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## Notes on Bolivian Mammals 6. The Genus *Ctenomys* (Rodentia, Ctenomyidae) in the Highlands

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### ABSTRACT

Tuco tuco (genus *Ctenomys*) of the Bolivian highlands are reviewed. Synonymies, references, a key for identification, lists of all known Bolivian specimens and localities, and new data on mor-

phology and karyology are given for the four species (*C. frater*, *C. opimus*, *C. lewisi*, and *C. leucodon*) present. Diploid chromosomes for these species number 52, 26, 56, and 36, respectively.

### RESUMEN

Se revisaron los tuco tuco (género *Ctenomys*) del altiplano boliviano. Se presentan sinonimos, referencias, listas de todos los especímenes conocidos, un clave por identificación, y nuevos datos sobre morfología y cariólogía. Se encontró que

existen cuatro especies (*C. frater*, *C. opimus*, *C. lewisi*, y *C. leucodon*). Sus números de cromosomas diploides son 52, 26, 56, and 36, respectivamente.

### INTRODUCTION

*Ctenomys* is a speciose genus of subterranean rodents that is endemic to southern South America. As is true for many rodent taxa of South America, the distribution and biology in general are poorly known for *Ctenomys*. Few specimens are available for

many of the estimated 30 (Mares and Ojeda, 1982) to 44 (Reig, 1986) species. *Ctenomys* is of considerable biological interest, however, as it is highly convergent ecologically and morphologically with North American pocket gophers (Geomyidae), with Middle

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Eastern and European mole-rats (Spalacidae), and with African mole-rats (Bathyergidae; Nevo, 1979). Karyotypic evolution has been extensive in those subterranean rodents and *Ctenomys* also exhibits extremely high chromosomal variation, with a diploid number ranging from 10 in *C. steinbachi* to 70 in *C. pearsoni* (Anderson et al., 1987). Comparative study of these taxa may lead to productive insights into the processes responsible for these similarities and for karyotypic evolution in general.

Six nominal species of *Ctenomys* were reported for Bolivia by Cabrera (1961) and the taxonomy of four lowland species was summarized by Anderson et al. (1987). The present paper lists all known literature references to actual specimens for four other species from highland Bolivia and all known specimens. Standard chromosomal and morphological variation within and among these highland species are described herein and the karyotypes of three of the four species are reported for the first time. Notes on *C. conoveri*, *C. steinbachi*, and "*C. minutus*" are added. Further study of the three Bolivian specimens previously and tentatively identified as *C. minutus* will establish their actual identity.

## MATERIALS AND METHODS

**TAXONOMIC SYNOPSIS:** This synopsis is based on literature and on examination of specimens in a number of major museums (by Anderson). Material from the Bolivian highlands, reported here for the first time, adds to knowledge of distributions and the morphological limits of *Ctenomys*. Museums and their acronyms were published earlier (Anderson et al., 1987).

**MORPHOLOGICAL ANALYSIS:** Standard external measurements from fresh specimens and cranial measurements (as figured previously, Anderson et al., 1987) taken with calipers are as follows (all measurements are in millimeters, except weight is in grams):

H&B	Length of head and body
TAI	Length of tail vertebrae
HF	Length of hind foot, including longest claw
EAR	Length of ear from notch
WT	Weight in grams
CRL	Condylbasilar length
CIL	Condylolincisive length

PRL	Palatilar length
MXL	Alveolar length of maxillary tooth row
DSB	Breadth of dental span
PRB	Breadth of palate between closest alveolar margins
ZYB	Greatest breadth across zygomatic arches
IOB	Breadth at interorbital constriction
LAB	Greatest breadth across lambdoidal ridges
SKD	Depth of skull from plane of occlusal surfaces to top of skull.

Using the following series, ratio diagrams (Anderson et al., 1987) were drawn in order to (1) visualize ontogenetic changes in proportions by comparing individuals of different ages in samples of sufficient size and (2) compare patterns for adults of five species.

*Ctenomys frater frater* from Potosí, 2 specimens; *C. f. mordosus* from near Tambo in Tarija, 12; *C. leucodon*, 5; *C. lewisi* from near Iscayachi in Tarija, 12, range only plotted; *C. lewisi* from Sama (probably at or near the preceding locality) in Tarija, 5; *C. opimus opimus* from Carikari in Potosí, 4; from Uyuni in Potosí, 4; from near Laguna Colorado in Potosí, 6; from near Huancaroma in Oruro, 28; from near Río Barros in Oruro, 9; and from near Sajama in Oruro, 11.

Based on comparisons of these diagrams with each other and with similar diagrams prepared for our earlier study of lowland species (Anderson et al., 1987), various differences in size and proportions of both external and cranial dimensions were evaluated and noted in the taxonomic comparisons below.

Measurements of series of *Ctenomys opimus opimus* from several localities were analyzed to evaluate differences relating to sex and estimated age. Three of the species were compared by analysis of Canonical Discriminant Functions to assess the amount of variation due to locality.

Measurements of selected specimens are included in table 2.

**SPECIMENS EXAMINED:** Sample localities for karyotypes are indicated in figure 1, along with all localities for highland *Ctenomys* known from the literature or from specimens examined by us. All specimens are listed in the taxonomic synopsis; those examined karyotypically for this study are indicated by NK numbers; and catalog numbers for those referred to specifically in text, figures, or ta-

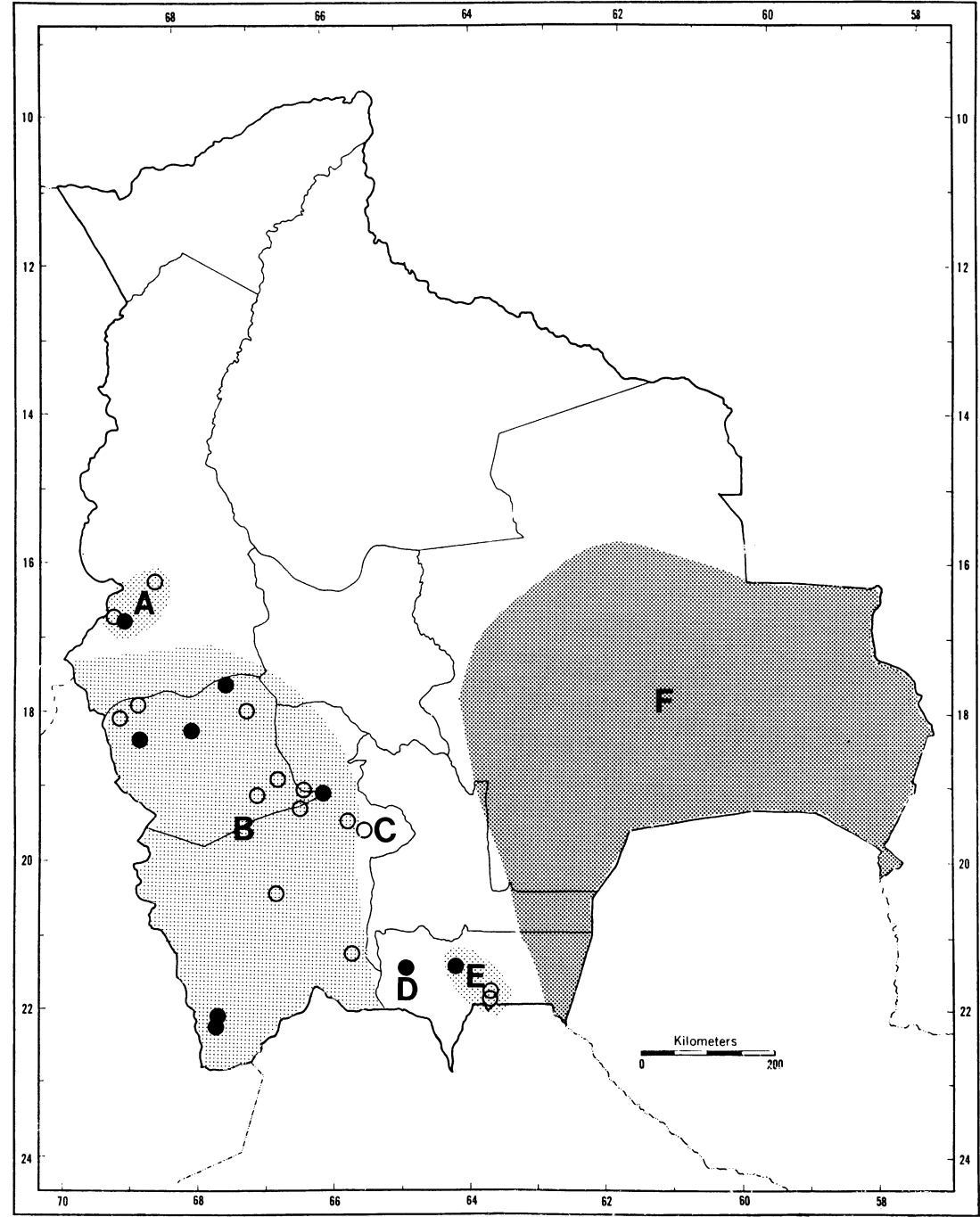


Fig. 1. Map of southwestern Bolivia showing all known localities of specimens of *Ctenomys* from highland Bolivia. Black dots are localities from which karyotypes have been examined. Taxa are: A. *C. leucodon*, B. *C. opimus*, C. *C. frater frater*, D. *C. lewisi*, and E. *C. frater mordosus*. F. Stippled area represents the distribution of lowland species of *Ctenomys* (Anderson et al., 1987).

bles also are given. Measurements in table 2 are of the largest specimen of a male and of a female for each species (in condylobasilar measurement).

**KARYOTYPIC ANALYSIS:** Nondifferentially stained karyotypes were prepared from 43 specimens representing four highland species of Bolivian *Ctenomys*. Specimens were collected using Macabee gopher traps or Victor steel traps. Traps were checked frequently to reduce mortality prior to karyotyping. Karyologic techniques were described in Anderson et al. (1987). Specimens of *Ctenomys opimus* were collected during expeditions in 1984 and 1986, while *C. frater*, *C. lewisi*, and *C. leucodon* were collected on the latter trip. Diploid number was verified by counting at least 10 cells per individual. Voucher specimens were deposited in the Mammal Division of the Museum of Southwestern Biology at the University of New Mexico, the Bolivian Museo Nacional de Historia Natural in La Paz, or in the Department of Mammalogy at the American Museum of Natural History.

