

Extreme High-Elevation Mammal Surveys Reveal Unexpectedly High Upper Range Limits of Andean Mice

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ABSTRACT: In the world's highest mountain ranges, uncertainty about the upper elevational range limits of alpine animals represents a critical knowledge gap regarding the environmental limits of life and presents a problem for detecting range shifts in response to climate change. Here we report results of mountaineering mammal surveys in the Central Andes, which led to the discovery of multiple species of mice living at extreme elevations that far surpass previously assumed range limits for mammals. We livetrapped small mammals from ecologically diverse sites spanning >6,700 m of vertical relief, from the desert coast of northern Chile to the summits of the highest volcanoes in the Andes. We used molecular sequence data and whole-genome sequence data to confirm the identities of species that represent new elevational records and to test hypotheses regarding species limits. These discoveries contribute to a new appreciation of the environmental limits of vertebrate life.

Keywords: Andes, distribution limits, high altitude, *Phyllotis*, Puna de Atacama, species limits.

Introduction

Identifying factors that influence geographic range limits of animal species is a long-standing goal in ecology and evolutionary biology. Elevational shifts in species' ranges are of special interest in the context of global climate change (Moritz et al. 2008; La Sorte and Jetz 2010; Rowe et al. 2010; Tingley et al. 2012; McCain et al. 2021; Storz and Scott 2024), and the conservation implications of such shifts underscore the need for accurate information about contemporary range limits. However, in the most mountainous regions of the planet—where potential elevational range limits are the highest—the upper limits of species' ranges are often poorly demarcated because of a paucity of survey data. For example, in the common South American rodent genus *Phyllotis* (Cricetidae: Sigmodontinae), latitudinal limits of nominal species are relatively well delineated (Steppan and Ramirez 2015; Jayat et al. 2021; Ojeda et al. 2021), but the upper elevational limits of species with montane distributions are known with far less certainty. This was highlighted by the results of a recent mountaineering mammal survey of Volcán Llullaillaco (Argentina, Chile) that recorded a new elevational record for *Phyllotis vaccarum* (previously recognized as *Phyllotis xanthopygus rupestris*) from the summit of the volcano at 6,739 m (Storz et al. 2020). This record surpasses previous records for *Phyllotis* by >1,700 m (Steppan and Ramirez 2015) and represents the highest specimen-based record for any mammalian species. This discovery highlights the need for novel

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survey approaches to document the elevational range limits of small mammals in remote, highly mountainous regions such as the Andean Altiplano.

Here we report results of five high-elevation mammal surveys (2020–2022) in the Puna de Atacama of northern Chile and bordering regions of Argentina and Bolivia. By conducting biological surveys at extreme elevations that had never been surveyed, we assessed whether small mammals inhabit higher elevations than previously supposed. The summits and upper reaches of >6,000-m Atacama volcanoes are extremely inhospitable environments for small endotherms because of the extreme cold, unceasing wind, and lack of oxygen. At an elevation of 6,700 m, for example, each breath of air contains ~44% of the oxygen available at sea level (45 kPa [337 mmHg] vs. 101 kPa [760 mmHg]), a level of hypoxia that imposes severe constraints on aerobic thermogenesis (Storz et al. 2010; Storz and Scott 2019). In the absence of evidence to the contrary, no biologist could be faulted for assuming that such extreme elevations are uninhabitable by mammals. Our high-elevation biological surveys were designed to assess the environmental limits of mammalian life and to help redress the so-called Wallacean shortfall (Hortal et al. 2015), which refers to the discrepancy between the known distributional limits of species and their actual limits.

The Central Andean dry puna ecoregion is characterized by montane grasslands and shrublands interspersed with salt flats, high plateaus, and snowcapped volcanoes. Our high-elevation surveys focused on 21 volcanoes distributed along the spine of the Andean cordillera and surrounding regions in the Altiplano. To obtain a broad picture of elevational distributions of small mammals in this remote and largely unexplored region, and to demarcate lower and upper range limits, we also surveyed small mammals at lower elevations in the Atacama Desert and along the Pacific coast of northern Chile (fig. 1; tables S1, S2; tables S1–S3 are available online). To resolve species limits and elevational distributions in *Phyllotis*, the most abundant taxon in our collection, we generated mitochondrial DNA (mtDNA) sequence data and whole-genome sequence (WGS) data for multiple species. The surveys yielded elevational records for multiple rodent species, providing a new appreciation of the environmental tolerances of mammals and the habitable limits of the high mountain biome.

Material and Methods

Elevational Surveys

In high-elevation expeditions between 2020 and 2022, we trapped small mammals (rodents and marsupials) at sites that spanned a diversity of habitats over a broad range of elevations (fig. 1A; table S1). For each of 21 surveyed volca-

noes (fig. 1B; table S2), we maintained a base camp for multiple days and maintained trap lines in the general vicinity, typically at elevations between 3,800 and 5,100 m. In the case of eight volcanoes with summits of 6,046–6,893 m (Nevado Sajama, Parinacota, Aucanquilcha, Acamarachi, Púlar, Socompa, Llullaillaco, and Ojos del Salado), we also maintained trap lines for 1–4 days at especially high elevations between 5,100 and 5,850 m.

