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VOLUME 1

BIOLOGY OF CAVIOMORPH RODENTS: DIVERSITY AND EVOLUTION

BIOLOGÍA DE LOS ROEDORES CAVIOMORFOS: DIVERSIDAD Y EVOLUCIÓN

Aldo Ivan Vassallo and **Daniel Antenucci**, EDITORS

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Biology of Caviomorph Rodents:
Diversity and Evolution

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In 2013, during the Annual Assembly of SAREM in the city of Mar del Plata, Dr. Mariano Merino, then President of the Society, together with the rest of the Directive Committee, announced the launch of a new editorial Project: **SAREM Series A: Mammalogical Research (Investigaciones Mastozoológicas).** The goal of this publication was to be the dissemination of scientific works on Neotropical mammals from wide and varied perspectives (evolutionary history, systematics, paleontology, biogeography, morphology, ecology, physiology, etology, conservation, genetics, etc.) aimed at a public formed by the mammalogy research community, graduates, students and other interested readers, at both national and international levels.

With this first book, *Biology of Caviomorph Rodents: Diversity and Evolution*, SAREM inaugurates the publication of novel works of a different nature compared to those already published in the journal Mastozoología Neotropical (Neotropical Mammalogy). In this series, each volumen will be dedicated to a specific subject, be it a particular taxon (*e.g.*, taxonomy of caviomorphs, marsupials, carnivores, primates, etc.) or discipline (*e.g.*, ecology of small mammals, conservation, etc.). This series is meant to allow publication of unpublished works and revisions resulting from scientific meetings, symposia or workshops, so that they may achieve wide distribution in the international scientific community.

It is our hope that this new series becomes a tool for further development of studies of mammals, one that can be used by the mammalogical community with the unwavering purpose of promoting the knowledge and dissemination of mammalogy in South America.

Dr. Emma Carolina Vieytes
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Foreword

The Caviomorpha is the most diverse clade of rodents when viewed by overall bauplan, and is by far the most species rich among any of its fellowhystricomorphous or hystricognathous cousins. No other group of rodents, or other mammalian lineage, can boast the body size diversity exhibited by caviomorphs through time –one covering five orders of magnitude, from ~100 g in the living octodontid *Spalacopus* to nearly a metric ton in the extinct dinomyid †*Josephoartigasia*. Nor does any other rodent group encompass the array of social and mating systems ofextant caviomorphs. Confined to the Neotropical Realm (with the single exception of the Nearctic porcupine, *Erethizon*), and distributed across every terrestrial biome from sealevel to well above treeline in the high Andes, and from rainforest to desert, the Caviomorpha is also among the oldest of all rodent groups,one represented byperhaps the best fossil record of any.

This wonderfully disparate assemblage is brought to life through the chapters in this volume, contributions by scholars who know these animals intimately, and from long personal experience in the field and/or in the laboratory. All have spent decadespicking fossils from matrix, handling live animals caught in traps, measuring physiological parameters, making direct or indirect observations, or examining specimens in the museum. As editors Vassallo and Antenucci note in their Introduction, this volume was conceived as "a new synthesis or integration ... made from different disciplines." As promised, both the individual and combined chapters do, indeed, provide the key overviews of current knowledge while also offering new insights into evolutionary history and diversification. In doing so, this volume constructsthe platform upon which the next generation of studies can, and will, be built.

My own introduction to the Caviomorpha began in graduate school when I took a seminar from George Gaylord Simpson, doyen of mammalian paleontology and anadvocate of "sweepstakes routes" and "waif dispersal" as fundamental principlesunderlying biogeographic pattern. This course coincided, in the mid-1960s, with the discovery of sea-floor spreading and, through a developing understanding of global plate tectonics, the re-wakening of Alfred Wegener's long discounted theory of continental drift. Today, one cannot doubt but that caviomorph entry into South America, from Africa, was promoted by plate dynamics, or that their subsequent diversification elegantly illustrates the "splendid isolation" of that continent championed by Simpson. At the very end of my graduate studies, I had the chance to experience caviormorph diversity first-hand in the eastern lowlands of Peru. Here I had my initial encounter with rainforest taxa like prehensile-tailed porcupines, pacas, agoutis, acouchis, and especially the bewildering diversity of spiny rats. It was also herewhere I became mesmerized by the staccato calls of bamboo rats at night along the river. My experiences with caviormorphs expanded in subsequent decades, during fieldwork centered in Amazonia but also ranging from the Patagonian steppe and *Nothofagus* forests of southern Argentina, through the Altiplano of Peru, and into the Atlantic Forest and Cerrado of Brazil. Much of my research passion over these decades, begun with that first experience in Peru, remained focused on diversification pattern and process among the highly speciose Echimyidae.

In their introduction, Vassallo and Antenucci detail the focus and primary coverage of each of the 10 contributions that follow. To their words, I offer a few of my own.

Vucetich and her co-authors, in Chapter 1, describe the tempo and mode of the fossil history of caviomorphs, and in so doing provide the critical backdrop to the queries of all interested in caviomorph diversity, no matter thespecific discipline. Many will immediately recognize the categorical placement of some of the superbly preserved skulls and teeth that are illustrated, or will otherwise marvel over those not so clearly recognizable. These authors importantly, and clearly, point to connections between fossil lineages and extant taxa, but also identify those either suspect or without an as yet firm understanding. While reading this contribution, I was reminded what my friend and Berkeley colleague, the late Vincent Sarich, often stated. Vince was one of the first molecular phylogeneticists to reconstruct rodent phylogeny, including that of caviomorphs. In discussions of the often-observedconflict between relationships posited from the fossil record and the molecular trees then being drawn, Vince would remind one, with his usual forceful candor: "we are certain that molecules had ancestors, but we can only hope that fossils had descendants." As Vucetich *et al.* demonstrate, many of the fossil taxa now known during the long and rich history of caviomorphs in South American clearly did leave off spring.

Both Upham and Patterson (Chapter 2) and Ojeda and colleagues (Chapter 3) illustrate the geographic pattern of extant taxon density, overall centered in the humid Amazonian and Atlantic forests but with each major clade exhibiting its own unique distribution pattern. While the former largely focuses on the timing and pattern of lineage diversification, the latter dissects current functional ecology, from range sizes and substrates to feeding niches. Rocha-Barbosa *et al.* (Chapter 4) and Morgan (Chapter 5) expand on Ojeda et alia's ecological perspective by incorporating, respectively, an ecomorphological locomotory axis and a functional shape analysis of postcranial elements to caviomorph diversification, the first noting in particular the numerous parallels with various small-bodied cervoid or bovoid lineages in paleo-tropical systems. And Álvarez and colleagues (Chapter 6) examine the primacy of a food axis through the combinatory lens of incisor structure, cheektooth specialization, and the craniomandibular masticatory apparatus, also employing a functional biomechanical approach and emphasizing constraint and opportunity driven by diversity in habitusand social system.

These first six chapters cover evolutionary history, phyletic relationships, and diversification, in bothecological and functional character contexts. The last four chapters zero in on the"non hard part" components of the living animals. These include social system (Herrera, Chapter 7) and energetics (Luna *et al*., Chapter 8), both as sets of adaptations importantly placed in the context of costs relative to diet, habitat, and sociality. MacManes *et al*. (Chapter 9) tie population parameters, like demography and demographic history, to social system ecology as well as to population genetic diversity in functional gene complexes, such as the MHC system. They show how high-throughput sequencing technology will revolutionize our ability to uncover the genetic basis of behavioral and/or ecological differences and commonalities, be these allelic changes in structural genes or those involving upstream or downstream regulation that underlietiming shifts in gene expression. While not explicitly covered, these same technologies will be equally critical in elucidating the genetic basis of functional-morphological adaptations, such as tooth crown height and occlusal surface changes, thus tying explicit genes and their control to the key innovations that drove caviomorph diversification.

Most of the chapters in the book are introspective, in that each focuses on diversity and disparity within the caviormoph lineage itself. The final contribution, that of Zapata and colleagues (Chapter 10), however, views caviomorphs vis-a-vis their pivotal role in structuring the communities in which they exist, in this case by regulating and sustaining the ecological diversity of their predators.We learn, for example, how caviomorph species in local communities not only support a diverse predator base but alsoinfluence trophic guildstructure. These observations, combined with those developed especially in Chapter 3, show how caviomorphs have both top-down and bottom-up influences on the larger communities, biotic and abiotic, in which they are members.

My own area of expertise is in systematics, which I define following G.G. Simpson as "the study of the diversity of life," a broadened view that provides the conceptual framework binding this volume together. I thus end by emphasizing two essential elements of Upham and Patterson's expansive presentation of caviomorph molecular phylogenetics. First, their analysis covers almost all extant genera for the first time, including those largely known only from a few, long-ago collected museum specimens. Their phyletic hypotheses will serve as the baseline for all future studies where phylogenetic inference is essential, even if not all nodes in the caviomorph tree are as yet firmly established. And, I especially encourage those who wish to unravel the diversification history of any and all modern South American groups, be these mammal or not, to reflect on Fig. 6 and the accompanying text, which integrate available information on the tectonic, landscape, and climate histories of South America from the Eocene to the present. Even if there remains much to understand of these separate histories, we should all remember that associations of taxa with the biomes of today, includingboth current composition and geographic placement, must be viewed within the context of a dynamic history involving many axes rather than through the myopic view of a single history static overboth time and space.

This is a rich volume, with state-of-the-art data presentations and analyses, and both thorough and substantive summaries of current knowledge. In its scope and coverage, therefore, this treatise truly does justice to the exceptionally diverse group that is the Caviomorpha.

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CAVIOMORPH RODENTS: AN INTRODUCTION

ROEDORES CAVIOMORFOS: UNA INTRODUCCIÓN

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Aims and scope

This book covers aspects of the evolutionary history and adaptive diversity of a group of rodents known as caviomorphs, one of whose main features is that they evolved in South America, where their common ancestor probably arrived from Africa. But in addition to focusing on a particular group of animals, this book aims to address general issues related to evolutionary biology. We asked the following question: what light may the study of caviomorphs shed on ecological evolutionary processes? Evolutionary biology is perhaps one of the most integrative fields in biology, as it draws on disciplines such as morphology, ecology, genetics, physiology, behavior, and biogeography. Thus, studying a particular taxonomic group while integrating different disciplines could help to answer more general questions concerning evolution.

By themselves, rodents are extremely diverse, including more than 2000 living species, thus constituting the most speciose mammalian order. In addition to the numerical contribution to the large number of species included in the Order Rodentia, caviomorphs also encompass a huge range of adaptive diversity. This diversity is probably the outcome of the ability of this group to respond to environmental challenges with very different morphological, physiological, and behavioral adaptations, which have given rise to a great diversity of ecological niches.The extent of these adaptations seems to surpass *qualitatively* the level of those that occur not only in other rodent groups, but also in other groups of mammals.This leads to the fact that the popular image, or physiognomy of a *typical* rodent (*e.g.*, *Rattus*; *Mus*; squirrel) differs greatly from that of a mara, capybara, or tuco-tuco. Currently, the study of the diversity and evolution of a particular group of organisms may be approached by very different disciplines with their particular methodologies, which permit answering increasingly narrow questions. However, it has been said that species evolve as a whole, responding in some way with all their phenotypic and genotypic baggage. One can hardly wonder about the adaptive value of a particular trait isolated and detached from the rest of the features of the species. In this book we have gathered several works on the biology of caviomorph rodents because in our opinion, knowledge of them has advanced significantly in the last two decades. Thus, we believe it is time to attempt a new synthesis or integration of the contributions made from different disciplines. We want to mention here the excellent book "The biology of hystricomorph rodents" (1974), edited by Barbara Weir and Idwal W. Rowlands, which is one of the most important background works on this group of rodents.

The Order Rodentia

A brief account of our current knowledge about the origin of this order is necessary to set the stage for the study of caviomorphs. Most of the 33 families of rodents (Wilson and Reeder, 2005) appeared as part of rapid cladogenesis during the late Eocene. The ischyromyids, extinct North American forms from the late Paleocene, are considered basal rodents; the genus *Paramys* would be one of these extinct basal forms (Kemp, 2004).These forms have the typical rodent dentition comprising two incisors in each jaw, with a layer of enamel on the labial side.This family diversified during the Eocene in North America, Eurasia and Africa and is probably the stem group of the infraorders Sciuromorpha (squirrels) and Myomorpha (mice). According to Kemp (2004, and references therein, see also Antoine *et al.,* 2011), the primitive genus *Cocomys* from China has dental affinities with the third major rodent infraorder, Hystricomorpha. A recent analysis based on extant species and using molecular characters (Fabre *et al.,* 2012; fig. 3 in Antoine *et al.*, 2011; Fig. 1) shows results largely consistent with those based on dental

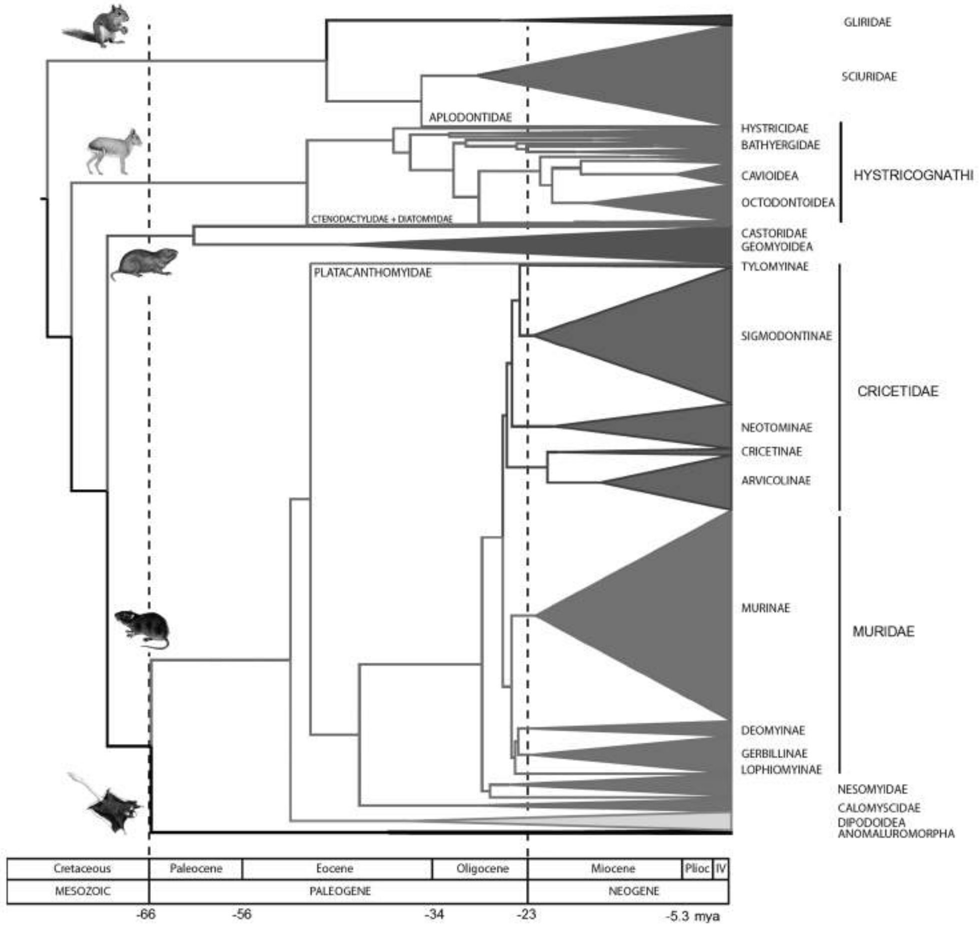

Figure 1. Time scale for rodent diversification. Modified from Fabre *et al*. (2012).

characters from extinct forms (*e.g.*, Marivaux *et al.,* 2004). These studies show the existence of three major clades within Rodentia: the squirrel-like clade (Sciuromorpha), the mice-vole clade (Myomorpha), and the clade called Ctenohystrica (Hystricomorpha + Phimorpha [African mole rats, Old World porcupines] + Ctenodactyloidea).

Hystricomorpha, Hystricognathi and Caviomorpha: some terminological issues

The so-called Hystricomorpha rodents have a particular arrangement of the masseteric musculature consisting of the presence of a belly of the masseter muscle, the medial masseter, which passes through the infraorbital foramen (Fig. 2). This belly of the masseter muscle arises from the sides of the anterior portion of the rostrum (the portion where the diastema is situated). Furthermore, the so-called Hystricognathi rodents have a particular condition of the lower jaw in which the angle of the jaw is lateralized with respect to the incisors (Fig. 3) in addition to the hystricomorph condition. This group includes living and extinct African, Asian and South American forms. The latter are known as Caviomorpha (= South American Hystricognathi).

How did caviomorphs originate? The most accepted hypothesis is that they dispersed from Africa to South America, through some kind of strategy that could include the crossing of the sea on floating debris or vegetation. Note that the distance between the two continents at the time this dispersion occurred, 35-41 million years ago, was substantially shorter than the current condition; nevertheless, they had to cross a large body of water (Fig.4). Another hypothesis is reviewed in the study by Huchon and Douzery (2001).

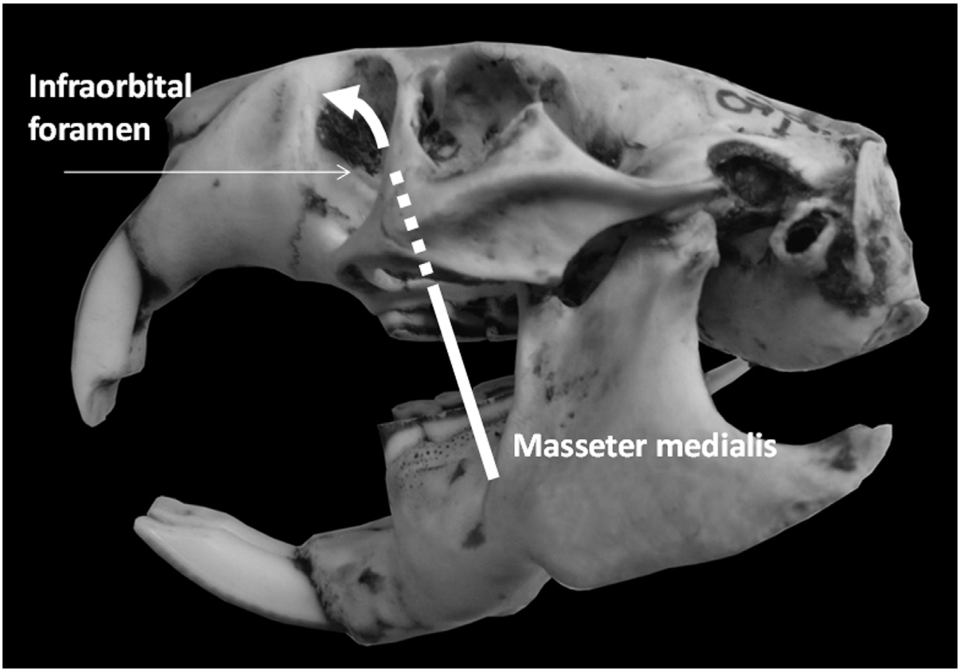

Figure 2. The hystricomorph condition as seen in *Ctenomys.*

The study by Antoine *et al.* (2011) reported the fossil remains of several species of basal caviomorphs, dated 41 million years ago, and belonging to the Yahuarango Formation in Peru. This study represents a backwards shift in the date of appearance of the first forms of caviomorph rodents, suggesting that the arrival and early evolution of the group may have occurred at a time around the Mid-Eocene Climatic Optimum characterized by relatively warm and humid climates, compared with the cooling that characterized the Eocene-Oligocene boundary (approx. 34 Ma). Apparently these animals had small body size (40-120 g) compared to the later body mass diversification experienced by several lineages within the group. According to the authors, the moderate disparity in dental morphological characteristics evidenced by these extinct species suggests that they represent the early stages of group diversification in South America, which subsequently experienced a marked divergence of mandibular morphology and dentition related to very different types of diet and habits (Álvarez *et al.*, this volume).

Just like other groups of typical South American mammals (*e.g.*, xenarthrans; notoungulates), it is often said that caviomorph rodents are *endemic* to this continent (endemism is the ecological state of a species, or a diverging species group, being unique to a defined geographical area). This is because from their arrival from Africa ~40 million years ago, until the formation of the Isthmus of Panama only about 3 million years ago, the caviomorphs experienced, in isolation from other rodent groups, the vast diversification made manifest by both extant and extinct forms. During this extended period South America experienced major changes in its climate, which resulted in the modification of the environmental characteristics of many macro-regions. One of the biggest changes was the increasing aridity and late Miocene global cooling, which particularly affected the south of South America, where open environments evolved. Caviomorphs weathered these environmental changes, generating –through different behavioral strategies and physiological adaptations– new ecological niches for themselves. A recent analysis shows that the two macrohabitats possessing the highest density of species are represented today by the Amazon and the Atlantic Forest (Ojeda *et al.*, this volume).

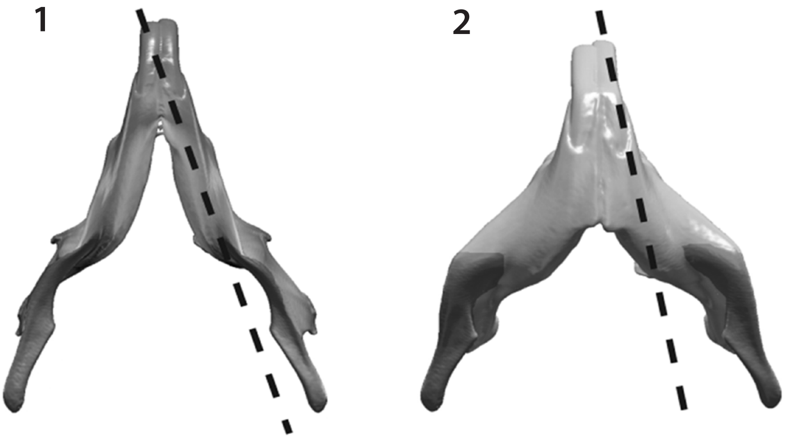

Figure 3. 1. Sciurognath and 2. hystricognath condition. In the former condition the angular process of the jaw (dark grey) almost coincides with a plane passing through the alveoli of the incisors (dotted line). In the second condition the angular process is lateral with respect to that plane. Modified from Hautier *et al.* (2001).

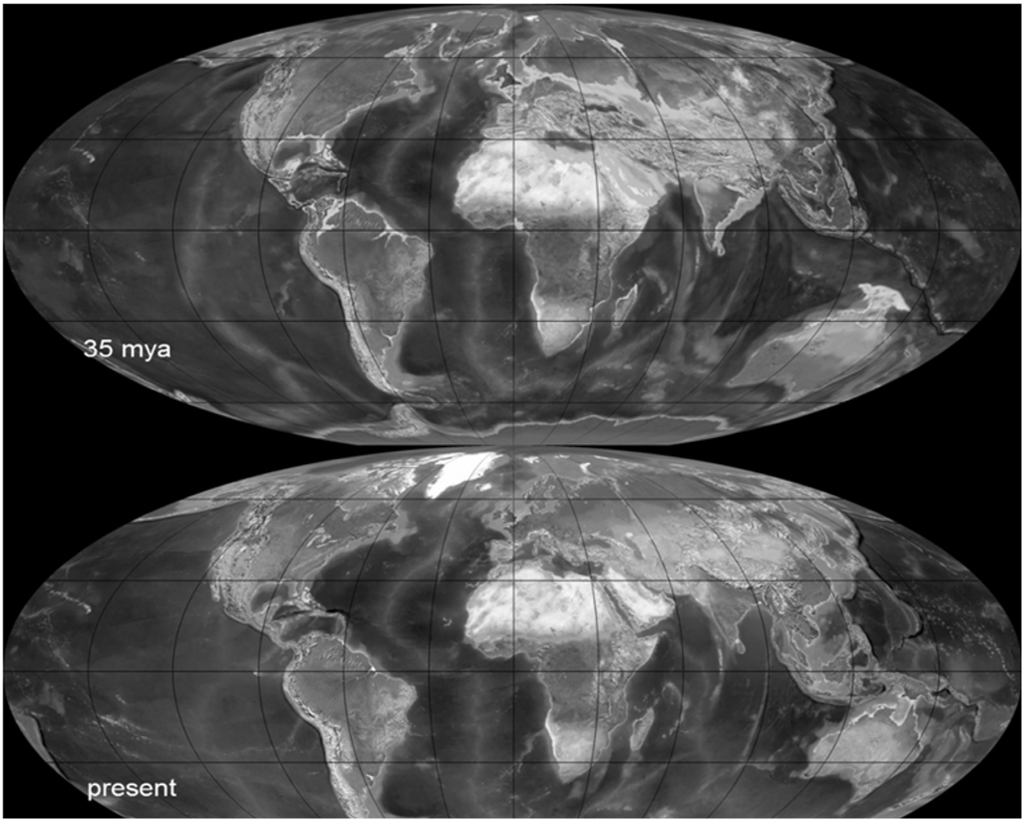

Figure 4. Continental masses at the time of hystricomorph arrival in South America (above) and at present (below). From http://cpgeosystems.com/paleomaps.html, Dr. Ronald Blakey.

Evolutionary comrades

Obviously, no caviomorph group experienced its diversification in isolation from other mammal taxa that either were already present in South America, or arrived later (Fig. 5). They coexisted with other herbivorous mammals, for example the extinct so-called South American ungulates (Meridiungulata), which included larger animals like *Macrauchenia* (Order Litopterna) and *Toxodon* (Order Notoungulata), as well as rodentiform, small-sized genera such as *Paedotherium* and *Pachyrukhos* (Order Notoungulata). Even though eutherian carnivores (*e.g.*, felids, canids, ursids) arrived recently in South America with the formation of the Isthmus of Panama ~3 million years ago, throughout much of their evolutionary history caviomorphs coexisted with several large sized marsupial predators such as *Borhyaena* and *Thylacosmilus*. Caviomorph rodents lived alongside xenarthrans whose main divergence, between sloths, anteaters and armadillos, had already occurred (according to recent dating based on molecular clocks, Delsuc and Douzery, 2008) before the ancestors of caviomorphs arrived in South America. Finally, we should mention the New World monkeys or Platyrrhini, which arrived in South America not long after the caviomorphs. The diversification into five families experienced by this group took place almost in parallel with the diversification of caviomorph rodents (Pérez *et al.*, 2013; Fig. 5).

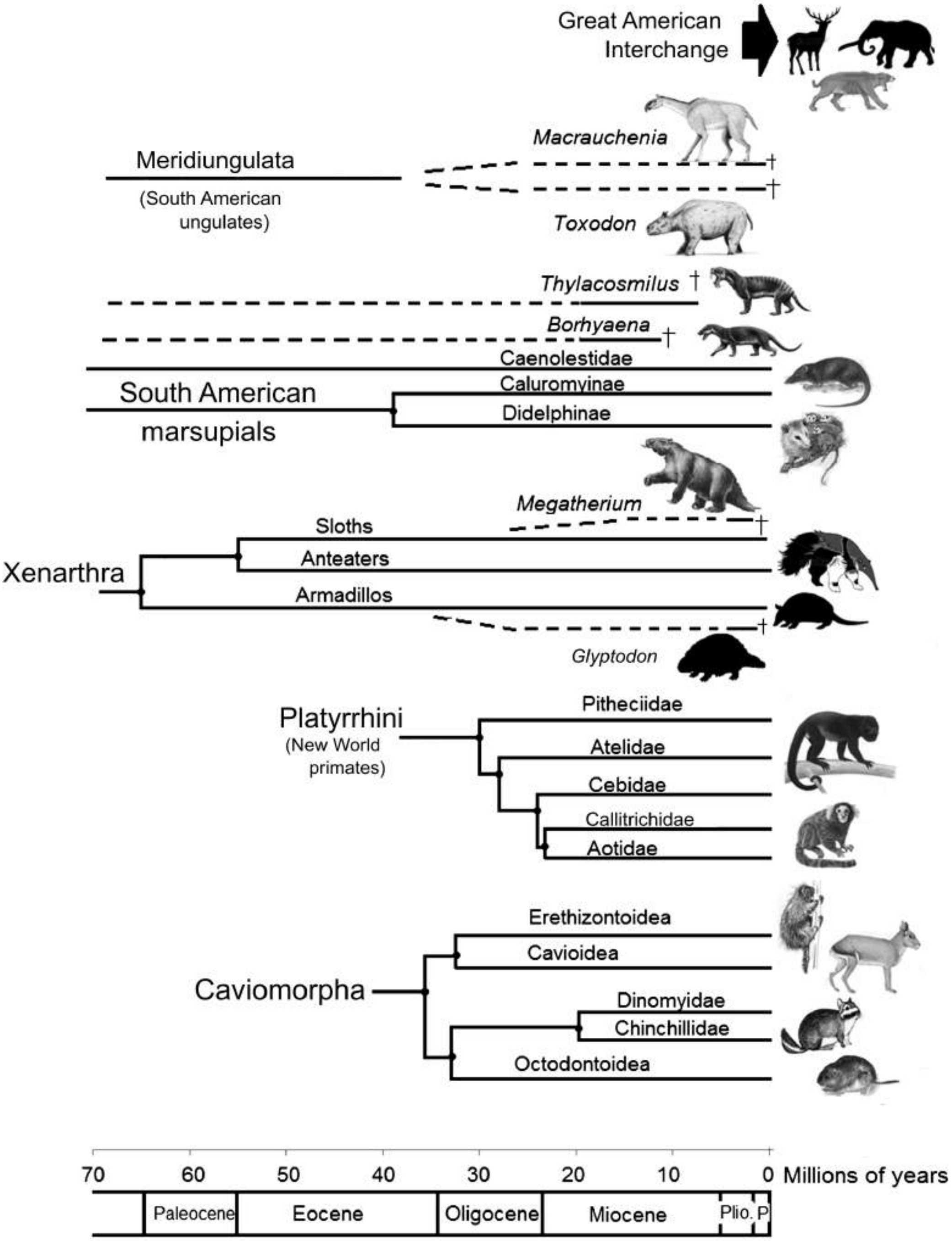

Figure 5. Time scale of the diversification of various lineages of mammals in South America. Based on different sources (Delsuc and Douzery, 2008; Meredith *et al*., 2008; Pérez *et al*., 2013; Upham and Patterson, this volume).

Role in South American ecosystems

Caviomorphs certainly play an important role in the ecological communities of South America. For example, studies have demonstrated the importance of agouti *Dasyprocta leporina* in seed dispersal in the Atlantic forest ecosystems, environments where this species seems to fulfill the role played during the late Pleistocene by extinct frugivorous mammals (Galetti *et al.*, 2010). In this volume, the role of caviomorphs as prey species of carnivorous mammals and raptors is analyzed and discussed thoroughly (Zapata *et al.*, this volume). Among other findings, this chapter shows that the frequency of occurrence of larger-sized species, such as *Hydrochoerus* sp. and *Dasyprocta* sp., in the diets of certain carnivores sometimes exceeds 60%, which clearly indicates their importance as prey. Strikingly, this strong representation in the diets of carnivores and raptors is also observed in forms such as the subterranean genus *Ctenomys* whose peculiar lifestyle would not appear to substantially protect them from predation -rather it is a way to save energy for thermoregulation (for example, Antenucci *et al.*, 2007). It is also surprising that a social lifestyle does not prevent predation when compared with solitary species, and that diurnal social species were found to be more preyed-upon than nocturnal ones.

Locomotion, size, and shape

The body plan of rodents lends to this group an important generalism in terms of the environments that they can inhabit. In general, rodents are able to travel with moderate skill in different habitats. Take, for example, what might be considered a typical representative of the Order Rodentia, *Rattus*. Rats are known to swim well, they are able to climb and dig burrows, and also move fast on land. Some species of rodents are more specialized to particular types of locomotion and habitats. For instance, squirrels (*Sciurus*) are very good climbers, beavers (*Castor*) are very good swimmers, while pocket gophers (*Geomys*) are excellent diggers. However, caviomorphs seem to have reached even greater ecological diversification, which is reflected largely in the structure of their postcranial skeleton (Morgan, this volume). No other group of rodents has reached the diversity of body sizes seen in caviomorphs. If we look at the extant forms, this is clear when comparing the body size of a coruro (*Spalacopus cyanus*), whose mass is around 150 g, with a capybara (*Hydrochoerus*), which can weigh up to 60 kg. This diversity becomes even more evident when extinct forms, whose estimated weight is ~700 kg, are taken into account (*e.g.*, † *Josephoartigasia monesi*). Why has this group achieved such disparity in body size? External causes have been invoked, such as the existence of vacant niches because South America had no native modern ungulates (they arrived in South America about 3 million years after the formation of the Isthmus of Panama). However, internal causes, such as the existence of marked size evolvability due to factors regulating size growth during ontogeny (*e.g.,* Berstein *et al.,* 2007), cannot be ruled out.

Many caviomorphs are able to climb, such as the spiny rats (spiny tree-rats, tree-rats, bamboo-rats) and the porcupine (*Coendou*) from Central and South America. When comparing other species, it is clear that evolution led to a dichotomy in limb morphology. In some species the limbs are elongated and hence adapted for speed, while in others they are adapted for strength, in which case they are short and stout. With regard to the ability to achieve fast locomotion, both maras (*Dolichotis*) and pacas (*Cuniculus*) have reached an important degree of specialization that allows them to run fast in the open environments of Patagonia as well as in environments with dense vegetation, showing several convergences with small ungulates (Rocha Barbosa *et al.*, this volume). Strong and robust limbs, on the other hand, are characteristic of swimmers like the semiaquatic coypu (*Myocastor*) and diggers such as the degus (*Octodon*), tuco-tucos (*Ctenomys*), and coruro (*Spalacopus*).

Behavior

The group shows significant diversity in behavioral aspects, particularly in relation to the degree of sociality (Herrera, this volume). There are several different mating systems (*i.e.,* how a group is structured concerning sexual and reproductive behavior) among caviomorph rodents, which include monogamy and communal care of offspring in the case of maras, and solitary behavior and polygyny in the subterranean rodent *Ctenomys*; and polygyny in conjunction with a certain degree of herding in *Cavia pamparum*. Capybaras form stable groups of 10 to 20 individuals of both sexes, which defend a common territory. By contrast, viscachas live in colonies consisting of 1-2 adult males and 1-2 adult females and their young. Females are philopatric, meaning that at the time of natal dispersal they remain in the vicinity of the colony, while males disperse to greater distances.

Genetic and physiological studies

The use of molecular techniques has helped to address quite different questions regarding the biology of caviomorphs. On the one hand, gene sequencing has provided an enormous number of molecular characters which, in conjunction with those provided by the morphological study of current and extinct forms, have enabled the production of robust phylogenies of the different caviomorph lineages at least at high taxonomic levels. The sequencing of other genes has permitted, on the other hand, answering questions about the relationship between intraspecific diversity at the population level, and its relationship to geography, within the framework of a relatively new discipline known as phylogeography. The use of another type of genetic material (*e.g.*, microsatellites) has been helpful in exploring both reproductive behavior (through providing knowledge about the paternity of offspring in natural populations) and the dispersal of individuals, two key demographic issues (Mora *et al.*, 2010; Zenuto *et al.*, 1999). In addition to studies on the evolution of insulin and major histoincompatibility complex genes, caviomorphs provide an interesting model for the implementation of massive sequencing techniques which allow us to address new questions, as shown by MacManes *et al.* (this volume). In this regard, caviomorphs have had the greatest role as study models for physiological research. It would be impossible to describe in this introduction the role of this group, but we wish to take into account merely the quantitative and qualitative importance of its contribution. A search for "guinea pig" –a single caviomorph species– in a popular scientific database, at the time we are writing these lines, yields 12,093 papers. As an example of its physiological distinctiveness, this group of rodents has a divergent insulin structure, as was pointed out by Opazo and coworkers (2005). Insulin in this group of rodents exhibits only 1-10% of biological activity in comparison to other mammals. Therefore, caviomorph rodents may hypothetically be unable to regulate blood glucose concentration in the manner of mammals. Because of their diverse habitat use which includes distinctive adaptive traits, as noted above, caviomorphs occupy very different environments and they show remarkably diverse physiological adaptations. A conspicuous example is represented by the subterranean forms belonging to the genus *Ctenomys*, which has been extensively studied. Other than the morphological adaptations for digging, it shows blood adaptations to hypoxia and hypercapnia, low basal metabolic rates that have been related to avoiding overheating, distinctive chemical and sound communication, etc. Recently, caviomorph genera such as *Octodon* and *Ctenomys* have been used as models for the study of the *stress axis* (*i.e.,* a component of the neuroendocrine system that controls responses to stress and regulates several body processes) both in captivity and in the wild. Studies evaluating the effect of stressors on learning capabilities and the immunological system are being carried out using *Ctenomys,* which represents a promising field of research to understand the biological meaning of stress responses. A chapter on energetics (Luna *et al*., this volume), aims to search for energetic patterns within caviomorph rodents and also explores reproductive patterns within this group.

We hope that this volume can provide a comprehensive overview of the main research lines on caviomorph rodents, and that it promotes interest and enthusiasm in continuing their study.

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1 | A BRIEF HISTORY OF CAVIOMORPH RODENTS AS TOLD BY THE FOSSIL RECORD

BREVE HISTORIA DE LOS ROEDORES CAVIOMORFOS SEGÚN EL REGISTRO FÓSIL

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Abstract. Caviomorph rodents have a very rich fossil record that provided good bases for understanding the major pathways of their evolution, at least in southern South America. The evolution of caviomorphs in intertropical South America is less known, although the knowledge of the Quaternary record has been improved in recent years. In this chapter we analyze this record and describe the most important features of their evolutionary history. The caviomorph ancestors probably entered South America during the middle Eocene by rafting from Africa, and the first steps of their evolution occurred in intertropical areas. The evidence strongly suggests that the initial radiation of caviomorphs was more complex than hitherto postulated, with the differentiation of some taxa that cannot be assigned to any of the major clades in which caviomorphs are classically divided (the superfamilies Octodontoidea, Erethizontoidea, Cavioidea, and Chinchilloidea). Caviomorphs arrived in Patagonia during the latest Eocene or early Oligocene, and by the late Oligocene they were highly diversified, with representatives of the four main lineages. A great morphological disparity, at least in tooth morphology, was then acquired mainly by the development of hypsodonty in several lineages. The early evolution of each of the major clades was also more complex than previously proposed, especially for chinchilloids and octodontoids. The first stages of the evolution of cavioids are more obscure because they are recognized through the relatively derived Deseadan species of Cavioidea *s.s.* Moreover, the steps that led to the differentiation of Dasyproctidae, Cuniculidae and some Oligocene - Miocene forms (*e.g.*, *Neoreomys*), are not known or not well understood yet. One of the most outstanding features of caviomorphs, the development of large size, appears as a complex phenomenon. Large size evolved independently in multiple lines, in what looks to be a coeval coordinated phenomenon.

Resumen. Los roedores caviomorfos poseen un registro paleontológico muy rico que permite establecer los patrones generales de su historia evolutiva, al menos para la parte austral de América del Sur (aproximadamente equivalente a la Subregión Patagónica de Hershkovitz, 1958). El registro de la región intertropical (aproximadamente equivalente a la Subregión Brasílica de Hershkovitz, 1958) es mucho más escaso y solo permite una visión muy limitada sobre la evolución del grupo en esta región, aunque el registro Cuaternario especialmente de Brasil se ha incrementado mucho recientemente. En este capí-

tulo analizamos el registro y describimos los rasgos más importantes de la historia evolutiva del grupo. Los caviomorfos habrían llegado a América del Sur durante el Eoceno medio desde África por medio de balsas naturales. Las primeras etapas de su evolución se habrían desarrollado en la región intertropical. Las evidencias disponibles hasta ahora, tanto provenientes del registro como de análisis filogenéticos con datos morfológicos indican que esta etapa habría sido más compleja de lo supuesto hasta ahora. Los nuevos aportes muestran que se habrían diferenciado taxones que no pueden ser clasificados en ninguno de los clados principales en que clásicamente se ha dividido a los caviomorfos (las superfamilias Octodontoidea, Erethizontoidea, Cavioidea y Chinchilloidea). La evolución temprana de cada uno de estos linajes principales también habría sido muy compleja, al menos para los chinchilloideos y octodontoideos. Las primeras etapas en la evolución de Cavioidea son menos conocidas principalmente porque es necesario resolver las afinidades de los taxones del Eoceno medio-Oligoceno temprano (*e.g.*, *Branisamys*, *Andemys*, etc.) propuestos para esta superfamilia. Sin embargo, análisis recientes focalizados en Cavioidea *sensu stricto* muestran una historia evolutiva compleja para este grupo a través de diferentes pulsos de diversificación, lo cual indicaría una diversidad taxonómica mayor de la conocida hasta ahora. Más aún, los pasos que llevaron a la diferenciación de los otros cavioideos (Dasyproctidae, Cuniculidae y otras formas del Oligoceno-Mioceno como *Neoreomys*), son prácticamente desconocidos. Los caviomorfos habrían llegado a latitudes altas (centro de Chile y Patagonia central) hacia el Eoceno tardío u Oligoceno más temprano. Esta migración quizá se haya visto favorecida por el cambio climático del límite Eoceno-Oligoceno que habría permitido el desarrollo de nuevos ambientes. Hacia el Oligoceno tardío (Edad Mamífero –SALMA por sus siglas en inglés– Deseadense) los caviomorfos ya estaban altamente diferenciados y se pueden reconocer claramente los representantes de las cuatro superfamilias. Los roedores deseadenses muestran una segunda etapa de radiación que es a su vez la primera radiación patagónica. En ellos se manifiesta una alta disparidad morfológica al menos a nivel dentario, que demuestra la adaptación a ambientes y dietas muy distintas. Aparecen, por ejemplo, las primeras especies con dientes de crecimiento contínuo. Durante el Mioceno más temprano (SALMAs Colhuehuapense y "Pinturense") se registra una muy alta diversidad con más de 36 especies. Para este período se conoce una gran diversidad de octodontoideos y corresponde, asimismo, al acmé de los puercoespines. Por otra parte, se registran todavía numerosos taxones que retienen caracteres primitivos, como la presencia del premolar deciduo 3 (DP3) en estadios juveniles. Durante el final del Mioceno temprano, representado por la SALMA Santacrucense, se produce un importante cambio con la reducción en diversidad de los pequeños octodontoideos braquiodontes y los puercoespines, pero con la diversificación de formas euhipsodontas de cavioideos y chinchilloideos. Este incremento de taxones euhipsodontes siguió el cambio climático y la subsecuente expansión de los ambientes abiertos. El Mioceno medio es un período relativamente poco representado, pero de singular importancia en la evolución de los caviomorfos ya que implica una modernización del grupo: se extinguen numerosos linajes antiguos, pero se desarrollan muchos linajes (familias y subfamilias) que tienen representantes vivientes como Caviinae, Dolichotinae e Hydrochoerinae. El Mioceno tardío (SALMAs Chasiquense y Huayqueriense) está muy bien representado en Argentina central y norte. Muchos linajes modernos tienen su primer registro o se hacen abundantes en este lapso. Los octodontoideos se hacen muy abundantes y diversos, representados por taxones claramente asociados a linajes con representantes vivientes, como el equímido *Theridomysops* estrechamente relacionado a *Clyomys* y *Euryzygomatomys*, o *Protabrocoma*, estrechamente relacionado a *Abrocoma*. Los octodóntidos y los hidroquerinos en particular son muy diversos. Un rasgo muy destacado es el registro detallado de etapas sucesivas en la adquisición de la hipsodoncia en varios linajes de octodontoideos provenientes de la Formación Cerro Azul en la provincia de La Pampa. Este es uno de los mejores ejemplos del desarrollo de la hipsodoncia en el que se observa claramente el cambio morfológico y la

modificación del *schmelzmuster* (distribución espacial de los tipos de esmalte) asociado al progresivo aumento de la altura de la corona. Se registra en este período el acmé de los dinómidos y es también el comienzo del período de gigantismo en los caviomorfos. Durante el Plioceno los caviomorfos del centro de Argentina experimentaron un fuerte empobrecimiento dado por la reducción en diversidad de los Dinomyidae y la extinción local de "Echimyidae" y Erethizontidae y la extinción de los Neoepiblemidae. Este cambio fue probablemente inducido por cambios climáticos y por el impacto producido por la llegada de los mamíferos holárticos participantes del Gran Intercambio Biótico Americano (GABI por sus siglas en inglés). Durante el Pleistoceno queda establecida la composición taxonómica de las faunas de roedores de Argentina, y solamente se observan fluctuaciones en la distribución geográfica de algunos taxones, en respuesta a las oscilaciones climáticas de los períodos glaciales e interglaciales. El registro intertropical es mucho más pobre, pero muestra el desarrollo de algunos linajes exclusivos de esta área, observado por ejemplo, en la fauna de La Venta, Colombia, referida al Mioceno medio. Asimismo, las faunas cuaternarias de Brasil muestran la supervivencia de linajes ya extintos en latitudes más altas por ejemplo, entre los octodontoideos el extinto *Dicolpomys* y los mismos *Clyomys* y *Euryzygomatomys*, así como los últimos dinómidos probablemente relacionados a los gigantes del Mio-Plioceno. Uno de los rasgos interesantes en la evolución de los caviomorfos es el desarrollo de numerosas formas grandes hasta alcanzar en algunos casos tamaños gigantescos para el Orden Rodentia. Este parece haber sido un fenómeno complejo ya que apareció paralelamente y en forma simultánea en todos los linajes principales.

Introduction

Caviomorphs are part of a rich rodent clade, the Ctenohystrica Houchon *et al.* (2000), differentiated in the early Eocene, which are recorded in Asia, Africa and more marginally in Europe (Houchon and Douzery, 2001; Sallam *et al.*, 2011). Caviomorphs reached South America probably during the middle Eocene perhaps synchronously with platyrrhine primates (Frailey and Campbell, 2004; Poux *et al.*, 2006; Vucetich *et al.*, 2010a; Bertrand *et al.*, 2012; Bond *et al.*, 2015). Since then, caviomorphs became one of the most important South American groups of mammals concerning their richness and diversity, particularly since the Oligocene.

Although some authors questioned the monophyly of caviomorphs (Woods, 1982; Bryant and McKenna, 1995; Candela, 1999; Coster *et al.*, 2010), data provided by molecular and morphological phylogenies support this group as monophyletic (Houchon *et al.*, 2000; Houchon and Douzery, 2001; Fabre *et al.*, 2012; Arnal *et al.*, 2014), and suggest an early? or middle? Eocene age for the moment of their differentiation from their African relatives (Poux *et al.*, 2006; Antoine *et al.*, 2012; Fabre *et al.*, 2012).

Living representatives occupy very different environments, from rain forests to puna deserts, and display a great variety of habits such as fossorial, arboreal, riparian and semiaquatic, and a great morphological disparity (Mares and Ojeda, 1982 ; Patton *et al.*, 2015). Living caviomorphs are grouped without difficulty within the four main clades classically recognized, namely the superfamilies Erethizontoidea (New World porcupines, =Erethizontidae for the purpose of this paper), Cavioidea (cavies, maras, mocos, capybaras and pacas), Octodontoidea (spiny rats, tuco-tucos, degus, coypus, and chinchilla rats), and Chinchilloidea (chinchillas, viscachas, and pacaranas) (see Simpson, 1945; Upham and Patterson, this volume). Their present distribution matches Hershkovitz's (1958; Fig. 1) main biogeographical subdivisons, with some groups restricted to the Patagonian Subregion (Chinchillidae, Octodontidae, Ctenomyidae, Abrocomidae), and others to the Brazilian Subregion [Dasyproctidae, Dinomyidae, Erethizontidae, and "Echimyidae" (quotation marks for Echimyidae are due to the disparate results of internal relationships in phylogenetic analyses; *e.g.*, Carvalho and Salles, 2004; Arnal *et al.*, 2014; Loss *et al.*, 2014; Verzi *et al.*, 2014; Arnal and Vucetich, in press; Upham and Patterson, this volume)]. But when the extinct taxa are included in the study, this systematic arrangement becomes less clear (Arnal, 2012; Antoine *et al.*, 2012; Arnal *et al.*, 2014; Vucetich *et al.*, 2014c), and the geographic distribution of taxa changes substantially, with almost all of the "Brazilian" lineages (*e.g.*, Erethizontidae, "Echimyidae") being represented up to southern Patagonia.

Some features that differentiate caviomorphs from other rodent clades are the great variety of adaptive types achieved along their history (Mares and Ojeda, 1982), the development of gigantic sizes, and the widespread and repetitive development of hypsodonty. In this chapter, the most important features of their evolution in South America will be analyzed through the evidence provided by the fossil record, with attention to the evolution of size and hypsodonty.

Geographic and temporal context

The Cenozoic South American record of continental mammals has a strong geographical bias. Most mammal-bearing localities are found in the southern half of the continent (approximately corresponding with the Patagonian Subregion *sensu* Hershkovitz, 1958). Moreover, Oligocene-early Miocene faunas come mostly from Patagonia (Fig. 1.1), whereas late Miocene-Pliocene faunas come from central to northern Argentina (Fig. 1.2). In northern South America (approximately coincident with the Brazilian Subregion *sensu* Hershkovitz, 1958; Fig. 1) the record is, in contrast, much poorer. This obviously results in a better knowledge of the evolutionary history of austral groups, and therefore of the differentiation, rhythms of evolution, and modes of adaptation of mammals to increasingly unfavorable climatic conditions throughout the Cenozoic, which is expressed more intensely in the southern part of the continent (Le Roux, 2012). Meanwhile, the paleontological record only gives a hint of the evolution of the rich Neotropical rodent fauna through the record in a few localities, especially in Brazil, Peru, and Colombia (Fig. 1). Thus, the knowledge of the history of the taxa currently living in the Brazilian Subregion has to be analyzed mostly on the basis of neontological data. This bias of the record has been reflected in several papers on the evolution of South American mammals (Pascual *et al.*, 1996; Ortiz-Jaureguizar and Cladera, 2006), and specifically of caviomorphs (Pérez and Pol, 2012). In this contribution, the Miocene-Holocene record of the Brazilian Subregion is described separately.

The temporal calibration of the continental Cenozoic of South America (Fig. 2) follows Dunn *et al.* (2013) for the Paleogene and early Neogene, Fleagle *et al.* (2012) and Deschamps *et al.* (2013 and literature therein) for the late Miocene-Pliocene, and Soibelzon *et al.* (2009) for the Quaternary. For the subdivision of the Cenozoic, here we followed the concept of land mammal ages (in our case, South American land mammal ages, SALMAs). "Land mammal ages subdivide geological epochs by recognizing distinctive assemblages of mammal species, each of which characterize a certain span of geological time" (Barnosky *et al.*, 2014: 2). Thus, these units are intervals of time as represented by fossils, based on mammalian evolution. In the current practice they are considered as biochronologic units (Woodbourne, 2004; Barnosky *et al.*, 2014).

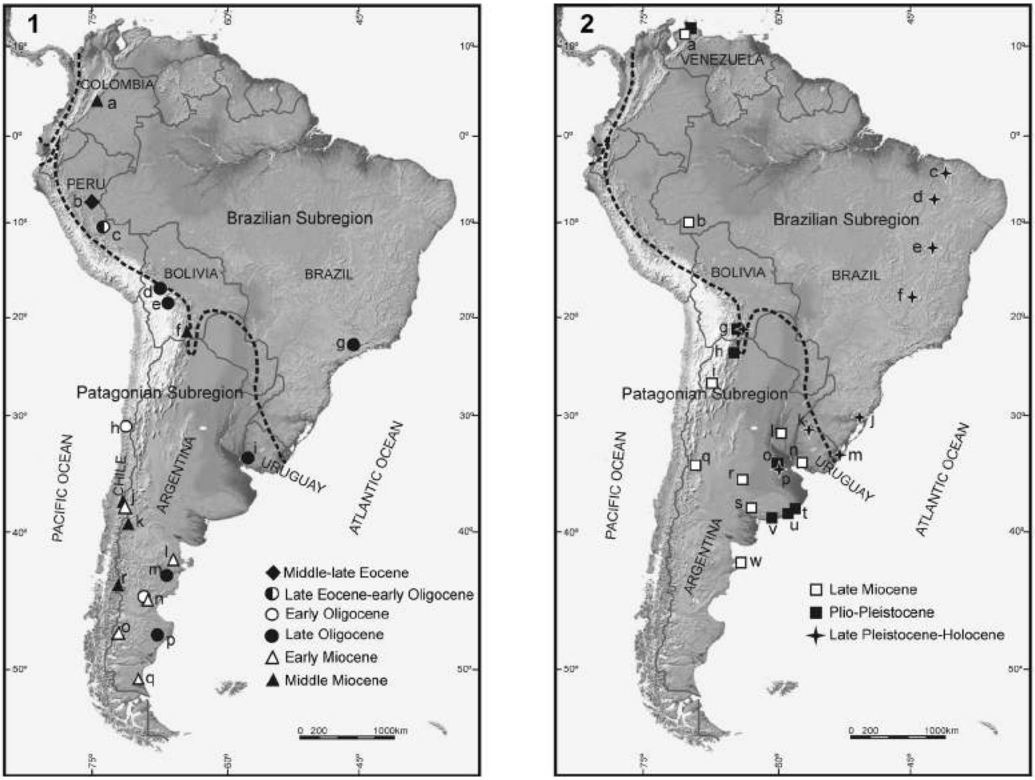


Figure 1. 1. Geographic distribution of most important Eocene-Middle Miocene and 2. Late Miocene-Holocene localities bearing fossil rodents. Dashed line, division between Brazilian and Patagonian subregions (Hershkovitz, 1958). 1. a, La Venta; b, Contamana; c, Santa Rosa; d, Salla-Luribay; e, Lacayani; f, Quebrada Honda; g, Taubaté Basin; h, Tinguiririca; i, Nueva Palmira; j, Laguna del Laja; k, Cañadón del Tordillo; l, Bryn Gwyn; m, Cabeza Blanca; n, Gran Barranca; o, Río Pinturas ; p, La Flecha; q, Río Santa Cruz and coastal area; r, Río Cisnes. 2. a, Urumaco; b, Acre region; c, Ubajara; d, Serra do Capivara; e, Caves of Bahia; f, Lagoa Santa; g, Tarija Valley; h, Uquía; i, Valle de Santa María; j, Río Grande do Sul; k, Sopas Formation, N Uruguay; l, Barrancas del Paraná; m, Chui Creek; n, Barrancas de San Gregorio; o, Toscas del Río de La Plata; p, Río Luján; q, Huayquerías de San Carlos; r, La Pampa (several localities); s, Arroyo Chasicó; t, Chapadmalal area; u, Necochea; v, Monte Hermoso; w, Rincón Chico, Península Valdés.

The fossil record

The oldest records

The oldest caviomorphs come from Peru [Contamana (Antoine *et al.*, 2012) and Santa Rosa (Frailey and Campbell, 2004)], Chile (Tinguiririca; Bertand *et al.*, 2012), and Argentina (La Cantera at Gran Barranca; Vucetich *et al.*, 2010c) (Fig. 1.1). The La Cantera fauna is likely between 30.77 and 30.617 Ma (Dunn *et al.*, 2013), whereas the Tinguiririca fauna is associated with tuffs with 40Ar/39Ar dates of 31.65 ± 0.32 Ma and 31.34 ± 0.17 Ma (Wyss *et al.*, 1993;

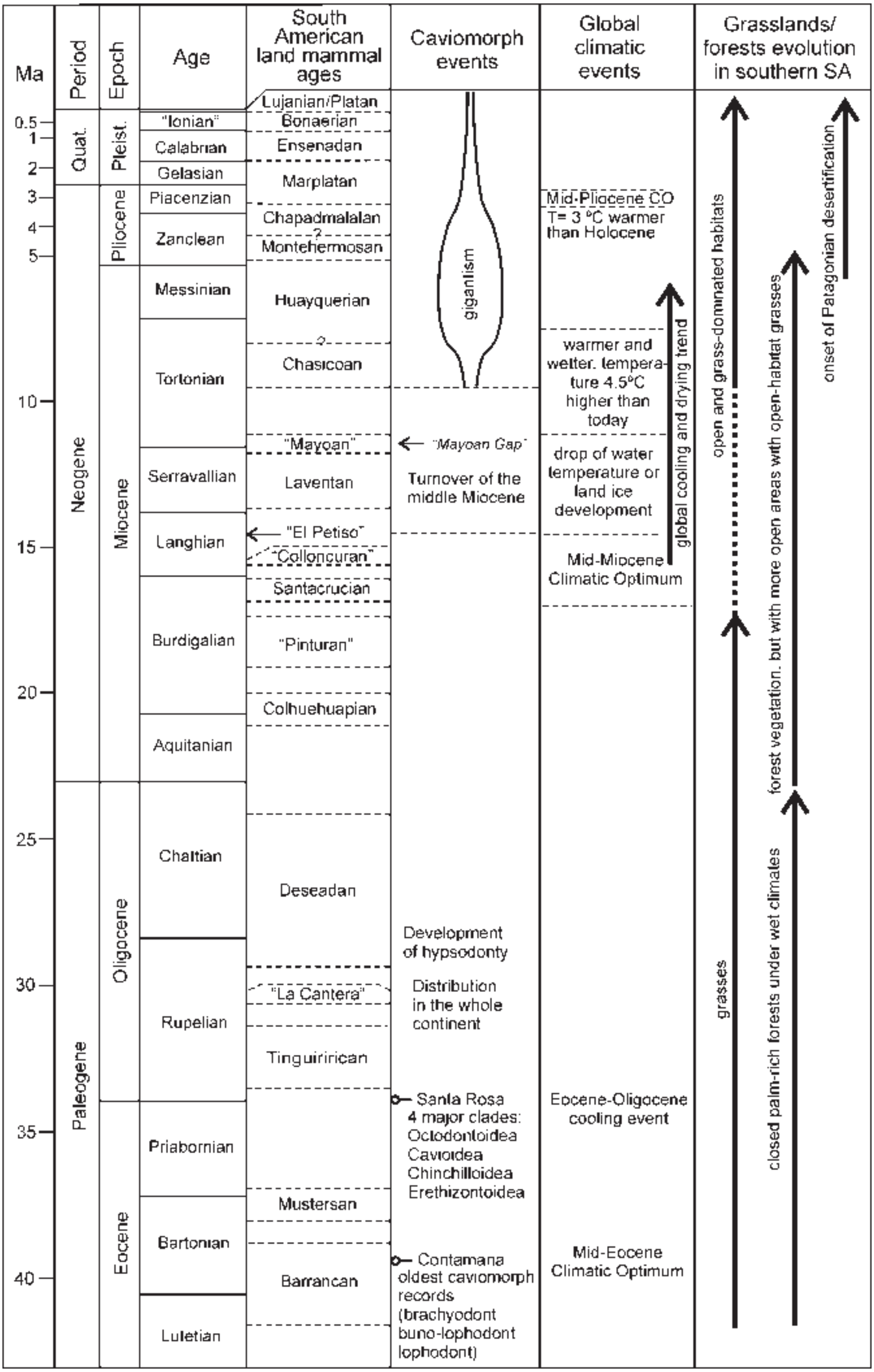


Figure 2. South American Cenozoic temporal calibration and the main events in caviomorph evolution.

Flynn *et al.*, 2003, Dunn *et al.*, 2013). So, both are likely to be early Oligocene in age and have scant rodent remains (see below).

The fauna from Contamana (locality CTA-27; Figs. 1.1.b, 2), was assigned to the middle Eocene (Antoine *et al.*, 2012), on the basis of numerical ages and biochronological data. In association with the rodents there are marsupials, dasypodids, notoungulates, and pyrotheres, known in higher latitudes from the Barrancan-Mustersan SALMAs (Fig. 2). In this locality, cavio-morphs are represented only by isolated teeth, which already display some taxonomic diversity within a relatively low morphological disparity. All the taxa are brachyodont, bunolophodont, or lophodont. Two genera and three species are exclusive to this fauna (*Cachiyacuy contamanensis*, *C. kummeli*, and *Canaanimys maquiensis*; Antoine *et al.*, 2012). According to morphological cladistic analyses (Antoine *et al.*, 2012; Arnal *et al.*, 2014) they are considered as stem caviomorphs. Although these assignments have to be proven by more inclusive phylogenetic analyses, the CTA-27 fauna would already record the first differentiation of at least some of the caviomorph lineages represented today, *e.g.*, pan-octodontoids.

The age of the fauna from Santa Rosa (Figs. 1.1.c, 2) is uncertain; lacking numerical ages, it has been referred to the middle Eocene-early Oligocene interval based on its mammal content. The oldest assignments are based especially on the marsupials, but taking together marsupials, cingulates, and notoungulates, a late Eocene-early Oligocene age is suggested (Campbell, 2004; Frailey and Campbell, 2004; Goin and Candela, 2004; Shockey *et al.*, 2004; Ciancio *et al.*, 2013). The rodent fauna, in particular, is taxonomically very rich, since about 17 species have been recognized. Moreover, Frailey and Campbell (2004) stated that among unstudied material there are other undescribed species. The Santa Rosa rodents were referred to three of the four major caviomorph lineages, Octodontoidea (*e.g.*, *Eodelphomys* Frailey and Campbell, 2004), Cavioidea (*e.g.*, *Eoincamys* Frailey and Campbell, 2004), and Erethizontoidea (*Eopululo* Frailey and Campbell, 2004), and even to families with modern representatives (Echimyidae, Dasyproctidae, Erethizontidae; App. 1). However, the relationships of the Santa Rosa taxa with the rest of the caviomorphs need further analyses (Vucetich *et al.*, 2014c; Arnal and Vucetich, 2014, in press). Concerning its age, two rodent taxa, *Eobranisamys* Frailey and Campbell, 2004 and *Eoespina* Frailey and Campbell, 2004 are probably shared with the Contamana fauna supporting its oldest age. However, one, *Eobranisamys*, could be shared with the fauna of La Cantera, in which case it suggests a younger age. The presence in Santa Rosa of *Eodelphomys* (the largest rodent of this fauna with a simplified occlusal surface) also suggests a younger age, as this taxon is morphologically similar to the Oligocene-early Miocene myocastorines (see below).

The rodents of these two old intertropical faunas are known mostly through isolated teeth, showing a certain morphological monotony compared to those of younger Patagonian and Bolivian faunas (*e.g.*, Deseadan). They are all brachyodont (or with an incipient degree of hypsodonty) and bunodont to bunolophodont. This monotony may be interpreted as a result of an evolution within a humid and warm, more or less stable environments. The lack of a more accurate temporal calibration has so far prevented any determination about whether or not this morphological monotony is also influenced by the closeness to the time of their arrival on the continent.

The Oligocene

The Oligocene (Tinguiririען and Deseadan SALMAs plus La Cantera fauna; Figs. 1, 2) has a rich record of caviomorphs showing a greater morphological disparity than older faunas. Representatives of the four superfamilies, with the archetypal dental features that characterize species of the subsequent SALMAs, can be clearly recognized, at least since the Deseadan SALMA. Although a few genera (*e.g.*, *Andemys* Bertrand *et al.*, 2012, *Branisamys* Hoffstetter and Lavocat, 1970) cannot be assigned with certainty to any supra generic taxa (see below).

Octodontoids are the richest and most diverse group (App. 1), including several genera and species. In turn, they represent different lineages (Wood 1949; Wood and Patterson 1959; Patterson and Wood 1982; Arnal *et al.*, 2014; Vucetich *et al.* 2014c, d), which will characterize the rodent faunas of the early and middle Miocene, at least in Patagonia. The Acaremyidae (Wood, 1949; Vucetich and Kramarz, 2003; Arnal and Pérez, 2013; Arnal and Vucetich, 2015; Vucetich *et al.*, 2014d) are likely a group of austral differentiation. The first representatives, the Deseadan *Platypittamys brachyodon* Wood, 1949, *Galileomys baios* Vucetich *et al.*, 2014c (Fig.3.1), and *Changquin woodi* Vucetich *et al.*, 2014d, attest to its differentiation into several lineages (Vucetich *et al.*, 2014c, d). They display a relatively low cheek tooth morphological disparity, as they are brachyodont to protohypsodont forms with different degrees of occlusal simplification within a tetralophodont pattern. They eventually acquired high-crowned cheek teeth and figure-eight occlusal surface, convergent with those of modern Octodontidae (Vucetich and Kramarz, 2003; but see Verzi *et al.*, 2014). The last representative, *Sciamys petisensis* Arnal and Pérez, 2013 persisted until the middle Miocene.

Several taxa from the Oligocene-middle Miocene such as *Ethelomys loomisi* (Wood and Patterson, 1959; Fig. 3.2), *Xylechimys obliquus* Patterson and Pascual, 1968, *Paradelphomys fissus* Patterson and Pascual, 1968, *Adelphomys* Ameghino, 1887a, *Stichomys* Ameghino, 1887a, were referred by Patterson and Pascual (1968) to the Subfamily Adelphomyinae within the Family Echimyidae. A recent cladistic analysis performed by Arnal and Vucetich (in press; Fig. 5) relates these genera to the living *Myocastor coypus*, and, by priority, Myocastorinae (Ameghino, 1902) would be the valid name for this clade (Fig. 5). This group is not related to the living echimyids but represents the sister group of the lineage formed by some living Echimyidae + Octodontidae. Myocastorines (App. 1) are represented in the Deseadan of Patagonia by *Ethelomys loomisi* (Fig. 3.2) and *Xylechimys obliquus*. They are also present in Santa Rosa with *Eodelphomys*. *Prospaniomys priscus* Ameghino, 1902 and *Deseadomys arambourgi* Wood and Patterson, 1959, originally described as echimyids, were since considered as myocastorine and adelphomyine respectively by Patterson and Pascual (1968), but in recent cladistic analyses (Arnal *et al.*, 2014; Arnal and Vucetich, in press) they appeared as a stem octodontoid and an early divergent member of crown Octodontoidea respectively (Fig. 5).

But probably the most interesting taxa of this time are those originally described as octodontoids (the Deseadan *Migraveramus* Patterson and Wood, 1982 and *Sallamys* Hoffstetter and Lavocat, 1970, plus the early Oligocene *Draconomys* Vucetich *et al.*, 2010c) as being small, brachyodont, or slightly hypsodont taxa with bunolophodont cheek teeth. But, according to recent morphological phylogenetic analyses, these taxa are excluded from Octodontoidea (Arnal *et al.*, 2014), or considered stem octodontoids (Arnal and Vucetich, in press). These taxa, together with the recently described *Llitun* Vucetich *et al.*, 2014c (Fig. 3.3) and *Leucokephalos*

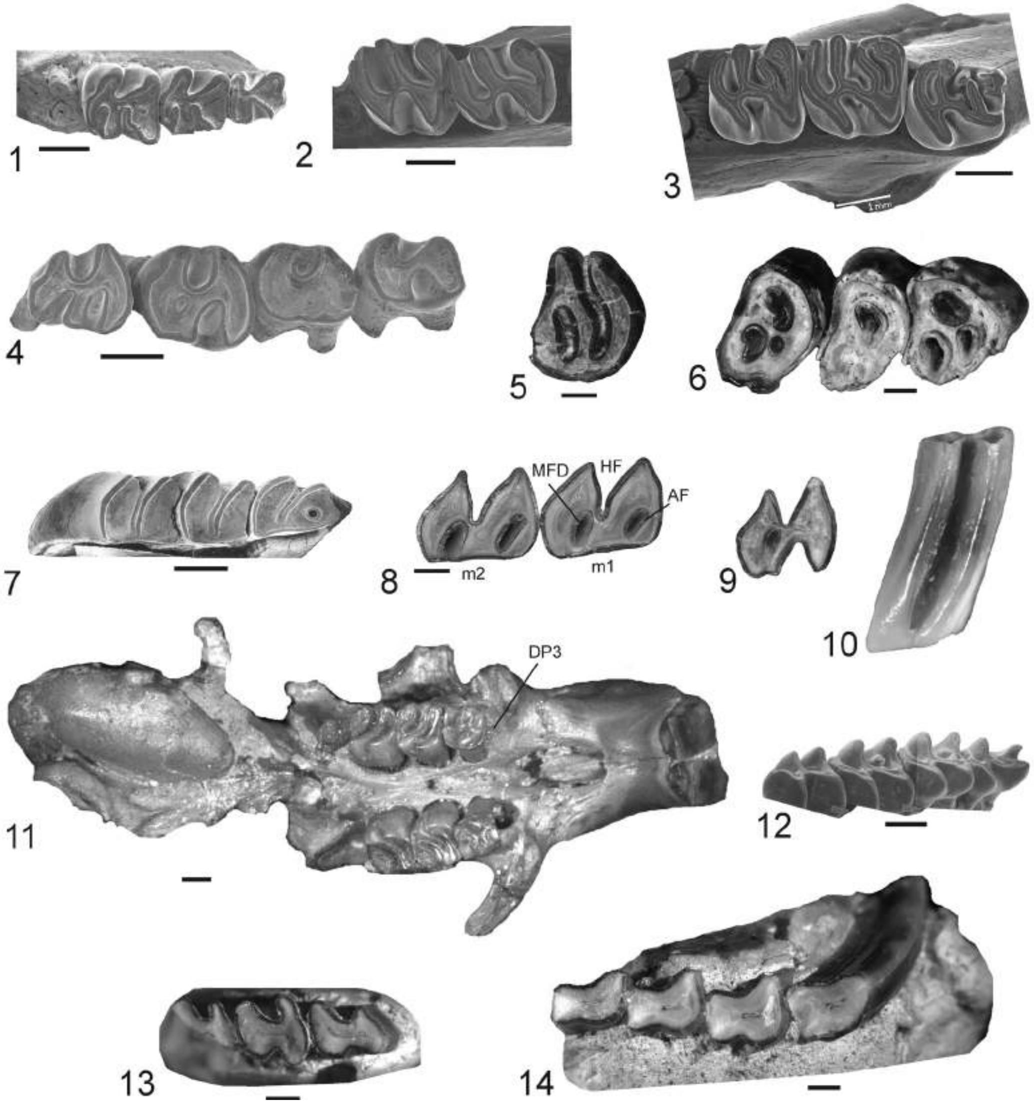


Figure 3. Oligocene-early Miocene caviomorphs. 1. *Galileomys baios* (p4-m3); 2. *Ethelomys loomisi* (m1-m2); 3. *Llitum notuca* (p4-m2); 4. *Leucokephalos zeffiae* (p4-m3); 5. *Incamys meniorum* (M1?); 6. *Leucoreios tretos* (P4-M2); 7. *Eoviscaccia boliviana* (p4-m2); 8. *Chubutomys simpsoni* (m1-m2); 9-10. *Cephalomys cecie* (m1?; 9. occlusal view; 10. external view); 11. *Protadelphomys latus* (skull in ventral view); 12. *Caviocricetus lucasi* (p4-m3); 13-14. *Cephalomyopsis hypselodontus* (13. p4-m2; 14. P4-M3). Anterior to the right. Scale 1 mm. **p**, **P**: lower and upper premolars; **m**, **M**: lower and upper molars.

Vucetich *et al.*, 2014c (Fig. 3.4) form a clade of stem octodontoids with a broad South American distribution that lived during the Oligocene and have no known descendants (Vucetich *et al.* 2014c; Arnal and Vucetich, in press). Thus, the relationships among these taxa, as well as with other caviomorphs, remain controversial.

Chinchilloids are represented by several genera, *Scotamys* Loomis, 1914; *Incamys* Hoffstetter and Lavocat, 1970 (see Vucetich *et al.*, 2014c; Fig. 3.5), *Eoviscaccia* Vucetich, 1989 (Fig.

3.7), and *Loncolicu* Vucetich *et al.*, 2014c, probably representing different lineages. *Incamys* and *Loncolicu* retain more generalized dental characters (*e.g.*, retention of fossetids on cheek teeth) than the oldest chinchilloid, the Tinguiririican *Eoviscaccia frasinetti* Bertand *et al.*, 2012, and they might represent basal chinchillids (Kramarz *et al.*, 2013; Fig. 6.2). *Incamys* was originally considered a dasyproctid (Lavocat, 1976), but currently, it is considered to be a probable chinchilloid (Vucetich *et al.*, 2014c). Generalized lineages such as that represented by *Loncolicu* may have persisted until the Colhuehuapian as *Garridomys* Kramarz *et al.* (2013), as they share some morphological similarities. *Scotamys* has been interpreted as a possible ancestor of the Chinchillidae *Prolagostomus* and *Pliolagostomus* (Wood and Patterson, 1959) or related to the gigantic neoepiblemids of the late Miocene (Bondesio *et al.*, 1975; Kramarz, 2002). *Eoviscaccia*, with several proto- to euhypsodont (*sensu* Mones, 1982) species, is the taxon most clearly related to the living Chinchillidae (*Chinchilla*, *Lagidium* and *Lagostomus*) as demonstrated by Kramarz *et al.* (2013). Chinchilloids represent the first caviomorph lineage to develop hypsodonty, at least during the early Oligocene (Bertrand *et al.*, 2012), being likely the first adapted to more arid environments and/or more abrasive diets, conditions already exploited in South America by other mammals such as several lineages of notoungulates (Reguero *et al.*, 2010).

Cavioids are comparatively scarce during the Oligocene. In Patagonia they are represented by three species of Cavioidea *s.s.* (Patterson and Wood, 1982), a subgroup within Cavioidea formed by the paraphyletic eocardiids (stem-group) and the family Caviidae (crown-group; Pérez, 2010b). One of them is the mesodont *Asteromys puctus* Ameghino, 1897, the most basal species within Cavioidea *s.s.* (see Pérez and Vucetich, 2012a). The other two species belong to *Chubutomys* [*C. simpsoni* Wood and Patterson, 1959 (Fig. 3.8) and *C. navaensis* Pérez, Krause and Vucetich, 2012], one of the most derived protohypsodont genera of this group (Pérez *et al.*, 2012).

Outside Patagonia no representatives of Cavioidea *s.s.* were recorded, but a couple of species have been tentatively assigned to the Cavioidea. *Branisamys luribayensis* Hoffstetter and Lavocat, 1970 from Salla and *Andemys termasi* Bertand *et al.*, 2012 from Tinguiririca, have been alternatively assigned to Dasyproctidae and to Dinomyidae (see Bertrand *et al.*, 2012 for detailed discussion). Both are relatively large compared to the other taxa, with a slight degree of hypsodonty and tetralophodont cheek teeth. The understanding of their relationships with other caviomorphs depends on thorough phylogenetic analyses and the finding of more and better material.

The peculiar *Cephalomys* Ameghino, 1897 (Fig. 3.9-10) is represented in Patagonia by at least three species (see Vucetich *et al.*, 2014c). They have meso- to protohypsodont cheek teeth with an asymmetrical morphology (between lower and upper teeth) that, although not exclusive (the octodontoids *Abrocoma* and *Massoiamys* are examples of this type of morphology), it has been difficult to homologize with that one of other caviomorphs. *Cephalomys* has been diversely considered as a dasyproctid (Wood and Patterson, 1959), a chinchilloid (Landry, 1957; Kramarz, 2001b), or a cavioid *inc. sedis* (Kramarz, 2005), but its relationships need to be analyzed with a broader phylogenetic approach.

Erethizontoids are little diversified, represented by a single genus in Patagonia, *Protosteiromys* Wood and Patterson (1959), and at least another one (unpublished) in Bolivia (Candela, 2000). This is probably the most conservative clade of caviomorphs, as all of them have brachyodont (to slightly more hypsodont) and bunolophodont or lophodont dental morphologies (the living *Chaetomys* being the single exception; Patterson and Wood, 1982: 394; but see Carvalho, 2000; Martin, 1994b), and are also very similar in skull morphology.

The Deseadan rodents attest to a second caviomorph radiation that represents the first caviomorph diversification in Patagonia (Pérez and Pol, 2012; Vucetich *et al.*, 2014c; Arnal and Vucetich, in press). Among Deseadan rodents there are several lineages that independently acquired some degree of hypsodonty. For example in Cabeza Blanca, the richest and most diverse Oligocene fauna (Vucetich *et al.*, 2014c), there is a marked trend to develop hypsodonty among different taxa. There are meso- (*Asteromys, Incamys*), proto- (*Chubutomys, Cephalomys*), and euhypsodont (*Scotamys*) taxa with a large variety of simplified occlusal morphologies. They suggest a relatively rapid adaptation to somewhat more open environments/dryer climates, which would have begun to develop more markedly after the cooling of the Eocene-Oligocene boundary (Goin *et al.*, 2012). However, the existence in Patagonia of large amounts of volcanic glass in the sediments is likely to have been another trigger for hypsodonty (Strömberg *et al.*, 2013).

The early Miocene

Miocene mammal-bearing sediments are widely represented in South America (Figs. 1, 2), and caviomorphs are profusely recorded there.

During the earliest Miocene (Colhuehuapian and "Pinturan" SALMAs; Fig. 2), there is a remarkable diversity of caviomorphs in central Patagonia. More than 36 brachyodont to euhypsodont species have been recognized in the two richest Colhuehuapian faunas, Gran Barranca and Bryn Gwyn (Figs. 1.1.l, n, 2), representing the four superfamilies and more than eight families (Vucetich *et al.*, 2010b).

About half of these Colhuehuapian caviomorphs have been considered octodontoids (Vucetich *et al.*, 2010b) representing several different lineages. Some of them have no descendants, and have dubious phylogenetic relationships within the superfamily, being recognized as basal octodontoids (Arnal, 2012; Arnal *et al.*, 2014) or stem and early divergent crown octodontoids (Arnal and Vucetich, in press; App. 1). Many of these stem octodontoids are restricted to the Colhuehuapian or are older taxa that persisted up to this SALMA. *Protadelphomys latus* Ameghino 1902 and its close relative *Willidewu esteparius* Vucetich and Verzi, 1991, are putative stem octodontoids of uncertain relationships (but see Verzi *et al.*, 2014) probably with digging habits, and a dental morphology similar to that of the phiomorph *Gaudeamus* Wood, 1968 (Fig. 3.11). Indeed, dental morphological similarities between *Gaudeamus* and the Peruvian *Sallamys* and *Incamys* led to the inference of caviomorphs in Africa or, alternatively, highlight a remarkable phenomenon of convergence, the latter being a more plausible interpretation (Sallam *et al.*, 2011). *Protadelphomys* was originally considered to be an echimyid (Ameghino, 1902) and was tentatively related to *Sallamys pascuali* (Vucetich and Verzi, 1991). It was also related to the living *Carterodon* because they share some dental characters such as upper incisor with a crest on the anterior face, an uncommon feature among Caviomorpha. *Caviocricetus lucasi* Vucetich and Verzi, 1996 is a small species common in central Patagonia with the most terraced molars (Fig. 3.12) known among caviomorphs. This kind of molars suggests a particular diet within caviomorphs including insects, berries, seeds and small invertebrates (Vucetich and Verzi, 1996: 301); living caviomorphs are essentially herbivorous, and only a few echimyids include non-plant items in their diet (Emmons, 1990). Another group of stem octodontoids are the acaremyids *Galileomys* and *Acaremys,* and *Protacaremys* Ameghino, 1902 (see Verzi *et al.*, 2014) originally decribed as an echimyid.

The lineage leading to crown octodontoids is represented by *Paradelphomys* Patterson and Pascual, 1968, described originally as an adelphomyine, but here considered as a putative myocastorine.

Chinchilloids have a relatively poor presence in the Colhuehuapian. They are represented by euhypsodont Neoepiblemidae and Chinchillidae. The latter are represented only by *Eoviscacia australis* Vucetich, 1989*,* whose occlusal pattern is as simplified as those of living viscachas. The euhypsodont neoepiblemids are more abundant and a little more diverse, with several species of *Perimys* Ameghino, 1887a (see Kramarz, 2002).

Cavioids are scarce in the Colhuehuapian (Fig. 2), represented by only two genera, the protohypsodont *Luantus* Ameghino, 1901 with a couple of species (*L. initialis* Ameghino, 1902 and *L. minor* Pérez, Vucetich and Kramarz, 2010), "*Chubutomys* " *leucoreios* Pérez, Vucetich and Kramarz, 2010, and *Australoprocta fleaglei* Kramarz, 1998, which was originally referred to the Dasyproctidae. During the rest of the early Miocene ("Pinturan" and Santacrucian) the record increases greatly with two species of *Neoreomys* Ameghino, 1887a (*N. pinturensis* and *N. australis*) and at least nine species of Cavioidea *s.s.* of the genera *Luantus*, *Phanomys* Ameghino, 1887a, *Schistomys* Ameghino, 1887a, and *Eocardia* Ameghino, 1887a.

Cephalomyids are represented by *Soriamys* Kramarz, 2001b, *Banderomys* Kramarz, 2005, and *Cephalomyopsis* Vucetich, 1985 (Fig. 3.13-14). The latter is an enigmatic taxon, whose dental morphology is somewhat similar to that of the African gundis *Ctenodactylus* (Vucetich, 1989, Vucetich *et al.*, 2014d; Vianey-Liaud *et al.*, 2010).

This time period is the moment of greatest diversity of erethizontoids (Candela, 2000; Kramarz, 2001a; 2004; 2006a; Kramarz and Bellosi, 2005; Vucetich *et al.*, 2010b). Four genera, *Eosteiromys* Ameghino, 1902 (Fig. 4.1), *Parasteiromys* Ameghino, 1904, *Hypsosteiromys* Patterson, 1958, and *Branisamyopsis* Candela, 2003, with several species (see Vucetich *et al.*, 2010b) have been recorded. During the Colhuehuapian one of these genera, *Hypsosteiromys* represents the single erethizontid with a hint of hypsodonty (Candela and Vucetich, 2002). This interval also represents the acme of primates in Patagonia (Fleagle *et al.*, 1997; Kay, 2010). This coincidence in the fossil record, repeated in other moments (see below), probably is produced by the existence of local environments with forests developed under temperate and humid conditions (Barreda and Palazzesi, 2014).

This great diversity (shown mostly by palatal and jaw fragments), accompanied by an increase in the degree of morphological disparity indicates that caviomorphs occupied a large variety of environments, although most of their modes of life and diet are still difficult to specify (see Álvarez and Arnal, in press, for an example for octodontoids).

Interestingly, several taxa of erethizontids and octodontoids retain generalized characters such as the presence of the deciduous premolar 3 (DP3) in juveniles of *Protadelphomys* (Vucetich *et al.*, 2010b; Fig. 3.11) and *Parasteiromys* (see Candela, 1999). *Protadelphomys* in particular, has a mosaic of generalized and specialized characters. Among the generalized ones is the normal

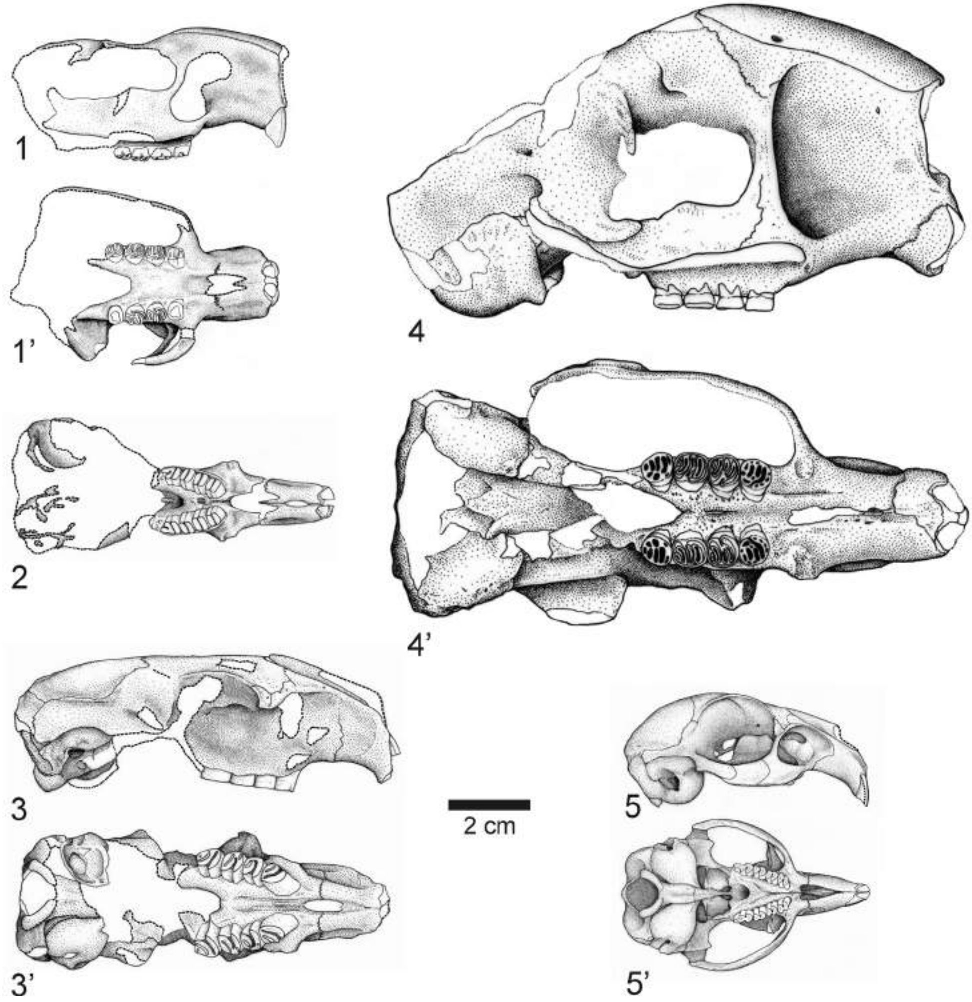


Figure 4. Skulls of erethizontids (1, 4), chinchillids (2), and cavioids (3, 5). 1-1'. *Eosteiromys homogenidens*; 2. *Prolagostomus* sp.; 3-3'. *Alloiomys friasensis*; 4-4'. *Neosteiromys pattoni*; 5-5'. *Dolicavia minuscula*.

replacement of the deciduous premolar 4 (DP4), in addition to the retention of a DP3 in juveniles. A derived character is the high obliquity of the lophs. The "transitional" type of incisor enamel (Vucetich and Vieytes, 2006; Box 1) is a derived character in the context of caviomorphs and a primitive one in the context of Pan-Octodontoidea (Fig. 5).

The rest of the mammal-bearing early Miocene corresponds to the Santacrucian SALMA (Fig. 2). The Santacrucian faunas were first studied by Ameghino (1887a) and played a central role in the understanding of the Miocene Patagonian faunas due to the abundant and excellently-preserved materials collected by Carlos Ameghino (see Scott, 1905; Vizcaíno *et al.*, 2012b). The Santacrucian faunas show a significant change with respect to those Colhuehuapian and "Pinturan" ones. Octodontoids underwent a reduction in diversity (Vucetich *et al*., 1999; Arnal, 2012). By contrast, several lineages experienced a progressive increase of hypsodonty, as in acaremyids and myocastorines among octodontoids (Kramarz, 2001a, 2004; Pérez and Vucetich, 2012b; Arnal and Pérez, 2013). The stem group of Cavioidea *s.s*. in particular, achieved euhypsodonty with a simplification of their occlusal pattern (Pérez and Pol, 2012). In addition, these forms greatly increased their specific richness, and *Neoreomys* became common. The taxonomic diversity of erethizontids decreased dramatically; it is represented by only the genus *Steiromys* Ameghino, 1887a. Concomitantly, the monkeys also decreased their diversity; they are represented by only two taxa (Ameghino, 1891; Tejedor *et al*., 2006).

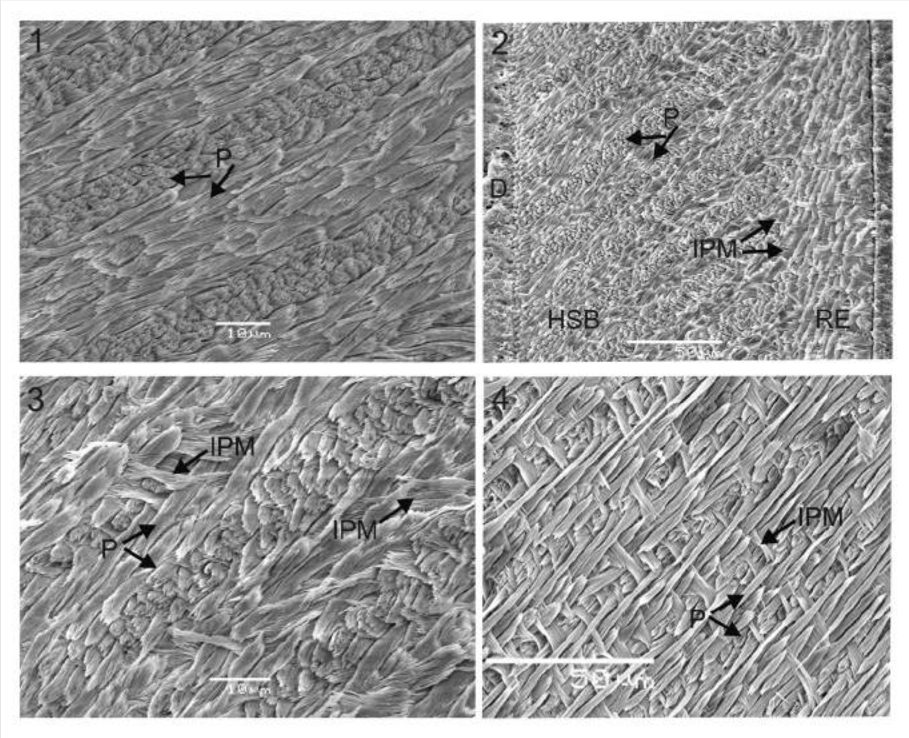
Such gradual increase in hypsodonty followed climatic deterioration with subsequent expansion of open environments, especially manifested in southernmost Patagonia during the Santacrucian. Very slowly, the most brachyodont forms diminished; however, some brachyodont

BOX 1

Incisor enamel evolution

Rodent incisor enamel microstructure is considered a useful tool for rodent phylogeny and systematics (Korvenkontio, 1934; Boyde, 1978; Martin, 1992, 1997). The incisor enamel has generally two layers, one inner portion (PI) with Hunter-Schreger Bands (HSB) and an external portion (PE) formed by radial enamel (RE) (Boyde, 1978; Koenigswald and Clemens, 1992). Among rodents, three types of HSB have been recognized: pauciserial (the most primitive), uniserial, and multiserial (Korvenkontio, 1934; Whalert, 1968; Martin, 1992, 1993, 1997). Multiserial HSB characterizes the Hystricognathi, some Eocene and post-Eocene Ctenodactyloidea, and *Pedetes*. Among Phiomorpha (African hystricognaths) this type is recorded since the late Eocene (Martin, 1992, 1993, 1994a). Classically three multiserial HSB subtypes have been recognized in which the interprismatic matrix (IPM) may run parallel (the most primitive subtype), at an acute angle (approximately 45°), or at right angles (rectangular) with respect to the prisms, this last considered to be the most derived (Martin, 1992, 1993, 1994a). Among caviomorphs, the first two subtypes are present in the superfamilies Chinchilloidea, Cavioidea, and Erethizontoidea, whereas the most derived subtype is restricted to the Octodontoidea and considered a synapomorphy of this superfamily (Martin, 1992). These three subtypes are already present in what are currently considered the most ancient caviomorphs (pre-Deseadan? of Santa Rosa, and Deseadan; Martin, 1992, 2004, 2005), but the incisor enamel of the Contamana and Tinguiririca rodents has not been studied yet. However, a transitional stage between the acute and rectangular subtypes was described for several Deseadan to "Colloncuran" (late Oligocene-middle Miocene) octodontoids (=Pan-Octodontoidea) (*e.g*., *Sallamys*, *Caviocricetus*, *Protadelphomys*, *Willidewu*, *Plesiacarechimys* and two taxa indet. of La Cantera; Martin, 1994b:126; Vieytes, 2003; Vucetich and Vieytes, 2006). The discovery of this transitional subtype of HSB, recorded as homoplasy in different taxa, allows new interpretations about the early evolution of octodontoids (Vucetich and Vieytes, 2006; Vucetich *et al*., 2010a; Arnal *et al*., 2014).

The presence of transitional IPM in different Pan-Octodontoid lineages, together with rectangular IPM in lineages not closely related to each other (*e.g*., Acaremyidae and Octodontidae; Vucetich and Kramarz, 2003) suggests independent development of the most derived subtype of HSB (Saether, 1979; Koenigswald, 1997) in different lineages of this monophyletic group, after the caviomorphs arrived in South America (Vucetich and Vieytes, 2006; Vucetich *et al*., 2010c). On the other hand, it could have evolved once, thus becoming a synapomorphy for the Pan-Octodontoidea; if this were so, *Caviocricetus*, *Sallamys-Protadelphomys-Willidewu*, and *Plesiacarechimys* would represent different lineages within stem Octodontoidea (but see Arnal *et al*., 2014). Any of these interpretations would reinforce the hypothesis that the early evolution of the octodontoids was more complex than previously supposed (Reig, 1989: 262; Vucetich and Kramarz, 2003; Arnal *et al*., 2014).



Microphotographs of the incisor enamel of two incisors in longitudinal section. 1, 2 and 3. Caviomorpha indet. from La Cantera, 1. detail of the Hunter-Schreger Bands (**HSB**) with parallel to acute interprismatic matrix (**IPM**); 2. detail of the HSB with acute IMP; 3. detail of the HSB with transitional IPM; 4. *Ctenomys* sp., detail of the HSB with rectangular IPM. **D**, dentine; **P**, prism.

species persisted until at least the early middle Miocene in northern Patagonia (Vucetich, 1994; Vucetich *et al*., 1993a; Vucetich and Vieytes, 2006) together with the last Patagonian monkeys (Kay *et al*., 1998).

The middle Miocene

Although poorly known, the middle Miocene ("Colloncuran", Laventan, and "Mayoan" SALMAs, plus "El Petiso", Fig. 2) is one of the most interesting periods for caviomorph evolution, especially from the point of view of the origin of modern taxa. Both paleontological (Vucetich *et al*., 1999; Pérez, 2010a, b; Vucetich and Pérez, 2011; Pérez and Pol, 2012) and neontological (Dunnum and Salazar-Bravo, 2010a, b; Opazo, 2005; Poux *et al*., 2006; Pérez and Pol, 2012; Upham and Patterson, 2012; Upham and Patterson, this volume) evidence states that the lineages that led to the differentiation of most of the living taxa likely originated during this time (but see Verzi *et al*., 2014).

The octodontoids from the middle Miocene are represented in Patagonia by several poorly-known species, *e.g.*, *Galileomys* sp. Vucetich and Kramarz, 2003, *Protacaremys denisae* Vucetich *et al.*, 1993a, *Maruchito trilofodonte* Vucetich *et al.*, 1993a, *Plesiacarechimys koenigswaldi* Vucetich and Vieytes, 2006, and *Sciamys petisensis* Arnal and Pérez*,* 2013 (the youngest and most hypsodont acaremyid), and several unnamed taxa found in the Cerro Boleadoras Formation (Vucetich, 1994, see App. 1). *Plesiacarechimys koenigswaldi* is especially interesting in this context because it shows the survival in northern Patagonia of an old lineage that retains primitive characters such as the transitional incisor enamel (Box 1) and generalized dental morphology. This species has also been recorded in the late Miocene of Entre Ríos (Candela *et al.*, 2012a) suggesting a biogeographic connection between the northeast of Argentina (Paraná River) and northern Patagonia (Fig. 1.1.k, 1.2.l).

Chinchilloids are represented by several species of the chinchillids *Prolagostomus* (Fig. 4.2) and *Pliolagostomus* that became more frequent than in the Santacrucian. The neoepiblemid *Perimys*, so frequent in the Santacrucian, is not recorded in the "Colloncuran" but is represented in the Cerro Boleadoras Formation (Vucetich, 1994).

A few species of Cavioidea from the middle Miocene were assigned to Dasyproctidae, such as *Neoreomys australis* Ameghino, 1887a, *Alloiomys pattersoni* Vucetich, 1979 (Fig. 4.3), and the Bolivian *Mesoprocta hypsodus* Croft *et al.*, 2011. However, their assignment to this family is dubious (Vucetich, 1984), and at least *Neoreomys* could be more closely related to the "eocardiids" than to living dasyproctids (Pérez, 2010a, b). A better understanding of the relationships of these taxa requires additional phylogenetic analyses with a larger taxon and character sampling. Besides, by these times ("Colloncuran" –post Colloncuran) six species of the stem group of Cavioidea *s.s.* are recorded (*Eocardia robertoi* Vucetich, 1984, *E. robusta* Vucetich, 1984, *Matiamys elegans* Vucetich, 1984, *Microcardiodon huemulesis* (Kraglievich, 1930), *M. williensis* Pérez and Vucetich, 2011 and *Guiomys unica* Pérez, 2010b). One of the most interesting species is *G. unica*, found in El Petiso (Chubut, Argentina; Villafañe *et al.*, 2008) and Quebrada Honda (Bolivia; Croft *et al.*, 2011). It is interesting because it has mandibular and dental characters intermediate between the basal Cavioidea *s.s.* and the family Caviidae (Pérez, 2010). Later, the "Mayoan" record of Cavioidea is extremely scarce ("Mayoan gap", Pérez and Pol, 2012; Figs. 2, 7) with only one isolated molar of Cavioidea *s.s.* (*Cardiomys? andinus*) which was considered by Vucetich and Pérez (2011) to be the oldest hydrochoerine.

Although represented by scant materials, porcupines were more diverse at this time than in the Santacrucian. They have been recorded in a single locality, Cañadón del Tordillo in Neuquén (Vucetich *et al.*, 1993a; Fig. 1.1.k), by three species representing three different lineages: *Branisamyopsis*, *Steiromys*, and *Neosteiromys*? (Candela, 2003; Candela and Morrone, 2003). In this case the monkeys apparently did not follow the diversity of porcupines, as they are here represented by only a single species (Kay *et al.*, 1998).

Early–middle Miocene mammal faunas, similar in family and genus composition to the Argentinean ones have been found in several localities in Chile (Flynn *et al.*, 2002; 2008; Bostelmann *et al.*, 2013); this is the classical middle Miocene fauna of the Río Cisnes (Fig. 1.1.r) that provided the basis for the recognition of the "Friasian" Age (Kraglievich, 1930; Vucetich, 1994; Marshall and Salinas, 1990).

The late Miocene

The late Miocene (Chasicoan and Huayquerian SALMAs, Fig. 1.2) is well represented in central and northern Argentina, with three most important areas: Northwest (Fig. 1.2.i, q), Northeast (Fig. 1.2.l), and Pampean region (Fig. 1.2.r, s). Northeast and Northwest areas represent clearly different biogeographic areas, the former being dominated by a diversity of environments related to the pre-Paraná River, under warm and humid conditions and with the development of gallery forests (see Brandoni and Noriega, 2013). Many modern caviomorph lineages have their first record, or became abundant during this period.

During these times crown-octodontoids became very rich and diverse, especially in the Huayquerian (Figs. 1.2, 2), represented by taxa clearly related to modern lineages. For example, among the echimyids *Theridomysops* Vucetich, 1995 is closely related to the living *Clyomys* and *Euryzygomatomys*; *Pampamys* Verzi *et al.*, 1995, is related to *Thrichomys*, whereas *Reigechimys* Verzi *et al.*, 1994, is related to extinct Brazilian forms that lived up to the Quaternary, such as *Dicolpomys* Winge, 1888 (Hadler *et al.*, 2008). Likewise, the first abrocomids are known from the Huayquerian (but see Verzi *et al.*, 2014) with *Abrocoma antiqua* Rovereto, 1914 and *Protabrocoma paranensis* Kraglievich, 1927.

In addition, several small brachyodont to mesodont caviomorphs recorded in Mendoza (Fig. 1.2.q) and Catamarca (Fig. 1.2.i), were erroneously referred to the most typical Pliocene genus *Eumysops* (see Rovereto, 1914; Vucetich, 1995; Olivares *et al.*, 2012).

An interesting issue is the acquisition of high degrees of hypsodonty, up to euhypsodonty among Octodontidae (Verzi, 2002). Several lineages, well recorded in different levels and localities of the Cerro Azul Formation (La Pampa; Fig. 1.2.r), provide one of the best examples of this process. In the lineages of *Chasichimys-Xenodontomys* (Ctenomyinae; Verzi *et al.*, 2004), *Neophanomys* (Octodontinae; Verzi *et al.*, 2011), and *Reigechimys* (Echimyidae; Verzi *et al.*, 1994; Sostillo *et al.,* 2014) a progressively increasing hypsodonty occurred together with changes of the dental gross morphology (*e.g.*, variation in the persistence of flexi/ids toward a simplification of the occlusal surface) and a modification of the enamel microstructure of the cheek teeth. This latter consists of the gradual secondary acquisition of radial enamel (RE) in the enamel pattern, first recorded in caviomorph rodents of the *Chasichimys-Xenodontomys* lineage (Verzi *et al.*, 2004). Such acquisition of RE strengthens the single enamel layer remaining as leading edge in the ctenomyine cheek teeth. These changes would represent a response to a more abrasive diet in progressively more desertic environments (Verzi *et al.*, 2004) that occurred as a result of the global cooling and drying trend (Pascual and Ortiz Jaureguizar, 1990; Janis, 1993; MacFadden and Cerling, 1996). This suggests that in caviomorphs the enamel pattern evolved in response to different functional requirements (Vieytes, 2003; Álvarez *et al.*, this volume).

Chinchilloids have their acme at the Huayquerian (Fig. 2). They are represented by the lagostomine *Lagostomus* (*Lagostomopsis*) Kraglievich*,* 1926, the gigantic neoepiblemids *Phoberomys* and *Neoepiblema*, probably of semiaquatic habits, and a great diversity of terrestrial eumegamyines (Dinomyidae). Excluding the octodontoids, dinomyids are one of the most diverse groups of caviomorphs with nearly 20 genera (App. 1), medium to large-sized, with multilaminated proto- to euhypsodont teeth, a great diversity of cranio-mandibular morphologies, and a wide distribution in central and northern Argentina, Brazil, and Uruguay (Frailey, 1986; Francis and Mones, 1966; Nasif, 2009; Nasif *et al.*, 2013; Perea *et al.*, 2013; Rinderknecht *et al.*, 2011a). This suggests that fossil dinomyids (the eumegamyines *in. lit.*) had diverse life strategies in varied environments.

Cavioids were very diverse in this period. Among them, the lineage of the caviid hydrochoerines reached their greatest diversity, especially during the Huayquerian, through a variety of the large semiaquatic capybaras, and the terrestrial extinct "cardiomyines" (Vucetich *et al.*, 2011, 2012; Deschamps *et al.*, 2013). Capybaras are represented by several species of *Cardiatherium* (Vucetich *et al.*, 2005a, 2014a; Deschamps *et al.*, 2007, 2013) that apparently had already achieved some biological and behavioral characteristics of modern capybaras, such as semiaquatic habits and living in herds. The extinct "cardiomyines" were diverse and abundant, and are represented by several genera and species (*Xenocardia* Pascual and Bondesio, 1963*, Procardiomys* Pascual, 1961, *Cardiomys* Ameghino, 1885, and *Caviodon* Ameghino, 1885; App. 1). They had a wide geographic distribution and, unlike hydrocherines, probably terrestrial habits. For example, in the Andalhuala Formation "cardiomyines" are recorded in the basal water-related levels together with capybaras (*Paraeuphractus prominens-Cardiomys ameghinorum-Cardiatherium* Zone) and continue up to the upper levels –despite the aridification trend (*Vassallia maxima-Pseudoplataeomys-Pithanotomys* Zone)– where capybaras are absent (see Esteban *et al.*, 2014). Caviines and dolichotines are also abundantly recorded in this period: *Allocavia* Pascual, 1962, *Neocavia* Kraglievich, 1932, *Prodolichotis* Kraglievich, 1932, *Pliodolichotis* Kraglievich, 1927, and *Paleocavia* Ameghino, 1889. These genera have several nominal species, which have not been revised recently. *Paleocavia* is a very interesting taxon because it shows similar dental characters to the living *Cavia* (Verzi and Quintana, 2005).

