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Notes on Bolivian Mammals 3: A Revised Diagnosis of *Andalgalomys* (Rodentia, Muridae) and the Description of a New Subspecies

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ABSTRACT

Reported characters of the phyllotine genus *Andalgalomys* are reviewed and a revised diagnosis is presented. *Andalgalomys* is phenetically more similar to *Graomys* than to *Calomys* or *Eligmodontia*. A new subspecies of *Andalgalomys pearsoni* is described from Bolivia. This, the first Bolivian record for the genus, extends the known range northward approximately 300 km. Karyotypes for both subspecies of *A. pearsoni* are: *A. p. pearsoni* has 78 chromosomes and *A. p.* n. ssp. 76. These are the highest reported diploid numbers for phyllotine rodents. The first specimens from Bolivia of *Thrichomys apereoides* and *Ctenomys minutus* are documented.

RESUMEN

Los caracteres descritos del género phyllotino *Andalgalomys* son revisados y un diagnosis corregido es presentado. Fenotípicamente *Andalgalomys* es más similar a *Graomys* que a *Calomys* o *Eligmodontia*. Una nueva subespecie de *Andalgalomys pearsoni* de Bolivia es descrita. Éste es el primer informe Boliviano para este género, extendiendo su distribución conocido aproximadamente 300 km al norte. Cariotipos para ambas subespecies de *A. pearsoni* estan: *A. p. pearsoni* tiene 78 cromosomas y *A. p.* n. ssp. 76. Éstos son los informes más altos del numero de cromosomas en los roedores phyllotinos. Los primeros especímenes de Bolivia de *Thrichomys apereoides* y *Ctenomys minutus* estan documentados.

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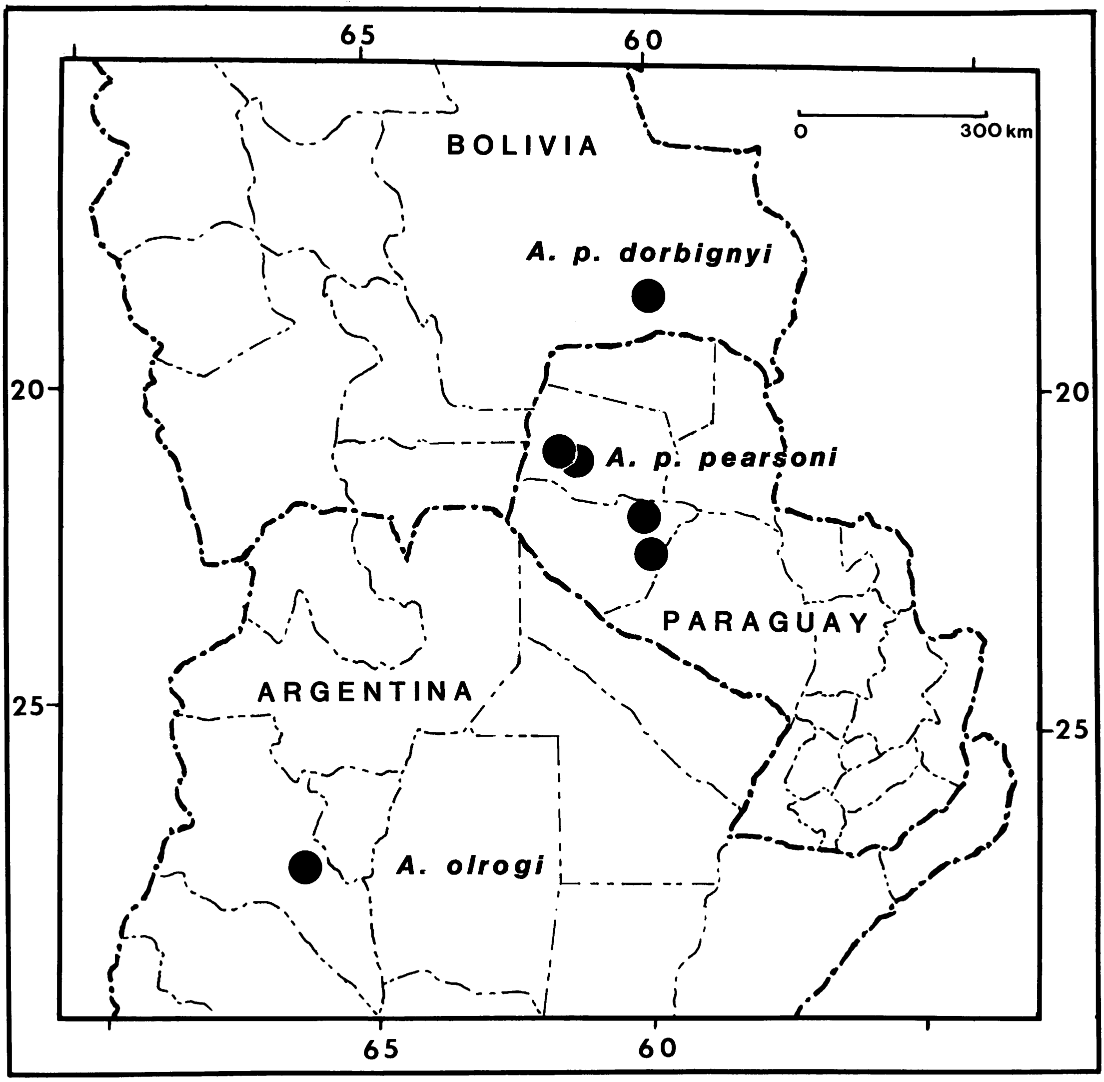

Fig. 1. Map of Paraguay and parts of Argentina and Bolivia. Localities shown are inhabited by *Andalgalomys* and are listed in the Appendix.

INTRODUCTION

In August of 1984, two specimens of *Andalgalomys* were trapped in the eastern part of Santa Cruz Department, Bolivia, in scrubby vegetation characteristic of the borders of the arid Chaco located to the south. These, the first Bolivian specimens of *Andalgalomys* (Anderson, 1985), extend the known range of the genus northward from Paraguay (fig. 1) and provide evidence of a morphologically distinct northern population of *Andalgalomys pearsoni*.

We document these geographic and taxonomic discoveries, add new comparative data, and reevaluate relationships at both the specific and generic levels. We review the published characters of the genus *Andalgalomys*, compare specimens, modify Williams and Mares' (1978) original description, and revise the diagnosis of the genus. Since Williams and Mares described *Andalgalomys*, additional specimens of *A. pearsoni* have been collected from Paraguay. The number of available specimens has approximately tripled and thus character variation within the genus can be assessed more adequately.

METHODS

We studied specimens (listed in the Appendix) of *Andalgalomys* and other phyllotine genera from the collections in the Museum of Southwestern Biology at the University of New Mexico (MSB), Albuquerque; the Carnegie Museum (CM), Pittsburgh; the Museum of Zoology at the University of Michigan (UMMZ), Ann Arbor; the American Museum of Natural History (AMNH), New York; the Museum of Vertebrate Zoology, University of California at Berkeley (MVZ); the National Museum of Natural History (USNM), Washington, D.C.; and the Field Museum of Natural History (FMNH), Chicago.

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

TOT	total length
HBL	head and body length
TAI	tail length
HFL	hind foot length
EAR	ear length

The weight in grams was also recorded. The following dimensions were measured with a stage craniometer to the nearest 0.01 mm (see Anderson, 1969, for definitions of the dimensions used):

BUL	length of bulla
MXL	alveolar length of maxillary tooth row
PRL	palatilar length
ZAL	length of zygomatic aperture
IFL	length of incisive foramina
CIL	condyloincisive length
MSB	breadth of mesopterygoid fossa
IDB	interdental palatal breadth
PDB	breadth of postdental constriction
BRB	breadth of rostrum
PLB	palatal breadth
POB	breadth across paroccipital processes
AZB	anterior zygomatic breadth
PZB	posterior zygomatic breadth
MTB	breadth of M1
OIL	occipito-interparietal length
ONL	occipitonasal length
NLL	nasal length
ROL	length of rostrum
IOB	interorbital breadth
BCB	breadth of braincase
IED	lateral incisor exposure
BUD	bullar depth
SKD	depth of skull
ZPW	width of zygomatic plate

Cell preparations of the new subspecies were made in the field from bone marrow of the femur as described by Baker et al. (1982). A slide of the cell suspension was prepared in the field and later stained with giemsa. A cell suspension for future banding analyses was preserved in liquid nitrogen and deposited in the frozen tissues division of the Museum of Southwestern Biology at the University of New Mexico. Dr. Philip Myers of the University of Michigan generously provided a chromosomal slide from the specimen from Paraguay. Determinations of diploid and fundamental numbers were based on examination of at least 20 metaphase spreads from each specimen.

