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EVOLUTIONARY SYSTEMATICS AND HETEROCHRONY IN *ABROTHRIX* SPECIES (RODENTIA, CRICETIDAE)

ANGEL E. SPOTORNO, CARLOS A. ZULETA & ARTURO CORTES

Departamento de Biología Celular y Genética,
Facultad de Medicina, U. de Chile, Casilla 70061,
Santiago 7, Chile, SA.
Departamento de Biología, Facultad de Ciencias, U. de La Serena,
La Serena, Chile, SA.
Departamento de Biología, Instituto Profesional de Osorno, Osorno, Chile
SHORT TITLE: Systematics and heterochrony in cricetids

ABSTRACT

Abrothrix and *Akodon* are two polytypic South American genera whose contents and limits have been unstable. One type species, *Abrothrix longipilis*, is probably heterochronic. Genetic and phenotypic divergence is examined by means of several analysis: protein electrophoresis (25 proteins in 55 samples), standard mitotic chromosomes (45 samples), craniomandibular and body morphometry (176 samples) and morphology of male genitalia (51 samples). *Abrothrix longipillis, Abrothrix sanborni, Akodon andinus,* and *Akodon olivaceus* show close Prevosti and Rogers genetic distances and share a single unique allele; *Akodon berlepschii* and *Akodon molinae* cluster in another distant branch defined by seven unique alleles. The former group, as well as *Abrothrix xanthorhinus* and *Akodon Jelskii,* all have a 2n = 52, NF = 59, a telocentric not larger than a 6.6% of the total karyotype length and two medium metacentric pairs; also, a reduced or absent distal baculum within an elongated penis. These derived features contrast with the full complex penis and the derived large chromosome 1 of *Akodon* and *Bolomys* species. Principal component analysis of 14 craniomandibular and four external body measurements of 17 species distribute specimens as above, mainly on the basis of body dimensions, postpalatal breaths, and bullar and mandible height. *Abrothrix*, which should include *andinus, olivaceus* and *jelskii,* is thus consistently distinct from *Akodon* and *Bolomys*. The distal bacular absence, modified accessory glands, increased body size and young with exceptional morphometric scores found in *Abrothrix longipilis* may compose an epigenetic cascade of developmental bounded phenotypes probably induced by a neonatal testosterone delay. Bacular simplification might be a secondary heterochronic effect triggered by few

mutations and possibly selected by ecological factors related to body size.

RESUMEN

Abrothrix y *Akodon* son dos géneros sudamericanos politípicos, cuyos contenidos y límites han sido inestables. Una de las especies tipo, *Abrothrix longipilis*, es probablemente heterocrónica. Se examina su divergencia genética y fenética por medio de varios análisis: electroforesis de proteínas (45 muestras), morfometría craneomandibular y corporal (176 muestras) y la morfología de la genitalia masculina (51 muestras). *Abrothrix longipilis*, *Abrothrix sanborni*, *Akodon andinus*, y *Akodon olivaceus* muestran cortas distancias genéticas de Prevosti y Rogers y comparten un único alelo; *Akodon berlepschii* y *Akodon molinae* se agrupan en otra rama distante, definida por siete alelos únicos. El primer grupo, así como *Abrothrix santhorhinus* y *Akodon jelskii*, tienen todos un $2n = 52$, $NF = 59$, un telocéntrico mayor que el 6.6% de la longitud total del cariotipo, y dos pares metacéntricos medianos; también un báculo distal reducido o ausente dentro de un órgano elongado. Estas características derivadas contrastan con el órgano complejo y el gran cromosoma 1 de las especies de *Akodon* y Bolomys. El Análisis de Componentes Principales de 14 medidas craneo-mandibulares y las cuatro medidas corporales externas de 17 especies ordenaron los especímenes como se indica arriba, principalmente sobre la base de las medidas corporales, ancho palatino, y altura de la bullae y mandíbula. *Abrothrix*, que debería incluir también a *andinus*, *olivaceus* y *jelskii*, es consistentemente distinto de *Akodon* y *Bolomys*. La ausencia del báculo distal, las glándulas accesorias modificadas, el tamaño corporal aumentado, y los juveniles con puntajes morfométricos excepcionales encontrados en *Abrothrix longipilis* pueden ser parte de una cascada epigenética de fenotipos ligados en el desarrollo, probablemente inducidos por atraso de la testosterona neonatal. La simplificación del báculo puede constituir un efecto heterocrónico secundario disparado por pocas mutaciones, y posiblemente seleccionado por factores ecológicos relacionados al tamaño corporal.

INTRODUCTION

Heterochrony, changes in the time of appearence of a structure during development, can be a major problem in systematics. The widespread assumption that morphological distances are robust estimates of genetic distances will induce oversplit or unstable classifications. If the type species of a morphologically defined genus happens to be heterochronic, subsequent assignation of related species might be severely misguided by affected characters. These will be erroneously interpreted as generic and

not as abrupt autopomorphies, exclusive of the type species. But heterochronies can be also instructive challenges, given that systematics seeks not only adequate classifications but also explanations; such cases of abrupt morphological divergence provide unique opportunities to detect mechanisms and identify factors acting on evolution.

The species of *Abrothrix* (Waterhouse 1837) and *Akodon* (Meyen 1832) are present in nearly all major South American habitats, and nearly a hundred nominal species have been described. Nevertheless, their extension and limits have been unstable and the two genera need urgent revision (Honacki et al., 1982). A first step has been taken by the recent removal of *Bolomys* species (Reig, 1987), previously considered a subgenus of *Akodon*. We report now genetic, reproductive and morphological data substantiating the phylogenetic unity and distinction of another group of Andean species; most of these have been included within *Abrothrix* but sometimes within *Akodon (Abrothrix)*.

During the course of such study, and heterochronic event involving the production of an unusual simple penis by a probable hormonal delay have been detected in *Abrothrix longipilis* (Spotorno, 1986), the type species of the genus. Since temporal disruptions of ontogeny, even when produced by few genetic changes (Bonner, 1982), might have a cascade of phenotypic and ecological effects (Gould, 1977), and since pleiotropic effects are expected from hormones with multiple targets, a variety of genetic, morphological, and reproductive characters will be compared in these two groups; furthermore, some ecological features will be reviewed to document the eventual association between ontogenetic heterochrony and the evolutionary divergence of such species.

MATERIAL AND METHODS

Specimens from which material have been examined are listed and documented in Appendix A. Scientific names follows Honacki et al. (1982).

