# Biology of Caviomorph Rodents:
## Diversity and Evolution

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## SAREM Series A
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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 This series is meant to allow publication of unpublished works and revisions resulting from scientific meetings, symposia or workshops, so that they may achieve wide distribution in the international scientific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.

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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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# 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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**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

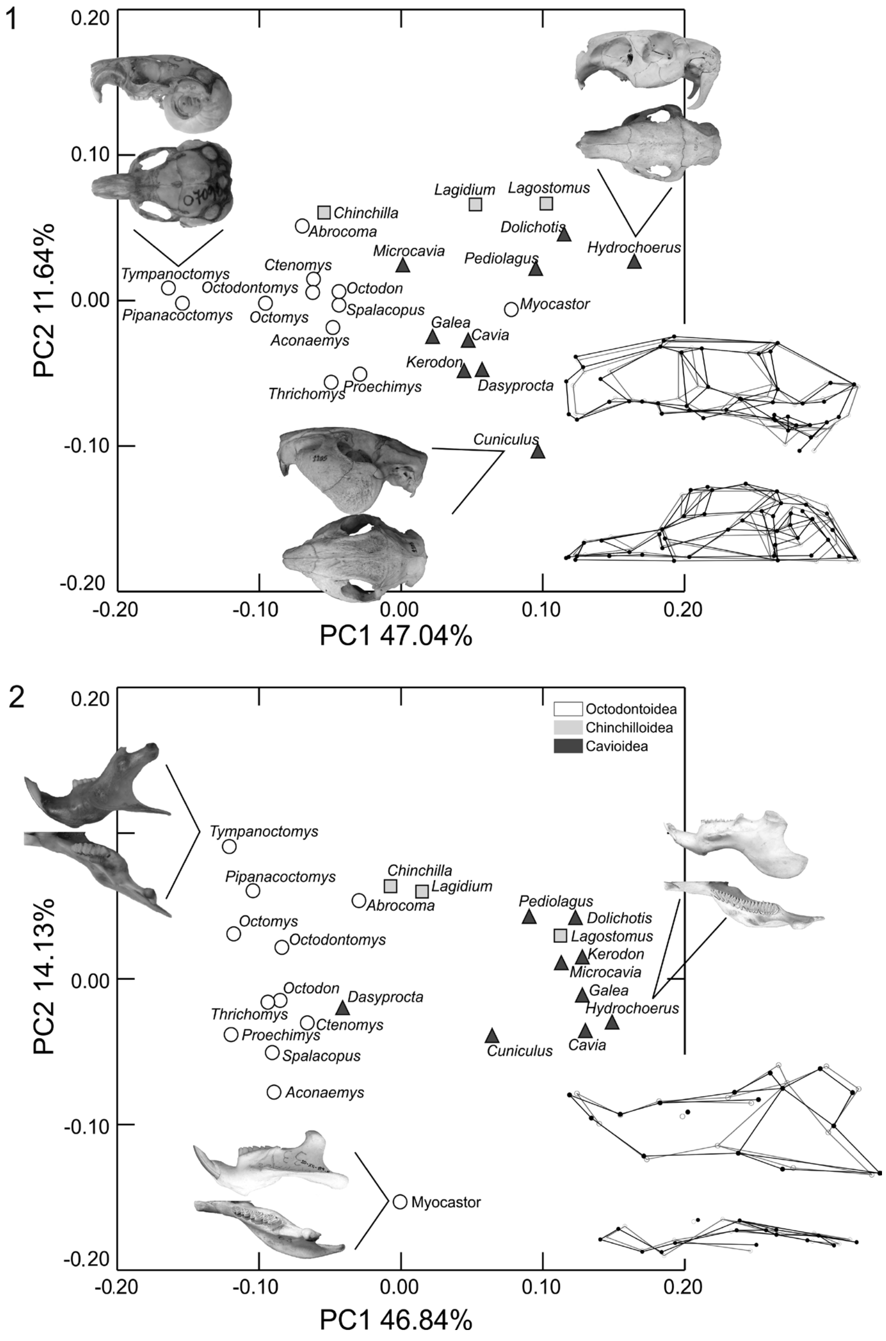

**Figure 1.** Ordination of the caviomorph genera in the morphospaces defined by the first two principal components (PCs) of the analyses of cranial 1. and mandibular 2. tri–dimensional shape variation. Shape changes associated with positive values of the first principal components (PCs) are shown as 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