Statistical analyses (Principal Components Analysis, Canonical Discriminant Analysis, univariate analyses) were done using the programs of the Statistical Analysis System (SAS Institute Inc., 1982) at the City University of New York Computer Center.

We compared specimens of comparable age between species, and examined sex and age differences within taxa. We found no obvious sexual dimorphism in species of *Andalgalomys,* but dimorphism might become evident if larger series were studied.

Dental terminology follows Hershkovitz (1962) and Williams and Mares (1978).

ACKNOWLEDGMENTS

The two specimens of the new Bolivian subspecies were obtained on an expedition supported in part by the National Science Foundation (Grants BSR 83-16740 and 84-08923, to Anderson and Yates, respectively). We acknowledge the field collectors J. A. Cook and D. L. Moore, the Carnegie Museum for lending specimens, curators at MCZ, FMNH, USNM, and UMMZ for use of their collections, P. Myers for sending the slide with unstudied chromosomes of *A. p. pearsoni* from Paraguay, N. A. Neff for checking locality records, C. J. Cole and M. Wasserman for use of their laboratories and assistance in karyotypic analyses, and C. W. Myers for photographic assistance. We thank A. L.

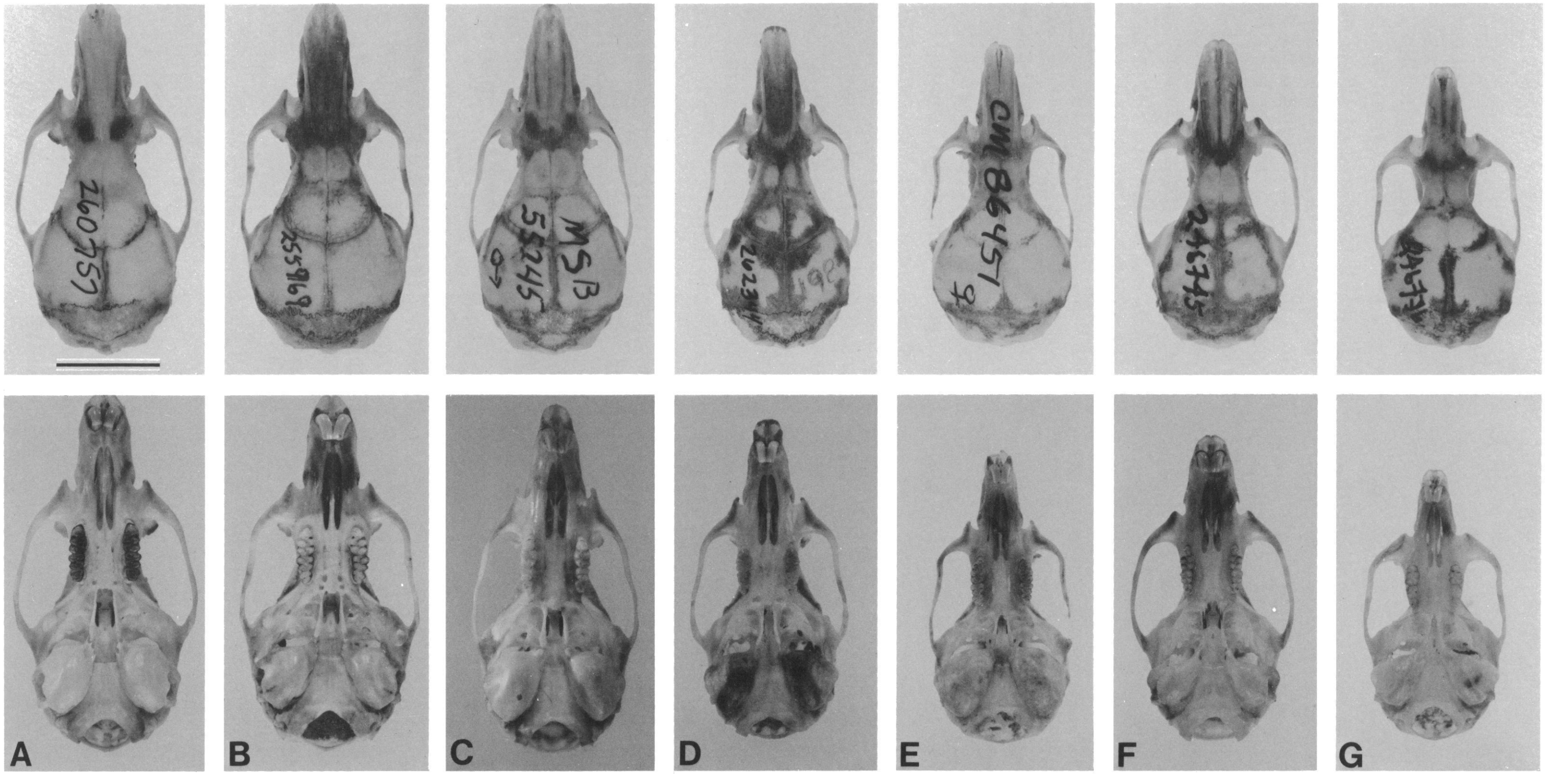

Fig. 2. Dorsal and ventral cranial views of species and subspecies of *Andalgalomys* and three other genera. **A.** *G. griseoflavus* (AMNH 260757), **B.** *Graomys domorum* (AMNH 255969), **C.** *A. pearsoni dorbignyi* (MSB 55245), **D.** *A. pearsoni pearsoni* (AMNH 262344), **E.** *A. olrogi* (CM 86451), **F.** *Calomys callosus* (AMNH 246745), and **G.** *Eligmodontia typus* (AMNH 246776). Scale shown represents 10 mm.

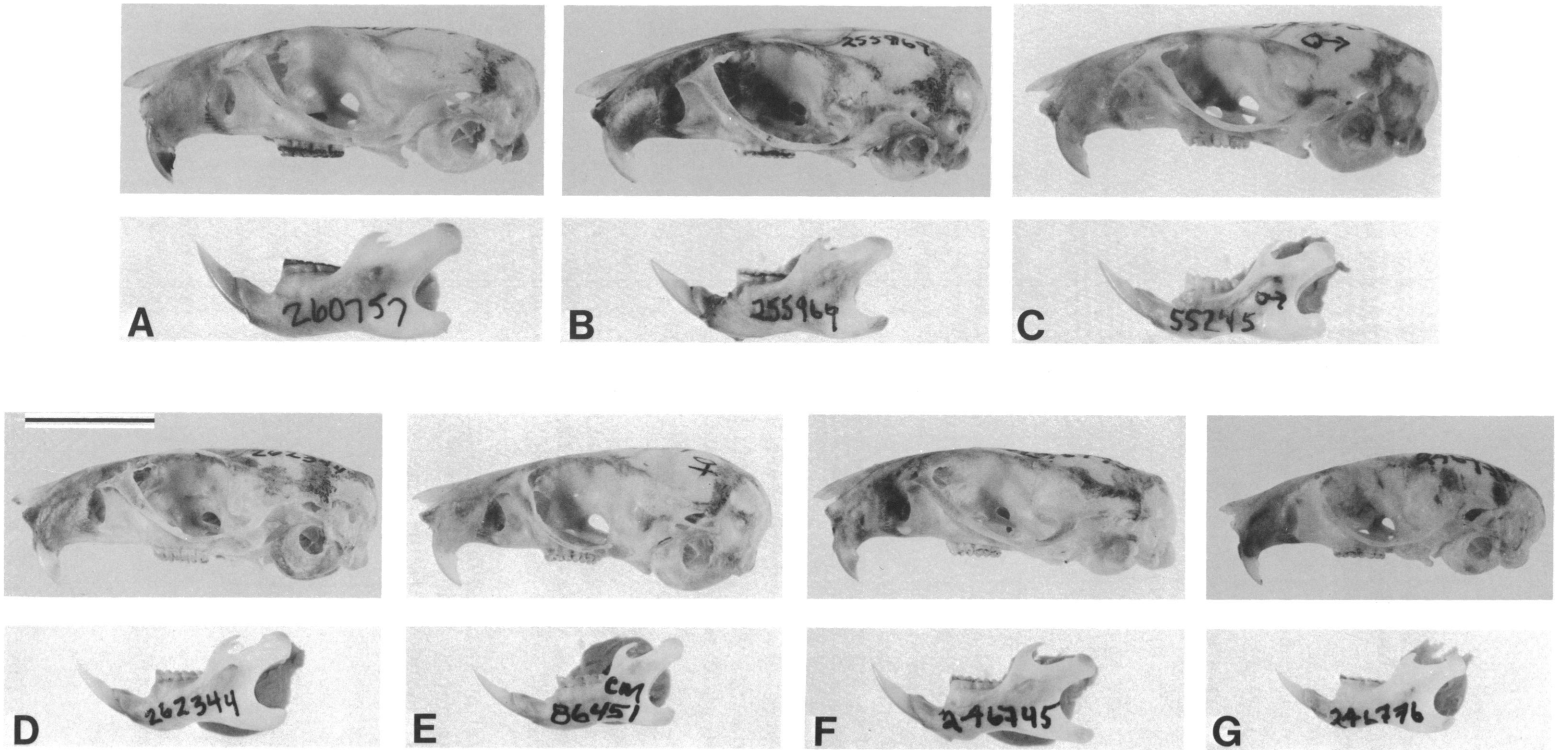

Fig. 3. Lateral views of crania and dentaries of specimens shown in figure 2. Scale shown represents 10 mm.

