Novitates

PUBLISHED BYTHE **AMERICAN** MUSEUM OF **NATURAL HISTORY** CENTRAL PARK WEST AT 79TH STREET. NEW N.Y. YORK. 10024 Number 2935, 22 pp., 10 figs., 2 tables April 20, 1989

Notes on Bolivian Mammals. 5. Taxonomy and Distribution of *Bolomys* (Muridae, Rodentia)

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ABSTRACT

The complex taxonomic history of the genus *Bolomys* Thomas, 1916, is reviewed, the diagnosis of *Bolomys* is revised, and the taxonomy and distribution of the three species now known from Bolivia are summarized. *Bolomys amoenus*, formerly known only from Peru, is reported from two central Bolivian localities at 3875 to 4000 m in

the department of Cochabamba, *B. lactens* of Argentina is now known from one Bolivian locality at 2100 m in Tarija, and *B. lenguarum* is known from dozens of localities mostly in the lowlands (below 500 m) of Beni and Santa Cruz but also up to 2500 m in Santa Cruz.

RESUMEN

La historia taxonomica del género *Bolomys* Thomas, 1916, es revisado, el diagnostico es revisado, y la taxonomia y distribución de las tres especies conocidas hasta ahora de Bolivia son sumarizados. *Bolomys amoenus*, antes conocido solamente en Perú, es descrita en dos localidades centrales de Bolivia de 3875 a 4000 m en el de-

partamento Cochabamba, *B. lactens* de Argentina es conocida ahora en una localidad boliviana a 2100 m en Tarija, y *B. lenguarum* es conocido en muchas localidades mayormente en las tierras bajas (menos de 500 m) de Beni y Santa Cruz, pero también hasta 2500 m en Santa Cruz.

INTRODUCTION

The genus *Bolomys* Thomas, 1916, has a complex taxonomic history, which we here summarize and bring up to date. Until recently (Reig, 1987), there has not been a clear statement of diagnostic characters for the genus with a list of included species, nor an adequate discussion of why *Bolomys* is a genus rather than a subgenus of *Akodon*.

Representatives of B. amoenus and B. lactens discovered in the collections at the

American Museum of Natural History and the British Museum (Natural History) provide the first records of these species from Bolivia.

We document these occurrences, report locality records for Bolivian specimens of the species tentatively identified as *B. lenguarum*, review the previously diagnosed characters of *Bolomys*, and revise the diagnosis of the genus.

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METHODS

We studied specimens of Bolomys and Akodon (listed in the Appendix) from the collections of the American Museum of Natural History in New York (AMNH), the National Museum of Natural History in Washington, D.C. (USNM), the Museum of Southwestern Biology, University of New Mexico, in Albuquerque (MSB), the Field Museum of Natural History in Chicago (FMNH), the Museum of Comparative Zoology at Harvard University in Cambridge (MCZ), the Museum of Vertebrate Zoology at the University of California in Berkeley (MVZ), the University of Michigan Museum of Zoology in Ann Arbor (UMMZ), the Michigan State University Museum of Zoology in East Lansing (MSU), the Carnegie Museum in Pittsburgh (CM), the Academy of Natural Sciences in Philadelphia (ANSP), the California Academy of Sciences in San Francisco (CAS). the Centro Nacional de Enfermadades Tropical in Santa Cruz (CENETROP), the Museo de Historia Natural "Noel Kempff Mercado" in Santa Cruz (MNK), the Museo Nacional de Historia Natural in La Paz (MNLP), and the British Museum (Natural History) in London (BMNH).

ABBREVIATIONS

External measurements (in mm) recorded from specimen labels are:

TL total length
T tail length
HF hind foot length

EAR length of ear from notch

The following dimensions (see Anderson, 1972) were measured to the nearest 0.01 mm with either a craniometer or digital calipers:

ONL occipitonasal length

LRS length of rostrum from anterior tip of nasals to posterior border of zygomatic

notch

BBC breadth of braincase BCH height of braincase

IOC least breadth of interorbital constriction

ZBR greatest breadth of zygomatic arches MAX crown length of the maxillary toothrow

PDB postdental breadth LM1 crown length of the M1

WM1 crown length of the M1 crown width of the M1

WRS width of rostrum

ZYN length of zygomatic notch

PAR length of the parietal bones at their su-

ture at the midline of skull length of the frontal bones at the midline

FRN length of the of the skull

NAS length of the nasal bones at the midline

In comparisons, we have used adults of comparable age when possible, or, when not possible, we have taken age differences into account before drawing conclusions about characters.

Dental terminology follows Reig (1977, 1987).

ACKNOWLEDGMENTS

We thank Drs. Philip Myers and James L. Patton for their help in identifying specimens in the collection at the American Museum of Natural History. Dr. Myers provided a version of an unpublished manuscript for our use.

We acknowledge the staff of the Photography Studio and the Interdepartmental Facilities of the AMNH for the photographs and SEM views.

Some specimens studied were obtained on expeditions supported in part by grants from the National Science Foundation to the AMNH (BSR 83-16740) and to the Museum of Southwestern Biology (BSR 84-08923).

We thank curators of the collections listed under Methods for allowing us to examine specimens in their care.

We thank Drs. M. A. Mares, P. Myers, B. D. Patterson, and R. S. Voss for critically reviewing earlier drafts of this work.

TAXONOMIC HISTORY

Tate (1932: 2) summarized the taxonomic history of the genus *Bolomys* from 1858 to 1926. Some of the history since then was summarized in Honacki et al. (1982: 400). At present, the most detailed and useful summary is included in a broader analysis of the tribe Akodontini by Reig (1987).

Below, we extend the taxonomic history of *Bolomys* since Tate's 1932 work, using the same format he used. We also include several references published prior to 1932 that, according to our current view of the contents of *Bolomys*, pertain to its history.

- 1839. Lund included the names Mus lasiotis and Mus lasiurus in an extract from larger memoirs presented to the Academy in Copenhagen. The names as used here are regarded as nomina nuda as no description was included.
- 1840. The names Mus lasiotus and Mus lasiurus were included in a translation of parts of Lund's memoirs subsequently published in 1841. The names as used here are also regarded as nomina nuda.
- 1841. Lund provided enough descriptive data to validate his names technically, but he did not refer explicitly to any of his specimens and the descriptions are not adequate for a useful diagnosis (the status of these names was not clarified until Langguth reported on Lund's specimens in 1975). The names Mus lasiurus and Mus lasiotis first appear on p. 50, measurements are on p. 280. Mus lasiotis was mistakenly designated type species of Thalpomys by Thomas, 1916; referred to Zygodontomvs by Gyldenstolpe, 1932; and to Bolomys by Reig, 1978 (see References for bibliographic details explaining different dates that have been cited).
- 1897. Allen (p. 38) proposed *Zygodontomys* with type species *Oryzomys cherriei* (now a subspecies of *Z. brevicauda*).
- 1898. Thomas described (p. 271) Akodon lenguarum and compared it with A. obscurus.
- 1916. Allen (p. 528) described Zygodontomys tapirapoanus, from Mato Grosso, Brazil, which extended the range of the genus south of the Amazon River.
- 1932. Glydenstolpe (p. 113) expanded Zygodontomys further by including Mus lasiurus Lund, 1841, Akodon fuscinus Thomas, 1897, and Oryzomys obtusirostris Allen, 1916. (We examined the holotype of the latter and agree with Tate, 1932, that it is a young individual of O. keaysi.)
- 1941. Ellerman (p. 415) reduced *Bolomys* to a subgenus of *Akodon* again and included *A. amoenus*, *A. albiventer*, *A. berlepschii*, *A. lactens*, *A. leucolimnaeus*, *A. negrito*, and *A. orbus*. He allocated other taxa recognized later

