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The role of the "Cordillera Blanca" (Ancash, Peru) in the evolutionary history of sigmodontinae rodents in northern Peru

Edgardo Manuel Rengifo Vásquez

Thesis presented to obtain the degree of Doctor in Science
Area: Applied Ecology

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2023

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Bachelor in Biological Sciences

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versão revisada de acordo com a Resolução CoPGr 6018 de 2011

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CONTENTS

RESUMO

O papel da "Cordillera Blanca" (Ancash, Peru) na história evolutiva dos roedores sigmodontinos no norte do Peru

A Cordilheira dos Andes é a cadeia montanhosa mais importante da América do Sul, possuindo uma notável riqueza de espécies que inclui um elevado número de táxons endêmicos. Além disso, os Andes representam uma área interessante para desenvolver estudos evolutivos e biogeográficos. Aqui, meu objetivo principal foi investigar como a elevação da Cordilheira Branca influenciou a história evolutiva dos roedores sigmodontíneos (subfamília Sigmodontinae) nas terras altas do departamento de Ancash, no norte do Peru. Primeiramente, apresentei os Andes mostrando a montagem da comunidade de pequenos mamíferos não-voadores e identifiquei o padrão de endemismo de roedores sigmodontíneos na região andina. Depois, dividi minha tese em três capítulos. O capítulo 1 é uma introdução geral na qual apresento brevemente os Andes, mencionando sucintamente os processos evolutivos que levaram a abrigar a diversidade atual; adicionalmente, também apresento a justificativa e as hipóteses de cada capítulo. O capítulo 2 tem como objetivo apresentar uma visão geral dos Andes, com uma atualização sobre o estado do conhecimento biogeográfico de pequenos mamíferos não-voadores e identificar áreas de endemismo dos roedores sigmodontíneos nos Andes. Para atingir este objetivo, i) compilei informações provenientes da montagem de comunidades de pequenos mamíferos não-voadores em regiões andinas altas ,e ii) para identificar as áreas de endemismo dos sigmodontíneos, empreguei uma análise de endemicidade usando o software NDM/VNDM. Como resultado, obtive informações de 630 comunidades de mamíferos de sete países Sul-americanos e compilei um total de 26.534 registros de indivíduos pertencentes a 241 espécies. A Ordem com maior número de registros foi Rodentia. A curva de acumulação de espécies apontou que o conjunto de dados cobre uma representação adequada, enquanto a análise de endemicidade recuperou oito áreas de endemismo (AoE). Em sentido amplo, os padrões de AoE aqui encontrados são congruentes com os previamente delimitados por outros métodos e em outros táxons. No capítulo 3, que visou avaliar a variação morfológica e genética intra e interpopulacional dos roedores distribuídos em ambos os lados da Cordilheira Branca, apliquei métodos morfológicos clássicos e a técnica ddRADseq nas oito espécies de sigmodontíneos mais abundantes que ocorrem nas terras altas do departamento de Ancash no Peru (Akodon mollis, Microryzomys altissimus, Oligoryzomys andinus, Calomys sorellus, Auliscomys pictus, Phyllotis andium, P. occidens e Thomasomys pretor). Os resultados mostraram que existe um padrão comum de relações estreitas entre as populações nas encostas leste e oeste da Cordilheira Branca, sugerindo que esta cadeia de montanhas não representaria uma barreira geográfica efetiva. Por outro lado, meus dados mostraram que as taxas de fluxo gênico na drenagem do rio Santa foram relativamente baixas ou nulas, sendo maiores nas cabeceiras. Nesse sentido, rejeitei a hipótese de que a Cordillera Blanca teria impulsionado a especiação alopátrica dos sigmodontíneos. Por fim, o Capítulo 4 apresentou uma síntese das principais conclusões e perspectivas futuras sobre o estudo dos sigmodontíneos nos Andes.

Palavras-chave: Andes, Sigmodontinae, Endemismo, Genômica, Morfologia

ABSTRACT

The role of the "Cordillera Blanca" (Ancash, Peru) in the evolutionary history of sigmodontinae rodents in northern Peru

The Andes are the most important mountain chain in South America, possessing a remarkable species richness, including many endemic taxa. Furthermore, the Andes represent an interesting area to develop evolutionary and biogeographical studies. Here, my main objective was to investigate how the uplift of the Cordillera Blanca has influenced the evolutionary history of sigmodontinae rodents on the highland of the Ancash department in Northern Peru. Firstly, I introduced the Andes showing the community assembly of small no-volant mammals, and identified the endemism pattern of sigmodontinae rodents in the Andean region. Afterward, I divided my thesis into three chapters. Chapter 1 is a general introduction in which I briefly present the Andes, succinctly mentioning the evolutionary processes that have led to harboring the current diversity; additionally, I also present each chapter's justification and hypotheses. Chapter 2 aims to raise an overview of the Andes, with an update on the status of the biogeographic knowledge for small non-volant mammals and identify areas of endemism of the rodents of the subfamily Sigmodontinae in the Andes. To accomplish this goal, i) I compiled information from non-volant small mammals community assembly in high Andean regions and ii) to identify the areas of endemism of the sigmodontinae I employed an analysis of endemicity using the NDM/VNDM software. As a result, I obtained information from 630 mammalian communities from seven South American countries and compiled 26,534 records of individuals belonging to 241 species. The Order with the highest number of records was Rodentia. The species accumulation curve suggests that the dataset covers an adequate representation. The Analysis of endemicity recovered eight areas of endemism (AoE); broadly, the patterns of AoE found here are congruent with those previously delimited using other methods and in other taxa. Chapter 3 aims to evaluate the intra and inter-populational morphologic and genetic variation of the rodents distributed on both sides of the Cordillera Blanca, I applied classical morphological methods and ddRADseq technique in the eight most abundant sigmodontinae species that occur in the highlands of Ancash department in Peru (*Akodon mollis*, *Microryzomys altissimus*, *Oligoryzomys andinus*, *Calomys sorellus*, *Auliscomys pictus*, *Phyllotis andium*, *P. occidens*, and *Thomasomys praetor*). The results showed a common pattern of close relationships between populations on the eastern and western slopes of Cordillera Blanca, suggesting that Cordillera Blanca would not represent an effective geographic barrier. Conversely, my data show that gene flow rates across the Santa River drainage are relatively low or null, greater at headwaters. In this sense, I reject the hypothesis that the Cordillera Blanca has driven the allopatric speciation of sigmodontinae. Lastly, Chapter 4 presents a synthesis of the main conclusions and future perspectives on the study of sigmodontinae in the Andes.

Keywords: Andes, Sigmodontinae, Endemism, Genomics, Morphology

1. GENERAL INTRUDUCTION

The Andes are the most important mountain system in South America. Its extension covers approximately 7,000 km along the entire continent, from Venezuela to Chile, throughout Colombia, Ecuador, Peru, Bolivia, and Argentina (Gregory-Wodzicki, 2000, Chen et al. 2019). Regarding the uplifting of the Andes, Zeil (1979) estimated that the process began well before the Mesozoic Era. According to Hoorn et al. (2010) the event of uplift had various stages, with the most intense orogenetic activities occurring during the late middle Miocene (~12 Ma) and early Pliocene (~4.5 Ma), being the subduction process between the Nazca and the South American plates the main force of this process (Gregory-Wodzicki, 2000; Garzione et al., 2008, Husson et al., 2012 Chen et al. 2019). Gansser (1973) proposed three zones for the Andes: first, the Northern Andes, which encompasses the northern Venezuelan, Colombian, and Ecuadorean Andes; second, the Central Andes, extending from the Golfo de Guayaquil to the Golfo de Penas in Chile; and third, the Southern Andes, from the southern Golfo de Penas through the Andes of Patagonia and the Andes of Tierra del Fuego.

Garreaud (2009) stated that the Andes play an important essential role in the climate and the water cycle, acting as a barrier to global atmospheric circulation and determining major climatic features in South America, being the eastern slope wetter than the western one (Gregory-Wodzicki, 2000). The Andes have a very complex geography, resulting in the existence of several types of habitats, presenting very steep elevational gradients with high mountains and deep valleys, numerous rivers originated in the slopes, and plateaus that flow into the Pacific Ocean or the Amazon River basin (Mcclain & Naiman, 2008; Weberbauer, 1945). The vegetation on the west side of the Andes is considerably scarce, and from 2,000 m, the landscape changes to environments where Andean pastures predominate (Weberbauer, 1945); on the eastern side, there is the opposite, with montane, Yungas, and Cloud, these super humid forests in the higher areas (above 1200-1500 m) and lowland Amazon rainforest in the lower portion of the slopes (Brown 1995; Swenson 2012).

In terms of biodiversity, the Andes harbor the highest species richness when compared to any other tropical mountain range in the world (Hughes & Eastwood, 2006) and also possesses the largest number of endemic species, both for vertebrate and plant species (Myers et al., 2000; Cracraft, 1985; Prado et al., 2015). This unique biodiversity is attributed to the Andean orogeny, which has had a solid and direct influence on the evolutionary processes of the biota (Haffer, 1967; Gentry, 1982; Lynch & Duellman, 1997; Velazco & Patterson, 2008). Two main modes of speciation have been proposed to explain this diversity: vicariance (Lessa et al., 2003; Coyne & Orr, 2004.) and ecological gradients (Endler, 1977, 1982; Patton & Smith, 1992; Patton et al., 1990; Smith. & Patton, 1991). The first mode refers to the allopatric speciation as a product of the isolation of the populations due to the emergence of physical barriers that interrupt the gene flow, and in an attempt to explain this isolation, the following models were proposed: Pleistocene refuge model (Haffer, 1967); riverine barrier model (Wallace, 1854; Patton & Smith, 1992), and mountain vicariance (Kuntze 1895; Cracraft & Prum 1988). The second mode is related to parapatric speciation, which suggests that marked environmental gradients result in adaptive divergence and speciation (Endler, 1973, 1977; Smith et al., 2001).

These features give the Andes an interesting area for the study of the evolution of biodiversity since, in biogeographic terms, these features could influence the processes of isolation and interruption of gene flow (Futuyma, 1998; Weir, 2006) and promote a relatively fast, speedy and extensive and adaptive differentiation (Reig 1986) Currently, there are studies in various taxa such as birds (e.g., Fjeldså et al. 2012, Hazzi et al. 2018), reptiles (e.g., Duellman 1979; Esquerré et al. 2019), invertebrates (e.g., Hutter et al. 2013, De-Silva et al. 2016, Ceccarelli et al. 2016), mammals (e.g., Reig, 1986, Patto et al 1990, Patton & Smith, 1992) among others; these studies, independently, contribute to a better understanding of the Andean system. Among the various taxa that can be studied, the subfamily Sigmodontinae of the Order Rodentia is an exciting group for biogeographical and evolutionary studies. This subfamily has a significant representation in museums and collections and many species (D'Elía and Pardiñas 2015); Likewise, Andes have the potential to promote a relatively speedy and extensive differentiation in this subfamily (Reig 1986).

Thus, the present document provide information on the diversity and biogeographic patterns of sigmodontine rodents throughout this mountain range. To reach this goal, I divided this thesis into three chapters; the first is develop here as a general introduction, the second and thrid chapters are organized as scientific manuscripts.

The second chapter aims to present an overview of the Andes, with an update on the status of the biogeographic knowledge for small non-volant mammals and identify areas of endemism of the rodents of the subfamily Sigmodontinae in the Andes. To accomplish this goal, I compiled information coming from non-volant small mammals community assembly in the high Andean region, considering as a selection criterion the elevation of 2,000 meters (Duellman 1979). It should be noted that this first stage was published (see Rengifo et al. 2022, as a datapaper on ECOLOGY journal), following the recent published data set of Atlantic forest (e.g., Bovendorp et al. 2017; Vancine et al. 2018, Culop et al. 2019, Souza et al. 2019, Silva et al. 2022). To identify the areas of endemism of the sigmodontine rodents in the Andes region, I employed the NDM/VNDM software (Szumik et al. 2002) as an alternative to methods such as parsimony and clustering (e.g., Morrone, 1994; Linder, 2001). Following Szumik & Goloboff (2004), an area of endemism is defined as a particular pattern of distribution pattern delimited by the congruence of at least two taxa restricted to one area. Platnick (1991) suggests that given the distributional range of a species is determined by historical and current factors; it can be assumed that if two species show similar ranges, they may have been affected by similar factors. Thus the identification of areas of endemism is essential to understand the spatial component of evolution and assist the identification of priority areas in need of conservation measures (Myers et al. 2000). Therefore, in this chapter, I tested the hypothesis that the resulting patterns from the analysis of endemism are congruent with areas previously delimited using other methods (such as those established by Herzog et al. 2011; Swenson 2012; Del Ventura 2013; Noguera-Urbano & Escalante, 2015; Pacheco et al. 2015; Sandoval et al. 2010, 2015, 2021)

In the third chapter, I aim to evaluate the intra and inter-populational morphologic and molecular variation of the species of rodents distributed on both sides of the Cordillera Blanca, intending to describe the demographic scenarios that led to the current distribution. I focused on the Cordillera Blanca in northern Peru, a smaller geographic region influenced by orogenic processes that exhibit dramatic environmental gradients over short geographic distances. Early hypothesis could drive allopatric speciation for sigmodontinae rodents (see Pacheco et al. 2015, Rengifo & Pacheco 2015). To accomplish this goal, I applied both morphological and genomic approaches. The morphological approach followed the traditional methodology of qualitative and quantitative analysis of characters (see Musser, 1968; Prado & Percequillo, 2017), aiming to understand the pattern of geographical variation between the populations and, lately, to solve the alpha taxonomy of species (see Prado & Percequillo, 2018). Genetic data was obtained through the ddRAD-Seq method, which allows the generation of multiple nuclear markers, with SNPs (unique site polymorphisms) detected at near-close readings or between restriction sites scattered throughout the nuclear genome, which do not require prior genome knowledge (Peterson et al., 2012). One of the advantages of using the ddRAD-Seq technique is that the generated data can be used for both phylogenetic analysis (Rubin et al. 2014, Eaton 2014) and phylogeographic analysis (McComack et al. 2013; Reitzel et al. 2013). It also can be used for detailed analysis of the genetic structure of populations, for example, to verify changes in the allele frequencies in space (e.g., van Heerwaarden 2010), to analyze the demographic history of the populations (e.g., if the populations underwent retraction events or expansion) and identify genes related to adaptation and specific environmental conditions (Hohenlode et al., 2010). The hypothesis that point that Cordillera Blanca drives allopatric speciation for sigmodontinae rodents has not been tested, Pacheco et al. (2014), Rengifo & Pacheco (2015) proposed it based on Cytb markers and only for the genus *Phyllotis*, that is why on the present chapter I tested the hypothesis that the orogenic process occurred at Cordillera Blanca between ~6 - ~ 2 Ma promoted the morphological and genetics patterns of sigmodontinae rodent having an important role on the evolutionary history of sigmodontine rodents that occurs in this region, differencing western and eastern populations.

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2. STATUS ON THE BIOGEOGRAPHICAL KNOWLEDGE FOR SIGMODONTINE RODENTS (RODENTIA: CRICETIDAE) IN THE ANDES

Abstract

Information from diversity inventories is used to study patterns of biodiversity and species distribution, to identify potential priority areas for conservation, and to guide future sampling efforts. In this context, In this second chapter I compiled information on non-volant small mammal communities from the high Andes (> 2,000 m.). Here, I present an dataset containing information on diversity (species composition, number of individuals captured), inventory design (type of traps, sampling efforts), and environment (habitat) for both unpublished and published information. This study covers 630 mammalian communities, geographically distributed throughout the seven countries. I compiled a total of 26,412 individual records belonging to 240 species; the order with greatest number of records was Rodentia (n=25,319, 96.06%), followed by Didelphimorphia (n=373, 1.42%), Eulipotyphla (n=358, 1.36%) and Paucituberculata, (n=307, 1.16%). In other hand in this same chapter I identify areas of endemism of the rodents of the subfamily Sigmodontinae in the Andes. I tested the hypothesis that the resulting patterns from the analysis of endemism are congruent with areas previously delimited using other methods. I used distributional records of a total of 198 species of subfamily Sigmodontinae among a total of 11,487 records distributed in 4095 localities; that were executed in NDM/VNDM software, with two different grid sizes of 0.5 ° and 0.75. Quantitative and qualitative analyses allowed the recognition of eight Areas of Endemism (AoE) throughout all Andes which I named as: i) Merida-Tama (MET), ii) Western Colombian (WC), iii) North-Central Ecuador (NCE),. iv) Huancabamba-Alto Marañon (HAM), v) Cuzco (CU) vi) Eastern Puno-La Paz (EPL) vii) Cochabamba (CO)) viii) Northwest Argentina (NWA). These results may corroborate and accept the hypotheses that patterns found here are congruent with previously delimited using other method and in other taxa. This study comprise the first attempt to identify area de endemism in the totality of the Andes using the most complete data set of records of sigmodontinae rodents

Keywords: Andes, Endemism, Sigmodontinae, NDM/VNDM

2.1. Introduction

Among mammals, members of the Orders Didelphimorphia, Microbiotheria, Paucituberculata, Eulipotyphla, and Rodentia (small non-volant mammals), are the most diverse vertebrate groups inhabiting the Andes (Gardner 2008, Hershkovitz 1962, 1972, Patterson et al. 2012, Patton et al. 2015). Generally, species of the Orders mentioned above are characterized by small body size, low vagility, and strong ecological dependence on specific habitats (e.g., Lima and Jaksic 1999, Kelt et al. 1999, Palmeirim et al. 2020). Beginning with Andean orogeny in the Miocene (Hoorn et al. 2010), ancestors of these lineages were affected by dispersal and vicariance events; Ecological adaptation and diversification across ecological gradients have resulted in a mammalian fauna whose elements are distributed according to environmental, latitudinal, and altitudinal features of each region (Endler 1977, Patton et al. 1990, Smith and Patton 1991, Patton and Smith 1992, Lessa et al. 2003, Coyne and Orr 2004, Patterson and Velazco 2008, Patterson et al. 2012).

Among the non-volant small mammals, the rodents of the subfamily Sigmodontinae (Rodentia: Cricetidae), *sensu* Wagner (1843), are the most diverse taxa in the Andes (Patton et al. 2015, D'Elía and Pardiñas 2015). This group has a remarkable ecological and zoonotic role; some species are important in seed and spore dispersal and also seed predation (e.g., Noblecilla and Pacheco 2012, Sahley et al. 2015, 2016); others are prey items for larger predators such as carnivore mammals, raptor birds, or snakes (e.g., Jaksik et al. 1999, Iriarte and Jaksic 2012, Fajardo et al. 2014, Brito et al. 2015, Orellana-Vasquez and Diaz 2019). Some others serve as reservoir hosts for important zoonotic infectious diseases such as Andean cutaneous leishmaniasis and hantavirus (e.g., Llanos et al. 1999 and Padula et al. 2004, respectively).

The Sigmodontinae is an interesting group for biogeographical studies due to its great representation in museums and collections, wide distribution, the large number of species, and its high level of endemism (D'Elía and Pardiñas 2015). Nonetheless, there are few studies with macro information about sigmodontine rodents in the Andes; Reig (1986) described the patterns of diversity of the sigmodontine for the high Andes, as well as possible areas of original differentiation (AOD) for the different tribes of these rodents. Other authors as Patterson et al. (2012), mentioned some generalities of the Andes and their influence on the processes of mammals' diversification, Patton et al. (2015) presented a review of sigmodontine rodents in which several Andean species were accounted for, presenting maps of distribution for each species. In contrast, Prado et al. (2015) presented the first study of areas of endemism of the Oryzomyini tribe, establishing the Northwestern part of South America as an area of endemism.

In this Chapter, I compiled a large dataset from inventories including all non-volant small mammal communities from the high Andes (see Rengifo et al. 2022), with the purpose of i). expanding the panorama of the small mammals' diversity and distribution throughout the extension of the high Andes; ii). describe the major patterns of data regarding species recorded and identify the gaps and well-studied areas, showing community assemblage in the Andean region; and iii). Finally, establish areas of endemism, employing Endemicity Analysis (EA) using the software NDM/VNDM (Szumik et al. 2002) to identify areas of endemism for the sigmodontinae rodents in the high Andes.

2.2. Methods

To assemble a comprehensive dataset, I considered two types of sources: (i) small mammal inventories in the Andes since 1939; and (ii) data available from museum and scientific collections databases.

2.2.1. Small mammal inventories in the Andes

Geographical information includes specific locality, province/department, and country; latitude and longitude coordinates are in decimal degrees. I defined non-volant small mammals as those species mainly under 1,000 g represented within the Orders Didelphimorphia, Paucituberculata, Eulipotyphla, and Rodentia (Gardner 2008, Patton et al. 2015); additionally, I included larger species in those Orders, such as the ones included in the genera *Didelphis*, *Cavia, Microcavia,* and *Galea*. In the same way, I added to the dataset non-small mammals that were captured only occasionally, such as *Coendou quichua*, *Lagidium viscacia*, *Mustela frenata*, *Sylvilagus andinus,* and *Notosciurus granatensis*. Missing information was labeled as "N/A". Small mammal information was compiled from literature (Pearson 1951, Dorst 1971, Pearson and Pearson 1978, Pizzimenti and de Salle 1981, Aagaard 1983, Simonetti et al. 1985, Reise and Venegas 1987, Zuñiga et al. 1988, Soriano et al. 1990, Leo and Romo 1992, Díaz de Pascual 1993, López-Arévalo et al. 1993, Yensen and Tarifa 1993, Arana-Cardó and Ascorra 1994, Durant and Diaz 1995, Gómez-Cervero 1996, Anderson 1997, Bonaventura et al. 1998, Barnett 1999, Jaksic et al. 1999, Castro and Román 2000, Solari et al. 2001, Voss 2003, Gómez 2004, Sánchez et al. 2004, Valencia et al. 2004, Pozo and Trujillo 2005, Haynie et al. 2006, Lee et al. 2006, Vivar 2006, Borghi and Giannoni 2007, Corredor-Carrillo 2007, Pacheco et al. 2007, Rodríguez et al. 2007, Tarifa et al. 2007, Vargas et al. 2007, Jayat et al. 2008, Ferro and Barquez 2008, Lee et al. 2008, Corrales and López 2009, Corporación Autónoma Regional de Cundinamarca - CAR 2009, Martínez et al. 2009, Montañez 2009, Prado and Bonilla 2009, Ramírez-Chaves et al. 2009, Tirira and Boada 2009, Castaño and Corrales 2010, Jayat et al. 2010, Zevallos and Carrera 2010, Jayat et al. 2011, Lee et al. 2011, Medina et al. 2012, Péfaur et al. 2012, Viancha et al. 2012, Jayat et al. 2013, Pacheco et al. 2013, Teta et al. 2013, Ferro and Barquez 2014, Mendoza and Sánchez 2014, Novillo and Ojeda 2014, Latorre and Arévalo 2015, Lee et al. 2015, Valladares et al. 2015, Brito and Ojala-Barbour 2016, Lobos and Alzamora 2016, Medina et al. 2016, Cairampoma 2017, Ferández de Córdova et al. 2017, Jayat et al. 2017, Medina et al. 2017, Jayat et al. 2018, Vargas-Ramírez et al. 2018, Bautista et al. 2018, Díaz-Beltran and Ladino-Moreno 2018, Lee et al. 2018, Vargas et al 2018, Beninato et al. 2019, Curay et al. 2019, Ojala-Barbour et al. 2019, Pacheco and Noblecilla 2019, Villarreal 2019, Storz et al. 2020, Lee et al. 2021, Urquizo et al 2021), and my own unpublished data.

Taxonomic identification was carefully checked; the nomenclature follows Gardner (2008) for the Orders Didelphimorphia, Microbiotheria, Paucituberculata, and Eulipotyphla, and Patton et al. (2015) for the Order Rodentia. When necessary, I updated the taxonomy of some taxa (Pacheco et al. 2014, Hanson et al. 2015, Rengifo and Pacheco 2015, Jimenez and Pacheco 2016, Quiroga-Carmona and Do Nascimiento 2016, Teta et al. 2017, Hurtado and D'Elía 2018, Brito et al. 2019, Noguera-Urbano et al. 2019, Voss et al. 2020, Hurtado 2021, Jayat et al. 2021).

To verify the accuracy of the information compiled here, I built an accumulated curve with 95% confidence intervals (shaded areas) from a dataset of non-volant small mammal communities from the High Andes. The 95% confidence intervals were obtained by a bootstrap method based on 1,000 replications. (Chao et al. 2009, Chao et al. 2014, Chao and Jost 2012).

2.2.2. Scientific database

For the purpose of performing the endemicity analysis, ocurrence data for sigmodontinae species from the Andes were obtained from online databases, namely the VertNet (https://www.vertnet.org) and GBIF (Global Biodiversity Information Facility https://www.gbif.org) as well from the compiled information of Rengifo et al. 2022 (see previous section). Though databases are an excellent instrument for obtaining biographical information, they are not always curated data, which is why it is necessary to perform a cleaning (Magdalena et al. 2018). I organized the data, including information relevant as institution name, collection catalog number, generic epithet, specific epithet, original database name, corrected database locality name, original coordinate, and corrected coordinate. I debugged the information, correcting erroneous coordinates. Whenever I identified questionable misidentification, I excluded it, or, when possible, I made the identification of specimens housed in MUSM (Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima Peru), FMNH (The Field Museum of Natural History, Chicago, USA), UMMZ (The University of Michigan Museum of Zoology), USNM (The National Museum of Natural History, Washington, USA) and AMNH (American Museum of Natural History, New York, USA). All coordinates were standardized to decimal degrees. Following Duellman (1979), I treated all species inhabiting areas above 2,000 m as Andean

2.2.3. Areas of endemism

The dataset with records were used to elaborate the distribution maps, which were used as a basis for delimiting areas of endemism. The search for areas of endemism carried out by the optimality criterion, known as endemicity analysis (EA), as proposed by Szumik et al. (2002) and Szumik & Goloboff (2004) and implemented in NDM/VNDM programs version 3.0 (Golo boff, 2011), two different grid sizes of 0.5 ° and 0.75° following the recommendations of Dalapicolla et al. (2021). The analyses were conducted using the following parameters: default-origin; temporarily save sets within 0.99 of the current score; save sets with two or more endemic spp.; save sets with a score above two.; keep overlapping subsets if 50% of species unique; Endemicity score above 1.0. Minimum endemicity score 0.4. Searches were repeated 100 times. I selected species with a minimum score of 0.4 (Escalante et al., 2013). and I computed the consensus areas of endemism using a cut-off of 100% similarity in species and the strict consensus (Szumik et al., 2002). To delimit the Areas of endemism, I followed the qualitative method suggested by DaSilva et al. (2015) with the modifications of Dalapicolla et al. (2021)

2.3. Results

2.3.1. Small mammals' inventories in the Andes

As results of an exhaustive bibliographic review, including published articles (n=66), book/book chapters (n=9), theses (n=6), technical reports (8), and unpublished data (n=45). I obtained information from 630 mammalian communities (or localities) from seven Andean countries: Argentina (n = 92), Bolivia (n = 82), Chile (n = 45), Colombia (n = 37), Ecuador (n = 38), Peru (n = 322), and Venezuela (n = 14) (Figures 1 and 2). Following the criteria proposed by Dinerstein et al. (2017), the communities were distributed across 22 ecoregions, with the Central Andean Puna the most frequently sampled (n = 109 communities), followed by the Central Andean Wet Puna (n = 94 communities), the Sechura desert (n = 79 communities), Central Andean dry Puna (n = 60 communities), the Peruvian Yungas (n = 57 communities), and Southern Andean Steppe (n = 39 communities); remaining ecoregions represent 192 communities (Figure 3). Only 29.5% of these localities fell within the boundaries of current protected areas.

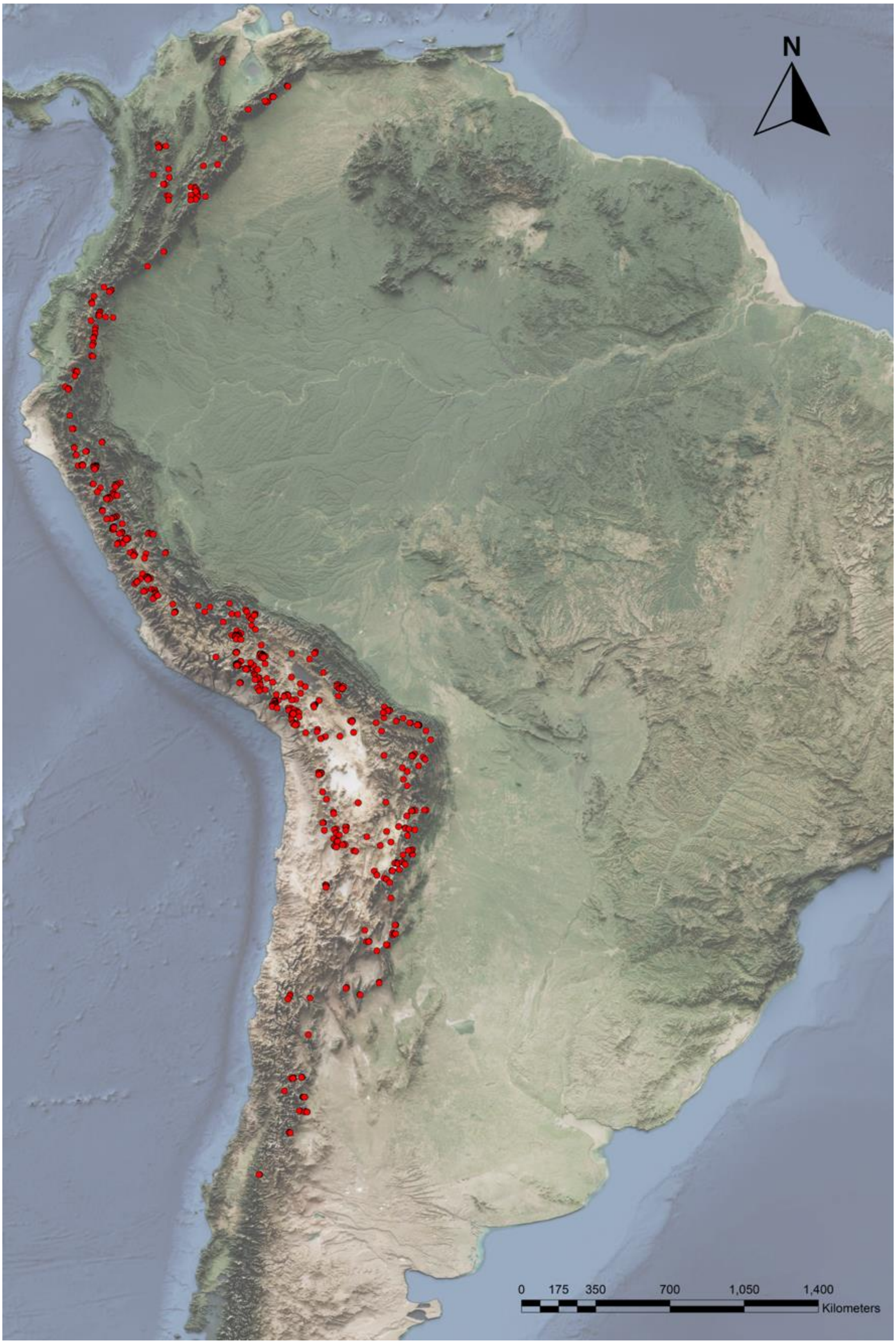

Figure 1. Distributional records of small mammal communities (red dots) compiled in the ANDEAN NON-VOLANT SMALL MAMMALS dataset.

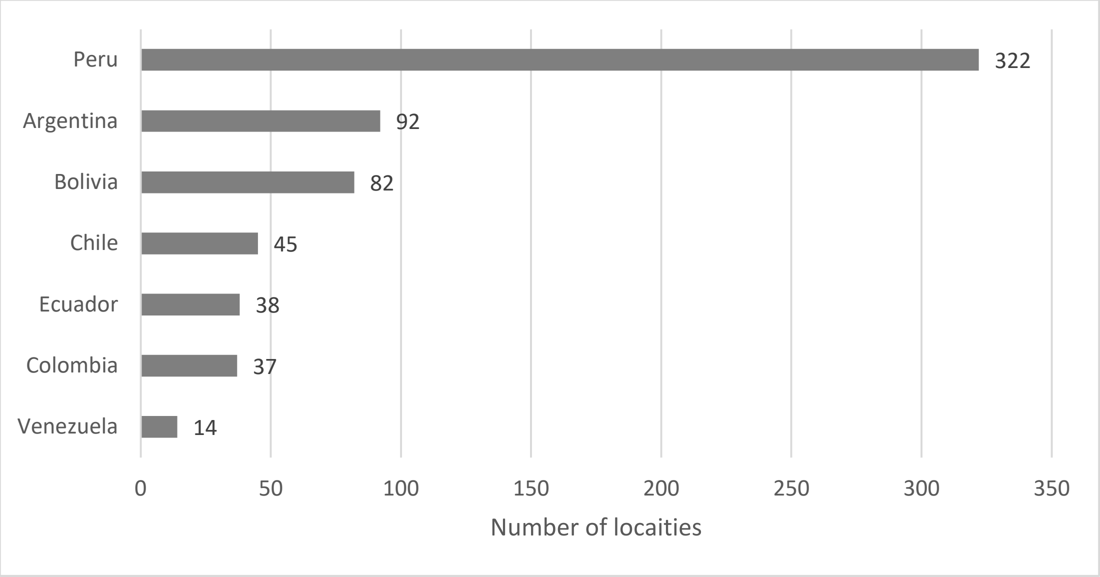

Figure 2. Total number of localities (or communities) sampled by country in the ANDEAN NON-VOLANT SMALL MAMMALS dataset. Countries were ordered from highest to lowest number of localities.

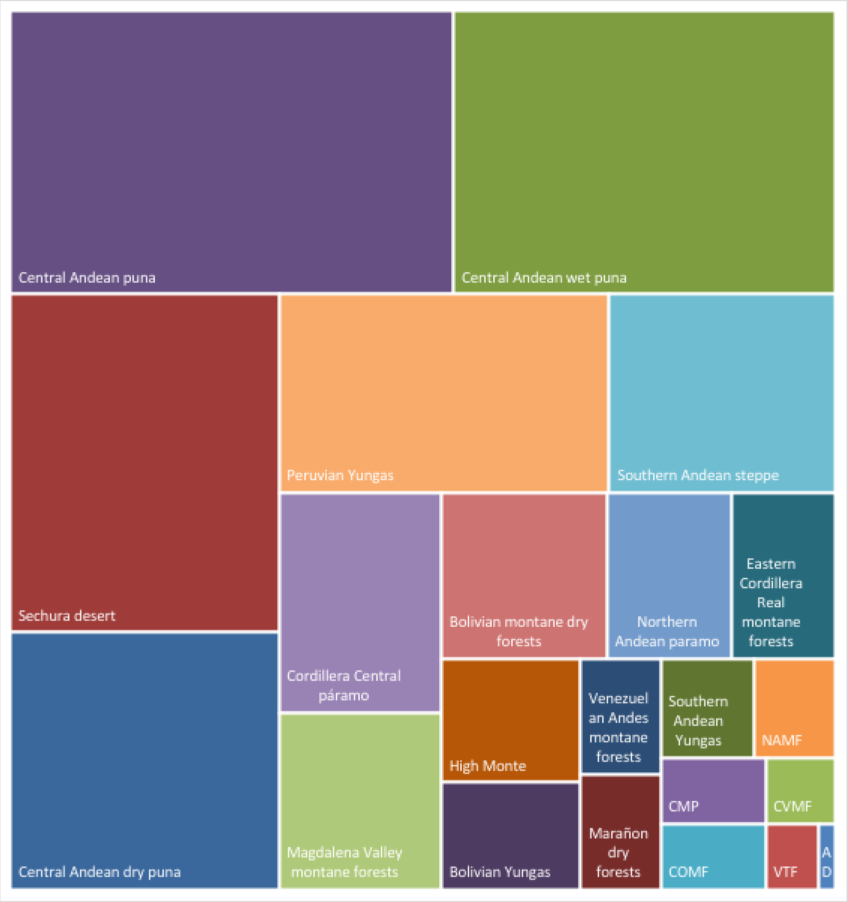

Figure 3. Proportion of localities sampled by ecoregion following the criteria of Dinerstein et al. (2017). Ecoregions of low proportional representation include: AD (Atacama Desert), VTF (Valdivian temperate forests), CVMF (Cauca valley montane forests), CMP: (Cordillera de Merida paramo) COMF (Cordillera oriental montane forests), NAMF (Northwest Andean montane forests).

The oldest study was conducted in 1939 (Pearson 1951); the subsequent years might be divided into two periods: 1) the period from 1960 to early 1990s with few studies (n=15), and 2) a period from 1993 to 2020, in which there was a substantial increase in the number of studies (n=115). This recent intensive sampling directly resulted from the formation and consolidation of local research groups (Figure 4). The elevation of most localities (n=187) sampled ranges from

3,500 to 4,000 m (Figure 5). The sampling effort varied from 18 trap-nights to 21,000 trap-nights (see Pacheco & Noblecilla 2019) for individual localities. Throughout the Andes, non-volant small mammal communities harbor 1-17 species, with 12.06% of sites being composed of a single species, 15.24% with two species, 20.16% with three species, 14.44% with four species, 12.06% with five species; 23.43% with species richness from six to ten, and 4.60% composed of more than ten species (Figure 6).

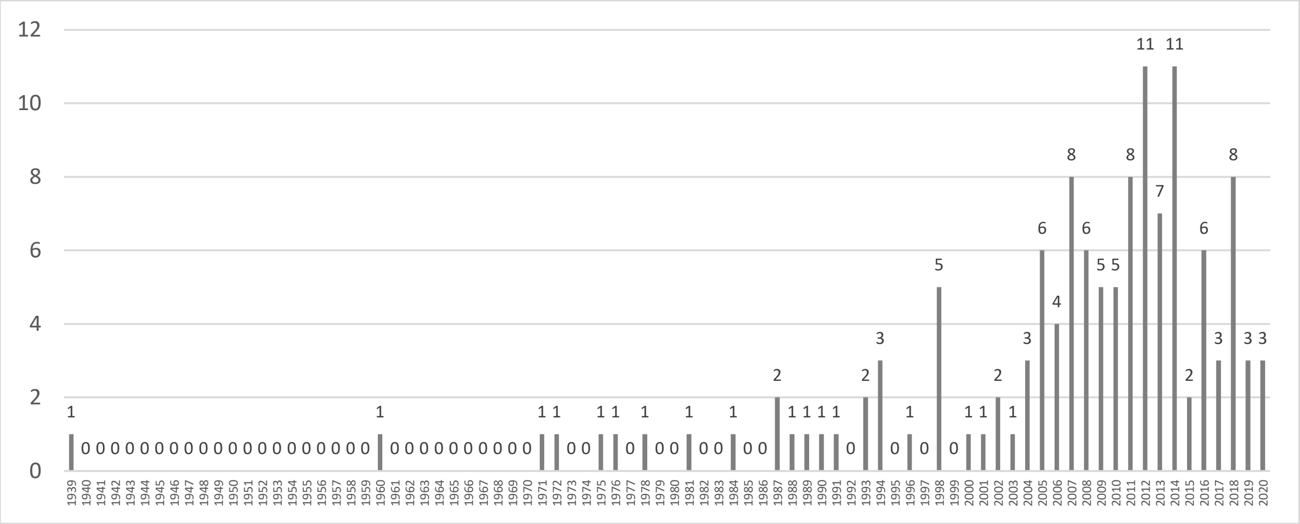

Figure 4. Number of studies with information available per year in the ANDEAN NON-VOLANT SMALL MAMMALS dataset. Only the first year of each study is included.

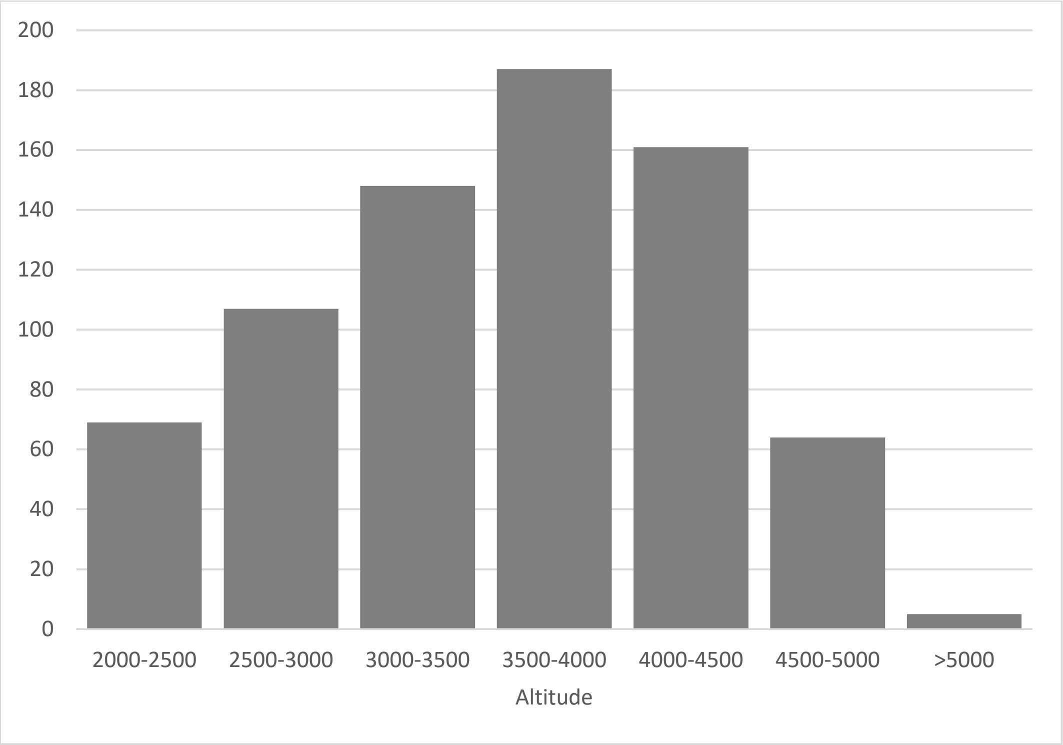

Figure 5. Total number of localities sampled per range in elevation in the ANDEAN NON-VOLANT SMALL MAMMALS dataset. Data include both exact elevation and range of elevation for each locality taken from each locality information given in each study.

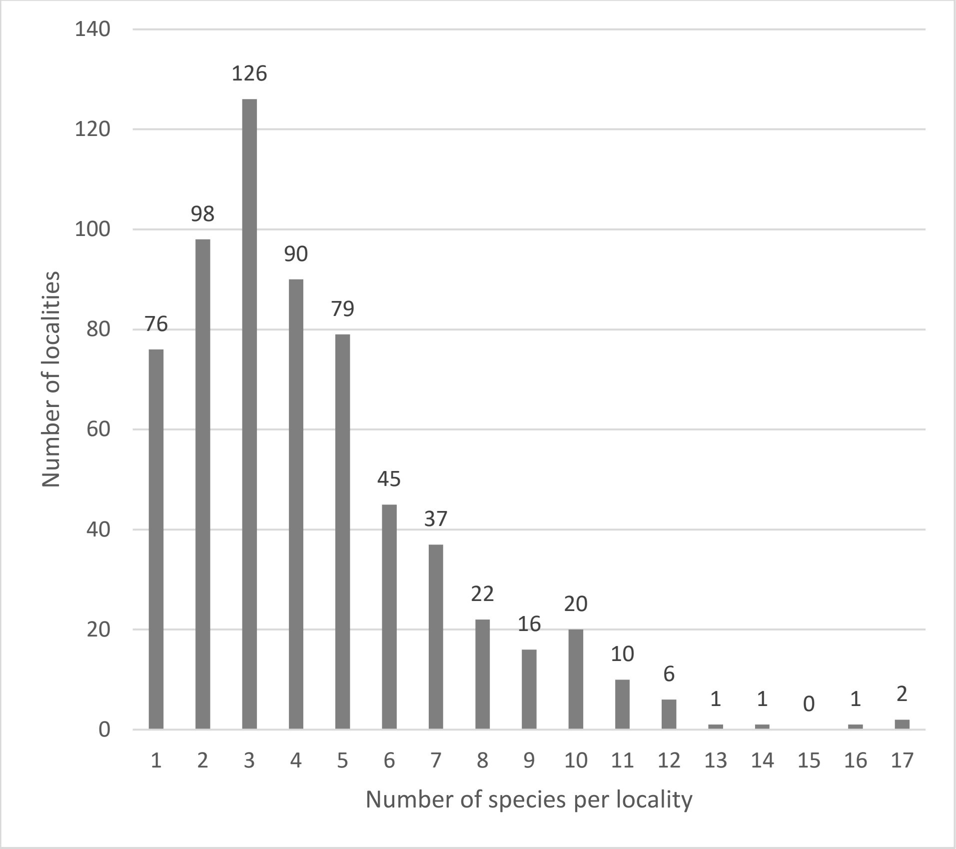

Figure 6. Number of species per locality; each bar shows the total number of localities per species richness, ordered from localities with one species to 17 species.

