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PHYLOGENETIC RELATIONSHIPS AND SPECIES LIMITS WITHIN *PHYLLOTIS* (RODENTIA: SIGMODONTINAE): CONCORDANCE BETWEEN MTDNA SEQUENCE AND MORPHOLOGY

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Phylogenetic relationships and species limits within the South American rodent genus *Phyllotis* were estimated using nucleotide sequence data from a 973 base-pair region of the mitochondrial gene, cytochrome *b*. Geographic variation and species limits were assessed by sequencing individuals from multiple populations and morphometric analyses of skulls and skins. Results supported the following clades: *Phyllotis* plus *Auliscomys* exclusive of *Graomys*, the *darwini* species group, and a northerly distributed species-pair of *P. amicus* and *P. andium*. The phylogeny, genetic divergence estimates, and morphology indicated that *P. xanthopygus rupestris* is polyphyletic and populations from the Pacific slope of the Andes currently assigned to that taxon are specifically distinct. These populations are placed in the newly elevated *P. limatus* and an emended diagnosis is provided. Biogeographic and phylogenetic patterns are most consistent with successive colonization of the Pacific slopes by *P. xanthopygus*, possibly through range expansion and contraction, over a short period of time relative to the age of the clade.

Key words: *Phyllotis*, phylogeny, cytochrome *b*, speciation, species limits, biogeography, Andes

Phyllotis is one of the most studied genera of South American rodents. Studies of its karyology, reproductive biology, morphology, and ecology have resolved its species-level taxonomy to a greater degree than perhaps any other comparable Neotropical rodent group. Nonetheless, this concentrated interest has failed to resolve phylogenetic relationships among species. Low bootstrap values for internal nodes (Steppan, 1993, 1995*a*, 1995*b*) and short branch lengths (Braun, 1993) characterize available morphology-based phylogenies. This lack of phylogenetic resolution within *Phyllotis* is significant for systematics well beyond the borders of the genus sensu stricto because *Phyllotis* may be paraphyletic with respect to some of the other genera within the tribe Phyllotini (Steppan, 1993, 1995*b*). This study sought to resolve relationships among species of *Phyllotis* by cladistic analyses of DNA sequence data from a 973 base-pair region of the mitochondrial cytochrome *b* gene. By sampling geographic variation within species, I evaluated concordance between species limits hypothesized by prior systematic studies and the mitochondrial gene tree. Additionally, fine scale geographic sampling of cranial morphometric data provided complementary data for revising species-level systematics.

This study focused on the *darwini* species group, the best supported *Phyllotis* clade from morphology-based phylogenies (Steppan, 1993, 1995*b*), but analyses presented here included 8 of the 13 species in the genus. The *darwini* species group includes the currently recognized species *darwini, caprinus, magister, osgoodi,* and *xanthopygus* (Fig. 1a). Members of the *darwini* species group are often the most abundant mammals at a locality (Meserve, 1981;

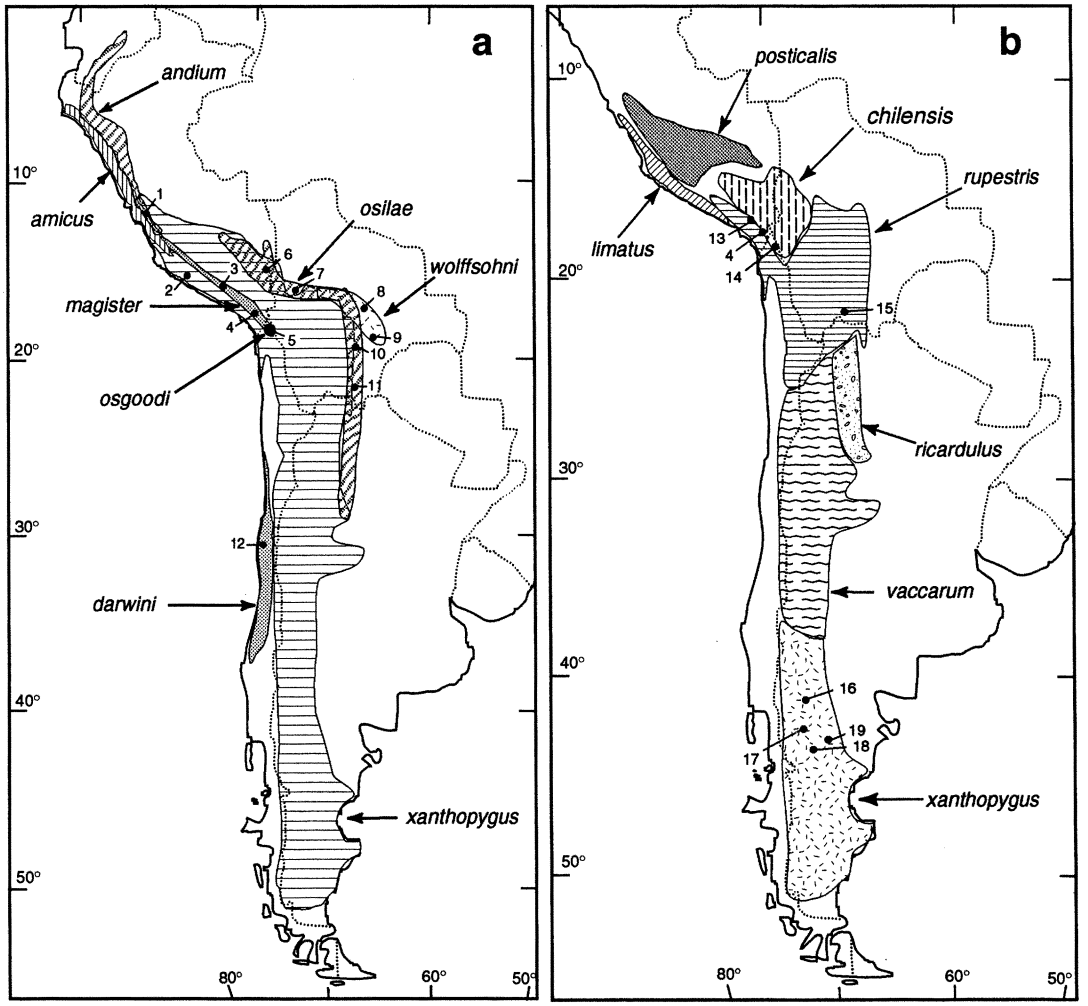

FIG. 1.—(a) Geographic distribution of *Phyllotis* species examined in this study. Numbers indicate localities of *Phyllotis* individuals that were included in the phylogenetic analyses. Locality numbers are cross referenced in Appendix I and used to identify individuals in the cladograms in Figs. 2 and 3. 1, Lima, Peru; 2, Atiquipa, Caraveli, Arequipa, Peru; 3, Chivay, Arequipa, Peru; 4, Tarata, Tacna, Peru; 5, Parinacota, Tarapacá, Chile; 6, Ilave, Puno, Peru; 7, Miña Lourdes, La Paz, Bolivia; 8, Quiñe, Santa Cruz, Bolivia; 9, Padilla, Chuquisaca, Bolivia; 10, Tarabuco, Chuquisaca, Bolivia; 11, Serrania Sama, Tarija, Bolivia; 12, Fray Jorge, Coquimbo, Chile. (b) Geographic distribution of all currently recognized subspecies of *Phyllotis xanthopygus*. Localities of individuals that were included in the phylogenetic analyses: 13, Torata, Moquegua, Peru; 14, Chapiquina, Tarapacá, Chile; 15, Iscayachi, Tarija, Bolivia; 16, Comallo, Río Negro, Argentina; 17, Cerro del Viento, Chubut, Argentina; 18, Pampa de Agnia, Chubut, Argentina; 19, Cerro Rosario, Chubut, Argentina. Sequences representing localities 17–19 were obtained from C. Phillips and I. Kim.

Pearson, 1958; Pearson and Ralph, 1978; Pizzimenti and de Salle, 1980; Reise and Venegas, 1987). The genus is distributed along the Andes and nearby xeric habitats from northern Ecuador to Tierra del Fuego (Fig. 1a). With many diagnosable species-level taxa (Hershkovitz, 1962; Pearson, 1958), *Phyllotis* is well suited to provide

insights into factors affecting speciation and the biogeographic history of the central and southern Andean region.

Systematic investigations in *Phyllotis* began when Darwin collected two species during the voyage of the Beagle: *xanthopygus* from eastern Patagonia and *darwini* from Coquimbo on the central Chilean coast. Species limits aside, there have been few hypotheses of interspecific relationships within *Phyllotis*. Pearson (1958) followed Ellerman (1941) and Osgood (1947) in recognizing a *Phyllotis* subgenus congruent with current concepts for the entire genus, except that they excluded *P. gerbillus* to the monotypic subgenus *Paralomys*. Hershkovitz (1962) did not recognize subgenera but did highlight a *darwini* complex that included *andium, darwini, haggardi,* and *osilae,* but not *amicus* and *gerbillus*. His polytypic *darwini* included the taxa *caprinus, definitus, magister, osgoodi, wolffsohni,* and *xanthopygus*—all now regarded as distinct species. Pearson and Patton (1976) used unbanded karyotypes and insights drawn from morphology and biogeography to propose an evolutionary scenario for the tribe Phyllotini. *Phyllotis osilae* was considered to possess the primitive karyotype and was placed at the base of a radiation that included *Phyllotis, Auliscomys, Eligmodontia, Graomys,* and *Reithrodon*. *Phyllotis wolffsohni, definitus,* and *andium* were successive sister taxa to an unresolved clade including *amicus, magister,* and two pairs of species, *haggardi* and *gerbillus,* and *darwini* and *caprinus*.

Karyotypic and breeding studies further divided the widespread and polytypic *P. darwini* into three species. Populations referred to *P. osgoodi* had a diploid count of 40 rather than the 38 that characterized most of the genus (Spotorno, 1976). Specific separation between coastal Chilean *P. d. darwini* and Andean *P. d. vaccarum* was demonstrated by the complete sterility of hybrids (Walker et al., 1984), leaving true *darwini* limited to a narrow strip along the central coast of Chile (Figs. 1a and 1b). The subspecies *rupestris* and *vaccarum* bred true for three generations, consistent with conspecificity. Remaining subspecies were allocated with them to *P. xanthopygus*.

Recent studies employing cladistic techniques have provided some minimal hypotheses within *Phyllotis,* but the object of those studies was the tribe Phyllotini, not the genus or *darwini* species group (Braun, 1993; Steppan, 1993, 1995*b*). Analyzing 98 morphological characters, I found the basal nodes of *Phyllotis* to be effectively unresolved (Steppan, 1993, 1995*b*). However, there is moderate support for a clade that consisted of *P. caprinus, P. darwini,* and *P. xanthopygus,* as well as evidence for two other clades: the *darwini* species group consisting of *P. magister* and the previous three species and a more inclusive clade designated *Phyllotis* sensu stricto that also included *haggardi, definitus,* and *osilae*. That concept of *Phyllotis* sensu stricto is not consistent with the hypotheses of Pearson and Patton (1976) that *osilae* is the basal member of *Phyllotis* and that its all-acrocentric karyotype is primitive for the genus. Other hypotheses from my morphological cladistic studies are that *wolffsohni* is related more closely to the *Auliscomys* or *Reithrodon* generic-groups than it is to *Phyllotis* sensu stricto, *P. andium* is a basal member of a probably paraphyletic *Phyllotis,* and *P. amicus* is more closely related to *Graomys* than it is to *Phyllotis* sensu stricto.

