

The evolutionary history of South American hystricognath rodents

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Abstract

Improvements in the knowledge of the temporal and geographic distribution of fossil caviomorph rodents, and on their systematics and phylogeny, allow tracing the major features of their evolutionary history. The fossil record shows that the splitting of most lineages of caviomorphs would have happened at least as early as the late Eocene. These lineages experienced their first important radiation in South America by the late Oligocene. After a subsequent period of relative stability (early Miocene to early-middle Miocene), the most important turnover in the history of caviomorphs occurred during the late-middle to late Miocene. It involved the evolution of several new families and subfamilies, the extinction of most of the ancient taxa, as well as a trend toward gigantism experienced in different lineages. This episode was part of a faunistic change recorded both worldwide and in southern South America, related to climatic change. The histories of the new families and subfamilies

recorded in this late Miocene “modernization” phase are quite dissimilar, however. Fossils of the "Caviid" and Dinomyidae groups show they were already differentiated before their diversification in the Chasicoan. Modern Octodontidae, on the other hand, differentiated during the late Miocene, whereas Hydrochoeridae, Abrocomidae, “Eumysopinae” and Erethizontinae appeared suddenly as differentiated groups at that time. Since the late-middle to late Miocene turnover, changes in caviomorph faunas were of lesser magnitude, with a gradual decrease in diversity in southern South America. However, an important pulse of extinction at the generic level occurred during the late Pleistocene-Holocene in intertropical areas, implying the extinction of ancient lineages. The record of Brazilian caviomorphs in the Quaternary of eastern Argentina supports this hypothesis.

Keywords: Caviomorphs, evolution, phylogeny, diversification events, Cenozoic.

Introduction

During the 1830s, Charles R. Darwin in Argentina and Peter W. Lund in Brazil discovered the first rodent fossils from South America. Since then, new discoveries and descriptions of fossil rodents were only sporadic until the 1880s, when Florentino Ameghino started what would become the continuous description of a huge number of new taxa from different regions of Argentina. He proposed numerous relationship schemes for South American hystricognaths (caviomorph rodents), many of which are still in use (e.g. Ameghino, 1889). Kraglievich continued this tradition in the decades of 1920-30, describing new taxa and formulating hypotheses of relationships and modes of evolution. The last 30 years again witnessed important progress in the knowledge of caviomorphs from Argentina, with systematic revisions and description of new taxa, formulation of new phylogenetic and evolutionary hypotheses, discovery of new localities representing new temporal spans, and refinement of chronological schemes (see list of references).

Most recently, the prospecting effort made in many countries other than Argentina (especially Bolivia, Brazil, Chile, Colombia, and Peru, see Figure 1), greatly enlarged knowledge of fossil caviomorph taxonomic diversity as well as their geographic and stratigraphic distribution (e.g. Walton, 1997; Flynn *et al.*, 2003; Frailey and Campbell, 2004; Hadler *et al.*, 2008; Chick *et al.*, 2008; Chick, 2009). In spite of this, the South American record still comes basically from the southern part of the continent, meaning that the tropical history of Neotropical rodents is almost unknown. Inferences about their tropical diversity can currently be done based mostly --or even only -- on indirect evidence (e.g. Vucetich and Verzi, 2002).

Caviomorphs are immigrants in South America. At present there is a relative consensus that caviomorphs are more closely related to the Old World hystricognaths than to

any other group of rodents, whether they are considered monophyletic or not (Bryant and McKenna, 1995; Candela, 1999; Huchon and Douzery, 2001; Marivaux *et al.*, 2002; Poux *et al.*, 2006; Blanda-Kanfi *et al.*, 2009; Sallam *et al.*, 2009; see discussion in Vilela *et al.*, 2009). It is also widely agreed that they probably came from Africa by rafting during the late Eocene (Vucetich *et al.* 2010a and bibliography therein).

From a macrosystematic point of view, caviomorphs have been classically divided in four superfamilies (Figure 2; Wood, 1955): Erethizontoidea (Erethizontidae; New World porcupines), Cavoidea [Caviidae, Hydrochoeridae, the extinct Eocardiidae, Dasyproctidae, and probably Cuniculidae (cavies, maras, capybaras, agouties, and pacas)], Chinchilloidea [(Chinchillidae, Dinomyidae and the extinct Neoepiblemidae (chinchillas, mountain viscachas, plain viscachas, pacaranas)], and the extraordinarily diverse Octodontoidea [Echimyidae, Octodontidae and Abrocomidae (spiny tree rats, casiraguas, guiaras, coypus, tuco-tucos, coruros, degus, chinchilla rats, and also the West Indian hutias, Figure 2)]. These groups, although arranged under different names and systematic ranks, have been recognized by many authors (Ellerman, 1940, Miller and Gidley, 1918; Simpson, 1945), before Wood and Patterson (in Wood, 1955) recognized the South American hystricognaths as a natural group, gathering them in the suborder Caviomorpha (currently without formal taxonomical category; see Woods and Kilpatrick, 2005).

