# Mice of the Akodon boliviensis Size Class <br> (Sigmodontinae, Cricetidae), with the Description of Two New Species from Brazil 


#### Abstract

Two species of Brazilian sigmodontine mice described as new are Akodon lindberghi, known from less than a hectare plot of cerrado near Brasília, DF, and Akodon sanctipaulensis, from the marshes at the eastern base of the Serra do Mar in southeastern São Paulo. Survival status of the first is discussed. Both species are included in the Akodon boliviensis size class, an assemblage of the 13 smallest species nearest the typical form of the genus. The larger species of Akodon, all in the $A$. mollis size class, are listed with taxonomic notes. The phyletic relationship between species within and between the size classes has not been determined. The provisional arrangement is for convenience of characterization of the two new species within a difficult, undefined genus. Other taxa of the akodont group used for reference are also discussed. Plectomys paludicola, a nomen nudum mentioned in the literature, is the same as Akodon lindberghi.


## Introduction

A collection of small mammals made during July and August 1986, in the cerrado region of Brasilia, Distrito Federal (fig. 1), includes two species of the sigmodontine genus Akodon. One, the wide-ranging Akodon cursor Lund, is represented by four specimens. The second, heretofore undescribed, is represented by seven specimens captured in a small segment of wet valley-side open grassland, or cerrado campo limpo. Intensive trapping and ecological studies of the small mam-
mals of the region during the last decade failed to reveal the presence of this savannah species outside the narrowly restricted plot of an otherwise extensive suitable habitat (fig. 1).

A third species of Akodon, from open, marshy fields on the eastern base of the Serra do Mar in southeastern São Paulo State, collected in 1961 by A. M. Olalla, also appears to be distinctive, and is described as new.

This is the first of a planned series of taxonomic and biogeographic papers on the small mammals of the Atlantic forest region of southeastern Brazil and the cerrado of central Brazil. Cooperative fieldwork with the Museu Nacional and the Universidade de Brasília was carried out in 1986, 1987, and 1988. It is expected that continued collaboration between the Brazilian scientific institutions and the Field Museum of Natural History will result in a thorough inventory of the small mammals of the highlands and fragmented remains of the coastal forest of Brazil.

## Material

Specimens examined of the tribe Akodontini in the collections of the Field Museum of Natural History (FMNH) represent nearly all species of all tribal genera except Blarinomys and Juscelinomys. They, together with others of the tribe, were studied in the Museu Nacional, Rio de Janeiro, and the British Museum (Natural History), London.

The last eight figures in the text (figs. 15-22) illustrate all cranial, dental and morphometric terminologies used here. Reference will be made to


Fig. 1. Map of southeastern São Paulo showing collecting localities $(2,3,4,5)$ of Akodon sanctipaulensis. Inset, map of Brazil showing States and collecting locality (1) of Akodon lindberghi in Distrito Federal (black square). Data for the São Paulo localities are from A. M. Olalla's field notes, a copy of which was loaned to me by M. Traylor through the courtesy of P. Vanzolini.
these illustrations in subsequent papers on Brazilian akodonts.

## Nomenclature

There is no distinctive vernacular equivalent for the generic name Akodon. The technical name itself, however, is apt for vulgarization. The epithet akodon is suggested. It slips easily off the tongue, particularly of Spanish and Portuguese speaking people of countries where the genus occurs. The name vole, sometimes applied to akodonts, is better left with the arvicolines where it belongs.

The abbreviation for molar is m whether upper or lower. Upper case $M$ as the first letter of a sentence means the same as lower case $m$. The identity of the upper or lower molars is indicated by a superscript or subscript (examples, $\mathrm{m}^{1}, \mathrm{~m}_{1}$ ).

## Discussion

Akodon, one of the most diversified and wide ranging genera of South American mammals, has never been formally revised taxonomically. Its systematic limits are unclear, the identities and assignments of some included species are confused. Cabrera (1961) admits 90 species and subspecies distributed among the subgenera Akodon (55), Abrothrix (12), Chroeomys (9), Deltamys (1), Hypsimys (1), Thaptomys (2), Thalpomys (1), Bolomys (5), and Microxus (4). The subgenus Akodon as understood by Cabrera is a composite of typical forms clustered around the type species $A$. boliviensis Meyen, a few species (and subspecies) of Abrothrix, and a few species of Bolomys.

A recent review of Akodon by Reig (1987), intended primarily as a background for descriptions of several fossil forms, provides, on the whole, a better understanding of the genus. Contrary to Ca -
brera, Reig treated Bolomys and Microxus as distinct genera. His restricted genus Akodon includes the subgenera Akodon (23 living species including Thalpomys reinhardti or lasiotis, and 3 species of Abrothrix), Abrothrix (7 species), and monotypic Chroeomys, Deltamys, and Hypsimys.

In the present account, the subgenus Akodon is comprised of about 21 species ranging in size from Akodon lutescens with average skull length about 22 mm to A. varius (sensu lato) with average skull length about 29 mm (table 1). The gradient can be conveniently divided into two size classes. The first, or typical Akodon boliviensis size class, is an assemblage of 13 species with greatest skull length of each species averaging less than 26 mm . The second, or $A$. mollis size class, contains 20 named forms representing about 8 species, with greatest skull length of each species averaging more than 26 mm . The classes overlap narrowly in cranial size, but differences other than size (mainly of the individual species), maintain separations between them. Phyletic relationship between the species of both groups has not been determined except cytogenetically to a limited extent. Only the Akodon boliviensis class, which includes the two new species, is described. Members of the A. mollis class are simply listed with taxonomic comments.

## Akodon boliviensis Size Class

Included Species (tables 1, 2)-Akodon alterus Thomas, 1919; A. azarae Fischer, 1829; Akodon boliviensis Meyen, 1833 (type species); A. caenosus Thomas, 1918; A. iniscatus Thomas, 1919; A. lutescens J. A. Allen, 1901; A. nucus Thomas, 1926; A. pacificus Thomas, 1902; A. puer Thomas, 1902; A. subfuscus Osgood, 1944; A. tucumanensis J. A. Allen, 1901; A. lindberghi (new species), and $A$. sanctipaulensis (new species).

## (Explanation of map, fig. 1)

1. Parque Nacional de Brasília, Brasília, DF; $15^{\circ} 35^{\prime}-15^{\circ} 45^{\prime} \mathrm{S}, 47^{\circ} 55^{\prime}-48^{\circ} 05^{\prime} \mathrm{W} ; 700-1,300 \mathrm{~m}$; area 28,000 ha; rolling plateau of quartzite and limestone; mean annual temperature $20.6^{\circ} \mathrm{C}$; annual rainfall $1,675 \mathrm{~mm}$; cerrado, campo cerrado cerradão, and Amazonian type gallery forests around springs and along valley streams. P. Hershkovitz and Scott Lindbergh, August 1986.
2. Iporanga, São Paulo; ca. $24^{\circ} 07^{\prime} \mathrm{S}, 47^{\circ} 38^{\prime} \mathrm{W} ; 40 \mathrm{~m}$; on Rio Açunguí (= Assunagui), 10 km above confluence with Ribeirão das Corujas; agriculture; second growth, patches primary forest. A. M. Olalla, October 1961.
3. Morretinho, São Paulo; ca. $24^{\circ} 01^{\prime} \mathrm{S}, 47^{\circ} 44^{\prime} \mathrm{W} ; 40 \mathrm{~m}$; said to be about 30 km NNW of Juquiá (ca. $24^{\circ} 19^{\prime} \mathrm{S}, 47^{\circ} 48^{\prime} \mathrm{W}$ ). A. M. Olalla, September 1961.
4. Primeiro Morro, São Paulo; $24^{\circ} 22^{\prime} \mathrm{S}, 47^{\circ} 49^{\prime} \mathrm{W}$; ca. 16 km NW Juquiá $\left(24^{\circ} 19^{\prime} \mathrm{S}, 47^{\circ} 38^{\prime} \mathrm{W}\right)$ on highway to Sete Barras ( $24^{\circ} 23^{\prime} \mathrm{S}, 47^{\circ} 55^{\prime} \mathrm{W}$ ); camp on left bank Ribeirão Fundo, where the stream crosses highway to Sete Barras and empties into the Rio Juquiá; swamps, second growth. A. M. Olalla, July, September, October 1961.
5. Quadro Penteado, São Paulo; ca. $24^{\circ} 20^{\prime} \mathrm{S}, 48^{\circ} 09^{\prime}$ W; $50 \mathrm{~m} ; 31 \mathrm{~km}$ W Sete Barras; camp near junction Rio Etá and Ribeirão Brazinho, in Rio Ribeira do Iguapé basin; mostly primary forest. A. M. Olalla, October, November 1961.