Erethizontoids were still diverse at this time. They are represented by the large *Neosteiromys bombifroms* Rovereto, 1914 and *N. pattoni* Candela, 2004 (Fig. 4.4) from the Andalhuala Formation, Catamarca (Fig. 1.2.i), *Paradoxomys cancrivorus* Ameghino, 1885 from the "conglomerado osífero" (see below), and another one, probably a third genus, from San Luis province (Pascual and Bondesio, 1981; Candela, 2004). The strong masticatory apparatus of *Neosteiromys* suggests they were adapted to more abrasive food and inhabited more open environments than the living porcupines (Candela, 2004).

A well-known fauna for its role in the history of the knowledge of Miocene mammals, is that from the "conglomerado osífero" of the Ituzaingó Formation, exposed at the cliffs of the Paraná River (Fig. 1.2.l), also known as "Mesopotamiense" (see Cione *et al.*, 2000). A great number of rodents with an important taxonomic diversity and morphological disparity is recognized in these sediments (Cione *et al.*, 2000; Candela *et al.*, 2012a; Nassif *et al.*, 2013). The octodontoids from these sediments, unlike those of La Pampa, are represented almost exclusively by "echimyids": "*Eumysops*" *parodii* and *Haplostropha scalabriniana*; the myocastorines *Myocastor paranensis* and *M. obesus* have been also mentioned in descriptions of this fauna. The presence of the abrocomid *Protabrocoma paranensis* with a dental morphology very similar to that of the living species of the Andean *Abrocoma* is noteworthy. Chinchilloids are the most outstanding group. They are represented by one species of *Lagostomus* Brookes, 1928, the gigantic neoepiblemids *Phoberomys* and *Neoepiblema*, and an overwhelming diversity of dinomyids, the greatest known for one locality with more than 30 species. These dinomyids ranged from protohypsodont and medium-sized species (*Paranamys typicus*, *Potamarchus murinus*, and *P. sigmodon*) to euhypsodont, large-sized species (*Gyriabrus holmbergi* and *G. rebagliatti*, several species of "*Tetrastylus*", *Carlesia pendolai*, *Eumegamys paranensis* (Fig. 10.5), *Isostylomys laurillardi*, *Eumegamysops praependens*; (Fig. 10.8) see App. 1 and Nasif *et al.*, 2013). Cavioids are represented by one species of capybara, *Cardiatherium paranense* (Ameghino, 1883) and several species of "cardiomyines" *Cardiomys* and *Caviodon* (Vucetich *et al*., 2005a, 2011), as well as *Paleocavia*, *Pliodolichotis* and *Prodolichotis* (Cione *et al*., 2000; Nasif *et al*., 2013). Erethizontids are represented by the large *Paradoxomys cancrivorus*, not related to the coeval *Neosteiromys* from Catamarca but closely-related to the living *Coendou*, being the oldest representative of the living porcupines (Vucetich and Candela, 2001; Candela and Morrone, 2003). Although many of these taxa have a wide geographic distribution (*e.g.*, *Cardiatherium*) some of them belong to typical Patagonian lineages (*e.g.*, *Protabrocoma* and *Lagostomus*), and others seem to be the southern expansion of Brazilian lineages (*e.g.*, *Phoberomys* and *Paradoxomys*). Thus, this region appears to be a transition zone (Morrone, 2006: 469).

The Pliocene

During the Pliocene the caviomorphs of central Argentina experienced a strong impoverishment due to the reduction in diversity of Dinomyidae and Echimyidae, the local extinction of Erethizontidae, and the extinction of Neoepiblemidae. This change was probably driven by climatic changes and the impact produced by the mammals of Holarctic origin participating in the Great American Biotic Interchange (GABI; Webb, 1985; Morgan, 2008; Woodburne, 2010).

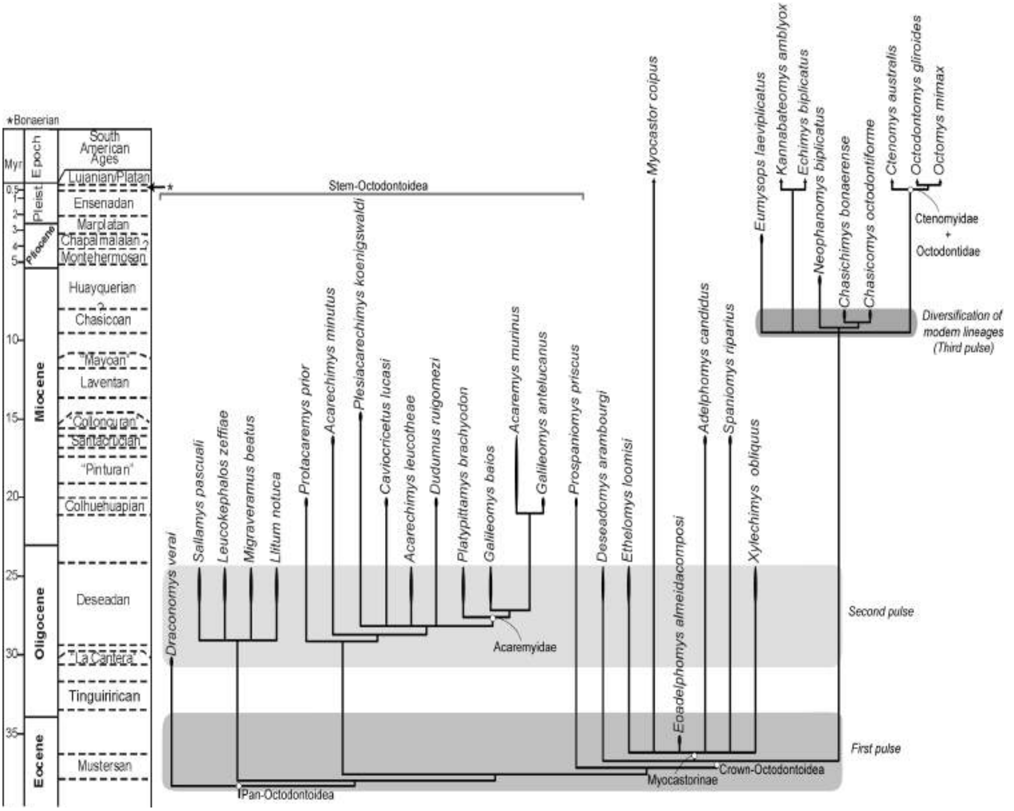


Figure 5. Evolutionary hypothesis of Octodontoidea based on phylogenetic analyses of Arnal and Vucetich (in press). Gray areas show main radiation events.

However, among octodontoids there is a notable diversification of Octodontidae probably associated also with climatic changes. The octodontids are common in the Pliocene of central and northwestern Argentina with the genera *Neophanomys*, *Phtoramys*, *Pithanotomys*, and *Pseudoplataeomys* (Marshall and Patterson, 1981; Deschamps *et al*., 2012; Tomassini *et al*., 2013). Ctenomyids, as well, are abundantly recorded with the genera *Eucelophorus* (the most specialized tooth-digger; Verzi and Olivares, 2006; Vieytes *et al*., 2007), *Actenomys*, *Praectenomys*, *Paractenomys*, and *Ctenomys*, which acquired different adaptations to digging and life underground (Verzi and Olivares, 2006; Lessa *et al*., 2008). *Eucelophorus* and *Ctenomys* independently acquired subterranean habits, whereas *Actenomys* probably had fossorial habits, spending part of its life above the surface (Verzi, 2008). "Echimyids" are represented by only *Eumysops* Ameghino, 1888 (Olivares *et al*., 2012; Olivares and Verzi, 2014) while *Paramyocastor,* usually considered an extinct "echimyid" (Verzi *et al*., 2002), represents a crown-octodontoid related to *Myocastor* (see Fig. 5). *Paramyocastor* is the only non-euhypsodont Pliocene caviomorph of southern South America. By the end of the Pliocene, a strong climatic deterioration can be recognized in Buenos Aires Province (Chapadmalal area; Fig. 1.2.t) through the record of the desert-adapted octodontoids *Abalosia* (a genus related to the living *Tympanoctomys*), *Pithanotomys*, and *Abrocoma* (Verzi and Quintana, 2005).

Chinchilloids are represented by several species of the chinchillid *Lagostomus*, with the diversity of chinchillines being conspicuously greater than today (Ameghino 1888, 1908). Nevertheless, the validity of these taxa must await a systematic revision (Francis and Mones, 1965; Rasia and Candela, 2013). Dinomyids were very scarce but still a few gigantic representatives inhabited central Argentina and Uruguay (see below).

Cavioids were abundant and diverse but are still poorly studied. Caviines are represented by the extinct genera *Neocavia* (Kraglievich, 1932)*, Dolicavia* (Ameghino, 1906; Fig. 4.5)*,* and *Paleocavia*, and the living *Cavia, Galea* (=*Pascualia* Ortega Hinojosa, 1963), and *Microcavia*, which are first recorded during this time (see Quintana, 1996, 1998; Verzi and Quintana, 2005). Dolichotines are represented by *Dolichotis chapalmalense* (=*Orthomyctera chapalmalense* Ameghino, 1889). Many species of *Prodolichotis* and *Orthomyctera* are recorded, being alternatively included in Dolichotinae or Caviinae, but these genera are a taxonomic hodge-podge and their numerous nominal species need a detailed revision.

Hydrochoerines are represented by *Hydrochoeropsis dasseni* Kraglievich, 1930, and at least three species of *Phugatherium* Ameghino, 1887b (Vucetich *et al*., 2014a; Figs. 9.1-2), which include the largest capybaras so far known (see below). Only *Caviodon* is still recorded among "cardiomyines", with several species in central Argentina: *C. australis* (Ameghino, 1888), *C. pozzi* Kraglievich, 1927, and *C. cuyano* Vucetich *et al*., 2011 (Fig. 10.1).

Pleistocene-Holocene

During this interval, the succession of glacial and interglacial periods played an important role in the setup of the mammal assemblages. Specific differences in the reaction to these changes resulted in the association of species that are today allopatric forming nonanalog assemblages typical of the Pleistocene (Bell *et al*., 2004). The legions of mammals that entered through the Panama corridor during the main phase of the GABI certainly contributed to shape the Quaternary faunas. In the case of caviomorphs, the modern taxonomic composition was already established (Vucetich and Verzi, 1999). Only fluctuations in their geographic distribution are seen as a response to climatic oscillations (glacial-interglacial). This is best recorded in an ecotonal area such as the Buenos Aires Province. Brazilian elements (such as the echimyid cf. *Clyomys* and the dasyproctid *Plesiaguti totoi* Vucetich *et al.*, 1997; Vucetich and Verzi, 2002; Vucetich *et al.*, 2005b) along the Atlantic coast attest to warm pulses. Opposite climatic conditions are evidenced by the caviid *Dolichotis salinicola* (Burmeister, 1875) and the octodontine desert-adapted *Tympanoctomys cordubensis* (Ameghino, 1889) recorded in the Pleistocene of the coastal area (Tonni, 1981; Verzi *et al.*, 2002 respectively). Outside of Buenos Aires Province, a nice example of a nonanalog assemblage was found in the Sopas Formation of northern Uruguay (Fig. 1.2.k) where the porcupine *Coendou*, the crown octodontoid *Myocastor*, and the caviids *Galea* and *Microcavia* were recorded together (Ubilla and Perea, 1999).

The great late Pleistocene extinction of large and megamammals (mostly xenarthrans, notoungulates, litopterns, equids, and gomphotheres) did not include the gigantic rodents which had already suffered a major extinction by the end of the Pliocene, of which the hydrochoerine *Neochoerus* –and perhaps the dinomyid *Josephoartigasia*– were the only survivors (see below).

The intertropical record

As noted above, the caviomorph fossil record in intertropical areas (the modern Brazilian Subregion, Fig. 1) is much poorer than that of southern South America. The oldest records belong to Contamana and Santa Rosa (Peru, see above; Fig. 1.1.b, c) in which almost exclusively brachyodont species are found. For the Deseadan only two Brazilian species are known, *Sallamys*? *minutus* Vucetich and Ribeiro, 2003, and *Paulacoutomys paulista* Vucetich *et al.*, 1993b, both referred originally to Echimyidae. Based on new cladistic analyses (Arnal and Vucetich, in press both species appeared to be stem-octodontoids rather than echimyids.

By contrast, the Miocene record is much richer and indicative. In the La Venta fauna (Laventan SALMA, middle Miocene, Colombia; Figs. 1.1.a, 2; Fields, 1957; Walton, 1997) there are some brachyodont or slightly higher crowned taxa referred by Walton (1997) to the families Echimyidae (*Acarechimys*, *Ricardomys*) and Erethizontidae (*Steiromys*, *Microsteiromys*); but most of the fauna is composed of high-crowned protohypsodont or euhypsodont forms (Fields, 1957). Among them, there are basal caviids such as *cf. Guiomys* (Pérez, 2010a), and other caviids such as *Prodolichotis pridiana* Fields, 1957 and Dolichotinae indet. (see Walton, 1997). Other taxa have uncertain relationships such as *Neoreomys*, *Microscleromys*, *Olenopsis*, "*Scleromys*" which have been referred to Dasyproctidae and/or Dinomyidae (Fields, 1957; Walton, 1997; Candela and Nasif, 2006; Kramarz, 2006b). More inclusive phylogenetic analyses are needed to resolve their relationships. In this fauna, some taxa with a wide geographic distribution up to Patagonia (*Acarechimys*, *Neoreomys*, *Steiromys*) coexisted with endemic taxa (*Microscleromys* and *Microsteiromys*) and others of intertropical distribution (*Ricardomys;* Madden and Vucetich, unpublished data). However, there were no acaremyids, chinchillids, or neoepiblemids, so frequent in the Miocene faunas of Patagonia. No capybaras have been reported; although their presence would have been expected in a warm intertropical fauna of this age (see Pérez and Pol, 2012). But some of the materials referred by Walton (1997) to *Prodolichotis pridiana* (*e.g.,* Walton, 1997 Fig. 24.7.I) could be "cardiomyines" based on their dental morphology (p4 with three complete lobes and an internal fissure in each lobe of m1-m3, see Vucetich and Pérez, 2011).

The contemporaneous fauna of Quebrada Honda (Bolivia; Croft *et al.*, 2011; Fig. 1.f.), is very interesting due to its geographical position between La Venta and Patagonia, within a cordilleran environment. Its rodent fauna (Croft *et al.*, 2011) is more similar to those of Patagonia, especially due to the presence of abundant chinchillids. However, as at La Venta, Quebrada Honda has some endemic taxa (*Mesoprocta hypsodus* Croft *et al.*, 2011, *Quebradahondomys potosiensis* Croft *et al.*, 2011) together with others of wide distribution (*Guiomys*, *Acarechimys*).

The late Miocene (Huayquerian SALMA, Fig. 2) of the Acre region in Brazil (Fig. 1.1) as well as in the adjacent area in Peru, has yielded numerous taxa among which there are capybaras, caviids, "cardiomyines", the gigantic neoepiblemids, some dinomyids, several poorly known brachyodont species of echimyids, and probably erethizontids, plus the oldest undoubted Dasyproctidae (Frailey, 1986; Sant'Anna, 1994; Campbell *et al.*, 2006; Antoine *et al.*, 2013; Kerber *et al.*, in press a). Studies in progress (Vucetich and Campbell, in prep.) suggest that as foreseen by some phylogenetic analyses (Fabre *et al.*, 2013), forms related to the living echimyids *Thrichomys* and *Proechimys* would have been present among the microrodents of this interval. In the Huayquerian of Venezuela, *Cardiatherium*, *Eumegamys* (Pascual and Díaz de Gamero, 1969), and the well known gigantic neoepiblemid *Phoberomys pattersoni* Mones, 1980 (see below) are recorded.

The Pliocene record is scanty. In Venezuela it is represented by isolated fragments of hydrochoerines, "cardiomyines", *Phoberomys*, *Neoepiblema* and a probable octodontoid *Marisela gregoriana* Vucetich *et al.*, 2010a found in the San Gregorio Formation of Falcón State (Fig.1.2.a). Recently, a Pliocene capybara was reported from northern Colombia (Moreno-Bernal *et al.*, 2013).

Our knowledge of the Quaternary rodents of Brazil began with the studies of Peter Lund in the first half of the XIX Century, with the discovery of fossils in the caverns of Lagoa Santa (Fig. 1.2.f; for an enjoyable story of these discoveries see Cartelle, 1994). Many other rodent faunas have been described since then, covering a wide region of eastern Brazil (*e.g.*, Hadler *et al.*, 2008; Kerber and Ribeiro, 2012; Kerber *et al.*, 2011, 2014, in press b; Oliveira *et al.*, 2013 and literature therein; Fig. 1.2.c-f, j). These rich faunas include numerous taxa with living representatives (*Coendou*, *Cavia*, *Kerodon, Hydrochoerus, Dasyprocta, Cuniculus*, *Dactylomys, Trinomys*, *Echimys*, *Mesomys*, *Nelomys*, *Callistomys, Carterodon, Myocastor*) showing a great diversity of echimyids. This assemblage proves that the modern caviomorph fauna of eastern Brazil was already established. However, extinct taxa, such as the echimyid *Dicolpomys* and the "eumegamyid" *Tetrastylus* show the survival in lower latitudes of lineages which became extinct earlier in higher latitudes. As well, the record of *Lagostomus* (Kerber *et al.*, 2011) and *Myocastor* (Kerber *et al.*, 2014), north of their modern distribution is especially interesting because it demonstrates the occurrence of cold pulses.

Evolutionary history

The most accepted theories state that rodents arrived in northern South America by rafting from Africa during the early to middle Eocene (Houle, 1998; Rowe *et al.*, 2010; Vucetich *et al.*, 2010c; Antoine *et al.*, 2012).

The fossil record together with phylogenetic analyses based on morphological data, show that the evolutionary history of caviomorphs occurred through pulses of diversification. The major events occurred in the middle? Eocene-early Oligocene (Vucetich *et al.*, 1999; Arnal and Vucetich, in press), late Oligocene (Pérez and Pol, 2012; Arnal and Vucetich, in press), and middle to late Miocene (Vucetich *et al.*, 1999; Pérez and Pol, 2012; Arnal and Vucetich, in press) (Fig. 5-7).

Although the middle Eocene–early Oligocene caviomorph record is poorly known, this interval was a key moment for the evolutionary history of the group. The relationships of Contamana rodents are still controversial. Some of them have been interpreted as stem caviomorphs not included in any of the modern superfamilies (Antoine *et al.*, 2012; Arnal *et al.*, 2014; Arnal and Vucetich, in press). The fauna of Santa Rosa, taxonomically richer than that of Contamana, otherwise shows that at least three of the four main lineages (Octodontoidea (Erethizontoidea + Cavioidea)) were already differentiated (Antoine *et al.*, 2012; Arnal *et al.*, 2014; Arnal and Vucetich, in press; Fig. 6.1). However, phylogenetic analyses are still in need to prove the relationships of these taxa among caviomorphs. These faunas would represent the first pulse of radiation that occurred in intertropical South America (Fig. 5).

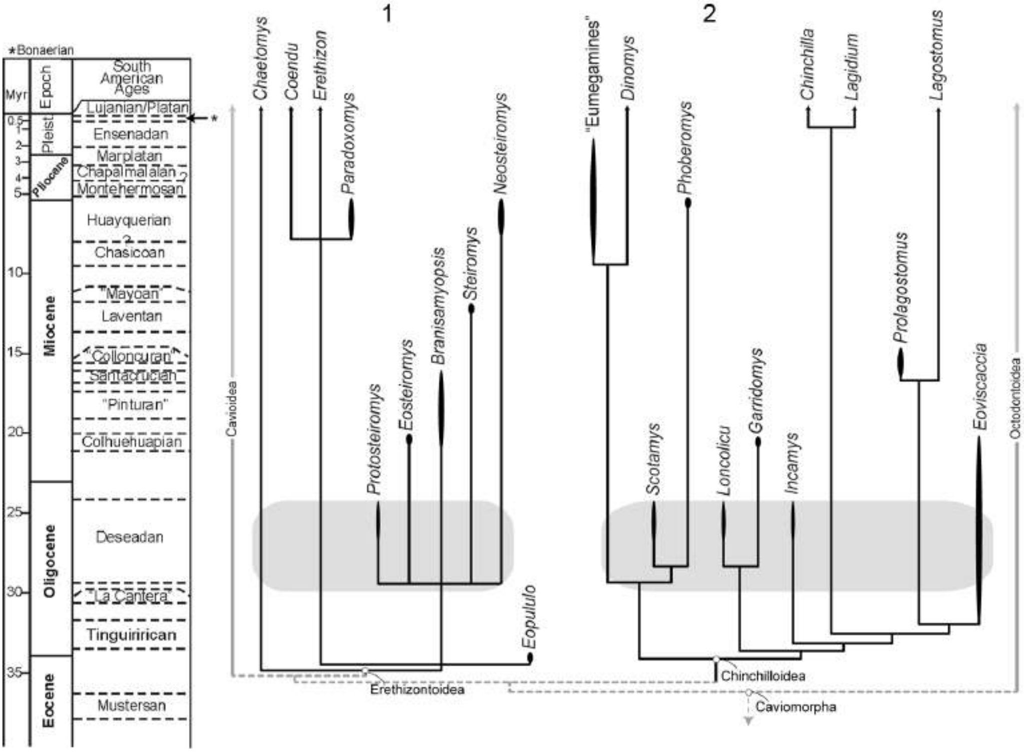


Figure 6. Graphical representation of evolutionary hypothesis of, 1. Erethizontoidea and, 2. Chinchilloidea based on phylogenetic analyses of Candela (2004), Kramarz *et al.* (2013), Sánchez Villagra *et al.* (2003), Antoine *et al.* (2012), Arnal *et al.* (2014), Arnal and Vucetich (in press), as well as on data in Vucetich *et al.* (2014c). Superfamilial relationships based on molecular data (Houchon and Douzery, 2001; Fabre *et al.*, 2012, 2013; Upham and Patterson, this volume) differ from the hypothesis presented here. Gray areas = second pulse of radiation.

Caviomorphs are first recorded in high latitudes in the earliest Oligocene of central Chile (Bertrand *et al.*, 2012 and literature therein) although they could have reached this area somewhat earlier. As a novelty, the fauna of Tinguiririca includes the oldest recognized chinchilloid. In central Patagonia they are first recorded a little later, during the early Oligocene (Vucetich *et al.*, 2010c; Figs. 1.1.h, n, 2). This southern migration likely occurred in response to the Eocene–Oligocene cooling that probably favored the settlement of new environments (Goin *et al.*, 2012; Fig. 2).

A second radiation, that also implies the first radiation detected in Patagonia, probably occurred during the earliest Oligocene and/or during most of the Oligocene (Arnal and Vucetich, in press). This is inferred from the rich record of the Deseadan SALMA (Fig. 2; Wood, 1949; Wood and Patterson, 1959; Hoffstetter and Lavocat, 1970; Patterson and Wood, 1982; Vucetich, 1989; Vucetich and Ribeiro, 2003; Pérez and Pol, 2012; Pérez *et al.*, 2012; Vucetich *et al.*, 2014c, d), showing that a moderate radiation had also occurred at least in three of the four superfamilies: Octodontoidea, Chinchilloidea, and Cavioidea (Figs. 5-7). Phylogenetic analyses of Octodontoidea (Arnal, 2012; Arnal *et al.*, 2014; Arnal and Vucetich, in press) indicate that its early evolutionary history was characterized by the differentiation of successive lineages that survived until the early or middle Miocene with no direct relationships with modern families (Fig. 5). Modern lineages are represented by a few taxa (*e.g.*, *Xylechimys*) although the diversity must have been higher because of the finding of several ghost lineages in phylogenetic analyses (Arnal and Vucetich, in press; Fig. 5).

The early radiation of chinchilloids (Fig. 6.2) also appears to be characterized by the differentiation of some taxa not directly related to modern lineages (Kramarz *et al.*, 2013; Vucetich *et al.*, 2014c); but the presence of *Eoviscaccia frassinetti* suggests that the lineage of living chinchillids was already differentiated in the Tinguiririean (early Oligocene; Bertrand *et al.*, 2012; Kramarz *et al.*, 2013).

Concerning erethizontoids, Candela (2004), based on a morphological phylogenetic analysis, proposed a basal dichotomy giving origin to the clade of the living forms and to that of the Oligocene–Miocene porcupines of Patagonia for which she proposed the subfamily Steiromyinae (Fig. 6.1). As in other groups (*e.g.*, "Echimyidae", platyrrhine primates; Patterson and Pascual, 1968; Kay *et al.*, 2008) it appears that the southern porcupines evolved separatedly from their intertropical representatives.

A recent phylogenetic analysis (Pérez and Pol, 2012) based on morphological and molecular data and calibrated with the geological age of the fossil taxa shows three major radiations in the evolutionary history of Cavioidea *s.s.* (Fig. 7). The first one is the radiation of the stem group of Cavioidea *s.s.* during the late Oligocene in the Deseadan SALMA. This was revealed through the record of three species and the presence of at least six ghost lineages in the phylogenetic analyses (Pérez, 2010b) that would extend back their age at least four million years before their first appearance in the fossil record of the early Miocene. The discovery of this Deseadan radiation contrasts with the traditional hypotheses that propose that the earliest evolutionary history of Cavioidea *s.s.* would have occurred through gradual changes from the Oligocene up to the early Miocene (see Kramarz, 2006a). The analysis of Pérez and Pol (2012) rejects such hypotheses because of the derived phylogenetic position of *Chubutomys*. These authors stated that during this radiation different evolutionary novelties were acquired, such as protohypsodonty, and the

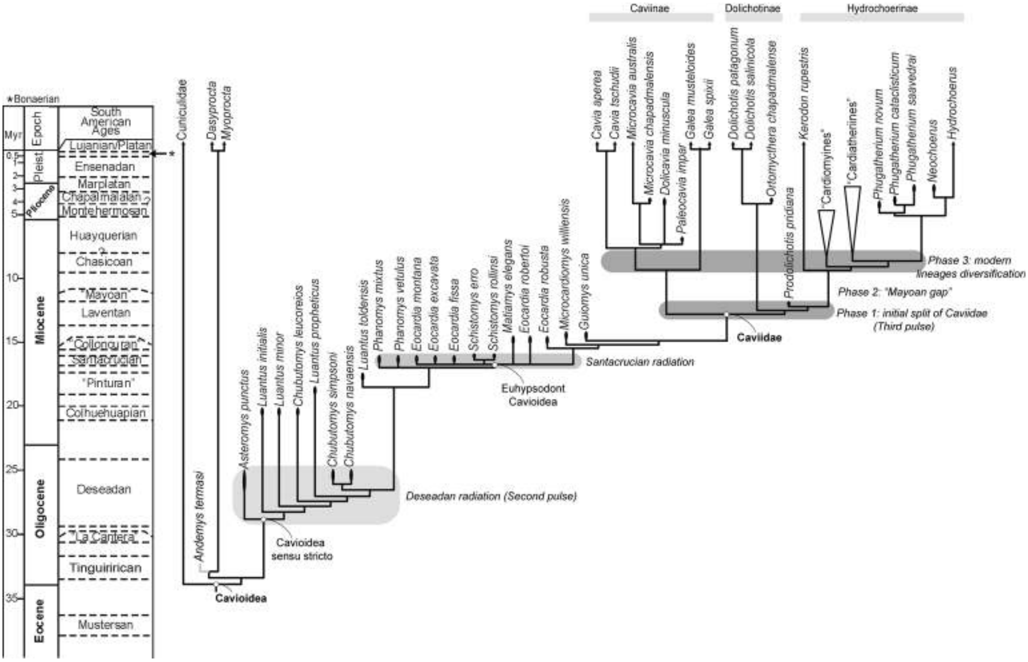


Figure 7. Evolutionary hypothesis of Cavioidea based on phylogenetic analyses of Pérez (2010a, b) and Vucetich *et al.* (2014a).

absence of the mesofossettid in lower cheek teeth in early ontogenetic stages, among other dental modifications. This first radiation of Cavioidea *s.s.* matches with that of Octodontoidea in Patagonia (second pulse of diversification= first Patagonian diversification, *sensu* Arnal and Vucetich, in press; Figs. 5, 7). During the Santacrucian (early Miocene) a second radiation of Cavioidea *s.s.* is recognized, evidenced by the record of seven species and the presence of three ghost lineages leading to "Colloncuran" forms and to the lineage that gave origin to the family Caviidae. The exceptional Santacrucian record and the sudden appearance of a high diversity of Cavioidea *s.s.* could be capturing the early offshoots of a major radiation, characterized by the acquisition of euhypsodonty, which is among the most important evolutionary novelties of the group (Pérez and Pol, 2012). Within Cavioidea, euhypsodonty is acquired only in Cavioidea *s.s.* This dental innovation must have been related to the adaptation to the main climatic-environmental changes recorded in Patagonia during the early Miocene (including great volcanic activity linked to the uplift of the Andes, a change toward more arid and colder biomes, and a general drop in humidity and temperature, etc.; Vizcaíno *et al.*, 2012b). The third radiation is the diversification of Caviidae (Pérez and Pol, 2012) that must have occurred at least at 12 Ma (initial split of Caviidae, named phase 1 in this radiation) with the appearance during the Chasicoan SALMA (phase 3; about 9 Ma) of the three modern lineages Caviinae, Dolichotinae, and Hydrochoerinae, which were already highly different in their anatomy, dentition, body size, and probably even in gregarious habits (Fig. 7).

Thus, the middle Miocene represents a significant period in the evolution of caviomorphs. An important extinction of several old lineages occurred, with the rate of extinctions largely surpassing that of first appearances at the genus level (Fig. 8; App. 1). The differentiation of several modern lineages (hydrochoerines, dolichotines, dinomyids, abrocomids) found for the first time in the late Miocene is not reflected in the middle Miocene probably because of the very poor record in the late middle Miocene, known as the "Mayoan gap" (phase 2 within the third radiation of Cavioidea *s.s.*; Fig. 7; Pérez and Pol, 2012). The late Miocene also witnessed the diversification of other modern lineages (eumysopines, octodontids, ctenomyids). No other period of such important turnover has been detected (compare Figs. 5-8).

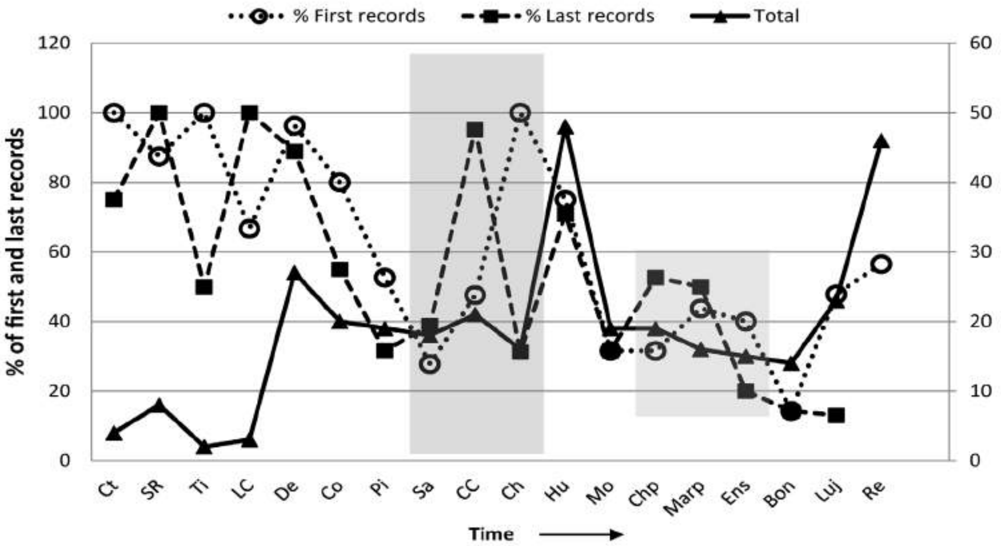


Figure 8. Percentages of first and last records of caviomorph genera through time. Gray areas show major turnover periods. Abbreviations for SALMAs and localities: **Bon**, Bonaerian; **CC**, "Colloncuran"; **Ch**, Chasicoan; **Chp**, Chapadmalalan; **Co**, Colhuehuapian; **Ct**, Contamana; **De**, Deseadan; **Ens**, Ensenadan; **Hu**, Huayquerian; **LC**, La Cantera; **Luj**, Lujanian; **Marp**, Marplatan; **Mo**, Montehermosan; **Pi**, "Pinturan"; **Re**, Recent; **Sa**, Santacrucian; **SR**, Santa Rosa; **Ti**, Tinguirirican.

Another important faunal change, although less important than the previous one, occurred between the end of the Chapadmalalan and the begining of the Ensenadan (Fig. 8) in southern South America. As with that of the middle Miocene, it also implies a certain modernization of the caviomorph fauna. The diversity of austral caviomorphs diminished gradually with the local extinction of Brazilian lineages, especially "echimyids" and erethizontids (App. 1). The gigantic hydrochoerines, dinomyids, and neoepiblemids diminished and eventually became extinct. However, many taxa closely related to living species are recorded since this period (*e.g., Lagostomus*, *Neochoerus*, *Cavia*, *Galea*, *Microcavia*, *Dolichotis*, *Ctenomys*, and *Pithanothomys*, a taxon practically indistinguishable from the living octodontine *Aconaemys*; Vucetich and Verzi, 1995; Verzi *et al.*, 2009; 2014). This pauperization was probably driven by climatic changes with a general trend to cooling and desertification.

Caviomorphs and gigantism

Living caviomorphs include several species which are very large within the context of rodents, including some around 10 kg: *e.g.*, *Lagostomus maximus* (Fig. 10.6), *Dinomys branickii* (Fig. 10.3), *Cuniculus paca*, and *Myocastor coypus* (Nowak and Paradiso, 1983), besides *Hydrochoerus hydrochaeris* (Fig. 9.6-7), the giant of the living rodents, with a body mass of about 50 kg. Among living hystricognaths, Old World porcupines also reach large sizes for rodents, with weights that may reach 30 kg (Nowak and Paradiso, 1983). This suggests that hystricognaths have, more than other groups of rodents, the capability (and/or the ecological opportunity; Losos, 2010) to increase size. Most outstanding is the fact that in the past, all caviomorph lineages excluding octodontoids developed large sizes, and even more, in two of them –chinchilloids and cavioids– gigantic sizes were reached. Gigantic fossil caviomorphs have been known since the XIX Century when several of the gigantic species were described (*e.g.*, Lund, 1839; Ameghino, 1886; Moreno, 1888), but in the last decade this issue took new impetus due to the estimation of the body masses of giant forms such as *Phoberomys pattersoni* Mones, 1980 and *Josephoartigasia monesi* Rinderknecht and Blanco, 2008 (Sánchez Villagra *et al.*, 2003 and Rinderknecht and Blanco, 2008 respectively). In order to explore the distribution and magnitude of this feature among caviomorphs, we estimated the body mass of several species that reached large sizes during the Neogene using geometric similarity with a phylogenetic modern relative of known mass (Tab. 1). Because fossil mammals are mostly known only through their dentitions, we followed Hopkins (2008) in using the length of the dental series (p4-m3 or P4-M3) as a proxy for size, a dimension that allows comparison among a greater number of species than postcranial bones. In the case of the Dinomyidae and Neoepiblemidae (chinchilloids), we used two living relatives for comparison, bearing in mind the great dispersion of values among the different methods used (*e.g.*, Rinderknecht and Blanco, 2008 *vs*. Millien and Bovy, 2010). With *Dinomys branickii* (Fig. 10.3), the single living dinomyid (and the putative closest phylogenetic relative with known body mass; Sánchez Villagra *et al.*, 2003), we obtained very large body masses, with values similar to those of Rinderknecht and Blanco (2008). Using *Lagostomus maximus* (Fig. 10.6), the largest living chinchillid, we obtained lower values, about 50% smaller than those mentioned above. With hydrochoerines we used the living capybara. In the case of those taxa with no modern representatives such as the "cardiomyines", we used the dolichotinae *Dolichotis patagonum* (Fig. 10.2) and the hydrochoerines *H. hydrochoerus* and *Kerodon rupestris* (Tab. 1).

Medium to large sizes were achieved already by at least the early Miocene (Tab. 1) in lineages as different as erethizontids, neoepiblemids, and Cavioidea *inc. sed*. (Tab. 1 and App. 1). But it was during the late Miocene–Pliocene when gigantic caviomorphs were abundant and diverse. In fact, the oldest caviomorphs over 20 kg in body mass come from the Chasicoan (Figs. 1.2.s, 2; Tab. 1), and by the latest Miocene, gigantic rodents were widely distributed across the continent.

Within Cavioidea, some Huayquerian (late Miocene) capybaras could have achieved the size of the living one, as *Cardiatherium paranense* (Ameghino, 1883) or be even larger, as *C. isseli* Rovereto, 1914 (see Deschamps *et al.*, 2013; Tab. 1). Incidentally, while the hydrochoerines increased in size during the late Miocene, caviines became smaller (M.E.P. personal observation). During the Pliocene, several species greatly surpassed the size of *H. hydrochaeris*, for example, the Montehermosan (early Pliocene of the Buenos Aires Province; Deschamps *et al.*, 2013, Vucetich

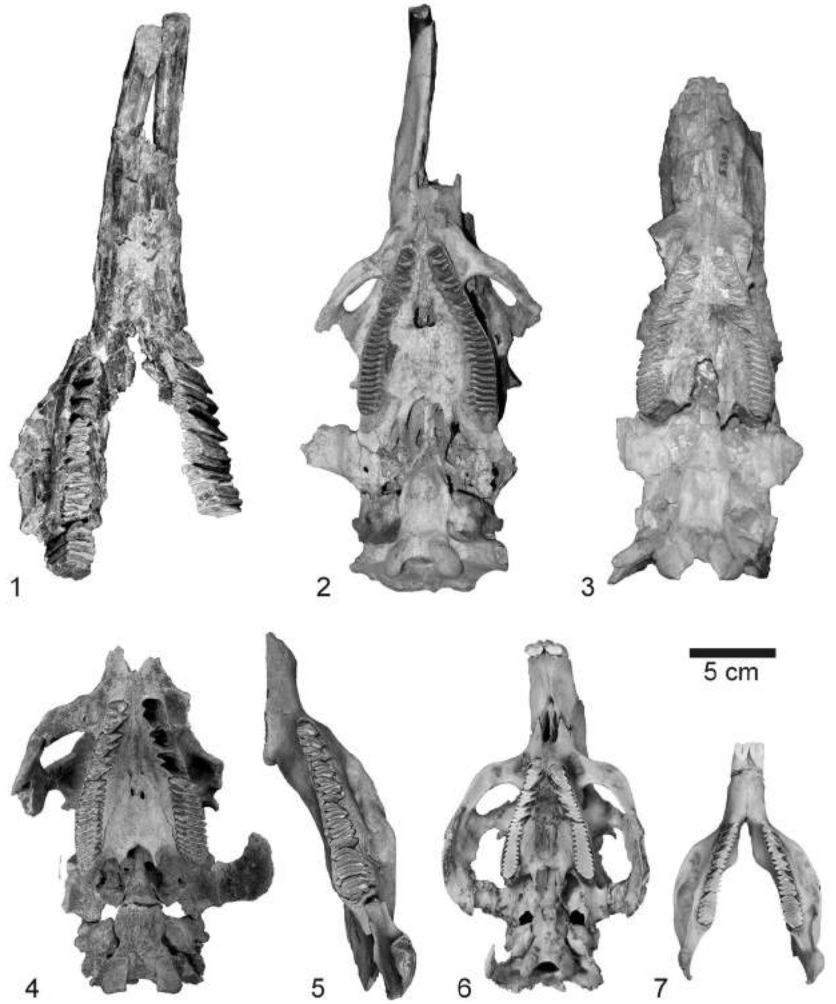


Figure 9. Gigantic hydrochoerines. 1. *Phugatherium cataclisticum*; 2. *Phugatherium novum*; 3. *Hydrochoeropsis dasseni*; 4. *Neochoerus cf. tarijensis*; 5. *Neochoerus* sp.; 6-7. *Hydrochoerus hydrochaeris*.

et al., 2014a) *Phugatherium cataclisticum,* which easily quadruples the body mass of the living capybara (Tab. 1, Fig. 9.1). The extinct "cardiomyines" also reached large size, although not as gigantic as capybaras. The largest was the Pliocene *Caviodon cuyano* Vucetich *et al.*, 2011 (Fig. 10.1), which probably greately exceeded *Dolichotis patagonum* in size (Tab. 1, Fig. 10.2).

Among Chinchilloidea, the Neoepiblemidae with *Phoberomys* Kraglievich, 1926 are among the most gigantic rodents (Fig. 10.7), and the estimation body mass in this genus has been long debated (Sánchez -Villagra *et al.*, 2003; Millien, *et al.*, 2006). Our estimations are similar to those of Sánchez Villagra *et al.* (2003), with the southern *P. burmeisteri* (Fig. 10.7) being even larger than the Venezuelan *P. pattersoni* (Tab. 1). Dinomyidae contain the greatest diversity

Table 1. Estimated body mass of some large and gigantic rodents.

Taxa	SALMA	Estimated body mass in kg	
		This paper	Previous papers
Hydrochoeridae			
Cardiatherium chasicoense	Chasicoan	12.88[a]	
Cardiatherium paranense	Huayquerian	29,55[a]	
Cardiatherium isselii	Huayquerian	90.58[a]	
Phugatherium cataclisticum	Montehermosan	238.9[a]	
Phugatherium novum	Chapalmalalan	115[a]	200 (1)
Hydrohoeropsis dasseni	post Chapalmalalan	93.68[a]	
Neochoerus	Ensenadan-Lujanian	195[a]	110 (1); 200 (2)
Cardiomys sp. nov.	Chasicoan	4.2[a] -10.68[b] -19.97[c]	
Caviodon cuyano	Chapalmalalan?	13[a] -37.66[b] - 61.62[c]	
Cavioidea in sed.			
Neoreomys australis	Santacrucian	8.42[d]	7.12 (3)
Neoepiblemidae			
Perimys sp.	Colhuehuapian	8.53[e]	
Phoberomys burmeisteri	Huayquerian	811.65[e] - 551[f]	
Phoberomys pattersoni	Huayquerian	654.85[e] - 444[f]	437-741 (6); 220-340 (7); 200-300 (8)
Dinomyidae			
Carlesia cf. *pendolai*	Chasicoan-Huayquerian	182[e] - 111.63[f]	
Eumegamysops praependens	Huayquerian	469.7[e] - 286[f]	
Eumegamys paranensis	Huayquerian	278.6[e] – 170[f]	
Potamarchus murinus	Huayquerian	18.99[e] – 12.9[f]	
Arazamys castiglionii	Huayquerian	455.83[e] - 309.4[f]	
Isostylomys laurillardi	Huayquerian	104[e] - 70.56[f]	
Telicomys giganteus	Montehermosan	137.5[e] - 93.24[f]	
Telicomys gigantissimus	Chapalmalalan	222.98[e] -136.2[f]	
Josephoartigasia monesi	Plio-Pleistocene	917.63[e] -622.78[f]	350 (4); 1211-2584 (5)
Erethizontidae			
Steiromys duplicatus	Santacrucian		14.17 (3)
Neosteiromys bombifrons	Huayquerian	40[g] - 58[h]	

***References.** (1) Vizcaíno *et al*., 2012a; (2) Ghizzoni, 2014; (3) Candela, Rassia and Pérez, 2012b; (4) Millien, 2008; (5) Rinderknecht and Blanco, 2008; (6) Sánchez Villagra *et al*., 2003; (7) Millien and Bovy, 2006; (8) Hopkins, 2008. The following modern species were selected for estimating body mass using geometric similarity: [a] *Hydrochoerus hydrochaeris* (50 kg), [b] *Kerodon rupestris* (1 kg), [c] *Dolichotis patagonum* (12 kg), [d] *Dasyprocta azarae* (4 kg), [e] *Dinomys branickii* (14 kg), [f] *Lagostomus maximus* (7 kg), [g] *Coendu prehensilis* (4 kg), [h] *Hystrix cristata* (22 kg).

of gigantic rodents, the most famous of which is the Plio-Pleistocene *Josephoartigasia monesi* Rinderknecht and Blanco 2008. The body mass of *J. monesi* has also been largely debated with results ranging from 200 to 2000 kg (Millien *et al.*, 2006; Hopkins, 2008; Rinderknecht and Blanco, 2008; Millien and Bovy, 2010). Many other dinomyids also reached gigantic size (Tab. 1), for example, *Carlesia pendolai*, *Telicomys gigantissimus* (Fig. 10.4) and *Eumegamysops praependens*, the latter with a skull almost the size of that of *J. monesi* (Fig. 10. 8). In fact many dinomyids exceeded 100 kg during that period. Although to a lesser degree, some Erethizontidae also achieved large sizes during this period. The skull of the Huayquerian *Neosteiromys bombifrons* Rovereto, 1914 was larger than that of *Erethizon dorsatum*, and it could have reached the size of some Old World porcupines (Tab. 1).

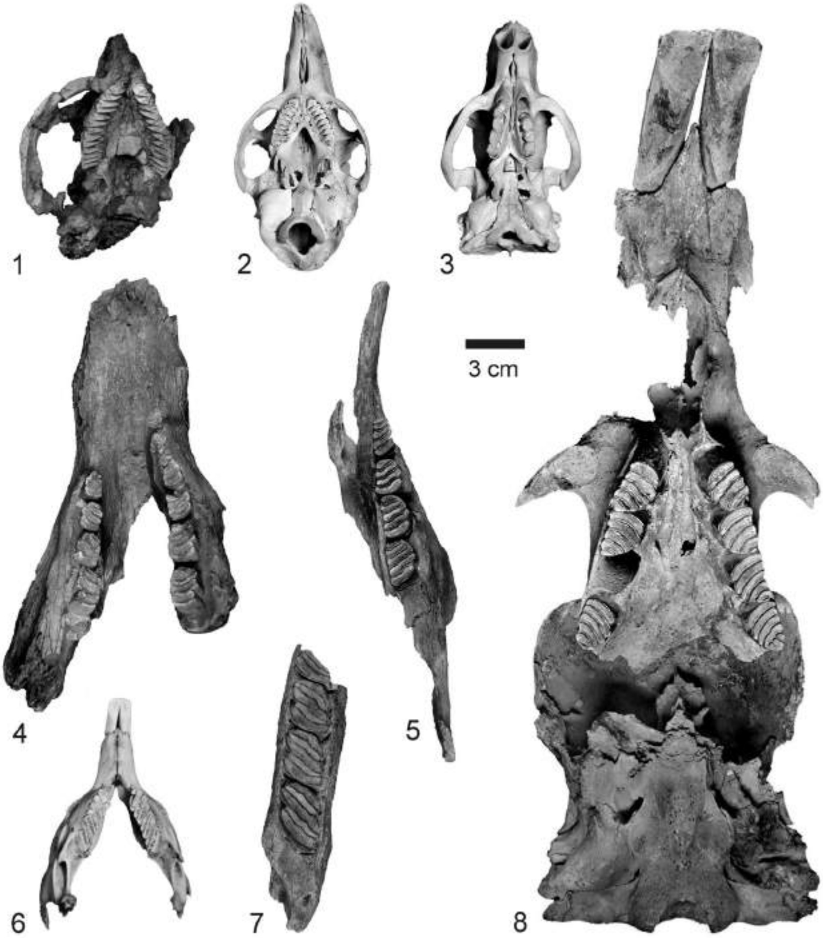


Figura 10. Large and gigantic cavioids and chinchilloids. 1. *Caviodon cuyano*; 2. *Dolichotis patagonum*; 3. *Dinomys branickii*; 4. *Telicomys gigantissimus*; 5. *Eumegamys paranensis*; 6. *Lagostomus maximus*; 7. *Phoberomys burmeisteri*; 8. *Eumegamysops praependens*.

Beyond the results of numerical estimations, some of these rodents were undoubtedly gigantic (see Figs. 9, 10). The evolution of gigantism appears as a complex issue, evolving in parallel on multiple lines, in what seems to be a coordinated phenomenon. The factors that led extinct taxa to develop such gigantic size are still under debate, but it is generally accepted that climatic change has been the driving force on evolution in size (Millien *et al*., 2006). A combination of climatic factors, mainly moisture and temperature, has been suggested as related to body size variation (James, 1970), with small body size being associated with warm and humid conditions and large size with cooler and drier conditions. Also latitudinal trends in body size have been explained as a response to temperature or water-related factors, which are predictors of primary production (Yom-Tov and Geffen, 2006). Other variables have also been proposed as important factors in the evolution of body size: basal metabolic rate, cost of transport, dominance in a community, success in mating, size and type of food, and competition (Millien *et al*., 2006 and literature therein).

In the specific case of South America, factors other than climatic change could have helped to trigger this spectacular coordinated phenomenon. On the one hand, the withdrawal of the Paranense Sea in the late Miocene allowed the development of wide plains (Pascual and Bondesio, 1982; Ortiz Jaureguizar and Cladera, 2006) represented, for example, by localities 35 and 36 in figure 2.2. On the other hand, the diversity of some large autochthonous herbivores decreased since the late Miocene (*e.g.*, the Astrapotheria which became extinct during the middle Miocene, or the large toxodont notoungulates which became very rare (Bond, 1999; Vizcaino *et al*., 2012a)). It is also possible that the appearance and diversification of eutherian carnivores on the continent (Prevosti and Soibelzon, 2012) also favored the development of large sizes as a way to avoid predation.

Species richness of gigantic caviomorphs

Among gigantic rodents, several species have been recognized exclusively on the basis of differences in size. One of the paradigmatic cases is that of the numerous nominal genera and species described for the assemblages of capybaras found at a single site (Deschamps *et al*., 2007; Vucetich, *et al*., 2005a, 2014a, b). Taking an ontogenetic approach, these materials turned out to be juveniles and adults of a single species. This led to a strong reduction in the number of capybaras species. Moreover, one single species of capybaras would be present in each locality (Deschamps *et al*., 2013; Vucetich *et al*., 2014b). In the case of capybaras, the change in size is associated with a strong morphological change in molars because teeth grow allometrically (Vucetich *et al*., 2005a).

The case of eumegamyines and neoepiblemids has been less explored (but see Vucetich *et al*., 2010a). In these two groups, teeth grow isometrically, and there is not a strong morphological difference between small and large specimens. For neoepiblemids in particular, several species have been recognized both for the "conglomerado osífero" and the Urumaco Formation (Mones, 1981; Horovitz *et al*., 2005), on the basis of a few morphological differences but mainly in differences in size. However, it is reasonable to think that in each locality, specimens of different sizes represent juveniles and adults of the same species. Rinderknecht *et al.* (2011b) reached a similar conclusion for the dinomyid *Isostylomys*.

Final remarks

Caviomorph rodents have a very rich fossil record that provided a good basis for understanding the major pathways of their evolution at least in southern South America. The evolution of caviomorphs in intertropical South America is less known, although our knowledge of the Quaternary record has been improved during recent years.

The caviomorph ancestors probably entered South America during the middle Eocene by rafting from Africa, and the first steps of their evolution occurred in intertropical areas. The evidence strongly suggests that the initial radiation of caviomorphs was more complex than hitherto postulated, with the differentiation of some taxa that cannot be assigned to any of the major clades in which caviomorphs are classically divided (the superfamilies Octodontoidea, Erethizontoidea, Cavioidea, and Chinchilloidea). Caviomorphs arrived in Patagonia during the latest Eocene or early Oligocene, and by the late Oligocene they were highly diversified, with the representatives of the four main lineages being recognizable already. A large morphological disparity, at least in tooth morphology was then acquired.

The early evolution of each large clade was also more complex than previously proposed, especially for chinchilloids and pan-octodontoids. The first stages of the evolution of cavioids are more obscure because they are recognized through relatively derived Deseadan species of Cavioidea *s.s.* and because it is necessary to resolve the relationships of the middle Eocene-early Oligocene taxa proposed as Cavioidea. The steps that led to the differentiation of Dasyproctidae, Cuniculidae, and the Miocene Patagonian forms such as *Neoreomys* are not known or not well understood yet.

A better understanding of the evolutionary history of caviomorphs requires more prospecting, especially in the intertropical region, in order to recover new and more complete materials. As well, new phylogenetic analyses including a larger number of taxa will shed light on their relationships, and further paleobiological studies are necessary to understand their response to the changing environments across the Cenozoic.

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Appendix 1. List of South American caviomorph taxa and their temporal distribution.

Taxa	**Ct**	**SR**	**Ti**	**“LC””**	**De**	**Co**	**“Pi”**	**Sa**	**CC**	**“EP”**	**LaV**	**“May”**	**Ch**	**Hu**	**Mo**	**Chp**	**Marp**	**Ens**	**Bon**	**Luj**	**Re**
Cavioidea																					
“Eocardiidae”																					
Asteromys					1																
Chubutomys					1	1															
Luantus						1	1														
Phanomys							1	1													
Schistomys								1													
Eocardia								1	1												
Matiamys									1												
Microcardiodon										1											
Guiomys										1	1										

Taxa	Ct	SR	Ti	“LC””	De	Co	“Pi”	Sa	CC	“EP”	LaV	“May”	Ch	Hu	Mo	Chp	Marp	Ens	Bon	Luj	Re
Caviidae																					
Prodolichotis											1		1	1							
Allocavia													1								
Orthomyctera													1	1	1	1	1				
Pliodolichotis														1							
Palaeocavia														1	1	1	1				
Microcavia															?	1	1	1	1	1	1
Neocavia																1					
Dolicavia																1					
Dolichotis																?	1	1	1	1	1
Cavia																	1	1	1	1	1
Propediolagus																		?			
Galea																		1	1	1	1
Cardiatherium													1	1							
Phugatherium															1	1					
Hydrochoeropsis																	1				
Neochoerus																		1	1	1	
Hydrochoerus																				1	1
Xenocardia													?								
Cardiomys												1	1	1							
Caviodon														1	1	1	1				
Procardiomys													1								
Kerodon																					1
Dasyproctidae																					
Plesiaguti																			1		
Dasyprocta?														1							
Dasyprocta																					1
Myoprocta																					1
Cavioidea inc. sedis																					
cf. *Eobranisamys*	1			1																	
Eobranisamys		1																			
Eopicure		1																			
Andemys			1																		
Branisamys					1																
Australoprocta							1														

Taxa	**Ct**	**SR**	**Ti**	**“LC””**	**De**	**Co**	**“Pi”**	**Sa**	**CC**	**“EP”**	**LaV**	**“May”**	**Ch**	**Hu**	**Mo**	**Chp**	**Marp**	**Ens**	**Bon**	**Luj**	**Re**
Neoreomys							1	1			?										
Scleromys							1	1	1												
Megastus									1												
Olenopsis									1												
Alloiomys											1										
Mesoprocta											1										
Microscleromys											1										
Cephalomyidae																					
Cephalomys					1																
Litodontomys					1																
Cephalomyopsis					1	1															
Palmiramys					1																
Soriamys						1	1														
Banderomys						1															
Cuniculidae																					
Cuniculus																				1	1
Basal Chinchillidae																					
Loncolicu					1																
Incamys					1																
Garridomys					1																
Neoepiblemidae																					
Scotamys					1																
Perimys						1	1	1													
Phoberomys														1							
Neoepiblema														1							
Dinomyidae																					
Eusigmomys												1		?							
Simplimus												1		?							
Carlesia													1	1							
Gyriabrus													1	1							
Arazamys														1							
Diaphoromys														1	1						
Tetrastylus														1							
Eumegamys														1	1						
Tetrastylopsis														1	?						

Taxa	**Ct**	**SR**	**Ti**	**“LC””**	**De**	**Co**	**“Pi”**	**Sa**	**CC**	**“EP”**	**LaV**	**“May”**	**Ch**	**Hu**	**Mo**	**Chp**	**Marp**	**Ens**	**Bon**	**Luj**	**Re**
Isostylomys														1	?						
Briaromys														1							
Doellomys														1							
Potamarchus														1							
Pentastylodon														1							
Rusconia														1							
Telodontomys														1							
Pseudosigmomys														1	1	1					
Pseudopotamarchus														1							
Telicomys														1							
Eumegamysops														1							
Protomegamys																1					
Josephoartigasia																	1				
Aenigmys																		1			
“Tetrastylus”																				1	
Dinomys																					1
Chinchillidae																					
Eoviscaccia			1		1	1															
Prolagostomus							1	1	1												
Pliolagostomus								1	1												
Lagostomus													1	1	1	1	1	1	1	1	1
Lagidium																				1	1
Chinchilla																					1
Pan-Octodontoidea																					
Stem Octodontoidea																					
Eoespina	1	1																			
Eosallamys		1																			
Eosachacui		1																			
Vallehermosomys				1																	
Draconomys				1																	
Acarechimys					1	1	1	1	1		1										
Protacaremys?					1																
Deseadomys					1																
Paulacoutomys					1																
Migraveramus					1																

Taxa	Ct	SR	Ti	“LC””	De	Co	“Pi”	Sa	CC	“EP”	LaV	“May”	Ch	Hu	Mo	Chp	Marp	Ens	Bon	Luj	Re
Leucokephalos					1																
Llitum					1																
Sallamys					1																
Protacaremys						1	1	1	1												
Dudumus						1															
Willidewu						1															
Protadelphomys						1															
Caviocricetus						1															
Prospaniomys						1															
Plesiacarechimys									1												
Acaremyidae																					
Platypittamys					1																
Changquin					1																
Galileomys					1	1	1	1	1												
Acaremys						1	1	1													
Sciamys								1	1	1											
Pseudoacaremys								1	1	1											
Crown-Octodontoidea																					
Chasicomys													1								
Chasichimys													1	1							
Neophanomys														1							
aff. *Neophanomys*															1						
Myocastorinae																					
Eodelphomys		1																			
Ethelomys					1																
Xylechimys					1																
Paradelphomys						1															
Prostichomys							1														
Stichomys							1	1	1												
Spaniomys							1	1													
Adelphomys							1	1													
Paramyocastor															1	1					
Tramyocastor																	?				
Myocastor														1				1	1	1	1
Octodontidae																					

Taxa	**Ct**	**SR**	**Ti**	**“LC”’**	**De**	**Co**	**“Pi”**	**Sa**	**CC**	**“EP”**	**LaV**	**“May”**	**Ch**	**Hu**	**Mo**	**Chp**	**Marp**	**Ens**	**Bon**	**Luj**	**Re**
Massoiamys									1	1											
Palaeoctodon													1	?	?						
Phtoramys														1	1						
Xenodontomys														1							
Pseudoplateomys														1	1						
Pithanotomys															1	1	1				
Abalosia																	1				
Aconaemys																					1
Octodon																					1
Octodontomys																					1
Octomys																					1
Tympanoctomys																		1			1
Spalacopus																					1
Actenomys															1	1	1				
Eucelophorus															1	1	1	1			
Praectenomys																?					
Ctenomys																	1	1	1	1	1
Echimyidae																					
Maruchito									1												
Gen. nov. 1									1												
Gen. nov. 2									1												
Gen. nov. 3									1												
Ricardomys											1										
Quebradahondomys											1										
Echimyidae indet.											1										
Pampamys														1							
Reigechimys														1							
Theridomysops														1							
Eumysops														?	1	1	1	1	1	1	
“E.” ponderosus														1							
“E.” intermedius														1							
“E.” serridens														?							
“E.” parodii														1							
Haplostropha														1							
Eumysopinae nov.																1					

Taxa	**Ct**	**SR**	**Ti**	**“LC””**	**De**	**Co**	**“Pi”**	**Sa**	**CC**	**“EP”**	**LaV**	**“May”**	**Ch**	**Hu**	**Mo**	**Chp**	**Marp**	**Ens**	**Bon**	**Luj**	**Re**
aff. *Clyomys*																			1		
Clyomys																				1	1
Euryzygomatomys																				1	1
Dicolpomys																				1	1
Callistomys																				1	1
Carterodon																				1	1
Dactylomys																				1	1
Echimys																				1	1
Thrichomys																					1
Proechimys																					1
Mesomys																					1
Hoplomys																					1
Trinomys																					1
Isothrix																					1
Lonchothrix																					1
Kannabateomys																					1
Olallamys																					1
Nelomys																					1
Toromys																					1
Pattonomys																					1
Phyllomys																					1
Abrocomidae																					
Protabrocoma													?	1	1						
Abrocoma																		1		1	1
Cuscomys																					1
Erethizontoidea																					
Erethizontidae																					
Eopululo		1																			
Protosteiromys					1																
Hypsosteiromys						1															
Eosteiromys						1	1														
Parasteiromys						1															
Branisamyopsis						1	1														
Steiromys							1	1	?		?										
Neosteiromys									?					1							

Taxa	**Ct**	**SR**	**Ti**	**“LC””**	**De**	**Co**	**“Pi”**	**Sa**	**CC**	**“EP”**	**LaV**	**“May”**	**Ch**	**Hu**	**Mo**	**Chp**	**Marp**	**Ens**	**Bon**	**Luj**	**Re**
Microsteiromys											1										
Paradoxomys														1							
Coendu																				1	1
Sphiggurus																					1
Chaetomys																					1
Erethizontidae?																					
Disteiromys												1									
Caviomorpha inc. sed.																					
Cachiyacuy	1																				
Canaanimys	1																				
Eoincamys		1																			
Luribayomys					1																

2 | EVOLUTION OF CAVIOMORPH RODENTS: A COMPLETE PHYLOGENY AND TIMETREE FOR LIVING GENERA

EVOLUCIÓN DE LOS ROEDORES CAVIOMORFOS: FILOGENIA Y ÁRBOL TEMPORAL COMPLETO DE LOS GÉNEROS VIVIENTES

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Abstract. The Caviomorpha is a diverse lineage of hystricognath rodents endemic to the Americas and Caribbean islands. We analyzed evolutionary relationships within 11 families of caviomorphs and their relatives in the suborder Ctenohystrica using a supermatrix of 199 taxa and DNA sequences from five genes. New gene sequences were generated for 33 genera, including 12 genera newly available for molecular analysis. Presented here are the analyses pruned to a single representative for each genus, totaling 68 of the 70 living genera in Ctenohystrica. Our analyses recovered strong support for Hystricognathi containing the monophyletic groups Hystricidae, Phiomorpha, and Caviomorpha, with the latter two groups as well-supported sister taxa. The analyses also strongly supported the monophyly of the four traditional superfamilies of caviomorphs, with Cavioidea + Erethizontoidea and Chinchilloidea (including Dinomyidae) + Octodontoidea. Cuniculidae + Dasyproctidae are recovered as sister to Caviidae (including *Hydrochoerus*). Abrocomidae (including *Cuscomys*) is sister to the remaining octodontoid families, consisting of the dyads Octodontidae + Ctenomyidae and Echimyidae (including *Myocastor*) + Capromyidae. The five genera of capromyids form a robustly monophyletic group, but they are allied to a group of Brazilian echimyids, rendering Echimyidae paraphyletic. We dated nodes in our tree by comparing eight sets of fossil calibrations, identifying a set of 22 calibrations that minimized internal age conflicts.The resulting timetree dates the Hystricognathi crown to the Middle Eocene, 44.9 Ma, and the phiomorph-caviomorph split to 42.0 Ma. Crown caviomorphs diverged at 35.7 Ma, and splits of Cavioidea-Erethizontoidea and Chinchilloidea-Octodontoidea occurred at 32.4 Ma and 32.8 Ma, respectively. Most families appeared in the late Oligocene-Early Miocene and virtually all genera are of Middle-Late Miocene age, with a few exceptions. We briefly consider geo-climatic changes that might have influenced the evolution of hystricognath rodents, deferring to another work a detailed analysis of their rates and ecological drivers of diversification.

Resumen. Los caviomorfos constituyen un linaje diverso de roedores histricognatos endémicos de las Américas y las islas del Caribe. En este estudio, analizamos secuencias de ADN (mitocondrial y exones nucleares) de cinco genes en el suborden Ctenohystrica, incluyendo roedores de las familias Diatomyidae, Ctenodactylidae, Hystricidae, Petromuridae, Thryonomyidae, Bathyergidae, y 11 familias de caviomorfos. Se generaron nuevas secuencias de cyt-*b*, 12S rRNA, GHR, vWF, y/o RAG1 para 33 géneros, 31 de estos caviomorfos, 12 de las cuales corresponden a secuencias nuevas disponibles para análisis filogenéticos. Se utilizó una supermatriz de 199 taxa y 5194 pb de ADN para el análisis de las relaciones evolutivas del

grupo. En este estudio, se redujeron los análisis a un solo representante por cada género, incluyendo un total de 68 de los 70 géneros vivientes de Ctenohystrica. Nuestros análisis recuperan un fuerte soporte para Hystricognathi: puercoespines del Viejo Mundo + fiomorfos + caviomorfos, con monofilia para los tres grupos: Phiomorpha con Bathyergidae y hermano de Petromuridae + Thryonomyidae; y los fiomorfos como grupo hermano de Caviomorpha. Los análisis también soportan fuertemente la monofilia de las cuatro superfamilias tradicionales de caviomorfos, con Cavioidea como hermana de Erethizontoidea y Chinchilloidea (incluyendo Dinomyidae) como hermana de Octodontoidea. Cuniculidae + Dasyproctidae fueron recuperadas como grupo hermano de Caviidae (incluyendo *Hydrochoerus*). Abrocomidae (incluyendo *Cuscomys*) aparece como hermana del resto de las familias de octodontoideos, consistiendo en las siguientes díadas: Octodontidae + Ctenomyidae y Echimyidae (incluyendo *Myocastor*) + Capromyidae. Aunque cinco géneros de caprómidos conforman un robusto grupo monofilético, fueron recuperados como grupo hermano de los equímidos brasileros (*Carterodon, Clyomys, Euryzygomatomys*, y *Trinomys*) quedando Echimyidae como parafilético. Datamos los nodos de nuestro árbol, comparando ocho grupos de calibraciones fósiles para identificar un grupo de 22 puntos de calibración, los que minimizaron los conflictos de edad entre las dataciones. El árbol calibrado resultante ubica el origen de la divergencia del grupo corona de Hystricognathi en el Eoceno medio (44.9 Ma), poco antes de la separación de Phiomorpha respecto de Caviomorpha hace 42.0 Ma. El grupo corona de caviomorfos divergió hace 35.7 Ma, separándose Cavioidea respecto de Erethizontoidea, y Chinchilloidea respecto de Octodontoidea hace 32.4 Ma y 32.8 Ma, respectivamente. El árbol datado muestra que la mayoría de las familias aparecieron en el Oligoceno tardío o en el Mioceno temprano. Virtualmente todos los géneros tuvieron su origen hacia el Mioceno medio a tardío, con algunas excepciones notables. Los antepasados de los caviomorfos habitaron ambientes variados y dinámicos durante el Eoceno medio-Reciente, historia que probablemente configuró su trayectoria evolutiva. La diversificación inicial de Caviomorpha en cuatro superfamilias fuertemente diferenciadas coincide con un evento de enfriamiento global dramático, cerca del límite Eoceno-Oligoceno, que representa la transición desde un "planeta invernadero" (caliente, húmedo y carente de casquetes polares) a un planeta más frío y seco, con presencia de glaciaciones. Durante el Mioceno medio (~15 Ma), el levantamiento de los Andes Centrales creó un patrón de lluvias en gran parte del este de América del Sur, con la transformación del continente, en términos generales, en biomas que fueron áridos en el sur y mésicos en el norte, cada uno con desafíos ambientales distintivos para los caviomorfos residentes. El registro fósil de Octodontoidea parece reflejar estos cambios. Así, el clado Echimyidae-Capromyidae adaptado a ambientes mésicos, se encuentra representado en las localidades de la Patagonia durante el Mioceno, pero es reemplazado posteriormente por una mayor diversidad de formas adaptadas a ambientes áridos, tales como Octodontidae-Ctenomyidae. Nuestro reloj molecular sugiere que estos clados principales de Octodontoidea experimentaron diversificaciones que son aproximadamente coetáneas (18.2 Ma y 18.9 Ma, respectivamente), más o menos concordantes con el principio de la diferenciación climática en todo el continente. Los datos espacio-temporales y ecomorfológicos del registro fósil necesitan correlacionarse, adicionalmente, con la aridez progresiva de la región, sobre todo ahora que la secuencia de eventos de diversificación del linaje se puede inferir a partir del reloj molecular. Nos resta abordar en futuros trabajos, una evaluación más detallada del tiempo, el modo y los factores ecológicos que estuvieron asociados a la diversificación biológica de los roedores caviomorfos.

Introduction

Studying how and when lineages diversify is a central strategy for illuminating the history of life. Yet investigating the timing and drivers of diversification requires first establishing a common timescale of evolutionary and geologic events. Whereas molecular phylogenies yield relative estimates of divergence timing in units of DNA substitutions, geologic ages (*e.g.*, from fossils) are needed to convert those molecular divergences to absolute time in years. Because the oldest diagnostic fossil in a clade establishes its minimum age, molecular rates can be calibrated to time and used with relaxed-clock models of among-species rate variation to estimate divergence times (Drummond *et al.*, 2006; Ho and Phillips, 2009). Phylogenetic trees that are scaled to time (hereafter referred to as "timetrees;" Hedges and Kumar, 2009) allow comparisons of timing and rates of diversification among clades, across taxa, and in relation to known geologic events (*e.g.*, Dávalos, 2010; Schenk *et al.*, 2013).The ability to contrast patterns of evolution in contemporaneous units enables the investigation of evolutionary tempo and mode from molecular phylogenies (Nee *et al.*, 1992), and presents new ways to test long-standing hypotheses, *e.g.*, assesing the biogeographic origins of lineages (Ronquist, 1997; Ree *et al.*, 2005).

Here we investigate the timescale of evolution across a speciose and fossil-rich clade of Neotropical rodents (Hystricognathi: Caviomorpha). This American and Caribbean lineage is an exceptionally diverse radiation comprised of four superfamilies, 11 families, and at least 244 living species. The Octodontoidea (spiny rats, degus, and their allies) are the most diverse, comprising 70% of caviomorph genera and 75% of living species. However, Cavioidea (guinea pigs and capybaras) and Chinchilloidea (chinchillas and pacaranas) both formerly exhibited considerably greater diversity: each superfamily was represented by 20 genera during the Late Miocene (11.2-5.3 Ma), alongside 18 genera of octodontoids from the same time period (McKenna and Bell, 1997; Upham, 2014). Analyses of their diversity over time are, however, beyond the scope of this paper and are instead the subject of a succeeding one. Here we focus on the phylogenetic relationships of living caviomorph genera.

Caviomorph rodents and each of the four superfamilies that comprise this group are mainly distributed in South America (Fig. 1). The overall pattern of caviomorph species richness (Fig. 1.1) is founded in that of Octodontoidea (Fig. 1.2); this group has concentrated richness in Amazonia and the Atlantic Forest but is distributed from the Greater Antilles and Central America to Tierra del Fuego and in most intervening habitats. Collectively, octodontoids exploit most niches available to rodents, assuming tree-living (arboreal and scansorial), burrowing (semi-fossorial and fossorial), terrestrial, rock-dwelling, and even semi-aquatic forms (Reig, 1981; Mares and Ojeda, 1982). The next-most diverse lineage is the Cavioidea (Fig. 1.3), whose geographic range is nearly as extensive as the octodontoids but with peak richness in the Guianan and Brazilian highlands. Cavioids encompass remarkable morphological disparity (including near-cursorial digitigrades and the largest living rodents), inhabit various ecosystems, and display diverse levels of sociality (Rowe and Honeycutt, 2002; Perez and Pol, 2012). The Erethizontoidea (Fig. 1.4) are widely distributed but only modestly diversified as medium-sized arboreal herbivores (Voss, 2011; Voss *et al.*, 2013); this group includes the only caviomorph lineage to colonize Nearctic portions of North America. Finally, the Chinchilloidea (Fig. 1.5) are represented by a couple of distantly related lineages that inhabit arid habitats and wet forests, respectively, in western South America (Mones, 1981; Spotorno *et al.*, 2004).

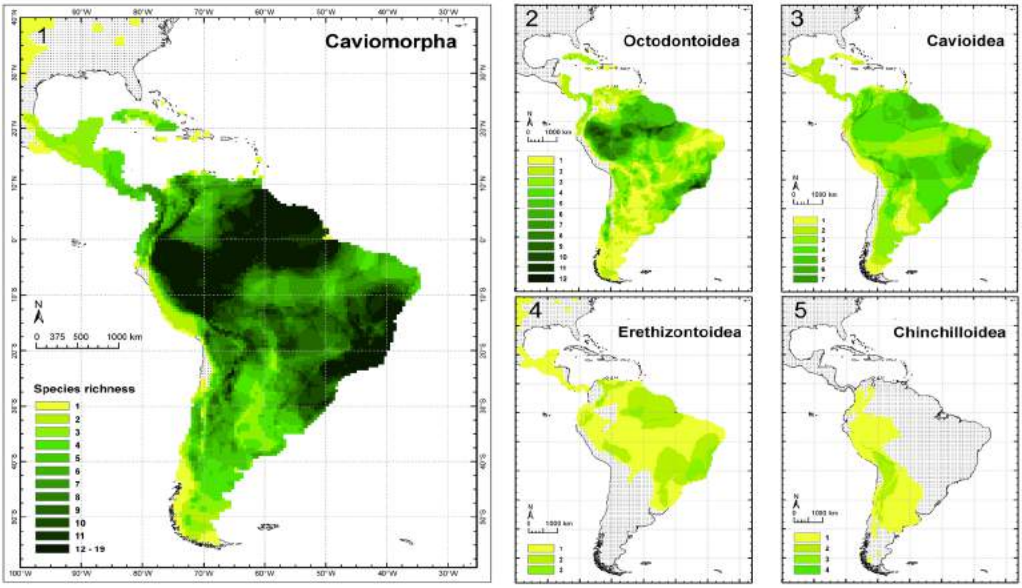

Figure 1. Species richness maps based on known geographic ranges and extant species of caviomorph rodents: 1. Caviomorpha, and its four component superfamilies; 2. Octodontoidea; 3. Cavioidea; 4. Erethizontoidea; and 5. Chinchilloidea. Species richness estimates are based on range overlap within 0.5 degree square grid cells, and are calculated using .shp files updated from the IUCN (2012) database.

Some caviomorphs adopt lifestyles exploited elsewhere by distantly related rodent groups like tree and ground squirrels, pocket gophers, and muskrats. Others may be ecological analogues to hyraxes (Hyracoidea: Procaviidae), duikers (Bovidae: Cephalophinae), rabbits and hares (Leporidae), hippos (Hippopotamidae), and chevrotains (Tragulidae; Mares and Ojeda, 1982). All of these other groups were absent from South America during most of its Cenozoic isolation as an island continent (Simpson, 1980). The sudden appearance of caviomorphs during the midst of this isolation (Wyss *et al.*, 1993; Campbell, 2004), their extensive fossil record back to the Middle Eocene (McKenna and Bell, 1997; Antoine *et al.*, 2012), and their modern ecological diversity and morphological disparity make Caviomorpha an excellent lineage for investigating biotic responses to changing landscapes (Veblen *et al.*, 2007; Madden *et al.*, 2010), climates (Hooghiemstra and van der Hammen, 1998), and biotas (Goin *et al.*, 2010).

We aim to construct a robust genus-level timetree from multiple genes and fossil calibrations to enable assessment of the patterns, tempo, and modes of diversification of Caviomorpha. In the present chapter we seek to: 1) identify its higher-level relationships to sister lineages in Africa and Asia; 2) identify and detail the relationships among all living caviomorph genera; and 3) reconstruct the timing of diversification throughout the group's Paleogene-to-Neogene radiation.

Materials and methods

Taxon sampling

The Suborder Ctenohystrica is one of three higher-level clades in Rodentia supported by recent molecular phylogenetic studies, others being the "mouse-related" and "squirrel-related" clades (Huchon *et al.*, 2000; Huchon *et al.*, 2007; Montgelard *et al.*, 2008; Blanga-Kanfi *et al.*, 2009; Churakov *et al.*, 2010; Fabre *et al.*, 2012a; Wu *et al.*, 2012). Some refer to this group as Hystricomorpha (Carleton and Musser, 2005), but to differentiate it from the hystricomorphous condition of rodent masseter muscles (not shared by all members) we employ the term Ctenohystrica (Huchon *et al.*, 2000).The Ctenohystrica includes 18 of the 33 living families of rodents, and is divided into the Ctenodactylomorphi, consisting of two small relict families in North Africa and Southeast Asia, and Hystricognathi, which consists of 16 tropical families, one reaching into North America (Carleton and Musser, 2005; Huchon *et al.*, 2007). Hystricognathi is then divided into the Old World porcupines (Hystricidae), Phiomorpha in Africa (three living families of mole-rats, dassie rats, and cane rats), and Caviomorpha in the Americas and Caribbean (11 living families, including *Myocastor* within Echimyidae, and *Hydrochoerus* within Caviidae) (Huchon and Douzery, 2001; Carleton and Musser, 2005; Martin, 2005; Opazo, 2005; Sallam *et al.*, 2009; Fabre *et al.*, 2012b; Upham and Patterson, 2012; Honeycutt, 2013).

Here we present patterns of evolution among genera that are based upon phylogenetic analyses conducted across 198 species in Ctenohystrica and presented in Upham (2014). In this study, we describe all aspects of the phylogenetic reconstruction –including DNA sequencing and alignments, GenBank accession numbers, gene combinability analyses, and fossil calibrations– in order to facilitate future work on this fascinating group of mammals.

Our analyses included dense taxon sampling across all families in Ctenohystrica, employing one representative per species and as many species as possible (Tab. 1; App. 1). We sampled 68 of 70 living genera in Ctenohystrica, all genera in Hystricognathi, and 69% of the living species (Tab. 1). Although most species sampled were from Octodontoidea (126 species), species sampling within superfamilies was roughly proportional to their extant diversity (62-88% of species; Tab. 1). The springhaas *Pedetes* (Anomaluromorpha) was the outgroup for all phylogenetic analyses because it is a member of the mouse-related clade most likely to be sister to Ctenohystrica (but see Huchon *et al.*, 2007; Montgelard *et al.*, 2008; Blanga-Kanfi*et al.*, 2009; Churakov *et al.*, 2010; Fabre *et al.*, 2012a). The classification, taxon and gene sampling, and GenBank accession numbers for this study are presented in Appendix 1.

Gene sampling

The gene sampling from two earlier studies of caviomorph rodent evolution (Upham and Patterson, 2012; Upham *et al.*, 2013) provided the foundation for this study. We generated an assortment of new DNA sequences for five genes that are listed in Appendix 1. These include two mitochondrial loci [mtDNA; cytochrome-*b* (cyt-*b*) and 12S ribosomal RNA (12S rRNA)] and three unlinked nuclear exons [growth hormone receptor exon 10 (GHR), von Willebrand factor exon 28 (vWF), and recombination activating gene 1 (RAG1)]. These genes were selected on the basis of variation in evolutionary rates (mitochondrial *vs.* nuclear), the diversity of taxa previously sampled, and their demonstrated utility in rodent phylogenetics (Huchon and Douzery, 2001; Honeycutt *et al.*, 2003; Galewski *et al.*, 2005; Opazo, 2005; Patterson and Velazco, 2008; Upham and Patterson, 2012). The use of cyt-*b* in this study lends breadth to our taxon sampling, particularly at the species-level (*e.g.*, in Ctenomyidae; Parada *et al.*, 2011), that has been lacking in evolutionary studies of Caviomorpha as a whole.

Table 1. Living diversity of rodent families in Ctenohystrica and the taxa sampled for one or more genes in this study. Taxonomy and counts are updated from Woods and Kilpatrick (2005). An asterisk (*) signifies all members sampled. Bold values differentiate higher clades from families.

Family	**Genera**			**Species**		
	Living	**Sampled**	**%**	**Living**	**Sampled**	**%**
CTENOHYSTRICA	70	68	97	288	198	69
CTENODACTYLOMORPHI	5	3	60	6	3	50
Ctenodactylidae	4	2	50	5	2	40
Diatomyidae	1	1	*	1	1	*
HYSTRICOGNATHI	65	65	*	282	195	69
Hystricidae	3	3	*	11	7	64
PHIOMORPHA	8	8	*	27	21	78
Bathyergidae	6	6	*	24	19	79
Petromuridae	1	1	*	1	1	*
Thryonomyidae	1	1	*	2	1	50
CAVIOMORPHA	54	54	*	244	167	68
ERETHIZONTOIDEA	3	3	*	16	14	88
Erethizontidae	3	3	*	16	14	88
CAVIOIDEA	9	9	*	34	21	62
Caviidae	6	6	*	19	14	74
Cuniculidae	1	1	*	2	2	*
Dasyproctidae	2	2	*	13	5	38
CHINCHILLIOIDEA	4	4	*	8	6	75
Chinchillidae	3	3	*	7	5	71
Dinomyidae	1	1	*	1	1	*
OCTODONTOIDEA	38	38	*	186	126	68
Abrocomidae	2	2	*	9	4	44
Octodontidae	8	8	*	13	12	92
Ctenomyidae	1	1	*	62	46	74
Echimyidae	22	22	*	89	56	63
Capromyidae	5	5	*	13	8	62

BOX 1

DNA sequencing from fresh and dried tissue

We isolated genomic DNA from frozen fresh tissues (liver, kidney or muscle) preserved in ethanol, or from dried tissues (muscle, skin) adhering to museum voucher specimens. Fresh tissue DNA was extracted from 37 specimens for this study, using either the DNeasy Blood & Tissue Kit (QIAGEN) or phenol-chloroform methods, both following standard protocols. Molecular laboratory work on fresh tissues was conducted in three labs depending on the source of the tissues: Pritzker Laboratory for Molecular Systematics and Evolution (Field Museum of Natural History, Chicago, IL, USA), Laboratory of Molecular Systematics (Royal Ontario Museum, Toronto, ON, Canada), and Laboratório de Mastozoologia e Biogeografia (Universidade Federal do Espírito Santo, Vitória, ES, Brazil). Nucleic acid concentrations were quantified using a NanoDrop spectrophotometer (Thermo Fisher Scientific).

Dried-tissue DNA, also called ancient DNA (aDNA), was extracted from eight specimens for this study and analyzed at the McMaster University Ancient DNA Centre (Hamilton, ON, Canada). These were: *Abrocoma boliviensis* [Museum of Vertebrate Zoology (MVZ) 120238, collected in 1955], *Santamartamys rufodorsalis* [American Museum of Natural History (AMNH) 34392, collected in 1912], *Diplomys labilis* [Field Museum of Natural History (FMNH) 70101, collected in 1954], *Pattonomys occasius* (FMNH 84259, collected in 1958), *Pattonomys semivillosus* (FMNH 69118, collected in 1953), *Toromys rhipidurus* (FMNH 87244, collected in 1960), *Geocapromys ingrahami* (FMNH 5624, collected in 1891), and *Plagiodontia aedium* (FMNH 63876, collected in 1948). *For Plagiodontia*, an additional fresh-tissue specimen [University of Vermont, Zadock Thompson Natural History Collections (ZTNH) 843] was sequenced for vWF and RAG1 and combined with cyt-b and GHR fragments from FMNH 63876 for analysis. We also included additional DNA sequences from dried tissues of *Olallamys albicauda, Toromys grandis, Isothrix barbarabrownae, I. orinoci*, and *I. pagurus* reported by Upham *et al.* (2013).

For aDNA specimens, dried tissues adhering to the cranium, mandible, and vertebrae ("crusties") were removed, shipped at ambient temperature to the Royal Ontario Museum (Toronto, Canada), and hand-carried to McMaster University. We used published aDNA protocols (Poinar *et al.*, 2006; Debruyne *et al.*, 2008) at McMaster, including the use of dedicated clean-room facilities for all pre-PCR work. Approximately 25 mg of each sample along with one extraction blank were incubated in 0.5 ml of 0.5 M EDTA pH 8.0 (EMD Chemicals) for 24 hours at 25º C using gentle agitation (1000 rpm). Samples were centrifuged at high speed and the EDTA supernatants were transferred to 5 ml tubes and processed separately. To the remaining tissue in each sample, we added 0.5 ml of custom digestion buffer [20 mMTris (EMD Chemicals) at pH 8.0, 0.5% N-Lauroylsarcosine (Sigma), 250 mg/ml Proteinase K (Thermo Fisher Scientific), 5 mM CaCl2 (EMD Chemicals), 50 mM DTT (EMD Chemicals), 1% PVP (EMD Chemicals), and 2.5 mM PTB (Prime Organics)]. After incubating at 55°C for 12-24 hours on a rotary wheel, samples were again spun down and the supernatant transferred to the same 5 ml tube. This demineralization-digestion process was repeated three times and the resultant ~3 ml of supernatant formed the raw DNA extract for further purification. Leftover tissue pellets were discarded or saved for future use. Organic purification was performed on each supernatant sample, first using 1.0 ml of phenol-chloroform-isoamylalcohol (25:24:1, pH 8, Fluka) and then 1.0 ml of chloroform (Fluka), retaining only the aqueous phase in each step. Samples were concentrated by ultrafiltration with Amicon Ultra 30K columns (Millipore), washed with three steps of 450 µl of 0.1x TE+Tween [10 mMTris, 0.1 mM EDTA, 0.05% Tween-20 (Sigma), pH 8.0], and the DNA was finally eluted in 80 µL of 0.1x TE+Tween.

Polymerase chain reaction (PCR) was carried out on all DNA extractions to amplify target genes. Each PCR had a reaction volume of 10 µl and contained 1.0 µl of DNA template, 1.0 µl 10x reaction buffer, 1.0 µl of 8 mM premixed deoxynucleotide triphosphates (dNTPs; 200 µM each nucleotide in final reaction), 1.0 µl of 25 mM $MgCl_2$, 0.5 µl of 10 mg/µl bovine serum albumin (Applied Biosystems), 4.4 µl of double-distilled H_2O (dH_2O), 0.1 µl of 5 U/µlAmpliTaq Gold™ DNA polymerase (Applied Biosystems), and 0.5 µl of each 10 µM priming oligonucleotide. PCRs performed on aDNA samples differed from fresh DNA reactions in the concentration of dNTPs (400 µM) and DNA polymerase (0.2 U), the targeting of smaller gene fragments (200-400 bp), and the inclusion of DNA extraction blanks. All PCR primers, primer pairs, reaction profiles, and DNA sequencing details are given in Upham *et al.* (2013). Sequences were edited and assembled using Geneious 6.1.6 software (Biomatters).

BOX 2

Sequence alignment and gene combinability

Of the five genes analyzed, cyt-*b* was sampled from all but 10 of 199 total taxa (95% complete), while the sampling of other gene alignments was less complete (12S rRNA, 58%; GHR, 47%; vWF, 42%; and RAG1, 32%; App. 1).Two taxa were represented by chimeras in order to sample all five genes: *Pedetes* (union of *P. capensis* and *P. surdaster*) and *Ctenodactylus* (union of *C. gundi* and *C. vali*). All other taxa were single species, although in many cases, they were composites of genes from multiple voucher specimens. The use of museum voucher specimens as tissue sources permits these sequences to be reassessed, re-evaluated, and possibly even re-identified with future systematic understanding.

Sequences from each gene were multiply aligned to establish character homology in relation to outgroups. For 12S rRNA, we aligned sequences based on the secondary structural model of Springer and Douzery (1996) after an initial alignment generated in MUSCLE (Edgar, 2004). At sites where multiple indels made sequence alignment ambiguous, we discarded a total of 198 base pairs (bp) from the initial alignment of 1035 bp (positions 70-93, 117-125, 219-236, 299-302, 326-333, 384-408, 426-437, 503-515, 711-719, 782-804, and 934-986). Alignment trials with Gblocks v0.91b (Castresana, 2000) for 12S rRNA using the same settings as recent studies of rodent phylogeny (Montgelard *et al.*, 2008; Fabre *et al.*, 2012a) failed to remove several ambiguous regions, so these results were discarded. For protein-coding genes, we aligned sequences using ClustalW 2.1 (Larkin *et al.*, 2007) and verified that indels were in sets of three bp. Details of our resulting alignments are listed in Table 2.

We explored the potential for mutational saturation in all genes, particularly cyt-*b* (Griffiths, 1997; Farias *et al.*, 2001), using Xia's test implemented in DAMBE v5.3.52 (Xia *et al.*, 2003; Xia, 2013). Xia's test compares a standard index of substitution saturation (Iss) with an index of critical substitution saturation (Iss.c) calculated from the data via a resampling process to conservatively assess the degree of saturation in a gene. We ran tests for all genes using all sites, 200 replicates, and specifying the proportion of invariant sites. We also visually examined cyt-*b* saturation with plots of pairwise transitions and transitions versus genetic distance on a per codon basis and over all sites (see App. 3).

Prior to combining gene alignments, we explored the possibility of incongruence between gene histories (Wiens, 1998). To compare gene-tree topologies most accurately among differentially sampled data sets, we pruned each alignment to the most inclusive set of 50 species that were sampled for all five genes. Identical 50-species analyses were also performed on mtDNA (cyt-*b* + 12S rRNA) and nuclear exon (GHR + vWF + RAG1) data sets to compare phylogenetic patterning among genome sources with different routes of inheritance. Maximum likelihood (ML) phylogenetic trees were constructed from each data set using RAxML-HPC2 v7.6.3 (Stamatakis, 2006) on the XSEDE online computing cluster accessed via the CIPRES Science Gateway (Miller *et al.*, 2010). The best-fit model of nucleotide evolution for each gene was general time-reversible (GTR) plus among-site rate variation (G), as found using jModelTest v2.1.4 (Darriba *et al.*, 2012). Models including G and the proportion of invariant sites (I) were in some cases better fitting, but concerns over the non-independence of I and G (Sullivan *et al.*, 1999; Mayrose *et al.*, 2005; Stamatakis, 2006) motivated us to employ the simpler GTR+G model in all cases. Rapid bootstrapping was performed for each gene alignment using the "–f a" option and 1000 bootstrap replicates, resulting in best-scoring ML trees annotated with values for bootstrap support (BS). We then compared topologies and nodal support values across data sets (Fig. 2; Tab. 3). The absence of topological conflict at basal nodes (Tab. 3; see Results for discussion) allowed us to concatenate the single-gene data sets into a supermatrix of characters for all 199 taxa, thereby maximizing both taxonomic and genetic diversity in the phylogeny (approach reviewed by de Queiroz and Gatesy, 2007). The presence of more than 2000 characters in the supermatrix for most taxa was expected to override any statistical biases resulting from missing data (Wiens, 2006; Lemmon *et al.*, 2009).

Table 2. DNA sequence characteristics for each single-gene alignment. Percent missing data was calculated without internal alignment gaps. Xia's test compares indices of substitution saturation for each gene alignment such that Iss > Iss.c indicates saturation, Iss < Iss.c indicates no saturation, and a non-significant difference ('NS') indicates some degree of saturation.

	mtDNA		**Nuclear exons**		
	cyt-*b*	**12S rRNA**	**GHR**	**vWF**	**RAG1**
No. taxa aligned	189	115	94	83	63
Total length (bp)	1140	837	884	1269	1064
Pars. inform. (all) (codons 1, 2, 3)	632 (166, 91, 375)	351	439	568	265
Missing data	13.70%	8.80%	8.60%	15.10%	16.60%
Invariant sites	31.70%	37.00%	13.40%	25.50%	47.10%
Base freq: A	30.80%	36.30%	29.20%	21.40%	26.10%
C	26.40%	21.60%	25.30%	28.90%	25.70%
G	12.60%	18.70%	22.50%	30.60%	26.80%
T	30.10%	23.40%	23.00%	19.20%	21.50%
Chi-square	577.5	128.5	118.6	158.1	80.8
df	564	342	279	246	186
P	0.338	~1.00	~1.00	~1.00	~1.00
Xia's test:	saturated	NS	unsaturated	NS	saturated
Iss	0.923	0.65	0.454	0.806	0.896
Iss.c	0.757	0.735	0.739	0.764	0.752
P	< 0.05	0.0725	< 0.05	0.1325	< 0.05

Phylogenetic analyses

The 5-gene supermatrix was analyzed using ML in RAxML and Bayesian inference (BI) in MrBayes version 3.2.1 (Ronquist and Huelsenbeck, 2003); both were run on the XSEDE computing cluster (Miller *et al.*, 2010). Both ML and BI analyses were partitioned using one DNA partition per gene and the GTR+G model specified, so that model parameters were estimated independently by partition. RAxML runs were executed using the rapid ML search and bootstrapping options with 1000 replicates and were repeated several times with random starting trees to verify both topology and clade support values (log-likelihood of -96325.2).

MrBayes runs were started with uniform priors and consisted of four concurrent incrementally heated chains (Metropolis-coupled Markov Chain Monte Carlo, MCMC; Ronquist and Huelsenbeck, 2003), sampling every 1000 generations over 40 million generations each. Six independent runs from random starting trees (three sets of two runs each) were compared by plotting -ln likelihood per generation in Tracer v1.5 (Rambaut and Drummond, 2007), and comparing marginal densities. After discarding the first 10% of samples as burn-in, convergent MCMC searches allowed us to combine a total of 216,000 trees (log-likelihood of -97040.3). We summarized the combined trees in TreeAnnotator v1.7.5 (Drummond and Rambaut, 2007), resulting in a single maximum-clade-credibility tree with the best *a posteriori* topology and nodes annotated with Bayesian posterior probabilities (PP).

Fossil calibrations

We assembled and evaluated the use of 25 fossil calibrations (points A-Y in Fig. 3; App. 2) for estimating clade divergence times in Ctenohystrica. These calibrations were grouped in eight different sets according to taxonomy, crown *vs*. stem placement, and previous analyses (Fig. 4.1). Resulting age estimates were then compared across calibrated nodes (Fig. 4.2), with non-overlapping 95% credibility intervals indicating that estimates were significantly different between calibration sets. The placement of calibrations relied on recent cladistic studies of living and fossil taxa (*e.g.*, Antoine *et al.*, 2012; Pérez and Pol, 2012; Verzi *et al.*, 2013) to allocate fossils among crown or stem groups depending on shared-derived morphological characters. Appendix 2 lists and justifies the minimum and maximum ages for each calibration point with reference to fossil taxa, locality and stratigraphic levels of collection, geologic age estimates, and analyses that identify the phylogenetic position of fossils, following recommendations by Parham *et al.* (2012). Minimum ages were set as lognormal priors, assuming that the oldest confidently assigned fossil in a group constrains that group's origination age. Soft maximum ages were set as the rear 5% of the lognormal distribution using dates from the youngest fossil assemblage that lacked fossils allied to the calibrated group (see App. 2).

Timetree analyses

We estimated clade divergence times using the Bayesian relaxed-clock model implemented in BEAST 1.7.5 (Drummond *et al.*, 2012), and a starting tree obtained from penalized likelihood (PL) analyses in r8s v1.8 (Sanderson, 2003).We used the PL starting tree to meet the age constraints of all fossil priors and prevent BEAST runs from crashing; subsequent analyses using the MCMC framework in BEAST allowed for information in the original molecular data to be incorporated into divergence-time estimates, and for the temporal influence of different fossil priors to be tested. We started the PL analyses using the 5-gene MrBayes tree pruned to 198 taxa (removing *Pedetes*) to achieve the fully bifurcating tree required by BEAST. We set PL constraints using the age minima and 95% maxima of all 25 calibrations (App. 2), with the exception of the Ctenohystrica root, which we fixed to the 50 Ma median age of its prior (r8s requires one fixed point). We arbitrarily changed several *Ctenomys* branch lengths that were near zero to the value "0.0011" to avoid the need to collapse branches (Sanderson, 2003). Cross-validation in r8s determined an optimal smoothing parameter of 2.5, and the resulting tree was used to start all BEAST runs.

We focused BEAST runs on estimating divergence times rather than topology by constraining the monophyly of all clades recovered from the MrBayes analysis (except those within *Ctenomys*). We ran BEAST analyses under the GTR+G model with four gamma categories, unlinking site models across the five gene partitions and estimating base frequencies. Relaxed clock models were unlinked except for the mtDNA genes (linked on the same strand) and rates were uncorrelated so that each branch was estimated from independent draws of a lognormal distribution. The universal clock mean priors were set to uniform with a large upper bound. Tree models were linked and the tree prior was set to Yule for the trial analyses with calibration sets 1-8. The final analysis used the birth-death tree prior with incomplete species sampling (Stadler, 2009), given 0.69 as the fraction of extant ctenohystricans sampled. MCMC chain lengths were set to 10 million generations with parameters sampled every 10,000 generations. For all analyses, eight independent runs were performed on the XSEDE computing cluster and combined after 10% burn-in, resulting in

7,200 trees (72 million generations) that in each case converged upon stable posterior distributions (determined using Tracer). Trees were summarized with the "maximum clade credibility" option using TreeAnnotator. Timetrees containing mean divergence times and 95% credibility intervals for each node were compared in R using the ape and phyloch packages (Paradis *et al.*, 2004). Below we report mean divergence times, but invite inspection of the associated error bars, which vary in width given the proximity and shape of age priors (Tab. 4 and Fig. 5).

Results

DNA sequence analyses

Table 2 contains DNA sequence characteristics for each of the five single-gene alignments. Although no parsimony analyses were conducted here, the number of parsimony-informative sites (PIS) per locus is an instructive metric of raw sequence variation. The cyt-*b* alignment contains more PIS than any other sampled gene, owing to its extensive taxonomic sampling and greater variability. Correcting for sites and taxa, vWF contains the most PIS (0.0054), followed by GHR, RAG1, 12S rRNA, and cyt-*b* (0.0053, 0.0040, 0.0036, and 0.0030, respectively). Both mtDNA genes contain fewer G nucleotides than do the nuclear exons, but no significant differences are found in nucleotide composition within each gene (P> 0.05; Tab. 2).

To verify aDNA results, we repetitively amplified each gene fragment and assembled multiple overlapping fragments for each gene (Pääbo *et al.*, 2004). Because instances of polymorphism among nuclear DNA fragments could reflect either DNA damage or diploid heterozygosity, we coded all polymorphic sites with the corresponding IUPAC ambiguity codes.

Results from Xia's test for substitution saturation show that four of the five sampled genes display some degree of saturation (Tab. 2). The cyt-*b* and RAG1 alignments each display significant saturation and only the GHR alignment is found to be significantly unsaturated. Plots of the pairwise number of transitions and transversions in cyt-*b* versus percent sequence divergence confirm substitution saturation across the breadth of the tree (App. 3). Given that cyt-*b*'s rapid evolution makes it a useful species-delimitation marker (*e.g.*, Baker and Bradley, 2006), saturation was actually expected at this taxonomic scale. Cyt-*b* nonetheless provides important resolution at terminal nodes (Tab. 3). Finding substitution saturation in 12S rRNA, vWF, and RAG1 was, however, unexpected, but follows from the Eocene-Recent range of divergences in each data set, especially given the conservative design of Xia's test (Xia and Lemey, 2009). We chose to proceed with caution, testing whether these varying degrees of saturation actually result in conflicting phylogenetic signal by comparing the statistical support for equivalent nodes in the phylogenies of each data partition.

Single-gene, mtDNA, and exon data sets: completely sampled trees

Results from comparisons of the 50-taxon trees, each completely sampled for all five genes, are displayed in Table 3 with node numbers from Figure 2. Across 48 total nodes, only three instances of significant conflict in topology are found among the single-gene data sets, each of which occurs at shallow nodes (Tab. 3). Because these conflicts exist among closely related taxa and involve support for alternative sister-relationships among species (node 42) or genera

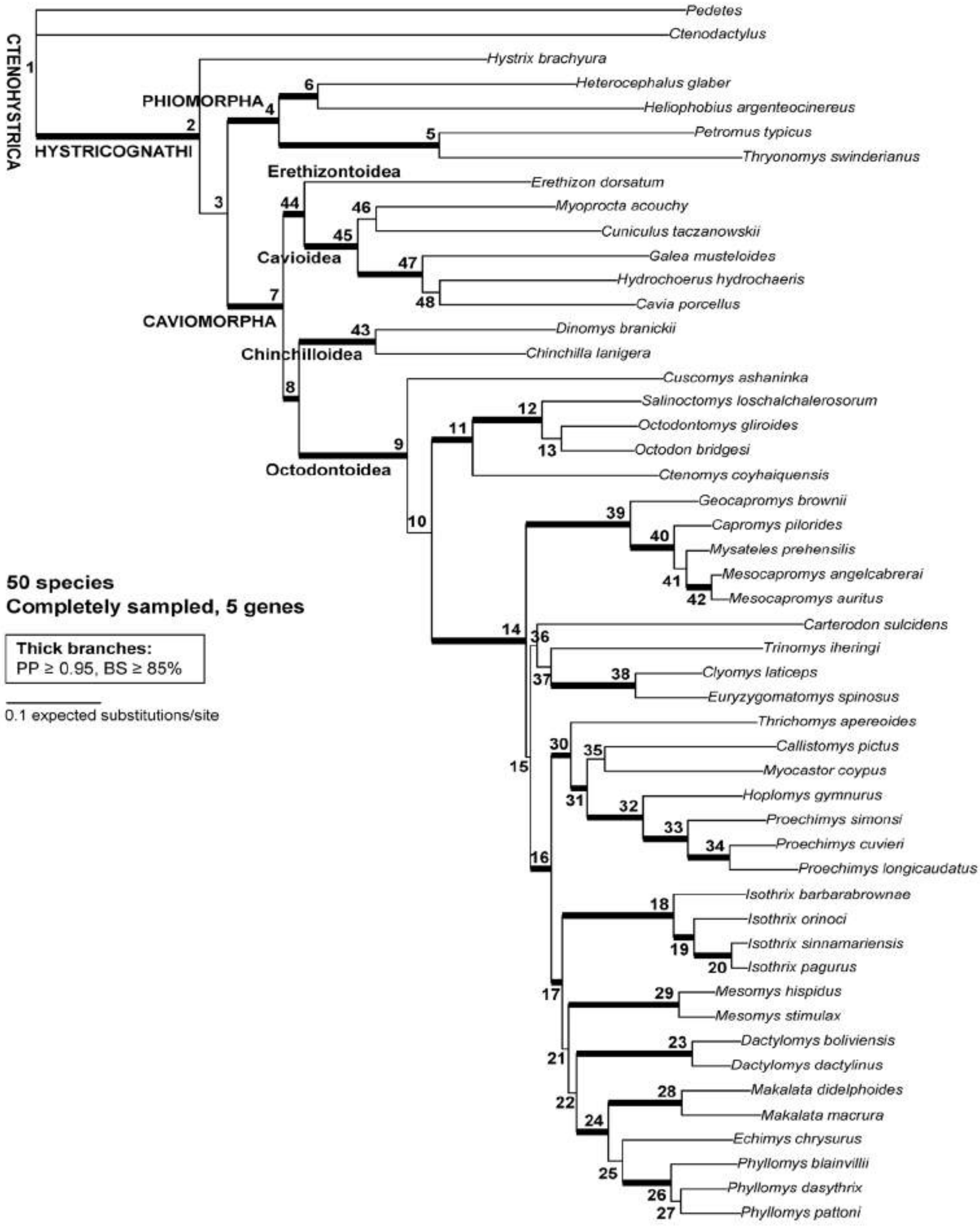

Figure 2. Phylogeny based on the concatenated analysis of 5 genes (cyt-*b*, 12S rRNA, GHR, vWF, and RAG1) that were completely sampled for 50 species representing all major groups of Ctenohystrica (Bayesian inference topology shown). Node numbers in this figure define groupings of taxa that facilitate comparisons of topology across single gene and concatenated gene data sets; support values for these permutations are displayed in Table 3. Thick branches indicate nodes with Bayesian inference posterior probability (**PP**) ≥ 0.95 and maximum likelihood bootstrap support (**BS**) ≥ 85%.

Table 3. Nodal support values for single genes and combined gene data sets constructed using only the 50 taxa that were sampled for all five genes. Node numbers are listed with reference to Figure 2. All values are maximum-likelihood bootstrap percentages (ML BP) except the column headed BI PP (Bayesian inference posterior probability). Boldface values indicate ML BP ≥ 85 or BI PP ≥ 0.95. Differences among data sets are marked as "-" if ML BP < 85, and with one or more asterisks (*) if they are statistically supported by ML BP ≥ 85 (see Table footnotes and Results section for further details).