Given the poor success provided by morphological characters at resolving relationships within the *darwini* species group, I sequenced a 973 base pair (bp) region of the mitochondrial gene, cytochrome *b*. This gene has the advantages of evolving rapidly, having resolved relationships at a comparable level in related groups of sigmodontine rodents (Smith and Patton, 1993), and because it is frequently used in other studies, ingroup and outgroup sequences were already available. Most morphological characters that are cladistically informative for this group are limited to a few phallic characters (Steppan, 1995*b*),

which were not included because of incomplete taxonomic sampling. Cranial measurements were taken from most specimens of the *darwini* species group present in museum collections to provide the systematic context for interpreting the molecular results.

Materials and Methods

DNA sequencing.—DNA was extracted from frozen tissue or dry museum skins by overnight digestion at 37°C using the SDS-proteinase K/phenol method (Maniatis et al., 1982). Portions of the mitochondrial cytochrome *b* gene were amplified using the polymerase chain reaction (PCR) and combinations of the following primers (5′ to 3′): B7 ccaatgatatgaaaaaccatcgttg (L14115); B7p cgaagcttgatatgaaaaaccatcgttg (L14115); B1a ccatccaacatctcagcatgatgaaa (L14233); B3 atctgcatctacctacacatcgg (L14434); B3p atctgcatattcctcacgtcggacg (L14437); B9 ggcattatcttattcctgaccactatagc (L14513); B5 accctagtagaatgagcctgagg (L14635); B8 ttcatctccggtttacaagac (H15309); B4 gatgaatgggtgttctactggttg (H15159); B10p gctggtgtataattatctgggtctccgag (H14886); B2 aaactgcagccccctcagaatgatatttgtcctca (H14541); B2p gtggcccctcagaatgatatttgtcctca (H14541). Primer names ending in "p" were designed specifically for phyllotines; numbers in parentheses refer to the position in the mtDNA sequence for *Mus musculus* (Bibb et al., 1981). L and H refer to light and heavy strands, respectively. This combination of primers results in a 973 bp region for specimens with complete sequence. A double-stranded product was amplified from the extract followed by asymmetric single-stranded amplification with one of the primers limiting (1:50 dilution). The limiting primer was then used for sequencing along with internal primers when needed. Typical temperature programs for amplification were denaturation at 93°C for 1 min, annealing at 50°C for 1 min, and extension at 71°C for 1.5 min with 35 cycles for double-stranded, and denaturation at 93°C for 1 min, annealing at 56°C for 1 min, and extension at 72°C for 1.5 min with 31 cycles for single-stranded. Extracts that did not amplify well initially were reamplified from plugs cut from 3% agarose gels. Plugs were cut from gels using individual flame-sterilized spatulas, then diluted in 250 µl ddH_2O before reamplification. The single-stranded product was then sequenced by the dideoxy chain termination method using ^{35}S-dATP (Sanger et al., 1977).

Sequenced specimens are listed in Appendix I. Taxonomy within *Phyllotis* follows Steppan (1995*b*) except for retaining *chilensis* within *xanthopygus*. Locality information for the measured specimens from the northern subspecies of *P. xanthopygus* is listed in Appendix II. Sequences have been submitted to GenBank and assigned accession numbers U86816-U86835.

Analysis.—Sequences were aligned by eye to maintain amino acid sequence. This presented no problem because sequence divergence was low and gaps were rare. Maximum parsimony analyses were conducted using PAUP 3.1.1 (Swofford, 1993) with the heuristic search algorithm, TBR branch-swapping, and 20 random addition replicates. MacClade (Maddison and Maddison, 1992) translated amino acid sequences from the DNA sequences. Analyses utilized combinations of several different weighting schemes based on codon position and transversion : transition ratio to compensate for differential rates of character evolution (Hillis et al., 1993). Frequencies of changes between states were estimated among each species with multiple representatives (*darwini, magister, osilae, wolffsohni, xanthopygus*) and for each codon position separately using MacClade. Frequencies were calculated from the mean in 50 random equiprobable trees, and summed over the five species to estimate transversion : transition and codon position ratios. Intraspecific comparisons are too recent for saturation of transitions and require the fewest a priori phylogenetic assumptions. More inclusive taxonomic groupings will encompass deeper regions of the phylogeny, more homoplasy, and thus will underestimate the differences in transformation frequencies.

A suite of weighting schemes based on transversion : transition ratios and codon position were applied to test for the sensitivity of bootstrap values and branching pattern to weighting. Only results from two schemes will be reported here: equal weighting and the a priori preferred analysis using weights derived from the inverse of the estimated evolutionary rates. Other commonly used weighting schemes, such as transversion only or first and second position only, resulted in trees that were less robust and less congruent with the best supported morphology-based hypotheses (Steppan, 1995*a*). They also are inadequate because they exclude potentially

informative data and thus are not discussed. The preferred weighting scheme is a six-parameter model (Hillis et al., 1993). For comparison, Kimura's two-parameter model (Kimura, 1980) weighs transversions differently from transitions, regardless of position, while a 12-parameter model (Arévalo et al., 1994) is based on estimated frequencies of all possible nucleotide transformations. Two-parameter models such as Kimura's (1980) or three-parameter models such as weighting by codon position are actually special cases among six-parameter models where one or more parameters are held constant. In the six-parameter scheme, codon positions were weighted 5:9:1 (first : second : third) and transversion weighting was applied to each codon position independently (3:1 for first position, 1:1 for second, 3:1 for third). Observed ratios were similar to those seen in another group of Andean sigmodontine mice with similar taxonomic sampling (Smith and Patton, 1991). Bootstrapping was used as an estimate of internal consistency in the data (i.e., robustness). Each bootstrap analysis consisted of 200 replicates. Repeatability of bootstrap percentages was estimated from 50 sets of 100 replicate analyses for the equal-weighting data set.

Calomys was designated as the outgroup in accordance with morphological phylogenies (Steppan, 1993, 1995*b*) and conventional estimates of phyllotine systematics. Members of the phyllotine genera *Auliscomys* and *Graomys* were included because *Phyllotis* may be paraphyletic with respect to them (Steppan, 1993, 1995*b*), and they are outside the focal *darwini* species group. Sequences for *Calomys* and *Auliscomys pictus* (801 bp) were acquired from M. Smith (Smith and Patton, 1993) and have been listed in GenBank. Sequences for *Graomys* and some Argentine *P. xanthopygus xanthopygus* (347 bp; localities 17, 18, and 19) were obtained from C. Phillips and I. Kim.

Twenty-three measurements were taken from skulls and jaws using digital calipers precise to 0.01 mm. External measurements were transcribed from skin tags. A total of 1,546 subadult and adult *Phyllotis* was measured (Table 1). Additional details of morphometric data collection and rationale were presented in Steppan (1995*a*, 1997).

RESULTS

Mean sequence divergences ranged from 3.7% (n = 15) within subspecies (roughly equivalent to phylogenetic species) to 7.6% (n = 45) within currently recognized biological species. Mean uncorrected sequence divergence among *Phyllotis* species was 13.6% (n = 183).

When the six-parameter weighting scheme based on observed transformation frequencies was used (positions 5:9:1, transversions : transitions 3:1, 1:1, 3:1), six most-parsimonious trees of 3,137 steps resulted (Fig. 2). All named taxa were monophyletic except for *Phyllotis* and *P. xanthopygus rupestris*. *Phyllotis* may be monophyletic because relative positions of *Auliscomys* and *P. wolffsohni* were unresolved. Placement of *Graomys* outside a clade that included *Auliscomys* and *Phyllotis* was supported strongly, found in 94% of bootstrap replicates. Excluding *P. wolffsohni*, the basal-most *Phyllotis* branch was the species pair *amicus-andium*. A *darwini* species group was supported moderately (found in 64% of bootstrap replicates), but interspecific relationships within *Phyllotis* were resolved more poorly, with a mean bootstrap percentage of 41% (n = 6, excluding the *amicus-andium* clade) for the remaining nodes.

All species or subspecies represented by multiple individuals appeared monophyletic, with the exception of *P. x. rupestris*. The *P. x. rupestris* individual from the eastern Andean slopes of Bolivia (locality 15) grouped with the western slope *P. x. chilensis* from Peru (locality 4) and Chile (locality 14) rather than the Peruvian *P. x. rupestris* (localities 4, 13). Furthermore, the *chilensis* clade was related more closely to the southern *P. x. xanthopygus* than to the Peruvian *P. x. rupestris*. In particular, although the *P. x. chilensis* and the *P. x. rupestris* individuals from Tacna were collected only two kilometers apart in the same river valley (locality 4), they did not group together and had a sequence divergence of 8.9%. The sequence divergence within the separate *chilensis* and *rupestris* clades ranged from 0 to 2.4% (n = 4), while the divergence between the members of these

TABLE 1.—*Mean measurements of subspecies of northern members of the* darwini *species group. Standard deviations and number of specimens examined are in parentheses. Taxonomy follows the systematic recommendations from the text and illustrated in figure 5.*

