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NEW SERIES, NO. 23

Systematics of Mice of the Subgenus *Akodon* (Rodentia: Cricetidae) in Southern South America, with the Description of a New Species

Bruce D. Patterson

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Kathy E. Freas

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Systematics of Mice of the Subgenus *Akodon* (Rodentia: Cricetidae) in Southern South America, with the Description of a New Species

Abstract

Two species of yellow-nosed mice (genus *Akodon*) occur in the forests and steppes of southern South America, but only one of these is currently named. *Akodon xanthorhinus* applies to the smaller, shorter-tailed species found over much of southern Chile and Argentina. A larger, longer-tailed form inhabits islands to the south, and this form is here described as new. Geographic variation throughout the range of *A. xanthorhinus* is examined to assess the taxonomic position of the new form. Clinal variation does not account for the substantial differences of the new form: specimens of *A. xanthorhinus* from geographically intermediate localities on Isla Grande de Tierra del Fuego are no more similar to the new form than are specimens from the mainland. The new form is therefore best considered a distinct species, *Akodon hershkovitzi*.

Introduction

The akodont rodents are an endemic Neotropical group that occupies a variety of habitats and presents an impressive array of morphologies fitting them to herbivorous, granivorous, omnivorous, or insectivorous diets. Trenchant differences among the various forms are lacking, however, and as a consequence, there is little agreement on the specific content of the tribe or even the genus (cf. Bianchi et al., 1971; Gardner & Patton, 1976; Reig, 1978). Conservative limits of the genus *Akodon* Meyen, 1833, include the *Akodon*, *Abrothrix*, *Thaptomys*, *Deltamys*, *Chroecomys*, *Hypsomyys*, and *Chalcomys* of various authors, totaling some 33 species (Honacki et al., 1982). Many of these species are included within the subgenus *Akodon*, which reaches its greatest specific diversity in the central

Andes. In southern South America, the subgenus *Akodon* currently includes the following taxa (from north to south): five subspecies of *Akodon olivaceus* (Waterhouse, 1837); three subspecies of *A. iniscatus* Thomas, 1919; monotypic *A. markhami* Pine, 1973; *A. xanthorhinus canescens* (Waterhouse, 1837); monotypic *A. llanoi* Pine, 1976; and *A. xanthorhinus xanthorhinus* (Waterhouse, 1837).

In early 1983, we collected mammals and birds in Magallanes, Chile. An *Akodon* we collected on a large island south of the Straits of Magellan, Isla Capitán Aracena, differed widely from related mice from Punta Arenas, currently referred to *A. x. xanthorhinus*. The new mouse weighed 50% more than comparable specimens from Punta Arenas, had an absolutely and relatively longer tail, and differed in details of its coloration. It therefore appeared to represent a new taxon. However, the taxonomy of mice of the subgenus *Akodon* from southern South America has not been comprehensively reviewed since Osgood's "The Mammals of Chile" (1943). Recently described taxa (Pine, 1973, 1976) and other additional specimens from marginal localities, especially islands in the Cape Horn group, permit a more detailed revision of this group than was possible in Osgood's time. We therefore undertook an analysis of geographic variation among southern *Akodon* to determine (1) the application of available names and (2) the relationships of the new mouse to previously described taxa.

Materials and Methods

We examined a total of 470 specimens from the collections of the following institutions: American

Museum of Natural History (AMNH), British Museum (Natural History) (BM[NH]), Field Museum of Natural History (FMNH), Instituto de la Patagonia (IP), Museum of Vertebrate Zoology, University of California (MVZ), Universidad Austral de Chile (UACH), and the (U.S.) National Museum of Natural History (USNM). Specimens were identified by comparisons with holotypes, original descriptions, and descriptions given in Osgood (1943). Published descriptions suffice to distinguish yellow-nosed akodons (including the taxa *xanthorhinus*, *canescens*, and *llanoi*) from other mice of the subgenus *Akodon* (Patagonian *iniscatus* and Pacific *olivaceus* and *markhami*), as well as those belonging to the subgenus *Abrothrix* (*Akodon longipilis* and *A. lanosus*). Series of specimens selected for use in the craniometric analysis were first subjected to a tooth-wear criterion for aging. We considered as adult those specimens in which the dentine visible between the hypocone and metacone of M1 approximated or exceeded in width the surrounding enamel layers (cf. Feito et al., 1981, figs. 2.2 and 2.3).

Nine cranial measurements were taken from adult specimens with dial calipers, graduated to 0.1 mm, as follows: condylobasal length, basilar length, palatilar length, length of the incisive foramina, alveolar length of the maxillary molar toothrow, upper diastema length (posterior alveolus I to anterior alveolus of M1), zygomatic breadth, least interorbital breadth, and cranial depth (measured at midline with cranium resting on a glass slide, minus the thickness of the slide). External measurements were taken from skin tags. Sexes were tallied separately. Means and standard deviations were computed on a desk calculator.

Results

Cursory inspection of adult specimens throughout the geographic range reveals two distinct size groups, one smaller (20–25 g, 95–105 mm head and body lengths), the other larger (30–45 g, 100–110 mm). Geographically, the two groups correspond to the mainland, Isla Grande de Tierra del Fuego, and Isla de los Estados on the one hand, and the outer islands (including Cape Horn) on the other (fig. 1). The mice also present two different, but intergrading, color forms whose geographic distributions do not coincide with those of the size groups. These color forms are grayish, slightly suffused with brown, characterizing ani-

mals from drier grasslands and steppes in eastern Patagonia, grading into richly rufescent in animals from more forested habitats to the west and south, both on the mainland and on adjacent islands.

When these patterns are superimposed on existing taxonomic divisions within the group, the following conclusions can be drawn. The small, grayish mouse of the Patagonian steppe can clearly be referred to Waterhouse's (1837) *canescens*, in agreement with Osgood's conception of this form. Similarly, the small, dark mouse of the southern forests fits Waterhouse's (1837) description of *xanthorhinus* (see also Osgood, 1943). Pine's (1976) name *llanoi* apparently refers to this same mouse. However, the large, dark mouse of the outer islands is apparently unnamed. Names are used in this manner in the accompanying table and figures, and are given greater justification below in the specific accounts.

The cranial morphology of southern *Akodon* is depicted in Figure 2, which illustrates the adult male specimen taken on Isla Capitán Aracena. Cranial data from representative populations of all taxa are given in Table 1. (Specimens of *hershkovitzi* from the Instituto de la Patagonia were examined in Punta Arenas where skin data were recorded, but skulls were not measured and could not be obtained in loan.) Sexual dimorphism is not apparent in these mice; no consistent mean differences between males and females were noted. All cranial characters appear to covary, much of the variation being attributable to simple size variation.

As previously noted, specimens of *canescens* and *xanthorhinus* are smaller than those of *hershkovitzi* in most measured characters; those characters in which no individual overlap was found are condylobasal length, basilar length, interorbital breadth, and length of the maxillary molar toothrow. Conversely, only minor cranial differences exist between populations referred here to *canescens* and *xanthorhinus*; widespread overlap exists between groups. The only geographic pattern of consequence among northern forms is the apparent tendency for island populations of *xanthorhinus* (from Isla Riesco and Isla de los Estados) to be somewhat larger in size than those from adjacent "continental" areas (the Brunswick Peninsula and Isla Grande, respectively). Larger body size of island populations is carried to an extreme in *hershkovitzi*, which insofar as known, is wholly restricted to the outer islands of the Chilean archipelago.

