Biology of Caviomorph Rodents:
Diversity and Evolution

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SAREM Series A
Mammalogical Research
Investigaciones Mastozoológicas

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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 This series is meant to allow publication of unpublished works and revisions resulting from scientific meetings, symposia or workshops, so that they may achieve wide distribution in the international scientific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 fellow hystricomorphous 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 of extant 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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5 THE POSTCRANIAL SKELETON OF CAVIO-MORPHS: 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 de-

sarrollo, 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 visca-

chas 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).
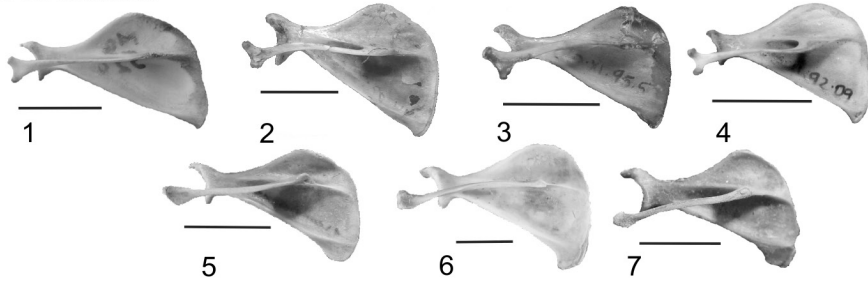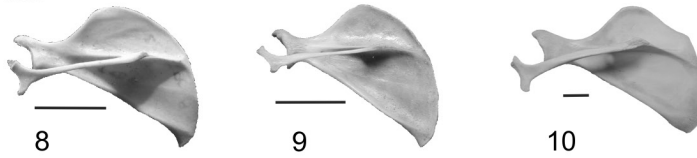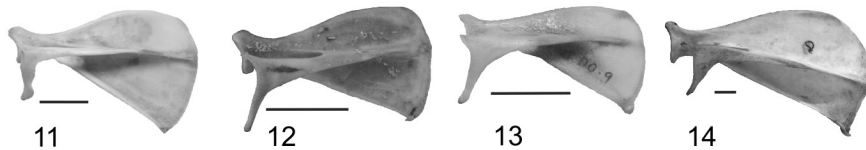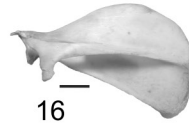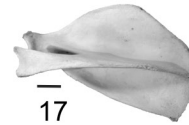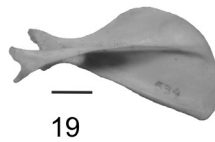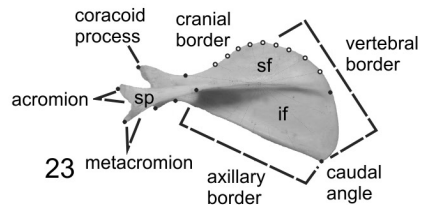