	Combined data sets				Single gene data sets				
	5-gene		2-gene	3-gene					
Node	BI PP	ML BP	mtDNA	exons	cyt-*b*	12S rRNA	GHR	vWF	RAG1
1	**1.00**	-	-	-	-	-	-	-	-
2	**1.00**	**100**	83	**100**	46	47	**100**	**88**	**98**
3	**0.99**	77	47	58	-	33	63	-	41
4	**1.00**	**100**	68	**99**	-	52	**100**	-	-
5	**1.00**	**100**	**98**	**100**	75	**93**	**100**	**100**	49
6	**1.00**	**98**	52	**97**	-	73	**98**	-	48
7	**1.00**	**100**	77	**100**	54	-	**94**	**98**	-
8	**1.00**	**90**	31	**88**	-	-	-	66	34
9	**1.00**	**100**	**95**	**100**	-	**90**	**100**	**100**	**100**
10	**1.00**	83	66	-	58	26	**88**	-	-
11	**1.00**	**100**	84	**99**	77	48	**91**	-	**95**
12	**1.00**	**100**	**98**	**100**	**93**	80	**100**	**91**	**97**
13	**1.00**	81	**91**	-	75	81	*	**85**	-
14	**1.00**	**100**	**94**	**100**	84	23	**100**	**98**	**100**
15	0.50	-	-	-	-	-	-	29	-
16	**1.00**	**99**	22	**97**	-	-	-	81	-
17	**1.00**	**97**	46	79	-	45	57	-	-
18	**1.00**	**100**	**100**	**100**	**100**	**100**	**100**	**99**	**98**
19	**1.00**	**91**	**97**	-	**99**	-	63	-	-
20	**1.00**	**100**	**100**	**98**	**92**	**99**	**97**	**89**	75
21	0.52	46	29	-	-	-	-	-	-
22	0.78	48	45	42	37	23	-	-	-
23	**1.00**	**100**	**100**	**100**	**100**	**100**	**100**	**100**	**100**
24	**1.00**	**100**	82	**100**	55	73	**92**	**85**	-
25	**1.00**	83	**94**	-	**86**	-	-	35	44
26	**1.00**	**100**	**100**	**100**	**100**	62	**96**	**96**	-
27	**0.95**	72	68	-	69	71	61	-	-
28	**1.00**	**100**	**100**	**100**	**100**	**97**	**99**	**99**	77
29	**1.00**	**100**	**100**	**100**	**100**	**100**	**100**	**100**	**86**
30	**1.00**	**100**	29	**99**	-	-	82	65	28
31	**1.00**	**97**	66	55	53	-	47	-	-
32	**1.00**	**100**	42	**100**	-	-	**100**	**100**	**91**
33	**1.00**	**100**	**100**	**100**	**96**	**96**	**94**	**100**	**98**
34	**1.00**	**100**	**100**	**100**	**98**	**94**	**99**	**99**	**100**
35	0.88	60	30	-	31	-	-	-	-
36	0.52	-	-	36	-	-	-	34	45
37	**0.96**	77	-	68	-	-	-	-	40
38	**1.00**	**100**	**100**	**100**	**100**	**100**	**100**	**88**	67
39	**1.00**	**100**	**100**	**100**	**100**	**92**	**100**	**100**	**93**
40	**1.00**	**100**	**97**	**100**	**92**	**90**	**100**	**99**	**85**
41	**1.00**	81	65	72	52	47	**91**	-	-
42	**1.00**	**100**	**100**	80	**100**	63	**97**	**	-
43	**1.00**	**100**	**100**	**100**	77	**99**	**98**	**98**	76
44	**1.00**	**98**	64	**92**	-	74	-	**95**	-
45	**1.00**	**100**	67	**100**	45	-	**97**	**99**	75
46	**1.00**	80	76	36	78	-	-	-	79
47	**1.00**	**100**	**95**	**100**	**93**	-	**100**	**97**	**99**
48	0.93	-	72	-	**97**	-	-	65	***

* GHR shows 86% support for *Octodontomys* – *Salinoctomys* relationship
** vWF shows 88% support for *Mesocapromys angelcabrerai* – *Mysateles prehensilis* relationship
*** RAG1 shows 88% support for *Hydrochoerus* – *Galea* relationship

(nodes 13, 48), they are likely the result of incomplete lineage sorting. In the absence of topological conflict at deeper nodes between single-gene trees, we concatenated data sets into 2-gene (mtDNA), 3-gene (exon), and 5-gene (combined) data sets. As expected, the greater degree of saturation in the mtDNA data set results in poor support at most basal nodes in the phylogeny (nodes 1-25 in Fig. 2) and higher nodal support among terminal branches, but there is no significant conflict between genes inherited maternally (mtDNA) and bi-parentally (nuclear exons; Tab. 3). The exon data set shows high resolution at basal nodes in the tree as well as at terminal branches, and agrees with each of the other data sets. The node-by-node concordance of all phylogenies from the 50-taxon data sets justifies the concatenation of data frames for all 199 taxa sampled, resulting in a 5-gene supermatrix.

5-gene data sets: completely sampled versus supermatrix trees

We compared the topology from the 5-gene completely sampled tree (CST; Fig. 2) with the positions of the same taxa in an analysis based on a supermatrix of all 199 taxa collapsed to genera (Fig. 3). Both analyses strongly support Hystricognathi (Old World porcupines, phiomorphs, and caviomorphs; node 2), but only the supermatrix strongly supports Hystricidae as sister to Phiomorpha + Caviomorpha (node 3). Both Phiomorpha and Caviomorpha are strongly recovered as monophyletic in both analyses (nodes 4 and 7). Within phiomorphs, strong evidence supports Bathyergidae (node 6) and Petromuridae + Thryonomyidae (node 5) in both sets of analyses. Within caviomorphs, both sets of analyses securely recover the four recognized superfamilies as monophyletic (nodes 45, 43, and 9) and forming sister pairs: Erethizontoidea + Cavioidea and Chinchilloidea + Octodontoidea (nodes 44 and 8).

At the family level, there is strong or moderate support for the monophyly of the caviomorph families Erethizontidae, Cuniculidae, Dasyproctidae, Caviidae, Dinomyidae, Chinchillidae, Abrocomidae, Octodontidae, Ctenomyidae, and Capromyidae. The CST (Fig. 2) loosely supports Cuniculidae + Dasyproctidae (node 46), whereas this group is moderately supported in the supermatrix analysis. Dinomyidae + Chinchillidae (node 43) are strongly supported as a clade in both analyses. Abrocomidae appears as the sister to all other octodontoid families (node 10), with strong support for its sisters, Ctenomyidae + Octodontidae (node 11) and Capromyidae + Echimyidae (node 14). However, whereas the CST analysis recovers a monophyletic Echimyidae (node 15), the supermatrix analysis finds Echimyidae paraphyletic with respect to Capromyidae (node 39); a group of eastern Brazilian taxa (*Carterodon, Clyomys, Euryzygomatomys,* and *Trinomys*) are loosely recovered as sister to the capromyids (Fig. 3).

At the genus level, there is also strong agreement between analyses in the recovered relationships. These include *Salinoctomys* (*Octodontomys*, *Octodon*); *Geocapromys* (*Capromys* (*Mysateles*, *Mesocapromys*); *Trinomys* (*Clyomys*, *Euryzygomatomys*); *Myocastor* (*Hoplomys*, *Proechimys*); and *Makalata* (*Echimys*, *Phyllomys*). However, minor differences are apparent in the topologies for a handful of genera. The supermatrix offers support for *Hydrochoerus* (*Cavia*, *Galea*), whereas the CST loosely recovers *Galea* as sister to *Cavia* + *Hydrochoerus* (nodes 47 and 48, Fig. 2). *Mesomys* and *Isothrix* form a moderately supported clade in the supermatrix, while in the CST they loosely appear as successive sisters to the remaining arboreal echimyids (nodes 17 and 21, Fig. 2). *Callistomys* and *Myocastor* appear as either successive sisters to *Hoplomys* + *Proechimys* (supermatrix) or as a poorly supported clade that is sister to them (CST).

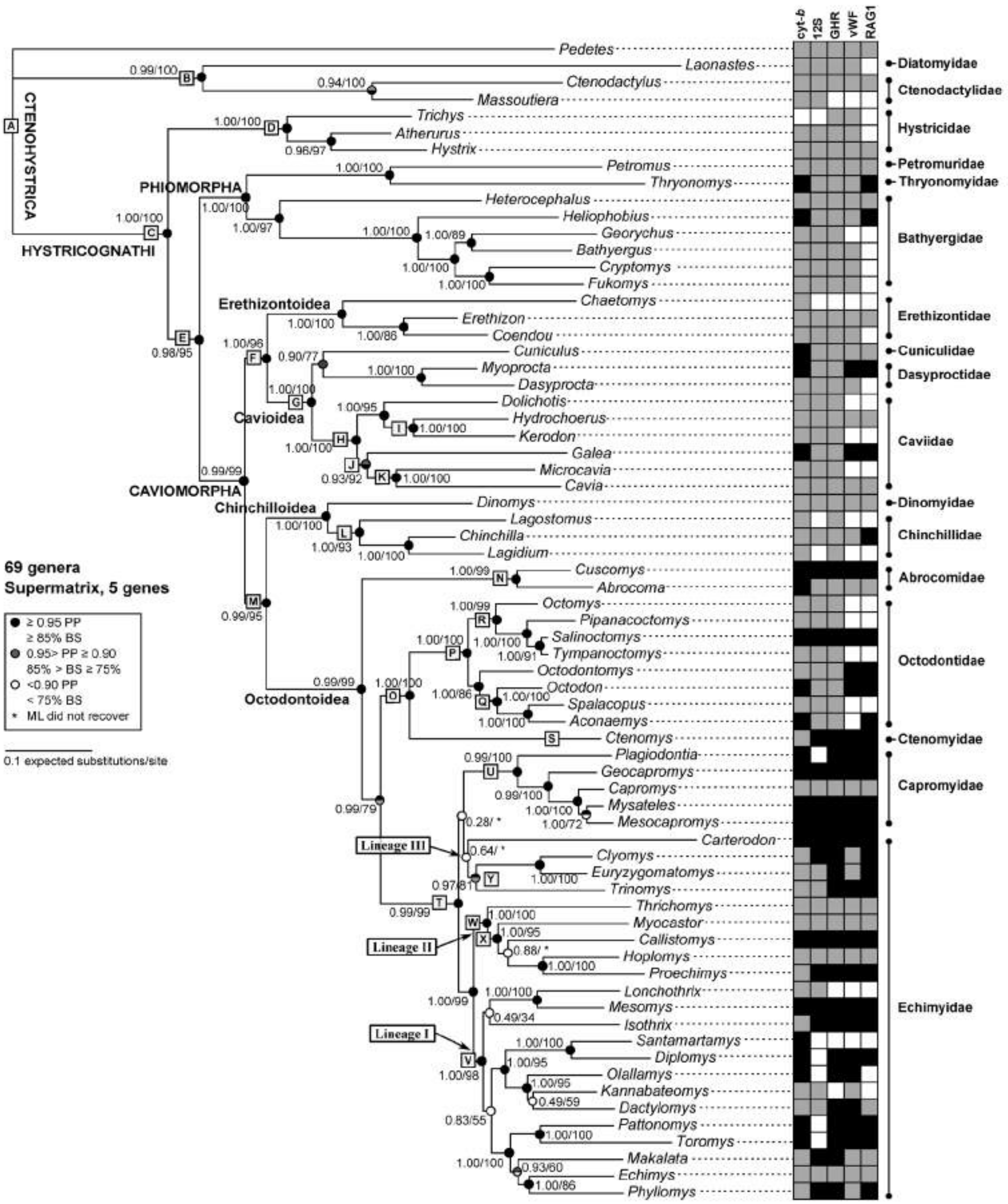

Figure 3. Genus-level phylogeny of Ctenohystrica from the 5-gene supermatrix (cyt–*b* + 12S rRNA + GHR + vWF + RAG1) focusing on the South American rodent clade Caviomorpha and including sister clades from Africa and Asia (Phiomorpha, Hystricidae, Diatomyidae, and Ctenodactylidae). The gene sampling matrix on the right is coded to show the sampling of genes for one or more species in a genus and the origin of the DNA sequences whether produced for the present study (black boxes), deposited on GenBank from previous studies (grey boxes), or currently unsampled (white boxes). Sequences from Upham *et al.* (2013) are included as black boxes. A total of 68 genera are represented in this phylogeny (Bayesian topology shown). Nodes are annotated with support values as indicated from Bayesian inference posterior probability (PP) and maximum likelihood bootstrap support (BS) analyses. Asterisks (*) denote instances where nodes were recovered in the Bayesian but not in the maximum likelihood analyses. Letters in boxes correspond to fossil calibration points, as detailed in Appendix 2. See text for details on lineages I, II, and III within Echimyidae.

Only the supermatrix analysis (Fig. 3) had the taxonomic scope to resolve a number of additional generic relationships. Within Hystricidae, there was strong support for *Trichys* (*Atherurus*, *Hystrix*). Within Bathyergidae, there was strong support for *Heterocephalus* as sister to all other mole-rats, followed by *Heliophobius*, and the remaining mole-rats form a monophyletic grouping of *Georychus* + *Bathyergus* and *Cryptomys* + *Fukomys*. Within Caviidae, *Dolichotis* is sister to *Hydrochoerus* + *Kerodon,* and this group is sister to *Galea* (*Microcavia*, *Cavia*). In Chinchillidae, *Lagostomus* is sister to *Chinchilla* + *Lagidium*. *Abrocoma* and *Cuscomys* are both placed in Abrocomidae. Octodontidae is recovered as two well-supported clades: *Octomys* (*Pipanacoctomys* (*Salinoctomys*, *Tympanoctomys*) and *Octodontomys* (*Octodon* (*Spalacopus*, *Aconaemys*). Within Echimyidae, there was strong support for –*Lonchothrix* + *Mesomys*; ((*Santamartamys*, *Diplomys*) (*Olallamys*, *Kannabateomys*, *Dactylomys*)), although the latter trichotomy could not be confidently resolved; and a lineage of arboreal rats comprised of two subclades, *Pattonomys* + *Toromys* and *Makalata* (*Echimys*, *Phyllomys*).

Timetree calibration trials

The eight sets of fossil calibrations (Fig. 4.1) form three groups that are statistically equivalent in terms of overlapping 95% credibility intervals on all calibrated nodes. These are group A, including sets 1, 4, and 6; group B, including sets 2, 3, and 8; and group C, including sets 5 and 7 (Fig. 4.1). Considering pairwise differences in sets across the 25 calibrated nodes, sets in group A find significantly different ages on an average of 8 nodes and 7 nodes from sets in groups B and C, respectively (ranges 4-13). The group A sets differ in number of calibrations (25, 20, or 7), but have in common the 7 stem fossils in set 6 (Fig. 4.1). The calibrations O and T are unique to the group A sets, and therefore appear to be responsible for the uniformly older age estimates in these sets versus those in groups B and C (Fig. 4.2). Excluding calibrations O and T (set 7) finds results that are equivalent to using 18 crown calibrations (set 5). These group C sets differ from those in group B on the age estimate for 1 calibrated node: U, the calibration for crown Capromyidae (~15 Ma *vs.* ~10 Ma; Fig. 4.2).The older age of node U when this node is calibrated highlights uncertainty regarding this fossil placement (MacPhee *et al.*, 2003), motivating us to exclude this calibration from further analyses (see also the "Capromyidae" section in the Discussion). We thus selected set 8 –excluding calibrations O, T, and U– for the final analyses. Set 8 provides estimates that are equivalent to sets with fewer calibrations (the group B sets 2 and 3), but because it retains information from 22 calibrations it does so with the most precision of any set evaluated (mean 95% credibility interval of 4.3 Ma, versus 5.9, 5.8, 4.8, 7.0, 5.5, 8.3, and 4.4 Ma for sets 1-7).

Timetree inferences

The divergence time analysis using calibration set 8 (log-likelihood of -93143.8) presents a calibrated chronology of group appearance within the Ctenohystrica (Fig. 5). Hystricognathi had appeared by roughly 50 Ma, and by 44.9 Ma, the Old World porcupines had diverged from them. The split between phiomorphs and caviomorphs is dated at 42.0 Ma, with the most recent common ancestor (MRCA) of phiomorphs dated to 36.3 Ma and the MRCA of caviomorphs to 35.7 Ma. Subsequent splits in these lineages took place in the early Oligocene;

1 Calibration sets

Set	*Results group*	# Calib.	Description	Calibration points
1	*A*	25	all calibrations	A B C D E F G H I J K L M N O P Q R S T U V W X Y
2	*B*	5	non-Caviomorpha	A B C D E
3	*B*	13	non-Octodontoidea	A B C D E F G H I J K L M
4	*A*	20	non-Cavioidea	A B C D E F L M N O P Q R S T U V W X Y
5	*C*	18	crown calibrations only	C D G H I J K L N P Q R S U V W X Y
6	*A*	7	stem calibrations only	A B E F M O T
7	*C*	23	all except O and T	A B C D E F G H I J K L M N P Q R S U V W X Y
8	***B***	**22**	**all except O, T, and U**	**A B C D E F G H I J K L M N P Q R S V W X Y**

2 Age estimates for calibrated nodes that differ among sets

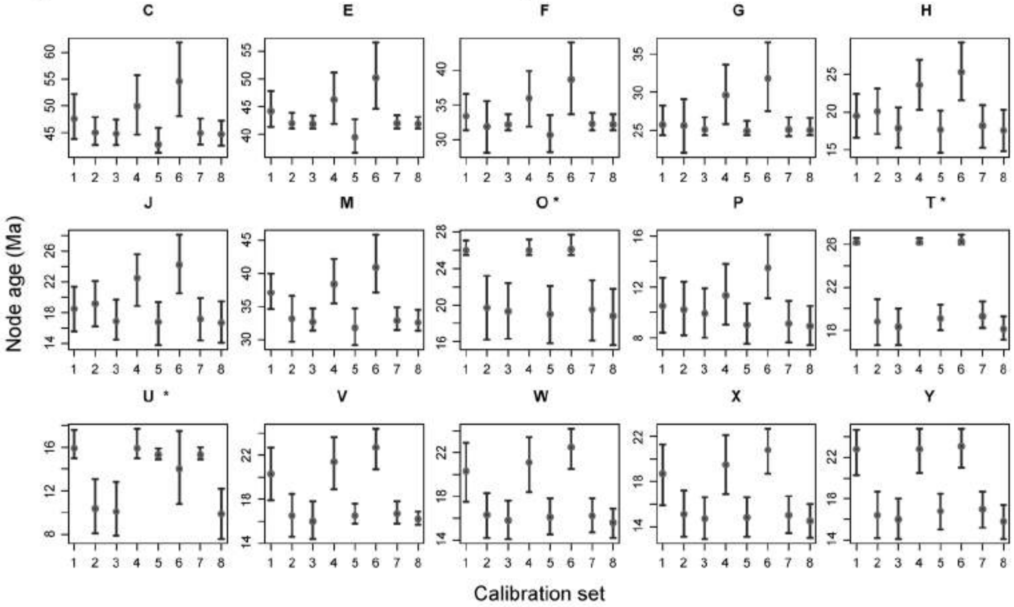

Figure 4. Comparison of eight sets of fossil calibrations that differ in their 1. inclusion of 25 calibrated nodes (AY), and 2. resulting influence on mean age estimates (red) and 95% credibility intervals (blue). Only the 15 calibrated nodes with age estimates that differed significantly among calibration sets are displayed; the other ten calibrated nodes had overlapping 95% credibility intervals across all sets. Asterisks (*) on plots for calibrations O, T, and U indicate that their inclusion in sets 1, 4, and 6 yielded results that were inconsistent with other sets. Exclusion of these three calibrations yielded the most consistent age estimates (set 8, in bold); results from this set of 22 calibrations are depicted in Figure 5 and discussed in the text. Nodes A–Y are labeled in Figure 3. Groups A, B, C indicate statistically equivalent sets (see Results). See Appendix 2 for calibration details and justifications.

the MRCAs of Diatomyidae + Ctenodactylidae (32.2 Ma), Bathyergidae (31.2 Ma), and the near-simultaneous divergences of Erethizontoidea + Cavioidea (32.4 Ma) and Chinchilloidea + Octodontoidea (32.8 Ma) all date to this interval. The crown radiations of Cavioidea (25.2 Ma) and Octodontoidea (25.6 Ma) were both initiated by the end of the Oligocene, followed closely by their subdivision into the cavioid families Cuniculidae, Dasyproctidae, and Caviidae (23.4 Ma), and the octodontoid family Abrocomidae and dyads of Octodontidae-Ctenomyidae and Echimyidae-Capromyidae (23.6 Ma).The two other caviomorph superfamilies have MRCAs during the early-to-mid Miocene: 17.5 Ma (Erethizontoidea) and 19.7 Ma (Chinchilloidea).

Other family and genus divergence timings are detailed in Table 4 along with a comparison of analogous results from other studies. Overall, our targeted effort to reconstruct the Ctenohystrica

Table 4. Comparison of divergence times among studies. All times are in millions of years and refer to the estimated ages (and confidence intervals) of the specified crown groups. Results from this study are from the timetree in Figure 4.

Clade	**This study**	**Upham and Patterson (2012)**	**Meredith *et al*. (2011)**	**Rowe *et al*. (2010)**	**Sallam *et al*. (2009)**	**Huchon *et al*. (2007)**
Ctenohystrica	50.0 (46.2-55.0)	50.8 (41.0–69.7)	61.1 (56.1–68.3)	92 (68–121)	55.6 (52.7–58.3)	61.3 (53.8–63.3)
Diato-Cteno	32.2 (28.5–37.6)	[b]	43.1 (38.2–49.0)	[b]	7.9 (5.2–12.1)	44.3 (37.6–51.1)
Ctenodactylidae	13.4 (7.3–20.5)	[a]	[a]	[a]	[a]	7.7 (5.1–10.9)
Hystricognathi	44.9 (42.5–47.4)	43.7 (37.2–51.0)	49 (41.9–56.7)	59 (44–74)	39.0 (36.1–41.9)	45.4 (39.7–50.5)
Hystricidae	12.7 (11.0–15.8)	[a]	[a]	[a]	15.7 (11.7–21.1)	[a]
Phiomorpha / Caviomorpha	42.0 (41.1–43.3)	40.4 (36.1–45.6)	47.2 (39.8–55.1)	[c]	36.1 (33.4–39.0)	42.7 (37.3–47.2)
Phiomorpha	36.3 (32.6–39.4)	36.3 (30.9–42.5)	42.0 (35.7–49.7)	55 (41–70)	32.1 (29.2–35.1)	38.0 (32.7–42.9)
Petro-Thryo	23.0 (17.6–28.1)	23.5 (17.5–29.5)	26.2 (18.3–33.3)	34 (22–49)	18.0 (14.8–21.3)	24.5 (19.8–42.9)
Bathyergidae	31.2 (26.7–35.1)	31.5 (25.3–37.4)	[a]	~46	26.3 (22.7–29.7)	32.8 (27.6–38.0)
Bathyergidae minus Heter	17.9 (14.3–21.8)	18.6 (13.6–23.4)	[b]	~15	[a]	[a]
Caviomorpha	35.7 (33.8–37.6)	34.1 (36.1–45.6)	42 (34.0–49.0)	45 (35–54)	30.1 (27.9–33.4)	34.3 (29.9–36.9)
Erethizontoidea /Cavioidea	32.4 (31.4–33.8)	30.6 (27.4–34.7)	40.9 (33.3–47.9)	[c]	28.6 (25.9–31.4)	31.7 (27.4–35.1)
Erethizontoidea	17.5 (11.3–24.0)	7.5 (5.0–10.4)	[a]	15 (8–23)	[a]	[a]
Cavioidea	25.2 (24.3–26.7)	30.6 (27.4–34.7)	32.2 (25.0–38.0)	37 (28–47)	23.1 (20.6–26.0)	24.1 (20.1–28.0)
Cunic-Dasyp	23.4 (21.0–25.7)	[c]	[c]	[c]	[b]	[b]
Dasyproctidae	8.1 (6.0–10.7)	10.2 (6.6–14.7)	[a]	9 (5–16)	[b]	[b]
Caviidae	17.6 (14.9–20.6)	19.2 (16.0–22.7)	19.9 (14.8–25.7)	~25	14.6 (12.4–17.2)	[a]
Chinchilloidea / Octodontoidea	32.8 (31.4–34.5)	32.7 (30.3–36.4)	38.9 (31.3–46.2)	43 (33–52)	29.0 (26.2–31.7)	33.3 (28.9–36.3)
Chinchilloidea	19.7 (14.8–24.7)	19.0 (13.7–25.1)	28.2 (24.3–34.7)	29 (20–38)	19.9 (16.5–23.2)	21.4 (17.9–25.6)
Chinchillidae	12.3 (9.3–15.9)	14.3 (8.1–21.2)	[a]	~24	[a]	[a]
Octodontoidea	25.6 (23.1–27.9)	26.8 (24.8–28.9)	28.2 (21.0–33.7)	~26	19.6 (17.1–22.2)	[b]
Abrocomidae	8.4 (7.2–15.0)	0.3 (0–1.8)	[a]	[a]	[a]	[b]
Octod-Cteno / Capro-Echim	23.6 (21.4–25.8)	25.3 (24.6–26.7)	26.7 (19.6–31.8)	~25	18.1 (15.7–20.6)	18.6 (15.3–21.8)
Octod-Cteno	18.9 (15.7–22.1)	19.1 (14.3–23.5)	22.9 (17.1–27.2)	22 (17–30)	[b]	[b]
Octodontidae	8.8 (7.3–10.4)	9.0 (6.7–11.6)	[a]	8 (5–12)	[a]	[a]
Ctenomyidae	6.0 (4.6–7.6)	4.3 (2.2–7.4)	[a]	[a]	[b]	[b]
Capro-Echim	18.2 (17.1–19.3)	18.8 (17.7–20.6)	20.0 (13.7–24.0)	15 (11–21)	12.3 (9.9–14.7)	12.4 (9.7–15.3)
Capromyidae	9.8 (7.4–12.3)	[a]	[a]	[a]	[a]	[a]
Echim: clade 1	16.7 (15.1–18.1)	16.4 (13.8 18.8)	[b]	[b]	[b]	[b]
Echim: clade 1-clade 2	17.1 (16.4–18.1)	16.6 (14.9–18.4)	[b]	~13	[b]	[b]
Echim: clade 2	15.5 (14.2–16.8)	14.9 (13.0–16.9)	[b]	~11	[b]	[b]
Echim: clade 3	16.2 (15.8–16.9)	15.6 (13.9–17.6)	[b]	~12	[b]	[b]

Abbreviations. Cteno, Ctenodactylidae; Cunic, Cuniculidae; Dasyp, Dasyproctidae; Diato, Diatomyidae; Heter, *Heterocephalus*; Petro, Petromuridae; Thryo, Thryonomyidae. Upham and Patterson (2012) analyzed 12S rRNA, GHR, vWF, and RAG1 for 51 ctenohystrican genera; Meredith *et al.* (2011) analyzed 26 gene fragments across mammalian families, including 19 genera in Ctenohystrica ("global mean" and "DNA all" analyses); Rowe *et al.* (2010) analyzed GHR and TTR for 39 ctenohystrican genera (U=55 Ma and "All/gap" analyses); Sallam *et al.* (2009) analyzed 115 morphological characters from Marivaux (2004) and ADRA2B, IRBP, vWF, GHR, RAG2, and CB1 from Blanga-Kanfi *et al.* (2009) for 18 ctenohystrican genera; and Huchon *et al.* (2007) analyzed ADRA2B, IRBP, vWF, GHR, cyt-*b*, and 12S rRNA for 16 ctenohystrican genera.

[a] Only one taxon sampled (no crown age); [b] One or more taxa not sampled in analysis; and [c] Analysis did not recover sister relationship.

timetree resulted in a greater breadth of sampled lineages and narrower nodal error bars than other recent timetrees (Tab. 4). Age estimates from the present study are comparable to our earlier study using five fossil calibrations (Upham and Patterson, 2012), but improved taxon sampling enables crown ages for several families to be estimated (*e.g.*, Abrocomidae, Capromyidae, Hystricidae). Prior estimates for the origin of crown Ctenohystrica varied from ~50 Ma (Sallam *et al.*, 2009; Upham and Patterson, 2012) to ~61 Ma (Huchon *et al.*, 2007; Meredith *et al.*, 2011) all the way to the mid-Cretaceous ~92 Ma (Rowe *et al.*, 2010).

Discussion

Appraisals of rodent evolution have taken enormous steps forward in recent years. The analysis of molecular datasets has offered a means to sidestep the morphological conservatism and parallelism (*e.g.*, Wood, 1935) that have plagued rodent systematics for more than a century (see also Castoe *et al.*, 2009). Comprehensively sampled molecular phylogenies across Rodentia (*e.g.*, Honeycutt, 2009; Fabre *et al.*, 2012a) and the present effort for hystricognath rodents now permit a fuller appraisal of rodent evolutionary and biogeographic diversification through time.

The Ctenohystrica and higher-level relationships

Our tree unambiguously recovers a monophyletic Hystricognathi, with Hystricidae sister to Caviomorpha + Phiomorpha sensu stricto (*i.e.*, Bathyergidae, Petromuridae, and Thryonomyidae). The same set of relationships was uncovered by the analyses of Adkins *et al.* (2001), Huchon *et al.* (2002), Huchon *et al.* (2007), Honeycutt (2009), Fabre *et al.* (2012a), and Voloch *et al.* (2013). Previous analyses had either regarded this as a trichotomy (Huchon and Douzery, 2001) or recovered Hystricidae as sister to Caviomorpha with Phiomorpha sister to this group (also called "Bathy-Phiomorpha"; Vilela *et al.*, 2009; Rowe *et al.*, 2010).

The Phiomorpha

Our trees robustly recover the sister-group relationship of Petromuridae with Thryonomyidae (Thryonomyoidea), and this group as sister to Bathyergidae. Nedbal *et al.* (1994) and Huchon and Douzery (2001) documented this same topology, as have others more recently (Sallam *et al.*, 2009; Rowe *et al.*, 2010; Meredith *et al.*, 2011).

One remarkable feature of the timetree is the very early divergence of the lineage leading to *Heterocephalus* from other mole-rats (Fig. 5), estimated at 31.2 Ma. Contemporaneously, on another continent, the early Oligocene witnessed the emergence of erethizontoids and cavioids (32.4 Ma) and of chinchilloids and octodontoids (32.8 Ma). The divergent gene sequences and early divergence time of *Heterocephalus* were noted in prior molecular studies (Allard and Honeycutt, 1992; Janecek *et al.*, 1992; Walton *et al.*, 2000). Currently, *Heterocephalus* is considered to be the lone member of the bathyergid subfamily Heterocephalinae (Woods and Kilpatrick, 2005). However, its morphological distinctiveness and early divergence from other mole-rats suggest that it should be elevated to family rank within the Bathyergoidea, *i.e.*, Heterocephalidae Landry, 1957 (Patterson and Upham, 2014).

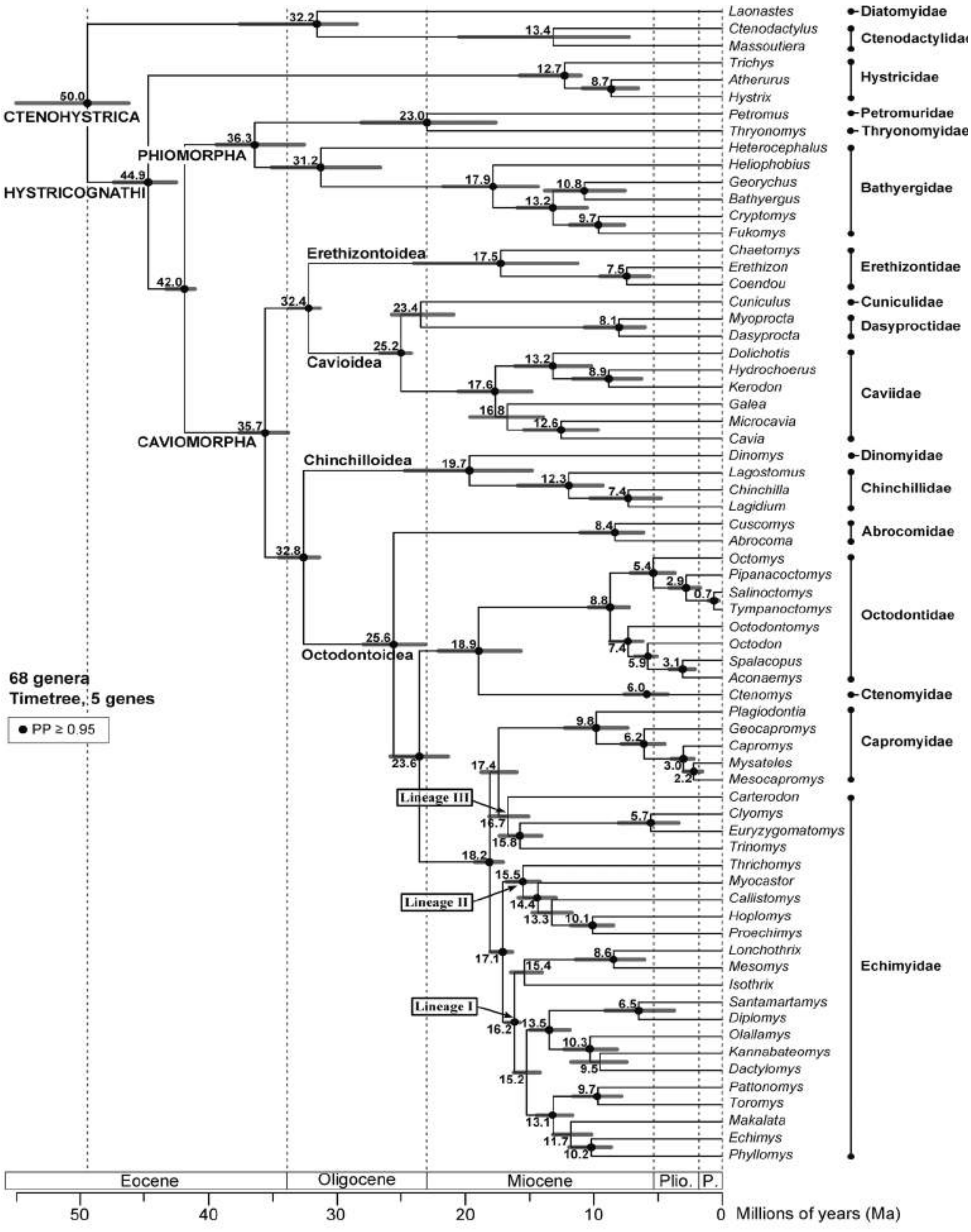

Figure 5. Molecular timetree of ctenohystrican rodent evolutionary history calibrated with 22 fossil priors in BEAST (see App. 2). Numbers above nodes are the mean divergence ages of clades, and node error bars correspond to 95% credibility intervals. Black dots on nodes correspond to MrBayes posterior probability (PP) values ≥ 0.95. The timing of geological epochs is from Gradstein *et al*. (2004). See text for details on lineages I, II, and III within Echimyidae.

The Phiomorpha-Caviomorpha split

Our phylogeny confidently recovers a sister-group relationship between the phiomorph rodents endemic to Africa (Thryonomyidae, Petromuridae, and Bathyergidae) and the American caviomorphs. We estimate their divergence time at 42.0 Ma (41.1-43.3), in the Middle Eocene (Fig. 5). This date is robust to recalculation excluding the fossil assemblage at Contamana, Peru (calibrations C and E in Fig. 3), yielding ages that are slightly younger, but not significantly so, for the phiomorph-caviomorph split (39.9 Ma [36.8-43.2]) and the Hystricognathi crown (43.2 Ma [39.3-47.1]; modified from calibration set 8). That Peruvian locality contains the oldest known hystricognath fossils in strata constrained to 41.6-40.94 Ma by a combination of radiometric and biochronological methods (see App. 2; Antoine *et al.*, 2012).

Our Middle Eocene estimate for the common ancestor of African and American hystricognaths is generally on par with recent molecular studies using a variety of markers and taxon-sampling strategies (Tab. 4). Using immunological distances, Sarich (1985) estimated their divergence at 45-48 Ma, in agreement with the Eocene divergences hypothesized by Woods (1982) and Wood (1985). An older estimate of ~85 Ma, consistent with vicariance via African and South American plate tectonics, was based on the mitochondrial divergence of cane rats from guinea pigs (Mouchaty *et al.*, 2001).The majority of DNA-based estimates place the Phiomorpha-Caviomorpha split in the Eocene, ruling out plate-tectonic explanations in favor of trans-oceanic dispersal to South America via one of three routes: North America, Africa, or an Australia-Antarctica landbridge (Huchon and Douzery, 2001). Molecular clock-based estimates vary across the Eocene, from the latest to the earliest stages (~34-56 Ma; Nedbal *et al.*, 1994; Huchon and Douzery, 2001; Opazo, 2005; Poux *et al.*, 2006; Huchon *et al.*, 2007; Vilela *et al.*, 2009; Voloch *et al.*, 2013). Several studies used the then-earliest known caviomorph fossil from the Tinguiririca of Chile (~31 Ma; Wyss *et al.*, 1993) to calibrate the phiomorph-caviomorph split, yielding estimates of 43-54 Ma (Huchon and Douzery, 2001), 34.0-39.2 Ma (Opazo, 2005), and 38.9-48.5 Ma (Poux *et al.*, 2006) depending on the calibration methods and genes analyzed. Rowe *et al.* (2010) instead used this fossil strictly as "dasyproctid indet." (Wyss *et al.*, 1993) to calibrate crown Cavioidea, yielding a considerably older date of 42-69 Ma for the stem divergence of caviomorphs (the uncertainty of this estimate derives from the poorly supported Caviomorpha-Hystricidae relationship recovered in that analysis). Recently, this Tinguiririca caviomorph was identified as *Andemys termasi*, Pan-Dasyproctidae (Bertrand *et al.*, 2012), and its age was further constrained to 31.6-33.6 Ma (Dunn *et al.*, 2013). The subsequent discovery of ~41 Ma caviomorph fossils in Peru (Antoine *et al.*, 2012) supports our use of *Andemys* as an age constraint inside Caviomorpha, treating it conservatively as a stem member of Cavioidea (App. 2; Pérez and Pol, 2012).

The most thorough previous effort to calibrate the divergence of Old and New World hystricognaths was the Mammalia-wide study of Meredith *et al.* (2011).They used seven fossil calibrations internal to Ctenohystrica (of 82 total for mammals), along with genetic sampling from all 17 extant families, to estimate an age of 39.8-55.1 Ma for the Phiomorpha-Caviomorpha split. A total of five calibrations, all placed internal to Ctenohystrica, were used in Upham and Patterson (2012) and yielded an estimated split of 36.1-45.6 Ma. Other recent efforts have included more calibrations external to Hystricognathi and Rodentia, estimating the phiomorph-caviomorph divergence as 33.4-39.0 Ma (Sallam *et al.*, 2009) and ~39-47 Ma (Voloch *et al.*, 2013).

Given the range of sampling in taxa and genes and the different methods employed, it is remarkable that nearly all of these molecular clock studies are in close agreement. Without exception, each of these works and the present one find evidence in support of an Old World-New World divergence prior to the Eocene-Oligocene boundary.

Our estimate for the Phiomorpha-Caviomorpha split, 42.0 Ma, approximately coincides with the Mid-Eocene Climatic Optimum (MECO –see Fig. 5; Zachos *et al.*, 2008), which occurred at ~41.5 Ma (Bohaty and Zachos, 2003). Given that the MECO event occurred shortly before the oldest known South American caviomorph fossils ~41 Ma and shortly after their inferred split from African phiomorphs, these biotic and abiotic events are coincidentally linked (Fig. 6). However, evidence that the MECO event initiated this biotic dispersal across the Atlantic Ocean is purely circumstantial, and unlikely to be corroborated because waif dispersals are by definition rare and idiosyncratic (*e.g.*, via rafts of floating debris; Lavocat, 1969; Martin, 1994a; Houle, 1998). Nevertheless, the scenario of trans-Atlantic dispersal is not altogether unrealistic. Houle (1998) used a model of paleocurrents and paleowinds for the Eocene Atlantic Ocean to estimate that floating debris would have crossed this oceanic barrier in ~11 days. This finding is consistent with studies that small-to-medium-sized mammals can survive 10-15 days without water, and suggests that caviomorph ancestors may have originated in temperate regions of Africa with discrete wet-dry seasonality (Houle, 1998; Houle, 1999). The MECO event is known from deep-sea isotope records in the Southern Atlantic and Indian Oceans –the same region where trans-Atlantic dispersal is hypothesized– and consisted of 4 °C warming in less than 1 Ma (Bohaty and Zachos, 2003). If the intensity of coastal storms in Africa increased from ocean warming, then caviomorph ancestors might have traveled a MECO "conveyer" of sorts, riding coastal debris across the Atlantic to South America.

South American primates also share an African or Asian ancestor (Kay *et al.*, 1998; Jaeger *et al.*, 2010), and our timetree does not rule out a single colonization event for both platyrrhine monkeys and caviomorph rodents to South America (Flynn and Wyss, 1998). The divergence of New World and Old World primates has generally been estimated to either the Late Eocene ~37 Ma (Poux *et al.*, 2006; Fabre *et al.*, 2009) or the Middle Eocene ~43 Ma (Eizirik *et al.*, 2004; Janecka *et al.*, 2007; Chatterjee *et al.*, 2009). In their analysis of divergence times in both monkeys and rodents, Poux *et al.* (2006) found evidence that caviomorphs diverged earlier in the Eocene than platyrrhines, but could not exclude the possibility that both groups dispersed contemporaneously to South America. If new fossil discoveries of South American primates can establish a minimum age on the continent prior to ~27 Ma (Hoffstetter, 1969), it would support the case for concurrent trans-Atlantic dispersal with rodents (Bandoni de Oliveira *et al.*, 2009; Antoine *et al.*, 2012). Earlier fossil finds for platyrrhine primates would also extend the age of their crown radiation, which has been estimated to ~26 Ma (Opazo *et al.*, 2006; Chatterjee *et al.*, 2009) or ~15 Ma (Poux *et al.*, 2006; Fabre *et al.*, 2009), and close the substantial gap relative to the ~40-30 Ma crown radiation of caviomorph rodents (Tab. 4).

Caviomorpha

The specter of paraphyly for caviomorphs (and rodents) has been raised on several occasions, notably by studies that questioned if "guinea pigs are rodents" (*e.g.*, Graur *et al.*, 1991; D'Erchia *et al.*, 1996). These early studies had woefully incomplete taxon sampling and their reconstructions were plagued by long-branch attraction. One credible challenge is that to Caviomorpha as a New World endemic, based on resemblances between the ~34 Ma African fossil *†Gaudeamus* and possibly contemporaneous fossil caviomorphs from Santa Rosa, Peru (*e.g.*, *†Eoincamys*); however, ecological convergence presumably explains their dental similarity (Sallam *et al.*, 2009; Coster *et al.*, 2010; Antoine *et al.*, 2012). The polyphyletic origin of caviomorphs involving two independent colonizations of South America has also been proposed on the basis of cephalic arterial patterns (Bugge, 1971, 1985) and myology (Woods and Hermanson, 1985). Incisor enamel microstructure shows similarities among South American octodontoids and African thryonomyoids (Martin, 1994a; Martin, 2005), which does not rule out polyphyly, but more parsimoniously suggests their common retention of an ancestral condition. Recent studies confidently support the monophyly of living caviomorphs using multiple data sources, including cranial and dental characters (Marivaux *et al.*, 2004; MacPhee, 2011), DNA sequences (*e.g.*, Nedbal *et al.*, 1994; Meredith *et al.*, 2011), and other genomic elements (*e.g.*, Huchon *et al.*, 2007; Churakov *et al.*, 2010).

Since Simpson (1945), there has been general agreement that living caviomorphs are divided into four superfamilies, although with more debate over their content: Erethizontoidea with a single family; Cavioidea with Caviidae, Dasyproctidae, Dinomyidae, and Hydrochoeridae; Chinchilloidea with a single family; and Octodontoidea, with Abrocomidae, Capromyidae, Ctenomyidae, Echimyidae, and Octodontidae (Patterson and Wood, 1982).The content of Octodontoidea was later expanded to include Myocastoridae (Woods, 1982), which had been treated as a subfamily of Echimyidae. Although the traditional arrangement placed Dinomyidae in Cavioidea, this family is now considered a chinchilloid (see also Spencer, 1987; Huchon and Douzery, 2001). For reasons mentioned above, African thryonomyids have also been placed in Octodontoidea (Simpson, 1945).

Relationships among these groups have slowly come into focus, limited mainly by inadequate taxonomic and genetic sampling. Using solely morphological evidence, McKenna and Bell (1997) treated both Hystricidae and Erethizontidae as *incertae sedis* within Hystricognathi. With a single gene, Huchon and Douzery (2001) recovered Erethizontoidea as sister to Octodontoidea + Chinchilloidea rather than Cavioidea. In an analysis that lacked chinchilloids, Vilela *et al.* (2009) recovered erethizontiods as sister to cavioids + octodontoids. However, our tree (Figs. 2 and 3) securely recovers the pairings Erethizontoidea + Cavioidea and Chinchilloidea + Octodontoidea, which were also supported by Honeycutt (2009), Meredith *et al.* (2011), Fabre *et al.* (2012a; 2012b), and Upham and Patterson (2012).

Erethizontoid relationships

Living erethizontoids all belong to the New World porcupine family Erethizontidae, which is recovered as strongly monophyletic. This family includes two lineages: *Chaetomys* on the one hand and *Erethizon* and *Coendou* on the other, with *Coendou* now including species previously allocated to *Echinoprocta* and *Sphiggurus* (Voss *et al.*, 2013). Because it retains deciduous premolars, *Chaetomys* had been considered a primitive echimyid (*e.g.*, Patterson and Wood, 1982) until molecular data clarified its relationships (Vilela *et al.*, 2009). However, Martin (1994b) had earlier correctly predicted the affinity of *Chaetomys* with Erethizontidae based on enamel microstructure. The lineage leading to *Chaetomys* diverged from other American porcupines 17.5 Ma (Fig. 5), soon after Dinomyidae separated from Chinchillidae (19.7 Ma) and Octodontidae separated from Ctenomyidae (18.9 Ma), and roughly coeval with the separation of Capromyidae and Echimyidae (17.4-18.2 Ma) and of subfamilies within Caviidae (16.8-17.6 Ma). This early divergence date and its morphological differentiation justify distinguishing *Chaetomys* in its own monotypic subfamily (*cf.* Martin, 1994b; Woods and Kilpatrick, 2005) or maybe even family. The fact that all other South American porcupines diversified after their divergence from *Erethizon* (7.5 Ma) also corroborates the decision of Voss (2011) to synonymize *Sphiggurus* and *Echinoprocta* with *Coendou.*

Cavioid relationships

Cavioidea is recovered as monophyletic, as are each of its families. Our analysis had moderate support for Caviidae as sister to Cuniculidae + Dasyproctidae. Using an eight-gene supermatrix and exemplar taxa, Fabre *et al.* (2012b) recovered Cuniculidae as sister to Dasyproctidae + Caviidae (see also Huchon and Douzery, 2001). Using a combination of morphological and molecular characters from four genes, Pérez and Pol (2012) posited a still different set of family relationships: Dasyproctidae as sister to Cuniculidae + Caviidae. Surely, confusion over the family-level relationships of cavioids is one of the major unresolved questions in caviomorph systematics. Given the group's rich fossil record, analyses that combine morphological and molecular approaches (*e.g.*, Pérez and Pol, 2012) are likely to be the most informative.

Caviidae

The Caviidae is currently thought to include three subfamilies: Dolichotinae, containing *Dolichotis;* Hydrochoerinae, containing *Hydrochoerus* and *Kerodon;* and Caviinae, containing *Cavia, Microcavia,* and *Galea*. Our reconstruction securely recovers Caviinae as sister to Hydrochoerinae + Dolichotinae and *Galea* as sister to *Cavia* + *Microcavia*, agreeing in detail with the analysis of Perez and Pol (2012). In addition, our timetree shows that the Hydrochoerinae-Dolichotinae MRCA (13.2 Ma) postdates the divergence of *Galea* from other caviines (16.8 Ma; Fig. 5). Because this family has numerous fossil members not included in our analysis, and because Fabre *et al.* (2012a) recovered a different topology for the *Hydrochoerus* clade, a comprehensive taxonomic revision is needed.

Chinchilloid relationships

Chinchilloidea is strongly supported, as are its two families: Chinchillidae and Dinomyidae, the latter represented by a single living species. Chinchillid relationships are securely recovered as *Lagostomus* sister to *Chinchilla* + *Lagidium.* Spotorno *et al.* (2004) recovered the same topological relationship in their analysis of cyt-*b* variation in species of Chinchillidae. Although some have considered Abrocomidae as a member of this lineage (*e.g.*, Glanz and Anderson, 1990), abrocomids are now known to be members of Octodontoidea.

The extinct Miocene and Pliocene diversity of chinchilloids is impressive, with the extinct families †Cephalomyidae and †Neoepiblemidae (Kramarz, 2002) and extinct dinomyid subfamilies †Eumegamyinae and †Potamarchinae (McKenna and Bell, 1997). The largest known fossil rodent, †*Josephoartigasia monesi*, is a dinomyid from the late Pliocene of Uruguay with an estimated body size of 350-1000 kg (Millien, 2008; Rinderknecht and Blanco, 2008). Clearly there is a fuller understanding of chinchilloid evolution to be gained by considering the broader geographic and ecological diversification of their fossil members in addition to their modern (primarily Andean) representatives (Fig. 1.5).

Octodontoid relationships

Octodontoidea is strongly supported as monophyletic, with five families: Abrocomidae, Octodontidae, Ctenomyidae, Capromyidae, and Echimyidae (without *Chaetomys* but including *Myocastor*). This content of the superfamily and families agrees with a developing consensus among molecular phylogenetic studies (*e.g.*, Huchon and Douzery, 2001; Leite and Patton, 2002; Galewski *et al.*, 2005; Fabre *et al.*, 2012a; Fabre *et al.*, 2012b). We securely recover Abrocomidae as the sister lineage to the remaining octodontoids, a finding with important biogeographic implications for the group as a whole (see Upham and Patterson, 2012). In an earlier single-gene analysis of the vWF exon, Octodontidae appeared to be sister to all other lineages within the superfamily (Huchon and Douzery, 2001). Again in agreement with traditional classifications (*e.g.*, Patterson and Wood, 1982), we find that the other octodontoid families form well-supported dyads: Octodontidae + Ctenomyidae and Capromyidae + Echimyidae.

Abrocomidae

Abrocoma and *Cuscomys* are the only living members of the family, so their robust grouping in Fig. 3 is unsurprising. However, this is the first molecular test of monophyly of this family, executed here with complete five-gene sampling and all plausible relatives. The modern specimen of *Cuscomys ashaninka* we sequenced is the only one known from this genus; its congener *C. oblativa* is known from historical material found alongside human burials at Machu Picchu (Emmons, 1999). *Abrocoma* and *Cuscomys* diverged 8.4 Ma (Fig. 5), approximately coeval with the split between the echimyid sister genera *Lonchothrix* and *Mesomys*.

Octodontidae

As in earlier analyses of Octodontidae, there is strong evidence for monophyly and good resolution of generic groupings. This group diverged from Ctenomyidae in the early Miocene (Fig. 5), but crown-group octodontids did not split into the two main lineages until the late Miocene, 8.8 Ma. One, the vizcacha-rat lineage, consists of a basal split of *Octomys* from the group containing *Pipanacoctomys* as sister to *Salinoctomys* + *Tympanoctomys.* These latter genera are arid-adapted and appear to be closely related, sharing a MRCA 2.9 Ma, with the *Salinoctomys-Tympanoctomys* divergence ~0.7 Ma during the mid-Pleistocene. Originally described by Mares *et al.* (2000), *Pipanacoctomys* and *Salinoctomys* are considered in synonymy with *Tympanoctomys* by some authors who question the morphological differences among these taxa (Díaz and Verzi, 2006; Pérez, 2013). This issue is not resolved, but the genetic similarity of *S. loschalchalerosorum* and *T. barrerae* indicates a divergence time younger than for any other caviomorph genus (Fig. 5).The recent description of a new species of vizcacha rat (*T. kirchnerorum*) (Teta *et al.*, 2014), and the putative whole genome duplication underlying their radiation (Suárez-Villota *et al.*, 2012), additionally call for a comprehensive revision of the vizcacha rats.

The other octodontid lineage consists of *Octodontomys* as sister to *Octodon* (*Spalacopus*, *Aconaemys*). Both *Octodontomys* and *Octodon* are terrestrial and/or saxicolous, whereas *Spalacopus* + *Aconaemys* appear adapted for fossoriality and, in the case of *Spalacopus*, subterranean life. *Spalacopus* is characterized by strongly procumbent incisors and short ears and tail, all associated with underground living (Lessa *et al.*, 2008) and clearly derived conditions within octodontids. The divergence of *Spalacopus* and 2 species of *Aconaemys* (*fuscus* and *sagei*) is dated as 3.1 Ma, in the late Pliocene; however, *Aconaemys* was found to be paraphyletic in our species-level analyses (not shown), with *A. porteri* weakly supported as sister to the remaining taxa. The paraphyly of *Spalacopus* and *Aconaemys* has been documented elsewhere (Gallardo and Kirsch, 2001; Honeycutt *et al.*, 2003; Upham and Patterson, 2012) and calls for a revision of this group, particularly considering the similarity between *Aconaemys* and the Plio-Pleistocene form †*Pithanotomys* (Reig, 1986).

Ctenomyidae

Our analysis recovered *Ctenomys*, the sole extant genus of ctenomyids, as a strongly supported monophyletic lineage that diverged from the Octodontidae roughly 18.9 Ma. However, most early branches in this family (all genera except *Ctenomys*) went extinct, and †*Ctenomys uquiensis* places a minimum age on the genus of ~3.5 Ma (Verzi *et al.*, 2010). We dated the crown Ctenomyidae radiation at 6.0 Ma (4.6-7.6), which differs from three estimates based exclusively on cyt-*b* data: 5.1 Ma (3.3-6.9; Lessa and Cook, 1998), 3.7 Ma (Castillo *et al.*, 2005), and 9.2 Ma (6.4-12.6; Parada *et al.*, 2011). Including data from two low-variability introns, Castillo *et al.* (2005) also estimated an age of 1.3 Ma that they recognized was inconsistent with the fossil record. Given the minimum inferred divergences of *Ctenomys*-†*Praectenomys* ~4 Ma and crown Ctenomyidae ~6.5 Ma (Verzi *et al.*, 2013), the fossil record agrees with molecular estimates that place the crown tuco-tuco radiation in the latest Miocene or earliest Pliocene.

Capromyidae

The Capromyidae (hutias) are recovered as monophyletic and well resolved, although they are nested within Echimyidae. The Hispaniolan *Plagiodontia* appears as the basal member of this clade, with the Jamaican and Bahamian *Geocapromys* as the next-most basal. These genera flank a clade of exclusively Cuban hutias, with *Capromys* as sister to *Mysateles* + *Mesocapromys*. The divergence of the three Cuban genera dates only to 3.0 Ma, in the Late Pliocene. In fact, *Mesocapromys* and *Mysateles* were regarded as subgenera of *Capromys* until Kratochvil *et al.* (1978) elevated them to generic rank (but see Woods, 1989). In view of their recent origins and morphological and genetic distinctions (*e.g.*, Camacho Pérez *et al.*, 1995; Borroto-Páez and Mancina, 2011; Kilpatrick *et al.*, 2012), this group also requires a revision with combined molecular and cladistic character analysis of fossil and living taxa.

The mid-Miocene (17.4 Ma) split between Capromyidae and a lineage of Brazilian echimyids considerably postdates GAAR (Greater Antilles + Aves Ridge; Fig. 6.2), a transitory corridor for dispersal from northern South America to the Caribbean ~34 Ma (Iturralde-Vinent and MacPhee, 1999).The delayed 9.8 Ma age for crown Capromyidae supports the idea that a considerable portion of this radiation is now extinct (Woods *et al.*, 2001; Borroto-Páez and Mancina, 2011). The oldest capromyid fossil, †*Zazamys*, was here assigned to the Capromyidae crown group as a stem member of Isolobodontinae following MacPhee *et al.* (2003), but this calibration point was excluded from the final analyses due to concerns about the significantly older node age upon its inclusion (Fig. 4.2). Until the phylogenetic position of †*Zazamys* relative to modern capromyids and recently extinct taxa (App. 1) can be confidently established, using this fossil as a crown constraint is questionable (see also Fabre *et al.* 2014).

Echimyidae

Our phylogenies identify three lineages of spiny rats (numbered "I", "II", and "III" in Figs. 3 and 4), two of which constitute well-supported clades. However, none support the traditional subdivision of living echimyids into the subfamilies Echimyinae, Dactylomyinae, and Eumysopinae (*e.g.*, Woods and Kilpatrick, 2005). Instead, echimyines appear in both lineages I and II, dactylomyines comprise a small part of a lineage I, and eumysopines are scattered across all three clades. The lineages we recover also conflict with the latest cladistic analyses of morphological variation in fossil and living taxa (*e.g.*, Olivares *et al.*, 2012). Nevertheless, our results agree with previous molecular studies in areas of overlap and strong statistical support (*e.g.*, Leite, 2003; Galewski *et al.*, 2005).

We recovered strong support for an arboreal lineage (I) that comprises all dactylomyines, most echimyines, plus a few eumysopines. This group includes the genera *Lonchothrix, Mesomys, Isothrix, Santamartamys, Diplomys, Olallamys, Kannabateomys, Dactylomys, Pattonomys, Toromys, Makalata, Echimys*, and *Phyllomys.* Some of these genera belong to well-supported dyads: *Lonchothrix* + *Mesomys, Santamartamys* + *Diplomys, Pattonomys* + *Toromys,* and *Echimys* + *Phyllomys.* Others, including *Isothrix* and *Makalata,* have less certain placements within the group. The three bamboo rat genera (*Olallamys, Kannabateomys*, and *Dactylomys*) are strongly supported as a group that shared a MRCA 10.3 Ma, but within that clade are unresolved, with weak support for a sister-group relationship between *Kannabateomys* and *Dactylomys*. Given the morphological and ecological distinctiveness of bamboo rats, the recovery of two erstwhile echimyine genera, *Diplomys* and *Santamartamys,* as their sister clade is remarkable. This is the first time *Olallamys, Diplomys,* and *Santamartamys* have been included in any molecular phylogeny, expanding the membership of this clade to non-bamboo rats and centering its geographic distribution in the Northern Andes.

We also found strong support for a widespread and ecologically diverse lineage (II), of which the terrestrial rodent *Thrichomys* appears to be the basal member. Our timetree (Fig. 5) dates the stem divergence leading to *Thrichomys* as 15.5 Ma. Using extensive sampling of *Thrichomys* populations across their geographic range, Nascimento *et al.* (2013) dated the *Thrichomys* crown group to the Late Miocene (~8.5 Ma). The next-most-basal member of this clade is *Myocastor*, which was thought to represent a separate family, Myocastoridae (Woods, 1993), until molecular phylogenetic analyses consistently recovered it as an echimyid (*e.g.*, Leite and Patton, 2002).

Myocastor is securely recovered as sister to a triad that includes the eumysopine pair *Proechimys* + *Hoplomys* plus the echimyine *Callistomys*. For most of the time since its initial description (Pictet, 1841), *Callistomys pictus* was recognized as a species of *Echimys* or *Isothrix*, both echimyines. Emmons and Vucetich (1998) recognized many differences in cranial characters between this form and other living echimyids and erected a new genus for it and a related fossil form. Recovery of *Callistomys* in lineage II with semi-aquatic *Myocastor* and the terrestrial spiny rats *Proechimys* + *Hoplomys* suggests that its soft fluffy pelage and arboreal or scansorial habits evolved independently from similar traits in lineage I (see also Upham, 2014; Loss *et al.*, 2014). Resemblances between *Callistomys* and extinct echimyid lineages in the mid-Miocene and earlier (*e.g.*, †*Maruchito*; Emmons and Vucetich, 1998; Verzi *et al.*, 2013) make it likely that the nearest relatives of *Callistomys* are missing from our phylogenetic tree.

The third echimyid lineage (III) is only partially supported and creates topological and nomenclatural issues for the Echimyidae by rendering the family paraphyletic with respect to Capromyidae. Galewski *et al.* (2005) were first to identify a clade of three Brazilian Shield taxa –*Trinomys* as sister to *Clyomys* + *Euryzygomatomys*– that joined to *Capromys* rather than the remaining echimyids (see also Fabre *et al.*, 2012b; Upham and Patterson, 2012).This relationship is unchanged by the addition of four additional capromyid genera, which join *Capromys* to form a robustly monophyletic group. It is also unaltered by the inclusion of *Carterodon*, a Cerrado endemic, which is recovered as sister to the other Brazilian Shield taxa or falls into a trichotomy with them and the capromyids (Fig. 3). Whereas the fossorial *Clyomys* and *Euryzygomatomys* diverged in late Miocene times (5.7 Ma; Fig. 5), other members of this lineage have much longer branches. The lineage leading to *Trinomys*, which was considered merely a subgenus of *Proechimys* until the molecular study of Lara *et al.* (1996), diverged from other echimyids 15.8 Ma, and the branch to *Carterodon* diverged still earlier, at 16.7 Ma. Carvalho and Salles (2004) grouped *Carterodon, Clyomys,* and *Euryzygomatomys* together with some fossil forms at the base of crown-group Echimyidae, which is consistent with our results. Olivares *et al.* (2012) found support for the Miocene fossil †*Theridomysops* as sister to *Clyomys* + *Euryzygomatomys*, joined next as sister by *Carterodon*, but they recovered *Trinomys* as sister to *Proechimys* rather than a member of this clade. Resolving this node may be clouded by the extinction of †*Theridomysops* and other forms, which would have pruned relatives that might help to resolve it.

There is also the possibility of a hard polytomy at the base of some echimyid lineages stemming from rapid or simultaneous divergence, an idea first posed to explain the lack of resolution in mtDNA phylogenies (Lara *et al.*, 1996; Leite and Patton, 2002). The inclusion of slower-evolving nuclear exons helped resolve some elements of this "star-phylogeny" (*e.g.*, Galewski *et al.*, 2005; Fabre *et al.*, 2012b), but it did not exclude the possibility that unresolved nodes were real polytomies (hard) rather than being due to lack of data (soft). Our expanded molecular sampling of echimyid genera helps to solidify the sister relationship between lineages I and II, and resolve the position of several Miocene-aged nodes (Figs. 3 and 5). Group membership for previously unsampled taxa (*e.g.*, *Pattonomys*, *Santamartamys*) is also clarified. Nevertheless, key nodes remain unresolved in lineage I (relative placement of *Isothrix, Mesomys* /*Lonchothrix*, bamboo rats, and tree rats) and, as detailed above, *Carterodon* relative to the clades of Antillean hutias and Brazilian echimyids. Not to be ignored, however, is the potential resolving power that molecular sequences from missing echimyids may still have on their inferred phylogeny. In particular, the historical extinction of Caribbean echimyids allied to †Heteropsomyinae (*e.g.*, *Boromys*; App. 1) presents a fascinating opportunity to include ancient DNA from this lineage. Considering echimyid fossils in this assessment is also necessary. Several mid-Miocene echimyids (*e.g.*, †*Stichomys*) cluster with living members of lineage I in recent cladistic analyses (Verzi *et al.*, 2013; Arnal *et al.*, 2014), reinforcing the idea that resolving the early history of Echimyidae hinges upon combined analyses of morphological and molecular diversity.

Environmental context for caviomorph rodent diversification

Geological and paleoclimatic studies allow us to glimpse the varied and dynamic environments that caviomorph ancestors would have experienced during their Middle Eocene-Recent evolutionary history (Fig. 6). Caviomorph ancestors inhabited a hot and wet "greenhouse" world that lacked polar icecaps and had mean global temperatures >10 °C warmer than they are today (Zachos *et al.*, 2008; Goin *et al.*, 2012). A dramatic global cooling event unfolded near the Eocene-Oligocene boundary that is linked to the opening of the Drake Passage between Cape Horn and Antarctica, formation of a strong Antarctic Circumpolar Current, and ensuing Antarctic glaciation (Livermore *et al.*, 2004; Zachos *et al.*, 2008; Lagabrielle *et al.*, 2009).

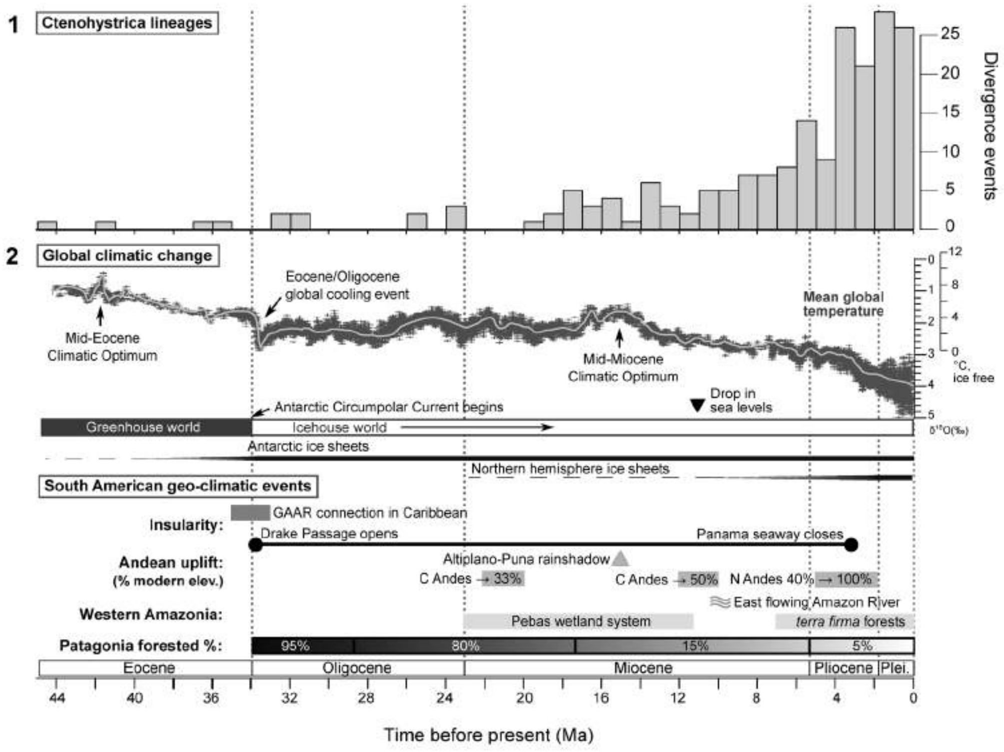

Figure 6. The timing of 1. divergence events throughout the molecular timetree of Ctenohystrica (grouped in 1 Ma bins from the species-level timetree [not shown]) in relation to 2. contemporaneous climatic and geologic events. Note that only the surviving lineages are represented in the timetree. The oxygen isotopic curve is modified from Zachos *et al.* (2008) and is used to represent global climatic changes. The temperature scale assumes an ice-free ocean, so only applies directly to the period prior to ~35 Ma (Eocene–Oligocene boundary), after which a global cooling event initiated ice sheets in Antarctica and a shift to an "icehouse" world (Livermore *et al.*, 2004; Lagabrielle *et al.*, 2009; Goin *et al.*, 2012). Other references for geoclimatic events are as follows: the GAAR (Great Antilles/Aves Ridge) land connection ~34 Ma for dispersal to the Caribbean from South America (Iturralde Vinent and MacPhee, 1999); global drop in sea levels ~11 Ma (Haq *et al.*, 1987); orogenic episodes and percentages of modern elevations in the Central Andes 22-20 Ma and 12-10 Ma, and Northern Andes 5-2 Ma (Gregory–Wodzicki, 2000; Lomize, 2008); Altiplano-Puna rainshadow by 15 Ma (Hartley, 2003); Pebas wetlands in Amazonia 23-11 Ma and *terra firma* forests beginning ~7 Ma (Hoorn *et al.*, 2010; Latrubesse *et al.*, 2010; Shephard *et al.*, 2010); establishment of the east flowing Amazon River between 10.6 and 9.7 Ma (Figueiredo *et al.*, 2010); and stages of decreasing forest cover in Patagonia (Barreda and Palazzesi, 2007; Barreda *et al.*, 2010). The timing of geological epochs is from Gradstein *et al.* (2004).

The subsequent "icehouse" world provided the backdrop for Caviomorpha's initial diversification ~32 Ma into four strongly differentiated superfamilies (Figs. 5 and 6). Several stages of Andean orogeny during the Miocene are well supported, with the first major uplift in the Central Andes by 20 Ma, followed by a later uplift 12-10 Ma to half of its modern elevation of ~3700 m in the Altiplano-Puna (Gregory-Wodzicki, 2000; Lomize, 2008). By ~15 Ma, Andean uplift created a rainshadow across much of eastern South America, especially in the south (Hartley, 2003), leading to a striking process of aridification throughout Patagonia and the Southern Cone. The middle to late Miocene drying of Patagonia reduced a formerly wet, forested biome to arid shrubland, desert, and relict montane forests (Barreda and Palazzesi, 2007; Barreda *et al.*, 2010). Major growth of the Northern Andes was not triggered until ~5 Ma, but subsequent uplift was rapid. By 2 Ma, the full modern elevation of both the Central and Northern Andes had been reached (Gregory-Wodzicki, 2000). Meanwhile in the Amazon Basin, the early stages of Andean orogeny took place as Western Amazonia was covered by the inland Pebas system of wetlands and floodplains, which lasted from ~23-11 Ma (Hoorn *et al.*, 2010; Latrubesse *et al.*, 2010). Shifting drainage patterns to the east and lowered global sea levels led to the Pebas system receding and establishing the east-flowing Amazon River (Haq *et al.*, 1987; Figueiredo *et al.*, 2010), so that by ~7 Ma, *terra firma* rainforests had expanded widely in the Amazonian lowlands (Hoorn *et al.*, 2010; Shephard *et al.*, 2010; Bonvicino and Weksler, 2012).

These geoclimatic events –individually and in concert– created major changes in South American biomes that certainly would have impacted the evolutionary diversification of caviomorphs. For example, episodes of Andean uplift provided novel highland habitats and opportunities for genetic isolation, promoting novel variants that might subsequently recolonize lowland habitats as incipient species. Evidence for transitions between lowland and highland habitats has been amassed within clades of Echimyidae (bamboo rats, spiny tree-rats, and brush-tailed rats; Upham *et al.*, 2013), as well as Andes-Amazon lineages of frogs (*e.g.*, Santos *et al.*, 2009), birds (*e.g.*, Weir, 2006), and mammals such as opossums (de la Sancha *et al.*, 2012) and olingos (Helgen *et al.*, 2013). Both directions of transition (lowland-to-highland and highland-to-lowland) appear to have been common in South America since the late Miocene (Upham *et al.*, 2013), supporting the thesis that processes of geoclimatic and biological evolution are intricately linked (Patterson *et al.*, 2012; Morrone, 2014).

Perhaps most dramatically for caviomorph rodents was the major differentiation of South American habitats into arid southern and mesic northern biomes after ~18 Ma. Substantial global cooling following the Mid-Miocene Climatic Optimum, along with the initiation of a rainshadow in most of the Southern Cone (Fig. 6.2), transformed the continent into multiple distinctive biomes, each with unique environmental challenges to resident caviomorphs (Croft *et al.*, 2009; Flynn *et al.*, 2012). The fossil record of Octodontoidea appears to especially reflect these changes, with the mesic-adapted clade of Echimyidae-Capromyidae represented in Patagonian localities during the Miocene (*e.g.,* Vucetich *et al.*, 1993), but replaced thereafter by a greater diversity of arid-adapted forms allied to Octodontidae-Ctenomyidae (Verzi *et al.*, 2008; Verzi *et al.*, 2013). According to our molecular timetree, these main clades of Octodontoidea have approximately coeval crown diversifications (18.2 Ma and 18.9 Ma, respectively; Fig. 5), roughly concordant with the timing of continent-wide climatic differentiation. This poses a key question about the subsequent evolution of these clades: What factors led to the greater longevity of lineages in Echimyidae-Capromyidae (many Miocene-aged lineages) compared to those in Octodontidae-Ctenomyidae (two surviving lineages from the late Miocene)? The fact that the southern clade of octodontids and ctenomyids had to adapt to arid climates unprecedented in the Paleogene (Fig. 6.2), suggests one reason for the apparently greater turnover of species during the initial stages of their radiation (Fig. 5; Upham, 2014). Spatiotemporal and ecomorphological data from the fossil record need to be reconciled with the region's progressive aridification, especially now that rates and sequences of lineage diversification can be inferred from the molecular timetree.

The juxtaposition of caviomorph diversification events (Fig. 6.1) along with the climatic and environmental factors that might have shaped their evolutionary history (Fig. 6.2) is intended only to be heuristic; we emphasize it is not exhaustive. In another study, we examine the tempo and mode of caviomorph diversification and disparification more directly. However, Figure 6 offers a glimpse of the major environmental factors that would have shaped caviomorph evolution from the Oligocene-Miocene, prior to the arrival of other rodent groups (including squirrels, beavers, and gophers) and placental lineages to South American ecosystems (Simpson, 1980). The opportunities that caviomorphs encountered and were able to exploit are directly reflected in their diversity and disparity, but we are still far from understanding this complementarity. The remarkable fossil and living diversity of caviomorph rodents deserves to be highlighted in evolution textbooks – this is truly an exemplar lineage for studying biological diversity and diversification through time.

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Appendix 1. Taxonomy and genetic sampling for this study, showing GenBank accession numbers for the five gene regions examined. Sequences in bold were generated newly for this study or Upham *et al*. (2013), and are associated with the listed museum voucher or collector numbers. Species listed without reference numbers are entirely from GenBank and are specimen chimeras in most cases. Species denoted with * lacked published DNA sequences prior to this study, and those with ‡ were sequenced from dried tissue. "NS" accompanies species not sampled here, and † denotes those recently extinct. This listing is updated from Woods and Kilpatrick (2005) using the IUCN Mammal Redlist (2012) and primary literature.

Species	**Museum voucher or collector number**	**Gene regions**				
		mtDNA		**Nuclear exons**		
		cyt-*b*	**12S rRNA**	**GHR**	**vWF**	**RAG1**
MOUSE-RELATED CLADE						
Pedetidae						
Pedetes	species chimera[b]	AJ389527 (s)	AY012113 (c)	AF332025 (c)	AJ238389 (s)	AY011882 (c)
CTENOHYSTRICA						
CTENODACTYLOMORPHI						
Diatomyidae						
Laonastes aenigmamus		AM407933	DQ139934	AM407901	AM407897	
Ctenodactylidae						
Ctenodactylus	species chimera[c]	AJ389532 (v)	AJ389543 (v)	AF332042 (g)	JN415077 (g)	JN633629 (g)
Felovia vae	NS					
Massoutiera mzabi		AJ389533	AJ389544			
Pectinator spekei	NS					
HYSTRICOGNATHI						
Hystricidae						
Atherurus africanus		HQ450774	AY093658			
Atherurus macrourus		FJ931121	U12451	JF938865	AJ251131	
Hystrix africaeaustralis		X70674	U12448	AF332033		
Hystrix brachyura		JQ991599	AY012117	JN414760	JN415082	AY011886
Hystrix crassispinis	NS					
Hystrix cristata		FJ472565	AY093659			
Hystrix indica		AY692229	AY093669			
Hystrix javanica	NS					
Hystrix pumila	NS					
Hystrix sumatrae	NS					
Trichys fasciculata				FM162081	AJ224675	
PHIOMORPHA						
Bathyergidae						
Bathyergus janetta		AF012241	AY425843			
Bathyergus suillus		AY425913		FM162080	AJ238384	
Fukomys amatus		AF012233	AY427021			
Fukomys anselli			AY427022			
Fukomys bocagei		AF012229	AF012213			
Fukomys damarensis		AF012220	AY427026	FN984748	FN984751	

Species	Museum voucher or collector number	Gene regions				
		mtDNA		Nuclear exons		
		cyt-*b*	12S rRNA	GHR	vWF	RAG1
Fukomys darlingi		AF012232	AY427033			
Fukomys foxi			AY427036			
Fukomys ilariae	NS					
Fukomys kafuensis		AY427037				
Fukomys mechowi		AF012230	AY427041			
Fukomys occlusus	NS					
Fukomys ochraceocinereus			AY427045			
Fukomys vandewoestijneae	NS					
Fukomys whytei			AY425863	AY427046		
Fukomys zechi	NS					
Cryptomys hottentotus		AY425885	AY427064	FJ855202	AJ251132	
Cryptomys anomalous			AY427054			
Cryptomys holosericeus			AY427051			
Cryptomys natalensis			M63568			
Cryptomys nimrodi	NS					
Georychus capensis		AF012243	AY427066	FJ855203		
Heliophobius argenteocinereus	FMNH 168421	KJ742646	AY427070	FJ855204	AJ251133	KJ742671
Heterocephalus glaber		AF155870	AY427075	AF332034	AJ251134	AY011889
Petromuridae						
Petromus typicus		DQ139935	M63571	JN414761	AJ251144	JN633636
Thryonomyidae						
Thryonomys gregorianus	NS					
Thryonomys swinderianus	FMNH 165618	KJ742647	NC_002658	AF332035	AJ224674	KJ742672
Caviomorpha						
Erethizontoidea						
Erethizontidae						
Chaetomyinae						
Chaetomys subspinosus		EU544660				
Erethizontinae						
Erethizon dorsatum		KC463889	AY012118	AF332037	AJ251135	AY011887
Coendou bicolor		KC463860				
Coendou ichillus		KC463861				
Coendou insidiosus		JX312693	JX312693			
Coendou melanurus		KC463862	AJ389549		AJ224664	
Coendou mexicanus		KC463863		FJ855212		
Coendou nycthemera		KC463864				
Coendou prehensilis	correction [d]	KC463873	AF520695	AF520663		
Coendou pruinosus		KC463880				

Species	Museum voucher or collector number	Gene regions				
		mtDNA		Nuclear exons		
		cyt-*b*	12S rRNA	GHR	vWF	RAG1
Coendou quichua		KC463882				
Coendou roosmalenorum	NS					
Coendou rufescens		KC463884				
Coendou spinosus		KC463887				
Coendou vestitus		KC463888				
Coendou villosus	NS					
Cavioidea						
Caviidae						
Caviinae						
Cavia aperea		GU136753	AF433908	AF433930		
Cavia fulgida		GU136737				
Cavia intermedia	NS					
Cavia magna		GU136734	AY765986			
Cavia patzelti	NS					
Cavia porcellus		AF490405	AF433909	AF433931	AJ224663	XM_003463833
Cavia tschudii		GU136731	AY012121	FJ855206		AY011890
Galea flavidens	NS					
Galea musteloides	FMNH 164943	KJ742648	AF433910	AF433933	KJ742608	KJ742673
Galea spixii		GU067491	AF433913	AF433935		
Microcavia australis		AF491750	AF433915	AF433937		
Microcavia niata		GU136725				
Microcavia shiptoni	NS					
Dolichotinae						
Dolichotis patagonum		GU136724	AF433917	AF433939		
Dolichotis salinicola		GU136723	AF433919	AF433940		
Hydrochoerinae						
Hydrochoerus hydrochaeris		GU136721	AF433924	FJ855208	AJ251137	AY011891
Hydrochoerus isthmius	NS					
Kerodon acrobata		GU477346				
Kerodon rupestris		GU136722	AY765988	AF433938		
Dasyproctidae						
Dasyprocta azarae	NS					
Dasyprocta coibae	NS					
Dasyprocta cristata	NS					
Dasyprocta fuliginosa		AF437784				
Dasyprocta guamara	NS					
Dasyprocta kalinowskii	NS					
Dasyprocta leporina		AF437791	AY093660	FJ855207	U31607	
Dasyprocta mexicana	NS					

Species	Museum voucher or collector number	Gene regions				
		mtDNA		Nuclear exons		
		cyt-*b*	12S rRNA	GHR	vWF	RAG1
Dasyprocta prymnolopha	NS					
Dasyprocta punctata			AF433921	AF433943	JN415079	
Dasyprocta ruatanica	NS					
Myoprocta acouchy	FMNH 160003	KJ742649	AF433922	AF433945	KJ742609	KJ742695
Myoprocta pratti		U34850	AF433923	AF433946		
Cuniculidae						
Cuniculus paca		AY206555	AF520693	AF433928	AJ251136	
Cuniculus taczanowskii	FMNH 170721	KJ742656	AY012125	AF433929	JN415074	AY011894
CHINCHILLOIDEA						
Chinchillidae						
Chinchilla chinchilla	NS					
Chinchilla lanigera	FMNH 178049	AF464760	AF520696	AF332036	AJ238385	KF590658
Lagidium peruanum		AY254885				
Lagidium viscacia		AY254886		FJ855209		
Lagidium wolffsohni		AY227023				
Lagostomus crassus	NS					
Lagostomus maximus		AF245485		FJ855210		
Dinomyidae						
Dinomys branickii		AY254884	AY012124	AF520659	AJ251145	AY011893
OCTODONTOIDEA						
Abrocomidae						
Abrocoma bennettii		AF244387		FJ855213	AJ251143	JN633625
*Abrocoma boliviensis**‡	MVZ 120238	KJ742657				
Abrocoma budini	NS					
Abrocoma cinerea		AF244388	AF520666	AF520643		
Abrocoma famatina	NS					
Abrocoma schistacea	NS					
Abrocoma uspallata	NS					
Abrocoma vaccarum	NS					
Cuscomys ashaninka *	LHE 1359	KJ742658	KJ742598	KJ742626	KJ742610	KJ742683
†*Cuscomys oblativus*	NS [e]					
Octodontidae						
Aconaemys fuscus		AF405351	AF520674	AF520657		
Aconaemys porteri			AF520671	AF520644		
Aconaemys sagei	MVZ 163419	KJ742650	AF520672	AF520645		KJ742675
Octodon bridgesi	MVZ 184958	KJ742651	AF520676	AF520646	KJ742611	KJ742676
Octodon degus		AF007058	AF520678	AF520647		
Octodon lunatus		AF227514	AF520681	AF520650	AJ238386	
Octodon pacificus	NS					

Species	Museum voucher or collector number	Gene regions				
		mtDNA		Nuclear exons		
		cyt-*b*	12S rRNA	GHR	vWF	RAG1
Octodontomys gliroides	FMNH 162890	AF370706	AF520683	AF520649	KF590672	KF590663
Octomys mimax		GQ121097	AF520686	AF520652		
Pipanacoctomys aureus		GQ121117	AY249753	AY249752		
*Salinoctomys loschalchalerosorum**	CML 3695	KJ742652	KJ742607	KJ742635	KJ742612	KJ742684
Spalacopus cyanus		AF007061	AF520688	AF520653		
Tympanoctomys barrerae		AF007060	AF520691	AF520655		
Ctenomyidae						
Ctenomys argentinus		AF370680				
Ctenomys australis		AF370697				
Ctenomys azarae		JN791407				
Ctenomys bergi		AF144284				
Ctenomys boliviensis		AF007038	U12446	FJ855214		JN633630
Ctenomys bonettoi		AF144286				
Ctenomys brasiliensis	NS					
Ctenomys budini	NS					
Ctenomys colburni		HM777474				
Ctenomys coludo	NS					
Ctenomys conoveri		AF007054				
Ctenomys coyhaiquensis	FMNH 134300	AF119112	KF590700	KF590678	KF590666	KF590659
Ctenomys dorbignyi		AF500044				
Ctenomys dorsalis	NS					
Ctenomys emilianus	NS					
Ctenomys famosus	NS					
Ctenomys flamarioni		AF119107				
Ctenomys fochi	NS					
Ctenomys fodax		HM777475				
Ctenomys frater		AF007045				
Ctenomys fulvus		AF370688				
Ctenomys goodfellowi		AF007050				
Ctenomys haigi		AF422920	AF422853			
Ctenomys ibicuiensis	new species [f]	JQ389020				
Ctenomys johannis	NS					
Ctenomys juris		AF144275				
Ctenomys knighti	NS					
Ctenomys lami		HM777477				
Ctenomys latro		HM777478				
Ctenomys leucodon		AF007056	HM544131			
Ctenomys lewisi		AF007049				
Ctenomys magellanicus		HM777479				

Species	Museum voucher or collector number	Gene regions				
		mtDNA		Nuclear exons		
		cyt-*b*	12S rRNA	GHR	vWF	RAG1
Ctenomys maulinus		AF370703			AJ251138	
Ctenomys mendocinus		HM777480				
Ctenomys minutus		HM777483				
Ctenomys nattereri		HM777484				
Ctenomys occultus		HM777485				
Ctenomys opimus		AF370700				
Ctenomys osvaldoreigi	NS					
Ctenomys pearsoni		HM777486				
Ctenomys perrensi		HM777489				
Ctenomys peruanus	NS					
Ctenomys pilarensis		AF144265				
Ctenomys pontifex	NS					
Ctenomys porteousi		AF370682				
Ctenomys pundit		HM777490				
Ctenomys rionegrensis		AF119103	HM544130			
Ctenomys roigi		HM777492				
Ctenomys saltarius		HM777493				
Ctenomys scagliai		HM777494				
Ctenomys sericeus		HM777496				
Ctenomys sociabilis		HM777495	HM544129			
Ctenomys steinbachi		AF007044	AF520667	AF520656		
Ctenomys sylvanus						
Ctenomys talarum		AF370699				
Ctenomys torquatus		AF119111				
Ctenomys tuconax		AF370684				
Ctenomys tucumanus		AF370691				
Ctenomys tulduco	NS					
Ctenomys validus	NS					
Ctenomys viperinus	NS					
Ctenomys yolandae		AF144285				
Echimyidae						
Dactylomyinae						
Dactylomys boliviensis		L23339	AF422875	JX515334	AJ849307	EU313298
Dactylomys dactylinus	USNM 579620	L23335	AF422874	KF590681	KF590667	EU313300
Dactylomys peruanus		EU313206				
Kannabateomys amblyonyx		AF422917	AF422850		AJ849310	
Olallamys albicauda *‡	FMNH 71128	KF590697		KF590690	KF590673	
Olallamys edax	NS					

Species	Museum voucher or collector number	Gene regions				
		mtDNA		Nuclear exons		
		cyt-*b*	12S rRNA	GHR	vWF	RAG1
Echimyinae						
*Callistomys pictus**	RM 233	KJ742659	KJ742594	KJ742627	KJ742614	KJ742677
Diplomys caniceps	NS					
*Diplomys labilis**‡	FMNH 70101	KJ742660		KJ742636	KJ742613	KJ742685
*Santamartamys rufodorsalis**‡	AMNH 34392	KJ742664				
Echimys chrysurus		L23341	AF422877	JX515333	AJ251141	EU313303
Echimys saturnus	NS [g]					
Echimys vieirai	NS					
Pattonomys occasius *‡	FMNH 84259	KJ742661		KJ742637		
Pattonomys semivillosus *‡	FMNH 69118	KJ742662			KJ742616	KJ742687
Isothrix barbarabrownae ‡	FMNH 170722	EU313214	KF590701	KF590682	KF590668	EU313304
Isothrix bistriata		L23349		JX515336	AJ849308	EU313307
Isothrix negrensis	mislabeled [h]	L23355	AF422873			
Isothrix orinoci‡	USNM 406370	EU313223	KF590702	KF590683	KF590669	KF590660
Isothrix pagurus ‡	USNM 555639	EU313227	KF590703	KF590684	KF590670	KF590661
Isothrix sinnamariensis	ROM 106624	AY745734	KF590704	KF590685	AJ849309	EU313312
Toromys grandis ‡	FMNH 92198	KF590699		KF590694	KF590676	EU313336
Toromys rhipidurus *‡	FMNH 87244	KJ742663		KJ742638	KJ742617	KJ742686
Makalata didelphoides	UFMG 3012	L23362	KJ742600	KJ742639	AJ849311	KJ742688
Makalata macrura	MVZ 153637 [i]	L23356	AF422879	KF590687	AJ849312	EU313328
Makalata obscura	NS [j]					
Phyllomys blainvillii	MVZ 197568	JF297836	KF590706	KF590692	JF297734	KF590664
Phyllomys brasiliensis		EF608182			JF297729	
Phyllomys dasythrix	MCNU 844	JF297832	KJ742605	KJ742641	JF297708	KJ742689
Phyllomys kerri	NS					
Phyllomys lamarum		EF608181			JF297730	
Phyllomys lundi		EF608183			JF297721	
Phyllomys mantiqueirensis		EF608179			JF297720	
Phyllomys medius	NS					
Phyllomys nigrispinus		JF297807			JF297714	
Phyllomys pattoni	MN 62391	EF608187	KJ742606	KJ742642	JF297744	KJ742690
Phyllomys sulinus		JF297833			JF297710	
Phyllomys thomasi	NS					
Phyllomys unicolor	NS[k]					
Eumysopinae						
*Carterodon sulcidens**	LGA 735	KJ742666	KJ742596	KJ742640	KJ742615	KJ742678
Clyomys bishopi	NS					
Clyomys laticeps	MCNM 2009	AF422918	KJ742597	KJ742628	AJ849306	KJ742679
Euryzygomatomys spinosus	UFMG 1948	EU544667	AF422854	KJ742629	AJ849319	KJ742680

Species	Museum voucher or collector number	Gene regions				
		mtDNA		Nuclear exons		
		cyt-*b*	12S rRNA	GHR	vWF	RAG1
Hoplomys gymnurus		AF422922	AF520668	AF520661	JN415080	JN633632
Lonchothrix emiliae		AF422921	AF422857			
Mesomys hispidus	MEPN 12212	KF590705	KF590696	KF590688	KF590671	KF590662
Mesomys leniceps						
Mesomys occultus	MVZ 194396	L23388	AF422858	KF590689		EU313331
Mesomys stimulax	UFROM 379	KJ742667	KJ742603	KJ742630	KJ742618	KJ742674
Myocastor coypus		EU544663	AF520669	AF520662	AJ251140	AY011892
Proechimys brevicauda	NS					
Proechimys canicollis	NS					
Proechimys chrysaeolus	NS					
Proechimys cuvieri	FMNH 175256	AJ251400	KF590707	KF590693	KF590675	KF590665
Proechimys decumanus	NS					
Proechimys echinothrix	NS					
Proechimys gardneri	NS					
Proechimys goeldii	NS					
Proechimys guairae	NS					
Proechimys guyannensis		AJ251396				
Proechimys hoplomyoides	NS					
Proechimys kulinae	NS					
Proechimys longicaudatus	MVZ 197574	HM544128	HM544128	KJ742643	KJ742619	KJ742681
Proechimys magdalenae	NS					
Proechimys mincae	NS					
Proechimys oconnelli	NS					
Proechimys pattoni	NS					
Proechimys poliopus	NS					
Proechimys quadruplicatus		U35413	AF422863		AJ849313	
Proechimys roberti		EU544666			AJ251139	
Proechimys semispinosus	NS					
Proechimys simonsi	FMNH 175283	U35414	AF422864	KJ742631	AJ849320	EU313332
Proechimys steerei	NS					
Proechimys trinitatus	NS					
Proechimys urichi	NS					
Thrichomys apereoides		EU313252	AF422855	JX515325	AJ849315	EU313334
Thrichomys inermis		AY083343				
Thrichomys pachyurus		AY083329				
Trinomys albispinus		U34856				
Trinomys dimidiatus	UFMG 1951	U35169	AF422867		KJ742620	KJ742682
Trinomys eliasi		U35166	AF422869			

Species	Museum voucher or collector number	Gene regions				
		mtDNA		Nuclear exons		
		cyt-*b*	12S rRNA	GHR	vWF	RAG1
Trinomys gratiosus		AF194281				
Trinomys iheringi	FMNH 141667	EU313254	AF422868	KF590695	KF590677	EU313337
Trinomys mirapitanga	NS					
Trinomys moojeni	NS					
Trinomys myosuros	NS					
Trinomys paratus		U35165	AF422866		AJ849316	
Trinomys setosus		AF422924	AF422871		AJ849317	
Trinomys yonenagae		AF194295	AF422865		AJ849318	
†Heteropsomyinae						
†*Boromys offella*	NS					
†*Boromys torrei*	NS					
†*Brotomys contractus*	NS					
†*Brotomys voratus*	NS					
†*Heteropsomys insulans*	NS					
Capromyidae						
Capromyinae						
Capromys pilorides		AF422915	AF433926	AF433950	AJ251142	JN633628
*Geocapromys browni**	ZTNH844	KJ742653	KJ742599	KJ742644	KJ742621	KJ742692
*Geocapromys ingrahami**‡	FMNH 5624	KJ742668				
†*Geocapromys columbianus*	NS					
†*Geocapromys thoracatus*	NS					
*Mesocapromys angelcabrerai**	RBP-A41	KJ742654	KJ742595	KJ742632	KJ742622	KJ742694
*Mesocapromys auritus**	RBP-B15	KJ742655	KJ742601	KJ742633	KJ742623	KJ742693
*Mesocapromys melanurus**	RBP-A25	KJ742669	KJ742602			KJ742691
Mesocapromys nanus	NS					
Mesocapromys sanfelipensis	NS					
Mysateles garridoi	NS					
Mysateles gundlachi	NS					
Mysateles meridionalis	NS					
Mysateles prehensilis *	RBP-B23	KJ742670	KJ742604	KJ742634	KJ742624	KJ742696
Plagiodontinae						
Plagiodontia aedium ‡	FMNH 63876	KJ742665		KJ742645		
	ZTNH 843				KJ742625	KJ742697
†*Plagiodontia araeum*	NS					
†*Plagiodontia ipnaeum*	NS					
†*Rhizoplagiodontia lemkei*	NS					
†*Hexolobodon phenax*	NS					

Species	Museum voucher or collector number	Gene regions				
		mtDNA		Nuclear exons		
		cyt-*b*	**12S rRNA**	**GHR**	**vWF**	**RAG1**
†Isolobodontinae						
†*Isolobodon montanus*	NS					
†*Isolobodon portoricensis*	NS					
†**"Heptaxodontidae"**						
†*Clidomys osborni*	NS					
†*Amblyrhiza inundata*	NS [l]					
†*Elasmodontomys obliquus*	NS [m]					
†*Quemisia gravis*	NS					

[a] Museum and collector abbreviations are as follows: **AMNH**, American Museum of Natural History; **CML**, Universidad Nacional de Tucumán, Colección de Mamíferos Lillo; **FMNH**, Field Museum of Natural History; **MCNM**, Museu de Ciências Naturais, Mammals Collection, Pontifícia Universidade Católica Minas Gerais; **MCNU**, Museu de Ciências Naturais da Universidade Luterana do Brasil; **MEPN**, Museo Escuela Politécnica Nacional, Ecuador; **MVZ**, University of California, Berkeley, Museum of Vertebrate Zoology; **MN**, Universidade Federal do Rio de Janeiro, Museu Nacional; **ROM**, Royal Ontario Museum; **UFMG**, Universidade Federal de Minas Gerais, Mammals Collection; **UFROM**, Universidade Federal de Rondônia, Mammals Collection; **USNM**, United States National Museum of Natural History; **ZTNH**, University of Vermont, Zadock Thompson Natural History Collections; **LGA**, collector number of Ana Paula Carmignotto and Roberta Paresque; **LHE**, collector number of Louise H. Emmons; **RBP**, Rafael Borroto-Paez collection (and specimen number); **RM**, collector number Raquel Moura.

[b] Chimera of *Pedetes* species *capensis* (c) and *surdaster* (s)

[c] Chimera of *Ctenodactylus* species *gundi* (g) and *vali* (v)

[d] Mislabeled 12S rRNA and GHR sequences on GenBank: as *Coendou bicolor*, but these represent *C. prehensilis* (R. Voss, in litt., 6 Mar 2012)

[e] Our attempts failed to amplify DNA from a ~500-year old bone specimen of *Cuscomys oblivatus* (YPM 3318; Machu Picchu). There were reports in 2009 of a *Cuscomys* individual sighted at Machu Picchu (L. Emmons in litt , 1 Aug 2011)

[f] Species was described by de Frietas *et al.* (2012)

[g] *Echimys saturnus* was recorded at Tiputini Biodiversity Reserve in 2005 (Blake *et al.*, 2010)

[h] Mislabeled cyt-*b* and 12S rRNA sequences on GenBank: *as Isothrix bistriata* but these are *I. negrensis* (Patterson and Velazco, 2008)

[i] Mislabeled cyt-*b* sequence on GenBank: as *Makalata didel phoides*, but this is *M. macrura* (Patterson and Velazco, 2008)

[j] The name *Makalata obscura* cannot be assigned to a specific population; holotype specimen is lost with an unknown locality (Emmons, 2005)

[k] The published cyt-*b* sequence of *Phyllomys unicolor* (EF608188) is a mitochondrial numt of *P. pattoni* (C. Loss in litt, 30 Nov 2012)

[l] *Amblyrhiza* is allied outside of Chinchilloidea based on basicranial characters (MacPhee, 2011)

[m] *Elasmodontomys is* allied outside the Echimyidae + Capromyidae clade (including *Myocastor*) based on basicranial characters (MacPhee, 2011)

Appendix 2. Detailed justification of the 22 fossil calibration points used in this study. Three additional calibration points were rejected because of the temporal inconsistencies they introduced during cross-validation analyses (see Rejected Calibrations below). Each entry begins with the constrained clade and its corresponding code (A-Y; see Fig. 3), then the lognormal prior's upper 95% range in millions of years (Ma) and its shape (mean, SD) as implemented in BEAST (an "R"next to the mean refers to the mean in "real space"). Each prior was offset to the minimum age of the oldest crown fossil assigned to that clade, and a soft maximum age set at the lower 5% of the prior. We then list fossil taxa supporting the minimum age estimates, museum voucher specimen (if any), role in our dating scheme, and references for their ancestry; we also include the geological formation used in minimum age estimates, aging method, and associated references. Horizons used in maximum age estimates and their references conclude each entry. SALMA refers to South American Land Mammal Age; see referenced publications for museum abbreviations and other details.

A - Ctenohystrica: 46.0–65.8 Ma (1.341,1)

Based on †*Chapattimys wilsoni*, the earliest confidently placed stem ctenodactyloid: 46–51 Ma, early-to-middle Eocene (Marivaux *et al.*, 2004; Sallam *et al.*, 2009; Sallam *et al.*, 2011; Antoine *et al.*, 2012). From the Subthu group, Kuldana Formation, India and Pakistan (Flynn *et al.*, 1986; Antoine *et al.*, 2012). Maximum: to the occurrence of eurymylids, *e.g.*, †*Heomys*, a primitive rodent from the early Paleocene, 65.8 Ma (Hussain *et al.*, 1978; Meredith *et al.*, 2011).

B - Diatomyidae–Ctenodactylidae: 28.3–46.0 Ma (1.230,1)

Based on †*Fallomus razae*, †*Fallomus ginsburgi*, and †*Fallomus quraishyi* (GSP 21218, DC 683, DC 438), the oldest stem diatomyid; crown member of Ctenodactylidae-Diatomyidae: >28.3 Ma, Rupelian stage, early Oligocene (Dawson *et al.*, 2006). From the Bugti Hills, Paali nala C2, Chitarwata Formation, Balochistan, Pakistan (Flynn *et al.*, 1986; Marivaux and Welcomme, 2003). Maximum: to the occurrence of †*Chapattimys*, 46 Ma (Flynn *et al.*, 1986; Antoine *et al.*, 2012).

C - Hystricognathi: 41.0–56.0 Ma (1.063,1)

Based on †*Cachiyacuy contamanensis*, †*Cachiyacuy kummeli,* †*Canaanimys maquiensis,* †*Gaudeamus hylaeus,* and †*Gaudeamus aslius* (MUSM 1871, MUSM 1882, MUSM 1890, CGM 66007, CGM 66006), the oldest crown hystricognaths in South America (see calibration E), Barrancan SALMA, middle Eocene. The oldest crown members in Africa (*Gaudeamus*) are younger at ~34 Ma (Sallam *et al.*, 2009; Sallam *et al.*, 2011; Antoine *et al.*, 2012). From the CTA-27 Locality, Yahuarango Formation, Contamana, Loreto, Peru; Jebel Qatrani Formation, Fayum Depression, Egypt (Sallam *et al.*, 2009; Sallam *et al.*, 2011; Antoine *et al.*, 2012). Maximum: to the early Eocene (56 Ma), the earliest proposed date for the Santa Rosa fauna, Peru (Frailey and Campbell, 2004; Meredith *et al.*, 2011).

D - Hystricidae: 11.0–15.0 Ma (R1.280,1)

Based on *Atherurus* indet (SA 64), the oldest confidently dated crown Hystricidae fossil: –11 Ma, early Vallesian (=MN 9), late Miocene(Mein and Pickford, 2006). From the Sheikh Abdallah, Western Desert, Egypt (Mein and Pickford, 2006). Maximum: to base of the Astaracian– 15 Ma (=MN 6), because of the putative *Atherurus* fossil (†*A. karnuliensis*, formerly †*Sivacanthion complicatus*) from the Lower Silwaliks of Pakistan (Colbert, 1935; van Weers, 2005).

E - Caviomorpha – Phiomorpha: 41.0–56.0 Ma (1.063,1)

Based on †*Cachiyacuy contamanensis*; †*Cachiyacuy kummeli*; †*Canaanimys maquiensis* (MUSM 1871, MUSM 1882, MUSM 1890), the oldest known caviomorphs in South America; stem Caviomorpha, not referable to any superfamily: ~41 Ma (40.94–45.94 Ma radiometric; 40.94–41.6 Ma including bio-chronology), Barrancan SALMA, middle Eocene (Antoine *et al.*, 2012). From the CTA-27 Locality, Yahuarango Formation, Contamana, Loreto, Peru. Radiometric age (^{40}Ar/^{39}Ar) and mammalian biochronology (Antoine *et al.*, 2012). Maximum: to early Eocene (56 Ma), in accordance with the earliest proposed date for the Santa Rosa fauna, Peru (Frailey and Campbell, 2004; Meredith *et al.*, 2011).

F - Cavioidea – Erethizontoidea: 31.3–41.0 Ma (0.63,1)

Based on †*Andemys termasi* (SGOPV 2933), oldest stem member of Cavioidea *sensu stricto*; may instead be basal members of Dasyproctidae: 31.3–33.6 Ma, Tinguirirican SALMA, late Eocene-early Oligocene (Wyss *et al.*, 1993; Bertrand *et al.*, 2012; Pérez and Pol, 2012;). From the Abanico (= Coya-Machalí) Formation, Tinguiririca River valley, Termas del Flaco, central Chile. Radiometric age: 40K/40Ar (Wyss *et al.*, 1990; Flynn *et al.*, 2003; Dunn *et al.*, 2013). Maximum: to the earliest caviomorph fossils in South America, ~41 Ma (Antoine *et al.*, 2012).

G - Cavioidea (=Caviidae, Cuniculidae, Dasyproctidae): 24.2–30.77 Ma (0.237,1)

Based on †*Asteromys punctus* and †*Chubutomys simpsoni*, oldest crown members of Cavioidea *sensu stricto* ("Eocardiidae"; stem members of Caviidae): 24.2–29.4 Ma, Deseadan SALMA, late Oligocene (Pérez and Pol, 2012). From Cabeza Blanca and Lagunade los Machos, Sarmiento Formation, Argentina (Pérez and Vucetich, 2011; Dunn *et al.*, 2013). Maximum: to the base of the youngest assemblage that lacks crown cavioid fossils, which is La Cantera, Gran Barranca, Argentina, 30.77 Ma (Vucetich *et al.*, 2010; Pérez and Pol, 2012; Dunn *et al.*, 2013).