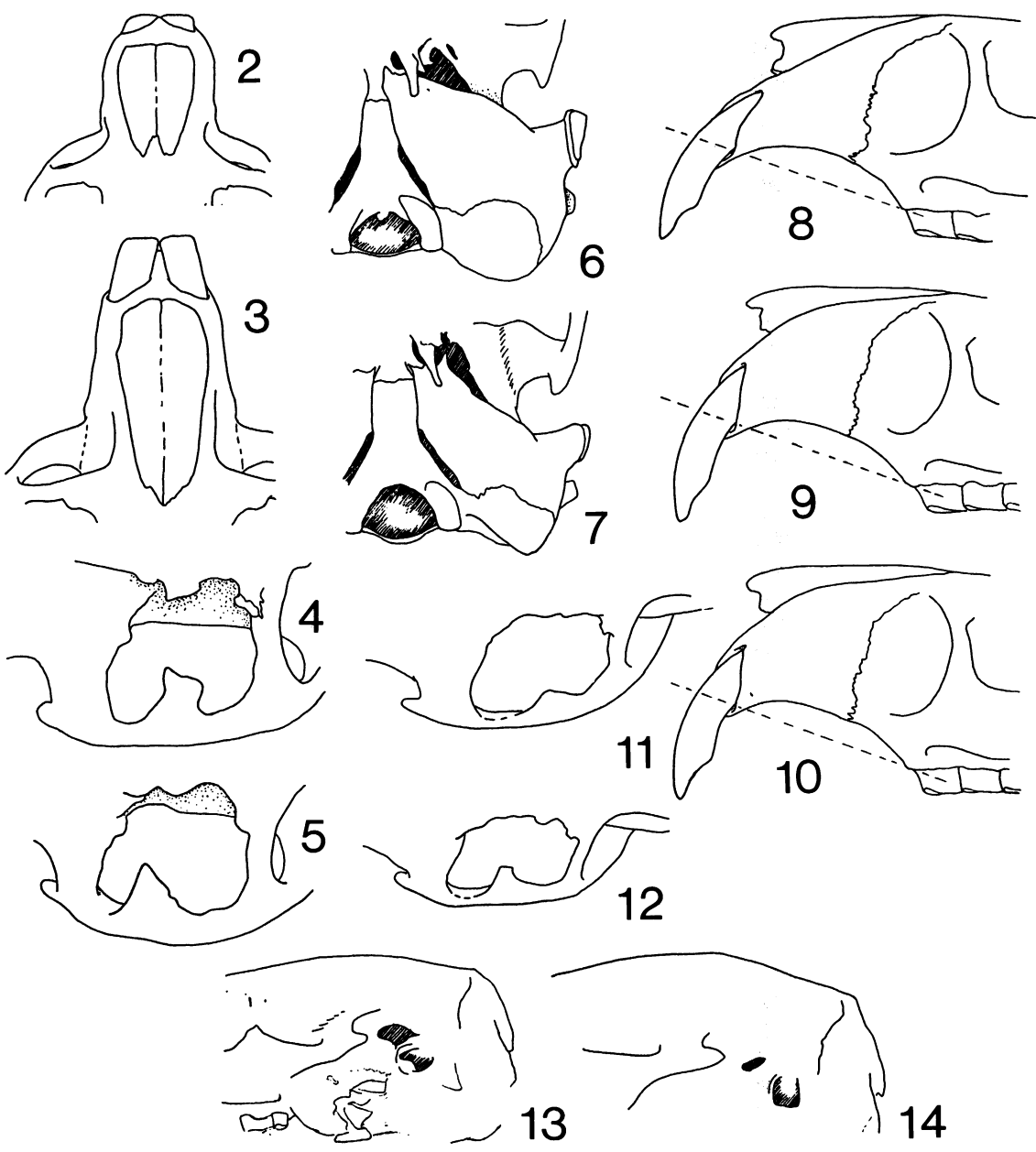
#### ACKNOWLEDGMENTS

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#### KEY TO BOLIVIAN SPECIES OF CTENOMYS

1. Size large, hind foot greater than 55 mm, greatest length of skull greater than 65; pelage coarse, shaggy, reddish brown; inhabiting the Gran Chaco in southeastern Bolivia; 2N = 48 ..... *Ctenomys conoveri*  
Size smaller, hind foot less than 55, greatest length of skull less than 65; pelage not as above ..... 2
2. Pelage short, few hairs of dorsum longer than 15 mm; nasal bones relatively short, broad, and truncated anteriorly (fig. 2) ..... 3  
Pelage long, most hairs of dorsum longer than 15; nasal bones longer, narrower, and not truncated anteriorly (fig. 3) ..... 5
3. Size small, hind foot less than 35 mm, head and body length less than 175, greatest length of skull less than 45; rostrum short (fig. 2); inhabiting eastern Santa Cruz .....  
..... "Ctenomys minutus"  
Size larger, hind foot more than 35, head and body length more than 175, greatest length of skull more than 45 ..... 4
4. Pelage blackish; postorbital processes farther forward (fig. 4); inhabiting western Santa Cruz; 2N = 10 ..... *Ctenomys steinbachi*  
Pelage brown; postorbital processes farther back (fig. 5); widely ranging in Santa Cruz; 2N variable, 36 to 46 ... *Ctenomys boliviensis*
5. Pelage pale reddish tan (in unworn pelage); bullae large (fig. 6); 2N = 26 .....  
..... *Ctenomys opimus*  
Pelage varying from tan to blackish; bullae not expanded (fig. 7) ..... 6
6. Dorsal pelage pale reddish tan; upper incisors unusually procumbent (fig. 8) and pale; dwelling to the south of Lake Titicaca; 2N = 36 ..... *Ctenomys leucodon*  
Dorsal pelage brown to blackish; upper incisors not unusually procumbent (fig. 9, 10) and pale; occurring in the Valles area from the city of Potosí southeastward ..... 7
7. Pelage usually with distinct cinnamon hue; width of an upper incisor greater than 3.3 mm; incisors more procumbent (fig. 9); postorbital process of jugal more anterior (fig. 11); braincases less vaulted (fig. 13); 2N = 56 ..... *Ctenomys lewisi*  
Pelage dark brown; width of an upper incisor less than 3.3; incisors less procumbent (fig.



Figures 2–14

10); postorbital process more posterior (fig. 12); braincase more vaulted (fig. 14); 2N = 52 ..... *Ctenomys frater*

TAXONOMIC SYNOPSIS

Genus *Ctenomys* Blainville, 1826

CONTEXT: Order Rodentia, superfamily Octodontoidea, family Ctenomyidae, in-

cludes five fossil genera but only one living genus, *Ctenomys* (Woods, 1984: 427).

CONTENT: *Ctenomys* includes about 33 recognized living species (Honacki et al., 1982) and some additional subspecies, and reaches its northern limits in Peru, Bolivia, and southern Brazil.

Data on three species of highland Bolivian *Ctenomys* (*C. opimus*, *C. lewisi*, and *C. frater*)

were analyzed separately for males and for females, with weights (in grams) and without weights, by Canonical Discriminant Function Analysis. In all four analyses, 100 percent were correctly classified as to group membership. This merely reinforces our earlier conclusion that every relatively complete specimen from the Bolivian highlands can be readily identified as to species. We have thus far discovered no complications such as we found earlier in lowland populations of *Ctenomys boliviensis* (Anderson et al., 1987).

*Ctenomys frater* Thomas, 1902

*Ctenomys frater frater* Thomas, 1902

*Ctenomys frater* Thomas, 1902: 228 (two from the type locality of Potosí, Bolivia). Neveu-Lemaire and Grandidier, 1911: 14 (Potosí).

*Ctenomys frater frater*: Cabrera, 1961: 548 (Potosí). Anderson, 1985: 14 (name only).

**CHARACTERISTICS:** Because species of *Ctenomys* tend to occupy mutually exclusive geographic ranges, the locality of origin of a specimen when compared with a map of distributions will usually provide an identification. However, many details of distribution remain to be discovered and all identifications should be checked on the basis of the visible morphological characters of the specimen, as outlined in the following notes.

**COMPARISONS:** In comparison with *Ctenomys boliviensis* (of both Bolivian subspecies), *C. frater* (of both Bolivian subspecies) having longer, softer, and darker, blackish, rather than brownish, pelage; throat collar indistinct; tail and hind foot both slightly shorter (relative to head and body length, HBL); skulls not noticeably different in dimensions used in the ratio diagrams (figs. 15 and 16). Based on direct comparison of skulls (of the subspecies *C. f. mordosus*, there being only three skulls of *C. f. frater* and none being available at the moment), *C. frater* smaller than *C. boliviensis*; incisors smaller and perhaps slightly less procumbent; anterior part of nasal seemingly less flattened and less shortened; zygomatic arch with lateral profile, in dorsal view, flattened in middle third rather than evenly, widely, and outwardly bowed; bullae much smaller, less inflated, less projecting, and less exposed posterior to lambdoidal crest; supraorbital process of frontal

small or absent rather than conspicuous, elevated, and continuing posteriorly onto the parietal as a distinct ridge; dorsal profile with concavity in frontal area rather than with concavity absent or slight.

In comparison with *C. conoveri*, *C. frater* having shorter, finer, and blackish, rather than brownish, pelage (figs. 17 and 18); tail, hind foot, and ears longer, relative to the HBL; and palatilar length (PRL) lesser, breadth of dental span (DSB) greater, breadth of palate between closest alveolar margins (PRB) greater, and depth of skull (SKD) lesser, all relative to the condylobasilar length (CRL). Based on direct comparison of skulls, *C. frater* smaller; upper incisors smoothly curved rather than with shallow longitudinal grooving (seen in no Bolivian *Ctenomys* except *C. conoveri*); anterior root of zygomatic arch projecting laterally rather than posterolaterally; supraorbital process small or absent; dorsal process of jugal relatively low and triangular rather than high and with a secondary point; postorbital breadth more than interorbital breadth rather than the reverse; lateral profile of arch in dorsal view slightly curved in medial third rather than sharply curved; mesopterygoid fossa an open V rather than more acuminate; bullae relatively less inflated, especially posteriorly.

In comparison with *C. leucodon*, *C. frater* (both subspecies) having darker, seemingly stiffer, less lax pelage; hind feet more slender; size slightly smaller; tail shorter, relative to HBL; and, relative to the CRL, condyloincisive length (CIL) shorter, tooth row (MXL) longer, and SKD shallower; and DSB/MXL less. Based on direct comparison of skulls, *C. frater* smaller; upper incisors less procumbent, anterior surface orange rather than pale orange or yellowish; anterior margin of zygomatic bridge in dorsal view sloping posterolaterally rather than nearly at right angle to longitudinal axis; dorsal process of jugal not so far posterior, orbit smaller; rostrum tapering but slightly anteriorly, rostral breadth near incisive alveoli broad, relative to size of skull; dorsal profile of skull less vaulted, slightly concave in frontal area, skull not so high; bullar tubes directed laterally rather than a bit more dorsolaterally (as a specialization for life in open places both eyes and ears may be placed high on the head as seen in *altiplano*