Livetrapping and Specimen Preparation. We captured all small mammals using Sherman live traps, in combination with Museum Special snap traps at several of the especially high-elevation sites. We euthanized animals in the field, prepared them as museum specimens, and preserved tissue samples as sources of DNA. All specimens are housed in the Colección de Mamíferos of the Universidad Austral de Chile, Valdivia, Chile (UACH), or in the Colección Boliviana de Fauna, La Paz, Bolivia (CBF). We identified all specimens to the species level based on external characters (Patton et al. 2015), and we later confirmed all uncertain field identifications with DNA sequence data.

In Chile all animals were collected in accordance with permissions to J. F. Storz and G. D'Elia from the following Chilean government agencies: Servicio Agrícola y Ganadero (6633/2020, 2373/2021, 5799/2021, 3204/2022, and 3565/2022), Corporación Nacional Forestal (171219 and 1501221), and Dirección Nacional de Fronteras y Límites del Estado (68 and 02/22). In Bolivia all animals were collected in accordance with permissions to A. Rico-Cernohorska, J. Salazar-Bravo, and J. F. Storz from the Ministerio de Medio Ambiente y Agua, Estado Plurinacional de Bolivia (026/09). All livetrapped animals were handled in accordance with protocols approved by the institutional animal care and use committee of the University of Nebraska (project IDs: 1919, 2100) and the bioethics committee of the Universidad Austral de Chile (certificate 456/2022).

Elevational Vegetation Surveys. For each of the 21 volcanoes that we surveyed, we treated the ascent route as an elevational transect, and we recorded the upper limits of vegetation. In many cases, we traversed the same route multiple times over several consecutive days, such as when making repeated trips from base camp to high camp.

*Resolving Species Limits of Highland *Phyllotis*: Molecular Sequence Data and Whole-Genome Polymorphism Data*

DNA Sequencing. To resolve species limits and refine upper elevational limits of highland *Phyllotis*, we sequenced the mitochondrial *cytochrome b* gene (*cytb*) of 89 specimens, seven of which had been published previously (Storz et al. 2020). We extracted DNA from liver samples, and we used polymerase chain reaction (PCR) to amplify the first

