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Notes on Bolivian Mammals 4: The Genus *Ctenomys* (Rodentia, Ctenomyidae) in the Eastern Lowlands

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ABSTRACT

Tuco tucos (genus *Ctenomys*) of lowland eastern Bolivia are reviewed. Synonymies, references, lists of all known specimens and localities, and new data on morphology and karyology are given for the four species (*C. steinbachi, C. minutus, C. conoveri,* and *C. boliviensis*) present. *Ctenomys boliviensis* displays some morphological variation and considerable karyological variation between localities. Diploid chromosome numbers of *Ctenomys* in lowland Bolivia range from 10 to 48.

RESUMEN

Los tuco tucos (género *Ctenomys*) de las tierras bajas del este de Bolivia son revisados. Sinónimos, referencias, listas de todos los especímenes conocidos, y nuevos datos sobre morfología y cariología son presentados. Cuatro especies (*C. steinbachi, C. minutus, C. conoveri, C. boliviensis*) existen allí y una de ellas (*C. boliviensis*) tiene algunas variaciónes morfológicas y mucha variación cariológica entre lugares. Numeros de cromosomas diploides en tierras bajas de Bolivia varian entre 10 y 48.

INTRODUCTION

Subterranean rodents are well known for their high variability in gross morphology and in chromosomes. Examples include North American pocket gophers (Geomyidae), Old

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TABLE 1
Diploid Chromosome Numbers of *Ctenomys*

Country, species	2N
Argentina (fn. 1)	
C. australis	46
C. azarae	48
C. latro	42
C. magellanicus	36
C. minutus	48, 50
C. occultus	22
C. opimus	26
C. porteousi	48
C. talarum	48
C. torquatus	68
C. tuconax	61
C. tucumanus	28
Brasil (fn. 2)	
C. torquatus	44, 46
Chile (fn. 3)	
C. opimus	26
C. robustus	26
C. fulvus	26
C. maulinus	26
C. magellanicus	34
Paraguay (none)	
Peru (none)	
Uruguay (fn. 4)	
C. torquatus	44
C. pearsoni	56, 64, 70
Bolivia (fn. 5)	
C. conoveri	48
C. steinbachi	10
C. boliviensis	36, 42, 44, 46

(1) Reig and Kiblisky, 1969; (2) Freitas and Lessa, 1984; (3) Gallardo, 1979; (4) Altuna and Lessa, 1985; Freitas and Lessa, 1984; Kiblisky et al., 1977; Novello and Lessa, 1986; (5) this study.

World mole-rats (Spalacinae), and African Bathyergidae.

Although not so well documented, chromosomal variability has also been reported for tuco tucos of the South American caviomorph genus *Ctenomys* (Freitas and Lessa, 1984; Gallardo, 1979; Kiblisky et al., 1977; Reig and Kiblisky, 1969; see table 1). These authors have reported diploid (2N) numbers among species of *Ctenomys* from Argentina, Brazil, and Uruguay ranging from 22 in *C. occultus* to 70 in *C. torquatus.* Except for *C. minutus* and *C. torquatus,* the diploid number within each species has not been found to vary. We report chromosome counts for three species of *Ctenomys* from lowland Bolivia (less than 500 m). No species of *Ctenomys* occurs in both highland (above 500 m) and lowland parts of Bolivia.

Prior to 1986, only five specimens belonging to two species of *Ctenomys* and from three localities in lowland Bolivia were mentioned in the literature. Thirty-three other unreported specimens are located in various museums. Since 1980 we have obtained 62 additional specimens from 20 additional localities (fig. 1) which represent at least four species.

We note morphological differences between these four clearly differentiated species and between populations within the species *C. boliviensis.*

MATERIALS AND METHODS

TAXONOMIC SYNOPSIS: This synopsis is based on a comprehensive review of the literature and examination of museum specimens (by Anderson). Six nominal Bolivian species were reported by Cabrera (1961). Two additional lowland species were included in a recently published list of scientific names (Anderson, 1985) and the specimens vouching for this listing are here reported.

Acronyms for museums used in the lists of specimens are:

AMNH	American Museum of Natural History, New York
BM	British Museum (Natural History), London
CM	Carnegie Museum of Natural History, Pittsburgh
FMNH	Field Museum of Natural History, Chicago
LACM	Los Angeles County Museum
MNLP	Museo Nacional de Historia Natural, La Paz
MSB	Museum of Southwestern Biology, Albuquerque
UMMZ	University of Michigan Museum of Zoology, Ann Arbor
USNM	United States National Museum of Natural History, Washington

In the lists of specimens, the latitude and longitude are given in abbreviated form for each locality, for example, "1647/6314" means 16°47′S and 63°14′W.

