. The ancestral node connecting the genus *Wiedomys* with the Abrothrichini extends its range into both ESA and the Southern Andes, when after a vicariance event the ancestors of this tribe have exclusive Southern Andean ancestral distributions. Likewise, the ancestral node to *Juliomys* and *Euneomys* plus *Irenomys* (Euneomyini) is distributed in ESA and the Southern Andes, with subsequent vicariance separating the new tribe in the Southern Andes.

Phylogenetic comparative analyses

The LTT plot with the numbers of lineages plotted on a logarithmic scale is expected to form a straight line when diversification rates are constant through time [88]. The observed LTT plot lays above this line; its shape is consistent with an initial burst of sigmodontine diversification

which correlates with a period of between-tribe differentiation that is followed by a subtle

tendency towards decreasing diversification rates (Fig. 2)

The optimal MEDUSA model identified two significant breakpoints in diversification

rates of the Sigmodontinae (Fig. 3), specified by a 5-parameter (Yule) model and AIC threshold

equal to 3.1838 (lnL = –213.4639, AICc = 437.5104). The background tempo of diversification

for the majority of nodes in the phylogeny is relatively modest (r = 0.4101 lineages per million

year), in contrast to diversification rates of the akodontine clades leading to *Akodon* and

Oxymycterus. These rate shifts occurred independently twice during the late Pliocene, the first

change was in the genus *Akodon* (r = 1.2456 lineages per million year) and the second in the

genus *Oxymycterus* (r = 1.3938 lineages per million year), which corresponds to a threefold

increase in the tempo of diversification for these diverse genera, with 43 and 17 extant species,

respectively. In contrast, we did not detect significant shifts in the diversification rates of other

species-rich genera, such as *Thomasomys*, *Rhipidomys* and *Oligoryzomys*.

Discussion

The final closure of the Isthmus of Panama at ~3.5 Ma (late Pliocene), which triggered the

GABI, is yet another episode in a series of events that comprise the biogeographic history of the

Sigmodontinae. The role and significance of the GABI in shaping sigmodontine biogeography

have been argued on the basis of extensive paleontological work during the last few decades, and

more recently in light of molecular phylogenetics. For example, the oldest South American fossil

remains found in Argentina and that can be putatively ascribed to sigmodontines date from late

Miocene to early Pliocene [48-50], whereas previous divergence time estimates place the origin

of sigmodontine radiation in the middle to late Miocene [35,53-55]. Clearly, fossil records and

molecular dating studies agree that diversification of sigmodontine rodents predates the GABI. However, details regarding the place and tempo of the initial sigmodontine diversification as well as the time of arrival and number of ancestral lineages that invaded South America need further clarification.

Previous phylogenetic studies using different molecular dating methods and sampling strategies (e.g., choice of taxa, molecular markers, and fossil calibrations) reached biogeographic conclusions similar to ours. That is, support for the hypothesis of an early arrival of sigmodontines in South America, although not as old (middle–late instead of early–middle Miocene) as envisioned by some early authors [e.g., 24,42,46,47]. Divergence date estimates provide substantial evidence (i.e., independent of the fossil record) to warrant a temporal framework to refute Simpson's late arrival hypothesis of sigmodontine invasion only after formation of the Panamanian land bridge [36,37]. However, we could not reject Marshall's hypothesis that sigmodontine ancestral lineages underwent further diversification in newly colonized areas of South America after crossing the Central American seaway [26]. Because divergence dates and credibility intervals estimated for the majority of crown groups, inclusive at tribal level, fall within the period of time postulated by Marshall as favoring waif dispersals due to a global sea level drop (ca. 5–7 Ma). Given the fragmentary Argentinean fossil record it is unclear, on the basis of divergence ages alone, if initial diversification of ancestral sigmodontines occurred in North America or not. Therefore, clarification of such biogeographic impasse would require incorporation of a spatial component.

Recently, Parada et al. [55] employed a method to reconstruct ancestral area distributions on the nodes of the Sigmodontinae phylogeny. They also provide estimates of divergence dates using a relaxed molecular clock. Despite taxonomic and molecular sampling designs similar to

that of our study, Parada et al. used only three fossil constraints to calibrate their molecular

dating analysis. In this study, we compare divergence dates from two different relaxed-clock

methods and employ 15 fossil calibrations, whose impact on estimation of node ages we explore

by means of jackknife analyses, in order to provide divergence time estimates with increased

precision. Although point estimates are comparable with those reported in Parada et al. [55], our

calibration strategy produced narrower confidence intervals that help to pinpoint important

biogeographic events on a temporal scale. Moreover, we reconstruct ancestral area distributions

using a higher geographic resolution in terms of the areas assigned to the Bayes-DIVA analysis

in an attempt to reveal areas of differentiation and probable routes of dispersal among tribes.

Finally, we also employ phylogenetic comparative methods of diversification rates, which

together allow for a better understanding of the patterns of sigmodontine diversity and

distribution.

Our analyses indicate that sigmodontine ancestral nodes have a distribution chiefly in

South America, as opposed to cricetid stem groups and other subfamilies which all show an

allochthonous ancestry. The only exceptions are the Central American lineage leading to

Sigmodontalia (Ichthyomyini and Sigmodontini) and the MRCA of the whole subfamily, the

latter of which node has an ancestral range also extending into South America (Fig. 1). Given

that the immediate ancestor of both tylomyines and sigmodontines has a distribution restricted to

Central America, such a dispersal event must have occurred prior to divergence of the basal

dichotomy within the Sigmodontinae. According to our relaxed molecular clocks, the initial

diversification of the subfamily occurred by middle to late Miocene (Fig. 1). Interestingly, a

regional unconformity at 14.8–12.8 Ma separates underlying open marine sequences from

depositional units of middle to late Miocene age with general shallowing depths [20]. In

addition, age estimates of the sigmodontine stem and crown nodes appear to be contemporaneous with a major eustatic lowering of 50 ± 5 m derived from offshore backstripping and $\delta^{18}O$ data [95,96].

It seems that episodes of low sea levels have been instrumental in facilitating the invasion of South America long before the onset of the GABI. However, the deepest part of the isthmus still had middle to upper bathyal depths (150–1500 m) in the upper middle Miocene [20]. Therefore, the stem cricetid ancestor must have entered South America via waif dispersal rather than by crossing a continuous dry-land pathway. The ancestor to sigmodontine rodents may have reached the new continent after traversing the Central American seaway, a 200-km wide strait east of the Panama Canal Basin connecting the Pacific Ocean and the Caribbean Sea [22], or alternatively, it may have entered South America by island-hopping via the Antilles [33]. We argue in favor of the first alternative as the most feasible route considering that southern Central America formed a subaerial peninsula connected to North America as early as ~19 Ma [23,25,27], whereas the Aves Ridge (SE Caribbean Sea) had undergone increased subsidence and subdivision by the middle Miocene [97,98]. We hypothesize that the ancestral sigmodontine lineage arrived in northwestern Colombia; most likely atop a raft made of entwined plant material washed ashore in the wake of river floods in the isthmian region. Similarly, transoceanic dispersals of caviomorph rodents and platyrrhine primates from Africa have been suggested as mechanisms for the South American colonization [99,100].

Although tectonically active settings of the isthmian region obscure potential relationships between global sea-level changes and the configuration of paleoenvironments in southern Central America [101], lowering sea levels may have exposed coastal areas with savanna-like environments [19]. In turn, such phenomena would have contributed, perhaps

synergistically, to the southward dispersal of a sigmodontine ancestor. However, late Tertiary palynofloras typically resemble modern tropical communities, suggesting that the impact of pre-GABI climatic conditions on patterns of vegetation distribution was less intense than paleophysiographic changes associated with tectonism [31]. Nevertheless, volcanic peaks 1400–4000-m high produced a rain-shadow zone within which paleosol differences indeed supported a variety of scrublands that are difficult to reconstruct from fossil floral assemblages alone [102]. Increasing elevations within this complex vegetation mosaic setting would have given rise to more temperate short-lived open habitats, under a climate that, albeit a less marked dry season, was drier and cooler than today.

This paleogeographic scenario agrees with a ice-growth phase after the middle Miocene Climate Optimum that culminated in the reestablishment of East Antarctic ice sheets by 10 Ma [103]. Moreover, the main pulses of the faunal interchange are dominated by taxa having affinity with temperate biotas and ecological adaptations to savanna-like ecosystems [104,105]. Therefore, it seems reasonable to conclude that the necessary environmental prerequisites for the opportunistic dispersal of a northern cricetid stock were in place long before the glacial phases that brought generalized favorable settings for the GABI episodes after completion of the land bridge [32]. Once the sigmodontine ancestor gained a foothold in South America it extended its range through savanna-like habitats mirroring conditions of tropical and subtropical open-country formations found in Central and North America. In this regard, Webb [105] envisioned two major corridors connecting disjunct South American savannas during Pleistocene glaciation times: the Andean route and the eastern route. As discussed above, such a scenario could also apply to the preexisting regional and global conditions established since the late middle Miocene.

According to Bayes-DIVA reconstruction the most likely utilized pathway was the eastern route, through which the ancestral sigmodontine lineage was able to reach ESA. Evidence that such a connection existed during the Tertiary is indicated by the close resemblance of relict shrub vegetation and savanna woodlands along the Caribbean coast and Llanos region of Colombia and Venezuela and the Guyana plateau, which at times would have been linked directly to open-dry formations of central and northeastern Brazil [106-109]. As a matter of fact, woodland savanna vertebrates are also represented in diverse fossil assemblages from the Miocene records of Colombia and Venezuela [105,110]. Subsequent to invasion of South America by this widespread sigmodontine ancestor, a vicariance event split the subfamily into two basal groups, each with restricted ancestral distributions: Sigmodontalia in Central America and Oryzomyalia in ESA. This event coincides with increased uplift of the Eastern Cordillera in the late middle Miocene that has shifted the course of the paleo-Orinoco river into its current west-east direction and permanently divided the Magdalena valley and Llanos basin [111,112]. Radiation of the two major sigmodontine lineages occurred within an interval of approximately three million years, and the majority of between-tribe level clades diverged shortly after that time period (Figs. 1 and 2). At least three other episodes of low sea level occurred during the late Miocene [29] in conjunction with a gradual cooling trend that lasted until the early Pliocene [103]. Despite widespread shallowing of southern Central America at 7.1 Ma [20], there is no signal of a second northern invasion or reinvasion by an autochthonous stock.

Based on patterns of diversity and distribution of the different sigmodontine tribes and genera, Reig [47] proposed that the Andean mountains represented the principal areas of differentiation in the subfamily. He also suggested that episodic dispersals within a north-to-south axis along the Andes gave rise to the main tribal lineages. Several nodes in the phylogeny

with Andean ancestral distributions support the view that the Andes provided numerous niche opportunities that ultimately fueled the remarkable radiation of sigmodontine rodents. On the other hand, the stem nodes of Oryzomyalia point to ancestral areas with chiefly eastern South American distributions. Therefore, ancestral lineages diverged in ESA and then radiated after having occupied the Andes multiple times (Fig. 1). We conclude that ESA served as source area for the initial burst of sigmodontine diversification (i.e., between-tribe differentiation; Fig. 2), rather than the Andes as previously postulated [47]. Dispersal episodes from ESA colonized distinct Andean regions independently, and each lineage involved underwent further diversification that accounted for the majority of modern genera (i.e., within-tribe differentiation). Interestingly, the extant taxonomic diversity within the subfamily is explained by a comparatively modest background rate of diversification across most sigmodontine lineages. The genera *Akodon* and *Oxymycterus* are an exception. These widespread akodontine clades, which are particularly more diverse in the Andes and the Atlantic region, experienced significant increases in the tempo of diversification relatively recently (Fig. 3). As a consequence, sigmodontine rodents overall do not represent an unexpectedly species-rich radiation considering their middle–late Miocene origin.

Even though there were cases of ambiguous ancestral area reconstructions, in particular those related to different Andean regions, we attempt to infer the most likely migratory route of each tribe. In the scenario above, where ancestral lineages departed originally from ESA, it is implied that dispersers reached the adjacent Andes through open-country formations distributed in a NE–SW direction. Ancestral areas indicate that, as opposed to Reig's hypothesis, such dispersal episodes did not necessarily follow a southward track. The Akodontini dispersed into the Central Andes at least three times during the radiation of its two major clades and arrived in

Amazonia also from ESA. The Phyllotini probably entered the Central Andes and from there spread into the Southern and Northern Andes. The pathway used by the paraphyletic Thomasomyini is tentatively associated with dispersal into the Northern Andes through Amazonia (and ESA) (*Rhipidomys*) and successive invasion of the Central Andes (*Thomasomys*), or alternatively a second episode of dispersal into the Northern Andes from the Central Andes. The Abrothrichini and Euneomyini are the only tribes with exclusive southern Andean distributions, and thus we suggest that each lineage dispersed only once into that particular region. The Oryzomyini has the most complex pattern of area distributions with a number of dispersals into the Northern Andes from either ESA or Amazonia, as well as several arrivals in Amazonia departing from ESA or the Northern Andes. In addition, some oryzomyines colonized areas in the Central and/or Southern Andes (*Nectomys* and *Oligoryzomys*), while other genera are the only sigmodontines to invade volcanic islands (*Nesoryzomys*) or to reinvade Central and North America (see Fig. 1). It is noteworthy that these northern hemisphere reinvasions occurred just prior to or after completion of the land bridge. Lastly, lineages comprising the Sigmodontini and Ichthyomyini, whose ancestors were confined to Central America, made their way into South America, but these more recent episodes of invasion are restricted to the continent's northwestern margin.

In summary, the remarkable diversification of the Sigmodontinae involved significant paleogeographic changes at the continental and global scales. The progressive bridging of the Central American seaway, aided by sea-level low stands and a gradual cooling trend since the late middle Miocene, triggered an intricate biogeographic history that is marked by the opportunistic invasion of South America by a single ancestral cricetid lineage. Given the antiquity of this biogeographic event, speciation proceeded at an expected background pace for

the majority of clades, except for a few exceptionally diverse akodontine genera. Overall, the sigmodontine radiation is biodiverse and provides numerous examples of ecomorphological adaptations. Indeed, sigmodontine rodents were very successful in colonizing novel habitats during the historical evolution of the group as a whole, which is intertwined with important landscape developments that have provided a number of opportunities for dispersal and specializations within the subfamily. Differential diversification rates may explain the observed patterns, but future studies are necessary to address the effect of shifting environmental conditions on species richness and ecomorphology among different lineages.

Acknowledgments

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Tables

Table 1. Divergence ages for major sigmodontine and other muroid crown groups.

Taxon	BEAST		Multidivtime	
	Node age	HPD 95%	Node age	HPD 95%
Cricetidae, Muridae	18.8	16.2–21.3	22.4	18.8–26.6
Cricetidae	16.0	14.3–17.8	18.7	16.3–21.7
Neotominae	13.8	12.5–15.1	16.0	14.0–18.5
Arvicolinae, Cricetinae	14.2	12.4–16.2	16.6	14.0–19.6
Sigmodontinae, Tylomyinae	14.3	12.5–16.1	16.7	14.2–19.7
Sigmodontinae	11.2	9.6–12.7	12.3	10.5–14.6
Oryzomyalia	9.5	8.4–10.8	10.6	8.9–12.7
Sigmodontalia	8.8	6.7–10.7	9.3	7.5–11.3
Oryzomyini	7.7	6.5–8.8	7.9	6.4–9.9
Akodontini	6.9	5.8–8.0	8.4	6.9–10.3
Abrothrichini, Wiedomyini	6.9	5.5–8.3	7.8	6.2–9.7
Phyllotini	6.3	5.3–7.3	7.0	5.7–8.7
Euneomyini	5.5	3.7–7.0	6.2	4.6–8.0
Abrothrichini	4.1	3.5–4.8	5.5	4.2–7.0
Sigmodontini	4.0	2.9–4.8	4.6	4.0–4.8

Node dates (Ma) and 95% highest posterior density (HPD 95%) interval estimated under rate variation (BEAST) and autocorrelation (Multidivtime) relaxed molecular clocks.

Figure Legends

Figure 1. Dated phylogeny with embedded ancestral area distributions for the Sigmodontinae (and other muroid rodents). Divergence ages were estimated under BEAST relaxed-clock model. Node bars are 95% highest posterior density credibility intervals; dashed-outline bars correspond to the 15 nodes constrained by fossil calibrations (see Table S2). Pie charts represent the marginal probability of ancestral area distributions inferred for each node using Bayes-DIVA; ancestral areas of highest probability are depicted from bottom-up in a clockwise order; stripped diagonal fill indicates an ancestral distribution in the two areas matching the color-code scheme on the left panel; colored squares next to species names symbolize their current distribution; pie charts at nodes with an exclusive ancestral distribution are downsized for clarity. Open circles at internal nodes indicate well-supported clades (PP $\geq$ 0.95; BS $\geq$ 75%). (I) Sigmodontinae; (II) Oryzomyalia.

Figure 2. Lineage through time plot of the subfamily Sigmodontinae. The number of lineages of sigmodontine rodents on a logarithm scale at any time before present as inferred from the Bayesian relaxed clock chronogram generated using BEAST. Dashed line represents accumulation of lineages under a constant rate of diversification. Gray shading indicates the time period of diversification between tribes.

Figure 3. MEDUSA analysis of diversification rate shifts across the generic-level phylogeny of the Sigmodontinae. Node numbers indicate the background tempo of diversification for most sigmodontine rodents (clade 1), and the order at which unusual rate shifts were identified by MEDUSA stepwise model fitting procedure. Clades 2 and 3 represent exceptionally diverse akodontine genera (*Akodon* and *Oxymycterus*, respectively) and are depicted thicker than usual. Horizontal bars indicate species richness per each genus.

Other Muroidea

Neotominae

Arvicolinae

Cricetinae

Tylomyinae

Ichthyomyini

Sigmodontini

Akodontini

Euneomyini

Thomasomyini A

Reithrodontini

Thomasomyini B

Wiedomyini

Abrothrichini

Phyllotini

Oryzomyini

Legend:
- Afrotropical
- Palearctic
- Nearctic
- Central America
- Eastern South America
- Northern Andes
- Central Andes
- Southern Andes
- Amazonia
- Galapagos Islands

Taxa:
Nesomys rufus
Acomys spinosissimus
Calomyscus baluchi
Neotoma albigula
Neotoma lepida
Baiomys taylori
Scotinomys teguina
Onychomys torridus
Reithrodontomys megalotis
Peromyscus truei
Peromyscus maniculatus
Eothenomys melanogaster
Myodes gapperi
Microtus oeconomus
Arvicola terrestris
Cricetulus longicaudatus
Cricetus cricetus
Mesocricetus auratus
Phodopus sungorus
Nyctomys sumichrasti
Tylomys nudicaudus
Rheomys raptor
Sigmodon hispidus
Sigmodon alstoni
Kunsia tomentosus
Scapteromys tumidus
Scapteromys aquaticus
Bibimys labiosus
Lenoxus apicalis
Brucepattersonius soricinus
Blarinomys breviceps
Juscelinomys huanchacae
Oxymycterus nasutus
Thaptomys nigrita
Thalpomys cerradensis
Necromys urichi
Deltamys kempi
Necromys lasiurus
Akodon azarae
Akodon montensis
Juliomys pictipes
Euneomys chinchilloides
Irenomys tarsalis
Rhipidomys macconnelli
Rhipidomys nitela
Reithrodon auritus
Rhagomys longilingua
Thomasomys aureus
Thomasomys ischyurus
Thomasomys baeops
Wiedomys pyrrhorhinos
Abrothrix longipilis
Abrothrix olivaceus
Geoxus valdivianus
Pearsonomys annectens
Notiomys edwardsii
Chelemys macronyx
Delomys sublineatus
Calomys lepidus
Calomys callosus
Eligmodontia typus
Graomys griseoflavus
Phyllotis xanthopygus
Auliscomys pictus
Loxodontomys micropus
Scolomys ucayalensis
Zygodontomys brevicauda
Euryoryzomys macconnelli
Transandinomys talamancae
Nephelomys albigularis
Hylaeamys megacephalus
Oecomys trinitatis
Oligoryzomys fulvescens
Oligoryzomys nigripes
Neacomys spinosus
Oreoryzomys balneator
Microryzomys minutus
Sooretamys angouya
Cerradomys subflavus
Holochilus brasiliensis
Pseudoryzomys simplex
Oryzomys couesi
Oryzomys palustris
Melanomys caliginosus
Nectomys squamipes
Nesoryzomys narboroughi
Nesoryzomys swarthi

I

II

Timescale: Oligo. | Early Miocene | Middle Miocene | Late Miocene | Early Pliocene | Late Plio. | Pleistocene

20   15   10   5   0 Ma

49

Biogeography and Evolution of Neotropical Small Mammals,

with Emphasis on Hystricognath Spiny Rats of the

Genus *Proechimys* (Family Echimyidae)

Rafael N. Leite

A dissertation submitted to the faculty of
Brigham Young University
in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

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July 2013

Supporting Information Tables

Table S1. Taxon sampling with GenBank accession numbers and classification scheme.

Taxon	*cytb*	*irbp*
Spalaciadae		
Myospalax aspalax	AF326272	AY326097
Muridae		
Acomys spinosissimus	AM409396	AY326074
Calomyscidae		
Calomyscus baluchi	AY288509	AY163581
Nesomyidae		
Nesomys rufus	AF160592	AY326099
Cricetidae		
Arvicolinae		
Arvicola terrestris	AY275106	AY277407
Eothenomys melanogaster	AM392374	AY163583
Microtus oeconomus	DQ452134	AY163593
Myodes gapperi	AY309431	AY326080
Cricetinae		
Cricetulus longicaudatus	AJ973386	AY326082
Cricetus cricetus	AJ490302	AY277410
Mesocricetus auratus	AM904612	AY163591
Phodopus sungorus	AJ973390	AY163631
Neotominae		
Baiomys taylori	AF548472	AY277408
Neotoma albigula	DQ179858	AY277411
Neotoma lepida	DQ179830	AY163599
Onychomys torridus	AY275110	AY277412
Peromyscus maniculatus	DQ385645	AY163630
Peromyscus truei	DQ861375	AY277413
Reithrodontomys megalotis	AF176248	AY277414
Scotinomys teguina	AF108705	AY163639
Tylomyinae		
Nyctomys sumichrasti	AY195801	AY163603
Tylomys nudicaudus	DQ179812	AY163643
Sigmodontinae		

Ichthyomyini		
Rheomys raptor	KU159017	AY163635
Sigmodontini		
Sigmodon alstoni	AF293397	AY163640
Sigmodon hispidus	AF425227	AY277479
Oryzomyalia		
Abrothrichini		
Abrothrix longipilis	U03530	AY163577
Abrothrix olivaceus	AF297879	AY277421
Chelemys macronyx	U03533	AY277441
Geoxus valdivianus	AY275116	AY277448
Notiomys edwardsii	U03537	AY163602
Pearsonomys annectens	AF108672	AY851749
Akodontini		
Akodon azarae	U03529	AY163578
Akodon montensis	AY273905	AY277426
Bibimys labiosus	DQ444329	AY277436
Blarinomys breviceps	AY275112	AY277437
Brucepattersonius soricinus	AY277486	AY277439
Deltamys kempi	AY195862	AY277444
Juscelinomys huanchacae	AY275119	AY277452
Kunsia tomentosus	AY275121	AY277454
Lenoxus apicalis	U03541	AY277456
Oxymycterus nasutus	AF175286	AY277468
Necromys lasiurus	AY273912	AY277459
Necromys urichi	AY273919	AY277463
Scapteromys tumidus	AY275133	AY163637
Scapteromys aquaticus	AY275132	AY277476
Thalpomys cerradensis	AY273916	AY277480
Thaptomys nigrita	AF108666	AY277482
Phyllotini		
Auliscomys pictus	APU03545	AY277434
Calomys lepidus	AF159294	AY163580
Calomys callosus	DQ447282	AY277440
Eligmodontia typus	AF108692	AY277445
Graomys griseoflavus	AY275117	AY277449
Loxodontomys micropus	AY275122	AY277457
Phyllotis xanthopygus	U86833	AY163632
Oryzomyini		
Cerradomys subflavus	AF181274	AY163626

Euryoryzomys macconnelli	GU126538	AY163620
Holochilus brasiliensis	GU126517	AY163585
Hylaeamys megacephalus	AY275124	AY163621
Melanomys caliginosus	EU340020	AY163590
Microryzomys minutus	AF108698	AY163592
Neacomys spinosus	AF108701	AY163597
Nectomys squamipes	GU126522	AY163598
Nephelomys albigularis	GU126532	AY163614
Nesoryzomys narboroughi	GU126523	AY163600
Nesoryzomys swarthi	GU126524	AY163601
Oecomys trinitatis	GU126527	AY163608
Oligoryzomys fulvescens	GU126529	AY163611
Oligoryzomys nigripes	GU126530	AY163612
Oreoryzomys balneator	GU126535	AY163617
Oryzomys couesi	DQ185386	AY163618
Oryzomys palustris	GU126539	AY163623
Pseudoryzomys simplex	GU126547	AY163633
Scolomys ucayalensis	AF108696	AY163638
Sooretamys angouya	GU126534	AY163616
Transandinomys talamancae	GU126544	AY163627
Zygodontomys brevicauda	GU126549	AY163645
Reithrodontini		
Reithrodon auritus	AY275129	AY163634
Thomasomyini		
Rhagomys longilingua	AY206770	DQ003723
Rhipidomys macconnelli	AY275130	AY277474
Rhipidomys nitela	AF108682	AY163636
Thomasomys aureus	TAU03540	AY277483
Thomasomys baeops	DQ914654	AY163642
Thomasomys ischyurus	AF108675	AY277484
Wiedomyini		
Wiedomys pyrrhorhinos	AY275134	AY163644
Incertae sedis		
Delomys sublineatus	AF108687	AY163582
Euneomys chinchilloides	AY275115	AY277446
Irenomys tarsalis	U03534	AY163587
Juliomys pictipes	EF127514	AY163588

Table S2. Fossil records used as calibration points in molecular dating analyses.

Node	Taxon	Fossil	Age (Ma)	Reference
1	Neotomini	*Neotoma [Paraneotoma] minutus*	8.3	[1]
2	Peromyscini	*Paronychomys* spp.	11.6	[2]
3	Cricetinae	*Cricetus kormosi*; *Cricetus lophidens*	6	[3,4]
4	Cricetinae	*Mesocricetus primitivus*	6	[4]
5	Arvicolinae	*Prosomys* (=*Promimomys*) *mimus*	5.5	[5]
6	Sigmodontini	*Prosigmodon oroscoi*	4.8	[6]
7	Akodontini	*Scapteromys aquaticus*	2.2	[7]
8	Akodontini	*Oxymicterus* cf. *rufus*	1	[8]
9	Akodontini	*Necromys bonapartei, Dankomys*	4	[8]
10	Akodontini	*Akodon lorenzinii*	2.7	[8]
11	Phyllotini	*Calomys laucha*	1	[8]
12	Phyllotini	*Auliscomys* sp.	4	[8]
13	Abrothricini	*Abrothrix* kermacki	3.5	[8]
14	Oryzomyini	*Oligoryzomys* cf. *flavescens*	0.8	[8]
15	Oryzomyini	*Holochilus brasiliensis*; *Holochilus prigimeus*	0.8	[8]

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Supporting Information Figures

Figure S1. Phylogenetic relationships of sigmodontine and other muroid rodents.
Topologies recovered from a concatenated dataset with two gene partitions (*cytb* and *irbp*). (A)
Best-scoring maximum likelihood tree inferred in RAxML using 200 initial rearrangements and
GTR+Γ_4 model of nucleotide substitution, with nodal support drawn from 1,000 nonparametric
bootstrap runs. (B) Maximum clade credibility Bayesian tree inferred in BEAST using GTR
model of substitution and rate heterogeneity, with posterior probabilities for each node.
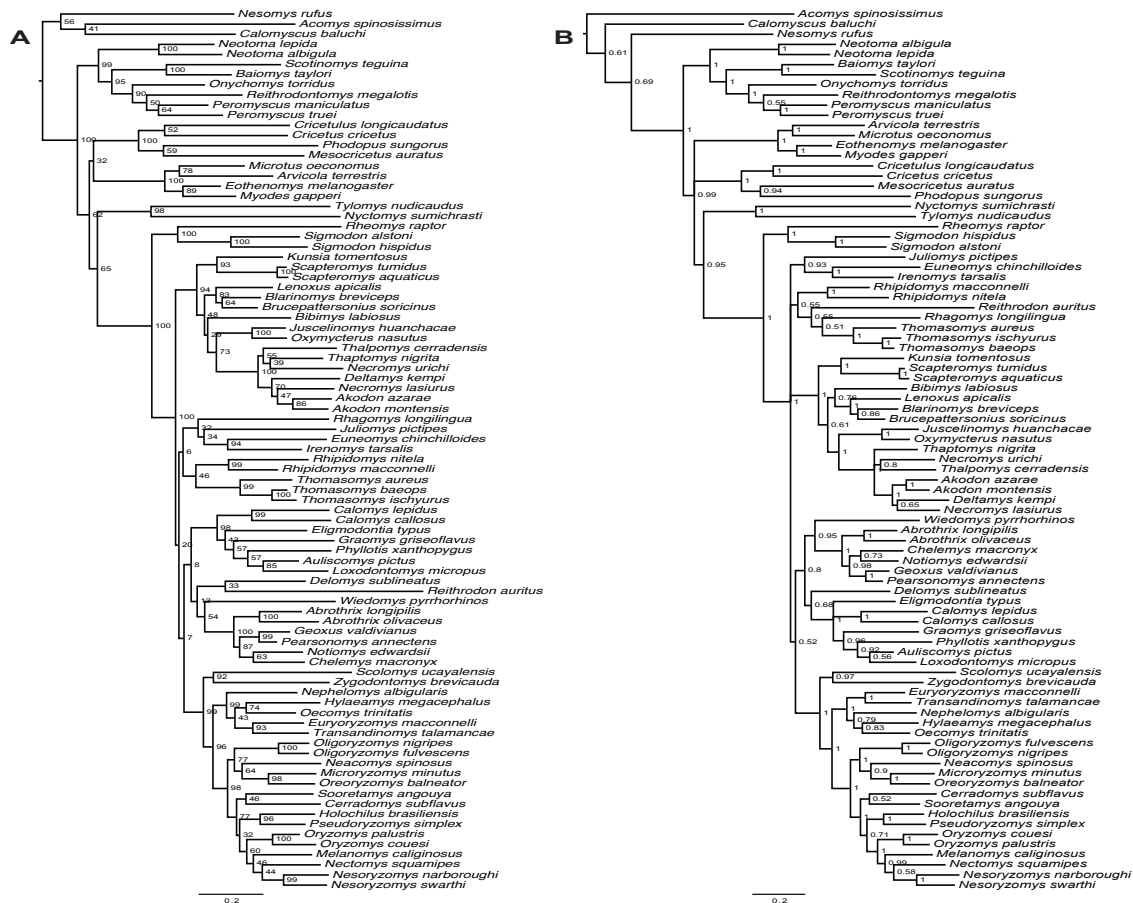
Figure S2. Time calibrated phylogeny of the Sigmodontinae (and other muroid rodents) as implemented in Multidivtime. The tree topology used for Multidivtime molecular dating was obtained from RAxML. Node bars indicate 95% credibility intervals for major clades listed in Table 1.
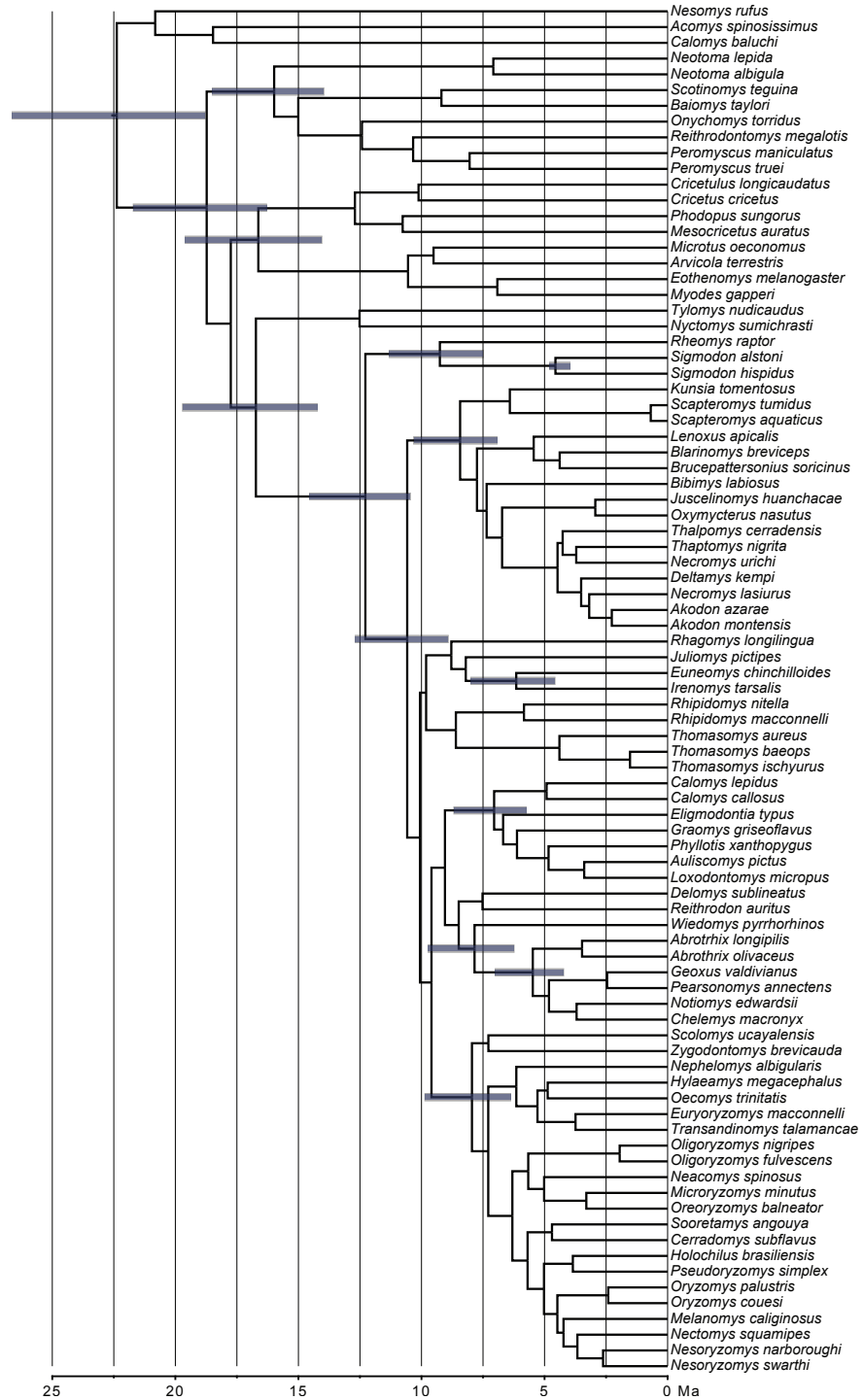
CHAPTER 2

**Revisiting Amazonian phylogeography: insights into
diversification hypotheses and novel perspectives**

Review paper in press at the journal *Organisms Diversity & Evolution*

REVIEW

ORGANISMS
DIVERSITY &
EVOLUTION

Revisiting Amazonian phylogeography: insights into diversification hypotheses and novel perspectives

Rafael N. Leite · Duke S. Rogers

Abstract The Amazon Basin harbors one of the richest biotas on Earth, such that a number of diversification hypotheses have been formulated to explain patterns of Amazonian biodiversity and biogeography. For nearly two decades, phylogeographic approaches have been applied to better understand the underlying causes of genetic differentiation and geographic structure among Amazonian organisms. Although this research program has made progress in elucidating several aspects of species diversification in the region, recent methodological and theoretical developments in the discipline of phylogeography will provide new perspectives through more robust hypothesis testing. Herein, we outline central aspects of Amazonian geology and landscape evolution as well as climate and vegetation dynamics through the Neogene and Quaternary to contextualize the historical settings considered by major hypotheses of diversification. We address each of these hypotheses by reviewing key phylogeographic papers and by expanding their respective predictions. We also propose future directions for devising and testing hypotheses. Specifically, combining the exploratory power of phylogeography with the statistical rigor of coalescent methods will greatly expand analytical inferences on the evolutionary history of Amazonian biota. Incorporation of non-genetic data from Earth science disciplines into the phylogeographic approach is key to a better understanding of the influence of climatic and geophysical events on patterns of Amazonian biodiversity and biogeography. In addition, achieving such an integrative enterprise must involve overcoming issues such as limited geographic and taxonomic sampling. These future challenges likely will be accomplished by a combination of extensive collaborative research and incentives for conducting basic inventories.

Keywords Amazonia · Terrestrial vertebrates · Biogeography · Evolutionary history · Phylogeography · Diversification hypothesis · Predictions · Coalescent

Introduction

The Amazon drainage basin is a major component of the Neotropical region that includes an area of over 8 million km^2 comprised mainly of lowland rainforest habitats (Sioli 1984). It extends across South America from the eastern Andean slopes towards the Atlantic coast and across the Brazilian and Guiana plateaus. There is large horizontal variation in relief across the basin (Bigarella and Ferreira 1985), and the overall warm and humid Amazonian climate also exhibits regional differences in precipitation and rainfall distribution (Salati 1985). Moreover, patterns of biotic composition and distribution have been influenced by a number of interrelated environmental features that have shaped the landscape development of Amazonia throughout its geological history (Hoorn et al. 2010c).

The analysis and interpretation of species evolution forms a strong basis for sustainable use and conservation planning strategies of species-rich regions such as Amazonia (Moritz 2002; Moritz and Faith 1998). Why Amazonia is so diverse relative to other regions on Earth is an important question in

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the discussion of large-scale species richness patterns. Time and variation in diversification rates are seen as major drivers of species richness patterns across different clades and regions, but this topic has been explored elsewhere (e.g., Mittelbach et al. 2007; Wiens 2011; Wiens et al. 2006). Nevertheless, understanding the link between Amazonia's intricate history and the mechanisms promoting and maintaining its high levels of species diversity remains a daunting task for evolutionary biologists (Moritz et al. 2000). Many alternative hypotheses have been proposed to explain species diversification in the Amazon Basin (reviewed in Haffer 1997). However, there is no agreement about the generality of any of these explanations, nor are they mutually exclusive (Hall and Harvey 2002; Patton and da Silva 1998). Difficulties exist in devising tests for competing hypotheses that lack temporal and spatial hierarchical division, as well as from the fact that organisms with inherently different life histories likely respond differentially to the same historical events (Moritz et al. 2000).

The integrative field of phylogeography plays a central role in elucidating the processes underlying patterns of genetic diversity at the species level (Avise 2000). Ever since its establishment as a discipline over two decades ago (Avise et al. 1987), phylogeographic methods have been employed to evaluate gene genealogies in a geographic context, and to infer biogeographic and demographic scenarios of interest (Avise 2009). More recently, advances based on the coalescent theory and technical developments have enhanced phylogeographic research (Knowles 2009) by establishing a rigorous statistical framework for the testing of explicit alternative models (Hey and Machado 2003; Hickerson et al. 2010). The coalescent is a retrospective approach that predicts the ancestry of DNA sequence samples (i.e., gene genealogies) under a mathematical model (Wakeley 2008). This theoretical approach forms the basis for a number of methodologies with varying assumptions that are implemented in different programs (Knowles 2004). Moreover, these methods are being applied to an increasing body of DNA sequence data derived from multiple loci (Brito and Edwards 2009) and from next-generation sequencing (Carstens et al. 2012; McCormack et al. 2012; Puritz et al. 2012). Therefore, the field of phylogeography is now equipped with innovative methods that will revolutionize the manner in which empirical data are evaluated. These new perspectives promise valuable insights for empirical studies concerned with species diversification in Amazonia.

Unfortunately, tropical countries lack many of the resources and infrastructure necessary to fully evaluate the mechanisms responsible for the formation and maintenance of their megadiverse biotas (Cracraft 2001). As a result, species-rich regions in the Southern Hemisphere such as

Amazonia have been understudied relative to temperate regions of the world (Beheregaray 2008). Additionally, there are a number of practical challenges involved in studying evolutionary processes governing Amazonia's biodiversity. These include insufficient biological inventories scattered over a vast area coupled with relatively high rates of habitat loss (Garda et al. 2010; Peres et al. 2010; Silva et al. 2005). Lastly, although terrestrial vertebrates comprise the majority of phylogeographic studies (Beheregaray 2008), only a small percentage of Amazonian mammals, birds, reptiles and amphibians has been evaluated.

In this context, we present a paleoenvironmental overview of the Amazon Basin to serve as a brief background of the historical settings considered in the formulation of Amazonian diversification hypotheses. We then proceed by reviewing major hypotheses of biotic diversification in light of the phylogeographic research achieved in Amazonia. We expand genetic and genealogical predictions derived from these major diversification hypotheses, and provide a synthesis of the current status of Amazonian phylogeography, focusing on terrestrial vertebrates. We also summarize information about the number of studies, their choice of genetic markers and analyses, as well as the distribution of targeted taxa in areas of endemism. Finally, we include an empirical example to illustrate how hypothesis-driven approaches can be used to discern alternative biogeographic scenarios and infer evolutionary processes involved in species diversification in the Amazon Basin. We discuss the prospects for future investigations with regard to phylogeographic approaches and suggest areas for new biological inventories in Amazonia. We anticipate that this review will improve the basis for the interpretation of the historical evolution underlying species diversity and distribution in Amazonia.

Historical setting

Geological processes have had great influence over the development of the Amazon Basin and its ecosystems. The modern drainage is the result of relatively recent geological events that caused drastic changes in the Amazonian landscape (Hoorn et al. 2010c), and account for much of the biotic diversification patterns seen today (Rull 2011, 2008). The debate on the geological history of Amazonia is as yet contentious; however, it gains momentum as geological studies present new data and insights into depositional patterns, drainage formation, edaphic variation, and past climate dynamics emerge (Hoorn and Wesselingh 2010). Linking both geological and biological data, as well as those derived from interdisciplinary

subareas, is key to interpreting patterns of biodiversity and biogeography (Riddle et al. 2008).

Several authors recently have emphasized the utility of placing inferences of the historical evolution of Amazonian organisms derived from molecular data within a geological context (e.g., Aleixo and Rossetti 2007; Antonelli et al. 2010; Pennington and Dick 2010). However, using a geological perspective for the design and testing of hypotheses of biological diversification in the Amazon Basin remains largely unexplored. This is complicated because geoscientific information over broad temporal and spatial scales is lacking due to difficult access to the terrain (Hoorn and Wesselingh 2010). As a result, geological frameworks attempting to resolve large-scale aspects of the history of the landscape in Amazonia (e.g., Campbell 2010; Figueiredo et al. 2009; Irion et al. 2005; Rossetti et al. 2005) often are subject to criticism and alternative interpretations of the data. Therefore, careful assessment of the historical settings should be made before any hypothesis can be applied as a working model to explain patterns of species diversity and distribution in the Amazon Basin. Nevertheless, the scarcity of solid paleoenvironmental data should not preclude Amazonian phylogeographic studies from exploring a priori hypotheses in experimental designs that seek to objectively integrate relevant information from biological and Earth sciences. Indeed, ad hoc explanations are potentially more misleading. Below, we summarize key aspects of the debate on geological history of the Amazon Basin and present alternative views of landscape evolution that are useful for interpreting species differentiation in a phylogeographic context.

Geology and landscape evolution

The modern Amazon Basin is composed of several sedimentary units that can be distinguished based on their distribution, age and composition (Bigarella and Ferreira 1985). However, the interplay of sedimentary processes, tectonics, and climate and sea level fluctuations controlling the geological history of Amazonia has been complex (Irion and Kalliola 2010). Perhaps one of the most striking characteristics of Amazonian geology is the dichotomy between eastern and western Amazonia (Aleixo and Rossetti 2007). To the east of Manaus, the Amazon drainage divides the Precambrian basement of the Amazonian Craton into the Guiana Shield to the north, and the Brazilian Shield to the south. These two regions constitute the source of most of the sediments of the intracratonic basins, with distinct fingerprints from sediments of Andean provenance (Kroonenberg and de Roever 2010). The sedimentary fill of the east–west trend rift separating the two shields was deposited during the Paleozoic, with renewed

subsidence in the Cretaceous and Cenozoic, although much less significant (Wanderley-Filho et al. 2010).

In contrast to eastern Amazonia, which remained mostly stable and had limited sediment deposition after the Late Cretaceous, western Amazonia experienced a much more recent and dynamic geological history (Aleixo and Rossetti 2007; Rossetti et al. 2005). This region is composed of numerous sedimentary units deposited during the Late Cenozoic (Hoorn 1994, 1993; Vonhof et al. 1998). Between Early and Middle Miocene, a distinct sedimentary record derived from the Andes is registered in western intracratonic and pericratonic basins, which marked the transition from craton-dominated fluvial systems to Andean-driven fluvio-lacustrine and lacustrine depositional environments (Hoorn et al. 2010a). The uplift of the Andes through the Late Miocene favored the development of a complex mega-wetland system with marginal marine influence, and the reversal of rivers flowing toward the west (Hoorn et al. 2010b; Hovikoski et al. 2010). Thus, throughout the Neogene, numerous geological transformations occurred in the western Amazon region and culminated with the establishment of modern landscape patterns (Fig. 1).

Detailed correlations between episodes of Andean uplift and drainage development remain to be described (Horton et al. 2010; Mora et al. 2010). However, tectonism in the northeastern Andes has played a major role in the genesis of the Amazon Basin, and an increased Andean deformation since the Late Miocene (Fig. 1a), presumably triggered the initial development of the transcontinental Amazon River (Figueiredo et al. 2009; Hoorn 1993; Hoorn et al. 1995). It was hypothesized that when the eastern margin of the Andes reached a critical elevation it became an orographic barrier that trapped moisture and supplied the western lowlands with greater sediment deposition. Then, overfilling of the foreland basin redirected the drainage towards the Atlantic and prompted the development of the transcontinental Amazonian network (Mora et al. 2010). In this context, the Amazon drainage basin acquired its modern configuration in the Pliocene, from ~7 Ma onwards, with the aid of global sea level changes (Figueiredo et al. 2009; Wesselingh et al. 2010). Support for the Late Miocene onset hypothesis comes from the initial buildup of the Amazon Fan at ~11 Ma, due to accumulation of Andean sediments in the Foz do Amazonas Basin (Figueiredo et al. 2009), and from the Ceará Rise, which increasingly received terrigenous sediments from the Andes off the Atlantic coast (Dobson et al. 2001).

Although Andean tectonism has been linked with the formation of major unconformities and depositional events throughout western Amazonia in the Miocene, Campbell et al. (2006) credited the establishment of the transcontinental drainage to terrain development within an erosional regime beginning in the Late Pliocene (~2.5 Ma). Under this scenario the Amazon River acquired its eastward flow by breaching the eastern rim of the
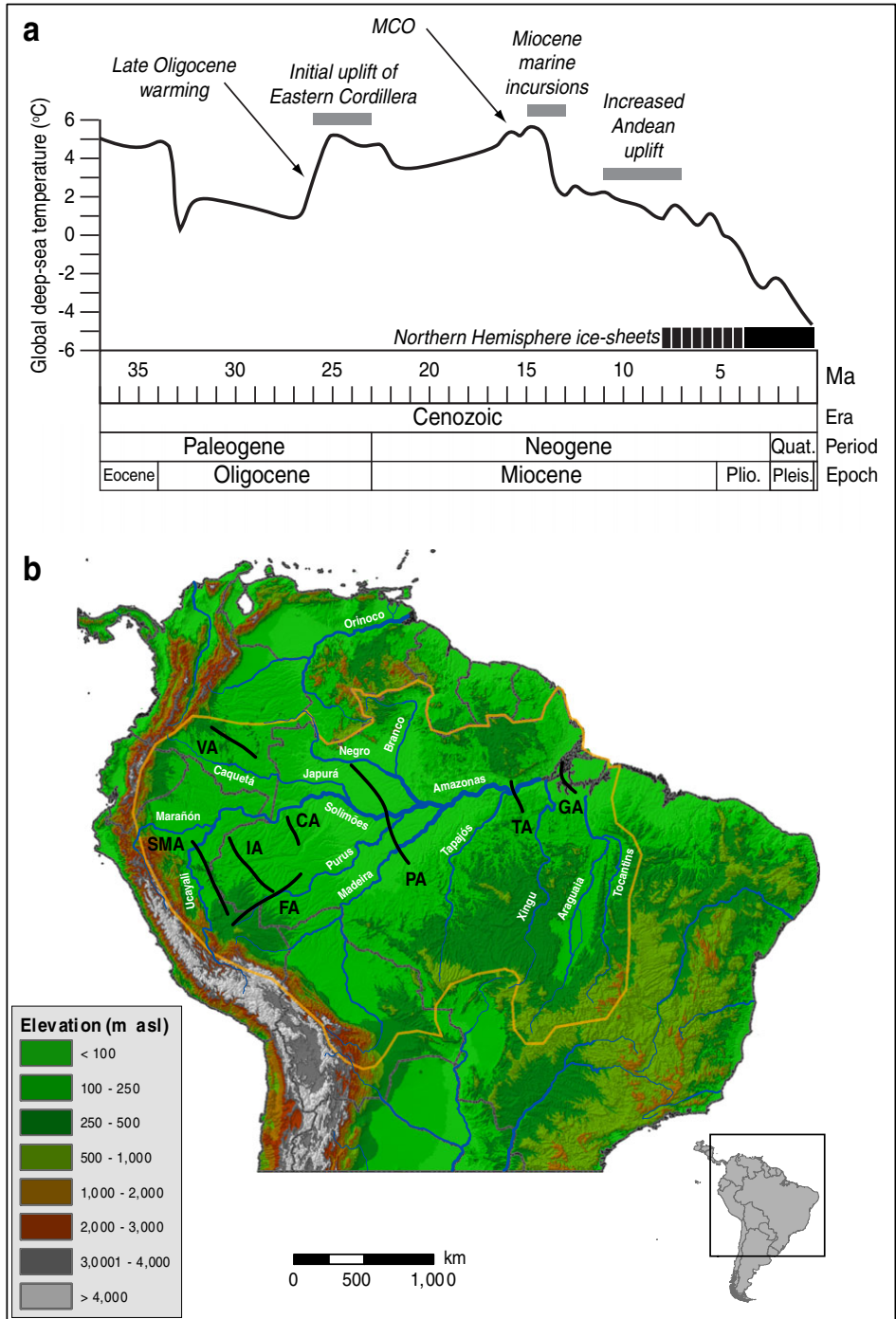
◀ **Fig. 1** **a** Schematic timeline of paleoclimate (adapted from Fig. 2 of Zachos et al. 2001) and major geological events in the course of Amazonian landscape development (based on Hoorn and Wesselingh 2010, and references therein). Ice coverage is represented by *dark dashed* (≤ 50%) and *full bars* (> 50% of present). **b** Present-day configuration of the Amazon drainage basin (*yellow outline*) depicting main rivers and presumed location of structural arches. *MCO* Miocene climate optimum, *Ma* mega-annum, *Quat.* Quaternary, *Plio.* Pliocene, *Pleis.* Pleistocene *GA* Gurupá Arch, *TA* Tapajós Arch (=Monte Alegre Arch), *PA* Purus Arch, *CA* Carauari Arch, *IA* Iquitos Arch, *SMA* Serra do Moa Arch (=Serra do Divisor Arch), *FA* Fitzcarrald Arch, *VA* Vaupés Arch (=Vaupés Swell)

sedimentary basin via overfilling, headward erosion of the proto-Amazon River, or both. Alternatively, Rossetti et al. (2005) proposed that the onset of the transcontinental Amazon did not take place until the Late Pleistocene. They postulated that Plio-Pleistocene fault reactivation caused subsidence of western Amazonia. After a period of stability and dominance of erosional processes, subsequent episodes of deposition resumed in the Late Pleistocene, which culminated in the development of the modern Amazonian drainage due to eastward fault reorientation, at ~32 ka (27,130±200 ^14C yr BP).

The limit between eastern and western Amazonian basins prior to the onset of the Amazon River also is contentious. Some authors suggest the site of this divide is contiguous with the Purus Arch (Rossetti et al. 2005) or that this feature conforms with the Purus Arch itself (Figueiredo et al. 2009), whereas its location can also be inferred further east on the Lower Tapajós Arch area (Campbell et al. 2006; Costa et al. 2001) (Fig. 1b). Most of these structural arches are buried under Cretaceous and Cenozoic sediments (Caputo 1991; Wesselingh and Salo 2006), and apparently have had no effect on deposition of Late Neogene–Quaternary sedimentary units of lowland Amazonia (Campbell et al. 2006; Rossetti et al. 2005). Conversely, distribution of the Solimões Formation, which is restricted to western lowlands, may suggest reactivation of the Purus Arch during deposition in the Miocene (Figueiredo et al. 2010).

Paleoclimate and paleovegetation dynamics

It is generally recognized that Amazonian plant diversity developed primarily during the Early–Middle Tertiary, when the climate was mostly warmer than today (Hooghiemstra and van der Hammen 1998; van der Hammen and Hooghiemstra 2000). Palynological records of the north-western Neotropics dating from the early Cenozoic suggest that plant diversity increased between the Middle Miocene and Pleistocene to reach its present-day levels (Jaramillo et al. 2006). Although the precise timing of this increase in floral diversity is unknown, seasonal rainfall patterns of Amazonia during the Miocene indicate that humid climatic conditions sufficient to sustain a rainforest existed as early as the Miocene Climate Optimum (MCO), at ~16 Ma

(Kaandorp et al. 2005) (Fig. 1a). Pollen records also support the existence of a *várzea* environment during Middle–Late Miocene. This type of rainforest seems to have persisted in the upper Amazon area despite a global cooling phase subsequent to the MCO (Hoorn 1994). Moreover, fossil trees dated from the Middle Miocene to the Pliocene demonstrate that the paleofloristic assemblage is comparable to the modern flora typical of terra firme lowland rainforests (Pons and De Franceschi 2007).

Despite important geological events, such as the Andean uplift and closure of the Panama seaway, and Milankovitch-driven climate cycles taking place in Neogene Amazonia, these potential influences on atmospheric circulation did not alter rainfall patterns in the Amazon Basin sufficiently to depart from a wet and warm tropical climate with monsoonal dynamics (Vonhof and Kaandorp 2010). Recent modeling of the effects of a lower relief during Andean uplift indicates that total precipitation remained fairly similar for the most part of the Amazon Basin, but because the Andes act as a moisture barrier for atmospheric circulation and influence zonal patterns of rainfall distribution, Amazonian climate likely experienced enhanced seasonality (Sepulchre et al. 2010).

Climatic alterations may have driven large-scale changes in the vegetation cover of Amazonia throughout the Cenozoic, with replacement of rainforests by relatively dry and open formations during cooler cycles, especially in the Pleistocene and early Holocene (Prance 1985). Records from the Ceará Rise support basin-wide Pleistocene climate variability (Harris and Mix 1999) and ice core paleoclimatic data (Thompson et al. 2000) reveal conditions of lower atmospheric humidity and precipitation at glacial stages, which suggest that rainforest cover was somewhat less extensive.