Protein electrophoresis.- Samples of liver and kidney were collected from recently killed animals, frozen in liquid nitrogen and stored in a deep freezer. Aqueous homogenates of tissues were subjected to starch gel electrophoresis according to the techniques described in Selander et al. (1971). Each locus was run in two different gel buffers to reduce convergence in electromobility (Johnson, 1977). Only those similarities that persisted in every run are reported here. Presumptive loci detected, number of specimens examined and gel-buffer systems employed are listed in Table 1. Genetic distances were calculated through the BIOSYST-1 computer

TABLE 1. **Allele designations and calculated gene frequencies for 30 presumptive genetic loci for 13 population and taxa of akodont rodents. Three *oryzomys longicaudatus* samples are included for comparison. Taxon abbreviations are those in Appendix A. N indicates sample size.**

		Olivaceus			Abrothrix andinu			longipi		san	Akodo		Geo	Che	Oryzomys longicaudat		
		beat	bra 2		and			moerens							phillip		lon
		bral			oli		dol	1	2		ber	mol			la	2v	
	N =	5	2	3	2	1	3	6	5	2	2	3	2	3	3	3	2
LOCUS	BUFFER																
GPD	TC 8	al	al	al	al	al	al	al	al	al	bl	bl	al	al	al	al	al
ALDH	Tris	a.6 c.4	al	cl	al	dl	al	cl	cl	cl	al	el	cl	cl	bl	b.5 c.5	b.5 c.5
EST D	LiOH	al	al	al	al	bl	al	a.3 c.7	a.9 c.1	al	al	gl	dl	bl	e.2 f.8	c.3 e.7	h.5 e.5
PEP B2	LiOH	a.8 b.2	al	a.7 b.3	al	cl	h.5 f.5	al	al	al	fl	fl	e.5 d.5	cl	dl	a.3 d.7	a.5 g.5
PEP B1	LiOH	a.9 b.1	a.5 b.5	a.8 b.2	a.5 b.5	bl	fl	al	al	al	fl	fl	d.5 c.5	cl	el	el	el
GOT - 1	LiOH	al	al	al	al	al	al	al	bl	al	al	bl	al	al	al	al	al
GOT + 2	LiOH	al	al	al	al	al	al	bl	al	bl	bl	bl	al	al	cl	cl	c.5 d.5
ICD - 1	TC 7	al	al	al	al	al	al	al	a.7 c.3	al	al	cl	al	al	bl	bl	bl
ICD +2	TC 7	a.8 c.2	al	al	al	al	al	a.5 c.5	al	al	bl	bl	al	al	a.5 c.5	al	al
SOD	TC 8	al	al	alp	al	al	al	al	al	al	bl	bl	al	al	bl	bl	a.5 c.5
ACON 1	TC 8	al	al	al	al	al	al	al	bl	al	cl	cl	bl	bl	al	cl	al
MPI	TC 8	al	al	al	al	bl	al	bl	bl	al	cl	cl	al	a.2 b.8	bl	bl	b.5 d.5
EAP	TC 7	al	al	a.2 b.8	al	al	cl	bl	al	bl	cl	cl	al	al	al	al	al
LDH 3	TC 7	al	al	al	al	al	al	al	al	al	bl	bl	al	al	al	al	al
MDH	TC 7	al	al	al	al	al	al	a.5 c.5	al	al	al	al	bl	al	cl	cl	a.5 c.5
PGM 3	TC 7	a.9 b.1	al	al	al	al	al	al	al	al	al	al	al	al	dl	dl	a.5 d.5
ENOL	TC 7	al	al	a.8 c.2	al	cl	al	al	al	al	al	al	al	al	d.7 e.3	dl	dl
GPI + 1	Paul	al	al	a.7 b.3	al	al	al	al	al	al	dl	dl	bl	bl	cl	cl	cl
G6PDH	TM	al	al	al	al	al	al	al	al	al	al	al	al	al	cl	bl	bl
6PGD	TM	a.7 b.3	al	al	al	al	al	bl	bl	bl	bl	al	al	cl	fl	dl	dl
ALD	TM	al	al	al	al	al	bl	bl	bl	bl	bl	bl	c.5 d.5	a.7 e.3	fl	fl	fl
ME 1	TC 8	al	al	al	al	al	al	al	al	al	cl	cl	bl	al	dl	al	el
SDH	TC 8	al	al	al	al	al	al	al	al	bl	bl	bl	al	al	a.3 c.7	al	al
ME - 2	TC8	al	al	al	al	al	al	al	al	al	al	al	al	al	al	al	al
GPI - 2	PGIp	al	al	al	al	al	al	al	al	dl	al	al	cl	cl	bl	bl	bl

Continue Table 1.

		Olivaceus			Abrothrix andinu			longipi		san	Akodon			Geo	Che	Oryzomys		
		beat	bra	2	and			moerens								longicaudat		
		bral			oli		dol	1	2		ber	mol				phillip	lon	
	N =	5	2	3	2	1	3	6	5	2	2	3	2	3	3	la	2v	2
LOCUS	BUFFER																	
PEP D	LiOH	a.6 b.4	a.5 c.5	a.7 c.3	cl	al	cl	c.5 f.3 g.2	cl	cl	bl	cl	dl	dl	c.2 e.8	c.3 e.7	bl	
PEP C1	LiOH	al	al	a.3 b.7	al	cl	al	bl	bl	bl	al	al	al	al	a.2 c.8	cl	cl	
GAPDH	PHOS	al	al	al	al	al	al	al	al	al	bl	bl	al	al	cl	al	a.5 c.5	
NP	TC 8	al	al	a.7 b.3	al	al	el	a.5 b.5	a.5 b.5	al	fl	gl	cl	cl	dl	dl	dl	
HF	TC 8	a.8 b.2	al	a.3 b.7	al	bl	fl	b.7 f.3	a.1 b.9	el	gl	gl	al	a.2 c.2 d.6	dl	d.5 e.5	el	

program (by D.L. Swofford and R.B. Selander), and dendrograms through the CLUST procedure (Aglomerative Hierarchical Clustering Program, by W.W. Moss).

Chromosomes.- Metaphase chromosomes were obtained by the well known colchicine-hypotonic technique. Chromosome measurements were made on photographic enlargements using the best single chromatid per pair, and values were transformed into percentages of the total haploid plus X set. Relative lengths were displayed in a scatter diagram called a karyo-idiogram (Spotorno et al., 1987), a device that allows eventual chromosome identification and comparison. Such procedure assumes the conservation of total nuclear DNA, which can be validated by direct DNA measurements, C-banding techniques or similarity of marker chromosomes (Spotorno, 1985). A karyo-idiogram also displays the two main indexes used in comparative cytogenetics: the total chromosome size (C = the sum of short and long arm lengths) and the centromeric index (i = 100 times the short arm length divided by C). The nomenclature for chromosome names follows Levan et al. (1964). Fundamental Number is the total number of arms visible in the female karyotype.

Penile morphology.- Penises were removed from dried specimens, placed within single vials and individually processed. Tap water was used for recovering full shape within a day or two. A first draft of external features was made under a Wild M5 stereomicroscope with a camera lucida attachment. A ventral or lateral cut then exposed the anterior bacular

mounds and urethral processes. After a second draft, each specimen was cleared in 1% KOH and stained with alizarin red, according to standard procedures (Lidicker, 1968). Finally, full dissection and removal of the proximal baculum together with its distal processes (still covered by soft mounds) allowed the production of drafts for ventral, lateral and dorsal views. Double staining with alcian blue and alizarin red, for cartilaginous and osseous tissues respectively (Wassersug 1976), was done on some additional specimens in the final stages of our work.

