Phylogenetic Relationships of New World Porcupines (Rodentia, Erethizontidae): Implications for Taxonomy, Morphological Evolution, and Biogeography

Authors: Voss, Robert S., Hubbard, Caldonia, and Jansa, Sharon A.

Phylogenetic Relationships of New World Porcupines (Rodentia, Erethizontidae): Implications for Taxonomy, Morphological Evolution, and Biogeography

ROBERT S. VOSS,[1] CALDONIA HUBBARD,[2] AND SHARON A. JANSA[2]

ABSTRACT

Phylogenetic analyses of cytochrome-*b* sequence data from 13 of the 15 currently recognized species of New World porcupines were used to test competing taxonomic hypotheses and to explore scenarios of morphological evolution and biogeography. Consistent with previous studies, the monophyly of Erethizontidae (*Chaetomys* + *Erethizon* + *Coendou*) and the monophyly of Erethizontinae (*Erethizon* + *Coendou*) were both strongly supported. However, cytochrome-*b* sequence data provide no support for the reciprocal monophyly of *Coendou*, "*Echinoprocta*," and "*Sphiggurus*" as those taxa were previously recognized by authors. All of the erethizontid species recognized in recent revisionary work and represented by multiple sequences in this study were recovered as monophyletic groups. Maximum-likelihood (ML) analyses of these data recovered the following phylogeny for 11 species of *Coendou*: ((*melanurus* (*ichillus* (*pruinosus* + *vestitus*))) ((*spinosus* (*bicolor* + *nycthemera*)) (*prehensilis* (*mexicanus* (*quichua* + *rufescens*)))))). Ancestral-state reconstructions based on the ML topology suggest that several morphological characters emphasized in past erethizontid classifications (size, nasofrontal sinus inflation, and long fur) have evolved homoplasiously. Maximum-likelihood inference of geographic range evolution suggests that the last common ancestor of living erethizontids was a cis-Andean species, and that most subsequent cladogenesis was also cis-Andean; however, at least two trans-Andean dispersal events are plausibly indicated, as well as two separate invasions of Andean landscapes. Among the most remarkable results of this study are almost-

[1] Division of Vertebrate Zoology (Mammalogy), American Museum of Natural History.

[2] Department of Ecology, Evolution, and Behavior; and J.F. Bell Museum of Natural History. University of Minnesota, 1987 Upper Buford Circle, St. Paul, MN 55108.

identical sequences of *Coendou prehensilis* from localities spanning 27° of latitude and 25° of longitude; we speculate that a trophic-niche shift might have allowed rapid range expansion of this species, which accounts for almost all known cases of geographic range overlap and sympatry in the genus *Coendou*.

INTRODUCTION

Recent New World porcupines (Erethizontidae) are arboreal caviomorph rodents that defend themselves with dangerous quills and eat leaves, bark, fruit, and immature seeds (Charles-Dominique et al., 1981; Roze, 1989; Chiarello et al., 1997; Emmons, 1997; Cherubini et al., 2003; Passamani, 2010). With the exception of one boreal North American species, erethizontids occur in tropical and subtropical habitats from southern Mexico to northern Argentina. Most Neotropical porcupines inhabit lowland rainforest, but some also occur in dry (deciduous) forests, and others are found in montane ("cloud") forests to at least 3500 m above sea level. Solitary, nocturnal, and silent, most erethizontids are seldom observed even where they are locally common, and several species are known from just a few museum specimens.

The current taxonomy (summarized by Voss, 2011) recognizes 15 erethizontid species in three genera (table 1). Two genera each include only a single living species: *Chaetomys* (containing only *C. subspinosus*, the Brazilian bristle-spined porcupine) and *Erethizon* (containing only *E. dorsatum*, the North American porcupine). The remaining 13 Recent species belong to *Coendou* (commonly known as prehensile-tailed porcupines), but some authors have recognized additional subgenera or genera within this group. Woods and Kilpatrick (2005), for example, referred several long-furred species of *Coendou* to the genus *Sphiggurus*, and the short-tailed species *C. rufescens* has long been referred to the monotypic genus *Echinoprocta*. Because these alternative usages were not based on any defensible hypothesis of reciprocal monophyly, Alberico et al. (1999) and Voss (2011) treated *Sphiggurus* F. Cuvier, 1823, and *Echinoprocta* Gray, 1865, as junior synonyms of *Coendou* Lacépède, 1799.

To date, erethizontid systematics has been almost entirely based on morphological data, only three DNA-sequencing studies having included multiple erethizontid exemplars (Bonvicino et al., 2002; Vilela et al., 2009; Leite et al., 2011). Taking synonymies and corrected identifications (Voss, 2011) into account, those studies suggest that (1) *Chaetomys* is the sister taxon of other living New World porcupines, (2) *Erethizon* is the sister taxon of *Coendou*, and (3) *Coendou spinosus* and *C. melanurus* are more closely related to one another than either is to *C. prehensilis*. However, most species of *Coendou* have not been sequenced for any gene, so existing molecular phylogenies are largely uninformative about erethizontid biogeography and morphological evolution.

This article reports the first phylogenetic analyses of New World porcupines based on a taxonomically dense molecular dataset; of the 15 currently recognized Recent species, only two (*Coendou insidiosus* and *C. roosmalenorum*) are not represented in this study. For several species with noteworthy geographic variation and/or problematic synonyms, we included multiple samples to test species monophyly. Because preserved tissue samples are unavailable for several species, we analyzed sequence data from the mitochondrial gene encoding cytochrome *b*,

TABLE 1. Classification and Distribution of Recent Erethizontids[a]

Taxon	Distribution
Chaetomyinae	
Chaetomys subspinosus	SE Brazil (cis-Andean)
Erethizontinae	
Coendou bicolor	Peru, E Bolivia, & NW Argentina (mostly cis-Andean)
Coendou ichillus[b]	E Ecuador & NE Peru (cis-Andean)
Coendou insidiosus[b]	SE Brazil (cis-Andean)
Coendou melanurus[b]	Guianas, E Venezuela, & N Brazil (cis-Andean)
Coendou mexicanus[b]	Mexico to W Panama (trans-Andean)
Coendou nycthemera	SE Amazonian Brazil (cis-Andean)
Coendou prehensilis	Colombia to N Argentina (mostly cis-Andean)
Coendou pruinosus[b]	NW Venezuela & NE Colombia (Andean)
Coendou quichua	Panama to Ecuador (Andean & trans-Andean)
Coendou roosmalenorum[b]	SW Amazonian Brazil (cis-Andean)
Coendou rufescens[c]	Colombia to N Bolivia (Andean)
Coendou spinosus[b]	SE Brazil to Uruguay (cis-Andean)
Coendou vestitus[b]	Colombia (trans-Andean)
Erethizon dorsatum	Mexico, United States, & Canada (trans-Andean)

[a] Based on taxonomy and geographic data summarized by Voss (2011). As defined by Haffer (1967), "cis-Andean" refers to distributions east of the Andes and "trans-Andean" refers to distributions west of the Andes (including inter-Andean Colombia, Central America, and North America). "Andean" species (our usage) are highland taxa that can occur on both eastern and western slopes and foothills. As noted in the text, two species with mostly cis-Andean distributions (*C. bicolor* and *C. prehensilis*) have isolated trans-Andean populations.
[b] Referred to *Sphiggurus* by Woods and Kilpatrick (2005).
[c] Referred to *Echinoprocta* by Woods and Kilpatrick (2005).

which can often be amplified from old museum skin-and-skull preparations. Our results corroborate some previous hypotheses about porcupine relationships, challenge others, and provide novel insights about porcupine morphological evolution and biogeography.

MATERIALS AND METHODS

VOUCHER SPECIMENS: Morphological voucher material for erethizontid DNA sequences analyzed in this report (tables 2 and 3) is preserved in the following institutional collections: American Museum of Natural History, New York (AMNH); Angelo State Natural History Collection, San Angelo (ASNHC); Estación Biológica de Rancho Grande, Maracay (EBRG); Field Museum of Natural History, Chicago (FMNH); Instituto Nacional de Pesquisas da Amazônia, Manaus (INPA); Biodiversity Research Center, University of Kansas, Lawrence (KU); Los Angeles County Museum, Los Angeles (LACM); Museu de Ciências Naturais da Universidade Luterana do Brasil, Canoas (MCNU); Muséum National d'Histoire Naturelle, Paris (MNHN);

TABLE 2. Erethizontid Specimens Sequenced for This Report

Species	Tissue[a]	Voucher[b]	Locality[c]	bp[d]
Coendou bicolor		AMNH 214612[e]	Bolivia: Beni (1)	682
Coendou bicolor	MVZ 196056	MUSM 9398[e]	Peru: Cajamarca (28)	1140
Coendou bicolor	EDH1	KU 144560[e]	Peru: Madre de Dios (31)	1140
Coendou bicolor	PMV 2311	FMNH 203679[e]	Peru: San Martín (32)	1140
Coendou ichillus	CLH 4709	TTU 115491[e]	Peru: Loreto (29)	1027
Coendou melanurus	T-1622	MNHN 1997.641	French Guiana (22)	1140
Coendou mexicanus	FN 30027	ASNHC 6407	Mexico: Campeche (23)	1140
Coendou nycthemera		USNM 519690[e]	Brazil: Pará (9)	795
Coendou nycthemera		USNM 519692[e]	Brazil: Pará (9)	794
Coendou prehensilis	NK 12984	AMNH 262274[e]	Bolivia: Santa Cruz (2)	1140
Coendou prehensilis	MVZ 191349	MVZ 191349[e]	Brazil: Acre (3)	772
Coendou prehensilis	MVZ 195088	INPA 2875[e]	Brazil: Amazonas (5)	788
Coendou prehensilis		USNM 281898[e]	Colombia: Cesar (18)	802
Coendou prehensilis		USNM 281904[e]	Colombia: Cesar (18)	678
Coendou prehensilis		USNM 528360[e]	Ecuador, Sucumbíos (21)	1140
Coendou prehensilis	T-1626	MNHN 1997.643	French Guiana (22)	795
Coendou prehensilis	MVZ 155200	MVZ 155200[e]	Peru: Amazonas (27)	768
Coendou prehensilis	MVZ 155201	MVZ 155201[e]	Peru: Amazonas (27)	772
Coendou prehensilis	DWF 554	AMNH 273130[e]	Peru: Loreto (30)	762
Coendou prehensilis	DWF 555	MUSM 15324[e]	Peru: Loreto (30)	762
Coendou prehensilis	ALG 14517	USNM 560869[e]	Venezuela: Amazonas (33)	802
Coendou prehensilis	T-3369	EBRG 23415	Venezuela: Bolívar (34)	798
Coendou prehensilis		USNM 443409[e]	Venezuela: Táchira (35)	802
Coendou pruinosus	RSV 1091	MHNLS 7692[e]	Venezuela: Zulia (36)	259
Coendou quichua		LACM 27376[e]	Colombia: Cesar (17)	1140
Coendou quichua	KMH 2218	USNM (uncataloged)[e]	Ecuador: Cotopaxi (20)	1114
Coendou quichua		USNM 296308[e]	Panama: "Canal Zone" (24)	682
Coendou rufescens		AMNH 181483[e]	Colombia: Cauca (16)	914
Coendou spinosus	MVZ 198208	UFMG 3043	Brazil: São Paulo (15)	1140
Coendou spinosus	GD 252	UMMZ (uncataloged)[e]	Paraguay: Itapúa (26)	1112
Coendou spinosus	GD 526	UMMZ 174975[e]	Paraguay: Caazapá (25)	1112
Coendou vestitus		AMNH 70596[e]	Colombia: Cundinamarca (19)	682
Erethizon dorsatum	J-557	USNM 568658	USA: Pennsylvania (37)	1140

[a] Sequences amplified from skins lack entries in this column.

[b] See Materials and Methods for explanations of museum acronyms.

[c] Country and next-largest administrative unit (state/department/province). Numbers in parentheses correspond to collection sites mapped in figure 1 and listed in the gazetteer (appendix 1).

[d] Sequenced base pairs of cytochrome *b*.

[e] Specimen examined by us.

TABLE 3. Erethizontid Sequences Downloaded from GenBank

Species	Genbank #	Voucher[a]	Locality[b]	bp[c]	Origin
Chaetomys subspinosus	EU544660	MCNU 918	Brazil: Bahia (6)	1140	Vilela et al. (2009)
Coendou melanurus[d]	AF411583	UFPB 3001	Brazil: Roraima (13)	786	Bonvicino et al. (2002)
Coendou prehensilis[e]	U34851	INPA 3919[f]	Brazil: Acre (4)	802	Lara et al. (1996)
Coendou prehensilis	AF411581	Manso 212	Brazil: Mato Grosso (8)	794	Bonvicino et al. (2002)
Coendou prehensilis	AF411582	Manso 138	Brazil: Mato Grosso (8)	781	Bonvicino et al. (2002)
Coendou prehensilis	AF411584	Manso 849	Brazil: Mato Grosso (8)	802	Bonvicino et al. (2002)
Coendou prehensilis	HM462243	MN 73383	Brazil: Pernambuco (10)	801	Leite et al. (2011)
Coendou spinosus[g]	EU544661	CIT 1326[h]	Brazil: Espirito Santo (7)	1140	Vilela et al. (2009)
Coendou spinosus[g]	AF407277	MN 46938	Brazil: Rio de Janeiro (11)	1071	Bonvicino et al. (2002)
Coendou spinosus[g]	AF411580	MN 46937	Brazil: Rio de Janeiro (12)	1106	Bonvicino et al. (2002)
Coendou spinosus[g]	EU544662	MZUSP 35142[i]	Brazil: São Paulo (14)	1140	Vilela et al. (2009)
Erethizon dorsatum	FJ357428	[unknown]	[unknown]	1140	Vilela et al. (2009)

[a] See Materials and Methods for explanations of museum acronyms.
[b] Country and next-largest administrative unit (state/department/province). Numbers in parentheses correspond to collection sites mapped in figure 1 and listed in the gazetteer (appendix 1).
[c] Sequenced base pairs of cytochrome *b*.
[d] Originally identified as "*Sphiggurus melanura.*"
[e] Originally identified as *Coendou bicolor*.
[f] Specimen examined by us.
[g] Originally identified as "*Sphiggurus villosus.*"
[h] Laboratory number (current whereabouts of morphological specimen unknown).
[i] Other numbers associated with this specimen are CIT 2113 and UNIBAN 2584 (A. Carmignotto, personal commun.).