Paleoenvironmental interpretations, mostly of pollen records, assume that mean temperatures in Amazonian lowlands were at least 4 °C cooler at the Last Glacial Maximum (LGM) than today, which, coupled with an approximate reduction in precipitation of 30–50%, may have resulted in widespread aridity and savanna expansion relative to lowland rainforests (van der Hammen and Hooghiemstra 2000). However, the relationship between cooling and reduced precipitation is difficult to interpret from the available palynological records (Colinvaux et al. 2000; Hooghiemstra and van der Hammen 1998). Fossil Poaceae pollen is often used as a proxy for paleoclimate, and these data are subject to specific settings of local habitat conditions that can be misleading (Bush 2002). Moreover, Amazonian rainforests apparently have remained quite resilient to climatic conditions significantly drier than today since the LGM (Mayle et al. 2004; Mayle and Power 2008)

Likewise, reinterpretation of geomorphologic evidence linking glacial cycles with rainforest contraction due to increased aridity refute this hypothesis as a viable scenario for

the vegetation dynamics of Cenozoic Amazonia (Colinvaux and De Oliveira 2001; Colinvaux et al. 2000). Despite some reduction in precipitation during ice-age conditions in northwestern Amazonia, decreases in rainfall apparently were most evident in wet season precipitation (Bush et al. 2004), supporting the continuous presence of mesic vegetation throughout the Late Pleistocene. Pollen and organic matter composition of the Amazon deep sea fan also indicates relatively mesic conditions at the LGM (Haberle and Maslin 1999; Kastner and Goñi 2003). Moreover, paleodistribution modeling do not indicate significant expansion of South American dry biomes into the core of the Amazon Basin (Werneck et al. 2011, 2012b).

These lines of evidence favor the alternate explanation that lowland forest assemblages changed in composition as a result of invasions of heat-intolerant montane taxa during cooler and relatively drier periods, albeit with localized peripheral displacements of savanna/forest ecotones in the southwestern portion of the basin (Bush 1994; Colinvaux et al. 1996, 2000). Yet, such views are not necessarily exclusive, and climatic changes mirroring both hypotheses may have occurred in distinct areas of the Amazon Basin and at different times, depending on climate constraints related to local environments (Hooghiemstra and van der Hammen 1998; van der Hammen and Hooghiemstra 2000).

Diversification hypotheses

Since the nineteenth century, a series of hypotheses has been proposed to explain the unprecedented levels of biodiversity and biogeographic patterns present in Amazonia (Hall and Harvey 2002). These models typically invoke historical or ecological processes promoting species diversification, and generally are associated with environmental shifts in a geographic context. Nevertheless, unambiguous temporal and/or spatial hierarchical explanations often are missing, and such omissions can hamper an objective testing of alternative hypotheses (Moritz et al. 2000). In part, this is due to the overall incompleteness of supporting evidence, particularly paleoenvironmental data (Aleixo and Rossetti 2007), necessary to formulate explicit models of population structure and species differentiation (Carstens and Richards 2007; Hickerson et al. 2010; Richards et al. 2007). Indeed, the majority of studies addressing Amazonian biogeography and speciation have based their conclusions on occurrence data or descriptive phylogenetics, and only a few have derived genetic or genealogical predictions from testable hypotheses.

In this section, we briefly review the main hypotheses of Amazonian diversification, followed by a synopsis of the literature that includes findings relevant to our discussion. Objective hypothesis testing is a key step for thoroughly characterizing the phylogeographic history of any particular

organism or, in a comparative context, the historical evolution of entire communities (Knowles 2009). In fact, this theme is central to our review paper, and hence we elaborate on the distinct evolutionary signatures derived from these major diversification models. Despite previous attempts to generalize such expectations within the context of Amazonia's biotic evolution (e.g., Aleixo 2004; Antonelli et al. 2010; Bonvicino and Weksler 2012; Haffer 1997; Noonan and Wray 2006), former compilations were limited with regard to genetic and genealogical predictions especially at the phylogeographic level (i.e., intraspecific), which we now formally underscore in light of the recent advances of phylogeography (Table 1).

Riverine barriers

The earliest hypothesis to explain patterns of animal distribution in Amazonia was advanced by Wallace in 1852 (Wallace 1852). Based on observations of primate species separated by major Amazonian rivers, he divided the basin into four biogeographic areas dissected by the Amazon-Solimões, Negro and Madeira rivers. The riverine barrier hypothesis postulates that large ancestral populations become fragmented into subpopulations upon the formation of major rivers in a once continuous forested region (Sick 1967). The river then acts as a barrier to gene flow, and thus favors differentiation between populations isolated by rivers (Gascon et al. 1998).

Under this vicariance model, populations from opposite riverbanks form sister lineages that share a most recent common ancestor (MRCA) across major river intersections, in contrast with descendent populations that would otherwise coalesce within the same interfluve. Moreover, the genetic divergence between sister populations along margins is reduced towards the headwaters, as the width and flow rate of a river decrease, allowing for gene flow and ultimately cases of admixture in contact zones (Haffer 1997; Lougheed et al. 1999; Patton et al. 1994). Accordingly, the riverine hypothesis is not a strictly allopatric model because of nonzero migration rates, especially in the headwaters (Table 1).

Therefore, the effect of a river as a barrier is dependent largely on whether the focal organism has low vagility, resulting in relatively high levels of genetic differentiation. Likewise, it is conditional on the geography and formation history of the drainage system. For instance, rivers whose headwaters are located in open-vegetation formations, such as the *cerrados* of central Brazil (e.g., Tapajós, Xingu and Araguaia rivers), are expected to limit gene flow between populations from opposite banks conditional on the degree to which the area of contact reduced to gallery forests may have an effect of restricting the range of forest-dwellers. Also, river channels that undergo fluvial disturbance may passively transfer populations from one bank to the other due to meander cutoffs, especially carved into soft molasse beds, or

Table 1 Summary of major hypotheses of diversification in the Amazon Basin and their evolutionary implications

Hypothesis	Geographic barrier (divergence mode)	Timing	Differentiation mechanism	Genetic predictions	Genealogical effects
Riverine barriers	Amazonian rivers (allopatric)	From Late Miocene onwards depending on which river is considered	Development of major rivers separates populations into opposite banks—isolating effect is less pronounced in the headwaters as the river width and flow rate decrease	Population divergence is higher between opposite banks near the mouth of the river and decreases gradually towards the headwaters. Rivers whose headwaters extend into dry regions are expected to show higher levels of genetic variation between opposite banks. Rivers with meandering cut-offs are expected to have little or no differentiation between banks	Lineages from opposite banks coalesce with each other and form sister relationships before finding the most recent common ancestor (MRCA) of the gene copies from within the same interfluve—that is, assuming a small to moderate migrant exchange with each margin. There is some haplotype sharing between opposite banks in the headwaters owing to nonzero rates of migration.
Refugia	Savannas and/or dry forests (allopatric)	Cenozoic	Climatic cycles oscillating between arid and mesic conditions fragment populations in areas of favorable relief (refugia) during cooler periods, with subsequent rainforest reconnection during warmer periods	Bottlenecks during episodes of refugium contraction may affect populations with small effective sizes and lower their genetic diversity. Reduced variability is expected given rapid demographic growth following rainforest reconnection in postglacial periods—especially for long distance dispersers, and due to founder events in areas newly colonized by expanding populations. Relatively higher genetic diversity is expected in stable (refugia) versus non-stable areas, and in older (Late Tertiary) versus more recent (Pleistocene) refugia	At the time of a severe bottleneck most gene copies coalesce, and the topology has short terminal branches if the bottleneck was a recent event, whereas it resembles the topology of an expanding population if the event was older. The genealogical effect of a moderate bottleneck is similar to that of a subdivided population. A genealogy under exponential growth has relatively shorter branches closer to the root than one under a constant coalescent process. A genealogy that diverged more recently in the past has shallower terminal branches with relatively shorter time until MRCA
Gradients	None—environmental gradients (parapatric)	Quaternary	Contiguous populations differentiate along (steep) ecogeographic clines driven by selective adaptation to habitat variation and isolation by distance	Genetic differentiation increases with distance along the gradient due to local drift. Greater genetic diversity is expected towards the center rather than at the extremes of a gradient. Heterogeneous habitats at the middle of gradients may favor balancing selection and retention of polymorphisms. Homogeneous habitats at the opposite ends of gradients may promote directional selection and the fixation of adaptive traits	Sister lineages are expected along a gradient in adjacent but distinct habitats. Time to the MRCA increases with geographic distance separating sampled genes and lineage-split times (backward in time) are greater towards the center than near the ends of the gradient. Selected loci have a local effect on genealogies. When there is balancing selection and low mutation rate most genes coalesce within each allelic type before finding the MRCA, resembling the genealogy of a subdivided population with limited gene flow. When a favorable allele

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Table 1 (continued)

Hypothesis	Geographic barrier (divergence mode)	Timing	Differentiation mechanism	Genetic predictions	Genealogical effects
					becomes fixed due to strong positive directional selection the genealogy resembles one of rapid population growth
Disturbance–vicariance	Unsuitable cold-related rainforest conditions (allopatric)	Cenozoic	Temperature oscillations affect vertical distribution ranges and fragment populations into suitable rainforest patches according to fine-scale habitat heterogeneity—cooling promotes downslope invasions of cold-adapted organisms	Genetic differentiation is higher at the perimeter of the Amazon Basin (particularly where both montane and lowland taxa shift their distributional ranges vertically) than at the core. Genetic diversity is expected to be lower towards central Amazonia since rainforest invasion decreases. Given the presence of a central dry corridor during Pleistocene glaciations, rainforest taxa adapted to warmer conditions show relatively higher genetic exchange between western and eastern populations (especially during interglacial periods) as compared to cold-adapted taxa	Sampled genes coalesce within the proximity of major mountain ranges before finding a MRCA in adjacent lowlands located further away in the core of the basin. The genealogy fits into a model of ancient subdivision where ancestral polymorphisms are retained between western and eastern Amazonia. Ecological disturbance may have an effect on the adaptation of selective traits associated with distinct habitat requirements
Marine incursions	High eustatic sea level (allopatric)	Middle Miocene	Marine embayments isolate populations in large landmasses above high sea level stand	Genetic diversity in western Amazonia is lower than in other regions not submerged by marine incursions. Levels of differentiation within the eastern Andean slopes, the Brazilian Shield, or the Guiana Shield are higher than within the western Amazonian lowlands. Demographic decline and exponential growth may also be predicted—but their effect (if any) may be detected only for western lineages	Coalescent events within western Amazonia occur more rapidly and lineages have short branches. Western lineages descend from the eastern Andean slopes, the Brazilian Shield, or the Guiana Shield, and coalesce within each of those ancestral lineages until ultimately finding their MRCA. The genealogy has long internal branches characteristic of an ancestral subdivision between three major landmasses
Structural arches	Intracratonic and foreland geologic arches (allopatric)	Pliocene and older depending on which arch is considered	Uplifting structural arches divide rainforest habitats into different drainage compartments and fragment populations	Levels of population divergence within drainages separated by arches are expected to be lower than between-drainage levels of differentiation	A large ancestral population is broken up into two daughter lineages connected by long branches

tectonics (Cheviron et al. 2005; Haffer 1997; Patton et al. 1994; Räsänen et al. 1987; Salo et al. 1986).

Early studies of allozyme variation in understory birds of the Peruvian Amazon support the notion that rivers preclude the exchange of alleles between populations on opposite banks, with considerably higher between-population differentiation than within (Capparella 1988, 1992). Similar conclusions based on mitochondrial DNA (mtDNA) sequence distances of nonpasserine taxa also indicate that the Amazon, Solimões and Ucayali rivers function as barriers to gene flow (Armenta et al. 2005). In addition, analyses of passerine distributions revealed limited dispersal across the lower Amazon for forest species restricted to upland (*terra firme*) habitats (Hayes and Sewlal 2004). Upland woodcreepers showed evidence of genetic divergence among populations from opposite margins of clear-water rivers, namely the Xingu and Tapajós, situated in crystalline rocks of the Brazilian Shield (Aleixo 2004). Furthermore, the temporal framework for the establishment of major Amazonian rivers has been linked with patterns of cladogenesis in trumpeter birds (Ribas et al. 2012). Regional primate assemblages also were correlated significantly with river attributes such as width and flow rate (Ayres and Clutton-Brock 1992). Likewise, patterns of haplotype networks for tamarin subspecies were consistent with distinct pelage color on opposite banks and intermediate phenotypes in the headwaters of the Juruá River (Peres et al. 1996).

Nevertheless, studies in support of the riverine hypothesis are equivocal. For example, ten bird species representing diverse guilds across a headwater tributary of the Tapajós exhibit varied levels of genetic differentiation without obvious correlation between their morphology-based taxonomy and ecology (Bates et al. 2004), and two floodplain-specialist birds along the Amazon and its main tributaries lack a geographic structuring consistent with river barriers (Aleixo 2006). In a *terra firme* frog, spanning the Juruá, Napo and Madre de Dios rivers, there is support for population divergence in the last intervening river, but evidence of population expansion is indicative only of a secondary contact area (Funk et al. 2007). Moreover, phylogenetic analyses of tamarin species recovered non-sister relationships between taxa from opposite margins of the Juruá (Jacobs et al. 1995), suggesting that this river is not the primary diversification driver in these primates. Genealogical relationships of an arboreal echimyid rodent along the Juruá revealed closer affinities between mouth and headwater areas, and greater haplotype sharing across banks of the mouth than the headwaters (Patton et al. 1994). Similarly, allozyme variation and mtDNA sequence data of frog populations found in *várzea* (floodplain) and *terra firme* are at odds with the riverine barrier hypothesis (Gascon et al. 1996, 1998; Lougheed et al. 1999; Symula et al. 2003). It is important to note, however, that the Late Tertiary to Quaternary sediments that shape most of today's river valleys

in western Amazonia are prone to the long-term fluvial disturbance typical of meandering rivers (Räsänen et al. 1987), as opposed to the crystalline beds of eastern Amazonian rivers.

Refugia

The refugia hypothesis invokes vicariant processes (Haffer 1982, 1969), and is by far the most widely discussed model of diversification in Amazonia (Moritz et al. 2000; Prance 1982, 1985; Whitmore and Prance 1987). Following Haffer's (1969) initial observations that closely related species of birds typically exhibit parapatric distributions in the Amazon Basin, core areas of endemism were inferred as regions of past climatic stability, the so-called refugia. Haffer proposed that alternating climate conditions during the Pleistocene led to cycles of rainforest fragmentation and reconnection, such that savanna or dry forest formations expanded at the expense of lowland rainforests under the assumption that cooler glacial phases accompanied a significant increase in aridity. Forest patches restricted to areas where surface relief favored mesic conditions then formed refugia. Isolation of populations into different refugia promoted allopatric differentiation, with high levels of species diversity resulting from repeated fluctuations (Haffer 1997, 1982, 1969). More recently, Haffer's original refugia model has been modified to accommodate not only Pleistocene events but also climatic oscillations driven by Milankovitch cycles throughout the Cenozoic (Haffer 1997, 1993; Haffer and Prance 2001).

First assessments of the validity of refugia for several groups of vertebrates, invertebrates and plants were based on distribution ranges and secondary contact zones between closely related taxa, below or above the species level, and often combining present-day rainfall patterns or other geoscientific data (Whitmore and Prance 1987, and references therein). However, there is no solid evidence to support the notion that cooler temperatures during glacial times reduced precipitation to the point where dry vegetation surrounded rainforest blocks (see section on Paleoclimate and paleovegetation dynamics). Lack of temporal and spatial hierarchical structure among refugia also precludes a more objective testing of this model due to particularly intractable lineage divisions linked with different refugia (Patton and da Silva 1998). Moreover, the location of putative refugia and secondary contact zones are uncertain and may be discordant depending on the set of taxa investigated (Lynch 1988; Moritz et al. 2000).

Aside from these drawbacks, much progress has been made with regard to deriving and testing genetic predictions of the refugia hypothesis (Table 1). Episodes of refugium contraction are expected to inflict demographic bottlenecks on isolated populations (Aleixo 2004; Moritz et al. 2000). These can

also be associated with founder effects, which reduce the genetic diversity in areas colonized by expanding populations (Hewitt 2000). Another expectation of the refugia hypothesis is demographic growth following postglacial rainforest reconnection (Lessa et al. 2003; Moritz et al. 2000). Typically, a genealogy experiencing exponential growth has relatively shorter branches closer to the root than one with constant size. Also, the genealogical effect of a bottleneck depends on how long ago it occurred as well as its severity and length (Hein et al. 2005). The impact of genetic drift during climate instability is expected to be stronger on very small effective population sizes, which can drastically impoverish the gene pool, and most gene copies likely will coalesce at that time. If samples diverged more recently in the past (perhaps during the Pleistocene as opposed to the Tertiary), then coalescence time until the MRCA (TMRCA) is shorter with relatively shallower coalescent events.

Variance in dispersal abilities also produces differences in the genetic variability of postglacial recolonization, such that range expansion of long-distance dispersers exhibit relatively large areas with low genetic diversity (Hewitt 1996; Ibrahim et al. 1996). As in a strict allopatric model, migration between local populations is null or negligible owing to an inhospitable matrix of open dry vegetation separating refugia. Clearly though, the level of genetic structure corresponding to the geographic structure of a species depends on assumptions made about the ecology, physiology and behavior of organisms, and our ability to model those overall effects in a tractable and biologically realistic framework (Wakeley 2008).

Lack of support for the refugia hypothesis is derived primarily from estimates of divergence times predating Pleistocene differentiation for the majority of taxa evaluated (Antonelli et al. 2010; Moritz et al. 2000). However, rejecting long-term paleoclimatic fluctuations (driven by orbital forcing cycles; see above discussion) is more challenging (Patton and da Silva 2001). Moreover, studies dealing with Amazonian refugia typically restrict their inferences to the Quaternary.

Lessa et al. (2003) implemented coalescent-based estimates of the growth rate parameter to examine the demographic histories of both Neotropical and Boreal mammals during favorable environmental conditions. These authors showed that lowland Amazonia taxa had genetic signatures consistent with limited signs of population expansion. Likewise, there was support for ancient divergence without gene flow among lineages of frogs in the upper Amazon, but distinct clades exhibit somewhat weak and conflicting evidences of recent population expansion (Elmer et al. 2007; Funk et al. 2007). Thus, rather discordant signatures of sudden demographic growth seem to be the norm for forest taxa, as was also

suggested for populations from different refugial areas of geographically widespread leafcutter ants (Solomon et al. 2008) and a *terra firme* bird (Aleixo 2004).

Phylogeographic studies of nonforest taxa, with disjunct distribution in open formations across the intervening Amazonian rainforest, are equally important because they can provide novel perspectives on the role of past vegetation dynamics and climatic oscillations. For example, a contentious but appealing work about the Neotropical rattlesnake proposed a dispersal route between northern and southern populations via a trans-Amazonian central corridor of dry forest or savanna habitats, which supposedly fragmented the rainforest in the Early–Middle Pleistocene (Gosling and Bush 2005; Quijada-Mascareñas et al. 2007; Wüster et al. 2005). Divergence and karyologic variation of cane mice in northern Amazonian savannas also rest on the influence of climate-driven fluctuations during the Middle–Late Pleistocene (Bonvicino et al. 2009). In addition, the patchy distribution and genetic subdivision of the red-footed tortoise—an inhabitant of savannas and adjacent forests—were attributed to dispersal during episodes of rainforest contraction and later differentiation in isolation, despite predating the Pleistocene (Vargas-Ramírez et al. 2010).

Gradients

The gradient hypothesis differs fundamentally from other models because allopatric isolation is not required. It postulates that centers of endemism occur in areas of relatively uniform environment—or habitat conformities—between contact zones formed by ecogeographic clines. Thus, contiguous populations differentiate along one (sharp) environmental continuum, and adaptation to selective habitat conformities may lead to parapatric divergence in spite of gene flow (Endler 1977, 1982). The extent of habitat variation and environmental stress balance the rates of adaptive divergence and levels of genetic exchange and phenotypic diversity (Ogden and Thorpe 2002; Orr and Smith 1998; Smith et al. 2001; Smith et al. 1997).

The gradient hypothesis essentially is a model of isolation by distance (Endler 1982), in which sister lineages are expected along a gradient in adjacent but distinct habitats (Moritz et al. 2000; Patton and Smith 1992). Accordingly, geographically distant individuals show higher genetic differentiation due to localized genetic drift such that TMRCA increases with separating distance and time is greater towards the center than near the ends of a continuous range (Wilkins and Wakeley 2002). Geographic structure will arise with limited gene flow across the habitat space, resulting in a greater genetic diversity along the gradient's core than at more

uniform opposite extremes. In addition, adaptive selection can often be incorporated into environmental gradient scenarios (Table 1). Therefore, it is important to understand how different patterns of selection may affect the underlying population structure, albeit selected loci have a local effect on genealogies (Nordborg 2001).

In the case of balancing selection, which favors polymorphisms, most genes will coalesce within each allelic type before finding the MRCA if mutation is rare. This situation resembles the topological effect of a subdivided population when the migration rate is small. Thus, coalescence events occurring more rapidly within types (or *patches*) give rise to many short terminal branches, whereas long branches connect the ancestral lineages after sufficient time has passed to allow mutation (or *migration*) between types (Hein et al. 2005; Nordborg 2001). On the other hand, when a favorable allele becomes fixed due to strong positive directional selection (also termed a selective sweep) the genealogy of the selected locus will look like one of rapid population growth (Nordborg 2001). Moreover, linked neutral variation can be fixed each time a selectively favored substitution sweeps through a population (also termed genetic hitchhiking), such that repeated selective sweeps tend to decrease the genetic variability in a particular genomic region unless the local rate of recombination is large (Kaplan et al. 1989).

The gradient hypothesis (in its original formulation) lacks any explicit spatial configuration except for the vague presence of ecotones between the rainforest and adjacent habitats. It also assumes that population divergence is driven by contemporary ecogeography, thus over a relatively short period despite having no definite time boundaries. However, understanding how past climate oscillations influenced the dynamics of environmental clines becomes more difficult the deeper we extend them into the past. In addition, adaptation of selective traits and differentiation patterns among taxa depend on how different ecophysiologic and behavioral organismal requirements correlate with habitat attributes across the gradient. Therefore, choosing an appropriate framework for testing predictions of the gradient hypothesis ultimately involves a critical assessment of the range and ecological steepness of a cline, as well as resource availability for the organism under study.

The role of environmental clines in promoting differentiation among Amazonian taxa was assessed along the eastern slope of the Andes (Antonelli et al. 2010). Insectivorous mice across a steep elevational gradient in the Andean valleys of Peru showed closer affinities between taxa from the same altitude rather than vertically within drainages (Patton and Smith 1992). Additional observations contrary to expectations of a parapatric model of isolation were also found in birds (Dingle et al. 2006) and an upland frog (Funk et al. 2007).

Nevertheless, support for the gradient hypothesis is suggested by paraphyly among lineages of mountain and lowland tapirs (de Thoisy et al. 2010), although this branching pattern could result from incomplete lineage sorting due to recent diversification. However, the application of geographic information system (GIS) to model niche distributions in Ecuadorian dendrobatid frogs demonstrated that parapatric speciation is facilitated across environmental gradients because of divergent selection and those lineages have a symmetric and substantial overlap in their range (Graham et al. 2004). In addition, genetic and phenotypic variation in montane versus lowland poison frogs from northwestern Amazonia suggested a rapid selective divergence in coloration across transition zones (Roberts et al. 2006, 2007).

Disturbance–vicariance

The disturbance–vicariance hypothesis counters the Pleistocene refugia in explaining Amazonian diversification on the basis of temperature fluctuations per se, rather than forest fragmentation due to increased aridity (Bush 1994; Colinvaux 1993). It proposes that past climatic shifts caused repeated lowland invasions by montane lineages during cooling phases and retraction into elevated areas in subsequent warmer periods. Regions of local higher precipitation and relief, likewise refugia, promoted allopatric differentiation and acted as centers of endemism, albeit as a result of population maximal disturbance rather than environmental stability (Colinvaux 1993; Haffer 1997; Patton and da Silva 1998).

This hypothesis was further elaborated by Bush (1994), who acknowledged that a southeast-to-northwest corridor below 1,500 mm of annual rainfall might have facilitated dry forest expansion given a moderate rainfall reduction (~20 %) during Northern Hemisphere glaciations (Fig. 1a). However, most of the lowlands persisted as two large forested blocks, with dispersal routes for cold-adapted taxa limited along the western and southern Amazonian flanks. Hence, cooling primarily facilitated a reassortment of rainforest communities without modern analogues, while unsuitable fine-scale habitat conditions and local competitive exclusion throughout the Late Cenozoic climate oscillations promoted allopatric divergence (Bush 1994).

Under this scenario, differentiation is expected to be greater at the perimeter of the Amazon Basin than at its core, particularly in the Andean forelands and the Guianan highlands, where both montane and lowland taxa shift their distribution ranges vertically. In addition, genetic diversity is expected to decrease towards central Amazonia since the rate of rainforest invasion is less intense. Genes will therefore coalesce within the proximity of major mountain ranges nearby western or

eastern Amazonia before finding their MRCA, so that ancestral polymorphisms are retained. A model of ancient subdivision may also incorporate episodes of population bottleneck and demographic growth, and ecological disturbance may have an effect on the adaptation of selective traits in populations with distinct habitat requirements (Table 1).

Additional predictions of the disturbance–vicariance hypothesis were derived from a niche modeling approach to cold-adapted species of Andean origin. According to Lötters et al. (2010), the Late Miocene cooling allowed Andean lineages to disperse through the Amazonian lowlands and reach the Guiana Shield. However, during the subsequent Pliocene warming, cold-adapted species became isolated by the intervening lowlands and differentiated while isolated in montane habitats on either side of the Amazon Basin. Because the range of vertical displacement for populations in upland areas of the Guianas was more limited than for western populations in the Andes, Lötters and colleagues postulated that eastern lineages have shifted their climate envelopes as a means to survive warmer periods. Moreover, western and eastern lineages continued to diverge during the Pleistocene glacial phases as a result of a postulated barrier of dry forests in central Amazonia which prevented the exchange of migrants between Andean and Guianan populations.

Phylogeographic studies have generally overlooked the context of past climatic oscillations under the disturbance–vicariance hypothesis, but a few recent examples are available from studies of anurans distributed in the Guiana Shield. Harlequin toads and dyeing poison frogs (Noonan and Gaucher 2005, 2006) represent cold-adapted lineages descendants of Andean invaders from the Late Tertiary. Diversification occurred within rainforest patches across a mountainous relief during the Quaternary, which resulted in significant genetic divergence and structure among populations despite geographically proximate and undisturbed regions. Evidence for multiple Quaternary refugia isolated by unsuitable (dry forest/savanna) habitats and a concordant phylogeographic break among 11 other lowland frog species also provide support for the disturbance–vicariance hypothesis (Fouquet et al. 2012).

Marine incursions

Periodic marine incursions caused by eustatic sea level fluctuations throughout the Tertiary (Haq et al. 1987; Miller et al. 2005) were responsible for the formation of an interior seaway in the Amazon Basin (Räsänen et al. 1995). These marine embayments affected the patterns of Amazonian diversification as the lowlands were flooded extensively during high sea stands (Webb 1995) via maritime connections with the Caribbean and perhaps southern South America. The marine incursion hypothesis postulates that sea level rise isolated three large blocks of land corresponding to elevated areas in the eastern slope of the Andes, the Guiana Shield, and the Brazilian Shield, which, as a result, favored allopatric differentiation (Aleixo 2004). The Middle Miocene is typically used as the temporal predictor for assessing the eustatically (and tectonically) controlled marine influence in Amazonia (see Hovikoski et al. 2010) (Fig. 1a). However, there is another episode of marine incursion during the Late Miocene predominantly controlled by tectonic loading of the Eastern Cordillera fold-and-thrust belt (Hernández et al. 2005). There is still some uncertainty associated with the timing, duration and magnitude of these incursions (Haq et al. 1987; Miller et al. 2005).

Nores (1999) traced a contour line of 100 m above modern sea level to map endemic bird taxa in the context of marine incursions, assuming that the relief of Mio-Pliocene Amazonia did not greatly differ from present-day topography (at least with regard to his mapping procedure, which left the southern and westernmost parts of the basin out). He identified areas of endemism congruent with two large islands to the north of the Amazon River as well as several smaller islands and archipelagos along the coast of Guiana and at the periphery of the basin. However, its core region would have been completely below sea level and surrounded by islands and archipelagos. Thus, numerous opportunities for population divergence and speciation would have existed. Once the sea level retracted, viable populations occurring in high water-free areas were able to disperse and establish in the interior lowlands. Consequently, the expected genealogical outcome of the marine incursions is that western lineages will coalesce more rapidly, prior to the coalescence within each ancestral lineage descending from one of the major landmasses, until ultimately finding their MRCA after some time has passed. Long internal branches conforming to an ancestral subdivision are expected unless there is sufficient gene flow to prevent the retention of ancient polymorphisms (Table 1). Predictions of the marine incursion hypothesis may also incorporate episodes of population bottleneck and expansion (Solomon et al. 2008). Nevertheless, signatures of demographic decline or exponential growth will likely not be as apparent (if at all) for the long lasting lineages distributed in the eastern Andean slopes, the Brazilian Shield, or the Guiana Shield, compared to the more recent western lineages. In addition, the genetic diversity in the Amazonian core is expected to be lower in comparison to other regions of the basin.

Only a few studies have addressed some predictions of the marine incursion hypothesis, perhaps because this requires extensive geographic sampling. It is uncertain whether

Miocene marine incursions may have contributed to differentiation in leafcutter ants despite the fact that the timing of population divergence falls within that period range (Solomon et al. 2008). Nevertheless, upland passerine woodcreepers diversified mainly from ancestral populations known to the Brazilian Shield inasmuch as its endemics form basal clades relative to samples from western Amazonia (Aleixo 2004). On the other hand, the geographic patterns observed in riverine habitat specialists differ strikingly in that there are no marked genetic structures associated with their presumed high dispersal rates (Aleixo 2006; Cadena et al. 2011). In addition, floodplain woodcreepers represent relict lineages whose hypothesized mode of diversification is consistent with episodes of population bottlenecks (during low sea level stands in glacial periods) and recent expansion since the establishment of floodplain forests in eastern Amazonia in the Holocene (Aleixo 2006).

Structural arches

Structural arches constitute major geological features present in the basement of intracratonic and foreland basins of Amazonia (Cunha et al. 2007; Räsänen et al. 1990; Wanderley-Filho et al. 2007) (Fig. 1b). By and large, arches played a role as drainage dividers and in the shaping of habitat heterogeneity, and despite encompassing different origins and a variety of features (Wesselingh and Salo 2006), they reputedly have been considered important barriers in explaining allopatric differentiation (Lougheed et al. 1999; Patton and da Silva 1998). Their direct influence, as an uplifting structure, on the biotic diversification of Amazonia is nonetheless questioned in favor of a long-term edaphic control and mosaicism of the forest bed (Wesselingh and Salo 2006; see above discussion).

It seems that some arches remained inactive deep in the subsurface after deposition of Early Tertiary and older overlaying formations (e.g., Gurupá Arch and Lower Tapajós Arch) (Caputo 1991; Costa et al. 2001), whereas orogenic events in the Andean front during the Neogene accounted for a more dynamic role of other arches in reorganizing the Amazonian forelands (Räsänen et al. 1987; Räsänen et al. 1990). For example, uplift and dissection of the Vaupés Arch (Late Miocene–Pliocene) and the Fitzcarrald Arch (Pliocene) apparently confined rivers flowing parallel to the Andes during an underfilled stage and changed respective paleocurrent directions (Espurt et al. 2010; Roddaz et al. 2010), which in turn rearranged drainage divides and catchment areas creating dynamic mosaics of the forest bed (Mora et al. 2010) for the associated biota. Also, the relief of the Carauari and Iquitos arches seem to have exerted some control

on the development of transverse megafans in the Late Miocene–Pliocene (Wilkinson et al. 2010).

Although largely undescribed, the timing and spatial configuration of the various geological arches present in the Amazon region, along with knowledge about their development and control patterns, are key elements for devising realistic hypothesis tests that relate to lineage splitting events and geographic structuring. Predictions of the structural arches are derived from a classical model of vicariance, wherein a large ancestral population is broken up into two sister populations and the specified arch forms the isolating barrier between them (Table 1).

The role of arches in promoting population differentiation was assessed for small mammal assemblages in western Amazonia, where deep phylogeographic breaks across the central section of the Juruá River, concordant with the hypothesized location and orogenesis of the Iquitos Arch, were identified for a number of rodents and marsupials (Patton and da Silva 1998; Patton et al. 2000). Similar conclusions were proposed for a dart-poison frog that also occurs along the Juruá (Lougheed et al. 1999). Finally, the location of several structural arches is generally consistent with the differentiation patterns of another group of poison frogs throughout most of the Amazon Basin, although the error associated with divergence time estimates were too broad to distinguish between vicariance due to the formation of geological archers or Miocene marine incursions (Symula et al. 2003).

Advances in Amazonian phylogeography

A series of studies have used a phylogeographic approach to explore hypotheses concerning the biogeography and evolution of terrestrial vertebrates distributed in the Amazon Basin and surrounding regions (e.g., Aleixo 2004; Cheviron et al. 2005; Noonan and Gaucher 2005; Patton et al. 2000; Quijada-Mascareñas et al. 2007; Vargas-Ramírez et al. 2010). These analyses provided valuable insights into the evolutionary processes underlying Amazonian diversification (Aleixo and Rossetti 2007; Antonelli et al. 2010; Moritz et al. 2000). However, phylogeographic inferences can attain a greater appreciation of the forces that govern population structure and divergence by incorporating the latest theoretical and methodological developments of phylogeography (Emerson and Hewitt 2005; Hickerson et al. 2010). As knowledge about Amazonia's paleoenvironmental history as a whole is still being compiled (Hoorn and Wesselingh 2010), such an integrative phylogeographic approach could aid in the formulation of an overall framework tying landscape and species evolution in Amazonia.

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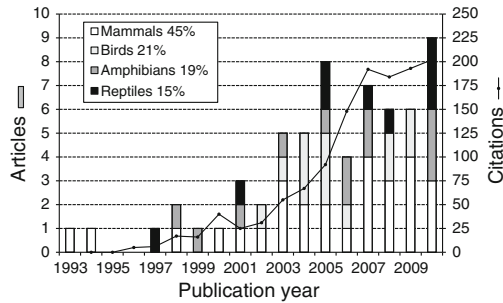
Fig. 2 Number of articles on Amazonian phylogeography sorted by major group of terrestrial vertebrates with corresponding number of citations; published from 1993 to 2010

including bird papers, and citations associated with this topic (Fig. 2). In the course of the nearly 20 years since da Silva and Patton's pioneering publication, studies dealing with mammals and birds, respectively, have comprised the majority of papers, which altogether correspond to two-thirds of all articles. The proportion of studies per taxonomic group is only a rough indication of the existing bias towards specific vertebrate taxa in Amazonia, as it does not reflect previous compilations of species richness for those groups (see Silva et al. 2005). It is also important to note that the current taxonomic knowledge of Neotropical biodiversity is changing. For example, the rate of mammalian species descriptions greatly exceeds that of birds in the Neotropics (Patterson 2000), and the number of reptile (Rodrigues 2005) and amphibian (Funk et al. 2012) species in Amazonia is grossly underestimated. This suggests that a greater deal of attention should be paid to such understudied taxa, but at the same time it does not mean that "well-studied" groups deserves lesser consideration in future phylogeographic studies. Indeed, there are sampling discrepancies even within "well-studied" groups and many collection gaps for virtually all species in the Amazon region that otherwise hamper any direct geographic and taxonomic comparisons.

To help illustrate trends of studies dealing with phylogeography of the Amazon region, we searched for scientific articles in the Web of Science^SM and Zoological Record® databases. Details of how we performed queries and treated records are available at the Appendix S1 in the Supporting Information. Although the results of our search are limited to articles from online databases, they serve as a general proxy for phylogeographic investigations focusing on Amazonian terrestrial vertebrates. Moreover, our discussion about current progress and future perspectives of Amazonian phylogeography encompasses a broader view of the field since it is not constrained by the records retrieved from those databases.

The first Amazonian phylogeographic study dealt with arboreal echimyid rodents as inferred from mtDNA haplotypes (da Silva and Patton 1993). This benchmark paper was followed by other contributions involving mainly small mammals, anurans, and lizards. A decade passed before there was a conspicuous increase in the number of articles,

The bulk of Amazonian phylogeographic papers have employed analyses of mtDNA sequences; used in 86% of the studies, followed by 10% and 3% of articles that also used nuclear sequence data (nuDNA) or microsatellites, respectively (Fig. 3). Of course, mtDNA offers some advantages for intraspecific studies over the use of nuclear markers because haploid mitochondrial genes have relatively high levels of informative polymorphisms due to shorter coalescent times as a result of smaller effective population sizes (Moore 1995). Moreover, mtDNA sequence data are relatively easy to generate, and there is no need for haplotype phase determination of heterozygous sites or testing for recombination. However, inferring population history based

Fig. 3 Number of Amazonian phylogeographic studies sorted by the types of molecular markers used; published from 1993 to 2010
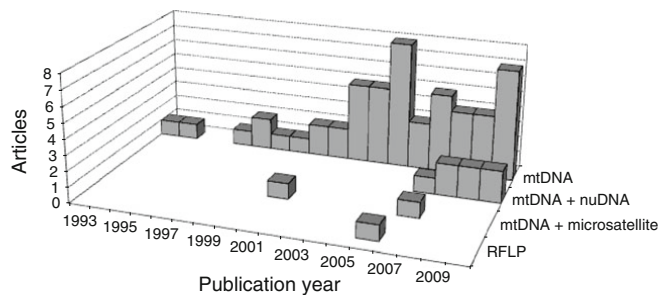
solely on this class of marker can be misleading, because the mitochondrial genome is inherited maternally as a single-linkage unit (Ballard and Whitlock 2004). The acquisition of nuclear data typically is more labor-intensive, but it can greatly extend the phylogeographic inferential approach with genealogical comparisons across unlinked loci (Brito and Edwards 2009; Edwards and Beerli 2000; Hare 2001). More recently, nuclear markers have been incorporated into phylogeographic inferences in Amazonia (Fig. 3), although these efforts are as yet modest.

Traditionally, phylogeographic studies have made historical inferences by describing hypotheses that underlie patterns of genetic diversity embedded on gene trees (Carstens et al. 2005; Garrick et al. 2010). This qualitative approach typically is combined with some measure of genetic variance within and among populations (see Pearse and Crandall 2004). Another common practice is to utilize molecular dating methods that do not take into account the stochastic variance of coalescence times in gene trees and assume equivalence between the timing of gene divergences and speciation events in the population history (see Knowles and Maddison 2002; McCormack et al. 2011). Recent meta-analyses lumping together various estimates of gene divergences for Neotropical biodiversity at the species-level (Rull 2011, 2008), disregard that gene trees contained in population trees produce dates that are overestimates of the population divergences (Arbogast et al. 2002; Edwards and Beerli 2000).

Descriptive assessments of topological relationships reconstructed via phylogenetic methods are routinely applied in studies of Amazonian phylogeography using varied taxonomic and geographic sampling. In this context, ad hoc explanations are devised to fit a posteriori hypotheses dealing with aspects of species diversification, such as population structure, historical biogeography or systematics. Exploratory analyses are important because they aid in the delineation of key evolutionary processes and provide a basic understanding of putative barriers or geological events and paleoenvironmental scenarios that are of interest in phylogeographic inferences (Garrick et al. 2010). Although, the majority of these studies lack a rigorous statistical framework of model-based inferences, integration of exploratory and model-driven approaches is what makes phylogeography a fundamental discipline for expanding research on Amazonian diversification. As a result, this discipline plays a central role in both testing existing hypotheses and generating new ones, the latter of which should be explored in more depth during the upcoming years.

Recently, studies also have combined several different analytical methods to examine questions about the evolutionary history of Amazonian organisms. Depending on the scope of the study and the set of assumptions regarding relevant biological properties of the target group, these analyses include (but are not limited to) topological tests, nested clade phylogeographic analyses, tests of neutrality and demographic equilibrium, as well as coalescent-based simulations and estimates of demographic parameters. Despite potential problems associated with the latter as to model misspecification and violation of underlying assumptions (Garrick et al. 2010; Nielsen and Beaumont 2009), model-based coalescent methods offer a robust statistical framework upon which alternative evolutionary scenarios and multiple genetic processes can be accommodated in models of population history (Knowles 2004, 2009). Moreover, coalescent methods explicitly consider the inherent variation in mutation rates and the stochasticity of genealogical processes (Knowles and Maddison 2002). Therefore, this model-driven approach has enabled testing of a priori hypotheses and estimation of biologically relevant demographic parameters useful for making phylogeographic inferences (Beaumont et al. 2010).

Phylogeographic studies in the Amazon Basin just have begun to explore some advantages of coalescent-based inferences, mostly by employing coalescent software for parameter estimation; also called genealogy samplers (see Kuhner 2008). These programs, which are available under different coalescent models and assumptions, calculate posterior probabilities or maximum likelihood estimates of various demographic parameters such as effective population sizes, migration rates and divergence times. Some findings that illustrate the application of coalescent-based estimates of demographic parameters on Amazonian phylogeographic studies include scenarios of recent (Quaternary) divergence coupled with negligible migration rates among populations of harlequin frogs (Noonan and Gaucher 2005), highly variable lineage-split times in several butterfly taxa distributed across a suture-zone (Dasmahapatra et al. 2010), and lack of substantial evidence for population growth in western small mammals (Lessa et al. 2003). In addition, DNA sequence data simulated along constrained gene trees under neutral coalescence were used to generate null distributions and test the fit of empirical data against a priori hypotheses concerned with the population history of dyeing poison frogs and lowland tapirs (de Thoisy et al. 2010; Noonan and Gaucher 2006). More recently, Fouquet et al. (2012) employed approximate Bayesian computation to test the synchrony of lineage-splits across 12 leaf-litter frog species codistributed in eastern Guiana lowlands. We provide an empirical illustration of how to explicitly design and test alternative models of Amazonian diversification under a coalescent-based approach in Box 1. Additional non-Amazonian examples on the use of coalescent-based analyses as well as complementary analytical methods to phylogeographic inference are reviewed in Garrick et al. (2010).

Box 1. Empirical example of how to design and test alternative hypotheses of Amazonian diversification within an explicit biogeographic context

Herein, we illustrate how competing models of population divergence in the Amazon Basin can be formulated and tested using a coalescent-based framework. Geological and paleoecological evidences (Salgado-Laboriau 1997; Costa et al. 2001; Rossetti and Valeriano 2007; Valente and Latrubesse 2012) suggest that neotectonics and climate fluctuations have played a role on the landscape formation of southeastern Amazonia. Specifically, such events were key for the configuration of modern drainage systems (e.g., Xingu and Araguaia/Tocantins sub-basins) and establishment of the ecotonal area between the Amazonia and Cerrado biomes, thereby shaping the phylogeographic history of forest-dwelling taxa found both in southeastern Amazon rainforests and Cerrado gallery forests. In this example, populations of the terrestrial spiny-rat *Proechimys roberti* (Fig. 4) are structured geographically at three divergent mitochondrial clades distributed, from west to east, in plateau (*orange*) or fluvial depression (*light blue*) areas of the Xingu–Araguaia/Tocantins interfluve, or east (*pink*) of the Araguaia/Tocantins drainage system (Fig. 5a), whereas there is substantial haplotype sharing across populations at multiple independent nuclear loci (Fig. 5b–f), indicating that elapsed time has been insufficient for complete lineage sorting since population divergence due to landscape rearrangements.
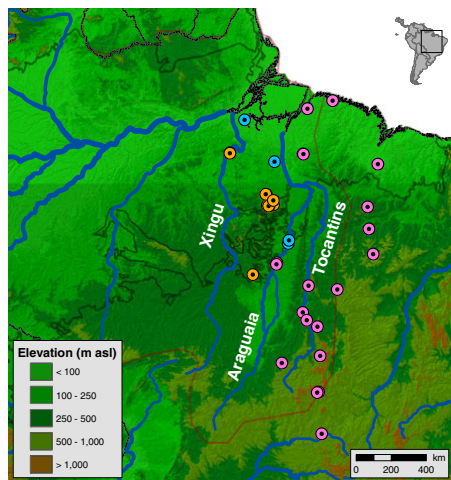
Fig. 4 Distribution of *Proechimys roberti* in plateau (*orange*), fluvial depression (*light blue*), and eastern (*pink*) populations. Major rivers are depicted in blue. Contour lines represent limits of the Amazon drainage basin (*red*) and Amazonian biome (*dark gray*)
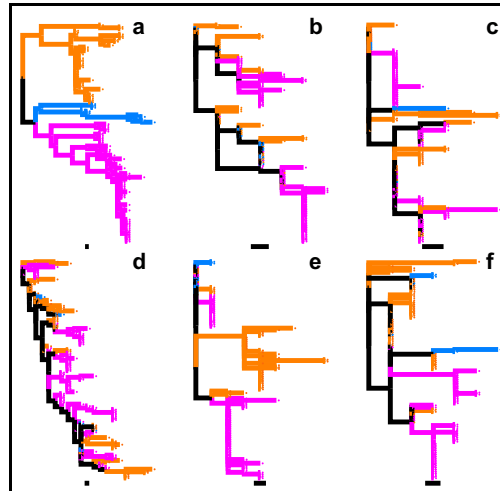
Fig. 5 Gene genealogies estimated for samples of *Proechimys roberti* from **a** one mitochondrial and five nuclear loci **b**–**f**. Colors correspond to plateau (*orange*), fluvial depression (*light blue*), and eastern (*pink*) populations, as referred in the text and map. *Scale bars* are drawn to proportion and equal 0.001 substitutions/site

Two competing hypotheses can be formulated according to this scenario: (1) establishment of the paleo-Tocantins River (Costa et al. 2001; Rossetti and Valeriano 2007) in the Plio-Pleistocene may have isolated *P. roberti* ancestral population within the interfluve region bounded on the west by the Xingu and on the east by the present-day Araguaia and lower Tocantins rivers (Fig. 4). More recently, formation of the fluvial depression of the Araguaia/Tocantins drainage basin in the Middle Pleistocene (e.g., Valente and Latrubesse 2012) may have prompted the differentiation of *P. roberti* into plateau and depression populations (LIM: late interfluve model). Capture of the lower Tocantins, due to fault reactivation with abandonment of the paleovalley (Rossetti and Valeriano 2007), and development of the Amazonia-Cerrado ecotone (e.g., Salgado-Laboriau 1997) during the Late Pleistocene may have promoted eastward expansion via the lower Tocantins or through gallery forests in the Araguaia/Tocantins headwaters, with subsequent differentiation between depression and eastern populations (Fig. 6a); (2) Alternatively, *P. roberti* ancestral population may have differentiated into western and eastern populations upon the formation of the paleo-Tocantins River (ERM: early riverine model), while development of the Araguaia/Tocantins fluvial depression may have driven divergence between western counterparts into plateau and depression populations (Fig. 6b). Establishment of the ecotonal region and reorganization of the lower Tocantins may have facilitated gene flow between these areas, but no significant

population expansion would be expected. This historical scenario, which is currently under investigation involving a comprehensive sampling (R.N. Leite et al., manuscript in preparation), has broader implications for Amazonian phylogeography as it illustrates the type of questions that can be considered within a testable hypothesis-driven framework.
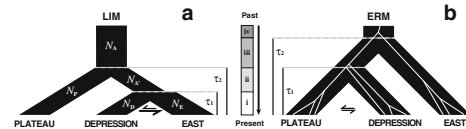
Fig. 6 Two competing hypotheses of population divergence for *Proechimys roberti* in southeastern Amazonia: **a** Late Interfluve Model, LIM; and **b** Early Riverine Model, ERM. Distinct divergence times (τ) and migration rates (*horizontal arrows*) are represented in schematic models **a** and **b**. Effective population sizes (*N*) also are shown in **a**—note the expanded size in eastern population, and a hypothetical gene genealogy is depicted in **b**. Letters in vertical timeline correspond to: (i) Late Pleistocene; (ii) Middle Pleistocene; (iii) Early Pleistocene; and (iv) Pliocene

Biogeographic hypotheses such as above—for example, derived from paleogeographic information—imply alternative population structures that can be modeled explicitly to reflect relevant attributes of the population history (i.e., population tree), and which can be tested statistically using a coalescent-based approach (see Hickerson et al. 2010, and references therein). The goal is to build simple yet biologically realistic models that are able to discriminate among alternative hypotheses. Gene genealogies mirroring demographic conditions of the organism's history are simulated by a neutral coalescent process within each model of population structure, and sequence data are simulated on these genealogies. Each of the simulated data set is then used to calculate a summary statistic that characterizes the data and a large number of replicates provides a null distribution for the summary statistic. The expected patterns of genetic variation corresponding to each hypothesis are evaluated by the fit of the observed data to the null distributions generated from these coalescent simulations, that is, the ability to reject or fail to reject the respective population model.

Historical scenarios may also be investigated using fully probabilistic methods that calculate from the molecular data demographic parameters under a specific coalescent model. Combined with a simulation approach and after careful consideration of the different underlying assumptions of these coalescent-based methods, parameter estimates provide an opportunity to understand in more detail evolutionary processes governing population structure. For example, estimates of effective population size and growth rate may reveal episodes

of bottleneck or population expansion, whereas migration rate estimates are useful for distinguishing patterns of gene flow. Moreover, divergence time estimates offer not only a quantitative framework for evaluating the timing of differentiation between populations, but also a means to assess the appropriateness of external sources (e.g., geological events) of divergence time used in simulations. Specifically, for *P. roberti* this means asking whether there is a significant signature of population expansion towards the east; whether migration between depression and eastern populations vs plateau and depression populations is appreciable considering both direction and magnitude of gene exchange; and whether divergence times support a model of late interfluve vs early riverine history of population differentiation (Fig. 6).

The Amazon region is not a homogeneous biogeographic unit. Rather, species distributions tend to form clusters arranged in a mosaic of different areas of endemism. Given that each harbors unique biotic assemblages (López-Osorio and Miranda-Esquivel 2010; Silva et al. 2005), these areas are useful for a basic understanding of Amazonian diversity and historical evolution. Hence, we counted how many times each area of endemism was covered by the taxon sampling in articles included in our survey. Although we recognize this is a very simplistic evaluation of the geographic complementarity of empirical studies in Amazonia, an exhaustive spatial analysis (see Kress et al. 1998) is beyond the scope of this review. Nevertheless, our assessment serves as an indication of how phylogeographic sampling efforts have been distributed in terms of the Amazonian areas of endemism, which seems appropriate since information about these areas can be used in conservation planning (e.g., López-Osorio and Miranda-Esquivel 2010).

The percentage of papers published among the eight Amazonian areas of endemism (according to Silva et al. 2005) illustrates obvious regional differences resulting from skewed taxon sampling (Fig. 7). More importantly, it demonstrates which areas have received less attention. Although some studies directed their efforts towards the Guiana and southwestern Amazonian areas (i.e., Napo, Inambari and Rondônia), fewer studies sampled the Imeri and other areas of endemism to the southeast (i.e., Xingu, Tapajós and Belém).

Remarkably, the former areas of endemism also were identified as the most valuable for conservation according to various diversity metrics based on evolutionary information (López-Osorio and Miranda-Esquivel 2010; Silva et al. 2005). However, areas ranked with the highest conservation priorities generally correspond to areas with ample collecting efforts (Kress et al. 1998; Nelson et al. 1990). Few areas in Amazonia have been inventoried in a fashion to permit definite conservation recommendations (Laurance 2005), but the disproportionate number of phylogeographic studies illustrated in Fig. 7
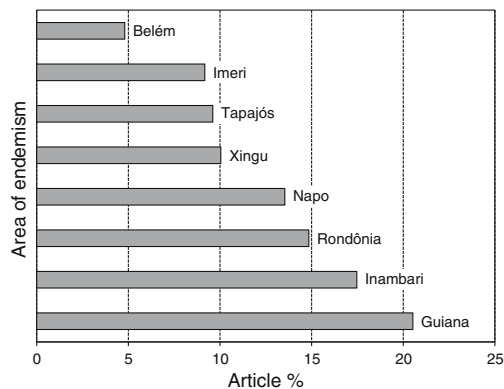
Fig. 7 Percentage of phylogeographic studies in each Amazonian area of endemism (according to Silva et al. 2005); published from 1993 to 2010

emphasizes that some of the least sampled areas, such as Xingu and Belém, also are among the most vulnerable and unprotected (see Silva et al. 2005). In addition, the Xingu figures as the second most critical area of endemism to preserve for complementary purposes (López-Osorio and Miranda-Esquivel 2010).

Future perspectives

It is clear that questions about the historical evolution of Amazonia's vertebrate biota, including the role of putative barriers and the relative influence of climatic and geological events for shaping present-day patterns of species diversity and distribution, have been refined by means of a phylogeographic approach. Based on our review of major diversification hypotheses and the emphasis given to an explicit hypothesis testing approach, together with our empirical example of how coalescent-based inferences can shed light into current trends of Amazonian phylogeography, we evaluate which directions investigators should consider in future research. We agree with Bush's assertion (1994) that no single model can indisputably explain the complex evolutionary history of the Amazon Basin and its biota. Indeed, the available hypotheses account for non-exclusive and simplified views of a handful of differentiation mechanisms (Moritz et al. 2000). Although a lack of consensus regarding geological and paleoclimatic events preclude an elaborate scheme to explain the history of Amazonian landscape and ecosystems, phylogeographers need to make the most of the existing data to aid in the analysis of population divergence and demographic histories, especially when trying to discriminate among alternative evolutionary scenarios. Nevertheless, the fortune of Amazonian phylogeography largely depends on implementing hypothesis-driven designs that are appropriate in terms of geographic sampling, target taxa, and molecular markers for the biological questions being considered.

At present, collection efforts are distributed unevenly among various taxonomic groups and account for sharp sampling disparities. This situation is probably due to the synergy between localized specimen collecting and an insufficient number of investigators working in the Amazon region. Moreover, research centers often undertake the challenge of accessing pristine areas to do fieldwork without collaboration from other institutions. All things considered, Amazonian phylogeography needs to expand its human resources, both in numbers and extent, across a diverse array of taxonomic expertise if we want to overcome intrinsic sampling biases and gain a detailed historical perspective.

Although mtDNA likely will continue to be the workhorse of future phylogeographic investigations (Zink and Barrowclough 2008), the potential utility of nuclear markers remains largely unexplored in Amazonian studies. Clearly, datasets incorporating nuDNA sequences, single nucleotide polymorphisms or microsatellites are better suited for inferring population genetic processes when based on genomic regions that offer informative variation at the population level (Brito and Edwards 2009; Hare 2001; Sunnucks 2000; Thomson et al. 2010), such as introns, anonymous nuclear loci, and highly polymorphic microsatellites (e.g., Bowcock et al. 1994; Lee and Edwards 2008). Nevertheless, assaying nuclear loci is not as straightforward as using markers from haploid genes, which can ultimately impact the number of populations screened and sample sizes evaluated (Garrick et al. 2010). However, advances in genomic technologies are expected to appreciably expand the cost-efficiency of sequencing multilocus datasets for use in phylogeographic studies with multiple individuals per population (Brito and Edwards 2009).