Gardner, L. F. Marcus, G. G. Musser, J. L. Patton, and D. F. Williams for critically reviewing an earlier draft of the manuscript.

Genus *Andalgalomys* Williams and Mares, 1978

Andalgalomys Williams and Mares, 1978: 197; type species *Andalgalomys olrogi*, op. cit.: 203, by original designation; also included *A. pearsoni* (Myers, 1977).

CONTEXT: Family Muridae, subfamily Sigmodontinae, tribe Phyllotini (see Olds and Anderson, in press, for diagnosis of tribe).

CONTENT: *Andalgalomys* includes *A. olrogi* (Williams and Mares, 1978) and *A. pearsoni* (Myers, 1977), the latter now represented by two subspecies.

DIAGNOSIS: A genus of Phyllotini distinguished by the following combination of characters: pelage yellowish-brown; small whitish subauricular spot; tail equal to or longer than head and body length; tail penicillate; soles of feet naked; supraorbital region with ledged and posteriorly divergent sides; nasals slender, straight, and long; bullae greatly inflated relative to those of other phyllotines; palatine with slits; molars brachydont, tuberculate, slightly crested, and with a tendency toward lamination in the upper molars; postcingulum of M1 with a slight notch or fold; anteroloph of M2 small and directed nearly anteriorly; major fold of M3 deep, separating metacone-hypocone from the protocone-paracone by a double enamel wall.

Williams and Mares (1978) presented a general description of *Andalgalomys* that includes some characters common to all phyllotines and some shared with other Sigmodontinae. Comparisons were in a separate section. We extracted the following characters for further consideration and comment as needed. The species of *Andalgalomys* are contrasted with representatives of *Calomys, Eligmodontia,* and *Graomys* in figures 2 and 3.

EXTERNAL CHARACTERS:

1. Size moderate (head and body lengths of adults now known to range from 85 to 125 mm).
2. Tail slightly to moderately haired and penicillate (unlike most phyllotines, but like *Phyllotis, Graomys, Irenomys,* and *Eligmodontia*).
3. Tail longer than head and body (unlike *Galenomys, Auliscomys, Calomys, Punomys, Chinchillula, Andinomys, Euneomys, Neotomys, Reithrodon*).
4. Pinnae moderately large and sparsely covered with fine hairs. True of many phyllotines.
5. Soles of feet naked (unlike *Eligmodontia* and *Galenomys*).

CRANIAL CHARACTERS (see figs. 2, 3):

6. Sides of interorbital region diverging posteriorly (like *Graomys* and some *Calomys* and unlike *Auliscomys, Phyllotis, Galenomys*).
7. Supraorbital region ledged (as in *Graomys* and some species of *Calomys*).
8. Nasals slender and straight. Also true of *Eligmodontia,* however, nasals relatively longer in *Andalgalomys.*
9. Molar rows parallel (or slightly convergent anteriorly). True of some phyllotines, but rows tending to converge anteriorly in *Neotomys, Reithrodon, Euneomys, Andinomys, Irenomys,* and *Punomys.*
10. Palatines usually having large slitlike foramina.
11. Parapterygoid fossa border ledged anteriorly and medially (as in phyllotines generally).
12. Bullae relatively greatly inflated (inflation greater in *A. olrogi* than in *A. pearsoni*). Bullae also somewhat enlarged in *Graomys* and in some species of *Eligmodontia.*

DENTAL CHARACTERS (see fig. 4):

13. Molars brachydont (as in *Calomys* and *Eligmodontia*).
14. Molar crowns tuberculate and slightly crested (as in *Calomys* and *Eligmodontia*), some tendency toward lamination in the upper molars (not present in *Calomys* and *Eligmodontia*).
15. M1 having well-developed anterior median fold and an anteromedian style. Not always true; fold often weakly developed

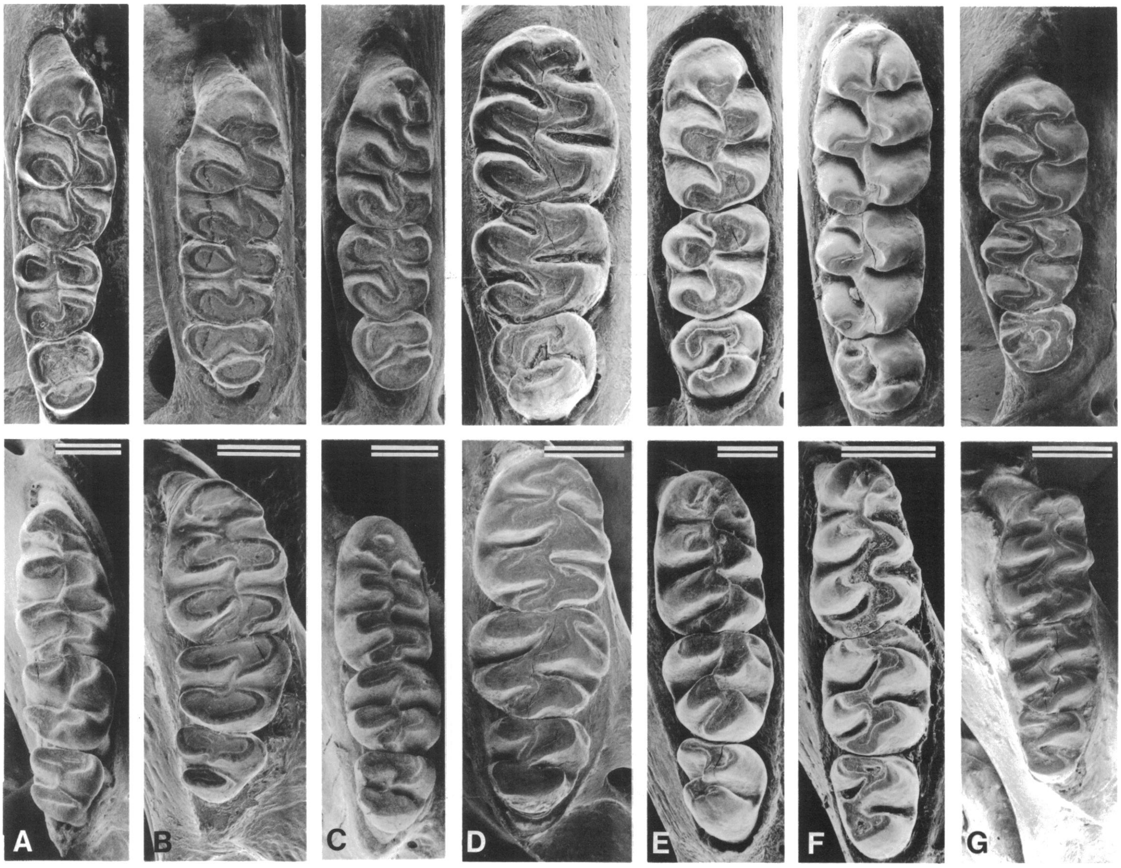

Fig. 4. Views of upper (above) and lower (below) right molar rows (SEM photos), of **A.** *A. pearsoni dorbignyi* (MSB 55245, holotype), **B.** *A. p. pearsoni* (AMNH 262345), **C.** *A. olrogi* (CM 44020), **D.** *Graomys domorum* (AMNH 260754), **E.** *Graomys griseoflavus* (AMNH 246848), **F.** *Calomys sorellus* (AMNH 231697), and **G.** *Eligmodontia typus* (AMNH 25702). Scales shown represent 1 mm.

in *Andalgalomys,* and style present or not. *Calomys* showing a similar pattern.

16. Postcingulum of M1 having slight notch or fold.
17. Anteroloph of M2 small and directed nearly anteriorly.
18. Major fold of M3 deep, separating the metacone-hypocone from the protocone-paracone by a double enamel wall that usually persists in worn teeth (*Graomys* tending to show this; but not *Calomys* and *Eligmodontia*).
19. Procingulum of m2 not apparent. Generally true of phyllotines.
20. Anteroconulid of m2 not apparent. Because anteroconulid a part of procingulum, redundant with 19.