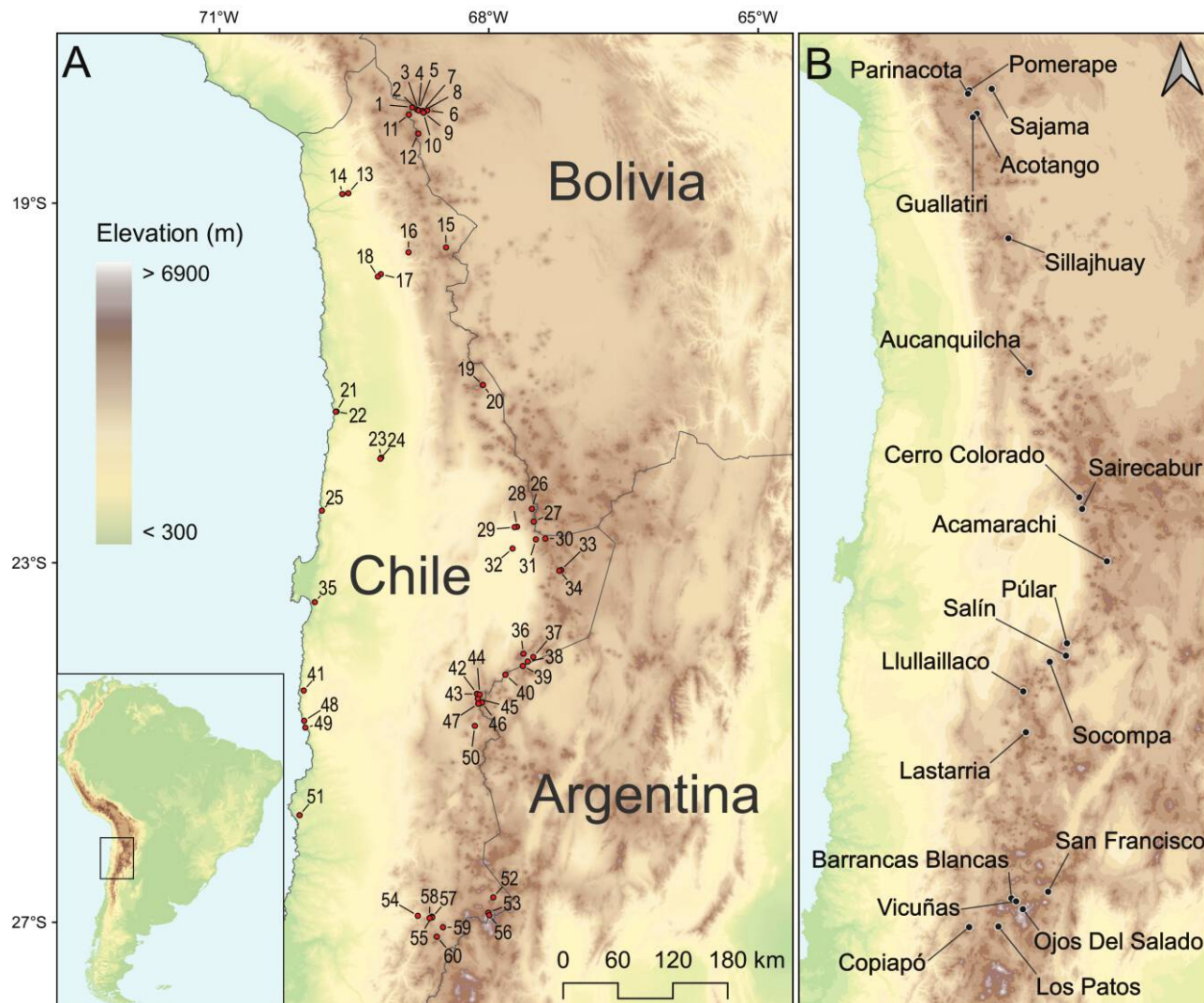


Figure 1: Collection localities. A, Sixty collection localities in northern Chile and bordering regions of Argentina and Bolivia, with elevations ranging from sea level to 6,739 m (see table S1 for details). B, Locations of 21 surveyed volcanoes along the spine of the Andean cordillera (see table S2 for details).

801 bp of *cytb* using the primers MVZ 05 and MVZ 16 (Smith and Patton 1993), following protocols of Salazar-Bravo et al. (2001) and Cadenillas and D'Elia (2021). All newly generated sequences were deposited in GenBank (OR784643–OR784661, OR799565–OR799614, OR810731–OR810743).

Taxon Sampling for Analysis of Whole-Genome Sequence Data. Using a chromosome-level reference genome for *Phyllotis vaccarum* (Storz et al. 2023), we generated low-coverage WGS data for a subset of 61 *Phyllotis* specimens (1.26–24.1-fold coverage, 2.86-fold median) to resolve uncertainty regarding species limits. We generated new WGS

data for 17 *Phyllotis* specimens that we then analyzed in conjunction with previously published genome sequence data for 44 specimens (Storz et al. 2023). We used WGSs from *P. chilensis* ($n = 2$) and *P. magister* ($n = 2$) for purposes of comparison. See the supplemental PDF for details regarding genomic library preparation, whole-genome sequencing, read quality processing, and read mapping to the reference genome.

Analysis of Genomic Variation in *Phyllotis*. We calculated genotype likelihoods for scaffolds 1–19 (covering >90% of the *Phyllotis* genome) for all samples in ANGSD (ver. 0.939; Korneliussen et al. 2014). We used -GL 1 to

specify the SAMtools model for genotype likelihoods, retained sites only with a probability of being variable $>1e-6$ with `-SNP_pval 1e-6`. We filtered out bad and nonuniquely mapped reads with `-remove_bads 1` and `-uniqueOnly 1`, respectively, and retained reads and bases only with a mapping quality higher than 20. We adjusted mapping quality for excessive mismatches with `-C 50` and recalculated base alignment quality with `-baq 1`. We used PCAngsd (ver. 0.99.0; Meisner and Albrechtsen 2018) to calculate the covariance matrix from genotype likelihoods and used a minor allele frequency filter of 0.05. We calculated eigenvectors and plotted the first and second principal components in R version 4.1.3 using the package ggplot2 (ver. 3.4.2; Wickham 2016).

Mitochondrial Genome Assembly. We used MitoZ (ver. 3.6; Meng et al. 2019) to create an initial de novo assembly of the mitochondrial genome for the *P. vaccarum* specimen from the summit of Volcán Llullaillaco (UACH8291). We then used NOVOplasty (ver. 4.3.3; Dierckxsens et al. 2017) to generate de novo assemblies for all remaining samples using the mitochondrial genome for UACH8291 as a seed sequence. We annotated assembled mitochondrial genomes with MitoZ to identify coding sequences. We generated a multiple alignment of coding sequence with MAFFT (ver. 7.508; Katoh and Standley 2013), using `-auto` flag to determine the best algorithm given the data.