Table 1. Measurements (in millimeters) and diploid chromosome numbers ( 2 n ) of taxa of Akodon boliviensis group and some related akodonts. Shown are means, extremes in parentheses, followed by number of specimens; sexes and localities of each taxon are combined. Numbered superscripts refer to notes on following page.

| Taxon | Head and body | Tail | Hind foot with claw | Ear from notch |
| :---: | :---: | :---: | :---: | :---: |
| lindberghi ${ }^{1}$ | $92(86-94) 6$ | 63 (56-66) 6 | 18.7 (18-19) 6 | 13.3 (13-14) 6 |
| sanctipaulensis ${ }^{2}$ | $93(86-100) 4$ | 72 (63-81) 4 | 23.8 (23.3-25) 4 | 15 (13-17) 4 |
| boliviensis ${ }^{3}$ | $99(90-115) 11$ | 62 (55-66) 11 | 21 (20-22) 11 | - |
| alterus ${ }^{4}$ | 91, 89, 100 | 63, 61, 78 | 19, 19, 20 | 13, 13, 13 |
| tucumanensis ${ }^{5}$ | $92(80-115) 10$ | 70 (50-75) 9 | 21 (18-25) 10 | - |
| subfuscus ${ }^{6}$ | 97 (83-107) 11 | $71(62-82) 11$ | 21 (19-23) 12 | - |
| azarae ${ }^{7}$ | $100(92-114) 24$ | $68(57-83) 24$ | 20.2 (19-22) 21 | - |
| puer | 84 (75-94) 5 | $71(70-75) 5$ | $18(15-20) 5$ | $15(15-15) 4$ |
| caenosus $^{8}$ | 98 (85-103) 9 | 60 (56-64) 9 | 19 (18.5-19.5) 9 | - |
| iniscatus ${ }^{9}$ | 95 (86-102) 5 | 63 (58-66) 5 | 19.7 (18-20) 5 | $12(11.5-13.5) 5$ |
| lutescens ${ }^{10}$ | $78(76-81) 5$ | 60 (57-64) 5 | 19.4 (19-20) 5 | - |
| amoenus ${ }^{11}$ | 93 (84-100) 5 | 63 (61-67) 5 | $21.2(21-22) 5$ | - |
| nigrita ${ }^{12}$ | $96(82-116) 15$ | 45 (30-50) 15 | 19 (16-20) 17 | $11(10-12) 12$ |
| dolichonyx ${ }^{13}$ | 87 (77-94) 14 | 55 (47-66) 14 | 20.3 (19-22) 14 | - |
| breviceps ${ }^{14}$ | 104.3 | 42.21 (30-52) 19 | 18.29 (16-21) 21 | 9.7 (8-10) 21 |
| xanthorhinus ${ }^{15}$ | 92 (88-94) 5 | 56 (52-58) 5 | 20.8 (20.5-21) 5 | - |
| longipilis ${ }^{16}$ | $126(118-141) 6$ | $91(79-105) 6$ | $29(28-31) 6$ | - |


| Taxon | Weight <br> $(\mathrm{g})$ |  | Greatest skull length | Condylobasal length |
| :--- | :--- | :--- | :--- | :--- | Zygomatic breadth | Z |
| :--- |
| lindberghi $^{1}$ |
| sanctipaulensis $^{2}$ |
| boliviensis $^{3}$ |


| Taxon | Least interorbital width | Braincase width | Frontal bone length | Nasal bone length |
| :---: | :---: | :---: | :---: | :---: |
| lindberghi ${ }^{1}$ | 4.8 (4.6-4.9) 5 | 11.12 (11.1-11.2) 5 | 8.7 (8.4-9.1) 5 | 8.2 (7.9-8.4) 5 |
| sanctipaulensis ${ }^{2}$ | 4.5 (3.5-5.3) 4 | 12.0, -, 11.9 | 8.5 (8.1-9.2) 4 | 10.1 (9.5-10.4) 4 |
| boliviensis ${ }^{3}$ | 4.2 (4.1-4.4) 10 | $11.2(10.8-11.5) 8$ | 9.2 (8.6-10.0) 10 | 8.5 (7.9-9.8) 9 |
| alterus ${ }^{4}$ | 4.2, 4.4, 4.3 | $-, 11.0,11.6$ | 8.7, 9.2, 9.9 | 8.5, 8.3, 9.2 |
| tucumanensis ${ }^{5}$ | 4.4 (4.1-4.7) 10 | 11.3 (10.7-11.7) 9 | 9.1 (8.7-9.8) 10 | 8.0 (8.4-9.7) 10 |
| subfuscus ${ }^{6}$ | 4.5 (4.2-4.7) 12 | 11.4 (11.1-11.7) 12 | 8.3 (6.7-9.5) 12 | 9.2 (8.0-10.6) 11 |
| azarae ${ }^{7}$ | 4.1 (3.8-4.5) 23 | 11.2 (10.7-11.7) 24 | 8.8 (8.2-9.4) 21 | 8.8 (8.1-9.8) 21 |
| puer | 4.3 (4.2-4.6) 4 | 10.8 (10.5-11.2) 4 | 7.9 (7.7-8.5) 9 | 8.9, -, 8.1, 8.4 |
| caenosus ${ }^{8}$ | 4.3 (4.1-4.4) 9 | 10.9 (10.4-11.2) 9 | 8.1 (7.7-8.5) 9 | 8.5 (7.7-8.5) 9 |
| iniscatus ${ }^{9}$ | $4.1(4.0-4.2) 5$ | 11.4 (11.2-11.9) 5 | 9.0 (8.5-9.6) 4 | 9.0 (8.6-9.5) 4 |
| lutescens ${ }^{10}$ | 4.1 (4.0-4.2) 5 | 10.7 (10.4-10.9) 5 | 7.9 (7.2-8.4) 5 | 7.8 (7.3-8.1) 4 |
| amoenus ${ }^{11}$ | 4.3 (4.1-4.6) 5 | 11.0 (10.8-11.3) 5 | 9.1 (8.7-9.3) 5 | 7.7 (7.2-8.3) 5 |
| nigrita ${ }^{12}$ | 5.0 (4.7-5.4) 17 | 11.5 (10.8-12.1) 12 | 7.4 (6.5-8.1) 8 | 9.2 (8.1-10.0) 14 |
| dolichonyx ${ }^{13}$ | 4.0 (3.8-4.1) 8 | 11.3 (10.9-11.8) 8 | 7.2 (5.8-7.9) 9 | 8.7 (7.6-9.3) 9 |
| breviceps ${ }^{14}$ | 6.79 (6.5-7.2) 20 | - | - | 11.3 (10.9-12.0) 4 |
| vanthorhinus ${ }^{15}$ | 3.9 (3.8-4.0) 5 | 11.5 (10.9-12.0) 5 | 7.5 (7.1-8.0) 5 | 9.5 (8.8-9.9)'5 |
| longipilis ${ }^{16}$ | 5.0 (4.8-5.2) 6 | 13.9 (13.4-14.1) 6 | 9.4 (8.5-9.8) 6 | 12.5 (11.6-13.1) 6 |


| Taxon | Incisive foramina | Palatal bridge | Mesopterygoid fossa | Zygomatic plate ant.-post. |
| :---: | :---: | :---: | :---: | :---: |
| lindberghi ${ }^{1}$ | 6.2 (5.9-6.7) 5 | 2.9 (2.7-3.1) 5 | 1.3 (1.0-1.4) 5 | 1.8 (1.7-1.9) 5 |
| sanctipaulensis ${ }^{2}$ | 5.9 (5.7-6.1) 4 | $3.5(3.2-4.1) 4$ | $1.6,1.4,2.0,-$ | 2.0 (1.9-2.0) 4 |
| boliviensis ${ }^{3}$ | 5.6 (5.2-5.9) 10 | 3.3 (3.0-3.8) 10 | 0.9 (0.6-1.0) 10 | 2.2 (2.0-2.6) 10 |
| alterus | 5.7, 5.5, 6.4 | $3.0,3.3,3.6$ | -, 1.2, 0.9 | 2.2, 2.2, 2.3 |
| tucumanensis | 6.1 (5.4-6.8) 9 | $3.2(3.0-3.4) 7$ | $1.0(0.9-1.1) 7$ | $2.2(1.8-2.5) 10$ |
| subfuscus ${ }^{\circ}$ | 5.9 (5.5-6.5) 11 | 3.3 (2.9-3.8) 12 | $1.3(1.0-1.8) 10$ | 2.0 (1.7-2.4) 12 |
| azarae ${ }^{7}$ | 6.1 (5.6-6.8) 23 | $3.2(2.1-3.6) 23$ | $1.3(0.9-1.6) 21$ | $2.2(1.9-2.4) 24$ |
| puer | 5.7 (5.4-6.2) 4 | $2.9(2.8-3.1) 4$ | $1.0(8.1-1.1) 4$ | 2.2 (2.0-2.5) 4 |
| caenosus ${ }^{8}$ | $5.7(5.1-6.1) 9$ | 3.1 (2.7-3.4) 9 | $0.99(0.8-1.2) 9$ | 2.0 (1.9-2.2) 9 |
| iniscatus ${ }^{9}$ | 5.8 (5.5-6.2) 5 | -,,- 3.6 | 0.98 (0.9-1.0) 5 | 2.6 (2.3-2.8) 5 |
| lutescens ${ }^{10}$ | 5.4 (5.1-5.7) 5 | $3.1(3.0-3.2) 5$ | $1.0(0.8-1.2) 5$ | $1.9(1.6-2.1) 5$ |
| amoenus ${ }^{11}$ | 5.6 (5.3-6.0) 5 | 3.7 (3.1-4.2) 5 | $1.1(1.0-1.2) 5$ | 2.5 (2.3-2.7) 5 |
| nigrita ${ }^{12}$ | 5.4 (4.9-5.9) 17 | $3.8(3.5-4.1) 16$ | $1.3(1.1-1.4) 12$ | 2.3 (2.0-2.7) 17 |
| dolichony $x^{13}$ | 5.2 (4.7-5.7) 10 | 3.5 (3.2-3.6) 10 | $1.2(1.0-1.3) 10$ | 2.16 (2.0-2.3) 9 |
| breviceps ${ }^{14}$ | 5.03 (4.3-5.4) 18 | - | - | - |
| xanthorhinus ${ }^{15}$ | 6.0 (5.3-6.3) 5 | 3.6 (3.4-3.7) 5 | $1.0(0.9-1.2) 5$ | $1.9(1.8-2.0) 5$ |
| longipilis $^{16}$ | 7.4 (6.9-7.9) 6 | $4.5(4.2-4.7) 6$ | $1.9(1.7-2.0) 6$ | 2.6 (2.4-2.9) 6 |