Spurious interpretations of the underlying population history may arise if discordance among reconstructed gene trees is ignored (Maddison 1997). However, when heterogeneity in topology and coalescent times from gene trees is taken into account appropriately, model inferences and demographic parameter estimates plus associated confidence intervals show improved accuracy overall (Carling and Brumfield 2007; Edwards and Beerli 2000; Felsenstein 2006). There is increased opportunity for Amazonian phylogeographers to add multiple independent loci that can capture a clearer view of the evolutionary processes shaping species diversity in the region. Variable nuclear markers are becoming more widely available for non-model species, and analytical methods are expected to improve on sophistication and flexibility to accommodate large amounts of data assembled via next-generation sequencing (Wakeley 2004). Nevertheless, research groups will have to consolidate the necessary laboratorial and computational infrastructure for widespread use of multiple loci and genome-wide datasets, which can be particularly challenging for the scientific community of developing Amazonian countries. Brazil has shown increased albeit incipient interest in scientific and technological innovation through investments in infrastructure and

education (Lemos 2012; Massarani 2012), an example to be adopted by and fully integrated among those nations.

In the meantime, phylogeographic studies based on single-locus datasets can be used as a "first pass" in making historical inferences about Amazonia's intricate ecosystems and biotic communities. For the same reason, exploratory methods will continue to contribute with de novo working hypotheses that form the basis for a detailed analytical framework (Garrick et al. 2010). However, assessing genealogical concordance of a collection of gene trees with tree-based approaches is rather cumbersome, particularly when attempting to account for complex historical scenarios because these methods disregard the inherent stochasticity of genetic processes (Brito and Edwards 2009).

In this context, coalescent theory provides a powerful mathematical framework in deriving common patterns of population ancestry drawn from a set of gene trees (Hey and Machado 2003), while offering statistical discrimination among alternative models (Nielsen and Beaumont 2009). The so-called statistical phylogeography posits a shift in how historical inferences are made by explicitly considering the stochastic variance of mutation and coalescence of gene lineages, as well as the processes generating genetic structure (Knowles 2004; Knowles and Maddison 2002). Hence, there are many possible historical scenarios in Amazonia amenable to testing via a coalescent-based approach (Table 1).

Although coalescent methods represent novel prospects for thoroughly evaluating genetic structure and population divergence, the decision on which analyses to use should be based on careful consideration of the underlying assumptions of each method. Otherwise, inferences may not capture any signal from the data or render incongruous results (Garrick et al. 2010). Moreover, the ability to formulate an objective experimental design ultimately rests on the researcher's ingenuity in translating plausible historical scenarios into a hypothesis-testing framework (Knowles 2009). For this reason, phylogeographic studies need not to be constrained by long-held biogeographic hypotheses in explaining Amazonian diversification. To the contrary, development of novel models will be required, or some combination of portions of available models may be appropriate for the study system under investigation (see Box 1 for an example). Nevertheless, such a decision depends on the manner in which historical scenarios may have affected target organisms. Therefore, acquaintance with the particulars of the paleogeographic setting is critical for devising and testing meaningful evolutionary hypotheses. With a good grasp of the study system, and given adequate taxon and geographic sampling, phylogeographers can put forward biologically realistic models that are readily testable.

There may be some occasions when plausible a priori hypotheses will comprise a variety of alternative candidate models, and researchers will be unable to differentiate among fail-to-reject null models (Anderson et al. 2000). This can be

the case for phylogeographic studies dealing with complex evolutionary histories in Amazonia. However, information-theoretic methods provide a means of measuring the fit of candidate models relative to one another, and so the ranking of alternative hypotheses can be used to scrutinize the influence of demographic processes or historical events shaping population structure (Carstens et al. 2009). In any case, informed methods of analysis should make comprehensive use of the historical features that might be relevant in the evolutionary context of any particular organism or biotic community while delimiting phylogeographic hypothesis (Buckley 2009).

For example, testing of riverine barriers entails discerning how surface relief, seasonal and long-term disturbances or the distribution of depositional units specifically affect river dynamics and relate to organismal idiosyncrasies (e.g., dispersal rates, mating systems, ecological requirements). Likewise, past climatic oscillations apparently provided different opportunities for species during Amazonian ice ages, whether or not aridity was ubiquitous. Amazonian phylogeographers need to pay greater attention to non-forest taxa because climate changes are expected to affect their evolutionary histories in ways that differ from their forest counterparts. This approach should shed additional light on overall patterns of forest cover dynamics from the perspective of open-habitat dwellers. Geological data are useful sources of external evidence while formulating alternative historical scenarios. However, there may be situations in which the available information is insufficient to outline the historical context of species diversification. In those instances, GIS-based environmental niche modeling (ENM) approaches have proven useful in delineating phylogeographic inferences (see Hickerson et al. 2010; Richards et al. 2007).

In the Brazilian Atlantic Forest, ecological niche models under different paleoclimate regimes revealed climatically stable areas and predicted patterns of genetic diversity (Carnaval et al. 2009). Likewise, paleodistribution modeling of Seasonally Dry Tropical Forests (Werneck et al. 2011) and the Cerrado (Werneck et al. 2012b) were used to identify areas of climatic stability during the Quaternary and further elaborate biogeographic hypotheses and identify research priorities for South American open vegetation biomes (Werneck 2011; Werneck et al. 2012a). ENM of Amazonian birds, woody plants and leafcutter ants projected onto LGM conditions also illustrated how paleodistribution limits may vary among taxa (Bonaccorso et al. 2006; Solomon et al. 2008). Moreover, phylogeographic inferential approaches based on information from ENM have key implications for the purpose of identifying cryptic refugia (Provan and Bennett 2008). Finally, GIS-based spatial analyses using Shuttle Radar Topography Mission (SRTM) data and floristic composition in western and central Amazonia verified that geological formations partition forest assemblages into large-area units due to edaphic control (Higgins et al. 2011). SRTM data in combination with regional geological information also provided a detailed

geomorphologic characterization of the lowest Amazon drainage basin, which formed the basis for reconstructing the geological history of this area during the Late Tertiary–Quaternary (Rossetti and Valeriano 2007).

Various unique types of transitional zones in the Amazon Basin await detailed phylogeographic study. Specifically, quantifying molecular and phenotypic variation in concert with key ecological attributes may reveal how adaptive selection and population divergence operate with respect to vertical gradients typical of mountainous regions, as well as horizontal contact zones between upland and floodplain forests or in savanna–forest interfaces. The consequences of disturbance–vicariance have been evaluated only for amphibians, which are known to exhibit restricted ecological requirements, and mostly within the Guiana Shield. Additional research focusing on whether or not other taxonomic groups with distinct or broader climatic regimes display similar phylogeographic patterns across the Guianas as well as other regions of the basin will improve our understanding of climatic events in the history of Amazonian biota. Finally, phylogeographic studies focusing on the extent and frequency of marine embayments, in addition to the tempo and mode of formation of different arches and the presumed location of paleo-channels, will be able to trace important pieces of Amazonian history.

It is clear, however, that the Amazon region constitutes an open laboratory for experimenting with the exploratory power of phylogeographic inference and hypothesis testing. As Amazonian phylogeographers engage in an active research program that integrates emerging analytical inferences with tools borrowed from related disciplines, new perspectives about the evolutionary histories of Amazonian organisms will be addressed in ways never envisioned before. To examine the evolution of Amazonian ecosystems as a whole, comparative phylogeography establishes the link between population processes and regional biodiversity patterns (e.g., areas of endemism) through comparison of multiple codistributed taxa within the geographic scale of entire communities (see Hickerson et al. 2010). This comparative approach provides a means to better understand the relationship between shared mechanisms driving biotic diversification and landscape formation despite the idiosyncratic variation of organisms' attributes in response to historical events (Arbogast and Kenagy 2001; Bermingham and Moritz 1998). Moreover, coalescent-based inferences can substantially extend the application of comparative studies by considering life-history parameters that are so important when testing for genealogical concordance among distinct organisms (Carstens et al. 2005).

The mapping of previous collection efforts is one of the first steps towards a precise identification of patterns of diversity and biogeography in the Amazon region. Although sampling gaps will exist for virtually all Amazonian taxa, this mapping procedure will facilitate new collecting efforts by indicating underrepresented areas. Natural history museums

have a fundamental role in coordinating these efforts effectively not only by serving as the final repositories of biological, geographic and genomic data of focal organisms and granting specimen loans whenever necessary, but also by providing information accessibility to these types of data (i.e., via online database systems, see Antonelli et al. 2010).

The Amazon region is contained within nine South American countries and borders three other major biogeographic units in the Neotropics (namely the Caribbean, Chacoan and Paranean regions). Its value in terms of environmental and biodiversity services are undeniable within a global context (Fearnside 1997), despite alarming conservation threats (Kirby et al. 2006). Due to its size, extensive regional and international collaborations are of utmost importance should we aspire to enhance biological inventories across political boundaries and benefit from recent theoretical and methodological advances (Barlow et al. 2011; Beheregaray 2008). At the same time, governmental and non-governmental agencies must work in concert with the scientific community to facilitate inventory programs by avoiding bureaucratic pitfalls that for instance delay issuance of scientific collecting permits (see Antonelli and Rodriguez 2009; Renner et al. 2012). Brazil, as the leading country in terms of Amazonian territory, has a central role in the integration of a conservation plan involving private sectors and public policies devoted to the sustainable social-economic development of the Amazon Basin, and that should also contemplate scientific research efforts within regional and international arenas.

Conclusions

The biotic diversification of Amazonia involves complex historical scenarios encompassing a range of temporal and spatial scales. Although generalizations are hard to make, emerging lines of geological and biological evidence indicate that landscape development, past-climate dynamics and biotic evolution in Amazonia shared some broad-spectrum attributes. In devising and testing meaningful models of Amazonian diversification, such commonalities need to be discerned on the basis of the requirements of each taxon or assemblage of interest and their resilience to potential environmental pressures through time. Relatively recent climatic oscillations apparently have had a more pronounced effect on taxa with narrower ecological and physiological requirements (i.e., within lineages), whose responses often are associated with shifts in distribution or niche envelopes. On the other hand, major geological events and long-term landscape changes played an important role for the geographic structuring of genetic diversity, especially at deeper hierarchical levels (i.e., among lineages).

Phylogeography has changed the way many questions concerned with the history of Amazonia's ecosystems and

its biota can be examined. However, in spite of an increasing number of empirical contributions, our appreciation of the diversification patterns as well as the evolutionary and geophysical processes shaping Amazonian diversity and biogeography is still far from complete. The exploratory yardstick of Amazonian phylogeographic inferences can now take advantage of the robustness offered by statistical discrimination of a priori models of organismal history applied to complementary multilocus datasets. The potential of these latest advances to assist Amazonian research also will depend on the ability to integrate reliable external information and overcome practical issues such as limited geographic and taxonomic sampling. Nevertheless, as we revisit major diversification hypotheses and consider future challenges for those studying Amazonian organisms, we also can anticipate that this renewed phylogeographic agenda will offer valuable insights into the evolution of Amazonian biota, and hopefully will help determine long-term conservation priorities for safeguarding the richest biota on Earth.

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Supplementary Material

Revisiting Amazonian phylogeography: insights into diversification hypotheses and novel perspectives

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Appendix. Supplementary Material

Detailed explanation of how article survey of online databases was conducted and the manner in which retrieved records were treated.

We conducted an online survey of articles published in scientific journals regarding the theme of our review (i.e., Amazonian phylogeography) with focus on terrestrial vertebrates. We searched the Web of Science[SM] and Zoological Record[®] databases; last updated on 12th and 11th of September 2011, respectively. To avoid missing any relevant publications from the online databases at first, we performed an intentionally broad query using the expression '*TS=(phylogeograph* AND amazon*)'* in the Advanced Search tab. Also, we did not include papers published in 2011 because more records from that same year are expected to be added to the databases until the end of 2011 and the beginning of the subsequent year. We retrieved a total of 157 and 103 records, respectively, but those articles stored in both databases were counted only once. We then refined our survey by downloading and examining each paper separately. Because we intended to select original research papers about terrestrial vertebrates within the scope of Amazonian phylogeography only, we excluded all other articles that matched any of the following criteria: 1) the focal group was comprised of non-vertebrate taxa (e.g., invertebrates, plants, and microorganisms); 2) the focal group strictly or primarily inhabited aquatic ecosystems (e.g., fishes, dolphins, manatees, turtles, and caimans); 3) the study did not include molecular data; 4) the paper was a review or book chapter; 5) the geographic scope of the study was outside the Amazon region; 6) the article dealt with humans or domesticated animals; 7) the article had a purely taxonomic scope.

We ended up selecting a total of 62 unique records, with 35 of those being present at both the Web of Science and Zoological Record databases, plus 16 and 11 exclusive ones, respectively. We classified the selected articles according to: 1) four major vertebrate groups: mammals, birds, reptiles or amphibians; 2) four types of genetic markers: mitochondrial sequence data (mtDNA), nuclear sequence data (nuDNA), microsatellites, or restricted fragment length polymorphism (RFLP); and 3) eight areas of endemism: Belém, Imeri, Tapajós, Xingu, Napo, Rondônia, Inambari, or Guiana (according to Silva *et al*., 2005a). For the classification of articles within areas of endemism, we counted every paper that had at least one locality present in a particular area of endemism; this procedure was based on a visual inspection of the map

depicting the taxon sampling of the respective article, but we inspected specific locality descriptions for a more accurate assessment whenever necessary. Below, we list all 62 articles that were used to produce the graphs presented in our review.

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CHAPTER 3

Genus *Proechimys*

Book chapter (in press) In: *Mammals of South America, Volume 2*
(Edited by J. L. Patton). University of Chicago Press, Chicago.

Genus *Proechimys* J. A. Allen, 1899

James L. Patton and Rafael N. Leite

Proechimys comprises the most speciose and geographically most widely distributed genus of the family Echimyidae. All species are essentially limited to lowland rainforest habitats in Central America and both cis- and trans-Amazonian South America, although a few reach elevations of 2,000 m on the lower slopes of the Andes or extend into dry forests in southeastern Bolivia and northern Paraguay and the Cerrado of central Brazil. These are the terrestrial spiny rats, often the most abundant non-volant mammal of lowland Neotropical forests, and perhaps the most easily recognizable. Individuals can be easily heard scurrying through the leaf litter and are readily seen at night, by virtue of their bright red or yellow eye shine, freezing when caught in a spotlight, or bounding off with a distinctive loping gait. They are important components of the terrestrial forest community, serving as seed predators and dispersal agents and as reservoirs of zoonoses, such as leishmaniasis, encephalitis, trypanosomiasis, and arboviruses.

In contrast to many other echimyids, all species of this diverse genus are terrestrial, with elongated heads and long rostra, large and erect ears, and narrow and long hind feet. Body size ranges extensively among species, with the smallest (e.g., *P. kulinae* or *P. pattoni*) averaging about 180 mm in head and body length and the largest (e.g., *P. semispinosus*, *P. quadruplicatus*) nearly 300 mm, but all are larger than any sympatric sigmodontine mice. The tail is always shorter than the head and body length (typically 65–70% of head and body length, but up to 85% in some species [e.g., *P. simonsi*]), and the dorsal pelage is a mixture of soft setiform hairs and expanded aristiform spines, varyingly stiffened among species and/or populations (see M. N. F. da Silva 1998 and Hoey et al. 2004 for descriptions of aristiform development among species). The dorsal and lateral color is generally reddish brown to gray-brown, often streaked with black

particularly along the mid-line, and the venter is white, although it can be tinged ochraceous or grayish, especially in the throat, thorax, and inner thighs. The narrow and elongate feet have slender toes and small plantar tubercles, the number of which may help define species (Patton and Gardner 1972). The color pattern on the dorsal surface of the foot is also often species specific (Patton and Gardner 1972; Gardner and Emmons 1984; Patton et al. 2000). The ears are distinctly larger than those of all similar-sized arboreal echimyid genera but are similar in length to those of the terrestrial spiny rats of the Atlantic Forest of Brazil, *Trinomys*.

The skull retains the same relatively narrow and elongated shape in all species currently recognized and despite substantial differences in overall size. A long rostrum, relatively narrow interorbital region with concave sides, and rounded cheek teeth with varying number of folds characterize the skull of all species. Characters such as the shape and structure of the incisive foramina, the degree of expression in temporal ridging, the degree of development of the groove on the floor of the infraorbital foramen produced by the passage of the maxillary nerve, the width and posterior palatal penetration of the mesopterygoid fossa, the size and construction of the postorbital process of the zygoma, the number and pattern of bullar septae, and the number of folds on both maxillary and mandibular cheek teeth (Patton and Gardner 1972; Gardner and Emmons 1984; Patton 1987; M. N. F. da Silva 1998; Patton et al. 2000) have proven useful in diagnosing species, as have bacular size and shape or the soft anatomy of the male glans penis (Patton and Gardner 1972; Patton 1987; M. N. F. da Silva 1998; Patton et al. 2000).

Moojen (1948) revised those species of the genus distributed in Brazil, following earlier authors in distinguishing two subgenera: *Proechimys*, which contains those species from Central America south through greater Amazonia, and *Trinomys*, which contains those species limited to the coastal Atlantic forest of Brazil. Cladistic analysis of morphological characters supports a

sister relationship between *Proechimys* and *Trinomys*, along with *Hoplomys* (Carvalho and Salles 2004), but molecular sequence analyses do not support the sister status of *Proechimys* and *Trinomys* (Lara et al. 1996; Leite and Patton 2002; Galewski et al. 2005). As a result, all recent literature has separated *Trinomys* from *Proechimys* (Carvalho and Salles 2004; Woods and Kilpatrick 2005) at the generic level. We agree with, and follow, these recent trends.

The extent of our knowledge of the systematics of this large and complex genus stands in stark contrast to their ubiquitous presence in all forest types, disturbed or pristine. The historically poor state of our understanding of the taxonomy of *Proechimys* is underscored by Oldfield Thomas's (1928b:262) famous statement: "The bewildering instability of the characters of these spiny rats makes it at present impossible to sort them according to locality into separate species, subspecies, or local races… I confess myself defeated in any attempt at present to distinguish the local races." A half-century later, Pine et al. (1981:267) echoed this sentiment, writing "among the rodents, *Proechimys* remains what may be the most problematical genus taxonomically in all mammaldom."

Moojen (1948) recognized only five species within *Proechimys* (*sensu stricto*) while Woods and Kilpatrick (2005) listed 25. Three to five species might be present at a single locality (Patton, et al. 2000); these may be truly syntopic, including sharing the same den sites on successive nights (Emmons 1982; Malcolm 1992), but they are often segregated by microhabitat (Patton et al. 2000; Voss et al. 2001). Although it is sometimes relatively easy to distinguish species when sympatric, identifying living animals to species takes a skilled eye, and defining species boundaries over larger segments of geography has proven very difficult. An extreme level of character variability, both within and among populations, hampered earlier studies attempting to diagnose species (Thomas 1928b; Moojen 1948; Hershkovitz 1948a). Even

karyotypes, which have proven useful in differentiating sympatric taxa (Patton and Gardner 1972; M. N. F. da Silva 1998), may be quite variable geographically (Reig, Aguilera et al. 1980; Gardner and Emmons 1984; Patton et al. 2000; Machado et al. 2005). Patton and Rogers (1983) documented that individual spiny rats essentially grow continuously throughout life, so that mensural variables may increase substantially with advancing age. As a consequence, one must be exceedingly careful in morphometric comparisons between taxa and not be confused by age-related variation.

Despite these complexities and problems, considerable advance has been made in our understanding of species boundaries, definable geographic ranges, and morphological variation in the past two decades. Much of this advance has been fueled by the application of new methodologies (chromosomes and molecular genetic characters) and detailed examination of qualitative morphological characters. For example, Patton and Gardner (1972) sorted co-occurring species in eastern Peru using concordant karyotypic, soft anatomical, and phallic (including bacular) characters. Gardner and Emmons (1984) utilized the septal patterns of the tympanic bullae to define species and group these into coherent units. Patton (1987) documented the utility of several qualitative cranial variables and bacular size and shape in allocating the 59 available names to one of nine species groups that he recognized. For each of these he provided hypotheses of species units and remarked on the probable geographic range of each. M. N. F. da Silva (1998) described four new species from the western Amazon of Brazil and presented the initial mitochondrial DNA sequence data to help define these and other sympatric species. Subsequently, in the most thorough analysis of the genus to date Patton et al. (2000) defined, described, compared, and mapped the eight species that are now recognized in western Amazonia. These authors also made recommendations regarding species units elsewhere in

Amazonia, based on patterns of morphological, karyotypic, and molecular phylogeographic variation. Reig, Aguilera et al. (1980) and Corti and Aguilera (1995) documented the distribution and limits of many species in Venezuela. Petter (1978), Steiner et al. (2000), and Voss et al. (2001) delineated sympatric species in French Guiana, describing morphological, molecular, and/or ecological differences. Weksler et al. (2001) revised one of the complexes of species occurring in eastern Amazonia and central Brazil. And, finally, Bonvicino (2005) delineated karyotypic and molecular diversification among populations in the Rio Negro drainage of Amazonian Brazil, and suggested limited taxonomic changes.

J. A. Allen (1899c) proposed *Proechimys* to replace *Echimys* I. Geoffroy St.-Hilaire (1840), which is not the same as *Echimys* F. Cuvier (1809). Fortunately, Allen designated *Echimys trinitatus* Allen and Chapman as the type species of his new genus, as *E. setosus*, the type of Geoffroy St.-Hilaire's *Echimys* is a species in the genus *Trinomys* Thomas. Voss and Abramson (1999) stated that the type species of the sigmodontine genus *Holochilus* Brandts at that time was *Mus leucogaster* Brandt, 1835, which was based on an example of the echimyid *Trinomys*, an oversight not previously recognized, and which would have necessitated the application of *Holochilus* Brandts as the senior synonym of *Trinomys* Thomas. In Opinion 1894 the ICZN (2001) asserted its plenary powers and fixed the type species of *Holochilus* Brandts as *H. sciureus* Wagner, thus keeping both *Proechimys* J. A. Allen and *Trinomys* Thomas on the Official List of Generic Names in Zoology.

SYNONYMS:

Echimys: I. Geoffroy St.-Hilaire, 1840; part; not *Echimys* F. Cuvier.

Proechimys J. A. Allen, 1899c:264; type species, *Echimys trinitatus* J. A. Allen and Chapman,

by original designation.

Proechinomys Elliott, 1904b:385; renaming of Allen's *Proechimys* based on the belief that it was

misspelled.

We organize the species accounts of *Proechimys* around the species groups defined by

Patton (1987), although these were established based simply on character similarity rather than

on an explicit phylogenetic hypothesis. One group recognized includes species described

subsequent to Patton's analysis (M. N. F. da Silva 1998), and species that do not fit comfortably

into these groups are treated separately. Phylogenetic data based on limited mitochondrial DNA

sequences generally support the groups recognized (M. N. F. da Silva 1998; Patton et al. 2000;

Weksler et al. 2001; Bonvicino 2005). However, while a reasonable understanding of species

limits and distribution is now available for some geographic regions (e.g., western Amazonia,

Guianan region), our understanding of the number of taxa for other regions (particularly northern

Venezuela, trans-Amazonian Colombia, and Ecuador) has progressed little since initial taxon

descriptions a century ago.

In the accounts that follow, 22 species of *Proechimys* are recognized. This list, however,

clearly underestimates the actual number of species in the genus as even the limited molecular

sequence data now available delineate deeply divergent phylogenetic clades within several of

these taxa (Patton et al. 2000; Bonvicino 2005) and substantial karyotypic differences

characterize others (Reig, Aguilera et al. 1980; Gardner and Emmons 1984; Patton et al. 2000;

Bonvicino 2005; Machado et al. 2005; Ribeiro 2006). These common and easily trapped rats are

ripe for both field and museum studies that must necessarily associate karyotypes and molecular

sequences to defined morphological entities, especially with reference to holotypes and type series, so that available names can be properly assigned and truly new forms recognized and properly described.

REMARKS: Carvalho and Salles (2004) questioned the monophyly of all species that have been traditionally included within the genus *Proechimys* (Moojen 1948 [subgenus *Proechimys*]; Patton 1987; Woods and Kilpatrick 2005), suggesting that some are more closely related to *Hoplomys* while others are aligned to *Trinomys*. Since most of the characters that support their phylogenetic hypothesis are details of the cheek teeth, especially construction of folds and contact between lophs (-ids), it is perhaps not surprising that highly varying fold number encountered among species of *Proechimys* partitions this genus into groups that align with the high fold count of *Hoplomys* and the low fold count of *Trinomys*. An expanded molecular analysis that includes the full range of taxa of all three genera is needed to resolve both generic limits and species assignments.

KEY TO THE SPECIES GROUPS OF *PROECHIMYS*:

1.   Head and body length short (< 185 mm); pelage harsh to touch, aristiform spines with blunt tips but moderate to broad in width; distribution in western Amazonia...*gardneri* species group (*Proechimys gardneri, Proechimys kulinae,* and *Proechimys pattoni*)

1′.   Head and body length larger (> 200 mm); pelage varying from very harsh to soft, aristiform spines usually with whip-like tip, rarely blunt; distribution including full range of genus...2

2.   Head and body length very large, up to 300 mm...3

2′.   Head and body length moderate to large, usually < 250 mm.............................4

3.   Dorsal color sandy fawn; pelage soft to touch, aristiform spines narrow; rostrum short

and broad; floor of infraorbital foramen smooth; mesopterygoid fossa narrow and deep,

reaching to M2; never four folds on upper cheek teeth, always two folds on lower m2 and

m3...*decumanus* species group

(*Proechimys decumanus*)

3′.   Dorsal color reddish brown; pelage stiff, aristiform spines moderate in width; rostrum

long and narrow; floor of infraorbital with groove; mesopterygoid fossa moderately wide,

reaching only to M3; four folds commonly on upper cheek teeth, rarely two folds on m2

and m3..*goeldii* species group

(*Proechimys goeldii*, *Proechimys quadruplicatus*, *Proechimys steerei*)

4.   Distribution non-Amazonian (western Peru, Ecuador, Colombia; northern Colombia and

Venezuela [except *Proechimys hoplomyoides*])..5

4′.   Distribution Amazonian, Guianan, or central Brazil...7

5.   Dorsal color grayish; pelage very soft, aristiform spines narrow with long whip-like tip;

tail with very narrow scale annuli (13–16 per cm); rostrum short and broad; postorbital

process of zygoma well developed; upper and lower molars always with two

folds...*canicollis* species group

(*Proechimys canicollis*)

5′. Dorsal color reddish yellow to reddish brown; pelage stiff, aristiform spines of moderate width or broad; tail with moderate to large scales (7–12 per cm); rostrum long and narrow; postorbital process of zygoma obsolete; always 3 (or more) folds on upper cheek teeth, usually 3 on lower cheek teeth..6

6. Dorsal color reddish yellow; tail indistinctly bicolored; incisive foramina oval in shape, anterior palate typically smooth; baculum long but stout..*trinitatus* species group (*Proechimys chrysaeolus*, *Proechimys guairae*, *Proechimys hoplomyoides*, *Proechimys mincae*, *Proechimys trinitatus*)

6′. Dorsal color reddish brown; tail sharply bicolored; incisive foramina lyrate in shape, anterior palate with median ridge; baculum short and broad with well developed apical wings...*semispinosus* species group (*Proechimys semispinosus*, *Proechimys oconnelli*)

7. Body size moderate (head and body length < 220 mm); pelage very stiff, aristiform spines very broad and blunt; floor of infraorbital foramen with groove and well-developed lateral flange...*echinothrix* species group (*Proechimys echinothrix*)

7′. Body size moderate to large (head and body length > 220 mm); pelage soft to moderately stiff, aristiform spines narrow to moderate in width, with whip-like tip; floor of infraorbital foramen smooth or with weakly developed groove...8

8.   Tail proportionately short (60–70% head and body length) and indistinctly bicolored; tail scales moderate, with annuli 9–10 per cm; pelage stiff, aristiform spines moderately wide; incisive foramina strongly lyrate in shape, anterior palate with strongly developed grooves and median ridge; mesopterygoid fossa broad and shallow; baculum massive and broad, with apical wings or extensions...................................*longicaudatus* species group (*Proechimys brevicauda*, *Proechimys cuvieri*, *Proechimys longicaudatus*)

8′.   Tail proportionately long (typically > 80% head and body length) and sharply bicolored; tail scales small, with annuli 10–13 per cm; pelage may be stiff, with aristiforms moderately broad, or soft, with narrow aristiforms; incisive foramina oval in shape, anterior palate smooth or with only weak grooves and no median ridge; mesopterygoid fossa narrow and deep; baculum long and narrow, without apical extensions or wings..9

9.   Tail proportionately very long (> 85% head and body length); plantar surface of hind feet with 5 pads, lacking hypothenar; pelage soft to touch, aristiform spines narrow, terminated with whip-like tip; range in western Amazonia.................*simonsi* species group (*Proechimys simonsi*)

9′.   Tail shorter (< 85% head and body length); plantar surface of hind feet with six pads, including hypothenar; pelage stiff to touch, aristiforms of moderate width, but with whip-like tip; range in Guianan region, eastern Amazonia, and central Brazil..*guyannensis* species group (*Proechimys guyannensis*, *Proechimys roberti*).

Proechimys canicollis species group

According to Patton (1987), this group is monotypic, containing the single species *P. canicollis* (J. A. Allen).

Proechimys canicollis (J. A. Allen, 1899)

Colombian Spiny Rat

SYNONYMS:

Echimys canicollis J. A. Allen, 1899b:200; type locality "Bonda, Santa Marta District," on Río

Manzanares, where joined by Quebrada Matogiro, 9 mi E Santa Marta (Paynter 1997),

Magdalena, Colombia.

[*Proechimys*] *canicollis*: J. A. Allen, 1899c:264; first use of current name combination.

Proechimys canicollis: J. A. Allen, 1904c:440; name combination.

DESCRIPTION: This is a moderate sized species of spiny rat, with the largest individuals

reaching a head and body length of approximately 225 mm, and with a proportionately short tail

(75% of head and body length). The pelage is relatively soft to the touch, particularly for a spiny

rat, and sparsely intermixed with weakly developed spines giving the body a distinctive soft

appearance. The aristiform hairs are long (22 to 25 mm) and quite narrow (0.02 to 0.03 mm),

terminating in a long whip-like tip. The dorsal color is pale yellowish brown or pale golden

brown sprinkled with black tipped spines on the back and paler and more gray on the sides. The

top of the head and nape is grayish, varied with black; sides of the head and neck are clear gray,

extending onto sides of the throat but becoming paler on the cheeks. The ventral color is white

along the midline from the throat to the inguinal region, but gray lateral bands encroach on the

midline from the sides and the chin and jowls are gray, completely so in some specimens. The

insides of the limbs are white, and may be continuous across the ankle to meet the whitish-gray upper surface of the hind feet. The ears are broad but short, brown in color, and appear naked. The tail is indistinctly bicolored, blackish above and dull-flesh colored below. It is moderately haired, with hairs partially concealing the narrow scale annuli, which range between 13 and 16 per centimeter.

The skull is moderate in size and, with the exception of a distinctively short and broad rostrum, conforms to the general shape of other species of *Proechimys*. Temporal ridges are absent, or extend only weakly from the supraorbital ledge onto the anterior parietals (Patton 1987:328, Table 2). The incisive foramina are broad and oval in shape, with weakly developed posterolateral flanges and thus an anterior palate that exhibits only faint grooves. The premaxillary portion of the septum is broad and long, occupying at least half of the opening; the maxillary portion is moderately to weakly developed, always in contact with the premaxilla, and sometimes with a keel that extends limitedly onto the anterior palate. The vomerine portion of the septum is usually hidden from view. The floor of the infraorbital foramen is smooth, with the occasional specimen with only a barely perceptible groove (Patton 1987:329, Table 3). The mesopterygoid fossa is relatively deep, extending to the anterior half of M3, and with an acute angle, averaging 54° (Patton 1987:331, Table 4). The postorbital process of the zygoma is moderately well developed, and may be comprised completely, or mostly, of either the squamosal or jugal in about equal frequency. The cheek teeth are the simplest of any spiny rat species, with a very uniform counterfold pattern of 3-2-2-2 for the upper series and 2-2-2-2 for the lower (Patton 1987:334–335, Table 5). This is the only species of *Proechimys* with only two folds on the 4th lower premolar.

The baculum is relatively short and stout with a rounded base, weakly concave sides, and a rather flat distal tip with only weakly developed apical wings (Patton 1987:Fig. 8c,d), similar in general size and characters to those of members of the *goeldii*-species group.

DISTRIBUTION: *Proechimys canicollis* inhabits the foothills of the Sierra de Perijá in northeastern Colombia and northwestern Venezuela.

MARGINAL LOCALITIES (Map 515): COLOMBIA: Atlántico, Ciénaga de Guájaro (Hershkovitz 1948a); Bolívar, San Juan de Nepumoceno (Patton 1987); Cesar, Río Guaimaral (= Río Garupal) (Patton 1987); Magdalena, Bonda (type locality of *Echimys canicollis* J. A. Allen), El Orinodo (Hershkovitz 1948a); La Guajira, Villanueva (USNM 280145). VENEZUELA: Zulia, Perijá (Patton 1987), Río Cachiri (Corti and Aguilera 1995).

SUBSPECIES: *Proechimys canicollis* is monotypic.

NATURAL HISTORY: This species occurs in dry tropical forest where it may be sympatric with both *P. mincae* and *P. chrysaeolus*. Handley (1976) reported that all captures in northwestern Venezuela were on the ground and equally in moist evergreen and dry deciduous forest, cropland, or orchards.

REMARKS: Gardner and Emmons (1985) placed *P. canicollis* in their "*brevicauda*-group" based on bullar septal patterns, but Patton (1987) considered it the sole member of its own group, not closely related to any other species in the genus, and "one of the more readily recognizable in the entire genus" by virtue of its reduced counterfold pattern and distinctive, almost bicolored, dorsal color pattern with the gray head and yellow brown back and rump. The karoytype consists of a $2n = 24$ and FN = 44, with minor differences in the number of arms in an autosomal pair between samples from northwestern Venezuela (Aguilera et al. 1979) and topotypes from Bonda, northeastern Colombia (Gardner and Emmons 1984). This species is positioned at the base of a

group of nine other species of spiny rats in a tree based on allozyme electrophoretic characters (Patton and Reig 1990).
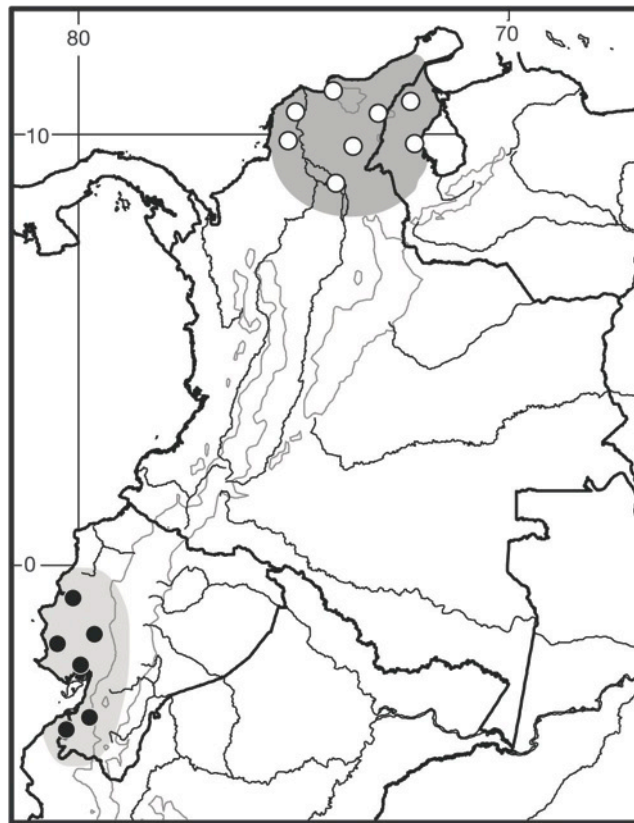
Map 515. Marginal localities for *Proechimys canicollis* (○) and *Proechimys decumanus* (●). Contour line = 2,000 m.

Proechimys decumanus species group

As currently understood, the *decumanus* group is monotypic, and with no apparent close relatives among other spiny rats (Patton 1987).

Proechimys decumanus (Thomas, 1899)

Pacific Spiny Rat

SYNONYMS:

Echimys decumanus Thomas, 1899c:282; type locality "Chongon, Guayas Province, west of

Guayaquil, Ecuador," ca. 100m, 25 km W of Guayaquil (Paynter 1993).

[*Proechimys*] *decumanus*: J. A. Allen, 1899c:264; first use of current name combination.

Proechimys cayennensis decumanus: Ellerman, 1940:120; name combination.

[*Proechimys semispinosus*] *decumanus*: Moojen, 1948:316; name combination.

DESCRIPTION: This is a large bodied spiny rat, with head-and-body length of adults

ranging from 260 to 300 mm, but with a proportionately short tail (about 65% of head and body

length). The dorsal color is coarsely grizzled sandy fawn with hairs. The sides are paler and

grayer, the face grizzled gray. The underside and inner sides of forearms and hips are pure white,

with hairs white to the base. The upper surfaces of the fore and hind feet are white, or slightly

washed yellow, and white on the inner thighs is continuous across the ankle to the foot. The

plantar pads of the hind foot are large, particularly both the thenar and hypothenar pads. The tail

is bicolored, dark above and pale below, and uniformly but thinly haired with scale annuli

narrow (averaging 13 per centimeter) and visible to the eye. Aristiform spines are long (25 to 27

mm in length) and thin (0.5 mm in width) and tipped with a long, flexible filament. As a

consequence, the pelage is inconspicuously spiny to the eye and to the touch.

The skull is large and elongated, but the rostrum is short and broad. Temporal ridges are

moderately developed and either continuous or interrupted across the parietals from the posterior

end of the supraorbital flange (Patton 1987:328, Table 2). The incisive foramina are oval to

slightly lyrate in shape and large, with weakly developed posterolateral flanges and weak

grooves extending onto the anterior palate. The premaxillary portion of the septum is long, but

tapers posteriorly and in direct contact with the maxillary portion, which is varyingly developed

as either a thin, spiculate bone or a broad shelf, often perforated by a small foramen, and with either no or only a limited keel that extends onto the anterior palate. The vomer is not visible along the septum. The floor of the infraorbital foramen is flat, rarely with limited evidence of a lateral flange indicating the passage of the maxillary nerve (Patton 1987:329, Table 3). The mesopterygoid fossa is moderately deep, reaching to the anterior half of M3, and rather narrow, with its angle averaging 53° (Patton 1987:331, Table 4). The postorbital process of the zygoma is obsolete. The cheek teeth are simple, typically with three counterfolds on all upper teeth (although rarely only two on M3) and with three folds on pm4 and m1 but only two folds on m2 and m3 (Patton 1987:Table 5, pp. 334–335). Counterfold formula is thus 3-3-3-(2)3 / 3-3-2-2.

The baculum is long but stout, among the longest of any *Proechimys* with average dimensions of 10–12 mm in length and 2.8–3.8 mm in maximal width (Patton 1987:315, Table 1). In both size and shape, this baculum is most similar to those of members of the *trinitatus*-group (Patton 1987:317, Fig. 7 and 8) with almost parallel sides, a rounded base, and a distal tip only slightly expanded with a weak median depression.

DISTRIBUTION: *Proechimys decumanus* is known only from the tropical dry forests of southwestern Ecuador and adjacent northwestern Peru.

MARGINAL LOCALITIES (Map 515): ECUADOR: El Oro, Santa Rosa (Patton 1987); Guayas, Chongón (type locality of *Echimys decumanus* Thomas), Manglar Alto (UMMZ 80040); Los Rios, Hacienda Pijigual (Patton 1987); Manabí, Bahia de Caraques (Patton 1987). PERU: Piura, Quebrada Bandarrango (Patton 1987; locality not located); Tumbes, Matapalo (FMNH 81197).

SUBSPECIES: *Proechimys decumanus* is monotypic.

NATURAL HISTORY: An inhabitant of tropical semi-deciduous forest, this large-bodied spiny rat has not been studied for any aspect of its ecology, reproduction, or behavior. It may be sympatric, or nearly so, with *Proechimys semispinosus* in SW Ecuador, with the latter presumably inhabiting patches of more mesic, evergreen forest.

REMARKS: Thomas (1899c) considered this species closely allied to *P. semispinosus* (Thomas) and Gardner and Emmons (1984) placed it with in their broadly encompassing *brevicauda*-group. In bacular characters, *P. decumanus* appears most similar to members of the *trinitatus*-group, and not at all close to any species within the *semispinosus* or *longicaudatus* groups (Patton 1987). Gardner and Emmons (1984) described a chromosomal complement of $2n$ = 30 and FN = 54 for topotypes, one indistinguishable from that of specimens of *P. semispinosus* from Costa Rica, but different from those of sympatric, or near-sympatric *P. semispinosus* from Ecuador.

Proechimys echinothrix species group

The single species within this group is the recently described *Proechimys echinothrix* Silva, which apparently has no close relatives within the genus (M. N. F. da Silva 1998). For the present, therefore, we list this as the sole member of another monotypic species group.

Proechimys echinothrix da Silva, 1998

Stiff-spined Spiny Rat

SYNONYM:

Proechimys echinothrix da Silva, 1998:441; type locality "Colocação Vira-volta, left bank Rio Juruá on Igarapé Arabidi, affluent of Paraná Breu, 66°14'W, 3°17'S, Amazonas, Brazil."

DESCRIPTION: This species is moderately large in overall size, averaging about 220 mm in head and body length. It has a distinctly robust body, long ears (24 mm), moderately and proportionately long tail (165 mm, on average; 77% of head and body length), and large hind feet (48 mm; Patton et al. 2000:Table 64). Overall, the dorsal color is uniformly reddish-brown, coarsely streaked on the back and sides with varying amounts of black; the interspersed heavy, dark brown guard hairs make the middorsum appear somewhat darker, but this grades evenly onto the brighter and paler sides of the body. The aristiform hairs are long (averaging 21 mm) and much broader (1.4 to 1.6 mm) than those of any other sympatric species, with distinctly strong and blunt tips that are conspicuous to the eye and touch, especially in the mid-dorsal region (M. N. F. da Silva 1998). The venter and inner surface of the limbs is pure white. The tail is indistinctly bicolored, dark above and white below. It is well haired, with the scales nearly completely obscured from view. The scales are small, with an average of 12 annuli per cm at mid-length. The hind feet are nearly unicolored white on their dorsal surfaces. All six pads are present on the plantar surface of the hind feet, but the hypothenar is weakly developed in relation to the thenar pad (M. N. F. da Silva 1998).

The skull is moderately large, with a long and narrow rostrum and a well-developed supraorbital ledge extending over the orbits but discontinuous across the parietals as a weakly developed temporal ridge. The zygoma usually lacks a postorbital process or, if present, it is low and rounded with equal contributions by the jugal and squamosal. A well-developed groove with a lateral flange is present on the floor of the infraorbital foramen. The incisive foramina are ovate to lyrate in general shape, with the posterolateral margins mostly flat, or only weakly flanged with very shallow grooves extending onto an anterior palate that lacks a median ridge. The premaxillary portion of the septum is long and narrow, extending between one half and two

thirds of the length of the opening; the maxillary portion is typically attenuate and has weak to no contact with the premaxillary portion; and the vomer is visible in most specimens. The mesopterygoid fossa is moderate in depth but broad, with an angle of indentation averaging about 70° and extending to the front of M3. The median number of lateral flexi on all upper cheek teeth is three, with M3 occasionally only with two. Counterfold formula is thus 3-3-3-3 / 3-3-3-3(2).

The baculum is massive and relatively short; its shaft is broad with a thick and expanded base and the distal end has a pair of divergent apical extensions that are separated by a shallow median depression. M. N. F. da Silva (1998) described the soft anatomy of the male phallus.

DISTRIBUTION: *Proechimys echinothrix* is known only from the western Amazon basin of Brazil, west of the Rio Madeira and on both sides of the Rio Solimões (Patton et al. 2000:230, Fig. 145; Schetino 2008:12, Fig. 2), possibly extending into Colombia in the upper Rio Negro drainage

MARGINAL LOCALITIES (Map 516): BRAZIL: Amazonas, Barro Vermelho (Silva 1998), Colocação Vira-Volta, left bank Rio Juruá (type locality of *Proechimys echinothrix* Silva), Comunidade Colina, Rio Tiquié (Patton et al. 2000), Lago Vai-Quem-Quer, right bank Rio Juruá (M. N. F. da Silva 1998), Macaco, Rio Jaú (Patton et al. 2000), alto Rio Urucu (M. N. F. da Silva 1998), Tambor, Rio Jaú (Patton et al. 2000), Comunidade Bela Vista (Schetino 2008).

SUBSPECIES: *Proechimys echinothrix* is monotypic.

NATURAL HISTORY (from Patton et al. 2000): This species typically inhabits upland, non-seasonally inundated (terra firme) forest, although it may be found along the margins of flooded várzea or igapó forest. Pregnant females have been taken in both dry and wet seasons in western Brazil, where modal litter size was two (range 1–3).

REMARKS: *Proechimys echinothrix* is one of the most readily recognizable among the sympatric assemblage of spiny rats of western Brazil, primarily due to the dense mid-dorsal cover of broad, stout, and blunt aristiform spines. Populations on opposite sides of the Rio Solimões are markedly distinct in mitochondrial DNA sequences (Patton et al. 2000), which might signal species-level differences. Both groups of populations, however, share the same karyotype and set of morphological attributes.
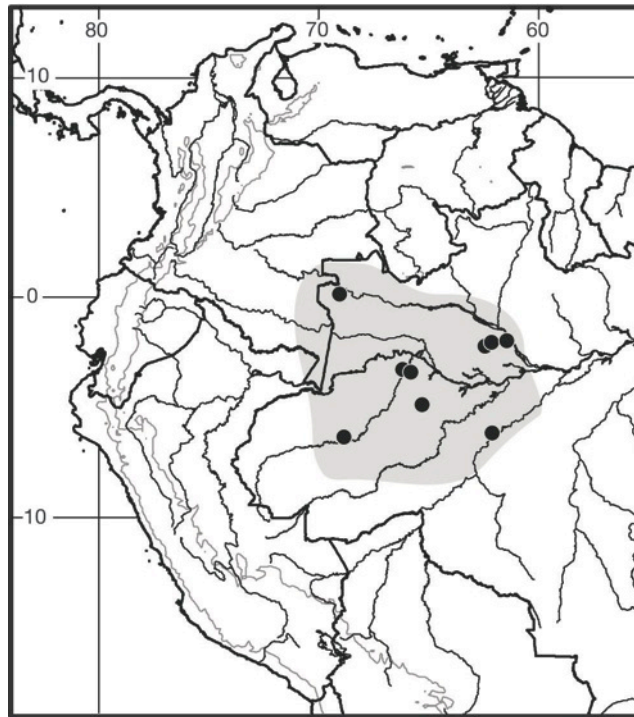
Map 516. Marginal localities for *Proechimys echinothrix* (●). Contour line = 2,000 m.

Proechimys gardneri species group

This complex includes three recently described species from the western Amazon of Brazil, Peru, and northern Bolivia (M. N. F. da Silva 1998). These are all of similar body size, with small ears, short hind feet, and a similarly proportioned tail. Species in this group differ markedly in characters of the cranium, phallus (including baculum), and karyotype, yet appear to

form a monophyletic clade based on mtDNA sequence data (M. N. F. da Silva 1998; Patton et al. 2000). The ranges of the three species are non-overlapping, as all three replace one another along the length, or on opposite banks, of the Rio Juruá in western Amazonian Brazil.

KEY TO THE SPECIES OF THE *PROECHIMYS GARDNERI* SPECIES GROUP:

1.   Aristiform spines on mid-dorsum thin so that pelage is relatively soft to the touch; tail not sharply bicolored; baculum stout and broad, with well-developed apical wings..*Proechimys pattoni*

1′.   Aristiform spines on mid-dorsum thick so that pelage is distinctly coarse to the touch; tail sharply bicolored; baculum without well-developed apical wings.....................................2

2.   Six tubercles on plantar surface of hind feet; scales of tail annuli small (11 per cm); post-orbital process of zygoma obsolete; mesopterygoid fossa long and narrow, reaching to M2; baculum broad with weak apical wings......................................*Proechimys gardneri*

2′.   Five tubercles on plantar surface of hind feet (missing hypothenar); scales of tail annuli large (nine per cm); post-orbital process of zygoma well-developed and formed by squamosal; mesopterygoid fossa short but narrow, reaching only M3; baculum short and narrow, without apical wings...*Proechimys kulinae*

Proechimys gardneri da Silva, 1998

Gardner's Spiny Rat

SYNONYM:

Proechimys gardneri da Silva, 1998:460; type locality "Altamira, right bank Rio Juruá, 68°54'W, 6°35'S, Amazonas, Brazil."

DESCRIPTION: One of three small-bodied species (head and body length averaging180 mm) of spiny rats from western Amazonia, *P. gardneri* has short ears (21 mm), short hind feet (40 mm), and a proportionately moderate length tail (125 mm; 70% of head and body length; Patton et al. 2000:Table 64). The overall body color is reddish brown or auburn, coarsely streaked with varying amounts of black both on the dorsum and sides; as with other sympatric species of spiny rats, the dorsum looks darker, especially on the rump, due to the presence of the heavy, dark brown aristiform spines. These spines are short (averaging 17 to 18 mm in length) and moderately wide (0.9 to 1.0 mm), with a blunt tip (M. N. F. da Silva 1998:Fig. 3), and provide a distinctly coarse, or stiff, texture to the dorsal pelage. The venter and chin are pure white, and most specimens have white lips. The inner surface of the hind limbs is pure white and extends across the ankle along the hind foot so that the ankle does not have a complete circular dark band. The dorsal surface of the hind foot is yellowish-white, not pure white, often with the distal parts of the toes brownish. The plantar surface of the hind foot has all six tubercles. The tail is sharply bicolored, dark brown above and cream to white below; the scales are relatively small (averaging 11 annuli per cm at mid length), but not completely hidden by hair.

The skull is small and delicate, with a relatively long and narrow rostrum and a beaded supraorbital ledge above the orbits, which extends posteriorly as a weakly developed ridge on the anterior parietals. The postorbital process of the zygoma is obsolete (M. N. F. da Silva 1998:Fig. 11). The floor of the infraorbital foramen is smooth, lacking a ventral groove. The incisive foramina are ovate to slightly lyrate in shape, with posterolateral margins lying flat or weakly flanged, and outlining only a shallow groove on the anterior palate. The maxillary portion of the septum is dorsoventrally compressed posteriorly and narrow anteriorly, visible over almost half the length of the foraminal opening, and fully connected to the premaxillary portion, which is

broad and usually about half the length of the foramen. The vomer is not visible on the ventral margin of the septum. The palate is smooth, without a median ridge. The mesopterygoid fossa is long and narrow, with the angle of indentation averaging 61°, and extends anteriorly to the middle of M2. The cheek teeth are remarkably small with the toothrow averaging only 7.5 mm in length. All upper teeth typically have three folds, with two occasionally present on M3. The lower pm4 has four (occasionally three) folds, m1 and m2 consistently have three, and m3 may have either two or three. Counterfold formula is thus 3-3-3-3(2) / 4(3)-3-3-2(3).

The baculum (M. N. F. da Silva 1998:Fig. 6) is massive and relatively long, especially in relation to the overall body size, with short, broad, and distolaterally directed apical extensions separated by a shallow median depression. The midshaft is relatively broad and the base is thick and expanded.

DISTRIBUTION: *Proechimys gardneri* is known only from only nine localities in western Amazonian Brazil and northern Bolivia, between the Rio Juruá and Rio Madeira (M. N. F. da Silva 1998; Schetino 2008).

MARGINAL LOCALITIES (Map 517): BRAZIL: Amazonas, Altamira, right bank Rio Juruá (type locality of *Proechimys gardneri* da Silva), alto Rio Urucu (M. N. F. da Silva 1998), Conunidade Bela Vista (Eler et al. 2012); Rondônia, Abunã, left bank Rio Madeira (Schetino 2008), Jirau, right bank Rio Madeira (Schetino 2008). BOLIVIA: Pando, San Juan de Nuevo Mundo (USNM 579615), Río Negro (USNM 579617).

SUBSPECIES: *Proechimys gardneri* is monotypic.

NATURAL HISTORY: This species has only been observed in upland, non-seasonally flooded (terra firme) forest. Pregnant females are known from the rainy season in western Brazil, although age structure suggests that breeding extends into the dry season. Subadults and

juveniles were collected in Pando in July (L. H. Emmons, pers. comm.). Modal litter size is two, with a range from 1–3 young (Patton et al. 2000).

REMARKS: This species is similar in most characters to *P. pattoni*, with which it is parapatric in distribution in western Brazil. On the Rio Juruá the two species share the same $2n = 40$, FN $= 56$ karyotype but differ in details of the baculum (M. N. F. da Silva 1998) and are strongly differentiated in mitochondrial DNA sequences (M. N. F. da Silva 1998; Patton et al. 2000). The karyotype of *P. gardneri* from the mid Rio Madeira is slightly different, with $2n = 40$, FN $= 54$ (Eler et al. 2012).
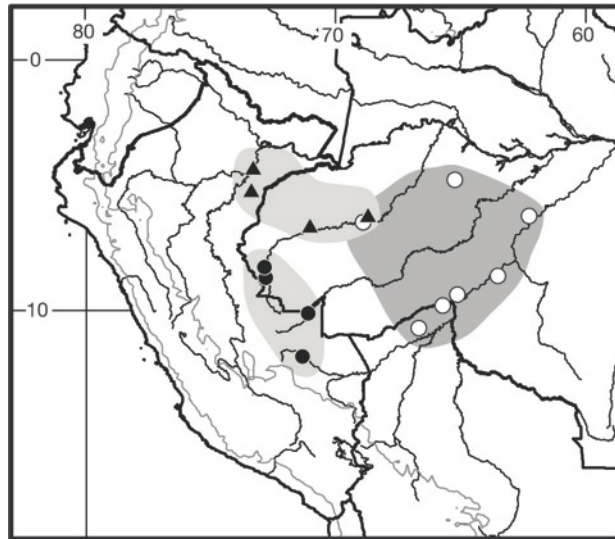
Map 517. Marginal localities for *Proechimys gardneri* (○), *Proechimys kulinae* (▲), and *Proechimys pattoni* (●). Contour line = 2,000 m.

Proechimys kulinae da Silva, 1998

Kulina Spiny Rat

SYNONYM:

Proechimys kulinae da Silva, 1998:451; type locality "Seringal Condor, left bank Rio Juruá,

70°51'W, 6°45'S, Amazonas, Brazil."

DESCRIPTION: Along with *P. gardneri* and *P. pattoni*, this is one of the smallest species of spiny rats, certainly the smallest in the western Amazon (head and body length averages 170 mm; Patton et al. 2000:Table 64). It is of slight build, with small ears (20 mm), short hind feet (41 mm), and a tail (120 mm) about 70% of head and body length. The dorsal color is uniform reddish brown, coarsely streaked with varying amounts of black on both the dorsum and sides. The dorsal pelage is interspersed with moderately thick (0.8 to 0.9 mm) but short (17 to 18 mm), dark brown aristiform hairs that form a darker medial band contrasting with the sides of the body. The tip of each aristiform is blunt (M. N. F. da Silva 1998:Fig. 3). The venter, chin, and undersurfaces of fore and hind limbs are pure white; the upper lips are dark, generally lacking patches of white hair; the tarsal joint is either ringed by dark and rusty-colored hair, or the tarsal ring is interrupted by white hair confluent with that of the undersurface of the hind limbs. The dorsal surface of the hind foot, including digits, is white, with golden tones in some individuals. The plantar surface typically posseses only five tubercles, with the hypothenar pad lacking in most specimens. The tail appears almost naked, is distinctly bicolored with dark brown above and white below, and has larger scales than other species in the group (averaging nine annuli per cm at mid-length).