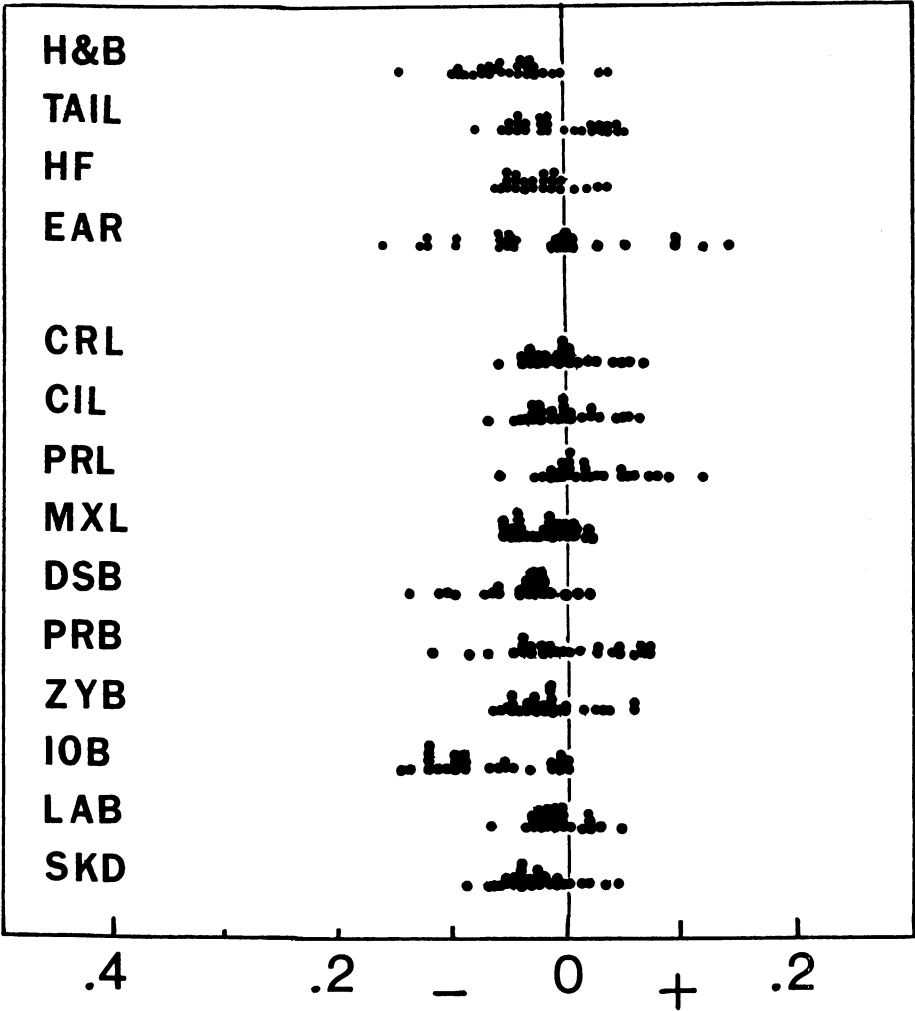


Fig. 15. Ratio diagram showing log differences for measurements of 28 specimens of *Ctenomys opimus* from near Huancaroma in Oruro, the largest series available for any highland tuco tuco in Bolivia. The standard is a specimen of *C. steinbachi* used in our earlier study of lowland *Ctenomys* (Anderson et al., 1987). No very juvenile animals are included in the series, but adults of various ages and of both sexes are included.

dwellers such as *Microcavia niata* and *Galenomys garleppi*).

In comparison with *C. lewisi*, *C. frater* is similar in darkness and color of dorsal pelage, venter less brightly ochraceous; smaller; hind foot smaller, relative to HBL; and (relative to the CRL) DSB, PRB, zygomatic breadth (ZYB), interorbital breadth (IOB), lambdoidal breadth (LAB), SKD, and MXL all greater. Based on direct comparison of skulls, *C. frater* smaller; upper incisors less procumbent, smaller; zygomatic bridge sloping posterolaterally (more than in *C. lewisi* but the

contrast less than between *C. frater* and *C. leucodon*); dorsal jugal process more posterior; bullae small relative to size of skull in both *C. frater* and *C. lewisi*.

In comparison with Bolivian *C. minutus* (which, as noted earlier, may eventually prove to be of some other species), *C. frater* having brownish pelage darker, especially middorsally where almost black; stiff hairs along lateral edge of manus whitish and contrasting with blackish dorsal pelage rather than reddish brown in both places; larger; ears larger relative to HBL; and, relative to CRL, PRL

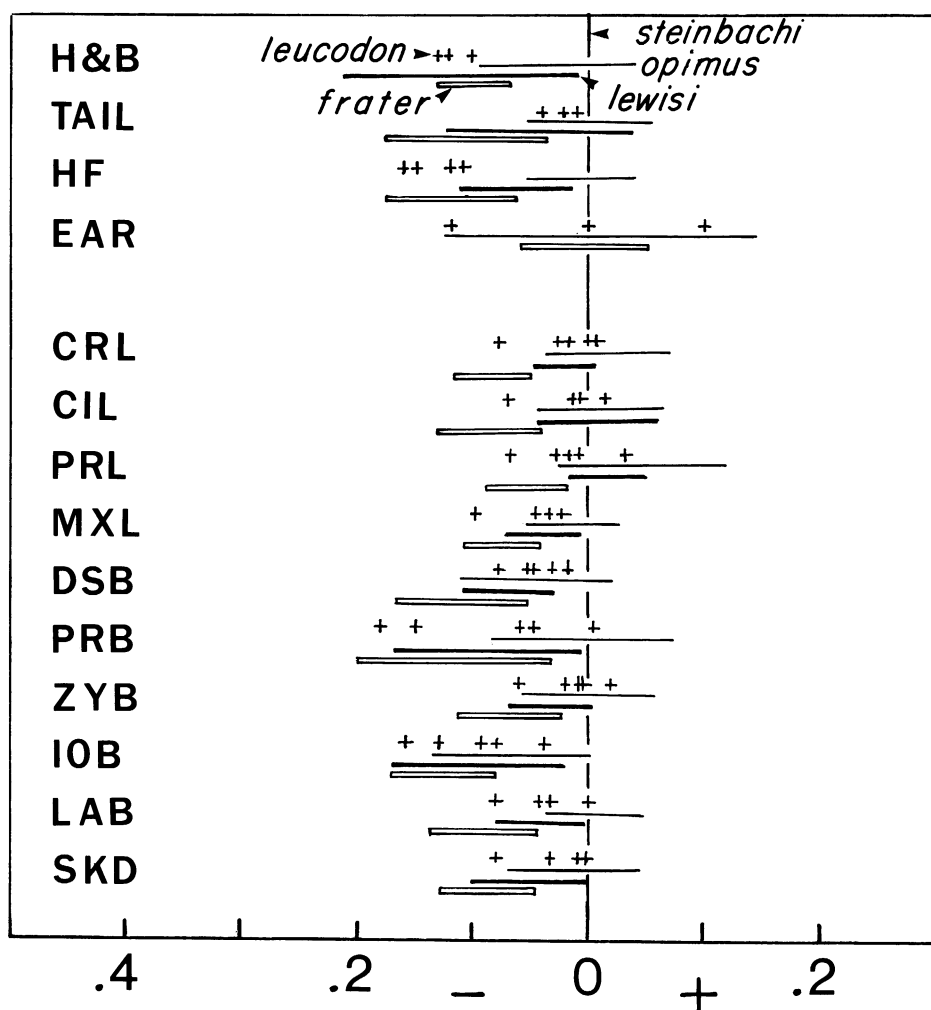


FIG. 16. Ratio diagram showing ranges of values for adults of four Bolivian highland species of *Ctenomys* compared to the same standard used in figure 15. The smallest individual of *Ctenomys opimus* in figure 15 has been omitted. Differences in proportions are discussed in text.

and PRB greater. Based on direct comparison of skulls, *C. frater* larger; rostrum relatively longer; bullae absolutely and relatively smaller.

In comparison with *C. opimus*, *C. frater* having dark brown dorsal pelage, relatively little contrast between the tips, and dark gray rather than tan bases of hairs, and with much contrast between pale tips and darker bases; pelage stiffer and less lax to the touch; size generally smaller; hind foot shorter, relative to HBL. Cranial proportions not very different. Based on direct comparison of skulls, *C. frater* smaller; orbit smaller, jugal process and

supraorbital process less conspicuous, smaller; auditory tube projecting laterally from a lower position on the bulla; bullae and some associated parts of skull smaller, volume estimated as one-fifth that of *C. opimus*, gap between anterior projections of bullae about 3 mm rather than 2 as in *C. opimus*; margin of mesopterygoid fossa a more open, less narrow, V-shape.

In comparison with *C. steinbachi*, *C. frater* having dark brownish rather than black glossy dorsal pelage; venter paler than dorsum but less markedly contrasting; less distinct pale throat collar; tail longer and ears larger, both





FIG. 17. Photographs of study skins in dorsal view of five taxa of *Ctenomys*. From top down, these are: *C. opimus opimus* (AMNH 263031 and 263035, the former with worn pelage), *C. leucodon* (AMNH 263028), *C. lewisi* (AMNH 263015), *C. frater mordosus* (AMNH 263014), and *C. frater frater* (BMNH 2.2.2.112). The scale represents 100 mm.



FIG. 18. Photographs of study skins in ventral view of five taxa of *Ctenomys*. Same specimens and scale shown in figure 17.

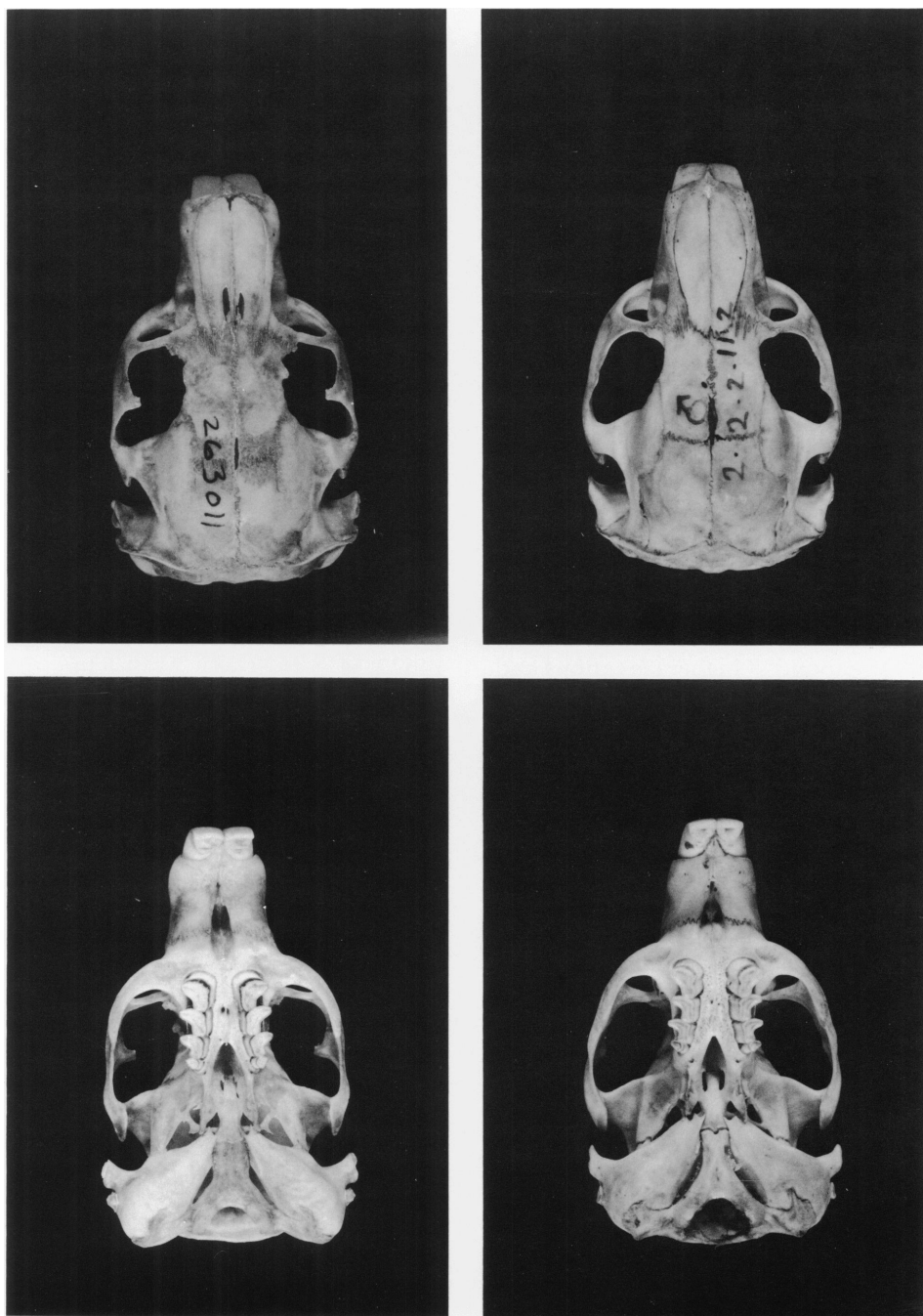


FIG. 19. Dorsal and ventral views of skulls of *Ctenomys frater mordosus* (left, AMNH 263011) and *C. frater frater* (right, BMNH 2.2.2.112). Same scale as figure 20.

relative to HBL; and, relative to CRL, greater PRL, greater PRB, and lesser IOB. Based on direct comparison of skulls, *C. frater* smaller; incisors less procumbent, smaller; nasals nar-

rower, less truncate anteriorly; rostrum not so broad; dorsal process of jugal more posterior, triangular rather than with secondary point; bullae less inflated (fig. 19).