Museo de Historia Natural La Salle, Caracas (MHNLS); Museu Nacional, Rio de Janeiro (MNRJ); Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima (MUSM); Museum of Vertebrate Zoology, University of California at Berkeley, Berkeley (MVZ); Museu de Zoologia da Universidade do São Paulo, São Paulo (MZUSP); Museum of Texas Tech University, Lubbock (TTU); Universidade Federal de Minas Gerais, Belo Horizonte (UFMG); Universidade Federal da Paraíba, João Pessoa (UFPB); University of Michigan Museum of Zoology, Ann Arbor (UMMZ); National Museum of Natural History, Washington, DC (USNM). The catalog numbers of specimens preserved in the mammal collection of the Manso hydroelectric dam (in Cuiabá) are prefixed with "Manso" (after Bonvicino et al., 2002).

DNA extraction, amplification, and sequencing: We extracted DNA from fresh tissues (heart, liver, or kidney) that had been preserved in ethanol or from dried material (skin fragments and/or quills) harvested from museum specimens. All DNA extractions were performed using a Qiagen DNA Minikit (Qiagen, Inc.). Ethanol-preserved tissue samples were extracted according to kit instructions, but dried skin fragments and quills required additional processing to yield uncontaminated DNA. All extractions from dried museum material were conducted in a UV-sterilized hood in a laboratory that had never been used to amplify mammalian DNA sequences. Skin samples were washed in a series of ethanol and water washes with overnight soaks (described in Giarla et al., 2010). Quills were similarly washed and soaked, but
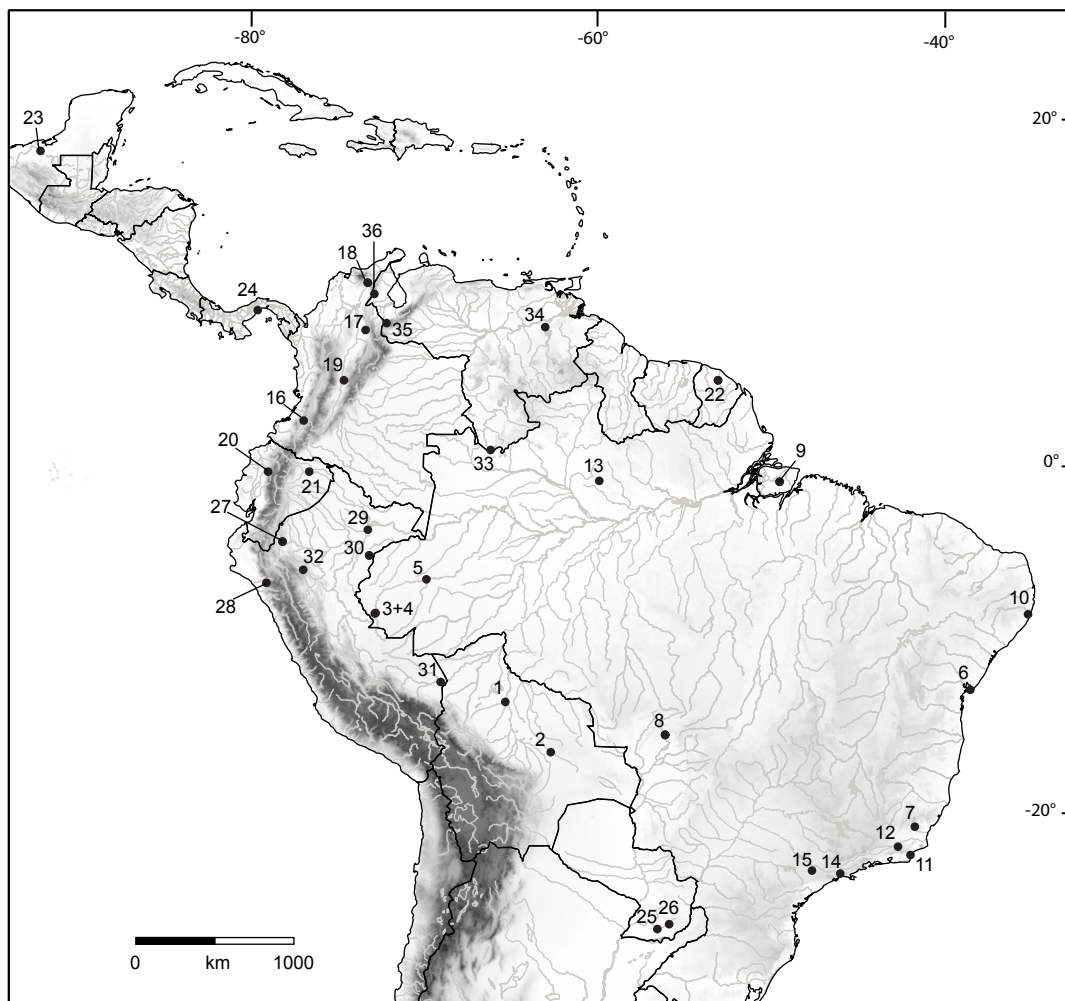
FIG. 1. Collection localities of sequenced specimens of Neotropical erethizontids (*Chaetomys* and *Coendou*). See gazetteer (appendix 1) for geographic coordinates and other information.

the time of each soak was shortened to 1 hour (rather than overnight). Washed skin samples were digested according to kit instructions, except that skin was allowed to sit in the lysis buffer + proteinase K mixture for two days with an extra 30 μL of proteinase K added on the second day. Quills were subjected to a similar two-day lysis, and 30 μL of 100 mg/mL dithiothreitol (DTT) was added to the digestion each day.

For most tissue samples, polymerase chain reaction (PCR) amplification of the entire mitochondrial gene encoding cytochrome *b* was done in two overlapping fragments of ~700 bp using primers MVZ05 paired with PorcCytb676R and either PorcCytb548F or PorcCytb565F paired with UMMZ04 (table 4, fig. 2). In cases where amplification of these two large fragments failed, the gene was amplified in four ~300–400 bp fragments using the following primer pairs: MVZ05/PorcCytb404R, PorcCytb323F/PorcCytb676R, PorcCytb565F/PorcCytb827R, and

TABLE 4. Primers Used to Amplify and Sequence the Cytochrome *b* Gene

Primer name[a]	Sequence
MVZ05	5′ CGAAGCTTGATATGAAAAACCATCGTTG
PorcCytb124F	5′ AAAYTTTGGATCCTTAYTAGG
PorcCytb234F	5′ ATATYTGCCGAGAYGTAAACTA
PorcCytb323F	5′ TAGGACGAGGAATTTACTAYGG
PorcCytb437F	5′ GGACAAATATCATTCTGAGGAG
PorcCytb478F	5′ CYTATCCGCAATCCCYTATG
PorcCytb548F	5′ GCRACCTTAACTCGATTCTTCG
PorcCytb565F	5′ TTAACTCGATTCTTCYCCTT
PorcCytb633F	5′ ACGAAACAGGATCAAACA
PorcCytb761F	5′ TTATTCTCACCAGACCTCCTA
PorcCytb944F	5′ CCACTCCTACATTCCTCAA
PorcCytb993F	5′ GCCAGTGCTTATTATGAWTACTAG
PorcCytb404R	5′ ACRTATCCTATGAAGGCTGTAGC
PorcCytb489R	5′ GTTGTACCGACATARGGGA
PorcCytb676R	5′ GAGTAGTATGGGTGGAATGG
PorcCytb694R	5′ CTTTAATTGAGTAGTATGGG
PorcCytb827R	5′ ATCATTCTGGTTTAATATGTGG
PorcCytb1059R	5′ AGGATRAATGGGTGTTCWA
UMMZ04	5′ TCTTCATTTYWGGTTTACAAGAC

[a] Numbers refer to sequence position as shown in figure 2. Primers MVZ05 and UMMZ04 were developed for studies of other taxa (Smith and Patton, 1993; Jansa et al., 1999). F = forward primer, R = reverse primer.

PorcCytb761F/UMMZ04. If PCR amplifications yielded sufficient product for sequencing, we sequenced this product directly; otherwise, we performed a second round of PCR using the same primers and 1 µL of the amplification product as template. All amplifications of tissue-derived DNA were done as 12.5 µL reactions using GoTaq Hot Start Polymerase (Promega Corp.) with 0.5 µL of each primer, 2.5 µL of reaction buffer, 1.0 µL of 25 mM $MgCl_2$, 0.25 µL of dNTP mix, 0.065 µL of polymerase, 1.0 µl of template (either DNA or PCR product), and 6.685 µL of dH_2O.

For museum skins and quills, cytochrome *b* was amplified in overlapping fragments of ~150–300 bp using various combinations of primers. In most cases, this initial amplification did not yield enough product for sequencing, so we performed a second round of PCR amplification as above. We used Platinum Taq (Life Technologies Corp.) for amplification of DNA derived from these degraded samples. Each reaction comprised 0.25 µL of each primer, 1.25 mL of reaction buffer, 0.375 µL of 50 mM $MgCl_2$, 0.25µL of dNTP mix, 0.05 µL of polymerase, 1.0 or 2.0 µL of template, and enough dH_2O to make a 12.5 µL reaction.

All PCR reactions using DNA as template were performed using a four-step touchdown protocol. Cycling started at an annealing temperature 2° C above the average primer-annealing
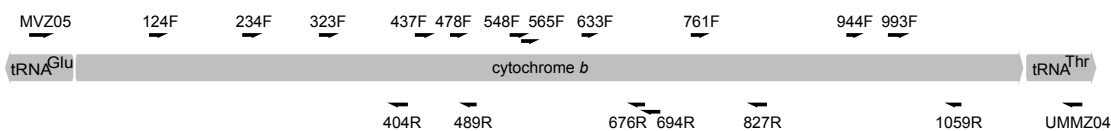
FIG. 2. Names and locations of primers (table 4) used to amplify and sequence cytochrome *b* for this study.

temperature and dropped by 2° increments for each step; the first three steps were run for 5 cycles, the last was run for 20 cycles. Any reamplification reactions were performed for 25 cycles using a single annealing temperature. Before sequencing, we used exonuclease I and shrimp alkaline phosphotase (Hanke and Wink, 1994) to remove primers and unincorporated nucleotides from the PCR product. Amplification products were sequenced in both directions on an ABI 3730 sequencer using amplification primers and dye-terminator chemistry (BigDye ver. 3.1 Cycle Sequencing Kit, Life Technologies Corp.). Sequences were edited and assembled using Sequencher ver. 4.7 (GeneCodes, Inc.) and were imported into Geneious ver. 5.6 (Drummond et al., 2011) to prepare files for analysis. All sequences newly obtained for this study have been deposited in GenBank (with accession numbers KC463857–KC463889).

Phylogenetic analysis and character optimization: We downloaded cytochrome-*b* sequences representing 14 non-erethizontid hystricognath genera from GenBank to use as outgroups in our phylogenetic analyses: *Hystrix* (GenBank accession FJ472565), *Bathyergus* (AF012241), *Cryptomys* (AF012233), *Thryonomys* (AJ301644), *Capromys* (AF422915), *Cavia* (AY382790), *Ctenomys* (AF370680), *Dasyprocta* (AF437784), *Galea* (GU067494), *Microcavia* (GU067490), *Myocastor* (AF422919), *Myoprocta* (AF437781), *Octodon* (AF007058), and *Proechimys* (AJ251400). Sequences were aligned using the MUSCLE algorithm (Edgar et al., 2004) as implemented in Genious ver. 5.6 (Drummond et al., 2011).

We analyzed our aligned sequence data using maximum parsimony (MP) and maximum likelihood (ML) methods. To reduce computational time for the MP analysis, we first deleted 16 of 19 nearly identical sequences (differing by <1%) of *C. prehensilis*; we chose the two individuals with the longest sequences (AMNH 262274 and USNM 528360, each 1140 bp long) as well as the specimen from Pernambuco (MN 73383; 801bp) to represent the genetic diversity of this clade. We analyzed this abbreviated (43-terminal) dataset using 20 replicates of random-taxon addition heuristic tree searches with TBR branch swapping as implemented by PAUP* ver. 4.0b10 (Swofford, 2003). To estimate nodal support under the MP criterion, we performed tree searches on 500 bootstrap replicates using 3 replicates of random-taxon addition and TBR branch swapping for each bootstrap replicate. For ML analysis, we used the full (59-terminal) dataset (including all 19 *C. prehensilis* sequences). We first determined the best-fitting model of sequence evolution using MrModelTest ver. 2.3 (Nylander, 2004). We specified the resulting model in two independent runs of maximum-likelihood tree searching using GARLi 2.0 (Zwickl, 2006), with two search replicates for each run and all other parameters set as defaults. To obtain estimates of nodal support, we used RaXML ver. 7.2.8 as implemented on the RAxML BlackBox web server (Stamatakis et al., 2008) to perform 500 replicates of rapid bootstrapping.