	Taxon						
Measurement	Northern *P. limatus*	Southern *P. limatus*	*P. x. posticalis*	*P. x. chilensis*	*P. x. rupestris*	*P. d. darwini*	*P. magister*
Body length	111.83 (8.69, 69)	108.66 (9.26, 215)	122.88 (13.47, 112)	113.11 (13.67, 415)	106.04 (9.35, 113)	121.13 (13.43, 164)	125.08 (12.47, 150)
Tail length	128.09 (10.13, 57)	114.04 (8.53, 182)	127.99 (12.12, 99)	113.97 (10.48, 376)	113.50 (9.85, 102)	120.91 (11.55, 128)	129.45 (11.26, 130)
Foot length	26.20 (0.95, 69)	24.59 (1.20, 215)	28.57 (1.61, 113)	27.00 (1.48, 416)	25.44 (1.31, 111)	27.79 (1.96, 168)	28.77 (1.29, 151)
Diastema length	7.55 (0.44, 80)	7.15 (0.46, 277)	8.08 (0.57, 114)	7.89 (0.54, 440)	7.51 (0.53, 124)	7.92 (0.65, 199)	8.11 (0.56, 155)
Molar row length	5.16 (0.23, 80)	5.03 (0.23, 277)	5.48 (0.27, 112)	5.12 (0.25, 443)	5.03 (0.28, 126)	5.28 (0.25, 201)	5.82 (0.25, 155)
Pterygoid length	6.74 (0.43, 80)	6.50 (0.43, 277)	6.98 (0.56, 114)	6.64 (0.49, 443)	6.44 (0.51, 125)	7.01 (0.58, 196)	6.88 (0.56, 155)
Basioccipital length	4.30 (0.27, 80)	4.28 (0.27, 275)	4.38 (0.34, 114)	4.24 (0.32, 433)	4.18 (0.31, 123)	4.61 (0.39, 196)	4.68 (0.35, 154)
Supraoccipital length	3.94 (0.31, 78)	3.95 (0.32, 277)	4.17 (0.34, 112)	4.00 (0.35, 439)	3.93 (0.36, 123)	4.25 (0.41, 197)	4.37 (0.34, 154)
Interparietal length	3.77 (0.34, 79)	3.61 (0.34, 276)	3.77 (0.33, 114)	3.53 (0.38, 442)	3.51 (0.44, 126)	3.94 (0.45, 200)	3.69 (0.38, 155)
Parietal length	5.33 (0.34, 79)	5.29 (0.39, 277)	5.78 (0.48, 114)	5.27 (0.42, 443)	5.38 (0.45, 126)	5.47 (0.46, 202)	5.67 (0.44, 155)
Frontal length	8.76 (0.49, 80)	8.32 (0.46, 277)	8.69 (0.70, 114)	8.26 (0.53, 443)	8.06 (0.66, 125)	8.68 (0.57, 202)	9.13 (0.49, 155)
Nasal length	12.40 (0.76, 78)	12.03 (0.68, 271)	12.91 (0.88, 111)	12.64 (0.81, 422)	12.03 (0.75, 122)	13.01 (0.99, 196)	13.26 (0.86, 154)
Nasal breadth	3.63 (0.26, 75)	3.55 (0.26, 276)	3.87 (0.36, 114)	3.54 (0.29, 437)	3.41 (0.29, 125)	3.58 (0.31, 202)	4.17 (0.39, 155)
Interorbital breadth	4.38 (0.19, 80)	4.25 (0.18, 275)	4.31 (0.18, 112)	4.21 (0.18, 437)	4.19 (0.17, 125)	4.26 (0.17, 200)	4.50 (0.18, 155)
Zygomatic breadth	15.02 (0.69, 80)	14.83 (0.58, 277)	15.77 (0.74, 114)	15.09 (0.69, 442)	14.74 (0.71, 126)	15.72 (0.95, 196)	16.23 (0.79, 155)
Anterior cranial breadth	7.87 (0.51, 80)	7.43 (04.2, 275)	7.64 (0.52, 113)	7.27 (0.52, 440)	7.56 (0.58, 126)	8.35 (0.51, 202)	7.83 (0.51, 155)
Posterior cranial breadth	11.95 (0.36, 80)	11.75 (0.31, 276)	12.19 (0.44, 112)	12.15 (0.41, 440)	11.78 (0.44, 125)	12.24 (0.47, 201)	12.33 (0.40, 155)
Condyle breadth	6.73 (0.19, 78)	6.55 (0.22, 274)	6.90 (0.26, 112)	6.79 (0.30, 434)	6.62 (0.27, 116)	7.00 (0.27, 187)	7.10 (0.23, 152)
Mesopterygoid breadth	1.17 (0.13, 80)	1.05 (0.13, 275)	1.29 (0.16, 113)	1.00 (0.18, 438)	0.99 (0.20, 125)	1.06 (0.19, 193)	1.32 (0.17, 155)
Parapterygoid breadth	5.78 (0.30, 80)	5.48 (0.25, 277)	5.58 (0.33, 114)	5.44 (0.76, 442)	5.41 (0.34, 125)	5.80 (0.34, 199)	5.73 (0.25, 155)
Palate breadth	2.82 (0.20, 80)	2.70 (0.19, 277)	2.91 (0.22, 114)	2.85 (0.22, 443)	2.72 (0.22, 125)	3.04 (0.29, 202)	3.12 (0.24, 155)
M1 width	1.61 (0.06, 79)	1.62 (0.22, 275)	1.63 (0.11, 113)	1.57 (0.23, 442)	1.52 (0.10, 126)	1.52 (0.09, 179)	1.75 (0.09, 154)
Incisor width	1.71 (0.15, 80)	1.64 (0.13, 275)	1.89 (0.16, 113)	1.81 (0.17, 443)	1.74 (0.15, 126)	1.83 (0.17, 199)	2.04 (0.17, 155)
Incisor depth	1.59 (0.14, 77)	1.59 (0.12, 274)	1.56 (0.16, 114)	1.44 (0.13, 441)	1.46 (0.12, 126)	1.46 (0.13, 199)	1.79 (0.15, 154)
Incisive foramina length	7.00 (0.39, 80)	6.85 (0.38, 277)	7.57 (0.54, 114)	7.17 (0.47, 443)	6.90 (0.51, 125)	7.23 (0.55, 201)	7.73 (0.51, 155)

TABLE 1.—*Continued.*

Measurement	Taxon						
	Northern *P. limatus*	Southern *P. limatus*	*P. x. posticalis*	*P. x. chilensis*	*P. x. rupestris*	*P. d. darwini*	*P. magister*
Bullar length	5.37 (0.22, 75)	4.86 (0.20, 275)	5.07 (0.22, 113)	5.01 (0.20, 442)	4.96 (0.25, 126)	5.46 (0.23, 200)	5.18 (0.20, 155)
Zygomata length	10.05 (0.47, 79)	9.85 (0.50, 277)	10.37 (0.54, 114)	9.69 (0.49, 443)	9.55 (0.53, 126)	10.34 (0.57, 201)	10.87 (0.50, 155)
Cranial depth	8.66 (0.29, 80)	8.56 (0.34, 271)	8.99 (0.38, 114)	8.72 (0.35, 434)	8.55 (0.34, 124)	9.14 (0.51, 195)	9.15 (0.37, 154)
Rostral depth	5.73 (0.36, 80)	5.60 (0.32, 275)	5.89 (0.42, 114)	5.47 (0.38, 443)	5.36 (0.39, 125)	5.81 (0.44, 202)	6.15 (0.35, 155)
Jaw length	18.08 (1.02, 79)	17.57 (0.89, 268)	19.29 (1.12, 113)	18.45 (1.09, 427)	17.82 (1.08, 122)	18.72 (1.20, 188)	19.87 (1.14, 139)
Moment-arm of masseter	7.69 (0.41, 80)	7.50 (0.41, 274)	7.91 (0.51, 113)	7.43 (0.47, 436)	7.32 (0.46, 123)	7.92 (0.58, 193)	8.25 (0.51, 152)

two clades ranged from 7.1–9.4% ($n = 6$, $\bar{X} = 8.9\%$).

In the equal weighting analysis (Fig. 3), *Auliscomys* and *Phyllotis* were paraphyletic, with *A. pictus* and *Graomys* unexpectedly comprising one *Phyllotis* branch and *A. sublimis* basal to another. *Phyllotis osilae* was still the sister species to the *darwini* species group (now lacking *P. magister*). True *P. x. xanthopygus* and *P. darwini* formed a clade, as did *P. x. rupestris* and *P. x. chilensis*. Mean overall bootstrap values were significantly lower than the six-parameter analyses (60.2% versus 65.1%; $SD = 1.1$, $P < 0.0001$), particularly in deeper nodes.

Morphometrics and species limits.—The most thoroughly documented boundary between taxa in *Phyllotis* is that between *P. x. chilensis* and *P. x. rupestris* in the southern Peruvian departments of Arequipa, Moquegua, and Tacna, having detailed transects, large population samples (ca. 600 individuals), and repeated collections over three decades. That permitted detailed elevational transects of the contacts between the two taxa. While most morphological features were similar, two distinct incisor morphologies could be recognized. Pacific slope *rupestris* had unusually deep and narrow incisors, but incisors of *chilensis* were wide and shallow, as was characteristic of the entire species group (Fig. 4). There was no evidence of intergradation. Data from the valley above Torata (Moquequa, Peru), Department of Arequipa in Peru, and Tarapacá Province in Chile showed the same general pattern (Steppan, 1995*a*), as did cranial morphometrics and spectrophotometric measurements of pelage (J.J. Pizzimenti, pers. comm.). Additionally, morphotypes remained distinct even in sympatric colonies near sea level (geographically isolated from parent distributions and possibly colonized during floods; Steppan, 1995*a*).

SYSTEMATICS

Based on molecular analyses in this study, *P. x. rupestris,* as currently defined, is polyphyletic. Mean percent sequence divergence among *P. x. chilensis* and the Bolivian *P. x. rupestris* (2.1%) was typical for within *Phyllotis* subspecies (3.7%, $n = 15$). But mean percent sequence divergence between members of the *chilensis* clade and western *rupestris* (8.5%) was more similar to the mean among members of the species group (11.8%, $n = 51$). Most notably, specimens of *P. x. chilensis* and *P. x. rupestris* from Tarata, Peru (locality 4), were collected only 2 km apart, but showed 8.9% sequence divergence and clustered into the two different clades supported by 87–100% bootstrap values.

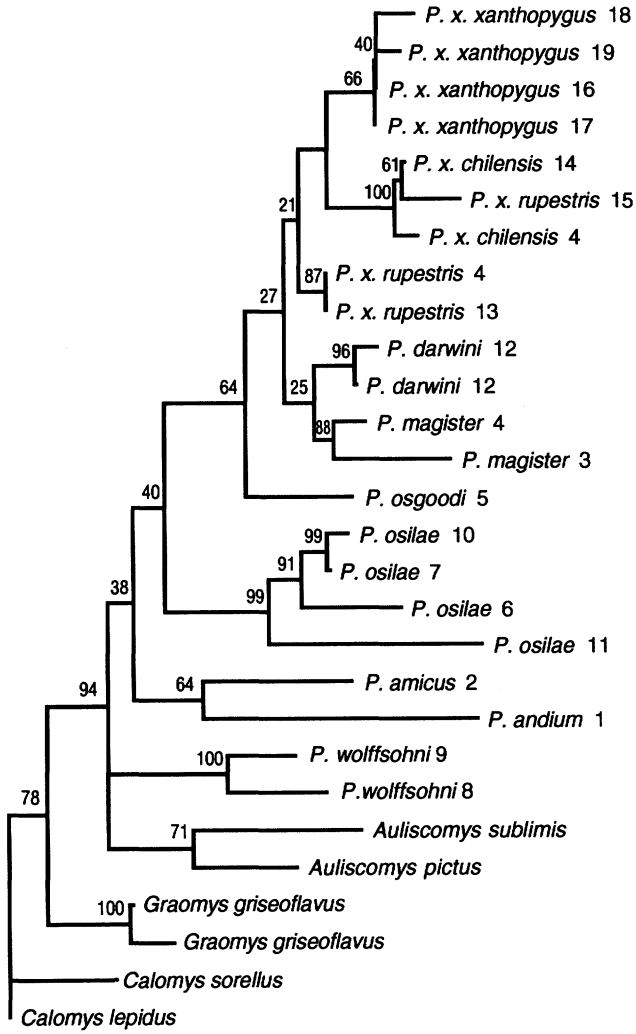

FIG. 2.—Strict consensus of the six most-parsimonious trees from the preferred six-parameter analysis. Each tree is 3,137 steps long. Numbers along the branches indicate percentage of bootstrap replicates including designated nodes. Branch lengths are proportional to the mean number of character state changes. Numbers following names of species indicate localities from Fig. 1.