The skull is relatively small, with a short and narrow rostrum and a well-developed supraorbital ledge extending onto the anterior portion of the parietals. The postorbital process of the zygoma is well developed and formed mostly by the squamosal. The floor of the infraorbital foramen is generally smooth, without a demonstrable groove for the maxillary nerve. The incisive foramen is mostly square to oval in shape, with nearly flat posterolateral margins; the

anterior palate is smooth, lacks grooves extending posteriorly from the incisive foramina, and lacks a median ridge; the premaxillary portion of the septum is short, extending for less than half the length of the foramen; the maxillary portion is variable, attenuate to expanded anteriorly, and usually in contact with the premaxillary part; and the vomer is either completely enclosed or only barely visible. The mesopterygoid fossa is narrow, with an angle of indentation averaging 57°; it is moderately deep, usually extending well into M3. All upper cheek teeth have three lateral folds, although M3 may, on occasion, have only two. Lower cheek teeth are uniform with four folds on pm4, three on m1 and m2, and only two on m3. Counterfold formula is thus: 3-3-3-3(2) / 4-3-3-2.

The baculum is elongate and relatively narrow, with stout and short apical extensions; the proximal and distal ends are about equal in width (M. N. F. da Silva 1998:Fig. 6).

DISTRIBUTION: *Proechimys kulinae* is known only from northeastern Peru, south of the Río Amazonas, and western Brazil along both sides of the central Rio Juruá.

MARGINAL LOCALITIES (Map 517): BRAZIL: Amazonas, Barro Vermelho (M. N. F. da Silva 1998), Seringal Condor (type locality of *Proechimys kulinae* da Silva). PERU: Loreto, Jenaro Herrera (AMNH 276708), Nuevo San Juan (MUSM 13340), San Pedro (MVZ 198489).

SUBSPECIES: *Proechimys kulinae* is monotypic.

NATURAL HISTORY (from Patton et al. 2002): This species is only known from primary or second growth upland, seasonally non-inundated (*terra firme*) forest. Pregnant females were taken only in the dry season in the Rio Juruá basin; the modal litter size was one young, maximum number two.

REMARKS: Substantial differences in mitochondrial DNA sequences are present between sampled localities, with samples from the central Rio Juruá in western Brazil and those from

northeastern Peru strongly separable from those towards the mouth of the Rio Juruá. Despite these molecular differences, all known specimens share the same general morphology, including bacular type, and karyotype (Patton et al. 2000). The chromosomal complement is $2n = 34$, FN = 52 (M. N. F. da Silva 1998). Aniskin (1993) described the same karyotype for specimens identified as *Proechimys* sp. from northeastern Peru; as noted by M. N. F. da Silva (1998), these likely represent *P. kulinae* as she allocated specimens from nearby localities to this species.

Proechimys pattoni da Silva, 1998

Patton's Spiny Rat

SYNONYM:

Proechimys pattoni da Silva, 1998:454; type locality "Igarapé Porongaba, right bank Rio Juruá, 72°47'W, 8°40'S, Acre, Brazil."

DESCRIPTION: This is the third small species occurring in western Amazonia, equal in size to *P. gardneri* and *P. kulinae* (head and body length averages 180 mm; Patton et al. 2000:Table 64). Individuals are slender with short ears (21 mm), a proportionally medium length tail (125 mm; 70% of head and body length), and short hind feet (41 mm). Overall, the color of the body varies between reddish brown and auburn, but is coarsely streaked with varying amounts of black both on the dorsum and sides. The interspersed dark brown aristiform spines give the dorsum a dark aspect, but the contrast between the color of the back and sides is not sharp. The dorsal pelage is stiff to the touch, with blunt tipped and shorter (16 to 17 mm), although narrower (0.6 t0 0.7 mm) aristiform spines compared to those of other species in the group (M. N. F. da Silva 1998:Fig. 3). The color of the venter and chin is pure white as are the sides of the upper lips. A dark ring around the tarsal joint interrupts the white color of the inner hind limbs. Dorsal

surfaces of the hind feet are entirely white. Six pads characterize the plantar surface of the hind feet. The dark brown dorsal surface of the tail grades evenly, rather than sharply contrasting, with the paler brown to cream color of its ventral surface. Scales are small, with 11 annuli on average per cm in the mid part of the tail.

The skull is small and delicate in appearance, with overhanging supraorbital ledges but with only weakly developed beading extending onto the temporal regions. A low but distinct post-orbital process of the zygoma is present, usually formed solely by the squamosal (M. N. F. da Silva 1998:Fig. 11). The floor of the infraorbital foramen is smooth, lacking even a hint of a groove. The incisive foramina are ovate to nearly square, with flat posterolateral margins, an attenuate or dorsoventrally compressed maxillary portion of the septum, and a broad and short premaxillary portion, which usually is not in contact with the maxillary portion. The palate is smooth, without a median ridge. The mesopterygoid fossa is long and narrow, the angle of indentation acute (50° to 60°), and may penetrate as far as M2. The cheek teeth are markedly small, with the entire toothrow less than 7.5 mm in length (M. N. F. da Silva 1998). All upper teeth typically have three lateral folds; lower cheek teeth typically have three folds, but pm4 may have four and m3 may only have two. Counterfold formula is: 3-3-3-3 / 3(4)-3-3-2(3).

The baculum is massive, especially in proportion to body size. It has a broad shaft, a thick and expanded base, and a long pair of divergent apical extensions separated by a wide and deep median depression (Patton and Gardner 1972; M. N. F. da Silva 1998; Patton et al. 2000).

DISTRIBUTION: *Proechimys pattoni* is known only from two localities in the headwaters of the Rio Juruá in western Amazonian Brazil and adjacent parts of eastern and southern Peru (M. N. F. da Silva 1998).

MARGINAL LOCALITIES (Map 517): BRAZIL: Acre, Sobral (M. N. F. da Silva 1998),

Acre, Igarapé Porongaba (type locality of *Proechimys pattoni* da Silva). PERU: Madre de Dios,

Pakitza (M. N. F. da Silva 1998); Puno, Putina Punco (M. N. F. da Silva 1998); Ucayali, Balta

(Patton and Gardner 1972, as *P. guyannensis*).

SUBSPECIES: *Proechimys pattoni* is monotypic.

NATURAL HISTORY (from Patton et al. 2000): This species is known only from upland,

non-seasonally flooded (*terra firme*) forest, where it might be found in undisturbed forest or in

disturbed areas dominated by bamboo. Pregnant females were taken in the rainy season in

western Brazil; modal litter size was two, with a range from one to two young.

REMARKS: This species was described and figured by Patton and Gardner (1972) based on

specimens from eastern Peru, but under the name *P. guyannensis*. The karyotype is $2n = 40$, FN

$= 56$ (Patton and Gardner, 1972), similar to that of *P. gardneri* (M. N. F. da Silva 1998).

Proechimys goeldii species group

Patton (1987) included 12 named taxa in this complex, but was unsure of how many of these

might represent valid species. Considerable karyotypic and molecular data are now available to

help define species limits and geographic ranges. Some of these data have been published (M. N.

F. da Silva and Patton 1998; Patton et al. 2000), but much remains unpublished. Because of the

relatively thorough geographic sampling, especially in regions that encompass most of the type

localities of the 12 names Patton (1987) placed in the group, we recognize three species and

assign with confidence the remainder of the available names to one or the other of these three.

Members of this group are restricted to the lowland rainforest of the Amazon basin where

they most commonly inhabit the seasonally inundated várzea or igapó forests, in contrast to their

sympatric congeners which live in non-seasonally flooded upland, or terra firme, forests (Patton et al. 2000). All three species have parapatric ranges, with rivers forming their common boundaries. These species are united by a uniformly large body size; by a common short, stout, but relatively narrow baculum (Patton 1987:316, Fig. 6); by skulls with weakly lyre-shaped or parallel-sided incisive foramina with a short premaxillary portion of the septum, typically attenuate maxillary portion sometimes not in contact with the premaxillary portion, and with the vomer only rarely exposed ventrally (Patton 1987:324, Fig. 15); a moderately narrow mesopterygoid fossa (angle 60° to 68°) that penetrates to the anterior part of M3 (Patton 1987:331, Table 4); and by upper cheek teeth typically characterized by four counterfolds (Patton 1987:332, Fig. 25; 334-335, Table 5).

KEY TO THE SPECIES OF THE *PROECHIMYS GOELDII* SPECIES GROUP:

1.   Distributed north of the Marañón-Solimões-Negro rivers in northern Peru, Ecuador, Colombia, north-central Brazil, and southern Venezuela; counterfold pattern of maxillary cheek teeth most commonly 4-4-4-4 ....*Proechimys quadruplicatus*

1′.   Distributed south or east of the Marañón-Solimões-Negro rivers in Peru, Bolivia, and Brazil; counterfold pattern of maxillary cheek teeth usually 3-3-3-3, but occasionally M3 and M4 with four folds...2

2.   Distributed in western Amazonia, west of the Rio Madeira; M3 and M4 commonly with four folds; dpm4 always with four folds; m1, m2 with three folds..*Proechimys steerei*

2′.   Distributed in eastern Amazonia, east of the Rio Madeira and mostly south of the Rio

Amazonas; M3 and M4 with three folds, only rarely with four; dpm4 often with three

folds; m1, m2, and m3 sometimes with two folds..................................*Proechimys goeldii*

Proechimys goeldii Thomas, 1905

Goeldi's Spiny Rat

SYNONYMS:

Proechimys goeldii Thomas, 1905a:587; type locality "Santarem, Lower Amazon," Rio Tapajós,

Pará, Brazil (locality of holotype given as "Santarem, Baras de Tapajoz" in catalog of the

Naturhistorisches Museum der Stadt Bern, Switzerland [Güntert et al. 1993]).

Proechimys cayennensis goeldii: Ellerman, 1940:12; name combination.

Proechimys goeldii goeldii: Moojen, 1948:340; name combination.

Proechimys guyannensis hyleae Moojen, 1948:361; type locality "Tauarí, Rio Tapajós, Porto de

Moz, Pará, Brazil; approximately 87 kilometers south of Santarem."

Proechimys guyannensis nesiotes Moojen, 1948:363; type locality "Ilha de Manapirí, Rio

Tocantins, Pará, Brazil."

Proechimys guyannensis leioprimna Moojen, 1948:364; type locality "Cametá, left bank of

Tocantins River, near its mouth, Cametá, Pará, Brazil."

DESCRIPTION: Size generally large, with head and body length averaging about 240 mm,

with long ears, large hind feet, and proportionately short tail (averaging about 68% of head and

body length). Dorsal color is dark reddish brown strongly mixed with black, especially over the

mid-back and rump, but specimens from more southern localities are distinctly paler and more

orangish-red in color. The venter is clear white from the chin to inguinal region; the inner thighs

are white, but separated from the dorsal foot color by a dark band. The dorsal surface of the hind foot is bicolored, with a dark lateral band and light inner band, a pattern also characteristic of both *P. quadruplicatus* and *P. steerei*. All plantar pads are well developed, with the thenar and hypothenar large and subequal in size. The tail is clothed with short, sparsely distributed hairs, so that it appears naked to the eye. Tail scales are rather small, with an average of 12 annuli per centimeter at mid-length. Aristiform spines are stout and stiff, averaging 18 to 20 mm in length and up to 1.1 mm in width, typically with a blunt tip.

The skull is similar in most respects to the other two species in the *goeldii*-group. It is large and elongate, broad across the zygomatic arches, with a relatively long but broad rostrum. Older specimens exhibit a weakly continuous temporal ridge extending from the supraorbital ledge across the parietals (Patton 1987:328, Table 2, Eastern Amazon sample). The incisive foramina are broadly open, weakly lyre-shaped or parallel sided, with the posterior margins slightly flanged and extending onto the anterior palate forming grooves; the premaxillary portion of the septum is short, usually less than one-half the length of the opening; the maxillary portion varies greatly, often weak and attenuate, perhaps not in contact with the premaxillary portion, or even spatulate and filling much of the posterior opening. The maxillary portion, however, has a slight keel that continues onto the palate as a median ridge. The vomerine portion is typically enclosed in the premaxillary sheath and thus not visible. The floor of the infraorbital foramen may be smooth, lacking any evidence of a groove, or with a groove defined by a moderately developed flange (Patton 1987:329, Table 3, Eastern Amazon sample). The mesopterygoid fossa is moderately broad, with an angle averaging 65°, but penetrates the posterior palate to about the mid-point of M3 (Patton 1987:331, Table 4, Eastern Amazon sample). The postorbital process of the zygoma is moderately developed and comprised mostly by the squamosal. The counterfold

pattern of the cheek teeth varies, with the number of folds decreasing from west to east and from north to south. Western samples typically have upper cheek teeth with 3-(3)4-(3)4-3 and lower cheek teeth with 4(rarely 3)-3-3-3 folds; eastern and southern samples have a reduced counterfold number of 3-3-3-3 above and 3(rarely 4)-3-3-3 or 2 below.

The baculum of *P. goeldii* is the same in general size and shape as those of the other members of this group, averaging slightly over 8 mm in length and nearly 3 mm in width (Patton 1987:321, Fig. 12). The sides are straight and parallel, the base slightly expanded, and the tip shows only faint development of apical wings and a median depression (Patton 1987:316, Fig. 6i).

DISTRIBUTION: *Proechimys goeldii* occurs in eastern Amazonian Brazil along both banks of the Rio Amazonas largely east of the Rio Madeira, in the states of Amazonas and Pará, and south along along the Tapajós, Xingu, and Tocantins-Araguaia rivers and their tributaries, reaching the Cerrado biome in Mato Grosso state.

MARGINAL LOCALITIES (Map 518): BRAZIL: Amazonas, Cachoeirinha (Schetino 2008), Itacoatiara (Patton 1987); Mato Grosso, Reserva Ecológica Cristalino (MVZ 197575), Serra da Chapada (Patton 1987), Utiariti (Patton 1987); Pará, Baião (Patton, 1987), Cametá (type locality of *Proechimys guyannensis leioprimna* Moojen), Fazenda Paraíso (Moojen 1948), Itaituba (Patton 1987), Óbidos (Moojen 1948), Project Pinkiati Research Station, Kayapo Indigenous Reserve (MVZ 199560), Vilarinho do Monte (Patton 1987).

SUBSPECIES: Both Moojen (1948) and Cabrera (1961) listed *steerei* Goldman as a valid subspecies, along with the nominate form. We consider *steerei* to be a separate species, following Patton et al. (2000). However, the several species-levels names we list above as

synonyms of *P. goeldii* may warrant formal recognition when appropriate analyses of geographic variation in morphological as well as molecular characters are undertaken.

NATURAL HISTORY: This species has not been studied in the field. Moojen (1948) stated that the holotype of his *leioprimna*, from the Rio Tocantins, was collected in seasonally flooded forest, which is consistent with the general habitat range of the two other species in the group. Moojen (1948) also recorded pregnant females in January for samples collected on the Rio Tapajós (*hylaea* Moojen) and Tocantins (*leioprimna* Moojen). *Proechimys goeldii* may be sympatric with two other species of spiny rats, commonly with *P. roberti* (of the *guyannensis*-group) and less commonly with *P. cuvieri* (of the *longicaudatus*-group).

REMARKS: Thomas (1920f:277) referred specimens from Manacaparú, west of Manaus, and Acajutuba, near Manaus, to *P. goeldii*. These are, however, most likely *P. steerei*, as both localities are within the known distribution of this species, which extends north of the Rio Solimões into the Imerí region between that river and the Rio Negro (see Patton et al. 2000, and the account for *P. steerei*). Moreover, the specimens to which Thomas referred (in the British Museum and American Museum collections) have the four folds that characterize the cheek teeth of *P. steerei*. Moojen (1948:341–342) also listed specimens from Manaus as P. *goeldii*, but Patton et al. (2000) allocated all specimens from the left bank of the lower Rio Negro to *P. quadruplicatus* based on DNA sequence analyses.

Osgood (1944:199) suggested that *P. goeldii* was a synonym of *P. oris* (= *P. roberti* herein), which he also thought indistinguishable from *P. cayennensis* (= *P. guyannensis*). We agree that *P. oris* shares characters with *P. guyannensis*, and for that reason Patton (1987) placed it within his *guyannensis*-group. However, both *P. oris* (= *P. roberti)* and *P. goeldii* are broadly sympatric throughout eastern Amazonia, are readily separable by a number of external and

craniodental traits (Patton 1987), and share no close phyletic relationship (J. L. Patton and R. N. Leite, unpublished DNA sequence data).

Moojen (1948:340) considered *P. goeldii* and *P. steerei* "clearly related," so much so that he included the latter as a subspecies of the former, an opinion followed by Cabrera (1961). While these two species are related, phylogenetic relationships based on mtDNA place *P. goeldii* as a basal node to the sister-species pair of *P. steerei* and *P. quadruplicatus* (Patton et al. 2000).

Machado et al. (2005) described and illustrated a karyotype with $2n = 15$, FN $= 16$ for a specimen from Juruena, Mato Grosso, Brazil (MZUSP 31924), which they identified as "*Proechimys* gr. *goeldii*." From their description of craniodental morphology, this specimen clearly belongs to the *goeldii*-group and is most likely assignable to *P. goeldii*, as currently understood, based on specimens that J. L. Patton examined from other localities in Mato Grosso. However, specimens from the Rio Xingu have a quite different karyotype of $2n = 24$, FN $= 44$ (L. H. Emmons, unpublished data). Available data from mtDNA sequences (J. L. Patton and R. N. Leite, unpublished data; Vilela 2005; Schetino 2008) also suggest two well-defined clades within *P. goeldii*, one of which occurs through eastern Amazonia in an area encompassing the type localities of *goeldii* Thomas, *hyleae* Moojen, *nesiotes* Moojen, and *leioprimna* Moojen. The second clade is known from Mato Grosso state and two additional localities in the mid to upper Rio Madeira in Amazonas and Rondônia states. The likelihood, therefore, is that each clade maps to the different karyotypes described above. Should these two clades be recognized as separate species based on future studies, there is no name currently available for the Mato Grosso clade.
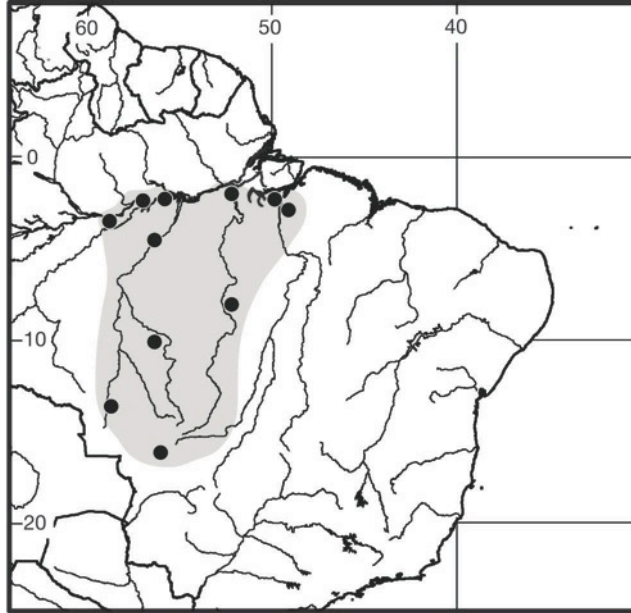
Map 518. Marginal localities for *Proechimys goeldii* (●).

Proechimys quadruplicatus Hershkovitz, 1948

Napo Spiny Rat

    SYNONYMS:

Proechimys quadruplicatus Hershkovitz, 1948a:138; type locality "Llunchi, an island in the Río

        Napo, about 18 kilometers below the mouth of the Río Coca, [Orellano,] eastern

        Ecuador."

Proechimys semispinosus amphichoricus Moojen, 1948:344; type locality "Mount Duida,

        Esmeralda, Amazonas, Venezuela; altitude 325 m."

    DESCRIPTION: This species is similar in all external and cranial characters to *P. steerei*,

but differs in karyotype and mtDNA sequences (M. N. F. da Silva and Patton 1998; Patton et al.

2000). Indeed, these two species are so alike that, at least until adequate analyses of

morphological characters are made, identification may rest solely on either chromosomes or molecules, or on general geographic ranges (Patton et al. 2000).

The body size is among the largest of all *Proechimys*, with adult weights averaging 450 to 500 g and head and body length about 250 mm. The tail is proportionately short, approximately 70% of head and body length. The overall color is ochraceous-orange, although it darkens considerably along the mid-line from the head to the rump. The venter may be pure white or lightly washed pale buff; a pale thigh stripe is usually confluent with the dorsal surface of the hind foot, which itself is characteristically bicolored, with an external dark longitudinal band encompassing digits IV and V contrasted with a pale internal band encompassing at least digits I and II, and usually III as well. The tail is bicolored, but not as sharply so as in sympatric *P. simonsi*, for example. The tail appears nearly naked from a distance, as the scales are large and conspicuous, averaging eight annuli per cm at mid length. The dorsal pelage is stiff to the touch, with well-developed aristiform spines about 20 mm long and 1.0 mm wide, terminated by a weakly developed whip-like tip. The distal one-third of the spines is black, which gives the overall darkened tone to the mid-line of the back and rump. Spines are most well developed in the mid-back, less so in the shoulder region or over the rump.

The skull is large and elongate with a long rostrum and heavy supraorbital ridges that extend posteriorly onto the parietals as distinct ridges, especially in older individuals. The incisive foramina vary from weakly lyre-shaped to oval, with the lateral margins tapering slightly posteriorly or parallel-sided. The premaxillary portion of the septum is short, usually one half or less the length of the foramen; the maxillary portion varies greatly, typically weak and attenuate, often not in contact with the premaxillary portion, but sometimes broadly spatulate and filling much of the foramen. The maxillary portion may be slightly ridged, but is never keeled; only

rarely does the ridge extend posteriorly to form moderately developed grooves on the anterior palate. The posterolateral margins of the foramen are only moderately flanged. Specimens for which Patton (1987:324, Fig. 15) illustrated the incisive foramina and called *P. steerei*, are actually *P. quadruplicatus* as now understood. A moderately developed groove is present in the floor of the infraorbital foramen, although its development varies among individuals. The mesopterygoid fossa is narrower than either *P. goeldii* or *P. steerei*, with the angle averaging 61°, and extending anteriorly to the middle of M3 (Patton 1987, 331, Table 4, Northern Peru sample). The counter fold pattern varies slightly, from 4(3)-4(3)-4(3)-4(3) / 4-3(4)-3(4)-3, but the characteristic four folds upon which Hershkovitz based his name *quadruplicatus* is the most common condition present in all samples (Patton 1987:334-335, Table 5, Colombia-Ecuador and Northern Peru samples). The counterfold pattern of the holotype of *amphichoricus* Moojen, however, is 3-3-3-3 / 3-3-3-3, which characterizes about half of all specimens examined from southern Venezuela and adjacent Brazil (Patton 1987).

The baculum is comparatively short and of moderate width, with nearly straight sides and only slightly flared apical wings and expanded base, similar to that of both *P. goeldii* and *P. steerei* (see Patton 1987:316, Fig. 6). Of the nine specimens of the "*goeldii*-group" figured by Patton (1987), those of Fig. 6a-d and f-g are *P. quadruplicatus* as this species is currently understood. Others in this figure are either of *P. goeldii* or *P. steerei* (see those accounts). Also, as noted by Patton (1987) this bacular type includes specimens described and figured by Didier (1962) both as *P. guyannensis* Type IV and as *P. quadruplicatus*. As with *P. steerei*, the rather short baculum underscores a surprisingly small phallus, contrasting with the large overall body size of this species and in comparison to other, smaller-bodied species (illustrations of the phallus in M. N. F. da Silva 1998).

DISTRIBUTION: *Proechimys quadruplicatus* occurs throughout the northwestern Amazon basin essentially north of the Río Marañón-Rio Solimões axis, in northern Peru, eastern Ecuador, southern Colombia, southern Venezuela, and northern Brazil on the left (= north and east) bank of the Rio Negro to its mouth near Manaus. This species is replaced to the south by the morphologically and ecologically similar *P. steerei* (see account of that species).

MARGINAL LOCALITIES (Map 519): BRAZIL: Amazonas, Arquipélago Anavilhanas (Patton et al. 2000), Lago Meduiním (Patton et al. 2000), Manaus (Moojen 1948), Tahuapunta (= Tauá) (Patton 1987). COLOMBIA: Caquetá, Mantanito (Patton 1987). ECUADOR: Napo, Llunchi (type locality, Hershkovitz 1948a); Orellana, San José de Payamino (MVZ 170291). PERU: Amazonas, La Poza (Patton et al. 2000); Loreto, El Chino (MVZ 198518), Pebas (Patton 1987), Río Tigre (FMNH 123013). VENEZUELA: Amazonas, Boca del Río Orinoco (AMNH 78031), Neblina base camp (USNM 560667), 18 km SSE Puerto Ayacucho (Patton 1987), San Carlos de Río Negro (Patton et al. 2000).

SUBSPECIES: *Proechimys quadruplicatus* is monotypic.

NATURAL HISTORY: As is true of *P. steerei*, *P. quadruplicatus* is most commonly found in seasonally flooded forest during the dry season, or along the margins of seasonally wet habitats during the flood season, in both black water and white water river systems, although this species may also be locally common in terra firme forest. Hice and Velazco (2012) recorded pregnant or lactating females in most months from January through at least September, and suggested that breeding was year-round. Litter size averaged 2.5 (range 1 to 4). In northern Peru and eastern Ecuador, it may be found sympatric with *P. brevicauda*, *P. cuvieri*, and *P. simonsi* (Hershkovitz 1948a; Patton et al. 1982; Hice and Velazco 2012).

REMARKS: The combination of large size, stiff pelage, bicolored hind feet, and four folds on most cheek teeth make this one of the most readily recognizable species of spiny rats in the northwestern Amazon basin. In comparison to other species, *P. quadruplicatus* is remarkable for uniformity in, and with low levels of, molecular diversification across the known range (Patton et al. 2000; Matocq et al. 2000). Both *quadruplicatus* Hershkovitz and *amphichoricus* Moojen were published in the same year, but as noted by Patton et al. (2000), Hershkovitz's paper appeared earlier and thus has date of publication priority. Minor geographic variation in karyotype has been recorded, with $2n$ varying from 26 (southern Venezuela) to 28 (Ecuador, Peru, and Brazil) and FN ranging from 42 to 44 (Reig and Useche 1976; Gardner and Emmons 1984; Patton et al. 2000; Bonvicino et al. 2005).

Specimens in the Field Museum of Natural History from Gualaquiza, Río Santiago, Ecuador referred to *P. semispinosus* (Tomes) by Osgood (1944:200–201) are *P. quadruplicatus*. Osgood's misidentification probably stemmed from the confusion regarding the type locality of Tomes' rat (Gardner 1983).
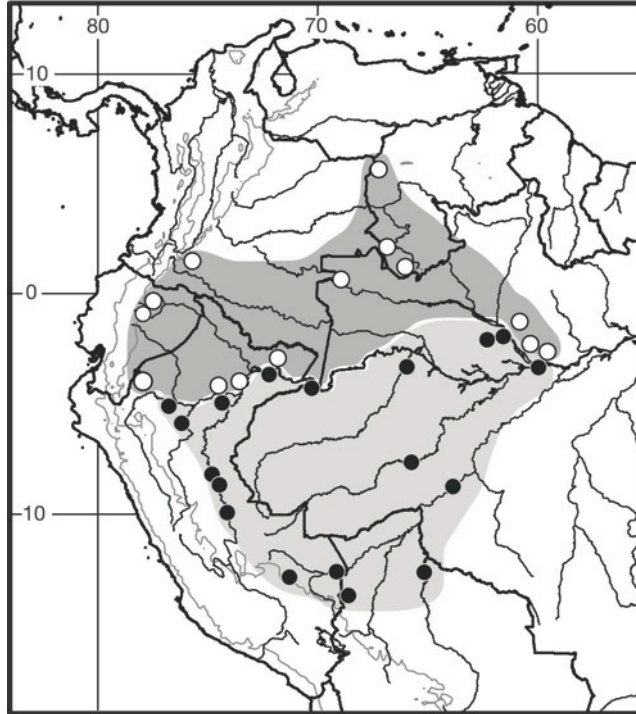
Map 519. Marginal localities for *Proechimys quadruplicatus* (○) and *Proechimys steerei* (●). Contour line = 2,000 m.

Proechimys steerei Goldman, 1911

Steere's Spiny Rat

SYNONYMS:

Proechimys steerei Goldman, 1911a:238; type locality "Rio Purus, a southern tributary of the Amazon, in northwestern [Amazonas] Brazil," amended to "Hyutánahan [Huitanaã], a small village of rubber gatherers, on the north side of the Rio Purus, in the upper part of its course" (Goldman 1912d).

Proechimys kermiti J. A. Allen, 1915b:629; type locality "Lower Rio Solimoens," amended to "Lower Rio Solimões (up the Solimões 50 to 60 miles on the north bank of the river), Manacaparú, Amazonas, Brazil" (Moojen 1948:345).

Proechimys pachita Thomas, 1923b:694; type locality "Puerto Leguia, 2000', Rio Pachitea,"

> Huánuco, Peru.

Proechimys hilda Thomas, 1924c:534; type locality "San Lorenzo. Alt. 500'. Marañon, just

> above the mouth of the Huallaga," Loreto, Peru.

Proechimys rattinus Thomas, 1926g:164; type locality "Ucayale, Tushemo, Masisea, 1000',"

> Ucayali, Peru.

Proechimys cayennensis pachita: Ellerman, 1940:121; name combination.

Proechimys cayennensis hilda: Ellerman, 1940:121; name combination.

[*Proechimys guyannensis*] *steerei*: Hershkovitz, 1948a:133; name combination.

[*Proechimys guyannensis*] *hilda*: Hershkovitz, 1948a:133; name combination.

[*Proechimys guyannensis*] *kermiti*: Hershkovitz, 1948a:133; name combination.

[*Proechimys guyannensis*] *pachita*: Hershkovitz, 1948a:138; name combination.

Proechimys goeldii steerei: Moojen, 1948:338; name combination.

[*Proechimys longicaudatus*] *pachita*: Moojen, 1948:316; name combination.

[*Proechimys longicaudatus*] *rattinus*: Moojen, 1948:316; name combination.

[*Proechimys semispinosus*] *hilda*: Moojen, 1948:316; name combination.

Proechimys semispinosus liminalis Moojen, 1948:343; type locality "Rio Quichito, affluent from

> the south of the Javarí River, near Benjamin Constant, Benjamin Constant, Amazonas,

> Brazil."

Proechimys semispinosus kermiti: Moojen, 1948:345; name combination.

DESCRIPTION: This is one of the largest species of terrestrial spiny rats, with an average body mass of 450 g but with some individuals reaching weights of more than 800 g. The head and body length can reach more than 300 mm; the ears and hind feet are large; and the tail is

proportionately short (65% of head and body length), bicolored with dark above and pale below, and clothed in fine hairs but with the scales conspicuous to the eye. There are typically 7 to 8 scale annuli per cm. The dorsal color is light reddish brown, only faintly streaked with darker hairs. Individuals vary in the degree to which they darken along the mid-line, but in general this species lacks the dark midline characteristic of most specimens of *P. quadruplicatus*. The venter is pure white, and the texture of the ventral fur is thicker and more velvety both to the eye and touch than in other species. The aristiforms of the dorsum are distinctly narrow, short, and lax, markedly softer in comparison with all other sympatric species in the genus (M. N. F. da Silva 1998) as well as to the other two species in the *goeldii*-group. The spines average only about 15 mm in length and 0.5 mm in width. The color of the dorsal surface of the hind foot is characteristic, with a pale to dark brown outer band and whitish inner band along the length of the foot, from the tarsal joint to the end of the toes.

The skull is large, with a long and narrow rostrum and a well-developed supraorbital ledge that extends onto the parietals as a weakly developed ridge (Patton 1987:328, Table 2, Central Peru and SE Peru-Bolivia samples). The incisive foramina are lyrate to oval in outline, with slightly to strongly flanged posterolateral margins that form grooves extending onto the anterior palate. The premaxillary portion of the septum is short, less than half the length of the opening, the maxillary portion is distinctly narrow, and both are in contact in most specimens; the vomer usually is not visible. A groove is present on the floor of the infraorbital foramen, but a lateral flange is only weakly developed (Patton 1987:328, Table 2, Central Peru and SE-Peru-Bolivia samples). The mesopterygoid fossa is relatively broad (averaging 67°), but penetrates to the mid-point of M3 (Patton 1987:331, Table 4, Central Peru and SE-Peru-Bolivia samples). The

counterfold pattern varies from 3(4)-3(4)-3(4)-4(3) / 4-3-3-3 (Patton 1987:334-335, Table 5, Central Peru and SE-Peru-Bolivia samples).

The baculum is comparatively short and of moderate width, with parallel or slightly concave sides, and similar in size and shape to those of *P. quadruplicatus* and *P. goeldii*. Of the series of specimens labeled as *P. steerei* and illustrated in Patton (1987:316), only those in Figs. 6d, 6e, and 6h are of this species; the rest are of *P. quadruplicatus* or *P. goeldii*, as herein understood (see those accounts). The male phallus itself is remarkably small, particularly for an animal as large as this species, with the prepuce extended as a narrow tube and terminated by a characteristic tuft of hairs, rather than rounded and blunt as in most *Proechimys* phalli.

DISTRIBUTION: *Proechimys steerei* is known from eastern and southern Peru south of the Río Marañón-Río Amazonas, northwestern Bolivia, and western Brazil south of the Rio Solimões to at least the Rio Purus, but extending north of the Rio Solimões into the Imerí region south and west of the lower Rio Negro (Patton et al. 2000: 250, Fig. 153). It is unclear if specimens from the lower Rio Madeira are of this species or represent *P. goeldii*.

MARGINAL LOCALITIES (Map 519): BOLIVIA: Beni, Río Mamoré, 17 km NNW Nuevo Berlín (Anderson 1997, as *Proechimys hilda*); La Paz, Río Madidi, Moira camp (Patton et al. 2000). BRAZIL: Amazonas, Huitanaã (type locality of *Proechimys steerei* Goldman), Ilha Paxiuba (Patton et al. 2000), right bank Rio Jaú above mouth (Patton et al. 2000), Rio Quichito (type locality of *Proechimys semispinosus liminalis* Moojen), mouth of Rio Solimões, near Manacaparú (type locality of *Proechimys kermiti* J. A. Allen), Tambor (Patton et al. 2000); Rondônia, Pista Nova (Patton 1987). PERU: Loreto, Orosa (Patton 1987), San Lorenzo (type locality *Proechimys hilda* Thomas), Loreto, Santa Elena (Patton 1987), Yurimaguas (Patton 1987); Madre de Dios, Albergue Cusco Amazónico (Patton et al. 2000), Itahuanía (Patton 1987);

Ucayali, Cumaría (Patton 1987), Tushemo (type locality of *Proechimys rattinus* Thomas),

Yarinacocha (Patton and Gardner 1972).

SUBSPECIES: By current understanding, *Proechimys steerei* is monotypic. The various

synonyms listed above generally belie the rather fairly uniform character variation among

populations of this species.

NATURAL HISTORY: This species prefers the seasonally flooded white-water (várzea) or

black-water (igapó) forests, where it is typically the only spiny rat present. It also occurs in

secondary and disturbed terra firme forests where water or moist areas are nearby, active and

abandoned gardens, and riverine or margins of flooded grasslands within the forest. Breeding

apparently takes place throughout the year in western Brazil, females begin to breed before they

have molted into their adult pelage, and modal litter size is three, with a range from one to seven

young (Patton et al. 2000). These reproductive characteristics suggest a more r-selected life

history, one adapted for living in seasonally available habitats. Emmons (1982) examined the

population ecology of *P. steerei* (she used the name *P. brevicauda* for this species, following

Patton and Gardner 1972) and sympatric *P. simonsi* in southern Peru, including nightly

movement pattern, seasonal home range, diet, and density. A notable finding was that both

species feed on sporocarps of mycorrhizal fungi, potentially a pivotal ecological service

(Emmons 1982, Janos et al. 1995).

Matocq et al. (2000) described molecular population genetic structure in relation to

riverine barriers and habitat range in western Brazil, contrasting those patterns with the co-

distributed *P. simsoni*. And, E. P. Lessa et al. (2003) provided estimates of late and post-

Pleistocene population expansion and stability based on coalescence analysis of molecular

sequence data.

REMARKS: Thomas (1926g:164) considered *rattinus* close to *P. hendeei* (= *P. simonsi*) in both pelage and cranial characters. Osgood (1944:202) also thought that *rattinus* Thomas might be a "lowland race or phase of *hendeei*." The holotype of *rattinus* Thomas is an adult, represented by a skull but not a skin; its cranial features are clearly those of *P. steerei*, not *P. simonsi* (= *P. hendeei*); see Patton (1987). Hershkovitz (1948a) noted that Thomas's description of *rattinus* was based on the skull of an adult female (designated as the type) and the skin of an immature female. He argued that the skull is referable to *guyannensis*, which is clearly wrong, and that the skin "agrees closely with that of the type of *P. hendeei*" (= *P. simonsi*). However, the skin (BM 24.2.22.18) has a gray throat patch, which is not typical of *simonsi*, although a note on the label reads: "the only skin of a dozen with belly other than wholly white." All specimens of spiny rats in the BM collection from the type locality of *rattinus* are *P. steerei*.

Thomas (1927f) assigned specimens from Tingo Maria and Chinchavita, Huánuco, Peru to his *Proechimys pachita* (= *P. steerei* Goldman); the entire series in the British Museum from both localities, however, are specimens of *P. brevicauda* Günther (see account of that species).

Osgood (1944:202) also considered *pachita* Thomas a synonym of *P. simonsi*, noting that it differed primarily by "having a longer palatal foramina." Thomas's holotype, however, clearly displays the incisive foramina and other characters of *P. steerei* and not *P. simonsi*, as described and defined by Patton (1987).

Moojen's *liminalis* can be assigned as a junior synonym to either *P. steerei* Goldman or *P. quadruplicatus* Hershkovitz based on Moojen's (1948:343) description of the structure and shape of the incisive foramina, the vomerine sheath, as well as the four counterfolds on both M2 and M3. However, since these two species appear separated south and north, respectively, of the Marañón-Amazonas-Solimões axis, and the type locality of *liminalis* is on the south side, we

assign the name to *P. steerei*. Should this prove incorrect, *liminalis* Moojen would become a

junior synonym of *quadruplicatus* Hershkovitz, which has date of publication priority in 1948.

      Proechimys steerei comprises two sharply divergent mtDNA clades (Patton et al. 2000),

one limited to the Imerí region sandwiched between the Rio Solimões on the south and Rio

Negro on the north and east, and the other south of the Rio Marañón-Rio Solimões axis in

western Brazil, Peru, and Bolivia. Should these two clades be recognized in the future as separate

taxa, then J. A. Allen's *kermiti*, with its type locality near Manacaparú on the north bank of the

Rio Solimões would be an available name for the clade in the Imerí region.

      Karyotypic variation is minimal geographically, with multiple samples available to

represent both mtDNA clades. All individuals for which voucher specimens have been examined

by J. L. Patton as assignable to *P. steerei* have a karyotype with $2n = 24$ and FN = 40 to 42

(Patton and Gardner 1972; Gardner and Emmons 1984; Patton et al. 2000; M. N. F. da Silva and

J. L. Patton unpublished data). Ribeiro (2006) also described a karyotype of $2n = 24$, FN = 42

from specimens from Pauiní, Amazonas, Brazil, which he ascribed to *P. steerei*. We have not

examined these. Patton et al. (2000) described a non-Robertsonian polymorphism in one pair of

biarmed autosomes in samples from the Rio Juruá in western Brazil.

Proechimys guyannensis species group

We list two species in this complex, which is distributed mostly in eastern Amazonia, from east

of the Rio Negro, including the Guianan region, and extending south into central Brazil. One

species, *P. guyannensis* occurs north of the Amazon, the other, *P. roberti*, occurs only to the

south of this river. Both species, however, exhibit phylogeographic structure in mitochondrial

DNA sequences (Weksler et al. 2001; Steiner et al. 2000; L. P. Costa, Y. L. R. Leite, and R. N.

Leite, unpublished data). Moreover, what we refer to here as *P. guyannensis* is also comprised of multiple karyotypic forms (Reig et al. 1976; Petter 1978; Weksler et al. 2001; Bonvicino 2005; Machado et al. 2006). Both of these "species" thus may prove to be composite. Since there are multiple names already available but currently listed only as synonyms, the challenge for future investigators will be to tie molecular clades and/or karyotypes directly to these names. Given that multiple species of spiny rats can co-occur at single sites, it is not sufficient to simply obtain "topotypes" for name application, as acknowledged by Hershkovitz (1948a) nearly 60 years ago, and care must be taken to compare karyotyped or sequenced voucher specimens with holotypes.

KEY TO THE SPECIES OF THE *PROECHIMYS GUYANNENSIS* SPECIES GROUP:

1.   Distributed north of the Rio Amazonas largely in the Guianan subregion; tail long, > 77% of head and body length; tail scales small with 11–14 annuli per cm; mid-dorsal aristoforms stout (0.9 to 1.0 mm in width); mesopterygoid fossa narrow (angle < 58°), penetrating to the level of M2...*Proechimys guyannensis*

1'.   Distributed south of the Rio Amazonas in eastern and central Brazil; tail short, < 70% of head and body length; tail scales large with 9–10 annuli per cm; mid-dorsal aristiforms narrow (0.6 to 0.8 mm); mesopterygoid fossa moderately wide (angle > 64°), penetrating only to level of M3...*Proechimys roberti*

Proechimys guyannensis (É. Geoffroy St.-Hilaire, 1803)

Guyenne Spiny Rat

SYNONYMS:

Mus guyannensis É. Geoffroy St.-Hilaire, 1803:194; type locality "Cayenne," French Guiana.

Echimys cayennensis Desmarest, 1817b:58; a redescription of *Mus guyannensis* É. Geoffroy St.-Hilaire.

echymis cayennensis: Desmarest 1822:292; inadvertent *lapsus*.

Proechimys cayennensis: J. A. Allen, 1899c:264; name combination.

Echimys cherriei Thomas, 1899d:382; type locality "Munduapo [= Monduapo, Paynter 1982], Upper Orinoco," on the right bank of the upper Río Orinoco at 4°45'N, 67°48'W, Amazonas, Venezuela.

[*Proechimys*] *cherriei*: J. A. Allen, 1899c:264; name combination.

Proechimys vacillator Thomas, 1903b:490; type locality "Kanuku Mountains, British Guiana. Altitude 600 feet," Upper Takutu-Upper Essequibo, Guyana.

Proechimys warreni Thomas, 1905b:312; type locality "Comackka, 80 miles up the Demerara River, British Guiana. Alt. 50 feet," Upper Demerara-Berbice, Guyana.

Proechimys cayennensis cherriei: Ellerman, 1940:121; name combination.

Proechimys cayennensis warreni: Ellerman, 1940:121; name combination.

[*Proechimys guyannensis*] *cherriei*: Moojen, 1948:316; name combination.

[*Proechimys guyannensis*] *vacillator*: Moojen, 1948:316; name combination.

[*Proechimys guyannensis*] *warreni*: Moojen, 1948:316; name combination.

Proechimys guyannensis: Moojen, 1948:355; first use of current name combination.

Proechimys guyannensis riparum Moojen, 1948:367; type locality "Manaus, Manaus, Amazonas, Brazil."

Proechimys guyannensis arabupu Moojen, 1948:369; type locality "Arabupu, Mount Roraima, Boa Vista, Territ. Rio Branco; about 1540 meters altitude," Roraima, Brazil. [Moojen's

designation of the type locality in Brazil is in error; Arabupu [=Arabopó] is on the Río

Arabopó, Bolívar, Venezuela; Paynter 1982.]

Proechimys canicollis vacillator: Cabrera, 1961:518; name combination.

DESCRIPTION: *Proechimys guyannensis* is a moderate-sized spiny rat, ranging about 180 to 230 mm in head and body length (Moojen 1948; Catzeflis and Steiner 2000; Voss et al. 2001). The tail is proportionately long, ranging from 77 to 87% of head and body length (Catzeflis and Steiner 2000; Voss et al. 2001). Samples across the northern Guianan region are light reddish to yellowish brown lined with black along the midback, distinctly paler on the lower sides, but abruptly meeting a pure white venter from chin to inguinal region. White inner thigh stripes are typically continuous across the ankle to the dorsal surface of the hind foot, which is typically light colored with only a slight brown patch on the tarsus below the 1st digit; all digits tend to be white. Plantar pads on the hind feet are only moderately developed, but both thenar and hypothenar are present and subequal in size. The tail is sharply bicolored, light brown above and cream below. The hairs on the tail are sparsely distributed and very short, so that from a distance the tail appears completely naked. The scales are small and the annuli consequently narrow, ranging between 11 and 14 per centimeter. The pelage is stiff to the touch, particular along the midback, with the aristiform spines rather short (16 to 19 mm long) and stout (0.9 to 1.0 mm wide); the tip is either blunt or terminates with a very short filament.

The skull conforms to that of virtually all spiny rats in general shape, but because body size is moderate, the skull appears small and rather delicate, lacking the heavy ridging that may be present in the skulls of larger species. As a result, temporal ridges are generally poorly developed, if at all, maximally just a short and weak posterior extension from the supraorbital ledges (Patton 1987:328, Table 2, Venezuela-Brazil and Surinam samples). The incisive

foramina are oval or teardrop in shape, with either no or only weakly developed posterolateral flanges so that the anterior palate is typically flat, or only very slightly grooved. The premaxillary portion of the septum is short, occupying less than half the opening, and usually not in contact with a very attenuate maxillary portion. The latter is short and unkeeled, such that the anterior palate lacks any medial ridging. A vomerine portion to the septum is typically not visible in ventral view (see Patton 1987:325, Fig. 18). This foraminal shape and structure is generally the same as that of *P. roberti*, described below, and also similar to that of *P. simonsi*. The floor of the infraorbital foramen may either lack evidence of a groove or have a moderately developed lateral flange that forms a groove for the passage of the maxillary nerve (Patton 1987:329, Table 3). The width of the mesopterygoid fossa ranges widely among geographic samples, but generally narrow with an angle < 58°. Nevertheless, the fossa penetrates to the level of the posterior half of M2 in nearly all specimens (Patton 1987:331, Table 4). The postorbital process of the zygoma is obsolete or only weakly developed; it is formed entirely by the squamosal. The number of folds on the upper cheek teeth is relatively constant, with three characterizing PM4, M1, and M2, and either three or less commonly two present on M3; the lower cheek teeth are more variable, as pm4 has three folds and m1-m3 typically only twu, but occasionally three (Patton 1987:334-335, Table 5). The counterfold formula is thus 3-3-3-(2)3 / 3-2(3)-2(3)-2(3). In comparison to sympatric *P. cuvieri*, the cheek teeth of *P. guyannensis* are also notably small in size, with the toothrow ≤ 8.0 mm in length (Voss et al. 2001).

The baculum is relatively long and narrow, the shaft straight with little dorsoventral curvature and only slightly tapered lateral indentations near mid-shaft. The proximal end is usually evenly rounded and paddle-shaped; the distal tip shows only slight development of apical wings and a moderate median depression (Patton 1987:313, Fig. 5 a-e; 314, Table 1).

DISTRIBUTION: *Proechimys guyannensis* is an Amazonian endemic largely confined in the Guiana subregion of eastern and southern Venezuela, Guyana, Surinam, French Guiana, and Brazil north and east of the Rio Negro and north of the Rio Amazonas (Patton 1987; Weksler et al. 2001; Voss et al. 2001: 163).

MARGINAL LOCALITIES (Map 520): BRAZIL: Amapá, Serra do Navio (Patton 1987); Amazonas, Faro (Patton 1987), Igarapé Araújo (Bonvicino et al. 2005, as "sp. A"), Manaus (type locality of *Proechimys guyannensis riparum* Moojen), São Gabriel da Cachoeira (INPA [JPB 0]). FRENCH GUIANA: Cayenne (type locality of *Mus guyannensis* É. Geoffroy St.-Hilaire). GUYANA: Demerara-Mahaica, Loo Creek (ROM 98216). SURINAM: Surinam, Santa Boma (Husson, 1978). VENEZUELA: Amazonas, Capibara (Patton 1987), Monduapo (type locality of *Echimys cherriei* Thomas), Neblina base camp (USNM 560675), Pozon (ROM 107892); Bolívar, Arabupu [= Arabopó] (type locality of *Proechimys guyannensis arabupu* Moojen), 3 km E Puerto Cabello del Caura (ROM 107944).

SUBSPECIES: The possible elevation of the various available names to the subspecies level must await delineation of species limits within this highly variable taxon (see Remarks).

NATURAL HISTORY: At Paracou in French Guiana, Voss et al. (2001) caught this species mostly in well-drained forest but also occasionally in creek-side forest, and significantly more commonly in primary forest than its sympatric congener, *P. cuvieri*. All but two specimens were collected on the ground; those that were not came from traps placed 0.5 to 1.5 m above ground in liana tangles. Spiny rats are important seed predators and dispersers of tropical forest trees in French Guiana (Forget 1991, 1996), although field ecological studies have been hampered by the difficulty in distinguishing sympatric species (Malcolm 1992). Consequently, the several published studies in French Guiana, or elsewhere in the Guianan region and northeastern

Amazonian Brazil, probably include data on *P. guyannensis*, but were unable to differentiate this species from sympatric *P. cuvieri*.

REMARKS: Woods (1993:795) used *cayennensis* Desmarest as the name for this species, following the argument of Wilson and Reeder (1993:831) that É. Geoffroy St.-Hilaire's 1803 publication did not meet the requirements of the International Code of Zoological Nomenclature and thus that his names were unavailable. However, the ICZN (ICZN 2002, Opinion 2005) subsequently validated É. Geoffroy St.-Hilaire, 1803, an action that makes *cayennensis* Desmarest a junior synonym of *guyannensis* É. Geoffroy St.-Hilaire.

As noted by Voss et al. (2001), Husson (1978) used the name *P. warreni* to refer to this species in his book on Surinam mammals, and applied *P. guyannensis* incorrectly to the larger-bodied species that has been identified by subsequent authors as *P. cuvieri*.

Patton (1987) incorrectly mapped the type locality of *cherriei* Thomas in the lower, instead of upper, Orinoco basin (see Voss et al. 2001).

Proechimys guyannensis, as defined here, is most likely composite given the extensive karyotype diversity described in the literature and the limited DNA sequence data available (Weksler et al. 2001; Bonvicino et al. 2005). Reig, Tranier, and Barros (1980) described a karyotype of $2n = 40$, FN = 54 from the type locality (Cayenne, French Guiana). Machado et al. (2005) reported a karyotype of $2n = 44$, FN = 52 from a specimen from Manaus, in Amazonas state, Brazil, which probably represents *P. guyannensis*, as L. H. Emmons (unpublished data) obtained the same karyotype from a specimen assignable to this species on morphological grounds and taken at 80 km N of Manaus (USNM 555638). Furthermore, Bonvicino et al. (2005) reported two different karyotypes for specimens that belong to *P. guyannensis* (*sensu lato*), what they called "*Proechimys* sp. A," with $2n = 38$ and FN = 52 (in the upper Rio Negro-Rio Aracá in Amazonas

state, Brazil), and "*Proechimys* sp. B," with $2n = 46$, FN = 50 (from the Rio Anauá, a tributary of the Rio Branco in Roraima state; the same karyotype obtained from the Rio Uatumã, in Amazonas state by Silva et al. 2012). They suggested that each karyotypic form represented a different species, and further suggested that *arabupu* Moojen was the correct name to apply to their "sp. B" because it's type locality is close to the locality of their specimen. However, the holotype of *arabupu* (AMNH 75816) came from Arabopó in southeastern Venezuela at the base of Mt. Roraima (not in Brazil as Moojen 1948 stated), some 450 km to the north of the locality for "sp. B." Moreover, there is a karyotype of $2n = 40$, FN = 50 for a specimen (MVZ 160094) collected near Icabarú, Bolívar, Venezuela, only 130 km west of the type locality of *arabupu* Moojen and with which it shares the same craniodental morphology. It is thus not possible to assign the name *arabupu* Moojen to the karyomorph Bonvicino et al. (2005) termed "sp. B" with any certainty. Eler et al. (2012) has also extended the distribution of the $2n = 38$, FN = 52 karyotype to the Rio Jari basin on the Amapá-Pará state boundary in eastern Amazonia, giving this chromosomal form a quite extensive range. Clearly, care must be taken before applying an available name to a karyotypic form because different karyotypes do not always signal reproductive incompatibility within the genus (Aguilera et al. 1995; M. N. F. da Silva 1998). Moroever, an effort must be made to obtain karyotypes and molecular sequences from topotypes that have been compared directly to relevant holotypes or type series, as two or more species of spiny rats may co-occur at single sites throughout the range of the genus.

Van Vuuren et al. (2004) described molecular sequence variation among populations in French Guiana, noted low molecular diversity and the lack of haplotype structure within this limited geographic region, and suggested that the sampled region had undergone a recent population expansion.
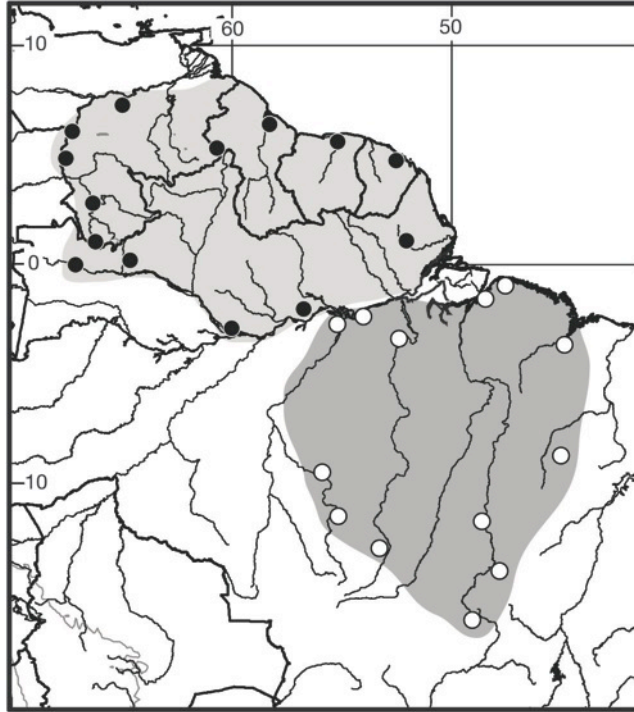
Map 520. Marginal localities for *Proechimys guyannensis* (●) and *Proechimys roberti* (○). Contour line = 2,000 m.

Proechimys roberti Thomas, 1901

Robert's Spiny Rat

SYNONYMS:

Proechimys roberti Thomas, 1901g:531; type locality "Rio Jordão, S. W. Minas Gerais [sic], Alt. 960 meters," Araguarí, Minas Gerais, Brazil.

Proechimys oris Thomas, 1904e:195; type locality "Igarapé-Assu, near Pará. Alt. 50 m," near Belém, Pará, Brazil (Moojen 1948:365).

Proechimys boimensis J. A. Allen, 1916c:523; type locality "Boim, Rio Tapajos," Pará, Brazil."

Proechimys cayennensis roberti: Ellerman, 1940:121; name combination.

Proechimys cayennensis oris: Ellerman, 1940:121; name combination.

Proechimys cayennensis boimensis: Ellerman, 1940:121; name combination.

