

University of California Press
(University of California, Office of the President)

Year 2005

Paper vol.133

Title: Mammalian Diversification: From
Chromosomes to Phylogeography (A
Celebration of the Career of James L.
Patton)

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**A Revision of the Genera of Arboreal Echimyidae
(Rodentia: Echimyidae, Echimyinae),
With Descriptions of Two New Genera**

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Most recent taxonomic works have recognized four or five genera of echimyines, *Echimys*, *Makalata*, *Diplomys*, *Phyllomys* and *Isothrix* (McKenna and Bell, 1997; Leite, 2003). Three of these genera include divergent arrays of species that do not cluster with each other in parsimony analyses based on morphology. From a phylogenetic hypothesis based on morphological characters, a revision of the arboreal Echimyid rodents (Echimyidae, Echimyinae) is proposed. The echimyine taxa are reorganized into eight genera, six of them based on previously defined groupings and names: *Echimys*, *Phyllomys*, *Isothrix*, *Diplomys*, *Makalata*, and *Callistomys*. Two new genera are named and diagnosed: *Pattonomys*, including three species formerly grouped under *Echimys semivillosus*; and *Santamartamys*, a monotypic genus based on *Diplomys rufodorsalis*. The eight genera are diagnosed and illustrated. Phylogenetic relationships between the genera are poorly resolved; the genus *Isothrix* is of uncertain affinity, but it is provisionally retained within the echimyines. Taxa formerly placed in the subfamily Eumysopinae do not appear to be paraphyletic but, as their monophyly cannot yet be rejected, the subfamily is retained pending a more thorough revision. These hypotheses based on morphology are consistent with recently constructed phylogenetic trees based on molecular characters (Leite and Patton, 2002).

SYSTEMATICS OF THE ECHIMYIDAE

The family Echimyidae Gray, 1825 is the most diverse of the South American hystricognath rodents, with 20 genera and 78 species recently recognized (Woods, 1993). The taxonomic history of the family has been chaotic; a number of generic names have been proposed, several have been abandoned, and the contents of numerous genera remain highly unstable. There have been no modern revisions of the family and several of the currently recognized genera do not appear to represent coherent taxonomic units from either a phenetic or phylogenetic perspective. Using morphology, I re-examine the supraspecific taxonomy of arboreal echimyids (subfamily Echimyinae) and other taxa recently included in the Echimyidae in an attempt to bring more coherence to the systematics of this group

and to provide morphological diagnoses for apparent taxonomic units. I first briefly summarize previous systematic views of the family and then describe the morphological character sets that I found to be most informative. The described characters are used to construct a phylogenetic hypothesis, from which I propose a revised generic classification.

Brief Taxonomic History

The family Echimyidae is of ancient origin in South America, found among the oldest fossil rodents of the late Oligocene (Patterson and Wood, 1982; Vucetich and Verzi, 1991). Recent work suggests that there was a diverse fauna of largely grassland (pampa) echimyids in the Miocene (Vucetich et al., 1993), but there is little early fossil record of the arboreal forest taxa. The family has recently been classified into three or four subfamilies (Table 1). The living Eumysopinae or Heteropsomyinae have been divided into six genera of terrestrial species and two of arboreal ones, with the greatest generic diversity among grassland taxa but the greatest number of species in the rainforest genus *Proechimys*. The Dactylomyinae includes three genera of specialized arboreal folivores of lowland and montane forests, while the Echimyinae has included five to six genera of large-bodied arboreal rats of forested or wooded habitats. Three small families or subfamilies (two of them monotypic) – Capromyidae, Chaetomyidae, Myocastoridae – have also been included by some authors.

When first discovered, the rat-like South American caviomorphs were placed in European rodent genera (e.g. *Myoxus chrysurus* Zimmermann 1780), but shortly thereafter they were recognized as distinct (*Echimys* Cuvier 1809). Nomenclatural confusion soon followed, with a rapid proliferation of names as new discoveries were sent to Europe and quickly described. As for many groups of South American mammals, the early taxonomy of echimyids was confounded by the use of separate generic classifications by French, German, Danish and English taxonomists, who named taxa or redefined their contents without viewing type material in other countries. Tate (1935) sifted through 150 years of publications in a heroic review of the taxonomic history of all caviomorph rodents. He reconciled many nomenclatural discrepancies and proposed a revised generic classification, but did not provide an extensive review of characters. His interpretation of the Echimyidae, in which he segregated the species of *Echimys* largely on the degree of hairiness of the tail (Table 2), left many questions unresolved. Tate's classification was adopted by most systematists until Cabrera (1961) again reviewed the family (together with all other South American mammals) and synonymized many named forms with little explanation. Cabrera's classification has been widely used until now (Honaki et al., 1983; Woods, 1993). Emmons and Feer (1990, 1997) proposed some revisions of the genera in field guide format, without explanation, including segregation of *Nelomys* from *Echimys* (1990); subsequently, these authors separated

Table 1. Recent classifications of the extant genera of Echimyidae. (*) refer to taxa included by Patterson and Wood (1982) but not by Patterson and Pascual (1968).

Patterson & Pascual 1968		Patton & Reig 1989	
*Patterson & Wood 1982	Woods 1982	Woods 1993	McKenna & Bell 1997
HETEROPSOMYINAE	ECHIMYINAE	EUMYSOPINAE	HETEROPSOMYINAE
<i>Carterodon</i>	<i>Carterodon</i>	<i>Carterodon</i>	<i>Carterodon</i>
<i>Clyomys</i>	<i>Clyomys</i>	<i>Clyomys</i>	<i>Clyomys</i>
	<i>Euryzygomatomys</i>	<i>Euryzygomatomys</i>	<i>Euryzygomatomys</i>
<i>Thrichomys</i>	<i>Thrichomys</i>	<i>Thrichomys</i>	<i>Thrichomys</i>
<i>Proechimys</i>	<i>Proechimys</i>	<i>Proechimys</i>	<i>Proechimys</i>
<i>Hoplomys</i>	<i>Hoplomys</i>	<i>Hoplomys</i> ¹	<i>Hoplomys</i>
		<i>Incertae sedis</i>	
<i>Lonchothrix</i>	<i>Lonchothrix</i>	<i>Lonchothrix</i>	<i>Lonchothrix</i>
<i>Mesomys</i>	<i>Mesomys</i>	<i>Mesomys</i>	<i>Mesomys</i>
ECHIMYINAE		ECHIMYINAE	ECHIMYINAE
<i>Echimys</i>	<i>Echimys</i>	<i>Echimys</i>	<i>Echimys</i>
	<i>Makalata</i>	<i>Makalata</i>	<i>Makalata</i>
<i>Diplomys</i>	<i>Diplomys</i>	<i>Diplomys</i>	<i>Diplomys</i>
<i>Isothrix</i>	<i>Isothrix</i>	<i>Isothrix</i>	<i>Isothrix</i>
DACTYLOMYINAE	DACTYLOMYINA	DACTYLOMYINAE	DACTYLOMYINAE
<i>Dactylomys</i>	<i>Dactylomys</i>	<i>Dactylomys</i>	<i>Dactylomys</i>
<i>Kannabateomys</i>	<i>Kannabateomys</i>	<i>Kannabateomys</i>	<i>Kannabateomys</i>
<i>Olallamys</i>	<i>Olallamys</i>	<i>Olallamys</i>	<i>Olallamys</i>
MYOCASTORINAE			MYOCASTORINAE
<i>Myocastor</i>			<i>Myocastor</i>
extinct genera			
CHAETOMYINAE	CHAETOMYINAE	CHAETOMYINAE	
<i>Chaetomys</i>	<i>Chaetomys</i>	<i>Chaetomys</i>	
*CAPROMYINAE			
*Subfamily Plagiodontinae			
*Subfamily Capromyinae			
*Subfamily Myocastorinae			

¹ *Hoplomys* included within *Proechimys* by Patton and Reig (1989)

additional species of *Makalata* from *Echimys* (1997). Patton and Emmons (1985) reviewed the genus *Isothrix* and, later, Emmons and Vucetich (1998) segregated a new genus, *Callistomys*, from *Isothrix*. Leite (2003), and Emmons et al. (2002) revised the Brazilian Atlantic tree rats, *Phyllomys* Lund, and showed the name *Nelomys* to have been incorrectly applied to this taxon. Emmons (1997) presented an outline of many of the characters and conclusions given here.

Several prior classifications have focused on the larger picture of placing caviomorph families in the context of the fossil record (Patterson and Wood, 1982; Woods, 1982), while a series of recent studies on molecular genetic relationships by J. L. Patton and his students have clarified the systematics of taxa within several genera (*Proechimys*, *Mesomys*, *Dactylomys*, *Phyllomys*): da Silva and Patton (1993), Patton (1994), Lara et al. (1996), Patton et al. (2000), and Leite (2003). Leite and Patton (2002) have presented a molecular phylogeny with the most taxonomically dense sampling of echimyid diversity. Carvalho (1999) recently analyzed phylogenetic relationships of living and fossil echimyids, with emphasis on the subfamily Eumysopinae; some of his results are similar to those presented below.

MATERIALS AND METHODS

Phylogenetic Assumptions and Taxon Sampling

The initial phylogenetic hypotheses were that (1) the Echimyinae, as defined by Patton and Reig (1989), form a monophyletic clade within the family Echimyidae (Tables 1, 2), and (2) within the subfamilial clade Echimyinae, species should group as six monophyletic clades representing the genera *Isothrix*, *Diplomys*, *Echimys*, and *Makalata* (Patton and Reig, 1989; Woods, 1993; McKenna and Bell 1997), as well as *Phyllomys* and *Callistomys pictus* (Emmons and Vucetich, 1998; Emmons et al., 2002; Leite, 2003).

For parsimony analysis I used one species as representative of each taxon for Eumysopinae and Dactylomyinae. For nominal species of *Diplomys*, only *D. labilis* and *D. rufodorsalis* are included, as adequate material of *D. caniceps* was unavailable. Likewise, two species of *Isothrix*, *I. pagurus* Wagner 1945, and *I. bistriata orinoci* (Thomas, 1899) were included as representatives of that taxon. Because some recent classifications have included *Myocastor coypus* among the Echimyidae (Table 1), this species was included in the analysis to explore its possible membership in Echimyinae or other subfamilial clades. The octodontid rodents, represented by *Octodon degus*, were chosen as the outgroup for the Echimyidae because they appear to be the most closely related clade at the family level (Woods, 1982) if myocastorids are included within the Echimyidae.

Table 2. Recent species classifications of the subfamily Echimyinae.

Tate 1935	Cabrera 1961	Woods 1993
	all Eumysopinae & <i>Mesomys</i>	
<i>Isothrix bistrata</i>	<i>Isothrix bistrata</i>	<i>Isothrix bistrata</i>
<i>Isothrix pagurus</i>	<i>Isothrix pagurus</i>	<i>Isothrix pagurus</i>
	<i>Isothrix picta</i>	
	<i>Diplomys caniceps</i>	<i>Diplomys caniceps</i>
	<i>Diplomys labilis</i>	<i>Diplomys labilis</i>
	<i>Diplomys rufodorsalis</i>	<i>Diplomys rufodorsalis</i>
"HAIRY-TAILED GROUP":		
<i>Echimys chrysurus</i>	<i>Echimys chrysurus</i>	<i>Echimys chrysurus</i>
	<i>Echimys blainvillei</i> (syn. <i>medius</i> , <i>thomasi</i>)	<i>Echimys blainvillei</i> (syn. <i>medius</i>)
<i>Echimys blainvillei</i>		
<i>Echimys pictus</i>		<i>Echimys pictus</i>
<i>Echimys lamarum</i>		<i>Echimys lamarum</i>
<i>Echimys grandis</i>	<i>Echimys grandis</i> (syn. <i>rhipidurus</i>)	<i>Echimys grandis</i>
<i>Echimys braziliensis</i>	<i>Echimys braziliensis</i>	<i>Echimys braziliensis</i>
<i>Echimys dasythrix</i>	<i>Echimys dasythrix</i> (syn. <i>lamarum</i>)	<i>Echimys dasythrix</i>
<i>Echimys rhipidurus</i>		<i>Echimys rhipidurus</i>
<i>Echimys saturnus</i>	<i>Echimys saturnus</i>	<i>Echimys saturnus</i>
"NAKED-TAILED GROUP"		
<i>Echimys semivillosus</i>	<i>Echimys semivillosus</i> (syn. <i>punctatus</i> , <i>carrikeri</i> , <i>flavidus</i>)	<i>Echimys semivillosus</i> (syn. <i>punctatus</i> , <i>carrikeri</i> , <i>flavidus</i>)
<i>Echimys punctatus</i>		
<i>Echimys carrikeri</i>		
<i>Echimys flavidus</i>		
<i>Echimys didelphoides</i>	<i>Echimys didelphoides</i> (syn. <i>occasius</i> , <i>guianae</i> , <i>longirostris</i>)	<i>Makalata didelphoides</i> (syn. <i>occasius</i> , <i>guianae</i> , <i>longirostris</i>)
<i>Echimys guianae</i>		
<i>Echimys longirostris</i>		
<i>Echimys obscura</i>		
<i>Echimys macrura</i>	<i>Echimys macrurus</i>	<i>Echimys macrurus</i>
<i>Echimys unicolor?</i>	<i>Echimys unicolor</i>	<i>Echimys unicolor</i>
<i>Echimys nigrispina</i>	<i>Echimys nigrispina</i>	<i>Echimys nigrispina</i>
<i>Echimys thomasi</i>		<i>Echimys thomasi</i>
<i>Echimys medius</i>		
<i>Echimys occasius</i>		

No echimyine taxon other than *Phyllomys* (Leite, 2003; Emmons et al., 2002) has received recent systematic or taxonomic revision, and most genera and species lack recent diagnoses. Resolution of the many nomenclatural problems and revision of all taxa of echimyines is beyond the scope of this paper, which is limited to supraspecific relationships of the arboreal taxa.

Phylogenetic Analysis

All parsimony analyses were implemented using PAUPTM 4.0b10 (D. L. Swofford, 1999) heuristic search option with all characters treated as unordered and equally weighted. The data set was subject to 100 random addition replicates with TBR branch swapping. Bootstrap values (Felsenstein, 1985) were calculated using 1000 bootstrap replicates with random searching. Patterns of character change were explored using MacClade 3.04 (Madison and Madison, 1992). Minimal numbers of characters were retained for analysis; for example, I include only 15 cheektooth features, although one could define a great many more in a loph-by-loph analysis. All relevant tooth characters and all parts of the skull involved in the chewing apparatus probably evolve in concert and the characters thus do not represent independent evidence of evolutionary change.

Specimens Examined

The specimens of Echimyinae preserved in the following museums were examined: National Museum of Natural History, USA (USNM); American Museum of Natural History (AMNH); Field Museum of Natural History (FMNH); Museum of Comparative Zoology, Harvard University (MCZ); Museum of Vertebrate Zoology, Berkeley (MVZ); Louisiana State University (LSU); Philadelphia Academy of Sciences (PAS); Natural History Museum, London (BMNH); Muséum National d'Histoire Naturelle, Paris (MNHN); Muséum d'Histoire Naturelle, Geneva (MHNG); Museum für Naturkunde der Humboldt-Universität zu Berlin (ZMB); Senckenburg Museum, Frankfurt (SMF); Naturhistorisches Museum, Vienna (NMW); Zoologisk Museum, Copenhagen (ZMC); Museo de Historia Natural, Lima (MHN); Escuela Politécnica Nacional, Quito; Museu de Zoologia, São Paulo (MZSP); Museu Nacional, Rio de Janeiro (MNRJ); Colección Boliviana de Fauna (CBF); Museo de Historia Natural Noël Kempff Mercado, Santa Cruz. The type material and a representative sample of specimens examined are listed below; many others were also examined.

Callistomys pictus: *Nelomys pictus* Pictet, 1841 MHNG 299.53, holotype; MNRJ 11027, 31545-6.

Diplomys: *Loncheres caniceps* Günther, 1876 BMNH 76.8.8.9, holotype. *Isothrix darlingi* Goldman 1913 USNM 179577, holotype; *D. labilis* USNM 296336-38, 305746, 460170-1, 396413, 339066, 335739-42, 178183, 457932.

Santamartamys: *Isothrix rufodorsalis* J. A. Allen, 1899 AMNH 14606, holotype; AMNH 34392.

Echimyis: *Echimyis saturnus* Thomas, 1928 BMNH 34.9.10.182, holotype; MCZ 41569; AMNH 71903, 98261; *Loncheres cristatus* Desmarest, 1817 MNHN 403, probable holotype; *E. chrysurus* USNM 460070, 549594-5, 549839-40, FMNH 93267, AMNH 96761-8.

Isothrix: *Isothrix bistrata* Wagner, 1845 NMW B 914, holotype; *Isothrix b. orinoci* USNM 406370, 406373-5, 496839; *Isothrix pagurus* Wagner, 1845 NMW B 913, holotype; USNM 555639; AMNH 95642, 95644, 95646-8, 95651.

Makalata: *Echimyis didelphoides* Desmarest, 1817 MNHN 404, probable holotype; USNM 460069, 549593, 549837-8, 581981-2; *Loncheres macrura* Wagner, 1842 NMW B921, holotype; USNM 406378, 406380-2, 406384, 406386, 406389-90, 406392, 406394-401, 496476, 496478, 496479-80, AMNH 92891-7, 93582-90, 96769-72, MVZ 153636-7, 157977; *Loncheres guianae* Thomas, 1888 BMNH 88.10.1.1, holotype; *Echimyis armatus handleyi* Goodwin, 1962 AMNH 184813 holotype; *Echimyis longirostris* Anthony, 1921 AMNH 42886, holotype; *Echimyis armatus castaneus* J. A. Allen, and Chapman, 1883, AMNH 6001/4728, holotype; *Loncheres grandis* Wagner, 1845 NMW 920, holotype; AMNH 92907-9, 92912-17, 92938-50, 93594-608, 93610-25, 94021-25, MCZ 32352-3; *Echimyis rhipidurus* Thomas, 1928 BMNH 28.7.21.89 holotype; AMNH 73231, 73267-8, 73270, 73273-4, 73276-7, 74084-6, 73791, BMNH 32.8.4.21, 32.8.4.22, 32.8.4.22a, FMNH 87243-49, 87251, 122991-2.

Pattonomys: *Nelomys semivillosus* I. Geoffroy 1838 MNHN 408b bis, possible holotype; USNM 280204-8; *Loncheres punctatus* Thomas, 1899: BMNH 98.12.1.18, holotype; BMNH 95.12.1.20, 52.12.3.21, 93.12.1.19; USNM 374741-2, 406402; *P. carrikeri* USNM 442715, 45629, 45636, 45643; *Loncheres flavidus* Hollister, 1914 USNM 63218, holotype; *Echimyis occasius* Thomas, 1921 BMNH 21.2.15.6, holotype; BMNH 34.9.10.202; MCZ 37964; FMNH 84259; AMNH 98262, 71897, 68177.