To obtain a time-scaled ultrametric phylogeny we employed Bayesian searches under a relaxed molecular clock model as implemented in BEAST ver. 1.7.2 (Drummond and Rambaut 2007; Drummond et al. 2006). We specified an HKY+Γ+I model of nucleotide substitiution with default priors, a Yule speciation process with a prior birth rate of 0.1, and a lognormal relaxed-clock model with mean = 0.01 and standard deviation = 0.333. We set a prior constraint on the height of the node defining Caviomorpha to have a normal distribution with a mean of 34.1 MYA and standard deviation of 3.5 MYA. This prior was based on the inferred mean date of origin (and associated error estimate) for crown-group Caviomorpha from a recent multilocus phylogenetic study of hystricognaths (Upham and Patterson, 2012). We performed 10 million generations of MCMC searches, with trees saved every 1000 generations and used Tracer ver. 1.5 (Rambaut and Drummond, 2007) to examine posterior parameter estimates and other output from the MCMC run.

We reconstructed the evolution of three discrete morphological traits on our time-scaled molecular phylogeny by coding binary traits for the 13 erethizontid species included in our study. To optimize character-state evolution, we trimmed our time-scaled molecular phylogeny to the species level, and used maximum-likelihood estimation under an equal-rates model of character evolution (Pagel, 1994) as implemented in the *ace()* command of the R-package APE 3.0-5 (Paradis et al., 2004). We reconstructed erethizontid biogeographic history using maximum-likelihood optimization under the the Dispersal-Extinction-Cladogenesis model implemented in the Python package LaGrange (Ree and Smith, 2008). We used the same time-scaled species-level tree that we used for morphological character optimization, but coded each terminal taxon as occupying one or more of three discrete areas. Dispersal among areas was unconstrained, but lineages were not allowed to occupy more than two areas (the maximum area occupancy observed among Recent species).

RESULTS

The 45 ingroup cytochrome-*b* sequences we analyzed range in length from 259 to 1140 bp (tables 2, 3), and no insertion-deletion events were required to align these or the 14 outgroup sequences that we obtained from GenBank, resulting in an aligned matrix with a total of 59 terminals. For parsimony analysis we removed 16 nearly identical sequences of *C. prehensilis* to yield a dataset with 43 terminals. There were 500 parsimony-informative characters in this reduced matrix, and tree searches resulted in 14 minimum-length trees (length = 2892; CI = 0.342; RI = 0.558) with the strict consensus shown in figure 3. For maximum-likelihood analyses we used the complete dataset of 59 terminals. Comparisons among 24 models of nucleotide substitution using the Akaike information criterion indicated that GTR+I+Γ was the best-fitting model for this dataset (table 5). Two independent searches using GARLi resulted in trees with identical topologies and likelihood scores (lnL = -12848.85; fig. 4).

Species limits, distance comparisons, and phylogeography: The monophyly of all erethizontid species represented by multiple terminals in our analyses (*Coendou prehensilis*, *C. spinosus*, *C. bicolor*, *C. quichua*, *C. nycthemera*, and *C. melanurus*) was strongly supported
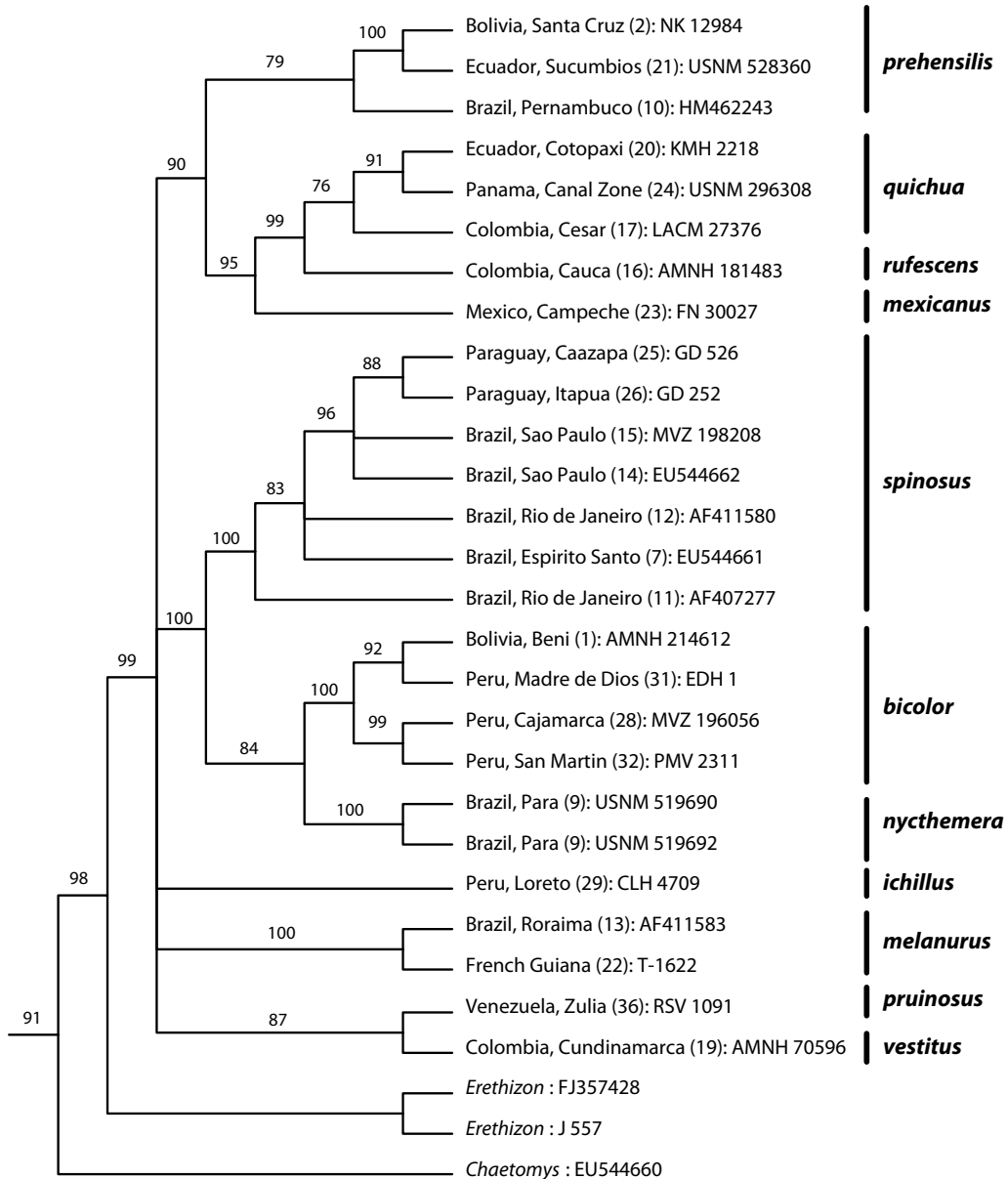
FIG. 3. Strict consensus of 14 equally most-parsimonious trees for 29 unique erethizontid cytochrome-*b* haplotypes (only ingroup relationships are shown). Sequenced specimens of *Coendou* are identified by country of origin, next-largest political unit (state, department, or province), collection locality number (mapped in fig. 1), and an alphanumeric identifier (tissue, voucher, or GenBank accession number; see tables 2 and 3). Nodal support values are bootstrap percentages.

(bootstrap > 75%) by both maximum-parsimony and maximum-likelihood analyses. Additionally, uncorrected mean intraspecific distances (table 6) for these taxa are well within the range of variation commonly observed for mammalian species, from 0.9% (in *C. prehensilis*) to 3.4% (in *C. quichua*), with an average value of 1.9%. By contrast, uncorrected interspecific distances

TABLE 5. Estimated Substitution Parameters
of the GTR+I+Γ Model

r(AC)[a]	0.182
r(AG)[a]	8.369
r(AT)[a]	0.515
r(CG)[a]	0.795
r(CT)[a]	5.655
r(GT)[a]	1.000
π (A)[b]	0.360
π (C)[b]	0.317
π (G)[b]	0.054
π (T)[b]	0.268
alpha[c]	0.657
P_{inv}[d]	0.407

[a] Substitution rates between nucleotides.
[b] Proportion of each nucleotide.
[c] The alpha parameter describes the shape of the
   gamma distribution.
[d] Proportion of invariant sites.

observed in this study range from 3.5% (between *C. pruinosus* and *C. vestitus*) to 12.1% (between *C. nycthemera* and *C. prehensilis*), with an average value of 9.1%.

Intraspecific haplotype variation is geographically structured in several species, notably *Coendou spinosus*, in which a northeast-to-southwest sequence links samples from coastal Brazil to those from Paraguay. In *C. bicolor*, samples from adjacent localities in northern Peru cluster together, as do samples from adjacent localities in southern Peru and northern Bolivia. In both of these examples, patterns of haplotype coalescence closely correspond to geographic expectations, but sequences of *C. quichua* from distant localities in Panama and western Ecuador are (anomalously) more closely related to one another than either is to a geographically intermediate sample from northern Colombia.

Remarkably, our samples of *Coendou prehensilis* consist of a single genetically divergent sequence from eastern Brazil (Pernambuco, locality 10) and a tight cluster of nearly identical sequences from 13 localities scattered throughout the rest of tropical South America. In this case, the tabulated mean intraspecific distance (0.9%) conceals substantial sequence heterogeneity, because HM462243 (the sequence from from Pernambuco) differs from other sequences of *C. prehensilis* by an average distance of 4.6%, whereas the latter differ among themselves by an average distance of just 0.5%.

Phylogenetic relationships: Parsimony and likelihood analyses both provide very strong support (bootstrap > 90%) for erethizontid monophyly (*Chaetomys* + *Erethizon* + *Coendou*) and for erethizontine monophyly (*Erethizon* + *Coendou*). Parsimony also provides very strong support for the monophyly of *Coendou*, but support for generic monophyly from maximum likelihood is notably weaker (83%). Because the species of *Coendou* (sensu Alberico et al., 1999; Voss, 2011) were formerly classified in three genera (see above), we used a likelihood-ratio test (Shimodaira and Hasegawa, 1999) to compare the topology in figure 4 with the alternative hypothesis that *Coendou* (sensu lato), *Sphiggurus*, and *Echinoprocta* are reciprocally monophyletic.[3] The resulting test statistic suggests that our sequence data are significantly (ΔlnL = 139.91; *P* = 0.000) less likely under the latter hypothesis, which can be rejected on this basis.

Although parsimony and likelihood analyses recovered different patterns of relationships among species of *Coendou*, all of the discrepant relationships are weakly supported. For exam-

---

[3] In the context of this test, *Coendou* (sensu lato) is equivalent to the group *bicolor* + *nycthemera* + *prehensilis* + *quichua*, *Sphiggurus* is equivalent to the group *ichillus* + *melanurus* + *mexicanus* + *pruinosus* + *spinosus* + *vestitus*, and *Echinoprocta* is equivalent to *rufescens* (table 1).
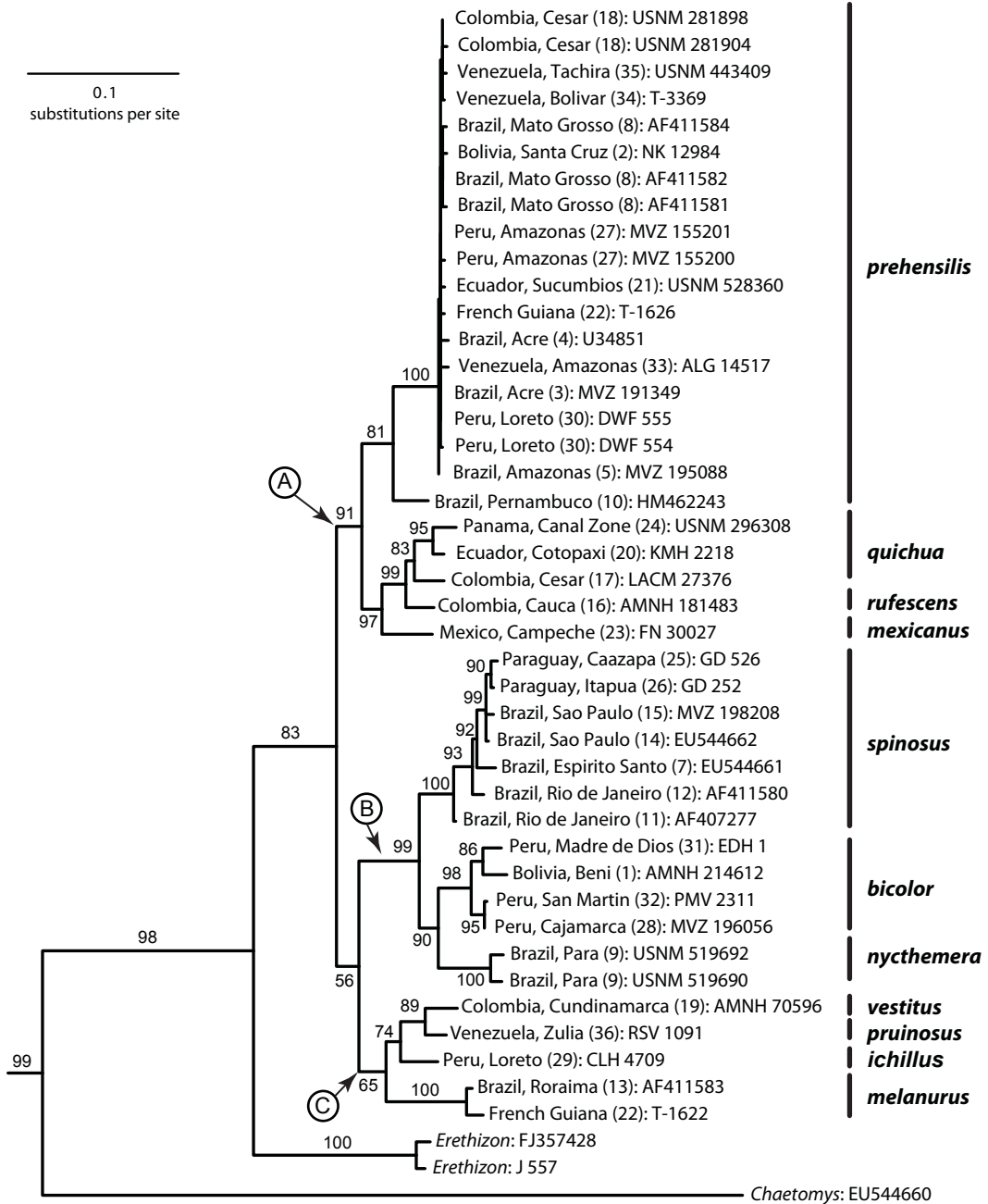
FIG. 4. Maximum-likelihood phylogeny for 45 ingroup (erethizontid) terminals; outgroup taxa are not shown. Labeling conventions and nodal support statistics are the same as in figure 3. Capital letters (A, B, C) indicate unnamed clades discussed in the text.

