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Phylogeny, evolution, and systematics of the *Galea musteloides* complex (Rodentia: Caviidae)

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As presently recognized, the genus *Galea* is composed of 3 species, *G. musteloides*, *G. flavidens*, and *G. spixii*. The most widely distributed species is *G. musteloides* (the common yellow-toothed cavy), ranging from southern Peru to southern Argentina and from sea level to over 4,000 m elevation. Our current taxonomic and systematic understanding of *Galea* is based primarily on morphological studies that have been limited in both taxonomic and geographic sampling. In this study phylogenetic analyses of sequences from the cytochrome-*b* gene were used to test hypotheses related to the content, limits, and systematic relationships within *G. musteloides*. Our data support restricting *G. musteloides* to the highlands of northwestern Bolivia, southeastern Peru, and extreme northeastern Chile. We elevate *G. leucoblephara* Burmeister, 1861, for populations occupying the lowlands of Bolivia and Paraguay to central Argentina, and we elevate *G. comes* Thomas, 1919, for populations from the Andes of southern Bolivia and northern Argentina. Our results also suggest the presence of a previously unrecognized form at midelevations in the southern Bolivian Andes. We find support for treating *G. spixii campicola* as a junior synonym of *G. l. demissa* and *G. monasteriensis* as a junior synonym of *G. musteloides boliviensis*. Most of the evolution of the taxa within the *G. musteloides* complex appears to have occurred in the Prepuna biogeographic province, with 2 independent vicariant events culminating in the separation of the *G. musteloides*, *G. comes*, and *G. leucoblephara* clades. Dating estimates suggest a late Miocene divergence between *G. spixii* and the *G. musteloides* group, followed by species-level divergence within the *G. musteloides* group during the Pliocene. DOI: 10.1644/08-MAMM-A-214R1.1.

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The genus *Galea* currently is composed of 1 monotypic species (*G. flavidens*) and 2 polytypic species (*G. musteloides* and *G. spixii*). *G. musteloides*, the common yellow-toothed cavy, is the most widely distributed of the 3, ranging from the highlands of Bolivia, Peru, and Chile to the eastern lowlands of Bolivia and Paraguay and the Patagonian steppe of southern Argentina (Agnolin et al. 2008; Woods and Kilpatrick 2005). This species was described from the high Andes of Peru (Meyen 1833) and, despite later revisionary works (Cabrera 1961; Hückinghaus 1961), a thorough understanding of species limits and phylogenetic relationships of *G. musteloides* is lacking.

Waterhouse (1847), Burmeister (1861), and Thomas (1911, 1919a, 1919b, 1921) described 7 *Galea* taxa that are currently regarded as subspecies or junior synonyms of *G. musteloides*. Four of these are from Argentina, with *G. m. leucoblephara* (Burmeister, 1861) present in the west-central lowlands; *G. m. littoralis* (Thomas, 1901) from Bahia Blanca, Buenos Aires; *G. m. negrensis* (Thomas, 1919a) from the upper Rio Negro Province; and *G. m. comes* (Thomas, 1919b) from the highlands of Jujuy Province. The other 3 are from Bolivia and Peru, with *G. m. boliviensis* (Waterhouse, 1847) from the central Bolivian Andes, *G. m. auceps* (Thomas, 1911) from the Altiplano region around Lake Titicaca, and *G. m. demissa* (Thomas, 1921) from the Bolivian lowlands adjacent to the Andean foothills.

Early taxonomic treatments for the genus were presented by Tate (1935) and Cabrera (1953, 1961), and a recent study based on morphology (Solmsdorff et al. 2004), the 1st in more than 40 years, recognized 5 subspecies of *G. musteloides* (*boliviensis*, *demissa*, *leucoblephara*, *littoralis*, and *musteloides*) and described a new species, *G. monasteriensis*, within the *G. musteloides* group. Solmsdorff et al. (2004) highlighted the lack of diagnostic information in pelage coloration, skull

size and shape, size of auditory bullae, and tooth morphology within *Galea*, although these characters had been the basis for previous taxonomic decisions. The absence of reliable diagnostic characters has been compounded by use of relatively small sample sizes and sparse geographic and taxonomic sampling in the majority of work done thus far, leaving the true levels of morphological variation within and between the named forms poorly understood.

Woods and Kilpatrick (2005) recognize 5 subspecies within *G. musteloides* (*auceps*, *demissa*, *leucoblephara*, *littoralis*, and *musteloides*), ranging from southern Peru to central Argentina at elevations from sea level to over 4,000 m and inhabiting grassland habitats from the high Andes, through the low Chaco, to the Atlantic coast. Other taxa of similarly large distributional ranges (e.g., the hispid cotton rat [*Sigmodon hispidus*] and eastern cottontail [*Sylvilagus floridanus*]) have been split into multiple species (Ruedas et al 1989; Ruedas and Elder 1994; Peppers and Bradley 2000; Peppers et al. 2002) despite appearing to represent single species on morphological grounds (Ruedas 1998; Voss 1992). Thus, analyses of morphological data alone may not be sufficient to elucidate species-level differences and may underestimate true diversity within taxa.

The biogeographic history of *Galea* is obscured by the lack of modern revisionary work. A hypothetical scenario for the evolution of caviioid rodents was advanced by Reig (1986), who suggested an origin for this group in the humid lowlands of South America with progressive adaptation to arid regions of the proto-puna in the Miocene and Pliocene before the final uplift of the Andes. This scenario is consistent with estimates by Opazo (2005) of origination time for the genus (16 million years ago [mya] ± 2.5 *SD*) and the divergence between *G. musteloides* and *G. spixii* (5.9 ± 1.6 mya).

Although molecular data for a few specimens of *G. musteloides* have been included in analyses of higher-level caviioid relationships (Opazo 2005; Rowe and Honeycutt 2002) and in work on other caviids (Spotorno et al. 2004), no comprehensive molecular-based phylogenetic analysis of *Galea* has been undertaken before this study. The objectives of this work are to conduct phylogenetic analyses of cytochrome-*b* (*Cytb*) sequence data and examine chromosomal data to assess hypotheses related to the content, limits, systematic relationships, and taxonomy of the *G. musteloides* group and provide a phylogenetic framework that can be used to assess the biogeographic hypotheses of Reig (1986) and Opazo (2005).

Materials and Methods

Specimens examined.—Forty-nine specimens from 34 localities spanning the known distribution of *Galea* were used in the phylogenetic analyses, including 43 *G. musteloides* (sensu Woods and Kilpatrick 2005), 1 topotype of *G. monasteriensis*, 3 specimens of *G. spixii campicola* (including 2 paratypes), and 2 of *G. spixii wellsi* (Fig. 1; Appendix I). One specimen each of *Cavia aperea* and *Microcavia niata* were used as outgroups (Opazo 2005; Rowe and Honeycutt 2002). No specimens of *G. flavidens* were available for this study; however, the status of this species is unclear (Paula Couto [1950] considered *G. flavidens* synonymous with *G. spixii*; but see Cabrera [1961]), and few specimens are known to exist. Bonvicino et al. (2005) tentatively referred specimens from the Cerrado of the Brazilian state of Goiás to *G. flavidens*.

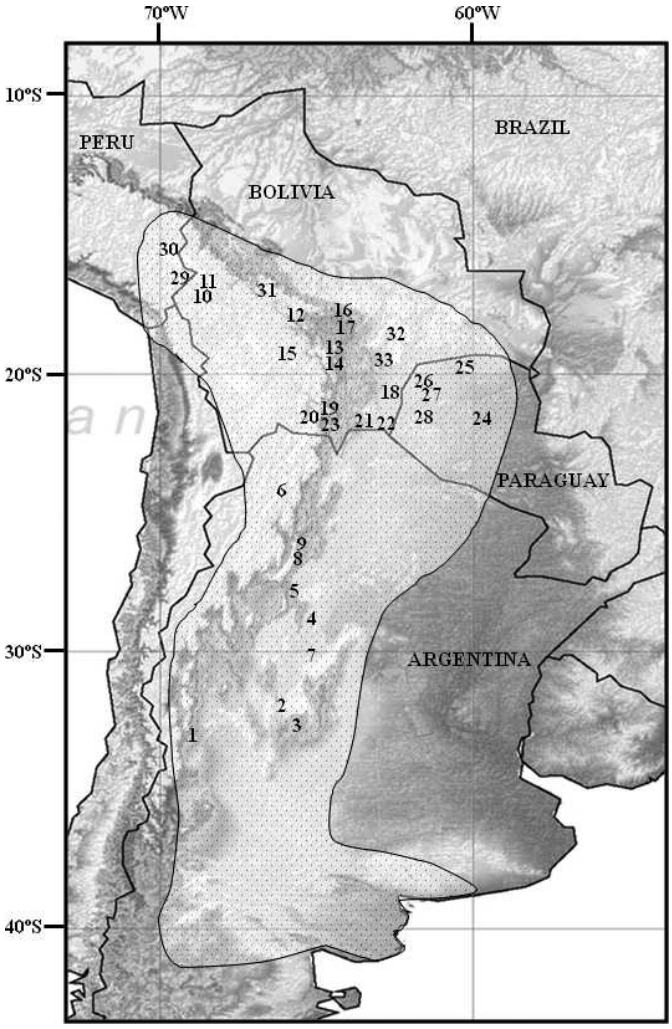

Fig. 1.—Map of collection localities (Appendix I) of specimens of *Galea* used in the present study. Stippled area represents the current known distribution of *Galea musteloides*.