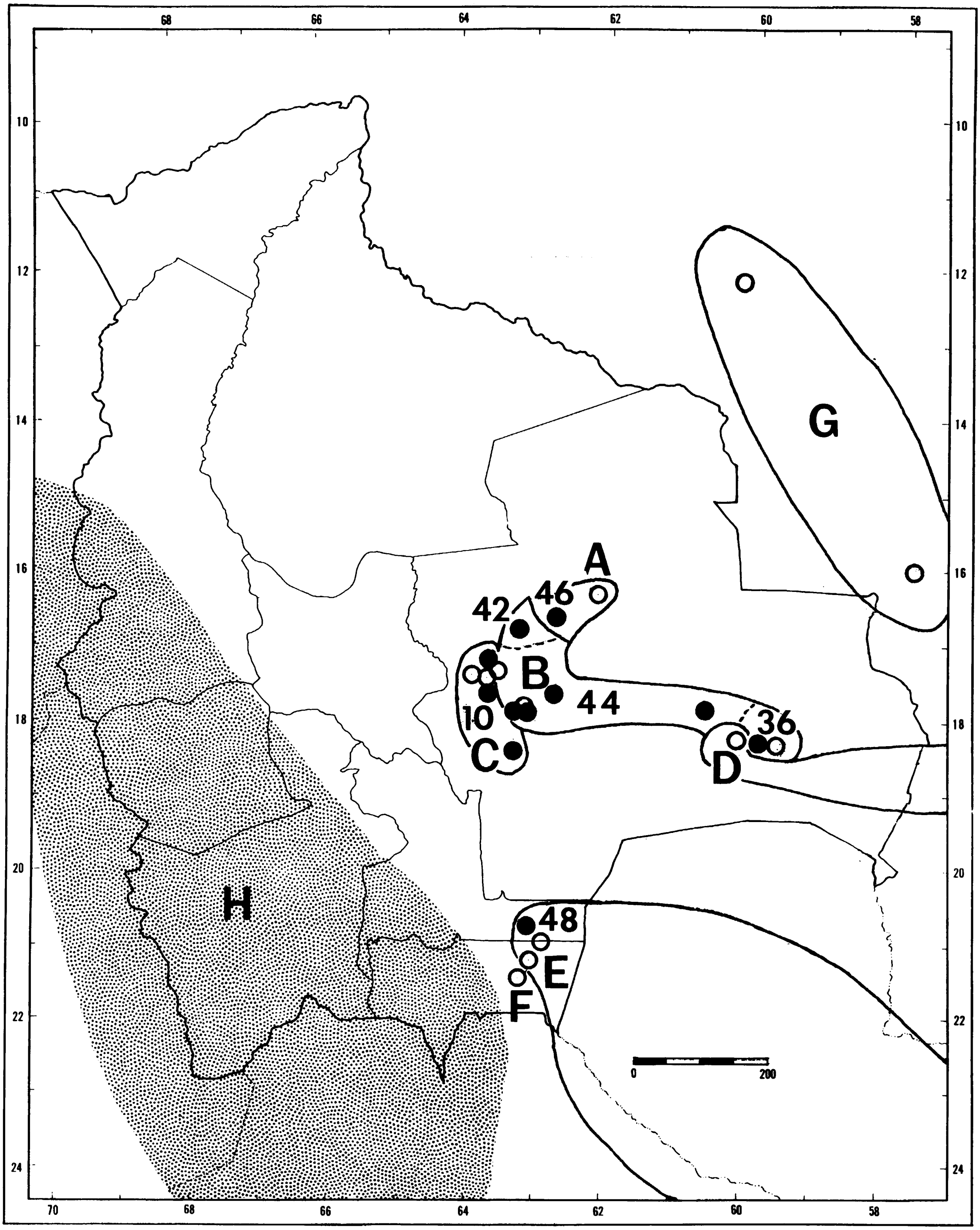

Fig. 1. Map of southeastern Bolivia showing all known localities of specimens of *Ctenomys* from lowland Bolivia. Numerals show diploid chromosome numbers found at localities shown as black dots. Currently recognized taxa are: **A.** *C. boliviensis goodfellowi,* **B.** *C. boliviensis boliviensis,* **C.** *C. steinbachi,* **D.** *C. minutus* ssp.?, **E.** *C. conoveri,* **F.** *C.* sp.?, **G.** *C. nattereri,* and **H.** distribution of highland species of *Ctenomys* to be reported in a later paper. The scale represents 200 km.

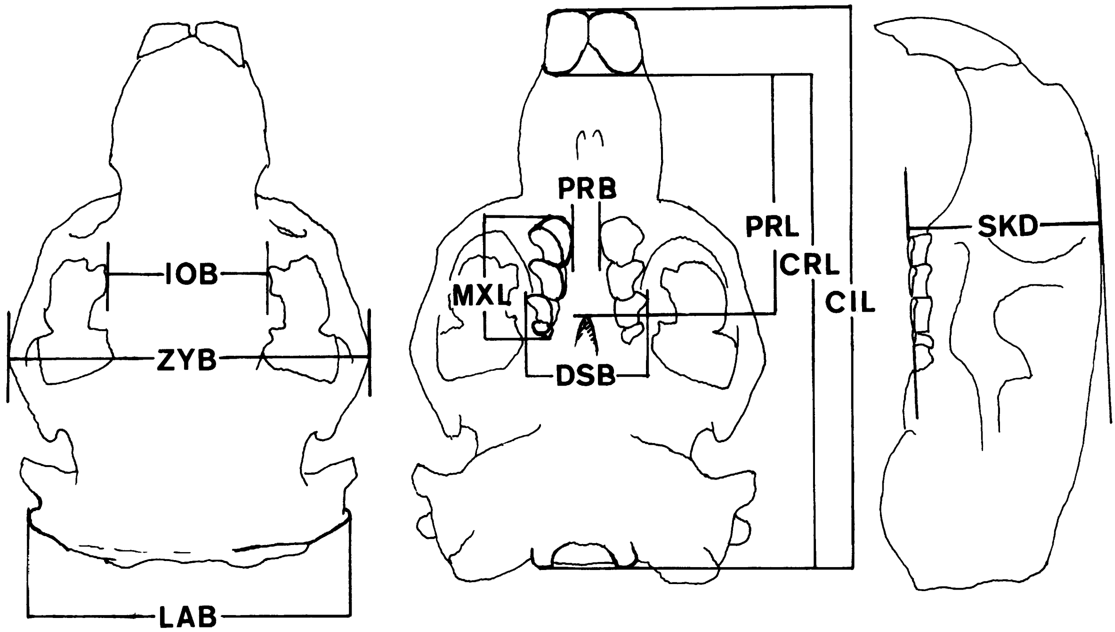

Fig. 2. Cranial dimensions noted in text and used in figure 3 and table 2.

Morphological Analysis: Standard external measurements from fresh specimens and cranial measurements taken with calipers are as follows (all measurements are in millimeters, except weight 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 Condylobasilar length
- CIL Condyloincisive 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

Cranial dimensions measured are shown in figure 2.

Ratio diagrams (see Anderson, 1972: 221, for comments on the method) were drawn in order to visualize ontogenetic changes in proportions by comparing skulls of different ages in the species *C. steinbachi* and *C. boliviensis.* Another ratio diagram compares adults of four species (fig. 3). A specimen of *C. steinbachi* was selected as a standard and one adult specimen of each of three other species was selected for comparison. The horizontal scale is the difference between the standard and the comparative specimen in the common log for each measurement. If the points for a comparative specimen were all equidistant from the points for the standard (so that the connecting lines were parallel), this would show that the two specimens were the same shape and differed only in size. The ratios between any two or more measurements can be directly compared. For example, *C. steinbachi* has a relatively broader interorbital region (IOB) than the other three species, hence the IOB points for these three species, when compared with other measurements in general or individual measurements such as the zygomatic breadth (ZYB, just above IOB in the diagram), are displaced to the left. The IOB/ZYB ratio is greatest in *C. steinbachi.*

The actual measurements of these four specimens and one other specimen for each species are in table 2. The two specimens of *C. minutus* are the only two for which we have measurements. The males of *C. steinbachi* and *C. boliviensis* are the largest specimens we have measured of these species.