**DISTRIBUTION:** *Ctenomys frater frater* is known only from the department of Potosí (see fig. 1). Cabrera, 1961: 547, recognized five subspecies, three in Argentina and two in Bolivia.

**SPECIMENS,** 3: dept. of Potosí: 1935/6545, Potosí, 2 BM (2.2.2.112 and 113), 1 ANSP (19352).

**REMARKS:** Thomas, 1902, distinguished *C. frater* from *C. opimus* and assigned specimens from [at or near the city of] "Potosí" to both species. In the paper with the original description, Thomas quoted the collector as having caught the specimens of *C. frater* "in ground in moist sand" whereas the specimens of *C. opimus* were taken "in sandy places on ridge" and "in decomposed trachyte soil on ridge." The exact distributions and habitats occupied by the two species near the city need to be studied further. We hypothesize that their precise local distributions will not overlap or be ecologically sympatric and that *C. opimus* will be found at higher elevations and *C. frater* at lower elevations. The identification of one young individual (ANSP 19352) is tentative. The back of the skull with the most diagnostic features of the bullae is missing.

*Ctenomys frater mordosus* Thomas, 1926

*Ctenomys sylvanus*: Thomas, 1925: 580 (Carapari), not of Thomas, 1919.

*Ctenomys sylvanus mordosus* Thomas, 1926: 325 (type locality Tambo, department of Tarija, Bolivia; also cited Melocoton). Rusconi, 1928: 247 (Tambo).

*Ctenomys frater mordosus*: Cabrera, 1961: 548 (Tambo). Anderson, 1985: 14 (name only).

*Ctenomys frater*: Lessa and Cook, 1989: 857 (8 km W of Rancho Tambo).

**CHARACTERISTICS:** Thomas (1926) characterized *C. s. mordosus* as having "size and general external appearance quite as in true *sylvanus*" [from Salta in Argentina, now considered to be a subspecies of *C. frater*] but the incisors were said to be much broader and heavier, "their combined breadth attaining 7 mm. in old specimens as compared with 5.5 mm. in equally aged specimens of *sylvanus*." The rostrum of *mordosus* is thickened, in a manner seen "to a still greater extent in *C. boliviensis*" and in *C. steinbachi*. "An allied species, with equally broad inci-

sors, is the *Ctenomys frater* of Potosí, but that has peculiarly narrowed bullae and is of a decidedly lighter colour." This summarizes relevant information in the literature.

**COMPARISONS:** *Ctenomys frater mordosus* is darker than *C. f. frater*, known from Potosí in a generally higher and drier area to the west. Additional specimens of the latter are needed in order to evaluate possible cranial differences.

**DISTRIBUTION:** *Ctenomys frater mordosus* occurs in Tarija east of the ranges of *Ctenomys frater frater* and of *C. lewisi*, as shown in figure 1.

**SPECIMENS,** 26 (New Mexico karyotype, or NK, numbers and sexes are in parentheses): Tarija: 2127/6419, Rancho Tambo, 61 km by road E of Tarija, 2 AMNH (including NK 14610 F, 14613 and 263014 F); 2127/6423, Tambo, 8 BM, 1 FMNH; 2127/6424, 8 km W of Rancho Tambo, 2 AMNH (263011, 263012), 1 MNLP, 2 MSB (NK 14621 F, 14622 M, 14623 M); 2149/6346, Carapari, 2 BM (Thomas, 1925); 2202/6345, Yacuiba, 2 BM; coordinates uncertain, Melocoton, 6 BM (including 26.1.1.126).

*Ctenomys leucodon* Waterhouse, 1848

*Ctenomys leucodon* Waterhouse, 1848: 281 (type locality San Andres de Machaca, south of Lake Titicaca, department of La Paz, Bolivia). Thomas, 1927: 552 (lectoparatypes). Rusconi, 1928: 239 (La Paz); Anderson, 1985: 14 (name only).

**CHARACTERISTICS:** Extremely proodont, relatively narrow, and pale upper incisors are noteworthy. *Ctenomys leucodon* exhibited a high-pitched whistle vocalization on several occasions. Individuals of this species seemed to spend more time at burrow openings than did other Bolivian tuco tuco. See other comparisons below.

**COMPARISONS:** In comparison with *C. boliviensis*, *C. leucodon* having longer softer pelage; no paler throat collar; plumbeous bases of ventral hairs longer and darker; hind foot shorter and condylobasilar (CRL) greater, relative to the head and body length (HBL); and, relative to CRL, breadth of palate between closest alveolar margins (PRB) narrower. Based on direct comparison of skulls, *C. leucodon* having more procumbent, small-

er, and paler upper incisors; rostrum narrower and more attenuate anteriorly; zygomatic arch and bridge more slender; arch less evenly, widely, and outwardly bowed; supraorbital process present, but process and ridge posterior to it are less conspicuous; lateral tubes of bullae perhaps more dorsolaterally directed; bullae smaller, less inflated.

In comparison with *C. conoveri*, *C. leucodon* having finer pale yellowish brown rather than coarse reddish brown pelage; tail longer, hind foot longer, and CRL greater, all relative to HBL; and, relative to the CRL, palatilar length (PRL) lesser, breadth of dental span (DSB) greater, interorbital breadth (IOB) less, and depth of skull (SKD) less. Based on direct comparison of skulls, *C. leucodon* much smaller; skull generally less massive; incisors more procumbent, narrower, and paler; anterior root of zygomatic arch projecting laterally rather than posterolaterally; outer margin of arch nearly parallel in middle third rather than conspicuously curved there; supraorbital process less conspicuous; bullae less inflated.

In comparison with *C. lewisi*, *C. leucodon* having paler, more yellowish, pelage; tail longer and hind foot shorter relative to HBL and relative to CRL; DSB greater relative to the length of the upper tooth rows (MXL). Based on direct comparison of skulls, *C. leucodon* smaller; incisors more slender and paler, although procumbent in both species; rostrum attenuate anteriorly, narrower; dorsal profile convex rather than concave in frontal area; dorsal process of jugal and supraorbital process more posterior; bullar tubes directed a bit more dorsolaterally rather than laterally; bullae roughly comparable in size, perhaps slightly smaller in relation to size of skull and more attenuate anteriorly in *lewisi*.

In comparison with Bolivian "*C. minutus*," *C. leucodon* having longer, more lax, paler, and more yellowish pelage; size larger; tail longer, hind foot shorter, CRL greater, all relative to HBL; and, relative to CRL, MXL slightly less. Based on direct comparison of skulls, *C. leucodon* much larger; incisors more procumbent and paler; anterior base of zygomatic arch in relation to position of zygomatic bridge more anterior; orbit seems relatively larger, dorsal jugal process more posterior; bullae relatively less inflated.

In comparison with *C. opimus*, *C. leucodon* is similar in color and texture of pelage; smaller; tail longer and hind foot shorter, both relative to HBL; and cranial proportions similar. Based on direct comparison of skulls, *C. leucodon* smaller; skull less massive; rostrum more attenuate, narrower; incisors more proodont, narrower, paler; bullar tubes directed dorsolaterally rather than laterally, but from a lower position on the bulla so that the external ears of both species are probably relatively high on the head; eyes of both seem comparatively large, supraorbital and dorsal jugal processes relatively posterior in position in both species; bullae much less inflated; gap between anterior processes of bullae nearer 3 than 2 mm (fig. 20).

In comparison with *C. steinbachi*, *C. leucodon* having paler reddish brown rather than glossy blackish dorsal pelage, and ochraceous, rather than grizzled, venter; venter not sharply contrasting with sides; no paler collar marking; tail longer, hind feet shorter, and CRL greater, all relative to HBL; and, relative to CRL, MXL less, breadth of palate between closest alveolar margins (PRB) less, and IOB less. Based on direct comparison of skulls, *C. leucodon* smaller, skull less massive, narrower; incisors more proodont, narrower, and paler; rostrum narrower, attenuate; orbit larger, supraorbital and dorsal jugal processes relatively posterior; bullae smaller, less inflated; interorbital area much narrower.

**DISTRIBUTION:** *Ctenomys leucodon* occurs in a relatively small area to the southeast of Lake Titicaca. See figure 1.

**SPECIMENS**, 9: dept. of La Paz: 1613/6827, Chilalaya, 1 BM (1901.6.7.56); 1644/6901, San Andres de Machaca, 4 BM; 1648/6853, 14 km by road SW of San Andres de Machaca, 2 AMNH (including 263028), 1 MSB (NK 14789 M, 14791 F, 14793 F). Department unknown: coordinates unknown, Comauchi, 1 BM.

#### *Ctenomys lewisi* Thomas, 1926

*Ctenomys lewisi* Thomas, 1926: 323 (type locality Sama, 4000 m, department of Tarija, Bolivia). Rusconi, 1928: 247 (Sama). Anderson, 1985: 14 (name only). Lessa and Cook, 1989: 857 (1 km E of Iscayachi).

