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A revision of the genus *Calomys* (Rodentia: Muridae)

Olds, Nancy, Ph.D.

City University of New York, 1988

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A REVISION OF THE GENUS CALOMYS (RODENTIA: MURIDAE)

by

Nancy Olds

A dissertation submitted to the Graduate Faculty
in Biology in partial fulfillment of the requirements
for the degree of Doctor of Philosophy, The City
University of New York

1988

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This manuscript has been read and accepted for the Graduate Faculty in Biology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

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Abstract

A Revision of the Genus Calomys (Rodentia, Muridae)

by

Nancy Olds

Advisors: Dr. Sydney Anderson and Dr. Max K. Hecht

The genus Calomys (Muridae: Sigmodontinae) includes ten species, C. bimaculatus, C. callosus, C. hummelincki, C. laucha, C. lepidus, C. murillus, C. musculus, C. sorellus, C. tener, and C. venustus. These species are separable on the bases of pelage characters, overall body size, tail length, cranial structures, and, in some cases, karyotypes. Diagnoses are given for the genus and all species. Descriptions, comparisons, and summaries of the taxonomic history for the genus and species are presented.

Age was found to be more important in intraspecific cranial variation than sex. Samples of two species, C. sorellus and C. callosus, show significant size changes with age. Young adults and juveniles are smaller than older adults, and very old adults are often smaller than middle-aged adults. An explanation for this is lacking at this time.

The fossil genus Bensonomys is not included in the genus Calomys. A comparison between the dentition of Bensonomys and Calomys is given. A close relationship is possible between these two genera, but further study, including a broad survey of all North and South American Recent and fossil Sigmodontinae is necessary before conclusions on the significance of Calomys in the diversification of the South American Sigmodontinae can be drawn. Necromys, a fossil genus of Sigmodontinae known from South America, is not included in Calomys, either.

Relationships within the genus Calomys are still uncertain; however, three species groups are postulated: C. callosus, C. venustus, and C. tener; C. laucha, C. bimaculatus, and C. hummelincki; and C. murillus and C. musculus. Calomys lepidus and C. sorellus do not fit in any of the above groups or with each other.

Calomys is most similar cranially and dentally to the phyllotine genera Eligmodontia, Andalgalomys and Graomys. A closer relationship to Eligmodontia and Andalgalomys is proposed.

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A REVISION OF THE GENUS CALOMYS (RODENTIA: MURIDAE)

INTRODUCTION:

Almost 42 percent (1750 of 4200 species) of living mammals are rodents. Approximately 1120 species, or about 64 percent of all rodents, belong to the family Muridae. This family includes most rats and mice, is cosmopolitan in distribution, and exists in a wide variety of habitats (Carleton and Musser, 1984). The subfamily Sigmodontinae (369 species in 73 genera), includes most New World rats and mice, occasionally referred to as the North American neotomine-peromyscines and the South American murids (Carleton, 1980).

The South American murids, like most South American groups, are poorly known, in comparison to those of North America. Two main reasons for this are habitat destruction leading to reduced species populations and ranges, and the difficulty of field work in South America, both of which are often compounded by a lack of local interest or resources for collecting, studying, and publishing results.

Some recent studies of ecology, physiology, and genetics on South American mammals are limited in usefulness because taxa are uncertain. In some cases, specific names are used that have little to do with the species actually studied. Unless voucher specimens of the animals studied are retained or adequate

measurements given, it is not possible to verify or revise identifications.

However, in recent years there has been increased collecting and more detailed analyses of ecology, biogeography, and systematics in South American mammalogy (Mares and Genoways, 1982). After looking at many of the unresolved problems in mammalian systematics with new data, recent workers have raised many new questions.

Early collectors of mammals sampled many sites and species and, fortunately, most of these specimens have been preserved in collections. However, considerable taxonomic confusion remains because most of these specimens have not been adequately examined since they were first collected or described.

Before higher level taxonomic relationships and larger biogeographic patterns can be addressed, the species and genera of many groups need to be clearly defined.

I chose the genus Calomys for several reasons, including the number of specimens already present in collections, the implication of several species as vectors of hemorrhagic fever and other diseases (Justines and Johnson, 1969; Karimi et al., 1976), and hypotheses of relationships that have arisen from earlier studies of the phyllotine group of rodents (Hershkovitz, 1962; Pearson and Patton, 1976). Other aspects of interest include a geographical range with a large gap in the Amazon basin, and a

tremendous altitudinal range (sea level up to approximately 5000 m).

Defining the genus and its species more precisely will aid in specimen identification. In addition, the revision of Calomys may help to answer one of the central questions in the study of New World rodent evolution: whether major diversification of murid rodents occurred in North America with subsequent movements into South America, or whether immigration was earlier and diversification in South America occurred at the same time as that in North America. Baskin's (1978) inclusion of Bensonomys, known from the Pliocene of the southwestern United States and Mexico, as a subgenus of Calomys supports a North American origin.

Calomys is considered to be the most primitive member of the tribe Phyllotini (Osgood, 1947; Hershkovitz, 1962; Williams and Mares, 1978), one of some eight tribes of South American murids (the number recognized depends on the source; see Carleton, 1980; Reig, 1980, 1986; and Olds and Anderson, in press, a). Diagnoses are lacking for some of these tribes. The phyllotine group was recognized as a loose, unnamed group by Thomas (1916a). Informal use of the name "phyllotine" dates from Tate (1932), and the group was recognized formally by Vorontsov (1959). However, only recently has a diagnosis of the group been provided (Olds and Anderson, in press, a).

As with most Sigmodontinae, rarely do unique characters separate groups. In fact, the subfamily Sigmodontinae is not defined by any unique character, but by being the residue after a number of distinctive groups of murids are separated (Carleton and Musser, 1984).

The most comprehensive examination of the phyllotine rodents, including Calomys, was by Hershkovitz (1962). He surveyed the genera he thought comprised the group. Although he provided no specific diagnoses for either the genera or the tribe, he did summarize much information. Olds and Anderson (in press, a) reviewed many of the characters he gave for the phyllotines and wrote a diagnosis. Characters at the generic level need the same treatment.

GENERAL BACKGROUND ON THE GENUS CALOMYS:

Cabrera (1961) listed 10 species of Calomys, with synonymies and geographic ranges. Hershkovitz (1962), recognized four species of Calomys; C. lepidus, C. sorellus, C. laucha, and C. callosus. A recent checklist of mammalian species by Corbet and Hill (1980) listed seven species of Calomys. Another recent checklist of species (Honacki et al., 1982) listed eight species, as did Carleton and Musser (1984). Reig (1984, 1986) included nine species in the genus. No new species were described between

these publications (the last species described was C. hummelincki, by Husson in 1960); differences are based solely on different interpretations of the literature and specimens.

Members of the genus Calomys are small (total length, including tail, approximately 120 to 220 mm; weight approximately 10 to 40 g), have prominent ears, narrow feet, and a short tail (rarely longer than the head and body). The larger members of Calomys resemble house mice (genus Mus). They inhabit temperate zone lowlands, scrublands, and forest fringes at elevations ranging from sea level to 5000 m. As defined by Hershkovitz (1962), C. sorellus and C. lepidus occur at high elevations in low scrubby vegetation, C. laucha occurs in the dry lowland grasslands and C. callosus occurs in the wetter lowlands. Calomys (excluding Bensonomys, see Baskin, 1978) is restricted to South America. The present range includes populations in Venezuela and the Netherlands Antilles which Hershkovitz (1962) thought to be introduced populations of C. laucha, but which others, including Handley (1976), considered endemic to those areas. The geographic distribution of the genus is shown in figure 8.

Several recent studies on rodent ecology in South America have included information on species of Calomys (Karimi et al., 1976; Pizzimenti and de Salle, 1980; 1981; Streilein, 1982a, b, c; Villafañe et al., 1973; Alho et al., 1986; Kravetz et al., 1975;

Kravetz and Villafañe, 1981; Crespo et al., 1970; Contreras and Rosi, 1980a, b). Several species of Calomys are known to be reservoirs for arboviruses that produce hemorrhagic fever in people (Johnson et al., 1965; Justines and Johnson, 1969; Roldan et al., 1985) and trypanosomes causing Chagas' disease (Ribeiro, 1973). Calomys has been implicated as a carrier of other infectious diseases, such as plague (Karimi et al., 1976). Concern about these diseases has led to extensive collecting and scientific research (including biochemical, ecological, karyological, and systematic studies) on Calomys (Hurtado de Catalfo and Wainberg, 1974; Contreras and Roig, 1976; Lisanti et al., 1976; Gardenal et al., 1977a, b; de la Barrera, 1936; Mello, 1978; Blanco and Gardenal, 1977; Villafañe et al., 1977).

Proposals have been made to split three of the four species of Calomys recognized by Hershkovitz (1962). Pearson and Patton (1976) described the karyotypes of three of these species. They found evidence that both C. sorellus and C. callosus should be divided. In another study, Massoia et al. (1968) reestablished a formerly synonymized species as a separate species (C. musculus, included in C. laucha by Hershkovitz, 1962) on the basis of karyology and morphology. As mentioned above, Handley (1976) referred the Venezuelan populations to a separate species (C. hummelincki).

The main questions addressed in this study are:

1. Is the genus Calomys clearly defined and separable from other genera?
2. How many species are there and how do they differ from each other?
3. How are these species related to each other?
4. Where do these species occur, geographically and ecologically?

Secondary questions that relate to the above include:

1. What, if any, character variation is geographic and intraspecific variation?
2. What significance did Calomys have in the diversification of the South American Muridae?

METHODS:

Specimens from the following collection were studied (abbreviations in parentheses): the American Museum of Natural History, in New York (AMNH); the National Museum of Natural History, in Washington, D. C. (USNM); the University of Michigan Museum of Zoology, in Ann Arbor (UMMZ); the Museum of Vertebrate Zoology, University of California, in Berkeley (MVZ); the Field Museum of Natural History, in Chicago (FMNH); the Carnegie Museum of Natural History, in Pittsburgh (CM); the British Museum (Natural History), in London (BMNH); the Natural History Museum of Los Angeles County, in Los Angeles (LACM); the California Academy of Sciences, in San Francisco (CAL); the Philadelphia Academy of Natural Sciences, in Philadelphia (ANSP); the Museum of Michigan State University, in East Lansing (MSU); the Museum of Southwestern Biology, University of New Mexico, in Albuquerque (MSB); the Museum of Comparative Zoology at Harvard College, in Cambridge (MCZ); the Museum of Natural History, University of Connecticut, in Storrs (UCONN); and the Zoological Museum in Amsterdam (ZAM). All specimens of Calomys examined and specimens of other genera used in illustrations and in analyses are listed in the Appendix. Many additional specimens and taxa were studied, using the extensive collections of the AMNH. For practicality, these are not listed individually unless reference is made to a particular specimen.

External measurement (in mm) recorded from specimen labels are (for definitions of the measurements, see DeBlase and Martin, 1974)

TL Total length

T Tail length

HF Length of hind foot, including claws

E Length of ear, from notch

The weight in grams and any other relevant information given on original labels was recorded.

The cranial and dental dimensions measured were selected to reflect aspects of skull shape and to be comparable with those in the literature. I chose some that would not be affected by growth, such as molar dimensions, and some that would reflect continuing growth. Many of the dimensions are length and breadth, which change with increasing age and are highly correlated with overall size, i.e., a large skull is large in most dimensions.

The measurements used are modified from standard measurements used by Anderson (1969), Musser (1979), Myers and Carleton (1981), and Taylor et al. (1982). Figure 1 shows a diagrammatic view of a Calomys skull (based on C. lepidus, AMNH 260626) with the bones and foramina labeled. Figure 2 shows the same skull with the dimensions labeled. The crown lengths and widths of the molars are not illustrated.

The cranial dimensions with abbreviations are as follows (see fig. 2):

ZYN	Length of zygomatic notch
LRS	Length of rostrum
GLS	Greatest length of skull
ZBR	Greatest breadth across zygomatic arches
BBC	Greatest breadth of braincase
IOC	Breadth of interorbital constriction
WRS	Width of rostrum at zygomatic notch
LINF	Length of incisive foramina
PAL	Length of palatal bridge
PPL	Post-palatal length
LBULL	Length of auditory bulla
MAX	Crown length of maxillary toothrow
DIAS	Length of diastema
LINCT	Length from anteriormost part of incisive foramina to alveolus of incisors
LM1, LM2, LM3,	Crown lengths of M1-3
WM1, WM2, WM3,	Crown widths of M1-3
PBR	Width of palate at M2
WINCT	Width of incisor tips
MESF	Width of mesopterygoid fossa
PARA	Width of parapterygoid fossa

Dimensions were measured with a stage craniometer to the nearest 0.01 mm (see Anderson, 1968).

Some dimensions were not used in later statistical analyses because the measurements were consistently too variable.

Figure 1. A) Ventral and B) dorsal views of a Calomys skull (drawing based on C. lepidus, AMNH 260626) with major structures labeled. Ab, auditory bulla; App, anterior palatal pits; As, alisphenoid; Bo, basioccipital; Bs, basisphenoid; Co, condyle; Eam, external auditory meatus; Fm, foramen magnum; Fo, foramen ovale; Fr, frontal; Ifo, infraorbital foramen; Inf, incisive foramen; Ipa, interparietal; Ju, jugal; La, lacrimal; Mlf, middle lacerate foramen; Mx, maxilla; Na, nasal; Oc, occipital; Pa, parietal; Pe, petrosal; Pl, palatine; Pmx, premaxilla; Pop, postorbital process; Pp, parapterygoid; Ppp, posterior palatal pits; Ps, presphenoid; Spv, sphenopalatine vacuities; Sq, squamosal; Stf, stapedial foramen. Bar represents 10 mm.

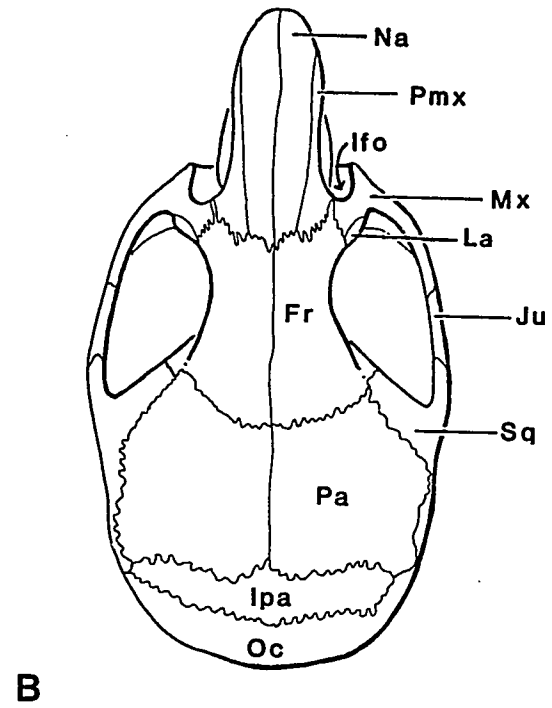
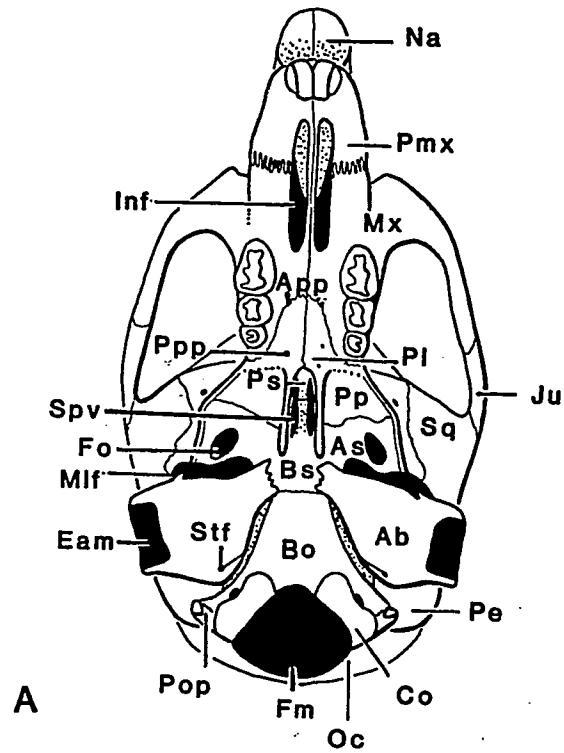
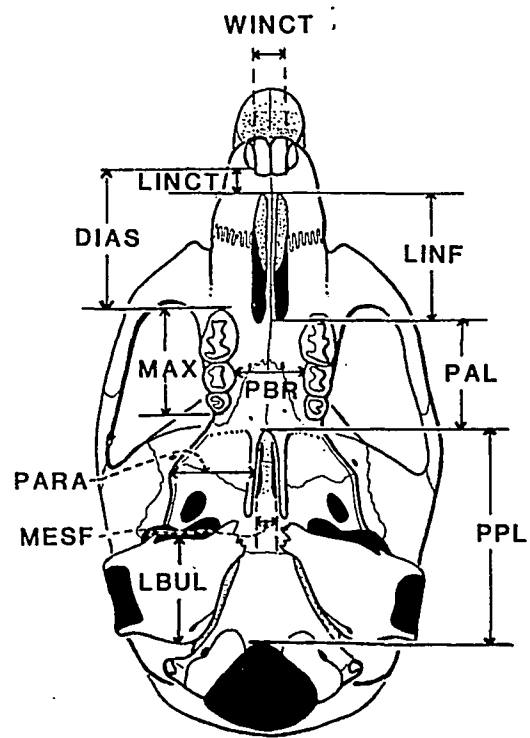
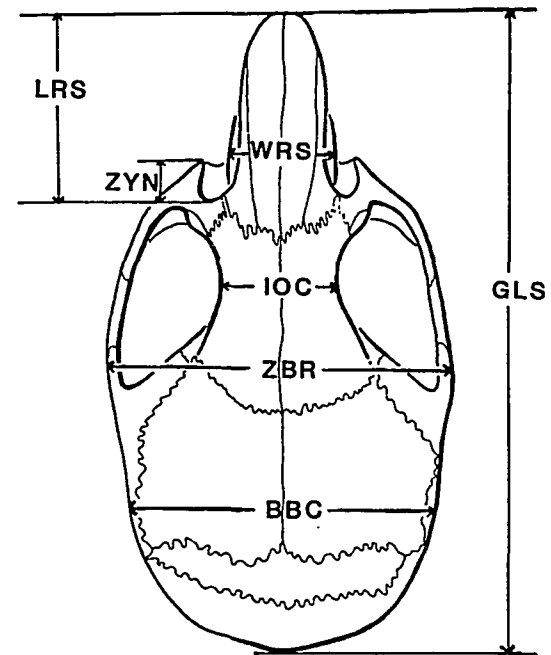


Figure 2. A) Ventral and B) dorsal views of a Calomys skull (drawing based on C. lepidus, AMNH 260626) showing dimensions measured. Measurements defined in "Methods" section. Bar represents 10 mm.



A



B

I used a slightly different set of measurements to compare Calomys with other phyllotine genera. This is an expansion of the results presented in Olds et al. (1987); additional specimens were measured, sample sizes increased, and additional taxa are included.

The dimensions measured for phyllotine comparisons (using the stage craniometer to the nearest .01 mm) are:

LRS	Length of rostrum
GLS	Greatest length of skull
ZBR	Greatest breadth across zygomatic arches
BBC	Breadth of braincase
IOC	Width of interorbital constriction
WRS	Width of rostrum
LINF	Length of incisive foramina
PAL	Length of palate
LBULL	Length of auditory bulla
PBR	Breadth of palatal bridge
PDB	Post-dental breadth
POB	Breadth across paroccipital processes
ZPW	Width of zygomatic plate
MESF	Width of mesopterygoid fossa
MAXA	Alveolar length of toothrow
LM1, LM2, LM3	Crown length of M1, M2, M3
WM1	Crown width of M1

All animals were assigned to an age class on the basis of tooth wear and general appearance of the skull using a modification of the tooth wear method of Myers and Carleton (1981) and Engstrom et al. (1982). These classes represent relative age only. I used seven age classes as follows:

0. M3 not erupted.
1. M3 just erupted and not worn. Anterior cusps of M1 not or barely worn.
2. Anterior cusps of M1 barely worn, the cusps of M2 showing a connected wear pattern, cusps still prominent, M3 showing some wear.
3. M3 flat, M2 with dentine pattern visible in a thick S-shape, connecting all cusps, M1 showing substantial wear, anterior conules still visible as separate structures.

4. M3 flat to concave, M2 with dentine lakes, M1 showing connected wear pattern, 3 cross lophs of dentine, cusps still discernable, amount of flexion of anteromedian flexus unclear.
5. M2 and M3 concave. M1 with discernable outline of cusps only.
6. M1, M2, and M3 concave, and usually damaged or otherwise distorted.

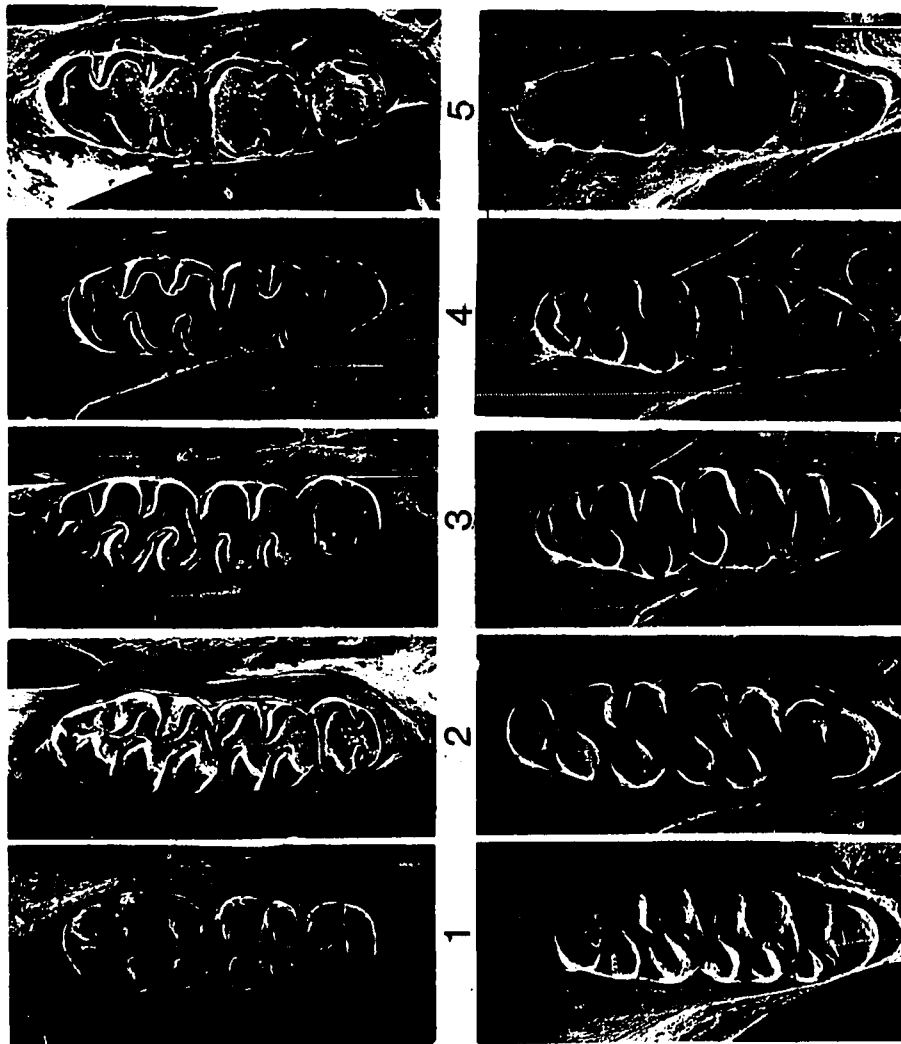
Individuals in age class 1 were considered to be subadults; age classes 2 through 4 were considered adults, and age classes 5 and 6, both rare in collections, were considered old adults. Juveniles, i.e. individuals in which the third molar has not yet erupted, were considered age class 0 and were not included in the study. Figure 3 shows age classes 1-5 in C. sorellus. Age classes 0 (M3 not erupted) and 6 (all surfaces concave) are easier to determine than classes 1 through 5, and are not shown. Different workers may assign animals that show an intermediate condition of tooth wear to different age classes. A conservative estimate was followed here.

Dental terminology follows Hershkovitz (1962) and Reig (1977). An upper case "M" signifies molars of the upper jaw, and a lower case "m", those of the lower jaw. Terminology for cranial foramina and other structures follows Wahlert (1974, 1985), Musser (1982), and Musser and Williams (1985).

Non-preferentially stained karyotypes of Bolivian specimens were prepared in the field from bone marrow cells of the femur as described by Baker et al. (1982). A cell suspension for future banding analyses was preserved in liquid nitrogen and deposited in the frozen tissues division of the MSB. Slides made from the cell suspension were stained with Geimsa and examined at AMNH. Non-preferentially stained slides of cells were generously sent by Dr. P. Myers from UMMZ and by Dr. J. Patton from MVZ. Dr. A. Gardner provided negatives of photographs of karyotypes he prepared.

Statistical analyses of the data were performed using the statistical programs of SAS (SAS Institute Inc., 1982) through the City University of New York (CUNY) Computer Center.

Figure 3. Upper and lower molar tooth rows of Calomys sorellus showing age classes 1 through 5. Age class 1, AMNH 231611; 2, AMNH 231602; 3, AMNH 231590; 4, AMNH 231591; and 5, AMNH 231556. Bar at right represents 1 mm.



TAXONOMY:

Superfamily Muroidea

Family Muridae

Subfamily Sigmodontinae

Diagnosis, general characters, distribution, included genera, and other information were given by Carleton and Musser (1984).

Tribe Phyllotini Vorontsov, 1959

Type genus: Phyllotis.

Diagnosis: "A tribe of Sigmodontinae distinguished by the following combination of characters: heel hairy; ears moderate to large, palate long (except in Irenomys), incisive foramina long, parapterygoid fossa relatively broader than mesopterygoid fossa (except in Punomys), sphenopalatine vacuities large, supraorbital region never evenly curved in cross-section, interparietal well developed, zygomatic notch deeply excised (less so in Irenomys), teeth tetralophodont, M3 more than half the length of M2" (Olds and Anderson, in press, a).

Distribution: Phyllotini are restricted to South America and are concentrated in southern South America. They range from sea level to approximately 5000 m in the Andes, and generally live in open grassland or at the edge of forests. Some are restricted

to the mountains, and others are known from the dry thorn-scrub of the Gran Chaco of Bolivia, Paraguay, and Argentina.

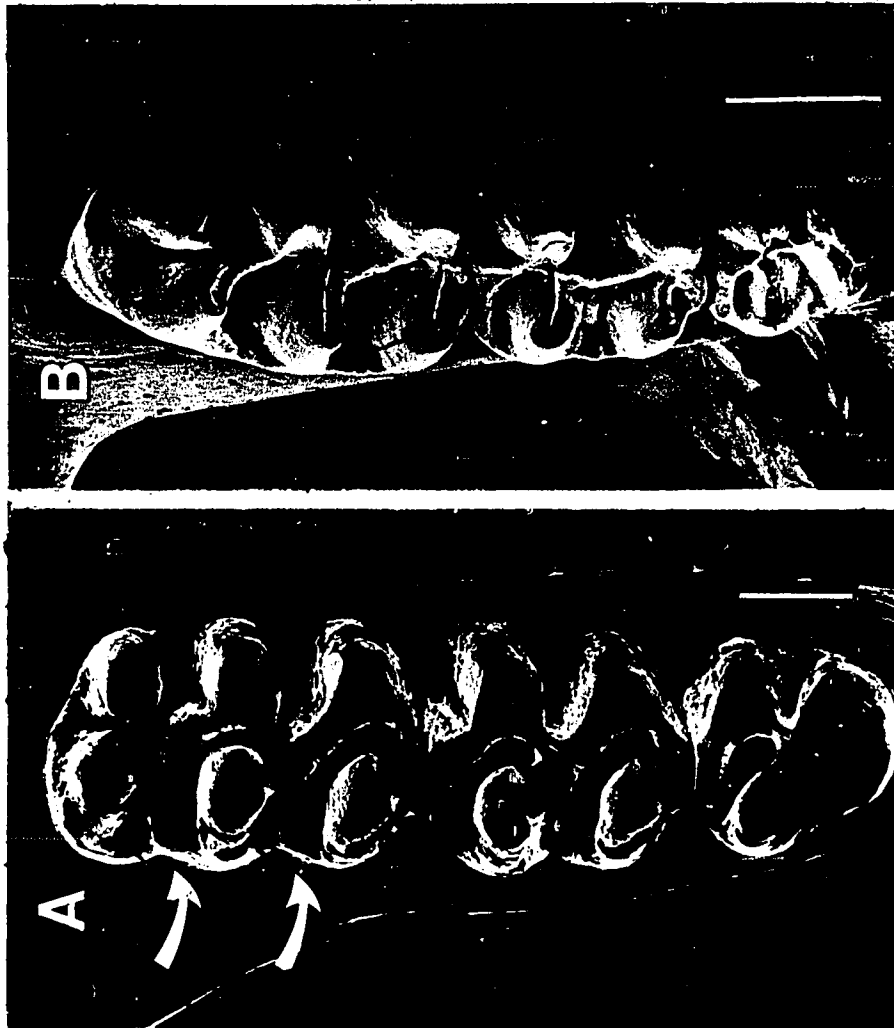
Content: Phyllotini include the following genera:

Andalgalomys, Andinomys, Auliscomys, Calomys, Chinchillula, Eligmodontia, Euneomys, Galenomys, Graomys, Irenomys, Neotomys, Phyllotis, Punomys, and Reithrodon (Olds and Anderson, in press, a).

Description and Comparisons: Phyllotines tend to have large ears, relatively small feet, and soft warm fur (because many live in cold climates at high elevation). Cranially, the phyllotines tend to have a lightly built skull and a long palate with perforations. Molars range from bunodont-brachydont (e.g. in Calomys, Eligmodontia, and Andalgalomys) to high-crowned and with terraced or planed occlusal surfaces in the other more derived genera. The M3 is always more than half the length of the M2. The teeth are not greatly narrowed; M1 has two to four roots and m1 has two to four roots. The front surface of each incisor is smooth or has one or two grooves. For further character descriptions see Herskovitz (1962) and Olds and Anderson (in press, a).

Herskovitz (1962) placed most of the New World Sigmodontinae into one of two basic dental patterns, pentalophodont or tetralophodont (fig. 4). Both patterns are subject to considerable variation. The more complex pentalophodont pattern is characterized by five primary transverse crests (p. 76). The

Figure 4. A) Pentalophodont and B) Tetralophodont patterns of molar teeth. A, Thomasomys aureus, AMNH 36279; B) Calomys venustus, AMNH 41870. Arrows point to the accessory lophs present in the pentalophodont pattern. Bars represent 1 mm.



"secondarily simplified" tetralophodont pattern has lost part or all of the middle or third crest. All simpler teeth are considered to be derived from the tetralophodont pattern (Herskovitz, 1962).

Dentally, tetralophodont phyllotines differ from the pentalophodont oryzomyines, thomasomyines, and scapteromyines. The molar teeth are relatively narrower in oxymycterines, scapteromyines (except Kunsia), akodonts, and ichthyomyines, than in phyllotines. The M3 is very small in oxymycterines, akodonts, scapteromyines and ichthyomyines. Akodonts and oxymycterines have simple cusp patterns that wear easily and early. Sigmodontini usually have large highly complex teeth. Figure 5 contrasts dentitions of representatives of Sigmodontini, Oryzomyini, Akodontini, and Phyllotini.

Skull shape is also useful in distinguishing tribes (figs. 6 and 7): cranial differences tend to be consistent at the tribal level. The oryzomyines have short incisive foramina; a short palate; a well-developed interparietal; a strong zygomatic notch; no sphenopalatine vacuities; and moderately wide mesopterygoid fossa. The akodonts (including the oxymycterines) have long incisive foramina, a long palate, an evenly curved supraorbital region in cross-section; weaker zygomatic notches, a very narrow parapterygoid fossa, small or no sphenopalatine vacuities; and a less well-developed interparietal. Sigmodonts (tribe

Sigmodontini) have extremely heavy rugose skulls, as do some scapteromyines. The tribes I stress in comparisons, the oryzomyines (including the thomasomyines) and akodonts (including the oxymycterines), are those that are most likely to be confused with the phyllotines in appearance.

Figure 5. SEM photographs of upper (top row) and lower (bottom row) molar tooth rows contrasting members of different tribes of Sigmodontinae. A) Holochilus brasiliensis, tribe Sigmodontini (AMNH 260771); B) Thomasomys aureus, tribe Oryzomyini (AMNH 36279); C) Oxymycterus paramensis, tribe Akodontini (AMNH 248999); and D) Calomys sorellus, tribe Phyllotini (AMNH 231697). Bars represent 1 mm.

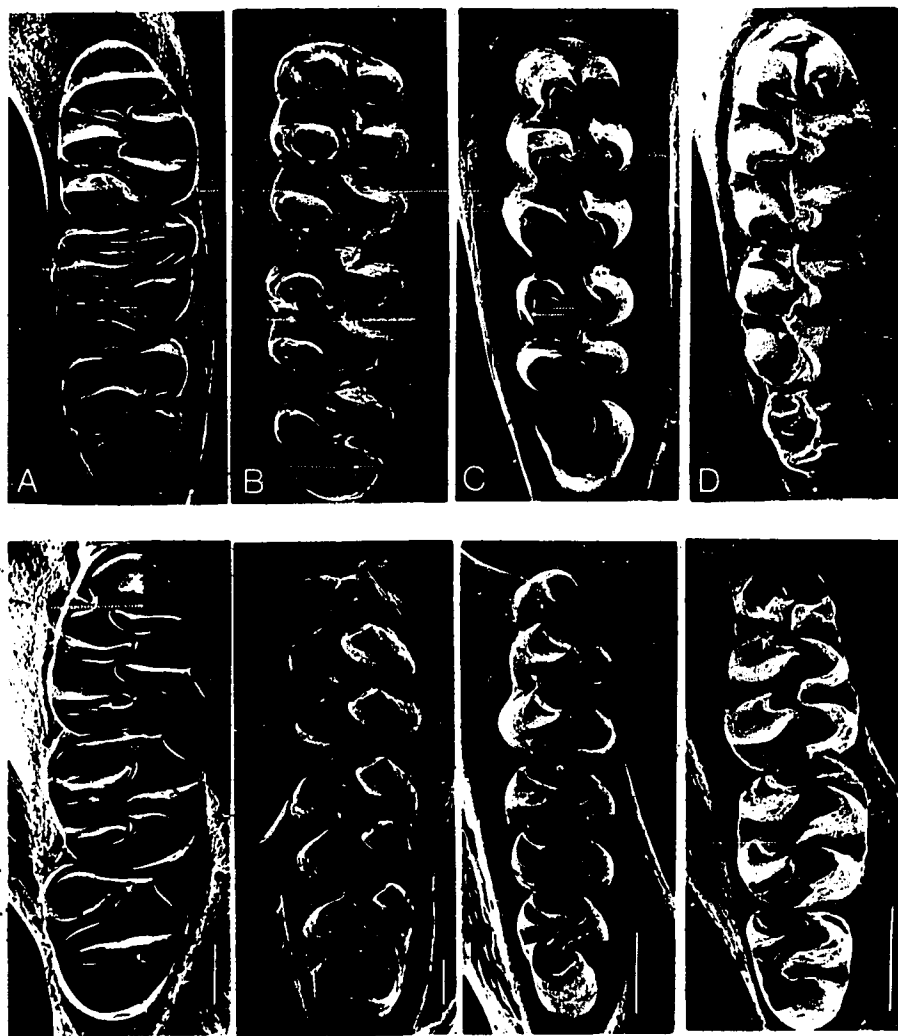


Figure 6. Dorsal (above) and ventral (below) views of skulls representing three tribes of Sigmodontinae. A) Oryzomys capito, tribe Oryzomyini (AMNH 209907); B) Akodon varius, tribe Akodontini (AMNH 260468); and C) Calomys callosus, tribe Phyllotini (AMNH 261961). Scale at right represents 10 mm.

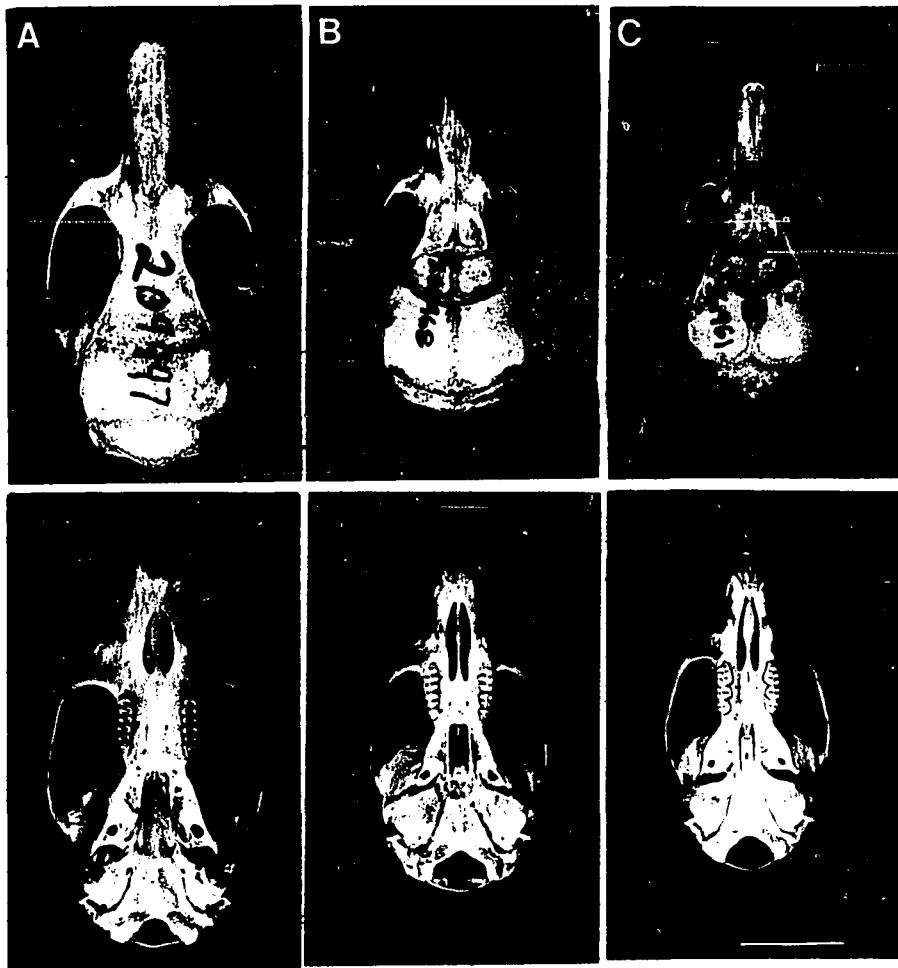


Figure 7. SEM photographs of the posterior palate showing variation within Sigmodontinae. A) Oryzomys nitidus, tribe Oryzomyini (AMNH 260377); B) Oxymycterus paramensis, tribe Akodontini (AMNH 248999); C) Akodon boliviensis, tribe Akodontini (AMNH 260455); D) Graomys domorum, tribe Phyllotini (AMNH 260754); E) Phyllotis osilae, tribe Phyllotini (AMNH 247880); and F) Calomys sorellus, tribe Phyllotini (AMNH 231602). Bars represent 1 mm.



Genus Calomys, Waterhouse, 1837

Calomys Waterhouse, 1837, p. 21. Type species Mus bimaculatus (loc cit., p. 18, by original designation). Also included Mus elegans and Mus gracilipes.

Hesperomys Waterhouse 1839, p. 75, type species Mus bimaculatus, by original designation.

Content: Calomys includes the following species: C. bimaculatus, C. callosus, C. hummelincki, C. laucha, C. lepidus, C. murillus, C. musculus, C. sorellus, C. tener, and C. venustus.

Diagnosis: A genus of Phyllotini distinguished by the following combination of characters: venter paler than dorsum; ears small to moderate; white or pale buffy post-auricular patch; feet small and white above; soles of feet naked; tail less than or equal to head and body length; tail not penicillate; edges of supraorbital region ledged or smoothly rounded, divergent or parallel; bullae not greatly inflated; nasals not noticeably narrowed; parapterygoid fossa much broader than the mesopterygoid fossa midway along their length; molars brachydont, tuberculate;

M1 generally with an anteromedian flexus dividing the anterocone into two anteroconules; M3 not greatly reduced.

Distribution: Calomys is restricted to the Neotropics as shown in figure 8. Members of the genus generally inhabit subtropical and temperate grasslands, scrublands and forest fringes (figs. 9 and 10 show the rainfall amounts and general vegetation zones in South America). Calomys ranges from northern Peru south to approximately 40°S in Argentina and east across southern Bolivia, Paraguay, Uruguay, and Brazil. There is a large gap in the Amazon region, then populations occur in Northern Venezuela, Eastern Colombia, Aruba, and Curaçao. The altitudinal range is from sea level to approximately 5000 m in the high Andes. (See Hueck and Siebert, 1972, for a detailed map of the vegetation of South America; regional descriptions are in Mares et al., 1981a, b; Streilein, 1982a; Vervoorst, 1982; Schaller, 1983; Mares et al., 1985a, b; Walter and Breckle, 1985, 1986; Alho et al., 1986; and Vuilleumier and Monasterio, 1986).

Figure 8. Map of South America showing the geographic range of Calomys. Note the disjunction in the Amazon region.

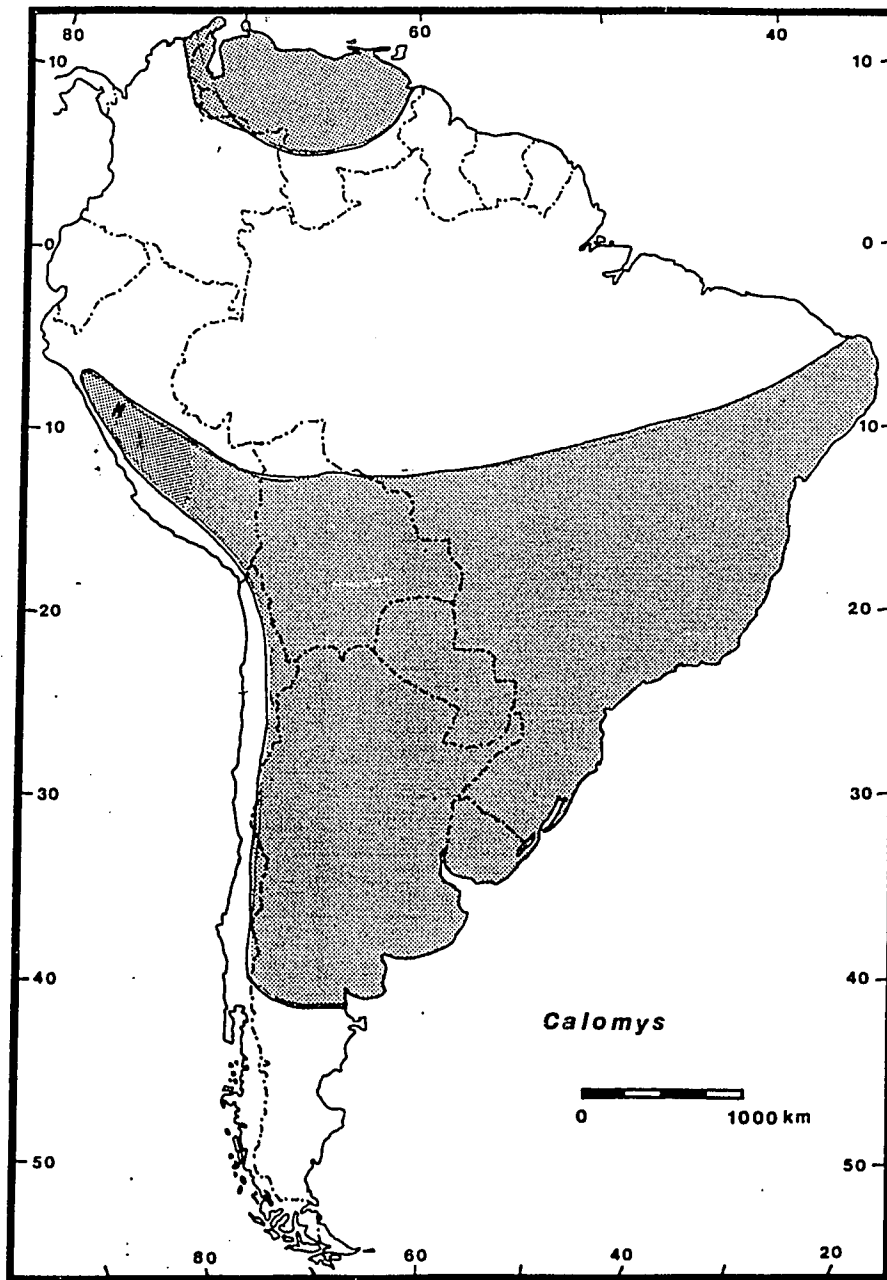
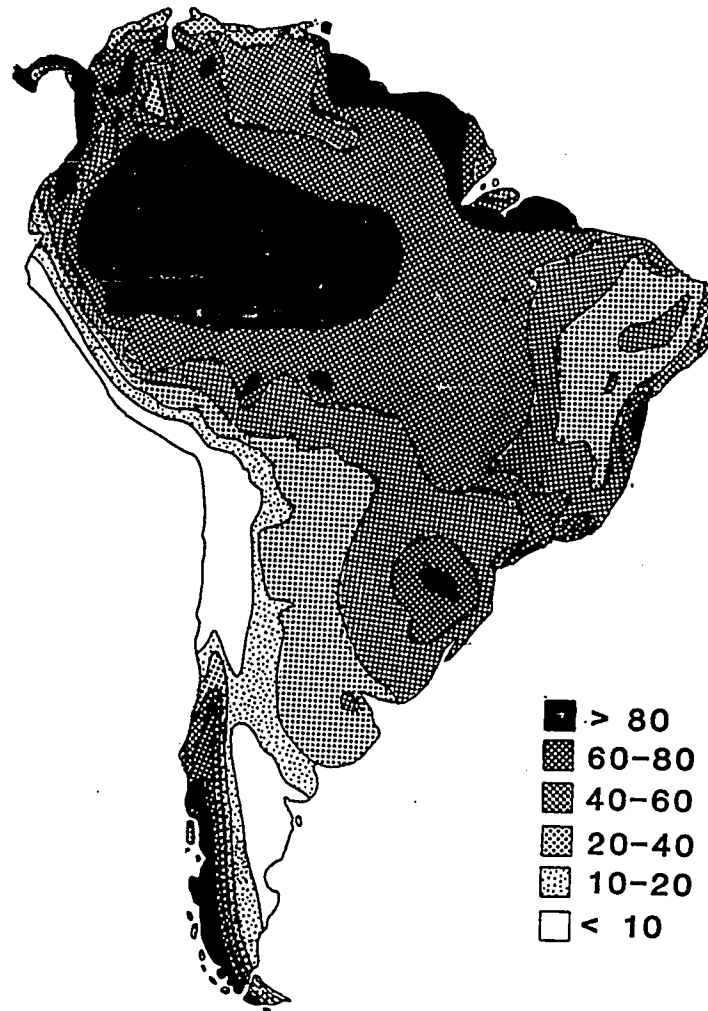


Figure 9. Map of South America showing the annual rainfall (in inches).



ANNUAL RAINFALL
(Inches)

Figure 10. Map of South America showing the major vegetation zones in South America.



-  Tropical Rain Forest
-  Mediterranean Vegetation
-  Tall Grass, Galleria Forest
-  Beech-Cedar Forest
-  Semideciduous Forest
-  Broadleaf Deciduous Galleria Forest
-  Araucaria Forest
-  Xerophytic Open Forest
-  Desert Shrub
-  Tall Grass
-  Low Grass, Desert Shrub
-  Montane Grass, Tola Shrub
-  Little or No Vegetation

MAJOR VEGETATION TYPES

General Description: External: Small; head and body length from approximately 70 to 125 mm; tail length from about 35 to 125 mm. Tail ranges from less than head and body length to equal to or slightly greater than head and body length. Pelage generally long, thick and smooth. Dorsal pelage ranging from bright buffy or pale yellowish-brown to dark brown or gray. Venter ranging from pure white, to white-tipped gray hairs, to medium gray, but never as dark as dorsum. Tail uniform in color to sharply bicolored and pale below. Feet small, generally white-haired above; plantar surface naked, with six small tubercles (see figure 7, p. 35, in Husson, 1960; and also figure 38, p. 146, in Hershkovitz, 1962). Ears small to moderate; length from notch ranging from less than, to equal to or slightly greater than, hind foot length; well haired with a white or light buffy post-auricular patch. Occasionally a pre-auricular buffy tuft is present. Juvenile pelage generally dark gray, very soft hairs. Mammae usually 8 to 10, but can range from 6 to 14.

Cranial (terminology follows Guthrie, 1963; Musser and Williams, 1985; and Wahlert, 1985; see also illustrations therein): Skull delicate to sturdy. Rostrum not narrowed, interorbital region parallel-sided to posteriorly divergent, with smooth edges or sharp beaded ridges. Suture between frontals and parietals rounded or angular, interparietal bone extending more than two-thirds the width of braincase. Zygomatic arches expanded

in adults, occasionally parallel-sided, anterior border of zygomatic plate slightly concave (with a slight notch), zygomatic notch strongly excised. Incisive foramina long, extending to level of middle of the M1, giving a slender impression. Palate long, extending past M3, usually with posterior palatal pits, either small or large, shallow or deep, and variable in number. A pair of posterior palatine foramina (anterior palatal pits of Hershkovitz, 1962) present at maxillary-palatine suture. Width of mesopterygoid fossa always less than width of parapterygoid fossa measured at the same transverse plane. Parapterygoid fossa shallow to slightly excavated, but never deeply excavated, and without perforations. Bullae not greatly enlarged. Length of auditory bullae approximately equal to crown length of maxillary toothrow. Sphenopalatine vacuities large. Alisphenoid strut present or absent (see fig. 11 and table 4), more often absent; sphenofrontal foramen present, squamosoalisphenoid groove present, very obvious in the small species, groove or trough for masticatory-buccinator branch of the maxillary nerve present, occasionally one or more foramina present at junction of squamosoalisphenoid groove and this trough present (see Musser and Williams, 1985). Stapedial foramen and carotid canal present. Foramen ovale generally large and distinct, but occasionally coalesced with post-alar fissure (and middle lacerate foramen). (Above description modified from Hershkovitz, 1962).

Figure 11. Lateral view of the posterior end of the skull showing the absence (A) and presence (B), as indicated by an arrow, of the alisphenoid strut. A, Calomys tener, USNM 484442 and B, C. sorellus, AMNH 231602. Bars represent 1 mm.



(See fig. 1 for bones and foramina, and table 5 for a summary of the frequency of occurrence of the structures associated with carotid circulation).

Dentition: (terminology follows Hershkovitz, 1962 and Reig, 1977): Upper incisors opisthodont to nearly proodont, ungrooved; molar rows usually parallel-sided.

In M1, an anteromedian fold or flexus usually dividing the anterocone into anterolabial and anterolingual conules. Anterolabial conule usually larger. This flexus sometimes absent and anterocone entire (see table 6). Anteromedian style present or not; present in different proportions in different species (see table 7). Anterolabial and anterolingual styles present or not, no anteroloph or anteroconule. First primary fold (paraflexus) present and large. Anterior secondary fold (anteroflexus) and anterior lingual fold (part of the protoflexus) absent. First minor fold (part of the protoflexus) present and large. Major cusps alternating in position, the lingual series anterior. Internal folds absent. A small mesostyle or enterostyle sometimes present, but no connecting lophs. Second primary fold (metaflexus) large. First secondary fold (mesoflexus) absent. Major fold (hypofold) large, without enteroloph in the middle. No posteroloph, posteroconule, or posterostyle. Second minor fold sometimes present as a small inflexion. Teeth ranging from evenly

rectangular to bowed in the middle on the lingual side if the procingulum constricted; generally 4-rooted.

In M2, an anteroloph and a small anteroconule present. Anteroloph about one-half of tooth width. First primary fold present and large, first minor fold present, although more like a fossa. Major cusps alternating, lingual series anterior. A small mesostyle or enterostyle sometimes present, but no paralophule, mesoloph, or enteroloph. Major fold large. Second primary fold large and in unworn teeth, merging with first secondary fold. No internal folds. Second secondary fold present in unworn teeth. Second minor fold a small notch. No posterostyle or posterior conule. Posteroloph present. Teeth generally square to rectangular and having 3 roots, occasionally an accessory rootlet (4-rooted appearance).

In M3, an anteroloph present but no anteroconule. First primary fold present, small, and occasionally closed off as an internal fold. Protocone and paracone readily discernable. Major fold small. Second secondary fold and second minor folds absent. No posteroloph, posteroconule, or metalophule. Mesostyle sometimes present. No enteroloph, enterostyle, or mesoloph. Second internal fold present, sometimes fused with PF2. Teeth usually rounded to ovate and having 3 roots. Length of M3 ranging from 64 to 77 percent of length of M2.

In m1, anteromedian fold or flexid present or absent. Anteromedian stylid rarely present. Conulids more or less equal in size, or if not, the larger one usually labial, but sometimes lingual. Procingulid sometimes narrower than rest of tooth. Major cusps alternately arranged, more so than in M1. Anterolingual and anterolabial stylids more often present than absent. No internal folds, no anterolophid, or anteroconulid. Anterolabial flexid and first minor fold (protoflexid) coalesced. Anterior primary fold (anteroflexid) and first secondary fold (metaflexid) coalesced. No mesolophid or ectolophid. Mesostylid and ectostylid present or absent, ectolophid present more often than mesostylid. Major fold (hypoflexid) large and well-opened. First primary fold (mesoflexid) large, obvious, and curving anteriorly. Second secondary fold (entoflexid) indistinct or absent. No entolophid. Second primary fold (posteroflexid) present and large. Posterostylid not present. Posterolophid present, large, and connected to a small posteroconulid. A notch or small fold present between the hypoconid and posterolophid. Tooth shape usually rectangular, although sometimes narrower at the anterior end. Teeth 3-4 rooted.

In m2, the major cusps alternating. Anteroconulid present, and with wear connecting to the anterolophid. First minor fold present and large. Anterolabial stylid present, anterolingual stylid absent. First secondary fold reduced or absent. First

primary fold large, second secondary fold obsolete. Mesolophid absent. Mesostylid occasionally present. No entolophid. Major fold large and well-opened. Ectolophid absent, ectostylid sometimes present. Second primary fold present. Posteroconulid present and joining with posterolophid. No posterostylid. A notch or small fold between the hypoconid and posteroconulid present or not. Teeth square to rectangular and generally having 3 roots.

In m3, first primary fold often enclosed as an internal fold. Major fold large and often bisecting tooth. Ectolophulid sometimes present. First internal fold sometimes present in unworn teeth. First minor fold small, if present. Large hypoconid present, either fusing with entoconid or entoconid absent. Second primary fold absent, no posterolophid or posteroconulid. Second internal fold small or absent. Second secondary fold small or coalesced with major fold. Mesostylid sometimes present. Mesolophid present. No entolophulid. Shape of tooth ranging from almost rectangular to triangular. Teeth generally three-rooted.

Hooper and Musser (1964) examined the male reproductive structures in C. callosus and "C. laucha" (probably = C. bimaculatus or C. murillus) and said of the genus: "exteriorly plain stubby glans, erect, blunt, smooth bacular mounds, the medial longer but much less robust than the lateral pair; deep

crater rimmed by a narrow band of nonspinous tissue; small slim dorsal papilla, its tip bearing a large recurved spine; long urethral flap, a row of recurved spines on the side of each process and a similar spine at its tip; prominent subapical midventral keel on the bone; and long, erect, cartilaginous digits, the medial one much less robust than the lateral pair" (p. 32).

Voss and Linzey (1981) gave a general description of the male reproductive tract of South American cricetine (= Sigmodontinae) rodents and noted that Calomys (they examined C. callosus and C. laucha) has a single pair of preputial glands which extend cranially beyond the ventral flexure of the penis; that the medial ventral prostates are longer than the lateral, vesiculars are lobed medially and along their greater curvatures, subterminal flexures appear lumpy and irregularly formed.

Massoia and Fornes (1967a) figured the baculum of Calomys "callosus" (probably = C. venustus) (plate 13).

Vertebral number based on examination of specimens of C. callosus, C. laucha, and C. lepidus in the AMNH collection is generally 7 cervical, 13 thoracic, with 13 pairs of ribs, 6-7 lumbar, 3-4 sacral, and 20-26 caudal.

Comparisons: Calomys can be distinguished from all non-phyllotines and from other phyllotines on the basis of the tribal and generic diagnoses. The non-phyllotine genera that are

found sympatrically and are most likely to be confused with Calomys are Akodon, Bolomys, Oryzomys (Oligoryzomys), and Mus.

Akodonts (including Akodon and Bolomys) usually have bigger, thicker, darker-haired feet, smaller ears, and often a very dark venter. Cranially, they have a more rounded supraorbital region in cross-section (this is occasionally ridged), a shallower zygomatic notch, narrower parapterygoid fossa, and the sphenopalatine vacuities are not as well developed, if present at all. Dentally, they have narrower and relatively larger molars.

Oryzomyines, especially Oryzomys (Oligoryzomys), Thomasomys, and Neacomys have larger feet, and very long tails. Oryzomys generally has a more orange dorsal color, Neacomys has spiny fur. Cranially, Calomys has longer incisive foramina, larger sphenopaltine vacuities, and a narrower mesopterygoid fossa. See figures 5, 6, and 7 for tribal differences.

Mus musculus, an introduced murine, has a grayer dorsum, darker venter, longer tail, and grayer feet. Dentally, Mus show three longitudinal rows of cusps, unlike any sigmodontine rodent.

Among the phyllotines, those that are most likely to be confused with Calomys are Eligmodontia, Andalgalomys, Graomys, and Phyllotis (all of which are sympatric with Calomys). These all have tails that are much longer than the length of the head and body, with a terminal brush, unlike that of Calomys. Eligmodontia has a hairy pad on the plantar surface of the hind feet and

softer, silkier fur. Auliscomys and Galenomys (also sympatric with Calomys) resemble C. lepidus; they have short tails (except A. boliviensis) and very short fur that is marbled in appearance, but both are larger than C. lepidus. Galenomys has hairy soles on the hindfeet.

The skulls of Andalgalomys and Graomys resemble those of C. callosus, C. venustus, and C. tener, in having posteriorly divergent, ridged supraorbital regions (fig. 12). Andalgalomys and Graomys are generally larger than Calomys, and have greatly inflated auditory bullae, deeper zygomatic notches, and a relatively narrower mesopterygoid fossa (fig. 12). Graomys tends to have an alisphenoid strut. Andalgalomys has a more slender rostrum than Calomys, lacks an alisphenoid strut, and tends to have slit-like foramina in the palatine bones. Skulls of Phyllotis, Auliscomys, and Galenomys generally have a strongly constricted interorbital region and greatly flared zygomatic arches, as well as larger size (except for two species of Phyllotis from Peru, P. andinus, P. amicus, and P. (Paralomys) gerbillus). Eligmodontia has a narrower rostrum, wider zygomatic notches, slightly more inflated braincase, and in some cases, more inflated bullae than Calomys (see fig. 13). For comparative measurements, see tables 2 and 3.

Dentally, Calomys most resembles Eligmodontia and Andalgalomys. Eligmodontia has slightly more hypsodont teeth and

Figure 12. Dorsal (upper row) and ventral (lower row) views of skulls of A) Graomys domorum, AMNH 260753; B) Andalgalomys pearsoni, AMNH 262346; and C) Calomys venustus, USNM 290914. Note the ridged and posteriorly divergent supraorbital region. Bar represents 10 mm.

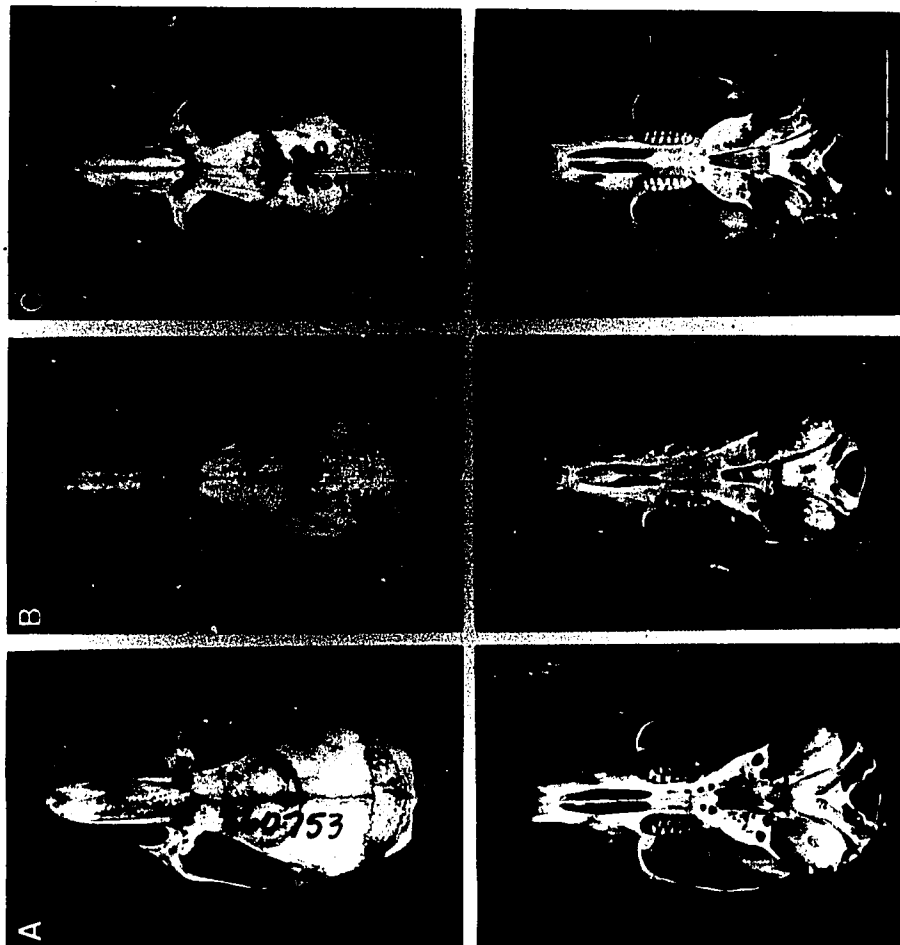


Figure 13. Dorsal (upper row) and ventral (lower row) views of skulls of A) Graomys domorum, AMNH 260753; B) Andalgalomys pearsoni, AMNH 262346; C) Phyllotis osilae, AMNH 247880; D) Eligmodontia typus, AMNH 246776; and E) Calomys musculus, MSB 55272. Bar represents 10 mm.

