

Phyllotis xanthopygus.

By Kristin M. Kramer, J. Adrian Monjeau, Elmer C. Birney,
and Robert S. Sikes

Published 5 May 1999 by the American Society of Mammalogists

Phyllotis Waterhouse, 1837

Phyllotis Waterhouse, 1837:28 (originally a subgenus of *Mus*; as a genus by Thomas, 1896). Type species *Hesperomys (Phyllotis) darwini* (Waterhouse, 1837:28), designated by Thomas, 1884:449.

CONTEXT AND CONTENT. Order Rodentia, Suborder Sciurognathi, Family Muridae, Subfamily Sigmodontinae, Tribe Phyllotini, Genus *Phyllotis*. Steppan (1995) considered nine species to form a monophyletic group—*caprinus*, *chilensis*, *darwini*, *definitus*, *haggardi*, *magister*, *osgoodi*, *osilae*, and *xanthopygus*. He also retained in the genus *andium*, *bonariensis*, and *wolffsohni*, as well as *amicus* and *gerbillus*. However, Braun (1993) previously had reassigned the latter two to *Paralomys*. Musser and Carleton (1993) considered *Paralomys* as a synonym of *Phyllotis*. Their classification subsequently was supported by Steppan (1995, 1998), who found no support for the hypothesis that *amicus* and *gerbillus* form a monophyletic group; instead, he determined that *amicus* was related most closely to *andium*. Steppan (1998) reclassified *P. chilensis* as *P. xanthopygus chilensis* and assigned populations of *P. xanthopygus rupestris* along the Pacific coast to *P. limatus*. Thus, *Phyllotis* should include *amicus*, *andium*, *bonariensis*, *caprinus*, *darwini*, *definitus*, *haggardi*, *gerbillus*, *limatus*, *magister*, *osgoodi*, *osilae*, *wolffsohni*, and *xanthopygus*.

Phyllotis xanthopygus (Waterhouse, 1837)

Patagonian Leaf-eared Mouse

Mus (Phyllotis) xanthopygus Waterhouse, 1837:28. Type locality “Santa Cruz.” Restricted to Santa Cruz, Santa Cruz Province, Argentina, by Pearson (1958:420) and Hershkovitz (1962:327).

Mus rupestris Gervais, 1841:51. Type locality originally given as “un trou de rocher des hautes montagnes de Cobija.” Osgood (1943:207) stated that “Cobija (formerly included in Bolivia) is on the arid coast of Chile between . . . Antofagasta and Tocopilla.”

Mus capito Philippi, 1860:159. Type locality “Hueso parado,” Chile, in the present range of *P. x. rupestris*. Name preoccupied by *Mus capito* Olfers, 1818, an *Oryzomys* according to Hershkovitz (1962:303).

Hesperomys glirinus Philippi, 1896:19. Type locality “Atacama,” Chile. Synonym of *P. x. rupestris* (Osgood, 1943:208).

Hesperomys lanatus Philippi, 1896:19. Type locality “Atacama,” Chile. Synonym of *P. x. rupestris* (Osgood, 1943:208).

Phyllotis xanthopygus Trouessart, 1898:535. First use of current name combination.

Phyllotis arenarius Thomas, 1902:224. Type locality “Sandy plateau of Bolivia. Type from Uyuni. Alt. 3,670 m.” Synonym of *P. x. rupestris* (Pearson, 1958:417).

Phyllotis darwini posticalis Thomas, 1912:406. Type locality “Galera, W. of Oroya, Department of Junín, Perú. Alt. 4,800 m.”

Phyllotis darwini vaccarum Thomas, 1912:408. Type locality “Las Vacas, Argentine slope of Cordillera opposite Mendoza. Alt. 2,500 m,” Mendoza Province, Argentina.

Phyllotis ricardulus Thomas, 1919:493. Type locality “Otro Cerro,” North-eastern Rioja, 45 km W Chumbicha, “Rioja” (= Catamarca), 3,000 m, Argentina. Although Hershkovitz (1962:304) listed *ricardulus* as a subspecies of *P. darwini*, he stated (p. 311) that “Clearly, *ricardulus* is nothing more than part of the cline leading from smaller *rupestris* to larger *vaccarum*.”

Phyllotis oreigenus Cabrera, 1926:319. Type locality “Laguna

Blanca, Catamarca (3,100 m. de altura),” Argentina. Synonym of *P. x. vaccarum* (Pearson, 1958:419).

Phyllotis wolffhuegeli Mann, 1944:108. Type locality “Bocatomá, Lo Valdés, Cajón del Río Volcán, a 1,800 m. de altura,” Chile. Synonym of *P. x. vaccarum* (Pearson, 1958:419).

Phyllotis arenarius chilensis Mann, 1945:84. Type locality “Parinacota,” Chile. Renamed as *P. darwini chilensis* by Pearson (1958:415), subsumed into *P. d. rupestris* by Hershkovitz (1962:304), recognized as *P. chilensis* by Steppan (1995:82), and returned to subspecific status as *P. x. chilensis* by Steppan (1998).

CONTEXT AND CONTENT. Context same as for genus. The taxonomic history of *P. xanthopygus* has been intertwined with that of *P. darwini*. For example, populations of *xanthopygus* were assigned to *darwini* at the species level as recently as 1992 (Redford and Eisenberg, 1992). Recent work on South American mammals (Anderson, 1997; Monjeau et al., 1994; Steppan, 1995) generally follows Spotorno and Walker (1983) and Walker et al. (1984), who presented substantial chromosomal evidence supporting recognition of the two as distinct species. Following Steppan (1998), we consider *Phyllotis xanthopygus* to be comprised of six subspecies:

P. x. chilensis Mann, 1945:84. See above.

P. x. posticalis Thomas, 1912:406. See above. Listed as a synonym of *P. darwini* by Musser and Carleton (1993), but as a subspecies of *P. xanthopygus* by Steppan (1997, 1998). Includes *abrocodon* as a synonym.

P. x. ricardulus Thomas, 1919:493. See above.

P. x. rupestris (Gervais, 1841:51). See above. Includes *arenarius*, *capito*, *glirinus*, and *lanatus* as synonyms.

P. x. vaccarum Thomas, 1912:408. See above. Includes *oreigenus* and *wolffhuegeli* as synonyms.

P. x. xanthopygus (Waterhouse, 1837:28). See above.

DIAGNOSIS. The sympatric genera we consider most likely to be confused with *Phyllotis xanthopygus* (Fig. 1) are *Auliscomys*, *Graomys*, and *Loxodontomys*. We follow Steppan (1995) in returning *Maresomys boliviensis* (Braun, 1993) to the genus *Auliscomys*. Relative to *Auliscomys* and *Loxodontomys*, *Phyllotis* has a distinctly penicillate tip on the tail that is lacking in the other two genera. When viewed from above, the outer margins of the zygomatic arches are convex in *Auliscomys pictus*, whereas they are



FIG. 1. Adult *Phyllotis xanthopygus* from Arroyo La Fragua, Río Negro Province, Argentina. Photograph by Jan Decher.