**CHARACTERISTICS:** Thomas (1926) characterized *C. lewisi* as a large reddish-brown

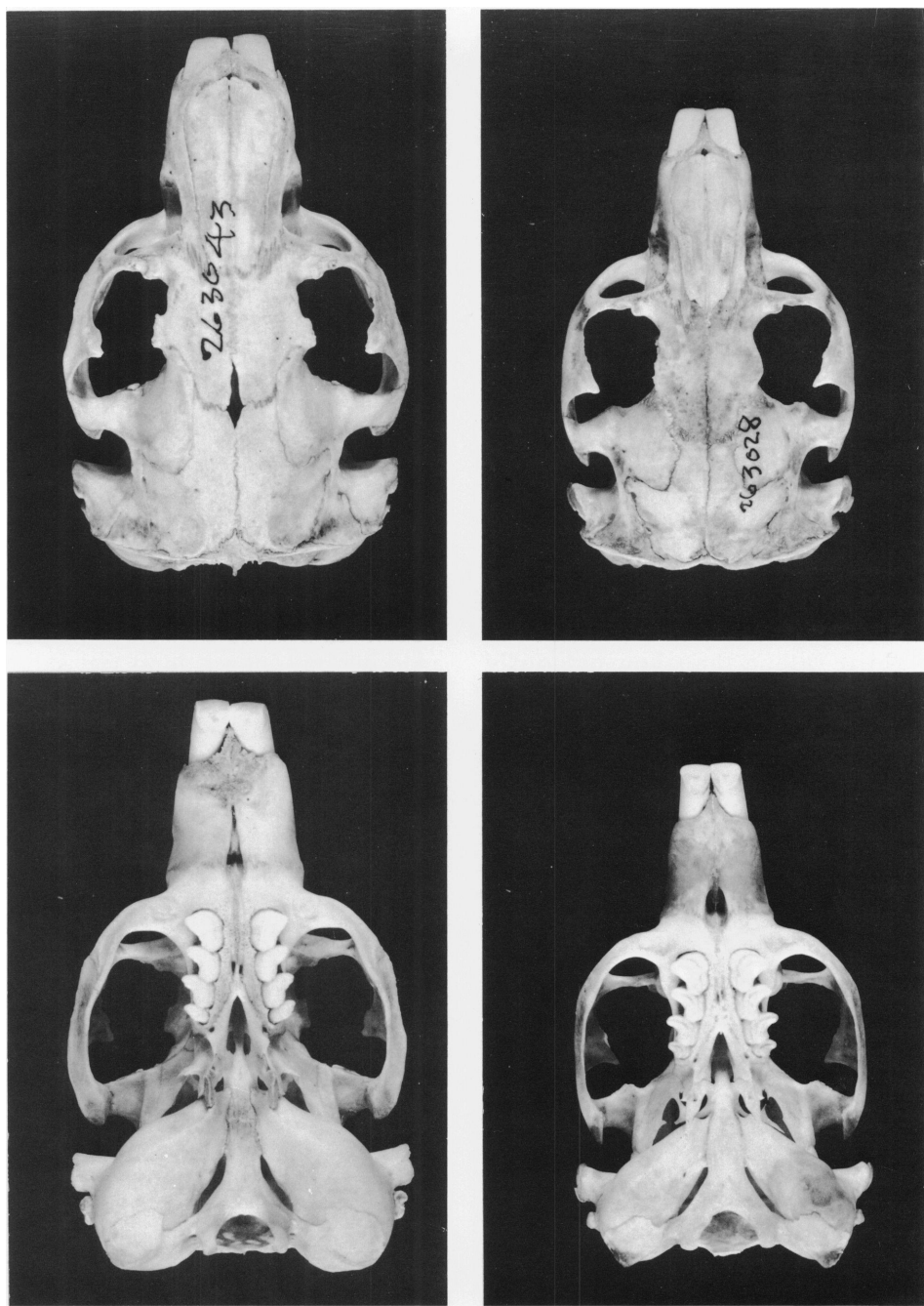


FIG. 20. Dorsal and ventral views of skulls of *Ctenomys opimus* (left, AMNH 263043) and *C. leucodon* (right, AMNH 263028). For scale, the zygomatic breadth of 263043 is 36.5 mm.

species with unusually proodont incisors (see figs. 17 and 18 for illustrations of skins). *Ctenomys leucodon* "has similarly proodont incisors, but these are comparatively slender,

are not so strongly flattened in front, and are almost unpigmented."

Some measurements of the holotype (a young adult male) and of an old female were:



head and body 219, 204; tail 68, 71; hind foot 37, 37; greatest length of skull 52, 50; condyloincisive length 54, 51.5; zygomatic breadth 33, 31; nasals  $17 \times 9.5$ ,  $17 \times 8.8$ ; interorbital breadth 13.5, 12.3; mastoid breadth 29.5, 29.2; breadth across muzzle 14, 12.8; palatilar length 25.8, 25; and combined breadth of incisors 9, 8.

**COMPARISONS:** In comparison with *C. boliviensis*, *C. lewisi* having longer, finer, darker and less reddish dorsal pelage; collar indistinct; plumbeous bases more distinct on ventral pelage; size smaller; tail shorter, relative to head and body length (HBL); and, relative to condylobasilar length (CRL), breadth of dental span (DSB), breadth of palate between closest alveolar margins (PRB), zygomatic breadth (ZYB), and interorbital breadth (IOB) all narrower. Based on direct comparison of skulls, *C. lewisi* having incisors more procumbent and wider; dorsal profile with concavity in frontal area; supraorbital process and ridge extending posteriorly from it less conspicuous; zygomatic arch less massive, less widely bowed; bullae smaller, less inflated (fig. 21).

In comparison with *C. conoveri*, *C. lewisi* having finer, longer, darker dorsal pelage; greater contrast between ochraceous tips and dark gray bases in ventral pelage rather than hairs more or less unicolored and with inconspicuous grayish bases; smaller; tail and hind foot both longer relative to HBL; and, relative to CRL, DSB greater, and palatilar length (PRL), PRB, ZYB, IOB, and depth of skull (SKD) all less. Based on direct comparison of skulls, *C. lewisi* smaller; incisors more procumbent, wider, on the average slightly darker orange; nasals slightly narrower and their anterior margins slightly nearer alveolar margins of incisors; dorsal profile of skull concave in frontal area rather than convex throughout; ratio of interorbital breadth to postorbital breadth at constrictions seems greater; lateral profile of zygomatic arch in dorsal view with greatest curvature in posterior third of arch rather than in middle third; anterior root of arch projecting laterally rather than posterolaterally; supraorbital process small and rounded rather than longer and pointed; bullae smaller, less inflated, especially posteriorly.

In comparison with Bolivian "*C. minu-*

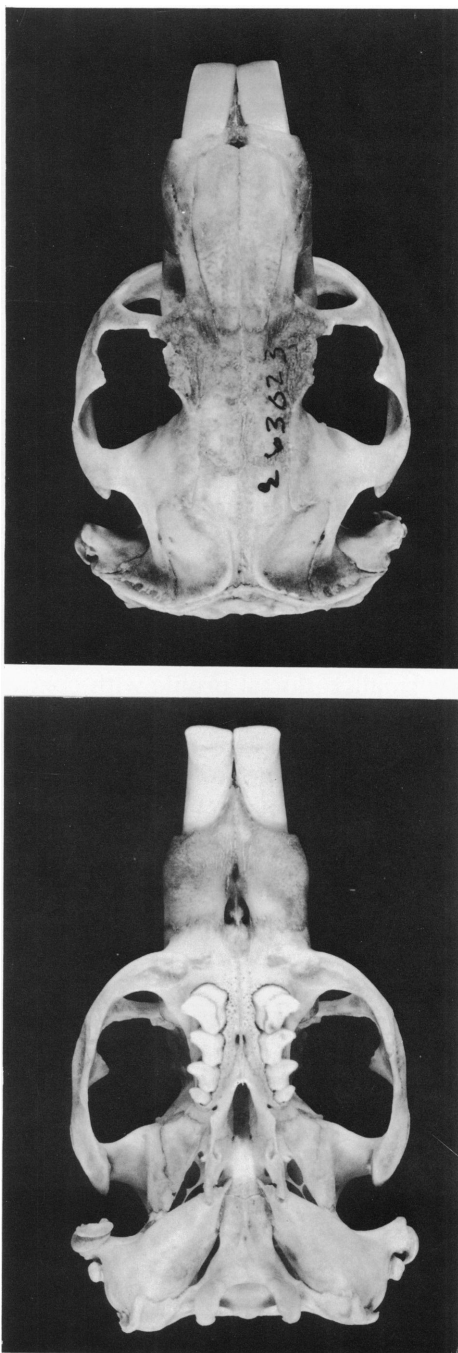


FIG. 21. Dorsal and ventral views of skull of *Ctenomys lewisii* (AMNH 263023). Same scale as figure 20.

*tus*," *C. lewisi* having darker and less reddish dorsal pelage and more ochraceous ventral pelage; larger in general; CRL greater relative

to HBL; and, relative to CRL, having greater PRL, and lesser MXL, DSB, and PRB. Based on direct comparison of skulls, *C. lewisi* much larger; incisors more procumbent, wider, orange in both species; anterior roots of zygomatic arch are, relative to position of bridge, more anterior; bullae relatively less inflated; skull more massive.

In comparison with *C. opimus*, *C. lewisi* much darker dorsally, more ochraceous ventrally; slightly smaller, but cranial proportions not very different.

In comparison with *C. steinbachi*, *C. lewisi* having reddish brown rather than glossy black dorsal pelage; venter not sharply contrasting with sides, venter ochraceous rather than paler and grizzled; indistinct collar on throat; tail shorter (in the non-Iscayachi series), and, relative to the CRL, greater PRL and lesser DSB, PRB, IOB, and SKD. Based on direct comparison of skulls, *C. lewisi* having incisors more procumbent, darker orange, wider; orbits smaller; dorsal profile with concavity in frontal area; anterior margin of mesopterygoid fossa less pointed, fossa wider; bullar tubes lower on bullae; bullae smaller; gap between anterior processes of bullae nearer 3 than 2 mm.

**DISTRIBUTION:** *Ctenomys lewisi* is known only from Tarija, see figure 1.

**SPECIMENS,** 35: Tarija; 2129/6457, 1 km E of Iscayachi, Rio Tomayapo, 13 AMNH (including 263015 and 263023), 1 MNLP, 5 MSB (NK 14650 F, 14651 F, 14652 F, 14653 and 57186 F, 14670 F, 14709 F); 2129/6502, Sama, 13 BM (including 26.1.1.116, the holotype, and 26.1.1.122; Thomas, 1926), 1 KU, 2 FMNH.

**REMARKS:** Semiaquatic habits of *C. lewisi* were suggested by captures in holes in wet stream banks (Thomas, 1926). No such habit has been suggested for any other *Ctenomys*. Some, but not all, of the specimens captured in 1986 near Iscayachi were in damp soil near the river, but there was no indication of a semiaquatic existence.

*Ctenomys opimus opimus* Wagner, 1848

*Ctenomys Brasiliensis*: Waterhouse, 1848: 274, pl. 8, fig. 6 (Potosí), not of Blainville, 1826.

*Ctenomys opimus* Wagner, 1848: 75 (type locality Bolivia, restricted by Thomas, 1900, to Mount Sahama, department of Oruro). Thomas, 1902:

227 (Oruro, Challapata, Pampa Aullaga, Livichuco, and 5 from Potosí). Osgood, 1916: 210 (Oruro). Neveu-Lemaire and Grandidier, 1911: 14 (Sahama). Anderson, 1985: 14 (name only). Lessa and Cook, 1989: 857 (four localities in department of Oruro).

*Ctenomys opimus opimus*: Yepes, 1930: 325 (Potosí, Pampa Aullaga, Livichuco).

**CHARACTERISTICS:** Large tuco tucos; pale yellowish, tending to become darker as tips of hairs wear, sometimes in patches, as on the top of the head; pelage long, soft, lax. *Ctenomys opimus* inhabited burrow systems with *Phyllotis xanthopygus* and *Galea musteloides* at sites near Cruce Ventilla (observations by Cook); and likewise with a murid mouse and a guinea pig, *Auliscomys boliviensis* and *Microcavia niata* respectively, at a site 45 miles distant and on a compass bearing of 123° from Challapata (observations by Anderson). See specific comparisons below, especially with *C. leucodon* and *C. frater*, the two Bolivian species occurring nearest to the large range of *C. opimus*.