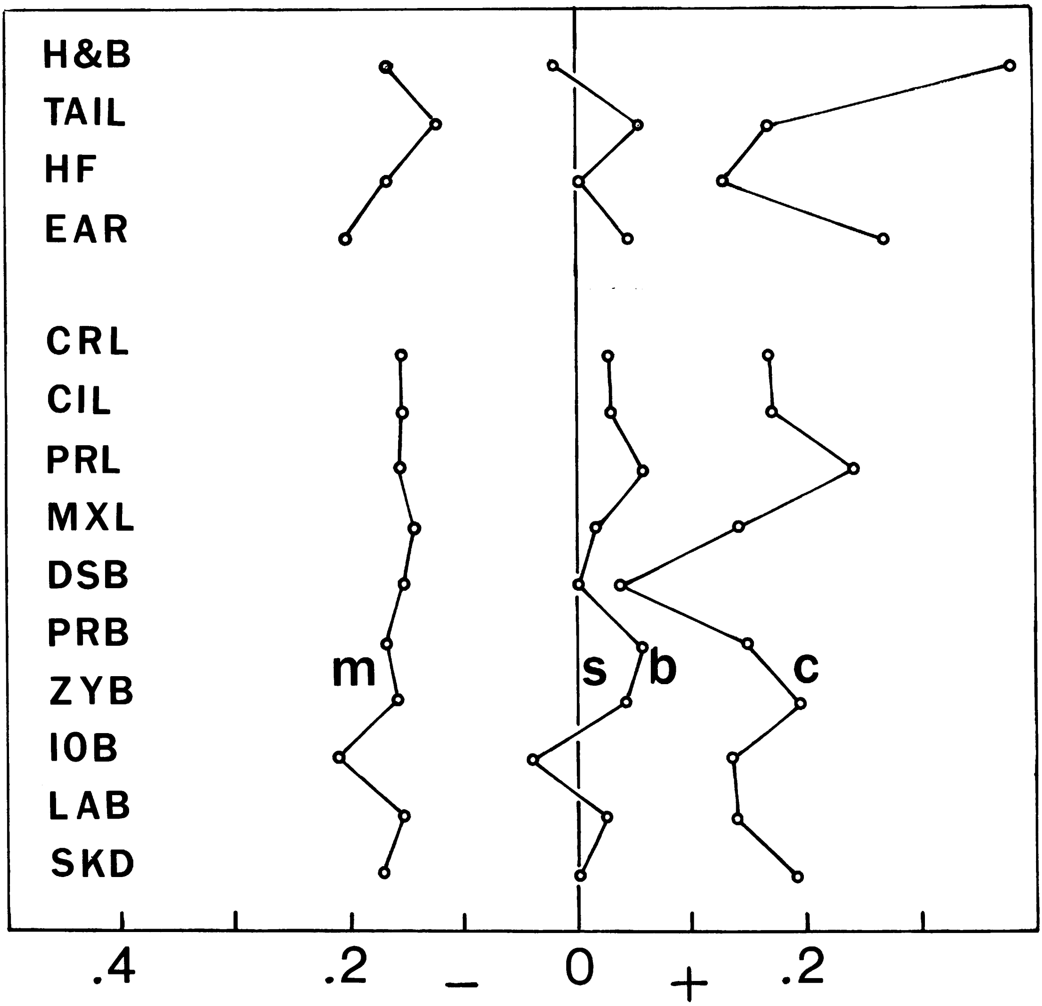

Fig. 3. A ratio diagram showing log differences for measurements of representative specimens of four species of Bolivian *Ctenomys*: **m** = *C. minutus* (AMNH 260835), **s** = *C. steinbachi* (AMNH 260853), **b**, = *C. boliviensis* (AMNH 260801), and **c** = *C. conoveri* (MSB 56088).

The specimens of *C. conoveri* are the largest and the smallest of the four we have measured. Sample sizes of the species are small and if subdivided by age, sex, and locality, samples are usually nonexistent or include only one. In spite of this, it is possible to take nearly any skin or any skull, young or old, and identify its species by comparing it with the illustrations and descriptions provided. In view of this, it seemed unproductive to use further statistical testing in the context of this paper.

SPECIMENS EXAMINED: Sample localities for karyotypes are indicated in figure 1, along with all localities for Bolivian lowland *Ctenomys* known from the literature or from specimens examined by us. All specimens are listed in the taxonomic synopsis and those represented by karyotypic preparations examined for this study are also noted there.

KARYOTYPIC ANALYSIS: Nondifferentially stained karyotypes were prepared from 30 specimens representing three lowland species of Bolivian *Ctenomys* using modifications of techniques described by Baker et al. (1982) and Lee and Elder (1980). Specimens were either injected with 0.01 percent Velban (Eli Lilly and Company) intraperitoneally and sacrificed after 10 minutes or one drop of Velban was added directly to the hypotonic cell suspension. When time permitted, animals were injected subcutaneously with a

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

	C. minutus		*C. steinbachi*		*C. boliviensis*		*C. conoveri*	
Dim.[a]	55367 Male	260835 Female	262297 Female	260853 Male	260804 Male	260801 Female	262291 Male	56088 Male
H&B	141	157	248	231	276	221	265	558
TAI	58	63	102	83	80	95	91	122
HF	30	30	45	44	46	45	54	60
EAR	5	5	8	8	12	9	15	15
WT	79	105	—	360	650	420	520	1200
CRL	29.2	33.3	48.4	47.1	53.8	50.8	53.6	70.0
CIL	31.9	36.0	53.7	51.0	60.1	55.2	—	76.4
PRL	13.8	15.7	24.4	22.3	27.1	25.6	26.6	39.4
MXL	8.0	8.8	12.7	12.2	13.2	12.7	14.0	17.0
DSB	7.1	8.5	11.9	12.0	12.6	12.2	13.0	13.3
PRB	1.9	1.7	2.3	2.5	2.5	2.9	2.8	3.6
ZYB	19.7	22.8	36.3	32.7	41.3	36.4	39.8	51.5
IOB	7.1	8.5	15.3	13.7	13.6	12.5	14.6	18.8
LAB	20.6	22.2	33.4	31.4	34.6	33.8	34.6	43.7
SKD	10.8	12.4	19.7	18.3	21.8	18.7	21.0	28.9

[a] Dimension. Abbreviations are spelled out in text.

suspension of live yeast cells (Lee and Elder, 1980) and sacrificed 24 to 48 hours later. In many cases Velban was not used in this procedure. Cells were incubated in 0.075 M KCl at body temperature (37°C) for 32 minutes. One minute prior to centrifugation, 1 ml of Cornoy's fixative was added to the cell suspension (R. J. Baker, personal commun.). Cell suspensions were fixed three times and one test slide was made and flame dried. The remaining suspension was placed in a Nunc tube, labeled in three places, and frozen in liquid nitrogen. Colored caps were used to distinguish cell suspensions from other samples for quicker sorting in the laboratory. This is desirable because cell suspensions sometimes explode after removal from nitrogen. Cell suspensions were stored by catalog number in wide-mouth liquid nitrogen tanks until processed. Slides are made directly from the suspensions and not refixed. Cells that were mitotically active when frozen tend to rupture when centrifuged. Some animals were karyotyped in the field 30 minutes after death with favorable results.

ACKNOWLEDGMENTS

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TAXONOMIC SYNOPSIS

Genus *Ctenomys* Blainville, 1826
Tuco tuco, topo, tojo, cujuchi

CONTEXT: Order Rodentia, superfamily Octodontoidea, family Ctenomyidae, which

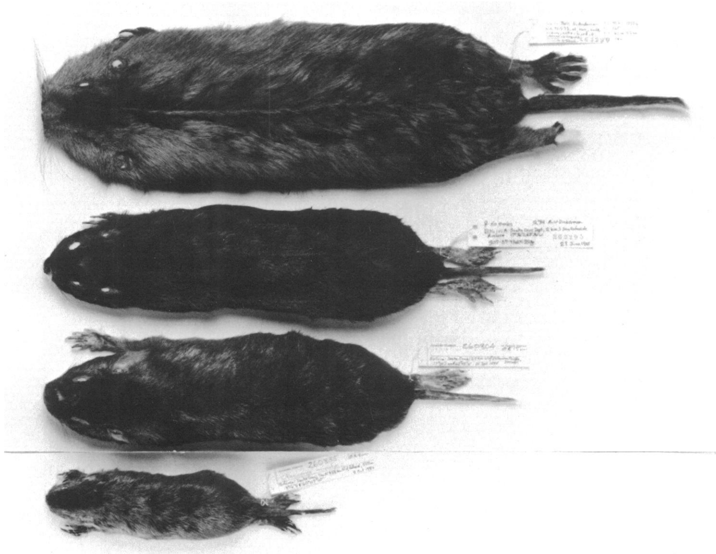

Fig. 4. Photograph of study skins of four species of *Ctenomys*. From top down, these are: *C. conoveri* (AMNH 262290), *C. steinbachi* (AMNH 262295), *C. boliviensis* (AMNH 260804), and *C. minutus* (AMNH 260835).

includes four fossil genera but only one living genus, *Ctenomys*.

CONTENT: *Ctenomys* includes 33 recognized living species (Honacki et al., 1982) some of which are divided into subspecies. *Ctenomys* reaches its northern limits in Peru, Bolivia, and Brazil.

The taxonomy of the four species known from the Bolivian lowlands is summarized here. All known literature references to actual specimens are cited and all known specimens are listed.

Ctenomys boliviensis Waterhouse, 1848

Ctenomys boliviensis boliviensis Waterhouse, 1848

Ctenomys Boliviensis Waterhouse, 1848: 278 (type locality Santa Cruz de la Sierra, Department of Santa Cruz, Bolivia).

Ctenomys boliviensis: Thomas, 1921: 136 (selected lectotype, BM 46.7.28.57); Rusconi, 1928: 238 (Santa Cruz de la Sierra).