TABLE 6. Mean Uncorrected Cytochrome-*b* Distances (scaled as percent sequence divergence; below diagonal) and Mean K2P-corrected Distances (above diagonal) among Sequenced Species of *Coendou*[a]

	bicolor	*ichillus*	*melanurus*	*mexicanus*	*nycthemera*	*prehensilis*	*pruinosus*	*quichua*	*rufescens*	*spinosus*	*vestitus*
bicolor	**2.3**	10.0	10.7	12.0	7.0	12.1	11.6	13.0	12.3	7.7	10.9
ichillus	9.1	—	7.0	10.7	11.5	9.7	4.8	10.7	10.1	10.2	5.6
melanurus	9.7	6.5	**1.3**	11.1	11.2	9.9	7.2	10.9	11.3	11.0	7.4
mexicanus	10.7	9.6	10.1	—	12.5	6.6	11.0	7.1	6.0	11.9	10.3
nycthemera	6.6	10.4	10.2	11.1	**1.6**	10.8	10.8	12.9	13.5	8.0	13.2
prehensilis	10.8	10.8	10.8	7.1	12.1	**0.9**	8.1	9.0	8.2	11.6	9.5
pruinosus	10.5	4.6	6.8	10.0	9.8	7.6	—	9.6	9.6	10.2	3.6
quichua	11.5	9.7	9.9	6.6	11.5	8.3	8.9	**3.4**	4.5	12.1	11.0
rufescens	11.0	9.2	10.2	5.7	11.9	7.6	8.9	4.3	—	11.5	11.4
spinosus	7.2	9.3	10.0	10.7	7.5	10.5	9.3	10.8	10.4	**2.0**	10.0
vestitus	9.9	5.3	6.9	9.4	11.7	8.7	3.5	9.9	10.3	9.1	—

[a] Diagonal elements (in boldface) are mean intraspecific distances.

FIG. 5. *Coendou prehensilis* (INPA 2875), the type species of *Coendou*. This is a long-tailed species that appears completely spiny because the quills conceal its short, sparse fur.

FIG. 6. *Coendou melanurus* (AMNH 266565), referred to *Sphiggurus* by Husson (1978) and other authors. This is a long-tailed species in which the quills are concealed beneath long, dense fur.

FIG. 7. *Coendou rufescens* (FMNH 88524), previously referred to *Echinoprocta* by many authors. This is a short-tailed species that (like *C. prehensilis*) appears completely spiny because the quills conceal its short, sparse fur.
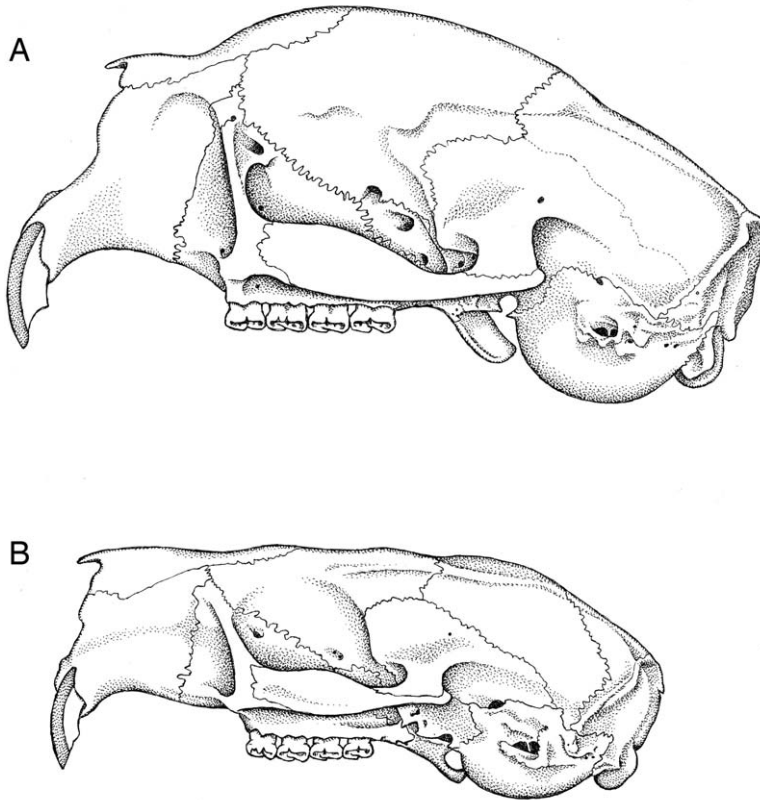
FIG. 8. Lateral cranial views: **A,** *Coendou prehensilis* (AMNH 134064); **B,** *C. melanurus* (AMNH 266565). The inflated nasofrontal sinuses of *C. prehensilis* (type species of the genus *Coendou*) result in a strongly convex dorsal profile by contrast with the flat dorsal profile of *C. melanurus* (referred to *Sphiggurus* by some authors; see text). Both skulls are life size (×1).

ple, parsimony recovered *melanurus*, *ichillus*, and *pruinosus + vestitus* as separate lineages in an unresolved basal polytomy, whereas likelihood recovered the same taxa as a weakly supported group (clade C in fig. 4). By contrast, both parsimony and likelihood provide strong support for two nested sets of relationships, one (clade A) consisting of (*prehensilis* (*mexicanus* (*rufescens + quichua*))), and the other (clade B) consisting of (*spinosus* (*bicolor + nycthemera*)). In the maximum-likelihood topology, clades B and C are weakly resolved as sister taxa.

DISCUSSION

The monophyly of Erethizontidae (*Chaetomys + Coendou + Erethizon*) is a noncontroversial result previously obtained from phylogenetic analyses of cytochrome-*b* sequence data by Vilela et al. (2009). The alternative hypothesis—implicit in classifications that formerly referred *Chaetomys* to the family Echimyidae (e.g., Miller and Gidley, 1918; Patterson and Wood, 1982)—has now been so convincingly refuted by multiple lines of evidence (Martin, 1994; Carvalho, 2000) that it no longer merits serious attention. The monophyly of Erethizontinae

TABLE 7. Selected Morphological Traits of 11 Species of *Coendou*[a]

	Dorsal fur	LT/HBL[b]	Nasofrontal sinuses	MTR (mm)[c]
bicolor	short & sparse	ca. 90–105%	inflated	20.1 (19.4–21.3) 9
ichillus	short & sparse	ca. 85%	not inflated	14.4 (14.0–15.2) 3
melanurus	long & dense	ca. 95%	not inflated	17.6 (15.7–19.4) 7
mexicanus	long & dense	ca. 65–80%	inflated[d]	19.6 (18.2–21.8) 26
nycthemera	short & sparse	ca. 90%	not inflated	15.3 (14.1–16.3) 25
prehensilis	short & sparse	ca. 100%	inflated	20.1 (18.6–22.2) 26
pruinosus	long & dense	ca. 50–70%	not inflated	15.1 (14.3–15.8) 12
quichua	short & sparse	ca. 55–90%	not inflated	17.8 (16.8–18.6) 29
rufescens	short & sparse	ca. 40%	not inflated	17.5 (16.7–19.2) 13
spinosus	long & dense	ca. 75%	not inflated	15.9 (15.1–17.0) 23
vestitus	long & dense	ca. 50%	not inflated	15.5 (14.7–16.4) 7

[a] Tabulated traits are modal conditions (the phenotype observed in most examined specimens) for species included in this study.

[b] Mean length of tail (LT) divided by mean head-and-body length (HBL) × 100, rounded to the nearest 5%. Apparently erroneous collector's measurements were omitted from the data used to calculate these values. Data are from Voss and Angermann (1997), Voss and da Silva (2001), Voss et al. (2001), and Voss (2011). Ranges are provided for species with noteworthy geographic variation (in each example, short-tailed populations are montane and long-tailed populations are from foothills or lowlands).

[c] Adult maxillary toothrow length (a proxy for size). Tabulated sample statistics include the mean, the observed range (in parentheses) and the sample size. Data are from Voss and Angermann (1997), Voss and da Silva (2001), Voss et al. (2001), and Voss (2011).

[d] In Mexican populations represented by analyzed sequence data; see Voss (2011) for remarks on geographic variation.

(*Erethizon* + *Coendou*), likewise recovered from a previous analysis of cytochrome-*b* sequence data (Vilela et al., 2009), is also noncontroversial.

By contrast, the generic classification of the Neotropical erethizontines variously referred by authors to *Coendou*, *Echinoprocta*, and *Sphiggurus* is fraught with controversy. Species referred to these genera differ in size and in qualitative external and craniodental characters (figs. 5–8; table 7). Because nomenclatural aspects of Neotropical erethizontid generic taxonomy have been reviewed elsewhere (Tate, 1935; Alberico et al., 1999), we limit our discussion to evidential support for monophyletic groups in the paragraphs that follow.

Generic Classification

Our results provide no support for the continued recognition of *Echinoprocta* and *Sphiggurus* as those taxa have traditionally been understood by authors (e.g., Cabrera, 1961; Husson, 1978; Honacki et al., 1982; Woods, 1984; Woods and Kilpatrick, 2005). As noted by Ellerman (1940) and White (1970), "*Echinoprocta*" *rufescens* is craniodentally indistinguishable from ordinary *Coendou*. Authors who recognize *Echinoprocta* as a valid genus emphasize its uniquely short and allegedly nonprehensile tail, but computed ratios of tail to head-and-body length (table 7) suggest that *rufescens* is simply the shortest-tailed member of a clade that exhibits continuous taxonomic

variation in this proportion. Additionally, most specimens of *rufescens* have a nearly hairless dorsal callus at the tip of the tail, suggesting that this stubby organ normally retains some prehensile ability (Alberico et al., 1999). Our phylogenetic analyses recovered *rufescens* as the sister taxon of *C. quichua*, montane populations of which are also short-tailed (Voss, 2011). Because recognizing a monotypic genus for *rufescens* would render *Coendou* nonmonophyletic, the continued recognition of *Echinoprocta* at any taxonomic rank is indefensible.

Modern recognition of *Sphiggurus* dates from Ellerman (1940), who ranked it as a subgenus of *Coendou*. According to Ellerman (1940: 185), members of the subgenus *Coendou* have "spines not mixed with hairy covering," whereas members of the subgenus *Sphiggurus* have "spines mixed with and typically covered by long woolly hair." Cabrera (1961) maintained Ellerman's subgeneric classification, but Husson (1978: 488) decided that two species of Surinamese porcupines "differ so strongly both in external and skull characters that their [generic] separation seems fully justified" and ranked *Sphiggurus* as a full genus. Although Husson provided detailed morphological comparisons of these two species—*C. prehensilis* (figs. 5, 8A) and "*S.*" *melanurus* (figs. 6, 8B)—he did not explain which of the characters that distinguish them serve to diagnose *Sphiggurus* from *Coendou* as supraspecific taxa, nor has any subsequent author who adopted Husson's generic taxonomy (e.g., Honacki et al., 1982; Woods, 1984). As noted by Handley and Pine (1992), the characters that differ between Husson's exemplar species are not consistently correlated among other Neotropical porcupines and cannot be used jointly to diagnose higher taxa. In fact, "*Sphiggurus*" (sensu Woods, 1984, 1993; Woods and Kilpatrick, 2005) is not diagnosable by any known morphological criterion (Voss, 2011).

Our phylogenetic results clearly indicate that *Sphiggurus* (as recognized by Ellerman, 1940; Cabrera, 1961; Honacki et al., 1982; Woods, 1984; Woods, 1993; Woods and Kilpatrick, 2005) is not monophyletic. Additionally, the principal morphological characters that differ between Husson's exemplar species of *Sphiggurus* and *Coendou* appear to have evolved homoplasiously in erethizontids (see below). As we have pointed out elsewhere (Voss, 2011), previous analyses of cytochrome-*b* sequence data alleged to support the reciprocal monophyly of *Sphiggurus* and *Coendou* (Bonvicino et al., 2002; Vilela et al., 2009) were compromised by taxonomic misidentifications of voucher specimens.