FURTHER COMMENTS ON DENTITION: In the general description given by Williams and Mares (1978), we found some discrepancies between their comments and the specimens we examined. These are summarized here.

The first primary fold of M2 is generally shallow, but not always. The first minor fold was said to be small and directed in an anteroposterior plane. This is confusing because the fold is horizontal along the anterior edge of the tooth and is oriented anteroposteriorly along the anteroloph.

In the M2, they said that the metacone is greater than or equal to the hypocone in size. Myers (1977, in describing *pearsoni*), said the opposite; to us they seem approximately equal in size. Williams and Mares also said that the paracone of the M2 is greater than or equal to the protocone; they seem approximately equal to us.

Anteromedian fold of the m1 was said to form a small notch or deep groove on the anterior surface of procingulum, but also to penetrate deeply as an enamel fold. We note considerable variation in this character; it may be present or absent; when present it is not always an enamel fold.

The anterolingual and anterolabial conulids were said to be usually not well differentiated from each other and usually of equal size. We note that the former may be larger.

The protoconid of the m1 was said to be nearly opposite the metaconid. This varies; the protoconid may be posterior to the metaconid. The hypoconid of the m1 was said to be opposite or behind the entoconid. We note that it is behind.

In the m2, the first minor fold was said not to be evident, however, it is evident in *A. pearsoni*.

In the m3, the first primary fold was said to be about midway on the tooth. It is more anterior in *A. pearsoni*.

BACULAR CHARACTERS FOR *ANDALGALOMYS* (characters from Williams and Mares, 1978; terminology and comparative data from Hooper and Musser, 1964):

21. Tridigitate (also true of other phyllotine and nonphyllotine genera).
22. Medial digit shorter than lateral digits, curved slightly dorsad (unlike *Calomys, Eligmodontia, Graomys,* and *Auliscomys*).
23. Lateral digits robust (true of others, including *Calomys* and *Eligmodontia,* but untrue of *Auliscomys*).
24. Proximal end of baculum expanded laterally and having straight edges. In this, *Andalgalomys* resembling *Eligmodontia* more than the three others in Hooper and Musser's figure 4.
25. Distal end slightly expanded and ball-shaped.
26. Bacular mounds extending beyond glans hood.
27. Glans penis as long as, or longer than, baculum (generally true of sigmodontine rodents).

COMPARISONS: Within the Phyllotini, *Andalgalomys* is most similar to *Calomys, Eligmodontia,* and *Graomys.* Williams and Mares (1978) noted these similarities and suggested (p. 199) that *Andalgalomys* is more closely related to the "*Calomys-Eligmodontia* complex than to *Graomys.*" Our interpretation of the morphology suggests that *Andalgalomys* may be more closely related to *Graomys.* Williams and Mares used two species of *Calomys* in their comparisons, *C. callosus* (*C. muriculus* is a synonym of *C. callosus*) and *C. musculinus,* of which they had only one specimen. *Calomys callosus* is more like *Andalgalomys* in many respects than *Andalgalomys* is like any other species of *Calomys. Graomys* is more similar to *Andalgalomys* externally and cranially than is *Eligmodontia.* The diagnosis given above will distinguish *Andalgalomys* from these other genera.

We summarize specific generic comparisons that seem meaningful (from Williams and Mares, 1978, and from our own observations) as follows:

Andalgalomys differs from *Eligmodontia* in having a longer tail, naked-soled feet, a larger, more wedge-shaped skull, longer rostrum (figs. 2, 3), and more ovate molar cusps (fig. 4). In *Andalgalomys* the M3 is larger and more triangular, the metacone is larger than the hypocone, the procingulum of the m2 is absent or obsolete, and the first primary fold of the m3 is in the middle of the tooth.

In comparison to *Calomys callosus, Andalgalomys* is larger and has a tail that is longer than the head and body, a more slender rostrum, larger bullae, a notch on the postcingulum of m1, and no evident procingulum of m2.

Andalgalomys differs from *Graomys* in being smaller, in lacking an alisphenoid strut, and in having more brachydont molars, more ovate cusps, an anterior fold and anteromedian style in the M1, no anteroloph of M3, and a rounded rather than ridged anteroconulid in the m2.

Andalgalomys differs from these three genera (and other phyllotine genera) in having a whitish subauricular patch; a tendency toward lamination in the upper molars; a slight notch in the postcingulum of M1; the anteroloph of M2 directed nearly anterior; and the deep fold of M3.

The ratio of crown lengths of M3/M2 (table 1) is greater in *Andalgalomys* than in *Calomys, Eligmodontia,* or *Graomys.* The crown length of the M3 is most reduced in *Eligmodontia.* In increasing order, the M1 is proportionally longer in *Graomys, Andalgalomys, Eligmodontia,* and *Calomys.* In the lower dentition, the m1 is relatively longer in *Andalgalomys* than in other genera and the length of m3 is approximately the same proportion of m2 in all.

TABLE 1
Means of Crown Lengths of Upper Molars and the Ratio M3/M2 in *Andalgalomys, Calomys, Eligmodontia,* and *Graomys*

Species	*n*	LM1	LM2	LM3	LM3/ LM2
C. callosus	28	1.89	1.18	0.87	73.73
C. lepidus	22	1.73	1.04	0.70	67.30
C. sorellus	9	1.79	1.09	0.76	69.72
C. tener	32	1.67	1.04	0.70	67.30
A. p. pearsoni	11	2.11	1.14	0.98	85.96
A. p. subsp. n.	2	2.43	1.29	1.08	84.05
A. olrogi	6	2.13	1.18	0.95	80.51
E. sp. A	5	1.69	1.09	0.72	66.06
E. sp. B	2	1.65	1.05	0.73	69.86
G. griseoflavus	7	2.43	1.50	1.15	76.60
G. domorum	6	2.37	1.47	1.05	71.43

Andalgalomys pearsoni dorbignyi, new subspecies

HOLOTYPE: Museum of Southwestern Biology catalog number 55245; adult male; skin and skeleton (plus frozen tissues and cell suspension with NK number 12402); prepared by Joseph A. Cook on October 7, 1984.

TYPE LOCALITY: Bolivia: Department of Santa Cruz; 29.5 km west of Roboré, 475 m (18°19′S, 60°02′W).

DISTRIBUTION: Known only from the type locality.

SPECIMENS: Holotype and AMNH 260762 (adult female with teeth slightly more worn than those of holotype).

DIAGNOSIS: A subspecies of *Andalgalomys pearsoni* distinguished from both *A. pearsoni pearsoni* and *A. olrogi* by larger size, more pronounced anterior zygomatic spines, broader mesopterygoid fossa, and 76 chromosomes.

DESCRIPTION: Any pale reddish brown mouse from southeastern Bolivia that has white spots below its ears, sharply demarked white belly, tail about the same length as head and body, total length (of adults) about 250 mm, hind foot about 26 mm, weight about 45 g, and a diploid number of 76 is probably *Andalgalomys pearsoni dorbignyi.* External, cranial, and dental characters for the genus are outlined above. Characters distinguishing species and subspecies within *Andalgalomys* are in the diagnosis immediately above and the comparisons immediately below. Measurements of the two specimens are listed in table 2.

COMPARISONS: *A. pearsoni dorbignyi* and *A. pearsoni pearsoni* can be distinguished from *A. olrogi* by larger size; broader posterior frontal region; broader rostrum; wider zygomatic plate; relatively smaller bullae; relatively shorter and less hairy tail; shorter and coarser hair; darker pelage, ears, and tail; and more chromosomes (76 in *A. p. dorbignyi,* 78 in *A. p. pearsoni,* and 60 in *A. olrogi*).

HABITAT: Arid, scrubby, low, partly open vegetation.

ASSOCIATED SPECIES: At the same locality or one of two nearby localities, the first Bolivian specimens of two species were captured: a young *Thrichomys apereoides* and three *Ctenomys minutus* (the former reported by name only as *Cercomys cunicularius,* and the latter as *Ctenomys minimus* by Anderson, 1985). Other mammals obtained were *Bolomys lasiurus, Chaetophractus vellerosus,* and *Tolypeutes matacus.* All are listed in the Appendix.

ETYMOLOGY: Because the previously recognized taxa of *Andalgalomys* were named for naturalists who worked in the area, we follow the same tradition and name this new subspecies for Alcide d'Orbigny, the first naturalist to collect in eastern Santa Cruz department (in 1830).