I compiled a total of 26,534 records of individuals belonging to 241 species (for a complete dataset see Rengifo et al. 2022); the Order with the highest number of records was Rodentia (n=25,319, 96.06%), with 204 species, assembled in eight families; Cricetidae was the most representative with 188 species (Table 1). The most frequently represented genera were *Akodon* (n=8,190), *Phyllotis* (n=4,674), and *Thomasomys* (n=3,419). Other registered Orders included Didelphimorphia (n=373, 1.42%) with 20 species, Eulipotyphla (n=358, 1.36%) with 12 species, and Paucituberculata, (n=307, 1.16%) with five species (Figures 7 and 8). The dataset contained 236 confirmed small non-volant species, including undescribed species from four different genera (*Nephelomys*, *Akodon*, *Thomasomys*, and *Chibchanomys*). I could not identify eleven species in seven genera (*Ctenomys, Eligmodontia, Handleyomys, Marmosa, Marmosops, Phyllotis,* and *Thomasomys*), due to ambiguous information or by the fact of two or more species of the same genus coexisting in the same locality.

Table 1. List of families, with number of species of the order Rodentia captured, across all inventories compiled in the ANDEAN NON-VOLANT SMALL MAMMALS dataset.

Families	Number of species
Cricetidae	188
Ctenomyidae	11
Caviidae	7
Abrocomidae	2
Muridae	2
Chinchillidae	1
Octodontidae	1
Heteromyidae	1

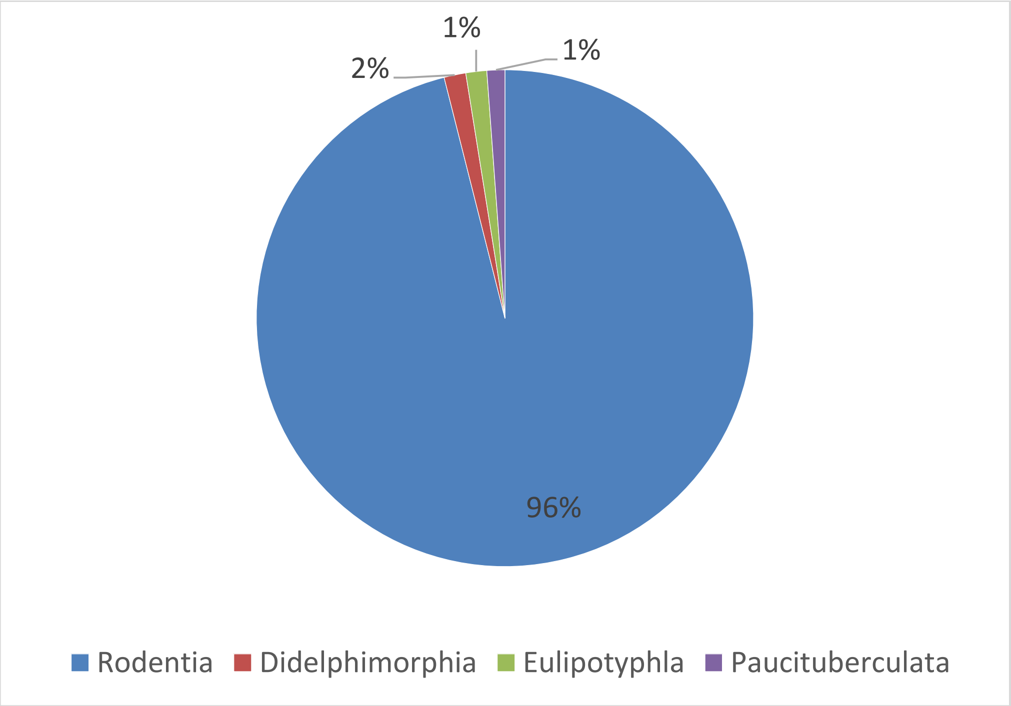

Figure 7. Pie chart showing the proportion of taxa captured in all inventories that I compiled in the ANDEAN NON-VOLANT SMALL MAMMALS dataset.

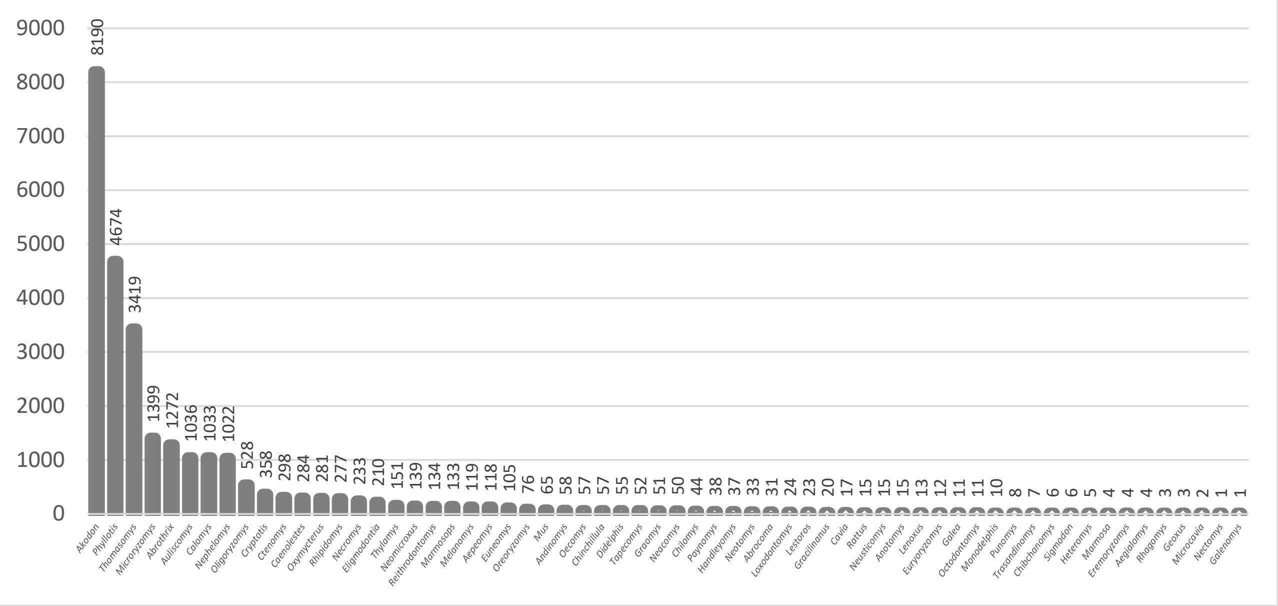

Figure 8. Number of individuals per genus recorded in the studies compiled in the ANDEAN NON-VOLANT SMALL MAMMALS data.

The Andes exhibit a large diversity of habitats; in the data, I identified eleven types: forests, geliturbed, grassland, shrubland, yaretal, paramo, wetland, rocky, riparian, plantation, xeric, and farm (see table 2 for definitions). Multiple sampling methods were used to survey non-volant small mammals; usually, these surveys included a combination of two or more types of traps, with the most representative snap-traps (Museum special and/or Victor rat traps) and live traps (Sherman) or combination of other trap types. Sherman traps were used in more than 81% of the studies; snap-traps were used in more than 50% of the studies; different trap types included Tomahawk (15%), pitfall (10%), Lux rat steel traps, and Berker traps (Figure 9). Voucher specimens collected were deposited in 38 research institutions (Appendix A). The species accumulation curve (Figure 10) shows a considerable increase until before the first 5k records, which is close to reaching an asymptote.

Table 2. Habitat and definition that I considered in the ANDEAN NON-VOLANT SMALL MAMMALS dataset. Based in Weberbauer 1945, Cano et al 2011, Trujillo 2013.

Habitat	**Definition**
Forest	Characterized by a wooded landscape with herbs and shrubs and mainly native trees, such as *Polylepis* or *Alnus*.
Geliturbed	Characterized by scattered and discontinuous vegetation cover, conditioned and adapted to the daily alternation of ice-thaw typical of high tropical mountains
Grassland	Composed primarily of herbaceous vegetation, such as the gramineous or hard grass genera *Festuca* and *Stipa*.
Shrubland	Characterized by the presence of woody and shrubby vegetation, with scattered trees and occasionally some cacti.
Yaretal	Dominated by a plant formation, characterized by its padded shape (*Azorella compacta*) predominates, with the presence of other species such as herbaceous vegetation.
Paramo	Characterized by the presence of shrubs and Poaceae such as the *Stipa* species as the predominant population.
Wetland	Characterized by areas of floodable soils and the presence of small water mirrors, with the presence of herbaceous vegetation adapted to areas with a high degree of water saturation, such as water cushion (*Distichia muscoide*s), paco (*Oxychloe andina*) and aquatic plants.
Rocky	Comprising rocks of different sizes arranged on slopes, its vegetation is represented by herbaceous and shrub species.
Riparian	Lands that occur along watercourses like rivers. Vegetation is present due to the humidity .
Plantation	Reforested areas usually with non-natives trees, like *Pinus* or *Eucalyptus*
Xeric	Characterized by low or moderate moisture supply and with plants adapted to water scarcity.
Farm	Lands used for agricultural practices, usually a few hectares of native food crops.

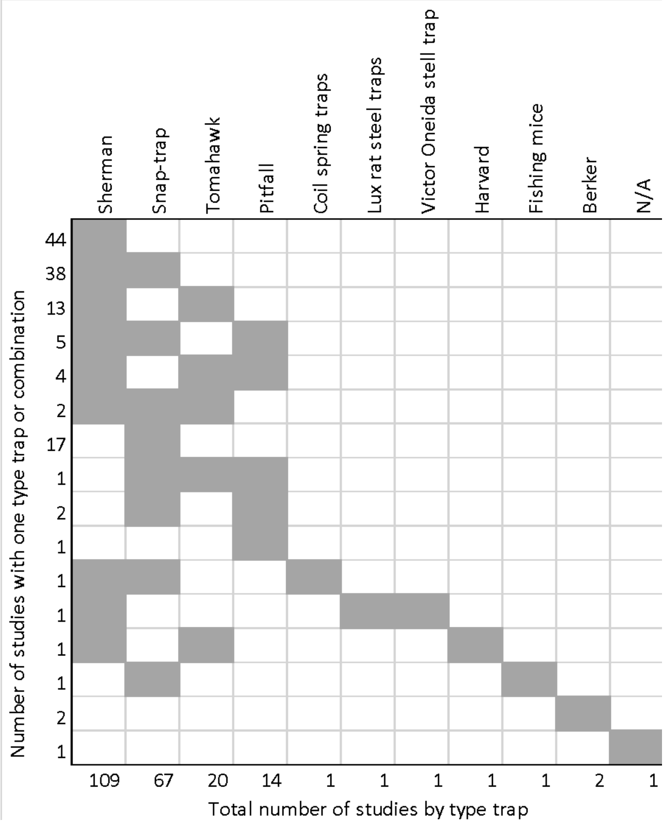

Figure 9. Type of traps or combinations (gray cells) used in the studies compiled in the ANDEAN NON-VOLANT SMALL MAMMALS dataset.

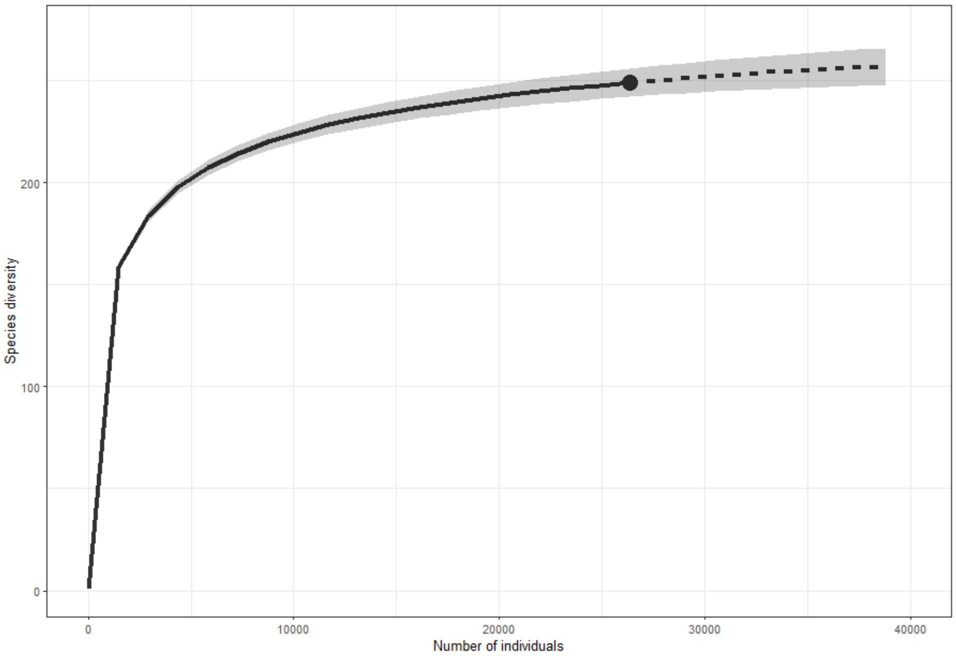

Figure 10. Species accumulation curve of the number of confirmed species. Sample-size-based rarefaction (solid line segment) and extrapolation (dotted line segments).

2.3.2. Area of endemism

A total of 198 species of the subfamily Sigmodontinae were analyzed here (See appendix B), among a total of 11,487 records distributed in 4095 localities (see figure 11). Quantitative analyses employing the 0.5° grid identified 19 areas of endemism and 14 consensus areas, and for 0.75° grid identified 35 areas of endemism and 27 consensus areas. After a qualitative analysis, ten consensus areas were retained for 0.5° grid size and nine for 0.75° grid size (See Appendix C). These 19 consensus areas allowed the recognition of eight areas of endemism throughout all Andes which (figure 12) I named as: **i) Merida-Tama (MET)**, located on Cordillera de Merida in Venezuela and extended beyond the Paramo of Tama at boundaries with Colombia, the species present in this area are *Aepeomys lugens*, *A. reigi*, *Chilomys fumeus*, *Thomasomys emeritus*, *T. vestitus,* and *Neusticomys mussoi.* **ii) Western Colombian (WC)**, in the western and central cordilleras of Colombia, it is supported by *Handleyomys fuscatus*, *Rhipidomys caucensis*, *Thomasomys contradictus*, *T. cinreiventer*, T. popayanus, Nephelomys pectoralis**, iii) North-Central Ecuador (NCE)**, occupying a large part of the western mountain ranges, the inter-Andean valley and the eastern mountain range from the Center to the north of Ecuador, the species that support this area are: *Mindomys hammondi*, *Neomicroxus latebricola*, *Phyllotis hagardi*, *Nephelomys moerex*, *Thomasomys fumeus*, *T. ucucha*, *T. erro*, *T. silvestris,* and *Sigmodon inopinatus* support this area. **iv) Huancabamba-Alto Marañon (HAM)**, located in northern Peru, in an area comprising the "Huancabamba depression" and the headwater of Marañon River, the species supporting this area are: *Eremoryzomys polius*, *Eremeryzomys mesocaudis*, *Akodon* sp 1., *Phyllotis stenops*, *Phyllotis pearsoni*, *Neacomys spinosus*, *Thomasomys elusis* and *T. praetor* **v) Cuzco (CU)** located at the north of Apurimac River in the Department of Cuzco (Peru), the species that support this area are: *Akodon surdus*, *Oxymycterus wilkaurco,* and *Thomasomys gracilis*, **vi) Eastern Puno-La Paz (EPL)** Located on the eastern Andes on south Peru and north Bolivia, between the Departments of Puno and La Paz, the species supporting this area are *Lenoxus apicalis*, *Oxymycterus nigrifrons*, *Punomys kofordi*, *Thomasomys ladewi*; **vii) Cochabamba (CO)** located south Bolivian Andes, occupying most of the province of Cochabamba and north Santa Cruz de la Sierra is supporting by *Akodon siberiae*, *Oxymycterus hucucha*, and *Thomasomys australis* (0.700) **viii) Northwest Argentina (NWA)**. Which occupies the west of Tucuman, south of Salta and north of Catamarca in Argentina. The species that support this area are *Eligmodontia bolsonensis*, *Phyllotis anitae*, *P. alisosiensis*, and *Oxymecterus wayku.*

Figure 11. Distributional records of all sigmodontinae Andean rodents used for search areas of endemism in the Andean region.

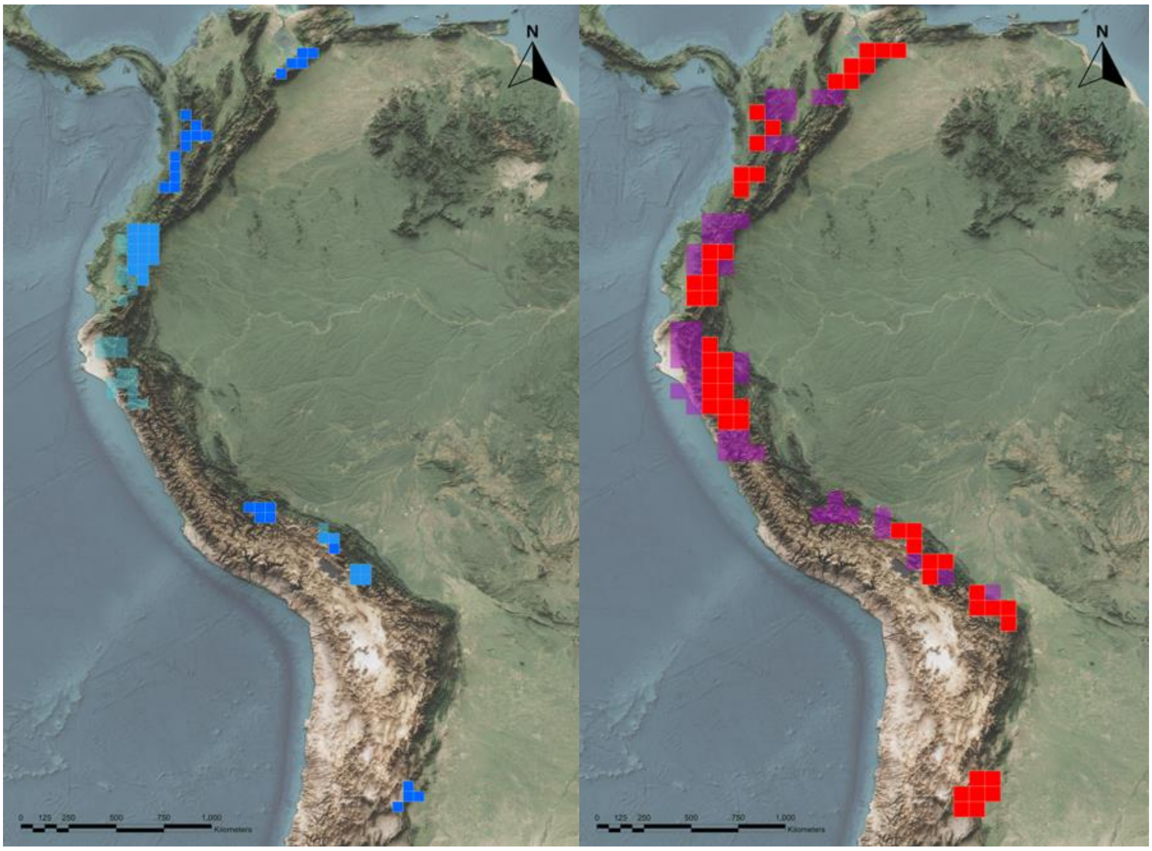

Figure 12. Results of numerical analyses on map. Cell-sets are the consensus areas for endemicity analysis with two grid sizes, left 0.75 size grid, and right 0.5 size grid. Solid color indicates areas retained and transparent color indicate areas removed in the qualitative analysis.

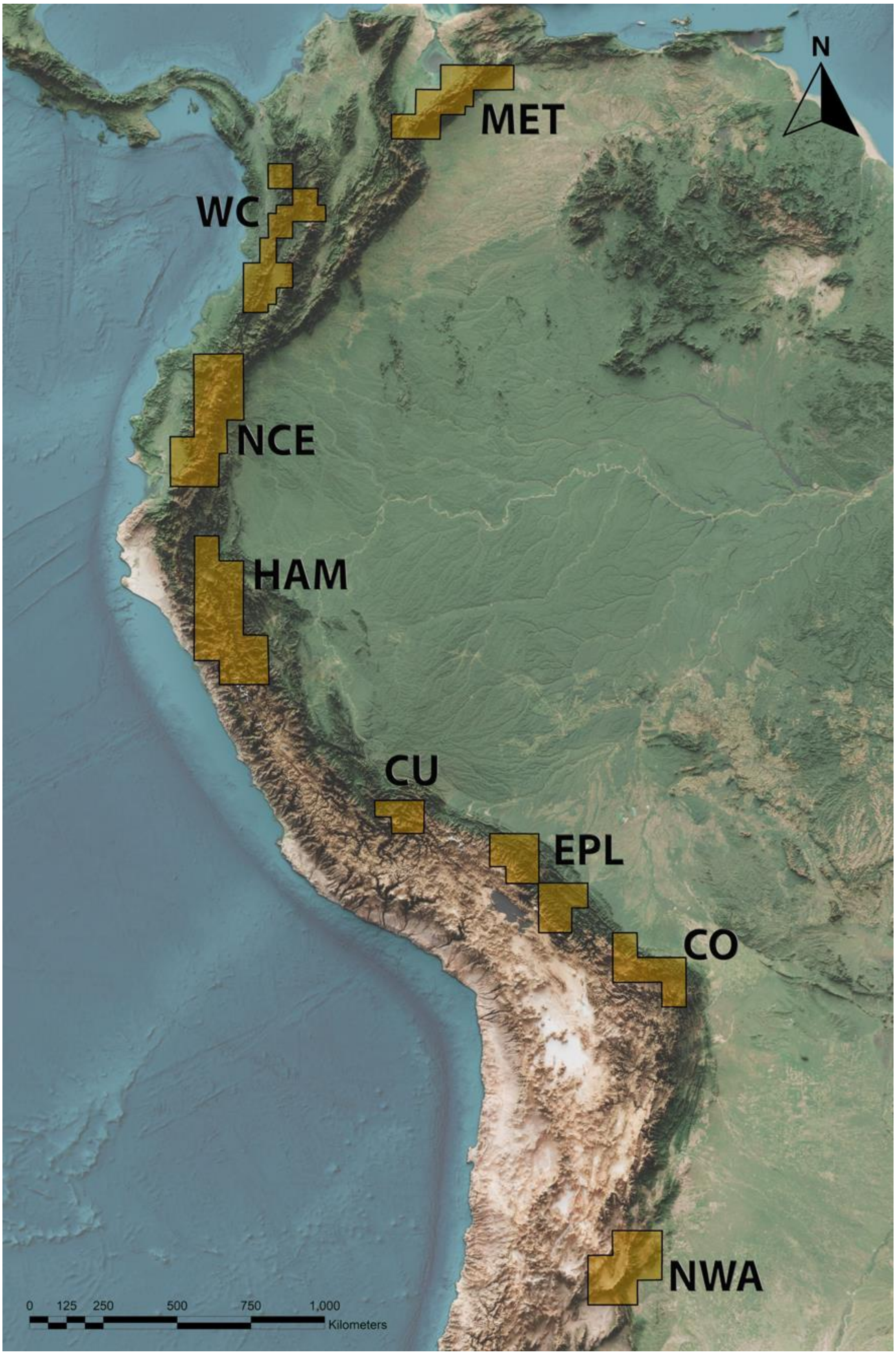

Fig. 3.—Areas of Endemism in the Andean region resulting of analysis for Sigmodontinae rodents. Merida-Tama (MET); Western Colombian (WC), North-Central Ecuador (NCE), Huancabamba-Alto Marañon (HAM); Cuzco (CU) vi) Eastern Puno-La Paz (EPL) vii) Cochabamba (CO) Northwest Argentina (NWA).

2.4. Discussion

Organizing and presenting information about the communities of non-volant small mammals from the high Andes represents a challenging and extensive task because of the large extension of the Andes, passing through several countries. The number of reported assemblages is still comparatively lower than in other regions, and in this dataset, 134 studies are reported. A similar number was reported by Bovendorp et al. (2017), who mentioned 136 studies for the Atlantic Forest (AF), considering that the AF is much smaller in extension when compared to the Andes. Nonetheless, among the 134 studies reported here, only 75 have been published in journals or books, suggesting a deficit of small mammal assemblage research in the current literature. On the other hand, the species accumulation curve comprising the 630 localities surveyed here, while still increasing, is close to reaching an asymptote, suggesting that the dataset covers an adequate representation of the Andean non-volant small mammal composition within the recorded communities

As with any extensive system, some areas of the Andes have been explored more than others. For example, the southern Colombian and central Peruvian Andes have been mostly neglected, likely due todifficulties of access and historical social conflicts (as "guerrillas" that arose during the 1980s and/or as drug trafficking). However, it is also true that other areas, such as the Chilean Andeswith no socio-political challenges, are far from well characterized. Regrettably, I acknowledge that a large amount of collected data remains unpublished, limiting our knowledge of the true diversity and distribution of small mammals inhabiting this unique region as it is the Andes.

As expected, the largest number of records belong to Rodentia (96%). The family Cricetidae, represented by the subfamily Sigmodontinae, adds up to 188 species. This great contrast concerning other taxa indicates that the Andes offer favorable environments for this group of mammals. In the same manner, the diversification process of Sigmondontinae was also intense. Genera such as *Akodon*, *Phyllotis*, and *Thomasomys* are good examples of this process; due to their abundance (in number records) could be considered as fairly-high-richness taxa in the Andes (Reig 1986, Pacheco 2015)

Numerous studies have documented that different traps are required to effectively sample the non-volant small mammal fauna more than any other areas within the Neotropics (McComb et al. 1991, Kalko and Handley 1993, Voss and Emmons 1996). However, here I show that most Andean surveys have the bias of using Sherman traps or a varied combination of Tomahawk traps, snap traps, and pitfall traps to a lesser extent. Pitfall traps are rarely used in Andes surveys, as the soil's rock layers are near the surface. Pitfall traps should be used more frequently in areas with deeper soils, such as alluvial and colluvial deposits,to take advantage of their full potential of capturing rare species (e.g., Luna and Patterson 2003, Medina et al. 2017).

Most endemism areas found with the NDM/VNDM method correspond to previously suggested endemism areas. The Mérida Mountain range has been mentioned as a potential area of endemism by Gutiérrez et al. (2015), Herzog et al. (2011), and Del Ventura (2013). In this study, this area represents the northernmost part of the Andes and is isolated by the Táchira depression and the Páramo de Tama (Merida-Tama, MET). In Colombia, there are three main chains of Andean mountains: Cordillera Occidental, Central, and Oriental. On the endemism analysis applied here, I found that the Cordillera Central and Occidental form a single area of endemism (Western Colombian, WC), coinciding with Quijano-Abril et al. (2006) and Escobar Prieto (2015), who classified it as an area of endemism formerly. In Ecuador, the Andes run across the country from south to north by one chain of mountains, which maintains an almost constant extension from west to east. The analysis of endemism shows an area of endemism from the province of Carchi to the north of Azuay (North-Central Ecuador, NCE). No studies have found similar results for mammals (see Noguera-Urbano & Escalante, 2015). Nonetheless, Tobar-Suárez et al. (2022) suggested the Ecuadorian montane cloud forests in the Andes as a possible area of endemism for amphibians. In north Peru, I found an area of endemism that has been widely studied, Huancabamba-Alto Marañon (HAM)known as the Huancabamba region and extended to the headwaters of the Marañón River. This region is considered a passage from East to West, connecting the Amazon with the Pacific Tropical Forest (see Parker et al. 1985; Carleton and Musser 1989; Cadle 1991). Previously, Swenson (2012) and Pacheco et al. (2015) identified a similar area of endemism; however, the area is wide and not delimited because the authors included rodents, such as bats and marsupials, which have different types of dispersal. Also, Noguera-Urbano & Escalante (2015) identified a similar area, which is wider than that of Pacheco et al. (2015) and includes part of Ecuadorian Andes; this difference could be to the inclusion of large mammals in South America. I think that the three studies are relevant for mammals in general. However, they do not fit for rodents, which have singular habits and display different ecological functions. Cuzco has a small endemism area (CUZ), which is consistent with other studies (e.g., Patton & Smith 1992, Pacheco et al. 2007, Herzog et al. 2011). Hazzi et al. (2018) found what they call a "Phylogenetics Allopatric Break" to the south of the area that delimits this area, known as the Apurimac River Valley. Hazzi et al. (2018) named this area the Apurimac Biogeographic Region. Previously, Swenson (2012), Noguera-Urbano & Escalante (2015), and Pacheco et al. (2015) identified a similar area but wider, given the taxa included in the analysis. I found an area of endemism in south Peru and north Bolivia which I called Eastern Puno-La Paz (EPL), with a predominant habitat of Bolivian Yungas. This area was previously identified in Noguera-Urbano & Escalante (2015) and Pacheco et al. (2015), but wider than in this study. In Swenson (2012), this area is identified only in the Bolivian Andes, probably for the taxa of mammals included. An additional area was also found further south, in the department of Cochabamba (CO), which agrees with the studies by Pacheco et al. (2007) and Harzong et al. (2011). In Swenson (2012), Noguera-Urbano & Escalante (2015), and Pacheco et al. (2015), found a similar area, which extension is similar to CO in this area, probably because of the taxa or because this area has a narrow extension. The EPL and CO areas are found in the same biogeographic region named by Dinerstein et al. (2017) as Bolivian Yungas and by Hazzi et al. (2018) only as Yungas. In northwest Argentina, an area of endemism (Northwest Argentina NWA) has been perhaps the most mentioned by other studies, some related to mammals as those presented by Sandoval et al. (2010, 2015, 2021). This area was not identified in Noguera-Urbano & Escalante (2015).

As expected, the genus *Thomasomys* was recorded in almost all the areas of endemism. Pacheco (2015) reported that some species of *Thomasomys* have reduced distributions and are primarily associated with montane forests. Coincidentally, all the areas of endemism in this study are found in this type of forest. Montane forests have been identified as an area of endemism by several authors, such as Young et al. (2007), and Quijano-Abril (2006). Other genera associated with montane forests are *Nephelomys* (Ruelas et al. 2021, Rico-Cernohorska et al. 2021), *Oxymycterus* (Oliveira & Gonçalves 2015), and *Akodon* (Myers & Patton 1989). On the other hand, species that occur in dryer habitats such as puna or desert (e.g. genus *Phyllotis*, *Calomys, Auliscomys*, *Abrotrix, Neotomys*) were not recovered in any area of endemism; that could be related to the fact that these species that occur in this habitat are widely distributed, which is not congruent to the concept that an Area of endemism as the smallest natural, spatial–historical hypotheses of biotic isolation (DaSilva et al. 2015).

I demonstrated by using NDM/VNDM methods was able to recover eight areas of endemism, likewise, none of them surprised due that other studies have mentioned them previously (see discussion above). These results may corroborate and accept the hypotheses that patterns found here are congruent with previously delimited using other methods and in other taxa. This study is the first attempt to identify area de endemism in the totality of the Andes using the most complete data set of records of sigmodontinae rodents, and will serve to other posterior analyses as in Mammals as others taxa.

2.5. Conclusions

In this second chapter, I compiled the largest dataset from inventories of non-volant small mammal communities from the high Andes; this allows me to have a good panorama about diversity and how the community of small mammals is assembling in the high Andes. I show what are the bibliographic sources that provide information, what are the most studied countries and ecoregions, as well as the increase in studies over the years. It was also possible to show the most used trapping methods, species richness as well as the most prevalent species, and the types of habitats where they occur, the species accumulation curve analysis suggesting the dataset is representative for the Andes region. Finally, when I performed the Endemicity Analysis (EA) using the NDM/VNDM software, I identified eight areas of endemism for the Sigomodontine rodents in the high Andes. These resulting areas corroborate and accept the hypotheses that patterns found here are congruent with previously delimited using other method and in other taxa

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Appendices

Appendix A. List of museum collections were the specimens collected are housed that I compiled in compiling the dataset.

Acronym	Full Name of museum (or collection)
ACUNHC	Abilene Christian University Natural History Collection, Texas, USA.
AMNH	American Museum of Natural History, New York, USA.
CBF	Colección Boliviana de Fauna, Instituto de Ecología y Museo de Historia Natural, La Paz, Bolivia.
CBG-UMSS	Centro de Biodiversidad y Genética de la Universidad Mayor de San Simón, Cochabamba, Bolivia.
CMI	Colección Mastozoológica del IADIZA, Mendaza, Argentina.
CML	Colección Mamíferos Lillo, Tucumán, Argentina.
CNP	Colección de Mamíferos, Centro Nacional Patagónico, Puerto Madryn, Chubut, Argentina.
CRILAR-Ma	Centro Regional de Investigaciones Científicas y Transferencia Tecnológica de La Rioja, La Rioja, Argentina.
CTUA	Colección Teriológica, Universidad de Antioquia, Medellín, Colombia.
CVULA	Colección de Vertebrados de la Universidad de Los Andes, Mérida, Venezuela.
CZUT-Ma	Colección Zoológica de la Universidad del Tolima, Tolima, Colombia.
CZZA	Colección Zoológica de Zonas Áridas y Andinas (CZZA030) de la Universidad de Tarapacá, Tarapacá, Chile.
DR	Detlef Reise Private collection.
FMNH	Field Museum of Natural History, Chicago, USA.
IAvH	Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Santafé de Bogotá, Colombia.
ICN	Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Santafé de Bogotá. Colombia.
JPJ	Juan Plabo Jayat Private collection.
MACN-Ma	Colección Nacional de Mastozoología, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires, Argentina.
MCNG	Museo de Ciencias Naturales de Guanare, Mesa de Cavacas, Guanare, Portuguesa, Venezuela.
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachussetts, USA.
MECN	Museo Ecuatoriano de Ciencias Naturales, Quito, Ecuador.
MEPN	Museo de Zoología, Escuela Politécnica Nacional de Ecuador, Quito, Ecuador.
MHNLS	Museo de Historia Natural La Salle, Caracas, Venezuela.
MHNUC	Museo de Historia Natural, Universidad de Caldas, Caldas, Colombia.
MHNUD-M	Museo de Historia Natural de la Universidad Distrital Francisco José de Caldas, Caldas, Colombia.
MSB	Museum of Southwestern Biology, University of New Mexico, Albuquerque, New Mexico, USA.
MUSA	Museo de Historia Natural, Universidad Nacional de San Agustín, Arequipa, Perú.
MUSM	Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Perú.
MVZ	Museum of Vertebrate Zoology, University of California- Berkeley, California, USA.
MZUA	Museo de Zoología de la Universidad del Azuay,Cuenca, Ecuador.
MZUCC	Museo de Zoología de la Universidad de Concepción, Biobío, Chile.

NHM	Natural History Museum, London, United Kingdom.
QCAZ	Museo de Zoología, Pontificia Universidad Católica del Ecuador, Quito, Ecuador.
TTU	The Museum, Texas Tech University, Lubbock, Texas, USA.
UACh	Colección de Mamíferos de la Universidad Austral de Chile, Valdivia, Chile.
UIS-MHN	useo de Historia Natural de la Universidad Industrial de Santander, Santander, Colombia.
UMMZ	University of Michigan Museum of Zoology, Ann Arbor, Michigan, USA.
USNM	National Museum of Natural History (formerly the United States National Museum), Washington, D.C., United States.

Appendix B. Species include in the NDM/VNDM method, reference were taken into account when I deciding the current distribution update for each species.

Taxonomy	Species	Reference
Subfamily Sigmodontinae Wagner, 1843		
Tribe Andinomyini Salazar bravo et al 2016		
Andinomys Thomas, 1902		
	Andinomys edax	Jayat et al. (2009)
Punomys Osgood, 1943		
	Punomys kofordi	Pacheco and Patton (1995), Salazar-Bravo et al. (2011)
	Punomys lemminus	Pacheco and Patton (1995)
Tribe Euneomyini Pardiñas teta salazar bravo 2015		
Euneomys Coues, 1874		
	Euneomys fossor	Braun and Pardiñas (2015)
	Euneomys mordax	Tammone et al (2016)
	Euneomys petersoni	Braun and Pardiñas (2015)
Neotomys Thomas, 1894		
	Neotomys ebriosus	Ferro and Barquez (2017)
Sigmodontinae *incertae sedis*		
Chinchillula Thomas, 1898		
	Chinchillula sahamae	Salazar-Bravo (2015)
Neomicroxus Alvarado-Serrano and D’Elía, 2013		
	Neomicroxus bogotensis	Alvarado-Serrano and D'Elía (2013a)
	Neomicroxus latebricola	Alvarado-Serrano and D'Elía (2013a), Curay (2019)
Tribe Abrotrichini D’Elía, Pardiñas, Teta, and Patton, 2007		
Abrothrix Waterhouse, 1837		
	Abrothrix andina	Ferro and Barquez (2008)
	Abrothrix jelskii	Jayat et al. (2013), Zuñiga and Tancara (2014), Valladares Faundez et al. (2015)
	Abrothrix olivacea	Rodríguez-Serrano et al. (2006)
Chelemys Thomas, 1903		
	Chelemys macronyx	Alarcón et al. (2011), Teta et al. (2014)
Tribe Akodontini Vorontsov, 1959		

Taxonomy	Species	Reference
Akodon Meyen, 1833		
	Akodon aenos	Pardiñas et al. (2015)
	Akodon aerosus	Pardiñas et al. (2015)
	Akodon aerosus baliolus	Pardiñas et al. (2015)
	Akodon affinis	Pardiñas et al. (2015)
	Akodon albiventer	Jayat et al. (2010)
	Akodon boliviensis	Patton and Smith (1992), Jayat et al. (2010)
	Akodon budini	Jayat et al. (2010)
	Akodon caenosus	Jayat et al. (2010)
	Akodon dolores	Pardiñas et al. (2015)
	Akodon fumeus	Jayat et al. (2010)
	Akodon josemariarguedasi	Jiménez et al. (2013), Jiménez and Pacheco (2016)
	Akodon juninensis	Myers (1990), Patton and Smith (1992)
	Akodon kofordi	Salazar-Bravo et al. (2002)
	Akodon kotosh	Jiménez and Pacheco (2016)
	Akodon lutescens	Patton and Smith (1992)
	Akodon mimus	Pardiñas et al. (2015)
	Akodon mollis	Alvarado-Serrano et al. (2013b)
	Akodon mollis sp. 1	Pacheco et al. (2009)
	Akodon orophilus	Jiménez et al. (2013), Jiménez and Pacheco (2016)
	Akodon siberiae	Pardiñas et al. (2015)
	Akodon simulator	Jayat et al. (2010)
	Akodon spegazzinii	Jayat et al. (2010)
	Akodon subfuscus	Myers (1990), Patton and Smith (1992)
	Akodon surdus	Pardiñas et al. (2015)
	Akodon torques	Myers (1990)
	Akodon varius	Pardiñas et al. (2015)
Lenoxus Thomas, 1909		
	Lenoxus apicalis	Patton (2015)
Necromys Ameghino, 1889		
	Necromys amoenus	D'Elía et al. (2008)
	Necromys lactens	D'Elía et al. (2008)
	Necromys punctulatus	D'Elía et al. (2008)
	Necromys urichi	D'Elía et al. (2008)
Oxymycterus Waterhouse,		

Taxonomy	Species	Reference
1837		
	Oxymycterus hiska	Oliveira and Gonçalves (2015)
	Oxymycterus hucucha	Oliveira and Gonçalves (2015)
	Oxymycterus inca	Hoffmann et al. (2002), Abreu-Júnior et al. (2016)
	Oxymycterus juliacae	Hoffmann et al. (2002)
	Oxymycterus nigrifrons	Hoffmann et al. (2002)
	Oxymycterus paramensis	Hoffmann et al. (2002), Jayat et al. (2008), d'Hiriart et al. (2015)
	Oxymycterus wayku	Jayat et al. (2008), d'Hiriart et al. (2015)
	Oxymycterus willkaurco	Zeballos et al. (2021)
Tribe Ichthyomyini Vorontsov, 1959		
Anotomys Thomas, 1906 281		
	Anotomys leander	Marín-C and Sánchez-Giraldo (2017)
Chibchanomys Voss, 1988		
	Chibchanomys orcesi	Jenkins et al. (1997)
	Chibchanomys sp.	Anderson (1997)
	Chibchanomys trichotis	Barnett (1997)
Ichthyomys Thomas, 1893		
	Ichthyomys hydrobates	Brito et al. (2015)
	Ichthyomys pinnei	Fernández de Córdova et al. (2020)
	Ichthyomys stolzmanni	Pacheco and Ugarte-Núñez (2011), Brito et al. (2016), Fernández de Córdova et al. (2020)
Neusticomys Anthony, 1921 287		
	Neusticomys monticolus	Velandia-Perilla and Saavedra-Rodríguez (2013)
	Neusticomys mussoi	Voss (2015)
	Neusticomys vossi	Hanson et al. (2015)
Tribe Oryzomyini Vorontsov, 1959		
Aegialomys Weksler, Percequillo, and Voss, 2006		
	Aegialomys baroni	Prado and Percequillo (2018)
	Aegialomys ica	Prado and Percequillo (2018)
Eremoryzomys Weksler, Percequillo, and Voss, 2006		
	Eremoryzomys polius	Uturunco and Pacheco (2016)

Taxonomy	Species	Reference
	Eremoryzomys mesocaudis	Uturunco and Pacheco (2016)
Handleyomys Voss, Gómez-Laverde, and Pacheco, 2002		
	Handleyomys fuscatus	Almendra et al. (2018)
	Handleyomys intectus	Almendra et al. (2018)
Hylaeamys Weksler, Percequillo, and Voss, 2006		
	Hylaeamys tatei	Brennand (2015)
Microryzomys Thomas, 1917		
	Microryzomys altissimus	Prado and Percequillo (2013)
	Microryzomys minutus	Prado and Percequillo (2013)
Mindomys Weksler, Percequillo, and Voss, 2006		
	Mindomys hammondi	Prado and Percequillo (2013)
Neacomys Thomas, 1900		
	Neacomys espinosus	Hurtado and Pacheco (2017)
	Neacomys vargasllosai	Hurtado and Pacheco (2017)
Nectomys Peters, 1861		
	Nectomys saturatus	Chiquito and Percequillo (2019)
Nephelomys Weksler, Percequillo, and Voss, 2006		
	Nephelomys albigularis	Prado and Percequillo (2013)
	Nephelomys auriventer	Prado and Percequillo (2013)
	Nephelomys childi	Prado and Percequillo (2013)
	Nephelomys keaysi	Prado and Percequillo (2013)
	Nephelomys levipes	Prado and Percequillo (2013)
	Nephelomys moerex	Prado and Percequillo (2013)
	Nephelomys nimbosus	Prado and Percequillo (2013)
	Nephelomys pectoralis	Prado and Percequillo (2013)
	Nephelomys ricardopalmai	Ruelas et al. (2021)
Oligoryzomys Bangs, 1900		
	Oligoryzomys andinus	Weksler and Bonvicino (2015)
	Oligoryzomys arenalis	Weksler and Bonvicino (2015)
	Oligoryzomys brendae	Teta et al. (2013)
	Oligoryzomys delicatus	Weksler and Bonvicino (2015)
	Oligoryzomys destructor	Hurtado and D'Elía (2019)
	Oligoryzomys destructor spodiurus	Hurtado and D'Elía (2019)
	Oligoryzomys flavescens	Weksler and Bonvicino (2015)
	Oligoryzomys griseolus	Weksler and Bonvicino (2015)
	Oligoryzomys guille	Hurtado (2021)
	Oligoryzomys longicaudatus	Weksler and Bonvicino (2015)
	Oligoryzomys pachecoi	Hurtado and D'Elía (2018)

Taxonomy	**Species**	**Reference**
Oreoryzomys Weksler, Percequillo, and Voss, 2006		
	Oreoryzomys balneator	Prado and Percequillo (2013)
Tanyuromys Pine, Timm, and Weksler, 2012		
	Tanyuromys thomasleei	Brito and Arguero (2016), Timm et al. (2018)
Zygodontomys Allen, 1897		
	Zygodontomys brunneus	Voss (2015)
Tribe Phyllotini Vorontsov, 1959		
Auliscomys Osgood, 1915		
	Auliscomys boliviensis	Salazar-Bravo (2015)
	Auliscomys pictus	Salazar-Bravo (2015)
	Auliscomys sublimis	Salazar-Bravo (2015)
Calomys Waterhouse, 1837		
	Calomys achaku	Zeballos et al. (2014)
	Calomys boliviae	Salazar-Bravo (2015)
	Calomys chinchilico	Zeballos et al. (2014)
	Calomys frida	Zeballos et al. (2014)
	Calomys lepidus	Ferro and Barquez (2008)
	Calomys miurus	Zeballos et al. (2014)
	Calomys musculinus	de Tommaso et al. (2014)
	Calomys sorellus	Zeballos et al. (2014)
Eligmodontia F. Cuvier, 1837		
	Eligmodontia bolsonensis	Mares et al. (2008)
	Eligmodontia hirtipes	Spotorno et al. (2013)
	Eligmodontia moreni	Mares et al. (2008)
	Eligmodontia morgani	Mares et al. (2008)
	Eligmodontia puerulus	Spotorno et al. (2013)
	Eligmodontia typus	Spotorno et al. (2013)
Galenomys Thomas, 1916		
	Galenomys garleppii	Salazar-Bravo (2015)
Graomys Thomas, 1916		
	Graomys domorum	Martínez and Gardenal (2016)
	Graomys griseoflavus	Udrizar Sauthier et al. (2011), Martínez and Gardenal (2016)
Phyllotis Waterhouse, 1837		
	Phyllotis alisosiensis	Jayat et al. (2016)
	Phyllotis amicus	Steppan and Ramírez (2015)
	Phyllotis andium	Rengifo and Pacheco (2015)

Taxonomy	Species	Reference
	Phyllotis anitae	Jayat et al. (2016)
	Phyllotis caprinus	Steppan and Ramírez (2015)
	Phyllotis definitus	Rengifo and Pacheco (2018)
	Phyllotis haggardi	Steppan and Ramírez (2015)
	Phyllotis limatus	Steppan (1998)
	Phyllotis magister	Steppan and Ramírez (2015)
	Phyllotis nogalaris	Jayat et al. (2016)
	Phyllotis occidens	Rengifo and Pacheco (2015)
	Phyllotis osgoodi	Steppan and Ramírez (2015)
	Phyllotis osilae	Jayat et al. (2016)
	Phyllotis perasoni	Pacheco et al. (2014)
	Phyllotis stenops	Rengifo and Pacheco (2015)
	Phyllotis tucumanus	Jayat et al. (2016)
	Phyllotis xanthopygus	Teta et al. (2018)
Tapecomys Anderson and Yates, 2000		
	Tapecomys primus	Barquez et al. (2006), Díaz et al. (2009), Pardiñas et al. (2015)
	Tapecomys wolffsohni	Pardiñas et al. (2015)
Tribe Reithrodontini Vorontsov, 1959		
Reithrodon Waterhouse, 1837		
	Reithrodon auritus	Pardiñas and Galliari (2001)
Tribe Sigmodontini Wagner, 1843		
Sigmodon Say and Ord, 1825		
	Sigmodon inopinatus	Tirira and Vallejo-Vargas (2015)
Tribe Thomasomyini Steadman and Ray, 1982		
Aepeomys Thomas, 1898		
	Aepeomys lugens	Pacheco (2015a)
	Aepeomys reigi	Ochoa et al. (2001)
Chilomys Thomas, 1897		
	Chilomys fumeus	Pacheco (2015b)
	Chilomys instans	Medina et al. (2016)
Rhagomys Thomas, 1886		
	Rhagomys longilingua	Medina et al. (2017)
Rhipidomys Tschudi, 1845		
	Rhipidomys caucensis	Tribe (2015)
	Rhipidomys fulviventer	García and Sánchez-González (2013)

Taxonomy	**Species**	**Reference**
	Rhipidomys latimanus	Tribe (2015)
	Rhipidomys ochrogaster	Pacheco and Peralta (2011)
	Rhipidomys similis	Tribe (2015)
	Rhipidomys sp.	
	Rhipidomys venustus	Tribe (2015)
Thomasomys Coues, 1884		
	Thomasomys andersoni	Pacheco (2015)
	Thomasomys apeco	Leo and Gardner (1993)
	Thomasomys aureus	Pacheco (2015)
	Thomasomys auricularis	Pacheco (2015)
	Thomasomys australis	Anderson (1997)
	Thomasomys baeops	Pacheco (2015)
	Thomasomys bombycinus	Pacheco (2015)
	Thomasomys caudivarius	Pacheco (2015)
	Thomasomys cinereiventer	Pacheco (2015)
	Thomasomys cinereus	Moreno Cardenas and Novillo-Gonzalez (2020)
	Thomasomys cinnameus	Pacheco (2015)
	Thomasomys contradictus	Pacheco (2015)
	Thomasomys daphne	Pacheco (2015)
	Thomasomys dispar	Pacheco (2015)
	Thomasomys eleusis	Pacheco (2015)
	Thomasomys emeritus	Pacheco (2015)
	Thomasomys erro	Pacheco (2015)
	Thomasomys fumeus	Pacheco (2015)
	Thomasomys gracilis	Pacheco (2015)
	Thomasomys hudsoni	Pacheco (2015)
	Thomasomys hylophilus	Pacheco (2015)
	Thomasomys incanus	Pacheco (2015)
	Thomasomys ischyrus	Pacheco (2015)
	Thomasomys kalinowskii	Pacheco (2015)
	Thomasomys ladewi	Pacheco (2015)
	Thomasomys laniger	Pacheco (2015)
	Thomasomys macrotis	Pacheco (2015)
	Thomasomys nicefori	Pacheco (2015)
	Thomasomys niveipes	Pacheco (2015)
	Thomasomys notatus	Pacheco (2015)
	Thomasomys onkiro	Luna and Pacheco (2002), Moreno and Albuja (2012)
	Thomasomys oreas	Pacheco (2015)

Taxonomy	Species	Reference
	Thomasomys paramorum	Pacheco (2015)
	Thomasomys popayanus	Pacheco (2015)
	Thomasomys praetor	Pacheco (2015)
	Thomasomys princeps	Pacheco (2015)
	Thomasomys pyrrhonotus	Pacheco (2015)
	Thomasomys rosalinda	Pacheco (2015)
	Thomasomys salazari	Brito et al. (2019)
	Thomasomys silvestris	Pacheco (2015)
	Thomasomys sp "bolivar"	Brito et al. (2019)
	Thomasomys sp "chaglla"	Noblecillas & Pacheco (2016)
	Thomasomys taczanowskii	Pacheco (2015), Pinto et al. (2018)
	Thomasomys ucucha	Pacheco (2015)
	Thomasomys vestitus	Pacheco (2015)
	Thomasomys vulcani	Pacheco (2015)

Appendix C. Summary of information on the consensus areas of the sigmodontinae rodent in the Andes, with information on the species composition with their respective score, number of cells for each area, the maximum scores and the grid sizes of each consensus areas. The * indicate all consensus areas include in an area of endemism. For qualitative combined criteria see DaSilva et al. 2015.