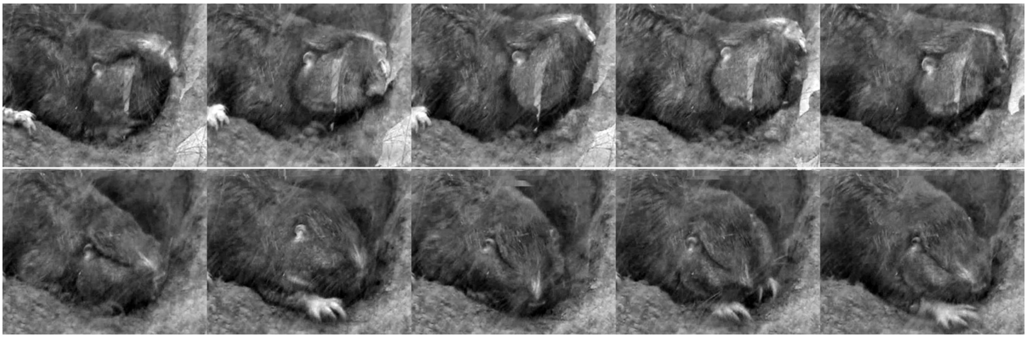

**Figure 2.** Burrow digging in *Ctenomys tuconax*. Above, pictures illustrate the use of incisors (chisel-tooth digging) for breaking rocks, fibrous roots or hard obstacles; below, pictures show the use of rapid alternating fore-claw movements (scratch-digging) to remove the loosened soil and rock fragments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

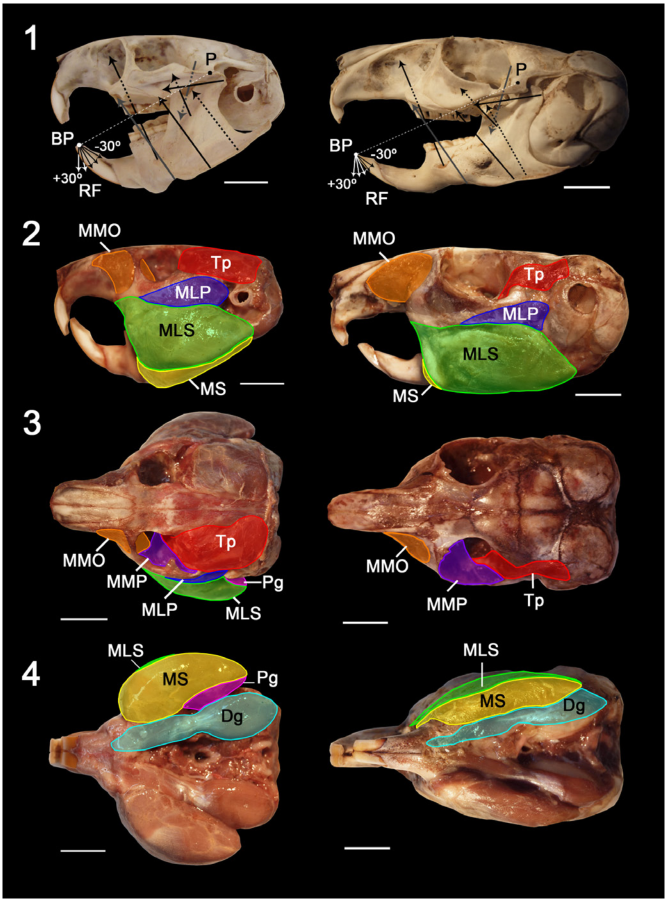

**Figure 3.** Skull and jaw of a tuco-tuco (*Ctenomys*; left) and chinchilla (*Chinchilla*; right) with 1. the biomechanical model used for bite force estimation at incisor tip, and the action lines of jaw adductor muscles, and 2. lateral, 3. dorsal, and 4. ventral views of those muscles. Model: **P**, 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