The incorporation of new methods of phylogenetic analysis, molecular techniques and modern geochronologic calibration has allowed development a more complete and clear picture of the fascinating history of caviomorph rodents. In this paper we summarize knowledge about the South American part of this history.

The included phylogenetic trees (Figures 2-6) attempt to reflect the state of the art. They are essentially based on published data but our unpublished results are also

incorporated. The temporal scheme used in this paper follows Flynn and Swisher (1995), updated with information in Ré *et al.* (2010 and references therein).

Caviomorphs begin

For many years the oldest South American caviomorphs were those from Tinguiririca (Chile, Figure 1; Wyss *et al.*, 1993), La Cantera (Gran Barranca, Argentina, Figure 1; Vucetich *et al.*, 2005b, 2010a,) and Santa Rosa (Peru; Figure 1; Frailey and Campbell, 2004). Tinguirirican rodents are not younger than 31.5 Ma [Tinguirirican South American Land Mammal Age (SALMA); Flynn *et al.*, 2003], those from La Cantera are somewhat younger, between 31.1 and 29.5 Ma (Ré *et al.*, 2010; Vucetich *et al.*, 2010a), whereas the Santa Rosa fauna has an imprecise age between late Eocene-early Oligocene or even late Oligocene (Goin and Candela, 2004 and Frailey and Campbell, 2004 vs. Shockey *et al.*, 2004)

The Tinguiririca fauna has yielded two rodent fossils; one is an unquestionable Chinchillidae Lagostominae, and the other was originally assigned to Dasyproctidae indet., but its affinities are less clear. The first one is especially interesting because it has derived bilaminar cheek teeth, which are startling considering the age of this old fauna. However, within Lagostominae, this dental morphology is consistent with this age because it is primitive for the subfamily (Vucetich *et al.*, 2010a).

The rodents from La Cantera are more abundant but more fragmentary, mostly known by isolated teeth. They represent an array of small and brachyodont species only one of which displays an incipient degree of hypsodonty. Although this is a very small fauna, Vucetich *et al.* (2010a) recognized six different types of dental morphologies (six species), but conservative enough to impede a clear assignment to familial taxa. The rodents from La Cantera are highly informative from a faunal perspective compared to the Tinguirirican fauna because the fossil-bearing level of La Cantera is placed within a very complete and rich

mammal sequence. The fossil-bearing level below La Cantera, named La Cancha, referred to the Tinguirirican SALMA (Goin *et al.*, 2010; Carlini *et al.*, 2010; Ré *et al.*, 2010), has yielded lots of small mammal remains, including a large number of isolated rodent-like incisors of marsupials (Goin *et al.*, 2010). However, not a single fossil from La Cancha can be referred to the Order Rodentia. The absence of rodent fossils at La Cancha reflects not a sampling artefact but a case of real absence. This implies that rodents arrived at the latitude of Gran Barranca not long before the deposition of La Cantera sediments.

Beyond the mentioned uncertainties concerning the age of Santa Rosa, its rodent assemblage is especially remarkable because it represents the richest old lowland intertropical caviomorph fauna. Santa Rosa rodents are brachyodont, mainly small-sized, and display a certain variety of occlusal designs, although within a monotonous pattern (Frailey and Campbell, 2004: 73-75, Figure 1, and Appendix 2). Frailey and Campbell (2004) referred these rodents to one species of Erethizontidae, eight of Dasyproctidae (Agoutidae Dasyproctinae in Frailey and Campbell, 2004), five of Echimyidae, and at least three species of uncertain affinities. In any case, the relationships of these early caviomorphs are unclear because, as occurs with the species of La Cantera, they are known mostly by isolate cheek teeth with a conservative morphology. However, some of these species are close to taxa represented in Salla (Bolivia, Desadan SALMA; Hoffstetter and Lavocat, 1970, Lavocat, 1976, Patterson and Wood, 1982) *i.e.* *Eobranisamys*, *Eoincamys* and *Eosallamys* are close to *Branisamys*, *Incamys* and *Sallamys* respectively. *Eodelphomys almeidacamposi* in particular, has a more derived pattern allowing a clearer systematic assignment to the Echimyidae (Frailey and Campbell, 2004; see octodontoid account below). Some of the putative dasyproctids such as *Eobranisamys* could be erethizontids (see Candela, 2002, for the affinities of the closely related *Branisamys*); other specimens such as 143375, assigned to Agoutidae, and 143271, assigned to Hystricognatha (Frailey and Campbell, 2004, Appendices

1 and 2), could also be erethizontids. If this were correct, the Santa Rosa rodent assemblage would be among the fossil faunas with the greatest diversity of porcupines (see Vucetich *et al.* 2010b).

Recently, Antoine *et al.* (2011) described a new caviomorph fauna from the locality of Contamana (Peru, Figure 1) with an estimated age of late middle Eocene. Caviomorphs are represented by three new species, some of which display characters that have been considered primitive for the group. For example the presence of a long metaloph almost isolated from adjacent lophs. Besides, two other of Contamana rodents are referred to Santa Rosa taxa.