The form described here as *hershkovitzi* also

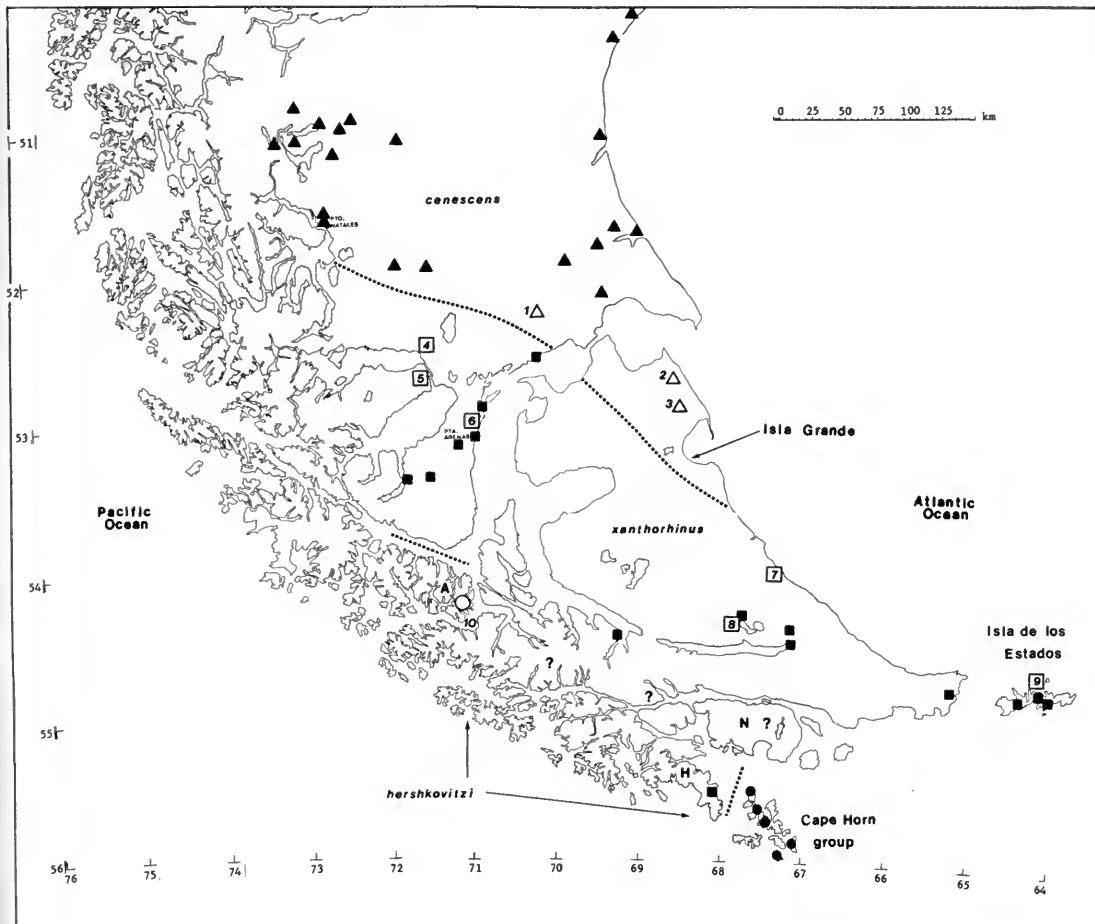


FIG. 1. Map of southern tip of South America, showing the distribution of the subgenus *Akodon*. Solid geometric symbols refer to localities of specimens examined; dashed lines indicate inferred distributional limits. Open, numbered symbols represent populations used in the craniometric analyses—Triangles, *Akodon x. canescens*: 1, Río Ciaike; 2, Arroyo Beta; 3, Estancia Cullen. Squares, *A. x. xanthorhinus*: 4, Río Verde; 5, Isla Riesco; 6, Mina Rica; 7, Estancia Vía Monte; 8, Lago "Yerwin"; 9, Isla de los Estados. Circle, *A. hershkovitzi*: 10, Isla Capitán Aracena. Letters indicate islands discussed in the text: A, Capitán Aracena; H, Hoste; and N, Navarino.

differs from *xanthorhinus* and *canescens* in tail length, exhibiting absolutely and relatively longer tails than either mainland taxon. Histograms of relative tail length (tail length divided by head and body length) for adult specimens of these taxa are shown in Figure 3. Both *canescens* and *xanthorhinus* have tail lengths averaging 55% to 58% of head and body length, whereas *hershkovitzi* tails average 72%. Relative tail length in *hershkovitzi* shows little overlap with either *canescens* or *xanthorhinus*, but is most closely approached by *xanthorhinus* from Isla de los Estados. Because this island represents the southeastern range limit of *xanthorhinus*, and *hershkovitzi* is found still further

to the south, the Isla de los Estados series of *xanthorhinus* raises the possibility that tail length variation in this group may simply be a product of clinal variation. This, however, does not appear to be the case. Both *xanthorhinus* and *canescens* are found on both the continent and Isla Grande (fig. 1); comparisons of mainland specimens of these taxa (open squares in fig. 3) with more southern specimens from Isla Grande (squares marked by ×'s) show no marked tendencies for more southern populations to have longer tails.

Discontinuous variation in tail length (and body size) distinguishes *hershkovitzi* from both *xanthorhinus* and *canescens*. The possible adaptive

TABLE 1. Means and standard deviations for ten populations of *Akodon* from southern South America (numbers refer to localities shown in fig. 1).

Sex	Sample size	Head and body length	Tail length	Hind foot length	Condylobasal length	Basilar length	Palatilar length
1. Río Ciatke, near Argentine frontier (<i>Akodon xanthorhinus canescens</i>)							
♂♂	6	92.3 ± 8.140	53.17 ± 1.941	20.33 ± .8165	21.60 ± .5967	18.17 ± .6439	9.63 ± .3670
♀♀	7	103.0 ± 3.464	52.57 ± 5.028	20.29 ± .5669	22.03* ± .4546	18.48* ± .4401	9.63 ± .2628
2. Arroyo Beta, Tierra del Fuego (<i>Akodon xanthorhinus canescens</i>)							
♂♂	6	98.8 ± 3.125	56.67 ± 2.944	21.58 ± .4916	22.62 ± .3188	19.10 ± .4147	10.00 ± .2449
♀♀	2	108.5 ± .7071	56.60 ± 4.950	21.50 ± .7071	22.35 ± .6364	18.90 ± .7071	9.80 ± .5657
3. Est. Cullen, Tierra del Fuego (<i>Akodon xanthorhinus canescens</i>)							
♂♂	3	101.3 ± 1.155	52.00 ± 2.000	21.67 ± .2887	22.73 ± .5033	19.10 ± .4583	10.00 ± .3606
♀♀	7	103.0† ± 3.367	56.75† ± 6.652	20.88† ± .6292	22.23* ± .6772	18.43* ± .3777	9.76 ± .4158
4. Est. Río Verde, east end Skyring Water (<i>Akodon xanthorhinus xanthorhinus</i>)							
♂♂	6	97.7 ± 5.715	55.00 ± 1.897	21.25 ± .6124	22.36† ± .7092	19.02† ± .7694	9.80 ± .4195
♀♀	5	104.6 ± 3.912	54.40 ± 1.673	20.90 ± .7416	22.14 ± .4827	18.50 ± .4637	9.78 ± .1924
5. East end, Riesco Island (<i>Akodon xanthorhinus xanthorhinus</i>)							
♂♂	3	103.0 ± 5.000	56.67 ± 3.215	21.83 ± .2887	23.30 ± .4583	19.77 ± .6110	10.43 ± .3055
♀♀	3	107.7 ± 3.512	57.00 ± 2.646	21.67 ± .5774	22.77 ± .6028	19.20 ± .6083	10.00 ± 0
6. Mina Rica, 12 mi N Punta Arenas (<i>Akodon xanthorhinus xanthorhinus</i>)							
♂♂	5	100.0 ± 4.062	58.80 ± 6.301	21.20 ± .4472	22.60 ± .2915	19.18 ± .4025	9.98 ± .1789
♀♀	3	103.7 ± 5.132	55.33 ± 1.528	20.67 ± .2887	22.33 ± .3786	18.83 ± .4041	9.80 ± .2000
7. Est. Via Monte, Tierra del Fuego (<i>Akodon xanthorhinus xanthorhinus</i>)							
♂♂	9	101.6 ± 2.186	57.89 ± 4.702	22.00 ± .8292	23.36 ± .4065	19.79 ± .4343	10.40 ± .2693
♀♀	6	104.3 ± 3.559	57.17 ± 3.312	22.08 ± .4915	22.68 ± .2927	19.02 ± .3601	9.88 ± .1722
8. Lago Yerwin (=Yehuín), Tierra del Fuego (<i>Akodon xanthorhinus xanthorhinus</i>)							
♂♂	9	99.4 ± 3.779	57.67 ± 4.183	22.33 ± .5590	23.00 ± .5408	19.33 ± .6837	10.14 ± .2698
♀♀	2	104.0 ± 7.071	57.50 ± 3.536	22.50 ± .7071	23.20 ± .4243	19.30 ± .2828	10.10 ± 0
9. Isla de los Estados (<i>Akodon xanthorhinus xanthorhinus</i>)							
♂♂	5	97.6 ± 3.362	63.80 ± 3.421	23.20 ± .837	23.20 ± .524	19.64 ± .673	10.18 ± .205
♀♀	3	94.67 ± 1.528	59.67 ± 3.512	22.67 ± .577	22.67 ± .321	19.10 ± .500	9.93 ± .321
10. Ba. Morris, Isla Capitán Aracena (<i>Akodon herskovitzi</i>)							
♂	1	104	71	24	24.2	20.8	10.6

TABLE 1. Continued.