Specimens were either wild-caught or procured via institutional loans from natural history collections. Field protocols followed guidelines approved by the American Society of Mammalogists (Gannon et al. 2007). All tissue samples included in our analyses are accompanied by voucher specimens (Appendix I). Taxonomy follows Woods and Kilpatrick (2005), and assignment of specimens to subspecies follows Anderson (1997) and Cabrera (1961).

DNA extraction, amplification, and sequencing.—Total genomic DNA was extracted from liver, muscle, or skin clips using either the DNeasy Tissue Kit (QIAGEN, Inc., Germantown, Maryland) or standard phenol–chloroform methods. Amplification of the *Cytb* gene was performed via polymerase

chain reaction using *Taq* PCR Core kit (QIAGEN, Inc.) in either 25- or 50-µl reactions. Negative controls were used in all amplifications. Combinations of the following primers were used: F78 and B149 (Spotorno et al. 2004); CB1-5′ and CB3-3′ (Palumbi 1996); L14724 (Irwin et al. 1991); and CAV2, CAV5,GAL3, GAL6, GAL7, GAL10, and GAL11 (designed for this study; Appendix II). Three thermal-cycling profiles were used: profile 1, initial denaturation at 95°C for 5 min, followed by 5 cycles at 94°C for 30 s, 48°C for 45 s, ramp of 0.5°C/s to 70°C, 70°C for 1 min, followed by 35 cycles of 94°C for 30 s, 54°C for 45 s, ramp of 1.0°C/s to 72°C, 72°C for 1 min, followed by 72°C for 7 min; profile 2, 30 cycles of 95°C for 45 s, 54°C for 30 s, 72°C for 1 min, followed by 72°C for 6 min (Spotorno et al. 2004); profile 3, 95°C for 3 min, followed by 40 cycles of 95°C for 30 s, 45°C for 30 s, 72°C for 1 min, followed by 72°C for 10 min. Profile 3 was used for animals of the type series of *G. s. campicola*.

Before sequencing, amplified products were cleaned using the QIAquick PCR Purification Kit protocol (QIAGEN, Inc.) and visualized on 0.8% agarose gels. Samples were cycle-sequenced with the same primers as above using 2 methods: method 1, BigDye Terminator v1.1 (Applied Biosystems, Inc., Foster City, California) for 25 cycles of 96°C for 10 s, ramp to 50°C at 1°C/s, 50°C for 5 s, ramp to 60°C at 1°C/s, 60°C for 4 min; method 2, CEQ Dye Terminator Cycle Sequencing Quick Start Kit (Beckman Coulter, Fullerton, California) for 30 cycles of 96°C for 20 s, 50°C for 20 s, 60°C for 4 min. Sequencing products were purified using Preforma DTR Gel Filtration Cartridges (Edge Biosystems, Gaithersburg, Maryland), then sequenced on either ABI Avant 3100 (Perkin Elmer, Waltham, Massachusetts) or CEQ2000 (Beckman Coulter) automated sequencers. Sequences were aligned using the software Vector NTI Advance 9.1.0 (Invitrogen Corp., Carlsbad, California) and proofread visually. Both strands of all sequences were obtained and were free of insertions–deletions (indels), premature stop codons, and ambiguities in forward and reverse directions, providing support for their mitochondrial origin (Triant and DeWoody 2007). All sequences have been deposited in GenBank (accession numbers GU067490–GU067523, GU067525–GU067538, and GU084285).

Phylogenetic analyses.—Phylogenetic relationships among taxa were assessed using maximum parsimony in PAUP* (Swofford 2000), maximum likelihood in RAxML (Stamatakis et al. 2008), and Bayesian analysis in MrBayes 3.1.1 (Ronquist and Huelsenbeck 2003). Pairwise genetic distances were calculated to assess within- and among-species differences using the Kimura 2-parameter method (Kimura 1980) in PAUP*.

Heuristic searches with 1,000 replicates (random-taxon addition) and tree bisection-reconnection branch swapping were performed in maximum parsimony on unordered and equally weighted characters. Strict consensus was used to obtain consensus trees. Nonparametric bootstrap analyses (Felsenstein 1985—1,000 pseudoreplicates and 10 random-sequence additions with each replicate) were run to assess support for individual nodes. Nodes with bootstrap support above 85% were considered well supported.

Modeltest v3.7 (Posada and Crandall 1998) was used to find the evolutionary model that best fit our data based on the Akaike information criteria. The General Time Reversible (GTR) model of substitution, taking into account the proportion of invariable sites and following a gamma distribution for variable sites (GTR + I + G), was determined to be the best fit.

The RAxML was run with 100 maximum-likelihood rapid bootstraps, the model of substitution and parameters suggested by Modeltest, and fast and slow maximum-likelihood optimizations. Bayesian analysis included 4 Markov chains run for 4,000,000 generations and sampled every 100 generations. For each analysis a model with 6 categories of base substitution, a gamma-distributed rate parameter, and a proportion of invariant sites was specified; all model parameters were estimated in MrBayes. Uniform interval priors were assumed for all parameters except base composition and GTR parameters, which assumed a Dirichlet process prior. To check for convergence on a stable log-likelihood value, we plotted the log-likelihood values against generation time for each run. The first 2,500 trees were discarded as burn-in, and the remaining 75,002 trees were used to compute a 50% majority rule consensus tree and obtain posterior probability estimates for each node. Branches with posterior probability $\geq$0.95 were considered well supported. Because Bayesian posterior probability values tend to be a less conservative estimate of node reliability than nonparametric bootstrap values (Alfaro et al. 2003; Erixon et al. 2003), inclusion of both support values on our trees represents the upper and lower bounds, respectively, of node reliability (Douady et al. 2003).

Chromosomal preparations were obtained for 4 individuals of *G. musteloides* following the methods of Anderson et al. (1987). Metaphase cells were photographed and scored to determine the diploid (2n) and fundamental (FN) numbers; a minimum of 30 metaphase plates from each individual were scored to verify the chromosome counts. Nomenclature for chromosome morphology and FN follows Patton (1967).

Biogeography and estimates of divergence dates.—Dispersal–vicariance analysis (DIVA; Ronquist 1996, 1997) was used to infer ancestral distributions of clades represented by each node in the haplotype phylogeny and dispersal and extinction events within an assumed vicariant framework. A species-area matrix was constructed in DIVA using the default options and an unconstrained maximum number of areas at nodes. One of the acknowledged pitfalls of DIVA is that ancestral area optimizations become less reliable as the analysis approaches the deepest nodes. To reduce this bias we used the distributions of the 2 outgroup taxa to restrict ancestral distributions at the internalmost node (Sanmartin 2003). Eight biogeographic units (equivalent to the biogeographic provinces of Cabrera and Willink [1973]) were used in the analyses: Cerrado, Caatinga, Prepuna, Puna, Alto Andina, Monte, Chaco, and Patagonica. Each of the 10 clades (8 clades in

Table 1.—Kimura 2-parameter genetic distances (mean and range) based on cytochrome-*b* (*Cytb*) sequence data for the major *Galea* clades. Only specimens with complete *Cytb* sequences were included in these calculations. Major clades are defined in Fig. 2.

	G. musteloides	*Galea* sp.	*G. comes*	*G. leucoblephara*	*G. spixii*
G. musteloides	3.1 (0.6–4.7)				
Galea sp.	8.2 (7.4–9.6)	0.3 (0.0–0.4)			
G. comes	9.7 (8.6–11.2)	6.3 (6.1–6.6)	0.9 (0.0–2.2)		
G. leucoblephara	9.0 (7.6–11.3)	5.9 (5.0–6.7)	4.8 (3.7–5.6)	2.5 (0.0–4.6)	
G. spixii	19.0 (18.5–20.1)	20.0 (19.8–20.3)	21.3 (21.2–21.5)	21.3 (20.5–22.0)	0.5 (0.5–0.5)

Galea and 2 outgroups) were scored according to their presence or absence in each of the 8 biogeographic regions.

Estimates of divergence time were calculated in a Bayesian Markov chain Monte Carlo framework using BEAST 1.4.6 (Drummond and Rambaut 2007). In contrast to other dating methods, BEAST simultaneously estimates topology and node ages, allowing sequence divergences to inform topology estimation (Drummond et al. 2006). We employed a relaxed clock, including an uncorrelated lognormal model for rate variation among branches, an assumption of independent rates among branches, and no a priori assumption of rate correlations between ancestor and descendant lineages (Drummond et al. 2006). A Yule prior on rates of evolution was employed because this more accurately resembles phylogenetic processes at the species level (Drummond et al. 2007). We used the SRD06 model of substitution, which has fewer parameters than the GTR + G + I model but has been shown to provide a better fit for protein-coding nucleotide data (Drummond et al. 2007).