KARYOTYPIC DATA: The karyotype of *A. pearsoni* differs considerably from that reported for *A. olrogi* (Williams and Mares, 1978). Diploid numbers (fig. 5) are 76 in *A. p. dorbignyi* and 78 in *A. p. pearsoni* compared to 60 in *A. olrogi.* Furthermore, in contrast to the all-biarmed karyotype of *A. olrogi, A. p. dorbignyi* and *A. p. pearsoni* have 10

TABLE 2

Measurements (in millimeters) of Species of *Andalgalomys* and Related Genera

(Mean and standard deviation are given for each dimension with the minimum and maximum measurements in parentheses.)

Dim.[a]	*A. p. dorbignyi* holotype MSB 55245	*A. p. dorbignyi* AMNH 260762	*A. p. pearsoni* ($n = 11$)	*A. olrogi* ($n = 6$)	*Graomys domorum* ($n = 11$)	*Graomys griseoflavus* ($n = 12$)	*Calomys callosus* ($n = 7$)	*Eligmodontia typus* ($n = 5$)
HBL	123	126	109.00 ± 9.37 (97–120)	106.50 ± 22.90 (86–136)	136.82 ± 11.40 (120–152)	131.55 ± 14.80 (111–159)	124.00 ± 5.57 (119–130)	89
TAI	136	129	114.30 ± 10.15 (97–129)	127.00 ± 2.16 (125–130)	124.91 ± 23.89 (83–165)	154.73 ± 15.67 (124–175)	96.75 ± 4.86 (94–104)	83
HFL	27	26	23.50 ± 0.81 (22–25)	24.38 ± 0.50 (23.8–24.9)	29.36 ± 1.86 (26–32)	29.00 ± 1.90 (25–31)	21.66 ± 1.15 (21–23)	29
EAR	24	23	19.45 ± 0.81 (18–21)	20.58 ± 0.97 (19.6–20.0)	25.09 ± 1.51 (22–28)	22.50 ± 2.26 (20–26)	19.33 ± 0.58 (19–20)	18
BUL	6.29	5.99	5.42 ± 0.34 (4.70–5.79)	6.32 ± 0.44 (5.74–6.82)	5.73 ± 0.20 (5.33–6.08)	6.22 ± 0.52 (5.41–6.93)	4.11 ± 0.42 (3.72–4.89)	4.10 ± 0.67 (3.33–4.83)
MXL	5.40	5.13	4.78 ± 0.29 (4.41–5.30)	4.74 ± 0.13 (4.60–4.97)	5.11 ± 0.31 (4.69–5.63)	5.04 ± 0.37 (4.82–5.88)	4.53 ± 0.18 (4.31–4.74)	3.94 ± 0.12 (3.78–4.12)
PRL	6.54	5.72	5.40 ± 0.40 (4.65–6.09)	5.36 ± 0.21 (5.15–5.71)	5.50 ± 0.32 (5.07–5.98)	5.65 ± 0.42 (5.11–6.50)	4.62 ± 0.34 (4.17–5.08)	4.40 ± 0.31 (3.97–4.73)
ZAL	8.73	9.28	9.01 ± 0.61 (7.80–9.67)	8.56 ± 0.59 (7.54–9.10)	9.53 ± 0.39 (9.00–10.16)	9.82 ± 0.55 (8.61–10.40)	8.15 ± 0.51 (7.36–8.85)	6.83 ± 0.38 (6.39–7.24)
IFL	6.84	7.89	6.46 ± 0.41 (5.62–7.08)	5.92 ± 0.88 (4.26–6.65)	7.14 ± 0.38 (6.66–7.66)	7.33 ± 0.66 (6.26–8.17)	6.47 ± 0.22 (6.13–6.72)	5.20 ± 0.27 (4.81–5.53)
CIL	29.20	28.40	26.76 ± 1.32 (24.54–28.54)	25.31 ± 1.21 (23.70–27.00)	29.52 ± 1.43 (27.40–31.14)	30.33 ± 2.10 (25.80–33.00)	25.44 ± 1.39 (23.20–27.10)	21.40 ± 1.08 (20.10–22.70)
MSB	1.51	1.55	0.87 ± 0.26 (0.46–1.27)	0.86 ± 0.14 (0.70–1.09)	1.56 ± 0.13 (1.39–1.89)	1.61 ± 0.19 (1.27–1.88)	1.12 ± 0.18 (0.89–1.41)	0.77 ± 0.22 (0.55–1.09)
IDB	2.81	2.70	2.75 ± 0.31 (2.10–3.10)	2.87 ± 0.14 (2.71–3.10)	2.76 ± 0.20 (2.49–3.15)	2.77 ± 0.20 (2.36–3.13)	2.50 ± 0.20 (2.33–2.85)	2.40 ± 0.18 (2.23–2.69)
PDB	4.81	4.48	4.51 ± 0.15 (4.33–4.68)	4.54 ± 0.24 (4.19–4.75)	5.03 ± 0.17 (4.83–5.27)	4.92 ± 0.24 (4.56–5.43)	4.24 ± 0.23 (4.01–4.60)	3.62 ± 0.28 (3.33–4.01)
BRB	5.65	3.79	4.94 ± 0.40 (4.42–5.80)	4.22 ± 0.49 (3.40–4.83)	5.62 ± 0.23 (5.25–6.05)	5.72 ± 0.63 (5.01–7.03)	5.15 ± 0.39 (4.38–5.51)	4.03 ± 0.16 (3.80–4.21)

TABLE 2
Continued

Dim.[a]	*A. p. dorbignyi* holotype MSB 55245	*A. p. dorbignyi* AMNH 260762	*A. p. pearsoni* (n = 11)	*A. olrogi* (n = 6)	*Graomys domorum* (n = 11)	*Graomys griseoflavus* (n = 12)	*Calomys callosus* (n = 7)	*Eligmodontia typus* (n = 5)
PLB	6.37	6.19	6.00 ± 0.37 (5.43–6.64)	6.02 ± 0.34 (5.74–6.63)	6.36 ± 0.24 (6.01–6.77)	6.26 ± 0.54 (4.99–7.00)	5.50 ± 0.32 (4.91–5.85)	4.92 ± 0.35 (4.58–5.40)
POB	9.05	8.93	8.40 ± 0.37 (7.86–9.13)	7.74 ± 1.25 (5.29–8.81)	9.65 ± 0.37 (9.00–10.27)	9.26 ± 0.37 (8.58–9.96)	7.89 ± 0.47 (7.29–8.43)	7.31 ± 0.43 (6.90–7.88)
AZB	13.80	12.30	13.11 ± 0.89 (11.70–14.36)	11.98 ± 0.85 (10.70–13.20)	14.75 ± 0.73 (13.31–15.90)	15.31 ± 0.84 (13.50–16.40)	13.40 ± 0.85 (11.90–14.20)	11.26 ± 0.87 (10.40–12.60)
PZB	15.30	15.10	14.46 ± 0.83 (12.90–15.45)	13.56 ± 0.49 (13.00–14.20)	16.46 ± 0.76 (14.89–17.15)	16.57 ± 0.96 (15.02–17.80)	14.41 ± 0.74 (13.20–15.30)	12.36 ± 0.64 (11.60–13.30)
MTB	1.54	1.53	1.51 ± 0.15 (1.27–1.75)	1.43 ± 0.03 (1.39–1.46)	1.64 ± 0.10 (1.49–1.86)	1.59 ± 0.10 (1.44–1.78)	1.32 ± 0.05 (1.23–1.39)	1.17 ± 0.11 (1.02–1.29)
OIL	4.40	4.08	4.27 ± 0.56 (3.27–5.25)	3.45 ± 0.24 (3.15–3.84)	4.18 ± 0.43 (3.75–5.14)	4.63 ± 0.37 (4.27–5.63)	3.90 ± 0.36 (3.37–4.48)	3.42 ± 0.23 (3.10–3.65)
ONL	32.50	31.70	29.74 ± 1.37 (27.51–31.93)	28.07 ± 1.47 (26.10–29.80)	32.64 ± 1.19 (30.60–34.15)	32.89 ± 1.95 (28.80–35.90)	26.96 ± 1.88 (23.90–28.80)	24.30 ± 0.91 (23.30–25.30)
NLL	12.40	12.70	11.60 ± 0.94 (10.29–13.19)	10.60 ± 0.94 (8.88–11.60)	13.03 ± 0.79 (11.90–14.37)	12.87 ± 1.37 (10.00–14.80)	10.44 ± 1.11 (8.32–11.60)	9.07 ± 0.20 (8.78–9.32)
ROL	9.88	10.60	9.46 ± 0.52 (8.62–10.16)	8.93 ± 0.70 (7.77–9.77)	10.44 ± 0.57 (9.70–11.33)	10.56 ± 1.10 (8.67–11.90)	8.44 ± 0.59 (7.52–9.15)	7.76 ± 0.20 (7.50–8.05)
IOB	5.30	4.43	4.68 ± 0.39 (3.97–5.30)	4.46 ± 0.15 (4.27–4.70)	5.44 ± 0.15 (5.07–5.56)	5.33 ± 0.39 (4.41–5.79)	4.06 ± 0.22 (3.76–4.34)	3.85 ± 0.13 (3.67–4.01)
BCB	13.60	12.00	12.56 ± 0.44 (12.10–13.35)	12.58 ± 0.20 (12.30–12.80)	14.10 ± 0.49 (13.09–14.74)	13.53 ± 0.55 (12.00–14.20)	11.36 ± 0.51 (10.70–12.10)	11.42 ± 0.52 (10.60–11.80)
IED	2.72	2.82	2.74 ± 0.34 (2.21–3.43)	2.30 ± 0.29 (1.78–2.62)	2.80 ± 0.31 (2.42–3.36)	2.91 ± 0.53 (2.02–3.74)	2.72 ± 0.37 (2.07–3.34)	2.22 ± 0.16 (2.02–2.41)
BUD	4.42	3.60	4.32 ± 0.24 (3.97–4.59)	4.72 ± 0.39 (4.16–5.31)	4.11 ± 0.25 (3.75–4.52)	4.30 ± 0.51 (3.13–4.95)	2.73 ± 0.32 (2.27–3.22)	3.46 ± 0.62 (2.90–4.14)
SKD	12.30	10.10	10.95 ± 0.48 (10.35–11.73)	11.12 ± 0.31 (10.80–11.70)	12.25 ± 0.31 (11.80–12.77)	12.23 ± 0.60 (11.10–13.30)	9.90 ± 0.90 (8.19–10.90)	9.50 ± 0.47 (8.93–10.10)
ZPW	3.36	2.22	2.89 ± 0.26 (2.41–3.20)	2.51 ± 0.21 (2.31–2.76)	3.39 ± 0.28 (2.90–3.69)	3.38 ± 0.35 (2.95–4.02)	2.85 ± 0.32 (2.29–3.31)	2.66 ± 0.25 (2.39–3.00)