Skull and body biometry.- Ten to twelve adult individuals were selected per species. Two or three juveniles were included in many species samples in order to study ontogenetic factors or when few adults were available. Four external body variables (recorded from the specimens tags) and fourteen skull variables were selected (among those proposed by Anderson, 1968). They are listed in Table 2 and illustrated in Spotorno and Walker (1983; see their Fig. 1). Skull measurements were taken with a caliper and recorded to the nearest 0.1 mm. All original data were analysed

TABLE 2. **Loadings of cranio-mandibular and body variables on the first three principal component axes for separate analyses of akodont rodents (percentages of total variation explained is indicated in parentheses).**

variable		Abrothrix + Akodon + Bolomys (77%)		
		I	II	III
a)	body length	0.85	0.17	0.08
b)	tail length	0.74	0.06	0.32
c)	ear length	0.82	-0.30	0.10
d)	hind foot	0.70	-0.48	-0.03
e)	skull length	0.96	0.11	0.00
f)	zygomatic breadth	0.91	0.17	-0.16
g)	diastema	0.89	0.32	-0.05
h)	incisive foramen	0.84	0.01	0.35
i)	palatal length	0.68	-0.25	-0.13
j)	cranium breadth	0.92	0.19	-0.12
k)	bullae	0.38	-0.33	-0.77
l)	postpalatal breadth	0.50	-0.74	0.01
m)	intermolar breadth	0.68	-0.33	0.03
n)	incisive breadth	0.63	0.08	0.13
o)	subdiastema	0.83	0.14	0.07
p)	subcondyle	0.94	0.22	-0.09
q)	subangular	0.91	0.30	0.05
r)	mandible height	0.70	0.23	-0.56

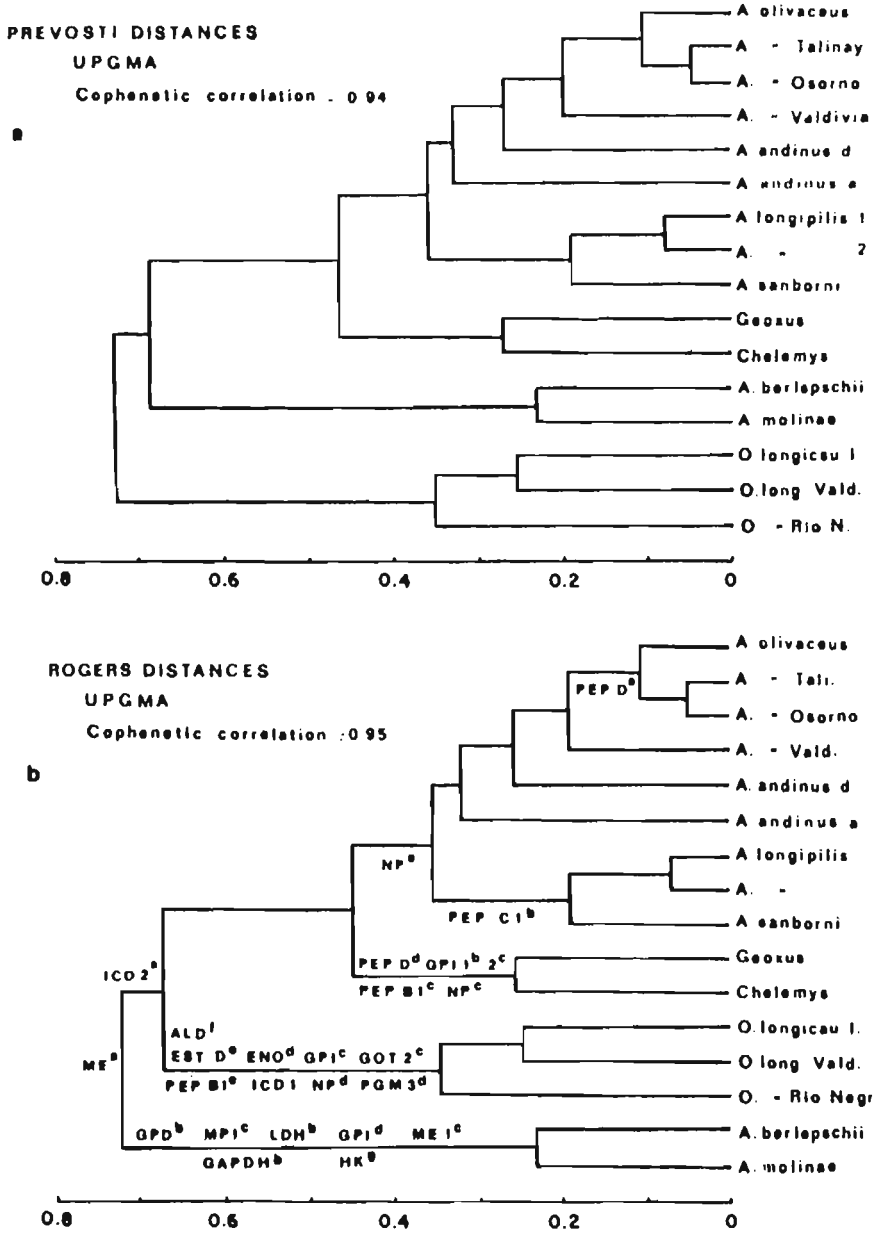

Fig. 1.- UPGMA dendrograms of electrophoretic distances among akodont rodents based on Prevosti and Rogers distances. *Oryzomys* samples are included as a reference.

by means of the Principal Component Analysis Computer Program available at the University of California, Berkeley (Duncan and Phillips, 1980). This is and ordination technique that usually results in distorted distances in close neighbors but derived distances between major groups or clusters are more faithfully represented than those obtained with other aglomerative techniques (Sneath and Sokal, 1973).

RESULTS

The electrophoretic analysis of akodonts were done examining 25 proteins encoded by 30 pressumptive loci in a total of 55 specimens from 16 populations; these represented eight akodont plus one oryzomylne species, the latter included as an outgroup. Table 1 shows allele designations and number of specimens per population studied. The number of alleles per locus found ranged from two to eight.

Genetic similarity indexes according to Prevosti (see Wright, 1978) and Rogers (1978) were calculated from allele frequencies of all electromorphs. Dendrograms based on Prevosti and Rogers genetic distances were generated using the UPGMA algorithm (Sneath and Sokal, 1973) (Fig. 1). Both had high cophenetic correlation coefficients with their correspondant data bases and displayed the same topology and taxa arrangement, save the most external branch: *Oryzomys* in the former and *Akodon* in the latter.

A search for alleles defining these branches gave nine exclusive alleles for *Oryzomys longicaudatus* populations, seven for *Akodon* species and five for *Geoxus-Chelemys* (Fig. 1). Surprisingly, no exclusive alleles shared by all *Akodon* species were found. But *Akodon berlepschii* and *A. molinae* shared seven of such alleles and the geographically southern species *A. olivaceus, A. andinus, A. longipilis,* and *A. sanborni* shared at least one allele not found in any other form. The last two species also exhibited two unique alleles.