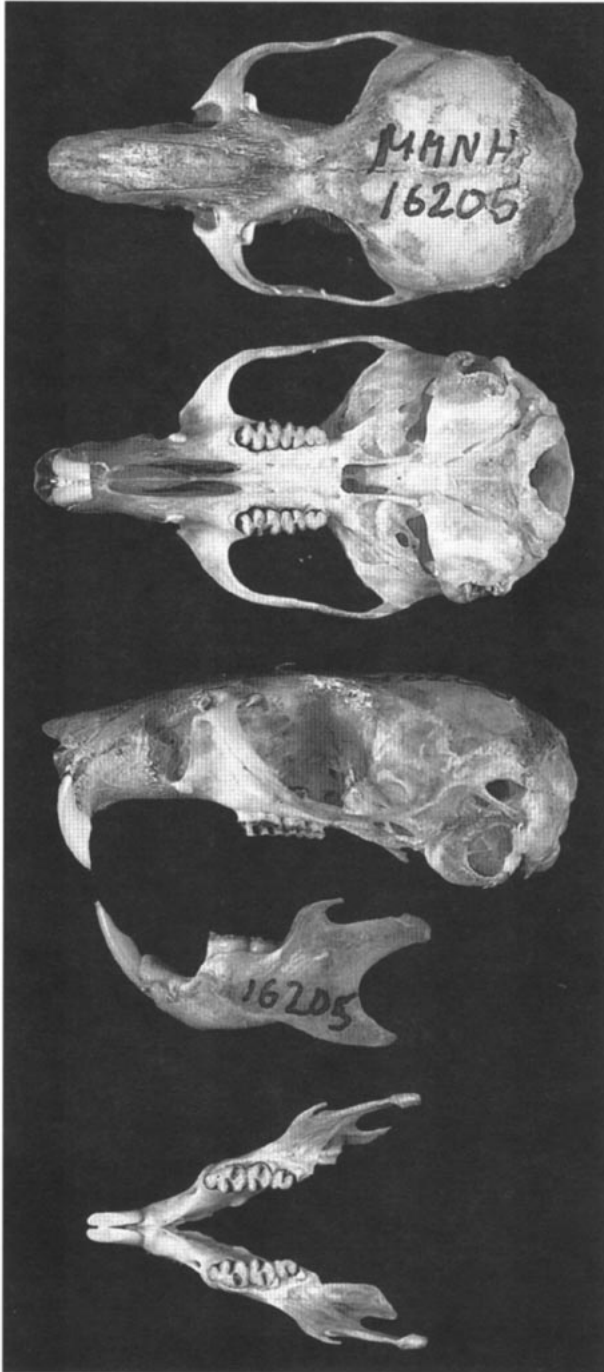


FIG. 2. Dorsal, ventral, and lateral views of the skull and dorsal and lateral views of the mandible of *Phyllotis xanthopygus* from Chubut Province, Argentina (female, Bell Museum of Natural History, MMNH 16205). Greatest length of skull is 31.16 mm. Photographs by Jan Decher.

linear to slightly concave in *Phyllotis*. Compared with *Loxodontomys*, the dorsal pelage of *Phyllotis* is lighter in color and the tail is more heavily furred and more sharply bicolored. The ventral pelage of both taxa is dark gray at the base but the distal half of the hairs are lighter and more buffy in *P. xanthopygus*, whereas only the very tips of the ventral hairs of *Loxodontomys* are light. *Phyllotis* has larger ears (>23 mm) and the mandibular condyloid process is not bent inward as in *Loxodontomys* (Fig. 2).

Graomys is perhaps the genus most similar to *Phyllotis* in size and external appearance. The ventral fur of *Phyllotis* is yellow to buff with a gray base, whereas it appears more nearly white in

Graomys. *Graomys* has a tail as long or longer than combined head and body length, whereas the tail of *Phyllotis* usually is less than the combined length of head and body (Hershkovitz, 1962). The orbital margin of the frontal bone forms a sharp edge in *Graomys* and is posteriorly divergent, whereas this margin is rounded and not markedly divergent in *Phyllotis*.

The eastern edge of the range of *Phyllotis darwini* meets the western edge of the range of *Phyllotis xanthopygus* in Chile. Although the two are quite similar in external appearance and their taxonomic histories are convoluted, karyotypic data as well as morphometric differences support specific recognition for each (Spotorno and Walker, 1983; Steppan, 1995). Identification of specimens based only on morphological characters remains troublesome, and we know of no single diagnostic morphological character for distinguishing the two species. Nevertheless, Spotorno and Walker (1983) separated specimens of *P. xanthopygus vaccarum* and *P. darwini* using discriminant function analysis of a suite of 18 body and cranial characters.

Based on molecular and morphological data, Pacific populations of *P. xanthopygus rupestris* were reassigned to *P. limatus* by Steppan (1998). *P. xanthopygus rupestris* reportedly has deep, narrow incisors, whereas *P. limatus* has wide, shallow incisors. Additionally, individuals of *P. limatus* tend to have relatively longer tails (115% of body length versus $\leq 105\%$ for *P. x. rupestris*) that often are white-tipped (Steppan, 1998). A key to species occurring in Bolivia was provided by Anderson (1997).

GENERAL CHARACTERS. Specimens from Río Negro, Chubut, and Santa Cruz provinces, Argentina, trapped in March and April were examined to provide the following description. *Phyllotis xanthopygus* is a mouse of large size (body mass of adults ca. 55 g) with large ears (length ca. 27 mm) and a tail close to the length of the head and body. The overall color is grayish brown with a faint buff or pale fulvous wash that is most prominent on the rump near the base of the tail in adults. The pelage is long and soft with gray bases and yellow to brown guard hairs that sometimes are black-tipped, especially along the dorsum. The chin, throat, and venter typically are light tan to pale buff with plumbeous underfur. The ears are lightly pigmented and sparsely furred in living individuals, but appear similar in color to the dorsum in museum specimens. Skin pigmentation and hair coloration on the tail are dark above and nearly white below, giving the tail a sharply bicolored appearance. The feet are covered by short, nearly white hairs and the soles are mostly naked with short, light-colored fur on the heel.

Seasonal variation in pelage characteristics of animals obtained in Santa Cruz, Argentina, was described by Allen (1905). He observed that adults trapped from February to April had thinner and darker pelage than those trapped in November. Young adults trapped in March and April had dark gray fur along the back changing to a more fulvous color on the lower sides (sometimes forming a distinct lateral band) and a still lighter-colored venter. Ventral color varied from faint buffy to strong buffy in the pectoral region during the same time period. Thomas (1884) reported two pairs each of pectoral and inguinal mammae.