| Taxon | Rostrum greatest breadth | Molar row (alveolar) | Greatest bullar width | Diploid chromosome number |
| :---: | :---: | :---: | :---: | :---: |
| lindberghi' | 4.4 (4.3-4.5) 5 | 4.0 (3.9-4.1) 5 | 3.9 (3.7-4.0) 5 | 42 (Svartman, pers. comm.) |
| sanctipaulensis ${ }^{2}$ | 4.3, -, 4.3, 4.3 | 4.15 (4.1-4.3) 4 | 4.4, -, -, - | - |
| boliviensis ${ }^{3}$ | 4.6 (4.4-4.8) 10 | 4.0 (3.9-4.1) 10 | 4.3 (4.1-4.6) 10 | 40 (Bianchi et al., 1971) |
| alterus ${ }^{\text {d }}$ | 4.2, 4.4, 4.6 | 4.3, 4.0, 4.4 | 4.2, 3.9, 4.1 | - |
| tucumanensis ${ }^{5}$ | 4.5 (4.3-4.8) 10 | $4.1(3.9-4.6) 10$ | 4.0 (3.8-4.2) 9 | 40 (Bianchi et al., 1971) |
| subfuscus ${ }^{\text {b }}$ | 4.4 (4.2-4.7) 11 | $3.9(3.5-4.5) 12$ | 4.0 (3.9-4.3) 12 | - |
| azarae' | 4.3 (3.9-4.7) 21 | 4.1 (3.8-4.3) 24 | 4.1 (3.9-4.6) 24 | 38/37 (Bianchi and Contreras, 1967) |
| puer | 4.0 (3.7-4.1) 4 | 3.6 (3.5-3.7) 4 | 4.0 (3.9-4.1) 4 | 34 (Vitullo et al., 1980) |
| caenosus ${ }^{\text {s }}$ | 4.2 (4.0-4.3) 9 | 3.5 (3.4-3.7) 9 | 3.9 (3.5-4.3) 9 | 34 (Barquez et al., 1980) |
| iniscatus ${ }^{9}$ | 4.62 (4.6-4.7) 4 | 3.9 (3.3-4.3) 5 | 4.0 (3.7-4.2) 5 | 33/34 (Barros et al., 1990) |
| lutescens ${ }^{10}$ | 4.1 (3.9-4.2) 5 | 3.6 (3.4-3.7) 5 | 4.02 (4.0-4.1) 5 | - |
| amoenus ${ }^{11}$ | 4.5 (4.2-4.8) 5 | 4.1 (3.9-4.3) 5 | 4.4 (4.3-4.6) 5 | 34 (Armada et al., 1983) |
| nigrita ${ }^{12}$ | 4.6 (4.4-5.0) 17 | $3.7(3.5-3.9) 17$ | 4.1 (3.9-4.2) 8 | 52 (Yonenaga, 1975) |
| dolichonyx ${ }^{13}$ | 4.2 (3.5-4.5) 9 | 3.4 (2.8-3.7) 9 | 4.4 (3.8-4.7) 8 | 52 (of Akodon andinus, Armada et al., 1983) |
| breviceps ${ }^{14}$ | - | 4.41 (4.42-4.6) 20 | - | Armad er al., 1983) |
| xanthorhinus ${ }^{\text {'s }}$ | 4.4 (4.2-4.5) 5 | 3.5 (3.4-3.8) 5 | 4.3 (4.2-4.6) 5 | 52 (Bianchi et al., 1971) |
| longipilis ${ }^{16}$ | 5.4 (5.1-5.7) 6 | 4.8 (4.5-5.1) 6 | 5.0 (4.8-5.2) 6 | 52 (Gallardo, 1982) |

${ }^{\text {' }}$ See Table 3 for individual measurements.
${ }^{2}$ See Table 4 for individual measurements.
${ }^{3}$ Akodon spegazzinii Thomas, 1897, with diploid chromosome number 40 (Bianchi et al., 1971), is treated as a subspecies by Cabrera (1961, p. 441).
${ }^{4}$ See 5 .
${ }^{5}$ Akodon tucumanensis J. A. Allen, 1901, is treated as a subspecies of Akodon bolivianus, with Akodon alterus Thomas, 1919, a synonym, by Cabrera (1961, p. 441 ).
${ }^{6}$ Originally described by Osgood (1944, p. 195), as a subspecies of Akodon boliviensis.
${ }^{7}$ Ratton agreste Brants, 1827, is a senior synonym of Mus azarae Fischer, 1829 (figs. 7-9 this paper); junior synonyms or subspecies include Mus (Habrothrix) arenicola Waterhouse, 1837, Akodon azarae bibianae Massoia, $1971(2 \mathrm{n}=38$, Vitullo et al., 1986), and possibly Habrothrix arenicola fossilis Ameghino, 1889. Akodon arenicola hunteri Thomas, 1917 and Akodon sylvanus Thomas, 1921, both treated as subspecies of Akodon azarae, by Cabrera (1961, pp. 440-441) may be conspecific with each other but apparently not with the smaller A. azarae. They are referred here to the Akodon mollis group.
${ }^{8}$ Originally described by Thomas, 1918 (p. 189) as a subspecies of Akodon puer Thomas, 1902, but Thomas (1920, p. 191) later regarded it as distinct.
${ }^{9}$ Includes collinus Thomas, 1919, as a subspecies; Akodon nucus Thomas, 1926, listed as a subspecies of puer by Cabrera (1961, p. 443) appears to be unrelated. Akodon iniscatus is notable for its extremely wide zygomatic plate with greater than usual projection beyond the anteorbital foramen.

Table 1. Continued.
${ }^{10}$ According to Sanborn (1949, p. 315) Akodon lutescens J. A. Allen, 1901, is a subspecies of Akodon andinus with Akodon andinus polius Osgood a synonym. However, A. lutescens, with polius a synonym, belongs to the Akodon boliviensis class whereas $A$. andinus does not (see 13 below).
${ }^{11}$ Bolomys amoenus Thomas, 1900, type species. Bolomys Thomas, 1916, is listed as a subgenus of Akodon by Cabrera (1961, p. 453), and as a genus by Reig (1987, p. 356), who includes the following named forms in the genus: amoenus Thomas, 1900
arviculoides Wagner, 1842 (as a synonym of lasiurus)
benefactus Thomas, 1919 (as a synonym of obscurus)
brachyurus Wagner, 1845 (as a synonym of lasiurus)
elioi Contreras, 1982 (as a subspecies of temchuki)
fuscinus Thomas, 1897 (as a possible subspecies of lasiurus)
lactens Thomas, 1918
lasiotis Lund, 1838 (as a synonym of lasiurus)
lasiurus Lund, 1838
lenguarum Thomas, 1898
leucolimnaeus Cabrera, 1926 (as a possible subspecies of lactens)
liciae Contreras, 1982 (as a subspecies of temchuki)
negrito Thomas, 1926 (as a synonym of lactens)
obscurus Waterhouse, 1837
orbus Thomas, 1919 (as a synonym of lactens)
pixuna Moojen, 1943 (as a possible subspecies of lasiurus)
tapirapoanus J. A. Allen, 1916 (as a probable synonym of lenguarum)
temchuki Massoia, 1982
The diploid chromosome number 34 has been recorded (cf. Reig, 1987, p. 356) for specimens referred to amoenus, elioi, lactens, lasiurus, lenguarum, liciae, obscurus, and temchuki. According to Maia and Langguth (1981), the basic diploid number for samples of arviculoides from Pernambuco is 16 (FN 26/25). This species, therefore, cannot be conspecific with lasiurus (figs. 3-5). It has been combined with Bolomys as well as Akodon but may belong with neither genus (cf. Ximénez and Langguth, 1970, for type skull of arviculoides). The taxonomic status of remaining named forms with karyotypes unknown or morphological affinities unclear, is subject to confirmation.
${ }^{12}$ Thaptomys nigrita Lichtenstein, 1829. Thaptomys Thomas, 1916, is listed as a subgenus of Akodon by Cabrera (1961, p. 452). According to Reig (1987, p. 358), "separation of Thaptomys from Akodon s.s. is unwarranted" because, he avers, nothing distinguishes the taxon "beyond the limits of variation with Akodon s.s." The peculiarity of a single pair of prostate glands in Thaptomys nigrita, demonstrated by Voss and Linzey (1981), was not esteemed by Reig, albeit its presence in Microxus bogotensis was deemed significant (Reig, 1987, p. 360). This derived character, found only in Thaptomys nigrita and Microxus bogotensis (a species questionably identified with Microxus) in a sampling of 59 species representing 35 genera of South American cricetids, cannot be judged arbitrarily. In addition, characters of Thaptomys such as the short tail, heavy skull, ridged parietals, short, thick rostrum with long nasal bones, wide interorbital region, squared braincase, relatively small molars, long powerful proodont incisors, and the diploid chromosome number 52, are singly or in combination non-Akodon.
${ }^{13}$ Hesperomys dolichonyx Philippi, 1896, treated as a subspecies of Akodon andinus by Osgood (1943, p. 179) is not an Akodon (sensu stricto).
${ }^{14}$ Blarinomys breviceps, type and only species; measurements from Abravaya and Matson (1975, p. 4), include total length ôo $142.4(129-157) 11$, $\uparrow 9152.1(143-161) 8$, sexes combined, $146.5(129-161) 19$; mean tail, sexes combined, 42.2; mean HB (= mean TL minus mean tail) 104.3; tail : HB, sexes combined, 40.4.
${ }^{15}$ Abrothrix xanthorhinus; regarded as a subspecies of olivaceus by Yañez et al. (1979).
${ }^{16}$ Abrothrix longipilis Waterhouse, 1837, type species (fig. 5, molars). Abrothrix Waterhouse, 1837, is listed as a subgenus of Akodon by Cabrera (1961, p. 454). Reig also treats Abrothrix as a subenus of Akodon with recognized species hershkovitzi, illuteus, lanosus, longipilis, mansoensis, sanborni, and xanthorhinus.