Chromosome analysis of the karyotypes from fourteen species (Fig. 2) allowed the assesment of chromosome similarities among these taxa, as well as the distinction of some groups. All species shared one small metacentric chromosome, very constant in shape (i = 50) and size (about 2%) (bottom of Fig. 2), perhaps with the exception of *A. arviculoides*, slightly larger. This conservation of the relative proportions of a marker chromosome in such a graph reinforces the idea of a gross constancy in DNA quantities in these akodonts and validates further comparisons by means of this karyo-idiogram.

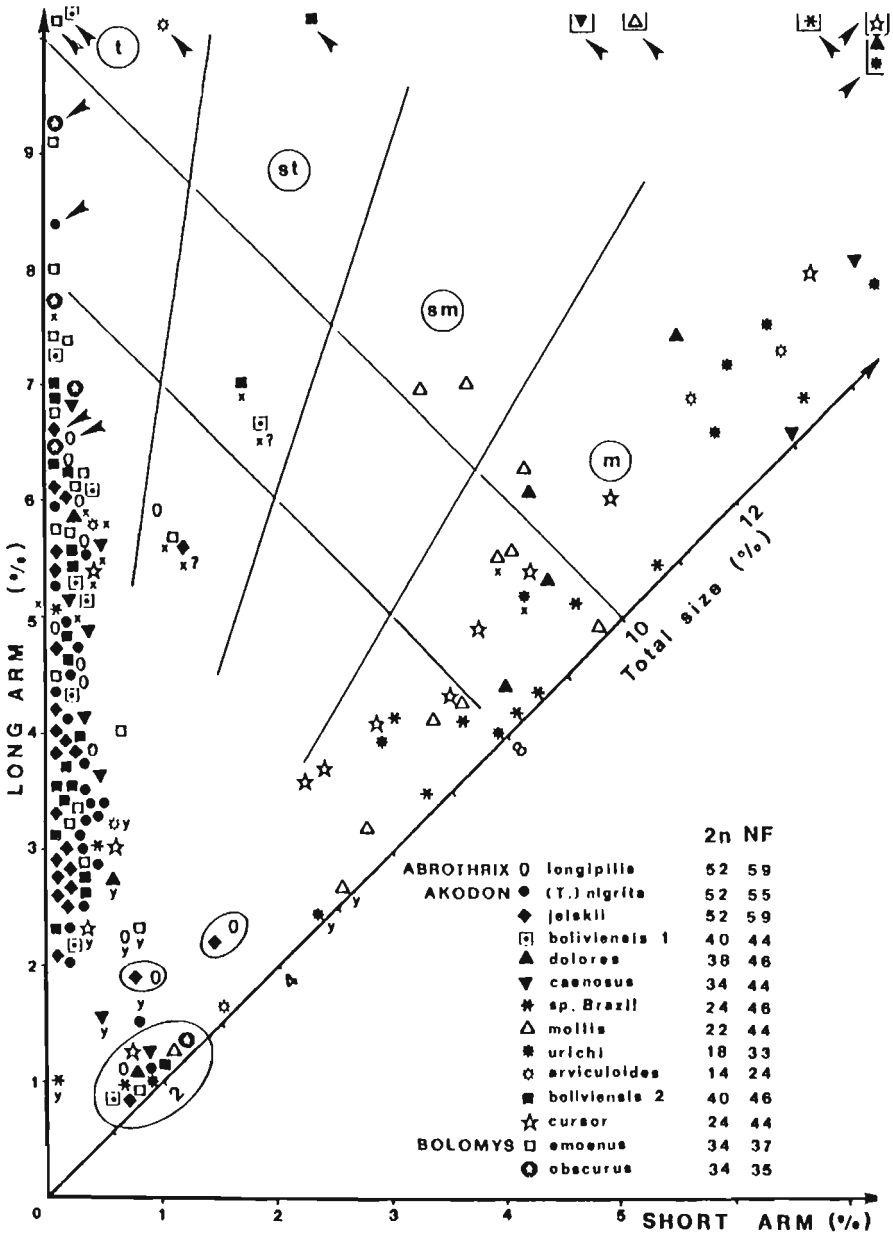

Fig. 2.- Karyo-idiogram displaying the chromosome relative lenghts from fourteen akodont karyotypes, based on the size of long and short arms of each chromosome in relation to the total length of the female haploid genome. Each symbol represents a separate chromosome (see text). X and Y designate sex chromosomes. Some telocentric elements are not displayed. The largest autosome is marked with arrow-head. Data sources are listed in Spotorno (1985).

Three chromosomes were found to be distinct for the above mentioned two groups: the largest autosome within each karyotype and two small metacentric ones. The largest autosome (arrow-heads in Fig. 3) was only 6.6% of the haploid genome length among the mostly telocentric (2n = 52) karyotypes of *A. longipilis* and *A. (Chroeomys) jeiskii*. By contrast, all other akodont karyotypes had at least one chromosome or arm larger than 8.5%, including *A. (Akodon) boliviensis, Bolomys amoenus, B. obscurus* and *A. (Thaptomys) nigrita*.

Two small submetacentric chromosomes (numbers 15 and 22 in the original karyotype description of *A. longipilis;* see Bianchi et al., 1971), having sizes 4 and 2.6% were also shared by the 2n = 52 karyotypes, with the notable exception of *A. (Thaptomys) nigrita*. No similar chromosomes were present in the karyotype of the latter or in the rest.

Metacentric and submetacentric autosomes found in the different karyotypes of akodonts showed a wide range of size and shape, with very few overlaps. This is the case for the extremely large biarmed chromosomes depicted in the upper right of the karyo-idiogram (Fig. 2), and of medium-sized ones near the diagonal in the same graph. This dispersion means that there is little similarity among them, and suggests that they are not homologous across the various karyotypes. Nevertheles, the chromosomal arm lengths of the medium-sized metacentrics fall within the same range as some telocentric ones, a similarity that might be due to inheritance from a common ancestry.

Penile morphology was also divergent in such two main groups. On one hand, the distal baculum of most species examined (including unreported material from the type species of *Bolomys)* showed three distal cartilaginous prongs or digits and a short osseous proximal baculum (Figs. 3b and c), similar to what is known as a complex baculum (Hooper and Musser, 1964). On the other hand, all examined specimens of *A. jelskii, A. olivaceus, A. xanthorhinus, A. longipilis* and *A. sanborni* always showed an elongated proximal baculum (Figs. 3e through i), which was extremely long in the last two species (Fig. 3a). This species pair also displayed a curved bacular bone in lateral view (Fig. 3i) and no distal digits at all. On the other hand, all the former species showed a small distal baculum. All these features were not known among South American cricetids, except *Nesoryzomys* (Patton and Haffner, 1970) with an elongated proximal baculum and a short distal baculum.