This geographic discontinuity in mtDNA lineages is precisely concordant with a pattern of discontinuity in incisor morphology that is itself consistent with species level separation (Fig. 4). Pacific slope *rupestris* have relatively deep and narrow incisors, and there is no evidence of intermediates, even in sympatry. The deep incisors of Pacific slope *rupestris* are unique within *Phyllotis*. Preputial gland complement also differs between the two taxa (Steppan, 1995*a*). Thus, given the concordance of the morphological and DNA patterns and the degree of genetic divergence, southern Peruvian *rupestris* appears specifically distinct from *P. x. chilensis* and Bolivian *P. x. rupestris*. Data support elevating to species status the Pacific slope populations that have been assigned historically to *rupestris* along with *limatus*, with which they share the derived-incisor morphology. The name *limatus* is the oldest available name for

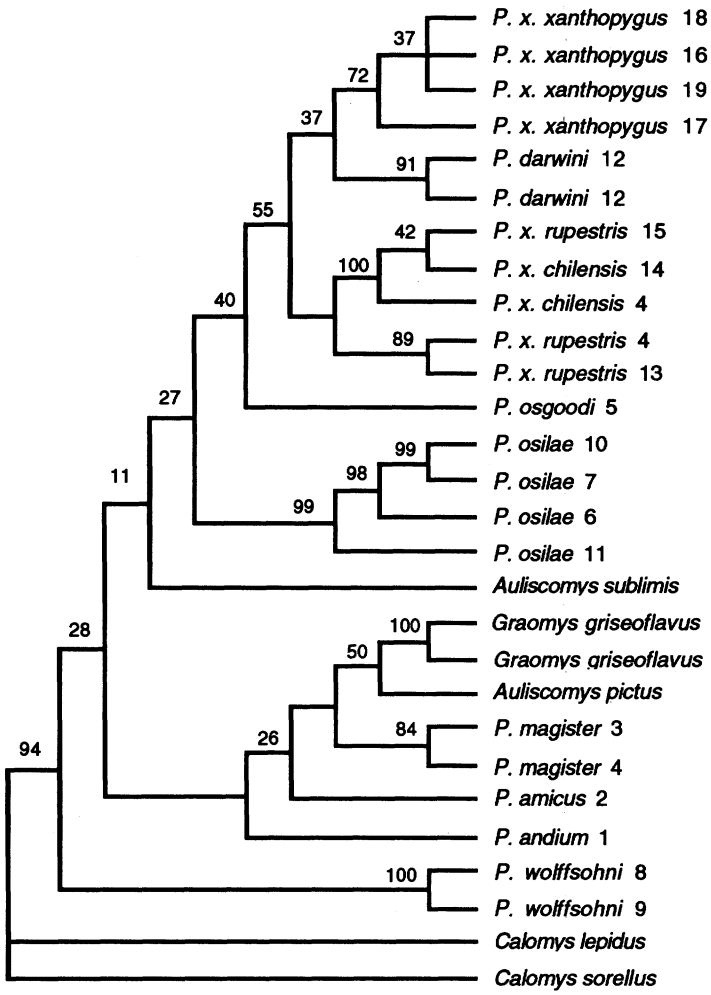

FIG. 3.—Equal-weighting analysis of raw sequence data. Strict consensus of three most-parsimonious trees, each 1,088 steps long. Numbers along branches indicate percentage of bootstrap replicates including designated nodes.

these Pacific slope populations. Older epithets *glirinus* Philippi and *lanatus* Philippi are from San Pedro de Atacama, Chile, near the southernmost population with deep incisors and could conceivably apply to these forms (the boundary with true *rupestris* is nearby). Because the Philippi types appear to be lost, it would be inappropriate to apply these names from the periphery of the range.

The type of *rupestris* is a complication. It is reportedly a mutilated skeleton that was not examined in previous revisions of the genus (Hershkovitz, 1962; Osgood, 1943; Pearson, 1958). The location is unknown, having been described imprecisely as "un trou de rocher des hautes montagnes de Cobija" (the high mountains of Cobija; Gervais, 1841:51). Cobija is on the coast in Antofagasta, Chile. Hershkovitz (1962) guessed that the type locality was in the coastal range, but Pearson (1958) considered localities further inland, just above San Pedro de Atacama, to be typical of the subspecies. The populations that Pearson specified were true *rupestris*. However, if the

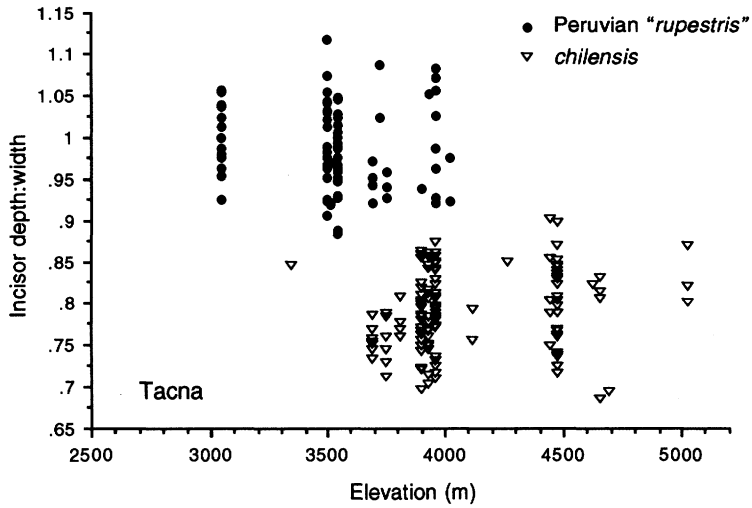

FIG. 4.—Elevational transects for incisor shape (depth : width) in the valley above Tarata, Department of Tacna, Peru.

type was from lower elevations, it conceivably could represent the deep-incisored forms of the Pacific slopes. Final resolution would require examining the type of *rupestris*, but that now seems unlikely as no specimen in Paris MNHN can be definitively associated with the type (J. Cuisin, pers. comm.). Given the uncertainty, it seems most conservative to follow Pearson (1958) and retain *rupestris* for eastern populations that occupy the majority of its range.

Phyllotis limatus Thomas

Phyllotis darwini limatus Thomas, 1912:407, Annals and Magazine of Natural History.

Phyllotis xanthopygus rupestris (Gervais), 1841: 51–53, Voyage autour du monde exécuté pendant les années 1836 et 1837 sur la corvette La Bonite commandée par M. Vaillant. Zoologie. (part)

Holotype.—Skin and skull of an old male, British Museum (BMNH) no. 0.5.7.43, collected 29 January 1900 by P. O. Simons, at Chosica, Dept. Lima, Peru, 3,000 ft.

Emended diagnosis.—A member of the *darwini* species group that can be distinguished from other members by deep and narrow upper incisors (depth at midarc >90% of width across both incisors at the cutting edge), short to moderate molar row (4.2–5.8 mm), light coloration, belly frequently white, two pairs of preputial glands, and karyotype 2n = 38. Comparative measurements are given in Table 1.

Geographic distribution.—Arid coast and Pacific slopes of the Andes in southern Peru and northern Chile from sea level to 2,500 m in the north and sea level to 4,000 m in the south (Fig. 5): departments of Arequipa, Ayacucho, Huancavelica, Ica, Lima, Moquegua, and Tacna in Peru, provinces of Antofagasta (San Pedro de Atacama) and Tarapacá in Chile.

Taxonomy.—The distinctive nature of subspecies *limatus* relative to "*rupestris*" has been well accepted. Even Hershkovitz (1962), who employed very inclusive species and subspecies concepts, retained *limatus* as a distinct subspecies. Tails have been described as relatively longer than those of "*rupestris*" (Hershkovitz, 1962; Pearson, 1958), but although they are significantly longer on average (115% body length versus 105%), variation appears to be clinal and is not a diagnostic character at the individual level. Tails of *limatus* often

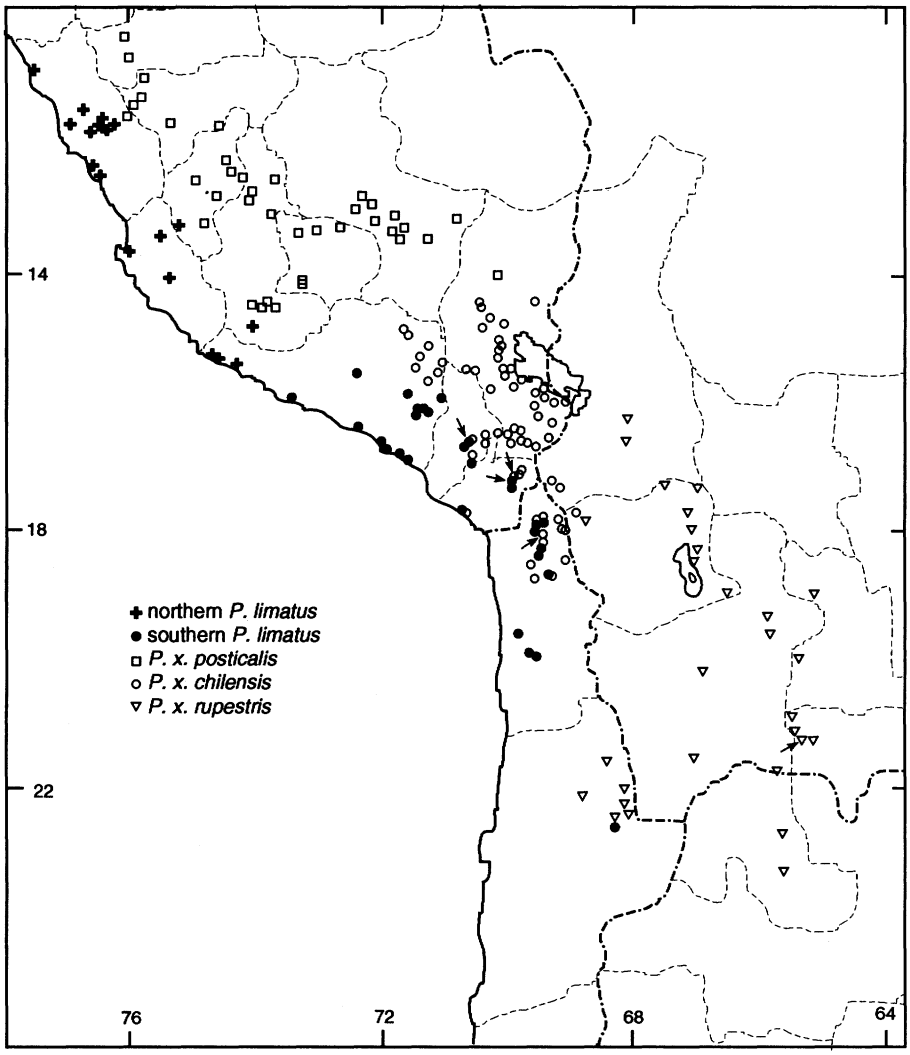

FIG. 5.—Geographic distribution of *Phyllotis limatus* and northern subspecies of *Phyllotis xanthopygus,* reflecting systematic changes presented in the text. Arrows identify localities of sequenced individuals.

have white tips, a rare trait in *Phyllotis,* but the feature is not universal. However, length of the auditory bulla (associated with ear size) shows a step-cline between northern ($\bar{X}$ = 5.4 mm) and southern populations ($\bar{X}$ = 4.8 mm). Using the break in the step-cline near 16°N latitude to define the boundary between these sets of populations moves the coastal section of the boundary 250 km to the northwest of its historical location (cf. Hershkovitz, 1962). No name for these Pacific slope "*rupestris*" populations currently exists, and further research may indicate that subspecific status is warranted. The distinctiveness of *limatus* may have been overemphasized by previous workers because they compared it to a composite taxon, "*rupestris.*" Therefore, at this time, I will not formalize the taxonomy and will instead categorize populations as "northern *limatus*" and "southern *limatus,*" referring to historical *limatus* and the

populations removed from *rupestris,* respectively.