Nodes with available fossil data were calibrated using a lognormal distribution, which assumes that the actual divergence event is most likely to have occurred at some time prior to the earliest appearance of the fossil evidence (Ho 2007). Thus, these priors were calibrated with the fossil date as the absolute minimum age for the node and a soft upper bound so that 95% of the prior weight fell on the specified interval. We used previously published divergence dates generated by Opazo (2005) for the Caviomorpha using growth hormone receptor (GHR) and 12S data and calibrated by the 1st caviomorph fossil at 31–37 mya (Wyss et al. 1993). Estimated divergence dates and standard deviations for the Caviidae and *Galea* from that study were used as approximate means when calculating our 95% confidence intervals (95% *CI*s). Posterior distributions for each parameter were obtained using a Markov chain Monte Carlo run for 10,000,000 generations and sampled every 1,000 generations. Three independent runs of the analysis were combined using Tracer version 1.3 (Rambaut and Drummond 2007) to assess convergence and achieve adequate sample sizes for all parameters. Trees were summarized as maximum clade credibility trees using the TreeAnnotator program in BEAST and visualized using FigTree version 1.0 (Rambaut 2006). The first 10% of samples was discarded to avoid sampling the burn-in phase.

Calibration priors were applied to the root height of the tree and the crown group of the genus *Galea*. The root height was set to correspond to the crown group of the family Caviidae using a lognormal prior distribution with an offset of 11.61 mya (minimum age of the oldest caviid fossil), a lognormal mean of 2.1, and a standard deviation of 0.5. These settings placed the mean of the divergence date at 18.5 mya, as estimated by Opazo (2005), and did not allow the 95% *CI* to exceed 30 mya (the crown age of the Cavioidea). The age prior for the genus *Galea* used a lognormal distribution with an offset of 1.2 mya (minimum age of the oldest *Galea* fossil), a lognormal mean of 1.9, and a standard deviation of 0.45. These settings placed the mean at 5.9 mya and did not allow the 95% *CI* to exceed 18 mya (crown age of the Caviinae). Priors for the other nodes of interest were assigned normal distributions with means and standard deviations following Opazo (2005), as follows: Caviinae (16.2 ± 2.5 mya), Dolichotinae (7.5 ± 4.8 mya), and Hydrochoerinae (12.28 ± 2.3 mya).

Results

Full *Cytb* sequences (1,140 base pairs [bp]) were obtained for 40 of 51 specimens, sequences for 9 specimens ranged in length from 787 to 1,125 bp, and approximately 200 bp of sequence were obtained for the specimens of the type series of *G. spixii campicola* (Appendix I). Genetic distances within the 4 major clades of *Galea* identified from within the *G. musteloides* complex in this study ranged from 0.3% within the *Galea* sp. clade to 3.1% within the *G. musteloides* clade (Table 1). Distances between clades ranged from 4.8% between the *G. comes* and *G. leucoblephara* clades to almost 10% sequence divergence between the *G. musteloides* and *G. comes* clades. Genetic distances between the ingroup taxa and both outgroups (*Cavia* and *Microcavia*) averaged approximately 22.0%. Genetic divergence between members of the 4 *Galea* clades within the *G. musteloides* complex and the 2 Brazilian samples of *G. spixii wellsi* ranged from 18.6% to 22.0%—comparable to distances measured between ingroup and outgroup specimens in this study.

Phylogenetic relationships.—Four major clades were resolved within *G. musteloides* regardless of the analytical method used (Fig. 2). RAxML analysis resulted in a log-likelihood of −6,084.384 and base compositions of 0.317 for adenine, 0.262 for cytocine, 0.122 for guanine, and 0.299 for thymine. Maximum parsimony analysis generated 1,312 most-parsimonious trees (length = 935, consistency index = 0.6214, homoplasy index = 0.3786, retention index = 0.8291), and 332 of the 1,140 *Cytb* sites were parsimony informative.

Our analyses place *G. spixii* as the sister taxon to a monophyletic clade containing the other 4 *Galea* taxa. Within this clade the *G. musteloides* clade (Fig. 2) is composed of

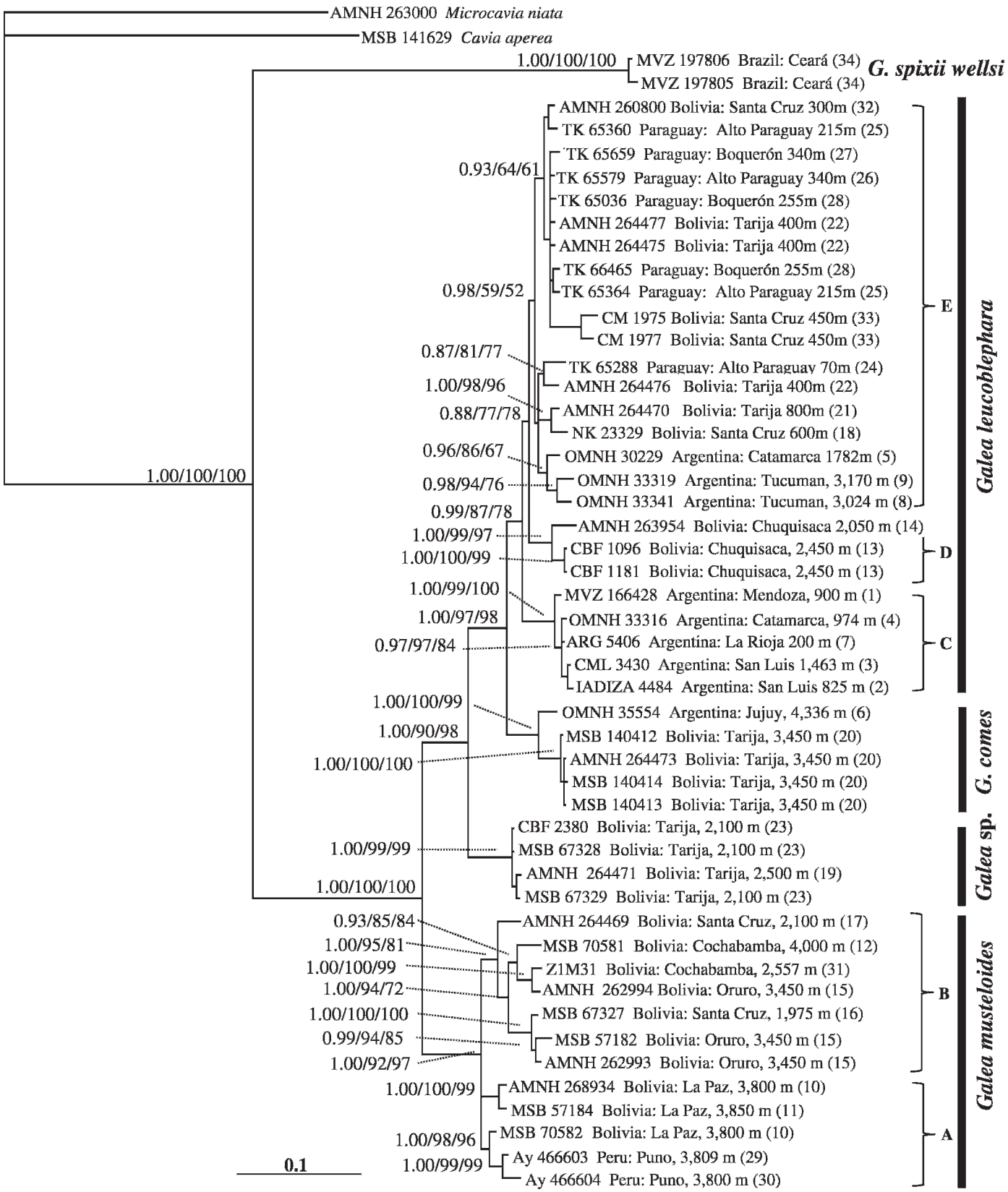

Fig. 2.—Phylogeny of the *Galea musteloides* group based on Bayesian, likelihood, and parsimony analyses of the cytochrome-*b* gene. Locality numbers (Appendix I) are listed for each specimen. Bayesian posterior probability, maximum-likelihood, and maximum-parsimony bootstrap support values (PP/ML/MP) are above nodes. The 2 specimens from locality 33 are currently recognized as *G. spixii campicola*, and the single specimen from locality 31 as *G. monasteriensis*. The taxonomic hypotheses presented in this report are reflected in the clade names. Major clades represent species level differentiation, and subclades A–E correspond to subspecies or distinct unnamed groups.