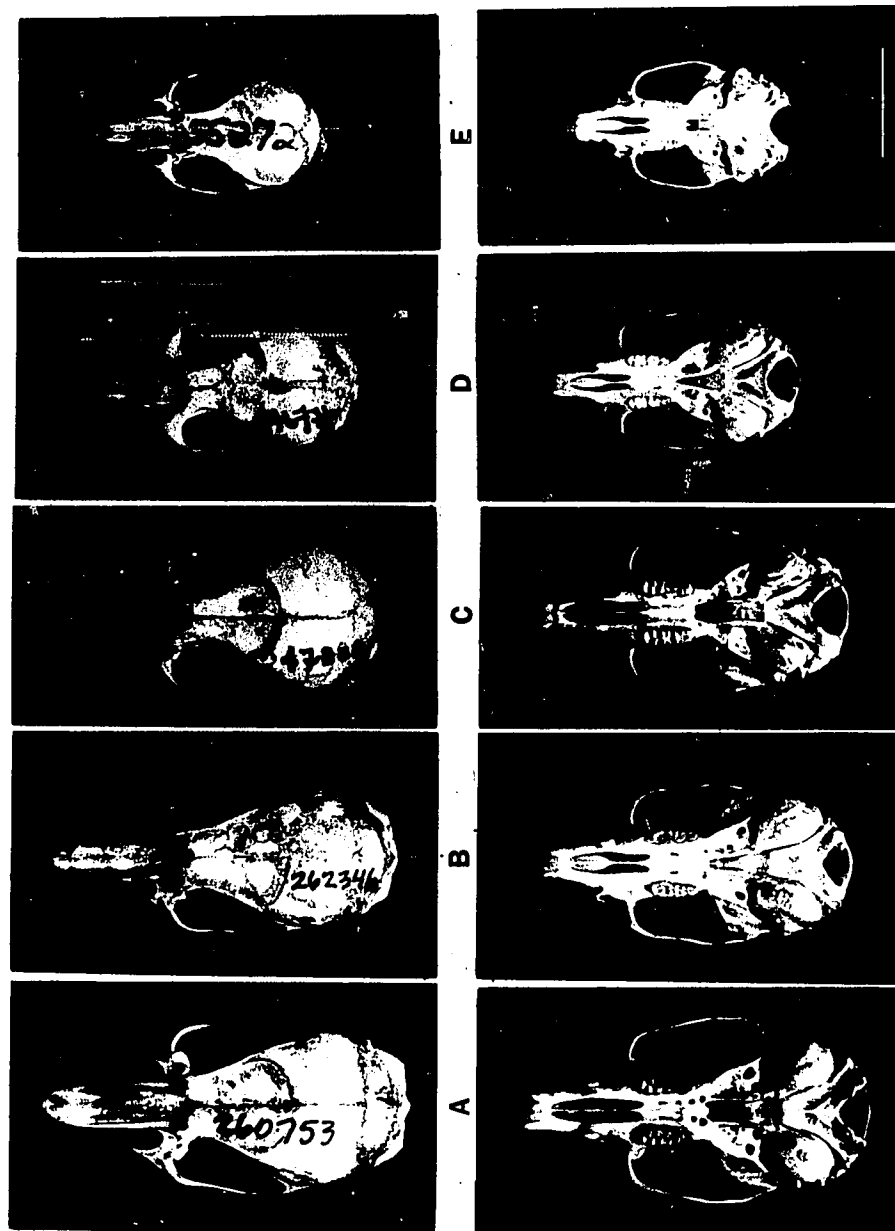


Figure 14. Comparison of the upper (above) and lower (below) molar tooth rows of selected general of Phyllotini. A) Calomys venustus, AMNH 41870; B) Eligmodontia typus, AMNH 25702; C) Andalgalomys olrogi, CM 44020; D) Andalgalomys pearsoni, AMNH 260762; E) Graomys domorum, AMNH 260754; and F) Graomys griseoflavus, AMNH 246848. Bars represent 1 mm.

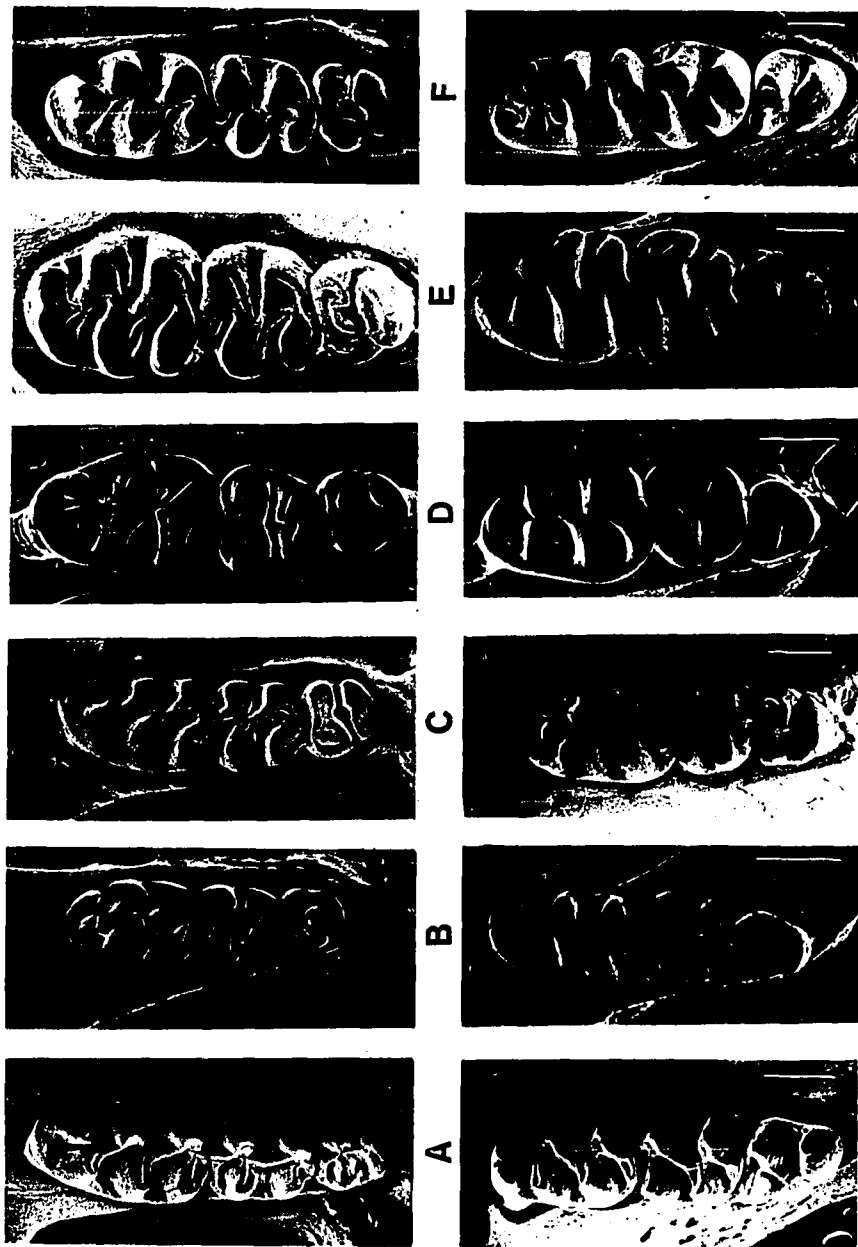


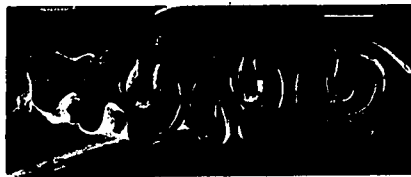
Figure 15 (14 cont'd). G) Phyllotis osilae, AMNH 247880; H) Auliscomys pictus, AMNH 231258; I) Chinchillula sahamae, AMNH 247886; J) Irenomys tarsalis, AMNH 256782; K) Andinomys edax, AMNH 249023; and L) Neotomys ebriosus, AMNH 231637. Bars represent 1 mm.



L



K



J



I



H



G



a less pronounced antero-median flexus. Molars of Andalgalomys have a tendency toward lamination, an anteriorly directed anteroloph on M2 (anterolabially directed in Calomys), and a notch on the postcingulid of m1. Graomys, Phyllotis, Auliscomys, and Galenomys all have much more hypsodont teeth, an entire anterocone (no anteromedian flexus or style), and a proportionally larger M3 (table 1). Thomas (1917) noted that the essential difference between Phyllotis and Hesperomys (= Calomys) is the greater hypsodonty of the molars of Phyllotis. For comparison of phyllotine dentition, see figures 14 and 15. For further comparisons, see Hershkovitz (1962), Williams and Mares (1981), Olds et al. (1987), and Olds and Anderson (in press, a).

Williams and Mares (1978) reported that the glans penis of Andalgalomys resembles that of Calomys callosus, except that in A. olrogi there is a dorsally-canted hood.

Baiomys has been confused with Calomys, for example, C. hummelincki was originally named as a Baiomys. The species of Baiomys are approximately the same body and cranial size as C. laucha, C. bimaculatus, and C. hummelincki. The cranial differences include a shallower zygomatic notch and a constriction at the anterior end of the parapterygoid fossa. The M3 is greatly reduced in Baiomys, less so in Calomys. See figures 16 and 17 for comparisons.

Table 1

Table of the lengths of M1, M2, and M3, and the ratio of the length of M3 to M2 for the species of Calomys and representative phyllotines.

Species	n	LM1	LM2	LM3	LM3/LM2
<u>C. bimaculatus</u>	6	1.59	1.00	0.64	.64
<u>C. callosus</u>	514	1.89	1.18	0.89	.75
<u>C. hummelincki</u>	8	1.59	0.96	0.67	.70
<u>C. laucha</u>	33	1.57	0.91	0.61	.67
<u>C. lepidus</u>	64	1.73	1.04	0.70	.67
<u>C. murillus</u>	61	1.72	1.03	0.74	.72
<u>C. musculus</u>	29	1.82	1.06	0.78	.74
<u>C. sorellus</u>	148	1.77	1.10	0.77	.70
<u>C. tener</u>	74	1.67	1.04	0.69	.66
<u>C. venustus</u>	220	2.07	1.29	0.99	.77
<u>E. typus</u>	5	1.69	1.09	0.73	.67
<u>A. olrogi</u>	6	2.13	1.18	0.95	.81
<u>A. pearsoni</u>	13	2.21	1.19	1.02	.86
<u>G. griseoflavus</u>	18	2.43	1.47	1.17	.80
<u>G. domorum</u>	17	2.40	1.50	1.14	.76
<u>P. osilae</u>	9	2.44	1.41	1.22	.87
<u>P. wolffsohni</u>	11	2.28	1.39	1.24	.89

Figure 16. Dorsal (upper row) and ventral (lower row) views of skulls of Baiomys musculus (A, C, AMNH 254782), and Calomys laucha (B, D, UMMZ 133929). Bar represents 10 mm.

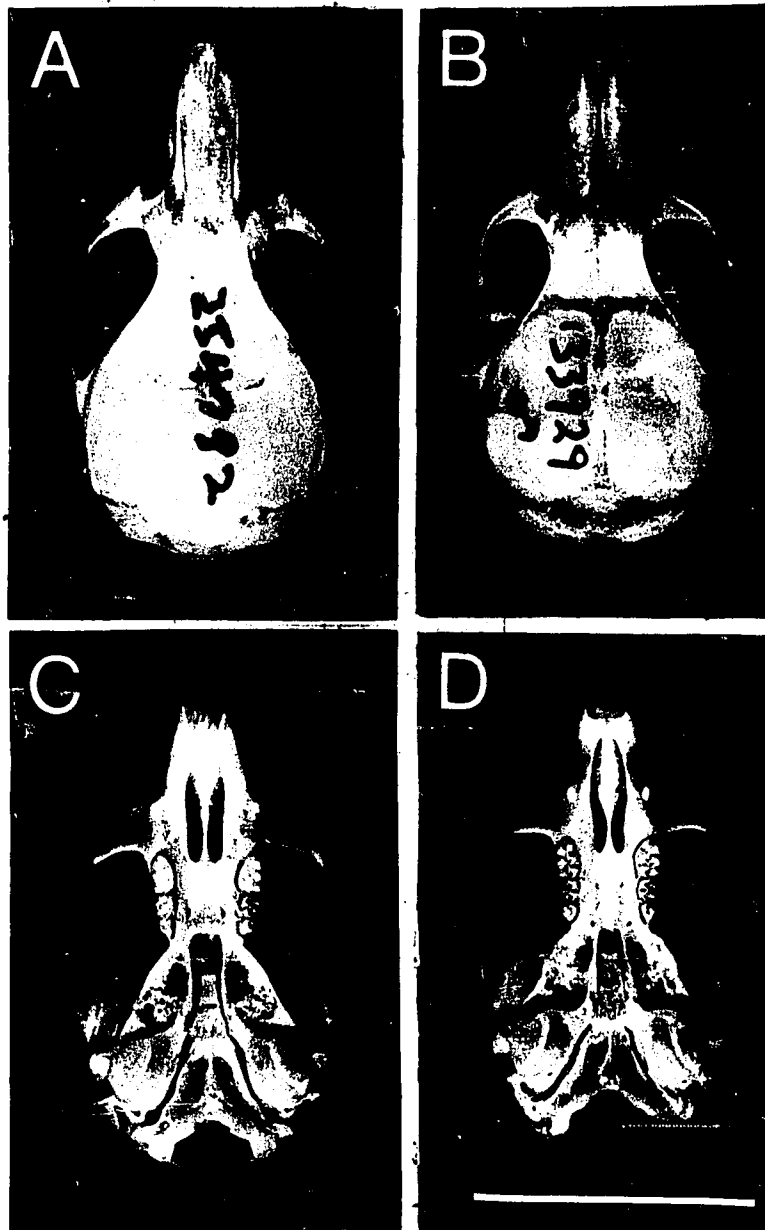


Figure 17. Comparison of the upper (A, B) and lower (C, D) molar tooththrows of Baiomys taylori (AMNH 177275) and Calomys laucha (AMNH 246867). Bar represents 1 mm.



Karyology: Karyotypes have been published for several of the species of Calomys. These are summarized in the species accounts. See also the discussion under relationships within Calomys.

Taxonomic History: The taxonomic history of this group is complicated (see Tate, 1932; Hershkovitz, 1962).

Early descriptions rarely included many useful characters and every new series of specimens was likely to be described as a different species.

Waterhouse (1837) used the name Calomys as a subgenus of Mus. He described several new species of murid rodents collected by Charles Darwin. All of the species described were placed in the genus Mus. Waterhouse wrote "Though in the foregoing description I have retained the generic title Mus, I . . . state that the above species naturally divide themselves into several subordinate groups, the characters of which are sufficiently evident, not only between themselves, but also between each group and that to which the term Mus ought . . . to be restricted, and of which our common mouse (Mus musculus) may be regarded as the type. To these groups I shall here assign subgeneric titles, and . . . point out their chief distinguishing characters. . ." (p. 20). He wrote of the subgenus Calomys "Fur moderate, soft. Tarsus almost entirely clothed beneath with hair. Front molar with three indentations of enamel on the inner side and two on the outer; second molar with

two on the inner and two on the outer; and the last molar with one on each side" (p. 21). He included as the type species, Mus (Calomys) bimaculatus, and two other species, Mus (Calomys) elegans, and Mus (Calomys) gracilipes, all of which were described therein. The measurements given for M. elegans include a tail length that is longer than the head and body, which suggests that it is not Calomys, but Eligmodontia (see below). The name Calomys, is from the Greek for "beautiful mouse".

In 1839, Waterhouse further described and illustrated the three species mentioned above, Mus elegans, M. bimaculatus, and M. gracilipes. Of M. elegans, he wrote "There appears to be but one large tubercle in the underside of the tarsus and this, which is situated near the base of the toes, is thickly covered with silvery-white hairs" (p. 41). This single large hairy pad is a character of Eligmodontia. He noted the similarities between the three species and did not want to separate Mus elegans from the other two at the generic level solely on the basis of the plantar pads.

Waterhouse then compared Old World murids, Mus musculus and Rattus rattus mostly with Mus bimaculatus, and on the basis of dental differences, the row of three versus two cusps, he proposed the genus Hesperomys to include all South American murids and those North American species that "agree with them in dentition" (p. 75). The species he specifically named as belonging in

Hesperomys are : Mus (=Calomys) bimaculatus, Mus (=Peromyscus) leucopus, Symidon hispidum (=Sigmodon hispidus), the species of Neotoma, and Mus (=Oryzomys) Galapagoensis, Mus (=Graomys) griseoflavus, Mus (=Phyllotis) xanthopygus, and Mus (=Phyllotis) Darwinii. Currently used names are from Hall and Kelson, 1959, and Cabrera, 1961).

Thomas (1882), in a report on specimens of Hesperomys collected in northern Peru, placed four species in the subgenus Calomys, H. laticeps, H. albigularis, H. longicaudatus and a new species, H. spinosus. Current taxonomy places the first three species in the genus Oryzomys, and the fourth in Neacomys (Cabrera, 1961).

Then in 1884, Thomas reviewed the genus Hesperomys and its subgenera. He wrote "In the subgeneric names used in 1882 I simply accepted the groups as defined by Baird, and used by other authors up to the present time; but on a closer investigation I find that the subgenera proposed by Waterhouse in 1837 should stand to a much greater extent than was allowed by Baird, who merely went upon Waterhouse's descriptions, without seeing any specimens of such subgenera as Phyllotis, Calomys, or Scapteromys, each of which is fully entitled to the same rank as the other groups" (1884, p. 448).

Of the subgenus Calomys, Thomas wrote "Form cricetine; tail short, hairy; fur very long and soft; feet small and slender, soles thickly hairy; mammae 2-2=8.

"Skull slightly made; interparietal very narrow from before backwards; interorbital edges square; palatine foramina long.

"Teeth as in the smaller Oryzomys" (p. 449).

He included Hesperomys bimaculatus, H. elegans, and H. gracilipes, and gave the range of the group as from "Peru across the continent southwards to Buenos Ayres (sic) and Bahia Blanca" (p. 449). Hesperomys laticeps, H. spinosus, H. longicaudatus, and H. albigularis were placed in the subgenus Oryzomys at this time.

He described Hesperomys (Calomys) bimaculatus, Waterh., var. lepidus, var. n., from the type locality of Junin, and said these specimens belong "to the rare and little known subgenus Calomys (s. s.), of whose subgeneric validity there can be no question, although, judged by the skull only, it might be joined with the great mass of Hesperomyes to which I apply the name Oryzomys. However, its members are so different externally from any of the other Vesper-mice . . ., that it is certainly worthy of the rank originally given it by Waterhouse. The only species belonging to it are H. bimaculatus, gracilipes, and elegans, to which some authors would perhaps think H. lepidus should be added as a distinct species; but without seeing more specimens of the true H.

bimaculatus, I do not care to describe the present form as more than a geographical variety of that animal" (1884, p. 455).

In 1916, Thomas reviewed the status of several genera of the phyllotines without referring to them as a group. He included H. elegans in Eligmodontia as a synonym of E. typus. He used the generic name Hesperomys, Waterhouse 1839, and said it was a synonym of Calomys, Waterhouse 1837, nec Callomys d'Orbigny and Geoffroy, 1830.

Thomas (1916a) wrote of Hesperomys (= Calomys) "size small or medium. Form delicate. Ears short. Tail short, rarely attaining the length of the head and body. Feet normal, slender, the pads 5-6, not covered by hair; surface of palms and soles generally naked, but occasionally hairy. Mammae variable, ranging from 2-2=8 or 3-2=10 to a continuous series attaining a total of 14, different numbers often occurring in the same species.

"Skull delicate, lightly built, the supraorbital edges square in old specimens, divergent and slightly ridged in the larger species; zygomatic plate not cut back anteriorly.

"Molars small, brachyodont" (1916a, p. 141).

He gave as the type species, H. bimaculatus (Mus bimaculatus, Waterhouse).

Other species he included (with original names in parentheses) were:

Hesperomys callosus, Rengger (Mus callosus)

- " " boliviae, Thomas (Eligmodontia c. boliviae)
- " carilla, Thomas (Eligmodontia carilla)
- " ducilla, Thomas (E. ducilla)
- " expulsus, Lund (Mus expulsus)
- " gracilipes, Waterhouse (Mus gracilipes)
- " laucha, Desmarest (Mus laucha)
- " " musculus, Thomas (Eligmodontia l.
musculina)
- " lepidus, Thomas (Hesperomys bimaculatus lepidus)
- " sorella, Thomas (Eligmodontia sorella)
- " tener, Winge.
- " venustus, Thomas (Oryzomys (?) venustus).

He also commented that the supraorbital edges of Graomys are ridged and divergent as in the larger species of Hesperomys and that the bullae of Phyllotis are larger than those of Hesperomys.

Gyldenstolpe (1932) treated the genus Hesperomys essentially as had Thomas (1916a). Gyldenstolpe included the following species and subspecies: H. bimaculatus, H. callosus callosus, H. callosus boliviae, H. laucha laucha, H. laucha musculus, H. laucha cortensis, H. gracilipes, H. lepidus, H. sorella, H. ducilla, H. carillus carillus, H. carillus marcarum, H. carillus argurus, H. murillus murillus, H. murillus cordovensis, H.

expulsus, H. tener, H. venustus venustus, H. venustus callidus, H. fecundus, H. muriculus, H. frida frida, and H. frida miurus. He gave brief descriptions, the type locality, and the original publication for each of the above.

Tate (1932) gave a chronological history of the genus Hesperomys. He included sixteen species, similar to those of Glydenstolpe (1932) except he referred to H. laucha, H. musculinus musculinus, H. musculinus cortensis, and H. lepidus lepidus. Tate provided the type localities as well.

Simpson (1945) included Paralomys in Hesperomys (Paralomys was included in Phyllotis by Hershkovitz, 1962).

Osgood (1947) recognized the "important" species of Hesperomys as "expulsus, tener, bimaculatus, laucha, muriculus, venustus, lepida, sorella, and frida". He said that "the essential character of Hesperomys which uniformly distinguishes it from Phyllotis and all other members of the group is found in its low-crowned teeth . . . almost tuberculate rather than flat-surfaced and prismatic. It may be concluded, therefore, that this is the most primitive of the living forms". He gave the generic range as from southeastern Brazil and Uruguay to northern Argentina, through southern Paraguay to Bolivia and, in diminished numbers, via Peru to southern Ecuador (one species only; at present there are no records for Calomys from Ecuador). Osgood described the group as being "rather small, some quite tiny, and

although most are short-tailed, a few have fairly long tails". He mentioned the widened frontals with ridged supraorbital edges in the larger species, and noted the resemblance between these and Graomys (p. 168).

Hershkovitz (1962) summarized the history of the use of the name Hesperomys and noted that the name, by virtue of its designated genotype, is an absolute synonym of Calomys Waterhouse.

Reig (1986) included nine species in the genus based on morphology and karyology. The names used here are given in parentheses, where different: C. callosus, C. boliviae (= C. callosus), C. sorellus, C. lepidus, C. musculus, C. murillus, C. laucha (= C. bimaculatus and C. laucha), C. tener and C. hummelincki (= C. hummelincki). He mentioned that C. bimaculatus may be a valid species.

Fossil History: Fossils belonging to Bensonomys have been included as a subgenus of Calomys (Baskin, 1978). Hershkovitz (1962) included Necromys, a fossil genus described by Ameghino (1889). Here, both are excluded from the genus Calomys, see below for discussion. Ameghino (1889) gave records and descriptions for Argentine fossils of Hesperomys, including some that were given names of living species. Critical examination of these specimens is needed before assigning them to species of Calomys.

Pleistocene fossils of C. hummelincki have been documented from the island of Tobago (Eschelman and Morgan, 1985). Pleistocene fossils identified as Calomys cf. laucha have been reported from the Tarija Basin (Hoffsteter, 1986). See discussion below.

Remarks: In a study of enzymes, Gardenal et al. (1977a) found no useful taxonomic characters among three species, but Blanco and Gardenal (1977) did, in species from Cordoba (C. laucha, C. musculus, and C. callosus (presumably = C. bimaculatus, C. murillus, and C. venustus). Bellocq and Kravetz (1983) found they could distinguish Calomys, Akodon, and Oryzomys (Oligoryzomys) using innominate bone characters. The anterior end of the bone is strongly flared in Oryzomys flavescens; Akodon has a relatively greater ratio of length of ilium to ischium. The two species of Calomys they examined were not separable. Scale structure of hair was studied in seven species of Sigmodontinae from Buenos Aires province, Argentina, including two species of Calomys (presumably, C. bimaculatus and C. murillus) by Piantanida and Petriella (1976). They concluded that because of the similarities in scale structure between all of the species examined, these characters were not useful taxonomically.

Roldan et al. (1985) studied cross fertilization among three species of Calomys. In some cases, fertilization occurred, but development never proceeded beyond 56 hours. They suggested that

fertilization is not strictly species-specific, but that there are factors reducing the efficiency of interspecific fertilization.

There is a problem with their use of the name C. callidus

(possibly = C. callosus, $2n=48$) for specimens from from El Palmar, Entre Rios, Argentina. Their other two species presumably were C. murillus and C. bimaculatus.

Species Accounts:

In the species accounts following the key to species, synonymies include only those names associated with type specimens. Hershkovitz (1962) provided an exhaustive list of published references to the species of Calomys in his synonomies. The literature abounds with misidentifications of the species of Calomys. For this reason, I have included museum catalog numbers with the locality records in the list of specimens examined (see the Appendix). For practical reasons, I have placed all species and specimens examined together in the Appendix.

Some species of Calomys are better studied than others; this is apparent when reading through the accounts, and was a contributing factor to the number of species I recognize here. Names are available for all ten species I recognize. It is possible that with future studies and more specimens from intermediate areas, some of these ten species will be found to intergrade, and their differences to be attributed to geographic variation. It is also possible that genetic studies will reveal more than the ten species I recognize. In the meantime, they are recognizable units, names are presently available, and it is convenient to summarize their distinctness as separate taxonomic units. I hope to encourage further work on all aspects of the biology of this group, including areas of possible sympatry or

integrgradation. It should be noted, however, that some of the species that I recognize here may never be found sympatrically, in part due to habitat destruction and lack of earlier collections.

KEY TO THE SPECIES OF Calomys

1a. Tail length always less than head and body length, but not greatly reduced; edges of supraorbital region of skull divergent posteriorly and with distinct ledges in adults, ... 2a

1b. Tail length variable; edges of supraorbital region of skull divergent posteriorly to parallel-sided, but never beaded or ledged in adults..... 4a

2a. Total length (including tail) of adults generally greater than 210 mm; length of maxillary toothrow generally greater than 4.10 mm (occasionally 4.00-4.10 mm); occurring at low to middle elevations (up to 2000 m) C. venustus

2b. Total length less than 210 mm; length of maxillary toothrow generally less than 4.00 mm; occurs at low elevation 3a

3a. Length of maxillary toothrow generally 3.70 to 4.00 mm; greatest length of skull of adults generally greater than 24.00 mm; total length generally greater than 170 mm and less than 210 mm; venter light to dark grey, no reddish tint above or below; alisphenoid strut not generally present, 2n=50 C. callosus

3b. Length of maxillary toothrow generally 3.20 to 3.60 mm;
greatest length of skull generally less than 24.00 mm; total
length generally less than above; venter often dark and body
frequently with a reddish or chestnut color, alisphenoid strut
usually present, 2n=66 C. tener

4a. Tail much shorter than head and body (generally less than 45
mm) and white, not bicolored; long, soft pelage with a marbled
appearance; rostrum relatively slender for genus; occurs at high
elevations (greater than 3000 m) C. lepidus

4b. Tail usually longer than 50 mm, bicolored; pelage long or
short but never marbled; nasals not noticeably slender; low to
high elevation 5a

5a. Tail generally 45-60 mm; pelage short, venter white or gray,
dorsum pale to buffy with gray; skull delicate, greatest length of
skull generally less than 22.00 mm; length of maxillary toothrow
generally less than 3.20 mm 6a

5b. Tail generally greater than 65 mm, approximately equal to or
longer than head and body length; pelage long or short, venter
light gray with white-tipped hairs; skull small, but not delicate,
greatest length of skull in adults generally greater than 21.00,

occasionally less; length of maxillary toothrow generally greater than 3.20 mm 8a

6a. Venter white, tail white, bright white post-auricular patches, dorsum pale yellow-brown to ochraceous 7a

6b. Venter pale or medium gray with white-tipped hairs, dorsum darker grey, post-auricular patches white or buffy; occurs in Uruguay, Argentina, and Brazil C. bimaculatus

7a. Dorsum yellow-brown, pale, not bright orange; occurs in the chaco of Bolivia, Paraguay, and northern Argentina C. laucha

7b. Dorsum bright buffy orange; occurs in the Netherlands Antilles, Venezuela, and Colombia C. hummelincki

8a. Edges of the supraorbital area parallel; pelage long, dark grey above, hairs of venter with grey bases and white tips; tail length slightly less than the head and body length; occurs at high elevation in Peru (greater than 3000 m) C. sorellus

8b. Edges of the supraorbital area slightly divergent; pelage yellow-brown with black lines, venter light in color; tail length

approximately equal to or greater than head and body length; low
to middle elevations 9a

9a. Bullae slightly enlarged; greatest length of skull in adults
generally greater than 22.00 mm; length of maxillary toothrow
generally greater than 3.40 mm; occurs at middle elevations in
Bolivia and Argentina C. musculus

9b. Bullae not enlarged; greatest length of skull in adults
generally less than 23.00 mm; length of maxillary toothrow less
than 3.50 mm; occurs at low to moderate elevations in Argentina,
(possibly Uruguay and eastern Paraguay) C. murillus

Calomys bimaculatus (Waterhouse, 1837)

Mus bimaculatus Waterhouse, 1837, p. 18, type locality: Maldonado, Uruguay. Type specimen: BMNH 55.12.24.172.

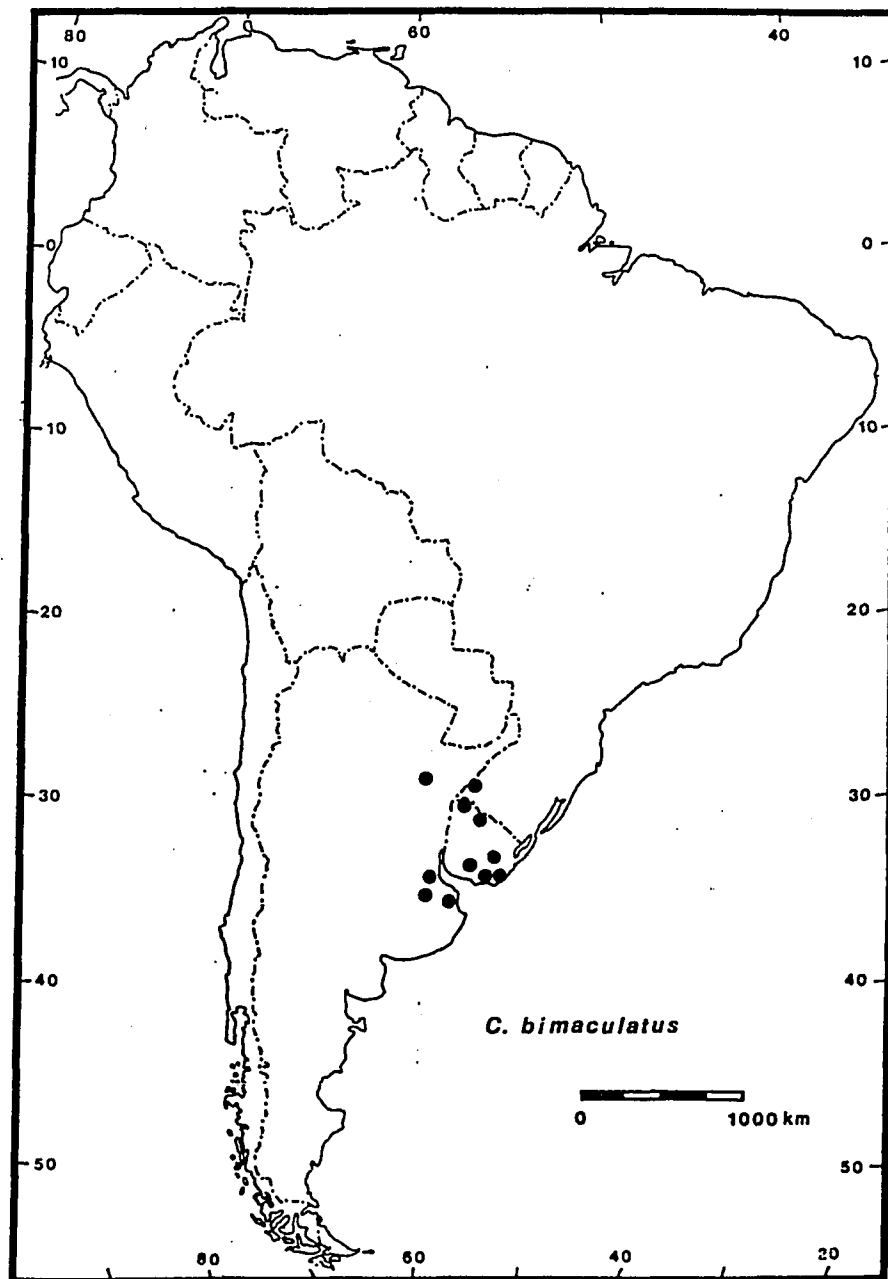
Mus gracilipes Waterhouse, 1837, p. 19, type locality: Bahia Blanca, Buenos Aires, Argentina. Type specimen: BMNH 0.8.5.2.

Hesperomys bimaculatus bonariensis Osgood, 1933, p. 14, type locality: Torrecita, Buenos Aires, Argentina. Type specimen: FMNH 23406.

Diagnosis: Calomys bimaculatus can be distinguished from all other species of Calomys on the basis of the following characters: body size small, total length less than 150 mm; tail short, generally less than 60 mm; dorsum with a dark gray to black dorsal stripe, venter pale to medium gray; skull delicate, post-auricular patches bright white; greatest length of skull of adults generally less than 21.0 mm; molar teeth delicate, maxillary tooththrow generally less than 3.3 mm.

Distribution: Lowlands of Argentina, Uruguay, and southern Brazil (see fig. 18).

Figure 18. Map of the known localities of Calomys bimaculatus.



Description and Comparisons: Calomys bimaculatus is among the smallest species in the genus. The tail is shorter than the head and body. The dorsum is gray, sides are mixed with brown. The venter is sharply demarcated from sides. Conspicuous white post-auricular patches are present. Hairs on the chin and throat are white to base, ventral hairs are white with grey bases, frequently appearing gray. The tail is shorter than the head and body, and is bicolored, dark above and pale beneath. The ears have black hairs on the back and are buffy inside; orange tufts that anterior to the ears. There are usually 5 pairs of mammae, 2 inguinal and 3 pectoral (the formula is 3-2=10). Thomas (1898a) reported 10-14 mammae in specimens from Chubut.

The skull is delicate. The sides of the supraorbital region are divergent posteriorly, but never ridged. An alisphenoid strut is absent (see table 4). A foramen is present at the junction of the squamosal groove and the groove for the masticatory-buccinator branch of the maxillary nerve (table 5). Table 5 contrasts the relative frequencies of structures associated with the carotid circulation.

Dentition is as described for genus; an anteromedian style is mostly present and the anteromedian flexus is well-developed (see tables 6 and 7 for relative frequency of dental structures). External and cranial measurements are given in table 2.

Calomys bimaculatus is readily distinguished from C. venustus, C. callosus, and C. tener by its small size and lack of either ridges or beading of the supraorbitals. It is distinguished from C. sorellus by smaller size, and posteriorly divergent supraorbitals, not parallel-sided as in C. sorellus. C. musculus and C. murillus are larger and have long tails; the tail of C. bimaculatus is never as long as the head and body length. This species is approximately the same size as C. laucha and C. hummelincki. It can be distinguished from both on coloration; both C. laucha and C. hummelincki have pure white venters, that of C. bimaculatus is more gray in appearance. Calomys bimaculatus has a darker dorsum than C. laucha and C. hummelincki, and has a broad dark dorsal band from the head to rump, formed by a concentration of blackish hairs. Calomys laucha is pale and sandy dorsally, and C. hummelincki has an orange dorsum. Calomys laucha is found in the Chaco of Paraguay, Bolivia, and Brazil, northwest of the range of C. bimaculatus, C. hummelincki is found in northern South America. See figures 32-35 for cranial and dental comparisons of the species of Calomys.

Compared to C. murillus, with which it is widely sympatric in Argentina (Massoia and Fornes, 1967b), C. bimaculatus has a shorter tail, the forward angle of the zygomatic plate passes behind incisors, the baculum is more expanded at tip and not evenly curved at base (Massoia et al., 1968).

Karyology: Brum (1962) (cited in Jotterand-Bellomo, 1984) reported a karyotype from a specimen (under the name C. laucha) from the department of Artigas in Uruguay as $2n = 56$ (FN = 60).

Gardenal et al. (1977b) published karyotypes (as C. laucha) from the Laguna Larga, Cosquin, and from a colony from Laboulaye (3405/6325), Province of Cordoba, Argentina. $2n=64$. They divided the chromosomes into 4 groups:

1. 1 pair large submetacentric, 1 pair large submetacentric with subterminal centromere, and 1 submetacentric chromosome.
2. 5 pairs large acrocentric, 19 pairs medium acrocentric.
3. 1 pair small metacentric, 1 pair small submetacentric.
4. 3 pairs plus 1 chromosome small acrocentric.

In summary, there are 2 large metacentric pairs, 2 pairs small metacentric, 5 pairs large acrocentric, 19 pairs medium acrocentric, and 3 pairs small acrocentric, plus the X and the Y. The number of autosomal arms is 70.

Massoia et al. (1968) (under the name C. laucha laucha) published a karyotype from individuals from the province of Buenos Aires, Argentina, as $2n = 62$ (fundamental number = 74), 6 pairs metacentric and submetacentric, and 24 pairs apparently acrocentric, and the X and Y.

Panzetta (1968) (cited in Gardenal et al., 1977b) cited a diploid number of 64 for individuals from Laguna Larga (also under the name C. laucha).

Taxonomic History: Waterhouse named and briefly characterized Mus bimaculatus and Mus gracilipes in 1837, and in 1839, published detailed descriptions. He compared M. bimaculatus to Mus musculus and commented on the similarities between Mus bimaculatus, Mus elegans (= Eligmodontia sp.), and Mus gracilipes (conspecific with bimaculatus). Mus gracilipes was treated the same way. The only differences between Mus bimaculatus and Mus gracilipes were grey based hairs on the venter of M. gracilipes, not on M. bimaculatus, and a little more hair on the feet of M. gracilipes. There are some inconsistencies in the account. Waterhouse wrote that the tail is about equal to the head and body length in M. bimaculatus, but, he gave as measurement for the head and body length, 3 inches 1 line (there are 12 lines per inch), and for the tail, 1 inch and 11 lines. This makes the tail about two-thirds as long as the head and body. M. gracilipes has similar, but slightly smaller measurements, 2 inches 10 lines for the head and body, and 1 inch and 7 lines for the tail. The tail is still much smaller than the head and body length. He noted that M. gracilipes has a more convex zygomatic arch, which projects more suddenly on the anterior part, and a smaller interparietal bone. The convexity of the zygomatic arch could be due to age, and whether by smaller he means a shorter or a narrower interparietal bone, is uncertain.

On the basis of page priority, Mus bimaculatus has priority over M. gracilipes in the publication.

Calomys bimaculatus was named for the two white patches behind the ears.

Osgood (1933) described Hesperomys bimaculatus bonariensis from Torrecita, Province of Buenos Aires, Argentina. He said that it is "Similar to typical bimaculatus, but decidedly smaller and somewhat darker-colored" (p. 14). The measurements given by Osgood fit well with typical M. bimaculatus; its short tail, greatest length of skull of 20.5 mm, and others.

Osgood commented on specimens collected from Uruguay by Sanborn. He noted their small size, short tails, and conspicuous post-auricular patches, but commented that they "do not wholly agree with Waterhouse's description and figure. They are darker in color than his figure and the hairs are not wholly white to the roots over the entire under parts, but only on the chin and throat. The extent of such white areas is often variable in other species and this discrepancy, therefore, may have no great significance" (Osgood, 1933, p. 14).

Calomys bimaculatus was synonymized with C. laucha by HersHKovitz (1962).

Remarks: Calomys bimaculatus is sympatric with C. murillus and C. venustus in Argentina (Massoia and Fornes, 1964, 1965; Thomas, 1898a, b; de la Barrera, 1936).

The name Calomys laucha has been used frequently in reference to this species (de la Barrera, 1936; Dalby, 1975; Reig, 1965; Barlow, 1969; de Fonollat, 1984; Vallejo and Gudynas, 1980; Crespo et al., 1970; Kravetz et al., 1975; Villafañe et al., 1977; Kravetz and Villafañe, 1981; Kravetz et al., 1981a, 1981b; and Corti et al., 1987). Specimens have not been retained or examined from all of these studies, so final identification is not certain, but is postulated on a geographical basis.

This species occurs in the pampa of Buenos Aires province, Argentina (Dalby, 1975), grasslands of the coastal belt of Buenos Aires province (Reig, 1965), arid and semiarid shrubby fields, margins of cultivated fields and in houses in Tucuman province, Argentina (de Fonollat, 1984), in both major "biotypes" of Uruguay, mixed herbaceous vegetation in rolling topography and the coastal sand dunes (Vallejo and Gudynas, 1980). It also occurs in wheat and corn fields in Buenos Aires Province (Massoia and Fornes, 1967b; Kravetz et al., 1975; Villafañe et al., 1977; Kravetz and Villafañe, 1981). The population in the fields is higher in the center of the field and lower at the edges (Kravetz and Villafañe, 1981).

Barlow (1969) said that in Uruguay the preferred habitat is "open grassland, rocky hillsides and edge situations but is also taken occasionally in the vicinity of marshes and swamps" (p. 34).

Waterhouse (1839) included Darwin's original notes on C. bimaculatus from Maldonado, Uruguay, "This mouse, when alive, had a very elegant appearance. A countryman, who brought it me, found six of them living together in one burrow" (p. 44) and on M. gracilipes (= C. bimaculatus), "This specimen was given me by Mr. Bynoe, the surgeon of the Beagle, who caught it amongst some long dry grass" (p. 46).

Thomas (1898b) wrote "[in La Plata city] it inhabits the Museum park and the fields round the town and a specimen or two may generally be kicked out from under any heap of weeds of [sic] faggots left lying about the houses. Adult specimens are however by no means easy to obtain, and the great majority of those I saw and trapped were little more than half grown" (p. 3). Thomas (1910) wrote "A specimen from eastern Buenos Aires province, Argentina was caught in esparto grass" (p. 242).

Notes from specimen labels of specimens from Concepcion, Province of Tucumán, Argentina, include "caught in forest", "caught in the grass", "trapped in the house", and "caught in the wood"; a specimen from Tacuarembó, Uruguay, was taken on a "dry, rocky hillside".

Capture rate has been reported as low (Dalby, 1975; Reig, 1965; Crespo et al., 1970) and as high (Vallejo and Gudynas, 1980; and especially during an unusually rainy summer in 1943-1944 by Crespo, 1945), frequently captured in agricultural fields, more frequently in the center of the field than the edges (Kravetz et al., 1975; Villafañe et al., 1977; Kravetz and Villafañe, 1981). Crespo et al. (1970) mentioned an increased frequency of capture between November and April in the province of Buenos Aires. Kravetz et al., (1981a) reported the maximum density to be in July and minimum in November and also that in March and June immatures comprise most of the population in the province of Cordoba, Argentina.

The species eats seeds (Dalby, 1975), small seeds and plants (de Fonollat, 1984), or is predominately herbivorous, but occasionally eats insects (beetle fragments found in one specimen) (Barlow, 1969).

It climbs well (de Fonollat, 1984; Barlow, 1969) and is nocturnal (Vallejo and Gudynas, 1980; Barlow, 1969).

Nests are found under boards and rocks, in crevices in the ground and in trees (Barlow, 1969). It nests on the ground and in old vegetation and fallen logs (de Fonollat, 1984). Field notes as reported by Thomas (1898a) stated that it "makes a nest in a thick bush about a foot above the ground. The nest is made of grass torn into fine fragments" (p. 211).

De la Barrera (1936) reported five, then three offspring in two consecutive matings in Buenos Aires province. De Fonollat (1984) reported one female with 9 embryos in the wild, while the maximum number of embryos found in captivity is 6. Vallejo and Gudynas (1980) said that the average number of embryos is usually two or three in Uruguay. Kravetz et al. (1981a) found that pregnant females were more common between December and July, that the number declined in late March, probably due to a drop in temperature, and that the average number of embryos ranged from 5.3 to 8.33 in March and April. They further noted that older females have a greater number of embryos on average. A specimen from Treinte y Tres, Uruguay, collected in March, had four embryos, with crown-rump measurements of 10 mm, and one from Zapican, Uruguay, had 6 embryos, 9 mm long. Barlow (1969) reported that females had an average of 6 embryos in late April.

Kravetz et al. (1981b) reported that the tooth row is fully emerged at 22 days. They suggested that growth slows in the autumn months and that this is possibly due to an increased metabolic rate brought on by a decrease in the ambient temperature.

Molt was described by Barlow (1969).

C. bimaculatus is a reservoir for hemorrhagic fever and bubonic plague (Massoia and Fornes, 1967b).

Calomys bimaculatus and C. laucha may, on further study, be proven to be conspecific. The pelage differences are enough to distinguish the two forms, and no intergradation has been observed. If they are found to be conspecific, the proper name will be C. laucha, and subspecies might be C. laucha laucha and C. laucha bimaculatus.

Other species commonly reported in association with C. bimaculatus include Holochilus brasiliensis, Reithrodon physodes, Oryzomys (Oligoryzomys) flavescens, Akodon spp. Specimen localities have been reported by Massoia (1962); Massoia and Fornes (1964); de Fonollat (1984); and Corti et al. (1987). For more information see Thomas (1898b), Thomas (1910), Reig (1965), Massoia and Fornes (1967b), Barlow (1969), and Dalby (1975).

Calomys callosus (Rengger, 1830)

Mus callosus Rengger, 1830, p. 231, type locality: banks of the Rio Paraguay under the 7th and 20th latitude, Paraguay, approx. 27°S, 58.5°W. Type specimen not preserved.

Mus expulsus Lund, 1839, p. 233, type locality: Rio das Velhas, Lagoa Santa, Minas Gerais, Brazil. Type specimen: Zool. Mus. Copenhagen, 236.

Hesperomys muriculus Thomas, 1921a, p. 623, type locality: Rio Parapiti, San Antonio, Santa Cruz, Bolivia, 600 m. Type specimen: BMNH 21.11.6.12.

Type specimen: none preserved.

Diagnosis: Calomys callosus can be distinguished from all other species of Calomys by the following characters: body size large, total length of adults generally 160 to 210 mm; tail moderate, neither greatly reduced nor as long as the head and body; dorsal pelage gray or brownish, lacking a reddish tint; skull robust for genus; supraorbital region distinctly ledged and divergent posteriorly; maxillary toothrow long, generally measures 3.7 to 4.1 mm.

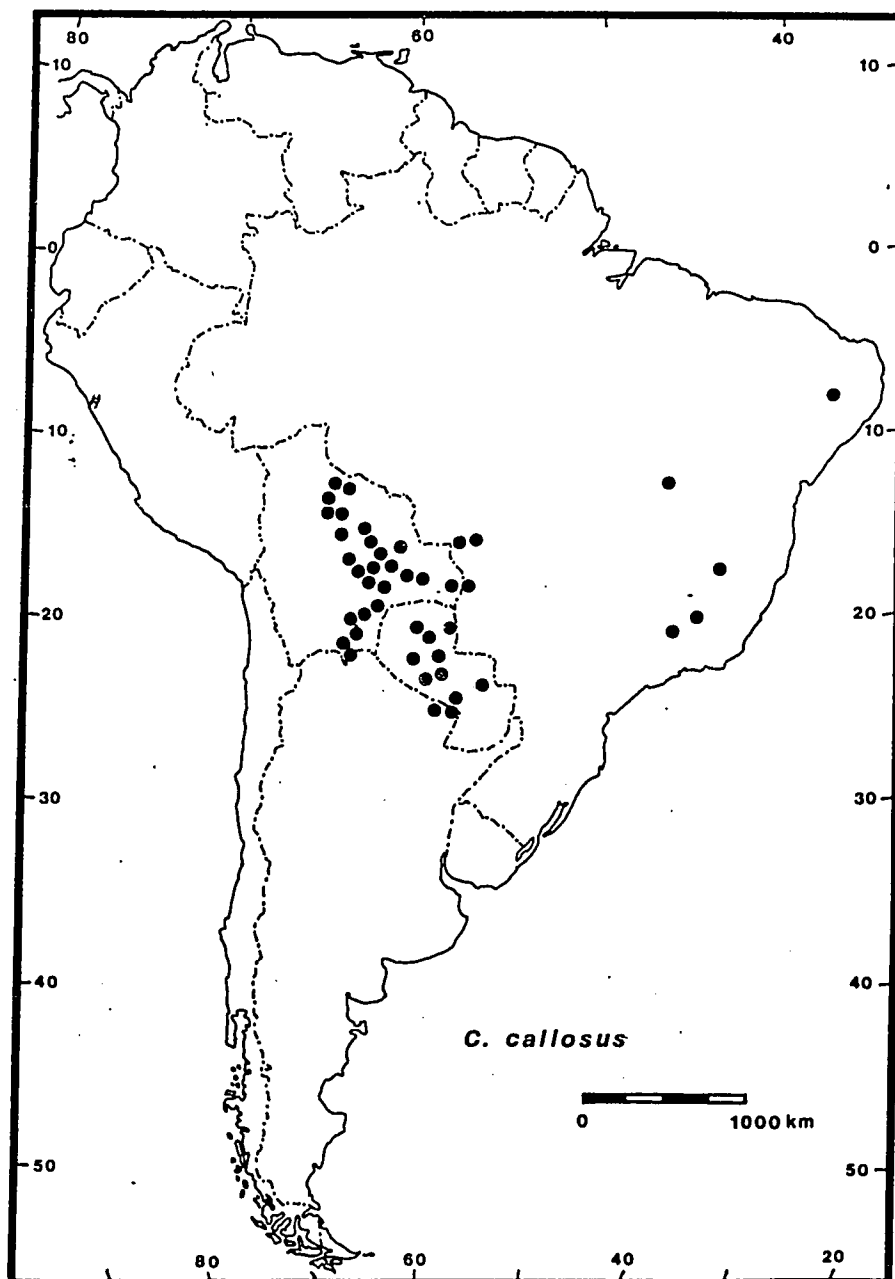
Distribution: Common in the lowlands of Bolivia, southern Brazil, Paraguay, and northern Argentina (see fig. 19). See Walter and Breckle (1986) for descriptions of the Cerrado and Caatinga habitats.

Description and Comparisons: The dorsum is dark gray or brown with black hairs, frequently giving a grizzled appearance. The venter is grayish with white-tipped hairs, sometimes a buffy wash is present. The sides are well marked from the venter. The hairs on the throat are gray at base, on the chin, white to base. The light post-auricular patches are small, but present. The nose is reddish. The dorsal surfaces of the feet are white. The soles of the feet are black, plantar pads are well separated. The tail is strongly bicolored, dark above, and light or white below. There are most commonly five pairs of mammae; 2 inguinal pairs, 1 pectoral, and 2 post-axial pairs ($3-2=10$). The number varies from 8 to 12 (including 9 and 11) in single populations.

The skull is strongly built for the genus, with marked ridges on the edges of the posteriorly divergent supraorbital region. An alisphenoid strut is rarely present (see table 4). Foramina are present about 50 percent of the time at the junction of the squamosal groove and the groove for the masticatory-buccinator branch of the maxillary nerve (see table 5).

Dentition is as for the genus; toothrows may show a slight posterior divergence. An anteromedian flexus is moderately to

Figure 19. Map of the known localities of Calomys callosus.



well developed, occasionally absent, an anteromedian style is present or absent, more often absent (see tables 6-7). External and cranial measurements are given in table 2.

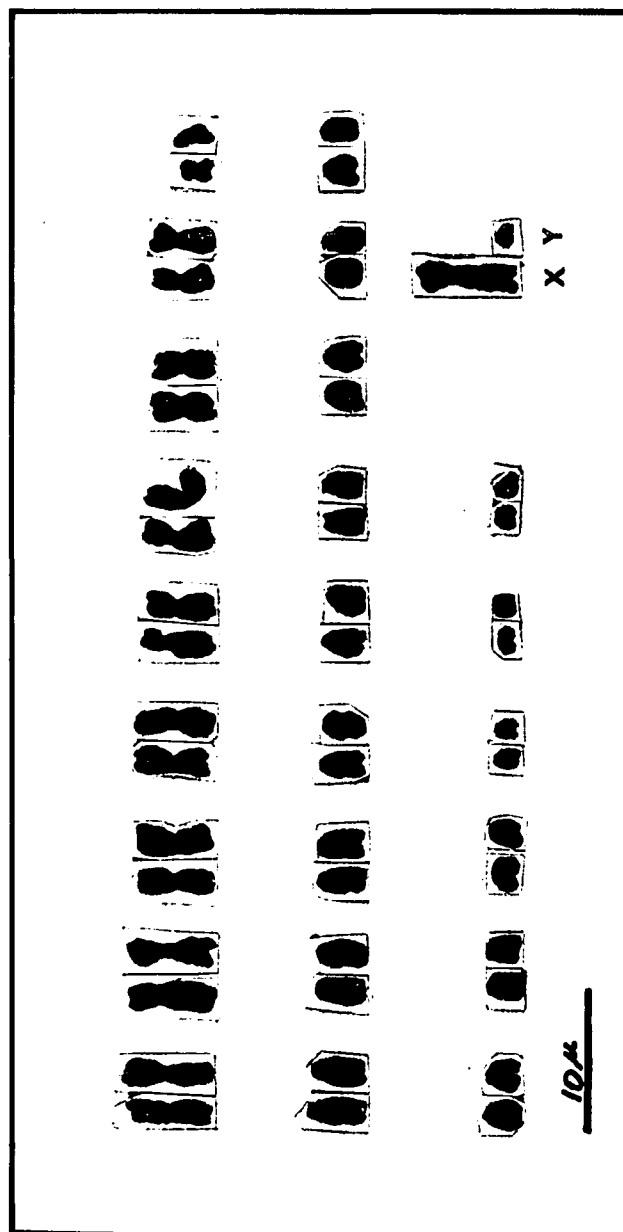
Calomys callosus is readily distinguished from all but C. venustus and C. tener on the basis of a ledged and posteriorly divergent supraorbital region. In body size, C. callosus is larger than all species but C. venustus. Calomys sorellus is slightly smaller and has a parallel-sided interorbital region. Calomys tener (which occurs sympatrically with C. callosus in parts of Brazil) is much smaller, has redder dorsal coloration and a darker venter. The diploid number is different in these as well, in C. callosus, $2n = 50$, in C. tener, $2n = 66$. Calomys venustus is difficult to distinguish from C. callosus as there are no obvious characters other than body size (C. venustus is larger in all dimensions). The most useful dimension for distinguishing these two is the length of the maxillary toothrow; in C. venustus it is generally greater than 4.1 mm, and in C. callosus is generally less than 4.1. See figures 32-35 for comparisons of the species of Calomys.

Karyology: Pearson and Patton (1976) published karyotypes and descriptions of C. callosus from 213 km by road NW Villa Hayes, Paraguay, and of "C. fecundus" from San Joaquín, 160 km N Trinidad, Department of Beni, Bolivia. They reported the Paraguayan karyotype as $2n = 36$, including 7 pairs of metacentric

autosomes; the X is probably a large metacentric and the Y a small acrocentric, leaving 10 pairs acrocentric. They reported the Bolivian karyotype as $2n = 50$; 9 pairs of metacentric autosomes, 1 pair much smaller than the rest, and 15 pairs of acrocentrics. The X is large and submetacentric, the Y is very small and acrocentric. They used the name C. fecundus for the Bolivian specimens, because of the large difference in the karyotype. I examined test slides of karyotypes from individuals from many localities in eastern Bolivia, and found most to have a diploid number of 50, and the same morphology as Pearson and Patton's (1976) C. fecundus (see figure 20). This also holds true for the Paraguay material I examined, courtesy of Dr. P. Myers. I tried to re-examine the slide from Paraguay that Pearson and Patton examined, but it is badly faded; I suspect an error in the analysis. The specimen is a young C. callosus. Unfortunately, this has compounded the taxonomic confusion within the genus (see Roldan et al., 1985). The type specimen of C. fecundus is not conspecific with C. callosus, but with C. venustus, so the karyotype given for "C. fecundus" is that for C. callosus. Reig (1986) separated C. callosus ($2n = 36$) from C. boliviae (including his fecundus, $2n = 50$).

Taxonomic History: Mus callosus was originally described by Rengger (1830). An English translation of the original German description was generously provided by Philip Myers.

Figure 20. Karyotype of Calomys callosus from San Joaquín,
Department of Beni, Bolivia (received from Drs. R. Pine, R. Baker,
and H. Genoways.)



Rengger said the pelage is gray, and that the upper and outer parts of the body have a reddish tinge. The whiskers and the snout are dark, the tail and the soles of the feet are dark gray. He reported that it resembles a young house rat in appearance. The tail does not project to a point, but ends in a stump, and curls like a prehensile tail. The nails of the thumb are entirely flat. On the soles of the feet there are three pairs of hard callouses, after which he named this species. He said they dig in the earth almost to the water, make long tunnels, which they inhabit in pairs. He saw them looking for food during the day, and said they eat seeds and roots.

Rengger's locality was modified by Hershkovitz to "opposite the mouth of Rio Bermejo, Department of Villa del Pilar, Paraguay" (p. 172). Gyldenstolpe (1932) wrote the type locality "Paraguay, Rio Paraguay, North of Villa Real" (p. 72).

Hesperomys muriculus was described by Thomas (1921a) from the southeastern Bolivian lowlands. He said it is "A comparatively large dark species, rather like Mus musculus.... General colour dark mouse-grey, the tips of the hairs slaty at base and washed terminally with dull whitish, far less white than in other species. Proectote of ears blackish, with buffy edges, metentote buffy brown; no white ear-patch. Hands and feet grey. Tail about as long as the body without the head, dark grey above, rather

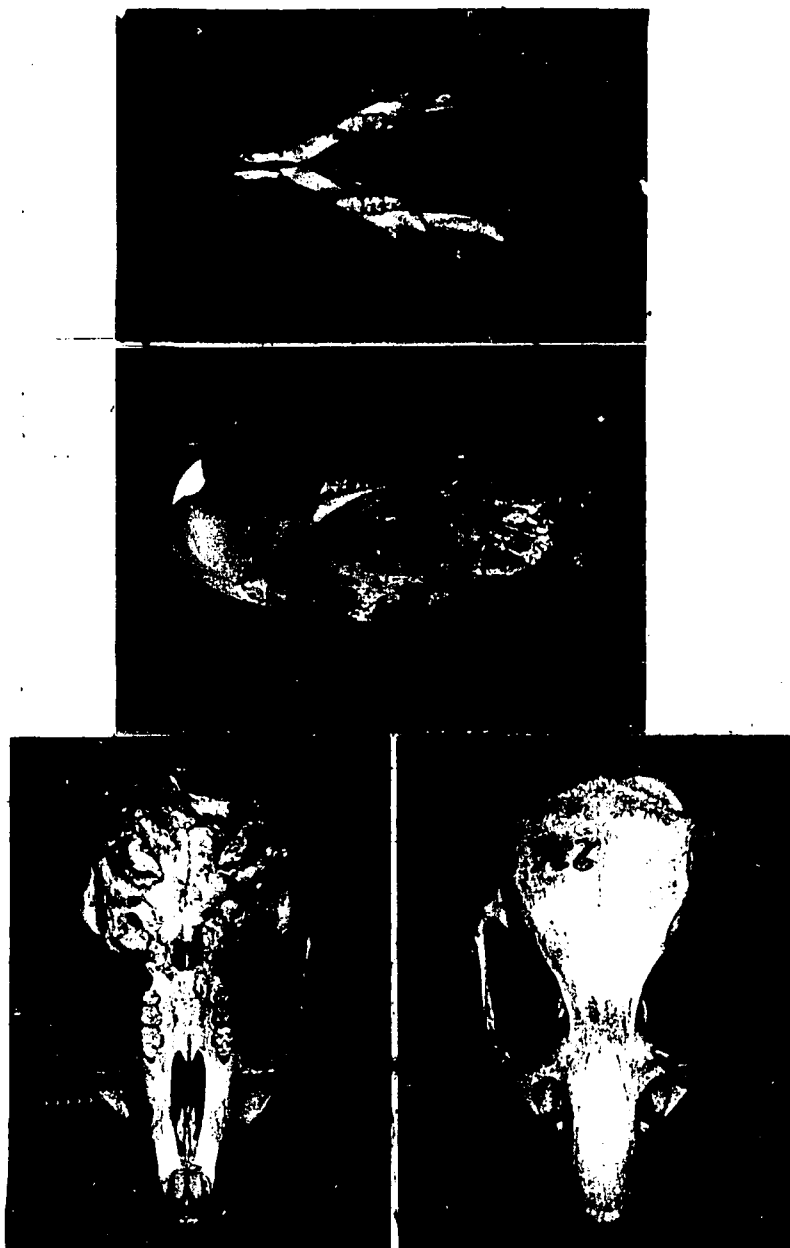
lighter below. Number of mammae not known" (Thomas, 1921a, p. 623).