The length-to-width ratio tends to be slightly greater in larger skulls, within either sex, and males differ from females (fig. 22) in being larger at a given estimated "age" or stage of development based on a composite length-to-width index ( $= \text{CIL} + \text{CRL}/2/((\text{ZYB} + \text{LAB})/2)$ ); abbreviations under Materials and Methods). Figure 22 compares CRL with the index in the Huancaroma sample of *C. opimus*. Most dimensions show this sexual difference to some degree. Considering external dimensions, based on visual comparisons of graphs, tail length and weight are seen to be clearly different between the sexes whereas head and body length, length of hind foot, and length of ear are not. Among the cranial dimensions, CIL, CRL, palatilar length (PRL), ZYB, LAB, interorbital breadth (IOB), and depth of skull (SKD) are noticeably different, whereas alveolar length of maxillary toothrow (MXL), palatal breadth (PRB), and dental span (DSB) are not.

**COMPARISONS:** In comparison with *C. boliviensis*, *C. opimus* with longer, softer, laxer, paler, more yellowish dorsal pelage and indistinct collar on throat; averaging smaller, and, relative to the condylobasilar length (CRL), having narrower interorbital breadth (IOB), breadth of palate between closest al-



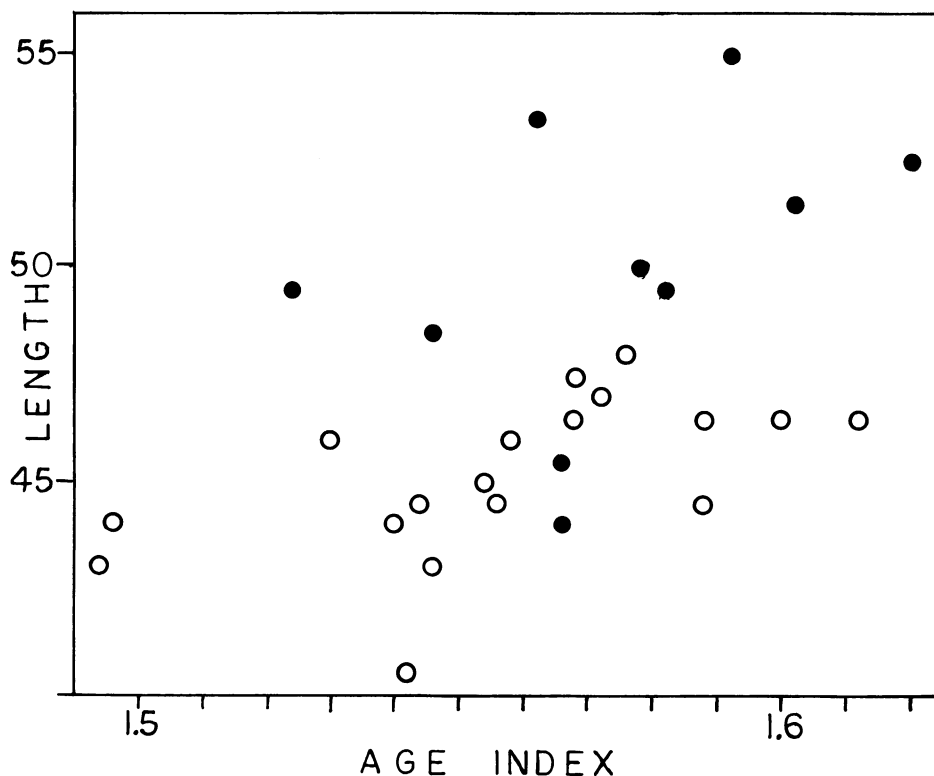


FIG. 22. Graph comparing males (dots) and females (circles) of *Ctenomys opimus* from near Huanacaroma and illustrating the generally larger size (condylobasilar length of skull in this case) in males of a given degree of maturity or age, estimated as described in text.

veolar margins (PRB), and zygomatic breadth (ZYB). Based on direct comparison of skulls, *C. opimus* averaging smaller; incisors narrower, less procumbent, paler orange; nasals and rostrum narrower; zygomatic arches less massive, less widely flaring, bridge relative to position of anterior root more posterior; dorsal process of jugal more posterior; supraorbital process and ridge posterior to it present in both species, but less conspicuous in *opimus*; bullae much larger, lateral tubes placed more dorsally on bullae, gap between anterior processes about 2 rather than 3 or more mm; mesopterygoid fossa more acuminate and with large rather than small fenestrae visible on either side of the anterior basisphenoid suture.

In comparison with *C. conoveri*, *C. opimus* having long, fine, pale yellowish tan pelage with contrasting tips and gray bases of hairs both dorsally and ventrally; smaller; tail longer, hind foot longer, and ear longer, all

relative to HBL; and, relative to CRL, lesser palatilar length (PRL), ZYB, IOB, and greater breadth of dental span (DSB) and lambdoidal breadth (LAB). Based on direct comparison of skulls, *C. opimus* much smaller; breadth at postorbital constriction greater than at interorbital constriction, rather than the reverse; zygomatic arch more evenly bowed rather than with strong curvature of lateral profile in dorsal view of middle of arch; bullae relatively more inflated although inflated in both species; postorbital process conspicuous in both, but less extended in *opimus*; auditory tube relatively dorsal on bullae; anterior root of zygomatic arch projecting laterally rather than posterolaterally; supraoccipital plate more vertical rather than sloping anterodorsally to lambdoidal crest.

In comparison with Bolivian "*C. minutus*," *C. opimus* having paler, longer, laxer pelage; larger; hind foot longer relative to HBL; and, relative to CRL, having smaller

MXL and DSB and longer breadth of palate between closest alveolar margins (PRB). Based on direct comparison of skulls, *C. opimus* much larger; rostrum relatively longer; bullae smaller relative to size of skull.

In comparison with *C. steinbachi*, *C. opimus* without sharp border between venter and sides, and without distinct paler collar on throat; pale brown rather than glossy black; hair longer and softer; averaging smaller in HBL but not in CRL; longer skull, CRL, tail, and HF, relative to HBL; and, relative to CRL, lesser DSB and IOB. Based on direct comparison of skulls, *C. opimus* having rostrum narrower; eyes larger, supraorbital and dorsal jugal processes more posterior; interorbital area narrower; bullae larger; nasals narrower; zygomatic arches more widely bowed.

In comparisons of population samples within the species *C. opimus*, the Sajama series has a relatively longer tail than others, including the Rio Barros series.

Data on six samples of *C. opimus* were analyzed separately for males and females. Samples from six numbered localities used for figure 23 (and numbers of females in each sample) were: 1—near Huancaroma (19), 2—near Esperanza (3), 3—near Oruro (6), 4—near Pomata Ayte (5), 5—near Cruce Ventilla (6), and 6—near ENDE camp (4). The percentages of correctly classified group memberships in an analysis of Canonical Discriminant Functions were: Group 1, 89.5; 2, 66.7; 3, 66.7; 4, 80.0; 5, 83.3; and 6, 100. Sufficient data on males were available for only two of the six geographic samples and the correctly predicted group memberships were: Group 1, 90.9, and 2, 100.

Although there is some geographic variation among local populations of *C. opimus* and the geographically most isolated sample (no. 6) is also the most isolated morphologically (fig. 23), we do not feel that recognition of more than one Bolivian subspecies is warranted at this time. The subspecies *C. o. luteolus* and *C. o. nigriceps*, known, respectively, from Argentina and Peru (following Cabrera, 1961: 554) need to be added to the analysis in order to evaluate the status of subspecies throughout the species' range.

**DISTRIBUTION:** Bolivian records are shown in figure 1. The species is reported to occur

north of Bolivia in Peru and south of Bolivia in Argentina, but we have not studied the specimens upon which these reports are based.

**SPECIMENS, 137:** **Dept. of La Paz:** 1749/6847, Esperanza, near Mt. Sahama, 5 BM, 14 FMNH. **Dept. of Oruro:** 1739/6728, 2.5 km NE of Huancaroma, 1 AMNH, 2 MSB (one karyotyped); 1740/6727, 3.5 km E of Huancaroma, 23 AMNH, 2 MSB (including 55378, NK 11513 F, 11541 F, 11568 M, 14765 F, 14766 F, 14767 M, 14768 F, 14769 F); 1740/6729, Huancaroma, 1 MSB; 1740/6732, 3 km W of Huancaroma, Río Desaguadero, 1 MSB (NK 14776 F, 14777 M, 14782 M); 1741/6731, 11.2 km S and 0.8 km W Eucaliptus, 2 AMNH; 1759/6707, 2 mi E Oruro, 1 MVZ; 1759/6709, Oruro, 9 BM (Thomas, 1902); 1807/6900, Sajama, 2 FMNH; 1819/6759, 5 km W and 1 km N of Pomata Ayte, Río Barros, 7 AMNH (including 263043), 3 MSB (including 57202, NK 14547 M, 14550 F, 14557 M, 14558 F, 14559 F); 1825/6844, 30 km S and 25 km E of Sajama, 2 AMNH, 1 MSB (NK 14542 F, 14546 M); 1854/6647, Challapata, 4 BM (Thomas, 1902); 1908/6607, 7 km S and 4 km E of Cruce Ventilla, 3 AMNH, 2 MSB (including 263031, NK 14740 M, 14745 F, 14747 F, 14748 F); 1908/6607, 7 km S and 3 km E Cruce Ventilla (NK 14750 F, 14751 F); 1908/6607, 6 km S and 4 km E of Cruce Ventilla, 1 MSB; 1910/6625, 45 km distant and on a compass bearing of 123° from Challapata, 2 AMNH; 1911/6705, Pampa Aullaga, 3 BM (Thomas, 1902). **Dept. of Potosí:** 1853/6628, Livichuco, 1 BM (Thomas, 1902); 1935/6545, Potosí, 4 ANSP (19348 to 19351), 5 BM (1902.2.2.99 to 103); 1939/6540, Caricari Mountains, also spelled Karikari, 13 ANSP; 2028/6650, Uyuni, 13 ANSP; 2115/6545, Chocaya, 1 ANSP; 2210/6742, 2 km E of ENDE camp, Laguna Colorado, 3 AMNH, 2 MSB (NK 14571 F, 14572 F, 14573 F, 14583 M); 2210/6745, 7 km E of ENDE camp, Laguna Colorado, 1 AMNH; 2218/6744, 21 km by road SE of ENDE camp, Laguna Colorado, 1 AMNH (NK 14584 F).