H - Caviidae (= Hydrochoerus, Kerodon, Dolichotis, Galea, Microcavia, Cavia): 11.8–13.8 Ma (0.640,1)

Based on†*Prodolichotis pridiana*, the oldest crown member of Caviidae: 11.8–13.5 Ma, Laventan SALMA, middle Miocene (Pérez and Pol, 2012). From the La Victoria and Villa Vieja formations, La Venta section of Colombia (Fields, 1957; Kay *et al.*, 1999). Maximum: to the start of the Colloncuran SALMA (13.8 Ma), since cavioid fossils of that period (*e.g.*, †*Guiomys unica*) are outside of crown Caviidae (Pérez and Pol, 2012).

I - Hydrochoerus – Kerodon: 6.1–11.8 Ma (0.095,1)

Based on †*Cardiomys cavinus* and †*Cardiatherium chasicoense*, the oldest crown hydrochoerines: 6.1–9.07 Ma, Chasicoan SALMA, late Miocene (Pérez and Pol, 2012). From the Arroyo Chasicó Formation, central Argentina. Radiometric age: correlated with Loma de Las Tapias Formation in northwestern Argentina (Deschamps *et al.*, 2009; Pérez and Pol, 2012). Maximum: to the start of the Laventan SALMA (11.8 Ma) since the cavioids of this period (*e.g.*, †*Prodolichotis*) are outside of crown Hydrochoerinae. This is the youngest, well-sampled rodent assemblage lacking forms potentially allied to Hydrochoerinae (Pérez and Pol, 2012).

J - Microcavia / Cavia – Galea: 6.1–11.8 Ma (0.095,1)

Based on †*Allocavia chasicoense*, oldest crown caviine: 6.1–9.07 Ma, Chasicoan SALMA, late Miocene (Pérez and Pol, 2012). From the Arroyo Chasicó Formation, central Argentina. Radiometric age: correlated with Loma de Las Tapias Formation in northwestern Argentina (Pascual, 1962). Maximum: to the start of the Laventan SALMA (11.8 Ma) since the cavioids of this period (*e.g.*, †*Prodolichotis*) are outside of crown Caviinae (Pérez and Pol, 2012).

K - Microcavia – Cavia: 4.0–9.07 Ma (R1.614,1)

Based on †*Paleocavia impar*, the oldest stem taxon to Microcavia: 4.0–5.3 Ma, Montehermosan SALMA, early Pliocene (Pérez and Pol, 2012). From the Monte Hermoso Formation, Argentina (Ameghino, 1889; Cione and Tonni, 1995; Schultz *et al.*, 2002). Maximum: to the base of the upper section of the Arroyo Chasicó Formation (9.07 Ma) to take into account possibly older fossils allied to this group in the Huayquerian (Pérez and Pol, 2012).

L - Chinchillidae: 9.07–19.04 Ma (0.655,1)

Based on †*Prolagostomus* sp. (AMNH DVP 99300; 9587 †*P. imperialis*), oldest crown members of Chinchillidae; stem members of the Lagostominae: 9.07–19.04 Ma, Pinturan SALMA, early-to-late Miocene (Kramarz, 2002; Croft *et al.*, 2011). From (youngest occurrence) Arroyo Chasicó Formation, central Argentina and (oldest occurrence) Pinturas Formation, Argentina (Bondesio *et al.*, 1980; Kramarz, 2002; Dunn *et al.*, 2013). Maximum: to the base of the Pinturan SALMA (19.04 Ma) based on the earliest occurrence of †*Proglagostomus* in the Pinturas Formation of southern Argentina (Kramarz, 2002; Dunn *et al.*, 2013).

M - Chinchilloidea – Octodontoidea: 31.3–41 Ma (0.627,1)

Based on †*Eoviscaccia frassinettii* (SGOPV 2935), oldest stem member of Chinchilloidea: 31.3–33.6 Ma, Tinguiriri_can SALMA, late Eocene-early Oligocene. *Eoviscaccia* is older than the oldest stem octodontoid, †*Draconomys verai,* from 30.62–30.77 Ma at La Cantera, Argentina (Wyss *et al.*, 1993; Vucetich *et al.*, 2010; Bertrand *et al.*, 2012). From Abanico (= Coya-Machalí) Formation, Tinguiririca River valley, Termas del Flaco, central Chile. Radiometric age: ^{40}K/^{40}Ar (Wyss *et al.*, 1990; Flynn *et al.*, 2003; Dunn *et al.*, 2013). Maximum: to the earliest caviomorph fossils in South America ~41 Ma (Antoine *et al.*, 2012).

N - Abrocomidae: 2.0–6.1 Ma (R1.305,1)

Based on *Abrocoma* (MMP 1059-M, MACN19722), oldest crown members of Abrocomidae (*Abrocoma* + *Cuscomys*): >2.0 Ma, Sanandresian substage, Upper Marplatan SALMA, late Pliocene (Verzi and Quintana, 2005b; Verzi *et al.*, 2013). From Punta San Andrés and Santa Isabel, Buenos Aires, Argentina. Biochronological and magnetostratigraphic age (Verzi and Quintana, 2005b). Maximum: to the start of the Huayquerian SALMA (6.1 Ma) based on the first occurrence of the stem abrocomid, †*Abrocoma* (*Protoabrocoma*) *antiqua*, in the late Miocene of Bolivia and western Argentina (Cione *et al.*, 2000; Verzi and Quintana, 2005b; Verzi *et al.*, 2013).

P - Octodontidae: 6.8–11.8 Ma (R1.590,1)

Based on †*Pseudoplateomys innominatus* (MACN 8363), the oldest crown octodontid (or octodontine *sensu* Verzi *et al.*, 2013): >6.8 Ma, Huayquerian SALMA, late Miocene (Verzi *et al.*, 2013). From Quebrada de La Troya, La Rioja, Argentina. Radiometric age (Ciccioli, Limarino and Marenssi, 2005). Maximum: to the start of the Laventan SALMA (11.8 Ma), beyond which no crown octodontid fossils are found, only stem fossils such as †*Acarechimys* (Verzi *et al.*, 2013).

Q - Aconaemys / Spalacopus – Octodon: 5.0–11.8 Ma (0.272,1)

Based on †*Pithanotomys* (MACN-A 1648, †*P. columnaris* holotype), crown octodontid, sister to *Aconaemys*: >5.0 Ma, Montehermosan SALMA, early Pliocene (Verzi *et al.*, 2013). From Farola Monte Hermoso, Buenos Aires, Argentina. Biochronological age (Zárate *et al.*, 2005; Verzi, 2008). Maximum: to the start of the Laventan SALMA (11.8 Ma), beyond which no crown octodontid fossils are found, only stem fossils such as †*Acarechimys* (Verzi *et al.*, 2013).

R - Octomys – Pipanacoctomys / Tympanoctomys / Salinoctomys: 2.0–6.8 Ma (R1.528,1)

Based on †*Abalosia castellanosi* (PVL 1252, †*Plataeomys castellanosi* holotype), oldest member of the desert-adapted clade in Octodontidae: >2.0 Ma, Sanadresian substage, Upper Marplatan SALMA, late Pliocene (Verzi *et al.*, 2013). From Punta San Andrés and Santa Isabel, Buenos Aires, Argentina. Biochronological and magnetostratigraphic age (Verzi and Quintana, 2005a). Maximum: to the minimum age for crown Octodontidae (6.8 Ma), based on †*Pseudoplateomys* (Verzi *et al.*, 2013).

S - Ctenomys: 3.5–5.3 Ma (R0.573,1)

Based on †*Ctenomys uquiensis* (MLP 96-II-29-1), the oldest member of *Ctenomys* crown group: ~3.5 Ma, Chapadmalalan SALMA, late Pliocene (Verzi *et al.*, 2013). From Esquina Blanca, Jujuy, Argentina. Radiometric andmagnetostratigraphic age (Reguero *et al.*, 2007; Verzi *et al.*, 2010). Maximum: to the last occurrence of the Ctenomys sister taxon, †*Praectenomys rhombidens*, 5.3 Ma, from the Umala Formation, Bolivia (Quintana, 1994; Verzi and Montalvo, 2008; Verzi *et al.*, 2013).

V - Echimyidae "arboreal clade": 15.7–24.2 Ma (0.495,1)

Based on †*Maruchito trilofodonte* (MLP 91-IV-1-22), crown echimyid; oldest stem taxon to *Echimys* + *Phyllomys*: ~15.7 Ma, Colloncuran SALMA, middle Miocene (Verzi *et al.*, 2013). From Cañadón del Tordillo, Neuquén, Argentina. Radiometric age (Vucetich *et al.*, 1993; Madden *et al.*, 1997). Maximum: to the start of the Deseadan SALMA, 24.2 Ma (Dunn *et al.*, 2013).

W - Thrichomys – Myocastor / Callistomys / Hoplomys / Proechimys: 6.0–11.8 Ma (0.113,1)

Based on †*Pampamys* (GHUNL-Pam 2214), crown echimyid; oldest stem taxon to *Thrichomys*: 6.0–9.3 Ma, Chasicoan - Huayquerian SALMA, late Miocene (Olivares *et al.*, 2012; Verzi *et al.*, 2013). From Laguna Chillué, Cerro Azul Formation, Bajo Giuliani, Telén, Loventué, La Pampa, Argentina. Biochronological age (Zárate *et al.*, 2005; Verzi *et al.*, 2008). Maximum: to the start of the Laventan SALMA, 11.8 Ma (Kay *et al.*, 1997).

X - Myocastor – Callistomys / Hoplomys / Proechimys: 6.0–11.8 Ma (0.113,1)

Based on *Myocastor* (MACN 5404, †*M. columnaris* holotype), crown echimyid; oldest *Myocastor* species: >6.0 Ma, Huayquerian SALMA, late Miocene (Verzi *et al.*, 2013). From the "Mesopotamiense" or "Conglomerado osífero", Ituzaingó Formation, Entre Ríos, Argentina. Biochronological age (Cione *et al.*, 2000; Candela and Noriega, 2004; Zárate *et al.*, 2005). Maximum: to the start of the Laventan SALMA, 11.8 Ma (Kay *et al.*, 1997).

Y - Trinomys – Euryzygomatomys / Clyomys: 6.0–11.8 Ma (0.113,1)

Based on †*Theridomysops* (MACN-Pv 8379, †*Eumysops parvulus* holotype), a crown echimyid; oldest stem taxon to *Euryzygomatomys* + *Clyomys*: 6.0–9.3 Ma, Chasicoan-Huayquerian SALMA, late Miocene (Verzi *et al.*, 2013). From Telén and Loventué, La Pampa, Argentina. Biochronological age (Zárate *et al.*, 2005; Verzi *et al.*, 2008). Maximum: to the start of the Laventan SALMA, 11.8 Ma (Kay *et al.*, 1997).

Rejected calibrations

O - Octodontidae – Ctenomyidae: 25.5–29.4 Ma (R1.24,1)

Based on †*Sallamys* (UATF-V 5000), the oldest stem ctenomyids (or ctenomyines *sensu* Verzi *et al.*, 2013): >25.5 Ma, Deseadan SALMA, late Oligocene (Verzi *et al.*, 2013). From the Salla Luribay, Bolivia. Radiometric and magnetostratigraphic age (Kay *et al.*, 1999). Maximum: to the base of the Deseadan SALMA, 29.4 Ma (Dunn *et al.*, 2013).

T - Echimyidae (including Capromyidae): 26.0–29.4 Ma (R1.083,1)

Based on †*Deseadomys* (*D. arambourgi,* MLP 93-XI-21-5, 95-III-10-13; *D. loomisi,* MPEF 571), the oldest crown member of Echimyidae: >26.0 Ma, Deseadan SALMA, late Oligocene (Verzi *et al.*, 2013). From the La Flecha and Las Cascadas, Chubut, Argentina, and Cabeza Blanca, Santa Cruz, Argentina. Biochronological age (Vucetich, 1989). Maximum: to the base of the Deseadan SALMA, 29.4 Ma (Dunn *et al.*, 2013).

U - Capromyidae: 14.86–29.4 Ma (1.032,1)

Based on †*Zazamys veronicae* (MNHNCu–P 3071), the oldest crown member of Capromyidae; recognized as stem isolobodontine from affinity of three teeth with †*Isolobodon* from Hispaniola: >14.86 Ma, early Miocene (MacPhee *et al.*, 2003; MacPhee, 2005). From the Lagunitas Fm (Cuba), Domo de Zaza, Sancti Spiritus. Radiometric age: Rb-Sr (also older results that compare to Santacrucian SALMA) (MacPhee, 2005). Maximum: to the base of the Deseadan SALMA, 29.4 Ma (Dunn *et al.*, 2013).

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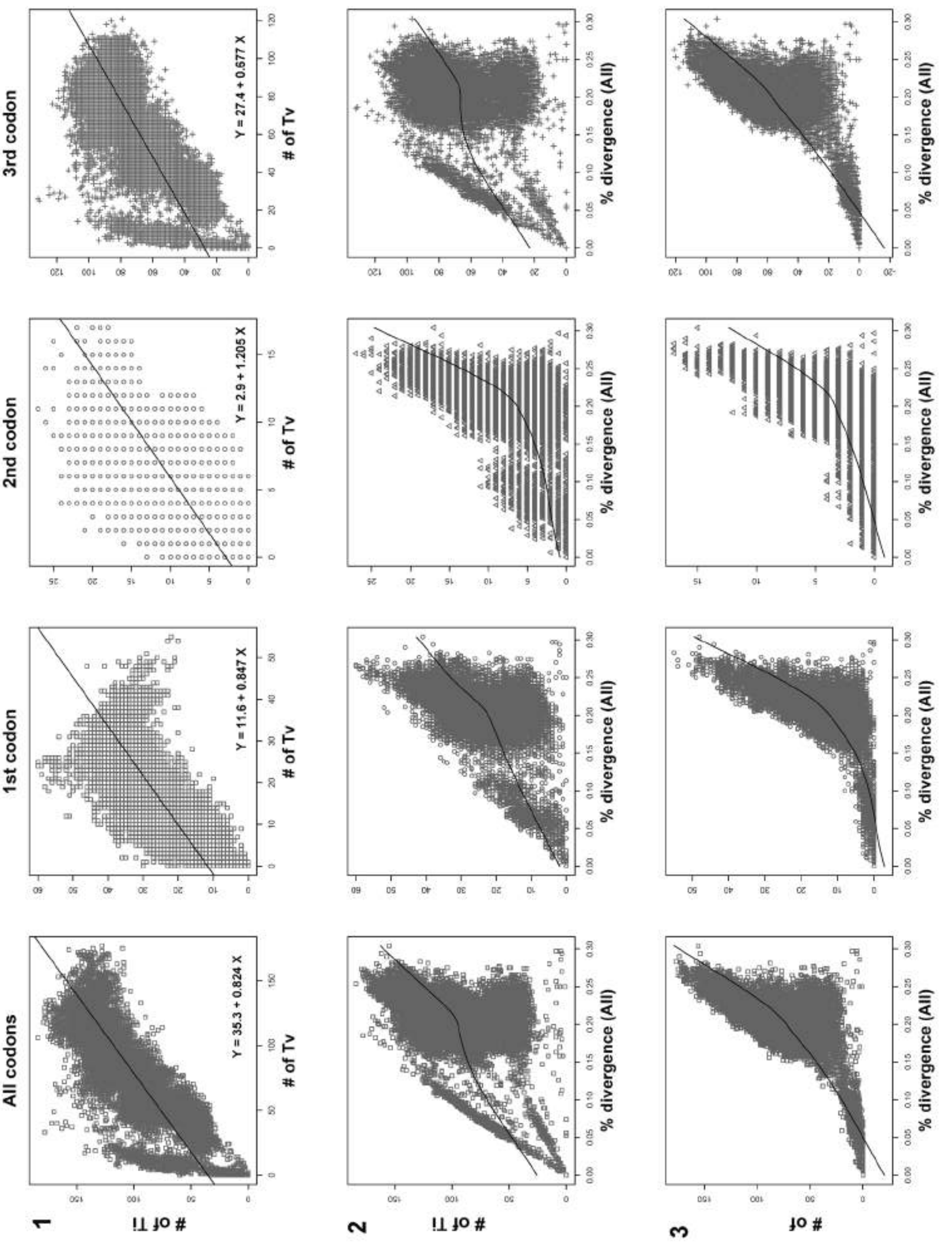
Appendix 3. Comparison of substitution saturation across codon positions in 1140 bp of the cytb mtDNA gene. Plotted are pairwise comparisons among taxa for 1. numbers of transitions (Ti) and transversions (Tv) and their corresponding linear models, 2. number of transitions versus percent sequence divergence (uncorrected–p) for all cyt–*b* codon positions, and 3) number of transversions versus cyt–*b* percent sequence divergence.



3 LARGE-SCALE RICHNESS PATTERNS, BIOGEOGRAPHY AND ECOLOGICAL DIVERSIFICATION IN CAVIOMORPH RODENTS

PATRONES DE RIQUEZA A GRAN ESCALA, BIOGEOGRAFÍA Y DIVERSIFICACIÓN ECOLÓGICA EN ROEDORES CAVIOMORFOS

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Abstract. Hystricognath rodents probably arrived from Africa and diversified rapidly into major clades during the Eocene-Early Oligocene. Caviomorph rodents radiated in different directions involving body size, ecomorphological, physiological and behavioral traits which make them convergent to several groups of mammals. The aim of this chapter is to analyze and integrate the biogeographical and ecological diversification within the phylogeny of the caviomorph major clades, followed by a case study of diversification of arid-land octodontids. Caviomorph rodents are grouped into four superfamilies (Cavioidea, Chinchi lloidea, Erethizontoidea and Octodontoidea), 13 families, 56 genera and 246 species. The major findings of our contribution are: a) the two macrohabitats with highest species density are the Amazonian and the Atlantic forest; b) approximately 35% of caviomorphs show small or restricted geographic ranges; c) species richness is linked to an effect of area and productivity; d) "Amazonia" is suggested as the most likely macrohabitat for the evolution of proto- caviomorphs; e) the most likely proto-caviomorph macroniches are associated with saxicolous modes of life and a diet of grasses, leaves and fruits; f) the proto- Monte arid-land has been suggested as the ancestral habitat of octodontids, followed by their biogeographical and ecological diversification associated with contrasting environmental conditions on both sides of the Andes; g) the colonization of a new adaptive zone and expanded geographic range of *Tympanoctomys* has been the result of the evolution of behavioral, ecomorphological, and physiological traits which enabled better utilization of open xeric habitats, and hypersaline food resources than its close relatives. The caviomorphs represent a good research model to explore and disentangle the biogeographical and ecological diversification of one of the most conspicuous native lineages of South American mammals. Our global analysis and proposed diversification hypotheses highlight some major findings and pinpoint research lines and gaps that deserve continuing investigations.

Resumen. Los caviomorfos, junto a los múridos, geómidos, sciúridos y heterómidos, son los distintos linajes de roedores que forman parte de la fauna de mamíferos de América del Sur. El segmento de roedores histricognatos neotropicales, los caviomorfos, ingresaron a América del Sur probablemente vía migración trans-Atlántica desde África, y a partir de su establecimiento radiaron hacia una amplia diversidad morfológica y ecológica en el Eoceno-Oligoceno temprano. La radiación adaptativa (*sensu* Simpson, 1950) es el marco conceptual donde enmarcamos la diversificación biogeográfica -ecológica de los caviomorfos hacia distintas zonas adaptativas. En términos generales la radiación adaptativa es la diversificación de un linaje en especies que pueden explotar una gran variedad de tipos de recursos o “zonas adaptativas” (alimentos, hábitat, modos de vida) y que difieren en atributos morfológicos y fisiológicos. No es objetivo de este trabajo discutir las distintas hipótesis y definiciones que han sido propuestas para la radiación adaptativa sino utilizarla como marco general o concepto heurístico donde analizar la diversificación de los caviomorfos. El ingreso del linaje de histricognatos a una “nueva” zona adaptativa y sin mayores competidores, representan las condiciones donde los caviomorfos experimentaron una extraordinaria diversificación en su morfología, ecología, fisiología y comportamiento, ocupando así toda la diversidad de ambientes de la Región Neotropical. Entre los resultados de esta radiación observamos un gran número de especies con características ecomorfológicas convergentes (también conocidos como equivalentes ecológicos) con ungulados, lagomorfos e hiracoideos (Mares y Ojeda, 1982; Rocha-Barbosa *et al.*, este volumen). La diversificación y biología de los caviomorfos han sido motivo de numerosos estudios, desde distintas disciplinas (sistemática, genética, anatomía, biogeografía, ecología, fisiología, comportamiento, paleontología, entre otras). Por otro lado, la aproximación integrativa entre filogenia, biogeografía y ecología ha estado limitada a algunas superfamilias y familias. En este capítulo ofrecemos una visión integradora de la diversificación biogeográfica y ecológica de los caviomorfos a partir de una matriz filogenética. Los caviomorfos comprenden en la actualidad 4 superfamilias, 13 familias, 56 géneros, y 246 especies. Entre los resultados de nuestra contribución destacamos: a) La mayor diversidad (densidad de especies) se localiza en los Andes tropicales húmedos, (Colombia, Ecuador, Perú, Bolivia), la cuenca amazónica, y la Selva Atlántica (Brasil); b) aproximadamente, el 35% de los caviomorfos muestra rangos geográficos pequeños o restringidos; c) la riqueza de especies está relacionada con un efecto fuerte de área y productividad; d) los análisis de ancestralidad de área sugieren a la “Amazonia” como el macrohábitat más probable en la evolución de los caviomorfos; e) el uso de sustrato del ancestro “proto-caviomorfo” está representado por un modo de vida saxícola; mientras que la dieta del ancestro “proto-caviomorfo” es ambigua, representada por pasto, hojas y frutos. Las diversificaciones “novedosas” de los caviomorfos, son las formas de vida terrestre, arborícola, escansorial y semiacuática, mientras que los fiomorfos se caracterizan por sus hábitos saxícolas, semifosoriales y subterraneos; f) el bioma del Desierto del Monte y el ecotono con la Protopuna habría sido el macrohábitat donde evolucionaron los protooctodóntidos. Su posterior diversificación en dos clados principales, el “chileno” y el “argentino” está fuertemente asociada al levantamiento de los Andes y los consecuentes cambios ambientales; g) la colonización de una nueva zona adaptativa y la ampliación del área de distribución geográfica de *Tympanoctomys*, ha sido el resultado de un conjunto de rasgos ecomorfológicos, fisiológicos y comportamentales que permitieron a la rata vizcacha una mejor utilización y competitividad. En conclusión, nuestro análisis ofrece una caracterización global e hipótesis sobre la diversificación biogeográfica y ecológica de un linaje conspicuo de mamíferos Neotropicales como son los caviomorfos. Se resaltan someramente algunos aspectos de este diverso grupo y se señalan líneas de investigación y vacíos que merecen ser indagados, en particular los relacionados con el papel y la integración de la filogenia asociada a la plasticidad de nichos y la estructura de los ensambles de caviomorfos.

Introduction

Caviomorph rodents are one of the most distinctive lineages of South American mammals. Their adaptive radiation in modern-day habitats of South America has resulted in 13 families and 246 species inhabiting the most diverse habitats (Upham and Patterson, 2012, this volume). The aim of this chapter is to narrow the gap between phylogeny, biogeography, and ecology of caviomorph rodents. Our approach seeks to analyze and integrate the biogeographical and ecological diversification of the major caviomorph clades (or superfamilies) within their phylogeny. In order to illustrate our aim, we discuss their overall radiation, followed by a case study of arid-land octodontids, with a particular focus on the evolution of their desert-adapted species.

Radiation of caviomorph rodents

"…The greatest interest of the phase of South American faunal history while the continent was an island lies in the fact that it is a sort of large-scale natural experiment in evolution….The first striking evolutionary phenomena illustrated are those of "explosive" or "eruptive" evolution and adaptive radiation... Everything here indicates the culmination of an exceptionally rapid and burgeoning expansion of the mammalian fauna into a great variety of ecological niches…When World Continent and South American lines became specialized for similar ecological roles, they also came to resemble each other functionally and morphologically. Parallel and convergent evolution was thus illustrated on a large scale... " (Simpson, 1950).

Caviomorph rodents colonized South America between 45.4 and 36.7 Ma through a trans-Atlantic migration from Africa (Poux *et al*., 2006). The oldest known records of small caviomorph rodents (30-120 g) in the Americas are from the Middle Eocene (about 41 Ma) of Peru (Antoine *et al*., 2011). Caviomorphs diversified rapidly after their arrival, before the Oligocene glaciations (Poux *et al*., 2006). The early diversification of caviomorphs from middle Eocene land-mammal bearing beds has been supported by the recent contributions of Antoine *et al*. (2011, and references therein) and Bertrand *et al*. (2012, and references therein). Antoine *et al*. (2011) hypothesized that the arrival and initial radiation of caviomorph rodents occurred during the warmer and wetter conditions of the Mid-Eocene Climatic Optimum. Bertrand *et al*. (2012) discovered remains of mandibles and teeth of fossil caviomorphs thought to be related to dasyproctids and chinchillids from the Early Oligocene of Chile (about 31-35 Ma). It is of particular interest that these caviomorph assemblages had high-crowned teeth, a condition called hypsodonty. Hypsodonty is well developed in mammals eating fibrous and abrasive foods that are most abundant in open and generally or seasonally dry environments (Jernvall and Fortelius, 2002). Hypsodonty prevents tooth erosion caused by abrasion (Samuels, 2009). In the Early Oligocene, these rodents inhabited open and arid landscapes with wind-blown dust and grasslands environments (Strömberg *et al*., 2013). Therefore, hypsodonty plausibly evolved in response to the presence of several abrasive conditions, due to exogenous (*e.g*., environment stressors dirt, ashes) and endogenous (diet with high fiber and silica content) factors (Williams and Kay, 2001). Likewise, a high level of hypsodonty is found in native South American ungulates that lived during the Eocene-Oligocene transition (Bertrand *et al*., 2012). Jernvall and Fortelius (2002) have proposed that mammal lineages possessing advanced or incipient hypsodonty may have been able to expand their share of habitats and food resources in the dry environmental conditions during the Late Miocene in Europe.

By the Late Oligocene, mammal trophic types were dominated by grazers, but browsers and frugivores were highly diverse. This diversity of trophic types indicates that mammals were part of a more open woodland savanna biota (Ortiz-Jaureguizar and Cladera, 2006 and references therein). Whereas in the Late Miocene, grasslands and grazer mammals were the dominant environments and trophic types in South America, while browsers and frugivores had very low diversity (Ortiz-Jaureguizar and Cladera, 2006 and references therein; Stromberg *et al.*, 2013).

The successful establishment and rapid adaptive radiation [diversification] of caviomorph rodents result from combining the colonization of a region, South America, practically devoid of competitors (*i.e.*, ecological equivalents), with ample diversity of "empty" niches of habitats and food resources. As Patterson and Pascual (1972, p. 278) pointed out, *"… Caviomorpha found a relatively clear field awaiting them. At the time of their first appearance … it is already possible…to recognize all four of the superfamilies"*. Thus, caviomorphs radiated in different directions involving body size and ecomorphological traits, with consequent diversifications in ecology, physiology and behavior which make them convergent to several groups of mammals such as hyracoid, ungulates and lagomorphs (Hershkovitz, 1972; Eisenberg 1981; Mares and Ojeda, 1982; Dubost, 1988; Sánchez - Villagra *et al.*, 2003; Lessa *et al.*, 2008). The purpose of our contribution is to disentangle the biogeographical and ecological diversification of the major caviomorph clades in South America.

Methodological considerations

We briefly outline some methodological considerations that were taken into account for the present chapter. We conducted an extensive search of specialized references (Eisenberg, 1989; Nowak, 1991; Redford and Eisenberg, 1992; Eisenberg and Redford, 1999; Wilson and Reeder, 2005) and databases (NatureServe, Patterson *et al.*, 2007; IUCN Red lists, 2012). We drew up a map of species richness based on geographic ranges in the NatureServe database. The distribution maps of each species were processed in ArcGIS 9.1 and rasterized in a 1° x 1° grid (ca. 111 km x 111 km). Species richness was estimated by superimposing all raster layers of the recorded species and adding up the number of species per cell. A relationship between species richness and latitude, area (*e.g.*, latitudinal band area) and productivity (*e.g.*, NDVI; Willmott and Matsuura, 2001) was evaluated.We followed the phylogeny and geographical regions of Upham and Patterson (2012), except for minor changes such as the Valdivian forest which we consider as a separate region. The historical biogeography of the caviomorphs was analyzed for eight main ecoregions: A: Amazonia, B: Atlantic forest; C: Caatinga-Cerrado-Chaco, D: Andean-Puna-Chilean Scrublands; E: Patagonia-Monte; F: Pampas; G: Valdivian Forest; H: areas outside South America. To reconstruct the possible ancestral ranges of the caviomorphs we used Bayesian binary MCMC analyses [BBM; Markov chain Monte Carlo (MCMC)] implemented in the Reconstruct Ancestral State in Phylogenies (RASP) (Yan *et al.*, 2011).

The evolutionary histories of the ecological traits (*i.e.*, substrate and feeding macroniches) were mapped onto the caviomorph phylogeny using Mesquite software, version 2.75 (Maddison and Maddison, 2011), which was also employed to reconstruct ancestral states using the Parsimony Ancestral States module. The characters were coded as multistate and unordered. Broad ecological niches dealing with substrate and food specializations (*i.e.*, macroniches) were defined according to modal strategies as proposed by Eisenberg (1981): saxicolous: species having morphological features and the ability to move on rock surfaces and using crevices among rocks for shelter. Their occurrence is strongly associated with the presence of rock outcroppings (*Octomys, Kerodon;* Lacher, 1981); semiaquatic: species that are primarily terrestrial, but spend part of the day in water (*Myocastor;* Mares and Ojeda, 1982); arboreal: species that spend most of their lives in trees (*Mesomys;* Eisenberg and Redford, 1999); scansorial: species that can both move on the ground and are capable of climbing (*Octodontomys, Octodon;* Gallardo *et al.*, 2007); terrestrial: species that perform their daily activities mainly on the ground (*Dasyprocta;* Nowak, 1991). The degree of fossoriality or burrowing behavior was defined as follows (Endries and Adler, 2005; *sensu* Lessa *et al.*, 2008; Almeida *et al.*, 2013). First, semifossorial*:* species that use natural crevices and pre-existing burrows *(Proechimys, Thrichomys)*. Second, fossorial: species that spend part of their lives above ground and are able to dig complex burrows of several openings, which are typically used as a refuge. Fossorial animals have the ability to move on the surface (*Microcavia, Tympanoctomys*, *Pipanacoctomys;* Tognelli *et al.*, 2001; Ojeda *et al.*, 2013). Finally, subterranean: species having specialized morphological features that allow them to be primarily active underground, but can also forage on the surface near the openings of their complex burrow systems (*Ctenomys, Spalacopus;* Contreras and Gutierrez, 1991). Regarding food specialization caviomorphs were classified according to major preferences (Nowak, 1991): herbivore: species feeding on grasses, forbs, stems, and leaves (*Lagostomus, Dolichotis*); herbivore/granivore: species feeding mainly on grasses, leaves and seeds (*Octodon*); frugivore /herbivore: species feeding on fleshy fruiting bodies, grasses and leaves (*Cuniculus, Coendou*); frugivore/granivore: species that have specialized in fruits, nuts and seeds (*Hoplomys,Trinomys*); rootivores: species feeding mainly on tubercles and roots (*e.g.,* the phiomorph African mole rats, *Heterocephalus, Bathyergus*).

Patterns of diversity in South America

A total of 47 genera and 214 species of caviomorphs have been recorded for South America, excluding Caribbean and North American forms. The first studies on diversity patterns of caviomorph rodents of South America date back to the early 1980s. Mares and Ojeda (1982) highlighted the limited information about this highly diverse group, including its phylogenetic affinities and its ecological attributes. These authors recorded a total of 41 genera with 125 species of South American caviomorphs. More recent studies have led to the identification of many additional species and genera (Gallardo and Palma, 1992; Patton *et al.*, 1994; Huchon and Douzery, 2001; Woods *et al.*, 2001; Honeycutt *et al.*, 2003; Castillo *et al.*, 2005; Galewski *et al.*, 2005). Most genera (40 %) are represented by only few species, while only 5 % of the genera are represented by more than five species (Fig. 1.1). The gopher-like tuco tuco, *Ctenomys*, and spiny rat, *Proechimys,* are the most speciose genera among South American caviomorphs. These genera encompass almost 40 % of caviomorph species (Fig. 1.2).

The spatial pattern of species richness shows two main areas with the highest species densities (Fig. 2). One is located in the Amazonian biome, in the central-western region of tropical South America (between 0° and 10° S), where it occupies the lowlands of western Brazil and parts of the eastern slopes of the Andes in Ecuador and Peru. The other one occurs along the eastern border of southern Brazil and mainly lies within the Atlantic forest biome. A similar pattern has been described for mammals of South America (Ruggiero and Kitzberger, 2004; Tognelli and Kelt, 2004), and for hystricognath rodents (Ruggiero, 1999). Furthermore, both of these regions are recognized as highly diverse areas rich in mammal endemism (Patterson and Costa, 2012; Solari *et al.*, 2012). Differences in the range size of South American mammals may affect our perception of species richness patterns at the continental scale (Ruggiero and Kitzberger, 2004).

Different taxa vary in their ecological requirements along with their diversification histories. As a consequence, they are not evenly distributed across the continent. Species richness of dif-

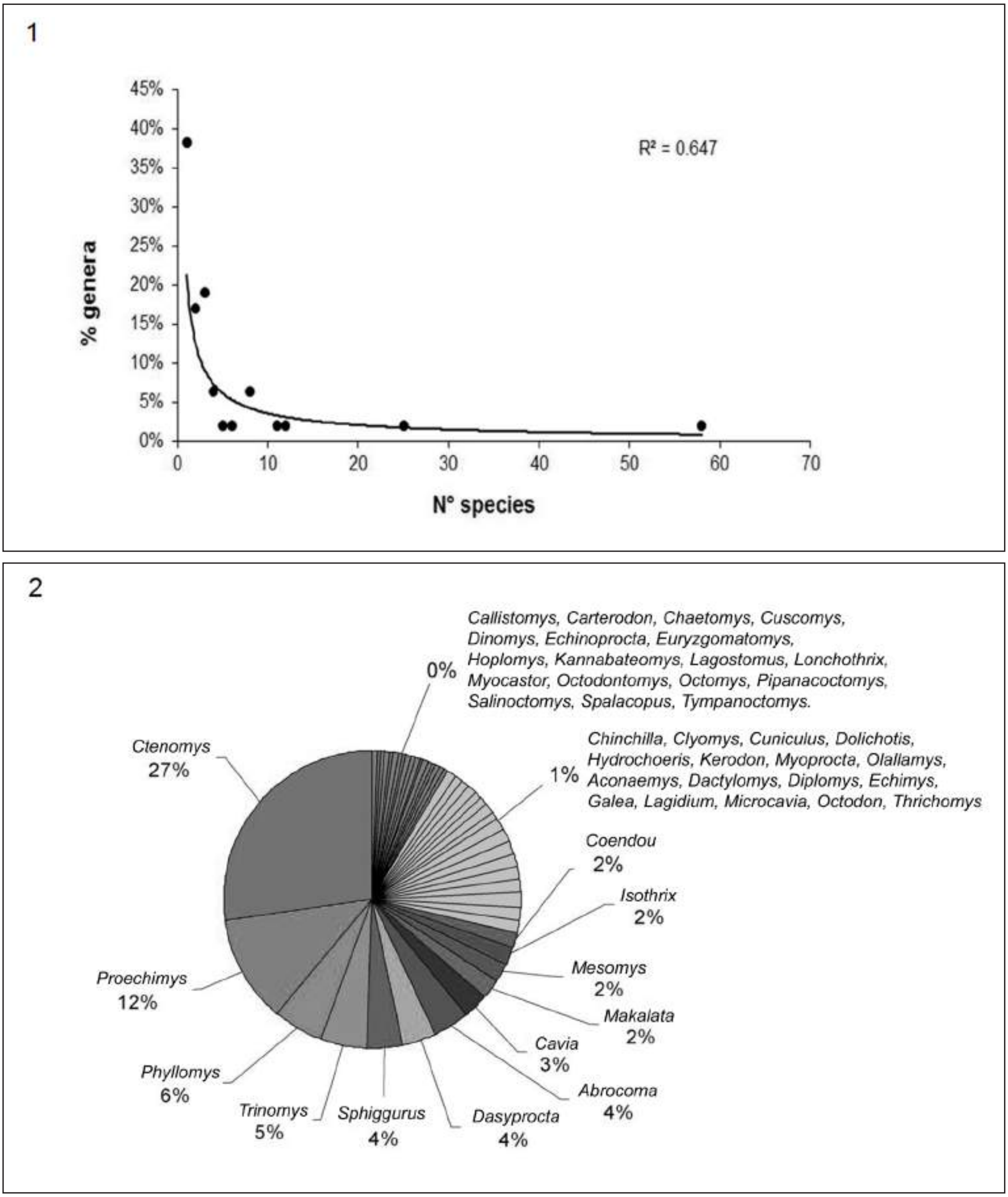

Figure 1. Diversity of living caviomorph rodents. 1. Number of species per genera (in percentages); 2. Relationship between genera and number of species (in percentages).

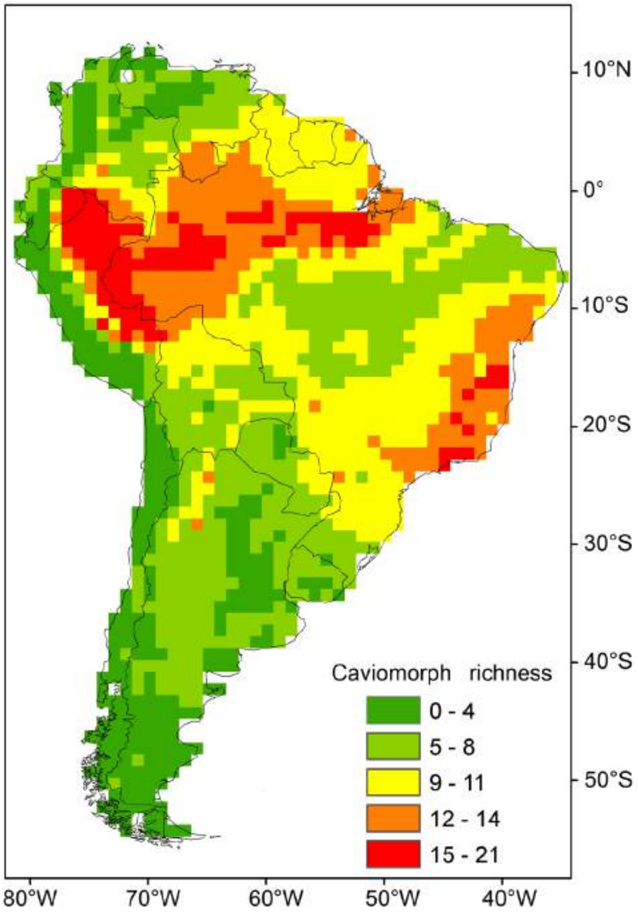

Figure 2. Caviomorph species density map based on occurrences in 1° by 1° grid cells (ca. 111 km x 111 km).

ferent mammalian orders peaks at different latitudes. Only the Erethizontidae (and perhaps the Dasyproctidae) show a linear decrease in species density with increasing southerly latitude. The families Echimyidae and Caviidae show maximum species densities between 10° and 20° S, with a decrease in species density both northwards (toward the equator) and southwards. The family Ctenomyidae reaches maximum species density values at latitudes between 20° and 30° S, while the species density of Octodontidae increases with increasing southerly latitude (Mares and Ojeda, 1982). The determining factors associated with richness may differentially affect species varying in body size (Ruggiero and Kitzberger, 2004), belonging to different trophic or spatial guilds (*e.g.*, Andrews and O'Brien, 2000), or having different dispersal capacities (Kerr and Currie, 1999), geographic range sizes (*e.g.*, Jetz and Rahbek, 2002) or evolutionary histories (*e.g.*, Lathman and Ricklefs, 1993). Approximately 35% of the caviomorph species of South America have rather small geographic ranges (Fig. 3). Similar results have been reported from a study of the environmental determinants of South American mammal richness patterns (Ruggiero and Kitzberger, 2004), in which most narrow-ranging species were located along the tropical and central Andes

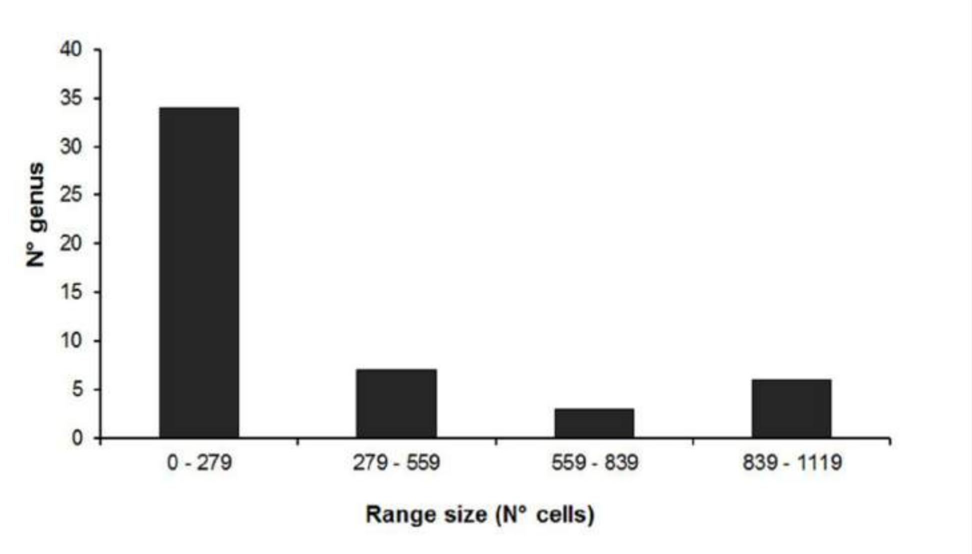

Figure 3. Caviomorph genera range sizes (by number of cells [ca. 111 km x 111 km] occupied).

while species with broad ranges were more frequent in lowlands.

The South American pattern of variation in mammal species richness mainly can be explained by the synergism between the normalized difference vegetation index (NDVI; productivity or available energy) and the effect of suitable area (Tab. 1). The species-energy hypothesis has frequently been mentioned as one of the main determinants of species richness patterns at

Table 1. Relationships between caviomorph richness and potential explanatory variables modeled using multiple ordinary least squares (**OLS**) regression and including in the model the spatial autocorrelation as an autocovariate (**ac**) (Dormann *et al.*, 2007).

Model	**lm(cavios-rich~ Area(km2) + NDVI + ac)**				
Predictor	Estimate	Std.Error	t value	Pr(>|t|)	
(Intercept)	2.55	0.59558	4.282	< 0.001	***
Area (km2)	-8.9422	0.74013	-12.082	< 0.001	***
NDVI	0.01673	0.00325	5.146	< 0.001	***
ac	1.25548	0.01893	66.341	< 0.001	***

Residual standard error: 1.611 on 1528 degrees of freedom

Multiple R-squared: 0.8397, Adjusted R-squared: 0.8394

F-statistic: 2668 on 3 and 1528 DF p-value: < 0.001

Signif.codes: ‘***’0.001 ‘**’0.01 ‘*’0.05 ‘.’0.1

broad scales (MacArthur, 1972; Hawkins *et al.*, 2003; Tognelli and Kelt, 2004).This is the case for South American mammals, although there are disagreements about which factors, productivity or environmental energy, are the main drivers for regulating the species richness pattern (Ruggiero, 1999; Tognelli and Kelt, 2004). Our analysis supports a strong effect of area, as Mares and Ojeda (1982) have pointed out, and associated with the productivity.

The presence of the Andes along the western margin of South America promotes high levels of heterogeneity associated with altitudinal changes and high productivity (Kerr and Packer, 1997; Rahbek and Graves, 2001). The variability in altitude seems to have a stronger influence on species richness patterns of rodents and artiodactyls, and this may be explained by the biogeographic history of these taxa that is clearly associated with Andean habitats (Reig, 1986; Marquet, 1989; Smith and Patton, 1993; Patterson *et al.*, 1998; Ruggiero and Kitzberger, 2004; Upham *et al.*, 2013).

Biogeographical and ecological diversification

Caviomorph rodents occur in a wide range of macrohabitats and have diversified into a broad variety of substrate and feeding niches. In this section we will characterize the hypothetical ancestral states of the major clades of caviomorphs and their subsequent diversification in the new "adaptive zones" (*e.g.*, macrohabitat and ecological niches) during their evolution in South America.

Macrohabitat diversification

Reconstruction of the ancestral areas (Bayesian binary MCMC) at the basal node (node 131, Fig. 4) provides ambiguous results. It suggests three possible ancestral ranges (A, D and E), with Amazonia (A, with 50.4 %) being the most likely macrohabitat for the evolution of the caviomorph group. These findings are supported by new fossil assemblages from the Middle Eocene of Peru (41 Ma; Antoine *et al.*, 2011). At the superfamily level, Amazonia appears as the ancestral macrohabitat of Erethizontoidea and Cavioidea (*e.g.*, high probability at node 130). Further on, Amazonia and the Atlantic forest (AB 53.36%) are suggested as the hypothetical ancestral areas for the Erethizontoidea (node 118), whereas Amazonia and the Caatinga-Cerrado-Chaco are proposed as the most likely ancestral macrohabitats for the Cavioidea (node 129; AC 63.15%). The arid and semiarid macrohabitats of the Andean-Puna-Chilean Scrublands and Patagonia-Monte (D-E) are the most likely ancestral areas for the evolution of the Octodontoidea (node 112; DE 56.21%; Ojeda *et al.*, 2013), while the Chinchilloidea evolved in the Andean-Puna-Chilean Scrublands macrohabitats (node 115; D).

Ecological diversification: feeding niches

Parsimony ancestral reconstructions for the character "diet" reveal a hypothetical ancestor with an ambiguous diet based on grasses, leaves and fruits (Fig. 5). This condition is common to the four superfamilies. Caviomorph families then radiated from these ancestral food habits into a diversity of feeding niches. For instance, the Abrocomidae, Octodontidae and Ctenomyidae shared an ancestral herbivorous feeding niche of grasses and leaves. The hypothetical ancestor of the arboreal forms of Echimyidae occupied a feeding niche of fruits and

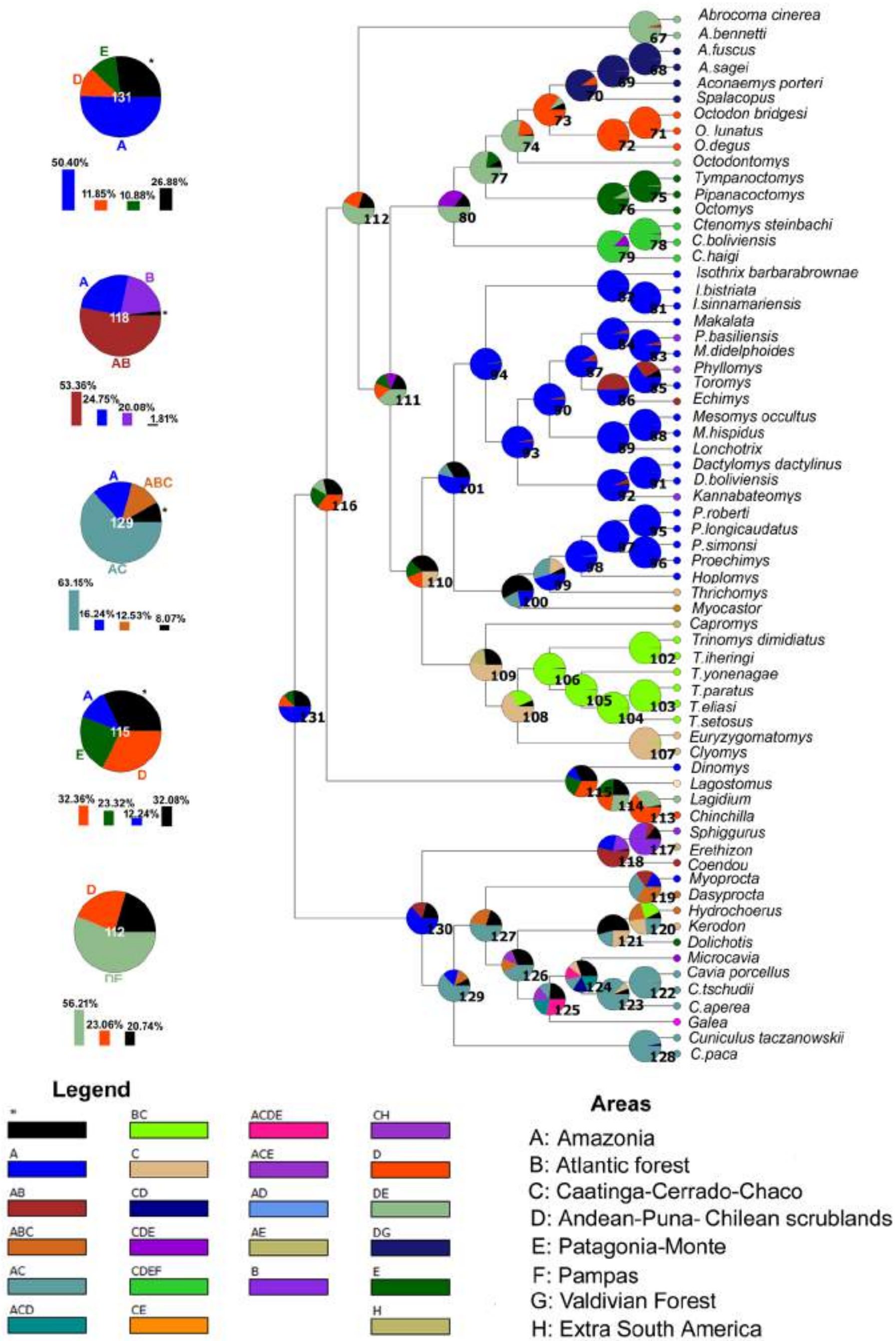

Figure 4. Ancestral areas reconstruction. Graphical output results of ancestral distributions at each node of the caviomorph phylogeny obtained from Bayesian Binary Analysis MCMC (**BBM**) (exported from RASP "Reconstruct Ancestral State in Phylogenies", Yan *et al.*, 2011). Alternative ancestral ranges of nodes 112, 115, 118, 129 and 131 (with frequency of occurrence) are shown in pie chart form. Color key represent possible ancestral ranges at different nodes; black with an asterisk represents other ancestral ranges. Areas: A, Amazonia; B, Atlantic forest; C, Caatinga-Cerrado-Chaco; D, Andean-Puna-Chilean Scrublands; E, Patagonia-Monte; F, Pampas; G, Valdivian Forest; H, areas extra South America.

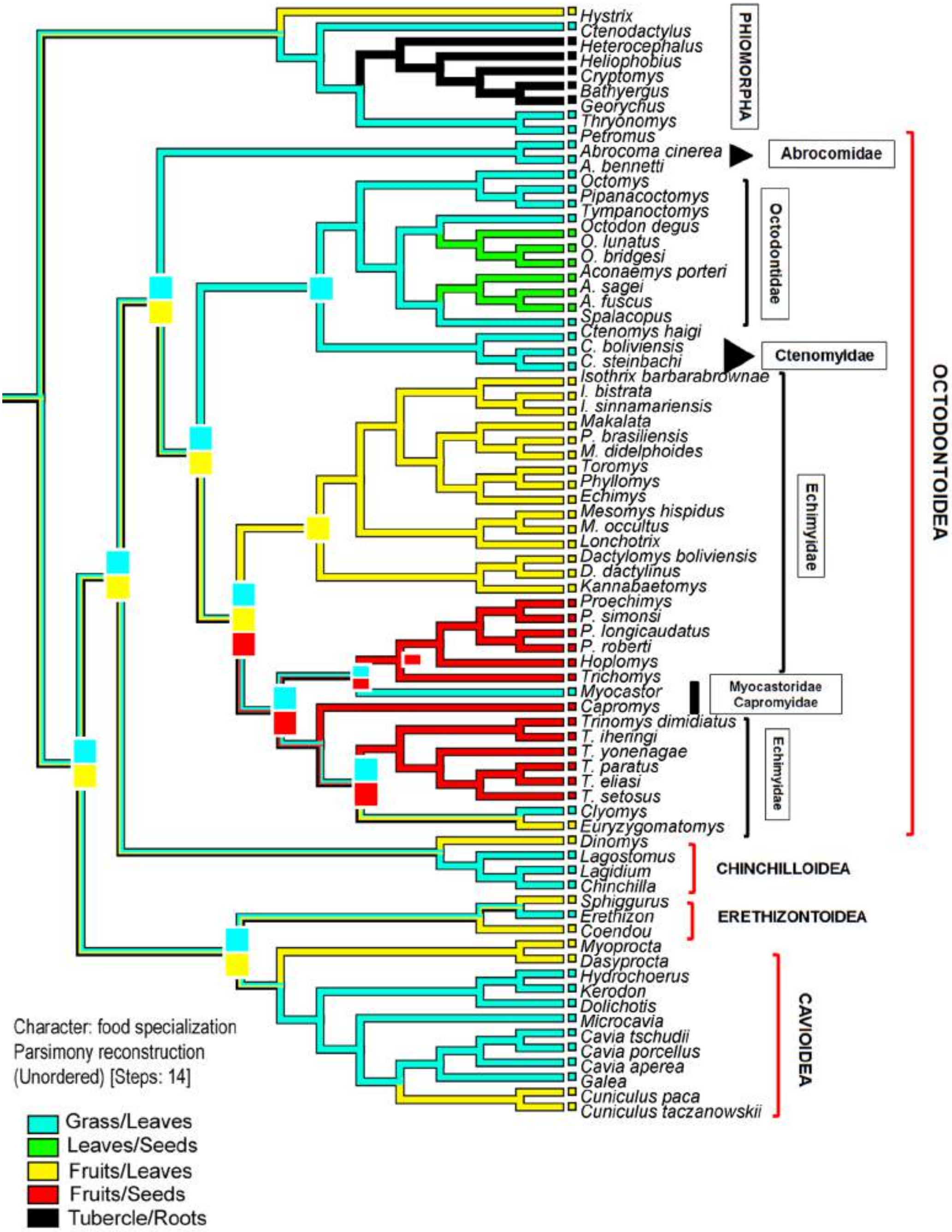

Figure 5. Parsimony ancestral state reconstruction of the ecological character "diet" in caviomorphs.

leaves, while the terrestrial forms of this family have ambiguous ancestral feeding niches based on grasses-leaves fruits-seeds, which is also shared with the Myocastoridae and Capromyidae. An ambiguous hypothetical ancestral state of grass-leaves/ fruits-leaves characterized the Chinchillidae + Dinomyidae*,* Erethizontidae and Dasyproctidae, while Caviidae and Cuniculidae are characterized by a grass-leaves food specialization.

Ecological diversification: substrate niches

The reconstruction of ancestral modes of life reveals a hypothetical saxicolous (rock dwelling) condition for the main node of caviomorphs (Fig. 6). The superfamilies Octodontoidea and Chinchilloidea retained the saxicolous character, whereas the Erethizontoidea and Cavioidea reveal an ambiguous ancestral condition of saxicolous, arboreal and terrestrial forms. Different families radiated from these ancestral characters to fill different substrate niches. The families Abrocomidae and Chinchillidae retained the saxicolous condition, while the Echimyidae diversified into arboreal, terrestrial, semifossorial and fossorial modes of life. Myocastoridae and Capromyidae evolved to semiaquatic and arboreal forms respectively. The Octodontidae are characterized by saxicolous/scansorial ancestral forms, while the Ctenomyidae filled the subterranean niche. Finally, the Erethizontidae are characterized by an ambiguous arboreal-terrestrial ancestral state, while the hypothetical ancestral state of Caviidae is terrestrial.

The aridland diversification of octodontids: a case study

The biogeographical and ecological diversification of octodontids throughout the western portion of southern South America, suggests that their evolution was associated with contrasting environmental conditions on both sides of the Andes produced by the Andean uplift (Ojeda *et al.*, 2013). The analysis of their historical biogeography proposed the Monte desert as the ancestral biome of the group, and that the octodontids subsequently expanded their geographic range and dispersed to other ecoregions (Ojeda *et al.*, 2013). The initial attributes of their ecological diversification are rather ambiguous. The ancestral macroniches were saxicolous, terrestrial generalist and semifossorial modes of life (Ojeda *et al.*, 2013), with fossorial habits appearing later in octodontid evolution and currently being represented by the monotypic *Spalacopus cyanus* in the Valdivian temperate forest. Ojeda *et al.* (2013) proposed a hypothetical ancestral proto-octodontid that was adapted to desert environments during the early evolution of the Octodontidae. The substrate niche of this proto-octodontid may have been saxicolous, semifossorial or terrestrial.

The ecomorphological diversity of the Octodontidae seems to be associated with a geographic subdivision within the family. Fossorial and semifossorial forms (*Spalacopus* and *Aconaemys*), as well as terrestrial generalists (*Octodon*) are adapted to Mediterranean sclerophyllous woodlands and semiarid open scrublands in central Chile; saxicolous (*Octomys*) and semifossorial xeric-adapted species (*Tympanoctomys*, *Pipanacoctomys*) inhabit arid-lands in Argentina; and *Octodontomys* occurs in pre-Andean Prepuna and Puna habitats in northern Argentina, southern Bolivia and north-eastern Chile (Contreras *et al.*, 1987). The diversification of species inhabiting arid macrohabitats is associated with the last uplift of the Andes (Diaguita phase)

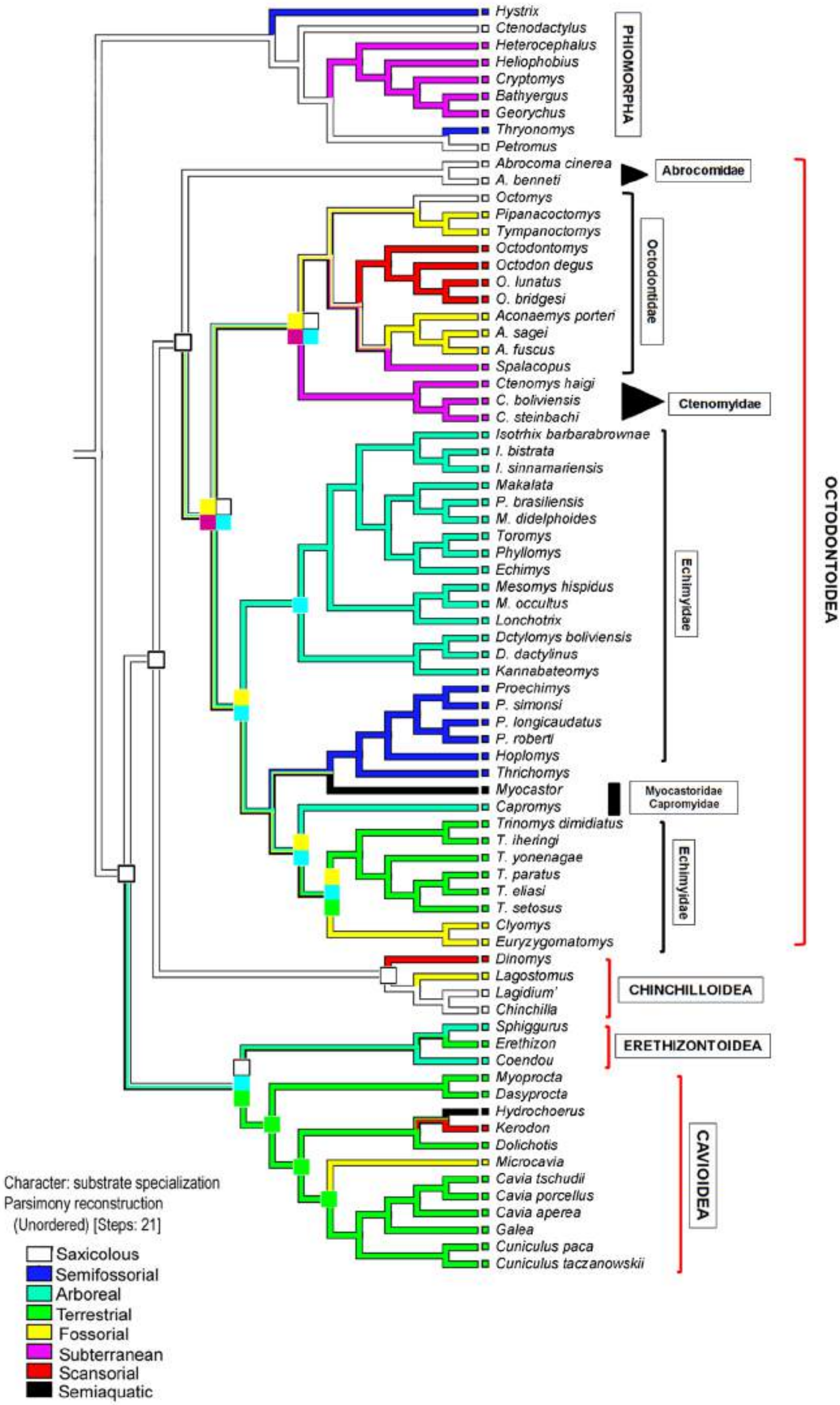

Figure 6. Parsimony ancestral state reconstruction of the ecological character "life modes" in caviomorphs.

during the Pliocene (4.28 ± 1.08 Ma). This uplift of the central Andes and Pampean Mountains had marked ecological consequences, as it enhanced the xeric conditions of the northern Monte Desert through a rain shadow effect (Ortiz-Jaureguizar and Cladera, 2006; Veblen *et al.*, 2007). In this scenario *Octomys* developed a saxicolous mode of life with a narrow geographic distribution and a saxicolous specialization for living and burrowing in rock formations of the Monte desert (Ebensperger *et al.*, 2008; Sobrero *et al.*, 2010). Its sister genera *Pipanacoctomys* and *Tympanoctomys* are semifossorial and strongly associated with salt basin habitats. However, the colonization of a "new adaptive zone" (*sensu* Simpson, 1944) and expanded geographic range of *Tympanoctomys*, have been the result of a set of behavioral, ecomorphological, and physiological traits which enabled the red vizcacha rat to better and more competitively utilize open xeric habitats, salt basins, and hypersaline food resources than its sister species *Pipanacoctomys* (Mares *et al.,* 1997; Ojeda *et al.,* 1999; Gallardo *et al.*, 2007). By contrast, the species inhabiting Mediterranean sclerophyllous woodlands and semiarid open scrublands in central Chile diversified into semi-fossorial and fossorial forms at a later stage of octodontid evolution. In this scenario, the evolution of semi-fossorial and fossorial habits in *Aconaemys* and *Spalacopus* may be associated with the appearance of novel habitats (*i.e.*, Chilean scrublands) after the Andean uplift. The Pleistocene paleoclimate subsequently cycled between global cool and warm phases and was accompanied by vegetational changes in the southern temperate ecosystems (Markgraf *et al.*, 1995), thus promoting the development of new habitats.

Concluding remarks

This paper represents the first attempt to integrate and synthesize the phylogeny of South American caviomorph rodents with their biogeographical and ecological diversification. Among the highlights of our contributing chapter are: a) the highest species density of caviomorphs was found in the forested macrohabitats of Amazonia and Atlantic Forest; b) there is a strong association of species richness with area and productivity; c) broad and small geographic range species were associated with lowlands and mountain macrohabitats respectively; d) we hypothesize that the Amazonia region appears to be the ancestral area in the diversification of proto-caviomorphs; e) the most likely proto-caviomorph macroniches were associated with saxicolous modes of life and a diet of grasses leaves and fruits; f) the arid-lands of the proto-Monte region appears to be the ancestral macrohabitat in the evolution of octodontids, followed by their biogeographical and ecological diversification associated with contrasting environmental conditions on both sides of the Andes; g) the colonization of new "adaptive zones" and expansion of geographic ranges by some arid -adapted octodontids (*e.g., Tympanoctomys*) has been the result of a set of behavioral, ecomorphological, and physiological traits which allow them a better and more competitive utilization of open xeric habitats and hypersaline food resources than some of their close relatives (*e.g.*, *Pipanacoctomys* and *Octomys*).

Future prospects

The phylogenetic matrix offers a proper framework for further research and hypothesis testing on the geographical distribution, diversification, and evolution of species ecological attributes. Our proposed biogeographical and ecological diversification hypotheses pinpoint major avenues of research that deserve in-depth study. Examples include the speciation -extinction dynamics within and between clades, ecological radiation and niche plasticity of major clades according to species attributes and environmental conditions (*e.g.,* climate, landscape heterogeneity), the role of niche conservatism (*i.e.,* climatic tolerances) in limiting geographic ranges, and species assembly at the regional and community level (Losos, 1996; Wiens and Donoghue, 2004; Wiens and Graham, 2005; Rickleffs, 2007). An example of further research is a closer inspection of the explosive radiation of the arboreal adaptive zone by the echimyid clade (Fabre *et al.*, 2012) and frugivory. An association of frugivory with the radiation of phyllostomid frugivorous bats has been proposed (Rojas *et al.*, 2012). There is evidence suggesting a mutualistic [plant-animal] interaction with bats acting as agents of seed dispersal and consequently maintaining the composition and structure of vegetation, which ultimately favor the evolution of frugivorous bat assemblages. Whether or not the same evolutionary link applies to the diversity of arboreal and terrestrial spiny rats is a matter of potential research. Recent contributions on the diversification of different caviomorph lineages (Fabre *et al.*, 2012; Upham and Patterson, 2012; Ojeda *et al.*, 2013; Upham *et al.*, 2013) are some examples of future directions of phylogenetic, biogeographic and ecological integrated research in one of the most conspicuous and oldest group of Neotropical mammals.

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4 ECOMORPHOLOGICAL AND LOCOMOTOR DIVERSITY IN CAVIOMORPH RODENTS WITH EMPHASIS ON CAVIOIDS

DIVERSIDAD ECOMORFOLÓGICA Y LOCOMOTORA EN ROEDORES CAVIOMORFOS CON ÉNFASIS EN CAVIOIDEOS

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Abstract. Caviomorphs are known for their controversial evolutionary history, which led to a great ecological and morphological diversity within the group. Among the many families are species that inhabit various habitats and occupy most rodent niches, from climbers to terrestrial, semi-aquatic to specialized fossorial, as well as more generalized forms. This chapter focuses on the main features related to caviomorph locomotor diversity, especially variations in size and shape, how they move on land and the different gaits they use. Special attention is given to the cursorial adaptations of some cavioid species and their conspicuous convergence on small artiodactyls. The postcranial skeleton of most caviomorph species considered cursorial is clearly distinguished by a set of features which includes, among others, relatively long metapodials and short phalanges; a tendency toward medial paraxony in the forefeet, and lateral paraxony in the hind feet; and a digitigrade posture, with unguligrade tendency. Like other quadrupedal mammals, caviomorph rodents usually use walking gaits at low speeds, trot at slow running gaits and gallop at higher speeds. Pacing is disadvantageous for short-legged animals as caviomorphs overall, because stability is reduced. However, its important advantage for long-legged animals lies in the fact that the hindlimb never interferes with a forelimb. Among caviomorphs, the long-legged *Dolichotis* is a recognized pacer. At higher speeds, several variants of galloping are recognized within cavioid rodents (*e.g.*, capybara). Virtual 3D reconstructions of some different-sized caviomorphs have already been accomplished, including for *Hydrochoerus*, *Dasyprocta* and *Cavia*. After each bone is digitized, the digital model can be exported to animation computer software, where the skeleton can be accordingly articulated and subsequently animated. These 3D models can be developed later to direct applications in biomechanics, such as analysis of posture, muscle insertion and ligament attachment, and analysis of their action, as well as in comparative biology.

Resumen. Los caviomorfos son conocidos por su historia evolutiva compleja, la que ha conducido a una diversidad ecológica y morfológica dentro de este grupo de roedores endémicos de Sudamérica e islas del Caribe. Uno de los aspectos más importantes es que las especies constituyentes ocupan muy diferentes tipos de hábitats y nichos ecológicos. Así, pueden observarse diferentes modos de locomoción asociados a la mencionada diversidad de hábitats y nichos, que incluyen formas trepadoras arborícolas y formas terrestres; formas semi-acuáticas y formas excavadoras o subterráneas, o bien formas corredoras de ambientes abiertos (*e.g.*, estepas patagónicas) así como también cerrados (selvas y forestas tropicales). También existen formas

generalizadas que pueden desempeñarse relativamente bien en diferentes hábitats. Este capítulo se focaliza en las principales características relacionadas con la diversidad ecomorfológica y locomotora de los caviomorfos, especialmente en los contrastes de tamaño y forma presentes en el grupo, cómo se desplazan estos roedores sobre la tierra, y qué tipos de paso utilizan al desplazarse a diferentes velocidades. Se presta especial atención a lo que se conoce como adaptaciones a la carrera presentes en algunas especies de cavioideos, las que son en gran medida convergentes con las que presentan los artiodáctilos de pequeño tamaño. Estas convergencias se ponen de manifiesto, en primera instancia, a través de una semejanza visual entre ambos grupos, que resulta a todas luces llamativa. Dubost (1968) fue uno de los primeros en señalar la aparente convergencia entre los roedores caviomorfos pertenecientes a la superfamilia Cavioidea y los rumiantes artiodáctilos del Viejo Mundo. Por ejemplo, el ciervo-ratón asiático (Familia Tragulidae), y los antílopes africanos pequeños conocidos como duikers (Cephalophinae) son semejantes al agutí sudamericano (Rodentia, Caviomorpha, Dasyproctidae,), ya que presentan hombros bajos con pendiente hacia adelante y, en contraste, cuartos traseros poderosos. Este *bauplan* estaría presente en varias especies de mamíferos herbívoros que se distribuyen, principalmente, en lo que se conoce como "Cinturón Verde de la Tierra" (esto es, los bosques y selvas tropicales; Fig. 5). Estos animales habitan ambientes similares con vegetación cerrada presentes en América, Asia, África y aún Australia, lo cual parece canalizar una morfología distintiva, y posiblemente también su comportamiento. Dubost (1968) ha propuesto la idea de que este diseño corporal particular, consistente en la posesión de relativamente cortas extremidades anteriores a la par de largas posteriores, determina una postura corporal inclinada hacia adelante. Esta fisonomía corporal general permitiría superar, o penetrar, la vegetación cerrada del estrato inferior de las selvas tropicales. Así, esta capacidad de maniobra los convierte en verdaderos "buceadores de la selva", lo que puede ser importante a la hora de esconderse o escapar de sus depredadores (ver Zapata *et al.*, este volumen). Varios de los análisis publicados sobre la morfología de las extremidades de los caviomorfos han identificado un importante solapamiento al comparar los distintos modos locomotores. Tanto si se analizan los huesos largos, como el esqueleto del autopodio o la escápula, esta congruencia en la morfología se debería, principalmente, al hecho de que varias especies de caviomorfos no se especializan en un modo locomotor particular sino que poseen un repertorio locomotor amplio. No obstante, el esqueleto post-craneal de las formas corredoras, especialmente las que se encuentran incluidas en la superfamilia Cavioidea, se distingue claramente debido a un conjunto de atributos conspicuos. Entre los mismos pueden mencionarse: 1) presencia de elementos metapodiales relativamente largos; 2) falanges cortas; 3) tendencia hacia una paraxonia medial en el miembro anterior (el eje pasando entre los dígitos III y IV) y 4) paraxonia lateral en el posterior, lo que se asocia con una evolución aparente a la posesión de 3 dígitos/4 dígitos en la mano, y un dígito funcional medial en el pie (mesaxonia); 5) postura digitígrada, con tendencia ungulígrada, a veces algún tipo de postura semi-digitígrada; 6) reducción de la clavícula, lo que permite incrementar el rango de movimiento del miembro anterior y, consecuentemente, la longitud de la zancada. Esto atributos sugieren que, durante la evolución de ciertas formas cavioideas, tuvieron lugar varios cambios en la morfología de los miembros y la postura corporal, tendientes a optimizar la capacidad de correr. En relación al comportamiento locomotor, algunas características morfológicas relacionadas con la velocidad, la aceleración, la maniobrabilidad, la resistencia y la estabilidad, parecen especialmente susceptibles de haber sido afectadas por la selección natural. Como otros mamíferos cuadrúpedos, los caviomorfos se desplazan caminando a bajas velocidades, trotan cuando alcanzan una velocidad mayor, y finalmente pasan al galope a altas velocidades. El trote y el "paso vivo" son considerados modos de andar simétricos, utilizados a velocidades moderadas. Al trotar, los pies opuestos diagonalmente se mueven en fase entre sí, mientras que durante el "paso vivo", los pies de un mismo lado del cuerpo son los que se mueven en fase. Ambos, el trote –que es el tipo más frecuente

de desplazamiento– y el "paso vivo", poseen la ventaja de que dos miembros trabajan en conjunto, ya sea para propulsar al animal así como también para amortiguar el contacto con el sustrato. El paso vivo es desventajoso para animales con miembros cortos, como es el caso de la generalidad de los roedores, debido a que la estabilidad se ve reducida ya que el centro de masa se descentra ligeramente durante el soporte. Sin embargo, la ventaja de este tipo de marcha para aquellas formas con largas extremidades, radica en que los miembros anteriores y posteriores no interfieren entre sí. La liebre patagónica, *Dolichotis*, de largas extremidades, utiliza este tipo de marcha. A mayores velocidades, diferentes variantes del andar conocido como "galope", se observan en los caviomorfos corredores. Por ejemplo, el galope rotatorio, que posee dos fases de suspensión (aéreas), puede observarse en especies de cavioideos que se asemejan, en este tipo de desplazamiento, a formas especializadas tales como *Chinchilla*, *Oryctolagus*, y *Spermophilopsis*. Se discuten finalmente técnicas para la reconstrucción virtual 3D del esqueleto y su combinación con programas que permiten su incorporación a animaciones, realizadas en *Hydrochoerus*, *Dasyprocta* y *Cavia*, y su implicancia en estudios biomecánicos y anatómicos.

Introduction

Caviomorphs underwent a particular evolutionary history that includes a rather controversial origin and radiation either from a lineage coming from North America (Patterson and Wood, 1982) or from an African ancestor (Lavocat, 1969; Hoffstetter, 1975; Martin, 1994; Huchon and Douzery, 2001), followed by at least two major moments of adaptive radiation, one at the Early Oligocene (28.5 Ma) and the other at the Middle/Late Miocene (11.2-5.3 Ma) (Vucetich *et al.*, 1999). These events are all evidence of their interesting and peculiar South-American journey and provided this group with great morphological and ecological disparity compared to other rodent groups.

Their ecomorphological and behavioral diversity is also reflected in the large number of families (12 extant families) included in this group, which comprises approximately 240 species (*sensu* Wilson and Reeder, 2005).

Throughout their range, they inhabit various habitats ranging from deserts to grasslands, tropical forests, coastal shrubs and rocky outcrops. Additionally, they exhibit most rodent locomotor specializations: climbers, like the erethizontoids *Coendou* (prehensile-tailed porcupines) and *Sphiggurus* (hairy dwarf porcupines) and the octodontoids *Phyllomys* and *Dactylomys* (spiny rats); cursors, like the cavioids *Dasyprocta* (agoutis) and *Dolichotis* (maras); diggers, like the chinchilloid *Lagostomus* (viscachas) and the specialized fossorial octodontoids *Ctenomys* (tuco-tucos) and *Spalacopus* (coruros); semi-aquatic, like the octodontoid *Myocastor* (coypus) and the cavioid *Hydrochoerus* (capybaras); as well as generalized forms, often terrestrial but capable of climbing, digging and swimming to some extent, such as the cavioids *Cuniculus* (pacas) and *Cavia* (guinea-pigs). Fig. 1 illustrates the variety of ecological niches and locomotor specializations found within the caviomorphs.

In this chapter, we attempt to highlight the main features of caviomorph ecomorphological and locomotor diversity, focusing on identifying their major differences regarding size and shape as well as how these morphologies can influence how caviomorphs move around and interact with their habitat. Special attention is given to species of Cavioidea because of their frequent association with cursorial adaptations (*i.e.,* running specializations).

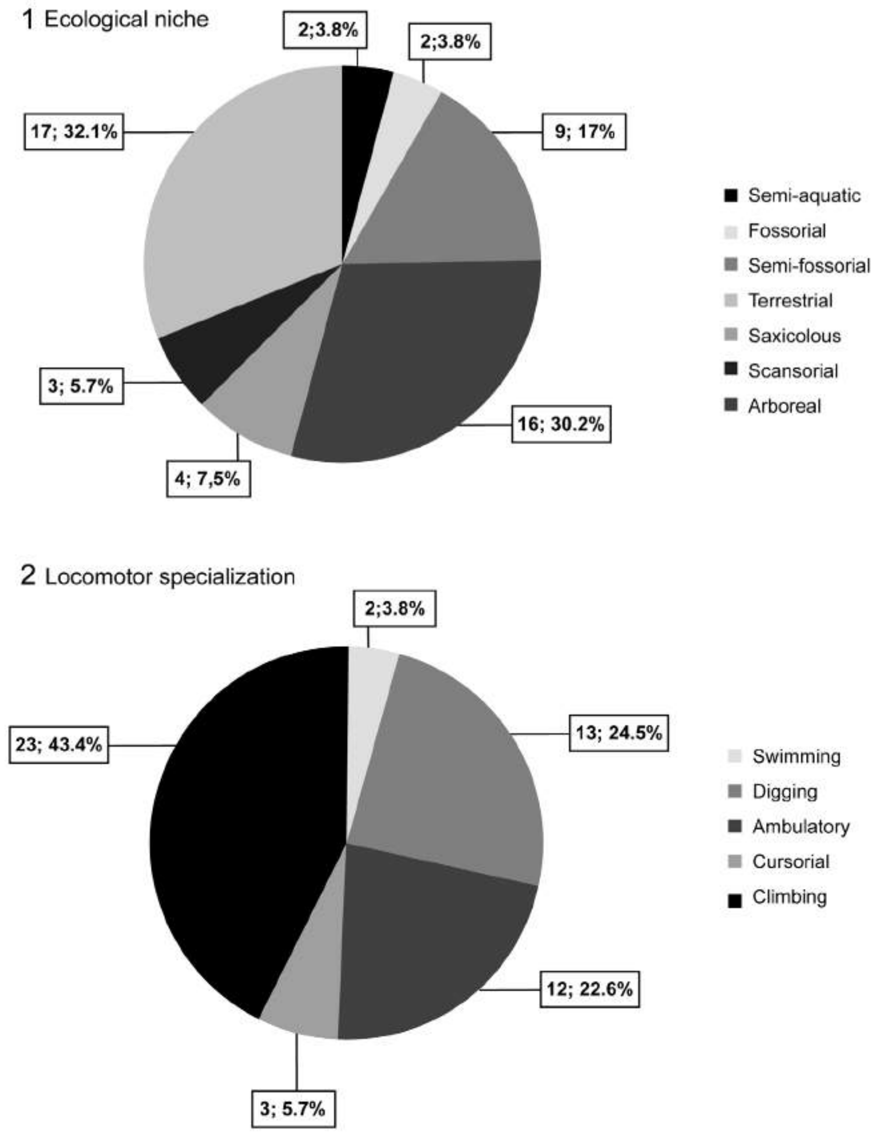

Figure 1. Diversity of extant caviomorph genera in numbers and percentage of, 1. ecological niches that they occupy and 2. locomotor specializations they have.

1. Size

Body mass in extant caviomorph rodents also ranges widely from the small coruros, some species of tuco-tucos and spiny rats (with body masses as low as 80 g), to medium-sized species such as the viscacha *Lagostomus* (around 3 kg), the coypu *Myocastor* (around 7 kg), the pacarana *Dinomys* (around 15 kg) or the porcupine *Erethizon* (around 18 kg), and to the largest living rodent, the capybara *Hydrochoerus* (around 50 kg; Nowak, 1991) (Fig. 2). However, if fossil species are considered, this range is considerably extended at its upper end.

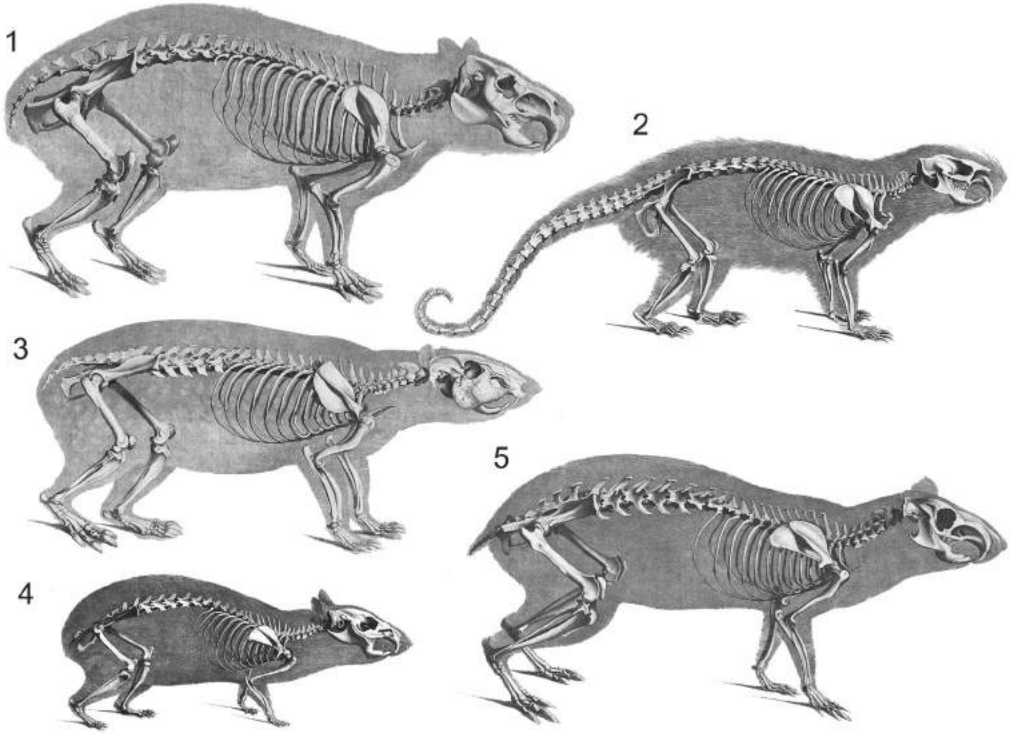

Figure 2. Diversity of size and shape in caviomorph rodents. Species are 1. capybara *Hydrochoerus hydrochaeris* (around 1.20 m in total length); 2. Brazilian porcupine *Coendou prehensilis* (around 0.60 m in total length); 3. paca *Cuniculus paca* (around 0.80 m in total length); 4. cavy *Cavia aperea* (around 0.25 m in total length) and 5. agouti *Dasyprocta leporina* (around 0.62 m in total length). Animals are not to scale. Modified from Pander and D´Alton (1821).

In the last 30 years, two species of giant caviomorph rodents have been described. †*Phoberomys pattersoni* (Neoepiblemidae) was described from the Upper Miocene Urumaco Formations of Venezuela (Mones, 1980). Using scaling equations, in which the sagittal diameters of the humeral and femoral diaphyses were regressed to body mass, its size was estimated at 436 kg and 741 kg, respectively (Sánchez-Villagra *et al.*, 2003). However, more recently, Millien and Bovy (2010) reviewed the evidence, and suggested a sensibly lower estimate between 220 and 280 kg.

More recently, another large rodent has been described: †*Josephoartigasia monesi* is known from an almost complete skull that was found in the Pliocene-Pleistocene layers of the San José Formation in Uruguay (about 4 Ma). The size of this animal has been debated. Rinderknecht and Blanco (2008) estimated it to be about 1,000 kg, or as much as 2,500 kg. However, Millien (2008) criticized the methodology used for these estimates, and proposed a body mass of no higher than 350 kg.

Even accepting the most conservative size estimates for these two fossil rodents, it is clear that they were between five (the Venezuelan species) and seven (the Uruguayan species) times larger than a capybara. Accepting a range between 6 g and 350 kg, we can conclude that the biggest known rodent was about 60 x 10^3 heavier than the smallest mouse. Probably no other order of placental mammals exhibits a similar difference. Considering mammals altogether, only diprotodontian marsupials display a greater size range (Sánchez-Villagra *et al.*, 2003).

Alexander (2003) discussed the advantages and disadvantages of such a large body size in the case of †*Phoberomys.* Some of his arguments can be applied to †*Josephoartigasia*, as in the case of digestion. Considering an equal food intake, the gut volume of herbivorous mammals is proportional to body mass. However, fermentation rates, necessary for transformation of cellulose into fatty acids, probably increase linearly with body mass, while metabolic rates scale to body mass to 0.75. This implies that a large herbivore can be more successful than a smaller one, in terms of energy extraction.

Normally in a terrestrial vertebrate, the strength of a bone is higher that the ultimate applied stress that can act on the bone in standard activities. For example, the safety factor of a femur is the quotient of the maximum strength (numerator) and the maximum stress (denominator) that can act on it during locomotion. The faster an animal is running, the higher are the stresses applied to the bones. A different mechanical issue (that cannot be applied to †*Josephoartigasia*, as only the skull is available) is whether the safety factor of the long bones of †*Phoberomys* was similar to that of a guinea pig, for example. In this context, the femur of †*Phoberomys* looks particularly weak. Considering that mass or volume increases by the third power of linear dimensions and surface area increases only by the square of linear dimensions, the cross-sectional area of the femur of a large mammal must support proportionally more load than that of a geometrically similar smaller mammal. The solution to this physical constraint is that large mammals usually keep their legs straighter than smaller ones. In this way, stresses on the bones are kept similar and the safety factor need not change.

So one can ask, why did these large rodents became extinct, if they displayed so many advantages in comparison to small rodents?

Alexander (2003) suggested that perhaps the different species of giant rodents, living from the Miocene to the Pleistocene, were more vulnerable to predation than other mammals of similar size, such as some ungulates. This question is related to an additional matter, shape (see below). For the moment the only analogy that we can use is the biggest extant rodent species, the capybara. Although the capybara is able to run, as are most rodents, it tires quickly and then it seeks water as a refuge. Some data seem to indicate that its inability to run during long periods of time is due to the fact that capybara has a small heart relative to its body mass. Were these extinct giants also inefficient runners? Other causes such as climate change or reduction in available resources deserve also to taken into account.

2. Shape

Consider a geometric figure like a cylinder, with a volume V. Its mass, M, is V times ρ, where ρ is density, which is constant for a given material. This volume or the corresponding mass can be distributed in different ways. We can imagine a very high cylinder, with a very narrow base, or a very short one, with a broad base. Although in real animals, the differences in mass distribution may not be so radical, two animals with the same body mass, can exhibit important differences in shape. For example, an antelope weighing about 40-50 kg looks quite different from a capybara, which easily attains a similar body mass. The question is whether this differential distribution of volume has mechanical consequences.

Similarly, if we consider different body parts separately, we can also observe some astonishing shape changes. This is the case of long bones. Bou *et al.* (1987) showed that rodent locomotor specialization can be associated with structural changes, with important differences in length and/or diameter, in such a way that a long bone typology, considering both length and sagittal diameter, can be established depending on the particular pattern of locomotion (Casinos, 1994). For example, the long bones of digging rodents tend to be short and thick, while in swimming rodents those bones are relatively slender. Such differences can be also observed between relatively closely-related rodents (*e.g.*, *Arvicola*, Cubo *et al.*, 2006). In this way, one can predict the lifestyles of extinct species, as is the case of the ancestors of the specialized digger *Ctenomys*, which were hypothesized to have lived above the ground (Casinos *et al.*, 1993).

In the particular case of caviomorphs, the correspondence between locomotor type and long bone morphology was analyzed by Elissamburu and Vizcaíno (2004), using shaft length and diameter, as well as some indexes, as variables. They obtained interesting correlations. In contrast, Weisbecker and Schmid (2007) failed to identify any differences between autopodial morphology and locomotor partterns in hystricognath rodents. However, Raich and Casinos (1991) and Llorente *et al.* (2008) had already shown that in many mammalian orders, as well as in chelonians, locomotor adaptations are reflected in metapodials. Weisbecker and Schmid (2007) concluded that their results may be a consequence of a lack of a strong locomotor specialization in the Hystricognathi. Nevertheless, this may be related to phylogeny rather than function.

Currently, most extant subterranean mammals are rodents. In caviomorphs, this adaptation is particularly frequent, especially in the genus *Ctenomys*, which experienced a relatively recent and extensive cladogenesis, in such a way that about 60 species are currently recognized, distributed from 17° to 54° latitude south. In fact, this genus comprises about 40% of the living subterranean rodents.

Digging strategies in subterranean mammals in general, and in rodents in particular, are not uniform. Most use one or both of two different tools: the skull and the limbs - the latter with a predominance of the forelimbs. The importance of these two kinds of tools is variable. Limbs are especially important in opportunistic species (Casinos *et al.*, 1983). On the other hand, the skull can be largely modified in the clades where it is the main digging tool; these modifications affect differing parts of it, tending to increase incisor procumbency and/or zygomatic width. Laville *et al.* (1989) showed an example of gradation of these changes from typical epigeous forms (*Microtus*) to highly specialized subterranean ones (*Spalax*), with an intermediate stage represented by *Arvicola.* In this view, the transformation of the skull in *Ctenomys* species is quite extreme (Becerra *et al.*, 2011).

3. Are cavioids ungulate substitutes?

> *"... 'Parallelism, parallelism, more parallelism and still more parallelism' is the evolutionary motto of the rodents..."*
>
> A.E. Wood (1935, p. 250)

Most morphological studies identify a large overlap in caviomorph limb morphology when comparing different locomotor modes. Whether analyzing the long bones (Biknevicius, 1993; Elissamburu and Vizcaino, 2004; Morgan and Álvarez, 2013; Echeverría *et al.*, 2014), autopodial skeleton (Weisbecker and Schmid, 2007) or scapula (Seckel and Janis, 2008; Morgan, 2009), this morphological congruence is mainly due to the fact that many species do not specialize in one locomotor mode but have a broader locomotor repertoire (Nowak, 1999). Significant phylogenetic signals also seem to be associated with variations in scapular (Morgan, 2009) and humeral shapes (Morgan and Alvarez, 2013), although only a few studies have really focused on macroevolutionary processes driving morphological variation of caviomorph rodents (Morgan and Alvarez, 2013; see Morgan, this volume).

Among caviomorphs, the Cavioidea (33 species) display a great diversity in behavior, habitat utilization, morphology, breeding system, and other life-history traits (Nowak, 1999). Based on behavioral and morphological features, the group can be divided into five categories: 1) terrestrial/cursorial (terrestrial forms that possess morphological specializations for running); 2) terrestrial/generalized (generalized terrestrial forms that climb, dig and swim to some extent); 3) terrestrial/occasional diggers (non-cursorial with some digging activity); (4) semi-aquatic/cursorial (cursorial forms that frequently swim); 5) terrestrial/scansorial (terrestrial forms that are also good climbers) (Tab. 1).

Table 1. Cavioidea genera, including number of species, common name, head and body length (**HB**), tail length (**T**), bodyweight (**W**), locomotor habits and habitat. References: Nowak, 1991; Redford and Eisenberg, 1992; IUCN, 2013.

Taxa (# of species)*	Common name	HB (mm)	T (mm)	W	Habit	Habitat
Caviidae						
Cavia (6)	cavy, guinea-pig cuis	265-310	vestigial	550-760 g	Terrestrial/ Generalized	Scrub grasslands, savannas, wetlands, primary and secondary forests
Galea (3)	Cuis	195-284	vestigial	140-560 g	Terrestrial/ Occasional digger	Open areas, s avanna and dry areas, primary and disturbed habitats
Microcavia (3)	Cuis, mountain cavy	170–245	vestigial	200–326 g	Terrestrial/ Occasional digger	Grasslands, arid and semiarid lowlands and valleys, riparian habitats, forested areas, or sandy forested flats

Taxa (# of species)*	**Common name**	**HB (mm)**	**T (mm)**	**W**	**Habit**	**Habitat**
Caviidae						
Dolichotis (2)	Mara	420-810	20-50	1.8-8.5 kg	Terrestrial/ Cursorial	Lowland habitats, including forest and creosote bush flats, arid Chaco, and dry, low, flat thorn scrub
Hydrochoeris (2)	capybara carpincho	1,070-1,340	10-20	35-65 kg	Semi-aquatic/ Cursorial	Lowland rainforest, dry forests, shrub, or grassland near water
Kerodon (2)	mocó, rocky cavy	384-410	vestigial	0.4-1.1 kg	Terrestrial/ Scansorial	Dry rocky areas with low scrub vegetation where they shelter in crevices
Dasyproctidae						
Dasyprocta (11)	Agouti	445-760	11-55	2.4-5.9 kg	Terrestrial/ Cursorial	Mature, disturbed, secondary evergreen, deciduous, gallery forests, montane forests, gardens and plantations
Myoprocta (2)	Acouchy	298-390	51-78	0.8-1.5 kg	Terrestrial/ Cursorial	Lowland forests
Cuniculidae						
Cuniculus (2)	Paca	616-775	12-32	5-13 kg	Terrestrial/ Generalized	Mature, disturbed, secondary evergreen, gallery forests, montane forests, gardens and plantations

*Classification based on Wilson and Reeder (2005).

Nonetheless, the postcranial skeleton of most caviomorph species considered cursorial (Box 1) is clearly distinguished by a set of features. These include relatively long metapodials and short phalanges (Weisbecker and Schmidt, 2007); a large humeral greater tuberosity, which restricts the range of shoulder movement to the parasagittal plane (Morgan and Álvarez, 2013); decreased humeral robustness; increased mechanical efficiency for speed of the m. gluteus medius (Elissamburu and Vizcaíno, 2004); a tendency to medial paraxony (foot axis passing between digits III and IV) in the forelimbs and lateral paraxony in the hindlimbs (Weisbecker and Schmidt, 2007), associated with an apparent three-digit/four-digit evolution in the forelimb and a prevailing functional median digit in the hindlimb (mesaxony, *i.e.*, foot axis passing through digit III) (Rocha-Barbosa *et al.*, 2007), indicating a common trend toward lateral digital reduction whether muscular or skeletal; a very reduced clavicle resembling a thin rod (Fig. 3), although they keep well-defined and separate mm. cleidobrachialis and cleidobasilaris, which also restricts forelimb excursions closer to the median plane (Rocha-Barbosa *et al.*, 2002); and finally they keep a digitigrade posture, with unguligrade tendency, and sometimes a kind of semi-digitigrade posture is observed (Rocha-Barbosa *et al.*, 1996; pers. obs.) (Fig. 4). It is clear now that during cavioid evolution, there have been many changes in limb morphology and posture to improve running performance.

Regarding locomotor behavior in general, some morphological features, such as those related to speed, acceleration, maneuverability, resistance, stability and energetic cost, seem to be favored by natural selection (Hildebrand and Goslow, 2006). The so-called cursorial adaptations (*i.e.*, running specializations) are commonly exemplified in mammals by a tendency towards digitigrady, an increase in length and proportion of the distal segments of the limbs, as well as a distal muscular reduction, clavicular reduction and/or absence, and the development of hooves (Hildebrand and Goslow, 2006).

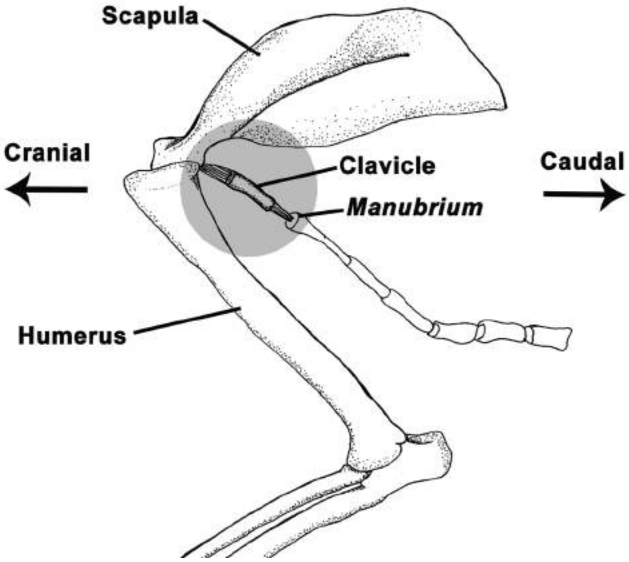

Figure 3. The agouti (*Dasyprocta*) clavicle. The circle indicates the thin rod-like clavicle. Modified from Rocha-Barbosa *et al.* (2001).

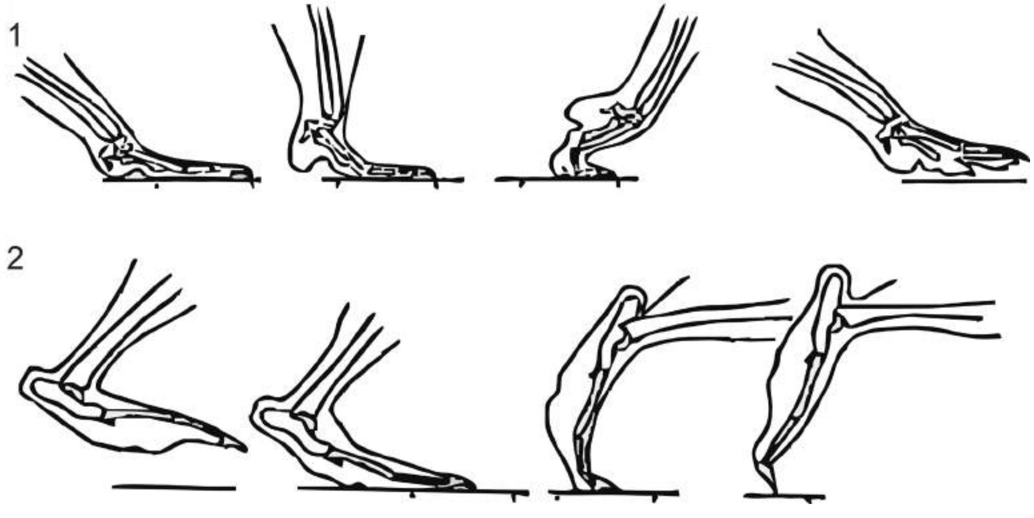

Figure 4. The cavy *Cavia porcellus* at stance phase of the forefoot 1. and hindfoot 2. Notice the semi-digitigrade posture during the middle of stance on the forefoot and throughout the stance phase on the hindfoot. Modified from Rocha-Barbosa *et al*. (1996)

In general, convergences and/or parallelisms are recognized by striking visual resemblances (Begon *et al*., 1990). These are the two possible kinds of homoplasy (Wiley, 1981) and, although there is considerable debate over the exact definition of both terms, there seems to be universal agreement that they convey the idea that sometimes distantly related organisms are similar because they share similar habitats, *i.e.*, this similarity is caused by adaptive evolution (McLennan and Brooks, 1993; Pagel, 1994; Larson and Losos, 1996; Schluter, 1988, 2000). Dubost (1968) was the first to notice a case of apparent parallelism between the Cavioidea and small ruminant artiodactyls of the Old World.

Both lineages (rodents and ruminants) had a very distant common ancestor, around 88 to 110 Ma, prior to the K-T boundary, in a clade named Boreoeutheria (Eizirik *et al*., 2001; Murphy *et al*., 2001; Archibald, 2003). Even though their evolutionary histories followed different paths, Asiatic mouse-deer (Tragulidae) and African duikers (Cephalophinae) resemble the South American agouti (Dasyproctidae, Rodentia), with forward-sloping shoulders and powerful hind quarters (Dubost, 1968; Bourlière, 1973; Nowak, 1991; Rocha-Barbosa, 1997). In fact, this *bauplan* is commonly found in small forest-dwelling herbivorous mammals throughout the world, mainly those living in the so called “Earth’s Green-Belt” (*i.e.*, rainforests of the world, Fig. 5). These animals share similar forested habitats, in America, Asia, Africa and even Australia, which seem to somehow constrain their morphology and perhaps their behavior. This particular *bauplan* of short forelimbs and longer hindlimbs in a somewhat forward-sloping body shape allows these animals to overcome the intertwined network of forest undergrowth (Dubost, 1968). This capacity for maneuverability, within this microhabitat, may be important for running and hiding from predators (Rocha-Barbosa, 1997).

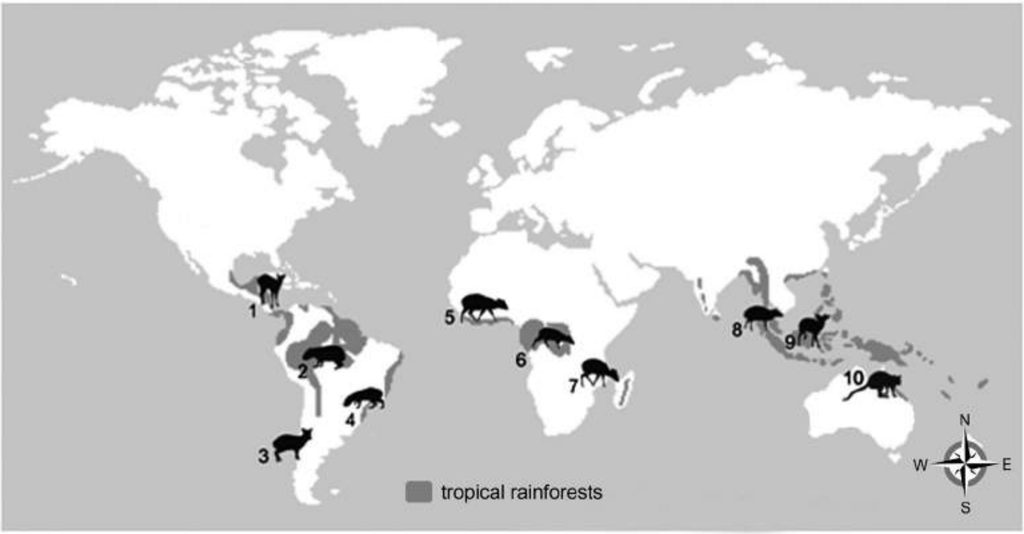

Figure 5. Geographical distribution of some caviomorph rodents, small artiodactyls and marsupials living in the Earth´s Green-Belt. Notice the forward-sloping shoulders and powerful hind quarters in all animals. 1. *Mazama americana*; 2. *Cuniculus paca*; 3. *Dasyprocta leporina*; 4. *Pudu puda*; 5. *Philantomba maxwellii*; 6. *Hyemoschus aquaticus*; 7. *Neotragus moschatus*; 8. *Tragulus napu*; 9. *Muntiacus atherodes*; 10. *Dorcopsis* sp. Source: Mariana Fiuza de Castro Loguercio; Rocha-Barbosa *et al*. (2001).

BOX 1

Defining cursoriality

Frequently when we read papers about mammalian locomotion we find expressions like "running mammal" or "cursorial mammal" to indicate that individuals of a particular species run. This terminology does not make sense, given that running is a characteristic of all mammals, with probably very few exceptions. We now know that even the biggest extant terrestrial mammals, elephants, run (Hutchinson *et al*., 2003). If mammals are able to run in a continuous way, while lizards, in contrast, run intermittently, it is because when mammals gallop, there is synchronization between locomotion and respiration. The mammalian back bends up and down (the reptilian one does it from side to side) and the animals breathe out and in during back flexion and extension, respectively. The consequence is that a horse, for example, only breathes once per stride.

In mammals, limbs are positioned under the body. However, important differences exist between small and large mammals regarding the extension and movement of the legs. While the latter tend to keep their legs in a rather straight position and move them in a strictly parasagittal way, small mammals walk and run with an important flexion at the different joints of the leg, concurrent to some lateral displacement (Fischer, 1994). In the first case, we classify those mammals as cursorial, in opposition to non-cursorial ones (Stein and Casinos, 1997). It is difficult to designate the body mass threshold between cursorial and non-cursorial mammals. Cursorial species very likely weigh more than 1 kg, and surely more than 5 kg.