Phylogenetic Analysis. Our *cytb* matrix for *Phyllotis* included newly generated sequences in combination with all nonredundant sequences available in GenBank for the species group *P. darwini* (Jayat et al. 2021; Ojeda et al. 2021) and sequences from each species in the *andium/amicus* and *osilae* species groups. We included sequences of the two most closely related genera in the tribe Phyllotini as out-groups. We aligned sequences using Clustal W (Thompson et al. 1997), as implemented in MEGA7 (Kumar et al. 2016). We conducted maximum likelihood phylogenetic analyses in IQ-TREE (Nguyen et al. 2015) using the W-IQ-TREE online implementation (<http://iqtree.cibiv.univie.ac.at>; Trifinopoulos et al. 2016), with the disturbance intensity set to 0.5, the term rule set to 100, and the substitution model TPM2u+F+I+G4 found by ModelFinder (Kalyanamoorthy et al. 2017) within IQ-TREE. Clade support was calculated via 1,000 ultrafast bootstrap pseudoreplicates.

For the whole mitochondrial genome dataset, we inferred a maximum likelihood phylogeny in IQ-TREE (ver. 2.2.0.3; Minh et al. 2020) using 1,000 ultrafast bootstrap replicates. The substitution model used for phylogenetic inference, GTR+F+I+G4, was chosen by ModelFinder (Kalyanamoorthy et al. 2017).

Results and Discussion

During five high-elevation expeditions and additional low-elevation collecting trips between 2020 and 2022, we livetrapped small mammals from ecologically diverse sites spanning ~6,700 m of vertical relief, from the Pacific coast of northern Chile to some of the highest summits of the Andean cordillera (fig. 1A; table S1). In the high-elevation expeditions, mammal trapping and vegetational surveys were centered on 21 volcanoes with summit elevations of 5,706–6,893 m (18,720–22,615 ft; fig. 1B; table S2). In total, we collected 500 small mammals, all of which were prepared as museum voucher specimens. The collection included 18 rodent species representing 12 genera (*Abrocoma*, *Abrothrix*, *Akodon*, *Auliscomys*, *Calomys*, *Eligmodontia*, *Oligoryzomys*, *Phyllotis*, *Punomys*, *Mus*, *Rattus*, and *Octodontomys*) and two marsupial species in the genus *Thylamys* (tables 1, S3). Photos of representative rodent taxa are shown in figure S1. Mice in the genera *Abrothrix* and *Phyllotis* were the most abundant taxa across the surveyed region, accounting for 27% and 49% of the total collection, respectively.

Vegetation surveys along the summit routes of the 21 volcanoes revealed a latitudinal trend in upper elevational limits (table S2). Among the volcanoes that we surveyed along the border of Chile and Argentina at latitudes $>26^{\circ}\text{S}$ (San Francisco, Barrancas Blancas, Vicuñas, Nevado Ojos del Salado, Los Patos [= Tres Quebradas], and Copiapó; fig. 1B), bunch grasses in the genera *Stipa* and *Festuca* and other vascular plants typically disappeared completely at elevations between ~4,600 and 4,900 m (table S2). By contrast, among the volcanoes that we surveyed on the border between Chile and Bolivia at latitudes $<20^{\circ}\text{S}$ (Nevado Sajama, Pomerape, Parinacota, Acotango, Guallatiri, and Sillajhuay; fig. 1B), multiple species of tropical alpine herbs and dwarf shrubs exceeded elevations of 5,200 m (fig. S2A; table S2). The flanks of Nevado Sajama harbor the highest tree line in the world, as stands of queñua (*Polylepis tarapacana*) reach elevations of ~5,200 m (Simpson 1979; fig. S2B, S2C).

Below, we highlight new elevational records for multiple rodent taxa. In the case of *Phyllotis*, we report results of molecular phylogenetic and genomic analyses that confirm species identities and place new elevational records in phylogeographic context.

Elevational Range Limits and Species Limits in *Phyllotis*

On the flanks of Ojos del Salado, we livetrapped six *Phyllotis* at 5,250 m (tables S1, S3), 650 m above the vegetation limits on the north face of the volcano (table S2). In addition to the live-captured specimen of *P. vaccarum* from the summit of Llullaillaco (6,739 m; Storz et al. 2020), identification of active burrows of *P. vaccarum* at 6,145 m on the same

Table 1: Elevational ranges of capture of small mammals in the surveyed region of the Puna de Atacama (Chile/Bolivia/Argentina) and Atacama Desert of northern Chile