Nevertheless, it is true that *prehensilis* (the type species of *Coendou*) and *spinosus* (the type species of *Sphiggurus*) belong to different lineages (clades A and B; fig. 4) that could validly be recognized as genera or subgenera. We see no purpose in doing so, however, because (1) neither clade seems to be morphologically diagnosable; (2) employing *Sphiggurus* in a completely different sense than that established by traditional usage would create needless confusion in the taxonomic literature with no compensatory advantage for scientific communication; and (3) a new generic name would then be needed for clade C, which remains weakly supported by available sequence data.

<div align="center">SPECIES LIMITS</div>

Phylogenetic analyses of cytochrome-*b* sequence data provide welcome support for several species concepts resulting from recent revisionary work. In particular, our results are consistent with the synonymy of lowland Panamanian populations that Thomas (1902) described as *Coen-*

dou rothschildi (represented by USNM 296308) with Ecuadorean material referable to *C. quichua* (represented by KMH 2218) as suggested by Voss (2011), and they refute previous concepts of *C. bicolor* that included *quichua* as a subspecies (Cabrera, 1961; Woods and Kilpatrick, 2005). Additionally, these data suggest the essential genetic continuity of long-furred porcupines from Paraguay to Rio de Janeiro, all of which should be referred to *C. spinosus* (as recommended by Voss, 2011; Junior and Leite, 2012), by contrast with the taxonomies suggested by Moojen (1952), Woods and Kilpatrick (2005), and others who recognized multiple species in this complex. Lastly, our results are consistent with the recognition of *C. melanurus* as a distinct Amazonian species (Voss and Angermann, 1997; Voss et al., 2001; Bonvicino et al., 2002), rather than as a subspecies (Cabrera, 1961) or synonym (Husson, 1978) of southeastern Brazilian taxa.

We made a particular effort to obtain sequence data from as many geographic localities as possible for *Coendou prehensilis*. Among the nominal taxa currently treated as synonyms of this widespread species, we analyzed sequences representing *boliviensis* (NK12984), *centralis* (AF411581, AF411582, AF411584), *longicaudatus* (T-1626), and *sanctaemartae* (USNM 281898, 281904). Additionally, we included sequence data from specimens previously misidentified as *C. bicolor* (see Voss, 2011) from eastern Ecuador (USNM 528360), northeastern Peru (MVZ 155200, 155201), western Brazil (MVZ 191349, U34851), and southwestern Venezuela (USNM 443409).

Although both parsimony and likelihood analyses provide strong support for the monophyly of *Coendou prehensilis*, it is noteworthy that the most divergent sequence we analyzed is HM462243, an 801 bp fragment that Leite et al. (2011) obtained from the recently designated neotype (MNRJ 73383). We have not examined this specimen, but Leite et al.'s exemplary description and illustrations match other material that we refer to *C. prehensilis* in most external and craniodental characters. However, the neotype has a smaller hind foot (76 mm) than any we have measured for this species (82–105 mm; Voss, 2011: table 7), and it has a narrower fourth premolar (4.9 mm versus 5.3–6.4 mm). Additional material from Pernambuco would be useful to put these unusual values in statistical perspective, but such comparisons—and others that can be made based on measurements in Leite et al. (2011) and Voss (2011)—suggest that the neotype is unusually small for Brazilian specimens traditionally referred to *C. prehensilis*.

The oldest available name that could be used for other geographic populations currently referred to *Coendou prehensilis* is *longicaudatus* Daudin, 1802, which was based on specimens from Cayenne, French Guiana. As no type material is known to exist (Rode, 1945), it would be sensible to designate a neotype if this taxon were to be recognized in any future revision of *Coendou*. The French Guianan voucher represented by sequence data in our analysis (MNHN 1997.643) is an obvious candidate for neotype designation.

<div align="center">OTHER RELATIONSHIPS</div>

The only clade recovered in our analyses that corresponds to a previously recognized group of *Coendou* species is the cluster of *vestitus*, *pruinosus*, and *ichillus* (in the ML tree; fig. 4), comprising part of the "Vestitus Group" of Voss and da Silva (2001). The missing member of the Vestitus Group is *roosmalenorum*, tissues of which were not obtained for this study. These species differ from other congeners by having bristle quills (long, wirelike, nondefensive quills)

in addition to the usual defensive quills and soft fur in their dorsal pelage (Voss and da Silva, 2001: fig. 1). Interestingly, the sister taxon to the Vestitus Group in our likelihood analysis, *Coendou melanurus*, also has three distinct structures in its dorsal pelage: defensive quills, soft fur, and yellow-tipped guard hairs (the latter producing the streaked effect seen in the dorsal pelage of this species; fig. 6). The guard hairs of *melanurus* are much finer and more flexible than the bristle-quills seen in members of the Vestitus Group, but it now seems plausible that these pelage structures are homologous.

The very strongly supported sister-group relationship that we recovered between *Coendou bicolor* and *C. nycthemera* contradicts Handley and Pine's (1992) hypothesis that *nycthemera*—a short-furred Amazonian species—is more closely related to the long-furred *C. spinosus* from the Atlantic forest of southeastern Brazil. Waterhouse (1848: 418–419) suspected that *bicolor* and *nycthemera* might be synonyms, but these taxa differ in size (indexed by toothrow measurements in table 7), nasofrontal sinus inflation, and cytochrome-*b* sequences (ca. 6.6%), so their current status as distinct species seems adequately supported. Although *C. spinosus* was recovered as the sister taxon of this pair, we suspect (based on morphology) that clade B will eventually prove to consist of ((*spinosus* + *insidiosus*) (*bicolor* + *nycthemera*)) when sequence data from *C. insidiosus* are analyzed.

Because *Coendou mexicanus*, *C. quichua*, and *C. rufescens* differ conspicuously in pelage and cranial traits, their close relationship was previously unsuspected. Nevertheless, this cluster makes sense biogeographically (see below), and we are not aware of any strongly contradictory evidence. Indeed, the genetic distance between *C. quichua* and *C. rufescens* (table 6) seems remarkably small given the traditional placement of these species in different genera. The sister-group relationship of *C. prehensilis* to this cluster is another unanticipated result, and one that merits testing with additional sequence data in future studies.

Morphological Evolution

Visually conspicuous morphological differences among Recent species of *Coendou* include variation in size, fur length and density, quill coloration, relative tail length, and nasofrontal sinus inflation[4] (Voss and Angermann, 1997; Voss and da Silva, 2001; Voss, 2011). As discussed above, Husson (1978) was so impressed by the differences he observed between *Coendou prehensilis* (a large, short-furred porcupine with inflated sinuses; figs. 5, 8A) and *C. melanurus* (a small, long-furred porcupine with uninflated sinuses; figs. 6, 8B) that he assigned these species to different genera. However, other porcupines exhibit trait combinations that make generic assignments problematic. *Coendou quichua*, for example, has short fur (and therefore appears completely spiny like *C. prehensilis*), but it is a small species with uninflated nasofrontal sinuses (like *C. melanurus*).

---

[4] The cranial structure responsible for the prominent convexity variously described as a "high dorsal hump" (Husson, 1978: 486) or "bulbous forehead" (Handley and Pine, 1972: 242) in some Neotropical porcupines is a pneumatic sinus that invades the substance of both the nasal and frontal bones. Sectioned skulls (e.g., USNM 36927) reveal that this sinus is divided by an unossified midsagittal septum and communicates with the nasal cavity by paired ventrolateral orifices.

Similarly, *C. mexicanus* has long fur (that conceals the underlying quills like *C. melanurus*), but it is a large species that usually has inflated nasofrontal sinuses (like *C. prehensilis*).

To explore historical patterns of phenotypic evolution among Recent erethizontids, we coded size, nasofrontal sinus inflation, and dorsal fur morphology for phylogenetic analysis. Lacking other suitable proxy measures of size (weight data, for example, are missing for several taxa), we scored species of *Coendou* as "small" if they had maxillary tooth rows < 18 mm or "large" if they had maxillary tooth rows > 19 mm (table 7). *Erethizon* (with maxillary tooth rows > 22 mm; Stangl et al., 1991) has teeth that are occlusally similar to those of *Coendou*, so this taxon can be scored for size by the same criterion. However, the laminar cheek teeth of *Chaetomys* are disproportionately longer and narrower than those of *Coendou*, so we scored this taxon based on other measurements (e.g., posterior zygomatic breadth; Voss and Angermann, 1997) and published weights (in Chiarello et al., 1997) that place it well within the size range of "small" species of *Coendou*.

We coded the nasofrontal sinuses of *Coendou* species as "inflated" or "not inflated" based on obvious external differences in cranial morphology (fig. 8). As noted elsewhere (Voss, 2011), the nasofrontal sinuses of *C. mexicanus* are geographically variable, but the modal sinus condition in this taxon (illustrated by Hall, 1980: fig. 501)—and the phenotype represented by material sequenced for this study—is inflated. The nasofrontal sinuses of *Erethizon* and *Chaetomys* are not inflated (for cranial illustrations, see Ellerman, 1940: figs. 43, 47).

We coded the dorsal fur of *Coendou* species as "long & dense" if it conceals the quills (fig. 6) or as "short & sparse" if it does not (figs. 5, 7). The length and density of the dorsal fur of *Erethizon* is seasonally variable (Po-Chedley and Shadle, 1955) and probably also varies with latitude and elevation, but the typical pelage morphology of this taxon more closely resembles the "long & dense" phenotype than it does the "short & sparse" condition. By contrast, the dorsal fur of *Chaetomys* is unambiguously short and sparse (Oliver and Santos, 1991: pl. 7; Voss and Angermann, 1997: fig. 8).

Maximum-likelihood optimizations (fig. 9) suggest that each of these characters has evolved homoplasiously in the erethizontid crown clade, but ancestral-state assignments are ambiguous at many internal nodes. This ambiguity has the unfortunate effect that different combinations of reversal and convergence are often equiprobable as alternative explanations for observed taxonomic differences. In particular, ambiguous state assignments for the last common ancestor of Recent erethizontids and for the last common ancestor of erethizontines (the two basalmost nodes of each tree in fig. 9) make it difficult to choose among alternative reconstructions of morphological evolution on the long branches that separate *Chaetomys*, *Erethizon*, and *Coendou*. Within *Coendou*, however, some probabilistic inference is possible.

SIZE AND SINUS INFLATION: Large size and nasofrontal sinus inflation are identically distributed among Recent species of *Coendou*, so it is not surprising that analyses of these traits yield similar patterns of ancestral-state probabilities. Based on our results, it seems likely that the last common ancestor of *Coendou* was a small species with uninflated nasofrontal sinuses, and that large size and inflated sinuses evolved convergently in *Coendou bicolor* and in clade A (*prehensilis + mexicanus + rufescens + quichua*). In the latter group, ancestral-state probabilities marginally favor the hypothesis that large size and inflated
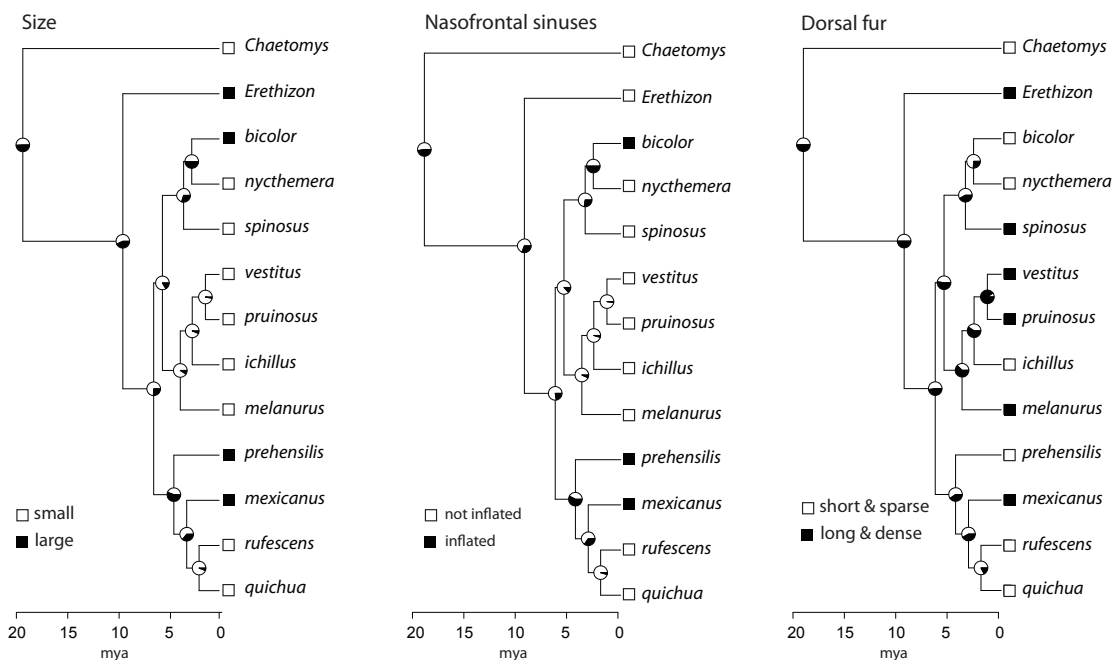
FIG. 9. Maximum-likelihood reconstructions of ancestral phenotypes for three morphological characters of Recent erethizontids. Branch tips representing species of *Coendou* are labeled with corresponding epithets only. See text for character definitions and scoring criteria and table 8 for divergence-date estimates. Pie diagrams at internal nodes represent estimated probabilities of alternative states.

sinuses evolved once (in a common ancestor) with a subsequent reversal to small size and uninflated sinuses on the branch leading to *C. rufescens* and *C. quichua*. However, it is almost equally likely that the common ancestor of clade A was small and had uninflated sinuses, in which case large size and sinus inflation must have evolved convergently in *C. prehensilis* and *C. mexicanus*.