Although the cavioid rodents do not show the extreme morphological modifications to cursoriality encountered in the large Artiodactyla and Perissodactyla, they do possess some adaptations, in convergence with other cursorial mammals, such as small artiodactyls, carnivores and lagomorphs (Elissamburu and Vizcaíno, 2004; Seckel and Janis, 2008) and notoungulates (Elissamburu, 2004; Croft and Anderson, 2008). In effect, during their evolutionary radiation in South America, caviomorphs have been hypothesized to fill niches that are occupied by lagomorphs, artiodactyls, and hyracoids in other continents (Mares and Ojeda, 1982; Dubost, 1988; Dubost *et al.*, 2005) and might have even competed with rodent-like native South American ungulates (Cifelli, 1985; Simpson, 1980).

4. How do caviomorphs move on land?

Locomotion as a whole has a fundamental role in vertebrate life, acting as a direct response to their environment, whether they are escaping from predators, searching for food or interacting with other organisms (Hildebrand and Goslow, 2006). The great mobility found in all mammals puts them in touch with a wide range of environments and, consequently, with varying biotic and abiotic factors.

According to Vásquez *et al.* (2002), the structural complexity of the habitat may also affect movement behavior through, 1) physically impeding locomotion (*e.g.*, Brownsmith, 1977; Crist and Wiens, 1994; Schooley *et al.*, 1996), 2) making movement more conspicuous and thus riskier (*e.g.*, Brillhart and Kaufman, 1991), 3) providing a higher density of resources, hence favoring slower speeds so that resource opportunities are not missed (see, Brownsmith, 1977), 4) increasing protection against predators through hiding cover (*e.g.*, Thompson, 1982), and/or 5) increasing visual obstruction, thus reducing the ability to detect predators (Metcalfe, 1984; Schooley *et al.*, 1996). Thus, how animals move is closely related to the complex tridimensional physical environment they live in and deal with.

During locomotion, animal limbs create a closed kinematic system which must perform three basic functions: i) propulsion, ii) support, and iii) shock absorption (Beaszczyk and Dobrzecka, 1989). Thus, in order to successfully carry out these functions, interlimb coordination must provide a smooth velocity of locomotion with a high margin of active equilibrium (Box 2).

Quadrupedal animals use a series of gaits that are divided into symmetrical and asymmetrical (Hildebrand, 1966, 1977). Symmetrical gaits include sequences in which the movement of a limb of one pair (*e.g.*, forelimb) is followed by movement of a limb of the other pair (*e.g.*, hindlimb) and, consequently, feet of the same pair land alternatively, evenly spaced in time. Symmetrical gaits include walk, pace, amble and trot (Hildebrand, 1966). On the other hand, asymmetrical gaits are those in which footfalls of a pair of feet are unevenly spaced in time, such as bound, half-bound, pronk and gallop (Hildebrand, 1977). During an asymmetrical gait, the one of a pair of feet which reaches the ground first is called trailing, while the other is called leading (Fig. 6).

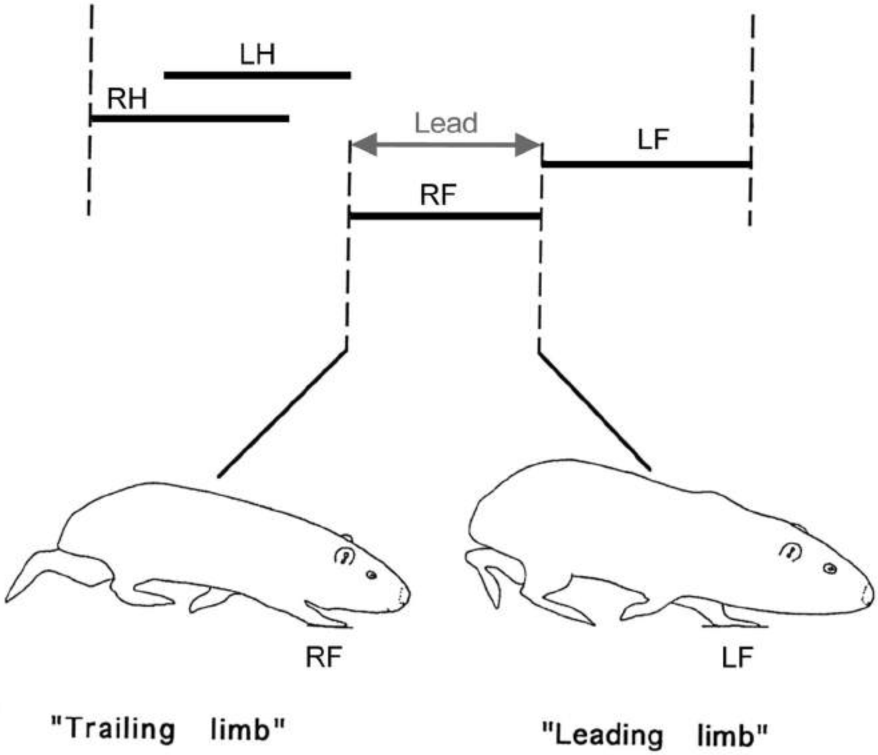

Figure 6. Gait diagram of galloping in *Cavia porcellus*, showing the trailing right forelimb and the leading left forelimb. **LH**, left hindfoot; **RH**, right hindfoot; **RF**, right forefoot; **LF**, left forefoot. Modified from Rocha-Barbosa (1997).

A locomotor cycle, also called stride cycle or gait cycle, starts when one foot makes contact with the ground and ends when that same foot contacts the ground again (Renous, 1994; Hildebrand and Goslow, 2006). Each limb undergoes a periodic motion, which is summarized by one cycle consisting of a stance and a swing phase (Alexander, 1984; Hildebrand, 1989). The stance and swing are perfectly recognizable phases. The first corresponds to the period when the foot touches the ground (touch-down), the latter when the limb is not in contact with the ground but accelerates forward looking for a new support (lift-off).

The behavior of the articulated limb during its gait cycle may be illustrated by the variation of the sum of the successive joint angles of the articular chain, which corresponds to sub-phases introduced by Philippson (1905) (Fig. 7). According to his definitions, the stance begins at the yield sub-phase (E2), corresponding to the extension of the distal joints and the flexion of all the other joints, owing to the contraction of certain extensor muscles. It allows the reduction of impact force at touchdown and the storage of elastic energy in tendons and muscles. The subsequent sub-phase (E3) corresponds to the propulsive momentum of the stance and starts when the proximal joint passes over the point of contact to the ground. An overall extension of the limb takes place as a result of the action of extensor muscles (Orsal, 1987). As soon as the foot leaves the ground and the swing phase begins, the limb undergoes an overall joint flexion owing to the action of flexor muscles (sub-phase F), which induces forward acceleration. Then, the limb is unfolded and decelerated to approach a new site of support by the action of extensor muscles (sub-phase E1) (Rocha-Barbosa *et al.*, 2005).

Although the limits of the stance-swing and swing-stance do not coincide with the maximal values of flexion and extension achieved by the sum of the joint angles, this division of the locomotor cycle into four sub-phases is clear for the minimum values of the sum of angles (Rocha-Barbosa, 1997). It also provides a conventional separation and a more perceptible observation of the stance and swing phase (Rocha-Barbosa *et al.*, 2005).

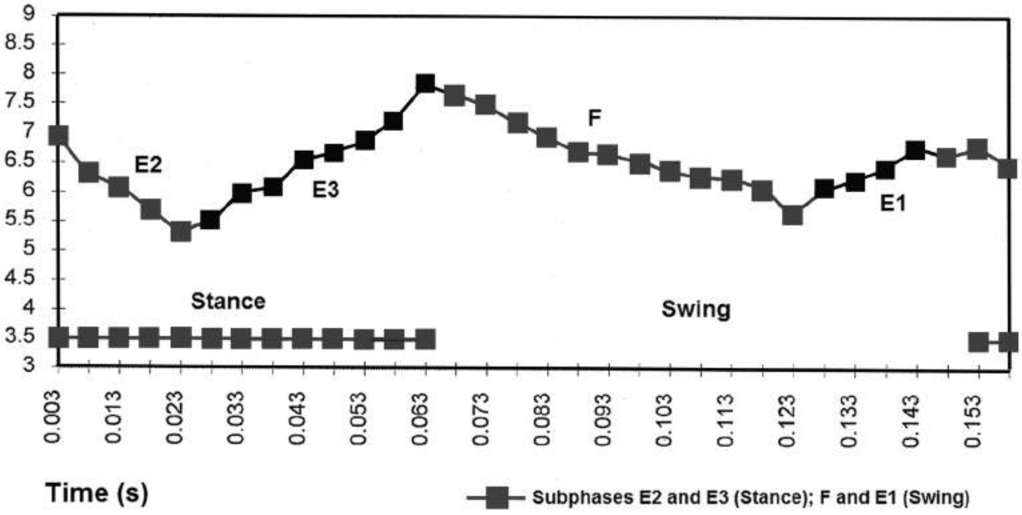

Figure 7. General pattern of the variation in the sum of angles of the limb (in radians) during one locomotor cycle, identifying the stance (touch-down) and swing (lift-off) subphases. An overall flexion of the articular chain can be seen in **E2** and **F**, while the overall extension is seen in **E3** and **E1**. Modified from Rocha-Barbosa (1997).

The gait used by each species can vary according to speed and habit. Quadrupedal mammals usually use walking gaits at low speeds, trot at slow running gaits and gallop at higher speeds (Alexander, 1984). Although there are relatively few studies on the biomechanics and kinematics of caviomorph rodents, we can hypothesize that they must follow this pattern.

In most mammals, during a normal walk, the forelimb reaches the ground soon after the ipsilateral hindlimb (lateral sequence) (Alexander and Jayes, 1983; Hildebrand and Goslow, 2006; Schmitt and Lemelin, 2002) (Fig. 9), with the footfall pattern LH-LF-RH-RF (Cartmill *et al.*, 2002). This particular movement seems to be important for static stability, but in this case the legs must be moved one at a time so that there are always three feet on the ground, keeping the center of mass over the triangle of support, which usually occurs only during slow walking (Alexander, 2003). Most caviomorphs walk exactly this way.

On the other hand, most primates and some other arboreal mammals use a diagonal sequence during walking, which can be identified when the forelimb reaches the substrate soon after the hindlimb from the opposite side, avoiding interlimb interference, with the footfall pattern LH-RF-RH-LF (Hildebrand and Goslow, 2006; Cartmill *et al*., 2002). Even if there is no study yet on the arboreal locomotion of scansorial and/or arboreal caviomorph species, we can assume that they probably move around trees and shrubs in a diagonal walk at low speeds.

With increasing speeds, mammals change from walking to running. The trot and pace are symmetrical quadrupedal runs, used mainly at moderate running speeds (Gambaryan, 1974; Alexander, 2003).

BOX 2

Step vs. Stride

Although these terms are sometimes used indistinctly in everyday language, in biomechanical terms, they are quite different. The step length is the amplitude of limb movement measured if the limb pivot point (or joint) were stationary, *i.e.*, it is the distance travelled while a foot is on the ground. On the other hand, stride length is simply the distance covered by the limb between two successive footfalls. In Fig. 8.1, the left hindlimb step length would be the distance travelled between a-e, while the stride length would be the distance travelled between f-i.

The same difference is evident when examining an animal trackway (Fig. 8.1- 8.3). The step length is the distance between one hind/forefoot to the other. The stride length is the distance between two placements of the same foot (=two steps). If the animal is a quadruped, these should be taken from the forelimbs and hindlimbs separately.

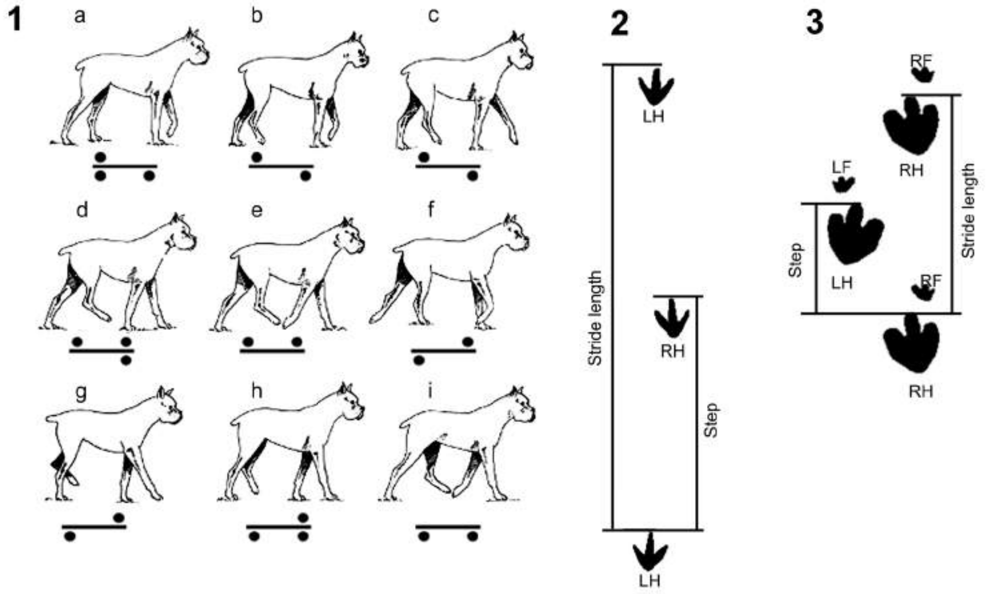

Figure 8. Differences between stride and step. 1. Walking gait of a dog, showing the stride cycle or locomotor cycle of the left hindlimb (a-e, stance; f-i, swing). Black dots are equivalent to when the limb is in contact with the ground. Modified from Nunamaker and Blauner (1985). Also, notice what is considered stride length and one step when looking at a trackway from a 2. bipedal animal and 3. quadrupedal one. **H**, hindlimb; **F**, forelimb; L, left; **R**, right. Modified from Over (1995).

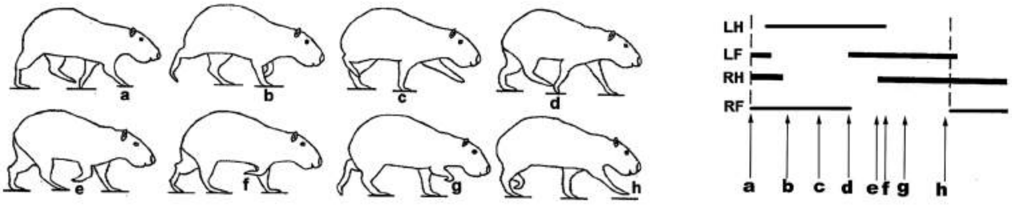

Figure 9. Moderate walk of *Agouti paca*. Gait diagram with the corresponding animal silhouette. **LH**, Left hindlimb; **LF**, Left forelimb; **RH**, Right hindlimb; **RF**, Right forelimb. Gap between two frames: 0.04 s. Modified from Rocha-Barbosa (1997).

In trotting, diagonally opposite feet move in phase with each other (Fig. 10), while in pacing, the two feet on the same side of the body move in phase with each other. Both trotters and pacers have the advantage that two limbs work together to propel the animal and to cushion the shock (Kar *et al.*, 2003). Trotting is more commonly observed than pacing.

Pacing is disadvantageous for short-legged animals like caviomorphs overall, because stability is reduced, as the center of mass is slightly decentered during support. But, its important advantage for long-legged animals lies in the fact that a hind foot cannot interfere with a forefoot. Although not all long-legged animals pace, animals that do pace are all long-legged (Kar *et al.*, 2003). Among caviomorphs, the cursorial and long-legged *Dolichotis* is a recognized pacer.

At higher running speeds, several variants of galloping (running asymmetrical gaits) are also recognized, but in general, they can be classified into transverse and rotatory (or rotary) (Hildebrand, 1977; Alexander, 2003).

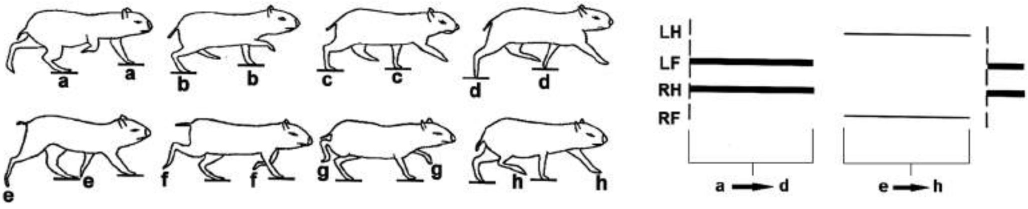

Figure 10. Typical trot of *Myoprocta acouchy*. Gait diagram with the corresponding animal silhouette. **LH**, Left hindlimb; **LF**, Left forelimb; **RH**, Right hindlimb; **RF**, Right forelimb. Modified from Rocha-Barbosa (1997).

The transverse gallop is a four-beat gait, with the footfall pattern LH-RH-LF-RF. The leading forelimb is the one that supports all the animal's weight right before suspension; it has a longer stride and its stance phase is also longer when compared to the trailing forelimb. In this gallop, the hindlimbs provide the major propulsive force. Whereas the leading hindlimb is more powerful in providing forward and upward thrust, the trailing forelimb is extended forward under the body and is more prone to injury because of the shock involved in catching the falling body weight. This gallop is often described as a single suspension gait because sometimes there is a single aerial phase, usually with the animal's limbs gathered beneath its body (gathered flight) soon before the leading forelimb leaves the ground and while the trailing hindlimb has not yet finished its swing phase.

The transverse gallop is the primary gallop of horses, cows, as well as other large ungulates. Among caviomorphs, the capybara also typically runs this way (Fig. 11). Overall, the trunk is held relatively rigid and undergoes a cranial-caudal rocking action. Dogs and other carnivores also exhibit the transverse gallop, but the rotatory gallop is their fastest gait.

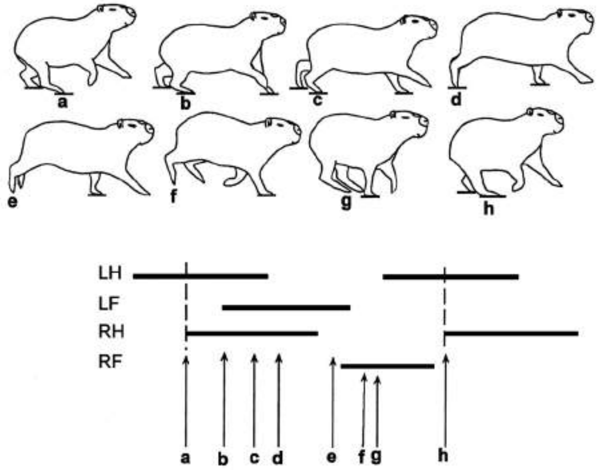

Figure 11. Four-beat gallop or transverse gallop of *Hydrochoerus hydrochaeris*. Gait diagram with the corresponding animal silhouette. **LH**, Left hindlimb; **LF**, Left forelimb; **RH**, Right hindlimb; **RF**, Right forelimb. Modified from Rocha-Barbosa (1997).

The other type of gallop is known as rotatory gallop (also called double suspension gallop) and it is also a four-beat gait, commonly used by carnivores, some rodents (including caviomorphs), and small ungulates (Gambaryan, 1974). The difference between the rotatory gallop and the transverse gallop is the footfall pattern LH-RH-RF-LF, which follows a clockwise footfall sequence (Fig. 12).

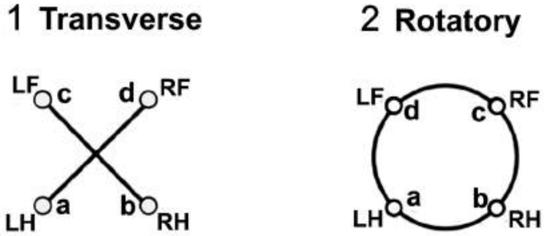

Figure 12. Gallops found in quadrupeds 1. transverse gallop; 2. rotatory gallop. Letters (a, b, c, d) indicate the footfall sequence. **LH**, Left hindlimb; **LF**, Left forelimb; **RH**, Right hindlimb; **RF**, Right forelimb. Modified from Kar *et al*. (2003).

In contrast to the transverse gallop, this gait has two suspension (aerial) phases. The first one is a gathered flight as in the transverse gallop while the other one is an extended flight, when both hind- and forelimbs are fully extended beneath the body and both pairs are in the middle of their swing phase. These two phases are always associated with flexion/extension of the vertebral column that helps increase stride length and consequently animal running speed. That is why the rotatory gallop is the fastest, but also the most tiring of all gaits, as it requires lots of energy. Thus, it is usually used during relatively short runs.

It is also considered more maneuverable than the transverse gallop although it is less stable (Hildebrand and Goslow, 2006). This is why some species, like the carnivores *Mustela* and *Lutra* and the rodents *Sciurus*, *Dolichotis* and *Hydrochoerus* tend to change from a four-beat gallop to a bound, as they continue to speed up (Hildebrand, 1977).

A bound is a two-beat gait where the hind feet and the forefeet strike the ground in unison (two-beat gallop). If the hindlimbs strike together while the forelimbs are out of phase with each other, the gait is termed as half bound (also called three-beat gallop). When all feet strike at the same time, this gait is called pronk. These three gaits are also referred to as in-phase gaits (Fischer *et al.*, 2002).

Rabbits, weasels and other mammals of similar size commonly use the half-bound (Hildebrand and Goslow, 2006), whereas squirrels and mice use the bound (Alexander, 2003).The capybara can also use a bound (see Casinos *et al.*, 1996), or according to Gambaryan (1974), the "primitive ricocheting jump", in what he considers as the characteristic rodent asymmetrical gait. In fact, all caviomorphs seem to use these previously-described gaits at higher speeds (Fig. 13).

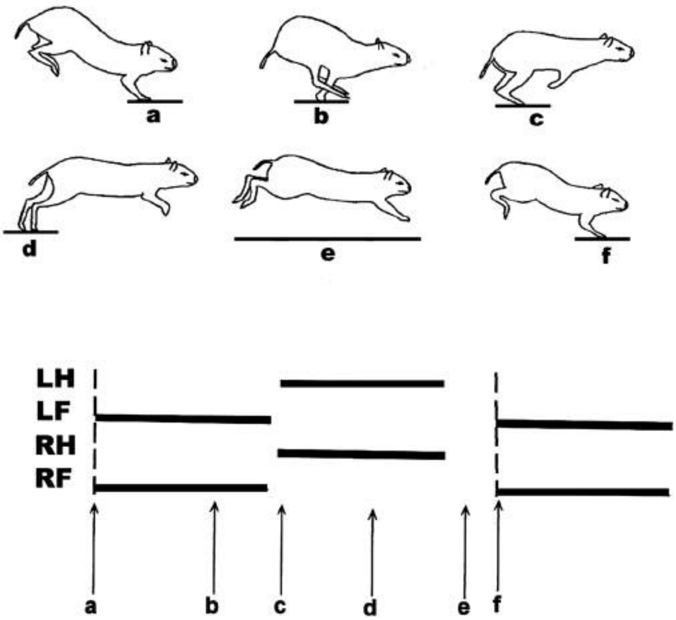

Figure 13. Bound of *Myoprocta acouchy*, asymmetrical gait characterized by the synchronic footfall of both forelimbs and both hindlimbs after an aerial phase. Gait diagram with the correspondent animal silhouette. **LH**, Left hindlimb; **LF**, Left forelimb; **RH**, Right hindlimb; **RF**, Right forelimb. Modified from Rocha-Barbosa (1997).

The difference between a bound and a half-bound is the lag between the footfalls of the forelimbs. During a bound, the forelimbs act exclusively to cushion the impact and a large shock-absorbing load is also brought to bear on the anterior section of the vertebral column (Gambaryan, 1974). Bound gaits, as such, are also observed in other rodents such as *Rattus*, *Cricetulus*, *Calomyscus*, and *Meriones* (Gambaryan, 1974) and even in marsupials, such as *Dendrolagus* and *Macropus* (Hildebrand, 1977).

In some species, we can observe two aerial phases, as in a rotatory gallop: a gathered flight and an extended flight. The gathered flight is usually reduced or even absent in species such as *Hydrochoerus* and *Myoprocta* (Rocha-Barbosa, 1997; Loguercio, 2005). The extended flight found in most Cavioid species is similar to that of species specialized for half-bounds, such as the *Chinchilla*, *Oryctolagus* (Lammers and German, 2002) and *Spermophilopsis* (Gambaryan, 1974), in which the hindlimbs are kept extended up until the forelimb footfall. Species specialized for the primitive ricocheting jump, such as the squirrels *Spermophilus* and *Sciurus*, keep their hindlimbs flexed during the extended flight (Gambaryan, 1974).

The extension and flexion of the vertebral column are sometimes more clearly observed during in-phase gaits than during gallops. These sagittal spinal movements contribute to increasing stride length and participate mainly in hindlimb progression, a fact that is common in small tailless mammals (Rocha-Barbosa, 1997; Fischer *et al.*, 2002; Witte *et al.*, 2002). This kind of spinal movement (similar to the one found during gallops), seen in members of the families Felidae and Canidae, is called dorso-mobile, whereas the other kind, found in the gallop of *Dasyprocta* and most ungulates, in which the vertebral column remains relatively rigid, is called dorso-stable (Gambaryan, 1974).

The variation in the participation of the vertebral column in movement is associated with the relatively high energetic cost of flexion/extension (Liem *et al.*, 2001). The need for fast sprinting, whether in escaping from a predator or in running after prey, would validate this kind of cost. By contrast, long-distance displacements, where endurance is needed, would not bear this extra cost. That is why dorso-mobile gaits are usually observed during short runs, either gallops or bounds. Extension and flexion of the vertebral column, which are especially important in very fast animals (for example, cheetahs), are also an elastic system that saves energy (Alexander, 1988).

5. Caviomorph biomechanics into the future

In the 1980s, new methods based on computer graphics underwent marked expansion, with the increasing use of computer tomography (CT-scan), magnetic resonance, videogrammetry, laser scanning and even three-dimensional animation programs (Fishman *et al.*, 1991). Due to reduced costs in computational resources, such techniques are gradually expanding and are being widely used in many areas of medicine and biology, as well as in diverse applications, thanks to the high resolution and the high level of detail for complex structures that these techniques offer.

Currently, using scanners and computational software, some three-dimensional (3D) animation programs permit the manipulation of three-dimensional models, as well as the testing and simulation of joint movement and the actions of muscles and ligaments (Wilhite, 2003).

In particular, 3D object modeling consists of the virtual reconstruction of a real object, allowing for manipulation of the geometric model on the computer (Werner and Lopes, 2009). This task can be performed either by scanners in a more automated way, or by computer graphics programs in a more manual way (Peixoto and Gattass, 2000). In general, the major challenge is to achieve the correct virtual representation of the main features of the object with the highest possible realism (Loguercio, 2009; Temba, 2010). When this is achieved, it is possible to simulate and/or analyze different virtual situations.

In this context, caviomorph rodents emerge as interesting models for three-dimensional analysis, enabling simulations and comparisons of species with high diversity of size and habits.

Virtual 3D reconstructions of some different-sized caviomorphs have already been accomplished, including *Hydrochoerus*, *Dasyprocta* and *Cavia* (Loguercio, 2009; Chagas, 2013; Santos, 2013). These skeletal models have been digitized through a process known as shape-from-silhouette (SFS) (Dardon *et al.*, 2010; Grillo *et al.*, 2011). This process involves a certain protocol from the shooting of a series of photos until the final model is complete. All bones must be processed individually for better resolution.

Initially, each bone is photographed from different angles in a photographic set that requires a pedestal, a background of contrasting color (chroma key) and a calibration mat (Fig. 14.1). This particular setting allows the software to identify the position of each photo in relation to the analyzed bone. As the process is called "shape-from-silhouette", in each photo the object needs to be highlighted from the background in a procedure known as masking, which can be accomplished manually or automatically via software (Fig. 14.2). This will identify the object silhouette in all photo positions.

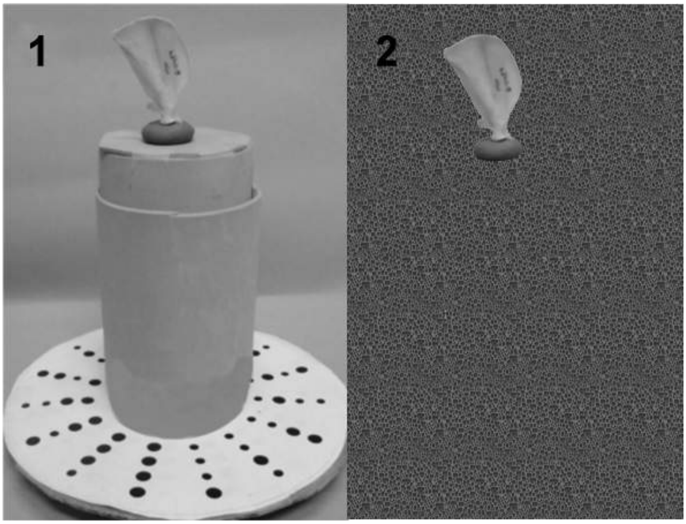

Figure 14. 3D shape-from-silhouette modeling of *Cavia aperea* scapula. 1. Photographic set with calibration mat, pedestal, and a chroma-key background; 2. Masking procedure in which the silhouette of the object is highlighted against the background. Modified from Santos (2013).

The final 3D model is complete after 1) the construction of the wireframe (polygonal mesh), 2) the optimization process, which defines and smoothes the polygonal surface and 3) the inclusion of a texture map that uses the colors from the original photos (Fig. 15).

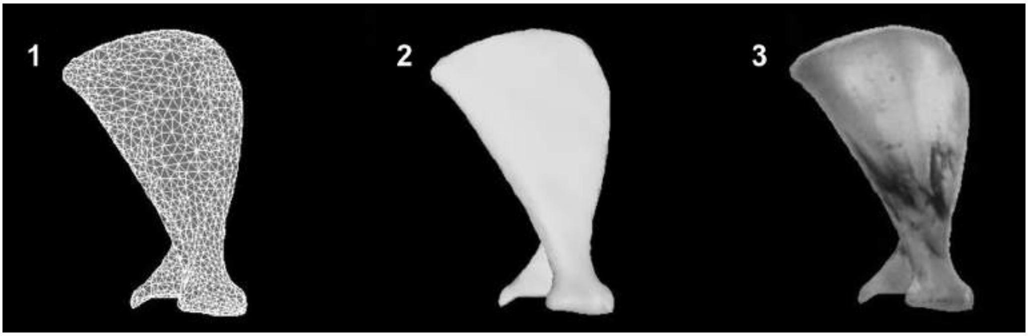

Figure 15. 3D model of the *Cavia aperea* scapula, in three stages 1. wireframe or polygonal mesh; 2. optimized surface; 3. textured surface. Modified from Santos (2013).

After each bone is digitized, the digital model can be exported to computer animation software, where the skeleton can be articulated and subsequently animated.

Overall, this modeling method demands more effort and attention to detail, mainly when shooting photos and masking bones, when compared to other more automated methods, such as CT-scans. On the other hand, the software interface is user-friendly and it is quite effective in modelling different-sized bones, such as large ones from *Hydrochoerus* as described by Loguercio (2009), medium-sized ones from *Dasyprocta* (Chagas, 2013), and even the smaller bones of *Cavia* (Santos, 2013) (Fig. 16). In contrast, this is usually a limitation of other techniques, such as the laser scanner (Dardon *et al.*, 2010).

This procedure is also less costly and although it does not offer high resolution details, the technique proves to be very effective in many studies that require a more practical 3D reconstruction, at a better cost/benefit ratio.

Additionally, these 3D models can be developed later for direct applications in biomechanics, such as analysis of posture, muscle insertion and ligament attachment, and analysis of muscle action, as well as in comparative biology. Finally, they constitute a valuable addition to collections of 3D virtual models for improving virtual databases that expand the exchange of information between researchers and institutions around the world.

Conclusion

Caviomorph rodents can be found in most habitats, including high- and low-altitude shrublands, coastal areas, and tropical forests, with numerous species having wide geographical ranges. Ecological niches range from arboreal to semiaquatic to subterranean. This high diversity makes caviomorph rodents ideal species for ecomorphological and locomotor studies.

Extant caviomorphs also vary in body mass, from small coruros at 80 g to the large capybara at around 50 kg. When considering fossil species, such as †*Phoberomys* and †*Josephoartigasia*, this range is increased considerably.

Variations in shape are commonly found in caviomorphs, especially when considering different locomotor specializations. Diggers and cursorials are usually at both extremes of the morphospace and can be easily recognized from the other groups.

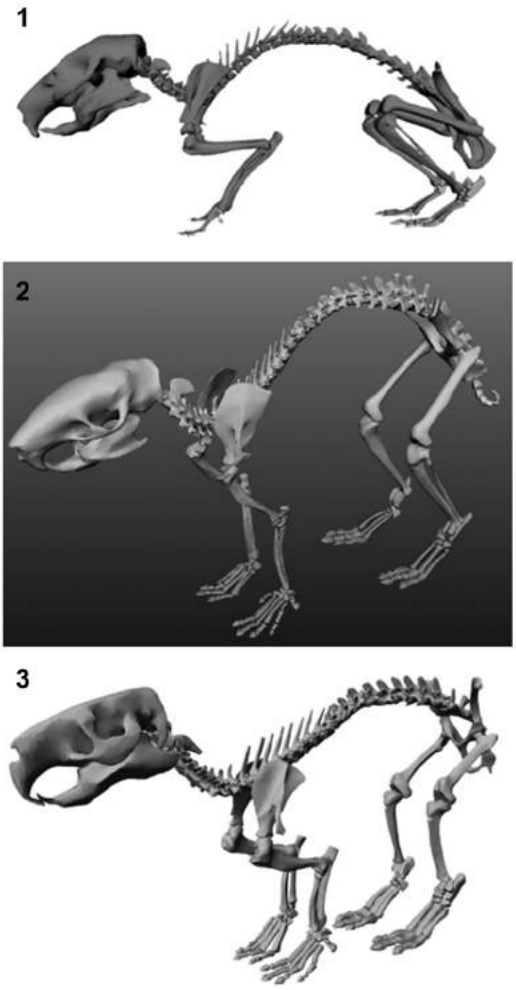

Figure 16. 3D complete skeleton reconstructions of three different-sized caviomorphs. 1. *Cavia aperea* (Santos, 2013); 2. *Dasyprocta azarae* (Chagas, 2013) and 3. *Hydrochoerus hydrochaeris* (Loguercio, 2009). Images are not to scale.

From an evolutionary point of view, most studies suggest certain morphological adaptations found in cursorial caviomorphs are convergent on other cursorial mammals, such as small artiodactyls and even carnivores and lagomorphs. Lateral digital reduction can be related to a better locomotor performance. Clavicle reduction helps increase the forelimbs' internal range of motion and, consequently, increases stride length. A more parasagittal limb posture raises the center of gravity and thus increases maneuverability when escaping from predators.

Overall, this chapter attempts to review some morphological and functional aspects of this interesting and diverse rodent group. Besides furnishing pure knowledge of biology, what we already know can also be applied in robotics to help mankind reach distant or dangerous places, as well as improving movies, animations and videogames, anything that uses 3D modelling and/or animal biomechanics.

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5 | THE POSTCRANIAL SKELETON OF CAVIOMORPHS: MORPHOLOGICAL DIVERSITY, ADAPTATIONS AND PATTERNS

EL ESQUELETO POSCRANEANO DE LOS CAVIOMORFOS: DIVERSIDAD MORFOLÓGICA, ADAPTACIONES Y PATRONES

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Abstract. This review focuses on the most recent advances in the study of the postcranial skeleton of South American Hystricomorpha ("caviomorphs"), with special focus on those made applying morphometric techniques to the shoulder girdle and forelimb skeleton, in a comparative phylogenetic context. In particular, morphometric analyses of the scapula and humerus are discussed with respect to the morphofunctional range of variation and evolutionary patterns recognized among caviomorphs. Scapular shape showed large differences and morphological features characteristic of each of the major caviomorph lineages, especially in the scapular spine; octodontoids and cavioids had the most divergent scapular morphologies. Body size showed only weak influence on scapular shape and most of the functional categories tested were not associated with a distinct scapular morphology. In the case of the humerus, the distribution of taxa in the morphospace was partially coincident with functional groups in some cases, and with phylogenetic proximity in others. The radius and ulna of octodontoids exhibited greater robusticity and curvature in diggers, while they were elongated in cursorial forms; in addition, in both of these functional types the shape of the radial fovea was asymmetrical, thus restricting rotation at the elbow level. The most specialized digger *Ctenomys* also showed mechanical restriction for rotation at wrist level. The hand skeleton also showed different morphological specializations within a conservative basic structure; *e.g.*, digit proportions and bone proportions were different (paraxony in generalized forms *vs*. mesaxony in diggers; less carpal mobility in diggers), and *Ctenomys* had the most modifications. Evidence from analyses of extinct representatives of several caviomorph families supports the hypothesis that morphological skeletal specializations were acquired early on in the history of the major caviomorph lineages.

Resumen. La presente revisión está enfocada en los más recientes avances en el conocimiento y estudio del esqueleto postcraneano de los roedores Hystricomorpha sudamericanos ("caviomorfos"), en particular en aquellos realizados mediante la aplicación de técnicas morfo-geométricas al esqueleto de la cintura escapular y miembro anterior, en un contexto filogenético comparativo explícito. Se discuten con mayor detalle análisis de la escápula y húmero realizados mediante morfometría geométrica, con respecto al rango morfofuncional de variación y los patrones evolutivos reconocidos dentro de los caviomorfos. La forma de la escápula mostró gran variación y rasgos morfológicos característicos de cada uno de los grandes linajes de caviomorfos, especialmente a nivel de la espina escapular. Los extremos de variación estuvieron representados por los octodontoideos, con espina escapular muy larga y muesca escapular muy extendida, y los cavioideos, con hoja escapular más alongada, espina corta y metacromion por lo general de gran desarrollo, mientras que los eretizontoideos y chinchilloideos mostraron forma escapular más generalizada. El tamaño corporal mostró débil influencia sobre el cambio de forma escapular, mientras que la mayoría de las categorías funcionales contrastadas (tipos de locomoción preferencial) no mostraron asociación con una morfología escapular particular, especialmente al analizarlas en un contexto filogenético comparativo. En el caso del húmero, la distribución de los taxones en el morfoespacio coincidió parcialmente con los grupos funcionales (tipos de locomoción) en algunos casos, mientras que en otros la agrupación se correspondió con la proximidad filogenética. En este caso fueron los cavioideos quienes presentaron la morfología humeral más distintiva, con diáfisis alongada, epífisis distal angosta y tuberosidad mayor de gran tamaño; estas características pueden correlacionarse con la especialización cursorial prevalente en dicho linaje. Los huesos del antebrazo fueron analizados con una metodología cuali-cuantitativa más tradicional, y la muestra consistió principalmente de octodontoideos. Tanto el radio como la ulna de estos últimos mostró grados variables de robustez y curvatura, mayor en las formas cavadoras, mientras que en los taxones cursoriales fueron más rectos y alongados. Además, tanto en cursoriales como en fosoriales, la carilla articular proximal del radio mostró un contorno asimétrico, restrictivo de la rotación a nivel del codo. El subterráneo excavador más especializado, *Ctenomys*, también presentó restricciones mecánicas para la rotación a nivel de la muñeca gracias a la posesión de una apófisis suplementaria en la epífisis distal del radio. El esqueleto de la mano de los octodontoideos también mostró diversas especializaciones morfológicas en el contexto de una estructura básica conservadora; estas especializaciones incluyeron diferencias en el desarrollo y largo relativo del metacarpo y dedos (paraxonia en las formas generalizadas *vs*. mesaxonia en los cavadores), y en el tamaño relativo y contacto entre los huesos carpianos de las series proximal y distal (escafolunar de gran tamaño y con más amplio contacto con el escafolunar y unciforme en cavadores especializados). Una vez más, el especializado *Ctenomys* mostró las modificaciones más acentuadas. Con respecto a taxones extintos, detallados análisis paleobiológicos han mostrado la existencia de especializaciones semiarborícolas, cursoriales, y subterráneas en representantes de los diversos linajes; de esta forma, los estudios funcionales paleontológicos apoyan también la hipótesis de que las especializaciones esqueletarias fueron adquiridas tempranamente durante la historia evolutiva de los principales linajes de caviomorfos. Es probable que estas morfologías características, combinadas con otros factores, hayan actuado canalizando y hasta cierto punto restringiendo la evolución morfológica y los nichos ecológicos explotados por cada clado. Futuros estudios con enfoque integrativo, que puedan incorporar mayor cantidad de taxones, datos ecológicos y de comportamiento actualizados y precisos, y filogenias moleculares para control filogenético de los análisis, permitirán comprender mejor los patrones detectados con el aporte de diversas disciplinas.

Introduction

The high diversity of caviomorph rodents became evident ever since they were first discovered and studied. In terms of species richness, the living representatives comprise about 250 species (Woods and Kilpatrick, 2005) in 14 families, and the numerous fossil taxa further add to this diversity (Vucetich *et al.*, this volume). Likewise, and as could be expected given the characteristics and history of the American continents, caviomorphs are also highly diverse with regards to ecological features such as habits, locomotor modes, substrate preferences and body size (Nowak, 1991; Grzimek, 2003). Indeed, the four major caviomorph lineages differ in their main ecological characteristics. The Erethizontoidea (porcupines) are medium- to large-sized semi-terrestrial and scansorial arboreal climbers. The Chinchilloidea (viscachas, mountain viscachas and chinchillas) include both primarily epigean ricochetal and fossorial forms, with a wide range of body sizes from the small, gracile chinchillas (*Chinchilla*) to the large, heavy viscachas (*Lagostomus*). The terrestrial pacarana (*Dinomys*) could also belong to this superfamily (Huchon and Douzery, 2001). The Cavioidea are mainly represented by epigean generalized and cursorial taxa that also range widely in body size, from the largest living rodent, the capybara (*Hydrochoerus hydrochaeris*), to the small mountain cavies (*Microcavia*). The most species-rich clade, the Octodontoidea, includes small- to medium-sized arboreal, terrestrial, aquatic, fossorial and completely subterranean species, with diverse climbing and digging specializations.

The postcranial skeleton of these rodents is expected to reflect both this ecological, adaptive diversity as well as their shared evolutionary history. But despite the fact that caviomorphs represent quite an interesting subject for this research, there is still much to learn about their postcranial skeletal anatomy. In fact, our current knowledge of the skeletal anatomy of caviomorphs is quite uneven. A considerable wealth of anatomical information is available for some species of special interest for man, be it because of their large size (*Hydrochoerus*), their use as anatomical models (*Cuniculus*) or their striking digging adaptations (*Ctenomys*). The history of the acquisition of this knowledge also reflects this heterogeneity. In the 19th century, Ramón de la Sagra (1845) provided one of the first descriptions of the caviomorph skeleton in his study of Antillean capromyids. Later on, some caviomorphs were included in anatomy treatises (Cuvier, 1835; Flower, 1885; Lessertisseur and Saban, 1967) as part of larger mammalian samples. It was only in the last decades of the 20th century that new approaches and contributions reflected a new and more specific interest in the morphology and adaptations of New World hystricomorphs.

Among other works, the anatomy of the guinea pig *Cavia*, a common laboratory animal, has been well studied (*e.g.,* Cooper and Schiller, 1975); Mones (1997) described the postcranial skeleton of *Dinomys*; and Bode *et al.* (2013) provided an anatomical description of the axial skeleton of *Hydrochoerus*, based on a small sample. Rocha-Barbosa and his collaborators have focused on the anatomy and kinematics of cavioids (see Rocha-Barbosa *et al.*, 2002, 2005; Rocha-Barbosa and Casinos, 2011; Rocha-Barbosa *et al.*, this volume). Living caviomorphs have also been studied as comparative material in analyses of fossil remains (*e.g.,* Biknevicius *et al.*, 1993; Fernández *et al.*, 2000; Candela and Picasso, 2008; Vucetich *et al.*, 2011); some taxa have been included in more encompassing analyses of locomotor adaptations of rodents (Samuels and Van Valkenburgh, 2008) and rabbits (Seckel and Janis, 2008).

Subterranean mammals and their adaptations have always appeared as an interesting topic, and thus several authors have focused on the specialized subterranean rodents included in the family Octodontidae. Lehmann (1963) analyzed morphological features of the forelimb in fossorial rodents, including *Ctenomys* and *Octodon*; Casinos *et al.* (1993) performed an allometric analysis of the long bones of living and extinct ctenomyines; and Vassallo (1998) compared two *Ctenomys* species and found differences at skull and forelimb level that could be correlated with their prevalent digging modes. Stein (2000) discussed some postcranial features of *Ctenomys* in her excellent synthesis of the morphology of subterranean rodents. Fernández *et al.* (2000) analyzed digging adaptations of the extinct ctenomyine †*Actenomys* and compared it with its living relatives. Other comparative analyses focused on the interpretation of extinct taxa include Candela and Vizcaíno (2007), Candela *et al.* (2012), Olivares (2009), and Olivares *et al.* (2010a). Regarding the autopodium, Ubilla and Altuna (1990) and Ubilla (2008) contributed detailed analyses of the anatomy and adaptations of the hand of some caviomorphs, while Weisbecker and Schmid (2007) analyzed the proportions of their autopodial skeleton.

Most of the aforementioned works were restricted to relatively few species, except for Elissamburu and Vizcaíno (2004), Candela and Picasso (2008) and Weisbecker and Schmid (2007) who analyzed taxonomically wide samples. In any case, the postcranial skeleton of most caviomorphs is poorly known or has not been studied at all. This paucity of information is particularly striking in the case of well-known, large-sized species that are exploited for their meat or fur, such as the viscachas (*Lagostomus*) or coypu (*Myocastor*).

The goal of this chapter is to review the most recent advances in the study of the caviomorph postcranial skeleton, with special focus on those made applying morphometric techniques in a comparative phylogenetic context. Most of these studies are focused on the forelimb skeleton; in addition, taxa belonging to the superfamily Octodontoidea will be particularly discussed, as their high ecomorphological and taxonomical diversity make for a very interesting model to analyze evolutionary patterns (see Rocha-Barbosa *et al.*, this volume, regarding Cavioidea).

The first section presents and summarizes recent analyses of postcranial elements. These include both published and unpublished qualitative and quantitative morphological analyses of the scapula, humerus, antebrachium and autopodium of living caviomorphs; some of them also included extinct taxa, when appropriate materials were available. The second section discusses the evolutionary implications of the patterns detected in these living taxa, while the third section integrates other recent, in-depth analyses of extinct caviomorphs that contribute to our understanding of the ecomorphological evolution of caviomorphs. The last section will briefly discuss a very recent analysis and suggest directions for future works to further explore the morphological adaptations and evolutionary patterns of caviomorph rodents in their historical and geographic context.

Insights from living forms

The morphological variation found in these comparative analyses was traditionally interpreted mostly in adaptive terms, linking anatomical features of the various taxa to locomotor modes or substrate preferences; particularly so in the case of paleobiological interpretations of extinct forms. However, in order to assess the relative importance of these or other causal factors in the generation of morphological disparity, any analysis must include, in addition to an estimation of phenotypical differences, also a phylogenetic framework and at least a gross description of the environment of each species (Straney and Patton, 1980). In this sense, the first approach to the study of the postcranium of caviomorphs that included an explicit comparative phylogenetic framework was a morphogeometric analysis of the scapula (Morgan, 2009a).

Shoulder girdle: the scapula

The mammalian scapula is a complex morphological structure (Monteiro and Abe, 1999) that plays a major role in mammalian locomotion (Fischer *et al.*, 2002), and its study is thus both appealing and intricate. Morphological and morphofunctional studies of the scapula had been performed for other mammalian taxa (Lessertisseur and Saban, 1967; Oxnard, 1968; Hildebrand, 1985; Taylor, 1997), including sciuromorph rodents (Price, 1993; Swiderski, 1993) and some hystricomorphs (Lehmann, 1963).

The functional factors that influence scapular morphology include the requirements of shoulder stabilization and limb mobility, as well as particular movements and forces linked to specialized locomotor modes. In addition, similar morphologies resulting from common ancestry are to be expected among closely related lineages. Previous works had highlighted some function-linked morphological features (Lehmann, 1963; Fernández *et al.*, 2000; Vassallo, 1998; Seckel and Janis, 2008), but this study was the first to show the strong influence of phylogenetic structure (estimated as phylogenetic inertia) on scapular morphology, thus shedding light on how these factors contribute to the evolution of scapular features.

Materials and methods. The shape of the scapula of adult caviomorphs was captured by means of few landmarks and several semilandmarks to describe its outline (see Fig. 1 and Box 1; also Morgan, 2009a). The sample included 22 species spanning the four major caviomorph clades, as well as the African *Hystrix cristata* (Old World porcupine; Hystricomorpha Hystricidae). After performing Procrustes superimposition and obtaining the consensus configurations for each taxon analyzed, a Principal Components Analysis (PCA) was used to explore the distribution of taxa in the morphospace, and shape changes were visualized by means of deformation grids. Centroid size (CS) was used as proxy for body size for regression analyses.

BOX 1

Quantitative approaches to the study of shape

There are two basic approaches to morphometrics or the quantitative analysis of shape: algebraic methods and coordinates-based ones. Within the algebraic methods, the use of linear measurements and indices built from the former have been classically used to describe and compare the shape of diverse organisms. Once the data are recorded, a large number of statistical analyses can be applied to single measurements (univariate) or sets of variables (multivariate) taken from diverse organisms (Sokal and Rohlf, 1995; Legendre and Legendre, 1998; Zar, 1998). Traditional morphometrics have been criticized because linear measurements of a given specimen often overlap, and especially because they provide little information about shape. Even the ratios of linear measurements, especially designed to reflect shape features such as "robusticity" (thickness/length), can be ambiguous (*e.g.*, is a bone more robust because it is longer or thicker than in other taxa?).

The landmark-based approach is based on "capturing" shape by means of the coordinates of particular points selected on an organism (homologous points or landmarks), which retain information both about distances between them (linear dimensions) and about the geometry of the shape being described (relative position of each point in space). Raw coordinates are superimposed in a process that removes differences due to position in space, rotation or size; the resulting data, expressed as Procrustes coordinates, can be subjected to different multivariate statistical analyses. In addition, the thin-plate splines technique developed by Bookstein (1991) on the basis of Thompson's (1917) original proposal, allows easy visualization of differences among complex shapes (Zelditch *et al.*, 2004) and makes it especially useful for the study of some biological materials.

Bookstein (1991) defined three types of biological landmarks: type 1 are located at the discrete juxtaposition of tissues or structures (*e.g.*, suture between nasal, maxillary and frontal bones); type 2 are points situated on local maxima or minima of curvature (*e.g.*, tip of a tooth); and type 3 are points that mark extreme distances from another point (*e.g.*, most proximal point of humeral head along longitudinal axis). Unlike Types 1 and 2, Type 3 landmarks are not defined by specific features, and currently, they are not usually considered as landmarks but as semilandmarks (*i.e.*, sets of sliding points placed along outlines and allowed to change their spacing along the curves they describe; Bookstein, 1997). Landmarks and semilandmarks can be captured as coordinates on 2D or 3D structures using various, more or less complex, equipment and software. Then, the effects of location, size and orientation ('nonshape variation', Rohlf and Slice, 1990) are removed by General Procrustes analysis (GPA; Gower, 1975; Rohlf, 1990). If semilandmarks are being used, they must be slid to minimize the variation tangential to the curve (Adams *et al.*, 2004), using one of two criteria: minimum bending energy or minimum squared Procrustes distance (see Perez *et al*., 2006). The Procrustes coordinates that result from these procedures can then be analyzed by diverse multivariate methods such as principal components analysis (PCA, also known as Relative Warps Analysis), discriminant analysis (DA), or partial least squares (PLS), among others.

In the field of morphological studies, both approaches have been developed in parallel, and they are among the most useful tools for quantitative analyses. The choice of either depends on the goals of the work; for instance, linear morphometry allows a more straightforward analysis in the case of functional models such as those that consider lever arms and force production. Conversely, in the case of morphologically complex structures with few or no landmarks, geometric morphometrics may represent the better approach, when linear measurements cannot fully capture the shape under study.

Either approach can be also used for the analysis of allometry, defined as differential growth of parts of an organism or "the relationship between changes in shape and overall size" (Levinton, 1988). Allometric equations summarize the differences between the growth rates of these parts, be it with respect to overall size of the organism or to other body parts. Thus, it is possible to identify shape changes that are directly related to overall size change; in turn, particular allometric trajectories may act as restrictions or channel the direction of shape changes at an ontogenetic or evolutionary scale. For traditional morphometrics, body size may be measured as body mass, or a variable highly correlated with it such as basilar length, other cranial, postcranial or dental measurements, or the geometric mean of other measurements. In geometric morphometrics, centroid size is used as a measure of size that is uncorrelated with shape for small isotropic landmark variation (Mitteroecker and Gunz, 2009).

At the time of the original analysis, no complete phylogenetic hypothesis that included all the taxa studied was available, and therefore a composite tree was constructed from several sources (Gallardo and Kirsch, 2001; Huchon and Douzery, 2001; Slamovits *et al.*, 2001; Rowe and Honeycutt, 2002; Honeycutt *et al.*, 2003; Spotorno *et al.*, 2004; Castillo *et al.*, 2005; Galewski *et al.*, 2005). Phylogenetic inertia was estimated by correlation (Mantel test) between matrices of phylogenetic and morphometric distances. Each species was assigned a locomotor habit based on information from the literature and relative involvement of the forelimb in a given mode; thus, species with no predominant locomotor mode were assigned to a generalized 'ambulatory' category. The relationship between shape changes and locomotor mode, and between the former and body size (as CS), were analyzed by means of ANOVA and post-hoc tests and multiple regressions, respectively. To account for the influence of phylogenetic structure, the data were reanalyzed using Generalized Estimating Equations (GEE), an extension of the Phylogenetic Generalized Least Squares regression model (PGLS; Martins and Hansen, 1997) that allows for the inclusion of multiple discrete or continuous variables (Paradis and Claude, 2002). These analyses were performed using various available free software packages: tps series (Rohlf, 2008), PAST 1.68 (Hammer *et al.*, 2001), and R (R Development Core Team, 2005) using the APE package (Paradis and Strimmer, 2004).

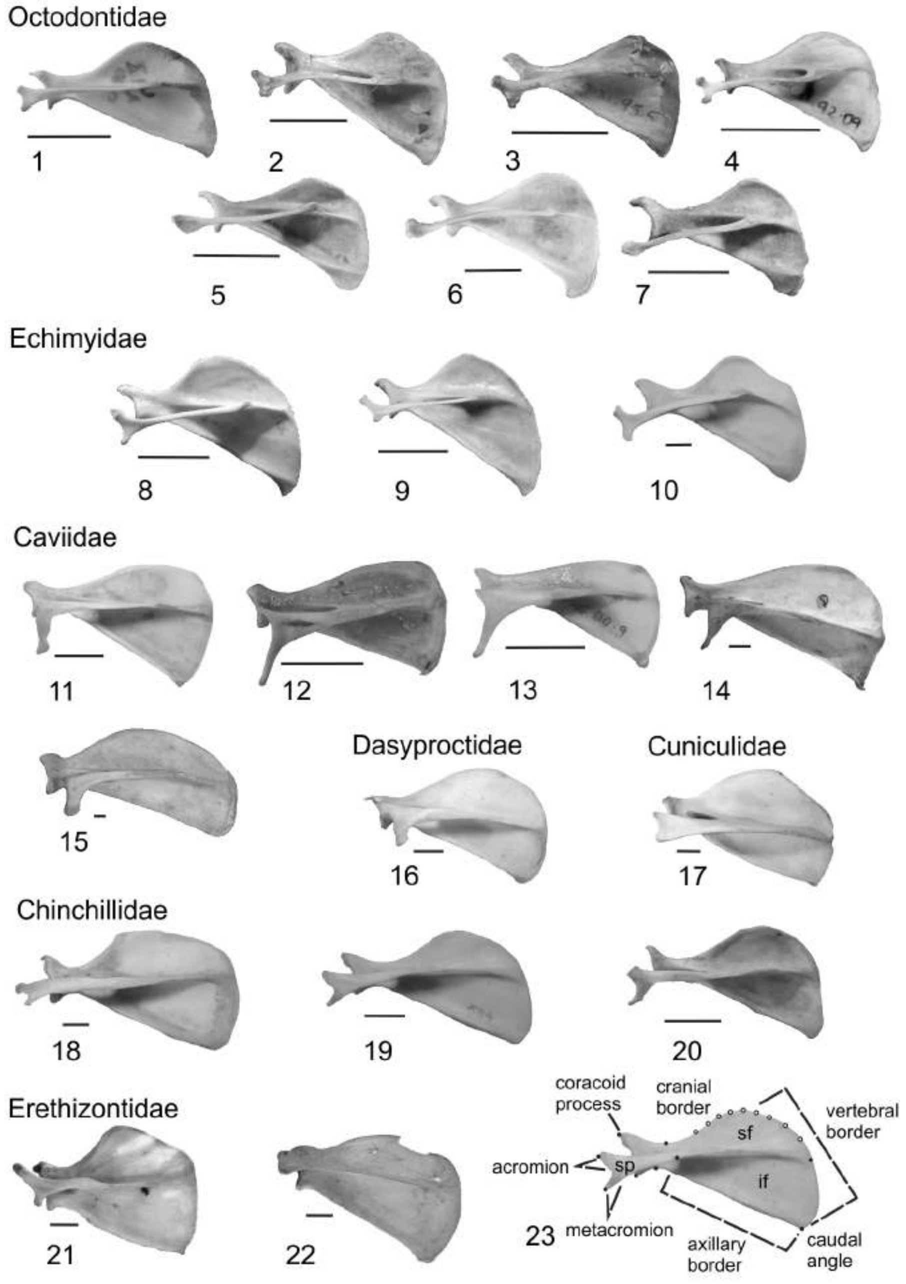

Figure 1. External view of left scapulae of Hystricomorpha included in the morphogeometric analysis. 1. *Octodontomys gliroides*; 2. *Octodon* sp.; 3. *Spalacopus cyanus*; 4. *Aconaemys* sp.; 5. *Ctenomys talarum*; 6. *C. australis*; 7. *C. rionegrensis*; 8. *Proechimys poliopus*; 9. *Thrichomys apereoides*; 10. *Myocastor coypus*; 11. *Cavia aperea*; 12. *Microcavia australis*, 13. *Galea* sp., 14. *Dolichotis patagonum*; 15. *Hydrochoerus hydrochaeris*; 16. *Dasyprocta* sp.; 17. *Cuniculus paca*; 18. *Lagostomus maximus*; 19. *Lagidium* sp.; 20. *Chinchilla* sp.; 21. *Coendou prehensilis*; 22. *Erethizon* sp.; 23. Left scapula of *Lagidium* sp. in external view showing landmarks (full circles) and semilandmarks (empty circles), and anatomical structures discussed in the text. **if**, infraspinous fossa; **sf**, supraspinous fossa; **sp**, scapular spine. Scale bar=1 cm.

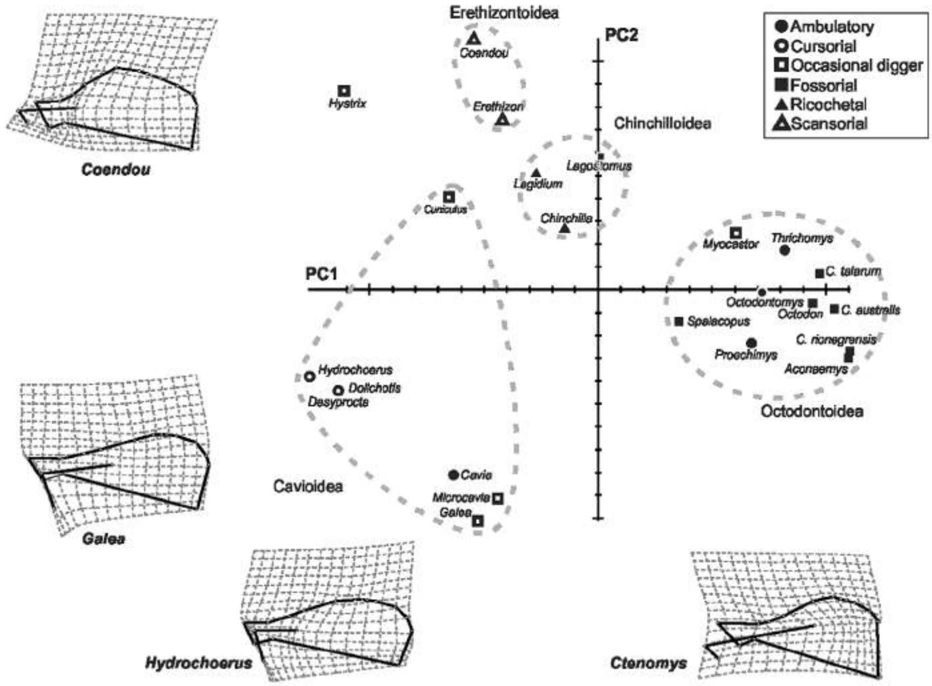

Figure 2. Principal Components Analysis of scapular shape: bivariate plot of taxon scores on first two principal components; locomotor habit for each species is indicated. Ellipses enclose all members of each superfamily. Deformation grids included for visualization of scapular shape changes. **PC1**, First Principal Component; **PC2**, Second Principal Component. Modified from Morgan (2009a).

Results and discussion. The first two principal components (PC) explained 72.14% of the observed variation. The distribution of taxa in the morphospace of these first two axes showed strong phylogenetic structure: the octodontoids occupied the extreme positive field along the PC1 axis, the chinchillids were located near the origin, while the erethizontids, cavioids, and *Hystrix cristata* had negative scores, with extreme negative values for *Dolichotis patagonum* (Patagonian cavy), *Dasyprocta* sp. (agouti) and *Hydrochoerus hydrochaeris* (capybara). The taxa belonging to different major clades were also separated along PC2: the erethizontoids and *Hystrix* had the highest positive scores, the chinchilloids and *Cuniculus paca* also presented positive scores, the octodontoids and most large-sized cavioids occupied intermediate values, and the smaller caviines presented extreme negative values. The deformation grids (Fig. 2) showed that PC1 summarized changes of the length and shape of the scapular spine (including relative development of the metacromion), extension of the coracoid process, size of the great scapular notch, and shape of the scapular blade, particularly at the cranial angle and vertebral border, while PC2 summarized mainly changes in shape of the scapular neck and the suprascapular fossa, the latter associated with the shape of the cranial border.

Thus, this analysis detected large differences in scapular shape characteristic of each of the major caviomorph lineages (Figs. 1, 2). The scapula of octodontoids is approximately triangular, with a long spine, large great scapular notch and well-developed coracoid process. In contrast, cavioids (with the exception of *C. paca*, discussed below) have a short scapular spine with well-developed metacromion. The shape of the scapular spine of chinchillids and erethizontids is intermediate between that of cavioids and octodontoids, with subequal acromion and metacromion and moderately developed great scapular notch. As noted above, the scapula of *C. paca* differs from that of other cavioids by having a relatively longer scapular spine and shorter metacromion, and is more similar to the chinchillid-erethizontid morphology (Fig. 1). The outgroup taxon, *Hystrix cristata*, was also more similar to Erethizontidae, Chinchillidae and *C. paca* in scapular shape. Certain scapular morphologies which were not found among caviomorphs, such as a scapula with both a long spine and long metacromion, may represent an incompatible combination of characters; indeed, Seckel and Janis (2008) suggested that a long scapular spine might be incompatible with a long metacromion process due to biomechanical constraints. This hypothesis should be tested by detailed biomechanical analysis applied to a wider sample of mammals, but it is noteworthy that such a morphology has not been recorded in other mammals either (Lessertisseur and Saban, 1967; Seckel and Janis, 2008).

This strong phylogenetic structure was confirmed by the high correlation between the Procrustes and phylogenetic distances (Mantel test, Pearson's $r=0.75$, $p<0.001$). In contrast, variation in centroid size (as proxy for body mass) was found to be statistically non-significant for shape changes (only 2.81% of the variation explained), both for raw and phylogenetically corrected data. In this analysis, shape changes were significantly related to locomotor mode for raw variables (ANOVA of species scores, Wilks' Lambda = 0.18, $F_{10,32}=4.40$, $p<0.001$), although the *post-hoc* pairwise analyses showed that only some locomotor modes were significantly different (see details in Morgan, 2009a). In contrast, for phylogenetically corrected data the effects of locomotor mode were non-significant.

The morphological characterization indicates that, at least at this scale of analysis, the similarities and differences in the scapular shape of caviomorphs are strongly linked to the common evolutionary history of the major lineages, as opposed to more immediate biomechanical or ecological factors. Body size showed only weak influence on scapular shape, as evidenced in the marked morphological similarity of scapular shape between closely related caviomorphs with very different body sizes (*e.g.*, *Cavia* and *Hydrochoerus*; *Ctenomys talarum* and *Myocastor coypus*). Furthermore, the multiple comparisons revealed that most of the functional categories were not associated with a distinct scapular morphology. This does not rule out the influence of adaptation, but suggests an agreement between habit and phylogeny in these rodents, similar to the high correlation found by Young (2004) between phylogenetic distance and locomotor similarity in primates. Thus, it is possible that the major features of scapular shape, and possibly the predominant locomotor modes, were established early on during the evolution of each caviomorph superfamily, and have since both facilitated and constrained the ecomorphological evolution within each lineage (Losos and Miles, 1994).

Morphofunctional interpretation. Large-scale changes of the scapular blade shape are closely related to the size and position of attached muscles, as well as the magnitude and direction of the forces they exert (Hildebrand, 1985; Szalay and Sargis, 2001; Sargis, 2002). Because a relatively long vertebral border provides ample attachment for the muscles involved in rotation and translation of the scapula (Woods, 1972; Fischer, 1994; Fischer *et al.*, 2002), and the large great scapular

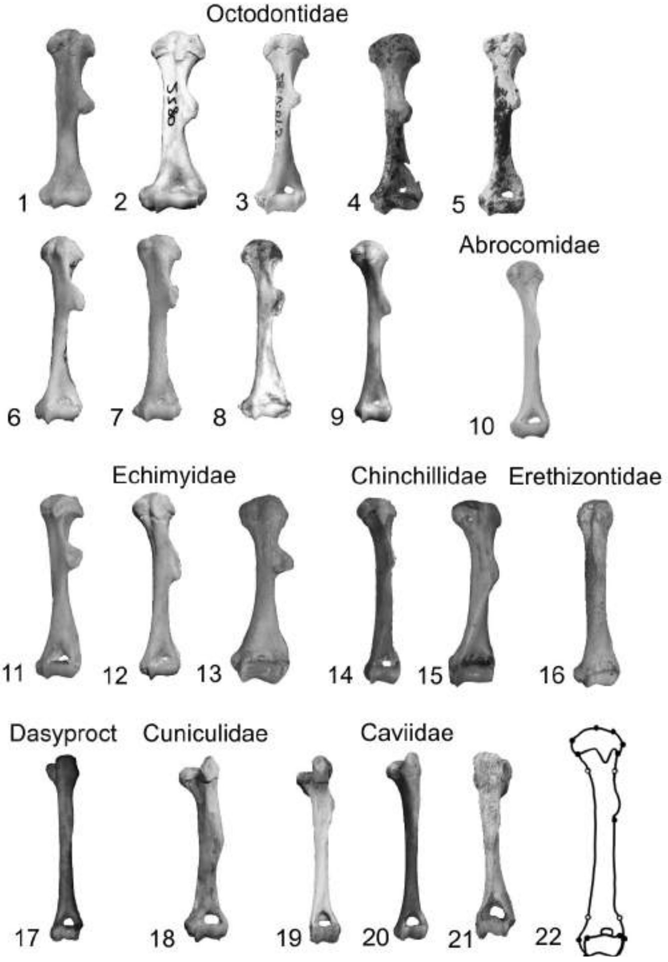

Figure 3. Anterior view of left humeri of some of the Hystricomorpha discussed in the text; only the living taxa were included in the morphogeometric analysis. 1. *Ctenomys talarum*; 2. C. *lewisi*; 3. *C. flamarioni*; 4. †*Eucelophorus* sp.; 5. †*Actenomys priscus*; 6. *Aconaemys* sp.; 7. *Octodon* sp.; 8. *Spalacopus cyanus*; 9. *Octodontomys gliroides*; 10. *Abrocoma* sp.; 11. *Clyomys laticeps*; 12. *Thrichomys apereoides*; 13. *Myocastor coypus*; 14. *Chinchilla* sp.; 15. *Lagostomus maximus*; 16. *Coendou* sp.; 17. *Dasyprocta* sp.; 18. *Cuniculus paca*; 19. *Dolichotis patagonum*; 20. *Microcavia* sp.; 21. *Hydrochoerus hydrochaeris*.; 22. Schematic drawing of left humeri showing landmarks (full circles) and semilandmarks (empty circles) used in the morphogeometric analysis. Abbreviations: Dasyproct=Dasyproctidae. Not to scale.

notch allows greater development of the shoulder stabilizer m. *infraspinatus*, the scapular shape of octodontoids might be advantageous for digging, although not a fossorial specialization. In contrast, the short vertebral border of cavioids could represent a constraint against fossorial locomotor activity, especially in the case of the cursorial cavioids whose elongate scapular blade is convergent with that of cursorial ungulates (Lessertisseur and Saban, 1967). The long scapular spine of octodontoids and the well-developed coracoid process restrict lateral movements of the humerus (Lehmann, 1963); in contrast, the relatively short spine of cavioids is associated with their reduced clavicle and greater angle of antero-posterior humeral mobility (Rocha-Barbosa *et al.*, 2002). The metacromion is relatively long in most cavioids, in contrast with other caviomorphs, and this feature, which is common to other small cursorial mammals, could be related to particular myological characters and to the evolution of cursorial, half-bounding habits (Seckel and Janis, 2008).

Forelimb: the humerus

Another major component of the forelimb skeleton, the humerus, provides much functional information. Accordingly, its morphology has been analyzed often (see Hildebrand, 1988; Polly, 2007 and literature cited therein). In particular, Elissamburu and Vizcaíno (2004) and Candela and Picasso (2008) studied the humerus of a wide caviomorph sample, while Morgan and Verzi (2006), Steiner-Souza *et al.* (2010) and Elissamburu and De Santis (2011) focused on the specialized subterranean genus *Ctenomys* and related taxa; in each case, proposing adaptive explanations for the variation found.

Materials and methods. This analysis (Morgan and Alvarez, 2013) included 28 genera in 9 families, comprising representatives of the ecological and morphological diversity of the four major caviomorph lineages (Fig. 3). Phylogenetic relationships among genera were studied through Bayesian Inference methods, using sequences from the Growth Hormone Receptor (GHR), Transtyrethin Hormone (TTH), the mitochondrial subunit 12S and cytochrome *b* (cytb).

To capture the morphological variation of the humerus, specimens were photographed in anterior view, with the plane formed by the diaphyseal axis and the transepicondylar axis (Boileau and Walch, 1999) parallel to the camera lens. Thirteen landmarks and 4 semilandmarks (Fig. 3) were digitized and then the landmark + semilandmark configurations were superimposed by Generalized Procrustes Analysis (see Box 1). As in the scapula analysis, shape variation was explored through PCA of the aligned Procrustes coordinates averaged by genus. The influence of phylogeny on shape variation was evaluated using the univariate *K* statistic (Blomberg *et al.*, 2003), and the multivariate *Tree length* test for phylogenetic signal (Laurin, 2004; Klingenberg and Gidaszewski, 2010). Possible association between humeral morphological variation and size was analyzed by ordinary least squares (OLS) regression analyses of Procrustes coordinates vs. size (log-transformed CS). The habit variable comprised four unordered habit categories, expressed as a dummy variable for the regression against the Procrustes coordinates; however, because habit categories are not exclusive and most caviomorphs are not greatly constrained to any particular locomotor mode (Elissamburu and Vizcaíno, 2004), those genera in which the relative involvement of the forelimb in running (cursorial), digging (fossorial) and/or climbing (scansorial/arboreal) activities is not predominant were classified as generalized ('ambulatory'), and the arboreal *Coendou* was pooled with the scansorial taxa.

Results. The first two PCs summarized 77.43 % of the shape variation (PC1 = 61.04%; PC2 = 16.39%). In the morphospace of these first two PCs (Fig. 4), most of the taxa were located near the origin along both axes. These taxa share a humeral morphology characterized by moderately slender diaphysis, proximal epiphysis with medium-sized tuberosities and humeral head almost level with the greater tuberosity, distal epiphysis with moderate entepicondyle development, and a deltoid process located on the proximal third of the diaphysis.

Within this central space, the scansorial echimyids *Phyllomys* and *Mesomys* were close to each other and to the cursorial cavioid *Hydrochoerus*. These scansorial forms showed more robust humeri, with the

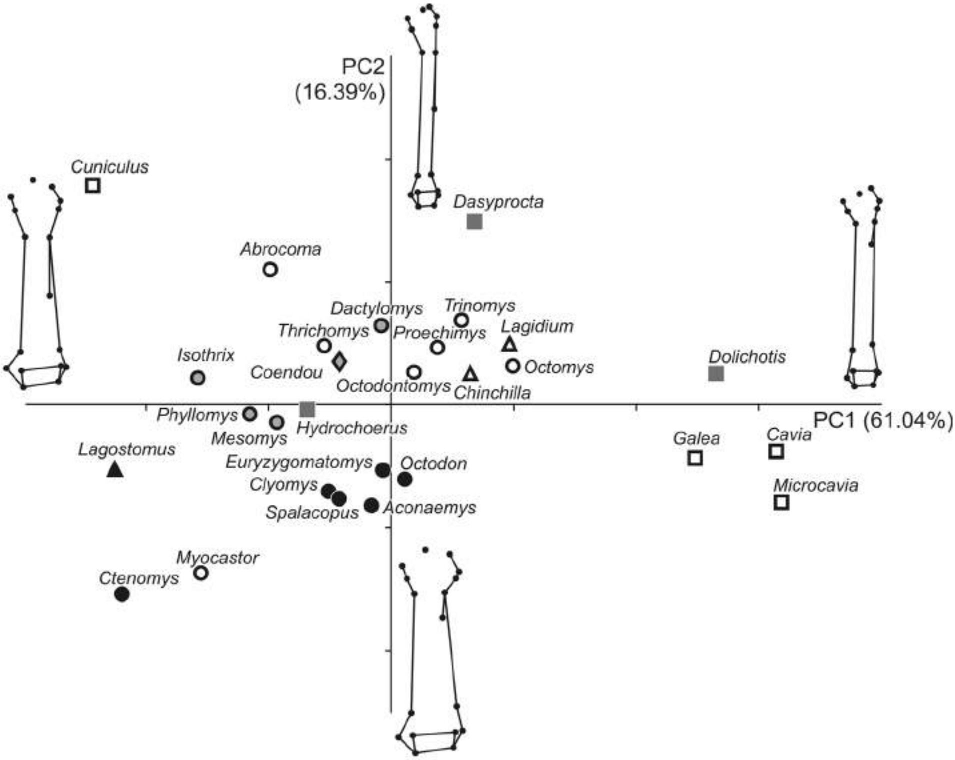

Figure 4. Principal Components Analysis of humeral shape: bivariate plot of caviomorph genera scores along the first two principal components. Deformation grids included for visualization of humeral shape changes. **PC1**, First Principal Component; **PC2**, Second Principal Component. Symbols for superfamilies: triangles, Chinchilloidea; circles, Octodontoidea; diamonds, Erethizontoidea; squares, Cavioidea. Colors indicate habit: full gray, cursorial; full black, digging; full white, ambulatory; black margin with gray fill, scansorial (including arboreal). Modified from Morgan and Álvarez (2013).

deltoid process extending more distally along the diaphysis. The fossorial octodontoids (the echimyids *Clyomys* and *Euryzygomatomys*, and the octodontids *Octodon*, *Spalacopus* and *Aconaemys*) formed a distinct group. Their humeri are more robust, with relatively broader proximal and distal epiphyses.

Along the main axis of variation (PC1), the caviids (minus *Hydrochoerus*) occupied extreme positive values, while the specialized digging ctenomyid *Ctenomys*, the fossorial chinchillid *Lagostomus* and the generalized cavioid *Cuniculus* were located at the negative end. *Ctenomys* also occupied the extreme negative values of PC2 along with the semiaquatic occasional digger *Myocastor*, while the extreme positive values along this axis corresponded to *Cuniculus* and another cavioid, the cursorial *Dasyprocta*. The humeri of the latter taxa have narrow epiphyses, a high greater tuberosity that surpasses the level of the articular head, and a relatively more proximal deltoid process.

The taxa with most negative values along PC1 have broader epiphyses, especially the entepicondyle, and a more distally extended deltoid process. These traits are associated with two distinct morphologies: one corresponds to *Ctenomys*, *Myocastor* and *Lagostomus*, with markedly more robust humeri (negative scores on PC2), and the other to *Cuniculus*, with a more slender humerus (extreme positive values on PC2).

Phylogenetic control. Given that the shape data displayed significant phylogenetic signal, subsequent analyses were made using both raw data and phylogenetic independent contrasts to account for phylogenetic structure. The regressions of shape on size were not significant for either raw values or independent contrasts; in contrast, the regression of shape on habit was significant for raw values, but not after phylogenetic control.

Morphofunctional interpretation. As in the case of the scapula, the considerable variation of humeral shape found in caviomorphs was primarily associated with their phylogenetic structure. Thus, it was possible to characterize a 'typical' humeral morphology for each lineage and identify variations of this morphology linked to adaptive differences. Octodontoids have moderately to very robust humeri with well-developed tuberosities and medial epicondyle. Among the range of morphological variation of this superfamily, the generalized taxa present a more gracile humerus with relatively less well developed processes, while the scansorial and fossorial genera show greater robusticity and better developed sites for muscle attachment, especially *Ctenomys*. The position of the deltoid process is relatively more distal in scansorial (*Mesomys*, *Phyllomys* and *Isothrix*) and fossorial taxa (*Myocastor*), and especially distal in the specialized subterranean *Ctenomys*. Greater robusticity provides resistance to the loads imposed by muscular action and substrate resistance during scratch-digging (Stein, 2000). Similarly, well-developed humeral tuberosities reflect powerful stabilizing shoulder muscles to withstand the forces applied across this joint during digging (Argot, 2001; Sargis, 2002). In any case, the humeral tuberosities of octodontoids never surpass the level of the humeral head, thus allowing a wide range of shoulder movements (Szalay and Sargis, 2001), especially in the generalized and scansorial taxa. In both digging and scansorial taxa, the expanded medial epicondyle provides a more extensive surface for carpal and digital muscles that provide more powerful flexion of the wrist and digits during scratch-digging and ensure a strong grasp during climbing (Hildebrand, 1985; Van Valkenburgh, 1987; Argot, 2001; Sargis, 2002). Similarly, the distal extension of the deltoid process observed in scansorial and some fossorial taxa enhances mechanical advantage by increasing the in-lever arm (*i.e.*, distance from muscle attachment to joint) of the deltoid and pectoral muscles that contribute to forelimb retraction (Hildebrand, 1985; Fernández *et al.*, 2000; Stein, 2000).

Among the Chinchillidae, the chinchillines *Lagidium* and *Chinchilla* have a gracile humerus, while the lagostomine *Lagostomus* is more similar to the digging octodontoids in humeral morphology. This agrees with their different habits: chinchillines use a half-bounding gait to move across rocky terrain (Lammers and German, 2002) that is not likely to exert a strong demand on the humerus, while the fossorial viscachas construct communal burrow systems presumably using their forelimbs (Fernández, 1949), and are thus under similar mechanical requirements as other scratch-diggers.

The humeral morphology of cavioids is quite distinctive, and set apart from that of other caviomorphs, as in the case of their scapula. In general, their humeri are comparatively slender, with narrow epiphyses and a strongly developed greater tuberosity that surpasses the level of the humeral head. The position of the deltoid process varies from markedly proximal in the caviine cavids (*Cavia*, *Microcavia* and *Galea*) to similar to that of most other caviomorphs in *Dasyprocta*, *Dolichotis* and *Hydrochoerus*. The peculiar cavioid *Cuniculus* is quite different from its relatives, with a more robust humerus and markedly distal deltoid process. In morphofunctional terms, the large greater tuberosity restricts the range of shoulder movements to the parasagittal plane; such restriction is characteristic of cursorial species (Argot, 2001; Sargis, 2002; Salton and Sargis, 2008). Concurrently, the proximally located deltoid process optimizes speed over force production, as expected for cursorial forms (Hildebrand, 1985; Polly, 2007). However, this structure is relatively more distal in *Hydrochoerus*; this may be related to different mechanical requirements linked to the large size of this rodent. The robust humerus of *Cuniculus*, with well-developed distal epiphysis and more distally extended deltoid process, may reflect the wide functional spectrum of this genus, which includes running, swimming and digging (Pérez, 1992). Likewise, the greater robusticity observed in *Microcavia* compared to other caviines could also be associated with its digging habit.

The arboreal erethizontid *Coendou* was close in the morphospace to the scansorial and some generalized taxa, with low tuberosities, moderately developed medial epicondyle and deltoid process on the proximal third of the diaphysis. *Coendou* is a tree-dweller, with a prehensile tail that reflects its arboreal specialization (Nowak, 1991; see also Candela and Picasso, 2008), but at least in this analysis, it did not occupy a distinct portion of the morphospace. A new analysis (currently in progress) with a larger sample of erethizontids will hopefully allow identification of morphological traits characteristic of this superfamily.

Forelimb: the antebrachium

Few studies have focused on the morphometrics of the radius and ulna, but the shape and robusticity of these bones, and their relative degree of development, are quite heterogeneous across the range of caviomorphs. This section will focus especially on octodontoids; see also Candela and Picasso (2008) for an analysis focused on erethizontoids.

Materials and methods. The sample included several species of living and extinct ctenomyines, octodontines and caviids, whose radii and ulnae were analyzed both qualitatively and quantitatively (Morgan, 2009b, unpublished thesis). On the basis of the qualitative analysis (visual inspection and comparison), linear measurements from each bone were selected and used to construct shape indices for quantitative analyses of robusticity, relative development of epiphyses and mechanical lever arms; descriptive statistics (mean and standard deviation) were calculated for all examined taxa and used for the comparisons.

Results. The radius of *Ctenomys* (Fig. 5) is a robust, curved bone, with an ovoid fovea (proximal articular surface) that is more or less symmetrical or pyriform depending on the species examined (Morgan, 2009b). The dorsoventral and lateromedial curvature of the radius also shows interspecific variation. The distal epiphysis is thicker than the diaphysis and ends in two well-developed structures: the medial styloid process and a lateral pseudostyloid process, both of which articulate with the proximal carpus. The radius of the related †*Actenomys* (not figured) is more gracile and less curved than that of *Ctenomys*, but it also has styloid and pseudostyloid processes. In contrast, octodontines and echimyids lack a pseudostyloid process; in both these clades, radial robusticity and curvature are greater in fossorial forms, but never as much as in *Ctenomys*. Caviids have a much more elongated and gracile radius; in addition, the radial fovea has a somewhat rectangular outline and its articular surface forms a veritable trochlear joint for the humerus.

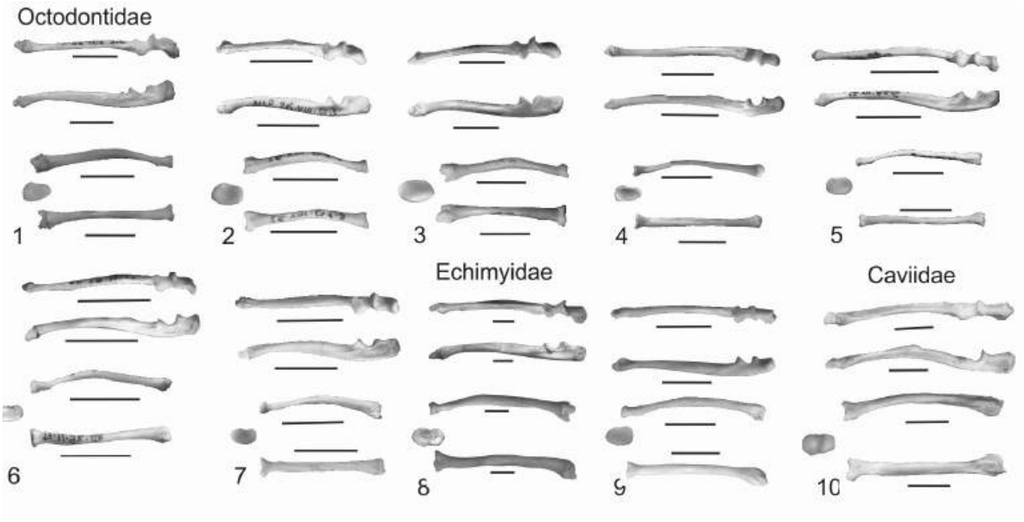

Figure 5. Right ulna (above) in anterior and medial views, and left radius (below) in medial, anterior and proximal views, of selected caviomorph taxa. 1. *Ctenomys australis*; 2. *C. talarum*; 3. *C. lewisi*; 4. *Octodontomys gliroides*; 5. *Octodon* sp.; 6. *Aconaemys* sp.; 7. *Euryzygomatomys spinosus*; 8. *Myocastor coypus*; 9. *Thrichomys apereoides*; 10. *Cavia aperea*. Scale: 1 cm. Modified from Morgan (2009a).

In particular, the contour of the radial fovea of both living and extinct caviomorphs was analyzed using geometric morphometrics, and preliminary results indicated the existence of significant phylogenetic signal (Morgan and Vieytes, 2010). Most of the variation detected was related to the relative elongation of this articular surface, as well as changes in the posterior half of its contour, at which level the curved outline ranged from smooth and symmetrical to quite irregular. Beyond the phylogenetic structure, cursorial, subterranean and occasional digging taxa presented a more irregular contour of the proximal articular surface, which could restrict antebrachial movements; in contrast, the symmetrical outline of generalized, ricochetal and fossorial taxa would allow pronation/supination. In this sense, the specialized subterranean tuco-tucos exhibited a strongly asymmetrical radial head contour, widely different from that of other octodontoids.

The ulna of *Ctenomys* is robust, laterally compressed and uniformly curved, with a well-developed olecranon that is curved medially (Fig. 5). The diaphysis is narrower distally and ends in a slightly broader segment that forms the basis of the conical styloid process. In the extinct †*Actenomys* the ulna is more gracile than in *Ctenomys* and shows only a slight lateral curvature; the olecranon is shorter and not markedly curved medially (Fernández *et al.*, 2000). Octodontines and echimyids have more gracile ulnae, except for *Spalacopus* in which it is as robust as in *Ctenomys*; in all cases the olecranon is relatively shorter. The ulna is quite different in caviids: it is moderately robust, straight, and much broader dorsoventrally than lateromedially. The olecranon is much shorter, and the distal epiphysis is blunt and almost as broad as the distal diaphysis.

Morphofunctional interpretation. The robusticity of the radius and ulna is linked to the development of strong tensional forces during digging; indeed, allometric analyses have shown that the diameter of these bones increases faster (at greater rate) in the dorsoventral than in the lateromedial dimension (Morgan, 2009b), thus resulting in reinforcement of mechanical resistance in the plane upon which the main loads are exerted. The marked curvature is directly related to the development of carpal and digital flexor muscles (pers. obs.). In contrast, these bones are elongated in cursorial forms such as the cavioids, as expected in animals whose limbs are required to produce fast but not strong movements.

An ovoid shape of the radial fovea restricts the extent of rotation at the elbow; however, although this has been mentioned as a characteristic of fossorial rodents (Stein, 2000), it cannot be considered as a specialization in the subterranean *Ctenomys* given that it is also present in other caviomorphs with different habits (Candela and Picasso, 2008). Indeed, as long as the fovea is smoothly concave and presents a convex margin, it will allow the radius to rotate on the humeral capitulum without markedly restricting its angle of rotation (MacLeod and Rose, 1993). In any case, the asymmetrical contour of this articular structure found in the subterranean *Ctenomys*, as well as the irregular outline of cursorial cavioids, would represent another morphological specialization to restrict rotation at this level (Morgan and Vieytes, 2010). The possession of a pseudostyloid process ensures stability and restriction of movements at wrist level in *Ctenomys* and its extinct relative †*Actenomys*. This feature and the styloid process typical of mammals articulate as wedges between the proximal carpal bones, thus allowing only flexion and extension of the hand and restricting other wrist movements in digging forms (Lehmann, 1963). A somewhat smaller pseudostyloid process has been described in members of the Geomyidae (*Geomys*, *Thomomys* and *Cratogeomys*) and in *Perognathus* pocket mice (Castorimorpha Heteromyidae; Hill, 1937).

Forelimb: the autopodium

The autopodial skeleton of caviomorphs has been relatively little studied, except for general descriptions of feet and digit reduction (Pocock, 1922). Forsyth Major (1899) and Ubilla and Altuna (1990) provided detailed descriptions of the hand skeleton of *Ctenomys*, and Ubilla (2008) described the manus of an extinct *Microcavia* species and compared it with living relatives. Weisbecker and Schmid (2007) included several caviomorphs in their analysis of the autopodial proportions of hystricognaths. In this context, Morgan and Verzi (2011) analyzed the morpho-structural variation of the autopodial skeleton of several octodontoid species, to assess the functional significance of the specialized traits found in octodontoids, and proposing possible evolutionary pathways for their acquisition.

Materials and methods. We examined the carpus and metacarpus of 27 species of extinct and living octodontoids, with the goal of detecting traits linked to functional requirements of scratch-digging (see Morgan and Verzi, 2011 for specimen data). When bone morphology was obscured due to the presence of tegumentary and muscular tissues, the latter were carefully removed from the specimen by placing dermestid larvae in contact with the materials for less than 24 hours, so as to ensure removal of tendon and muscle tissues but avoid disarticulation. Specimens were then observed and photographed under light binocular microscope to obtain accurate descriptions of the shape and relative size of each bone, as well as arrangement and degree of contact between them. Length and width of metacarpal bones were measured using digital calipers. Identification and nomenclature of bones followed Flower (1885) and Lessertisseur and Saban (1967).

Results. The comparative analysis showed that the carpal structure of octodontoids follows the basic structural plan described for rodents (Flower, 1885; Holliger, 1916; Lessertisseur and Saban, 1967; *contra* Prochel *et al.*, 2014). The descriptions below are focused on particular features of each taxon, especially those that had not been previously described (see Forsyth Major, 1899; Dubost, 1968; Ubilla and Altuna, 1990 for *Ctenomys*, and Reig and Quintana, 1992 for partial descriptions of †*Eucelophorus* and †*Actenomys*).

The carpus of echimyids ranges from relatively gracile in *Proechimys* and *Thrichomys*, less so in *Euryzygomatomys*, and markedly more robust in *Clyomys* (Fig. 6). The scapholunar is proximodistally short and lateromedially broad; it contacts the unciform only at its latero-distal margin. The centrale is the smallest carpal bone, about half the size of the trapezoid, and triangular in dorsal view. The magnum is rhomboidal in dorsal view; it is most elongated in *Proechimys*, less so in *Thrichomys* and *Euryzygomatomys*, and almost quadrangular in *Clyomys*. The trapezium is narrower and more elongated than the trapezoid in the four genera. The dorsal outline of the trapezoid is pentagonal in *Proechimys* and *Thrichomys*, due to the greater contact between this

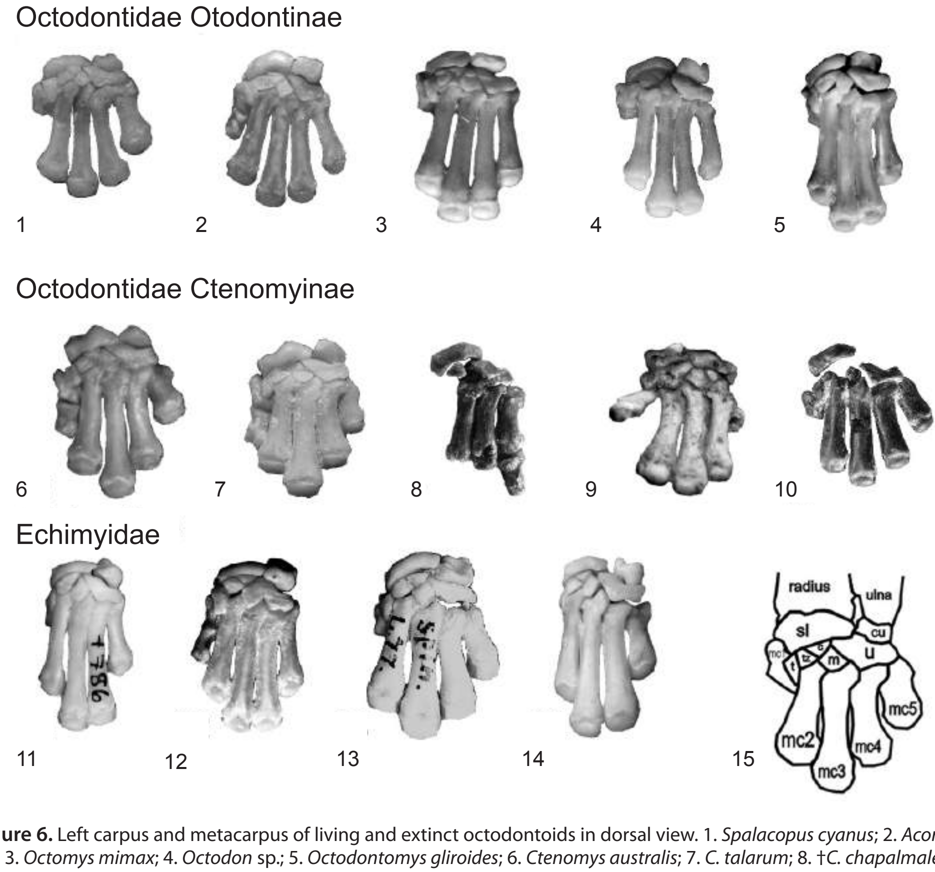

Figure 6. Left carpus and metacarpus of living and extinct octodontoids in dorsal view. 1. *Spalacopus cyanus*; 2. *Aconaemys* sp.; 3. *Octomys mimax*; 4. *Octodon* sp.; 5. *Octodontomys gliroides*; 6. *Ctenomys australis*; 7. *C. talarum*; 8. †*C. chapalmalensis*; 9. †*Actenomys priscus*; 10. †*Eucelophorus cabrerai*; 11. *Proechimys poliopus*; 12. *Thrichomys apereoides*; 13. *Clyomys laticeps*; 14. *Euryzygomatomys spinosus*; 15. Schematic representation of carpal-metacarpal skeleton. Abbreviations: **c**, centrale; **cu**, cuneiform; **m**, magnum; **mc1-5**, metacarpals 1-5; **sl**,scapholunar; **t**, trapezium; **tz**, trapezoid; **u**, unciform. Not to scale.

bone and the magnum compared with the condition in *Euryzygomatomys*, in which the outline of the trapezoid is tetragonal; *Clyomys* resembles *Euryzygomatomys* in this respect, according to available photographs. In *Euryzygomatomys*, *Thrichomys* and *Proechimys*, the prepollex is a flat ovoidal bone, often lost in skeletonized specimens, and smaller than the more cylindrical pisiform. The relative size of these elements in *Clyomys* could not be assessed.

The morphological variation among octodontids ranges from the relatively gracile carpus of *Octodontomys*, *Octodon* and *Octomys*, through the more robust structure of *Aconaemys*, to the especially broad and short carpus of *Spalacopus* (Fig. 6). The scapholunar is similar to that of echimyids in that its proximal articular surface is smoothly concave, but it is relatively thicker anteroposteriorly in *Aconaemys* and *Spalacopus*. The contact between the scapholunar and unciform is slight in *Octodon*, *Octomys*, *Octodontomys* and *Aconaemys*, and greater in *Spalacopus*. In all the octodontids examined, the centrale is about half the size of the magnum. The prepollex is similar to that of the echimyids, and only slightly smaller than the pisiform. In *Ctenomys*, the scapholunar is the largest carpal bone; its proximal articular surface is irregular, with a transverse ridge that fits between the styloid and pseudostyloid processes of the radius. The cuneiform is flat in dorsal view and bears a well-defined concavity on its proximal articular surface for the ulnar styloid process. As in the other taxa examined, the centrale is the smallest carpal bone. The unciform is smaller than the scapholunar, and the contact between these two carpals is generally greater than in the echimyids and octodontids analyzed, with some interspecific variation. The pisiform is well developed, cylindrical, broader at its base where it forms a concavity for ulnar articulation together with the cuneiform, and ending distally in a rounded, somewhat bulbous and medially hooked tip. The prepollex is paddle-shaped, with a slightly concave palmar surface, and longer than the pisiform, reaching the level of the joint between mc1 and the proximal phalanx of the first ray. Carpal morphology was very similar in the 14 living *Ctenomys* species examined, with some variation in the extent of contact between the scapholunar and unciform.

Among the extinct ctenomyid genera, the carpus is known only for †*Eucelophorus* and †*Actenomys*. A single fragmentary carpus is known from the type specimen of †*E. cabrerai* MACN 7294 (Reig and Quintana, 1992: fig. 9a). In this specimen, the proximal articular surface of the scapholunar is convex with a slight central concavity, and the extent of the contact between the scapholunar and the unciform cannot be evaluated. The carpus of †*A. priscus* could be analyzed in an exceptionally well-preserved specimen deposited in the Paleontology collection of Museo Municipal de Mar del Plata, Argentina (MMP 703-S). In dorsal view, the scapholunar is flatter than that of *Ctenomys* and it presents a simpler, slightly concave proximal surface; it contacts the unciform only at its lateral tip. The centrale is almost as large as the trapezoid. The prepollex and pisiform could not be observed because only the dorsal aspect of the hand is exposed.

With respect to the relative development of digits, the echimyids *Proechimys*, *Thrichomys* and *Euryzygomatomys* have paraxonic hands. In the first two genera, the metacarpals (mc) 3 and 4 are subequal and longest, while mc2 is shorter than mc4, and mc5 is about 2/3 of the length of mc4; in *Euryzygomatomys* mc3 is slightly longer than mc4 while mc2 is much shorter than the latter. The hand of *Clyomys* is mesaxonic. The metacarpals are gracile in *Proechimys*, *Thrichomys* and *Euryzygomatomys*, and more robust in *Clyomys*, in which the epiphyses are markedly broadened. The proximal ends of mc2 and mc3 are oriented at an obtuse angle with respect to the main metacarpal axis.

The hands of the octodontines *Octomys*, *Octodontomys* and *Octodon* are paraxonic, with mc3 and mc4 subequal and longest. The condition in *Aconaemys* is somewhat different, with mc3 slightly longer than mc4, while the latter is longer than mc2. The hand of *Spalacopus* is mesaxonic; in addition, mc5 in this genus is short and broader than the other metacarpals. The metacarpals show only slight expansion of their distal epiphyses in *Octomys*, *Octodontomys* and *Octodon*, whereas the metacarpals of *Aconaemys* and especially those of *Spalacopus* are more expanded distally. The proximal ends of the metacarpals are oriented laterally as in the Echimyidae. The hand of *Ctenomys* is mesaxonic, and mc1 and mc5 are more reduced, especially the former (Ubilla and Altuna, 1990; Reig and Quintana, 1992). These elements are relatively short and robust, with both the proximal and distal articular surfaces expanded, and the proximal ends of metacarpals 2, 3 and 4 laterally deflected and firmly wedged between the distal carpals. The morphology of mc5 is remarkable: this bone is not only shortened (as already observed by Reig and Quintana, 1992), but also noticeably more robust than the remaining metacarpals (at least 1/3 broader in dorsal view; Fig. 6). This relative robustness of mc5 is evident in all the living species examined, as well as in the extinct †*C. chapalmalensis*.

The metacarpals of †*Eucelophorus* are robust but not expanded distally; the hand is mesaxonic and the relative lengths of metacarpals are similar to those of *Ctenomys*. Its mc5 is relatively robust, but not so much as in *Ctenomys*, and it is relatively longer than in the latter genus. In †*Actenomys*, mc3 is longest and mc4 is clearly longer than mc2. Mc5 is no more robust than the remaining metacarpals. The pisiform and prepollex, located on the palmar surface, could not be examined in this specimen.

Discussion. Mapping of these morphological differences onto a composite phylogeny of octodontoids indicated that mesaxony appeared to have evolved independently in the three families studied here. At least in an incipient state, this metacarpal condition was present in both fossorial and subterranean ctenomyids. Among octodontids it was restricted to the clade formed by the fossorial *Aconaemys* and the subterranean *Spalacopus*; in both cases the predominance of ray 3 was less marked. Among echimyids, mesaxony occurred in only the fossorial *Clyomys*. Robusticity of mc3 (calculated as the width at midshaft / total length ratio) was greatest in ctenomyids and in the echimyid *Clyomys*. A broadened mc5 and greater contact between scapholunar and unciform occurred independently in some ctenomyids and the octodontid *Spalacopus*. Finally, the complex-shaped scapholunar was only present in *Ctenomys*, although this carpal bone was also relatively thick in other ctenomyids and octodontids.

These results show that, in addition to the expected morphological resemblance between closely related species at family level, more distantly related taxa with digging habits share carpal-metacarpal specializations that provide greater stability and probably ensure better distribution of forces, thus supporting the adaptive value of the latter. In this context, the unique carpal morphology of *Ctenomys* highlights the morphological specialization of this genus among the relative morphological uniformity of octodontoids.

Patterns of morphological evolution: living forms

Previous morphofunctional analyses of the postcranial skeleton of caviomorphs have shown that most taxa are not highly specialized for any single locomotor mode, but often combine two or more of them (Elissamburu and Vizcaíno, 2004; Weisbecker and Schmid, 2007); however, it is interesting to consider each of the derived morphologies characteristic of the major lineages of caviomorphs, as they could represent unique functional capabilities and constraints and thus be closely associated with the evolution of prevalent locomotor modes within each clade.

In the case of the scapula, octodontoids and most cavioids possess distinct morphologies, while in contrast, the chinchilloids, erethizontids and *C. paca* are morphologically more similar to each other (and to the African hystricognath *Hystrix*; see Morgan, 2009a). This suggests that a roughly rectangular blade, moderately-sized great scapular notch, intermediate spine length and subequally-sized acromion and metacromion could be plesiomorphic for the scapula of caviomorphs, and that octodontoids and cavioids would have acquired their characteristic morphologies early on during the evolution of each lineage.

Similarly, the association between humeral shape and both phylogeny and habit suggests an early ecomorphological diversification of caviomorphs accompanying their phylogenetic divergence. As in the case of the scapula, the major clades of caviomorphs may be distinguished by characteristic humeral features. Other mammalian groups (*e.g.*, scandentians: Sargis, 2002; carnivorans, Meloro and O´Higgins, 2011, Meloro *et al.*, 2011; platyrrhines, Perez *et al.*, 2011) exhibit comparable phylogenetic constraints on their morphological patterns. In any case, these analyses attempt to shed some light on the macroevolutionary processes linked to the morphological variation of caviomorphs. While craniomandibular shape variation has been shown to have significant phylogenetic signal and simultaneously a strong allometric component (Álvarez, 2012; Alvarez *et al.*, this volume), the variations in scapular shape agree with the phylogenetic pattern rather than with the different habits of these rodents, and humeral morphology appears to be influenced by both phylogenetic (historical) and adaptive (ecological) factors.

Although the analysis of the autopodial skeleton did not span the diversity of caviomorphs, this sample comprised the ecomorphological variation of Octodontoidea. Previous analyses of the ecomorphological evolution of this diverse superfamily (Galewski *et al.*, 2005; Vassallo and Mora, 2007; Hadler *et al.*, 2008; Lessa *et al.*, 2008; Verzi, 2008; Olivares, 2009) have suggested that fossorial habits, without marked morphological adaptations, would have been present in the ancestors of both modern octodontids and ctenomyids, and that digging specializations would have been acquired in association with increasing burrowing frequency in some lineages, derived from increased underground performance of biological functions (Vieytes *et al.*, 2007; Lessa *et al.*, 2008). Accordingly, the specialized subterranean taxa (*Ctenomys*, †*Eucelophorus* and *Spalacopus*) presented the most derived carpal and metacarpal morphology, combined with strong cranial and dental specializations for digging. The fact that metacarpal modifications especially advantageous for digging are also present in fossorial octodontoids that lack marked craniodental adaptations, such as †*Actenomys* and *Clyomys*, suggests that scratch-digging specialization preceded the acquisition of tooth-digging traits; this would be the expected evolutionary scenario according to the claim that scratch-digging is the primary digging strategy for burrowing mammals (Lessa *et al.*, 2008).