Multivariate analysis of skull and body measurements of 176 specimens of *Abrothrix, Akodon* and *Bolomys* gave principal component scores which tended to be similar for individuals belonging to a particular spe-

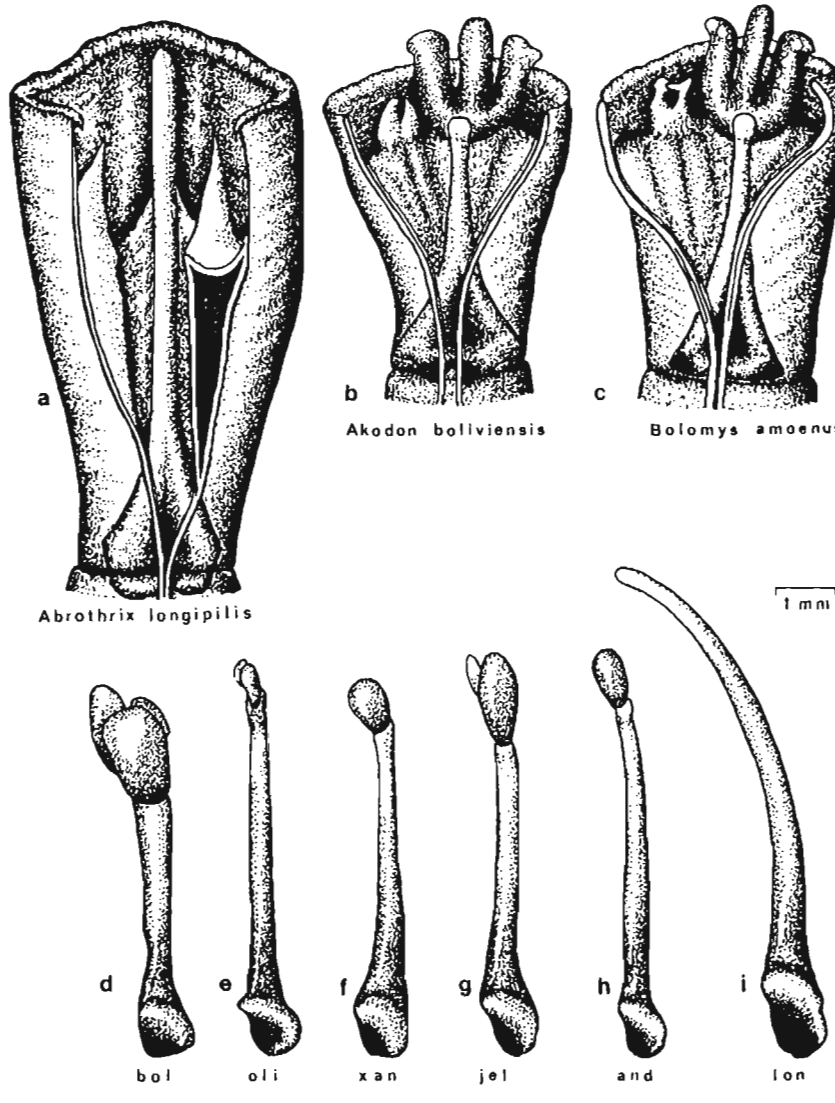

Fig. 3.- Penis morphology in akodont rodents. a) through c) ventral view of whole dissected organs; d) though i) lateral view of bacular apparatus (dorsal, non-urethral side to the right). Species name abreviations from Appendix A. (In *b*, specimen MVZ 115655, lately identified as *A. subfuscus arequipae* of the *boliviensis* group; see Myers et al., 1990).

cies, although identification of specimens was not considered in calculations. This analysis defined a first axis that explained a 61.9% of the total variation contained in the original data set. The large positive correlations of this axis (Table 2) with skull (0.96) and craniomandibular lengths (0.94) as well as with many other variables suggested that total body size was the most influencing factor in this axis. Juveniles usually had the lowest scores within specific samples, thus confirming that such axis represented size.

The second principal component, which was calculated orthogonal to the first and therefore statistically independent, explained 8.77% of the total variation, mainly on the basis of postpalatal breadth (correlation = 0.74) and hind foot length (-0.48) (Table 2). *Bolomys* specimens had the highest scores (top of Fig. 4), all *Akodon* species with full complex penis result with intermediate ones, and species with elongated proximal bacula had the lowest scores (bottom of Fig. 4). The third principal component, also orthogonal to the first and second axis and recovering 7.15% of total variation, spread the different specimens mainly on the basis of bullae (-0.77) and mandible height (0.56). The first three axis accumulated 77.22% of the total variation.

Juvenile specimens seem to follow a regular pattern according to the second and third principal component scores. They usually had the least extreme values within a specific sample (in the bivariate, towards the center of Fig. 4, where scores approach zero). An exception is *A. longipilis*, whose juveniles took comparatively extreme scores, and therefore peripheral positions (bottom of Fig. 4).

The fact that *A. longipilis* differed from congeneric forms not only in having a simple penis (Fig. 3), the largest body size (Fig. 4) and unusual position of juveniles in a multivariate morphospace (Fig. 4) prompted us to study other reproductive features in *Abrothrix*. We choose to examine litter size as revealed by embryo counts in field pregnant females, and in relation to their respective body size. Data for 33 females (Fig. 5) showed a significant correlation ($r = 0.<$, $P<0.05$) between such variables. Moreover, *A. longipilis* had the smallest litter size (mean = 3.46; N = 13) of all species here studied (Fig. 5). This is further confirmation on the divergent nature of *A. longipilis* when compared with related species.

DISCUSSION

Within the large species group currently included in *Abrothrix* and *Akodon*, two particular subsets seem to be clearly distinct. We will in-