He said the skull of adults has very well-developed supraorbital ledges. He gave the head and body length as 89 mm, the tail length as 69 mm, the length of the hind foot as 20 mm, and the length of the ear as 16 mm.

He said "This very distinct little species, found in company with, and almost mistakeable for, Mus musculus, is . . . readily recognizable by its comparatively dark color" (p. 623). The collector's (Wavrin) notes say "Trapped in a house surrounded by bush".

Lund (1839) first used the name Mus expulsus in a list of the living and fossil species of mammals from Rio das Velhas, Brazil (the confluence of Rio de S. Francisco and Rio de Paraopeba). Lund (1841a, b) further mentioned Mus expulsus from the same locality, but did not provide much additional information. Mus expulsus was extensively described and figured by Winge (1888). Figure 21 shows views of the skull of the type specimen. The photographs are courtesy of Alfred Gardner. Notes on the type specimen from Dr. Gardner include, that it is a brown mouse with buffy-white underparts, the digital brushes longer than and tending to hide nails, the supraorbital ridges are well-developed and arching over interorbital region, the zygomatic plate is broad and projecting anteriorly, and the lacrimal large. Winge (1888)

Figure 21. Dorsal, ventral, and lateral views of the cranium, and dorsal view of the mandibles of the type specimen of Hesperomys expulsus (= Calomys callosus). Negatives courtesy of Dr. A. L. Gardner. The greatest length of the skull measures 27.5 mm.



included external and cranial measurements, and illustrations of the skull and mandible (plate II), and the head and hind foot (plate I). The hind foot shows six tubercles, the ears are round and of moderate size.

Remarks: C. callosus can be a crop and house pest, it frequently occurs in disturbed habitats. It is known to be a reservoir for hemorrhagic fever. Machupo virus, the aetiological agent of Bolivian hemorrhagic fever, was found in populations of C. callosus from San Joaquín, Beni, Bolivia (Johnson et al., 1965, and Justines and Johnson, 1969). Machupo virus is related to Junin virus, which caused a similar hemorrhagic syndrome in Argentina (Johnson et al., 1965). These mice are also known to be a reservoir for Trypanosoma cruzi, an agent for Chagas' disease (Ribeiro, 1973).

This species is found in thickets at the edge of pastures, ravines and forest roads in the pantanal of Brazil (Schaller, 1983), in caatinga, cerrado, evergreen mesophytic forest, pampa, but not chaco of Brazil (Mares et al., 1985b), in scrub areas with low trees in the cerrado of Goias, Brazil (Mello, 1977, 1978), in cerrado of Brasilia, which is loosely called savannah, a mixture of small trees and xeromorphic vegetation, including the cerrado gallery forest (Alho, 1981), rare in caatinga of Brazil (Streilein, 1982c), in cerrado and caatinga of Pernambuco, Goias and D.F., Brazil (Alho, 1982), not in cerrado gallery forest of

Brazil (Nitikman and Mares, 1987, and Ernest and Mares, 1986), in second growth habitats in mesic forested areas, such as stream areas, road cuts, old fields, grassy areas, sugar cane fields, and river banks of chacoan thorn scrub, transitional forest, humid forest and precordillera monte desert of Salta, Argentina (Mares et al., 1981a), abandoned fields of Brazil (Mares et al., 1981b), and the chaco of Paraguay (Myers, 1982). It is found in Polygenis sp. and piles of dried grasses (Karimi et al., 1976). "Caatinga Baixa and later stages of old field succession are preferred habitats" (Mares et al., 1981b). Mares et al. (1985b) reported that most species in the caatinga also occur in cerrado, the caatinga is a subset of the cerrado habitat. Much of the contradiction above reflects a lack of extensive collection in regions of Brazil.

Alho (1981) reported two species of Calomys as common in the cerrado at Fazenda Agua Limpa, Brasilia, Brazil (1557/4754); C. callosus in the gallery forest, and C. expulsus (common) in campo. In the text (p. 226), however, he reported C. callosus as the widespread species. In my judgement, the widespread species probably is C. callosus and the other is C. tener. Presumably, there are two species in this habitat, C. callosus and C. tener. No voucher specimens were retained, however. In later studies, he used the name C. tener (Alho, 1982; Alho et al. 1986) and reported tener from the cerrado of the same area of Brazil. Alho et al. (1986) reported two species, C. callosus and C. tener from Fazenda

Agua Limpa, Brasilia, Brazil, and the National Park of Brasilia. He described the cerrado and noted that both species are most common in open habitats, especially valley-side wet campo (50%), along gallery forest campo (25%), and strict cerrado (25%).

Lange and Jablonski (1979) included C. callosus (as Hesperomys callosus callosus) in their list of rodents from the state of Parana, Brazil. However, they gave no locality records. Also included in Hesperomys, was H. leucodactylus, which is Rhipidomys leucodactylus (Cabrera, 1961).

Notes from labels on specimens from the department of Tarija, Bolivia, include, "dense forest 15 m height, dense understory of 6 m shrubs. 80% ground cover of forbs, grasses and bromeliads" and "dense shrubs 8 m high, scattered trees 10 m high with understory of smaller shrubs, forbs, grasses". Notes from field labels of specimens from Paraguay, include "tufts of grass nr. thorn edge", "thorn thicket in field", "edge thorn forest", "Trapped under brush on river bank", "caught in house", "snap trap at edge of canadon nr. growth of Bromelia balansae". This species was often captured in burrows under logs or rocks, or tangled roots (Mares et al., 1981a).

Field notes on Fazenda San Martin, Brazil (CM specimens, collected by Doult in the dry season) describe the habitat as flat country with low ridges (approximately 600-900 m) in height and dense vegetation along the Paraguay River. The high ground had

palms, the lower ground had shrubby grassy vegetation. There was much swampy land, grazed by cattle. Crocodilians were observed in an abandoned river channel. Jaguar trails, capybara tracks, and parrots were seen.

Calomys callosus has been reported as rare in abandoned fields and Caatinga Baixa of Brazil (Mares et al., 1981b); never in large numbers in Caatinga (Streilein, 1982a); at low density in Pernambuco, Brazil (less than 1.7 % of all rodents trapped in study area in a 4 year period; Karimi et al., 1976); at low numbers in the Pantanal of Brazil (Schaller, 1983); common in the Cerrado of Brazil (Mello, 1977, 1980; Alho, 1981; and Alho et al., 1986); and common in Salta Province, Argentina (Mares et al., 1981a).

Mello (1980) found a population peak of C. callosus in July 1975, then another in August-November of 1976, in the northern part of the state of Goias, Brazil. Out of a total number of 963 captured rodents, individuals of C. callosus comprised about 41 percent (398/963) over 2.5 years; 44.2 % were females, and 55.8 % males. Many of the females were immature.

Density has been reported as 3-4 individuals per hectare (Alho et al., 1986). Home range is limited according to Mello (1977), and about 100-1000 m² according to Alho et al. (1986).

The species is nocturnal (Karimi et al., 1976; Mares et al., 1981a, b; Streilein, 1982a; and Alho et al., 1986). It eats

arachnids (Karimi et al., 1976) and seeds, moths, and beetles (Streilein, 1982a).

Contradictory reports on the arboreality of this species exist: C. callosus has been reported as not appearing to climb (Mares et al., 1981a), as an agile, active climber that uses its tail as a climbing aid, and shows a tendency toward arboreal activity in the laboratory (Streilein, 1982a, and Mares et al., 1981b). Streilein (1982a) also noted that adults were capable of vertical leaps of 0.7-0.8 m.

It is a useful laboratory animal and easy to maintain (Mello, 1978; Karimi et al., 1976; Streilein, 1982a; and Alho et al., 1986).

Molt was described by Mares et al. (1981a) in Salta, Argentina.

Nests have been described as made of dried herbs (Karimi et al., 1976) and as being spherical and made of "finely shredded, interwoven plant material found in depressions hollowed in the ground, camouflaged with twigs and leaves" (Alho et al., 1986, p. 453). Nests are generally above the ground surface in clumps of grass or in branches of dead trees (Mello, 1978). Streilein (1982a) found that nests in the laboratory were spherical, made of finely shredded, interwoven plant material, while those in the field were simple depressions hollowed in the ground 10-15 cm deep

and wide, and camouflaged with twigs and leaves. He noted occasional stores of seeds found near the nests.

In a laboratory colony from Exú, Pernambuco, Brazil, Petter et al. (1967) found the number of embryos to range from 1 to 10, the newborn weight to range from 1.3 to 2.5 g, more males to be born than females (181:148), the gestation period to be 19 to 22 days, adults to weigh 35-45 g, eyes to open after 7-8 days, the lower incisors to erupt after 6-7 days, and the upper incisors to erupt after 7-8 days. The dorsal pelage is gray on the third day and measures about 2 mm.

Mello (1978) reported the average litter size to be 4.5, the range was 2-9, and the length of gestation to be 21.8 days, with a range of 20-23 days. The ratio at birth of males to females was 1.05:1. The eyes open 6-7 days after birth, weaning occurs 15-17 days after birth, and pelage cover is complete on the 6th day.

Mello (1980) reported gestation to require 21.8 days in the laboratory, intervals between matings to be 30 to 50 days, and the average number of embryos per litter to be 4.5. Animals were sexually mature at 22-23 g, embryos were present in June 1975 (8 in 1 female), September (4 and 2, in 2 females), October (1 female with 4), November (2 females, both with 4), January (1 female with 3), and April (2 females, 4 and 7). Mello further noted that the reproductive periods were coincident with the end of the rainy season.

The average litter size in field studies in Brazil was 4.4, the range was 2-8 (Streilein, 1982a). Reproductive information from his study included 1 lactating female in September, 2 lactating females in October, 1 pregnant and 1 lactating female in November, 2 lactating females in February, 1 lactating female in April, and 1 female with no reproductive activity in May.

Specimens from the department of Tarija, Bolivia, taken in May, show a range of 5 to 13 embryos, ranging in crown-rump length from 5 to 21 mm. Two lactating females were also collected. In the department of Santa Cruz, Bolivia, 1 lactating female was collected in August; a pregnant female with 4 embryos, measuring 22 mm (crown-rump) in September, and a pregnant female with 7 embryos of 17 mm length in October.

Schaller (1983) gave the average weight for C. callosus as 15 g, which is low for this species. Average weight from a series from the Estancia Cachuela Esperanza, Department of Santa Cruz, Bolivia, is 35.84 g, and the range for adults is 19.5-60 g.

Karimi et al. (1976) studied this species in relation to the plague; they said it is not implicated in the epizootology of the disease because of its low population density.

The baculum of C. callosus was figured in Massoia and Fornes, (1976b), as no locality or specimen reference was given, it is unclear if the baculum is that of C. callosus or C. venustus.

Predators include owls as evidenced by pellet remains (AMNH 263186).

Other species commonly reported in association with C. callosus include Oryzomys (Oligoryzomys) eliurus, O. subflavus, Bolomys lasiurus, and Holochilus brasiliensis. See Karimi et al. (1976); Mello (1977); Mares et al. (1981a, b); Alho (1982); Streilein (1982a); Mares et al. (1985b); and Alho et al. (1986).

Calomys hummelincki (Husson, 1960)

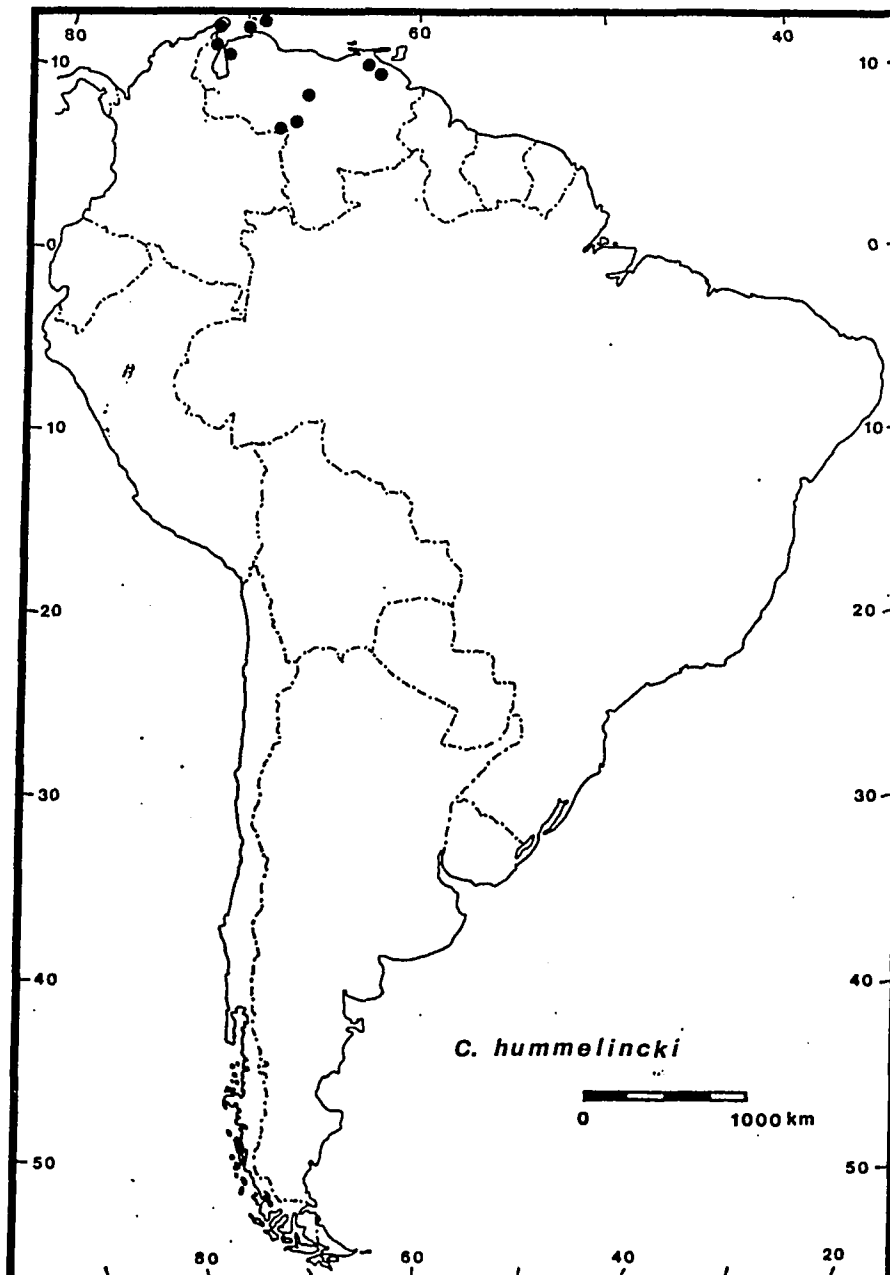
Baiomys hummelincki Husson, 1960, p. 34, type locality: Klein Santa Martha, Curaçao, Netherlands Antilles. Type specimen: Leiden Museum 15994 (not seen).

Diagnosis: Calomys hummelincki can be distinguished from all other species of Calomys on the basis of the following characters: body size small, total length less than 130 mm; tail much shorter than head and body length; dorsum with a distinct orange color, venter white; post-auricular patches distinct; tail weakly bicolor, pale above, and white below; skull delicate, greatest length of skull of adults generally less than 21.00 mm; molar toothrow generally less than 3.3 mm.

Distribution: Grasslands on sandy soils, Venezuela, Colombia, islands of the Netherlands Antilles, Curacao, and Aruba (see fig. 22). For the vegetation of Venezuela, see Walter and Breckle (1985; 1986), also see August (1984) for descriptions of some habitats.

Description and Comparisons: The dorsal pelage has an orange tint and the hairs are short and adpressed. The middorsum is dark, buffy brown or orange to dark brown and extends onto head.

Figure 22. Map of the known localities of Calomys hummelincki.



The rump and sides are sandy orange, the hairs of sides are gray-based with rufous tips. The sides are well marked from the venter by an orange line. The hairs of the venter are gray with white tips, but it has a distinctly white appearance. The hairs of the chin and throat are white to the base. The tail is weakly bicolored, pale above, lighter below; dorsal parts of the feet are white. Light-colored post-auricular patches are present (but not bright white). Buffy preauricular tufts are present. There are usually 4 pairs of mammae, $2-2=8$.

The skull is small and delicate, the supraorbital region is posteriorly divergent, but not ridged. The alisphenoid strut is absent (see table 4), foramina are frequently present along squamosal-alisphenoid groove (see table 5). Dentition is as for the genus; the anteromedian flexus is well-developed and the anteromedian style is occasionally present, (tables 6-7). External and cranial measurements are given in table 2.

Calomys hummelincki can be distinguished from C. callosus, C. venustus, and C. tener by its small size, lack of a ridged, posteriorly divergent supraorbital region, and orange dorsal color. It can be distinguished from C. musculus and C. murillus by its shorter tail, never as long as the head and body length, its smaller body size, and orange dorsal color. Calomys sorellus is larger, darker, and has a parallel-sided interorbital region. Calomys lepidus is larger, has long silky fur, a marbled dorsum,

and a narrower rostrum. The species most likely to be confused with C. hummelincki are C. laucha and C. bimaculatus: they are all similar in size and overall appearance. Calomys hummelincki can be distinguished on the basis of coloration; neither of the others have an orange dorsum. Calomys laucha is more sandy colored, and C. bimaculatus is darker and has a gray venter. It may have a relatively longer rostrum than the others, as well. Calomys hummelincki may be confused with house mice, but Mus is larger, has a longer tail, and longer hind foot (Husson, 1960). For comparisons with the other species of Calomys, see figures 32-35.

Karyology: Reig (1986) reported that the chromosomes differ from those of C. laucha in morphology (Reig, 1986). However, his C. laucha equals C. laucha and C. bimaculatus. Pérez-Zapata et al. (1987) reported the karyotype of a male from Los Cocos, Venezuela, as $2n = 60$, $FN = 64$, and compared this to the karyotype of C. laucha (= C. bimaculatus).

Taxonomic History: Baiomys hummelincki was described by Husson in 1960. He assigned the species to Baiomys because of the shape and structure of the last upper molar and noted that in Hesperomys (= Calomys), the last upper molars are not evidently reduced in relation to the second upper molars, being of about equal width and more or less pronouncedly triangular, while the inner reentrant angle is distinctly visible. In B. hummelincki, the M3 is strongly reduced in relation to the width of M2, being

more or less ring-shaped while the inner reentrant angle is obliterated or possibly altogether absent. In this, he wrote that it fits with B. taylori. Interparietal in size and shape resembles that of Hesperomys laucha and H. lepidus. In Baiomys taylori and B. musculus, the interparietal is relatively broad antero-posteriorly and short (extending across one half of braincase). The rostrum of Baiomys is short compared with that of Hesperomys. See figures 16 and 17 for comparisons of the cranium and dentition in Baiomys and C. hummelincki.

Hershkovitz (1962) synonymized C. hummelincki with C. laucha. He thought the northern populations resulted from artificial introductions of C. laucha.

Remarks: C. hummelincki occurs in the llanos of the Orinoco and deserts around Golfo de Venezuela in tropical thorny forest, in tropical very dry forest, and in tropical dry forest of Venezuela at elevations of 15 to 76 m (Handley, 1976). Husson (1960) reported that the specimen from W of Barranca Corra was caught under a stone and that from Seroe Blanco was taken in a maize field, under a stone. Handley (1976) reported the frequency of captures in different places: caught on the ground (100 %); usually in moist (86 %) but occasionally in dry sites (14 %); in grass (86 %), houses (9 %), and in nests under a slab of bark and under a bottle (5%); in sandy grassland (95 %), thorn forest (2.5 %), and yards (2.5 %). The species is possibly rare, specimens

are not common in collections, and it has not been reported in ecological studies, such as the one by August (1984).

Notes from specimen labels include, " around dwellings", "caught under log", "inside log in meadow", "under trash box", "open savannah - short grass", "short grass - mesa slope", "short grass, mesa summit", and "long grass".

Pleistocene fossils are known from Tobago (Eshelman and Morgan, 1985), where it is unknown in the Recent fauna.

Ibáñez and Moreno (1982) reported a very low capture rate for C. hummelincki (5/551 total) in the llanos of Apure, Venezuela. Other species they reported in association included Sigmomys alstoni, Bolomys brevicauda (= Zygodontomys brevicauda), Oryzomys concolor, O. fulvescens, and Holochilus brasiliensis.

Reproductive information is scarce. Information from specimen labels includes 6 pregnant females with 2-5 embryos from Aguaro Guariquito, N.P. Llanos Centrales, Venezuela. These specimens are somewhat grayer than typical hummelincki, unfortunately, no skulls were preserved. Sperm morphology was described by Pérez-Zapata et al. (1987).

Additional specimen localities have been reported by Husson (1960); Handley (1976); Ibáñez and Moreno (1982); and Pérez-Zapata et al. (1987). For additional information on the fauna of Curaçao and Aruba, see Hummelinck (1940).

Calomys laucha, Olfers, 1818

M[us] laucha Olfers, 1818, p. 209, type locality: Paraguay. Type specimen: lost or never preserved (see "Taxonomic History").

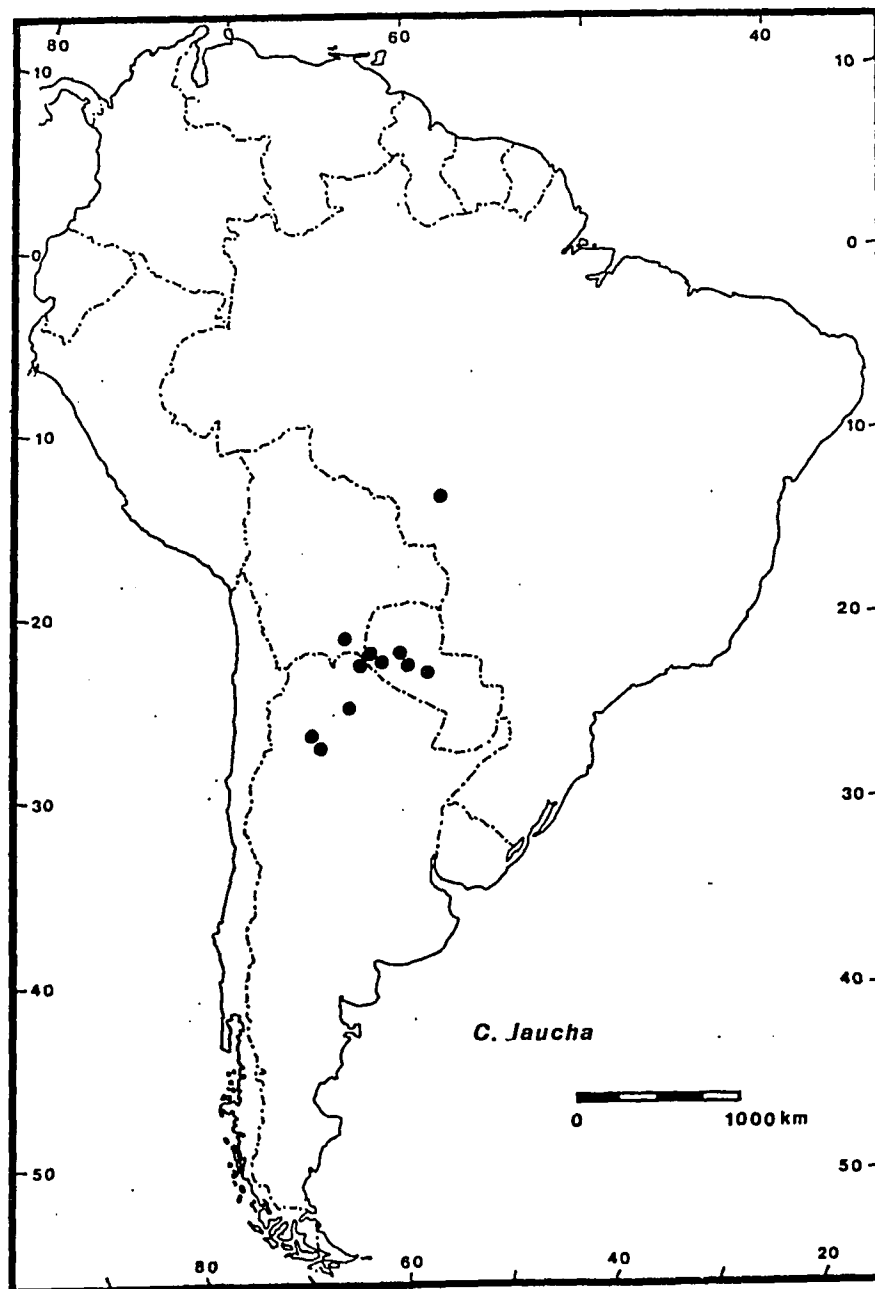
Type Locality: Restricted to the neighborhood of Asunción, Paraguay, by Hershkovitz (1962).

Diagnosis: Calomys laucha can be distinguished from all other species of the genus Calomys on the basis of the following characters: body size small, total length less than 145 mm; tail short, less than 65 mm; dorsum gray, sometimes with a buffy tint; venter pure white; tail weakly bicolored, dark above and pale below; cheeks white; skull small and delicate, greatest length of skull generally less than 22.5 mm; maxillary toothrow generally less than 3.3 mm.

Distribution: Chaco of southeastern Bolivia, western Paraguay, northeastern Argentina, and western Brazil (see fig. 23).

General Description and Comparisons: The dorsal pelage is golden-brown with black hairs. The venter, including the chin and throat, is pure white. The tail is bicolored, light brown above, white below. The cheeks are white. There are buffy tufts anterior to ears. There are generally four pairs of mammae, 2-2=8.

Figure 23. Map of the known localities of Calomys laucha.



The skull is delicate. The sides of the supraorbital region diverge posteriorly, but never have ridges. An alisphenoid strut is generally present (see table 4). A foramen at the junction of squamosal-alisphenoid groove is generally present (table 5). Dentition is as for the genus; the anteromedian flexus well-developed, and an anteromedian style is present (tables 6-7). The M1 occasionally has the procingulum constricted. External and cranial measurements are given in table 2.

Calomys laucha can be distinguished from C. callosus, C. venustus, and C. tener by its small size, lighter color, and lack of a strongly ridged, posteriorly divergent supraorbital region. It can be distinguished from C. musculus and C. murillus by its smaller size, and shorter tail (never as long as the head and body). It is smaller and paler than C. sorellus, which has a distinctly parallel-sided interorbital region. Calomys lepidus is larger, has long, silky fur, a marbled appearance, and a relatively shorter tail. In size and general appearance, C. laucha is similar to C. bimaculatus and C. hummelincki (see those species accounts, also); it differs from them in having a pure white venter and paler dorsal coloration. The dorsal coloration is typical of other chacoan species, a pale sandy color, as in Graomys griseoflavus chacoensis, Andalgalomys pearsoni, Oryzomys chacoensis. For comparisons with other species of Calomys, see figures 32-35.

Karyology: A preliminary examination of material from 8 km NE of Juan de Zalazar, President Hayes Department, Paraguay, suggests a high diploid number, $2n=64$ (FN=66), with many very small elements (Myers, pers. comm.). Clearly, future studies will be of interest.

Taxonomic History: The first description of Calomys laucha was by Azara (1801, pp. 102-104) as "rat septième ou rat laucha" in his description of the mammals of Paraguay. He applied the vernacular name "laucha" to this species. He did not assign a type specimen, and gave only general localities: "a pile of maize stalks on a farm in the province of 'Buenos Ayres,' and a second in the 'pampas' abound 25°S Lat." (Hershkovitz, 1962, p. 153). As Hershkovitz pointed out, Buenos Aires then included Uruguay, and several provinces of Argentina. The type locality was restricted to the vicinity of Asunción, Paraguay by Olfers (1818, cited in Hershkovitz, 1962).

Gyldenstolpe (1932) and Cabrera (1961) credited Desmarest (1819) with the first use of the name. Desmarest (1819, 1822) used Mus laucha.

Hershkovitz (1962) cited Olfers (1818) as an earlier reference for the name Mus laucha (= C. laucha).

Langguth (1966) proposed that several of Azara's names, including "laucha", be credited to Fischer (1814, cited in Langguth, 1966). However, Myers and Carleton (1981), in a

discussion of the taxonomic history of Oryzomys (Oligoryzomys) nigripes, claimed that Fischer's (1814) names are not available because he did not consistently use binomial nomenclature.

Honacki et al. (1982) credited the name C. laucha to Olfers (1818), but commented (under Reithrodon physodes, p. 459) that Langguth responded and still maintained that Fischer's 1814 work is valid.

Remarks: This is among the smallest species of Calomys and seems rare and difficult to catch based on field notes and the limited number of specimens in collections. It is sympatric with C. callosus in Bolivia, Brazil, and Paraguay.

Notes from specimen labels from Paraguay include "thorn forest", "grass in thorn forest", and from the department of Tarija, Bolivia, include "dense forest 15 m height, dense understory of 6 m shrubs, 80% ground cover of forbs, grasses and bromeliads".

Mares et al. (1981a) reported that Calomys laucha is rare in the chacoan thorn scrub of Salta Province, Argentina. They reported two specimens from 4 km NE Santa Victoria, Province of Salta, Argentina, a place characterized by xeric thorn scrub. These specimens were caught in October under sparse bushes, the female was lactating, and the male had large scrotal testes. They described the area as "dry chaco thorn forest with widely-spaced trees (Acacia, Prosopis, Geoffroea) on hard-packed soils" (p.

157). A third specimen was reported, but examination shows it to be C. musculus.

Calomys cf. laucha was reported from the Tarija Basin by Hoffstetter (1986). This locality is currently at 2000 m, and in the past was higher. This identification is questionable.

For other species associated with C. laucha, see Myers (1982). For additional localities, see Thomas (1898b).

Calomys lepidus (Thomas, 1884).

Hesperomys (Calomys) bimaculatus, Waterh., var. lepidus, var.

n., Thomas, 1884, p. 454, type locality: Lake Junin,
Department Junin, Peru. Type specimen: BMNH 85.4.1.43.

Eligmodontia ducilla Thomas, 1901a, p. 182, type locality: San

Anton, Lake Titicaca, Peru, 3800 m. Type specimen: BMNH
1.1.1.1.

Eligmodontia carilla Thomas, 1902a, p. 133, type locality: Choro,

Department of Cochabamba, Bolivia, 3500 m. Type specimen:
BMNH 2.1.1.55.

Hesperomys carillus marcarum Thomas, 1917, p. 1, type locality:

Lauramarca, Department of Cuzco, Peru, 3995 m. Type
specimen: BMNH 3.2.9.8.

Hesperomys carillus argurus Thomas, 1919a, p. 130, type locality:

Abrapampa, Peru, 3500 m. Type specimen: BMNH 19.8.1.21.

Hesperomys lepidus montanus Sanborn, 1950, p. 4, type locality:

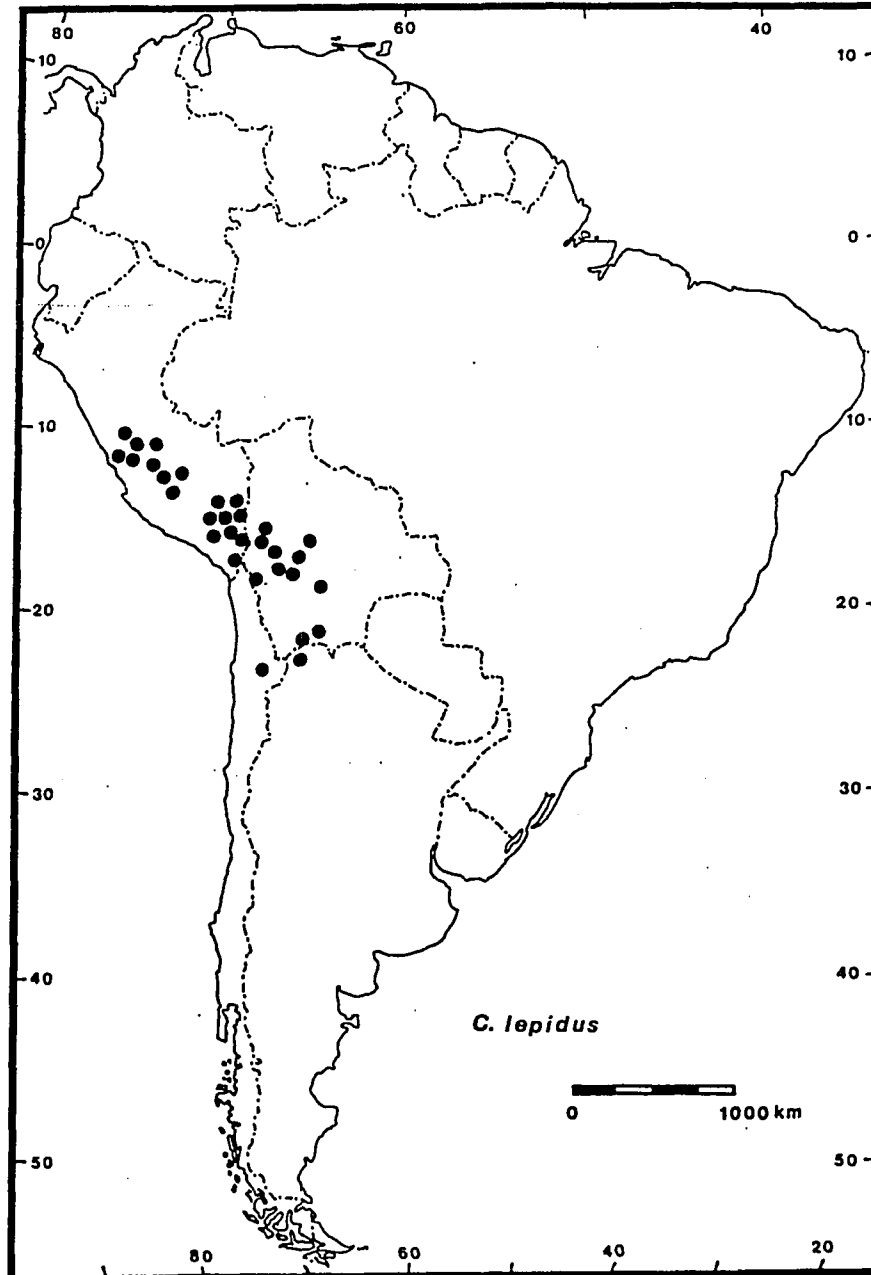
El Cumbre, Department of La Paz, Bolivia, 15,200 ft. Type
specimen: AMNH 72683.

Diagnosis: Calomys lepidus can be distinguished from all other species of the genus Calomys on the basis of the following characters: body size moderate, total length less than 140 mm; tail very short, less than 50 mm; ears large, length of ears from notch is generally equal to or greater than the length of the hind foot; pelage thick, hairs long and soft; dorsum pale gray marbled with light brown; venter with white-tipped gray hairs; skull small, greatest length of skull in adults generally ranges from 20.5 to 23.5 mm; nasals narrowed, bullae slightly enlarged, teeth small, but not delicate, maxillary toothrow generally 3.3 to 3.7 mm; occurring at high elevations, over 2500 m.

Distribution (see fig. 24): High elevations in Peru, Bolivia, northern Chile, and probably northern Argentina (although no specimens are reported from there, see Mares et al., 1981a).

General Description and Comparisons: The fur is long, soft and silky, the general color dull fawn or grayish fawn, somewhat darker on the center of the back, because of an intermixture of numerous longer black hairs. The dorsum has a marbled appearance, and is nearly uniform in tone from head to rump. The venter is white, not sharply defined laterally, the hairs are gray basally and white terminally. The ears are of medium length, pale brown; with a conspicuous white post-auricular spot. The tail is less than half the length of the head and body, uniformly hairy, weakly bicolored, sandy white above, clear white below. The soles of the

Figure 24. Map of the known localities of Calomys lepidus.



hind feet are hairy for their proximal two thirds, the pads are small and crowded towards the distal end of the sole. The feet are white above. There are eight mammae, two pectoral and two inguinal pairs (2-2=8).

The skull is light and delicate, the frontal outline markedly convex, the supraorbital edges square, but not ridged. The interorbital constriction is more parallel-sided than most of the species of Calomys, but less parallel-sided than that of C. sorellus. There are five interdental palate-ridges. An alisphenoid strut is frequently present (table 4). A foramen is generally present along the squamosal-alisphenoid groove (table 5). Dentition is as described for the genus, an anteromedian style is occasionally present and the anteromedian flexus is well-developed (see tables 6-7). External and cranial measurements are given in table 2. (Above description modified in part from Thomas, 1884, 1901a).

Calomys lepidus is readily distinguished from C. callosus, C. venustus, and C. tener by its smaller size, very short tail, marbled pelage, and lack of ridged, posteriorly divergent supraorbital region. It is larger than C. bimaculatus, C. laucha, and C. hummelincki, all of which have shorter hair, and relatively longer tails. Tail length also will distinguish C. lepidus from C. musculus and C. murillus, the latter two have long tails (equal to the head and body length), as well as shorter hair, and

broader nasals. Calomys lepidus is found sympatrically with C. sorellus; C. sorellus is larger, has a longer tail, darker dorsal and ventral pelage, and a parallel-sided interorbital area. See figures 32-35 for comparisons of the species of Calomys.

Karyology: Pearson and Patton (1976) published the karyotype of this species. Their specimens came from the departments of Puno and Junin, Peru. The karyotype reported has a diploid number of 36; all autosomes are metacentric, the X is medium-sized and subtelocentric; the Y is subtelocentric, the smallest of the series. They commented that this karyotype shows a perfect Robertsonian relationship to C. sorellus.

Preliminary analysis of a karyotype of a specimen from the vicinity of Huancaroma, Department of Oruru, Bolivia, suggests a diploid number of 44.

Taxonomic History: Thomas (1884) described Hesperomys (Calomys) bimaculatus var. lepidus from the "Region of the 'puna,' or mountain grass-land, close to the lake of the same name, called also Lake Chinchacocah, one day distant from Tarma, the capital of the Department of Junin. The lake is situated in the centre of a marshy prairie abounding in small lakes and streams, and covered in many places with thick patches of rushes" (p. 447). The type specimen is an old adult, the skin is BM 85.4.1.43, the skull is numbered BM 85.4.1.45.

Thomas reported that C. lepidus differs from C. bimaculatus by its larger size, longer and differently shaped ears, shorter tail, longer fur, slate-mixed instead of pure-white belly, and by the absence of supraorbital ridges on the skull. It is unclear what species was represented by the specimens for which he used the name bimaculatus.

In 1901, Thomas described Eligmodontia ducilla, an Eligmodontia of the short-tailed group, with a striking superficial resemblance to Phyllotis sublimis (= Auliscomys sublimus), though smaller and with shorter fur. He said its size was about as in E. lepida, and its teeth of the "complicated brachyodont character found in E. laucha and its allies, very different to those of Phyllotis, which are of a more simple, though semi-hypsodont and zig-zag pattern" (Thomas, 1901a, p. 182).

In comparing E. ducilla with E. lepida, Thomas wrote "This pretty little mouse is most nearly allied to E. lepida and sorella, but may be readily distinguished from both by its much paler and more fawny colour. Its superficial resemblance to Phyllotis sublimus is so great that at first sight it might be taken for a smaller shorter haired subspecies of that animal" (p. 182).

In 1902, Thomas described Eligmodontia carilla from Choro, Bolivia, 3500 m. He said it was "Closely similar externally, in

size, colour, and character of fur, to the Peruvian E. sorella. General colour slightly paler (about isabella colour of Ridgway), the postauricular spots rather larger, and the longer hairs mixed with the fur less numerous; in other respects the description of E. sorella will apply verbatim to this species. . . Tail much shorter than in E. sorella, longer than in E. ducilla, grey above, white below and laterally.

"Skull almost exactly similar to that of E. ducilla, the brain-case short and broad, not elongated as in E. sorella" (Thomas, 1902a, p. 133-134).

He did note that the skull is more like "that of the still shorter-tailed E. ducilla" (p. 134). A topotype of H. carillus is dark, small with a gray belly.

Hesperomys carillus marcarum was described by Thomas in 1917. He noted that it is duller colored than true carillus, the tail is white above; and the soles of the feet are more hairy.

Hesperomys carillus argurus was described by Thomas in 1919 from Abapampa, Peru, 3500 m, "On the bank of the laguna, in humid pasture-land". He said the "Essential characters apparently quite as in the true H. carillus, but colour throughout much paler" (Thomas, 1919a, p. 130). He reported 10 mammae, 3-2=10, and skull similar to that of carillus, but the zygomatic plate slightly broader (there was only one example of carillus). He wrote "This pretty little mouse is evidently the dry-area representative of

the forest H. carillus, from which it differs by its conspicuously lighter colour" (p. 130).

In 1920, Thomas further compared Hesperomys carillus marcarum with H. carillus of the Yungas region of Bolivia. He said marcarum was "distinguished 1) by the general color being duller and grayer, with less buffy infusion: 2) by the upper side of the tail being, like the sides and below, quite white instead of more grayish buffy; and 3) by the palms and soles being considerably more hairy. In true carillus the soles, along their middle line at least, are naked almost to the heels, while in all the five available specimens of H. c. marcarum, taken at different seasons, the soles are hidden by the hairs to the level of the fifth or sixth sole pad" (Thomas, 1920a, p. 231).

Sanborn (1950) described H. lepidus montanus from Bolivia: El Cumbre, 15,200 ft. (4600 m). He reported it to be similar in size to H. l. ducilla from the Titicaca Lake region of southern Peru, but much darker. General color of back near Clove Brown, lighter on head and sides. A narrow line, close to Ochraceous Buff, extends from below the eye to the rump and separates color of upper parts from the dark grayish-white under parts. All hairs with long slaty bases. Skull as in ducilla. He remarked that "This dark race is closely related to ducilla on the north and on the south probably to H. carillus from northwest of Cochabamba,

from which it differs by its darker color, shorter tail, and lack of a prominent post-auricular patch" (p. 5).

Remarks: Sympatric with C. musculus in Bolivia, and C. sorellus in Peru (Dorst, 1971, 1972a). Can be a crop pest, as in the vicinity of the Salar de Uyuni, Bolivia, in the winter of 1986 (personal observation).

Pearson (1982) included C. lepidus in a group that is widespread at high elevation in the altiplano. Dorst (1972b) reported elevations of 3800-4300 m. Dorst (1971) said that C. lepidus, while sympatric with C. sorellus is less common in the same habitat, and that preferred habitat was grassy areas, never in denser vegetation. Pearson and Ralph (1978) collected specimens in the sparsely vegetated portions of their trap grid.

Many names have been used for this species, see for example Pearson (1951), Soukup (1961), and summaries in the taxonomic history above. It is possible that there is seasonal variation in color, i.e., the bright and dusky phases of Hershkovitz (1962). The bright specimens could be in winter pelage from August to October, and the darker specimens, in summer pelage, caught mostly in May. Further study, including additional specimens from the southern portion of the range will be critical in deciding which, if any, subspecies should be recognized. The preliminary karyotypic work, $2n=36$ in Junin and Puno, Peru, and $2n=44$ in

Oruro, Bolivia, suggests that subspecific recognition may be warranted.

Notes from specimen labels include "caught overnight in small rocks in grass", "at night by rock wall", "caught under rocks in barren thorn sage", "rocky-grassy hill top, overnight", "in grassy gully, overnight", "sand among spiny Festuca clumps" from localities in Peru, and "sandy soil hillside with shrubs and grass", and "wet grassy area adjacent to stream" from the department of Oruro, Bolivia. A specimen from the province of Antofagasta, Chile, was caught "in dry bunchgrass alongside a stream" (Koford, 1955, p. 466).

Dorst (1972b) reported the heart weight to be 0.70 to 0.84 % of the body weight in adults.

Reproductive information includes a female from the department of Oruro, Bolivia, with four embryos that measure 6 mm (crown-rump) in August, and a lactating female and a female with 4 embryos measuring 14 mm (crown-rump) from the department of Tarija, Bolivia, in September. Specimens from departments in Peru: from Arequipa, a pregnant female in December, and one with 5 embryos, 12 mm (crown-rump length) in April; from Ancash, a female with 4 embryos measuring 2 mm in September; from Lima, a pregnant female in July; from Moquegua, a female with 5 embryos in January; and from Puno, a female with 4 embryos measuring 10 mm in August,

and a lactating female in February. This species appears to be reproductively active all year.

Other species commonly associated with C. lepidus include Eligmodontia typus, Auliscomys pictus, A. sublimus, Akodon boliviensis, A. albiventer, A. jelskii, Phyllotis xanthopygus, and P. osilae. See Thomas (1884, 1902a, 1919a, 1920a), Pearson and Ralph (1978) and Pearson (1982) for a more complete list. Also see Osgood (1943) for the species of northern Chile, although he did not include Calomys lepidus in the Chilean fauna. The first published record from Chile was by Koford (1955). Predators include Canis culpaeus andinus (stomach contents of AMNH 262663, from Estancia Agua Rica, 40 km E and 22 km S of Sajama, Department Oruro, Bolivia, 18°20'S, 68°36'W).

Calomys murillus (Thomas, 1916)

Hesperomys murillus Thomas, 1916b, p. 183, type locality:

La Plata, Province of Buenos Aires, Argentina. Type
specimen: BMNH 6.4.6.26.

Hesperomys murillus cordovens Thomas, 1916b, p. 184, type

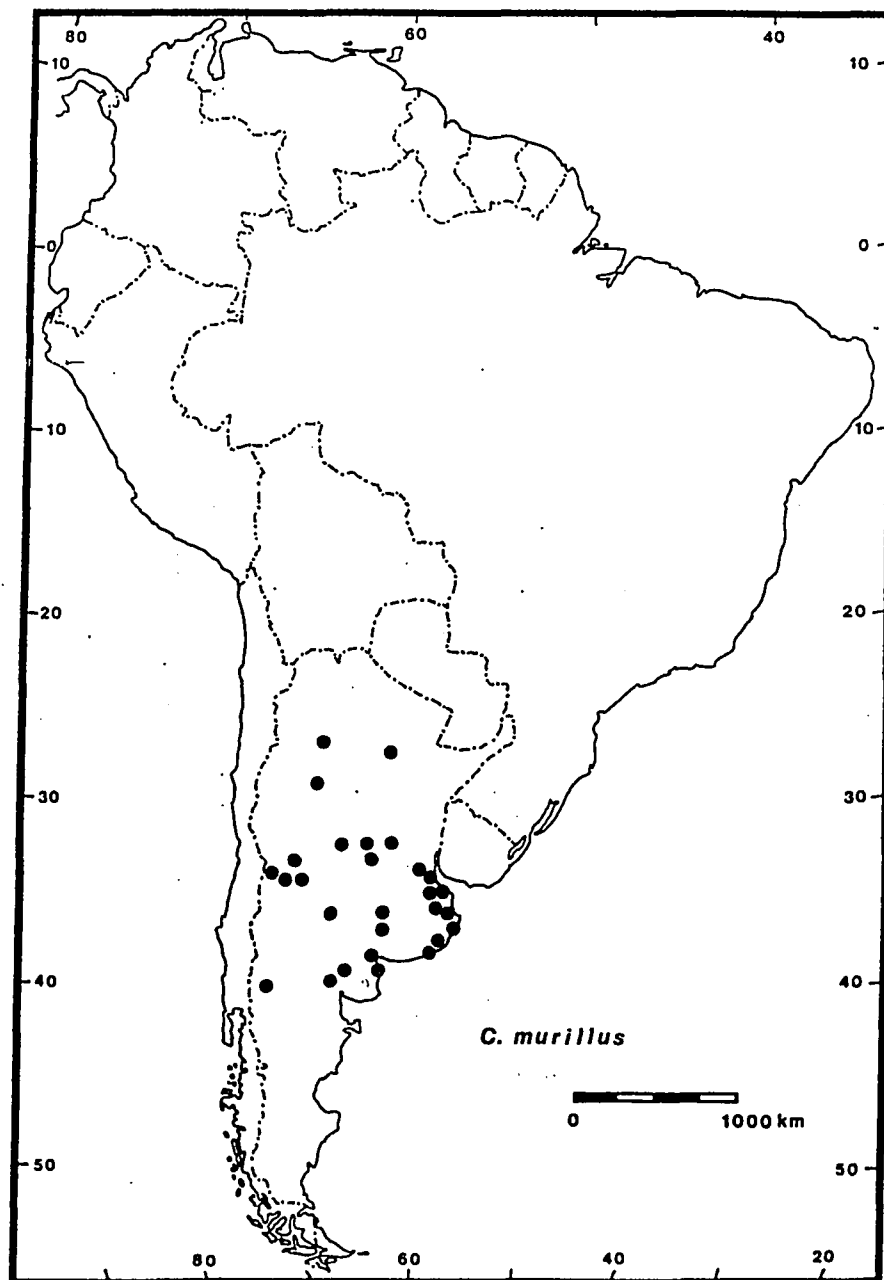
locality Yacanto, near Villa Dolores, Province of Cordoba,
Argentina. Type specimen: BMNH 16.1.6.24.

Diagnosis: Calomys murillus can be distinguished from all other species of the genus Calomys on the basis of the following characters: body size moderate for genus, total length of adults 140 to 175 mm; tail long, equal to or longer than head and body length; dorsum gray, occasionally with a darker appearance at rump, venter gray, hairs with white tips; skull small, greatest length of skull in adults generally 20 to 23 mm; maxillary toothrow generally 3.15 to 3.5 mm; occurring at low to moderate elevations in eastern Argentina, generally less than 1200 m.

Distribution: Low to moderate elevations in Argentina (see fig. 25).

General Description and Comparisons: Thomas (1916b) in his original description wrote that the color is "mouse-grey above,

Figure 25. Map of the known localities of Calomys murillus.



slightly more drabby posteriorly, an inconspicuous buffy wash along the sides; under surface greyish white, the bases of the hairs slaty" (p. 13).

The dorsum is brown with black hairs. The venter occasionally has a buffy wash. The ears are medium-sized, greyish brown, with a well-marked postauricular white patch and small buffy preauricular tufts. The nose is paler than the head. Chin hairs are white to base. Cheeks are buffy brown. The tail is usually equal to or longer than the head and body length, but sometimes slightly shorter; bicolored dark brown above, slightly darkening terminally, whitish below. The number of mammae is variable, one specimen had six pairs (3-3=12), five pairs were also observed (3-2=10).

The skull is small. The supraorbital region is divergent posteriorly, but without marked supraorbital ridges or ledges. An alisphenoid strut is rarely present (table 4). Foramina are present at the junction of squamosal-alisphenoid groove and the groove for the masticatory-buccinator branch of the maxillary nerve (table 5). Dentition is as described for the genus; the anteromedian flexus is well-developed and an anteromedian style is generally present (tables 6-7). External and cranial measurements are given in table 2.

Calomys murillus differs from C. callosus, C. venustus, and C. tener by smaller size, longer tail, and lack of a ridged

supraorbital region. It is readily distinguished from C. lepidus and C. sorellus by a longer tail, smaller body and skull size, paler dorsal pelage and shorter hair. The long tail and larger body and skull size distinguish C. murillus from C. laucha, C. bimaculatus, and C. hummelincki. Compared to C. bimaculatus, with which it is sympatric in Argentina (Massoia and Fornes, 1964), C. murillus is slightly larger, has a longer tail, a different number of chromosomes, and a line continuing the angle of the zygomatic plate forward passes in front of the incisors. The baculum differs (Massoia et al., 1968), also. The rostrum is more pointed in C. murillus than in C. laucha, and the bullae are more rounded. It is difficult to distinguish C. murillus from C. musculus; the most obvious difference is in size (see table 2 for comparative measurements), although a small or young individual of C. musculus is about the size of an adult C. murillus. Calomys murillus tends to have smaller bullae, slightly darker dorsal pelage, and occurs at lower elevation than C. musculus. See figures 32-35 for comparisons of the species of Calomys.

Karyology: There is some uncertainty about the karyotype. Massoia et al. (1968) published the karyotype of C. musculus murillus from the province of Buenos Aires, Argentina, as $2n = 38$ with a fundamental number of 50. They said it had 6 pairs of

large metacentric chromosomes, 12 pairs of large and probably acrocentric, and an "X" and "Y".

Gardenal et al. (1977b), published the karyotype for C. musculus from Laguna Larga and Cosquin, Province of Cordoba, Argentina, as $2n = 38$, number of autosomal arms = 56. They divided the chromosomes into 5 groups:

1. 1 pair large and metacentric, 1 pair large and acrocentric.
2. 5 pairs medium and acrocentric.
3. 4 pairs medium and submetacentric, 2 pairs medium and metacentric, 1 pair submetacentric with subterminal centromere, and 1 metacentric chromosome with morphology similar to group "1", the shortest.
4. 1 pair small and metacentric, 1 pair small and submetacentric.
5. 2 pairs plus 1 chromosome, small and acrocentric.

Summary: 1 large and metacentric pair, 7 medium metacentric pairs, 2 small metacentric pairs, 1 large acrocentric pair, 5 medium acrocentric pairs, and 2 small acrocentric pairs, and the X and Y. They frequently observed satellites, secondary constrictions, and association of acrocentrics.

Taxonomic History: Calomys murillus was first described by Thomas (1916b) from La Plata City, Las Talas, Ensenada, and Bahia Blanca, Buenos Aires, Argentina. He said the general appearance resembled that of Mus musculus, and that "This mouse is readily

distinguishable from H. laucha by its conspicuously longer tail, but is otherwise closely like that species. It is the only member of the restricted genus Hesperomys in which the tail is proportionally so long" (p. 184). Body measurements given for the type specimen are: head and body length 72 mm; tail length 72 mm; hindfoot length 16.5 mm; and ear length 13.5 mm.

H. murillus cordovensis was described by Thomas in the same paper (1916b) from the province of Cordoba. He wrote that the "general characters as in true murillus of La Plata, but the colour paler and less saturate, the back nearly matching "drab" of Ridgway; sides rather more buffy. Under surface more heavily washed with buffy whitish, the slaty bases of the hairs less evident. Colour of crown especially lighter and more drabby than in true murillus" (p. 184). He suggested that the braincase may be more inflated than in murillus, but did not have enough specimens to compare.

Calomys murillus was synonymized with C. laucha by Hershkovitz (1962).

Contreras and Justo (1974) used the name Calomys musculus murillus.

Contreras and Rosi (1980b) used the name C. musculus cordovensis, as a separate subspecies from C. musculus murillus. They wrote that the tail length was more frequently longer than the head and body length in cordovensis than in

murillus (69 % of specimens vs. 51.6 %, respectively).

Remarks: Much confusion has been associated with the names used for this species, C. laucha, C. bimaculatus and C. musculus (most frequently, C. musculus), partly because they were all synonymized by Hershkovitz (1962). In some of the studies it is impossible to know which species is being referred to because no measurements or descriptions are given (for example Dalby, 1975) and C. bimaculatus and C. murillus are widely sympatric in parts of Argentina, especially in the province of Buenos Aires, where many studies are done (Massoia and Fornes, 1964, 1967b). Possibly C. murillus and C. musculus are both found in Catamarca Province, Argentina. It is possible that with further study these will be found to be conspecific, if so, C. musculus has priority as a name. The subspecies might be C. musculus musculus for the larger mice at higher elevations and C. musculus murillus for the smaller mice at lower elevations and more southerly areas. Until further work is done, including more collecting from intermediate areas and more genetic studies, I prefer to recognize two separate species, as they are separable on the basis of size and pelage coloration.

Thomas (1916b) wrote of C. murillus that "this animal is not much of a burrower, but lives about in the grass, and examples may be easily obtained by kicking up loose heaps of hay, thistle-stalks, or other rubbish, under which the mice take

refuge. One specimen I have marked as found under a heap of thistle-stalks, in a round nest, the size of a tennis-ball, made of thistle-down. Another was dug up, semi-torpid, in very cold weather, from about 6 inches below the surface of the ground" (p. 184).

Notes from specimen labels from La Plata, the type locality include "At mouth of hole in field full of Acodon [sic] runs, Museum park", "Sound asleep in a round nest 6 inches underground", "caught by museum boy. Species this size will not enter traps", "Found under heap of thistle stalks, with round nest, size of tennis ball made of thistle down", "under thistle stalks in fields beyond hippodrome", "in hole in museum park", "fields by hippodrome, cheese bait", "museum park", "among Tala trees", others from Buenos Aires Province, "amongst tall grass in poplar plantation", "in sheeps skull in carcase heap". Specimens from Tucumán, have notes that say "eye black, "caught by the hand", "eye black, caught by a dog". Specimens from Chumbicha were "caught among the wild cactus-plants" (E. Budin, collector's notes, in Thomas, 1919b). Specimens from Catamarca were caught in a hilly district and "Caught among the piles of branches in the cultivated fields" (E. Budin, collector's notes from Thomas, 1920b).

Fornes and Massoia (1965) reported the common name as "laucha manchada mediana".

This species was trapped in an arroyo in Buenos Aires (Fornes and Massoia, 1965); was trapped at the foot of arid monte, ca. 900 m, (Contreras and Roig, 1976); is known from the pampas (Thomas 1927a), and from crop fields in Buenos Aires (Massoia and Fornes, 1967b).

It is rare in Buenos Aires (Fornes and Massoia, 1965), captured in low frequency in Buenos Aires (Kravetz et al., 1975), common in Cordoba (Crespo et al., 1970), common in corn and wheat fields, more common in the center of the fields than along the borders (Kravetz and Villafañe, 1981; Villafañe et al., 1977), and common in Mendoza (Contreras and Rosi, 1980b).

Contreras and Rosi (1980a) reported that this species accounted for 94 out of 330 captures (28.5 %) of which 21 individuals accounted for 90 of the 94 (22.33 %), and that males outnumbered females (12 to 9). They reported the species to be territorial, and to have an average home range size of 366.07 m².

Kravetz et al. (1975) suspected competition with Mus musculus.

Dalby (1975) used the name C. musculus for the second species of Calomys in Barcarce, province of Buenos Aires, Argentina. He gave no measurements and mentioned no specimens, so his identification is unverifiable. The comments he gave on "C. musculus" include low density in traps, higher in owl pellets

(Asio flammeus), and scat of Galictis cuja. Of 28 rodent prey items, 57.1 % were Calomys. These mice appeared mainly as winter season transients and were never more than 8 % of daily catch. Owl pellets accounted for 75 % of the "C. musculus" caught (12/16). These seed-eaters were caught in corn fields, with Mus musculus and were often affected by skin mites. Calomys are associated with human habitation, and are reservoirs of Junin virus (a virus causing Argentine Hemorrhagic fever), and bubonic plague (Contreras and Justo, 1974; Massoia and Fornes, 1967b).

Reproductive information is scarce. Females of 16 g and up tend to be sexually mature (Crespo et al., 1970; Villafañe, 1981), and maturity is reached in 72.5 days (Villafañe, 1981). Males reach sexual maturity after 82 days and at about 19.8 g (Crespo et al., 1970; Villafañe, 1981). Gestation lasts about 24.5 days and the length of the estrous cycle is about 5.7 days (Villafañe, 1981). Crespo et al. (1970) reported reproductive activity in males from September to April, with a concentration between November and February, and females were active from November to June, with the most activity between November and April, with only a small percentage of individuals were reproductively active between October and November. They said the greatest number of pregnant females were caught from October to January, and March to April.

The number of embryos ranged from 2 to 11, with an average from 5.7 to 8.5 (Crespo et al., 1970), and the average was 5.4 according to Villafañe (1981). Villafañe (1981) found the sex ratio of the litter to be 1.25 females per 1 male. A specimen from the province of Cordoba had 7 embryos in March, and a second had 3 embryos in March, a female from Neuquen had 9 embryos in November.

Ectoparasites were reported by Fornes and Massoia (1965).

Some commonly associated species include Akodon azarae, A. obscurus, and Oryzomys (Oligoryzomys) nigripes (for other species associated see Thomas, 1919b, 1920b, 1921b, 1927a; Crespo et al., 1970; Villafañe et al., 1973; Contreras and Justo, 1974; Dalby, 1975; and Kravetz et al., 1975). For specimen records see Thomas (1926a, 1927a); Massoia and Fornes (1964); Fornes and Massoia (1965); Massoia et al. (1968); Contreras and Justo (1974); Contreras and Roig (1976); and Corti et al. (1987).

Calomys musculus (Thomas, 1913)

Eligmodontia laucha musculina Thomas, 1913, p. 138, type locality:

Maimara, Province of Jujuy, Argentina, 2230 m. Type

specimen: BMNH 12.12.12.9.