Thus, the evidence suggests that during the late Eocene-early Oligocene caviomorphs were represented mostly by brachydont species, that at least a moderate radiation had already occurred, and that probably it was not until the end of the early Oligocene when caviomorphs were distributed within the whole continent.

What is striking among early neotropical caviomorph assemblages is that, in spite of the alleged differences in age, they share the same or at least closely related genera especially between Contamana and Santa Rosa but also with Salla, implying long periods of at least relative stasis. It also points out the necessity of a better understanding of the Santa Rosa fauna age.

Caviomorph radiation

By the Deseadan SALMA (late Oligocene) caviomorphs had achieved a higher degree of diversification than in Tinguiririca, La Cantera and Santa Rosa. Almost 20 genera can be referred to several families (Patterson and Wood, 1982; Vucetich, 1989, 1991; Vucetich *et al.* 1993a, 2010a; Vucetich and Ribeiro, 2003; Shockey *et al.*, 2009), the number varying according to the criteria used by various authors. Regardless of the number of families, the four classical caviomorph superfamilies are already represented in the Deseadan (Figure 2).

Interestingly, several lineages had by then developed very high-crowned molars with a correlated simplification of their occlusal patterns (e.g. *Scotamys*, *Cephalomyopsis*, *Eoviscaccia*; Wood and Patterson, 1959; Vucetich, 1985, 1989). By the late Oligocene, caviomorphs occupied an array of ecological niches, probably in detriment to the marsupials (Goin *et al.*, 2010). Since then, caviomorphs became diverse and abundant in every South American mammal-bearing deposit, where clear evidence of their radiation is recorded.

The Cavioids

Cavioidea is a highly diverse group, displaying extensive variation in size, dental morphology, and life history. Although some rodents from Tinguiririca, La Cantera and Santa Rosa were assigned to this superfamily (Figure 3), undoubted cavioids are only recorded since the Deseadan. They belong to the Cavioidea *sensu stricto* (Patterson and Wood, 1982), i.e. cavioids with double-heart cheek teeth (see Pérez, 2010a and Figure 3). Other Deseadan rodents have been referred to Dasyproctidae (see for example McKenna and Bell, 1997, and Vucetich *et al.*, 2010a, and the position of *Branisamys* in Figures 3-5), but this familial assignment requires re-consideration.

The Deseadan witnessed the first radiation of the Cavioidea *sensu stricto* within rodents classically grouped as “Eocardiidae” (Figure 3). Different hypotheses have been proposed to explain this radiation. Wood and Patterson (1959) suggested the group split into a very early dichotomy of two lineages. Kramarz (2006), in contrast, claimed the existence of a phyletic lineage, *Asteromys-Luantus-Phanomys*, that eventually gave rise to modern taxa. Pérez (2010a) postulated a very extensive Deseadan cladogenesis of protohypodont species, denying the existence of both an early dichotomy and a phyletic line. Additionally, she considered “Eocardiidae” as paraphyletic (Figure 3). Hypsodonty in this group developed through a first Deseadan to “Pinturan” (late Oligocene-early Miocene) cladogenesis. Another

cladogenesis occurred during the Santacrucian SALMA and the “Colloncuran” (late early Miocene - early middle Miocene) involving euhypsodont eocardiids (Figure 3). Then, an important radiation occurred between the “Colloncuran” and the Chasicuan SALMA, which gave rise to the modern Caviioidea, i.e., caviids and hydrochoerids (Figure 3; Vucetich *et al.*, 1999). Pérez (2010a) also supported the monophyly of Caviidae + Hydrochoeridae, and she used the name Medialis Series for this clade. This term was created by Miller and Gidley (1918; Figure 3) to separate both families from the rest of the hystricognaths. It has the same taxonomic content (plus related fossil taxa) as Caviidae *sensu* Woods and Kilpatrick (2005) and we use this latter criterion here (Figure 3).

The relationships among the members of the Caviidae are still controversial (Figure 3), thus the internal systematics of this clade remains unstable (compare for example Ameghino, 1889, to Wilson and Reeder, 2005). The conflicts are based mainly on two issues. One is the position of *Kerodon*, which was alternatively related to the Caviidae (both to Dolichotinae and Caviinae; Quintana, 1998 and literature therein) and to Hydrochoeridae (Woods and Kilpatrick, 2005 and literature therein). The other issue concerns the relationships of Dolichotinae. While usually considered as caviids in the classical meaning, Rowe and Honeycutt (2002) considered them to be the sister group of *Hydrochoerus* + *Kerodon*. Other evidence (Pérez, 2010a; Vieytes *et al.*, 2001) suggests that Dolichotinae is the sister group of Caviinae + Hydrochoerinae (Figure 3). In turn, Vucetich and Deschamps (in press), in opposition to the classical proposal, postulated that the extinct cardiomyines are more closely related to hydrochoerines than to caviines.