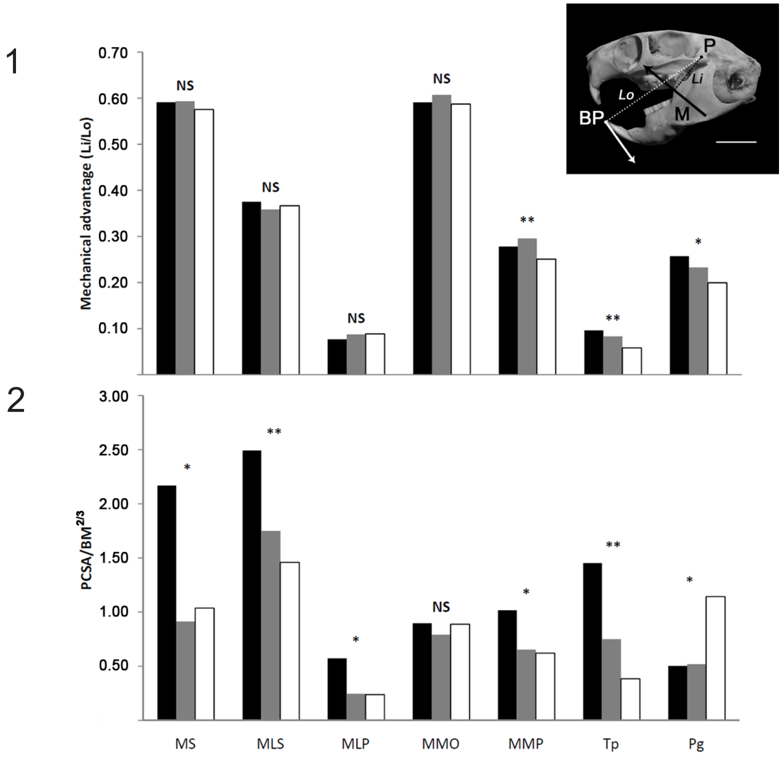

**Figure 4**. Bar-plots of 1. mechanical advantage and 2. physiological cross-sectional area (**PCSA**) standardized by body mass (**BM**) of all adductor muscles, comparing three caviomorph rodents with different ecologies but similar body size. Black bars, *Ctenomys* (solitary, subterranean); gray 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).