Hesperomys musculus cortensis Thomas, 1920a, p. 190, type

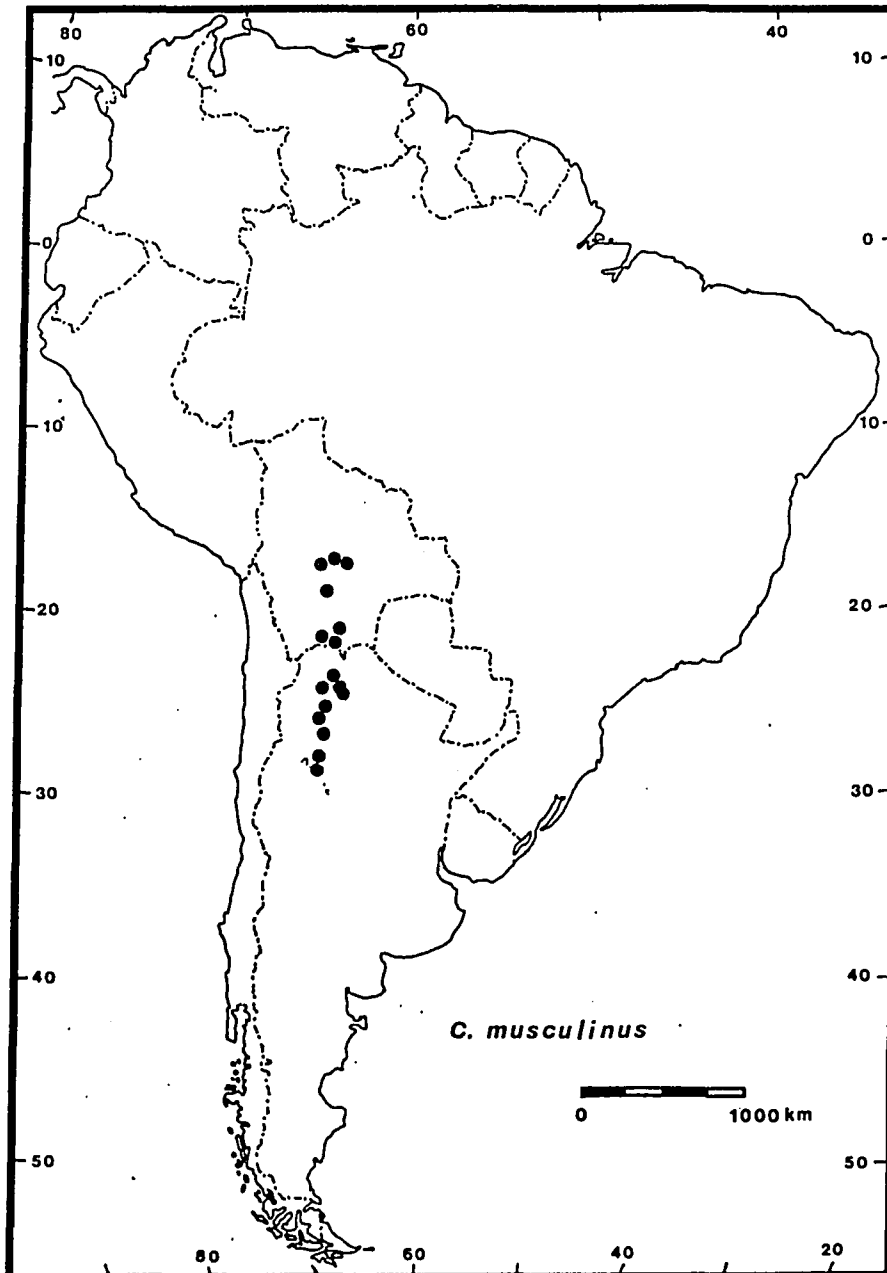
locality: Jujuy, Province of Jujuy, Argentina, 1200 m. Type

specimen: BMNH 20.1.7.46.

Diagnosis: Calomys musculus can be distinguished from all other species of the genus Calomys on the basis of the following characters: body size moderate, total length of adults generally 155 to 200 mm; tail long, equal to or slightly longer than head and body length; dorsum sandy brown, frequently lined with black hairs, venter white, hairs gray at base; skull medium in size, greatest length of skull in adults generally 22 to 26 mm; auditory bullae slightly inflated; maxillary toothrow moderate, 3.4 to 3.8 mm; occurring at moderate to high elevation, 1000 to 3500 m.

Distribution: Moderate to high elevations in the eastern slopes of the Andes mountains in Bolivia and northern Argentina (see fig. 26).

Figure 26. Map of the known localities of Calomys musculus.



General Description and Comparisons: In the original description, Thomas wrote of the color that the "general colour above rather paler, drab-grey; under surface greyish white, with a slight drabby tinge. White post-orbital patch less conspicuous" (Thomas, 1913, p. 138). The tail is weakly bicolored, darker above.

The skull is moderate in size for the genus, not delicate. The auditory bullae are slightly inflated, the supraorbital edges are not beaded or ledged, but do diverge posteriorly. An alisphenoid strut is rarely present (table 4). Foramina along squamosal-alisphenoid groove are frequently present (table 5). Dentition as for genus, an anteromedian style is frequently present and the anteromedian flexus is well-developed (tables 6-7). External and cranial measurements are given in table 2.

Calomys musculus can be distinguished from all species of Calomys except C. murillus, by its very long tail, medium size, lack of ridges on the supraorbital region, and sandy dorsal coloration. See the previous accounts for specific comparisons, especially that of C. murillus with which C. musculus is most likely to be confused. It differs from C. murillus in its larger size (see table 2), longer toothrow, and slightly inflated bullae. See figures 32-35 for comparisons to other species of Calomys.

Karyology: No karyotype of this species has been published. Preliminary analysis of a karyotype from an individual from the vicinity of Comarapa, Department of Santa Cruz, Bolivia, suggests a diploid number of 38, which is the same as that reported for C. murillus. Reig (1986) remarked that although the karyotype is unpublished, it is morphologically different from that of C. murillus.

Taxonomic History: Thomas (1913) described Eligmodontia laucha musculina from Maimara, Argentina, 2230 m. He said the skull is "decidedly larger than is normal in E. laucha, though unusually large examples of the latter may just attain the size of small specimens of E. l. musculina". He gave body measurements of the type (an adult male) as head and body length 100 mm; tail length 98 mm; hind foot length 21 mm; and ear length 16 mm.

He further wrote "I have been in some doubt as to whether this mouse ought not to be called a separate species, as its skull is so much larger than that of ordinary Buenos Aires specimens of E. laucha. But both forms seem to vary a good deal in size, while there are no other distinctions of importance, and therefore it may, for the present, be attached to E. laucha in order to emphasize its difference from the still larger E. callosa, in which supraorbital beads are developed in old examples" (Thomas, 1913, p. 138).

Thomas (1920a) described Hesperomys musculus cortensis, a new subspecies from Jujuy, Province of Jujuy, Argentina, at 1200 m. He wrote "Size rather less than in true musculus of Maimara, feet and tail averaging shorter. Colour above slightly duller, browner, and less clear, and below, where the difference is more noticeable, the tone is a dull pale drabby, approaching (though much less than) that found in Mus musculus, while in true musculus the colour is a clear greyish white, with scarcely any suspicion of drabbiness" (p. 191), and that "This laucha is no doubt very closely allied to the true musculus of Maimara, with which it shares the number of 14 mammae; but on comparison of 15 specimens with 6 of musculus it proves to have so uniformly drabbier an under surface, while both feet and tail average shorter, that I have thought it worthy of having a distinctive name" (p. 191).

Herskovitz (1962) synonymized this species with C. laucha.

Remarks: Information on this species is scarce. The type specimen of C. musculus cortensis was "caught in straw-yard" according to the collector, E. Budin (in Thomas, 1920a). Notes from specimen labels include "habitat dense shrubs (3 m ht) adjacent to cloud forest. 100 % ground cover of ferns and grasses" and "in vineyard", both from Bolivia.

Mares et al. (1981a) in their account of Calomys laucha, in Salta Province, Argentina, included one specimen that I have

identified as C. musculus. This specimen was collected at 5 km NE Cafayte, at 1660 m, in Precordillera Monte desert, in a sandy area. This area was described as "Extreme Prosopis forests predominate in mesic localities, whereas Larrea forms the major vegetation on the bajadas. Tall cacti (Trichocereus) are common" (p. 159).

De Fonollat (1984) reported localities in Tucuman, Argentina and habits of C. musculus. He gave the tail length as 80, but little other descriptive information, thus the identification is uncertain. He said the species was found in shrubby fields, forests, and savannah, frequently in houses, and that it is a good runner and jumper.

Reproductive information is not available for this species.

For associated species see Thomas (1920a) and Mares et al., 1981a). Additional localities were reported by Thomas (1920b, 1926a) and Dalby and Mares (1974).

Calomys sorellus (Thomas, 1900)

Eligmodontia sorella Thomas, 1900, p. 297, type locality: 8 mi S of Huamachuca, Department of La Libertad, Peru, 3500 m. Type specimen: BMNH 0.6.6.29.

Hesperomys frida Thomas, 1917, p. 1, type locality: Chospyoc, Department of Cuzco, Peru, 10,000 ft. (3050 m). Type specimen: USNM 194779.

Hesperomys frida miurus Thomas, 1926b, p. 314, type locality: Yano Mayo, Rio Tarma, Peru, 8500 ft. (2590 m). Type specimen: BMNH 26.2.1.26.

Diagnosis: Calomys sorellus can be distinguished from all other species of the genus Calomys on the basis of the following characters: body size moderate to large, total length 145 to 190 mm; tail moderately long, but always less than the head and body length; dorsum dark grayish brown, sides paler, often with a buffy line separating the venter, venter whitish, hairs gray at base and white at tip; fur long and soft; skull moderate to large, greatest length of skull 22.5 to 27.5 mm; interorbital region parallel-sided; molar teeth moderate in size, maxillary toothrow

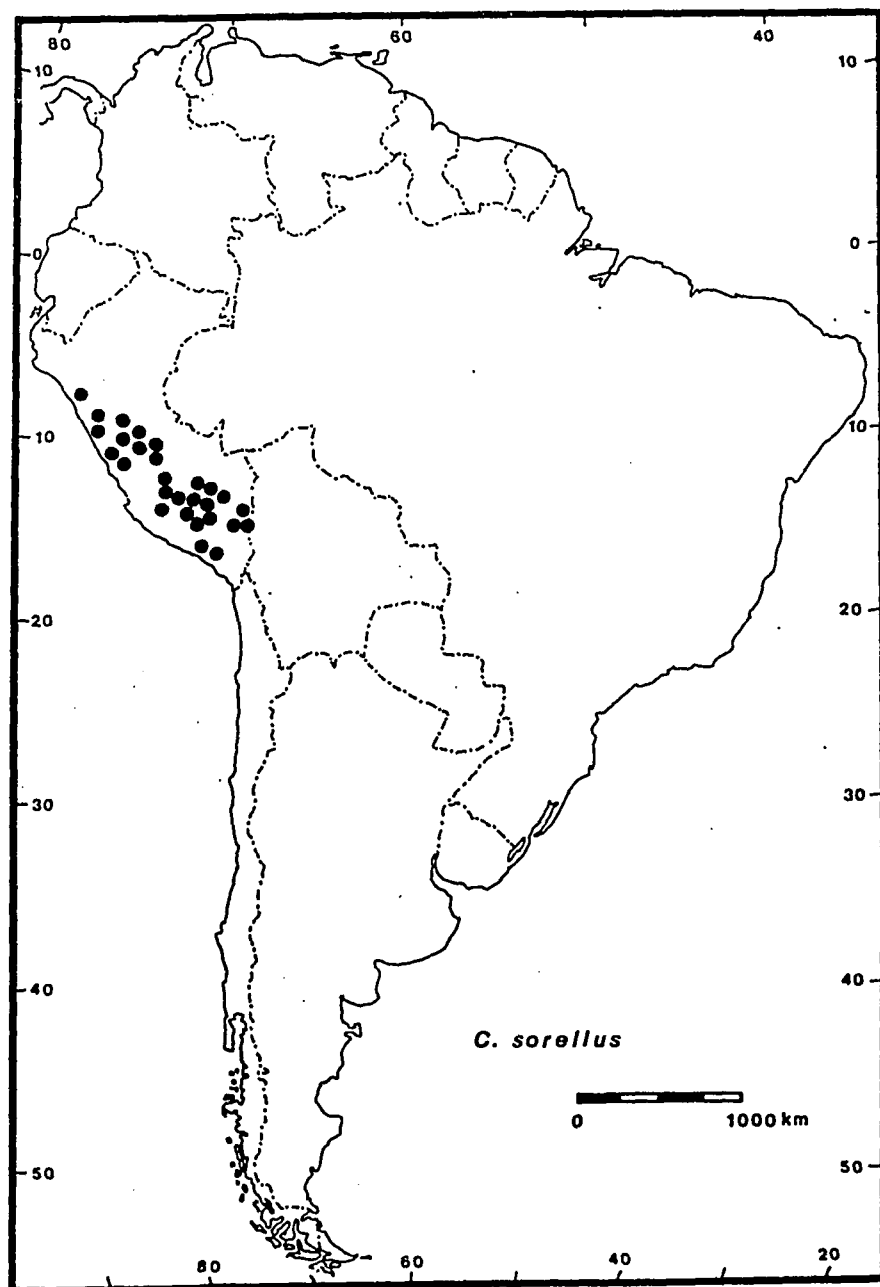
generally 3.4 to 3.8 mm; occurring at high elevations in Peru, generally over 2500 m.

Distribution: High elevation in Peru, possibly occurs in Bolivia in the vicinity of Lake Titicaca (see fig. 27). For a description of the vegetation of the Puno, see Walter and Breckle (1986).

General Description and Comparisons: Calomys sorellus has long, smooth, very soft and fine fur, about 9 mm long on the back and 6-7 mm ventrally. The dorsum is mixed with longer hairs, which are about 16 mm in length. General dorsal color grayish brown, sometimes dark brown, closely lined with black. The sides are paler and have a well-defined buffy line separating the venter. The tips of the longer dorsal hairs are silvery. The venter is whitish, the hairs are slaty gray basally and white terminally. The face is slightly grayer than the back. The ears are of medium length, their visible surface when folded brownish, colored like the head, and with a white post-auricular patch. The upper surface of hands and feet pure white; the proximal third of soles is thinly hairy. The tail is shorter than the head and body length, is sharply bicolored, brownish above, darkening nearly to black at the tips, white below and on the sides. There are four pairs of mammae, 2-2=8.

The skull is moderate to large in size for the genus. The interorbital region is flat, its edges square but not beaded,

Figure 27. Map of the known localities of Calomys sorellus.



giving a parallel-sided appearance. The auditory bullae are small. An alisphenoid strut is absent (table 4). Foramina along squamosal-alisphenoid groove are present (table 5). (Description modified from Thomas, 1900, 1920c).

Dentition is as described for the genus, an anteromedian style is present or absent and the anteromedian flexus is well developed (see tables 6-7). External and cranial measurements given in table 2.

Calomys sorellus can be distinguished from all other species of Calomys on the basis of size and its parallel-sided interorbital region. It is larger than C. bimaculatus, C. laucha, C. hummelincki, C. lepidus, C. tener, and C. murillus. It is smaller than C. callosus and C. venustus. It is somewhat similar in size to C. musculus, but has a shorter tail. Calomys tener and C. venustus both have ridged, posteriorly divergent supraorbitals, as does C. callosus. See also comparisons in the previous species accounts.

Compared to C. lepidus, with which it is sympatric in Peru, C. sorellus has a longer tail, is larger bodied, is less marbled in appearance, and has a grayer venter. See figures 32-35 for comparison to the other species of Calomys.

Karyology: Pearson and Patton (1976) published karyotypes of C. sorellus from several localities in Peru. They noted a basic karyotype of $2n = 64$, with three small metacentric pairs,

and the rest of the autosomes, acrocentric. The subtelocentric X is the largest, and the acrocentric or subtelocentric Y is the smallest. They mentioned that several pairs of the autosomes seem to be subtelocentric. One specimen from the department of Apurimac had a diploid number of 62. They suggested that this species may need to be divided later, on the basis of karyotypes.

Taxonomic History: Thomas (1900) described Eligmodontia sorella from 8 mi S of Huamachuca, in northwestern Peru, at 3500 m. The type is an adult; body measurements given were head and body length 72 mm, tail length 62 mm, hind foot length 18 mm (cu 19.5), and ear length 17 mm.

Thomas wrote of this species, "This pretty little mouse has no near relation to the E. lepida of Central Peru, which is one of the very short-tailed species, but is most closely allied to the Argentine and Paraguayan E. laucha Desm., from which it differs by its longer and softer fur, more fawny colour, longer and slenderer feet, and other details" (Thomas, 1900, p. 298).

In 1917, Thomas, described Hesperomys frida from Peru. He said it was large with a comparatively long tail and that the supraorbital ridges were little divergent. Measurements given were head and body length of 102 mm, tail length of 91 mm; hind foot length of 19 mm, and ear length of 18 mm. He gave a more complete description of this species in 1920 and said "This

species differs strikingly from the other equal-sized species of restricted Hesperomys by the Phyllotis-like build of its interorbital region, the edges of which are symmetrically concave, and without the broadly divergent ridges found in H. venustus and its allies and also in Graomys. From Phyllotis it is distinguished by its absolutely brachyodont molars, these being semihypsodont in that genus" (Thomas, 1920a, p. 231).

Thomas did not compare Hesperomys frida with Eligmodontia sorella. The measurements given for H. frida are larger, possibly due to an older individual, but measurements for both specimens are well within the range for the species (see table 2).

In 1926, Thomas described Hesperomys frida miurus from Yana Mayo, Rio Tarma, 8500 ft., Peru. He said it was similar to typical H. frida but that the tail was uniformly shorter. The number of mammae was given as the same as typical H. frida. He also commented that it is more difficult to distinguish Hesperomys and Phyllotis in Peru, than further south. There are some small species of Phyllotis in Peru that are more similar cranially (but not dentally) to Calomys, such as P. andinus and P. amicus (Thomas, 1926b).

Remarks: Calomys sorellus occurs at high elevations in Peru, above 4200 m (Pizzimenti and de Salle, 1981), 3800-4300 m (Dorst, 1972a, b; Pizzimenti and de Salle, 1980).

C. sorellus is widely sympatric with C. lepidus in Peru (Pearson, 1982; Dorst, 1971, 1972a).

This species is found in diverse rocky habitats dominated by "ichu" grass and Tola shrubs (Pizzimenti and de Salle, 1980); in short mountain scrub, bunch grass, "yareta" (Pizzimenti and de Sale, 1981); grassland and or Pampa Steppe is a preferred habitat, the dominant plants there are Festuca, Calamagrostis, and Stipa (Dorst, 1971, 1972a).

Dorst (1971) reported that the percentage of the rodent biomass comprised of C. sorellus ranged from 4.2 to 40.7 percent at different stations and that C. sorellus accounted for the highest biomass in steppe habitats. Dorst found the population to be 22 % young, and 78 % adults, the weights given were 15 g for young individuals and 20 g for adults. Dorst (1972a) reported the density of C. sorellus as 8 to 9 individuals per hectare, and the biomass of this species ranging from 20 to 40 percent of the total rodent biomass in their studies.

Pearson (1982) included C. sorellus in a group of high elevation species that occur across the Andes on the altiplano.

Notes from specimen labels include "trapped in rocks in thicket", "trapped in hole in the ground near grain field", "trapped in rocks by grain field", "trapped under rocks in

brush, "trapped by wall by grain field", "caught in weed patch in daytime", "trapped in dry maguey hedge", "trapped by stream", "trapped in bushy dell above corn field", and "trapped in rocks in thicket".

The species is nocturnal, with most activity between 1800 and 0500 hours and the maximum activity period between 1900 and 2200 hours (Dorst, 1971).

Pizzimenti and de Salle (1980) reported the diet to be unlike that of other phyllotines; C. sorellus nearly exclusively feeds on insects. Insects accounted for 92 % of the diet; forbs 4 %, and grass 4 %. No seeds were eaten. They wrote that this species exhibited a narrow and invariable food niche. Dorst (1971) described this species as a granivore that eats grains of diverse species of little herbaceous plants (mainly from the mustard and composite families).

Dorst (1972b), found the heart weight to be slightly larger for males, and heart weight/body weight to equal 0.84-0.86 % in adults.

Reproductive information is scarce. Dorst (1971) reported that females have 3 or 4 embryos. Specimen labels show 3 pregnant females in August. One female had 2 embryos measuring 14 mm (crown-rump), the other two had 4 embryos each, in one case they measured 22 mm (crown-rump). Others include, from Ancash, a pregnant female, one with 2 embryos measuring 14 mm

(crown-rump), 2 lactating females, and one with 4 embryos, 22 mm (crown-rump) in August, a lactating female in September; from Ayacucho, a lactating female in May; from Huancavelica, a lactating female in August; and from Lima, 2 pregnant females in July and August. This species appears to be reproductively active during the winter months.

There is some geographic variation in color, specimens from northern Peru are paler and more grizzled, while those from further south are darker and more brown. Possibly, these are subspecific differences, the dark ones in the south, which may be slightly larger also, would then be Calomys sorellus frida, and the northern population would be C. sorellus sorellus.

Additional specimen localities were reported by Thomas (1920c, 1926b, 1927b). Some commonly associated species include Phyllotis xanthopygus, Akodon boliviensis, and Auliscomys pictus. For other associated species see Thomas (1927b), Pearson (1982), Pizzimenti and de Salle (1980).

Calomys tener (Winge, 1888)

Hesperomys tener Winge, 1888, p. 15, type locality: Rio das Velhas, Lagoa Santa, State of Minas Gerais, Brazil. Type specimen: Zoological Museum, Copenhagen, 252 (fig. 28, views, photos courtesy of Dr. Alfred Gardner).

Diagnosis: Calomys tener can be distinguished from all other species of Calomys on the basis of the following characters: body size moderate, total length of adults generally 125 to 165 mm; tail moderate to long, not as long as head and body length; dorsum often dark reddish, the hairs gray at base, venter pale to dark gray; skull moderate in size, greatest length of skull of adults 21.0 to 24.5 mm; supraorbital region distinctly ledged and divergent posteriorly; alisphenoid strut generally present; maxillary toothrow generally 3.2 to 3.6 mm; occurring in coastal and southern Brazil.

Distribution: Brazil (see fig. 29). For descriptions of the cerrado and caatinga habitats see Walter and Breckle (1986).

General Description and Comparisons: Calomys tener is moderately sized for the genus. The dorsal color is gray and frequently has a reddish hue. The venter varies from a light gray to a very dark gray that is almost indistinguishable from the

Figure 28. Dorsal, ventral, and lateral views of the cranium, and dorsal view of the mandible of the type specimen of Calomys tener. Negatives courtesy of Dr. A. L. Gardner. The greatest length of the skull measures 21.5 mm.

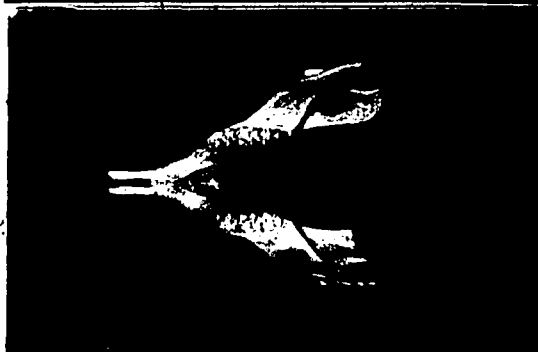
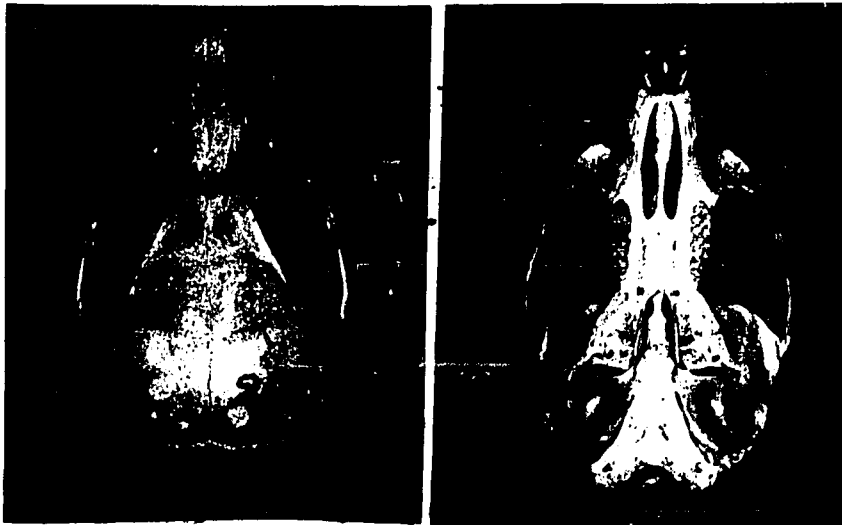
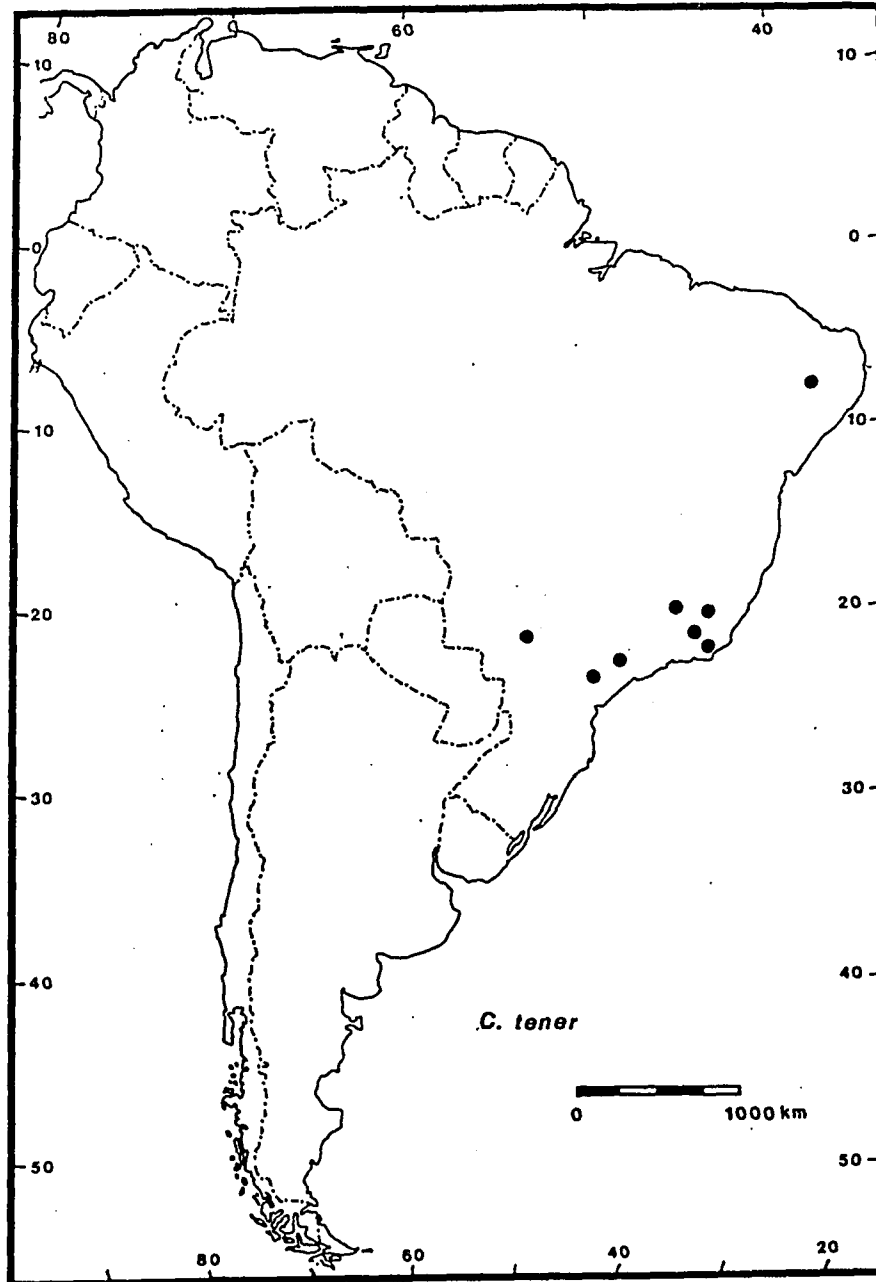


Figure 29. Map of the known localities of Calomys tener.



dorsal color. The tail is bicolored, dark above and pale below. It is never as long as the head and body length. Orange pre-auricular spots are present. There appear to be five pairs of mammae, 3-2=10; 3 pairs pectoral and 2 inguinal. In one specimen only 3 pairs were visible, 2 pectoral and 1 inguinal.

The skull is medium-sized for the genus. Distinct ridges are present at the edges of the supraorbital region. An alisphenoid strut is generally present (table 4). Foramina are present along the squamosal-alisphenoid groove (see table 5). Dentition as for genus, an anteromedian style is present or absent and the anteromedian flexus is moderately to well-developed (tables 6-7). External and cranial measurements are given in table 2.

Notes on the type specimen (courtesy of Dr. Alfred Gardner), a female, include information on pelage: hairs are white to base on throat (but not all specimens have a white throat), underparts appear buffy white, with a wash over the gray underfur. Digital brushes are present but sparse, some are longer than nails. He recorded the greatest length of skull as 21.5 mm, and the length of the maxillary toothrow as 3.3 mm. Many specimens I examined did not have white throats, the hairs were gray at the base.

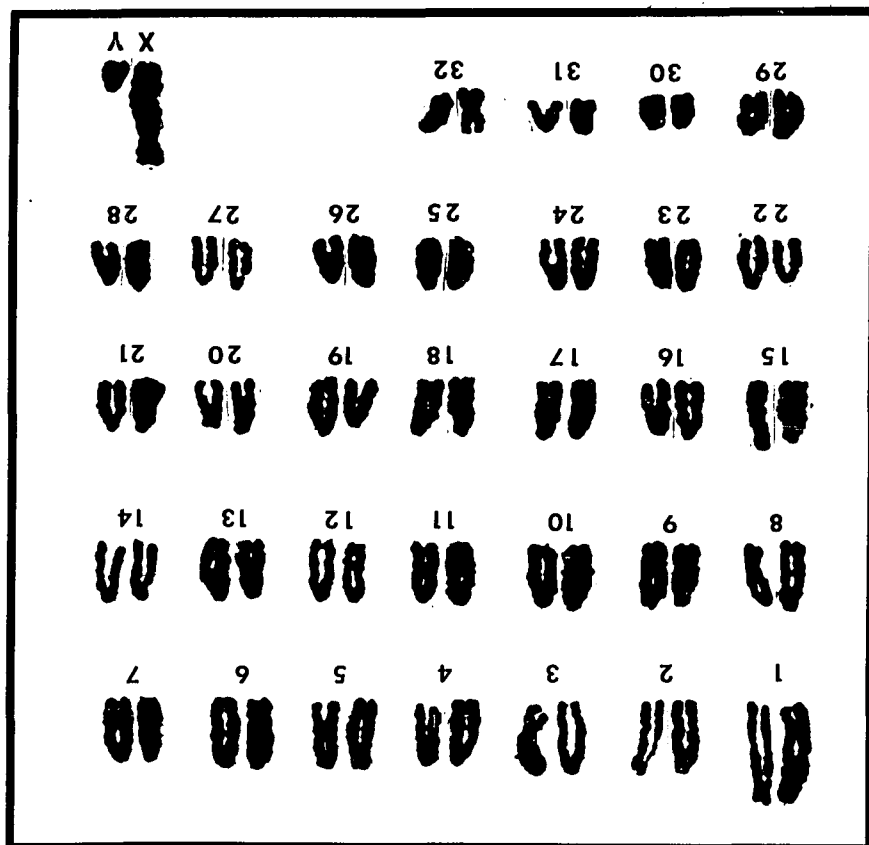
This species is occasionally misidentified as Thalpomys, on the basis of color and size. Examination of the skull and dentition will separate Thalpomys from Calomys, also, C. tener has

pale post-auricular patches and the dorsal surface of the feet are whiter.

Calomys tener can be distinguished from all species of Calomys except C. venustus and C. callosus by the presence of ridges along the sides of the supraorbital region. It is larger and has a relatively longer tail than C. bimaculatus, C. laucha, and C. hummelincki. Calomys murillus and C. musculus have relatively longer tails and tend to lack an alisphenoid strut. The pelage is much shorter than that of either C. lepidus or C. sorellus, both of which also have a more parallel-sided interorbital region. Calomys tener is smaller than either C. callosus or C. venustus and has an alisphenoid strut, which the others generally lack. See further comments under previous species accounts. See figures 32-35 for comparisons of the species of Calomys.

Karyology: Yonenaga (1975) reported a karyotype for Calomys sp. from Itapetininga, São Paulo, Brazil, as $2n = 66$. No mention was made of where the specimens were deposited. Slides prepared from specimens in the field from the vicinity of Exú (Brazil: Pernambuco; Exú), by Dr. A. Gardner, have a similar karyotype (fig. 30). Unfortunately, the location of these specimens is uncertain at this time, probably they are at the museum in São Paulo. I have examined a large series of specimens from Itapetininga, and they are all C. tener. It is assumed

Figure 30. Karyotype of a specimen of Calomys tener from Itapetininga, State of São Paulo, Brazil. Courtesy of Dr. A. L. Gardner.



tentatively, until examination of the specimens that were karyotyped, or until voucher specimens are clearly deposited, that this is the karyotype of C. tener. Yonenaga (1975) described the karyotype as $2n = 66$; all autosomes, except 1 small metacentric pair are acrocentric, and graded in size. The X is submetacentric and the largest in the complement.

Taxonomic History: Hesperomys tener (= Calomys tener) was described by Winge (1888). He gave external measurements for three specimens, two females and one male, and cranial measurements for a female (presumably, the type specimen). Also included were views of the cranium and mandible (plate 2).

Hershkovitz recognized C. laucha tener as a subspecies of C. laucha (Hershkovitz, 1962).

Recently, Mares used the name C. tener (Mares et al., 1981b).

Remarks: Data on this species are scarce. The habitat has been described by Alho (1982), Alho et al. (1986), and Dietz (1983). Dietz (1983) described his study area in central Brazil as characterized by paralld ridges nearly 1500 m in elevation, extending the length of the park (Serra da Canastra Natonal Park) and descending into valleys of approximately 800 m. The habitat is about 50 % grassland, 35 % cerrado vegetation - campo cerrado, and 15% seasonal tropical forest. The climate is subtropical and has well-defined wet and dry seasons. Annual precipitation is

1300-1700 mm. Disturbed habitat is present. He reported that C. tener was captured more frequently in the wet season (13/15) than the dry (2/15), that 30.8 % of the animals captured in the wet season were reproductively active while 50 % of those caught in the dry season were. Of the 15 individuals captured, 5 (33.3%) were caught in grassland, 9 (60%) in cerrado, and 1 (6.7%) in the forest.

Alho (1982) reported C. tener from the Atlantic forest of Minas Gerais. Alho (1981) reported two species in the cerrado in Fazenda Agua Limpa, Brasilia. He used the names C. callosus and C. expulsus. Perhaps one of these refers to C. tener (see discussion under "remarks" of the account of C. callosus). Alho et al. (1986) reported C. tener and C. callosus from this same locality. They noted that both species are most common in open habitats, especially valley-side wet campo (50 % of the captures), gallery forest campo (25%), and strict cerrado (25 %).

Notes from specimen labels include "in longhouse at base camp", and "farmed area 10 km S base camp" from specimens from Mato Grosso, and "trapped in cerrado", "short grass", "forest", "dry weedy area, near pond", and "grass pasture" from specimens from Minas Gerais.

Reproductive notes from Dietz (1983) include 2 lactating females in November, and 2 females with 4 embryos each in January and February. Notes from specimen labels (Dietz specimens)

include 1 female with 4 embryos measuring 3 mm (crown-rump) in February, a female with 4 embryos measuring 7 mm in November, and a female with 4 embryos measuring 4 mm in January. This species appears to be reproductively active during the summer months.

Ribeiro (1973) reported natural infection in the population of C. tener from northeastern São Paulo, Brazil, of Trypanosoma cruzi, the etiological agent for Chagas' Disease. Although he used the name C. tener, he gave no other data, so identification is not definite.

Other species with habitat preferences similar to those of C. tener are Bolomys lasiurus, Thalpomys lasiotis, and possibly Oxymycterus roberti (Dietz, 1983, see for further information). Additional specimen localities have been reported by Alho et al. (1986).

Calomys venustus (Thomas, 1894)

Oryzomys (?) venustus Thomas, 1894, p. 359, type locality:

Cosquin, Province of Cordoba, Argentina. Type specimen:

BMNH 83.4.16.1.

Eligmodontia callosa boliviae Thomas, 1901b, p. 253, type locality:

Rio Solocame, Department of La Paz, Bolivia, 1200 m. Type

specimen: BMNH 1.6.7.43.

Hesperomys venustus callidus Thomas, 1916b, p. 182, type locality:

Goya, Province of Corrientes, Argentina, 600 ft. Type

specimen: BMNH 98.12.3.12.

Hesperomys fecundus Thomas, 1926a, p. 321, type locality: Tablada,

Department of Tarija, Bolivia, 2000 m. Type specimen: BMNH

26.1.1.33.

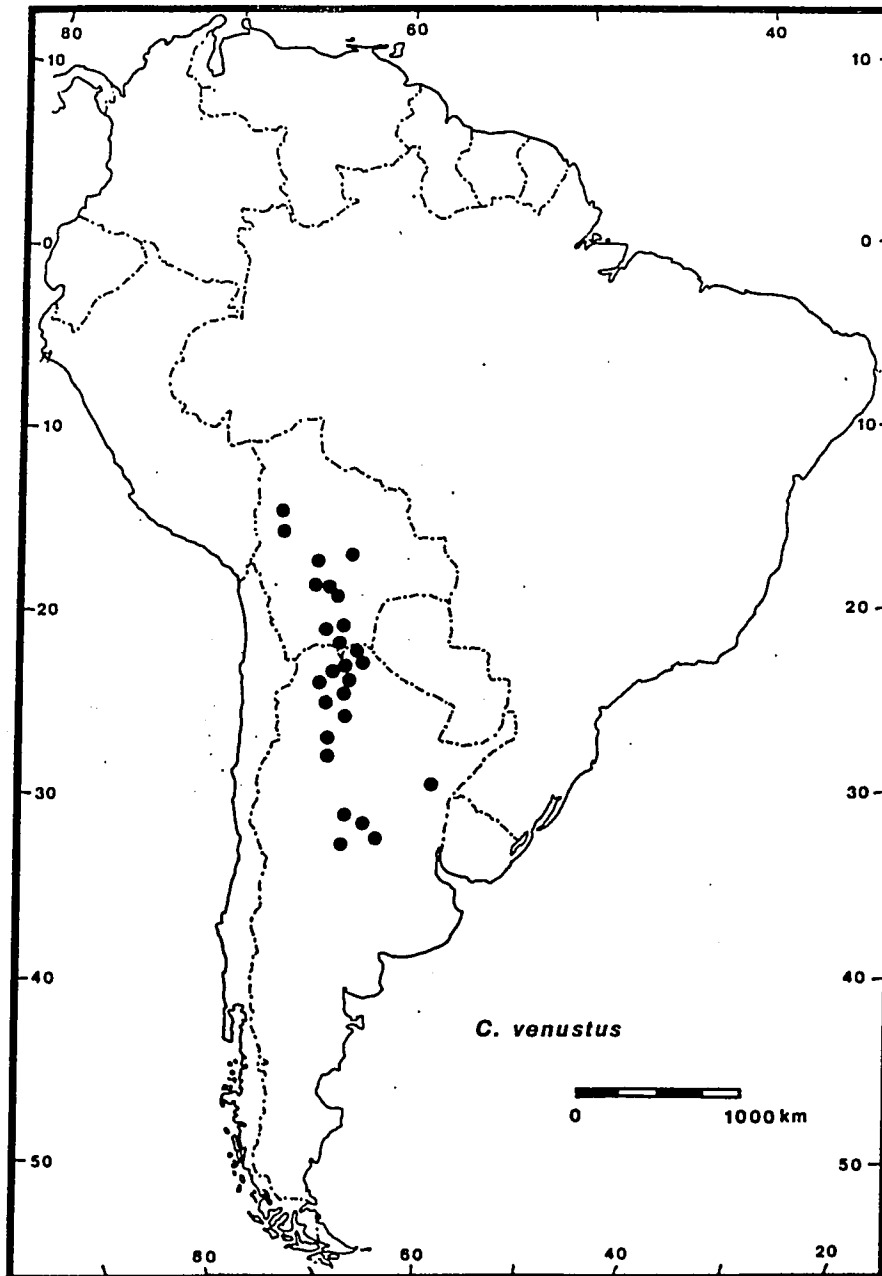
Diagnosis: Calomys venustus can be distinguished from all other species of the genus Calomys on the basis of the following characters: body size large, largest species of genus, total length of adults generally 185 to 240 mm; tail moderate, less than head and body length; dorsum gray or brownish gray, venter pale

gray with white-tipped hairs; skull large, greatest length of skull of adults generally 25 to 30 mm; supraorbital region distinctly ledged and divergent posteriorly, rostrum heavy for genus; teeth large, maxillary toothrow 3.9 to 4.4 mm; occurring at moderate elevations in Bolivia and Argentina.

Distribution: Low to moderate elevations in Argentina and Bolivia (higher elevations in Bolivia than in Argentina), on the eastern slopes of the Andes (see fig. 31).

General Description and Comparisons: Calomys venustus is the largest species in the genus Calomys. The dorsal pelage is a pale or yellowish gray to dark gray. The sides are paler. The tips of the hairs are buffy, finely lined with blackish. Fur long, soft and fine; on the back the hairs are about 13 mm in length. The face is like the back and the cheeks are like the sides. The venter is pale buffy white, the hairs are gray at the base and white at the tips, the venter usually appears a pale gray. The hairs of the chin are white to the base. An indistinct buffy line separates the sides and the venter. The ears are medium to large, their visible parts when folded are thinly haired, brown or gray; a buffy tuft is at the base of the ears, the post-auricular spot is whitish, but is less obvious than in other species of the genus. The hands and feet are well-haired and white as in the other species. The tail is shorter than the head and body length,

Figure 31. Map of the known localities of Calomys venustus.



is well-haired, and is distinctly bicolored, brown above and white on the sides and below.

The number of mammae is variable. Five to seven pairs have been observed. Sometimes the mammae are spaced evenly along the body (5 pairs in CM 86475), sometimes not. A specimen from Cuyabuyo, Bolivia has 7 pairs of mammae, as do specimens from specimens from Tucuman, Argentina, and Tablada, Bolivia; specimens from Goya, Argentina, have five pairs, 3-2=10.

The skull is strongly built: the rostrum is broad, especially in older individuals; the interorbital region is flat and has strongly ridged edges that diverge posteriorly. An alisphenoid strut is absent (table 4). Foramina along squamosal-alisphenoid groove are frequently present (table 5). Dentition as for the genus, an anteromedian style is frequently present and the anteromedian flexus is less well developed than in other species of the genus (tables 6-7). Description modified from Thomas, 1894, 1901b). External and cranial measurements are given in table 2.

Calomys venustus can be distinguished from any other species of Calomys on the basis of size. It is much larger than any other species, except very old or large individuals of C. callosus. It has strongly ridged, posteriorly divergent supraorbitals, like C. callosus and C. tener, but is much larger than either of those. Calomys venustus and C. callosus are similar; there are no

characters other than size that will serve to separate the two consistently; size is not always reliable, either. In general, the length of the maxillary toothrow is the most useful in separating these species: the toothrow is generally greater than 4.1 mm in C. venustus and less than 4.1 in C. callosus. Calomys callosus tends to have 10 mammae, while C. venustus may have up to 14 (there is variation in this in both species). The diploid number seems to be different in these species, $2n = 50$ in C. callosus, and the reported numbers for C. venustus are $2n = 54$, 56. See table 2 for comparative measurements, and figures 32-35 for views of the skulls and dentition of the species of Calomys. See also previous species accounts for more comparisons.

Karyology: Gardenal et al. (1977b) published the karyotype for C. callosus from Coisquin, province of Cordoba, Argentina, as $2n = 56$, number of autosomal arms = 66. They divided the karyotype into 4 groups:

1. 1 large submetacentric pair, 1 pair large metacentrics, 1 pair medium submetacentrics, 1 pair medium metacentrics, 1 pair submetacentrics with subterminal centromere, and 1 chromosome, a submetacentric with morphology similar to the first, but smaller.
2. 7 pairs large acrocentrics, and 12 pairs medium acrocentrics.
3. 1 small metacentric pair.
4. 2 pairs and 1 chromosome acrocentric.

Summary: 2 large metacentric pairs, 3 medium metacentric pairs, and 1 small metacentric pair; 7 large acrocentric pairs, 12 medium acrocentric pairs, and 2 small acrocentric pairs, and the X and Y. They noted small secondary constrictions and association of acrocentrics.

Hurtado de Catalfo and Wainberg (1974) published the karyotype of C. c. callosus (= C. venustus) from the department of Famaila, province of Tucuman, Argentina, as $2n = 54$, $FN = 70$. They noted 4 medium pairs plus the X, 20 small pairs, and 2 pairs of microchromosomes plus the Y; of these, 7 pairs were metacentric and 19 were acrocentric. Of the 7 metacentric, 1 pair was submetacentric, 6 pairs (and the X) were metacentric.

Lisanti et al. (1976) published the karyotype for C. c. callosus from 3 localities in the province of Cordoba, Argentina (Cosquin, Chucul, and Las Albahacas), as $2n = 56$; 6 biarmed pairs of autosomes, 21 telocentric pairs of autosomes, X submetacentric, and Y acrocentric. They compared their karyotype to that published by Hurtado de Catalfo and Wainberg (1974) and have 2 more telocentric chromosomes present.

Taxonomic History: Oryzomys (?) venustus was described by Thomas in 1894. He gave as body measurements, head and body length 94 mm; tail length 72 mm; hindfoot length 21 mm; and ear length 16 mm.

Thomas wrote "This pretty little species, although by its skull apparently an Oryzomys, much resembles externally a diminutive Phyllotis both in general coloration, character of fur, and size of ears; but I know no species of that or any other group with which it could be confounded" (p. 360).

Eligmodontia callosa boliviae was described by Thomas in 1901 from Rio Solocame, Bolivia, 1200 m. He wrote the "Skull very like that of the typical form, with the same evenly divergent, well-marked, supraorbital ridges, long palatal foramina, and other details. Molars smaller and lighter throughout" (Thomas, 1901b, p. 253). Measurements given were head and body length 106 mm; tail length 82 mm; hind foot length (su) 21 mm; and ear length 19 mm. He said "This Eligmodontia is clearly the Bolivian representative of E. callosa Rengg., from which it differs by its rather smaller teeth and more buffy under surface" (p. 254).

Thomas (1916b) described H. venustus callidus from Goya, Corrientes, Argentina; he wrote "This mouse may be distinguished from the true H. venustus of Cordova by its darker, less drabby colour, shorter fur, and apparently rather longer ears" (p. 183). Body measurements given were head and body length 115 mm; tail length 77 mm; hind foot length 21 mm; and ear length 18 mm.

Hesperomys fecundus was described by Thomas (1926a) from Tablada, Tarija, Bolivia, as similar to H. venustus, but with 14 mammae. He wrote of this taxon that its "size among the largest

of the genus. Colour and general appearance very much as in the H. venustus of Cordova and Salta, with the same drabby-grey back, clearer and more buffy sides, and grey-mixed belly. Ears with a buffy tuft at their anterior bases, and a white one posteriorly. Hands and feet white. Tail brown above, whitish below. Mammae, in 3 specimens=14, 5-2=14; but the gap between the thoracic and inguinal pairs is not great.

"Skull about as in venustus, the supraorbital ridges well developed" (Thomas, 1926a, p. 321). Body measurements given were head and body length 124 mm, tail length 90, hindfoot length 21, and ear length 18.

He noted that 14 mammae are also found in C. musculus, which is smaller, and a member of the "laucha" group.

This species was synonymized with C. callosus by Hershkovitz (1962).

Remarks: Data on this species are scarce. De Fonollat (1984) reported of C. c. callosus from Tucumán, Argentina. He said they are of large size, live in arid and semiarid forests, thickets, and are common in cultivated fields. The species builds runways, is terrestrial and nocturnal. It is herbivorous and granivorous. They nest on the ground in dense vegetation.

Notes from specimen labels include "arid country, rocky cactus, algarroba", "caught in house, edge of town", "caught

inside adobe hut", "in rock pile", "by stone pile", "in bush", "common, killed in grass in the quinta", "common killed in maize field" "trapped in quinta", "common found among grass and weeds in chaco", "common, trapped in monte". Notes from specimens from Concepcion, Tucuman, Argentina, say "caught in the grass" (or on the grass), "caught in the wood", "from the wood region". Other notes include "common, found among grass and weeds in chaco", "killed in maiz field", "trapped in chaco", "trapped in barn", "common, trapped in quinta", and "Caught in woods".

Reproductive data are scarce. One lactating female was caught in February in Tucumán Province.

There is a problem with some specimens in the literature from Tucumán, Tafi del Valle, in the CM collection. Examination shows them to be C. venustus. However, Dalby and Mares (1974) reported specimens collected from that place as C. musculus. This locality is at a high elevation according to their paper, near the 3043 m elevation marker, and located in an area of dense bunch grass cut by numerous small rocky gullies. The specimens at CM were collected in 1974, the paper was published in 1974, and the Reithrodon specimens that they reported there were collected in 1972 and 1973.

Specimen localities have been reported by Thomas (1901b, 1919c, 1920a, 1925, 1926a, c); Massoia and Fornes (1965); Hurtado

de Catalpo and Wainberg (1974); Massoia (1974); de Fonollat (1984); and Corti et al. (1987).

For associated species, see Thomas (1902b, 1920a, 1925, 1926a, c); and Massoia and Fornes (1965).

Problem names:

Mus pusillus Philippi, type locality: Chile: Santiago, ca. 33°S, 70°W (see Osgood, 1943).

Mus pusillus was described by Philippi in 1858 (see Osgood, 1943). The type specimen is in the Santiago Museum, with the skull left inside the skin. Osgood pointed out specific problems with the date of collection on the label and the date of the original description. He says "It is a small, soft-haired, grayish mouse with a white belly. . . the ears have been shriveled by preservative. . . Only one remains and this measures about 11 mm. . . The hairs of the chin and upper throat are practically all white; those of chest have dark bases. The hind foot in good condition is 21" (p. 239). Osgood says it is doubtful that this species belongs to the Chilean fauna and that possibly it belongs to Hesperomys (=Calomys). Clarification of this name awaits study of the type specimen. Hershkovitz (1962) included M. pusillus in C. laucha laucha.

Table 2

Means and standard deviations of selected measurements of the species of Calomys. Minimum and maximum measurements given in parentheses.

MSMT	<u>C.</u> <u>bimaculatus</u> (n=6)	<u>C.</u> <u>hummelincki</u> (n=8)	<u>C.</u> <u>laucha</u> (n=33)	<u>C.</u> <u>lepidus</u> (n=64)
ZYN	0.98 ± 0.12 (0.81-1.13)	1.19 ± 0.37 (0.92-1.45)	1.15 ± 0.16 (0.87-1.63)	1.42 ± 0.20 (1.02-1.83)
LRS	5.89 ± 0.51 (5.00-6.47)	5.89 ± 0.13 (5.75-6.17)	5.70 ± 0.35 (5.19-6.58)	6.65 ± 0.42 (5.92-7.87)
GLS	21.08 ± 1.21 (19.32-22.38)	20.87 ± 0.54 (20.04-21.66)	20.03 ± 0.91 (18.45-22.95)	21.99 ± 0.78 (20.43-23.55)
ZBR	11.32 ± 0.79 (10.18-12.32)	11.51 ± 0.50 (10.63-12.13)	10.76 ± 0.67 (9.14-12.45)	11.64 ± 0.60 (10.25-13.34)
BBC	9.93 ± 0.34 (9.41-10.25)	9.32 ± 0.14 (9.06-9.46)	9.56 ± 0.31 (8.99-10.30)	10.21 ± 0.32 (9.58-11.02)
IOC	3.60 ± 0.21 (3.31-3.82)	3.52 ± 0.13 (3.34-3.76)	3.44 ± 0.16 (3.04-3.74)	3.52 ± 0.19 (3.10-4.04)
WRS	4.04 ± 0.41 (3.48-4.52)	4.19 ± 0.23 (3.85-4.55)	3.70 ± 0.35 (2.83-4.53)	3.97 ± 0.27 (3.26-4.59)
LINF	5.15 ± 0.28 (4.86-5.48)	4.66 ± 0.25 (4.16-4.92)	4.62 ± 0.41 (3.44-5.68)	4.84 ± 0.29 (4.29-5.71)
PAL	3.13 ± 0.18 (2.88-3.28)	3.34 ± 0.26 (2.99-3.73)	3.19 ± 0.17 (2.80-3.60)	3.61 ± 0.23 (2.75-4.14)
PPL	7.25 ± 0.38 (6.81-7.72)	7.31 ± 0.19 (6.97-7.56)	6.79 ± 0.54 (6.00-8.21)	7.55 ± 0.43 (6.63-8.68)
LBULL	3.19 ± 0.29 (2.60-3.36)	3.19 ± 0.18 (2.98-3.51)	3.20 ± 0.23 (2.84-3.97)	3.42 ± 0.19 (3.00-4.04)
MAX	3.17 ± 0.11 (3.03-3.28)	3.15 ± 0.09 (3.05-3.31)	3.07 ± 0.12 (2.84-3.34)	3.49 ± 0.14 (3.20-3.86)

Table 2 cont'd.

	<u>C.</u> <u>bimaculatus</u>	<u>C.</u> <u>humelincki</u>	<u>C.</u> <u>laucha</u>	<u>C.</u> <u>lepidus</u>
DIAS	5.03 $\pm$ 0.27 (4.73-5.42)	5.07 $\pm$ 0.22 (4.59-5.30)	4.71 $\pm$ 0.35 (4.05-5.43)	4.97 $\pm$ 0.34 (4.22-5.74)
INCTL	0.62 $\pm$ 0.06 (0.54-0.67)	0.93 $\pm$ 0.19 (0.69-1.26)	0.59 $\pm$ 0.11 (0.38-0.79)	0.69 $\pm$ 0.14 (0.46-1.15)
LM1	1.59 $\pm$ 0.06 (1.51-1.66)	1.59 $\pm$ 0.05 (1.52-1.65)	1.57 $\pm$ 0.10 (1.36-1.76)	1.73 $\pm$ 0.09 (1.50-1.92)
LM2	1.00 $\pm$ 0.05 (0.91-1.06)	0.96 $\pm$ 0.04 (0.89-1.01)	0.91 $\pm$ 0.06 (0.77-1.03)	1.04 $\pm$ 0.06 (0.91-1.20)
LM3	0.64 $\pm$ 0.08 (0.56-0.75)	0.67 $\pm$ 0.07 (0.58-0.78)	0.61 $\pm$ 0.05 (0.51-0.73)	0.71 $\pm$ 0.06 (0.57-0.90)
WM1	0.98 $\pm$ 0.05 (0.94-1.05)	1.01 $\pm$ 0.06 (0.91-1.13)	0.90 $\pm$ 0.07 (0.65-1.05)	1.07 $\pm$ 0.07 (0.91-1.25)
WM2	0.87 $\pm$ 0.05 (0.80-0.94)	0.86 $\pm$ 0.05 (0.81-0.96)	0.82 $\pm$ 0.06 (0.69-0.95)	0.91 $\pm$ 0.10 (0.73-1.32)
WM3	0.72 $\pm$ 0.03 (0.68-0.76)	0.67 $\pm$ 0.04 (0.63-0.74)	0.65 $\pm$ 0.09 (0.47-0.79)	0.76 $\pm$ 0.09 (0.55-0.96)
PBR	2.20 $\pm$ 0.08 (2.08-2.29)	2.32 $\pm$ 0.13 (2.05-2.45)	2.17 $\pm$ 0.17 (1.83-2.53)	2.31 $\pm$ 0.19 (1.83-2.71)
WINCT	1.07 $\pm$ 0.11 (0.98-1.24)	1.28 $\pm$ 0.05 (1.20-1.33)	0.94 $\pm$ 0.12 (0.74-1.24)	1.08 $\pm$ 0.12 (0.57-1.38)
PARA	2.53 $\pm$ 0.19 (2.29-2.72)	2.25 $\pm$ 0.12 (2.08-2.39)	2.34 $\pm$ 0.18 (2.01-2.86)	2.78 $\pm$ 0.20 (1.99-3.33)
MESF	0.96 $\pm$ 0.21 (0.66-1.19)	1.07 $\pm$ 0.13 (0.91-1.32)	0.81 $\pm$ 0.12 (0.51-1.02)	0.67 $\pm$ 0.16 (0.35-1.04)
TL	132.40 $\pm$ 8.38 (123-142)	108.80 $\pm$ 9.36 (95-120)	120.37 $\pm$ 10.10 (105-145)	118.36 $\pm$ 8.89 (101-139)

Table 2 cont'd.

	<u>C.</u> <u>bimaculatus</u>	<u>C.</u> <u>humelincki</u>	<u>C.</u> <u>laucha</u>	<u>C.</u> <u>lepidus</u>
T	55.20 $\pm$ 3.11 (52-59)	38.00 $\pm$ 5.66 (33-47)	51.17 $\pm$ 4.74 (42-65)	41.25 $\pm$ 5.56 (30-52)
HF	16.80 $\pm$ 0.76 (15.5-17.5)	14.13 $\pm$ 1.46 (11-15)	14.70 $\pm$ 1.52 (10-18)	16.63 $\pm$ 1.00 (14-19)
E	13.00 $\pm$ 1.00 (12-14)	13.13 $\pm$ 1.64 (10-15)	13.33 $\pm$ 1.14 (11-16)	16.41 $\pm$ 1.30 (12.5-19)

Table 2 cont'd.

MSMT	<u>C.</u> <u>murillus</u> (n=61)	<u>C.</u> <u>musculus</u> (n=29)	<u>C.</u> <u>sorellus</u> (n=148)	<u>C.</u> <u>tener</u> (n=74)
ZYN	1.44 ± 0.14 (1.07-1.70)	1.63 ± 0.22 (1.32-2.37)	1.36 ± 0.20 (0.89-1.66)	1.13 ± 0.19 (0.78-1.79)
LRS	6.35 ± 0.43 (5.58-7.78)	7.17 ± 0.59 (6.13-8.60)	7.50 ± 0.53 (5.86-8.70)	6.58 ± 0.38 (5.72-7.31)
GLS	21.62 ± 1.08 (19.80-25.23)	23.69 ± 1.38 (20.61-26.34)	24.15 ± 1.26 (20.54-27.86)	22.87 ± 0.88 (21.08-24.96)
ZBR	11.49 ± 0.55 (10.53-12.63)	12.25 ± 0.79 (10.80-13.66)	12.47 ± 0.70 (10.31-14.12)	12.06 ± 0.57 (10.45-13.49)
BBC	9.99 ± 0.31 (9.23-10.54)	10.43 ± 0.38 (9.34-11.15)	11.04 ± 0.29 (9.78-11.66)	10.38 ± 0.26 (9.73-10.91)
IOC	3.51 ± 0.15 (3.23-3.89)	3.71 ± 0.21 (3.16-4.10)	3.86 ± 0.14 (3.52-4.21)	3.73 ± 0.18 (3.37-4.25)
WRS	3.99 ± 0.27 (3.32-4.74)	4.32 ± 0.36 (3.35-4.90)	4.47 ± 0.27 (3.69-5.17)	4.15 ± 0.24 (3.78-4.85)
LINE	4.73 ± 0.35 (3.55-5.74)	5.29 ± 0.34 (4.58-5.99)	5.49 ± 0.36 (4.29-6.26)	5.20 ± 0.28 (4.62-5.84)
PAL	3.32 ± 0.19 (2.74-3.73)	3.52 ± 0.32 (2.63-4.02)	3.74 ± 0.26 (2.90-4.46)	3.54 ± 0.23 (3.07-4.25)
PPL	7.54 ± 0.60 (6.39-8.94)	8.37 ± 0.72 (7.19-9.75)	8.07 ± 0.54 (6.53-9.66)	7.70 ± 0.49 (6.22-8.80)
LBULL	3.24 ± 0.19 (2.75-3.59)	3.44 ± 0.18 (3.17-4.05)	3.65 ± 0.15 (3.30-4.05)	3.42 ± 0.17 (2.96-3.84)
MAX	3.37 ± 0.13 (3.10-3.67)	3.55 ± 0.16 (3.35-3.89)	3.64 ± 0.13 (3.30-4.01)	3.45 ± 0.14 (2.81-3.63)

Table 2 cont'd.

	<u>C.</u> <u>murillus</u> (n=61)	<u>C.</u> <u>musculus</u> (n=29)	<u>C.</u> <u>sorellus</u> (n=148)	<u>C.</u> <u>tener</u> (n=74)
DIAS	5.02 ± 0.37 (4.30-6.25)	5.64 ± 0.47 (4.78-6.49)	5.57 ± 0.43 (4.12-6.51)	5.35 ± 0.30 (4.78-6.10)
INCTL	0.68 ± 0.12 (0.45-1.02)	0.78 ± 0.17 (0.51-1.23)	0.76 ± 0.13 (0.38-1.09)	0.73 ± 0.12 (0.47-1.08)
LM1	1.72 ± 0.19 (1.52-1.88)	1.82 ± 0.09 (1.65-2.05)	1.77 ± 0.08 (1.52-1.96)	1.67 ± 0.08 (1.46-1.83)
LM2	1.03 ± 0.06 (0.89-1.16)	1.06 ± 0.06 (0.95-1.19)	1.10 ± 0.05 (0.93-1.28)	1.04 ± 0.07 (0.87-1.22)
LM3	0.74 ± 0.07 (0.53-0.91)	0.78 ± 0.08 (0.62-1.00)	0.77 ± 0.06 (0.60-0.90)	0.69 ± 0.06 (0.52-0.90)
WM1	0.97 ± 0.05 (0.87-1.08)	1.02 ± 0.07 (0.88-1.12)	1.10 ± 0.06 (0.94-1.26)	0.95 ± 0.06 (0.73-1.09)
WM2	0.90 ± 0.06 (0.76-1.02)	0.95 ± 0.07 (0.83-1.08)	1.00 ± 0.06 (0.85-1.19)	0.87 ± 0.05 (0.73-0.98)
WM3	0.75 ± 0.05 (0.55-0.84)	0.80 ± 0.07 (0.66-0.94)	0.82 ± 0.05 (0.68-0.97)	0.74 ± 0.05 (0.59-0.86)
PBR	2.38 ± 0.17 (2.08-2.88)	2.54 ± 0.17 (2.22-2.83)	2.51 ± 0.17 (2.01-2.92)	2.41 ± 0.14 (2.13-2.74)
WINCT	1.05 ± 0.11 (0.51-1.22)	1.20 ± 0.16 (0.99-1.77)	1.22 ± 0.11 (0.78-1.50)	1.23 ± 0.10 (0.96-1.58)
PARA	2.74 ± 0.18 (2.07-3.07)	2.76 ± 0.24 (2.08-3.10)	2.79 ± 0.18 (2.22-3.24)	2.44 ± 0.18 (2.09-3.24)
MESF	0.79 ± 0.14 (0.41-1.11)	0.89 ± 0.13 (0.71-1.17)	0.91 ± 0.15 (0.46-1.30)	1.10 ± 0.17 (0.80-1.95)
TL	150.96 ± 14.42 (118-187)	175.56 ± 17.89 (143-206)	160.69 ± 15.73 (114-196)	143.18 ± 9.83 (120-165)

Table 2 cont'd.