Sex	Sample size	Incise foramina length	Zygomatic breadth	Cranial depth	Interorbital breadth	Tooththrow length	Diastema length
1. Río Cialke, near Argentine frontier (<i>Akodon xanthorhinus canescens</i>)							
♂♂	6	5.15 ± .0548	12.18 ± .5345	9.17 ± .2160	3.90 ± .0894	3.45 ± .1225	6.05 ± .4461
♀♀	7	5.39 ± .1773	12.41 ± .2545	9.34 ± .2699	3.94 ± .1512	3.43 ± .0756	6.14 ± .2299
2. Arroyo Beta, Tierra del Fuego (<i>Akodon xanthorhinus canescens</i>)							
♂♂	6	5.67 ± .2422	12.70 ± .2550	9.41 ± .0753	4.13 ± .0816	3.47 ± .0516	6.28 ± .1835
♀♀	2	5.45 ± .2121	12.50 ± .4243	9.30 ± .1414	4.00 ± .1414	3.55 ± .2121	6.15 ± .3536
3. Est. Cullen, Tierra del Fuego (<i>Akodon xanthorhinus canescens</i>)							
♂♂	3	5.63 ± .2082	12.90 ± .4359	9.60 ± .3000	4.10 ± .1000	3.50 ± .1000	6.23 ± .1528
♀♀	7	5.47 ± .1890	12.40† ± .4848	9.48* ± .3545	4.01 ± .1464	3.47 ± .0756	6.06 ± .2149
4. Est. Río Verde, east end Skyring Water (<i>Akodon xanthorhinus xanthorhinus</i>)							
♂♂	6	5.52 ± .2317	12.52 ± .3869	9.22‡ ± .2280	4.02‡ ± .0447	3.50 ± .1414	6.15 ± .2074
♀♀	5	5.42 ± .1643	12.48 ± .1789	9.36 ± .2302	4.00 ± .1000	3.44 ± .0548	6.06 ± .1140
5. East end, Riesco Island (<i>Akodon xanthorhinus xanthorhinus</i>)							
♂♂	3	5.70 ± .1732	13.00 ± .1000	9.47 ± .0577	4.03 ± .1155	3.60 ± .1000	6.47 ± .2309
♀♀	3	5.80 ± .100	12.67 ± .5033	9.47 ± .4041	4.03 ± .1528	3.67 ± .0577	6.37 ± .2082
6. Mina Rica, 12 mi N Punta Arenas (<i>Akodon xanthorhinus xanthorhinus</i>)							
♂♂	5	5.54 ± .2074	12.58 ± .3633	9.18 ± .1304	3.98 ± .0447	3.46 ± .0894	6.32 ± .2280
♀♀	3	5.47 ± .2517	12.57 ± .5686	9.43 ± .0577	3.93 ± .2082	3.43 ± .0577	6.20 ± .1732
7. Est. Via Monte, Tierra del Fuego (<i>Akodon xanthorhinus xanthorhinus</i>)							
♂♂	9	5.74 ± .1740	12.94 ± .1944	9.56 ± .1740	4.04 ± .0882	3.58 ± .0441	6.50 ± .2236
♀♀	6	5.52 ± .1602	12.82 ± .2229	9.50 ± .1265	4.12 ± .0408	3.57 ± .0816	6.22 ± .1472
8. Lago Yerwin (=Yehuín), Tierra del Fuego (<i>Akodon xanthorhinus xanthorhinus</i>)							
♂♂	9	5.74 ± .2007	12.84 ± .3245	9.54 ± .1590	4.14 ± .1014	3.58 ± .0972	6.30 ± .2000
♀♀	2	5.55 ± .4950	12.55 ± .0707	9.40 ± .2828	4.10 ± 0	3.60 ± 0	6.25 ± .0707
9. Isla de los Estados (<i>Akodon xanthorhinus xanthorhinus</i>)							
♂♂	5	5.62 ± .130	12.34 ± .207	10.52 ± .130	4.30 ± .071	3.68 ± .045	6.48 ± .259
♀♀	3	5.40 ± .173	12.05§ ± .495	10.37 ± .231	4.27 ± .115	3.63 ± .058	6.30 ± 0
10. Ba. Morris, Isla Capitán Aracena (<i>Akodon hershkovitzi</i>)							
♂	1	6.1	13.2	9.6	4.4	3.9	6.7

* Sample size equals 6. † Sample size equals 4. ‡ Sample size equals 5. § Sample size equals 2.

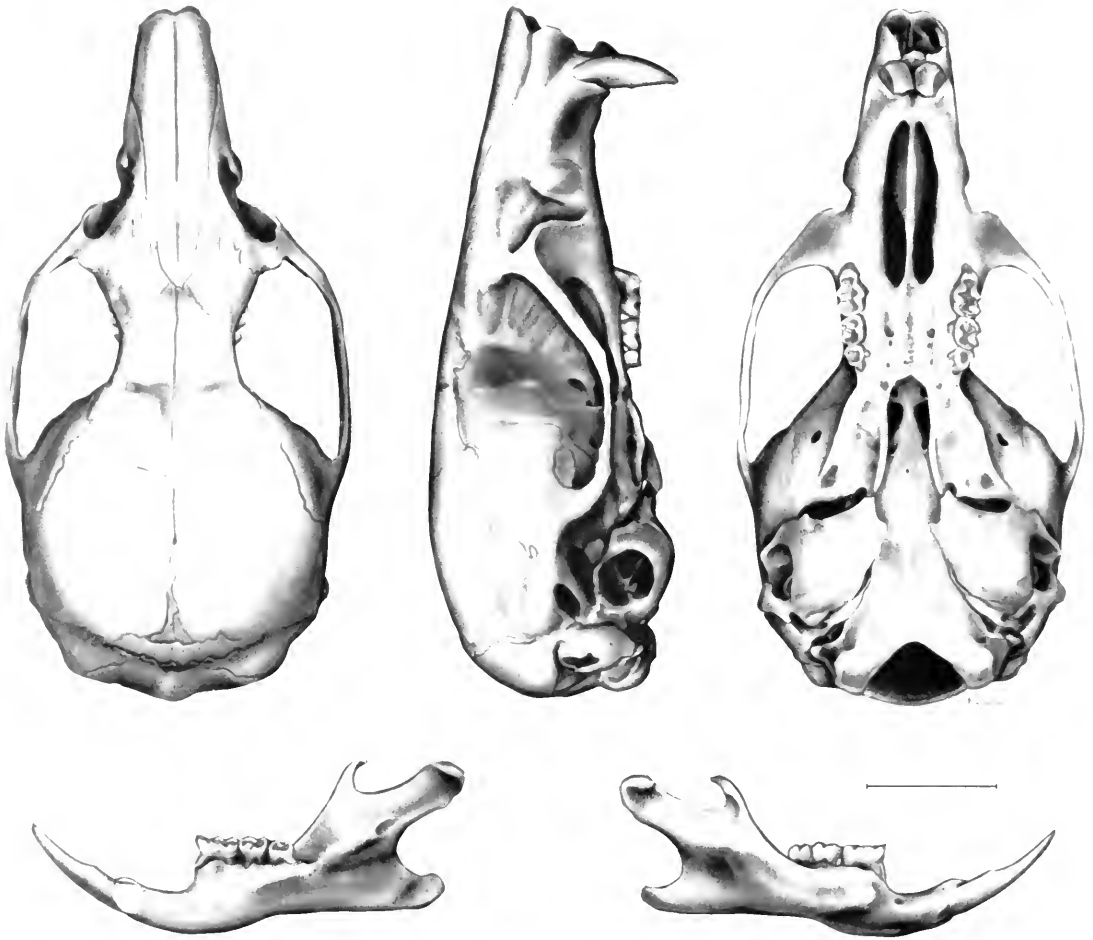


FIG. 2. Skull of *Akodon hershkovitzi* (FMNH 124544) from Isla Capitán Aracena. Compare with skull of *A. xanthorhinus* depicted in Plate XI, Figure 1 of Allen (1905). Only mensural cranial characters are known to definitively separate these taxa.

significance of tail length variation is unclear, as Allen's Rule would predict shorter, not longer, tails in more polar populations. Patterns in tail length of these *Akodon* may represent allometric responses to body size variation, in which larger body size in more polar populations (in accordance with Bergmann's Rule) might coincidentally produce a proportionately longer tail. This interpretation is consistent with the finding that *xanthorhinus* from Isla de los Estados, which is slightly larger than most mainland and Isla Grande populations (table 1), also has a relatively longer tail (fig. 3).