TABLE 2
Continued

Dim.[a]	A. p. dorbignyi holotype MSB 55245	A. p. dorbignyi AMNH 260762	A. p. pearsoni ($n = 11$)	A. olrogi ($n = 6$)	Graomys domorum ($n = 11$)	Graomys griseoflavus ($n = 12$)	Calomys callosus ($n = 7$)	Eligmodontia typus ($n = 5$)
LM1	2.57	2.29	2.11 ± 0.05 (2.07–2.17)	2.13 ± 0.06 (2.00–2.23)	2.39 ± 0.11 (2.27–2.62)	2.45 ± 0.14 (2.21–2.72)	1.91 ± 0.05 (1.81–1.97)	1.69 ± 0.11 (1.53–1.77)
LM2	1.27	1.30	1.14 ± 0.08 (1.05–1.23)	1.18 ± 0.06 (1.11–1.26)	1.50 ± 0.08 (1.35–1.61)	1.46 ± 0.10 (1.27–1.62)	1.21 ± 0.03 (0.85–0.93)	1.09 ± 0.06 (1.04–1.16)
LM3	1.12	1.04	0.98 ± 0.06 (0.92–1.06)	0.95 ± 0.10 (0.82–1.09)	1.11 ± 0.09 (0.97–1.27)	1.15 ± 0.08 (1.04–1.30)	0.89 ± 0.03 (0.85–0.93)	0.72 ± 0.03 (0.69–0.76)

[a] Dimension measured. Abbreviations are spelled out in the Methods section.

and 12 pairs of uniarmed and 28 and 27 pairs of biarmed chromosomes, respectively. The sex chromosomes in *A. pearsoni* are both acrocentric rather than biarmed as in *A. olrogi.* The X in the former is the largest element in the karyotype and the Y is a medium-size acrocentric.

The diploid numbers observed in *A. pearsoni* (both subspecies) are the highest reported for any phyllotine rodent. Pearson and Patton (1976) hypothesized that a basic trend in chromosomal evolution among these rodents has been a decrease in diploid number through Robertsonian fusion. If this is correct, *A. pearsoni* may possess close to the primitive condition for the phyllotines and the hypothetical primitive diploid number would be about 78. The totally uniarmed autosomal complement proposed by these authors, however, is not consistent with the large number of biarmed chromosomal pairs (fig. 5) found in *A. pearsoni.* The karyotypes of *A. pearsoni* may contain a number of heterochromatic arms although this cannot be determined without banding analysis. Changes within chromosomes, as well as changes in number of chromosomes, must also have occurred if the *A. olrogi* karyotype was derived from the condition found in *A. pearsoni.* In diploid number, *Andalgalomys* is closer to the 70 found in *Neotomys ebriosus* and *Phyllotis osilae* and the 64 as in *Calomys sorellus* (as suggested by Williams and Mares, 1978, than to any species of *Graomys, Eligmodontia,* or other *Calomys* studied by them).

Numerical Analyses: We selected two multivariate analyses, principal components and canonical variates: the first was used to explore the general pattern of variation and to see whether groupings appeared in the data when our concept of taxonomy was not specified, and the second analysis was used to observe the clustering of individuals within and between our specified groups. The latter relates to the recognizability of the genus *Andalgalomys* and its affinities with the three other genera represented. There are other analyses that would express the phenetic affinities more completely or quantitatively. We calculated Mahalanobis distances and decided that these data did not alter our tentative conclusions about relationships and did not warrant inclusion.

We performed principal components analysis with the PRINCOMP procedure of SAS

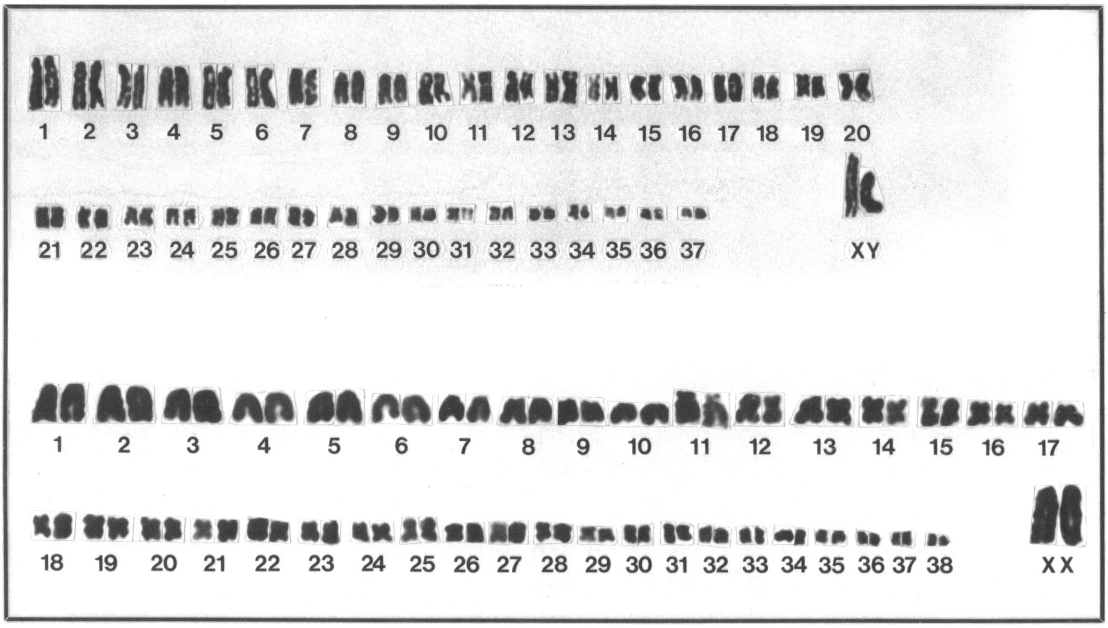

Fig. 5. Karyotypes of *A. pearsoni dorbignyi,* AMNH 260762 (above) and *A. pearsoni pearsoni,* UMMZ 134386 (below).

(SAS Institute Inc., 1982) using the correlation matrix on specimens of *Andalgalomys olrogi* ($n = 6$) and *A. pearsoni dorbignyi* ($n = 2$), *A. p. pearsoni* ($n = 11$), and on the following species: *Calomys callosus* ($n = 7$), *Eligmodontia* sp. A ($n = 9$), *E.* sp. B ($n = 2$), *Graomys domorum* ($n = 11$), and *G. griseoflavus* ($n = 12$). Initially, we used 28 cranial and dental variables. After examination of coefficients of variation from an analysis of sample means, we excluded the most variable, thereby reducing the number of variables to 21 (see table 3). Table 3 gives the eigenvectors for each variable on the first three principal components.