**REMARKS:** Waterhouse, 1848: 275, referred to "numerous specimens" brought to England by Mr. Bridges "from the neighborhood of the town of Potosi" and to "others in which the colouring was somewhat richer," the latter comment suggesting the pos-

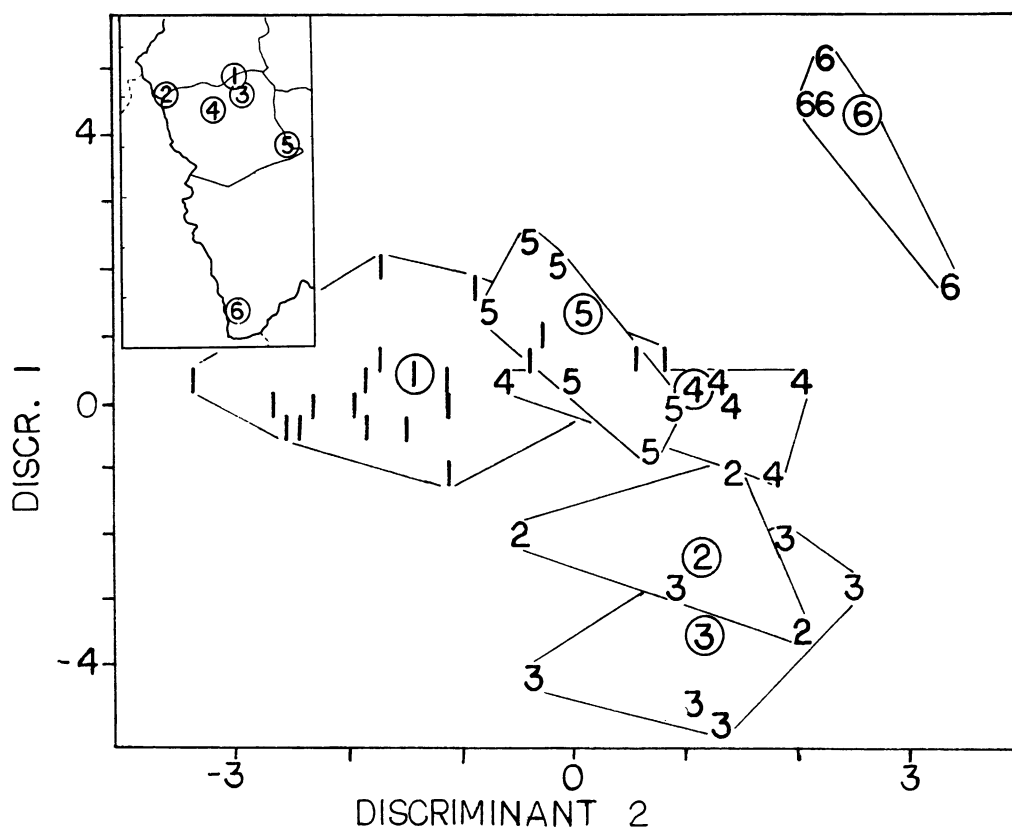


FIG. 23. Graph comparing samples of six different local populations of *Ctenomys opimus* as described in text. Values for individuals are indicated by uncircled numbers and sample centroids by circled numbers. The inset map of southwestern Bolivia shows the six geographic localities represented. The abscissa is the second discriminant function and the ordinate is the first discriminant function, based on analysis of females only.

sibility of *C. frater*. Waterhouse compared the skulls and found "no differences which would lead us to suppose there was more than one species amongst the Potosi specimens." The skull of one of these was figured on plate 8 (fig. 6) and it is clearly *C. opimus* and not *C. frater*. The skulls of these two species are sufficiently different that we suppose Waterhouse would not have made the above statement if both species were present in his sample; however, he did group the specimens from Potosí with specimens (from Maldonado, Uruguay, and elsewhere) that are not now considered to be conspecific. Waterhouse included measurements of four Bolivian specimens (external data on p. 276 and cranial data on p. 284) but cited no catalog numbers. We know of only four specimens of *Ctenomys* in the British Museum (Natural History) ob-

tained by Bridges that came from, or might have come from, the vicinity of the city of Potosí. These are: 45.11.18.6 (this one simply from "Bolivia"), 45.11.18.7, 45.11.18.8 (the skull of which is numbered 45.12.8.2), and a skull with no registry number and with zygomatic breadth of 33.03 mm. We conclude that the four specimens noted are the four that Waterhouse provided measurements for, including the one figured, and that they are *C. opimus*. Waterhouse's measurements are either difficult to equate with ours or are not useful in distinguishing *C. opimus* from *C. frater*, the two species now known to occur at or near the city of Potosí.

NOTES ON *CTENOMYS CONOVERI*, *C. STEINBACHI*, AND "*C. MINUTUS*": Previously unidentified specimens reported earlier (Anderson et al., 1987) from Palo Marcado in

TABLE 1  
Diploid Chromosome Numbers of *Ctenomys*

Country and species	2N
ARGENTINA	
<i>Ctenomys australis</i>	46
<i>Ctenomys azarae</i>	48
<i>Ctenomys latro</i>	42
<i>Ctenomys magellanicus</i>	36
<i>Ctenomys minutus</i>	48, 50
<i>Ctenomys occultus</i>	22
<i>Ctenomys opimus</i>	26
<i>Ctenomys porteousi</i>	48
<i>Ctenomys talarum</i>	46, 48
<i>Ctenomys torquatus</i>	68
<i>Ctenomys tuconax</i>	61
<i>Ctenomys tucumanus</i>	28
<i>Ctenomys haigi</i>	50
BRAZIL	
<i>Ctenomys torquatus</i>	44, 46
<i>Ctenomys minutus</i>	46, 50, 54, 55
<i>Ctenomys flamarioni</i>	48
CHILE	
<i>Ctenomys opimus</i>	26
<i>Ctenomys robustus</i>	26
<i>Ctenomys fulvus</i>	26
<i>Ctenomys maulinus</i>	26
<i>Ctenomys magellanicus</i>	34
URUGUAY	
<i>Ctenomys torquatus</i>	44
<i>Ctenomys pearsoni</i>	56, 64, 70
BOLIVIA	
<i>Ctenomys opimus</i>	26
<i>Ctenomys conoveri</i>	48
<i>Ctenomys steinbachi</i>	10
<i>Ctenomys boliviensis</i>	36, 42, 44, 45, 46
<i>Ctenomys leucodon</i>	36
<i>Ctenomys lewisi</i>	56
<i>Ctenomys frater</i>	52

1) Argentina: Reig and Kibliskey, 1969; Pearson, 1984; Vidal-Rioja, 1985; 2) Brazil: Reig and Kibliskey, 1969; Freitas and Lessa, 1984; Freitas and Travi, 1982; 3) Chile: Gallardo, 1979; 4) Uruguay: Altuna and Lessa, 1985; Freitas and Lessa, 1984; Kibliskey et al., 1977; Novello and Lessa, 1986; 5) Bolivia: Anderson et al., 1987.

Tarija have been identified by Dr. Gerhard Storch, using characterizations given in our paper, as *C. conoveri*. Krumbiegel (1941: 131; quoted by Krieg, 1948: 119) cited specimens from Villa Montes, 21°15'S, 63°30'W, Tarija, under the name *Ctenomys leucodon* that are

*C. conoveri*, based on his description of the animals and on distributional considerations.

The legend of figure 8 in our earlier paper (Anderson et al., 1987) needs clarification. The male sex chromosomes of *Ctenomys steinbachi* were not mislabeled, as stated. The photo of the Y-chromosome is not to the same scale as the other chromosomes shown but is much more enlarged. The Y-chromosome is actually smaller than the X-chromosome.

We wish to stress here that the three small Bolivian specimens from near Roboré previously (Anderson et al., 1987) identified very tentatively as *Ctenomys minutus* are not of that species. Their identity will be dealt with in a later paper.

KARYOLOGICAL RESULTS

**KARYOLOGY:** Nondifferentially stained chromosomes from four nominal highland species, *C. opimus* (N = 29), *C. leucodon* (N = 3), *C. frater* (N = 5), and *C. lewisi* (N = 6) were examined. The diploid number (2N) varies among species (table 1), but intraspecific variation was not found in our samples, except for a questionable situation noted for *C. leucodon*. The number of autosomal arms (FN) range from 48 in *C. opimus* to 78 in *C. frater*.

*Ctenomys opimus:* Individuals from eight localities in Bolivia have a 2N of 26 and an FN of 48 (fig. 24). This karyotype is similar to that reported by Reig and Kibliskey (1969) for specimens collected in Jujuy Province, Argentina, and Gallardo (1979) for specimens collected in Tarapaca Province, Chile. The karyotype consists of three pairs of large metacentric, three pairs of medium metacentric, two pairs of medium subtelocentric, two pairs of small metacentric, and two pairs of small submetacentric autosomes. The morphology of the X-chromosome does not agree with the metacentric condition reported by Reig and Kibliskey (1969), but more closely resembles the submetacentric condition reported by Gallardo (1979). The Y-chromosome is minute and appears to be subtelocentric as reported by the above authors.

*Ctenomys leucodon:* Two females from two localities west of San Andres de Machaca have a 2N of 36 and an FN of 68 (fig. 24). This is

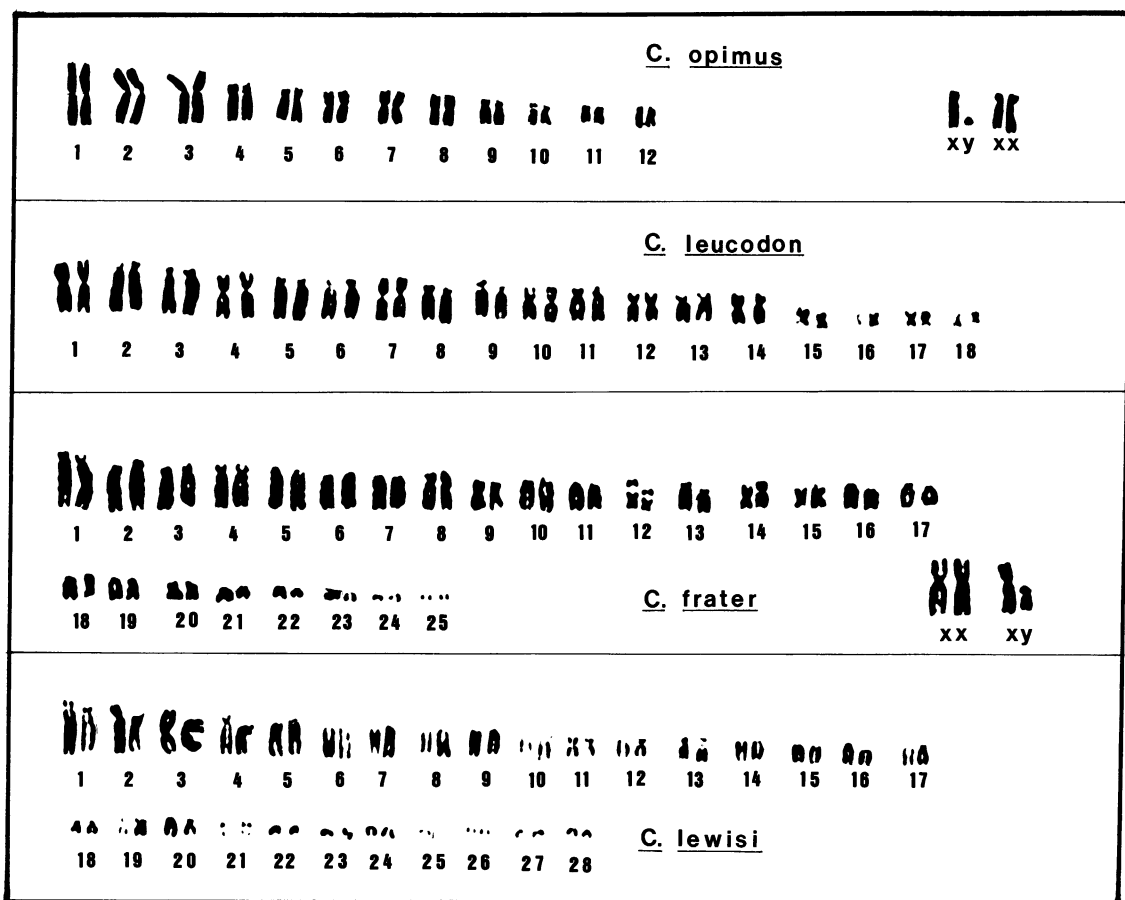


FIG. 24. Karyotypes (top to bottom) of *Ctenomys opimus* (catalog no. MSB 55376, NK 11568, and AMNH 260838, NK 11513, now in the Museo Nacional de Historia Natural in La Paz, for chromosomes of female); *C. leucodon* (AMNH 263028, NK 14793, female); *C. frater mordosus* (AMNH 263011, NK 14622, male; and 263012, NK 14610 for chromosomes of female); and *C. lewisi* (MSB 57186, NK 14653, female).

the first reported karyotype for this species. The karyotype is entirely biarmed with a fairly continuous gradation in size among the large and medium size chromosomes. These include four metacentric pairs and ten submetacentric or subtelocentric pairs. The remaining four small pairs appear to be metacentric. Cells of one male were examined and each of the 11 cells counted had 35 chromosomes. It is unclear whether this is an intraspecific polymorphism or results from variation in the sex chromosomes. Further banding studies and samples from other localities are needed to address this question.

