Journal of Mammalogy, 95(2):201–215, 2014

A new genus of sigmodontine rodent from eastern Brazil and the origin of the tribe Phyllotini

Ulyses F. J. Pardiñas,* Gisele Lessa, Pablo Teta, Jorge Salazar-Bravo, and Edeltrudes M. V. C. Câmara

Centro Nacional Patagónico, Casilla de Correo 128, 9120 Puerto Madryn, Chubut, Argentina (UFJP, PT)
Museu de Zoologia, Departamento de Biologia Animal, Universidade Federal de Viçosa, 36571-000 Viçosa, Minas Gerais, Brasil (GL)
Department of Biological Sciences, Texas Tech University, Lubbock, TX 79409, USA (JSB)
Museu de Ciências Naturais da Pontifícia Universidade Católica de Minas Gerais and Bicho do Mato Instituto de Pesquisa, Belo Horizonte, Minas Gerais, Brasil (EMVCC)

* *Correspondent: ulyses@cenpat.edu.ar*

We describe a new living genus and species of Sigmodontinae currently only known from the Brazilian National Park Sempre Vivas, Minas Gerais State. This rodent is characterized by a unique combination of traits that include, among others, a long tail, with its distal tip (approximately 2.5 to 5 cm) entirely white; skull with domed profile; long rostrum with an incipient rostral tube; and noticeable small brachyodont molars with reduced mesolophs and mesostyles present on the 1st and 2nd upper molars. Cladistic analyses of molecular (1 mitochondrial and 1 nuclear marker) and morphological characters indicate that the new genus belongs to the Phyllotini and is sister to the remainder genera of this tribe. However, contrary to other known phyllotines, the new genus shows vestigial mesolophs and mesostyles. Phyllotines are widespread in open areas, in particular desert and semideserts, mostly in the western portion of South America. The new genus described herein expands the diversity of the tribe and suggests an ancient event of diversification in eastern Brazil.

Key words: Brazil, *Calomys*, Cerrado, Cricetidae, Sigmodontinae

DOI: 10.1644/13-MAMM-A-208

Phyllotini includes several genera of small- to medium-sized rodents widely distributed in south-central and southern South America, often associated with Andean, Patagonian, and Chacoan distributions. The maximum species diversity for the tribe occurs in the Puna, deserts, and semideserts of western South America (Hershkovitz 1962; Musser and Carleton 2005; Salazar-Bravo et al. 2013). The taxonomic history of the tribe is convoluted and it did not reach some level of stability until recently when molecular data suggested that several genera of high-elevation rodents (e.g., *Andinomys*, *Chinchillula*, *Neotomys*) were not closely related to the members of the Phyllotini and were better considered Sigmodontinae incertae sedis (Martínez et al. 2012; Salazar-Bravo et al. 2013). Therefore, as currently understood, the tribe is composed of 10 genera: *Andalgalomys*, *Auliscomys*, *Calomys*, *Eligmodontia*, *Galenomys*, *Graomys*, *Loxodontomys*, *Phyllotis*, *Salinomys*, and *Tapecomys*. With the exception of *Calomys* and *Graomys*, the remaining members of the tribe are primarily associated with habitats on the western and southwestern half of South America. In fact, the imbalance in the geographic distribution of the members of the tribe is such that large portions of the Guianan shield and the Brazilian territory only host the widespread genus *Calomys*, whereas *Graomys* has only marginal records near the Paraguayan border (Hershkovitz 1962). As far as it is known, no phyllotines occur in the Amazonian basin proper; this pattern of geographic distribution was used by Hershkovitz (1962), Reig (1984, 1986), and others (Braun 1993; Steppan 1995) to either propose or support the Altiplano and Puna as the area of original differentiation for the tribe.

The origin of the Phyllotini was a matter of a candent discussion in the early 1980s; on the basis of fossils recovered in southern United States (e.g., †*Bensonomys*), Baskin (1978, 1986) stated that phyllotines initially evolved in North America during the Pliocene to later reach South America after the closure of the Panama land bridge. Contradicting Baskin's

---

† Represents the extinct (fossil) condition of this genus.

arguments, Reig (1980, 1984, 1986) strongly defended a South American origin for the tribe. This author disregarded the allocation of †*Bensonomys* (sometimes considered as subgenus of *Calomys*) in Phyllotini, or even in Sigmodontinae, invoking convergence to explain the observed morphological similarities. Although Steppan (1995), diagnosing cladistically *Calomys*, excluded †*Bensonomys* from it, the tribal or subfamiliar allocation of the latter is still unstable (cf. McKenna and Bell 1997; Pardiñas et al. 2002; Musser and Carleton 2005). Moreover, †*Symmetrodontomys*, another North American fossil, is uncritically considered sister of *Calomys* (Lindsay 2008) and the debate about phyllotine origins remains open and has increased with the addition of putative candidates such as †*Antecalomys* (e.g., Korth 1998).

Here we describe a new living genus and species of Phyllotini currently found in only a small number of localities in Minas Gerais state, eastern Brazil. Phylogenetic analyses based on combined nuclear and mitochondrial molecular markers place this form as sister to the remaining genera of the tribe (Parada et al. 2013; Salazar-Bravo et al. 2013). Noteworthy, morphological traits present in the new genus (e.g., the persistence in the 1st and 2nd upper molars of vestigial mesolophs and mesostyles) are unique within Phyllotini and prompted us to address the origin of this group in the context of the evolution of South American open environments.

MATERIALS AND METHODS

Our study was based on 6 specimens livetrapped following the procedures of the American Society of Mammalogists (Sikes et al. 2011) in Sempre Vivas National Park, Minas Gerais, Brazil. In addition, at least another 13 individuals were captured and karyotyped but solely preserved as skins in fluid or histological preparations of some anatomical portions. A more detailed inspection of these animals in the cabinet revealed a set of traits that separates this rodent from all sigmodontines previously known. From this primary morphological inspection overall similarities were detected with *Calomys* and, to a minor extent, *Wiedomys* and *Zygodontomys*. As *Delomys* is consistently recovered as associated with Phyllotini (Parada et al. 2013; Salazar-Bravo et al. 2013), it was, together with the mentioned genera, included in the comparisons (see below). Four specimens of the new form described here, including the holotype, are housed in the Coleção de Mamíferos do Museu de Ciências Naturais da Pontifícia Universidade Católica de Minas Gerais (MCN/PUC-MG), Minas Gerais, Brazil. Two more have been deposited in the collections of the Centro Nacional Patagónico (CNP, Puerto Madryn, Chubut, Argentina) and the Museu de Zoologia, Departamento de Biologia Animal, Universidade Federal de Viçosa (MZUFV, Viçosa, Minas Gerais, Brazil). All specimens examined, including those used in comparisons, are listed in Appendix I.

Anatomical descriptions and terminology follow Reig (1977), Carleton (1980), Voss (1988), Carleton and Musser (1989), and Weksler (2006); scale pattern on guard hairs was described according to Day (1966) and the nomenclature of Carleton (1980) and Myers and Patton (1989) was used to describe the anatomy of the soft palate. Standard external measurements (total length, length of tail, length of hind foot with and without claw, length of ear from notch, in millimeters) and weights (W, in grams) were transcribed from the specimens' labels as originally recorded by the collectors. Craniodental dimensions were taken using digital calipers and recorded to the nearest 0.01 mm following the definitions provided by Hershkovitz (1962) and Voss (1991). They are arranged in alphabetical order as follows: breadth across both incisive foramina; breadth of braincase; breadth of rostrum; breadth of the 1st maxillary molar; breadth of the mesopterygoid fossa (maximum); breadth of the palatal bridge (measured between the M1 protocones); breadth of the zygomatic plate; condyloincisive length; least interorbital breadth; length of diastema; length of 1 incisive foramen; nasal length; occlusal length of the dentary molar row; occlusal length of the maxillary molar row; and zygomatic breadth. Taking into account the similarities in dental pattern between the new genus and *Zygodontomys*, for the age classification of the individuals examined we adopted the toothwear classes defined by Voss (1991:16).

Karyotypic data were obtained for 3 males and 1 female of the new form following protocols outlined in Verma and Babu (1995); briefly, bone marrow was incubated in 0.1 ml (0.05%) of colchicine plus 9.9 ml of KCl (0.075 M) for 40 min at 37°C and subsequently fixed in 3:1 methanol : glacial acetic acid.

To further guide our analyses and to place the new genus herein described in a phylogenetic context, we obtained the complete sequence of the mitochondrial cytochrome *b* gene (*Cytb*) of MCN/PUC-MG 2650 and a fragment of 759 base pairs of the 1st exon of the nuclear gene interphotoreceptor retinoid binding protein (IRBP) for MCN/PUC-MG 2646. Sequences were navigated and translated to proteins to proof for stop codons using SeqManII 5.07 (DNAStar 2003). The 2 markers were analyzed by Parada et al. (2013) and Salazar-Bravo et al. (2013) as part of their broad phylogenetic analyses where the new genus appears as Phyllotini, new genus; details of phylogenetic analyses are provided therein.

RESULTS

FAMILY CRICETIDAE FISCHER, 1817
SUBFAMILY SIGMODONTINAE WAGNER, 1843
TRIBE PHYLLOTINI VORONTSOV, 1959
Calassomys, gen. nov.

Type species.—*Calassomys apicalis*, gen. et sp. nov.

Etymology.—In memory of A. Calaça do Espírito Santo, father of one of the authors (EMVCC).

Geographic distribution.—Known from the eastern portion of Brazil, state of Minas Gerais, in the rocky outcrops of Serra do Espinhaço, Sempre Vivas National Park, above 1,000 m above seal level (asl).

Chronological distribution.—Recent. No fossils are known.

Fig. 1.—Holotype of *Calassomys apicalis*, gen. et sp. nov., from Sempre Vivas National Park, Minas Gerais, Brazil (MCN/PUC-MG 2785): skull in right lateral (top), dorsal (left) and ventral (right) views, and right dentary in labial view. Scale = 5 mm.

Contents.—Exclusively the type species.

Morphological diagnosis and description.—As for the single included species, below.

Calassomys apicalis, gen. et sp. nov.
Figs. 1–6

Holotype.—MCN/PUC-MG 2785, an adult male (tooth-wear class [TWC] 3 sensu Voss [1991]) preserved as skull (Fig. 1), partial postcranial skeleton, study skin (in good condition), mounted karyotype, cell suspension and alcohol-preserved tissue; collected by E. Câmara and C. Guimarães Costa in November 2006.

Type locality.—Brazil, Minas Gerais, Sempre Vivas National Park, 3.25 km by road NW Macacos, Pedreira do Gaio (17°57′50″S, 43°47′18″W, 1,251 m asl).