The first principal component is related to size (fig. 6) in that the larger species, *Graomys domorum* (M) and *G. griseoflavus* (G), are at the right; the medium-size species of *Andalgalomys* (D, O, P) are in the center; and the small species, *Calomys callosus* (C) and both species of *Eligmodontia* (E), are at the left. The overlapping of *G. domorum* and *G. griseoflavus* suggests their overall cranial similarity. *Andalgalomys olrogi* is well separated (by the second principal component) from *A. p. pearsoni* and *A. p. dorbignyi.* The two specimens of *A. p. dorbignyi* bridge the scatters of *A. p. pearsoni* and *G. griseoflavus.* These two specimens are different in age, sex, and

TABLE 3

Eigenvectors for the First Three Principal Components

(The cumulative percentage of variance explained by each component is given at the bottom of the table.)

Dim.[a]	PC1	PC2	PC3
BUL	0.21	0.32	−0.16
MXL	0.22	0.03	−0.02
PRL	0.21	0.23	−0.08
ZAL	0.24	0.01	0.12
IFL	0.22	−0.23	0.15
CIL	0.24	−0.11	0.06
IDB	0.16	0.37	0.68
PDB	0.22	0.08	0.07
PLB	0.22	0.18	0.32
POB	0.21	−0.17	−0.01
AZB	0.22	−0.29	0.10
PZB	0.23	−0.21	0.05
MTB	0.22	0.07	−0.05
ONL	0.24	−0.06	0.02
NLL	0.24	−0.11	0.03
ROL	0.23	−0.10	−0.00
IOB	0.23	−0.06	−0.22
BCB	0.21	0.07	−0.23
BUD	0.15	0.55	−0.39
SKD	0.24	0.04	−0.22
ZPW	0.19	−0.31	−0.20
Cum. %	77.2	84.0	86.8

[a] Dimension measured. Abbreviations are spelled out in the Methods section.

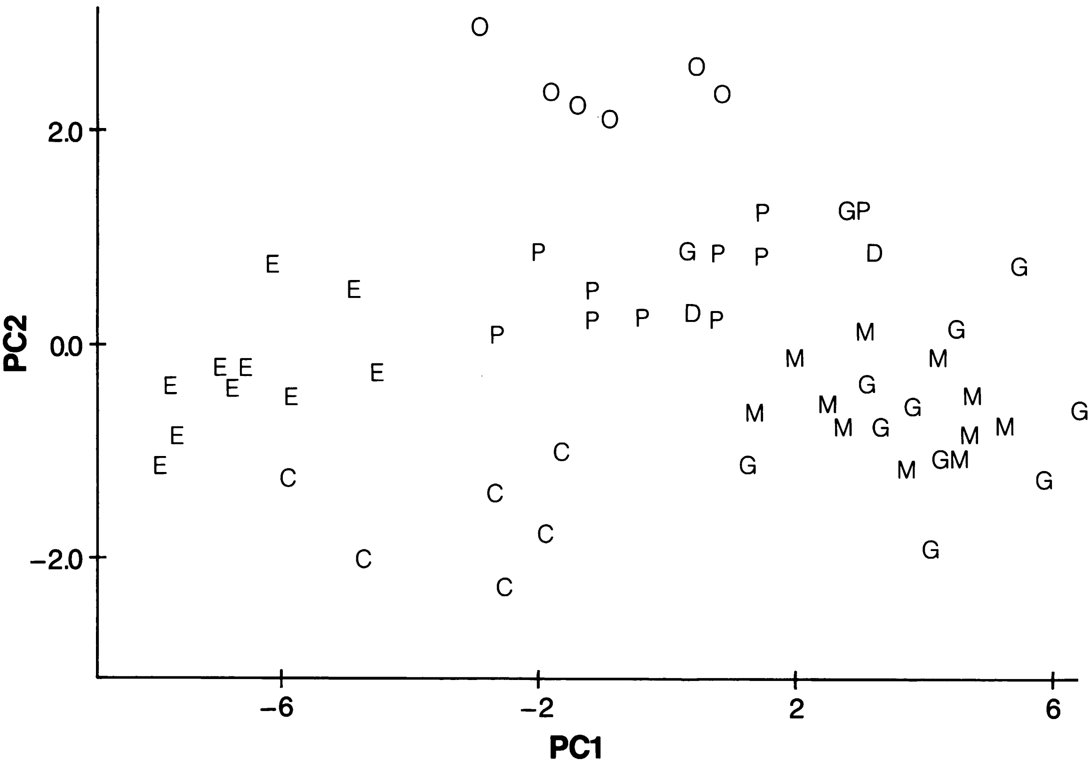

Fig. 6. Graph of the results of a principal components analysis; Principal Component 1 (PC1) versus Principal Component 2 (PC2). C = *Calomys callosus*, D = *Andalgalomys pearsoni dorbignyi*, E = *Eligmodontia typus*, G = *Graomys griseoflavus*, M = *G. domorum*, O = *A. olrogi*, and P = *A. p. pearsoni*.

size; the older (based on tooth wear) specimen (AMNH 260762) is slightly smaller than the younger one (MSB 55245).

We did a canonical variates analysis (CANDISC procedure of SAS) using the same samples as above (except omitting two specimens of *Eligmodontia* referred to *E.* sp. B), and using the reduced number of variables (21). This analysis uses specified groups (the species above). In a plot of Canonical Variate 1 versus Canonical Variate 2 (fig. 7), the two species of *Graomys* lie close together; *A. p. dorbignyi* is between them and *A. p. pearsoni* while *A. olrogi* is further away. *Eligmodontia* and *C. callosus* are well removed from the other clusters at the bottom of the graph. In the graph of Canonical Variate 1 versus Canonical Variate 3 (fig. 7), there is more separation of the species of *Graomys*; *A. p. pearsoni* lies between *Eligmodontia* and *A. p. dorbignyi*, and *A. p. dorbignyi* lies near *C. callosus*. *A. olrogi* and *Eligmodontia* overlap.

DISCUSSION: Data presented show (1) that the two Bolivian phyllotine specimens (on the basis of which a new subspecies is here named) are morphologically (phenetically) different from other phyllotines, (2) that they are nearer to the two previously recognized taxa of *Andalgalomys* than to any other phyllotine, and (3) that, within *Andalgalomys*, they are nearer to *A. pearsoni* than to *A. olrogi*. It is possible to interpret some of the diagnostic characters of *Andalgalomys* as synapomorphies and thus develop a cladistic hypothesis of monophyly. Within the genus it is more difficult to interpret any shared characters of *A. pearsoni* and the new taxon as synapomorphies rather than as primitive plesiomorphies. The distinctive characters of *A. olrogi* may be interpreted as derived from those of *A. pearsoni*. Within the known range of *A. p. pearsoni* in Paraguay, no geographic cline in size is noticeable in the limited number of specimens available.