The following list of cranial characteristics was taken from descriptions of subspecies (Hershkovitz, 1962) now recognized as *Phyllotis xanthopygus*: moderately inflated auditory bullae; length of the auditory bullae minus tubes is usually less than alveolar length of molar row; bullar tubes usually short; mesopterygoid fossa measured at base of hamular processes usually less than the width of, but sometimes as wide as, parapterygoid fossa measured on the same plane; proximal ends of nasals pointed to truncate; and alveolar length of molar tooththrow 15–20% of greatest length of skull. Kelt (1994) provided comments on additional cranial characters of *P. xanthopygus* as follows: M2 larger than M3; terminal end of palate lies posterior to anterior end of tooththrow; and posterior margins of incisive foramina are posterior to the anterior edge of the tooththrow. Thomas (1884) noted five interdental ridges on the soft palate.

Means (\pm SD) for skull characters (in mm; $n = 20$) of *P. xanthopygus* from the Aisén region, Chile, (Kelt, 1994) are as follows: total length, 241.6 (15.0); tail length, 120.4 (7.7); hind foot length, 29.2 (1.0); ear length, 25.4 (1.1); greatest length of skull, 31.4 (1.0); length of nasal bone, 13.2 (0.8); length of maxillary diastema, 7.8 (0.5); length of maxillary tooththrow, 5.5 (0.1); length of palate, 13.8 (0.6); breadth across rostrum, 4.3 (0.2); breadth

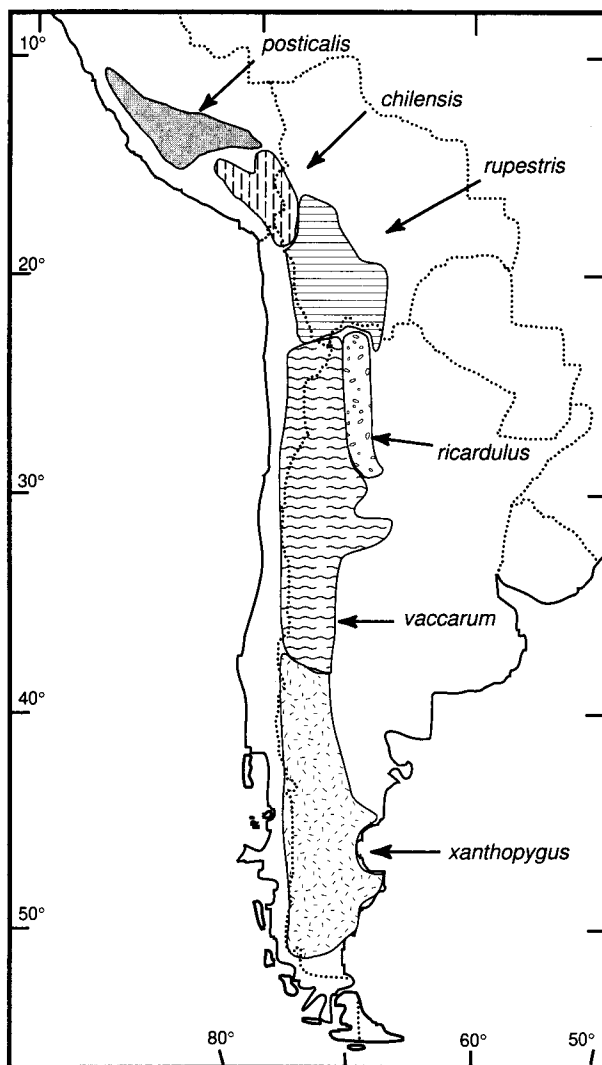


FIG. 3. Distribution of *Phyllotis xanthopygus*. Distributions of the six currently recognized subspecies, *P. x. chilensis*, *P. x. posticalis*, *P. x. ricardulus*, *P. x. rupestris*, *P. x. vaccarum*, and *P. x. xanthopygus*, are indicated. Map provided by Scott Stepan.

across braincase, 13.8 (0.3); breadth across zygomatic arches, 16.0 (0.6); width of incisors, 2.8 (0.2); length of mandibular diastema, 3.4 (0.3); length of mandibular toothrow, 5.7 (0.2); greatest length of mandible, 16.8 (0.7); mandibular depth, 5.5 (0.3); and length of coronoid process, 1.3 (0.1). Mean body mass was 57.6 (10.9) g. Detailed descriptions of all six subspecies (considered at the time to be subspecies of *P. darwini*) are provided by Pearson (1958).

DISTRIBUTION. *Phyllotis xanthopygus* occurs in and along the Andes from southern Peru into Patagonia from ca. 15°S to 51°S (Fig. 3). Habitats include grasslands and desert regions at altitudes ranging from sea level to 5,600 m. De Fonollat et al. (1989) and Halloy (1991) recorded *P. x. rupestris* at 5,570 m on the border between Chile and Argentina (24°S, 68°W) where steam vents and warm vapor from volcanic activity warmed the immediate vicinity (Halloy, 1991).

Phyllotis xanthopygus shares localities of sympatry with seven of its congeners and its range borders that of two additional congeners. In the northwestern part of its range, in Peru, *P. xanthopygus* is sympatric with *P. andium* and *P. amicus* (Stepan, 1998). Farther south, *P. xanthopygus* shares the western portion of its range in northernmost Chile and into Peru with *P. magister* (Stepan, 1998). Sympatry with *P. osgoodi* is known for a small area in northernmost Chile (Pearson, 1958; Stepan, 1998). The eastern portion of its range is shared as follows: with *P. osilae* in

Argentina, Bolivia, and Peru; with *P. wolffsohni* in Bolivia; and with *P. caprinus* in Argentina and Bolivia (Stepan, 1998). Western portions of the range of *P. xanthopygus* border that of *P. darwini* in Chile from ca. 30–35°S and that of *P. limatus* in western Peru (Stepan, 1998).

In the southern and western portions of the species distribution, *P. x. chilensis* intergrades with *P. x. rupestris*. The two subspecies likely intergrade along the Bolivian plateau as well (Pearson, 1958). Pearson (1958) reported an extensive contact zone between these two subspecies in the Peruvian departments of Arequipa, Moquegua, and Tacna. In the western part of the distribution, *P. x. vaccarum* intergrades with *P. x. xanthopygus* to the south and with *P. x. rupestris* to the north and northeast (Pearson, 1958). In central Chile, *P. darwini* occurs at the coast and in the central valley with *P. xanthopygus vaccarum* occupying mountain tops at altitudes >2,000 m (Spotorno and Walker, 1983).