Paratypes.—MCN/PUC-MG 1244, an adult male (TWC 3) preserved as skull, partial postcranial skeleton, and skin in poor condition, collected by R. Parisi Dutra on 2 July 2005. MCN/PUC-MG 1142, an adult male (TWC 3) preserved as skull, partial postcranial skeleton, and skin, collected by F. Freire Diniz and K. Leal on 26 August 2005. MCN/PUC-MG 1144, an adult individual, sex unknown (TWC 3) preserved as skull (nasal damaged on tip, right zygomatic arch broken) and partial skeleton, collected by K. Leal and C. Guimarães Costa on 27 August 2005. MZUFV 2237, an adult male (TWC 4) preserved as skull, partial postcranial skeleton, and skin in poor condition, collected by K. Leal and D. G. Saraiva on 12 October 2007. CNP 3437, a subadult male (TWC 2) preserved as eviscerated body in ethanol and cleaned skull, collected by K. Leal and G. Rocha on 12 October 2007 (field number DG 88).

Distribution.—Known from only 3 localities in the Cerrado ecoregion. In addition to the type locality, *C. apicalis* was collected in 2 additional locations in the Sempre Vivas National Park, Campo de Pedras (17°57′56″S, 43°48′04″W; 1,421 m) and Arrenegado (17°33′42″S, 43°44′24″W; 1,140 m), the latter about 46 km N of Macacos.

Etymology.—The specific epithet is a reference to the white color on the distal portion of the tail, a remarkable and uncommon external feature of this new form; *apicalis*, meaning "pertaining to the tip" (from Latin, *apex* + *alis*, *alius*).

Measurements of the holotype (mm).—Total length = 274; length of tail = 157; length of hind foot with (and without) claw = 25 (23); length of ear from notch = 19; weight = 46 g; breadth across both incisive foramina = 2.31; breadth of braincase = 13.29; breadth of rostrum = 5.74; breadth of the 1st maxillary molar = 1.24; breadth of the mesopterygoid fossa = 2.07; breadth of the palatal bridge = 3.55; breadth of the zygomatic plate = 2.34; condyloincisive length = 27.15; least interorbital breadth = 5.07; length of diastema = 8.06; length of 1 incisive foramen = 6.25; nasal length = 11.63; occlusal length of the dentary molar row = 4.3; occlusal length of the maxillary molar row = 4.14; and zygomatic breadth = 15.07.

Morphological diagnosis.—A member of the subfamily Sigmodontinae with the following combination of characters: size medium (head and body length ~110 mm; condyloincisive length ~27.1 mm); moderately large ears (~20 mm); numerous and long mystacial vibrissae, the longest surpassing the tips of the ears when bent backward; long tail, with distal tip ranging from 2.5 to 5 cm entirely white, including a short terminal tuft of hairs; skull with domed profile; long rostrum; nasals and premaxilla produced anteriorly, forming an incipient rostral tube; inconspicuous zygomatic notches; interorbit convergent anteriorly with sharp frontal borders; rounded and smooth braincase; carotid circulatory pattern 1 (Voss 1988); palate wide and short; mesopterygoid fossa especially broad; parapterygoid plates reduced; middle lacerate foramen conspicuously open; suspensory process of squamosal and tegmen tympani present; alisphenoid strut typically present; opisthodont upper incisors; noticeably small (upper tooth-row length ~4.1 mm)

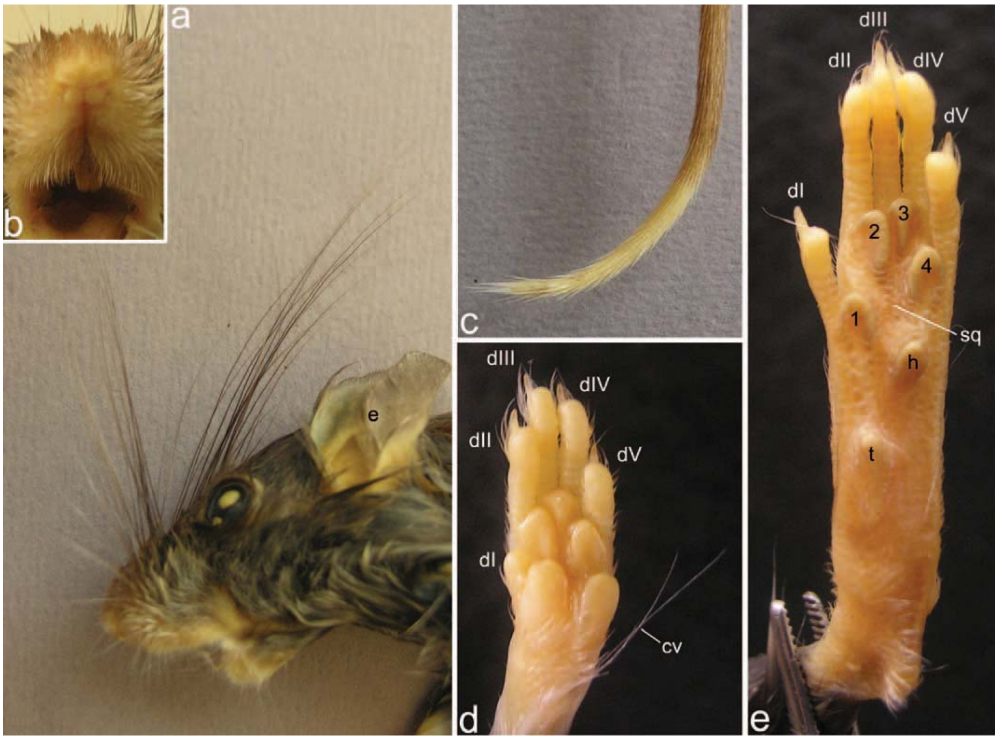

Fig. 2.—Anatomical external details of *Calassomys apicalis*, gen. et sp. nov., based on the young fluid-preserved individual CNP 3437 (Sempre Vivas National Park, Minas Gerais, Brazil): a) head in lateral view; b) muzzle in frontal view; c) distal portion of tail; d) manus in palmar view; e) pes in palmar view. Abbreviations are 1, 2, 3, 4, interdigital pads; cv, carpal vibrissae; dI, dII, dIII, dIV, dV, digits; e, ear; h, hypothenar pad; sq, squamae; t, thenar pad.

and simplified brachyodont molars with crested surfaces and main cusps in opposite pattern; anteromedian flexus/id absent; vestigial mesoloph, mesostyle, and parastyle typically present on M1 and M2; gall bladder present.

Morphological description.—*C. apicalis* is a medium-sized sigmodontine rodent (Table 1) with moderately large and naked ears, conspicuous, long mystacial vibrissae, and a long tail with a totally white distal end (Fig. 2). The available specimen s for study are markedly homogeneous in age (being 5 adults and only 1 young), measurements (see Table 1), and general morphology. The following description is based on all specimens at hand.

Eyes of regular size with a conspicuous black eye-ring (Fig. 2a). Numerous dark and white mystacial vibrissae, the longest surpassing the tips of the ears when bent backward; 2 short superciliary and 1 genal vibrissae also present, the latter reaching the earbases when bent backward (Fig. 2a). Upper lips densely covered by white hairs (Fig. 2b). Ears moderately large, rounded, partially naked, covered internally and externally by short and delicate brown hairs; concha and tragus strikingly yellow resembling the condition displayed by some marsupials (e.g., *Thylamys*). Dorsal and ventral colors subtly delimited with weak countershading. Dorsal fur with dark gray base and brown-ochraceous or brown-yellowish tips, long (guard hairs ~15 mm) and soft; individual hairs in the ventral fur with plumbeous gray bases and whitish tips; muzzle and cheeks whitish gray. Scale pattern on guard hairs lanceolate, changing to mosaic toward the distal one-half; medullae biseriate along most of the hair, becoming uniseriate at the extremes. Long tail, clearly longer than combined head and body lengths, bicolored dorsoventrally—brown above, white below—except for the distal 2.5 to 5 cm white all around, sparse apical tuft present conformed by white hairs of about 5 or 6 mm in length (Fig. 2c); tail covered by sets of 3 delicate hairs per scale, each dorsal hair covering 2 scale rows. Manus dorsally covered with short whitish hairs; digit III and dIV subequal in size, with dIII slightly longer than dIV; dII and dV shorter than dIII and IV, with dII clearly longer than dV; dI vestigial and with a small nail; dII–V with inconspicuous claws (~1.8 mm), dorsally covered by whitish ungueal hairs; ventral surface naked and unpigmented, with 2 carpal and 3 interdigital pads large and fleshy, almost equal in size (Fig. 2d); a heart-shaped callus is present on each interdigital pad. Pes enlarged and narrow; dI and dV much shorter than II–IV; claw of dI extending to middle of 1st phalange of dII, claw of dV extending to middle of 2nd phalange of dIV; ungal tufts whitish, level at or slightly surpassing the tips of the short unkeeled claws (~1.8 mm); pedal dorsum sparsely covered by entirely whitish hairs; plantar surface naked, unpigmented, and slightly squamated (sensu Pacheco 2003), with 4 large, nearly ovate interdigital pads; hypothenar pad subequal in size to the 1st interdigital and intermediately located between the 1st interdigital and thenar pads; thenar pad enlarged and narrow,

Fig. 3.—Cranial details of *Calassomys apicalis*, gen. et sp. nov., based on adult individuals MCN/PUC-MG 2785, 1144, and MZUFV 2237 (Sempre Vivas National Park, Minas Gerais, Brazil): a) rostrum in dorsal view; b) interorbital region; c) left zygomatic plate; d) left squamosal region; e) diastemal palate; f) pterygoid region; g) auditory bulla in laterointernal view. Abbreviations are b, auditory bulla; cc, carotid canal; cs, coronal suture; et, eustachian tube; f, frontal; fl, lacerate foramen; h, hamular process; if, incisive foramen; l, lacrimal; mf, mesopterygoid fossa; n, nasal; p, parietal; pgf, postglenoid foramen; pm, premaxillary process; pp, parapterygoid plate; s, origin of the superficial masseter; sq, squamosal; ssf, subsquamosal fenestra; stf, stapedial foramen; tt, tegmen tympani; zp, zygomatic plate.

except for the calluses on the plantar pads (Fig. 2e); long hairs at the sides of the heel partially cover the calcaneum area.