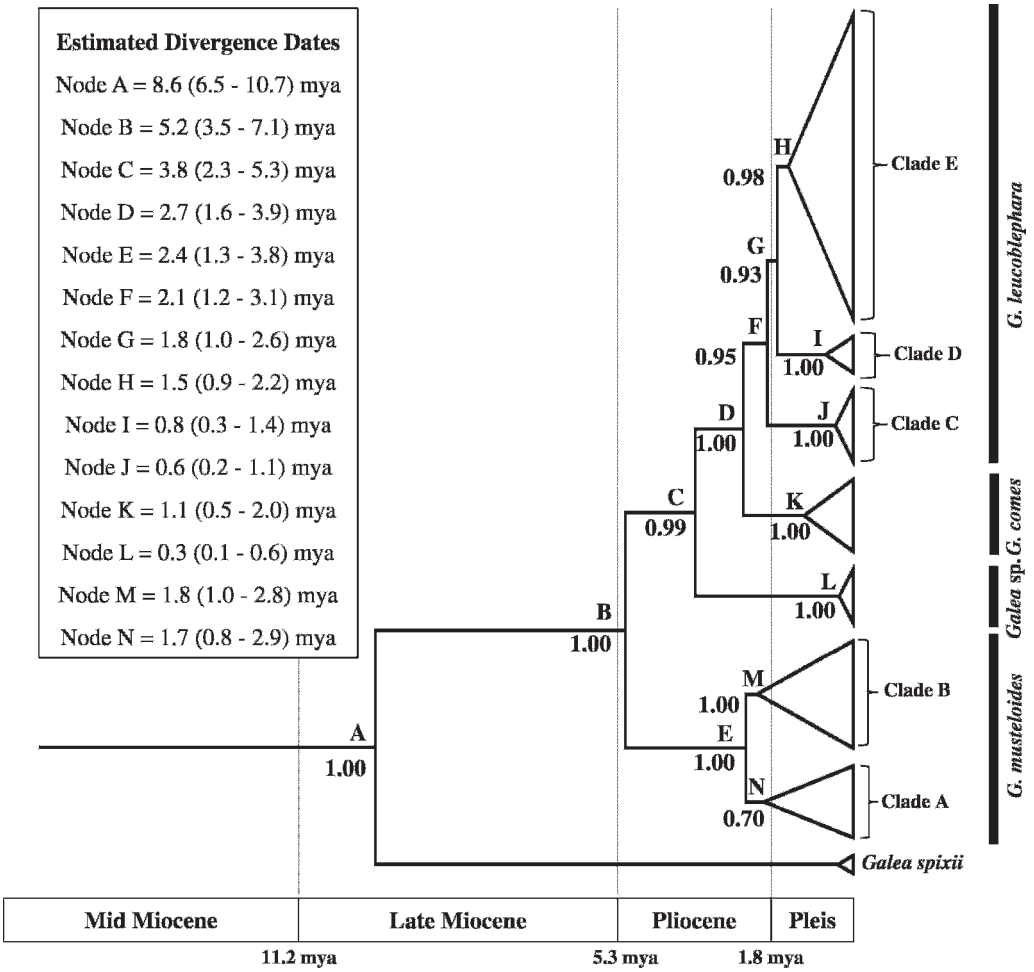

Fig. 3.—Phylogeny and estimates of divergence times for *Galea* generated using BEAST and a relaxed clock model. Bayesian posterior probability (PP) values are below nodes. Outgroup taxa are not shown, but the Caviinae divergence is estimated at 16.2 mya (95% highest posterior density 13.6–19.3 mya). Letters above nodes refer to divergence values in the legend. Geological times follow the *Geologic Time Scale* of the Geological Society of America (1999).

specimens from southeastern Peru and the northern and central Bolivian Andes (2,000–3,850 m elevation). This clade includes specimens associated with the nominal forms *G. m. musteloides*, *G. m. auceps*, *G. m. boliviensis*, and the recently described *G. monasteriensis* (Solmsdorff et al. 2004). The *Galea* sp. clade (Fig. 2) is composed of specimens from 2 neighboring localities (Erquis and Tucumilla, Tarija Department, Bolivia) on the eastern versant of the southern Bolivian Andes (2,100–2,500 m). The *G. comes* clade (Fig. 2) includes specimens from localities 300 km apart in the highlands of northern Argentina (Jujuy Department; 4,336 m) and southern Bolivia (Iscayachi Department; 3,450 m). The *G. leucoblephara* clade is composed predominantly of lowland specimens (usually below 1,000 m, with several exceptions up to 3,024 m). This clade has regional substructure and can be subdivided into at least 3 mitochondrial DNA (mtDNA) subclades (C–E in Fig. 2). BEAST analyses recovered the same well-supported tree topology and suggest a Miocene divergence between *G. spixii* and the *G. musteloides* complex, followed by species-level divergence within the *G. musteloides* complex during the Pliocene (Fig. 3).

Karyotypes.—All karyotypes analyzed had 2n = 68 and FN = 132, and in all preparations the X chromosome was a large submetacentric and the Y chromosome a small metacentric (Fig. 4). The only difference observed among the karyotypes was in the morphology of one of the medium pairs; it is subacrocentric in a representative of the *Galea* sp. clade (MSB 67329) but metacentric to submetacentric in specimens from the other clades.

Discussion

Following initial descriptions of *G. musteloides* and *G. leucoblephara* by Meyen (1833) and Burmeister (1861), the taxonomic history of *Galea* lies predominantly with the descriptive works of Thomas (1901, 1911, 1919a, 1919b, 1921), followed by subsequent synonymization of many nominal forms by Osgood (1916) and Thomas (1926, 1929). Our phylogenetic hypotheses correspond well with the geography and biomes of central South America, and the phylogroups we identify reflect some of these past taxonomic hypotheses while also suggesting presence of previously

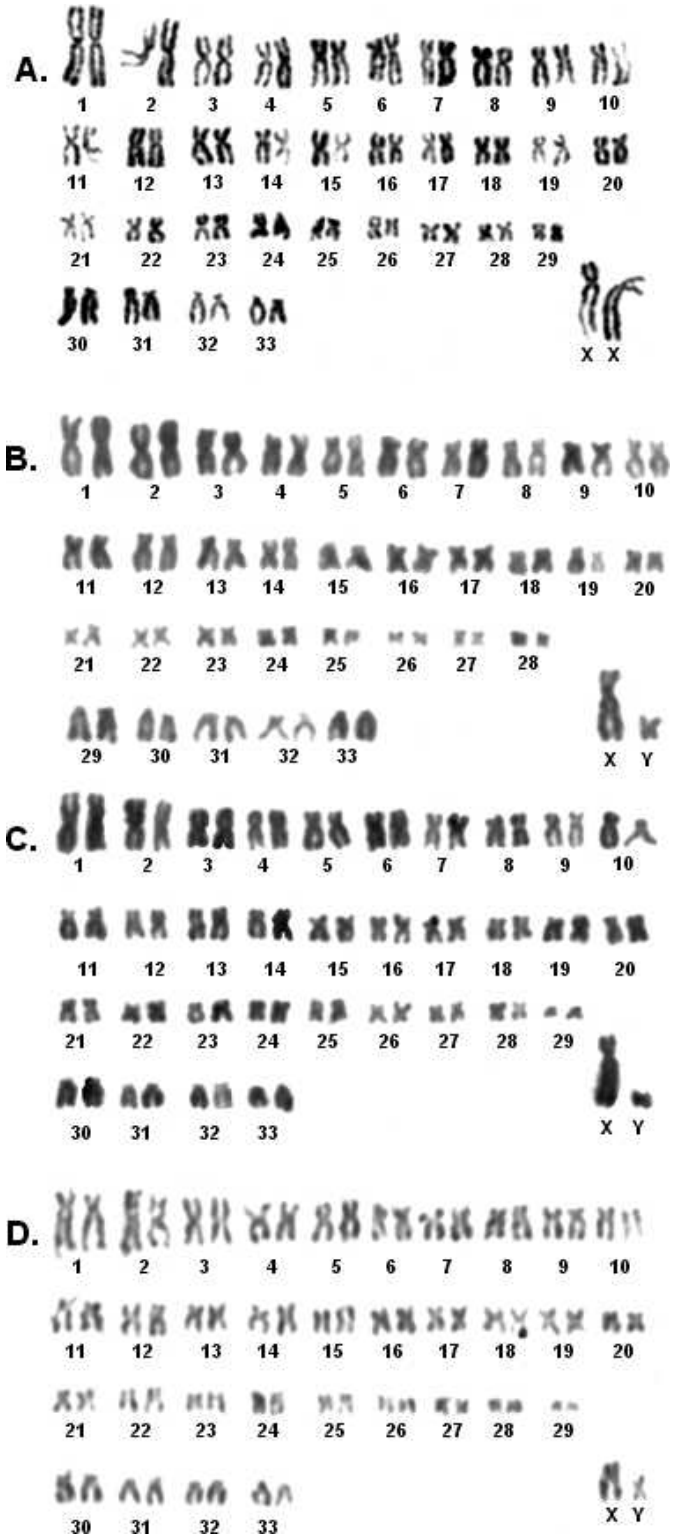

Fig. 4.—Karyotypes of representative specimens from each of the major *Galea* clades in Fig. 2. A) *G. musteloides* clade (MSB 67327, female); B) *Galea* sp. clade (MSB 67329, male); C) *G. comes* clade (MSB 140412, male); D) *G. leucoblephara* clade (AMNH 264470, male). All karyotypes have 2n = 68, FN = 132; the X chromosome is a large submetacentric, and the Y chromosome is a small metacentric. Specimen numbers as in Appendix I.

unrecognized forms. Recent revisionary work on other South American taxa from this general area has resulted in similar patterns of relationships (D'Elía et al. 2008; Voss et al. 2004, 2005; Weksler 2003). Moore (1995) and Wiens and Penkrot (2002) suggested that mtDNA has an important advantage in species delimitation relative to nuclear-based markers because the smaller effective population size of the mitochondrial genome means that the mtDNA haplotypes of a given species should coalesce 4 times more rapidly than will nuclear markers. Thus, newly formed species should become distinct in their mtDNA haplotype phylogenies before they become distinct in nuclear-based markers (but see Hudson and Turelli 2003). Given the potential for mitochondrial introgression and incomplete lineage sorting of mitochondrial haplotypes, taxonomic decisions based on a single gene tree must be scrutinized carefully. However, the concordance of our mitochondrial-based trees with earlier trees based on nuclear-encoded data (morphology) suggests that our gene trees reflect the actual species phylogeny of *Galea*.