Hydrochoerines are among the most peculiar rodents, not only because they are the giants among extant representatives, but also because their cheek teeth grow anisometrically. This produced high dental variability that led to the multiplication of taxonomic names among

the fossils (see Mones, 1991). A new interpretation of tooth growth has led to a substantial reduction in the number of taxa (Vucetich *et al.*, 2005a).

New phylogenetic results relate *Neoreomys* to Caviioidea s.s. (Pérez, 2010a, Figure 3) rather than to Dasyproctids as was classically thought. This result suggests that the clade containing the living Dasyproctidae could have always been restricted to northern South America, as reported by Vucetich (1984). But surprisingly, a primitive dasyproctid was found in the Pleistocene of central Argentina (Figure 1B, locality 33; Vucetich and Verzi, 2002).

The Erethizontoids

Erethizontoidea groups the New World porcupines, which are small to medium sized, brachydont, arboreal rodents (Candela and Picasso, 2008, and literature therein). They are recorded at least since the Deseadan SALMA (Wood and Patterson, 1959), but the porcupine fossils from Santa Rosa might represent an older record. Erethizontids had their acme during the Colhuehuapian SALMA and the “Pinturan” (early Miocene; Figure 4; Kramarz *et al.*, 2010; Kramarz and Bellosi, 2005). They are a conservative group, at least in dental morphology, but during the Colhuehuapian, one lineage (*Hypsosteiromys*) developed an incipient hypsodonty (Candela and Vucetich, 2002). In addition, the living *Chaetomys* has many peculiar dental, osteological, and molecular characters that justify its separation in a different subfamily, Chaetomyinae (Thomas, 1897; Martin, 1994; Carvalho, 2000; Vilela *et al.*, 2009). Recently, Candela (2004) divided the porcupines other than Chaetomyinae, into Erethizontinae and Steiromyinae. Erethizontinae includes the living species, which have mostly a Brazilian distribution, and Steiromyinae, the extinct species with an essentially Patagonian distribution (Candela and Morrone, 2003).

During the Huayquerian SALMA (late Miocene), erethizontids achieved their largest body size (Candela, 2004) in *Neosteiromys bombifrons* from central Argentina (Rovereto,

1914), which is the last record of Steiromyinae. The oldest record of Erethizontinae (*Paradoxomys*) is also from the Huayquerian but from eastern Argentina (Vucetich and Candela, 2001; see Figure 4). By the Montehermosan SALMA (early Pliocene), porcupines vanished from southern South America, except for the record of *Erethizon* in the late Pliocene of Uquía (Jujuy province; Figure 1; Reguero *et al.*, 2007). This is the oldest fossil record of the otherwise living North American porcupine genus.

The Chinchilloids

Chinchilloidea comprise the families Dinomyidae, Chinchillidae and Neoepiblemidae. They include rodents with a very typical laminar dental pattern and an enormous size range, ranging from small-sized to the most gigantic rodents that ever existed (Sánchez Villagra, *et al.*, 2003; Rinderknecht and Blanco, 2008, but see Millien and Bovy, 2010). The family Cuniculidae has been occasionally included in this superfamily (Wood and Patterson, 1959).

Chinchillids are known since the Tinguirirican SALMA, but they have become common, although never diverse, since the Santacrucian SALMA. They are represented for the most part by Lagostominae, but Flynn *et al.* (2002) reported a Chinchillinae from the middle Miocene of the Chilean Altiplano (see Figure 5). Differentiating quite early, the two lineages may have evolved differences in their geographic distribution and habitat requirements (Figure 5).

The systematic position of the families Dinomyidae (pacaranas) and Cuniculidae (pacas) have been uncertain among the caviomorphs because they have poor fossil records and retain several primitive characters (Patterson and Wood, 1982:511 and 523). Both families were alternatively classified as chinchilloids or cavioids. Recent phylogenetic analyses, including morphological and/or molecular characters, shed some light on their relationships. Opazo (2005) and Huchon and Douzery (2001) considered the peculiar pacas as

cavioids on the basis of molecular information. But the dinomyids are clearly more closely related to chinchillids than to caviids (Huchon and Douzery, 2001; Sánchez Villagra *et al.*, 2003; Opazo, 2005; Poux *et al.*, 2006), and the gigantic extinct neoepiblemids appear to be more closely related to dinomyids than to any other group (Sánchez Villagra *et al.*, 2003). In addition, Vucetich *et al.* (2005c) stated that dinomyids share some apomorphic characters of the enamel microstructure with the West Indian heptaxodontids, which exclude them from the cavioids. This composition makes the Chinchilloidea a moderately diversified caviomorph clade.

Chinchilloids developed hypsodonty several times in parallel, and they were the caviomorphs that developed this characteristic earliest. In fact, a typical chinchillid with high crowned molars and a simplified bilaminar occlusal structure is recorded in the Tinguirirican SALMA (Flynn *et al.*, 2003; Vucetich *et al.*, 2010a). Interestingly, this pattern remained almost unchanged during 30 my in the Lagostominae, and nowadays can be seen in plain viscachas. By the Deseadan SALMA, some chinchilloids had already attained evergrowing cheek teeth, such as the neoepiblemid *Scotamys*. Chinchillid molars became euhypsodont in the Colhuehuapian SALMA. However, more primitive chinchilloids, currently under study, have also been recorded in younger sediments (Kramarz and Vucetich, 2009; Vucetich *et al.*, 2010b).