FOSSIL RECORD. Fossils of *Bensonmys* from the late Hemphillian White Cone fauna of Arizona, dated 6–8 × 10⁶ years ago (Baskin, 1978), appear to be the oldest known representatives of the subfamily Sigmodontinae. The earliest South American records of Sigmodontinae are from the Montehermosan Land Mammal Age (mid to upper Pliocene, 4 × 10⁶ years ago—Reig, 1978). Members of the tribe Phyllotini (*Auliscomys*, *Reithrodon*, and *Graomys*) were already present in southern Argentina during the lower and upper Pliocene (Mares, 1985). Because *Graomys*, a possible offshoot of *Phyllotis*, was present in the Monte-Patagonian-Chacoan area during the late Pliocene, it is likely that *Phyllotis* occupied the rocky fringes of the deserts during this period (Mares, 1985). Specimens of the genus *Phyllotis* have been found in Bolivia in the basins of Tarija, Concepción (= Uriondo), and Poceya and were dated at 0.7–0.97 × 10⁶ years ago and 0.2–0.25 × 10⁶ years ago by different methods (Hoffstetter, 1986; Pardiñas and Galliari, 1998). Fossils of the genus also have been found in Argentina in Bajo San Jose and Bahía Blanca (Buenos Aires Province) in Ensenadean beds from the middle to lower Pleistocene, and in Camet (Mar del Plata, Buenos Aires Province—Pardiñas and Deschamps, 1996). Fossils of *Phyllotis* dated at 20,000–16,000 B.C. (Lujanian/Holocene) are abundant in the Ayacucho area (Pikimachay Cave) in the central Andes of Peru (Hoffstetter, 1986), and fossils from the Lujanian Age, tentatively identified as *Phyllotis*, have been found in Talera (Piura, Peru—Lemon and Churcher, 1961; Marshall et al., 1984). Representatives of the genus also were found in the San Andrés Formation, Buenos Aires Province, from the Uquian Land Mammal Age, Pleistocene (Quintana, 1994). In Argentina, specimens of *Phyllotis* cf. *xanthopygus* from the Holocene were found in Río Negro Province (dated at 3,230 ± 60 to 1,370 ± 60 years ago), Neuquén Province (9,970–320 years ago), and in Buenos Aires Province from the upper Holocene (Centinela del Mar, General Alvarado—Pardiñas, 1995). *P. xanthopygus* specimens also have been found in numerous archaeological sites in Patagonia from 12,000 years ago to present (Pardiñas and Deschamps, 1996).

The origin of the genus *Phyllotis* is unclear. Fossil comparisons, host-parasite distribution, and penile morphology indicate that South American sigmodontines might be related more closely to certain Old World muroids than to North American neotomine-peromyscines (Jacobs and Lindsay, 1984). However, this conclusion was based primarily upon the identification of fossil specimens of *Bensonmys*, then considered to be a subgenus of *Calomys*. Stepan (1995) argued that certain characteristics of the teeth in these fossils are not present in extant *Calomys* or in other phyllotines; thus, these fossils should not be assigned to *Calomys*. Furthermore, only characters of the molars and mandible were visible in the fossils. Stepan (1995) found that dental characters were not particularly informative for determination of relationships at the subfamily level. Thus, the conclusion that phyllotines might be more closely related Old World muroids than to North American neotomine-peromyscines seems unwarranted.

In a study of a 10,000-year accumulation of owl pellets in a cave in Trafal Valley, Neuquén Province, Argentina, Pearson (1987) found that remains of *Phyllotis* generally were present at a frequency <5%. A notable exception was the period from ca. 5,000–2,500 years ago when an increase of ca. 25% in the frequency of *Phyllotis* was observed. It is likely that *Phyllotis* produced the deposits of solidified urine present in caves near Confluencia Trafal, Neuquén Province, Argentina, dating from 3,610 to 4,357 years ago (Pearson and Christie, 1993).



FIG. 4. Representative habitat of *Phyllotis xanthopygus*. Meseta de Somuncurá, Río Negro Province, Argentina.

FORM AND FUNCTION. Although detailed studies of the internal morphology of *Phyllotis xanthopygus* are few in number, *P. x. rupestris* reportedly has highly developed olfactory senses (Mann, 1945). Mann also noted that mice of this subspecies have a long colon and well-developed cecum that aids in fermenting cellulose. *P. xanthopygus* also is characterized by semi-determinate growth as individuals continue to grow as adults before bone length reaches an asymptote (Steppan, 1997).

Although the phyllotine rodents show considerable diversity in glans morphology, all eight taxa examined by Hooper and Musser (1964), including *Phyllotis darwini* (*P. xanthopygus* not examined), share the following characteristics: exterior spines moderate in size and shape, bacular mounds without tubercles, urethral flap longer than wide, robust baculum with a ventrally concave base, and distal part of the shaft laterally compressed. Spotorno (1986) reported that the phallus of *P. x. xanthopygus* is barrel shaped, slightly elongated, has well-defined craters, well-developed distal processes, a central digit slightly longer than the lateral digits, and lateral digits with wide, pointed hooks. Proximally, the baculum is short with a wide base, a median notch, and lateral basilar condyles (Spotorno, 1986).

The lower limit of the thermoneutral zone of *P. x. rupestris* at ambient temperatures from 0 to 32.5°C is ca. 28°C (Bozinovic and Marquet, 1991). Basal metabolic rate was $1.26 \pm 0.21 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$, and the mean body temperature was $37.1 \pm 1.1^\circ\text{C}$ (Bozinovic and Marquet, 1991). Bozinovic and Rosenmann (1988) reported a basal metabolic rate of $1.03 \pm 0.08 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ for mice of this subspecies. They also reported that thermal conductance averaged $0.123 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$, body temperature averaged $37.3 \pm 0.9^\circ\text{C}$, and metabolic rate increased linearly with decreasing temperature at temperatures $<28.9^\circ\text{C}$. Bozinovic and Marquet (1991) induced torpor in *P. x. rupestris* by depriving animals maintained at either 12.5 or 20°C of food for 2 days.

ECOLOGY. *Phyllotis xanthopygus* is found in fields of basaltic boulders, rock piles created by erosion, and top rims of volcanic hills (Fig. 4). In 2,460 trap nights in Río Negro, Chubut, and Santa Cruz provinces, Argentina, Kim et al. (1998) captured only four specimens of *P. xanthopygus* >100 m from rocky areas and interpreted these to be dispersing individuals. Monjeau (1989) reported no captures outside of rocky areas in a review of 263 trap sites (ca. 25,000 trap nights) in northern Patagonia. Simonetti et al. (1985) reported that *P. xanthopygus* accounted for 76.9% of the animals trapped in rocky outcrops and only 6.1% of those trapped in nearby shrub. Traps placed in pampa or in open areas yielded no captures. In a study of the relationship between small mammal assemblages and landscape classification systems in northern Patagonia, Monjeau et al. (1997) trapped *P. xanthopygus* along with *Abrothrix xanthorhina*, *Akodon niscatus*, *Eligmodontia morgani*, *E. typus*, *Graomys griseoflavus*, *Lestodelphys halli*, *Oligoryzomys longicaudatus*, *Reithrodon auritus*, and *Thylamys pusillus*. All localities where *P. xanthopygus* was captured were semidesert with at least some rocky habitat. In contrast to other Patagonian small mammals, Monjeau et al. (1998) found no recognition of semidesert landscape boundaries in the distribution

of *P. xanthopygus* (i.e. between Occidental and Oriental Patagonia).