Size grid	Initial Area (number)	Consensus areas (number)	Selected áreas and qualitative combined criteria (DaSilva et al. 2015).	Araea of endemism	Maximun score	Number of cell	Endemic species
0.5	0	0	*C2	NCE	2.381	6	*Mindomys hamondi* (0.476), *Neomicroxys latebricola* (0.428), Nephelomsy moerex (0.476), *Thomasomys silvestris* (0.428), *Thomasomys ucucha* (0.571)
0.5	1	1	*C2	NCE	2.163	11	*Neomicroxus latebricola* (0.772), *Thomasomys erro* (0.8681), *Thomasomys fumeus* (0.709)
0.5	2	2			2.347	8	*Mindomys hamondi* (0.534), *Nephelomys moerex* (0.937), *Thomasomys silvestris* (0.875)
0.5	3	3	*C1	WC	2.071	7	*Handleyomys fuscatus* (0.635), *Nephelomys pectoralis* (0.436), *Thomasomys cinereiventer* (0.524), *Thomasomys popayanus* (0.476)
0.5	8	3	*C1	WC	2.071	7	*Handleyomys fuscatus* (0.635), *Nephelomys pectoralis* (0.436), *Thomasomys cinereiventer* (0.524), *Thomasomys popayanus* (0.476)
0.5	4	4	*C1	WC	2.166	9	*Nephelomys pectoralis* (0.770), *Thomasomys cinereiventer* (0.722), *Thomasomys popayanus* (0.674)
0.5	15	4	*C1	WC	2.148	6	*Nephelomys pectoralis* (0.777), *Thomasomys cinereiventer* (0.555), *Thomasomys popayanus* (0.815),
0.5	5	5	*C1	WC	2.138	9	*Nephelomys pectoralis* (0.777), *Rhipidomys caucensis* (0.631), *Thomasomys cinereiventer* (0.729)
0.5	9	5	*C1	WC	2.111	7	*Nephelomys pectoralis* (0.888), *Rhipidomys caucensis* (0.698), *Thomasomys cinereiventer* (0.524)
0.5	6	6			2.149	14	*Oligoryzomys arenalis* (0.649), *Thomasomys cinereus* (0.815), *Thomasomys pyrrhonotus* (0.685)
0.5	12	6			2.149	14	*Oligoryzomys arenalis* (0.649), *Thomasomys cinereus* (0.815), *Thomasomys pyrrhonotus* (0.685),
0.5	7	7			2.285	7	*Lenoxus apicalis* (0.857), *Oxymycterus nigrifrons* (0.786), *Punomys kofordi* (0.643)
0.5	10	8	*C2	NCE	3.081	7	*Neomicroxus latebricola* (0.735), Nephelomys moerex (0.612), Thomasomys erro (0.459), *Thomasomys silvestris* (0.561), *Thomasomys ucucha* (0.714)
0.5	17	8	*C2	NCE	2.966	7	*Neomicroxus latebricola* (0.576), *Nephelomys moerex* (0.628), *Thomasomys erro* (0.471), *Thomasomys silvestris* (0.576),

Size grid	Initial Area (number)	Consensus areas (number)	Selected áreas and qualitative combined criteria (DaSilva et al. 2015).	Araea of endemism	Maximun score	Number of cell	Endemic species
							Thomasomys ucucha (0.714)
0.5	11	9	*C2	MET	2.442	5	*Aepeomys lugens* (0.642), *Thomasomys emeritus* (1.000), *Thomasomys vestitus* (0.800)
0.5	13	10	*C1	CU	2.26	5	*Akodon surdus* (0.700), *Oxymycterus willkaurco* (0.560), *Thomasomys gracilis* (1.000)
0.5	14	11	*C1	NWA	2	4	*Oxymycterus wayku* (0.500), *Phyllotis alisosinsis* (0.750), *Phyllotis anitae* (0.750)
0.5	16	12	*C2	EPL	2.744	7	*Lenoxus apicalis* (0.673), *Oxymycterus nigrifrons* (0.786), *Punomys kofordi* (0.643), *Thomasomys ladewi* (0.643)
0.5	18	13			2.188	18	*Phyllotis haggardi* (0.720), *Thomasomys paramorum* (0.745), *Thomasomys fumeus* (0.722)
0.75	0	0			2.495	11	*Emeroryzomys polius* (0.487), *Oligoryzomys arenalis* (0.405), *Thomasomys cinereus* (0.864), *Thomasomys pyrrhonotus* (0.740)
0.75	1	0			2.25	8	*Emeroryzomys polius* (0.413), *Oligoryzomys arenalis* (0.4375), *Thomasomys cinereus* (0.700), *Thomasomys pyrrhonotus* (0.700)
0.75	4	0			2.495	11	*Emeroryzomys polius* (0.487), *Oligoryzomys arenalis* (0.405), *Thomasomys cinereus* (0.863), *Thomasomys pyrrhonotus* (0.740)
0.75	19	0			2.5	11	*Emeroryzomys polius* (0.454), *Oligoryzomys arenalis* (0.4545), *Thomasomys cinereus* (0.864), *Thomasomys pyrrhonotus* (0.727)
0.75	2	1	*C1	HAM	2.7051	6	*Eremeryzomys mesocaudis* (0.666), *Eremeryzomys polius* (0.6346), *Neacomys spinosus* (0.448), *Phyllotis stenops* (0.666)
0.75	3	2	*C1	MET	2.433	5	*Aepeomys lugens* (0.9), *Chilomys fumeus* (0.533), *Neusticomys mussoi* (0.4666), *Thomasomys emeritus* (0.5333)
0.75	5	3			2.015	12	*Akodon orophillus* (0.531), *Eremeryzomys polius* (0.791), *Thomasomys cinereus* (0.692),
0.75	6	4			3.87	6	*Handleyomys fuscatus* (0.6666), *Nephelomys pectoralis* (0.555), *Rhipidpmys caucensis* (0.66666), *Thomasomys cineriventer* (0.740)*Thomasomys contradictus* (0.4166) *Thomasomys popayanus* (0.416),
0.75	10	4			4.203	6	*Handleyomys fuscatus* (0.6666), *Nephelomys pectoralis* (0.712), *Rhipidpmys caucensis* (0.8333), *Thomasomys cineriventer* (0.740)*Thomasomys contradictus* (0.4166) *thomasomys popayanus* (0.8333,
0.75	7	5			2.14	6	*Aepeomys lugens* (0.833)), *Chilomys fumeus* (0.833), *Neusticomys mussoi* (0.476)

Size grid	Initial Area (number)	Consensus areas (number)	Selected áreas and qualitative combined criteria (DaSilva et al. 2015).	Araea of endemism	Maximun score	Number of cell	Endemic species
0.75	8	6			2.182	12	*Oligoryzomys arenalis* (0.656), *Thomasomys cinereus* (0.833), *Thomasomys pyrrhonotus* (0.692),
0.75	9	7	*C1	MET	2.125	4	*Aepeomys reigi* (0.75), *Thomasomys emeritus* (0.625), *Thomasomys vestitus* (0.75)
0.75	11	8			2.2556	13	*Emeroryzomys polius* (0.769), *Thomasomys cinereus* (0.807), *Thomasomys popayanus* (0.678)
0.75	12	9			2.2	12	*Akodon kofordi* (0.6172), *Akodon mimus* (0.9166), *Oxymycterus hiscka* (0.666)
0.75	13	10	*C1	HAM	2.875	5	*Akodon* sp 1 (0.800), *Phyllotis pearsoni* (0.800), *Thomasomys eleusis* (0.610), *Thomasomys praetor* (0.400)
0.75	20	10	*C1	HAM	3.061	7	*Akodon* sp 1 (0.710), *Phyllotis pearsoni* (0.714), *Thomasomys eleusis* (0.714), *Thomasomys praetor* (0.6122)
0.75	14	11			2.15	5	*Oxymycterus wayku* (0.750), *Phyllotis alisosinsis* (0.700), *Phyllotis anitae* (0.700)
0.75	15	12			2.825	5	*Akodon orophillus* (0.400), *Akodon* sp 1 (0.613), *Phyllotis pearsoni* (0.6125), *Thomasomys eleusis* (0.800), *Thomasomys praetor* (0.400)
0.75	16	13	*C1	EPL	2.916	6	*Lenoxus apicalis* (0.916), *Oxymycterus nigrifrons* (0.666), *Punomys kofordi* (0.666), *Thomasomys ladewi* (0.6666)
0.75	27	13	*C1	EPL	3	3	*Lenoxus apicalis* (0.500), *Oxymycterus nigrifrons* (0.833), *Punomys kofordi* (0.8333), *Thomasomys ladewi* (0.833)
0.75	17	14			2.919	9	*Akodon orophillus* (0.888), *Eremeryzomys polius* (0.681), *Neacomys spinosus* (0.6818), *Thomasomys eleusis* (0.666)
0.75	31	14			2.769	8	*Akodon orophillus* (0.937), *Eremeryzomys polius* (0.402), *Neacomys spinosus* (0.740), *Thomasomys eleusis* (0.687),
0.75	18	15			2.372	11	*Phyllotis haggardi* (0.863), *Thomasomys fumeus* (0.681), *Thomasomys paramorum* (0,827),
0.75	21	16			2.3111	12	*Neusticomys vossi* (0.686), *Thomasomys fumeus* (0.666), *Thomasomys paramorum* (0,958)
0.75	22	17			2.218	8	*Handeyomys intectus* (0.656), *Thomasomys bombycinus* (0.687), *Thomasomys nicefori* (0.875)
0.75	23	18	*C2	WC	4.21	6	*Handleyomys fuscatus* (0.8333), *Nephelomys pectoralis* (0.672), *Rhipidomys caucensis* (0.833), *Thomasomys cineriventer* (0.9166), *Thomasomys popayanus* (0.8333)
0.75	24	19	*C1	CO	2.3	5	*Akodon siberiae* (0.900), *Oxymycterus hucuha* (0.700), *Thomasomys australis* (0.700)
0.75	25	20	*C2	NWA	2.469	7	*Eligmodontia bolsonensis* (0.51), *Oxymycterus wuayku* (0.673), *Phyllotis alisosiensis* (0.642), *Phyllotis anitae* (0.642)
0.75	26	21			4.902	7	*Mindomys hamondi* (0.714), *Neomicroxys latebricola* (0.701), *Nephelomsy moerex* (0.701), *Thomasomys erro* (0.785), *Thomasomys fumeus* (0.584), *Thomasomys silvestris* (0.701), *Thomasomys ucucha* (0.714)

Size grid	Initial Area (number)	Consensus areas (number)	Selected áreas and qualitative combined criteria (DaSilva et al. 2015).	Araea of endemism	Maximun score	Number of cell	Endemic species
0.75	28	22			2.25	13	*Calomys sorrelus* (0.684), *Oligoryzomys andinus* (0.800), *Thomasomys praetor* (0.769)
0.75	29	23			2.375	4	*Akodon surdus* (0.750), *Oxymycterus willkaurco* (0.875), *Thomasomys gracilis* (0.750)
0.75	30	24			2.71	5	*Chilomys fumeus* (0.571), *Neusticomus mussoi* (0.800), *Oligoryzomys griseolus* (0.700), *Thomasomys hylphilus* (0.643)
0.75	32	25			2.8	5	*Aepeomys lugens* (0.900), *Thomasomys emeritus* (0.900), *Thomasomys vestitus* (0.700)
0.75	33	26	*C1	NCE	2.128	7	*Phyllotis haggardi* (0.866), *Sigmodon inopinatus* (0.643) , *Thomasomys fumeus* (0.619)
0.75	34	9			2.2	12	*Akodon kofordi* (0.6172), *Akodon mimus* (0.9166), *Oxymycterus hiscka* (0.666)

3. MORPHOLOGIC AND GENETIC PATTERNS OF VARIATION ON SIGMODONTINE RODENTS OF THE CORDILLERA BLANCA (ANCASH PERU)

Abstract

The Cordillera Blanca is one of the highest areas in the Andes, with mountains reaching more than 6,000 m in the central region of Peru (in the Ancash Department). The uplift of Cordillera Blanca began at ~ 8 MYA intensifying between ~ 6 and ~ 2 MYA, a period that coincides with the origin and diversification of the rodents of the subfamily Sigmodontinae, estimated at 8.24 to 3.5 MYA. The goal of this study was to evaluate if the orogenic process that occurred at the Cordillera Blanca had played an important role in the morphological and genetic variation of rodent species inhabiting this region, and to test this, we intend to evaluate classical and ddRADSeq technique of samples obtained at this region. I focused on the eight most abundant species: *Akodon mollis*, *Calomys sorellus*, *Oligoryzomys andinus* and *Microryzomys altissimus, Auliscomys pictus, Calomys sorellus Phyllotis occidens*, *P. andium*, and *Thomasomys praetor*. The results showed a common pattern where the mountain chain located on the southern portion of the area of study does not represent a barrier between populations on the western and eastern slopes. On the contrary, the Santa River seems to represent a present barrier to populations; however, the headwater portion of this river may likely act as a corridor that unites both sides of the river. My demographic analyses suggested that the history of *Akodon mollis* and genus *Phyllotis* is best described by a model of isolation with migration. The date for the isolation event coincides with the date of the uplift of Cordillera Blanca. I have to reject this hypothesis because my results show a pattern opposite to that expected; there is a common pattern of close relationships between populations on the eastern and western slopes of Cordillera Blanca. This data suggest that gene flow and morphological traits, in all species, between both slopes of the Cordillera are not interrupted, suggesting that the Cordillera Blanca could not be an effective barrier.

Keywords: Cordillera Blanca, genomics, Morphology, demography

3.1. Introduction

Along the Andes are zones formed by sets of high-altitude mountains, and one of the highest zones is located in the central Andes, called the Cordillera Blanca, whose highest mountain is the Nevado Huascaran, with 6,768 m. The Cordillera Blanca is located in the department of Ancash, in the north of Peru, between 08º12' to 10º01' S. Much of its extension falls within the National Park of Huascarán, having approximately 200 peaks that surpass 5,000 m and 30 of them with more than 6,000 m; Additionally, the Cordillera Blanca represents the most ice-covered mountainous masses of the tropic (SERNANP, 2011). This region exhibits dramatic environmental gradients over short geographic distances; the Cordillera Blanca is the primary geological formation in northern Peru, and much of its melting process gives origin to several rivers, such as the Santa River, which flows into the Pacific Ocean, and the Marañón

River, one of the tributaries of the Amazon River. From a biogeographic perspective, this provides a rich system to examine evolutionary scenarios of organisms on a fine spatial scale. However, the studies of this area are very scarce, and the role of the Cordillera Blanca in the evolutionary processes of the fauna has not been investigated in detail until now.

Nevertheless, some studies point out the role of the Cordillera Blanca as a geographical barrier or area of endemism. Fjeldså & Irestedt (2009) and Schulenberg et al. (2010) show that the distribution of some birds is limited to the east and west of the mountain range, and some are restricted to this zone, as in the case of *Atlapetes rufigenis*, *Leptasthenura yanacensis*, and *Scytalopus affinis*. For small mammals, two main hypotheses have been proposed to explain diversification in the high-Andean region of Ancash. The first suggests the Cordillera Blanca as a source of speciation for the genus *Sturnira* and *Phyllotis* (Pacheco & Petterson 1992; Pacheco et al. 2014; Rengifo & Pacheco 2015), following the Montane Vicariance hypothesis (Coyne and Orr, 2004), and the second that suggested that the presence of the Santa River acts a possible geographic barrier (Pacheco 2002, Rengifo & Pacheco 2018) following the Riverine Barrier hypothesis (Wallace, 1854; Ayres and Clutton-Brock, 1992; Patton et al., 1994, Capparella 1988). Pearson (1982) mentioned that some species of rodents, which he called "Peri-Andinos", are distributed in both the western slope and in the Marañón River basin (in eastern Cordillera Blanca). However, to date, no studies are corroborating if there is any gene flow between both sides of the Cordillera Blanca.

The Order Rodentia represents an excellent model to test biogeographic and diversification theories since this group usually exhibits a high species richness associated with diverse types of habitats present in several areas where they occur (Steppan et al. 2004, Rundell & Price 2009, Rowe et al. 2011). Speciation in rodents has been strongly influenced by geographic barriers such as deep valleys, rivers, and high mountains (Patton & Smith, 1992; Patton et al., 2000; Pacheco, 2002). It is estimated that the Cordillera Blanca was formed recently, approximately ~8 MYA (Montario, 2001), with a higher intensity between ~6 to ~2 Ma (Late Miocene to Early Pleistocene) (Montario et al., 2005). This recent rise of Cordillera Blanca produced geographic traits in northern Peru (see paragraph above, Montario et al., 2005), and many species of rodents have likely been affected by this uplifting. These date estimates agree with the processes of diversification of sigmodontine rodents, as evidenced in recent studies that estimated the times of divergence of the various tribes in South America (Parada et al. 2013, Leite et al. 2014, Parada, et al., 2015): to Akodontini ~4.86 − 6.75 Ma, Oryzomyini ~5.29−7.16 Ma; Phyllotini ~5.33−7.03 Ma; Thomasomyini ~5.02−7.04 Ma. These dates provide an overview of evolution at the level of tribes, consequently, the diversification process at the species level should be much more recent, as inferred from Leite et al. (2014: Figure 1) in which the processes of speciation of some taxa occurred between ~3 and ~2 Ma.

Rodents of the subfamily Sigmodontinae that inhabit the region around the Cordillera Blanca currently comprise 19 species, corresponding to nine genera and six tribes, of which 11 are distributed on both sides of the mountain range, four inhabit only the western part, and four only the eastern part (Table 1). It should be noted that most genera inhabiting the Cordillera Blanca have a wide distribution in the Andes, but some are very rare. Thus, species that are distributed on both sides of the Cordillera Blanca, except rare species, will be good candidates to employ as models to test diversification, and these are *Akodon mollis*, *Oligoryzomys andinus, Microryzomys altissimus, Auliscomys pictus, Phyllotis andium, Phyllotis occidens, Calomys sorellus and Thomasomys praetor*.

The soft grass mouse, *Akodon mollis*, is widely distributed from Ecuador to northern Peru. Luna (2012) indicated differences between northern and southeastern populations that could be employed to distinguish them in different taxa; nonetheless, Luna's (2012) analysis did not include specimens from the western slope of the Cordillera Blanca, creating a geographical information gap. Following Alvarado & Luna (2013) *A. mollis* occurs in a wide variety of habitats such as the puna, yungas and dry forest.

The Andean colilargo, *Oligoryzomys andinus*, following Hurtado (2021), has a distribution in northwestern Peru; however, there is little information about geographic variation (Musser & Carleton, 2005) and no data on ecology (Weksler & Bonvicino 2015) *Oligoryzomys andinus* is monotypic.

The Páramo colilargo, *Microryzomys altissimus*, has a preference for more open areas, such as the Puna, and is mainly distributed in the eastern part of Andes (Carleton & Musser, 1989) but also occurs in a known locality in the western part - Quilcayhuanca (Ancash - Peru), being relatively isolated from its eastern distribution. Unfortunately, nothing is known about the western populations of *Microryzomys altissimus* and their relationships with the eastern populations, so a current systematic study is needed. Carleton & Musser (1989) suggested that this species inhabits the paramo, Polylepis forest, arid scrub, and humid temperate forest just below the timberline. Carleton and Musser (1989) treated *Microryzomys minutus* as monotypic.

The painted big-eared mouse, *Auliscomys pictus*, is widely distributed in the Andes of Peru, northern Bolivia, and Chile (Salazar-Bravo, 2015). Pearson (1951) reported *A. pictus* in stone walls and places far from water, and Pizzimenti and DeSalle (1980) trapped it in habitats containing an abundance of grasses (mostly Stipa ichu) and other herbaceous vegetation at high elevations. No subspecies are recognized for this taxon, and no taxonomic revisions have not been performed since Pearson (1958) and Hershkovitz (1962). Thus, a taxonomic update becomes urgent.

The genus *Phyllotis* is represented by five species in northern Peru: *Phyllotis amicus*, *P. andium, P. definitus, P. pearsoni and P. occidens* (Rengifo & Pacheco, 2015). *P. amicus, P. definitus, and P. occidens* are distributed on the western side of the Andes, whereas *P. pearsoni* and *P. andium* occur on the eastern side. According to Pacheco et al. (2014) and Rengifo & Pacheco (2015), the Cordillera Blanca may have acted as a geographic barrier for this genus. These authors base their hypotheses on the close relationship between *P. pearsoni* - *P. definitus* and between *P.andium* - *P. occidens* and, although they are morphologically different, they are closely related at cytogenetically and molecularly levels. These two latter species are found in brushy habitats (Pearson 1972, Rengifo & Pacheco 2015). *P. andium* and *P. occidens* have no subspecies from the Ancash region.

The Peruvian Vesper Mouse *Calomys sorellus* occurs on both sides of the Cordillera Blanca. Following the taxonomic review of Zeballos et al. (2014), C. sorellus is from La Libertad to north of Lima and Junín. Osgood (1914) mentioned that collected in tall grass and weeds growing about the bases of rough limestone exposures on the very top of the mountains, but no more information about natural history was published before. This species is monotypic.

The Cajamarca *Thomasomys*, *Thomasomys praetor*, occurs from the northern Andes in Peru, south of Huancabamba depression, to the Cordillera Negra in the Ancash department (Pacheco 2015). No information regarding the ecology or other aspects of the natural history of this species is known, and the scarce knowledge of this species is only based on collecting information. Thomas (1900), Osgood (1914), and Pacheco (2015) mentioned that *T. praetor* was collected in páramo, and at the edge of the timberline in the dry forests of the Río Marañón valley and dense and tall shrub habitats on rocky substrates, near rivers or streams. *Thomasomys praetor* is monotypic.

There is a lack of knowledge regarding the population variation and the phyletic relationships (as well as the taxonomy and systematics) of the populations occurring on the western side of the Cordillera Blanca, nor any study comparing these populations with the eastern ones. Therefore, in this contribution, I aim to explore the speciation processes and evolutionary trends of the fauna of this region, employing morphological and genomic data. This approach will enhance our understanding of the diversification processes operating in this region. The goal was to evaluate the intra and inter-morphological variation of the most predominant populations distributed on both sides of the Cordillera qualitatively and quantitatively, to determine the genetic structure of sigmodontine rodent populations in the Andean region of the department of

Ancash, and to describe the demographic scenarios that led to the current patterns of genetic variation and geographic distribution of the most predominant species in the Cordillera Blanca

TABLE 1. Species of rodents of subfamily Sigmodontinae distributed on the western and eastern slopes of Cordillera Blanca. Bold indicates the species with larger series of available specimens in scientific collections and, therefore, more appropriate for the purposes of this study.

TAXA		West	East
Tribu Abrotrichini	*Abrothrix jelskii*	x	x
Tribe Akodontini	***Akodon mollis***	x	x
	Akodon juninensis	x	x
Tribe Oryzomyini	*Aegialomys ica*	x	
	Microryzomys altissimus	x	x
	Microryzomys minutus		x
	Oligoryzomys andinus	x	x
	Oligoryzomys arenalis	x	
Tribe Phyllotini	***Auliscomys pictus***	x	x
	Calomys lepidus	x	x
	Calomys sorellus	x	x
	Phyllotis amicus	x	
	Phyllotis andium		x
	Phyllotis definitus	x	
	Phyllotis pearsoni		x
	Phyllotis occidens	x	
	Phyllotis xanthopygus		x
Tribe Thomasomyini	***Thomasomys praetor***	x	x
	Thomasomys cinereus		x
Incertae sedis	*Neotomys ebriosus*	x	x

3.2. Methods

3.2.1. Study area and samples

The study area was located in the high Andes of the department of Ancash, northern Peru. There are two main mountain ranges, one on the eastern side called "Cordillera Blanca" with peaks over 5,000 meters and the presence of perennial snow-capped mountains, and one on the western side the mountain range called "Cordillera Negra" with maximum heights that barely exceed 5,000 meters, without perennial snow; from south to the north rises the Rio Santa, which separates both mountain ranges (Figure 1).

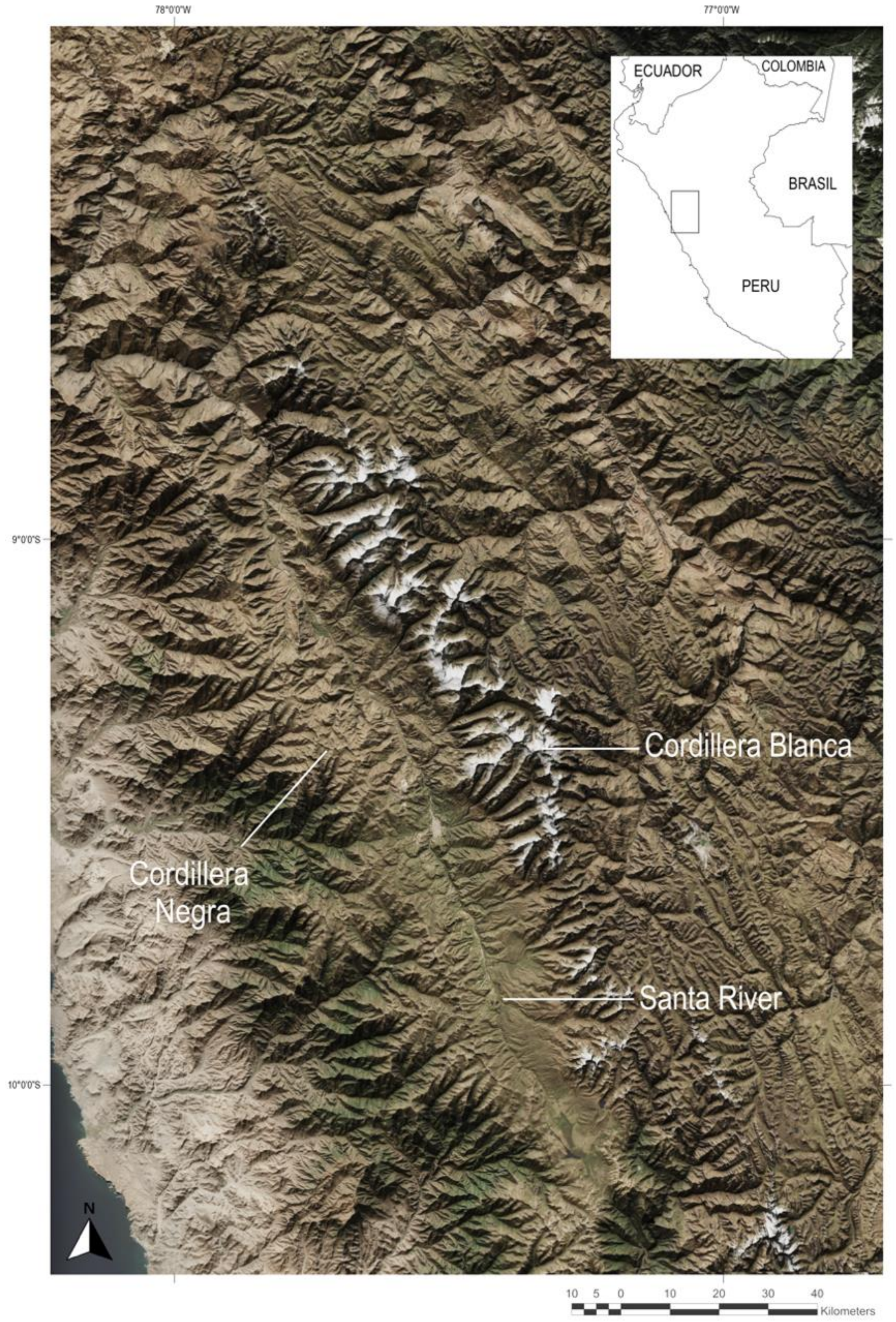


Figure 1. Study area in Northern Peru, the image shows the geographic features in this region, the Cordillera Negra, the Cordillera Blanca, and Santa river are marked. Small map (in the upper right corner) indicates the location in South America.

The sampling design was established to analyze populations of sigmodontine rodents located on the eastern and western sides of the Cordillera Blanca, as well as populations on the western side of the Santa River, on the Cordillera Negra. Three sampling sites were arranged to the north, center, and south of both mountain systems (See figure 2).

Available data suggests that 19 species of sigmodontinae rodents occur in Ancash. In this study, I analyzed those with larger numbers of available specimens corresponding to the following genera: *Auliscomys, Akodon, Phyllotis, Calomys, Oligoryzomys, Thomasomys, and Microryzomys.* These specimens are housed in the following mammal collections: FMNH (The Field Museum, Chicago, USA), USNM (The National Museum of Natural History Washington, USA), and MUSM (Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Perú) (see appendix A, B and C).

To fill sampling gaps recovered by analyzing the abovementioned collections, I conducted field surveys along three transects crossing both the Cordillera Blanca and the Cordillera Negra, on its northern, central, and southern portions. I used the conventional capture techniques with Sherman traps, following the Guidelines of the American Society of Mammalogists for using wild mammals in research (Sikes et al. 2011). All collected sites are shown in figure 2. Collected specimens were used for both morphological and genetic analysis. Voucher specimens and tissue samples that were used in this study were deposited at the Museo de Historia Natural de la Universidad Nacional Mayor de San Marco (MUSM) in Lima, Peru (Table 2).

Tabla 2. Names of sampling sites from the study area, with coordinates in decimals.

Abbreviation	Sampling sites	Latitude	Longitude
PAL	Pallasca*	-8.188155	-77.794428
MAC	Macate	-8.773998	-78.043632
CHA	Chalhuas	-9.021525	-77.492435
BAQ	Baqueria	-9.045292	-77.563214
POR	Portachuelo	-9.051013	-77.587399
CHI	Chinancocha	-9.078713	-77.651089
CHP	Chircarhuapunta	-9.113612	-77.869715
HUA	Huari**	-9.31443	-77.20697
TUL	Tullparaju*	-9.425	-77.3425
HUZ	Huaraz*	-9.533334	-77.533333
ESC	Escalon**	-9.550479	-77.635379
TAM	Tambillo	-9.67267	-77.212444
CAH	Cahuish	-9.689218	-77.255542
QUE	Querococha	-9.725251	-77.333061
TIC	Ticapampa*	-9.75	-77.45
HLL	Huallanca	-9.92	-76.955833
HAT	Hatun Machay	-10.099995	-77.345057
CON	Conococha	-10.115624	-77.273555
CHQ	Chiquián	-10.146973	-77.17132
CAJ	Cajacay**	-10.158396	-77.417389

No asterisk indicates populations sampled only in the fieldwork. One asterisk (*) indicates populations with specimens previously captured and deposited in museums that were not sampled in the current fieldwork. Two asterisks (**) indicate populations with specimens previously captured and deposited in museums and sampled again in the current fieldwork,

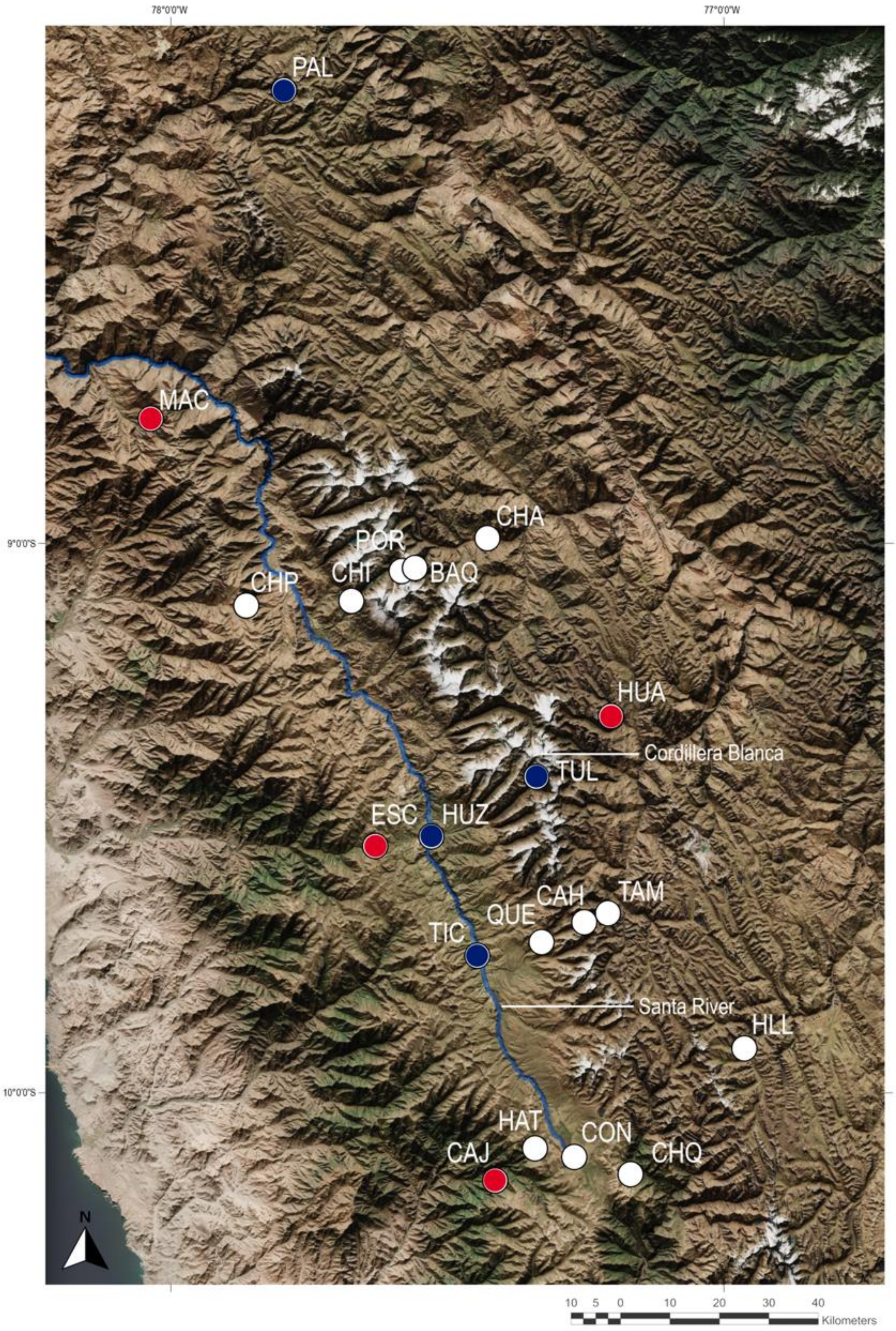


Figure 2. Map of all sampling sites from the study area; for abbreviation, see table 2. White dots indicate populations sampled only in the fieldwork. Blue dots indicate populations with specimens previously captured and deposited in museums that were not sampled in the current fieldwork. Red dots indicate populations with specimens previously captured and deposited in museums and sampled again in the current fieldwork

3.2.2. Library preparation and sequencing

I extracted genomic DNA from the liver and muscle samples of the individuals (see appendix B) using DNeasy Blood and Tissue Kit (Qiagen, Valencia, CA), following the manufacturer's instructions. I established three ddRAD libraries: the first composed by only individuals of Akodon mollis, the second by individuals of *Thomasomys praetor*, *Oligoryzomys andinus,* and *Microryzomys minutus*, and the third by individuals of *Phyllotis andium*, *Phyllotis occidens*, *Auliscomys pictus*, and *Calomys sorellus*. Using the ddRAD-Seq technique following the protocol of Peterson et al. (2012). The DNA is digested with the high-fidelity restriction enzymes EcoRI and MseI (New England Biolabs) in this method. Digestion reactions are cleaned with the commercial Agencourt AMPure XP Beads (Beckman Coulter, Brea, CA, USA), DNA concentrations are quantified using the Qubit dsDNA Assay Kit (Invitrogen), digested fragments are ligated to barcodes for each individual and to adapters for sequencing. DNA fragments are automatically selected by size (between 300 and 450 bp) through Pipin Prep (Sage Science, Beverly, MA) after PCR amplifies fragments. All libraries were sequenced in three lanes of HiSeq2000 (Illumina, San Diego, CA) according to instructions of the manufacturer to generate 150 base pairs, single-end reads in the Hospital for Sick Children (Toronto, Ontario, Canada)

3.2.3. Identifying and genotyping SNPs

I used the software STACKS v 2.41 to process the raw data (Catchen et al. 2013). Initially, raw sequences were demultiplexed, barcodes removed, and low-quality reads were filtered using process_radtags (Catchen et al. 2013). All sequences were processed in USTACKS to produce consensus sequences of RAD tags. The program USTACKS takes a set of short-read sequences from a single sample as input and aligns them into exactly matching stacks. CSTACKS was used to build a catalog of consensus loci containing all the loci from all the individuals and merging all alleles. Each genotype was then compared against the catalog using SSTACKS. Then, I used TSV2BAM to associate the pair-end read to each single-end locus and used GSTACKS to assemble the pair-end contigs. Using the POPULATIONS software (Catchen et al., 2011, 2013), I obtained the loci that were present in at least 85% of individuals (-r 0.85), minimum depth of coverage required to create a stack (m) = 6, maximum distance between stacks (M) = 3, and maximum mismatches between loci when building the catalog (n) = 2, and ddRAD tags were requested to be present in all locations (-p 3). In addition, I used a Minor Allele Frequency (MAF) of 5% (–min_maf 0.05) to filter out allelic types—with a count of one—that may mask population structure (e.g., Rodriguez-Ezpeleta et al. 2016). Lastly, I only included the first SNP per locus in the final analysis.

3.2.4. Data analysis

Maximum likelihood phylogeny based on SNPs was inferred using the Randomized Accelerated Maximum Likelihood (RAxML) algorithm version 7.0.4 (Stamatakis 2006) with 1,000 bootstrap pseudo-replicates to search for the best tree and bootstrap support (BS). The PCA was performed in R (R Core Team 2015) through RStudio (Team RS 2018) using the prcomp function and visualized using the package GGPLOT2 (Wickham H. 2016).

Genetic structure was examined using the software STRUCTURE v. 2.3.4, which separates groups according to allelic frequencies (Pritchard et al., 2000). The hypothetical number of subpopulations (K) was set as a continuous series of K from 1 to 10 in 10 independent runs. A burn-in period of 100,000 steps was followed by 100,000 Monte Carlo Markov Chain (MCMC) iterations (Evanno et al., 2005). The CLUMPAK online server (https://clumpak.tau.ac.il/contact.html) was used to average iterative runs of K and determine an optimal estimate of the number of distinct genetic clusters using the delta K method (Evanno et al. 2005; Kopelman et al. 2015; Meirmans 2015, 2019; Janes et al. 2017).