Proechimys cayennensis arescens Osgood, 1944:198; type locality "Roca, near Fazenda Inhuma, below Santa Philomena [= Filomena], upper Rio Parnahyba [= Vitoria do Alto Parnaiba], Maranhão, Brazil" (Moojen 1948:366).

[Proechimys guyannensis] boimensis: Hershkovitz, 1948: 128; name combination.

Proechimys longicaudatus boimensis: Moojen, 1948:350; name combination.

Proechimys longicaudatus roberti: Moojen, 1948:353; name combination.

Proechimys guyannensis oris: Moojen, 1948:365; name combination.

Proechimys guyannensis arescens: Moojen, 1948:366; name combination.

DESCRIPTION: This is a moderate sized spiny rat similar in size to *P. guyannensis*, with which it shares a number of morphological attributes (Patton 1987). Head and body length varies from 200 to 230 mm but the tail is distinctly shorter, both absolutely and proportionately, than that of *P. gu*yanennsis, averaging only 70% of head and body length. In this respect alone the typical *P. roberti* from south of the Amazon can be distinguished from the typical *P. guyannensis* from north of this river. The dorsal color ranges from reddish brown in the northern part of the range in Amazonia proper to pale buff in samples at the southern terminus of the range in the dry and gallery forests of the Cerrado, a difference in color that reinforced the species status of *P. roberti* when Thomas (1904e) described *P. oris* a few years later. The venter is white from chin to the inguinal region, but the white of the inner thigh is discontinuous, broken by a dark ankle band, with the pale surface of the hind feet. In many specimens, there is a brownish patch extending from the tarsus to the lateral toes. The pads on the plantar surface of the hind foot are only moderately developed, but both the thenar and hypothenar are present and subequal in size. As in *P. guyannensis*, the tail is very sparsely covered with short hairs so that is

appears completely naked to the eye from a distance. The scales are large, with 9–10 annular rings per centimeter. The pelage is stiff to the touch, although much softer in southern samples; aristiform development is, however, moderate, as spines are relatively short (20 mm in length) and narrow (0.6 to 0.8 mm in width), each terminating in a long whip-like tip. The difference in softness of the pelage between Amazonian and Cerrado specimens is mostly in aristiform density, not any appreciable difference in the width or other features.

The skull is similar in all respects to that of *P. guyannensis*; of medium length but rather narrow and with a narrowed, tapering rostrum. Slight temporal ridges extend posteriorly onto the parietals from the supraorbital ledge in older individuals, but most specimens lack ridges altogether (Patton 1987:328, Table 2, Goiás and Pará samples). The incisive foramina cannot be distinguished from those of *P. guyannensis* in any single feature. They are relatively wide, oval to teardrop in shape, with little or no posterolateral flange so that the anterior palate is either flat of only weakly grooved. The premaxillary portion of the septum is short, less than half the opening, and either connected to a very attenuate maxillary portion or separated from the latter entirely. The maxillary portion is unkeeled, so that anterior palate lacks a medial ridge; the vomerine portion may be visible ventrally, but not always (Patton 1987:325, Fig. 18d). The floor of the infraorbital foramen is either flat or with only a hint of a groove formed by a weakly developed lateral flange (Patton 1987:329, Table 3). The mesopterygoid fossa is intermediate in width, with an angle averaging 64° to 67°; it penetrates the posterior palate to the anterior half of M3 (Patton 1987:331, Table 4). The postorbital process of the zygoma is weakly to moderately developed, but formed completely by the squamosal. The characteristic number of folds on the upper cheek teeth is three on all teeth except M3, which occasionally has only two. On the lower cheek teeth, the number of folds is more variable, with three (or occasionally four) on pm4, and

either two (usually) or three on each lower molar. The counterfold count is thus 3-3-3-(2)3 / 3(4)-2(3)-2(3). As with other species of spiny rats whose populations span a range of forest types, southernmost samples of *P. roberti* in the drier Cerrado forests typically have simpler teeth, with a higher proportion of individuals with only two folds on the lower molars, for example (Patton 1987:334–335, Table 5, Goiás and Pará samples of *guyannensis*-group).

The baculum is long and narrow, with general features as described above for *P. guyannensis*, above, except specimens from the southern part of the range tend to be smaller in length and width (Patton 1987).

DISTRIBUTION: *Proechimys roberti* occurs throughout the rainforest of Amazonian Brazil south of the Rio Amazonas and extends south to the Cerrado biome in east-central Brazil, in the states of Pará, Maranhão, Tocantins, Mato Grosso, Goiás, and Minas Gerais (Weksler et al. 2001).

MARGINAL LOCALITIES (Map 520): BRAZIL: Goiás, Anápolis (Patton 1987), Fazenda Fiandeira (Weksler et al. 2001); Maranhão, Fazenda Lagoa Nova (Weksler et al. 2001); Mato Grosso, Gaúcho do Norte (Machado et al. 2005), Cláudia (Machado et al. 2005), Reserva Ecológica Cristalino (MVZ 197576); Minas Gerais, Rio Jordão (type locality of *Proechimys roberti* Thomas); Pará, 52 km SSW Altamira (Weksler et al. 2003), Belém (MVZ 196096), Boim, Rio Tapajós (type locality of *Proechimys boimensis* J. A. Allen), Curuá-Una (Weksler et al. 2001), Igarapé-Assú (type locality of *Proechimys oris* Thomas); Piauí, Estação Ecológica de Uruçuí-Una (Machado et al. 2005); Tocantins, Rio Santa Teresa (MVZ 197585).

SUBSPECIES: Populations in lowland Amazonian rainforest could be considered a subspecies (*P. r. oris*) separate from those in the semideciduous forests of the Cerrado (*P. r.*

roberti), although the limited analyses available suggest clinal variation between these geographic and ecological extremes (Weksler et al. 2001).

NATURAL HISTORY: Neither the ecology nor life history of *P. roberti* have been studied extensively in the field, although Alho (1981) examined homing ability using radio telemetry in the Brazilian Cerrado. This species is sympatric with *P. goeldii* along the southern margins of the Rio Amazonas in eastern Brazil, and with *P. longicaudatus* in the dry forests of the Cerrado in central Brazil.

REMARKS: In his original description of *P. roberti*, Thomas (1904e:196) suggested that his new species agreed "very closely with *P. oris* in its cranial characters, but differs by its paler and more uniformly buffy color, its fully haired under surface, and its much longer and softer fur, of which the spines form a less considerable proportion than usual." The pelage characters, both color and spine development, are typical of populations of spiny rats that live in more open, drier forests in comparison to conspecific populations in denser, more humid forests. Weksler et al. (2001) reviewed geographic variation in both *P. roberti* and *P. oris* and concluded that both belonged to the same taxon on morphological, karyotypic, and molecular grounds, a conclusion contrary to a more geographically limited morphometric study of Pessôa et al. (1990). Weksler et al. (2001) examined specimens that filled the large geographic hiatus between the ranges of the Amazonian lowland *P. oris* Thomas and the Cerrado isolate *P. roberti* Thomas, samples that documented clinal rather than discordant variation in morphological characters across the north-to-south range encompassing both taxa, and thus reinforcing the conclusion of conspecificity. Molecular sequence data reported by Weksler et al. (2001) for specimens spanning this geographic range, from the mouth of the Amazon to south of Brasília, indicate only minor interpopulation differences (maximum sequence divergence 2.4%). However, specimens from

Mato Grosso and Pará states, in the Tapajós-Xingu interfluvial region, not included in the Weksler et al. analyses, are somewhat different morphologically and twice as divergent in mtDNA sequence (Vilela 2005; Schetino 2008; Y. L. R. Leite, L. P. Costa, and R. N. Leite, unpublished data). Further analyses may warrant segregation of more than one species unit within what is considered as a single species (this account; Weksler et al. 2001).

Gardner and Emmons (1984), Leal-Mesquita (1991), Weksler et al. (2001), Machado et al. (2005), and Ribeiro (2006) described and figured the karyotype, as $2n = 30$ and FN = 54 to 56, noting limited regional differences in the number of small biarmed versus uniarmed autosomal pairs. Valim and Linardi (2008) described the host association of ectoparasitic lice in the genus *Gryopus*.

Proechimys longicaudatus species group

Patton (1987) included nine taxa within his concept of the *longicaudatus*-group, and suggested that at least two species were recognizable among them: *P. longicaudatus* Rengger, from the dry forests of southeastern Bolivia east across northern Paraguay to the Cerrado of central Brazil, and *P. brevicauda* Günther, from the lowland rainforest in northern Bolivia, eastern Peru, eastern Ecuador, southeastern Colombia, and western Amazonian Brazil. Gardner and Emmons (1984) had previously suggested that samples from northern Peru and eastern Ecuador might be separable from *P. brevicauda* as a third species, *P. gularis* Thomas, based on chromosomal differences. While Patton (1987) did not include *P. cuvieri* Petter within his *longicaudatus*-group, available DNA sequence data suggest a relationship between this species and those members of the *longicaudatus*-group that he recognized (Vilela 2005; Schetino 2008; J. L. Patton and R. N. Leite, unpublished data). Because of this apparent phyletic coupling and the

fact that each of these species shares a similar suite of craniodental features, we include *P. cuvieri* along with *P. longicaudatus* and *P. brevicauda* within the *longicaudatus*-group here. Common characters that uniquely unite this group of species include lyrate and strongly flanged incisive foramina, broad and long maxillary portion to the septum with the vomerine portion exposed, and deep groves extending onto the anterior palate; a broad and relatively shallow mesopterygoid fossa; a smooth floor to the infraorbital foramen; and a generally uniform three counterfolds on each cheek tooth, with virtually never four folds on any upper tooth, but with two folds characterizing the lower posterior molars of a substantial portion of individual samples. All three share a wide baculum.

Two of these species (*P. brevicauda* and *P. cuvieri*) have been found in sympatry at several localities in the western Amazon (Patton et al. 2000), but the "test of sympatry" has not been established for *P. brevicauda* and *P. longicaudatus*. These two seem to grade from one to the other through the transition between the lowland rainforest of western Amazonia (*brevicauda*) to the dry forests of eastern Bolivia and central Brazil (*longicaudatus*). Whether or not these two are best treated as a single species that varies substantially over this transition area or as the two that we recognize herein must await further critical sampling. Regardless of the status of *brevicauda* and *longicaudatus*, however, the number of species in the group is likely much greater. The limited mtDNA sequence data synthesized in Patton et al. (2000) indicate well-defined geographic clades that differ by considerable levels of divergence within both *P. brevicauda* and *P. cuvieri*, and unpublished morphological and sequence data as well as published karyotypes (Machado et al. 2005; Eler et al. 2012), suggest the presence of an undescribed species in the mid and upper part of the Rio Madeira in western Brazil. Clearly, this is a group ripe for additional research.

KEY TO THE SPECIES OF THE *PROECHIMYS LONGICAUDATUS* SPECIES GROUP:

1.	Dorsal color dark, rich reddish brown; distributed in lowland rainforest of the Guianan region and Amazon basin...2

1′.	Dorsal color pale, yellowish brown; distributed in the dry forests of eastern Bolivia, northern Paraguay, and central Brazil...*Proechimys longicaudatus*

2.	Ventral color always white; aristiform spines long, stout, and with a blunt tip; well-developed postorbital process of zygoma comprised mostly of squamosal; mesopterygoid fossa moderately wide (angle < 73°), penetrating to middle of M3; baculum nearly as wide as long, with deep median depression and elongated apical extensions...*Proechimys cuvieri*

2′.	Ventral color often brownish gray or reddish-buff; aristiform spines short and narrow with elongated tip; postorbital process of zygoma obsolete; mesopterygoid fossa broad (angle >73°) and shallow, penetrating barely to posterior edge of M3; baculum nearly twice as long as wide, with a shallow, or no, median depression and without apical extensions...*Proechimys brevicauda*

Proechimys brevicauda (Günther, 1877)

Short-tailed Spiny Rat

	SYNONYMS:

Echimys brevicauda Günther, 1877:748; type locality "Chamicuros, Huallaga river," (lectotype selected by Thomas, 1900f:301), Loreto, Peru.

Thricomys brevicauda: Trouessart, 1897:607; name combination.

Tricomys brevicauda: Trouessart,1904:504; name combination.

Proechimys bolivianus Thomas, 1901h:537; type locality "Mapiri, Upper Rio Beni, N.W. [La Paz,] Bolivia. Altitude 1000m."

Proechimys securus Thomas, 1902b:140; type locality "Charuplaya, 1350–1400 m," Río Sécure, Cochabamba, Bolivia.

Proechimys gularis Thomas, 1911c:253; type locality "Canelos, Rio Bobonaza, Oriente of [= Pastaza] Ecuador. Alt. 2100'."

Proechimys brevicauda: Ihering, 1904:422; first use of current name combination.

Proechimys brevicaudus securus: Osgood, 1916,209; name combination.

Proechimys cayennensis bolivianus: Ellerman, 1940:121; name combination.

Proechimys cayennensis brevicauda: Ellerman, 1940:120; name combination.

Proechimys cayennensis gularis: Ellerman, 1940:120; name combination.

Proechimys cayennensis securus: Ellerman, 1940:121; name combination.

Proechimys hendeei elassopus Osgood, 1944:203; type locality "Santo Domingo, Rio Inambari, Puno, Peru. Altitude 6,000 ft."

Proechimys "hendeei" elassops [sic]: Hershkovitz, 1948a:138; incorrect spelling of *elassopus* Osgood.

P[*roechimys*]. *guyannensis gularis*: Hershkovitz, 1948a:138; name combination.

[*Proechimys guyannensis*] *brevicauda*: Hershkovitz, 1948a:138; name combination.

[*Proechimys guyannensis*] *bolivianus*: Moojen, 1948:316; name combination.

[*Proechimys longicaudatus*] *elassopus*: Moojen, 1948:316; name combination.

Proechimys longicaudatus brevicauda: Moojen, 1948:349; name combination.

[*Proechimys longicaudatus*] *securus*: Moojen, 1948:316; name combination.

[*Proechimys semispinosus*] *gularis*: Moojen, 1948:316; name combination.

Proechimys guyannensis bolivianus: Cabrera, 1961:519; name combination.

Proechimys guyannensis gularis: Cabrera, 1961:520; name combination.

DESCRIPTION: This is a moderate sized spiny rat with a reddish-brown overall dorsal color, dark feet and short and weakly bicolored tail. Head and body length varies from approximately 235 to 250 mm, and tail length from 150 to 170 mm (averaging 65% of head and body length). Overall color of the head, back, and rump is reddish brown, but not as dark along the mid line as in *P. cuvieri*, although overall tones lighten in samples in central Bolivia where the range of *P. brevicauda* approaches that of its close relative, *P. longicaudatus*. A fulvous lateral stripe characteristically separates the darker dorsal pelage from the lighter venter, but the venter is varyingly colored in different parts of the geographic range, being brownish or grayish in parts of eastern Ecuador (as in the named form *gularis* Thomas) or reddish-buff throughout most of northern and central Peru and western Brazil, and clear white in most individuals from southern Peru and Bolivia (Patton and Gardner 1972 [as *P. longicaudatus*]; Patton et al. 2000).

Osgood (1914b:168) noted the extensive variation in color and color pattern of the venter in specimens from Yurimaguas, in northern Peru near the type locality of Günther's *brevicauda*, "which can scarcely be said to be exactly alike in any two individuals. Fulvous and white are distributed in varying proportions, in general occupying about equal areas of the under parts. The chin and throat with scarcely any exception are fulvous and likewise the sides of the belly. Sometimes the white is reduced to a small pectoral and an inguinal patch or it may cover practically the entire belly and run forward to the middle of the throat." The fulvous lateral stripe continues across the ankle to a small paler patch at the proximal base of the metatarsal area on the dorsal surface of the hind feet. Otherwise, the upper surfaces of the hind feet, including all

five toes, are uniformly dark. The tail is sparsely haired, much less so and with distinctly shorter hairs than that of *P. cuvieri*; scale annuli average 9 to 10 per cm at mid-length. The dorsal pelage is stiff to the touch, but aristiform hairs are less well developed than in *P. cuvieri*. Length varies from 18 to 20 mm and width from 0.6 to 0.8 mm; a distinctly tapering tip is present on all aristiforms.

Cranially, *P. brevicauda* is similar to the two other species within the *longicaudatus*-group, being of moderate size with an elongated but relatively broad rostrum. The temporal ridge is moderately to weakly developed, often with an anterior parietal portion separated from a posterior lambdoidal portion (Patton 1987:328, Table 2). The incisive foramina are typically strongly lyrate in shape, distally flanged so that the anterior palate is deeply grooved with a median ridge, and with a complete and keeled septum (Patton 1987:Fig. 13). The postorbital process of the zygoma is nearly obsolete and comprised predominantly by the jugal. The mesopterygoid fossa is shallow, generally only barely reaching the posterior margins of M3, and wide (the angle varies from 73° to 80° among geographic samples; see Patton 1987:331, Table 4). The floor of the infraorbital foramen is smooth, lacking a grove indicative of the infraorbital nerve (Patton 1987:329, Table 3). The counterfold pattern of the cheek teeth is uniformly 3-3-3-3 above and 3(4)-(2)3-(2)3-(2)3 below. In rare individuals the upper M2 and M3 may have a remnant fourth fold, and southern samples exhibit a higher frequency of only two folds on the m3 (Patton 1987:334–335, Table 5).

The baculum is massive, long and wide, with slight but broad apical wings and an expanded base (Patton and Gardner 1972; Patton 1987; Patton et al. 2000). The rather massive size and length of the baculum make the phallus itself long and distinctly heavy or broad in

appearance; palpating the phallus in live males is an easy way to distinguish this species from sympatric congeners in the field.

DISTRIBUTION: *Proechimys brevicauda* occurs throughout the western Amazon basin, from southern Colombia and eastern Ecuador south throughout eastern Peru, northwestern Bolivia, and east into Acre state in western Brazil.

MARGINAL LOCALITIES (Map 521): BOLIVIA: Beni, Río Mamoré, 5 km NE Río Grande mouth (Patton 1987), 10 km E San Antonio de Lora (Anderson 1997); Cochabamba, Charuplaya (type locality of *Proechimys securus* Thomas), El Palmar (Patton 1987), Mission San Antonio (Patton 1987); La Paz, Mapirí (type locality of *Proechimys bolivianus* Thomas). BRAZIL: Acre, Sobral, Rio Juruá (Patton et al. 2000). COLOMBIA: Caquetá, La Murelia (Patton 1987); Putumayo, Río Mecaya (Patton 1987). ECUADOR: Orellana, San José Abajo (Patton 1987); Pastaza, Canelos, Río Bobonaza (type locality of *Proechimys gularis* Thomas). PERU: Amazonas, Huampami (Patton et al. 2000); Huánuco, Chinchavito (Thomas 1927f); Loreto, Pebas (Thomas 1928c), San Fernando, Río Yavari (Patton 1987); Pasco, Montsinery (Patton 1987); Puno, Santo Domingo (type locality of *Proechimys hendeei elassopus* Osgood); Ucayali, Balta (Patton and Gardner 1972, as *P. longicaudatus*).

SUBSPECIES: The number of taxa assigned to this species, as well as both variation in karyotype and the limited molecular sequence data, could signal valid geographic units, but the analyses needed to determine such have as yet to be done. For the present we regard *P. brevicauda* as monotypic.

NATURAL HISTORY: This species typically occupies upland, non-seasonally inundated (*terra firme*) lowland rainforest, both undisturbed and disturbed forest and second growth, where it is likely to be the most common spiny rat present. It is often found in garden plots (*chacras*),

where individuals feed on yucca and plantains (Osgood 1914b). The few reproductive data, from northern Peru and western Brazil, suggest that breeding commences by the end of the dry season (Patton et al. 2000). *Proechimys brevicauda* may be sympatric with up to four other species of spiny rats throughout much of its range, typically with *P. simonsi*, *P. quadruplicatus*, and more rarely *P. cuvieri* in northern Peru, Ecuador, and Colombia; with *P. simonsi*, *P. steerei*, *P. cuvieri*, and *P. pattoni* in eastern Peru and western Brazil (Patton and Gardner 1972; Patton et al. 2000); and with *P. steerei* and occasionally *P. simonsi* in northern Bolivia (Anderson 1997, who listed *P. steerei* as *P. hilda*). Valim and Linardi (2008) described the host association of ectoparasitic lice in the genus *Gryopus*.

REMARKS: Günther (1877) based his description of *brevicauda* on two specimens, one from Chamicuros, Río Huallaga and the other from a locality recorded only as "Upper Amazons." Thomas (1900f:301) selected the specimen (a skin with a distinctly rufous throat and belly) from Chamicuros as the lectotype. Stephens and Traylor (1983) state that Chamicuros is on the upper Río Samiria, about 35 miles east of Santa Cruz, which is on the Río Huallaga.

Specimens in the American Museum from Inca Mines, on the Río Inambari, Puno, Peru, and referred by J. A. Allen (1900a, 1901b) to *P. simonsi*, are *P. brevicauda*. Patton and Gardner (1972) applied the name *longicaudatus* Rengger to specimens from eastern Peru that Gardner and Emmons (1984) and Patton (1987) referred correctly to *P. brevicauda* (Günther).

Thomas (1901h) regarded his *bolivianus* to be "most nearly allied to *P. simonsi*, but larger and different in cranial details." The skull of the holotype, however, possesses all of the cranial attributes of *P. brevicauda* although the underparts of the skin are pure white, not with the varying degrees of fulvous in typical *brevicauda*, but characteristic of the white venter of all specimens we assign to this species from the southern part of its range in southern Peru and

Bolivia. If this assignment of *bolivianus* Thomas to *brevicauda* Günther, following Patton (1987), is in error, the only other species we recognize to which this name could apply based on its characters is *P. steerei* Goldman. If this is true, then *bolivianus* Thomas would be senior to Goldman's name.

Thomas (1911c) considered *P. brevicauda* to be the closest ally to his *gularis*, differing primarily by the dark-colored throat of the latter in comparison to the buffy venter of *brevicauda*. Gardner and Emmons (1984) suggested that *gularis* Thomas is a valid species, based on karyotypic and color differences. However, Osgood (1944:201) noted that variation in specimens of *Proechimys gularis* Thomas from the vicinity of the type locality "are practically identical with some of the variations of typical *brevicauda*. It is, therefore, doubtful that the name should stand, even for a subspecies."

Patton et al. (2000) noted the molecular uniqueness of *elassopus* Osgood from southern Peru but nevertheless included it within their concept of *P. brevicauda*. Gardner and Emmons (1984) described the karyotype as $2n = 28$, FN $= 48$, based on specimens from nearby localities in southern Peru. This karyotype differs from that of *P. brevicauda* from northern Peru with the same $2n$ and FN in the number of different classes of biarmed autosomes (Patton et al. 2000). The type series of *elassopus* Osgood has cranial features generally consistent with those of typical *longicaudatus*-group animals, yet differs in a more attenuate and weak maxillary portion to the septum of the incisive foramina with the vomer not visible and in a wide but much deeper anterior margin of the mesopterygoid fossa that penetrates the posterior palate to the level of M2. In many respects, these are features also shared with *bolivianus* Thomas and *securus* Thomas, both from Bolivia and also from the lower Andean slopes. Future studies may well conclude that

these three taxa deserve species status. If so, and if all three names belong to the same entity, then *bolivianus* Thomas would be the earliest name available.

The karyotype is geographically variable, ranging from $2n = 30$, FN = 48 in northern Peru and Ecuador (Gardner and Emmons 1984) to $2n = 28$, FN = 48 to 50 in central Peru and western Brazil (Patton and Gardner 1972; Gardner and Emmons 1984; M. N. F. da Silva 1998; Patton et al. 2000). Aniskin et al. (1991) described a similar karyotype, presumably of this species, from Peru south of the Río Marañon-Río Amazonas axis. The specimen referred to *P. longicaudatus* from Usina Hidrelétrica Samuel, in Rondônia state, Brazil, by Machado et al. (2005) is probably *P. brevicauda*. It has a karyotype with $2n = 28$ and FN = 48 and an acrocentric, not biarmed, Y-chromosome typical of other samples of *P. brevicauda* from eastern Peru and western Brazil, and the locality is within lowland Amazonian rainforest rather than the tropical dry forest habitat characterizing *P. longicaudatus*. To whichever species these specimens can be assigned with confidence, it is apparently sympatric with an undescribed member of the *longicaudatus*-group that has a different karyotype ($2n = 30$, FN = 52), and that Machado et al. assign to the *longicaudatus*-group (MZUSP 27396). Specimens with this karyotype have both the enlarged baculum similar to other members of this group (Martin 1970; Patton 1987) and their mtDNA sequences are positioned with other group members. This undescribed entity is known from Amazonas, Rondônia, and Mato Grosso states, where it can be sympatric with *P. roberti* and *P. goeldii* in the mid to upper Rio Madeira and headwaters of the Rio Tapajós, but likely extends to near the mouth of these rivers as well (Vilela 2005; Schetino 2008; Eler et al. 2012; M. N. F. Silva, J. L. Patton, and R. N. Leite, unpublished data). Additional sampling for DNA sequences and careful morphological comparisons of sequenced specimens to those already present in museum collections will be required to accurately map the ranges of *P.*

brevicauda, *P. longicaudus*, and this undescribed taxon in the southwestern Amazon basin of Bolivia and Brazil.
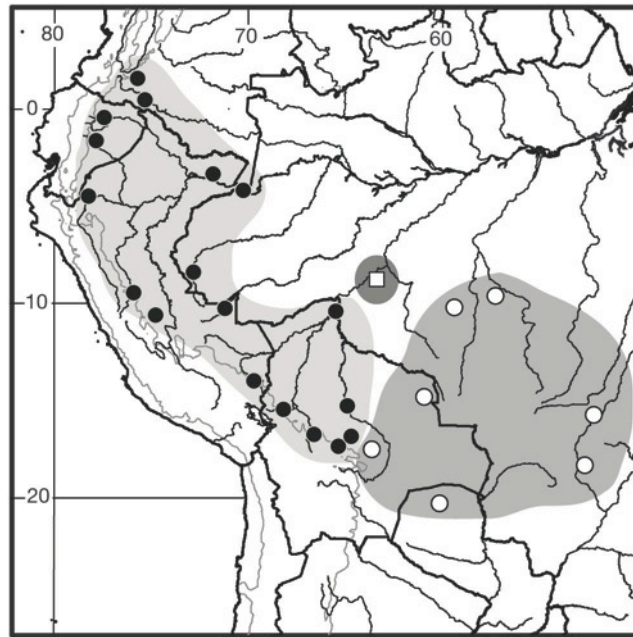
Map 521. Marginal localities for *Proechimys brevicauda* (●), *Proechimys longicaudatus* (○), and *Proechimys* sp. from the central Rio Madeira (□). Contour line = 2,000 m.

Proechimys cuvieri Petter, 1978

Cuvier's Spiny Rat

SYNONYM:

Proechimys cuvieri Petter, 1978:263; type locality "Saül (S 21), Guyane française," French Guiana.

DESCRIPTION: This is a moderate-sized species closely similar in external and craniodental characters to sympatric samples of *P. brevicauda* in the western part of its range (Patton et al. 2000), but markedly distinct from sympatric *P. guyannensis* (Catzeflis and Steiner 2000; Voss et al. 2001) in the Guianan region. Head and body length averages about 230 mm;

the tail is proportionately short (approximately 70% of head and body length). The overall color

is dark reddish orange, with the mid-line of the back darker than the sides, which contrast sharply

with the white venter. Specimens from western Brazil may have a slight fulvous edge to the

ventral fur in some individuals, but the generally bright white contrasts sharply with the typically

buffy venter of sympatric *P. brevicauda*. The dorsal surface of the hind foot is dark on the toes

and lateral margin, but the short hairs above the metatarsals are silverish in color, or at least

distinctly paler in color than the toes. This also generally contrasts with the color pattern of *P.

brevicauda*, where the dorsal surface of the hind feet is overall dark and dull. The tail is sharply

bicolored and clothed in long, slightly curved and dark hairs, which gives it a distinctly "shaggy"

appearance, rather remarkable for a *Proechimys* (Malcolm 1992; Voss et al. 2001). Nevertheless,

the tail scales are visible to the eye. Scale annuli range from 9 to 12 per centimeter at mid-tail.

The dorsal pelage is stiff to the touch, with well-developed aristiform spines averaging 0.9 mm

in width and 20 to 21 mm in length. Some geographic variation in spine development is apparent

in the samples J. L. Patton has examined, with narrower spines in those from the Guianan region

and tips with a whip-like extension in those from south of the Amazon in eastern Brazil;

otherwise, samples are characterized by rather blunt-tipped spines (Patton et al. 2000). The head,

rump, and sides are devoid of spines, as with most spiny rats.

The skull is relatively large, with a long but relatively broad rostrum and well-developed

supraorbital ridges, but with weakly developed temporal ridges (Patton 1987:Table 2, p. 328).

The incisive foramina are lyrate in shape with only moderate posterior constrictions. The

posterolateral margins are flanged, but not as strongly so as in species such as *P. brevicauda*, and

extend onto the palate forming only weak grooves (Patton 1987:322, Fig. 14 a-c). The

premaxillary portion of the septum is long and typically in contact with the maxillary portion,

which may be either keeled or smooth; the vomer is slightly to well exposed ventrally. The groove on the floor of the infraorbital foramen is absent or only weakly developed, as is the lateral flange of this groove (Patton 1987:329, Table 3). The postorbital process of the zygoma is well developed and formed completely by the squamosal, or with only a minimal jugal contribution. The mesopterygoid fossa is relatively broad but penetrates the posterior palate into M3, with a mean angle ranging from 66° to 73°, depending on geographic samples (Patton 1987:Table 4, p. 331). The cheek teeth are large, with the length of the maxillary toothrow ≥ 8.2 mm (Voss et al. 2001). Three folds are typically present on all four upper and lower cheek teeth, although some variation in number exists among geographic samlpes (Patton 1987:334–335, Table 5). In particular, dpm4 may have either three or four folds, and m3 may likewise have either two or three folds. Counterfold formula is thus 3-3-3-3 / 3(4)-3-3-(2)3.

The baculum is short and massive, with a broad but short shaft, expanded base, and deep notch in the distal portion resulting in distinct apical extensions (Patton 1987; M. N. F. da Silva 1998; Patton et al. 2000). A similar shaped, but smaller, baculum is found in *Proechimys pattoni* (Patton and Gardner 1972 [as *P. guyannensis*]; Patton 1987 [in his "*cuvieri*-group"]; M. N. F. da Silva 1998; and Patton et al. 2000).

DISTRIBUTION: *Proechimys cuvieri* is widely distributed throughout the Amazon basin, from eastern Ecuador and Peru to eastern Brazil, Venezuela and the Guianas.

MARGINAL LOCALITIES (Map 522): BRAZIL: Acre, Igarapé Porongaba (Patton et al. 2000); Amapá, 4 km N Amapá (Patton 1987); Amazonas, Barro Vermelho (Patton et al. 2000), Comunidade Colina (Patton et al. 2000), Lago Meduiním, left bank Rio Negro (Patton et al. 2000); Pará, Foresta Nacional Tapirapé-Aquiri (Patton et al. 2000), Ilha do Taiuno (Patton 1987). ECUADOR: Sucumbios, Laguna Grande, Río Cuyabeno (FMNH 125088). FRENCH GUIANA:

vicinity of Cayenne (Catzeflis and Steiner 2000). GUYANA: Barima-Waini, Baramita (ROM 100890). PERU: Amazonas, La Poza (Patton et al. 2000); Loreto, Santa Luisa, Río Nanay (Patton 1967), Sarayacu, Río Ucayali (Patton 1987). SURINAM: Surinam, Lelydorpplan (Patton 1987). VENEZUELA: Bolívar, 69 km SE Río Cuyuni (Patton et al. 2000).

SUBSPECIES: *Proechimys cuvieri* is monotypic.

NATURAL HISTORY: Habitat associations of *P. cuvieri* have been studied limitedly both in western (Patton et al. 2000) and central (Malcolm 1992) Amazonian Brazil, and French Guiana (Guillotin 1983; Voss et al. 2001; Adler et al. 2012). In all three areas, the species inhabits upland, or terra firme rainforest, but may be found equally in locally inundated forest or secondary upland forest and abandoned gardens. Malcolm (1992), for example, found *P. cuvieri* proportionally more abundant than sympatric *P. guyannensis* in early-successional and edge-dominated habitats. Patterson (1992b) also reported on specimens from the central Rio Juruá in western Brazil that were taken from dense virgin forest in hilly terrain, particularly within palm stands along an igarapé and on the margins of igapó or várzea seasonally inundated forest. At Paracou in French Guiana, both Voss et al. (2001) and Adler et al. (2012) took most specimens in traps placed on the ground, but Voss et al. captured two individuals in liana tangles up to 1 m above the ground. The species was taken in well-drained primary forest, creek-side primary forest, and secondary vegetation beside logs, at the bases of trees, among stilt roots, on top of logs and under masses of fallen branches.

Proechimys cuvieri is broadly sympatric with *P. guyannensis* throughout the Guianan region (Voss et al. 2001) and northern Amazonian Brazil (Malcolm 1992), and may co-occur with up to four other species along the Rio Juruá in western Brazil, being absolutely syntopic with as many as three others on the same trap lines (Patton et al. 2000).

In western Brazil pregnant females were only observed in the months of February and March, during the wet season, but data are too limited to define the actual length of the breeding season. Only adult females reproduce, and litter size were always comprised of two young (Patton et al. 2000). In French Guiana, juveniles were taken in every month of the year, although at a substantially higher proportion in March through May, suggesting that reproduction is continuous but with a peak in births also coinciding with the rainy season (Guillotin 1983).

Proechimys cuvieri has also been implicated as a vector for leishmania in French Guiana (Dedet et al. 1984).

REMARKS: Husson (1978) incorrectly identified specimens of this species from Surinam as *P. guyannensis guyannensis* (see Voss et al. 2001). Four strongly divergent geographic clades are defined by the limited mtDNA sequence data available (up to 10% divergence; Patton et al. 2000). One of these is distributed across the Guianan region and eastern Amazonian Brazil, east of the lower Rio Negro along both sides of the Rio Amazonas. A second is known from the Rio Juruá basin in western Brazil and northeastern Peru south of the Río Marañón. A third is known only from northern Peru, north of the Río Marañón. And a fourth is known only from the upper Rio Negro in Brazil, near the Colombian border. Each of these varied geographic clusters share the same basic set of morphological attributes, including the same bacular and glans characters and karyotype, with $2n = 28$ and FN = 46 to 48 (Reig, Tranier, and Barros 1980; Maia and Langguth 1993; M. N. F. da Silva 1998; Patton et al. 2000; Ribeiro 2006; Eler et al. 2012; Silva et al. 2012). However, as noted by Voss et al. (2001), differences in the relative proportions of the qualitative cranial features described by Patton (1987) are apparent in separate geographic regions such that more rigorous analyses of larger samples may well distinguish morphological groupings coincidental with the markedly distinct mtDNA clades. Should more than a single

species be recognized for this group of geographic units, only that from the Guianan region, which contains the type locality of *P. cuvieri* Petter, would have a name to which it can be reliably referred. The remaining clades would lack a name. As with so many other "species" of *Proechimys*, here is another rich opportunity for further research to elucidate species boundaries and their geographic ranges. Steiner et al. (2000) and Van Vuuren et al. (2004) provided more detailed analyses of molecular genetic population structure for samples in the Guianan region, where there is higher sequence diversity and greater geographic structure than in the co-distributed populations of *P. guyannensis*.

Guillotin and Ponge (1984) doubted that *P. cuvieri* could be distinguished from sympatric *P. guyannensis* in French Guiana by standard craniodental measurements, but Catzeflis and Steiner (2000) countered this conclusion by a thorough morphometric analysis of appropriately aged samples. These latter authors also provided a detailed distribution map of known localities in French Guiana. Voss et al. (2001) extended the Catzeflis and Steiner (2000) analysis and evaluated a number of qualitative characters that distinguish *P. cuvieri* from *P. guyannensis*. For example, the single, and easily measured, metric of maxillary toothrow length is non-overlapping between their large series of both species (7.0 to 8.0 mm in *guyannensis* and 8.2 to 9.3 in *cuvieri*; Table 45, p. 157). Malcolm (1992) documented that these two species were also readily separable by toothrow length as well as hind foot length for populations in the central Brazilian Amazon near Manaus. In males, the difference in baculum width and shape is easily palpated in living specimens, even in juveniles (L. H. Emmons, pers. comm.). Lara et al. (1992) examined age and sex components of craniodental metrical dimensions in a large sample from Amapá state, eastern Brazil.
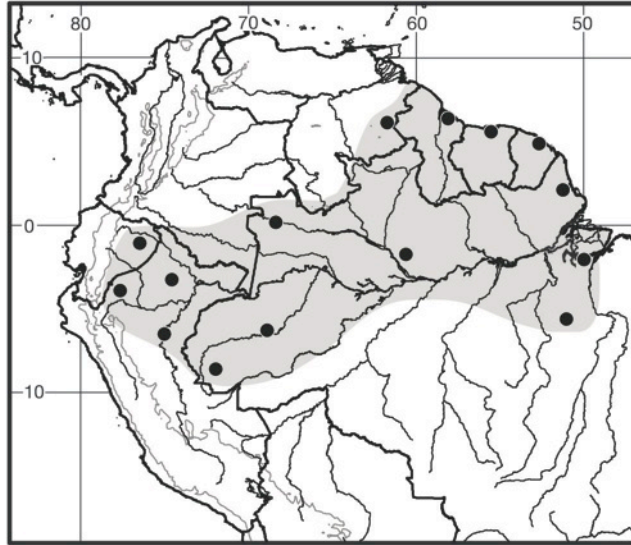
Map 522. Marginal localities for *Proechimys cuvieri* (●). Contour line = 2,000 m.

Proechimys longicaudatus (Rengger, 1830)

Long-tailed Spiny Rat

SYNONYMS:

Echimys longicaudatus Rengger, 1830 236, type locality "Northern Paraguay."

Loncheres myosurus Lichtenstein, 1830:plate 36, fig. 2, and unnumbered text; not *myosurus*

Lichtenstein.

Echimys myosurus: I. Geoffroy St.-Hilaire, 1840:15, 17; name combination.

Echimys cayennensis: Pictet, 1841b,145; name combination; not *Echimys cayennensis*

Desmarest.

P[*roechimys*]. *longicaudatus*: Thomas, 1901g:532; first use of current name combination.

Proechimys cayennensis longicaudatus: Ellerman, 1940:121; name combination.

Proechimys leucomystax Miranda-Ribeiro, 1914:42, type locality "Utiariti, Rio Papagaio," Mato

Grosso, Brazil.

Proechimys longicaudatus: Moojen, 1948:346; name combination.

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Proechimys longicaudatus longicaudatus: Moojen, 1948:351; name combination.

Proechimys longicaudatus leucomystax: Moojen, 1948:352; name combination.

Proechimys guyannensis villacauda Moojen, 1948:355; type locality "Tapirapoã, Rio Sepotuba, Cáceres, Mato Grosso, Brazil."

Proechimys guyannensis ribeiroi Moojen, 1948:361; type locality "Rio 12 de Outubro, affluent of the Camararé, Mato Grosso, Mato Grosso, Brazil; about 190 kilometers west of Utiarití; altitude 414 meters."

DESCRIPTION: This is a medium sized species with head and body length averaging about 220 to 250 mm, and with a proportionately short tail, averaging about 60–63% of head and body length. The dorsal color is distinctly pale reddish or yellowish-brown, streaked with dark brown, contrasting sharply with the dark reddish brown mixed with black of both *P. brevicauda* and *P. cuvieri*. The venter is pure white, without a hint of buffy overtones. The dorsal surface of the hind feet can be highly variable, from uniformly white, including the toes (most specimens), to mostly dusky, or dusky laterally and white medially. A dark ankle band may or may not separate the white inner thigh from the white foot. The tail is bicolored, thinly haired with the scales obvious, and with scale annuli averaging 9 to 10 per centimeter at mid-length. The fur is relatively soft to the touch, with the aristiforms narrow (0.6 to 0.7 mm), rather short (17 to 18 mm), and terminating with a long whip-like tip.

Cranially, *P. longicaudatus* is similar in nearly all features to other members of this complex, but the skull is generally smaller than that of either *P. brevicauda* or *P. cuvieri*. The temporal ridge varies from weakly continuous across the parietals or is limited to a simple posterior extension of the supraorbital ledge (Patton 1987:328, Table 2). The incisive foramina are lyrate in shape, as in *P. brevicauda* and *P. cuvieri*, with typically well-developed

posterolateral flanges that extend onto the anterior palate forming deep groves, and an expanded and long premaxillary portion of the septum with a short, often thin, but typically keeled maxillary portion that continues as a median ridge onto the anterior palate; the vomerine portion of the septum is short but exposed (Patton 1987). The floor of the infraorbital foramen is smooth, without a groove for the infraorbital nerve (Patton 1987:329, Table 3). The postorbital process of the zygoma is well developed and comprised equally by both jugal and squamosal. The mesopterygoid fossa is broad (the angle averages 78°), but penetrates the posterior palate to the middle of M3 (Patton 1987:331, Table 4). All maxillary cheek teeth have three counterfolds; mandibular cheek teeth vary from three (rarely four) on pm4 to two or three folds on each lower molar. The counterfold formula is thus 3-3-3-3 / 3(4)-2(3)-2(3)-2(3). Population samples of *P. longicaudatus* have a higher percentage of individuals with two folds on the lower molars than do the other two species (Patton 1987:334–335, Table 5). This pattern fits a general trend of decreasing counterfold number in species, and/or their populations, along an environmental gradient from extremely wet forests (trans-Amazonian Cocó and western Amazon) to dry forests (eastern Amazonia and central Brazil; Patton 1987). Other examples of this trend are *P. quadruplicatus* in the western Amazon versus *P. goeldii* in the east, or samples of *P. semispinosus* from the Chocó in western Colombia versus those of the isolated population of this species (*rosa* Thomas) in southern Ecuador.

The baculum is robust, long, and wide, with short, stout apical wings. In these general features it is virtually identical to that of *P. brevicauda* (Patton 1987:318, Fig. 9g-h; 321, Fig. 12).

DISTRIBUTION: *Proechimys longicaudatus* occurs in the dry tropical forests of eastern Bolivia, northern Paraguay, and central Brazil.

MARGINAL LOCALITIES (Map 521): BOLIVIA: Santa Cruz, Buenavista (Anderson 1997), Santa Cruz, El Refugio (USNM 588195). BRAZIL: Goiás, Parque Nacional das Emas (Machado et al. 2005); Mato Grosso, Apiacás (Machado et al. 2005), Aripuanã (Machado et al. 2005), Fazenda São Luis (MVZ 197661); Mato Grosso do Sul, Urucum (Patton 1987). PARAGUAY: Alto Paraguay, 54 km E Agua Dulce (Patton 1987).

SUBSPECIES: The number of taxa assigned to this species could signal valid geographic units, but the analyses needed to determine such have not as yet been done. Consequently, *P. longicaudatus* is treated as monotypic.

NATURAL HISTORY: Little has been published about the natural history or population biology of this species. Anderson (1997) recorded pregnant females in March and August in Bolivia. Emmons (2009) found that reproduction seems to begin after a hiatus about the first week in September, with appearance of lactating and late-gestation females, shortly after which young began to appear in the traps. This species was the most common rodent in some dry forests, where its populations remained stable over 10 years. The species also bred in mid-savanna grassland habitats shaded by trees and shrubs, where it denned in holes in termite mounds and in armadillo burrows (Emmons 2009, and pers. comm.) Three species of fleas have been reported, also from Bolivian specimens (Smit 1987). Valim and Linardi (2008) described the host association of ectoparasitic lice in the genus *Gryopus*.

REMARKS: The exact locality from which the type specimen was collected has not been determined, although Thomas (1903c:240) wrote that "Rengger's type was obtained on the 21st parallel of latitude, therefore not far south of Corumbá" (state of Mato Grosso do Sul, Brazil). He considered it "nearly allied to my *P. bolivianus* [herein = *P. brevicauda* Günther], which differs from it by the cranial characteristics given in the description of the latter." Moojen (1948)

assigned specimens from Utiarití on the Rio Papagaio in Mato Grosso, the type locality of Miranda-Ribeiro's *leucomystax*, to both *leucomystax* and *villacauda* Moojen, considering these to belong to separate species based on differences in counterfold counts of the lower pm4 and m1. Our view is that these are the same taxon with a varying expression of counterfold number, which is common in samples examined by J. L. Patton from eastern Bolivia and western Brazil (Patton 1987:334–335, Table 5). However, as noted in the account of *P. brevicauda*, a clear understanding of both geographic and character range must wait additional sampling that explicitly focuses on the undescribed species we mention above. It is likely that northern localities in Brazil herein ascribed to P. longicaudus may actually represent this new taxon.

Machado et al. (2005) report karyotypic variation of $2n = 28$ with the FN varying from 48 to 50 for samples from Mato Grosso and Goiás states in west-central Brazil. These karyotypes are the same as that described for *P. brevicauda* from Amazonian Brazil and Peru (Patton et al. 2000), except the Y-chromosome is biarmed rather than uniarmed.

Proechimys semispinosus group

Patton (1987) included 13 named taxa in his concept of the *semispinosus*-group, most of which had been regarded in earlier literature as subspecies of *P. semispinosus* or as synonyms. He further suggested that only two valid species were contained within the group, *P. semispinosus* and *P. oconnelli*. Among South American taxa, the insular *P. gorgonae* Bangs and *P. rosa* Thomas from southern Ecuador had been recognized by some authors as species, but listed as subspecies by others. Here we follow Gardner and Emmons (1984) and Patton (1987) in recognizing two species, the widespread *P. semispinosus* and the limited range *P. oconnelli*.

KEY TO THE SPECIES OF THE *PROECHIMYS SEMISPINOSUS* SPECIES GROUP:

1.   Distributed in Central American south from Honduras along the west coast of Colombia

        and Ecuador; temporal ridge well developed; cheek teeth complex, typically with four

        counterfolds commonly present on both upper and lower molar series and especially on

        lower pm4..*Proechimys semispinosus*

1′.   Distributed east of the Cordillera Oriental in the northwestern Amazon; temporal ridge

        nonexistent or only weakly developed; cheek teeth simplified, with three counterfolds on

        upper cheek teeth and lower pm4, and two to three counterfolds on lower molar

        series...*Proechimys. oconnelli*

Proechimys oconnelli J. A. Allen, 1913

O'Connell's Spiny Rat

   SYNONYMS:

Proechimys oconnelli J. A. Allen, 1913a:479; type locality "Villavicencio (alt. 1600 ft.),

        Colombia," Meta.

Proechimys cayennensis o'connelli: Tate, 1939:178; name combination but incorrect use of an

        apostrophe (ICZN 1999; Art. 32.5.2.3).

[Proechimys guyannensis] oconnelli: Hershkovitz, 1948a:133; name combination.

   DESCRIPTION: This is a moderately large-bodied species, with head and body length up to

250 mm in adult individuals, and with a medium-length tail (about 70% of head and body

length). The dorsal color is orange rufous finely lined with black, paler on the sides than the mid-

back and rump. The venter is pure white, sharply defined against the color of the sides. A pale

inner thigh stripe is continuous across the ankle onto the dorsal surface of the hind foot, which is

two-toned, pale cream on the inner half and light brown on the outer half, with the dark color typically extending to the 4th and 5th toes. Plantar pads are moderate in size, with the thenar and hypothenar pads subequal. The tail is sharply bicolored, dark brown above and creamy-white below, and thinly clothed with short, fine hairs. The visible scale annuli are relatively wide, averaging nine per centimeter along the mid-length of the tail. The pelage is neither distinctly nor heavily spinous, as the aristiforms are weakly developed, long (18 to 21 mm) and thin (0.8 to 0.9 mm), and tipped with a long whip-like filament.

The skull is unremarkable, with an elongated and tapering rostrum. The temporal ridge is either non-existent or only weakly developed, extending posteriorly from the supraorbital ledge onto the parietals. In this aspect, *P. oconnelli* contrasts sharply with its presumptive sister species, *P. semispinosus* (see Patton 1987:328, Table 2). The incisive foramina are angular or lyrate in shape, with moderately developed posterolateral flanges that extend onto the anterior palate forming grooves on either side of the midline, and despite only moderate development of a maxillary keel and median palatal ridge. The premaxillary portion of the septum is well developed and elongated, encompassing more than half the opening; the premaxillary portion is well developed and always in contact with the premaxillary portion. The vomer is completely encased and not visible in ventral aspect. The floor of the infraorbital foramen has an obvious groove supporting the passage of the maxillary nerve, and formed by a distinct lateral flange (Patton 1987:329, Fig. 22 a, b, Table 3). The mesopterygoid fossa is moderate in width, with an angle averaging 63°, and penetrating to the middle of M3 (Patton 1987:331, Table 4). The postorbital process of the zygoma is obsolete, but formed completely by the jugal. The cheek teeth both above and below are simplified, with three counterfolds on each upper tooth and the

lower pm4 and two to three counterfolds on the lower molars. Hence, the counterfold pattern is 3-3-3-3 / 3-(2)3-(2)3-2(3) (Patton 1987:334–335, Table 5).

The baculum is of medium length but broad (Patton 1987:Fig. 12), with the blunt and thickened base and indented sides typical of *P. semispinosus*, but without the distal apical extensions characteristic of that species (Patton 1987:320, Fig. 11f and g).

DISTRIBUTION: *Proechimys oconnelli* is known only from east central Colombia, east of the Cordillera Oriental in the headwaters of the Río Meta and Río Guaviare.

MARGINAL LOCALITIES (Map 523): COLOMBIA: Cundinamarca, Mámbita (USNM 240036); Meta, Barrigona (Patton 1987), Meta, La Macarena Parque (FMNH 88051); Cundinamarca, La Aguadita (Patton 1987).

SUBSPECIES: *Proechimys oconnelli* is monotypic.

NATURAL HISTORY: There have been no published studies on the ecology or population biology of this species.

REMARKS: Both Gardner and Emmons (1984), using bullar septal patterns and karyotypes, and Patton (1987), using bacular and other craniodental characters, suggested that *P. oconnelli* was the only Amazon-drainage spiny rat to have a close affinity with the trans-Andean *P. s*emispinosus. This hypothesis, however, has as yet to be tested by a cladistic analysis of any character set, morphological or molecular. Gardner and Emmons (1984) described and illustrated a karyotype of $2n = 32$, FN = 52 from a topotype, which differs from that of *P. se*mispinosus mainly in the presence of two medium acrocentrics instead of a single large submetacentric.
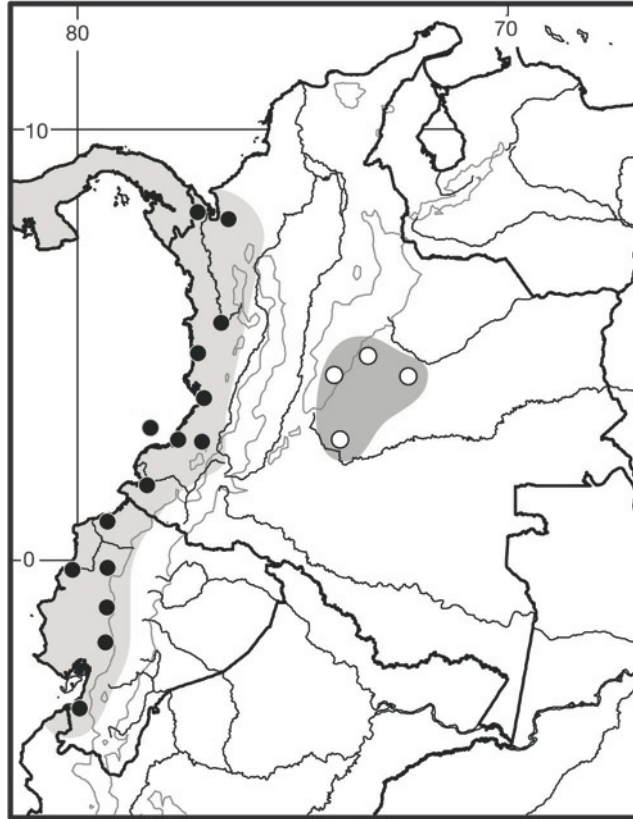
Map 523. Marginal localities for *Proechimys occonnelli* (○) and *Proehcimys semispinosus* (●). Contour line = 2,000 m.

Proechimys semispinosus (Tomes, 1860)

Tome's Spiny Rat

SYNONYMS:

Echimys semispinosus Tomes, 1860b:265; type locality "Gualaquiza, southeastern Ecuador," amended to "Esmeraldas, Prov. Esmeraldas, on the Pacific coast of Ecuador" (Gardner 1983a).

Echinomys semispinosus: Thomas, 1882:101; name combination.

Echinomys semispinosus True, 1889:467; type locality "San Emilio, Lake Nicaragua, Nicaragua;" not *Echimys semispinosus* Tomes.

Echinomys centralis Thomas, 1896:312; renaming of *Echinomys semispinosus* True; not

   Echimys semispinosus Tomes.

[*Proechimys*] *semispinosus*: J. A. Allen, 1899c:264; first use of current name combination.

Proechimys rosa Thomas, 1900b:219; type locality "Santa Rosa, S. W. [= El Oro] Ecuador. Alt.

   10 meters."

Proechimys centralis panamensis Thomas, 1900b:220; type locality "Savanna near Panama,"

   Panama, Panama.

Proechimys centralis chiriquinus Thomas, 1900b:220; type locality "Bugava [=Bugaba],

   Chiriqui, N. W. Panama," Chiriqui, Panama.

Proechimys burrus Bangs, 1901:640; type locality "Isla San Miguel, Archipelago de las Perlas"

   Golfo de Panama, Panama.

Proechimys gorgonae Bangs, 1905:89; type locality "Gorgona Island," about 50 km W Punta las

   Reys, Cauca, Colombia.

Proechimys semispinosus calidior Thomas, 1911c:254; type locality "San Javier, Lower Cachavi

   R., N.W. [= Esmeraldas] Ecuador. Alt. 60 feet."

Proechimys rubellus Hollister, 1914a:57; type locality "Angostura Valley, Costa Rica," but

   holotype actually came from "Pacuare, Costa Rica" (True, 1889:467; Gardner, 1983:136).

Proechimys centralis colombianus Thomas, 1914c:60; type locality "Condoto, Choco, W.

   Colombia. Alt. 300'."

Proechimys semispinosus panamensis: Goldman, 1920:120; name combination.

Proechimys semispinosus burrus: Goldman, 1920:122; name combination.

Proechimys semispinosus goldmani Bole, 1937:178; type locality "altos Cacao, Prov. Veraguas,

   Panama."

Proechimys cayennensis semispinosus: Ellerman, 1940:120; name combination.

Proechimys cayennensis burrus: Ellerman, 1940:120; name combination.

Proechimys cayennensis centralis: Ellerman, 1940:120; name combination.

Proechimys cayennensis panamensis: Ellerman, 1940:120; name combination.

Proechimys cayennensis rubellus: Ellerman, 1940:120; name combination.

Proechimys cayennensis colombianus: Ellerman, 1940:120; name combination.

Proechimys cayennensis calidior: Ellerman, 140:120; name combination.

Proechimys cayennensis gorgonae: Ellerman, 140:120; name combination.

Proechimys cayennensis rosa: Ellerman, 1940:120; name combination.

Proechimys semispinosus ignotus Kellogg, 1946:61, type locality "Isla San José, Archipelago de

      las Perlas, Golfo de Panama, Panama."

 [*Proechimys guyannensis*] *calidior*: Hershkovitz, 1948a:133; name combination.