	<u>C.</u> <u>murillus</u>	<u>C.</u> <u>musculus</u>	<u>C.</u> <u>sorellus</u>	<u>C.</u> <u>tener</u>
T	72.88 ± 8.04 (49-86)	84.96 ± 10.15 (64-111)	73.52 ± 9.18 (52-94)	63.81 ± 7.12 (40-87)
HF	17.22 ± 1.00 (14.5-20)	19.10 ± 1.11 (17-21)	19.69 ± 1.40 (13-22)	15.79 ± 1.57 (8-19)
E	13.99 ± 0.99 (12.5-16.8)	15.28 ± 1.09 (13-17.5)	17.46 ± 1.29 (13-20)	14.16 ± 1.40 (11.5-18)

Table 2 cont'd.

MSMT	<u>C.</u> <u>callosus</u> (n=514)	<u>C.</u> <u>venustus</u> (n=220)
ZYN	1.72 ± 0.25 (1.00-2.39)	1.90 ± 0.23 (1.37-2.54)
LRS	7.85 ± 0.60 (6.15-9.39)	8.29 ± 0.65 (6.64-10.19)
GLS	26.20 ± 1.45 (21.66-30.15)	27.11 ± 1.60 (23.08-31.26)
ZBR	13.93 ± 0.83 (11.31-17.32)	14.43 ± 0.90 (12.34-16.98)
BBC	11.36 ± 0.37 (10.05-12.47)	11.66 ± 0.37 (10.62-12.74)
IOC	4.28 ± 0.39 (3.58-5.12)	4.24 ± 0.22 (3.65-4.82)
WRS	5.02 ± 0.39 (3.71-6.38)	5.06 ± 0.36 (4.28-6.25)
LINF	6.02 ± 0.42 (4.48-7.24)	6.24 ± 0.48 (5.04-7.71)
PAL	4.35 ± 0.34 (3.18-6.14)	4.65 ± 0.34 (3.66-5.60)
PPL	9.14 ± 0.71 (7.02-11.20)	9.24 ± 0.84 (7.46-11.57)
LBULL	3.81 ± 0.18 (3.19-4.32)	3.93 ± 0.24 (3.04-5.62)
MAX	3.93 ± 0.16 (3.18-4.49)	4.28 ± 0.15 (3.87-4.63)

Table 2 cont'd.

	<u>C.</u> <u>callosus</u> (n=514)	<u>C.</u> <u>venustus</u> (n=220)
DIAS	6.31 ± 0.50 (4.93-7.83)	6.48 ± 0.56 (4.98-8.29)
INCTL	0.87 ± 0.18 (0.35-1.72)	0.95 ± 0.20 (0.43-1.77)
LM1	1.89 ± 0.09 (1.64-2.15)	2.07 ± 0.09 (1.69-2.30)
LM2	1.18 ± 0.06 (1.02-1.41)	1.29 ± 0.07 (1.10-1.49)
LM3	0.89 ± 0.07 (0.68-1.18)	0.99 ± 0.08 (0.79-1.25)
WM1	1.16 ± 0.07 (0.98-1.38)	1.29 ± 0.08 (0.89-1.55)
WM2	1.08 ± 0.07 (0.79-1.27)	1.18 ± 0.07 (0.99-1.41)
WM3	0.92 ± 0.06 (0.73-1.12)	1.01 ± 0.07 (0.80-1.18)
PBR	2.60 ± 0.21 (2.02-3.39)	2.73 ± 0.21 (2.27-3.28)
WINCT	1.45 ± 0.16 (0.88-1.84)	1.55 ± 0.16 (1.11-1.98)
PARA	2.76 ± 0.21 (2.18-3.51)	2.95 ± 0.21 (2.37-3.61)
MESF	1.21 ± 0.18 (0.51-1.71)	1.16 ± 0.21 (0.65-1.64)
TL	173.16 ± 18.27 (115-222)	188.59 ± 20.16 (145-245)

Table 2 cont'd.

	<u>C.</u> <u>callosus</u>	<u>C.</u> <u>venustus</u>
T	70.81 $\pm$ 10.90 (39-115)	82.42 $\pm$ 9.37 (40-110)
HF	19.84 $\pm$ 1.96 (14-25)	21.58 $\pm$ 1.53 (18-29)
E	16.38 $\pm$ 1.81 (10-23)	18.27 $\pm$ 1.89 (10.7-23.4)

Table 3

Means and standard deviations of selected measurements for selected phyllotine species. The minimum and maximum measurements are given in parentheses. (All measurements in mm).

MSMT	<u>Andalgalomys</u>	
	<u>pearsoni</u> (n=11)	<u>olrogi</u> (n=6)
LRS	9.46 ± 0.52 (8.62-10.16)	8.93 ± 0.70 (7.77-9.77)
GLS	29.74 ± 1.37 (27.51-31.93)	28.07 ± 1.47 (26.10-29.80)
ZBR	14.46 ± 0.83 (12.90-15.45)	13.56 ± 0.49 (13.00-14.20)
BBC	12.56 ± 0.44 (12.10-13.35)	12.58 ± 0.20 (12.30-12.80)
IOC	4.68 ± 0.39 (3.97-5.30)	4.46 ± 0.15 (4.27-4.70)
WRS	4.94 ± 0.40 (4.42-5.80)	4.22 ± 0.49 (3.40-4.83)
LINF	6.46 ± 0.41 (5.62-7.08)	5.92 ± 0.88 (4.26-6.65)
PAL	5.40 ± 0.40 (4.65-6.09)	5.36 ± 0.21 (5.15-5.71)
LBULL	5.42 ± 0.34 (4.70-5.79)	6.32 ± 0.44 (5.74-6.82)
PBR	2.75 ± 0.31 (2.10-3.10)	2.87 ± 0.14 (2.71-3.10)
PDB	4.51 ± 0.15 (4.33-4.68)	4.54 ± 0.24 (4.19-4.75)

Table 3 cont'd.

	<u>Andalgalomys</u>	
	<u>pearsoni</u>	<u>olrogi</u>
POB	8.40 $\pm$ 0.37 (7.86-9.13)	7.74 $\pm$ 1.25 (5.29-8.81)
ZPW	2.89 $\pm$ 0.26 (2.41-3.20)	2.51 $\pm$ 0.21 (2.31-2.76)
MESF	0.87 $\pm$ 0.26 (0.46-1.27)	0.86 $\pm$ 0.14 (0.70-1.09)
MXL	4.78 $\pm$ 0.29 (4.41-5.30)	4.74 $\pm$ 0.13 (4.60-4.97)
LM1	2.11 $\pm$ 0.05 (2.07-2.17)	2.13 $\pm$ 0.06 (2.00-2.23)
LM2	1.14 $\pm$ 0.08 (1.05-1.23)	1.18 $\pm$ 0.06 (1.11-1.26)
LM3	0.98 $\pm$ 0.06 (0.92-1.06)	0.95 $\pm$ 0.10 (0.82-1.09)
WM1	1.51 $\pm$ 0.15 (1.27-1.75)	1.43 $\pm$ 0.03 (1.39-1.46)
HBL	109.00 $\pm$ 9.37 (97-120)	106.50 $\pm$ 22.90 (86-136)
TAI	114.30 $\pm$ 10.15 (97-129)	127.00 $\pm$ 2.16 (125-130)
HFL	23.50 $\pm$ 0.81 (22-25)	24.38 $\pm$ 0.50 (23.8-24.9)
EAR	19.45 $\pm$ 0.81 (18-21)	20.58 $\pm$ 0.97 (19.6-20.0)

Table 3 cont'd.

MSMT	<u>lepidus</u> (n=22)	<u>Calomys</u> <u>tener</u> (n=26)	<u>callosus</u> (n=41)
LRS	6.47 ± 0.37 (5.69-7.07)	6.68 ± 0.38 (5.77-7.29)	8.18 ± 0.50 (7.11-9.15)
GLS	21.65 ± 0.85 (19.83-22.82)	22.99 ± 0.96 (21.52-24.96)	27.02 ± 1.33 (23.90-29.39)
ZBR	11.42 ± 0.57 (10.20-12.40)	12.19 ± 0.44 (11.56-13.01)	14.39 ± 0.70 (13.17-15.77)
BBC	10.14 ± 0.27 (9.58-10.82)	10.39 ± 0.24 (9.78-10.79)	11.41 ± 0.35 (10.59-12.10)
IOC	3.46 ± 0.11 (3.30-3.65)	3.78 ± 0.16 (3.51-4.06)	4.24 ± 0.22 (3.76-4.76)
WRS	3.83 ± 0.15 (3.54-4.13)	4.14 ± 0.22 (3.82-4.68)	5.09 ± 0.40 (4.29-6.03)
LINF	4.71 ± 0.27 (4.19-5.03)	5.24 ± 0.26 (4.72-5.71)	6.28 ± 0.31 (5.44-6.93)
LPAL	3.54 ± 0.26 (2.90-4.03)	3.57 ± 0.24 (3.11-4.25)	4.50 ± 0.32 (3.72-5.09)
LBULL	3.47 ± 0.12 (3.14-3.61)	3.30 ± 0.18 (2.96-3.60)	3.93 ± 0.23 (3.58-4.89)
PBR	2.30 ± 0.14 (2.09-2.56)	2.49 ± 0.14 (2.31-2.74)	2.69 ± 0.24 (2.31-3.39)
PDB	3.49 ± 0.11 (3.32-3.77)	3.65 ± 0.17 (3.38-4.02)	4.19 ± 0.23 (3.69-4.68)

Table 3 cont'd.

	<u>Calomys</u> <u>lepidus</u> (n=22)	<u>C.</u> <u>tener</u> (n=26)	<u>C.</u> <u>callosus</u> (n=41)
POB	6.57 ± 0.24 (6.06-6.95)	6.50 ± 0.19 (6.29-6.89)	7.71 ± 0.38 (6.79-8.45)
ZPW	2.18 ± 0.18 (1.73-2.43)	2.39 ± 0.14 (2.19-2.74)	2.82 ± 0.25 (2.29-3.31)
MESF	0.55 ± 0.10 (0.35-0.74)	1.10 ± 0.15 (0.82-1.38)	1.22 ± 0.19 (0.87-1.60)
LM1	1.73 ± 0.07 (1.56-1.84)	1.69 ± 0.07 (1.46-1.79)	1.90 ± 0.08 (1.90-0.08)
LM2	1.04 ± 0.06 (0.91-1.15)	1.06 ± 0.07 (0.87-1.22)	1.19 ± 0.06 (1.02-1.30)
LM3	0.70 ± 0.05 (0.61-0.78)	0.67 ± 0.06 (0.56-0.85)	0.90 ± 0.06 (0.76-1.08)
WM1	1.04 ± 0.07 (0.90-1.14)	0.95 ± 0.05 (0.79-1.04)	1.19 ± 0.09 (1.03-1.39)
HBL	*	*	*
TAIL	*	*	*
HF	*	*	*
EAR	*	*	*

Table 3 cont'd.

MSMT	<u>Graomys</u>		<u>Eligmodontia</u>
	<u>domorum</u> (n=17)	<u>griseoflavus</u> (n=18)	<u>typus</u> (n=5)
LRS	10.51 ± 0.50 (9.70-11.33)	10.53 ± 0.94 (8.67-11.90)	7.76 ± 0.20 (7.50-8.05)
GLS	32.70 ± 1.03 (30.60-34.15)	32.74 ± 1.65 (28.80-35.90)	24.30 ± 0.91 (23.30-25.30)
ZBR	16.45 ± 0.69 (14.89-17.15)	16.47 ± 0.83 (15.02-17.80)	12.36 ± 0.64 (11.60-13.30)
BBC	14.22 ± 0.46 (13.09-14.74)	13.65 ± 0.52 (12.00-14.29)	11.42 ± 0.52 (10.60-11.80)
IOC	5.41 ± 0.15 (5.07-5.60)	5.25 ± 0.35 (4.41-5.79)	3.85 ± 0.13 (3.67-4.01)
WRS	5.63 ± 0.21 (5.25-6.05)	5.66 ± 0.53 (5.01-7.03)	4.03 ± 0.16 (3.80-4.21)
LINF	7.10 ± 0.34 (6.66-7.66)	7.32 ± 0.58 (6.26-8.17)	5.20 ± 0.27 (4.81-5.53)
PAL	5.56 ± 0.31 (5.07-6.08)	5.66 ± 0.35 (5.11-6.50)	4.40 ± 0.31 (3.97-4.73)
LBULL	5.63 ± 0.31 (4.95-6.08)	6.06 ± 0.49 (5.41-6.93)	4.10 ± 0.67 (3.33-4.83)
PBR	2.84 ± 0.21 (2.49-3.15)	2.86 ± 0.22 (2.36-3.24)	2.40 ± 0.18 (2.23-2.69)
PDB	5.05 ± 0.14 (4.83-5.27)	4.99 ± 0.24 (4.56-5.43)	3.62 ± 0.28 (3.33-4.01)

Table 3 cont'd.

	<u>domorum</u>	<u>Graomys</u> <u>griseoflavus</u>	<u>Eligmodontia</u> <u>typus</u>
POB	9.72 $\pm$ 0.33 (9.00-10.27)	9.34 $\pm$ 0.41 (8.58-10.22)	7.31 $\pm$ 0.43 (6.90-7.88)
ZPW	3.46 $\pm$ 0.24 (2.90-3.69)	3.27 $\pm$ 0.35 (2.67-4.02)	2.66 $\pm$ 0.25 (2.39-3.00)
MESF	1.57 $\pm$ 0.13 (1.39-1.89)	1.57 $\pm$ 0.22 (1.27-1.90)	0.77 $\pm$ 0.22 (0.55-1.09)
MXL	5.29 $\pm$ 0.37 (4.69-6.04)	5.44 $\pm$ 0.32 (4.82-5.88)	3.94 $\pm$ 0.12 (3.78-4.12)
LM1	2.40 $\pm$ 0.10 (2.27-2.62)	2.43 $\pm$ 0.15 (2.08-2.72)	1.69 $\pm$ 0.11 (1.53-1.77)
LM2	1.50 $\pm$ 0.07 (1.35-1.63)	1.47 $\pm$ 0.11 (1.27-1.73)	1.09 $\pm$ 0.06 (1.04-1.16)
LM3	1.14 $\pm$ 0.08 (0.97-1.27)	1.17 $\pm$ 0.09 (1.04-1.32)	0.72 $\pm$ 0.03 (0.69-0.76)
WML	1.64 $\pm$ 0.10 (1.49-1.86)	1.60 $\pm$ 0.09 (1.44-1.78)	1.17 $\pm$ 0.11 (1.02-1.29)
HBL	136.82 $\pm$ 11.40 (120-152)	131.55 $\pm$ 14.80 (111-159)	89
TAI	124.91 $\pm$ 23.89 (83-165)	154.73 $\pm$ 15.67 (124-175)	83
HFL	29.36 $\pm$ 1.86 (26-32)	29.00 $\pm$ 1.90 (25-31)	29
EAR	25.09 $\pm$ 1.51 (22-28)	22.50 $\pm$ 2.26 (20-26)	18

Table 3 cont'd.

MSMT	<u>Phyllotis</u>	
	<u>osilae</u> (n=9)	<u>wolffsohni</u> (n=11)
LRS	9.21 ± 0.54 (8.64-10.02)	9.96 ± 0.67 (9.17-11.37)
GLS	29.34 ± 1.06 (28.07-30.87)	30.23 ± 1.05 (28.98-32.41)
ZBR	15.22 ± 0.53 (14.32-16.03)	15.41 ± 0.34 (15.04-16.20)
BBC	13.45 ± 0.30 (12.97-13.83)	13.45 ± 0.33 (12.90-14.18)
IOC	4.18 ± 0.14 (3.98-4.43)	4.17 ± 0.18 (3.95-4.55)
WRS	5.22 ± 0.28 (4.92-5.68)	5.31 ± 0.29 (4.80-5.81)
LINF	6.87 ± 0.34 (6.51-7.45)	7.29 ± 0.35 (6.81-7.87)
LPAL	4.77 ± 0.28 (4.30-5.15)	5.09 ± 0.36 (4.59-5.79)
LBULL	4.15 ± 0.23 (3.87-4.48)	4.20 ± 0.20 (3.93-4.64)
PBR	2.83 ± 0.25 (2.44-3.18)	2.73 ± 0.12 (2.46-2.87)
PDB	4.56 ± 0.17 (4.39-4.96)	4.06 ± 0.20 (3.71-4.34)

Table 3 cont'd.

	<u>Phyllotis</u>	
	<u>osilae</u>	<u>wolffsohni</u>
POB	8.61 ± 0.32 (7.85-8.92)	8.58 ± 0.26 (8.24-8.94)
ZPW	2.93 ± 0.14 (2.78-3.21)	2.89 ± 0.20 (2.69-3.33)
MESF	1.60 ± 0.11 (1.43-1.74)	1.39 ± 0.16 (1.13-1.57)
MXL	5.43 ± 0.15 (5.15-5.62)	5.49 ± 0.19 (5.14-5.69)
LM1	2.44 ± 0.10 (2.31-2.65)	2.28 ± 0.13 (2.05-2.48)
LM2	1.41 ± 0.07 (1.32-1.53)	1.39 ± 0.08 (1.29-1.50)
LM3	1.22 ± 0.07 (1.12-1.36)	1.24 ± 0.14 (1.00-1.44)
WM1	1.57 ± 0.08 (1.47-1.69)	1.53 ± 0.07 (1.46-1.68)
HB	109.11 ± 10.25 (98-125)	110.55 ± 5.15 (107-125)
T	127.56 ± 9.21 (116-145)	130.00 ± 8.61 (110-145)
HF	27.50 ± 0.90 (26-29)	26.55 ± 1.57 (24-29)
EAR	23.11 ± 0.78 (22-24)	21.00 ± 1.00 (19-22)

Table 4

Table showing the frequency of the presence of the alisphenoid strut in the species of Calomys.

Species	N	Alisphenoid Strut	
		Number	Percent
<u>C. bimaculatus</u>	12	0	0.00
<u>C. callosus</u>	156	4	2.56
<u>C. hummelincki</u>	12	0	0.00
<u>C. laucha</u>	35	32	91.43
<u>C. lepidus</u>	97	66	68.04
<u>C. murillus</u>	48	1	2.08
<u>C. musculus</u>	33	2	6.06
<u>C. sorellus</u>	58	0	0.00
<u>C. tener</u>	86	77	89.53
<u>C. venustus</u>	44	0	0.00

Table 5

Table of the frequency of structures associated with the carotid circulation in the species of Calomys. Number of individuals observed with the structure above, the frequency, in percent, in parentheses. Stf, Stapedial foramen; sqg, squamosal groove; spf, sphenofrontal foramen; vg, vertical groove; unf, unnamed foramen; exf, extra foramina along the squamosal groove.

Species	Stf	Sqg	Spf	Vg	Unf	Exf
<u>C. bimaculatus</u> (n=8)	8 (100)	8 (100)	8 (100)	8 (100)	8 (100)	0 (0)
<u>C. callosus</u> (n=50)	50 (100)	48 (96)	50 (100)	50 (100)	21 (42)	0 (0)
<u>C. hummelincki</u> (n=20)	15(15) (100)	20 (100)	19 (95*)	20 (100)	15 (75)	6 (30)
<u>C. laucha</u> (n=27)	27 (100)	27 (100)	27 (100)	27 (100)	20 (74.1)	0 (0)
<u>C. lepidus</u> (n=37)	37 (100)	37 (100)	37 (100)	37 (100)	32 (86.5)	0 (0)
<u>C. murillus</u> (n=6)	6 (100)	6 (100)	6 (100)	6 (100)	5 (83.3)	0 (0)
<u>C. musculus</u> (n=11)	11 (100)	11 (100)	11 (100)	11 (100)	4 (36.4)	0 (0)
<u>C. sorellus</u> (n=48)	48 (100)	48 (100)	48 (100)	48 (100)	38 (79.2)	9 (18.8)
<u>C. tener</u> (n=43)	43 (100)	42 (97.7)	43 (100)	43 (100)	25 (58.1)	2 (4.7)
<u>C. venustus</u> (n=34)	34 (100)	34 (100)	33 (97.1)	34 (100)	12 (35.3)	1 (2.9)

* in one specimen, coalesced with optic foramen.

Table 6

Table showing the frequency of the presence of the anteromedian style in the species of Calomys.

Species	N	Anteromedian Style	
		Number	Percent
<u>C. bimaculatus</u>	12	7	58.33
<u>C. callosus</u>	154	39	25.32
<u>C. hummelincki</u>	12	1	8.33
<u>C. laucha</u>	34	34	100.00
<u>C. lepidus</u>	95	32	33.68
<u>C. murillus</u>	48	32	66.67
<u>C. musculus</u>	33	12	36.36
<u>C. sorellus</u>	55	24	43.64
<u>C. tener</u>	81	42	51.85
<u>C. venustus</u>	41	13	31.71

Table 7

Table showing the variation in the division of the anterocone on the M1 in the species of Calomys, (percent in parentheses). 0, Anterocone entire, no anteromedian flexus; 1, anterocone with anteromedian flexus, but fused at base of cusp; 2, anterocone with deep anteromedian flexus, well separating the two conules.

Species	N	Division of Anterocone		
		0	1	2
<u>C. bimaculatus</u>	12	0 (0.00)	1 (8.33)	11 (91.67)
<u>C. callosus</u>	139	12 (8.63)	67 (48.20)	60 (43.17)
<u>C. hummelincki</u>	7	0 (0.00)	3 (42.86)	4 (57.14)
<u>C. laucha</u>	34	0 (0.00)	8 (23.53)	26 (76.47)
<u>C. lepidus</u>	69	0 (0.00)	3 (4.35)	66 (95.65)
<u>C. murillus</u>	47	0 (0.00)	1 (2.13)	46 (97.87)
<u>C. musculus</u>	33	0 (0.00)	1 (3.03)	32 (96.97)
<u>C. sorellus</u>	57	0 (0.00)	6 (10.53)	51 (89.47)
<u>C. tener</u>	76	1 (1.32)	37 (48.68)	38 (50.00)
<u>C. venustus</u>	39	0 (0.00)	29 (74.36)	10 (25.64)

Figure 32. Dorsal views of skulls of representatives of Calomys:
A) C. venustus, USNM 290914; B) C. callosus, AMNH 261961; C) C. tener, USNM 440557; D) C. sorellus, FMNH 75396; E) C. musculus, MSB 55272; F) C. murillus, FMNH 23395; G) C. lepidus, AMNH 260609; H) C. hummelincki, USNM 460440; I) C. bimaculatus, AMNH 206333; and J) C. laucha, UMMZ 133929. Bar represents 10 mm.

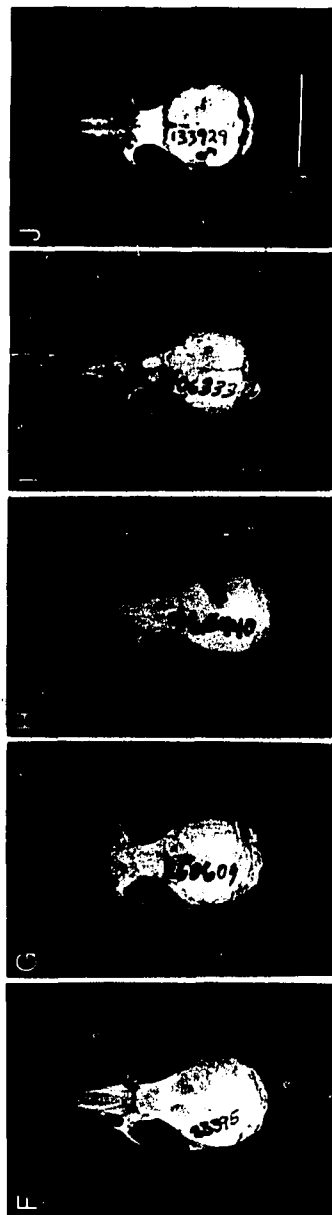
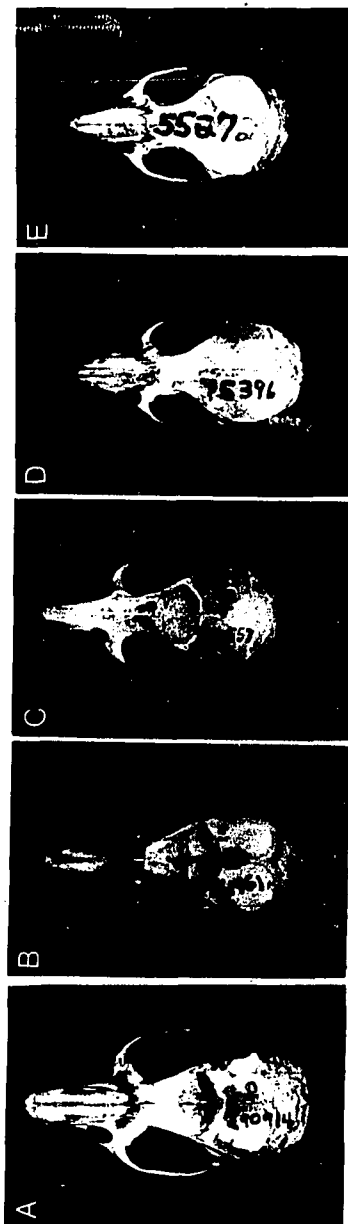


Figure 33. Ventral views of skulls of representatives of
Calomys. Species and specimens as in figure 32.

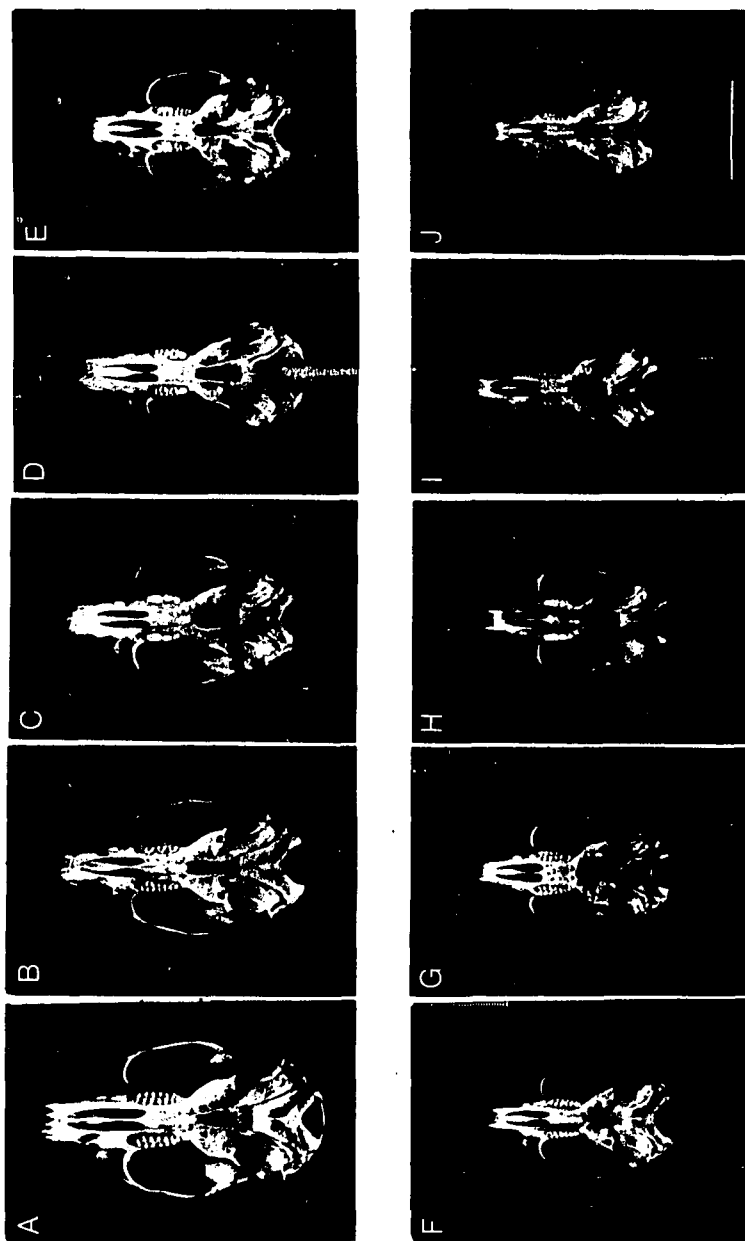


Figure 34. SEM photographs of the upper (top row) and lower (bottom row) molar toothrows in the different species of Calomys: A) C. venustus, AMNH 41870; B) C. callosus, AMNH 260718; C) C. tener, USNM 460553; D) C. sorellus, AMNH 231697; and E) C. musculus, AMNH 260666. Bars represent 1 mm.

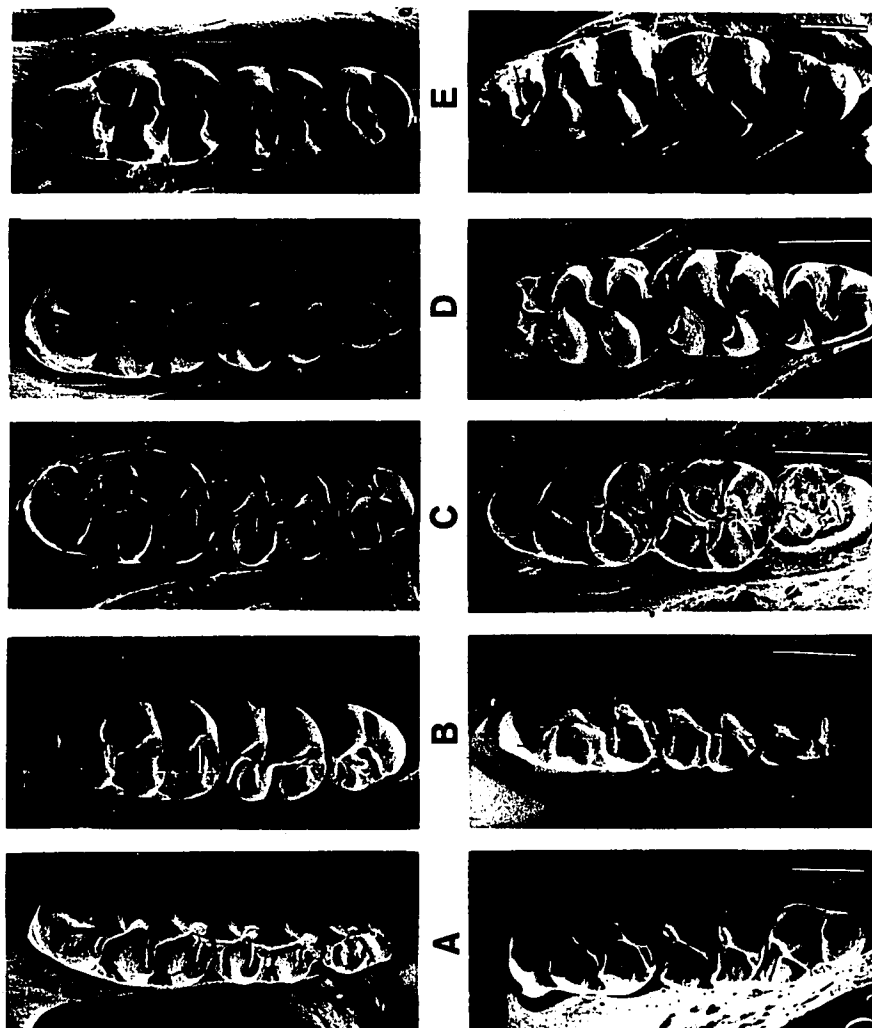
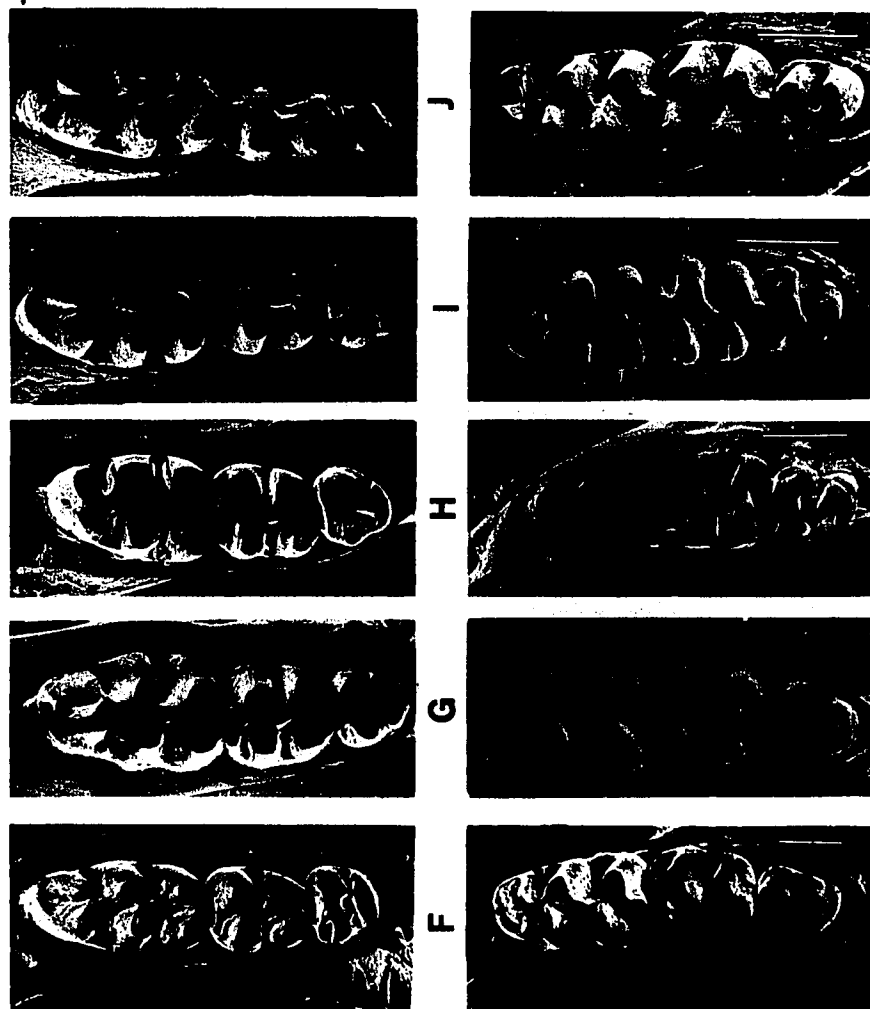


Figure 35 (fig. 34 cont'd). From left to right; F) C. murillus, FMNH 29102; G) C. lepidus, AMNH 260608; H) C. hummelincki, USNM 460441; I) C. bimaculatus, AMNH 206340; and J) C. laucha, AMNH 246867. Bars represent 1 mm.



SEXUAL DIMORPHISM AND AGE-RELATED VARIATION:

Sexual dimorphism is readily apparent in many species of mammals, but is not generally important taxonomically in murid rodents (Myers and Carleton, 1981; Engstrom et al., 1982; Koh and Peterson, 1983; Airoidi and Hoffman, 1984; Bergstrom, 1984; Xia and Millar, 1987; Olds et al., 1987; Tolliver et al., 1987, and Olds and Anderson, in press, b).

Many genera of sigmodontine rodents are poorly defined taxonomically because of the lack of clear diagnostic characters and the presence of considerable overlap in mensural characters. Age-related size variation is often a confounding problem for systematic studies because the adults may continue to grow throughout life (Koh and Peterson, 1983). Frequently, old adults of one species resemble young adults of another. Thus, I was concerned with age variation as a confounding problem in species recognition and future analyses. Age-related size variation is significant in some murid rodents (Koh and Peterson, 1983; Airoidi and Hoffman, 1984; Xia and Millar, 1987; and Tolliver et al., 1987). Hershkovitz (1962) noted considerable size variation within Calomys. He stressed the variation within C. laucha (see p. 147), but his C. laucha included five species, C. bimaculatus, C. hummelincki, C. laucha, C. murillus, and C. musculus.

I analyzed the largest series available for both C. callosus and C. sorellus. The sample of C. sorellus (n = 68), is from 6.3

mi W of Casapalca, Province of Lima, Peru, at 12,600 feet (3840 m); and the series of C. callosus (n = 240) is from San Joaquín, Department of Beni, Bolivia, a lowland locality, approximately 300 m in elevation. The age class distributions of the two samples are shown in fig 36: in both samples, the predominant age class is 2, the next most abundant are 1 and 3 and the remaining age classes accounted for just over 10 % of the population in C. sorellus and just under 10 % in C. callosus. The sex ratios of the two samples are similar, in C. sorellus, males comprise 54.4 % of the total, in C. callosus, males account for 56.25 % (fig. 36 A).

Tables 8 and 9 give the means, standard deviations and ranges of the data for age classes 1 through 6 for C. callosus and C. sorellus.

The results of two-way analyses of variance of age and sex on these data for the series of C. callosus and C. sorellus are given in tables 10-11. I used the General Linear Models procedure in SAS because of unbalanced cells in the data. The F value from the type III sum of squares is given. For discussions of the problems and possible solutions relating to analysis of variance on unbalanced data and the different sums of squares, see Sokal and Rolf (1981), Freund and Littell (1981), and Leamy (1983).

Figure 36. Histograms showing age class distribution and sex ratios for a series of Calomys sorellus (above) from 6.3 mi W Casapalca, Province of Lima, Peru (n=68) and a series of C. callosus (below) from San Joaquin, Department of Beni, Bolivia (n=240).

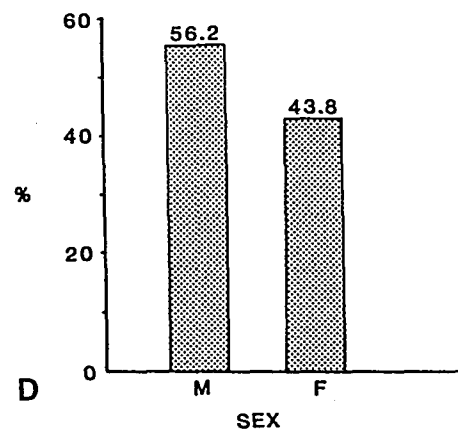
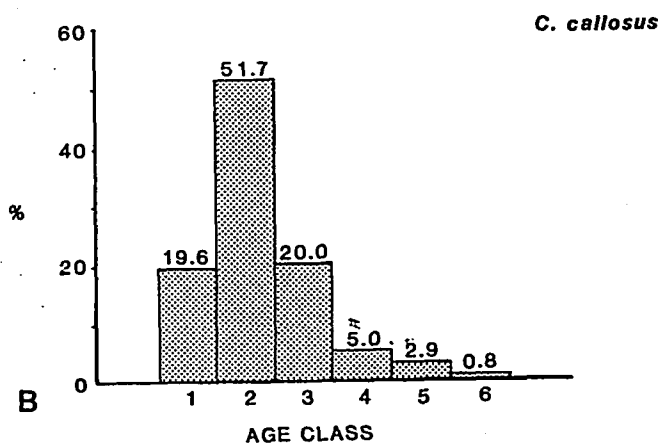
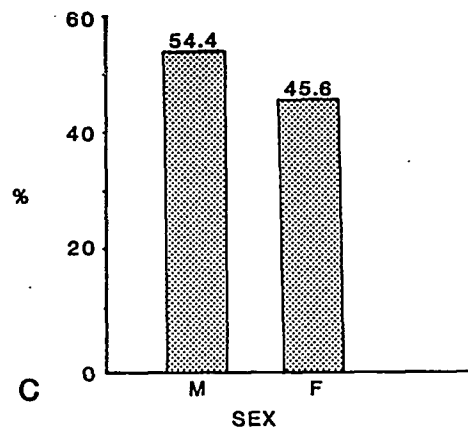
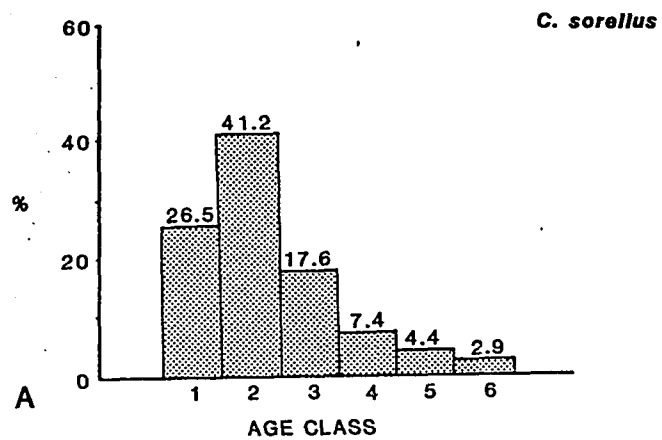


Table 8

Means and standard deviations of measurements taken on the different age classes of C. callosus from San Joaquín, Department of Beni, Bolivia. Minimum and maximum measurements in parentheses. All measurements in mm.

MSMT	AGE CLASS 1 (n=48)	AGE CLASS 2 (n=127)	AGE CLASS 3 (n=48)
LRS	6.86 ± 0.59 (5.56-7.86)	7.69 ± 0.54 (6.38-9.39)	7.92 ± 0.43 (6.84-8.96)
GLS	23.93 ± 1.32 (21.24-26.69)	25.95 ± 1.22 (23.09-29.21)	26.44 ± 1.16 (23.64-28.89)
ZBR	12.81 ± 0.70 (11.50-14.16)	13.87 ± 0.69 (11.78-15.88)	14.16 ± 0.73 (12.25-15.81)
BBC	11.09 ± 0.34 (10.47-11.78)	11.39 ± 0.32 (10.65-12.22)	11.39 ± 0.34 (10.49-11.97)
IOC	4.14 ± 0.23 (3.68-4.58)	4.34 ± 0.22 (3.92-4.93)	4.33 ± 0.26 (3.78-5.12)
WRS	4.58 ± 0.36 (3.84-5.68)	5.05 ± 0.33 (4.24-6.18)	5.21 ± 0.32 (4.56-5.92)
LINE	5.50 ± 0.33 (4.83-6.22)	5.95 ± 0.40 (5.06-7.23)	6.08 ± 0.35 (5.21-6.70)
PAL	3.97 ± 0.24 (3.58-4.41)	4.31 ± 0.30 (3.64-5.09)	4.38 ± 0.28 (3.80-5.01)
PPL	8.10 ± 0.61 (6.62-9.43)	9.14 ± 0.65 (7.58-10.91)	9.35 ± 0.60 (8.03-10.51)
LBULL	3.70 ± 0.12 (3.39-3.98)	3.82 ± 0.14 (3.46-4.32)	3.85 ± 0.17 (3.40-4.15)
MAX	3.90 ± 0.12 (3.67-4.20)	3.91 ± 0.14 (3.61-4.22)	3.91 ± 0.15 (3.64-4.25)

Table 8 cont'd.

	AGE CLASS 1	AGE CLASS 2	AGE CLASS 3
DIAS	5.57 $\pm$ 0.40 (4.76-6.62)	6.25 $\pm$ 0.44 (5.22-7.37)	6.48 $\pm$ 0.35 (5.83-7.15)
INCTL	0.71 $\pm$ 0.13 (0.44-0.96)	0.85 $\pm$ 0.16 (0.56-1.72)	0.89 $\pm$ 0.17 (0.58-1.36)
LM1	1.87 $\pm$ 0.08 (1.68-2.07)	1.88 $\pm$ 0.08 (1.69-2.10)	1.89 $\pm$ 0.08 (1.74-2.12)
LM2	1.19 $\pm$ 0.04 (1.11-1.30)	1.18 $\pm$ 0.06 (1.02-1.33)	1.18 $\pm$ 0.05 (1.07-1.34)
LM3	0.86 $\pm$ 0.06 (0.74-1.00)	0.87 $\pm$ 0.06 (0.68-1.03)	0.88 $\pm$ 0.07 (0.74-1.09)
WM1	1.13 $\pm$ 0.06 (1.00-1.25)	1.15 $\pm$ 0.06 (0.98-1.27)	1.16 $\pm$ 0.05 (1.05-1.30)
WM2	1.07 $\pm$ 0.05 (0.96-1.19)	1.08 $\pm$ 0.06 (0.94-1.23)	1.11 $\pm$ 0.05 (1.01-1.20)
WM3	0.92 $\pm$ 0.05 (0.80-1.05)	0.92 $\pm$ 0.06 (0.75-1.05)	0.92 $\pm$ 0.05 (0.80-1.06)
PBR	2.35 $\pm$ 0.18 (2.03-2.69)	2.51 $\pm$ 0.17 (2.16-3.11)	2.57 $\pm$ 0.20 (2.02-3.01)
WINCT	1.29 $\pm$ 0.14 (0.74-1.61)	1.50 $\pm$ 0.13 (1.23-1.84)	1.58 $\pm$ 0.10 (1.28-1.74)
PARA	2.51 $\pm$ 0.15 (2.17-2.79)	2.63 $\pm$ 0.17 (2.22-3.07)	2.65 $\pm$ 0.18 (2.32-3.02)
MESF	1.26 $\pm$ 0.13 (0.99-1.55)	1.27 $\pm$ 0.15 (0.91-1.70)	1.22 $\pm$ 0.18 (0.82-1.53)
TL	148.93 $\pm$ 14.19 (108-182)	165.29 $\pm$ 14.99 (115-195)	166.94 $\pm$ 14.01 (130-194)
T	60.67 $\pm$ 7.03 (35-76)	66.41 $\pm$ 8.03 (40-80)	63.21 $\pm$ 9.93 (39-80)

Table 8 cont'd.

	AGE CLASS 1	AGE CLASS 2	AGE CLASS 3
HF	18.30 ± 1.64 (15-22)	19.26 ± 1.71 (14-23)	19.46 ± 1.61 (14-21)
E	14.78 ± 1.53 (11-19)	15.67 ± 1.37 (12-19)	15.77 ± 1.29 (12-19)

Table 8 cont'd.

MSMT	AGE CLASS 4 (n=12)	AGE CLASS 5 (n=7)	AGE CLASS 6 (n=2)
LRS	7.96 $\pm$ 0.49 (7.31-8.79)	8.43 $\pm$ 0.43 (7.87-8.92)	8.40 $\pm$ 0.27 (8.21-8.59)
GLS	26.60 $\pm$ 1.00 (25.45-28.19)	27.53 $\pm$ 0.56 (26.97-28.25)	27.97 $\pm$ 1.14 (27.16-28.77)
ZBR	14.13 $\pm$ 0.53 (13.39-15.12)	14.68 $\pm$ 0.43 (14.13-15.19)	14.49 $\pm$ 0.58 (14.08-14.89)
BBC	11.44 $\pm$ 0.41 (10.81-12.02)	11.71 $\pm$ 0.19 (11.44-11.98)	11.73 $\pm$ 0.31 (11.51-11.95)
IOC	4.33 $\pm$ 0.20 (3.99-4.74)	4.55 $\pm$ 0.13 (4.32-4.69)	4.87 $\pm$ 0.04 (4.84-4.90)
WRS	5.26 $\pm$ 0.37 (4.75-5.95)	5.45 $\pm$ 0.24 (5.04-5.74)	5.56 $\pm$ 0.16 (5.45-5.67)
LINE	6.07 $\pm$ 0.26 (5.85-6.73)	6.47 $\pm$ 0.42 (6.01-7.12)	6.75 $\pm$ 0.47 (6.42-7.08)
PAL	4.43 $\pm$ 0.21 (4.05-4.90)	4.51 $\pm$ 0.33 (4.05-5.00)	4.51 $\pm$ 0.05 (4.47-4.54)
PPL	9.43 $\pm$ 0.48 (8.56-10.18)	9.86 $\pm$ 0.47 (9.03-10.49)	10.19 $\pm$ 0.66 (9.72-10.65)
LBULL	3.78 $\pm$ 0.14 (3.61-3.95)	3.89 $\pm$ 0.12 (3.76-4.08)	3.91 $\pm$ 0.18 (3.78-4.04)
MAX	3.77 $\pm$ 0.15 (3.57-3.96)	3.71 $\pm$ 0.28 (3.18-4.02)	3.78 $\pm$ 0.14 (3.68-3.88)

Table 8 cont'd.

	AGE CLASS 4 (n=12)	AGE CLASS 5 (n=7)	AGE CLASS 6 (n=2)
DIAS	6.66 $\pm$ 0.33 (6.14-7.16)	7.01 $\pm$ 0.32 (6.66-7.56)	7.35 $\pm$ 0.49 (7.00-7.69)
INCTL	0.95 $\pm$ 0.14 (0.72-1.20)	0.89 $\pm$ 0.10 (0.75-1.07)	1.01 $\pm$ 0.14 (0.91-1.11)
LM1	1.81 $\pm$ 0.08 (1.69-1.93)	1.82 $\pm$ 0.09 (1.69-1.96)	1.80 $\pm$ 0.10 (1.73-1.87)
LM2	1.13 $\pm$ 0.06 (1.03-1.21)	1.12 $\pm$ 0.04 (1.06-1.17)	1.16 $\pm$ 0.08 (1.10-1.22)
LM3	0.87 $\pm$ 0.05 (0.80-0.98)	0.90 $\pm$ 0.08 (0.76-1.02)	0.86 $\pm$ 0.08 (0.80-0.91)
WM1	1.14 $\pm$ 0.08 (1.04-1.27)	1.15 $\pm$ 0.06 (1.10-1.26)	1.19 $\pm$ 0.05 (1.15-1.22)
WM2	1.08 $\pm$ 0.06 (0.98-1.18)	1.06 $\pm$ 0.11 (0.94-1.22)	1.11 $\pm$ 0.02 (1.09-1.12)
WM3	0.89 $\pm$ 0.05 (0.77-0.99)	0.91 $\pm$ 0.08 (0.81-1.07)	0.87 $\pm$ 0.05 (0.83-0.90)
PBR	2.53 $\pm$ 0.19 (2.19-2.82)	2.66 $\pm$ 0.16 (2.43-2.87)	2.61 $\pm$ 0.16 (2.49-2.72)
WINCT	1.55 $\pm$ 0.11 (1.38-1.82)	1.66 $\pm$ 0.10 (1.50-1.77)	1.61
PARA	2.64 $\pm$ 0.17 (2.36-2.89)	2.70 $\pm$ 0.13 (2.57-2.86)	2.68 $\pm$ 0.06 (2.64-2.72)
MESF	1.20 $\pm$ 0.20 (0.92-1.53)	1.15 $\pm$ 0.19 (0.88-1.40)	1.04 $\pm$ 0.06 (1.00-1.08)
TL	171.42 $\pm$ 12.47 (155-195)	168.71 $\pm$ 10.84 (159-186)	170.00 $\pm$ 14.14 (160-180)
T	65.75 $\pm$ 9.06 (45-75)	63.43 $\pm$ 4.69 (58-69)	68.50 $\pm$ 6.36 (64-73)

Table 8 cont'd.

	AGE CLASS 4	AGE CLASS 5	AGE CLASS 6
HF	18.50 ± 2.20 (15-21)	19.57 ± 1.13 (17-20)	18.50 ± 2.12 (17-20)
E	15.08 ± 2.07 (10-17)	16.57 ± 1.27 (15-18)	16.00 ± 0.00 (16-16)

Table 9

Means and standard deviation of measurements on the age classes of C. sorellus from 6.3 mi W of Casapalca, Department of Lima, Peru. Minimum and maximum measurements in parentheses. All measurements in mm.

MSMT	AGE CLASS 1 (n=18)	AGE CLASS 2 (n=28)	AGE CLASS 3 (n=12)
LRS	6.41 $\pm$ 0.23 (6.03-6.86)	6.83 $\pm$ 0.47 (5.86-7.70)	7.52 $\pm$ 0.21 (7.16-7.88)
GLS	21.62 $\pm$ 0.59 (20.23-22.52)	22.52 $\pm$ 1.04 (20.54-24.32)	24.14 $\pm$ 0.65 (22.88-25.34)
ZBR	11.23 $\pm$ 0.41 (10.42-11.70)	11.71 $\pm$ 0.56 (10.31-13.01)	12.59 $\pm$ 0.48 (12.11-13.58)
BBC	10.71 $\pm$ 0.30 (10.27-11.17)	10.87 $\pm$ 0.30 (9.78-11.41)	10.96 $\pm$ 0.31 (10.44-11.65)
IOC	3.96 $\pm$ 0.15 (3.72-4.27)	3.90 $\pm$ 0.14 (3.62-4.16)	3.89 $\pm$ 0.11 (3.66-4.04)
WRS	4.13 $\pm$ 0.22 (3.80-4.59)	4.26 $\pm$ 0.25 (3.73-4.72)	4.58 $\pm$ 0.20 (4.23-4.91)
LINF	4.80 $\pm$ 0.22 (4.39-5.15)	5.06 $\pm$ 0.33 (4.29-5.65)	5.49 $\pm$ 0.14 (5.33-5.72)
PAL	3.46 $\pm$ 0.16 (3.17-3.68)	3.59 $\pm$ 0.27 (2.90-4.10)	3.67 $\pm$ 0.15 (3.32-3.87)
PPL	7.00 $\pm$ 0.30 (6.38-7.50)	7.44 $\pm$ 0.45 (6.53-8.52)	8.05 $\pm$ 0.27 (7.45-8.27)
LBULL	3.51 $\pm$ 0.10 (3.32-3.68)	3.58 $\pm$ 0.12 (3.30-3.80)	3.66 $\pm$ 0.14 (3.40-3.82)
MAX	3.56 $\pm$ 0.08 (3.44-3.77)	3.62 $\pm$ 0.14 (3.31-4.00)	3.59 $\pm$ 0.10 (3.42-3.72)

Table 9 cont'd.

	AGE CLASS 1 (n=18)	AGE CLASS 2 (n=28)	AGE CLASS 3 (n=12)
DIAS	4.69 ± 0.24 (4.26-5.08)	5.03 ± 0.32 (4.27-5.64)	5.60 ± 0.21 (5.23-5.86)
INCTL	0.56 ± 0.08 (0.38-0.69)	0.65 ± 0.08 (0.48-0.79)	0.81 ± 0.15 (0.60-1.01)
LM1	1.70 ± 0.06 (1.60-1.82)	1.74 ± 0.09 (1.52-1.95)	1.73 ± 0.07 (1.63-1.82)
LM2	1.10 ± 0.04 (1.02-1.16)	1.12 ± 0.06 (1.00-1.28)	1.10 ± 0.05 (1.02-1.18)
LM3	0.72 ± 0.03 (0.66-0.78)	0.74 ± 0.04 (0.69-0.84)	0.74 ± 0.06 (0.63-0.83)
WM1	1.08 ± 0.06 (0.95-1.17)	1.08 ± 0.08 (0.94-1.21)	1.08 ± 0.03 (1.01-1.14)
WM2	0.98 ± 0.06 (0.89-1.08)	1.00 ± 0.06 (0.89-1.11)	1.03 ± 0.04 (0.93-1.08)
WM3	0.79 ± 0.05 (0.69-0.88)	0.82 ± 0.05 (0.73-0.92)	0.82 ± 0.05 (0.75-0.88)
PBR	2.24 ± 0.11 (2.02-2.43)	2.35 ± 0.11 (2.15-2.59)	2.55 ± 0.13 (2.32-2.76)
WINCT	1.08 ± 0.07 (0.95-1.19)	1.14 ± 0.07 (1.04-1.38)	1.22 ± 0.07 (1.07-1.35)
PARA	2.67 ± 0.16 (2.40-2.97)	2.77 ± 0.17 (2.35-3.09)	2.77 ± 0.09 (2.61-2.94)
MESF	0.77 ± 0.09 (0.60-0.90)	0.83 ± 0.15 (0.48-1.06)	0.82 ± 0.13 (0.58-0.99)
TL	130.33 ± 8.42 (115-146)	139.15 ± 11.15 (114-168)	157.42 ± 11.88 (131-173)
T	57.67 ± 6.33 (46-66)	62.84 ± 5.97 (53-75)	67.45 ± 6.71 (58-79)

Table 9 cont'd.

	AGE CLASS 1	AGE CLASS 2	AGE CLASS 3
HF	18.71 ± 0.92 (17-20)	18.78 ± 1.75 (13-21)	19.00 ± 1.48 (16-21)
E	15.50 ± 1.83 (13-18)	16.60 ± 1.93 (13-19)	17.33 ± 1.50 (15-20)

Table 9 cont'd.

MSMT	AGE CLASS 4 (n=5)	AGE CLASS 5 (n=3)	AGE CLASS 6 (n=2)
LRS	7.88 $\pm$ 0.22 (7.70-8.27)	7.62 $\pm$ 0.30 (7.40-7.83)	7.56 $\pm$ 0.11 (7.48-7.63)
GLS	24.96 $\pm$ 0.37 (24.61-25.50)	24.46 $\pm$ 0.58 (24.05-24.87)	24.58 $\pm$ 0.28 (24.38-24.77)
ZBR	13.00 $\pm$ 0.33 (12.51-13.26)	12.36 $\pm$ 0.22 (12.16-12.59)	12.96
BBC	10.95 $\pm$ 0.11 (10.86-11.13)	10.98 $\pm$ 0.34 (10.60-11.25)	10.89 $\pm$ 0.01 (10.88-10.89)
IOC	3.92 $\pm$ 0.09 (3.85-4.08)	3.82 $\pm$ 0.13 (3.68-3.93)	3.91 $\pm$ 0.04 (3.88-3.94)
WRS	4.80 $\pm$ 0.10 (4.66-4.90)	4.75 $\pm$ 0.31 (4.48-5.09)	4.92 $\pm$ 0.11 (4.84-4.99)
LINF	5.67 $\pm$ 0.21 (5.41-6.00)	5.75 $\pm$ 0.09 (5.66-5.83)	5.67 $\pm$ 0.02 (5.65-5.68)
PAL	3.85 $\pm$ 0.25 (3.57-4.13)	3.53 $\pm$ 0.04 (3.48-3.56)	3.70 $\pm$ 0.07 (3.65-3.75)
PPL	8.51 $\pm$ 0.39 (7.97-8.92)	8.36 $\pm$ 0.27 (8.10-8.64)	8.29 $\pm$ 0.34 (8.05-8.53)
LBULL	3.53 $\pm$ 0.06 (3.46-3.59)	3.62 $\pm$ 0.24 (3.35-3.81)	3.54 $\pm$ 0.11 (3.46-3.62)
MAX	3.66 $\pm$ 0.09 (3.56-3.79)	3.54 $\pm$ 0.01 (3.53-3.55)	3.48 $\pm$ 0.14 (3.38-3.58)

Table 9 cont'd.

	AGE CLASS 4 (n=5)	AGE CLASS 5 (n=3)	AGE CLASS 6 (n=2)
DIAS	5.70 $\pm$ 0.33 (5.29-6.17)	5.78 $\pm$ 0.06 (5.72-5.84)	5.63 $\pm$ 0.04 (5.60-5.66)
INCTL	0.69 $\pm$ 0.04 (0.65-0.74)	0.88 $\pm$ 0.06 (0.83-0.94)	0.84 $\pm$ 0.10 (0.77-0.91)
LM1	1.71 $\pm$ 0.06 (1.65-1.78)	1.68 $\pm$ 0.04 (1.65-1.72)	1.68 $\pm$ 0.04 (1.65-1.71)
LM2	1.10 $\pm$ 0.03 (1.07-1.14)	1.05 $\pm$ 0.01 (1.05-1.06)	1.05 $\pm$ 0.03 (1.03-1.07)
LM3	0.80 $\pm$ 0.02 (0.78-0.84)	0.78 $\pm$ 0.04 (0.73-0.81)	0.74 $\pm$ 0.08 (0.68-0.80)
WM1	1.12 $\pm$ 0.08 (1.03-1.23)	1.10 $\pm$ 0.10 (0.99-1.17)	1.18 $\pm$ 0.03 (1.16-1.20)
WM2	1.04 $\pm$ 0.05 (0.97-1.09)	1.03 $\pm$ 0.03 (1.00-1.05)	1.00 $\pm$ 0.01 (0.99-1.01)
WM3	0.85 $\pm$ 0.04 (0.81-0.90)	0.80 $\pm$ 0.02 (0.78-0.81)	0.77 $\pm$ 0.02 (0.75-0.78)
PBR	2.62 $\pm$ 0.14 (2.41-2.74)	2.53 $\pm$ 0.06 (2.46-2.56)	2.40 $\pm$ 0.32 (2.17-2.62)
WINCT	1.17 $\pm$ 0.07 (1.10-1.28)	1.16 $\pm$ 0.06 (1.10-1.22)	1.28 $\pm$ 0.02 (1.26-1.29)
PARA	2.78 $\pm$ 0.10 (2.66-2.89)	2.71 $\pm$ 0.09 (2.62-2.79)	2.66 $\pm$ 0.07 (2.61-2.71)
MESF	0.95 $\pm$ 0.09 (0.81-1.03)	0.92 $\pm$ 0.15 (0.77-1.07)	1.12 $\pm$ 0.07 (1.07-1.17)
TL	158.50 $\pm$ 11.36 (150-174)	156.33 $\pm$ 5.51 (150-160)	147.50 $\pm$ 0.71 (147-148)
T	66.00 $\pm$ 5.48 (62-74)	67.33 $\pm$ 3.79 (63-70)	65.00 $\pm$ 9.90 (58-72)

Table 9 cont'd.

	AGE CLASS 4	AGE CLASS 5	AGE CLASS 6
HF	20.00 $\pm$ 0.82 (19-21)	19.67 $\pm$ 1.15 (19-21)	19.00 $\pm$ 1.41 (18-20)
E	18.00 $\pm$ 2.16 (15-20)	16.67 $\pm$ 2.08 (15-19)	17

Table 10

Two-way analysis of variance on a sample of Calomys callosus from San Joaquín, Department of Beni, Bolivia, 300 m (n=244).

Character	Error df	F (sex)	F (age)	F (interaction)
LRS	216	0.29	25.02***	0.69
GLS	216	2.52	28.41***	1.19
ZBR	226	3.17	25.47***	0.56
BBC	228	2.80	8.67***	0.47
IOC	228	0.12	5.34***	0.54
WRS	228	1.50	25.25***	0.87
LINF	228	0.97	18.73***	2.50*
PAL	227	2.19	13.90***	0.99
PPL	216	4.96*	28.16***	0.64
LBULL	219	0.01	6.62***	1.34
MAX	220	0.11	3.88**	1.16
DIAS	228	2.31	39.84***	1.47
INCTL	228	0.34	10.39***	0.53
LM1	228	1.24	2.44*	0.86
LM2	228	0.97	3.66**	0.80
LM3	228	3.91*	1.15	1.40
WM1	228	1.43	1.90	0.84
WM2	228	0.66	2.73*	0.90
WM3	227	0.10	1.07	0.68
PBR	228	0.48	9.73***	1.11
WINCT	223	1.46	29.70***	1.23
PARA	224	0.12	4.53***	0.41
MESF	218	0.33	1.83	2.15

* $p \leq .05$, ** $p \leq .01$, *** $p \leq .001$

Table 11

Two-way analysis of variance on a sample of Calomys sorellus from 6.3 mi W of Casapalca, Department of Lima, Peru, 3800 m (n=68).