Phyllomys: *Phyllomys brasiliensis* Lund, 1839 lectotype and other type material from Lagoa Santa, ZMC (not numbered); *Nelomys blainvillii* Jourdan, 1837 MHNG 250/19, lectotype; MNHN nos. 310, 402; A7789, MZUSP 6146, 6147; USNM 304580, MNHN 14868, MNRJ 1345, 1350, 1512, 1516, 1517, 1521, 1523, 1528, 1548, 1762, 2238; *Phyllomys dasythrix* Hensel, 1872 ZMB 38800 lectotype, 38794, 38799, paralectotypes; *Phyllomys kerri* Moojen, 1950 MNRJ 6241, holotype; *Nelomys lamarum* Thomas, 1916

BMNH 3.9.5.96, holotype; BMNH, 3.9.5.92, 3.9.5.93, 3.9.5.94, 3.9.5.95, 3.9.5.97, 3.9.5.98, 3.9.5.99, 3.9.5.101, 3.9.5.102, 3.9.5.103, 3.9.5.104; FMNH 35356; *Loncheres medius* Thomas, 1909 BMNH 3.4.1.84, holotype; *Loncheres nigrispina* Wagner, 1842 NMW B 918, holotype; BMNH 33.10.9.18, 33.10.9.19; FMNH 93045, 94358, 94359; MZUSP 175, 1950, 1951, 1952, 1953; *Mesomys thomasi* Ihering, 1897, MZUSP 47 lectotype; MZUSP 45, 51, 223, 526, 527, 532 FMNH 41360 (ex MZUSP 1408); BMNH 2.8.25.2 (ex MZUSP 224), paralectotypes; *Loncheres unicolor* Wagner, 1842, SMF 4319, holotype.

RESULTS

Character Descriptions

There are few sets of discrete and stable characters with which to diagnose supra-specific levels of echimyine taxa. Many morphological characters were rejected during this study as being too variable among individuals. As my interest was in understanding the Echimyinae, I did not make a detailed study of the characters of Eumysopinae or other caviomorphs that might better illuminate those taxa, although some are included in the analysis. Most taxa of echimyids have indeterminate growth, so that measurements are best compared only between like-aged individuals (Patton and Rogers, 1983; Pessôa and dos Reis, 1991; Leite 2003). This limits the usefulness of morphometrics to taxa for which large series of specimens are available. Unfortunately, this is rarely the case for arboreal species. Skull nomenclature follows Woods and Howland (1979), tooth nomenclature (Figure 1) follows Emmons and Vucetich (1998). The states of the characters given below and the associated matrix by taxon (Appendix 1) were used to construct a phylogenetic hypothesis by parsimony analysis and to support the resulting generic classification.

External Morphology:

Character 1. *Pelage of lower back spiny (1); bristly (2); stiff (3), or soft (4).* Echimyidae owe their name to the stiff, spiny or bristly guard hairs characteristic of many taxa. With a few exceptions, spines are visually inconspicuous; they lie flat and are surrounded by slender hairs and are best detected by running a finger lightly backward against the tips of the rump pelage. Spiny pelage (1) has its most robust guard hairs petiolate, stiff, and strongly flattened, with the tip forming a sharp, abruptly narrowing point in strong-spined species. The strongest spines usually occur on the lower back; they bend most readily at the petiolate base, so that they rise vertically when stroked backward. In bristly pelage (2), the tip of the most robust hairs is prolonged into a long, flexible hairlike process and the hair is narrower. When rubbed backward, the hairlike process bends back and the hair is felt as very stiff or prickly but it does not impale the finger; pushed further, the hair

bends at its base and stands upright. Stiff pelage (3) is resistant but not prickly when rubbed backward; the hairs bend in the middle but do not stand upright. A few taxa of echimyids are soft-furred (4); their guard hairs feel soft and bend easily if rubbed backward. Guard hairs of these four types are illustrated by Leite (2001) and Emmons et al. (2002).

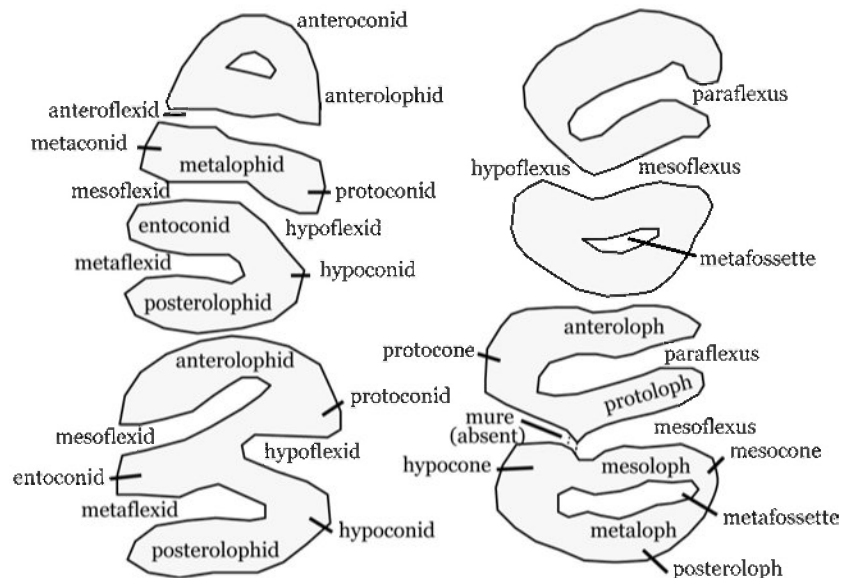


Figure 1. Terminology of the occlusal surface of the cheekteeth (after Emmons and Vucetich, 1998).

Character 2. *Guard hairs without dorsal sulcus (1) or with sulcus (2)*. Whether guard hairs are soft, stiff, or spiny, all but one of the taxa surveyed possess a dorsal, longitudinal groove that runs the length of the hair. The guard hairs are nearly circular in cross-section and it requires a microscope to detect the sulcus in the fine-haired *Callistomys pictus*. Of the taxa reviewed here, only *Myocastor coypus* lacks a sulcus; *O. degus* has a sulcus.

Character 3. *Crest of longer hair on crown and nape absent (1); or present (2)*. The crests of longer hairs on the crown and nape of some echimyine taxa are often composed of paler pelage bordered with contrasting darker stripes or are entirely black, contrasting with paler cheeks. Presumably, these crests can be erected in display, but there are no published descriptions of such behavior.

Character 4. *Guard hairs banded (1) or unbanded (2)*. Dorsal guard hairs can be banded, usually with pale gray bases, dark subterminal bands, and pale tips, or unicolored.

Character 5. *Tail "naked" (1) slightly hairy (2) or well clothed with hair, usually with a terminal tuft (3)*. Distal to the body fur the tail can range from "naked" or thinly clothed with inconspicuous short hairs that do not hide any scales; to slightly hairy, with conspicuous hairs throughout, but scales still partly visible; to "hairy" with the scales completely covered by dense long pelage. The tail tip may or may not have a pencil of long hair. Tail hairs of echimyines are monocolored and tend to curl away from the surface, which enhances visibility of the hairs. Tate (1935) strongly emphasized tail hairiness in his generic classification of the arboreal Echimyidae, however, the most polytypic taxa (*Makalata*, *Phyllomys*) have species with each state.

Character 6. *Tail tip colored as basal third of tail (1) sharply contrasting pale (2) or sharply contrasting black or darker (3)*. Color of the tail tip, especially in hairy-tailed species with tufts (but not all such), can contrast sharply from the base: species in three taxa have white tail-tips, those in two taxa can have tails tipped with orange or black. When most specimens had unicolored tails but rare individuals had a small pale tip, the species was scored as (1).

Character 7. *Extension of body fur onto tail base less than two cm (1) or more than two cm (2)*. Echimyids have either a significant (3-4 cm) extension of the dorsal pelage onto the tail base (species in most echimyine taxa) or the body fur ends abruptly where the tail joins the body (two echimyine species, many other echimyids).

Character 8. *Tiny tubercles cover naked plantar soles of feet (1) or tubercles only present between raised, smooth, well-developed pads (2) or tubercles absent (3)*. Many caviomorphs have no distinct firm, smooth, raised plantar pads under the foot joints, but have the soles of the feet covered with tiny tubercles (illustrated for *Cuscomys* in Emmons 1999 [Figure 3]); this state (1) is found in all taxa of Abrocomidae and Capromyida as well as species of *Ctenomys*, *Octodon*, *Myocastor*, and others. It is this taxonomic distribution that suggests that it is the plesiomorphic condition. The Echimyidae possess a variable degree of retention of tiny tubercles on the soles, from entirely covering the soles (all dactylomyines, state 1) to strong development of smooth raised pads under weight-bearing joints, but tiny tubercles present around and between the pads (most echimyines, state 2); or smooth raised pads with no surrounding tubercles (*Diplomys* spp., state 3). The tubercles may provide friction for gripping smooth surfaces.

Character 9. *Hind foot without raised, smooth, firm, well-developed plantar pads (1), with five pads and the lateral metatarsal pad and first digital pads joined as a single pad (2) or six*

pads, with the lateral metatarsal pad and first digital pad not joined (3). The number and development of the raised smooth pads under the foot joints varies among taxa (see character 8). Fluid preserved specimens were not available for all taxa, and the characters are difficult to see in skin preparations.

Character 10. *Mammae arranged in two pairs (1), three pairs (2), or four or more pairs (3).* With the possible exception of *S. rufodorsalis*, Echimyinae have two to five pairs of mammae found under the lateral body fur between elbow and hip in the dorsal pelage field, well above its line of demarcation from the ventral field. There are three principal patterns of mammae: (a) as many as 5 lateral pairs, which include three pairs about equally spaced along the sides in the dorsal pelage field, with another pair intercalated between each of the anterior and medial, and the medial and posterior pairs; (b) three lateral pairs of mammae that are about equally spaced along the sides in the dorsal pelage field (one anterior, one medial, and one posterior), and one inguinal pair on the ventral field; c) two functional lateral pairs which seem to correspond to the medial and posterior lateral pairs of (b), with an occasional inguinal pair. When pairs are reduced, the anteriormost lateral pair appears to be the first one lost, followed by the inguinal pair. Because of their placement below dense dorsal pelage, unused lateral mammae are difficult to detect and mammae counts from skins of echimyids can be ambiguous.

Character 11. *Maxillary cheekteeth brachydont, with 4 roots (1), hypselodont with 3 roots (2), or hypsodont and unrooted (3).* Characters of the dental roots appear to distinguish higher (subfamilial) levels of Echimyidae. When the teeth are four-rooted and brachydont, (1), the cheekteeth are straight-sided; when the molars have three roots (2), the crown of the tooth is strongly bent laterally; when the teeth are hypsodont, with single, open roots, the crowns tend to be straight sided. Most echimyines have state 1, and eumysopines state 2.

Character 12. *Occlusal plane tip flattish relative to plane of palate (1), weak tip (2), or strong tip (3).* When the cheekteeth are 4 rooted (character 11) the occlusal plane may be parallel to the hard palate (state 1, only in dactylomyines) or tipped laterally with the labial maxillary gumline above the palatal line (state 2, Figure 2). When the teeth are three rooted and unilaterally hypsodont, the crown of the tooth may be straight sided and the occlusal plane parallel to the palate (state 1), or weakly (state 2), or strongly bent laterally (state 3, Figure 2) such that the maxillary occlusal surfaces face laterally. In this case the labial gumlines are about on a plane with the palatal gumline. When the maxillary occlusal plane is tipped laterally, the mandibular occlusal surfaces correspondingly tip medially for occlusion.

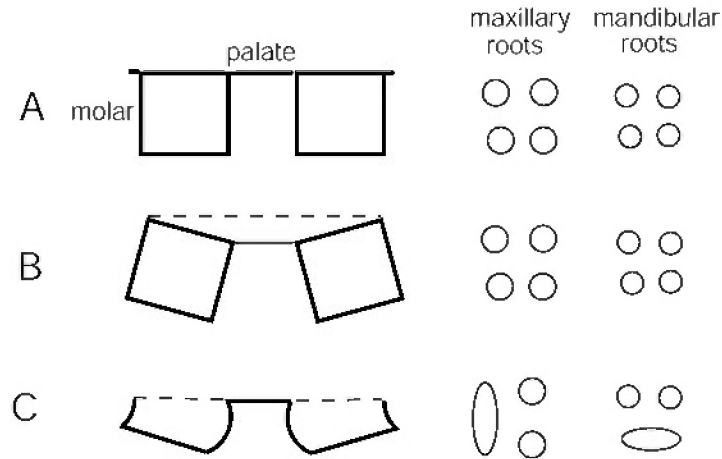


Figure 2. Schematic of maxillary cheek tooth angles in relation to palate, and associated molar root patterns. (a) Occlusal plane parallel to palate (i.e., dactylomyines), (b) straight-sided teeth tipped, occlusal surface at an angle (most echimyines), (c) teeth bent, occlusal surface at angle (eumysopines, *Callistomys* spp.).

Character 13. *Upper incisor root originates within the maxillary root of zygoma, posterior to the root of the zygoma (1) or level with or outside zygoma (2).* The root of the upper incisors may extend into the infraorbital foramen to nearly contact the molar roots (1). The bulge at the base of the root forms beneath it the canal for the infraorbital nerve on the floor of the interior, medial surface of the inferior zygomatic root. Alternatively, the incisor root may be short, with its base level with or anterior to the vertical part of the maxillary root of the zygoma (2). In this case, the medial ventral wall of the infraorbital foramen is smooth. The condition of long incisor roots and a well-developed infraorbital canal, with a sheetlike dorsal extension of the maxillary over the canal to form a closed tube at maximal development, may be the plesiomorphic state, as it is present in octodonts.

Character 14. *Lower incisor root originates posterior to m3, high in coronoid process (1) below m3 (2) or anterior to m3 (3).* The lower incisor root can extend posteriorly high up the condylar process of the mandible, which is then extremely robust (state 1); or it can be much shorter, originating below or anterior to the third molar. The mandibular foramen lies posterodorsally to the incisor root, such that when the roots are long, it is high up near the condyloid process.

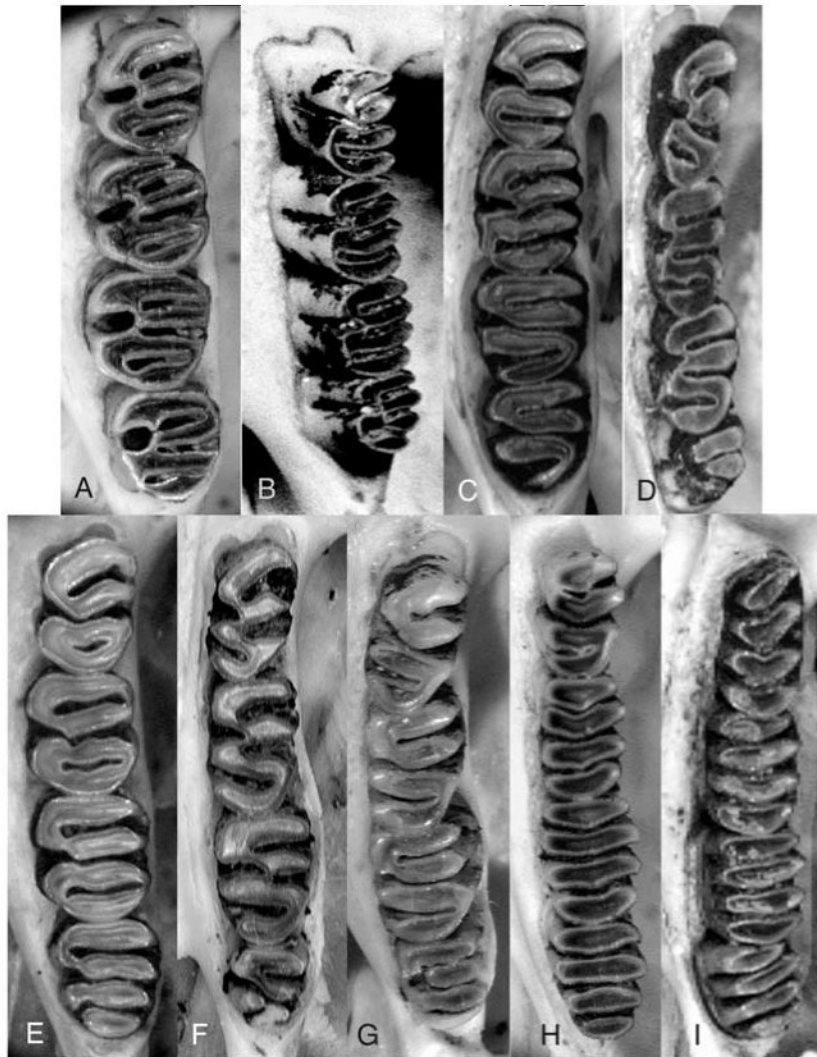


Figure 3. Occlusal aspect of left maxillary cheekteeth. (a) *Isothrix bistriata* USNM 460375, (b) *Callistomys pictus* BMNH 80.9.15.1, (c) *Makalata macrura* USNM 40638, (d) *Pattonomys occasius* FMNH 84259, (e) *Echimys chrysurus* USNM 549594, (f) *Pattonomys carrikeri* USNM 45642, (g) *Santamartamys rufodorsalis* AMNH 34392, (h) *Phyllomys nigrispina* MZSP 1951, (i) *Diplomys labilis* USNM 296337.

Character 15. Occlusal surface of maxillary cheekteeth with one short lingual flexus/fossette and two labial flexi/fossettes (1, *Proechimys* pattern), one lingual flexus and three labial flexi (2, *Echimys* pattern), two lingual flexi, two labial flexi (3, *semivillosus* pattern), four separate and parallel laminae (4, *Phyllomys* pattern), none of these (5), 1 lingual flexus, 4 labial flexi/fossettes (6, *Mesomys* pattern), or polymorphic (2) and (3), (7). All patterns

refer to unworn or little-worn teeth; the pattern can change with wear. Teeth of state (2) are subcircular in shape with one re-entrant lingual flexus that penetrates less than a half-width of the tooth (Figure 3a). Teeth of state (3) are elongate, with two lingual flexi, the anterior one may completely divide tooth and connect to mid-tooth labial flexus, and two labial flexi (Figure 3d, f); teeth of state (4) are elongate, with three flexi that completely cross teeth and split them into 4 sub-parallel, laminar lophes (Figure 3h, i); state (5) refers only to the outgroup, *Octodon degus*, which has no enamel flexi or fossettes; while state 6 was found uniquely in *Mesomys* c.f. *hispidus*. Whether the posterior flexus opens lingually or labially is variable in *Makalata macrura*, such that an individual can have both patterns in the corresponding teeth on opposite sides of the mouth. In species with laminar teeth, the lophes often join with wear. The pattern in which this occurs, like the original pattern of lophes and flexi, depends upon the vertical depth of each part of each flexus. In unworn teeth, the eventual wear pattern can be predicted from the relative depth of the flexi as viewed from the side of the tooth.

Character 16. *M3 with four or more well-developed lophes (1) or with reduced posteroloph (2) or with three or fewer lophes (3) or polymorphic for (1) and (2) (4) or polymorphic for (2) and (3) (5)*. The fourth or posteriormost loph of M3 can be well developed and extend the full width of the tooth (1, Figure 3e, i); or be reduced in size to half or less of the width of the anterior lophes of M3 (2, Figure 3c); or else completely absent (3, Figure 3d).

Character 17. *M3 mesoloph similar in size to protoloph (1 Figure 3c) or much shorter than protoloph (2 Figure 3d)*.