3.2.5. Demographic history

To infer possible demographic scenarios, I used the software package momi2 - MOran Models for Inference - (see Kamm et al., 2019). I only performed this analysis for *Akodon mollis* and the genus *Phyllotis*, as they were the only groups with adequate samples and specimens to attend to the minimal sample size required for these analytical procedures (Kamm et al., 2019). I tested multiple models with different demographic scenarios for the groups identified previously by genetics analyses, RAXML and STRUCTURE. The groups used for the species analyzed were northern, southern, and western groups for *Akodon mollis,* and the Phyllotis genus used *P. andium* and *P. occidens* (Figure 3). In general, the aim was to identify if there were migration pulses posterior to the divergences found by the RAxML/structure analyses among these populations. Due to computational restrictions, for the *Akodon mollis* models, I ran a preliminary model without migration (only divergence times and populational size were estimated) to set up the other models. From this first run, the following models estimated the migration pulses among the populations with these two a priori parameters. For the Phyllotis complex, I ran all models estimating the abovementioned parameters. For each model, I implemented 100 runs to avoid suboptimal results, and based on the run with the highest likelihood for each model, the best-fit scenario was selected using the Akaike Information Criterion (AIC, Akaike, 1973). At the same time, I set the mutation rate for each model in 2.9x10^-8 substitutions per site per generation (Abreu et al., 2022) and the generation time of 1.61 years, following Pacifici et al. (2013). Finally, I ran 100 bootstrap simulations on the best-selected model by the AIC criterion to estimate confidence intervals and plotted the results. I performed only this analysis on *Akodon mollis* and the genus *Phyllotis* (*P. andium* and *P. occidens*) because they were the best sampling species, and they can explain the orogeny process determined demographic history.

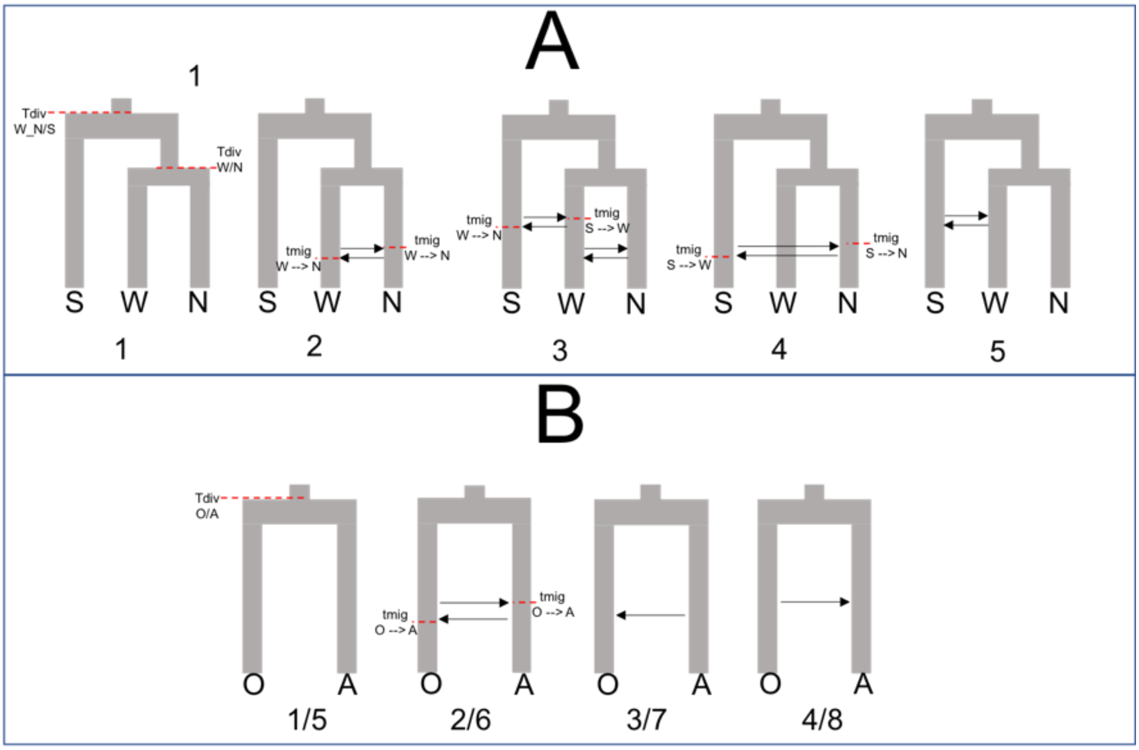


Figure 3. Demographic models tested in momi2 using ddraq-seq. (A) Schematic of the alternative demographic models tested for *Akodon mollis*. Numbers represent the five tested models. (B) Schematic of the alternative demographic models tested for genus *Phyllotis*. Numbers represent the eight tested models; 1, 2, 3, and 4 tested 4Ma divergence, and 5, 6, 7, and 8. tested 2.5Ma divergence. Model parameters are noted as follows: tdiv N/W: divergence time between population N and W; tdiv N_W/S: divergence time between ancestral population N_W and population C; tmig N-> W: migration time from population N to W; tmig W-> N: migration time from population W to N; tmig N-> S: migration time from population N to C; tmig S->N: migration time from population S to N; tmig W-> S: migration time from population W to S; tmig S->B: migration time from population S to W. tdiv O/A: divergence time between *Phyllotis occidens* and *P. andium*; tmig O-> A: migration time from population *P. occidens* to *P. andium*; tmig A-> O: migration time from population *P. andium* to *P. occidens*: S: Southern populations; W: western-populations; N: northern populations Amazonia; O: *Phyllotis occidens*; A: *Phyllotis andium*.

3.2.6. Morphological analysis

External and cranial characters were examined, and the descriptions follow the morphological terminology of Carleton (1980), Voss (1988, 1993), Carleton and Musser (1989), Voss and Carleton (1993), Steppan (1995) and Pacheco (2003). The nomenclature of Reig (1977) and Hershkovitz (1994) were followed for teeth morphology. All analyzed specimens were adult (age classes 3, 4, and 5, following Steppan 2007 and Voss 1991; see Appendix A).

Morphological characters were treated here to verify the frequency with which each character state occurs in the sample (Musser, 1968; Prado & Percequillo, 2017). These frequencies were inserted into the geographical space, allowing the observation of the geographical boundaries of each state. Based on this approach, it was possible to test the degree of polymorphism, evaluating the level of information of each character (Wiens, 2000) within and among geographic samples.

Cranial measurements were taken following Myers et al. (1990): Condyle-incisive length, CIL: distance from the anterior edge of the upper incisors to the posterior face of the occipital condyles. Zygomatic breadth, ZB: the greatest distance between the outside margins of the zygomatic arches. Braincase breadth, BB: the greatest breadth of the braincase at a point just superior to the zygomatic root of the squamosal. Interorbital constriction, IC: the least distance across the interorbital region. Rostral length, RL: the diagonal distance from the orbit's anterior margin to the nasals' anterior tip. Nasal length, NL: the length of the nasal bones measured at the midline. Rostral width, RW: the breadth of the rostrum across the nasolacrimal capsules. Mid-rostral width, RW2: the breadth of the rostrum measured at the top of the arc formed by the roots of the incisors as they pass posteriorly; this arc is visible as a raised curve along the rostra1 walls. Orbital length, OL: the greatest longitudinal distance across the inside of the orbit. Diastema length, DL: the length of the diastema from the posterior margin of the upper incisors to the anterior margin (root) of M1. Maxillary toothrow length, MTRL: the greatest length of the upper tooth row taken at the alveolus. Incisive foramen length, IFL: the greatest length of the incisive foramen. Alveolar width, AW: the width of the palate measured across the labial margins of alveoli of the right and left M1's. Breadth of palatal bridge, BPB: measured between the protocones of the first maxillary molars- Occipital condyle width, OCW: the width across the occipital condyles. Zygomatic plate breadth, ZP: the greatest longitudinal distance, taken at approximately mid-height. Cranial depth, CD: the depth of skull, measured by placing the skull on a glass slide, measuring the distance from the bottom of the slide to the top of the cranial vault, and subtracting the thickness of the slide. Height of braincase HBC: Distance from basisphenoid and basioccipital bones to the top of the braincase.

All cranial and dental measurements were recorded in millimeters and were first assessed for univariate normality by performing a Kolmogorov-Smirnov test. For each species, imputations for missing data were carried out using the expectation-maximization with bootstrapping algorithm proposed by Honaker and King (2010). All variables were converted to "standard size variables," following Mosimann (1970), which reduces the effect of size and maintains the same units as the original variables and then were log-transformed. After this process, Principal Component Analyses were performed, grouping specimens according to Sampling sites. Linear Discriminant Analysis (LDA) was computed using the scores' principal components to explore the morphometric relationships among specimens from different sampling sites in the multivariate craniometrics space. All analyses were carried out using the PAST software (Hammer et al. 2001). In the software R 4.2.1, mainly, imputations were performed using the package Amelia II (Honaker et al. 2011), while the rest were performed using the MASS package (Ripley et al. 2013) and in-built R functions.

3.3. Results

3.3.1. Genomic data

The first library produced an average of 1,864,003 (range 661,514–3,812,301) raw sequence reads per sample. After removing poor-quality sequences, an average of 1,765,047 (range 630,469–3,585,046) After filtering loci, the final data set of 51 individuals of *Akodon mollis* contained 3,124 SNPs with a proportion of missing data of 25%.

The second library produced an average of 1,838,700 (range 718,782–4,240,935) raw sequence reads per sample. After removing poor-quality sequences, an average of 1,757,705 (range 694,218–4,085,146) reads were available. After filtering loci, the final data set of 8 individuals of *Thomasomys praetor* contained 880 SNPs, 18 individuals of *Oligoryzomys andinus* had 1,672 SNPs, and 31 individuals of *Microryzomys minutus* contained 1,846 SNPs, in the three cases with a proportion of missing data of 25%.

The third library produced an average of 1,260,466 (range 632,567–2,333,218) raw sequence reads per sample. After removing poor-quality sequences, an average of 1,232,750 (range 621,738–2,302,017) After filtering loci, the final data set of 38 individuals of *Phyllotis genus* contained 3,761 SNPs, 14 individuals of *Auliscomys pictus* had 1,267 SNPs and 24 individuals of *Calomys sorellus* contained 979 SNPs, in the all cases with a proportion of missing data of 25%.

3.3.2. Phylogenetics and genetic structure

The phylogenetic relationship for *Akodon mollis* determined that the 15 populations sampled are divided into three groups; one formed by the populations of Macate (MAC), Chircarhuapunta, (CHP), and Cajacay (CAJ), which I named as Western Clade; other formed by the populations Pallasca (PAL), Chinancocha (CHI) and Challhuas (CHA), which I called as North clade, and the other formed by the populations of Portachuelo (POR), Baqueria (BAQ), Huari (HUA), Tambillo (TAM), Cahuish (CAH), Querococha (QUE), Huallanca (HLL), Chiquian (CHQ), Conocochas (CON), Hatun machay (HAT), and Escalon (ESC), which I named as South clade. The PCA showed three clusters corresponding to the Western, North, and South clade. The STRUCTURE analysis identified three distinct genetic populations, with a K=3 as the most probable (Figure 4).

The phylogenetic relationship for *Microryzomys altissimus* determined that the 11 populations sampled are divided into two groups, one formed by Chinancocha (CHI), Portachuelo (POR), Baqueria (BAQ), CHallhuas (CHA), Huari (HUA), Huallanca (HLL), Cahuish (CAH) Tambillo (TAM), Querococha (QUE) and CHiquian (CHQ), which I named as South clade, and the other formed only by Pallasca (PAL) population, which I named as north clade. The PCA showed two clusters corresponding to the south and North clade. The STRUCTURE analysis also identified two distinct genetic populations, with a K=4 as the most probable (Figureo 5).

The phylogenetic relationship for *Oligoryzomys andinus* determined that the five populations sampled are divided into two groups, one formed by the populations of Macate (MAC), Cajacay (CAJ), Escalon (ESC), and Chinancocha (CHI), which I named as Western clade, and the other formed only by Pallasca (PAL) population, which I called as north clade. The PCA showed two clusters corresponding to the Western and North clade. The STRUCTURE analysis also identified two distinct genetic populations, with a K=4 as the most probable (Figureo 6).

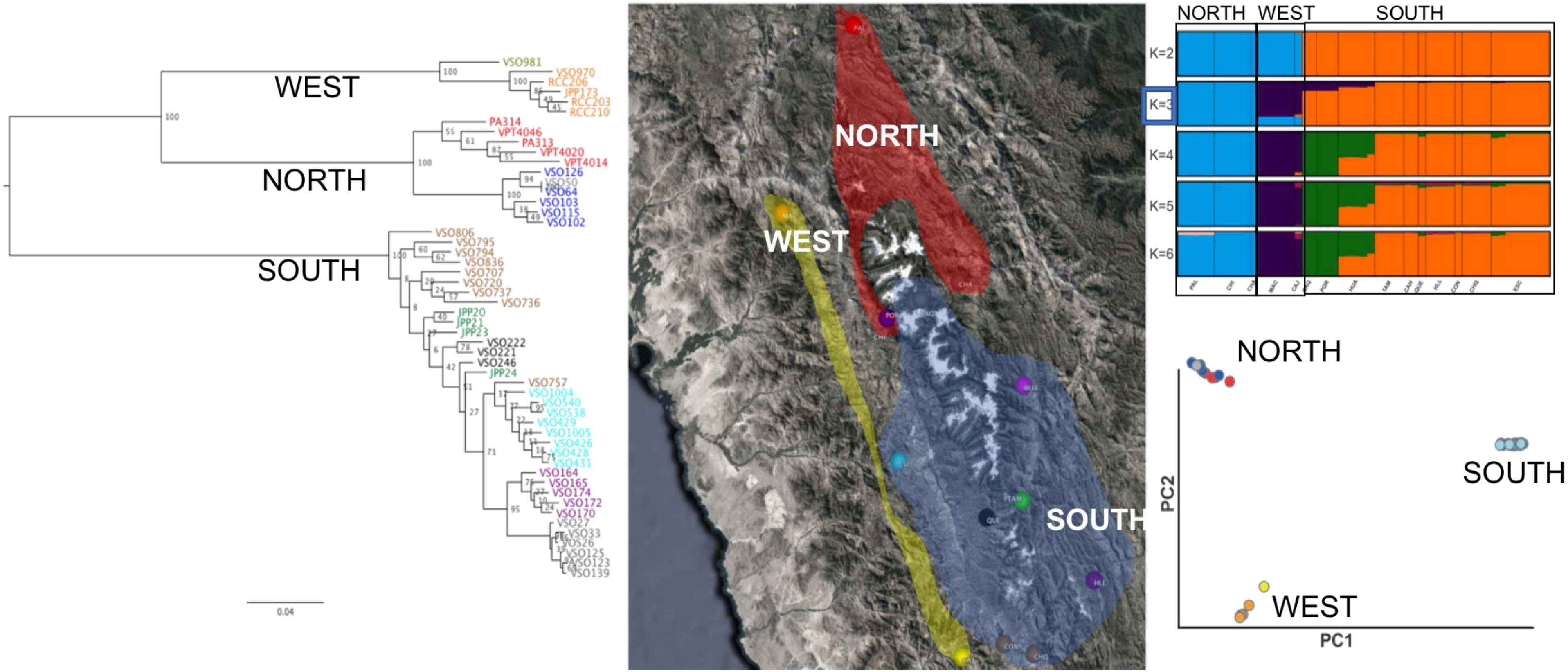
The phylogenetic relationship for *Auliscomys pictus* determined that the five populations sampled are divided into two groups, one formed by Chinancocha (CHI) and Pallasca (PAL), which I named as north clade, and the other formed by Tambillo (TAM), Huallanca (HLL) and Conocochas (CON) which I called as south clade. The PCA showed two clusters corresponding to the north and South clades. The STRUCTURE analysis also identified two distinct genetic populations, with a K=3 as most probable. (Figureo 7).

The phylogenetic relationship for *Calomys sorellus* determined that the 11 populations sampled are divided into three groups, one formed by Portachuelo (POR) and Huari (HUA), which I named as north clade, other composed by the samples of Tambillo (TAM), Cahuish

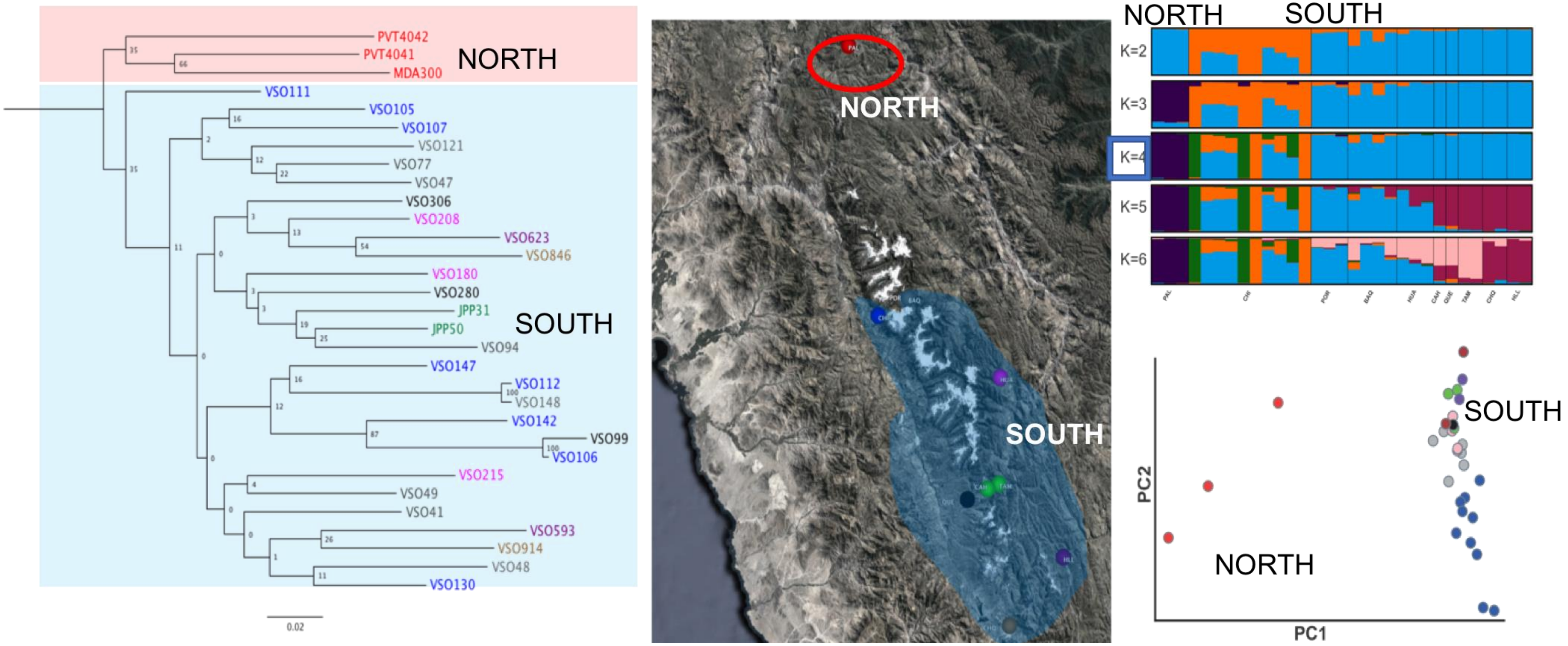
(CAH), Querococha (QUE), Huallanca (HLL), Chiquian (CHQ) and Conocochas (CON), which I named as north-south clade, and other formed by Escalon (ESC), Macate (MAC) and Chircarhuapunta, (CHP), I called as western clade. The PCA showed none of the populations overlap andthe north clade is only represented by one specimen respectively. The western and north clades are segregated. The STRUCTURE analysis also identified three distinct genetic populations, with a K=4 as the most probable. (Figureo 8).

The phylogenetic relationship for *Phyllotis* determined that the nine populations sampled are divided into two main groups, one formed by Pallasca (PAL), Challhuas (CHA) and Huari (HUA), which corresponds to *Phyllotis andium,* and the other formed by Escalon (ESC), Macate (MAC) and Chircarhuapunta, (CHP), Cajacay (CAJ), Conocochas (CON) and Chiquian (CHQ), that corresponds to *P. occidens*. The PCA showed three clusters when all specimens of *Phyllotis occidens* are very close and overlap, and on the other hand *P. andium* has two clusters, one grouped with Huari (HUA) and Challhuas (CHA) populations and other with specimens of Pallasca (PAL) of the north. The STRUCTURE analysis also identified two distinct genetic populations corresponding to *P. occidens* and *P. andium*, with a K=3 as the most probable. (Figureo 9).

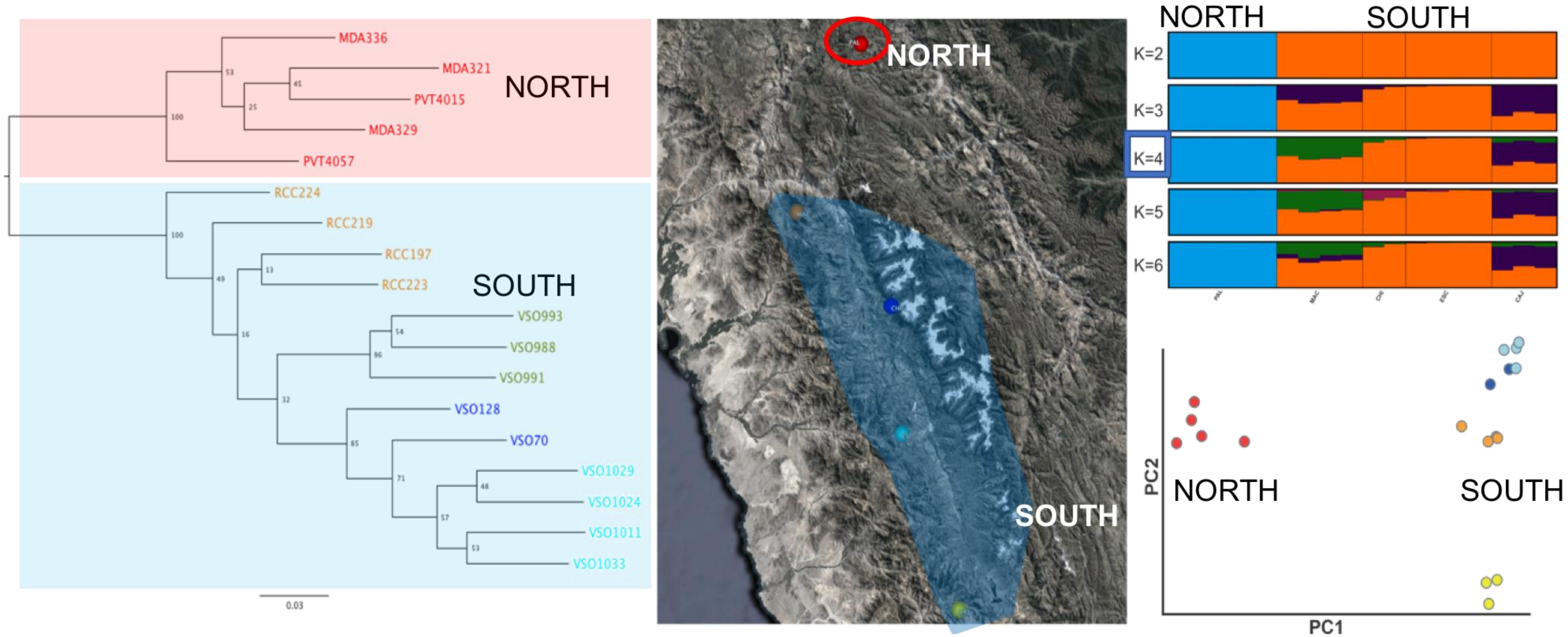
The phylogenetic relationship for *Thomasomys praetor* determined that the four populations sampled are divided into two groups, one formed by Chinancocha (CHI) and Pallasca (PAL), which I called as north clade, and the other formed by Baqueria (BAQ) and Tambillo (TAM) which I called as south clade, The PCA recovered the same two clusters (South and North clade). The STRUCTURE analysis also identified two distinct genetic populations, with a K=4 as the most probable. (Figureo 10).



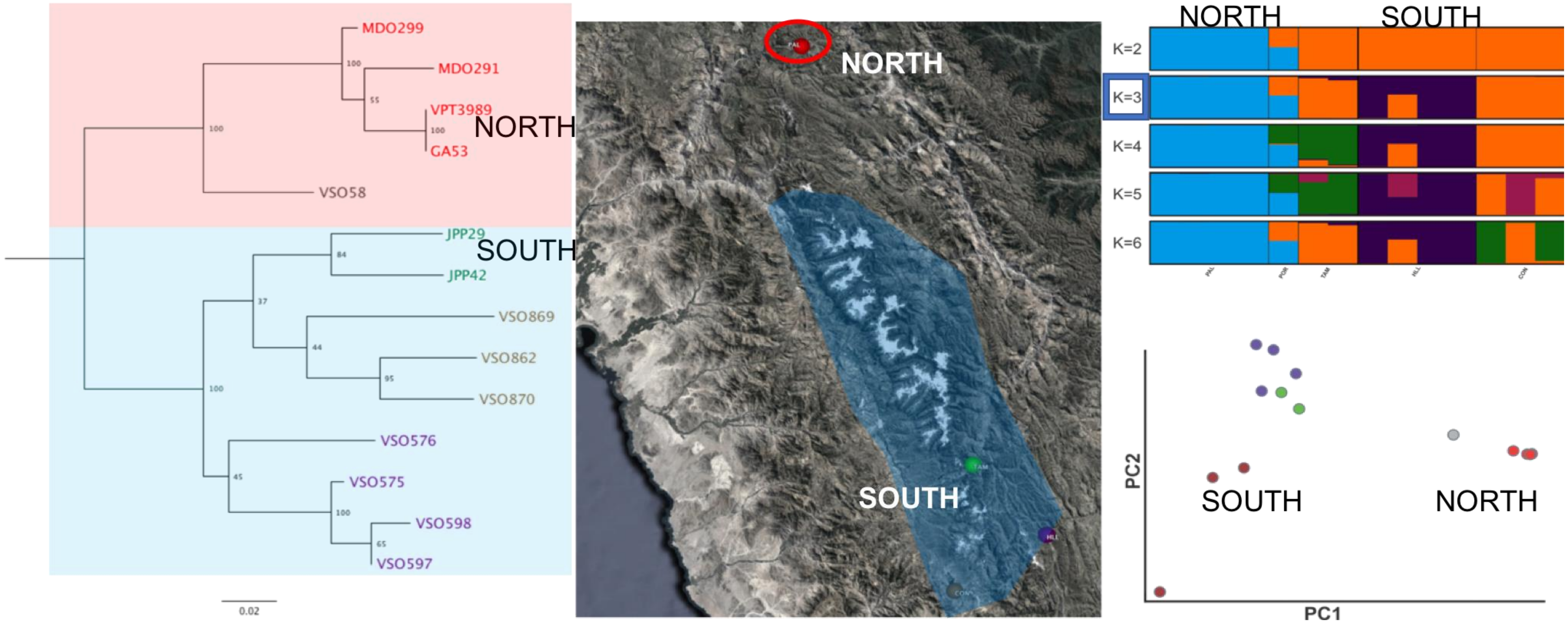
Figureo 4. Phylogenetic tree for *Akodon mollis* inferred under maximum likelihood (ML) with RAxML. Numbers on the nodes indicate the bootstrap values. Information about samples is in the Appendix C. Map shows the locations of samples analyzed. STRUCTURE analysis plots with sampling sites and a number of classes (K) from 2 to 6. Samples sites are mentioned as an abbreviation (see Table 2). PCA of samples with the first and second principal components (PC). For abbreviation of sampling sites see Table 2. Each color in the phylogenetic tree, map, and PCA are related.



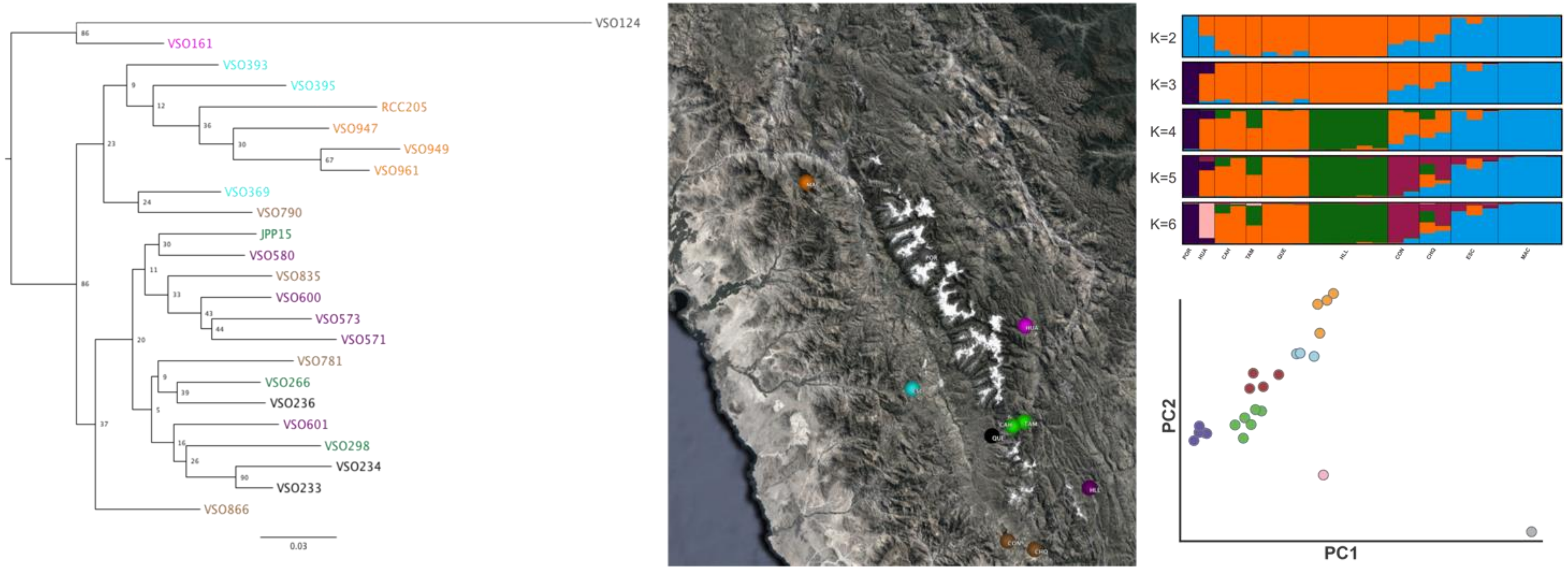
Figureo 5. Phylogenetic tree for *Microryzomys altissimus* inferred under maximum likelihood (ML) with RAxML. Numbers on the nodes indicate the bootstrap values. Information about samples is in Appendix C. The map shows the locations of samples analyzed. STRUCTURE analysis plots with sampling sites and a number of classes (K) from 2 to 6. Samples sites are mentioned as an abbreviation (see Table 2). PCA of samples with the first and second principal components (PC). For an abbreviation of sampling sites see Table 2. Each color in the phylogenetic tree, map, and PCA are related.



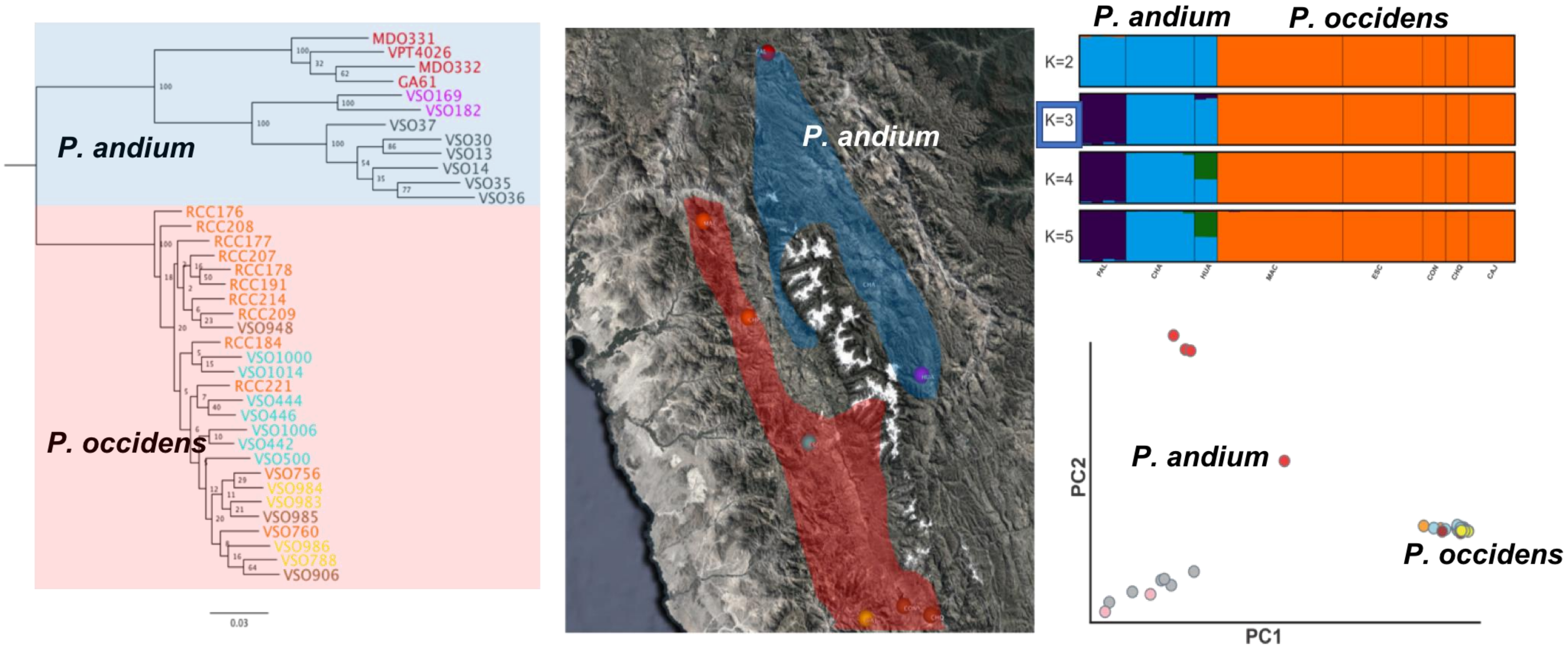
Figureo 6. Phylogenetic tree for *Oligoryzomys andinus* inferred under maximum likelihood (ML) with RAxML. Numbers on the nodes indicate the bootstrap values. Information about samples is in Appendix C. The map shows the locations of sampled analyzed. STRUCTURE analysis plots with sampling sites and a number of classes (K) from 2 to 6. Samples sites are mentioned as an abbreviation (see Table 2). PCA of samples with the first and second principal components (PC). For abbreviation of sampling sites see Table 2. Each color in the phylogenetic tree, map, and PCA are related.



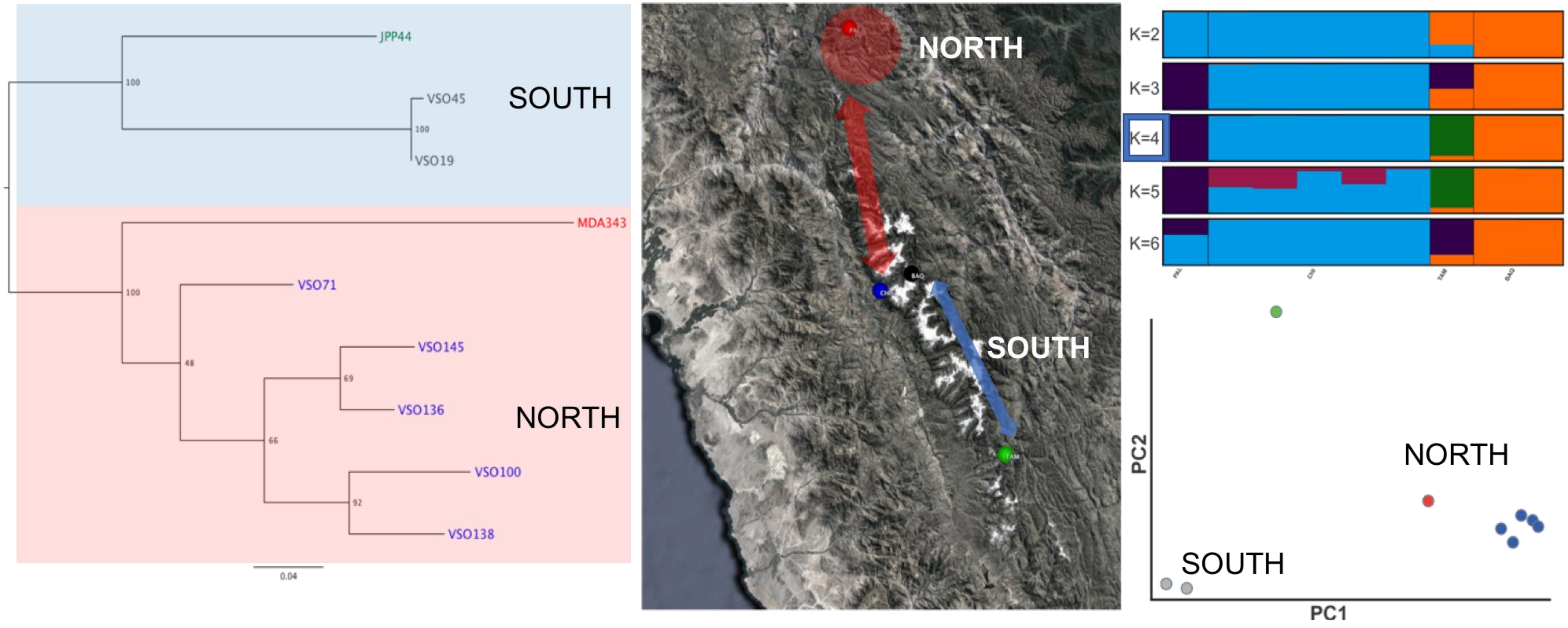
Figureo 7. Phylogenetic tree for *Auliscomys pictus* inferred under maximum likelihood (ML) with RAxML. Numbers on the nodes indicate the bootstrap values. Information about samples is in Appendix C. The map shows the locations of samples analyzed. STRUCTURE analysis plots with sampling sites and a number of classes (K) from 2 to 6. PCA of samples with the first and second principal components (PC). For abbreviation of sampling sites see Table 2. Each color in the phylogenetic tree, map, and PCA are related



Figureo 8. Phylogenetic tree for *Calomys sorellus* inferred under maximum likelihood (ML) with RAxML. Numbers on the nodes indicate the bootstrap values. Information about samples is in Appendix C. The map shows the locations of samples analyzed. STRUCTURE analysis plots with sampling sites and a number of classes (K) from 2 to 6. PCA of samples with the first and second principal components (PC). For abbreviation of sampling sites see Table 2. Each color in the phylogenetic tree, map, and PCA are related.



Figureo 9. Phylogenetic tree for *Phyllotis occidens and P. andium* inferred under maximum likelihood (ML) with RAxML. Numbers on the nodes indicate the bootstrap values. Information about samples is in Appendix C. The map shows the locations of samples analyzed. STRUCTURE analysis plots with sampling sites and a number of classes (K) from 2 to 6. Samples sites are mentioned as an abbreviation (see table 2). PCA of samples with the first and second principal components (PC). For abbreviation of sampling sites see Table 2. Each color in the phylogenetic tree, map, and PCA are related.



Figureo 10. Phylogenetic tree for *Thomasomys praetor* inferred under maximum likelihood (ML) with RAxML. Numbers on the nodes indicate the bootstrap values. Information about samples is in Appendix C. The map shows the locations of samples analyzed. STRUCTURE analysis plots with sampling sites and a number of classes (K) from 2 to 6. Samples sites are mentioned as an abbreviation (see Table 2). PCA of samples with the first and second principal components (PC). For abbreviation of sampling sites see Table 2. Each color in the phylogenetic tree, map, and PCA is related.

3.3.3. Demography history

The demographic history of *Akodon mollis* and the species of the genus *Phyllotis* were consistent with a model of isolation with migration. The magnitude and direction of migration events was not the same; in *Akodon mollis* I found evidence of lower migration levels between the North and South population. Nevertheless, in *Phyllotis*, the confidence interval pointed to a high probability of high levels of migration (~40% of Ne) between the *P. andium* and *P. occidens* at different times.

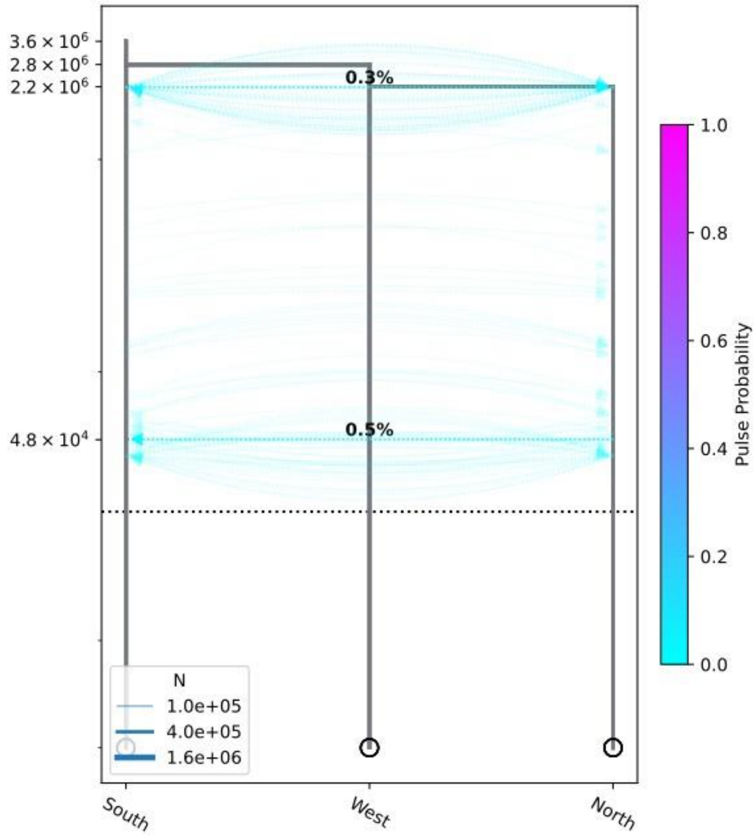
For *Akodon mollis*, A single model of bidirectional and asymmetrical lower migration levels between the North and South populations provided the best fit to this dataset (model 6; log-lik = −-13,489.42963, AIC = 26986.85927; ωi = 1) (Table 3, Figureo 11). After bootstrapping, I dated the divergence of the South group from the other groups to be approximately 2.8 Ma (95% CI 2.5–3.0 Ma), whereas the divergence between the Western and North group was estimated at around 2.2 Ma (95% CI 2.0–2.5 Ma). In this model, events of migration were identified around 2.2 Ma from South to North, and 48 ka from North to South, and in both cases, the pulses of migrations are no higher than ~0.5% of Ne. For the genus *Phyllotis*, the best-fit demographic model exhibits bidirectional and asymmetrical with a high migration level from *P. occidens* to *P. andium* and a significantly lower migration level from *P. andium* to *P. occidens* (model 6; log-lik =-12120.128, AIC = 24254.2557; ωi = 1) (Table 4, Figure 12). I dated the divergence between these two species as 3.4 Ma (95% CI 2.8–3.9 Ma), the events of migration identifies occur in two possible dates, the first with a high pulse (~40% of Ne) around 0.43Ma ka from *P. occidens* to *P. andium*, and the second with a lower pulse (~3.2% of Ne) from 0.018 Ma *P. andium* to *P. occidens*.

Table 3. Summary of the results of demographic model selection with *momi2 for Akodon mollis*. Values of composite likelihood (Max ln(likelihood); the number of parameters of the model (N Parameters); Akaike Information Criterion (AIC); the difference between AIC values of each model and that of the best-ranked model (ΔAIC); and Akaike weights (ωi) for the five models. Model numbers refer to the schematic models in Fig. 3.