Character	Error df	F (sex)	F (age)	F (interaction)
LRS	51	0.14	22.73***	0.86
GLS	50	1.52	22.55***	0.41
ZBR	53	0.39	21.40***	2.61*
BBC	56	0.41	2.96*	2.02
IOC	55	0.05	0.47	0.47
WRS	55	1.65	13.67***	1.82
LINF	57	0.06	20.49***	1.29
PAL	57	0.80	2.33	0.32
PPL	53	0.62	16.57***	0.36
LBULL	57	4.12*	2.55*	1.70
MAX	57	0.51	1.41	0.31
DIAS	57	0.01	27.15***	1.65
INCTL	57	0.01	14.52***	1.13
LM1	57	0.09	0.82	0.71
LM2	57	0.61	1.84	0.20
LM3	57	1.54	2.02	0.54
WM1	57	0.04	1.57	2.06
WM2	57	0.19	1.74	0.36
WM3	57	0.82	1.89	0.36
PBR	57	0.60	13.52***	1.33
WINCT	56	2.04	8.07***	1.33
PARA	55	1.32	2.08	2.54*
MESF	55	1.28	2.05	2.52

* $p \leq .05$, ** $p \leq .01$, *** $p \leq .001$

Table 12

Two-way analysis of variance on a sample of Calomys callosus from 50 km WSW Fortín Madrejon, Department of Chaco, Paraguay (n=28).

Character	Error df	F (sex)	F (age)	F (interaction)
LRS	19	0.90	19.05***	0.25
GLS	19	0.40	21.19***	0.42
ZBR	19	0.09	23.27***	0.55
BBC	19	0.07	4.05*	0.43
IOC	19	0.27	6.25**	0.35
WRS	19	0.55	12.41***	0.30
LINF	19	0.35	12.55***	0.31
PAL	19	1.33	10.12***	1.76
PPL	19	2.40	31.23***	0.73
LBULL	19	2.65	4.24*	0.06
MAX	19	0.24	1.59	2.38
DIAS	19	0.13	23.23***	0.86
INCTL	19	1.22	3.09*	1.52
LM1	19	1.73	1.36	1.52
LM2	19	0.00	2.27	0.50
LM3	19	3.44	3.46*	2.48
WM1	19	1.94	3.51*	0.70
WM2	19	0.00	0.53	1.06
WM3	19	2.58	2.67	0.17
PBR	19	0.82	13.41***	1.52
WINCT	19	0.11	10.27***	1.35
PARA	19	0.29	6.36**	0.13
MESF	19	2.29	1.46	0.67

* $p \leq .05$, ** $p \leq .01$, *** $p \leq .001$

Table 13

Two-way analysis of variance on a sample of Calomys callosus from Huacaraje, Department of Beni, Bolivia, ca. 300 m (n=24).

Character	Error df	F (sex)	F (age)	F (interaction)
LRS	17	0.27	15.78***	1.33
GLS	17	4.15	8.61**	.
ZBR	18	0.51	8.59***	0.26
BBC	18	3.10	0.04	0.43
IOC	18	0.10	1.53	0.55
WRS	18	0.89	3.76*	0.11
LINF	18	0.20	3.79	0.05
PAL	17	1.07	2.63	0.32
PPL	17	0.02	10.21***	0.83
LBULL	18	0.71	2.15	1.32
MAX	18	1.89	0.88	1.86
DIAS	18	0.21	9.08***	0.86
INCTL	18	0.05	3.30*	1.06
LM1	18	2.07	0.37	1.10
LM2	18	0.01	0.18	0.01
LM3	18	0.07	2.80	2.29
WM1	18	2.99	1.01	2.34
WM2	18	1.70	0.68	0.64
WM3	18	0.00	0.77	0.00
PBR	18	1.10	4.02*	7.50*
WINCT	18	1.52	5.71**	1.41
PARA	18	1.23	0.65	0.00
MESF	18	0.02	1.23	0.56

* $p \leq .05$, ** $p \leq .01$, *** $p \leq .001$

The F value for age is significant in almost all characters; molar dimensions are less significant, if at all, and sex was insignificant in most characters. This is consistent in the results. In general, molar dimensions are age-stable characters. However, with wear, these dimensions decrease: a drop in toothrow length occurs because the widest part of the tooth is worn along with the cusps, leaving a smaller tooth in old animals.

This pattern holds for some other samples analyzed: C. callosus from 50 km WSW Fortín Madrejon, Chaco, Paraguay (table 12); C. callosus from Huacaraje, Beni, Bolivia, 300 m (table 13); and C. venustus from Sarmiento, Argentina, 500 m.

I then chose seven characters (greatest length of skull, GLS; length of rostrum, LRS; breadth of zygomatic arches, ZBR; breadth of braincase, BBC; length of incisive foramina, LINF; length of palate, LPAL; post-palatal length, PPL; and length of maxillary toothrow, MAX), some that were expected to increase with age and some that were not, and fit a quadratic equation (using Proc GLM of SAS) to obtain predicted values. In most of the characters analyzed, the data and the model show a distinct dropoff at age classes 5 and 6.

Of the dimensions examined, LINF, LRS, ZBR, LPAL, and PPL, are all highly correlated with overall cranial size. MAX shows only a slight decrease in size, for the reasons given above. Some possible hypotheses to explain the drop in dimensions in old

animals include bone resorption in old age, sampling artifacts, or possibly differential mortality. This pattern has been noted in populations of the genus Oryzomys, subgenus Oligoryzomys (Olds and Anderson, in press, b), but not sufficiently studied. Tolliver et al. (1987) noted a high correlation with age in many cranial and external dimensions, and that age had little influence on toothrow, hind foot and palate length.

Principal Components Analysis (PCA) was done using the correlation matrix on these two series (see Neff and Marcus, 1980, and Sokal and Rolff, 1981, for a discussion of this method). The eigenvectors are given in tables 14 and 15. In both cases, Principal Component 1 separated the specimens by size, and thus in most cases, age; the youngest animals are to the left. Age class 2 is the largest and most variable in size, and this was apparent in the plots; tooth measurements are especially important in Principal Component 2. It separates the larger toothed from the smaller toothed.

In the samples examined, age variation is highly significant while sexual dimorphism is not. Adult animals do grow, although growth slows considerably after age class 3. In many cases, the older animals are smaller, especially in C. sorellus, and an explanation is lacking at this time. Two possible explanations are 1) that the animals do actually get smaller as they get older, and 2) that smaller adults are able to live longer. Resolution of

this question requires analysis of more large series including samples of other Sigmodontinae and ecological experiments.

Airolidi and Hoffmann (1984) summed up much of the problem in intraspecific variation "...skulls exhibiting similar morphological features may not be the same age, while skulls of the same age are not necessarily morphologically identical, even when growth is completed.." (p. 4).

Tolliver et al. (1987) clearly stated the relevance of these analyses, "In taxonomic studies, it is important to know which traits vary least with sex, age or sex by age interaction because these effects must be accounted for before comparisons are made with other taxa" (p. 426). These studies are also important to show how traits vary between populations of the same species, before comparisons with other taxa are made.

As a result of these analyses, sexes were combined in later procedures. Adults of age class 2 and greater were included. Animals of age class 1 are much smaller than the older adults. Most individuals in the samples examined were either age class 2 or 3.

Table 14

Eigenvectors from a principal components analysis on a sample of Calomys callosus from Bolivia: Dept. Beni; San Joaquin, 300 m (N=197). (The cumulative percentage of variance explained by each component is given at the bottom of the table).

Character	Prin1	Prin2	Prin3
LRS	0.2937	-.0935	0.0745
GLS	0.3094	-.0783	0.0401
ZBR	0.2974	-.0612	0.0270
BBC	0.2264	0.0004	0.0346
IOC	0.1360	-.0458	-.2437
WRS	0.2907	-.0574	-.0130
LINF	0.2504	-.1234	0.1697
PAL	0.2347	0.0259	-.0570
PPL	0.2899	-.1189	0.0249
LBULL	0.2071	0.0510	0.0302
MAX	0.1109	0.4636	-.0588
DIAS	0.2907	-.1563	0.0762
INCTL	0.1868	-.0556	-.1763
LM1	0.0880	0.3504	-.0567
LM2	0.0499	0.3971	0.0265
LM3	0.1176	0.3011	-.0483
WM1	0.1241	0.2648	0.0761
WM2	0.1264	0.3454	0.0933
WM3	0.0801	0.3471	0.0378
PBR	0.2197	-.0905	0.0698
WINCT	0.2479	-.1008	0.0866
PARA	0.1647	0.0045	-.5035
MESF	-.0098	0.0381	0.7546
CUMULATIVE %	41.91	55.72	61.12

Table 15

Eigenvectors from a principal components analysis on a sample of Calomys sorellus from Peru: Dept. Lima; Prov. Huarachiri, 6.3 mi W. Casapalca, 3800 m (N=51). (The cumulative percentage of variance explained by each component is given at the bottom of the table).

Character	Prin1	Prin2	Prin3
LRS	0.2891	-.1172	0.0523
GLS	0.2966	-.0973	0.0616
ZBR	0.2953	-.0647	0.0929
BBC	0.1867	0.1215	0.1409
IOC	-.0414	0.1435	0.4782
WRS	0.2529	-.1059	0.0771
LINF	0.2800	-.1474	-.0013
PAL	0.1757	0.2047	0.2169
PPL	0.2824	-.1445	-.0268
LBULL	0.1927	0.0399	-.0208
MAX	0.1661	0.3994	-.2014
DIAS	0.2731	-.1767	0.0790
INCTL	0.1706	-.2647	-.0015
LM1	0.1253	0.4225	-.1755
LM2	0.0835	0.4021	-.0309
LM3	0.1490	-.0371	-.1965
WM1	0.1729	0.2162	-.1919
WM2	0.1875	0.2027	-.2245
WM3	0.1655	0.3014	0.0687
PBR	0.2393	-.1271	-.0959
WINCT	0.2186	-.0199	0.0899
PARA	0.1669	0.0510	0.4586
MESF	0.1138	-.1992	-.4955
CUMULATIVE %	45.05	59.79	66.09

Numerical Analyses within Calomys:

Distinguishing the species of Calomys is more difficult than separating Calomys from other genera because there are few taxonomically useful characters. Much of the variation between species is in size: there is considerable overlap in almost all characters, except between the very small and very large species (fig. 37, table 2). Tail length separates some species, pelage coloration, presence or absence of the alisphenoid strut, beaded or unbeaded edges of the supraorbitals, karyotypes, and habitat separate others. Dentally there is little variation among species within the genus, except in the frequency of certain structures, such as the anteromedian flexus and style.

The cranio-dental mensural data were submitted to Principal Components Analysis (PCA) and Canonical Variates Analysis (CVA). External measurements were excluded from analyses because of extremely high coefficients of variation, possibly caused by age or differences in measuring by different collectors. For general descriptions of the statistical methods and assumptions involved see Neff and Marcus (1980).

Because the plots of the above PCA and CVA analyses of individual specimens are difficult to interpret (due to the number of individuals included), sample means were used in additional PCA and CVA analyses. There are large differences in numbers of samples, and sample sizes between different species (table 16).

Figure 37. Graphs of the mean (horizontal line), range of measurement, and two standard errors of the mean (black rectangle) for two dimensions, greatest length of skull (GLS) and length of maxillary tooththrow (MAX), in the species of Calomys, showing size overlap. Sample sizes are given in table 2. A, C. laucha; B, C. bimaculatus; H, C. hummelincki; T, C. tener; MR, C. murillus; L, C. lepidus; MS, C. musculus; S, C. sorellus; C, C. callosus; and V, C. venustus.

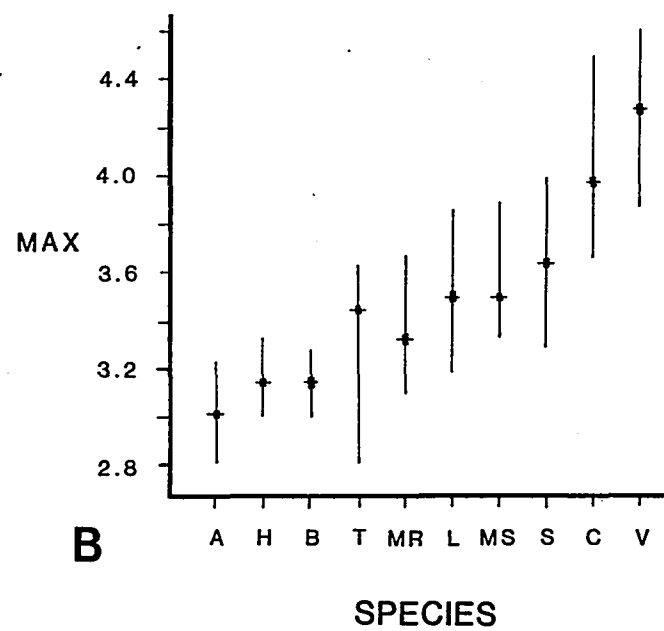
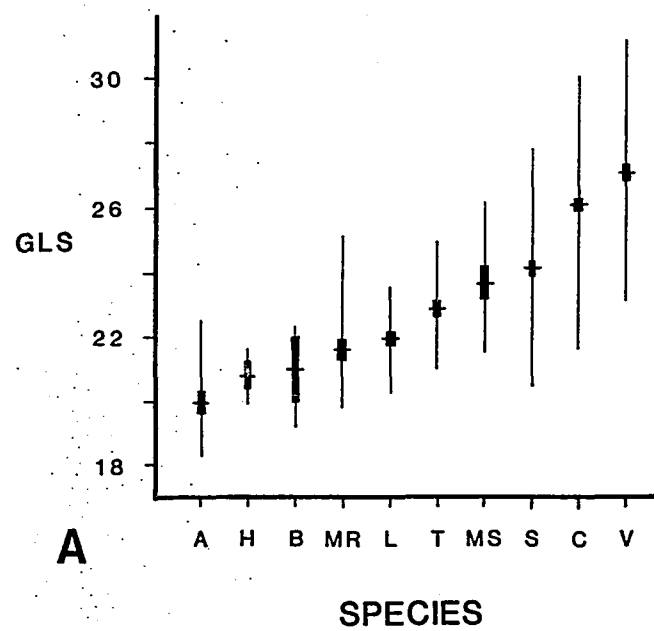


Table 16

The number of samples per species of Calomys and the number of observations per sample.

Species	Sample Size (N)									
	1	2	3	4	5	6-10	11-20	21-50	50+	Total
<u>C. bimaculatus</u>	1	0	0	0	1	0	0	0	0	2
<u>C. callosus</u>	4	4	0	3	3	3	9	3	1	30
<u>C. hummelincki</u>	0	1	0	0	0	1	0	0	0	2
<u>C. laucha</u>	4	2	1	0	0	0	0	1	0	8
<u>C. lepidus</u>	11	6	1	1	2	1	1	0	0	23
<u>C. murillus</u>	3	3	1	1	2	5	0	0	0	15
<u>C. musculus</u>	3	0	2	0	0	3	0	0	0	8
<u>C. sorellus</u>	3	1	3	2	1	7	1	0	1	19
<u>C. tener</u>	1	1	0	0	0	1	1	0	1	5
<u>C. venustus</u>	3	5	2	0	2	8	5	2	0	27
Total	33	23	10	7	11	29	17	6	3	139

All samples of one individual from one locality were excluded. Samples of two individuals were generally excluded, except in certain cases to increase the representation of those species known from only a few specimens (i.e., C. hummelincki and C. laucha). A total of 86 samples, representing 10 species were used in these analyses.

In both the PCA and CVA analyses of sample means, the means were weighted by the sample size (using the WEIGHT statement in SAS). The results of a PCA on unweighted sample means were similar to those of a weighted analyses, but the results of a CVA on unweighted sample means were very different; the Mahalanobis Distances were greatly inflated over those from the analysis of individuals. The spatial relationships on the plots were similar in both PCA and CVA on weighted and unweighted sample means.

The results of a Principal Components Analysis (PCA) on the correlation matrix of all individuals of age class 2 and older are given in table 17 (eigenvectors). The first eigenvector is positive, accounts for approximately 71 % of the variance, and corresponds to cranial size.

In Principal Component 2, which accounts for 7 % of the variance, the dental dimensions dominate. This separates the smaller animals from the larger ones. Principal Component 3 accounts for 5 % of the variance; it weighs heavily on the widths of the parapyerygoid and mesopterygoid fossae. I also tried a PCA

on the covariance matrix of the log-transformed variables and the correlation matrix from the raw data with no noticeable difference. A PCA was done using only animals of age class 2, to eliminate some of the age-related size effects. The results are similar to those above. The pattern within the eigenvectors, positive on the first, dominance of fossae widths on the second or third and of dental dimensions on the second or third, tends to be somewhat consistent in all PCA analyses of individuals of Calomys (see tables 14-15, also).

The results of a PCA analysis using sample means weighted by sample size are given in table 18 (eigenvectors). Principal component 1 is positive and accounts for about 85 % of the variance. It separates the species by size. In figure 38 A, the largest species, C. callosus and C. venustus, are well to the right of the others, and the smallest species, C. laucha, C. bimaculatus, and C. hummelincki, are to the left. Calomys tener, C. lepidus, and C. murillus are all approximately the same size and C. musculus and C. sorellus are slightly larger. In principal component 2, which accounts for about 6.7 % of the total variance, the relative widths of the parapterygoid and mesopterygoid fossae are stressed. This tends to separate C. lepidus, C. murillus, C. musculus, and C. sorellus from C. hummelincki, C. laucha, C. bimaculatus, and C. tener. It also separates C. callosus and C. venustus from each other (fig. 38 A).

Table 17

Results of a Principal Components Analysis on individuals representing the species of Calomys (n=970). (The cumulative percentage of variance explained by each component is given at the bottom of the table)

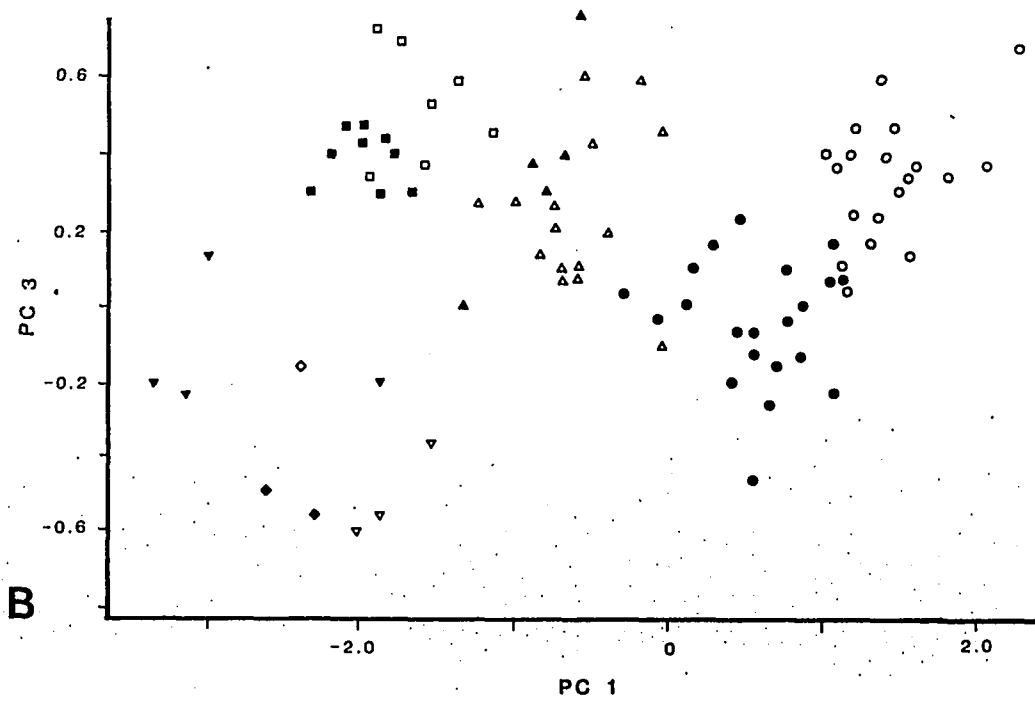
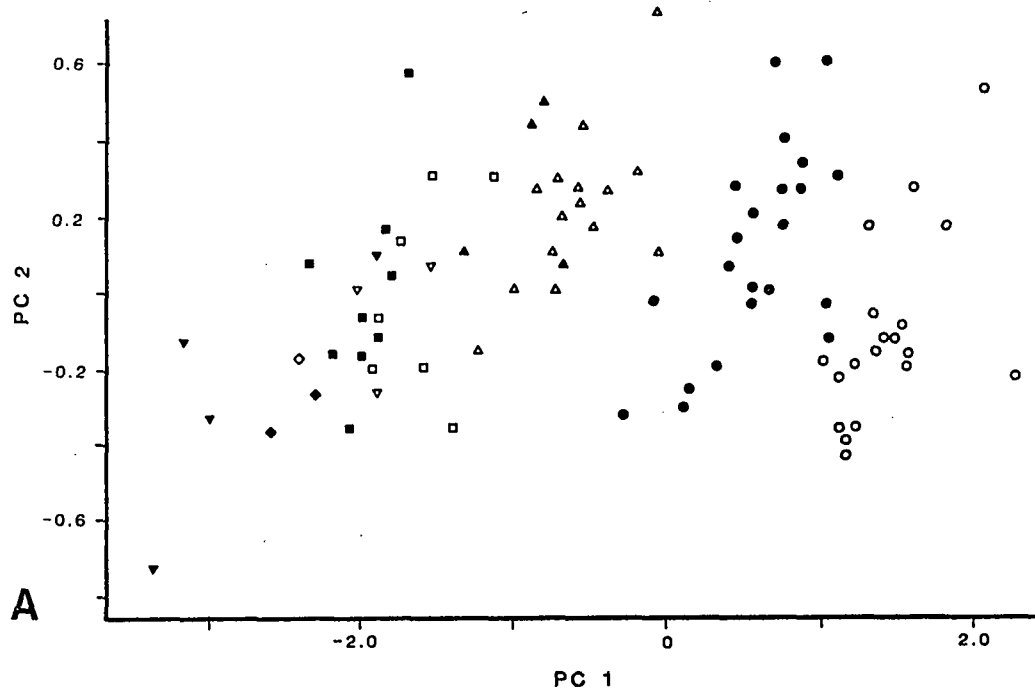
MSMT	Prin1	Prin2	Prin3
LRS	0.2314	-.1699	0.1294
GLS	0.2430	-.1706	0.0419
ZBR	0.2390	-.1565	0.0399
BBC	0.2303	-.0076	0.0238
IOC	0.2146	-.1287	-.1183
WRS	0.2283	-.2038	-.0521
LINF	0.2279	-.1837	-.0040
PAL	0.2239	-.0030	-.0114
PPL	0.2230	-.2721	0.0534
LBULL	0.2105	-.0341	0.0061
MAX	0.2273	0.3046	-.0066
DIAS	0.2296	-.2637	0.0115
LM1	0.2004	0.3548	0.0286
LM2	0.2075	0.3173	-.0735
LM3	0.2166	0.1936	-.0372
WM1	0.2002	0.3332	0.0303
WM2	0.2125	0.2842	-.0646
WM3	0.2126	0.2631	-.0969
PBR	0.1827	-.1648	0.2060
WINCT	0.2130	-.1570	-.1172
PARA	0.1382	0.0665	0.6883
MESF	0.1420	-.0824	-.6383
CUMULATIVE %	70.94	78.10	83.40

Table 18

Eigenvectors from a Principal Components Analysis on sample means of the species of Calomys (10 species, 86 observations) weighted by the sample size. The cumulative percentage of variance explained by each component is given at the bottom of the table).

Character	Prin 1	Prin 2	Prin 3
LRS	0.2175	0.0675	0.3020
GLS	0.2274	-.0533	0.1758
ZBR	0.2265	-.0837	0.1014
BBC	0.2222	-.0199	0.1020
IOC	0.2085	-.2723	0.0346
WRS	0.2197	-.1901	0.0905
LINF	0.2237	-.0926	0.1482
PAL	0.2243	-.0348	-0.766
PPL	0.2177	-.1411	0.2333
LBULL	0.2169	-.0247	0.0536
MAX	0.2229	0.1464	-.2271
DIAS	0.2220	-.1558	0.1877
LM1	0.2127	0.2171	-.2611
LM2	0.2176	0.1241	-.2764
LM3	0.2208	0.1082	-.1751
WM1	0.2090	0.2271	-.2922
WM2	0.2181	0.1293	-.2728
WM3	0.2230	0.0788	-.2298
PBR	0.1974	0.1737	0.3688
WINCT	0.2131	-.1962	-.0610
PARA	0.1491	0.5688	0.3331
MESF	0.1608	-.5079	-.1932
CUMULATIVE %	84.76	91.47	94.14

Figure 38. Results of a Principal Components Analysis on weighted sample means of the species of Calomys, A) PC 1 vs. PC 2, B) PC 1 vs. PC 3. closed inverted triangle, C. laucha; open diamond, C. bimaculatus; closed circle, C. callosus; closed diamond, C. hummelincki; open square, C. lepidus; closed triangle, C. musculus; closed square, C. murillus; open triangle, C. sorellus; open inverted triangle, C. tener; and open circle, C. venustus.



In principal component 3, which accounts for about 2.7 % of the total variance, LRS, PBR, PARA, and dental dimensions dominate. This is a reverse of the pattern in the analyses presented above (see tables 14-15, 18). In a plot of PC1 vs. PC3 (fig. 38 B), C. murillus, C. laucha, C. hummelincki, C. bimaculatus, and C. tener are separated from C. sorellus, and C. musculus. Calomys lepidus is not distinct from either of the above.

The results of a Canonical Variates Analysis (CVA) of individuals are given in table 19. This analysis uses specified groups, here, the species of Calomys. In table 19 of Mahalanobis Distances, notice the smaller distances between laucha and bimaculatus, callosus and venustus, and murillus and musculus. A CVA was done using only animals of age class 2, also. The results were similar to these.

The results of a CVA of weighted sample means are given in table 20 and figure 39. The Mahalanobis Distances in table 20 are less than those in table 19, the results of a CVA on individuals. This analysis, using weighted sample means, gives conservative estimates of the distances between species centroids. The distances are smallest between C. musculus and C. murillus, C. laucha and C. bimaculatus, C. callosus and C. venustus, and C. lepidus and C. murillus, C. musculus, and C. tener. In the plot of CAN1 versus CAN2 (fig. 39 A), C. callosus and C. venustus are close together; C. sorellus is isolated, and the rest of the

species cluster together with some internal separation; C. hummelincki and C. tener are well separated. In the lower plot of CAN1 vs. CAN3 (fig. 39 B), there is separation between a grouping of C. murillus and C. musculus from C. laucha, C. bimaculatus, C. hummelincki, and C. tener. Calomys tener and C. sorellus are fairly close together. The two largest species, C. callosus and C. venustus remain separate from the rest.

Some of the resulting spread in the results of PCA and CVA analyses (figs. 38-39) may be due to geographic variation between samples. I did one-way analyses of variance of locality (using the GLM procedure of SAS and the NESTED procedure to get estimates of the percent of variation due to locality) in the four species with the greatest number of samples, C. callosus, C. lepidus, C. sorellus, and C. venustus. The results of these analyses are given in tables 21-24. I used all adults of age class 2 and older in one analysis of variance, and the nested analysis of variance, and only age class 2 animals in another analysis of variance. The results of these analyses are given in the tables. In C. callosus (table 21), most characters are significant for locality. This is the species represented from the greatest number of localities. While the F values are significant, the variance contributed by locality is small. In C. lepidus (table 22), most characters are not significant for locality. The results in C. sorellus (table 23) and C. venustus (table 24) show significant for some

Table 19

Mahalanobis Distances between the species of Calomys based on analysis of individuals (n=963): A, C. laucha; B, C. bimaculatus; C, C. callosus; H, C. hummelincki; L, C. lepidus; MR, C. murillus; MS, C. musculus; S, C. sorellus; T, C. tener; and V, C. venustus.

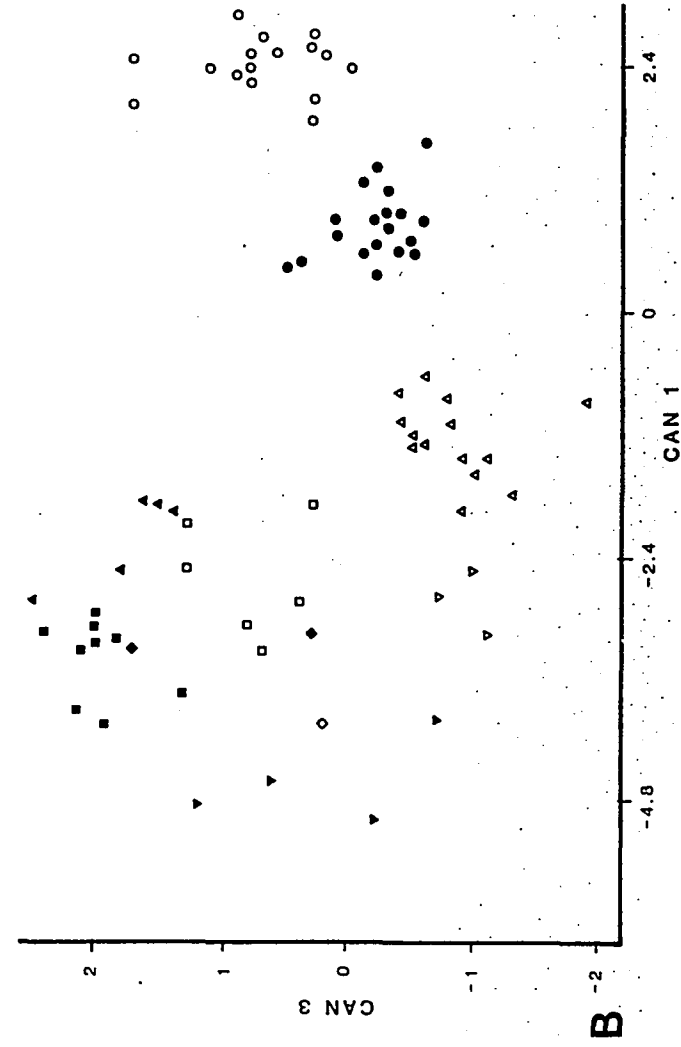
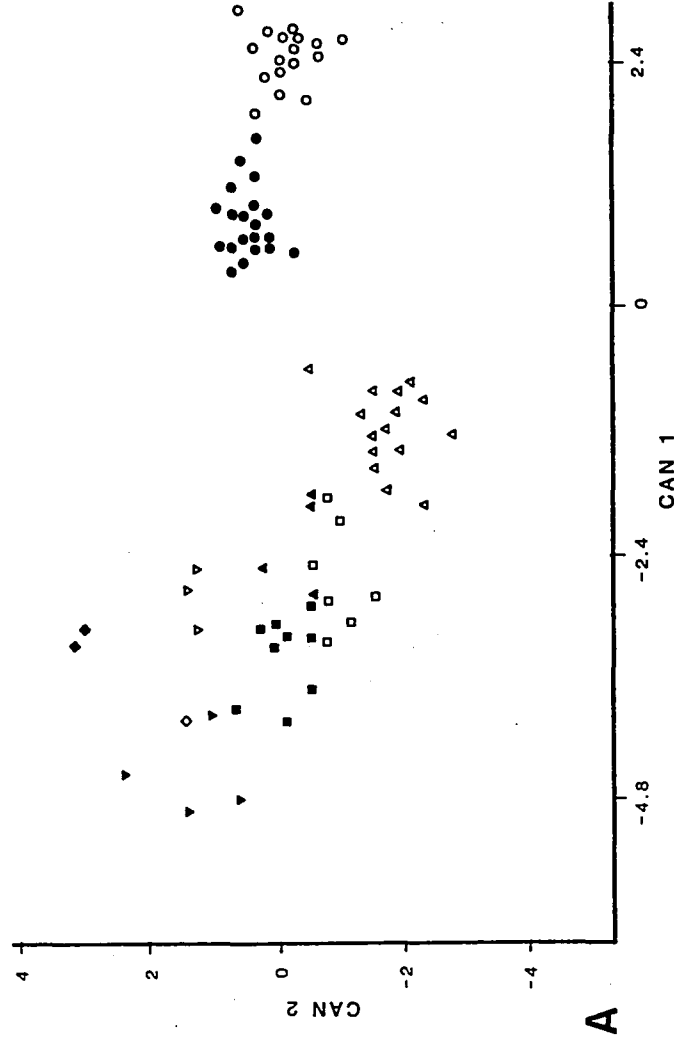
	A	B	C	H	L	MR	MS	S	T
B	3.62								
C	7.86	6.83							
H	4.31	4.75	8.16						
L	4.52	4.88	6.02	6.14					
MR	3.63	4.13	6.76	5.07	3.09				
MS	4.88	5.00	5.63	6.00	3.46	2.37			
S	6.37	5.90	4.46	7.90	3.66	5.16	4.30		
T	4.10	3.85	5.14	4.97	4.42	1.05	4.00	4.55	
V	10.16	9.03	3.06	10.12	7.58	8.61	7.30	5.98	7.45

Table 20

Table of Mahalanobis Distances from a Canonical Variates Analysis on the sample means of species of Calomys (86 samples representing 10 species) weighted by sample size. Species abbreviations are given in table 19.

	A	B	C	H	L	MR	MS	S	T
B	2.28								
C	5.97	5.34							
H	3.80	3.39	5.71						
L	3.59	3.32	4.32	4.93					
MR	3.40	3.15	4.92	4.17	2.24				
MS	4.22	3.82	3.94	4.62	2.45	1.75			
S	5.09	4.72	3.29	6.18	2.70	3.27	4.00		
T	3.05	2.81	3.92	3.93	3.30	3.52	3.64	3.59	
V	7.67	6.97	2.21	7.10	5.52	4.99	6.14	4.22	5.68

Figure 39. Results of a Canonical Variates Analysis on the weighted sample means representing the species of Calomys, A) CAN 1 vs. CAN 2, B) CAN 1 vs. CAN 3. Symbols as in figure 38.



characters. In the latter three, the percent contribution of locality to variance is also low. In the species represented by more than 25 localities, in most characters the among locality variance accounted for between 10 and 20 percent of the species variance. Some of the percent of among locality variance is due to different age composition of different samples.

A stepwise discriminant analysis (STEPDIS in SAS) was done on the data. No characters were discarded.

Table 21

Results of a one-way analysis of variance of locality in C. callosus on all animals of age class 2 and older (n = 514, 30 localities). The among locality variance is given as a percentage.

MSMT	Error df	F (loc)	% Variance (loc)
LRS	468	3.85***	16.58
GLS	464	4.12***	18.03
ZBR	481	4.34***	18.56
BBC	481	3.52***	14.72
IOC	480	3.46***	14.41
WRS	483	3.50***	14.51
LINF	482	3.39***	14.04
PAL	481	2.85***	11.22
PPL	459	3.46***	14.90
LBULL	471	5.18***	22.45
MAX	483	2.68***	10.23
DIAS	482	3.43***	14.20
LM1	483	3.22***	13.13
LM2	484	2.64***	10.02
LM3	484	2.33***	8.28
WM1	483	2.96***	11.75
WM2	483	2.57***	9.63
WM3	483	3.67***	15.38
PBR	483	4.59***	19.64
WINCT	476	6.93***	28.92
PARA	475	6.55***	27.72
MESF	469	2.88***	11.59

* $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$

Table 22

Results of a one-way analysis of variance of locality on all adults of C. lepidus (n = 64, 22 localities). The among locality variance is given as a percentage.

MSMT	Error df	F (loc)	% Variance (loc)
LRS	40	1.62	19.31
GLS	38	1.18	6.73
ZBR	38	1.06	2.33
BBC	37	1.21	7.93
IOC	41	1.39	12.96
WRS	40	1.32	10.89
LINF	42	1.75	21.87
PAL	41	1.67	20.17
PPL	36	0.83	0.00
LBULL	37	0.99	0.00
MAX	42	1.53	16.63
DIAS	42	1.60	18.21
LM1	42	1.20	6.79
LM2	42	1.54	16.76
LM3	42	0.91	0.00
WM1	42	1.84*	23.92
WM2	41	1.85*	24.35
WM3	42	2.08*	28.82
PBR	42	1.64	19.21
WINCT	42	1.46	14.54
PARA	38	1.05	1.98
MESF	38	1.94*	27.33

* $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$

Table 23

Results of a one-way analysis of variance for locality on all adults of C. sorellus (n = 148, 19 localities). The among locality variance is given as a percentage.

MSMT	Error df	F (loc)	% Variance (loc)
LRS	117	4.32***	33.81
GLS	114	4.65***	35.42
ZBR	125	6.74***	45.53
BBC	128	3.07***	22.87
IOC	126	2.45**	17.42
WRS	128	1.84*	10.72
LINF	129	3.95***	29.64
PAL	129	3.73***	28.03
PPL	121	5.00***	35.21
LBULL	129	3.23***	24.16
MAX	129	2.76***	20.03
DIAS	129	5.46***	38.90
LM1	129	3.28***	24.52
LM2	129	0.94	0.00
LM3	129	3.80***	28.55
WM1	129	1.72*	9.35
WM2	129	2.21**	14.70
WM3	129	1.89*	11.32
PBR	129	1.95*	11.93
WINCT	128	4.66***	34.39
PARA	128	4.88***	35.71
MESF	127	2.50**	17.81

* $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$

Table 24

Results of a one-way analysis of variance of locality on all adults of C. venustus (n = 220, 27 localities). The among locality variance is given as a percentage.

MSMT	Error df	F (loc)	% Variance (loc)
LRS	187	2.19**	13.51
GLS	183	2.82***	19.09
ZBR	191	2.32***	14.57
BBC	190	2.61***	16.78
IOC	193	1.83*	9.58
WRS	192	2.33***	14.57
LINF	192	3.18***	21.88
PAL	190	1.41	5.09
PPL	181	2.74***	18.60
LBULL	189	2.25**	13.59
MAX	191	1.75*	8.79
DIAS	191	2.49***	16.10
LM1	193	1.48	5.83
LM2	189	2.96***	20.32
LM3	190	2.72***	18.26
WM1	193	3.52***	24.35
WM2	190	3.85***	27.00
WM3	191	2.30***	14.35
PBR	192	1.15	1.95
WINCT	187	1.85*	10.10
PARA	185	1.73*	8.64
MESF	184	3.94***	27.52

* $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$

DISCUSSION OF RELATIONSHIPS WITHIN Calomys:

Hershkovitz (1962) considered Calomys sorellus to be the most "generalized member" of the genus. He considered C. laucha (which included C. laucha, C. bimaculatus, C. hummelincki, C. murillus, and C. musculus) to be "generalized" as well. He regarded C. callosus (which included C. callosus and C. venustus) to be specialized, mostly on the basis of the ridges in the interorbital area.

Williams and Mares (1981) produced two phenograms using dental, cranial and external characters of various South American Sigmodontinae. Included were three species of Calomys, C. callosus (probably = C. venustus), C. muriculus (= C. callosus), and C. musculus. In the phenogram based on taxonomic distance, C. callosus and C. muriculus (C. venustus and C. callosus) cluster together and C. musculus, while in the same larger cluster, is as distant from those two as from Oryzomys longicaudatus and Eligmodontia typus. The latter two species and C. musculus are all much smaller than the first two species mentioned and have relatively longer tails. In their second phenogram, based on correlations (in which taxa most similar in proportions will exhibit the highest positive similarity), all three species of Calomys cluster together, with C. callosus and C. musculus (= C. venustus and C. musculus) closer to each other than to C.

muriculus (= C. callosus). They used small sample sizes. C. callosus and C. venustus are extremely similar according to this study, see species accounts, and should show a close relationship (they do in karyotypes).

Pearson and Patton (1976) discussed relationships within Calomys based on karyology (see fig. 4, p. 345). They suggested that C. sorellus shows the primitive state (having a high diploid number), that C. laucha from Argentina (perhaps = C. bimaculatus) is closely related, and that C. musculus (= C. murillus), C. lepidus, and C. callosus (from Paraguay, error in the diploid number count, see species account of C. callosus) are a group. C. fecundus (= C. callosus) occupies an intermediate position. They further suggested that C. lepidus, which, with a high number of autosomal arms, is divergent karyotypically, may be more closely related to C. fecundus (= C. callosus). Table 25 summarizes the published diploid numbers for Calomys (see also Reig, 1986, p. 407). In most instances, these are based on single individuals. There is little information available on karyotypic variations within a sample or a species. The only reported polymorphism is by Pearson and Patton (1976) for C. sorellus.

Corti et al. (1987) performed Canonical Variates Analysis on characters of the lower jaw of three species of Calomys, C. bimaculatus, C. murillus, and C. venustus (using the names C. laucha, C. musculus, and C. callosus, respectively). They found

C. venustus to discriminate easily from the other two species, which are morphologically very similar. The former two species, C. bimaculatus and C. murillus were separable on the second Canonical Variate.

On the basis of skull shape, tail length, and diploid number, the following relationships or species groups are proposed:

1. C. callosus and C. venustus: Calomys tener probably belongs in this group. These species have widely divergent, beaded supraorbitals, moderate tail length, and a moderate to high diploid number (50-66).
2. C. murillus and C. musculus: on the basis of a low diploid number, ($2n = 38$, identical according to Reig, pers. comm.), long tails, medium body size, and moderately divergent supraorbitals.
3. C. laucha, C. bimaculatus, and C. hummelincki: on the basis of relatively short tails, small body size, grassland habitats, delicate skulls, small-toothed, moderately divergent supraorbitals in adults, and a high diploid number.

The other two species, C. sorellus and C. lepidus, are considered to fall somewhere between the "laucha" group and the "musculus" group. C. sorellus is closer to the "laucha" group on the basis of diploid number ($2n = 64$, Pearson and Patton, 1976), but it is morphologically different; it has a fairly long tail and a distinctly parallel-sided interorbital region which is unique within Calomys. Calomys lepidus has a relatively low

diploid number, close to the "musculus" group, but has a very short tail, and cranially, does not resemble any other species.

Further study is necessary before an assessment of relationships within Calomys can be determined with greater confidence. Studies of banded karyotypes and protein similarities will be most useful.

The species of Calomys occur in mostly distinct geographic areas and elevational ranges. The species occurring at high elevations are C. sorellus and C. lepidus; the species occurring at middle to high elevations is C. musculus; species occurring at low to middle elevations are C. murillus and C. venustus; and the species occurring at low elevations are C. bimaculatus, C. callosus, C. hummelincki, C. laucha, and C. tener.

The Andes rise from 500 m on the eastern slopes to several thousand meters very quickly, thus producing a geologically and ecologically complicated area. There is no doubt that much more study is required to understand species' distributions there.

Koopman (1978) studied the relationship of ranges of bats to the Andes in Peru and found 1000 m in elevation to separate low and high elevation species. An elevation of 1000 m tends to separate the low elevation species of Calomys from the moderate and high elevation species, but there is some overlap.

Myers (1982) wrote that the Paraguay River is a geographic barrier for small mammals, especially Calomys: C. callosus and C.

laucha occur on the west side of the river, only. Myers gave a general description of Paraguay, and predicted that the species on the western side of the Paraguay River should be most closely associated with strongly seasonal environments and the eastern species with more tropical or subtropical environments (he associated C. musculus with temperate species). There is a specimen (skull only) from the east side of the river, Department Misiones, Paraguay. Myers (1982) identified this as C. musculus. It is not C. musculus, but could be either C. laucha, C. bimaculatus, or C. murillus. For the latter two species, this would represent a northern range record. Further collections will be necessary to clarify this problem.

Table 25

The reported diploid numbers and authors for the species of Calomys. The specific name used in the publication is listed.

Species	Name used	2n	Author
<u>bimaculatus</u>	<u>laucha</u>	64	Panzetta, 1968*
	<u>laucha</u> <u>laucha</u>	62	Massoia et al., 1968
	<u>laucha</u>	64	Gardenal et al., 1977b
	<u>laucha</u>	56	Brum, 1962**
<u>callosus</u>	<u>callosus</u>	36	Pearson and Patton, 1976
	<u>fecundus</u>	50	Pearson and Patton, 1976
<u>lepidus</u>	<u>lepidus</u>	36	Pearson and Patton, 1976
<u>murillus</u>	<u>musculus</u> <u>murillus</u>	38	Massoia et al., 1968
	<u>musculus</u>	38	Gardenal et al., 1977b
<u>sorellus</u>	<u>sorellus</u>	64	Pearson and Patton, 1976
		62	Pearson and Patton, 1976
<u>tener</u>	sp.	66	Yonenaga, 1975
<u>venustus</u>	<u>callosus</u>	56	Gardenal et al., 1977b
	<u>callosus</u> <u>callosus</u>	54	Hurtado de Catalfo and Wainberg, 1974
	<u>callosus</u> <u>callosus</u>	56	Lisanti et al., 1976
sp.?	<u>callosus</u> <u>callosus</u>	66	Matthey, 1968***

* cited in Gardenal et al. (1977b)

** cited in Jotternad-Bellomo (1984)

*** cited in Matthey (1973)

Fossil Genera and Calomys

Bensonomys and Calomys:

Bensonomys includes several species of fossil Sigmodontinae from the southwestern United States and Mexico (Gidley, 1922; Gazin, 1942; Baskin, 1978, 1979; Lindsay, 1984; Lindsay and Jacobs, 1985; and Czaplewski, 1987). The first described species was Eligmodontia arizonae (Gidley, 1922). It was assigned to a new genus, Bensonomys by Gazin (1942), and later included as a subgenus of Calomys (Baskin, 1978). Baskin (1978, 1979) hypothesized a North American origin for Calomys, and the South American Sigmodontinae, on the basis of these fossils.

These fossils have implications for the evolutionary history of the South American Sigmodontinae. Excellent summaries of the hypotheses proposed and much of the supporting data were given by Baskin (1986) and Czaplewski (1987; see also Slaughter and Uberlaker, 1984; Lindsay and Jacobs, 1985; Reig, 1980, 1986; Flynn et al., 1985; Marshall et al., 1983; and Marshall et al., 1984).

After study of casts of representative fossils of Bensonomys (courtesy of E. Lindsay and L. Flynn, see fig. 41), I do not think that it is congeneric with Calomys. However, there is tremendous similarity between them, and to properly assess the relationship between these genera will require a more detailed character survey than is now available of North and South American Recent and fossil Sigmodontinae. There are no reports of fossil Calomys from

southern South America (except Ameghino, 1889, see below). There are Pleistocene fossils of Calomys from the island of Tobago, near Trinidad, off the north coast of South America (Eshelman and Morgan, 1985).

Gidley (1922) described late Pliocene fossils from the San Pedro Valley, Arizona, as Eligmodontia arizonae, on the basis of lower jaws. He gave the length of the cheek tooth series as 3.6 mm. He noted a distinct notch in the anterior lobe of the m1, the anterior re-entrant angle, which he said was usual in Peromyscus, in contrast to a usually convex lobe in the living species of Eligmodontia. He included these fossils in Eligmodontia on the basis of (1) the masseteric ridge (which extends forward to the extreme anterior border of the cheek-tooth series), (2) the capsular process for the reception of the base of the incisor (which is placed high upon the ascending ramus and is marked by a decided sulcus between it and the coronoid), and (3) by the last cheek tooth (m3), which in species of Eligmodontia is more reduced than in Peromyscus. He distinguished E. arizonae from E. morgani (a Recent species currently synonymized with E. typus) by the relatively greater depth of the jaws of E. arizonae, its decidedly shorter symphysis, and the less reduced condition of the last molar.

Gazin (1942) described the genus Bensonmys as being "Near Eligmodontia with knoblike process at anterior extremity of

masseteric crest on lower jaw, last lower cheek tooth reduced, and sulcus between capsular and coronoid processes. Removed from Eligmodontia in having deeper lower jaw, dorsally placed mental foramen closer to process at extremity of masseteric crest, more brachydont cheek teeth, notch on anterior lobe of first lower cheek tooth better developed, lower incisor more procumbent" (p. 489).

Gazin (1942) distinguished Bensonomys from Eligmodontia morgani by a deeper lower jaw, more brachydont teeth, a more procumbent incisor, distinctly better developed notch in the anterior lobe of M1, slightly less reduced M3, and somewhat more dorsally placed mental foramen which is closer to the prominence at the anterior end of the masseteric crest.

Hershkovitz (1962), in a discussion of the characters of Galenomys, said "However, in Bensonomys (sic) Gazin of the Kansas Pleistocene, the lower incisors are similarly procumbent, and the lower molars show the same enamel pattern as in Galenomys" (p. 466).

Baskin (1978) included Bensonomys as a subgenus of Calomys and gave a diagnosis of Bensonomys. He wrote of Bensonomys that they are small, very brachydont cricetines (= Sigmodontinae) with a bilobed anterocone (-id) on the M1 and m1; the M3 and m3 are reduced as much as in Recent Peromyscus; the anterior limit of a heavy masseteric crest is situated at the anterior root of m1; the

mental foramen is very high on the dentary; the M1 is usually 3 rooted; and the m1 is usually 2 rooted. Baskin then added that Calomys is distinguished from Eligmodontia and other phyllotines by having more brachydont teeth and a more bifurcated anterocone (-id).

Reig (1980) disagreed with Baskin's conclusions. He wrote that similarities between Bensonomys and Calomys in enamel pattern and other aspects of molar structure are due to convergence, as is common within rodents. He noted that the molars of Calomys are more lophate than those of Bensonomys; that Calomys has narrower molars; that there is no posteroloph in the M1 of Calomys; no external shelf of the M1 running from procingulum to the paracone; that Calomys has a relatively short and narrow procingulum on the m1, which is more so in Eligmodontia; that the depth of the ramus decreases markedly backwards; and the lower masseteric crest is strongly marked in Eligmodontia and Calomys, and goes forward to a level usually beyond the anterior end of the m1, projecting above the mental foramen. He commented that an anteromedian flexid may or may not be present in species of Calomys, that there is no metaflexid in Calomys or Eligmodontia, that an enamel island, the posterofossetid, is often present in the M3 of Calomys, that the molars of Bensonomys are more bunodont, the posteroloph (= posterior cingulum) which is lacking in Calomys is present in two species of Bensonomys, and that the m1 of Calomys and Bensonomys

differs in the relative development of the procingulum, which is wider and longer in Calomys. Reig commented that Calomys is an advanced sigmodontine in many characters, including dentition and "cannot be postulated as ancestral to the more primitive oryzomyine, akodontine, or scapteromyine cricetids" (p. 278). He also pointed out that if Bensonomys and Calomys are related and share a common ancestor with Peromyscus (possibly Copemys), then we should see many similarities, but that on the basis of many structures, Calomys seems more closely related to other South American Sigmodontinae (i.e., penile morphology, stomach morphology, and skull structure).

Jacobs and Lindsay (1984) considered Calomys (Bensonomys) primitive for phyllotines, and phyllotines primitive for sigmodontines by extension. They gave a list of primitive dental characters based on this assumption, including many of the characters described above.

Lindsay and Jacobs (1985) described two new species of Bensonomys from Mexico, giving thorough descriptions of the dentition (as available). They commented on the similarity between Calomys (Bensonomys) and Eligmodontia, said that these two are closely related, and noted that many details of dental and mandibular morphology are shared by Calomys (Bensonomys) and other sigmodontine rodents.

Baskin (1986) enumerated many of the distinctions between Bensonomys and Recent Calomys, some of which are pointed out above. He noted that "The most extreme conclusion that can be drawn from these comparisons is that perhaps Bensonomys should be retained as the slightly more primitive, albeit very close relative of Calomys. To emphasize the relationship, I prefer to recognize Bensonomys as a subgenus of Calomys. The name of this taxon, however, is not important" (p. 295).

Czaplewski (1987) briefly summarized the hypotheses on the diversification of the South American sigmodontine rodents. He reported and described specimens of Calomys (Bensonomys) arizonae. He then gave a short history of Bensonomys and mentioned some of the species of Bensonomys (see references therein). He stated that most of the differences pointed out by Reig (1980) between Bensonomys and Calomys do not hold up for all species of Bensonomys. He viewed the morphological differences between the species of Bensonomys as being part of a continuum "that exhibits progressive hypsodonty, lophodonty, and narrowing" (p. 186). At the end of this discussion, he mentioned that living Calomys (such as C. musculinus), have weakly bilobed or undivided anteroconids and said this characteristic is variable from species to species of Calomys. He said "This more hypsodont mouse [presumably C. musculinus] resembles Eligmodontia in several respects. Eligmodontia appears to be among the most derived

phyllotines in terms of crown morphology. Toward the other end of the spectrum are C. fecundus and C. lepidus whose molars are very similar (too similar to be discussed as merely convergent) in crown morphology to those of C. (Bensonomys) spp." (p. 186). He also stated that "A case could probably be made for maintaining Bensonomys as a distinct genus, although closely related to Calomys" (p. 186).

I agree that the relationship is more important than the name. However, I feel that including Bensonomys in Calomys may obscure the more probable phylogeny. There is no doubt that they are very similar, but surveys of character variation in living and fossil forms such as those done by Guilday (1982) on three species of Microtus; Wolfe and Layne (1968) on Peromyscus floridanus; Dalquest and Stangl (1983) on characters of the lower jaw; and Yáñez and Jaksic (1977) on Akodon are necessary before conjectures can be made based on the characters that have been used to unite Bensonomys and Calomys.

Comments on the characters above:

In many phyllotine genera there is a sulcus between the capsular and coronoid processes. The mental foramen is generally dorsally located. Reduction of the m3 occurs in many phyllotines, and also in some peromyscines, e.g. Baiomys. The M3 is more

reduced in Eligmodontia than Calomys, and more reduced in Baiomys than in Eligmodontia.

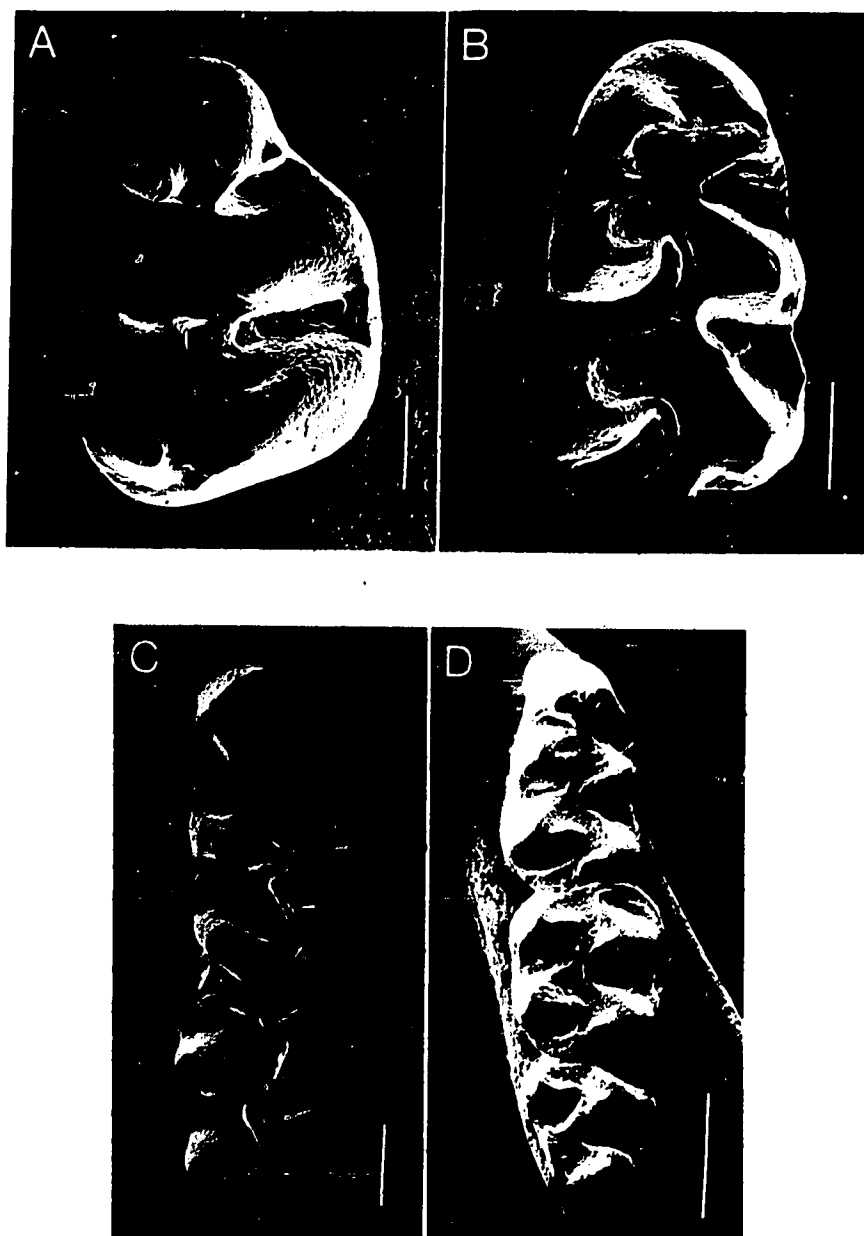
Baskin's (1978) character "small" is not helpful as a real character, and there are many brachydont cricetines. Brachydont teeth and a bifurcated anterocone (-id) are primitive characters for Sigmodontinae. Eligmodontia and Andalgalomys have brachydont teeth. A bilobed anterocone (-id) occurs in Calomys, Eligmodontia, Andalgalomys, some Baiomys (not as strongly as in Calomys, but present), as well as representatives of other tribes. It more consistently occurs in Calomys, but there is some variation (see table 5) and it is rarely as pronounced as in Bensonomys (fig. 40). Gidley (1922) mentioned this as occurring in Peromyscus, but he also said that Bensonomys is closer to Eligmodontia which lacks this division.

The proportions of the m1 and m2 in Eligmodontia are like Calomys, not Bensonomys. In Peromyscus, the procingulum may be pinched at the anterior end, also the M3 is reduced. There is a knob-like anterior limit of the masseteric crest, small and below the anterior root of m1, less anterior than in Calomys. Some of the Peromyscus have a heavy masseteric crest. In Calomys the mental foramen is more dorsally placed than in Peromyscus. The knob-like process is more anterior than in Peromyscus, but is not always there.

In Calomys there is a moderately heavy masseteric ridge, and process at the anterior root of the m1. The m1 shows weak bifurcation of the anteroconid, the mental foramen is high on the dentary. The m2 is relatively large in the molar row. There is some variation in the placement of the mental foramen.

A proper assessment of the relationship of Bensonomys to living genera will require an extensive examination of all living and fossil New World Sigmodontinae, and a review of the species of Bensonomys, as well.

Figure 40. SEM photographs of casts of teeth of representative species of Bensonomys. A) Right M1, 1134; B) right m1, IGCU 1224; C) right M1-2, WC 188; and D) right m1-3, UMMP 28173. A, B, and C, scale equals 400 microns; D, scale equals 1 mm.



Dental Comparison between Bensonomys and Calomys:

(Based on casts of specimens received from Lindsay representing several species of Bensonomys, see the Appendix).

M1: The procingulum of Bensonomys is distinct generally and pinched off from the rest of the tooth. The lingual side of the tooth (middle and posterior) bulges out unlike that of Calomys. In some Bensonomys, the tips of the anterior conules are widely separated in unworn teeth - they are not connected (fig. 40 A, C). In Calomys, if conules are divided, the tips converge and are only visible as separate in very young animals. Generally, the conules are connected for at least the bottom 1/3 to 1/2 of their length. Styles in folds are present in most of Bensonomys and also, frequently in Calomys. The cusps seem to be more alternate in Bensonomys. In Calomys, the tooth is more rectangular. In Bensonomys, according to Baskin (1978), M1 is 3 rooted, in Calomys it is 4 rooted (HersHKovitz, 1962). Wear across the protocone and paracone tends to form a horizontal loph in Calomys, in Bensonomys it is not loph-like, but bent. The folds between the major cusps are broader in Bensonomys.

M2 (1 specimen of Bensonomys, WC 188, fig. 40 C): The folds between the cusps are broader, more alternately arranged. The

lingual side has an anterior spur of the tooth not found in Calomys. Styles are present generally in both genera.

M3: The fold (PF1) is generally deeper in Bensonomys. The teeth are simpler than in Calomys. The specimens all show some wear.

m1 (fig. 40 D): In Bensonomys, the same general shape as in Calomys, although in Calomys m1 tends to be more rectangular. The anteroconid in Bensonomys may be always divided with two conulids. In Calomys, the loph of wear connecting the protoconid and metaconid has a smooth curve, in Bensonomys, it is much more linearly slanted. The cusps are more alternate, the folds are broader in Bensonomys. The procingulum with 2 anteroconules - they are very close together in Bensonomys; in Calomys, they may be separate, partly fused, or fused into 1 structure. Roots are two in Bensonomys (Baskin), 3-4 in Calomys (Herskovitz, 1962). In the m1 of Bensonomys, the primary folds (of Herskovitz) are prominent, deep and well curved. In Bensonomys, there is an angular projection of the enteconid, not seen in Calomys. These folds are large in Calomys, but show less curvature. Also the first secondary fold of Calomys is more open.

m2 (fig. 40 D): The m2 is very similar in Bensonomys and Calomys. The folds are a little broader in general in Bensonomys, and the cusps are more alternately arranged. This tooth in Bensonomys is broader than the m1 and is almost equal in length to the m1. In Calomys, the m2 and m1 are approximately equal in breadth and the m2 is less than two-thirds of the length of the m1. The labial shelf is bigger in Bensonomys.

m3 (fig. 40 D): The cusps may be more nearly opposite in Bensonomys than in Calomys. The folds are broad, especially the major fold between the protoconid and the hypoconid.