Figure 1. External view of left scapulae of Hystricomorpha included in the morphogeometric analysis. 1. *Octodontomys gliroides*; 2. *Octodon* sp.; 3. *Spalacopus cyanus*; 4. *Aconaemys* sp.; 5. *Ctenomys talarum*; 6. *C. australis*; 7. *C. rionegrensis*; 8. *Proechimys poliopus*; 9. *Thrichomys apereoides*; 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.
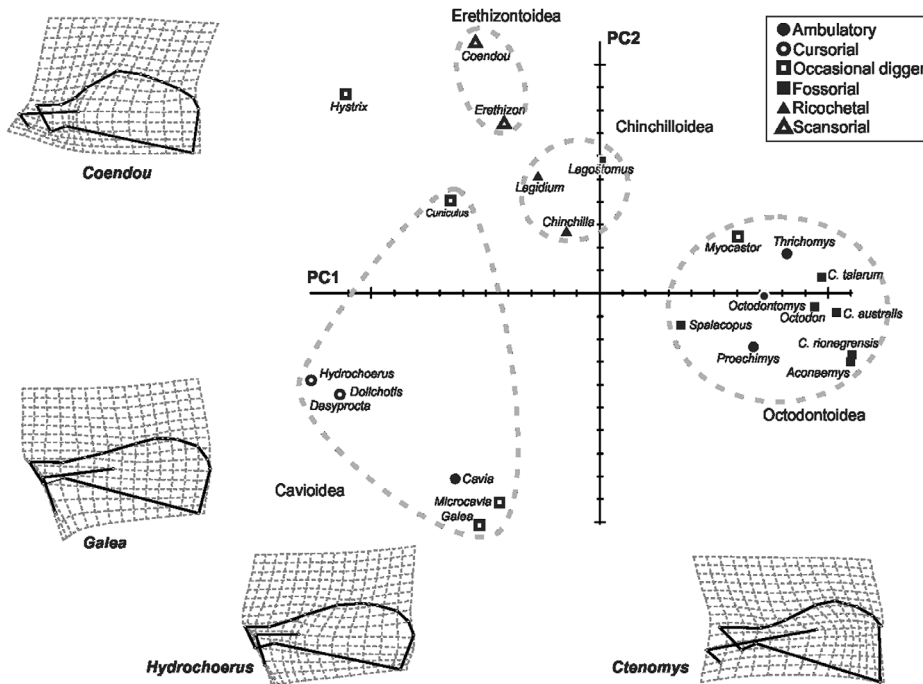
Figure 2. Principal Components Analysis of scapular shape: bivariate plot of taxon scores on first two principal components; locomotor habit for each species is indicated. Ellipses enclose all members of each superfamily. Deformation grids included for visualization of scapular shape changes. **PC1**, 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
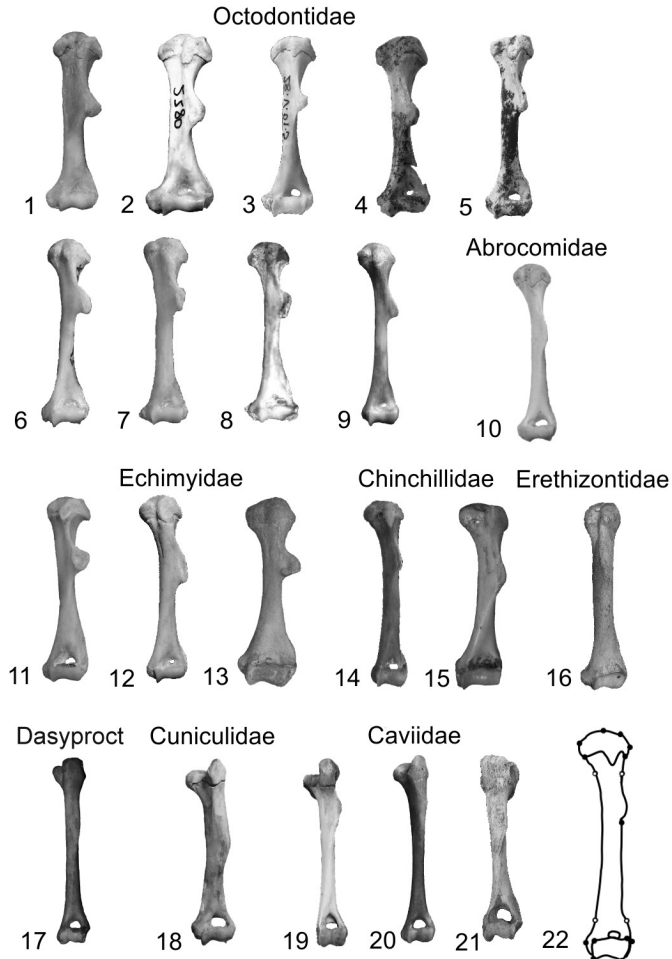
Figure 3. Anterior view of left humeri of some of the Hystricomorpha discussed in the text; only the living taxa were included in the morphogeometric analysis. 1. *Ctenomys talarum*; 2. C. *lewisi*; 3. *C. flamarioni*; 4. †*Eucelophorus* sp.; 5. †*Actenomys priscus*; 6. *Aconaemys* sp.; 7. *Octodon* 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
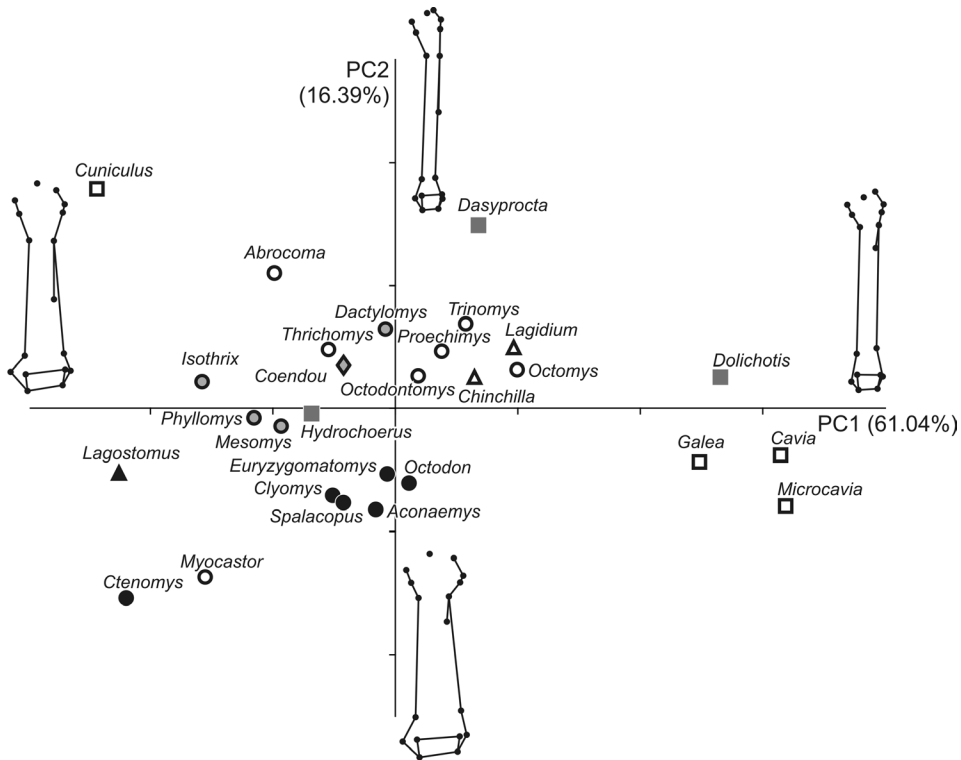