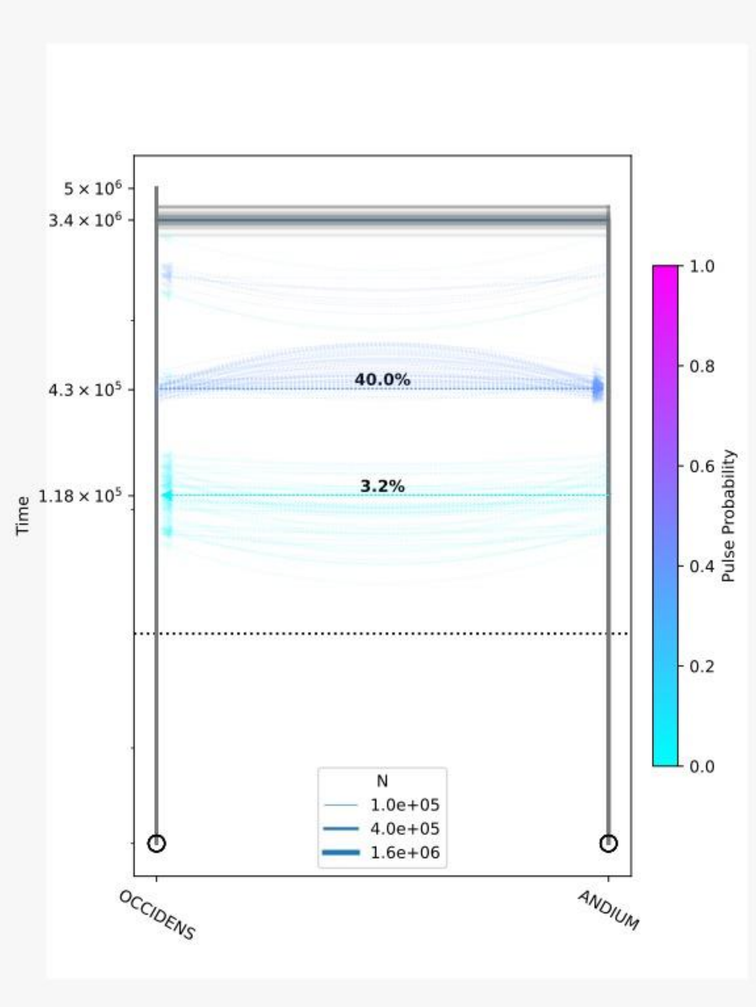
Model	**Max ln (likelihood)**	**N parameters**	**AICs**	**Δ AIC**	**ωi**
4	-13489.42963	4	26986.85927	0	1
5	-13512.58268	4	27033.16536	46.30609157	8.81E-11
3	-13526.33819	8	27068.67638	81.81710843	1.71E-18
2	-13541.35597	4	27090.71195	103.8526787	2.81E-23
1	-13570.58233	5	27151.16465	164.3053844	2.10E-36

Table 4. Summary of the results of demographic model selection with *momi2 for Phyllotis genus*. Values of composite likelihood (Max ln(likelihood); the number of parameters of the model (N Parameters); Akaike Information Criterion (AIC); the difference between AIC values of each model and that of the best-ranked model (ΔAIC); and Akaike weights (ωi) for the eight models. Model numbers refer to the schematic models in Fig. 3.

Model	**Max ln (likelihood)**	**N parameters**	**AICs**	**Δ AIC**	**ωi**
6	-12120.12785	7	24254.2557	0	1
1	-12158.45161	7	24330.90321	76.6475144	2.27E-17
8	-12169.17036	5	24348.34073	94.08503084	3.71E-21
5	-12175.47986	5	24360.95971	106.704012	6.75E-24
3	-12175.47866	7	24364.95732	110.7016216	9.15E-25
4	-12424.44728	5	24858.89455	604.6388545	5.06E-132
7	-12424.4473	5	24858.89461	604.6389114	5.06E-132
1	-12462.91161	3	24931.82322	677.5675196	7.38E-148



Figureo 11. Schematic of the demographic model and parameter estimates for *Akodon mollis* with the bootstrap replicates (model 6 in Figs. 3A). Values associated with migration events (light blue arrows) represent the percentage of Ne that migrated



Figureo 12. Schematic of the demographic model and parameter estimates for *Phyllotis andium* and *P. occidens* with the bootstrap replicates (model 6 in Figs. 3B). Values associated with migration events (light blue arrows) represent the percentage of Ne that migrated

3.3.4. Morphological variation

I recovered discrete morphological characters for the species analyzed here (for brief descriptions of each taxa see appendix D). The type and number of the traits that present informative variation throughout the geography, varied for each species analyzed.

Akodon mollis

When performing the morphological analysis of *A. mollis*, I found six discrete morphological characters (Figure 13 and 14), as follows:

i) Antorbital bridge. In the frontal view of the skull. very broad (0), broad (1), or very thin (2);

ii) Anterior margin of the zygomatic plate. Straight (0), sigmoid (1), or bulky (2),

iii) Foramen oval (in ventral view), diminutive as small as a dot (0), small (1), or very large (2);

iv) Capsular process of the jaw . Absent (0) or present (1);

v) Hamular process. Broad (0) or thin (1);

vi) Stapedial spine of auditory bulla. A notorious Stapedial spine (0) or very diminutive (1).

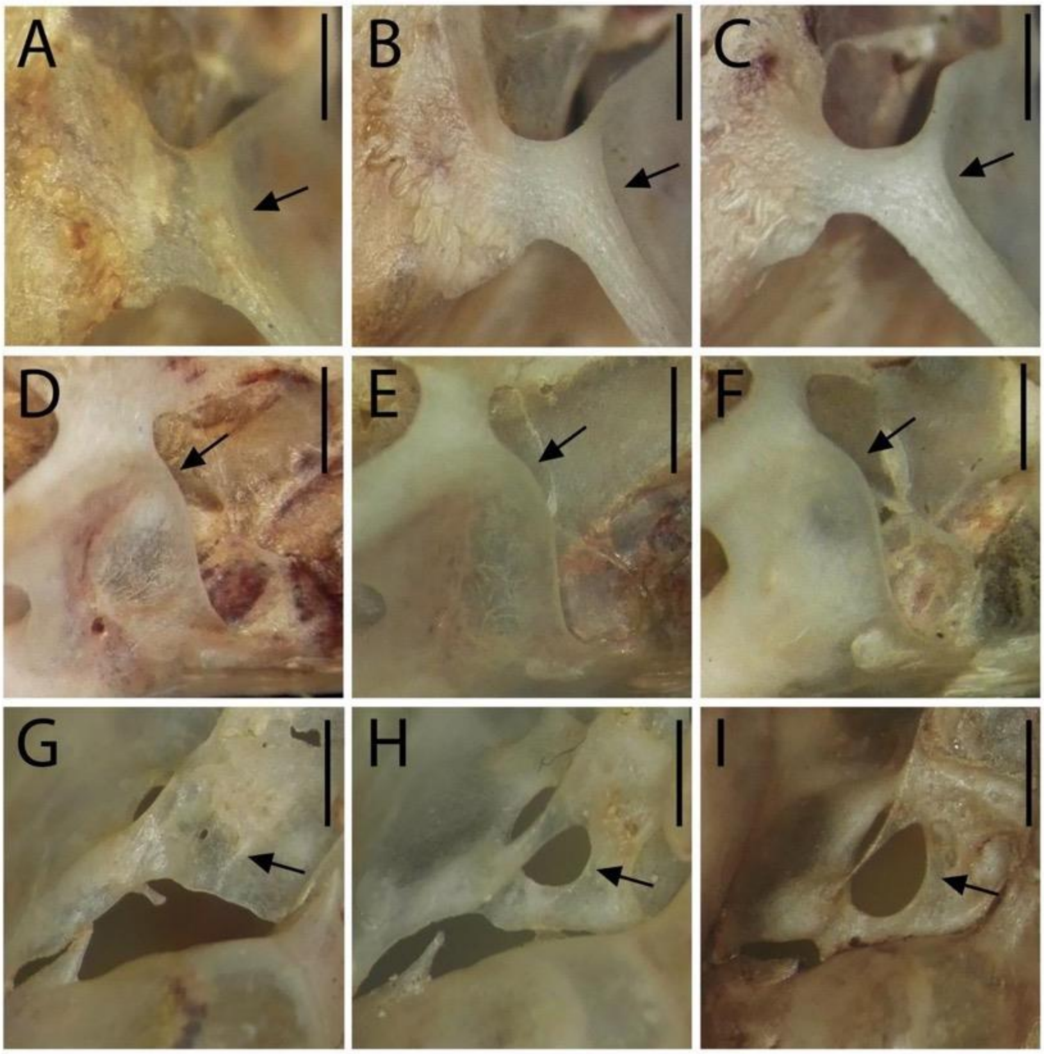


Figure 13. Character states evaluated for *Akodon mollis*. Antorbital bridge (A, B, C): state 0 (A – MUSM 50121), state 1 (B – MUSM 49208), state 2 (C – MUSM 40150). Stapedial spine of auditory bulla (D, E, F): state 0 (D – MUSM 49074), state 1 (E – MUSM 49224), state 2 (F – MUSM 5779). Foramen oval (G, H, I): state 0 (G – MUSM 49212), state1 (H – MUSM 49153), state 2 (I – MUSM 3635).

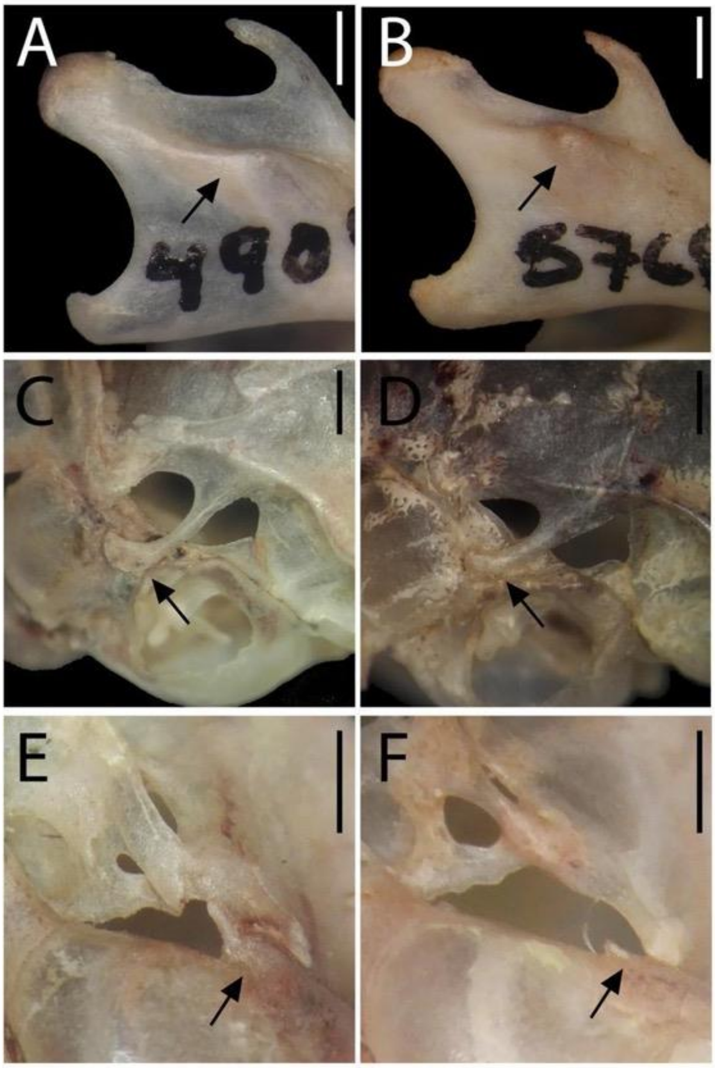


Figure 14. Character states of *Akodon mollis*. Capsular process. (A, B): state 0 (A – MUSM 49097), state 1 (B – MUSM 5768). Hamular process (C, D): state 0 (C – MUSM 49074), state 1 (D – MUSM 49130). Stapedial spine of auditory bulla (E, F): state 0 (E – MUSM 50118), state 1 (F – MUSM 49445

Microryzomys altissimus

For this species, I recovered two discrete morphological characters that were informative (Figure 15), namely:

i) Fronto-nasal suture, aligned with the premaxillar nasal suture (0) or projected beyond the premaxillar nasal suture (1);

ii) Foramen oval. Large (0) or small (1)

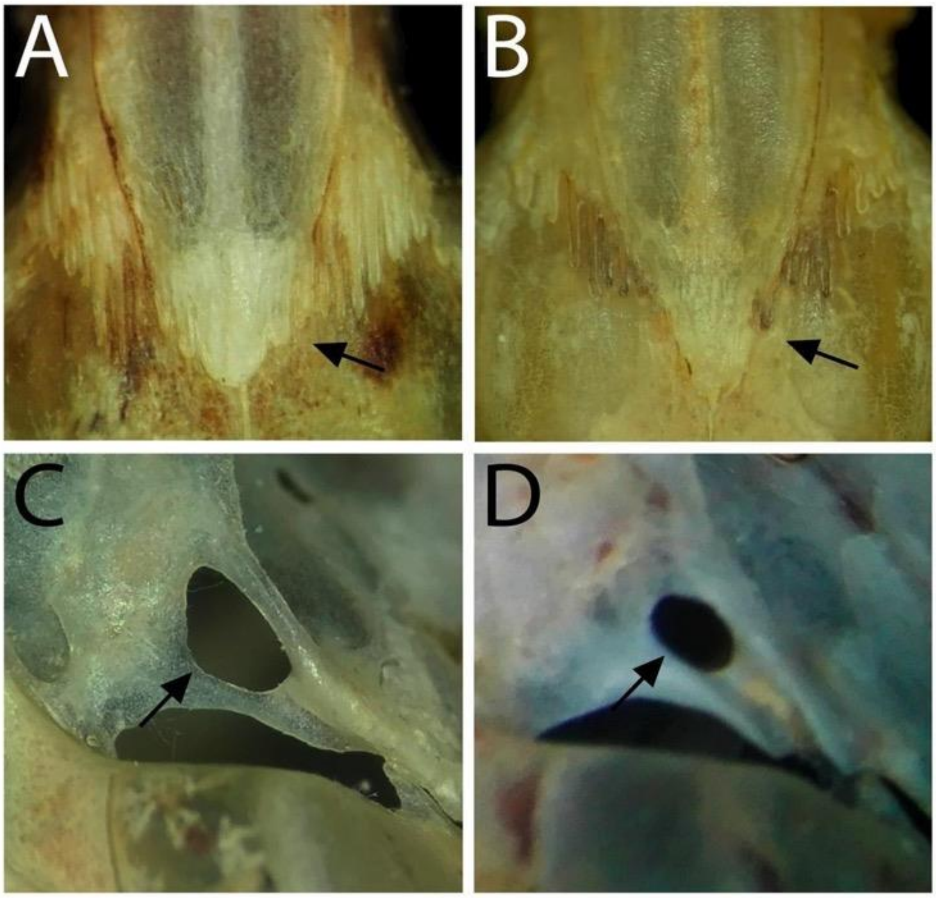


Figure 15. Character states for *Microryzomys altissimus*. Fronto-nasal suture (A, B): state 0 (MUSM 49915), state 1 (MUSM 49892). Foramen ovale (C,D): state 0 (MUSM 49894), state 1 (MUSM 49914).

Oligoryzomys andinus

For this species, I found four discrete morphological characters (Figure 16 and 17) which were:

i) Foramen ovale. Large (0) or small (1);

ii) Sphenopalatine foramen. Larger than the ethmo-turbinate (0) or as large as the ethmo-turbinate (1);

iii) Fronto-nasal suture. Below the fronto-premaxillary suture (0) or aligned (1);

iv) Middle lacerate foramen. Large (0) or reduced (1).

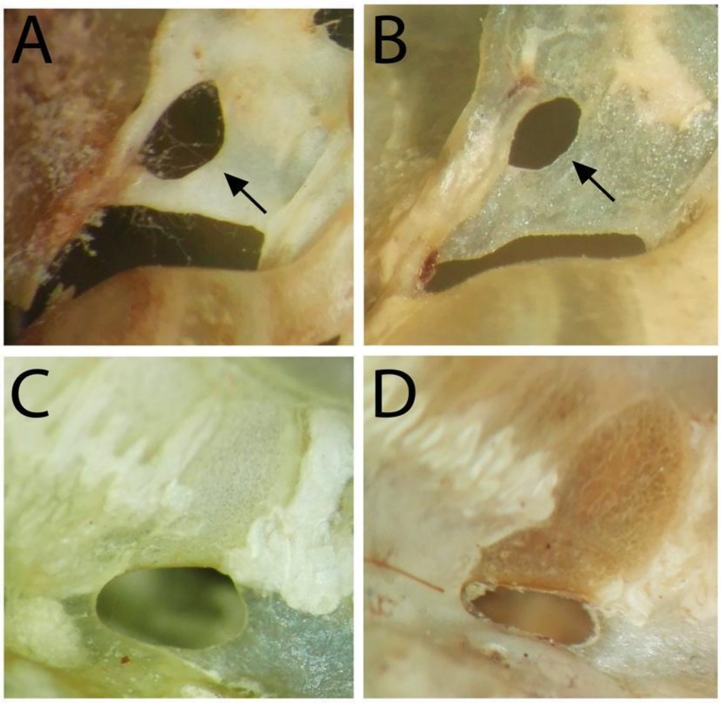


Figure 16. Character states *Oligoryzomys andinus*. Foramen ovale (A, B): state 0 (MUSM 5407), state 1 (MUSM 49938). Sphenopalatine foramen/ethno turbinate (C, D): state 0 (MUSM 40184), state 1 (MUSM 23227).

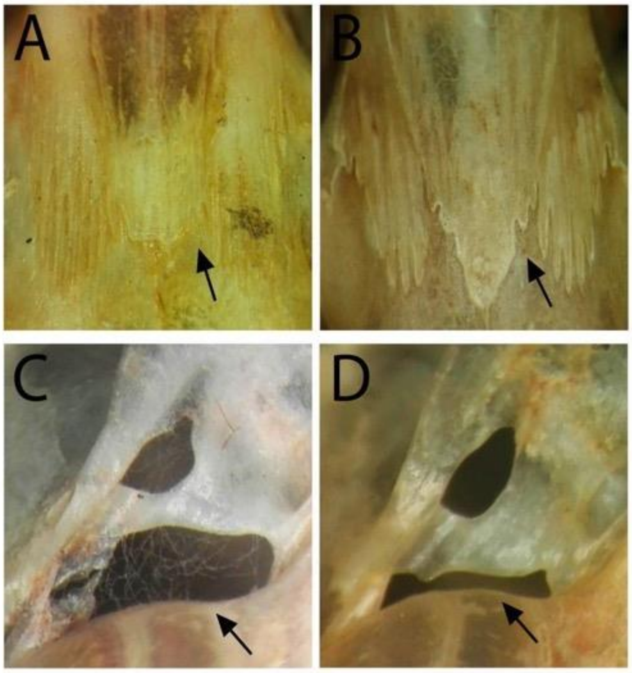


Figure 17. Character states *Oligoryzomys andinus*. Frontonasal suture (A, B): state 0 (MUSM 5403), state 1 (MUSM 23227). Middle lacerate foramen (C, D): state 0 (MUSM 23299), state 1 (MUSM 49929).

Auliscomys pictus

The evaluation of the samples of this species revealed six discrete morphological characters that exhibited discontinuities along the geography (Figure 18, 19 and 20):

i) Incisive foramina. Width (0) or narrow (1);

ii) Nasal tip. Broad (0) or slender (1);

iii) Fronto-nasal suture. Aligned with the fronto-premaxiliar suture (0) or beyond than fronto- premaxiliar suture (1);

iv) Small palatal process on mesopterygoid fossa. Present (0) or absent (1);

v) Zygomatic spine. Absent (0) or present (1);

vi) Stapedial foramina. Absent (0) or present (1).

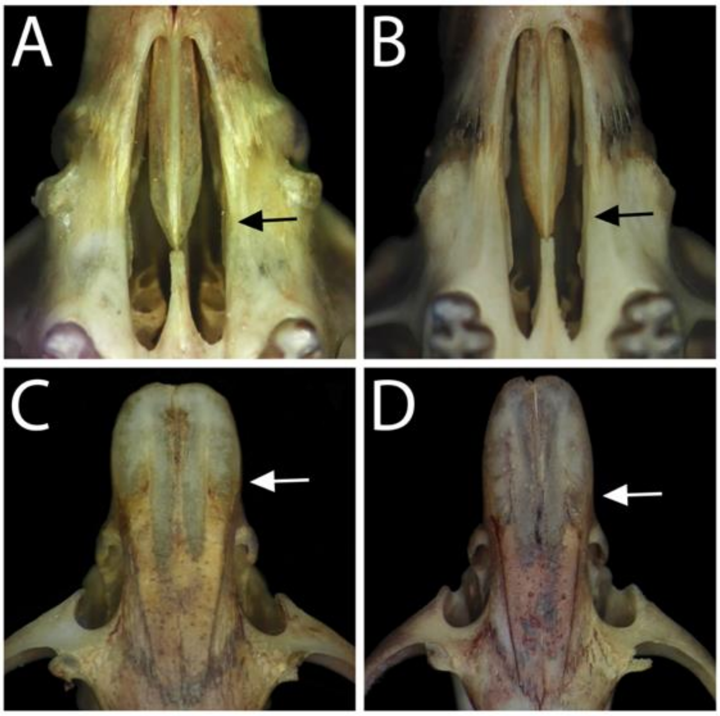


Figure 18. Character states *Auliscomys pictus*. Incisive foramen (A, B): state 0 (MUSM 49622), state 1 (MUSM 49624). Nasal tip: state 0 (MUSM 49626), state 1 (MUSM 49623).

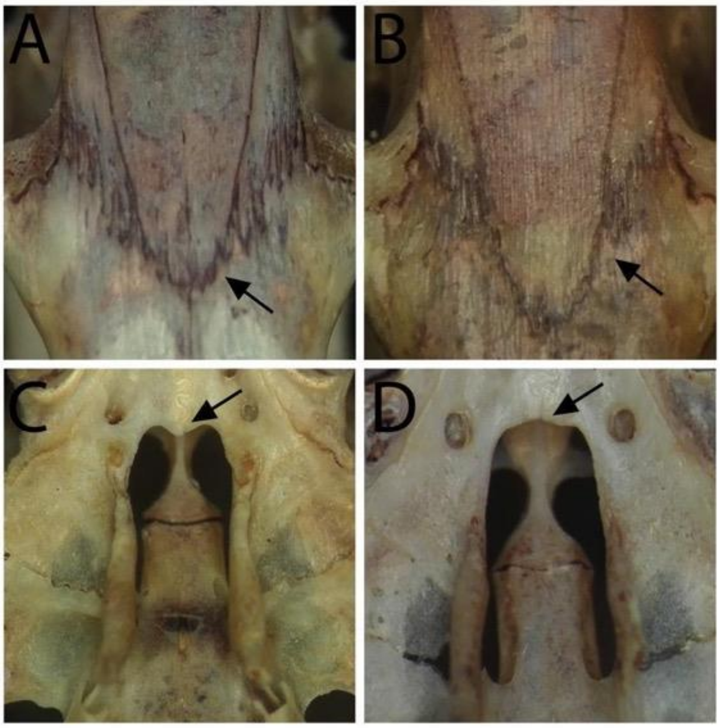


Figure 19. Character states *Auliscomys pictus.* Frontonasal suture (A, B): state 0 (MUSM 49624), state 1 (MUSM 49622). Small palatal process on mesopterygoid fossa: state 0 (MUSM 49644), state 1 (MUSM 49613).

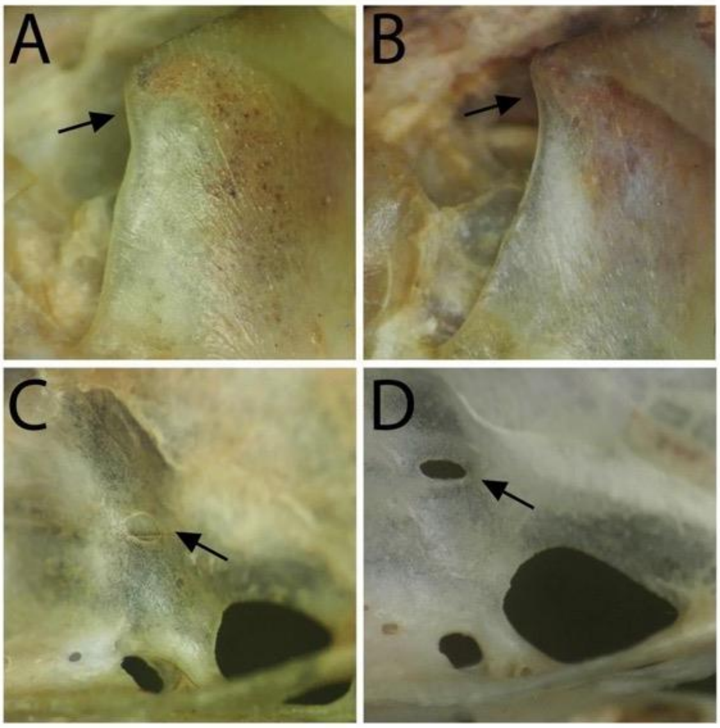


Figure 20. Character states *Auliscomys pictus.* Zygomatic spine (A, B): state 0 (MUSM 49623), state 1 (MUSM 49596). Stapedial foranmina state 0 (MUSM 49618), state 1 (MUSM 49613).

Calomys sorellus

I found six discrete morphological characters which are (Figure 21, 22, 23):

i) Posterior palatine foramen. Located distant from the maxillo-palatal suture (0) or located on the maxillo-palatal suture (1);

ii) Incisive foramina. The posterior margin of the foramina reaching the second root of the first molar (0) or does not reach the second root of the first molar (1);

iii) Buccinator-masticatory foramen. Small (0) or large (1);

iv) Sphenopalatine foramen. Larger than the ethno-turbinate (0) or equally large (1);

v) Foramen ovale. Very large (0) or small (1);

vi) Middle lacerate foramen. Large (0) or reduced (1).

vii) Mesopterygoid fossa in V shape (0) or bounded shape (1).

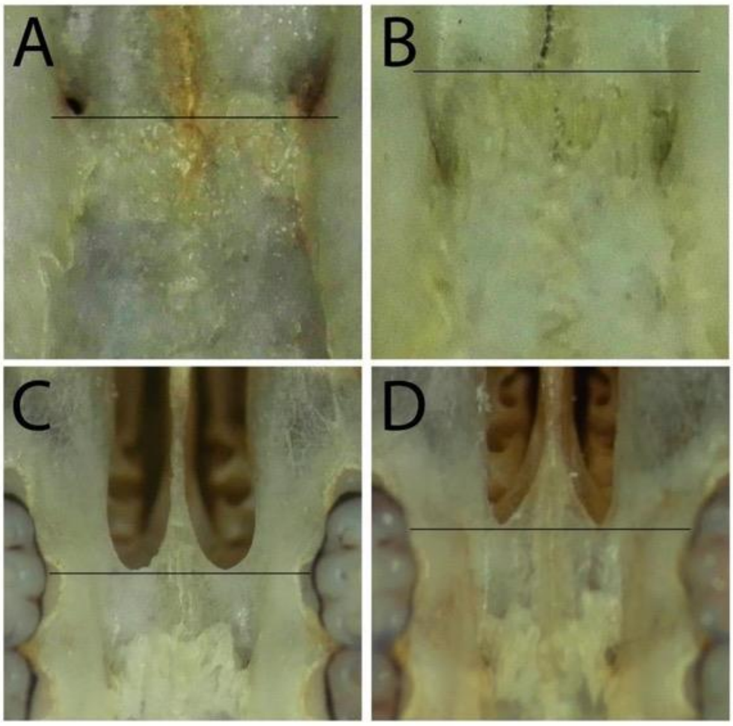


Figure 21. Character states *Calomys sorellus*. Antero-palate pits (A, B): state 0 (MUSM 40061), state 1 (MUSM 49662). Incisive foramen (C, D): state 0 (MUSM 49663), state 1 (MUSM 49655).

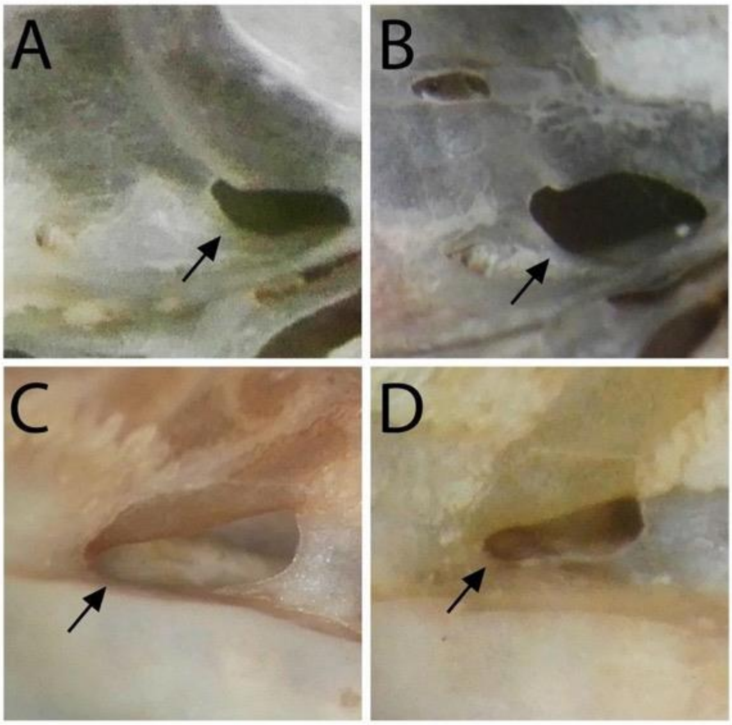


Figure 22. Character states *Calomys sorellus*. Foramen ovale (A, B): state 0 (MUSM 49747), state 1 (MUSM 49697). Sphenopalatine foramen (C, D): state 0 (MUSM 40061), state 1 (MUSM 49655).

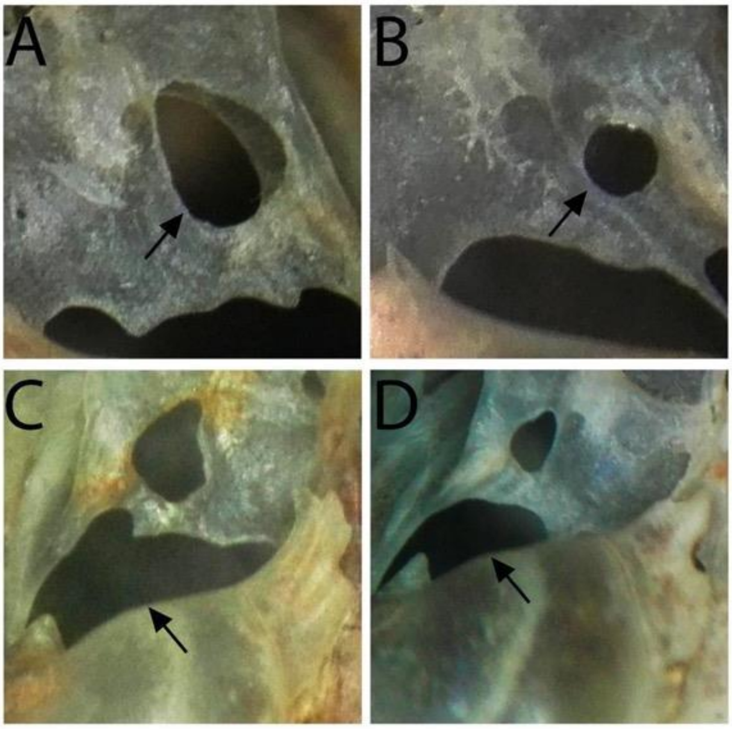


Figure 14. Character states *Calomys sorellus*. Foramen ovale (A, B): state 0 (MUSM 49656), state 1 (MUSM 49697). Middle lacerate foramen (C, D): state 0 (MUSM 49851), state 1 (MUSM 49755).

Genus *Phyllotis*

both *P. andium* and *P. occidens* I found six discrete morphological characters (Figure 15 and 16):

i) Fronto nasal suture. Aligned with the fronto-premaxiliar suture (0) or beyond than fronto-premaxiliar suture (1);

ii) Posterior palatine foramen. Located close to the incisive foramen (0) or close to the maxillary portion of the palatine (1);

iii) Palatal process. Absent (0) or present (1) ,

iv) Zygomatic spine. Absent (0) or present (1);

v) Hamular process. Moderately broad (0) or thin (1);

vi) Eustachian tube. Subequal to the posterior lobe of the pterygoid process (0) or in contact with the parapterygoid process (1).

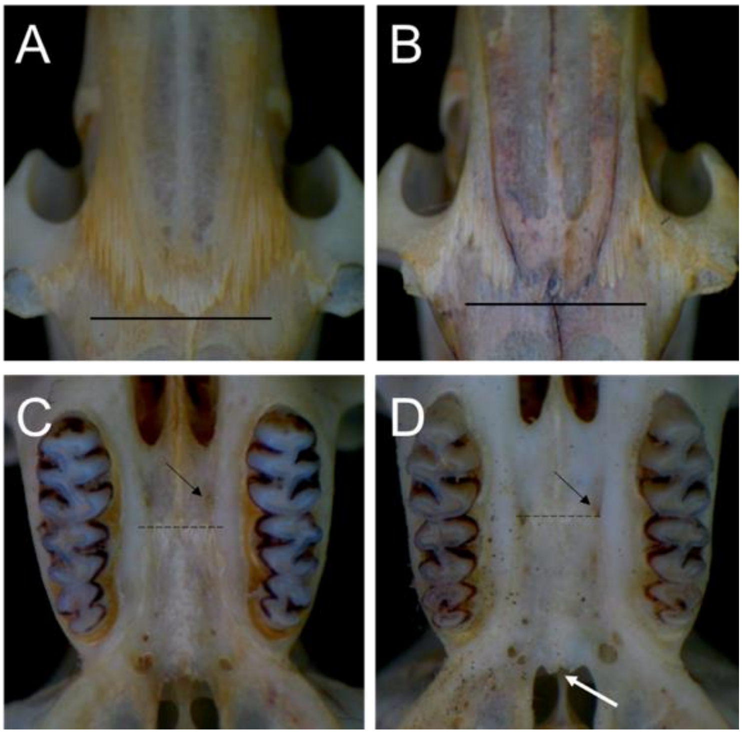


Figure 15. Character states for the genus *Phyllotis*. Fronto nasal suture (A, B): state 0 (MUSM 40197), state 1 (MUSM 50020). Posterior palatine foramen (C, D): state 0 (MUSM 40197), state 1 (MUSM 45211) black arrow indicate position in relation to maxillo-palatine suture. Palatal process (C, D): state 0 (MUSM 40197),), state 1 (MUSM 45211).

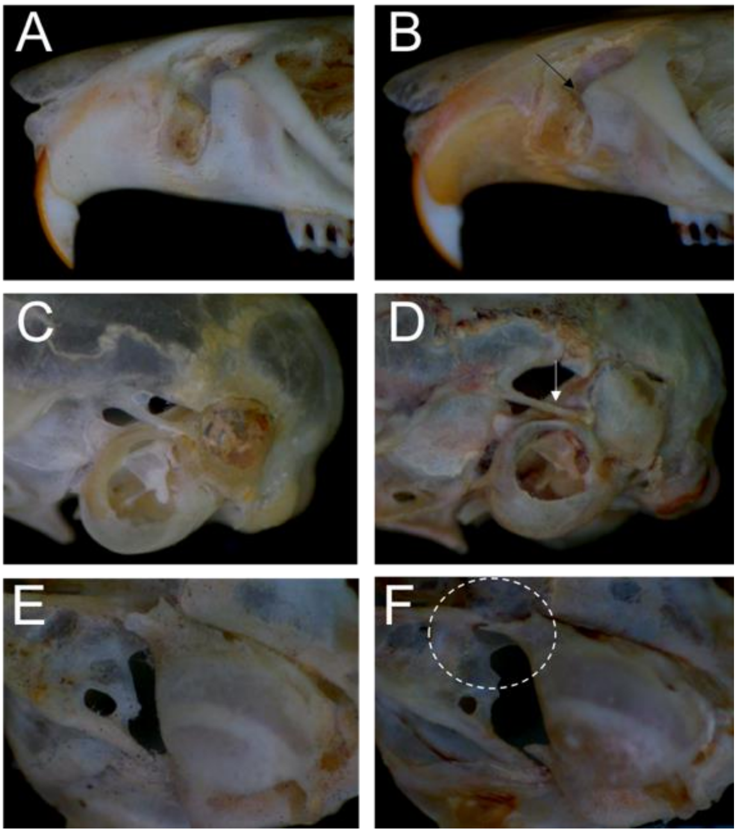


Figure 16. Character states *Phyllotis* Zygomatic spine. (A, B): state 0 (MUSM45211), state 1 (MUSM 50020). Hamular process. (C, D): state 0 (MUSM 23932), state 1 (MUSM 50020). Eustachian tube. (E, F): state 0 (MUSM 40197), state 1 (MUSM 45211).

Thomasomys praetor

Four discrete morphological characters were found (Figure 17):

i) Mesopterygoid fossa. Narrow (0) or broad (1);

ii) Stapedial spine of auditory bulla. Reach to posterior border of parapterygoid (0) or don’t reach to posterior border of parapterygoid (1)

iii) Fronto nasal suture: beyond than fronto-premaxillary suture (0) or Aligned with the fronto-premaxillary suture (1)

iv) Nasal tip. Slender (0) or broad (1);

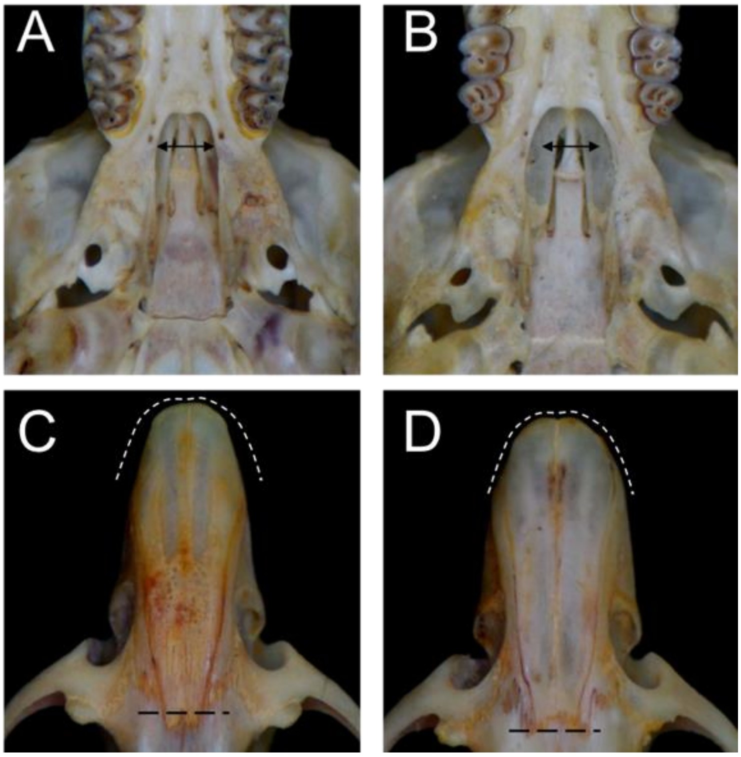


Figure 17. Character states *Thomasomys praetor* Mesopterygoid fosse (A, B): state 0 (MUSM 50030), state 1 (MUSM 50037). Stapedial spine of auditory bulla (A, B): state 0 (MUSM 50030), state 1 (MUSM 50037). Fronto nasal suture (C, D): state 0 (MUSM MUSM 40209), state 1 (MUSM 50036). Nasal tip (C, D): state 0 (MUSM 40209), state 1 (MUSM 50036).

When mapping, the scoring of each analyzed specimen, some patterns of geographic variation arise. The results for *Akodon mollis* show the grouping of three large morphological populations (Figure 18), the first located to the north, including the localities of Pallasca (PAL), Chinancocha (CHI), and Chalhuas (CHA), the second located to the South including the localities of Portachuelo (POR), Baqueria (BAQ), Huari (HUA), Tambillo (TAM), Cahuish (CAH), Querococha (QUE), Huallanca (HLL), Chiquian (CHQ), Conocochas (CON), Hatun Machay (HAT), Escalon (ESC); and the third located on the western side formed by the localities Macate (MAC), Chichuarapunta (CHP) and Cajacay (CAJ).

The two discrete characters found for *Microryzomys altissimus* do not show geographic patterns. They varied indistinctly throughout its distribution (Figure 19). Likewise, in *Oligoryzomys andinus*, the four discrete characters showed no pattern of variation associated with geography (Figure 20).

For *Auliscomys pictus*, a slight clinal variation was distinguished from north to south, where there are two groups, populations of Pallasca (PAL) and Portachuelo (POR) for the north. The Huari (HUA), Hyallanca (HLL), Tambillo (TAM), and Conococchas (CON) populations, to the south, Hatun machay (HAT) and Chichuarapunta (CHP) only have a single individual but can be considered as part of South (Figure 21).

The character states are very constant in the individuals of each species, with some variations (Figure 23). For *Calomys sorellus* the six discrete characters showed no clear distribution pattern of variation, but the specimens of Pallasca (PAL) are slightly different from the others (Figure 22). Regarding the genus *Phyllotis*, it was possible to recover a clear morphological difference between the two species present in the area, *Phyllotis occidens*, which covers the localities Macate (MAC), Chichuarapunta (CHP), Escalon (ESC), Hatun Machay (HAT), Conocochas (CON), Chiquian (CHQ), and *Phyllotis andium* that covers the localities of Pallasca (PAL), Challhuas (CHA), Chinancocha (CHI), Huari (HUA).

For *Thomasomys praetor*, the four characters do not show a clear geographic pattern; nevertheless, individuals of Pallasca (PAL) are slightly different from Baqueria (BAQ); Chinancocha (CHI), and Tambillo (TAM) (Figure 24).

3.3.5. Morphometric analysis

Principal Component Analysis (PCA) conducted on *Akodon mollis* showed that PC1 accounts for 23.33% of the variation, PC2 for 19.53% and PC3 for 12.82% of the variation, PC1 has high positive loadings from DL and BPB and high negatives loadings for BB, IC, MTRL, OCW and CD, PC2 has high positive loadings from NL and IFL and high negatives loadings for ZP (Appendix E). The dispersal of individual scores throughout the multivariate space of the LDA forms three groups: a cluster restricted to the superior portion of axis two that correspond to northern populations, a cluster occupying an intermediate position of axis two, and a slightly right portion of the axis one that corresponds to southern populations, and finally a cluster nested in a cloud in the left portion of the axis one that corresponds to western population (Figure 18).

PCA conducted on *Microryzomys altissimus* showed that PC1 accounts for 30.55% of the variation, PC2 for 17.18%, and PC3 for 10.67%. PC1 has high positive loadings from IC and HBC and high negative loadings for NL, and PC2 has high positive loadings from OCW and high negative loadings for RW (Appendix E). The multivariate space of the LDA forms two groups, a separate cluster to the left portion of axis one that corresponds to northern populations, and another cluster occupying mainly the right portion of axis one that corresponds to southern populations (Figure 19).

PCA conducted on *Oligoryzomys andinus* showed that PC1 accounts for 29.13% of the variation, PC2 for 12.73%, and PC3 for 12.38% of the variation. PC1 has high positive loadings from BB, IC, MTRL, and HBC and high negatives loadings for NL and ZP, PC2 has high positive loadings from IFL, ZP and high negatives loadings for RW, AWand BPB (Appendix E). The multivariate space of the LDA forms two groups, a separate cluster to the inferior portion of axis two that correspond to northern populations and another cluster occupying mainly the intermediate and superior portion of axis two that correspond to southern populations (Figure 20).

PCA conducted on *Auliscomys pictus* showed that PC1 accounts for 44.38% of variation, PC2 for 13.72%, and PC3 for 11.57%. PC1 has high positive loadings from RL, NL, DL and high negative loadings for BB, IC, and MTRL. PC2 has high positive loadings from ZP and high negative loadings for RW, RW2, and BPB (Appendix E). The multivariate space of the LDA shows disperse groups, one located mainly to the right portion of axis 1, which corresponds to northern populations. Another located on the left portion of axis one, which corresponds to the Eastern population; and finally, a cluster nested in a cloud on the inferior portion of the axis two that correspond to south-western population (Figure 21)

PCA conducted on *Calomys sorellus* showed that PC1 accounts for 28.63% of the variation, PC2 for 15.05%, and PC3 for 13.64% of the variation, PC1 has high positive loadings from NL and RW and high negatives loadings IC, MTRL, OCW, CD, and HBC, PC2 has high positive loadings from BPB, and high negatives loadings for ZP (Appendix E). The multivariate space of the LDA shows all groups overlapped, without clear patterns.

PCA conducted on the genus *Phyllotis* showed that PC1 accounts for 34.67% of the variation, PC2 for 13.24%, and PC3 for 10.46% of the variation. PC1 has high positive loadings from BB, IC, and CD and high negative loadings BPB, and PC2 has high positive loadings from ZP, and high negative loadings for BPB (Appendix E). Here the multivariate space of the LDA shows all groups overlapped. Northern and eastern populations (that correspond to *P. andium*) are located mainly to the intermediate and superior portion on axis two. In contrast, the western and southern populations (that correspond to *P. occidens*) are located in the intermedium portion of axis two (Figure 23).