Growth curves for tail length constructed from both juvenile and adult specimens of *xanthorhinus* and *hershkovitzi* appear in Figure 4. These curves

indicate that *hershkovitzi* is not simply an overgrown *xanthorhinus*; at all body sizes, *hershkovitzi* has a longer tail than *xanthorhinus* and at no point do the curves show appreciable overlap. This difference implicates differences in the initiation and duration of growth. This fact and the failure of specimens of *xanthorhinus* and *canescens* from geographically intermediate Isla Grande to more closely approach *hershkovitzi* in body size and tail length suggest that *hershkovitzi* is genetically differentiated from both forms. Further, the geographic position and genetic differentiation of *hershkovitzi* indicate genetic isolation from both northern taxa. The results of these findings can be summarized in the following key.

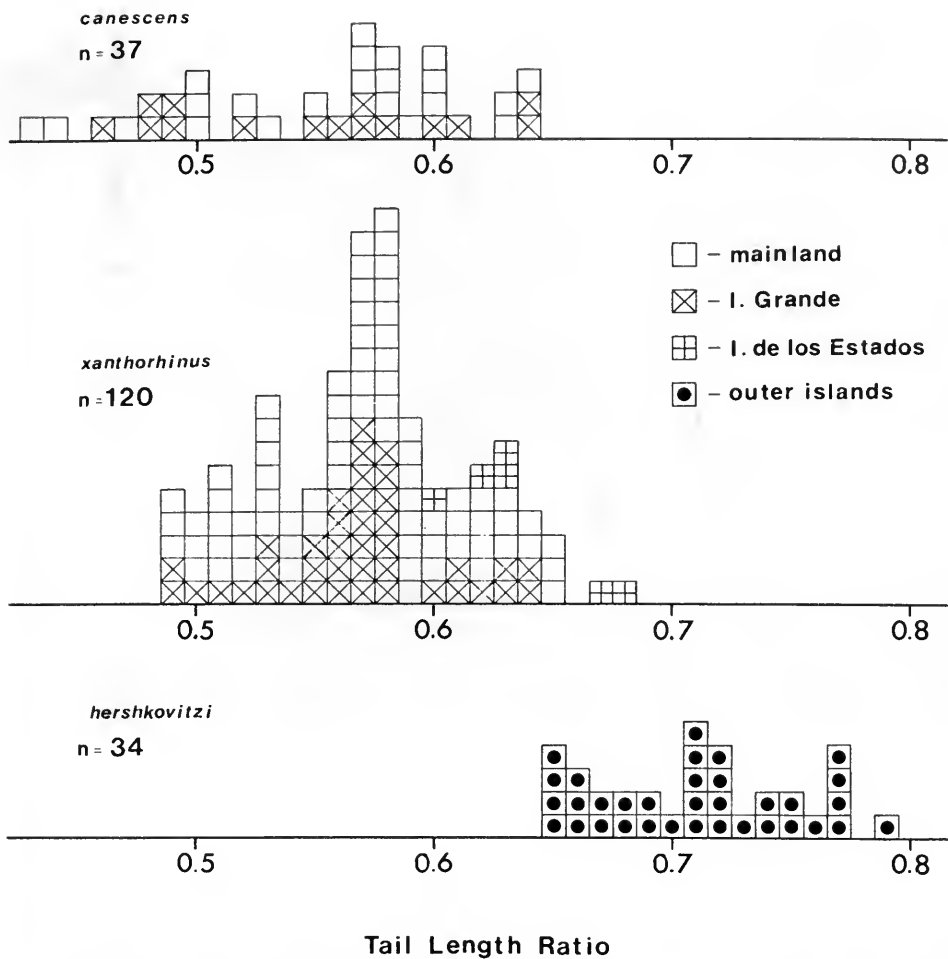


FIG. 3. Histograms of adult tail length ratios (tail length divided by head and body length) for three taxa of southern *Akodon*. Animals weighing at least 20 g or exhibiting complete, somewhat worn dentitions were considered adult. Specimens of *canescens* and *xanthorhinus* overlap broadly; their subspecific distinction rests chiefly on pelage characters. Neither taxon of *A. xanthorhinus* overlaps appreciably with *A. herskovitzi* (dotted squares), although the latter are most closely approached by *xanthorhinus* from Isla de los Estados (squares marked by +’s). Specimens of both *canescens* and *xanthorhinus* from geographically intermediate Isla Grande de Tierra del Fuego (squares marked by ×’s) are no more similar to *herskovitzi* than are more distant mainland specimens (open squares).

Key to Southernmost *Akodon*

- A. Size large, adult weight at least 30 g; tail long relative to head and body, exceeding 65%; condylobasal length greater than 23.5 mm; rostrum long, with somewhat trumpeted nasals and premaxillae, the maxillary diastema exceeding 6.5 mm. . . . *Akodon herskovitzi*
- A'. Size small, adult weight less than 30 g; tail shorter than 65% head and body length; condylobasal length less than 23.5 mm; rostrum shorter, with less trumpeted nasals, the maxillary diastema rarely reaching 6.5 mm. . . B

- B. Dorsal coloration predominately grayish brown; coloration of dorsum of feet light, the manus tan, the pes darker and more rufescent; yellow-orange color of nose more or less defined on all specimens; generally smaller size.
Akodon xanthorhinus canescens
- B'. Dorsal coloration brownish, suffused with rufus; coloration of dorsum of feet darker, the manus with traces of orange, the pes predominately rufescent; nose proportionately darker, in some specimens quite brown and blending in with the facial pelage.
Akodon xanthorhinus xanthorhinus

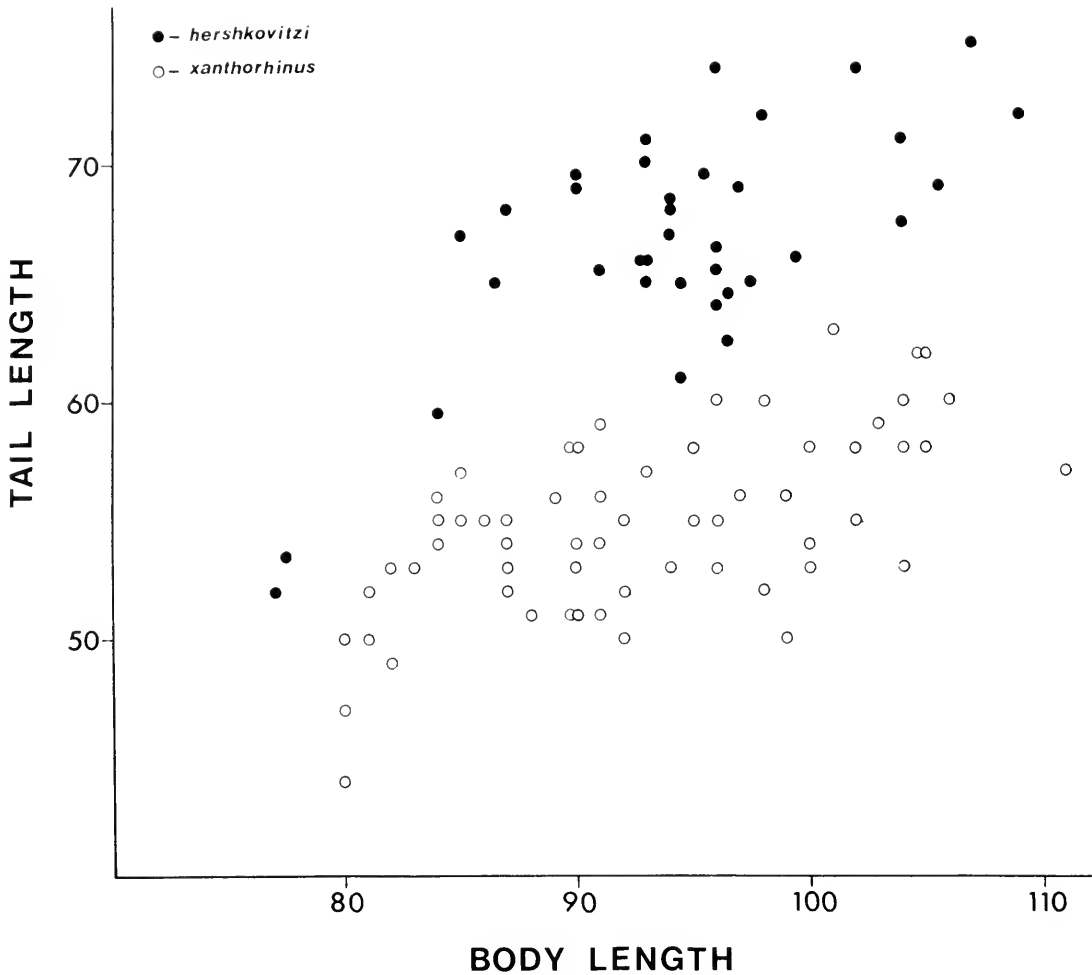


FIG. 4. Growth curves for tail length as a function of head and body length for specimens of *Akodon hershkovitzi* (dots) and *A. x. xanthorhinus* from near Punta Arenas (circles). Throughout later development, *A. hershkovitzi* have tail lengths absolutely and relatively greater than those of *A. xanthorhinus*.