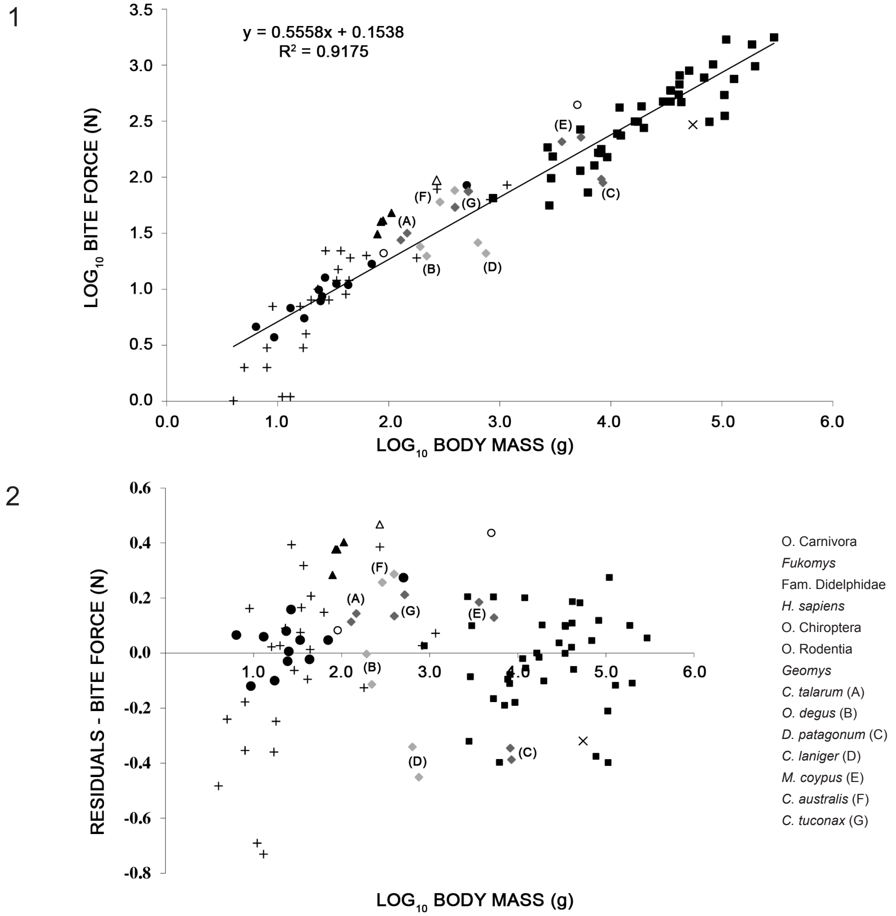

**Figure 5**. 1. Regression and 2. residuals of the bite force *vs.* body mass, corresponding to several mammalian taxa. Grayscale diamonds represent different caviomorph species. Modified from Becerra *et al.* (2014).

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

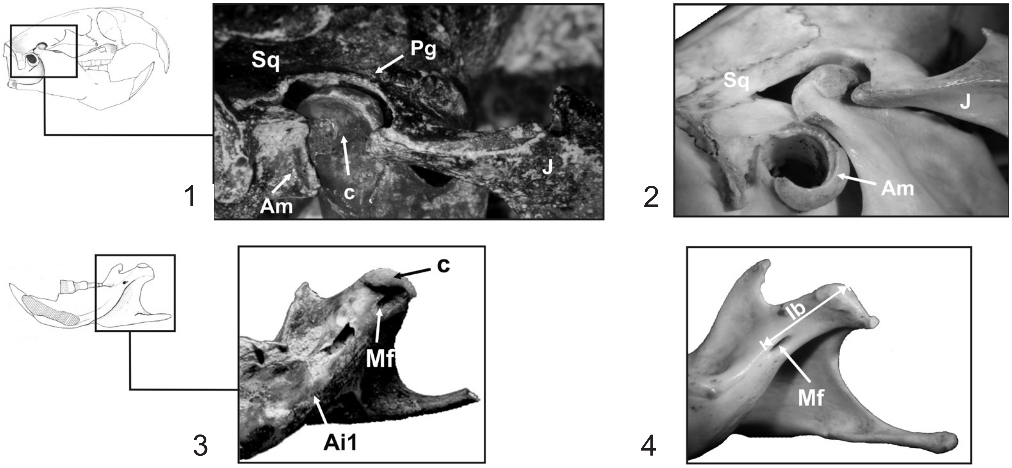

**Figure 6.** 1. Detail of the jaw joint in the extinct †*Eucelophorus chapalmalensis* (cranium and mandible correspond to different specimens with equal length of the molar series) and 2. *Ctenomys fulvus*. 3. Detail of the internal view of the right hemimandible of †*Eucelophorus* and 4. *Ctenomys 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-