Skull domed on lateral profile and braincase moderately dominating the dorsal aspect (Fig. 1). Rostrum long and moderately broad (Fig. 3a); rostral sides taper gradually but the premaxillary bones can be seen to extend for almost their entire length along the nasal margins. Nasals broad and especially projected in their anterior third, in conjunction with the premaxillaries forming an incipient rostral tube or "trumpet" and totally covering incisors when the skull is viewed from top; nasals parallel sided and slightly turned down at tips. Large lacrimals (Fig. 3a). Interorbital region wide and dorsally flat; interorbital constriction immediately behind inconspicuous frontal sinuses; margins of frontal bones sharp and posteriorly divergent but not to the point of producing supraorbital shelves (Fig. 3b). Coronal suture open "V"-shaped (Fig. 3b). Braincase large and rounded, temporal and lambdoidal ridges absent; suture between parietals and squamosals concealed by a slightly developed bony ridge in adult specimens. Interparietal large. Zygomatic plate narrow and high (Fig. 3c) with a moderate forward extension forming a free anterodorsal margin and defining a shallow zygomatic notch. Zygomatic arches delicate, their midportions dip ventrally but remain discernibly above the level of the orbital floor. Jugal short but distinctly separates the maxillary and squamosal portions of the arch. Parietals without extensions in lateral view. Hamular process of the squamosal long, thick, and with an unexpanded posterior end; subsquamosal fenestra reduced with respect to the postglenoid foramen (Fig. 3d). Tegmen tympani contacting and overlapping a suspensory process of the squamosal bone. Incisive foramina long and wide, compressed anteriorly, with posterior ends rounded and slightly surpassing the anterior roots of M1; premaxillary processes occupying three-fourths in length of the incisive foramina (Fig. 3e). Palate wide and short, vaulted, with diminutive posterolateral palatal pits at the sides of the mesopterygoid fossa. Mesopterygoid fossa especially wide, with anterior borders reaching posterior face of M3; anterior portion slightly lyre-shaped with median palatine

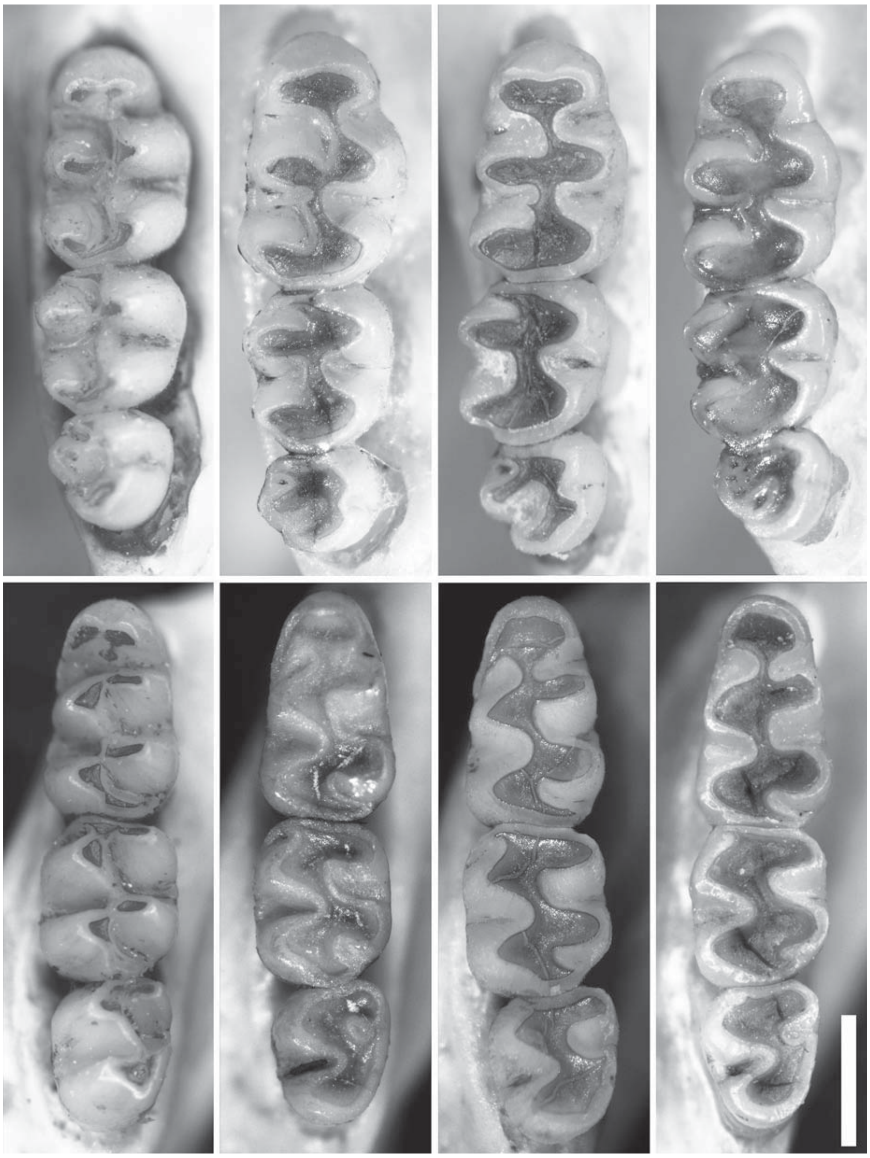

FIG. 4.—Occlusal view of upper (upper) and lower (bottom) tooth rows in *Calassomys apicalis*, gen. et sp. nov., from Sempre Vivas National Park, Minas Gerais, Brazil, arranged from left to right (CNP 1286, MCN/PUC-MG 1142, 1144, and 2785) by increased wear. Scale = 1 mm.

process (Fig. 3f). Roof of mesopterygoid fossa presenting open sphenopalatine vacuities as narrow slits (see "Variation"). Pterygoids short, small, and parallel. Parapterygoid plates flat and reduced in size with respect to mesopterygoid fossa (Fig. 3f). Posterior opening of the alisphenoid canal moderate in size associated with a well-marked groove for the infraorbital branch of the stapedial artery. Middle lacerate foramen well opened (Fig. 3f). Auditory bullae of medium size, flat and subtriangular in outline, with a short and wide bony Eustachian tube; carotid canal present as a groove (Fig. 3g). Squamosal–alisphenoid region characterized by a foramen ovale sometimes divided by an alisphenoid strut (see "Variation"); a well-expressed trough for masticatory–buccinator nerve present in all individuals examined, ending in a small foramen; squamosoalisphenoid grooves also visible, confluent with the sphenofrontal foramina. Inferred carotid circulatory "pattern 1" (sensu Voss 1988).

Mandible enlarged with the ascendant portion subtriangular in outline (Fig. 1). Anterior point of diastema located slightly below alveolar plane. Posterior face of diastema smooth and mental foramen moderately visible from labial view. Masseteric crest evident with upper and lower ridges meeting to produce a thick edge running from the plane defined by the m1 posterior face to slightly above the mental foramen level. Capsular projection conspicuous, lying near the base of coronoid process. Coronoid process reduced and slightly inflected backward; condyloid process short and wide; angular process short. Lunar notch scarcely developed. Mandibular foramen compressed and located above mylohyoid line; retromolar fossa moderately enlarged.

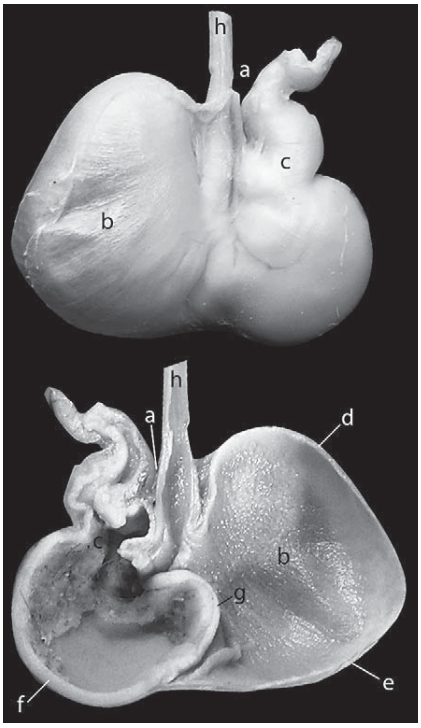

FIG. 5.—Gross stomach morphology in *Calassomys apicalis*, gen. et sp. nov., based on the young fluid-preserved individual CNP 3437 (Sempre Vivas National Park, Minas Gerais, Brazil): dorsal half in external (top) and internal (bottom) view. Abbreviations are a, incisura angularis; b, corpus; c, antrum; d, fornix ventricularis; e, cornified squamous epithelium; f, glandular epithelium; g, bordering fold; h, posterior end of esophagus.

Upper incisors with bright orange enamel, opisthodont, smooth, narrow, with juxtaposed tips showing a straight cutting edge; dentine fissure as a long straight slit (sensu Steppan 1995). Upper molars crested, with labial cusps higher than lingual ones, markedly opposite in pattern, brachyodont, and small with respect to the skull (Figs. 1 and 4). M1 trilophodont, subrectangular in outline; procingulum well developed without anteromedian flexus (see "Variation"); mures longitudinally oriented; hypo- and protoflexus transverse; proto- and hypocone subequal in size; minute mesoloph consistently present; parastyle and mesostyle usually present as thickening of labial cingula. Anteroloph and mesoloph showing a tendency to coalesce with paracone and metacone, respectively. Hypoflexus wide and posteriorly directed. M2 square in outline, bilophodont; anteroloph reduced or absent, mesoloph typically present; wide mesoflexus opposite to hypoflexus. M3 cylindriform, moderately reduced with respect to the M2; vestigial hypoflexus; mesoflexus persisting as a small fossette. Root numbers unknown but lateral inspection suggests M1 and M2 are 3-rooted and M3 with 1 or 2 roots. Lower molars crested, transversally compressed, main cusps moderately alternating, mesolophids and mesostyles absent (Fig. 4). Trilophodont m1 with a well-developed fan-shaped procingulum without anteromedian flexid (see "Variation"); especially wide mesoflexus; proto- and hypoconid areas subtriangular in outline; enlarged and bulbous entoconid; reduced posterolophid. In the m2, bilophodont, posterolophid reduced. The m3 subtriangular in outline, sigmoid, and with a reduced mesoflexid.

On the basis of 5 individuals, *C. apicalis* presents 12 thoracic ribs, 12 thoracic vertebrae, 7 lumbar vertebrae, and 30 caudal vertebrae. The neural spine of the 2nd cervical vertebra is enlarged, has a distinct knob, and does not overlap with the 3rd cervical vertebra. The tuberculum of the 1st rib articulates with the transverse process of the 7th cervical vertebra in addition to the 1st thoracic vertebra. The neural spine of the 2nd thoracic vertebra is conspicuously enlarged, twice or more as long as nearby spines. Hemal arches are absent from the caudal vertebrae; hemal processes are present, starting between the 2nd and 3rd caudal vertebrae, becoming most pronounced between the 4th and 5th, and then decreasing in size until disappearing at the last 4th vertebrae. Humerus lacks of entepicondylar foramen and the supratrochlear fossa is perforated. The position of deltoid tuberosity, as defined by Steppan (1995:49), is $<$ 59% of the total length from the condyle.