Dinomyids, in turn, exhibit protohypsodonty up to the middle Miocene (Vucetich, 1984), and became euhypsodont later, in the Chasicuan SALMA. A spectacular late Miocene radiation is recorded in the Huayquerian (see Mones, 1981, for a taxonomic synthesis) followed by a very important extinction during the Pliocene. The relationships among the different genera have not been deeply explored, but Nasif (2010) developed a new and interesting phylogenetic proposal.

Chinchilloids enjoyed their acme in the late Miocene, especially due to the high diversification of large-bodied to huge dinomyids, the eumegamyines (Figure 5). A few of these eumegamyines survived during the Pliocene (Francis and Mones, 1966), and one unexpected primitive rodent related to dinomyid-neoepiblemids has been recorded in the Quaternary of eastern Argentina (Vucetich *et al.*, 2005c). In the Pliocene, the diversity of chinchilloids diminished dramatically, and only four genera are now still living.

The extinct family Cephalomyidae has sporadically been assigned to this superfamily (Landry, 1957; Kramarz, 2001, 2005, Vucetich *et al.* 2010b), or to the Caviodea dasypsectids (e.g. Wood and Patterson, 1959), but its relationships are still uncertain (Figure 2 and 5). A comprehensive systematic and phylogenetic revision is necessary in order to elucidate the status of the included taxa.

The Octodontoids

Octodontoidea is the most diverse caviomorph clade, and the most diverse among the hystricomorphs. They are represented in South America by nearly 80 living and extinct genera belonging to three families: Echimyidae (spiny rats; including coypus of the subfamily Myocastorinae), Octodontidae (degus, viscacha rats; including tuco-tucos of the subfamily Ctenomyinae) and Abrocomidae (chinchilla rats) (McKenna and Bell, 1997; Frailey and Campbell, 2004; Woods and Kilpatrick, 2005; Emmons, 2005; D.H.V. and M.G.V., unpubl.). Most species are small to middle-sized rat-like caviomorphs, with terrestrial to fossorial or arboreal habits.

Early octodontoids have a conservative dental morphology which makes the interpretation of their affinities quite difficult. Uncertainties lie especially in the familial assignment of some Oligocene to middle Miocene species (e.g. Reig, 1989; Verzi, 2001, 2002; Vucetich and Kramarz, 2003; Vucetich and Vieytes, 2006).

The most ancient octodontoids are recorded in La Cantera (Vucetich *et al.*, 2010a) and in Santa Rosa (Frailey and Campbell, 2004), although the age of the latter is still under discussion (see above and Figure 6). These ancient species are represented mainly by low-crowned molars with little varied occlusal morphology, and most of them cannot be easily assigned to families. Frailey and Campbell (2004) included the Santa Rosa genera *Eosallamys*, *Eoespina*, *Eosachacui* and *Eodelphomys* in Echimyidae, and ascribed the affinities of the former to octodontids (Frailey and Campbell, 2004: 89). We think that only *Eodelphomys* can be confidently assigned to the Echimyidae because its occlusal morphology, characterized by three very oblique lophids, resembles that of the Colhuehuapian echimyid *Paradelphomys* (Frailey and Campbell, 2004: 91; Carvalho and Salles, 2004).

Echimyidae is one of the caviomorph families that experienced relatively few morphological changes throughout its evolutionary history (Reig, 1986). Although the interrelationships among living species have been relatively well studied, the suprageneric taxonomic compositions are still unstable. For example, according to molecular and morphological information, the conventionally recognized subfamilies Echimyinae and Eumysopinae would not be monophyletic (Figure 6; Leite and Patton, 2002; Carvalho and Salles, 2004; Galewski *et al.*, 2005; Emmons, 2005; Olivares *et al.*, 2012). Similarly to molecular results (Galewski *et al.*, 2005), in a recent morphological analysis including living and extinct species, two major clades of echimyids were recovered. One of them included the living fossorial eumysopines (Tribe Euryzygomatomyini of Emmons 2005), and the other clustered terrestrial eumysopines with arboreal echimyines-dactylomyines (Olivares *et al.*, 2012: fig. 5).