- (Honacki et al., 1982) as belonging to Bolomys under the following names: Akodon (Akodon) obscurus lenguarum, A. (Akodon) benefactus, A. (Akodon) lenguarum, A. (Akodon) obscurus, A. (Thalpomys) lasiotis, Zygodontomys fuscinus, Z. lasiurus, and Z. tapirapoanus. The name Z. obtusirostris [=Oryzomys keaysi] was also used.
- 1943. Osgood expressed dissatisfaction with *Bolomys* as then constituted but made no changes in taxonomy.
- 1943. Moojen described *Zygodontomys pix-una* from Crato, Ceará, Brazil, and contrasted it with *Z. lasiurus*.
- 1951. Pearson included *Bolomys* as a subgenus of *Akodon*, with the species *Akodon* (*Bolomys*) amoenus and *A*. (*Bolomys*) berlepschii.
- 1961. Cabrera (p. 444) included in the subgenus Bolomys the species Akodon albiventer, A. amoenus, A. berlepschii, and A. lactens (with subspecies A. l. lactens and A. l. leucolimnaeus). Akodon orbus and A. negrito were considered synonyms of A. l. lactens. Akodon lasiotis was retained in the subgenus Thalpomys and A. benefactus, A. obscurus, and A. lenguarum were retained in the subgenus Akodon as subspecies of A. obscurus. Akodon (Akodon) tapirapoanus tapirapoanus and A. (Akodon) tapirapoanus dayi were recognized. Zygodontomys lasiurus was recognized, with subspecies Z. l. fuscinus, Z. l. lasiurus, and Z. lasiurus pixuna.
- 1962. Hershkovitz (p. 196) regarded all of the members of a "southern group" of Zygodontomys as subspecies of Z. lasiurus except Z. [?lasiurus] tapirapoanus and Z. [?lasiurus] lenguarum. He noted the uncertain status of tapirapoanus and lenguarum and the possibility that they may or may not eventually prove to be conspecific with lasiurus by use of the bracketed comments.
- 1964. Hooper and Musser (p. 36) included the species Z. brevicauda and Z. lasi-urus in Zygodontomys, and noted that in many features of the male repro-

- ductive tract Z. lasiurus resembles Akodon, and Z. brevicauda resembles oryzomyines and, in overall bacular shape, Calomys.
- 1967. Massoia and Fornes proposed the new genus *Cabreramys* (with *C. obscurus* as its type species and with *C. benefactus* and *C. lenguarum* assigned to it).
- 1975. Langguth examined the holotypes of Lund's Mus lasiotis and Mus lasiurus, considered them conspecific, used the name Akodon lasiurus for the species, and suggested that Akodon reinhardti should be designated by the International Commission on Zoological Nomenclature as the type species of the subgenus Thalpomys of Thomas. We do not know that this was ever formally submitted to the Commission or acted upon.
- 1976. Gardner and Patton restricted Zygodontomys to Z. brevicauda in northern South America and so transferred lasiurus from Zygodontomys back to Akodon on the basis of diploid number, lasiurus having 2n = 34 and the brevicauda group 2n = 84-88. They included albiventer (2n = 40) in Bolomys.
- 1978. Reig included in the genus Bolomys the species B. amoenus, B. obscurus, B. lactens (including orbus and negrito as Tate had done, and also leucolimnaeus), B. lasiurus, B. lenguarum (including tapirapoanus), and a Pliocene fossil species B. bonapartei. He did not include albiventer or berlepschii in his list of recognized species of Bolomys. He further included B. brachyurus, B. fuscinus, B. pixuna, and B. arviculoides in B. lasiurus.
- 1978. Pearson and Ralph did not recognize the generic distinction of *Bolomys* and included its type species, *B. amoenus*, in *Akodon*.
- 1978. Mann F. used the name Akodon (Bolomys) berlepschii, but commented on the need for a reevaluation of the phylogenetic status of the subgenus Bolomys.
- 1979. Pine et al. (p. 348) quoted a letter from A. Spotorno stating that *albiventer* and

- berlepschii "are good Akodon s.s. and not Bolomys."
- 1980. Corbet and Hill (p. 151) included in Bolomys, B. albiventer, B. amoenus, B. berlepschii, and B. lactens. They included in Cabreramys, C. benefactus, C. lenguarum, and C. obscurus, and in Zygodontomys, Z. lasiurus.
- 1980. Massoia (p. 179) described Cabreramys temchuki from the Province of Misiones, Argentina, and compared it with C. obscurus. He separated these species on the basis of external characters only. He used the name Cabreramys lasiurus.
- 1981. Maia and Langguth used the names Bolomys lasiurus, B. amoenus, and B. obscurus and noted that they are closely related and "probably belong to a distinct and well defined group at the generic level within the Akodontini"; excluded Akodon arviculoides from Bolomys, although Reig (1978) had regarded it as a synonym of B. lasiurus; and regarded Cabreramys as a junior subjective synonym of Bolomys.
- 1981a. Mares et al. used the name *Bolomys* lenguarum in their list of species possibly occurring in Salta province, Argentina. They also used the name Akodon albiventer, as have other authors since Reig (1978), and thus recognized the exclusion of this species from Bolomys.
- 1981b. Mares et al. used the name *Bolomys* lasiurus in their account of mammals in northeastern Brazil, and listed specimens from the following states: Alagoas, Bahia, Ceará, Minas Gerais, and Pernambuco.
- 1981. Voss and Linzey referred Zygodontomys lasiurus to Akodon and recommended that Zygodontomys be restricted to the brevicauda group on the basis of diploid number (= 84-88 in brevicauda), dentition, and structure of the ventral prostates.
- 1982. Myers used the name Akodon lasiurus, and included A. lenguarum in that species. He also included "Zygodontomys" lasiurus fuscinus and stated that A. lasiurus is closely allied with A. ob-

- scurus from east-central Argentina and Uruguay.
- 1982. Contreras described two new subspecies of *Bolomys temchuki* (B. t. elioi and B. t. liciae) from northeastern Argentina.
- 1982. Honacki et al. (p. 400) recognized Bolomys amoenus, B. lactens, B. lasiurus, B. lenguarum, B. obscurus, and B. temchuki. They noted that "there is no consensus concerning the content of this genus" (p. 401).
- 1985. Anderson used the names *Bolomys* lenguarum and *B. lasiurus lasiurus* in reference to Bolivia.
- 1987. Macêdo and Mares analyzed sexual dimorphism and geographic variation in samples presumed to be Bolomys lasiurus from Brazil, Bolivia, and Paraguay. They recognized (p. 591) two subspecies, B. l. fuscinus from near the mouth of the Amazon, and B. l. lasiurus for all other populations. They did not provide explicit synonymies but did imply the inclusion of arviculoides in B. l. lasiurus, thus following Reig (1978) rather than Maia and Langguth (1981). Diagnostic characters by which Bolomys differs from Akodon or by which B. lasiurus differs from B. lenguarum were not given. Other related taxa, such as B. lactens in Argentina and B. obscurus in Uruguay, were not mentioned, nor were any of the large dark species of Akodon such as A. davi, A. varius, and A. cursor.
- 1987. Reig summarized the history of the Akodontini including *Bolomys*; presented a detailed diagnosis and illustrations; discussed confusion in the literature about *arviculoides* Wagner (= a synonym of *B. lasiurus*, based on study of the holotype); provided a tentative list, with synonyms, of eight recognized species of *Bolomys* (seven extant and one fossil); explained why *Mus lasiotis* Lund, "1838," but not *Thalpomys lasiotis* as used by Thomas, 1916, is a subjective synonym of *Mus lasiurus* Lund, "1837," and *Thalpomys* Thomas, 1916, is a syn-

onym of *Bolomys* Thomas, 1916; and regarded *tapirapoanus* as a probable junior synonym of *B. lenguarum*, a species separate from *B. lasiurus*.

Analysis of Characters:

Reig (1987: 354) listed the following characters as diagnostic for *Bolomys*. His terminology, in quotes, is followed by our comments.

It should be explained that Reig (1987: 364) presented his method of characterizing the Akodontini, and the included genera, as one of "conventional intension" or "defining the intensional meaning of various taxa by commonality of character-states, abjuring the typological claim of exclusive sharing of one or another of all the alternative states of the characters used in defining taxa of the same rank and which belong to the same taxon of immediate higher rank." Taxa thus defined are polythetic (in the sense of Sneath and Sokal, 1973). Thus, Reig did not claim that any one character state was necessarily present in all taxa of a group being characterized. He (p. 395) viewed his presentation as "a set of working hypotheses open to partial or overall modification ... and, therefore, a heuristic framework for further advances in the knowledge of the evolution of these rodents." It is in this spirit that we offer the following analyses. We are examining how the character states are distributed among the species being considered, and, in a sense, specifically searching for synapomorphies. We do this not to be typological, but because we think the presence of such character states, if they exist, would strengthen the hypothesis of monophyly of *Bolomys*. If no synapomorphies exist, that is also interesting taxonomic information.