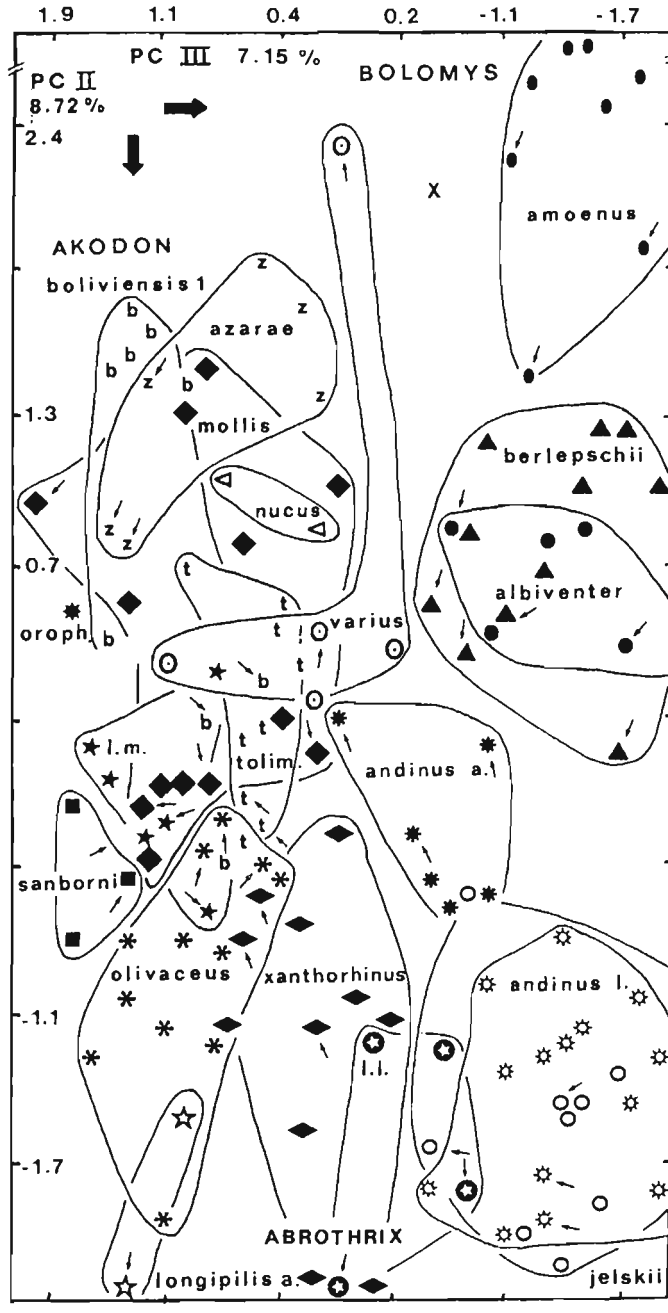

Fig. 4.- Bivariate plot of principal component scores on the first two axes of specimens of akodont rodents. Major generic groups are indicated. Percentages represent the proportion of the total variation explained by each component. Small arrows point juvenile specimens.

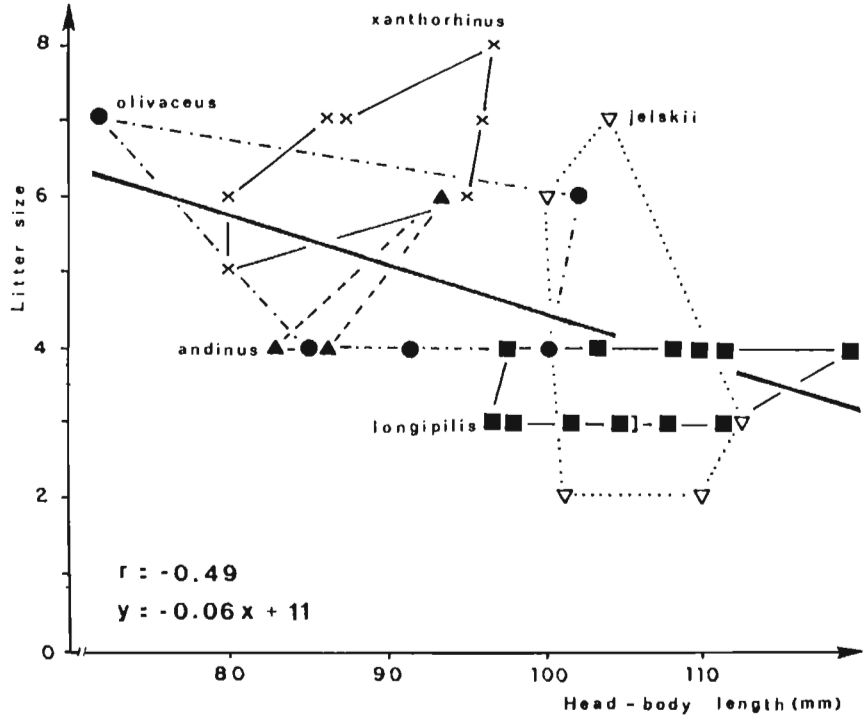

Fig. 5.- Bivariate plot of litter size and head-body length of each mother in some species of *Abrothrix* and *Akodon*.

terpret our findings in this light first, trying to assess the phylogenetic distinction of such subsets. Afterwards, we will examine the taxonomic status of what seems to be two different phylogenetic clades. Finally, we will explore and evaluate the factors that might have influenced the evolutionary history of these species.

The close relationships of *A. longipilis, A. sanborni, A. olivaceus, A. andinus, A. xanthorhinus* and *A. jeiskii* are clearly demonstrated by genetic and morphological data. All populations of the first four species consistently show close genetic distances (Table 1) as to cluster together in all UPGMA dendrograms (Fig. 1). Such branch can be uniquely defined by a single allele. Surprisingly, the other two *Akodon* (subgenus Akodon) species included here are placed well appart, in a branch clearly defined by seven unique alleles (Fig. 1). Also, A. *xanthorhinus* is electrophroretically well apart from seven species of *Akodon* and *Bolomys* (Apfelbaum & Reig 1989); the same can be said of *Bolomys amoenus* in relation to the *Akodon boliviensis* complex (Myers et al., 1990). Thus, three frequently confused species groups are electrophoretically distinct.

Cytogenetic data are consistent in separating this species group from *Akodon* s.s. species. The subset of six species all exhibit a diploid number of 52 chromosomes, a Fundamental Number of 59 (Bianchi et al., 1961; Gardner and Patton, 1976), a chromosome 1 with a length of 6.6%, and two small submetacentrics. Such array of characters is not present in any of the nearly twenty other *Akodon* species cytogenetically studied until now (Spotorno, 1986); rather, all species of *Akodon* s.s. show a 2n ranging from 22 to 43, FN from 39 to 46 as well as a chromosome 1 larger than 8.5% (review in Spotorno, 1986). In particular, *Akodon boliviensis* and *Bolomys amoenus*, the type species of their genera, have the distinct diploid numbers of 40 and 34, and Fundamental numbers of 44 and 37 respectively. Thus, these species groups can now be uniquely defined by the possession of such characters.

A generic status for the subgenus *Chroeomys*, based on protein electrophoresis data, have been recently proposed (Patton et al., 1989). Al though in such a study the genetic distinction of *Akodon (Chroeomys) jelski* from *Akodon* (s.s.), *Microxus, Bolomys, Oxymycterus,* and *Lenoxus* is clearly demonstrated, unfortunately "no other taxa allocated to *Abrothrix* were examined..." (p.357). Perhaps most of the 9 unique fixed alleles that are divergent in such a species (see their Table 5) belong not only to the former but also to the *Abrothrix* clade, as here understood. In fact, 4 of such alleles seem to be the same loci that separate *Abrothrix* from *Akodon* (s.s.) (my Table 1): GPD, ICD, LDH, and GAPDH. On the other hand, one of such authors listed at least three skull features shared by *A.*

inclusion of the Atlantic forms *obscurus* and *azarae* was probably the source of the taxonomic confusion created around the content of *Abrothrix*. We now know they both have a standard complex penis (Hooper & Musser, 1964), derived karyotypes, one pair of preputial glands and craneo-mandibular features like the rest of *Akodon* and *Bolomys* species. Accordingly, they should be excluded from *Abrothrix*.

Abrothrix seems to deserve a generic status. Most subgenera originally proposed by Waterhouse (1837) are now recognized as well estabilseh genera, e.g. *Scapteromys, Oxymycterus, Calomuys* and *Phyllotis*. Gray (1843) raised it to a full genus, as well as Thomas (1916), but many authors considered it unsufficiently different from *Akodon* s.s. But recently Bianchi et al. (1961) suggested a generic status, a step fully taken by Hershkovitz (1966), Gardner and Patton (1976), Voss and Linzey (1981), and Carleton and Musser (1984). All our data, particularly genetic data (see Table 1 and Fig. 1 and 2), clearly suggest that a distinct substantial gap separates this phyletic line from the rest of the *Akodon* genera.