Taxon	Elevational range of captures (m)	Previous elevational record (m)
Didelphimorphia, Didelphidae:		
<i>Thylamys elegans</i> ($n = 2$)	85	
<i>Thylamys pallidior</i> ($n = 12$)	40–4,183	
Abrocomidae:		
<i>Abrocoma cinerea</i> ($n = 6$)	3,100–4,543	
Cricetidae:		
<i>Abrothrix andina</i> ($n = 46$)	2,370– 5,837	5,000 (Mann 1978; Patterson 2015)
<i>Abrothrix olivacea</i> ($n = 88$)	4–3,100	
<i>Akodon albiventer</i> ($n = 41$)	3,380– 5,221	4,500 (Pardiñas et al. 2015)
<i>Auliscomys sublimus</i> ($n = 1$)	4,807	
<i>Calomys lepidus</i> ($n = 3$)	4,183–4,330	
<i>Eligmodontia hirtipes</i> ($n = 2$)	4,362	
<i>Eligmodontia puerulus</i> ($n = 6$)	1,360–4,099	
<i>Oligoryzomys flavescens</i> ($n = 1$)	790	
<i>Phyllotis darwini</i> ($n = 21$)	40–360	
<i>Phyllotis limatus</i> ($n = 19$)	650–3,380	
<i>Phyllotis magister</i> ($n = 7$)	974–3,380	
<i>Phyllotis chilensis</i> ($n = 50$)	3,380– 5,221	4,700 (Rengifo et al. 2022)
<i>Phyllotis vaccarum</i> ($n = 147$)	49– 6,739	5,030 (Steppan and Ramirez 2015)
<i>Punomys lemmingus</i> ($n = 1$)	5,461	4,877 (Pacheco and Patton 1995)
<i>Mus musculus</i> ($n = 21$)	4–1,440	
<i>Rattus norvegicus</i> ($n = 25$)	4–1,440	
Octodontidae:		
<i>Octodontomys gliroides</i> ($n = 1$)	3,380	

Note: Maximal elevations that represent new species-specific records are shown in bold. See tables S1 and S3 for detailed locality information and capture records.

volcano (Steppan et al. 2022), and the discovery of desiccated cadavers (“mummies”) of *P. vaccarum* on the summits of multiple >6,000-m peaks (Storz et al. 2023), the live-capture records reported here confirm that this species is a regular denizen of the barren world of rock, ice, and snow at extreme elevations in the Puna de Atacama.

Phylogenetic analysis of *cytb* DNA sequences revealed that high-elevation *Phyllotis* specimens collected from Chilean and Bolivian Altiplano localities from Volcán Sairecabur northward (fig. 1B) are referable to *P. chilensis* (sensu Pearson 1958; fig. 2). By contrast, all high-elevation *Phyllotis* specimens from Altiplano localities to the south of Sairecabur fell into two distinct *cytb* clades (fig. 2): one representative of *P. vaccarum* and one that appears to represent a southern subclade of *P. limatus*. The latter finding is surprising because we collected mice with *limatus*-type *cytb* at sites in the Chilean Altiplano far south of the previously assumed range limits of *P. limatus* (fig. 3A, 3B). Previous records of mice with *limatus*-type *cytb* on the flanks of Llullaillaco were interpreted as evidence that *P. limatus* occurred at more southern latitudes (and higher elevations) than previously assumed (Storz et al. 2020). Notably, some of the highest-elevation *Phyllotis* specimens that we collected south of the Tropic of Capricorn have *limatus*-type *cytb* haplotypes, including all six mice collected from 5,250 m

on the flanks of Ojos del Salado and three other mice from elevations of 5,070–6,052 m on the flanks or summits of other Atacama volcanoes (figs. 2, 3B). If any of those specimens are indeed referable to *P. limatus*, they would far surpass the reported upper elevational range limit of that species (~4,000 m; Steppan and Ramirez 2015) and would also represent a considerable southward extension of the species’ known latitudinal range (fig. 3A, 3B). As expected, the *cytb* results were corroborated by the analyses of whole mitochondrial genomes (fig. 3C). Coding sequence divergence (d_{xy}) between the mitogenomes of southern and northern *limatus*-type subclades was 0.011, whereas d_{xy} between *vaccarum* and the two alternative *limatus*-type subclades was 0.022 in both pairwise comparisons. To obtain more conclusive insights into species limits, we generated low-coverage WGS data for representative subsets of our high-elevation *Phyllotis* specimens that carried *cytb* haplotypes from the *vaccarum* clade ($n = 36$) and the southern *limatus*-type subclade ($n = 15$), along with specimens from more northern localities within the known range of *P. limatus* (and well outside the known range of *P. vaccarum*), all of which carried *cytb* haplotypes from the northern *limatus*-type subclade ($n = 6$; fig. 3B).

Analysis of WGS data revealed that representatives of the *vaccarum* mitochondrial clade and the southern