Ctenomys boliviensis boliviensis: Cabrera, 1961: 546 (Santa Cruz de la Sierra); Anderson, 1985: 14 (name only).

CHARACTERISTICS: A species of *Ctenomys* of moderately large size (see photos of study skin of adult in figure 4, of skull in figures 5 and 7, comparisons of species in figure 3, and measurements in table 2); pelage reddish brown, with darker areas middorsally, especially on head and nape. Chromosomes are discussed below.

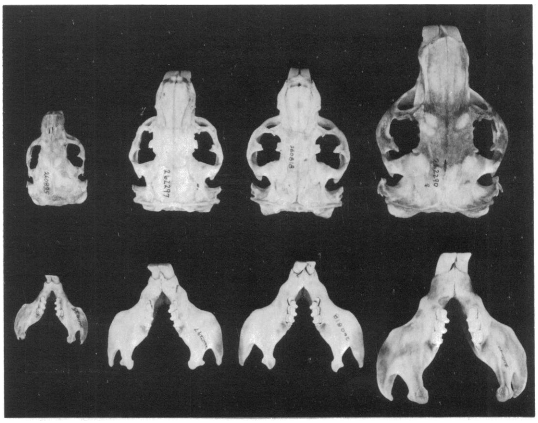

Fig. 5. Crania and mandibles of four species of *Ctenomys* to show relative sizes. From left to right, *C. minutus* (AMNH 260835), *C. steinbachi* (AMNH 262297), *C. boliviensis* (AMNH 260818), and *C. conoveri* (AMNH 262290). For scale, the zygomatic breadth of the largest skull is 50.0 mm.

Fig. 6. Dorsal and ventral views of skulls of *Ctenomys minutus* (left, AMNH 260835) and *C. steinbachi* (right, AMNH 262297).

COMPARISONS: *Ctenomys boliviensis* differs from *C. conoveri* of the Gran Chaco region in being smaller, darker, shorter haired, and in having a relatively (in comparison to head and body length) longer tail and hind foot, and cranially in having relatively lesser palatilar length and relatively greater dental span (fig. 3).

C. boliviensis differs externally from *C. minutus* in being larger and darker and cranially in having smaller bullae (relative to skull size), and greater rugosity and outward bowing of zygomatic arches.

C. boliviensis is roughly the same size as *C. steinbachi* but has more reddish (less blackish) and duller (less glossy) dorsal pelage. *C. boliviensis* differs in ochraceous (rather than mixed or grizzled whitish and blackish) ventral pelage, relatively longer tail, and narrower interorbital, postorbital, and postzygomatic constrictions. Zygomata are widest anteriorly or medially (rather than posteriorly as in *C. steinbachi*, fig. 6).

A comparison of five external and ten cranial measurements of three males and three females (ranging from 188 to 243 mm in H&B) in a ratio diagram revealed no noticeable difference in size or proportions between males and females. The hind foot, tail, and ear (all relative to H&B) are longer in smaller animals. Cranially, there are no major changes in proportions with increasing size.

Morphologically (including color, size, and cranial features), the populations of *C. boliviensis* are closer to each other than to any of the populations we refer to other species. As in North American geomyids, slight differences are usually observable between local populations if several individuals of each are available. Among the populations of *C. b. boliviensis*, three skins from the Estancia Cachuela Esperanza are slightly darker and less ochraceous on the sides than skins from near Santa Cruz but are not different from two skins from near Roboré. Slight differences in darkness are noticeable even between skins from 12 km S of Santa Cruz and those from two nearby localities (8.5 and 10.5 km S of Santa Cruz). The degree of whitish spotting or blotching on venters is variable within a single local sample, but, on average, there is more white on skins from near Estación Pailón than from other samples.

Cranially, as externally, the population samples of *C. boliviensis* are nearer each other than to those of any of the other species. Given the considerable range of sizes (and hence ages) in local samples, it is useful to select pairs of skulls matched by size for comparisons. Among samples of *C. b. boliviensis*, two skulls from near Roboré (AMNH 260817 and 260818 having 2N = 36, compared with 260821 and 260824, respectively, from 22 km SW of Santa Cruz, 2N = 44) have a smaller orbital opening (the supraorbital and dorsomedial processes of zygoma are more anterior); the nasals are relatively broader, shorter, and more flattened and depressed anteriorly; and the premaxillaries as seen in dorsal view are wider and the angularity of the dorsal margin of the infraorbital foramen is more pronounced. The same differences are observed in comparing the two from near Roboré with two individuals from the Estancia Cachuela Esperanza (260802 and 260801, 2N = 42) or with two from near Estación Pailón (260811 and 260806 or 260804, 2N = 44). Three skulls from Estancia Cachuela Esperanza (260802, 260803, and 260801) compared with three matched skulls from near Estación Pailón (260811, 260814, and 260806) have narrower rostra and less pointed supraorbital processes. No differences were observed in comparing the three from near Estancia Cachuela Esperanza with three from near Santa Cruz de la Sierra (2N = 44, 260830, 260826, and 260827), nor in comparing the three from near Estación Pailón with three from near Santa Cruz (260829 replaced 260826 in this sample).

In summary, there are slight differences in coloration and cranial morphology between local samples of *C. boliviensis*. Some samples also have different numbers of chromosomes than others (as noted in the separate section on karyology). The magnitude of the morphological differences is less than the differences distinguishing the four species we recognize from lowland Bolivia. Pending further study, we continue to recognize *C. boliviensis*, with three subspecies (two Bolivian and one Brazilian).

DISTRIBUTION: Inhabits part of the Department of Santa Cruz, Bolivia, and part of the state of Mato Grosso, Brasil (fig. 1); re-