The primary samples used in the comparisons below (but not the only specimens examined, as noted in the Appendix) were small samples of four to six adults of each of the following taxa: Akodon dayi (from Ayacucho, Santa Cruz), A. toba (from 8 km S and 10 km E of Villa Montes, Tarija), A. varius (from Parotani, Cochabamba), Bolomys amoenus (from the vicinity of Puno, Peru), B. amoenus (from near Rodeo, Cochabamba), B. lactens (from Rancho Tambo, Tarija), B. lenguarum (from Boca del rio Baures, Beni), and B. len-

TABLE 1					
Measurements (in mm) of Samples of Bolomys					
(Minimum and maximum values are given for each dimension))				
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	B. amoenus Peru (n = 5)	B. amoenus Bolivia (n = 4)	B. lactens Bolivia (n = 4)	B. lenguarum (Beni) (n = 6)	B. lenguarum (Santa Cruz) (n = 8)
ONL	24.95–26.01	25.59–26.40	26.31–30.27	28.55-30.49	27.63–29.28
LRS	6.61-7.34	7.30-7.84	7.19-8.45	8.13-8.78	8.00-8.65
BBC	10.98-11.57	11.23-11.69	11.99-12.93	12.16-12.63	11.74-12.81
BCH	8.26-8.71	8.85-8.97	8.85-9.71	8.89-9.83	8.75-9.68
IOC	4.54-4.76	4.52-4.65	4.87-5.61	4.72-5.23	4.60-5.30
ZBR	13.92-15.17	14.44-14.92	14.40-16.84	15.10-16.47	14.30-15.70
MAX	3.93-4.12	3.98-4.21	4.47-4.92	4.43-4.79	4.57-5.05
PDB	2.77-2.98	2.95-3.28	2.79-3.01	3.26-3.89	3.22-3.88
LM1	1.99-2.16	2.80-2.14	2.12-2.58	2.23-2.57	2.25-2.53
WM1	1.14-1.36	1.19-1.33	1.44-1.50	1.25-1.45	1.21-1.42
WRS	4.89-5.13	5.36-5.46	4.90-5.88	5.32-5.88	4.90-5.53
ZYN	1.28-1.55	1.48-1.72	1.44-1.67	1.79-1.99	1.60-2.26
PAR	5.17-5.88	4.74-5.63	4.98-6.10	4.82-5.70	4.56-5.61
FRN	9.02-9.79	9.54-10.35	10.03-11.37	10.26-11.97	10.41-11.23
NAS	7.43-8.41	8.27-8.66	8.25-9.40	9.20-9.90	8.63-9.61
TL	160-165	174–179	172–216	190-212	172-206
T	63–70	71–79	73–86	77–86	70–86
HF	20–22	20–22	23–26	20.5–26	24-26.5
EAR	10–13	12–14	14–19	16–17	15–18

guarum (from San Miguel Rincón, Santa Cruz).

The adults are not of identical age as judged from tooth wear in any one sample except for the Bolivian *B. amoenus* which are all relatively old. Measurements are listed in tables 1 and 2.

"Braincase broad and deep"—We measured breadth of braincase, depth from the suture between the basioccipital and basisphenoid bones to the top of the braincase, and occipitonasal length. Breadth of braincase and depth of skull were plotted against occipitonasal length. There was no noticeable difference in the breadth of braincase to length of skull ratio between these samples, and certainly not between Akodon and Bolomys. The depth of braincase to length of skull ratio was more that 0.33 in B. amoenus, less than 0.33 in A. toba and A. dayi, but A. varius, B. lenguarum, and B. lactens overlapped each other and the 0.33 dividing line. Thus, neither breadth of braincase nor depth of skull is diagnostic (in the restricted sense now being examined) of Bolomys (see fig. 1). This does not eliminate the possibility that other measurements or methods of comparison might exhibit differences. Breadth of braincase, like many other cranial characters, varies with age; it may become greater with age, but as a ratio of total length of skull it becomes less, as is true of muroid rodents in general. In any event, in order to deal scientifically with shape or size, definitions of measurements or other methods of comparison need to be in a form that can be repeated by other investigators with the same results. Problems often arise when direct comparisons seem to show differences that are extremely difficult to quantify or describe.

"Occipital region short" and "truncated"—We found the shape of this region to be too varied in both *Bolomys* and *Akodon* to show clear differences (fig. 2).

"Rostrum rather short and markedly tapering forward in lateral view"—In figure 3 the length of rostrum measured from the posterior margin of the zygomatic notch to the anterior margin of the nasals is plotted against the occipitonasal length of skulls in several samples of Akodon and Bolomys. The specimens representing the three Bolivian species of Bolomys all have a relatively shorter rostrum than the specimens of Akodon. In most of the specimens of Bolomys, the length of the rostrum is less than 30 percent of occip-

TABLE 2

Measurements (in mm) of Samples of Akodon
(Minimum and maximum values are given for each dimension)

	A. varius (n = 5)	A. dayi (n = 6)	A. toba (n = 6)
ONL	26.66–30.01	28.70-30.96	27.33–30.04
LRS	7.99-9.15	8.78-9.56	8.00-9.18
BBC	12.20-12.74	12.20-13.22	11.85-12.49
BCH	8.89-9.75	8.62-9.54	8.33-9.32
IOC	4.81-5.32	4.6-5.15	4.76-5.19
ZBR	14.01-16.04	14.86-15.82	14.28-15.24
MAX	4.50-4.96	4.50-4.80	4.38-4.82
PDB	3.69-4.12	4.03-4.35	3.60-4.13
LM1	2.31-2.55	2.35-2.50	2.15-2.59
WM1	1.27-1.44	1.26-1.41	1.22-1.40
WRS	5.21-5.82	5.05-5.98	5.32-5.66
ZYN	1.47-1.75	1.24-1.73	1.61-1.92
PAR	4.81-5.75	4.36-5.41	4.69-5.47
FRN	8.25-10.00	9.99-11.28	9.58-11.24
NAS	9.75-11.01	10.31-11.14	9.29-10.73
TL	180-222	195-213	193-226
T	75-100	76–90	84-100
HF	23-25	25.5-28.5	22–27
EAR	14–18	16–19	16–20

itonasal length. In most of the specimens of Akodon, the length of the rostrum is more than 30 percent (fig. 3). Then, to examine the "tapering," we drew a diastemal baseline on drawings prepared by us and by Reig (1987) of lateral views of the skulls of Akodon and Bolomys (see fig. 4) and a line (not shown in the figures) through the dorsal profile of the nasals. The acute angle of intersection of this line and the diasternal baseline was then measured. In general, the angle is more than 20° in Bolomys and less than 20° in Akodon. However, in a few specimens the difference is 19° versus 20° and the error of measurement can be this great, the principal difficulty being the placement of the line through the dorsal profile of the nasals. On average, skulls of Bolomys have straighter dorsal profiles than the more bowed profiles of Akodon.

"Upper profile of skull gradually sloping forward from the middle of parietals"—If the skull is oriented so that the highest point is the middle of the parietals, it is always true that the profile gradually slopes forward and downward, although this slope is not uniform nor is it noticeably different between *Bolomys* and *Akodon*. We drew a baseline through the tip of upper incisors and ventralmost point

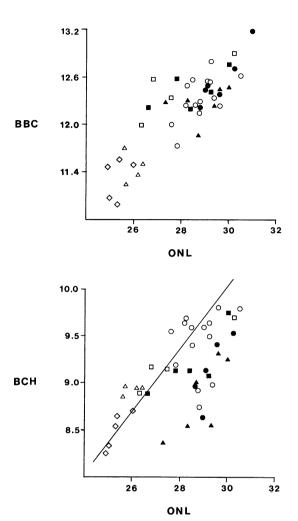


Fig. 1. Graphs contrasting the breadth of braincase (BBC, top) and depth of braincase (BCH, bottom) to the occipitonasal length (ONL) in species of *Bolomys* (open symbols) and *Akodon* (closed symbols). *Bolomys amoenus* from Peru (♦), *B. amoenus* from Bolivia (△), *B. lactens* from Bolivia (□), *B. lenguarum* from Bolivia (○), *Akodon dayi* from Bolivia (●), *A. varius* from Bolivia (■), and *A. toba* from Bolivia (▲). Line on bottom plot represents one-third of ONL. See Appendix for specimens and localities.

on bulla on a series of drawings of Reig (1987) and on our own drawings, and we did not find that the highest point from this baseline was in the middle of the parietals. It was generally near the back of the frontal bone in both Akodon and Bolomys. This character is not useable as stated or as measured here.

"Nasals short, with anterior border well

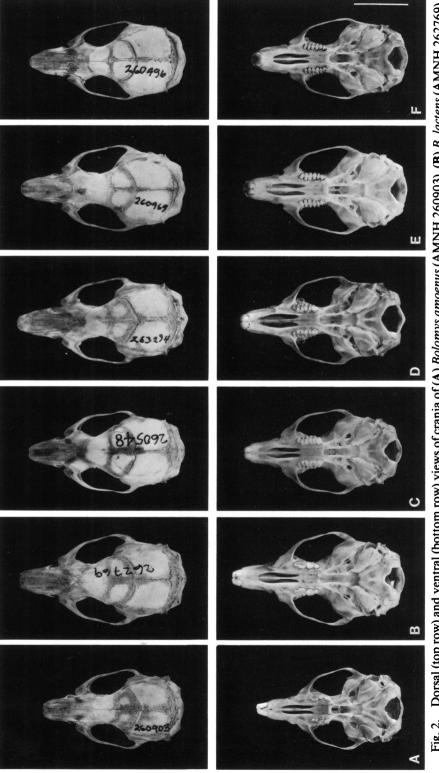


Fig. 2. Dorsal (top row) and ventral (bottom row) views of crania of (A) Bolomys amoenus (AMNH 260903), (B) B. lactens (AMNH 262769), (C) B. lenguarum (AMNH 260548), (D) Akodon dayi (AMNH 263294), (E) A. toba (AMNH 260469), and (F) A. varius (AMNH 260496). Scale at lower right represents 10 mm.