Species Accounts

Akodon hershkovitzi, new species

HOLOTYPE—Adult male, skin, complete skeleton, and stained glans penis preserved in glycerin, Field Museum of Natural History (FMNH) No. 124544, collected on 8 Feb. 1983 by B. D. Patterson (BDP/MHG 968).

TYPE LOCALITY—Chile: Magallanes Province: Isla Capitán Aracena, head of Bahía Morris, elev. ca. 60 m; 54°14'S, 71°30'W. See Figure 5.

DISTRIBUTION—Magellanic steppe (=tundra *magellanica*) and coastal forests of outer islands

in the Chilean archipelago. Presently recorded from a majority of islands in the Cape Horn group, including Isla Hornos (56°S, 67°W), and Isla Capitán Aracena (54°15'S, 71°W). Probably occurs on intervening and adjacent islands, including Isla Grande and Isla Hoste, where its range would approach that of *xanthorhinus*. See Figure 1.

DIAGNOSIS—A medium-sized *Akodon*, larger than any other species of the subgenus *Akodon* in southern South America except *A. markhami*. In pelage coloration, generally darker than other yellow-nosed akodons, especially in ears, sides of nose, and dorsum of tail. Pelage apparently more coarse grained than that of *A. xanthorhinus*. Cranial mor-



FIG. 5. Habitat at type locality of *Akodon hershkovitzi*, showing *Nothofagus betuloides* tree amidst *tundra magellanica*. The type specimen was captured in one such clump at the head of Bahía Morris, Isla Capitán Aracena.

phology similar to *xanthorhinus*, but differing in larger size, less developed interparietal, and less pigmented incisors.

DESCRIPTION—Medium-sized *Akodon*. Pattern of pelage similar to *xanthorhinus* in agouti head, back, and sides, buffy white chin and venter, rufescent dorsum of feet, tricolored tail, and differentially pigmented sides of the nose. Grain of dorsal agouti generally coarse, although the grain may be influenced by the specimen's being in molt. Dorsum of feet tanner than rufescent. Tail heavily pigmented dorsally, with rufescent band on sides and white venter. Sides of nose yellowish brown. Cranial and external measurements of the holotype are given in Table 1.

COMPARISONS—Compared with *A. x. canescens*, *A. hershkovitzi* has darker dorsal pelage than any of 92 specimens on hand; skin of ears and nose is also darker than that of any individual *canescens*. Coloration of dorsum of feet similar in *canescens* and *hershkovitzi*, being rufescent proximally grading to whitish buff on toes. Tail coloration of *hershkovitzi* averaging distinctly darker than *canescens*. Compared with *A. x. xanthorhinus*, the

nose of *hershkovitzi* is darker brown than that of any of 123 *xanthorhinus* on hand; its ears are also darker than those of any *xanthorhinus*, although it is approached in this character by some (e.g., FMNH 50110 from Via Monte). Dorsum of feet of *hershkovitzi*, in contrast, averages paler than that of *xanthorhinus*. General pelage condition more coarse grained, light yellowish hairs standing out against a dark background; in *xanthorhinus*, dorsal pelage shows less contrast. In body size *hershkovitzi* is larger than any known specimen of *A. xanthorhinus* and additionally has an absolutely and relatively longer tail (see figs. 3 and 4). In cranial morphology, *A. hershkovitzi* may be distinguished from *A. xanthorhinus* by the larger size of mensural cranial characters (condylobasal length, basilar length, interorbital breadth, and length of the maxillary molar tooththrow show no individual overlap among specimens examined). Present materials are insufficient to evaluate the discrimination of certain qualitative cranial characters (e.g., reduction of the interparietal, less pigmented incisors, more vertical anterior edge of zygomatic plate, greater relative size of auditory bullae).

Compared with *Akodon (Abrothrix) lanosus*, the only member of this subgenus whose range approaches it, *A. hershkovitzi* can be distinguished by its lighter pelage, darker feet, tricolored tail, and uncleft M1 (see Osgood, 1943).

REMARKS—The typical characters that distinguish *A. hershkovitzi* from *A. xanthorhinus* are usually considered adaptive ones (e.g., body size, tail length). They are therefore especially subject to convergent selection pressures. Thus, it is possible that populations of large mice might have arisen independently on islands in the Cape Horn group and those to the west. Present data are insufficient to evaluate this proposal, which would make *A. hershkovitzi* as presently constituted a polyphyletic group, and hence would require the description of an additional taxon. Biochemical data on southernmost *Akodon* could shed much light on the phyletic relationships of these mice. Morphological characters in these mice cannot be established as apomorphic and pleisiomorphic, whereas electrophoretic data might contribute to such analyses.

ETYMOLOGY—We are pleased to name this species after our friend and colleague, Philip Hershkovitz, on the occasion of his 74th birthday Oct. 12, 1983, in tribute to his enormous contributions to South American mammalogy.

SPECIMENS EXAMINED (34 TOTAL)—CHILE: Magallanes: Isla Bayly, Sursidero Romanche (5, IP); Isla Cabo de Hornos (12, IP); Isla Capitán Aracena, Ba. Morris, head, 54°14'S, 71°1'30"W (1, holotype, FMNH); Isla Deceit, Caleta Toledo (9, IP); Isla Grevy (5, IP); Isla Wollaston, Caleta Lien-tur (2, IP).

Akodon xanthorhinus canescens (Waterhouse, 1837)

Mus canescens Waterhouse, 1837, Proc. Zool. Soc. Lond. 1837:17. Waterhouse, 1839, Zool. Voy. Beagle, Pt. II, Mamm., p. 54.

Mus [(*Abrothrix*)] *canescens* Waterhouse, 1837, Proc. Zool. Soc. Lond. 1837: 21. Philippi, 1900, Anal. Mus. Nac. Chile 14: 7.

Hesperomys canescens Wagner, 1843, Schreber's Säugth. Suppl. III, p. 522. Burmeister, 1879, Descr. Phys. Rep. Argentine 3: 227.

[*Hesperomys (Akodon)*] *canescens* Trouessart, 1881, Bull. Soc. Etudes Sci. Angers, 1880, 10(1): 141.

[*Akodon*] *canescens* Trouessart, 1897, Cat. Mammal. 3: 537.

Akodon canescens Thomas, 1898, Proc. Zool. Soc. Lond. 1898: 211. Allen, 1905, Mamm. Patagonia, p. 73. Thomas, 1919, Ann. Mag. Nat. Hist. (9)3: 205, 207. Thomas, 1927, Ann. Mag. Nat. Hist. (9)19: 550. Thomas, 1927, Ann. Mag. Nat. Hist. (9)20: 201.

Akodon xanthorhinus canescens Osgood, 1943, Field

Mus. Nat. Hist., Zool. Ser. 30: 182. Cabrera, 1958–1961, Rev. Argent. Cienc. Nat. "Bernardino Rivadavia" 4: 450. Pine, 1973, Anal. Inst. Patagonia 4: 425. Mann, 1978, Gayana, Zool. 40: 144. Pine et al., 1979, Mammalia, 43(3): 351.

Akodon olivaceus canescens Yañez et al., 1979, Arch. Biol. Med. Exp. 12: 202.

Hesperomys (Abrothrix) xanthorhinus Thomas (not Waterhouse), in Milne-Edwards, 1890, Mission Sci. Cap Horn, 6, Zool., Mamm., p. A.28.

[*Akodon*] *xanthorhinus* Wolffsohn (not Waterhouse), 1923, Rev. Chilena Hist. Nat. 27: 163.

Akodon xanthorhinus Thomas (not Waterhouse), 1929, Ann. Mag. Nat. Hist. (10)4: 42. Gyldenstolpe, 1932, Kungl. Svenska Vetenskapsakad. Handl. 11(3): 107. Ellerman, 1941, Families and genera of living rodents, II, p. 413.

TYPE LOCALITY—Santa Cruz, Santa Cruz Province, Argentina.