[*Proechimys guyannensis*] *semipsinosus*: Hershkovitz, 1948a*:*133; name combination.

Proechimys semispinosus gorgonae: Moojen, 1948:316; name combination.

Proechimys semispinosus rosa: Moojen, 1948:316; name combination.

Proechimys guyannensis gorgonae: Cabrera, 1960:520; name combination.

    DESCRIPTION: This is a moderately variable species geographically, larger in body size in

Central America and northern Colombia than in the southern part of its range in Ecuador.

Panamanian specimens, for example, range up to nearly a kilogram in body mass (Adler 1996).

Head and body length varies from about 290 mm in northern Colombia to 240 mm in

northwestern Ecuador, with tail length also varying proportionally from about 63% of head and

body length in the north to 70% in the south. Dorsal color in South America is rather consistently

dark reddish brown liberally speckled with black, and with the sides only slightly lighter to

contrast sharply with the uniformly white venter. The pale inner thigh stripe does not continue across the ankle onto the dorsal surface of the hind foot, which is uniformly dark. The plantar pads are well developed and the thenar and hypothenar pads enlarged and subequal in size. The tail is sharply bicolored, dark brown above and pale below, particularly in northern samples, but less bicolored in southern samples from northwestern Ecuador. Hairiness of the tail varies among individuals, with some moderately clothed in elongated hairs such that the tail scales are nearly hidden from view while others, from the same population sample, have more typically sparsely haired tails. Scale annuli are well developed and usually obvious to the eye, averaging 7 to 8 per centimeter. The dorsal pelage is stiff to the touch, but aristiform development also varies from north to south. These spines are of equal length (19 to 21 mm) in all populations, but vary in width, and hence stiffness (0.9 to 1.1 mm in northern samples and 0.6 to 0.8 in southern ones). Nevertheless, each aristiform terminates in an elongated, filament-like, not blunt, tip.

The skull is large and broad across the zygomatic arches, but with an elongated and narrowed rostrum. This species is uniquely characterized among spiny rats by its well-developed temporal ridges extending from the supraorbital ledge across the length of the parietals (Patton 1987:328, Table 2). Only rarely is this ridge interrupted into anterior and posterior segments. The incisive foramina of specimens from Colombia and Ecuador are rather narrow, with almost parallel sides, or weakly lyre-shaped. The posterolateral margins are usually strongly flanged, creating deep grooves extending onto the anterior palate despite only moderate development of a medial ridge. The premaxillary portion of the septum is long, encompassing nearly the entire length of the opening. The maxillary portion varies from well developed to attenuate, is only weakly keeled at best, and is nearly always in contact with the premaxillary portion. The vomer is completely hidden from ventral view. The floor of the infraorbital foramen has a groove

supporting the maxillary nerve, formed by a well-developed lateral flange (Patton 1987:329, Table 3). The mesopterygoid fossa is of moderate width, but the angle becomes broader from north to south (57° to 62°; Patton 1987:311, Table 4). In contrast to *P. oconnelli*, the postorbital process of the zygoma is moderately well developed and more commonly formed (especially in northern samples, less so in southern ones) by the jugal. Finally, the counterfold pattern is similar to that of species of the *goeldii*-group, with four folds commonly present on all upper cheek teeth and on the lower pm4, and less commonly on lower m2 and even m3. However, fold number decreases in samples from northern Colombia to southern Ecuador (samples of *rosa* Thomas), where four folds are rare on all teeth and two folds may be found on M3 and all lower molars (Patton 1987:334–335, Table 5).

DISTRIBUTION (South America only): *Proechimys semispinosus* is found along the coastal lowlands of western Colombia and Ecuador, from the Panama border in the north to near the Peruvian border in the south.

MARGINAL LOCALITIES (Map 523): COLOMBIA: Cauca, Isla Gorgona (type locality of *Proechimys gorgonae* Bangs), Cauca, Río Saija (Patton 1987); Nariño, Barbacoas (AMNH 34172); Chocó, Bagado (Patton, 1987), Río Docompado (Patton 1987), Unguía (Patton 1987); Cordoba, Socorré (Patton 1987); Valle de Cauda, Zabaletas (FMNH 86766). ECUADOR: Chimborazo, Puente de Chimbo (Patton 1987); El Oro, Santa Rosa (type locality of *Proechimys rosa* Thomas); Esmeraldas, Esmeraldas (corrected type locality of *Echimys semispinosus* Tomes; see Gardner 1983); Guayas, Bucay (Patton 1987); Manabí, Cuaque (Patton 1987); Pichincha, Santo Domingo (Patton 1987).

SUBSPECIES: Hall (1981) recognized six subspecies in Central America (*burrus* Bangs, *centralis* Thomas, *goldmani* Bole, *ignotus* Kellog, *panamensis* Thomas [with *chiriquinus*

Thomas as a synonym], and *rubellus* Hollister. The number and range of subspecies in the South American part of the distribution has not been assessed. The insular *gorgonae* Bangs averages smaller than samples from the Colombian mainland, and is unique in its very dark brown, almost black, dorsal color, and gray-brown infusion across the chin, throat, upper chest, and encroachment along the sides to the inguinal region. This taxon might justify status as a valid subspecies on the basis of its unique coloration alone.

NATURAL HISTORY: Extensive ecological and life history studies of this species have been published for populations in Panama, including microhabitat use and spacing patterns (Adler et al. 1997; Tomblin et al. 1998; Lambert and Adler 2000; Endries and Adler 2005), seed predation and food habits (Bonaccorso et al. 1980; Adler 1995; Hock and Adler 1997; Adler and Kestell 1998; Mangan and Adler 1999; Adler 2000); growth and reproduction (Tesh 1970b; Gliwicz 1984; Adler and Beatty 1997), life span (Oaks et al. 2008), and comparative life history (Fleming 1971). Adler et al. (2003) described infestation by bot flies, Durette-Desset (1970a) described nematode parasites, and McKee and Adler (2002) documented tail autotomy. Little apparent ecological or life history data are available for populations in South America. Bangs (1905) did note, however, that spiny rats on Isla Gorgona were so common that not all specimens trapped could be preserved before the crabs ate them. Valim and Linardi (2008) described the host association of ectoparasitic lice in the genus *Gryopus*.

REMARKS: Thomas (1900b:219), in describing *P. rosa*, considered it "most nearly allied to *P. chrysaeolus*" and not belonging to *P. semispinosus* Tomes, although he also thought *P. rosa* was "allied to the Central American species *P. centralis*," which now is considered a synonym (and valid subspecies) of *P. semispinosus* (Hall 1981).

Bangs (1905), in his description of *P. gorgonae* from Isla Gorgona off the Pacific coast of southwestern Colombia, stated that this "species" was marked only by its unique color, as its skull was indistinguishable from mainland samples of *P. centralis* (= *P. semispinosus*).

Specimens in the Field Museum from Lagunas, near the junction of the Marañón and Ucayali rivers, in northern Peru that Osgood (1944:200–2001) referred to *P. semispinosus* are *P. steerei* (see that account).

Patton and Gardner (1972) described and figured a karyotype of $2n = 30$, FN = 54 from Costa Rica, and Gardner and Emmons (1984) reported intraspecific variation in the morphology and two pairs of small autosomes, with $2n = 30$ but FN = 50 to 54, in samples from Panama, Colombia, and Ecuador, including near-topotypes of *rosa* Thomas. Gómez-Laverde et al. (1990) described and figured the karyotype of *gorgonae* Bangs as $2n = 30$, FN = 56, and Bueno and Gómez-Laverde (1993) recorded two karyotypes for the Pacific lowlands of Colombia, both $2n = 30$, FN = 56, that differ in the amount and pattern of constitutive heterochromatin. Based on similarities in C-banding patterns, Bueno and Gómez-Laverde (1993) suggested a close relationship between *gorgonae* Bangs and mainland populations of *P. semispinosus* in southern Colombia and western Ecuador.

Proechimys simonsi species group

This group is defined on the basis of its relatively large size; long and slim body form with elongated and narrow head and skull; absolutely and proportionately long tail, bright white venter and white hind feet; distinctive, rather oval shaped incisive foramina with a noticeably weak maxillary part to the septum often not in contact with the premaxillary portion; flat and smooth anterior palate without a median ridge; narrow and deeply penetrating mesopterygoid

fossa; and long and narrow baculum (Patton 1987). Only a single species is currently recognized, but deeply divergent and geographically structured DNA sequence clades may underlie greater levels of species diversity than presently understood (Patton et al. 2000; R. N. Leite and J. L. Patton, unpublished data).

Proechimys simonsi Thomas, 1900

Simons' Spiny Rat

SYNONYMS:

Proechimys simonsi Thomas, 1900f:300; type locality "Perené River, Junin Province, Peru. Altitude 800 m."

Proechimys hendeei Thomas, 1926g:162; type locality "Puca Tambo, 5100'," 1,480 m, on trail from Chachapoyas to Moyobamba, Río Huallaga drainage (Stephens and Traylor 1983), San Martín, Peru.

Proechimys cayennensis simonsi: Ellerman, 1940:121; name combination.

Proechimys hendeei nigrofulvus Osgood, 1944:199; type locality "Montalvo, Rio Bobonaza, southeast of Sarayacu," Pastaza, Ecuador.

[*Proechimys longicaudatus*] *hendeei*: Moojen, 1948:316; name combination.

[*Proechimys longicaudatus*] *nigrofulvus*: Moojen, 1948:316; name combination.

[*Proechimys longicaudatus*] *simonsi*: Moojen, 1948:316; name combination.

Proechimys rattinus: Cabrera, 1961:524; referral of paratype (BM 24.2.22.18), but not holotype, to *P. hendeei* (= *P. simonsi* Thomas).

Proechimys pachita: Cabrera, 1961:526; name combination.

DESCRIPTION: This is one of the largest species in the genus, equaled or exceeded in body size only by *P. semispinosus*, *P. quadruplicatus*, and *P. steerei* (head and body length ranges to 250 mm; Patton et al. 2000). It has a characteristic elongated body, long and narrow face, long ears, absolutely as well as proportionately long tail (85% of head and body length), and long, narrow hind feet. The tail is sharply bicolored, dark above and white below; it is covered by sparse, fine hair, although the small scales remain conspicuous to the eye, with 9 to 13 annuli per cm. The middorsal color is darker than that of the sides, reddish brown in tone, coarsely streaked with black hairs and interspersed by dark brown aristiforms. The aristiform hairs are long (22 to 24 mm) and thin (0.2 to 0.4) with a distinctly whip-like tip (Patton et al. 2000). The venter, chin, sides of the upper lips, undersurfaces of forelimbs, and hind limbs are pure white. The white of the inner leg typically extends across the tarsal joint onto the hind foot, which is usually white above. As noted by Patton and Gardner (1972), *P. simonsi* is apparently unique among all species of the genus in lacking the hypothenar pad on the plantar surface of the hind feet.

The skull is large, the rostrum is distinctly long and narrow, and supraorbital ridges are well developed, but do not extend onto the parietals as a temporal ridge. The incisive foramina are diagnostic in its ovoid shape, sometimes slightly elongated but never with strongly constricted posterior margins, flat posterolateral margins lacking grooves extending onto the anterior palate, short and rounded premaxillary portion of the septum that is usually no more than half the length of the opening, and an attenuate maxillary portion usually not in contact with the premaxillary part. The floor of the infraorbital foramen is usually grooved, with a moderately developed lateral flange. The anterior border of the mesopterygoid fossa is acutely angled (49° to 53°) and penetrates deeply into the palate, reaching the anterior half of M3 or the middle of M2. PM4 and M1 typically have three folds while M2-M3 have three or four. The number of folds,

particularly on the lower pm4, varies from north to south from four to three. The counterfold formula is 3-3-3(4)-3(4) / (3)4-3-3-(2)3.

The baculum is long and narrow, with a rounded and slightly broadened base (Didier 1962:416–417, 419, and 422 [as *P. guyannensis brevidauda* and *P. hendeei*]; Patton and Gardner 1972 [as *P. hendeei*]; see Patton 1987).

DISTRIBUTION: *Proechimys simonsi* occurs in the western Amazon basin, including the eastern Andean slopes, from southern Colombia through eastern Ecuador, eastern Peru, northern Bolivia, and into western Brazil.

MARGINAL LOCALITIES (Map 524): BOLIVIA: Beni, Río Mamoré (Anderson 1997); La Paz, Alto Río Madidi, Moira Camp (USNM 579259); Pando, 18 km north of San Juan de Nuevo Mundo (USNM 579616). BRAZIL: Amazonas, Altamira, Rio Juruá (Patton et al. 2000), Colocação Vira-Volta, Rio Juruá (Patton et al. 2000), alto Rio Urucu (Patton et al. 2000). COLOMBIA: Caquetá, La Morelia (Patton 1987); Putumayo, Río Mecaya (Patton 1987). ECUADOR: Morona-Santiago, Gualaquiza (Patton 1987); Napo, San Francisco (UMMZ 80046); Orellana, San José Abajo (Patton 1987); Pastaza, Río Pindo Yacu (Patton 1987). PERU: Amazonas, Yambrasbamba (Patton 1987); Cajamarca, Huarandosa (Patton 1987); Cusco, Consuelo, 15.9 km SW Pilcopata (Solari et al. 2006), 2 km SW Tangoshiari (USNM 588058); Huánuco, Tingo Maria (FMNH 24800); Loreto, Boca Río Curaray (Patton 1987), Orosa (Patton 1987); Madre de Dios, Río Tavara, Fila Boca Guacamayo (USNM 579696); Pasco, San Pablo (Patton 1987); San Martín, Puca Tambo (type locality of *Proechimys hendeei* Thomas).

SUBSPECIES: As currently understood, *P. simonsi* is monotypic (but see Remarks).

NATURAL HISTORY: This species primarily inhabits upland, non-seasonally flooded or terra firme forests, including undisturbed rainforest and secondary or disturbed forests and

garden plots in the western Amazon basin. However, it extends upwards to above 2,000 m in montane forest on the eastern slope of the Andes, and thus has the broadest elevational range of any species of *Proechimys*. In western Brazil, reproductive females (those pregnant or lactating) were taken in all seasons, suggesting that breeding may take place throughout the year. The modal litter size was two, with the range in embryo number from one to three. Both males and females apparently do not reach reproductive maturity until they are fully grown and have molted into their adult pelage (Patton et al. 2000).

Emmons (1982) examined the population ecology, including habitat association, home range size, nightly movement patterns, and density in sympatric populations of *P. simonsi*, *P. steerei*, and *P. brevicauda* in southeastern Peru (for which she used the names *hendeei*, *brevicauda*, and *longicaudatus*, respectively, following Patton and Gardner 1972). Females appear to be territorial, which is likely the reason they reproduce only as adults (they may be unable to acquire territories on which to breed as subadults, Emmons 1982, and pers. comm.).

REMARKS: In his description of P. *simonsi*, Thomas (1900f) considered it externally similar to *P. chrysaeolus* and *P. rosa* (= *P. semispinosus* herein), with the skull "scarcely distinguishable from that of the outwardly very different *P. brevicauda*" (p. 300–301). Osgood (1944:202) referred specimens from the Río Perené at an altitude of 800 ft in central Peru to *P. simonsi*, stating that the species is "probably allied to *brevicauda*, from which it differs at least in immaculate white under parts." It is, however, difficult to reconcile either of these comparisons, as *P. simonsi* is perhaps the most easily recognizable spiny rat, readily separable from all others externally by virtue of its elongated body, pure white venter, and elongated and sharply bicolored tail, and five hind foot pads; and cranially by its uniquely shaped and constructed incisive foramina and narrow, deeply penetrating mesopterygoid fossa (Patton 1987; Patton et al. 2000),

conditions that do not even approach those of the other species to which both Thomas and Osgood referred.

Cabrera (1961:524) referred the paratype of *Proechimys rattinus* used by Thomas (1926g) in his description of this species to *P. hendeei* (= *P. simonsi* herein). This specimen (BM 24.2.22.18) is a skin only of a young animal, with juvenile pelage still on the lower back and rump. It is dark colored with a white venter but gray throat patch but a proportionately long tail (79% of head and body length). Without a skull, identification is difficult, but Cabrera's allocation appears to be correct.

Two markedly divergent geographic clades are apparent in the limited mtDNA sequence data available (Patton et al. 2000). One of these is in northern Peru, north of the Río Marañón-Río Amazonas axis and the second covers the remainder of the range in eastern and southern Peru, western Brazil, and northern Bolivia. If subsequent studies document that these clades correspond to diagnosable taxa, then *nigrofulvus* Osgood would be an available name for the northern clade. The karyotype varies only minimally throughout the sampled range, from eastern Ecuador to southern Peru and western Brazil, with $2n = 32$ and FN = 56 or 58 (Patton and Gardner 1972; Gardner and Emmons 1984; Patton et al. 2000; Ribeiro 2006). Reig and Useche (1976) described an identical karyotype for specimens from southern Colombia, but we have not examined the vouchers and thus cannot unequivocally allocate them to *P. simonsi*. Similarly, Aniskin et al. (1991) described a $2n = 32$, FN = 58 karyotype from northern Peru but without a morphological description to assign those specimens to *P. simonsi* with confidence.

Matocq et al. (2000) described molecular population genetic structure in relation to riverine barriers and habitat range in western Brazil, contrasting those patterns with the co-distributed *P. steerei*. And, E. P. Lessa et al. (2003) provided estimates of late and post-

Pleistocene population growth and stability based on coalescence analysis of these same molecular sequence data. Milishnikov (2006) contrasted patterns of variation in allozyme loci between *P. simonsi* and other co-occurring species of spiny rats in northern Peru.
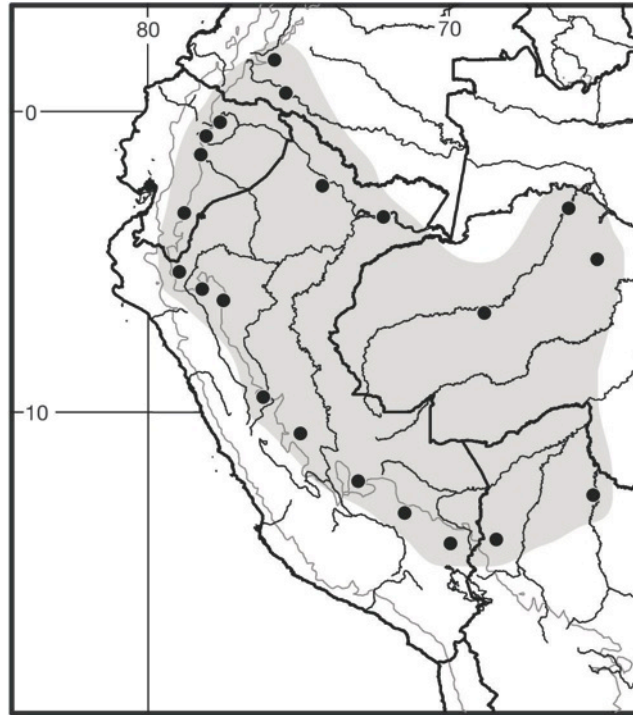
Map 524. Marginal localities for *Proechimys simonsi* (●). Contour line = 2,000 m.

Proechimys trinitatus species group

Patton (1987) assigned nine taxa to this group, but made no recommendations as to the actual number of species. Curiously, most members of this group have been better studied with a broader range of methods and characters than any other group of spiny rats, yet species boundaries remain uncertain and phylogenetic relationships among species unclear. Karyotypic variation is extensive (reviewed by Reig et al. 1970; Reig and Useche 1976; Reig, Aguilera et al. 1980; Reig 1981) and both karyotypic and electromorphic data (Benado et al. 1979; Reig, Aguilera et al. 1980) differentiate a *guairae* superspecies (including *guairae* Thomas and

poliopus Osgood) and a *trinitatus* superspecies (composed of *trinitatus* Allen and Chapman and

urichi Allen). The *guairae* superspecies exhibits a sequence of karyotypic diversity from $2n = 42$

to 62, FN = 72 to 76 that form a ring of ill-defined species or subspecies around the eastern-most

branch of the northern Andes (Benado et al. 1979; Reig, Aguilera et al. 1980; Corti et al. 2001).

While acknowledging the extensive karyotypic diversity, for the present we consider these forms

to represent a single species, *P. guairae*. Karyotypic intermediates are known from points of

geographic contact between some of these chromosomal forms (Aguilera et al. 1995), all

karyotypic forms are very closely related, based on protein allozyme comparisons (Benado et al.

1979; Pérez-Zapata et al. 1992), and all share a similar craniometric morphology (Aguilera and

Corti 1994; Corti and Aguilera 1995; Corti et al. 2001). Following the arguments of Reig,

Aguilera et al. (1980) in their delineation of the *trinitatus* superspecies, we place both *trinitatus*

Allen and Chapman and *urichi* Allen into the single species *P. trinitatus*. Linares (1998),

however, included all members of both the *P guairae* and *P. trinitatus* superspecies (sensu Reig,

Aguilera et al. 1980) in the single species *P. trinitatus*, recognizing three subspecies (*P. t.

trinitatus* from the Cordillera Oriental and Orinoco delta; *P. t. guairae* from the Cordillera

Central, Llanos, and flanks of the Mérida Andes; and *P. t. ochraceus* from the Maracaibo Basin).

We retain the usual consideration of *P. mincae* as a valid species, although Gardner and Emmons

(1984) suggested that it is also a member of the *guairae* superspecies. Finally, we recognize that

P. chrysaeolus Thomas (including *magdalenae* Hershkovitz) and *P. hoplomyoides* Tate, while

members of Patton's (1987) *trinitatus* group, are outside of either the *P. guairae* or *P. trinitatus*

superspecies. We thus retain each as a separate species, at least until additional data can verify

both the phylogenetic cohesion of this group of taxa as well as help resolve species boundaries

within them.

The *trinitatus* group of *Proechimys* is defined by a moderate to large body, relatively soft fur with narrow and elongated aristiform spines (except in *P. chrysaeolus* or *P. hoplomyoides*), a long but stout baculum in males, weakly developed or non-existent temporal ridges, large and open incisive foramina with an attenuated maxillary portion to the septum that is seldom connected to the premaxillary portion, a groove present on the floor of the infraorbital foramen, a narrow and deeply penetrating mesopterygoid fossa, and simplified cheek teeth with many individuals expressing only two folds on the lower molars.

KEY TO THE SPECIES OF THE *PROECHIMYS TRINITATUS* SPECIES GROUP:

1. Body size large (average head and body length > 260 mm); pelage relatively soft to the touch, as aristiform spines are thin (0.4–0.5 mm in width) and terminate with a long whip-like tip..*Proechimys trinitatus*

1′. Body size moderate (average head and body length < 240 mm); pelage stiff to touch, with of aristiforms moderate (0.6–0.8 mm) to wide (0.9–1.1) and often with blunt tip..............2

2. Tail proportionately long (85–90% of head and body length); aristiform spines of moderate width; lower molars with only 2 counterfolds..3

2′. Tail proportionately short (70–75% of head and body length); aristiform spines well developed and wide; all lower molars usually with 3 counterfolds...................................4

3. Floor of infraorbital foramen with groove and lateral flange to accommodate maxillary nerve; range limited to lower Madgalena Valley in northern Colombia...*Proechimys mincae*

3′.   Floor of infraorbital foramen smooth, or with only weakly developed groove; range in Colombia east of Sierra de Perijá and Cordillera Oriental, otherwise range in Venezuela..*Proechimys guairae*

4.   Narrowed mesopterygoid fossa, penetrating to M2; baculum long and narrow; range Guianan and Amazonian Venezuela..*Proechimys hoplomyoides*

4′.   Mesopterygoid fossa wide, penetrated only to M3; baculum long but broad; range restricted to northern Colombia..*Proechimys chrysaeolus*

Proechimys chrysaeolus (Thomas, 1898)

Boyacá Spiny Rat

SYNONYMS:

Echimys chrysaeolus Thomas, 1898b:244; type locality "Muzo, N. of Bogota," Cundinamarca, Colombia (but see Hershkovitz 1948a, who questioned the designation of Muzo as the type locality).

Proechimys chrysaeolus: J. A. Allen, 1899c:264; first use of current name combination.

P[*roechimys*]. *xanthaeolus* Thomas, 1914c:61; incorrect subsequent spelling of *chrysaeolus* Thomas.

Proechimys cayennensis chrysaeolus: Ellerman, 1940:120; name combination.

Proechimys guyannensis chrysaeolus: Hershkovitz, 1948a:136; name combination.

Proechimys guyannensis madgalenae Hershkovitz, 1948a:136; type locality "Río San Pedro, a small stream in the northern foothills of the Cordillera Central, above the village of Norosí altitude 178 meters, department of Bolívar, Colombia."

[*Proechimys*] *magdalenae*: Gardner and Emmons, 1984:14; name combination.

DESCRIPTION: This is a moderate sized spiny rat, with head and body length averaging about 210 to 220 mm, with a medium length tail averaging 70 to 75% of head and body length. The overall dorsal color is dark yellowish to reddish brown speckled with black, with the sides only marginally paler than the mid back and abruptly contrasting with the venter white from the chin to the inguinal region. The white inner thigh stripe is discontinuous with the few white hairs on the dorsal surface of the hind foot by a broad, dark ankle band. The hind foot varies in color above, but is typically dark or may have silvery hairs across the metatarsals; the toes are always dark brown. All plantar pads are well developed, with the thenar and hypothenar subequal in size. The tail is dark brown above and pale below, sparsely haired, appears naked to the eye, and with the scale annuli forming distinct rings, more so than in most other species of spiny rats, with 10 to 13 per centimeter. The pelage is stiff and bristly to the touch, with well-developed aristiform hairs averaging 20 to 22 mm in length and 0.9 to 1.1 mm in width, terminating with either a very short whip-like or blunt tip.

The skull is robust, but long and narrow, with a particularly elongated rostrum. A temporal ridge is absent or only weakly developed, extending onto the anterior parietals from the supraorbital ledge if present (Patton 1987:Table 2). The incisive foramina are oval to teardrop in shape, tapering slightly with weak posterolateral flanges extending onto the anterior palate forming a shallow groove. The premaxillary portion of the septum is well developed, broad, and extends at least half the length of the opening; the maxillary portion may be broad or narrow, but always contacts the premaxillary portion so that the vomerine portion is not visible. The maxillary part of the septum is unkeeled, so that the palate lacks a median ridge. The floor of the infraorbital foramen may be entirely smooth or with only a moderately developed groove resulting from a slight lateral flange (Patton 1987:Table 3). The mesopterygoid fossa is

moderately wide, with an angle averaging 59° and a depth penetrating to the middle of M3, on average (Patton 1987:Table 4). The counterfold pattern of all maxillary cheek teeth is uniformly 3-3-3-3; that of the lower cheek teeth varies slightly, as pm4 typically has three folds, but rarely four, m1 always with three folds, and m2 and m3 with either two or three folds, and in about equal frequencies (Patton 1987:334–335, Table 5). Counterfold formula is thus 3-3-3-3 / 3(4)-3-2(3)-2(3).

The baculum is long (averaging about 10 mm) but relatively broad (2.5 to 2.8 mm in width), with a bulbous base with a median depression and slightly developed apical wings with a median notch at the distal end (Patton 1987:Fig. 7a,b). It is similar in size and shape to other members of the *trinitatus* group, and also to the baculum of *P. decumanus*.

DISTRIBUTION: *Proechimys chrysaeolus* occurs in northern Colombia from the Caribbean coast into the lower Cauca and Madgalena valleys west of the Cordillera Oriental.

MARGINAL LOCALITIES (Map 525): COLOMBIA: Antioquia, Puri (Patton 1987); Bolívar, above Norosí (type locality of *Proechimys guyannensis madgalenae* Hershkovitz), San Juan Nepomuceno (Patton 1987); Boyacá, Muzo (type locality of *Echimys chrysaeolus* Thomas), Puerto Boyacá (Bueno et al. 1989); Córdoba, Catival (Patton 1987), Socorre (Patton 1987); Norte de Santander, Guamalito (Hershkovitz 1948a); Santander, Finca San Miguel (MVZ 196095); Sucre, Las Campanas (Patton 1987).

SUBSPECIES: *Proechimys chrysaeolus* is monotypic, although the relationships between typical *P. chrysaeolus* and *magdalenae* Hershkovitz are unresolved and may signal racial, or even species-level, differences.

NATURAL HISTORY: This species has not been studied in the field. *Proechimys chrysaeolus* may be found in sympatry with *P. canicollis*. It is apparently an important zoonotic

vector in equine encephalitis in Colombia, where a laboratory colony has been established in the Instituto Nacional de Salud in Bogotá (Bueno et al. 1989).

REMARKS: In his original description (Thomas 1898b:244) stated that *P. chrysaeolus* was similar in pelage and cranial characters to *P. trinitatus*. Hershkovitz (1948a:136) suggested that the holotype must have come from further down the Magdalena Valley and not from Muzo, which he argued was at an elevation (1,240 m) too high for this species. We provisionally include *magdalenae* Hershkovitz in our concept of *P. chrysaeolus*, although Hershkovitz (1948a:136–137) specifically compared his *magdalenae* to the geographically adjacent *P. chryaesolus*, both of which he assigned as valid subspecies of *P. guyannensis* É. Geoffroy St.-Hilaire. Hershkovitz believed that *magdalenae* was more similar to what he termed the "western" forms of the races of *P. guyannensis* (in which he included *decumanus* Thomas, *panamensis* Thomas, and *califior* Thomas; the former now a species unto itself and the latter two are synonyms of *P. semispinosus*) than to the geographically adjacent *mincae* J. A. Allen or *chrysaeolus* Thomas by virtue of a consistent three folds on each lower molar. However, *P. decumanus* has only two folds on each lower molar, samples of *P. semispinosus* from western Colombia and Ecuador may have either two or four folds, in addition to the more typical three, and most individuals of *P. chrysaeolus* have three folds on their lower molars (Patton 1987: 335, Table 5). Consequently, *magdalenae* Hershkovitz falls within the range of counterfold number found in *P. chrysaeolus*. Gardner and Emmons (1984) placed *magdalenae* Hershkovitz in their *brevicauda*-group, not in their *guairae*-group, on the basis of bullar septal pattern. These authors did not examine specimens of *P. chrysaeolus*. Because J. L. Patton has seen specimens from the INS laboratory colony in Bogotá which he regards as *P. chrysaeolus*, we believe those specimens

from the same colony for which Bueno et al. (1989) described and figured a karyotype of $2n = 32$, FN = 54 are this species.
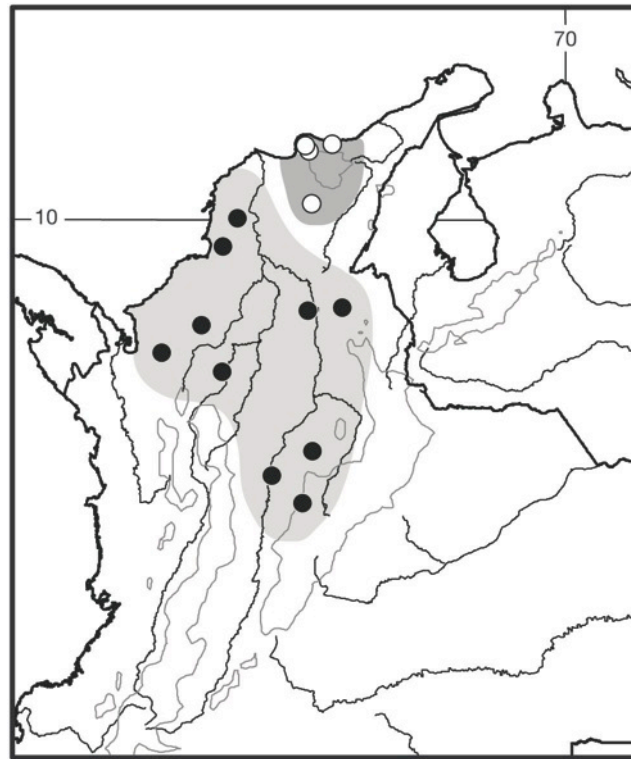
Map 525. Marginal localities for *Proechimys chrysaeolus* (●) and *Proechimys mincae* (○). Contour line = 2,000 m.

Proechimys guairae Thomas, 1901

Guaira Spiny Rat

SYNONYMS:

Proechimys guairae Thomas, 1901a:27; type locality "La Guaira," Distrito Federal, Venezuela.

Proechimys ochraceus Osgood, 1912:56; type locality "El Panorama, Rio Aurare, Zulia, Venezuela."

Proechimys poliopus Osgood, 1914a:141; type locality "San Juan de Colon, State of Tachira, Venezuela. Altitude, 2500 ft."

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Proechimys cayennensis guairae: Ellerman, 1940:121; name combination.

[Proechimys guyannensis] ochraceus: Hershkovitz, 1948a:133; name combination.

Proechimys guyannensis poliopus: Hershkovitz, 1948a:133; name combination.

[*Proechimys guyannensis*] *guairae*: Moojen, 1948:316; name combination.

DESCRIPTION: *Proechimys guairae* is a moderate to large bodied spiny rat, with a head and body length of adults ranging from 210 to 240 mm. The tail is absolutely and proportionately long, averaging nearly 85% of head and body length. Dorsal coloration is light reddish brown lined with black, along the southern slopes of the Merida Andes, but distinctly paler and more yellowish brown in the drier forests around Lake Maracaibo. The ventral color is white from chin to the inguinal region, including white inner thighs where the stripe may be continuous across the ankles onto the dorsal surface of the hind feet. As a consequence, the hind feet are pale above, but often with a lateral light brown stripe extending from the ankle to cover digits IV and V. Plantar pads of the hind feet are well developed, with the thenar and hypothenar pads large and subequal in size. The tail is bicolored, light brown above and pale below, lightly haired so that the large scales are obvious to the eye; scale annuli average 7 to 8 per centimeter. The pelage is coarse but relatively soft to the touch, with long (20 to 22 mm) and narrow (0.5 to 0.7 mm) aristiform spines tipped with a whip-like extension.

The skull is unremarkable, sharing the conformational shape of most spiny rats. Temporal ridges are undeveloped, or present only as a weak and short posterior extension from the supraorbital ledge (Patton 1987:328, Table 2). The incisive foramina are broad and long, oval to slightly teardrop in shape, and with weakly developed posterolateral flanges that extend onto the anterior palate forming slight moderate grooves. The premaxillary portion to the septum is narrow, extends at least to the mid point of the septal opening, but may be only weakly

connected to the maxillary portion, or not at all. The maxillary portion of the septum is thin and attenuated, slightly keeled so that a medial ridge may be present on the anterior palate. The vomer is visible between the premaxillary and maxillary septal elements in ventral view. The floor of the infraorbital foramen may be either smooth or with a slight groove developed by a short lateral flange (Patton 1987:329, Table 3). The mesopterygoid fossa varies from narrow to moderate in width, with an angle ranging from 47° to 55°, but it penetrates typically to at least the posterior margins of M2 and commonly even deeper (Patton 1987:331, Table 4). The postorbital process of the zygoma is moderately developed and comprised of the jugal alone or by equal contributions of jugal and squamosal. Three folds are uniformly present on PM4, M1, and M2, with M3 having either two or three folds in about equal proportions within samples. Lower cheek teeth are uniform with three folds on pm4 and two folds on the molar series. The counterfold formula is 3-3-3-(2-3) / 3-2-2-2.

The baculum has the same shape and general size as other species in the *trinitatus* group, about 10 mm long and 3.4 mm wide, with a bulbous base notched at the midline and weakly developed apical wings (Patton 1987:317, Fig. 7c, 315, Table 1).

DISTRIBUTION: *Proechimys guairae* occurs in northern and western Venezuela in the foothills of both sides of the Andes and upper Llanos north of the upper Río Orinoco, including around Lake Maracaibo and the eastern slopes of the Sierra de Perijá, and into adjacent northeastern Colombia.

MARGINAL LOCALITIES (Map 526): COLOMBIA: Arauca, Fatima (FMNH 92608), Río Arauca (FMNH 92576); Norte de Sandander, San Calixto (USNM 280182), Tarrá (Reig, Aguilera et al. 1980). VENEZUELA: Anzoátequi, Cueva de Agua (Corti and Aguilera 1995); Apure, Guasdualito (Reig, Aguilera et al. 1980); Aragua, Ocumare de la Costa (Aguilera et al.

1995); Barinas, Buena Vista (Reig, Aguilera et al. 1980); Cojedes, El Baul (Reig, Aguilera et al. 1980); Distrito Federal, La Guaira (type locality of *Proechimys guairae* Thomas); Falcón, Carrizalito (Aguilera et al. 1995), Sanare (Reig, Aguilera et al. 1980); Monagas, San Juan (Pérez-Zapata et al. 1992); Guárico, Dos Caminos (Reig, Aguilera et al. 1980); Táchira, San Juan de Colón (Reig, Aguilera et al. 1980); Zulia, El Panorama (type locality of *Proechimys ochraceus* Osgood), Los Angeles del Tucuco (Corti and Aguilera 1995).

SUBSPECIES: Reig, Aguilera et al. (1980) delineated the extensive karyotypic variation they described in *P. guairae* and regarded each chromosomal "segment" in the circular distribution of forms as either species (*poliopus* Osgood plus the unnamed "Barinas" species) or subspecies (*guairae* Thomas and *ochraceus* Osgood, plus two to four unnamed races). Counterclockwise around the ring, beginning in Apure and Barinas states in southwestern Venezuela, these included: "Barinas" ($2n = 62$, FN = 72; Reig and Useche 1976; Reig, Aguilera et al. 1980), "ssp." ($2n = 48$ to 50, FN = 72; Reig and Useche 1976; Reig, Aguilera et al. 1980), *guairae guairae* ($2n = 46$, FN = 72; Reig et al. 1970; Reig and Useche, 1976), *guairae ochraceous* ($2n = 44$, FN = 76; Reig, Aguilera et al. 1980), and, finally, *guairae poliopus* ($2n = 42$, FN = 76; Reig and Useche 1976; Reig, Aguilera et al. 1980). A geographically disjunct $2n = 52$, FN = 74 karyomorph is also known from Anzotegui and Monagas states. Samples of each of these races can be delineated by both standard multivariate morphometrics (Aguilera and Corti 1994; Corti and Aguilera 1995) and geometric morphometrics (Corti et al. 2001), but a formal taxonomy defining and diagnosing each subspecies has yet to be produced.

NATURAL HISTORY: Aguilera (1999) examined the population ecology of *P. guairae* at a single site in coastal Venezuela, including home range size, density, reproductive schedule, and spatial organization of the sexes, and estimated the census effective population size. Handley

(1976) included both *P. guairae* and *P. quadruplicatus* within a taxon he recognized as "*P. semispinosus*" from Venezuela. While it is possible to allocate the specimens in his list of localities (p. 57) to either of these two species, it is unfortunately not possible to parse the habitat and trap data he provides in the same manner. Osgood (1912) collected specimens from the roots of the wild pineapple in the arid parts of the northeastern slope of Lake MarAcaibo, where he found spiny rats to be common. Valim and Linardi (2008) described the host association of ectoparasitic lice in the genus *Gryopus*.

REMARKS: Thomas (1901a:28), in his description of *P. guairae*, recognized that it was "…evidently closely allied to *P. trinitiatis* and its continental representatives of *P. urichi* and *P. mincae*" but differed from them primarily by a much paler color. Osgood (1912) believed that *P. ohcraceus* was most similar to *P. guairae*, but smaller and paler. Two years later when he described *P. poliopus*, Osgood (1914a:141) regarded this new species to be most similar to *ochraceus*. He also made comparisons to *P. guairae*, as well as with *P. mincae* and *P. canicollis*, stating that *poliopus* was "doubtless related" to *P. guairae*, which is distinguishable by its larger size and white feet.
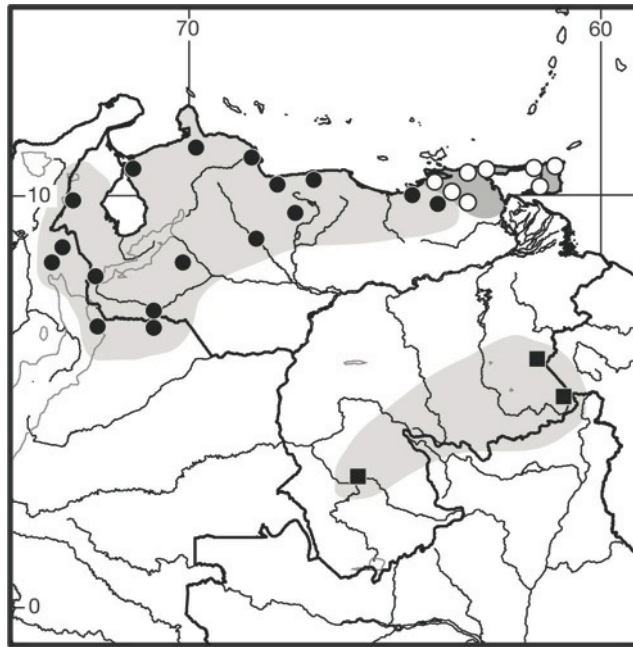
Map 526. Marginal localities for *Proechimys guairae* (●), *Proechimys hoplomyoides* (■), and *Proechimys trinitatus* (○). Contour line = 2,000 m.

Proechimys hoplomyoides Tate, 1939

Guianan Spiny Rat

SYNONYMS:

Proechimys cayennensis hoplomyoides Tate, 1939:179; type locality "Rondon Camp, Mt. Roraima, 6800 feet," Bolívar, Venezuela.

Hoplomys hoplomyoides: Moojen, 1948:315; name combination.

Hoplomys gymnurus hoplomyoides: Cabrera, 1961:532; name combination.

Proechimys hoplomyoides: Handley, 1976:57; first use of current name combination.

Proechimys guyannensis hoplomyoides: Linares, 1998:238; name combination.

DESCRIPTION: This is another moderate sized spiny rat species (head and body length of the holotype 213 mm; Tate 1939:179) with a moderately long tail (72% of head and body

length). Tate diagnosed the species by its blackish-brown and heavily spinose dorsal pelage and slightly larger cheek teeth in comparison to other spiny rats nearby (which would have been samples of *P. guyannensis*). Indeed, the broad and very stiff aristiform spines were so reminiscent of those of *Hoplomys* that Moojen (1948), and subsequently Cabrera (1961), placed *P. hoplomyoides* in that genus. No data are available, however, on aristiform dimensions, characters of the tail scales and scale annuli, or number and size of plantar tubercles. Indeed, so few specimens (six) are known that an adequate understanding of character variation is not possible at present. However, as detailed by Patton (1987) the skull is relatively long and narrow, with an elongated rostrum characteristic of all spiny rats. Temporal ridges extending posteriorly from the supraorbital ledges are absent (Patton 1987:328, Table 2); the floor of the infraorbital foramen is smooth, without a groove indicative of the passage of the maxillary nerve (Patton 1987:329, Table 3); the incisive foramina are somewhat lyre-shaped with weakly flanged posterolateral margins that define grooves extending on the anterior palate; the premaxillary portion of the septum of the foramen is enlarged, extending at least one half the length of the opening, but the maxillary portion is attenuate and not in contact with the premaxilla. The mesopterygoid fossa is narrow and deeply penetrating, to at least the level of the posterior half of M2 (Patton 1987:331, Table 5). And, the counterfold pattern is simple, with three folds on each upper and lower tooth (Patton 1987:334–335, Table 5). The counterfold pattern is thus 3-3-3-3 / 3-3-3-3

The baculum is long and rather narrow (Patton 1987:Fig. 7f), more so than any other species of spiny rat, including other members of the *trinitatus* group (Patton 1987:Fig. 12).

DISTRIBUTION: The known range of *Proechimys hoplomyoides* is limited to the tepui area of southeastern and southern Venezuela. This the only species in the *trinitatus* group with a distribution south of the Río Orinoco and within Amazonia and the Guianan region.

MARGINAL LOCALITIES (Map 526): VENEZUELA: Amazonas, Tamatama (Handley 1976); Bolívar, km 125, 85 km SSE El Dorado (Handley 1976), Rondon Camp (type locality of *Proechimys cayennensis hoplomyoides* Tate).

SUBSPECIES: *Proechimys hoplomyoides* is monotypic.

NATURAL HISTORY: *Proechimys hoplomyoides* is known from evergreen rainforest and gardens, near streams or other moist areas (Handley 1976). The holotype was taken at the highest elevation (6,800 ft, or 2,000 m) recorded for any spiny rat in the Guianan region (Tate 1939).

REMARKS: Moojen (1948) placed *P. hoplomyoides* in the genus *Hoplomys* because of the heavy and dense spines, an action followed by Cabrera (1961). The bullar septal pattern, however, is close to other species in the *trinitatus* group (Gardner and Emmons 1984) although the long and narrow baculum is more similar to that of *P. simonsi* than to those of other species in the *trinitatus* group (Patton 1987:Fig. 12, p. 321). Linares (1998) assigned the species as a valid subspecies of *Proechimys guyannensis*, likely following Tate (1939) in his original description, but without comment. The species is known from only six specimens, including the holotype, and four localities in southern Venezuela.

Proechimys mincae (J. A. Allen, 1899)

Minca Spiny Rat

SYNONYMS:

Echimys mincae J. A. Allen, 1899b:198; type locality "Minca, Santa Marta District," Magdalena,

Colombia.

[*Proechimys*] *mincae*: J. A. Allen, 1899c:264; first use of current name combination.

Proechimys cayennensis mincae: Ellerman, 1940:120; name combination.

Proechimys guyannensis mincae: Hershkovitz, 1948a:134; name combination.

DESCRIPTION: This is a moderately large spiny rat (head and body length about 220 to 230

mm) with a proportionately long tail (90% of head and body length). Coloration across the

dorsum is reddish brown speckled with black, becoming slightly paler on the sides, and with a

white venter from chin to inguinal region but varyingly bordered by light buff margins. A white

inner thigh stripe passes weakly across the ankle to be confluent with a basically dirty white

dorsal surface of the hind foot, with the toes only slightly darker. All plantar pads are enlarged

and well developed, with the thenar and hypothenar large and subequal in size. The tail is

bicolored, brownish gray above and pale cream below. The tail is thinly haired with the scales

large, irregular in shape, and readily visible to the eye; scale annuli average 8–9 per centimeter.

The aristiform spines are long (20 to 22 mm) and thin (0.6 to 0.8 mm) but stiff, giving the pelage

a raspy texture when brushed. The tip of each aristiform may terminate in a short, whip-like

extension or be blunt.

The skull is similar to that of most species of *Proechimys*, elongated, relatively narrow,

and with a tapering rostrum. The temporal region of the braincase is smooth, lacking virtually

any evidence of ridges extending posterior to the supraorbital ledge (Patton 1987:328, Table 2).

The incisive foramina are wide and with somewhat rounded sides giving the opening an oval

shape; posterolateral flanges are either non-existent or so weakly developed that the anterior

palate lacks grooves. The premaxillary portion of the septum is well developed and long, filling

more than half the distance of the opening, but either does not or only rarely contacts a greatly attenuated maxillary portion. The mid palate may have a small medial ridge, but the small maxillary portion of the septum lacks any hint of a keel. The vomer can often be seen in ventral view. The floor of the infraorbital foramen is typically grooved resulting from the moderate development of a lateral flange (Patton 1987:329, Table 3). The mesopterygoid fossa is moderately broad, opening at an angle averaging 57°, and penetrating the posterior palate to the level of M2 (Patton 1987:331, Table 4). The cheek teeth are relatively simple, with never more than three folds above, but often only two folds on M2 and especially M3; the lower cheek teeth typically have three folds on pm4 but only two on each molar (Patton 1987:334–335, Table 5). The counterfold formula is thus 3-3-2(3)-2(3) / 3-2-2-2.

The baculum of *P. mincae* is long and stout, similar in size and shape to that of other species in the *trinitatus* group, except that of *P. hoplomyoides* (Patton 1987:315, Table 1).

DISTRIBUTION: *Proechimys mincae* is known only from the lower Magdalena valley in northern Colombia to the west and south of the Sierra Nevada de Santa Marta.

MARGINAL LOCALITIES (Map 525): COLOMBIA: Cesar, Colonia Agricola de Caracolicito (USNM 280198); Magdalena, Bonda (Patton 1987), Don Dago (= Don Diego) (Patton 1987), Minca (type locality of *Echimys mincae* J. A. Allen).

SUBSPECIES: *Proechimys mincae* is monotypic.

NATURAL HISTORY: *Proechimys mincae* has not been studied in the field. It is sympatric with *P. canicollis* at Bonda, the type locality of the latter species (J. A. Allen 1899b).

REMARKS: Gardner and Emmons (1984) described and figured the karyotype of *P. mincae* as 2*n* = 48 and FN = 68, similar to that of some karyotypes of *P. guairae*. In his description of this species, J. A. Allen (1899b) noted that it belonged to the same group as *P.*

trinitatus, with the "…same white belly, the same general proportions, and practically the same dentition." He considered it separate from *P. trinitatus* by virtue of smaller size and golden brown rather than dark chestnut brown dorsal color. However, the skull of *P. mincae* is more different in geometric shape than any members of Reig, Aguilera et al.'s (1980) *P. guairae* or *P. trinitatus* superspecies groups, and even the unrelated *P. canicollis* (Corti et al. 2001).

Proechimys trinitatus (J. A. Allen and Chapman, 1893)

Trinidad Spiny Rat

SYNONYMS:

Echimys trinitatus J. A. Allen and Chapman, 1893:223; type locality "Princestown [= Princes Town], Trinidad, " Trinidad and Tobago.

E[*chinomys*] *trinitatus*: Thomas, 1896:313; name combination.

Echimys urichi J. A. Allen, 1899b:199; type locality 'Quebrada Secca," Villarroel, Sucre, Venezuela.

[*Proechimys*] *trinitatus*: J. A. Allen, 1899c:264; first use of current name combination.

[*Proechimys*] *urichi*: J. A. Allen, 1899c:264; name combination.

Proechimys urichi: Pittier and Tate, 1932:264; name combination.

Proechimys cayennensis trinitatus: Ellerman, 1940:121; name combination.

Proechimys cayennensis urichi: Ellerman, 1940:121; name combination.

[*Proechimys guyannensis*] *trinitatus*: Moojen, 1948:316; name combination.

[*Proechimys guyannensis*] *urichi*: Moojen, 1948:316; name combination.

Proechimys guyannensis urichi: Cabrera, 1961:523; name combination.

DESCRIPTION: This is a moderately large bodied species (head and body length ranging between 265 and 270 mm in mature adult individuals), with a proportionately long tail (75–80% of head and body length). The dorsal color is brownish orange heavily mixed with black lines, only slightly paler on the sides, and contrasting with a pure white venter. A white inner thigh stripe may continue across the ankle to the medial side of the hind foot surface, which is otherwise brownish in color. The plantar pads of the hind foot are well developed with both the thenar and hypothenar pads enlarged and subequal in size. The tail is covered very sparsely with short hairs so that it appears quite naked to the eye. The tail scales are large, almost oval in shape, and only 6 to 7 annuli per centimeter along the mid-tail. The pelage is relatively soft to the touch, with aristiform spines long (20 to 22 mm), thin (0.3 to 0.5 mm), and terminating in an extended whip-like tip.

The overall shape of the skull is similar to most other species of spiny rats, relatively narrow and elongated, with a long and tapering rostrum. Weak temporal ridges that extend back to mid-parietal from the supraorbital ledges are present in older individuals, and are less obvious in younger specimens (Patton 1987:328, Table 2). The incisive foramina are wide and oval in general shape, with only weakly posterolateral flanges, if at all, so that the anterior palate is either flat or weakly grooved. The premaxillary portion of the septum is variable in size laterally and may extend virtually the entire length of the opening or only to the mid point. The maxillary portion is narrow and weakly developed, barely in contact with the premaxilla, and only weakly keeled, typically without extending onto the anterior palate as a continuing medial ridge. Nevertheless, the vomerine portion of the septum is usually not visible in ventral view. The floor of the infraorbital foramen is grooved which is bordered laterally by typically moderately developed flange (Patton 1987:329, Table 3). The mesopterygoid fossa is relatively narrow,

forming an angle of about 53°, and deep, typically penetrating to the anterior edge of M3 or posterior edge of M2. The postorbital process of the zygoma is weakly to moderately developed, and composed entirely of the squamosal. The upper cheek teeth are uniform with three folds on each, except that M3 occasionally has only two. The lower cheek teeth all have three folds, with each molar often with only two. Consequently, the counterfold pattern is 3-3-3-(2)3 / 3-(2)3-(2)3. The paroccipital processes are distinctly broad, flattened, and tightly appressed to the bulla, more so than in any other species of *Proechimys*.

Patton (1987:Fig. 7, e) illustrated the baculum of *P. trinitatus*; it is elongated but moderately wide, with a slightly expanded base with a median notch, straight sides, and slight apical wings, similar to that of other species within the *trinitatus* group (with the slight exception of the baculum of *P. hoplomyoides*).

DISTRIBUTION: *Proechimys trinitatus* occurs on the island of Trinidad and the adjacent coastal lowlands of northern Venezuela (see maps in Pérez-Zapata et al. 1992; Corti and Aguilera 1995).

MARGINAL LOCALITIES (Map 526): TRINIDAD AND TOBAGO: Trinidad, Chaguaramas (MVZ 168949), Oropuche Heights (FMNH 20960), Princes Town (type locality of *Echimys trinitatus* J. A. Allen and Chapman). VENEZUELA: Monagas, 6.5 km NE Cachipo (Pérez-Zapata et al. 1992), Guanaguana (Aguilera et al. 1995); Sucre, El Argarrobo (Aguilera et al. 1995), Guaraunos (Aguilera et al. 1995), Quebrada Seca (type locality of *Echimys urichi* J. A. Allen).

SUBSPECIES: Spiny rats from the Venezuelan mainland are somewhat smaller than those on the island of Trinidad. Ellerman (1940), Moojen (1948), and Cabrera (1961) regarded these mainland populations as a distinct subspecies, but listed it as *P. guyannensis urichi* (J. A. Allen).

NATURAL HISTORY: Everard and Tikasingh (1973a) examined the population ecology of *P. trinitatus* on Trinidad, including recapture rates, home range and movement patterns, longevity, reproduction, sex ratio, and parasites. Everard et al. (1974) examined filarial nematodes and Stunkard (1953) described cestodes. This species is common in secondary rainforest on the island of Trinidad. Valim and Linardi (2008) described the host association of ectoparasitic lice in the genus *Gryopus*.

REMARKS: Reig and colleagues (Reig et al. 1979; Reig, Aguilera et al. 1980; Pérez-Zapata et al. 1992) report a karyotype of $2n = 62$, FN = 80 for both Trinidad and Venezuelan populations of *P. trinitatus*. Benado et al. (1979) examined allozyme relationships and show that *P. trinitatus* is the sister to a group of four karyomorphs of the *P. guairae* superspecies. However, Patton and Reig (1990) showed that *urichi* Allen (= *P. trinitatus*) is nested phylogenetically within three karyomorphs of *P. guairae*, including two examined by Benado et al. (1979; $2n = 46$ and 62 forms) plus $2n = 42$ *poliopus* Osgood. If more sophisticated molecular analyses support the phylogenetic position of *P. trinitatus* within the *P. guairae* superspecies, then Linare's (1998) conspecific hypothesis should be re-evaluated.