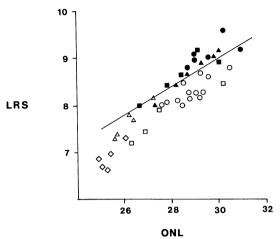
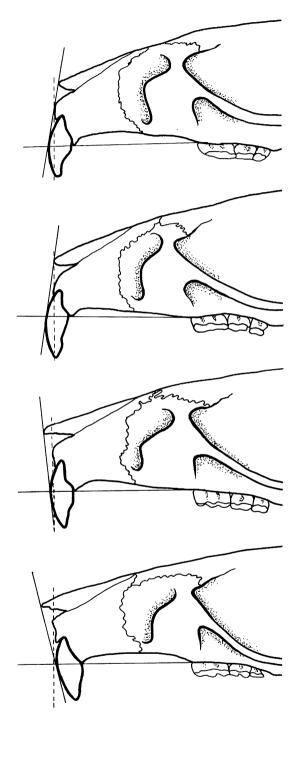


Fig. 3. Length of rostrum (LRS) plotted against occipitonasal length (ONL) in species of *Akodon* and *Bolomys*. Symbols and samples as in figure 1. Line represents 30 percent of ONL.

posterior to level of anterior border of incisors"-Nasals tend to be shorter and less projecting anteriorly in Bolomys than in Akodon. but there is considerable variation in each genus so that a nearly unbroken continuum in degrees of projection can be found (see fig. 4). Among the three species of Bolomys in Bolivia, B. amoenus and B. lactens have shorter nasals than do the lowland populations of B. lenguarum (fig. 4). The former two species have more proodont incisors as well, which adds to the impression of shorter nasals. Specimens of B. lenguarum can show nasals extending as far anterior as in some specimens of Akodon. This character generally holds, but not in all individual cases.

Fig. 4. Lateral views of the anterior cranium of (top to bottom) Bolomys amoenus (AMNH 260904), B. lactens (AMNH 262769), B. lenguarum (AMNH 263286), and Akodon dayi (AMNH 263304). Scale represents 5 mm. The horizontal line is the diastemal baseline drawn through the anterior alveolar edge of the M1 and the posterior alveolar edge of the incisor. The dotted vertical line drawn tangential to the premaxillae is perpendicular to the diastemal baseline and serves both to orient the skulls and to show the relative positions of the incisors to the premaxillae. The third line is drawn through the anterior point of the nasals and the anterior edge of the incisors and shows the proodonty of the incisors.



"Frontals long, always longer than nasals"—We measured the length of the nasal bones and the length of the frontal bones on the midline for the individuals above. In the specimens of *Bolomys*, the frontals are always longer than the nasals, the nasal/frontal ratio ranging from 0.76 to 0.95. In the specimens of Akodon examined, the frontals range from longer to shorter than the nasals. In the samples of Akodon toba, the frontals are always longer than the nasals, the nasal/frontal ratio ranging from 0.92 to 0.97; in A. varius, the frontals are usually shorter than the nasals, the nasal/frontal ratio ranging from 1.00 to 1.18; in A. dayi, the frontals are shorter or longer than the nasals, the nasal/frontal ratio ranging from 0.94 to 1.10. The nasals are shorter than the frontals in *Bolomys*, but some individuals of Akodon have relatively short nasals. The best separation point might be 0.95, less for most Bolomys and more for most Akodon.

"Parietals short, less than half the length of frontals, and extending forward anterolaterally by means of narrow spines penetrating between frontals and temporals"—We measured the parietal and frontal lengths on the midline. In Bolomys, we found the parietal/ frontal ratio to range from 0.41 to 0.60 (averaging 0.59 in B. amoenus from Peru, 0.51 in B. amoenus from Rodeo, 0.50 in B. lactens from Tambo, 0.48 in B. lenguarum from the Beni, and 0.48 in B. lenguarum from Santa Cruz). In Akodon, the ratio ranged from 0.42 to 0.54 (averaging 0.46 in A. dayi from Ayacucho, 0.50 in A. varius from Parotani, and 0.48 in A. toba from Tarija). The quoted statement is not true in regard to the parietal/ frontal ratio and is not useful as a diagnostic character. There is an anterolateral projection of the parietals that can be spinelike (fig. 5), but is variable in shape in both *Bolomys* and Akodon and there is some overlap. Thus, these processes are not useful as a diagnostic character either, although we have the subjective impression that the process is more slender and longer in Bolomys.

"Interparietal noticeably reduced anteroposteriorly and transversely"—The shape and size of the interparietal bone are too variable in both *Bolomys* and *Akodon* to be useful (see reverse situation in fig. 5). It is reduced in akodonts in general.

"Interorbital area with well-formed, anteriorly convergent borders"—True of *Bolomys*, this is useful. *Bolomys* shows a distinctly ridged, posteriorly divergent interorbital area (see fig. 2). Some specimens of *Akodon varius* have slightly convergent borders with slight ridging, but not so distinct as in *Bolomys*.

"Posterior palate moderately long and wide. the median posterior border of palatines behind the posterior border of M3"-Moderately long is defined but "wide" needs an explicit definition. The "posterior border of the M3" might refer to the crown or to the alveolar margin. The palate in both Bolomys and Akodon extends posteriorly at the anterior margin of the mesopterygoid fossa to or, in most cases, slightly beyond the level of the molar crowns. Since the mesopterygoid border lies dorsal to both the crown and the alveolar margin, the orientation of the skull needs to be defined in order to measure or observe this feature in a comparable way. There does not seem to be a relative difference of palate width between Bolomys and Akodon (fig. 6, and see fig. 2).

"Zygomatic plate broad and strong, with anterior border straight or slightly concave, perpendicular to diastema"—This is true of Bolomys (fig. 4) and some species of Akodon. It serves to separate Bolomys from the oxymycterine group (see Hinojosa et al., 1987), including Microxus and some species of Akodon, but is not useful in distinguishing other species of Akodon and Bolomys.

"Upper incisors orthodont or proodont"—In *Bolomys*, the upper incisors range from being slightly opisthodont to somewhat proodont (fig. 4). *Bolomys amoenus* and *B. lactens* show a greater degree of proodonty than *B. lenguarum* (fig. 4) and all are slightly more proodont than *Akodon*. In *Bolomys*, the premaxillae do not extend beyond the level of the anterior face of the incisors. The differences between species of *Akodon* and *B. lenguarum*, however, are slight (fig. 4).

"Molars mesodont, terraced with moderate wear, broad and robust"—The former two characters are generally true of *Bolomys* and *Akodon*. "Broad and robust" may be misleading, as akodonts generally have relatively narrower molars than do other sigmodonts. We measured the crown length and width of the M1 and then compared the width-to-

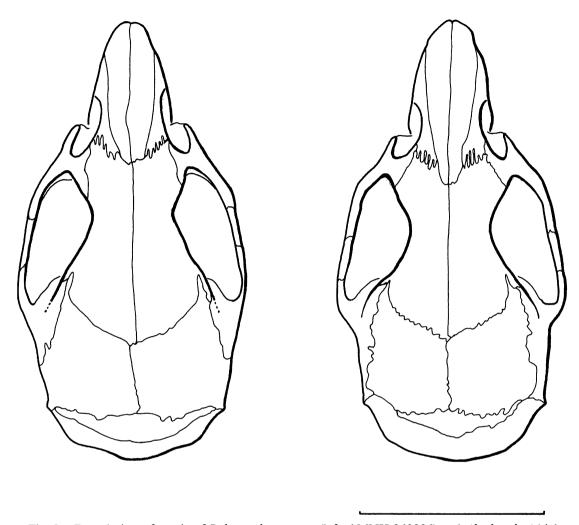


Fig. 5. Dorsal view of crania of *Bolomys lenguarum* (left, AMNH 263286) and *Akodon dayi* (right, AMNH 263304). Scale at bottom represents 10 mm.

length ratio of the M1. There is no consistent difference between Akodon and Bolomys. In B. amoenus from Peru, the ratio ranged from 0.53 to 0.63; in B. amoenus from Rodeo, 0.57 to 0.63; in B. lactens from Tambo, 0.58 to 0.70; in B. lenguarum from the Beni, 0.49 to 0.60; in B. lenguarum from Santa Cruz, 0.51 to 0.59; in Akodon dayi from Ayacucho, 0.52 to 0.59; in A. varius from Cochabamba, 0.52 to 0.61; and in A. toba from Tarija, 0.47 to 0.61. The M1 tends to be relatively wider in the highland Bolomys, B. amoenus and B. lactens. We also compared the length of the M1 to occipitonasal length in all samples, and found no obvious difference between species.