Character 18. *Lower premolar anteroloph not triangular (1) or triangular with a flexid opening lingually or apparently so (2) or triangular with flexid open labially (3, Figure 4f) or triangular with flexid open posteriorly (4) or an enclosed triangle with a central fossetid (5, Figure 4c) or loph triangular or oblong, with no fossetid (6)*. The anterior lophes of the unworn lower premolar have some of the most trenchant characters for distinguishing echimyid taxa (Figure 4). In most echimyines the anterior loph forms a roughly triangular, pointed or rounded structure, which varies in the orientation of its single flexid (2, 3, 4) or whether this is enclosed as a central fossetid (5) or is completely absent (6).

Character 19. *Lower premolar without separate (metalophid) bar in middle (1, Figure 4b, F) or bar is present (2, Figure 4c, E) or other (3)*. I provisionally follow Vucetich and Verzi (1992) in considering the pentalophodont molariform tooth as plesiomorphic among echimyids, but I am uncertain of the homologies of the anterior lophes of p4. I consider the anteroconid and anterolophid (Figure 1) as two lophids, but where the metalophid bar is absent (compare Figure 4b to 4c), it is unclear whether it is the

metalophid or the anterolophid that is lacking, or whether they have merged into a single loph. *Myocastor coypus* has premolars of a different form (state 3) not classifiable for this character.

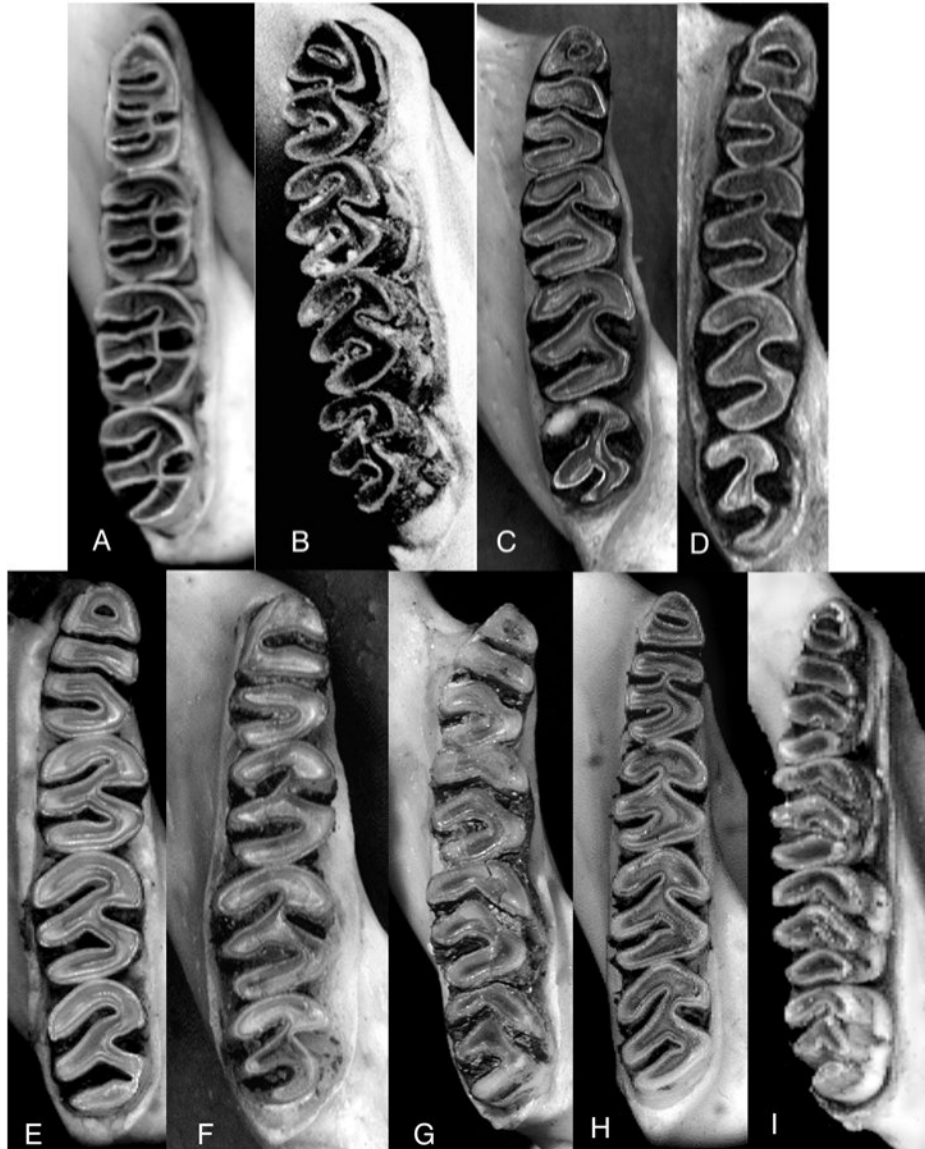


Figure 4. Occlusal aspect of the right mandibular cheek teeth. Specimens as in Figure 3.

Character 20. Anterior edge of crowns of m2-3 almost a straight line at right angle to tooth axis (1) or curved with radius like part of a circle encompassing tooth, or caret shaped (2, Figure 4, all) or a straight diagonal line relative to tooth axis (3).

Character 21. Lower molar labial and lingual flexids slanted forward, medial end anterior to labial end, m2-3 metaflexid well separated from hypoflexid (1, Figure 4b-e) or labial and lingual flexids about 90° to tooth axis, metaflexid meets or almost meets hypoflexid in mid-tooth (2, Figure 4a).

Character 22. Lower molars with no separate laminar lophs (1, Figure 4a-f) or with one separate anteroloph (2, Figure 4g) or with three separate lophs (3, Figure 4i) or with one separate posteroloph (4). State (1) is the condition of most caviomorphs and echimyids, and likely plesiomorphic. Only *Phyllomys* spp. share state (2), only *Diplomys* spp. have state (3), and only *Dactylomys* spp. state (4).

Character 23. Hypoflexid slants posteriorly (1, Figure 4a) or slants weakly anteriorly (2, Figure 4d, e) or slants strongly anteriorly (3, Figure 4b, h).

Character 24. Mandibular toothrows strongly convergent anteriorly (1) slightly convergent anteriorly (2) or parallel or divergent (3).

Character 25. Relative length of upper toothrow/basilar length of Hensel very short, 20-22% (1), short 23-24.4% (2), intermediate 24.4-25.7% (3, Figure 11), or long, 26.9-31% (4, Figure 14).

Character 26. Lower incisors strongly curved (1, Figure 13) or straightish (2, Figure 11).

Character 27. Squamosotympanic fenestra a large open slit (1, Figure 5b) or a tube enclosed in bone (2, Figure 5a). The squamosotympanic fenestra is an elongate open slit along the squamosal suture in some echimyids. This is likely to be the plesiomorphic state, as it is thus in capromyids, octodontids, abrocomids, and cuniculids. In most echimyini, the fenestra is closed posteriorly to form a tube that opens anteriorly. Functionally, this fenestra in caviomorphs is likely the same as the post-glenoid foramen of murids.

Character 28. Masticatory foramen and foramen ovale accessorius (foa) are separated by a bony strut that is absent, or no masticatory foramen (1); a narrow strut (2, Figure 6e); a medium width strut (3, Figure 6b); a wide strut (4, Figure 6f); or are polymorphic 2 and 3 (5). The strut of bone that separates the foa and masticatory foramina is narrow or very narrow, or the masticatory foramen is lacking, in most Eumysopinae, which likely possess the plesiomorphic state. It is narrow to absent in *Dactylomys* spp., and varies from narrow to wide in other echimyines.



Figure 5. Auditory bullar region of Echimyids. (a) *Echimyus chrysurus* USNM 549594 (reversed), (b) *Isothrix bistriata* USNM 406375, (c) *Makalata didelphoides* MDC572, (d) *Santamartamys rufodorsalis* AMNH 34392 (reversed), (e) *Phyllomys nigrispina* USNM 484508, (f) *Diplomys labilis* USNM 296337. Arrows denote crest on the ventral border of the squamosotympanic foramen, with depression below, in (c) and space above meatus in (e).

Character 29. A small (interparietal) foramen between foa and masticatory foramen is present (1, Figure 6a) or absent (2, Figure 6c) or 3 polymorphic for (1) and (2). This foramen was considered present in a specimen if it was found on both or only one side of a specimen.

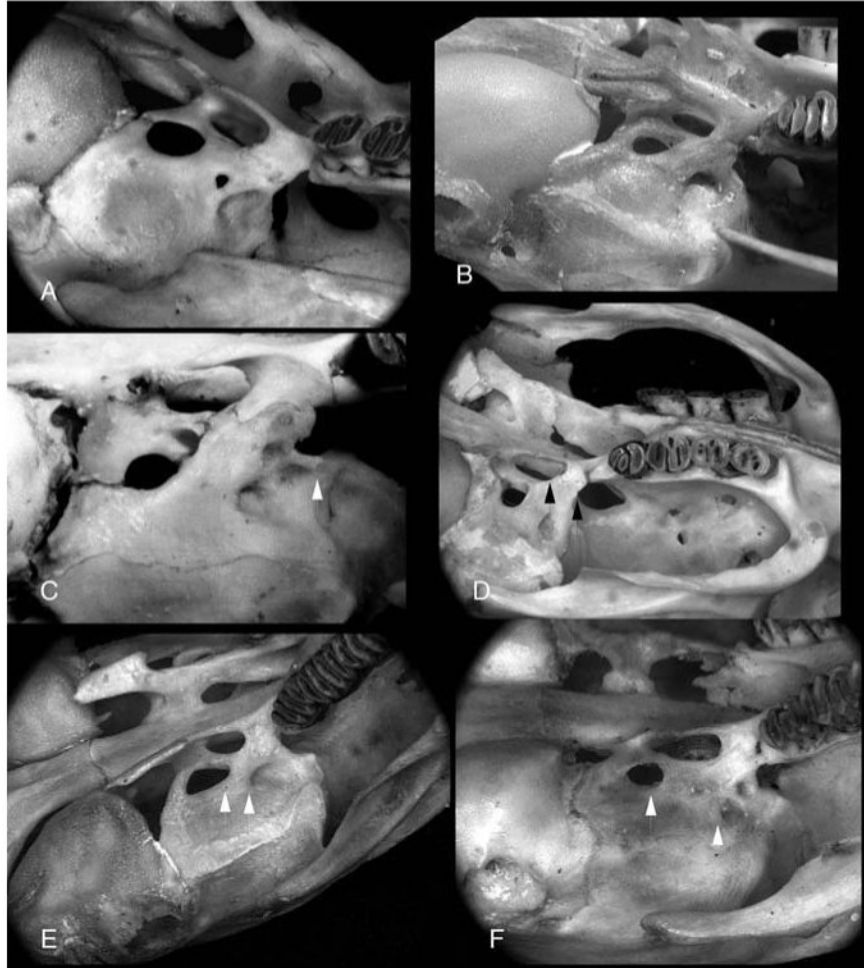


Figure 6. Alisphenoid region of (a) *Isothrix bistrata* USNM 406375, (b) *Echimys chrysurus* USNM 549594, (c) *Makalata grandis*, (d) *Pattonomys occasius* MVZ 37964, (e) *Diplomys labilis* USNM 296337, (f) *Santamartamys rufodorsalis* AMNH 34392. Arrows in (d-f) bracket the distance from the foramen ovale accessorium to the masticatory foramen; arrow in (c) points to the buccinator foramen.

Character 30. Slant of lateral tube of auditory meatus straight out or slightly forward (1, Figure 5c) or slanted strongly forward or downward (2, Figure 5f) or slanted upward and backward (3). Because the ear pinnae of echimyines are tiny and likely immobile, the direction of slant of the outer ear canal may be associated with the directionality of hearing; the functional significance of the different character states among echimyids is unclear, as all species are arboreal. Specimens often have bony rings external to the tubes (Figure 5e, on lower right of meatus), but these are usually lost in skinning or skull preparation and their presence/absence could not be scored. Nevertheless, bony rings seem more common in some taxa than in others (*Phyllomys* spp., *semivillosus* group).

Character 31. Premaxillary and maxillary portions of septum within incisive foramen separate, maxillary portion dipping in dorsally (1, Figure 7a) or fused and maxillary portion dipping in dorsally (2) or broadly fused, in the same plane as rim of foramen (3, Figure 7b). Characters of the incisive foramen have proved extremely useful for distinguishing *Proechimys* species (Patton, 1988). Among the Echimyinae, most have configuration (1), which is likely plesiomorphic, as it is widely distributed among caviomorphs. *Makalata* skulls can often be distinguished from other genera by this character alone. In very old animals, some fusion of the elements of state (1) can occur.

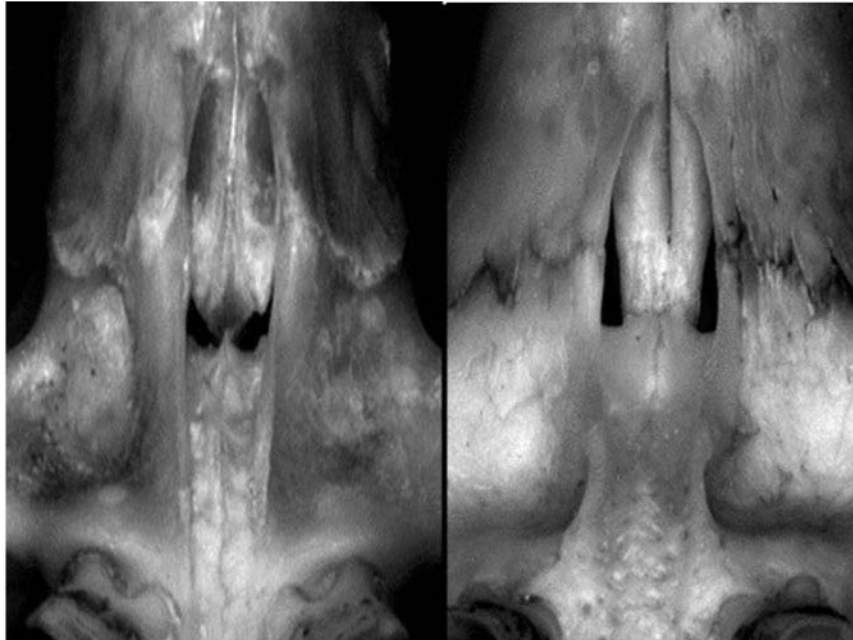


Figure 7. Incisive foramen of (a) *Pattonomys carrikeri* USNM 45629 and (b) *Makalata macrura* USNM 406380.

Character 32. *Anterior jugal hugely expanded in depth, more than 1/2 width of infraorbital foramen (1) or wide, but less than 1/2 width of infraorbital foramen (2) or narrow (3).* The most extreme expansion of the jugals is found in the semi-fossorial taxa *Euryzygomatomys spinosus*, *Carterodon sulcidens* and *Clyomys laticeps*, and in the semiaquatic *Myocastor coypus*, while the next widest condition is possessed by terrestrial taxa such as *Thrichomys aperioides* and *Proechimys longicaudatus*, and one arboreal species, *Callistomys pictus*. Most arboreal species have relatively slender jugals (Figure 12), suggesting an ecological association with jugal development.

Character 33. *Jugal fossa, anterior point diffuse and broad anteriorly (1) or comes to a sharp point (2, Figure 12).* State (1) is shared only by three terrestrial taxa and *C. pictus*, again suggesting an ecological association.

Character 34. *Inferior jugal process (jp) inconspicuous and forward of superior jp (1, Figure 17) or elongate and about level with or posterior to sjp (2, Figure 12).*

Character 35. *Jugal fossa, width of angle from upper rim to lower border of inferior process 10° or less (1), about 20° (2), about 30° (3, Figure 12), or about 40° or more (4, Figure 14).*

Character 36. *Infraorbital canal well developed with sharp crest or closed beneath a bony shelf (1) or present only as a groove (2) or completely absent (3) or polymorphic for 2 and 3 (4).* This canal or groove on the medial floor of the infraorbital canal was described and illustrated by Patton (1988) as a character of *Proechimys* spp. See notes for character 13. Most arboreal taxa lack a canal.

Character 37. *Ventral lip of squamosotympanic fenestra smooth, without a beaded rim or a depression ventrad (1, Figure 5f) or raised as a beaded rim, with distinct depression below it (2, Figure 5c arrow).*

Character 38. *Large palatal vacuities present in alisphenoid-basisphenoid region such that parapterygoids are freestanding (1) or small, distinct round openings of unfused sutures persisting to adulthood (2, Figure 11) or with sutures either completely fused in adults, or with only hairline slits present (3, Figure 12).* This character must be evaluated in adult specimens; vacuities in juveniles may fuse with maturity.

Character 39. *Buccinator foramen with no medial wall and open space below pterygoid (1) or with a bony shelf on foramen floor beside alisphenoid (2) or with a shelf and medial wall or partial wall forming a closed foramen (3).* This structure can only be seen in well-cleaned skulls, as it is deep in the medial cranium. It is viewed by holding the skull at eye level and sighting posteriorly through the infraorbital foramen along the plane of the buccinator foramen.

Character 40. Mandibular foramen near top of the condylar process of mandible (1) or on low or mid ramus anterior to a blade-like condyloid ridge (2, Figure 8a) or at the base of ramus near toothrow on posterior edge of condyloid ridge (3, Figure 8c) or at base of ramus near toothrow on anterior side of condyloid ridge (4, Figure 8d). See note for character 13.

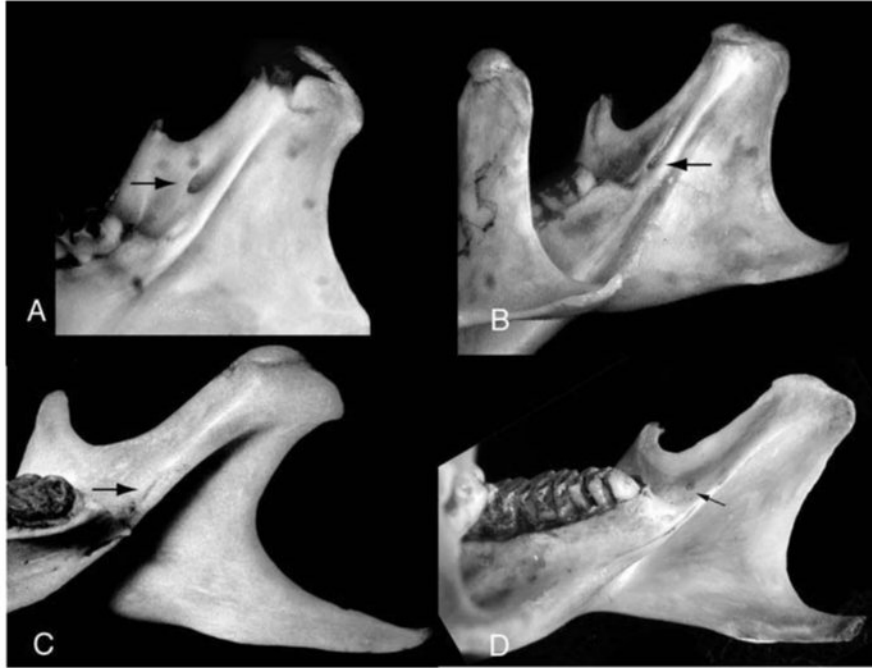


Figure 8. Position of mandibular foramen (arrows). (a) *Isothrix bistrata*, (b) *Echimys chrysurus*, (c) *Phyllomys medius*, (d) *Diplomys labilis*.