Figure 4. Principal Components Analysis of humeral shape: bivariate plot of caviomorph genera scores along the first two principal components. Deformation grids included for visualization of humeral shape changes. **PC1**, First Principal Component; **PC2**, Second Principal Component. Symbols for superfamilies: 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.
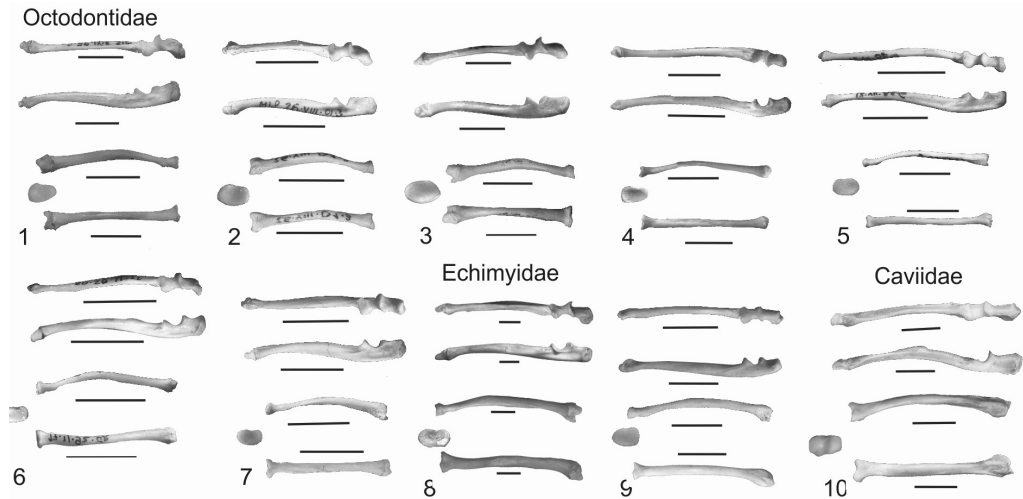
Figure 5. Right ulna (above) in anterior and medial views, and left radius (below) in medial, anterior and proximal views, of selected caviomorph taxa. 1. *Ctenomys australis*; 2. *C. talarum*; 3. *C. lewisi*; 4. *Octodontomys gliroides*; 5. *Octodon* sp.; 6. *Aconaemys* sp.; 7. *Euryzygomatomys spinosus*; 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
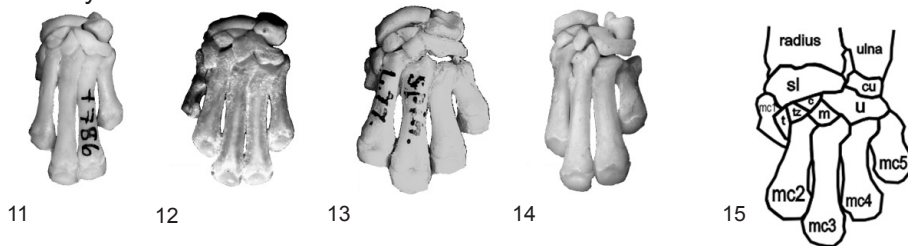
Figure 6. Left carpus and metacarpus of living and extinct octodontoids in dorsal view. 1. *Spalacopus cyanus*; 2. *Aconaemys* sp.; 3. *Octomys mimax*; 4. *Octodon* sp.; 5. *Octodontomys gliroides*; 6. *Ctenomys australis*; 7. *C. talarum*; 8. †*C. chapalmalensis*; 9. †*Actenomys priscus*; 10. †*Eucelophorus 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).
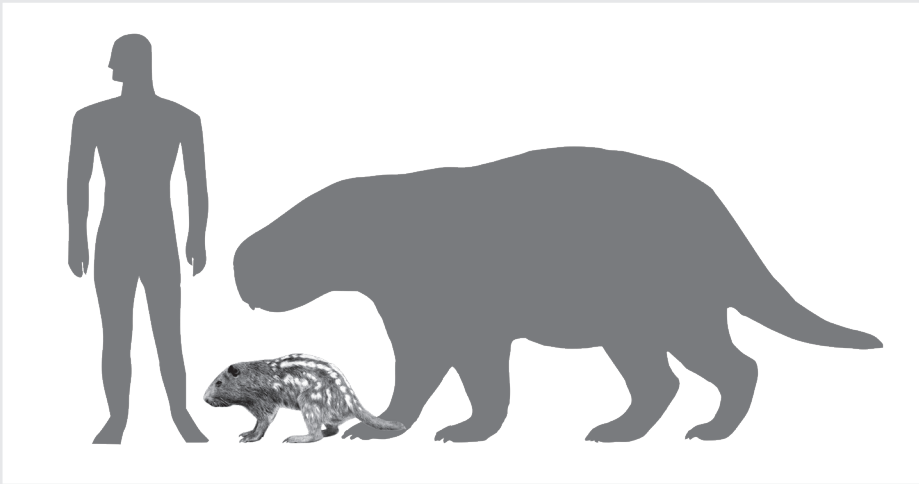
Figure 1 Box. Estimated size of †*Josephoartigasia monesi* (large grey silhouette) compared with its living relative *Dinomys branickii* (pacarana) and a human being. Modified from unpublished original by A. Rinderknecht.