PCA conducted on *Thomasomys praetor* showed that PC1 accounts for 41.80% of the variation, PC2 for 23.78%, and PC3 for 10.41% of the variation. PC1 has high positive loadings from IC, AW, BPB, and high negatives loadings from IFL and ZP, while PC2 has high positive loadings from BPB and ZP (Appendix E). The multivariate space of the LDA shows two groups, one that corresponds to northern populations that are located mainly to the right portion on axis two, whereas the southern population is located in the left portion of axis 2 (Figure 24)

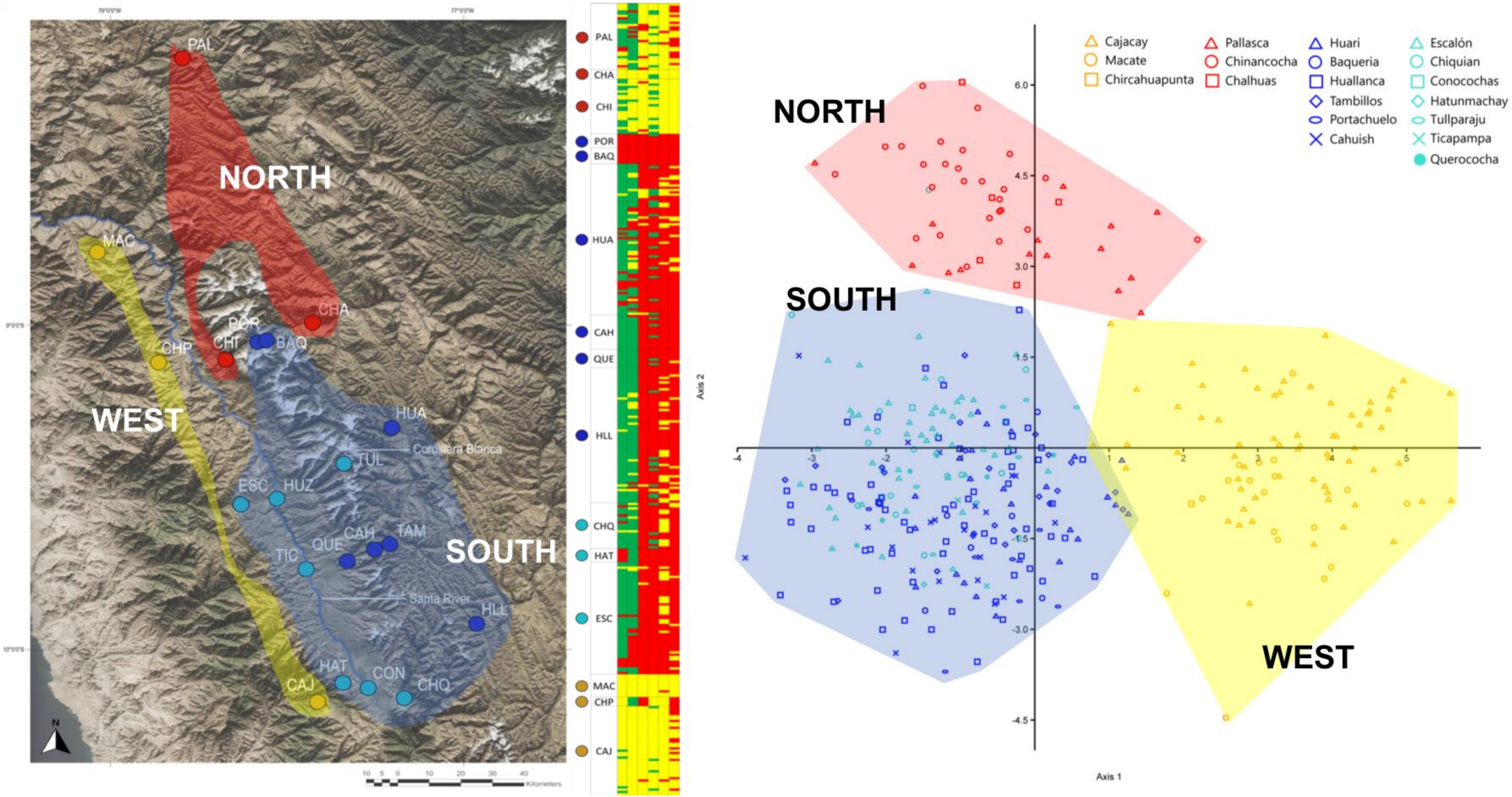


Figure 18. The map represents sampling sites for *Akodon mollis*. Figures show the qualitative morphological analysis and Linear Discriminant analysis. Red dots indicate sites from northern, Blue dots indicate sites from high altitudes and the eastern slope of Cordillera Blanca, Light blue dots indicate sites related to the Santa River basin, Yellow dots indicate sites from dry ecosystems on the Cordillera Negra. Each column represents a character, and each row represents a scored specimen. For characters with two state of character, character 0 correspond to the red cell, and character 1 correspond to the yellow cell. For a character with three states of character, character 0 corresponds to the red cell, character 1 corresponds to the green cell, and character 2 corresponds to the yellow cell.

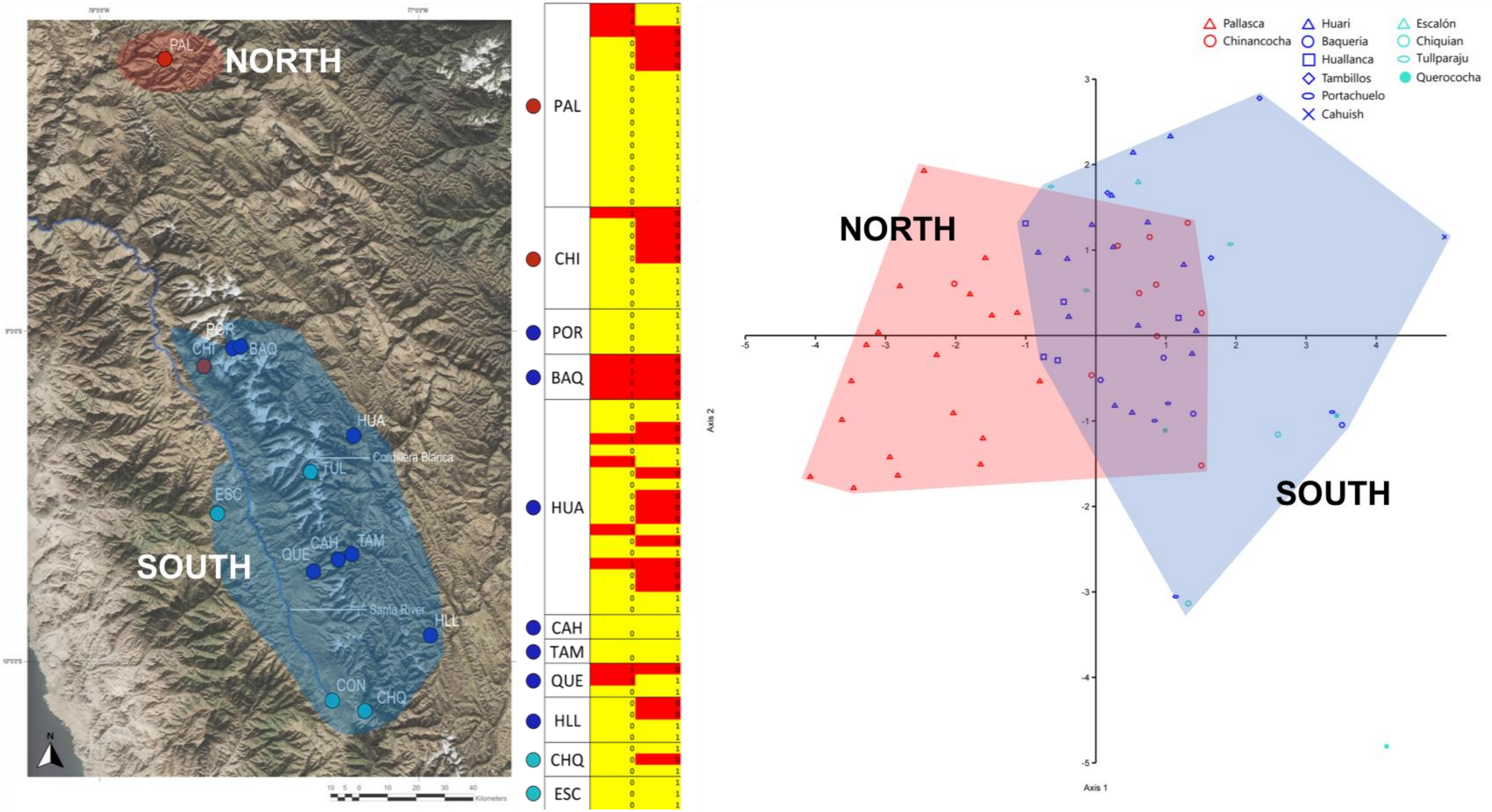
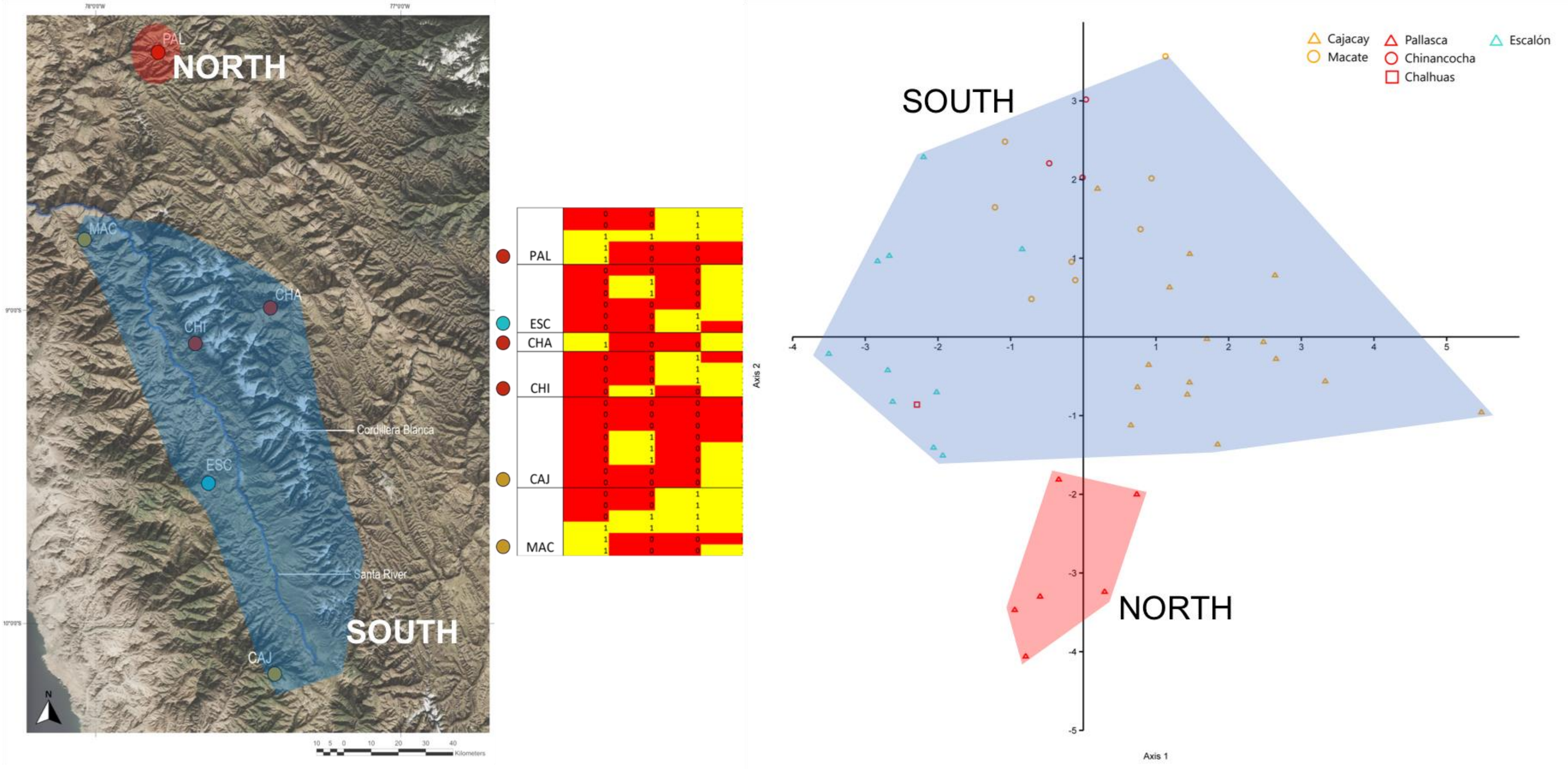


Figure 19. The map represents sampling sites for *Microryzomys altissimus*, figures show the morphological qualitative analysis and Linear Discriminant analysis. red dots indicate sites from northern, blue dots indicate sites from high altitudes and eastern slope of Cordillera Blanca, light blue dot indicate sites related with Santa River basin. Each column represents a character and each row represents a scored specimen. Each column represents a character and each row represents a scored specimen. Character 0 correspond to red cell, and character 1 correspond to yellow cell.



● PAL	0	0	1	🟨
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	1	0	0	🟥
	1	0	0	🟥
● ESC	0	0	0	🟨
	0	1	0	🟨
	0	1	0	🟨
	0	0	0	🟨
	0	0	1	🟨
	0	0	1	🟥
● CHA	1	0	0	🟨
● CHI	0	0	1	🟥
	0	0	1	🟨
	0	0	1	🟨
	0	1	0	🟨
● CAJ	0	0	0	🟥
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Figure 20. The map represents sampling sites for *Oligoryzmys andinus*, figures show the morphological qualitative analysis and Linear Discriminant analysis. Red dots indicate sites from northern. Light blue dot indicate sites related with Santa River basin; Yellow dots indicate sites form dry ecosystems on Cordillera Negra. Each column represents a character and each row represents a scored specimen. Character 0 correspond to red cell, and character 1 correspond to yellow cell

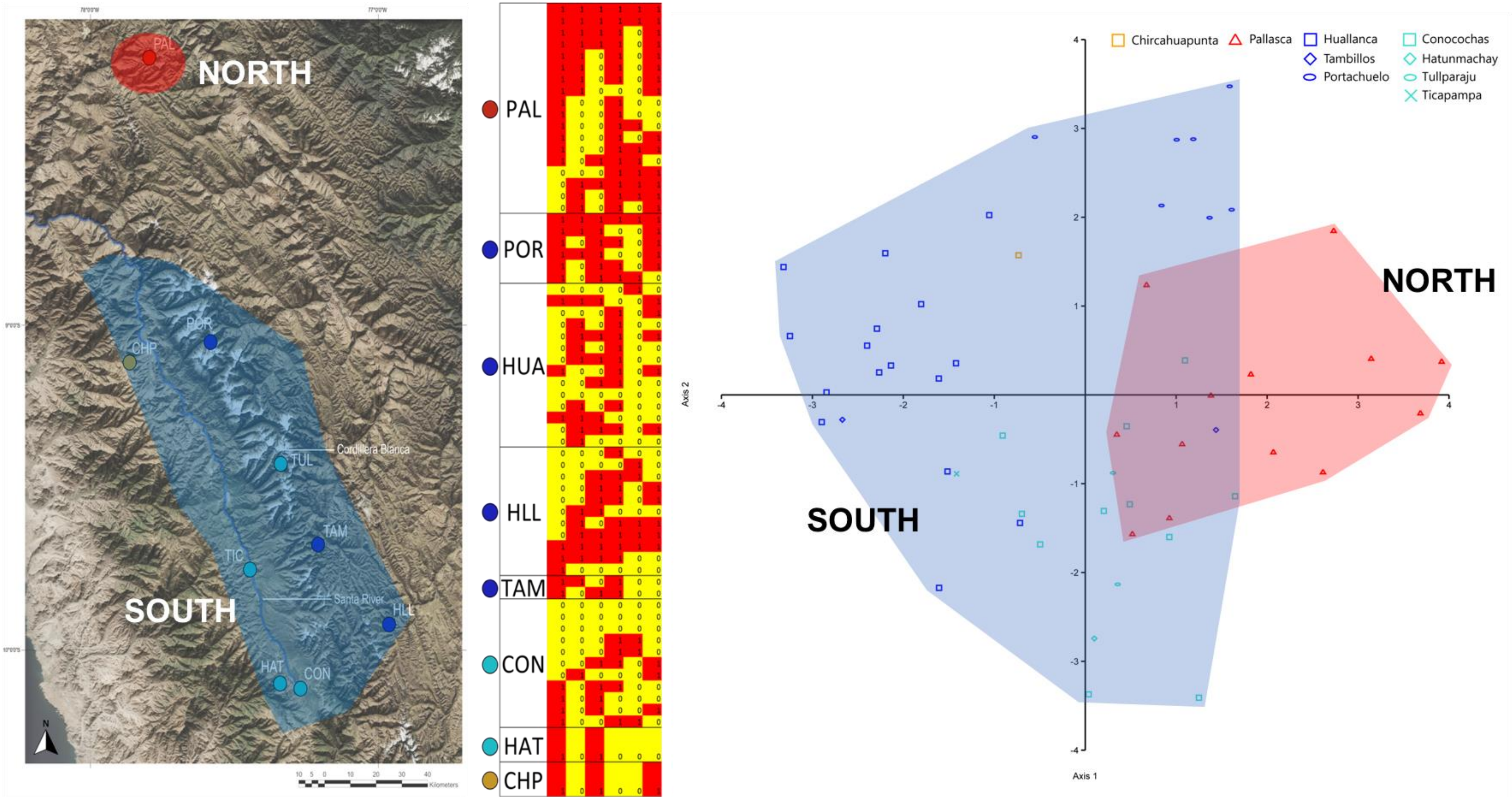


Figure 21. The map represents sampling sites for *Auliscomys pictus*, figures show the morphological qualitative analysis and Linear Discriminant analysis. Red dots indicate sites from northern, Blue dots indicate sites from high altitudes and eastern slope of Cordillera Blanca, Light blue dot indicate sites related with Santa River basin; Yellow dot indicates sites form dry ecosystems on Cordillera Negra. Each column represents a character and each row represents a scored specimen. Character 1 correspond to red cell, and character 0 correspond to yellow cell

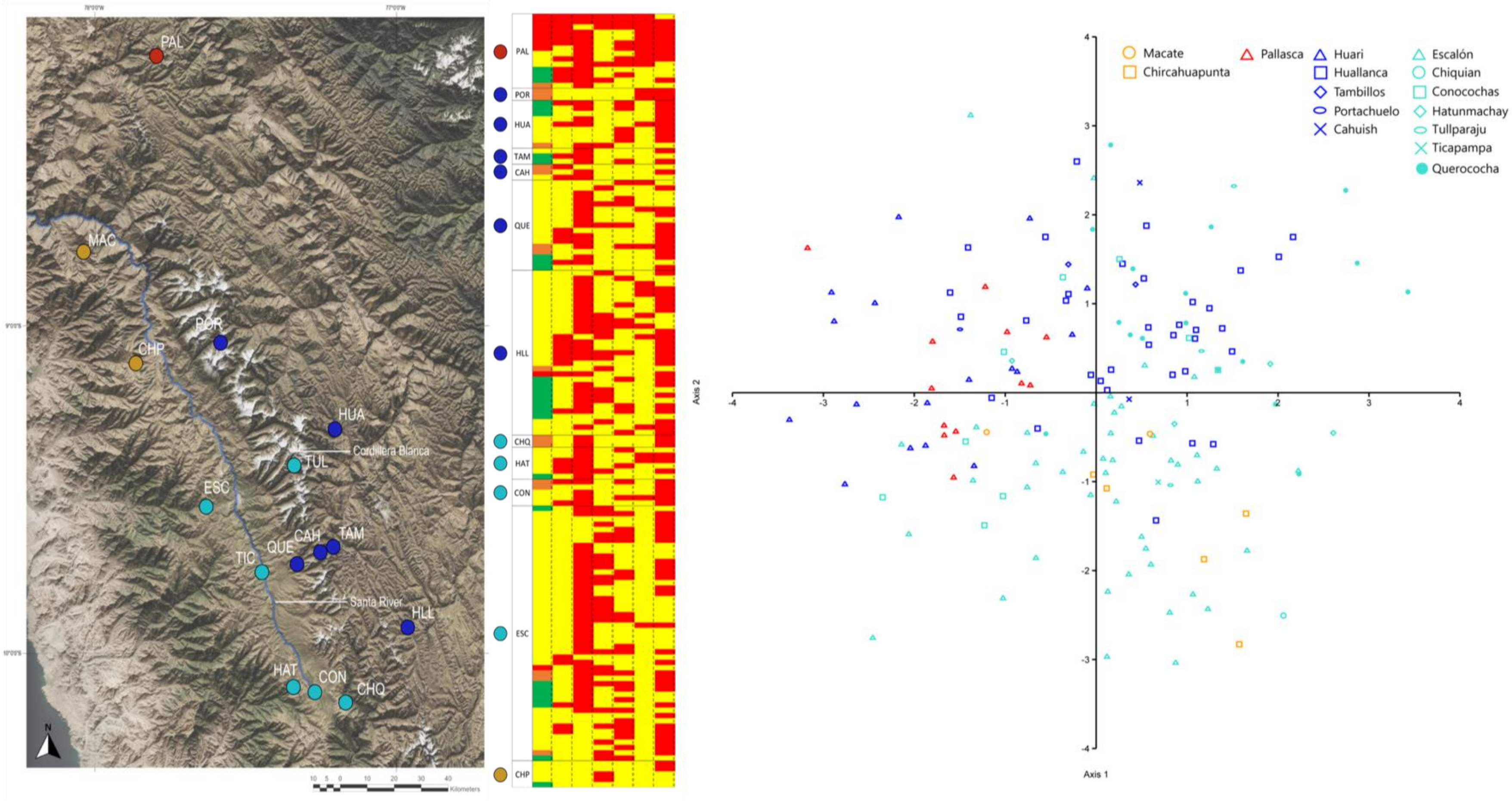


Figure 22. The map represents sampling sites for *Calomys sorellus*, figures show the morphological qualitative analysis and Linear Discriminant analysis. Red dots indicate sites from northern, Blue dots indicate sites from high altitudes and eastern slope of Cordillera Blanca, Light blue dot indicate sites related with Santa River basin; Yellow dots indicate sites form dry ecosystems on Cordillera Negra. Each column represents a character and each row represents a scored specimen. For characters with two state of character, character 0 correspond to red cell, and character 1 correspond to yellow cell, For character with four state of character, character 0 correspond to red cell, character 1 correspond to orange cell, character 2 correspond to yellow cell, and character 3 correspond to green cell.

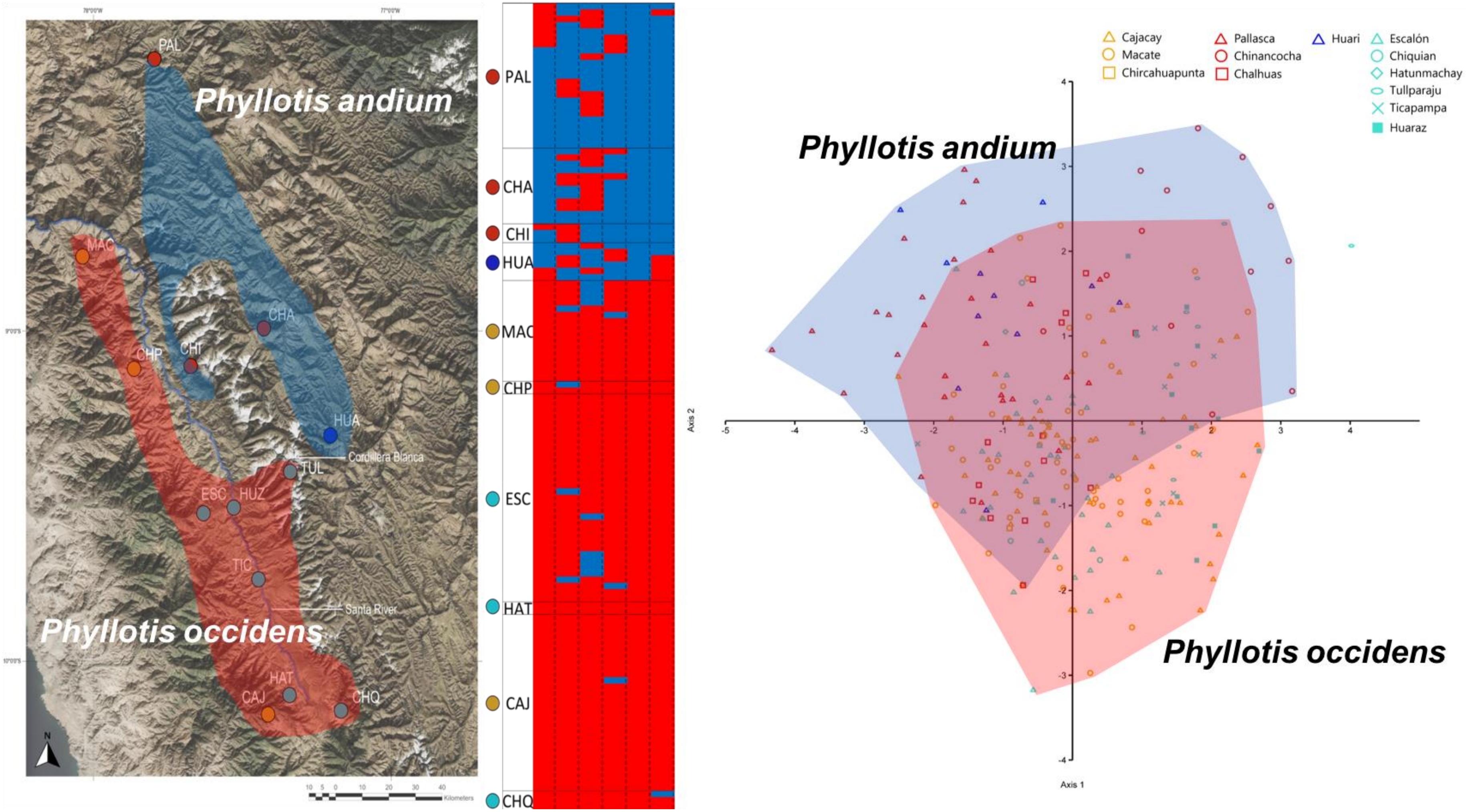
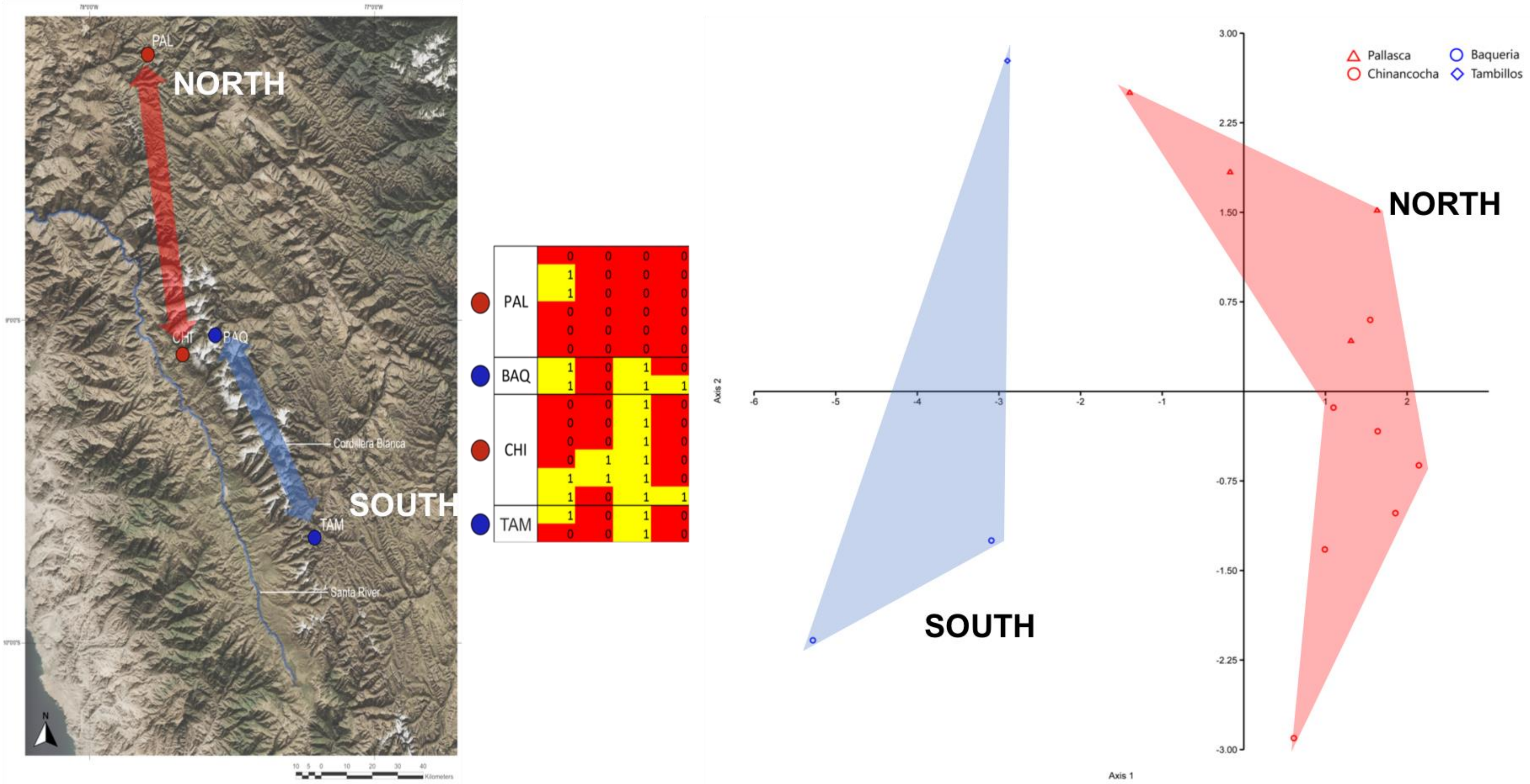


Figure 23. The map represents sampling sites for *Phyllotis andium and P. occidens*, figures show the morphological qualitative analysis and Linear Discriminant analysis. Red dots indicate sites from northern, Blue dots indicate sites from high altitudes and eastern slope of Cordillera Blanca, Light blue dot indicate sites related with Santa River basin; Yellow dots indicate sites form dry ecosystems on Cordillera Negra. Each column represents a character and each row represents a scored specimen. Character 0 correspond to red cell, and character 1 correspond to blue cell



🟥	PAL	0	0	0	0
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🔵	BAQ	1	0	1	0
		1	0	1	1
🟥	CHI	0	0	1	0
		0	0	1	0
		0	0	1	0
		0	1	1	0
		1	1	1	0
		1	0	1	1
🔵	TAM	1	0	1	0
		0	0	1	0

Figure 24. The map represents sampling sites for *Thomasomys praetor*, figures show the morphological qualitative analysis and Linear Discriminant analysis. Red dots indicate sites from the northern region, Blue dots indicate sites from high altitudes and eastern slope of Cordillera Blanca. Each column represents a character and each row represents a scored specimen. Character 0 correspond to red cell, and character 1 correspond to yellow cell

3.3.6. Pattern summary

As seen in the previous morphological and genetic analyses, when combining both pieces of evidence, the patterns of variation are similar and coincident, and it is possible to differentiate populations. The variation indicates the same geographic pattern for all species, with i) populations of the northern region, including both slopes at the northern Cordillera Blanca forming one group; and ii) populations from the southwestern portion of the highland of Ancash forming one distinct region, in the case of *Akodon mollis* formed another group only for the western portion, in the case of genus, *Phyllotis andium* fit on the northern group, and *P. occidens* fit on the southwest group but without populations on eastern and highest sampling sites of cordillera blanca. For all species, the mountain chain located on the southern portion of the study area does not represent a barrier between populations situated on the western and eastern slopes. On the contrary, the Santa River represents a present barrier to populations; however, the headwater portion of this river may likely act as a corridor that unites both sides of the river, as no variation was observed in this area, but this pattern doesn't work for the Oryzomini of the assemble, *Microryzomys altissimus* and *Oligoryzomys andium* do not exhibit differences between the right and left side of the river.

3.4. Discussion

In this study, I analyzed the morphologic and genomic variation of the eight species of sigmodontinae rodents to evaluate if the orogeny process of the Cordillera Blanca in northern Peru played an important and decisive role in the rise of population differences. This integrative approach revealed that there are sharp population patterns of variation that are coincident with geography in the Andean highlands of this region. These results showed that despite the area being mainly drawn by a high mountain range, the Cordillera Blanca, the discontinuities are associated to the drainage of the Rio Santa River. Though the geographic system affects all species almost equally, each has its own unique singularities, as described in the following.

Akodon mollis shows a population structure with three well-defined groups. This pattern was not found by Alvarado-Serrano & Luna (2013), who point to Puna high-elevation in the southern portion of Ancash shows morphological differences with other populations, which agrees with my results; this I called the "Southern population." It should be noted that the analyses by Alvarado-Serrano & Luna (2013) included very few individuals from the "Western population" (on the left bank of the Santa River), so my results are based on a more robust sample. Here I called the "Northern population," the specimens from Pallasca, Chinancocha, and Challhuas sampling localities. Pacheco et al. (2009) and Rengifo et al. (2022) noted the existence of an undescribed species of *Akodon* (*Akodon* sp.1) from Pallasca. Still, my revision of these specimens revealed that they do not match the specimens analyzed in the present study. According to Voss (2003), *Akodon mollis* exhibits substantial geographic variation, and despite some taxonomic studies found well-differenced populations (Alvarado-Serrano & Luna 2013; Pozo-Rivera et al. 2019), not enough evidence has been found in the present integrative approach to recognize these specimens as different species.

The results obtained for *Auliscomys pictus* do not show a clear geographic structure. It can only be recovered that there are at least two slightly differentiated populations, one to the North and the other to the South. Both Pearson (1958) and Hershkovitz (1962) and the present sampling effort show that this species inhabits high areas. Therefore, it is not surprising that this species has managed to get through passes of the Cordillera Blanca. Like *Akodon mollis*, the mountain range to the south does not acted as a barrier that separates populations from the east and west. Unfortunately, the number of samples for the left bank of the Santa River is too small to determine if the Santa River fulfills any function.

The results for *Calomys sorellus* obtained here show an intrapopulation variation. Still, it is not structured, except for individuals from the North (Pallasca), which differentiate them from the rest. Like *Akodon mollis* and *Auliscomys pictus*, *C. sorellus* can cross passes of the cordillera Blanca on the southern portion of the highland Ancash, which fits perfectly on the definition of Pearson (1982) that mentioned *C. sorellus* as a trans-Andean species. My results also indicate that *C. sorellus* do not cross the Santa River at lower parts of the basin. Still, there is a relationship in the headwaters, similar to the pattern of Patton et al. 2000, who found shared haplotypes of populations of small nonvolant mammal species across Headwater in the Jurua River. This also could be conditioned whit the habitats preference, Osgood (1914) mentioned that *C. sorellus* was "caught in tall grass and weeds growing about the bases of rough limestone exposures on the very top of the mountains," that is the typical habitat found on headwater of Santa River.

The genus *Phyllotis* has been the only one that has recent studies for the area. Rengifo & Pacheco (2015, 2018) postulated that the mountain range plays an important role in the diversification of this genus, similar to Pacheco (2002) and Rengifo & Pacheco (2018), that mentioned that *P. definitus* has its distribution limited by the Santa River. It should be noted that all these works suggested making a greater effort to corroborate their statements because their conclusions were based on morphological and Cyt-b evidence only.

My results clearly show that there is a definite difference between *Phyllotis andium* and *P. occidens*, agreeing with the initial hypothesis of Rengifo & Pacheco (2015) when separating these species; the morphological and molecular data were very congruent, but the morphometric results were not; the Linear Discriminant Analysis (LDA) shows an overlap of all the populations, failing to separate the species, it is not common for this type of multivariate analysis results between species. However, some examples include the case between *Hylaemys yunganus* and *H. perenensis* in the Peruvian Amazon (Hice & Velazco 2012); species that cannot be separated by multivariate analysis. Notably, the distribution of *P. andium* borders the western slope of the Cordillera Blanca, reaching south to Chinancocha, and the distribution of *P. occidens* can reach Huaraz. Unfortunately, there are no data between these localities to indicate that there is a contact or hybridization zone.

The samples available to carry out the analysis of *Thomasomys praetor* were limited, but with the few specimens analyzed it was possible to recover results similar to those of the other species. The population of Pallasca is related to Chinancocha on the western slope of the Cordillera Blanca, a similar result to *Phyllotis andium* and *Akodon mollis*. Likewise, the population of Baqueria related to Tambillo on the eastern slope of the Cordillera Blanca, a result similar to that of *Akodon mollis*. *Thomasomys praetor,* unlike the other species, has a high preference for dense and tall shrub habitats on rocky substrates near rivers or streams (Pacheco 2015). According to my observations, the possibility of a connection between forest patches is very difficult, which decreases the probability of events of migration or interbreeding between populations. In this way, Fjeldså & Irestedt (2009) also noted that some bird species are isolated to *Polylepis* forest in the Cordillera Blanca. I suggest carrying out studies on this species and the small patches of *Polylepis* forests in the area.

The results of *Microryzomys altissimus* and *Oligoryzomys andiuns* are discordant with the other species. The morphological and genomic results only showed a slight intrapopulation variation without geographic structure. Pallasca was recovered as a population isolated from the rest for both species, but the Santa River does not act as a barrier for both species. These results were not surprising based on the natural history reported for these two species. For the *M. altissimus*, Carleton & Musser (1989) stated that adaptation to different microhabitats and concomitant differences in the degree of arboreality could be to promote the interchange between these species. A similar situation could be proposed for the genus *Oligoryzomys*, with Hurtado & D’Elía (2017) suggesting that rivers might act as semipermeable barriers in these taxa.

My demographic analyses suggested that the history of *Akodon mollis* and genus *Phyllotis* is best described by a model of isolation with migration. The date for the isolation event coincides with the date of the uplift of Cordillera Blanca (Montario et al., 2005) around ~6 to ~2 Ma (Late Miocene to Early Pleistocene). Furthermore, these dates coincide with an estimation by Parada et al. (2015) for the genus *Akodon* and *Phyllotis*. Although this would suggest that the Cordillera Blanca might have a role in driving population differentiation, the rise of the Rio Santa and the uplift of Cordillera Blanca are contemporary due to the majority of glaciers terminating in watersheds that are drained by the Rio Santa (Vilímek et al. 2000). In this scenario, the effect of both geological processes could be determinant in the diversification of these taxa. *Akodon mollis* shows very low pulses of migrations, suggesting that the probability was very low if there was gene flow. On the contrary, in *Phyllotis*, the confidence interval pointed to a high likelihood of high levels of migration (~40% of Ne), the estimated date ~0.43 Ma, coinciding with an event of glaciation of Pleistocene occurs around ~0.424 Ma (Lisiecki & Raymo 2005), which would indicate that there was a genetic flow between these two species, I suppose that could have occurred in one zone of the western slope of the Cordillera Blanca, but at this moment I am not able to accurate.

Many works have investigated geographic barriers' effectiveness in diversifying organisms. In particular, rivers and geological processes as rivers and geological events have gathered much literature (Lougheed et al., 1999; Murienne et al., 2022; Patton & da Silva, 1998; Pirani et al., 2019, among others).

For the Neotropics, there is evidence of rivers acting as diversification barriers, avoiding the gene flow with diverse levels of effectiveness. For example, rivers such as the Rio Paraná are a weak barrier in the dispersion of four species of small mammals (Cáceres, 2007). Andean rivers such as Marañon, Huallaga, Apurimac, and Inambari have driven the speciation in Andean *Neacomys* and *Akodon* genus (Patton & Smith, 1992, Hurtado & Pacheco, 2017). Similar situations happen in the Tapajós River, in the Amazon (Maximiano et al., 2020). The Marañon River Valley is also considered a main geographical barrier blocking the dispersion of organisms between the Northern and Central Andes, as proposed by Hazzi et al. (2018).

On the other hand, other works have emphasized that rivers are ineffective barriers for many species (Santorelli et al., 2018). Sandoval-H et al. (2017) found that the Magdalena River is a permeable barrier for some species of birds, with gene flow across the river facilitated by narrow headwaters and the dynamic seasonality of the river. Hurtado & D'Elía (2018) also found Eastern Andean rivers (Huallaga, Apurimac, and Inambari) might be acted as semipermeable barriers for *Oligoryzomys destructor*. In a recently published paper, Janiak et al. (2022) tested the influence of Amazonian rivers as drives of speciation in multiple species of primates from this region, with conflicting results; at least for small taxa, the rivers are a strong barrier, but for larger monkeys, there is a minimal or absent capacity of avoid gene flow. Dalapicolla et al. (2021) with two co-distributed species of *Proechimys*, where *P. steerei* from the várzea forests showed more robust genetic structure, higher heterozygosity, and lower inbreeding than *P. simonsi* from the terra-firme forests

Concerning geological events acting as barriers among populations, a lot of literature can be found (Ebach & Michaux, 2020; Mendoza et al., 2019; Naka et al., 2012; Prieto-Torres et al., 2018; Pujolar et al., 2022; Quintana et al., 2017). The tectonic processes suffered in the Andean regions have been pointed out as the main drivers of speciation and diversification of taxa inhabiting there. The different environmental gradients produced by the rise of the Andean orogeny allowed ecological specialization and minimized the gene flow among populations (Kröemer et al., 2005; Medina et al., 2021; Pujolar et al., 2022; Rodríguez-Cajarville et al., 2022).

According to my early impressions of the geographic features of the high-andean region of Ancash, the Montane Vicariance hypothesis was the candidate to promote speciation or interpopulation variation due to event of recent uplift of the Cordillera Blanca. However, I have to reject this hypothesis because my results show a pattern opposite to that expected; there is a typical pattern of close relationships between populations on the eastern and western slope of Cordillera Blanca. This data suggest that gene flow and morphological traits, all species, between both slopes of the Cordillera is not interrupted, suggesting that the Cordillera Blanca could not be an effective barrier. This pattern contradicts the results of Pacheco & Petterson (1992), Pacheco et al. (2014), and Rengifo & Pacheco (2015), who noted that this Mountain range separates sister species of the genus *Sturnira* and *Phyllotis*. And on the contrary, it supports the idea that some species of rodents range high enough to cross the lowest passes ("abras"); Pearson (1982) called these species "*transandinas*" (trans-Andean).

Conversely, my data show that gene flow rates across the Santa River drainage are relatively low or null but were greater at headwaters. This shows the basin acting as a barrier to support the Riverine Barrier hypothesis (Wallace, 1854; Patton et al., 1994). These results are congruent with Pacheco (2002), Rengifo & Pacheco (2018), and DuBay (2012), who subtly mention the presence of the Santa River as a possible geographic barrier. One example of another taxon with the same patterns is the bird *Atlapetes rufigenis* (García-Moreno & Fjeldså, J. 1999) which is able to cross passes the south region of the cordillera Blanca and cross only the headwater of Rio Santa, which gives empirical support to my hypothesis about these taxa.

3.5. Conclusions

In this third chapter, I performed classical and modern techniques to obtain robust results that help understand the variations between rodent populations in northern Peru. My results reject the initial hypotheses that the orogenic process at the Cordillera Blanca between ~6 - ~ 2 Ma promoted the morphological and genetic patterns of sigmodontine rodents in this region, differencing western and eastern populations. The patterns of variation are similar and coincident with one population of the northern region, including both slopes at the north of Cordillera Blanca and populations from the southwestern portion of the highland of Ancash forming one distinct cluster. The mountain chain located on the southern portion of the study area does not represent a barrier between populations situated on the western and eastern slopes. On the contrary, the Santa River represents a present barrier to populations; but the headwater portion of this river may likely act as a corridor, but this pattern doesn't work for *Microryzomys altissimus* and *Oligoryzomys andium* does not exhibit differences between the right and left side of the river. My demographic analyses suggested that the history of *Akodon mollis* and genus *Phyllotis* is best described by a model of isolation with migration. The date for the isolation event matches the date of the uplift of Cordillera Blanca.