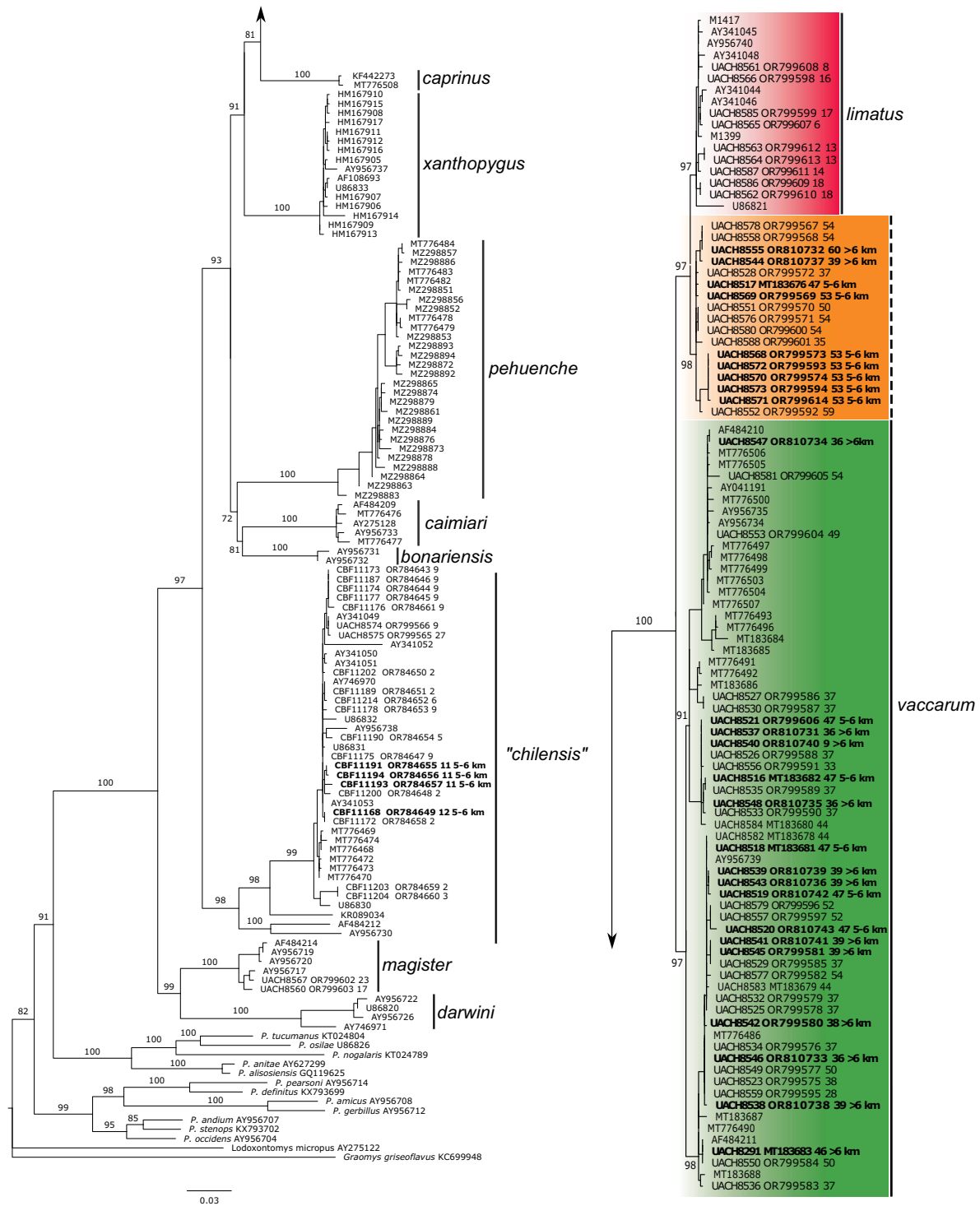
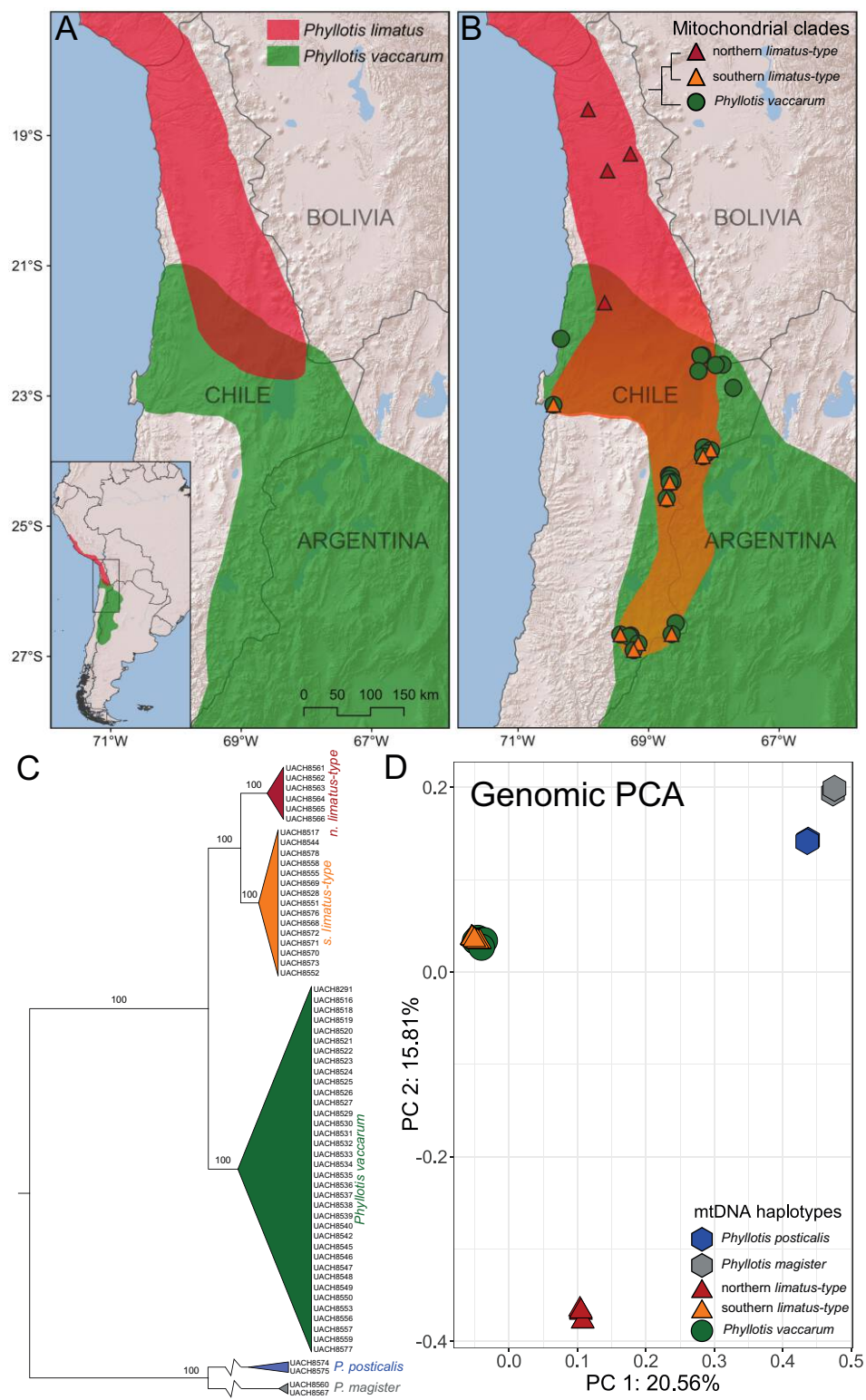