The length of the M1 is from 7.3 to 9.2 percent of the occipitonasal length in all specimens examined. The largest and smallest values of this ratio are from individuals of Akodon varius and A. toba, respectively. Thus, Bolomys does not consistently have broader and more robust molars than the larger species of Akodon (fig. 7).

"Upper molars with lophs almost completely transverse, and mesoloph usually completely coalesced with paraloph"—This is not useful; while true of *Bolomys*, it is generally true of *Akodon* (see fig. 7).

"Procingulum of M1 simple, with anteromedian flexus absent or only slightly devel-

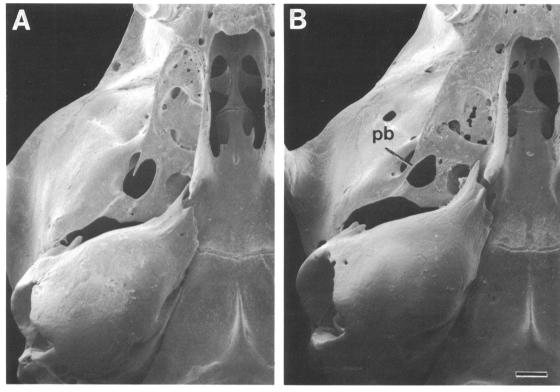


Fig. 6. SEM views of the basicrania of (A) Bolomys lenguarum (AMNH 210065) and (B) Akodon toba (AMNH 246756) with pterygoid bridge (pb) labeled. Scale represents 1 mm.

oped"—This is true of *Bolomys* and is generally useful in separating *Bolomys* from *Akodon* in which the anteromedian flexus is deeper on the average (see fig. 7). However, the range of variation in *Akodon* is such that some individuals are not different in this character from some individuals of *Bolomys*, which also have a slightly developed anteromedian flexus.

"Lower molars with lingual cusps somewhat anterior to the labial ones, with mesolophid remnants and mesostylids usually absent"—This is not useful as it is generally true of *Bolomys* and *Akodon* (fig. 7).

Myers (in prep.) noted the following characters as useful in distinguishing *Bolomys* from species of *Akodon* in the Chaco region of Bolivia, Paraguay, and Argentina. We examined these characters to determine whether they are more broadly applicable.

"Narrower, more strongly divergent interorbital region with much more strongly ledged sides"—Differences in shape relating to divergence and ledges are discussed above. The interorbital region of *Bolomys* is not noticeably narrower at the point of greatest interorbital constriction in specimens of *Bolomys* than in skulls of comparably sized specimens of *Akodon*.

"Dorsoventral bowing of skull tends to be more pronounced"—See comments above.

"Wider rostrum"—The rostrum is relatively shorter and has a broader appearance in *Bolomys* (see figs. 2 and 8). We measured the width of the rostrum and plotted these data against occipitonasal length (fig. 8). The ratio is approximately 0.19 in all species measured of both *Akodon* and *Bolomys*. The ratio is slightly more than 0.19 in adult skulls of *B. amoenus* from Bolivia. In the species of *Akodon* and *B. lenguarum* from Santa Cruz, there is nearly complete overlap; therefore this is not a useful diagnostic character.

"Broader zygomatic notches"—This is useful. *Bolomys* does show a broader zygomatic notch (see figs. 2 and 5), but this is a

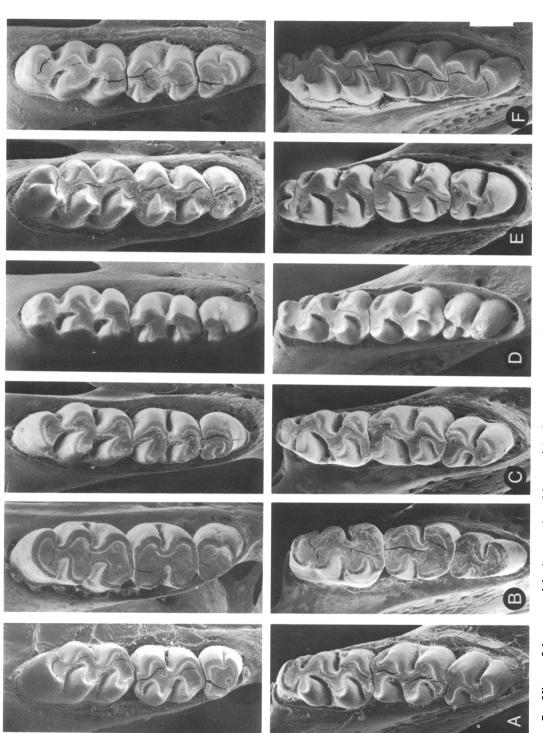


Fig. 7. Views of the upper right (top row) and lower right (bottom row) maxillary toothrows of (A) Bolomys amoenus (AMNH 213564), (B) B. lactens (AMNH 262761), (C) B. lenguarum (AMNH 260530), (D) Akodon dayi (AMNH 263289), (E) A. toba (AMNH 246699), and (F) A. varius (AMNH 38688). Scale at lower right represents 1 mm.

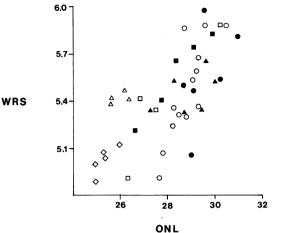


Fig. 8. Plot of rostrum width (WRS) against occipitonasal length (ONL). Symbols and samples as in figure 1.

highly variable character that overlaps somewhat between Akodon and Bolomys. We measured the depth of the zygomatic notch to ascertain the relative size difference (width is difficult to quantify); the notch is generally deeper in Bolomys. In B. lenguarum and the comparably sized species of Akodon, the zygomatic notch ranges from 1.60 to 2.26 mm in Bolomys lenguarum; from 1.24 to 1.73 mm in A. dayi, from 1.47 to 1.75 mm in A. varius, and from 1.61 to 1.92 mm in A. toba.

Zygomatic arches "less flared"—We were not certain what was meant, so we measured the greatest zygomatic breadth and plotted these data against occipitonasal length (fig. 9). The highland Bolomys (B. amoenus and B. lactens) tend to have zygomatic-breadthto-skull-length ratios greater than 0.55, whereas B. lenguarum and the comparably sized Akodon of the lowlands tend to be less than 0.55 (fig. 9). Thus, the relative width of the zygomatic arch is not very useful as a diagnostic character of the genus although it may be useful in distinguishing certain pairs of species or in certain local areas. Myers (in litt.) defines less flared as lesser breadth in the anteriormost part of the arch. The arch becomes broader, both anteriorly and at its greatest breadth, with increasing age, so that characters relating to the arch need to be compared in mice at similar developmental stages. The same consideration applies to many other cranial characters. Other mea-

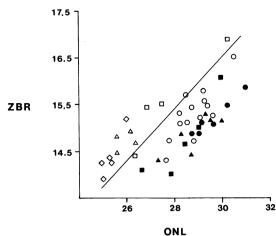


Fig. 9. Plot of zygomatic breadth (ZBR) against occipitonasal length (ONL). Symbols and samples as in figure 1. Line drawn represents 55 percent of ONL.

surements of the arch are needed to evaluate possible differences in its shape.

"Considerably smaller bullae" (than in A. varius and A. toba)—This is generally true when lowland Bolomys and Akodon are compared. Bolomys amoenus has relatively large bullae, actually larger than those of B. lactens, which is larger overall. This is not a generic character. However, there may be average differences between species within Akodon and Bolomys. See figures 2 and 6.

"Narrower incisive foramina" (than in A. varius and A. toba)—This generally holds also as a generic character when species other than those of the chaco are compared. In absolute width, the incisive foramina of small species of Akodon such as A. andinus and A. boliviensis are as narrow as in Bolomys amoenus, but the ratio of width-to-length of the foramina seems greater in the species of Akodon (see fig. 2).

"Narrower pterygoid wings" (than in A. varius and A. toba)—This character, narrower parapterygoid fossa in our terminology, is useful. The parapterygoid fossae of Bolomys are much narrower than those of any of the species of Akodon we examined (figs. 2 and 6). However, there is noticeable variation among species of Akodon and to a lesser degree between individuals. This is difficult to quantify adequately, but is evident in figures 2 and 6.