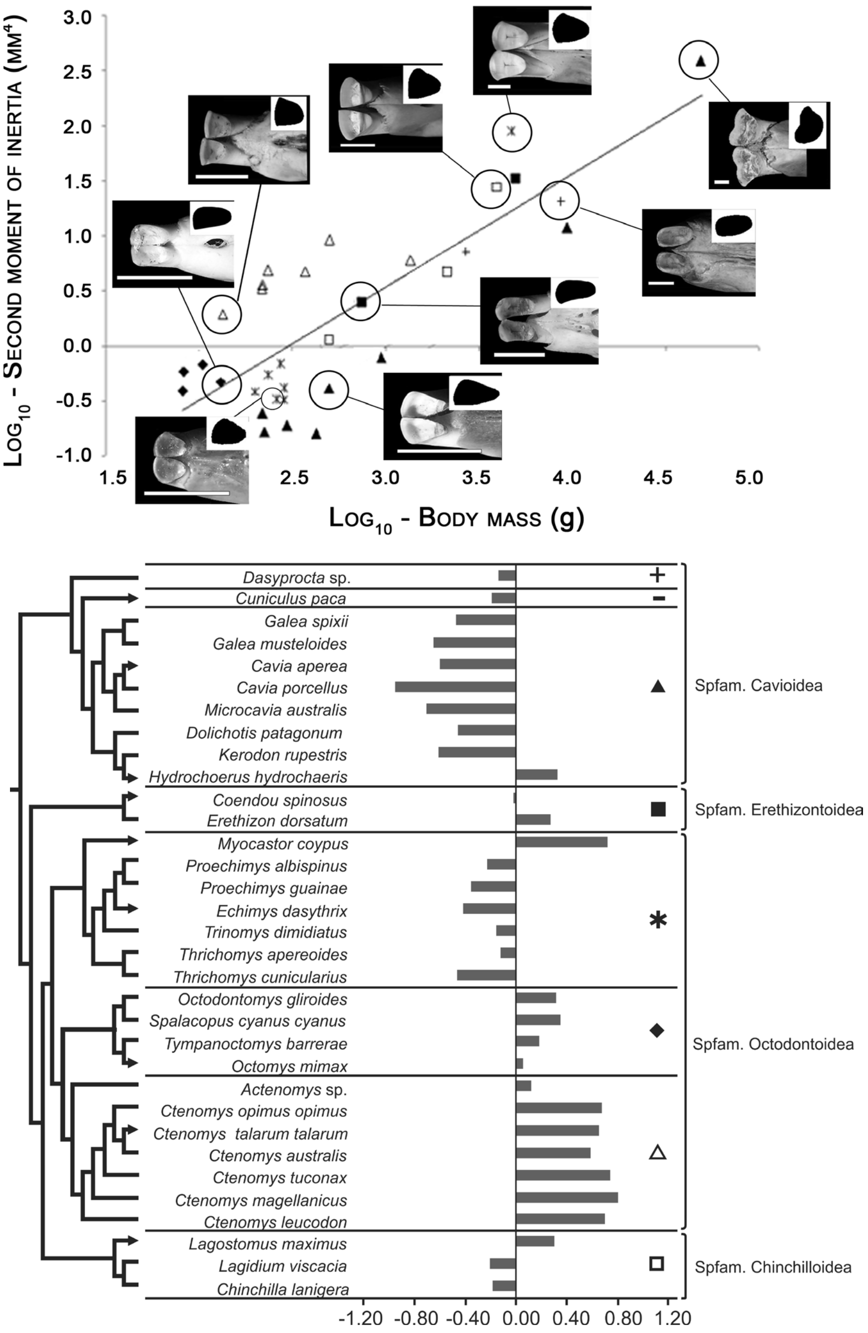

**Figure 7.** 1. Regression of the second moment of inertia of the upper incisors *vs*. body mass in caviomorph rodents, with a representation of the upper incisor diversity and detailed shape of left tooth cross-sectional area; and 2. residual values organized by their phylogenetic position. Highlighted 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).