The full extension of such monophyletic line remains to be completed. As here understood, *Abrothrix* comprises a geographic chain of six species now living only in southern South America; it probably evolved there along the Andes mountains (Reig, 1987). It is very probable that other Chilean southern forms like *Akodon markhami* Pine 1973 and *Akodon hershkovitzi* Patterson, Gallardo and Freas 1984 might belong to it; the same is true for the Argentinian *A. illuteus*, with a karyotype identical to that of *Abrothrix longipilis* (Liascovich et al., 1989). These must await further empirical research.

The ocurrence of a simple penis within the large group of South American cricetids thought to possess mainly full complex penises is a striking fact demanding explanation. The natural differentiation of the complex baculum in many muroids, including the ossification of the proximal baculum, is an event ocurring at 4 to 6 days after birth (Glucksmann et al., 1976). A reduction of the distal baculum can be experimentally induced in males of complex penis species by means of neonatal castration (Howard, 1959). Testosterone counteracts such effect, but only when injected before the fourth day of age; after such critical age, a simplified distal baculum remains (Gluksmann et al., 1976). Assuming that hormonal patterns are general for muroids, which include cricetids, a temporal delay of testosterone during development might be a proximal cause of bacular simplification.

There are some strong evidence that such hormonal heterochrony have in fact ocurred during the ontogeny of *A. longipilis*. Neonatal testosterone effects in muroids include not only differentiation of distal baculum and

TABLE 3. **Ecological characteristics of *Abrothrix longipilis* compared with those of *Abrothrix olivaceus* (m = male, f = female)**

Characteristic	*A. longipilis*	*A. olivaceus*	Source
Mean body weight of adults in g (range)	m 38.2 ± 0.5 (25-51) f 36.9 ± 0.7 (23-60)	28.2 ± 0.6 (20-36) 25.8 ± 1.0 (19-35)	Pearson, 1983
Mean body length of adults in mm (range)	m 104.9 ± 0.6 (91-122) f 105.4 ± 0.8 (88-121)	95.6 ± 0.9 (86-103) 93.2 ± 1.3 (84-108)	"
Longevity (months)	24	12	"
Distance moved (m)	46	29	"
Litter size (mean)	3.78 ± 0.11	5.08 ± 0.38	"
Reproduction	continuous	seasonal	Fulk, 1975
Density (animals/hectare) in Aug-Nov-Feb-May	8.7-4.8-7.1-7.9	30.3-97-78.6-62.7	"
Survivorship (%) in Aug-Nov-Feb-May	100-46-46-39	100-48-20-3	"
Behavior	peacefull, sociable	agressive	Pearson, 1983
Hydric efficiency	less	more	Cortes, 1986
Bioenergetic efficiency	less	more	Rau et al., 1981
Microhabitat	dense cover	varied, in patches	Pearson, 1983

the evolution of *A. longipilis* the main feature selected for was an increase in body size and for some but not necessarily all of their correlated reproductive characters. According to this view, a simple penis would not be a state particularly selected, but only a secondary consequence of broad phenotypic changes developmentally bounded. Some of such features would not be adaptations, but effects (Gould and Vrba, 1982); that is, the origins of some of such features do not have to be adaptive (Hoenigsberg, 1988). Indeed, two of such effects seems to be even maladaptive: hydric and bioenergetic efficiencies in the advanced *longipilis* are low compared with those of *olivaceus* (Table 3). It might be the case that the reported habitat selection of *longipilis* is forced by this physiological constraint ori-

ginally produced by an heterochronic event. Comparative and experimental tests of these hypothesis are now under way in our laboratory.

Although the particular genetic basis for such a large evolutionary change are largely unknown, our present data suggest that few genetic changes might be involved. First, the genetic distances found between *longipilis, olivaceus* and *andinus* are relatively low, at least similar to those separating subspecies of *Oryzomys longicaudatus* (Table 1 and Fig. 1) or to those between *Homo sapiens* and related pongids (O'Brien et al., 1985). Second, the chromosomes of *longipilis* are identical to those of the rest of congeneric species (Spotorno, 1986), even when-G and C-bands are examined (Gallardo, 1982). If hormonal heterochrony have occurred as outlined above, only a few genes regulating neonatal testosterone discharge are in principle required to induce an array of abrupt phenotypic changes from a generalized plastic body plan. In such a case, there would be no correlation between the amounts of genetic and phenotypic changes.

A reduced distal baculum was thought to be characteristic of North American cricetids (Hooper and Musser, 1964), in contrast with the complex penis of South American ones. Such macroevolutionary character have been considered key to understand the origin of American cricetids (Slaughter and Uberlaker, 1984). Our results suggests that the simple penis independently evolved in parallel within the two groups and we suspect by means of homologous ontogenetic mechanisms and under similar ecological factors. Further data substantiating these views will be published elsewhere.

ACKNOWLEDGEMENTS

This work was supported by Projects FONDECYT 86-1412, 88-1013 and DIB B-2689-8713, U. de Chile. We also thanks the accession to the Electrophoresis Laboratory and to specimens from the Museum of Vertebrate Zoology, U. of California, Berkeley, during post-graduate studies of the senior author supported by OEA and UNESCO. Some specimens were kindly provided by Drs. R. Murua, L. González and M. Gallardo from U. Austral, Valdivia.

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APPENDIX A. SPECIMENS EXAMINED

All specimens represented by standard museum preparations (skin with skull) are deposited in the Museum of Vertebrate Zoology, U. of California, Berkeley, USA, unless otherwise indicated. For each species (names usually taken from labels supra-specific names following Carleton & Musser, 1984), the country, province or department, specific locality, elevation, and number of specimens examined are given. This is followed by an asterisk if the specimen is deposited in the collection of the

Laboratorio de Citogenética de Mamíferos, F. de Medicina, U. de Chile and by one or more letters in parenthesis indicating materials additionally examined: C = chromosomes; E = electrophoretic material; S = skull and body; and P = phallus. The abreviations used in the tables and figures follow the species name.

ORYZOMYINI

Oryzomys longicaudatus (Orl). ARGENTINA. Rio Negro; La Veranada, 38 Km SSW Bariloche, 3 (E). CHILE. La Serena 1a, Quebrada Monardes, 2* (E). Valdivia 2v, Fundo Rucapangui, 3* (E).

AKODONTINI

Geoxus valdivianus (Geo). ARGENTINA. Neuquen: Arroyo Chacabuco, 5 km NW Nahuel Huapi, 1 (S); 2 km NW Confluencia, 2 (SP); Lago Correntoso, Ruca Malen, 5 (SP); Rio Negro: 43 km SSW Bariloche, 6 (ES).

Chelemys macronyx (Che). ARGENTINA. Rio Castano Overo, 44 km W Bariloche, 8 (ES); 43 km SSW Bariloche, 6 (SP); Cerro Leones, 15 km ENE Bariloche, 1 (S).