Although these observations suggest that large size and nasofrontal sinus inflation might be developmentally or functionally correlated, it is noteworthy that *Erethizon* (the largest living erethizontid) does not have inflated sinuses, nor did some large fossil erethizontids (e.g., *Hypsosteiromys* from the early Miocene of Argentina; Dozo et al., 2004). Convincing explanations for the evolution of mammalian cranial sinuses are elusive (Moore, 1981: 277–279), perhaps because sinuses have different functions in different clades. To the best of our knowledge, no hypothesis about the functional significance of nasofrontal sinus inflation among New World porcupines has been suggested, but we hypothesize that this trait might help protect the soft tissues of the head from attacking predators.

Functional analyses of porcupine quill erection (Chapman and Roze, 1997) suggest that these defensive spines can only be erected to an angle of about 90° from the underlying dermal surface, so fully erected quills on a flat skull can only stick straight up. Nasofrontal sinus inflation increases the cranial surface area for quill deployment and allows erected quills to point anteriorly and laterally (fig. 10), effectively protecting the eyes and nose. High in the canopy,

FIG. 10. *Coendou prehensilis* with erected cranial quills. The inflated nasofrontal sinuses of this species provide increased surface area for quill deployment, and their convex margins allow erected quills to point anteriorly and laterally to protect adjacent soft tissues. Photographed at the Frankfurt Zoo in 2008 (courtesy of Marek Polster).

Neotropical porcupines are perhaps safe from most nonavian predators, but they are probably more vulnerable on the ground. Swollen nasofrontal sinuses may confer an adaptive advantage for *Coendou* species that often descend to the ground for geophagy (Montenegro, 2004; Blake et al., 2011) or to cross canopy gaps (Montgomery and Lubin, 1978), where they might be exposed to terrestrial predators such as pumas (Chinchilla, 1997; Novack et al., 2005; Foster et al., 2010) and large boas (Cherubini et al., 2003; Duarte, 2003).

PELAGE: Reconstructions of dorsal fur evolution in *Coendou* are minimally constrained by inferred ancestral-state probabilities. Parsimony analyses (not shown) indicate that at least four state transformations are necessary to explain observed taxonomic variation in dorsal-fur morphology among *Coendou* species, but many alternative scenarios of convergence and reversal are almost equally likely and it would be pointless to enumerate all of them here. Clearly, however, dorsal-fur character-state transformations have occurred rather frequently in the genus, and it would be interesting to know why.

The reason is not immediately obvious. Although fur length and/or density seem to vary with elevation within some widespread species (e.g., *Coendou mexicanus*; Voss, 2011), pelage traits are not correlated with elevation across species, as one might expect if the primary function of fur were thermoregulatory. Thus, porcupines with long/dense fur include both lowland species (e.g., *C. melanurus*) and highland species (*C. pruinosus*); likewise, porcupines with short/sparse fur include lowland species (*C. prehensilis*) and highland species (*C. rufescens*). Instead, taxonomic variation in fur length and density might result from divergent selection for aposematism versus crypsis, defensive adaptations that often involve evolutionary tradeoffs (Ruxton et al., 2004).

The black-and-white banding pattern of porcupine quills is a classic example of warning coloration (dangerous spines in many other animals are similarly colored; Inbar and Lev-Yadun, 2005; Speed and Ruxton, 2005; Caro, 2009). Openly displaying such weapons might be advantageous for deterring attacks by predators that kill by biting (e.g., felids; Emmons, 1987; Moreno et al., 2006), which must often result in a painful (or even lethal) mouthful of spines.

TABLE 8. Estimated Divergence Dates (millions of years) for Selected Erethizontid Clades

Crown clade	Mean[a]	Credibility interval[b]
Erethizontidae	19.1	12.8–27.1
Erethizontinae	9.4	5.9–13.9
Coendou	6.4	4.2–9.1
Clade A	4.4	2.8–6.6
Clade B	3.5	2.2–5.0
Clade C	3.8	2.3–5.8

[a] Calculated from the posterior distribution of node age estimates from Bayesian dating analysis.
[b] The 95% highest posterior density of node age estimates from Bayesian dating analysis

On the other hand, hiding quills under a long, thick coat of background-matching fur might be advantageous for avoiding detection by predators that kill with armored talons (e.g., harpy eagles; Izor, 1985; Piana, 2007), against which spines might be ineffective. Unfortunately, evidence of taxonomic variation in habits that expose porcupines to different sets of predators is almost entirely anecdotal, consisting of chance observations (e.g., fig. 11) that might not represent typical behaviors.

Biogeography

Recent erethizontids occur in lowland habitats either on the east or the west side of the Andes, but some are highland species (Voss, 2011). To explore erethizontid biogeographic history, we scored species as "cis-Andean" if they occur in lowland habitats east of the Andes, as "trans-Andean" if they occur in lowland habitats west of the Andes, or as "Andean" if they occur primarily in Andean landscapes (including adjacent foothills and piedmonts; table 1). For the purpose of this analysis we scored *Coendou bicolor* and *C. prehensilis* as cis-Andean species, despite the fact that an isolated montane population of *C. bicolor* occurs on the west side of the Andes in northern Peru (fig. 1: locality 28), and that an isolated lowland population of *C. prehensilis* occurs in northern Colombia west of the Serranía de Perijá (fig. 1: locality 18).

Maximum-likelihood modeling of geographic range evolution based on these data provides the first phylogeny-based reconstruction of erethizontid crown-clade biogeography (fig. 12). In this scenario, the last common ancestor of living erethizontids was an Early Miocene (ca. 19.1 Mya; table 8) cis-Andean species, but the erethizontine lineage (ancestral to *Erethizon* and *Coendou*) dispersed into the transAndean lowlands and subsequently split at about 9.4 Mya, giving rise to one trans-Andean daughter species ancestral to *Erethizon* and a second species, ancestral to *Coendou*, that was widespread in both cis- and trans-Andean lowlands. The latter split at about 6.4 Mya, producing a cis-Andean daughter species ancestral to clades B (*bicolor* + *nycthemera* + *spinosus*) and C (*vestitus* + *pruinosus* + *ichillus* + *melanurus*), and a widespread species ancestral to clade A (*prehensilis* + *mexicana* + *rufescens* + *quichua*). Whereas clade B

FIG. 11. Camera-trap photograph of two *Coendou bicolor* visiting a mineral lick near the Centro de Investigación Río Los Amigos, Madre de Dios, Peru (courtesy of Dyana LaRosa). In situations like this, porcupines are probably exposed to a greater risk of predation than they would be in the canopy. *Coendou prehensilis* is the only other Neotropical species known to frequent mineral licks (Montenegro, 2004; Blake et al., 2011).

remained cis-Andean, two dispersal events occurred in clade C: once into the trans-Andean lowlands and another, subsequently, into Andean landscapes. A basal split in clade A at about 4.4 Mya resulted in a cis-Andean species (*prehensilis*) and a trans-Andean lineage (*mexicana + rufescens + quichua*), one branch of which (*rufescens + quichua*) subsequently dispersed into the Andes.

This reconstruction of erethizontid crown-clade historical biogeography suggests that the cis- and trans-Andean lowlands have hosted more-or-less separate porcupine faunas since the Pliocene. From a Recent perspective, the persistence of a widespread (cis- and trans-Andean) lineage from about 10 to 5 Mya seems implausible, but the northern Andes did not reach their currently formidable elevations until about 3 Mya (Gregory-Wodzicki, 2000), so it is not impossible that one or more paleospecies maintained reproductive continuity across these mountains when they were substantially lower. Indeed, at least three Recent species (*Coendou mexicanus*, *C. pruinosus*, and *C. quichua*; Voss, 2011) have elevational ranges that are known to extend from near sea level to at least 2000 m, suggesting that the Andes were not insurmountable barriers to Miocene gene flow.
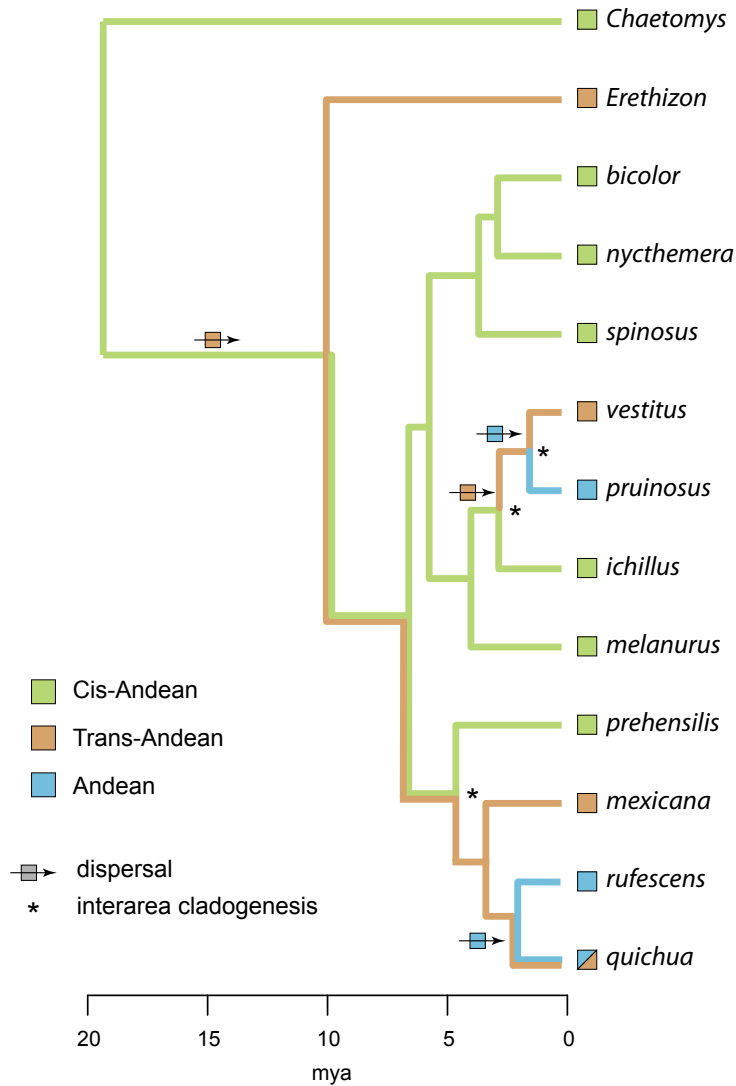
FIG. 12. Maximum-likelihood reconstruction of geographic range evolution for the erethizontid crown clade. See table 1 (footnote) for range descriptors and table 8 for divergence-date estimates.

Genetic Uniformity in a Widespread Species

The striking absence of phylogeographic structure and sequence divergence among samples of *Coendou prehensilis* representing populations that span 27° of latitude (northern Colombia to eastern Bolivia) and 25° of longitude (French Guiana to northern Peru) is among the most remarkable results of this study. Such genetic uniformity would seem to suggest either very recent range expansion or extensive contemporaneous gene flow. Both explanations imply that geographic or biotic barriers that inhibit dispersal in other porcupines are (or were) easily surmounted by *C. prehensilis*.

Most Neotropical porcupines are restricted to humid forests, but *Coendou prehensilis* also occurs in dry forests and savannas (Montgomery and Lubin, 1978; Parker et al., 1993; Emmons et al., 2006; Bruna et al., 2010) and seems to be more eurytopic than other congeneric species. Additionally, *C. prehensilis* may occupy a different trophic niche than other porcupines. Whereas field studies of *Chaetomys subspinosus* and *Coendou spinosus* suggest that these species are almost exclusively folivorous (Giné et al., 2010; Lima et al., 2010; Passamani, 2010), direct observations of feeding behavior by *C. prehensilis* suggests that this species feeds primarily on seeds from immature fruits (Charles-Dominique et al., 1981). Either or both of these ecological traits (eurytopy and granivory) might account, in part, for the broad geographic distribution of this species and its ability to coexist with other porcupines. Indeed, it is noteworthy that most species of *Coendou* are allopatric (possibly because they occupy the same trophic niche), whereas *C. prehensilis* accounts for almost all known examples of geographic range overlap and sympatry in the genus (table 9). An ecological niche shift followed by rapid range expansion is one scenario that might account for these observations.

Directions for Future Research

The phylogenetic analyses of this study are based on sequence data from a single mitochondrial gene, so obtaining additional data from other (preferably nuclear) loci is an obvious future priority. Also of interest would be the discovery of craniodental characters that could be used to place fossil and Recent erethizontids in a common phylogenetic framework and thereby provide internal constraints for future attempts to date key events in erethizontid phylogeny. Unfortunately, most craniodental characters known to vary among Recent erethizontids are either autapomorphies (e.g., the exceptionally deep jugal, well-developed postorbital processes, and laminar molars of *Chaetomys*), or they are so variable within species as to be effectively useless for phylogenetic analysis.

Another productive avenue for future research concerns erethizontid natural history, about which we remain profoundly ignorant. Although much fascinating detail is now available concerning key aspects of the behavior, physiology, and functional morphology of the North American porcupine (reviewed by Roze, 2009), available information about most Neotropical species is pitifully limited to chance observations and results from short-term field studies. Without reliable data about diet, activity patterns, dispersal ability, predation, and other relevant topics, the adaptive hypotheses suggested in this report will remain untested.