To sum up, the analyses of living caviomorphs in a phylogenetic context indicate that the influence of complex factors on different skeletal elements is disparate, and may facilitate or constrain ecomorphological evolution within each lineage (Miles and Dunham, 1993; Losos and Miles, 1994).

Patterns of morphological evolution: what the fossils tell

Concerning octodontoids, morpho-functional analyses of the postcranial skeleton have been performed for the echimyid †*Eumysops* and the ctenomyine †*Actenomys*, and preliminary analyses have been made for the octodontine †*Pithanotomys*, while the postcranium of the ctenomyine †*Eucelophorus* has also been partially described (Reig and Quintana, 1992; Morgan, 2009b). The Plio-Pleistocene †*Eumysops* is a relatively large echimyid, whose well-preserved postcranial skeleton has allowed for both qualitative and quantitative analyses (Olivares, 2009; Olivares *et al.*, 2010b) that indicate it had primarily terrestrial habits, with some specialized features that seem to be favorable for jumping, as previously suggested by Horovitz (1991) and Olivares (2009). The unique combination of skeletal specializations of this genus suggests its behavior and ecology were different from those of any living echimyid, and likely more similar to those of other open-areas caviomorphs such as caviines. †*Actenomys* is a large ctenomyine whose known postcranial skeleton indicates that it had some morphological specializations which indicate fossorial habits: the humerus bears a well-developed deltoid process, the scapula appears to have had a small *teres major* process, and the hand is relatively robust (Fernández *et al.*, 2000; Morgan and Verzi, 2006, 2011). The skeletal morphology of the Pliocene octodontine †*Pithanotomys* was preliminarily assessed by Olivares *et al.* (2010a); in this case, only the hindlimb was available for morphometric analysis. The analyses of cranial indices of this genus compared with other living and extinct octodontoids suggested fossorial habits; regarding the known postcranium, the great robusticity of the femur could be related to the large size of †*Pithanotomys* compared to other octodontids. The Plio-Pleistocene †*Eucelophorus* shows the most extreme craniodental specializations for digging and subterranean life among ctenomyines; accordingly, its known postcranium also comprises robust bones, with well-developed muscle attachment sites and stabilized joints (Fig. 3.4).

Candela and Picasso (2008) performed an in-depth morphofunctional analysis of the limb bones of two extinct erethizontids, the Miocene †*Steiromys duplicatus* and †*Neosteiromys pattoni*. Their study showed that these species had skeletal characteristics compatible with scansorial ability, including a forelimb with low humeral tuberosities, a well-developed and distally placed deltoid crest, joints capable of pronation and supination, and a well developed medial epicondyle. The morphology of the hindlimb skeleton also suggested a good ability for abduction and external rotation of the femur, similar to that of their living relatives, and for lateral and rotational movements at the hip, knee and ankle joints. Thus, Candela and Picasso (2008) concluded that †*S. duplicatus* would have been semi-arboreal, while in the case of †*Neosteiromys*, a giant form for which fewer skeletal remains are known, the evidence was less conclusive but climbing ability could not be dismissed.

In their detailed paleobiological analysis of the extinct caviomorph fauna from the Santa Cruz Formation (Miocene of Patagonia), Candela *et al.* (2012) summarized their previous studies on the dasyproctid †*Neoreomys australis* and the eocardiid †*Eocardia fissa*, in addition to the analysis of †*Steiromys*. They estimated body masses for these rodents on the basis of allometric equations from long bone diameters (Biknevicius, 1993), and performed morphofunctional analyses of postcranial features associated with different locomotor habits. Their results suggest that these species were middle- to large-sized in the context of living caviomorphs (approx. 14 kg for †*Steiromys*, ~ 3 kg for †*Eocardia* and ~ 7 kg for †*Neoreomys*; Candela *et al.*, 2012). They also confirmed the interpretation of †*S. duplicatus* as a semi-arboreal form, with some climbing ability but less skeletal specialization than in the extant arboreal *Coendou*. The postcranial skeleton of †*E. fissa* is less well known, but features of its tibia, femur and fragmentary ulna suggest it was an agile cursor, similar in habit to the living *Pediolagus* (Candela *et al.*, 2012). †*N. australis* was also cursorial, but with a relatively robust skeleton more similar to that of *Cuniculus paca* and likely with similar habits (Candela and Vizcaíno, 2007).

†*Eumysops* (Echimyidae), †*Pithanotomys* (Octodontinae) and †*Actenomys* (Ctenomyinae) are much larger than living members of their respective families (with the exception of the semiaquatic coypu *Myocastor*, in the case of echimyids), and this is a relevant characteristic that must be taken into account when analyzing putative skeletal adaptations of these taxa. They represent morphotypes that are currently absent from the octodontoid range of morphological variation and permit us a glimpse of the past diversity of the clade. Similarly, the extinct giant caviomorphs that evolved within different lineages (see Box 2) are quite different from any living forms. The fact that these extinct caviomorphs show degrees of specialization at least comparable to those of their living counterparts, and in some cases even greater morphological differentiation, agrees with the results from the comparative analyses of extant forms made in a phylogenetic context, in indicating that the differentiation of habits and morphologies occurred early in the evolution of caviomorph lineages.

The future: integrating data

In a very recent paper, Alvarez *et al.* (2013) performed a morphometric analysis of the lumbar vertebrae, pelvis and hindlimb of several mammals, including in their sample some caviomorph taxa. Using geometric morphometrics in a phylogenetic context, they explored shape differences among these mammals grouped according to gait type, estimated phylogenetic inertia for the data and analyzed the possible influence of body mass and other ecological variables on shape variation. They were able to identify morphological traits that characterize caviomorphs, including relatively rigid backs, ability for wide flexion and extension of the knee in the parasagittal plane, and a typically crouched posture of the hindlimb; these characteristics were shared with other rodents, macroscelideans and also, in part, with lagomorphs (see Alvarez *et al.*, 2013).

This type of integrated approach is quite interesting, and similar studies will no doubt contribute to the advancement of our understanding of the history of caviomorphs, as it has been the case with other rodents (for example, Neotropical sigmodontines studied by Carrizo *et al.*, 2013). The addition of more caviomorph taxa, both living and extinct whenever possible, to these analyses, will also broaden our perspective and permit testing of these and other hypotheses. At the same time, the abundance of new molecular-based phylogenetic analyses highlight the lack of basic ecological and morphological information on many taxa. For instance, characterization of a species' ecology should not only include the type of habitat occupied by it (*e.g.*,

BOX 2

The giant relatives

An intriguing element of the diversity of caviomorphs is represented by the giant extinct forms belonging to various families. Unfortunately, the postcranial skeleton is known for only few of them, such as †*Phoberomys pattersoni* (Neoepiblemidae) and †*Amblyrhiza inundata* (Heptaxodontidae), and partially at best. A detailed analysis of these forms is beyond the scope of this chapter, but current knowledge about them will be summarized briefly because of the significance of their size range in the context of the ecomorphological diversity of caviomorphs. For in-depth reports and analyses of these and other giant caviomorphs, see Biknevicius *et al*. (1993), Sanchez-Villagra *et al*. (2003), Horovitz *et al*. (2006), Blanco (2008), Millien (2008), Rinderknecht and Blanco (2008), Millien and Bovy (2010), Rinderknecht *et al*. (2011), Blanco *et al*. (2012).

The first of these giant forms to be discovered, †*A. inundata*, was collected from Quaternary cave deposits in the Lesser Antilles and described by Cope (1869), who remarked on its extremely large size. It is currently recognized as the largest island rodent, with estimates of its body mass ranging between 50 kg and 178 kg (Biknevicius *et al*., 1993). These estimates, calculated from measurements of available humeral and femoral fragments, have been questioned because of the wide discrepancy between these values. Furthermore, "small" and "large" morphotypes have been recognized, and given that †*Amblyrhiza* has not been assigned to a particular locomotor habit (either specialized or generalized), it is not at present possible to evaluate whether the different results yielded by humeral and femoral measurements could be related to functional factors (Biknevicius *et al*., 1993); unfortunately, the postcranial fragments illustrated by Cope (1869: Plates IV and V) are quite incomplete.

The title of largest fossil rodent is currently held by the Pliocene dinomyid †*Josephoartigasia monesi*, from Uruguay (Fig. 1 Box). Dinomyids are currently represented by a single species, the middle-sized (15 kg) pacarana *Dinomys branickii* (Fig. 2 Box), but their past diversity and body size range were much greater, including other giant forms such as †*Isostylomys* (Montes and Castiglioni, 1979) and the recently described †*Arazamys castiglionii* (Rinderknecht *et al*., 2011). Although the description of †*J. monesi* is very recent (Rinderknecht and Blanco, 2008), the only known specimen was discovered more than 20 years ago. It was deposited in the paleontological collection of the "Museo Nacional de Historia Natural y Antropología" in Uruguay and remained overlooked until 2006, when it was 'rediscovered' by museum staff.

Fossil dinomyids are known mostly from isolated teeth or small cranial or mandibular fragments (Mones, 1986). However, in the case of †*Josephoartigasia*, the largely complete skull has permitted estimating its body mass, from skull and dental measurements, at over 1000 kg (range 468 kg – 2,586 kg, Rinderknecht and Blanco, 2008; 630 kg-1,515 kg, Blanco *et al*., 2012), although these estimates have been contested and a body mass of as low as 350 kg was proposed (see Millien, 2008 and response in Blanco, 2008). Unfortunately, although the cranial remains are quite complete (even allowing estimation of bite forces; see Blanco *et al*., 2012), no postcranial remains of †*Josephoartigasia* have been described so far.

†*Phoberomys* is the largest genus of the extinct family Neoepiblemidae (middle Miocene to Pliocene), which also includes †*Neoepiblema* and †*Eusigmomys* (Horovitz *et al*., 2006). Most species of this genus are known only from dental remains found in Argentina, Brazil and Venezuela, but the finding of postcranial elements of †*Phoberomys* pattersoni enabled a more reliable estimate of its body mass. These estimates ranged from 436 kg to 741 kg, using humerus and femur, respectively (Sanchez-Villagra *et al*., 2003), and these authors considered that the femur-based estimate was more reliable because of the greater involvement of the hindlimbs in locomotor propulsion. More recently, Hopkins (2008) and Millien and Bovy (2010) challenged these body mass estimates; these latter authors argued that the values are probably overestimated because this giant form has markedly robust bones and thus, long bone diameters are relatively large. By their own estimates, the body mass of †*Phoberomys*, estimated from measurements of teeth, humerus and femur, may have ranged between 220 kg and 340 kg (Millien and Bovy, 2010).

The known postcranial skeleton of this species comprises the atlas, forelimb long bones, hindlimb long bones and some tarsal elements, which have been described and compared with its living close relative *Dinomys* (Sanchez-Villagra *et al*., 2003, Supplementary Online Information; Horovitz *et al*., 2006).

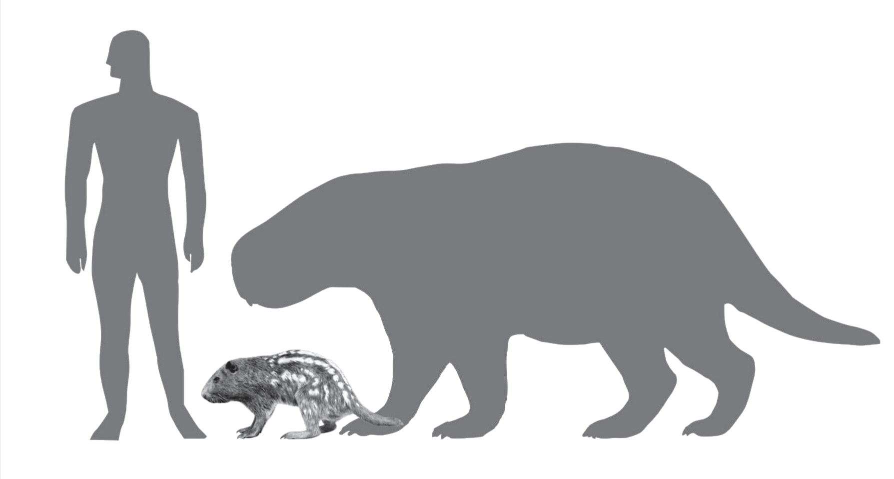

Figure 1 Box. Estimated size of †*Josephoartigasia monesi* (large grey silhouette) compared with its living relative *Dinomys branickii* (pacarana) and a human being. Modified from unpublished original by A. Rinderknecht.

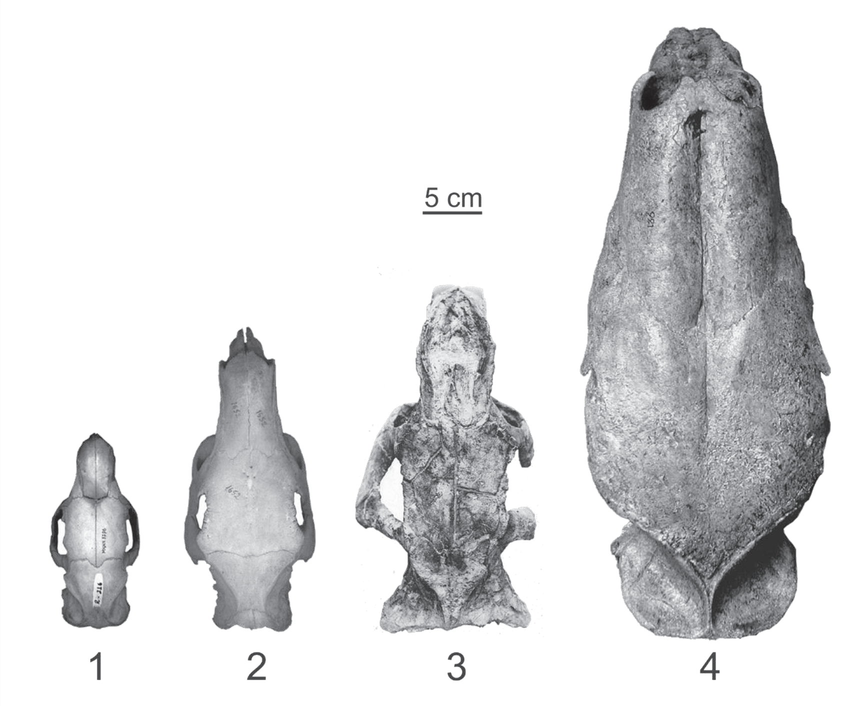

Figure 2 Box. Skulls in dorsal view of 1. *Dinomys branickii* (pacarana), 2. *Hydrochoerus hydrochaeris* (capybara), 3. †*Telicomys giganteus* MACN 8011, and 4. †*Josephoartigasia monesi* **MNHN** 921. **MACN**, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (Argentina); **MNHN**, Museo Nacional de Historia Natural y Antropología (Uruguay). Unpublished original illustration provided by A. Rinderknecht.

Paleoenvironmental reconstructions of Urumaco Formation suggest a coastal wetland according to its sedimentology, and on this basis, semiaquatic habits have been suggested for †*Phoberomys* (Horovitz *et al.*, 2006), but no morpho-functional analyses have been attempted using a wider comparative sample.

Interestingly, Geiger *et al*. (2013) studied both the morphological variation and the bone microstructure of femora from these giant forms. According to their analysis, four different morphotypes (according to relative robusticity or gracility) were distinguishable among the available materials, and this would indicate that the diversity of giant caviomorphs in northern South America was greater than previously supposed. These authors provided complementary estimates of body mass based on different methods, including femoral diameters and length, and toothrow length; their results range between 200 kg and 330 kg (using femur and toothrow lengths) and 395 kg to 488 kg (using femoral diameters). In addition, bone microstructure was similar to that of living caviomorphs, and thus did not support the semiaquatic habitats hypothesized for these taxa (Millien and Bovy, 2010).

Beyond any conflicting body mass data, it is evident that these fossil rodents were an order of magnitude larger than their living relatives, and likely affected by different biomechanical constraints and requirements, as in the case of other large mammals. This must be taken into account when undertaking any morphofunctional analysis and interpretation of those (unfortunately few) cases in which the postcranial skeleton is well known.

forest, grassland, desert, etc.), but also, and more importantly, describe its locomotor mode (*e.g.*, cursorial, saltatorial, scansorial, etc.) and distinguish that from its substrate preferences (*e.g.*, arboreal, terrestrial epigean, subterranean, aquatic, etc.). Such information is scarce for many caviomorph species, but it is fundamental in order to make sense of the patterns detected (conversely, mistaken characterizations extracted from the literature will lead to wrong conclusions) and for making paleobiological interpretations of extinct forms. This imbalance will need to be addressed by those researchers interested in the evolution of these diverse South American rodents, bearing in mind that studies based on multiple sources and approaches are able to provide insight into significant evolutionary events and patterns (*e.g.,* Verzi *et al.*, 2013).

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6 | DIVERSITY OF CRANIOMANDIBULAR MORPHOLOGY IN CAVIOMORPH RODENTS: AN OVERVIEW OF MACROEVOLUTIONARY AND FUNCTIONAL PATTERNS

DIVERSIDAD DE LA MORFOLOGÍA CRANEOMANDIBULAR EN ROEDORES CAVIOMORFOS: UNA REVISIÓN DE LOS PATRONES MACROEVOLUTIVOS Y FUNCIONALES

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[4]CONICET.

Abstract. Caviomorphs are a broadly diversified rodent clade. Accordingly, a great morphological disparity has been detected. This variation bears a clear phylogenetic signal, and a strong allometric component was also detected. Morphological variation is associated with the habitat occupied by each species, with the most divergent condition seen in species with burrowing habits. These species present a massive skull associated with strong masticatory musculature and a stabilized temporomandibular joint that allows the generation of high bite forces. These features are present in species that use incisors in digging or in aggressive encounters during courtship or territorial defense, as in the case of *Ctenomys*. Exertion of higher bite forces also influences dental morphology and enamel microstructure. Procumbent incisors, deeply implanted, with high resistance to flexion-torsion forces, are observed in species that display the aforementioned features. Features with opposite trait values are present in species that exhibit lower bite forces. With respect to the molar enamel microstructure, a generalized pattern linked to brachydont teeth can be observed; by contrast, a secondary gradual acquisition of radial enamel, strengthening the enamel band and favoring the formation of sharp edges, is related to the acquisition of hypsodonty. The strong phylogenetic signal of morphological variation observed among extant caviomorphs may be explained by an early establishment of the major pathways of craniomandibular specialization in the evolutionary history of these rodents. However, phylogenetic structure alone does not explain morphological changes. Several variables such as size, habitat, diet, habits, and diverse aspects of the life history of species, such as burrow construction and social interaction are also linked to the observed morphological variation. The integration of macroevolutionary and morpho-functional studies in future comprehensive studies that involve both approaches, together with paleoenvironmental inferences, would improve the understanding of the evolution of this exceptional group of rodents.

Resumen. La complejidad del aparato masticatorio de los roedores, vinculado no sólo a las funciones de aprehensión y masticación, sino también a diversas funciones como la excavación de túneles, hace de éste un excelente modelo para el estudio de patrones y procesos asociados a la evolución morfológica. En particular, los roedores Caviomorpha comprenden un grupo ampliamente diversificado, se distribuyen en una gran variedad de ambientes (áridos a selváticos), presentan diferentes modos de vida (epigeos a subterráneos) y estrategias locomotoras (cursoriales a arborícolas). En concordancia con la amplia variación ecológica exhibida por los caviomorfos, se ha detectado una gran disparidad morfológica. El estudio de esta variación ha sido llevado a cabo en los últimos años principalmente bajo dos enfoques, uno macroevolutivo, que observa y analiza los patrones a escala evolutiva, y otro morfo-funcional, que estudia las causas de la variación. En esta contribución se recopila e integran los principales hallazgos relacionados a la variación morfológica cráneo-mandibular y dentaria en este grupo de roedores. El resultado principal de los estudios a escala macroevolutiva involucra la detección de una clara señal filogenética en la variación morfológica, esto es, las relaciones filogenéticas entre los taxa representan una de las dimensiones a tener en cuenta para entender los patrones observados. Las técnicas de morfometría geométrica han sido de las más utilizadas en los estudios más recientes sobre la variación morfológica cráneo-mandibular. La distribución de los taxones obtenida en los morfoespacios refleja, en gran medida, las relaciones filogenéticas entre estos. Como patrón general, gran parte de los octodontoideos muestran cráneos robustos, con rostros y diastemas cortos, bullas auditivas grandes, órbitas relativamente más pequeñas. Los cavioideos y el chinchilloideo *Lagostomus* muestran características opuestas. Los chinchíllidos y el octodontoideo *Abrocoma* presentan rostros más largos y bajos y márgenes de las órbitas más amplios. En cuanto a la variación de la mandíbula, los octodontoideos son morfológicamente más dispares aunque como patrón general presentan un cuerpo mandibular más alto, proceso angular corto, procesos condilar y coronoides más altos y series dentarias más cortas. Los cavioideos y chinchillideos muestran características opuestas. Por otro lado, la variación cráneo-mandibular se asocia a los cambios de tamaño y al hábitat ocupado por las especies. Dentro del amplio espectro morfológico que exhiben los caviomorfos, la morfología más evidente y divergente (y quizás por ello, la más estudiada) es la presente en especies con hábitos excavadores, y especialmente aqué-llas con un modo de vida subterráneo. En mayor o menor medida, la mayoría de los trabajos que se han llevado a cabo bajo un enfoque morfo-funcional se han enfocado en estudiar cómo, y en qué grado, estos hábitos influencian la variación morfológica. El rasgo más conspicuo que poseen las especies cavadoras, y en particular las dento-excavadoras, es la presencia de un cráneo macizo asociado a una musculatura masticatoria bien desarrollada y una articulación cráneo-mandibular estabilizada que permiten la generación de grandes fuerzas a nivel de incisivos. Estudios recientes en morfología funcional indican que las diferencias en dichas fuerzas están asociadas en gran medida al desarrollo muscular. Se ha observado que, luego de controlar el efecto del tamaño, aquellas especies de caviomorfos que enfrentan estreses mecánicos altos a nivel de los incisivos (*e.g.*, dentoexcavación, enfrentamientos durante el cortejo o defensas territoriales, como es el caso de *Ctenomys*) presentan mayor fuerza de mordida que las especies que no presentan estos hábitos, como *Chinchilla* y *Dolichotis*. La variación morfológica vinculada a mayores fuerzas de mordida también se reconoce a nivel de la morfología dentaria y de la microestructura del esmalte. Se ha encontrado una fuerte relación entre la morfología de los incisivos y el requerimiento de fuerzas de mordida elevadas y la resistencia de éstos a altos esfuerzos de corte (consumo de alimentos duros o corte de raíces). Las especies con las características recién mencionadas, presentan incisivos procumbentes y profundamente implantados, con alta resistencia a fuerzas de flexión-torsión, mientras que incisivos procumbentes pero cortos, de implantación menos profunda, están presentes en especies que no presentan estas características. Un ejemplo extremo lo representa el ctenómido subterráneo †*Eucelophorus* (Plioceno–Pleistoceno medio de Argentina), con fuertes adaptaciones a la dentoexcavación, que presenta, entre ellas, rasgos marcados en el esmalte de sus incisivos que incrementan la resistencia a la fractura y abrasión, sugiriendo un incremento en la frecuencia de uso o la ocupación de suelos más duros. Estos caracteres son recurrentes en clados distantes de roedores dentoexcavadores. En cuanto a la morfología de los molares, ésta se asocia claramente con los modos de masticación, especialmente la disposición de las bandas de esmalte, que se disponen perpendicularmente a la dirección masticatoria. En cuanto a la microestructura del esmalte de los molares, puede observarse un patrón generalizado asociado a dientes braquiodontes, presente en taxones no estrechamente relacionados. A su vez, en distintos linajes ocurren diversas variaciones vinculadas mayormente al desarrollo homoplásico de la hipsodoncia, como la adquisición secundaria y gradual de esmalte radial en respuesta a diversos requerimientos funcionales (*e.g.*, refuerzo de la banda de esmalte que favorece la formación de bordes cortantes). El establecimiento temprano de las principales rutas de especialización cráneo-mandibular podrían explicar la fuerte señal filogenética de la variación morfológica observada en los roedores caviomorfos. Sin embargo, la estructura filogenética por sí sola no explica los cambios morfológicos. Distintas variables se han relacionado a esta variación: tamaño, hábitat, hábito, dieta y diversos aspectos de la historia de vida de cada especie, como construcción de galerías o interacción entre individuos. Varios rasgos morfológicos descriptos en este capítulo muestran una clara señal filogenética, en particular las especializaciones craneomandibulares desarrolladas por la superfamilia Octodontoidea, particularmente en ctenómidos, estrechamente asociadas a la historia paleoclimática del Cenozoico. La integración de estos dos aspectos, morfofuncional y filogenético, presentada en este capítulo y futuros estudios que incorporen inferencias paleoambientales podrían mejorar la comprensión de la evolución de este interesante grupo de roedores.

Introduction

The morphology of an organism results from the interplay of several factors, including history, function, and developmental processes. In mammals, the morphology of the masticatory apparatus has received great attention, given the key changes experienced by this complex of characters in the history of the group (Turnbull, 1970; Novacek, 1993; Feldhamer *et al.*, 1999; Hiiemae *et al.*, 2000; Ungar, 2010). Functional and phylogenetic approaches have prevailed in the study of the cranial and mandibular evolution (Turnbull, 1970; Allin, 1975; Greaves, 1982; Radinsky, 1985; Russell and Thomason, 1993; Janis, 1995; Feldhamer *et al.*, 1999; Kielan-Jaworowska *et al.,* 2004; Ungar, 2010).

The complexity of the masticatory apparatus has promoted the emergence of adaptations beyond its primary specializations related to prehension and mastication (exaptations *sensu* Gould and Vrba, 1982). In particular, the unique design of the masticatory apparatus in rodents, characterized by the complexity of its zygomasseteric structure, the presence of a diastema (*i.e.*, a large gap between the incisors and premolars), and euhypsodont incisors, has led to a separation of the functions of gnawing and chewing. This functional duality may have facilitated the acquisition of secondary functions such as chisel-tooth digging (in fossorial and subterranean species; Hildebrand, 1985; Lessa, 1990; Stein, 2000), which in turn may have led to different functional demands promoting both complex coadaptation (Hildebrand, 1985; Lessa, 1990; Stein, 2000; Olivares *et al.*, 2004; Hautier *et al.*, 2012) and functional-structural constraints (*i.e.*, interdependent evolution) among character complexes (Greaves, 1982, 1985; Verzi and Olivares, 2006; Hautier *et al.*, 2009). Therefore, the complexity presented by the masticatory apparatus, and in general the rodent skull, makes this an excellent model for the study of patterns and processes associated with morphological evolution (Duarte *et al.*, 2000; Cardini, 2003; Klingenberg *et al.*, 2003; Renaud and Michaux, 2003; Monteiro and Dos Reis, 2005; Zelditch *et al.*, 2008; Hautier *et al.*, 2009).

Caviomorphs are a highly diversified rodent clade, living in a variety of environments (from the open arid Andean-Patagonian region to the Brazilian rainforests; Hershkovitz, 1969; Nowak, 1999) and presenting very different modes of life (epigean to subterranean, diurnal to nocturnal) and locomotor strategies (cursorial to arboreal; Mares and Ojeda, 1982; Elissamburu and Vizcaíno, 2004; Hautier *et al.*, 2012). They show great variation in body size, from the tuco-tucos (*Ctenomys*) and red vizcacha rat (*Tympanoctomys*) with a body mass of only 50–80 g, to the capybara (*Hydrochoerus*) with a body mass of 50-60 kg (Mones and Ojasti, 1986; Nowak, 1999; Teta *et al.*, 2014), and even up to ~ 350–1000 kg in the extinct *Josephoartigasia* (Millien, 2008; Rinderknecht and Blanco, 2008). This rich diversity makes of these rodents a very interesting model to study macroevolutionary patterns of diversification.

A fair amount of attention has been paid to the craniomandibular morphology and of the masticatory apparatus function among caviomorphs. Earlier work goes back to the 19th century and was basically centered on the characterization of the hystricomorph and hystricognath conditions and the description of the muscular system in the head (*e.g.*, Mivart and Murie, 1866; Alston, 1876; Beddard, 1891; Parsons, 1894; Windle, 1897). More recently, several studies focused on muscular anatomy (*e.g.*, Woods, 1972; Woods and Howland, 1979; Woods and Hermanson, 1985; Cox and Jeffery, 2011; Hautier *et al.*, 2011). Hystricomorphy involves the forward spread of the anterior part of the medial masseter muscle from the inner surface of the zygomatic arch through the infraorbital foramen onto the snout; hystricognathy is a condition defined by a deflected angle of the jaw from the incisive vertical plane (Wood, 1965). Biomechanical studies are also fairly abundant in the literature. Traditional approaches have been applied to the study of the function of the masticatory apparatus, focusing mainly on the variation among variables (usually linear ones) with functional significance (*e.g.*, Landry, 1957; Wilkins and Cunningham, 1993; De Santis *et al.*, 1998; Vassallo, 1998, 2000; Vassallo and Verzi, 2001; Mora *et al.*, 2003; Olivares *et al.*, 2004; Verzi and Olivares, 2006; Lessa *et al.*, 2008). Because the anatomical bases of animal capacities are analyzed from dry skulls and mandibles, actual performances are out of the scope of study. Thus, the integrative study of both form and function, "two sides of the same coin", may offer an insight into the fine tuning in the evolutionary design of living beings (Liem *et al.*, 2001). Functional morphology (by combining *in vivo* records and anatomical measurements) is one of several disciplines that study how structures and complex functional units within organisms perform in certain conditions and how specific designs evolved from pre-existing musculoskeletal structures to highly specialized functional tools. Thus, morpho-functional approaches involving the modern techniques are currently being applied to caviomorphs (Becerra *et al.*, 2011, 2012a, 2013, 2014; see Box 1). Additionally, there is a body of recent work focusing on craniomandibular morphological variation within macroevolutionary and phylogenetic comparative frameworks (Samuels, 2009; Wilson and Sánchez-Villagra, 2010; Álvarez *et al.*, 2011a, b, 2013; Hautier *et al.*, 2012).

Consistent with the enormous ecological variation exhibited by caviomorphs, a great morphological disparity has been detected. Initially, researchers aimed at recognizing morphologies that characterize different clades (*e.g.*, superfamilies). This was evidenced in studies involving different taxonomical levels throughout the phylogeny of caviomorphs (Vassallo and Verzi, 2001; Samuels, 2009; Wilson and Sánchez-Villagra, 2010; Álvarez *et al.*, 2011a, 2013; Becerra *et al.*, 2012b; Hautier *et al.*, 2012). The results of these studies brought to light a significant phylogenetic signal in morphological variation, together with a strong relationship between this variation and variables such as size, habitat, habits, and diet. Within the broad morphological variation displayed by caviomorphs, one of the most divergent morphologies (and, maybe for this reason, most studied) is that presented by burrowing species, and especially those with a subterranean mode of life. Most of the morpho-functional studies mentioned above have at least partially focused on analyzing how, and to what extent, fossorial habits influence morphological variation.

In this chapter, we summarize the main findings from studies on craniomandibular and dental variation in caviomorph rodents. We describe the main proposed morpho-functional and macroevolutionary patterns. Finally, with the scope of available knowledge in mind, we attempt to denote steps that should be followed in order to improve our understanding of the morphological evolution of caviomorphs.

BOX 1

Morphofunctional analysis of masticatory muscles

Because muscle complexes allow an extensive modulation of external force, and slight morphometric differences may determine morphofunctional shifts (Cleuren *et al*., 1995), it is important to study the parameters of every single muscle. For this purpose, the whole mandibular adductor musculature (*i.e*., the pterygoid, temporal and masseter complex –superficial, both lateral, and both medial layers; (Figs. 3.2–4, 4) is carefully dissected, photographed, weighed and digested using HNO_3. The physiological cross-sectional area (**PCSA**) of a muscle is estimated as: PCSA = $[m * \cos(\alpha)] / (\rho * l)$, where **m** is the muscle mass (kg), α is the mean angle of pinnation, **ρ** is the density of muscle tissue, and **l** is the mean fiber length (m). Then, muscle force (*i.e*., the in-force; F_{IN}) is deduced as the product of PCSA and the maximum isometric stress of striated muscle (Alexander, 1983).

Macroevolutionary Morphological Patterns

Large-scale evolutionary morphological patterns

The factors responsible for morphological diversification at a macroevolutionary scale have been discussed recently (Schluter, 2000; Wainwright, 2007; Gavrilets and Losos, 2009; Losos and Mahler, 2010). Caviomorphs represent an excellent model to explore this issue, as they are the most ecologically diverse group of rodents, and have early divergent lineages (Antoine *et al*., 2012). In accordance with their current wide ecological diversity, great disparity has been detected in their morphology at the craniomandibular level. Although part of this disparity has been shown to be related to ecological factors at lower levels of phylogenetic divergence (Perez *et al*., 2009), morphological variation has shown a strong phylogenetic signal at higher taxonomic levels. At the same time, a strong ecological imprint on morphological variation was found (Hautier *et al*., 2012; Álvarez *et al*., 2013).

Currently, geometric morphometric techniques have become some of the most commonly used tools to study morphological variation (Álvarez *et al*., 2011a, b, 2013; Hautier *et al*., 2012). Figure 1 shows the ordination obtained in analyses of cranium and mandible shape variation in caviomorphs. The phylogenetic structure is immediately noticeable as a clear separation of major caviomorph clades can be observed (detailed analyses and interpretation of this issue

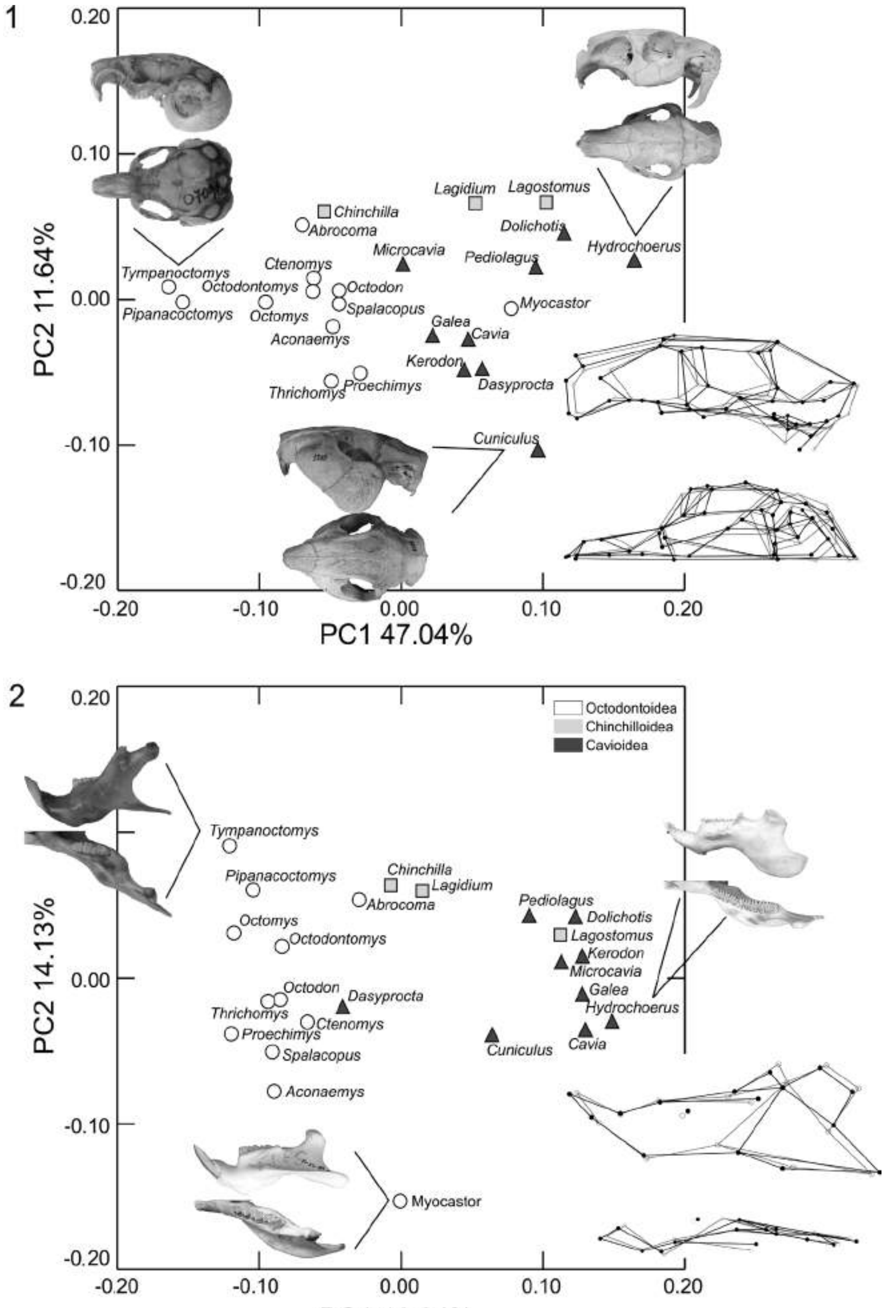

Figure 1. Ordination of the caviomorph genera in the morphospaces defined by the first two principal components (PCs) of the analyses of cranial 1. and mandibular 2. tri–dimensional shape variation. Shape changes associated with positive values of the first principal components (PCs) are shown as wireframes: black dots and lines indicate shape changes with respect to the mean configuration (grey dots and lines). Crania and mandible images are included to show part of the morphological diversity represented in the analyses. Modified from Álvarez *et al.* (2013).

are described in Hautier *et al.*, 2012 and Álvarez *et al.*, 2013). Octodontoids are positioned towards the negative side of the first axis (PC1 in Fig. 1.1). These taxa can be described as having a relatively shorter rostrum, a larger auditory bulla, and a smaller orbit. In addition, the zygomatic arch is located dorsally with respect to the upper cheek teeth, the cranial vault is lengthened antero-posteriorly, and the occipital region tends to be more vertically oriented. Cavioids and *Lagostomus* are located towards the positive side of PC1, and show the opposite morphological traits. Chinchillids and *Abrocoma* have positive values of PC2; they bear a lower and longer rostrum and a rostral masseteric fossa, a wider posterior margin of the orbit, and a shorter cranial vault that is associated with a more ventrally facing occipital region. The cavioid *Cuniculus* is positioned towards the negative side of PC2; features displayed by this genus are a lower cranium, deeper maxillary and jugal portions of the zygomatic arch generating a larger antero-ventral surface area, and a smaller auditory bulla.

Mandible shape presents a similar phylogenetic pattern of variation among caviomorphs (Fig. 1.2). Octodontoids and cavioids occupy opposite ends of the first axis (positive and negative values of PC1 in Fig. 1.2, respectively) with a few exceptions. Chinchilloids are centrally positioned on this axis, except for *Lagostomus* which falls among the cavioids. Octodontoids are morphologically more diverse, showing a greater dispersion along the second axis. As a general pattern, an octodontoid mandible is characterized by a deep corpus, a shorter angular process, higher condylar and coronoid processes, and shorter tooth rows. *Myocastor* departs from this pattern with a massive mandible with relatively low coronoid and condylar processes and a posteriorly extended angular process. By contrast, cavioids present a more restricted variation characterized mainly by features opposed to those described for octodontoids. *Dasyprocta* represents an exception to this pattern as it has a morphologymore similar to that of the octodontoids.

The size of an organism has long been considered a significant source of morphological variation through allometric changes (LaBarbera, 1989; Emerson and Bramble, 1993). Within a group displaying such a broad body size range as caviomorphs, size could be expected to be one of the most important dimensions of shape diversification. Along these lines a strong allometric pattern in the craniomandibular shape variation has been detected (Hautier *et al.*, 2012; Álvarez *et al.*, 2013). This becomes obvious for the cranium (Fig. 1.1), where the larger cavioids, *Myocastor* and *Lagostomus* are located on one extreme and most of the small octodontoids occupy the opposite extreme of the axis of shape variation. Species with larger skulls present a more elongated rostrum and rostral masseteric fossa, reduced auditory bulla, a deeper zygomatic arch, and a relatively shorter vault. Regarding the allometric patterns in the mandible, two groups can be clearly differentiated: octodontoids show no obvious relationship between mandible shape and size, whereas cavioids and chinchilloids do. In the latter clades, larger mandibles tend to have a larger diastema, angular processes that are posteriorly extended and dorsoventrally developed. In addition, the coronoid processes are shorter and the tooth rows are larger. Part of this shape divergence in caviomorphs appears to have taken place at the same time as the phylogenetic divergence in size (Álvarez, 2012). This correspondence between size and phylogeny is evidenced by the distribution of size among clades: the largest extant rodents, the capybara *Hydrochoerus* and the paca *Cuniculus*, belong to Cavioidea, while all South American Octodontoidea are medium- to small-sized caviomorphs, with the exception of *Myocastor*. The Chinchilloidea include medium to large-sized representatives.

However, phylogeny and size do not explain all the shape variation we see; ecological attributes can also be regarded as potential explanatory variables (Hautier *et al.*, 2012; Álvarez *et al.*, 2013). Among these, habitat adaptation is worth noting. Shape differences such as the size of the auditory bullae (and associated development of basicranium) and the position of the orbits, are assumed to be related to differences in habitat usage (open environments *vs.* forested habitats; Hautier *et al.*, 2012; Álvarez *et al.*, 2013). Caviomorphs (or even rodents broadly) adapted to semiarid and arid environments have enlarged auditory bullae (Braun and Mares, 1996; Cortés *et al.*, 2003; Gallardo *et al.*, 2009; Traba *et al.*, 2010). Bullar hypertrophy is especially marked in the desert-adaptated octodontids *Tympanoctomys* and *Pipanacoctomys* (Ojeda *et al.*, 1999; Mares *et al.*, 2000; Verzi, 2001). The adaptive hypothesis of increasing sensitivity to low-frequency sounds as a strategy to detect predators in open environments is the most accepted, but remains controversial (Lay, 1993). On the other hand, greater bullar size in *Ctenomys* may reflect good low-frequency audition and could be an adaptation for subterranean vocal communication (Schleich and Vassallo, 2003). Hautier *et al.* (2012) highlighted the position and convergence of the orbits as key features to understand the cranial evolution of rodents. It has been thought that changes in these traits would promote changes in the arrangement of masticatory muscles and associated cranial and mandibular morphology (Hautier *et al.*, 2012). On the other hand, there is no noticeable pattern when interpreting changes in the mandible associated with habitat variation. However, even if complex, the interpretation of the patterns of morphological variation becomes clearer when other factors, such as diet, are also taken into account. Thus, the preference for and capabilities to obtain certain food items are strongly related to the habitat where species live. Those species that inhabit open environments usually have a grass-based diet which is related to morphologies modified to easily crop and process these dietary items (*e.g.*, longer diastema, enlarged temporal fossae, shallow mandible with enlarged angular process, euhypsodonty and associated modifications of enamel microstructure; Satoh, 1997; Verzi *et al.*, 2004; Hautier *et al.*, 2012; see below). By contrast, hard-fruit eaters (such as *Cuniculus* and *Dasyprocta*) show skulls with a relatively narrow zygomatic arch and cranial vault, and a moderately developed nuchal region and basicranium (see also Samuels, 2009). This is accompanied by mandibles with shorter diastemata and poorly developed angular processes (Fig. 1.2).

Although studies at macroevolutionary scales did not show a clear influence of modes of life (*i.e.*, epigean, semi-fossorial to subterranean) on cranial morphology (Álvarez *et al.*, 2011a, 2013; but see Hautier *et al.*, 2012), several craniomandibular morphological traits are traditionally associated with habit variation. This issue represents one of the main hypotheses of the bulk of morpho-functional studies carried out on the masticatory apparatus of caviomorph rodents. The next sections of this chapter deal with these kinds of studies.

Functional morphology of the masticatory apparatus

Because caviomorph rodents have evolved divergent habitat adaptations (*e.g.*, from Andean-Patagonian aridity to Amazonian wetness), social behaviors (*e.g.*, solitary to colonial) and habits (*e.g.*, subterranean to arboreal), most of the species have developed morphological adaptations to confront different ecological requirements. In particular, fossorial, semi-fossorial

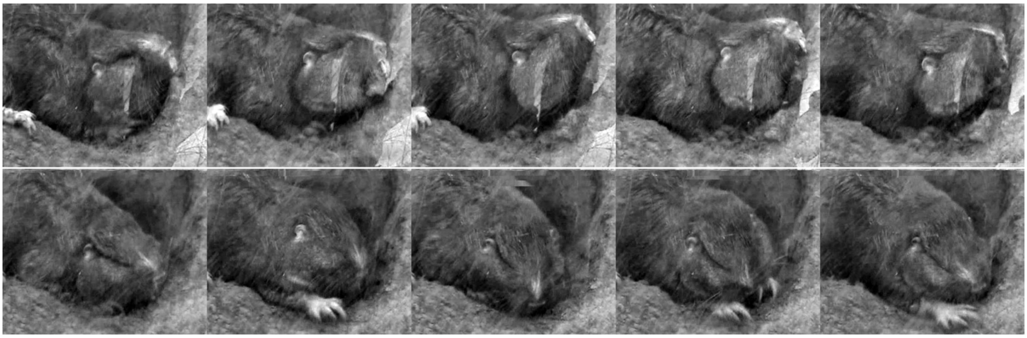

Figure 2. Burrow digging in *Ctenomys tuconax*. Above, pictures illustrate the use of incisors (chisel-tooth digging) for breaking rocks, fibrous roots or hard obstacles; below, pictures show the use of rapid alternating fore-claw movements (scratch-digging) to remove the loosened soil and rock fragments .

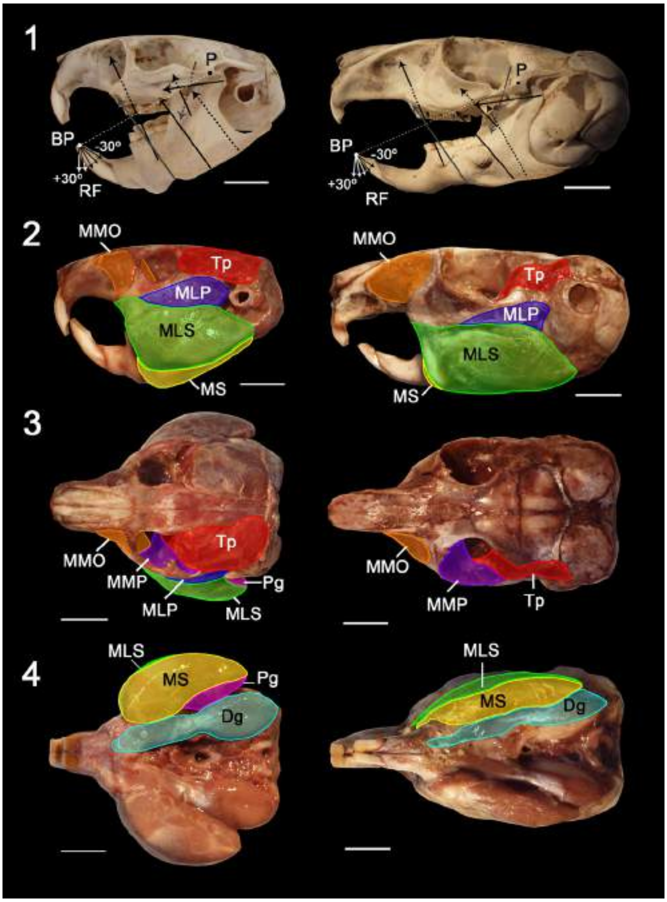

Figure 3. Skull and jaw of a tuco-tuco (*Ctenomys*; left) and chinchilla (*Chinchilla*; right) with 1. the biomechanical model used for bite force estimation at incisor tip, and the action lines of jaw adductor muscles, and 2. lateral, 3. dorsal, and 4. ventral views of those muscles. Model: **P**, pivot (mandibular joint); **BP**, bite point; **RF**, food/soil reaction force. Muscles: **MS**, superficial masseter; **MLS**, lateral masseter-superficial part; **MLP**, lateral masseter-posterior part; **MMO,** medial masseter–anterior part; **MMP**, medial masseter-posterior part; **Tp**, temporal; **Pg**, pterygoideus; **Dg**, digastricus (jaw abductor). Scale bar: 1 cm. Modified from Becerra *et al*. (2013) .

BOX 2

Estimation of the bite force

In a static biting model, the in- and out- moment (*i.e.*, the mechanical relationship of the forces and their associated lever arms) should be equal, *i.e.*, the sum of muscles' moments across the temporo-mandibular joint (**TMJ**) equals the food or soil reaction force moment. Thus, $F_{OUT} * L_{OUT} = \Sigma (F_{IN} * L_{IN})$, where F_{OUT} is the bite force, F_{IN} is the muscle force, and L_{IN} and L_{OUT} are the in- and out- lever arms to the TMJ of muscles and bite point, respectively (Hildebrand and Goslow, 2001). Muscles' action lines are considered to pass through the centroid of muscles' origin and insertion but, in the case of meandering muscles, only the section involved in the movement should be considered. Due to the bilateral condition of musculature, the effective force does not include the medio–lateral component. Estimations are considered at a similar gape angle to that used in the bite force measurements (~10º)

In vivo bite force measurement

Individual bite forces are registered by means of bite plates connected to a strain gauge load cell force transducer, during trials in which animals defensively bite the plates at a similar gape angle (~10º). Each session consists of trials that include several bites, until animals refuse to approach the plates. Then, experimental values are saved on a computer, and the strongest record is assumed to be the maximal bite performance of each individual (Becerra *et al.*, 2011, 2012a, 2013).

and subterranean species have been described as having compact bodies, short and powerful limbs, and a reinforced and massive skull to enhance their underground performance (Nevo, 1995; Vassallo, 1998; Hildebrand and Goslow, 2001; Lessa *et al.*, 2008). Some species even use their incisors like digging tools (chisel-tooth digging; Fig. 2) displaying high biting forces, which relate to the muscle force (F_{IN}) and the in- and out-lever arm ratio (L_{IN}/L_{OUT} or mechanical advantage). Previous studies by Lessa, Verzi, Vassallo and collaborators, have suggested that higher biting forces might be achieved by enlarging the jaw adductor muscles (larger F_{IN}), moving the muscle line of action farther from the jaw condyle (longer L_{IN}), reducing the distance between the bite point and the condyle (shorter L_{OUT}), or a combination thereof (Box 2). In particular, hystricomorph rodents are characterized by a forwardly-displaced origin, through the infraorbital foramen, of the anterior part of the medial masseter muscle, which increases the in-lever arm and the bite force (Fig. 3.1; Cox *et al.*, 2013; and references therein). Concurrently, this displacement also enhances fine control at the incisors and the horizontal component of the pressure exerted at the molars, *e.g.*, for the processing of food, without substantially affecting cranial deformation (Cox *et al.*, 2013). On the other hand, the shortening of the skull should affect the performance during biting events, as it was also described for other mammalian taxa (see for example, Van Valkenburgh and Ruff, 1987; Christiansen and Adolfssen, 2005; Wroe *et al.*, 2005; Nogueira *et al.*, 2009; Slater *et al.*, 2009; Santana *et al.*, 2010). Nonetheless, it appears that, in caviomorph rodents of equivalent body size, an ecological diversification involving substantially different mechanical demands (*e.g.*, ground-dwelling *vs.* subterranean –chisel-tooth digging– lifestyles) has not modified the lever arm relationships (Fig. 4.1; Becerra *et al.*, 2014). In other words, shorter skulls would also imply that the adductor muscles are shifted closer to the temporo-mandibular joint (TMJ), resulting in a relatively constant ratio of the incisors-to-TMJ and muscles-to-TMJ distances. Hence, rather than affecting muscle lever arms, skeletal

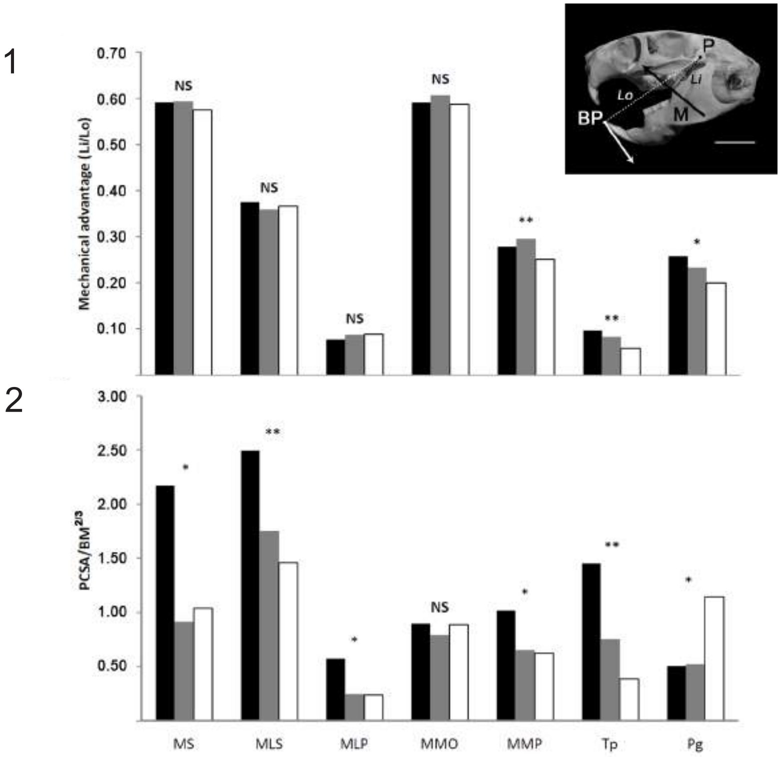

Figure 4. Bar-plots of 1. mechanical advantage and 2. physiological cross-sectional area (**PCSA**) standardized by body mass (**BM**) of all adductor muscles, comparing three caviomorph rodents with different ecologies but similar body size. Black bars, *Ctenomys* (solitary, subterranean); gray bars, *Octodon* (social, fossorial); white bars, *Chinchilla* (colonial, ground-dweller). **NS**, non–significant differences; *, p-value < 0.05; **, p-value < 0.01. **BP**, bite point; **P**, pivot; **M**, muscle force; **Li** and **Lo**, in– and out–lever arms (black and white dashed lines, respectively). References for muscles and detailed muscle lines of action in Fig. 3. Modified from Becerra *et al*. (2014).

differences such as the lateral expansion of the mandible mainly offer a larger insertion site for a stronger adductor musculature, the main cause of a higher bite force (high PCSA values; Fig. 4.2). This fact can be observed, for example, in the subterranean genus *Ctenomys* which presents strikingly hypertrophied superficial and lateral masseter muscles (responsible for about 60% of the total bite force), inserted on a laterally expanded angular process (Fig. 3.3-4; Becerra *et al*., 2014).

According to Schmidt-Nielsen (1991), because bite force is proportional to the physiological cross-sectional area of the muscle, it should scale to body mass to the power of 0.667. Nevertheless, previous analyses on mammalian taxa have established that bite force scales to body size with negative allometry (with a coefficient of 0.558; Van Daele *et al*., 2009; Becerra *et al*., 2011, 2013; Box 2), which means that smaller animals bite relatively harder than expected, and/or larger animals bite relatively less hard than expected. Within caviomorph rodents, it was found that, after controlling for the effect of body size, those species which face high mechanical stresses [*e.g.*, chisel-tooth digging and aggressive encounters during courtship or territorial defense as *Ctenomys*, or hard alimentary items in *Myocastor* (Parry, 1939; Mares and Ojeda, 1982)], are relatively much stronger biters than their counterparts, such as ground-dwellers and colonial animals (*e.g.*, *Chinchilla* and *Dolichotis*; Fig. 5). Previous studies on non-caviomorph subterranean rodents also recorded much higher bite forces than expected for their body sizes (Freeman and Lemen, 2008; Van Daele *et al.*, 2009; see *Fukomys* and *Geomys* in Fig. 5). In particular, in the semi-fossorial *Octodon degus*, a social species which constructs its burrows primarily by scratch-digging, it was observed that biting performance achieves values very close to those expected by body size. Previous studies on bite force in caviomorph rodents have shown that no matter if males are larger or smaller than females, males bite harder (Becerra *et al.*, 2011). Furthermore, in solitary and territorial species of the subterranean *Ctenomys*, the observed sexual dimorphism in bite force has been linked to particular behaviors such as high inter-male aggression during the establishment of hierarchical relationships in the context of a polygynous mating system (*i.e.*, sexual selection; Zenuto *et al.*, 1999; Becerra *et al.*, 2012a).

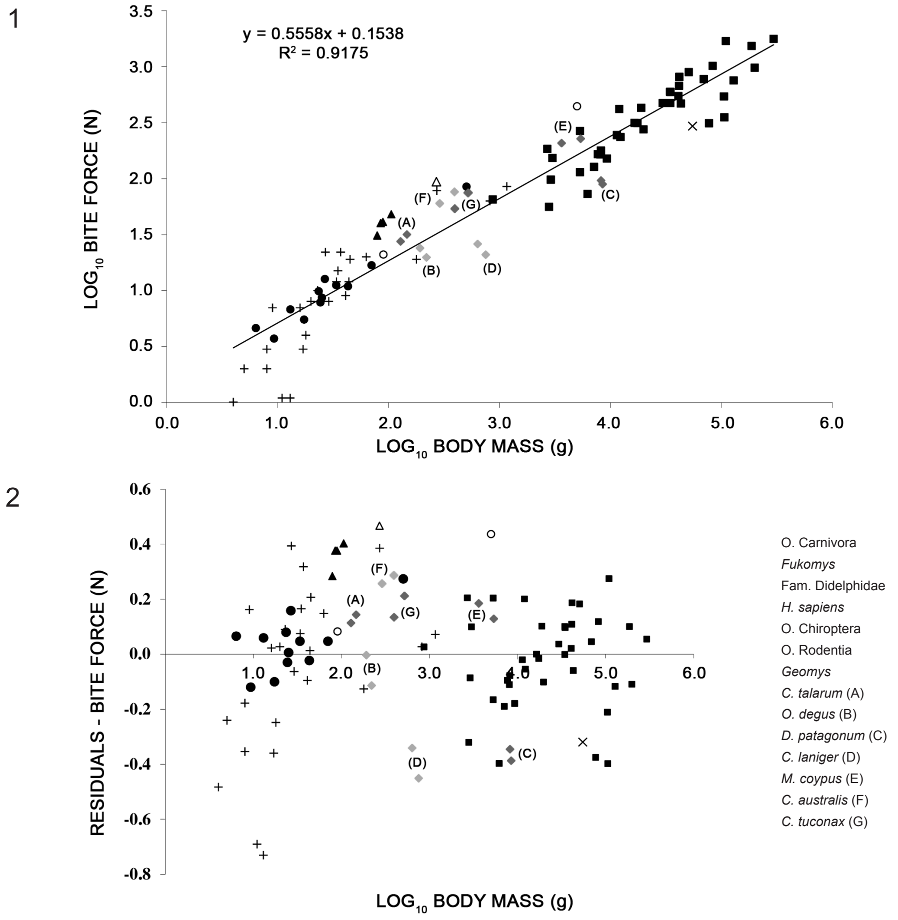

Figure 5. 1. Regression and 2. residuals of the bite force *vs.* body mass, corresponding to several mammalian taxa. Grayscale diamonds represent different caviomorph species. Modified from Becerra *et al*. (2014).

The theoretical bite forces based on anatomical (musculoskeletal) features were higher than forces recorded *in vivo* at the tip of the incisors. However, the magnitude of that difference might be behaviorally-biased, according to the natural aggressiveness of each species (*e.g.*, solitary species of *Ctenomys*, the social *Octodon* and the colonial *Chinchilla* bite at 83.80%, 55.20% and 35.19% of the theoretical force, respectively; Becerra *et al.*, 2014). The high theoretical values might be explained by the assumption of the model that all muscles are fully contracted at the same time and due to the absence of inertial forces of the structure. On the other hand, the calculation of bite forces at different angles might reflect the actual performance of the animal due to the broadly and unpredictable orientation of the reaction force depending on the texture of the soil or food item (for example, until ±30° away from the incisors' tip-to-TMJ lever arm or from the orthogonal angle to the molar grinding surface; see Fig. 3.1). However, it has been found that the variation of the estimated bite force at the tip of the incisors does not statistically differ at different angles of reaction force, but this changes if one focuses on the molars (*e.g.*, harder bites would be obtained at backward molar occlusion; Becerra *et al.*, 2013).

Increased bite forces in burrowing species are expected to impact the morphology of the temporomandibular joint (TMJ). The TMJ receives higher loads in generating a reaction force both to the contraction of jaw muscles (Herring, 2003; Greaves, 2012) and to the postero-dorsal forces transmitted to the condyle through the lower incisor. Thus, stabilization of the TMJ is a prerequisite for tooth digging. In tooth-digging caviomorphs the acquisition of a postglenoid fossa for hosting the condyle fulfils this requirement. This fossa is particularly marked in the ctenomyids *Ctenomys* and †*Eucelophorus* (from the Plio-Pleistocene of Argentina), the latter being the South American rodent with the most remarkable craniodental adaptations to a subterranean life (Reig and Quintana, 1992; Verzi, 2002; Verzi and Olivares, 2006; Lessa *et al.*, 2008). This fossa is formed by a laterally expanded

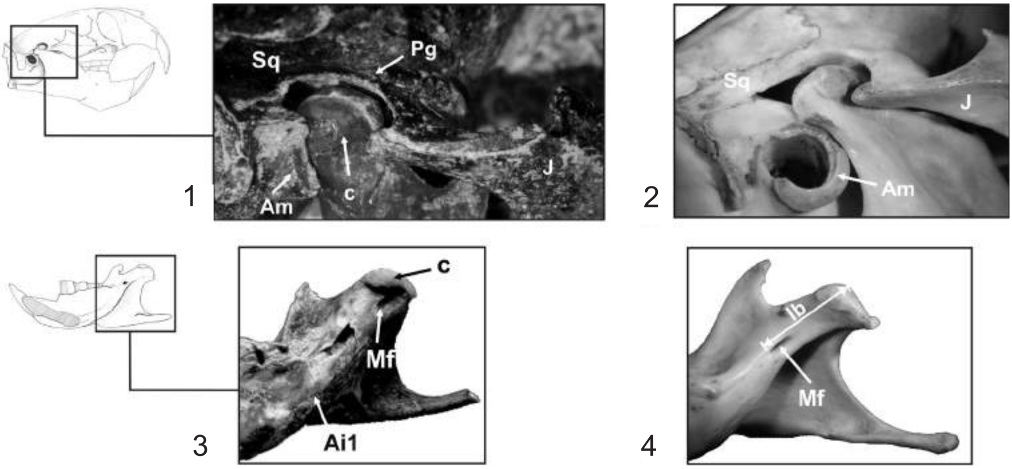

Figure 6. 1. Detail of the jaw joint in the extinct †*Eucelophorus chapalmalensis* (cranium and mandible correspond to different specimens with equal length of the molar series) and 2. *Ctenomys fulvus*. 3. Detail of the internal view of the right hemimandible of †*Eucelophorus* and 4. *Ctenomys fulvus* . **Ai1**, alveoli of lower incisors; **Am**, external auditory meatus; **c**, condyle; **Ib**, Insertion depth of the lower incisor (as indicated by length between the anterior margin of the mandibular foramen, which accompanies the base of the incisor, and the dorsum of the condyle); **j**, jugal; **Mf**, mandibular foramen; **Pg**, postglenoid fossa; **Sq**, squamosal's posterior apophysis. Not to scale.

posterior apophysis of the squamosal bone and the protruding auditory meatus (Fig. 6.1 *vs*. Fig. 6.2; Verzi and Olivares, 2006). The presence of a postglenoid articular region implies a new position of the mandible when digging, different from those involved in gnawing (when incisors are in occlusion) and chewing (when molars are in occlusion). This third position allows for the TMJ to be stabilized when the incisors attack the soil or an obstacle (such as roots), preventing dislocation. Interestingly, burrowing representatives of Castorimorpha (Geomyidae) and Myomorpha (Muridae, Rhizomyinae, Spalacinae and Myospalacinae) have non-homologous, and even more specialized, postglenoid cavities (Hafner *et al*., 2004: fig. 6; Neveu and Gasc, 1999; Samuels and Van Valkenburgh, 2009), showing the common need to stabilize the mandibular joint when strong forces are exerted at the level of the incisors (Verzi and Olivares, 2006).

At least in caviomorphs, the proposed mandibular function imposes a mechanical constraint on size and shape of the auditory bullae because inflated bullae preclude a satisfactory opening of the mandible when the condyle articulates in the postglenoid region. In a general context, this constraint would explain the peculiar pear-shaped gross morphology of the bullae of †*Eucelophorus* and *Ctenomys* (Verzi and Olivares, 2006).

Functional morphology of the teeth

Biomechanics of the incisors

Caviomorph rodents have evolved one of the most specialized and differentiated masticatory apparatus, and they display a great diversity at the rostral region. Not only their behavioral characteristics, but also their diet and their environmental conditions (*e.g*., food hardness and aridity) have shaped incisor morphology.

A recent study on several caviomorph species, belonging to seven different families, has focused on the resistance of incisors to bending and/or shearing stresses exerted on their tips by means of the calculation of their cross sectional area, and second and polar moments of inertia (Becerra *et al*., 2012b). These last two geometric parameters, which can be measured from photos of the cross sectional area, are proportional to the bending and torsional strength of a structure, respectively, helping one to understand the robustness of teeth. In this study, a strong relationship between the morphology of incisors and digging behavior, and/or food cutting efforts was observed (Fig. 7). Moreover, those species with the most resistant incisors also possess the most massive adductor musculature, and are the strongest biters. Animals with highly fossorial and subterranean behaviors, especially chisel-tooth diggers, and/or hard food consumers, share more robust and tougher incisors (Fig. 7). Procumbency, *i.e.*, the forward orientation of the incisors, not only seems to be related to digging behavior, as it was observed by Lessa *et al.* (2008) in several living and extinct octodontoid diggers, but also to social interaction (*e.g.*, aggressive agonistic encounters) since more proodont animals have a better angle for attacking both soil and opponents (Fig. 8; Becerra *et al*., 2011, 2012b; but see Verzi and Olivares, 2006). Intraspecific analyses on the Los Talas' tuco-tuco (*C. talarum*) showed dramatic dimorphism in the second moment of inertia of incisors, which was higher in males. This difference may be explained by the great bending stress suffered during agonistic struggling when their incisors are locked (Becerra *et al*., 2012a).

Another dental specialization that is present in fossorial to subterranean caviomorphs such as †*Eucelophorus*, the tooth diggers *Ctenomys* and *Spalacopus,* and the fossorial echimyids *Clyomys* and *Carterodon*, involves a very long root for the lower incisors - their bases reach the condyle or the vi-

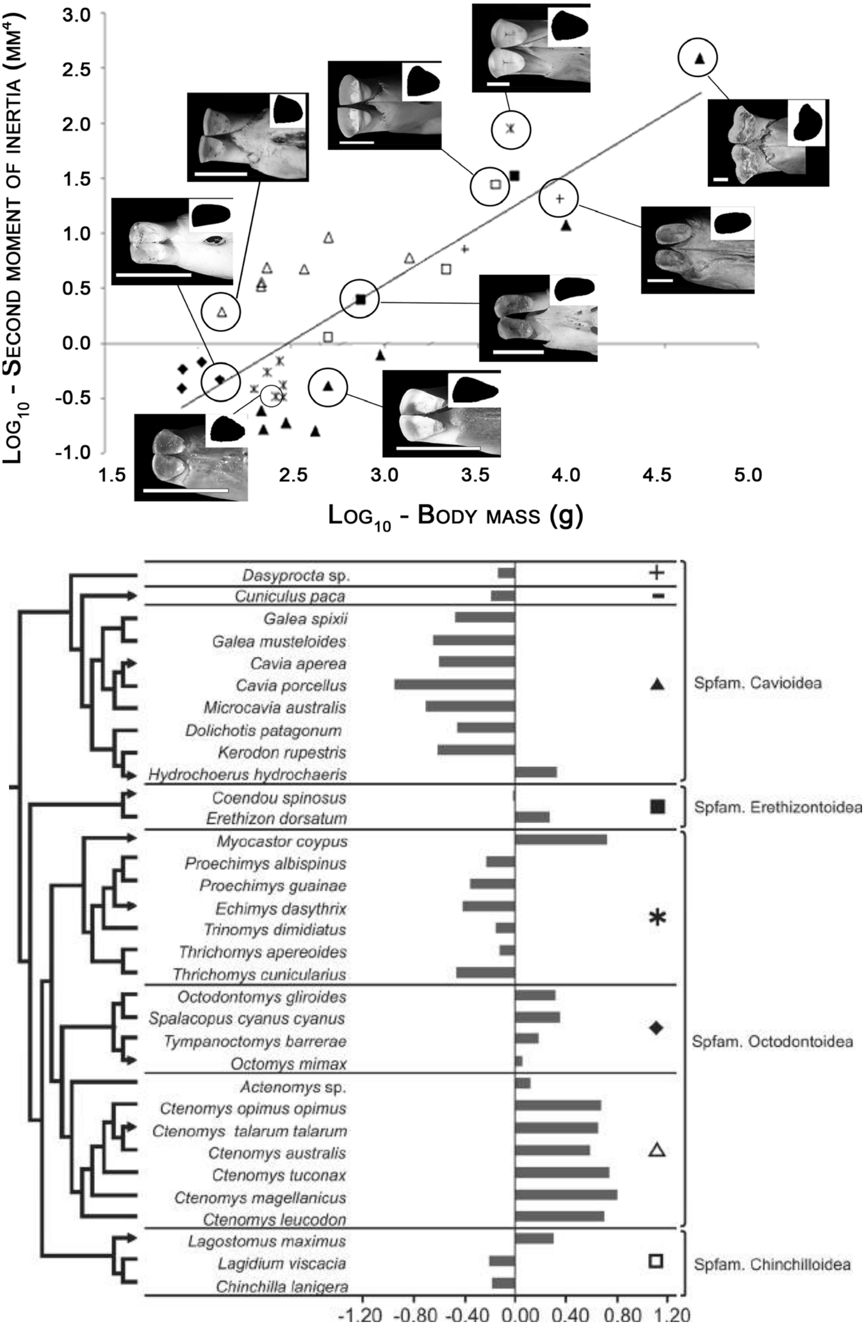

Figure 7. 1. Regression of the second moment of inertia of the upper incisors *vs*. body mass in caviomorph rodents, with a representation of the upper incisor diversity and detailed shape of left tooth cross-sectional area; and 2. residual values organized by their phylogenetic position. Highlighted species 2. correspond to detailed observation on the incisors 1. Note, for example, the more robust incisors (*i.e.*, more resistant to bending stress) of the subterranean/burrowers *Ctenomys*, *Lagostomus* and *Myocastor*; compared to the more slender ones of the arboreal/ground–dwellers *Coendou*, *Cuniculus*, *Echimys* and *Cavia*. Open squares, Chinchillidae; open triangles, Ctenomyidae; solid squares, Erethizontidae; solid triangles, Caviidae; solid diamonds, Octodontidae; asterisks, Echimyidae; vertical cross, Dasyproctidae; dash, Cuniculidae. Scale bar: 5 mm. Modified from Becerra *et al.* (2014).

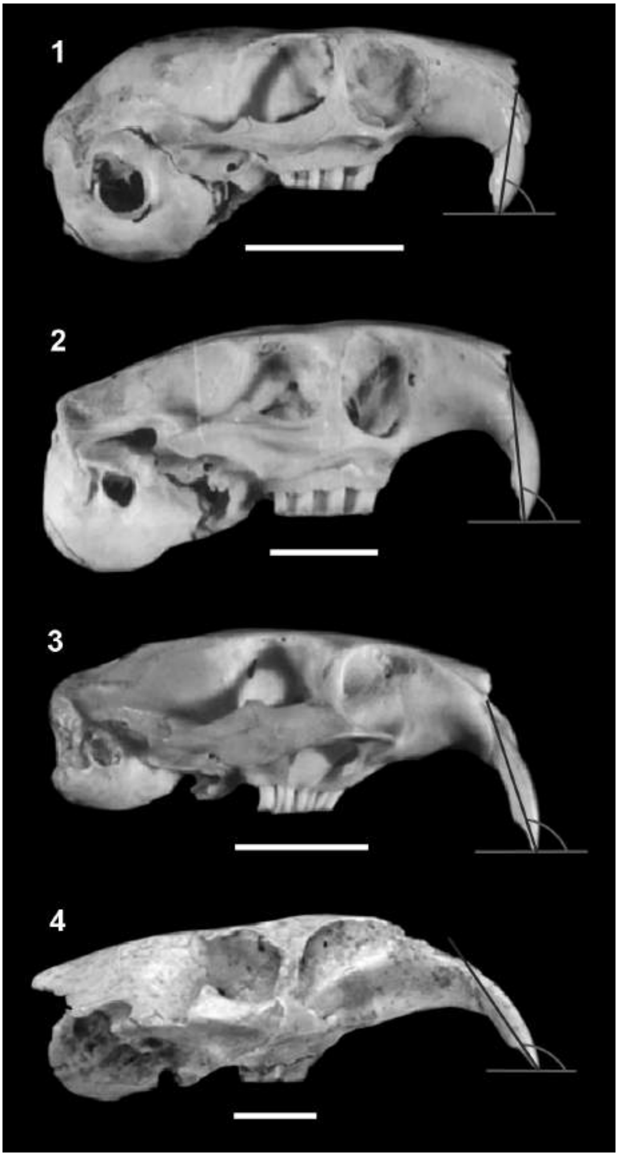

Figure 8. Lateral view of the skull of octodontid and ctenomyid rodents, with their respective angle of procumbency 1. *Octodontomys gliroides* (fossorial); 2. *Ctenomys australis* (highly fossorial, scratch-and chisel tooth-digger); 3. *Spalacopus cyanus* (subterranean, chisel–tooth digger); 4. †*Eucelophorus zaratei* (inferred to be subterranean and chisel-tooth digger). Scale bar: 1 cm. Modified from Lessa *et al.* (2008).

cinity thereof (Fig. 6.3; Verzi and Olivares, 2006). This disposition implies that the longer teeth have the basal generative zone far from the point on which bite pressure is exerted (Landry, 1957; Stein, 2000; Zuri and Terkel, 2001). Furthermore, longer lower incisors transmit the force applied on their tip during excavation more directly to the condyle (Verzi and Olivares, 2006). The depth of insertion of the lower incisors could be a better indicator of tooth-digging capacity than procumbency *per se* (Verzi and Olivares, 2006: fig. 6). The average angle of procumbency of *Lagostomus maximus* (103°)

and *Myocastor coypus* (102°) are more similar to the tooth diggers *Spalacopus cyanus* (108°), *Ctenomys leucodon* (116°) and †*Eucelophorus* (122°). These high values could indicate a particular use of the incisors, but only the tooth digger species have deeper lower incisors, *i.e.*, shorter distance between the anterior margin of the mandibular foramen (which accompanies the base of the incisor) and the dorsum of the condyle (Ib, see Fig. 6, and Verzi and Olivares, 2006: fig. 1). Indeed, *Spalacopus* has an Ib of 1.94 mm (standardized by Basilar length, SBL=0.05), *C. leucodon*, 4.60 mm (SBL=0.11) and †*Eucelophorus*, 2.86 mm (SBL=0.09). The procumbent, but not tooth digging, *Lagostomus* and *Myocastor* have shorter lower incisors [*i.e.*, greater length, 21.39 mm (SBL=0.21) and 17.45 mm (SBL=0.23), respectively]. These results show that species with similar procumbency of the incisors may exhibit strong differences in the insertion depth of these teeth, indicating divergent functional specializations (Verzi and Olivares, 2006).

Enamel microstructure of the incisors

The enamel is a conspicuous feature of teeth which is clearly influenced by mechanical demands. In particular, the analysis of its microstructure can provide abundant functional information (Koenigswald, 1988; Pfretzschner, 1988; Rensberger, 1997). As in other rodents, the enamel pattern or *schmelzmuster* (*sensu* Koenigswald, 1980; see Box 3 for an explanation of several terms related to this issue) of caviomorph incisors is double-layered (Fig. 9), with an external layer (portio externa, PE) of radial enamel (RE), occasionally a zone of prismless enamel (PLEX; Martin, 1992), and an internal layer (portio interna, PI) formed by multiserial Hunter-Schreger bands (HSB). Within this pattern, variation in relative thickness of enamel types (EI) and HSB inclination can be related to different functional requirements (Koenigswald, 1985; Flynn *et al.*, 1987; Martin, 1999). The angular arrangement of the interprismatic matrix (IPM) strengthens the enamel in the third dimension (see Box 3). In the most derived multiserial HSB, the IPM runs perpendicularly to the prism long axes and forms plates between the prism rows; this enamel type is considered an octodontoid synapomorphy (Martin T., 1992, 1993, 1994, 1997, 2005).

Vieytes *et al.* (2007) analyzed the morpho-functional and adaptive significance of variation in the upper incisor enamel of ctenomyids and other octodontoid rodents with different digging strategies, habits and habitats (Fig. 10). A specialized subterranean tooth-digger, the extinct

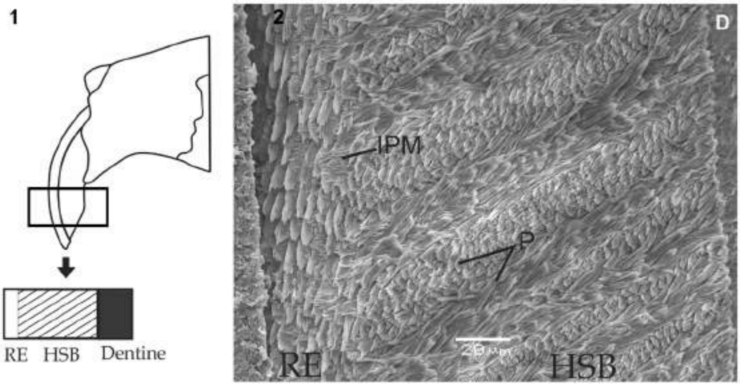

Figure 9. 1. Diagram of the longitudinal section of an upper incisor showing enamel types and dentine. 2. Micrograph of enamel rodent incisor. **RE**, radial enamel; **HSB**, Hunter Schreger bands; **D**, dentine; **P**, prisms; **IPM**, interprismatic matrix.

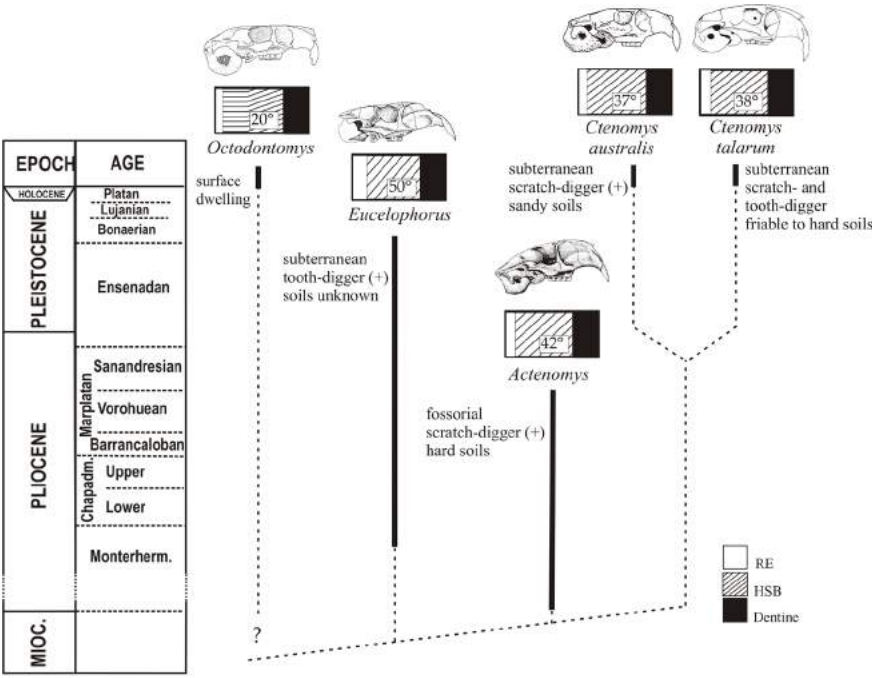

Figure 10. Known or inferred habits, digging modes and occupied soils of several octontoid species (after Contreras *et al*., 1987; Verzi and Alcover, 1990; Reig and Quintana, 1992; Quintana, 1994; Vassallo, 1998; Fernández *et al*., 2000; Patton *et al*., 2000; Morgan and Verzi, 2006; Verzi and Olivares, 2006). Phylogenetic relationships (dotted lines) and biochrons (solid lines) after Honeycutt *et al*. (2003), Opazo *et al*. (2005) and Verzi (2002). (+) indicates the predominant digging mode. **RE**, radial enamel; **HSB**, Hunter Schreger bands.

BOX 3

Enamel

The mammalian enamel is formed by hydroxyapatite crystallites that are bundled into enamel prisms (**P**) and has a second structural element, the interprismatic matrix (**IPM**), in which the crystallites are arranged in parallel but are not bundled (Fig. 9). These crystallites run parallel – at an acute or right angle – to the prisms, the former being the plesiomorphic condition. The primary prism organization is radial enamel in which all prisms run parallel to each other, straight or slightly bent from the enamel-dentine junction to the outer enamel surface (Fig. 9). This type of enamel prevails in non–specialized teeth, and seems to fulfill the basic functional requirements because the orientation of the closely packed prisms minimizes wear rates (Rensberger and Koenigswald, 1980; Boyde and Fortelius, 1986). However, this parallel arrangement of prisms involves a trade-off between this minimized wear rate and a greater vulnerability to interprismatic fractures created by tensional forces (Koenigswald, 1988; Pfretzschner, 1988). When the enamel achieves a higher level of complexity, the prisms are arranged in decussating layers at a high angle, the Hunter–Schreger bands (**HSB**; Fig. 9), which are interpreted as an adaptation to strengthen the enamel by dissipating tensional stresses when chewing stress is increased (Koenigswald *et al*., 1987; Pfretzschner, 1988). An increasing inclination of HSB, in the same direction as the applied forces, enhances their efficiency for fracture arrest (Rensberger and Koenigswald, 1980; Martin, 1999). Thus, mammalian teeth display combinations of different types of enamel to fulfill diverse biomechanical requirements during chewing.

ctenomyid †*Eucelophorus chapalmalensis* was included in this study. Despite the strong differences in habits, digging behavior and substrates occupied among the studied species, the values of enamel traits with a morpho-functional meaning (see Vieytes *et al.*, 2007) were quite similar, suggesting a phylogenetic constraint in Octodontoidea. However, †*Eucelophorus* had the highest values of HSB inclination and EI (Box 3), which would increase the resistance to both fracture and abrasion, in agreement with its exceptional craniomandibular tooth-digging specialization (Fig. 10). These results suggest an increased frequency of incisor use for digging in †*Eucelophorus*, which could be related to an extreme tooth-digging strategy and/or the occupancy of hard soils. Higher EI values are a recurrent pattern in distant clades of tooth-digging rodents (Flynn *et al.*, 1987), which would be in support of the adaptive significance of this trait.

Biomechanics of the molariforms

Regarding the caviomorph molariforms, their most conspicuous feature is the occlusal surface and, as for incisors, variation in their shape and area holds significant functional information. While the total occlusal surface area seems to respond basically to a molar *baüplan* (*i.e.*, scales isometrically to body size), the grinding capacity, analyzed by means of the molar enamel length divided by its occlusal area (*i.e.*, the relative length of enamel edges which process the food), might be associated with the environmental conditions, the hardness, and the nutritional quality of the food sources (Becerra *et al.*, 2012b). With the single exception of the semi-aquatic *Myocastor*, caviomorphs that inhabit southern South America have euhypsodont molars (Vucetich and Verzi, 1999). Euhypsodont molars of Caviidae, Octodontidae, Ctenomyidae, and Chinchillidae show a shorter enamel perimeter (*e.g.*, Vieytes, 2003; Verzi *et al.*, 2004; Box 4). This could be related to the exertion of higher occlusal pressures which increases the capability to consume the relatively less nutritious and more abrasive vegetation typical of arid environments (Becerra *et al.*, 2012b; Fig. 11).
Interestingly, the extinct genus *Actenomys*, the ancestor of the living *Ctenomys*, possessed a more generalized condition showing a higher relative length of enamel edges than other ctenomyid rodents, equivalent to the value in *Octodontomys gliroides* (see the lowest ctenomyid and the highest octodontid PC2-values in Fig.11.2; Becerra *et al.*, 2012b). This overall clustering fits quite well with the ecological and geographical distribution of these taxa, even though it does not show as strong a phylogenetic signal as other caviomorph cranio-dental morphological features do (Álvarez *et al.*, 2011 but see Verzi, 1994).

Molar enamel microstructure

Another important feature of cheek teeth is their enamel structure (see Box 3 for a detailed description) and several associated traits. As was observed for the incisors, there exists a direct rtionship between the distribution of enamel types (*schmelzmuster*) and the functional requirements of rodent molars (Koenigswald, 1980). The asymmetric wear of the enamel-dentine interface enables the identification of both the direction of jaw movement and the leading (first exposed to the occlusion) and trailing (the opposite) edges of molars (Fig. 12; Greaves, 1973; Rensberger, 1973; Koenigswald *et al.*, 1994). Enamel scars permit the detection of the direction of the mandibular movement (Greaves, 1973; Olivares *et al.*, 2004). The cutting edges of the enamel band are more efficient when they are mostly perpendicular to the mandibular movement (Rensberger, 1973). In rodents with hypsodont molars (see Box 4), unlike other mammals, microstructure is a determining factor in the degree of abrasion of the enamel, and the disposition of different enamel types (with different functional value) is closely related to the trailing and leading edges. In general, radial enamel (RE) develops on the "pushing side" of the leading and trailing edges and receives the first hit during mastication, whereas the "pulling side" shows crossing elements (*i.e.*, HSB) that are resistant to breaks (Fig. 12). As the RE is the enamel type most resistant to abrasion, its position on the "pushing side" of the enamel layer favors the formation and maintenance of self-sharpening cutting edges (Koenigswald, 1982; Koenigswald and Sander, 1997; see Box 3). However, as the HSB are formed by layers of prisms in different directions, they intercept the mastica-

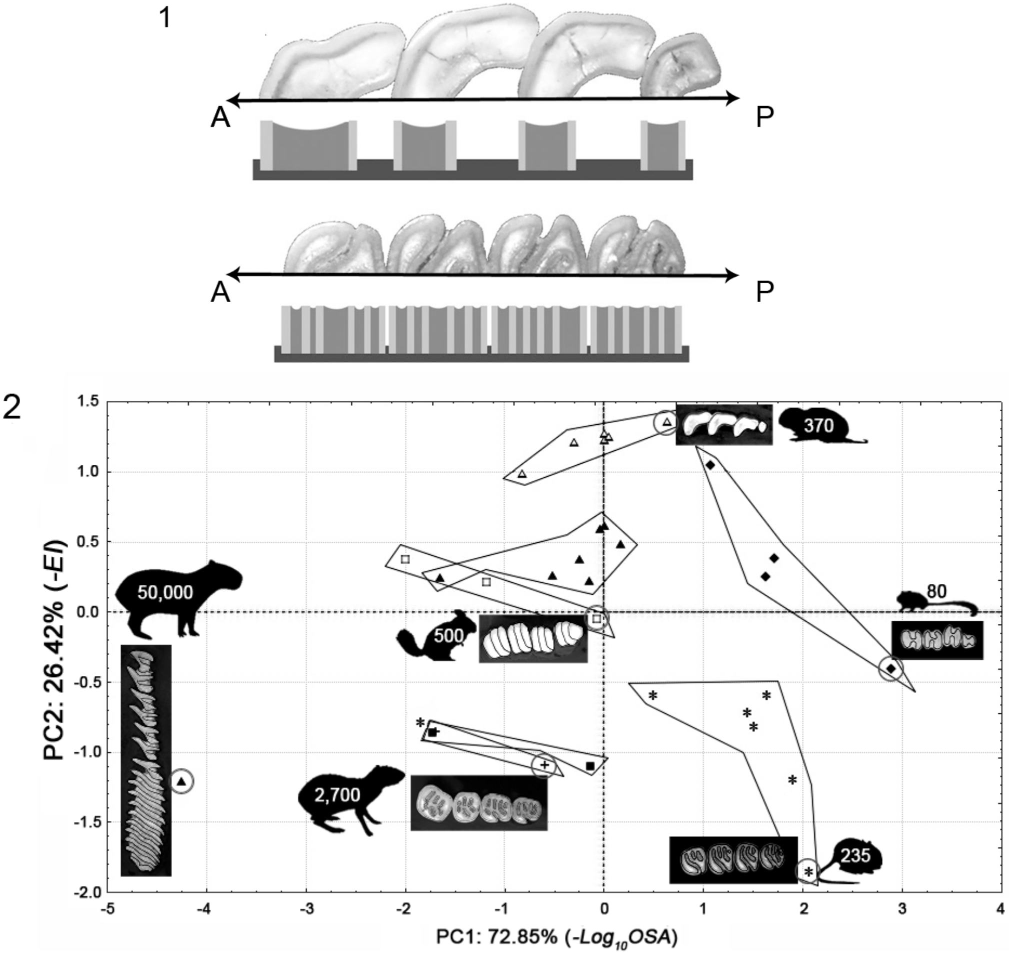

Figure 11. 1. Parasagittal profile through upper molar row of the subterranean *Ctenomys* (above) and the ground-dweller *Trinomys* (below); note the striking difference in the number of enamel edges (light gray bars). 2. PCA ordination of 33 caviomorph species belonging to seven different families, according to occlusal surface area (PC1) and the relative amount of enamel edges (PC2), which separates the Brazilian taxa (negative values) from the Andean–Patagonian taxa (nearly neutral to positive values), *sensu* Hershkovitz (1969). Silhouettes, body mass (g) and molar rows with highlighted enamel bands correspond to the highest and lowest PC1 values (*Tympanoctomys* and *Hydrochoerus*, respectively), the two highest and lowest PC2 values (*Trinomys*, *Dasyprocta* and *Ctenomys*, respectively), and the neutral value for both factors (*Chinchilla*). **A**, anterior end; and **P**, posterior end of the molar row; **OSA**, occlusal surface area; and **EI**, enamel index (*i.e.*, relative enamel band length). Symbols for families as in Fig. 7. Modified from Becerra *et al.* (2012b).

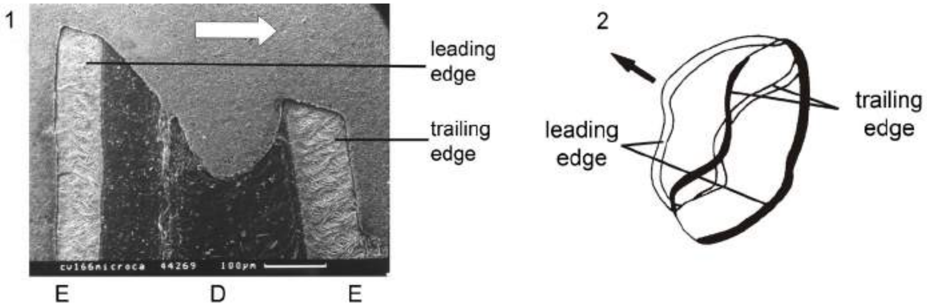

Figure 12. 1. Longitudinal section of a molar of the cavioid *Microcavia* showing the asymmetric wear of dentine. The arrow indicates direction of masticatory movement relative to the antagonist molar. On the trailing edge (**TE**), the increased abrasion due to accumulation of food particles produces a step of enamel above the dentine. 2. Occlusal pattern between the upper first molar (white) and the lower first molar (black) of the octodontoid *Ctenomys*. Arrow indicates direction and orientation of masticatory movements. **E**, enamel; **D**, dentine. Modified from Verzi *et al*. (2004) .

tory forces at higher angles than the RE, reducing their resistance to wear. In addition, because of the crossing disposition of the prisms, the enamel density, and consequently its hardness, is lower; thus, the HSB have an effective design to stop breaks, but are not able to form cutting edges.

If the design of the enamel structure is primarily adaptive, it is expected that the *schmelzmuster* is modified when functional requirements change (*e.g.*, during acquisition of euhypsodonty; Koenigswald, 1997a, b, c). Thus, the increasing complexity of the *schmelzmuster* allows the thinning of the enamel layer, favoring the formation of sharp cutting edges (Martin L.D., 1993). Caviomorph molar enamel microstructure shows remarkable *schmelzmuster* diversity, in contrast with the low diversity observed in other rodents. This diversity is correlated with the disparity in the degree of hypsodonty and associated dental morphologies; *e.g.*, taxa with low dental gross morphology variation, such as Erethizontidae and Chinchillidae, display low or nonexistent *schmelzmuster* diversity. The *schmelzmuster* found in erethizontids and various genera of the Cavioidea and Octodontoidea with primitive molar structure and low-crowned molars (an apical layer of RE, covering an inner layer of HSB forming the rest of the enamel band) was interpreted as the primitive and ancestral condition for the enamel pattern of all caviomorphs (Vieytes, 2003). With the acquisition of hypsodonty, the original apical portion of the crown is lost, thus the apical RE layer disappears and the entire enamel band is formed by HSB alone. In the Octodontoidea, Cavioidea and Chinchilloidea, a pattern of change was detected in which RE is repeatedly added to a *schmelzmuster* formed only by HSB (Fig. 13). This secondary and progressive acquisition of RE, related to the homoplastic development of hypsodonty may be hypothesized as a possible evolutionary pattern for the caviomorphs, as a response to functional requirements, reinforcing the enamel band and favoring the formation of sharp cutting edges (Verzi *et al.*, 2004). This hypothesis is supported by the gradual addition of a layer of the aforementioned enamel type that has been recorded along the two progressively hypsodont lineages of †*Chasichimys-Xenodontomys* and *Neophanomys* (Octodontidae, Late Miocene) (Verzi *et al.*, 2004, 2011). These changes probably resulted as a response to a more abrasive diet (Janis, 1988; Martin L.D., 1993) related to increasing aridity and the development of open environments in southern South America during the Cenozoic (Pascual *et al.*, 1996 and literature therein).

In summary, not only has the overall morphology of the dentition of caviomorphs been shaped by the mechanical demands of living in a broad range of habitats, differential habits

BOX 4

Hypsodonty and molar function

Herbivorous mammals acquired the ability to increase the functional durability of teeth as a structural response to their abrasive diet. This capability to recover the crown worn through a prolonged or continuous generation/growth of dental tissue is known as hypsodonty (Koenigswald and Golenishev, 1979; Janis, 1988). Another way to increase the wear resistance is by increasing the total thickness of the enamel layer; however, a thick layer is useful in crushing molars (*e.g.*, some primates, insectivorous and suids), but not in grinding molars (Janis, 1988). In the latter, cutting edges are formed by differential wear of enamel and dentine, after losing the apical portion of the crown; in this way, a secondary occlusal surface is formed, which is always functional by continuous wear. Frequently, rodent hypsodont molars are characterized by a simplified morphology, a flat occlusal surface, and highly unidirectional masticatory stresses acting on the molariforms (Fortelius, 1985; Koenigswald *et al*., 1994; Schmidt-Kittler, 1984). This means that the perimeter of enamel exposed on the masticatory surface decreases together with the loss of enamel structures (*e.g.*, loss of flexi/flexids). After reaching euhypsodonty, the next step is to recover enamel perimeter through an increase in length of the cutting edges, by lengthening the lophs or increasing the number of lophs or laminae (Verzi, 1994; Verzi *et al*., 2004). By increasing the enamel perimeter, the ability of molars to subdivide the food increases as well, but there is a threshold of occlusal pressure that determines whether food is divided or not (Rensberger, 1973) that varies inversely to the contact area between teeth. In many rodents the correct occlusal pressure is achieved through patterns of enamel crests in opposite curves in upper and lower molars (Fig. 12), which generate minimum contacts at each moment of the occlusal event (Verzi, 1994, 2002; Verzi *et al*., 2004). This generates high occlusal pressures, and an effective control on the movements of food particles (Fortelius, 1985; Verzi, 2002).

and diets, social interactions and locomotor modes, but even the microscopic structure of the teeth has been adapted to those conditions. Thus, in general terms, octodontoids, cavioids and chinchillids, especially fossorial and subterranean species, which have evolved in association with the more arid and open environments with more abrasive and less nutritious foods in southern South America, developed much stiffer, more massive and microstructurally complex teeth.

Concluding remarks

In the last few years, much effort has been put into understanding the morphological variation of caviomorph rodents and the factors responsible for it. The two main approaches that encompass most of these studies have been addressed in this chapter. Although they have been presented separately, there is an evident link between them.

Large-scale evolutionary patterns concern the variation detected across phylogenies; factors generating and/or influencing them may be found at different levels.

The noticeable morphological differences observed among caviomorph clades, especially at the superfamilial level, were interpreted as a result of the long-standing evolutionary history of the major lineages of these rodents. This would have been accompanied by morphological divergence. Thus, the early establishment of the main pathways of craniomandibular specialization would explain the strong phylogenetic signal in morphological variation among major clades of extant caviomorphs.

However, phylogenetic structure alone does not explain morphological diversity. Other variables have been related to the observed variation, such as body size, habitat, diet, habits, and

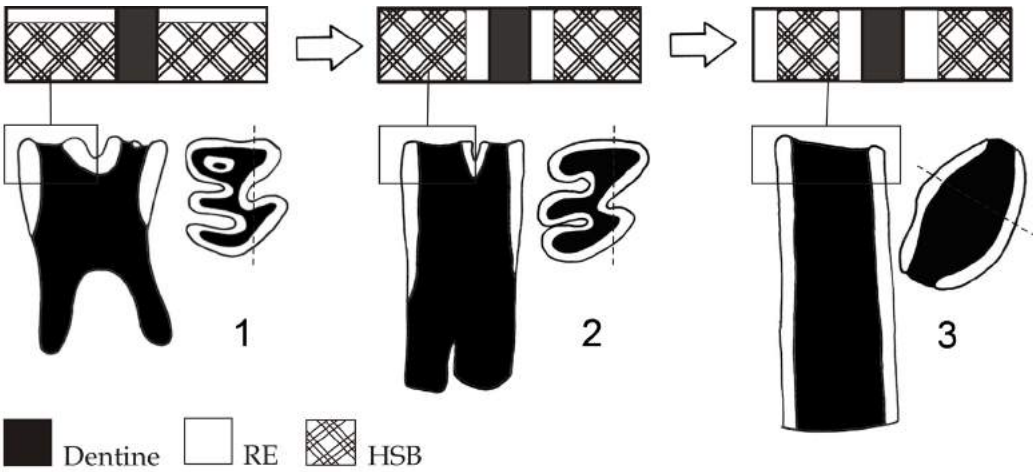

Figure 13. Hypothetical transformation of schmelzmuster (above), hypsodonty and occlusal morphology (below) in octodontoids (not to scale). Right lower first molars are shown for 1. †*Sciamys*, 2. †*Chasichimys* and 3. †*Xenodontomys*. *Schmelzmuster* schemes represent longitudinal sections. Dotted lines indicate longitudinal plane analyzed. **RE**, radial enamel; **HSB**, Hunter Schreger bands. Modified from Verzi *et al*. (2004).

diverse aspects of the life history of the species, such as burrow construction and interactions among individuals. All of them can be regarded as part of the proximate causes of morphological variation, and the morpho-functional approaches have as a main goal to study how the aforementioned variables influence it. From a comprehensive standpoint of the study of morphological evolution, this approach may represent the structural and/or adaptive perspective through which immediate causes of change can be determined.

As Cracraft (1990: 23) pointed out: "Manifestations of pattern above the level of differentiating populations, or basal taxa, are epiphenomena, or effects, of lower level processes". Thus, phylogenetically structured morphological variation, implying an early (in the evolutionary history) acquisition of major shape features, does not exclude an adaptive approach that claims that any trait historically structured could represent an adaptation to the conditions that prevailed in its origin. The integration of the two approaches presented in this chapter, and further comprehensive studies that involve both of them together with paleoenvironmental inferences would improve the understanding of the evolution of caviomorph rodents.

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7 | SOCIAL AND MATING SYSTEMS OF CAVIOMORPH RODENTS

SISTEMA SOCIAL Y REPRODUCTIVO DE LOS ROEDORES CAVIOMORFOS

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Abstract. The caviomorphs (American Hystricognathi) are a highly diverse group of rodents, both in anatomical characters as well as in behavioral features. Virtually all mating and social systems described for mammals (the exception being eusociality, exhibited by another Hystricognath family, the African Bathyergidae) are present in one or other of the species in this group. In this chapter I list all families of caviomorphs and describe the mating tactics and social systems representative of each family (except when information is too scant to allow this). For example, in the family Caviidae, monogamy, polygyny and promiscuity are present: *Cavia aperea* is quite strictly polygynous, *Dolichotis patagonum* is notably monogamous and *Galea musteloides* is basically promiscuous. These seem to be independent evolutionary events and examples of the relation between ecology and mating system, as illustrated by the maras where dispersed and unpredictable resources force the male into monogamy. In the burrowing caviomorphs, Octodontidae and Ctenomyidae, sociality and solitary living are both present. Group living in burrowing species seems to have evolved independently in these two families. Burrowing in many cases promotes grouping, although many ctenomyids are solitary. Caviomorphs provide a wide array of examples of social and mating systems among rodents, or in mammals in general, but clearly further study is necessary to fully understand the social and reproductive tactics of this unique group of rodents.

Resumen. Los caviomorfos (Hystricognathi americanos) son tal vez el grupo más diverso entre los roedores. Al menos en cuanto a nichos y modos de vida sin duda lo son: están los coipos y capibaras, de gran tamaño y semi-acuáticos; los tuco tucos y degus, de hábitos subterráneos; las pacas y agutíes, del bosque tropical; y las chinchillas y *Kerodon*, habitantes de montañas y rocas, entre otros. En lo que respecta a su comportamiento social y reproductivo también son extremadamente diversos, mostrando todas las formas de sociedad y de sistemas de apareamiento. Tal como han encontrado muchos autores, el comportamiento social y reproductivo suele mostrar estrecha relación con la ecología. Así por ejemplo, los mamíferos herbívoros de gran tamaño y de sabana suelen vivir en grupos mientras los de menor porte y de bosque suelen ser solitarios y territoriales. En este trabajo, se revisa sistemáticamente las formas de vida social y los sistemas de apareamiento de los caviomorfos, intentando relacionar estos aspectos con el modo de vida y la ecología de cada grupo (especie o género) así como con la posición filogenética del taxón. Encontramos que en la familia Caviidae se dan todos los sistemas sociales y de apareamiento descritos para mamíferos: dentro de la subfamilia Caviinae, *Cavia aperea* es claramente monógamo y no forma grupos mientras *Galea musteloides* presenta un comportamiento sexual promiscuo y vive en grupos mixtos con una jerarquía de dominancia entre los machos. Este es un caso interesante porque implica un origen independiente de estos tipos de comportamiento dada la cercanía filogenética de estos géneros.