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Appendices

Appendix A List of analyzed specimens per sampling sites for morphometrics analyses. MUSM (Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima Peru) FMNH (The Field Museum of Natural History Chicago USA) USNM (The National Museum of Natural History Washington USA)

Akodon mollis (n=360)

Pallasca (n = 15): MUSM 40009; MUSM 40090; MUSM 40092; MUSM 40100; MUSM 40106; MUSM 40128; MUSM 40131; MUSM 40133; MUSM 40136; MUSM 40140; MUSM 40145; MUSM 40150; MUSM 40154; MUSM 40156; MUSM 40157

Chinancocha (n=26): MUSM 49138; MUSM 49139; MUSM 49143; MUSM 49145; MUSM 49146; MUSM 49147; MUSM 49148; MUSM 49150; MUSM 49151; MUSM 49152; MUSM 49153; MUSM 49444; MUSM 49445; MUSM 49446; MUSM 49447; MUSM 49448; MUSM 49449; MUSM 49450; MUSM 49454; MUSM 49455; MUSM 49456; MUSM 49457; MUSM 49458; MUSM 49459; FMNH 81350; FMNH 81351)

Challhuas (n 5):MUSM 49129; MUSM 49130; MUSM 49131; MUSM 49132; MUSM 49443

Baqueria (n=6): MUSM 49069; MUSM 49070; MUSM 49071; MUSM 49072; MUSM 49074; MUSM 49077

Portachuelo (n=8) MUSM 49434; MUSM 49435; MUSM 49436; MUSM 49437; MUSM 49438; MUSM 49440; MUSM 49441; MUSM 49442

Huari (n=25): MUSM 49338; MUSM 49339; MUSM 49340; MUSM 49341; MUSM 49342; MUSM 49343; MUSM 49344; MUSM 49345; MUSM 49348; MUSM 49350; MUSM 49353; MUSM 49354; MUSM 49358; MUSM 49367; MUSM 49388; MUSM 49389; FMNH 129212; FMNH 129213; FMNH 129215; FMNH 129216; FMNH 129218; FMNH 129219; FMNH 129224; FMNH 129225; FMNH 12922

Tambillo (n= 23) MUSM 49517; MUSM 49518; MUSM 49519; MUSM 49520; MUSM 49521; MUSM 49522; MUSM 49523; MUSM 49524; MUSM 49526; MUSM 49527; MUSM 49528; MUSM 49529; MUSM 49530; MUSM 49531; MUSM 49532; MUSM 49533; MUSM 49534; MUSM 49535; MUSM 49536; MUSM 49537; MUSM 49538; MUSM 49544; MUSM 49545

Querococha (n=26) MUSM 49460; MUSM 49462; MUSM 49463; MUSM 49467; MUSM 49496; MUSM 49515

Huallanca (n=64) MUSM 49208; MUSM 49210; MUSM 49211; MUSM 49212; MUSM 49213; MUSM 49214; MUSM 49215; MUSM 49216; MUSM 49217; MUSM 49218; MUSM 49220; MUSM 49221; MUSM 49222; MUSM 49223; MUSM 49224; MUSM 49225; MUSM 49228; MUSM 49229; MUSM 49230; MUSM 49231; MUSM 49232; MUSM 49233; MUSM 49234; MUSM 49235; MUSM 49236; MUSM 49237; MUSM 49239; MUSM 49240; MUSM 49241; MUSM 49243; MUSM 49245; MUSM 49247; MUSM 49251; MUSM 49252; MUSM 49258; MUSM 49260; MUSM 49264; MUSM 49265; MUSM 49266; MUSM 49269; MUSM 49270; MUSM 49271; MUSM 49272; MUSM 49273; MUSM 49274; MUSM 49275; MUSM 49276; MUSM 49277; MUSM 49278; MUSM 49317; MUSM 49318; MUSM 49324; MUSM 49325; MUSM 49326; MUSM 49327; MUSM 49328; MUSM 49329; MUSM 49331; MUSM 49332; MUSM 49333; MUSM 49334; MUSM 49335; MUSM 49336; MUSM 49337

Chiquian (n=16) MUSM 49165; MUSM 49167; MUSM 49168; MUSM 49170; MUSM 49172; MUSM 49173; MUSM 49177; MUSM 49179; MUSM 49181; MUSM 49404; MUSM 49405; MUSM 49408; MUSM 49409; MUSM 49421; MUSM 49424; MUSM 49429

Conocochas (n=1) MUSM 49287

Hatanmachay (n=1)MUSM 49310

Cajacay (n=66) MUSM 3601; MUSM 3605; MUSM 3608; MUSM 3611; MUSM 3626; MUSM 3630; MUSM 3632; MUSM 3635; MUSM 3637; MUSM 3638; MUSM 3639; MUSM 3640; MUSM 3641; MUSM 3643; MUSM 3645; MUSM 3646; MUSM 3647; MUSM 3650; MUSM 3651; MUSM 3652; MUSM 3653; MUSM 3654; MUSM 3655; MUSM 3657; MUSM 3658; MUSM 3659; MUSM 5425; MUSM 5750; MUSM 5751; MUSM 5753; MUSM 5755; MUSM 5756; MUSM 5757; MUSM 5758; MUSM 5759; MUSM 5760; MUSM 5761; MUSM 5762; MUSM 5764; MUSM 5765; MUSM 5766; MUSM 5768; MUSM 5769; MUSM 5770; MUSM 5773; MUSM 5774; MUSM 5776; MUSM 5777; MUSM 5779; MUSM 5781; MUSM 5783; MUSM 5784; MUSM 5785; MUSM 5786; MUSM 5789; MUSM 5790; MUSM 5792; MUSM 5793; MUSM 5794; MUSM 5795; MUSM 5796; MUSM 5797; MUSM 50102; USNM 302999

Escalon (n=49) MUSM 49078; MUSM 49079; MUSM 49080; MUSM 49087; MUSM 49090; MUSM 49091; MUSM 49094; MUSM 49096; MUSM 49097; MUSM 49098; MUSM 49100; MUSM 49105; MUSM 49106; MUSM 49108; MUSM 49110; MUSM 49111; MUSM 49112; MUSM 49113; MUSM 49114; MUSM 49115; MUSM 49116; MUSM 49123; MUSM 49128; MUSM 49195; MUSM 49199; MUSM 49204; MUSM 50103; MUSM 50104; MUSM 50105; MUSM 50106; MUSM 50107; MUSM 50108; MUSM 50109; MUSM 50114; MUSM 50115; MUSM 50116; MUSM 50117; MUSM 50118; MUSM 50119; MUSM 50120; MUSM

50121; MUSM 50122; MUSM 50123; MUSM 50124; MUSM 50125; MUSM 50126; MUSM 50127; MUSM 50128; MUSM 50129

Chircahuapunta (n=1) MUSM 49315

Macate (n=18) MUSM 50043; MUSM 50044; MUSM 50046; MUSM 50047; MUSM 50048; MUSM 50049; MUSM 50050; MUSM 50051; MUSM 50052; MUSM 50053; FMNH 20899; FMNH 20902; FMNH 20903; FMNH 20905; FMNH 20908; FMNH 20909; FMNH 20910; FMNH 21144

Ticapampa (n=2) FMNH 81349; FMNH 81375

Tullparaju (n =7) FMNH 81348; FMNH 81368; FMNH 81370; FMNH 81371; FMNH 81372; FMNH 81373; FMNH 81374

Microryzomys altissimus (n=70)

Pallasca (n=19)MUSM 23220; MUSM 23221; MUSM 23222; MUSM 23223; MUSM 23224; MUSM 23225; MUSM 23298; MUSM 40065; MUSM 40066; MUSM 40067; MUSM 40174; MUSM 40175; MUSM 40176; MUSM 40177; MUSM 40178; MUSM 40179; MUSM 40180; MUSM 40181; MUSM 40182

Chinancocha (n=10)MUSM 49897; MUSM 49898; MUSM 49899; MUSM 49900; MUSM 49901; MUSM 49902; MUSM 49903; MUSM 49918; MUSM 49919; MUSM 49920

Baqueria (n=4) MUSM 49891; MUSM 49892; MUSM 49893; MUSM 49894

Portachuelo (n=4) MUSM 49914; MUSM 49915; MUSM 49916; MUSM 49917

Huari (n=15) MUSM 23846; MUSM 23878; MUSM 23879; MUSM 23886; MUSM 23906; MUSM 23920; MUSM 23973; MUSM 23974; MUSM 23977; MUSM 24091; MUSM 24092; MUSM 24094; MUSM 24102; MUSM 49909; MUSM 49910

Huallanca (n=5) MUSM 49904; MUSM 49905; MUSM 49906; MUSM 49907; MUSM 49908.

Chiquian (n=2) MUSM 49912; MUSM 49913.

Escalon (n =1) MUSM 49895

Tullparaju (n=3) FMNH 81434; FMNH 81433; FMNH 81432

Oligoryzomys andinus (n=43)

Pallasca (n=6) MUSM 23227; MUSM 23228; MUSM 23299; MUSM 40184; MUSM 40186; MUSM 40189

Chinancocha (n=3) MUSM 49938; MUSM 49939;MUSM 49940

Challhuas (n=1) MUSM 49929

Cajacay (n=15) MUSM 5400; MUSM 5401; MUSM 5402; MUSM 5403; MUSM 5407; MUSM 5408; MUSM 5836; MUSM 5838; MUSM 5840; MUSM 5841; MUSM 50132; MUSM 50133; MUSM 50134; USNM 302982; USNM 302983

Escalon (n=10) MUSM 11630; MUSM 50135; MUSM 50136; MUSM 50137; MUSM 50138; MUSM 50139; MUSM 50140; MUSM 50141; MUSM 50142; MUSM 50143

Macate (n=8)MUSM 50058; MUSM 50059; MUSM 50060; MUSM 50061; MUSM 50062; FMNH 20962; FMNH 20961; FMNH 20963

Auliscomys pictus (n=41)

Portachuelo (n=7) MUSM 49636; MUSM 49637; MUSM 49638; MUSM 49639; MUSM 49643; MUSM 49644; MUSM 49645

Tambillo (n=2) MUSM 49646; MUSM 49649

Huallanca (n=16)MUSM 49596; MUSM 49597; MUSM 49598; MUSM 49599; MUSM 49600; MUSM 49601; MUSM 49602; MUSM 49606; MUSM 49612; MUSM 49613; MUSM 49614; MUSM 49615; MUSM 49628; MUSM 49629; MUSM 49630; MUSM 49631

Conocochas (n=11)MUSM 49616; MUSM 49617; MUSM 49618; MUSM 49619; MUSM 49620; MUSM 49621; MUSM 49622; MUSM 49623; MUSM 49624; MUSM 49625; MUSM 49626

Hatanmachay (n=1) MUSM 49627

Chircahuapunta (n=1)MUSM 49595

Ticapampa (n=1) FMNH 81284

Tullparaju (n=2) FMNH 81228 ;FMNH 81282

Calomys sorellus (n=161)

Pallasca (n=12)MUSM 40061; MUSM 40062; MUSM 40063; MUSM 40064; MUSM 40167; MUSM 40168; MUSM 40169; MUSM 40170; MUSM 40171; MUSM 40172; MUSM 40173; MUSM 41523

Portachuelo (n=1) MUSM 49850

Huari (n=18)MUSM 23848; MUSM 23850; MUSM 23851; MUSM 23854; MUSM 23862; MUSM 23866; MUSM 23867; MUSM 23872; MUSM 23875; MUSM 23891; MUSM 23907; MUSM 23914; MUSM 23928; MUSM 23931; MUSM 24087; MUSM 24089; MUSM 24090; MUSM 49849

Tambillo (n=2) MUSM 50041; MUSM 50042

Cahuish (n=2) MUSM 49887; MUSM 49888

Querococha (n=17) MUSM 49851; MUSM 49852; MUSM 49853; MUSM 49854; MUSM 49856; MUSM 49858; MUSM 49859; MUSM 49864; MUSM 49867; MUSM 49868; MUSM 49869; MUSM 49874; MUSM 49878; MUSM 49879; MUSM 49881; MUSM 49882; MUSM 49884

Huallanca (n=39) MUSM 49651; MUSM 49652; MUSM 49653; MUSM 49761; MUSM 49762; MUSM 49763; MUSM 49764; MUSM 49765; MUSM 49766; MUSM 49767; MUSM 49771; MUSM 49772; MUSM 49773; MUSM 49774; MUSM 49779; MUSM 49780; MUSM 49781; MUSM 49782; MUSM 49783; MUSM 49785; MUSM 49786; MUSM 49787; MUSM 49788; MUSM 49789; MUSM 49790; MUSM 49791; MUSM 49806; MUSM 49807; MUSM 49810; MUSM 49811; MUSM 49812; MUSM 49813; MUSM 49814; MUSM 49815; MUSM 49816; MUSM 49845; MUSM 49846; MUSM 49847; MUSM 49848

Chiquian (n=1) MUSM 49731

Conocochas (n=9) MUSM 49821; MUSM 49822; MUSM 49824; MUSM 49825; MUSM 49826; MUSM 49828; MUSM 49829; MUSM 49832; MUSM 49834

Hatunmachay (n=4) MUSM 49841; MUSM 49842; MUSM 49843; MUSM 49844

Escalon (n=45) MUSM 11625; MUSM 11627; MUSM 11628; MUSM 49654; MUSM 49655; MUSM 49656; MUSM 49658; MUSM 49659; MUSM 49661; MUSM 49662; MUSM 49663; MUSM 49664; MUSM 49668; MUSM 49669; MUSM 49671; MUSM 49673; MUSM 49674; MUSM 49675; MUSM 49677; MUSM 49679; MUSM 49680; MUSM 49681; MUSM 49682; MUSM 49684; MUSM 49685; MUSM 49696; MUSM 49697; MUSM 49702; MUSM 49703; MUSM 49705; MUSM 49706; MUSM 49713; MUSM 49715; MUSM 49716; MUSM 49717; MUSM 49719; MUSM 49720; MUSM 49726; MUSM 49744; MUSM 49746; MUSM 49747; MUSM 49749; MUSM 49751; MUSM 49752; MUSM 49755

Chircahuapunta (n= 5) MUSM 49734; MUSM 49735; MUSM 49737; MUSM 49738; MUSM 49742

Macate (n=2) MUSM 50056; FMNH 20942

Ticapampa (n=1) FMNH 81289

Tullparaju (n=3) FMNH 81216; FMNH 81286; FMNH 81287

Phyllotis andium (n=68)

Pallasca (n=30) MUSM 23229; MUSM 23230; MUSM 23231; MUSM 23233; MUSM 23234; MUSM 23236; MUSM 23237; MUSM 23239; MUSM 23240; MUSM 23242; MUSM 23243; MUSM 40070; MUSM 40072; MUSM 40074; MUSM 40075; MUSM 40190; MUSM 40191; MUSM 40192; MUSM 40193; MUSM 40194; MUSM 40195; MUSM 40197; MUSM

40198; MUSM 40199; MUSM 40200; MUSM 40201; MUSM 40202; MUSM 40203; MUSM 40204; MUSM 40205

Chinancocha (n=13) MUSM 49955; MUSM 49956; FMNH 81237; FMNH 81238; FMNH 81239; FMNH 81240; FMNH 81241; FMNH 81242; FMNH 81243; FMNH 81244; FMNH 81245; FMNH 81246; FMNH 81247

Challhuas (n=14)MUSM 49941; MUSM 49942; MUSM 49948; MUSM 49949; MUSM 49950; MUSM 49951; MUSM 49952; MUSM 49953; MUSM 49957; MUSM 49958; MUSM 49959; MUSM 49960; MUSM 49961; MUSM 49962

Huari (n=11)MUSM 23835; MUSM 23844; MUSM 23924; MUSM 23932; MUSM 49943; MUSM 49944; MUSM 49945; MUSM 49946; MUSM 49947; FMNH 129248; FMNH 129249

Phyllotis occidens (n=187)

Chiquian (n=3) MUSM 50010; MUSM 50011; MUSM 50012

Hatunmachay (n=2) MUSM 50020; MUSM 50024

Cajacay (n=60) MUSM 4502; MUSM 4503; MUSM 4505; MUSM 4506; MUSM 4507; MUSM 4516; MUSM 4517; MUSM 4518; MUSM 4520; MUSM 4521; MUSM 4523; MUSM 4524; MUSM 4525; MUSM 4527; MUSM 4528; MUSM 4529; MUSM 4532; MUSM 4534; MUSM 4536; MUSM 4538; MUSM 4539; MUSM 4541; MUSM 4542; MUSM 4551; MUSM 4556; MUSM 4560; MUSM 4561; MUSM 4562; MUSM 4563; MUSM 4566; MUSM 4575; MUSM 4595; MUSM 5578; MUSM 49965; MUSM 49966; MUSM 49967; MUSM 49968; MUSM 49969; MUSM 49970; MUSM 49971; MUSM 49972; MUSM 49973; MUSM 49974; MUSM 49975; MUSM 49976; MUSM 49977; MUSM 49978; MUSM 49979; MUSM 50144; MUSM 50145; MUSM 50146; MUSM 50147; MUSM 50148; MUSM 50149; MUSM 50150; MUSM 50151; MUSM 50152; MUSM 50153; MUSM 50154; MUSM 50155

Escalon (n=36) MUSM 11633; MUSM 11634; MUSM 11637; MUSM 11638; MUSM 11639; MUSM 11640; MUSM 11641; MUSM 12664; MUSM 12665; MUSM 12666; MUSM 12668; MUSM 12670; MUSM 12671; MUSM 49988; MUSM 49989; MUSM 49991; MUSM 49992; MUSM 49993; MUSM 49994; MUSM 49995; MUSM 49996; MUSM 49998; MUSM 49999; MUSM 50001; MUSM 50004; MUSM 50006; MUSM 50016; MUSM 50156; MUSM 50157; MUSM 50158; MUSM 50159; MUSM 50160; MUSM 50161; MUSM 50162; MUSM 50163; MUSM 50164

Chircahuapunta (n=2) MUSM 50014; MUSM 50025

Macate (n=55) MUSM 50063; MUSM 50064; MUSM 50065; MUSM 50066; MUSM 50068; MUSM 50069; MUSM 50070; MUSM 50071; MUSM 50072; MUSM 50074; MUSM

50075; MUSM 50076; MUSM 50077; MUSM 50078; MUSM 50079; MUSM 50081; MUSM 50084; MUSM 50085; MUSM 50086; MUSM 50087; MUSM 50088; MUSM 50089; MUSM 50090; MUSM 50091; MUSM 50092; MUSM 50093; MUSM 50094; MUSM 50095; MUSM 50096; MUSM 50098; MUSM 50099; MUSM 50100; MUSM 50101; FMNH 20914; FMNH 20916; FMNH 20918; FMNH 20924; FMNH 20925; FMNH 20928; FMNH 20933; FMNH 20934; FMNH 20935; FMNH 20943; FMNH 20945; FMNH 20946; FMNH 20950; FMNH 20953; FMNH 20954; FMNH 20955; FMNH 20956; FMNH 20957; FMNH 21146; USNM 259595; USNM 259596; USNM 259597

Ticapampa (n=7)FMNH 81229; FMNH 81230; FMNH 81231; FMNH 81233; FMNH 81234; FMNH 81235; FMNH 81236

Tullparaju (n=10) FMNH 81217; FMNH 81218; FMNH 81219; FMNH 81221; FMNH 81222; FMNH 81223; FMNH 81224; FMNH 81225; FMNH 81226; FMNH 81227

Thomasomys praetor (n=10)

Chinancocha (n=7)MUSM 50029; MUSM 50030; MUSM 50031; MUSM 50032; MUSM 50033; MUSM 50035; MUSM 50036

Baqueria (n=2) MUSM 50027; MUSM 50028

Tambillo (n=1) MUSM 50037

Appendix B. list of analyzed specimens per sampling sites for morphological analyses. MUSM (Museo de Historia Natural de la Univerisidad Nacional Mayor de San Marcos, Lima Peru) FMNH (Field Museum of Natural History Chicago USA)

Akodon mollis ***(n=337)***

Pallasca (n=29) MUSM 4011; MUSM 40010; MUSM 40012; MUSM 40014; MUSM 40015; MUSM 40016; MUSM 40018; MUSM 40020; MUSM 40021; MUSM 40023; MUSM 40027; MUSM 40035; MUSM 40089; MUSM 40096; MUSM 40098; MUSM 40099; MUSM 40102; MUSM 40104; MUSM 40107; MUSM 40108; MUSM 40109; MUSM 40110; MUSM 40130; MUSM 40137; MUSM 40142; MUSM 40146; MUSM 40149; MUSM 40151; MUSM 40152

Chinancocha (n=24) MUSM 49138; MUSM 49139; MUSM 49141; MUSM 49143; MUSM 49145; MUSM 49146; MUSM 49147; MUSM 49148; MUSM 49150; MUSM 49151; MUSM 49152; MUSM 49153; MUSM 49444; MUSM 49446; MUSM 49447; MUSM 49448; MUSM 49449; MUSM 49450; MUSM 49454; MUSM 49455; MUSM 49456; MUSM 49457; MUSM 49458; MUSM 49459

Challhuas (n=4)MUSM 49129; MUSM 49130; MUSM 49132; MUSM 49443;

Baqueria (n=8) MUSM 49069; MUSM 49070; MUSM 49071; MUSM 49072; MUSM 49074; MUSM 49075; MUSM 49076; MUSM 49077;

Portachuelo (n=6) MUSM 49435; MUSM 49437; MUSM 49438; MUSM 49440; MUSM 49441; MUSM 49442

Huari (n=67)MUSM 4675; MUSM 4965; MUSM 4966; MUSM 4968; MUSM 23834; MUSM 23836; MUSM 23838; MUSM 23839; MUSM 23840; MUSM 23841; MUSM 23842; MUSM 23843; MUSM 23845; MUSM 23847; MUSM 23852; MUSM 23853; MUSM 23855; MUSM 23856; MUSM 23857; MUSM 23858; MUSM 23860; MUSM 23861; MUSM 23865; MUSM 23880; MUSM 23881; MUSM 23882; MUSM 23884; MUSM 23885; MUSM 23887; MUSM 23888; MUSM 23889; MUSM 23890; MUSM 23895; MUSM 23896; MUSM 23898; MUSM 23900; MUSM 23901; MUSM 23905; MUSM 23915; MUSM 23916; MUSM 23917; MUSM 23918; MUSM 23921; MUSM 23922; MUSM 23923; MUSM 23925; MUSM 23926; MUSM 23927; MUSM 23929; MUSM 24052; MUSM 24073; MUSM 49338; MUSM 49339; MUSM 49340; MUSM 49341; MUSM 49342; MUSM 49343; MUSM 49344; MUSM 49345; MUSM 49348; MUSM 49350; MUSM 49353; MUSM 49354; MUSM 49358; MUSM 49367; MUSM 49388; MUSM 49389

Cahuish (n=17)MUSM 49550; MUSM 49551; MUSM 49552; MUSM 49554; MUSM 49555; MUSM 49556; MUSM 49560; MUSM 49562; MUSM 49564; MUSM 49565; MUSM 49566; MUSM 49567; MUSM 49585; MUSM 49586; MUSM 49588; MUSM 49590; MUSM 49593;

Querococha (n=7)MUSM 49460; MUSM 49462; MUSM 49463; MUSM 49464; MUSM 49467; MUSM 49515; MUSM 49594

Huallanca (n=58) MUSM 49208; MUSM 49210; MUSM 49211; MUSM 49212; MUSM 49213; MUSM 49214; MUSM 49215; MUSM 49216; MUSM 49217; MUSM 49218; MUSM 49220; MUSM 49221; MUSM 49222; MUSM 49223; MUSM 49224; MUSM 49225; MUSM 49228; MUSM 49229; MUSM 49230; MUSM 49231; MUSM 49232; MUSM 49233; MUSM 49234; MUSM 49235; MUSM 49236; MUSM 49237; MUSM 49240; MUSM 49241; MUSM 49244; MUSM 49248; MUSM 49251; MUSM 49252; MUSM 49260; MUSM 49264; MUSM 49265; MUSM 49266; MUSM 49269; MUSM 49271; MUSM 49272; MUSM 49274; MUSM 49275; MUSM 49276; MUSM 49277; MUSM 49278; MUSM 49317; MUSM 49319; MUSM 49324; MUSM 49325; MUSM 49326; MUSM 49327; MUSM 49329; MUSM 49330; MUSM 49331; MUSM 49332; MUSM 49333; MUSM 49334; MUSM 49335; MUSM 49336

Chiquian (n=17) MUSM 23997; MUSM 24001; MUSM 24005; MUSM 24014; MUSM 49165; MUSM 49167; MUSM 49168; MUSM 49170; MUSM 49172; MUSM 49173; MUSM 49179; MUSM 49404; MUSM 49405; MUSM 49408; MUSM 49409; MUSM 49421; MUSM 49424

Conocochas (n=1) MUSM 49067

Hatunmachay (n=1) MUSM 49310

Cajacay (n=39)MUSM 3612; MUSM 3628; MUSM 3629; MUSM 3630; MUSM 3631; MUSM 3635; MUSM 3640; MUSM 3643; MUSM 3645; MUSM 3646; MUSM 3647; MUSM 3649; MUSM 3652; MUSM 3654; MUSM 3657; MUSM 3658; MUSM 5746; MUSM 5750; MUSM 5753; MUSM 5755; MUSM 5756; MUSM 5757; MUSM 5758; MUSM 5759; MUSM 5760; MUSM 5761; MUSM 5762; MUSM 5769; MUSM 5779; MUSM 5783; MUSM 5784; MUSM 5785; MUSM 5786; MUSM 5789; MUSM 5790; MUSM 5792; MUSM 5793; MUSM 5794; MUSM 5797

Escalon (n=47) MUSM 45070; MUSM 45072; MUSM 45075; MUSM 45079; MUSM 45080; MUSM 45082; MUSM 45083; MUSM 45084; MUSM 45085; MUSM 45086; MUSM 45154; MUSM 45165; MUSM 45166; MUSM 45189; MUSM 45190; MUSM 45225; MUSM 45227; MUSM 45228; MUSM 45234; MUSM 45235; MUSM 45236; MUSM 49048; MUSM 49078; MUSM 49079; MUSM 49080; MUSM 49087; MUSM 49090; MUSM 49091; MUSM

49094; MUSM 49096; MUSM 49097; MUSM 49098; MUSM 49100; MUSM 49105; MUSM 49106; MUSM 49108; MUSM 49110; MUSM 49111; MUSM 49112; MUSM 49113; MUSM 49114; MUSM 49115; MUSM 49116; MUSM 49123; MUSM 49128; MUSM 49198; MUSM 49204

Chicarhuapunta (n=2) MUSM 49185; MUSM 49315

Macate (n=10) MUSM 50043; MUSM 50044; MUSM 50046; MUSM 50047; MUSM 50048; MUSM 50049; MUSM 50050; MUSM 50051; MUSM 50052; MUSM 50053

Microryzomys altissimus (n=68)

Pallasca (n=18)MUSM 23220; MUSM 23222; MUSM 23223; MUSM 23224; MUSM 23225; MUSM 23297; MUSM 23298; MUSM 40065; MUSM 40066; MUSM 40067; MUSM 40174; MUSM 40175; MUSM 40176; MUSM 40177; MUSM 40178; MUSM 40179; MUSM 40181; MUSM 40182;

Chinancocha (n=9)MUSM 49897; MUSM 49898; MUSM 49899; MUSM 49900; MUSM 49901; MUSM 49902; MUSM 49903; MUSM 49918; MUSM 49920;

Baqueria (n=3)MUSM 49891; MUSM 49892; MUSM 49894

Portachuelo (n4)=MUSM 49914; MUSM 49915; MUSM 49916; MUSM 49917

Huari (n=19)MUSM 23846; MUSM 23878; MUSM 23879; MUSM 23886; MUSM 23906; MUSM 23920; MUSM 23973; MUSM 23974; MUSM 23975; MUSM 23976; MUSM 23977; MUSM 24091; MUSM 24092; MUSM 24093; MUSM 24094; MUSM 24095; MUSM 24102; MUSM 49909; MUSM 49910

Tambillo (n=1) MUSM 49925

Cahuish (n=1) MUSM 49927

Querococha (n=3) MUSM 49921, MUSM 49922, MUSM 49923

Huallanca (n=5)MUSM 49046; MUSM 49904; MUSM 49905; MUSM 49906; MUSM 49907; Chiquian (n=2)MUSM 49912; MUSM 49913

Escalon (n=3)MUSM 45205; MUSM 45206; MUSM 49895

Oligoryzomys andinus (n=30)

Pallasca (n=5)MUSM 23227; MUSM 23228; MUSM 23299; MUSM 40184; MUSM 40189

Chinancocha (n=4)MUSM 5406; MUSM 49938; MUSM 49939; MUSM 49940;

Challhuas (n=1)MUSM 49929;

Cajacay (n=8)MUSM 5399; MUSM 5400; MUSM 5401; MUSM 5402; MUSM 5403; MUSM 5404; MUSM 5407; MUSM 5837; MUSM 45208;

Escalon (n=6)MUSM 45245; MUSM 45247; MUSM 45248; MUSM 45250; MUSM 45253;

Macate (n=6)MUSM 50057; MUSM 50058; MUSM 50059; MUSM 50060; MUSM 50061; MUSM 50062

Auliscomys pictus (n=64)

Pallasca (n=18)MUSM 23209; MUSM 23210; MUSM 23212; MUSM 23213; MUSM 23214; MUSM 23280; MUSM 23287; MUSM 23910; MUSM 40055; MUSM 40056; MUSM 40059; MUSM 40060; MUSM 40160; MUSM 40161; MUSM 40162; MUSM 40163; MUSM 40164; MUSM 41522

Portachuelo (n=6)MUSM 49636; MUSM 49637; MUSM 49638; MUSM 49639; MUSM 49644; MUSM 49645

Huari (n=14)MUSM 23868; MUSM 23869; MUSM 23870; MUSM 23873; MUSM 23874; MUSM 23876; MUSM 23877; MUSM 23899; MUSM 23902; MUSM 23908; MUSM 23913; MUSM 23972; MUSM 24084; MUSM 24085

Tambillo (n=2) MUSM 49649; MUSM 49949

Huallanca (n=11)MUSM 49596; MUSM 49597; MUSM 49598; MUSM 49600; MUSM 49602; MUSM 49606; MUSM 49613; MUSM 49615; MUSM 49628; MUSM 49630; MUSM 49631

Conocochas (n=11) MUSM 49616; MUSM 49617; MUSM 49618; MUSM 49619; MUSM 49620; MUSM 49621; MUSM 49622; MUSM 49623; MUSM 49624; MUSM 49625; MUSM 49626;

Hatunmachay (n=1)MUSM 49627

Chircahuapunta (n=1)MUSM 49595

Calomys sorellus (n=143)

Pallasca (n=13)MUSM 40061; MUSM 40062; MUSM 40064; MUSM 40166; MUSM 40168; MUSM 40169; MUSM 40170; MUSM 40171; MUSM 40172; MUSM 41080; MUSM 41081; MUSM 41484; MUSM 41523;

Portachuelo (n=1)MUSM 4985

Huari (n=10)MUSM 23848; MUSM 23849; MUSM 23851; MUSM 23854; MUSM 23867; MUSM 23872; MUSM 23928; MUSM 23931; MUSM 24089; MUSM 49849;

Tambillo (n=3)MUSM 49546; MUSM 50041; MUSM 50042;

Cahuish (n=3)MUSM 49887; MUSM 49888; MUSM 49889

Querococha (n=16)MUSM 49851; MUSM 49852; MUSM 49853; MUSM 49854; MUSM 49856; MUSM 49858; MUSM 49859; MUSM 49867; MUSM 49868; MUSM 49869; MUSM 49874; MUSM 49878; MUSM 49879; MUSM 49881; MUSM 49882; MUSM 49884

Huallanca (n=32)MUSM 49249; MUSM 49653; MUSM 49762; MUSM 49763; MUSM 49764; MUSM 49765; MUSM 49766; MUSM 49767; MUSM 49771; MUSM 49772; MUSM 49773; MUSM 49779; MUSM 49780; MUSM 49781; MUSM 49782; MUSM 49783; MUSM 49785; MUSM 49787; MUSM 49788; MUSM 49790; MUSM 49791; MUSM 49806; MUSM 49807; MUSM 49810; MUSM 49811; MUSM 49812; MUSM 49814; MUSM 49815; MUSM 49816; MUSM 49846; MUSM 49847; MUSM 49848;

Chiquian (n=1)MUSM 24086;

Conocochas (n=8)MUSM 49821; MUSM 49822; MUSM 49824; MUSM 49825; MUSM 49828; MUSM 49829; MUSM 49832; MUSM 49834

Hatunmachay (n=3)MUSM 49841; MUSM 49842; MUSM 49844

Escalon (n=48) MUSM 11625; MUSM 11628; MUSM 45087; MUSM 45088; MUSM 45089; MUSM 45091; MUSM 45199; MUSM 45201; MUSM 45202; MUSM 49654; MUSM 49655; MUSM 49656; MUSM 49658; MUSM 49662; MUSM 49663; MUSM 49664; MUSM 49668; MUSM 49669; MUSM 49673; MUSM 49674; MUSM 49675; MUSM 49676; MUSM 49680; MUSM 49682; MUSM 49684; MUSM 49685; MUSM 49697; MUSM 49698; MUSM 49702; MUSM 49703; MUSM 49705; MUSM 49706; MUSM 49713; MUSM 49715; MUSM 49716; MUSM 49717; MUSM 49719; MUSM 49720; MUSM 49726; MUSM 49744; MUSM 49746; MUSM 49747; MUSM 49749; MUSM 49751; MUSM 49752; MUSM 49755; MUSM 49876; MUSM 49890;

Chircahuapunta (n=5) MUSM 49734; MUSM 49735; MUSM 49737; MUSM 49738; MUSM 49742

Phyllotis andium (n=42)

Pallasca (n=23MUSM 23230; MUSM 23221; MUSM 23234; MUSM 23235; MUSM 23236; MUSM 23238; MUSM 23239; MUSM 23243; MUSM 40071; MUSM 40072; MUSM 40075; MUSM 40190; MUSM 40191; MUSM 40192; MUSM 40193; MUSM 40194; MUSM 40197; MUSM 40198; MUSM 40199; MUSM 40200; MUSM 40202; MUSM 40204; MUSM 40205;

Chinancocha (n=2)MUSM 49955; MUSM 49956

Challhuas (n=11)MUSM 49942; MUSM 49949; MUSM 49950; MUSM 49951; MUSM 49952; MUSM 49953; MUSM 49957; MUSM 49958; MUSM 49959; MUSM 49961; MUSM 49962;

Huari (n=6)MUSM 23932; MUSM 49943; MUSM 49944; MUSM 49945; MUSM 49946; MUSM 49947

Phyllotis occidens (n=83)

Chiquian (n=3) MUSM 50010; MUSM 50011; MUSM 50012;

Hatunmachay (n=2)MUSM 50020; MUSM 50024

Cajacay (n=28)MUSM 4519; MUSM 4521; MUSM 4523; MUSM 4524; MUSM 4525; MUSM 4527; MUSM 4529; MUSM 4553; MUSM 4559; MUSM 4560; MUSM 4566; MUSM 4572; MUSM 4595; MUSM 4601; MUSM 49965; MUSM 49966; MUSM 49967; MUSM 49968; MUSM 49969; MUSM 49970; MUSM 49971; MUSM 49972; MUSM 49974; MUSM 49975; MUSM 49976; MUSM 49977; MUSM 49978; MUSM 49979

Escalon (n=32) MUSM 49988; MUSM 49989; MUSM 49990; MUSM 49992; MUSM 49994; MUSM 49995; MUSM 49996; MUSM 49998; MUSM 49999; MUSM 50001; MUSM 50004; MUSM 50006; MUSM 50016; MUSM 45098; MUSM 45099; MUSM 45102; MUSM 45103; MUSM 45104; MUSM 45106; MUSM 45108; MUSM 45109; MUSM 45123; MUSM 45210; MUSM 45211; MUSM 45212; MUSM 45213; MUSM 45214; MUSM 45215; MUSM 45216; MUSM 45218; MUSM 45220; MUSM 45255;

Chircahuapunta (n=2)MUSM 50014; MUSM 50025

Macate (n=16)MUSM 50074; MUSM 50075; MUSM 50076; MUSM 50077; MUSM 50078; MUSM 50079; MUSM 50084; MUSM 50087; MUSM 50088; MUSM 50092; MUSM 50093; MUSM 50094; MUSM 50095; MUSM 50096; MUSM 50100; MUSM 50101

Thomasomys praetor (n=16)

Pallasca (n=6)MUSM 23248; MUSM 23330; MUSM 23332; MUSM 40080; MUSM 40209; MUSM 40211;

Chinancocha (n=6) MUSM 50029; MUSM 50030; MUSM 50031; MUSM 50032; MUSM 50033; MUSM 50036;

Baqueria (n=2)MUSM 50027; MUSM 50028;

Escalon (n=2)MUSM 11644; MUSM 45112

Appendix C. List of analyzed specimens per populations for genetics analyses. MUSM (Museo de historia Natural de la Univerisidad Nacional Mayor de San Marcos, Lima Peru) Codes in brackets are the collector number (it is showing in the figures)

Akodon mollis (n=51)

Pallasca (n=5)MUSM 40089 [VPT 4020]; MUSM 40112 [VPT 4014]; MUSM 40143 [PA 313]; MUSM 40144 [PA 314]; MUSM 40158 [VPT 4046];

Chinancocha (n=5)MUSM 49142 [VSO 102]; MUSM 49143 [VSO 103]; MUSM 49145 [VSO 115]; MUSM 49446 [VSO 064]; MUSM 49457 [VSO 126];

Baqueria (n=1 MUSM 49075 [VSO 050];

Portachuelo (n=3)MUSM 49437 [VSO 125]; MUSM 49438 [VSO 139]; MUSM 49442 [VSO 123];

Huari (n=4)MUSM 49350 [VSO 164]; MUSM 49351 [VSO 165]; MUSM 49354 [VSO 170]; MUSM 49356 [VSO 172]; MUSM 49358 [VSO 174];

Tambillo (n=4) MUSM 49524 [JPP 020]; MUSM 49525 [JPP 021]; MUSM 49527 [JPP 023]; MUSM 49528 [JPP 024];

Cahuish (n=2)MUSM 49553 [VSO 221]; MUSM 49554 [VSO 222];

Querococha (n=1)MUSM 49466 [VSO 246];

Huallanca (n=6)MUSM 49273 [VSO 720]; MUSM 49274 [VSO 736]; MUSM 49275 [VSO 737]; MUSM 49304 [VSO 757]; MUSM 49316 [VSO 970]; MUSM 49324 [VSO 707]; Chiquian (n=4)MUSM 49161 [VSO 794]; MUSM 49162 [VSO 795]; MUSM 49167 [VSO 836]; MUSM 49401 [VSO 806];

Cajacay (n=1) MUSM 50102 [VSO 981];

Escalon (n=9)MUSM 49088 [VSO 426]; MUSM 49090 [VSO 428]; MUSM 49091 [VSO 429]; MUSM 49093 [VSO 431]; MUSM 49198 [VSO 538]; MUSM 49199 [VSO 540]; MUSM 50103 [VSO 998]; MUSM 50108 [VSO 1004]; MUSM 50109 [VSO 1005];

Macate (n=4)MUSM 50044 [RCC 173]; MUSM 50045 [RCC 206]; MUSM 50046 [RCC 210]; MUSM 50049 [RCC 203]

Microryzomys latissimus (n=24)

Pallasca (n=3)MUSM 40065 [MDA 300]; MUSM 40179 [VPT 4041]; MUSM 40180 [VPT 4042];

Chinancocha (n=3)MUSM 49899 [VSO 111]; MUSM 49900 [VSO 112]; MUSM 49920 [VSO 130];

Baqueria (n=4)MUSM 49891 [VSO 041]; MUSM 49892 [VSO 047]; MUSM 49893 [VSO 048]; MUSM 49894 [VSO 049];

Portachuelo (n=3)MUSM 49915 [VSO 077]; MUSM 49916 [VSO 094]; MUSM 49917 [VSO 121];

Huari (n=3)MUSM 49909 [VSO 180]; MUSM 49910 [VSO 208]; MUSM 49911 [VSO 215];

Tambillo (n=2)MUSM 49924 [JPP 031]; MUSM 49926 [JPP 050];

Cahuish (n=1)MUSM 49927 [VSO 306];

Querococha (n=1)MUSM 49923 [VSO 280];

Huallanca (n=2)MUSM 49905 [VSO 593]; MUSM 49906 [VSO 623];

Chiquian (n=2)MUSM 49912 [VSO 846]; MUSM 49913 [VSO 914]

Oligoryzomys andinus (n=24)

Pallasca (n=5)MUSM 40183 [MDA 336]; MUSM 40185 [MDA 321]; MUSM 40186 [MDA 329]; MUSM 40188 [VPT 4057]; MUSM 40189 [VPT 4015];

Chinancocha (n =8)MUSM 49930 [VSO 099]; MUSM 49931 [VSO 105]; MUSM 49932 [VSO 106]; MUSM 49933 [VSO 107]; MUSM 49934 [VSO 142]; MUSM 49935 [VSO 147]; MUSM 49936 [VSO 148]; MUSM 49938 [VSO 070]; MUSM 49940 [VSO 128];

Cajacay (n=2) MUSM 50133 [VSO 991]; MUSM 50134 [VSO 993];

Escalon (n=4)MUSM 50135 [VSO 1011]; MUSM 50138 [VSO 1024]; MUSM 50139 [VSO 1029]; MUSM 50141 [VSO 1033];

Macate (m=4)MUSM 50058 [RCC 219]; MUSM 50059 [RCC 223]; MUSM 50060 [RCC 224]; MUSM 50061 [RCC 197]

Auliscomys pictus (n=14)

Pallasca (n=4)MUSM 40055 [MDA 299]; MUSM 40057 [MDA 291]; MUSM 40058 [GA 053]; MUSM 40059 [VPT 3989];

Portachuelo (n=1)MUSM 49643 [VSO 058];

Tambillo (n=2)MUSM 49646 [JPP 029]; MUSM 49649 [JPP 042];

Huallanca (n=4)MUSM 49597 [VSO 575]; MUSM 49598 [VSO 576]; MUSM 49599 [VSO 597]; MUSM 49600 [VSO 598];

Conococha (n=3)MUSM 49618 [VSO 862]; MUSM 49620 [VSO 869]; MUSM 49621 [VSO 870]

***Calomys sorellus* (n=24)**

Portachuelo (n=1)MUSM 49850 [VSO 124];

Huari (n=1)MUSM 49849 [VSO 161];

Tambillo (n=2) MUSM 50041 [JPP 015];

Cahuish (n=2)MUSM 49888 [VSO 266]; MUSM 49889 [VSO 298];

Querococha (n=3) MUSM 49853 [VSO 233]; MUSM 49854 [VSO 234]; MUSM 49856 [VSO 236];

Huallanca (n=5) MUSM 49764 [VSO 571]; MUSM 49765 [VSO 573]; MUSM 49766 [VSO 580]; MUSM 49772 [VSO 600]; MUSM 49773 [VSO 601];

Chiquian (n=2) MUSM 49730 [VSO 790]; MUSM 49731 [VSO 835];

Conocochas (n=2) MUSM 49824 [VSO 781]; MUSM 49834 [VSO 866];

Escalon (n=3) MUSM 49659 [VSO 369]; MUSM 49677 [VSO 393]; MUSM 49678 [VSO 395];

Chircahuapunta (n=3)MUSM 49736 [VSO 947]; MUSM 49737 [VSO 949]; MUSM 49739 [VSO 961];

Macate (n=1)MUSM 50056 [RCC 205]

***Phyllotis andium* (n=12)**

Pallasca (n=4)MUSM 40072 [GA 061]; MUSM 40194 [MDA 331]; MUSM 40195 [MDA 332]; MUSM 40205 [VPT 4026];

Challhuas (n=6)MUSM 49941 [VSO 013]; MUSM 49942 [VSO 014]; MUSM 49951 [VSO 035]; MUSM 49952 [VSO 036]; MUSM 49953 [VSO 037]; MUSM 49958 [VSO 030];

Huari (n=2) MUSM 49945 [VSO 169]; MUSM 49946 [VSO 182];

***Phyllotis occidens* (n=25)**

Chiquian (n=2) MUSM 50011 [VSO 788]; MUSM 50012 [VSO 906];

Hatunmachay (n=2)MUSM 50021 [VSO 756]; MUSM 50022 [VSO 760];

Cajacay (n=4)MUSM 50145 [VSO 983]; MUSM 50146 [VSO 984]; MUSM 50147 [VSO 985]; MUSM 50148 [VSO 986];

Escalon (n=7) MUSM 49995 [VSO 442]; MUSM 49996 [VSO 444]; MUSM 49997 [VSO 446]; MUSM 50016 [VSO 500]; MUSM 50157 [VSO 1000]; MUSM 50158 [VSO 1006]; MUSM 50159 [VSO 1014];

Macate (n=10)MUSM 50070 [RCC 176]; MUSM 50071 [RCC 177]; MUSM 50072 [RCC 178]; MUSM 50074 [RCC 207]; MUSM 50075 [RCC 208]; MUSM 50076 [RCC 209]; MUSM 50078 [RCC 214]; MUSM 50086 [RCC 221]; MUSM 50091 [RCC 184]; MUSM 50098 [RCC 191]

Thomasomys praetor (n=9)

Pallasca (n=1)MUSM 40210 [MDA 343];

CHinancocha (n=5)MUSM 50029 [VSO 100]; MUSM 50032 [VSO 136]; MUSM 50033 [VSO 138]; MUSM 50034 [VSO 145]; MUSM 50035 [VSO 071];

Baqueria (n=2)MUSM 50027 [VSO 019]; MUSM 50028 [VSO 045];

Tambillo (n=1)MUSM 50037 [JPP 044]

Appendix D. Qualitative morphological species descriptions

Tribe Akodontini Vorontsov, 1959
Genus *Akodon* Meyen, 1833
Akodon mollis Thomas, 1894
Soft Grass Mouse
(Figure 1A)

Description: Small rodent with long and soft pelage with a mixed olive brown and yellowish coloration; a dark basal band; hair longitude up to 10 mm over the rump; the ventral fur is clearer with a grayish basal band followed by a yellowish-brown band. The pinnae are short and covered with olive-colored hairs. The mystacial vibrissae are short and reach the posterior border of the pinna when laid back against the head. The dorsal surface of the forefoot is covered with gray hairs with a dark base. The tail is short, measuring nearly the length of the head and the body together and it is faintly bicolored, dark above and pale gray below; both dorsum and venter are covered with few fine hairs that gives a semi-naked appearance to the tail.