Two recent reviews summarized the major species concepts currently recognized in the literature and their operational criteria for making decisions about species boundaries in nature (Sites and Marshall 2003, 2004). In our view, species are populations or groups of populations that share a unique phylogenetic history and are diagnosable by molecular, chromosomal, behavioral, morphological, or any combination of these or other genetically encoded characters. Therefore, the groups of populations we identify below are diagnosed by the combination of mitochondrial characters (base pairs of the *Cytb* gene) that contribute to the phylogenetic patterns presented in Fig. 2. Where chromosomal, behavioral, and other kinds of data exist, we use these data to support or refute our contention that the major groups of *Galea* we identify merit species-level recognition.

The G. musteloides clade.—This clade is composed of animals from the Andes of central Bolivia and southeastern Peru, and it includes animals formerly assigned to the subspecies *G. m. auceps* and *G. m. boliviensis* and the topotype of *G. monasteriensis* (a direct descendant of the holotype of this taxon). The description of *G. musteloides* by Meyen (1833) is based on a single skull from Tacna Pass on the road to Lake Titicaca, Peru. Waterhouse (1847:175) subsequently described *Cavia boliviensis* from the ''… high tableland between Cochabamba and La Paz [Bolivia] …'' and remarked that Meyen's *Galea* was surely the same animal. Thomas (1911:255) subsequently restricted the type locality for *G. boliviensis* to ''Paratani [sic], close to Cochabamba.'' Later, Osgood (1916:211) stated ''… it is reasonably certain that *boliviensis* is at most no more than a subspecies of *musteloides*.'' With the exception of Solmsdorff et al. (2004), most subsequent authors do not recognize *G. m. boliviensis* as a valid subspecies of *G. musteloides*.

Thomas (1911:255) described *G. auceps* from ''Guarina (alt. 4000 m.), near the south-east, the Bolivian, end of the lake [Titicaca]'' and restricted its distribution to the highland areas of western La Paz Department, Bolivia, and adjacent

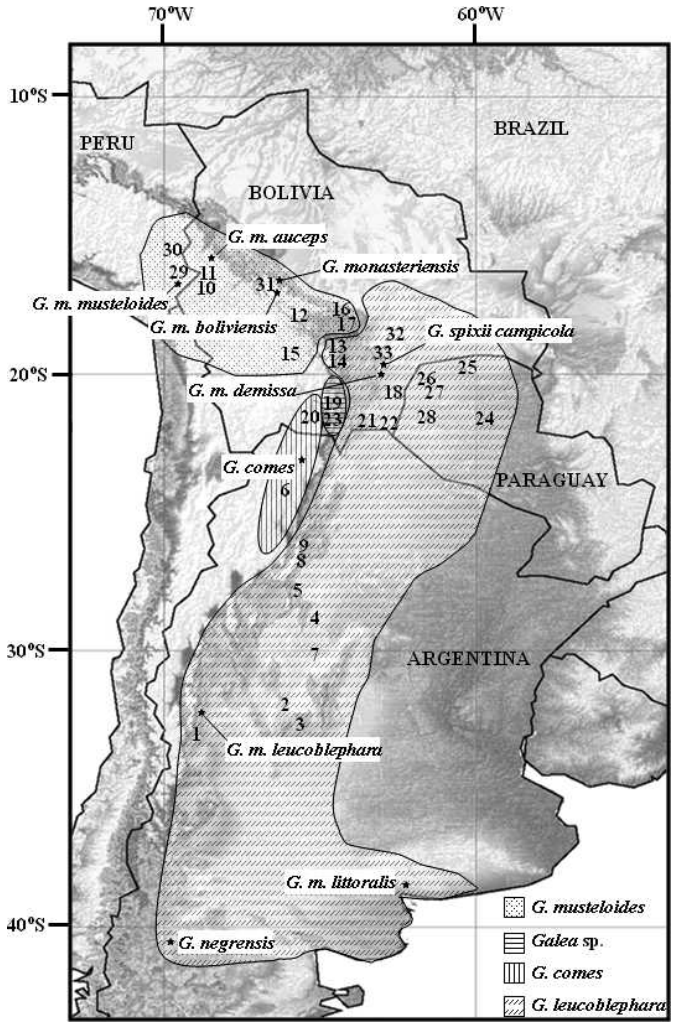

FIG. 5.—Map of major *Galea* clades identified in this study. Stars represent type localities of nominal forms (taxonomy follows Woods and Kilpatrick 2005). Numbers correspond to localities in Appendix I.

areas of Peru. Anderson (1997) suggested that this form was diagnosable by its pale, yellowish coloration in contrast to the darker color of the nominate subspecies.

The initial evidence for presence of an undescribed species of *Galea* (*G. monasteriensis*) came during an attempt to supplement laboratory colonies of *Galea* at the Universities of Bielefeld and Muenster, Germany, with new animals from the Bolivian highlands (Valle Hermoso, Cochabamba Department, Bolivia; 2,557 m). The newly imported animals would not interbreed with colony animals, leading Solmsdorff et al. (2004) and Hohoff et al. (2002, 2003) to investigate morphological, behavioral, and reproductive differences between the 2 forms and eventually recognize the imported animals as a new species, *G. monasteriensis*. However, our investigation of the literature shows that the founding population for the University of Bielefeld laboratory colony and the previously studied wild populations were not from other highland populations of *G. musteloides*, but rather from lowland populations representing *G. leucoblephara*. Thus, the species-level differences documented between the new and resident animals in the University of Bielefeld laboratory colony are actually evidence of species-level differences between *G. musteloides* (the imported animals) and *G. leucoblephara* (the resident laboratory animals and previously studied populations). This explains why our sample of *G. monasteriensis* is placed well within the *G. musteloides* (sensu stricto) clade (Fig. 2). The type locality of *G. monasteriensis* (Valle Hermoso, Cochabamba) is separated from that of *G. boliviensis* (a recognized synonym of *G. musteloides*) by only 30 km of continuous habitat (Fig. 5).

Trillmich et al. (2004) used mtDNA sequence data from the 12S and 16S genes to show >30% sequence divergence between *G. monasteriensis* and *G. musteloides*. Although this evidence seems to challenge our contention that *G. monasteriensis* is actually a junior synonym of *G. musteloides*, Trillmich et al. (2004) also reported that *Galea* was genetically more similar to *Mus musculus* than it was to other members of the Caviidae. Unfortunately, our suspicions about the reliability of the findings of Trillmich et al. (2004) cannot be investigated because the authors did not list the specimens used in their study, and sequences for only 4 specimens from their study were submitted to GenBank.

Within *G. musteloides* we identified an unresolved trichotomy (Fig. 2) that we subdivide tentatively into 2 subclades (as recovered in the BEAST phylogeny; Fig. 3). One of these subclades includes the 2 clades from the vicinity of Lake Titicaca (subclade A in Fig. 2) where *G. m. musteloides* and *G. m. auceps* were described. We retain the subspecific names *G. m. musteloides* and *G. m. auceps* to recognize the 2 clades within subclade A. The other subclade (B in Fig. 2) includes populations from the Bolivian departments of Oruro, Cochabamba, and Santa Cruz. *G. m. boliviensis* and *G. monasteriensis* (now *G. musteloides*) were described from this region, and we retain the trinomen *G. m. boliviensis* for subclade B. Our usage of subspecific epithets is in agreement with the genetic definition of Lidicker (1962).

Upon examination of specimens from 3 localities in the southern Bolivian department of Tarija (Tablada, 2,000 m; Carlazo, 2,300 m; and Sama, 4,000 m; specimens from these localities not sampled in this study), Thomas (1926) reassessed his description of *G. comes* (Thomas, 1919a) from northern Argentina and the description by Waterhouse (1847) of *G. boliviensis* from central Bolivia and concluded that all populations of these species are referable to *G. musteloides*. However, examination of our molecular data suggests that Thomas (1919a) may have been correct in his original assessment of multiple discrete forms in this region. Our samples from Erquis (locality 23 in Fig. 5) and Tucumilla (locality 19) form a well-supported clade (Fig. 2) and are at the same elevation and within 30 km of Tablada and Carlazo. In contrast, Iscayachi (locality 20) is within a few kilometers of Sama and belongs to a different clade (*G. comes*; Fig. 2). Thus, initial hypotheses of Thomas based on morphology are consistent with our molecular results, and it appears that at least 2 forms of *Galea* occur in southern Bolivia and northern Argentina.

The Galea sp. clade.—This as yet unnamed clade contains animals from midelevations (2,100–2,500 m) at Erquis (locality 23) and Tucumilla (locality 19) in Tarija Department, Bolivia. To our knowledge, no names are available for this well-supported clade (Fig. 2), and the distributional extent of this taxon remains unknown. A recently described extinct species of *Galea* (*G. ortodonta*—Ubilla and Rinderknecht 2001) is known from this region, so comparison of our specimens to *G. ortodonta* is warranted before naming this newly recognized *Galea* sp. clade.

The G. comes clade.—In his examination of mammals from the Jujuy region of northern Argentina, Thomas (1913, 1919a) noticed the close affinity of the highland Jujuy fauna to that of the southern Bolivian highlands to the north. Our molecular data are consistent with this observation, because populations of *Galea* from the highlands of southern Bolivia (locality 20 in Fig. 5) unite with those from the highlands of Jujuy (locality 6) to form a well-supported clade (*G. comes*; Fig. 2).