"Broader teeth"-See comments above.

Upper incisors tend "to be more proodont," but with "considerable variation"— See comments above.

Procingulid of m1 "always lacks an anteromedian flexid"—This appears to be true and useful (see fig. 7).

An additional character that is useful in distinguishing *Bolomys* from *Akodon* is the reduced or absent pterygoid bridge (see fig. 6, terminology from Musser and Newcomb, 1983), a strut of bone over the foramen ovale visible in ventral view. In species of *Akodon*, the pterygoid bridge is well developed and readily apparent. In most specimens of *Bolomys*, it is delicate or missing. However, in some specimens of *B. lactens*, the pterygoid bridge is present and approaches the condition observed in *Akodon*.

The number of chromosomes known in species of Bolomys (e.g., B. amoenus, B. obscurus, B. lasiurus [under name arviculoides], B. lasiurus, "probably" B. lenguarum, and B. temchuki) is a uniform 2n of 34. For Akodon that have been studied, numbers of 14, 16, 24, and 40 have been reported, but never 34. These data (from various sources, summarized in Reig, 1987: 354, 356) support the possible monophyly of *Bolomys*. Karyology, of additional species and using banding techniques, offers a source of valuable new taxonomic information relating to the phylogeny of akodontine rodents. Electrophoresis and other biochemical methods also offer promise of helping to clarify phylogeny in the group.

Genus Bolomys Thomas, 1916

CONTEXT: Order Rodentia, suborder Sciurognathi, infraorder Myomorpha, superfamily Muroidea, family Muridae, subfamily Sigmodontinae (Carleton, 1984; Carleton and Musser, 1984), tribe Akodontini (Reig, 1987). The genus *Bolomys* is one of some 73 Recent genera in the subfamily and has been regarded as a subgenus of *Akodon* by some authors.

SYNONYMY:

Bolomys Thomas, 1916: 339. Type species Akodon amoenus Thomas, 1900: 468, by original designation.

Thalpomys Thomas, 1916: 339. Type species said to be Mus lasiotus Lund, 1838 = Bolomys lasiurus (Lund, 1837), but Thomas' description and concept of Thalpomys were actually based on a

misidentified specimen of Akodon and not the type specimen of Mus lasiotus (Langguth, 1975), in which case the type species of Thalpomys should be fixed by the Commission according to Article 70 (b) of the Code, and this has not been done to our knowledge.

Cabreramys Massoia and Fornes, 1967: 418. Type species Akodon obscurus (Waterhouse, 1837).

DIAGNOSIS: The following characters seemed to be those most diagnostic of *Bolomys*. Other characters discussed above are less useful because of their variability in species studied. Some of those characters may be useful when comparing specimens from a local area or a restricted subset of species, but not over the wide geographic ranges of *Akodon* and *Bolomys*.

Bolomys can be distinguished from other genera of Akodontini by the combination of the following characters (our concept of combination is more restricted than that of Reig, in that all of the Bolomys examined by us have the character states listed below). The characters are not, however, unique to the genus, all occurring in some form in some other genus of Sigmodontinae or even genera of other family-level groups. The characters of other species of Akodon need to be critically compared to refine this diagnosis further. The diagnostic characters, in this sense, are: short rostrum, deeper and often wider zygomatic notches, posteriorly divergent interorbital region with ridged edges, relatively narrow incisive foramina, narrow parapterygoid fossae, reduced or absent pterygoid bridges, anterior face of upper incisors anterior to premaxillae, reduced anteromedian flexus on M1, lack of anteromedian flexid on m1, see figures 2, 4, 5, 6, and 7.

KEY TO BOLIVIAN SPECIES OF BOLOMYS

- 1b. Nasals slightly longer, incisors not visible from above, incisors not obviously proodont, incisors yellow, zygomatic breadth generally less than 0.55 of occipitonasal length B. lenguarum
- Smaller body size (total length generally less than 180 mm), pelage paler, skull smaller,

occipitonasal length of adults generally less than 26.5 mm, relatively large bullae, sphenopalatine vacuities present, occurs at high elevations, known only from Cochabamba B. amoenus

Bolomys amoenus Thomas, 1900

Akodon amoenus Thomas, 1900: 468 (type locality "Calalla, Rio Colca, near Sumbay, Peru. Altitude 3500 metres").

Recently discovered in the department of Cochabamba (see fig. 10 and the Appendix for details), the occurrences there extend the known range at least 500 km southeastwardly from Peru and provide the first records for Bolivia. These two localities are at 4000 (Colomi) and 3875 m (near Rodeo) in elevation.

Bolomys amoenus differs from other Bolivian Bolomys in being smaller, paler, and in having relatively larger bullae. Externally, B. amoenus is quite different from the other Bolomys, it has a whitish venter which is sharply demarked from darker sides, smaller, paler hind feet with ochraceous dorsal hue, and vellowish sides of head. The venter in B. lactens is darker and ochraceous and in B. lenguarum darker and grayish. Bolomys amoenus also differs from B. lenguarum in having shorter nasals and rostrum, and paler and more proodont upper incisors. Cranially, B. amoenus and B. lactens are similar in having a short rostrum, pale, almost white proodont upper incisors, relatively broad zygomatic arches, and relatively broad M1; however, B. amoenus is more extreme in rostral shortening and incisive proodonty. B. amoenus differs from B. lactens in having sphenopalatine vacuities, the anterior margin of the mesopterygoid fossa occurring at about the level of the posterior alveolar margin of M3 rather than anterior to this margin.

In external characters, B. amoenus may be confused with certain species of Akodon, especially A. albiventer, which occurs at similar elevations, is the same size, and has a whitish venter. Bolomys amoenus differs in having

less blackish ears, less blackish dorsal stripe on tail, and more evident ochraceous or yellowish hue on sides of head, on feet, and on sides of tail. Cranially, both species have relatively larger bullae than their congeners.

Bolomys lactens Thomas, 1918

Akodon lactens Thomas, 1918: 188 (type locality "Leon, Jujuy, 1500 m," Argentina).

Recently discovered from Rancho Tambo (2100 m) in the department of Tarija (see fig. 10 and the Appendix for details), this occurrence extends the known range northward from Argentina and provides the first record for Bolivia.

Bolomys lactens differs from B. amoenus as described above and from B. lenguarum in being generally larger and most noticeably in having an ochraceous rather than grayish venter. Cranially, B. lactens differs from B. lenguarum in having a relatively shorter rostrum and nasals, more proodont upper incisors, relatively greater zygomatic breadth, and relatively broader M1.

Externally, B. lactens may be confused with certain species of Akodon in southeastern Bolivia, including A. pervalens, A. toba, A. simulator, and A. varius of the varius group (Myers, in prep.). Field identifications based on external characters are generally not reliable. However, cranial differences in the supraorbital area and anterior rostrum between Akodon and Bolomys are visible on uncleaned skulls in the field.

Bolomys lenguarum Thomas, 1898

Akodon lenguarum Thomas, 1898: 271 (type locality "Waikthlatingmayalwa, Northern Chaco of Paraguay"); Thomas, 1925: 579 (Caraparí).

Zygodontomys tapirapoanus Allen, 1916: 528 (type locality "Tapirapoan, Rio Sepotuba, Matto Grosso, Brazil").

Zygodontomys lasiurus: Gyldenstolpe, 1932: 113; Voss and Linzey, 1981: 41 (5 km E Mizque).

Zygodontomys [?lasiurus] tapirapoanus: Hershkovitz, 1962: 207 (Buenavista).

Bolomys lenguarum: Reig, 1978; 1987; Anderson, 1985: 13 (name in list, based on record from Caraparí).

Bolomys lasiurus lasiurus: Anderson, 1985: 13 (name in list); Macêdo and Mares, 1987: 591 (various localities in Beni and Santa Cruz).

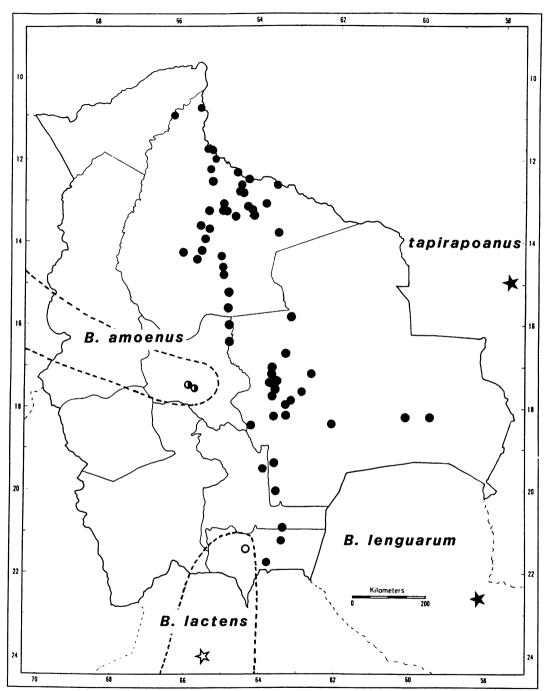


Fig. 10. Map of known Bolivian localities of *Bolomys lenguarum* (\bullet), *B. lactens* (\circlearrowleft), and *B. amoenus* (\bullet). Type localities of *B. lactens* (\nwarrow) and *B. l. lenguarum* (\bigstar , Paraguay) and *B. l. tapirapoanus* (\bigstar , Brazil) are also given.