Figure 2: Maximum likelihood tree (ln = -8,956.735) estimated for *cytb* gene sequences of *Phyllotis*. Numbers at nodes correspond to ultrafast bootstrap support values (only values for species and relationships among species are shown). For specimens collected as part of the present study, terminal labels refer to specimen catalog numbers, GenBank accession numbers, and localities (table S1). For sequences downloaded from GenBank, terminal labels refer to accession numbers. *Phyllotis* specimens that we collected from especially high elevations are labeled "5-6 km" and ">6 km". The clade shown in orange comprises *Phyllotis* specimens with *limatus*-like *cytb* haplotypes that we collected well outside the known range of *P. limatus* in northern Chile (see text for details).



limatus-type mitochondrial subclade cluster together to the exclusion of mice from the northern *limatus*-type subclade (fig. 3D). At the whole-genome level, d_{XY} between *vaccarum* and representatives of the southern *limatus*-type mitochondrial subclade was 0.0041, whereas d_{XY} between *vaccarum* and the northern *limatus*-type mitochondrial subclade was 0.0054. Results of the WGS analysis clearly indicate that mice with the southern *limatus*-type mtDNA haplotypes are referable to *P. vaccarum*, whereas those with northern *limatus*-type mtDNA haplotypes represent a distinct species (*P. limatus*). The WGS results are far easier to reconcile with the traditional understanding of the geographic distributions of the two species (fig. 3A; Steppan et al. 2007; Steppan and Ramirez 2015). The WGS data also confirm that all extreme high-elevation *Phyllotis* mice from elevations of 5,070–6,739 m on the flanks or summits of five different volcanoes (Púlar, Salín, Lullaillaco, Ojos del Salado, and Copiapó) are referable to *P. vaccarum*, not *P. limatus*. Causes of the discordance between mitochondrial and nuclear genomic variation in these mice remain to be elucidated and could potentially reflect incomplete lineage sorting and/or a history of introgressive hybridization between *P. limatus* and *P. vaccarum*. Whatever the cause, the results demonstrate that mtDNA sequence data alone do not always provide a reliable basis for distinguishing species of *Phyllotis*.

Notably, high-elevation specimens of *P. vaccarum* exhibited close genetic affinities with multiple specimens that we collected at or near sea level along the coast of northern Chile (fig. 2). Thus, this species not only inhabits higher elevations than any other mammal but also has by far the broadest elevational range, from sea level to >6,700 m.

Elevational Records Provide a New Appreciation of Environmental Limits of Vertebrate Life

Our high-elevation surveys yielded new elevational records for five rodent species, including previously reported rec-

ords for *P. vaccarum* (Storz et al. 2020) and *P. lemminus* (Quiroga-Carmona et al. 2023; table 1). Our record capture of *Abrothrix andina* at 5,837 m on the flanks of Ojos del Salado far surpasses the previously reported limit of ~5,000 m (Mann 1978; Patterson et al. 2015). In western Bolivia, we captured multiple *Akodon albiventer* from 5,020 to 5,221 m on the flanks of Nevado Sajama and Volcán Parinacota (the species had not been previously recorded >4,500 m; Pardiñas et al. 2015), and we captured multiple *Phyllotis chilensis* from 5,027 to 5,221 m on the flanks of Acotango and Parinacota (the species had not been previously recorded >4,700 m; Rengifo et al. 2022).