Competition with *Akodon andinus* appears to limit occupation of shrubby areas by *Phyllotis* along the Andes in central Chile. When *A. andinus* was removed from shrubby areas, captures of *P. xanthopygus* increased markedly, and when *P. xanthopygus* was removed from rocky areas, captures of *A. andinus* increased (Simonetti et al., 1985). Hershkovitz (1962) noted that the range of *P. x. rupestris* included xerophytic scrub, grassland, and puna. Osgood (1943) reported that *P. x. xanthopygus* lived in open pampa or low brush along waterways but did not appear to extend far into the mountains in the west.

Phyllotis xanthopygus has been described as a frugivore and granivore (Bozinovic and Rosenmann, 1988) and as a full herbivore (Monjeau, 1989), but others have observed high levels of insectivory (Mann, 1944; Pizzimenti and de Salle, 1980). Some variation in diet has been reported among subspecies. *P. x. rupestris* shows less variability in diet than *P. x. chilensis*; the diet of *P. x. rupestris* included fewer total items, fewer items per locality, and a single species (not named) of forb comprised 25% of its diet (Pizzimenti and de Salle, 1980). In contrast, *P. x. chilensis* did not concentrate on any one item throughout its range, but populations sometimes shifted to dietary extremes. At one site *P. x. chilensis* fed exclusively on leafy vegetation, and at another site it fed mostly on insects. Diet composition of *P. x. rupestris* sampled at seven different sites was 2% grass, 39% forb, 4% seed, and 54% insect, whereas that of *P. x. chilensis* sampled at sixteen different sites was 15% grass, 37% forb, 13% seed, and 35% insect (Pizzimenti and de Salle, 1980). *P. x. rupestris* showed increased insectivory at higher altitudes and in the presence of two potential competitors. Pizzimenti and de Salle (1980) noted that females consumed 18–22% more insects than did males.

Population levels of *Phyllotis* apparently increase after volcanic eruptions. Sixteen months after the eruption of Volcán Hudson, at a site 130 km SE of the volcano, *P. xanthopygus* was much more numerous than expected given the absence of cliffs or rocky habitat, and the population consisted of a higher proportion of young individuals than in previous years (Pearson, 1994). Saba and de Lamo (1994) found that the increase in *P. xanthopygus* after the eruption was correlated with vegetation recovery. Of 11 animals examined, all were in reproductive condition and in good health.

Little information is available on the population structure of *P. xanthopygus*. Kelt (1994) reported that in March most animals trapped are young, nonreproductive individuals. In November and December, five of seven males trapped had descended testes (Kelt, 1994). Parous females were trapped in November, February, and March, whereas pregnant females were obtained in November, December, and February (Kelt, 1994). By March and April, most females collected were either young, nulliparous individuals or larger lactating individuals (Kelt, 1994).

Mammals that are potential predators of *P. xanthopygus* include *Lestodelphys*, *Lycalopex*, *Lyncodon*, *Conepatus*, *Galictis*, *Oncifelis*, *Puma*, and *Mustela*. Owls of the genera *Tyto*, *Bubo*, and *Athene* undoubtedly prey on this mouse as well. Birney et al. (1996) trapped *P. xanthopygus* along with the highly carnivorous marsupial *Lestodelphys halli* at two localities in Argentina; thus we consider this didelphid to be a likely predator of young and perhaps even adult *P. xanthopygus*.

Jaksic and Simonetti (1987) observed that escape behavior is seen more often in response to silhouettes of large rather than small raptors. They also noted that tail "autotomy" has been observed in this species and suggested this might be an adaptation to escape predation (Jaksic and Simonetti, 1987).

The following Siphonapterans were obtained from *P. xanthopygus*: *Plocopsylla chiris* (Jameson and Fulk, 1977), *Plocopsylla achilles* (Hershkovitz, 1962), *Neotyphloceras crassispina chilensis* (Jameson and Fulk, 1977), *Delostichus phyllotis* (Jameson and Fulk, 1977), *Tetrapsyllus bleptus* (Hershkovitz, 1962), *Plocopsylla inti* (Hershkovitz, 1962), *Sphinctropsylla inca* (Hershkovitz, 1962), *Tiamastus subtilis* (Hershkovitz, 1962), *Craneopsylla minerva wolffhuegeli* (Hershkovitz, 1962). One anopluran, *Hoplopleura affinis*, was recorded from *P. xanthopygus* (Hershkovitz, 1962). Acarins identified include *Parasecia argentinensis* (Goff and Gettinger, 1995), *Andalgalomacarus xanthopyga* (Goff and Gettinger, 1995), and *Ornithodoros* (Hershkovitz, 1962). Only one endoparasite, *Taenia taeniaformis*, has been recorded from *P. xanthopygus* (Cubillos et al., 1991).

BEHAVIOR. Only scant information is available on the behavior of this species. Field investigations indicate the species is inactive during the daylight hours, and we surmise that activity is strongly related to avoidance of predators. Laboratory studies have shown that although they tend to be nocturnal, exposure to light intensities even half that of full moonlight during their dark period shifts activity from a strictly nocturnal schedule to activity bouts throughout a 24-hour period (Kramer, 1998). Kramer (1998) also found that males became active earlier in the evening than females and that their peak in activity occurs ca. 45 min before that of females.

GENETICS. A karyotype consisting of 68 acrocentric autosomes ($2n = 70$) appears to be ancestral for the tribe Phyllotini (Pearson and Patton, 1976). Within *Phyllotis*, the number of autosomes seems to have changed from 68 (now observed only in *P. osilae*) to 36 as presently observed for *P. xanthopygus*, *P. darwini*, and closely related species (Pearson and Patton, 1976). Both sex chromosomes in *P. x. xanthopygus* are larger than sex chromosomes in *P. x. vaccarum* and *P. x. rupestris*, and the Y chromosome and the terminal segments of the long arm of the X chromosome of *P. x. xanthopygus* are slightly heterochromatic.