*Ctenomys frater*: Individuals from two localities within the range of the subspecies *C.*

*f. mordosus* have a 2N of 52 and an FN of 78 (fig. 24). This is the first reported karyotype for this species. The autosomal complement comprises two pairs of large subtelocentric chromosomes, 12 pairs of medium to small submetacentric to subtelocentric chromosomes, nine pairs of medium to small acrocentrics, and two pairs of micro or dot chromosomes. The X-chromosome is large and submetacentric and the Y-chromosome is small and submetacentric. Secondary constrictions were noted in chromosome pair 12. The constrictions presumably correspond to regions of nucleolar organization, although silver staining was not conducted.

*Ctenomys lewisi*: Individuals from the type

TABLE 2  
Measurements of Four Species of Bolivian Highland *Ctenomys*

Dim. <sup>a</sup>	<i>C. frater</i>		<i>C. opimus</i>		<i>C. leucodon</i>		<i>C. lewisi</i>	
	26.1.1.126 Male	2.2.2.113 Female	55378 Male	57202 Female	1901.6.7.56 Male	263028 Female	26.1.1.116 Male	26.1.1.122 Female
H & B	192	160	251	201	200	172	150	133
TAI	76	72	89	81	85	79	69	71
HF	35	35	45	41	34	34	37	37
EAR	—	9	11	9	8	4	—	—
WT	—	—	457	280	—	—	—	—
CRL	41.8	40.8	55.2	49.7	47.3	44.4	47.8	45.2
CIL	46.6	45.0	59.3	53.9	52.4	49.4	55.4	50.7
PRL	21.2	21.0	29.2	24.1	23.8	22.9	25.2	24.5
MXL	11.6	10.6	12.4	11.2	11.0	11.5	11.2	11.6
DSB	10.8	10.4	10.2	11.5	10.6	11.4	10.5	9.9
PRB	2.0	2.2	3.0	2.7	2.6	2.3	2.1	2.0
ZYB	28.2	30.7	37.5	33.1	34.2	31.3	32.8	30.8
IOB	10.0	10.5	14.1	12.0	12.3	9.5	12.7	11.9
LAB	27.4	28.2	34.4	31.7	31.5	28.7	29.8	28.9
SKD	15.1	16.4	20.1	18.2	18.3	16.9	17.6	16.9

<sup>a</sup> Dimension. Abbreviations are spelled out in text.

locality have a 2N of 56 and an FN of 74 (fig. 24). This is also the first reported karyotype for this species. All six individuals examined were females so the morphology of the sex chromosomes could not be determined. Four pairs are large and submetacentric to subtelocentric, 7 pairs medium to small and submetacentric to subtelocentric, 3 pairs large and acrocentric, 11 pairs medium to small and acrocentric, and 3 pairs micro chromosomes. *Ctenomys lewisi* and *C. frater* are the only Bolivian *Ctenomys* with microchromosomes although these appear to be common among some of the species of *Ctenomys* with higher diploid numbers (Kiblisky et al., 1977).

DISCUSSION

The genus *Ctenomys*, although found throughout the highlands of Bolivia, generally exhibits a patchy distribution typical of subterranean rodents. *Ctenomys opimus* ranges throughout the altiplano, while *C. leucodon* is restricted to the northern altiplano, and *C. frater* and *C. lewisi* occur in highlands southeast of the altiplano.

The wide geographic range of *C. opimus* is not accompanied by substantial morphometric or chromosomal variation. Analyses

of existing specimens suggest that in *C. opimus* some degree of morphological divergence has occurred among populations, but not to the extent seen in some other subterranean rodents such as North American pocket gophers of the genus *Thomomys* (as reflected by the numerous subspecies mapped by Hall, 1981). The *Ctenomys opimus* specimens used in this study are chromosomally monomorphic in populations from relatively distant parts of the range. Karyotypes of *C. opimus* from Chile (Gallardo, 1979) and Argentina (Reig and Kiblisky, 1969) are similar to those of the Bolivian specimens, except for a possible slight variation in the X-chromosome morphology reported by Reig and Kiblisky (1969).

Ctenomyids are closely related to Octodontidae (including the genera *Octodontomys*, *Octodon*, *Spalacopus*, *Aconaemys*, *Tympanoctomys*, and *Octomys*). Pascual et al. (1965) and others have included *Ctenomys* (as the subfamily Ctenomyinae) in the Octodontidae and placed the other genera in the Octodontinae. Chromosomal variation in the octodontid genera (*Spalacopus cyanus* 2N = 58, *Octodon degus* 2N = 58, *Octodontomys gliroides* 2N = 38) was thought to be less than in *Ctenomys* until recent studies of other octodontids revealed extremely differ-

ent karyotypes in *Tympanoctomys barrae* ( $2N = 102$ ; Contreras and Torres-Mura, 1987) and *Octodon lunatus* ( $2N = 78$ ; Spotorno et al., 1988). Together, the Octodontidae and Ctenomyidae range from 10 in *C. steinbachi* to 102 in *T. barrae*, and thus span nearly the entire range of diploid chromosomal variation known for mammals. The causes of this extreme variation are not clear.

Reig (1970) and Reig et al. (1972) hypothesized that the contrast in population structure between *Ctenomys* and the octodontid genera (e.g., *Spalacopus*) explained the increased chromosomal variability found in tuco tucos. These authors suggested that the subterranean *Ctenomys* have solitary habits and a low capacity for dispersal which has led to reduced gene flow and increased differentiation in this group, while the lack of chromosomal variation in octodontid species was due to increased dispersal and gene flow. It seems clear, with the recently reported karyotypes of *Octodon lunatus* and *T. barrae*, that a difference in population structure between *Ctenomys* and the octodontids is not a sufficient explanation for the karyotypic diversity found in these groups.

Diploid chromosomal numbers among the seven species of Bolivian *Ctenomys* range from 10 in *C. steinbachi* to 56 in *C. lewisi*. Intraspecific chromosomal variation also may be substantial as has been noted for *C. boliviensis* (Anderson et al., 1987), with five chromosomal forms known, although two of these may be distinct species. This amount of intraspecific variation is similar to that found in *Spalax ehrenbergi* (Wahrman et al., 1969, 1985) and *Thomomys bottae* (Patton, 1972; Hafner et al., 1983) complexes.

In general, however, species of *Ctenomys* exhibit less intraspecific chromosomal variation than other subterranean rodents. It is our subjective judgment, based on familiarity with *Thomomys* and other geomyids in North America, that intraspecific morphological variation also is less in *Ctenomys*, and that this difference will not disappear with further taxonomic revision. However, considering the complexity of the situation and our relatively greater ignorance of *Ctenomys*, this judgment is best considered to be a hypothesis for further testing. Chromosomal polymorphisms have been reported for only five *Ctenomys*

species (table 1), but the paucity of reported intraspecific polymorphisms may be due to limited sampling as relatively few species have been examined over wide geographic areas. It is also possible that populations that seem identical based on nondifferentially stained chromosomes will be found to differ structurally when examined using chromosome banding techniques, as has been noted for the subterranean Insectivora (Yates and Moore, in press).

Considerable care must be taken when attempting to draw systematic conclusions from the analysis of standard karyotypes (Baker et al., 1987), however, a few preliminary generalizations may be made from the data now available for Bolivian tuco tucos. Based strictly on diploid number, some species (e.g., *C. boliviensis* and *C. steinbachi*) that are geographically closest to each other do not appear to be sister taxa, while other geographically proximate species (e.g., *C. lewisi* and *C. frater*) are very similar karyotypically. If similarity of diploid number is representative of the history of chromosomal evolution in this group, then the historical biogeography of *Ctenomys* in Bolivia is more complex than a simple lowland/highland dichotomy. Although we had no a priori theoretical basis for predicting elevational or geographic correlations with diploid number, we thought it worth examining whether such correlations were noteworthy in the present case. Correlations are not noteworthy among the seven species that were examined. Low diploid numbers ( $< 30$ ) are found in both the lowlands (*C. steinbachi*) and highlands (*C. opimus*) and the same is true for the higher diploid numbers.

Chromosomal variation among fossorial rodents (see Nevo, 1979; and Patton and Sherwood, 1983, for reviews) has received considerable attention in the literature, however, relatively little is understood about the mechanisms that allow this variation. Recent use of banding techniques has elucidated some of the types of rearrangements that have occurred in *Thomomys* (Patton and Sherwood, 1982; Barros and Patton, 1985), *Geomys* (Qumsiyeh et al., 1988), and *Spalax* (Wahrman et al., 1985). Preliminary G- and C-bands from Bolivian tuco tucos (Cook and Yates, unpubl. data) reveal that substantial changes,

including fission/fusion events and non-Robertsonian rearrangements, have taken place within the Bolivian group. Although the process-level explanations for chromosomal differentiation in subterranean rodents have generally focused on population structure (Patton, 1985) or environmental correlates (Nevo et al., 1988), Sites and Moritz (1987) listed other processes that might be important. Additionally, factors intrinsic to the genome (Greenbaum et al., 1986; Meyne et al., 1989, in press) may have a role in chromosomal evolution.

The extreme chromosomal variation found in *Ctenomys* ( $2N = 10-70$ ), wide geographic distribution, and large number of species provide a prime mammalian example of explosive diversification with rapid rates of evolution as the earliest known fossils of *Ctenomys* are from the Pleistocene (Mones and Castiglioni, 1979; Frailey et al. 1980; Patterson and Wood, 1982). Detailed studies of this genus should provide powerful insights into the processes responsible for extensive chromosomal evolution.

A synthetic and eclectic approach is needed to help resolve the systematic relationships within the Ctenomyidae. In addition to expanded chromosome analyses (including G- and C-band studies) and the morphometric analyses presented in this paper, recent studies of protein electrophoretic variation (Sage et al., 1986), sperm morphology (Feito and Gallardo, 1982; Feito and Barros, 1982; Altuna et al., 1985; Vitullo et al., 1988), and phallic morphology (Altuna and Lessa, 1985) provide data sets that are useful in addressing the systematics of this diverse group. Brooks (1988) reviewed the evidence for phyletic coevolution in host/parasite systems and he and Kluge (1989) concluded that parasites may be used to develop strong hypotheses of host relationships. Phylogenetic relationships of the nematode parasites of the Bolivian tuco tucos have recently been proposed by Gardner (1988) and provide additional testable hypotheses of the host relationships. Due to the wide geographic range and large number of species found in this group, *Ctenomys* may be an excellent model to use in developing hypotheses of both biogeographic and faunal relationships in Bolivia and the southern cone of South America.

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