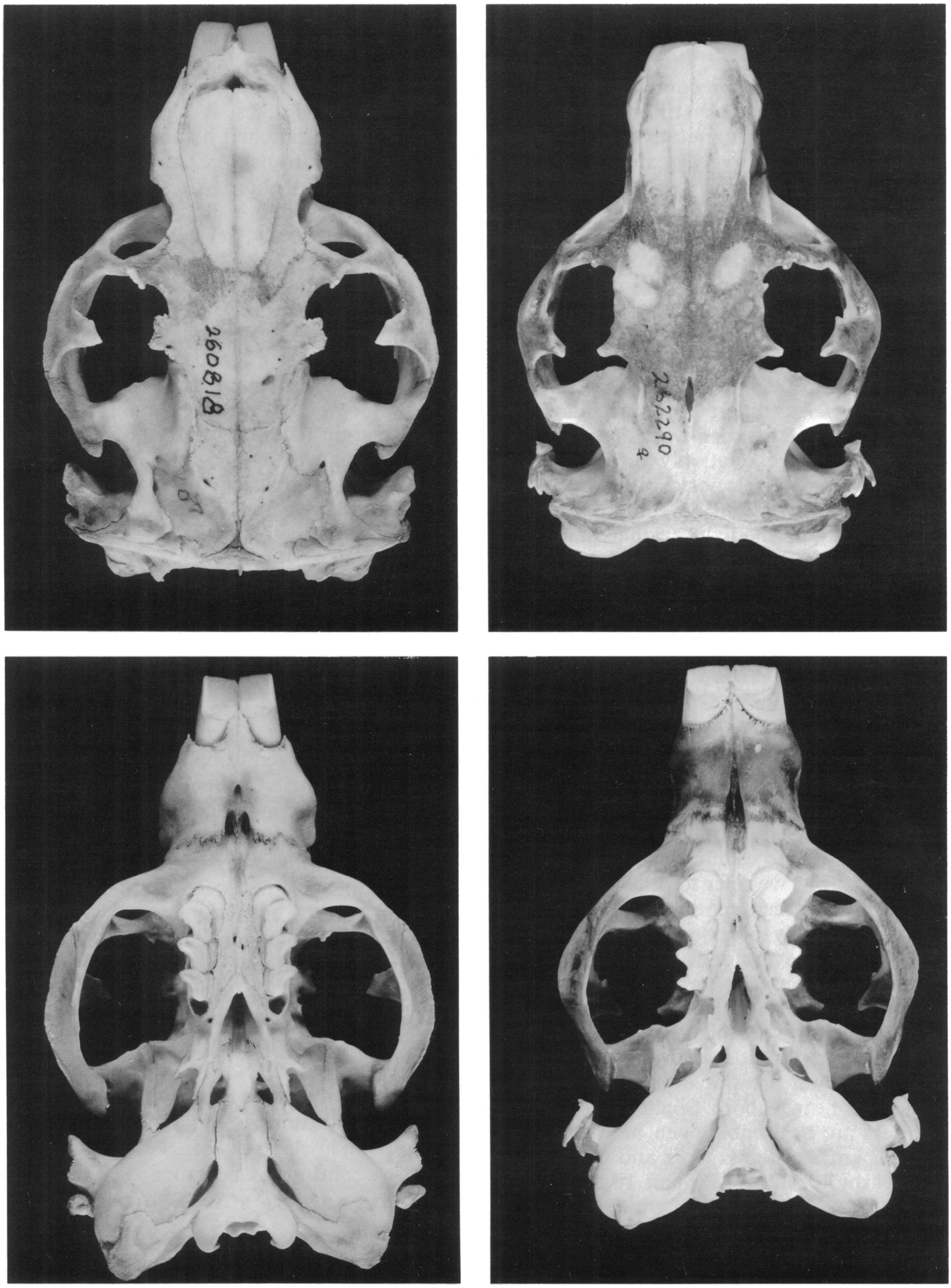

Fig. 7. Dorsal and ventral views of skulls of *Ctenomys boliviensis* (left, AMNH 260818) and *C. conoveri* (right, AMNH 262290).

ported also for northern Argentina (Olrog and Lucero, 1981, specimens not listed).

Specimens, 58 (number karyotyped in parentheses): Department of Santa Cruz: 1647/6314, Estancia Cachuela Esperanza, 3 AMNH, 3 MSB (2); 1723/6332, San Miguel Rincón, 1 AMNH, 1 MSB; 1739/6245, 3.5 km W of Estación Pailón, 12 AMNH, 4 MSB (3); 1748/6310, Santa Cruz de la Sierra, 1 BM (Thomas, 1927), 3 CM; 1752/6031, 4 km S and 24 km E of San José de Chiquitos, 1 MSB (1); 1752/6311, 8.5 km S of Santa Cruz de la Sierra, 1 AMNH, 1 MSB; 1753/6311, 10.5 km S of Santa Cruz de la Sierra, 3 AMNH (1); 1754/6311, 12 km S of Santa Cruz de la Sierra, 5 AMNH, 1 MSB (1); 1755/6319, 22 km SW of Santa Cruz de la Sierra, 4 AMNH, 1 MNLP, 4 MSB (1); 1756/6311, 12 km S and 8 km E of Santa Cruz, 2 AMNH; 1815/5951, 9 km N and 10 km W of Roboré, 2 AMNH, 2 MSB (2); 1819/5934, Santiago, province of Chiquitos, 3 FMNH.

REMARKS: *Ctenomys boliviensis* was the third (see below) species of *Ctenomys* to be described. Tate (1935) summarized the taxonomic history of the genus. Whether Waterhouse's *C. boliviensis* or Wagner's *C. nattereri* was published earlier in 1848 is not clear from the original publications which do not give month and day of publication. We regard *C. boliviensis* and *C. nattereri* as conspecific, and as first revisers (under Article 24 of the International Code of Zoological Nomenclature), select Waterhouse as the first author.

A specimen (AMNH 37121) of *Ctenomys boliviensis nattereri* from Jose Bonefacio, 12°10′S, 60°12′W, in the present state of Rondônia, Brazil, was obtained by Leo E. Miller on the Roosevelt Expedition (Miller, 1918: 238). This specimen differs from most Bolivian specimens referred to *C. boliviensis* in minor ways, the upper incisors are less procumbent, the bullae are larger, the lateral fenestrae of basisphenoid are larger, and the tail is shorter. However, when all of the Bolivian specimens of *C. boliviensis* are considered, this falls within the range of variation.

The original description (Wagner, 1848) of *C. nattereri* (based on two specimens from "Caissora," = Caceres, 16°00′S, 57°45′W, in Mato Grosso, Brazil) does not include comparisons with any *Ctenomys* from lowland Bolivia and does not include any character that distinguishes *C. nattereri* from *C. boliviensis* as now known within Bolivia.

In view of the above, we recognize *Ctenomys boliviensis nattereri* as a subspecies. More specimens are needed to determine whether geographic differences will warrant continued recognition of the presently recognized three subspecies (or possibly additional subspecies or species, as suggested in the discussion of karyotypes).

Ctenomys rondoni Ribeiro, 1914, was treated as a synonym of *C. nattereri* by Cabrera (1961: 553). The type locality of *C. rondoni* is Rio Juruena, Mato Grosso. The head of this river lies at about 14°40′S and 59°10′W and its mouth at about 12°00′S and 58°35′W. We have not been able to ascertain the exact type locality, but it probably is within the area mapped as G in figure 1.

Ctenomys boliviensis was mapped by Olrog and Lucero (1981) in the province of Formosa in northern Argentina, but the specimens upon which the report is based are not known to us. Likewise, they mapped *Ctenomys juris* in the province of Salta adjacent to southern Bolivia. Cabrera (1961: 552) had treated *juris* as a subspecies of *C. mendocinus*. More taxa of *Ctenomys* have been recognized in Argentina than in all other areas occupied by the genus. Revisionary work is needed there in order to assess relationships of Bolivian *Ctenomys*.

Ctenomys boliviensis goodfellowi Thomas, 1921

Ctenomys goodfellowi Thomas, 1921: 136 (type locality Esperanza, near Concepción, province of Nuflo de Chaves, Department of Santa Cruz, Bolivia).

Ctenomys Goodfellowi: Rusconi, 1928: 246 (Esperanza).

Ctenomys boliviensis goodfellowi: Cabrera, 1961: 546 (Esperanza); Anderson, 1985: 14 (name only).

CHARACTERISTICS: The description of *C. goodfellowi* was based on the comparison by Thomas (1921) of one specimen with one of the two cotypes of *C. boliviensis,* so it is possible that most or all of the cranial differences that he noted are examples of individual variation rather than of geographic or taxonomic significance. Thomas wrote that "This tucutucu is no doubt nearly allied to *C. bolivien-*

sis." In 1985, we quadrupled the number of specimens by trapping three at La Laguna, north of San Ramón. Four specimens are still too few to evaluate geographic variation with any precision.

COMPARISONS: Two skulls of *C. boliviensis goodfellowi* (2N = 46, AMNH 262288 and 262289) differed from two matched skulls of *C. b. boliviensis* from near Santa Cruz de la Sierra (2N = 44, 262284 and 260829) in having narrower rostra, narrower interorbital constriction, and less inflated bullae. Two skins of *C. b. goodfellowi* (same two specimens) can be matched closely by two skins of *C. b. boliviensis* from near Santa Cruz de la Sierra (260830 and 260832). *C. goodfellowi* was said to be smaller than *C. boliviensis* and to have a smaller and less heavily ridged skull (even though the specimen of *C. goodfellowi* was thought to be rather older); shorter, narrower, and more parallel-sided nasals; broader interorbital breadth with nearly parallel-sided overhanging ledges; more slender zygomata; shorter orbital fossa with ascending process of jugal almost in center of orbitotemporal fossa rather than nearer its posterior end; bullae smaller; and meatal tube unusually elongated.