Thomas (1919a) included specimens from Abrapampa, Jujuy (3,500 m), in his description of *G. comes* and designated as holotype a specimen collected previously (Thomas 1913) from Maimará (2,230 m), which is located approximately 100 km south of Abrapampa in contiguous Andean habitat. Although we lack specimens from either Maimará or Abrapampa, our available samples from Iscayachi (locality 20) and Jujuy (locality 6) bracket them to the north and the south, respectively.

The G. leucoblephara clade.—This is a large and reasonably well-supported clade (Fig. 2) that is sister to *G. comes*. We recognize this clade as *G. leucoblephara* (Burmeister, 1861), this being the oldest available name for these populations. As recognized here, *G. leucoblephara* occurs from central Bolivia through Paraguay into southern Argentina and includes *G. demissa* (including *G. s. campicola* in synonymy) and *G. littoralis*. *G. leucoblephara* contains 3 well-supported subclades (C–E in Fig. 2).

Galea l. leucoblephara (subclade C).—Burmeister (1861:425) described *G. leucoblephara* without designating a holotype and provided only a general type locality, ''Die Art war haüfig bei Mendoza wie bei Tucuman'' (roughly, Mendoza to Tucuman, Argentina). Yepes (1936) restricted the type locality to Mendoza, but also failed to designate a holotype (subsequently designated by Solmsdorff et al. [2004]). Cabrera (1953) listed the distribution of *G. leucoblephara* as western Argentina in the provinces of Mendoza, San Juan, and San Luis, the mountains of Córdoba, and possibly southern La Rioja. In our analyses a well-supported group of samples from those provinces (clade C in Fig. 2) supports this distribution, but our findings also extend the distribution northward into southern Catamarca (locality 4). The sample from central Catamarca (locality 5) and the eastern slopes and valleys of the pre-Andean chains in Tucuman (localities 8 and 9) fall more closely with the Paraguayan and Bolivian populations (clade E in Fig. 2).

G. leucoblephara (subgroup D).—This well-supported clade consists of 2 midelevation populations along the eastern versant in the department of Chuquisaca, Bolivia (localities 13 and 14). We know of no available names for this group.

G. l. demissa (subclade E).—Thomas (1921:623) described *G. musteloides demissa* based on a skull from ''San Antonio, Parapiti [sic], Bolivia. Alt. 600 m,'' about 250 km south of Santa Cruz de la Sierra, Santa Cruz Department, Bolivia. Cabrera (1961) restricted the distribution to central Bolivia, Santa Cruz Department, at the base of the mountain zone, whereas Hückinghaus (1961) thought it had a broader distribution encompassing the flatlands of southeastern Bolivia. Specimens included in our analyses that can be associated with the name *D. l. demissa* include those from lowland Bolivia (localities 18, 21, 22, 32, and 33), the northern Chaco regions of Paraguay (localities 24–28), and northern Argentina (localities 5, 8, and 9).

Doutt (1938:100) described *G. spixii campicola* from ''Campo de Guanacas'' [sic] in Santa Cruz Department, Bolivia (450 m), based on the overall size and coloration of the type series. By current taxonomy this form would represent the extreme westernmost point in the distribution of *G. spixii*, a taxon thought to occur mostly in eastern Brazil. Cabrera (1961) and Anderson (1997) accepted Doutt's description of *G. s. campicola* without providing any further diagnosis or comparison with other lowland Bolivian forms of *Galea*. Solmsdorff et al. (2004) stated that *G. s. campicola* resembled *G. musteloides* and suggested that it may represent a northern extension of *G. m. demissa*. Woods and Kilpatrick (2005) include *G. s. campicola* in the synonymy of *G. s. spixii*. In the original description Doutt (1938) made no comparisons to *G. m. demissa* when diagnosing *G. s. campicola*, although the type locality of *G. m. demissa* is approximately 100 km southwest of the type locality of *G. s. campicola*. Our molecular data provide no support for the distinction between these 2 forms. A specimen assigned to *G. s. campicola* by Anderson (1997—locality 32, approximately 150 km north of the type locality) and 2 specimens from the type series of *G. s. campicola* (locality 33) showed no affinity with the Brazilian specimens of *G. spixii*, but fell solidly within the well-supported lowland *G. leucoblephara* clade (Fig. 2).

The southern forms *G. m. littoralis* and *G. m. negrensis* (the latter a junior synonym of *G. m. littoralis*) were not sampled for this analysis. However, reproductive and behavioral studies (Rood 1972; Solmsdorff et al. 2004) suggest that these forms are conspecific with Argentinian *G. leucoblephara*. Thus, until further evidence suggests otherwise, we refer to the southernmost form as *G. leucoblephara littoralis*.

Chromosomal variation in Galea.—George et al. (1972) reported the karyotype for *G. musteloides* from Buenos Aires as $2n = 68$, $FN = 132$, X chromosome submetacentric, and Y chromosome metacentric. Based on our taxonomy, this specimen is referable to *G. leucoblephara littoralis*. This karyotype differs only slightly from those of specimens we karyotyped from southern Bolivia (localities 16, 20, 21, and 23) by presence of a secondary constriction on 1 of the larger chromosomes not evident in our preparation. Thus, chromosomal information from our study and that of George et al. (1972) has limited taxonomic value within the *G. musteloides* group. However, chromosomal information does distinguish

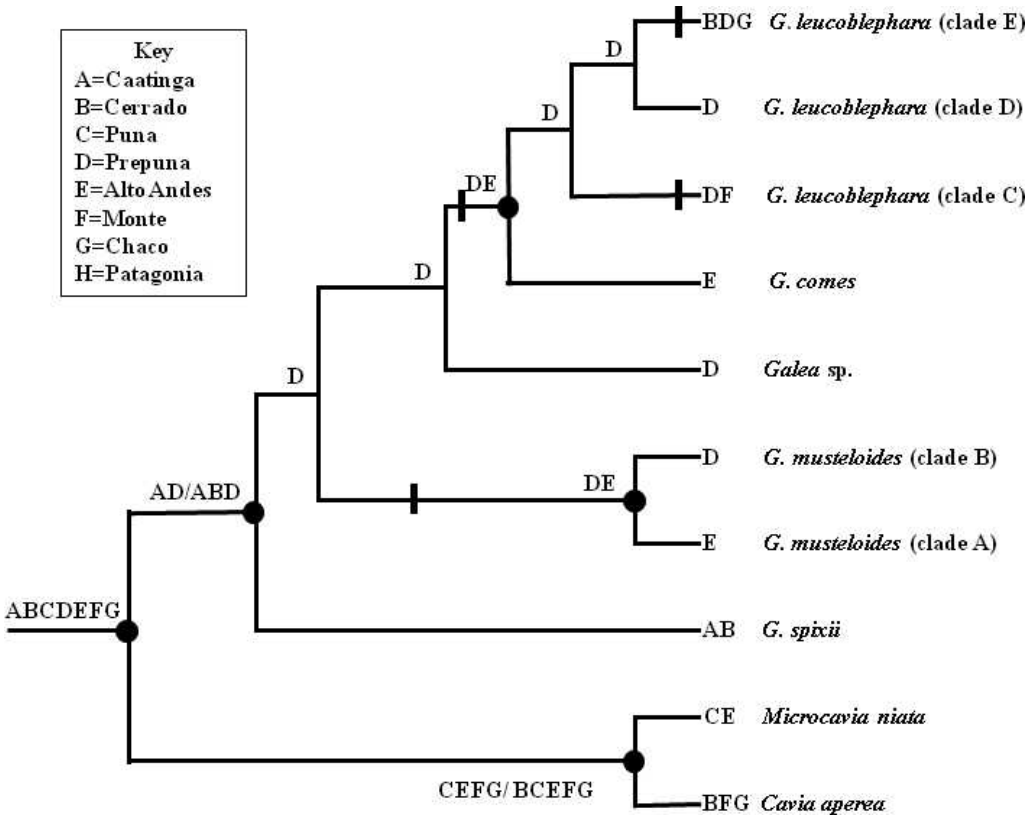

FIG. 6.—Ancestral area relationships reconstructed using DIVA (Ronquist 1996, 1997) for the phylogeny of *Galea* presented in Fig. 2. Letters at nodes correspond to the biogeographic provinces listed in the legend. Black circles indicate vicariant events, and tick marks indicate dispersal events to new biogeographic provinces.

the *G. musteloides* group (restricted thus far to 2n = 68, FN = 132) from *G. spixii* (2n = 64, FN = 118—Maia 1984). This chromosomal difference between *G. spixii* and members of the *G. musteloides* group is accompanied by genetic differentiation that exceeds that measured between other caviomorph genera (e.g., *Myoprocta* and *Dasyprocta*—Rowe and Honeycutt 2002).

Biogeography and dating of divergence times.—Reig (1986) postulated that the Caviidae originated in northeastern Brazil, followed by 2 bouts of diversification, 1 in the biomes to the south, and the other associated with the uplift of the Andes. He speculated that the latter event was responsible for the evolution of various highland forms, including *Galea*.