Subspecific differences exist in chromosomal banding patterns of *P. xanthopygus*. Walker et al. (1991) reported that although most chromosomes of *P. x. xanthopygus* ($n = 2$) have tiny pericentromeric C-bands, this band was large in one member of chromosomal pair 15. *P. x. rupestris* ($n = 2$) has large pericentromeric C-bands in all autosomes and in the X chromosomes. In contrast, G-banding patterns of autosomes are similar in *P. x. rupestris*, *P. x. vaccarum* ($n = 2$), and *P. x. xanthopygus* except that the terminal region of the long arm of the X chromosome of *P. x. xanthopygus* has a few well-differentiated G-bands that were not seen in the other subspecies (Walker et al., 1991).

Walker and González-Providell (1995) found that pericentromeric regions of the chromosomes of these three subspecies differ in their GGCC content and suggested that these differences might be correlated to ancestral and derived conditions. They also reported significantly larger genomes for *P. x. rupestris* and *P. x. vaccarum* relative to *P. x. xanthopygus*. *P. x. rupestris* and *P. x. vaccarum* also were found to have defined pericentromeric bands on the autosomes and on the X chromosome, which are lacking in *P. x. xanthopygus*. These bands are larger in *P. x. vaccarum* than in *P. x. rupestris*. Finally, Walker and González-Providell (1995) found that Hin dIII recognition sites were rare or nonexistent in *P. x. xanthopygus* but frequent in the heterochromatin of some chromosomes of *P. x. vaccarum* and *P. x. rupestris*.

Phylogeographic analyses of mitochondrial DNA sequences (mtDNA) from *P. xanthopygus* trapped in southern Argentina revealed two distinct haplotype clades, one of which was found only in populations presently occurring north of Río Chubut (Kim et al., 1998). The existence of two relatively deep clades suggested to the authors that the distribution of this species probably was separated by some event or barrier, perhaps early in the Pleistocene.

Kim et al. (1998) reported considerable variation in mtDNA haplotypes both within and between localities from both large and small populations of *P. x. xanthopygus*. Although, *P. xanthopygus* occurs in rocky outcrops that were hypothesized to act as habitat islands, no evidence of genetic isolation of local populations was detected. Instead, it is likely that the smaller islands of rocky habitat act as sinks because resources there are highly variable, and although dispersal rates seemingly are high, predominant matrilineages generally are absent from at least the smaller islands.

REMARKS. *Phyllotis xanthopygus vaccarum* was separated taxonomically from *P. d. darwini* by Spotorno and Walker (1983) based on chromosomal differences. Few studies have been published on the ecology, physiology, or behavior of *P. xanthopygus*, but pertinent information on *P. darwini* is available (Agüero and Simonetti, 1988; Bravo et al., 1990; Fuentes and Campusano, 1985; Jaksic et al., 1992; Jiménez et al., 1992; Mares, 1977; Meserve, 1978, 1981; Meserve and Glanz, 1978; Pearson, 1975; Péfaur et al., 1979).

The generic name, *Phyllotis*, is derived from the Greek root *phyll-* meaning leaf. The species epithet, *xanthopygus*, is derived from the Greek roots *xanth-* and *pyg-*, meaning yellow and rump, respectively. Woodman (1993) argued that the species name should be changed to "*xanthopyga*" because the generic name, *Phyllotis*,

is derived from a Greek, feminine noun. Pritchard (1994) pointed out that "*Phyllotis* is a latinized Greek word and in Latin *-is* is feminine, masculine, or neuter, and therefore '*xanthopygus*' should be retained." The vernacular name we have adopted for *P. xanthopygus*, "Pericote orejudo andino-patagónico," refers to its distribution along the Andean mountains and the Patagonian semi-deserts.

We thank J. Decher for taking photographs of the live animal and skull. S. J. Steppan contributed to this account in many ways, generously sharing insights and making helpful comments in addition to providing the distribution map.

LITERATURE CITED

- AGÜERO, T., AND J. A. SIMONETTI. 1988. Home range assessment: a comparison of five methods. *Revista Chilena de Historia Natural*, 61:223–229.
- ALLEN, J. A. 1905. Mammalia of southern Patagonia. Reports of the Princeton University Expeditions to Patagonia, 1896–1899, *Zoology*, 3:(Part I)1–210.
- ANDERSON, S. 1997. Mammals of Bolivia, taxonomy and distribution. *Bulletin of the American Museum of Natural History*, 231:1–652.
- BASKIN, J. A. 1978. *Bensonomys*, *Calomys*, and the origin of the Phyllotine group of neotropical cricetines (Rodentia: Cricetidae). *Journal of Mammalogy*, 59:125–135.
- BIRNEY, E. C., J. A. MONJEAU, C. J. PHILLIPS, R. S. SIKES, AND I. KIM. 1996. *Lestodelphys halli*: New information on a poorly known Argentine marsupial. *Mastozoología Neotropical*, 3: 171–181.
- BOZINOVIC, F., AND P. A. MARQUET. 1991. Energetics and torpor in the Atacama desert-dwelling rodent *Phyllotis darwini rupestris*. *Journal of Mammalogy*, 72:734–738.
- BOZINOVIC, F., AND M. ROSENMANN. 1988. Comparative energetics of South American cricetid rodents. *Comparative Biochemistry and Physiology*, 91A:195–202.
- BRAUN, J. K. 1993. Systematic relationships of the tribe Phyllotini (Muridae: Sigmodontinae) of South America. Special Publication, Oklahoma Museum of Natural History, Norman, 50 pp.
- BRAVO, H., J. OLAVARRIA, AND F. TORREALBA. 1990. Comparative study of visual inter and intrahemispheric cortico-cortical connections in five native Chilean rodents. *Anatomy and Embryology*, 181:67–73.
- CABRERA, A. 1926. Dos roedores nuevos de las montañas de Cautamarca. *Revista Chilena de Historia Natural Pura y Aplicada*, 30:319–321.
- CUBILLOS, V., P. TORRES, AND M. GALLARDO. 1991. Aspectos histopatológicos en un nuevo hospedador de *Taenia taeniaformis*. *Archivos de Medicina Veterinaria*, 23:77–79.
- DE FONOLLAT, A. M. P., M. M. LUCERO, AND G. J. SCROCCHI. 1989. Nuevos datos para dos especies de Cricétidos: *Akodon andinus dolichonyx* (Philippi, 1896) y *Phyllotis darwini rupestris* (Gervais, 1841), en la provincia de Salta (Argentina). *Acta Zoológica Lilloana*, 39:111–112.
- FUENTES, E. R., AND C. CAMPUSANO. 1985. Pest outbreaks and rainfall in the semi-arid region of Chile. *Journal of Arid Environments*, 8:67–72.
- GERVAIS, P. 1841. Mammifères. Pp. 1–68, in *Voyage autour du monde exécuté pendant les années 1836 et 1837 sur la corvette La Bonité commandée par M. Vaillant* (A. Bertrand, ed.). *Zoologie* (Eydox and Souleyet, eds.), Paris, 1:1–334.
- GOFF, M. L., AND D. GETTINGER. 1995. New genus and six new species of chiggers (Acari: Trombiculidae and Leeuwenhoekeidae) collected from small mammals in Argentina. *Journal of Medical Entomology*, 32:439–448.
- HALLOY, S. 1991. Islands of life at 6000 m altitude: the environment of the highest autotrophic communities on earth (Socoma Volcano, Andes). *Arctic and Alpine Research*, 23:247–262.
- HERSHKOVITZ, P. 1962. Evolution of neotropical cricetine rodents (Muridae) with special reference to the Phyllotine group. *Fieldiana: Zoology*, 46:1–524.
- HOFFSTETTER, R. 1986. High Andean mammalian faunas during the Plio-Pleistocene. Pp. 218–245, in *High altitude tropical biogeography* (F. Vuilleumier and M. Monasterio, eds.). Oxford University Press, New York, New York, 649 pp.
- HOOPER, E. T., AND G. G. MUSSER. 1964. The glans penis in neotropical cricetines (Family Muridae) with comments on clas-