Discussion

Phylogenetic relationships.—Well supported hypotheses of relationship are few in the phyllotines, but three key hypotheses involving taxa in this study include a monophyletic *Auliscomys* (Pearson and Patton, 1976; Steppan, 1993, 1995*b*; Walker and Spotorno, 1992), a *Calomys* that may be monophyletic or paraphyletic, but not polyphyletic (Steppan, 1993, 1995*b*), and a *darwini* species group (Steppan, 1993, 1995*b*). These three hypotheses are found in the six-parameter analysis. The equal-weighting (Fig. 3) and amino acid (Steppan, 1995*a*) analyses failed to recover all three of these hypotheses.

Starting with the most basal nodes, this analysis refutes a close relationship between *Phyllotis* and *Graomys* and specifically between *P. amicus* and *Graomys.* Morphology-based phylogenetic analyses led me to suggest that *P. amicus* and *P. gerbillus* might be related more closely to the *Graomys* group (*Eligmodontia* and *Graomys,* including *Andalgalomys* in synonymy) than to other members of *Phyllotis* (Steppan, 1993, 1995*b*). However, basal branches of *Phyllotis* were poorly resolved in the morphological analysis and many alternative arrangements were nearly as optimal (Steppan, 1995*b*). In the preferred six-parameter analysis, the node joining *Phyllotis* and *Auliscomys* to the exclusion of *Graomys* and *Calomys* was found in 94% of bootstrap replicates (Fig. 2). Therefore, this analysis also contradicts the hypotheses that *Graomys* is related more closely to the *darwini* species group and *Auliscomys* than it is to *P. amicus* (Braun, 1993), or that *Auliscomys* and *Graomys* are sister taxa (Reig, 1986). The hypothesis of Reig (1986) finds weak support in the equal-weighting analysis (Fig. 3), but that analysis also presents the incongruous topology of splitting the species pair *A. pictus* and *A. sublimis* far apart.

No support is found for removing *P. amicus* to the newly resurrected *Paralomys* as was done by Braun (1993) and weakly supported by my morphological analysis (Steppan, 1993). Instead, the six-parameter analysis moderately supports *P. amicus* as closely related to *P. andium* and that *Phyllotis* may be monophyletic. The status of *wolffsohni* is uncertain, with its position relative to *Auliscomys* unresolved (Fig. 2). The paraphyly of *Phyllotis* with respect to *wolffsohni* in some of the most-parsimonious trees is consistent with my morphological analyses, which placed *wolffsohni* near the base of a radiation that included the *Reithrodon, Auliscomys,* and *Andinomys* groups (Steppan, 1995*b*), although supported by very low bootstrap values (<15%). Confident assessment of *Phyllotis* monophyly from this study is compromised by the limited sampling from the other 12 phyllotine genera.

Pearson and Patton (1976) proposed that *P. osilae* possessed the ancestral karyotype for phyllotines in general and *Phyllotis* in particular (all acrocentric, 2n = 70), and thus occupied the basal position within a paraphyletic *Phyllotis.* Each of the figured analyses in this study place other *Phyllotis* species with lower diploid numbers basal to *P. osilae* (usually *P. amicus* 2n = 38, *andium* 2n = 64, and *wolffsohni* 2n = 54). The shortest trees that place *osilae* basal to the other *Phyllotis* are 31 steps longer than the most-parsimonious six-parameter trees overall (22 steps longer in equal weighting analyses). Mapping karyotypes onto the phylogeny (Fig. 2) indicates possible convergence on the 2n = 38 karyotype shared by *P. amicus* and most of the *darwini* species group. Alternatively, 2n = 38 could be the plesiomorphic karyotype for *Phyllotis* excluding *wolffsohni,* as that reconstruction is not much less parsimonious given the difficulties in hypothesizing chromosomal transformation series. Simple Robertsonian fusion, as proposed by Pearson and Patton (1976) and Gardner and Patton (1976), and subsequently used to polarize chromosomal

phylogenies among phyllotines (e.g., Vitullo et al., 1990; Zambelli et al., 1994), is contradicted as the primary model of chromosome evolution, and may be of opposite polarity in some instances.

This study provides moderate support for both a *darwini* species group and a *Phyllotis* sensu stricto clade (Steppan, 1995*b*) that includes the *darwini* species group plus *osilae*. The preferred six-parameter analysis also agrees with dendrograms calculated from allozyme data that place *P. osgoodi* outside a clade consisting of *P. darwini, P. x. xanthopygus,* and *P. x. chilensis* (Spotorno and Walker, 1983). Electrophoretic dendrograms of Spotorno and Walker (1983) differ from the DNA sequence tree in indicating that *P. x. chilensis* is related more closely to *P. darwini* than to true *P. x. xanthopygus*. Firm conclusions regarding relationships within the *darwini* species group can not be made because of the poor resolution of the internal nodes, as reflected by the low bootstrap values.

Prior studies also have been unable to draw strong hypotheses about the *darwini* species group, at least relative to the taxa included in this study. The cladogram in Braun (1993) is generally discordant with this study, presenting the following topology for a paraphyletic *Phyllotis*: (*andium* (*osilae* (*wolffsohni* (*Auliscomys*-plus eight other phyllotine genera), (*magister, xanthopygus*)))). Unfortunately, the most-parsimonious tree or trees are not reported in that study, only a composite from subset analyses. Pearson and Patton (1976) recognized a clade that included *amicus, magister,* and *xanthopygus* but excluded *wolffsohni, andium,* and *osilae*. This study provides no support for inclusion of *amicus* in the former clade.

Species limits in Phyllotis xanthopygus.—The molecular data by itself would be insufficient to hypothesize specific separation between Peruvian "*rupestris*" and *P. x. chilensis*. Several factors independent of reproductive isolation can cause phylogenetic analyses based on single genes to segregate fully interbreeding populations to different lineages, causing biological species to appear paraphyletic (Avise et al., 1990; Patton and Smith, 1994). One factor is introgression of mitochondrial haplotypes due to post-isolation hybridization or secondary contact. Another possible cause for this observed discontinuity is differential fixation of ancestral polymorphisms (Avise et al., 1987), also known as lineage sorting. Over time, effects of lineage sorting should disappear, and taxa will become monophyletic with respect to the gene genealogy (Neigle and Avise, 1986; Pamilo and Nei, 1988). Conspecific populations are likely to be so recently differentiated or isolated that apparent paraphyly will be common. In this case, the precise concordance between the mtDNA phylogeny and morphological data makes the argument for specific separation compelling.

Pearson (1958) noted a clear distinction in size and darkness between *chilensis* and Pacific slope "*rupestris*" [= southern *limatus*], and the presence of apparent intermediates in a narrow transition zone (2–3 km) led him to treat the populations as two subspecies of *P. darwini*. Hershkovitz (1962) examined the same material but concluded that there was a smooth altitudinal cline in thickness and length of the darker guard hairs and he considered *chilensis* to be only a junior synonym of the subspecies *rupestris*. However, more detailed morphometric analyses clearly demonstrate specific separation of these taxa (Steppan, 1995*a*, this study). Thus, *P. xanthopygus* becomes limited to high elevations (>2,500 m) and the eastern slopes and the foothills. Additional work is needed to test if the distinctive subspecies *posticalis* and *xanthopygus* are truly conspecific with the central complex of *chilensis-rupestris-vaccarum-ricardulus*.

Additional insights into species limits and a possible explanation for the morphological divergence can be found in a comparison of diets and cranio-mandibular morphology between *chilensis* and Peruvian *ru-*

pestris. In their study of dietary and morphometric variation in Peruvian rodent communities, Pizzimenti and de Salle (1980:274) found that "the morphological variation of this group [*Phyllotis*] can be explained on the basis of changes in the trophic apparati and suggests that interspecific variation reflects, to some extent, feeding niches." Pizzimenti and de Salle (1980) found that Peruvian *rupestris* and *chilensis* had markedly different diets. Peruvian *rupestris* ate less seed and more insects while *chilensis* ate more of the abrasive grasses and a higher diversity of forbs. Morphological divergence between these two taxa may be associated with dietary specializations.

Biogeography and speciation.—Two partitions are apparent in *Phyllotis. Phyllotis amicus* and *P. andium* are hypothesized to be sister species (Fig. 2) and are the northern-most species sampled in this study (Fig. 1a). The western cordillera of the Andes appears to divide basal members of the *darwini* species group (*osgoodi, darwini, magister,* Peruvian *rupestris* [=*limatus*]) from an altiplano-eastern slope clade (*chilensis,* Bolivian *rupestris, xanthopygus*). Further taxonomic sampling is needed to confirm these patterns. For example, does the northern clade also include the distinctive *P. gerbillus,* found only along the desert coast of northern Peru and morphologically associated with *P. amicus,* or *P. haggardi,* the northern-most species from Ecuador, which may be most closely related to *P. osilae* (Steppan, 1995*b*)? Additionally, does *P. caprinus* belong to the eastern clade? *Phyllotis caprinus* is a member of the *darwini* species group from the eastern slopes of the Andes in southern Bolivia and northern Argentina, but insufficient DNA sequence was obtained for analysis.

Absence of robust structure among basal branches of the *darwini* species group suggests that divergence of mtDNA lineages leading to extant taxa occurred over a short period of time relative to the age of the species group. The biogeographic pattern in *Phyllotis* suggests a history of peripatric speciation, with a widely distributed central species (*xanthopygus*) surrounded by species with small ranges on the periphery (e.g., *limatus, caprinus, darwini, osgoodi, magister, definitus*). In peripatric speciation, species that formed from peripheral isolates initially would be related more closely to some members of the central species than those members are to other populations of the central species. The expected phylogenetic pattern would be paraphyletic ancestral species (Patton and Smith, 1994; Theriot, 1992). A similar pattern may be expected from repeated range contractions and expansions, where alternating periods of isolation of populations and reestablishment of gene flow obscures the sequence of phenotypic differentiation. Such a biogeographic history may be expected in the topographically complex Andes under climatic fluctuations of the Pleistocene. Interestingly, the preferred mtDNA phylogeny does not coincide with the expectation of a widespread and possibly paraphyletic species occupying a basal position relative to the peripheral species (Theriot, 1992). Instead, *P. xanthopygus* is monophyletic and distal relative to the geographically peripheral species, suggesting a sequential pruning of peripheral ranges. A more likely model, given the Pacific slope distribution of the basal branches of the *darwini* species group, would be for successive waves of expansion by *xanthopygus* from the east, each followed by divergence and reproductive isolation of populations of the Pacific slope. If those waves of expansion were not evenly distributed temporally but clustered early in the history of the species group and if the Pacific slope species were each derived from different geographic lineages of *xanthopygus* (cf. *darwini* and *limatus*), the expected result would be relatively poor resolution of the basal nodes as seen here. More detailed geographic sampling and examination of nuclear genes are needed to test this model.