The distribution of this species is shown in figure 10. Most localities are at elevations below 500 m in the extensive lowlands of

northeastern Bolivia; however, the species is known from Comarapa at about 2500 m and Vermejo at 1100 m in the eastern foothills of the Andes. In this area Bolomys lenguarum is geographically sympatric (or perhaps parapatric on an ecological or local scale) with Akodon varius (specimens from 8 km west of Comarapa, for example). At Caraparí in Tarija (at 2149/6346 and at 1000 m in elevation), Bolomys lenguarum (BMNH 25.2.1.51 and 52) occurs with at least three species of Akodon, A. pervalens (BMNH 25.2.1.55 and 56), A. boliviensis (BMNH 25.2.1.57 to 60), and A. toba (BMNH 25.2.1.53 and 54). Furthermore, Bolomys lactens and other species of Akodon occur in other parts of Tarija. Clearly a diverse akodont fauna occurs there.

Hershkovitz (1962: 203) provisionally accorded specific rank to a northern group and a southern group of *Zygodontomys* and contrasted them. Specifically, he compared the northern species *Z. brevicauda* with *Z. lasiurus* of Brazil. He did not provide diagnoses for *Z. lenguarum* or *Z. tapirapoanus* or assign them to *Z. lasiurus*, although he implied their possible conspecificity.

Macêdo and Mares (1987) found significant age-related cranial variation in *Bolomys* (assigned by them to *lasiurus*) from central Bolivia. They found sexual dimorphism to be present as well, with males slightly larger in most of the craniodental characters they examined. They assigned specimens from a number of Bolivian and Paraguayan localities to *B. lasiurus* and did not directly comment on the possible status of *B. lenguarum* or *B. tapirapoanus*.

Reig (1987), the most recent revisor, examined relevant specimens and clearly recognized *Bolomys lenguarum* as separate from *B. lasiurus* in the taxonomic sense. However,

he provided no data or specific comparisons as evidence for how they may be clearly recognized in a morphological sense.

We are reasonably certain that *Bolomys* from the Bolivian lowlands are not distinguishable at the subspecific level from *Bolomys tapirapoanus* from Mato Grosso, but we are uncertain how these populations may differ from Paraguayan *B. lenguarum* although we think that they are probably not distinguishable at the specific level. Detailed study of geographic variation based on more material is needed to resolve these questions. Further study is also needed to resolve the question of whether *B. lenguarum* and *B. lasiurus* are conspecific. For the moment we follow Reig's (1987) nomenclature.

Comparisons of *Bolomys lenguarum* to *B. amoenus* and to *B. lactens* are included in those accounts. Although superficial similarities in size, bodily proportions, and color make identification difficult in the field, *B. lenguarum* and species of *Akodon* seem separable on cranial characters in areas of geographic sympatry.

Specific localities in the departments of Chuquisaca and Santa Cruz, Bolivia, where Bolomys lenguarum occurs with Akodon dayi or A. toba, include the following: Chuquisaca: Laguna Palmar (with A. toba); Ayacucho (1751/6320); Santa Cruz: 6 km N of Buen Retiro; 3.5 km W of Estación Pailón; 8 km SE of Tita; 6 km W of Ascención; San Rafael de Amboró; Santiago de Chiquitos; Ayacucho (1700/6355); San Miguel Rincón; Buenavista; Warnes; río Pitasama; and Vallegrande.

APPENDIX: LIST OF SPECIMENS

All Bolivian specimens of *Bolomys* definitely identified by us, selected localities and specimens of Bolivian *Akodon*, and selected specimens of both genera beyond Bolivia are listed. Latitude and longitude are given in coded form (1428/6734 represents 14°28′S and 67°34′W) for Bolivian localities. Catalog numbers are given for selected specimens, including those specifically referred to in text, tables, or legends to figures, and those where some uncertainty might persist about the exact specimens referred to.

Akodon dayi. BOLIVIA: Beni: 1428/6734, Rurrenabaque, 9 AMNH; 1450/6623, Beni Reserve, río Curiaba, 1 MNLP. Cochabamba: 1620/6645, Yungas, 17 AMNH; 1648/6508, Todos Santos, 26 AMNH, 1 BMNH 20 FMNH, 1 MCZ; 1700/6550, Yungas, 1 AMNH; 1751/6440, 25 km by road W of Comarapa, 6 UMMZ. La Paz: 1401/6731, río Beni, 3 AMNH, 2 MSB; 1529/6731, 1 mi W of Puerto Linares, 8 MSU; 1540/6735, 35 km by road N of Caranavi, 2 AMNH. Santa Cruz: 1543/6309, 6 km by road W of Ascención, 3 AMNH, 5 MSB; 1635/6412, Punta Rieles, 4 AMNH, 7 CENETROP; 1636/6242, 10 km N of San Ra-

món, 3 AMNH, 1 MSB; 1637/6246, río Quiser, 3 CM (one with uncertain locality); 1649/6237, Palmarito, río San Julian, 5 CM; 1700/6355, Ayacucho, 14 AMNH, 1 CENETROP, 1 MNK; 1713/6338, 6 km N of Buen Retiro, 4 AMNH (includes 260474); 1724/6346, 25 km by road W of Buenavista, W bank of río Yapacani, 3 UMMZ (156305, 156306, 156245); 1727/6340, Buenavista, 1 BMNH; 1730/6310, Warnes, 2 USNM; 1736/6336, San Rafael de Amboró, 3 AMNH (includes 261922), 4 MSB.

Akodon simulator tartareus. BOLIVIA: Tarija: 2128/6429, 38 km by road ENE of Tarija, Carlazo, 3 UMMZ; 2133/6447, Tablada, 8 BMNH; 2136/6445, 5 mi S Tarija, 2 MVZ; 2212/6436, 8 km by road N of Cuyambuyo, 1 UMMZ.

Akodon toba. BOLIVIA: Chuquisaca: 2045/6313, Porvenir, 1 AMNH, 1 MSB; 2056/6321, 2 km S and 10 km E of Tiquipa, Laguna Palmar, 1 AMNH. Santa Cruz: 1739/6245, 3.5 km W of Estación Pailón, 4 AMNH; 1818/5936, 4 km N and 1 km W of Santiago de Chiquitos, 2 AMNH; 1825/6210, Tita, 2 AMNH, 1 MNLP, 2 MSB; 1828/6407, 8 km SE of Tita, 1 AMNH (260532); 1857/5751, Puerto Suarez, 2 CM. Tarija: 2119/6325, 8 km S and 10 km E of Villa Montes, 34 AMNH (includes 246756), 1 MNLP.

Akodon varius. BOLIVIA: Chuquisaca: 1914/ 6513, Pulce, 1 AMNH. Cochabamba: 1721/6552, Colomi, 1 FMNH; 1724/6609, Cochabamba, 2 BMNH, 6 FMNH; 1726/6619, Vinto, 12 AMNH; 1731/6623, 15 mi E of Tapacari, 1 MVZ; 1731/ 6636, Tapacari, W of Cochabamba, 3 BMNH; 1734/6621, Paratani, 16 AMNH, 1 BMNH, 1 FMNH; 1742/6509, Totora, 1 BMNH. Potosi: 1918/6612, río Cachimayo, 4 AMNH. Santa Cruz: 1649/6237, Palmarito, río San Julian, 400 m, 5 CM; 1751/6440, 25 km by road W of Comarapa, 2800 m, 5 UMMZ; 1754/6432, 8.5 km by road W of Comarapa, 2300 m, 1 MSB; 1754/6434, 5 mi (8 km) W of Comarapa, 2310 m, 1 MVZ; 1755/ 6434, 1 km N and 8 km W of Comarapa, 2450 m, 3 AMNH; 1830/6406, Vallegrande, 1980 m, 2 USNM.