Abrothrix Waterhouse, if restricted to A. longipilis, A. sanborni, and possibly A. illuteus, has the semblance of a valid genus separable from all other genera. The baculum of the first two species is simple, exceptional for sigmodontines including all akodonts, but obviously derived from the complex type. It is poles apart from the simple peromyscine type derived independently from a complex type (but see Carleton, 1980). Akodon longipilis and $A$. sanborni also share similar karyotypes $(2 \mathrm{n}=52, \mathrm{FN}=58)$. That of A. illuteus is the same (Liascovich et al., 1989), but morphology of its baculum is unknown. The karyotype of Akodon xanthorhinus is characterized by $2 \mathrm{n}=52$, $\mathrm{FN}=56$. Those of $A$. lanosus, $A$. hershkovitzi, and $A$. mansoensis are unknown.
Table 2. Ratios $(\times 100)$ of some cranial and external measurements of taxa in Table 1.

| Taxon | Zygomatic plate | Interorbital | Interorbital | Nasals | Tail |
| :---: | :---: | :---: | :---: | :---: | :---: |
|  | Interorbital | Braincase | $\overline{\text { Skull greatest length }}$ | Frontal | Head and body |
| lindberghi | $39(35-40) 5$ | 42.6 (41-44) 5 | 20.0 (19.5-21.0) 5 | $94(92-95) 5$ | $70(64-76) 6$ |
| sanctipaulensis | -, 57, 40 | $-,-, 41,45$ | -, - -, 19.1 | $118(110-125) 4$ | 77 (69-87) 4 |
| boliviensis | 51 (48-62) 10 | $38(37-39) 8$ | 17.2 (16.4-17.8) 9 | 93 (87-102) 10 | $63(52-72) 11$ |
| alterus | 52, 50, 53 | -, 40, 37 | $17.5,19.3,16.5$ | $98,90,93$ | $69,69,78$ |
| tucumanensis | $49(41-57) 10$ | $39(38-41) 8$ | 18.1 (16.7-18.5) 9 | $98(93-108) 10$ | 75 (62-90) 9 |
| subfuscus | 45 (40-52) 6 | $39(37-41) 12$ | 18.2 (17.6-18.9) 11 | 108 (93-117) | 74 (62-93) 11 |
| azarae | 53 (46-62) 22 | 37 (34.5-40.5) 23 | 17.0 (15.3-19.0) 20 | 99 (93-108) 19 | 67 (58-79) 23 |
| puer | 51 (46-58) 4 | $40(38-44) 4$ | 17.6, -, 18.3, 17.7 | 107, -, 103, 105 | $85(80-93) 5$ |
| caenosus | 46 (43-51) 9 | 39.4 (38.5-40.4) 9 | $18.2(17.5-19.1) 9$ | $105(98-110) 8$ | 61 (55-67) 9 |
| iniscatus | $64(57-70) 5$ | 36 (34-37) 5 | $15.9,15.7,17.0$ | $100(94-107) 4$ | 65 (64-67) 4 |
| lutescens | 46 (40-50) 5 | 38.6 (37.4-39.6) 5 | 18.3 (18.1-18.6) 5 | $99(91-110) 4$ | $76(70-84) 5$ |
| amoenus | 58 (53-61) 5 | $40(38-43) 5$ | 18.0 (17.2-18.7) 5 | $82(78-87) 5$ | $68(65-73) 5$ |
| nigrita | 45 (38-50) 17 | $43(38-47) 12$ | 20.9 (20.0-21.8) 12 | 126 (100-139) 8 | $47(34-53) 15$ |
| dolichonyx | 54 (49-58) 9 | $35(34-36) 8$ | $16.9(15.9-18.1) 8$ | $121(106-140) 9$ | $63(52-78) 14$ |
| breviceps | - | - | - | - | $40.4^{1}$ |
| xanthorhinus | 48 (45-50) 5 | 34.2 (31.7-35.8) 5 | 15.8 (15.0-16.6) 5 | $126(115-139) 5$ | $60(55-62) 5$ |
| longipilis | $52(49-59) 6$ | 35.8 (34.8-37.2) 6 | 15.6 (14.7-16.6) 6 | $135(122-155) 6$ | 72 (66-79) 6 |

Table 3. External and cranial measurements (in millimeters) of Akodon lindberghi.

| FMNH $n$ \%. | Sex | Head and body | Tail Hind foot |  | t Ear | Weight (g) | Greatest skull length | Condylobasal length | Zygomatic breadth | interorbital | Interparietal width/length |  | Braincase width/ length |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| $128292^{1}$ | ¢ | 86 | 65 | 19 | 13 | 21 | 24.4 | 22.7 | 12.1 | 4.9 |  |  | 1.1/16.3 |
| 128293 | ¢ | 92 | 65 | 19 | 13 | - | 24.3 | 22.9 | 12.0 | 4.8 |  |  | 1.1/17.0 |
| 128294 | ¢ | 93 | 62 | 18 | 14 | - | - | - | - | - |  |  | - |
| 128295 | ¢ | 91 | 66 | 19 | 13 | 16 | 24.3 | 22.9 | 12.4 | 4.8 |  |  | 1.1/17.2 |
| 128297 | ¢ | 87 | 56 | 18 | 14 | 16 | 23.5 | 21.7 | 11.8 | 4.6 |  |  | 1.1/16.3 |
| 128298 | ¢ | 93 | 63 | 19 | 13 | 19 | 24.1 | 22.3 | 12.1 | 4.7 |  | 1.7 | 1.2/16.9 |
| $128296^{2}$ | ¢ | 67 | 49 | 17 | 13 | 11 | - | - | 11.2 | 4.6 |  |  | 0.9/15.1 |
| FMNH $n$ \% | Frontal bone length | Parietal sutures (across) |  | sals I <br> width  | Incisive foramina | Palatal bridge | Diastema | Mesopterygoid fossa | Zygomatic plate | Rostrum | Molar row | Greatest bullar width | Mandible length |
| $128292^{1}$ | 9.1 | 8.3 |  | /3.6 | 6.1 | 3.0 | 6.3 | 1.4 | 1.7 | 4.5 | 4.1 | 3.8 | 15.0 |
| 128293 | 9.0 | 7.2 |  | /3.6 | 6.7 | 2.7 | 6.1 | 1.4 | 1.9 | 4.4 | 4.1 | 3.8 | 14.4 |
| 128294 | - | - |  | /- | - | - | - | - | - | - | - | - | - |
| 128295 | 8.5 | 8.7 |  | /3.8 | 6.5 | 3.1 | 6.2 | 1.2 | 1.9 | 4.5 | 4.1 | 3.7 | 15.0 |
| 128297 | 8.4 | 7.7 |  | /3.3 | 5.9 | 2.8 | 5.2 | 1.0 | 1.8 | 4.4 | 4.0 | 4.0 | 14.9 |
| 128298 | 8.5 | 8.2 |  | /3.5 | 6.0 | 2.9 | 6.1 | 1.3 | 1.9 | 4.3 | 3.9 | 4.0 | 14.9 |
| $128296{ }^{2}$ | - | 8.1 |  | /3.0 | 5.6 | 2.8 | - | - | 1.5 | - | 3.9 | 3.6 | 13.2 |

## Characters (figs. 2-6)

Morphometric (tables 1, 2) - External measurements by various collectors recorded here are not strictly comparable and some may be misleading; cranial measurements are by the author. Combined head and body length between 73 and 117 (?); tail between $49(?)$ and 85 , tail relative to head and body length between $52 \%$ and $94 \%$; hind foot to longest toe with claw between $15(?)$ and 26 ; ear, usually hidden in fur, between 12 and 15 ; weight probably between 15 and 22 grams; greatest skull length, 22-27; condylobasal length, 20.1-24.8; interorbital constriction, 3.8-4.9; alveolar length of upper molar row, 3.3-4.6
External-Upper parts of body from tip of rostrum to tail base dominantly dark brown (exceptionally dominantly buffy or ochraceous), the hairs blackish (eumelanin) with a single narrow subterminal ochraceous or buffy (pheomelanin) band, length middorsally $5-10 \mathrm{~mm}$; contrastingly colored pheomelanin eye ring and dominantly or entirely pheomelanin snout sometimes present; cheeks like crown or contrastingly ochraceous; whitish postauricular patch absent, mystacial vibrissae short, when laid back extending to between eye and middle of ear base. Sides of body like back or with pheomelanin subterminal band of hairs broader and usually more saturate, to ochraceous orange, lateral stripe present or absent. Underparts from chin to tail base weakly to sharply defined from sides of body, the hairs dominantly ochraceous or buffy superficially, the slaty basal portion showing prominently at the surface; chin like throat or chest, rarely contrastingly whitish. Tail more or less uniformly colored to sharply bicolor, thinly pilose, the scales fully exposed or partially concealed. Hind feet with upper surface thinly to thickly covered with stiff ochraceous to buffy or whitish hairs, the scaly brown skin fully exposed to nearly entirely concealed; digital bristles varying from short or thin, the claws fully exposed, to long, thick, nearly completely concealing claws; fifth digit, less claw (s.u.), extending to base of first, second, or rarely third phalanx of fourth digit; first digit with or without claw never extending beyond base of second digit; claws of middle digits from 2 to 4 mm long, extending $1.5-3 \mathrm{~mm}$ beyond phalangeal tips. Extension of webbing between toes and fingers from slightly proximad to slightly distad of base of second phalanges; two middle toes and two middle fingers sometimes syndactylous; thumb with nail not extending to base of second digit.