DISTRIBUTION—Grasslands and steppes of Argentine Patagonia, from Neuquén south to the Atlantic coast of Isla Grande. The range of *canescens* extends to the Pacific coast near Puerto Natales (51°30'S) and also in Aysén Province, Chile, where it is recorded from Puerto Ibañez (47°S) and the Río Nireguao (45°S). The range of *canescens* is broadly apposed to that of *xanthorhinus*, where the two apparently intergrade (see fig. 1).

REMARKS—Allen (1905) and Osgood (1943) give suitable descriptions of *A. x. canescens*. Unfortunately, the Darwin specimens on which Waterhouse's names *xanthorhinus* and *canescens* are based were mislabeled, leading to some confusion in published literature over the types. Allen (1905, p. 75) examined both specimens of *canescens* collected by Darwin, BM(NH) 55.12.24.157 from Santa Cruz and 55.12.24.173 from Port Desire (which Allen reported mistakenly as "55-12-24-143"). Only Port Desire is given in the original description (Waterhouse, 1837), but both localities are given in the account of the voyage of the H.M.S. *Beagle* (Waterhouse, 1839). Thomas (1919, p. 205) selected 55.12.24.157 as lectotype, fixing the type locality at Santa Cruz.

East of the Andes, in Río Negro and Neuquén provinces, Argentina, the similar species *Akodon iniscatus* Thomas, 1916, occurs. Southern *canescens* can be immediately distinguished from *iniscatus* by numerous characters, including a flatter dorsum of cranium, more elongated nasals, a narrower zygomatic plate, a narrow interorbital region that is dorsally flatter and more rounded at the orbital margins, a tricolored rather than bicolored tail, and larger ear pinnae. However, specific differences are reduced among specimens from

more proximate localities. The two species are sympatric at Rawson (Chubut Province), where they show no signs of intergradation. However, the Rawson specimens are sufficiently similar that Osgood himself confused an *A. iniscatus* specimen (FMNH 35248) as a *canescens*. The significance of such superficial similarities in areas of range overlap is at present uncertain. Oliver Pearson (pers. comm.) has informed us that specimens in the British Museum establish the sympatric occurrence of *canescens* and *iniscatus* not only at Rawson but also at four other Argentine localities: Maiten, Pico Salamanca, Valle de Lago Blanco, and Cholila. Specimens of both species from the last locality are labeled "in barn," suggesting the two occur in microsympatry.

Yañez et al. (1979) considered *xanthorhinus* and *canescens* as subspecies of *Akodon olivaceus*, basing their argument on clinal variation in mensural cranial characters that transcends the boundary between *A. olivaceus brachiotis* and *A. x. canescens* in Aysén Province, Chile. However, clinal variation need not imply genetic intergradation, and almost certainly does not in this case. Although sympatry has yet to be established, *A. o. brachiotis* and *A. x. canescens* are known to have overlapping ranges in Aysén Province, Chile. Specimens of *brachiotis* from Río Aysén and *canescens* from Río Nireguao (both at FMNH) show no signs of intergradation in pelage color, tail length and color, and in details of cranial shape, although the two taxa are of similar size, as demonstrated by Yañez et al.

SPECIMENS EXAMINED (168 TOTAL)—ARGENTINA: Chubut: Rawson (3, FMNH). Neuquén: 5 km N Las Coloradas (1, MVZ); Parque Nacional Laguna Blanca, 31 km SW Zapala (1, MVZ). Río Negro: Pilcaneu (1, FMNH). Santa Cruz: ** (3, FMNH); Arroyo Aike (10, AMNH); Upper Río Chico (4, USNM); Upper Río Chico, near Cordilleros (2, AMNH; 2, FMNH; 8, USNM); Río Coy [Coig] (2, FMNH; 11, USNM); Cape Fairweather (1, FMNH; 13, USNM); Río Gallegos, Halliday Ranch (5, USNM); Río Gallegos, Ramon Crossing (2, USNM); Mt. Observation (1, AMNH); Rudd Ranch (1, FMNH; 7, USNM); 30 mi S Santa Cruz on coast (1, AMNH). Tierra del Fuego: Arroyo Beta (11, FMNH); Estancia Cullen (15, FMNH). **CHILE:** Aysén: Puerto Ibañez (4, USNM); Río Nireguao (2, FMNH). Magallanes: Estancia Río las Chinas (2, IP); Río Ciaiike, near Argentine boundary (16, FMNH); Río Ciaiike, North Arm Station (10, FMNH); Tom Gould's Lagoon, NE of Punta Arenas, ca. 100 mi (1,

AMNH); Laguna Lazo, Ultima Esperanza (12, FMNH); Seccion Lazo (3, IP); Puerto Natales (4, FMNH); Cerca Salto Grande (Paine), fin de Lago Pehoe (1, IP); Río Rubens, on Natales Road (1, FMNH); Lake Sarmiento, Ultima Esperanza (7, FMNH).

Akodon xanthorhinus xanthorhinus (Waterhouse, 1837)

Mus xanthorhinus Waterhouse, 1837, Proc. Zool. Soc. Lond. 1837: 17. Waterhouse, 1839, Zool. Voy. Beagle, Pt. II, Mamm., p. 53. Gay, 1847, Hist. Chile, Zool. 1: 116.

Mus (Abrothrix) xanthorhinus Waterhouse, 1837, Proc. Zool. Soc. Lond. 1837: 21.

Mus (Abrothrix) xanthorhinus Philippi, 1900, Anal. Mus. Nac. Chile 14: 7, 13.

Hesperomys xanthorhinus Wagner, 1843, Schreber's Säugth. Suppl. III, p. 522.

[*Hesperomys (Akodon) xanthorhinus* Trouessart, 1881, Bull. Soc. Études Sci. Angers, 1880, 10(1): 142.

Hesperomys (Akodon) xanthorhinus Matschie, 1898, Hamburger Magalh. Sammelreise, Säugeth., p. 7.

Hesperomys (Habrothrix) xanthorhinus Thomas, 1881, Proc. Zool. Soc. Lond. 1881: 5.

[*Hesperomys (Habrothrix) xanthorhinus* Thomas, 1884, Proc. Zool. Soc. Lond. 1884: 450.

[*Akodon xanthorhinus* Trouessart, 1897, Cat. Mammal. 3: 537.

Akodon [Akodon] xanthorhinus Allen, 1905, Mamm. Patagonia, p. 71. Thomas, 1919, Ann. Mag. Nat. Hist. (9)3: 205; 1929, Ann. Mag. Nat. Hist. (10)4: 41. Gyldestolpe, 1932, Kungl. Svenska Vetenskapsakad. Handl. 11(3): 107. Ellerman, 1941, Families and genera of living rodents, II, p. 413.

[*Akodon xanthorhinus* Thomas, 1916a], Ann. Mag. Nat. Hist. (8)17: 187 + footnote.

Akodon xanthorhinus xanthorhinus Osgood, 1943, Field Mus. Nat. Hist., Zool. Ser. 30: 180. Cabrera, 1958–1961, Rev. Argent. Cienc. Nat. "Bernardino Rivadavia" 4: 450. Pine, 1973, Anal. Inst. Patag. 4: 425. Pine et al., 1978, Mammalia, 42(1): 106. Mann, 1978, Gayana, Zool., 40: 144 (part).

"*Akodon xanthorhinus*" Bianchi et al., 1971, Evolution 25: 728 ("probably belongs to the genus *Abrothrix*").

Abrothrix xanthorhinus Gardner and Patton, 1976, Occas. Pap. Mus. Zool. La. State Univ. 49: 28.

Akodon olivaceus xanthorhinus Yañez et al., 1979, Arch. Biol. Med. Exp. 12: 202.

Akodon (Akodon) xanthorhinus Reig, 1980, J. Zool., (Lond.) 192: 263.

Hesperomys (Habrothrix) olivaceus Thomas (not Waterhouse), in Milne-Edwards, 1890, Mission Sci. Cap Horn, 6, Zool., Mamm., p. A.28.

Akodon llanoi Pine, 1976, Mammalia, 40: 63.

TYPE LOCALITY—"Hardy Peninsula, Tierra del Fuego" [actually the southeastern extension of Isla Hoste, ca. 55°30'S, 68°W], Magallanes Province, Chile.

DISTRIBUTION—Forests and adjacent meadows of southernmost South America, from the Brunswick Peninsula through southern Isla Grande to Isla de los Estados. Weakly differentiated populations occur on Isla de los Estados and Isla Riesco. The southernmost localities at which this form has been documented are: Bahía Parry, Isla Grande; Hardy Peninsula, Isla Hoste; and Isla de los Estados (see fig. 1). Intergradation of *xanthorhinus* and *hershkovitzi* is presently unknown.