Frey (1993) argued that when the widespread central species is relatively apomor-

phic, the phylogenetic pattern was consistent with the centrifugal speciation model (CSM). In the CSM, new phenotypes are more likely to be fixed in central populations due to a large source pool, more optimal and diverse habitats, and other factors. If poor resolution within the *darwini* species group reflects the true phylogenetic pattern rather than insufficient data, then the results under the CSM would indicate sequential colonization from isolate to isolate (Frey, 1993). However, because branch lengths leading to the central species (*xanthopygus*) are not significantly longer than those of the peripheral species, the data are not fully congruent with the CSM expectations. Under the peripheral isolates model (PIM), a polytomous pattern would be expected given independent colonizations or by range subdivision (i.e., range retraction or microvicariance—Frey 1993). Additional data are needed to clarify the results.

Poor resolution within the *darwini* species group resembles that seen among a group of central to north Andean *Akodon* mice with restricted distributions (Smith and Patton, 1993). Although Smith and Patton (1993) found several of the species to be paraphyletic or polyphyletic, the species here are relatively well characterized, at least given the limited sampling. Smith and Patton (1993) suggested that retention of ancestral polymorphisms or lineage sorting may have been obscuring the "true" phylogenetic relationships within a group that underwent a rapid period of speciation after episodic glaciations.

The pattern in *osilae* contrasts with that in the *darwini* species group by exhibiting strong intraspecific phylogenetic structure. The pattern of relationship is (((central Bolivia, northern Bolivia), southern Peru), southern Bolivia). The cause of the pattern is unclear, but because the range of *osilae* runs in a relatively narrow strip along the eastern slope of the Andes (Fig. 1a), and *osilae* is generally limited to bunch grass (*Stipa ichu*) habitats, gene flow may be restricted.

Conclusions

As was found in the phylogenies based on morphology, interspecific relationships within *Phyllotis* are not well resolved. Nonetheless, my analysis of cytochrome *b* sequence does provide several hypotheses. Contrary to some evidence from morphological phylogenies, *P. amicus* is not related more closely to *Graomys* than to other *Phyllotis*. Instead, *Graomys* is basal to a clade that includes *Phyllotis* and *Auliscomys,* and *P. amicus* is related closely to *P. andium.* Both the *darwini* species group (consisting of *P. darwini, magister, osgoodi,* and *xanthopygus*) and *Phyllotis* sensu stricto (consisting of the *darwini* species group plus *osilae*) hypothesized by the morphological phylogenies are supported by this data set. *Phyllotis xanthopygus* appears to be composite with a geographic discontinuity in mtDNA lineages corresponding to a discontinuity in morphology. Populations currently assigned to *P. x. rupestris* from the Pacific slopes of the Andes in Peru and northern Chile are likely conspecific with *limatus* to the north. Together, these Pacific slope forms with derived incisor morphology are elevated to the species *P. limatus.* The preferred analysis indicates a northern *Phyllotis* clade and a clade distributed over the altiplano and eastern Andean slope. The biogeographic pattern is most consistent with successive colonization of western slopes, possibly by range expansion and contraction over a short period of time relative to the age of the clade. However, support for internal nodes is weak, and sequencing of additional genes, along with more complete taxonomic sampling of *Phyllotis* species and the remaining *P. xanthopygus* subspecies, is needed to test these hypotheses. In particular, intraspecific relationships of the widespread *P. xanthopygus* are likely to be very complex, and further evidence for paraphyly might be expected.

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Literature Cited

Arévalo, E., S. K. Davis, and J. W. Sites, Jr. 1994. Mitochondrial DNA sequence divergence and phylogenetic relationships among eight chromosome races of the *Sceloporus grammicus* complex (Phrynosomatidae) in central Mexico. Systematic Biology, 43:387–418.

Avise, J. C., C. D. Ankney, and W. S. Nelson. 1990. Mitochondrial gene trees and the evolutionary relationships of mallard and black ducks. Evolution, 44: 1109–1119.

Avise, J. C., et al. 1987. Intraspecific phylogeography: the mitochondrial bridge between population genetics and systematics. Annual Review of Ecology and Systematics, 18:489–522.

Bibb, M. J., R. A. Van Etten, C. T. Wright, M. W. Walberg, and D. A. Clayton. 1981. Sequence and gene organization of mouse mitochondrial DNA. Cell, 26:167–180.

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.

Ellerman, J. R. 1941. The families and genera of living rodents. Family Muridae. British Museum of Natural History, London, United Kingdom, 2:1–690.

Frey, J. K. 1993. Modes of peripheral isolate formation and speciation. Systematic Biology, 42:373–381.

Gardner, A. L., and J. L. Patton. 1976. Karyotypic variation in oryzomyine rodents (Cricetinae) with comments on chromosomal evolution in the neotropical cricetine complex. Occasional Papers of the Museum of Zoology, Louisiana State University, 49: 1–48.

Gervais, P. 1841. Mammifères. Pp. 1–68, *in* Voyage autour du monde exécuté pendant les années 1836 et 1837 sur la corvette La Bonite commandée par M. Vaillant. Zoologie (E. A. Soulet, eds.). Paris, France, 334 pp.

Hershkovitz, P. 1962. Evolution of Neotropical cricetine rodents (Muridae) with special reference to the phyllotine group. Fieldiana: Zoology, 46:1–524.

Hillis, D. M., M. W. Allard, and M. M. Miyamoto. 1993. Analysis of DNA sequence data: phylogenetic inference. Methods in Enzymology, 224:456–487.

Kimura, M. 1980. A simple model for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. Journal of Molecular Evolution, 16:111–120.

Maddison, W. P., and D. R. Maddison. 1992. MacClade: analysis of phylogeny and character evolution. Version 3.0. Sinauer Associates, Inc., Publishers, Sunderland, Massachusetts, 398 pp.

Maniatis, T., E. F. Fritsch, and J. Sambrook. 1982. Molecular cloning. A laboratory manual. Cold Spring Harbor, New York, 545 pp.

Meserve, P. L. 1981. Trophic relationships and small mammals in a Chilean semiarid thorn scrub community. Journal of Mammalogy, 62:304–314.

Neigle, J. E., and J. C. Avise. 1986. Phylogenetic relationships of mitochondrial DNA under various demographic models of speciation. Pp. 515–534, *in* Evolutionary processes and theory (E. Nevo and S. Karlin, eds.). Academic Press, New York, 786 pp.

Osgood, W. H. 1943. The mammals of Chile. Field Museum of Natural History, Zoological Series, 30: 1–268.

———. 1947. Cricetine rodents allied to *Phyllotis*. Journal of Mammalogy, 28:165–174.

Pamilo, P., and M. Nei. 1988. Relationships between gene trees and species trees. Molecular Biology and Evolution, 5:568–583.

Patton, J. L., and M. F. Smith. 1994. Paraphyly, polyphyly, and the nature of species boundaries in pocket gophers (genus *Thomomys*). Systematic Biology, 43: 11–26.

Pearson, O. P. 1958. A taxonomic revision of the rodent genus *Phyllotis*. University of California Publications in Zoology, 56:391–477.

Pearson, O. P., and J. L. Patton. 1976. Relationships among South American phyllotine rodents based on chromosome analysis. Journal of Mammalogy, 57: 339–350.

Pearson, O. P., and C. P. Ralph. 1978. The diversity and abundance of vertebrates along an altitudinal gradient in Peru. Memorias del Museo de Historia Natural "Javier Prado," 18:1–97.

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.

Reig, O. A. 1986. Diversity patterns and differentiation of high Andean rodents. Pp. 404-439, *in* High altitude tropical biogeography (F. Vuilleumier and M. Monasterio, eds.). Oxford University Press, London, United Kingdom, 649 pp.

REISE, D., AND W. S. VENEGAS. 1987. Catalogue of records, localities and biotopes from research work on small mammals in Chile and Argentina. Gayana, Zoology, 51:103–130.

SANGER, F., S. NICKLON, AND A. R. COULSON. 1977. DNA sequencing with chain terminating inhibitors. Proceedings of the National Academy of Sciences, 74:5463–5467.

SMITH, M. F., AND J. L. PATTON. 1991. Variation in mitochondrial cytochrome *b* sequence in natural populations of South American akodontine rodents (Muridae: Sigmodontinae). Molecular Biology and Evolution, 8:85–103.

———. 1993. The diversification of South American murid rodents: evidence from mitochondrial DNA sequence data for the akodontine tribe. Biological Journal of the Linnean Society, 50:149–177.

SPOTORNO, A. E. 1976. Análisis taxonómico de tres especies altiplánicas del género *Phyllotis* (Rodentia: Cricetidae). Anales del Museo de Historia Natural, Valparaiso, 9:141–161.

SPOTORNO, A. E., AND L. I. WALKER. 1983. Análisis electroforético de dos especies de *Phyllotis* en Chile Central y sus híbridos experimentales. Revista Chilena de Historia Natural, 56:51–59.

STEPPAN, S. J. 1993. Phylogenetic relationships among the Phyllotini (Rodentia: Sigmodontinae) using morphological characters. Journal of Mammalian Evolution, 1:187–213.

———. 1995*a*. Phylogenetic relationships of the phyllotine rodents (Sigmodontinae) and the evolution of phenotypic patterns of covariation in *Phyllotis*. Ph.D. dissertation, University of Chicago, Illinois, 136 pp.

———. 1995*b*. Revision of the leaf-eared mice Phyllotini (Rodentia: Sigmodontinae) with a phylogenetic hypothesis for the Sigmodontinae. Fieldiana: Zoology, 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.

SWOFFORD, D. L. 1993. PAUP: Phylogenetic analysis using parsimony. Version 3.1.1. Illinois Natural History Survey, Champaign, 257 pp.

THERIOT, E. 1992. Clusters, species concepts, and morphological evolution of diatoms. Systematic Biology, 41:141–157.

VITULLO, A. D., M. B. ESPINOSA, AND M. S. MERANI. 1990. Cytogenetics of vesper mice, *Calomys* (Rodentia; Cricetidae): Robertsonian variation between *Calomys callidus* and *Calomys venustus*. Zeitschrift für Säugetierkunde, 55:99–105.

WALKER, L. I., AND A. E. SPOTORNO. 1992. Tandem and centric fusions in the chromosomal evolution of the South American phyllotines of the genus *Auliscomys* (Rodentia, Cricetidae). Cytogenetics and Cell Genetics, 61:135–140.

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.

ZAMBELLI, A., L. VIDAL-RIOJA, AND R. WAINBERG. 1994. Cytogenetic analysis of autosomal polymorphism in *Graomys griseoflavus* (Rodentia, Cricetidae). Zeitschrift für Säugetierkunde, 59:14–20.