Character 41. Angular process of mandible short posteriorly, about as long as condylar process (1, Figure 8b) or long, much longer than condylar process (2, Figure 8c). The relative length of the angular process is gauged by setting the mandible on a flat surface and looking straight down on it from above, over the condylar process.

Character 42. Dorsal rim of auditory meatus close to squamosal suture, space above meatus is narrower than width of auditory meatus (1, Figure 5a) or with wide flat space, almost as wide or wider than meatus, between it and the suture (2). A wide space above the meatus is found only in *Phyllomys* species (Figure 5e, between arrows) and *Myocastor*.

Character 43. *Posterior maxillary notch of maxillary and palatine behind M3 enclosed as a foramen, with maxillary fused with suture to alisphenoid (1, Figure 6f) or open as notch, alisphenoid not fused to maxillary (2, Figure 6e) or polymorphic for 1 and 2 (3).*

Character 44. *Coronoid process of mandible higher than condylar process (1) or lower than condylar process (2).*

Character 45. *Fourth premolar deciduous (1) or not deciduous (2).* A diagnostic character of the family Echimyidae is the presence of a premolar retained throughout life that is not preceded by an erupted deciduous tooth. This tooth is likely the homologue of the deciduous premolar of other hystricognath rodents. I designate it as P4/p4, without judgment as to its homology. The bristle-spined porcupine, *Chaetomys subspinosus*, previously considered an echimyid, has a deciduous premolar that is replaced by a permanent tooth. A specimen in Senkenburg Museum, Frankfurt, (SMF 11045) has an unworn P4 beside well-worn molars, a state that does not occur in echimyids, where the cheekteeth always show decreasing wear from P4/p4 to M3/m3.

Character 46. *Squamosoparietal suture raised in a ridge extending across parietal (1) or smooth, with no raised ridge (2).*

Character 47. *Squamosal width at squamosotympanic foramen ≤ 1 mm (1) or 1 to ≤ 2 mm (2) or 2 to ≤ 3 mm (3).*

Phylogenetic Hypothesis

The above characters were used to construct a phylogenetic hypothesis. The bootstrap 50% majority rule consensus tree suggests the following relationships (Figure 9a): (1) a clade of taxa including all genera placed in Echimyinae by Patton and Reig (1989) and McKenna and Bell (1997) is weakly supported, but, unlike their classifications, it includes *Mesomys* sp., *Lonchothrix emiliae*, *Dactylomys boliviensis* and *Myocastor coypus*, (2) taxa formerly all synonymized under the genus *Echimyis* (Tate 1935) group into four units, including *Makalata* species, *Echimyis* species, *Phyllomys* species, and the *semivillosus* group of Caribbean coastal species, with which the Amazonian *occasius* associates, (3) *Isothrix* species, *Callistomys pictus*, *Diplomys labilis* and *rufodorsalis* do not cluster with others, (4) the eumysopines (sensu Patton and Reig, 1989) do not segregate as a monophyletic clade, but (5) the three semi-fossorial taxa cluster as a sister group to all the other Echimyidae.

Bootstrap analysis (Figure 9a) strongly supports clades of *Echimyis* species and *Isothrix* species, as well as a clade including the three semifossorial taxa (*Carterodon sulcidens*, *Clyomys laticeps*, *Euryzygomatomys spinosus*). Clades of *Makalata* species and *Phyllomys* species are more weakly supported. McKenna and Bell (1997) placed

Myocastor among the Echimyidae, a view that seems supported by this character set. However, other characters of this taxon were not examined in detail and I consider the subfamilial affinity of *Myocastor* unresolved by this data set.

These results reveal some close similarities to patterns seen in molecular studies of a range of caviomorphs (Lara et al. 1996, Leite and Patton 2002, Figure 9b). Those analyses also grouped all taxa seen above the first node of Figure 9a and found little resolution at the base of the family, but indicated monophyly of the four included taxa of echimyines (*Echimys*, *Phyllomys*, and two taxa of *Makalata*). Like Figure 9a, the molecular analysis (Figure 9b) does not support monophyly of Eumysopinae sensu Patton and Reig (1989) and places *Euryzygomatomys* and *Clyomys* as a sister group to all other echimyids, which may be associated with *Myocastor*. My results also agree with the molecular hypothesis in showing separation of *Proechimys* from *Trinomys*. Leite (2003) recently analyzed complete cyt b gene sequences of *Phyllomys* from populations throughout the entire geographic range, with *Echimys chrysurus* and two *Makalata* species as outgroups. His molecular data set shows that the 33 individuals from populations of nine *Phyllomys* species form a strongly supported monophyletic clade with respect to the outgroups, but there are several divergent clades within *Phyllomys*. Of the four *Phyllomys* taxa analyzed here, Leite (2003) shows *P. lamarum* grouped in a clade with *P. blainvillii*, with *P. nigrispinus* in a more distant sister group to these, while *P. dasythrix* is widely divergent in a sister group to the clade including those three. This structure is partially mirrored in Figure 9a.

I find the molecular evidence compelling and I here conclude that on both morphological and molecular grounds there is as of yet no clear basis for assigning several taxa of Echimyidae into subfamilies with other genera, including *Myocastor*, *Dactylomys* spp., *Isothrix* spp. and *Mesomys/Lonchothrix* spp. Furthermore, as also concluded by Lara et al. (1996) and Leite and Patton (2002), a subfamilial clade Eumysopinae is not supported. With the caveats noted below, I provisionally define Echimyinae as the taxa grouped above *Proechimys* in Figure 9a, and grouped likewise above the arrow in Figure 9b. Nonetheless, I will follow recent authors (Table 1) and maintain the dactylomyines and *Myocastor* in their own subfamilies, pending more comprehensive and convincing systematic studies of those taxa. In this report I revise all the arboreal echimyine genera with the exception of *Mesomys* and *Lonchothrix* species.

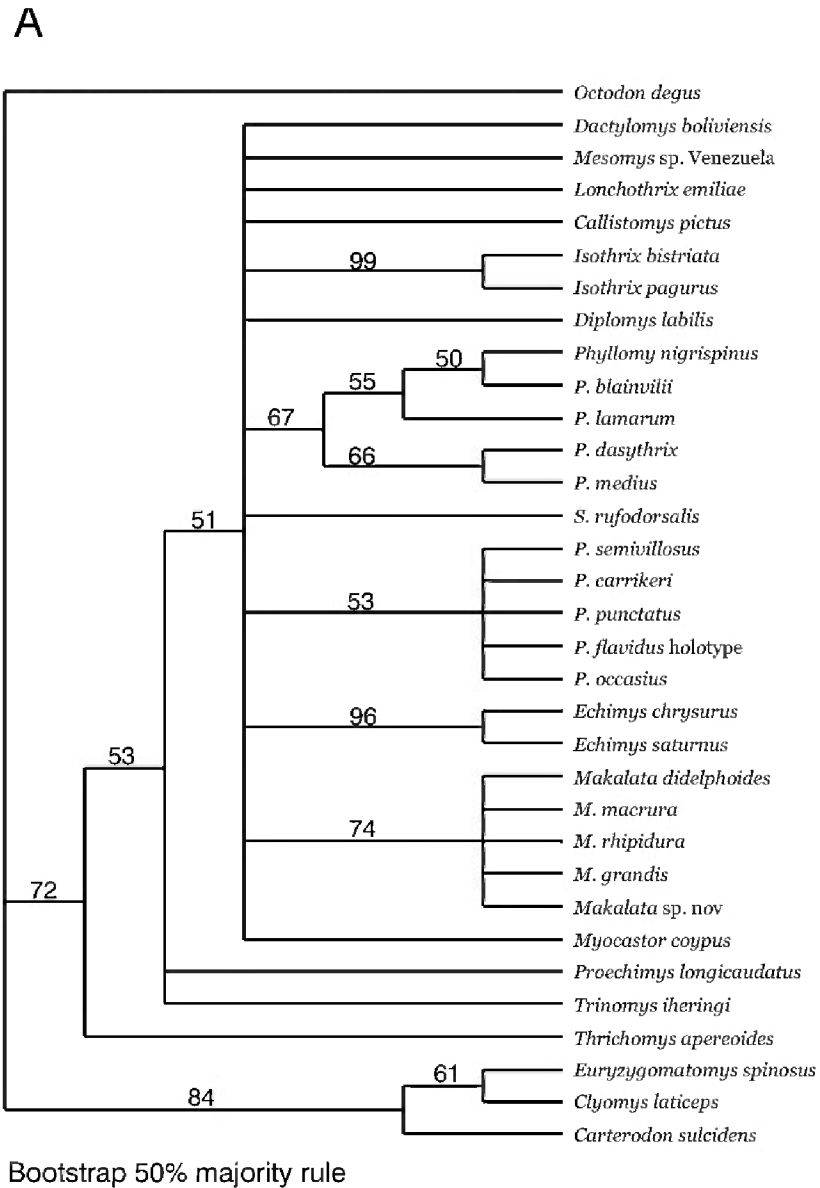


Figure 9a. Tree generated by 50% majority-rule bootstrap analysis of morphological characters. Bootstrap values from heuristic search in boldface italics; values $\geq 50\%$ shown above branches.

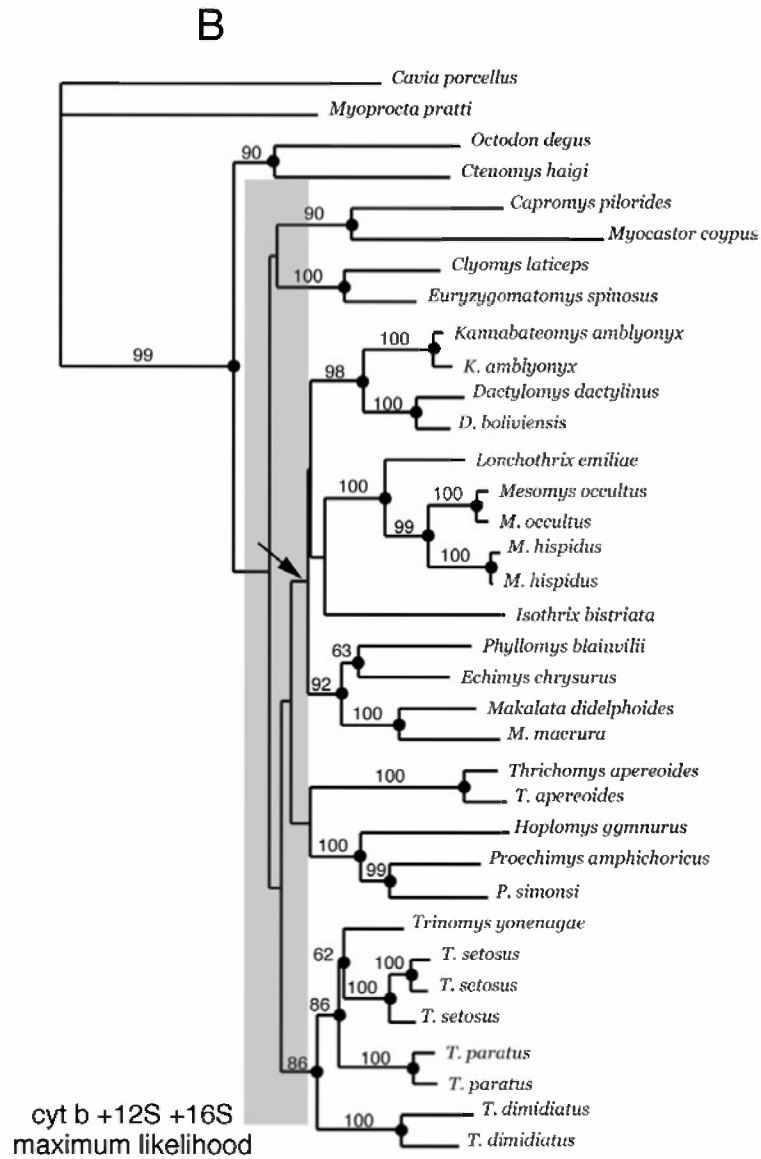


Figure 9b. Highest likelihood tree based on molecular characters of combined cyt b, 12S, and 16S genes. Percent bootstrap values shown above branches, gray area of tree has no resolution (from Leite and Patton, 2002).

The Family Echimyidae Gray, 1825

Before defining the genera of the subfamily Echimyinae, I briefly outline the most significant characters, primarily of dentition, that separate the Echimyinae from the other echimyid taxa provisionally grouped under Dactylomyinae and the likely paraphyletic Eumysopinae sensu Patton and Reig (1989). I retain the subfamily Eumysopinae pending a stronger case for rejecting it and substituting another, but I propose a tribal grouping within it, based on morphological characters and the molecular results of Leite and Patton (2002).

Subfamily Eumysopinae Rusconi, 1935

Diagnosis: Cheekteeth hypselodont (unilaterally hypsodont), with uppers on the lingual side and lowers on the labial side. Occlusal plane tipped at a sharp angle away from the palate, produced by bending of the tooth so that labial gum lines are close to the same plane as the palate (Figure 2c). Upper molars with three roots; the lingual, hypsodont side with a single, longitudinal, narrow root running the length of the tooth and the labial side with two small roots. Lower molars with three roots; one long narrow transverse root across the posterior side and two small anterior roots. Hypoflexids of m1-3 slant posteriorly (internal end more posterior to external, labial, end). Root of lower incisor reaches to M3 or posterior to it. Root of upper incisor originates within the orbit, posterior to the inferior zygomatic root. Upper cheekteeth subcircular in occlusal section, with one lingual flexus (hypoflexus) which penetrates less than half the width of tooth; no reentrant flexi from labial side, cheekteeth not split into separate lophs by deep transverse flexi. Tooththrows short, less than 25% of basilar length of Hensel.

Remarks: The above characters are shared by many eumysopine taxa and may be plesiomorphic, as noted by Patton and Reig (1989). I list them here for heuristic comparison with characters of the echimyines described below. For brevity, below I use the term Eumysopinae to designate the group of taxa placed there by Patton and Reig (1989), without implying that I consider them to be a monophyletic group.

Tribe Euryzygomatomini

*Included genera:**Euryzygomatomys* Goeldi, 1901*Clyomys* Thomas, 1916*Carterodon* Waterhouse, 1848

Diagnosis: Fossorially adapted rodents. Tail much shorter than head and body (about 50% or less of HB length), claws of forefoot greatly elongated. Root of lower incisor extends high above line of cheekteeth into ramus of mandible. Mandibular foramen high near top of ramus; coronoid process of mandible higher than condyloid process. Infraorbital canal strongly developed. Jugals often broadly expanded dorsoventrally, with the maxillary ascending portion of zygomatic arch usually broad. Basisphenoid above palatal notch completely surrounded by large vacuities.

Remarks: This cluster of monotypic genera likely deserves subfamilial rank, but detailed studies are needed of the molecular genetics and the morphology of both fossil and living forms.

*Incertae Sedis*Genus *Proechimys* Allen, 1899synonym *Hoplomys*, Allen, 1908Genus *Thrichomys* Trouessart, 1880Genus *Trinomys* Thomas, 1921Genus *Mesomys* Wagner, 1845Genus *Lonchothrix* Thomas, 1920

Subfamily Dactylomyinae Tate, 1935

*Included genera:**Dactylomys* I. Geoffroy, 1838*Kannabateomys* Jentink, 1891*Olallamys* Emmons, 1988

Diagnosis: Arboreally adapted rodents. Pelage without spines or bristles. Tails much longer than head and body length. Feet with no raised, smooth palmar or plantar pads, palmar and plantar skin evenly and densely covered with tiny

tubercles, toes elongate and slender. Cheekteeth brachydont, with four roots. Occlusal plane approximately parallel (in the same plane as) to palate. Cheekteeth extremely enlarged, broader than long, forming broad flat plates. Cheekteeth split by deep flexi into four lophs in two V-shaped pairs that open labially and come to a gradual point lingually. Lower molars split by transverse flexids into three lophs, an anterior, single, lamellar loph and a posterior, V-shaped pair of joined lophs. Alisphenoid with reduced or no bony bridge from foramen ovale to basisphenoid posterior to base of parapterygoid processes. Paraoccipital processes projecting laterally. Where diet is known, all taxa feed chiefly on bamboo.

Subfamily Echimyinae Gray, 1825

Included genera:

Echimyys F. Cuvier, 1809

Phyllomys Lund, 1839

Makalata Husson, 1978

Diplomys Thomas, 1916

Callistomys Emmons and Vucetich 1998

Two new genera

Diagnosis: Arboreally adapted rodents with pelage spiny, bristly, or soft; tail as long as or longer than head and body length. Feet with raised, smooth plantar pads developed under joints. Molars brachydont, with four roots (except in *Callistomys*), but crowns often high. Posterior tip of lower incisor root terminates anterior to m3. Occlusal plane tipped away from plane of palate, achieved by tipping of straight-sided teeth, so that labial gumline is higher than palatal (Figure 2b, except in *Callistomys*). Cheekteeth with deep reentrant flexi/ids that may split teeth into separate, parallel laminae. One to three deep flexi present on labial side of maxillary cheekteeth. Maxillary zygomatic process and jugal usually slender. Toothrows long, over 25% of basilar length of Hensel.

*Incertae Sedis**Isothrix* Wagner, 1845Genus *Isothrix* Wagner, 1845*Type species: Isothrix bistriata* Wagner, 1845*Included species:**Isothrix bistriata* Wagner, 1845*Isothrix pagurus* Wagner, 1845*Loncheres [bistriata] orinoci* Thomas, 1899*Isothrix [bistriata] negrensis* Thomas, 1920*Isothrix sinnamariensis* Vié et al. 1996

Diagnosis: Large arboreal rats; fur soft; tail covered with long, unbanded hair that curls outward like a bottle-brush but may not completely hide scales. Mammary numerous, three to five lateral pairs and usually one inguinal pair. Phallus of *I. bistriata* short and blunt, with deep longitudinal grooves on sides, lappet above urethra not salient from crater (Figure 10e). Maxillary toothrows short, $\leq 26.8\%$ of basilar length of Hensel, with small, short, subcircular teeth (Figures 3a, 11). Maxillary cheekteeth not strongly tipped laterally as in other echimyines, but occlusal surface nearly on a plane parallel to the palate. All hypoflexi/ids of both upper and lower premolars and molars are oval to subcircular, with a mure; the adjacent loph curve around the hypoflexi to nearly close at the rim of the tooth (Figures 3a, 4a). Mandibular cheekteeth with hypoflexids slanting slightly backward, with the internal end of the flexid slightly posterior to the external end (Figure 4a). Lower premolar pentalophodont, hypoflexid short, with a mure, and other flexids close to parallel and all opening lingually when unworn. Tooth quickly wears to a pointed oval with three parallel lingual fossettes and a round labial fossette derived from the hypoflexid. Cranium broad, with short, broad rostrum; zygomatic arches strongly bowed outward anterior to squamosal (Figure 11). Auditory tympanic bullae moderately inflated, auditory meatus medium-sized, near squamosal, short auditory tube strongly slanted forward. Squamosotympanic fenestra a long, open slit that reaches posteriorly to base of mastoid process (Figure 5b). Post-palatal notch deep, to middle of M2; incisive foramina large and wide. In pterygoid region, there is no shelf of bone behind base of parapterygoid (hamular) processes on the wall of the buccinator foramen. Below the presphenoid-basisphenoid suture a round vacuity connected to a slitlike vacuity along the side of the presphenoid is shaped like a written musical note. Base of

mandible with strongly developed masseteric and pterygoid crests; mandibular foramen anterior to the condyloid ridge and not in a fossa (Figure 8a).