As in recent subfamilies, the status of the extinct “Adelphomyinae” is also unstable. According to morphological information it would be a non-monophyletic taxon, which would include species closely related to living taxa (Scott, 1905; Carvalho and Salles, 2004; Figure

6). At least the Colhuehuapian *Paradelphomys*, and perhaps also *Eodelphomys* (Oligocene?) and the Deseadan *Xylechimys* (Patterson and Pascual, 1968; Patterson and Wood, 1982), would be related to the living arboreal “dactylomyines” (Carvalho and Salles, 2004). The early to middle Miocene “adelphomyines,” *Adelphomys* and *Stichomys*, would be part of the stem group of the “echimyines” + “dactylomyines” (Scott, 1905; Carvalho and Salles, 2004; Figure 6). The “echimyines”, a group of genera closely related to “dactylomyines” and also with arboreal habits (Galewski *et al.*, 2005), are represented in the “Colloncuran” by *Maruchito* (Emmons and Vucetich, 1998). Thus, this radiation of arboreal echimyids, today restricted to the forests of northern South America and Central America (Emmons and Feer, 1997), would have been present at least since the late Oligocene in Patagonia and perhaps earlier in Peru.

“Eumysopines” and Myocastorinae are first recorded during the late Miocene (Verzi *et al.*, 1994, 1995; Vucetich, 1995; Candela and Noriega, 2004), although the origin of both groups is probably older (Galewski *et al.*, 2005; Opazo, 2005) (Figure 6). These two groups are the only echimyids recorded in southern South America from this period on (except for “*E.*” *parodii*). The record of “eumysopines” in Argentina has been interpreted as southern expansions of Brazilian radiations, an early one occurring after the withdrawal of the Paranense Sea (Verzi, 2002; see Pascual *et al.*, 1985; Webb, 1995; Figure 1 A), and a more recent one related to warm climatic cycles in the Pleistocene. In these Pleistocene events, as well as in the late Pleistocene-Holocene of southern Brazil, “eumysopines” are represented by species related to the living *Clyomys* and *Euryzygomatomys* (Vucetich *et al.*, 1997; Hadler *et al.*, 2008).

Early Octodontidae with primitive low-crowned molars (Figure 6) include some of the most primitive caviomorphs (Wood, 1949; Wood and Patterson, 1959), and they have a complex taxonomic history. The early Miocene *Acaremys* and *Sciamys* (and alternatively the

early to middle Miocene *Protacaremys* and *Galileomys*, and the late Oligocene *Platypittamys*) were considered to be members of a suprageneric assemblage, *Acaremyidae* (or *Acaremyinae*). *Acaremyids* were alternatively included among the *Myomorpha* (Ameghino, 1893), *Erethizontidae* (Ameghino, 1902; Scott, 1905; Bordas, 1939), and *Octodontoidea* (Wood and Patterson, 1959; Vucetich and Kramarz, 2003), or even among *caviomorphs* without clear relationships (Wood, 1949). In addition, the Deseadan *Sallamys*, the Colhuehuapian *Prospaniomys*, *Protadelphomys* and *Willidewu*, and the early to middle Miocene *Acarechimys* were included among *Echimyidae* (Ameghino, 1902; Hoffstetter and Lavocat, 1970; Patterson and Pascual, 1968; Patterson and Wood, 1982; Vucetich and Verzi, 1991; Carvalho and Salles, 2004), whereas the Deseadan *Sallamys quispea*, the Colhuehuapian *Caviocricetus*, and the “Colloncuran” *Plesiicarechimys* were described as *Octodontoidea* without familial assignment (Vucetich and Verzi, 1996; Vucetich and Vieytes, 2006; Shockey *et al.*, 2009).

Here we use the masseteric configuration of the mandible and morphology of lower molars to delimit *Octodontidae* (Verzi *et al.*, 1994; Verzi, 1999). In *Octodontidae*, the masseteric crest is not aligned with the notch for the tendon of the M. masseter medialis anterior in the adult. In the lower first and second molars, the mesoflexid is more persistent than the metaflexid. Based on these criteria, we propose that the above mentioned octodontoids are more closely related to the modern *Octodontidae*, as partially suggested in previous papers (Winge, 1887; Wood and Patterson, 1959; Verzi, 2002; Arnal and Kramarz, 2011). Relationships among most of these early species remain uncertain. Nevertheless, a cohesive clade formed by *Acaremys*, *Sciamys* and *Galileomys* was proposed by Vucetich and Kramarz (2003) (Figure 6). In addition, a close relationship among *Sallamys*, *Protadelphomys* and *Willidewu* was recognized by Vucetich and Verzi (1991); *Eosallamys* probably belongs to this group (Frailey and Campbell, 2004).

Since the late Miocene, crown octodontids are represented by two clearly defined groups, the subfamilies Ctenomyinae and Octodontinae (Reig, 1989; Honeycutt *et al.*, 2003; Verzi, 2008). Their differentiation would have been a consequence of increasing specializations linked to open environments, such as molar hypsodonty and digging adaptations (Pascual, 1967; Lessa *et al.*, 2008; Verzi, 1999, 2008). The relationships of species of these modern subfamilies with older octodontids, or even with primitive representatives of the late Miocene “modern stage” (*Chasicomys*, *Neophanomys*, *Phthoromys*; Figure 6), remain controversial. Abundant materials of the “Colloncuran”, Chasican and Huayquerian from Patagonia and central Argentina, currently under study, could contribute to a better understanding the affinities among ancient and modern species.