Lastly, we encourage field biologists to make greater efforts to collect porcupines. New species almost certainly remain to be discovered, and available sample sizes for some described species (e.g., *Coendou ichillus* and *C. roosmalenorum*; Voss and da Silva, 2001) are too small to support confident inference about size and other metrical traits. Because most porcupines are hard to observe even where they are locally common, advantage should be taken of rare opportunities (e.g., flooding by hydroelectric dams) to obtain large series.

TABLE 9. Geographic Relationships among Species of *Coendou*[a]

	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.
1. *bicolor*	–												
2. *ichillus*	A	–											
3. *insidiosus*	A	A	–										
4. *melanurus*	A	A	A	–									
5. *mexicanus*	A	A	A	A	–								
6. *nycthemera*	A	A	A	A	A	–							
7. *prehensilis*	O	O	O[b]	O[c]	A	O[d]	–						
8. *pruinosus*	A	A	A	A	A	A	O	–					
9. *quichua*	A	A	A	A	P[e]	A	O	A	–				
10. *roosmalenorum*	A	A	A	A	A	A	O	A	A	–			
11. *rufescens*	?	A	A	A	A	A	A	?	?	A	–		
12. *spinosus*	A	A	A	A	A	A	O[f]	A	A	A	A	–	
13. *vestitus*	A	A	A	A	A	A	A	A	A	A	?	A	–

[a] Table entries: A, allopatric; O, broad range overlap (frequent potential sympatry); P, parapatric (potential for narrow sympatry). See Voss (2011) for a synopsis of distributional data.
[b] Sympatric at several localities in SE Brazil (Oliver and Santos, 1991: appendix 1).
[c] Sympatric at several Guianan localities (e.g., Voss et al., 2001; Lim et al., 2005).
[d] Sympatric on Marajó Island and at Cametá (on the lower Tocantins; Handley and Pine, 1992).
[e] Sympatric at Boquete, in Chiriquí province, Panama (Voss, 2011).
[f] Sympatric at Lagoa Santa, Minas Gerais, Brazil (Voss, 2011).

ACKNOWLEDGMENTS

REFERENCES

Alberico, M., V. Rojas-Díaz, and J.G. Moreno. 1999. Aporte sobre la taxonomía y distribución de los puercosespines (Rodentia: Erethizontidae) en Colombia. Revista de la Academia Colombiana de Ciencias Exactas, Físicas, y Naturales 23 (suppl. esp.): 595–612.

Anderson, S. 1997. Mammals of Bolivia, taxonomy and distribution. Bulletin of the American Museum of Natural History 231: 1–652.

Blake, J.G., et al. 2011. Mineral licks as diversity hotspots in lowland forest of eastern Ecuador. Diversity 3: 217–234.

Bonvicino, C.R., V. Penna-Firme, and E. Braggio. 2002. Molecular and karyologic evidence of the taxonomic status of *Coendou* and *Sphiggurus* (Rodentia: Hystricognathi). Journal of Mammalogy 83: 1071–1076.

Bruna, E.M., et al. [nine other coauthors]. 2010. Mammalia, Estação Ecológica do Panga, a cerrado protected area in Minas Gerais state, Brazil. Checklist 6: 668–675.

Cabrera, A. 1961. Catálogo de los mamíferos de América del Sur. Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (Ciencias Zoológicas) 4 (2): v–xxii, 309–732.

Cadle, J.E. 1991. Systematics of lizards of the genus *Stenocercus* (Iguania: Tropiduridae) from northern Peru: new species and comments on relationships and distribution patterns. Proceedings of the Academy of Natural Sciences of Philadelphia 143: 1–96.

Caro, T. 2009. Contrasting coloration in terrestrial mammals. Philosophical Transactions of the Royal Society of London B Biological Sciences 364: 537–548.

Carvalho, G. 2000. Substitution of the deciduous premolar in *Chaetomys subspinosus* (Olfers, 1818) (Hystricognathi, Rodentia) and its taxonomic implications. Zeitschrift für Säugetierkunde 65: 187–190.

Chapman, D.M., and U. Roze. 1997. Functional histology of quill erection in the porcupine, *Erethizon dorsatum*. Canadian Journal of Zoology 75: 1–10.

Charles-Dominique, P., et al. 1981. Les mammifères frugivores arboricoles nocturnes d'une forêt guyanaise: inter-relations plantes-animaux. Revue d'Écologie (la Terre et la Vie) 35: 341–435.

Cherubini, A.L., T.H. Barrela, and R.J. da Silva. 2003. Death of *Boa constrictor amarali* (Serpentes, Boidae) after ingestion of a tree porcupine (Rodentia). Journal of Venomous Animals and Toxins, Including Tropical Diseases 9 (1): 117–124.

Chiarello, A.G., M. Passamani, and M. Zortéa. 1997. Field observations on the thin-spined porcupine, *Chaetomys subspinosus* (Rodentia: Echimyidae). Mammalia 61: 29–36.

Chinchilla, F.A. 1997. La dieta del jaguar (*Panthera onca*), el puma (*Felis concolor*) y el manigordo (*Felis pardalis*) (Carnivora: Felidae) en el Parque Nacional Corcovado, Costa Rica. Revista de Biología Tropical 45: 1223–1229.

D'Elía, G., I. Mora, P. Myers, and R.D. Owens. 2008. New and noteworthy records of Rodentia (Erethizontidae, Sciuridae, and Cricetidae) from Paraguay. Zootaxa 1784: 39–57.

DMA. 1988. Gazetteer of Colombia (3rd ed.). Washington, DC: Defense Mapping Agency.

Dozo, M.T., M.G. Vucetich, and A.M. Candela. 2004. Skull anatomy and neuromorphology of *Hypsosteiromys*, a Colhuehuapian erethizontid rodent from Argentina. Journal of Vertebrate Paleontology 24: 228–234.

Drummond, A.J., and A. Rambaut. 2007. BEAST: Bayesian evolutionary analysis by sampling trees. BMC Evolutionary Biology 7 (214). [doi:10.1186/1471-2148-7-214]

Drummond, A.J., S.Y.W. Ho, M.J. Phillips, and A. Rambaut. 2006. Relaxed phylogenetics and dating with confidence. PLoS Biology 4 (5). [doi: 10.1371/journal.pbio.0040088]

Drummond, A.J., et al. [14 coauthors]. 2011. Geneious v5.4. Internet resource (http://www.geneious.com/).

Duarte, M.R. 2003. Prickly food: snakes preying upon porcupines. Phyllomedusa 2: 109–112.

Edgar, R.C. 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. Nucleic Acids Research 32: 1792–1797.

Ellerman, J.R. 1940. The families and genera of living rodents, vol. 1. Rodents other than Muridae. London: Trustees of the British Museum (Natural History).

Emmons, L.H. 1997. Neotropical rainforest mammals, a field guide (2nd ed.). Chicago: University of Chicago Press.

Emmons, L.H., et al. 2006. The non-flying mammals of Noel Kempff Mercado National Park (Bolivia). Revista Boliviana de Ecología y Conservación Ambiental. 19: 23–46.

Fairchild, G.B., and C.O. Handley, Jr. 1966. Gazetteer of collecting localities in Panama. In R.L. Wenzel and V.J. Tipton (editors), Ectoparasites of Panama: 9–22. Chicago: Field Museum of Natural History.

Foster, R.J., B.J. Harmsen, B. Valdes, C. Pomilla, and C.P. Doncaster. 2010. Food habits of sympatric jaguars and pumas across a gradient of human disturbance. Journal of Zoology London 280: 309–318.

Gardner, A.L. (editor). 2008 ("2007"). Mammals of South America, Volume 1: Marsupials, xenarthrans, shrews, and bats. Chicago: University of Chicago Press.

Giarla, T.C., R.S. Voss, and S.A. Jansa. 2010. Species limits and phylogenetic relationships in the didelphid marsupial genus *Thylamys* based on mitochondrial DNA sequences and morphology. Bulletin of the American Museum of Natural History 346: 1–67.

Giné, G.A.F., J.M.B. Duarte, and D. Faria. 2010. Feeding ecology of a selective folivore, the thin-spined porcupine (*Chaetomys subspinosus*) in the Atlantic forest. Journal of Mammalogy 91: 931–941.

Gregory-Wodzicki, K.M. 2000. Uplift history of the central and northern Andes: a review. GSA Bulletin 112: 1091–1105.

Haffer, J. 1967. Speciation in Colombian forest birds west of the Andes. American Museum Novitates 2294: 1–57.

Hall, E.R. 1980. Mammals of North America. 2 vols., 2nd ed. New York: John Wiley.

Handley, C.O., Jr. 1976. Mammals of the Smithsonian Venezuelan Project. Brigham Young University Science Bulletin (Biological Series) 20 (5): 1–89, map.

Handley, C.O., Jr., and R.H. Pine. 1992. A new species of prehensile-tailed porcupine, genus *Coendou* Lacépède, from Brazil. Mammalia 56: 237–244.

Hanke, M., and M. Wink. 1994. Direct DNA sequencing of PCR-amplified vector inserts following enzymatic degradation of primer and dNTPs. BioTechniques 17: 858.

Honacki, J.H., K.E. Kinman, and J.W. Koeppl. 1982. Mammal species of the world, a taxonomic and geographic reference. Lawrence, KS: Allen Press.

Husson, A.M. 1978. The mammals of Suriname. Leiden: E.J. Brill.

Inbar, M., and S. Lev-Yadun. 2005. Conspicuous and aposematic spines in the animal kingdom. Naturwissenschaften 92: 170–172.

Izor, R.J. 1985. Sloths and other mammalian prey of the harpy eagle. In G.G. Montgomery (editor), The evolution and ecology of armadillos, sloths, and vermilinguas: 343–346. Washington, DC: Smithsonian Institution Press.

Jansa, S.A., S.M. Goodman, and P.K. Tucker. 1999. Molecular phylogeny and biogeography of the native rodents of Madagascar (Muridae: Nesomyidae): a test of the single origin hypothesis. Cladistics 15: 253–270.

Jarrín-V., P. 2001. Mamíferos en la niebla[:] Otongo, un bosque nublado del Ecuador. Quito: Museo de Zoología, Pontifica Universidad Católica del Ecuador.

Junior, V.C., and Y.L.R. Leite. 2012. Geographic variation in hairy dwarf porcupines of *Coendou* from eastern Brazil (Mammalia: Erethizontidae). Zoologia 29: 318–336.

Lara, M.C., J.L. Patton, and M.N.F. da Silva. 1996. The simultaneous diversification of South American echimyid rodents (Hystricognathi) based on complete cytochrome b sequences. Molecular Phylogenetics and Evolution 5: 403–413.

Leite, Y.L.R., et al. 2011. Designation of a neotype for the Brazilian porcupine, *Coendou prehensilis* (Linnaeus, 1758). Zootaxa 2791: 30–40.

Lima, R.B.S., P.A. Oliveira, and A.G. Chiarello. 2010. Diet of the thin-spined porcupine (*Chaetomys subspinosus*), an Atlantic forest endemic threatened with extinction in southeastern Brazil. Mammalian Biology 75: 538–546.

Lim, B.K., et al. [eight additional coauthors]. 2005. Results of the Alcoa Foundation-Suriname Expeditions. XIV. Mammals of Brownsberg Nature Park, Suriname. Annals of Carnegie Museum 74: 225–274.

Linares, O.J. 1998. Mamíferos de Venezuela. Caracas: Sociedad Conservacionista Audubon de Venezuela.

Martin, T. 1994. On the systematic position of *Chaetomys subspinosus* (Rodentia: Caviomorpha) based on evidence from the enamel microstructure. Journal of Mammalian Evolution 2: 117–131.

Miller, G.S., Jr., and J.W. Gidley. 1918. Synopsis of the supergeneric groups of rodents. Journal of the Washington Academy of Sciences 8: 431–448.

Montenegro, O.L. 2004. Natural licks as keystone resources for wildlife and people in Amazonia. Ph.D. dissertation, University of Florida, Gainesville.

Montgomery, G.G., and Y.D. Lubin. 1978. Movements of *Coendou prehensilis* in the Venezuelan llanos. Journal of Mammalogy 59: 887–888.

Moojen, J. 1952. Os roedores do Brasil. Rio de Janeiro: Instituto Nacional do Livro.

Moore, W.J. 1981. The mammalian skull. Cambridge: Cambridge University Press.

Moreno, R.S., R.W. Kays, and R. Samudio, Jr. 2006. Competitive release in diets of ocelot (*Leopardus pardalis*) and puma (*Puma concolor*) after jaguar (*Panthera onca*) decline. Journal of Mammalogy 87: 808–816.

Nava, S., P.M. Velazco, and A.A. Guglielmone. 2010. First record of *Amblyomma longirostre* (Koch, 1844) (Acari: Ixodidae) from Peru, with a review of this tick's host relationships. Systematic and Applied Acarology 15: 21–30.

Novack, A.J., M.B. Main, M.E. Sunquist, and R.F. Labisky. 2005. Foraging ecology of jaguar (*Panthera onca*) and puma (*Puma concolor*) in hunted and non-hunted sites within the Maya Biosphere Reserve, Guatemala. Journal of Zoology London 267: 167–178.

Nylander, J.A.A. 2004. MrModeltest v2. Program distributed by author. Evolutionary Biology Centre, Uppsala University.

Oliver, W.L.R., and I.B. Santos. 1991. Threatened endemic mammals of the Atlantic forest region of south-east Brazil. Wildlife Preservation Trust Special Scientific Report 4: 1–125.