Before our Andean surveys, the mammalian species with the highest specimen-based elevational record was the long-eared pika, *Ochotona macrotis*, with two Himalayan specimens from 5,182 m (US National Museum 198648 and 198649). In the Andean Altiplano, the highest records reported by Rengifo et al. (2022) were for *Abrothrix jelskii* from 5,100 m in the Central Andean puna of southern Peru (Museo de Historia Natural, Universidad Mayor de San Marcos, MUSM37711–37727). Our high-elevation Andean expeditions yielded a total of 26 specimens of five different species that surpass those elevations, including the highest elevational record for mammals (*P. vaccarum*) as well as species with the second- to fifth-highest records (table 1). These specimen-based records greatly extend the known limits of what can be considered habitable environments for mammals.

New Frontiers of Biological Surveys

Biological surveys of the abyssal and hadal zones of deep ocean trenches have yielded novel discoveries about the environmental limits of marine life by using specialized approaches (e.g., manned and unmanned submersibles) distinct from those employed in surveys of upper pelagic zones. Likewise, surveys of terrestrial mammals at extreme

Figure 3: Genomic tests of alternative hypotheses regarding the latitudinal and elevational range limits of *Phyllotis limatus*. A, Southern range limit of *P. limatus* and northern range limit of *P. vaccarum*, according to traditional criteria based on morphological variation and mitochondrial DNA (mtDNA) variation (Steppan et al. 2007; Steppan and Ramirez 2015). B, Hypothesis for revised range limits of *P. limatus* based on the collection of mice with *limatus*-like *cytb* haplotypes in northern Chile (forming the southern *limatus* clade shown in fig. 2) that occur well outside the traditionally assumed range of the species (but that occur well within the known range of *P. vaccarum*). Symbols denote collection localities where we recovered mice with *cytb* haplotypes that fall into three well-supported clades, one representative of *P. vaccarum*, one representative of *P. limatus* as traditionally recognized (northern *limatus*-type), and one that appears to represent a southern subclade of *P. limatus* (southern *limatus*-type). If mice with the southern *limatus*-type mtDNA are in fact referable to *P. limatus*, the newly collected specimens would represent a considerable southward extension of the species' known latitudinal range and a >1,250-m upward extension of the species' known elevational range (Steppan and Ramirez 2015). The inset tree depicts inferred relationships among the three abovementioned *cytb* clades, according to the phylogeny estimate shown in figure 2. C, Estimated phylogeny based on whole mitochondrial genomes recovers the same topology as the *cytb* tree for *vaccarum* and the two *limatus* subclades (fig. 2). D, In contrast to the relationships based on mtDNA, principal components analysis of whole-genome polymorphism data demonstrates that mice with southern *limatus*-type mtDNA group with *vaccarum* to the exclusion of mice with northern *limatus*-type mtDNA. The genomic data indicate that mice with the southern *limatus*-type mtDNA haplotypes are in fact referable to *P. vaccarum*, whereas those with the northern *limatus*-type mtDNA haplotypes are referable to *P. limatus*.

elevations require the specialized logistics and acclimatization protocols of a full-fledged mountaineering expedition, with the establishment of base camps and high camps for the daily monitoring of trap lines. Using this approach, our trapping surveys of Nevado Sajama, Volcán Llullaillaco, Ojos del Salado, and other volcanoes >6,000 m have yielded surprising elevational records for multiple rodent species, all of which are cataloged as museum voucher specimens. These records provide valuable baseline data for monitoring effects of climate change on the elevational distributions of Andean mammals, and they also prompt new questions about basic ecology and mechanisms of physiological adaptation to environmental extremes.

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Statement of Authorship

J.F.S., S.L., M.Q.-C., G.D., and J.M.G. designed the research; J.F.S., M.Q.-C., N.M.B., J.S.-B., A.R.C., and G.D. performed the fieldwork; S.L. performed the laboratory work; S.L., N.D.H., M.Q.-C., J.S.-B., J.C.O., G.D., and J.M.G. analyzed data; J.F.S., S.L., M.Q.-C., N.M.B., G.D., and J.M.G. prepared figures and wrote the manuscript.

Data and Code Availability

All sequence data reported in this study are archived in the National Center for Biotechnology Information/GenBank. Raw sequencing reads are available in the Sequence Read Archive, and all genome sequences are available in GenBank under BioProject PRJNA950396. Data and code associated with this study are publicly available at Zenodo (<https://doi.org/10.5281/zenodo.8270684>; Storz et al. 2024).

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