Abrocomidae are first recorded in the late Miocene of western and central Argentina by the extinct *Protabrocoma* (Rovereto, 1914; Kraglievich, 1940; Rodríguez Brizuela and Tauber, 2009). The available materials of this genus provide little or no information about the origin of the group, however, which is certainly older (Opazo, 2005) (Figure 6). The modern *Abrocoma* is undoubtedly recorded in the late Pliocene Sanandresian (Verzi and Quintana, 2005), although Rodríguez Brizuela and Tauber (2006) reported its presence in the late Miocene of western Argentina.

Discussion and Conclusions

Although fossil caviomorphs come basically from southern South America, improvements in our knowledge of their temporal and geographic distributions, together with available information on caviomorph systematics and phylogeny, allows us to trace the major features of the evolutionary history of this group.

The fossil record indicates that caviomorphs would have already radiated in South America in the late Eocene. The diversity of the oldest faunas, those of Tinguiririca, La

Cantera and presumably Santa Rosa, suggests either that caviomorphs entered South America much earlier than their first record (e.g., Vucetich et al., 1999) or that their first evolutionary diversification on the continent was quite rapid. New discoveries in Peru support the first hypothesis. The age for the oldest caviomorphs reported by Antoine et al. (2011) is even younger than data provided by molecular analyses (e.g., Opazo, 2005; Poux *et al.*, 2006; Sallam *et al.*, 2009).

Concerning the splitting of most lineages, paleontological estimations are older than those based on molecular studies. For example, most molecular estimations indicate that the divergence between *Chinchilla* and *Dinomys* occurred during the early Miocene (Opazo, 2005; Poux *et al.*, 2006; Sallam *et al.*, 2009). But available fossil data suggest it occurred at least in the early Oligocene. In general, the topologies expressing relationships among fossil and modern caviomorphs suggest that the four superfamilies and at least the families Chinchillidae, Dasyproctidae, Erethizontidae, Abrocomidae, Echimyidae and Octodontidae, have already originated in the Oligocene (> 25 Ma).

By the Deseadan (late Oligocene), caviomorphs had achieved a higher degree of diversification at the family level than in the early Oligocene. During the Colhuehuapian (early Miocene), the great diversity and disparity recorded by the caviomorphs suggests that they had already differentiated into a large variety of adaptive types, in accordance with warm and humid climatic conditions of the Miocene Climatic Optimum (Madden *et al.* 2010; Vucetich *et al.*, 2010b). From the Colhuehuapian SALMA up to the “Colloncuran”, there is relative faunal stability and almost no new caviomorph family or subfamily is recorded, as noted by Vucetich *et al.* (1999).

The most important turnover in the history of caviomorphs occurred during the late-middle Miocene to the late Miocene (post “Colloncuran” – Huayquerian), as well documented in the late Miocene record of central Argentina (see Figure 1B). The exposures representing

the latter interval belong to a sedimentary cycle which followed the withdrawal of a widespread marine transgression that extended from central Argentina to western Uruguay and southern Paraguay (“Mar Paranense” Figure 1A; see Pascual *et al.*, 1985, 1996). The withdrawal of this sea would have been synchronous with a marked global sea level fall near 10 Ma (Haq *et al.*, 1987; Verzi, 1999; Schultz *et al.*, 2004).

The magnitude of this turnover may be exaggerated by the bias of the fossil record, especially because of the paucity, or lack, of the record for the Oligocene – middle Miocene in northern Patagonia, the late Miocene in Patagonia, and a gap in the late middle Miocene in southern South America. However, this turnover is not an artefact caused by the geographic distribution of fossil localities. Instead, it is part of a faunistic change recorded both worldwide and in southern South America. This change was triggered by physical changes (consequences of astronomical climatic cycles, and diastrophic events), involving climatic changes (Vrba *et al.*, 1995) that resulted in arid environments in austral areas (*e.g.* Pascual and Ortiz Jaureguizar, 1990).

Among caviomorphs, this episode involves the appearance of several new families and subfamilies, the extinction of most of the ancient taxa in the late Miocene, as well as a trend toward gigantism in different lineages. The evolutionary histories of the new families and subfamilies recorded in this late Miocene “modern” stage are quite dissimilar. “Caviids” and Dinomyidae have a southern fossil record that shows they were already differentiated before the Chasicuan (Figures 3 and 5) when they underwent a large diversification. In contrast, the differentiation of modern Octodontidae of the subfamilies Ctenomyinae and Octodontinae occurred during the late Miocene, whereas their most important diversification occurred later (see Figure 6). On the other hand, Hydrochoeridae, Abrocomidae, “Eumysopinae” and Erethizontinae were already well differentiated in the late Miocene. Although their origin is undoubtedly earlier, it is not evidenced in the southern fossil record (Figures 3, 4 and 6),

suggesting they would have differentiated in intertropical South America (but see Vucetich and Pérez, 2011). The presence of the “eumysopines”, in particular, has been interpreted as a result of a southern expansion of an ancient Brazilian radiation that occurred after the withdrawal of the Paranense Sea (Verzi, 2002). This scenario is in agreement with the one proposed by Vucetich *et al.* (1999).