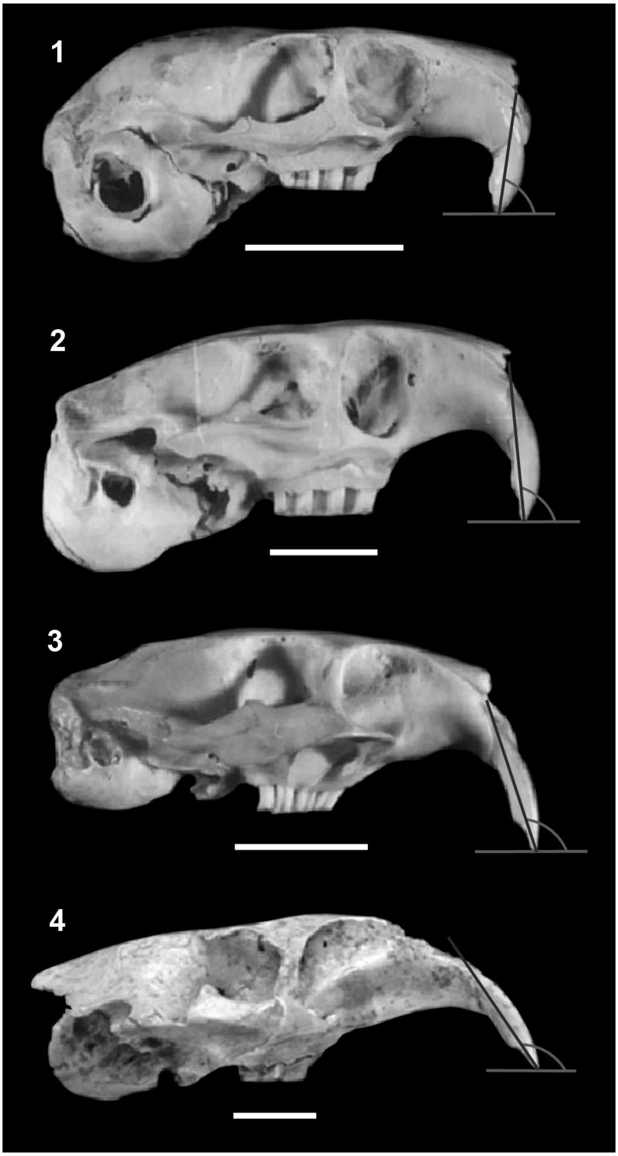

**Figure 8**. Lateral view of the skull of octodontid and ctenomyid rodents, with their respective angle of procumbency 1. *Octodontomys gliroides* (fossorial); 2. *Ctenomys australis* (highly fossorial, scratch-and chisel tooth-digger); 3. *Spalacopus cyanus* (subterranean, chisel–tooth digger); 4. †*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* (103º) and *Myocastor coypus* (102º) are more similar to the tooth diggers *Spalacopus cyanus* (108º), *Ctenomys leucodon* (116º) and †*Eucelophorus* (122º). 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

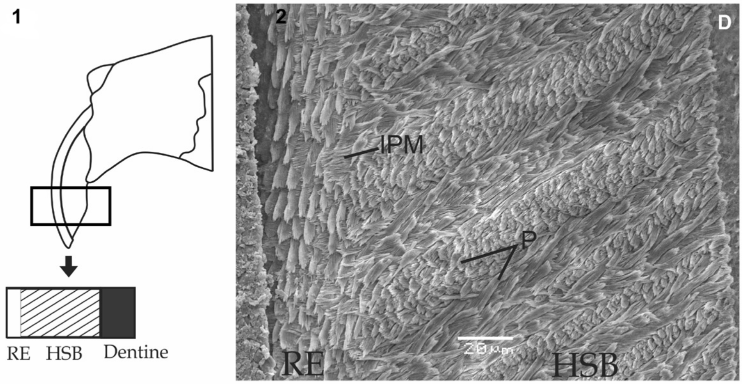

**Figure 9**. 1. Diagram of the longitudinal section of an upper incisor showing enamel types and dentine. 2. Micrograph of enamel rodent incisor. **RE**, radial enamel; **HSB**, Hunter Schreger bands; **D**, dentine; **P**, prisms; **IPM**, interprismatic matrix.