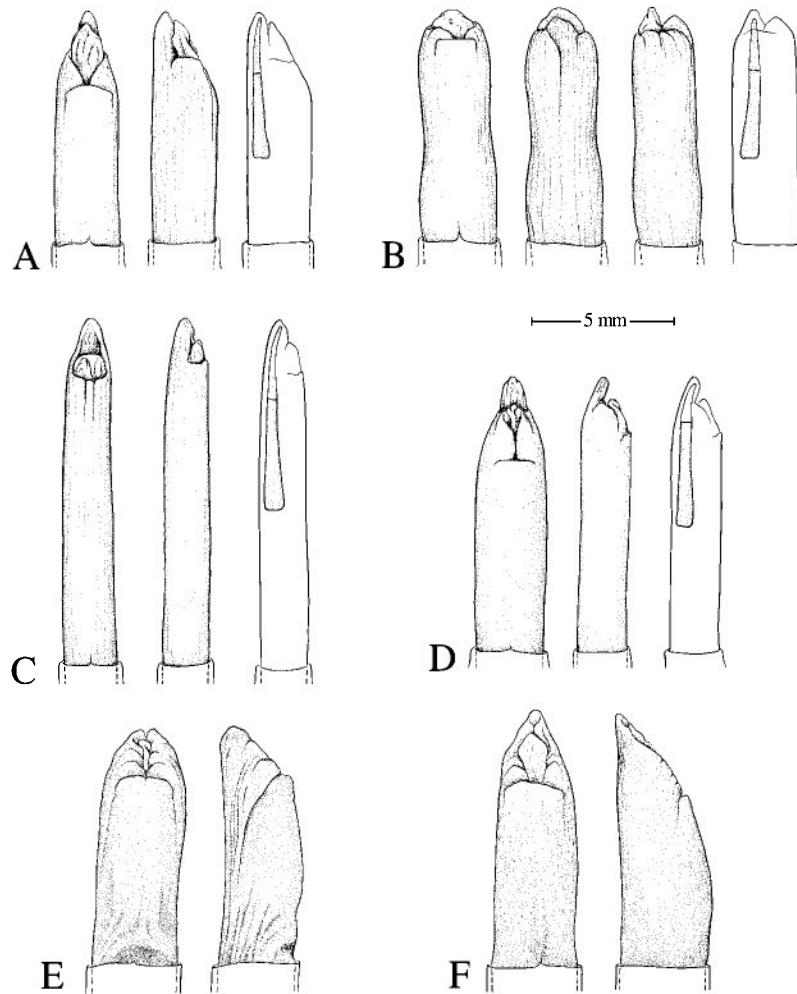


Figure 10. Preserved phalli, with prepuce folded back. Ventral (left) and lateral views. The unshaded (right) figures show the position of the rodlike bacula, with proximal bone shaded darkly and the distal cartilage shaded lightly. (a) *Makalata didelphoides* LHE 632, (b) *Echimys chrysurus* LHE 632 – ventral, dorsal, and lateral views, (c) *Pattonomys carrikeri* USNM 496508, (d) *Diplomys labilis* USNM 460179, (e) *Isothrix bistrata* MVZ 191300, (f) phallus of *Phyllomys medius* EDR 8 (from a photo by Yuri Leite, specimen courtesy of L. C. Machado Ribeiro, Museu de Zoologia de Universidade Católica do Paraná).

Remarks: Members of this genus, like *Callistomys* spp., have some characters shared with eumysopines but not with other echimyines, including small round cheekteeth with only the hypoflexi/ids open (other flexi/ids appearing as closed enamel folds) and an open squamosotympanic fenestra. Cyt b sequence data (Lara et al., 1996) fails to group *Isothrix* spp. with four echimyine taxa; its phylogenetic position is therefore equivocal. Molecular data has begun to resolve some species-level biogeographical questions within *Isothrix* (Patton and Emmons, 1985; Patton et al., 2000). I segregate *I. negrensis* and *I. orinoci* from *I. bistriata* because of the cranial distinctiveness of the former and the molecular distinctiveness of the latter, following the results of Patton and Emmons (1985) and Patton et al. (2000). However, as noted by those authors, additional work is needed and the geographic and morphological limits of the *bistriata* group of species need to be clarified.

Genus *Callistomys* Emmons and Vucetich, 1998

Type species: *Nelomys pictus* Pictet, 1843

Included species:

Callistomys pictus (Pictet, 1843)

Callistomys sp. (Emmons and Vucetich, 1998)

syn. *Lasiuromys villosus* Winge, 1888

Diagnosis: Large, soft-furred, arboreally adapted rats with striking black and white pelage pattern; tail completely covered with hair. Guard hairs fine, underfur dense and wavy. Two pairs of lateral mammae. Cheekteeth apparently three-rooted, high crowned, P4 and M1 unilaterally hypsodont (lingual side of crown higher than labial side, crown curved outward); P4-M3 tetralophodont, with three labial flexi and one lingual flexus; hypoflexi and mesoflexi deep, P4 completely divided by the joined hypoflexus-metaflexus into two, U-shaped lophs, with no mure (Figure 3b). Hypoflexids of p4-m3 set at a strong oblique angle. Lower premolars tetralophodont, anteroconid and protoconid united, enclosing the anteroexternal flexid as a slitlike fossetid; anterior half of the tooth approximates a triangle; the hypoflexids and metaflexids do not join (p4 is not divided by a continuous flexid, (Figure 4b). Skull with jugals expanded dorsoventrally, lateral jugal fossa wide and diffuse anteriorly, not coming to a sharp point; anterior edge of fossa above P4. Superior zygomatic root of maxillary expanded posteriorly. Tympanic auditory bulla inflated. Angular process of mandible strongly projecting ventrally with respect to the inferior projection of the symphysis, such that an angle drawn between the ventral posterior tip of the angular process and the occlusal plane of the toothrow, with the apex at the anterior edge of the occlusal surface of p4, is

greater than 30° (description from Emmons and Vucetich, 1998, crania are illustrated therein).

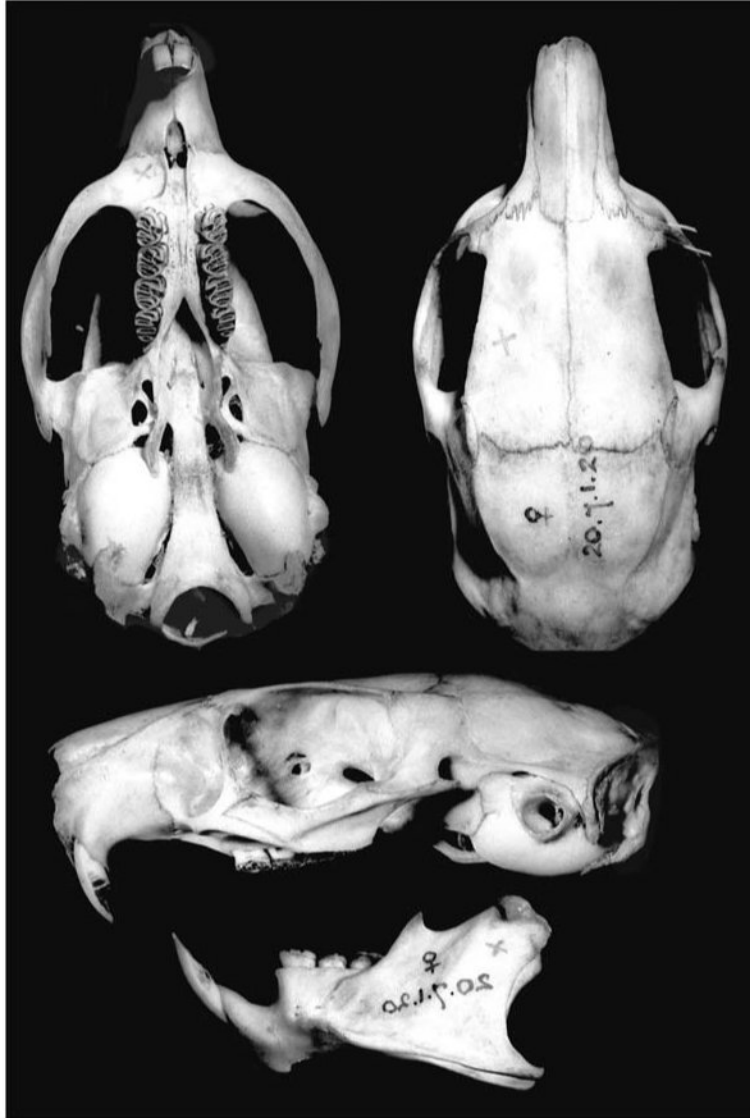


Figure 11. Cranium and mandible of *Isothrix negrensis* holotype BMNH 20.7.1.20.

Remarks: The characters of *C. pictus* were discussed by Emmons and Vucetich (1998). The following two major features distinguish this taxon from other Echimyinae and raise questions about whether it belongs in the subfamily: (1) possession of the “eumysopine” cheektooth root pattern and hypselodonty; and (2) greatly dorso-ventrally expanded jugals and anterior zygomatic arch. These features are in common with the Eumysopinae (Euryzygomatini) but are not shared by any other living echimyine.

Genus *Makalata* Husson, 1978

Type species: *Echimys didelphoides* Desmarest, 1817

Included species: This genus includes two species groups:

didelphoides group

- Echimys didelphoides* Desmarest, 1817
- Loncheres guianae* Thomas, 1888
- Loncheres macrura* Wagner, 1842
- Loncheres castaneus* Allen and Chapman, 1893
- Echimys longirostris* Anthony, 1921
- Echimys handleyi* Goodwin, 1962
- Loncheres obscura* Wagner, 1840 (?)

grandis group

- Loncheres grandis* Wagner, 1845
- Echimys rhipidurus* Thomas, 1928
- Makalata* sp. nov.

Diagnosis: Arboreally adapted rats with short legs and long backs; pelage including spines (*didelphoides* group) or stiff bristles (*grandis* group); tail about as long as head and body length, sparsely (*didelphoides* group) to completely covered (*grandis* group) with stiff hair. Two pairs of functional lateral mammae and occasionally a third, apparently obsolete, pair. Phallus of *M. didelphoides* slender, heavily ridged on sides, with long pointed dorsal bacular papilla; urethral lappet anterior to it extruded, large, and pointed; ventral lip of crater forms a deep V-shaped notch proximally abutting a straight, horizontal fold (Figure 10a). Maxillary tooththrows parallel or slightly divergent at either end (Figure 12), cheekteeth squarish to rectangular, longer than wide, with crowns of medium height, usually two lingually opening flexi (hypoflexus, metaflexus) and two labially opening flexi (paraflexus and mesoflexus), so that M1-2 have two, U-shaped loph opening in opposite directions (Figure 12); but several species have one lingual and three labial flexi in some or all molars (Figure 3c). Para, meso, and metaflexi extending two-thirds or more across P4-M1-3, but hypoflexi short, crossing about one quarter of

the width of the tooth. Lower molars with hypoflexids at an oblique angle, such that ectolophids at anterior tip of flexids are narrower than lophid posterior to tip (Figure 4c). Lower premolar pentalophodont, with anteroconid pointed; when unworn usually with flexid not enclosed by lophids (no central fossette), but opening posteriorly, such that anterior loph is an inverted V. Metaflexids of m1-2 bent posteriorly at internal tip, and mesoflexids bent forward; hypoflexid often curved forward. Lower incisors not strongly curved. Auditory tympanic bullae moderately inflated; auditory meatus medium sized to small; auditory tube short, outwardly or slightly forwardly directed; meatus close to squamosal suture. Squamosotympanic fenestra slitlike but short, with ventral lip raised in a ridge with a depression below (Figure 5c). Incisive foramen with maxillary septum broadly fused to premaxillary portion (Figure 7b). Mandibular foramen in a fossa with base on condyloid ridge; condyloid process of mandible short and dorsoventrally wide; masseteric crest strongly developed.

Remarks: The holotype of *Loncheres obscura* Wagner, 1840, collected by Spix in Brazil, has apparently been lost (Dr. Richard Kraft, pers. com.). It appears from the original description and figures to be a *Makalata* (Wagner 1840), but the name currently cannot be assigned to a specific population. Many of the *didelphoides* group species are colored warm brown with reddish rostrum forward of eyes; *grandis* group species are more blackish or dark-lined.

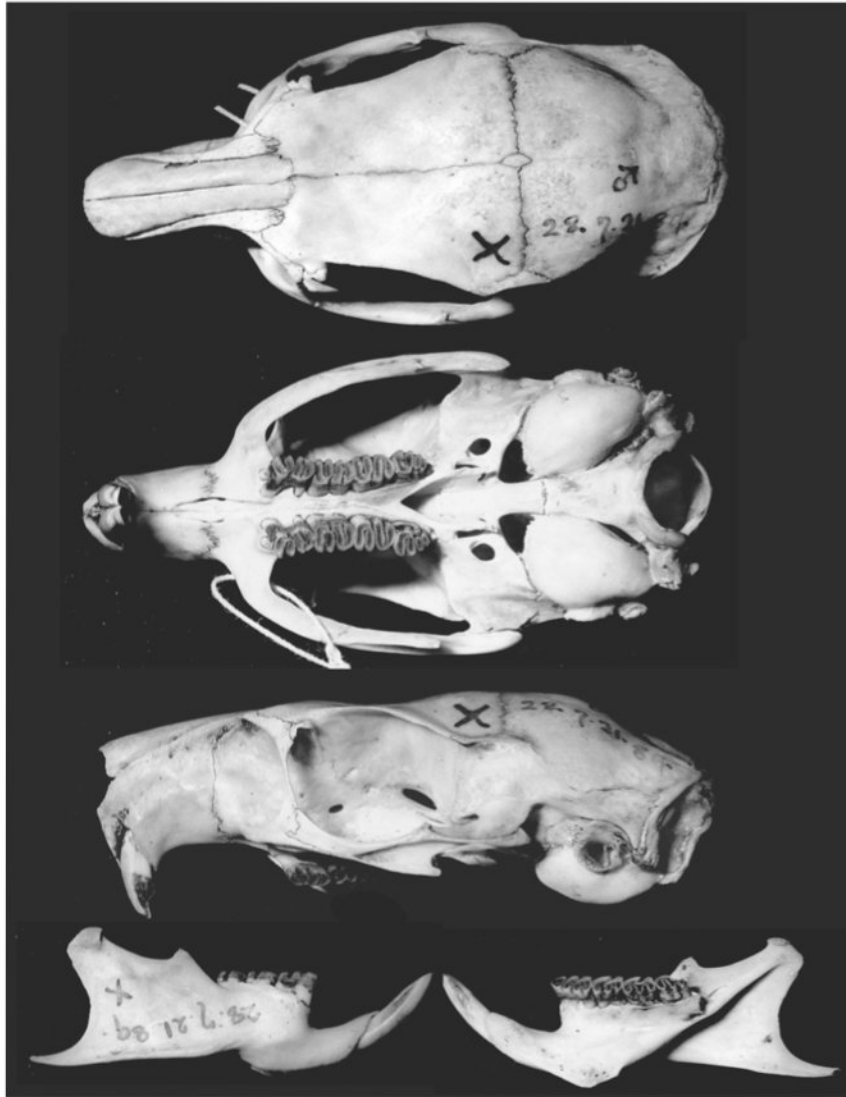


Figure 12. Cranium and mandible of *Makalata rhipidura*, holotype BMNH 20.7.1.20, mandible photo reversed.

Genus *Pattonomys*, gen. nov.

Type species: Nelomys semivillosus I. Geoffroy, 1838

Included species:

Nelomys semivillosus I. Geoffroy, 1838

Loncheres punctatus Thomas, 1899

Echimys carrikeri J. A. Allen, 1911

Loncheres flavidus Hollister, 1914

Echimys occasius Thomas, 1921

Etymology: The genus is named to honor James L. Patton, whose many key contributions to echimyid systematics have brought light to a dark place. The name *Pattonomys* is in recognition of his outstanding generosity in sharing his knowledge with students and colleagues.

Diagnosis: Medium to large, arboreally adapted rats; pelage color generally gray on head and sides, often with yellowish cast; back tinged brown; tail uniformly reddish brown, lightly clothed throughout length with fine hairs. Pelage including strong spines, many on rump tipped whitish, imparting a speckled appearance. Two pairs of lateral mammae. Phallus long and slender, with long, pointed bacular papilla, a small urethral lappet, and with border of ventral crater wall a straight line, without a V- or U-shaped ventral fold (Figure 10c). Maxillary cheekteeth squarish to rectangular, longer than wide, posterior loph rounded. Teeth have an uneven occlusal appearance due to unequal loph sizes (Figures 3f, 4f). P4-M3 always with two labial and two lingual flexi. Para- and mesoflexi short, most reach only to mid-tooth; hypoflexi long, likewise reaching midway across tooth, and opening at a wide angle. P4 and M1 always with a mure in the center of the tooth; M2-3 with or without a mure. Chief diagnostic features of the upper teeth include widely open flexi, some nearly as wide as the lophs, and anteroposteriorly expanded protocone and posteroloph (probably metaloph and posteroloph combined). These expanded lophs are accentuated with wear. The four lophs of P4-M2 are markedly unequal in length and width: the anteroloph is broad and squared linguallly, tapering labially; and the posteroloph is pointed labially and strongly curved along the posterior margin of the tooth. The paraflexus and metaflexus of P4-M2 slant in markedly opposite directions, with the metaflexi slanting posteriorly from the labial to medial edges of the tooth (Figure 3f). Lower premolar tetralophodont, with two labial and two lingual flexids; tooth usually divided by one central flexid into two V-shaped lophs (Figure 4f), but it may have a central mure. Flexids of m1-2 form nearly straight-sided Vs. Lower incisors not strongly curved. Cranium short and broad, with expanded, winglike supraorbital shelf that curves upward from frontals; supraorbital region broad, especially developed in *P. carrikeri*, much narrower in *P.*

semivillosus (Figure 13). Tympanic auditory bulla moderately to considerably inflated, auditory meatus high, near squamosal, directed outward; auditory tubes short, their role taken by the formation of two overlapping bony rings, especially well developed in old individuals. Mastoid process short, usually to middle of auditory meatus, not extending ventrally beyond lower edge of meatus. Angular process of mandible slender; condyloid process narrow; mandibular foramen usually in a fossa on condyloid ridge; masseteric crest strongly developed anteriorly.

Remarks: The teeth of members of this genus are so distinctive that any single tooth is diagnostic except m1-3, and often these are too. The named forms of the genus were all synonymized under the name *semivillosus* by Cabrera (1961) and subsequent authors. However, all but *P. flavidus* are cranially distinctive and readily diagnosable. I consider them all to be valid species, but they merit further study. The form *P. flavidus* is cranially similar to coastal specimens of *P. carrikeri*, and may be synonymous, but as it also has distinctive features, such as an extremely deep mandible, I provisionally recognize it pending additional specimens and molecular genetic analysis. It is unlike the geographically closer *P. punctatus*.