Since this turnover, changes in caviomorph faunas are less profound, as they gradually decrease in diversity in southern South America. However, an important extinction at the generic level occurred during the late Pleistocene-Holocene in intertropical areas (Hadler *et al.*, 2008 and references therein), implying for some cases (*e.g. Plesiaguti, Dicolpomys*) the extinction of old lineages. Although scarce and marginal, the record of certain rodent taxa of intertropical origin (such as, aff. *Clyomys*, *Plesiaguti*, *Aenigmys*, Figures 3, 5 and 6; Vucetich *et al.*, 1997, 2005c; Vucetich and Verzi, 2002; Verzi *et al.*, 2004) in the Quaternary of eastern Argentina supports this hypothesis. These records have been interpreted as representing invasions from the north in response to warm climatic pulses. These taxa not only quickly vanished from Argentine latitudes, but also some, such as the lineages of *Plesiaguti*, *Aenigmys*, and *Dicolpomys*, also became extinct.

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Captions for figures

Figure 1. Main or classical localities bearing fossil caviomorphs. A, Eocene-Middle Miocene; B, Late Miocene-Holocene. Dashed line, Paranense Sea (Hernández *et al.*, 2009). 1, La Venta; 2, Contamana; 3, Santa Rosa; 4, Salla-Luribay; 5, Lacayani; 6, Quebrada Honda; 7, Taubaté Basin; 8, Tinguiririca; 9, Nueva Palmira; 10, Laguna del Laja; 11, Río Collón Curá; 12, Gaiman; 13, Cabeza Blanca; 14, Gran Barranca; 15, La Flecha; 16, Río Pinturas; 17, Río Santa Cruz and coastal area; 18, Urumaco; 19 Acre region; 20, Tarija; 21, Uquía; 22, Lagoa Santa; 23, Valle de Santa María; 24, Barrancas del Paraná; 25, Río Grande do Sul; 26, Barrancas de San Gregorio; 27, Toscas del Río de La Plata; 28, Río Luján; 29, Huayquerías de San Carlos; 30, La Pampa (several localities); 31, Arroyo Chasicó; 32, Chapadmalal area; 33, Necochea; 34, Monte Hermoso; 35, Rincón Chico, Península Valdés.

Figure 2. Chronological distribution and hypotheses of relationships among caviomorph families (dotted lines indicate the uncertain age of Santa Rosa).

Figure 3. Relationships among Caviioidea and stratigraphic based on Miller and Gidley, 1918; Hoffstetter and Lavocat, 1970; Lavocat, 1976; Patterson and Wood, 1982; Wyss *et al.*, 1993; Quintana, 1998; Rowe and Honeycutt, 2002; Vieytes, 2003; Frailey and Campbell, 2004; Opazo, 2005; Pérez, 2010a; Vucetich and Pérez, 2011. Gray rectangles, non-monophyletic taxa; black circles, monophyletic taxa; question marks, controversial relationships; dotted lines, dubious horizon.

Figure 4. Relationships among Erethizontoidea based on Martin, 1994; Candela, 2000, 2004; Carvalho, 2000; Vucetich and Candela, 2001; Vucetich and Ribeiro, 2003; Kramarz, 2004; Reguero *et al.*, 2007 and references therein. Black circles, monophyletic taxa; question marks, controversial relationships; X, dubious systematic assignment for “Colloncuran” material of *Neosteiromys*.

Figure 5. Relationships among Chinchilloidea and stratigraphic based on Wood and Patterson, 1959; Frailey, 1980; Vucetich, 1984, 1989; Vucetich and Verzi, 1993; Kramarz,

2001, 2005; Sánchez Villagra *et al.*, 2003; Pérez and Vucetich, 2008; Chick, 2009. Black circles indicate monophyletic taxa; question marks indicate controversial relationships; dotted lines indicate dubious record/horizon.

Figure 6. Relationships among Octodontoidea and stratigraphic based on Scott, 1905; Wood y Patterson, 1959; Pascual, 1967; Patterson and Pascual, 1968; Vucetich and Verzi, 1991, 1996; Vucetich *et al.*, 1993b; Vucetich, 1995; Emmons and Vucetich, 1998; Verzi, 2001, 2002, 2008; Kramarz, 2001; Leite and Patton, 2002; Vucetich and Kramarz, 2003; Honeycutt *et al.*, 2003; Frailey and Campbell, 2004; Carvalho and Salles, 2004; Galewski *et al.*, 2005; Emmons, 2005; Iack-Ximenes *et al.*, 2005; Verzi and Arnal, 2007; Olivares, 2009; Blanga-Kanfi *et al.*, 2009; Chick, 2009, Arnal and Kramarz, 2011; Olivares *et al.*, 2012. Gray rectangles, non-monophyletic taxa; black circles, monophyletic taxa; dotted lines, dubious horizon; A, Adelphomyinae; H, Heteropsomyinae.

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