The skull profile is convex, barely more swollen in the interorbital region. The rostrum is moderately long. In dorsal view, the nasolacrimal capsule is softly broader than the anterior portion of the rostrum. The nasal is conical, long, and slightly broader towards the tip. The fronto-nasal suture is faintly posterior to the fronto- premaxillary suture; the premaxillary-naso-frontal joint is anterior to the maxillary-fronto-lacrimal joint. The premaxillary projects anteriorly to the plane of the incisors; the gnathic process is conspicuous. The zygomatic plate is narrow and slightly oblique at the border, the anterodorsal spinous process is absent; the zygomatic notch is superficial; the infraorbital foramen is slightly broad, the antorbital bridge is wide. The sides of the zygomatic arch are barely convergent anteriorly; the zygomatic process of the maxillary is narrower than the antorbital bridge; the jugal is long and very thin. The interorbital region is broad and moderately concave, the bases of the molars are nearly indistinguishable from the dorsal view, the supraorbital margin exhibits round and smooth edges, the lacrimal bone is small. The frontal bone is wide from the dorsal view and slightly swollen from the lateral view and it does not present a medial depression. The braincase is rounded whereas the fronto-parietal suture is smooth and convex; the parietal edge is quite smooth without forming a crest; the interparietal is small and thin, the interparietal-parietal suture is smooth and the interparietal-supraoccipital suture is serrated.

The palatal region is long and narrow. The diastema is flat from the lateral view. The incisive foramen is long and narrow, and slightly concave at the level of the nasolacrimal capsule. The premaxillary portion of the septum builds a medial ridge overlapping the vomer, the vomer is long and marginally broad; the maxillary portion of the septum is moderately thin. The bony palate is moderately wide and long, extending behind the posterior plane of M3. The palatal lateral grove is shallow. The posterolateral palatal pit is wide and placed next to the mesopterygoid fossa. The mesopterygoid fossa is wide and square-shaped with parallel sides. The palatal process is absent. The sphenopalatine vacuities are narrow. The presphenoid is thick. The parapterygoid fossa is triangular and wide with small vacuities. The parapterygoid process is long. The middle lacerate foramen is open. The alisphenoid strut is present. The anterior opening of the alisphenoid canal is smaller than the foramen ovale.

The auditory region is composed of moderately large-sized ectotympanic bullae. The tegmen tympani is small and may reach the suspensory process of the squamosal. The Eustachian tube bone is short and reaches the base of the parapterygoid process. The anterior process of the ectotympanic (stapedial spine) is small and, in most specimens, does not reach the posterior margin of the alisphenoid bone. The postglenoid foramen is larger than the subsquamosal fenestra; the hamular process of the squamosal is thick. The lambdoid ridge is barely visible. The basioccipital is narrow and has a trapezoid shape; it presents a medial spine that extends to the basioccipital—basisphenoid suture. The mastoid (the periotic capsule of the petrosal) is square-shaped with an open mastoid fenestra and a conspicuous mastoidoccipital opening. The occipital condyle is not evident in the dorsal view; the paraoccipital process is medium-sized.

The upper incisors are ortodont, the M1 and M2 are trilofodont, the anteroloph is reduced, the mesoloph and the posteroloph are distinguishable; the M3 is bilophodont and reduced. The ventral margin of the mandible is slightly concave, the diastema is slightly long. The capsular process is present but small. The coronoid process is long, placed at the level of the condyle process, forming a slightly deep sigmoid notch. The condylar process is rounded and reaches the level of the angular process which has a deep angular notch.

Figure A1 Dorsal, ventral and lateral views of the cranium and the mandible of *Akodon mollis* (MUSM 49070)

Tribe Oryzomyini Vorontsov, 1959

Genus *Microryzomys* Thomas, 1917

Microryzomys altissimus (Osgood, 1933)

Highland Small Rice Rat

(Figure A2)

Description: Small rodent with a soft and long fur with a cinnamon gray coloration, a middle band faintly darker than the lateral ones, and hair longitude of approximately 10 mm over the rump; the ventral fur is creamy composed of a gray basal band followed by a brownish-beige band. The pinnae are short and have few hairs. The mystacial vibrissae reach the posterior border of the pinna when laid back against the head. The dorsal surface of the fore foot is covered with fine white hairs and a few black hairs. The hind foot is thin and moderately long with white hairs and a few black hairs. The tail is longer than the body and head together, faintly bicolored, and presents a very little brush at the end of the tail.

The skull profile is slightly convex. The rostrum is short and narrow. The nasal is conical, long, and slightly broader towards the tip. The fronto-nasal suture is placed posterior to the fronto- premaxillary suture; the premaxillary-naso-frontal joint is at the same level as the maxillary-fronto-lacrimal joint. The premaxillary projects anteriorly to the plane of the incisors and behind the tip of the nasal, the gnathic process is very small.

The zygomatic plate is broad with vertical dip, the anterodorsal spinous process is absent; the zygomatic notch is shallow, the infraorbital foramen is barely wide, and the antorbital bridge is thin. The zygomatic arch has a robust appearance and exhibits slightly rounded sides. The zygomatic process of the maxillary is thinner than the antorbital bridge, the jugal is considerably reduced.

The inteorbital is faintly broad and concave, the molar bases are recognizable from a dorsal view; the supraorbital margin shows round and smooth edges; the lacrimal is small but visible. The frontal bone is narrow from the dorsal view, it presents a slight medial depression that lengthens the premaxillary bone.

The braincase is rounded, the fronto-parietal suture is serrated and converges posteriorly, the parietal edge does not form a crest, the interparietal is large and has a trapezoid shape, and both the interparietal-parietal and interparietal-supraoccipital sutures are somewhat dentated.

The palatal region is long and slightly narrow. The diastema is flat in the lateral view. The incisive foramen is slightly long and narrow, the premaxillary portion of the septum is thin and does not build a medial ridge, the vomer is wide, the maxillary portion of the septum is moderately broad. The bony palate is moderately wide and long, extending behind the posterior plane of M3. The palatal lateral groves are depthless. The posterolateral palatal pit is wide and located next to the mesopterygoid fossa.

The mesopterygoid fossa is wide and oval-shaped with softly convergent sides posteriorly. The sphenopalatine vacuities are large. The presphenoid is thin. The parapterygoid fossa is triangular and quite wide with vacuities. The parapterygoid process is short. The middle lacerate foramen is almost closed. The alisphenoid strut is absent. The anterior opening of alisphenoid canal is smaller than the buccinator-masticatory and foramen ovale joint.

The auditory region is formed by moderately large-sized ectotympanic bullae. The tegmen tympani is small and does not reach the suspensory process of the squamosal. The bony Eustachian tube is short and does not reach the parapterygoid process. The anterior process of the ectotympanic (stapedial spine) is small and reaches the posterior edge of the alisphenoid bone.

The postglenoid foramen is larger than the subsquamosal fenestra; the hamular process of the squamosal is thin and reaches the mastoid bone. The lambdoid ridge is absent. The basioccipital is narrow and trapezoid- shaped, showing a medial spine that extends to the basioccipital—basisphenoid suture. The mastoid (the periotic capsule of the petrosal) is square-shaped with a visible mastoid fenestra and a distinguishable mastoid-occipital opening. The occipital condyle is not evident in the dorsal view; the paraoccipital process is small.

The upper incisors display a slightly opistodont orientation. The tooth topography follows a pentalofodont pattern. The procingulum of M1 is divided by a visible anteromedial flexus. The M2 presents a very evident anteroloph, paracone, mesoloph, metacone, and posteroloph. The ventral margin of the mandible is barely concave, the diastema is short. The capsular process is present but small. The coronoid process is short, and placed at the level of the condyle process, forming a shallow sigmoid notch between them. The condylar process is rounded and reaches the level of the angular process which has a superficial angular notch.

Figure 2B Dorsal, ventral and lateral views of the cranium and the mandible of *Microryzomys altissimus* (MUSM 49917)

Genus *Oligoryzomys* Bangs, 1900

Oligoryzomys andinus (Osgood, 1914)

Andean Pygmy Rice Rat

(Figure A3)

Description: Small rodent with a soft and long fur with a reddish-cinnamon coloration, dark gray at the base, and hair longitude is about 10 mm over the rump; the dorsal fur has some dispersed black hairs, and the ventral fur is creamy composed of a pale gray basal band followed by a cream band. The pinnae are short and have few hairs. The mystacial vibrissae exceed the posterior border of the pinna when laid back against the head. The dorsal surface of the forefoot is covered with fine white hairs. The hind foot is thin with long white hairs. The tail is considerably longer than the body and head together, faintly bicolored, and presents a very little brush at the end of the tail.

The skull profile is slightly convex. The rostrum is short and narrow. The nasal is conical, long, and softly broader towards the tip. The fronto-nasal suture is located anterior to the fronto-premaxillary suture; the premaxillary-naso-frontal joint is at the same level as the maxillary-fronto-lacrimal joint. The premaxillary is in the plane of the incisors and behind the tip of the nasal, the gnathic process is very small.

The zygomatic plate is broad with bent margins, anterodorsal spinous process is absent, the zygomatic notch is moderately deep; the infraorbital foramen is narrow; the zygomatic arch exhibits anteriorly convergent sides. The zygomatic process of the maxillary is wider than the antorbital bridge. The jugal is very reduced and might be imperceptible.

The interorbital region is narrow and concave, the bases of the molars are indistinguishable in dorsal view, the supraorbital margin displays square-shaped edges, the lacrimal is small. The frontal bone is narrow from the dorsal view, it presents a slight medial depression that lengthens the premaxillary bone.

The braincase is rounded, the fronto-parietal suture is somewhat serrated and converges posteriorly, the parietal edge forms a smooth and almost invisible crest, the interparietal is large and trapezoid-shaped, both the interparietal-parietal and interparietal-supraoccipital sutures are dentated.

The palatal region is long and narrow. In lateral view the diastema is flat. The incisive foramen is long and narrow with slightly convex margins interiorly. The premaxillary portion of the septum is thin and builds a medial ridge, the vomer is wide, the maxillary portion of the septum is moderately thin. The bony palate is moderately narrow and long, extending behind the posterior plane of M3. The palatal lateral groves are shallow. The posterolateral palatal pit is wide and located anteriorly to the mesopterygoid fossa.

The mesopterygoid fossa is narrow and square-shaped with parallel sides. The sphenopalatine vacuities are large. The presphenoid is thin. The parapterygoid fossa is triangular and wide with vacuities. The parapterygoid process is long.

The middle lacerate foramen is faintly opened. The alisphenoid strut is absent. The anterior opening of alisphenoid canal is smaller than the buccinator-masticatory and foramen ovale joint.

The auditory region is composed of moderately large-sized ectotympanic bullae. The tegmen tympani does not reach the suspensory process of the squamosal. The bony Eustachian tube is short and does not reach the parapterygoid process. The anterior process of the ectotympanic (stapedial spine) is moderately large and does not reach the posterior margin of the alisphenoid bone.

The postglenoid foramen is much larger than the subsquamosal fenestra, the hamular process of the squamosal is wide and reaches the mastoid bone. The lambdoid ridge is present. The basioccipital is wide and has a trapezoid shape, it shows a smooth medial spine that extends to the basioccipital—basisphenoid suture. The mastoid (the periotic capsule of the petrosal) is square-shaped with a visible mastoid fenestra and a recognizable mastoid-occipital opening. The occipital condyle is not evident in dorsal view; the paraoccipital process is small.

The upper incisors display an opistodont orientation. The tooth topography is determined as a pentalofodont pattern. The procingulum of M1 shows a visible anteromedial flexus. The M2 presents very evident anteroloph, paracone, mesoloph, metacone, and posteroloph. The ventral margin of the mandible is slightly concave, the diastema is short. The capsular process is distinguishable. The coronoid process is small and extends posteriorly to the angular process, the angular notch is slightly deep.

Figure A3 Dorsal, ventral and lateral views of the cranium and the mandible of *Oligoryzomys andinus* (MUSM 23227)

Tribe Phyllotini Vorontsov, 1959

Genus *Auliscomys* Osgood, 1915

Auliscomys pictus (Thomas, 1884)

Painted Big-eared Mouse

(Figure A4)

Diagnosis. Pelo largo y suave, con un tono gris y ligeramente amarillento a los costados, cola tenuemente bicoloreada, sutura fronto-nasal esta posterior a la sutura fronto-premaxilar, margen supraoccipital muestra bordes suaves y redondos, foramen palatal anterior localizado cerca a la sutura maxilo-palatina; proceso medial del paladar posterior está presente y muy visible, tubo de Eustaquio corto, no llega al nivel del proceso del parapterigoideo; proceso hamular del escamosal delgado. M2 presenta paraflexus evidentemente profunda, el proteflexido m2 es desarrollado.

Diagnosis. Long and soft hair, with a gray and slightly yellowish hue on the sides, faintly bicolored tail, fronto-nasal suture is posterior to the fronto-premaxillary suture, the supraoccipital margin shows smooth and rounded edges, anterior palatal foramen located near the maxillary suture -palatine; medial process of posterior palate present and visible, Eustachian tube short, not reaching the level of the parapterygoid process; hamular process of the thin squamosal. M2 presents evidently deep paraflexus, the proteflexid m2 is developed.

Description: Small rodent with soft and long fur. The coloration of the dorsal fur has an ochre hue with intermixed dark and brownish hairs that are light gray at the base. The length of the hairs is up to 10 mm over the rump; the lateral sides have a clearer brownish coloration: the ventral fur is grayish, composed of a dark gray basal band followed by a light gray band. The pinnae are long and covered with brownish hairs. The mystacial vibrissae are long and reach the posterior border of the pinna when laid back against the head. The dorsal surface of the forefoot is covered with fine white hairs. The dorsal surface of the hindfoot is thin and short, with white hairs. The tail is short, it does not exceed the length of the body and head together, and it is slightly bicolored: black above and gray below, both back and venter are furry.

The skull profile is convex. The rostrum is short and narrow. The nasal is conical, long, and slightly broader towards the tip. The fronto-nasal suture is placed posterior to the fronto-premaxillary suture; the premaxillary-naso-frontal joint is anterior to the maxillary-fronto-lacrimal joint. The premaxillary is short and does not reach the plane of the incisors; the gnathic process is reduced.

The zygomatic plate is broad with the edge softly concave and presents a smooth anterodorsal spinous. The zygomatic notch is deep, the infraorbital foramen is narrow at the base and slightly open at the level of the antorbital bridge, which is wide. The zygomatic arch is robust and has softly bent sides. The zygomatic process of the maxillary is wider than the antorbital bridge, the jugal is long and thin.

The interorbital region is quite broad and concave, the molar bases are very distinguishable from the dorsal view, the supraorbital margin exhibits slightly square-shaped edges, the lacrimal bone is large. The frontal bone is narrow and does not have a medial depression.

The braincase is rounded, the fronto-parietal suture is slightly serrated and convex, the parietal edge is smooth and does not form a crest, the interparietal is wide and has a rhomboid shape, both the interparietal-parietal and interparietal-supraoccipital sutures are dentated.

The palatal region is long and narrow. The diastema is flat from the lateral view. The incisive foramen is long and narrow with edges that softly converge posteriorly, the premaxillary portion of the septum determines a medial ridge overlapping on the vomer, the vomer is short and narrow, the maxillary portion of the septum is thin. The bony palate is narrow and long. The palatal lateral groves are shallow. The posterolateral palatal pit is small and located next to the mesopterygoid fossa.

The mesopterygoid fossa is wide and slightly square-shaped with parallel sides that converge posteriorly, the palatal process is not very noticeable, the sphenopalatine vacuities are large. The presphenoid is thick. The parapterygoid fossa is triangular with vacuities, the parapterygoid process is long.

The middle lacerate foramen is open, the alisphenoid strut is absent. The anterior opening of alisphenoid canal is considerably smaller than the buccinator-masticatory and foramen ovale joint.

The auditory region is formed by large ectotympanic bullae. The tegmen tympani overlaps the posterior suspensory process of the squamosal. The bony Eustachian tube is short and does not reach the anterior margin of the middle lacerate foramen. The anterior process of the ectotympanic (stapedial spine) is long and reaches the posterior edge of the alisphenoid.

The postglenoid foramen is smaller than the subsquamosal fenestra, the hamular process of the squamosal is barely thick and reaches the mastoid bone. The lambdoid ridge is present. The basioccipital is narrow and has a trapezoid shape, showing a well-defined medial spine that extends to the basioccipital—basisphenoid suture. The mastoid (the periotic capsule of the petrosal) is square-shaped with a large mastoid fenestra and a distinguishable mastoid-occipital opening. The occipital condyle is barely recognizable from a dorsal view, the paraoccipital process is long.

The upper incisors have a protodont orientation. The tooth topography is determined as having a tetralophodont dental pattern. The procingulum of M1 is small and not divided. The M2 has an "S" shape with an evident anteroloph. The M3 is smaller than the M2. The ventral margin of the mandible is softly concave, the diastema is long. The capsular process is very reduced or absent. The coronoid process is long and placed at the level of the condyle process, forming a superficial and slightly concave sigmoid notch. The condylar process is rounded and lengthens the level of the angular process which has a deep angular notch.

Figure A4 Dorsal, ventral and lateral views of the cranium and the mandible of *Auliscomys pictus* (MUSM 49613)

Genus *Calomys* Water house, 1837

Calomys sorellus (Thomas, 1900)

Peruvian Vesper Mouse

(Figure A5)

Description: Small rodent with soft and long fur. The coloration of the fur is grayish with intermixed dark and brownish dorsal hairs that are dark gray at the base; the lateral band is much clearer and has a creamy tone; the hairs measure up to13 mm over the rump; whitish ventral fur composed of a gray basal band followed by a white band. The pinnae are long and are covered with brownish hairs; the auricular patch is conspicuous. The mystacial vibrissae surpass the posterior border of the pinna when laid back against the head. The dorsal surface of the forefoot is covered with fine white hairs. The hind foot is thin and moderately short with white hairs at the dorsal surface. The tail measures nearly the same as the body and head together, and it is bicolored: dark above and clearer below. Both the dorsum and venter are furred.

The skull profile is convex, barely more bloated in the interorbital region. The rostrum is short. The nasal is conical, long, and has a narrow tip. The fronto-nasal suture is faintly posterior to the fronto-premaxillary suture; the premaxillary-naso-frontal joint is anterior to the maxillary-fronto-lacrimal joint. The premaxillary is short and narrow, it marginally projects anteriorly to the plane of the incisors and behind the tip of the nasal; the gnathic process is small.

The zygomatic plate is narrow with a vertical dip and does not present an anterodorsal spinous process, the zygomatic notch is deep, the infraorbital foramen is wide; the antorbital bridge is thin. The parallel sides of the zygomatic arch are softly convergent anteriorly. The zygomatic process of the maxillary is narrow and as thick as the antorbital bridge, the jugal is long and thin.

The interorbital region is broad and moderately concave, the crowns of the molars are visible from the dorsal view, the supraorbital margin exhibits round and flatten edges, the lacrimal bone is slightly large, and it is projected on the supraorbital ridge. The frontal bone is moderately broad from the dorsal and does not present a medial depression.

The braincase is rounded and the fronto-parietal is slightly serrated and convex, the parietal edge is smooth without forming a crest, the interparietal is moderately large and long, both the interparietal-parietal and interparietal-supraoccipital sutures are somewhat dentated.

The palatal region is long and narrow. The diastema is flat from the lateral view. The incisive foramen is long and narrow with parallel margins. The premaxillary portion of the septum builds a conspicuous medial ridge overlapping the vomer, the vomer is thin and long, the maxillary portion of the septum is thin. The bony palate is moderately wide and long, extending behind the posterior plane of M3, the palatal lateral groves are shallow. The posterolateral palatal pit is quite wide and located anteriorly to the mesopterygoid fossa.

The mesopterygoid fossa is quite narrow with parallel sides. The palatal process is absent. The sphenopalatine vacuities are large. The presphenoid is quite wide. The parapterygoid fossa is triangular and quite broad, may or may not present small vacuities. The parapterygoid process is long.

The middle lacerate foramen is moderately open. The alisphenoid strut is absent. The anterior opening of alisphenoid canal is much smaller than the buccinator-masticatory and foramen ovale joint.

The auditory region is formed by large ectotympanic bullae. The tegmen tympani overlaps on the suspensory process of the squamosal. Although the bony Eustachian tube is short, it exceeds the anterior edge of the middle lacerate foramen but does not reach the parapterygoid process. The anterior process of the ectotympanic (stapedial spine) is middle-sized and rarely reaches the posterior edge of the alisphenoid bone.

The postglenoid foramen is smaller than the subsquamosal fenestra, the hamular process of the squamosal is thin and reaches the mastoid bone. The lambdoid ridge is present. The basioccipital is wide and has a trapezoid shape, it shows a medial spine that lengthens to the basioccipital—basisphenoid suture. The mastoid (the periotic capsule of the petrosal) is square-shaped with a mastoid fenestra and an evident mastoid-occipital opening. The occipital condyle is not evident in the dorsal view; the paraoccipital process is small.

The upper incisors exhibit an ortodont or slightly opistodont orientation. The tooth topography follows a tetralofodont pattern. The alveolus of M1 is placed anterior to the incisive foramen and marginally behind the posterior margin of the zygomatic plate. The procingulum of M1 is small and divided.

The ventral margin of the mandible is concave, the diastema is long. The capsular process is very reduced, the coronoid process is long and located at the level of the condyle process and the sigmoid notch formed is slightly deep. The condylar process is rectangular-shaped and extends to the same level as the angular process which has a deep angular notch.

Figure A5 Dorsal, ventral and lateral views of the cranium and the mandible of *Calomys sorellus* (MUSM 45199)

Genus *Phyllotis* Water house, 1837

Phyllotis andium Thomas, 1912

Andean Leaf- eared Mouse

(Figure A6)

Description: The dorsal pelage is composed of rich-brow hairs that have neutral grey at the base, the dorsal band on the dorsum is inconspicuous; the hairs are dense and long and average 13 mm over the rump; the ventral pelage is whitish with a short grey basal band followed by a white band. The pinnae are comparatively short in comparison to congeners; the auricular patch is inconspicuous; an orbicular ring is absent. The mystacial vibrissae reach the posterior border pinna when laid back against the head. The tail is barely longer than the head and the body together. The dorsal surface of the manus are covered with fine white hairs and the ungual tuft is present but not very dense and is dimly bicolored, being dark above and pale neutral gray below, and both the dorsum and venter are furred.

The skull profile is convex and slightly more swollen in the interorbital region. The rostrum is short. The nasal is conical and long and anteriorly it is broad; in lateral view, it projects anterodorsally beyond the premaxillae and the anterior border of the incisors. The fronto-nasal suture is aligned to the fronto-premaxillary suture; the premaxillary-naso-frontal joint is anterior to the maxillary-fronto-lacrimal joint. The premaxillary is short and narrow; it projects slightly anteriorly to the plane of the incisors.

The zygomatic plate is moderately broad with a vertical dip and the anterodorsal spinous process is absent; the zygomatic notch is deep; the infraorbital foramen is narrow. The zygomatic arch has parallel sides, which are slightly convergent anteriorly; the zygomatic process of the maxillary is narrow; it is barely wider than the antorbital bridge; the jugal is long and very thin.

The interorbital region is narrow and moderately concave, the molar bases are visible in dorsal view; the supraorbital margin has sharp edges; the lacrimal is large and projects over the antorbital bridge. The frontal bone is moderately narrow in dorsal view and slightly swollen in the lateral one and it does not have a medial depression.

The braincase is rounded and the fronto-parietal suture is slightly serrated and convex; the parietal edge (on the squamosal-parietal suture) is smooth; the interparietal is small with a trapezoid-shape and both the interparietal-parietal and interparietal-supraoccipital sutures are dentated.

The palatal region is long and narrow. The incisive foramen is long and narrow with parallel margins, extending to the M1 alveolus. The premaxillary portion of the septum builds a medial ridge overlapping the vomer; the maxillary portion of the septum is moderately thin. The bony palate is moderately wide and long, extending behind the posterior plane of M3. The palatal lateral grove is shallow. The posterolateral palatal pit is small and placed anterior to the mesopterygoid fossa.

The mesopterygoid fossa is narrow and square-shaped with parallel sides. The palatal process is absent. The sphenopalatine vacuities are large and reach halfway to the basisphenoid. The presphenoid is present but thin. The parapterygoid fossa is triangular and wide, but with inconspicuous or absent vacuities. The parapterygoid process is long and projected outside. The middle lacerate foramen is moderately open. The alisphenoid strut is absent. The anterior opening of the alisphenoid canal is smaller than the buccinator-masticatory and foramen ovale joint.

The auditory region is formed by moderate-sized ectotympanic bullae. The tegmen tympani overlaps the posterior suspensory process of the squamosal. The bony Eustachian tube is long; it exceeds or is at the same level as the anterior margin of the middle lacerate foramen, in some cases, it contacts the parapterygoid process. The anterior process of the ectotympanic (stapedial spine) is moderate-size.

The postglenoid foramen is smaller than the subsquamosal fenestra; the hamular process of the squamosal is moderately broad and reaches the mastoid bone. The lambdoid ridge is absent. The basioccipital is narrow with a trapezoid shape; it shows a medial spine that extends to the basioccipital—basisphenoid suture. The mastoid (the periotic capsule of the petrosal) is squared-shaped with an open mastoid fenestra and a conspicuous mastoidoccipital opening. The occipital condyle is not evident in the dorsal view; the paraoccipital process is small.

The upper incisor has an orthodont orientation. The tooth topography is determined as having a tetralophodont dental pattern. The alveolus of M1 is placed anterior to the incisive foramen and slightly behind the posterior margin of the zygomatic plate. The procingulum of M1 is small and undivided. The M2 has an "S" shape. The ventral margin of the mandible is slightly concave; the diastema is short with a weakly acute angle formed by the root of m1. The capsular process, although small, is present. The coronoid process is small but at the same level with the condyle process, forming a shallow sigmoid notch. The condylar process is rounded and is level with the angular process which has a deep angular notch.

Figure A6 Dorsal, ventral and lateral views of the cranium and the mandible of *Phyllotis andium* (MUSM 40071)

Phyllotis occidens Rengifo & Pacheco 2015

Western Leaf-eared Mouse

(Figure A7)

Description: Middle-sized rodent with long and soft fur. The dorsal pelage is composed of rich-brow hairs that have neutral grey at the base, the dorsal band on the dorsum is inconspicuous; the hairs are dense and long and average 13 mm over the rump; the ventral pelage is whitish with a short grey basal band followed by a white band; a pectoral streak is present but barely conspicuous. The pinnae are comparatively short in comparison to congeners; the auricular patch is inconspicuous, represented by some flew hairs over and under the ears. The mystacial vibrissae reach the posterior border pinna when laid back against the head. The dorsal surface of the fore foot is covered with fine white hairs. The hind foot is long and thin with white hairs on the dorsal surface. The tail is barely longer than the head and the body together, being dimly bicolored, dark above and pale neutral gray below and both the dorsum and venter are furred.

The skull profile is convex and slightly more swollen in the interorbital region. The rostrum is short. The nasal is conical and long and anteriorly broad; in lateral view, it projects anterodorsally beyond the premaxillae and the anterior border of the incisors. The fronto-nasal suture is posterior to the fronto- premaxillary suture; the premaxillary-naso-frontal joint is anterior to the maxillary-fronto-lacrimal joint. The premaxillary is short and narrow, it projects slightly anteriorly to the plane of the incisors, the gnathic process is very reduced.

The zygomatic plate is moderately broad with vertical dip, anterodorsal spinous process is absent; the zygomatic notch is deep; the infraorbital foramen is narrow; the antorbital bridge is broad. The zygomatic arch exhibits parallel sides, which are slightly convergent anteriorly; the zygomatic process of maxillary is narrow; narrow; it is barely wider than the antorbital bridge; the jugal is long and very thin. The interorbital region is narrow and moderately concave, the molar bases are visible from the dorsal view; the supraorbital margin has sharp edges; the lacrimal bone is large and projects over the antorbital bridge. The frontal bone is moderately narrow (in the dorsal view) and slightly swollen (in the lateral view) and it does not have a medial depression.

The braincase is rounded and the fronto-parietal suture is slightly serrated and convex; the parietal edge (on the squamosal-parietal suture) is smooth and does not form a crest; the interparietal is small with a trapezoid shape and both, the interparietal-parietal and interparietal-supraoccipital sutures, are dentated.

The palatal region is long and narrow. The diastema is flat from the lateral view. The incisive foramen is long and narrow with parallel margins, the premaxillary portion of the septum builds a medial ridge overlapping on the vomer, the vomer is short and narrow; the maxillary portion of the septum is moderately thin. The bony palate is moderately wide and long, extending behind the posterior plane of M3. The palatal lateral grove is shallow. The posterolateral palatal pit is small and placed anterior to the mesopterygoid fossa, but in some cases beside it.

The mesopterygoid fossa is narrow and square-shaped with parallel sides. The palatal process is present and very visible. The sphenopalatine vacuities are large and reach halfway to the basisphenoid. The presphenoid is present and thin. The parapterygoid fossa is triangular and wide with inconspicuous or absent vacuities. The parapterygoid process is long.

The middle lacerate foramen is moderately open. The alisphenoid strut is absent. The anterior opening of the alisphenoid canal is smaller than the buccinator-masticatory and foramen ovale joint.

The auditory region is formed by moderate-sized ectotympanic bullae. The tegmen tympani overlaps the posterior suspensory process of the squamosal. The bony Eustachian tube is short at same level or posterior of the anterior margin of the middle lacerate foramen, it does not reach to level parapterygoid process. The anterior process of the ectotympanic (stapedial spine) is moderate size, but rarely reaches the posterior edge of the alisphenoid bone.

The postglenoid foramen is smaller than the subsquamosal fenestra; the hamular process of the squamosal is thin and reaches the mastoid bone. The lambdoid ridge is absent. The basioccipital is narrow with a trapezoidshape; it shows a medial spine that extends to the basioccipital—basisphenoid suture. The mastoid (the periotic capsule of the petrosal) is squared-shaped with an open mastoid fenestra and a conspicuous mastoidoccipital opening. The occipital condyle is not evident in the dorsal view; the paraoccipital process is moderate-sized.

The upper incisor has an orthodont orientation. The tooth topography is determined as having a tetralophodont dental pattern. The alveolus of M1 is placed anterior to the incisive foramen and slightly behind the posterior margin of the zygomatic plate. The procingulum of M1 is small and undivided. The M2 has an “S” shape. The M3 is smaller than the M2.

The ventral margin of the mandible is barely concave, the diastema is short. The capsular process is present and small. The coronoid process is slightly long, placed at the level of the condyle process, forming a shallow sigmoid notch between them. The condylar process is rounded and reaches the level of the angular process having a superficial angular notch.

Figure A7 Dorsal, ventral and lateral views of the cranium and the mandible of *Phyllotis occidens* (MUSM 50020)

Tribe Thomasomyini Steadman and Ray, 1982

Genus *Thomasomys* Coues, 1884

Thomasomys praetor (Thomas, 1900)

Cajamarca Oldfield mouse

(Figure A8)

Description: Large rodent with soft and long fur. The dorsal fur coloration is olive-gray with a darker tone in the middle and more yellowish in the lateral areas. The longitude of the hairs averages 13 mm over the rump; the ventral fur is grayish-creamy composed of a gray basal band followed by a creamy-gray band. The pinnae are short and have scarce hairs and present an auricular patch of gray hairs. The mystacial vibrissae surpass the posterior border of the pinna when laid back against the head. The dorsal surface of the forefoot is covered with fine white hairs. The hind foot is thin and short with white hairs. The tail is longer than the body and head together, it has a single color and presents few hairs giving a naked appearance.

The skull profile is softly convex. The rostrum is slightly long and narrow. The nasal is conical, long, and barely broader towards the tip. The fronto-nasal suture is aligned with the fronto-premaxillary suture; the premaxillary-naso-frontal joint is located at the same plane of the incisors and behind the tip of the nasal, the gnathic process is very reduced.

The zygomatic plate is broad with vertical dip, the anterodorsal spinous process is absent, the zygomatic notch is moderately deep, the infraorbital foramen is narrow; the antorbital bridge is wide. The zygomatic arch has a robust appearance, and its sides softly converge forward. The zygomatic process of the maxillary is thinner than the antorbital bridge, the jugal is long and thin.

The interorbital is narrow and concave, the molar bases are recognizable from a dorsal view, the supraorbital margin has square-shaped edges, the lacrimal is very small. The frontal bone is narrow from the dorsal view and presents a slight medial depression.

The braincase is slightly oval, the fronto-parietal suture is smooth and converges posteriorly, the parietal edge forms a crest, the interparietal is large and has a rectangular shape, the interparietal-parietal suture is smooth while the interparietal-supraoccipital suture is somewhat dentated.

The palatal region is long and narrow. The diastema is flat from the lateral view. The incisive foramen is long and narrow with slightly convex margins interiorly; the premaxillary portion of the septum is thin and builds a medial ridge overlapping the vomer, the vomer is short and thin, the maxillary portion of the septum is thin. The bony palate is moderately narrow and short, extending behind the posterior alveolus of the M3. The palatal lateral groves are slightly deep. The posterolateral palatal pit is small and placed next to the mesopterygoid fossa and behind the toothrow.

The mesopterygoid fossa is wide and oval-shaped with softly bent sides. The sphenopalatine vacuities are very small. The presphenoid is thin. The parapterygoid fossa is narrow with small vacuities. The parapterygoid process is short.

The middle lacerate foramen is open, the alisphenoid strut is present. The anterior opening of alisphenoid canal is smaller than the foramen ovale.

The auditory region is composed of relatively small ectotympanic bullae. The tegmen tympani overlaps on the suspensory process of the squamosal. The bony Eustachian tube is short but contacts the parapterygoid process. The anterior process of the ectotympanic (stapedial spine) is large and does not reach the posterior edge of the alisphenoid bone.

The postglenoid foramen has the same size as the subsquamosal fenestra; the hamular process of the squamosal is quite wide and reaches the mastoid bone. The lambdoid ridge is very evident. The basioccipital is broad and has a trapezoid shape, it shows a medial spine that extends to the basioccipital—basisphenoid suture. The mastoid (the periotic capsule of the petrosal) is square-shaped with a small mastoid fenestra and a recognizable mastoid-occipital opening. The occipital condyle is noticeable in dorsal view, the paraoccipital process is very conspicuous.

The upper incisors display a slightly opistodont orientation. The tooth topography follows a pentalofodont pattern. The M2 presents very evident anteroloph, paracone, mesoloph, metacone, and posteroloph. The ventral margin of the mandible is softly concave, the diastema is short. The capsular process is absent. The coronoid process is long and is higher than the condyle process, forming a deep and concave sigmoid notch. The condylar process is rounded and extends behind the angular process which has a slightly deep angular notch.

Figure A8 Dorsal, ventral and lateral views of the cranium and the mandible of *Phyllotis occidens* (MUSM 50020)

Appendix E. Factor loadings on the first three axes of a principal component analysis for adult specimens of *Akodon mollis, Microryzomys altissimus, Oligoryzomys andinus, Auliscomys pictus, Calomys sorellus, Phyllotis andium, P. occidens and Thomasomys praetor*. Morphological variables that most influence the dispersion of scores are in bold

	Akodon mollis			*Microryzomys altissimus*			*Oligoryzomys altissimus*			*Auliscomys pictus*			*Calomys sorellus*			genus *Phylllotis*			*Thomasomys praetor*		
	PC 1	PC 2	PC 3	PC 1	PC 2	PC 3	PC 1	PC 2	PC 3	PC 1	PC 2	PC 3	PC 1	PC 2	PC 3	PC 1	PC 2	PC 3	PC 1	PC 2	PC 3
CIL	0.10	0.07	-0.03	-0.10	0.13	-0.01	-0.12	0.06	0.12	0.11	0.10	0.08	0.10	-0.11	0.08	-0.11	-0.04	-0.13	-0.07	-0.06	-0.03
ZB	-0.01	-0.08	0.10	0.03	0.03	0.00	-0.02	-0.01	0.00	0.03	0.08	-0.02	-0.03	0.08	-0.06	0.00	-0.04	-0.03	-0.09	0.01	-0.14
BB	**-0.30**	-0.08	-0.02	0.17	0.16	-0.09	**0.29**	0.03	0.01	**-0.28**	0.11	0.12	-0.26	-0.01	0.02	**0.29**	-0.06	-0.01	0.24	-0.16	0.00
IC	**-0.35**	-0.17	**0.43**	**0.61**	-0.11	**0.34**	**0.35**	-0.26	0.00	**-0.46**	0.07	-0.07	**-0.38**	0.18	0.08	**0.47**	-0.12	0.13	**0.36**	-0.05	**0.59**
RL	0.14	0.25	0.04	-0.22	0.12	0.10	-0.24	-0.02	0.20	**0.31**	0.06	0.12	0.27	-0.17	0.15	-0.19	0.00	-0.14	-0.13	0.04	**-0.34**
NL	0.15	**0.43**	0.07	**-0.40**	0.08	0.21	**-0.33**	-0.16	0.19	**0.28**	0.01	0.16	**0.27**	-0.20	0.11	-0.19	0.02	-0.25	-0.07	-0.14	-0.26
RW	0.16	-0.16	0.08	-0.07	**-0.65**	**0.35**	-0.21	**-0.30**	0.09	0.18	**-0.54**	0.24	**0.29**	0.18	0.00	-0.22	0.07	**0.49**	-0.06	0.12	-0.04
RW2	0.09	-0.14	0.13	-0.17	-0.21	-0.01	-0.22	0.07	**-0.51**	-0.07	**-0.33**	0.01	0.10	0.12	-0.03	-0.14	0.18	**0.61**	-0.18	0.18	0.14
OL	-0.01	0.08	-0.18	-0.06	0.08	-0.01	-0.02	-0.02	0.21	0.02	0.14	0.20	0.04	-0.11	0.07	-0.01	-0.10	-0.18	-0.14	-0.19	-0.06
DL	**0.28**	0.21	-0.10	-0.26	0.04	-0.03	-0.17	0.13	0.26	**0.31**	0.15	0.16	0.24	-0.18	**0.34**	-0.27	-0.22	-0.21	-0.27	0.02	-0.01
MTRL	**-0.27**	-0.04	-0.02	0.22	0.05	-0.14	**0.35**	0.19	0.00	**-0.32**	-0.05	0.18	**-0.32**	-0.15	-0.03	0.23	0.23	-0.05	0.11	-0.26	0.12
IFL	0.25	**0.31**	-0.25	-0.17	0.24	-0.09	-0.09	**0.33**	**0.45**	0.23	0.02	0.22	0.19	-0.18	0.26	-0.23	-0.18	**-0.30**	**-0.28**	-0.19	-0.04
AW	0.00	-0.21	0.18	0.01	0.12	0.02	0.21	**-0.27**	-0.18	-0.10	-0.08	-0.17	-0.03	0.25	-0.07	0.09	-0.03	0.11	**0.31**	0.14	0.18
BPB	**0.40**	-0.12	**0.51**	-0.22	-0.01	0.28	-0.01	**-0.61**	-0.10	0.20	**-0.40**	**-0.66**	0.19	**0.76**	-0.08	**-0.28**	**-0.48**	0.26	**0.33**	**0.73**	**-0.32**
OCW	-0.28	0.00	0.00	0.13	**0.28**	**-0.29**	0.16	0.11	-0.03	-0.25	0.05	0.21	**-0.30**	-0.11	-0.09	0.23	0.01	-0.03	0.25	-0.09	0.09
ZP	0.26	**-0.64**	**-0.53**	-0.01	**-0.52**	**-0.71**	**-0.41**	**0.29**	**-0.51**	0.21	**0.59**	**-0.38**	0.20	-0.27	**-0.85**	-0.25	0.75	-0.15	**-0.53**	**0.33**	**0.45**
CD	**-0.33**	0.13	**-0.23**	0.21	0.18	-0.03	0.24	0.19	-0.02	-0.20	0.01	-0.16	**-0.27**	-0.02	0.01	**0.31**	0.06	-0.03	0.15	-0.18	-0.18
HBC	-0.26	0.14	-0.19	**0.29**	-0.02	0.12	**0.27**	0.26	-0.17	-0.19	0.01	-0.22	**-0.31**	-0.07	0.09	0.26	-0.04	-0.09	0.07	-0.25	-0.14
Eigenvalue	1.02E-03	8.55E-04	5.62E-04	1.31E-03	7.39E-04	4.59E-04	1.12E-03	4.90E-04	4.75E-04	2.48E-03	7.66E-04	6.46E-04	1.11E-03	5.83E-04	5.28E-04	1.52E-03	5.81E-04	4.59E-04	2.81E-03	1.60E-03	6.99E-04
% variance	23.33	19.53	12.83	30.55	17.18	10.67	29.13	12.76	12.38	44.38	13.72	11.57	28.63	15.05	13.64	34.67	13.24	10.46	41.80	23.78	10.41

4. SYNTHESIS, RECOMMENDATIONS AND FUTURE PERSPECTIVE

The Ph.D. thesis has been divided into two chapters. The first discloses general aspects about the communities of small non-volant mammals in the Andean region. The second shows the morphological and genetic variation in a community of sigmodontinae rodents in the high Andes of the department of Ancash in Peru. At the end of this thesis, I was able to compile and organize an extensive database to obtain the best information on the distribution of Andean species and combine results obtained from morphological/morphometric and genomic data to interpretthe Andean geography.

The first chapter is subdivided into two sections. In the first section, I present the most complete dataset of non-volant small mammal species of the Andes. The one that was published (see Rengifo et al, 2022). Although it is improbable for different studies to standardize their sampling design, I strongly recommend that for future sampling efforts, all sampling methods, including trapping design, effort, and capture success, should be properly informed, to allow relevant comparisons when necessary. I expect that this dataset will be used for several purposes, for instance, to identify gaps of knowledge and local fauna that has been adequately sampled, and to recognize potential areas to guide future sampling efforts. The present contribution could also guide the design of strategies for conserving non-volant small mammals or even prompt research into macroecological and biogeographical patterns of the Andes. The other one is the first research that uses a very accurate database of Andean sigmodontinae rodents to identify areas of endemism. In addition, this research is one of the few that use NDM/VNDM for the Andes region; I would like that it to serve as an example in initiatives in other taxa; in this way, I recommend it to other researchers who study fauna and flora to continue with this type of analysis, to refute or accept the areas of endemism presented here.

The second chapter has as characteristic the use and integration of different methods, classical morphological/morphometric analysis, with modern methods as the application of ddRAD-seq technology; in this way, my data represent a robust result because both classical and modern methods were very congruent. Given the results, the main conclusion was that the mountain chain does not represent a barrier for the species of sigmodontine rodents; on the contrary, the Santa River is the one that promotes the population structuring of the species, demographic data applied to the genus *Akodon* and *Phyllotis* show that the divergence between populations coincides with the uplift of the Cordillera Blanca. This is a significant contribution, because currently public policies in the Peruvian state in the environmental field are evolving, with the opening of new conservation strategies, using the integration of scientific knowledge in decision-making. In this way, this work could be an example for other taxonomic groups and other geographic areas that need strategic conservation planning.

My perspective is to continue working on these data. For the first chapter, at less two contributions could to published, one that shows the updated distributions of sigmodontinae rodents in the Andes and another that covers the areas of endemism found in this study. The second chapter also has a high potential to be published; the data is robust and can be improved by including other analyses or increasing samples. Likewise, the data give the option of carrying out conservation genetics analysis, which would be interesting given that a large part of the study area is located in a protected natural area, "Huascaran National Park".