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CHAPTER 4

Phylogeography of *Proechimys roberti* (Rodentia, Echimyidae): implications for the evolutionary history of southeastern Amazonia and the Cerrado ecotone

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Short title: *Proechimys roberti* phylogeography

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Introduction

The Neotropical lowlands harbor the richest fauna on Earth, as a result of both high species turnover between habitats (beta diversity) and regions (gamma diversity) (Cody 1996; Hoorn *et al.* 2010b). Such vast biodiversity has fascinated and challenged researchers for over a century (Moritz *et al.* 2000), and yet the specific mechanisms responsible for promoting and maintaining such high levels of biodiversity are not well understood. Several alternative hypotheses have been proposed to account for patterns of diversification in the Neotropical lowlands, with special reference to the Amazon Basin. Alfred Russel Wallace (1852) advanced the first of these hypotheses based on riverine barriers, while other factors that promote speciation were subsequently attributable to Pleistocene refugia (Haffer 1969), sharp environmental gradients (Endler 1982), long-term paleoclimatic shifts (Bush 1994), fine-scale habitat heterogeneity (Tuomisto *et al.* 1995), marine transgressions (Nores 1999) and neotectonics (Rossetti *et al.* 2005). Not surprisingly, there is no agreement about the generality of any of these hypotheses, which in turn are not mutually exclusive and could potentially influence any group of taxa (Hall & Harvey 2002). Moreover, confounding issues in finding a model consensus include the fact that organisms with different inherent life histories are likely to respond uniquely to the same historical events, and from the difficulty in devising tests to falsify particular hypotheses that lack hierarchical temporal and/or spatial division (Colinvaux *et al.* 1996; Patton & da Silva 1998).

Traditionally, molecular-based studies have been based on qualitative assessments and *ad hoc* explanations of bifurcating phylogenetic trees that describe the underlying patterns of genetic diversity (Knowles & Maddison 2002; Liu & Pearl 2007). When data from multiple loci are available, such topological inferences also are often treated with concatenation and consensus

tree approaches (Carstens & Knowles 2007). This inferential procedure has formed the basis for a number of studies supporting hypotheses concerned with species diversification in Amazonia and adjacent regions (Leite & Rogers in press). Nevertheless, over-interpretations may arise because these approaches fail to incorporate the stochastic variance of genealogies into the phylogenetic inferential procedure (Maddison & Knowles 2006) and potentially complex and varied histories of species are overlooked (Edwards & Beerli 2000). More recently, inferences within a rigorous statistical framework are explicitly considering the stochasticity inherent to the coalescence of gene lineages and the genetic processes shaping population structure and speciation events (Knowles & Maddison 2002; Nielsen & Beaumont 2009). As a result, coalescent-based methods allow for the testing of alternative historical hypotheses devised *a priori* to accommodate biologically more realistic models while providing relevant parameter estimates (Knowles 2009). At the same time, testing historical hypotheses within a statistical framework requires reasonable deliberation of three key steps that involve: (1) defining a set of hypotheses; (2) deciding on the model's complexity; and (3) integrating information from external data (e.g., paleogeographic data) (Knowles 2004). Therefore, tests of hypotheses in statistical phylogeography should be able to accommodate geographically structured genetic variation while providing parameter estimates that are relevant to a biologically realistic model built upon external evidence (Carstens *et al.* 2005).

Notably, phylogeographic studies are skewed toward temperate organisms from North America and Europe, whereas research efforts have devoted comparatively less attention to the southern hemisphere (Beheregaray 2008). Neotropical countries in particular harbor megadiverse biotas that can be investigated under a statistical phylogeographic approach, and thus can provide insights into the evolutionary history of biotic diversification in such species-rich regions.

Moreover, South American ecosystems exhibit an array of biogeographic scenarios that have been shaped in varying degrees by geological events and climatic alterations during the course of the continent's landscape evolution (Turchetto-Zolet *et al.* 2013). As a result, there has been a renewed interest in evaluating biogeographic hypotheses proposed for the Neotropical region within an explicit phylogeographic context. Recent studies have involved the testing of climatic stability in the Atlantic Forest (Carnaval *et al.* 2009), alternative diversification models of the open dry biomes (Werneck *et al.* 2012), and simultaneous divergence across a suture zone in northwestern Amazonia (Dasmahapatra *et al.* 2010). These empirical examples demonstrate how a hypothesis-driven framework can provide a better understating of the patterns of species diversity and distribution in the Neotropics and the evolutionary processes governing them. Insights into major hypotheses of diversification have been discussed more specifically for Amazonia under the tenets of coalescent theory and recent developments of phylogeography, and future research perspectives highlight the importance of formulation and testing of *a priori* alternative hypotheses for critically evaluating the many historical scenarios involved in Amazonia's intricate biotic evolution (Leite & Rogers in press). However, this is a challenging task considering our incipient scientific knowledge of the history of this region, and thus new empirical studies are necessary.

Spiny rats of the genus *Proechimys* form an amenable and very interesting group for exploring the geography of genetic variation in the Neotropical region. They constitute the most speciose and most widely distributed genus among the echimyid rodents (da Silva & Patton 1998), and are essentially inhabitants of lowland rainforests of Central America and the Amazonia, although a few species extend their limits onto the lower slopes of the Andes or gallery forests in southeastern Bolivia and central Brazil. The genus was formally divided into

nine species groups defined on the basis of several craniodental and bacular characters (Patton 1987), and each of these groups pertains to a more or less well-defined subregion within the total distribution of the genus. The geographic context of genetic variation among and within populations of the species of *Proechimys* stimulate a variety of hypotheses concerning their historical relationships and patterns of species diversity which can provide new insights into the biogeographic scenarios of diversification in the Neotropical region. More specifically, *P. roberti* occurs south of the mid-lower Amazon River in three distinct sub-basins, namely the Tapajós, Xingu and Araguaia/Tocantins, also extending towards adjacent drainages south and east of the Amazon Basin.

Here we use a coalescent-based framework to investigate the phylogeography of *P. roberti*, and test alternative population divergence models based on geological and paleoecological data from southeastern Amazonia (Costa *et al.* 2001; Rossetti & Valeriano 2007; Salgado-Labouriau 1997; Valente & Latrubesse 2012). Such evidence suggests that neotectonics and climate fluctuations have played a key role on the landscape formation and configuration of modern drainage systems (e.g., Xingu and Araguaia/Tocantins sub-basins) and establishment of the ecotonal area between the Amazonia and Cerrado biomes, therefore shaping the phylogeographic history of forest-dwelling taxa found both in southeastern Amazonian rainforests and gallery forests of the Cerrado. To investigate the diversification of this species and test for explicit historical scenarios in the Amazon Basin, we have obtained a dense geographical and molecular dataset, which is perhaps the most comprehensive intraspecific sampling ever employed for any Amazonian vertebrate.

Materials and Methods

Taxon sampling and sequence data

Samples were obtained through tissue loans from several scientific collections and museums (Table S1, Supporting Information) and complemented during fieldwork led by RNL. Our complete dataset includes 187 individuals from 35 localities spanning the geographic range of *P. roberti* (Figure 1). We used six other *Proechimys* species from five different species group (following Patton & Leite in press) as outgroups in the phylogenetic analyses. We sequenced 801 base pairs of the mtDNA Cytochrome *b* (Cyt *b*) gene for all individuals, and then subset at least one individual from all unique mtDNA haplotypes and/or geographical localities for sequencing six autosomal nuclear loci.

The mtDNA Cyt *b* gene was amplified using the primers: L14724 (Irwin *et al.* 1991) and MVZ16 (Smith & Patton 1993). We implemented the EvolMarkers bioinformatic pipeline (Li *et al.* 2010; Li *et al.* 2012) for mining molecular markers across annotated genomes at the Ensembl database. We chose three rodent taxa for which genomic data were available: *Cavia porcellus*, *Rattus norvegicus* and *Mus musculus*. The first is the closest relative of *Proechimys* (family Echimyidae) and the other two are the commonly used laboratory mouse and rat, respectively. We compared conserved genomic regions and searched for exon-primed intron-crossing (EPIC) markers. We then designed three novel EPICs, which primers were tested in the laboratory bench and successfully amplified DNA sequence fragments of ~800 base pairs. In addition, we manually browsed three other genes in order to design new primers for previously described markers that did not amplify across all studied taxa (Matthee *et al.* 2001; Wickliffe *et al.* 2003). Table 1 lists measures of sequence variation that summarize characteristics of the multilocus dataset generated for this study.

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We extracted genomic DNA with the DNAeasy Qiagen kit. The PCR amplification conditions differed across loci, but basically included a initial denaturation at 94°C for 5 min, followed by 40 cycles each consisting of 94°C denaturation (1 min); 45-63 °C annealing (0.5-1 min), 72 °C extension (1 min), and a final extension at 72 °C for 5-7 min. PCR products were vacuum purified using MANU 30 PCR plates Millipore and subsequently resuspended with HPLC water. Sequencing reactions used the ABI Big-Dye Terminator v3.1 Cycle Sequencing Kit. Sequencing products were purified with Sephadex G-50 Fine (GE Healthcare) and sequenced on an ABI 3730xl DNA Analyzer at the BYU DNA Sequencing Center.

Chromatogram assembly and editing was performed with Sequencher v4.9 (Gene Codes Corporation), and the resulting consensus sequences were aligned with MAFFT (Katoh *et al.* 2002). Alleles with length variation (heterozygous indels) were phased using Champuru v1.0 (Flot 2007). We resolved the gametic phase of heterozygotes with PHASE v2.1.1 (Stephens *et al.* 2001), implementing the default iterative scheme of 100 main iterations, 100 burn-in iterations, one thinning interval per iteration, and confidence probability thresholds of 0.90. Input files for PHASE were prepared with SeqPHASE, as well as the output files from PHASE were converted back into FASTA alignments with SeqPHASE (Flot 2010). The heterozygous indels that were present in some individuals were specified as known phases in a separate input file (.known) that was phased along with base polymorphisms, as PHASE tends to perform better when known phases are available. When phase certainty was inferior to the probability threshold we selected the reconstructions with the highest posterior probability, to avoid the omission of unresolved genotypes that can introduce biases into downstream inferences (Garrick *et al.* 2010a). Recombination tests performed using the Difference of Sum of Squares test with TOPALi v2.5 (Milne *et al.* 2009) revealed no significant recombination regions for the nuclear loci. Models of

DNA evolution were selected based on AIC criterion with jModelTest v0.1.1 (Posada 2008).

Gene trees, genetic diversity and distances

We performed maximum likelihood phylogenetic inference in RAxML v7.2.6 (Stamatakis 2006) to reconstruct gene trees for each locus using the GTR + Gamma model with 200 independent ML searches, and 1,000 nonparametric bootstrap replicates to assess nodal support (Felsenstein 1985). Individuals were assigned to populations based on their presence in major distinct landscape compartments of southeastern Amazonia and the Cerrado, which were mostly congruent with the overall geographical structure of *P. roberti* with respect to the mtDNA Cyt *b* gene. This population assignment approach is frequently used for poorly known geographic regions and groups with taxonomic uncertainty (Werneck *et al.* 2012). These assignments were used for subsequent species tree, demographic analyses, and hypothesis testing.

We estimated relative mutation rates among all loci and theta ($\theta = 4N_e\mu$) for each population across all loci as implemented in Migrate-n v3.2.15 (Beerli 2006; Beerli & Felsenstein 2001), using a Bayesian approach and thermodynamic integration of four chains with a static heating swap scheme (temperatures: 1.0, 1.5, 3.0, 10^6), sampling at every 100th increment for a total of 50,000 steps and burn-in of 50,000 steps. We calculated the following genetic diversity parameters in DnaSP v5.10.1 (Librado & Rozas 2009): number of haplotypes (H), haplotype diversity (Hd), Watterson's theta (θ_w), nucleotide diversity per site (Pi), average number of nucleotide differences between sequences (k), and number of segregating sites (S). Net among group distances between mtDNA haploclades and outgroup species were computed in MEGA v5.1 (Tamura *et al.* 2011) using uncorrected and Tamura-Nei corrected (Tamura & Nei 1993) distances, and 500 bootstrap replicates to estimate standard errors.

Species tree and species delimitation

We estimated the species tree and divergence times for *P. roberti* under a coalescent model using *BEAST v2.0.2 (Drummond *et al.* 2012) and uncorrelated relaxed clocks to allow for rate heterogeneity among lineages. We used a Yule prior for the species tree, and a normal prior distribution (mean = 0.00523 substitutions/million years; SD = 0.0013075) on the global substitution rate of Cyt *b* (following Ho 2007; Ho & Phillips 2009) to calibrate the estimation of divergence times based on 5.23×10^{-9} substitutions per site per year for *Rattus norvegicus* (Bininda-Emonds 2007). For the nuclear loci, we estimated the substitution rates relative to the rate of Cyt *b* and used the default gamma prior for ucld.mean and exponential prior for ucld.stdev, with a mean of 0.5. We performed five independent runs of 200 million generations sampled every 20,000 generations, to obtain a total of 10,000 trees per run from the posterior distribution. We examined parameter traces with Tracer v1.5 (Rambaut & Drummond 2007) to check for stationarity, high ESS, and convergence between independent runs. We annotated tree files with TreeAnnotator v1.7.5 to estimate a maximum clade credibility (MCC) tree after removing a burn-in of 10% in each independent run that were combined in LogCombiner v1.7.5 (Drummond *et al.* 2012).

We implemented a Bayesian species delimitation approach for assessing the limits of distinct evolutionary lineages within *P. roberti* using the program BPP v2.1 (Yang & Rannala 2010). This method is based on reversible-jump Markov chain Monte Carlo (rjMCMC) that samples from the posterior distribution of species divergence (τ) and population size (θ) parameters to estimate the posterior probability of species delimitation models. BPP has shown to be accurate and was successfully used in several empirical studies (Camargo *et al.* 2012;

Fujita *et al.* 2012; Leaché & Fujita 2010). BPP implementation takes a fully resolved guide tree

that is specified *a priori* and evaluates alternative models of species limits from a set of nested

species trees by collapsing internal nodes on the guide tree. This coalescent framework

accommodates variation in θ along the species phylogeny and gene tree uncertainty and assumes

no gene flow between species. We used algorithm 0 with fine-tuning parameter $\varepsilon = 2$ and input

as guide tree the same topology of the species tree inferred using *BEAST. We employed

different combinations of the parameters α and β that specifies the gamma $G(\alpha, \beta)$ prior

distributions for θ and τ to assess a range of demographic scenarios: relatively large ancestral

population sizes and deep divergences, both priors $G(2, 10)$; small population sizes and shallow

divergences, both priors $G(2,1000)$; and large population sizes and shallow divergences, $G(2,10)$

for θ and $G(2,1000)$ for τ (Leaché & Fujita 2010).

Continuous diffusion and population size trajectories

We used a time-heterogeneous Relaxed Random Walk (RRW) Bayesian approach with the Cyt *b*

dataset to infer the geographic location of ancestors and the continuous diffusion of lineages over

space and time while accommodating for genealogical uncertainty (Lemey *et al.* 2010). Time-

homogeneous spatial diffusion models assume a Brownian constant rate among discrete

locations and make the assumption that the diffusion process and the diffusion rates are

homogeneous over the entire phylogeny (Lemey *et al.* 2009), which can be a unrealistic

assumption for heterogeneous landscapes that were subject of major landscape rearrangements

and climatic fluctuations, as the ecotonal area between the Amazonia and Cerrado biomes at

southeastern Amazonia. So we implemented the spatio-temporal phylogeographic

reconstructions in BEAST v1.7.5 (Drummond *et al.* 2012) and used the time-heterogeneous log-

normal RRW model that extends the time-homogeneous approach and allows for variation in the diffusion rates across branches of the phylogeny (Lemey *et al.* 2010). We also used a Bayesian Skyride model as the demographic tree prior for the RRW analyses to simultaneously reconstruct the change in effective population size through time (Minin *et al.* 2008). A likelihood ratio test rejected the null hypothesis of a molecular clock for Cyt *b* ($P = 0.008$; *ln*L $_{\text{with clock}} = -3103.33$, *ln*L $_{\text{without clock}} = -2983.46$), so we applied a uncorrelated relaxed clock model (Drummond *et al.* 2006) with the same substitution rate and normal prior distribution used for Cyt *b* in *BEAST analysis. After initial runs that failed to converge and recovered low effective sample sizes (ESS) values and some parameter values jumping between alternative values, we subsampled the complete Cyt *b* dataset ($n = 187$) to select one individual representing each unique haplotype found in a given locality, reducing the dataset to 97 individuals.

We performed five independent runs of 200 million generations sampled every 20,000 generations and, as for the species tree analysis, we examined parameter traces with Tracer v1.5 (Rambaut & Drummond 2007), annotated tree files and estimate a maximum clade credibility (MCC) tree with TreeAnnotator v1.7.5 (Drummond *et al.* 2012). We then produced a reconstruction representing the spatial diffusion of lineages for visualization in Google Earth, using the Continuous Tree module from SPREAD v1.0.7 and used Time Slicer to summarize the variation in diffusion rate over time at selected time slices (Bielejec *et al.* 2011).

Isolation with migration models

We used the isolation with migration model (Hey & Nielsen 2004) implemented in the program IMa2 (Hey 2010) to estimate joint posterior probabilities of migration rates and divergence times for our multiple population dataset. IMa2 requires a user-specified rooted tree with known

sequence of splitting events for internal nodes, for which we provided the species tree inferred in

*BEAST. We ran 20 metropolis-coupled chains with geometric heating (h1 = 0.96, h2 = 0.90)

and set the upper bounds for $\theta = 15$, $\tau = 10$, and $M = 1.5$ following the manual's

recommendations. The ranges on mutation rates were included as priors on mutation rate scalars,

but since the mutation rates for nuclear loci are unknown, we used the relative mutation rates

estimated in Migrate-n to calculate the mutation rate per each nuclear locus based on the Cyt b

rate of 5.23×10^{-9} substitution per site per year for *Rattus norvegicus* (Bininda-Emonds 2007).

We combined four independent runs each with 25,000 states after a burn-in of 100,000 states for

a total of 100,000 sampled states and specified a full model with migration between each pair of

populations that coexist over one or more time intervals. We compared the full model with a

model of migration only between sister populations and a model of migration only between

sampled populations using likelihood ratio tests and χ^2 statistic (Hey & Nielsen 2007)

implemented in IMa2 in L-mode. Given that some migration parameters were fixed at the

boundary of the parameter space (i.e., migration set to zero) the test distribution is a mixture, and

we used a conservative approach to calculate the statistic with all degrees of freedom in the

nested model, following the author's recommendation in isolation with migration discussion

forum.

Species distribution modeling

To support and hypothesize demographic scenarios for *P. roberti* across the Quaternary climatic

fluctuations we used the maximum entropy machine-learning algorithm implemented by Maxent

(Phillips *et al.* 2006) to infer the potential geographic range of the species at the present and at

three past time periods (120, 21, and 6 ka). Models were based on paleo-climatic layers from the

WorldClim database (Hijmans *et al.* 2005), for the Last Interglacial (120 ka, LIG) we followed

Otto-Bliesner et al. (2006), while for the Last Glacial Maximum (21 ka, LGM) and mid-

Holocene (6 ka) we used the ECHAM3 atmospheric General Circulation Model (DKRZ 1992).

All bioclimatic layers used span from 12°47' N to 34°46' S and from 78°31 W to 35°00' W, a

larger spatial range than the current *P. roberti* distribution.

To avoid the use of redundant climatic variables, we generated correlation matrices

between them with ArcGIS version 10 (ESRI). Highly correlated variables ($r > 0.9$) were

removed until we reached a final set of 9 bioclimatic variables (bio3 – Isothermality, bio4 –

Temperature Seasonality, bio7 – Temperature Annual Range, bio10 – Mean Temperature of

Warmest Quarter, bio11 – Mean Temperature of Coldest Quarter, bio14 – Precipitation of Driest

Month, bio15 – Precipitation Seasonality, bio16 – Precipitation of Wettest Quarter, and bio17 –

Precipitation of Driest Quarter), plus altitude. We evaluate model performance using the curve

(AUC) of the receiver operating characteristic (ROC) plot, a threshold-independent measure as

compared to null expectations.

We did species-specific tuning under the current climatic conditions to increase model

performance (Anderson & Gonzalez Jr. 2011). We explored the strength of protection against

over-fitted models (regularization), often represented by complex and irregular response curves,

which can affect model generality and transferability (Phillips *et al.* 2006). We investigated 12

values for the regularization multiplier (from 0.5 to 6.0, in increments of 0.5) under the auto-

features which allows all the set of feature classes (linear, quadratic, hinge, product, and

threshold) to depend on the number of presence records. For each regularization multiplier we

conducted 5 replicated runs and recorded model performance and the shape of the variable

response curves. We then retained the best parameter set that produced smoothest distributions of

the variable response curves, making them more regular and achieving the highest mean AUC

and lowest average differences between training and test AUCs (Anderson & Gonzalez Jr. 2011).

The intermediate values for the regularization led to improved models, while lower and higher

multipliers achieved reduced performances (results shown in Table S2 and Figure S1, Supporting

Information). We selected the regularization multiplier of 3.5 in order to increase the model

quality and confidence of our subsequent analyses and projections to the past climate scenarios

(Elith *et al.* 2010). Finally, we performed a 10-replicates run with the selected regularization

multiplier, an occurrence dataset of 128 geographical records of *P. roberti*, and the set of

selected bioclimatic variables, which were projected onto the three past time periods. We used a

cross-validation testing procedure that divides the occurrence points into training and test points

based on the number of replicates (e.g., for the 10-fold cross-validation a test percentage of 10%

is used). For the maps we display the point-wise means of the 10 output grids.

Hypothesis testing

Hydrological and climatic changes influenced the paleogeography of the Neotropical region and

constitute important factors that contributed to the development of present-day drainage patterns

in southeastern Amazon Basin and the ecotonal area between Amazonia and Cerrado biomes

(e.g., Figueiredo *et al.* 2009; Salgado-Labouriau 1997). We used mtDNA Cyt *b* haplotypes for

which *P. roberti* exhibits geographical structuring to formulate and test two alternative

diversification hypotheses based on the available geological data for the study area. In common,

the two hypotheses assume that the basal split between *P. roberti* ancestral populations,

distributed either to the west or to the east of the Xingu River, occurred in response to landscape

rearrangements that established the modern configuration of this river during the Plio-

Pleistocene, at ~2.6 Ma (Costa *et al.* 2001). Also, in both models we postulate that divergence of the western ancestral population into the lower reaches or headwaters of the Tapajós–Xingu interfluve took place in the Middle Pleistocene, at ~781 ka (Figure 2).

However, these two hypotheses differ in relation to population divergence times and structure of the *P. roberti* eastern clade. The first hypothesis (Late Interfluve Model, hereafter termed LIM; Figure 2a) postulates that the eastern ancestral population was isolated in the interfluve bounded by the rivers Xingu and Araguaia/lower Tocantins upon establishment of the modern Amazon drainage system in the Late Tertiary (Figueiredo *et al.* 2009). More recently, during the late Middle Pleistocene fluvial sedimentation in the Araguaia River valley since ~240 ka (Valente & Latrubesse 2012) promoted differentiation between populations in plateau and fluvial depression areas, while divergence between fluvial depression and eastern populations was favored by development of the Amazonia-Cerrado ecotone (Ledru 2002), or as early as ~126 ka due to reorganization of the lower Tocantins (Rossetti & Valeriano 2007) during the Late Pleistocene. Alternatively, the second hypothesis (Early Riverine Model, hereafter termed ERM; Figure 2b) postulates that the *P. roberti* eastern ancestral population was separated into an area limited to the Xingu–Araguaia/Tocantins interfluve and another to the east of the Araguaia/Tocantins drainage upon formation of the paleo-Tocantins during the Early Pleistocene, at ~1.8 Ma (Rossetti & Valeriano 2007). Then, development of the Araguaia River valley in the late Middle Pleistocene (~240 ka) promoted differentiation between plateau and fluvial depression populations.

These two evolutionary scenarios have different expectations of population structure that we explicitly modeled and compared for statistical significance to our empirical data. We built null distributions of the expected genetic variation under the two historical models using the *s*

statistic of Slatkin and Maddison (1989), which measures the discord between the genealogy and

population subdivision. We used the average effective population size estimated in Migrate-*n* for

Cyt *b* (N_e = 478,011) to perform coalescent simulations assuming that ancestral population sizes

were constant over time and generation length was one year. First, we simulated 1,000

genealogies constrained within each model of population structure using the program Mesquite

(Maddison & Maddison 2011). We then simulated DNA sequence matrices on each of the

replicated gene trees using a model of nucleotide evolution that matched the same parameters of

our empirical data, selected with jModelTest. We also simulated genealogies under neutral

coalescent for each simulated DNA sequence dataset to generate a null distribution of the

expected population structure model.

Results

Genetic diversity, mtDNA gene tree and genetic distances

Our mtDNA and nuclear datasets included 801 and 4,871 base pairs, respectively, for a total of

5,672 base pairs. Nucleotide diversity ranged from 0.35% (Cad) to 4.5% (Cyt *b*) and we

observed maximum haplotype and nucleotide diversity of phased nuDNA for Fgb, and minimum

for Cad (Table 1). All nuclear markers had individuals with length variation with the exception

of Fgb.

The Cyt *b* maximum likelihood inference indicates that *Proechimys roberti* populations

are geographically structured in western and eastern clades that are further structured into five

main mitochondrial haploclades (Figure 3). These five haploclades have variable levels of

support and are distributed from west to east as follows: the lower west (LW) course of the

Xingu River; the upper west (UW) section in the headwaters of the Xingu River; the plateau (PL)

located east of the Xingu River; the fluvial depression (FD) within the interfluve area delimited

by the Xingu and Araguaia/lower Tocantins rivers; and east (EA) of the Araguaia/Tocantins

drainage system (Figure 3).

The only individual from a given geographic area that was grouped with a different

geographical haploclade is UFES1866 from Canaã dos Carajás, Pará, which is distributed at the

PL region but clusters with the FD haploclade (Figure 3). On the other hand, there is substantial

haplotype sharing across geographic regions for the nuclear loci (Figure S2, Supporting

Information), indicating that there has not been sufficient time for complete lineage sorting since

population divergence due to landscape rearrangements. However, with the exception of the

Sptbn1 gene, there is no nuclear haplotype sharing between western and eastern lineages,

confirming the major W–S splitting pattern with moderate levels of support across most

individual nuclear gene trees (Figure S2, Supporting Information).

Corrected mitochondrial distances between *P. roberti* main clades and the outgroups are

all higher than 12%, while corrected distances between the western and the eastern clades is

8.3% (Table 2). The corrected mitochondrial distances between the five *P. roberti* haploclades

ranged from 3.5% (between PL and FD) to 8.8% (between UW and EA), with overall higher

distances between the western clades and the remaining clades (Table 3).

Species tree and species delimitation

The species tree runs based on all seven loci attained high ESS values (> 200) and strong

convergence for all sampled parameters. The inference recovered *P. roberti* intraspecific

relationships with strong support and narrow divergence times confidence intervals (Figure 4).

As for the outgroup taxa, their relationships showed variable support and broader confidence

intervals (Figure 4). *P. roberti* diverged at the Pliocene-Pleistocene transition (~3.026 Ma; 95%

HPD: 1.83-4.65 Ma), with all internal diversification events occurring during the Pleistocene

(Figure 4). Western clades of the Xingu River diverged at around 538 ka (95% HPD: 301-869

ka). Compared to the Cyt *b* gene tree, the species tree recovered a closer relationship between

Fluvial Depression and Plateau samples that dated to 277 ka (95%-HPD: 129-473 ka), while

Eastern individuals diverged at around 715 ka (95%-HPD: 433ka-1.11 Ma).

The Bayesian species delimitation supported the presence of all nodes with posterior

probability of 1.0 in the guide tree. The use of different priors for θ and τ did not change

speciation probabilities for the nodes, but different combinations of priors had an impact on

population sizes and divergence times. Differences in θ were more evident and varied among

populations with estimates for θ_{LW}, θ_{FD} and θ_0 presenting the highest (two-fold) variation. Priors

on τ affected divergence time estimates to a much lesser extent with τ_0 showing relatively more

variation. Nevertheless, BPP results were consistent across runs and mean divergences times

(assuming a mean mutation rate across all loci of 2.1×10^{-9}) fall within the 95% HPD of

divergence dates estimated in *BEAST.

Continuous diffusion and population size trajectories

The RRW diffusion pattern based on the MCC tree shows that the ancestral origin of *P. roberti* is

located ~430 km (straight line distance) to the east of Xingu River (4.581 S, 51.504 W). The

coupled divergence times dated the tree root and the main west-east split within *P. roberti* to

have occurred at 4.35 Mya (95%-HPD: 2.35-7.89), the divergence between upper and lower west

clades at 3.28 Mya (95%-HPD: 1.59-6.19), and the diversification between the three eastern

clades (FD, PL, and EA) at 3.50 (95%-HPD: 1.94-6.29), which are older estimates than those

obtained from the multi locus species tree in *BEAST, even though there is overlap at the 95%
confidence intervals for the *P. roberti* root. However, the uncertainty associated with these dates
is quite large (Figure S3, Supporting Information).

The spatio-temporal reconstruction indicates 3 main colonization phases: (1) long-
distance westward and eastward dispersals that were completed around 2.10 Ma; (2) subsequent
dispersal towards the southern and northeastern ranges that began around 1.30 Ma and was
complete before 750 ka; and (3) a final expansion towards the southeastern range of the species
that took place in the last 750 ka (Figure 5). The mean diffusion rate for *P. roberti* 151.45 km per
million years (95%-HPD: 70.64-232.15), with considerable variation among times slices.
Dispersal rates at 3.80 Ma were 184.98 km/Myr and increased during the initial long-distance
west-east dispersal when it reached the maximum rate of 216.16 km/Myr at 2.90 Ma. During the
southern and northern colonization phase, dispersion rates were still high with little fluctuation,
but gradually decreased in the last 700 ka with a value of 100.84 km/Myr at the LGM (21 ka).
The Bayesian Skyride shows that although range expansion was higher in the initial long-
distance west-east colonization phase, population sizes were relatively stable until about 705 ka,
when a noticeable growth is detected until the present population sizes were reached (Figure 6).

Isolation with migration models

We rejected the model with migration only between sampled populations ($P = 0.029$, $df = 12$),
but we could not reject the model with migration only between sister populations ($P = 0.99$, $df =$
24). The high point estimates for population times of splitting between the most recent and the
older split-events are overall concordant with divergence times from the species tree analysis,
albeit with broader values for the highest posterior density intervals. However, the divergence

times between populations distributed west of the Xingu (LW–UW) and between the ancestor population of plateau and fluvial depression and the eastern population are almost two-folds older (Table 4). The estimated population migration rates listed in Table 5 are given as $2N_iM_i{>}j$, which forward in time is the rate at which immigrant genes from population j replace genes from population i, and the migration rates $m_{LW}{>}UW$ and $m_{PL|FDa}{>}EA$ are statistically significant in the likelihood ratio test of Nielsen and Wakeley (2001).

Species distribution modeling

The average test AUCs for the 10 replicate runs conducted under each regularization multiplier during the tuning phase were moderate and varied slightly (between 0.881 and 0.891—Table S2, Supporting Information). For the 10-fold runs and paleo-climate projections that used the particular regularization multiplier of 3.5 the average test AUC was 0.884 (SD = 0.029), indicating reasonable and consistent model performance. Variables of precipitation seasonality (bio15) and precipitation of wettest quarter (bio16) had the highest two contributions to the model, with a cumulative percent contribution of 65.6% (Table S3, Supporting Information).

During the LIG, areas of potential paleo-distribution of *P. roberti* were distributed in a relatively homogeneous fashion towards the southeastern portion of the species range, albeit with only intermediate logistic probabilities (Figure 7). Since the LGM, the potential distribution surfaces depict overall higher suitability areas concentrated at the northern and southeast extremes; indicating favorable conditions for at least two possible range expansion events (Figure 7). After these inferred potential range expansions, the predicted *P. roberti* distribution did not change significantly from the LGM to the present. In all models, areas of over prediction were identified in northwestern South America (Figure 7).

Hypotheses testing

The null model is rejected when the observed value *s* of Slatkin and Maddison (Slatkin &

Maddison 1989) falls outside the 95% confidence interval for the *s* values computed from the

simulated gene trees. For our empirical gene tree we calculated Slatkin and Maddison's *s* = 5.

We were able to reject the LIM hypothesis (average *s* = 8.624; *P* < 0.001), but the ERM

hypothesis could not be rejected (average *s* = 5.604; *P* = 0.115; Figure 8). Therefore, coalescent-

based simulations indicate that the population structure model predicted by the ERM is

congruent with our data.

Discussion

Phylogeographic studies dealing with aspects of Neotropical diversification customarily base

their conclusions on somewhat qualitative assessments of gene genealogies in an effort to

explain the patterns of species diversity and distribution for that region. These notions are

described by a number of non-exclusive biogeographic hypotheses that cannot be easily

reconciled to explain the mechanisms responsible for generating and maintaining such

biodiversity patterns given the complex geological and climatic history of the Neotropics.

Moreover, examples of phylogeographic studies that make use of an adequate sampling, both in

terms of geographic coverage of the focal group and molecular markers, are not commonplace in

the region as yet (but for examples see Camargo *et al.* 2012; Werneck *et al.* 2012). This by and

large has prevented an explicit hypothesis-driven approach that is key to unraveling central

questions about the evolutionary history of the Neotropical ecosystems and their associated

biota. Herein, we demonstrate how an extensive taxon sampling can be employed to that purpose

through estimation of relevant demographic parameters and testing of *a priori* alternative hypotheses concerned with the population structure and historical biogeography of *P. roberti*, thereby contributing to a better understanding of the biotic diversification particularly in the Amazonia and Cerrado biomes.

Molecular systematics and taxonomy

The five Cyt *b* haploclades that we recovered are in agreement with major landscape compartments in southeastern Amazonia and Cerrado presently separating populations of *P. roberti*. The geographic structuring of Cyt *b* haploclades seems intimately associated with the drainage patterns of the Xingu and Araguaia/Tocantins sub-basins. Genetic distances based on the mtDNA Cyt *b* for the comparison of *P. roberti* and other species of the genus are within the range previously reported for between-species distances (da Silva 1998; Patton *et al.* 2000). The distance between western and eastern clades is relatively high when compared to sequence divergence among populations within each respective clade, and almost as high as that observed between formally recognized species of *Proechimys*. UW and EA populations have the highest mean genetic distance between the two clades, whereas sequence divergence between populations within the western clade (i.e., UW and LW) is higher than between populations within the eastern clade (i.e., PL, FD and EA).

Genetic distances from this study are higher than the 2.4% sequence divergence reported for eastern Amazonia and Cerrado in a previous work limited to four localities east of the Xingu River (Weksler *et al.* 2001). These authors evaluated the taxonomic status of *P. roberti* and *P. oris* (name attributed to a form in eastern Amazonia, near Belém, state of Pará) based on karyologic, morphometric, morphologic and molecular data, and recognized the latter as a junior

synonym of *P. roberti*. Although their molecular and morphologic sampling did not include any samples from west of the Xingu, they were able to analyze morphometrically a series of individuals from one locality (Curuá-Una) in that area, whose specimens showed some degree of separation in morphometric space. However, this was ascribed to intraspecific differences and clinal phenotypic variation along Amazonia and Cerrado. Likewise, substantial variability is documented for karyomorphs of *P. roberti* distributed from west of the Xingu to east of the Tocantins (Gardner & Emmons 1984; Machado *et al.* 2005; Weksler *et al.* 2001).

Nevertheless, the lack of significant morphologic and karyotypic variation also emphasizes the cryptic status of the different evolutionary lineages identified here. Indeed, the species limits and geographic ranges within the genus *Proechimys* awaits detailed investigation, but the distinct geographic distribution of the well-supported western clade of *P. roberti*, presently separated from its eastern counterparts by the Xingu River, with relatively high mtDNA sequence divergence and no instances of nuclear haplotype sharing but for Sptbn1, suggests that the western clade is a candidate species and its populations are distributed within the Tapajós–Xingu interfluve. Should *P. roberti* prove to be a composite taxon, other named forms such as *arescens* and *boimensis* (Moojen 1948) are currently listed as synonyms, and thus the next step would be to obtain data from topotypes that can associate this candidate species with available names or verify that it belongs to an undescribed taxon. However, taxonomic reassessments will require careful examination of sequenced and karyotyped vouchers with holotypes because multiple species of spiny rats can occur syntopically (Patton & Leite in press).

P. guyannensis and *P. roberti* do not for a sister group and the *guyannensis* species group as proposed by Patton (1987) is not a natural group, suggesting that evolutionary convergence in

morphological traits possibly related to use of food resources in generally similar rainforests located on the Guiana and Brazilian shields of Precambrian origin has occurred.

Population structure and biogeography

All populations of *P. roberti* have high posterior probability in species tree and species delimitation analyses, indicating that our population assignment based on the distribution of sampled individuals and overall structure of Cyt *b* haploclades is adequate for the scenario investigated here, which is consistent with the presence of major topographic features in southeastern Amazonia and adjacent Cerrado. Similar procedures also have demonstrated that considering the variation of mtDNA data can be relevant for the task of population assignment (Sousa-Neves *et al.* 2013; Werneck *et al.* 2012), and we advocate that information on geographic ranges should be included whenever possible. However, we stress that such schemes may be not justified for taxa with shallow mtDNA divergence distributed over geographic regions without conspicuous landscape subdivision.

The distribution of *P. roberti* spans an extensive area south of the lower Amazon River, and encompasses parts of the two largest South American biomes. Despite obvious environmental clines between Amazonia and Cerrado, the population structure of *P. roberti* is primarily conditioned by an west-east direction paralleling the main axis of the Amazon, rather than by a north-south trend as would be expected if environmental differences between the two biomes were the primary drivers of population structure. On the one hand, the presence of major tributaries flowing towards the Amazon River dictates the first level of geographic structuring of *P. roberti* populations. Situated in the Brazilian Shield, from west to east, the Tapajós, Xingu and Araguaia/Tocantins rivers cut through old rocks of the basement and intersect the landscape of

southeastern Amazon Basin more or less perpendicularly. On the other hand, terrain development also played an important role in shaping the population structure of *P. roberti*, which by erosional and depositional processes throughout the geological history of the Amazonian craton has created areas of relatively higher versus lower relief (Kroonenberg & de Roever 2010). These areas represent the second level of geographic structure for *P. roberti* populations and are delimited differentially by presence of interfluves; within the Tapajós–Xingu interfluve between-population differentiation follows a north-south direction, whereas within the Xingu–Araguaia/Tocantins interfluve it conforms to a west-east trend.

The notion of rivers as barriers that promote biological divergence forms the basis of the oldest hypothesis of diversification formally proposed to explain patterns of species diversity and distribution in the Amazon Basin (Wallace 1852). Frequently, phylogeographic studies conclude that rivers are areas of secondary contact and not the primary drivers of differentiation because lineages from opposite banks fail to coalesce with each other before finding their most recent common ancestor within the same interfluve (Leite & Rogers in press). However, as evidenced here, rivers do play a fundamental role as primary diversification barriers, but one favoring population divergence that is often perceived only at the deeper levels of the intraspecific relationships. Topographic features shaping relief variation are intimately associated with patterns of drainage configuration that are conditioned by formation of the river itself (Hoorn *et al.* 2010a). Likewise, differentiation between populations due to variation in relief is expected to contribute to more recent coalescence events. In addition, the impact of rivers and relief variation is expected to differ in relation to gene flow because the former has a stronger isolating effect on population structure. However, neotectonic events have been documented for several portions of

the basin (Latrubesse & Franzinelli 2005; Latrubesse & Rancy 2000; Rossetti & Valeriano 2007) and may have contributed to gene flow due to relatively recent drainage reorganizations.

The splitting times between ancestor populations of *P. roberti* are in agreement with recent geological data that propose a Late Tertiary onset of the transcontinental Amazon River (Hoorn *et al.* 2010b) in response to an increased Andean orogeny in the Late Miocene (Mora *et al.* 2010). The extensive and drastic rearrangements of the landscape culminated with the redirection of the Amazon drainage basin towards the Atlantic and its modern configuration in the Pliocene, at ~7 Ma (Figueiredo *et al.* 2009). Accordingly, intracratonic rivers such as the Tapajós, Xingu and Araguaia/Tocantins changed their paleocourses to conform to this new drainage pattern with substantial sediment influx of Andean origin (Hoorn *et al.* 2010a). The paleoenvironmental evolution of the Amazon Basin followed a west-to-east direction, and our data support this hypothesis inasmuch as establishment of the modern Xingu drainage in the Late Pliocene (Costa *et al.* 1996) was likely the cause of the first split observed between western and eastern ancestral populations of *P. roberti* at that age (Fig. 3; Table 5). More recently, development of the drainage system of the paleo-Tocantins (Rossetti & Valeriano 2007) triggered the differentiation of the eastern ancestral population into either the Xingu–Araguaia/Tocantins interfluve or east of the Tocantins in the Early–Middle Pleistocene.

We found almost two-fold differences in divergence times estimated in *BEAST versus IMa2 for two nodes of the population tree (Table 4). Notably, likelihood ratio tests (Nielsen & Wakeley 2001) implemented in the latter program indicate significant migration rates between populations involved in those two splitting events (Table 5). In *BEAST, the species tree reconstruction and divergence time estimation assume that uncertainty in the population tree is due to incomplete lineage sorting (Drummond *et al.* 2012), whereas in IMa2 population

divergence with gene flow in both directions between populations is allowed (Hey & Nielsen 2004). Nevertheless, population subdivision can increase time for coalescence because genes in different populations cannot coalesce until migration brings them together in the same population (Nordborg 1997). Hence, in situations of substantial migration rate between populations the species tree model assumed in *BEAST may underestimate divergence times, thus an isolation with migration model seems more realistic despite broad 95% HPD intervals.

The causal link between paleoenvironmental evolution and the role played by rivers as primary drivers of diversification has been recently emphasized for birds (e.g., Fernandes *et al.* 2013; Ribas *et al.* 2012), but the influence of relief variation on population structuring and differentiation remains largely unexplored for lowland vertebrate taxa. Andean uplift is considered a major driver of speciation in the Neotropical region because mountain building creates topographically complex areas that promote opportunities for species differentiation (Badgley 2010; Hoorn *et al.* 2013; Weir & Price 2011). Nevertheless, we demonstrate for *P. roberti*, a typical inhabitant of lowland rainforests of southeastern Amazonia and Cerrado, that even with comparatively small differences in topography there will be important implications for population structure, and that relief variation within interfluves is responsible for divergence in spite of gene flow. Spiny rats are known for their ability to use diverse food resources such as fruits, seeds and fungi spores (Adler 1995; Mangan & Adler 1999) and for their ubiquity in heterogeneous tropical forests, but the influence of forest structure is not as important as forest diversity (Adler 2000). Therefore, the effect of relief variation on gene flow probably is indirectly mediated by differences in the composition of myco and phytoassemblages that respond to soil heterogeneity and topography (e.g., Braga-Neto *et al.* 2008; Kahn 1987; Vormisto *et al.* 2004), which in turn are associated with landscape development of river

drainages (Irion & Kalliola 2010). However, the rejection of the full migration model against one allowing for migration only between sister populations demonstrates the importance of rivers in the allopatric differentiation of populations presently separated by the Xingu–Araguaia/Tocantins interfluve and by the Xingu itself.

In addition, zero migration has been detected between ancestral populations divided by the Xingu, which reinforces the isolating effect of rivers on spiny rats in southeastern Amazon Basin, particularly the Xingu (Table 5). Interestingly, our analyses also revealed unidirectional gene flow from the eastern population towards the ancestral population of plateau and fluvial depression separated upon establishment of the paleo-Tocantins. The paleogeography along the Amazon and its tributaries is largely attributed to neotectonics (Costa *et al.* 2001). Several normal faults with a N-S orientation control the course of the Xingu, whereas thrust faults west of the Araguaia were responsible for the vertical displacement of several hills up to 800 meters present in that area (Costa *et al.* 1996). The geodynamics associated with reactivation of these different fault types may explain why no migration has been detected between populations on opposite banks of the Xingu, where normal faults are associated with crust extension, whereas formation of ramps typically associated with thrust faulting may permit unidirectional migration.

Nevertheless, there is substantial gene flow between populations within interfluves. For instance, population LW receives immigrants from UW and vice-versa, but the population migration rate is more intense from population UW into LW than in the opposite direction, in agreement with the prediction that topographically complex areas in higher relief contribute considerably more to species differentiation (Badgley 2010). However, we observed a reverse gene flow direction prevailing in the Xingu–Araguaia/Tocantins interfluve, which is indicative that such prediction does not hold for areas where relief variation exists but is not comparable to

mountainous settings, or perhaps because of geologically dynamic and relatively recent formation history of the fluvial valley of the Araguaia/Tocantins (e.g., Morais *et al.* 2008; Valente & Latrubesse 2012). Although, climatic fluctuations have drastic implications for distributional patterns in typical montane species (Weir & Price 2011), the core of the Amazonian biome has been quite resilient to past climatic alterations (Bush *et al.* 2004; Colinvaux & De Oliveira 2001; Mayle *et al.* 2000), except for localized peripheral displacements of forest/savanna ecotones (Mayle *et al.* 2007; Mayle & Power 2008). This may explain the contrasting gene flow patterns seen in *P. roberti* populations from different interfluves.

The Bayesian phylogeographic analysis allowed us to infer the area of origin and dispersal routes among major clades of *P. roberti*. The geographic origin of the *P. roberti* ancestral population was inferred as the east bank of the Xingu drainage, around the mid-section of this river system in the micro-interfluve bounded by the main course of the Xingu and its second order tributary the Bacajá River, within the sub-basin of the same name (Figure 5). Interestingly, this area of the upper Bacajá is controlled by several dextral strike-slip faults which displacement mainly in a right-lateral horizontal direction of rock strata of older ages (Costa *et al.* 1996) may have promoted the differentiation of *P. roberti* ancestral populations. The transcurrent faulting zone in this area extends further east for more than 500 km and is connected to the Serra do Carajás hill system, all of which had been reactivated during the Late Tertiary (Miocene–Pliocene) and formed the general configuration of the southeastern drainages (Costa *et al.* 2001; Costa *et al.* 1996). We propose that neotectonic events have played an important role in the divergence of *P. roberti* ancestral populations given that the inferred dispersal route tracks the general orientation of these fault zones.

The Bayesian continuous diffusion reconstruction has the advantage of providing the spatial and temporal dynamic of range distribution patterns instead of averaged estimates of historical range expansion, providing the means to decouple it from demographic expansion patterns (Camargo *et al*. 2013). Indeed, results show that the initial long-distance westward and eastward dispersals were not accompanied by demographic expansion, because an increase in effective population size was not detected until relatively recently when dispersal rates have decreased (Figure 6). However, time estimates inferred from the Cyt *b* data only are older than coalescent times estimated using multiple loci because discordance due to incomplete lineage sorting tend to produce younger dates in the species tree (Drummond *et al.* 2012). The species distribution modeling suggests that in the last 120 ka there existed climatic conditions for a relatively widespread distribution of *P. roberti* and suitable climate envelopes could have supported range expansions since at least the LGM, especially towards the northeastern and southeastern extremes of the potential distribution surface (Figure 7). Although this spatial pattern is congruent with the final phase of range diffusion recovered in the RRW analysis, the timing of predicted range distribution is much younger than the time of population size expansion inferred by the Bayesian Skyride, even if uncertainty in divergence times from single-gene analysis relative to multilocus approaches is taken into account. The lack of climatic layers for periods preceding the LIG precludes paleomodeling analyses to confirm whether population expansion is supported by suitable climatic envelops before then. However, the Bayesian diffusion reconstruction suggests that favorable environmental conditions for the establishment of *P. roberti* populations were present throughout the Plio-Pleistocene.

Reconstructing the evolutionary history of species by taking environmental changes into account through geological time is critical to understand the mechanisms associated with

Amazonian diversification (Rossetti & de Toledo 2007). Moreover, these sources of external

data constitute key information upon which to build testable a priori hypotheses about biotic

evolution (Riddle *et al.* 2008). Although paleogeographic data are still fairly incomplete for the

Amazon Basin as a whole (Aleixo & Rossetti 2007), a recent framework based on new

geological data was proposed to explain landscape evolution of southeastern Amazonia (Rossetti

& Valeriano 2007). The influence of such a historical scenario on patterns of genetic variation

has been investigated for two lizard species distributed in that region. However this attempt was

mostly limited to qualitative assessments of area cladogram relationships (Avila-Pires *et al.*

2012). Instead, we evaluate this recently proposed geological scenario for the lower Amazon

area within an objective hypothesis-driven framework. By incorporating coalescent stochasticity

in a simulation approach we were able to reject the model of population structure consistent with

a scenario of recent differentiation within the eastern clade of *P. roberti*, which could be

explained by the capture of the lower Tocantins River. Therefore, neotectonics and depositional

processes involved in such paleogeographic events must have had no or only minor effects on

the major patterns of genetic structuring evident in *P. roberti*.

Phylogeographic investigations in the Amazon Basin typically involve mtDNA (Leite &

Rogers in press), which is a marker of choice for exploratory analytical purposes (Garrick *et al.*

2010b), but we also have demonstrated how future empirical studies in the region can take

advantage of the growing body of paleogeographic evidence (Hoorn & Wesselingh 2010), so as

to formulate and test alternative historical hypotheses within an explicit statistical framework.

Importantly, rigorous hypothesis testing can be performed using a simulation approach that takes

into account coalescent stochasticity even if mtDNA sequence data are the only class of markers

being utilized. Of course, the robustness of coalescent simulations depends on the use of

appropriate summary statistics that can discriminate alternative models, and the adequacy of model assumptions based on biologically realistic models of population history that mirror relevant demographic parameters accurately estimated from the data (Carstens *et al.* 2005). However, it is clear that after careful consideration about the historical setting and taxa of interest, hypothesis testing via coalescent simulations can bring important insights into phylogeographic studies (Knowles 2004).

Here, we were able to elucidate key aspects of the evolutionary history of spiny-rats inhabiting rainforests of southeastern Amazonia and the Cerrado by means of coalescent-based estimates of relevant demographic parameters and simulations of alternative models of population structure, which are integrated with geological data and information from ecological niche modeling and continuous spatial diffusion. We now can better understand the role of rivers and topographic heterogeneity as isolating barriers and the influence of neotectonics and Quaternary climatic changes on the geographical structuring of *P. roberti* populations. Moreover, our findings will serve as a baseline for more detailed investigations (e.g., applying fine-scale landscape genetics) about major environmental attributes and their interplay with phenotypic variation and ecological interactions across the geographic distribution of these spiny-rats. We also anticipate that our model-based phylogeography of *P. roberti* will prompt future studies interested in other taxonomic groups and ecosystems to objectively quantify patterns and processes of Neotropical diversification. In turn, this joint enterprise will provide a strong framework for conservation decisions.

Conservation implications

The geographic setting of this study comprises three of the most threatened areas of endemism (AOE) in the Amazon Basin, namely the Tapajós, Xingu and Belém AOEs (Silva *et al.* 2005). These areas have the highest rates of land-use change and the least amount of formally protected areas (Garda *et al.* 2010), and are bordered to the south and west by the Cerrado biome which is highly impacted by human activities as well (Klink & Machado 2005). These AOEs also figure amongst the least studied areas in terms of phylogeographic efforts (Leite & Rogers in press). Conservation practices should focus on preserving the ongoing mechanisms of isolation in allopatry and in the presence of gene flow by implementing regional biodiversity corridors (Garda *et al.* 2010) on the core of AOEs and ecotonal zones between Amazonia and Cerrado since these two major South American biomes harbor a number of shared taxa. Coalescent stochasticity, when taken into consideration, accounts for important information to be used in conservation decision-making because it provides a clear view of the patterns of genetic variation and underlying evolutionary processes in these areas and may reveal instances of cryptic diversity. Thus, ignoring this source of uncertainty in historical inferences can have serious implications for the proper management of protected areas and conservation planning.

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Tables

Table 1. Molecular markers used in this study included mitochondrial (mtDNA) and nuclear genes (NPCL: nuclear protein coding locus; EPIC: exon-primed intron crossing), and are ranked by nucleotide diversity (bp: base pairs; n: number of individuals; l: number of localities; H: number of haplotypes; Hd: haplotype diversity; Pi: nucleotide diversity per site; θ_w: Watterson's theta; k: average number of nucleotide differences between sequences; S: number of segregating sites).

Marker	Name	Type	Size (bp)	n/l	H/Hd	Pi (%)	θ_w	k	S
Cyt *b*	Cytochrome *b*	mtDNA	801	187–46	97–0.99	4.498	0.0395	35.1	180
Fgb§	Fibrinogen beta chain	EPIC	876	85–31	78–0.98	1.107	0.0164	9.70	82
Exoc3‡	Exocyst complex component 3	EPIC	844	86–33	40–0.92	0.724	0.0120	5.98	57
Sptbn1§	Spectrin, beta, non-erythrocytic 1	EPIC	713	81–30	50–0.95	0.635	0.0116	4.44	46
Kitlg§	KIT ligand	EPIC	772	81–30	41–0.93	0.568	0.0127	4.26	54
Clptm1‡	Cleft lip and palate associated transmembrane protein 1	EPIC	856	88–30	45–0.94	0.547	0.0108	4.65	53
Cad‡	Carbamoyl-phosphate synthetase 2, aspartate transcarbamylase, and dihydroorotase	EPIC	810	69–25	41–0.75	0.346	0.0109	2.78	48

§ New primers; ‡ Novel markers

Table 2. Net among group mtDNA genetic distances between *Proechimys roberti* major clades (Western and Eastern) and *Proechimys* outgroup species. Values below the diagonal are uncorrected *p*-distances and above the diagonal are Tamura-Nei (Tamura and Nei 1993) corrected *p*-distances, with respective standard errors in parenthesis calculated using 500 bootstrap replicates (EC: *P. echinothrix* [*echinothrix* species group], GA: *P. gardneri* [*gardneri* species group], CU: *P. cuvieri* [*longicaudatus* species group], GO: *P. goeldii* [*goeldii* species group], GY: *P. guyannensis* [*guyannensis* species group], SI: *P. simonsi* [*simonsi* species group]).

	Western	Eastern	EC	GA	CU	GO	GY	SI
Western		0.083 (0.010)	0.159 (0.016)	0.155 (0.017)	0.128 (0.013)	0.164 (0.016)	0.146 (0.015)	0.176 (0.018)
Eastern	0.075 (0.008)		0.160 (0.016)	0.142 (0.015)	0.128 (0.013)	0.132 (0.014)	0.154 (0.016)	0.164 (0.015)
EC	0.133 (0.011)	0.133 (0.011)		0.151 (0.016)	0.148 (0.016)	0.156 (0.016)	0.150 (0.016)	0.169 (0.017)
GA	0.131 (0.011)	0.123 (0.010)	0.130 (0.011)		0.145 (0.016)	0.053 (0.008)	0.140 (0.015)	0.155 (0.017)
CU	0.112 (0.010)	0.112 (0.010)	0.127 (0.011)	0.125 (0.011)		0.128 (0.014)	0.126 (0.014)	0.153 (0.016)
GO	0.139 (0.011)	0.116 (0.010)	0.134 (0.011)	0.050 (0.007)	0.114 (0.011)		0.134 (0.016)	0.146 (0.016)
GY	0.124 (0.011)	0.128 (0.011)	0.127 (0.011)	0.121 (0.011)	0.111 (0.011)	0.116 (0.011)		0.147 (0.016)
SI	0.146 (0.012)	0.138 (0.011)	0.144 (0.011)	0.134 (0.012)	0.131 (0.012)	0.126 (0.011)	0.126 (0.011)	

Table 3. Between group mean distance for the five major *Proechimys roberti* mtDNA haploclades. Values below the diagonal are uncorrected *p*-distances and above the diagonal are Tamura-Nei (Tamura and Nei 1993) corrected *p*-distances, with respective standard errors in parenthesis, calculated using 500 bootstrap replicates Color codes follow Figure 2 (UW: upper west; LW: lower west; PL: plateau; EA: east, FD: fluvial depression)

	UW	LW	PL	EA	FD
UW		0.061 (0.009)	0.078 (0.010)	0.088 (0.011)	0.082 (0.010)
LW	0.057 (0.008)		0.075 (0.010)	0.084 (0.011)	0.083 (0.011)
PL	0.071 (0.008)	0.069 (0.008)		0.037 (0.006)	0.035 (0.006)
EA	0.079 (0.009)	0.076 (0.009)	0.036 (0.006)		0.037 (0.005)
FD	0.074 (0.008)	0.075 (0.008)	0.034 (0.005)	0.035 (0.005)	

Table 4. Divergence time estimates and highest posterior density intervals based on *BEAST and IMa2.