Little information is available on the soft anatomy of *C. apicalis*. There are 2 diastemal and 5 interdental palatal rugae. The 1st and the 2nd diastemal rugae are arched and have a slight depression at midpoint. All 5 interdental are incomplete and their ridges slope sharply caudally toward the midline. According to the single available fluid-preserved specimen (CNP 3437) the gall bladder is present and the stomach corresponds to the unilocular–hemiglandular pattern (sensu Carleton 1973; Fig. 5), with the antrum slightly smaller than the corpus. The bordering fold crosses the lesser curvature at the apex of the incisura angularis and the greater curvature at a locus opposite of the incisura angularis; the glandular epithelium extends past the esophageal orifice and protrudes in a wide bulge into the corpus.

Karyological data.—*C. apicalis* presents, on the basis of 4 individuals analyzed (holotype, male, MCN/PUC-MG 2785; male, MCN/PUC-MG 2187; male, MCN/PUC-MG 2645; female, MCN/PUC-MG 2646), a diploid number of 62 chromosomes and an autosomal fundamental number of 116. The karyotype consists of 28 pairs of biarmed autosomes (20 pairs of metacentrics, 8 pairs of submetacentrics) and 2 pairs of acrocentric autosomes. The X chromosome is a medium-sized acrocentric, intermediate between pairs 5 and 6, whereas the Y is acrocentric.

Variation.—Minor variation of morphological traits was detected in *C. apicalis*. Externally, the distal white portion of the tail varies in extension, although it never decreases below ~2.5 cm. For example, in specimen MCN/PUC-MG 1244 the white portion is ~50 mm in length, whereas in specimen MCN/PUC-MG 2785, the holotype, it is 30 mm. The sphenopalatine vacuities display some degree of variation (Figs. 6a and 6b): all the examined animals have them developed as narrow slits, but whereas in 4 these are short and restricted to the sides of the presphenoid, in the remaining 2 they are also sided by the basisphenoids. The presence of alisphenoid strut is also polymorphic (Figs. 6c and 6d):

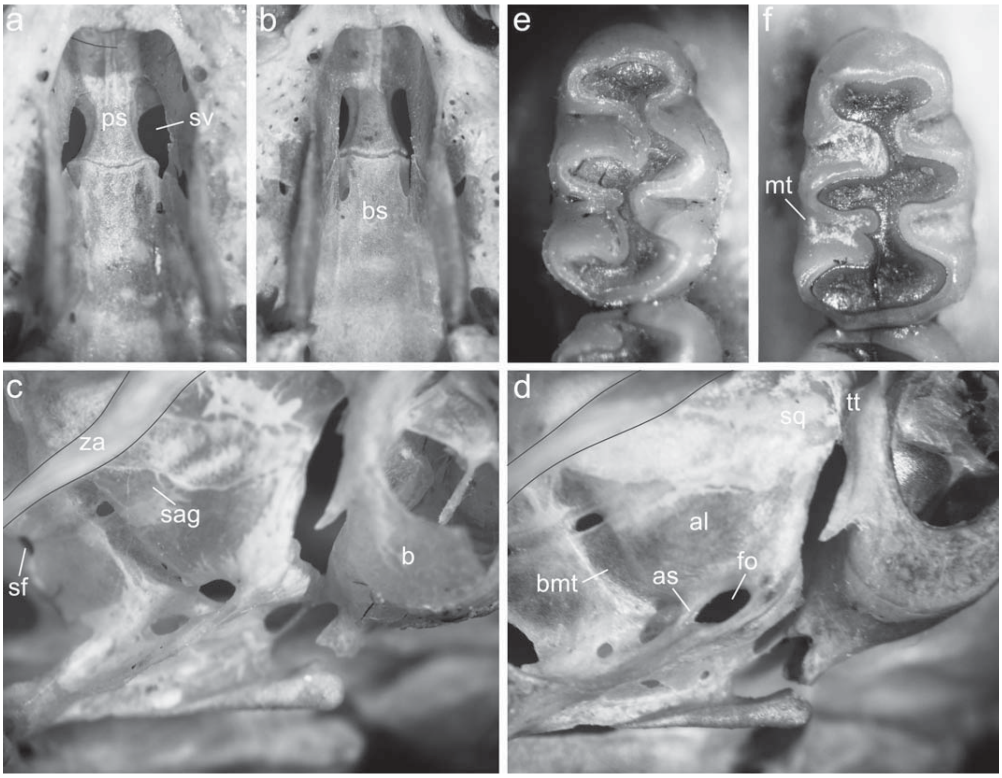

Fig. 6.—Selected cranial and dental traits of *Calassomys apicalis*, gen. et sp. nov., from Sempre Vivas National Park, Minas Gerais, Brazil, to show examples of variation in the degree of extention of the sphenopalatine vacuities (a, MCN/PUC-MG 1142; b, MCN/PUC-MG 1244), the occurrence of the alisphenoid strut (c, MZUFV 2237; d, MCN/PUC-MG 1244), and the connection or disconnection between the mesoloph and the mesostyle on M1 (e, MCN/PUC-MG 1142; f, MCN/PUC-MG 1144). Abbreviations are al, alisphenoid; as, alisphenoid strut; b, auditory bulla; bmt, trough for masticatory–buccinator nerve; bs, basisphenoid; fo, foramen ovale; mt, mesostyle; ps, presphenoid; sag, squamosal-alisphenoid groove; sf, sphenofrontal foramen; sq, squamosal; sv, sphenopalatine vacuities; tt, tegmen tympani; za, zygomatic arch.

specimens MCN/PUC-MG 2237, 1244, and CNP 3437 present this structure on both sides of the skull; specimen MZUFV 2237 lacks the left strut; in specimen MCN/PUC-MG 1144 the left strut is filiform and incomplete, whereas specimen MCN/PUC-MG 1142 lacks the strut on both sides of the cranium. Dental morphology also shows minor variations. Although the anteromedian flexus was recorded as absent, specimen MCN/PUC-MG 1144 has the procingulum indented by a very shallow notch. The young individual CNP 3437 has the procingulum slightly dissected by this structure being the lingual conule slightly smaller than the labial one (Fig. 4). The juvenile dentition of this specimen also shows a very shallow anteromedian flexid combined with an anteromedian fossetid labially open in the procingulum of the m1. Finally, the mesostyle condition on the M1 varies from a narrow short crest (MCN/PUC-MG 1244) to, more frequently, an enamel spur (Figs. 6e and 6f).

Phylogeny.—Results of the phylogenetic analysis of the combined data set (*Cytb* + IRBP, see Salazar-Bravo et al. [2013] for full details) indicate that *Calassomys* n. gen. (there labeled as Phyllotini new genus) is resolved as the sister taxon to the remaining Phyllotini (see also Parada et al. 2013). In addition, this analysis also indicates that Phyllotini s.s. is the sister group to *Delomys*.

Comparisons.—*Calassomys* differs strongly from the remainder of phyllotines and sigmodontines by a set of external and craniodental features (Table 2). Although the general external morphology, especially the abundant and long mystacial vibrissae combined with the long tail, resembles some medium-sized oryzomyines and thomasomyines, the skull and molars clearly link this rodent with the phyllotines (Hershkovitz 1962; Braun 1993; Steppan 1995). Within this tribe, morphology suggests major affinities with *Calomys*. The phylogenetic position of *Calassomys* n. gen. within the Phyllotini (i.e, sister to the clade formed by all other phyllotines) invites comparison with *Delomys*, a sigmodontine usually recovered as sister to the tribe (e.g., Salazar-Bravo et al. 2013). It is also interesting to note a general skull resemblance between *Calassomys* and the Caatinga endemic *Wiedomys*; a comparison is included here to avoid misidentifications. Finally, the dental simplification achieved by *Calassomys* are also present in *Zygodontomys* (Fig. 7) and to some degree in *Necromys* (not shown); however, both of these genera are otherwise so distinct from *Calassomys* and phylogenetically so distant that further comparisons are unwarranted.

Representatives of *Calomys* can be easily separated from *Calassomys* by having the tail usually shorter, more rarely

Table 1.—Selected measurements (in mm) of the paratypes and additional material of *Calossomys apicalis*, gen. et sp. nov., from Sempre Vivas National Park, Minas Gerais, Brazil.

	MCN/PUC-MG[a]			MZUFV	CNP	MCN/PUC-MG	
	1244	1144	1142	2237	3437	7 females $\bar{X} \pm$ SD	6 males $\bar{X} \pm$ SD
Toothwear class	3	3	3	4	2	-	-
Total length	283		255	259	240	255.67 ± 18.21	254.00 ± 14.56
Length of tail	158		149	156	130[c]	142.17 ± 14.96	143.17 ± 9.58
Length of hind foot with claw	27		26	29	27[c]	26.80 ± 0.84	25.80 ± 2.17
Length of ear from notch	20		20[b]	21	18[c]	18.86 ± 2.19	18.25 ± 1.50
Weight (g)	36.5		29	55	25	38.57 ± 6.48	34.50 ± 3.21
Breadth across both incisive foramina	2.40	2.43	2.30	2.36	2.47		
Breadth of braincase	13.40	13.16	13.52	13.45	13.28		
Breadth of rostrum	5.63	5.66	5.66	5.65	5.17		
Breadth of the first maxillary molar	1.29	1.22	1.25	1.27	1.25		
Breadth of the mesopterygoid fossa	2.18	2.14	2.34	2.05	1.79		
Breadth of the palatal bridge		3.71	3.53	3.47	3.20		
Breadth of the zygomatic plate	2.53	2.42	2.51	2.52	2.37		
Condyloincisive length	27.84	26.67	26.69	27.48	24.80		
Least interorbital breadth	4.67	4.76	4.87	4.86	4.75		
Length of diastema	7.49	7.75	7.66	7.98	7.21		
Length of one incisive foramen	6.33	6.47	6.18	6.25	5.35		
Nasal length	12.87		12.66	12.98	11.54		
Occlusal length of the dentary molar row	4.55	4.48	4.32	4.47	4.47		
Occlusal length of the maxillary molar row	4.22	3.98	4.01	4.03	4.18		
Zygomatic breadth	15.06		14.78	14.71	13.51		

[a] MCN/PUC-MG, Coleção de Mamíferos do Museu de Ciências Naturais da Pontifícia Universidade Católica de Minas Gerais; MZUFV, Museu de Zoologia, Departamento de Biologia Animal, Universidade Federal de Viçosa; CNP, Centro Nacional Patagónico.