- sification of muroid rodents. Miscellaneous Publications of the Museum of Zoology, University of Michigan, 123:1-57.
- JACOBS, L. L., AND E. H. LINDSAY. 1984. Holarctic radiation of neogene muroid rodents and the origin of South American cricetids. *Journal of Vertebrate Paleontology*, 4:265-272.
- JAKSIC, F. M., AND J. A. SIMONETTI. 1987. Predator/prey relationships among terrestrial vertebrates: an exhaustive review of studies conducted in southern South America. *Revista Chilena de Historia Natural*, 60:221-244.
- JAKSIC, F. M., J. E. JIMÉNEZ, S. A. CASTRO, AND P. FEINSINGER. 1992. Numerical and functional response of predators to a long-term decline in mammalian prey at a semi-arid Neotropical site. *Oecologia*, 89:90-101.
- JAMESON, E. W., JR., AND G. W. FULK. 1977. Notes on some fleas (Siphonaptera) from Chile. *Journal of Medical Entomology*, 14:401-406.
- JIMÉNEZ, J. E., P. FEINSINGER, AND F. M. JAKSIC. 1992. Spatiotemporal patterns of an irruption and decline of small mammals in northcentral Chile. *Journal of Mammalogy*, 73:356-364.
- KELT, D. A. 1994. The natural history of small mammals from Aisén Region, southern Chile. *Revista Chilena de Historia Natural*, 67:183-207.
- KIM, I., ET AL. 1998. Habitat islands, genetic diversity, and gene flow in a Patagonian rodent. *Molecular Ecology*, 7:667-678.
- KRAMER, K. M. 1998. The effect of light intensity and motivational state on the activity patterns of Patagonian leaf-eared mice, *Phyllotis xanthopygus*. M.S. thesis. University of Minnesota, St. Paul, 59 pp.
- LEMON, R. R. H., AND C. S. CHURCHER. 1961. Pleistocene geology and paleontology of the Talara region, northwest Peru. *American Journal of Science*, 259:410-429.
- MANN, F. G. 1944. Dos nuevas especies de roedores. *Biológica*, 1:95-113.
- . 1945. Mamíferos de Tarapaca. *Biológica*, 2:23-96.
- MARSHALL, L. G., ET AL. 1984. Mammals and stratigraphy: geochronology of the continental mammal-bearing quaternary of South America. *Palaeovertebrata*, Montpellier, Mémoire Extraordinaire, 1984:1-76.
- MARES, M. A. 1977. Water balance and other ecological observations on three species of *Phyllotis* in northwestern Argentina. *Journal of Mammalogy*, 58:514-520.
- . 1985. Mammal faunas of xeric habitats and the great American interchange. Pp. 489-520, in *The great American biotic interchange* (F. Stehli and S. D. Webb, eds.). Plenum Press, New York, 532 pp.
- MESERVE, P. L. 1978. Water dependence in some Chilean arid zone rodents. *Journal of Mammalogy*, 59:217-219.
- . 1981. Trophic relationships among small mammals in a Chilean semiarid thorn scrub community. *Journal of Mammalogy*, 62:304-314.
- MESERVE, P. L., AND W. E. GLANZ. 1978. Geographical ecology of small mammals in the northern Chilean arid zone. *Journal of Biogeography*, 5:135-148.
- MONJEAU, A. 1989. Ecología y distribución geográfica de los pequeños mamíferos del Parque Nacional Nahuel Huapi. Ph.D. dissertation. Universidad Nacional de La Plata, La Plata, 253 pp.
- MONJEAU, A., N. BONINO, AND S. SABA. 1994. Annotated checklist of the living land mammals in Patagonia, Argentina. *Mastozoología Neotropical*, 1:143-156.
- MONJEAU, J. A., R. S. SIKES, E. C. BIRNEY, N. GUTHMANN, AND C. J. PHILLIPS. 1997. Small mammal community composition within the major landscape divisions of Patagonia, southern Argentina. *Mastozoología Neotropical*, 4:113-127.
- MONJEAU, J. A., E. C. BIRNEY, L. GHERMANDI, R. S. SIKES, L. MARGUTTI, AND C. J. PHILLIPS. 1998. Plants, small mammals, and the hierarchical landscape classifications of Patagonia. *Landscape Ecology*, 13:285-306.
- MUSSER, G. G., AND M. D. CARLETON. 1993. Family Muridae. Pp. 501-756, in *Mammal species of the world: a taxonomic and geographic reference*. Second ed. (D. E. Wilson and D. M. Reeder, eds.). Smithsonian Institution Press, Washington, D.C., 1206 pp.
- OSGOOD, W. H. 1943. The mammals of Chile. *Field Museum of Natural History, Zoological Series*, 30:1-268.
- PARDIÑAS, U. F. J. 1995. Novedosos cricétidos (Mammalia, Rodentia) en el Holoceno de la Región Pampeana, Argentina. *Ameghiniana*, 32:197-203.
- PARDIÑAS, U. F. J. AND C. DESCHAMPS. 1996. Sigmodontinos (Mammalia, Rodentia) pleistocénicos del sudoeste de la Provincia de Buenos Aires (Argentina): aspectos sistemáticos, paleoogeográficos y paleoambientales. *Estudios Geológicos*, Madrid, 52:367-379.
- PARDIÑAS, U. F. J., AND C. A. GALLIARI. 1998. Sigmodontinos (Rodentia, Muridae) del Holoceno Inferior de Bolivia. *Revista Española de Paleontología*, 13(1):17-25.
- PEARSON, O. P. 1958. A taxonomic revision of the rodent genus *Phyllotis*. University of California Publications in Zoology, 56:391-496.
- . 1975. An outbreak of mice in the coastal desert of Peru. *Mammalia*, 39:375-386.
- . 1987. Mice and the postglacial history of the Trafal Valley of Argentina. *Journal of Mammalogy*, 68:469-478.
- . 1994. The impact of an eruption of Volcán Hudson on small mammals in Argentine Patagonia. *Mastozoología Neotropical*, 1:103-112.
- PEARSON, O. P., AND M. I. CHRISTIE. 1993. Rodent guano (amberat) from caves in Argentina. *Studies on Neotropical Fauna and Environment*, 28:105-111.
- PEARSON, O. P., AND J. L. PATTON. 1976. Relationships among South American Phyllotine rodents based on chromosome analysis. *Journal of Mammalogy*, 57:339-350.
- PEFAUR, J. E., J. L. YANEZ, AND F. M. JAKSIC. 1979. Biological and environmental aspects of a mouse outbreak in the semi-arid region of Chile. *Mammalia*, 43:313-322.
- PHILIPPI, R. A. 1860. Reise durch die Wüste Atacama auf Befehl der chilenischen Regierung im Sommer 1853-54 unternommen und ausgeführt von R. A. Philippi. Eduard Anton, Halle, pp. 192 + 62, map, 27 pls.
- . 1896. Descripción de los mamíferos traídos del viaje de exploración a Tarapacá, hecho por orden del gobierno en el verano de 1884 a 1885, por Federico Philippi, descrita por el Dr. R. A. Philippi. *Anales del Museo Nacional de Chile, Zoología*, 13a:1-24.
- PIZZIMENTI, J. J., AND R. DE SALLE. 1980. Dietary and morphometric variation in some Peruvian rodent communities: the effect of feeding strategy on evolution. *Biological Journal of the Linnean Society*, 13:263-285.
- PRITCHARD, P. C. H. 1994. Comment on gender and declension of generic names. *Journal of Mammalogy*, 75:549-550.
- QUINTANA, C. A. 1994. Notas para una actualización del conocimiento de la fauna de la "formación" San Andrés (Pleistoceno inferior), Provincia de Buenos Aires. *Ameghiniana*, 31:331-332.
- REDFORD, K. H., AND J. F. EISENBERG. 1992. Mammals of the Neotropics. The southern cone: Chile, Argentina, Uruguay, Paraguay. The University of Chicago Press, Chicago, 2:1-430.
- REIC, O. A. 1978. Roedores cricétidos del Plioceno superior de la Provincia de Buenos Aires (Argentina). Publicaciones del Museo Municipal de Ciencias Naturales de Mar del Plata "Lorenzo Scaglia," 2:164-190.
- SABA, S. L., AND D. A. DE LAMO. 1994. Dynamic responses of mammals to the eruption of Volcán Hudson. *Mastozoología Neotropical*, 1:113-122.
- SIMONETTI, J. A., E. R. FUENTES, AND R. D. OTAIZA. 1985. Habitat use by two rodent species in the high Andes of central Chile. *Mammalia*, 49:19-25.
- SPOTORNO, A. O. 1986. Systematics and evolutionary relationships of Andean Phyllotine and Akodontine rodents. Ph.D. dissertation. University of California, Berkeley, 219 pp.
- SPOTORNO, A. E., AND L. I. WALKER. 1983. Análisis electroforético y biométrico de dos especies de *Phyllotis* en Chile central y sus híbridos experimentales. *Revista Chilena de Historia Natural*, 56:51-59.
- STEPAN, S. J. 1995. Revision of the tribe Phyllotini (Rodentia: Sigmodontinae), with a phylogenetic hypothesis for the Sigmodontinae. *Fieldiana: Zoology, New Series*, 80:1-112.
- . 1997. Phylogenetic analysis of phenotypic covariance structure. I. Contrasting results from matrix correlation and common principal component analyses. *Evolution*, 51:571-586.
- . 1998. Phylogenetic relationships and species limits within *Phyllotis* (Rodentia: Sigmodontinae): concordance between