Method	τ_{PL-FD}	τ_{LW-UW}	$\tau_{PL|FDa-EA}$	τ_{W-E}
*BEAST	0.277	0.538	0.715	3.026
	(0.129–0.473)	(0.301–0.869)	(0.433–1.11)	(1.83–4.65)
IMa2	0.204	0.948	1.112	2.660
	(0.070–0.625)	(0.625–1.41)	(0.862–1.51)	(1.87–6.06)

Table 5. Population migration rates from IMa2 (0: LW; 1: UW; 2: PL; 3: FD; 4: EA; 5: PL|FDa; 6: Wa; 7: Ea). Asterisks indicate significant migration rates ($P < 0.05$).

$2N_0M_0{>}1$	$2N_1M_1{>}0$	$2N_2M_2{>}3$	$2N_3M_3{>}2$	$2N_4M_4{>}5$	$2N_5M_5{>}4$	$2N_6M_6{>}7$	$2N_7M_7{>}6$
0.56*	0.09	2.29	0.67	0	0.66*	0	0

Figure Legends

Figure 1. Distribution of sampled localities for *Proechimys roberti* and the current Amazon drainage basin configuration (yellow outline). South America digital elevation model and major rivers are also depicted. Localities codes follow the major geographical clades recovered in this study: Upper West (dark blue), Lower West (light blue), Plateau (orange), Fluvial Depression (yellow), East (pink). Numbers correspond to population codes as used in Table S1.

Figure 2. Illustration of the two alternative models for the population structure of *Proechimys roberti* tested under the simulation approach. (a) Early Riverine Model (ERM) and (b) Late Interfluve Model (LIM).

Figure 3. Maximum likelihood mtDNA gene tree. Colors for the major clades correspond to those used in the geographical locations in Figure 1, with the exception of Fluvial Depression populations (represented in yellow in Figure 1). See Table S1 for details regarding samples.

Figure 4. *Proechimys roberti* and outgroups species tree (maximum clade credibility tree) and divergence time estimates, as inferred under a coalescent model based on all seven loci with ⋆BEAST. Node numbers represent divergence times/posterior probabilities, with values >0.95 depicted by an asterisk (*).

Figure 5. Spatial projection of *Proechimys roberti* diffusion pattern through time, based on the maximum clade credibility tree estimated with a time-heterogeneous Relaxed Random Walk (RRW) Bayesian phylogeography approach at six time slices (from 3.8 Ma to the present). The red lines represent the MCC tree branches, and blue shading represents the 80%-HPD uncertainty in the location of ancestral branches with a color gradient representing older (lighter) and younger (darker) diffusion events.

Figure 6. Variation through time in *Proechimys roberti* effective population size based on Bayesian Skyride analyses. Blue areas above and below the mean parameter values represent 95%-HPD.

Figure 7. Potential distribution range of *Proechimys roberti* across Quaternary climatic fluctuations and current climate. Warmer colors represent regions modeled as having higher probability of occurrence in the species distribution modeling analyses.

Figure 8. Simulated null distributions for the value *s* of Slatkin and Maddison (Slatkin & Maddison 1989) corresponding to the Early Riverine Model (ERM; a) and the Late Interfluve Model (LIM; b). Arrows indicate empirical values, and P values are probabilities that observed values of *s* are smaller that expected simulated means (1,000 simulations). The red lines represent the 95% confidence intervals of the simulations.

Elevation (m asl)

	< 100
	100 - 250
	250 - 500
	500 - 1,000
	1,000 - 2,000
	2,000 - 3,000
	3,0001 - 4,000
	> 4,000

(a) LIM

LW   UW   PL   FD   EA

126 ka
240 ka

781 ka

2.6 Ma

(b) ERM

LW   UW   PL   FD   EA

240 ka

781 ka

1.8 Ma

2.6 Ma

267

LOWER WEST (LW)

UPPER WEST (UW)

PLATEAU (PL)

FLUVIAL DEPRESSION (FD)

EAST (EA)

0.0080

■ bootstrap > 0.90
■ bootstrap > 0.80
□ bootstrap > 0.70

8.4997/*

P. simonsi

P. cuvieri

10.4577/0.66

P. guyannensis

9.7068/0.40

P. echinothrix

P. gardneri

8.1683/0.85

4.2284/*

P. goeldii

11.9942/*

0.5382/* Upper West

Lower West

3.0257/*

East

0.7152/*

Plateau

0.2772/* Fluvial
Depression

2.0

| Early Miocene | Middle Miocene | Late Miocene | Pliocene | Pleistocene |

20.0   17.5   15.0   12.5   10.0   7.5   5.0   2.5   0.0 Mya

269

a) 120ka (LIG)

b) 21ka (LGM)

c) 6ka (Holocene)

b) Present

a) ERM model

P = 0.115

b) LIM model

P < 0.001

Number of trees

s value
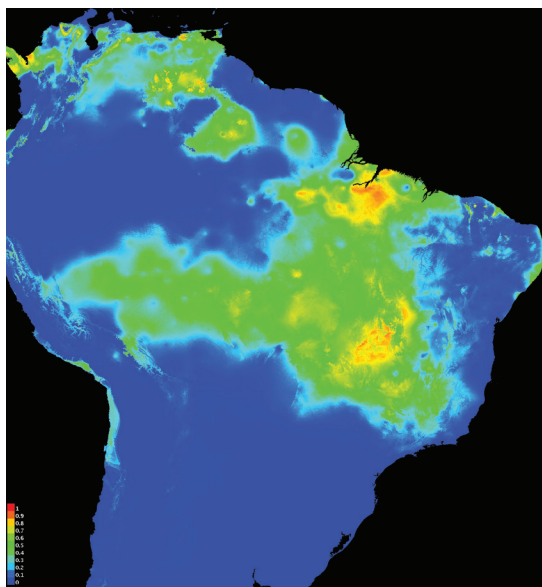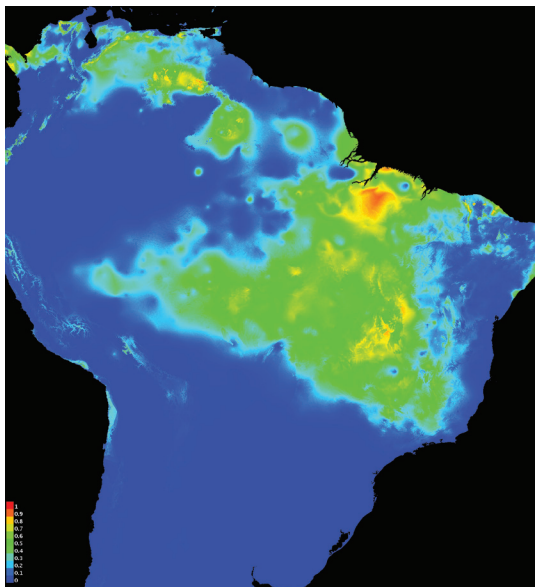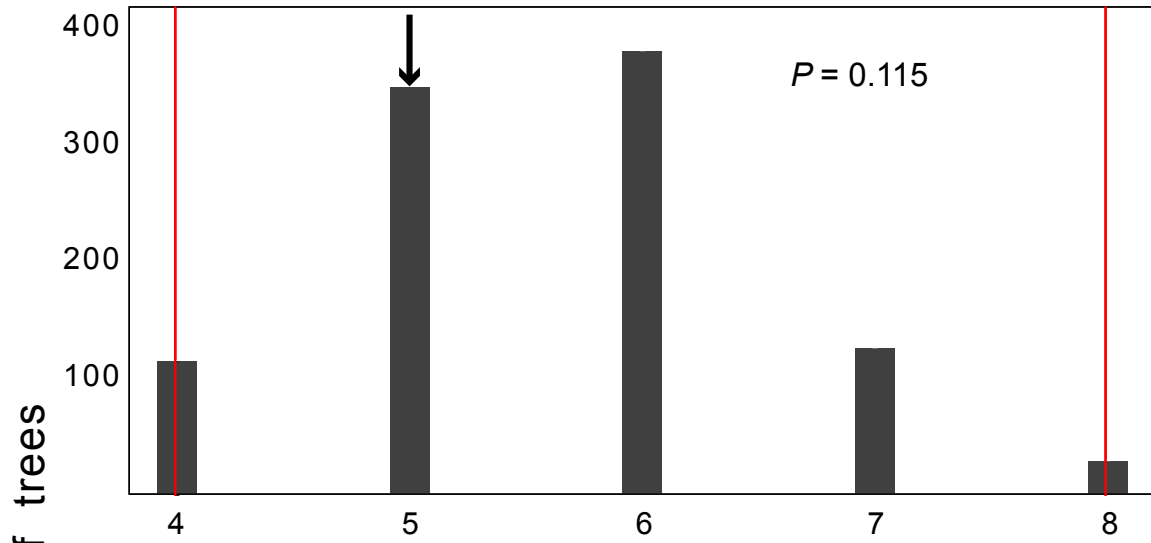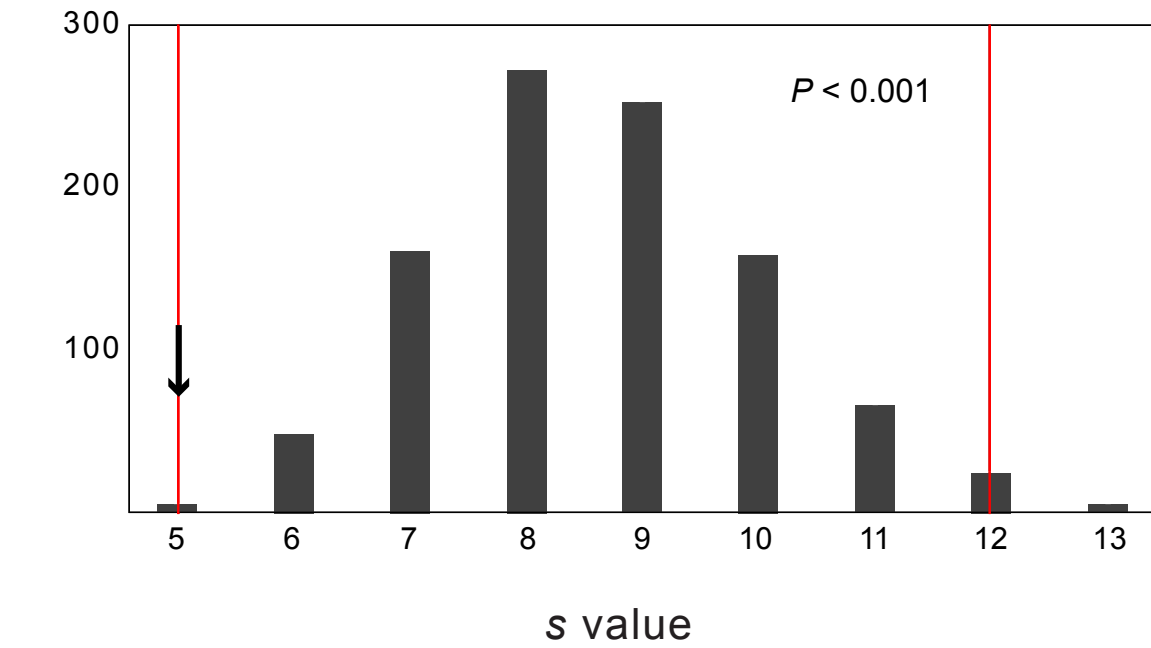
Supplementary Material

Supporting Information Tables

Table S1. Details of material examined, with locality data for all species examined. Locality numbers (Loc #) correspond to sampled localities depicted in Figure 1. Population acronyms (Pop): lower west (LW); upper west (UW); plateau (PL); fluvial depression (FD); east (EA). Brazilian States: Distrito Federal (DF); Goiás (GO); Maranhão (MA); Mato Grosso (MT); Pará (PA); Piauí (PI); Tocantins (TO).

Catalog	Field	Institution	Pop	County	Code	State	Lat	Long	Loc #	Short Locality
CIT458	M97003	CIT	UW	Cláudia	Clau	MT	-11.583	-55.167	8	Claudia
CIT464	M97009	CIT	UW	Cláudia	Clau	MT	-11.583	-55.167	8	Claudia
CIT483	M97032	CIT	UW	Cláudia	Clau	MT	-11.583	-55.167	8	Claudia
CIT497	M97137	CIT	UW	Cláudia	Clau	MT	-11.583	-55.167	8	Claudia
CIT511	M97180	CIT	UW	Cláudia	Clau	MT	-11.583	-55.167	8	Claudia
CIT589	M90	CIT	UW	Paranatinga	GauN	MT	-13.083	-53.283	10	Gaucha do Norte
CIT591	M97	CIT	UW	Paranatinga	GauN	MT	-13.083	-53.283	10	Gaucha do Norte
CIT714	APC273	CIT	PL	Vila Rica	ViRi	MT	-9.900	-51.200	26	Vila Rica
CIT753	APC274	CIT	PL	Vila Rica	ViRi	MT	-9.900	-51.200	26	Vila Rica
CIT1359	UUPI9	CIT	EA	Baixa Grande do Ribeiro	UUna	PI	-8.850	-45.017	34	ESEC Uruçuí-Una
CIT1402	MRT3925	CIT	EA	Paranã	Parn	TO	-12.583	-47.883	41	Parana UHE Peixe
CIT1457	UUPI372	CIT	EA	Baixa Grande do Ribeiro	UUna	PI	-8.850	-45.017	34	ESEC Uruçuí-Una
CIT1465	UUPI412	CIT	EA	Baixa Grande do Ribeiro	UUna	PI	-8.850	-45.017	34	ESEC Uruçuí-Una
CIT1476	APC847	CIT	EA	Peixe	Peix	TO	-12.250	-48.433	40	Peixe UHE Peixe

CIT1488	APC825	CIT	EA	Peixe	Peix	TO	-12.250	-48.433	40	Peixe UHE Peixe
INPA2746	CS14	INPA	PL	Marabá	Tapi	PA	-5.800	-50.500	18	FLONA Tapirape-Aquiri
INPA2747	CS21	INPA	PL	Marabá	Tapi	PA	-5.800	-50.500	18	FLONA Tapirape-Aquiri
INPA2748	CS25	INPA	PL	Marabá	Tapi	PA	-5.800	-50.500	18	FLONA Tapirape-Aquiri
INPA2749	CS27	INPA	PL	Marabá	Tapi	PA	-5.800	-50.500	18	FLONA Tapirape-Aquiri
INPA2750	CS34	INPA	PL	Marabá	Tapi	PA	-5.800	-50.500	18	FLONA Tapirape-Aquiri
INPA2751	CS36	INPA	PL	Marabá	Tapi	PA	-5.800	-50.500	18	FLONA Tapirape-Aquiri
INPA2752	CS46	INPA	PL	Marabá	Tapi	PA	-5.800	-50.500	18	FLONA Tapirape-Aquiri
INPA2753	CS63	INPA	PL	Marabá	Tapi	PA	-5.800	-50.500	18	FLONA Tapirape-Aquiri
INPA2756	CS100	INPA	PL	Marabá	Tapi	PA	-5.800	-50.500	18	FLONA Tapirape-Aquiri
INPA2757	CS113	INPA	PL	Marabá	Tapi	PA	-5.800	-50.500	18	FLONA Tapirape-Aquiri
INPA2775	CS132	INPA	PL	Marabá	Tapi	PA	-5.800	-50.500	18	FLONA Tapirape-Aquiri
INPA2776	CS135	INPA	PL	Marabá	Tapi	PA	-5.800	-50.500	18	FLONA Tapirape-Aquiri
INPA2781	CS149	INPA	PL	Marabá	Tapi	PA	-5.800	-50.500	18	FLONA Tapirape-Aquiri
	CMS1	INPA	LW	Santarém	Strm	PA	-2.537	-54.911	1	Anisio
	CMS5	INPA	LW	Santarém	Strm	PA	-2.581	-54.899	4	Jacu
	CMS6	INPA	LW	Santarém	Strm	PA	-2.581	-54.899	4	Jacu
	CMS7	INPA	LW	Santarém	Strm	PA	-2.582	-54.902	4	Paraiso

	CMS14	INPA	LW	Santarém	Strm	PA	-2.582	-54.902	4	Paraiso
	CMS17	INPA	LW	Santarém	Strm	PA	-2.607	-54.904	5	Ilha Grande
	CMS56	INPA	LW	Santarém	Strm	PA	-2.541	-54.957	2	Sao Luiz
	MNFS2157	INPA	LW	Santarém	Mraj	PA	-2.549	-54.899	3	Marajuba
	PEM5	INPA	EA	Mirador	Mrad	MA	-6.433	-45.308	32	Parque Estadual Mirador
	PEM20	INPA	EA	Mirador	Mrad	MA	-6.433	-45.308	32	Parque Estadual Mirador
	PEM24	INPA	EA	Mirador	Mrad	MA	-6.433	-45.308	32	Parque Estadual Mirador
MN50195	CRB861	MN	EA	Cavalcante	Fian	GO	-14.066	-47.750	42	PARNA Chapada dos Veadeiros
MN50196	CRB862	MN	EA	Cavalcante	Fian	GO	-14.066	-47.750	42	PARNA Chapada dos Veadeiros
MN50197	CRB863	MN	EA	Cavalcante	Fian	GO	-14.066	-47.750	42	PARNA Chapada dos Veadeiros
MN50198	CRB864	MN	EA	Cavalcante	Fian	GO	-14.066	-47.750	42	PARNA Chapada dos Veadeiros
MVZ197576	LPC505	MVZ	UW	Alta Floresta	Crst	MT	-9.596	-55.930	7	RESEC Cristalino Alta Floresta
MVZ197577	LPC508	MVZ	UW	Alta Floresta	Crst	MT	-9.596	-55.930	7	RESEC Cristalino Alta Floresta
MVZ197578	LPC509	MVZ	UW	Alta Floresta	Crst	MT	-9.596	-55.930	7	RESEC Cristalino Alta Floresta
MVZ197579	LPC513	MVZ	UW	Alta Floresta	Crst	MT	-9.596	-55.930	7	RESEC Cristalino Alta Floresta
MVZ197580	LPC522	MVZ	UW	Alta Floresta	Crst	MT	-9.596	-55.930	7	RESEC Cristalino Alta Floresta
MVZ197581	LPC523	MVZ	UW	Alta Floresta	Crst	MT	-9.596	-55.930	7	RESEC Cristalino Alta Floresta
MVZ197582	LPC524	MVZ	UW	Alta Floresta	Crst	MT	-9.596	-55.930	7	RESEC Cristalino Alta Floresta

MVZ197583	LPC531	MVZ	UW	Alta Floresta	Crst	MT	-9.596	-55.930	7	RESEC Cristalino Alta Floresta
MVZ197585	LPC714	MVZ	EA	Peixe	RSTe	TO	-11.842	-48.635	39	Rio Santa Teresa Peixe
MVZ197970	LPC532	MVZ	UW	Alta Floresta	Crst	MT	-9.596	-55.930	7	RESEC Cristalino Alta Floresta
MVZ197975	LPC538	MVZ	UW	Alta Floresta	Crst	MT	-9.596	-55.930	7	RESEC Cristalino Alta Floresta
MVZ197976	LPC539	MVZ	UW	Alta Floresta	Crst	MT	-9.596	-55.930	7	RESEC Cristalino Alta Floresta
MVZ197977	LPC547	MVZ	UW	Alta Floresta	Crst	MT	-9.596	-55.930	7	RESEC Cristalino Alta Floresta
MVZ197979	LPC549	MVZ	UW	Alta Floresta	Crst	MT	-9.596	-55.930	7	RESEC Cristalino Alta Floresta
MVZ197980	LPC550	MVZ	UW	Alta Floresta	Crst	MT	-9.596	-55.930	7	RESEC Cristalino Alta Floresta
MVZ197981	LPC551	MVZ	UW	Alta Floresta	Crst	MT	-9.596	-55.930	7	RESEC Cristalino Alta Floresta
MVZ197982	LPC552	MVZ	UW	Alta Floresta	Crst	MT	-9.596	-55.930	7	RESEC Cristalino Alta Floresta
MVZ197983	LPC553	MVZ	UW	Alta Floresta	Crst	MT	-9.596	-55.930	7	RESEC Cristalino Alta Floresta
MVZ197988	LPC558	MVZ	UW	Alta Floresta	Crst	MT	-9.596	-55.930	7	RESEC Cristalino Alta Floresta
MVZ197992	LPC571	MVZ	UW	Alta Floresta	Crst	MT	-9.596	-55.930	7	RESEC Cristalino Alta Floresta
MVZ197993	LPC540	MVZ	UW	Alta Floresta	Crse	MT	-9.596	-55.928	7	Left bank Cristalino River
MVZ198003	LPC572	MVZ	UW	Alta Floresta	Crse	MT	-9.596	-55.928	7	Left bank Cristalino River
MVZ198004	LPC573	MVZ	UW	Alta Floresta	Crse	MT	-9.596	-55.928	7	Left bank Cristalino River

MVZ198115	LPC704	MVZ	EA	Peixe	RSTe	TO	-11.842	-48.635	39	Rio Santa Teresa Peixe
	APC1217	MZUSP	EA	Mateiros	SGTO	TO	-10.666	-46.866	38	ESEC Serra Geral do TO
	PG3	UEMA	EA	Bacabal	Bacb	MA	-4.225	-44.780	31	Bacabal
	PG4	UEMA	EA	Bacabal	Bacb	MA	-4.225	-44.780	31	Bacabal
	PG7	UEMA	EA	Ribeiro Gonçalves	RibG	PI	-7.558	-45.241	33	Ribeiro Goncalves
UFES1388	RGR4	UFES	EA	Caseara	CntP	TO	-9.303	-49.958	35	Mata do Sitio Velho PE Cantao
UFES1389	RGR5	UFES	EA	Caseara	CntP	TO	-9.303	-49.958	35	Mata do Sitio Velho PE Cantao
UFES1390	RGR8	UFES	EA	Caseara	CntP	TO	-9.303	-49.958	35	Mata do Sitio Velho PE Cantao
UFES1391	RGR11	UFES	EA	Caseara	CntP	TO	-9.303	-49.958	35	Mata do Sitio Velho PE Cantao
UFES1392	RGR9	UFES	EA	Caseara	CntP	TO	-9.303	-49.958	35	Mata do Sitio Velho PE Cantao
UFES1393	RGR35	UFES	EA	Caseara	CntA	TO	-9.384	-49.975	36	Mata do Paredao APA Cantao
UFES1394	RGR36	UFES	EA	Caseara	CntA	TO	-9.384	-49.975	36	Mata do Paredao APA Cantao
UFES1395	RGR37	UFES	EA	Caseara	CntA	TO	-9.384	-49.975	36	Mata do Paredao APA Cantao
UFES1396	RGR39	UFES	EA	Caseara	CntP	TO	-9.303	-49.958	35	Mata do Sitio Velho PE Cantao
UFES1397	RGR40	UFES	EA	Caseara	CntP	TO	-9.303	-49.958	35	Mata do Sitio Velho PE Cantao
UFES1398	RGR41	UFES	EA	Caseara	CntP	TO	-9.303	-49.958	35	Mata do Sitio Velho PE Cantao
UFES1400	RGR43	UFES	EA	Caseara	CntA	TO	-9.384	-49.975	36	Mata do Paredao APA Cantao
UFES1401	RGR44	UFES	EA	Caseara	CntA	TO	-9.384	-49.975	36	Mata do Paredao

										APA Cantao
UFES1402	RGR45	UFES	EA	Caseara	CntA	TO	-9.384	-49.975	36	Mata do Paredao APA Cantao
UFES1403	RGR53	UFES	EA	Caseara	CntA	TO	-9.384	-49.975	36	Mata do Paredao APA Cantao
UFES1404	RGR66	UFES	EA	Caseara	CntP	TO	-9.303	-49.958	35	Mata do Sitio Velho PE Cantao
UFES1405	RGR188	UFES	EA	Caseara	CntP	TO	-9.303	-49.958	35	Mata do Sitio Velho PE Cantao
UFES1445	RGR187	UFES	EA	Caseara	CntA	TO	-9.384	-49.975	36	Mata do Paredao APA Cantao
UFES1566	DPO9	UFES	PL	Canaã dos Carajás	Cana	PA	-6.376	-50.383	23	Canaã dos Carajás
UFES1569	DPO18	UFES	PL	Canaã dos Carajás	Cana	PA	-6.347	-50.446	22	Canaã dos Carajás
UFES1570	DPO19	UFES	PL	Canaã dos Carajás	Cana	PA	-6.380	-50.360	24	Canaã dos Carajás
UFES1580	BAC320	UFES	PL	Canaã dos Carajás	Cana	PA	-6.343	-50.423	21	Canaã dos Carajás
UFES1583	BAC331	UFES	PL	Canaã dos Carajás	Cana	PA	-6.344	-50.408	21	Canaã dos Carajás
UFES1842	BAC321	UFES	PL	Canaã dos Carajás	Cana	PA	-6.343	-50.423	21	Canaã dos Carajás
UFES1866	BAC350	UFES	FD	Canaã dos Carajás	Cana	PA	-6.329	-50.127	20	Canaã dos Carajás
UFES1873	BAC300	UFES	PL	Canaã dos Carajás	Cana	PA	-6.400	-50.435	25	Canaã dos Carajás
UFES1877	BAC308	UFES	PL	Canaã dos Carajás	Cana	PA	-6.400	-50.435	25	Canaã dos Carajás
UFES1887	BAC349	UFES	PL	Canaã dos Carajás	Cana	PA	-6.329	-50.127	20	Canaã dos Carajás
	APS6	UFMT	UW	Cláudia	Clau	MT	-11.588	-55.292	9	Fazenda Continental
	APS13	UFMT	UW	Cláudia	Clau	MT	-11.588	-55.292	9	Fazenda Continental
	APS19	UFMT	UW	Cláudia	Clau	MT	-11.588	-55.292	9	Fazenda Continental
	APS25	UFMT	UW	Cláudia	Clau	MT	-11.588	-55.292	9	Fazenda Continental
	MAR466	UFMT	FD	Melgaço	Caxi	PA	-1.960	-51.615	11	PPBio Caxiuana

MAR946	UFMT	FD	Melgaço	Caxi	PA	-1.960	-51.615	11	PPBio Caxiuana
MAR1085	UFMT	FD	Melgaço	Caxi	PA	-1.960	-51.615	11	PPBio Caxiuana
MAR1271	UFMT	FD	Melgaço	Caxi	PA	-1.960	-51.615	11	PPBio Caxiuana
MAR1298	UFMT	FD	Melgaço	Caxi	PA	-1.960	-51.615	11	PPBio Caxiuana
PAB19	UFMT	EA	Belém	Blem	PA	-1.386	-48.397	28	Parque Ambiental de Belém
PSA77	UFMT	PL	Marabá	Tapi	PA	-5.781	-50.530	17	FLONA Tapirape-Aquiri
PSA111	UFMT	PL	Marabá	Tapi	PA	-5.781	-50.530	17	FLONA Tapirape-Aquiri
PSA153	UFMT	PL	Marabá	Tapi	PA	-5.781	-50.530	17	FLONA Tapirape-Aquiri
PSA156	UFMT	PL	Marabá	Tapi	PA	-5.781	-50.530	17	FLONA Tapirape-Aquiri
PSA163	UFMT	PL	Marabá	Tapi	PA	-5.781	-50.530	17	FLONA Tapirape-Aquiri
PSA174	UFMT	PL	Marabá	Tapi	PA	-5.781	-50.530	17	FLONA Tapirape-Aquiri
PSA175	UFMT	PL	Marabá	Tapi	PA	-5.781	-50.530	17	FLONA Tapirape-Aquiri
PSA191	UFMT	PL	Marabá	Tapi	PA	-5.781	-50.530	17	FLONA Tapirape-Aquiri
PSA193	UFMT	PL	Marabá	Tapi	PA	-5.781	-50.530	17	FLONA Tapirape-Aquiri
PSA196	UFMT	PL	Marabá	Tapi	PA	-5.781	-50.530	17	FLONA Tapirape-Aquiri
PSA197	UFMT	PL	Marabá	Tapi	PA	-5.781	-50.530	17	FLONA Tapirape-Aquiri
PSA198	UFMT	PL	Marabá	Tapi	PA	-5.781	-50.530	17	FLONA Tapirape-Aquiri
PSA206	UFMT	PL	Marabá	Tapi	PA	-5.781	-50.530	17	FLONA Tapirape-Aquiri

	PSA207	UFMT	PL	Marabá	Tapi	PA	-5.781	-50.530	17	FLONA Tapirape-Aquiri
	TC54	UFMT	EA	Primavera	Prim	PA	-0.979	-47.112	27	Primavera
	TC59	UFMT	EA	Primavera	Prim	PA	-0.979	-47.112	27	Primavera
	TC60	UFMT	EA	Primavera	Prim	PA	-0.979	-47.112	27	Primavera
	TC64	UFMT	EA	Primavera	Prim	PA	-0.979	-47.112	27	Primavera
	TC73	UFMT	EA	Primavera	Prim	PA	-0.979	-47.112	27	Primavera
	TC100	UFMT	EA	Primavera	Prim	PA	-0.979	-47.112	27	Primavera
	TC102	UFMT	EA	Primavera	Prim	PA	-0.979	-47.112	27	Primavera
	TC113	UFMT	EA	Primavera	Prim	PA	-0.979	-47.112	27	Primavera
	TC124	UFMT	EA	Primavera	Prim	PA	-0.979	-47.112	27	Primavera
	TC126	UFMT	EA	Primavera	Prim	PA	-0.979	-47.112	27	Primavera
	TC137	UFMT	EA	Primavera	Prim	PA	-0.979	-47.112	27	Primavera
	UTP90	UFMT	UW	Paranaíta	TePi	MT	-9.451	-56.472	6	Rio Teles Pires
	UTP100	UFMT	UW	Paranaíta	TePi	MT	-9.451	-56.472	6	Rio Teles Pires
	UTP124	UFMT	UW	Paranaíta	TePi	MT	-9.451	-56.472	6	Rio Teles Pires
	UTP128	UFMT	UW	Paranaíta	TePi	MT	-9.451	-56.472	6	Rio Teles Pires
	UTP173	UFMT	UW	Paranaíta	TePi	MT	-9.451	-56.472	6	Rio Teles Pires
	UTP184	UFMT	UW	Paranaíta	TePi	MT	-9.451	-56.472	6	Rio Teles Pires
	UTP192	UFMT	UW	Paranaíta	TePi	MT	-9.451	-56.472	6	Rio Teles Pires
	UTP194	UFMT	UW	Paranaíta	TePi	MT	-9.451	-56.472	6	Rio Teles Pires
	UTP196	UFMT		Paranaíta	TePi	MT	-9.451	-56.472	6	Rio Teles Pires
	UTP197	UFMT	UW	Paranaíta	TePi	MT	-9.451	-56.472	6	Rio Teles Pires
	UTP198	UFMT	UW	Paranaíta	TePi	MT	-9.451	-56.472	6	Rio Teles Pires
	UTP662	UFMT	UW	Paranaíta	TePi	MT	-9.451	-56.472	6	Rio Teles Pires
	UTP663	UFMT	UW	Paranaíta	TePi	MT	-9.451	-56.472	6	Rio Teles Pires
	UTP1012	UFMT	UW	Paranaíta	TePi	MT	-9.451	-56.472	6	Rio Teles Pires
UFPA115	CAR139	UFPA	PL	Parauapebas	Carj	PA	-6.100	-50.150	19	FLONA Carajas

UFPA129	CAR65	UFPA	PL	Parauapebas	Carj	PA	-6.100	-50.150	19	FLONA Carajas
UFPA140	CAR87	UFPA	PL	Parauapebas	Carj	PA	-6.100	-50.150	19	FLONA Carajas
UFPA175	CAR12	UFPA	PL	Parauapebas	Carj	PA	-6.100	-50.150	19	FLONA Carajas
UFPA181	CAR144	UFPA	PL	Parauapebas	Carj	PA	-6.100	-50.150	19	FLONA Carajas
UFPA211	CAR135	UFPA	PL	Parauapebas	Carj	PA	-6.100	-50.150	19	FLONA Carajas
UFPA221	CAR32	UFPA	PL	Parauapebas	Carj	PA	-6.100	-50.150	19	FLONA Carajas
UNB2671	ARB658	UNB	EA	Palmas	Palm	TO	-10.467	-48.340	37	Irrigacao Sao Joao Taquaralto
UNB2673	ARB662	UNB	EA	Palmas	Palm	TO	-10.467	-48.340	37	Irrigacao Sao Joao Taquaralto
UNB2719	ST10	UNB	EA	Santa Terezinha de Goiás	STrz	GO	-14.438	-49.706	43	Santa Terezinha de Goias
UNB2723	ST9	UNB	EA	Santa Terezinha de Goiás	STrz	GO	-14.438	-49.706	43	Santa Terezinha de Goias
UNB2850	SF29	UNB	EA	Catalão	Faca	GO	-18.066	-47.666	46	UHE Serra do Facao
	RNL72	UNB	FD	Conceição do Araguaia	Cabe	PA	-8.297	-49.382	14	Fazenda Cabeceira
	RNL76	UNB	FD	Conceição do Araguaia	Cabe	PA	-8.297	-49.382	14	Fazenda Cabeceira
	RNL77	UNB	FD	Conceição do Araguaia	SJFo	PA	-8.142	-49.339	13	Fazenda Sao Jose da Fortaleza
	RNL85	UNB	FD	Novo Repartimento	Arat	PA	-4.105	-50.092	12	Fazenda Aratau
	RNL91	UNB	FD	Novo Repartimento	Arat	PA	-4.105	-50.092	12	Fazenda Aratau
	RNL92	UNB	FD	Novo Repartimento	Arat	PA	-4.105	-50.092	12	Fazenda Aratau
	RNL96	UNB	EA	Goianésia do Pará	Capm	PA	-3.715	-48.602	30	Fazenda Rio Capim
	RNL97	UNB	EA	Goianésia do Pará	Capm	PA	-3.715	-48.602	30	Fazenda Rio Capim
	RNL98	UNB	EA	Goianésia do Pará	Capm	PA	-3.715	-48.602	30	Fazenda Rio Capim
	RNL99	UNB	EA	Goianésia do Pará	Capm	PA	-3.715	-48.602	30	Fazenda Rio Capim
	RNL101	UNB	EA	Goianésia do Pará	Capm	PA	-3.709	-48.620	29	Fazenda Rio Capim
	RNL102	UNB	EA	Goianésia do Pará	Capm	PA	-3.715	-48.602	30	Fazenda Rio Capim
	RNL123	UNB	EA	Goianésia do Pará	Capm	PA	-3.715	-48.602	30	Fazenda Rio Capim

	RNL150	UNB	EA	Brasília	IBGE	DF	-15.955	-47.889	45	Corrego Taquara RECOR IBGE
	RNL151	UNB	EA	Brasília	IBGE	DF	-15.955	-47.889	45	Corrego Taquara RECOR IBGE
	RNL152	UNB	EA	Brasília	IBGE	DF	-15.955	-47.889	45	Corrego Taquara RECOR IBGE
USNM549581	LHE506	USNM	PL	Altamira	Altm	PA	-3.650	-52.366	15	Altamira left bank Rio Xingu
USNM549582	LHE512	USNM	PL	Altamira	Altm	PA	-3.650	-52.366	15	Altamira left bank Rio Xingu
USNM549583	LHE513	USNM	PL	Altamira	Altm	PA	-3.650	-52.366	15	Altamira left bank Rio Xingu
USNM549584	LHE525	USNM	PL	Altamira	Altm	PA	-3.650	-52.366	15	Altamira left bank Rio Xingu
USNM549585	LHE526	USNM	PL	Altamira	Altm	PA	-3.650	-52.366	15	Altamira left bank Rio Xingu
USNM549586	LHE527	USNM	PL	Altamira	Altm	PA	-3.650	-52.366	15	Altamira left bank Rio Xingu
USNM549587	LHE533	USNM	PL	Altamira	Altm	PA	-3.650	-52.366	15	Altamira left bank Rio Xingu
USNM549588	LHE580	USNM	PL	Altamira	Altm	PA	-3.650	-52.366	15	Altamira left bank Rio Xingu
USNM549589	LHE591	USNM	PL	Altamira	Altm	PA	-3.650	-52.366	15	Altamira left bank Rio Xingu
USNM549590	LHE618	USNM	PL	Altamira	Altm	PA	-3.666	-52.366	16	Altamira left bank Rio Xingu
USNM549821	MDC592	USNM	PL	Altamira	Altm	PA	-3.650	-52.366	15	Altamira left bank Rio Xingu
	JB216		EA	Brasília	JBBr	DF	-15.925	-47.834	44	Jardim Botânico Brasilia

Table S2. Summary of the results from the species-specific tuning carried on with 10 replicated runs each under the current climatic conditions. The selected regularization parameter was 3.5, marked in bold (see variable response curves below).
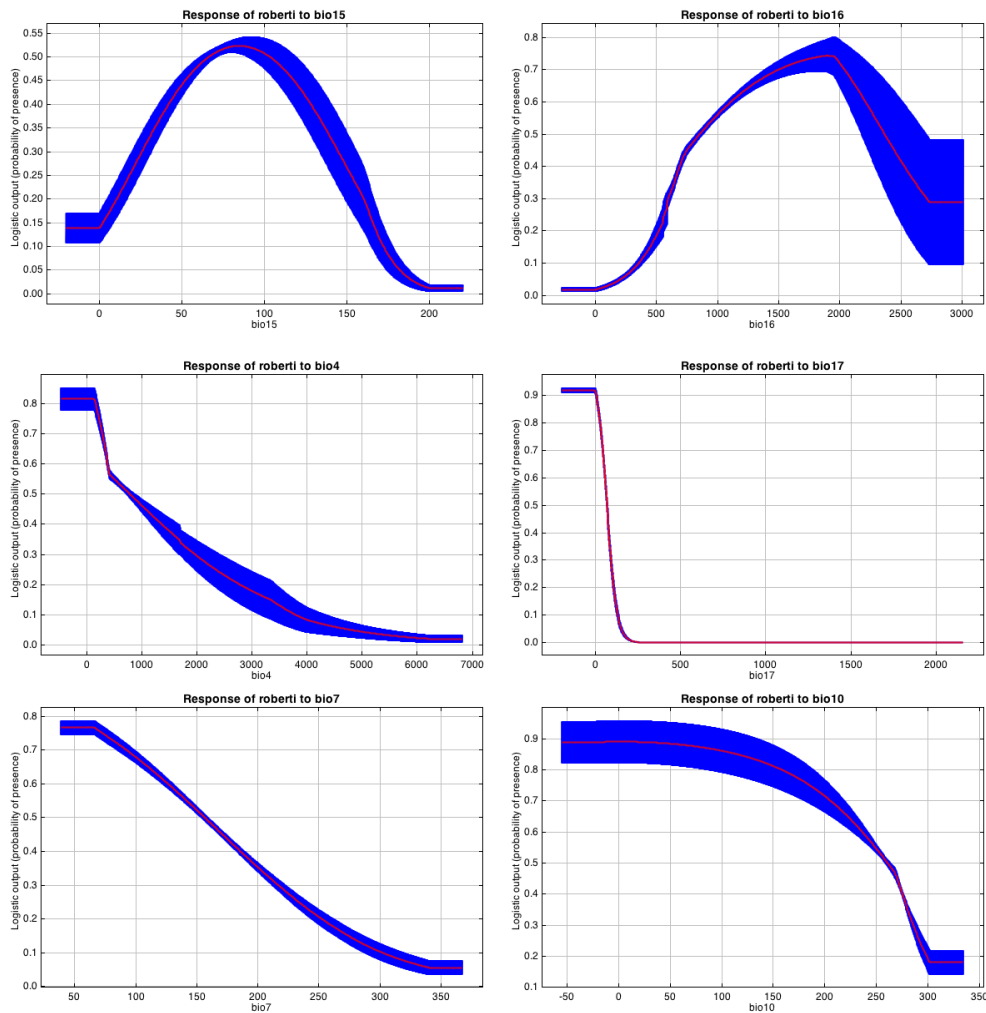
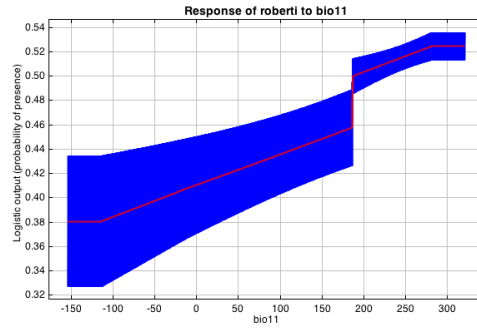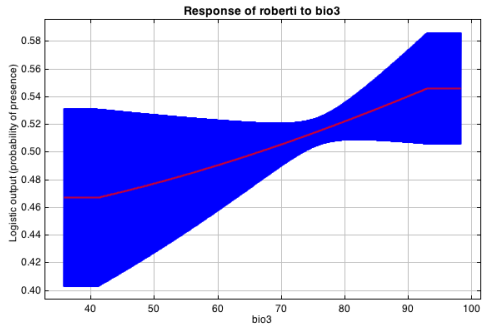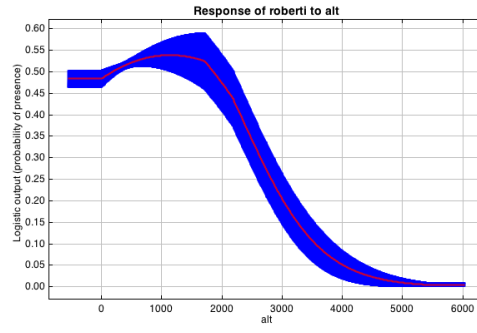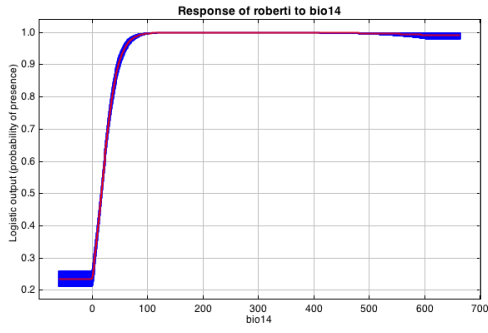| Regularization parameter	Average test AUC for replicate runs (SD)	AUC differences (traininig – test AUCs)	Average 10 percentile training presence	Minimum training presence test omission rates	Variable response curves
0.5	0.886 (0.013)	0.07	0.3082	0.0546	Highly irregular
1	0.893 (0.012)	0.0378	0.3112	0.0548	Highly irregular
1.5	0.893 (0.014)	0.0258	0.3382	0.065	Less irregular, but not smooth
2	0.891 (0.017)	0.019	0.3396	0.0796	Less irregular, but not smooth
2.5	0.89 (0.019)	0.015	0.3368	0.0896	Less irregular and smooth
3	0.887 (0.02)	0.0148	0.3418	0.096	Less irregular and smooth
3.5	**0.885 (0.02)**	**0.0162**	**0.3466**	**0.986**	**Regular and smooth**
4	0.884 (0.019)	0.0134	0.3478	0.0978	Regular and smooth
4.5	0.883 (0.019)	0.0118	0.3354	0.095	Regular and smooth
5	0.882 (0.018)	0.011	0.3344	0.0946	Regular and smooth
5.5	0.881 (0.019)	0.0098	0.3298	0.0914	Less regular and smooth
6	0.881 (0.019)	0.0072	0.3278	0.0952	Less regular and smooth

Table S3. Estimates of relative contributions of the environmental variables for the 10-fold run Maxent model including the past climate projections and implementing the selected regularization multiplier (3.5). Variables are ranked according to their percent contributions to the models.

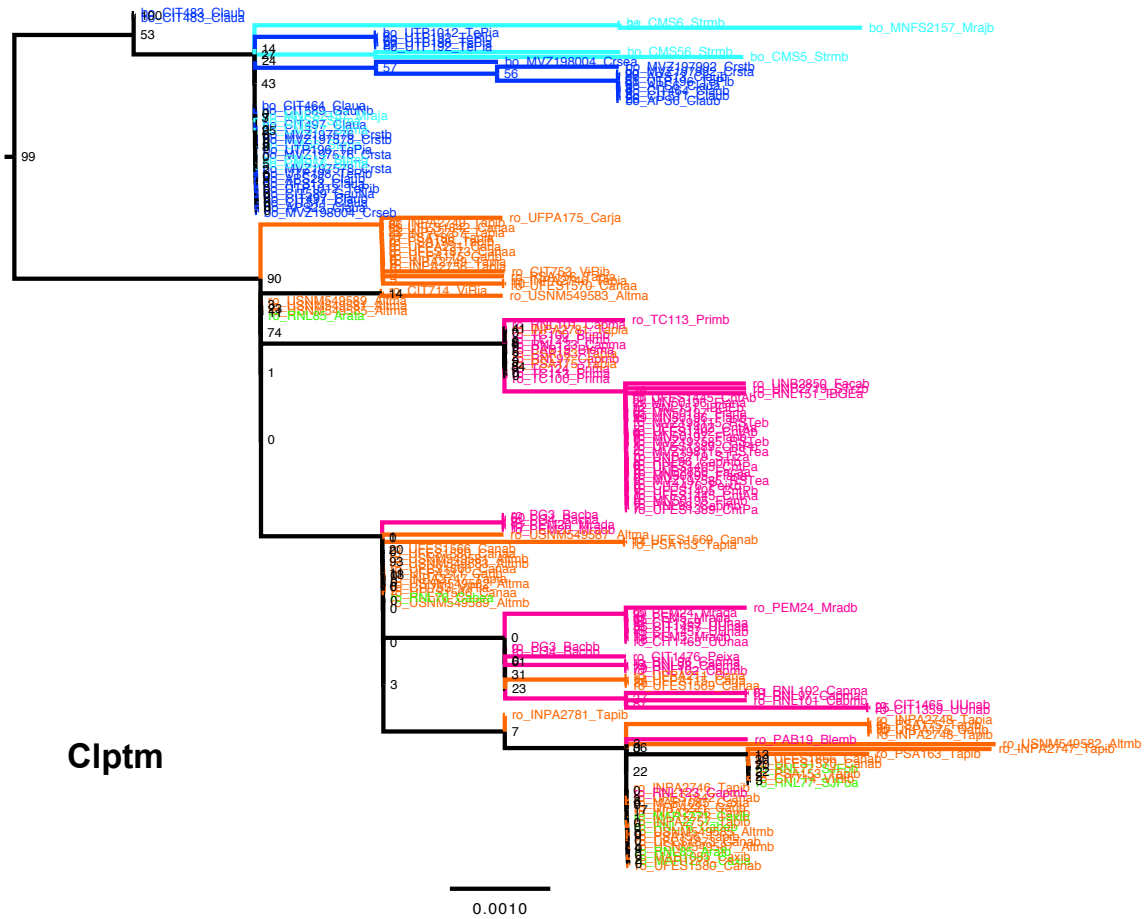| Variable	Percent Contribution	Permutation Importance
bio15: precipitation seasonality (coefficient of variation)	39.7	9.1
bio16: precipitation of wettest quarter	25.9	14.4
bio4: temperature seasonality (standard deviation × 100)	18.9	8.6
bio17: precipitation of driest quarter	5.2	40.9
bio7: temperature annual range (bio5-bio6)	3	5.6
bio10: mean temperature of warmest quarter	2.5	3.9
bio14: precipitation of driest month	1.4	14.3
alt: altitude	1.3	2.6
bio3: isothermality ((bio2 ÷ bio7) × 100)	1	0.3
bio11: mean temperature of coldest quarter	1	0.4

Supporting Information Figures

Figure S1. Individual variable response curves for the regularization parameter selected (= 3.5). These curves show how the logistic Maxent prediction changes as each environmental variable is varied, keeping all other environmental variables at their average sample value.
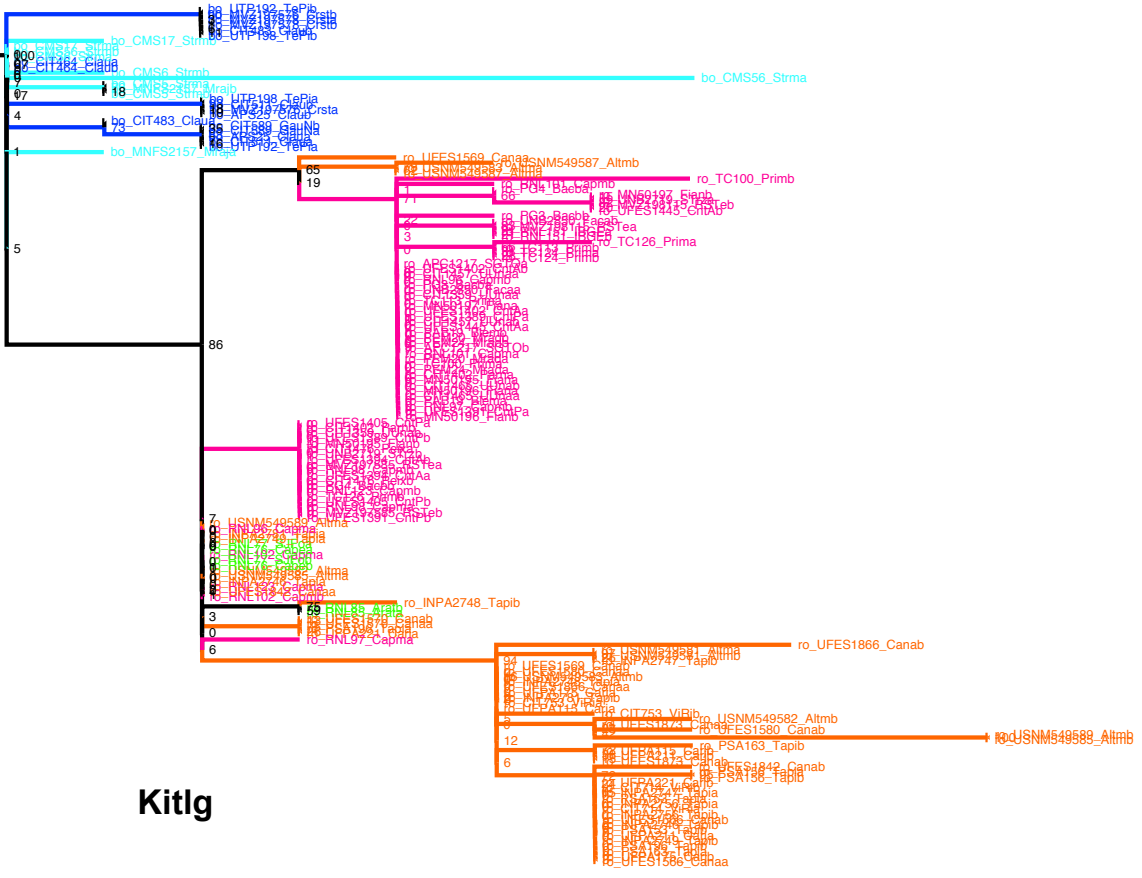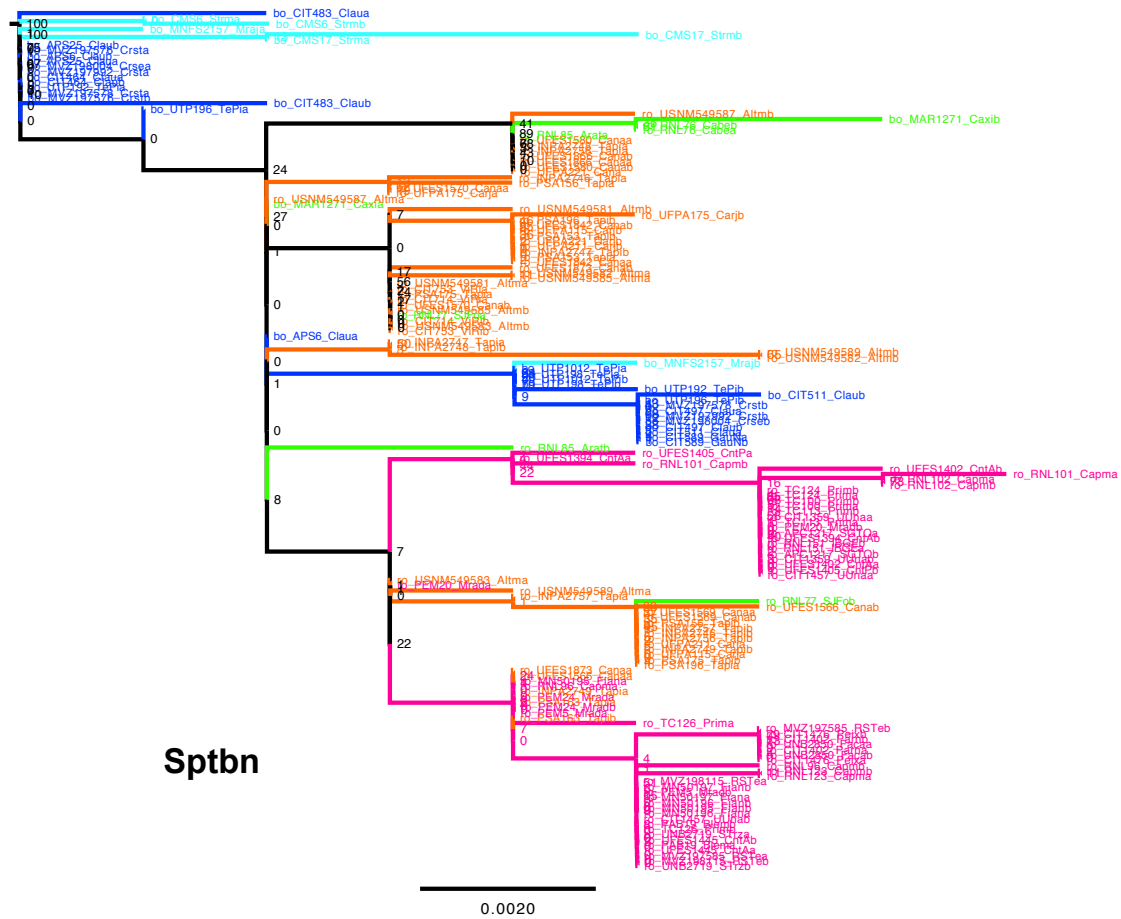
Figure S2. Individual nuclear gene trees based on maximum likelihood inference.

Cad

0.0010

Clptm

0.0010

Exoc3

0.0020

Fgb

0.0030

Kitlg

0.0020

Sptbn

0.0020

Figure S3. Maximum clade credibility tree from Bayesian phylogeography RRW analysis showing estimated divergence times and 95% confidence intervals. The numbers in the nodes correspond to clades posterior probability.