Galea musteloides, además, ilustra muy bien el proceso conocido como competencia espermática, que ocurre en especies promiscuas, al presentar testículos muy grandes para su tamaño, generados justamente como resultado de esta forma particular de competencia post-cópula. En esta familia está también uno de los mejores ejemplos de monogamia en mamíferos como es el caso de la mara, *Dolichotis patagonum* (subfamilia Dolichotinae). Las hembras de esta especie del semi-desierto patagónico, se mueven amplia e impredeciblemente por el ecosistema, obligando a cada macho a seguir a una hembra a donde vaya, de modo de estar presente en el momento en que se haga sexualmente receptiva, generando una monogamia. Los carpinchos (capibaras o chigüires, *Hydrochoerus hydrochaeris*) son, junto con *Kerodon*, los únicos miembros de la subfamilia Hydrochoerinae, dentro de Caviidae. Los carpinchos forman grupos sociales mixtos estables, con una estricta jerarquía de dominancia entre los machos. El sistema de apareamiento parece ser básicamente poligínico (un macho, varias hembras), parecido al de *G. musteloides*, aunque posiblemente menos promiscuo. Es interesante notar que los carpinchos presentan una alta variabilidad en su comportamiento social en relación al ambiente en que se encuentran. Así, se han observado carpinchos formado parejas (o tríos) posiblemente monógamas en el bosque amazónico de Perú. El otro caviomorfo relativamente grande y de hábitos más acuáticos que el carpincho es el coipo (*Myocastor coypus*), que también forma grupos mixtos con jerarquía de dominancia entre los machos. Un grupo particularmente interesante de los caviomorfos son los subterráneos formados por las familias Ctenomyidae (tucotucos) y Octodontidae (degus). Los tucotucos consisten de más de 60 especies en un solo género (*Ctenomys*), la mayoría solitarias, pero algunas son sociales. De entre estas últimas, *Ctenomys sociabilis* forma grupos compuestos por un macho y 2-6 hembras, aunque en muchas de estas unidades sociales, el macho está ausente. *C. haigi* es una especie de tucotuco solitaria, mientras *C. talarum* varía entre solitaria y grupal con jerarquía de dominancia entre los machos y un sistema de apareamiento aparentemente poligínico. A diferencia de los tucotucos, la familia Octontidae consiste de ocho géneros y unas 13 especies. El degu común, *Octodon degus*, vive en grupos de 2-5 hembras emparentadas con un sistema de apareamiento probablemente poligínico. Poco se sabe del comportamiento de las otras especies en esta familia. Entre los caviomorfos solitarios están las pacas (*Cuniculus paca*) y los agutíes (*Agouti* spp.), cuyos hábitos de deambular por el bosque en búsqueda de plantas nutritivas no parecen permitir la formación de grupos, favoreciendo una aparente monogamia. En contraste con esto, la familia Chinchillidae (vizcachas, chinchillas), tienden a ser sociales, pero su sistema de apareamiento no se ha dilucidado. La familia Echimyidae es muy amplia, comprendiendo un gran número de especies en 21 géneros. Sin embargo, se conoce muy poco de su comportamiento, aunque se ha observado gran variabilidad en sistemas sociales y de apareamiento en función de la densidad, encontrándose mayor promiscuidad a altas densidades, tendencia a la monogamia en bajas densidades y poliginia en casos intermedios. En esta revisión se muestra cómo los caviomorfos presentan la gama completa de sistemas sociales y de apareamiento descritos para los mamíferos, y se ilustra la relación entre las circunstancias ecológicas y las estrategias comportamentales que llevan a los sistemas sociales y de apareamiento. Sin embargo, hay que tener en cuenta la filogenia antes de concluir que estas relaciones se deben a presiones selectivas recientes: en muchos casos se puede tratar de rasgos heredados filogenéticamente de un ancestro común. A pesar de una gran cantidad de estudios muy completos del comportamiento de los caviomorfos, está claro que falta mucho por hacer. Grupos importantes como los equímidos y otros más crípticos como las familias Abrocomidae y Capromyidae requieren mayores estudios para comprender sus estrategias comportamentales. La diversidad de los caviomorfos y su amplia gama de adaptaciones los hacen un grupo ideal para poner a prueba hipótesis acerca de la evolución de sistemas sociales y de apareamiento en mamíferos.

Introduction

Caviomorphs, the American Hystricognaths, are an extremely diverse mammalian group, with species displaying semiaquatic, rock-dwelling and arboreal habits and niches such as cursorial browsers and savanna grazers. They are found in virtually all major habitats in South America (Upham and Patterson, 2012, this volume; Ojeda *et al.,* this volume). Arguably, they cover more niches and ways of life than all other rodent taxa. This is neatly exemplified in Figure 1 of Kay and Hoekstra's (2004) primer on "Rodents", which, with the aim of illustrating the diversity of rodents' forms and habits, shows eight photographs, five of which are caviomorphs. As explained elsewhere in this book (McManes *et al.*, this volume; Vucetich *et al.*, this volume), caviomorphs evolved in South America during a long period when the subcontinent was an island (Oligocene-Pliocene, or 40 to 3 million years before the present; Wood, 1974; Ricklefs, 2002; Poux *et al.*, 2006; Antoine *et al.*, 2011), whence they evolved into myriad of forms, many reminiscent of small antelopes, such as the paca, *Cuniculus paca*. The paca is extremely similar in appearance to the forest-dwelling African chevrotain (*Hyemoschus aquaticus*), complete with spots on the back, and roughly filling its niche in the neotropical forests. Despite the diversity of species found this group, caviomorphs in general share a number of features, in particular reproductive traits such as precocity (with the possible exceptions of tuco-tucos and degus), small litter sizes and long gestations (Weir, 1974).

As I will show in this chapter, caviomorphs exhibit the full array of social and mating systems described for mammals. Unfortunately, some interesting groups are not very well known. I will select from among the best studied groups a few examples to illustrate 1) social systems and 2) reproductive strategies as reflected in the mating system; and the relation between these, if any. I will take a systematic approach to show how each group has evolved its strategies, whether as a unique solution to their particular ecological and social situation or as a phylogenetically inherited character. This approach assumes that behavioral tactics, be they social or sexual, are naturally selected adaptations and therefore genetically determined (to a point), but clearly, there is also behavioral flexibility and geographical/ecological variation in social and mating systems, which I will also point out when relevant. As Trillmich *et al.* (2004) have remarked, the relationship between phylogeny and social system in caviomorphs is not a simple one, with phylogenetic or ecological constraints varying in their relative importance over the origin of the mating or social system. For the sake of completeness, I will list each family in alphabetical order, but in some cases there will be little to say, since the group is almost unstudied, at least as far as my aims are concerned. But first, I will briefly discuss a few basic concepts, relevant to an understanding of the social and reproductive strategies of animals in general.

Mating systems

As animals evolve mating tactics to maximize their reproductive success, mating systems emerge, namely, monogamy, polygyny (one male, several females), polyandry (one female, several males) and promiscuity. The mating system is determined mainly by the relative investment (in energy and resources) in the reproductive act by the male and the female (Davies *et al.*, 2012) and by resource distribution, both in time and space (Clutton-Brock, 1989). Basically, the sex that invests most (usually females) is the limiting factor and the more selective member of the pair. This is also the less competitive one intrasexually. Individuals of the opposite sex (usually males), on the other hand, invest less and compete for access to the other sex. When the difference in relative investment is great, the less-investing sex becomes polygamous. Thus, in mammals, where females invest significantly more than males, males compete among themselves for access to females, while females tend to form groups, leading to a polygynous mating system: 97% of mammalian species are polygynous (Kleiman, 1977). To illustrate the opposite situation, in birds, where both sexes invest more equally (as the eggs are laid, both parents can contribute to incubating and rearing), monogamy is more common (Greenwood, 1980). However, it must be stressed that within the widespread apparent monogamy of birds, more promiscuous mating systems can occur via extra-pair copulations, whose frequency depends on ecological, genetic and demographic circumstances (Petrie *et al.*, 1998; Westneat and Stewart, 2003). Monogamy in mammals can occur when resource distribution and availability does not permit the monopolization of a group of females by a male (Kleiman, 1977) and when offspring are altricial (born underdeveloped) requiring care from both parents, as in humans.

Sexual selection

Sexual selection can be understood as a kind of natural selection for traits that increase the chances of access to the opposite sex (Jennions and Kokko, 2010). It can also be viewed as the process through which secondary sexual characters (bright plumage, antlers, etc.) evolve. Sexual selection has two components: an intrasexual component, originated by competition within one sex, usually males, which gives rise to "weapons" such as antlers or large teeth, and sexual dimorphism in size, with males heavier than females. Intersexual or epigamic sexual selection, on the other hand, is usually driven by female choice and generates sexually dimorphic characters such as ornaments (*e.g.*, bright plumage, manes, antlers). Sexual selection is still a hot topic of research, with several hypotheses competing as the explanation for this process. One is Fisher's (1930) runaway sexual selection, which states roughly that if a female prefers a particular trait in a male (say, a long tail), then the male character (long tail) will become linked to the female character (preference for a long tail). This leads to a positive feedback process which produces the evolution of exaggerated characters until costs outweigh benefits, even if the character does not give any direct advantage to the male. The "good genes" hypothesis, on the other hand, posits that a conspicuous secondary sexual character is an honest indicator of health, because it is costly (Zahavi, 1975), or that it shows a lack of parasites since only a parasite-free male can "afford" to grow exaggerated characters (Hamilton and Zuk, 1982). By preferring healthy and energetic mates with "indicator" characters, females promote the evolution of ornaments such as bright colors in birds, and manes, antlers (which double as weapons) and/or scent glands in mammals (Zahavi, 1975; Hamilton and Zuk, 1982; Grafen, 1990).

Sperm competition

Sperm competition occurs when a female copulates with more than one male within a single ovulation event, causing the ejaculates in her reproductive tract to compete for fertilization of her eggs (Parker, 1970). When present for sufficient evolutionary time, sperm competition leads to the evolution of large testes, high concentration of sperm in semen and other traits (Ramm *et al.*, 2005). Typically, in clearly polygynous (where a male monopolizes a group of females) and monogamous systems (where a male guards his partner and does not allow other males to mate with her) little or no sperm competition occurs and males therefore tend to have small testes (for their size) and low sperm counts. Under more promiscuous systems, males tend to develop large testes. A female can also develop mechanisms to choose which ejaculate will fertilize her ova, leading to so-called cryptic female choice. A typical example of the extremes or sperm competition and no sperm competition are chimpanzees (*Pan troglodytes*) and gorillas (*Gorilla gorilla*) (Harcourt *et al.*, 1981). Chimpanzees, being rather omnivorous, roam widely around their home ranges in search for food. This precludes the possibility of mate guarding by males, making their mating system very promiscuous. Thus, there is little sexual dimorphism and chimp males have very large testes for their size. Gorillas, on the other hand, being totally herbivorous, spend much of their time sitting, eating and digesting their food. There, males can defend a group of females, leading to a strictly polygynous mating system. Since large males are the ones that can defend a group of females, this scenario has generated, over evolutionary time, a marked sexual dimorphism in size and small testes in gorillas. In caviomorphs, as we shall see in the case studies below, when it occurs, sperm competition has a significant effect in the development of large testes, such that highly promiscuous species have very large testes for their size.

Case studies

Family Abrocomidae

Not much is known about members of this family (commonly known as chinchilla rats), which consists of two genera, *Abrocoma* (8 species) and *Cuscomys* (2 species). The family is restricted to rocky habitat in the high, dry Andes, 2000- 5000 m above sea level. *Abrocoma schistacea* form small groups of 3-4 animals (1 male, 2 females or 2 males and 2 females) and live in communal burrows (Taraborelli*et al.*, 2011). Lack of sexual dimorphism suggests this species is probably not strictly polygynous.

Family Capromyidae

Hutias are found in Cuba and on nearby islands, including the Bahamas and Jamaica. There are at least 13 species in 4 subfamilies (Wilson and Reeder, 2005). In contrast to most rodents but similar to other caviomorphs, they are rather large, with species weighing up to 7 kg. There is even an arboreal species with a prehensile tail, *Mysateles prehensilis*, which is endemic to Cuba and listed as near endangered by the IUCN.

The behavior of hutias is nearly unknown, but the Jamaican hutia (*Geocapromys brownii)* appears to form social groups of 2-6 individuals (Anderson *et al.*, 1983). Bahamian hutias, *G. ingrahami*, now restricted to the small island of East Plana Cay and also endangered, weigh around 700 g, with males being about 8% heavier than females (Clough, 1972). Hutias are usually seen in solitary or in pairs in the wild. According to observations in captivity, there appears to be a significant degree of social tolerance, including the use of squeaks to attract conspecifics as well as allogrooming and nuzzling (Clough, 1972). This author also described chases, which suggests some kind of dominance hierarchy. Howe (1974) in a study of marking behavior by the Bahamian hutia refers to this species as "gregarious" and concludes that marking behavior is a non-agonistic social behavior possibly contributing to group cohesion.

Family Caviidae

This is a large and diverse family with three subfamilies (Caviinae, Hydrochoerinae and Dolichotinae) and 18 species. In this family we encounter virtually every kind of social and mating system described for mammals.

Capybaras. Capybaras (genus *Hydrochoerus*) are in a subfamily (Hydrochoerinae) with the genus *Kerodon*, the rock cavy (Rowe and Honeycutt, 2002). There are two species of capybara, *H. hydrochaeris* and *H. isthmius*. The former is the largest extant rodent (50 kg), and it is distributed in all South American countries except Chile. The latter *H. isthmius* is the second largest species (35 kg) and is found in Northwestern Venezuela, Northern Colombia and in Panama, west of the Andes. Since nothing is known about this species' social or sexual behavior, no more is going to be said about it here.

Capybaras are grazers common in the wetlands and seasonally flooded savannas of tropical and subtropical South America (Ojasti, 2011). They are also found in the Amazonian rainforest (Moreira *et al.,* 2012). In the wetlands and savannas, capybaras form stable social groups ranging in size from 10 to 20 animals, composed of both males and females with a sex ratio ranging from 1.2:1 to 2.0:1 (female: male) (Herrera *et al.*, 2011). These groups defend a common territory and are characterized by relatively long-term stability in their membership and a strict dominance hierarchy among the males (Herrera and Macdonald, 1987, 1989, 1993). The defendable resource here appears to be a water body that will retain some water into the dry season, while having neighboring patches of grass and high ground for the wet season (Herrera and Macdonald, 1987). There is some degree of cooperation within capybara groups, as all members –males and females- defend the territory against intruders (Herrera and Macdonald, 1989) and females communally nurse their young (Macdonald, 1981).The mating system is clearly polygynous, so that the main advantage for the dominant male is priority of access to receptive females (Herrera and Macdonald, 1993). It is worth mentioning that subordinate males also obtain a not-insignificant number of matings. Unfortunately no data on paternity are at present available to ascertain the degree of actual monopoly the dominant capybara male exerts over females' sexual receptivity and parentage within groups. Capybaras share social dynamics and features of the mating system with both *Cavia aperea* (strictly polygynous) and *Galea musteloides* (large mixed sexes groups, with male linear hierarchy and polygynous-promiscuous mating system; Adrian *et al.,* 2005). The relatively small testes (Herrera, 1992) and lack of sexual size dimorphism of capybaras suggest that the mating system in this species is more polygynous (*i.e.*, less promiscuous) than that of *G. musteloides* (see below).

There is a further remarkable feature of the capybaras' social system: its flexibility. Observations by Soini and Soini (1992) in the Peruvian Amazon indicate that in contrasting habitats (forest vs. savanna), capybaras form pairs and occasionally trios. This illustrates both the species' adaptability to different ecological situations and the relation between ecology and social system: where resources and structural features of the habitat (trees, shrubs, etc.) do not favor aggregations, animals form pairs, while in open habitats where grouping appears to provide protection against predators (Hamilton, 1971; Brashares *et al.,* 2000), capybaras are social.

Kerodon. The behavior of rock cavies has not been well studied, unfortunately. Lacher (1981) describes the social system of *Kerodon rupestris* as "resource defense polygyny", although he bases his conclusions on ecophysiological characteristics of the species, not on direct behavioral observations. Interestingly, Tasse (1986) found that both males and females impart equal amounts of parental care to the offspring, but this does not seem to benefit the young since young cared by the mother alone put on more weight than young cared by both parents, although this result should be accepted with caution since it was obtained in captivity. Such behavior on the part of the male indicates either monogamy or strict polygyny. Further study is needed for a better understanding of the social and mating system of this highly peculiar caviomorph.

The closeness of this animal to the capybara (its closest relative; Rowe and Honeycutt, 2002; Trillmich *et al.*, 2004) linked with its peculiar adaptation to rock-living suggests this animal evolved and diverged greatly and quickly from other caviomorphs. However a number of behavioral features such as chases and "lunges" by the dominant male (Lacher, 1981) indicate that some characters are shared through common descent with capybaras and cavies. Still, social features such as the social hierarchy are somewhat different: stable, strictly linear and rigid among male capybaras (Herrera and Macdonald, 1993) and "weakly linear" in *Kerodon*, with many more male-female interactions than in capybaras (Lacher, 1981).

The cavies. The Caviinae subfamily comprises three genera, *Cavia*, *Microcavia* and *Galea*. This is a very interesting group of species and it is here that we find the extreme variety of mating systems mentioned above. I will choose just three cases to illustrate the subfamily, *Cavia aperea*, *Galea musteloides* and *Galea monasteriensis*.

In the wild, *Cavia aperea* forms pairs or trios (1 male, 2 females) and they are territorial (Asher *et al.,* 2004, 2008). Asher *et al.* (2008) attribute the small size of groups to a predation strategy involving reducing detectability. Using genetic techniques, Asher *et al.* (2004) found that the only two juveniles they tested were fathered by the resident male of the territory. This, together with the sexual dimorphism (males 10% heavier than females) and small testes of males (Adrian and Sachser, 2011), points strongly to a strictly polygynous mating system. Also, females nurse their own young exclusively, as do maras (Taber and Macdonald, 1992a), but contrary to what female capybaras do (Macdonald, 1981).

Galea musteloides is a habitat generalist. This species forms larger groups of both sexes where mating appears to be promiscuous (Sachser *et al.,* 1999). However the dominant male obtains significantly more copulations than subordinates (Keil *et al.,* 1999) and home ranges of males overlap with those of several females, making the system intermediate between polygyny and promiscuity. The large size of the testes (relative to their body size) of *G. musteloides* is consistent with the promiscuous sexual behavior observed, indicating that sperm competition is common in this species.

Galea monasteriensis (referred to as "*Galea* sp." by Hohoff *et al.,* 2002, and later named *G. monasteriensis* by Solmsdorff *et al.,* 2004) has been described as monogamous, based on evidence of experiments on mate choice and the presence of reverse sexual dimorphism (females larger than males; Hohoff *et al.,* 2002). It is interesting that male *G. monasteriensis* show paternal care, at least in terms of social play and grooming (Adrian *et al.,* 2005), a most uncommon behavior in male mammals. The fact that two closely related species of the genus *Galea* (*G. musteloides* and *G. monasteriensis*) contrast so strikingly in their mating behavior is indicative that such behavior is a recent adaptation to specific ecological circumstances and not an product of phylogenetic closeness (Trillmich *et al*., 2004).

The maras. Two species comprise the Dolichotinae subfamily, the Patagonian mara *Dolichotis patagonum* and the Chacoan mara *Dolichotis salinicola*. Only the former will be mentioned here since little is known about the latter.

The Patagonian mara is possibly one of the best examples of monogamy among mammals (Genest and Dubost, 1974; Kleiman, 1977; Taber and Macdonald, 1992a). In the Patagonian semi-desert where they live, females are widely dispersed and males can only follow one, so as to be ready when she comes into estrus during the few rainy days of the year. This makes the males closely attached to the female, following her wherever she goes, virtually never losing sight of her (Dubost and Genest, 1974; Taber and Macdonald, 1992a). Interestingly, although the mating system is monogamous pairs, the breeding system (*i.e*., birthing and nursing) is communal: Taber and Macdonald (1992b) described how several pairs coalesce around a dry lagoon bed where the pairs dig burrows inside of which females give birth and around which they tend to the young. Despite this apparent cooperative breeding (see Lukas and Clutton-Brock, 2012), pairs do not really help each other or cooperate in any way. In fact, females reject any young not their own who attempt to suckle from them (Taber and Macdonald, 1992b).

Family Chinchillidae

This is a family with three genera (*Chinchilla*, *Lagidium* and *Lagostomus*) with two species each, none of which are very much studied in terms of behavior. Genus *Chinchilla* forms colonies from a few individuals to several hundred (Mohlis, 1983, cited by Jimenez, 1996) which in turn form an "archipelago". Nothing has been published on its mating system (Mignani and Beach, 1968, only describe physiological aspects of mating behavior).

Viscachas, *Lagostomus maximus*, are relatively large caviomorphs with marked sexual dimorphism in size, males weighing at 5-6 kg (up to 9) and females around 3-4 kg (Jackson *et al*., 1996). They live in colonies composed of one or more males, two or more females and their young, totaling up to 17 members (Branch, 1993). Dominance relations among males were difficult to detect and non-existent among females. Dispersal patterns (females phylopatric; males dispersers, albeit late) suggest that females in colonies may be related (Branch, 1993). The mating system appears to be polygynous, as suggested by the body size dimorphism, but no hard data on this are available.

Family Ctenomyidae

Tuco-tucos (genus *Ctenomys*, the only genus in the family) constitute a large family with more than 60 species. All are fossorial and only a handful have been studied. Most are solitary (Lacey *et al.,* 1998 and references therein) but a few are social. As with the cavies, the ctenomyids can illustrate the evolutionary origin of mating and social systems in mammals. I will mention here three species in the genus, since they illustrate contrasting points on the continuum solitary-social.

Ctenomys haigi, the Patagonian tuco-tuco, does not form groups; burrows are used by a single animal and there was no overlap in home ranges of animals of either sex (Lacey *et al.,* 1998). Unfortunately, the mating system, whether monogamous or promiscuous (polygyny can clearly be dismissed from space use data), has not been ascertained.

A well-known and so far the only social tuco-tuco is *Ctenomys sociabilis*, which is restricted to the Limay Valley, in the province of Neuquén, Argentina. Interestingly, *C. haigi*, with its contrasting non-social habits, is found just across the river Limay, some 500 m away (Lacey *et al.,* 1998). In *C. sociabilis*, live-trapping has shown extensive burrow sharing, with burrows containing 1-6 females (Lacey *et al.*, 1997; Lacey and Wieczorek, 2004). There was no evidence of reproductive monopoly by a single female in a group (as in naked mole-rats, Jarvis, 1981) since all females captured were lactating (Lacey *et al.,* 1997). The mating system, again, is unknown, but is likely to be polygynous, since no more than one male appeared to share the burrow with a group of females (Lacey and Wieczorek, 2004)

Ctenomys talarum is a tuco-tuco whose behavior has been described as solitary and territorial (Busch *et al.*, 1989). In a comparative study of two *C. talarum* populations, Zenuto *et al.* (2002) found that in a high density location, males formed a dominance hierarchy, with an apparently polygynous mating system, while at the lower density population, males appeared to court a single female. However, in both populations sexual dimorphism favoring males, small relative testes size and sperm morphology suggest that a male can monopolize sexual access to females, *i.e.*, that the mating system is rather more strictly polygynous (Zenuto *et al.*, 1999; Zenuto *et al.,* 2003).

Family Cuniculidae

This family (the pacas) contains only the genus *Cuniculus*, which was changed from *Agouti* since the re-validation of some of Brisson's generic names by the International Commission for Zoological Nomenclature (1998). This has helped avoid confusion between the common name "agouti" for *Dasyprocta* with the generic name *Agouti* for the paca.

Pacas, *Cuniculus paca*, are tropical caviomorphs of 6-12 kg, which roam in the Neotropical forests foraging for fruit (Pérez, 1992). They are described as solitary, territorial and generally aggressive. No detailed study of their mating system has been published, but they are thought to be monogamous (Pérez, 1992). Enurination behavior, where one male urinates on "his" female, is thought to be a type of mate-guarding behavior, consistent with monogamy (Smythe and Brown de Guanti, 1995). It is interesting to note that the male paca's penis has horny spines (Matamoros, 1980) which may serve to ensure fertilization. This suggests that there is post-mating competition, or sperm competition, among paca males, which in turn indicates that a certain degree of promiscuity is likely.

Family Dasyproctidae

Dasyprocta (commonly known as agoutis) is a speciose genus: 11 species and many subspecies, according to Wilson and Reeder (2005). Smythe (1970) mentioned the existence of monogamous pairs in *Dasyprocta agouti*, supported by the description of specific behaviors used by the male to ensure "possession" of the female, such as enurination. The male is attentive to the female, while the latter pays him little attention (similar to maras, see above). Smythe (1970) suggests that monogamy in this species is adaptive because of food scarcity in the dry season. At this bottle-neck time, aggression from neighboring males or couples promotes the shared defense of the hoarded seeds between members of the pair, leading to monogamy.

Family Dinomyidae

Pacaranas or Mountain pacas (*Dinomys branickii*) are large (10-15 kg; third largest caviomorph after the two species of capybaras), montane forest-dwelling caviomorphs from the mid- to Northern Andes (White and Alberico, 1992). Young pacaranas are good climbers (White and Alberico, 1992). They have varied means of communication (as do other caviomorphs) such as several sounds and a scent gland around the eyes (White and Alberico, 1992). Saavedra-Rodríguez *et al*. (2012) found that they live in pairs with their young, sharing several burrows and moving around 2.45 ha home ranges. Although Saavedra-Rodríguez *et al*. (2012) call these family associations "groups", there is no indication that they constitute social groups.

Family Echimyidae

This is the largest family of the hystricomorphs, commonly known as spiny rats. It is divided in 4 subfamilies with a large number of species grouped in 21 genera (Wilson and Reeder, 2005). The species in this family have been well studied in aspects such as taxonomy (although this is not quite clear yet; Wilson and Reeder, 2005), chromosomal speciation (*e.g.,* Reig *et al.,* 1980 and many others) and ecology (*e.g.,* Aguilera, 1999). Despite their abundance and diversity, little is known of echimyid behavior, social or otherwise, possibly because of their small size, nocturnal habits and the forested habitat where they are found. One species, the bamboo rat, *Kannabateomys amblyonyx*, has been described as monogamous in areas with low and patchy resource density and more polygynous in higher quality, more continuous habitat (Silva *et al.,* 2008). Such intraspecific variation in echimyids has been generalized by Adler (2011) who, using information on radio-tracking of movements as well as behavioral observations of several echimyid species from his own studies and others from the literature, found that at high densities echimyids tend to be promiscuous while at low densities they are monogamous, and polygynous at intermediate densities. Such patterns were also found inter-specifically (Adler, 2011).

Family Erethizontidae

This is the family of the New World porcupines, and includes the only member of the caviomorphs found in North America, namely, *Erethizon dorsatum*. This species is described as generally solitary, although several individuals may share a den in the winter (Woods, 1973). There are another four genera of this family in South America, the best known of which is *Coendou*. *Coendou prehensilis*, the most common and widely distributed species of the genus, is described in captivity as "socially tolerant, but not overtly gregarious" (Roberts *et al*., 1985). No more information on the social or sexual behavior of *Coendou* was found.

Family Myocastoridae

Coypus (*Myocastor coypus*) are the only species in this family. They are a smaller (5-9 kg) ecological equivalent to the Northern hemisphere beaver (*Castor* sp., 18 kg). Coypus have been introduced to several regions in the northern hemisphere, having achieved pest status in some places (Gosling and Baker, 1989).

Coypus are semi-aquatic and they form groups of some five adults, 1-5 males and 2-6 females (Guichón *et al.,* 2003) plus a variable number of subadults and young. Groups were socially cohesive and frequent "amicable" behaviors were observed. In such groups, one of the males is clearly dominant and tends to be the largest individual in the group, suggesting a polygynous mating system (Guichón *et al.,* 2003; Túnez *et al.*, 2009). Túnez *et al.* (2009), using microsatellite markers, assessed both relatedness among group members and reproductive skew among the males within a group in the two populations studied by Guichón *et al.* (2003). They found that groups were in fact kin clusters, with females within groups being significantly more closely related than females from different groups. These authors also found that the apparent dominant male in the groups of one population was in fact the father of 87% of the young of the group while in the other population paternity was more evenly distributed among males (Túnez *et al.*, 2009). Thus, the degree of polygyny can be quite high in some cases, but less so in others. The ecological reasons for this are not clear but Túnez *et al.* (2009) suggest that such flexibility can help individuals survive catastrophic events and improve their colonizing ability.

Family Octodontidae

The degus are a family of caviomorphs closely related to tuco-tucos (Ctenomyidae) (Wilson and Reeder, 2005). There are eight genera but only *Octodon* (degus) and *Spalacopus* (coruros) have been studied in any detail. Both are found in Southern South America where they live in groups sharing burrows. Not much more in known about coruro social and sexual behavior, so I will restrict my comments to the degus.

Degus (*Octodon degus*) are medium sized caviomorphs (170-300 g) who live in groups of 2-5 related females in communal burrows (Ebensperger *et al.*, 2004). Females sharing a nest constitute a stable social unit (Ebensperger *et al.,* 2004). The main benefit of sociality in these groups is predation (Ebensperger and Wallen, 2002) and increased efficiency in burrowing (Ebensperger and Bozinovic, 2000). There is variation in group size and composition among populations and it has been shown to be related to variation in predation and burrowing costs (Ebensperger *et al.*, 2012). The mating system of this species has not been completely elucidated but the sharing of a burrow between several females and one (sometimes more than one) male suggests polygyny (Ebensperger *et al.*, 2011).

Final remarks

From the point of view of sociality and mating systems, caviomorphs are unparalleled among mammals: all conceivable social and mating systems are present in one or other family. In particular the Caviidae, the Ctenomyidae and the Octodontidae contain examples for all of these cases. Interestingly, despite the great variety of behavioral tactics observed in many of these taxa, a number of common features recur, many possibly phylogenetically inherited rather than evolved *de novo* and hence convergent. Among these are the aggressive behaviors, shown mainly by males. The most common is the simple chase, observed in many taxa. A male would approach another and the other would simply step away. Sometimes this becomes a lunge where the attack is more violent. In most cases, this is the end of the interaction with one animal retreating while the other is the "winner". This commonly generates a dominance hierarchy, which is another recurrent feature of caviomorph social systems. The existence of a hierarchy is also a typical example of how individual behaviors displayed to obtain individual benefits (access to resources or mates) result in emergent properties at the next level, namely, the social group, where the hierarchy is observed. The hierarchy usually occurs among males and it is sometimes quite clear-cut and stable (*i.e.*, capybaras, Herrera and Macdonald, 1993) and sometimes it is difficult to ascertain (*i.e.*, viscachas, Branch, 1993). In the case of *Cavia aperea*, the hierarchy is clearer among females, which is interesting since females tend to compete less among them than males do. So, why do females "organize" themselves in a hierarchy in *C. aperea*? First I must point out that this was observed in captivity so it may be an artifact of this situation. If true, this implies strong competition among females with important consequences since only top ranking females breed successfully (Adrian and Sachser, 2010). Because the dominant male has been observed to provide parental care (Adrian *et al.,* 2005), perhaps it is this "resource" over which females are competing.

Two ecological factors associated with sociality are also exemplified by caviomorphs: predation and burrowing (Ebensperger and Cofré, 2001). Capybaras are the prime example of how predation favors aggregation, as is also shown in many African antelopes (Jarman, 1974; Brashares *et al.,*2000). Burrowing is also present and observed in several species of social tuco-tucos, degus and coruros (Ebensperger and Cofré, 2001). Interestingly, the vast majority of burrowing tuco-tucos are solitary, which suggests that, as a general rule, burrowing and sociality are not associated. Further research is needed to shed light on this.

Finally, caviomorphs also contain an example of the least common mating system among mammals. Since females carry by far the most of the reproductive cost in mammals, males, by contributing basically just an ejaculate and the genes therein, are free to leave and attempt to find another female to mate with, hence the typical polygynous mating system of mammals (Greenwood, 1980). The ecological conditions needed to overcome this extreme asymmetry in parental investment and generate a monogamous mating system occur at least twice in caviomorphs, the clearest example being the maras. Here, extreme ecological conditions of dryness and unpredictability of resources force males to remain with one female, possibly for life. The proximate mechanism for this may be something we humans would call "love": male maras follow "their" female everywhere they go and when she is lost, they do not try to join another female, even when they are available (Genest and Dubost, 1974).

Although much work is still needed to complete our picture of caviomorph social and mating systems, this group has generated a great deal of information which has helped advance our understanding of the evolution of such systems in mammals, their relation to ecological conditions, their biogeographic distribution and their phylogenetic origins. In the near future, since this is an active area of research, much light will be thrown on the evolution of social and mating tactics among mammals from the information gleaned from this unique group of rodents.

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8

MACROPHYSIOLOGICAL PATTERNS IN THE ENERGETICS OF CAVIOMORPH RODENTS: IMPLICATIONS IN A CHANGING WORLD

PATRONES MACROFISIOLÓGICOS EN LA ENERGÉTICA DE ROEDORES CAVIOMORFOS: IMPLICANCIAS EN UN MUNDO CAMBIANTE

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Abstract. In this article we review literature-based data on energy metabolism of caviomorph species in a changing world. The pioneer work of Arends and McNab (2001) analyzed the energetics of 30 caviomorph species, specifically the effect of their food habits and habitat preferences on basal metabolic rates. We would go further and test for the effect of body mass and geo-climatic factors (latitude, altitude, ambient temperature, precipitation) on caviomorph comparative energetic diversity. We analyze the relationship between changes in basal metabolic rate (BMR) and thermal conductance (C_{min}) by using conventional statistics and phylogenetically informed analyses. As this group is so diverse in terms of habitat use and distribution, for instance, we were not able to find any exogenous factor affecting energy metabolism and thermal conductance. Moreover, as the variance of BMR (~96 %) or C_{min} (~85 %) is explained almost entirely by body mass, it is understandable that it is not easy to correlate the residual percentage with geographical or climatic variables. We further discuss the effect of diet (quality, availability, predictability) on caviomorph energetics. As we performed an interspecific analysis (macroevolutionary) to test for correlations between metabolic variables and geo-climatic traits, we did not take into account the individual and/or population variability, then we discuss the proximate factors (*i.e.*, ambient temperature, diet) responsible for differences in the rate of metabolism and thermal conductance and their underlying mechanism in species belonging to this group. Furthermore, we also analyze the cost of different behaviors and activities that influence caviomorph lifestyles. We believe that there is valuable non-basal energetic information available that could be used to understand the whole picture of energy metabolism and thermal biology among caviomorph rodents. There is compelling evidence of climatic warming at a global scale (IPCC 2013). Searching for global patterns of physiologic variables in endotherms is an effort to understand and to predict the scope of these changes. With the available data from caviomorph rodents, we observed that no clear energetic trend appears in this group, because no geo-climatic variable affects patterns of minimal metabolism and thermal conductance. We are far from a complete understanding of the effect of climate change on caviomorph rodents; however, this review is an endeavor in this sense. Certainly, more studies analyzing physiological diversity in different taxonomic groups taking into account large geographic and temporal scales are needed to understand climate change effects. This kind of study must not only consider the predicted increase in ambient temperature, but also it needs to go beyond and search for global-scale patterns in other environmental factors such as photoperiod or seasonal timing. We review physiological information for many caviomorph species; however, for many others, neither physiological nor ecological or genetic information is available. As we outlined, some relevant issues must be taken into account (intraspecific-interpopulation physiological information). As more of this knowledge becomes available, we may be able to predict more accurately the responses of individuals, species or taxa to future changes, and predict as to whether climate change will harm or benefit individuals of a particular species.

Resumen. En este artículo se revisan datos de la literatura sobre el metabolismo energético de especies de caviomorfos en un mundo cambiante. El trabajo pionero de Arends y McNab (2001) evaluó el efecto de variables como hábitos alimentarios y preferencia de hábitats sobre la tasa metabólica basal de 30 especies de caviomorfos. En este trabajo nos propusimos dar un paso más y poner a prueba los efectos de la masa corporal y factores geo-climáticos en la diversidad energética comparada de los roedores caviomorfos. Se analiza la relación entre los cambios en la tasa metabólica basal (BMR) y la conductancia térmica ($C_{\min}$), utilizando estadística convencional y análisis filogenéticamente informados. La base de datos que utilizamos incluye una importante cantidad de especies con modo de vida subterráneo, por lo que se procedió, en primera instancia a analizar si este modo de vida influye en la relación entre la BMR o la $C_{\min}$ y la masa corporal. No se observaron diferencias entre las ecuaciones alométricas obtenidas excluyendo las especies subterráneas de la base de datos o utilizándola en forma completa, tanto para los análisis convencionales como los filogenéticamente informados. Por lo que en esta revisión se reportan los datos alométricos entre las variables fisiológicas y la masa corporal para todas las especies de roedores caviomorfos, independiente de su modo de vida. Asimismo, ya que la BMR y la conductancia térmica forman parte de un sistema coordinado de regulación de la transferencia de calor corporal, se evaluó explícitamente si estas variables están correlacionadas, observándose una relación positiva entre ambas variables. Posteriormente, analizamos si variables geo-climáticas de la zona que habitan las especies de caviomorfos (latitud, altitud, temperatura anual, temperatura mínima, rango de temperatura anual, estacionalidad de la temperatura, rango de temperatura mensual de las precipitaciones) explican la variación tanto de la BMR como de la $C_{\min}$. No observamos ningún factor exógeno que afecte el metabolismo energético y la conductancia térmica, posiblemente debido a la diversidad que presenta este grupo en cuanto a, por ejemplo, al uso del hábitat y la distribución. Por otra parte, como la varianza de BMR (~96 %) o la $C_{\min}$ (~85 %) se explica casi en su totalidad por efecto de la masa corporal, es comprensible el hecho de no observar correlaciones entre la variación residual con variables geográficas o climáticas. Posteriormente, discutimos el efecto de la dieta (calidad, disponibilidad, previsibilidad) en la energética de caviomorfos. Dado que realizamos análisis interespecíficos (macroevolutivos) para evaluar la existencia de correlación entre variables metabólicas y características geo-climáticas, no se tomó en cuenta la variabilidad individual y/o poblacional -asumimos que tal variabilidad es despreciable-, discutiendo solo acerca de los factores proximales (*i.e.,* temperatura ambiental, dieta) responsables de las diferencias en la tasa metabólica y la conductancia térmica, y sus mecanismos subyacentes en especies pertenecientes a este grupo. Además, analizamos los costos de diferentes comportamientos y actividades que influencia su estilo de vida. Existe información disponible valiosa sobre energética, más allá de la basal, que podría ser utilizada para comprender el cuadro completo del metabolismo energético y la biología térmica en los roedores caviomorfos. Hay suficiente evidencia del calentamiento climático a escala global (IPCC 2013). La búsqueda de patrones fisiológicos en endotermos representa un esfuerzo destinado a entender y a predecir el alcance de estos cambios. Con la base de información disponible de roedores caviomorfos, nosotros no pudimos encontrar para este grupo un patrón claro de relaciones entre variables ambientales y variables energéticas, dado que no se observo un efecto de las variables geo-climáticas evaluadas sobre el metabolismo mínimo y la conductancia térmica. Estamos lejos de comprender como los cambios climáticos afectan a la biología de los roedores caviomorfos, sin embargo, esta revisión es un esfuerzo en este sentido. Se necesitan más estudios que se dediquen a analizar la diversidad fisiológica en diferentes grupos taxonómicos, teniendo en cuenta que se necesitan de grandes escalas geográficas y temporales para entender los efectos del cambio climático. Los estudios a encarar no solamente podrían considerar la elevación predicha en la temperatura ambiente, podrían estar dirigidos también a la búsqueda de patrones a escala global de efectos de variables secundarias. Nosotros reunimos información fisiológica de muchas especies de caviomorfos, pero existe mucha información ecológica y genética disponible con una enorme potencialidad para efectuar metanálisis. Cuanto más esté disponible este conocimiento, más vamos a ser capaces de predecir cambios en las respuestas a nivel individual, de especies o taxa, y predecir cuándo y en qué nivel el cambio climático será perjudicial o beneficioso.

Introduction

Caviomorph rodents comprise a diverse group of species that inhabits almost all habitat types in Central and South America, and also some areas of North America (Upham and Patterson, 2012). Caviomorphs are considered a monophyletic group that has diversified since approximately 35 Ma (Opazo, 2005; Upham and Patterson, 2012). This group has diversified more than any other group of Neotropical mammals (Hershkovitz, 1972), occupying almost all available habitats from cold to tropical, from mountain slopes to coastal grasslands. Besides type of habitat, species of this group also varies in its habits, from semiaquatic or terrestrial to subterranean. Their social structure ranges from solitary-living to highly gregarious species (Redford and Eisenberg, 1992). Variation in body mass is important, it comprises species weighing only a few grams (*e.g., Ctenomys talarum*) to large species weighting over 50 kg (*e.g., Hydrochoerus hydrochaeris*); however, all of them are narrowly herbivorous. The diversity of caviomorph rodents encouraged Arends and McNab (2001) to compare the energetics of caviomorph rodents evaluating the effect of their food habits and habitat preferences on basal metabolic rates. This gives us the basis to take a step forward on the analysis of other variables that could account for energetic variability of caviomorphs. So we evaluated the effects of geographical distribution and geo-climatic traits on the energetics of caviomorphs, in relation to their current and future climatic conditions.

Our planet is experiencing a substantial change in its environmental conditions, particularly in temperature and habitat loss. It is expected that Earth's temperature will increase due to global climate change (IPCC 2013), representing one of the major challenges that individuals must confront in the near future (Parmesan, 2006). While some species can deal with these changes through migration or altering their range, for some this is not an option. Even when animals are able to move, the response is often too slow, resulting in a potentially deleterious effect (Pörtner and Farrell, 2008; Inouye *et al.*, 2000; Visser, 2012). In particular, physiological responses to changes in climatic variables give an excellent opportunity to know how global or local changes in environmental factors might affect individual fitness, species distribution, and trophic interactions in a community (Spicer and Gaston, 1999; Chown *et al.,* 2004). Moreover, Cooke *et al.* (2013) posit that using physiology as an integrative term of the functional and mechanical responses of individuals, we are able to develop and define strategies for conservation of populations, species and ecosystems, hence biodiversity (Bernardo and Spotila, 2006; Bernardo *et al.,* 2007; Rodriguez-Serrano and Bozinovic, 2009; Bozinovic *et al.*, 2011; Huey *et al.*, 2012; Cooke *et al.*, 2013).

Given the central role that energy metabolism plays in all biological processes (acquisition, transformation and use of energy), it is not surprising that several studies focus on correlations among energetics of different populations or species and variation in geographical and climatic factors. In fact, those correlations generally have been seen as evidence of adaptation. Most endotherms are homeothermic and use behavioral, morphological, and especially, physiological adjustments to maintain a high and relatively constant body temperature (T_b). One of the main aspects to take into account is the amount of energy destined to maintain T_b constant, thus maintaining a balanced daily energy budget. Constant T_b, within a certain range of ambient temperature, is maintained by the interaction between basal metabolic rate (BMR) and minimal thermal conductance (C_{min}, Bozinovic *et al.,* 1995; McNab, 2002).

Basal metabolic rate (BMR) is a standardized measurement of minimal energy required to maintain individual homeostasis (McNab, 2002; for discussion about definition and controversies, see Speakman *et al.*, 1993; Speakman, 2000). Since Kleiber (1932), body mass has been described as one of the main determinants of BMR. When the effect of body mass is statistically removed, the residual variation has been attributed to food habits (McNab, 1992), habitat productivity (Mueller and Diamond, 2001; White, 2003), climate (Lovegrove; 1996; 2003; Rezende *et al.,* 2004; Withers *et al.*, 2006), and latitude (Lovegrove, 2003), among other factors. Besides, although endotherms have a high capacity to face environmental changes and buffer them (McNab, 2002), they are not unaffected by changes in specific climatic factors -mainly, ambient temperature (Welbergen *et al.*, 2008; McKecknie and Wolf, 2010). On the other hand, minimal thermal conductance (C_{min}, Scholander *et al.*, 1950) is another predictor of energy expenditure, because it gives insight on the thermal balance between individuals and the environment. As with BMR, minimal thermal conductance is a standardized measurement and accounts for the thermal-isolation properties of individuals (McNab, 2002) affected by climatic factors (Naya *et al.*, 2013a). Thus, estimation of minimal energy metabolism and thermal balance would allow us to understand the underlying mechanisms that allow different caviomorph species to live in the environment where they are found and potentially assess whether these species are vulnerable to the predicted increase of ambient temperature (Hofmann and Todgham, 2010; Huey *et al.*, 2012; IPCC 2013). Correspondingly, the relationship between energy metabolism and body mass would also allow us to evaluate, in species of this group that differ in almost 300-fold in body mass, the effects on the thermal biology within their wide distribution range over the Americas. Therefore, the aim of the present study is to assess how changes in geographic and climatic factors influence energetic and thermal variables in caviomorph rodents. This approach attempts to characterize the patterns of variability in energy metabolism and thermal biology in the interspecific framework of caviomorph biodiversity. Furthermore, with this approach we would explore the ecological implications of such pattern on physiological diversity (Bernardo and Spotila, 2006; Bernardo *et al.*, 2007).

In this review, we present new approaches to analyzed literature-based data of energy metabolism of caviomorph species and we discuss it in light of the new scenarios of climate change. In the first section, we analyze the relationship between changes in BMR and C_{min} of caviomorph rodents using two different methodological approaches, conventional statistics and phylogenetically informed analyses. In the second part, we analyze the cost of different behaviors and activities that influence the lifestyles of species.

Interspecific variation of basal energetics and thermal conductance

As presented before, BMR and C_{min} are probably the most often used predictors of the energy expenditure of organisms (McNab, 2002), affected mainly by body mass (see Kleiber, 1932). The range of body masses that are observed in caviomorph rodents implies that a substantial variation in BMR or C_{min} might be present. To our knowledge, several studies focus on the relationship between both BMR or C_{min} and body mass in different mammal species (McNab, 2002; see Riek and Geiser, 2013 for allometry of thermal variables). In this review, we introduce a new approach to evaluate these variables using data from caviomorphs rodents. The relationship of both BMR and C_{min} with body mass was analyzed, using both conventional analysis (Ordinary Least Squares, OLS) and phylogenetically comparative methods (Phylogenetically Independent Contrasts, PIC). For a brief explanation of the methodology see Box 1.

BOX 1

Database

From the literature, we collected data on basal metabolic rate (BMR), minimal thermal conductance (C_{min}), delta of body temperature (ΔT_b), and body mass (M) for 42 populations (belonging to 39 species) of caviomorph rodents. Species included in the database represent 24 genera and 12 families (Fig. 1 Box). To build up this database (available upon request), we considered only studies that included BMR measured in animals captured in the field, and we discarded those studies that reported resting metabolic rate (RMR) instead BMR. For each species, we gathered geographic coordinates or locality information for the collecting sites from the original work. For each data point we downloaded, from the WorldClim dat base (http://www.worldclim.org/), the altitude (Altitude, in m) and several climatic variables. Climatic data from an area of ~1 km^2, were: a) mean annual temperature (T_{med}, in ºC), b) minimum temperature of the coldest month (T_{min}, in ºC), c) annual temperature range (TAR: difference between the maximum temperature of the warmest month and the minimum temperature of the coldest month, in ºC), d) temperature seasonality (TS: standard deviation of the mean monthly temperature, in ºC), e) monthly temperature range (TMR; the average differences between the maximum and minimum monthly temperatures), and f) precipitation seasonality (PS; the standard deviation of the mean monthly rainfall). As used in Naya *et al.*, 2012, we used the variable CorLat to assess the combined effect of latitude and altitude. CorLat is estimated according Price *et al.* (1998), using the following formula: CorLat = (altitude / 76.25) / latitude.

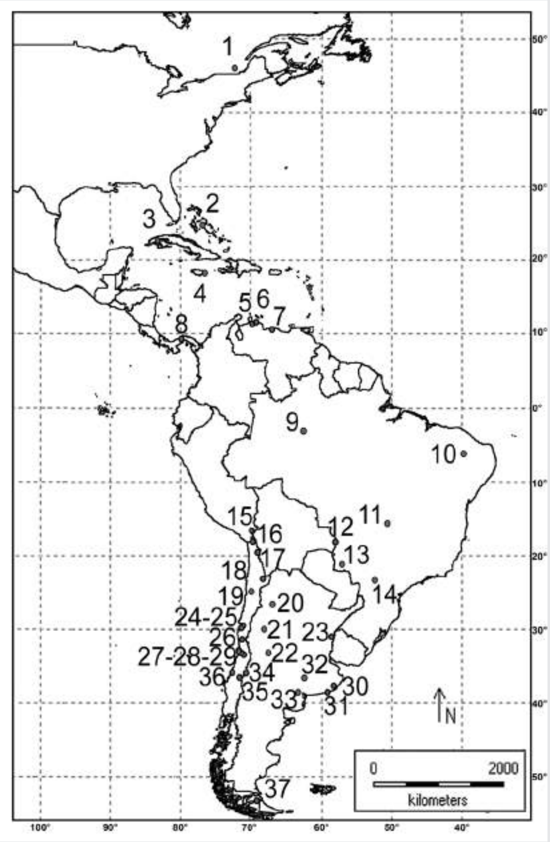
Statistics

We evaluated physiological data using two different approaches. All allometric regressions were computed using both conventional statistics (OLS) and phylogenetically independent contrasts (PIC, see below). Because our data set of caviomorph species includes a large number of subterranean species, we compared allometric regressions with and without subterranean species using ANCOVA, to compute parallelism and intercept differences for both regressions. Partial regression analysis was used to test the effect of M and the proposed geographic and environmental variables on energetic and thermal variables. Different models (OLS or PIC) were compared using the Akaike Information Criterion (AIC; see Burnham and Anderson, 2001). The best model of the set is that with the lowest AIC value. We also measured the Akaike weight (ω_i) to estimate the probability that any given model is the best fit compared with the other models.

Phylogenetically independent contrasts

We evaluated the effect of phylogeny on the relationship between BMR and environmental factors, using phylogenetically independent contrasts. First, we constructed a phylogenetic tree that includes all the species/populations present in our caviomorph sample, using the tree described in Upham and Patterson (2012). The arbitrary branch length transformation of Pagel (1992) was used to standardize branch lengths in the tree. The relationships between energetic and thermal variables and environmental factors were evaluated through independent contrasts (Felsenstein, 1985), computed with the PDAP module (Midford *et al.*, 2010) of the Mesquite program (Maddison and Maddison, 2006). A log10 transformation was applied to BMR, $C_{\min}$, ΔT_b and M raw data in order to meet the assumption of normality. No transformations were performed on altitude measurements or climatic data.

Localities of caviomorph species (gray) used in the analysis.



1. *Erethizon dorsatum;* 2. *Geocapromys ingrahami;* 3. *Capromys pilorides/Myocastor coypus;* 4. *Geocapromys brownii;* 5. *Hydrochoerus hydrochaeris;* 6. *Cuniculus paca;* 7. *Dasyprocta leporina;* 8. *Proechimys semispinosus;* 9. *Myoprocta acouchy;* 10. *Kerodon rupestris;* 11. *Thrichomys apereoides;* 12. *Galea musteloides;* 13. *Dolichotis salinicola;* 14. *Dasyprocta azarae;* 15. *Ctenomys peruanus;* 16. *Microcavia niata/Octodontomys gliroides;* 17. *Ctenomys opimus;* 18. *Ctenomys fulvus* (2 data points)*;* 19. *Chinchilla chinchilla;* 20. *Ctenomys tuconax;* 21. *Octomys mimax;* 22. *Tympanoctomys barrerae;* 23. *Lagostomus maximus;* 24. *Octodon lunatus;* 25. *Lagidium viscacia;* 26. *Chinchilla lanigera;* 27. *Abrocoma bennetti/Spalacopus cyanus (*low altitude population)*;* 28. *Spalacopus cyanus* (high altitude population)*;* 29. *Octodon degu;* 30. *Ctenomys talarum;* 31. *Ctenomys australis/C. talarum;* 32. *Ctenomys porteousi;* 33. *Ctenomys chasiquensis;* 34. *Aconaemys fuscus;* 35. *Ctenomys maulinus;* 36. *Octodon bridgesi;* 37. *Ctenomys magellanicus.*

Our data set of caviomorph species includes a large number of subterranean species. Subterranean species show morpho-physiological traits related to life underground, when compared with surface dwelling species. These include compact bodies, microphtalmic eyes, short tails, large and powerful forefeet, low BMR compared to surface-dwelling species of same body mass, among others (Nevo, 1999). Therefore, in a preliminary analysis, we tested if commitment to subterranean life influences the allometric equation for all caviomorph species.

No differences were observed in allometric equations of BMR vs. body mass (M) when all species of the group were used, compared to those equations obtained when subterranean species were excluded from the regression. This pattern was similar when either OLS (Slope, $F_{1, 64} = 0.04$, $P = 0.84$, Intercept, $F_{1, 65} = 0.27$, $P = 0.61$) or PIC were used (Slope, $F_{1, 63} = 0.58$, $P = 0.45$, Intercept, $F_{1, 64} = 1.05$, $P = 0.31$). In a similar way, no differences were observed in allometric equations of the relationship between C_{min} and body mass when subterranean species were excluded (OLS, Slope, $F_{1, 59} = 0.17$, $P = 0.68$, Intercept, $F_{1, 60} = 0.34$, $P = 0.56$; PIC, Slope, $F_{1, 57} = 0.91$, $P = 0.34$, Intercept, $F_{1, 58} = 1.18$, $P = 0.28$).

As no differences were found when subterranean species were included, we used the entire data set of species in our further analysis. Slopes and intercepts of the relationship between BMR and M tested with conventional or phylogenetically independent analyses were similar. In all cases, the 95% confidence intervals for the equations obtained using phylogenetic and non-phylogenetic method overlapped (Tab.1).

Table 1. 95% confidence intervals of slopes and intercepts of regressions of basal metabolic rate (**BMR**) or thermal conductance (**C_{min}**) with body mass of all data set of caviomorphs, obtained with ordinary least squares (**OLS**) and phylogenetically independent contrasts (**PIC**) analysis.

		OLS	PIC
BMR	Slope (95% CI)	0.70 – 0.79	0.70 – 0.81
	Intercept (95% CI)	1.99 – 3.95	2.25 – 3.97
C_{min}	Slope (95% CI)	0.53 – 0.72	0.51 – 0.70
	Intercept (95% CI)	0.27 – 0.86	0.31 – 0.99

Note: data are $\log_{10}$ transformed.

The standard allometric equation calculated for the entire data set of caviomorph rodents (Fig. 1.1) using OLS analysis was

$$\text{BMR (ml O}_2\text{/h)} = 2.80\ M^{0.76 \pm 0.01}$$

$$(R^2 = 0.95,\ F_{1, 40} = 813.46,\ P < 0.001)$$

When same data set was analyzed taking into account phylogeny, the obtained allometric equation was

$$\text{BMR (ml O}_2\text{/h)} = 2.98\ M^{0.74 \pm 0.02}$$

$$(R^2 = 0.97,\ F_{1, 39} = 1098.75,\ P < 0.001)$$

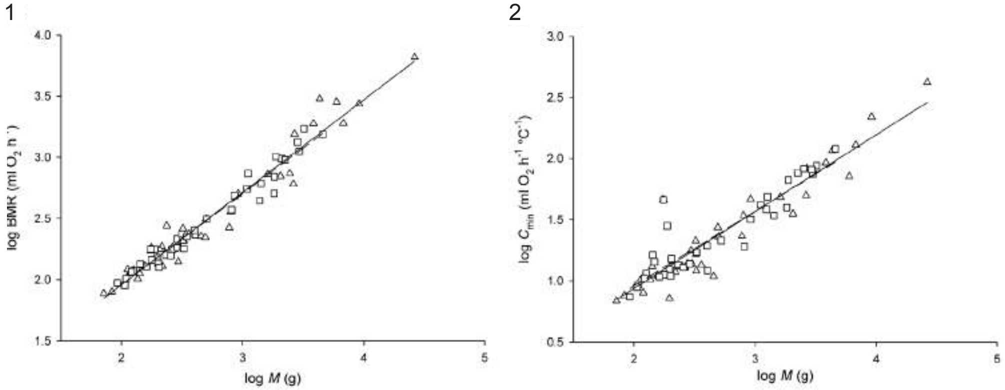


Figure 1. 1. Relationship between log-transformed basal metabolic rate (**BMR**), -or log-transformed minimal thermal conductance $\boldsymbol{C}_{\mathbf{min}}$, and 2. log-transformed body mass (***M***) among caviomorph rodents, obtained with ordinary least squares (**OLS**, triangles) and phylogenetically independent contrasts (**PIC**, squares) analysis. Solid line: **OLS** regression. Dashed lines: **PIC** regression.

In both cases, *M* is body mass (g). A detailed discussion about the value of the allometric exponent and the mechanistic basis of the allometric scaling in the relationship between BMR and body mass are included among the aims of this review. Interesting reviews are found on the literature dealing with this issue (Savage *et al.*, 2004; White and Seymour, 2005; White *et al.,* 2007; Capellini *et al.*, 2010; White, 2011). We found that allometric equations in caviomorph rodents, using OLS or PIC, are fairly similar to those proposed by Kleiber (1932).

In the same way, regression equations of C_{min} vs. body mass were similar regardless of which statistical method we used (Tab. 1). Allometric equations calculated for studied caviomorph species (Fig. 1.2) using conventional analysis was

$$C_{\mathrm{min}}\ (\mathrm{ml\ O_2/h\ °C}) = 0.49\ M^{\,0.63 \pm 0.02}$$

$$(R^2 = 0.84,\ F_{1,\,37} = 196.83,\ P < 0.001)$$

When evaluating C_{min} corrected for the effect of phylogeny to render data independent, we obtained the following equation

$$C_{\mathrm{min}}\ (\mathrm{ml\ O_2/h\ °C}) = 0.55\ M^{\,0.61 \pm 0.02}$$

$$(R^2 = 0.87,\ F_{1,\,36} = 177.85,\ P < 0.001)$$

The scaling relationship between BMR and body mass is different from the relationship observed between C_{min} and body mass. In a previous study, Arends and McNab (2001) reported similar allometric coefficients for both variables using a database of 30 caviomorph species.

Recently, it has been proposed for mammals that similar environmental factors might affect the evolution of both BMR and C_{min}, and that both variables are part of a coordinated system of heat transfer regulation, hence body temperature (Naya *et al.*, 2013b). In the same way, Luna *et al.* (2009) posit that it could be a trade-off between low thermal conductance and low BMR in *Ctenomys* species that accounts for the prevention of either hyperthermia at high ambient temperatures or hypothermia at low ambient temperatures. In this context, we explicitly tested the correlation between body mass-controlled BMR and body mass-controlled C_{min}. We found that, independent of the type of statistical analysis, residuals of BMR are related positively to residuals of C_{min} (OLS, $r = 0.40$, $P = 0.01$; PIC, $r = 0.61$, $P < 0.01$; Fig. 2).

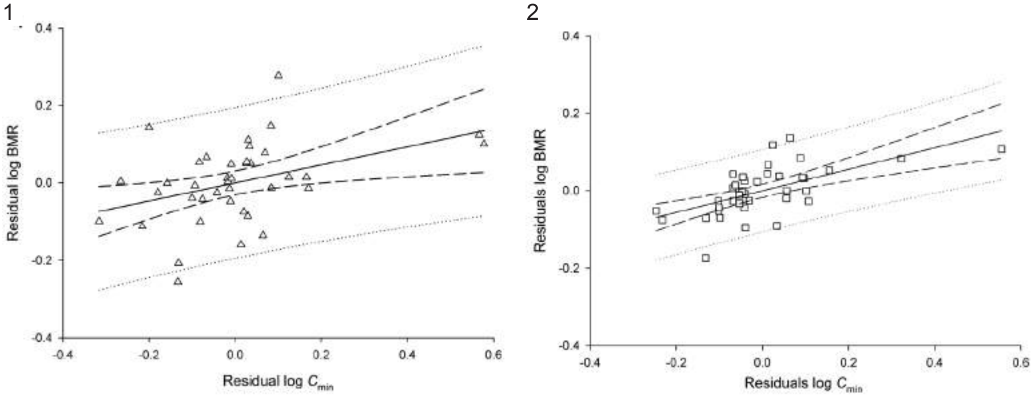


Figure 2. Regression between residuals of log-transformed basal metabolic rate (**BMR**) and log-transformed minimal thermal conductance (**C_{min}**), 1. obtained with ordinary least squares (**OLS**, triangles) and 2. phylogenetically independent contrasts (**PIC**, squares) analysis.

After allometric analyses, we tested if geographical and climatic variables explain the residual variation of BMR or C_{min} among caviomorph rodents (for a brief explanation of methods, see Box 1). Conventional analysis showed no correlation between BMR and geographical or climatic variables. Similar pattern was observed in C_{min}: body mass is the only explicatory variable (Table 2). In accordance, Arends and McNab's (2001) conventional analysis reported that body mass was the main factor affecting BMR and C_{min}. They also found no effect of climate –in that case used as categorical variable– on these variables.

Studies of BMR or C_{min} variation have been attempted to elucidate the factors determining such variability in several taxa and taxonomic affiliation (Hayssen and Lacy, 1985; Lovegrove, 2000; Rezende *et al.*, 2004; McNab, 2008; White, 2011). By contrast, none of these factors affect variation in caviomorphs (Tab. 2); this probably reflects the intrinsic interspecific variation in the lifestyles of the studied species. As this group is so variable in their biology (habitats, diet, distribution, etc.), we are not able to find any exogenous factor affecting energy metabolism and thermal conductance. Moreover, as the variance of BMR (~96 %) or C_{min} (~85 %) is explained almost entirely by body mass, it is reasonable that it is not easy to correlate the remaining percentage with geographical or climatic variables.

Thermoregulatory abilities of individuals are related to the balance between heat production and heat loss (McNab, 2002). As we collected BMR and C_{min} for each species, and body mass-controlled BMR and body mass-corrected C_{min} are correlated (see before, Fig. 2.1 and 2.2, we calculate the differential of body temperature at the lower limit of thermoneutrality (ΔT_b) for each caviomorph species.

The standard allometric equation calculated for ΔT_{b} vs. body mass (Fig. 3.1) using OLS analysis was

$$\Delta T_{\mathrm{b}}\ (^{\circ}\mathrm{C}) = 5.47\ M^{0.14 \pm 0.04}$$

$$(R^2 = 0.23,\ F_{1,\ 37} = 10.74,\ P = 0.003)$$

and using PIC was

$$\Delta T_{\mathrm{b}}\ (^{\circ}\mathrm{C}) = 5.03\ M^{0.15 \pm 0.04}$$

$$(R^2 = 0.31,\ F_{1,\ 36} = 15.99,\ P < 0.001)$$

Table 2. Partial regression between basal metabolic rate (**BMR**) or thermal conductance (***C*$_{\text{min}}$**) and environmental variables and body mass of caviomorphs, obtained with ordinary least squares (**OLS**) and phylogenetically independent contrasts (**PIC**) analysis.

	BMR				**C$_{\text{min}}$**			
	OLS		**PIC**		**OLS**		**PIC**	
	r	**P**	**R**	**P**	**r**	**P**	**r**	**P**
Latitude	0.001	0.56	0.002	0.23	-0.002	0.59	<-0.001	0.86
Altitude	<0.001	0.11	<0.001	0.23	<0.001	0.52	<0.001	0.82
CorLat	0.004	0.29	0.003	0.58	-0.009	0.29	-0.002	0.84
T_{med}	-0.014	0.61	-0.004	0.87	-0.039	0.35	0.002	0.95
T_{min}	0.013	0.60	<0.001	0.92	0.028	0.49	-0.003	0.93
TMR	0.015	0.73	0.037	0.25	-0.041	0.56	-0.038	0.42
TS	-0.001	0.69	<0.001	0.62	-0.001	0.73	-0.001	0.43
TAR	0.019	0.68	-0.02	0.55	0.038	0.62	0.026	0.60
PS	<0.001	0.79	<-0.001	0.61	<0.001	0,91	<-0.001	0.21
M	0.80	<0.001	0.76	<0.001	0.60	<0.001	0.65	<0.001

In evolutionary terms, besides modifications in BMR or C_{min}, at any given mass, a caviomorph rodent may increase ΔT_{b} by increasing body mass. In this context, for example, combination of low BMR and high C_{min}, might lead to a low temperature differential. However, the interaction among these variables is complex, and difficult to ascribe to a particular environmental factor. Thus, if BMR and C_{min} were maintained allometrically in a similar way throughout the range of body masses of caviomorphs, in evolutive terms, the almost exclusive way to cope with a decrease in T_{a} is to increase body mass.

Bergmann's rule (1847) is one of the oldest biogeographic relationships proposed, and after several reformulations (see Meiri and Dayan, 2003), states that body mass of congeneric species or populations is greater in colder regions compared to those species or populations living in warmer regions (Mayr, 1963; also see Blackburn *et al.*, 1999). Underlying mechanisms responsible for this pattern would be related to thermal adaptations to different environmental conditions. For example, with higher body surface-to-volume ratio at high temperatures, individuals

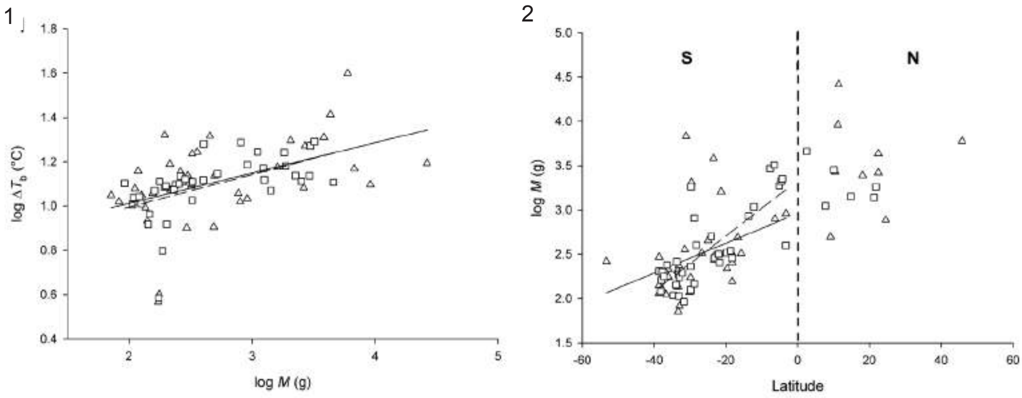


Figure 3. 1. Relationship between log-transformed delta of body temperature (**ΔT_b**) and log-transformed body mass (***M***), and 2. relationship between log-transformed body mass (***M***) and latitude among caviomorph rodents, obtained with ordinary least squares (**OLS**; triangles) and phylogenetically independent contrasts (**PIC**, squares) analysis. Solid line: **OLS** regression. Dashed lines: **PIC** regression. Only regression of southern caviomorph species are shown in Fig 3.2.

are allowed to dissipate heat effectively, whereas, at low temperatures, the low surface-to-volume ratio ensures a reduction in heat loss (Mayr, 1963). Therefore, since temperature and other environmental variables are highly correlated with latitude, a positive relationship between latitude and body mass is expected (Ashton *et al.,* 2000; Meiri and Dayan, 2003). By extending this idea, we might expect a change in body mass according to latitude over time to account for climate warming (see Millien *et al.,* 2006). Several examples can be found in the literature that show a change in body mass over time (Millien and Damuth, 2004; Millien, 2004; Yom-Tov and Yom-Tov, 2004). These results have been interpreted as evidence of adaptation to climate change (Yom-Tov, 2001, but see Teplitsky *et al.,* 2008).

Different large-scale interspecific studies have shown a clear Bergmann-like pattern between body mass and latitude in mammals from the northern Nearctic (Blackburn and Hawkins, 2004), and Western Palaearctic (Rodríguez *et al.*, 2006), but in Neotropical mammals an inverse pattern was found (Rodriguez *et al.*, 2008). Interestingly, despite using only species for which BMR data were reported and the relative significant influence of *Erethizon dorsatum* in the regression -high body mass at high latitude-, a converse to Bergmann's rule pattern was also observed in this group of Neotropical mammals. Both conventional and phylogenetically informed analyses showed a negative relationship between body mass and latitude. Based on the Akaike Criterion, the model of body mass in terms of latitude, controlled by phylogeny, is better than a conventional proposed model (OLS, AIC = -92.76, $\omega_i = 0.01$; PIC, AIC = -107.50, $\omega_i = 0.99$). Interestingly, when we analyzed this relationship using northern or southern species exclusively, we found that body mass of southern caviomorph species decreased with the increment of latitude, either using OLS ($R^2 = 0.14$, $F_{1,31} = 5.10$, $P = 0.03$) or PIC ($R^2 = 0.62$, $F_{1,33} = 54.69$, $P < 0.01$); however, northern species showed no relationship between latitude and body mass (OLS, $R^2 = 0.001$, $F_{1,7} = 0.01$, $P = 0.91$; PIC, $R^2 = 0.30$, $F_{1,4} = 1.70$, $P = 0.26$, Fig. 3.2).

This pattern must be taken with caution because we used a small data set from all extant caviomorphs. In this sense, data for body mass of the capybara (*Hydrochoerus hydrochaeris*) correspond to individuals from populations in Venezuela. The distribution of *H. hydrochaeris* is wider, occurring from Venezuela to central areas of Argentina (Redford and Eisenberg, 1992). Alternatively, this pattern can be ascribed to the presence of subterranean species in the data analysis. An inverse pattern appears to be rather usual in subterranean caviomorph rodents. Medina *et al.* (2007) found that among *Ctenomys* species, which are distributed in the southern cone of South America (Redford and Eisenberg, 1992), body mass decreases with the increment of latitude. Moreover, at the intraspecific level, the same pattern is found. Both, *C. talarum* (Buenos Aires Province, Argentina) and *C. perrensi* (Corrientes Province, Argentina) follow the converse to Bergmann's rule (Medina *et al.*, 2007). Therefore, the same selective pressure, other than ambient temperature, might be operating on caviomorph rodents to determine the converse pattern, and this factor might be operating at different levels. The converse to Bergmann's rule in southern species would be related to diet, habitat productivity or seasonality, (Ashton *et al.*, 2000; Meiri *et al.*, 2007). For example, Yom-Tov and Yom-Tov (2005) found a converse pattern in *Sorex cinereus*. They suggest that lower body mass at high latitudes was due to low food availability in winter months. Moreover, it could be reasonable to consider that in strictly herbivorous species, such as *Ctenomys* spp., an inverse trend might be related to the high diversity and availability of plants at low latitudes when compared with high latitudes (Medina *et al.*, 2007). Finally, seasonality has been proposed to explain the converse pattern. At least for ectotherms, a shorter productive season through high latitudes progressively limits the time available for foraging, growth and development, hence increments of body mass can be restricted (Blanckenhorn and Demont, 2004). This pattern can also be attained in endotherms directly or indirectly via other environmental parameters (*e.g.*, variability of precipitation; see Medina *et al.*, 2007).

Extending this idea, could the same factors account for the residual variation of BMR –or C_{min}– in caviomorph rodents? As we proposed, residual variation of BMR among mammals has been ascribed to several biotic and abiotic factors, one of them being diet. McNab (1986) hypothesized that variations in the quality, availability and predictability of food resources can affect BMR (food habitat hypothesis). According to the food habitat hypothesis, species living in areas with low food availability and/or predictability (Cruz-Neto and Jones, 2005), or low energy content and/or low digestibility of the food (Cruz-Neto *et al.*, 2001), tend to show low mass-specific BMR (McNab, 2002). Most studies in which the relationship between BMR and diet was evaluated have utilized geographical and climatic variables, such as latitude, temperature, etc., as proxies for the effect of quality, availability and predictability of food resources (see Cruz-Neto and Bozinovic, 2004). For instance, when a broad characterization of diet categories is used, the feasible variation of food items that are consumed by individuals of particular species is eventually ignored (see Cruz-Neto and Bozinovic, 2004). Thus, an adequate characterization of diet quality can avoid misleading interpretations in interspecific analyses of diet quality (McNab, 2002; Muñoz-Garcia and Williams, 2005). Although all caviomorphs are herbivorous, food habits can be characterized even further. Arends and McNab (2001) found that when only food habits were included in the analysis, BMR of folivorous caviomorphs is lower than BMR of grazers, frugivores and seed-eating species. As was proposed by McNab (1978), low BMR in folivorous species would be due to interaction between high fiber content, presence of secondary compounds in leaves and/or low muscle mass. In our analysis, most of the folivorous species belonging to the genus *Capromys* and *Geocapromys* are also island endemics. So this correlation might lead to ambiguous interpretations because, as capromyids belong to a monophyletic group among caviomorphs (Upham and Patterson, 2012), it would be difficult to differentiate if food habits or phylogenetic relatedness is the best predictor of BMR variation (Cruz-Neto *et al.*, 2001; Rezende *et al.*, 2004; but see Muñoz-Garcia and Williams, 2005).

On the other hand, the effect of food availability and predictability cannot be easily excluded, due to correlation with other habitat characteristics. A good candidate to represent those variables, but mainly food availability, is net primary productivity (NPP). As NPP represents the rate of resource accumulation (Waide *et al.*, 1999; White *et al.,* 2007), it would be reasonable to assume that it would be linked to BMR. At the intraspecific level, Bozinovic *et al.* (2009) examined BMR of *Octodon degus* from populations from different habitats in Chile, and found that individuals from populations with low NPP -and low annual precipitation- consistently show low BMRs. As seen in *Peromyscus* species (Mueller and Diamond, 2001), mass-independent BMR of *O. degus* is positively correlated with habitat productivity. Notwithstanding this finding, Luna *et al.* (2009) established that NPP was not a variable that affects BMR within the subterranean genus *Ctenomys*. Undoubtedly, more data are needed for interspecific assessment of the effect of diet (quality, availability and predictability of food resources) on BMR among caviomorph rodents.

Intraspecific variation of basal energetics and thermal conductance

We performed an interspecific analysis to test correlations between metabolic variables and geo-climatic traits. We did not take into account the individual and/or population variability in BMR or C_{min}, instead we assume that such variability lies within a narrow range for each species. The potential pitfall of the interspecific studies can be offset by an intraspecific approach. While interspecific studies focus on the macroevolutionary factors that affect physiological variables –in our case, BMR and C_{min}–, intraspecific analyses look for the proximate factors responsible for differences in the rate of metabolism and their underlying mechanism. Our interspecific analysis excludes the possibility of adjustments in the former variables, but we do not deny that this adjustment can occur. Intraspecific variability could be wide and biologically significant, being the substrate of natural selection (Bartholomew, 1987; Speakman *et al.,* 2004). The apparent divergence between the two types of approaches would not constrain a full analysis of animal energetics; thus, intraspecific studies can complement interspecific ones (Ives *et al.*, 2007).

It is widely recognized that BMR and C_{min} of individuals can vary in time and space (see McNab, 2002; Piersma and van Gils, 2011). Microevolutionary factors affecting BMR can be assessed in an ecological context by testing differences among geographically separated populations in order to account for patterns of environmental variability (spatial scale) or testing individuals from a single population confronting seasonal variation or lab-controlled conditions. Given that differences in BMR among populations of different species were included in our previous analyses (*Ctenomys talarum*, *C. fulvus*, and *Spalacopus cyanus*), we provide an overview of the phenotypic flexibility in metabolic variables found in caviomorph species.

Temperature

Phenotypic flexibility in BMR of endotherms is a central issue in seasonal habitats. In animals that remain active during winter, survival is linked to the ability to conserve heat (McNab, 2002). Seasonal changes of BMR also can be correlated to variation in C_{min} as well as to modifications in thermogenic capacity (Bozinovic *et al.*, 1990; Nespolo *et al.*, 1999; Rezende *et al.*, 2001). It is interesting to note that only a few caviomorph species have been studied in the context of seasonal variations of BMR and C_{min}. Moreover, the available data came from studies in which BMR was not the focus variable, as in the case of *Octodon degus* (Bozinovic *et al.*, 2004) or *Ctenomys talarum* (Luna *et al.*, unpublished data). Both works showed that BMR does not vary seasonally. Furthermore, when phenotypic flexibility in metabolic variables was tested in laboratory conditions, BMR suffered small variations, as in the case of *S. cyanus* (Nespolo *et al.*, 2001a), or showed no modification, as in *C. talarum* (Luna *et al.,* 2012) and in *O. degus* (Nespolo *et al.*, 2001b). On the other hand, Nuñez-Villegas *et al.* (2014), evaluated the effect of social grouping in *O. degus* on the flexibility of BMR after an acclimation to low T_as, and found that BMR of huddling individuals was 40% lower than that of individuals housed alone.

In all of these cases, focus variables were related to metabolic heat production at low temperatures. In general, small mammals mainly increase total heat production to maintain constant body temperature to cope with cold stress (Heldmaier, 1989). In this regard, total heat production for thermoregulation, hence thermogenic capacity, is derived from shivering (ST) and non-shivering thermogenesis (NST). Jansky (1973) suggested that ST is less efficient than NST, because heat is produced by the muscles at the periphery of the body, where conductance is higher. In contrast, NST has been proposed to be a more plastic element in the machinery of heat production (Cannon and Nedergaard, 2004), responding rapidly to cold acclimation (Jansky, 1973). Nespolo *et al.* (2001b) established that NST in *O. degus* increases with acclimation to low temperatures, being less plastic than that observed in surface-dwelling *Phyllotis* species (*Phyllotis darwini*, Muridae) living in the same area of central Chile. Moreover, during acclimation to low T_as, *S. cyanus* shows a small increment of NST (only 15%, Nespolo *et al.,* 2001a), but no effect was reported for *C. talarum* (Luna *et al.,* 2012). In *S. cyanus*, NST is the main thermogenic mechanism, showing a total absence of ST, while in *C. talarum*, a close relative, NST accounts for less than 40% of total heat production. It should be borne in mind that both species are subterranean, so their underground lifestyle might strongly influence the observed results (see below). Clearly, NST is able to vary from cool to cold conditions (acclimation or acclimatization) allowing a quick increase in heat production. In spite of such flexibility, Rodriguez-Serrano and Bozinovic (2009) identified a positive relationship between NST and latitude, as a result species from high latitudes exhibited higher mass-independent NST than species from low latitudes. Moreover, as these kind of seasonal thermoregulatory responses may vary with body mass (Lovegrove, 2005), and the main thermogenic mechanism could differ among species of similar size range (Luna *et al.*, unpublished data), total thermogenic capacity, as well as their flexibility, may be a key factor underlying ecological and evolutionary success, being decisive to allow thermal adaptation (Pörtner *et al.*, 2006).

Diet

As we have seen before, diet can affect BMR among species, and its effect might also be extended to the intraspecific level. In particular, Cork (1994) postulated that small mammals might decrease BMR to survive on a low quality diet. To our knowledge, only a few studies of caviomorph rodents explored this possibility experimentally. Veloso and Bozinovic (1993) found that individuals of the semifossorial *O. degus* decreased their BMR after they were maintained with a diet high in dietary fiber (low quality diet). In addition, taking into account acclimation type, Veloso and Bozinovic (2000a) proposed that high quality diet allowed *O. degus* females to increase their BMR. In the same way, Perissinotti *et al.* (2009) established that diet quality and also soil type affect BMR in the subterranean rodent *C. talarum*. In both cases, a concomitant variation in digestive efficiencies was observed. Feeding on a low quality diet affects digestive efficiencies, hence the rate at which energy and materials are acquired (Mangione and Bozinovic, 2003). A common strategy to maximize digestive efficiencies in both species includes an increase in feeding rate, or time devoted to feeding activities, and feces production, but a decrease in transit time and apparent digestibility. In this context, as Veloso and Bozinovic (1993) hypothesized for *O. degus*, diet quality constitutes a useful signal that promoted changes in minimal metabolism.

Non-basal energetics and behavior

Although this is not the main focus of this review, we believe that there is valuable energetic information available that could be used to understand the whole picture of energy metabolism and thermal biology among caviomorph rodents. Measurement of non-basal metabolism in a wide range of conditions would add information about the energy balance at different time scales. As in basal conditions, scaling of non-basal metabolism has received increased attention over time (Rosenmann and Morrison, 1974; Nagy *et al.*, 1999; Weibel *et al.*, 2004; White and Seymour, 2005). Within caviomorphs only two groups have been extensively studied in terms of energetic costs of different activities. These groups have different life history features. Both families, Ctenomyidae and Octodontidae, have been used as models for several physio-ecological studies of non-basal energetics. Those studies deal with costs of digging in subterranean species (Ebensperger and Bozinovic, 2000; Luna *et al.*, 2002; Bozinovic, *et al.*, 2005; Luna and Antinuchi, 2006, 2007a, 2007b), and several energy expenditures associated with activities and/or behaviors sustained over time (Bozinovic *et al.*, 2004; Zenuto *et al.*, 2002).

Digging energy expenditure

As was shown earlier, caviomorph species include a large number of subterranean species. In contrast to some semifossorial species that inhabit relatively short and simple tunnel systems but forage mostly on the surface, subterranean species construct a more complex and intricate burrow (Reichman and Smith, 1990). In this case, they need to construct new tunnels to have access to new patches of plants (Nevo, 1999). In general, construction of new tunnels implies an extremely high cost of digging (see Vleck, 1979). Ebensperger and Bozinovic (2000) studied digging energetics in the semifossorial *Octodon degus*, which is found in semi-arid scrub areas of central Chile. When digging metabolic rate (DMR) was analyzed, they found that it was similar to unrelated subterranean rodents (Luna *et al.*, 2002). However, digging efficiency –estimated as the rate of soil removal– was lower than more fossorial species (Camin *et al.*, 1995; Ebensperger and Bozinovic, 2000; Luna *et al.,* 2002). Interestingly, when DMR is compared to phylogenetically-related subterranean species, such as *C. talarum* (Luna *et al.*, 2002) and *S. cyanus* (Peichl *et al.*, 2005), *O. degus* expends more energy while digging than its subterranean counterparts. During digging, *C. talarum* expended energy at 53% and *S. cyanus* at 71% when compared with *O. degus* (see Tab. 3). Thus, it appears that among caviomorph species, subterranean dependence might establish restrictions on the total energetic budget, and as a consequence, subterranean species are more efficient in terms of digging energetics than semifossorial species, despite the fact that all studied species use a similar mode to break the soil (Luna *et al.,* 2002).

Table 3. Body mass (***M***), basal metabolic rate (**BMR**), digging metabolic rate (**DMR**) of subterranean caviomorph rodents.

	BMR ($ml\ O_2/h$)	DMR ($ml\ O_2/h$)	DMR – BMR ($ml\ O_2/h$)	*M* (g)	Type of soil	References
Ctenomys talarum[a]	114.8	408.3	293.5	130.7	Hard soil*	Luna and Antinuchi (2006)
	125.7	267.6	141.9	125.7	Soft soil*	
C. talarum[b]	119.1	494.9	375.8	125.3	Hard soil	Luna and Antinuchi (2007b)
	127.7	455.1	327.4	124.0	Soft soil	
C. australis	207.4	772.9	565.5	314.2	Hard soil	Luna and Antinuchi (2007b)
	225.6	828.3	602.7	322.3	Soft soil	
Spalacopus cyanus	58.4[c]	161.8	103.4	89.9	Hard soil	Bozinovic *et al.* (2005)
	45.4[d]	217.7	172.3	70.6	Soft soil	

[a]Northern population (Mar de Cobo, Argentina). [b]Southern population (Necochea, Argentina). [c]Southern population (Valparaíso, Chile). [d]Northern population (La Serena, Chile). *differences in DMR between soils conditions.

The influence of underground lifestyle is so important that several hypotheses were proposed to explain convergent morpho-physiological features found in subterranean species. In particular, it has been proposed that mass-specific BMR is low compared to that observed in surface-dwelling rodents of similar body mass and that this is an adaptation to live in this environment (McNab, 1966). The thermal-stress hypothesis proposed that low BMR could minimize the risk of overheating within burrows, where convective and evaporative heat loss are restricted (McNab, 1966, 1979). By contrast, the cost-of-burrowing hypothesis posits that low BMR may balance the high cost of digging during foraging activities (Vleck, 1979, 1981). So far, White (2003) compared BMR of unrelated subterranean and semifossorial species from arid and mesic environments, and no definite conclusions were obtained. This fact lead the author to conclude that in some cases (subterranean mammals from mesic environments) the thermal-stress hypothesis is supported but in others (subterranean species from arid habitats) the cost-of-burrowing hypothesis is verified. Thus, in some cases, either the thermal stress hypothesis or the cost-of-burrowing hypothesis could drive similar interpretations, indicating that these hypotheses are not mutually exclusive.

Because subterranean species are well represented in caviomorphs, several studies were conducted to test both hypotheses. Two species of *Ctenomys* rodents were analyzed, comparing their BMR and digging metabolic rate (DMR) using different soil types (Luna and Antinuchi, 2007b). Also, one study compared BMRs and digging energy expenditures of *S. cyanus* from different localities with contrasting soil characteristics (Bozinovic *et al.*, 2005). Surprisingly, both studies failed to support either cost-of-burrowing or the thermal-stress hypotheses. Although neither hypothesis was fully accepted, they were not discarded, and thus they were used to make some approximations about digging energetics. Luna and Antinuchi (2007a) evaluated digging metabolic rate in relation to ambient temperature. At low T_as, individuals of *C. talarum* increase DMR, thus the energy generated during digging was used to, in part, furnish the energy required for thermoregulation. However, at high T_as, body temperature was maintained through conduction to the soil. Increases in soil hardness should affect daily energy balance directly by increasing burrowing costs (Vleck, 1979), or indirectly due to animals consuming poor quality food items associated with low primary productivity in harder soils (Vleck, 1981; Andersen, 1982). In *C. talarum* from a population characterized by soft soils, DMR are augmented when individuals from this population are exposed to hard soil (Luna and Antinuchi, 2006). However, when individuals from a population living permanently in hard soils were analyzed, DMR maintains similar values to when individuals dig in soft soils. Thus, irrespective of differences observed between genetically contrasting populations (Cutrera *et al.*, 2006), digging energetics can show plasticity. The obtained results for other subterranean representatives among caviomorphs appear to contradict this fact. As also observed in bathyergids species (*Fukomys mechowii* and *Heliophobius argenteocinereus*; Zelová *et al.*, 2010), soil hardness did not affect DMR in *C. australis* and *S. cyanus* (Luna and Antinuchi, 2007b; Bozinovic *et al.,* 2005; respectively). Besides differences in DMR, burrow architecture could be modeled by external factors. As digging construction angle increase, DMR also suffers a concomitant increase, thus tunnel angles of more than 40° in natural burrows are extremely rare (Luna and Antinuchi, 2007c). In conclusion, digging expenditure represents a high physiological cost for individuals, being determined by intrinsic factors rather than external effects (for example, ambient temperature or soil hardness). At the interspecific level, cost of digging appears to be a critical factor that determines convergent physiological features among subterranean and fossorial species, having a profound effect on their distribution (McNab, 1979; Vleck, 1981).

Energetics of reproduction and growth

Numerous studies have proposed that mammalian reproduction is the most energetically costly period of female´s life (see Thompson, 1992), implying an increase of almost 50% of the annual energy budget (Kenagy, 1987). Despite this increment, energy expenditure is not sustained over the entire reproductive period. Gestation is considered a relatively inexpensive process, representing only 20% of the total cost of reproduction (Gittleman and Thompson, 1988).

During pregnancy there is an increase in the body mass of females due to the intake of energy and materials both for the growth of fetuses and for development of accessory reproductive structures. In this processes, minimal energetic requirements of females (pregnant female resting metabolic rate) might be modified. For many species gestation cost –besides the cost of producing new tissue– is related to the accumulation of lipids that will be used during the lactation period (see Thompson, 1992). During the lactation period, energy expenditure increase more than

2 or 3 times the cost observed during gestation (Künkele, 2000a; Veloso and Bozinovic, 2000b). Also, lactation cost can vary depending of several factors (*e.g.,* diet quality, litter size). Thus, from an evolutionary perspective, there is a trade-off between duration of gestation/lactation and energy requirement of both processes, and such a trade-off might vary depending on life-history (McClure, 1987; see Thompson, 1992). Pup development can also differ according to a species' life-history. A great diversity of offspring development types can be observed in mammals; this is associated with the use of energy for growth and thermoregulation. Altriciality and precociality are considered as extremes of a continuum in pup development (Antinuchi *et al.*, 2007; see Hill, 1992). Whereas altricial pups are born almost naked, in a relatively helpless and uncoordinated state, with a postnatal period of extreme dependence on their parents, precocial pups are born in a comparatively advanced state, almost furred and with their eyes open. These pups mature their locomotor skills, as well as achieving thermal independence, comparatively early.

It is not our intention to perform an exhaustive review of the energy balance (acquisition-expenditure) during reproduction, however some considerations can be offered. In general, it is widely recognized that caviomorphs show long gestation periods and produce few and precocial pups (Weir, 1974). Caviomorph rodents have much lower reproductive output rates than do other rodent species (Weir, 1974). Besides that several studies were performed to investigate reproductive biology among caviomorph species (*Cavia aperea, Galea musteloides* and *Microcavia australis*, Rood and Weir, 1970; *Myoprocta pratti*, Weir, 1971a; *Dasyprocta aguti*, Weir, 1971b; *Kerodon rupestris***,** Roberts *et al.*, 1984; *Thrichomys apereoides*, Roberts *et al.*, 1988; *Spalacopus cyanus*, Begall *et al.*, 1999; *Cavia magna*, Kraus *et al.*, 2005; *Ctenomys pearsoni*, Pereira, 2006; *Cavia intermedia*, Salvador and Fernandez, 2008; *Ctenomys mendocinus*, Camín, 2010; *Octodon degus*, Long and Ebensperger, 2010), only a few studies evaluate the energetics of reproduction and growth. Those examples came from species of *Cavia*, *Ctenomys talarum* and *Octodon degus*.

As a typical caviomorph, *Cavia porcellus* produces precocial pups, and has a long gestation period (~68 days), however precociality is so extreme that pups start to eat solid food a very early stage (~3 days). In this context, this species was used as a model to evaluate the cost of gestation and lactation in relation to this unusual life-history strategy (Künkele and Trillmich, 1997; Künkele, 2000a). The pattern of energy expenditure differs substantially from that of other rodents because mothers have lower peak energy demands during lactation than those observed in altricial species, but overall reproductive cost appears to be similar. In this context, peak energy expenditure during lactation is almost 1.9 times BMR (Künkele and Trillmich, 1997). Moreover, when peak energy expenditure between gestation and lactation were performed, no differences were found (gestation: 1.6 times BMR; lactation: 1.5 times BMR; Künkele, 2000a). Although those stages are energetically similar, the duration of gestation implies a high energy transfer to litters, determining an efficiency of gestation nearly twice as high as the energetic efficiency during lactation (62% vs. 35%, respectively). It is important to note that the efficiency of energy conversion into pups was not affected by the size of the litter (Künkele, 2000b). The precocial *Octodon degus* increases its metabolic rate during lactation (a maximum of 39%), but this was not affected during gestation or in non-reproductive females (Veloso and Bozinovic, 2000b). Furthermore, diet quality has a profound effect on metabolic rate of lactating females (Veloso and Bozinovic, 2000a), being related to the increase of mass in several internal organs, such as liver, intestines, cecum and stomach (Naya *et al.*, 2008b). Finally, females of the subterranean *Ctenomys talarum* increase their metabolic rate during the entire reproductive period, remaining similar between gestation and lactation (128% and 151% over non reproductive females, respectively; Zenuto *et al.*, 2002). As in *Cavia porcellus*, the total energy cost of gestation was similar to the cost of lactation. Therefore, as was proposed for precocial species (Künkele and Trillmich, 1997), for this small set of caviomorph species, the maximum rate of production (conversion of energy into pup mass) occurs during late gestation -early lactation, as opposed to the condition in altricial rodent species in which maximum rate of production takes place during late lactation. The only available energetic data on pups themselves comes from *C. talarum*. Interestingly, and probably due to the particular life style, pups are altricial at birth but start to eat solid food very early during their development. Thus, a bimodal pattern for metabolic rate is observed (Zenuto *et al.*, 2002), showing an increase until day 10 -the day on which pups start to eat solid food-, decreasing to the adult level just before dispersion (~90 days).

Looking to the future

One of the approaches that should be addressed in the future is to examine the relationship between metabolic amplitude (an instantaneous measurement of phenotypic flexibility -which refers to a reversible change in phenotypic traits due to endogenous or exogenous factors) and environmental factors. In this context, we are able to assess the correlation between the absolute metabolic scope and different geographic and climatic variables in caviomorphs rodents. Metabolic scope is defined here as maximum metabolic rate (MMR) minus BMR. This type of analysis is complex, but would complement the classical analysis of thermal tolerance because it seeks the causal mechanisms behind the observed pattern. So, we collected the available data of MMR of different caviomorphs species (Tab. 4) and conducted an analysis of metabolic scope among caviomorphs. Interestingly, we found that metabolic scope is greater in surface dwelling species than in subterranean species after the effect of body mass was removed (ANCOVA, $F_{1,9} = 14.05$, $P < 0.001$, Tab. 4). Despite the small and limited data and preliminary analysis performed, subterranean species appears to show a restricted metabolic scope. In this regard, it has recently been suggested that the ability of species to cope with rapid changes in climatic conditions is closely related to flexibility of physiological traits (Hofmann and Todgham, 2010; Hoffmann and Sgro, 2011; Naya *et al.*, 2012). Recently, a macrophysiological hypothesis was proposed that links phenotypic flexibility and latitude (Chown *et al.*, 2004). The Climatic Variability Hypothesis (CVH) proposes that because the range of climatic fluctuations experienced by individuals increases with latitude, those individuals require wide ranges of tolerance or the capacity to acclimatize, allowing them to live in those sites. Therefore, a relationship between phenotypic flexibility and latitude is expected (Naya *et al.*, 2012, 2013b). Naya *et al.* (2008a) demonstrated a positive relationship between latitude and flexibility of the length of small intestine in rodents. Metabolic flexibility of mammalian species is also positively correlated with latitude (Naya *et al.*, 2012). Although few data are available to emphasize a latitudinal pattern of metabolic flexibility within caviomorphs (Tab. 4), the difference between species with different modes of life can be seen as a model for this. Given the possibility of climate change, physiological responses would be different between the subterranean and surface-dwelling species. Surface-dwelling species are able to occupy different environments or shift their geographic

Table 4. Body mass (*M*), basal metabolic rate (**BMR**), and maximum metabolic rate (**MMR**) of species of caviomorph rodents.

	BMR (ml O_2/h)	MMR (ml O_2/h)	MMR – BMR (ml O_2/h)	*M* (g)	References
Chinchilla brevicaudata	227.2	1145.1	917.9	454.4	Cortes *et al.* (2003)
C. lanigera	240.9	1408.9	1168.0	365.0	Cortes *et al.* (2000)
Microcavia niata	176.1	1791.5	1615.4	255.2	Naya *et al.* (2012)
Octodon bridgesi	183.1	774.8	591.7	176.1	Bozinovic (1992)
O. degus	181.4	1072.5	891.2	195.0	Rosenmann (1977)
O. lunatus	171.5	927.5	756.0	174.1	Bozinovic (1992)
Spalacopus cyanus	76.0	439.0	363.0	108.8	Nespolo *et al.* (2001a)
Ctenomys talarum	157.5	572.9	415.4	175.7	Luna *et al.* (2012)
C. tuconax	217.5	544.1	326.6	334.1	Luna (unpublished data)
C. australis	189.5	507.5	318.0	260.2	Luna (unpublished data)
C. roighi	89.3	264.0	174.7	151.2	Luna (unpublished data)
C. porteousi	163.4	551.4	388.0	193.4	Luna (unpublished data)

ranges or phenologies to avoid heat stress (see Chown *et al.*, 2010). However, in subterranean species, this possibility is restricted because they are restricted to friable soils into which they can dig (Nevo, 1999). This substantial difference, added to the low metabolic scope, could have significant effects on individual survival. For example, the suitable habitat of occurrence for *Ctenomys porteousi* represents only 10% of the total distributional range (Mapelli and Kittlein, 2009). Restriction on habitat occupancy, coupled with the low metabolic scope, might have profound effects on survival of this species under a climate warming scenario. Consequently, it is clear that the identification of global patterns of phenotypic flexibility, particularly metabolic flexibility, should be considered as an important feature in current ecological studies (Naya *et al.*, 2012).

Conclusion

There is compelling evidence of climatic warming at a global scale (IPCC 2013). Searching for global patterns of physiologic variables in endotherms is an effort to understand and to predict the scope of these changes. With the available data of caviomorph rodents, we observed that no clear energetic trend appears in this group, because no geo-climatic variable affects the pattern of minimal metabolism and thermal conductance. We are far from a complete understanding of the effect of climate change on caviomorph rodents; however, this review is an attempt to address this issue. Certainly, more studies analyzing physiological diversity in different taxonomic groups taking into account large geographical and temporal scales are needed to understand climate change effects. This kind of study not only must consider the predicted increase in ambient temperature, but also needs to go beyond and search for global-scale patterns in other environmental factors (for example photoperiod or seasonal timing; see Bradshaw and Holzapfel, 2010).We considered physiological information for many caviomorph species; nevertheless, for many others no physiological, ecological, or genetic information is available. As we outlined, some relevant issues must be taken into account (intraspecific-interpopulation physiological information). As more of this knowledge becomes available, we may be able to predict more accurately the responses of individuals, species or taxa to future changes, and predict as to whether climate change will harm or benefit individuals of a particular species (Somero, 2010; Huey *et al.*, 2012).

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9 | GENETICS, GENOMICS, AND EVOLUTIONARY THEMES IN CAVIOMORPH RODENTS

GENÉTICA, GENÓMICA Y CUESTIONES EVOLUTIVAS EN ROEDORES CAVIOMORFOS

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Abstract. Caviomorph rodents provide multiple important opportunities to explore fundamental evolutionary and biomedical questions due to their diversity and their typically marked divergence from other rodent lineages. Now that the phylogenetic position of caviomorphs within Rodentia has been firmly established –due in part to advances in obtaining and analyzing gene sequence data– the evolution of these intriguing animals can be explored in greater detail. In this chapter, we consider the potential for High Throughput Sequencing (HTS) to contribute to studies of caviomorph diversity. Specifically, we review progress made over the last few decades with regard to two aspects of caviomorph biology: 1) the evolution of the unusual insulin genes found in this clade and 2) the impacts of demography and social structure on immunogenetic variation in ctenomyids. While molecular genetic data have already yielded important insights into each of these lines of inquiry, such data have also revealed new and puzzling aspects of the biology of caviomorphs, resolution of which may be facilitated by the ability of HTS to generate data regarding variation at large numbers of loci. We conclude by outlining several promising directions for future studies of caviomorphs that will likely benefit from the use of HTS “omic” approaches to analyses of caviomorph biology.

Resumen. Los caviomorfos proveen múltiples e importantes oportunidades para explorar preguntas evolutivas y biomédicas fundamentales, debido tanto a su diversidad como a su típicamente marcada divergencia con respecto a otros linajes de roedores. La posición filogenética de los caviomorfos dentro de los roedores histricomorfos está firmemente establecida, en parte gracias a avances en la obtención y análisis de datos de secuencias de genes, así como a importantes hallazgos paleontológicos. Tanto los datos moleculares como el registro fósil señalan que los caviomorfos han existido en Sudamérica por unos 40 Ma. Estos avances facilitan el estudio comparativo de la evolución de estos peculiares animales en mayor detalle. En este capítulo, consideramos el potencial que tienen los métodos de secuenciación masiva (HTS: high throughput sequencing) de contribuir a los estudios de la diversidad de los caviomorfos. HTS ofrece varias ventajas sobre las estrategias de secuenciación basadas en el método de Sanger. Primero, HTS no se basa en PCR y no requiere el uso de cebadores (primers) taxón-específicos para amplificar las regiones de interés del genoma o transcriptoma. Segundo, HTS provee datos en cantidades de pares de bases que son órdenes de magnitud mayores en relación a la inversión que los métodos tradicionales, llegando a la escala de genomas y transcriptomas completos. Finalmente, los análisis de mRNA mediante HTS pueden usarse para investigar problemas difíciles hasta hace poco tiempo, tales como la detección de evidencia de selección natural y el examen de diferencias en expresión génica. En suma, pese a que los desafíos planteados para el análisis de datos generados por HTS, este enfoque ofrece múltiples e importantes oportunidades para la investigación evolutiva. En este capítulo, resumimos varios aspectos de la biología de los caviomorfos que prometen beneficiarse de estudios basados en HTS. Específicamente, revisamos el progreso realizado en las últimas décadas con respecto a los dos aspectos siguientes de la biología del grupo: 1) Evolución de la insulina y genes asociados en caviomorfos. Aunque la hormona proteica que representa la insulina es generalmente conservada entre los mamíferos, la insulina de los caviomorfos difiere de la de otros roedores (y más en general, otros mamíferos) tanto en estructura como en función. En consecuencia, los estudios de genes de la insulina en caviomorfos proveen una importante oportunidad de examinar las relaciones entre la diversidad genotípica, la acción de la selección natural, y diferencias funcionales entre los diferentes fenotipos. Análisis de secuencias de ADN que codifican para los péptidos A y B de la insulina han permitido establecer que la selección positiva ha contribuido significativamente a la diversificación del locus en caviomorfos, tanto con respecto a otros mamíferos como dentro del grupo. Dichos estudios han identificado codones que han evolucionado en respuesta a la selección positiva. Futuros análisis basados en HTS prometen mejorar significativamente nuestra comprensión de las causas y consecuencias de la selección, al permitir la exploración simultánea de cambios en secuencias y en patrones de expresión en múltiples loci funcionalmente asociados a la acción de la insulina y la proinsulina, esta última recientemente asociada al desarrollo embrionario. 2) Impactos de la demografía y la estructura social en la variación inmunogenética en ctenómidos. Los datos genético-moleculares ya han resultado en importantes avances en cada una de estas líneas de investigación; dichos datos también han revelado nuevos y enigmáticos aspectos de la biología de los caviomorfos. Por ejemplo, estudios que han examinado múltiples genes en el complejo mayor de histocompatibilidad (MHC) han encontrado que la naturaleza e intensidad de la selección natural varían entre loci, por lo que es difícil identificar efectos generales de la demografía y el comportamiento en la variación inmunogenética. Análisis basados en estrategias de HTS prometen resolver este problema al permitir cuantificar simultáneamente la variación en un gran número de genes codificantes para proteínas, permitiendo por tanto la detección de patrones globales de selección entre individuos comportamental o demográficamente diferentes. En resumen, HTS ofrece múltiples y atractivas oportunidades para mejorar nuestra comprensión de la biología evolutiva. Como se esboza en este capítulo, las estrategias de HTS generan conjuntos de datos apropiados para abordar problemas fundamentales relacionados con la filogenia, la filogeografía y la estructura genética poblacional, así como también aspectos de la evolución de genes y genomas. La capacidad de HTS de cuantificar patrones de expresión génica (y proveer al mismo tiempo información sobre las secuencias subyacentes) es particularmente promisoria, ya que permite examinar problemas de importancia pero mal comprendidos de la biología de las poblaciones naturales. Dada su diversidad, historia evolutiva y múltiples características fenotípicas de interés, creemos que los roedores caviomorfos proveen evidentes e importantes blancos para futuros estudios que utilizan HTS para abordar temas relevantes de biología evolutiva.

Introduction

Caviomorph rodents –their current diversity, their geographic distributions, and their evolutionary origins– have long intrigued biologists. Caviomorphs are unusual among rodents in that they encompass a broad range of body sizes, have longer than expected gestation times, display diverse social systems, and diverge from other mammals at genes that are usually conserved (Rowlands and Weir, 1974; Landry, 1977; Wriston, 1984). The increasing use of molecular technologies in organismal and evolutionary biology over the past few decades has produced a dramatic increase in our understanding of some of these aspects of caviomorph biology. For example, the phylogenetic position of caviomorphs within Rodentia has now been firmly established, due in part to advances in our abilities to generate and to analyze gene sequence data (*e.g.,* Poux *et al.*, 2006). At the same time, sequence data have revealed unexpected patterns of divergence at genes coding for insulins (see below) as well as growth hormones and their receptors (Adkins *et al.*, 2000). In conjunction with detailed field studies, genetic analyses have also generated important insights into the evolutionary implications of differences in demography and social structure (see below).