Remarks on Tegumentary Coloration (fig. 2)The primitive agouti cover-hair pattern for the Akodon boliviensis group and all other akodonts is characterized by a single pheomelanin band between eumelanin tip and eumelanin basal portion of the hair. The typical ancestral mammalian agouti pattern with two pheomelanin bands on the terminal portion of the hair was modified by reduction and elimination of one pheomelanin band in the dorsal pelage, and reduction to nearly complete or complete elimination of the terminal eumelanin band in the ventral pelage. This may be accompanied in some species by expansion of the eumelanin base of the hairs. The evolutionary trend in others may be toward partial or complete dominance on both upper and lower parts of the body by either of the two melanins. Markings, or contrasted chromogenetic fields such as eye rings, snout tip, chin, postauricular patches, pectoral streak, and spotting, vary from saturate (reddish or orange) to bleached (buffy or whitish) monochromatic pheomelanin. Markings in dominantly pheomelanin akodonts may be either eumelanin (brownish) or a contrasted tone of pheomelanin.

Primitive sensory hairs, not the same as the strictly mammalian cover hairs, were inherited from the reptilian ancestry. They appear as vibrissae, guard hairs, interscutellate tail hairs, and digital bristles. Such hairs are typically monochromatic eumelanin, often bleached to grayish or white. Variation and evolution of mammalian tegumentary colors, termed metachromism, are discussed in detail by Hershkovitz in several publications, the first in 1968, the most recent in 1988.

Cranial (figs. 3, 4)-Smooth, without sagittal, lambdoidal, occipital, interorbital, or temporal crests, ridges, or beading; dorsal contour from nasal tips to parietal bones broadly arced to nearly plane; nasal bones tapered distally, length about $10 \%$ shorter to $17 \%$ longer than frontal bone at midline suture, tips rounded to pointed, not flared or trumpet-shaped, and separated from and extending distad of premaxillary bone; sides of interorbital region nearly parallel to concave with divergence posteriorward; rostrum in front of opposing zygomatic plates from slightly wider to slightly narrower than width of interorbital region at constriction; braincase moderately inflated, rarely globose, the supraoccipital bone rounded above, rounded to nearly plane behind, occipital condyles not projected behind vertical plane of supraoccipital bone; zygomatic arches convergent anteriorly, the bones delicate, the jugal often threadlike; zygomatic plate narrow, more or less


Fig. 2. Saturation of agouti cover-hair through eumelanin (blackish-brown) pathway and pheomelanin (reddishyellow) pathway. In model shown, only terminal portion of hair is banded and subject to saturation. The basal portion is saturate melanin. Two or three pheomelanin bands separated by eumelanin bands is regarded as the primitive mammalian pattern. The modified agouti (2) hair of the eumelanin pathway is primitive for dorsum and sides of akodonts, the same or the modified agouti (2) of the pheomelanin pathway is primitive for the underparts, certain markings, rarely for dorsum and sides. Saturation may proceed stepwise in either pathway, as shown here, or may leap from agouti to stage 3,4 , or 5 . The basal portion of the hair is chromogenetically independent from the terminal portion. It is also subject to saturation and bleaching. The rates of change are usually uneven, but insofar as known the direction of change is irreversible. (Adapted from Hershkovitz, 1968.)
upright or reclined, little to hardly projected anteriorly beyond antorbital foramen; incisive (anterior) palatal foramina long, extending back to anterior plane of $\mathrm{m}^{1}$ or beyond to midplane of tooth, the foramina expanded anteriorly, contracted posteriorly but always wider than mesopterygoid fossa at palatal border; palate extending to posterior plane of $\mathrm{m}^{3}$ or slightly beyond; molar rows parallel-sided to slightly convergent behind, palatal width between molar rows greater than length of first molar; sphenopalatine vacuities usually widely expanded but sometimes narrowed to
short slits or almost completely absent; tympanic bullae not conspicuously inflated.

Dental (fig. 5)-Upper incisors orthodont to opisthodont, never proodont, enamel pigmented yellow to orange, length in straight line from symphysis subequal to length of $\mathrm{m}^{1-2}$ but less than that of $\mathrm{m}^{1-3}$.

Upper molars moderately hypsodont, unworn crowns crested or bilevel. First molar with anteromedian flexus usually deeply penetrant, sometimes not defined, the procingulum biconulate with anterolabial and anterolingual conules usually well
defined, sometimes not defined; talon and trigon minus procingulum subequal in width and length; paralophule (pseudomesoloph) present, often fused with metalophule if present. Second molar shorter than first minus procingulum, otherwise similar. Third molar as large as, to slightly smaller than, talon of second molar, hypoflexus and posteroflexus shallow but often persistent in worn tooth, the latter as an island.

Lower molars moderately hypsodont, the first molar with staggered cusps, procingulum slightly larger than half bulk of trigonid, anteromedianflexid penetrant, exceptionally absent, anterolabial and anterolingual conulids well defined, exceptionally not defined (mainly in A. mollis class), protolophid and posterolophid present, sometimes not well defined. Second molar with trigonid and talonid subequal in length and breadth; cusps of opposite sides staggered or opposed; protolophid, mesolophid, and posterolophid present, ectolophid weakly defined or absent. Third molar narrower but longer than talonid of second molar; trigonid and talonid subequal; cusps usually staggered; posteroflexid suppressed.
Remarks on Dental Morphology and Terminology (figs. 20-22) - Unworn akodont molars are hypsodont (high crowned), the crowns bilevel, sometimes crested, with well defined cones (-ids), conules (-ids), lophs (-ids), lophules (-ids), and styles (-ids). The first (anterior) molar is ovoid or oblong, larger, and more complicated than the others. This is mainly due to expansion and differentiation of the anterior portion of the cingulum, termed procingulum, into a functional and similitudinal replacement of the lost fourth premolar. The second molar, effectively wedged between first and third, is more nearly square, its procingulum abbreviated. The reduced third molar erupts last, the eruption sometimes delayed past weaning.

Erosion of the molar crown topography is rapid. At the time of the individual's maturity, the crown surface may already have been ground to a dished eight-shaped pattern with few of the cingular elements persistent or clearly defined.

The enamel pattern of sigmodontine molar crowns was described and figured by me in 1944, refined with additions in 1962. The diagrammatic pattern and terminology for coronal elements were adopted by various students of New World cricetid dentition, most recently by $\operatorname{Reig}(1980,1987)$. The present plan replaces my term "enamel fold" with Reig's "flexus" each with a distinguishing prefix derived from the name of the enamel element defined by it.

Terminology for sigmodontine molar elements is, in all cases, based on the traditional and still useful Cope-Osborn concept of molar evolution. The similar terms used for upper and lower molar elements distinguished by the suffix "-id," however, do not imply homology between them. This defect of the Cope-Osborn terminology has been explained elsewhere (Hershkovitz, 1970). The system based on homologies of nonrodent crown elements has yet to be effectively extended to the special molar crown patterns of sigmodontines and rodents generally.

Projection of the upper incisor with reference to the basal incisive plane varies from opisthodont to orthodont and proodont (fig. 22).

Karyotypic - The diploid chromosome number is known for 8 of the 13 species of the Akodon boliviensis class (table 1). The number varies from 34 in puer and caenosus, 38/37 in azarae, 40 in alterus, boliviensis, and tucumanensis, to 42 in Akodon lindberghi (Svartman, pers. comm.).

Remarks - The distinctive characters of the two new species described below extend the erstwhile parameters of the Akodon boliviensis class considerably beyond what they would be without them. A better known A. sanctipaulensis might indicate generic separation.

## Akodon mollis Size Class

An alphabetical list of the larger species of Akodon Meyen, 1833 (sensu stricto) follows. Taxa in parentheses may be subjective synonyms, subspecies, or nearest related species of the apposed taxa. The known diploid chromosome numbers, from 24 (cursor) to 44 (dolores, molinae, serrensis), indicate that the class is heterogeneous. Identifications of the specimens listed by name have not been verified against the type specimens. Omitted from the list are species questionably referred to Akodon by authors, and others properly referred to the subgenera or genera Abrothrix Waterhouse, 1837; Chroeomys Thomas, 1916; Chalcomys Thomas, 1916; Deltamys Thomas, 1917; Hypsimys Thomas, 1918; Microxus Thomas, 1909; Thalpomys Thomas, 1916; Thaptomys Thomas, 1916. Skull and molars of Akodon cursor are figured (figs. 3-5) as representative of the $A$. mollis class.

An anteromedianflexus (-id) is probably present in all bonafide species of the Akodon mollis size class. In most type specimens of the species, however, presence or absence of the character cannot


Bolomys lasiurus
 Akodon andinus
 xosxns uopoxy



Fig. 4. Skulls and mandibles, left side of same specimens shown in Figure 3: a, Akodon boliviensis; b, Akodon cursor; c, Akodon andinus dolichonyx; d, Bolomys lasiurus. White bar $=1 \mathrm{~cm}$.
be ascertained because of the excessive coronal wear of their first molars.

> altorum Thomas, 1913 (see mollis) cursor Winge, 1888 (includes montensis)
dolores Thomas, 1916 (includes molinae Contreras, 1968)
fulvescens Hershkovitz, 1940 (see mollis)
fumeus Thomas, 1902 (see mollis)
glaucinus Thomas, 1919 (see varius)


Fig. 5. Right upper and lower left molars of same specimens except $c$ and $d$, shown in Figures 3 and 4: a, Akodon boliviensis; b, Akodon cursor; c, Abrothrix longipilis (FMNH 23123); d, Bolomys lasiurus (FMNH 28336). White bar $=$ 1 mm .
hunteri Thomas, 1917
leucogula Miranda Ribeiro, 1905 (originally proposed as "[Hesperomys] (A[kodon]) serrensis var. leucogula)
markhami Pine, 1973
molinae Contreras, 1968 (see dolores) mollis Thomas, 1894 (includes altorum Thomas, 1913, fumeus Thomas, 1902, fulvescens Hershkovitz, 1940)
montensis Thomas, 1913 (see cursor)
neocenus Thomas, 1919 (see varius)
pervalens Thomas, 1925 (see serrensis)
serrensis Thomas, 1902 (includes pervalens
Thomas, 1925)
simulator Thomas, 1916 (see varius)
surdus Thomas, 1917
tartareus Thomas, 1919 (see varius)
toba Thomas, 1921 (see varius)

Fig. 6. Akodon lindberghi: Cheiridia, dorsal and ventral surface of right hand (upper) and foot (lower). Drawn from dry skin, partially reconstituted by moistening; volar pads are semidiagrammatic. Black bar $=5 \mathrm{~mm}$.