[b] Measured from dry skin.

[c] Measured from fluid.

subequal, than combined head and body, without both an apical tuft and white terminal portions, the mystacial vibrissae much less conspicuous, the plantar and palmar pads less developed, the fingers shorter, the general back fur shorter, more hirsute ears and tail, and the postauricular patches typically present. Cranially, differences are also trenchant. *Calomys* has the rostrum shorter and broader than *Calassomys*, the nasals not anteriorly projected, the zygomatic notches well developed, the mesopterygoid fossa narrower and the parapterygoid plates enlarged and excavated, the bullae smaller, and the parietals with a lateral projection over the temporal area. The mandible in *Calomys* is shorter and higher than in *Calassomys*, with the coronoid well developed, the notches well excavated, and the masseteric ridges typically more

Table 2.—Morphological comparisons of selected traits among *Calassomys* n. g. and other related sigmodontines.

Characters	*Calassomys*	*Calomys*	*Wiedomys*	*Delomys*
Plantar pads	Six, fleshy, prominent	Six, small	Six, fleshy	Six, fleshy, prominent
HB/TL	HB < TL	HB ≥ TL	HB < TL	HB < = > TL
Tail distal portion white	Yes	No	No	Sometimes white tips
Mystacial vibrissae	Numerous and long	Short	Numerous and long	Numerous and long
Parietal lateral expansion	No	Yes	Yes	No
Rostrum	Long; nasals anteriorly projected	Short	Short	Rostral tube developed
Zygomatic notch	Shallow	Well defined	Well defined	Shallow
Zygomatic plate	Narrow	Broad	Narrow	Narrow
Palate	Short	Long	Short	Short
Palatal pits	Minute	Medium	Large	Minute
Incisive foramen	Eeven M1	Protocone M1	Protocone M1	Not reaching M1
Mesopterygoid [M]/Parapterygoid [P] fossae	M > P	M << P	M ≥ P	M = P
Sphenopalatine vacuities	Slits	Large	Large	Slits
Alisphenoid strut	Typically present	Typically absent	Present or absent	Absent
Capsular process	Present, small	Present, large	Present, small	Absent
Coronoid process	Small	Large	Small	Medium
Molar design	Opposite pairs	Slightly alternating	Slightly alternating	Opposite pairs
Coronal type	Crested	Crested	Crested	Terraced
Anteromedian flexus	Not patent	Patent	Patent	Patent
Mesoloph on M1	Small	Absent	Large	Large
Number of ribs	12	12 or 13	12	13

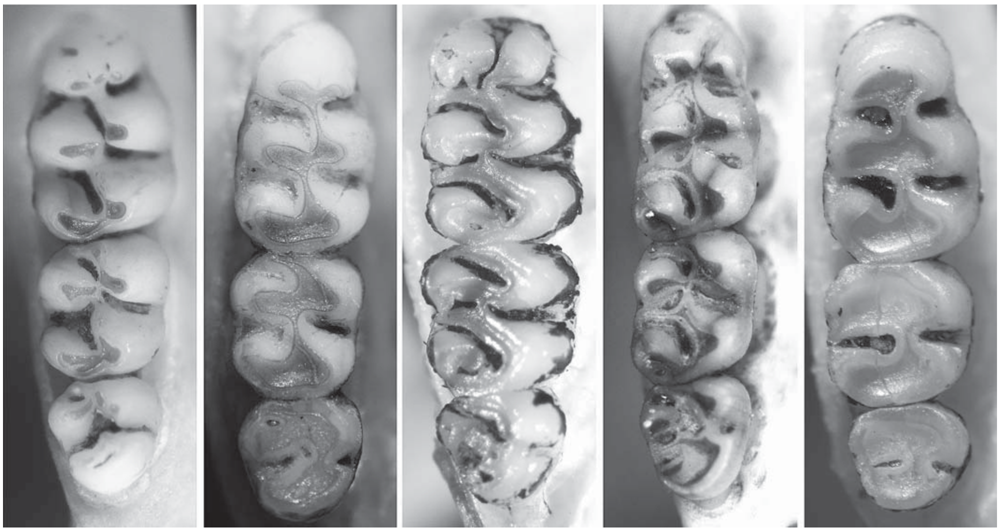

Fig. 7.—Upper right molar tooth rows in occlusal view in *Calomys*, *Delomys*, *Wiedomys*, and *Zygodontomys* to compare with those of *Calassomys apicalis*, gen. et sp. nov., from Sempre Vivas National Park, Minas Gerais, Brazil. From left to right, *Calomys callidus*, young individual (CNP 2395), *C. callidus*, adult individual (CNP 1650, reversed), *Delomys dorsalis* (MACN 22256), *Wiedomys pyrrhorhinos* (CNP 3643), and *Zygodontomys* sp. (MVZ 113957). Not to scale.

marked or directly showing a bony excrescence. Finally, among the main differential dental traits, *Calomys* has crown-crested molars, the main cusps arranged in a more alternate pattern, the mures more obliquely oriented, a well-developed anteromedian flexus that deeply divides the M1 procingulum, the posteroloph present, the M3 hypoflexus more developed, an accessory labial root on M1, and an M3 with 3 roots. In addition, *Calomys* lacks mesolophs (Fig. 7).

Skull differences between *Delomys* and *Calassomys* are evident. The main contrasting morphological traits of the former are its long rostrum with its anterior portion forming a tube or trumpet, the small zygomatic notches, an interorbital region hourglass-shaped with smoothly rounded supraorbital margins, the large interparietal, the short and broad incisive foramina, and the mesopterygoid fossa anterior margin between M3 (Voss 1993). The upper dentition in *Delomys* is characterized by a greater occlusal complexity than that of *Calassomys*, including well-developed anterolophs and mesolophs (Fig. 7).

Finally, *Wiedomys* has the rostrum shorter than the new Cerrado endemic described here, and the interorbital region flattened, narrower, and with the frontal sinuses clearly less developed (Gonçalves et al. 2005). In addition, auditory bullae in *Wiedomys* are bigger and more rounded, with the stapedial process laterally appressed. Upper molars in *Wiedomys* are easily distinguishable from those of *Calassomys* by their larger mesolophs, well-developed parastyles and anterolophs, deep and displaced anteromedian flexus, and large, 3-rooted, complex M3 (Fig. 7).

Natural history.—*C. apicalis* inhabits rocky outcrops within the ‘‘campos rupestres,’’ an open physiognomy that characterizes the plateaus and mountaintops in Sempre Vivas National Park. The vegetation, with marked xerophytic adaptations, is supported by acidic or lithosolic, poorly developed soils; exposed rock is often covered by lichens and rupestrial plants (Giulietti et al. 1997; Conceição and Pirani 2005). A sample of 11 individuals collected in July (winter) 2008 included 4 males and 7 females, with an average weight of 36 ± 5 g; no reproductive data were recorded. Other species of small mammals trapped in the same trap lines were the cricetids *Calomys* sp. and *Cerradomys subflavus*, the echymyids *Thrichomys apereoides* and *Trinomys albispinus*, and the marsupial *Monodelphis domestica*.

Discussion

As with other endemic mammals from the Cerrado, *Calassomys apicalis* has a restricted range distribution (cf. Carmignotto et al. 2012); according to the available data, this species is found in an area of approximately 1,000 km^2 on the Serra do Espinhaço. Specimens were captured among rocky outcrops in campo rupestre montane savannas. Because the Espinhaço range is not continuous, but separated by deep and extensive river valleys, the campos rupestres have a patchy distribution, which may promote speciation in allopatry (Harley 1988). At least 1 other sigmodontine rodent, *Oligoryzomys rupestris*, is also restricted to this kind of habitat, with scattered populations in the Brazilian states of Goiás, Minas Gerais, and Bahia at elevations above 1,000 m (Weksler and Bonvicino 2005). The Espinhaço range has been recognized as a center of endemism for plants (Giullietti and Pirani 1988; Harley 1988; Davis et al. 1997), lizards (Rodrigues 1988), amphibians (Costa et al. 1998), and birds (Stattersfield et al. 1998). Several endemic taxa occur along this entire region, but others are restricted to 1 or few patches, indicating considerable species turnover within isolated stands of campos (e.g., Stattersfield et al. 1998 for birds).

Carmignotto et al. (2012) recognized 2 main groups of mammal endemism for Cerrado and Caatinga: 1 composed of species in genera that diversified in the rain-forest biomes of the Amazonia or Atlantic forest, and another including taxa derived from lineages that diversified in South American open biomes; *C. apicalis* belongs to the 2nd group. Among others, this group encompasses most of the mammals endemic to the Cerrado and Caatinga regions including marsupials (e.g., *Cryptonanus agricolai*, *Thylamys velutinus, T. karimii*) and several sigmodontine (e.g., *Cerradomys*, *Juscelinomys*, *Kunsia*, *Thalpomys*, *Wiedomys*) and hystricognath genera (e.g., *Carterodon*, *Clyomys*, *Kerodon*, *Thrichomys*).

The last 2 decades have witnessed a deep split between paleontologists and neontologists regarding the origin of both phyllotines as well as the entire sigmodontine radiation (Pardiñas et al. 2002; Jacobs and Flynn 2005; Prevosti and Pardiñas, in press). Several authors claim, on the basis of fossil evidence, that the oldest representatives of several sigmodontine tribes, such as Phyllotini, Akodontini, or Oryzomyini, are present in North American Miocene deposits (e.g., Baskin 1978, 1986, 1989; Czaplewski 1987a, 1987b; Morgan and Lucas 2003; Lindsay and Czaplewski 2011). In fact, the number of extinct genera and species attributed to sigmodontines from Mio-Pliocene United States and Mexico is increasing, whereas at the same time these taxa, as well as the hypotheses built upon them, are overlooked in studies of systematics and historical biogeography; the latter are mostly based on molecular data (e.g., Weksler 2003; Almeida et al. 2007; Parada et al. 2013). Indeed, †*Bensonomys*, †*Antecalomys*, and †*Postcopemys* are among the fossil genera that have been directly linked to the origin of *Calomys* and the Phyllotini (Lindsay and Czaplewski 2011 and the references therein).