In our biogeographic analysis a species-area matrix was constructed in DIVA using the default options and an unconstrained maximum number of areas at nodes. One of the acknowledged pitfalls of DIVA is that ancestral area optimizations become less reliable as the analysis approaches the deepest nodes. To reduce this bias we used the distributions of the 2 outgroup taxa to restrict ancestral distributions at the internalmost node (Sanmartin 2003). Eight biogeographic units (equivalent to the biogeographic provinces of Cabrera and Willink [1973]) were used in the analyses: Cerrado, Caatinga, Prepuna, Puna, Alto Andina, Monte, Chaco, and Patagonica. Each of the 10 clades (8 clades in *Galea* and 2 outgroups) were scored according to their presence or absence in each of the 8 biogeographic regions.

Our analysis of species-area relationships in DIVA yielded 1 exact solution (Fig. 6). The analysis identified a broad ancestral distribution for the entire group, followed by a vicariant event that separated *G. spixii* from the *G. musteloides* group. Most of the evolution of the *G. musteloides* group appears to have occurred in the biogeographic province of Prepuna, with 3 subsequent vicariant events separating the *G. musteloides* (sensu stricto) clades, the *Galea* sp. clade, and the *G. comes* clade from *G. leucoblephara*. Two independent dispersal events from the Prepuna toward the lowlands of eastern and southeastern South America also appear to have occurred, 1 that includes animals from *G. leucoblephara* clade C, which appears to have invaded the Monte province, and 1 invasion of members of the *G. leucoblephara* clade E to the provinces of Cerrado, Chaco, and Patagonia.

Estimates of divergence dates from our BEAST analyses (Fig. 4) are congruent with the biogeographic hypotheses obtained in DIVA. By the time the central Andes had neared their current height in the late Miocene (Garzione et al. 2008; Sempere et al. 2006), 2 distinct lineages of *Galea* were present, 1 in the lowlands of eastern South America (*G. spixii*), and a western form that rose with the Andes (the *G. musteloides* group). The highland form spread southward in the early Pliocene and reinvaded the lowlands through the northern Argentinian Andes in the late Pliocene. Once in the lowlands of north-central Argentina, a Pleistocene expansion northward into the Chacoan regions of Paraguay and Bolivia

resulted in the current distribution. This pattern is consistent with that of other Chacoan species; for example, Myers (1982) reported that sister groups of most Chacoan species of both cricetines and hystricognaths are either southern or Andean, and many come from the dry forests or grasslands of the eastern slopes of the Bolivian Andes. Based on both fossil and archaeological evidence, the present distribution of the *G. musteloides* group (sensu Woods and Kilpatrick 2005) was established by the late Holocene, with specimens found at localities from northern Chile (Mann Fischer 1978) to the Argentinean province of Rio Negro (Massoia 1982).

The phylogeny and current distribution of *Galea* reflects the geographic history and topography of central South America and the restrictions they impose on grassland species. The Andes contain several discrete forms of *Galea*, each with a relatively small distribution and high level of genetic divergence from other highland forms. In contrast, the relatively recent invasion of the lowlands by *Galea* has resulted in a single, wide-ranging species with low genetic divergence among regional subclades that are restricted to different lowland biomes (e.g., the Chaco and scrub desert of west-central Argentina) or different elevations (e.g., midelevational outcroppings in Catamarca and Tucuman and Andean foothills in Chuquisaca).

Our phylogeny and revised taxonomy of *Galea* provides a foundation for not only further molecular investigations of the genus but also future morphological studies that hold the potential of revealing new and useful diagnostic characters for *Galea* taxa. In addition, a greater understanding of systematic relationships within another animal taxon that spans both the Andes and lowlands of central and southern South America provides further insight into the role of the Andes in shaping the evolutionary history of the rich fauna associated with the diverse grasslands of South America.

Resumen

Hoy por hoy, el género *Galea* está compuesto de 3 especies: *G. musteloides*, *G. flavidens* y *G. spixii*. La especie *G. musteloides* es la de más amplia distribución con poblaciones conocidas desde el centro de Perú hasta el sur de la Argentina y desde el nivel del mar hasta más de 4,000 m. El conocimiento taxonómico y sistemático del género *Galea* están sustentados principalmente en estudios de caracteres morfológicos, sesgados por pequeños tamaños muestrales con pobre representación geográfica y taxonómica. En este trabajo y basados en un muestreo detallado de taxa y poblaciones reconocidas para *G. musteloides* utilizamos secuencias de un gen mitocondrial (citocromo *b*), con el objetivo de poner a prueba hipótesis de limites específicos y relaciones filogenéticas de varios grupos nominales. Nuestros resultados sugieren que *G. musteloides* debería estar restringido al taxon con poblaciones en el altiplano de Bolivia, sur del Perú y extremo noreste de Chile. Sugerimos reconocer *G. leucoblephara* Burmeister, 1861, para las poblaciones distribuidas en los llanos del oriente de Bolivia, partes de Paraguay y de ahí hasta Argentina central, además de que sugerimos reconocer el nombre *G. comes* Thomas, 1919, para poblaciones distribuías en los Andes del sur Bolivia y norte de la Argentina. También proponemos la existencia de un taxon actualmente innominado en elevaciones medias (aproximadamente 1,800 m) del sur de Bolivia. Utilizando muestras de las series típicas de las formas nominales *G. spixii campicola* y *G. monasteriensis* sugerimos que la primera (*G. spixii campicola*) debería ser considerada un sinónimo subjetivo de *G. l. demissa* y que las segunda (*G. monasteriensis*) es un sinónimo subjetivo de *G. musteloides boliviensis*. La evolución de *G. musteloides* parece haber ocurrido en la provincia biogeográfica de la Prepuna seguida de 2 eventos vicariantes independientes que culminaron en la separación de los clados *G. musteloides*, *G. comes* y *G. leucoblephara*. La separación entre *G. spixii* y las especies del grupo *G. musteloides* sucedió en el Mioceno tardío mientras que la divergencia entre las especies de complejo *musteloides* sucedió en el Plioceno.

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Appendix I

Specimens used in the phylogenetic analyses of the cytochrome-*b* gene, GenBank accession numbers, and locality information. Locality numbers refer to Figs. 1, 2, and 5. Taxonomy follows Woods and Kilpatrick (2005) and subspecies designations are as outlined in Anderson (1997) and Cabrera (1961). The specimen of *Galea monasteriensis* is a descendant of animals from type locality of this species (Bolivia: Cochabamba; Valle Hermoso, 2,557 m). Asterisks (*) denote GenBank sequences from Spotorno et al. 2004. Daggers (†) denote specimens accompanied by karyotypes. Acronyms are as follows: American Museum of Natural History (AMNH); Carnegie Museum of Natural History (CM); Colecćion Boliviana de Fauna, La Paz, Bolivia (CBF); Colecćion de Mamíferos Lillo, Universidad Nacional de Tucumán, Tucumán, Argentina (CML); Colecćion Mastozoológica, Instituto Argentino de Investigaciones de las Zonas Aridas, Mendoza, Argentina (IADIZA); Laboratorio de Citogenética Mammiferos, Universidad de Chile (LCM); Museo Noel Kempff Mercado, Santa Cruz, Bolivia (MNK); Museum of Southwestern Biology, Division of Genomic Resources, University of New Mexico (NK); Museum of Southwestern Biology, University of New Mexico (MSB); Museum of Vertebrate Zoology, University of California Berkley (MVZ); Sam Noble Oklahoma Museum of Natural History (OMNH); Sam Noble Oklahoma Museum of Natural History Argentina collection (ARG); Texas A&M University tissue collection (AK); Texas Tech University tissue collection (TK).