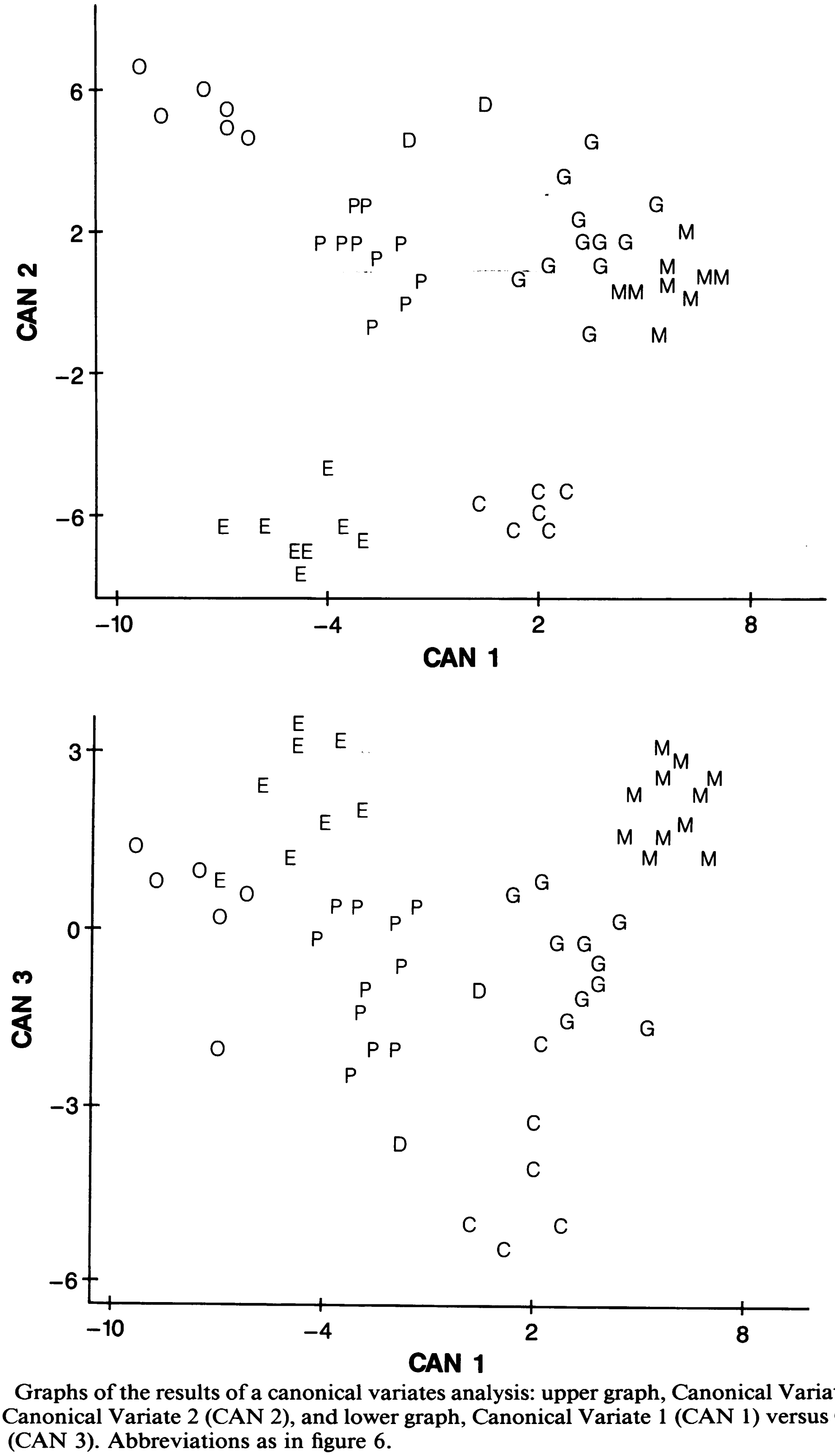

Fig. 7. Graphs of the results of a canonical variates analysis: upper graph, Canonical Variate 1 (CAN 1) versus Canonical Variate 2 (CAN 2), and lower graph, Canonical Variate 1 (CAN 1) versus Canonical Variate 3 (CAN 3). Abbreviations as in figure 6.

Generally, the concept of subspecies is used for well-marked populations with contiguous geographic ranges that are hypothesized to interbreed with one or more other subspecies of the species. This assumes the "biological species concept." There is no consensus on how "well marked" the population must be or how narrow or sharp the zone of intergradation between subspecies must be.

Recognition of a new subspecies, *Andalgalomys pearsoni dorbignyi,* for the two Bolivian specimens is based on the highly probable distinctness of the population they represent and the hypothesis that *A. p. dorbignyi* and *A. p. pearsoni* will be found to intergrade somewhere in the area between the presently known geographic localities of these subspecies. An alternative hypothesis is that these two taxa will be found sympatrically in this area and maintain their morphological distinctness. These alternative hypotheses can be tested by further collecting in the intervening area.

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APPENDIX. SPECIMENS EXAMINED OR REPORTED

A. olrogi (6): Argentina: Catamarca; 15 km S of Highway 62 on Río Amanao and W of Andalgala, CM 44020. Argentina: Catamarca; "Km marker 10" on Highway 62, 10 km W of Andalgala, CM 44021. Argentina: Catamarca; 15 km W (on Route 62) of Andalgala on W bank Río Amanao, CM 44022–44024 (44024 = holotype). Argentina: Catamarca; 8 km W of Andalgala on Highway 62, CM 86451. (Andalgala = 1060 m; 27°36′S, 66°19′W; Amanao = 27°33′S, 66°31′W.)

A. pearsoni pearsoni (24): Paraguay: Boqueron; 410 km by road NW of Villa Hayes, MVZ 145276 (holotype) (Villa Hayes = 25°06′S, 57°34′W). Paraguay: Boqueron; 15.6 km by road N of Filadelphia, UMMZ 134386. Paraguay: Nueva Asunción; 0.5 km S of Teniente Enciso, UCONN 17579, 17580, Teniente Enciso (cited as 2.5 km S by Myers, 1977), UCONN 17562, 17563, 17566, 17568, 17575. Paraguay: Nueva Asunción; 1 km SW km 620 on the Trans-Chaco Road, AMNH 262344–262347, UMMZ 158621, 130037, and the following uncataloged specimens at UMMZ, collected by T. W. Nelson: TWN 183, 184, 193, 195, 201, 202, 218, 229, 233.

A. pearsoni dorbignyi (2): Bolivia: Santa Cruz; 29.5 km W of Roboré, 475 m (18°19'S, 60°02'W), AMNH 260762, MSB 55245.

Calomys callosus (35): Bolivia: Tarija; 8 km S and 10 km E Villa Montes, 467 m (21°19'S, 63°25'W), AMNH 246740, 246760. Bolivia: Tarija; 2 km S and 10 km E Tiquipa, Laguna Palmar, 555 m (20°56'S, 63°21'W), AMNH 246745, 246834, 246857, 246860, 246862. Paraguay: Chaco; 50 km WSW Fortín Madrejon, AMNH 248449–248452, 248455–248459; UMMZ 124232, 124233, 124237–124250, 125460–125462.

Calomys lepidus (22): Bolivia: Oruro; 3.5 km E Huancaroma, 3720 m (17°40'S, 67°27'W), AMNH 260607–260614, 260616, 260619–260624. Bolivia: Oruro; 2.5 km NE Huancaroma, 3720 m (17°40'S, 67°28'W), MSB 55264, 55266–55271.

Calomys sorellus (9): Peru: Huancavelica; Lircay, 3278 m, FMNH 95396–95399, 95415–95417, 95548, 95549.

Calomys tener (32): Brasil: São Paulo; Itapetininga, USNM 460552–460554, 462124–462126, 484409, 484411–484415, 484417–484419, 484430, 484432, 484434, 484436–484439, 484443–484445, 484450–484452, 484470–484472, 543055.

Eligmodontia sp. A (9): Argentina: Patagonia; Arroyo Aike, AMNH 25702, 25703. Argentina: Mendoza; 312 km (by El Manzano Rd) of Tunuyán, CM 43657, 43671, 43673, 43675, 43681, 43682. Bolivia: Oruro; 12 km S and 1.5 km E Eucaliptus, Lecheria, 3359 m (17°42'S, 67°30'W), AMNH 246776.

Eligmodontia sp. B (2): Argentina: Mendoza; La Paz, MCZ 41079, 41100. All *Eligmodontia* have been referred to *E. typus* (Hershkovitz, 1962); however, our sample includes two species. We are not certain of their correct names.

Graomys domorum (11): Bolivia: Santa Cruz; 5 km by road SE of Comarapa, 1695 m (17°58'S, 64°29'W), AMNH 260748, 260751–260754. Bolivia: Cochabamba; Cochabamba, 2600 m (17°24'S, 66°09'W), FMNH 50961–50963, 50967–50969.

G. griseoflavus (12): Bolivia: Tarija; 8 km S and 10 km E Villa Montes, 467 m (21°19'S, 63°25'W), AMNH 246761, 246770, 246771, 246773, 248438. Bolivia: Santa Cruz; Tita, 300 m (18°25'S, 62°10'W), AMNH 260757. Argentina: Jujuy; Santa Barbara, AMNH 185222. Paraguay: Chaco; Guachalla, FMNH 54359–54361, 54363, 54364.

Bolomys lasiurus (9): Bolivia: Santa Cruz; 7 km N and 38 km W of Roboré, 550 m (18°16'S, 60°07'W), AMNH 260552, 260553, 260509–260513, MSB 55250. Bolivia: Santa Cruz; 29.5 km W of Roboré, 475 m (18°19'S, 60°02'W); AMNH 260507.

Thrichomys apereoides (1): Bolivia: Santa Cruz; 7 km N and 38 km W of Roboré, 550 m (18°16'S, 60°07'W), AMNH 260860.

Ctenomys minutus (3): Bolivia: Santa Cruz; 41 km by road W of Roboré, 550 m (18°18'S, 60°02'W), AMNH 260835, 260836, MSB 55367.

Chaetophractus vellerosus (1): Bolivia: Santa Cruz; 41 km by road NW of Roboré, 500 m (18°18'S, 60°02'W), AMNH 260318.

Tolypeutes matacus (1): Bolivia: Santa Cruz; 29.5 km W of Roboré, 475 m (18°19'S, 60°02'W), AMNH 260320.