Echimys occasius Thomas, 1921 was formerly placed in *Makalata* (Emmons and Feer, 1990), which it resembles in pelage color, smaller size, and geographic distribution in Amazonia. It does not possess several of the more diagnostic characters *Makalata*. In parsimony analyses, it groups with *Pattonomys*, where it is tentatively placed here. It may be a relictual form close to the common ancestor of *Makalata* spp. and other *Pattonomys*. Molecular studies are needed to better clarify its relationship. Thomas did not give the etymology of his name *occasius*. I surmise that from its purported type locality west of the Andes (likely erroneous), he derived the name from the Latin *occasus*, meaning western (to set as the sun), with the comparative superlative ending *ius*, or westernmost. The suffix therefore does not change with the gender of the generic epithet.



Figure 13. Cranium and mandible of *Pattonomys semivillosus* USNM 280205, scale 0.5 cm.

Genus *Echimyys* F. Cuvier, 1809

Type species: Myoxus chrysurus Zimmermann, 1780

Included species:

Echimyys chrysurus (Zimmermann, 1780)

Echimyys saturnus Thomas, 1928

Diagnosis: Large arboreal rats with pelage including stout spines; tail longer than head and body length, completely, densely covered with hair that forms a pencil at tip. Four pairs of mammae, three lateral and one inguinal. Phallus of *E. chrysurus* stout, strongly ridged on sides, dorsal tip with short, triangular dorsal bacular papilla; ventral lip of urethral crater forms a short, U-shaped fold above a straight line lip (Figure 10b). Maxillary toothrows parallel, not converging anteriorly, cheekteeth rectangular, longer than wide, with tall crowns; only one lingual flexus, (the hypoflexus) that usually joins with mesoflexus to completely divide tooth into two, U-shaped lophs (no mure); three labial flexi (Figure 3e). The four lophs of P4-M2 are subequal in length and width and nearly parallel. Paraflexus and metaflexus long, about two-thirds or more of the width of the tooth, and parallel; hypoflexus or its trace, short, about one quarter to one third of the width of the tooth. Lower molars with hypoflexids reaching less than half way across tooth, opening at a wide angle, and scarcely, if at all angled forwards, such that lophs adjoining the tip of hypoflexid are about equal in width. Metaflexids of m1 and more prominently, m2, with angled internal tip with two points (perhaps outlining a mesoconid) and bending slightly posteriorly; mesoflexid with internal tip bending slightly anteriorly (Figure 4e). Lower premolar pentalophodont, completely divided by two flexids into the following three parts: (1) a symmetrical triangular anterior loph, rounded at its anterior tip and enclosing a subcircular fossetid, (2) a single, laminar, central metalophid bar, (3) posterolophid and entoconids of posterior third of tooth united labially into a single, V-shaped loph that opens lingually. Lower incisors not strongly curved. Auditory tympanic bulla small to medium-sized, with a small meatus on a short auditory tube directed straight outward at nearly a right angle to the skull axis; meatus near (less than half its diameter) squamosal suture (Figures 5a, 14, 15). Mastoid process short. Squamosotympanic fenestra small and subcircular, with no raised ventral lip, entirely anterior to auditory meatus. Incisive foramen with premaxillary part of septum free posteriorly. Jugal deep below post-orbital process, jugal fossa very broad, forming an angle of at least 40.° Mandibular foramen anterior to condyloid ridge, not in a fossa with base in ridge (Figure 8b); masseteric crest weakly developed.

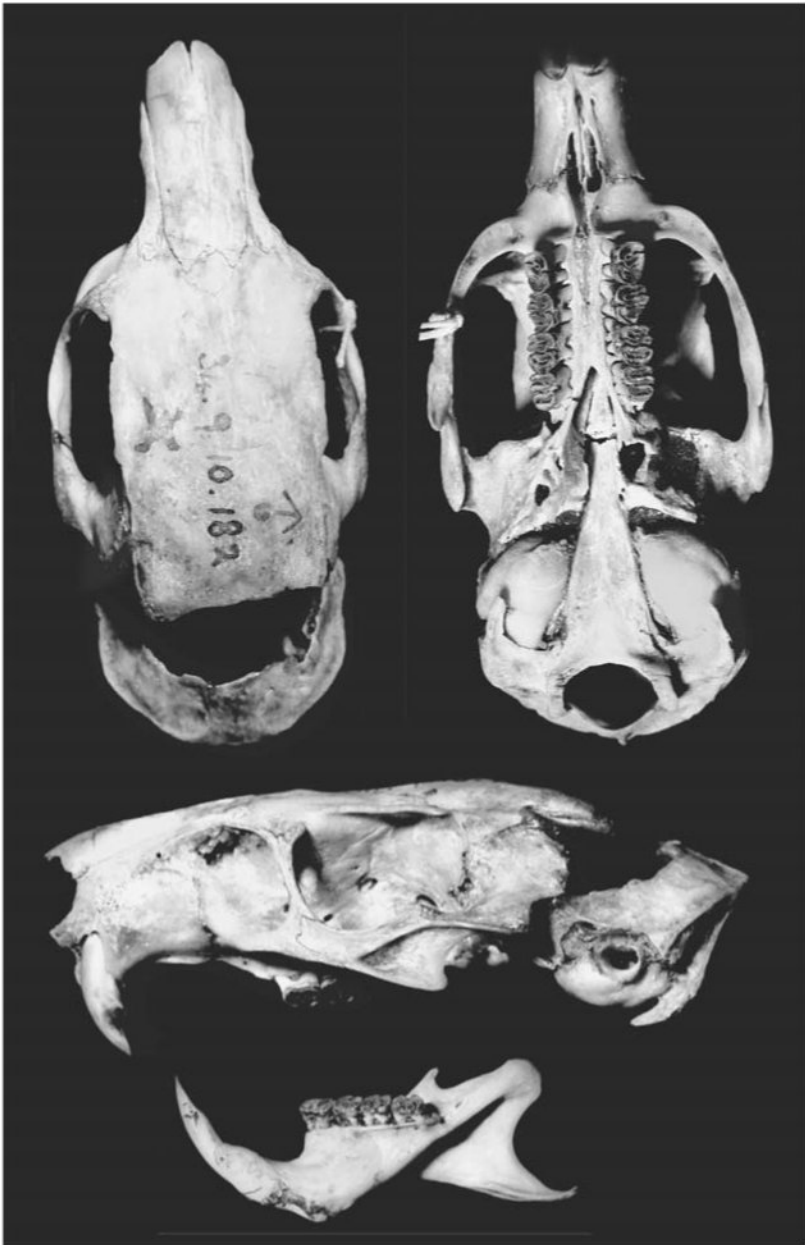


Figure 14. Cranium and mandible of *Echimys saturnus*, holotype BMNH 34.9.10.182.



Figure 15. Cranium and mandible of *Echimys chrysurus* USNM 549594.

Genus *Phyllomys* Lund, 1839

Type species: *Phyllomys brasiliensis* Lund, 1840

Included species:

- Nelomys blainvillii* Jourdan, 1837
- Phyllomys dasythrix* Hensel, 1872
- Phyllomys kerri* Moojen, 1950
- Nelomys lamarum* Thomas, 1916
- Phyllomys lundi* Leite, 2003
- Phyllomys mantiqueirensis* Leite, 2003
- Loncheres medius* Thomas, 1909
- Loncheres nigrispina* Wagner, 1842
- Mesomys thomasi* Ihering, 1897
- Loncheres unicolor* Wagner, 1842
- Phyllomys pattoni* Emmons, Leite & Costa, 2002

Diagnosis: Medium-sized to large arboreal rats with pelage including spines or bristles, or soft furred; tail sparsely to densely haired, with or without pencil or tuft at tip. Four pairs of mammae, three lateral and one inguinal. Phallus of *P. medius* robust, pointed, with triangular tip, large urethral lappet extrudes in an inverted pear-shape below pointed bacular papilla; ventral fold short and forming a U-shape with sides bordering lappet (Figure 10f). Maxillary teeth rectangular; longer than wide, unworn teeth completely split by three flexi into four nearly parallel laminae or lophs of quite uniform width; posterolophs crescent-shaped (Figure 3h). The two posterior lophs unite labially with wear; the anterior lophs unite lingually. Lower premolar pentalophodont, split by two flexids into three parts; unworn anterior loph including lingually opening flexid, this tending to close with wear to form a triangle with a central subcircular fossette (Figure 4h). Lower molars with narrow lophids; metaflexid long, often dividing tooth, hypoflexids at strong oblique angle. Lower incisors usually strongly curved. Auditory tympanic bullae with auditory meatus low, directed slightly forward, with a space as wide as meatus between meatus and squamosal (Figures 5e, 16). Additional rings of bone external to meatus often present. Mandibular foramen in fossa on base of condyloid ridge (Figure 8c); condyloid process narrow, angular process reflected ventrad with respect to occlusal plane of toothrow (Figure 16); masseteric crest weakly to moderately developed anteriorly.

Remarks: The taxonomy and status of all named forms of *Phyllomys* were recently reviewed by Emmons et al. (2002) and Leite (2003). Diagnoses and descriptions of all species listed above, with discussion of nomenclatural issues, are found therein. The systematics and phylogeography are reviewed in Leite (2001)

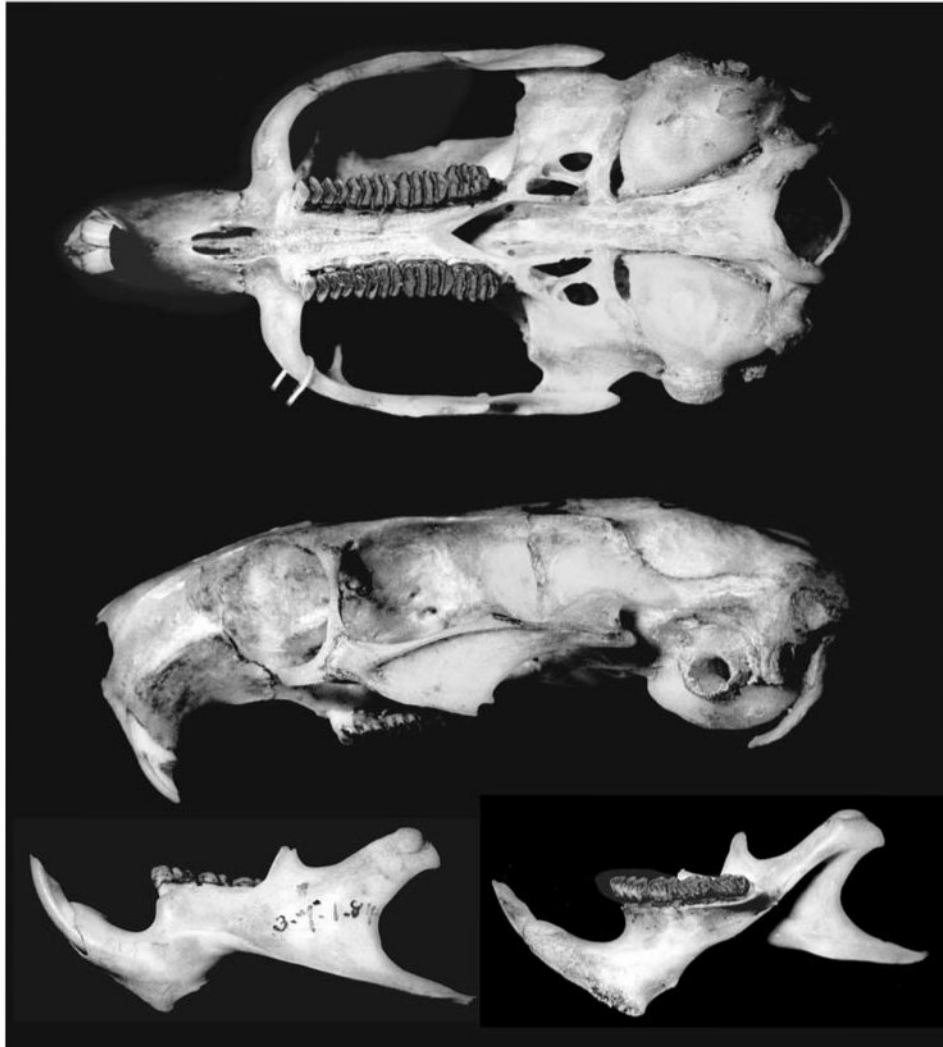


Figure 16. Cranium and mandible of *Phyllomys medius*, holotype MBNH 3.7.1.84.

Genus *Diplomys* Thomas, 1916

Type species: Loncheres caniceps Günther, 1877

Included species:

Loncheres caniceps Günther, 1877

Loncheres labilis (Bangs, 1901)

synonym: *Isothrix darlingi* (Goldman, 1913)

Diagnosis: Large arboreal rats without spines, but guard hairs flattened and slightly stiff, with deep dorsal sulcus; guard hairs 1.8-2.0 cm long on dorsum; underhairs few, fine and inconspicuous. Tail with dorsal body fur extension 1.5-5 cm onto base; distal part fully but moderately clothed with stiff, bristlelike, brown hairs, scales visible beneath. Two pairs of lateral mammae. Feet without tiny tubercles between pads. Phallus without deep lateral ridges, dorsal tip with a long, slender, bacular papilla; inconspicuous urethral lappet, ventral surface with a long, longitudinal slit distal to a short transverse fold (Figure 10d). Maxillary cheekteeth large, toothrow relatively long, teeth as in *Phyllomys* spp., divided by three flexi into four laminae; laminae parallel in M1-3; P4 with labial ends of the two anterior lophs bent forward (Figure 3i). Flexi of even depth, such that with wear, three straight fossettes are centered on molars. In mandibular cheekteeth, all flexids may traverse all lophs in unworn teeth (Figure 4i); but with wear the metaflexid divides m1-3 into a free posterolophid; middle loph (entoconid + hypoconid) usually connected to anterolophid at near its midpoint by a short mure, forming a highly distinctive pattern of two, crescent-shaped lophids connected by a central stem, like an Inuit knife. Hypoflexids at an oblique angle (Figure 4i). Lower premolar split into three or four parts by two or three flexids; anterior loph a rounded triangle enclosing a flattened oval transverse fossette, metalophid a separate lamina, and entoconid and posterolophid either joined labially, or divided into separate parts by metaflexid (Figure 4i). Lower incisors strongly curved (Figure 17). Cranium long and narrow, dorsal surface curved throughout length from nasals to occiput when viewed laterally (Figure 17); auditory tympanic bullae not inflated; auditory meatus close to squamosal; auditory tubes well developed, directed strongly forward, so that inner ear bones not visible from side (Figure 5f). Alisphenoid with distance between foramen ovale and masticatory foramen usually very short (Figure 6e, between arrows); ventral roof of this canal often nearly obsolete. Hamular process of pterygoid with prominent, anteriorly directed spur (Figure 6e). Large oval sphenopalatine vacuity present below presphenoid-basisphenoid suture (Figure 17). Squamosotympanic fenestra tubelike, opening forward, without depression on squamosal below (Figure 6e). Jugal narrow below postorbital process, with ventral process inconspicuous and well forward of dorsal process (Figure 17). Angle of sigmoid notch between angular and condyloid processes of mandible shallow;

mandibular foramen on side of ramus, far anterior to condyloid ridge, not in a fossa (Figure 8d). Masseteric crest large.

Remarks: There is much variability in which of m1-3 the "Inuit knife" wear pattern appears.

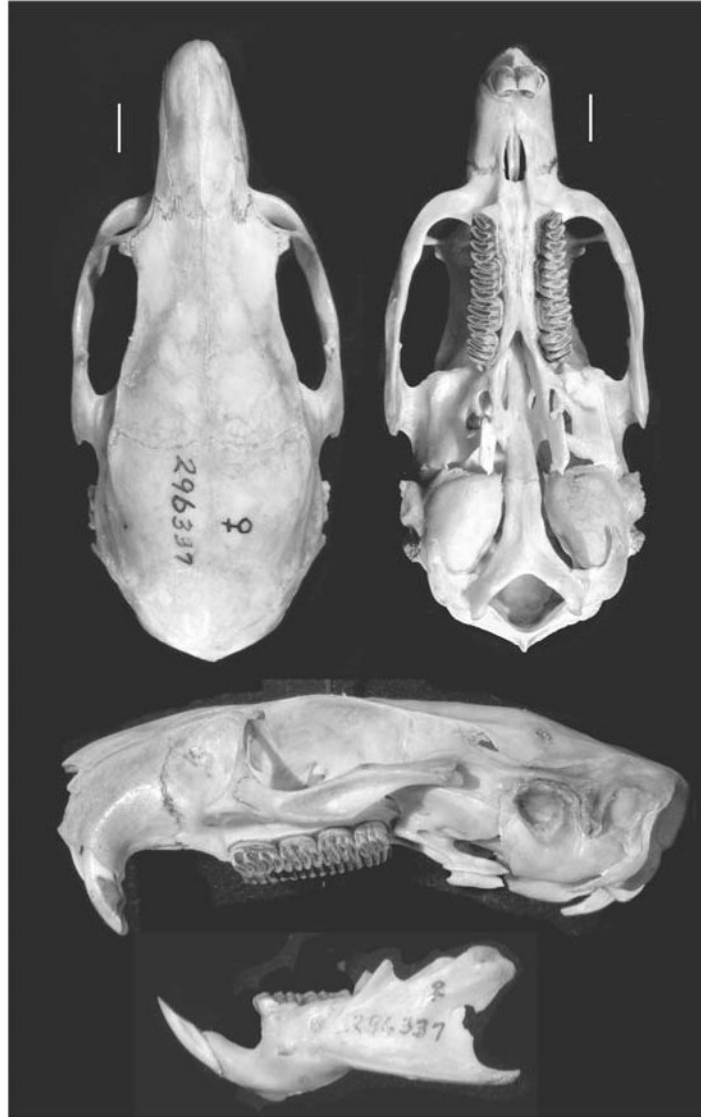


Figure 17. Cranium and mandible of *Diplomys labilis* USNM 296337.

Santamartamys gen. nov.

Type species: Isothrix rufodorsalis Allen, 1899
synonym.—*Diplomys rufodorsalis* (Tate, 1935)

Included species: Only one species is recognized, it is known from only two specimens.

Etymology: Named for the type locality and origin of both known specimens, the Sierra Nevada de Santa Marta, Colombia.