As technology continues to change, new possibilities for exploring caviomorph biology are emerging. We believe that the advent of High Throughput Sequencing (HTS) represents a particularly large leap forward that will substantially change the way that organismal and evolutionary biologists study genetic diversity. In brief, this technology allows researchers, including those studying non-model organisms, to generate large quantities of sequence data (*e.g.*, entire genomes) much more rapidly and efficiently than in the past, thereby avoiding many of the more laborious and costly aspects of more traditional genetic analyses. In this chapter, we explore the opportunities created by HTS for genetic studies of caviomorph diversity and evolution. We begin by offering a brief account of the phylogenetic position and current diversity of the Caviomorpha. This is followed by an overview of HTS, with emphasis on the costs and benefits of this approach relative to more traditional Sanger sequencing. Finally, we review the progress made over the last few decades with regard to two areas of research on caviomorph diversity. These themes, drawn from our own research programs, consist of 1) the evolution of the unusual insulin genes found in this clade and 2) the impacts of demography and social structure on immunogenetic variation in ctenomyids. In both cases, we summarize the state of our knowledge of these topics and identify important questions that have yet to be answered. We then consider how use of HTS approaches may generate new insights into these aspects of caviomorph biology by shifting the scale of genetic analyses from one or a few to hundreds or thousands of loci. Our goal is not to provide a comprehensive review of the use of genetic data to study caviomorph diversity but, rather, to offer a few specific examples how use of HTS may improve our understanding of the evolutionary history and biomedical potential of these animals.

Phylogenetic framework

The phylogenetic position of caviomorphs has long been controversial, with both paleontologists and neontologists divided between those favoring a close connection to the bathyergids and their allies and those favoring independent origins for South American and African taxa (reviewed by Reig, 1981). Analyses based on immunological distances and molecular clocks favored the former scheme (Sarich, 1985) but were called in to question as part of larger controversies surrounding those early uses of molecular phylogenetics. A decade later, Graur *et al.* (1991) questioned the monophyly of the Rodentia based on multiple protein sequences suggesting that guinea pigs (and, by extension, other caviomorphs and hystricognaths) were not part of this clade. Reanalyses of these data by Hasegawa *et al.* (1992), however, quickly reaffirmed the monophyly of rodents. In addition to highlighting the distinctiveness of caviomorphs, these discrepancies tended to enhance distrust of molecular systematics by researchers employing morphological or other more traditional data sets. Now, roughly 40 years later, much of this controversy has subsided as 1) strict molecular clocks have given way to more flexible methods that incorporate fossil data to provide multiple calibration points and 2) molecular phylogenies based on multiple loci have become more common. Indeed, an increasing number of phylogenetic analyses integrate fossil, modern anatomical, and molecular data to explore apparent evolutionary relationships among organisms (*e.g.*, Lessa *et al.*, 2008; O'Leary *et al.*, 2013).

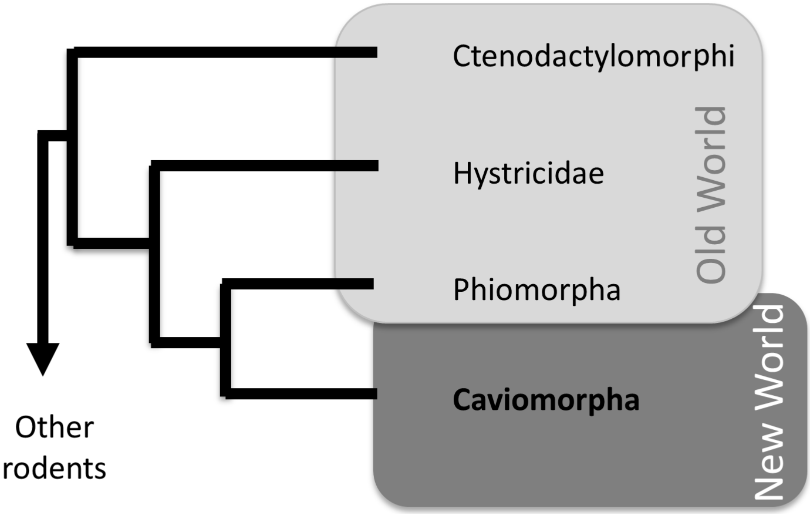

Figure 1. Phylogenetic relationships of hystricognath rodents. A more complete taxonomy of these animals is given in Table 1; Upham and Patterson (this volume) provide a detailed discussion of the phylogenetics of the Caviomorpha.

Our current understanding of phylogenetic relationships within the Caviomorpha –as well as the relationships of this group to other African and Asian rodents currently placed in the Suborder Hystricomorpha– are discussed in detail by Upham and Patterson (this volume). Here, we briefly summarize these relationships as a framework for our review of the population and evolutionary genetics of caviomorph rodents. A plethora of morphological and molecular data supports the monophyly of the Caviomorpha (New World hystricomorphs) and their close relationship to Old World hystricomorphs. Molecular data suggest that the divergence between the phiomorphs and the living caviomorphs occurred 43-45 million years before present (Mybp), with early branching within the caviomorphs dating to 37-38 Mybp (Poux *et al.*, 2006; Voloch *et al.*, 2013). Recent fossil findings are generally consistent with these dates, indicating that the appearance and early divergence of caviomorphs occurred at least 41 Mypb (Vucetich *et al.*, 2010; Antoine *et al.*, 2012; Bertrand *et al.*, 2012). Caviomorphs are thought to be sister to the Phiomorpha (African mole-rats, dassies and cane-rats); this relationship is consistent with the hypothesis that both groups descended from a single lineage of African origin (see Reig, 1981 and Upham and Patterson, this volume, for an historical account and discussion), although alternative scenarios cannot be ruled out (see Sallam *et al.*, 2011).The Old World porcupines (family Hystricidae), in turn, appear to be sister to the caviomorph-phyomorph clade, although this is relationship has been less strongly supported. Together, the caviomorphs, phiomorphs and hystricids comprise the Infraorder Hystricognathi, which is sister to the Ctenodactylomorphi (African gundis and the Laotian rock rat) (Fig. 1). It should be noted that some of the major groups mentioned here –especially the Caviomorpha and Phiomorpha– are often used informally (*i.e.*, caviomorphs, phiomorphs) or not at all in the literature, as categories that are intermediate between Order and Family are not mandatory in most phylogenetic classifications.

Diversity of extant caviomorphs

Living caviomorphs comprise 11 families, grouped into four superfamilies (Tab. 1). In addition, the recently extinct Heptaxodontidae are often included within this clade. Members of the superfamily Cavioidea are noteworthy for their striking diversity in body size, which ranges from less than 200 g in some cavies (*Microcavia*) to over 50 kg in capybara (*Hydrochoerus*). At the same time, this clade includes a number of morphologically unusual forms such as the Patagonian hare or mara (*Dolichotis*), which displays a number of striking convergences with members of the Lagomorpha. The Chinchilloidea comprise vizcachas (*Lagidium, Lagostomus*) and chinchillas (*Chinchilla*), as well as the larger-sized pacaranas (Dinomyidae). One fossil dinomyid was reported to have the largest body sizes among rodents (median estimates 900 - 1,100 kg, Rinderknecht and Blanco, 2008; Millien, 2008). The Erethizontoidea comprise the New World porcupines. The final superfamily, the Octodontoidea, is the most taxonomically diverse lineage, including five families and some 193 species (Upham and Patterson, 2012). This superfamily also displays considerable diversity with respect to natural history; members include (but are not limited to) subterranean tuco-tucos and coruros, fossorial octodontids, and arboreal spiny rats.

Population and evolutionary genetics of caviomorphs

Due to their diversity, their intriguing evolutionary history, and their prominence in many South American landscapes, caviomorph rodents have been the subjects of multiple studies aimed at exploring the population and evolutionary genetics of these animals. Beginning with early allozyme studies and continuing through to Sanger sequencing of mitochondrial and nuclear loci, patterns of genetic variation have now been explored for numerous species of caviomorphs (*e.g.*, Opazo *et al.*, 2005; Cutrera and Lacey, 2007; Opazo *et al.*, 2008; Mora *et al.*, 2010; Tomasco and Lessa, 2011; MacManes and Lacey, 2012a). Members of the Octodontoidea have been particularly well studied with respect to genetic themes (Honeycutt *et al.*, 2003; Upham and Patterson, 2012 and references therein) and thus much of this chapter focuses on this superfamily. Within the Octodontoidea, genetic variation has been quantified using every major technique employed by evolutionary biologists and the resulting studies using allozymes (D'Elía *et al.*, 1998), DNA fingerprinting (Zenuto *et al.*, 1999), microsatellite loci (Lacey, 2001; Lopes *et al.*, 2013), and mitochondrial and nuclear DNA sequencing (Adkins *et al.*, 2001; Castillo *et al.*, 2005) have generated important insights into multiple fundamental questions regarding organismal diversity. Given this rich background of molecular genetic research, it is perhaps not surprising that caviomorphs are now at the forefront of efforts to apply emerging high-throughput DNA sequencing strategies to studies of evolutionary biology.

Table 1. Taxonomy of living caviomorph and closely related hystricomorph rodents (Suborder Hystricomorpha) based on analyses by Upham and Patterson (this volume) as well as Wilson and Reeder (2005).

INFRAORDER	MAJOR GROUP	SUPERFAMILY	FAMILY	COMMON NAME
Ctenodactylomorphi				
			Ctenodactylidae	African gundis
			Diatomyidae	Laotian rock rat (*Laonastes*)
Hystricognathi				
	Phiomorpha		Hystricidae	Old World porcupines
			Bathyergidae	African mole-rats
			Petromuridae	African dassie rats
			Thryonomyidae	African cane rats
	Caviomorpha	Erethizontoidea	Erethizontidae	New World porcupines
		Chinchilloidea	Chinchillidae	Chinchillas, viscachas
			Dinomyidae	Pacaranas
		Cavioidea	Caviidae	Cavies, includes *Hydrochoerus*
			Dasyproctidae	Agoutis, acouchis
			Cuniculidae	Pacas, Agoutidae as junior synonym
		Octodontoidea	Ctenomyidae	Tuco-tucos
			Octodontidae	Cururos, degus
			Abrocomidae	Chinchilla rats
			Echimyidae	Spiny rats, includes *Myocastor*
			Capromyidae	Hutias, may include recently Extinct Heptaxodontidae

New frontiers: the age of "omics"

The advent of PCR-based Sanger sequencing techniques revolutionized organismal and evolutionary biology by making it possible to document nucleotide-level variation within the genomes of countless non-model taxa. While the importance of this sequencing strategy to biological (including biomedical) research cannot be overemphasized, use of Sanger sequencing is necessarily limited in at least two important ways. First, Sanger sequencing is fundamentally tied to PCR amplification (or cloning) of known target DNA fragments. Development of PCR primers typically requires knowledge of homologous sequences from related taxa; for researchers interested in generating sequence data for a target whose sequence is not known or one that occurs in a poorly characterized lineage, this constraint may prove to be a significant challenge. Second, although the number of base pairs that can be sequenced per PCR reaction has increased markedly over time, this approach typically remains limited to analysis of a single locus per sequencing effort. Sequencing additional regions multiplies the associated cost and effort by the number of loci characterized, with the result that Sanger sequencing is not an efficient strategy for exploring large portions of a genome. Thus, while Sanger sequencing has proven invaluable to studies of genetic and phylogenetic diversity, it is also subject to important limitations as a tool for evolutionary research.

High throughput sequencing (HTS). Evolutionary biology is now entering the age of "omics." Rather than sequencing one or a few genes to address evolutionary questions, it is now increasingly possible to sequence entire genomes or transcriptomes (the expressed portion of the genome) with a single run of a sequencing machine. Detailed descriptions of the molecular bases for HTS (*e.g.*, Illumina sequencing, Pacific Biosystems sequencing, Ion Torrent sequencing) are provided elsewhere (Quail *et al.*, 2008; Nagalakshmi *et al.*, 2010; Cahais *et al.*, 2012); here, we focus on the relative benefits of this technology for addressing questions regarding organismal diversity and evolution. In addition to generating many orders of magnitude more data than Sanger sequencing, HTS does not require a priori knowledge of the genes of interest. HTS strategies are not PCR-based but instead employ a "universal" adaptor sequence that, when ligated to DNA or RNA, serves as a starting point for sequencing at large numbers of locations throughout the genome (Fig. 2). As a result, HTS can be applied to any organism from which nucleic acids can be extracted.

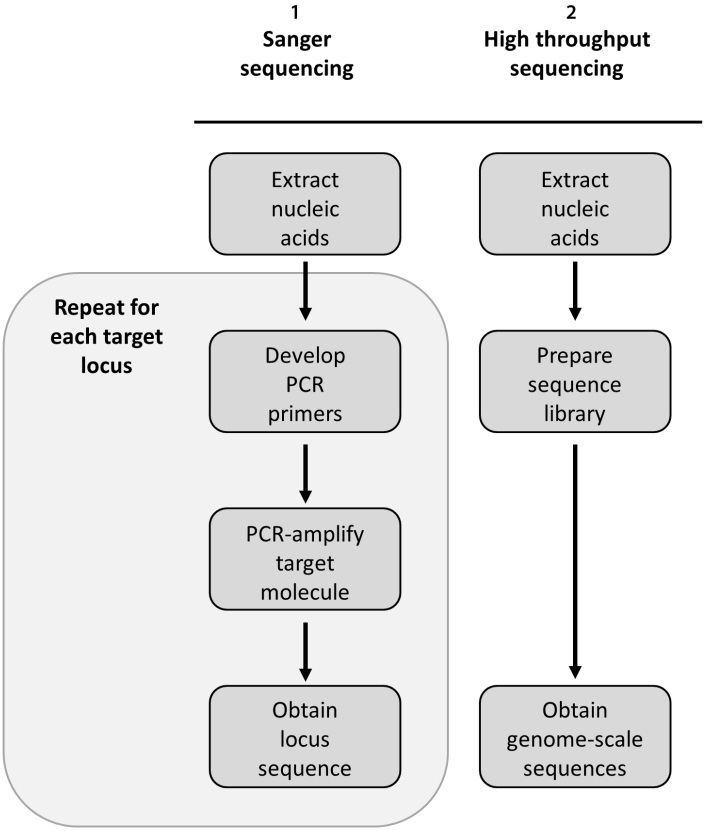

Figure 2. Comparison of the primary procedures involved in 1. Sanger sequencing and 2. high throughput sequencing techniques including both genome and transcriptome approaches. The current relative costs and analytical challenges of each strategy are described in the text.

Practical considerations. From an economic perspective, use of HTS entails a series of tradeoffs relative to Sanger sequencing and other PCR-based techniques. Initial preparation of samples for HTS sequencing is relatively inexpensive and technically easy to complete. At present, the cost of running one lane of HTS is ~100 times greater than that of a single 96-well plate of Sanger sequencing. Due to the considerably greater output of the former, however, the cost per base pair of HTS is markedly less than that for Sanger sequencing. The economic efficiency of HTS can be enhanced by including samples from multiple individuals in a single lane of sequencing; such multiplexing reduces the depth of coverage (number of copies) at which the initial pool of DNA or RNA molecules is sequenced but, depending upon the specific application, the resulting coverage is typically sufficient for addressing evolutionary questions. The reagents required to provide each individual with a distinctive label (barcode) require an initial investment but, again, this cost is typically recovered through the volume of sequence data generated. In sum, although the costs of HTS are more concentrated (*i.e.*, the cost of a lane of sequence), the overall expense of this strategy is less than that of Sanger sequencing when differences in the amount of data generated by these techniques are taken into account. For many researchers and projects, the initial investment is more than repaid by the returns in terms of data generated, especially when the organism sequenced is the focus of medium- or long-term study.

Analyses of HTS data. While HTS is more efficient than Sanger sequencing for generating data, analysis of HTS output is considerably more computationally intensive than are analyses of traditional sequence data. A single HTS run can generate millions or even billions of short, unordered sequence fragments that must be assembled or aligned and then annotated to produce a single consensus record of an individual's genotype. Base calling error rates are higher for HTS, although this tends to be offset by the inclusion of multiple reads covering the same genomic region. With regard to hardware, analyses of HTS data typically require the use of a dedicated workstation computer or access to supercomputing facilities (*e.g.*, XSEDE https://www.xsede.org.). With regard to software, although an increasing number of analytical programs designed for HTS data are available (*e.g.*, ABySS [Simpson *et al.*, 2009], AllPaths-LG [Maccallum *et al.*, 2009], Trinity [Haas *et al.*, 2013]), many tools are still under development and thus a relatively sophisticated understanding of bioinformatics is required. While these challenges should become more manageable over time (*e.g.*, The Galaxy Project, Goecks *et al.*, 2010), there is no question that generating several orders of magnitude more data increases the effort required to analyze those data.

Emerging opportunities

The initial and, to date, primary use of HTS in evolutionary research has been to generate genome (Kim *et al.*, 2011) and transcriptome (Trapnell *et al.*, 2010) sequences for an increasing number of species. Such data have allowed greater resolution of difficult-to-interpret-phylogenies (Decker *et al.*, 2009; Siepel, 2009; Casci, 2011; Struck *et al.*, 2011), have generated new insights into evolutionary changes in genome structure (Groenen *et al.*, 2009; Miles *et al.*, 2009; Wong *et al.*, 2010), and have allowed detection of genome-wide patterns of natural selection (Kosiol *et al.*, 2008; Jin *et al.*, 2012; Pespeni and Palumbi, 2013). As use of HTS strategies has increased and new molecular and analytical tools have been developed, additional applications for these data have emerged that make it increasingly possible to use HTS to address population-level questions regarding genetic variability (*e.g.*, Faircloth *et al.*, 2012; Reitzel *et al.*, 2013) as well as questions related to patterns of gene expression. These emerging uses for HTS strategies include the following:

Improved phylogenetic resolution. HTS - in particular transcriptome sequencing- is playing an increasingly important role in phylogenetic inference (Dunn *et al.*, 2008; Smith *et al.*, 2011). Unlike shotgun genomic sequencing strategies that generate data regarding randomly selected portions of the genome, whole-transcriptome sequencing offers substantial benefits to the study of evolutionary relationships among taxonomic groups. The most obvious of these is the large number of phylogenetically informative markers that can be generated, although because HTS of transcriptomes captures variation only at expressed genes, assembly and annotation of the resulting data may be more feasible than when working with complete genomes. At the same time, because expressed genes are commonly thought to be subject to purifying selection, identifying homologies between sequences from distantly related organisms may be facilitated. Phylogenetic methods appropriate to handling hundreds if not thousands of loci are emerging (Zieliński *et al.*, 2014; Dunn *et al.*, 2013), which suggests that HTS technologies will increasingly be used to address phylogenetic and phylogeographic research questions.

Analyses of gene expression. Because HTS generates data regarding the absolute abundance of the different nucleic acids in a sample, HTS of transcriptomes (*i.e.*, mRNA, or transcribed genes) can be used to examine patterns of gene expression (*e.g.*, MacManes and Lacey, 2012a). In contrast, while Sanger sequencing documents nucleotide variation, it does not generate information regarding levels of gene expression. Although quantitative PCR is routinely used to document patterns of gene expression, this technique - like Sanger sequencing - is locus-specific and does not offer the same comprehensive perspective on patterns of expression that HTS does. Thus, use of HTS to quantify gene expression facilitates exploration of previously intractable aspects of genetic variation in natural populations of organisms.

Array capture studies. HTS also serves as the foundation for a growing number of array-based studies of genomic DNA. Once a reference genome or transcriptome has been generated, a variety of protocols can be implemented to develop arrays (or other physical supports) capable of capturing allelic variants at multiple distinct loci (*e.g.*, Bi *et al.*, 2012; Linnen *et al.*, 2013). Such arrays can then be used to generate high coverage sequence data for many individuals, thereby allowing analyses of population-level patterns of nucleotide diversity. Although the sequence data captured by an array represent only a small subset of the genome, the information obtained far exceeds that produced by more traditional population-level approaches such as locus-specific Sanger sequencing or microsatellite analyses, and thus may offer an important compromise between targeted studies using Sanger sequencing and the more extensive data sets generated by HTS. The number of array-based protocols available to researchers is increasing rapidly and this strategy for capturing sequence data for a large number of targeted loci promises to have a significant impact on organismal and evolutionary research.

Detecting selection. By generating data for extensive portions of the genome, HTS provides a convenient basis for detecting evidence of selection on individual loci. Statistical procedures for detecting selection typically rely on comparing DNA sequence (and allele frequency) data for loci presumed to have been under selection with data from putatively neutral portions of the genome (Nielsen, 2005). One challenge with these analyses is to select appropriate regions for comparison. For example, while microsatellite loci have often been used to provide a neutral contrast to nuclear loci subject to selection (*e.g.*, Cutrera *et al.*, 2010), microsatellites have a distinctive underlying mutational process that complicates use of some statistical models. In contrast, genome wide data provide a broad background against which to examine loci that are putatively subject to selection, thereby accounting for variation in mutational patterns as well as potential footprints of demographic history (*e.g.*, Novembre and Di Rienzo, 2009).

HTS and caviomorph rodents: potential applications

Caviomorph rodents provide highly appropriate targets for studies employing HTS strategies given their taxonomic diversity, their phenotypic variability, and their phylogeographic importance to understanding mammalian evolution. Previous research using Sanger sequencing and other more “traditional” methods of quantifying genetic variation has generated significant insights into multiple aspects of the biology of these rodents. At the same time, these analyses have revealed a number of intriguing evolutionary puzzles, resolution of which may be facilitated by application of HTS. To illustrate the apparent potential of this technology to address evolutionary problems, below we summarize several lines of research on caviomorph rodents that will likely benefit from the extensive nucleotide information –as well as the information on gene expression– that can be obtained from HTS analyses.

Evolution of caviomorph insulin genes

Caviomorphs are characterized by an unusual suite of traits related to insulin physiology. Insulin is a protein hormone best known for its role in down-regulating glucose levels in blood and its association with diabetes mellitus (Fig. 3). Although generally highly conserved among mammals, the insulin of caviomorphs is structurally distinct from that of other members of this clade. The first hint of this distinctiveness came from studies indicating that antibodies developed for other mammalian insulins did not neutralize these proteins in capybaras (Cavioidea) or coypus (Octodontoidea) (Davidson *et al.*, 1968, 1969). Subsequent research (Zimmerman *et al.*, 1974 and references therein) revealed that in guinea pigs, receptor affinity for insulin is greatly reduced but that circulating (blood) levels of this hormone are markedly elevated, perhaps as a means of compensating for seemingly impaired receptor function. Within caviomorphs, insulin activity varies greatly among species, with chinchillas and vizcachas (Chinchilloidea) displaying levels comparable to other mammals but degus, tuco-tucos and spiny rats (Octodontoidea) displaying considerably reduced activity (Zimmerman *et al.*, 1974; Horuk *et al.*, 1979; Bajaj *et al.*, 1986). Interestingly, regulation of blood glucose levels appears to be normal in caviomorphs (Opazo *et al.*, 2004), although Vera *et al.* (2008) reported reduced glucose tolerance in tuco-tucos. It has been postulated that, in addition to elevated circulating insulin levels, caviomorphs may possess additional compensatory mechanisms (*e.g.*, increased numbers of insulin receptors) that allow regulation of blood glucose levels, although the occurrence of such mechanisms has not been confirmed.

In most mammals, inactive insulin is stored in the pancreas in a hexameric form with a zinc ion core. Caviomorph insulin, however, cannot hexamerize (Wood *et al.*, 1975); based on studies of coypu, Bajaj *et al.* (1986) hypothesized that this inability may reflect several amino acid changes in the region of the insulin protein that is involved in hexamerization. This region, which is structurally distinct in caviomorphs, appears to function as a second binding site for the hormone (De Meyts, 1994; Shäffer, 1994; Menting *et al.*, 2013; see also Hubbard, 2013). Functionally, while caviomorph insulins have low biological activity with respect to glucose regulation, they have enhanced growth-promoting (mitogenic) capabilities and, especially in the proinsulin configuration (Fig. 3), function in part as insulin-like growth factors (King and Kahn, 1981; King *et al.*, 1983). These two functions seemed to have evolved in non-parallel fashion, such that increased efficiency in one is not associated with a concordant change in the other. A similar reduction in glucose regulation but increase in mitogenic activity has been reported in some other vertebrate lineages – notably lampreys and hagfishes (see De Meyts, 2012) – although at present it is not known if this similar change in function reflects convergent structural and molecular level differences among taxa.

Collectively, these observations raise several intriguing questions regarding the evolution of insulin proteins in caviomorph rodents. First, if maintenance of a specific protein structure required for glucose regulation is no longer critical, release from purifying selection may be

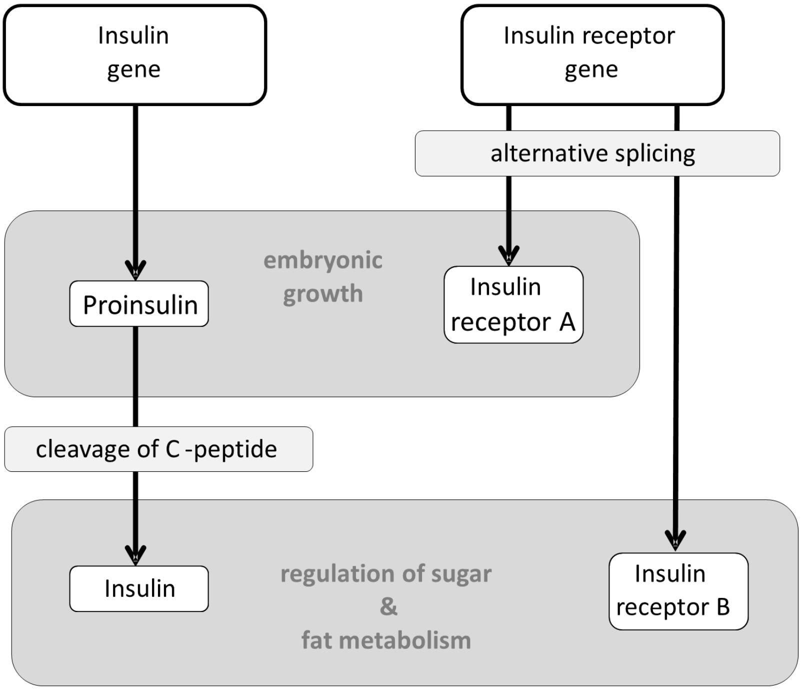

Figure 3. Schematic of the roles of proinsulin, insulin, and their receptors in embryonic growth and key metabolic processes. Only a few primary interactions are depicted. Functional receptors are homo- or hetero-dimeric forms; the latter may be combinations of A and B with each other or with receptors of insulin-like growth factors.

responsible for the relatively rapid divergence of caviomorph insulins compared to those in other mammalian lineages. At the same time, adaptations associated with other functions (*e.g.*, mitogenesis) may have dominated the evolution of caviomorph insulins, resulting in strong directional selection for distinct forms of these proteins. Opazo *et al.* (2005) tested these hypotheses by sequencing the exons in the insulin gene that code for chains A and B (the functional portion of insulin) in 21 species representing three of the four caviomorph superamilies (Tab. 1). Using phylogeny-based tests of variation in dN/dS (the ratio of non synonymous to synonymous changes in coding sequences), these authors rejected neutral explanations (*e.g.*, relaxed purifying selection) in favor of positive, directional selection as an explanation for changes in specific codons of this gene. Interestingly, these codons are thought to be associated with the region of the protein that participates in hexamerization of insulin in the pancreas and that contains a second receptor binding site in caviomorphs (De Meyts, 1994; Shäffer, 1994), suggesting a potential causal link between selection on these codons and the unusual aspects of insulin function in this lineage of rodents.

A role for HTS. As this overview suggests, the evolution of caviomorph insulin genes is complex and raises a number of important questions concerning the effects of multiple, potentially competing selective pressures on these portions of the genome. For example, given their relative shift in function from glucose regulation to mitogenesis, it seems plausible that changes in insulin genes have occurred in concert with changes at other, functionally associated loci such as the genes coding for insulin-like growth factors, growth hormone, and prolactin, all of which play important roles in fetal development (Wriston, 1984; Fowden and Forehead, 2009). While concordant changes in nucleotide sequences at these loci could be examined using Sanger sequencing, HTS analyses provide a much more efficient way of exploring correlations between nucleotide –and thus amino acid– changes at multiple genes, including loci that may not yet have known associations with insulin physiology in caviomorphs. Using HTS to examine patterns of gene expression also offers considerable potential; insulin is known to affect the expression of more than 150 genes (Mounier and Posner, 2006), suggesting that comparative analyses of simultaneous activity at insulin and other loci would be informative. Transcriptomes can provide sequence and expression data from multiple genes without requiring previous identification of candidate genes, but require an appropriate definition of targeted tissues and developmental stages. Array capture, on the other hand, can simultaneously target large numbers of previously selected genes (whose reference sequences may be obtained from the guinea pig genome) at the expense of expression data. Thus, HTS may provide an important means of generating new insights into the selective causes and functional consequences of the distinctive insulin physiology of caviomorph rodents.

Immunogenetic variation in caviomorph rodents

The genes of the Major Histocompatibility Complex (MHC) have played a fundamental role in efforts to understand the effects of selection on genetic variation in natural populations of vertebrates. While Class I MHC loci are thought to participate in the detection of intracellular pathogens such as viruses (Bjorkman and Parham, 1990), Class II loci code for the glycoproteins that recognize extra-cellular pathogens such as bacteria (Kumánovics *et al.*, 2003). By binding and then presenting such pathogens to T-cells, these glycoproteins initiate the adaptive immune response (Klein, 1986; Spurgin and Richardson, 2010). Accordingly, greater allelic diversity at Class

II loci should lead to detection of a wider range of pathogens and thus Class II genes are generally expected to be subject to strong balancing (diversifying) selection (Satta *et al.*, 1994; Bernatchez and Landry, 2003). At the same time, because stabilizing selection may favor the maintenance of particularly beneficial alleles (Takahata, 1990), conservation of specific Class II variants across species (*i.e.*, trans-specific allelism) has also been observed in multiple lineages of vertebrates (Cutrera and Lacey, 2007; Kikkawa *et al.*, 2009; Wei *et al.*, 2010). In sum, the selective forces acting on Class II MHC genes are complex and may operate over multiple time scales, thereby offering a rich context in which to evaluate the effects of selection on specific loci.

Multiple environmental factors are believed to influence the nature and magnitude of selection on Class II MHC genes. For example, pathogen exposure may vary as a function of multiple demographic parameters, including population density, dispersal patterns, and degree of generational overlap (Kimura and Ohta, 1974; Takahata, 1990; Fu and Li, 1993). Exposure may also be affected by patterns of social behavior, notably the frequency and duration of contact among conspecifics as well as the number of reproductive partners per individual (Hambuch and Lacey, 2002; MacManes and Lacey, 2012b). These factors are routinely documented as part of studies of the behavior and ecology of free-living populations of vertebrates, many of which have revealed that these parameters vary within as well as among species. This variation, coupled with the comparatively well-understood function of Class II MHC genes, provides an ideal system in which to examine potential causal relationships among environmental conditions, pathogen exposure, and selection on MHC loci.

Demography and selection on MHC loci. Locus-specific studies of selection on MHC genes have been conducted for several species of ctenomyids as part of research aimed at understanding the effects of demography and behavior on selection on immunogenes (Fig. 4). Analyses of the effects of inter- and intra-specific differences in demography have been completed using comparative studies of two species – the talas tuco-tuco (*Ctenomys talarum*) and the austral tuco-tuco (*C. australis*) – both of which occur in coastal regions of central eastern Argentina. Although these species are partially sympatric, they display differences in micro-habitat use (Vassallo, 1993) that are associated with pronounced differences in patterns of individual space use (Cutrera *et al.*, 2006a, 2010) and demography (Malizia *et al.*, 1995). Additionally, *C. talarum* displays considerable intraspecific variation in demography, including well-documented differences in population density, adult sex ratio, and effective population size (Busch *et al.*, 1989; Malizia *et al.*, 1991, Zenuto *et al.*, 1999; Cutrera *et al.*, 2006b).

Comparisons of two well-studied populations of *C. talarum* at Mar de Cobo and Necochea, Argentina, have revealed that genetic effective population size is smaller and that neutral genetic variation is more spatially structured at Mar de Cobo, which is the population characterized by a greater density of individuals and greater degree of inbreeding among conspecifics (Cutrera *et al.*, 2005, 2006b). Parasite loads are also greater in the Mar de Cobo population (Rossin *et al.*, 2010), leading to the expectation that selection on Class II MHC loci should be stronger in this population than at Necochea. To test this prediction, Cutrera and Lacey (2006) compared patterns of variation at the Class II DRB and DQA genes in these two populations of conspecifics. Their analyses indicate that while, as expected, both loci reveal greater evidence of selection at Mar de Cobo, levels and patterns of variability differ markedly between these genes, leading Cutrera and Lacey

(2006) to conclude that although demography and parasite load are important correlates of MHC variation, the intensity of selection on individual MHC loci varies, perhaps reflecting differences in the function of specific immunogenes (Fig. 4).

With regard to interspecific comparisons, analyses of mtDNA have revealed that while genetic structure in *C. talarum* is consistent with a stable demographic history and equilibrium between gene flow and genetic drift, *C. australis* appears to have undergone a rapid historical demographic expansion such that genetic and geographic distance are not correlated in this species (Mora *et al.*, 2006). Based on these differences, Cutrera *et al.* (2010) predicted that evidence of recent balancing selection should be less pronounced for *C. australis*. Using sequence data from the Class II loci DRB and DQA, these authors found that, contrary to expectation, estimates of selection were greater for *C. australis* than for *C. talarum*. More specifically, evidence of selection based on codon changes was greater for *C. australis*, suggesting that selection has acted on MHC genes in this species over relatively long time periods. In contrast, evidence of selection based on allele frequencies was greater for *C. talarum*, suggesting that current selection on MHC genes is greater in this species. Collectively, these findings led Cutrera *et al.* (2010) to conclude that interspecific differences in demography can have significant impacts on selection at MHC loci but that these effects may vary temporally, making it challenging to assess the role of selection in shaping variation at MHC genes (Fig. 4).

Social behavior and selection on MHC loci. A second set of comparative studies of ctenomyids has examined the effects of differences in social structure on selection at MHC genes. While most ctenomyid species are believed to be solitary – meaning that each adult inhabits its own burrow system –the colonial tuco-tuco (*C. sociabilis*) is social, with multiple adults routinely sharing a single burrow system and nest site (Lacey *et al.*, 1997; Lacey, 2000). Burrow sharing arises due to natal philopatry by females, with the result that social groups consist of several closely related adult females, their dependent young, and a single adult male (Lacey and Wieczorek, 2004). This species is endemic to Neuquén Province, Argentina, where it inhabits mesic areas along the eastern slope of the Andes (Tammone *et al.*, 2012). Also found in this region is the ecologically less specialized Patagonian tuco-tuco (*C. haigi*), which is solitary (Lacey *et al.*, 1998). Both species occur in the Limay River Valley in southwestern Argentina, providing an ideal opportunity for comparative studies of selection on MHC genes in these syntopic yet behaviorally distinct congeners.

Increased exposure to pathogens has long been believed to be a cost of sociality (Alexander, 1974) and thus it has been postulated that burrow-sharing by *C. sociabilis* should lead to increased selection on Class II MHC loci in this species compared to *C. haigi*. An initial study of selection on the Class II DQB locus in one population per species was consistent with this prediction; when corrected for interspecific differences in effective population size, evidence of selection based on departures from neutrality was greater for the group-living *C. sociabilis* (Hambuch and Lacey, 2002). However, subsequent analyses of the same populations using two additional loci - the Class II DRB and DQA genes –failed to reveal the same outcome. Thus, as in studies of *C. talarum* and *C. australis*, patterns of selection on MHC loci are complex, making it difficult to draw general conclusions regarding relationships between parameters such as social structure or demography and selection on immunogenes.

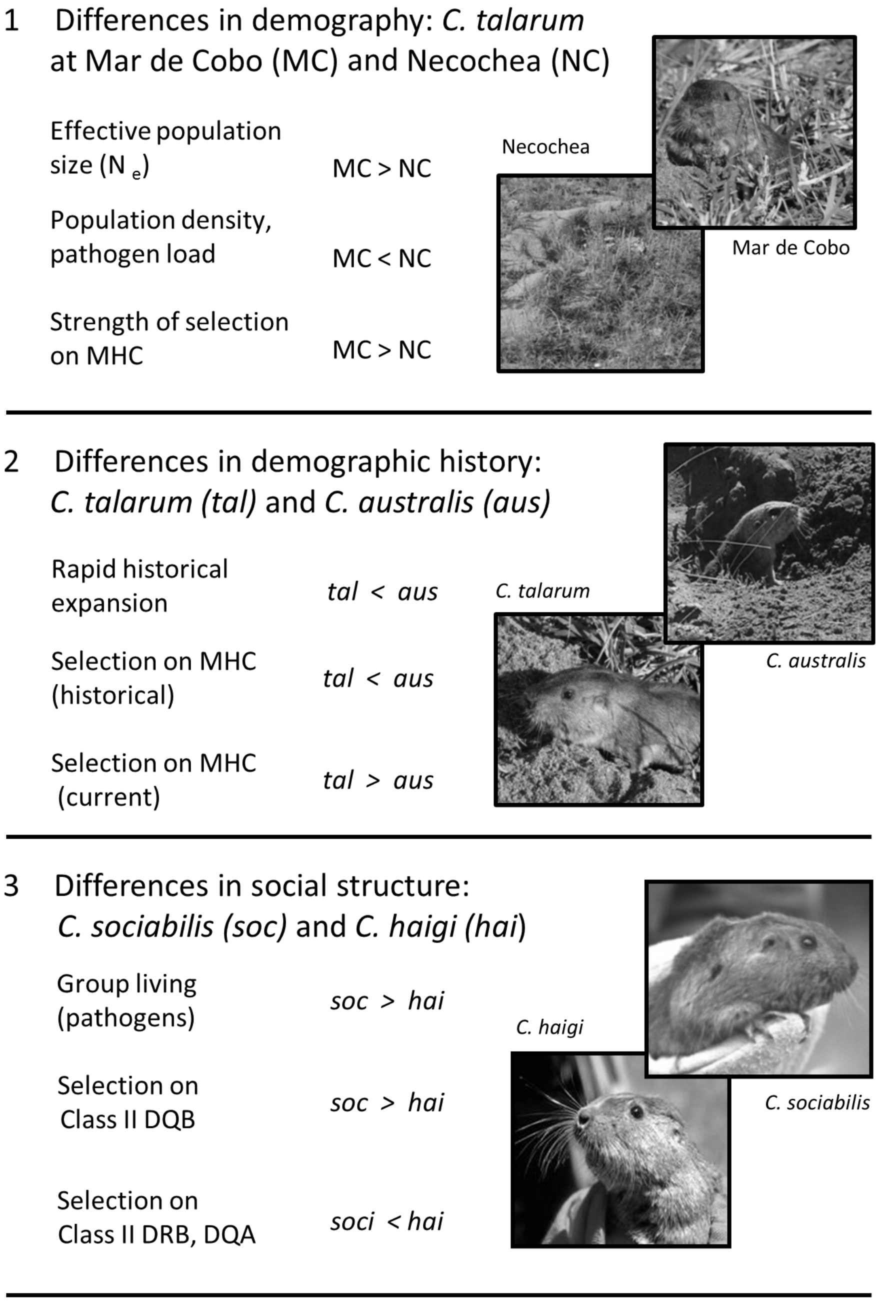

Figure 4. Synopsis of locus-specific studies of selection on **MHC** genes in tuco-tucos (*Ctenomys*). Analyses of three **MHC** Class II loci (DQA, DQB, DRB) have been used to examine patterns of selection associated with 1. intraspecific differences in demography; 2. interspecific differences in demographic history, and 3. interspecific differences in social structure. In each case, results varied by locus suggesting that a more comprehensive (*i.e.*, multi-locus) perspective on **MHC** variation in these animals would be informative. Details of each study and associated literature citations are provided in the text. Photos in parts 1 and 2 of figure courtesy of Matías Mora.

Roles for HTS. In sum, studies of ctenomyids provide multiple lines of evidence that differences in demography and behavior influence selection on MHC loci. At the same time, these analyses consistently reveal unexpected variation or even contradictory information regarding how selection acts on different Class II MHC genes within the same population or species. In some ways, this variation is not surprising, given the complexity of the immune response and the number of genes associated with detecting and neutralizing pathogens. While this variation can be informative, it also makes it more challenging to identify general relationships between demographic or other parameters and selection on immunogenes, particularly when examining only one to a few loci.

Future studies that employ HTS strategies to assess variation at MHC genes have the potential to resolve these challenges. By documenting variation at a large number of protein-coding loci, transcriptomic sequencing will provide a much more comprehensive data set that includes information from all functional MHC loci as well as other immunologically actives genes (*e.g.*, toll-like receptors, or TLRs), thereby allowing detection of overall patterns of selection on immunogenes in relation to demography and behavior. At the same time, such analyses will allow improved detection of differences in selection among loci that may reflect the different functions of individual genes or gene families. Finally, use of transcriptome data will allow exploration of patterns of immunogene expression, an aspect of immune response that has to date remained largely unstudied for natural populations of vertebrates.

Concluding thoughts

As this review suggests, HTS offers multiple opportunities to improve our understanding of evolutionary biology. Use of HTS promises to generate data sets suitable for addressing phylogenetic, phylogeographic, and population genetic questions, as well as questions regarding the evolution of genes and genomes. At the same time, the enhanced ability to examine patterns of gene expression allows the exploration of this important but poorly studied aspect of the biology of natural populations. While we are clearly enthusiastic about HTS, it is ultimately the ability to better resolve evolutionary problems that drives our interest in this technology. As we hope this review indicates, the Caviomorpha – a large, diverse clade of rodents with a complex evolutionary history – provide an important target for the application of this technology. As exemplified by our descriptions of ongoing research regarding insulin and MHC genes, there are multiple puzzling aspects of caviomorph biology that will benefit from use of this technology. We hope that the information provided here will facilitate future studies aimed at gaining further understanding of the evolutionary biology of these fascinating animals.

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10 | CAVIOMORPHS AS PREY: GENERAL PATTERNS FOR MAMMALIAN CARNIVORES AND A LOCAL STUDY FOR RAPTORS IN PATAGONIA

CAVIOMORFOS COMO PRESAS: PATRONES GENERALES PARA MAMÍFEROS CARNÍVOROS Y UN ESTUDIO LOCAL PARA AVES RAPACES EN PATAGONIA

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Abstract. South American caviomorph rodents occur in a broad range of ecosystems, display a great diversity of habits, and the greatest morphological and ecological disparity among rodents, and as primary consumers, they constitute the food of a large number of predators. We reviewed 127 studies, which included 249 diets of mammalian carnivores from South America, to investigate the importance of caviomorphs as their prey, and patterns of predation on the latter. We also present a case study to evaluate the importance of two caviomorph species in the structure of a raptor assemblage. Results indicate that consumption of caviomorphs is a common event for carnivores; they were present in 76% of the diet samples. At a biogeographical scale, the probability of consumption of caviomorphs increases with increasing predator body weight, decreasing species richness in predator diets, and decreasing longitude. Several carnivore species exhibited local trophic specialization toward some caviomoph species, which can explain the negative relationship between frequency of occurrence of caviomorphs in predators' diets and dietary richness. We found an east-west longitudinal gradient in frequency of occurrence of caviomorphs in diets, which could be related to a gradient of biodiversity and availability of prey (different from caviomorphs) for predators. Sociality does not prevent predation, when comparing predation on solitary species with social species, and diurnal social species were more preyed-upon than nocturnal ones. There was no overlap between activity patterns of predators and prey for diurnal caviomorphs, enhancing the importance of this prey to carnivores. Our case study shows that both *Ctenomys haigi* and *Microcavia australis* were important prey for the entire assemblage of raptors and were responsible for the formation of a trophic guild based on their consumption.

Resumen. Los roedores caviomorfos se encuentran en una gran variedad de hábitats, tienen hábitos diversos, y una gran disparidad en el tamaño corporal. Como consumidores primarios, constituyen una oferta de alimento importante para los predadores. Revisamos 127 trabajos que incluyeron 249 dietas de mamíferos carnívoros con el fin de detectar la presencia de caviomorfos en sus dietas. Identificamos cuales fueron las especies más consumidas y exploramos los posibles patrones de predación a escala biogeográfica. Para esto exploramos la relación entre la frecuencia de ocurrencia (FO) de caviomorfos en la dieta de carnívoros con el peso corporal de éstos y el de sus presas (caviomorfos); con la riqueza específica de las

dietas y con posibles variaciones geográficas (latitud y longitud). Por otro lado exploramos la relación entre aspectos de sociabilidad de caviomorfos con la predación por carnívoros, así como la superposición en el tiempo de actividad de predadores y presas (caviomorfos). Finalmente presentamos un estudio que resalta la importancia de dos especies de cavimomorfos como estructurantes de un ensamble de aves rapaces en la estepa Patagónica. Identificamos 51 especies de caviomorfos pertenecientes a 11 familias, en las dietas de 10 especies de félidos, en ocho especies de cánidos, dos de mustélidos y un prociónido. *Ctenomys* spp., *Hydrochoerus* sp. y *Dasyprocta* spp., fueron más consumidos por félidos; *Clyomys* spp. y *Cavia* spp. por cánidos. Dentro de los géneros que aparecieron con mayor frecuencia en las dietas de los carnívoros, las especies de mayor tamaño corporal, *Hydrochoerus* sp. y *Dasyprocta* spp. tuvieron en general una alta representación, superando en algunos casos el 60% de las FO, al igual que *Ctenomys* spp. Por el contrario, *Cavia* spp., *Microcavia* spp. y *Abrocoma* spp. tuvieron una representación menor, llegando ocasionalmente al 30% de FO en las dietas de los carnívoros evaluados. Los predadores de mayor tamaño tienden a consumir presas de mayor tamaño (como el yaguareté, *Panthera* onca, quien selecciona carpincho, *Hydrochoerus hydrochaeris*, en muchas áreas de su distribución), otras especies de gran tamaño como el puma (*Puma concolor*) se alimentan de caviomorfos de una gran variedad de tamaños a lo largo de su distribución. Las especies de caviomorfos de mayor tamaño tuvieron una representación mayor en las dietas individuales de los carnívoros que las de menor tamaño. La importancia de los caviomorfos como presas de carnívoros a una escala biogeográfica surge de la relación negativa entre las FO de caviomorfos y la riqueza en la dieta de los carnívoros, la cual suele interpretarse como indicativa de especialización trófica. Por otro lado, encontramos un gradiente longitudinal este-oeste en el incremento de las FO de los caviomorfos presa, desde el Cerrado y la Mata Atlántica de Brasil, hacia el oeste de Argentina y Chile, que fueron las áreas que concentraron los estudios de las dietas. Este gradiente fue relacionado con la mayor riqueza de especies (distintas de caviomorfos) disponibles para los carnívoros en los biomas de Brasil mencionados arriba. Las especies de caviomorfos sociales fueron igualmente consumidas que las solitarias, y dentro de las sociales las de hábitos diurnos fueron significativamente más depredadas. Por otro lado, las especies con hábitos nocturnos fueron más depredadas que aquellas con hábitos diurnos, lo que no es sorprendente dado que la mayoría de los predadores son crepusculares y nocturnos. Sin embargo, los caviomorfos diurnos también fueron más consumidos por éstos predadores, lo que pone de manifiesto que, si bien los factores que explican los patrones de actividad de los mamíferos carnívoros son complejos, pueden ajustar sus tiempos de actividad al de sus presas. Finalmente presentamos los resultados de un estudio sobre la importancia de dos especies de caviomorfos, el tuco-tuco patagónico (*Ctenomys haigi*) y el cuis chico (*Microcavia australis*) en las dietas y en la estructura de un ensamble de aves rapaces en un área protegida semi-árida de la estepa Patagónica, el Monumento Natural Bosques Petrificados (MNBP). Estas dos especies tienen mayor peso corporal que el resto de los roedores presentes en el MNBP, y por lo tanto constituyen un recurso ventajoso (desde el punto de vista energético) para sus predadores. De hecho estuvieron presentes en las dietas de las seis especies de aves rapaces estudiadas, llegando a representar más del 40% de la biomasa consumida del aguilucho común (*Geranoetus polyosoma*), el águila mora (*G. melanoleucus*) y el búho magallánico (*Bubo virginianus magellanicus*). Tanto los tuco-tucos como los cuises (con hábitos nocturnos y diurnos respectivamente) fueron consumidos por rapaces diurnas y nocturnas, aunque en distinta proporción, por lo que el tiempo de actividad no sería un factor determinante de su vulnerabilidad. Creemos que las áreas abiertas características del MNBP, carentes de matorrales altos o árboles que podrían ofrecerles protección de las aves rapaces, aumentan su riesgo de predación. Las dos especies de caviomorfos promovieron la formación de un gremio trófico basado en su consumo, lo que resalta su importancia como presas estructuradoras del ensamble de aves rapaces en el MNBP.

Introduction

South American caviomorph rodents (New World hystricognaths) occur in a broad range of ecosystems and include species that are arboreal (Adler, 2011), semiaquatic (Macdonald *et al.*, 2007), semifossorial (Ebensperger and Blumstein, 2006; Lacey and Ebensperger, 2007), and subterranean (Lacey and Ebensperger, 2007). Some species have wide geographical ranges with different populations experiencing very different ecological conditions (Lacey and Ebensperger, 2007). Many caviomorphs are solitary (Adler, 2011), or display diverse levels of sociality (Rowe and Honeycutt, 2002; Silk, 2007). Caviomorphs constitute the rodent clade with the greatest morphological and ecological diversity, including the broadest range of body size within Rodentia (Sánchez-Villagra *et al.*, 2003; Woods and Kilpatrick, 2005). They occupy a great variety of niches and, as primary consumers, they constitute the food of a great number of predators. Predation upon caviomorph species has been documented along their range as being part of the diets of carnivorous mammals, birds of prey (this chapter and references therein), reptiles (Soini and Soini, cited in Eisenberg and Redford, 1999) and even humans (Zapata Ríos, 2001; Santos Moreno and Pérez-Irineo, 2013). Despite their diversity in body size, this group sustains many species in animal communities (Farías and Jaksic, 2007a; Zapata *et al.*, 2007). Here we review the diets of carnivorous mammals from South America to evaluate the role of caviomorphs as their prey at a biogeographical scale (an area large enough to include different climates, vegetation and species assemblages, see Cueto, 2006). Then we present a case study which highlights the importance of two species of caviomorphs in the structure of an assemblage of raptors in southern Argentinean Patagonia.

Methods

Literature review: mammalian carnivores and predation on caviomorphs

We searched for studies of South American carnivore diets by consulting databases (*e.g.*, IngentaConnect; Google Scholar), and publisher websites (*e.g.*, ScienceDirect; SpringerLink; Wiley InterScience), by asking researchers in South American countries (colleagues working on carnivore ecology) for information, and by consulting our own collection of studies of carnivores (App.1). Studies presenting diet information for more than one study area, or for different time periods in the same area, were considered as different diet samples (see methods for considerations regarding potential spatial autocorrelation in data and presence of pseudo-replications). Most of the studies expressed their diet results as frequency of occurrence (FO) of the different prey types in carnivore diets.

We recorded geographical variables (latitude and longitude, in degrees) either from the studies themselves or, if they were not provided, from Google Earth (http://earth.google.com), for the construction of a map with these studies area locations. We also constructed maps with the distribution of the FO of the most consumed genera of caviomorphs, and others with the distribution of the FO of caviomorphs in the diets of felids and canids. We included only those species widely distributed along South America (Redford and Eisenberg, 1992). All maps were constructed by using the software Arc View 3.2 (ESRI, Redlands, California, USA).

Biogeographical patterns of predation

To test patterns of predation on caviomorphs we selected the following variables:
1) Predator and prey body weights. Small predators tend to eat small prey, whereas larger predators attack predominantly larger prey; body weight data were taken from Eisenberg and Redford (1999); Redford and Eisenberg (1992) and Zapata (2005). 2) Species richness in predators' diets, to evaluate the existence of a relationship between predation on caviomorphs and number of other types of prey in diets. 3) Latitude and longitude, to search for geographic differences in consumption of caviomorphs by predators.

Data analyses. We used linear mixed-effects models (GLMM; Crawley, 2007) using a binomial distribution for errors of the response variable (the frequency of occurrence of caviomorph species in predators' diets) and a logit link function (Crawley, 2007). We did not include caviomorphs from diets of *Potos flavus, Galictis vittata, Pseudalopex fulvipes, Dusycion sechurrae, Leopardus guigna* and *Eira Barbara* in these analyses because of the small sample sizes for the diets of these carnivores. As few studies presented the percentage of prey in terms of biomass consumed, we did not include them in these models. To avoid pseudo-replication among studies performed on the same geographic site, and to avoid dependencies among the response variable (FO) and explanatory variables, the different localities (study sites) and predator species were included in the model as random effects. To assess the extent of spatial auto-correlation among samples, we first used a spline correlogram (Bjørnstad and Falck, 2001). To produce the correlogram we used the nfc package (Bjørnstad and Falck, 2001). As we detected significant positive spatial auto-correlation at distances of less than 200 km, we looked at the spatial auto-correlation in the Pearson residuals of the model (Rhodes *et al.*, 2009). After fitting the GLMM we observed that there was no obvious increase in spatial auto-correlation at those short distances suggesting that the mixed effects model successfully accommodated the spatial auto-correlation within localities. The GLMM models were carried out using the packages LME4 (Bates *et al.*, 2011). Akaike´s Information Criterion, with small-sample bias adjustment (AICc) (Burnham and Anderson, 2002), was used to select the most parsimonious models that best fit the data; here we used the package "Mumin" (Barton, 2012). We selected the model with the lowest AICc score as the best model. Analyses were carried out using R 2.15.1. statistical software (R Development Core Team, 2012).

Finally, to assess any relationship between aspects of the sociality of prey species and predation by carnivores, *i.e.,* that sociality enhances predator detection or group defense (Maher and Burger, 2011) we assigned the categories "solitary" or "in groups" to caviomorphs species (Eisenberg and Redford, 1999; Redford and Eisenberg, 1992). We also considered overlap in activity time of both predator and prey, assigning categories "diurnal", "crepuscular" and "nocturnal" to predators and "diurnal" or "nocturnal" to prey (Eisenberg and Redford, 1999; Redford and Eisenberg, 1992; Zapata, 2005). The relationship between sociality of prey and predation, as well as overlap in activity time of both predator and prey were evaluated using Chi-squared-test.

Results

Carnivore predation on caviomorphs

Our review comprised 127 studies (App. 1) which included 249 diets of 10 canids, 10 felids, four mustelids, two procyonids, and two mephitid species. From the total of diet samples revised, 76% of them contained some caviomorph species. Predation upon caviomorphs seems to be widespread in South America, with some areas concentrating more studies on predation like southeastern Brazil and western Argentina and Chile (Fig. 1). In our revision, 51 species of caviomorphs were identified, which represent 57% of the extant genera (according to Upham and Patterson, 2012) and cover most of the families (11 out of 13) of the Caviomorpha (App. 2). The consumption of caviomorphs is a common event among carnivores; they were reported in the diets of all the felid species studied, in eight canid species; and in two and one species of mustelids and procyonids, respectively (Tabs. 1, 2, and 3). In general, the same genera of caviomorphs were preyed-upon and consumed by both felids and canids (Tabs. 1, 2). However, three of the four species of porcupines (*Chaetomys subspinosus, Coendou prehensilis,* and *C. rufescens,* these two last spe-

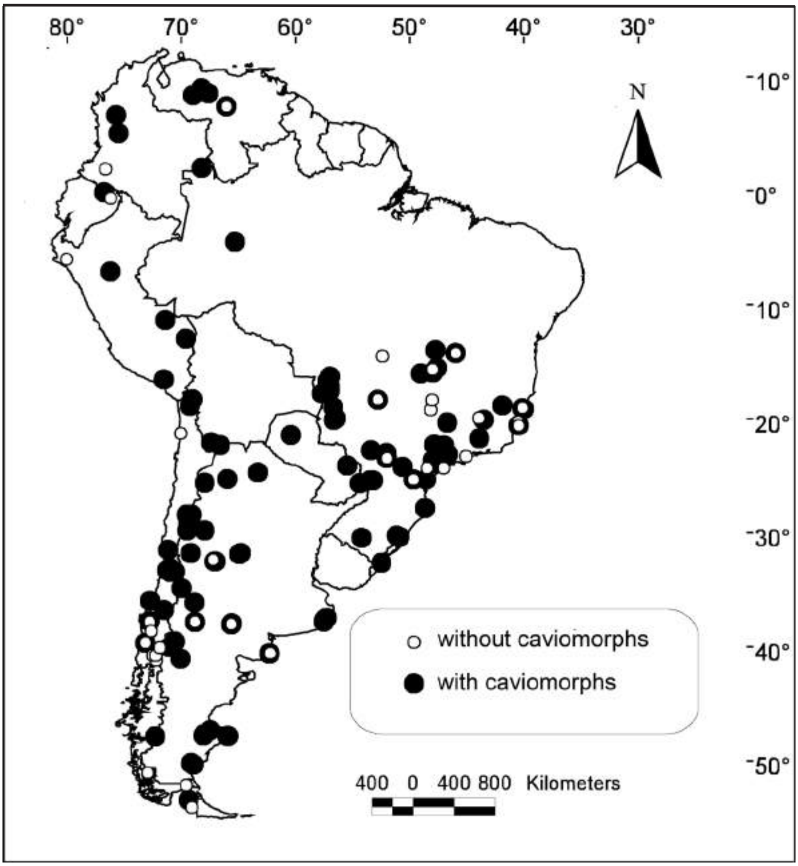

Figure 1. Geographical distribution of the studies of carnivore diets with (black circles) and without (white circles) caviomorphs included in our review.

cies as *Coendou* spp. in Tab. 1), one octodontoid (*Octodontomys gliroides*), two echimyids (*Mesomys hispidus, Dactylomys* sp.), and the dinomyid (*Dinomys branickii*) were consumed only by felids. By contrast, also according to these studies, two octodontoids (*Aconaemys* sp. and *Spalacopus* sp.) and two echimyids (*Euryzygomatomys* sp. and *Olallamys* sp.) were consumed by only canids (Tab. 2). Moreover, *Ctenomys* spp., *Hydrochoerus* sp., and *Dasyprocta* spp., were more frequently consumed by felids (Fig. 2.1); and *Clyomys* spp., and *Cavia* spp. by canids (Fig. 2.2).

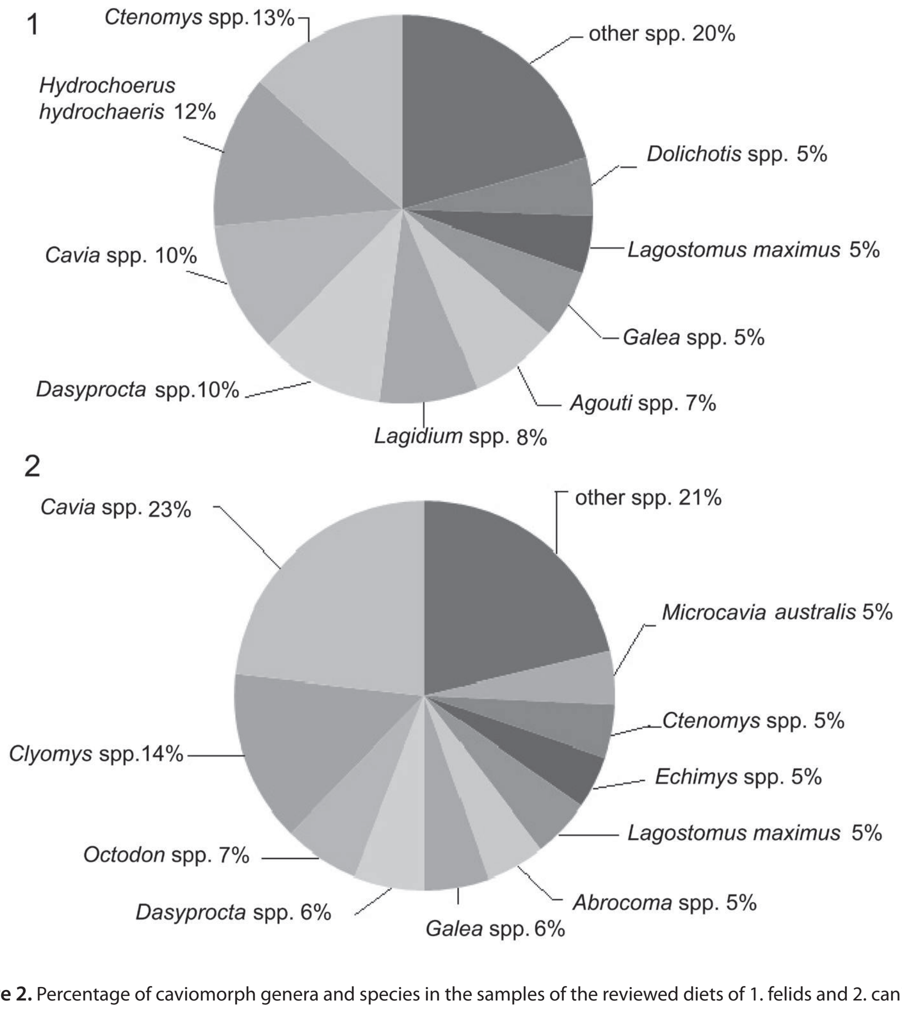

Figure 2. Percentage of caviomorph genera and species in the samples of the reviewed diets of 1. felids and 2. canids.

At a biogeographical scale, when analyzing the frequencies of occurrences of the most consumed genera of caviomorphs in carnivore diets, we saw that those species with large body size (more than 2 kg) were better represented in carnivore diets than smaller ones (Fig. 3). This is, *Hydrochoerus* and *Dasyprocta*, accounted for more than 30% of the diets of predators, and in some cases they represented more than 60% of occurrences in diets. By contrast, *Cavia* spp.,

Table 1. Presence of caviomorph species in the diets of felids. Numbers indicate the number of studies with and without these species.

Caviomorph spp.	***P. onca***	***P. concol***	***L. colocolo***	***L. geoffroyi***	***L. guigna***	***L. jacobita***	***L. pardalis***	***L. tigrinus***	***L. wiedii***	***P. yagoua***
Chaetomys subspinosus	1									
Coendou spp.							3			
Sphiggurus villosus							4			
Dasyprocta spp.	6	8					8	2		
Myocastor coypus		1		4						
Myoprocta pratti							1			
Agouti spp.	6	3	1				5	1		1
Dinomys branickii							1			
Cavia spp.		1	2	11		2	1	2		3
Galea spp.	1	10	2				4			
Microcavia australis		3	1							
Dolichotis spp.	1	9		1						
Hydrochoerus sp.	22	5		2						
Octodon spp.					1					
Octodontomys gliroides			2							
Ctenomys spp.		19	9	3						
Dactylomys sp.							1			
Mesomys hispidus							1			
Proechimys spp.	1	1					3			
Thrichomys spp.							2			
Clyomys spp.							4			
Euryzygomatomys sp.							2			
Echimys spp.		1					1	1	3	3
Lagostomus maximus		11								
Chinchilla spp.		2								
Lagidium spp.		4	7	1		7				
Abrocoma spp.			7			3				
Without caviomorphs		15		1			4	1	2	2

Note: *P. onca, Panthera onca; P. concol, Puma concolor; L. colocolo, Leopardus colocolo; P. yagoua, Puma yagouaroundi.*

Table 2. Presence of caviomorph species in the diets of canids. Numbers indicate the number of studies with and without these species.

Caviomorphs spp.	***C. thous***	***C. brachy.***	***L. culpae***	***L. griseus***	***L. gymnoc.***	***S. venatic***	***A. microtis***	***L. fulvipes***	***L. vetulus***	***L. sechur***
Sphiggurus villosus	2									
Dasyprocta spp.	2	4				5	1			
Myocastor coypus			1							
Myoprocta pratti						1	1			
Agouti spp.		1	3			2				
Cavia spp.	7	14	15	5	6					
Galea spp.	2	3	2	3	1					
Microcavia australis			4	4	1					
Dolichotis spp.			1	2	1					
Hydrochoerus sp.	2	1								
Aconaemys fuscus			2					1		
Octodon spp.			10	2				1		
Spalacopus cyanus			1	1						
Ctenomys spp.				9						
Olallamys albicauda	1									
Proechimys spp.		1								
Thrichomys spp.	2	4								
Clyomys spp.	4	7	18							
Euryzygomatomys sp.	1									
Echimys spp.	2	5				1	1			
Lagostomus maximus			2	2	6					
Chinchilla spp.			2	2						
Lagidium spp.			6	1						
Abrocoma spp.			9	1						
Without caviomorphs	5	2	4	6	1		1		4	1

Note: *C. thous, Cerdocyon thous; C. brachy, Chrysocyon brachyurus; L. culpae., Lycalopex culpaeus; L. gimnoce, L. gymnoc.; L. sechur, L. sechurae; S. venatic, Speothos venaticus; A. microtis, Atelocynus microtis.*

Microcavia spp., and *Abrocoma* spp. accounted for less than 30% of occurrences in diets (Fig. 3) meaning that species of these genera often occur with other prey in the diets of carnivores, except for *Ctenomys* spp. In fact, *Hydrochoerus* and *Dasyprocta* spp. were more frequently consumed by the biggest carnivores, jaguar (*Panthera onca*) and puma (*Puma concolor*); *Dasyprocta* spp. were also consumed by ocelot (*Leopardus pardalis*) (Tab. 1).

With respect to predators, also at a biogeographical scale, the puma, jaguar and ocelot consumed caviomorphs along their distributional ranges, and caviomorphs occurred in highest frequencies in the diets of pumas and jaguars (Fig. 4.1). Regarding canids, both culpeo (*Lycalopex culpeus*) and grey (*L. griseus*) foxes also consume caviomorphs along their ranges, although at a relative low frequency; maned wolf consumed caviomorphs in Brazil only (Fig. 4.2).

Table 3. Presence of caviomorph species in the diets of mustelids, procyonids and mephitids. Numbers indicate the number of studies with and without these species.

Caviomorphs spp.	*G. cuja*	*G. vittata*	*E. barbara*	*L. longica*	*P. cancrivo*	*N. nasua*	*P. flavus*	*C. humbol*
Dasyprocta spp.						2		
Myocastor coypus						1		
Agouti spp.						1		
Cavia spp.					3			
Microcavia australis	3							2
Hydrochoerus sp.	1							
Ctenomys spp.	5							2
Proechimys spp.			1					
Abrocoma spp.	1							
Without caviomorphs		1		3	2	2	1	1

Note: *G. cuja, Galictis cuja; E. barbara, Eira barbara; L. longica, Lontra longicaudis; P. cancrivo, Procyon cancrivorus; N. nasua, Nasua nasua; P. flavus, Potos flavus; C. humbol, Conepatus humboldtii.*

Biogeographical patterns of predation

Predation and body weights of both predators and prey; richness in predator diets; and biogeographical patterns of predation. The best model describing predation on caviomorphs included longitude, species richness in predator diets, and predator body weights (Tab. 4). Accordingly, the probability of consumption of caviomorphs increased with decreasing longitude (parameter estimates = -0.031 ± 0.018; CI 95%: -0.067 -0.002, excluding 0), with increasing predator body weight (parameter estimates = $1.12 \times 10^{-2} \pm 5.407 \times 10^{-3}$; CI 95%: 0.002 -0.021, excluding 0), and with decreasing species richness in predator diets (parameter estimates = $-0.012 \pm 2.95 \times 10^{-3}$; CI 95%: -0.018 -0.006, excluding 0). Random effects of predators contributed significantly to the model (X^2, $P < 0.001$).

Predation and sociality. We did not find differences between "solitary" or "in groups" predation on caviomorphs (Tab. 5). Nevertheless, nocturnal "solitary" caviomorphs were consumed more frequently than diurnal ones; on the other hand diurnal "in groups" were consumed more often than nocturnal "in groups" caviomorphs ($X^2 = 25.15$, $p<0.01$, Tab. 5).

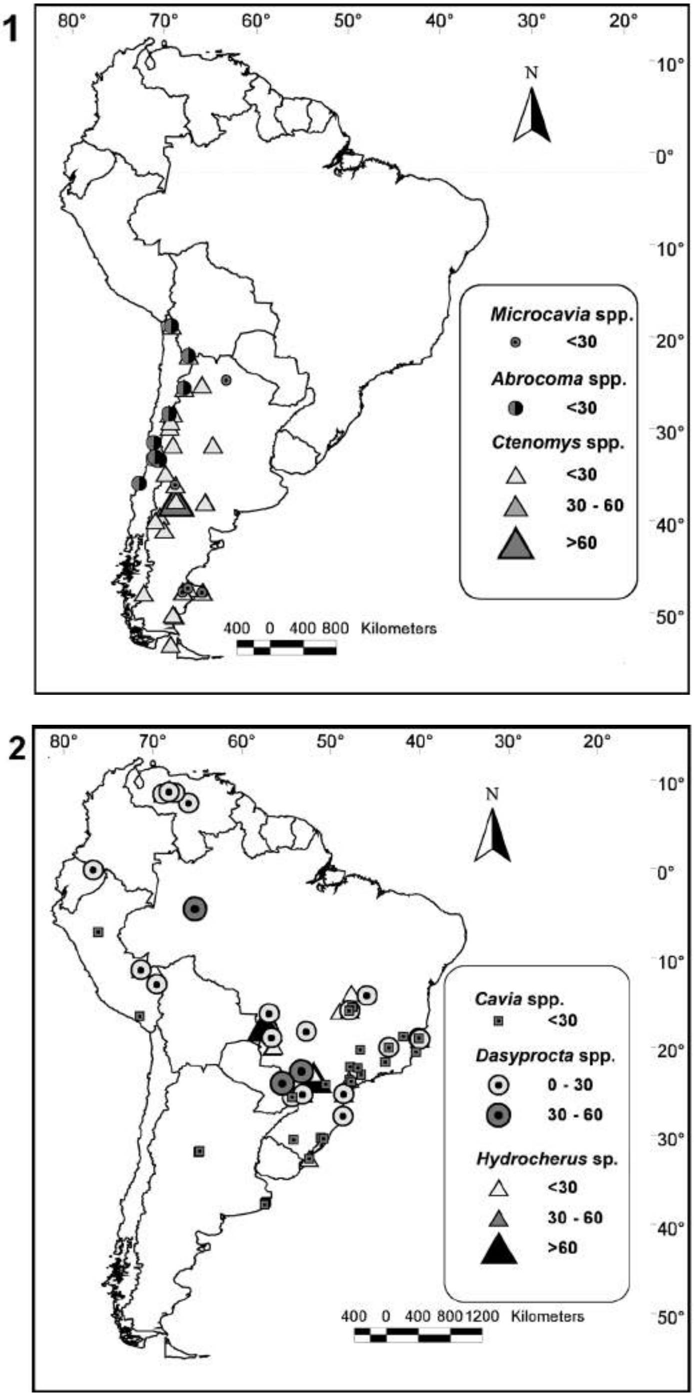

Figure 3. Frequencies of occurrence of caviomorphs in the diets of carnivores from reviewed studies. Frequencies were grouped into <30; between 30 and 60; and >60. 1. Frequencies of *Ctenomys* spp., *Microcavia* spp. and *Abrocoma*; 2. Frequencies of *Hydrochoerus* sp., *Dasyprocta* spp. and *Cavia* spp.

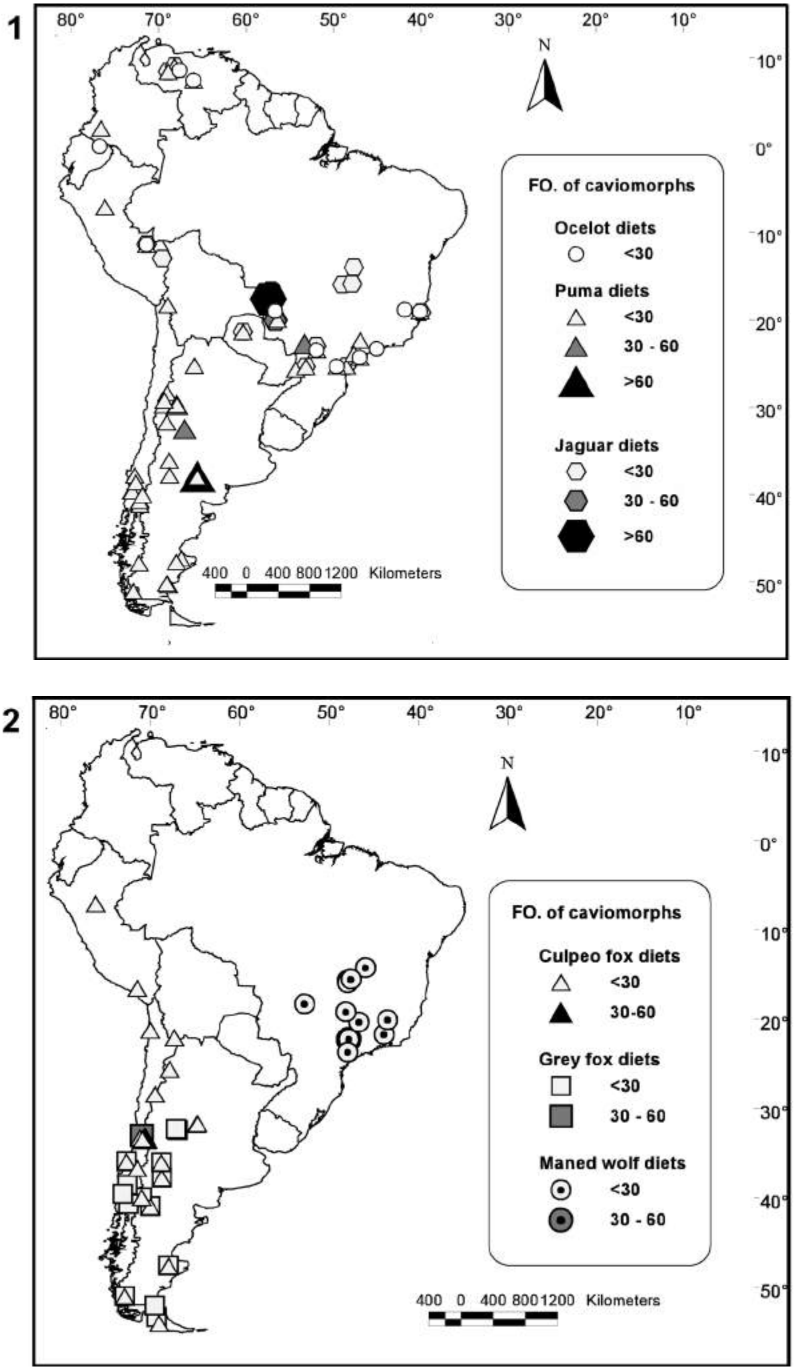

Figure 4. Frequencies of occurrence of caviomorphs in the diets of carnivore predators. Frequencies were grouped into <30; between 30 and 60; and >60. 1. diets of ocelots, pumas and jaguars; 2. diets of culpeo and grey foxes, and maned wolf.

Table 4. Model selection results for the four highest-ranked candidate models that explain the frequencies of occurrences of caviomorphs in carnivore diets from revised studies.

Model	parameters	LogLik	AICc	ΔAICc	AICcWeight
LONG + WPRED + RICH	6	-705.78	1423.98	0.00	0.35
WPREDED + RICH	5	-707.09	1424.48	0.50	0.27
LTA+ LONG +WPRED+RICH	7	-705.08	1424.72	0.74	0.24
LAT+WPRED+ RICH	6	-706.77	1425.96	1.98	0.13

LONG, Longitude; **WPRED**, predator weights; **RICH**, diet richness of predators; **LAT**, Latitude

Table 5. Frequency of occurrence (%) of consumed caviomorphs in carnivore diets according to their activity and sociality.

Sociality / Activity	Diurnal	Nocturnal	Total
Solitary	5.95	42.26	48.21
In group	33.01	18.75	51.79
Total	38.99	61.01	100

Predation and activity pattern of both predator and prey. In general, "nocturnal" caviomorphs were consumed more frequently than "diurnal" ones ($X^2 = 9.32$, $p < 0.01$, Tab. 6). "Nocturnal" caviomorphs were preyed-upon more frequently by "crepuscular" predators; the same is true of "nocturnal" predators (Tab. 6). "Diurnal" caviomorph species were also often consumed by "crepuscular" predators; the same is true of "nocturnal" predators (Tab. 6).

Table 6. Frequency of occurrence (%) of consumed caviomorphs in carnivore diets according to both predator and prey activity.

Predator / Prey	Diurnal	Nocturnal	Total
Diurnal	2.68	2.98	5.65
Crepuscular	17.56	21.73	39.29
Nocturnal	18.75	36.31	55.05
Total	38.99	61.01	100

Discussion

Our revision shows that predation on caviomorphs by mammalian carnivores is a widespread phenomenon in most South American study areas. We could not collect diet information from central Brazil and/or from a great part of Bolivia, probably due to the small number of field studies on carnivores from those areas (Brito *et al.*, 2009). The great representation of caviomorph families in carnivores' diets (11 of 13 listed in Upham and Patterson, 2012) suggests that despite their great morphological and ecological disparity, wherever a caviomorph occurs, it will constitute a potential prey for carnivores. Predators with wider geographic ranges included a great diversity of caviomorphs in their diets. Therefore, the dietary flexibility of generalist predators like pumas (*Puma concolor*), ocelots (*Leopardus pardalis*) (Sunquist and Sunquist, 2002), and Patagonian foxes (culpeo and grey fox, *Lycalopex culpaeus* and *L. griseus*, respectively, Zapata *et al.*, 2007) reflects the distribution of their caviomorphs prey.

Caviomorphs of a broad range of body sizes are important prey for carnivores. In our revision, the largest caviomorph, the capybara (*Hydrochoerus hydrochaeris*), was an important prey for the jaguar (*Panthera onca*), the largest felid of the Neotropics, which displays feeding specialization and selection toward this large-bodied prey (40 kg) in many areas of its distribution (Cascelli de Azevedo and Murray, 2007). By comparison, one of the smallest caviomorphs in our study, *Ctenomys haigi* (113 g) constitutes an important resource for a wide variety of predators ranging from the large bodied puma to the pampas cat (*Leopardus colocolo*) and the small grey fox (Zapata, 2005).

Predation can be influenced by several factors, for example, the size of predators determines the range of prey sizes they can feed upon (Zapata *et al.,* 2013). A positive correlation between prey size and predator size is usually the rule for sympatric carnivores (see Zapata, 2005 and references therein). We found a positive relationship between FO of caviomorphs and predator body weight at a geographical scale, meaning that body size of predator is an important factor to explain patterns of predation on these prey species. As seen above, caviomorphs occurred in highest frequencies in the diets of predators of great body size, *i.e.*, pumas and jaguars.

The importance of caviomorphs as prey for carnivores at a biogeographical scale arises from the negative relationship between the FO of caviomorphs and species richness in carnivore diets. A negative relationship between a given food group and dietary diversity is usually interpreted as indicating trophic specialization (Futuyma and Moreno, 1988; Fedriani *et al.*, 1998, Díaz-Ruiz *et al.*, 2013). In our revision, several carnivore species exhibited local specialization toward some caviomoph species. For example puma on plains viscacha, (*Lagostomus maximus*, Branch *et al.*, 1996), and agutí bayo (*Dasyprocta azarae,* Ludwig *et al.*, 2007); pampas cat on tuco-tuco (*Ctenomys* sp., Palacios *et al.*, 2012); the short-eared fox (*Atelocynus microtis*) and bush dog (*Speothos venaticus*) on *Proechimys* sp. and Echimyinae (Peres, 1991); and the Andean cat (*Leopardus jacobita*) on mountain viscacha (*Lagidium viscacia*, Viscarra Siñani, 2008), among others. Also the negative relationship between longitude and the FO of caviomorphs in carnivore diets, which corresponds to an east-west gradient, could be related to species richness. In our revision, most studies took place in southeastern Brazil and western South America, mainly in Argentina and Chile. The first area corresponds to Brazil´s Atlantic Forest and the Cerrado, which are considered hotspots of biodiversity (Brooks *et al.*, 2002). Predators in these areas have a wide range of available prey that could be reflected in their diets, increasing the numbers of different kinds of prey, other than caviomorphs.

Sociability has been described in species representing several caviomorph families. Ecological factors, including the distribution of resources such as food, soil conditions associated with digging, and predation risk have been identified as potential causes for the formation of social groups (Hayes *et al.,* 2011). Regarding predation, it has been suggested that sociality enhances predator detection or group defense (Lacey and Ebespenger, 2007); accordingly, at our broad scale, it may be expected that social caviomorphs suffer less predation when compared with their solitary counterparts. Contrary evidence arises from our revision. In our study, both solitary and social species were equally preyed-upon, supporting the suggestion that in some species like capybara, sociality may be related to predation whereas in other caviomorphs it is more related to cooperation in burrowing (Ebespenger and Cofré, 2001). Ebespenger and Blumstein (2006) found a link between predation risk and sociality in caviomorphs to explain the reasons of this behaviuor for diurnal species. They linked selection of predators to larger rodents, the greater exposure of rodents when foraging due to their larger bodies, and more vulnerability to predators during the day. Then, by being social, diurnal species could engage in corporate vigilance and increase the rate at which they detect predators (Ebespenger and Blumstein, 2006). In fact, in our revision, most of the social species consumed were diurnal.

Another factor to consider when searching for patters of predation is the overlap in activity pattern of both predator and prey. Caviomorph species with nocturnal habits were more frequently preyed-upon than diurnal ones. This is not surprising because the majority of predators considered in this revision have crepuscular and nocturnal habits (Eisenberg and Redford, 1999; Redford and Eisenberg, 1992; Zapata, 2005). What seems to be unexpected is that caviomorphs with diurnal habits were also more consumed by crepuscular and nocturnal predators. Although the factors that explain the daily activity patterns of carnivore predators are complex (Lucherini *et al.*, 2009), there are numerous examples of predators changing their activity time to avoid competitors or to adjust their activity to that of their prey (Neale and Sacks, 2001; Di Bitetti *et al.*, 2009).

Case study: Patagonian predators and caviomorphs

To illustrate predation on caviomorphs we examined the diets of a raptor assemblage from Santa Cruz province, Argentinean Patagonia. We conducted our fieldwork in different sites of a protected area, the Monumento Natural Bosques Petrificados (MNBP). The area is a flat steppe at 800-900 m of altitude with shrublands and grasslands interrupted by ravines and rock outcrops. The vegetation cover does not usually exceed 50%. The weather is dry and cold, with frequent frosts. Mean annual temperatures are about 10°C, with highest temperatures during summer (30°C for January and February) and lowest during autumn and winter (-10°C from May to July). Annual rainfall ranges between 100 and 200 mm. The assemblage consisted of six raptor species: Black-chested Eagle (*Geranoetus melanolecus*), Variable Hawk (*Geranoetus polyosoma*), American Kestrel (*Falco sparverius*), Austral Pygmy Owl (*Glaucidium nanum*), Magellanic Horned Owl (*Bubo virginianus magellanicus*) and Barn Owl (*Tyto alba*). We focused on two of the three caviomorph species found in the area, the lesser cavy (*Microcavia australis*) and the Patagonian tuco-tuco (*Ctenomys haigi*). The third species, the mara (*Dolichotis patagonum*), was not found in the diet of these species. The lesser cavy is a 286 g semifossorial member of the family Caviidae, widely distributed in Argentina. It forms groups composed of several females, one or a few males, and their young. Cavies forage around a burrow and/or make short incursions along activity paths. Cavies do not need the burrow for their daily forage and use it for sleeping at night, napping during the day, parturition and litter rearing, group nesting (social thermoregulation), and for avoiding inclement weather (Ebensperger *et al.*, 2006; Taraborelli, 2009). The Patagonian tuco-tuco (Ctenomyidae) is a 113.23± 23.6 g (own data, n= 18) solitary, nocturnal and subterranean rodent, with each adult occupying a different burrow system (Lacey *et al.*, 1998). It is known from the Argentina provinces of Chubut and Río Negro (Pearson, 1984) and it is also present in our study area. Unlike the lesser cavy, the Patagonian tuco-tuco is rarely seen above ground.

To evaluate the importance of both caviomorph species as prey for raptors, we examined raptor diets from pellets collected in the study area from February 1999 to September 2009. Collected material was hydrated and broken apart by hand, and prey items were identified using reference collections of the Centro de Investigaciones de Puerto Deseado (CIPD) and keys (Chehébar and Martin, 1989; Pearson, 1995). We estimated the biomass of rodent and avian prey items from the literature and our unpublished records. Following Vargas *et al.,* (2007), we assigned a biomass of 1 g to each invertebrate prey item. We calculated the biomass contribution of each prey type as a percent of the total biomass of all prey consumed. To test the importance of caviomorphs in the community structure of raptors, (*i.e.*, trophic guild structure *sensu* Root, 1967) we used the clustering technique unweighted pair-group method with arithmetic averaging (UPGMA), previously used by other authors and in our previous work, to obtain a dendrogram from which to identify guilds with statistical significance (Zapata, 2005; Zapata *et al.*, 2007, 2013). Once guilds were identified, Principal Component Analysis (PCA), calculated on a correlation matrix, was used to assess which food categories generated the pattern found in the cluster analysis (Manly, 1994).

Results

Diets of raptors from MNBP: importance of caviomorphs

Both the tuco-tuco and the lesser cavy were important prey for raptors. The tuco-tuco represented 40% of the total ingested biomass for the Variable Hawk, and achieved the highest occurrence in its diet (38% frequency of occurrence). For the rest of the raptors of the assemblage, it represented more than 10% of the total biomass. The lesser cavy was by far the most consumed species by the Variable Hawk, the Black-chested Eagle, and the Magellanic Horned Owl with 42.2%, 56.2% and 58.12% of consumed biomass respectively (Tab. 7). Both caviomorphs were present in the diet of all raptor species of the assemblage, irrespective of their body weights and activity pattern, although the heaviest species consumed them in large proportion (Tab. 7).

Trophic guild identification: community structure based on the consumption of caviomorphs

Raptors were separated into two trophic guilds which contained species that exploit resources in a similar way, and were named according to the dominant prey consumed by their members. The cut-off point in the dendrogram was achieved at a similarity level of 75% ($p < 0.05$) (Fig. 5). Each guild was composed of three species and they were: 1) Guild I: composed

Table 7. Food categories in the diet of the six raptor species from **MNBP** expressed in percentage of consumed biomass; raptor weights and activity times.

Food Categories	***G. melanoleucus***	***G. polyosoma***	***Falco***	***Bubo***	***Tyto***	***Glaucidium***
Microcavia	56.3	42.4	24.8	58.1	20.9	24
Ctenomys	10.1	40.8	6.4	10.4	16.2	11.2
Small mammals (<100g)	0.55	2.5	18.2	9.21	61.25	38.08
Hares	11.21	4.4	0	10.91	0	0
Other mammals	16.24	0	0	0	0	0
Birds	5.48	1.9	18.2	10.51	1.7	20.46
Reptiles	0.13	0.86	22.6	0	0	7.95
Invertebrates	0.26	0.19	9.8	0.78	0.1	1.08
Raptor weight (kg)	2	0.95	0.12	2	0.4	0.0805
Raptor activity time	diurnal	diurnal	diurnal	nocturnal	nocturnal	nocturnal
Number of pellets analyzed	338	268	56	112	175	364

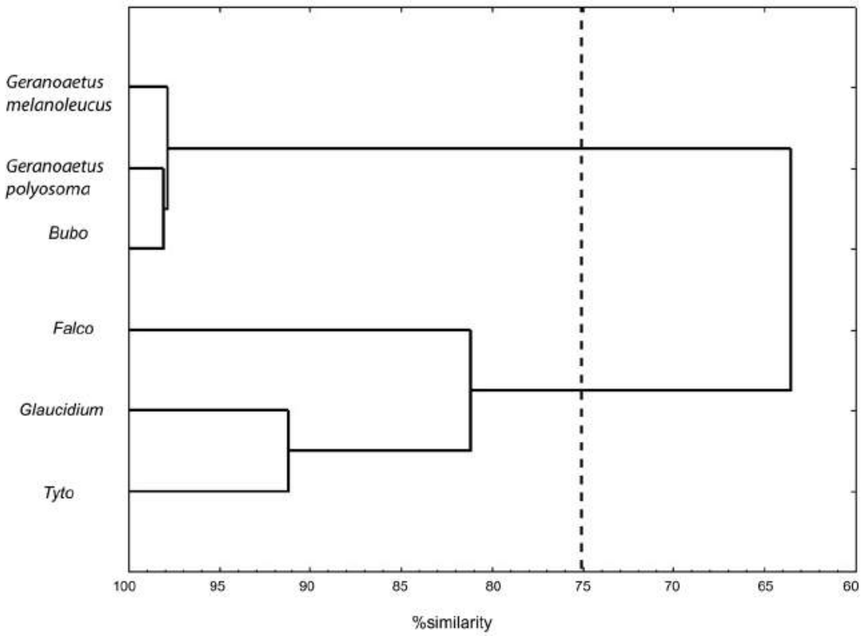

Figure 5. Trophic guild structure of raptor assemblage from **MNBP**, Argentine Patagonia. Dotted line at 75% of similarity indicates the existence of two guilds.

of the Variable Hawk, the Black-chested Eagle and the Magellanic Horned Owl, these species converged mainly in the consumption of lesser cavies and tucos, and hares to a lesser extent, so we named it the "caviomorphs-hares" trophic guild. 2) Guild 2: composed of the Barn Owl, the Austral Pygmy Owl, and the American Kestrel, these species converged in the consumption of small mammals (< 100g, mainly *Abrothrix* sp. and *Eligmodontia* sp.), and birds, reptiles and invertebrates to a lesser extent (Tab. 7), so we named it the "omnivorous" trophic guild. Principal components 1 and 2 explained 52.38% and 24.43% respectively of the overall variance of the diet of the six raptor species. The main food categories that contributed to the first axis were caviomorph rodents, hares and "other mammals" (xenarthrans and carnivores) on the negative side, where Variable Hawk, Black-chested Eagle and Magellanic Horned Owl were located. On the positive side, birds and reptiles contributed to this axis, where American Kestrel was located (Fig. 6). The food categories that contributed to the second axis were small mammals (< 100g) on the positive side, where the Barn Owl and the Austral Pygmy owl were located. The American Kestrel was located on the negative side, where invertebrates and reptiles were the food categories that most contributed to this axis (Fig. 6).

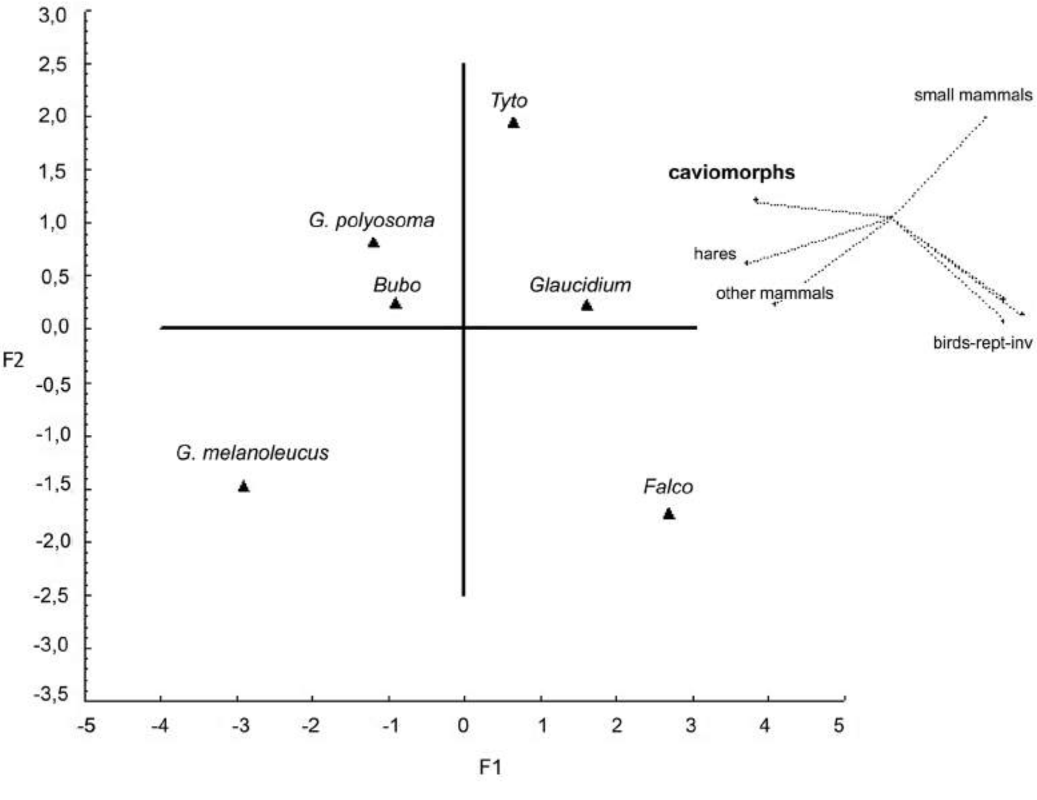

Figure 6. Principal component analysis (**PCA**) of the diets of raptors from **MNBP**, Argentine Patagonia and projection of the variables (different prey) on the factor plane (1x2). Principal components (F1 and F2) explained 52.38% and 24.43% respectively of the overall variance of the diet.

Discussion

Rodents from desert and semi-desert environments are the most diverse and abundant group, with a known range of behavioral, physiological, and ecological adaptations which allow their persistence (Letnic, 2007; Taraborelli *et al.*, 2009). Rodent communities from arid zones have been the focus of an important number of long term studies around the world, to understand how biotic and abiotic factors interact to determine community structure (Dickman *et al.*, 2010, Shenbrot *et al.*, 2010; Thibault *et al.*, 2010). Among these factors, the effects of predation on these communities may be very important (Previtali, 2006) to null (Previtali *et al.*, 2009, Gutierrez *et al.*, 2011). From the predators' point of view, rodents constitute the principal resource in arid environments, probably due to the scarcity of alternative prey (Farías and Jaksic, 2007a, b; Zapata *et al.*, 2007). In our study area, caviomorphs are heavier than the rest of rodent species and for this reason, they constitute an energetically profitable prey for predators. In fact, they were present in the diets of the entire assemblage of raptors. One of the factors associated with patterns of predation is the overlap in activity pattern of both predator and prey, to ensure encounters between them (Taraborelli, 2008). In our study, cavies and tuco-tucos (with diurnal and nocturnal habits respectively) were consumed by both diurnal and nocturnal raptors, although in different proportions, suggesting that activity time is not a determinant factor that can explain their vulnerability. For example, tuco-tucos were highly consumed by the Variable Hawk, and cavies by the Magellanic Horned Owl. Baladrón *et al.* (2009) described a close trophic association between hawks and tuco-tucos in a coastal locality of Buenos Aires province, because, as seen above, they are profitable prey in terms of energy available and handling costs. The diet of the Magellanic Horned Owl has been well studied in Patagonia (see Formoso *et al.*, 2012 and references therein) and cavy species seem to be less important for this owl in other sites than in MNBP. The fact that cavies were highly consumed (not only in biomass but also in frequency) may be due to an opportunistic behavior of the Magellanic Horned Owl, taking advantage of an abundant resource (Trejo *et al.*, 2005). Unfortunately quantitative data on lesser cavy abundances in the sites where the owl's diet was studied are not available.

Another important factor to take into account is the avoidance of predation risk. For desert rodents, available evidence supports the idea that shrub habitats provide lower predation risk than exposed areas (Ebespenger and Wallem, 2002). The open area characteristics of MNBP, without dense shrubs or trees that could give vertical protection from raptors, can increase rodent predation risk because predators prefer to attack in these areas, decreasing the likelihood of escape (Taraborelli, 2008). On the other hand, these open areas would allow rodents to detect the approach of terrestrial mammalian predators (Taraborelli, 2008). In MNBP both caviomorph species were present in the diets of terrestrial carnivores, although in lesser proportion than in raptors (Zapata *et al.*, 2007), implying that predation risk by terrestrial carnivores would decrease in these areas with low shrub cover.

In semiarid environments in Chile, Farías and Jaksic (2007b) determined the existence of two trophic guilds (specialized mammal eaters and omnivorous species with emphasis on arthropods) in a similar assemblage of raptors (although they included a terrestrial carnivore species in their study). As in MNBP, the largest predators fed mainly on caviomorphs (*Octodon degus* and *Abrocoma bennetti*) and formed the "mammal eaters" guild, when these species became more abundant (Farías and Jaksic, 2007b). In our study, tuco-tucos and cavies were important prey for individual species of raptors, but they were also very important in raptors community structure because they were responsible for the formation of a trophic guild based on their consumption.

Concluding remarks

Caviomorph rodents are important prey for mammalian carnivores. Biogeographical patterns of predation on caviomorphs in South America are related to geographical variables, species richness and predator body weights, which affect the probability of being preyed upon. Sociality does not prevent predation when comparing with predation on solitary species, and diurnal social species were more preyed upon than nocturnal ones. There was no overlap between activity time of both predators and prey for diurnal caviomorphs, highlighting the importance of these prey species to carnivores. At an ecological scale, caviomorphs played a fundamental role in the structure of raptor communities.

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Appendix 2. List of caviomorph species, in the reviewed studies of carnivore diets, sorted by families.

Erethizontidae
Chaetomys subspinosus
Coendou prehensilis
Coendou rufescens
Sphiggurus villosus

Dasyproctidae
Dasyprocta agouti
Dasyprocta azarae
Dasyprocta leporina
Dasyprocta punctata
Dasyprocta variegata
Myoprocta pratti

Agoutidae
Agouti paca
Agouti taczanowski

Dinomyidae
Dinomys branickii

Caviidae
Cavia aperea
Cavia fulgida
Cavia tschudii
Galea musteloides
Galea spixii
Microcavia australis
Dolichotis patagonum
Dolichotis salinicola
Hydrochoerus hydrochaeris

Octodontidae
Aconaemys fuscus
Octodon bridgesi
Octodon degus
Octodontomys gliroides
Spalacopus cyanus

Ctenomyidae
Ctenomys azarae
Ctenomys haigi
Ctenomys magellanicus
Ctenomys mendocinus
Ctenomys opimus

Echimyidae
Dactylomys sp.
Olallamys albicauda
Mesomys hispidus
Proechimys Iongicaudatus
Proechimys semiespinosus
Thrichomys apereoides
Thrichomys pachyurus
Trinomys sp.
Clyomys bishopi
Clyomys laticeps
Euryzygomatomys spinosus
Echimys semivillosus

Myocastoridae
Myocastor coypus

Chinchillidae
Lagidium peruanum
Lagidium viscacia
Lagostomus maximus
Chinchilla lanigera

Abrocomidae
Abrocoma bennetti
Abrocoma cinérea

PLATES

Plate 1. Representative caviomorphs. Superfamily Cavioidea

Figure 1. Family Cuniculidae: *Cuniculus paca*, the 'paca', inhabits tropical forests of South America. Photograph credits: Richard Culbert.

Figure 2. Family Dasyproctidae: *Dasyprocta punctata*, 'agouti', with adaptations for fast locomotion in forest environments. Photograph credits: Geoff Gallice.

Figure 3. Family Caviidae: *Dolichotis patagonum*, "mara", a monogamous species with marked adaptations for fast locomotion in open environments. Birthing and nursing are communal in maras. Photograph credits: Jason Hollinger (Creative Commons Attribution-Share Alike 2.0 Generic license).

Figure 4. Family Caviidae: The polygynous *Cavia aperea*, 'cui', inhabitant of the Pampas grasslands; its domesticated form is known as 'guinea pig' or 'cobayo'. Photograph credits: Cecilia C. Morgan.

Figure 5. Family Caviidae: *Kerodon rupestris*, the 'rock cavy', inhabits rocky habitats where it lives in groups. Photograph credits: Brian Gratwicke.

Figure 6. Family Caviidae: The semiaquatic *Hydrochoerus hydrochaeris*, 'carpincho' or 'capybara', the largest living rodent. This species lives in stable groups that defend a common territory. Photograph credits: Anouchka Unel.

Plate 1

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Plate 2. Representative caviomorphs. Superfamily Octodontoidea

Figure 1. Family Echimyidae: *Mesomys hispidus*, 'spiny tree rat', a species widespread in evergreen forest and low cloud forest. Its presence is common around tree falls, disturbed areas and around villages. Photograph credits: Thiago Semedo.

Figure 2. Family Echimyidae: *Proechimys roberti*, 'Roberto's spiny rat'. Spiny rats inhabit forest habitats of central and northern South America. Echimyids are morphologically conservative (i.e. present a rat-like physiognomy) and comprise numerous species able to climb and dig moderately well. Photograph credits: Thiago Semedo.

Figure 3. Family Echimyidae: Swimming adaptations in *Myocastor coypus*, 'coypu', a species that probably has a polygynous mating system. Photograph credits: Cecilia C. Morgan.

Figure 4. Family Octodontidae: The robust subterranean *Ctenomys*, known as 'tuco tuco' or 'oculto', has specialized digging adaptations and a polygynous mating system; it is highly territorial. Photograph credits: Cláudio Dias Timm (Creative Commons Attribution-Share Alike 2.0 Generic license).

Figure 5. Family Octodontidae: *Tympanoctomys barrerae*, 'plains viscacha rat' or 'red vizcacha rat', a desert specialist endemic to the arid plains of mid-western Argentina. Photograph credits: Michael A. Mares (Creative Commons Attribution-Share Alike 3.0 Unported license).

Figure 6. Family Octodontidae: The social species *Octodon degus*, 'degu'; although able to dig extensive burrows, the degu performs many activities aboveground. Photograph credits: Jacek555 (Creative Commons Attribution-Share Alike 1.0 Generic license).

Plate 2

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Plate 3. Representative caviomorphs. Superfamilies Chinchilloidea, Erethizontoidea and Octodontoidea

Figure 1. Family Chinchillidae (Chinchilloidea): The colonial and burrowing species *Lagostomus maximus*, 'viscacha' lives in communal burrows, known as 'viscacheras', occupied by up to 50 individuals. Females are highly phylopatric. Photograph credits: Cecilia C. Morgan.

Figure 2. Family Chinchillidae (Chinchilloidea): *Lagidium viscacia*, the 'southern viscacha', lives in small groups in rocky mountain areas, where it moves with agility. Photograph credits: Cody Hinchliff.

Figure 3. Family Dinomyidae (Chinchilloidea): 3. *Dinomys branickii*, 'pacarana', lives in tropical forests and is a living relative of the giant extinct rodents Phoberomys pattersoni and Josephoartigasia monesi. Photograph credits: Benjamin Frable.

Figure 4. Family Erethizontidae (Erethizontoidea): 4. *Erethizon dorsatum*, the 'porcupine', a scansorial species able to climb and also travel well on land. Photograph credits: Norbert Potensky (Creative Commons Attribution-Share Alike 1.0 Generic license).

Figure 5. Family Erethizontidae (Erethizontoidea): *Coendou prehensilis*. As its name indicates, the 'prehensile tail porcupine' has a prehensile tail and front and hind feet specialized for grasping; these rodents spend most of their lives on trees. When threatened, they roll themselves into a ball covered by hard and sharp quills. Photograph credits: Bart van Dorp.

Figure 6. Family Capromyidae (Octodontoidea): *Capromys pilorides*, 'hutia', endemic to Cuba. Hutias normally live in pairs, but can be found as solitary individuals or in small groups. Photograph credits: Yomangani.

Plate 3

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Caviomorph rodents evolved in South America, diversifying in shape and size and occupying disparate habitats. Because of their diversity and their peculiar evolutionary history, they are particularly interesting for biologists. Throughout its chapters, this volume provides new and updated information on caviomorph skeletal morphology, their locomotor behavior, size range, physiology, social and reproductive structure, and ecological relationships. The historical dimension is not overlooked: biogeography, genetic studies, and phylogenetic relationships of living and extinct representatives are also covered. We hope that such an integrative approach to the study of caviomorphs will also contribute to shed light on more general evolutionary biology issues.

Aldo Ivan Vassallo and **Daniel Antenucci**
Editors

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