Necromys and Calomys:

Necromys conifer Ameghino (1889), described from the Pleistocene (Uquian age) of Buenos Aires, Argentina, was included in Calomys (with a question mark) by Hershkovitz (1962). Osgood (1947) commented on the similarity of Necromys (and three other fossil genera, Ptyssophorus, Tretomys, and Bothriomys) to Andinomys, a Recent phyllotine.

Patterson and Pascual (1972) wrote that Calomys is known from the early Pleistocene of South America. This was not referenced, but presumably refers to Necromys. Marshall et al. (1984) document Calomys (= Necromys) from the Ensenadan and

Lujanian ages of Argentina. They mention that there may be problems with the proper assignment of dates of some previously considered Uquian material.

A review of the original description of Necromys and analysis of dental characters show that Necromys is not congeneric with Calomys, although it is a phyllotine. A critical examination of the original material and comparison with Recent genera are necessary. The molars of Necromys are more hypsodont and prismatic than in Calomys. The fossil record of Calomys is thus more poorly known than previously thought.

Fossil Calomys:

Ameghino (1889) also assigned some fossils to Hesperomys, including some contemporary species. His descriptions and illustrations are not adequate to evaluate his assignments. A thorough review of the fossils he described is necessary before these can be properly assigned to species and genera.

Osgood (1947) mentioned that "the name Hesperomys has been applied to certain South American Pliocene fossils but that their generic identity with modern forms is more than doubtful" (p. 168). He may have been referring to Ameghino's descriptions.

Eschelman and Morgan (1985) reported Pleistocene fossils of C. hummelincki from cave deposits on the island of Tobago. They suggested that "the vegetation over much of Tobago in the late Pleistocene may have been similar to the present-day llanos [of Venezuela]" (p. 148). This species is not known today from Trinidad or Tobago. The present vegetation is more mesic, less like the more typical grassland habitat of this species, and most other species in the genus.

Hoffstetter (1986) included Calomys cf. laucha in a faunal list from the Tarija Basin (Pleistocene in age). It is considered to be an Andean fauna. This area is currently at approximately 2000 m in elevation. The species of Calomys that are currently known from that vicinity include C. lepidus, C. musculus, and C. venustus. Possibly, the specimen (or specimens) reported are one of these species. The former two species are currently part of the Andean fauna. Other sigmodontines listed included Kunsia fronto, Oxymycterus cf. paramensis, Nectomys cf. squamipes, Phyllotis cf. darwini, and Andinomys cf. edax (Hoffstetter, 1986).

RELATIONSHIP OF CALOMYS TO OTHER PHYLOTINES

Calomys has long been considered the most primitive genus of the living phyllotines (Osgood, 1947; Hershkovitz, 1962; Gardner and Patton, 1976; Williams and Mares, 1981; Jacobs and Lindsay, 1984); and Reig (1984, 1986).

Calomys exhibits the primitive state for most of the phyllotine characters (see Olds and Anderson, in press, a); it has bunodont, cuspidate molars, non-prismatic wear surfaces, a simple posterior palate, unspecialized bullae, a generally unconstricted interorbital region, moderately sized ears, and an unspecialized skull. According to Carleton (1980), Calomys shows the primitive sigmodontine condition in carotid circulation (see Guthrie, 1963, for a description of the pattern).

Dentally and cranially, its nearest relative seems to be Eligmodontia. Andalgalomys may be the next nearest, and then Graomys (see Reig, 1986). As discussed in the generic account, Calomys is most similar dentally to Eligmodontia and Andalgalomys; Graomys molars are more hypsodont and the anterocone is always entire (see figs. 14-15). Phyllotis, Auliscomys, and Galenomys, show more derived dentition and skull shapes. These patterns become more extreme in Andinomys and Chinchillula. The "Reithrodon-group" (see Anderson and Olds, in press, a), Reithrodon, Neotomys, and Euneomys show a derived state in many

characters of the posterior palate and dentition that set them apart from the rest of the phyllotines. Irenomys and Punomys are problematic genera, their relationships are unclear (see Olds and Anderson, in press, a).

Herskovitz (1962) stated that Eligmodontia is "nearest" Calomys, and is most like C. laucha. He also considered Zygodontomys to be closely related to Calomys and Eligmodontia. In his usage, Zygodontomys included Zygodontomys and Bolomys. He also noted that the phyllotine ancestor probably resembled either C. sorellus or C. laucha.

Pearson and Patton (1976) stated that "Calomys has traditionally been considered to be closely related to Phyllotis" (p. 347). Previously, Phyllotis included Graomys, Auliscomys, and Galenomys (Cabrera, 1961). They postulated that the karyotype of C. sorellus can be derived directly from that of Phyllotis osilae by three autosomal fusions and a change in centromere position of "X". Dentally, Phyllotis and Calomys are quite different (see figs. 14-15). Pearson and Patton did not suggest any close relationship between Calomys and Eligmodontia.

Gardner and Patton (1976) suggested that Calomys is primitive for phyllotines, and did not suggest any close relationship with any phyllotine genus, but suggested that Calomys is an earlier spinoff from all phyllotines. They also suggested that the phyllotines are related to the sigmodonts and scapteromyines.

Williams and Mares (1981) placed Calomys and Eligmodontia close together. They placed Calomys as the most primitive group of phyllotines, and closest phenetically to oryzomyines. They give as primitive traits: 1. persistently brachydont, tuberculate teeth; 2. classically "murine" skull (sharply ridged supraorbital region, relatively unconstricted interorbital, and a robust rostrum); and 3. generally unspecialized appendages. In regard to trait 2 above, not all Calomys have sharply ridged supraorbital regions, in fact, most species do not, C. sorellus has a constricted interorbital region, less so than in Phyllotis and some more derived phyllotines, but obvious, and C. lepidus has a slender rostrum. Most of their analyses pointed to a close relationship between Calomys, Andalgalomys, and Eligmodontia, based on dental traits, morphometric analyses, phallic morphology, and karyology. They proposed a fairly generalized, Mus-like ancestor as the prototype phyllotine (i.e. something like Calomys that inhabited dry-grassland or chaco). They wrote that there is much evidence to support a close relationship between Calomys and Eligmodontia, but felt that Eligmodontia is separable at the generic level.

Jacobs and Lindsay (1984) wrote that Calomys (Bensonomys) exhibits many characters primitive for sigmodontines, and by extension, that phyllotines are primitive among the Sigmodontini. The characters they gave as primitive for Sigmodontini are:

1. relatively low height of crown.
2. strongly bifurcated anterocone on M1.
3. weakly bifurcated anteroconid on m1.
4. short mesoloph (and mesolophid).
5. moderately small M3 with a minute metacone.
6. moderately large m3 with a minute entoconid.
7. minute accessory rootlets, especially on M1.
8. a posteriorly directed short lophule on the paracone.

Results of statistical analyses:

Principal Components Analysis (PCA, using the correlation matrix) and Canonical Variates Analysis (CVA) were done on the cranio-dental data in table 3. These analyses used individuals from 1 sample where possible (see the Appendix). The sample sizes are given in table 3. The species selected represent those genera most closely related to Calomys: Eligmodontia, Andalgalomys, Graomys, and Phyllotis. The species of Calomys (C. lepidus, C. callosus, and C. tener) were chosen to reflect the shape differences in the genus. Other species included Andalgalomys pearsoni, A. olrogi, Graomys domorum, G. griseoflavus, Eligmodontia typus (and a second species, the proper name of which is uncertain, see Olds and Anderson, in press, a), Phyllotis osilae, and P. wolffsohni. The more "derived" phyllotine genera were omitted from these two analyses because these analyses

exclude many of the important dental characters, and size would be a confounding factor. Eigenvectors from the PCA are given in table 26.

The first principal component is positive, accounts for 93.33 percent of the variance, and reflects cranial size. The larger species, both species of Graomys, both of Phyllotis, and A. pearsoni, are to the right of the species of Calomys, Eligmodontia, and A. olrogi. The second principal component, which accounts for about 2 % of the total variance, weighs heavily on LBULL, and separates A. olrogi, which has greatly inflated bullae, from the balance of the taxa (fig. 41 A). The next most important dimensions are ZBR, WRS, LINF, and LPAL. The species of Graomys are not separated, nor are the species of Phyllotis. Phyllotis have relatively smaller bullae than Graomys, A. pearsoni, and Eligmodontia. Calomys lepidus has relatively greater bullae than C. callosus and C. tener. The third principal component, which accounts for about 1.4 % of the total variance, weighs heavily on BBC; it is not easily interpretable (fig. 41 B).

I also did Canonical Variates Analysis (CVA) on the same data and taxa. Mahalanobis Distances are given in table 27. Note the small distances between the species of Graomys, those of Phyllotis, C. lepidus and C. tener, and C. callosus and C. tener. The distance is not especially small between C. callosus and C. lepidus. Also on the low side are the distances between the

species of Andalgalomys, and Eligmodontia and C. lepidus and C. tener. The largest distances are between G. domorum and C. lepidus, Andalgalomys olrogi and both species of Phyllotis, C. tener and G. domorum and also A. olrogi.

Figure 42 shows plots of individual specimens on the Canonical Variates 1, 2, and 3. In the plot of CAN 1 versus CAN 2 (fig. 42 A), the species of Graomys form a tight cluster as do the species of Phyllotis, A. pearsoni and A. olrogi form a looser cluster and the three species of Calomys and Eligmodontia form a large cluster. CAN 1 represents overall cranial size, CAN 2 appears to reflect relative size of the bullae. CAN 3 versus CAN 1 (fig. 42 B) is less easily interpretable. Phyllotis and Andalgalomys are close together there. All groups are concentrated in the center of CAN 3.

Table 26

Eigenvectors from a Principal Components Analysis on genera of phyllotine rodents. (The cumulative percentage of variance explained by each component is given at the bottom of the table).

DIMENSION	Prin1	Prin2	Prin3
LRS	0.2878	0.0203	-.1655
GLS	0.7473	0.0110	-.2505
ZBR	0.3306	-.4247	-.0316
BBC	0.2539	0.1214	0.7964
IOC	0.1097	0.1457	-.0702
WRS	0.1187	-.2716	-.0949
LINF	0.1702	-.2639	-.1184
PAL	0.1427	0.2477	-.0136
LBULL	0.1657	0.7335	-.1884
PBR	0.0350	-.0176	0.0047
PDB	0.0937	0.1211	0.0694
POB	0.2055	0.0283	0.2888
ZPW	0.0710	-.0507	-.0592
MESF	0.0479	-.1226	0.1016
MAXA	0.1230	-.0643	0.2663
WML	0.0438	0.0320	0.0944
LM1	0.0522	0.0187	0.1207
LM2	0.0299	-.0171	0.0872
LM3	0.0355	-.0348	0.0837
CUMULATIVE %	93.33	95.28	96.67

Figure 41. Results of a Principal Components Analysis on representatives of the tribe Phyllotini, A) PC 1 vs. PC 2, B) PC 1 vs. PC 3. Closed circle, Calomys callosus; open triangle, Eligmodontia typus; open inverted triangle, Graomys griseoflavus; open square, Calomys laucha; closed diamond, Graomys domorum; open diamond, Andalgalomys olrogi; closed square, Andalgalomys pearsoni; closed triangle, Phyllotis osilae; closed inverted triangle, Calomys tener; and open circle, Phyllotis wolffsohni.

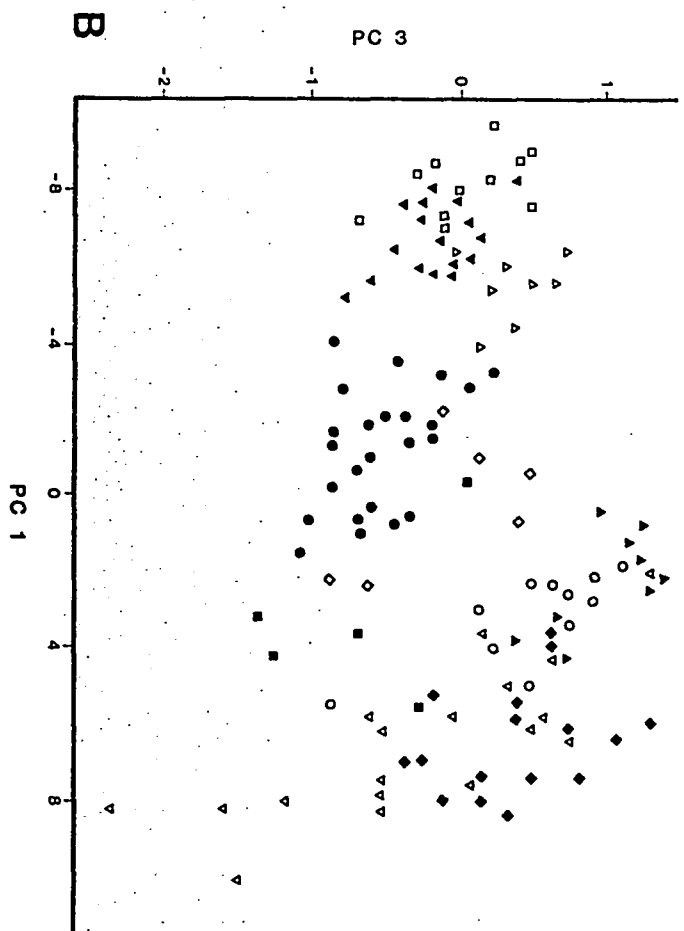
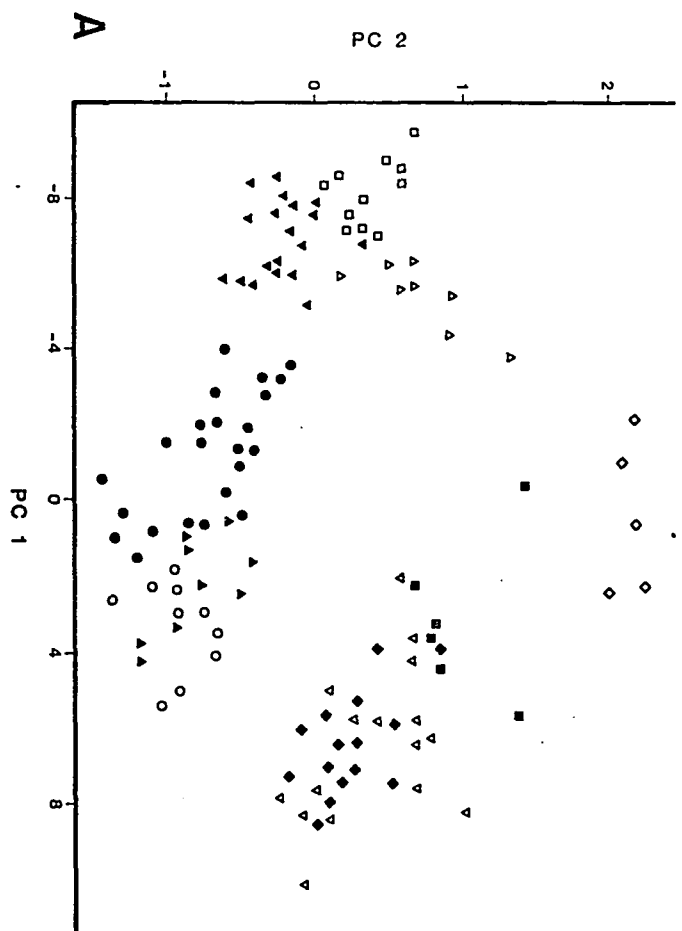
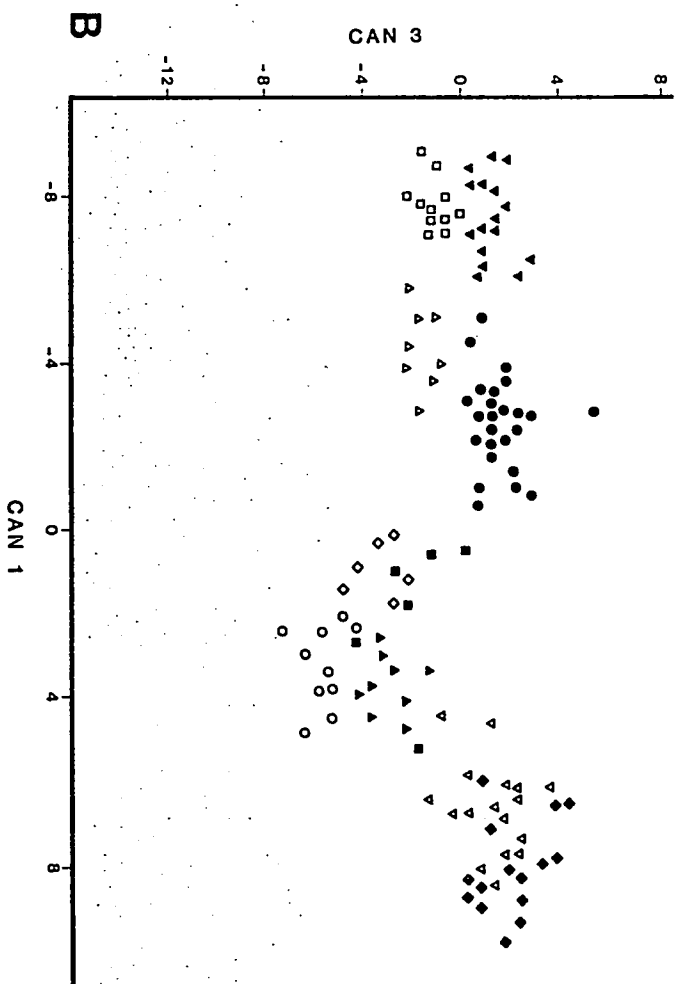
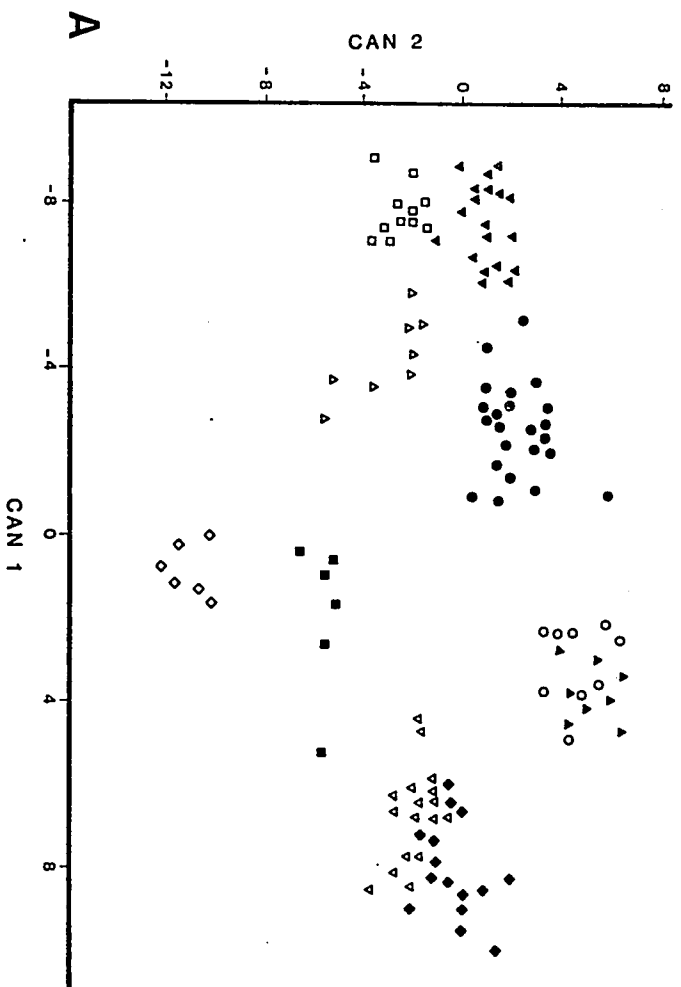


Table 27

Table of Mahalanobis Distances between different phyllotine genera: C, Calomys callosus; E, Eligmodontia typus; G, Graomys griseoflavus; L, C. lepidus; M, G. domorum; O, Andalgalomys olrogi; P, A. pearsoni; R, C. tener; S, Phyllotis osilae; W, P. wolffsohni.

	C	E	G	L	M	O	P	R	S
E	8.34								
G	10.24	12.62							
L	8.60	6.38	15.06						
M	11.61	13.45	4.34	16.54					
O	14.78	11.33	11.99	13.12	14.65				
P	10.05	9.11	7.66	11.64	10.44	6.93			
R	5.78	7.15	14.51	5.76	15.82	15.41	12.42		
S	8.86	12.72	9.13	14.43	9.40	16.85	11.84	12.84	
W	9.63	12.05	10.05	14.25	10.67	16.34	11.57	13.10	4.46

Figure 42. Results of a Canonical Variates Analysis on
representatives of the tribe Phyllotini, A) CAN 1 vs. CAN 2, B)
CAN 1 vs. CAN 3. Series and abbreviations as in figure 41.



SUMMARY

I have attempted in this work to answer the questions proposed in the introduction.

The genus Calomys is clearly definable and separable from other genera. It has few unique characters, as is often found in genera of Sigmodontinae. I recognize ten species, all of which are separable from each other on the basis of morphological and karyological characters.

The relationships among the species in the genus remains inconclusive. I recognize three species clusters, the "C. callosus" group, the "C. musculus" group, and the "C. laucha" group. Two species, C. sorellus and C. lepidus, do not fall into any of the above. Further study will help to clarify their relationships.

The secondary questions indicate other areas for future study. Geographic variation is evident in some characters, most notably external coloration. Further collection of specimens will help to address this.

As far as the role that Calomys had in the diversification of the South American Muridae, I conclude that Calomys is primitive for the tribe Phyllotini and that there is tremendous dental similarity between Calomys and the fossil genus Bensonomys. A survey of character variation in the species of Bensonomys and

comparisons with other groups of Sigmodontinae, including peromyscines, is necessary before conclusions as to the center of origin for these groups can be hypothesized.

APPENDIX: SPECIMENS EXAMINED

Note: Coordinates are given where possible in an abbreviated form. For example, 3012/5736 stands for 30 degrees 12 minutes South, and 57 degrees 36 minutes West. In all cases except Calomys hummelincki, Thomasomys aureus, Baiomys musculus, and B. taylori, the first coordinates are degrees and minutes South, in these three species, the first coordinates are degrees and minutes North. The museum abbreviations are defined in the "Methods" section.

Akodon boliviensis

BOLIVIA:

Santa Cruz:

1751/6437 21 km by rd W of Comarapa, 2900 m, AMNH 260455.

Akodon varius

BOLIVIA:

Santa Cruz:

1825/6210 Tita, 300 m, AMNH 260468.

Andalgalomys olrogi

ARGENTINA:

Catamarca:

? 15 km S of Highway 62 on Río Amanao and W of
Andalgala, CM 44020.

- ? Km marker 10 on Highway 62, 10 km W of Andalgala, CM 44021.
- ? 15 km W (on Route 62) of Andalgala on W bank Río Amanao, CM 44022-44024 (44024 = holotype).
- ? 8 km W of Andalgala on Highway 62, CM 86451 (Andalgala = 1060 m; 2736/6619; Amanao = 2733/6631).

Andalgalomys pearsoni pearsoni

PARAGUAY:

Boqueron:

- ? 410 km by road NW of Villa Hayes, MVZ 145276 (holotype) (Villa Hayes = 2506/5734).
- ? 15.6 km by road N of Philadelphia, UMMZ 134386. (Philadelphia = 2221/6002).

Nueva Asuncion:

- ? 0.5 km S of Teniente Enciso, UCONN 17579-17580.
- ? Teniente Enciso (cited as 2.5 km S by Myers, 1977), UCONN 17562-17563, 17566, 17568, 17575.
- ? 1 km SW km 620 on the Trans-Chaco Road, AMNH 262344-262347, UMMZ 158621, 130037, and the following uncataloged specimens at UMMZ, collected by T. W. Nelson, TWN 183-184, 193, 195, 201-202, 218, 229, 233.

Andalgalomys pearsoni dorbignyi

BOLIVIA:

Santa Cruz:

1819/6002 29.5 km W of Roboré, 475 m, AMNH 260762, MSB 55245

(type specimen).

Andinomys edax

BOLIVIA:

La Paz:

1659/6749 Caracato, 2900 m, AMNH 249023.

Auliscomys pictus

PERU:

Lima:

1137/7617 Prov. Huarachiri, 1.2 mi NW Chinchán, 15,600 ft., AMNH

231258 (coordinates approximate).

Baiomys musculus

MEXICO:

Jalisco:

? 5 mi W Cihuatlan, AMNH 254782.

Baiomys taylori

MEXICO:

San Luis Potosí:

? El Salto, AMNH 177275.

Bensonomys (casts received from E. Lindsay, and L. Flynn):

Univ. Arizona Paleontology Lab.:

B. (=Cimmaronomys) stirtoni, UMMP 28173.

B. yazi: WC 188.

B. gidleyi: WC 198, 206, 211-212, 222, 230.

B. elachyi: IGCU 1174, 1178, 1187, 1199.

B. baskini: IGCU 1211, 1224-1225, 1227-1231, 1234.

B. sp.: Y3/143, IGCU 1192.

Bolomys lasiurus

BOLIVIA:

Santa Cruz:

1816/6007 7 km N and 38 km W of Roboré, 550 m, AMNH

260552-260553, 260509-260513, MSB 55250.

1819/6002 29.5 km W of Roboré, 475 m, AMNH 260507.

Calomys bimaculatus:

URUGUAY:

Artigas:

3012/5736 Yuqueri, Río Cuareim, 32 km NW Artigas (coordinates
approximate), AMNH 232505.

LaValleja:

3331/5455 12 km WSW Zapican, AMNH 206331-43.

3353/5503 Polanco, FMNH 29248.

3423/5514 Minas, Río Cebollati, FMNH 29246-47.

Tacuarembó:

? 40 km N Tacuarembó (Tacuarembó = 3144/5559),
AMNH 206344.

Treinte y Tres:

? Dept. only, AMNH 206345.

Maldonado:

3454/5457 Maldonado, BMNH 55.12.24.172 (type of C. bimaculatus).

BRAZIL:

Rio Grande do Sul:

2945/5705 Uruguaiana, Rio Uruguay, AMNH 235982-235983.

ARGENTINA:

Buenos Aires:

3436/5838 Hurlingham, 20 m, UMMZ, 109227.

3603/5907 Flores, 35 m, BMNH 67.1655.

3622/5643 LaValle, Estancia Tuyu, 15 mi S Cape San Antonio, 0
m, USNM 236272.

3624/5658 Luiconia Ayo, BMNH 9.12.1.19 (coordinates approximate).

3843/6217 Bahía Blanca, 20 m, BMNH 0.8.5.2, 14.4.4.12 (type
locality of M. gracilipes).

? Los Ynaglese, Ajo, 0 m, BMNH 20.2.7.17 (Ajo = General
LaValle).

Santiago del Estero:

? Rapelli, MCZ 41085-41088.

Tucumán:

2630/6445 Cerro Campo, Burruyacu, 800 m, BMNH 26.2.13.48.

2720/6335 Concepción, 400 m, FMNH 35011-12, JM 296, BMNH
 25.12.13.32, 26.1.9.17, 25.3.1.11,
 26.8.3.13-26.8.3.15.

Province unknown:

Lujan, AMNH 188215 (there are several places named
 Lujan in Argentina).

C. callosus:

ARGENTINA:

Formosa:

2605/5750 Km 182, 10 mi NW Riacho Pilaga, ca. 100 m (= Estancia
 Linda Vista in gazeteer), USNM 236242,
 236244-236247, 236249-236251.

Salta:

- ? Cerrillos Dept., Inta Station, CM 43536-37 (Cerrillos
 Dept. = 2500/6525).
- ? General Ballivian, 20 km W on Puerto Baules Rd., CM
 43538-43539.

PARAGUAY:

Alto Paraguay:

- ? 69 km W Puerto Sastre, UCONN 19177-19178 (Puerto
 Sastre = 2206/5759).
- 2102/5754 Olimpo Fuerte Olimpo, AMNH 234789, ca. 200 m (probably
 this department).

Boquerón:

2330/5918 2 km NE Pozo Colorado, UCONN 17590 (coordinates for Pozo Colorado).

2230/6221 Pedro P. Pena (= Dr. Pedro P. Pena in atlas, near

? Puerto La Paz, Salta, Argentina, coordinates for Puerto La Paz) USNM 390154; UCONN 19202.

? 0.5 km NE Teniente Enciso, UCONN 17244, 17246.

? Teniente Enciso, UCONN 17241-17242, 17386.

? Estancia Iparoma, 19 km N Filadelfia, UCONN 19210, 19222 (Filadelfia = 2221/6002).

? Río Verde, 300 km NW Villa Hayes by rd, MVZ 145217-145220.

? Vic. of Teniente Ochoa, UCONN 15916, 15924, 15934-15936, 15951-15952, 16001-16003, 16010, 16012-16016, 16876.

Chaco:

2037/6031 50 km WSW Fortín Madrejon, Cerro Leon, AMNH 248446-248447, 248449-248454, 248555-248559; UMMZ 124231-124250, 125460-125466, 125468-125477, 125607-125612.

? 65 km N Fortín Madrejon, UMMZ 125467.

2521/5742 Río Pilcomayo, 15 mi W Río Paraguay, FMNH 53954-53958, 53466, 53482-53485, AMNH 143890-143891.

? 120 km E of Lagerenza, Agua Dulce, UCONN 19169.

- ? 123 km E Mayor Pablo Lagarenza, Park Hdq., Agua Dulce,
 UCONN 19145, 19149, 19152, 19158, 19161, 19153, 19163,
 19166, 19169-19170, 19276, 19289-19290, 19294-19295.

Concepción:

- ? Concepción, BMNH 11.11.19.17-11.11.19.18.

Nueva Asunción:

- ? 19 km by road WSW km 588, Trans Chaco Rd.,
 (uncataloged specimens at MSU collected by T.W.
 Nelson, 297, 299, 349-350, 353, 392, 401,
 409-410.
- ? Teniente Enciso, UCONN 17572, 17574 (possibly same
 locality as above, but specimen labels say Nueva
 Asunción).

Presidente Hayes:

- 2225/5810 Chaco Boreal (Waikthalating Mayliva =
 Wailthlatingmayalwa, a mission in the Gran Chaco,
 coordinates approximate) BMNH 98.5.14.5.
- 2238/6118 8 km NE Juan de Zalazar, UMMZ 133915-22, 134399,
 134401 (coordinates for Juan de Zalazar).
- 2243/5750 Puerto Pinasco, Km 80 W, USNM 236255-236258,
 236297-236298 (coordinates for Puerto Pinasco).
- 2230/5850 Pozo Colorado, km 250 Trans-Chaco Hwy, UCONN 17581,
 17584, 17587-17588, 17591-17592, 17594-17595 (see
 also series under Boquerón).

- 2306/5918 Juan de Zalazar, UCONN 15652-15654, 15680-15705,
15706-15708, 15715-15719, 15721-15726, 15728-15729,
15731-15735, 15737, 15739-15740, 15742-15743,
15745-15746, 15748-15755, 15907-15909, 15912-15913,
15931-15933, 15998-16000, 16004-16009, 16011,
16510-16537, 16737-16738, 16836, 16838-16841,
17216-17221, 17249-17251, 17314.
- 2506/5734 24 km NW Villa Hayes (coordinates for Villa Hayes),
UMMZ 133923-27, 137066-67.
- ? 85 km E Loma Plata, Estancia Laguna Para de la Colonia
Fernhiem, 175 m, UCONN 19121, 19123, 19126, 19128,
19132-19133, 20354-20357 (Colonia Fernhiem =
2220/5955).
- ? 213 km by road NW Villa Hayes, MVZ 145222.
- ? 69 km by road NW Villa Hayes, MVZ 145221.
- ? 295 km NW Villa Hayes on Trans-Chaco Hwy., MVZ 145216,
145223-145244.
- ? 15.5 km NNW Chaco-i, UMMZ 125958, 136071-73.
- San Pedro:
- 2325/5646 Aca Poi, Tacuati (coordinates for Tacuati) USNM 293149.
- Dept. Unknown:
- ? Alto Paraguay, nr. Puerto Braga, BMNH 11.10.27.2
(presumably on the Río Paraguay).

- ? Jesamatathla, Chaco W of Concepción, BMNH
20.12.18.21-20.12.18.22 (possibly in Argentina).
- ? Chaco, N. Paraguay, BMNH 99.11.1.1.

BRAZIL:

Mato Grosso:

- 1415/5733 Tapirapoan, Siputuba River, AMNH 37520-21
- 1514/5621 Fazenda Acurizal, Rio Paraguai, Pantanal, USNM 531282.
(coordinates for Acurizal).
- 1605/5740 Cáceres, Limao Balsa, USNM 390392-93 (coordinates for
Cáceres).
- ? Cáceres, Limao, 48 km W Cáceres, west bank Rio Jauru,
USNM 390392-403, 391552.
- 1645/5740 Descalvados, FMNH 28359, 28361-63.
- 1900/5735 Urucum de Corumba, FMNH 26790, 26792, 26794-96, 26799,
26802-03, 26813, USNM 259644-259645, BMNH 29.3.17.73
(coordinates are for Corumba, those for Urucum are
1908/5733).
- ? Corumba, São Marcus Road, 10 km NE Urucum, USNM
390201-03, 390376-83, 390387-390391, 391550.
- 1900/5735 Corumba, USNM 390392-390393.
- ? Ladario, 6 km E of Corumba, USNM 390192-392193.
- ? Santa Theresa, 7 km WSW Urucum, USNM 390194-390196,
390198-390200, 390384-390385, 391549, 391551.

1908/5733 Urucum, 22 km S Corumba, USNM 390197.

? Fazenda San Martin, ca. 150 km S Corumba, CM
62056-62062, 62064-62076, 62078-62081.

? Descalvados Ranch, Boa Vista Camp, BMNH 29.3.17.74.
(= Tapirapua, Sepotuba River).

? San Juan (probably in Mato Grosso), AMNH 37087,
37106-07, 37109.

? Faz. Joffie, Transpantanal Hwy., USNM 531283-531284.

Minas Gerais:

1720/4454 Pirapora, MCZ 25751.

1939/4344 Lagoa Santa, BMNH 88.1.9.7 (topotype of M. expulsus).

2045/4638 Passos, 728 m, USNM 304609.

? Parque Forestal do Rio Doce, uncat. Florida State
Museum, JRS 319 (coordinates approximately 21 S, 43 W).

? Fazenda Montes Claros, uncataloged specimens at
Florida State Museum, 102P (coordinates approximately
20°S, 42°30'W).

Goiás:

1339/4657 Nova Roma, MCZ 36278.

? Barro do Rio São Domingas, MCZ 34046-47, 34054, 34061,
34063-64; FMNH 48923 (= head of Rio São Domingos; São
Domingos = 1325/4619).

Pernambuco:

0728/3945 1 km S Exú; uncataloged specimen, KES 468.

" Exú, KES 449.

" Escola Agricola de Exú, KES 345, 610.

Bahia:

? Lamiarao, BMNH 3.9.5.64-3.9.5.65.

BOLIVIA:

Santa Cruz:

1543/6309 6 km by road W Ascención, 250 m, AMNH 261979.

1557/6442 Ichilo, nr. Buen Retiro, FMNH 72285.

1623/6059 San Ignacio, USNM 391530-391548.

1636/6242 10 km N San Ramón, 250 m, AMNH 261975-261978; MSB
55983-55985.

1647/6314 Estancia Cachuela Esperanza, 300 m, AMNH 260644-65,
MSB 55274-80.

1649/6237 Río San Julian, Palmarito, Chiquitos, 400 m, CM
4996-4997 (4996, skull = Bolomys), BMNH
22.3.1.12-22.3.1.16.

1703/6335 7 km N. Santa Rosa, Pucia Sara (Province Sara?), AMNH
254582-94.

1713/6338 6 km N of Buen Retiro, 300 m, AMNH 260627-43.

1723/6332 San Miguel Rincon, 300 m, AMNH 260686-90; MSB 55282.

1724/6345 San Carlos, Pr. Tchilo (possibly = Puertochuelo), FMNH
51930-33716.

1724/6351 Prov. Sara, Rio Surutu, 450 m, CM 2181.

1727/6340 Buenavista, FMNH 25269-70, BMNH 26.2.4.47, 28.2.9.43;
UMMZ 55919.

- 1736/6336 San Rafael de Amboro, 400 m, AMNH 261956-261974; MSB 55972-55982.
- 1739/6245 3.5 km W of Estacion Pailon, 300 m, AMNH 260671-81; MSB 55281.
- 1739/6348 Hunting camp at 4 km S, 13 km W San Rafael de Amboro, 400 m, AMNH 263186.
- 1748/6310 Santa Cruz, 450 m, CM 1936.
- 1752/6031 4 km S and 24 km E San José de Chiquitos, 400 m, AMNH 260682-85.
- 1808/6312 7 km E, 3 km N Ingeniero Mora, 490-580 m, AMNH 247824-247849, 247887-247889, 249895-249897.
- 1809/6312 Los Tajibos, 2 km N, 7 km E Ingeniero Mora, MSU 31053.
- 1818/5936 4 km N, 1 km W of Santiago de Chiquitos, 700 m, MSB 55283-84; AMNH 260307-260309, 261212-261213.
- 1825/6210 Tita, 300 m, AM 260691-97.
- 1828/6207 8 km SE of Tita, 290 m, AM 260698-260747; MSB 55285-89.
- 1845/6406 La Hoyada, 30 km S Valle Grande, MVZ 134660-134661.
- 1857/5751 Puerto Suarez, 150 m, CM 1855.
- 2001/6313 San Antonia, Río Parapiti, 600 m, BMNH 21.11.6.10-21.11.6.13, 21.11.6.15 (21.11.6.11 = type H. muriculus).
- 2005/6334 Camiri and Charcti Region, USNM 269113-269114 (coordinates approximate).

Beni:

- 1248/6422 Cdo. en N. Calama, Río Iténez (Nueva Calama), USNM 460798.
- 1254/6421 Teremaca, USNM 460796.
- " Teremaca, Iténez, USNM 460797.
- 1304/6449 San Joaquín, FMNH 118589, 118595, 118615, 117852, 117247-49, 117251-52, 117255-56, 117258-61, 117265-68, 117273, 117867, 118507-08, 118511, 118513, 118520, 118524, 118534, 118536, 118542, 118547, 118549, 118560-61, 118567-68, 118570, 118573, 118577, 118581, 118585-86, 117960-61, 117971-73, 117311, 117319, 117321, 117324, 117326, 117329-31, 117333, 117335, 117338-39, 117344, 117274-75, 117277, 118144-46, 118148-51, 118154-55, 118157, 118165, 118167-68, 118170-74, 118176, 118178, 118180, 117871, 117873, 117875, 117880-82, 117918, 117922-24, 117928, 117931, 117933, 117944-45, 117948-50, 117952, 117958-59, 117278, 117281, 117285-86, 117288-91, 117925, 117977, 117981, 117987, 117991, 117998-99, 117348, 117350, 117366-67, 117235-36, 118235-36, 118238, 118256-57, 118263, 118265, 118267-68, 118136-39, 119141-42, 118192, 118194-95, 118200-01, 118203, 118374, 118377, 118382-83, 118387-88, 118204-09, 118217-23, 118229-30, 118334, 118344-46, 118348-53, 118357, 118359-60,

118364-66, 118368, 118370-73, 118284-85, 188288-90,
 118300-01, 118306-08, 118317-18, 118321-24, 118327,
 118329, 118331-33, 117237-39, 117245, 117293-96,
 117301-02, 117306-08, 117811, 117813, 117826,
 118269-70, 118275-76, 118278, 118181-82, 118185,
 118191, 118014, 118018-19, 118029-30, 118037, 118048,
 118131-35, AMNH 212334, 213138, MVZ 143937-143938;
 USNM 364832-364864, 364866-364889, 364891-364899,
 364900-364919, 390736-390737, 391320-391323, 391333,
 391359-391360, 391372-391375, 391385-391390, 391392,
 460193-460203, 460205-460208, 460283-460299,
 460301-460327, 460329-460345, 460347-460363, 460365,
 460368-460415, 460432-460434, 460756-460790,
 460799-460862, 460879-460946, 460973-460974.

1306/6525 Prov. Yakuma, Mangal, 25 km NW Exaltacion, USNM 461359.
 1312/6410 Cachuelita, USNM 460794-460795.
 1315/6448 Yutirole-San Joaquín, USNM 460435-460436.
 1315/6449 Totai, USNM 460863-460878.
 ? Prov. Iténez, Gualeva, USNM 460355-461356.
 1317/6438 Huerrasca, USNM 364816-364831, 364802-364812,
 364814-364815.
 1317/6443 San Ramón, USNM 460431.
 1318/6409 Magdalena, La Granja Río Honama, USNM 460793.

- 1320/6408 Magdalena, USNM 390753-54, 460977-4610021,
461023-461024, 461357-461358.
- 1324/6404 Achachairu, Río Itorama (Itonamas), USNM 460791-460792.
- 1333/6345 Huacaraje, FMNH 118714-18, 118725, 118728-32,
118734-36, 118738-39, 118741, 118760-62, 118769,
118779-81.
- 1356/6340 El Carmen, 210 m, AMNH 164779.
- 1420/6455 Mamoré River, ca. 10 km W San Pedro, AMNH 214598.
- 1447/6447 Trinidad, FMNH 21519.
- 1448/6414 Casarabe, 230 m, AMNH 261980-261981.
- 1454/6422 6 km W Casarabe, 230 m, AMNH 255964.

Tarija:

- 2056/6321 2 km S, 10 km E Tiquipa, Laguna Palmar, 555 m, AMNH
246731-246732, 246734, 246736-246737, 246749-246752,
246678-246686, 246690-246691, 246739, 246745-246747,
246923-246932.
- 2115/6330 Villa Montes, FMNH 34237-38.
- 2119/6325 8 km S, 10 km E Villa Montes, 467 m, AMNH 246677,
246696-246698, 246706, 246740, 246753-246754,
246892, 246915-246916.
- 2122/6358 18 km W of Palos Blancas (by rd), AMNH 244650.
- 2149/6334 Caiza (=Villa Ingavi), 600 m, BMNH 97.2.25.26.

Chuquisaca:

- 1955/6334 17 km N Camiri, AMNH 261955.
 2041/6309 10 km NE Porvenir, AMNH 261954.
 2045/6313 Porvenir, 675 m, AMNH 261953; MSB 55971.
 2058/6251 30 km SE Carandayti, LACM 60646-60660, 60662.

Department Unknown:

- ? nr. Carimi, S. Bolivia, CAL 13806-13811 (possibly in
 Santa Cruz).
 ? Bolivia only, BMNH 50.6.5.4.

C. hummelincki (Note that the first coordinates are minutes and
 degrees North):

COLOMBIA:

Guajira:

- 1200/7130 W. Pto. Lopez, E. Maicao, 50 m, USNM 486982-486983
 (coordinates approximate).

VENEZUELA:

Apure:

- ? Rio Cinaruco, 41 km NW Puerto Páez, 76 m, USNM 374523,
 374525-374526 (Puerto Paez = 0613 N/6728).

Monagas:

- ? 45 km S Maturín, close to bank of Rio Tigre, 75 m, USNM
 460437-48 (Maturín = 0945/6311; possibly = 0927/6225).
 ? 42 km SE Maturín, LACM 13795-98.

? 47 km SE Maturín, USNM 388104-388105, 388107,
388110-388113, 388115-388116, 388118-388119.

Bolívar:

? Raudal Cabure, 70 km from mouth of Rio Suapure, 110 m,
AMNH 180400 (Cabure = 1108N/6938; Isla Cabure =
0721N/6633).

Zulia:

? 114 km N and 32 km W Maracaibo, USNM 442441 (Maracaibo
= 1040N/7137).

Falcón:

? 49 km N and 34 km W Coro, USNM 456385 (Coro =
1125N/6941).

Aguaro:

0836/6631 Guariquito N.P. Llanos Centrales, 120 m, BMNH
82.601-82.623 (0836N).

C. laucha:

ARGENTINA:

Salta:

2215/6458 4 km NE Santa Victoria, CM 43603-43604.

2313/6406 Embarcación, 286 m, BMNH 19.6.26.8 (left
bank upper Rio Bermejo).

2553/6508 Arenal, 750 m, BMNH 4.10.2.8.

Corrientes:

2908/5916 Goya, BMNH 98.12.3.15-98.12.3.17.

BRAZIL:

Mato Grosso:

1300/5820 Utiariti, Papagaio River, 1500-2500 ft., AMNH 37543.

BOLIVIA:

Tarija:

2025/6317 Boyube, nr. Carimi (= Boyuibe), CAL 13813.

2119/6325 8 km S, 10 km E Villa Montes, E bank Río Pilcomayo, 467
m, AMNH 246672-75, 246666-68, 246841, 246844, 246867,
246883, 246907, 246917-246918.

PARAGUAY:

Boquerón:

2221/6002 Filadelfia, UMMZ 134402.

? Estancia Iparoma, 19 km N Filadelfia, UCONN 19209,
19213, 19231 (Filadelfia = 2221/6002).

2227/6220 Pedro P. Pena, Guachalla, 250 m, USNM 390204-390210,
391553.

2227/6220 Guachalla, Río Pilcomayo, 580 km W Ascensión, 250 m,
FMNH 54371-80.

? Teniente Ochoa, UCONN 15917, 16028-16030.

Chaco:

? Chaco, FMNH 54343.

Misiones:

- ? 2.7 km (by rd) N San Antonio, UMMZ 124310 (coordinates approximately 2500/5600; identification uncertain, skull only).

Nueva Asunción:

- ? Trans-Chaco Hwy, UMMZ 125297-125298.
- ? Km 589 Trans-Chaco Copagro, Hotel San Francisco del Chaco Boreal, UCONN 18857-18858, 18860.
- ? Nueva Asunción, UCONN 18873, 18885-18886.

Presidente Hayes:

- 2238/6118 8 km NE Juan de Zalazar (coordinates for Juan de Zalazar), UMMZ 133928-29.
- 2306/5918 Vic. of Juan de Zalazar, UCONN 15655-15656, 16026-16027, 16551.
- ? 85 km E Loma Plata, Estancia Laguna Para, UCONN 19122, 19120, 19125.

C. lepidus:

BOLIVIA:

Cochabamba:

- 1630/6635 Ayopaya, 3500 m, FMNH 74864.
- 1656/6642 Choro, 3500 m, BMNH 2.1.1.55 (type of H. carillus).

La Paz:

- 1503/6916 Ulla ulla, UMMZ 121081.

1622/6803 La Cumbre, 4675 m, AMNH 72681, 72683, 72685, 72688

(72683 type of H. lepidus montanus).

1647/6809 20 mi S La Paz, 13,000 ft., MVZ 119949.

1712/6757 Viscachani, 3780 m, AMNH 255963.

Oruro:

1740/6727 Huancaroma, 3720 m, AMNH 262786, 262788, MSB 57104.

1740/6727 3.5 km E of Huancaroma, 3720 m, AMNH 260607-260624.

1740/6728 2.5 km NE Huancaroma, 3720 m, MSB 55264, 55266-71.

1740/6728 2 km E Huancaroma, 3720 m, AMNH 260626.

1740/6732 3 km W Huancaroma, Río Desaguadero, 3720 m, AMNH
262787, MSB 57105.

1745/6656 20 mi NE Oruro, 14,000 ft., MVZ 119950.

1809/6724 37 km SW of Oruro, 3.5 km NE of Toledo, 3650 m, AMNH
262790.

1810/6855 6 km NE Laguna, foothills of Nevado Sajama, 4200 m,
AMNH 260912-260914.

1819/6759 5 km W and 1 km N Pomata Ayte, río Barros, 3800 m, AMNH
262789.

1820/6836 Estancia Agua Rica, 40 km E and 22 km S of Sajama, 3850
m, AMNH 262783-262785, MSB 57103.

Potosí:

2154/6536 5 mi N Villazon, 11,500 ft., MVZ 119951.

Tarija:

2129/6457 1 km E of Iscayachi, río Tomayapo, 3450 m, AMNH 262791-
262797, MSB 57106-57107.

CHILE:

Antofagasta:

? Ojos San Pedro, 55 mi NE Calama, 12,500 ft., MVZ 116789.
(Calama = 2230/6855).

PERU:

Ancash:

? Rachacoca, 45 km S Huaras, 11,000 ft., MVZ
135689-135690.

Arequipa:

1558/7123 Sumbay, 13,500 ft., FMNH 49562.

1602/7050 Huaylarco, 52 mi ENE Arequipa, 15,000 ft., MVZ
116018-116019.

" Huaylarco, 55 mi ENE Arequipa, 15,300 ft., MVZ
116020-116022.

1620/7105 Salinas, 14,000 ft. (4270 m), FMNH 49551-53, 49752,
50551-52.

1622/7108 Lago Salinas, 14,100 ft., MVZ 115751-115754.

Ayacucho:

1300/7400 San Miguel, Tambo, Polanco, 3500 m, FMNH 75419
(coordinates approximate).

Cuzco:

- 1342/7119 Lauramarca, 3995 m, BMNH 3.2.9.8-3.2.9.9, 3.2.9.11
(3.2.9.8. type of H. carillus marcarum).

Junin:

- 1055/7602 Carhuamayo, 14,500 ft., FMNH 54743, 54745.
1102/7606 Lake Junin, BMNH 85.4.1.43 (type of Mus bimaculatus
var. lepidus).
1110/7600 Junin, central Peru, BMNH 85.4.1.18 (coordinates for
city of Junin).
1146/7608 Pomacocha; Yauli Valley, 14,200 ft., MVZ 137988.

Huancavelica:

- 1312/7505 Santa Inez, Sandenaro (coordinates for Santa Inés, note
spelling) FMNH 75420.

Lima:

- 1137/7617 Prov. Huarachiri, 1.2 mi NW Chinchán, 15,600 ft., AMNH
231506-12.
1139/7614 1 mi E Casapalca, 14,000 ft., MVZ 119952.
" 2 mi N Casapalca, 14,400 ft., MVZ 137611-137612.

Moquegua:

- ? Pampa de Huaitire, Tutupaca, 14,500 ft., MVZ 115755
(Huaitara = 1336/7521, Volcano Tutupaca = 1700/7022).

Pasco:

- ? Ninacaca, 13,500 ft., MVZ 119953.

Puno:

- 1408/6942 4 mi SSW Limbani, 13,000 ft., MVZ 139555.
- 1433/6948 Picotani, 14,000 ft. (4390 m), FMNH 52661.
- 1447/7021 Hac. Posoconi, 3 mi W of Asillo, 13,500 ft., FMNH
51249-52.
- 1449/7001 Hacienda Checayani, 20 km NE Azangaro, 13,200 ft., MVZ
136260-136261.
- 1503/7022 2 mi NNW Pucara, 12,700 ft., MVZ 116119-116120.
- 1530/7008 6 km NNW Juliaca, MVZ 139262-139264 (coordinates
approximate).
- 1542/7036 Santa Lucia, 4039 m, FMNH 51361.
- 1548/6924 Lake Titicaca, AMNH 16504.
- 1552/7045 Tincopalca, 13,800 ft., MVZ 115767.
- 1553/6953 Chucuito, 3870 m, FMNH 52660.
- 1605/6940 Caccachara, SW of Ilave, 16,000 ft., MCZ 42831.
- " W of Ilave, 13,000 ft., MCZ 42894.
- " Santa Rosa, SW of Ilave, 15,000 ft., MCZ 42910.
- " Hacienda Payrumani, SW of Ilave, 13,500 ft., MCZ
42911-12 (coordinates for Ilave).
- 1613/6927 4 km E Juli, 12,700 ft., MVZ 115759 (coordinates
approximate).
- 1615/6905 6 mi S of Yunguyo, 3826 m, FMNH 51301-03.
- 1638/6920 Huacullani, 3910 m, FMNH 52657-59.
- 1645/6944 Mazocruz, 13,000 ft., MVZ 115760-115761.

1712/6939 Pampa de Ancomarca, 123 km S Ilave, 13,800 ft., MVZ
115757.

? Hac. Collacachi, FMNH 49555-61, 49749.

? Río Huanque, 13,100 ft., MVZ 136265-136267,
136269-136270, 139257-139261.

? 15 km W Puno, 13,000 ft., MVZ 115762-115763.

? 82 km W Puno, 14,000 ft., MVZ 115764-115766.
(Puno = 1550/7022).

? 25 km NW Ayaviri, 12,900 ft., MVZ 115758 (Ayaviri =
1453/7035).

? 22 km (by rd) N Mazocruz, MVZ 139257 (Mazo Cruz
ca. 4000-4500 m, 1645/6944).

? Hacienda Pichupichuni, 6 km NW Huacallani, 12,800 ft.,
MVZ 139553-139554 (Nev. Pichupichu = 1629/7115).

? Dept. Puno only, MVZ 141864, 137242-137246.
San Antonio, Lake Titicaca, 3800 m, BMNH 1.1.1.1. (type
H. ducilla) (possibly Puno, possible coordinates
1435/7019).

Tacna:

1714/6947 0.5 mi 3 E Challapalca, MVZ 141359-141360 (near Tacna
border).

Department Unknown:

? La Paya Pass, Araranca, 14,000 ft., BMNH 22.1.1.60.

ARGENTINA:

Jujuy:

2243/6542 Abrapampa, 3500 m, BMNH 19.8.1.17-19.8.1.22

(19.8.1.21. = type of H. carillus argurus).

C. murillus:

ARGENTINA:

Buenos Aires:

3436/5827 Flores, Capital Federal, 0 m, FMNH 95142, BM 62.1927,
63.1445, 67.1656.

3436/5838 Hurlingham, 20 m, UMMZ 109227.

3446/5813 Hudson, Pdo. Berazategui, 20 m, UMMZ 115502.

3455/5757 La Plata, 20 m, BMNH 99.1.1.25-99.1.1.29,
6.4.6.25-6.4.6.31, 89.8.1.3-89.8.1.4 (type of C.
murillus, 6.4.6.26).

3618/6143 Nr. Henderson, 100 m, USNM 259646, FMNH 23394-95,
23397-98.

3622/5643 LaValle, Estancia Tuyu, 15 mi S Cape San Antonio, 0 m,
USNM 236265.

3627/6126 Torrecita, 108 m, FMNH 23400-02, 23404-05, 23407,
23409-10, 23413-14; MCZ 27021-22, USNM 259647,
BM 29.11.7.52.

3633/6235 Papin, nr. Bonifacio, F.C.S., 50 m, (see Garré) BMNH
16.10.3.18-16.10.3.20.

3649/6213 Bonifacio, 50 m, F.C.S., BMNH 16.10.3.21-16.10.3.29.

3711/6244 Carhue, 100 m, USNM 236308.

3750/5815 Partido de Balcarce, Inta, R 7, CM 86622 (coordinates for Balcarce, 108 m).

3800/5745 Partido de General Pueyrredon, Arroyo Corrientes, CM 86623 (coordinates for Partido de General Pueyrredon, a small district).

3833/5845 Necochea, Pdo. Necochea, 10 m, UMMZ 115503.

3842/6117 10 km NW of Dorrego, 113 m, (= Coronel Dorrego) FMNH 50939-45.

3843/6217 Bahia Blanca, 20 m, BMNH 0.8.5.1.

? Partido de General Pueyrredon, Estafetz Playa

? Chapadmalal, CM 86624-86625.

? Nuñez, MVZ 134247.

? Los Yngaleses, Ajo, 0 m, BMNH 20.2.7.16,
20.2.7.18-20.2.7.21.

? Villa Garibaldi, 10 mi E La Plata, BMNH
6.4.6.32-6.4.6.33.

? Las Talas, Ensenada, La Plata, BMNH 99.1.1.30
(Ensenada = 0 m, 3451/5755).

Catamarca:

2804/6734 Tinogasta, 1200 m, BMNH 20.5.11.52.

2852/6614 Chumbicha, 600 m, FMNH 29102, BMNH 18.11.11.5,
 18.11.11.7-18.11.11.9, 18.11.11.11-18.11.11.13,
 18.11.11.15-18.11.11.16, field nos. only, E. Budin 304,
 298, 14.

? 23 km SW Chumbicha, CM 43600.

? Puntilla Tinogasta, 1000 m, BMNH 20.5.11.1-20.5.11.5.

? Otro Cerro, 3000 m, BMNH 20.3.17.20-20.3.17.21.

Chaco:

2719/6117 General Pinedo, 93 m, AMNH 41746.

Cordoba:

2952/6407 Los Hoyos, UMMZ 109229.

3203/6503 Yacanto-Cordoba Range, 900 m, BMNH 16.1.6.24-16.1.6.26
 (type of H. murillus cordovensis, 16.1.6.24).

3205/6502 El Carrizal, Cordoba Range, 1000 m, BMNH
 16.1.6.27-16.1.6.31.

3222/6219 Noetinger-F.C.C.A., 100 m, BMNH 17.1.25.18-17.1.25.25.

3300/6228 La Maya, 45 km SE Belle Ville, MVZ 134248,
 134250-134251.

La Pampa:

3613/6527 Victoria, 311 m, USNM 236301.

Mendoza:

3315/6809 Santa Rosa, 601 m, MCZ 41095.

3334/6901 Tunuyán, 874 m, MCZ 19206, USNM 236284.

3436/6820 San Rafael, 686 m, MCZ 41081, 41104.

3436/6754 2 mi N Monte Coman, 400 m, MVZ 151015.

? 2.5 km S Chacras de Coria, 900 m, MVZ 166067
(coordinates for Chaceras de Coria = 3300/6852).

? 31 km (by El Manzano Rd) W Tunuyán, CM 43610.
(Tunuyán, 875 m, =3334/6901).

Neuquén:

4005/7010 Collon Cura; 16 km SE La Rinconada, MVZ 163802-163803.

? 6 km NNE Junin de los Andes, MVZ 171142 (coordinates for
Junin de los Andes = 3956/7105).

Río Negro:

3910/6609 Chimpay, 175 m, FMNH 50932-38.

3916/6541 Choele choel, 130 m, FMNH 83843.

Santa Fe:

3233/6124 Germania, 50 m, MCZ 38317.

? Las Rosas, 100 m, BMNH 17.5.2.6-17.5.2.11.

Tucumán:

2649/6513 Tucumán, 450 m, BMNH 0.7.9.6-0.7.9.10.

? Norcos Vipos, 2500 m, BMNH 26.2.13.55-26.2.13.57
(Vipos = 2629/6522).

C. musculus:

ARGENTINA:

Catamarca:

2726/6619 Immed N Andalgalá, CM 43606-43607.

" Southern outskirts of Andalgalá, CM 43608.

2726/6619 7.5 km W Andalgala, CM 43601-43602 (coordinates for Andalgala).

? La Toma Dept., 6.5 km N jct. Hwy. 63 (to Chagiago) and La Toma Rd, CM 43605.

Jujuy:

2157/6604 Sta. Catalina, 4500 m, BMNH 26.6.12.43-26.6.12.44.

2334/6522 Tilcara, 8000 ft., AMNH 41878.

2337/6524 Maimara, 2300 m, FMNH 85842, BMNH 12.12.12.7-12.12.12.11, 34.11.4.57, plus one uncataloged specimen, E. Budin 16 (type of C. musculus, 12.12.12.9).

2403/6526 1 mi W Leon, 5800 ft., MVZ 119954.

2411/6518 Jujuy, 1258 m, BMNH 20.1.7.43-20.1.7.57 (type of H. musculus cortensis, 20.1.7.46).

? Yala Dept., along Yala Laguna Rd, CM 43609 (Yala = 2407/6523, 1445 m.

2407/6429 Sunchal, Sierra Sta. Barbara, 1200-1500 m, BMNH 21.1.1.41.

Salta:

? INTA Station, Cerillos, CM 44030 (Cerillos = 2454/6529, ca. 1000 m).

? M. Sola, 2500 m, BMNH 34.11.4.56 (= Palma Sola?, 2359/6418).

? 5 km NE Cafayate, 1660 m, CM 43602 (Cafayate =
2605/6558).

San Juan:

2159/6833 Canada Honda, 500 m, BMNH 21.4.8.2-21.4.8.3.

Tucumán:

2647/6533 Nr. Tucumán, Mala Mala, BMNH 1.6.3.10.

BOLIVIA:

Cochabamba:

1727/6547 10 mi NE Punata, 10,500 ft., MVZ 119955.

1748/6445 10 km by road SE Epizana, Siberia cloud forest, 2989 m,
AMNH 246798 (coordinates approximate).

Potosí:

2127/6543 Tupiza, 2000 m, BMNH 26.6.12.37-26.6.12.42.

2143/6534 Yuruma; 20 mi SSE Tupiza, 10,500 ft., MVZ 119956.

Santa Cruz:

1751/6437 21 km by road W of Comarapa, 2900 m, AMNH 260670.

1755/6434 1 km N and 8 km W of Comarapa, 2450 m, AMNH 260666-69;
MSB 55272-73.

Tarija:

2128/6429 38 km (by rd) ENE Tarija, Carlazo, 2400 m, UMMZ 156314.

2129/6457 1 km E of Iscayachi, río Tomayapo, 3450 m, AMNH
262798-262800.

2129/6502 Sama, 4000 m, BMNH 26.1.1.41.

2133/6447 Tablada, 2000 m, BMNH 26.1.1.40.

Calomys sorellus:

PERU:

Ancash:

- 0924/7723 Huaraz, Quilcayhuanca, 4000 m, FMNH 81286-87.
- 0932/7732 Huaraz, Tullparaju, 4300 m, FMNH 81216, 81285.
- 0945/7727 Recuay; Ticapampa, Hda. Catac, 3500 m, FMNH 81288-89.
- 1307/7234 Macate, 2700 m, FMNH 20942.
- ? 6 mi WSW Cahul Tunnel, 13,000 ft., MVZ 137989-137997
- ? Callon, 2 km S and 11 km W Huaras, 13,000 ft., MVZ
135683, 137998 (coord for Huaras = 0932/7732).
- ? 25 mi S Huaras, 12,500 ft., MVZ 137999.
- ? 3 km S and 11 km W Huaras, 12,500 ft., MVZ
135686-135688.
- ? Tres Cruces, ca. 12 km W Huaras, 4200 m, MVZ 139253
- ? Rachacoca; 45 km S Huaras, 11,000 ft., MVZ
135684-135685.
- ? 45 km S Huaras, 11,000 ft., MVZ 135681-135682.
- ? Pass about 12 km W Huaras, 12,650 ft., MVZ 139252.
- ? 4 mi S and 8 mi E of Recuay, 12,500 ft., MVZ
138004-138006, 138009-138014, 138016-138021
(Recuay = 0943/7728).
- ? 2 km E Tinco, 11,950 ft., MVZ 139254.