5 cm

1   2   3   4
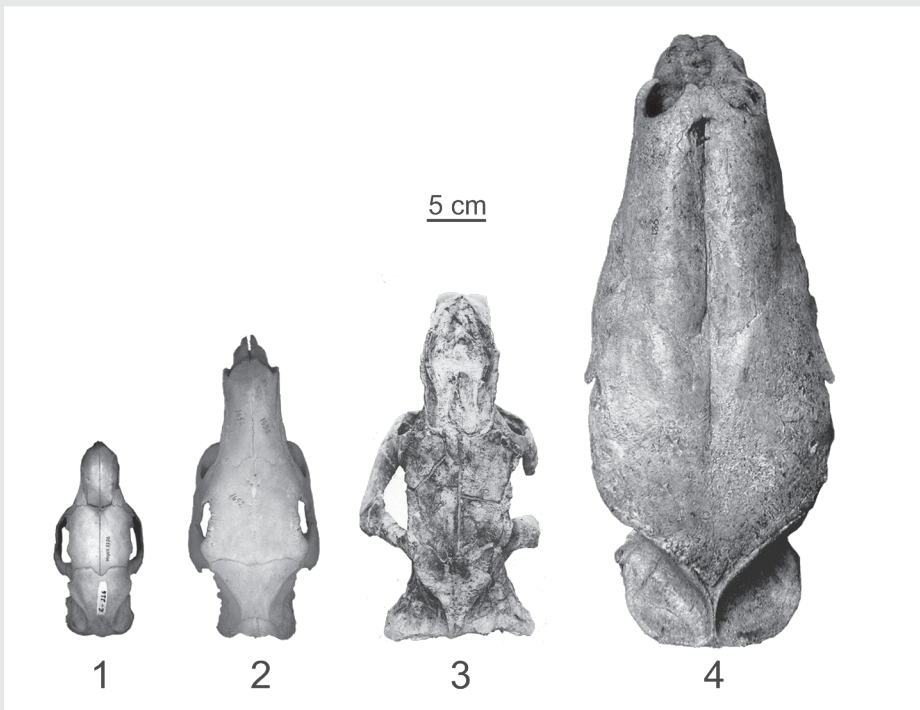
Figure 2 Box. Skulls in dorsal view of 1. *Dinomys branickii* (pacarana), 2. *Hydrochoerus hydrochaeris* (capybara), 3. †*Telicomys giganteus* MACN 8011, and 4. †*Josephoartigasia monesi* **MNHN** 921. **MACN**, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (Argentina); **MNHN**, Museo 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).

Acknowledgments

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