Bolomys amoenus. BOLIVIA: Cochabamba: 1721/6552, Colomi, 3800–4000 m, 2 BMNH (unregistered skins only, F. B. Steinbach field nos. 266 and 267); 1740/6535, 9.5 km by road SE of Rodeo, then 2.5 km on road to ENTEL antenna, 3875 m, 5 AMNH (260890, 260903–260906). PERU: Puno: 5 mi NW Puno, 3850 m, 8 AMNH (213559–213562, 213564–213567); 8 mi NW Puno, 3850 m, AMNH 213563, 232150; Puno, 3800 m, 13 AMNH (213552–213558, 213568–213572, 232151); Sangero, 4000 m, 1 BMNH (1.1.1.12). Peru only: 3 AMNH (232156, 232157, 232160).

Bolomys lactens lactens. ARGENTINA: Catamarca: Las Pavas, Aconguija, 2 BMNH

(25.12.13.40 and 41); Aconguija, 1 BMNH (28.10.14.6). **Jujuy**: Río Lavallen, 1 BMNH (20.1.7.100). **Tucumán**: Norco-Vipos, 4 BMNH (26.2.13.122 to 125). BOLIVIA: **Tarija**: 2127/6419, Rancho Tambo, 61 km by road E of Tarija, 2100 m, 4 AMNH (262761, 262764, 262767, 262769).

Bolomys lenguarum tapirapoanus. BOLIVIA: Beni: 1048/6525, 1.5 km NW Guayaramerin, 15 AMNH; 1048/6526, 1 mi NW Guayaramerin, 10 AMNH: 1059/6606, Riberalta, 1 USNM; 1142/ 6516, 4 km S Santa Rosa, 3 AMNH; 1149/6506, 7 km N Lagoinha on río Mamoré, 1 AMNH; 1200/ 6506, Puerto More, 4 AMNH; 1200/6502, río Iténez, 20 km above mouth, 2 AMNH; 1213/6513, Cascajal, across river from, 2 AMNH; 1225/6428, río Iténez, bank opposite Principe da Beira [Brazil], 11 AMNH; 1228/6417, río Iténez, 1 km above Costa Marques [Brazil], 3 AMNH; 1229/6415, río Iténez, 4 km above Costa Marques, 5 AMNH; 1229/6418, río Iténez, 1.5 km below Costa Marques, 1 AMNH; 1229/6418, río Iténez, below Costa Marques, 2 AMNH; 1229/6417, río Iténez, bank opposite Costa Marques, 52 AMNH; 1230/6418, mouth of rio Baures, 30 AMNH; 1230/6415, Pampa de Meio, 42 AMNH; 1232/6509, 17 km NNW Nuevo Berlin, 1 AMNH; 1234/6425, 15 km above Horquilla on río Machupo, 14 AMNH; 1240/6330, mouth of río Curiche, 6 AMNH; 1244/ 6428, Las Peñas, 4 FMNH, 1 USNM; 1248/6422, Nueva Calama, 1 USNM; 1304/6448, Camino Vilches, 8 FMNH; 1304/6449, San Joaquín, 26 FMNH, 7 USNM; 1306/6348, Boa Vista, 29 km NE San Joaquín, 3 USNM; 1310/6413, Cayoba, 1 USNM; 1310/6449, San Marco, 2 FMNH; 1312/ 6410, Cachuelita, 1 USNM; 1313/6448, Barranquita, 1 FMNH; 1315/6448, Yutiole, 7 AMNH; 1316/6515, Exaltación, 3 FMNH; 1320/6408, Magdalena, province of Iténez, 3 USNM; 1325/ 6435, Cafetal, 1 USNM; 1334/6154, Remansos, 1 AMNH: 1338/6525, río Yacuma, 2 km from mouth, 1 AMNH; 1338/6526, río Yacuma, 4 km from mouth, 1 AMNH; 1343/6521, Puerto Caballo, 146 AMNH; 1346/6330, Lago Victoria, province of Iténez, 1 FMNH, 4 USNM; 1355/ 6520, río Mamoré, 4 AMNH; 1412/6528, Fortaleza, province of Yacuma, 8 USNM; 1412/6527, Palacio Ranch, 90 km S Santa Ana, province of Ykuma, 2 USNM; 1420/6455, 10 km W San Pedro, 8 AMNH; 1420/6450, San Pedro, 1 FMNH; 1425/6532, La Esperanza, 7 USNM; 1434/6455, 23 km W San Javier, on río Mamoré, 12 AMNH; 1447/6451, río Ibare, 26 km from mouth, 1 AMNH; 1448/6414, Casarabe, 4 AMNH, 1 MSB; 1519/6444, Camiaco, 4 AMNH; 1534/6446, 15 km S Limoquije, 1 AMNH; exact coordinates unknown, río Iténez, 1 AMNH. Chuquisaca: 1931/ 6409, Monte Cantu, province of Tomina, 1 USNM;

2056/6321, 2 km S and 10 km E of Tiquipa, Laguna Palmer, 12 AMNH, Cochabamba: 1558/ 6442, mouth of rio Chapare, 1 AMNH. Santa Cruz: 1543/6309, 6 km by road W of Ascención, 2 AMNH, 5 MSB; 1557/6441, 2 km N of mouth of río Chapare, 1 AMNH; 1628/6444, río Ichilo, 52 km S of mouth of río Chapare, 1 AMNH; 1647/ 6314, Estancia Cachuela Esperanza, 21 AMNH, 3 MSB; 1700/6355, Ayacucho, 2 AMNH; 1703/ 6335, 7 km N Santa Rosa, 1 AMNH; 1713/6338, 6 km N of Buen Retiro, 9 AMNH, 2 MSB; 1723/ 6332, San Miguel Rincón, 13 AMNH, 5 MSB; 1727/6340, Buenavista, 19 BMNH; 1730/6310, Warnes, province of Warnes, 17 USNM; 1736/ 6336, San Rafael de Amboró, 13 AMNH, 3 MSB: 1739/6245, 3.5 km W of Estación Pailón, 7 AMNH, 1 MSB; 1745/6340, 4.5 km N and 1.5 km E of Cerro Amboro, río Pitasama, 1 AMNH; 1748/6310, Santa Cruz, province of Ibañez, 23 USNM; 1748/6310, "Santa Cruz" (city?), 1 USNM; 1748/6314, Km 7 on Santa Cruz to Cochabamba highway, 1 MSU: 1751/6309, Palmar, province of Ibañez, 4 USNM; 1751/6320, Ayacucho, province of Ibañez, 5 USNM; 1754/ 6326, Km 15 (SW) from Santa Cruz, 1 USNM; 1754/6429, Comarapa, 9 BMNH; 1808/6312, 7 km E and 3 km N Ingeniero Mora, 22 AMNH; 1810/6336, Vermejo, 8 AMNH; 1816/6007, 7 km N and 38 km W of Roboré, 8 AMNH, 1 MSB: 1818/5936, 4 km N and 1 km W of Santiago de Chiquitos, 9 AMNH, 5 MSB; 1819/6002, 29.5 km W of Roboré, 1 AMNH; 1828/6207, 8 km SE of Tita, 15 AMNH, 6 MSB; 1830/6406, Vallegrande, province of Vallegrande, 1 USNM (290910); 1925/ 6334, Gutierrez, province of Cordillera, 1 USNM; 2005/6334, near Camiri, 1 CAS. Tarija: 2149/ 6346, Caraparí, 2 BMNH (Thomas, 1925); 2241/ 6426, río Lipeo, 5 ANSP. BRAZIL: Mato Grosso: Tapirapoan, Siputuba River, 2 AMNH; Utiarity, near Salto Bello, 460-770 m, 2 AMNH; Urucum, 1 AMNH; Tres Buretys, 1 AMNH; Base camp, 264 km N of Xavantina, Serra do Roncador, 11 BMNH.

Bolomys lenguarum lenguarum: ARGEN-TINA: Chaco: Avia Terai, 1 BMNH (34.11.4.77). Corrientes: Goya, 1 BMNH (98.12.3.25). PAR-AGUAY: Caaguazú: Caaguazú, 2 AMNH. Chaco: 50 km WNW Fortín Madrejón, Cerro Leon, 2 AMNH; Jesamatathla, BMNH 20.12.18.17 to 19; "N. Paraguay," 5 BMNH (99.11.1.2 to 6). Presidente Hayes: Puerto Piñasco, 1 USNM (236254).

Bolomys obscurus obscurus: URUGUAY: Canelones: Km 36 Interbalnearia, E of Montevideo, 1 AMNH. Montevideo: Colon, near Maldonado, 4 BMNH (99.1.1.1 to 4).

Bolomys obscurus benefactus: ARGENTINA: Buenos Aires: Bonifacio, F.C. Sud Argentina, 4 BMNH (16.10.3.34 and 36 to 38). Dept. unknown: El Chaco Austral. 1 BMNH (12.9.6.2).

Bolomys n. sp. (to be described by Reig): AR-GENTINA: **Buenos Aires**: Sierra de la Ventana, 3 BMNH (79.1664 to 1666).

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