Thomas compared *C. goodfellowi* with Ribeiro's *C. rondoni* and *C. bicolor,* but not with Wagner's *C. nattereri.*

DISTRIBUTION: Northern Santa Cruz Department, Bolivia (fig. 1).

Specimens, 4: Department of Santa Cruz: 1615/6204, Esperanza, 1 BM (the type); 1636/6242, 10 km N of San Ramón, 2 AMNH, 1 MSB (3).

Ctenomys conoveri Osgood, 1946

Ctenomys (*Chacomys*) *conoveri* Osgood, 1946: 47 (type locality Colonia Frenheim, 16 km W of Filadelphia, Paraguay, 60°10'W and 22°15'S); Anderson, 1985: 14 (name only).

CHARACTERISTICS: The largest species in the genus *Ctenomys* (measurements of adult in table 2). Pelage relatively long, lax, and shaggy. Dorsal hairs with pale grayish basal part about 10 mm long, then brownish part about 7 mm, then blackish tips. Some longer guard hairs have paler tips. Many hairs are longer than 20 mm. Overall color of dorsum is brown, darker middorsally, especially on head and nape, and around the mouth; venter is paler and more reddish. Hind foot is broad.

COMPARISONS: *Ctenomys conoveri* is much larger than *C. minutus,* has shaggier longer hair, shorter tail and hind foot (these relative to H&B length), and relatively greater palatilar length and lesser dental span (fig. 3).

C. conoveri is also larger than *C. steinbachi,* is brown (rather than blackish) in the dorsal pelage, and is pale brown (rather than grizzled whitish and blackish) ventrally.

DISTRIBUTION: Occurs in the Gran Chaco of northern Paraguay, northeastern Argentina, and southeastern Bolivia. Two skulls (probably both from the Department of Santa Cruz, the label on one mentions the province of Cordillera in that department) were obtained for the Carnegie Museum at different times prior to 1930 by José Steinbach. They seem weathered and probably were found and picked up in the field. The exact localities for these are uncertain. The presence of the species along the northern edge of the Gran Chaco in Santa Cruz is probable but needs confirmation.

Specimens, 8: Department of Chuquisaca: 2046/6300, 9.7 km by road E of Carandayti, 1 AMNH (1); 2045/6313, 9 km by road E of Carandayti, 1 MNLP, 1 MSB (2); 2046/6301, 8 km by road E of Carandayti, 1 AMNH (1); 2058/6251, 30 km SE of Carandaiti (spelling from original field label), 1 LACM. Department of Santa Cruz: 2 CM. Department of Tarija: 2113/6300, 10 km S of Capirenda, 1 LACM.

Ctenomys minutus Nehring, 1887

Ctenomys minutus Nehring, 1887: 47 (type locality campos east of Mondo Novo, Rio Grande do Sul, Brasil); Olds and Anderson, in press.
Ctenomys minimus: Anderson, 1985: 14 (name misspelled).

CHARACTERISTICS: The smallest Bolivian species of the genus. Measurements of linear dimensions (table 2) are about 60–70 percent of those of *C. boliviensis* (which occurs near the Bolivian locality from which *C. minutus* is known). Pale brown dorsally and even paler ventrally.

COMPARISONS: *Ctenomys minutus* differs from *C. steinbachi* in being smaller, reddish tan (rather than blackish) dorsally, and tan (rather than grizzled whitish and blackish) ventrally, in having relatively longer tail (compared with head and body length), and relatively less interorbital breadth. See previous accounts for other comparisons.

DISTRIBUTION: Southern Brasil, eastern Bolivia, and northern Argentina.

Specimens, 3: Department of Santa Cruz: 1816/6007, 7 km N and 38 km W of Roboré, 1 AMNH, 1 MNLP, 1 MSB.

REMARKS: These, the first Bolivian specimens of the species, were obtained in 1984. Because of their small size, they were killed by the Macabee traps used and karyotype preparations were not obtained. Special traps would be useful in obtaining these animals alive.

The wide geographic range, the chromosomal variation (see table 1), and the absence of any critical taxonomic revision suggest that more than one species may be represented. Two subspecies of *C. minutus* were recognized in Brasil by Cabrera (1961). Evaluation of geographic variation awaits more specimens than are available now. For these reasons our assignment of the Bolivian specimens to the species, and not to any previously recognized subspecies, seems to be a reasonable working taxonomic hypothesis, although quite tentative. There are other small *Ctenomys* (*C. sericeus* and *C. pundti*; Olrog and Lucero, 1981) in Argentina, but their known ranges are separated from, rather than contiguous with, the range of *C. minutus.*

Ctenomys steinbachi Thomas, 1907

Ctenomys Steinbachi Thomas, 1907: 164 (type locality campo of province of Sara, near Santa Cruz de la Sierra, Department of Santa Cruz, Bolivia; here restricted as noted in Remarks below); Neveu-Lemaire and Grandidier, 1911: 14 (citing Thomas); Rusconi, 1928: 243 (citing Thomas).

Ctenomys steinbachi: Anderson, 1985: 14 (name only).

CHARACTERISTICS: Blackish dorsal pelage and grizzled or mixed whitish and blackish ventral pelage.

COMPARISONS: A ratio diagram comparing five external and ten cranial measurements of five males and five females (ranging from 139 to 235 mm in length of head and body, H&B) reveals no noticeable difference in size or proportions between males and females. The noticeable differences in proportions are those that occur in mammals generally, the hind feet and to a lesser degree the tail, relative to H&B length, are longer in younger (smaller) animals. Most cranial proportions are relatively constant, in comparison to those of some other rodents, for example. Only two dimensions provide noticeable exceptions. The depth of skull (relative to lambdoidal breadth or to most other measurements), is relatively less in smaller animals. The breadth between the upper molar tooth rows (PRB) changes relatively little with increasing size of skull and is thus relatively less in larger skulls.

DISTRIBUTION: Parts of western Santa Cruz Department in Bolivia (see fig. 1).

Specimens, 41: Department of Santa Cruz: 1713/6338, Campo of province of Sara, 2 BM (Thomas, 1907); 1713/6338, 6 km N of Buen Retiro, 8 AMNH, 1 MNLP, 4 MSB (6); 1724/6351, Río Suruto, 1 CM; 1727/6340, Buenavista, 3 AMNH, 1 ANSP, 9 BM, 2 CM, 4 FMNH, 3 UMMZ; 1736/6336, San Rafael de Amboró, 1 AMNH, 1 MSB (2); 1736/6336, 1 km S of San Rafael de Amboró, 1 AMNH (1); 1737/6336, 2 km S of San Rafael de Amboró, 2 AMNH (2); 1823/6313, 10 km S of Zanja Honda, 1 AMNH, 1 MSB (1).

REMARKS: The type locality "campo of province of Sara" is a large area. In 1907, Sara included what is now divided into the provinces of Santiesteban, Ichilo, and present day Sara. Not all of this area is known to be occupied by *C. steinbachi*; some is known to be occupied by *C. boliviensis.* Therefore, we restrict the type locality to 6 km N of Buen Retiro, 17°13'S, 63°38'W.

Ctenomys sp.?