Apurimac:

- 1339/7323 Andahuaylas, Mozobamba, 2300 m, FMNH 75377-78, 75534,
75539-40.
- 1339/7324 Andahuaylas, Hda. Palmira, 2200 m, FMNH 75291, 75372-75,
75387, 75537-38.
- 1339/7324 Andahuaylas, Hacienda La Laguna, 3040 m, FMNH 75376,
75433.
- 1327/7344 Andahuaylas, Uripa, 3100 m, FMNH 75541.
- 1344/7255 Quebrada Matara, Hac. La Victoria, 6200-7000 ft.,
FMNH 52648-56, 59496-97.
- ? 10 mi N Abancay, 8000 ft., MVZ 119957-119958
(Abancay = 1335/7255).
- ? 10 km SSE Abancay, 6250 ft., MVZ 115648-115649.
- ? 22 km S Chalhuanca, 10,700 ft., MVZ 136271
(Chalhuanca - 1417/7315).

Arequipa:

- 1548/7422 2 mi E Atiquipa, 12,000 ft.(?), MVZ 145615 (coordinates
for Atiquipa).

Ayacucho:

- 1251/7400 San Miguel, Tambo, 3200 m, FMNH 75381-84, 75388-89,
75402-04, 75544.
- 1256/7401 Tapuna Pass (6 mi NNE Tambo, 12,300') AMNH 208086,
208097 (coordinates for Tambo).
- 1256/7401 3 mi N Tapuna Pass, 10,700 ft., AMNH 208098.

- 1256/7415 Huanta, 2628 m, FMNH 75405-08.
- 1256/7415 2 mi SE Huanta, 9090 ft., MVZ 141362
(Huanta = 1256/7415).
- 1307/7413 0.5 mi NW Ayacucho, 9700 ft, AMNH 208085.
- 1312/7348 Ocos, Hda. Pajonal, 2000 m, FMNH 75401, 75434.
- 1324/7354 Ocos, Ocos, 3150 m, FMNH 75379-80, 75543.
- ? Ocos, Puente Pajonal, 1900 m, FMNH 75435, 75542.
- ? Chunyacc, 3600 m, UMMZ 120287.
- ? Pacaicasa 2560 m, UMMZ 120288-120289.
- ? Ticumachay, 4250 m, UMMZ 120290.
- ? Jawaymachay Cave, 3400 m, UMMZ 120291.
- ? 2 mi E Puquio, 11,000 ft., MVZ 136272, 139255.
- ? 18 km NW Puquio, 11,500 ft., MVZ 115927-115928.
- ? 11 mi NW Puquio, 11,500 ft., MVZ 116030.
- ? 10 mi WNW Puquio, 13,000 ft., MVZ 138002-138003
(Puquio = 1442/7408).

Cuzco:

- 1243/7314 Chirapata, Cosireni Pass, Lucura, 3000 m, FMNH 43391,
USNM 194710; BM 22.1.1.59 (coordinates for Yuvini).
- 1310/7230 Torontoy, USNM 194690.
- 1316/7221 Chospiyoc, 10,000', USNM 194726, 194779 (type of H.
frida), 194780, 194782; BMNH 22.1.1.56-22.1.1.58.
- 1318/7200 Hacienda Urco, nr. Calca, 9500-1000 ft, FMNH 49496,
49657-66, 49668-70 (coordinates for Hacienda Urco).

1325/7154 Calca, Hda. Paullo Grande, 2900 m, FMNH 84361-64.

1325/7213 Huarcocondo, 3331 m, USNM 194715, 194766-194769, 194771,
194775, 194778; MCZ 19672-73; BMNH 22.1.1.55.

1332/7157 Cuzco, 3400 m, FMNH 52662-64, 52666-67.

Huancavelica:

1217/7355 Rio Mantaro, 8500 ft., MVZ 119959.

1229/7501 3 mi SE Izcuchaca, MVZ 141363-141365.

1239/7423 Locroja, Hda. Piso, FMNH 75391-92, 75409.

1241/7424 Mayoc, 1500 m, FMNH 75390.

1245/7503 Huancavelica, 3650 m, FMNH 48312-13, 75545-47, 75385-86,
75393-95, 75410-14; BM 1938.9.26-1938.9.32.

1259/7444 Lircay, 3278 m, FMNH 75396-99, 75415-17, 75548-49.

Huanuco:

0923/7642 Cullcui, Marañon River, 10,400 ft., FMNH 23762.

0948/7645 Huanuco Viejo, 12,700 ft., FMNH 23763, JTZ 327.

0950/7602 Panao Mountains, 10,300 ft., FMNH 23747-48, 23760;
BMNH 29.11.7.53.

0954/7609 Huanuco mountains, 12,200 ft., FMNH 23758-59.

0955/7614 Huanuco, 1900 m, FMNH 23751-54, 23756-57; USNM 259648.

Junin:

1055/7602 Carhuamayo, 14,500 ft., FMNH 54744.

1122/7524 Maraynioc (45 mi NE Tarma), 12,000 ft., MCZ 38600-06.

1125/7542 Río Tarma, Yana Mayo, 8500 ft., FMNH 29103; BMNH
26.2.1.20-26.2.1.33 (type of H. frida miurus 26.2.1.26).

1132/7554 Oroya, 3750 m, FMNH 20964-65; BMNH 26.2.1.18-26.2.1.19,
66.1567.

1132/7554 Prov. Yauli, 9.5 mi N La Oroya, 13,000 ft. (3965 m),
AMNH 231786-231788, 232651-23652 (coordinates for
Oroya).

1146/7608 Pomacocha; Yauli Valley, 14,200 ft., MVZ 137613,
13800-13801.

? 17 mi WNW Huancayo, MVZ 141361, 141366-141368
(coordinates for Huancayo = 1204/7514).

? Huariaca, 9000 ft., BMNH 27.11.1.155-27.11.1.158.

? Alcas, 25 mi NE Cerro Junin, 11,500 ft., BMNH
27.11.1.159-27.11.1.161.

? Hacienda Asocsaico, 13,500 ft., BMNH 26.2.1.17.

? ? Junin, Acoria, 10,400 ft., BMNH
1938.9.26.33-1938.9.26.35 (Huancavelica, Acoria =
1237/7453, 3167 m).

La Libertad:

0754/7835 Mountains near Otuzco, 10,000 ft., 3050 m, FMNH
19209-10.

? 15 mi W Quiruvilca, 11,000 ft., MVZ 138015
(Quiruvilca = 0800/7819).

? 10 mi WNW Santiago, 3100 m, MVZ 138022
(Santiago de Chuco = 0809/7811).

- ? S of Huamachuco, BMNH 0.6.6.29 (type of C. sorellus)
(Huamachuco = 0748/7804, 3169 m).

Lima:

- 1119/7633 Culluay, 12,500 ft., MVZ 119963-119964 (= Cullhuay?).
1125/7638 1 mi W Canta, 8800 ft., MVZ 119960 (Canta=1128/7639).
1137/7617 Prov. Huarachira, 1.2 mi NW Chinchán, 15,600 ft.,
AMNH 231535-41.
1139/7614 1 mi E Casapalca, 14,000 ft., MVZ 119961.
" 1 mi W Casapalca, 14,000 ft., MVZ 119962.
" 2 mi N Casapalca, 14,400 ft., MVZ 137614-137616.
" 2 mi SW Casapalca, 13,300 ft., MVZ 137617-137623.
1143/7616 Prov. Huarachira, 6.3 km W Casapalca, 12,600 ft., AMNH
230981, 231543-231597, 231599-231615, 231694-231698,
231707-231709, 231711-231715, 231720, 231744,
231759-231760, 231775-231785, 232653-232663.
? Below Huaros, 11,500 ft. MVZ 119965.
? Villavista, 12,200 ft., MVZ 119967-119969.
? 10 mi NE Cerro de Pasco, 13,000 ft., MVZ 119970
(Cerro de Pasco = 1041/7616).

Pasco:

- 1036/7610 La Quina, 11,600 ft., FMNH 24715-23, USNM 259649.

Puno:

- 1447/7021 5 mi S Asillo, 13,000 ft., MVZ 116180.

1449/7001 Hacienda Checayani, 20 km NE Azangaro, 13,200 ft., MVZ
139256, 136273-136274.

1502/6956 Hacienda Calacala, 7 mi SW Putina, 13,200 ft., MVZ
114674, 116671-116675.

1508/7007 3 mi NE Arapa, 12,600 ft., MVZ 116667-116670.

? Alta Calacala, 40 mi NNE Juliaca, 13,400 ft., MVZ
139556-139558 (Juliaca = 1530/7008).

? 3 mi SE Nunoa, 13,400 ft., MVZ 139559 (Nunoa =
1429/7039).

Peru Only:

? AMNH 231839-231847.

C. tener:

BRAZIL:

Minas Gerais:

2045/4255 Viçosa, USNM 541497.

- ? Parque Nacional de Sierra de Canasta, (PNSC),
 - ? 23 km W of S. Roque de Minas, MSU 29251
 - ? Faz de Pedras, MSU 29252-53, 29256, 29259, 29306.
 - ? Retiro Pedras, MSU 29583-85, 29588.
 - ? 19 km W of S. Roque de Minas, MSU 29307, 29333.
 - ? Retiro M. Carmo, MSU 29587.
 - ? Zezim Condidos, MSU 29589.
- (coordinates for Carmo are 2154/4237).

São Paulo:

- 2224/4646 Itapira, LACM 55269-70 (55270 possibly = Ourinhos).
 2336/4807 Itapetininga, USNM 460552-57, 462124-28, 484408-484417,
 484419-484454, 484470-72, 485173-485174, 543054-543056.
 ? Braunau, MCZ 25795.

Rio Grande do Sul:

- ? Harmonia Estancia, AMNH 235979-235981 (in old NY Times
 Atlas, Harmonia is in the state of Parana).

Pernambuco:

- 0728/3945 Exú, uncataloged specimen at CM, KES 185.
 " 0.5 km S Exú, uncataloged specimen at CM, KES 470.
 " Escola Agricola de Exú, uncataloged specimen at CM, KES
 515.

Minas Gerais:

- 1939/4344 Lagoa Santa, BMNH 88.1.28.3 (co-type of C. tener).

Mato Grosso:

- ? Base camp, 264 km N Xavantina, Serra do Roncador, BMNH
 81.301-81.314, 81.316-81.317, 86.1129
 (Xavantina = 2121/5246).

State Unknown:

- ? Sierra Azul (either Para or Mato Grosso in Atlas),
 uncataloged specimen at Florida State Museum, no. 7.

C. venustus:

ARGENTINA:

Catamarca:

2810/6458 La Merced, near abandoned RR tunnels, MSU 19235-38

(near Tucumán).

? La Mendicta (= Mendicita?), BMNH 25.3.1.45.

Cordoba:

3044/6448 Cruz de Eje, 600 m, BMNH 2.2.5.18.

3115/6429 Cosquín, ca. 700 m, BMNH 83.4.16.1 (type of C. venustus).

3203/6503 Yacanto-Cordoba Range, 900 m, BMNH 16.1.6.14-16.1.6.20,
16.1.6.22-16.1.6.23.

3222/6219 Noetinger, F.C.C.A., 100 m, BMNH 17.1.25.12-17.1.25.17.

Corrientes:

2908/5916 Goya, USNM 94163-64; BMNH 98.12.3.11-98.12.3.14 (type
of H. venustus callidus, 26.12.3.12).

Jujuy:

2344/6435 Caimarcito, 400 m, BMNH 21.1.2.1-21.1.2.2.

2347/6447 Calilegua, FMNH 22235, 23372-74, 23376-78, 23393,
23430-31.

2359/6418 El Simbolar Dept. 25 km S Palma Sola, CM 43508 (ca.
1000 m, coordinates for Palma Sola).

2411/6518 Jujuy, 1258 m, BMNH 20.1.7.22-20.1.7.26.

? 4 km W jct. hwys 34 and 3, CM 43509-43523.

- ? 6 km W jct. hwys 34 and 3, CM 43524-43527.
- ? Yuto, AMNH 182586, 182926-182930.
- ? Sta. Barbara, AMNH 185239.
- ? Palma Sola, AMNH 185240.
- ? Sunchal, Sierra Sta. Barbara, 1200-1500 m, BMNH
21.1.1.42-21.1.1.53 (Sta. Barbara = 2467/6429).
- ? Villa Carolina, Rio Lavellen, 500 m, BMNH
20.1.7.27-20.1.7.42, 66.1707 (Laveyen = 2412/6443).

Salta:

- 2232/6349 Piquirenda Viejo, 30 km N Tartagal, CM 72385-72390
(coordinates for Tartagal, 502 m).
 - 2232/6349 Tartagal, 600 m, BMNH 19.7.25.1.
 - 2308/6420 15 km S Oran, CM 43544 (coordinates for Oran, ca. 360
m).
 - 2553/6508 Arenal, 450 m, BMNH 4.10.2.9-4.10.2.12.
 - ? Anta Dept., 21 km N Anta, CM 43528-43531, 43533-34
(Anta = 2455/6428).
 - ? Pocoy Dept., 4 km S Pocoy, CM 43540, 43543, 86602.
 - ? " " Ala Laguna Dept. Pocoy, CM 43542.
 - ? 15 km S, 15 km W Oran, CM 43545-43547.
 - ? Arroyo de los Puestos, 200 m from entrance of Parque
 - ? Nacional El Rey, CM 72380-72384.
- Santiago del Estero:
- ? Rapelli, MCZ 41084, 41106, 41110.

Tucumán:

- 2614/6529 11 km S San Pedro de Colalao on San Pedro Rd, CM 86475
(coord for San Pedro de Colalao, ca. 1000 m).
- 2630/6445 Burruyacu, 800 m, FMNH 29099-29101; BMNH
26.2.13.42-26.2.13.54, 66.1708-66.1709.
- 2641/6516 El Cadillal (Sierra Medina) 2 km Embarcadero, CM
86460-86474, 86479 (86378, skin = Calomys, skull =
Oryzomys) (17 km N San Miguel de Tucumán, coord for El
Cadillal, 683 m).
- 2644/6516 Cerro de Tafi Viejo, 1000 m, FMNH 85845.
- 2644/6516 Tafi Viejo, ca. 700 m, CM 4923.
- 2647/6518 Horco Molle Dept., 25 km W San Miguel de Tucumán, CM
43591-43595 (coordinates for Horco Molle, ca. 550 m).
- 2649/6513 Tucumán, 450 m, (San Pablo on label), BMNH 2.1.5.7.
- 2649/6513 El Cadillal Dept., 25 km N San Miguel de Tucumán, CM
43550-43584, 44031-44032 (coordinates for San Miguel de
Tucumán, 450 m, foothills of Andes in central Tucumán).
- 2652/6519 Quebrada de Lules, 8 km SW San Pablo, CM 43596-98
(ca. 500 m, coordinates for San Pablo).
- 2652/6541 El Infiernillo Dept., NW of Tafi del Valle, CM
43585-43590 (coordinates for Tafe del Valle, ca 2000 m).
- 2720/6535 Concepción (ca. 200-500 m), FMNH 30135, 30137-38,
30141, 30143, 30145-49, 30151-62, 30164-74, 30176,
30178, 30197; MCZ 23211-20, 23222-23; USNM 236317,

259259-259263, 259265-259270; BMNH 25.3.1.12,
 25.12.13.28-25.12.13.31, 26.1.9.18, 26.5.9.3-26.5.9.6,
 26.8.3.7-26.8.3.12, 66.2267-66.2269, 66.4352.

- 2724/6541 Sarmiento, 1700 ft., AMNH 41738-39, 41758, 41762,
 41766, 41768, 41770, 41772-76, 41778, 41783, 41785,
 41790-94, 41797-99, 41825 (province uncertain, some
 labels say Chubut, but possibly is Cordoba).
- ? Cevil Pozo Dept., Cevil Pozo, CM 43548-43549.
- ? Tucumán, 500 m (Vipos on label), BMNH 21.1.5.3.
- ? Tala, BM 20.7.6.5-20.7.6.6 (El Tala = ca. 900 m,
 2607/6517).

BOLIVIA:

Chuquisaca:

- 1905/6424 Tomina Prov., Llantocsillos, USNM 461043.
- 1911/6430 Tomina Prov.; Tomina, 2200 m, USNM 271404-271405,
 271592.
- ? Tomina Prov.; Rosal, 1800 m, USNM 290904, 290918.
- 1927/6407 Tomina Prov.; Tolo Orko, 40 km from Padilla, 2100 m,
 USNM 271430, 271595-271598, 545224 (coordinates
 approximate).
- 1929/6433 Horcus, 80 km SE Sucre, 6000 ft., MVZ
 134644-134647, 134650-134652.
- 1934/6408 Tomina Prov.; Tihumayu, 1500 m, USNM 290905, 290912-17.

Cochabamba:

1829/6510 2 km NW of Peña Blanca, 1700 m, AMNH 255962.

La Paz:

1608/6744 Chijchipani, 20 km by rd from Coroico, 850-1400 m, AMNH
262780-262782.

1616/6733 Astillero, 2700 m, BMNH 1.6.7.42 (coordinates
approximate).

1618/6732 Río Solocama, 1400 m, BMNH 1.6.7.43-1.6.7.45 (type of
E. callosa boliviae, 1.6.7.43).

1621/6747 Pitiguaya, 5800 ft., AMNH 72679-80.

Tarija:

2128/6432 Carlazo, 2300 m, BMNH 26.1.1.39.

2132/6412 Prov. O'Connor, Entre Rios, 1200 m, USNM 271402-03.

2133/6447 Tablada, 2000 m, BMNH 26.1.1.27-26.1.1.38 (type of H.
fecundus 26.1.1.33).

2149/6346 Carapari, 1000 m, BMNH 25.2.1.40-25.2.1.45.

2202/6345 Yacuiba, 600 m, BMNH 25.2.1.46-25.2.1.48.

2213/6436 4 km (by road) N Cuyambuyo, 980 m, UMMZ 155869,
156200-156202, 156318-156322.

Department Unknown:

? Yungas, BMNH 1.6.7.46.

? Bolivia only, BMNH 45.12.8.4, 45.12.18.10.

Chinchillula sahamae

BOLIVIA:

La Paz:

1502/6913 5 km E Ulla Ulla, 4460 m, AMNH 247886.

Eligmodontia sp. A

ARGENTINA:

Mendoza:

? 312 km (by El Manzano Rd) of Tunuyán, CM 43657, 43671,
43673, 43675, 43681-43682 (Tunuyán = 3334/6901). 4

Patagonia:

? Arroyo Aike, AMNH 25702-25703.

BOLIVIA:

Oruro:

1742/6730 12 km S and 1.5 km E Eucaliptus, Lecheria, 3359 m, AMNH
246776.

Eligmodontia sp. B

ARGENTINA:

Mendoza:

3328/6733 La Paz, 500 m, MCZ 41079, 41100;

All Eligmodontia have been referred to E. typus (HersHKovitz, 1962); however, this sample includes two species, the names are not certain (see Olds and Anderson, in press, a).

Graomys domorum

BOLIVIA:

Santa Cruz:

1758/6429 5 km by road SE of Comarapa, 1695 m, AMNH 260748,
260751-260754.

Cochabamba:

1724/6609 Cochabamba, 2600 m, FMNH 50961-50963, 50967-50969.

1734/6621 Parotani, 8800 ft., AMNH 38678, 38686, 38693.

1829/6510 2 km NW Peña Blanca, 1700 m, AMNH 255966-255973.

Graomys griseoflavus

BOLIVIA:

Santa Cruz:

1825/6210 Tita, 300 m, AMNH 260757.

Tarija:

2056/6321 2 km S, 10 km E Tiquipa, Laguna Palmar, 555 m, AMNH
246769, 246778.

2119/6325 8 km S and 10 km E Villa Montes, 467 m, AMNH 246761,
246770-246773, 246784-246786, 248438.

ARGENTINA:

Jujuy:

2336/6504 Santa Barbara, AMNH 185222.

PARAGUAY:

Boquerón:

2227/6220 Guachalla, ca. 250 m, FMNH 54359-54361, 54363-54364.

Holochilus brasiliensis

BOLIVIA:

Santa Cruz:

1828/6207 8 km SE of Tita, 290 m, AMNH 260771.

Irenomys tarsalis

ARGENTINA:

Rio Negro:

4102/7149 Puerto Blest, ca. 767 m, AMNH 256782.

Neotomys ebriosus

PERU:

Junin:

1132/7554 Prov. Yauli, 9.5 mi N La Oroya, 13,000 ft., AMNH 231637

(coordinates approximate).

Oryzomys capito

BOLIVIA:

Beni:

1228/6417 Río Iténez, opp. Costa Marques, AMNH 209997.

Oryzomys nitidus

BOLIVIA:

Santa Cruz:

1828/6207 8 km SE of Tita, 290 m, AMNH 260377.

Oxymycterus paramensis

BOLIVIA:

La Paz:

1659/6749 Caracato, 2900 m, AMNH 248999.

Phyllotis osilae osilae

BOLIVIA:

La Paz:

1448/6904 Pelechuco, 3650 m, AMNH 247880.

1512/6902 Charazani, 3450 m, AMNH 247867-247873.

1512/6903 ca. 2 km W of Charazani, 3800 m, AMNH 247874-247876.

P. wolffsohni:

BOLIVIA:

Cochabamba:

1740/6535 9.5 km by road SE of Rodeo, then 2.5 km on road to

ENTEL antennae, 3875 m, AMNH 260922-260939.

Punomys lemminus

PERU:

Puno:

? 8 mi SSW Limbani, 15,000 ft., AMNH 256780 (Limbani =
1408/6942).

Reithrodon physodes

URUGUAY:

Artigas:

? 6 km NNW Belén, AMNH 206346 (Belén = 3047/5747).

Thomasomys aureus

ECUADOR:

Pichincha:

0007/7850 Gualea, AMNH 36279 (= 0007 N).

LITERATURE CITED

Airolidi, J. P., and R. S. Hoffmann. 1984. Age variation in voles (Microtus californicus, M. ochrogaster) and its significance for systematic studies. Occas. Papers Mus. Nat. Hist., Univ. Kansas, no. 111, 45 pp.

Alho, C. J. R. 1981. Small mammal populations of Brazilian cerrado: the dependence of abundance and diversity on habitat complexity. Rev. Brasil. Biol., 41: 223-230.

_____. 1982. Brazilian rodents: their habitats and habits. Pp. 143-166 in M. A. Mares and H. H. Genoways (Eds.), Mammalian Biology in South America. The Pymatuning Symposia in Ecology, vol. 6, Univ. Pittsburgh.

Alho, C. J. R., L. A. Pereira, and A. C. Paula. 1986. Patterns of habitat utilization by small mammal populations in cerrado biome of central Brazil. Mammalia, 50(4): 447-460.

Ameghino, F. 1889. Contribucion al conocimiento de los mamiferos fósiles de la República Argentina. Acta Acad. Nac. Cienc., Córdoba, 6: 1-1027, + 98 plates.

Anderson, S. 1968. A new craniometer and suggestions for craniometry. J. Mamm., 49(2): 221-228.

_____. 1969. Taxonomic status of the woodrat, *Neotoma albigula*, in southern Chihuahua, Mexico. Misc. Publ. Univ. Kansas Mus. Nat. Hist., 51: 25-50.

August, P. 1984. Population ecology of small mammals in the llanos of Venezuela. Special Publ. Mus. Texas Tech Univ., no. 22: 71-104.

Azara, F. de. 1801. Essais sur l'Histoire Naturelle des Quadrupedes de la Province du Paraguay. Charles Pougens, Paris, 2 volumes.

Baker, R. J., M. W. Haiduk, L. W. Robbins, A. Cadena, and B. F. Koop. 1982. Chromosomal studies of South American bats and their systematic implications. Pp. 303-327, in Mares, M. A., and H. H. Genoways (Eds.). Mammalian Biology in South America. The Pymatuning Symposia in Ecology, vol. 6, Univ. Pittsburgh.

Barlow, J. C. 1969. Observations on the biology of rodents in Uruguay. Life Sci. Contrib. Royal Ontario Mus., no. 75, 59 pp.

Barrera, J. M. de la. 1936. Peste Rural. Rev. Inst. Bacteriologico, Buenos Aires, 7(3): 439-506.

Baskin, J. A. 1978. Bensonomys, Calomys, and the origin of the phyllotine group of neotropical cricetines (Rodentia; Cricetidae). J. Mamm., 59(1): 125-135.

_____. 1979. Small mammals of the Hemphillian Age White Cone local fauna, Northeastern Arizona. J. Paleontol., 53(3): 695-708.

_____. 1986. The late Miocene radiation of Neotropical sigmodontine rodents in North America. Contrib. to Geol., Univ. Wyoming, Special Paper 3: 287-303.

Belloq, M. I., and F. O. Kravetz. 1983. Identificacion de especies, sexo y edad relativa a partir de restos oseos de roedores de la provincia de Buenos Aires, Argentina. Hist. Nat., Corrientes, Argentina, 3(10): 101-112.

Bergstrom, B. J. 1984. Morphologic variation between long-established and pioneer populations of the meadow vole (*Microtus pennsylvanicus*) in Illinois. Amer. Midl. Natur., 112(1): 173-177.

Blanco, A., and C. N. Gardenal. 1977. Polimorfismo eszimatico en poblaciones de roedores cricetidos. Medicina (Buenos Aires), 37:suppl. 3: 141-148.

Cabrera, A. 1961. Catalogo de los mamiferos de America del Sur. Rev. Mus. Argent. Cienc. Nat. "Bernardino Rivadavia", Cienc. Zool., 4(2): 309-732.

Carleton, M. D. 1980. Phylogenetic relationships in neotomine-peromyscine rodents (Muroidea) and a reappraisal of the dichotomy within New World Cricetinae. Misc. Publ. Mus. Zool., Univ. Mich. no. 157, 146 pp.

Carleton, M. D., and G. G. Musser. 1984. Muroid rodents. Chapter 11, pp. 289-379 In, S. Anderson and J.K. Jones, Jr. (Eds.). Orders and Families of Recent Mammals of the World. John Wiley and Sons, New York.

Contreras, J. R., and E. R. Justo. 1974. Aportes a la mastozoologia pampeana. I. Nuevas localidades para roedores Cricetidae (Mammalia, Rodentia). Neotropica, Buenos Aires, 29(62): 91-96.

Contreras, J. R., and V. G. Roig. 1976. Biota centro-andina. I. Presencia en la provincia de Mendoza del raton Calomys musculus (Thomas) (Rodentia, Cricetidae). Neotropica, 22: 15-16.

Contreras, J. R., and M. I. Rosi. 1980a. Comportamiento territorial y fidelidad al habitat en una poblacion de roedores del centro de la provincia de Mendoza. Ecologia, Argentina, 5: 17-29.

_____. 1980b. El raton de campo Calomys musculus cordovensis (Thomas) en la Provincia de Mendoza. I. Consideraciones taxonomicas. Hist. Nat., 1(5): 17-28.

Corbet, G. B., and J. E. Hill. 1980. A World List of Mammalian Species. British Museum, London.

Corti, M., M. S. Merani, and G. de Villafañe. 1987. Multivariate morphometrics of vesper mice (Calomys): preliminary assessment of species, population and strain divergence. Z. Saugetierkunde, 52: 236-242.

Crespo, J. A. 1945. Relaciones entre estados climaticos y la ecologia de algunos roedores del campo (Cricetidae). Rev. Argentina Zoogeog., 4(3):137-144.

Crespo, J. A., M. S. Sabattini, M. J. Piantanida, and G. de Villafañe. 1970. Observaciones sobre densidad, reproduccion y estructura de comunidades de roedores silvestres en el sur de Cordoba. Estudios ecologicos sobre roedores silvestres, Buenos Aires, 45 pp.

Czaplewski, N. J. 1987. Sigmodont rodents (Mammalis; Muridae; Sigmodontinae) from the Pliocene (early Blancan) Verde Formation, Arizona. J. Vert. Paleontol., 7(2): 183-199.

Dalby, P. L. 1975. Biology of Pampa rodents, Balcarce area, Argentina. Publ. Mus. Mich. State Univ., Biol. Ser., 5(3): 149-272.

Dalby, P. L., and M. A. Mares. 1974. Notes on the distribution of the coney rat Reithrodon auritus, in northwestern Argentina. Amer. Midl. Natur., 92(1): 205-206.

Dalquest, W. W., and F. B. Stangl, Jr. 1983. Identification of seven species of Peromyscus from Trans-Pecos Texas by characters of the lower jaws. Occas. Papers Mus. Texas Tech. Univ., no. 90, 12 pp.

DeBlase, A. F., and R. E. Martin. 1974. A Manual of Mammalogy. Wm. C. Brown Company Publishers, Dubuque, Iowa.

Desmarest, M. A. G. 1819. Pp. 40-86, in Nouveau Dictionnaire d'Histoire Naturelle, vol. 29, Deterville, Paris.

_____. 1822. Mammalogie ou Description des Especes de Mammiferes. Mme. Veuve Agasse, Imprimeur Libraire, Paris, part 2: 277-555.

Dietz, J.M. 1983. Notes on the natural history of some mammals in central Brazil. J. Mamm., 64(3): 521-523.

Dorst, J. 1971. Nouvelles reserches sur l'ecologie des rongeurs des hauts plateaux peruvians. Mammalia, 35(4): 515-547.

_____. 1972a. Premières recherches sur la densité, la biomasse et la spécialization écologique de quelques rongeurs de hautes Andes du Perou. C.R. Acad. Sc. Paris, 274(6): 940-942.

_____. 1972b. Poids relatif du coeur de quelques rongeurs des hautes Andes peruvienes. Mammalia, 36(3): 389-394.

Engstrom, M. D., D. J. Schmidly, Jr., and P. K. Fox. 1982. Nongeographic variation and discrimination of species within the Peromyscus leucopus species group (Mammalia: Cricetinae) in Eastern Texas. Texas J. Science, 34(2): 149-162.

Ernest, K. A., and M. A. Mares. 1986. Ecology of Nectomys squamipes, the neotropical Water rat, in central Brazil: home range, habitat selection, reproduction and behaviour. J. Zool., London (A), 210: 599-612.

Eshelman, R. E., and G. S. Morgan. 1985. Tobagan Recent mammals, fossil vertebrates, and their zoogeographical implications. Nat. Geog. Soc., Res. Reports, vol. 21: 137-143.

Flynn, L. J., L. L. Jacobs, and E. H. Lindsay. 1985. Problems in muroid phylogeny: relationship to other rodents and origin of major groups. In Luckett, W.P.; and J.L. Hartenberger (Eds). 1985. Evolutionary Relationships among Rodents. Plenum Press, New York.

Fonollat, A. M. de. 1984. Cricetidos de la provincia de Tucuman (Argentina). Acta Zool. Lilloana, 37(2): 219-225.

Fornes, A., and E. Massoia. 1965. Micromamíferos (Marsupialia y Rodentia) recolectados en la localidad bonaerense de Miramar. *Physis*, 25: 99-108.

Freund, R. J., and R. Littell. 1981. SAS for Linear Models. Cary, N. C.: SAS Institute Inc.

Gardenal, C. N., A. Blanco, and M. S. Sabattini. 1977a. Contribucion al conocimiento de tres especies del genero Calomys (Rodentia, Cricetidae). II. Analisis electroforetico de formas multiples de enzimas como criterio de diferenciacion taxonomica. *Physis secc. C.*, Buenos Aires, 36(92): 179-188.

Gardenal, C. N., N. Triay de Juarez, M. Gutierrez, and M. S. Sabattini. 1977b. Contribucion al conocimiento de tres especies del genero Calomys (Rodentia, Cricetidae). I. Estudios citogeneticos. *Physis secc. C.*, Buenos Aires, 36(92): 169-178.

Gardner, A. L., and J. L. Patton. 1976. Karyotypic variation in oryzomyine rodents (Cricetinae) with comments on chromosomal evolution in the Neotropical cricetine complex. *Occas. Pap. Mus. Zool. Louisiana State Univ.*, no. 49, 48 pp.

Gazin, C. L. 1942. The late Cenozoic vertebrate fauna from the San Pedro Valley, Arizona. *Proc. U. S. Nat. Mus.*, 92: 475-578.

Gidley, J. W. 1922. Preliminary report on fossil vertebrates of the San Pedro Valley, Arizona with descriptions of new species of Rodentia and Lagomorpha. *U.S. Geol. Survey Prof. Paper* 131-E: 119-131.

Guilday, J. E. 1982. Dental variation in Microtus xanthognathus, M. chrotorrhinus, and M. pennsylvanicus (Rodentia: Mammalia). *Ann. Carnegie Mus.*, 51(11): 211-230.

Guthrie, D. A. 1963. The carotid circulation in the Rodentia. *Bull. Mus. Comp. Zool.*, Harvard Univ., Cambridge, 128(10): 455-481.

Gyldenstolpe, N. 1932. A manual of Neotropical sigmodont rodents. *Kungl. Sv. Vet. Akademiens Handlingar.*, 11(3): 1-164 + 18 plates.

Hall, E. R.; and K. R. Kelson. 1959. The Mammals of North America. Ronald Press Co., New York, Vol. 2: 547-1083.

Handley, C. O., Jr. 1976. Mammals of the Smithsonian Venezuelan Project. Brigham Young Univ. Sci. Bull., Biol. Ser., 20(5): 1-91.

Hershkovitz, P. 1962. Evolution of Neotropical cricetine rodents (Muridae) with special reference to the phyllotine group. Field. Zool., 46: 1-524.

Hoffstetter, R. 1986. High Andean mammalian faunas during the Plio-Pleistocene. Pp. 218-245, in Vuilleumier, F., and H. Monasterio (Eds.). High Altitude Tropical Biogeography. 1986. Oxford University Press, New York.

Honacki, J. H.; K. E. Kinman; and J. W. Koepl (Eds.). 1982. Mammal Species of the World. A Taxonomic and Geographic Reference. Allen Press, Inc. and the Associations of Systematics Collections, Lawrence, Kansas.

Hooper, E. T., and G. G. Musser. 1964. The glans penis in Neotropical cricetines (Family Muridae) with comments on the classification of muroid rodents. Misc. Publ. Mus. Zool., Univ. Michigan, no. 123, 57 pp.

Hueck, K.; and P. Seibert. 1972. Vegetationskarte von Sudamerika. Gustav Fisher Verlag, Stuttgart (71 pp. + map).

Hummelinck, P. W. (Ed.). 1940. Studies on the fauna of Curacao, Aruba, Bonaire and the Venezuelan Islands. 2 vols., The Hague.

Hurtado de Catalfo, G. E., and R. L. Wainberg. 1974. Citogenetica de Calomys callosus callosus (Rengger 1830) (Rodentia, Cricetinae). Analisis metrico del cariotipo somatico. Physis, secc. C, 33: 215-219.

Husson, A. M. 1960. A new species of the rodent Baiomys from Aruba and Curaçao. Studies on the fauna of Curaçao and other Caribbean Islands, (43): 33-40.

Ibáñez, C., and S. Moreno. 1982. Ciclo reproductor de algunos cricetidos (Rodentia Mammalia) de los llanos de Apure (Venezuela). Actas VIII Congr. Latinoamer. Zool., Merida, Venezuela, 1980: 471-480.

Jacobs, L. L., and E. H. Lindsay. 1984. Holarctic radiation of neogene muroid rodents and the origin of South American cricetids. J. Vert. Paleo., 4(2): 265-272.

Johnson, K. M., R. B. MacKenzie, P. A. Webb, and M. L. Kuns. 1965. Chronic infection of rodents by Machupo virus. *Science*, 150: 1618-1619.

Jotterand-Bellomo, M. 1984. New developments in vertebrate cytotaxonomy VII. Les chromosomes de Rongeurs (Ordre Rodentia Bowich, 1821). *Genetica*, 64: 3-64.

Justines, G., and K.M. Johnson. 1969. Immune tolerance in Calomys callosus infected with Machupo virus. *Nature*, 222: 1090-1091.

Karimi, Y., C. Rodrigues de Almeida, and F. Petter. 1976. Note sur les rongeurs du Nord-Est du Bresil. *Mammalia*, 40(2): 257-266.

Koford, C. B. 1955. New rodent records for Chile and for two Chilean provinces. *J. Mamm.*, 36(3): 465-466.

Koh, H. S., and R. L. Peterson. 1983. Systematic studies of deer mice, Peromyscus maniculatus Wagner (Cricetidae, Rodentia): analysis of age and secondary sexual variation in morphometric characters. *Can. J. Zool.*, 61: 2618-2628.

Koopman, K. 1982. Biogeography of the bats of South America. Pp. 273-302 in Mares, M. A.; and H. H. Genoways (Eds.). *Mammalian Biology in South America*, Vol. 6, Pymatuning Laboratory of Ecology, Univ. Pittsburgh.

Kravetz, F. O., M. C. Manjón, M. Busch, R. E. Percich, P. N. Marconi, and M. P. Torres. 1981a. Ecología de Calomys laucha (Rodentia, Cricetidae) en el departamento de Río Cuarto (Córdoba). 1. Dinámica de población. *Ecologia* (Buenos Aires), 6: 15-22.

Kravetz, F. O., M. Busch, R. E. Percich, M. C. Manjón, and P. N. Marconi. 1981b. Ecología de Calomys laucha (Rodentia, Cricetidae) en el departamento de Río Cuarto (Córdoba). 2. Criterios para la determinación de edades y crecimiento.. *Ecologia* (Buenos Aires), 6: 35-44.

Kravetz, F. O., and G. de Villafane. 1981. Poblaciones de roedores en cultivos de maíz durante las etapas de Madurez y Rastrojo. *Hist. Nat.*, Mendoza, Argentina, 1(31): 213-232.

Kravetz, F. O., G. de Villafane, M. P. Torres, and M. J. Piantanida. 1975. Poblaciones de roedores en un campo de Trigo. *Physis secc. C. Cont. Org. Terr.*, 34(89): 187-197.

Lange, R. B., and E. F. Jablonski. 1979. Roedores do Parana. Estudos de Biologia, Publ. Univ. Catolico do Parana, no. 2, 15 pp.

Langguth, A. 1966. Application to place on the appropriate official list the names given by G. Fischer 1814 to the cricetid rodents described by Felix de Azara in the French translation of "Essais sur l'Histoire Naturelle des Quadrupedes du Paraguay," 1801. Z. N. (S.) 1774. Bull. Zool. Nomencl., 23(6): 285-288.

Leamy, L. 1983. Variance partitioning and effects of sex and age on morphometric traits in randombred house mice. J. Mamm., 64(1): 55-61.

Lindsay, E. H. 1984. Late Cenozoic mammals from northwestern Mexico. J. Vert. Paleontol., 4(2): 208-215.

Lindsay, E. H., and L. L. Jacobs. 1985. Pliocene small mammal fossils from Chihuahua, Mexico. Paleont. Mex., no. 51, 53 pp.

Lisanti, J. A., F. O. Kravetz, and C. L. del V. Ramirez. 1976. Los cromosomas de Calomys callosus (Rengger) (Rodentia Cricetidae) de la Provincia de Cordoba. Physis secc. C. Cont. Org. Terr., 35(91): 221-230.

Lund, P. W. 1839. Coup-d'oeil sur les espèces etientes de mammifères du Brésil; extrait de quelques mémoires présentés a l'Académie royale des Sciences de Copenhague. Ann. Sci. Nat., Paris, second series, 11: 214-234.

_____. 1841a. Blir paa Brasiliens dyreverden för Sidste Jordomvaeltning. K. Danske Vidensk. Selsk. Afhandl. Nat. Math., 8: 61-144.

_____. 1841b. Tillaeg til de to sidste afhandlinger over Brasiliens dyreverden för Sidste Jordomvaeltning. K. Danske Vidensk. Selsk. Afhandl. Nat. Math., 8: 273-296.

Mares, M. A., and H. H. Genoways (Eds.). 1982. Mammalian Biology in South America. The Pymatuning Symposia in Ecology, vol. 6, Univ. Pittsburgh.

Mares, M. A., J. Morello, and G. Goldstein. 1985a. The Monte desert and other subtropical semi-arid biomes of Argentina, with comments on their relation to North American arid areas. Pp. 203-237 in Evani, M; I. noy-Meir; and D. W. Goodall (eds.). 1985. Hot Deserts and Shrublands, A. Ecosystems of the World, 12A. Elsevier Science Publishers, Amsterdam.

Mares, M. A., R. A. Ojeda, and M. P. Kosco. 1981a. Observations on the distribution and ecology of the mammals of Salta Province, Argentina. Ann. Carnegie Mus., 50(6): 151-206.

Mares, M. A., M. R. Willig, and T. E. Lacher, Jr. 1985b. The Brazilian Caatinga in South American Zogeography: tropical mammals in a dry region. J. Biogeog., 12: 57-69.

Mares, M. A., M. R. Willig, K. E. Streilein, and T. E. Lacher, Jr. 1981b. The mammals of northeastern Brazil: a preliminary assessment. Ann. Carnegie Mus., 50(4): 81-137.

Marshall, L. G., A. Berta, R. Hoffstetter, R. Pascual, O. A. Reig, M. Bombin, and A. Mones. 1984. Mammals and stratigraphy: geochronology of the continental mammal-bearing Quaternary on South America. Palaeovertebrata, Montpellier, Mem. Extr. 1984: 1-76.

Marshall, L. G., R. Hoffstetter, and R. Pascual. 1983. Mammals and stratigraphy: geochronology of the continental mammal-bearing Tertiary of South America. Palaeovertebrata, Montpellier, Mem. Extr. 1983: 1-93.

Massoia, E. 1962. Sobre los cricetidos de la selva marginal de Punta Lara. Physis, 23: 108.

_____. 1974. Ataques graves de Holochilus y otros roedores a cultivos de caña de azúcar. Inst. Nac. Tec. Agropec., 321/24: 1-12.

Massoia, E., and A. Fornes. 1964. Tres notas sobre el genero Calomys (Rodentia, Cricetidae). Physis, 24: 490-491.

_____. 1965. Nuevos datos sobre la morfologia, distribucion geografica y etoecologia de Calomys callosus callosus (Rengger) (Rodentia-Cricetidae). Physis, 25(70): 325-331.

_____. 1967a. El estado sistematico, distribucion geografica y datos etoecologicos de algunos mamiferos neotropicales (Marsupialia y Rodentia) con la descripcion de *Cabreramys*, genero nuevo (Cricetidae). *Acta Zool. Lilloana*, 23: 407-430.

_____. 1967b. Roedores recolectados en la Capital Federal (Caviidae, Cricetidae y Muridae). *Rev. Inst. Nacional Tecnologia Agropecuaria*, no. 240: 47-53.

Massoia, E., A. Fornes, R. L. Wainberg, and T. G. de Fronza. 1968. Nuevos aportes al conocimiento de las especies bonaerenses del genero *Calomys* (Rodentia-Cricetidae). *Revta Investnes Agropec. (VBiol. Prod. anim.)*, 5: 63-92.

Matthey, R. 1973. The chromosome formulae of eutherian mammals. Pp. 531-616 in Chiarelli, A. B., and E. Capanna (Eds.). 1973. *Cytotaxonomy and Vertebrate Evolution*, Academic Press, London.

Mello, D. A. 1977. Observações preliminares sobre a ecologia de algumas espécies de roedores do cerrado, Município de Formosa, Goiás, Brasil. *Rev. Bras. de Pesquisas Med. e Biol.*, 10(1): 39-44.

_____. 1978. Biology of *Calomys callosus* (Rengger, 1830) under laboratory conditions (Rodentia, Cricetinae). *Rev. Brazil. Biol.*, 38(4): 807-811.

_____. 1980. Estudo populacional de algumas espécies de roedores do cerrado (Norte do município de Formosa, Goiás). *Rev. Brazil. Biol.*, 40(4): 843-860.

Musser, G. G. 1979. Results of the Archbold Expeditions. No. 102. The species of *Chiropodomys*, arboreal mice of Indochina and the Malay Archipelago. *Bull. Amer. Mus. Nat. Hist.*, 162: 379-445.

_____. 1982. Results of the Archbold Expeditions. No. 108. The definition of *Apomys*, a native rat of the Philippine Islands. *Amer. Mus. Novitates*, no. 2746, 43 pp.

Musser, G. G., and M. M. Williams. 1985. Systematic studies of oryzomyine rodents (Muridae): definitions of *Oryzomys villosus* and *Oryzomys talamancae*. *Amer. Mus. Novitates*, no. 2810, 22 pp.

Myers, P. 1977. A new phyllotine rodent (genus *Graomys*) from Paraguay. *Occas. Pap. Mus. Zool. Univ. Michigan*, no 676, 7 pp.

_____. 1982. Origins and affinities of the mammal fauna of Paraguay. Pp. 85-93 in Mares, M. A., and H. H. Genoways. Mammalian Biology in South America. The Pymatuning Symposia in Ecology, vol. 6, Univ. Pittsburgh.

Myers, P., and M. D. Carleton. 1981. The species of Oryzomys (Oligoryzomys) in Paraguay and the identity of Azara's "Rat sixieme ou Rat a Tarse Noir". Misc. Publ. Mus. Zool., Univ. Mich., no. 161, 41 pp.

Neff, N. A., and L. F. Marcus. 1980. A Survey of Multivariate Methods for Systematics. New York, privately published.

Nitikman, L. Z., and M. A. Mares. 1987. Ecology of small mammals in a gallery forest of central Brazil. Ann. Carnegie Mus., 56(2): 75-95.

Olds, N., and S. Anderson. In press (a). A diagnosis of the tribe Phyllotini (Rodentia, Muridae). Memorial volume for R. M. Wetzel, University of Florida Press, Gainesville.

_____. In press (b). Notes on Bolivian mammals 2. Taxonomy and distribution of rice rats of the subgenus Oligoryzomys. Fieldiana Zool., Festschrift for P. Hershkovitz.

Olds, N., S. Anderson, and T.L. Yates. 1987. Notes on Bolivian mammals 3: A revised diagnosis of Andalgalomys (Rodentia, Muridae) and the description of a new subspecies. Amer. Mus. Novitates, no. 2890, 17 pp.

Olfers, I. von. 1818. Bemerkungen zu Illiger's Ueberblick der Saugthiere nach ihrer Vertheilung uber die Welttheile, rucksichtlich der Sudamericanischen Arten (Species). Vol. 15, no. 2, pp. 192-237, in Eschwege, W. L., Journal von Brasilien, Neue Bibliothek der Reisebeschreibungen zur Erweiterung der Erd-und Volderkunde, Weimar.

Osgood, W. H. 1933. Two new rodents from Argentina. Field Mus. Nat. Hist., Zool. ser., 20: 11-14.

_____. 1943. The mammals of Chile. Field Mus. Nat. Hist., Zool. ser., 30: 1-268.

_____. 1947. Cricetine rodents allied to Phyllotis. J. Mamm., 28(2): 165-174.

Patterson, B., and R. Pascual. 1972. The fossil mammal fauna of South America. Pp. 247-309, in Keast, A; F.C. Erk; and B. Glass (Eds). 1972. Evolution, Mammals, and Southern Continents. State University of New York Press, Albany.

Pearson, O. P. 1951. Mammals in the highlands of southern Peru. Bull. Mus. Comp. Zool., 106 (3): 117-174.

_____. 1982. Distribucion de pequenos mamiferos en el altiplano y los desiertos del Peru. Pp. 263-284, in Salinas, P. (Ed.). 1982. Zoologia Neotropical. Actas del 8th Congreso Latinoamericano de Zoologia, Merida, Venezuela.

Pearson, O. P., and J. L. Patton. 1976. Relationships among South American phyllotine rodents based on chromosome analysis. J. Mamm., 57(2): 339-350.

Pearson, O. P., and C. P. Ralph. 1978. The diversity and abundance of vertebrates along an altitudinal gradient in Peru. Memorias Mus. Hist. Nat. "Javier Prado", Lima, no. 18, 97 pp.

Pérez-Zapata, A., A. D. Vitullo, and O. A. Reig. 1987. Karyotypic and sperm distinction of Calomys hummelincki from Calomys laucha (Rodentia: Cricetidae). Acta Cient. Venez., 38: 90-93.

Petter, F., Y. Karimi, and C. R. de Almeida. 1967. Un nouveau rongeur de laboratoire le cricetide Calomys callosus. C.R. Acad. Sc. Paris, Serie D, 265: 1974-1976.

Piantanida, M. J., and A. M. Petriella. 1976. Estudio morfologico de los pelos de algunas especies de roedores de la provincia de Buenos Aires con el microscopio electronico de Barrido. Physis secc. C. Cont. Org. Terr., 35(90): 105-124.

Pizzimenti, J. J., and R. de Salle. 1980. Dietary and morphometric variation in some Peruvian rodent communities; the effect of feeding strategy on evolution. Biol. J. Linnean Soc., 13: 263-285.

_____. 1981. Factors influencing the distributional abundance of two trophic guilds of Peruvian cricetid rodents. Biol. J. Linnean Soc., 15(4): 339-354.

Reig, O. A. 1965. Datos sobre la comunidad de pequenos mamiferos de la region costera del Partido de General Pueyrredon y de los partidos limitrotes (Prov. de Buenos Aires, Argentina). *Physis*, 25: 205-211.

_____. 1977. A proposed unified nomenclature for the enamelled components of the molar teeth of the Cricetidae (Rodentia). *J. Zool.*, London, 181: 227-241.

_____. 1980. A new fossil genus of South American cricetid rodents allied to Wiedomys, with an assessment of the Sigmodontinae. *J. Zool.*, London, 192: 257-281.

_____. 1984. Distribuição geográfica e história evolutiva dos roedores muroideos sulamericanos (Cricetidae: Sigmodontidae). *Rev. Brasil. Genet.* 7(2): 333-365.

_____. 1986. Diversity patterns and differentiation of high Andean rodents. Pp. 404-439, in Vuilleumier, F., and M. Monasterio (Eds.). 1986. *High Altitude Tropical Biogeography*. Oxford University Press, New York.

Rengger, J. R. 1830. *Naturgeschichte de Saeugethiere von Paraguay*. Schweighauserschen Buchhandlung, Basel.

Ribeiro, R. D. 1973. Novos reservatórios do Trypanosoma cruzi. *Rev. Brasil. Biol.*, 33(3): 429-437.

Roldan, E. R. S., A. D. Vitullo, M. S. Merani, and I. von Lawzewitsch. 1985. Cross fertilization in vivo and in vitro between three species of vesper mice, Calomys (Rodentia, Cricetidae). *J. Exper. Zool.*, 233: 433-442.

Sanborn, C. C. 1950. Small rodents from Peru and Bolivia. *Publ. Mus. Hist. Nat. "Javier Prado"*, Ser. A, *Zool.*, Lima, no. 5, 16 pp.

SAS Institute Inc. 1982. *SAS User's Guide: Statistics*, 1982 Ed. Cary, N. C.: SAS Institue Inc.

Schaller, G. B. 1983. Mammals and their biomass on a Brazilian ranch. *Arq. Zool.*, Sao Paulo, 31(1): 1-36.

Simpson, G. G. 1945. The principles of classification and a classification of mammals. *Bull. Amer. Mus. Nat. Hist.*, 85: 1-350.

Slaughter, B. H., and J. E. Ubelaker. 1984. Relationship of South American cricetines to rodents of North America and the old world. *J. Vert. Paleo.*, 4(2): 255-264.

Sokal, R. R., and F. J. Rolff. 1981. *Biometry*. W. H. Freeman and Company, San Francisco.

Soukup, J. 1961. Materiales Para El Catalogo de los Mamiferos Peruanos. *Biota*, 3 (26): 240-276.

Streilein, K. E. 1982a. Ecology of small mammals in the semiarid Brazilian Caatinga. I. Climate and faunal composition. *Ann. Carnegie Mus.*, 51: 79-107.

_____. 1982b. Ecology of small mammals in the semiarid Brazilian caatinga. II. Water relations. *Ann. Carnegie Mus.*, 51(6): 109-126.

_____. 1982c. Ecology of small mammals in the semiarid Brazilian caatinga. III. Reproductive biology and population ecology. *Ann. Carnegie Mus.*, 51(13): 251-269.

Tate, G. H. H. 1932. The taxonomic history of the South American cricetid genera Euneomys (subgenera Euneomys and Galenomys), Auliscomys, Chelemyscus, Chinchillula, Phyllotis, Paralomys, Graomys, Eligmodontia and Hesperomys. *Amer. Mus. Novitates*, no. 541, 21 pp.

Taylor, J. M., J. H. Calaby, and H. M. Van Deusen. 1982. A revision of the genus Rattus (Rodentia, Muridae) in the New Guinean region. *Bull. Amer. Mus. Nat. Hist.*, 173(3): 177-336.

Thomas, O. 1882. On a Collection of Rodents from North Peru. *Proc. Zool. Soc. London*, 1882: 98-111 + 1 plate.

_____. 1884. On a Collection of Muridae from Central Peru. *Proc. Zool. Soc. London*, 1884: 447-458 + 2 plates

_____. 1894. Descriptions of some new Neotropical Muridae. *Ann. Mag. Nat. Hist.*, ser. 6, 14: 346-366.

_____. 1898a. On some Mammals obtained by the late Mr. Henry Durnford in Chubut, E. Patagonia. *Proc. Zool. Soc. London*, 1898: 210-212.

_____. 1898b. On the small mammals collected by D'Borelli in Bolicia and Northern Argentina. Boll. Musei di Zoologia ed Anatomia comparata della R. Universita di Torino, 13(315): 1-4.

_____. 1900. Descriptions of new Rodents from Western South America. Ann. Mag. Nat. Hist., ser. 7, 11: 294-302.

_____. 1901a. New Mammals from Peru and Bolivia, with a List of those recorded from the Inambari river, Upper Madre de Dios. Ann. Mag. Nat. Hist., ser. 7, 7: 178-190.

_____. 1901b. New Neotropical Mammals, with a Note on the Species of Reithrodon. Ann. Mag. Nat. Hist., ser. 7, 8: 246-255.

_____. 1902a. On Mammals from Cochabamba, Bolivia, and the Region north of that place. Ann. Mag. Nat. Hist., ser. 7, 9: 125-143.

_____. 1902b. On Mammals collected at Cruz del Eje, Central Cordova, by Mr. P. O. Simons. Ann. Mag. Nat. Hist., ser. 7, 9: 237-245.

_____. 1910. A Collection of Mammals from Eastern Buenos Ayres, with Descriptions of related new Mammals from other Localities. Ann. Mag. Nat. Hist., ser. 8, 5: 239-247.

_____. 1913. On Small Mammals collected in Jujuy by Senor E. Budin. Ann. Mag. Nat. Hist., ser. 8, 11: 136-143.

_____. 1916a. On the grouping of the South-American Muridae that have been referred to Phyllotis, Euneomys, and Eligmodontia. Ann. Mag. Nat. Hist., ser. 8, 17: 139-143.

_____. 1916b. Notes on Argentine, Patagonian, and Cape Horn Muridae. Ann. Mag. Nat. Hist., ser. 8, 17: 182-187.

_____. 1917. Preliminary diagnoses of new mammals obtained by the Yale-National Geographic Society Peruvian Expedition. Smithsonian Misc. Coll., 68(4): 1-3.

_____. 1919a. List of Mammals from the Highlands of Jujuy, North Argentina, collected by Sr. E. Budin. Ann. Mag. Nat. Hist., ser. 9, 4: 128-135.

_____. 1919b. On some small Mammals from Catamarca. Ann. Mag. Nat. Hist., ser. 9, 3: 115-118.

_____. 1919c. Two new Rodents from Tartagal, Salta, N. Argentina. Ann. Mag. Nat. Hist., ser. 9, 4: 154-156.

_____. 1920a. A Further Collection of Mammals from Jujuy. Ann. Mag. Nat. Hist., ser. 9, 5: 188-196.

_____. 1920b. On Mammals from near Tinogasta, Catamarca, collected by Sr. Budin. Ann. Mag. Nat. Hist., ser. 9, 6: 116-120.

_____. 1920c. Report on the Mammalia collected by Mr. Edmund Heller during the Peruvian Expedition of 1915 under the auspices of Yale University and the National Geographic Society. Proc. National Mus., 58: 217-249 + plates 14 and 15.

_____. 1921a. New Hesperomys and Galea from Bolivia. Ann. Mag. Nat. Hist., ser. 9, 8: 622-624.

_____. 1921b. On Mammals from the Province of San Juan, Western Argentina. Ann. Mag. Nat. Hist., ser. 9, 8: 214-221.

_____. 1925. The Spedan Lewis South American Exploration. - I. On Mammals from Southern Bolivia. Ann. Mag. Nat. Hist., ser. 9, 15: 575-582.

_____. 1926a. The Spedan Lewis South American Exploration. - II. On Mammals collected in the Tarija Department, Southern Bolivia. Ann. Mag. Nat. Hist., ser. 9, 17: 318-328.

_____. 1926b. The Godman-Thomas Expedition to Peru. - I. On Mammals collected by Mr. R. W. Hendee near Lake Junin. Ann. Mag. Nat. Hist., ser. 9, 17: 313-318.

_____. 1926c. The Spedan Lewis South American Exploration. - III. On Mammals collected by Sr. Budin in the Province of Tucuman. Ann. Mag. Nat. Hist., ser. 9, 17: 602-609.

_____. 1927a. On further Patagonian Mammals from Neuquen and the Rio Colorado collected by Senor E. Budin. Ann. Mag. Nat. Hist., ser. 9, 20: 199-205.

_____. 1927b. The Godman-Thomas Expedition to Peru. - VI. On Mammals from the Upper Huallaga and neighbouring Highlands. Ann. Mag. Nat. Hist., ser. 9, 20: 594-608.

Tolliver, D. K., J. R. Choate, D. W. Kaufman, and G. A. Kaufman. 1987. Microgeographic variation of morphometric and electrophoretic characters in *Peromyscus leucopus*. *Amer. Midl. Nat.*, 117(2): 420-427.

Vallejo, S., and E. Gudynas. 1980. Aspectos biogeograficos de *Calomys laucha* (Rodentia: Cricetidae) en al Rep. O. del Uruguay. *Res. Jorn. C. Nat.*, Montevideo, 1: 83-84.

Vervoorst, F. 1982. Noroeste. Pp. 9-24, in *Conservacion de la Vegetacion Natural en la Republica Argentina*, Simposio 18 Jornadas Argentina de Botanica, Ministerio de Cultura y Educacion, Fundacion Miguello Lillo, Sociedad Argentina de Botanica, Tucumán.

Villafañe, G. de. 1981. Reproduccion y crecimiento de *Calomys musculinus murillus* (Thomas, 1916). *Hist. Nat.*, Mendoza, Argentina, 1(33): 237-256.

Villafañe, G. de, F. O. Kravetz, O. Donadio, R. Percich, L. Knecher, M. P. Torres, and N. Fernandez. 1977. Dinamica de las comunidades de roedores en agro-ecosistemas pampasicos. *Medicina (Buenos Aires)*, 37(suppl. 3): 128-140.

Villafañe, G. de, Kravetz, F. O., M. J. Piantanida, and J. A. Crespo. 1973. Dominancia, densidad e invasion en una comunidad de roedores de la localidad de Pergamino (Provincia de Buenos Aires). *Physis secc. C. Cont.Org. Terr.*; 32(84): 47-59.

Vorontzov, N. N. 1959. The system of hamster (Cricetinae) in the sphere of the world fauna and their phylogenetic relations. *Byull. MOIP, otd. biol.*, 64(5): 134-137 (in Russian).

Voss, R. S., and A. V. Linzey. 1981. Comparative gross morphology of male accessory glands among Neotropical Muridae (Mammalia: Rodentia) with comments on systematic implications. *Misc. Publ. Mus. Zool., Univ. Michigan*, no. 159, 41 pp.

Vuilleumier, F., and M. Monasterio (Eds.). 1986. *High Altitude Tropical Biogeography*. Oxford University Press, New York.

Wahlert, J. H. 1974. The cranial formaina of protogomorphous rodents; an anatomical and phylogenetic study. *Bull. Mus. Comp. Zool.*, 146(8): 363-410.

_____. 1985. Cranial foramina of rodents. Pp. 311-332 In Luckett, W. P.; and J. L. Hartenberger (Eds.). 1985. Evolutionary Relationships Among Rodents: A Multidisciplinary Analysis. Plenum Press, New York.

Walter, H., and S.-W. Breckle. 1985. Ecological Systems of the Geobiosphere. 1. Ecological Principles in Global Perspective. Springer-Verlag, Berlin.

_____. 1986. Ecological Systems of the Geobiosphere. 2. Tropical and Subtropical Zonobiomes. Springer-Verlag, Berlin.

Waterhouse, G. R. 1837. Characters of new species of the genus Mus from the collection of Mr. Darwin. Proc. Zool. Soc. London, 1837, part 5: 15-21.

_____. 1839. The Zoology of the Voyage of H. M. S. Beagle under the Command of Captain Fitzroy, R. M. During the Years 1832 to 1836. Part 2. Mammalia. Smith, Elder and Co., London, 97 pp, + 35 plates.

Williams, D. F., and M. A. Mares. 1978. A new genus and species of phyllotine rodent (Mammalia: Muridae) from Northwestern Argentina. Ann. Carnegie Mus., 47: 193-221.

Winge, H. 1888. Jordfundne og nulevende Gnavere (Rodentia) fra Lagoa Santa, Minas Geraes, Brasilien. E. Museo Lundii, 1 (3): 178 pp. + 8 plates.

Wolfe, J. L., and J. N. Layne. 1968. Variation in dental structures of the Florida mouse, Peromyscus floridanus. Amer. Mus. Novitates, no. 2351, 7 pp.

Xia, X., and J. S. Millar. 1987. Morphological variation in deer mice in relation to sex and habitat. Can. J. Zool., 65: 527-533.

Yáñez, J., and F. Jaksic. 1977. Variacion geografica de la morfologia dentaria en subespecies del genero Akodon. Bol. Mus. Nac. Hist. Nat. Chile, 35: 105-112.

Yonenaga, Y. 1975. Karyotypes and chromosome polymorphism in Brazilian Rodents. Caryologia, 28(3): 269-286.