Diagnosis: A medium-sized, bright rust-red arboreal rat with long, lax overhairs, 2.0–3.8 cm in length on dorsum; pelage not stiff or bristly, underfur dense, wavy, gray. Overhairs so slender that they are difficult to distinguish from other pelage. Dense woolly pelage covers legs to ankles and wrists. Crest of long hair on crown between ears. Longest genal and mystacial vibrissae 5 cm, vibrissae present on wrist. Two pairs of lateral mammae on abdominal edge of lateral pelage, in ventral pelage field. Tail robust, covered with extension of dorsal pelage for 2.5 cm, well clothed distally with fine hairs, basal half brown, distal half pure white. Feet without tiny tubercles between pads, pollux with a nail. Maxillary cheekteeth rectangular, longer than wide, teeth and toothrow relatively long, bowed inward (Figure 18); P4-M3 split by a deep flexus into two parts, anterior loph with flexi opening labially and posterior loph with flexi opening lingually; protocones broad, conferring a wishbone shape to joined anteroloph/protoloph pairs, especially on P4 (Figure 3g). Lower molars split by meso- and hypoflexid into two parts, a curved, laminar anterolophid, and a somewhat wishbone-shaped entoconid/posterolophid (Figure 4g). Lower premolar split by two flexids into a small closed triangular anterior loph apparently lacking a fossette; a laminar metalophid, and a wishbone-shaped posterior loph that opens lingually. Hypoflexids strongly oblique; protoconids large and squarish. Lower incisors strongly curved (Figure 18). Cranium conspicuously curved in dorsal profile, rostrum short and broad. Auditory tympanic bullae small and flattened; merging with alisphenoid at a shallow angle (Figures 5d, 6f, 18). Auditory meatus small, placed high near the squamosal; auditory tube short, strongly directed anteriorly; mastoid process extremely short (Figure 5d). Bony bridge between foramen ovale and masticatory foramen exceptionally long (Figure 6f, between arrows); there seems to be a small oval vacuity below the presphenoid-basisphenoid suture (Figure 18). Condylod process of mandible deep; angle of sigmoid notch between angular and condylod processes of mandible shallow (Figure 18); mandibular foramen in a fossa beside the condylod ridge. Masseteric crest of lower edge of mandible poorly developed and shallow, pterygoid shelf small.



Figure 18. Cranium and mandible of *Santamartamys rufodorsalis* AMNH 34392.

Remarks: *Santamartamys rufodorsalis* seems closely allied to members of the genus *Diplomys*, where it has recently been placed. It shares with *Diplomys* a number of probable apomorphies, as well as a close geographic affinity. I segregate it as a genus primarily because of its distinctive cheektooth occlusal morphology, which is different from all other living Echimyidae. This taxon also has unique pelage, mammae placement, and bullar and alisphenoid configurations. The descriptions above were largely based on AMNH 34392, a young female with little-worn dentition. The teeth of the holotype, AMNH 14606, are extremely worn. Because only two specimens are known, the diagnosis is expanded with descriptive material to aid those unable to view the specimens.

Comparisons Between Genera

Pelage: All species in the genera *Isothrix*, *Santamartamys*, *Callistomys*, and all Dactylomyiines are soft furred, while the guard hairs of *Diplomys* spp. and the eumysopine *Thrichomys* spp. are flattened and somewhat stiff, but nearly soft. Most members of other Echimyid genera are spiny or have stiff, bristly dorsal guard hairs, which is likely the plesiomorphic condition for the family. However, it is noteworthy that species in all three of the largest echimyid genera, *Proechimys*, *Phyllomys*, and *Makalata*, range from heavily spined to stiff- or soft-furred (*Phyllomys* only), thus spininess is not evolutionarily stable.

Mammae: *Echimys* and *Phyllomys* species have three lateral pairs of mammae that are about equally spaced along the sides in the dorsal pelage field (one anterior, one medial, and one posterior), and one inguinal pair on the ventral field. Species of *Callistomys*, *Makalata*, *Pattonomys*, *Diplomys*, and *Santamartamys rufodorsalis*, have only two functional lateral pairs that seem to correspond to the medial and posterior lateral pairs of *Echimys* spp. Some individuals of *Makalata* spp. have an inguinal pair of mammae that appears to be non-functional. *Isothrix pagurus* can have as many as 5 lateral pairs, including the three standard pairs, with another pair intercalated between the anterior and medial and the medial and posterior pairs. *Isothrix bistriata* can have three lateral pairs: medial, posterior, and one between these, and an inguinal pair. The patterns typical of *Isothrix* spp. are thus not found among other genera. The lateral mammae of *S. rufodorsalis* are placed in the ventral pelage field on the edge of the dorsal field, a unique condition among the Echimyinae for which the pattern mammae placement is known. This observation needs confirmation as it is based on a single specimen but, because the species has (with *C. pictus*) the longest, densest, and finest fur of the genus, I speculate that the mammae may have "migrated" to the abdominal field because the unusually dense pelage interferes with nursing.

Phallus: Too few species and individuals – often only one individual per genus – were examined for confident intergeneric comparison but, based on the material seen, the phallus of *Phyllomys medius* is very similar to that of *Makalata didelphoides* (Figure 10). The phallus of *Pattonomys carrikeri* is uniquely long, slender, and of simple structure at the tip, while that of *Diplomys labilis* is remarkable for its smooth, unridged exterior and elongated, digitlike tip. The phallus of *Echimys chrysurus* almost lacks the bacular papilla seen in other genera so it is shorter and blunt rather than pointed at the tip. The phallus of *Isothrix bistriata* appears to have a much broader tip above the ventral fold than do those of other taxa and the tip is grooved, rather than forming a solid papilla. I did not examine the specimens of *I. bistriata* and *P. medius*, which were illustrated from photos supplied by Yuri Leite. Leite (2003) illustrated the phallus of several *Phyllomys* species.

Squamosal and auditory region: This cranial region has some of the most useful characters for diagnosing the genera of Echimyinae. The low placement of the auditory meatus, with an expanse of bone wider than the meatus between it and the squamosal suture (Figure 5), distinguishes *Phyllomys* species from members of all other genera, although there is some species-level variation in width of the supra-meatal area within *Phyllomys*. *Santamartamys rufodorsalis* is distinct from members of all other genera in possessing a highly flattened and ossified junction between the small, flattened, auditory tympanic bulla and the alisphenoid (Figure 18). The squamosotympanic fenestra is an elongate open slit along the squamosal suture in *Isothrix* spp. alone among Echimyinae, a condition that they share with the echimyids *Euryzygomatomys*, *Carterodon*, *Clyomys*, and some *Proechimys* and *Myocastor*. In the other echimyines, the suture is closed and the foramen opens from a bony tube (Figure 5). In *Makalata* species the tubelike development is most accentuated, with a slight to well developed bony crest or ventral lip to the foramen that is more or less continuous with the rim of the auditory meatus. There is a distinct depression on the squamosal ventrad to this crest (Figure 5c). This crest and depression are universally developed only among *Makalata* species, although one individual of *P. semivillosus* had a similar crest. In *Makalata* species, the mastoid process is long (usually reaching ventrad of the lower rim of the auditory meatus) and is free of the cranium at its tip, whereas in other echimyines it is short and adpressed to the cranium, enclosed medially in bone.

Alisphenoid and parapterygoid region: The strut of bone which separates the foramen ovale accessorius and masticatory foramen is narrow to absent in *Dactylomys* spp., narrow in *Diplomys* spp., *Echimys chrysurus* and *Callistomys pictus*, and exceptionally wide in *Santamartamys rufodorsalis* (Figure 6). In the other Echimyinae it is wide. The buccinator foramen is enclosed by a medial wall, partly enclosing it below the pterygoid process, in *Santamartamys*, *Echimys*, *Pattonomys*, and some *Makalata* and *Phyllomys* species. It has a dorsal shelf partly enclosing it in some species of

Phyllomys and *Makalata*. In *Isothrix*, *Diplomys*, and *Dactylomys* species and all eumysopines, the foramen is open and unenclosed medially.

Incisive foramen: In *Makalata* species, the premaxillary portion of the septum in the incisive foramen is broad and broadly fused to the maxillary; in all other genera, including all Eumysopinae other than some *Proechimys* and *Trinomys*, the premaxillary portion is slender and dips dorsally, leaving a gap between it and the maxillary (Figure 7).

Occlusal pattern of the cheekteeth: The molar roots and occlusal patterns of lophi and flexi of the cheekteeth provide important characters for distinguishing the echimyid taxa defined here, despite some intraspecific variation.

The maxillary cheekteeth of *Isothrix* spp. are small and nearly circular in occlusal outline (Figure 3a), with a short, subcircular to oval hypoflexus less than half the width of the tooth. The para-, meso- and metaflexi are short (about 2/3 the width of the tooth) and parallel sided. In all other echimyines, the molariform teeth are large and roughly square (some *Makalata* spp., *Echimys* spp.) or rectangular (all others). In unworn teeth of *Diplomys* spp. and *Phyllomys* spp., three flexi completely cross each molar, separating the lophi into four approximately parallel laminae (Figure 3h, i). In *C. pictus*, *Echimys* spp., *Makalata* spp. and *S. rufodorsalis*, all four cheekteeth are each split by the joined mesoflexus and hypoflexus into two halves, each of which is a pair of joined lophi (Figure 3). The paired lophi of some *Makalata*, *C. pictus*, and all *Echimys* spp. approach a laminar design (nearly parallel, straight lophi and flexi). In contrast, *Pattonomys* species have a unique occlusal pattern, characterized by the presence of a mure about 2/5 to 1/2 of the distance across the tooth between hypoflexus and mesoflexus. The hypoflexus and mesoflexus are short and wide, and the hypocone, protocone and protoloph are broad antero-posteriorly.

In mandibular cheekteeth, all taxa but *C. pictus* and *Pattonomys* species have a distinctly pentalophodont p4. In *Isothrix* spp., the anterolophid is visible as a small projection in unworn teeth, with wear it merges with the anteroconid and becomes indistinguishable (Figure 4a). In the other taxa, the metalophid of p4 is a bar entirely separated from the adjacent lophi by transverse flexi that completely cross the tooth (Figure 4). *C. pictus* differs from *Makalata* species in lacking a metalophid bar (Figure 4b). Lower premolars of *Pattonomys* spp. differ from those of all other taxa in the combination of lacking both a metalophid bar and a mure medial to the hypoflexid (Figure 4f). The lower cheekteeth of *Isothrix* spp. differ from those of all other echimyine genera in having sub-circular hypoflexids, and meso- and metaflexids nearly at right angles to the axis of the tooth row and nearly closed at the lingual margins by curvature of the tips of the lophi (Figure 4a). The hypoflexids of *Isothrix* spp. are slightly angled in the opposite direction from those of all other taxa (Emmons and Vucetich, 1998), where the medial end is anterior to

the labial opening of the flexid. *Diplomys* spp. are unique among echimyines in always having all lower cheekteeth completely split into three laminae by three flexids that completely traverse the tooth, (Figure 4i). *Santamartamys rufodorsalis* has the mesoflexid and hypoflexids of m1-3 united to traverse the tooth, creating one free anterior loph, but in contrast to *Diplomys* spp., the metaflexids do not traverse the teeth. A similar condition is sometimes observed in *Phyllomys* species. In all the other genera the lophids of m1-3 are W-shaped and differ chiefly in the angle and breadth of the hypoflexids, which are steeper and narrower in *Callistomys* and *Phyllomys* species.

Incisors and mandible: In Echimyinae, Dactylomyinae, and Eumysopinae other than Euryzygomatomini, the lower incisor roots originate below the molar toothrow, and the mandibular foramen is low on the ramus (Figure 8). The mandibular foramina of *Dactylomys* spp., *Diplomys* spp., *Isothrix* spp., *Echimys* spp., and *S. rufodorsalis* are above and anterior to the condyloid ridge, while the foramen of *Makalata* spp. is either directly on the spine of the condyloid ridge, or above it; at the bottom of a small fossa on the ridge, while those of *Phyllomys* spp. are close behind the molar toothrow and on the condyloid ridge. In *Echimys* spp. and *Makalata* spp., the condyloid ridge retains a sharp keel almost to the articulation on the posterior tip of the condyloid process, whereas among the other genera the ridge tends to flatten out and merge with the process farther below the condyle (Figure 8). The angular process of the mandible is short, reaching posteriorly about the same length as the condylar process in Eumysopini, *Isothrix* spp., *Diplomys* spp., and *C. pictus*. It is longer than the condylar process in Euryzygomatomini, Dactylomyinae and all the other echimyines.

DISCUSSION

The Echimyinae, as I propose here (Table 3), include seven or eight genera and about 38 species of arboreal rats. Several species await description and there are likely more than 50 extant species, but the number of species now grouped under most echimyid genera, including *Isothrix*, *Dactylomys*, *Mesomys*, *Makalata*, and *Pattonomys*, will be unclear until each has been revised. In both morphological (here) and molecular (Lara et al., 1996, Leite and Patton, 2002) analyses, the relationships between genera are poorly resolved, remaining consistent with the conclusion drawn by Lara et al. (1996) and reconfirmed by Leite and Patton (2002) that the genera in the family Echimyidae:

“. . . may well represent a star-phylogeny, with an origin in the late Miocene resulting in a set of polytomous relationships reflecting that cladogenic history rather than to inadequate data. . . True polytomous relationships, as opposed to demonstrably dichotomous ones, are an expected outcome of

rapid and near-simultaneous divergence of multiple lineages. As a consequence, resultant taxa are likely to be composites of shared-primitive and uniquely derived characters, and relationships based on any character set will be difficult to establish" (p. 411).

This appears to be the case for several morphological characters, with the species in two of the eight echimyine genera, *Callistomys* and *Isothrix*, possessing suites of composite characters that make their affinities ambiguous; the same is true for *Mesomys*, *Dactylomys*, *Thrichomys*, and others. Although the phylogenetic relationships between the echimyine genera I define here may prove difficult or impossible to resolve if they evolved as a star-phylogeny, the monophyly of the generic groupings I propose will be testable with molecular techniques when tissues become available, as has recently been the case for *Phyllomys* (Leite, 2003).

Living Echimyinae can be placed in the following sequence of development of cheekteeth with increasingly parallel and separate laminae: *Isothrix*, *Pattonomys*, *Makalata*, *Santamartamys*, *Callistomys*, *Echimys*, *Phyllomys*, and *Diplomys*. Of major systematic interest is whether the laminar molars of *Phyllomys* species are synapomorphic with those of *Diplomys* species. I conjecture that they are not, and are homoplasies, chiefly because the closest living relative to *Diplomys* is clearly *S. rufodorsalis*, which does not have a laminar occlusal pattern; instead, *S. rufodorsalis* has a unique occlusal pattern, albeit with similarities to that of *Diplomys* species. It seems unlikely to have evolved by reversal from the laminate pattern of *Diplomys* spp., although it could have done so. The near laminarity of the teeth of *Echimys* species may reflect a closer phylogenetic relationship of *Echimys* to *Phyllomys* than of *Echimys* to either *Makalata* or *Pattonomys*, as is suggested by the molecular data sets of Leite and Patton (2002; Figure 9b). Too little is known of the diet of any species to evaluate whether, as might be predicted, increasing cheektooth laminarity is associated with increasing folivory or a diet including coarse vegetation such as stems and petioles.

The echimyine genera are segregated geographically, with *Phyllomys* and *Callistomys* species restricted to the Atlantic forests of eastern Brazil, *Echimys*, *Makalata*, and *Isothrix* species found only in Amazonia (including the Guianas), *Pattonomys* and *Santamartamys* species restricted to the northern coastal forests of Colombia and Venezuela (with the exception of the West-Amazonian *P. occasius*), and *Diplomys* isolated alone in Central America and coastal Colombia and Ecuador. A number of divergent taxa, often in genera that are monotypic or with few species, are endemic to small regions around the periphery of the continent, including *C. pictus*, *S. rufodorsalis*, *D. caniceps* and *D. labilis*, and, to a lesser extent, *P. occasius*. The Dactylomyine species of *Dactylomys peruanus* and both *Olallamys* species are likewise narrow endemics of small peripheral Andean regions. This centrifugal distribution of highly differentiated and now relictual forms suggests a long history of radiation in the Neotropical forests, with likely centers of speciation in the central

Table 3. A classification of the Echimyinae. Genera are arranged in order of increasing laminarity of the maxillary cheekteeth, without implication that this represents a phylogenetic series.

INCERTAE SEDIS	<i>Rhipidura</i> group:
Genus <i>Mesomys</i>	<i>M. grandis</i>
<i>M. hispidus</i>	<i>M. rhipidura</i>
<i>M. stimulax</i>	<i>M. sp. nov.</i>
<i>M. occultus</i>	
Several other species	Genus <i>Santamartamys</i> :
	<i>S. rufodorsalis</i>
Genus <i>Lonchothrix</i>	Genus <i>Callistomys</i> :
<i>L. emiliae</i>	<i>C. pictus</i>
Genus <i>Isothrix</i> :	Genus <i>Echimyis</i> :
<i>I. bistrata</i>	<i>E. chrysurus</i>
<i>I. orinoci</i>	<i>E. saturnus</i>
<i>I. negrensis</i>	
<i>I. pagurus</i>	
<i>I. sinamariensis</i>	
ECHIMYINAE	Genus <i>Phyllomys</i> :
Genus <i>Pattonomys</i>	<i>P. brasiliensis</i>
<i>P. semivillosus</i>	<i>P. blainvillii</i>
<i>P. punctatus</i>	<i>P. lamarum</i>
<i>P. carrikeri</i>	<i>P. lundi</i>
<i>P. flavidus</i>	<i>P. mantequeirensis</i>
<i>P. occasius</i>	<i>P. dasythrix</i>
	<i>P. unicolor</i>
Genus <i>Makalata</i> :	<i>P. medius</i>
Didelphoides group:	<i>P. thomasi</i>
<i>M. didelphoides</i>	<i>P. nigrispinus</i>
<i>M. guianae</i>	<i>P. kerri</i>
<i>M. castanea</i>	<i>P. pattoni</i>
<i>M. handleyi</i>	
<i>M. longirostris</i>	Genus <i>Diplomys</i> :
<i>M. macrura</i>	<i>D. caniceps</i>
<i>M. obscura?</i>	<i>D. labilis</i>

Amazonian and Atlantic coastal regions. These peripheral taxa are those currently at most risk of extinction. Several taxa are known from fewer than 10 specimens: *S. rufodorsalis* has not been reported since the two specimens were collected in the late 1800's, its locality is now severely degraded and the species could even be extinct. *Phyllomys unicolor* is known only from the holotype collected in 1824 and is likewise possibly extinct. *P. brasiliensis* is represented by only three specimens, one of which is recent (Emmons et al., 2002). *C. pictus* is rare in a small region of intensely exploited habitat. *E. saturnus* occupies a small geographic area of unknown extent at the Andean base of Ecuador and N. Peru; this area currently has considerable forest, but there are few specimens and less information. As I conjectured earlier for an arboreal murid on the Sunda Shelf (Emmons, 1993), specialized arboreal morphology and habits, such as that of folivory, might allow the persistence of primitive or relictual taxa in the presence of invasions or radiations of more advanced taxa such as murid rodents. This might partially explain the high diversity of rainforest arboreal echimyid genera (twelve) relative to terrestrial forms (two genera, each with many species).

The three Amazonian genera of echimyines overlap widely in geographic range, suggesting differentiated ecological roles. Of these, *Isothrix bistrata* and all *Makalata* species seem restricted to waterside and floodplain forests (Emmons and Feer, 1990; Patton et al., 2000), while *Echimys chrysurus* has a wider habitat range in both floodplain and terra firme interfluvial forests. *Dactylomys* species in Amazonia are restricted to bamboo-dominated lowland and/or floodplain habitats or to montane forests, where they feed on bamboos (Emmons, 1981; pers. obs. of *D. bolivianus*, *D. dactylinus* and *D. peruanus*). Consistent with their large, tall-crowned, laminar or near-laminar teeth and large to enormous hindgut fermentation compartments (Dactylomyines, Emmons 1981; pers. observation of specimens of all Amazonian genera), nearly all large-bodied arboreal Echimyidae may be strongly folivorous. Nonetheless, I have watched *E. chrysurus* feed on fruit and *M. didelphoides* feed on leaves and fruit. Floodplain forests, on younger alluvial soils than forests on adjacent uplands, may provide plant resources with higher protein, mineral, or other nutrient content or fewer toxic secondary compounds than those of terra firme. Howler monkeys (*Alouatta seniculus*), the most folivorous of Amazonian primates, are likewise chiefly restricted to floodplain forests in Amazonia (Peres, 1997; personal observation), but they use terra firme in the Guiana region (north of the Rio Amazon and east of the Rio Negro), where, interestingly, *Isothrix pagurus* (unlike *I. bistrata* in Amazonia) is also found in terra firme forests. The cause of this habitat change in Guianan forests is not understood, but I speculate that from deposition of marine aerosols, terra firme Guianan forests are more mineral-rich than are forests of Central Amazonia, where many herbivores, including *Alouatta* spp., frequent both natural and artificial sodium sources and mineral licks (Emmons, unpublished data).