To connect fossil and recent evidence is not an easy task; this is even more difficult when the fields using these approximations have been isolated for a long time. In fact, even in relatively well-known taxa, linking results on the basis of fossils and molecular data is problematic. For example, when discussing the origin of cotton-rats (*Sigmodon*) after obtaining a well-supported molecular-based hypothesis of South American ancestry, Peppers et al. (2002:404) attempted to reconcile their findings with those of the fossil record by arguing "if one assumes that *P*[*rosigmodon*]. *oroscoi*… represents the most immediate ancestor to *Sigmodon*, then a North American origin for *Sigmodon* seems most probable. This would imply that an *S. alstoni*–like ancestor arose in North America and dispersed to South America. However, as *S. alstoni* (South American in distribution) is the basal-most member of the extant species of *Sigmodon*, it may be that an *S. alstoni*–like ancestor arose in South America after the divergence of *Sigmodon* from a *Prosigmodon*–like ancestor. Given the lack of data for *Sigmodon* fossils, it is difficult to distinguish among these competing hypotheses concerning the origin of the genus." A 3rd hypothesis, of course, is that *Prosigmodon* is unrelated to *Sigmodon*, an issue that can be solved only with morphological and/or morphological–molecular combined approaches. Against this, previous authors claimed that *Prosigmodon* is a junior synonym of *Sigmodon* (Peláez-Campomanes and Martin 2005), an unsupported proposition that axiomatically places the origin of the subfamily Sigmodontinae in North America.

The placement of *Calassomys* as the sister species to the remaining Phyllotini constitutes a refreshing finding, which helps reappraise the origin of the tribe and, by inference, the morphology of their putative ancestor. First, *Calomys* was always treated as the genus with the largest suite of primitive characters in the Phyllotini (e.g., Pearson and Patton 1976; Braun 1993; Steppan 1995), mainly by its brachyodont and bunodont teeth; *Calassomys* shares with *Calomys* many character states in teeth as well as in cranial morphology. Second, the complete loss of the mesoloph was one of the traits identified by Steppan (1995:72) as diagnostic for his concept of the Phyllotini, a concept that also included *Andinomys, Chinchillula,* etc., in addition to the 10 genera currently accepted (Salazar-Bravo et al. 2013). An independent phylogeny based on a reanalysis of the morphological matrix constructed by Steppan (1995) also retrieved *Calassomys* as the sister group to the remaining Phyllotini (Supporting Information S1), in concordance with the molecular-based approach (Fig. 8; Salazar-Bravo et al. 2013). More important, other taxa (e.g., †*Bensonomys*) were not included in this analysis due the paucity of data and the temporary impossibility of inspecting appropriate material personally. Significantly, several dental traits present in †*Bensonomys* preclude its consideration as a primitive member of the phyllotini. According to Kelly (2007), †*Bensonomys* lacks mesolophs and presents a greatly reduced anteroconid. In contrast *Calassomys* combines the presence of mesolophs with moderately developed anteroconids (Fig. 4). However, there is substantial variation in the presence or absence of mesolophs or mesolophids among species assigned to †*Bensonomys*. For example, a mesoloph was reported for the M2 of †*B. baskini* and †*B. gidleyi*, and the holotype of †*B. hershkovitzi* is characterized by mesolophids (absent in the paratype—Martin et al. 2002:fig. 5a). A detailed study, far beyond the scope of this contribution, is necessary to rule out †*Bensonomys* from among the set of possible candidates as phyllotine ancestors; however, with the evidence at hand—including the traits showed by *Calassomys*—the highlighted similarities between †*Bensonomys* and *Calomys* seem to be convergent rather than the result of common ancestry (Reig 1980:277). A cursory inspection of the many available figures of †*Bensonomys* molars indicate m1 procingulum from almost nonexistent (cf. *B. gidleyi*—Baskin 1978:fig. 1c) to reduced, undivided, and connected by a thin enamel ridge (cf. *B. baskini*—Carranza-Castañeda and Walton 1992:plate 1O); upper molar mures as sharp enamel ridges mainly longitudinally oriented; reduced exposure of dentine in protocone/id and hypocone/id areas; and dentine exposure tending toward labial side of the molars, producing a somewhat "asymmetric" effect. In all these characters †*Bensonomys* departs from *Calomys* (and in general

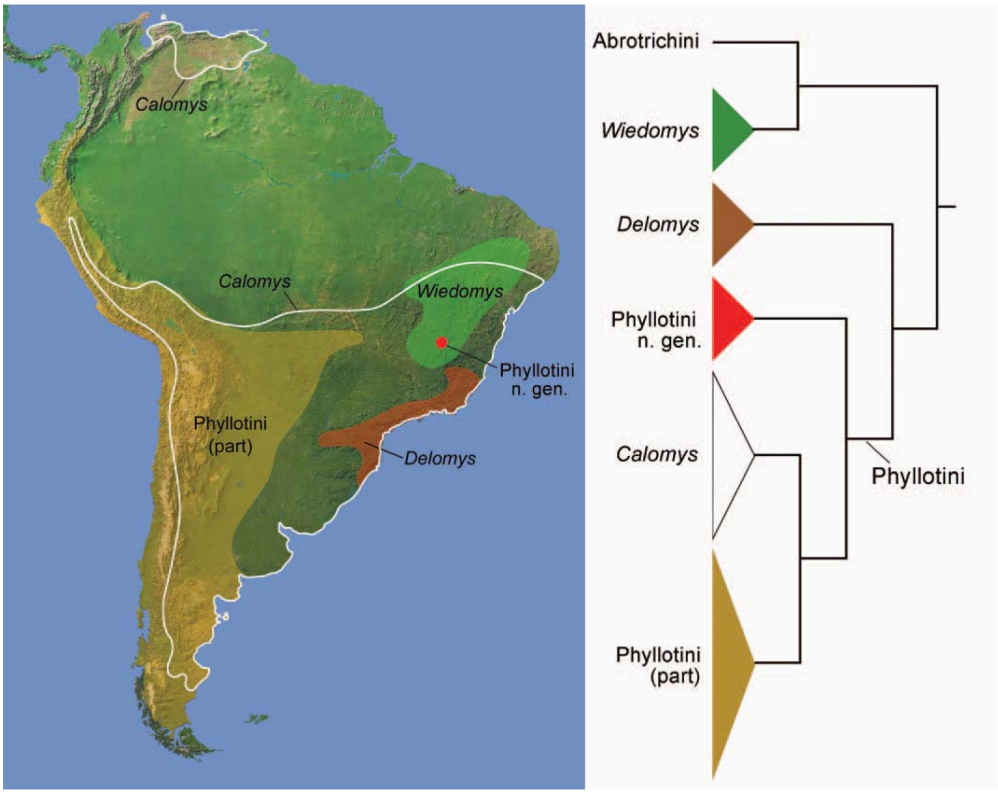

FIG. 8.—Schematic geographic distributions and phylogeny of the tribe Phyllotini and the main genera discussed in the text; the type locality of *Calassomys apicalis*, gen. et sp. nov., is indicated on the right panel by a dot.

other Sigmodontinae) and resembles †*Copemys* and the Neotominae.

Considering the hypothesis of that *Calassomys apicalis* is the sister to the remaining members of the Phyllotini, then we could argue that the ancestor of the phyllotine crown group ranged outside the Andes (Fig. 8). Even when the phyllotines were usually considered as typically Andean elements (e.g., Reig 1986), the known distribution of this tribe, as it is currently understood (i.e., excluding several Andean genera, such as *Andinomys*, *Neotomys*, or *Punomys*), is more closely linked to low to middle elevations in arid to semiarid open environments east of the Andes (Salazar-Bravo et al. 2013). To date, the evolution of the Phyllotini s.s. is thought to be strongly associated to the Altiplano of Bolivia, Peru, and northern Argentina and Chile (e.g., Reig 1986, Smith and Patton 1999), whereas the distribution of members of the tribe in extra Andean habitats (e.g., several species of *Graomys* in the Chaco of S Bolivia and NE Argentina, or *Calomys* in the grasslands of N Venezuela and Colombia) was thought to be mainly the result of secondary dispersal from the highlands, as these groups diversified (Salazar-Bravo et al. 2001; Almeida et al. 2007). The discovery of *Calassomys* in the Cerrado of Brazil bears important consequences for our understanding of the biogeographic setting for the origin and evolution of phyllotines. It indicates that whatever processes responsible for the diversification of the Phyllotini at approximately 7 million years ago (cf. clade C in Parada et al. 2013:fig. 2), they may be geographically linked to the evolution of the biomes typical of the SE lowlands of Bolivia, N Paraguay, and SW Brazil. Whatever these processes are, they may also be responsible for the relationship between *Delomys* and (Phyllotini s.s. + *Calassomys*); *Juliomys* with respect to (*Andinomys* + *Punomys*); and *Wiedomys* with respect to the Abrothrichini, to cite only some examples (cf. Salazar-Bravo et al. 2013). These paired examples of groups of Andean and Cerrado or Atlantic Forest endemics indicate potentially shared historical and ecological factors that shaped the range limits and patterns of speciation of these and potentially other organisms in those regions; currently, however, it is premature to hypothesize what these processes may have been.

The discovery of *Calassomys*, as well as the recently described *Drymoreomys* from Serra do Mar, Brazil (Percequillo et al. 2011), eloquently highlights the incomplete knowledge of Sigmodontinae diversity. The subfamily is composed of a wide array of forms including 84 living genera (Patton et al., in press). Interestingly, *Calassomys* is a clear example of a new entity raised from field efforts. The last coined sigmodontine genus in this condition from Cerrado biome was *Microakodontomys*, 2 decades ago (Hershkovitz 1993). The existence of a rodent such as *Calassomys* living in a moderately open physiognomy and overlooked to date constitutes a call for attention to intensify primary biodiversity surveys, an issue sometimes considered complete in the scientific policies in the countries of the region.

RESUMEN

Describimos un nuevo género y especie de Sigmodontinae actualmente sólo conocido para el Parque Nacional brasilero Sempre Vivas, Estado de Minas Gerais. Este roedor se caracteriza por una combinación única de rasgos que incluyen, entre otros, una cola larga con su porción distal (ca. 2,5 a 5 cm) enteramente blanca; cráneo con perfil abovedado; rostro largo con tubo rostral incipiente; molares braquiodontos notablemente pequeños con pequeños mesolofos y mesostilos presentes en los primeros y segundos molares superiores. Análisis cladísticos de caracteres moleculares (un marcador mitocondrial y un marcador nuclear) y morfológicos indican que el nuevo género pertenece a los Phyllotini y es hermano de los restantes géneros de la tribu. Sin embargo, contrariamente a los otros filotinos conocidos, el nuevo género muestra mesolofos y mesostilos vestigiales. Los filotinos están ampliamente distribuidos en zonas abiertas, en particular en desiertos y semidesiertos, mayormente en la porción occidental de América del Sur. El nuevo género aquí descripto expande la diversidad de la tribu y sugiere un antiguo evento de diversificación en Brasil oriental.