REMARKS—Waterhouse (1837) gave the type locality for *xanthorhinus* as “Santa Cruz” [Santa Cruz Province, Argentina], but later emended it as “Hardy Peninsula, Tierra del Fuego” (Waterhouse, 1839). In an attempt to clarify this situation, Allen (1905) created more confusion. He mistakenly stated that one of the types had been lost (it is not, being BM[NH] 55.12.24.168) and that the other, given as “55-12-24-156” from the Hardy Peninsula, Tierra del Fuego [Isla Hoste], should stand as the type. Thomas (1919, pp. 205, 206) repeated the latter facts, designating 55.12.24.156 as lectotype. However, this registration number is a *lapsus calami* of 55.12.24.158, which is the proper registration number for the immature specimen described in Waterhouse (1839) and designated by Thomas (1919) as lectotype (Thomas, 1927; M. C. Perry, pers. comm.). The adult specimen 55.12.24.168, collected by Capt. P. P. King, served as the basis of Waterhouse’s (1837) original species description (Thomas, 1927).

In keeping with earlier workers (e.g., Osgood, 1943; Mann, 1978), we have applied the name *xanthorhinus* to the smaller of the two species inhabiting the Chilean and Argentine archipelago. However, the existence of two species was unknown to these workers, and hence the critical nomenclatural nature of this determination was unappreciated. The name *xanthorhinus* has seniority over all other names for these mice; its type locality falls well within the documented range of the larger species, and is well beyond the otherwise substantiated range of the smaller species. Indeed, on these grounds we initially applied *xanthorhinus* to the larger species. However, *xanthorhinus* and *hershkovitzi* can be reliably distinguished by a single compound character, relative tail length, which fortunately figured in Waterhouse’s original descriptions. His 1837 description of *xanthorhinus* gave a relative tail length of 47%; his later (1839) description gave a 50% figure. Both of these figures are far less than the shortest *hershkovitzi* (65%), indeed one being shorter than

the shortest *xanthorhinus* (49%; fig. 3). Comparable figures are given for *canescens* in the same works: correcting the 1837 account to read “1 inch, 10 lines” rather than “2 inches, 10 lines” (or 86% of body length!), he gives 56% and 59%, respectively, in the 1837 and 1839 descriptions. This accords well with current understanding of *A. x. canescens*. Whether his figures for *xanthorhinus* are artifactually small or instead reflect novel responses at its southern range limit still remains to be seen. We feel comfortable, on the basis of tail growth curves for *hershkovitzi* (fig. 4), that Waterhouse’s *xanthorhinus* cannot apply to the form named here as new.

This admitted impression is reinforced by our examination of a young female topotype, BM(NH) 85.6.4.5, obtained on loan. Relative tail length of this specimen from Orange Bay, Hardy Peninsula, is 59%. Other characters preserved in its broken cranium likewise indicate the smaller, shorter-tailed species.

Pine (1976) described *A. llanoi* from Isla de los Estados, believing it to be specifically distinct from the *Akodon* of the surrounding region. This assessment was based on limited material, specifically on differences between mice of Isla de los Estados and those found at the nearest point on Isla Grande (at Bahía Buen Suceso), referred to *Akodon x. xanthorhinus*. The crux of his argument lay in the shape of the rostrum of *llanoi*, which is more slender and narrow than in mice from Buen Suceso; externally, *A. llanoi* appeared “at most to be subspecifically distinct from [*A. xanthorhinus*]” (Pine, 1976, p. 64). While the rostrum of some southern *Akodon* indeed resembles the condition in *Abrothrix*, this character varies smoothly over its range. Specimens of *canescens* from the Straits of Magellan have longer and more fluted rostra than mice to the north, and *hershkovitzi* to the south has more fluted nasals and premaxillae than any other southern form of the subgenus *Akodon*. In the context of geographic variation, cranial distinctions of *llanoi* disappear; specimens from Isla de los Estados and from Isla Riesco tend to be larger than “mainland” specimens (including those from Isla Grande). Additionally, *llanoi* do possess longer, more plumbeous pelage than is characteristic of *xanthorhinus* over its entire range. Nevertheless, these features are not judged to merit taxonomic recognition, and *llanoi* is treated as a synonym of *A. x. xanthorhinus*.

SPECIMENS EXAMINED (267 TOTAL)—ARGENTINA: Tierra del Fuego: Isla de los Estados: Puerto Basil Hall (1, USNM); Bahía Capitán Canepa

(7, USNM); Bahía York, Puerto Celular (2, USNM); Puerto Vancouver (1, USNM). Isla Grande: Bahía Buen Suceso (3, USNM); Lago Yerwin (=Yehuín) (11, FMNH); Estancia Via Monte (15, FMNH). CHILE: Magallanes: Pali-Aike (Mte. Aymond) (12, IP); Laguna Azul en el Lado Norte (3, IP); Estancia La Cumbre, Cordillera Baguales (Río Baguales) (1, IP); Río Bandurria, Sierra Baguales (8, IP); Lago Blanco, Tierra del Fuego (1, IP); Aserradero "Lago Blanco," Tierra del Fuego (5, IP); Lago Blanco (aserradero) Pozo No. 2 (ENAP) (3, IP); Pta. Entrada (afuera y debajo una casa) (1, IP); San Gregorio (1, IP); Hotel San Gregorio (después del 1^{er} chorillo) (4, IP); Bahía el Indio (4, IP); Río Leon, Seno Skyring, 65 km N, 80 km W Punta Arenas (1, IP); Mina Rica, 10 mi N Punta Arenas (16, FMNH); Mina Rica, 12 mi N Punta Arenas (19, FMNH); Bahía Parry, Tierra del Fuego, 170 k S, 100 k E Punta Arenas (4, IP); Punta Arenas (17, IP); Punta Arenas, Estancia María Cristina (1, IP); Punta Arenas, Parque Nacional Río Las Minas, 500 m N "Grupo D," 390 m (27, FMNH+UACH); Punta Arenas, Quinta Emilia (atrás I de la P) (2, IP); Punta Arenas, 3 km N, 3 km W (16, IP; 3, USNM); Punta Arenas, "Quinta Emilia," 3.5 km WNW Av. España y Abello (34, FMNH+UACH); Punta Arenas (3 km W), Río de los Ciervos (1, IP); Punta Arenas, hills 5 mi W (1, FMNH); Punta Arenas, ridge 8 km W (1, FMNH); Punta Arenas, 8 km W (along Río de las Piedras), 1200 ft (4, USNM); East end of Isla Riesco (8, FMNH); Estancia Río Verde, E. end of Skyring Water (15, FMNH); Tierra del Fuego (1, IP).

Discussion

Generic Affinities

We have treated *Akodon hershkovitzi* and *Akodon xanthorhinus* as members of the genus and subgenus *Akodon*. Others (Bianchi et al., 1971; Gardner & Patton, 1976) have considered *xanthorhinus* as an *Abrothrix*, citing Reig (unpubl. data) as an authority, primarily if not solely, on karyotypic grounds. Both *xanthorhinus* and *longipilis* (the type species of *Abrothrix*; Waterhouse, 1837) share diploid numbers of 52 chromosomes and autosomal fundamental numbers of 56 (fig. 6; Spotorno & Fernández, 1976; Gallardo, 1982), not 54 as given by Bianchi et al. (1971). These karyotypes differ considerably from that of *A. boliviensis*, the

type species of *Akodon* ($2n = 40$, $FN = 40$), and other related taxa (Gardner & Patton, 1976), but are identical to *Akodon (Akodon) olivaceus* and *Akodon (Abrothrix) sanborni* (Spotorno & Fernández, 1976; Gallardo, 1982). However, as noted by Gardner & Patton (1976, p. 30), the karyotypes of *xanthorhinus* and *longipilis* "are similar in many respects to the broadly based group ($2n = 52$ to 64 , $FN = 54$ to 68) typified by *Oryzomys palustris* and encompassing species belonging to every suprageneric group [of Neotropical cricetines] except the scapteromyines and ichthyomyines." Shared, apparently primitive, characters such as these are a poor basis for supraspecific groupings.

Thomas (1916b) divided the akodont rodents previously referred to *Akodon* into seven genera. In discussing the shortcomings of this classification, Osgood (1943, p. 186) noted:

In the case of *Abrothrix*, it seems impossible to find characters which are not repeated elsewhere in the akodont group or which, still more significantly, do not grade almost or quite insensibly from one species to another. Therefore, *Abrothrix* as a genus seems indefensible, and even as a subgenus its position is doubtful. For the present it may be accepted as a subgenus at least to maintain connection with previous concepts until thorough studies have been made.