In the only two echimyine genera known to include sympatric congeners - *Phyllomys* (Yuri Leite, pers. com.) and *Makalata* - sympatry seems restricted to members of different species groups, such as *Makalata grandis* with *M. macrura*. Too little is known of the ecology of echimyines to lend much insight into either their biogeography or evolution; both merit further research.

ACKNOWLEDGEMENTS

This work was done over the course of many years, with the help and support of a great many colleagues. For their hospitality and for facilitating access to specimens in their care, I thank Paulina Jenkins (BMNH), Hans Baagoe and Mogens Anderson (ZMC), Michel Tranier and Jacques Cusin (MHNP), Manuel Ruedi (MHNG), Luis Flamarion and Leandro Salles (MNRJ), Guy Musser and Robert Voss (ANMH), Bruce Patterson (FMNH), Victor Pacheco (MHNP), James Patton; (MVZ), Dieter Kock (ZSM), Maria Rutzmoser (MCZ), and Barbara Hertzog (NMW). My travel to the BMNH was generously supported by the American Museum of Natural History, facilitated by Guy Musser. I am grateful to Alfred Gardner, Sharon Jansa, James Patton and particularly Robert Voss for meticulous critical reviews that improved the manuscript. To Sharon Jansa I owe a special debt for her help with the parsimony analyses. For stimulating discussions, moral support, and help in resolving problems or providing material throughout the years that this work was in progress, I thank Alfred Gardner, Yuri Leite, Guíomar Vucetich, Robert Voss, and especially James Patton, whose generosity in sharing ideas, information and parts of his own data were instrumental in completing this work. Figure 10 was drawn by Karolyn Darrow.

LITERATURE CITED

Cabrera, A.

- 1961 Catálogo de los mamíferos de America del Sur. Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" e Instituto Nacional de Investigación de las Ciencias Naturales Zoologia 4:309-732.

Cuvier, F.

- 1809 Extrait des premiers Mémoires de M. F. Cuvier, sur les dents des mammifères considérées comme caractères génériques. Nouveau Bulletin des Sciences, par la Société Philomatique. 1:393-395.

da Silva, M. N. F., and J. L. Patton

- 1993 Amazonian phylogeography: mtDNA sequence variation in arboreal echimyid rodents (Caviomorpha). *Molecular Phylogenetics and Evolution* 2:243-255.

Emmons, L. H.

- 1981 Morphological, ecological, and behavioral adaptations for arboreal browsing in *Dactylomys dactylinus* (Rodentia, Echimyidae). *Journal of Mammalogy* 62:183-189.
- 1993 A new genus and species of rat from Borneo (Rodentia: Muridae). *Proceedings of the Biological Society of Washington* 106:752-761.
- 1997 A revision of the genera of arboreal echimyid rodents (Echimyidae, Echimyinae). *Seventh International Theriological Congress, Acapulco, Mexico. Paper read and Abstracts*, p. 96.
- 1999 A new genus and species of abrocomid rodent from Peru (Rodentia: Abrocomidae). *American Museum Novitates* 3279:1-14.

Emmons, L. H., and F. Feer

- 1990 *Neotropical rainforest mammals: A field guide*. University of Chicago Press, Chicago, IL.
- 1997 *Neotropical rainforest mammals: A field guide*. 2nd ed. University of Chicago Press, Chicago, IL.
- 1999 *Mamíferos de los bosques húmedos de América tropical: Una guía de campo*. Editorial F.A.N, Santa Cruz, Bolivia.

Emmons, L. H., Y. L. R. Leite, D. Kock, L. P. Costa

- 2002 A review of the named forms of *Phyllomys* (Rodentia: Echimyidae) with the description of a new species from coastal Brazil. *American Museum Novitates* 3380:1-40.

Emmons, L. H., and M. G. Vucetich

- 1998 The identity of Winge's *Lasiuromys villosus* and the description of a new genus of echimyid rodent (Rodentia: Echimyidae). *American Museum Novitates* 3223:1-12.

Felsenstein, J.

- 1985 Confidence limits on phylogenies: An approach using the bootstrap. *Evolution* 39:783-791.

Honacki, J. H., K. E. Kinman, and J. W. Koeppel

- 1982 *Mammal species of the World: A taxonomic and geographic reference.* The Association of Systematics Collections, Lawrence, KS.

Jourdan, C.

- 1837 Mémoire sur quelques mamifères nouveaux. *Comptes Rendues Hebdomadaires des Séances de l'Académie des Sciences (Paris)* 5 (juillet-décembre 1837): 521-524.

Lara, M. C., J. L. Patton, and M. N. F. da Silva

- 1996 The simultaneous diversification of South American Echimyid rodents (Hystricognathi) based on complete cytochrome b sequences. *Molecular Phylogenetics and Evolution* 5:403-413.

Leite, Y. L. R.

- 2003 Evolution and systematics of the Atlantic tree rats, genus *Phyllomys* (Rodentia, Echimyidae), with description of two new species. *University of California Publications in Zoology* 132:1-118.

Leite, Y. L. R., and J. L. Patton

- 2002 Evolution of South American spiny rats (Rodentia, Echimyidae): the star-phylogeny hypothesis revisited. *Molecular Phylogenetics and Evolution* 25:455-464.

Lund, P. W.

- 1839 Coup d'oeil sur les espèces éteints de Mamifères du Brésil; extrait de quelques mémoires présentés à l'Académie royale des Sciences de Copenhague. *Annales de Sciences Naturelles, ser. 2*, 11:214-234.

- 1840 Nouvelles recherches sur la faune fossile du Brésil. *Annales de Sciences Naturelles, ser. 2*, 13:310-19.

- 1840a Blik paa Brasiliens Dryerverden för Sidste Jordonvaeltning. Tredie Afhandling: Fortsaettelse af Pattendryne. *Det Kongelige Danske Videnskabernes Selskabs Naturvidenskabelige og Mathematisk Afhandlinger* 8:217-272.

Maddison, W. P., and D. R. Maddison

- 1992 MacClade: Analysis of phylogeny and character evolution. Version 3.0. Sinauer Associates, Sunderland, MA.

McKenna, M. C., and S. K. Bell

- 1997 Classification of mammals above the species level. Columbia University Press, New York.

Patterson, B., and R. Pascual

- 1968 New Echimyid rodents from the Oligocene of Patagonia, and a synopsis of the family. *Breviora* 301:1-14.

Patterson, B., and A. E. Wood

- 1982 Rodents from the Deseadan Oligocene of Bolivia and the relationships of the Caviomorpha. *Bulletin of the Museum of Comparative Zoology* 149:371-543.

Patton, J. L.

- 1988 Species groups of spiny rats genus *Proechimys* (Rodentia: Echimyidae). *Fieldiana Zoology* 39:305-345.

Patton, J. L., and L. H. Emmons

- 1985 A review of the genus *Isothrix* (Rodentia, Echimyidae). *American Museum Novitates* 2817:1-14.

Patton, J. L., M. N. F. da Silva, and J. R. Malcolm

- 1994 Gene genealogy and differentiation among arboreal spiny rats (Rodentia: Echimyidae) of the Amazon basin: a test of the riverine barrier hypothesis. *Evolution* 48:1314-1323.

- 2000 Mammals of the Rio Juruá and the evolutionary and ecological diversification of Amazonia. *Bulletin of the American Museum of Natural History* 244:1-306.

Patton, J. L., and O. A. Reig

- 1989 Genetic differentiation among echimyid rodents, with emphasis on spiny rats, genus *Proechimys*. Pp. 75-96 in *Advances in Neotropical Mammalogy* (K. H. Redford and J. F. Eisenberg, eds.). Sandhill Crane Press, Gainesville, FL.

Patton, J. L., and M. A. Rogers

- 1983 Systematic implications of non-geographic variation in the spiny rat genus *Proechimys* (Echimyidae). *Zeitschrift für Säugetierkunde* 48:363-370.

Peres, C.

- 1997 Primate community structure at twenty western Amazonian flooded and unflooded sites. *Journal of Tropical Ecology* 13:381-405.

Pessôa, L. M., and S. F. dos Reis

- 1991 Cranial intraspecific differentiation in *Proechimys iheringi* Thomas (Rodentia: Echimyidae). *Zeitschrift für Säugetierkunde* 56:34-40.

Santos Carvalho, G. A. dos

- 1999 Relações filogenéticas entre formas recentes e fósseis de Echimyidae (Rodentia: Hystricognathi) e aspectos da evolução da morfologia dentária. MS thesis, Univ. Fed. Rio de Janeiro, Rio de Janeiro.

Swofford, D. L.

1998. *PAUP**. Phylogenetic Analysis Using Parsimony (*and Other Methods). Sinauer Associates, Sunderland, MA.

Tate, G. H. H.

1935. The taxonomy of the genera of Neotropical hystricoid rodents. *Bulletin of the American Museum of Natural History* 68:295-447.

Thomas, O.

- 1921 New *Sigmodon*, *Oryzomys*, and *Echimys* from Ecuador. *Annals and Magazine of Natural History* 7:448-450.

Voss, R. S., and R. Angermann

- 1997 Revisionary notes on Neotropical porcupines (Rodentia: Erethizontidae). 1. Type material described by Olfers (1818) and Kuhl (1820) in the Berlin Zoological Museum. *American Museum Novitates* 3214:1-44.

Vucetich, M. G., M. M. Mazzoni, and U. F. J. Pardiñas

- 1993 Los rodeores de la formación Collón Cura (Mioceno Medio), y la ignimbrita Pilcaniyeu, Cañadon del Tordillo, Neuquen. *Ameghiniana* 30:361-381.

Vucetich, M. G., and D. H. Verzi

- 1991 Un nuevo Echimyidae (Rodentia, Hystricognathi) de la edad Colhuehuapense de Patagonia y consideraciones sobre la sistematica de la familia. *Ameghiniana* 28:67-74.

Wilson, D. E., and Reeder D. M. (eds.)

- 1993 *Mammal species of the world: A taxonomic and geographic reference*. 2nd ed. Smithsonian Institution Press, Washington, D.C.

Woods, C. A.

- 1979 Adaptive radiation of capromyid rodents: Anatomy of the masticatory apparatus. *Journal of Mammalogy* 60:95-116.
- 1982 The history and classification of the South American Hystricognath rodents: Reflections on the far away and long ago. *Pymatuning Laboratory of Ecology Special Publication* 6:377-392.
- 1991 Suborder Hystricognathi. Pp. 771-806 in *Mammal species of the world: A taxonomic and geographic reference* (D. E. Wilson and D. M. Reeder, eds.). 2nd ed. Smithsonian Institution Press, Washington DC.

Woods, C. A., and E. B. Howland

- 1979 Adaptive radiation of capromyid rodents: anatomy of the masticatory apparatus. *Journal of Mammalogy* 60:95-116.

Appendix 1. Character matrix for morphological analyses of relationships among echimyine rodents. Each character is identified by the number assigned to it in the text (e.g., character 1 = pelage of lower back). Character states correspond to those identified for each trait in the text

Taxon	Character															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
<i>Octodon degus</i>	4	2	1	1	3	3	1	2	3	2	3	1	1	1	5	3
<i>Dactylomys boliviensis</i>	4	2	2	1	1	1	1	1	1	1	1	1	2	3	2	3
<i>Euryzgomatomys spin.</i>	2	2	1	1	2	1	1	3	3	2	2	2	1	1	1	3
<i>Carterodon sulcidens</i>	2	2	1	1	2	1	1	3	?	2	2	1	1	1	1	1
<i>Clyomys laticeps</i>	2	2	1	1	2	1	2	3	2	1	2	1	1	1	1	3
<i>Trichomys apereoides</i>	3	2	1	1	3	1	2	3	3	2	2	2	1	2	1	3
<i>Proechimys longicaud.</i>	2	2	1	1	2	1	2	3	3	2	2	2	1	2	2	1
<i>Trinomys iheringi</i>	1	2	1	1	2	1	2	2	3	?	2	2	1	2	2	3
<i>Mesomys sp Venez.</i>	1	2	1	1	3	1	2	3	3	2	2	2	1	2	6	3
<i>Lonchothrix emiliae</i>	1	2	1	1	3	1	2	?	?	?	2	3	1	2	2	1
<i>Callistomys pictus</i>	4	2	2	2	3	2	2	2	?	1	2	3	2	3	2	1
<i>Isothrix bistrata</i>	4	2	2	1	3	3	2	2	3	3	1	2	1	3	2	1
<i>Isothrix pagurus</i>	4	2	2	1	3	1	2	2	2	3	1	2	1	3	2	1
<i>Diplomys labilis</i>	3	2	1	2	3	1	1	3	2	1	1	3	2	3	4	1
<i>Phyllomys nigrispinus</i>	2	2	1	1	2	1	1	2	3	3	1	3	2	3	4	1
<i>P. blainvilli</i>	2	2	1	1	2	1	1	2	?	3	1	3	2	3	4	5
<i>P. lamarum</i>	2	2	1	1	1	1	1	2	?	?	1	3	2	3	4	2
<i>P. dasythrix</i>	3	2	1	1	1	1	1	2	?	?	1	3	2	3	4	1
<i>P. medius</i>	3	2	1	1	1	1	1	2	2	?	1	3	2	3	4	1
<i>S. rufodorsalis</i>	3	2	2	2	3	2	1	3	2	1	1	3	2	3	3	1
<i>P. semivillosus</i>	1	2	1	1	1	1	1	2	3	2	1	3	2	3	3	2
<i>P. carrikeri</i>	1	2	1	1	1	1	1	2	3	2	1	3	2	3	3	2
<i>P. punctatus</i>	1	2	1	1	1	1	1	2	3	?	1	3	2	3	3	2
<i>P. flavidus holotype</i>	1	2	1	1	1	1	1	2	3	?	1	3	2	3	3	2
<i>Echimyus chrysurus</i>	1	2	2	2	3	2	2	2	2	3	1	3	2	3	2	1
<i>Echimyus saturnus</i>	1	2	2	2	3	2	2	2	?	1	3	2	3	2	2	1
<i>Makalata didelphoides</i>	1	2	1	1	3	1	1	3	2	2	1	3	1	3	3	1
<i>M. macrurua</i>	1	2	1	1	2	1	1	3	2	2	1	3	1	3	7	1
<i>M. rhipidura</i>	2	2	1	1	3	1	1	2	3	2	1	3	1	3	3	2
<i>M. grandis</i>	2	2	1	1	3	1	1	2	2	?	1	3	1	3	3	4
<i>Makalata sp nov</i>	2	2	1	1	2	1	1	2	3	2	1	3	1	3	3	2
<i>P. occasius</i>	1	2	1	1	1	1	2	2	3	2	1	2	2	3	3	3
<i>Myocastor coypus</i>	4	1	1	1	1	1	1	1	1	3	2	3	1	2	2	1

Appendix 1 continued.

Taxon	Character														
	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47
<i>Octodon degus</i>	2	1	2	1	1	1	1	2	2	1	1	2	1	2	2
<i>Dactylomys boliviensis</i>	2	2	3	3	1	3	1	2	2	1	1	2	2	1	2
<i>Euryzygomatomys spin.</i>	2	2	3	1	1	1	1	2	1	1	1	1	2	2	2
<i>Carterodon sulcidens</i>	2	1	2	1	2	1	1	1	2	1	1	1	2	?	?
<i>Clyomys laticeps</i>	1	2	2	1	1	1	1	1	2	1	1	1	2	2	2
<i>Trichomys apereoides</i>	1	1	2	2	1	1	1	2	2	1	1	2	2	2	1
<i>Proechimys longicaud.</i>	2	1	2	2	1	3	1	2	1	1	2	2	2	1	1
<i>Trinomys iheringi</i>	2	2	4	2	1	3	1	2	1	1	2	2	2	2	1
<i>Mesomys</i> sp Venez.	2	2	2	3	1	3	1	2	1	1	1	2	2	2	3
<i>Lonchothrix emiliae</i>	2	2	3	3	1	3	1	2	1	1	1	2	2	2	3
<i>Callistomys pictus</i>	1	1	3	?	1	2	1	3	2	1	1	1	2	2	3
<i>Isothrix bistrata</i>	2	1	3	3	1	2	1	2	1	1	2	2	2	1	1
<i>Isothrix pagurus</i>	2	1	3	3	1	2	1	2	1	1	2	2	2	1	1
<i>Diplomys labilis</i>	2	1	2	3	1	2	1	2	2	1	2	2	2	1	2
<i>Phyllomys nigrispinus</i>	2	2	3	3	1	3	2	4	2	2	3	2	2	1	2
<i>P. blainvilli</i>	2	2	4	3	1	3	1	4	2	2	2	2	2	2	2
<i>P. lamarum</i>	2	2	3	3	1	3	1	4	2	2	2	2	2	1	2
<i>P. dasythrix</i>	2	2	4	3	1	3	3	4	2	2	2	2	2	1	2
<i>P. medius</i>	2	2	4	3	1	3	?	4	2	2	2	2	2	1	2
<i>S. rufodorsalis</i>	2	1	3	3	1	3	3	2	2	1	1	2	2	1	2
<i>P. semivillosus</i>	2	2	3	3	1	3	1	3	2	1	2	2	2	2	2
<i>P. carrikeri</i>	2	2	4	3	2	3	3	4	2	1	3	2	2	2	2
<i>P. punctatus</i>	2	2	4	3	1	3	3	3	2	1	1	2	2	2	2
<i>P. flavidus holotype</i>	2	2	4	3	1	3	1	4	2	1	1	2	2	2	2
<i>Echimyis chrysurus</i>	2	2	4	3	1	3	3	3	2	1	2	2	2	2	3
<i>Echimyis saturnus</i>	2	2	4	3	1	3	3	2	2	1	2	2	2	1	3
<i>Makalata didelphoides</i>	2	2	3	3	2	3	3	2	2	1	2	2	2	1	3
<i>M. macrurua</i>	2	2	3	4	2	3	3	3	2	1	2	2	2	1	3
<i>M. rhipidura</i>	2	2	3	4	2	3	3	3	2	1	2	2	2	1	2
<i>M. grandis</i>	2	2	4	3	2	3	3	3	2	1	2	2	2	1	3
<i>Makalata</i> sp nov	2	2	3	3	2	3	3	3	2	1	2	2	2	1	2
<i>P. occasius</i>	2	2	3	2	2	3	1	3	2	1	3	2	2	2	2
<i>Myocastor coypus</i>	1	2	1	3	1	2	1	4	2	1	1	2	2	3	3

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