FIG. 7. Skulls of Akodon: Dorsal and ventral aspects of a, Akodon sanctipaulensis (FMNH 94516, holotype); b, Akodon lindberghi (FMNH 128292, holotype); c, Akodon azarae (FMNH 27619). White bar $=1 \mathrm{~cm}$.
varius (specific synonyms or nearly related species include glaucinus, neocenus, simulator, tartareus, toba)

## Akodon lindberghi, new species (Matosa akodon)

Holotype ${ }^{1}$ - Adult male, skin and skull, Field Museum of Natural History no. 128292; collected 7 August 1986, by Philip Hershkovitz and Scott Lindbergh; original number 9589.

COTYPES-Adult males, skin and skulls, FMNH

[^0]nos. 128293, 128295, 128297, 128298; skin only 128294; juvenal female, skin and skull, FMNH no. 128296; all collected by Philip Hershkovitz and Scott Lindbergh.

Etymology-Named for Scott Morrow Lindbergh, without whose devoted and unstinted assistance this species would not have been discovered.

Type Locality - Matosa, a former fazenda now part of the Parque Nacional de Brasilia, about 20 km NW of Brasília, Distrito Federal, Brazil; altitude about $1,100 \mathrm{~m}$.

Distribution (Fig. 1)-All known individuals were captured within a half hectare plot on the periphery of an extensive wet valley side grassland


Fig. 8. Skulls and mandibles of same specimens as shown in Figure 7. a, Akodon sanctipaulensis, right side of skull and right mandible reversed; b, Akodon lindberghi, right mandible reversed; c, Akodon azarae. White bar $=1$ cm.
(campo limpo) cerrado in the Parque Nacional de Brasília, Brasília, DF, Brazil. For a description of cerrado landscape habitats in the Brasilia area see Alho (1982).

Diagnostic Characters - Moderately sized small-footed member of the Akodon boliviensis class; tail about $70 \%$, hind foot about $21 \%$ of combined head and body length; interorbital region extremely broad, mean $20 \%$ of greatest skull length, $43 \%$ of braincase width, incisive foramina extremely long (mean 6.2 mm ); strongly reclined zygomatic plate extremely narrow antero-posteriorly, about $39 \%$ of interorbital breadth, and barely projecting beyond interorbital foramen as seen
from above; auditory bullae small; diploid number of chromosomes, 42.

Measurements-See Tables 1-3.
Comparisons - Long, lax pelage, extremely narrow, strongly reclined interorbital plate, and diploid chromosome number 42 distinguish $A$. lindberghi from all other species of the Akodon boliviensis group.

## Characters (figs. 6-10)

External-Coat thick, hairs of upper and lower surface of body long, lax; dorsal surface from tip of rostrum to tail base dark olivaceous agouti, the


Fig. 9. Molars, right upper and lower left of same specimens shown in Figures 7 and 8. a, Akodon sanctipaulensis; b, Akodon lindberghi; c, Akodon azarae. White bar $=1 \mathrm{~mm}$.
individual hairs $8-10 \mathrm{~mm}$ long middorsally, with one narrow subterminal buffy (pheomelanin) band; mystacial vibrissae short, when laid back extend from between eyes to middle of ears; sides of body brighter, the pheomelanin band broader; lateral line absent; cheeks like sides. Underparts from chin to tail base not sharply defined from sides, hairs buffy to ochraceous terminally, slaty basally, the color broadly exposed at the surface. Tail dark brown above, little paler beneath, thinly pilose, the scales fully exposed. Hind feet (fig. 6) thinly covered with grayish or buffy hairs above, the brown scaly skin exposed; fifth digit less claw extending to base of second phalanx of fourth digit; first digit less claw extending to base of first pha-
lanx of second digit; claws comparatively thick, moderately curved, length (middle pair) about 4 mm , of shortest (first digit) about 3 mm , all extending 2 mm beyond tip of distal phalanges; digital bristles thin, short, not concealing claws; forefeet small, thick, claws extending about 1.2-1.4 mm beyond phalangeal tips. Webs between middle digits of hands and feet extending from slightly distad to slightly proximad to base of second phalanges; plantar tubercles large, the palmar postdigitals apparently adapted for clutching grass stems and slender twigs.

Cranial (figs. 7, 8)-Bones thin, translucent; dorsal contour nearly plane; paired anterior frontal sinuses notably inflated; braincase rounded but


Fig. 10. Akodon lindberghi (FMNH 128292): Glans penis, partially reconstituted from dry tissue and cleared in KOH to reveal baculum. A, baculum from ventral aspect; $\mathbf{B}$, three quarter ventral view of cartilaginous bacular digits; C, lateral view of baculum. a, base of proximal bony shaft. See Figure 11 for identification of other parts. Black bar $=1 \mathrm{~mm}$.
not globular; interparietal bone comparatively long anteroposteriorly; interorbital region extremely wide relative to greatest skull length; zygomatic plate extremely narrow, reclined, hardly or not projecting beyond antorbital foramen as seen from above; width of rostrum in front of zygomatic plates less than least interorbital breadth; zygomatic arches extremely weak, convergent anteriorly; foramen magnum positioned forward, the occipital condyles not produced behind vertical plane of supraoccipital bone; auditory bullae comparatively small; mesopterygoid fossa comparatively wide, parapterygoid fossa as wide proximally, becoming
wider distally; sphenopalatine vacuities widely open; combined foramina ovale and spinosum crossed by pterygoid bridge.

Upper teeth (fig. 9) - Incisors more often orthodont than opisthodont, enamel pigmented yellow to orange; molar rows parallel-sided to slightly convergent behind, crowns moderately hypsodont, persistently cuspidate. First molar with procingulum slightly more than half bulk of trigon, anterior median fold or flexus deeply penetrant and persistent in worn tooth, the anterolingual and anterolabial conules well defined; anteroloph moderately developed; paralophule present in ab-


Fig. 11. Glans penis, partially reconstituted from dry tissue and cleared in KOH to reveal baculum. A, Akodon boliviensis (FMNH 75494), ventral aspect; B, Bolomys lasiurus, ventral aspect; C, Bolomys lasiurus, lateral aspect. a, proximal baculum or bony shaft; $\mathbf{b}$, lateral bacular process or lateral cartilaginous digit; $\mathbf{c}$, distal baculum or middle cartilaginous digit; d, outer crater; $\mathbf{e}$, inner crater; $\mathbf{f}$, dorsal papilla. Black bar $=1 \mathrm{~mm}$.
sence of mesoloph; posteroloph short but well defined. Second molar like first but shorter, the procingulum reduced; talon narrower than trigon. Third molar less than half bulk of second; talon less than bulk of either cusp of trigon; hypoflexus shallow, obliterated with wear, shallow posteroflexus more persistent.

Lower teeth (fig. 9). Incisors with enamel paler than that of corresponding upper incisors. First molar with procingulum slightly more than half bulk trigonid; anteromedianflexid penetrant, anterolingual and anterolabial conulids well defined; accessory features include protolophid, protostylid, ectolophid, ectostylid usually fused with ectolophid, mesostylid, anterolophid, mesolophid, metalophid, metastylid and posterolophid often fused with entoconid; talon wider than trigon and subequal in bulk to trigon plus procingulum; cusps staggered. Second molar with protolophid, ectostylid, mesostylid, posterolophid present, ectolo-
phid weakly defined or absent; lacking are anterolophid, protostylid, and mesolophid; trigonid and talonid subequal in length and breadth; cusps slightly staggered. Third molar with hypoflexid present often as a midcoronal island; posterolophid almost vestigial, usually undefined in worn tooth, posteroflexid suppressed; protolophid greatly reduced; talonid narrower than trigonid but subequal in bulk; cusps staggered.

Karyotype-The diploid number of 42 chromosomes for the species was determined from bone marrow preparations of specimens FMNH 128295 ㅎ and 1282969 by Marta Svartman of the Universidade de São Paulo, São Paulo. Her formal description of the karyotype awaits publication of the name Akodon lindberghi.

Genitalia (fig. 10)-The dried penis of the holotype (FMNH 128292), preserved on the dry skin, was detached and partially reconstituted with water and by clearing in potassium hydroxide $(\mathrm{KOH})$;


Fig. 12. Abrothrix longipilis: Glans penis, partially reconstituted from dry tissue and cleared in KOH to reveal baculum. A, dorsal aspect of proximal baculum; B, ventral aspect showing urinary meatus and ventral lappet; C, lateral aspect; a, enlarged section of penial skin with spines; $\mathbf{b}$, ventral lappet; $\mathbf{c}$, ventral. Black bar $=1 \mathrm{~mm}$ for baculum, .5 mm for spines.
the bone and cartilage were then stained. Nearly all soft parts of the glans were lost. The baculum itself (fig. 10) resembles that of Akodon boliviensis (fig. 11 A ) more nearly than that of Bolomys lasiurus (figs. 11B,C) and differs widely from that of Abrothrix longipilis (fig. 12). Detailed descriptions of the complete glans penis of Akodon boliviensis, and some related species including those of $A$. azarae, Bolomys lasiurus, and other sigmodontines, are given by Hooper and Musser (1964).

Specimens Examined-Total 7. Matosa, Parque Nacional de Brasília, Brasília, DF, 7 (FMNH, holotype and 6 cotypes).