ACKNOWLEDGMENTS

We are grateful to several individuals and institutions for providing help, specimens, and funds. Inventory work at Sempre Vivas National Park was accomplished with the assistance of C. Costa, K. Leal, G. Rocha, F. Vieira, É. Carmo, T. Paula, D. Saraiva, R. Dutra, D. Ziviani, K. da Silva, F. Diniz, and E. Lima and sponsored by IBAMA, Fundação Boticário, FIP PUC Minas, and PROBIC PUC Minas. We are also indebted to the curators D. Flores (Colección Nacional de Mastozoología, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires, Argentina), J. Patton (Museum of Vertebrate Zoology, Berkeley, California), and J. Alves de Oliveira (Museu Nacional, Rio de Janeiro), who kindly loaned us specimens of *Delomys*, *Zygodontomys*, and *Wiedomys*. Many thanks also to our colleagues G. D'Elía, C. Bonvicino, M. Weksler, A. Percequillo, E. Manduca, C. Galliari, and P. Ortiz for sharing their impressions and systematic knowledge about the new genus described herein. The help and kindness of G. D'Elía, who formerly produced in his lab the *Cytb* sequence of the new genus and allowed us to use these data, and the careful revision of the manuscript made by A. Percequillo, are deeply appreciated. Finally, N. Czaplewski contributed greatly by sending key literature about the North American fossil record. This paper was partially funded by Agencia Nacional de Promoción Científica y Tecnológica (PICT 2008-547) and CONICET (to UFJP) and funds from the American Philosophical Society, the Systematics Research Fund of the Systematics Association, and Faculty Research Award from Texas Tech University (to JSB). This is Grupo de Estudios de Mamíferos Australes contribution #4.

SUPPORTING INFORMATION

Supporting Information S1.—Cladistic analysis of the Phyllotini based on morphological data.
Found at DOI: 10.1644/13-MAMM-A-208.S1

LITERATURE CITED

ALMEIDA, F. C., C. R. BONVICINO, AND P. CORDEIRO-ESTRELA. 2007. Phylogeny and temporal diversification of *Calomys* (Rodentia, Sigmodontinae): implications for the biogeography of an endemic genus of the open/dry biomes of South America. Molecular Phylogenetics and Evolution 42:449–466.

BASKIN, J. A. 1978. *Bensonomys*, *Calomys*, and the origin of the phyllotine group of Neotropical cricetines (Rodentia: Cricetidae). Journal of Mammalogy 59:125–135.

BASKIN, J. A. 1986. The late Miocene radiation of Neotropical sigmodontine rodents in North America. Contributions to Geology, University of Wyoming, Special Paper 3:287–303.

BASKIN, J. A. 1989. The initial origin and diversification of the Neotropical Sigmodontinae (Rodentia: Muridae)—a perspective from the North American fossil record. Fifth International Theriological Congress, Rome. Abstracts of Papers and Posters, pp. 263–264.

BRAUN, J. K. 1993. Systematic relationships of the tribe Phyllotini (Muridae: Sigmodontinae) of South America. Oklahoma Museum of Natural History Special Publication, pp. 1–50.

CARLETON, M. D. 1973. A survey of gross stomach morphology in New World Cricetinae (Rodentia, Muroidea), with comments on functional interpretations. Miscellaneous Publications, Museum of Zoology, University of Michigan 146:1–43.

CARLETON, M. D. 1980. Phylogenetic relationships in neotomine–peromyscine rodents (Muroidea) and a reappraisal of the dichotomy within New World Cricetinae. Miscellaneous Publications, Museum of Zoology, University of Michigan 157:1–146.

CARLETON, M. D., AND G. G. MUSSER. 1989. Systematic studies of oryzomyine rodents (Muridae, Sigmodontinae): a synopsis of *Microryzomys*. Bulletin of the American Museum of Natural History 191:1–83.

CARMIGNOTTO, A. P., M. DE VIVO, AND A. LANGGUTH. 2012. Mammals of the Cerrado and Caatinga. Distribution patterns of the tropical open biomes of Central South America. Pp. 307–350 in Bones, clones and biomes. The history and geography of recent Neotropical mammals (B. D. Patterson and L. P. Costa, eds.). University of Chicago Press, Chicago, Illinois.

CARRANZA-CASTAÑEDA, O., AND A. H. WALTON. 1992. Cricetid rodents from the Rancho el Ocote, Late Hemphillian (Pliocene), state of Guanajuato. Universidad Nacional Autonoma de Mexico, Instituto de Geología, Revista 10:71–93.

CONCEIÇÃO, A. A., AND J. R. PIRANI. 2005. Delimitação de hábitats em campos rupestres na Chapada Diamantina, Bahia: substrato, composição florística e aspectos estruturais. Boletim de Botânica da Universidade de São Paulo 23:85–111.

COSTA, C. M. R., G. HERRMANN, C. S. MARTINS, L. V. LINS, AND I. R. LAMAS. 1998. Biodiversidade em Minas Gerais—um Atlas para sua conservação. Fundação Biodiversitas, Belo Horizonte, Minas Gerais, Brasil.

CZAPLEWSKI, N. J. 1987a. Sigmodont rodents (Mammalia: Muroidea: Sigmodontinae) from the Pliocene (early Blancan) Verde Formation, Arizona. Journal of Vertebrate Paleontology 7:183–199.

CZAPLEWSKI, N. J. 1987b. Middle Blancan vertebrate assemblage from the Verde Formation, Arizona. Contributions to Geology, University of Wyoming 25:133–155.

DAVIS, S. D., V. H. HEYWOOD, O. HERRERA-MACBRYDE, J. VILLA-LOBOS, AND A. C. HAMILTON. 1997. Centres of plant diversity: a guide and strategy for their conservation. IUCN Publications Unit, Cambridge, United Kingdom.

DAY, M. G. 1966. Identification of hair and feather remains in the gut and faeces of stoats and weasels. Journal of Zoology (London) 148:201–217.

FISCHER, G. 1817. Adversaria zoologica. Fasciculus primus. Quaedam ad Mammalium systema et genera illustranda. Memoires de la Societe imperiale des naturalistes de Moscou 5:357–446, 2 pls.

GIULIETTI, A. M., AND J. R. PIRANI. 1988. Patterns of geographic distribution of some plant species from the Espinhaço Range, Minas Gerais and Bahia, Brazil. Pp. 39–69 in Proceedings of a workshop on neotropical distribution patterns (P. E. Vanzolini and W. R. Heyer, eds.). Academia Brasileira de Ciências, Rio de Janeiro, Brazil.

GIULIETTI, A. M., J. R. PIRANI, AND R. M. HARLEY. 1997. Espinhaço range region. Eastern Brazil. Pp. 397–404 in Centres of plant diversity. A guide and strategy for their conservation. Vol. 3. The Americas (S.D. Davis, V. H. Heywood, O. Herrera-MacBryde, J. Villa-Lobos, and A. C. Hamilton, eds.). WWF/IUCN, Cambridge, United Kingdom.

GONÇALVES, P. R., F. ALMEIDA, AND C. R. BONVICINO. 2005. A new species of *Wiedomys* (Rodentia:Sigmodontinae) from Brazilian Cerrado. Mammalian Biology 70:46–60.

HARLEY, R. M. 1988. Evolution and distribution of Eriope (Labiatae), and its relatives, in Brazil. Pp. 71–120 in Proceedings of a workshop on neotropical distribution patterns (P. E. Vanzolini and W. R. Heyer, eds.). Academia Brasileira de Ciências, Rio de Janeiro, Brazil.

HERSHKOVITZ, P. 1962. Evolution of Neotropical cricetine rodents (Muridae) with special reference to the phyllotine group. Fieldiana, Zoology 46:1–524.

HERSHKOVITZ, P. 1993. A new central Brazilian genus and species of sigmodontine rodent (Sigmodontinae) transitional between akodonts and oryzomyines, with a discussion of muroid molar morphology and evolution. Fieldiana, Zoology, n.s. 75:1–18.

JACOBS, L. L., AND L. J. FLYNN. 2005. Of mice… again: the Siwalik rodent record, murine distribution, and molecular clocks. Pp. 63–80 in Interpreting the past: essays on human, primate, and mammal evolution in honor of David Pilbeam (D. E. Leiberman, R. J. Smith and J. Kelley, eds.). Brill Academic Publishers Inc., Boston, Massachusetts.

KELLY, T. 2007. A new species of *Bensonomys* (Rodentia, Cricetidae) from the late early Hemphillian (late Miocene), Coal Valley Formation, Smith Valley, Nevada. Paludicola 6:125–138.

KORTH, W. W. 1998. Rodents and lagomorphs (Mammalia) from the late Clarendonian (Miocene) Ash Hollow Formation, Brown County, Nebraska. Annals of Carnegie Museum 67:299–348.

LINDSAY, E. H. 2008. Cricetidae. Pp. 456–479 in Evolution of tertiary mammals of North America. Volume 2: small mammals, xenarthrans, and marine mammals (C. M. Janis, G. F. Gunnell, and M. D. Uhen, eds.). Cambridge University Press, Cambridge, United Kingdom.

LINDSAY, E. H., AND N. J. CZAPLEWSKI. 2011. New rodents (Mammalia, Rodentia, Cricetidae) from the Verde Fauna of Arizona and the Maxum Fauna of California, USA, early Blancan Land Mammal Age. Palaeontologia Electronica 14(3), 29A, pp. 16; palaeo-electronica.org/2011_3/5_lindsay/index.html

MARTIN, R. A., T. GOODWIN, AND J. O. FARLOW. 2002. Late Neogene (Late Hemphillian) rodents from the Pipe Creek Sinkhole, Grant County, Indiana. Journal of Vertebrate Paleontology 22:137–151.

MARTÍNEZ, J. J., L. I. FERRO, M. I. MOLLERACH, AND R. M. BARQUEZ. 2012. The phylogenetic relationships of the Andean swamp rat genus *Neotomys* (Rodentia, Cricetidae, Sigmodontinae) based on mitochondrial and nuclear markers. Acta Theriologica 57:277–287.

MCKENNA, M. C., AND S. K. BELL. 1997. Classification of mammals above the species level. Columbia University Press, New York.

MORGAN, G. S., AND S. G. LUCAS. 2003, Mammalian biochronology of Blancan and Irvingtonian (Pliocene and Early Pleistocene) faunas from New Mexico. Bulletin of the American Museum of Natural History 279:269–320.