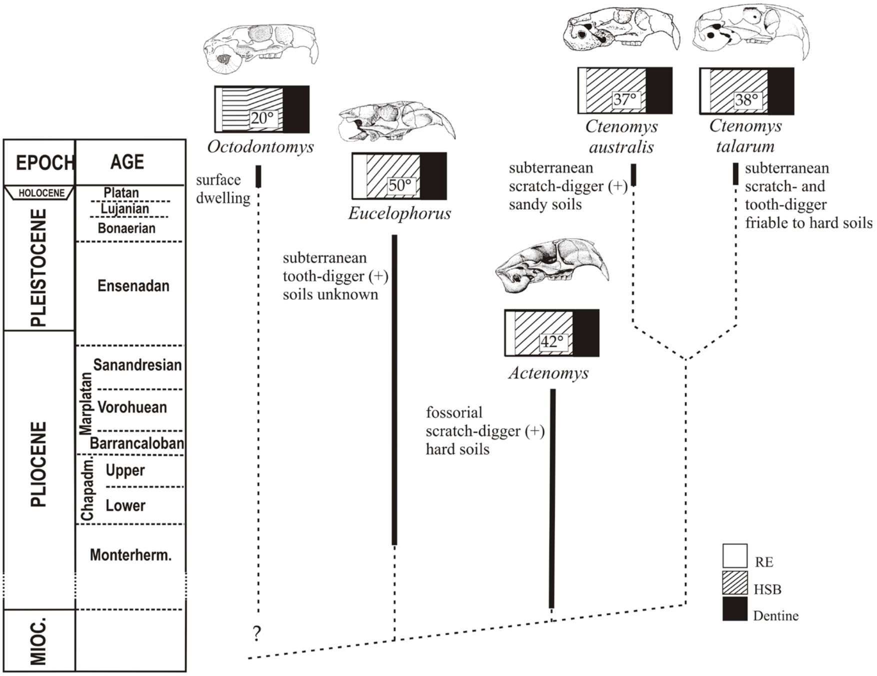

**Figure 10.** Known or inferred habits, digging modes and occupied soils of several octontoid species (after Contreras *et al*., 1987; Verzi and Alcover, 1990; Reig and Quintana, 1992; Quintana, 1994; Vassallo, 1998; Fernández *et al*., 2000; Patton *et al*., 2000; Morgan and Verzi, 2006; Verzi and 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-