## Akodon lindberghi and the Nomen Nudum Plectomys paludicola

A report by Borchert and Hansen (1983) on the effects of flooding and wildfire on sigmodontines in the Parque Nacional is of particular relevance to the probable history of Akodon lindberghi. Their study areas, .74 hectares each, denominated unburned A, and burned B, were located 1 km apart in the valley side wet campo behind the old Matosa farmhouse, now type locality of $A$. lindberghi. The 147 mice captured during the study included, in
decreasing order of abundance, Bolomys (their Zygodontomys) lasiurus, 42\%; Oxymycterus sp. (their $O$. roberti), $31 \%$; their Plectomys paludicola, 20\%; Oryzomys "eliurus," .05\%; Akodon cursor (their Akodon arviculoides cursor), $01 \%$. Their observations focused on the most abundant species, Bolomys lasiurus, Oxymycterus sp., and the socalled Plectomys paludicola.

The last binomial is puzzling. To my knowledge, neither the generic nor specific name of Plectomys paludicola has ever been described. The name, with no mention of holotype, no indication of a distinguishing character, reference to author, or where or when published, was used by Borchert and Hansen (1983). It was also used in two unpublished student theses on the ecology of cerrado rodents shown me in Brasilia, and in a publication by Alho et al. (1986, pp. 447, 451-452, 454). Notwithstanding, the mice conceived as Plectomys paludicola must be real, and their attributes, including habitat preference, relative abundance, food habits, and circadian rhythms (Borchert \& Hansen, 1983) cannot be dismissed for having been reported under an unrecognized name. In any event, all authors agree that mice they called Plectomys paludicola were found only in the Parque Nacional de Brasília, specifically the Matosa area.

Trapping by me and Scott Lindbergh (fig. 13) in cerrado habitats of the Parque Nacional de Brasilia during August 1986 yielded the following sigmodontines (number of specimens in parentheses): Bolomys lasiurus (12), Oxymycterus sp. (7), Akodon lindberghi (7), Oryzomys subflavus (5), Thalpomys sp. (2), and Thalpomys lasiotis (1). The last binomial takes priority over Akodon reinhardti proposed by Langguth (1975, p. 45) for Ha brothrix lasiotis Winge, 1887, p. 29, and Thalpomys lasiotis Thomas, 1916, p. 339, not the Mus lasiotis of Lund (1840, p. 55).

The above mentioned species, except Akodon lindberghi, are widely distributed throughout the central Brazilian cerrado. The seven specimens of Akodon lindberghi were captured within the Borchert and Hansen (1983) study area A, still identifiable at the time by their grid marking stakes. At least two of the mice were trapped in daylight.

Thalpomys lasiotis, Oryzomys subflavus, and the erstwhile undescribed Akodon lindberghi, are area species not mentioned by Borchert and Hansen. Habitat, distribution, demography, and possibly habits attributed to Plectomys paludicola point more certainly to identity of that mouse with Akodon lindberghi than to either of the others, which are distinctive and too well known to be confused with anything else. Furthermore, the number of


Fig. 13. Matosa habitat of Akodon lindberghi in Parque Nacional de Brasilia, DF; Scott Lindbergh is shown holding live-trapped Oxymycterus sp. with right hand and Oryzomys subflavus with left hand, both species taken in the same trapline with Akodon lindberghi.

Akodon lindberghi captured by us holds a roughly proportional relationship to that of our capture of Bolomys lasiurus and Oxymycterus sp., comparable to the proportional number of Bolomys, $O x$ ymycterus, and Plectomys paludicola trapped by Borchert and Hansen (1933) in the same general area. The fact that the distinctive Matosa akodon lacked a valid scientific name at the time may have invited the use of the unpublished manuscript name Plectomys paludicola, of an anonymous author, possibly João Moojen (1965), the discoverer of Juscelinomys candango of the same region.

## Population Dynamics

All cerrado habitats in Brasília, DF, including the one occupied by Akodon lindberghi, have been thoroughly investigated during the last decade by students of mammalian ecology and demography including, among others, Mello and Moojen (1979), Borchert and Hansen (1983), da Fonseca and Redford (1984), Redford and da Fonseca (1986), Mares
et al. (1986), Nitikman and Mares (1987), Alho (1981), Alho and Pereira (1985), Alho et al. (1986), and Alho and Souza (1982). As noted above, two of the cited references mention the nomen nudum Plectomys paludicola; Borchert and Hansen (1983, p. 237) provide more information than mere name and locality. Excerpts from their paper are quoted below.

## Plectomys paludicola

had a narrow habitat breadth and an even narrower microhabitat preference in wet campo. While the capture distributions of the other two [study] species [Bolomys lasiurus, Oxymycterus "robert""] on area A expanded and contracted during the study, that of $P$. paludicola remained remarkably constant even though its population level fluctuated considerably. Very few individuals were captured at Paspalum [spp. grasses] stations 20 m from the border [of the campos] even after the flood water receded. Apparently, this species travelled along the border because of the frequency with which individuals were captured on opposite borders of the marsh on consecutive nights, but never in the central portion. Nor were captures common in [the introduced grass] Hypahrrenia even though food, at least grass seed, was far more abundant in this area than along the Paspalum border.

Preceding the above statements, Borchert and Hansen (1983, p. 237) note that unlike the more abundant Oxymycterus "roberti" and "Zygodontomys" lasiurus, which were not limited in movements by flooding, their Plectomys paludicola
avoided standing water, yet its own movements were only partially influenced by flooding. Several lines of evidence suggest that this species moves to and from wet campo seasonally, departing after the beginning of the rainy season and returning when the marsh begins to dry. First, individuals disappeared from area A by April even though the preferred microhabitat did not flood. Second, specific attempts to snap trap this species during the rainy season on unburned mounds surrounded by water and along the wet campo border were fruitless, while upland burned and unburned low-tree and scrub savanna yielded a number of individuals. Third, at least one marked male from area A was snap trapped $500-600 \mathrm{~m}$ from the grid in bordering low-tree and scrub savanna, 100 m from the nearest wet campo. Finally, we noted a sudden increase in the abundance of this species in wet campos that were beginning to dry suggesting an influx of individuals from other habitats.

Response to wet campo, altered by an intensive wildfire in late 1978 that burned $60 \%$ of the Parque, also differed significantly among the species. According to Borchert and Hansen (1983, p. 238), Bolomys lasiurus and Plectomys paludicola, both seasonal inhabitants of wet campo, recolonized
area B not long after the fire. Oxymycterus roberti was continuously present in the marsh after the fire. Plectomys paludicola, however, "was the last species to appear in the burned area."

## Survival Status

What is known of Akodon lindberghi, granting identity with Plectomys paludicola, suggests that its restricted geographic range may be too small for survival of the species should the habitat suffer exceptionally severe and long term alteration by flood and fire. Addition of competition by the larger, ubiquitous, and resilient Bolomys and Oxymycterus can result in catastrophic effects. Skulls and molars of Bolomys lasiurus are shown in Figures 3-5.

Our trapping in 1986, and that of Borchert and Hansen (1983) in the wet valleyside grassland (campo limpo) cerrado in the Parque Nacional uncovered a total of eight sigmodontine species. Gallery forest mice in Brasilia are distinct and of no consideration here. Trapping during the same period in 1986, and again in 1988, in surrounding unprotected campo limpo drastically modified by excessive burning, agriculture, and cattle grazing indicated that ultimately only Bolomys and Calomys survive there. Both genera include plague or ratada species, which are the principal reservoirs of pathogenic viruses. In contrast, mice as delicately balanced ecologically as Akodon lindberghi, and the fossorial oxymycterine Juscelinomys candango Moojen (1965), the primary object of our trapping, may not survive in altered habitats. The latter species was discovered in 1960 at the time its natural cerrado niche was being destroyed for accommodation of human facilities. The animal has not been seen since despite intensive search.

The Matosa mouse is neither fossorial nor cryptic. Its existence, almost certainly confined to a small plot of campo limpo in the Parque Nacional de Brasília, is precariously balanced between strong competitors and an undefined microhabitat that narrows progressively with each overall environmental modification.

## Akodon sanctipaulensis, new species (São Paulo marsh akodon)

Holotype-Adult female, skin and skull, fMNH no. 94516 , collected 13 July 1961, by A. M. Olalla, original number 1166 .

Type Locality - Primeiro Morro, São Paulo, Brazil.

Distribution (fig. 1)-Known only from the

north bank of the Rio Juquiá and Rio Etá (between $24^{\circ} 00^{\prime}-24^{\circ} 25^{\prime} \mathrm{S}, 47^{\circ} 35^{\prime}-48^{\circ} 10^{\prime} \mathrm{W}$ ) on the Atlantic coastal plain at the base of the Serra do Mar, extreme southeastern São Paulo State, Brazil.

Diagnostic Characters-Tail relatively long, about $77 \%$ of head and body length; average size of hind foot about 24 mm or extreme for the $A$. boliviensis class; braincase globular, interorbital region short, wide; zygomatic arches extremely delicate, convergent; nasals long, ratio of length to frontal bone at midline high, as in Abrothrix rather than Akodon (s.s.); upper incisors extremely short, length from symphysis less than combined length of $\mathrm{m}^{1-2}$, enamel pale orange to pale yellow; procingulum of first upper molar biconulate, of lower uniconulate or biconulate; $\mathrm{m}_{2}$ with mesolophid present; $\mathrm{m}_{3}$ with posterolingual flexid persistent, usually as island in worn tooth; complete eruption of upper and lower third molars delayed to post weaning juvenal or early subadult stage.

Measurements-See Tables 1, 2, and 4.
Comparisons-Large feet, globular braincase with short interorbital region, relatively long nasals, short incisors, combine to distinguish Akodon sanctipaulensis from equal-aged individuals of all other species of Akodon.