- mtDNA sequence and morphology. *Journal of Mammalogy*, 79: 573–593.
- THOMAS, O. 1884. On a collection of Muridae from central Peru. *Proceedings of the Zoological Society of London*, 1884:447–451.
- . 1896. On the genera of rodents: an attempt to bring up to date the current arrangement of the order. *Proceedings of the Zoological Society of London*, 1896:1012–1028.
- . 1902. On mammals collected by Mr. Perry O. Simons in the southern part of the Bolivian plateau. *Annals and Magazine of Natural History*, ser. 7, 9:222–230.
- . 1912. New bats and rodents from S. America. *Annals and Magazine of Natural History*, ser. 8, 10:403–411.
- . 1919. On small mammals from “Otro Cerro,” north-eastern Rioja, collected by Sr. L. Budin. *Annals and Magazine of Natural History*, ser. 9, 3:489–500.
- TROUËSSART, E. L. 1898–1899. *Catalogus mammalium tam viventium quam fossilium*. R. Friedländer & Sohn, 1:1–664.
- WALKER, L. I., AND S. GONZÁLEZ-PROVIDELL. 1995. Heterochromatic DNA evolution in phyllotine rodents: restriction enzyme bands. *The Journal of Heredity*, 86:240–243.
- WALKER, L. I., A. E. SPOTORNO, AND J. ARRAU. 1984. Cytogenetic and reproductive studies of two nominal subspecies of *Phyllotis darwini* and their experimental hybrids. *Journal of Mammalogy*, 65:220–230.
- WALKER, L. I., A. E. SPOTORNO, AND J. SANS. 1991. Genome size variation and its phenotypic consequences in *Phyllotis* rodents. *Hereditas*, 115:99–107.
- WATERHOUSE, G. R. 1837. Characters of new species of the genus *Mus* from the collection of Mr. Darwin. *Proceedings of the Zoological Society of London*, 1837:15–32.
- WOODMAN, N. 1993. The correct gender of mammalian generic names ending in *-otis*. *Journal of Mammalogy*, 74:544–546.
- Editors of this account were ELAINE ANDERSON and LESLIE N. CARRAWAY. Managing editor was BARBARA H. BLAKE.
- K. M. KRAMER, E. C. BIRNEY, R. S. SIKES, BELL MUSEUM OF NATURAL HISTORY AND DEPARTMENT OF ECOLOGY, EVOLUTION, AND BEHAVIOR, UNIVERSITY OF MINNESOTA, ST. PAUL, MINNESOTA 55108; J. A. MONJEAU, DEPARTAMENTO DE ECOLOGÍA, UNIVERSIDAD NACIONAL DEL COMAHUE, CC. 1336 (8400) BARILOCHE, RÍO NEGRO, ARGENTINA.