MUSSER, G. M., AND M. D. CARLETON. 2005. Superfamily Muroidea. Pp. 894–1531 in Mammal species of the world: a taxonomic and geographic reference (D. E. Wilson, and D. M. Reeder, eds.). 3rd ed, Johns Hopkins University Press, Baltimore, Maryland.

MYERS, P., AND J. L. PATTON. 1989. A new species of *Akodon* from the cloud forests of Eastern Cochabamba department, Bolivia (Rodentia: Sigmodontinae). Occasional Papers of the Museum of Zoology, University of Michigan 720:1–28.

PACHECO, V. 2003. Phylogenetic analyses of the Thomasomyini (Muroidea: Sigmodontinae) based on morphological data. Ph. D. dissertation, City University of New York.

PARADA, A., U. F. J. PARDIÑAS, J. SALAZAR-BRAVO, G. D'ELÍA, AND E. PALMA. 2013. Dating an impressive Neotropical radiation: molecular time estimates for the Sigmodontinae (Rodentia) provide insights into its historical biogeography. Molecular Phylogenetics and Evolution 66:960–968.

PARDIÑAS, U. F. J., G. D'ELÍA, AND P. E. ORTIZ. 2002. Sigmodontinos fósiles (Rodentia, Muroidea, Sigmodontinae) de América del Sur: estado actual de su conocimiento y prospectiva. Mastozoología Neotropical 9:209–252.

PATTON, J. L., U. F. J. PARDIÑAS, AND G. D'ELÍA. In press. Mammals of South America. Volume 2, Rodents. University of Chicago Press, Chicago, Illinois.

PEARSON, O. P., AND PATTON, J. L. 1976. Relationships among South American phyllotine rodents based on chromosome analysis. Journal of Mammalogy 57:339–350.

PELÁEZ-CAMPOMANES, P., AND R. MARTIN. 2005. The Pliocene and Pleistocene history of cotton rats in the Meade Basin of southwestern Kansas. Journal of Mammalogy 86:475–494.

PEPPERS, L. L. , D. S. CARROLL, AND R. D. BRADLEY . 2002. Molecular systematics of the genus *Sigmodon* (Rodentia: Muridae): evidence from the mitochondrial cytochrome-*b* gene. Journal of Mammalogy 83:396–407.

PERCEQUILLO, A. R., M. WEKSLER, AND L. P. COSTA. 2011. A new genus and species of rodent from the Brazilian Atlantic Forest (Rodentia: Cricetidae: Sigmodontinae: Oryzomyini), with comments on oryzomyine biogeography. Zoological Journal of the Linnean Society 161:357–390.

PREVOSTI F. J., AND U. F. J. PARDIÑAS. In press. The heralds: carnivores (Carnivora) and sigmodontine rodents (Cricetidae) in the Great American Biotic Interchange. Pp. xxx–xxx in Origins and evolution of Cenozoic South American mammals (A. L. Rosenberger and M. F. Tejedor, eds.). Vertebrate palebiology and paleoanthropology. Springer, New York.

REIG, O. A. 1977. A proposed unified nomenclature for the enamelled components of the molar teeth of the Cricetidae (Rodentia). Journal of Zoology (London) 181:227–241.

REIG, O. A. 1980. A new fossil genus of South American cricetid rodents allied to *Wiedomys*, with an assessment of the Sigmodontinae. Journal of Zoology (London) 192:257–281.

REIG, O. A. 1984. Distribuiçao geográfica e história evolutiva dos roedores muroideos sulamericanos (Cricetidae: Sigmodontinae). Revista Brasileira de Genética 7:333–365.

Reig, O. A. 1986. Diversity patterns and differentiation of high Andean rodents. Pp. 404–439 in High altitude tropical biogeography (F. Vuilleumier and M. Monasterio, eds.). Oxford University Press, New York.

Rodrigues, M. T. 1988. Distribution of lizards of the genus *Tropidurus* in Brazil (Sauria, Iguanidae). Pp. 305–315 in Proceedings of a workshop on neotropical distribution patterns (P. E. Vanzolini and W. R. Heyer, eds.). Academia Brasileira de Ciências, Rio de Janeiro.

Salazar-Bravo, J., J. W. Dragoo, D. S. Tinnin, and T. L. Yates. 2001. Phylogeny and evolution of the neotropical rodent genus *Calomys*: inferences from mitochondrial DNA sequence data. Molecular Phylogenetics and Evolution 20:173–184.

Salazar-Bravo, J., U. F. J. Pardiñas, and G. D'Elía. 2013. A phylogenetic appraisal of Sigmodontinae (Rodentia, Cricetidae) with emphasis on phyllotine genera: systematics and biogeography. Zoologica Scripta 42:250–261.

Sikes, R. S., W. L. Gannon, and the Animal Care and Use Committee of the American Society of Mammalogists. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 92:235–253.

Smith, M. F., and J. L. Patton. 1999. Phylogenetic relationships and the radiation of sigmodontine rodents in South America: evidence from cytochrome *b*. Journal of Mammalian Evolution 6:89–128.

Stattersfield, J. A., M. J. Crosby, A. J. Long, and D. C. Wege. 1998. Endemic bird areas of the world: priorities for biodiversity conservation. Burlington Press Ltd., Cambridge, United Kingdom.

Steppan, S. J. 1995. Revision of the tribe Phyllotini (Rodentia: Sigmodontinae), with a phylogenetic hypothesis for the Sigmodontinae. Fieldiana, Zoology, n.s. 80:1–112.

Verma, R. S., and A. Babu. 1995. Human chromosomes. Principles and techniques. McGraw-Hill, Inc., New York.

Vorontsov, N. N. 1959. The system of hamsters (Cricetinae) in the sphere of the world fauna and their phylogenetic relations. Byulleten' Moskovskovo Obshchestva Ispytatelei Prirody, Otdel Biologicheskii 64:134–137 [in Russian].

Voss, R. S. 1988. Systematics and ecology of Ichtyomtinae rodents (Muroidea): patterns of morphological evolution in small adaptive radiation. Bulletin of the American Museum of Natural History 188:262–493.

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. 1993. A revision of the Brazilian muroid rodent genus *Delomys* with remarks on "Thomasomyine" characters. American Museum Novitates 3073:1–44.

Wagner, J. A. 1843. Supplementband. Dritte Abtheilung: Die Beutelthiere und Nager (erster Abschnitt). Pp. 137–614 in Die Säugthiere in Abbildungen nach der Natur mit Beschreibungen, J.C.D. von Schreber, Leipzig.

Weksler, M. 2003. Phylogeny of Neotropical oryzomyine rodents (Muridae: Sigmodontinae) based on the nuclear IRBP exon. Molecular Phylogenetics and Evolution 29:331–349.

Weksler, M. 2006. Phylogenetic relationships of oryzomine rodents (Muroidea: Sigmodontinae): separate and combined analyses of morphological and molecular data. Bulletin of the American Museum of Natural History 296:1–149.

Weksler, M., and C. R. Bonvicino. 2005. Taxonomy of pigmy rice rats (genus *Oligoryzomys*, Rodentia: Sigmodontidae) of the Brazilian Cerrado, with the description of two new species. Arquivos do Museu Nacional 63:113–130.

Submitted 26 August 2013. Accepted 12 October 2013.

Associate Editor was Ryan W. Norris.

Appendix I

Specimens examined belong to the following mammal collections: CEM, Colección Elio Massoia (acquired by the Fundación de Histora Natural Félix de Azara, Buenos Aires, Argentina); CNP, Colección de Mamíferos del Centro Nacional Patagónico, Chubut, Argentina; MZUFV, Museu de Zoologia, Departamento de Biologia Animal, Universidade Federal de Viçosa, Viçosa, Minas Gerais, Brazil; MACN, Colección Nacional de Mastozoología, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires, Argentina; MCN/PUC-MG, Coleção de Mamíferos do Museu de Ciências Naturais da Pontifícia Universidade Católica de Minas Gerais, Minas Gerais, Brazil; MLP, Museo de La Plata, La Plata, Buenos Aires, Argentina; MN, Museu Nacional, Rio de Janeiro, Brazil; MVZ, Museum of Vertebrate Zoology, Berkeley, California.

Calassomys apicalis, gen. et sp. nov. ($n = 19$): Brazil, Minas Gerais, Sempre Vivas National Park, 3.25 km by rd NW Macacos, Pedreira do Gaio (MCN/PUC-MG 1142, 1144, 1244, 2785 [holotype], MZUFV 2237, CNP 3437), Campo de Pedras (MCN/PUC-MG 1728, 2176, 2187, 2188, 2202, 2244), Arrenegado (MCN/PUC-MG 2645, 2646, 2647, 2648, 2649, 2650, 2651).

Calomys callidus ($n = 7$): Argentina, Entre Ríos, Santa Ana de Carpinchorí (CNP 1650, 2394, 2395, 2401, 3432, 3433); Corrientes, Estación Biológica Corrientes (CNP 3479).

Calomys callosus ($n = 4$): Argentina, Chaco, 5 km W Pto. Las Palmas (CNP 3429), 7 km W Pto. Las Palmas (CNP 3431); Formosa, río Bermejo (CNP 3535, 3537).

Calomys expulsus ($n = 3$): Brazil, Minas Gerais, Viçosa, Mata do Paraíso (MZUFV 2354, 2826), Araguari (MZUFV 2216).

Calomys laucha ($n = 3$): Argentina, Misiones, Leandro N. Alem (CNP 799); Santiago del Estero, Estación Experimental INTA "La María" (CNP 2359); Tucumán, intersección entre la Ruta Nacional 9 y el arroyo India Muerta (CNP 2360).

Calomys musculinus ($n = 10$): Argentina, Neuquén, Zapala (CNP 3430); Chubut, Puerto Madryn (CNP 3506), Los Altares (CNP 1624, 1635, 1652), Puerto Lobos (CNP 1005, 1007, 1012, 1019, 1037).

Calomys tener ($n = 4$): Brazil, Minas Gerais, Belo Horizonte (MZUFV 701, 732), Salto da Divisa (MZUFV 1088, 2009).

Delomys dorsalis ($n = 4$): Argentina, Misiones, General Manuel Belgrano, Reserva Vida Silvestre Urugua-í (MACN 22253, 22254, 22255, 22256).

Wiedomys pyrrhorhinos ($n = 6$): Brazil, Bahía, locality unknown (CNP 3643, CEM 3718), Vitória da Consquista, Faz. Batalha (MN 60783), Serrinha, Faz. Cruzeiro (MN 18445), Seabra, Sítio Mariano (MN 18516), Seabra, Sítio Lapao 2° (MN 18707).

Zygodontomys sp. ($n = 1$): Colombia, Huila, 17.5 km SE Villavieja (MVZ 113957).