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APPENDIX I

Specimens sequenced.—Numbers in brackets correspond to the locality numbers identified in Fig. 1. Abbreviations are as follows: FMNH, The Field Museum; LCM, Laboratorio de Citogenetica Mammiferos, Universidad de Chile; MFS, uncatalogued material, Margaret F. Smith, Museum of Vertebrate Zoology, University of California, Berkeley; MSB, Museum of Southwestern Biology, University of New Mexico.

Auliscomys sublimis PERU. Arequipa: Chivay, 5 km S (FMNH 107711).

Phyllotis amicus [2] PERU. Arequipa: Caraveli, Atiquipa (FMNH 107392).

Phyllotis andium [1] PERU. Lima: Lima, 1/2 mile NNE, Santa Eulalia canyon (FMNH 107361).

Phyllotis darwini darwini [12] CHILE. Coquimbo: Parque Nac. Fray Jorge (MSB 69976, 69977).

Phyllotis magister magister [4] PERU. Tacna: Tarata, 3 km NE (FMNH 107611). [3] PERU. Arequipa: Chivay, 5 km NE (FMNH 107691).

Phyllotis osgoodi [5] CHILE. Tarapacá: Parinacota (LCM 638).

Phyllotis osilae osilae [6] PERU. Puno: Chicuito, Ilave (FMNH 107870). [10] BOLIVIA. Chuquisaca: Tarabuco, 2 km N, 3 km E (MSB 63366). [7] BOLIVIA. La Paz: Miña Lourdes (MSB 65839). [11] BOLIVIA. Tarija: Serrania Sama (MSB 67256).

Phyllotis wolffsohni [9] BOLIVIA. Chuquisaca: Padilla, 9 km W (MSB 63364). [8] BOLIVIA. Santa Cruz: Quiñe, 17 km S (MSB 67270).

Phyllotis xanthopygus chilensis [14] CHILE. Tarapacá: Chapiquina, 10 km S (FMNH 133830). [4] PERU. Tacna: Tarata, 5 km NE (FMNH 107606).

Phyllotis xanthopygus rupestris [15] BOLIVIA. Tarija: Iscayachi, 4.5 km E (MSB 67261). [13] PERU. Moquegua: Torata, 16 km NE (FMNH 107476). [4] PERU. Tacna: Tarata, 3 km NE (FMNH 107615).

Phyllotis xanthopygus xanthopygus [16] ARGENTINA. Río Negro: Comallo (MFS 1324).

APPENDIX II

Measurements were made of skulls and jaws from specimens of *Phyllotis* belonging to the following collections: American Museum of Natural History (AMNH), The Field Museum (FMNH), Laboratorio do Citogenética Mamíferos, Facultad de Medicina, Universidad de Chile (LCM), Museum of Comparative Zoology, Harvard (MCZ), Museo Nacional de Historia Natural, Santiago, Chile (MNHN), The Museum, Michigan State University (MSU), Museum of Vertebrate Zoology, University of California, Berkeley (MVZ), University of Michigan, Museum of Zoology (UMMZ), National Museum of Natural History, Smithsonian Institution (USNM).

Phyllotis magister (*n* = 155). CHILE. Tarapacá: Belen (USNM 541798, 541799); Putre (LCM 196, 251; USNM 541790, 541794–541797). PERU. Arequipa: Chihuata, 2 mi. E (MVZ 116680–116682); Chivay (MVZ 174035–174038), 5 km NNE (FMNH 107683, 107690–107692); Mt. Misti (FMNH 35360); Tingo (AMNH 74152); Yura (FMNH 49475). Huancavelica: (MVZ Ticrapo, 2 km E (MVZ 136335, 136336). Lima: Yauyos, 8 mi. NE (MVZ 137662, 137663, 141412). Moquegua: Ilubuya, 3 km NE Torata (FMNH 107417, 107460, 107469, 107480, 107481); Toquepala, 5 mi. NW (MVZ 145610); Rio Torata, 15 km NE Torata (FMNH 107436; MVZ 115792, 115794, 115795). Tacna: Moro Sama, 65 km W Tacna (MVZ 143705–143712, 143717, 143739, 143747, 143749); Tarata (FMNH 107611–107613, 107616, 107620, 107622, 107623, 107625, 107629, 107631, 107653, 107654; MVZ 141513–141534, 141536, 141537, 115874–115884, 139384–139432, 139438–139445).

Phyllotis darwini darwini (*n* = 201). CHILE. Aconcagua: Longotoma (FMNH 22355); Papudo (FMNH 22680–22685, 23884–23886, 24062). Antofagastsa: Paposo (MVZ 119158–119161, 119163–119189, 119191–119199), 4 mi. E (MVZ 150058). Atacama: Caldera, 10 mi. N (MVZ 150056); Quebrada La Huerta, Alto de Carmen (MNHN 1457); Rio Carmen, 5 km SSE Alto de Carmen (MNHN 1279); Vallenar (MVZ 118658, 118659), 10 mi. S, Estancia Romero (MVZ 150057). Coquimbo: Asentamiento Ceeres, La Serena (MNHN 973, 974, 975); Huentelauquen (FMNH 133894, 133896); Illapell, 7.5–10 km E (USNM 541756, 541758); Las Breas (LCM 674); La Serena, Rio Limon (LCM 365); Las Palmas, 95 km N Los Vilos (MVZ 150060); Las Tacas (LCM 220, 221, 233, 234, 258, 262, 263, 693, 790); Los Villos, 4 km S (USNM 541759); Parque Nacional Fray Jorge (FMNH 119512, 133874, 133877, 133881, 133894; MNHN 319; 1212, 1214–1220, 1222, 1223, 1227; MVZ 118662); Cerro Potrerillos, 4 km E Guanaqueros (MVZ 150059); Puerto Los Molles, 10 km N (FMNH 119507–115909, 119511); Romero (FMNH 22325–22329). Linares: Palo Negro, 8 km N Quirihue (MNHN 656, 659, 732–735). Santiago: Auco (LCM 723); Bocatoma (AMNH 391807); 2.5 km NE Cerro Manquehue (FMNH 119491–119493, 119496–119500, 119504, 119505); Farellones (LCM 737, 741, 746); Fundo Santa Laura (MVZ 150061–150063, 150065, 150066); La Dehesa (LCM 318); Las Condes (AMNH 391805); Los Dominicos (MNHN 535, 538, 544, 548); Quebrada de la Plata, Maipu (MNHN 643, 644, 646, 665, 677–680, 747, 753, 756); Rinconada de Maipu (AMNH 541761); San Cristobal (FMNH 35901, 35902); Til Til (FMNH 119505, 119506; MNHN 977). Talca: Siete Tazas, 50 km E Molina (USNM 541787–541789). Valparaíso: Buen Retiro, Calera (FMNH 23889–23890); 4.5 km N Caleta Los Molles (MNHN 573); Cuesta Las Chilcas, Com. Llay Llay (MNHN 1234, 1235, 1273, 1456); La Rojas (FMNH 23882, 23883) Olmue (FMNH 22347, 22348); Palmilla (FMNH 24394); Penuelas (MNHN 1166, 1167, 1169, 1364, 1365, 1370); 7 km SSE Papudo (MNHN 708); Quilpue (MSU 2102); Reserva Forestal Penuelas (MNHN 1090, 1094,1102, 1131, 1133, 1172, 1174, 1183, 1186).

Northern *Phyllotis limatus* (*n* = 86). PERU. Arequipa: Bella Union, 8 mi. NNW (MVZ 145562–145581); Chala, 16 km ESE (MVZ 139311, 139312); La Planta (MVZ 145582, 145583); Ayacucho: Nazca, 35 mi. ENE (MVZ 138091–138094). Huancavelica: Ticrapo, 2 km E, Pisco Valley (MVZ 136309–136311, 136313–136319). Ica: Hac. San Jacinto (FMNH 53162, 53163); Humay, 3 km E, Pisco Valley (MVZ 136320–136325); Pisco, 10 km SSE (MVZ 136326–136328). Lima: Chilca, 8 mi. SE (MVZ 138089, 138090); Chillon Valley, 2 mi. SW Quives (MVZ 136329, 136330); Chosica (FMNH 53164, 53169, 53170; MVZ 120058–120063, 120066); Nana (MVZ 120066); Oscolla (FMNH 53056); Pucusana (MVZ 137657, 137658, 138715, 138725, 139213, 138214); Ri-

mac Valley (MVZ 120067–120071); San Bartolome Station (MVZ 119966, 120026, 120072, 120073); Santa Eulalia (MVZ 120074–120078); Yangas (MVZ 136332).

Southern *Phyllotis limatus* (*n* = 328). CHILE. Tarapacá: Belen (USNM 541748); Canchones, SE Pozo Almonte (MNHN 1416, 1418, 1421); Caritaya, 75 mi. SE Arica (MVZ 116792); Cruce (MNHN 4431); La Guaica, SE Pozo Almonte (MNHN 1396, 1397, 1400, 1403; USNM 541763, 541766); Putre (FMNH 133837, 133839, 133844, 133846–133848, 133851; MNHN 4382, 4394; USNM 541747, 542255, 542267); Quebrada El Condor (MNHN 1207); Rio Tingamar (USNM 541750, 541751); San Perdo de Atacama, 5 mi. S (MVZ 150067–150069); Zapahuira (MNHN 1208). PERU. Arequipa: Arequipa (FMNH 35358, 35359), 7 km E (MVZ 115779–115785), 12 km E (MVZ 136300–136307), 12 km SSW (MVZ 115786–115789), 15 km E (MVZ 139560), 28 km N by rd., Loma Huanuconcha (MVZ 174024, 170432–170434); Atico, 3 mi. W (MVZ 114704, 114705, 116676, 116677); Balneario de Jesus (FMNH 50991–51002, 53161); Camana, 5 mi. ENE (MVZ 143701–143704); Chucarapi, Tambo Valley (MVZ 116678, 116679); Mitarani (MVZ 145584, 145585); Molendo, 3 mi. N (MVZ 145586–145596); Salinas (FMNH 49480–49488, 49637); Yura (FMNH 49451–49479, 49608, 49748). Moquegua: Toquepala, 5 mi. NW (MVZ 145597–145608); Torata, 3 km N to 20 km NE (FMNH 107403–107411, 107413–107415, 107418, 107420–107427, 107429–107432, 107435, 107437, 107438, 107440, 107442, 107443, 107444, 107476, 107477, 107482, 107484; MVZ 115790, 115791, 115793, 115796–115800). Tacna: Moro Sama, 65 km W Tacna (MVZ 141492–141500, 141501–141509, 143713–143716, 143718–143738, 143741, 143742, 143744, 143750, 143751, 143757, 143758) Tarata, 16 km S to 8 km NE (FMNH 107574, 107575, 107598, 107602, 107603, 107605, 107609, 107610, 107614, 107615; MVZ 115837, 115838, 115840–115846, 116788, 139313–139333, 139335–139341, 139348, 139365, 139369, 139370, 139376, 139378, 141423, 141634–141636, 141639–141651, 141653–141659, 141661–141666); Rio Torata, 10 km NE Torata (MVZ 115799, 115800), 15 km NE Torata (MVZ 115790, 115791, 115793, 115796–115798).