Bolomys amoenus. PERU. Puno: Hda. Ontave, 12900 ft, 2 (S); Hda. Calacala, 7 mi SE Putina, 13000 ft, 2 (SP), Hda. Pairumani, 24 mi S Ilave, 13000 ft, 2 (SP); 15 km W Puno, 13000 ft, 2 (S); 13300 ft, 1 (S); 82 km W Puno, 14000 ft, 3 (S); Hda. Checayani, 20 km NE Azangaro, 13200 ft, 2 (CSP).

Bolomys lactens. ARGENTINA, Jujuy: 1 mi W Leon, 5800 ft, 1 (S).

Akodon albiventer. ARGENTINA, Jujuy: 0.5 ml E Tilcara, 8500 ft, 1 (S). BOLIVIA. Oruro 40 mi S Oruro, 12000 ft, 1 (S). Potosi: 4 mi E Uyuni, 12600 ft to 13000 ft, 2 (SP); 5 mi N Villazon, 11500 ft, 1 (SP). Tarija: 25 mi SSE Camatazuri, 1 (S).

Akodon azarae: ARGENTINA. Buenos Aires: 25 mi S Azul, 1000 ft, S (S); 20 km S Ezeiza, 2 (SP); Laboratory stock IMBICE, 1* (P).

Akodon berlepschii (ber). CHILE. Parinacota: 25 mi NEE Caritaya, 12000 ft, 2 (S); 2 km E Putre, 3650 m, 8* (CE). PERU: Tacna: 2 km N Tarata, 10500 ft, 1 (P); 1.5 ml N Tarata, 11600 ft, 2 (S); Pampa de Titire, 8 km NE Tarata, 14600 ft, 1 (SP); 8 mi NE Tarata, 2 (S).

Akodon (boliviensis 2).PERU. Puno: Río Huanque, 13100 ft, 2 (CS). Tacna: 15 mi N Tarata, 11600 ft, 2 (CS).

Akodon molinae (mol). ARGENTINA: Buenos Aires: Laboratory stock IMBICE, 3* (E).

Akodon mollis (moll). ECUADOR. Pichincha: 26 km NNE Quito, 2800 m, 1 (P). PERU. Piura: 6 mi NE Canchaque, 5500 ft, 7 (CSP); 2 KM Porculla, 6500 ft, 1 (S).

Amazonas: 5 Km N, 5 Km E Pomacocha, 6000 ft, 4 (SP).

Akodon nucus. ARGENTINA. Neuquén: 5 km N Las Coloradas, 2 (P).

Akodon orophilus (oro). BOLIVIA. Cochabamba: 20 mi E Totora, 9700 ft, 1 (SP). PERU. Amazonas: 15 km N, 5 km E Pomacocha, 6000 ft, 4 (SP).

Akodon subfuscus (boliviensis 1). PERU. Apurimac: 22-24 Km S Chalhuanca, 10700 – 11700 ft, 2 (CSP); 24 km S Chalhuanca 14500 ft, 1 (S); 40 km S Chalhuanca, 14700 ft, 1 (SP). Ayacucho: 10 mi NWN Puquio, 11500 – 13000 ft, (3) (S); 9 mi NE Puqulo, 13500 ft, 2 (S). Arequipa: 12 mi E Arequipa, 10600 ft, 1 (S).

Akodon tolimae (tol.). COLOMBIA. VALLE: 4 km NW San Antonio, 6500 ft, 12 (SP).

Akodon torques (tor). PERU. Cuzco: 90 km SE Quillabamba, 2 (P).

Akodon varius (var). ARGENTINA: Córdova: La Maya, 4,5 km SE Bell Ville, 1 (S). BOLIVIA. Cochabamba: 15 mi E Tapacari, 9000 ft, 1 (S). Santa Cruz: 5 mi W Comarapa, 7500 ft, 1 (SP). Tarija: 5 mi S Tarija, 6700 ft, 2 (SP).

Abrothrix andinus andinus (and). CHILE. Santiago: Farellones, 51 km E Santiago, 10* (CS).

Abrothrix andinus dolichonyx (and 1). CHILE. Parinacota: 3 km S Parinacota, 4100 m 3* (CE). El Loa: San Pedro, 35 mi NE Calama, 12500 ft, 3 (SP). PERU. Arequipa: Lago Salinas, 22 mi E Arequipa, 14100 – 15000 ft, 5 (S). Moquegua: 5 km E Lago Suche, 14600 ft, 1 (S). Tacna: 2 km N Nevado Livina, 15300 ft, 4 (S); 13 – 29 km NE Tarata, 14600 ft, 3 (SP).

Abrothrix jeiskii. PERU. Pasco: 10 mi Cerro de Pasco, 13000 ft, 1 (S). Lima: 1,5 mi W Casapalca, 13200 ft, 1 (S); 1 mi NR Challapalca, 1 (C). Puno: Hda. Onayo, 15 mi S Juliaca, 3 (S); 1 mi S Limbani, 11500 ft, 1 (S); Hda. Pairumani, 24 mi S Ilave 13000 ft, 2 (SP); 4 km NW Pomata, 12500

ft, 1 (P). Arequipa: Lago Salinas, 25 mi E Arequipa, 14200 ft, 1 (SP). Moquegua: Lago Suche, 14500 ft, 2 (S); Lago Vizcacha, 14900 ft, 1 (S).

Abrothrix longipilis. ARGENTINA. Neuquén: 30 km S San Martín de los Andes, 2 (S); Arroyo Chacabuco, 5 km NW Nahuel Huapi, 2 (SP); 3 Km NW Confluencia, 2 (SP) Lago Correntoso, 1 (P). Río Negro: 19 km NNE El Bolsón, 1 (P); La Veranada, 39 km SSW Bariloche, 3 (E). CHILE. Elqui, Coquimbo: Fray Jorge, 1000 ft, 2 (ESP). Chacabuco: Fundo STa. Laura, Cta. Dormida, 10 Km W Tiltil, 1100 m, 4 (CSP). Malleco: Nahuelbuta, 3 (S). Valdivia: Fundo San Martín, 5* (E). Osorno La Picada, Volcán Osorno, 3* (P).

Abrothrix olivaceus (oli). ARGENTINA. Rio Negro: Bariloche, 790 m, 3 (SP); 112 to 14 km W Bariloche, 7 (ESP); 44 km W to SSW Bariloche, 890 to 1030 m, 5 (ES). Chubut: La Catarata, El Hoyo 600 ft, 1 (S); Lago Puelo, 2 (S). CHILE. Ovalle: Las Breas, 4* (CS). Limarí: Talinay, 2* (E). Santiago: Farellones, 2800 m, 1* (E). Valdivia: Fundo San Martín, 3* (E). Osorno: La Picada, Volcán Osorno, 2* (E).

Abrothrix sanborni (san). CHILE. Osorno: La Picada, Volcán Osorno, 3 (S) plus 2* (EP).

Abrothrix xanthorhinus. ARGENTINA. Neuquén: Parque Laguna Blanca, 31 km SW Zapala, 1 (S); 5 km N Las Coloradas, 1 (S); 3 km NW Confluencia, 5 (SP); Arroyo Corral Quemado, 16 km NNE Nahuel Huapi, 2 (S). Rio Negro: Cerro Leones, 15 km ENE Bariloche, 2 (S).