Specimens, 3: Department of Tarija: 2127/6307, Palo Marcado, 2 Frankfurt (Felten, in litt.). Department unknown: "Bolivia," 1 Frankfurt (Felten, in litt.).

EXTINCT SPECIES OF *CTENOMYS* IN BOLIVIA

Ameghino (1902) described three species of *Ctenomys* from Tarija, *C. subassentiens, C. subquadratus,* and *C. brachyrhinus,* based on incomplete fossil skulls, and allied them with the "grupo *brasiliensis-boliviensis*" rather than with smaller species such as "*Ctenomys magellanicus, lujanensis,* or *Puncti*" or with *C. leucodon* of the altiplano.

Frailey et al. (1980) considered the differences distinguishable in material reported by Ameghino to be the result of individual variation rather than characters of species. These authors redescribed *Ctenomys subassentiens* Ameghino, 1902, a large robust tuco-tuco, with new and more complete material from middle Pleistocene deposits in the Tarija Basin and compared it with nine specimens representing *Ctenomys lewisi, C. sylvanus, C. mendocinus,* and *C. torquatus.* The largest and one of the most robust species of living *Ctenomys* is *C. conoveri,* which has now been compared (by Anderson). *C. subassentiens* differs noticeably from *C. conoveri* in having smaller size (occipitonasal length, 46.6, compared to more than 60 in a large *C. conoveri*), relatively broader rostrum, relatively smaller bullae, and flatter dorsal profile of skull. In all of these characters, *C. subassentiens* has a closer resemblance to *C. boliviensis* than to *C. conoveri.* However, *C. subassentiens* differs from *C. boliviensis* in having a more massive rostrum and relatively broader interorbital region. Both *C. opimus* and *C. steinbachi* have narrower rostra, narrower incisors, and more inflated bullae than *C. boliviensis* and *C. subassentiens. C. subassentiens* seems more closely related to *C. boliviensis* than to any other species of *Ctenomys* with which it has been compared.

KARYOLOGICAL RESULTS

KARYOLOGY: Nondifferentially stained karyotypes from three species, *C. steinbachi* (N = 12), *C. conoveri* (N = 4), and *C. boliviensis* (N = 14) were examined. The diploid number (2N) ranges from 10 in *C. steinbachi* to 48 in *C. conoveri.* The number of autosomal arms (FN) ranges from 16 in *C. steinbachi* to 70 in *C. conoveri.* Intraspecific variation was found only in *C. boliviensis.* The known localities for each cytotype are shown in figure 1.

Ctenomys steinbachi: Specimens from three localities consistently have a 2N of 10 and an FN of 16. The karyotype consists of four pair of metacentric to submetacentric autosomes, a small acrocentric Y-chromosome, and a medium-size subtelocentric X-chromosome (fig. 8). No variation or polymorphism was observed.

Ctenomys conoveri: All specimens had a 2N of 48 (fig. 8) and an FN of 70. Centromere position and size of the autosomes differed markedly when compared to those of *C. boliviensis* and *C. steinbachi* as did the size and morphology of the sex chromosomes. The autosomal complement includes the following pairs of chromosomes: seven pair are large and submetacentric to subtelocentric, one is large and acrocentric, four are medium and submetacentric to subtelocentric, two are medium-size and acrocentric, one is small and submetacentric, and nine are acrocentric. In one pair of small acrocentric chromosomes, each has a secondary constriction. The X- is large and subtelocentric and the Y-chromosome is medium-size and submetacentric.

Ctenomys boliviensis: Eight scattered localities were sampled. Three samples differed from the other five in diploid number or in fundamental number. The easternmost specimens had a 2N of 36 and an FN of 64 (from near Roboré, locality A, fig. 1). Northern individuals (of *Ctenomys boliviensis goodfellowi*) from near San Ramón had a 2N of 46 and an FN of 68 (locality B, fig. 1). Individuals from near the Estancia Cachuela Esperanza to the north of Santa Cruz de la Sierra all had a 2N of 42 and an FN of 64 (locality C, fig. 1). Specimens from all other localities had a 2N of 44 and an FN of 68, except for one individual from 10.5 km S of Santa Cruz de la Sierra which had a 2N of 45.

This initial general pattern of geographic variation needs to be clarified with chromosomal banding data and appropriate outgroup comparisons. Clearly, both numerical and structural differences occur between local populations (fig. 9). Observed differences involve the medium and small autosomes. The three largest elements (one metacentric and two submetacentric/subtelocentric) appear to have been unchanged. Likewise, the large subtelocentric X-chromosomes appear identical among the four karyotypic forms as do the large submetacentric Y-chromosomes. The 44-chromosome form has five pair of chromosomes that are submetacentric to

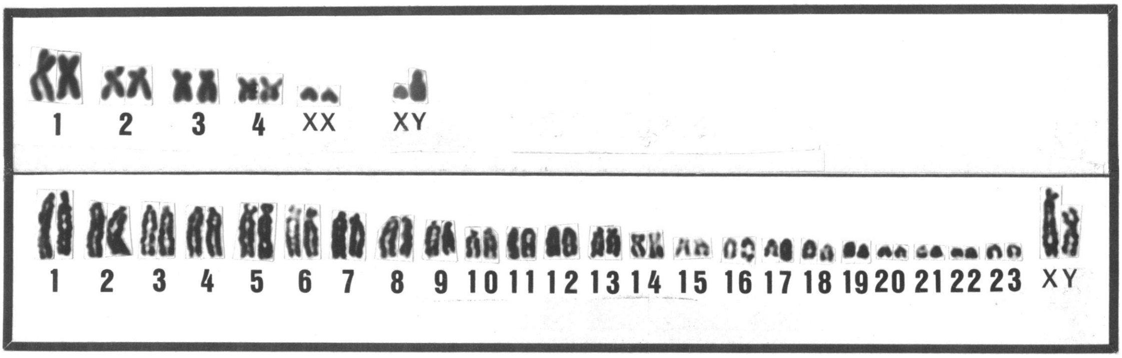

Fig. 8. Karyotypes of *Ctenomys steinbachi* (above) and *C. conoveri* (below). The male sex chromosomes for *C. steinbachi* are mislabeled, the smaller one is the Y-chromosome. The male chromosomes are enlarged more than the female chromosomes.

subtelocentric and three that are acrocentric and of medium size as compared to three and four, respectively (plus one pair that are of medium size and metacentric) for the 42-chromosome form. The former (2N = 44) also has five pair of submetacentric to subtelocentric elements and five pair of acrocentric elements compared to two and four for the 42-chromosome form. The latter (2N = 42) appears to have three small metacentric chromosomes, although the resolution in these smaller elements is not clear. Even if all structural variations in the smaller elements are sufficiently dubious that they should be discounted, the two cytotypes differ by at least one fusion (or fission) and two pericentric inversions or other structural changes. The 46- differs from the 44-chromosome form only in diploid number, having one extra pair of acrocentric elements (fig. 9).

The 42-chromsome form differs from the 36-chromosome form by at least three fission/fusion events (and possibly by other structural changes as well) and in having one less pair of medium-size metacentrics and two pair more of acrocentric chromosomes. In addition, the former (2N = 42) has two less pair of biarmed and four pair more of uniarmed elements than the latter (2N = 36). Standard karyotypes for all four forms are presented in figure 9.

Ctenomys boliviensis may include three or more cryptic species, based on the chromosomal data. Relatively minor differences between local samples are evident. Gross morphological differences that provide consistent phenetic separation of individuals or clearly diagnostic characters are not evident. Further sampling and study are needed to determine whether intergradation or hybridization will be found between local populations with different karyotypes and to define more subtle but distinctive morphological differences.