The need for further revisionary work on the akodonts has since been echoed by Hershkovitz (1962), Bianchi et al. (1971), and Gardner & Patton (1976), but a comprehensive study has yet to be conducted. In recent work, Reig (1978, 1980) has accorded *Abrothrix* only subgeneric status and, moreover, has treated *Akodon xanthorhinus* as a member of the subgenus *Akodon*, an assessment with which we tentatively agree.

The Reference of Philippi's *Mus infans*

Most current synonymies of *Akodon xanthorhinus* (e.g., Gyldenstolpe, 1932; Osgood, 1943; Mann, 1978) include *Mus infans* Philippi, 1900. This assignment was made independently by at least Gyldenstolpe and Osgood (see Osgood, 1943, p. 181). Determination of its proper application is hindered by the absence of the type (Osgood, 1943) and a provenance of "*Ex provinciis centralibus?*" (Philippi, 1900, p. 41). However, some understanding of Philippi's *infans* can be gained by examining the color plates included in his work.

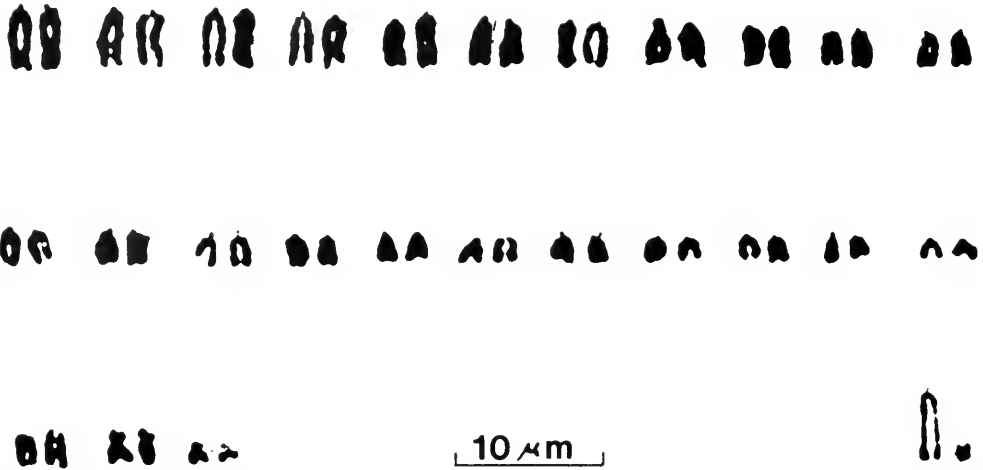


FIG. 6. Karyotype of male *Akodon x. xanthorhinus* (BDP/MHG 1038) collected at Parque Nacional Río las Minas near Punta Arenas. The karyotype has three pairs of metacentric autosomes, a diploid number of 52, and an autosomal fundamental number of 56.

These indicate that *infans* is not a synonym of *xanthorhinus*. While Philippi's "*Mus darwini*" (pl. II) appears to be only a slightly modified version of the depiction of that form in Waterhouse (1839, pl. 23), his "*Mus xanthorhinus*" (pl. II) differs from Waterhouse's plate (pl. 17) in head posture, tail carriage, and the position of the feet. These facts suggest that Philippi recorded his own impressions of *xanthorhinus* rather than reiterating the work of Waterhouse. The obvious contrast between *xanthorhinus* and *infans* as depicted by Philippi (pl. II vs. XVII) suggests they pertain to different taxa; the animals figured in these plates differ noticeably in ear length, foot and rhinarium coloration, and tail length and color.

In assigning *Mus infans* to the synonymy of *Akodon xanthorhinus*, Osgood (1943, p. 181) stated that the colored figure [of *infans*], with its ochraceous ears and muzzle, its small size, etc., can only apply to this species [*xanthorhinus*], "despite the miniscule ears, highly bowed skull, long but not sharply bicolored tail, and a provenance of central Chile. *Akodon xanthorhinus* occurs nowhere north of Aysén (45°S), and typical material is lacking north of 52°S latitude. Apparently overlooked by Osgood in this connection, the similar-sized *Akodon iniscatus nucus* Thomas and St. Leger, 1926,

approaches the Chilean frontier in Neuquén, Argentina (type locality, Chos Malal, ca. midpoint of Chile's latitudinal extent). Like *infans*, *A. iniscatus* has small ears, a highly bowed skull which persists to adulthood, and somewhat dark sides of the rhinarium. The latter, suggestive character is lacking in the four representatives of *A. iniscatus* that Osgood had on hand in 1943. Thus, we believe it warranted to remove *infans* from the synonymy of *A. xanthorhinus*, believing it probable but by no means certain that *infans* referred to what was later named *A. iniscatus*. We recommend that *Mus infans* Philippi be considered a *nomen dubium* that should be rejected.

Island Populations

We believe *A. hershkovitzi* to be an insular derivative of *A. xanthorhinus*. The occurrence of these akodons on islands in the Chilean and Argentine archipelago appears directly related to aspects of their ecology. *Akodon xanthorhinus* inhabits a wide range of mainland habitats, ranging geographically from the humid, forested region of southern and western Patagonia to the drier, open grasslands and steppes of the north and east. Even within the forested region, as in Parque Nacional

Río las Minas and Estancia "Quinta Emilia," both near Punta Arenas, catholic habitat requirements are evident. We collected *A. x. xanthorhinus* in low numbers in closed *Nothofagus pumilio* forest with little ground cover and in dense swampy grasslands filled with *Agrostis magellanica* and the introduced grasses *A. stolonifera* and *Poa praetensis*. Most animals were captured in ecotonal areas between forest and field, which supported these plant species as well as *Gunnera magellanica*. At Quinta Emilia, ecotonal areas supporting the introduced grasses *Holcus lanatos*, *Agrostis* sp., and *Deschampsia* sp., and the native shrubs *Pernettya mucronata* (in drier, open sites) and *Berberis buxifolia* (in more shaded, moist locations) yielded the greatest numbers of captures. Osgood (1943, p. 181) noted the numerical dominance of *A. x. xanthorhinus* over every other species of mammal in this region, an observation also supported by our studies.

Good colonizing abilities of *Akodon xanthorhinus* are evident in the nearly ubiquitous distribution of this species in various mainland habitat patches. Ecological characteristics that are apparently related to this distribution include a high intrinsic rate of increase, which results in population pressures favoring local emigration, and generalized trophic and habitat requirements, which permit at least temporary exploitation of marginal habitats. Similar, if more marked, characteristics are found among some North American *Microtus*, which also occur on coastal oceanic islands (e.g., Crowell, 1973).

The distribution of *Akodon hershkovitzi* on islands in the Cape Horn group need not have entailed over-water dispersal. All the islands (Grevy, Bayly, Wollaston, Hermite, Herschel, Deceit, Hall, and Hornos) are presently separated by marine channels no deeper than 60 m and were broadly connected by land bridges during the latest Pleistocene, when eustatic changes in sea level exceeded 100 m (e.g., Milliman & Emery, 1968). Such changes would have connected the Cape Horn group to Isla Navarino and thence to Isla Hoste and Isla Grande (Tierra del Fuego). Akodons could have moved more or less freely through newly emergent habitats. Indeed, if *Akodon hershkovitzi* diverged from some *xanthorhinus*-like ancestor on the Cape Horn islands during oceanic isolation prior to the latest glaciation, then it may well have moved north out of the Cape Horn group during the latest glaciation. In this scenario, one would expect to find sympatry or parapatry between *Akodon xanthorhinus* and *A. hershkovitzi* in south-

western Isla Grande or Isla Hoste. Existing collections are insufficient to determine whether this is in fact the case, but the occurrence of *A. xanthorhinus* on Isla Hoste, between areas supporting *A. hershkovitzi*, suggests divergence of these forms took place prior to the Recent. Otherwise, Cape Horn populations of *Akodon* would probably have evolved independently of *A. hershkovitzi* (*sensu stricto*), and hence would require separate taxonomic distinction.

However, over-water dispersal would have been necessary for the colonization of Isla Capitán Aracena. The Magellanic Straits which bound this island's northern coast generally exceed 400 m in depth, and the Cockburn and Magdalena canals on the southern and eastern borders are only slightly shallower (380 and 300 m minimal depths, respectively). Eustatic sea level changes associated with Pleistocene glaciations never emptied canals this deep. However, swimming and rafting are well known in small rodents (Sheppe, 1965; Cameron, 1959), and strong currents might have quickened the passage through frigid waters. Minimal distances from Isla Capitán Aracena to the Brunswick Peninsula and Isla Grande, where related forms occur, are 8.88 and 3.05 km, respectively.

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