Phyllotis xanthopygus chilensis (*n* = 525). BOLIVIA. Oruruo: Sajama, 40 km E, 18° 20′ S 68° 36′ W (AMNH 262972, 272976); Mt Sajama region, Pr. Caranges (FMNH 53614–53616). CHILE. Tarapacá: Belen (USNM 541749); Caritaya, 75 mi. SE Arica (MVZ 116782, 116784, 116785); Chapiquina, 10 km S, 72 km E Arica (FMNH 133830, 133832, 133835, 133836; MNHN 4373); Choquelimpe, Putre (MNHN 1218); Cotacotani (MNHN 431, 432); Cruce, 5 km S (MNHN 4419); Guallatiri (USNM 541754); Lake Chungara (USNM 541744), SW shore (FMNH 133856); Minita (MNHN 670, 952); Parinacota (FMNH 133853–133855; MNHN 4407; USNM 391801, 391804, 542257, 542258); Putre (FMNH 22697–22699, 22701–22705; USNM 542259, 542260, 542265, 542266, 542568, 542269); Timar (USNM 391808). PERU. Arequipa: Cailloma (FMNH 49507–49515, 49519–49525, 49533, 49626–49630, 49632–49635; MVZ 174039); Cailloma, 16–20 km SE (FMNH 107757, 107759, 107773, 107775) Callalli, 15 km S (MVZ 174028–174031); Chiguata, 8–10 km E (FMNH 107778–107782, 107778–107790, 107796, 107798, 107800, 107802); Chivay (FMNH 107668, 107672, 107677, 107682, 107685, 107686, 107695, 107697, 107706, 107708, 107715, 107730); Huayarco, 52 mi. ENE Arequipa (MVZ 115807, 115884, 116124–116126); Imata, 6 mi. SSE (MVZ 116127); Salinas, 22 mi. E Arequipa (MVZ 116128, 116129); Sibayo (FMNH 39508, 39509, 39511–39513); Sumbay (FMNH 49501–49506, 49516–49518, 49609, 49610, 49612, 49625; MVZ 174025–174027). Moquegua: Lago Loriscota, 5 km N (MVZ 145555–145561); Lago Suche (MVZ 115810, 115812, 115813); Lago Viscacha (MVZ 115811); Tala, 5 km NE (MVZ 115801, 115802); Torata, 7 km NE (FMNH 107412, 107419, 107428), Torata, 19 km NE (FMNH 107494–107496), Torata, 24–27 km NNE (FMNH 107445–107452, 107454–107456, 107458, 107459, 107471, 107473, 107474, 107485–107487, 107489, 107490), Torata, 31–35 km NNE (FMNH 107498–107508, 107510, 107512–107515, 107519, 107520, 107524, 107527, 107529, 107537, 107545). Puno: Ananea, 11 km W 12 km S (MVZ 172772–172774); Arapa (MVZ 116685); Asillo, (FMNH 51245–51248), 5 km S Asillo, (MVZ 116130); Caccachara (MCZ 39500, 42833, 42909, 42913–42918; MVZ 115814); Chucuito (FMNH 52584,

52586, 52588–52592, 52595); Hac. Collacachi (MCZ 49526–49532, 49534, 49535, 49776); Huacullani (FMNH 52576, 52577, 52580, 52581); Rio Huanque (MVZ 136333, 139382); Ilave, 15 km S (MVZ 115816, 115817, 115886); Imata, 6 mi. S (MVZ 116131, 116132); Juli (MCZ 39502, 39503, 39506; MCZ 39502, 39503, 39506; MVZ 115818–115821, 115885); Juliaca, (FMNH 49489, 49490, 49621), Juliaca, 6 km NNW (136334, 136340–136342), Juliaca, 3 mi. SW (MVZ 116690); Mazocruz, 30 mi. S (MVZ 116786); Occomani (FMNH 53182); Hac. Pairumani, 24 mi. S Ilave (MCZ 39518, 42906; MVZ 114684, 115815, 115887); Pampa de Ancomarca (MVZ 115822–115824); Pisacoma (FMNH 52601–52604); Pomata (MVZ 115873, 115970); Pucara (MVZ 172776); Puno (AMNH 213613, 213615, 213617–213619, 213623, 213625; FMNH 51366; MVZ 116133, 116146), 5–15 km W Puno (MVZ 115825, 115826, 115888, 115889, 115891), 82 km W Puno (MVZ 115827, 115828); Rio Santa Rosa, 20 km W Mazocruz (MVZ 115829–115831); San Antonio de Esquilache (FMNH 49638, 49709); San Ignacio (MCZ 39507, 39514, 39515); Santa Rosa, (MCZ 42832, 42851, 42852, 42889, 42890,42903, 42905–42908, 42919–42921), Santa Rosa, 3–12 km W (FMNH 107898–107905, 107907, 107909–107911, 107914–107916, 107924, 107927, 107929, 107933–107939, 107942, 107945, 107947–107949, 107955–107958, 107961, 107963–107966, 107971–107973, 107977, 107978, 107980, 170982, 107986, 107992, 107994, 107996), Santa Rosa, 2 mi. W, 10 mi. W Mazocruz (MVZ 114685, 114686); Sibayo (MCZ 39508, 39509, 39511–39513); Soropa (AMNH 91502, 91503); Tincopalca, 13 mi. E (MVZ 116134); Hac. Umayo, 15 mi. S Juliaca (MVZ 116691, 116694–116696); Yunguyo (FMNH 51266). Tacna: Challapalca (MVZ 141421); Livine, 21 mi. NE Tarata (MVZ 114687–114690); Nevado Livine, 2 km NW (MVZ 115839); Moro Sama, 65 km W Tacna (MVZ 141491, 143746, 143748); Tarata, 2.6 mi. N (MVZ 139342–139347, 139349, 139351, 139353, 139355–139363, 139366–139368, 139371–139375, 139377, 139379–139381), Tarata, 4 km N (MVZ 115832, 115833, 115835, 115836, 115847, 115848), Tarata, 2 km NE (MVZ 141638), Tarata, 5–8 km NE (FMNH 107550–107552, 107556–107560, 107562–107567, 107569, 107571, 107572, 107576, 107577, 107582–107584, 107586, 107588, 107590, 107636–107638, 107595, 107596, 107604, 107606–107608, 107635, 107648; MVZ 141422, 141424–141431, 141433–141440, 141442–141446, 141448–141458, 141460–141462, 141553–141555, 141557, 141564–141566), Tarata, 13 km NE (MVZ 141463, 141465–141477, 141480–141482, 143753–143756), Tarata, 20–25 km NE (MVZ 115849–115854), Tarata, 10 km S (MVZ 141652); Volcan Tutupaca (MVZ 115803–115805).

Phyllotis xanthopygus posticalis (n = 122). PERU. Apurímac: Abancay, 18 km NE (MVZ 139302, 139305); Andahuaylas, Hac. Palmira (FMNH 75428–75432); Chalhuanca, 22 km S (MVZ 1393603, 139304), 36 km S (MVZ 174040, 174041); Huancarani (MVZ 171526–171528). Ayacucho: Ayacucho (AMNH 208091–208093); Huanta, 2 mi. SE (MVZ 141585–141591); Orcos, Hac. Pajonal (FMNH 75421–75423); Puquio, 2 km E (MVZ 139306–139309), Puquio, 18 km E (MVZ 174042), Puquio, 35 km E (MVZ 115808), Puquio, 15–21 km NE (MVZ 115809, 116024), Puquio, 10–15 km WMW (MVZ 138098, 138099–138113). Cuzco: Ampay, Pisac (FMNH 84356, 84358); nr Calca, Hac. Paullo Grande (FMNH 84359, 84360), Hac. Urco (FMNH 49492, 49493, 49495); Chospyoc (USNM 194573, 194574, 194718, 194720); Cuzco (FMNH 52607–52610); Marcapata, Ccolina (FMNH 75464); Ollantaytambo (USNM 194577); Ocongate, Hac. Ccapana (FMNH 66407); Fundo Perayoc (FMNH 83473); Sacsahuaman, nr Cuzco (FMNH 49498–49500, 49624, 49629). Huancavelica: Huancavelica (FMNH 75427, 75441, 75443–75455); Lircay (FMNH 75456–75459); Locroja, Hac. Piso (FMNH 75425, 75426); Mayoc (FMNH 75436, 75439); Rio Montaro, 3 mi. SE Igcuchaca (MVZ 120006, 120007, 141592–141594); San Jenaro (FMNH 75437, 75460–75462, 75465). Junín: Carhuamayo (FMNH 54726–54732); Jauja, 20 km W (MVZ 139310); Junín (FMNH 20912, 20913); Oroyo (FMNH 20911, 29166).

Phyllotis xanthopygus rupestris (n = 129). ARGENTINA. Jujuy: Tilcara (MVZ 120090–120096, 141414, 141417–141419); Tres Cruces (FMNH 41288, 41289). BOLIVIA. Chiquisaca: Camargo, 68 km N by rd., 20° 09′ S 68° 17′ W (AMNH 262969–262971); Tarabuco, 2 km N (AMNH 263739, 263899–263905, 263907). La Paz: Amullachta, 5 km below Caracato (MVZ

121051–121055); La Paz, 20 mi. S (MVZ 120054–120057); Estancia Perez, Pr. Pacajes (FMNH 53600–53606, 53608–53611, 53613); Viscachi (AMNH 255974, 255976). Oruro: Cruce Ventilla, 7 km S, 4 km E, 19° 08′ S 66° 07′ W (AMNH 262977–262979); Eucaliptus, 9–12 km S (AMNH 246774, 246873); Huancaroma (AMNH 262980); Lagunas, 6 km NE, 18° 10′ S 68° 55′ W (AMNH 260940, 260941, 260943–260945); Machacamarca, 11 km N (AMNH 244648); Oruro (MVZ 120099, 120100); Finca Santa Helena, 10 km SW Panza (MVZ 155852, 155853). Potosi: Lipez (FMNH 29108–29110); Potosi, 20 mi. S (MVZ 120101–120106); Villazon, 5 mi. N (MVZ 120107, 120108), Villazon, 25 mi. NE (MVZ 120109–12112). Tarija: Camataqui, 25 mi. SSE (MVZ 120141–120148); Iscayachi, 12 mi. NW (MVZ 141582, 141583), Rio Tomayapo, 21° 29′ S 64° 57′ W (AMNH 262983). CHILE. Antofagasta: Calama (USNM 273261); Ojos San Pedro, 50 mi. NE Calama (MVZ 116777, 116790, 118660, 118661); Pocos (MVZ 119555); San Pedro de Atacama (MNHN 305, 306, 359, 376, 378, 511, 535, 568), 20 mi. E (FMNH 22303, 22304, 22307–22313, 22315–22317, 22322, 22324, 25282, 25283; MCZ 27026); Tatio Geysers (MVZ 116791); Toconce, 60 mi. ENE Calama (MVZ 116778–116780).