Pagel, M. 1994. Detecting correlated evolution on phylogenies: a general method for the comparative analysis of discrete characters. Proceedings of the Royal Society of London B Biological Sciences 255: 37–45.

Paradis, E., J. Claude, and K. Strimmer. 2004. APE: analyses of phylogenetics and evolution in R language. Bioinformatics 20: 289–290.

Parker, T.A., III, A.H. Gentry, R.B. Foster, L.H. Emmons, and J.V. Remsen, Jr. 1993. The lowland dry forests of Santa Cruz, Bolivia: a global conservation priority (RAP Working Papers 4). [Washington, D.C.]: Conservation International.

Patterson, B., and A.E. Wood. 1982. Rodents from the Deseadan Oligocene of Bolivia and the relationships of the Caviomorpha. Bulletin of the Museum of Comparative Zoology 149: 371–543.

Passamani, M. 2010. Use of space and activity pattern of *Sphiggurus villosus* (F. Cuvier, 1823) from Brazil (Rodentia, Erethizontidae). Mammalian Biology 75: 455–458.

Patton, J.L., B. Berlin, and E.A. Berlin. 1982. Aboriginal perspectives of a mammal community in Amazonian Peru: knowledge and utilization patterns among the Aguaruna Jivaro. *In* M.A. Mares and H.H. Genoways (editors), Mammalian biology in South America (Pymatuning Symposia in Ecology 6): 111–128. Pittsburgh: Pymatuning Laboratory of Ecology.

Patton, J.L., M.N.F. da Silva, and J.R. Malcolm. 2000. Mammals of the Rio Juruá and the evolutionary and ecological diversification of Amazonia. Bulletin of the American Museum of Natural History 244: 1–306.

Paynter, R.A., Jr. 1993. Ornithological gazetteer of Ecuador. 2nd ed. Cambridge, MA: Museum of Comparative Zoology (Harvard University).

Paynter, R.A., Jr. 1997. Ornithological gazetteer of Colombia. 2nd ed. Cambridge, MA: Museum of Comparative Zoology (Harvard University).

Paynter, R.A., Jr., and M.A. Traylor, Jr. 1991. Ornithological gazetteer of Brazil. Cambridge, MA: Museum of Comparative Zoology (Harvard University), 2 vols.

Piana, R.P. 2007. Anidamiento y dieta de *Harpia harpyja* Linnaeus en la comunidad nativa de Infierno, Madre de Dios, Perú. Revista Peruana de Biología 14: 135–138.

Po-Chedley, D. S., and A. R. Shadle. 1955. Pelage of the porcupine, *Erethizon dorsatum*. Journal of Mammalogy 36: 84–95.

Rambaut, A., and Drummond, A.J. 2007. Tracer v1.5. Internet resource (http://beast.bio.ed.ac.uk/Tracer).

Ree, R.H., and S.A. Smith. 2008. Maximum likelihood inference of geographic range evolution by dispersal, local extinction, and cladogenesis. Systematic Biology 57: 4–14.

Rode, P. 1945. Catalogue des types de mammifères du Muséum National d'Histoire Naturelle, IV. Ordre des rongeurs. Paris: Muséum National d'Histoire Naturelle.

Roze, U. 2009. The North American porcupine (2nd ed.). Ithaca, NY: Cornell University Press.

Ruxton, G.D., T.N. Sherratt, and M.P. Speed. 2004. Avoiding attack: the evolutionary ecology of crypsis, warning signals, and mimicry. Oxford: Oxford University Press.

Shimodaira, H., and M. Hasegawa. 1999. Multiple comparisons of log-likelihoods with applications to phylogenetic inference. Molecular Biology and Evolution 16: 1114–1116.

Smith, M.F., and J.L. Patton. 1993. The diversification of South American murid rodents: evidence from mitochondrial DNA sequence data for the akodontine tribe. Biological Journal of the Linnean Society 50: 149–177.

Speed, M.P., and G.D. Ruxton. 2005. Warning displays in spiny animals: one (more) evolutionary route to aposematism. Evolution 59: 2499–2508.

Stamatakis, A., P. Hoover, and J. Rougemont. 2008. A rapid bootstrap algorithm for the RAxML Web Servers. Systematic Biology 57: 758–771.

Stangl, F.B., Jr., R.D. Owen, and D.E. Morris-Fuller. 1991. Cranial variation and asymmetry in southern populations of the porcupine, *Erethizon dorsatum*. Texas Journal of Science 43: 237–259.

Stephens, L., and M.A. Traylor, Jr. 1983. Ornithological gazetteer of Peru. Cambridge, MA: Museum of Comparative Zoology (Harvard University).

Swofford, D. 2002. PAUP*: Phylogenetic analysis using parsimony (and other methods); 4.0 beta version for Macintosh. Sunderland, MA: Sinauer Associates.

Tate, G.H.H. 1935. The taxonomy of the genera of Neotropical hystricoid rodents. Bulletin of the American Museum of Natural History 68: 295–447.

Thomas, O. 1902. Diagnosis of a new Central American porcupine. Annals and Magazine of Natural History (ser. 7) 10: 169.

Upham, N.S., and B.D. Patterson. 2011. Diversification and biogeography of the Neotropical caviomorph lineage Octodontoidea (Rodentia: Hystricognathi). Molecular Phylogenetics and Evolution 63: 417–429.

Vilela, R.V., et al. 2009. The taxonomic status of the endangered thin-spined porcupine, *Chaetomys subspinosus* (Olfers, 1818), based on molecular and karyologic data. BMC Evolutionary Biology 9: 29. [doi: 10.1186/1471-2148-9-29]

Voss, R.S. 1991. An introduction to the Neotropical muroid rodent genus *Zygodontomys*. Bulletin of the American Museum of Natural History 210: 1–113.

Voss, R.S. 2011. Revisionary notes on Neotropical porcupines (Rodentia: Erethizontidae). 3. An annotated checklist of the species of *Coendou* Lacépède, 1799. American Museum Novitates 3720: 1–36.

Voss, R.S., and R. Angermann. 1997. Revisionary notes on Neotropical porcupines (Rodentia: Erethizontidae). 1. Type material described by Olfers (1818) and Kuhl (1820) in the Berlin Zoological Museum. American Museum Novitates 3214: 1–44.

Voss, R.S., and M.N.F. da Silva. 2001. Revisionary notes on Neotropical porcupines (Rodentia: Erethizontidae). 2. A review of the *Coendou vestitus* group with descriptions of two new species from Amazonia. American Museum Novitates 3351: 1–36.

Voss, R.S., and D.W. Fleck. 2011. Mammalian diversity and Matses ethnomammalogy in Amazonian Peru. Part 1. Primates. Bulletin of the American Museum of Natural History 351: 1–81.

Voss, R.S., D.P. Lunde, and N.B. Simmons. 2001. The mammals of Paracou, French Guiana: a Neotropical lowland rainforest fauna. Part 2. Nonvolant species. Bulletin of the American Museum of Natural History 263: 1–236.

Waterhouse, G.R. 1848. A natural history of the Mammalia, vol. II. Containing the order Rodentia, or gnawing Mammalia. London: Hippolyte Ballière.

White, J.A. 1970. Late Cenozoic porcupines (Mammalia, Erethizontidae) of North America. American Museum Novitates 2421: 1–15.

Woodman, N., et al. 1991. Annotated checklist of the mammals of Cuzco Amazonico, Peru. Occasional Papers of the Museum of Natural History (University of Kansas) 145: 1–12.

Woods, C.A. 1984. Hystricognath rodents. *In* S. Anderson and J.K. Jones, Jr. (editors), Orders and families of Recent mammals of the world: 389–446. New York: John Wiley & Sons.

Woods, C. A. 1993. Suborder Hystricognathi. *In* D.E. Wilson and D.M. Reeder (editors), Mammal species of the world, 2nd ed.: 771–806. Washington, DC: Smithsonian Institution Press.

Woods, C.A., and C.W. Kilpatrick. 2005. Infraorder Hystricognathi Brandt, 1855. *In* D.E. Wilson and D.M. Reeder (editors), Mammal species of the world, 3rd ed., 2: 1538–1600.

Zwickl, D. 2006. Genetic algorithm approaches for the phylogenetic analysis of large biological sequence datasets under the maximum likelihood criterion. Ph.D. dissertation, University of Texas at Austin.

APPENDIX 1

Gazetteer of Collecting Localities

Below we list all of the localities where sequenced erethizontid specimens were collected, including those newly sequenced for this report and others sequenced for previous molecular studies (Bonvicino et al., 2002; Vilela et al., 2009; Leite et al., 2011). Italics identify the largest administrative unit (department, province, state) within each country, and geographic coordinates are provided parenthetically with a cited source for these data. Neotropical collection localities are mapped in figure 1.

BOLIVIA

1. *Beni,* Río Mamoré (13°42′S, 65°19′W; Anderson, 1997).

2. *Santa Cruz,* 10 km N San Ramón (16°36′S, 62°42′W; Anderson, 1997).

BRAZIL

3. *Acre,* right bank Rio Juruá, Ocidente (8°34′S, 72°48′W; Patton et al., 2000).

4. *Acre,* left bank Rio Juruá, Fazenda Santa Fé (8°36′S, 72°51′W; Patton et al., 2000).

5. *Amazonas,* left bank Rio Juruá, Eirunepé (6°38′S, 69°52′W; Patton et al., 2000). Note that Lara et al. (1996), who also sequenced MVZ 195088 (= MNFS 439), gave incorrect coordinates for this locality, placing it almost 1000 km to the east; Vilela et al. (2009: table 4) repeated their mistake.

6. *Bahia,* Salvador (13°00′S, 38°30′W, near sea level; Vilela et al., 2009).

7. *Espírito Santo,* Usina Hidrelétrica de Rosal (20°54′S, 41°42′W; Vilela et al., 2009).

8. *Mato Grosso,* Usina Hidrelétrica de Manso (15°36′S, 56°06′W; Bonvicino et al., 2002).

9. *Pará,* Ilha de Marajó (ca. 1°00′S, 49°30′W; Paynter and Traylor, 1991).

10. *Pernambuco,* Mata Xanguá (8°39′S, 35°10′W; Leite et al., 2011).

11. *Rio de Janeiro,* Rio das Ostras (22°32′S, 41°57′W; Bonvicino et al., 2002).

12. *Rio de Janeiro,* Sumidouro (22°03′S, 42°40′ W; Bonvicino et al., 2002).

13. *Roraima,* São João da Baliza (00°57′S, 59°54′W; Bonvicino et al., 2002).

14. *São Paulo,* Biritiba Mirim (23°36′S, 46°00′W; Vilela et al., 2009).

15. *São Paulo,* 20 km NW Sorocaba (23°26′S, 47°38′W; L.P. Costa, personal commun.).

COLOMBIA

16. *Cauca*, Quintana (in western Andes near Cerro Munchique [ca. 2°32′N, 76°57′W; DMA, 1988], not "La Quintana," a locality said to be on the western slopes of the Central Andes; Paynter, 1997: 236)

17. *Cesar,* San Alberto (ca. 7°45′N, 73°23′W; Paynter, 1997).

18. *Cesar,* Valledupar (10°29′N, 73°15′W; Paynter, 1997).

19. *Cundinamarca*, San Juan de Río Seco (4°51′N, 74°38′W; Paynter, 1997).

ECUADOR

20. *Cotopaxi,* Otonga (0°25′S, 79°00′W; Jarrín, 2001).

21. *Sucumbíos,* Río Napo, Limoncocha (ca. 0°25′S, 76°38′W; Paynter, 1993).

FRENCH GUIANA
     22. Petit Saut (ca. 4°51′N, 53°03′W; F. Catzeflis, personal commun.).
MEXICO
     23. *Campeche,* 4 km N and 0.5 km E Jonuta (ca. 18°05′N, 92°08′W).
PANAMA
     24. "Canal Zone," Fort Kobbe (8°54′N, 79°36′W; Fairchild and Handley, 1966).
PARAGUAY
     25. *Caazapá*, Estancia dos Marías (26°48′S, 56°33′W; D'Elía et al., 2008).
     26. *Itapúa,* Estancia San Isidro (26°31′S, 55°52′W; D'Elía et al., 2008).
PERU
     27. *Amazonas,* Río Cenepa, Huampami (ca. 4°27′S, 78°10′W; Patton et al., 1982).
     28. *Cajamarca,* 2.5 km N Monte Seco (ca. 6°50′S, 79°06′W; Cadle, 1991).
     29. *Loreto,* Iquitos (3°46′S, 73°15′W; Stephens and Traylor, 1983).
     30. *Loreto,* Río Gálvez, Nuevo San Juan (5°15′S, 73°10′W; Voss and Fleck, 2011).
     31. *Madre de Dios,* 15 km NE Puerto Maldonado (12°33′S, 69°03′W; Woodman et al., 1991).
     32. *San Martín,* Área de Conservación Municipal Mishquiyacu-Rumiyacu y Almendra (6°05′S, 76°59′W; Nava et al., 2010).
VENEZUELA
     33. *Amazonas,* Cerro Neblina Base Camp (0°50′N, 66°10′W; Gardner, 2008).
     34. *Bolívar,* Río Caroní (7°55′N, 63°01′W; F. Catzeflis, personal commun.).
     35. *Táchira,* Las Mesas (8°09′N, 72°10′W; Handley, 1976).
     36. *Zulia,* Misión Tukuko (9°50′N, 72°52′W; Voss, 1991).
UNITED STATES
     37. *Pennsylvania,* near Rauchtown (41°51′N, 77°16′W; J. Jacobs, personal commun.).