DISCUSSION

Subterranean rodents in general have high levels of chromosomal variation and polymorphism (Nevo, 1979; Nevo et al., 1986). Diploid numbers for *Ctenomys* range from 10 to 48 in Bolivia and 10 to 70 in South America. This variation spans much of the total diploid number range known for mammals. Although relatively few cytogenetic studies of *Ctenomys* have been published, extensive inter- and intraspecific variation in both diploid number (table 1) and fundamental number has been documented.

Samples of three of the four Bolivian species examined (the fourth is *C. opimus* from the altiplano, to be reported in a subsequent paper) have been found to be homogeneous karyotypically with respect to diploid number; only *C. boliviensis* is heterogeneous. These data are consistent with those reported by other workers for *Ctenomys* (table 1). Our samples are not sufficient from a geographic standpoint to demonstrate that karyotypes are uniform throughout the range of each species but in at least two of the three cases (*C. steinbachi* and *C. opimus*) there is enough evidence to suggest that they may be. Diploid

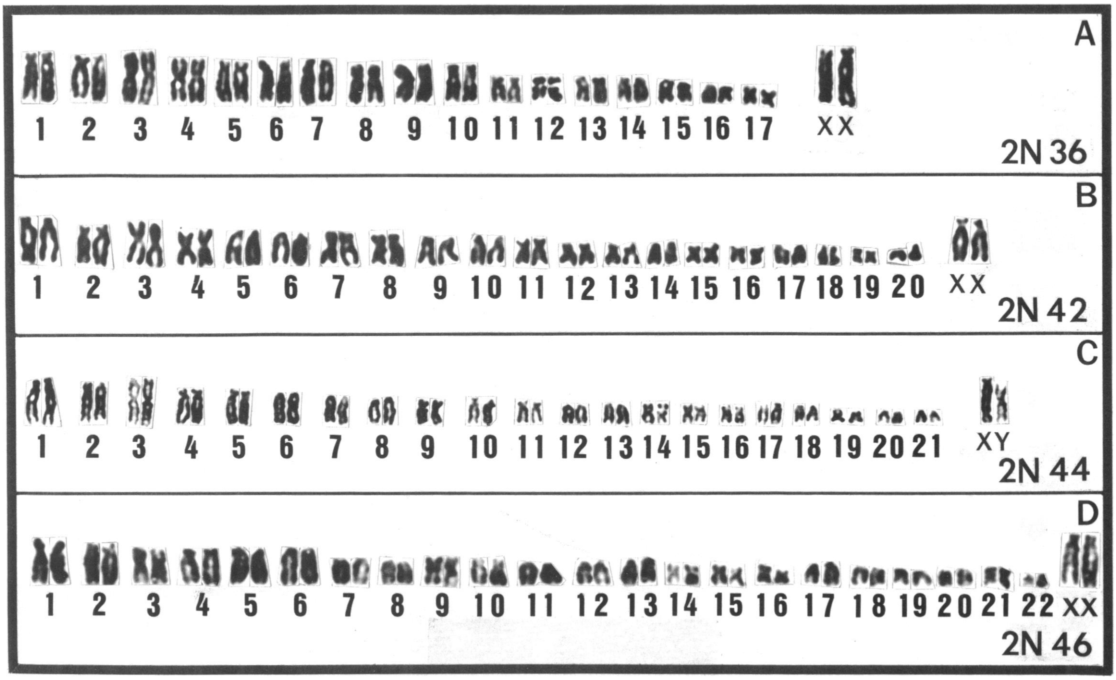

Fig. 9. Four different karyotypes found in populations of *Ctenomys boliviensis* in lowland Bolivia (see fig. 1). Reference numbers of the specimens at MSB are: A. NK 12439, Roboré; B. NK 11808; C. NK 11689; and D. NK 13031.

numbers for samples of *C. steinbachi* from throughout its known range are uniform. Banding data have not been examined in this species, however, and the possibility of additional structural variation at a finer level still needs study. Taxonomic revision using all available characters is needed along with further karyological work. Mares and Ojeda (1982) indicated that the systematic status of most forms is unclear. While some nominal species will on further study probably be reduced to subspecies or synonyms, it is also likely that undescribed species (some morphologically cryptic) are to be found in the genus as well (Sage et al., 1986). Similar situations have been reported for other fossorial rodent genera where zones of contact have been examined (Patton, 1973; Thaeler, 1974; Tucker and Schmidly, 1981; Nevo, 1985).

Analyses of zones of contact within *Ctenomys* should greatly enhance our understanding of variation within and among species. No definite case of sympatry between species is known. One place of relatively close occurrence of two species is near Roboré, between *C. minutus* and *C. boliviensis*. However, these species differ markedly in size, morphology, and habitat, and it is unlikely that they would interbreed. Also, *C. steinbachi* and *C. boliviensis* have been taken within 15 km of each other east of Buenavista. It is also doubtful whether these two would hybridize, considering the large difference in chromosome number and structure. The potential for contact among the various chromosomal forms of *C. boliviensis* seems greater. We have taken 42- and 44-chromosome forms within 40 km of each other. Perhaps some of the chromosomal forms of *C. boliviensis* reported here will not be found to interbreed and will thus represent distinct species while others do interbreed and represent chromosomal races. The finding of one individual 10.5 km S of Santa Cruz de la Sierra with a 2N of 45 suggests that hybridization may be occurring in that region. However, the alternative, that this individual represents local polymorphism, cannot be ruled out at this time.

Despite the apparent taxonomic problems

in the group, sufficient data are available to suggest some initial hypotheses. In *Ctenomys,* taxa with higher diploid numbers seem to have more intraspecific chromosomal variation and polymorphism. Available data suggest that *Ctenomys* species with 26 or fewer chromosomes are less likely to have populations which vary in diploid number than those with more chromosomes. Additional sampling is needed to validate and determine the extent of this pattern. Whether rates of genic mutation or chromosomal breakage are different cannot be determined with data currently available.

Other interesting hypotheses relate to the broader question of what are the phyletic or cladistic relationships among the entire diverse group of species comprising the genus and, at higher levels, among genera of octodontoid rodents generally. The monophyly of *Ctenomys* and relationships within *Ctenomys* need to be tested with appropriate phylogenetic analyses of additional morphological, parasitological, and genetic data. Representatives of the family Octodontidae as well as additional species of *Ctenomys* will need to be included in the analysis. Fossoriality did evolve more than once from different octodontoid rodent lineages, as is evidenced by *Spalacopus* and *Ctenomys.*

Whatever the phylogenetic history of the group, it remains clear that the extent of chromosomal evolution in the genus *Ctenomys* is among the highest known for mammals. In Bolivia as well as other parts of the range of the genus, numerical as well as structural changes within chromosomes have been fixed relatively extensively (and perhaps at a high rate although times of divergence are unknown). Preliminary C-band data from our study and C-band data published for *C. torquatus* (Freitas and Lessa, 1984) and *C. talarum* (Vidal-Rioja, 1985) suggest that relatively little heterochromatin is present in karyotypes of these species. Too few species have been examined using C-bands to generalize these findings to the entire genus.

Probably, much of the variation thus far reported involves euchromatin changes of types theoretically expected to cause severe problems in meiosis. Whether such changes are being fixed by random genetic drift, selection, and/or by somehow avoiding negative heterosis such as is known in the genus *Peromyscus* (Greenbaum et al., 1986) are questions yet to be answered.

Why some groups of animals are highly variable chromosomally and others are not, and what role, if any, the karyotype plays in evolution and speciation are not known. The extensive range of chromosomal variation found in the genus *Ctenomys* may provide an important means of addressing these and other evolutionary questions.

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