Taxon	Specimen no.	GenBank no.	Locality no.	Locality	Latitude and longitude	No. base pairs
Galea mustelides leucoblephara	MVZ 166428	GU067495	1	Argentina: Mendoza; Lujan, Chacras de Coria, 900 m	−33.05, −68.86	1–1,140
G. m. leucoblephara	IADIZA 4484 (AK 13772)	GU067529	2	Argentina: San Luis; Ayacucho, 825 m	−32.36 −66.13	1–370, 560–1,140
G. m. leucoblephara	CML 3430 (AK 13818)	GU067528	3	Argentina: San Luis; 9 km N Paso del Rey, 1,463 m	−32.83 −66.00	1–1,140
G. m. leucoblephara	OMNH 33316 (ARG 5720)	GU067533	4	Argentina: Catamarca; El Alto, Bella Vista, 974 m	−28.63, −65.50	1–801
G. m. leucoblephara	OMNH 30229 (ARG 4663)	GU067535	5	Argentina: Catamarca; Ambato, Estancia Narvaez, 5.5 km N Chacritas on Ruta Provincial 1, 1,782 ± 150 m	−27.65, −65.93	1–787
G. m. leucoblephara	OMNH 35554 (ARG 6777)	GU067530	6	Argentina: Jujuy; 12.3 km N, 11.5 km W of San Antonio de los Cobres, 4,336 m	−24.14, −66.41	1–1,140
G. m. leucoblephara	ARG 5406 (TK 85602)	GU067534	7	Argentina: La Rioja; La Paz, Salinas Grandes, 26 km SW Quimilo, 200 m	−30.05, −65.52	1–787
G. m. leucoblephara	OMNH 33341 (ARG 6044)	GU067532	8	Argentina: Tucumán; Tafí del Valle, 20.6 km W Tafí, 3,024 m	−26.74, −65.75	1–787
G. m. leucoblephara	OMNH 33319 (ARG 6305)	GU067531	9	Argentina: Tucumán; Trancas, 24 km NW Hualinchay, 3,170 m	−26.37, −65.67	1–1,140
G. m. auceps	MSB 70582 (NK 30655)	GU067504	10	Bolivia: La Paz; 11.5 km W San Andres de Machaca, 3,800 m	−17.00, −69.00	1–1,140
G. m. auceps	AMNH 268934 (NK 30656)	GU067503	10	Bolivia: La Paz; 11.5 km W San Andres de Machaca, 3,800 m	−17.00, −69.00	1–1,140
G. m. auceps	MSB 57184 (NK 14792)	GU082485	11	Bolivia: La Paz; 14 km SW San Andres de Machaca, 3,850 m	−16.80, −68.88	1–1,140
G. m. musteloides	MSB 70581 (NK 30468)	GU067505	12	Bolivia: Cochabamba; 7.5 km SE Rodeo Curubamba, 4,000 m	−17.68, −65.60	1–1,140
G. m. musteloides	CBF 1181 (NK 21624)	GU067522	13	Bolivia: Chuquisaca; 12 km N, 11 km E Tarabuco, 2,450 m	−19.07, −64.82	1–1,140
G. m. musteloides	CBF 1096 (NK 21625)	GU067521	13	Bolivia: Chuquisaca; 12 km N, 11 km E Tarabuco, 2,450 m	−19.07, −64.82	1–1,140
G. m. musteloides	AMNH 263954 (NK 21540)	GU067523	14	Bolivia: Chuquisaca; 11 km N and 16 km W of Padilla, 2,050 m	−19.20, −64.45	25–1,140
G. m. musteloides	AMNH 262993 (NK 14737)	GU067527	15	Bolivia: Oruro; 7 km S, 4 km E Cruce Ventilla, 3,450 m	−19.13, −66.12	1–1,140
G. m. musteloides	AMNH 262994 (NK 14738)	GU067526	15	Bolivia: Oruro; 7 km S, 4 km E Cruce Ventilla, 3,450 m	−19.13, −66.12	1–1,140

Appendix I.—Continued.

Taxon	Specimen no.	GenBank no.	Locality no.	Locality	Latitude and longitude	No. base pairs
G. m. musteloides	MSB 57182 (NK 14739)	GU067525	15	Bolivia: Oruro; 7 km S, 4 km E Cruce Ventilla, 3,450 m	−19.13, −66.12	1–1,140
G. m. musteloides	MSB 67327 (NK 22819)†	GU067520	16	Bolivia: Santa Cruz; 6 km NNE Quiñe, at Estancia Jahue, 1,975 m	−18.03, −64.32	1–1,140
G. m. musteloides	AMNH 264469 (NK 22940)	GU067519	17	Bolivia: Santa Cruz; 17 km S of Quiñe, at Estancia Laja, 2,100 m	−18.20, −64.30	1–1,140
G. m. musteloides	NK 23329 (MNK)	GU067518	18	Bolivia: Santa Cruz; 53 km E of Boyuibe, 600 m	−20.45, −62.83	1–1,140
G. m. musteloides	AMNH 264471 (NK 23720)	GU067509	19	Bolivia: Tarija; 1 km E de Tucumilla, 2,500 m	−21.45, −64.82	1–1,140
G. m. musteloides	MSB 140412 (NK 23579)†	GU067513	20	Bolivia: Tarija; 1 km E of Iscayachi, Rio Tomayapo, 3,450 m	−21.48, −64.95	1–1,140
G. m. musteloides	MSB 140413 (NK 23581)	GU067512	20	Bolivia: Tarija; 1 km E of Iscayachi, Rio Tomayapo, 3,450 m	−21.48, −64.95	1–1,140
G. m. musteloides	MSB 140414 (NK 23590)	GU067511	20	Bolivia: Tarija; 1 km E of Iscayachi, Rio Tomayapo, 3,450 m	−21.48, −64.95	1–1,140
G. m. musteloides	AMNH 264473 (NK 23591)	GU067510	20	Bolivia: Tarija; 1 km E of Iscayachi, Rio Tomayapo, 3,450 m	−21.48, −64.95	1–1,140
G. m. musteloides	AMNH 264470 (NK 23372)†	GU067517	21	Bolivia: Tarija; 2 km S and 5 km E of Palos Blancos, 800 m	−21.43, −63.73	1–1,140
G. m. musteloides	AMNH 264475 (NK 25145)	GU067505	22	Bolivia: Tarija; 4 km N Estancia Bolivar, 400 m	−21.60, −62.57	1–1,140
G. m. musteloides	AMNH 264476 (NK 25201)	GU067506	22	Bolivia: Tarija; 5 km W Estancia Bolivar, 400 m	−21.63, −62.62	1–1,140
G. m. musteloides	AMNH 264477 (NK 25186)	GU067507	22	Bolivia: Tarija; 5 km W Estancia Bolivar, 400 m	−21.63, −62.62	1–1,140
G. m. musteloides	MSB 67328 (NK 23463)	GU067516	23	Bolivia: Tarija; Erquis, 2,100 m	−21.47, −64.80	1–1,140
G. m. musteloides	CBF 2380 (NK 23464)	GU067515	23	Bolivia: Tarija; Erquis, 2,100 m	−21.47, −64.80	1–1,140
G. m. musteloides	MSB 67329 (NK23503)†	GU067514	23	Bolivia: Tarija; Erquis, 2,100 m	−21.47, −64.80	1–1,140
G. m. musteloides	TK 65288	GU067501	24	Paraguay: Alto Paraguay; Estancia Tres Marias, 70 m	−21.28, −59.62	1–1,140
G. m. musteloides	TK 65360	GU067500	25	Paraguay: Alto Paraguay; Palmar de Las Islas, approximately 215 m	−19.63, −60.61	1–1,140
G. m. musteloides	TK 65364	GU067499	25	Paraguay: Alto Paraguay; Palmar de Las Islas, approximately 215 m	−19.63, −60.61	1–1,140
G. m. musteloides	TK 65579	GU067498	26	Paraguay: Alto Paraguay; Fortin Pikyrenda, approximately 340 m	−20.09, −61.79	1–1,140
G. m. musteloides	TK 65659	GU067497	27	Paraguay: Boquerón; Parque Cue, approximately 340 m	−20.13, −61.76	1–1,140
G. m. musteloides	TK 66465	GU067496	28	Paraguay: Boquerón; Parque Nacional Teniente Enciso (approximately Puesto Siracua), 255 m	−21.04, −61.76	1–1,140
G. m. musteloides	TK 65036	GU067502	28	Paraguay: Boquerón; Parque Nacional Teniente Agripino Enciso, 255 m	−21.04, −61.75	1–1,140
G. m. auceps	LCM 2494	AY46660*	29	Peru: Puno; Desaguadero, 3,809 m	−16.57, −69.05	1–1,125
G. m. auceps	LCM 2496	AY46660*	30	Peru: Puno; Sillustani, 3,800 m	−15.73, −70.17	1–1,125
G. monasteriensis	Z1M31	GU067494	31	University of Muenster laboratory colony	−17.38, −66.15	1–1,114

Appendix I.—Continued.

Taxon	Specimen no.	GenBank no.	Locality no.	Locality	Latitude and longitude	No. base pairs
G. spixii campicola	AMNH 260800 (NK 12269)	GU067493	32	Bolivia: Santa Cruz; 3.5 km W of Estación Pailón, 300 m	−17.65, −62.75	1–1,140
G. s. campicola	CM 1975	GU067536	33	Bolivia: Santa Cruz; Campo de Guanacas, 450 m	−19.00, −63.00	244–416
G. s. campicola	CM 1977	GU067537	33	Bolivia: Santa Cruz; Campo de Guanacas, 450 m	−19.00, −63.00	244–416
G. s. wellsi	MVZ 197805	GU067492	34	Brazil: Ceará; Baixo dos Aleida, 41 km NW Crato	−07.03, −39.72	1–1,140
G. s. wellsi	MVZ 197806	GU067491	34	Brazil: Ceará; Baixo dos Aleida, 41 km NW Crato	−07.03, −39.72	1–1,140
Microcavia niata	AMNH 263000 (NK 14529)	GU067490		Bolivia: Oruro; 30 km S, 25 km E Sajama, 3,850 m	−18.25, −68.48	1–1,140
Cavia aperea	MSB 141629 (NK 116565)	GU067538		Bolivia: La Paz; Apa Apa, 1,605 m	−16.38, −67.52	1–1,140

Appendix II

Cytochrome-*b* (*Cytb*) primers designed for this study. Location corresponds to the approximate start point of targeted *Cytb* sequence. R = reverse primer; F = forward primer.

Primer	Sequence	Strand	Location
CAV2	AAKGATATTTGYCCYCATGG	R	399
CAV5	ATTGTTTATACTACCAGGGC	R	>1,140
GAL3	ATCATTCAGGTTTAATGTGTG	R	796
GAL6	CCATCAAATATCTCAGCATGATGAAA	F	96
GAL7	GACAAAGCAACCCTAACACGAT	F	533
GAL10	CTCCATGCCAATGGCGCATCAATA	F	244
GAL11	GTGTGGCGGTGTGTTTAAAGGGTT	R	801