## Characters (figs. 7-9, 14)

External (fig. 14) - Pelage dense, the hairs 7-9 mm long middorsally; dorsal surface from rostrum to tail base nearly uniformly blackish, the hairs blackish (eumelanin) with a single narrow buffy (pheomelanin) subterminal band broader on anterior than on posterior half of trunk; sides of trunk with pheomelanin band wider, more saturate, lateral line absent; cheeks like crown, mystacial vibrissae when laid back extend from eye to midear base. Underparts not defined from sides, dominantly ochraceous orange, the pheomelanin terminal portion and eumelanin basal portion of hairs not banded, chin not contrastingly whitish. Tail brown above, slightly paler beneath, hairs short, the scales fully exposed. Hind feet thinly covered grayish or buffy, brown of scaly skin fully exposed; fifth digit less claw extending to base of first phalanx of fourth digit, first digit less claw extending to base of second digit; claws moderately curved,
of middle digits about 4.5 mm long and extending about 1 mm beyond phalangeal tips; digital bristles short, thin, not concealing claws. Webbing of middle digits of hands and feet usually extending from slightly proximad to slightly distad of second phalanges; in FMNH 94573, middle digits of right hand completely syndactylous, of left hand united to base of distal phalanges, middle digits of right and left feet entirely syndactylous, webbing of adjacent digits extend to base of second phalanges (fig. 14).
Cranial (figs. 7, 8)-Bones smooth, delicate, translucent, dorsal contour with globular braincase raised above long, pointed slender rostrum; paired midfrontal sinuses notably inflated, anterior frontal sinuses less inflated; zygomatic plate reclined but anterior border projecting, as usual, beyond antorbital foramen as seen from above; interorbital region short, wide, the sides strongly divergent; width of rostrum in front of zygomatic plates less than least interorbital width; zygomatic arches extremely weak, convergent; mesopterygoid fossa comparatively wide; parapterygoid fossa wider, with greatest expansion behind; pterygoid bridge complete; sphenopalatine vacuities absent to present and widely expanded; auditory bullae well inflated; interparietal bone little developed.
Dental (fig. 9)-Upper incisors extremely short, opisthodont; upper and lower molars essentially as in the Akodon boliviensis class, except procingulum of $m_{1}$ uniconulate or weakly biconulate as in holotype, incisor enamel extremely pale.

Karyotype-Unknown.
Remarks-Available skulls are of juvenals, young adults, and a skin without skull (FMNH 95413) of an old male. Procingulum of first lower molar is uniconulate in one juvenal and one adult, biconulate in four specimens. Third molar eruption in the juvenals appears to be retarded compared with dental eruption in comparably aged juvenals of other akodonts.

The distinctive characters of Akodon sanctipaulensis suggest those typical of juvenals or newborn. These traits, however, are not shared with comparably aged young of all other Akodon species examined. The 10 specimens of sanctipaulensis were taken by the same collector in the same places at the same times with 91 specimens of Akodon cursor, and 2 of a third unidentified species of

Fig. 14. Akodon sanctipaulensis: Cheiridia, dorsal and ventral surface of right hand (upper) and foot (lower). Drawn from dry skin, partially reconstituted by moistening; digits 3 and 4 of hands and feet are syndactylous, volar pads are semidiagrammatic. Black bar $=5 \mathrm{~mm}$.
Table 4. External and cranial measurements (in millimeters) of Akodon sanctipaulensis.


[^1]

Fig. 15. Skull, dorsal and palatal aspects showing cranial measurements used in text: a, rostrum width; b, least interorbital breadth; c, zygomatic breadth; d, mid-frontal expansion; e, braincase, greatest width.


Fig. 16. Akodont type skull, dorsal aspect.
Explanation of Figures 16-18. Practically all topographic features of the sigmodontine skull are shown except cranial crests and ridges absent in Akodon.

## Bones

```
1 nasal
2 \text { frontal}
3}\mathrm{ parietal
4 interparietal
5 \text { occipital}
6 premaxillary
7 \text { maxillary}
8 jugal; zygomatic
9 squamosal; temporal
```

10 lacrymal
11 auditory or tympanic bulla
12 mastoid, periotic capsule
13 infraorbital foramen or fissure
14 alisphenoid
15 orbitosphenoid
16 basisphenoid
17 presphenoid
18 palatine
(Continued on opposite page)

Akodon. The A. cursor series includes 11 juvenals and young comparable in age to those of the sanctipaulensis series. The latter species differs in the same respects from young A. cursor as it does from the adults. It is apparent that in Akodon, cranial growth pattern from juvenal to adult is one of increase in size with little change in proportions and overall shape. The same likely holds for Akodon sanctipaulensis.

Specimens Examined-Total 10 (table 3), all fmnh. Primeiro Morro 6 (holotype and 5 paratypes); Quadro Ponteado, 2; Morretinho, 1; Iporanga, 1.

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(Fig. 16, continued from previous page)

Foramina, Fissures, Sutures, Processes, Fossae, Others
a coronal suture
sagittal suture
suprafrontal foramen
parapterygoid fossa of pterygoid; external pterygoid process (of alisphenoid, 14)
e hamular process of pterygoid (internal pterygoid process of alisphenoid, 14)
f squamosal or temporal process of zygomatic arch (9)
g petrotympanic fissure (middle lacerated foramen, Glasserian fissure)
h foramen ovale and foramen spinosum
i auditory meatus
temporal vacuity (postglenoid foramen, subsquamosal foramen)
k hamular process of squamosal (9)
1 condyle of occipital or occipital condyle (5)
m paraoccipital process
n capsular projection for upper incisor, and nasopharyngeal foramen of maxillary (7)
preorbital foramen
zygomatic plate of maxillary (7)
anteorbital bridge of maxillary (7)
anterior palatine foramen
optic foramen
sphenopalatine vacuity (anterior alar fissure, anterior lacerated foramen)
$\mathrm{u} \quad$ malar process of maxillary (7)
v anterior and posterior ethmoidal foramina
w alisphenoid foramen or canal
x basioccipital of occipital (5)
y palatal process of premaxillary (6)
z palatal process of maxillary (7)
aa mesopterygoid fossa (craniopharyngeal canal; posterior nares) between internal pterygoid processes (see fig. 15 for points of measurement)
bb postincisor foramen
cc posterior palatine foramen (foramina) of maxillo-
palatine $(7,8)$ and/or palatine (18)
dd palatine process of premaxillary (6)
ee posterior palatine foramina or pits
$\mathrm{ff} \quad$ alveolar process of maxillary (7)
gg sphenoidal fissure
hh sphenofrontal foramen
ii glenoid fossa of squamosal (9)
jj stapedial foramen
kk interpterygoid foramen (foramen Civinini)
11 Eustachian canal
mm carotid canal (posterior lacerated foramen)
nn jugular foramen
oo mastoid process of mastoid (12)
pp stylomastoid foramen
qq hypoglossal foramen or canal
rr buccinator-masticatory foramen (partially concealed by alisphenoid, 15)
ss foramen magnum of occipital (5)

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Fig. 17. Akodont type skull, palatal aspect. For names of parts and foramina see Figure 16 caption.

 symphysis; d, angular process; e, condyloid process; f, coronoid process; $\mathbf{g}$, alveolar process; $\mathbf{h}$, capsular projection of incisor root; $\mathbf{i}$, sigmoid or superior notch; $\mathbf{j}$, inferior or lunate notch; $\mathbf{k}$, superior masseteric ridge; $\mathbf{l}$, inferior masseteric ridge; m, mylohyoid line; $\mathbf{n}$, mental foramen; $\mathbf{o}$, mandibular or dental foramen; $\mathbf{p}$, alveolar foramen.

Explanation of symbols used for molar crown elements of akodont rodents (fig. 20):

## Upper Right Molars

Main Cusps (large numbers)

1. paracone
2. metacone
3. protocone
4. hypocone

Lophs, Conules, Conulids, Styles ${ }^{1}$
(medium-sized numbers)
5. anterolabial conule
6. anterolingual conule
7. parastyle
8. anteroloph
9. anteroconule
10. mesostyle
11. paralophule
12. mesoloph
13. metalophule
14. posteroloph
15. mure
16. enterostyle

Flexi or Enamel Folds ${ }^{1}$
(small numbers)
17. anteromedianflexus
18. anteroflexus
19. paraflexus
20. mesoflexus
21. metaflexus
22. posteroflexus
23. protoflexus
24. hypoflexus

## Lower Left Molars

Main Cusps (large numbers)

1. metaconid
2. entoconid
3. protoconid
4. hypoconid

Lophs, Conules, Conulids, Stylids ${ }^{1}$
(medium-sized numbers)
5. anterolabial conulid
6. anterolingual conulid
7. protostylid
8. anterolophid ${ }^{2}$
9. anteroconulid ${ }^{3}$
10. metastylid
11. metalophulid
12. mesolophid
13. entolophid
14. posterolophid
15. murid
16. mesostylid


Fig. 21. Molar crowns of sigmodontine rodents; evolutionary stages from primitive crested to derived plane in side and crown views (from Hershkovitz, 1955).
(Fig. 20, continued from opposite page)

## Flexids or Enamel Folds ${ }^{1}$

(small numbers)
17. anteromedianflexid
18. anteroflexid
19. metaflexid
20. mesoflexid
21. entoflexid
22. posteroflexid
23. protoflexid
24. hypoflexid

## Addendum

25. ectostylid
26. anterolophulid ${ }^{4}$

[^2]

Fig. 22. Sigmodontine incisor curvature with reference to the basal-incisive plane (a-b) and vertical-incisive plane (from Hershkovitz, 1962, p. 103).

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[^0]:    ${ }^{1}$ Deposited in the Museu Nacional, Rio de Janerio, Brazil.

[^1]:    ${ }^{1}$ Holotype.

[^2]:    ${ }^{\prime}$ Numbers $5,6,7,8,9,17,18$ of upper and lower first molars and number 10 of first lower molar are elements of the procingulum. Numbers 8,9 may also be present in second and third upper and lower molars.
    ${ }^{2}$ Commonly coalesced with metaconid.
    ${ }^{3}$ Commonly coalesced with anteroloph and metaconid.
    ${ }^{4}$ Anterolabial cingulum of Reig (1987).