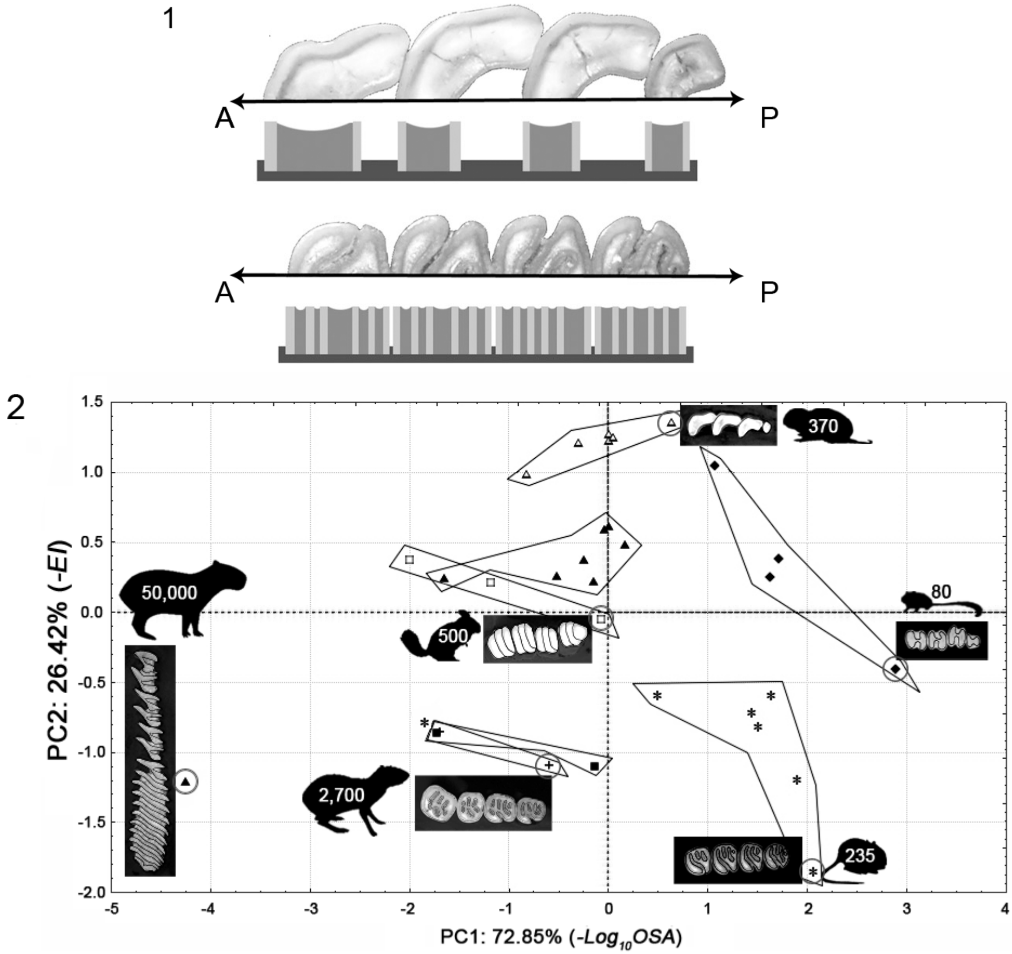

**Figure 11**. 1. Parasagittal profile through upper molar row of the subterranean *Ctenomys* (above) and the ground-dweller *Trinomys* (below); note the striking difference in the number of enamel edges (light gray bars). 2. PCA ordination of 33 caviomorph species belonging to seven different families, 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).

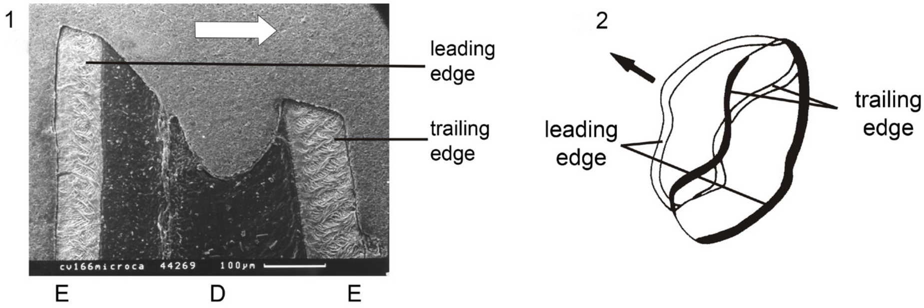

**Figure 12.** 1. Longitudinal section of a molar of the cavioid *Microcavia* showing the asymmetric wear of dentine. The arrow indicates direction of masticatory movement relative to the antagonist molar. On the trailing edge (**TE**), the increased abrasion due to accumulation of food particles produces 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

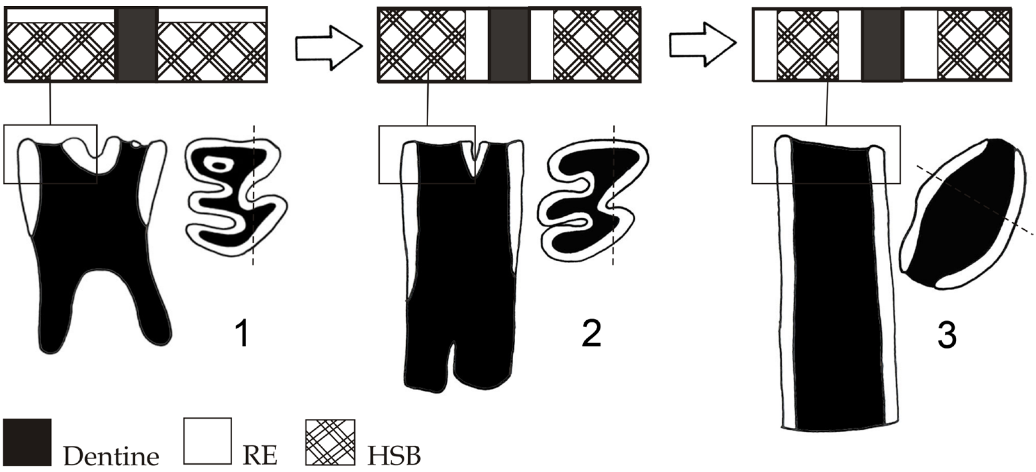

**Figure 13.** Hypothetical transformation of schmelzmuster (above), hypsodonty and occlusal morphology (below) in octodontoids (not to scale). Right lower first molars are shown for 1. †*Sciamys*, 2. †*Chasichimys* and 3. †*Xenodontomys*. *Schmelzmuster* schemes represent longitudinal sections. Dotted 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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