Journal of Zoology. Print ISSN 0952-8369

# Phylogeny and adaptive diversity of rodents of the family Ctenomyidae (Caviomorpha): delimiting lineages and genera in the fossil record

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**Keywords**
Rodentia; Ctenomyidae; phylogeny; burrowing adaptations; fossil record.

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Received 14 September 2007; accepted 7 November 2007

doi:10.1111/j.1469-7998.2007.00398.x

## Abstract

Differentiation of genera of the modern (Late Miocene to Recent) South American rodent family Ctenomyidae would have been linked to the acquisition of disparate adaptations to digging and life underground. In accordance with this hypothesis, the delimitation of lineages and genera in the ctenomyid fossil record is evaluated here following an adaptation-rooted criterion that involves both an assessment of the monophyly and of the adaptive profiles of recognized clades. The application of such a criterion, including morphofunctional information, delimited four cohesive lineages among crown ctenomyids (i.e. euhypsodont species of the Late Miocene to Recent): *Eucelophorus* (Early Pliocene–Middle Pleistocene), *Xenodontomys-Actenomys* (Late Miocene–Pliocene), *Praectenomys* (Pliocene) and *Ctenomys* (including *Paractenomys*; Pliocene–Recent); in addition, the results supported the status of *Xenodontomys* as a paraphyletic ancestor of *Actenomys*. The cladogenesis that gave rise to the crown group would have occurred immediately after the acquisition of euhypsodonty in a *Xenodontomys simpsoni*-like ancestor during the Late Miocene. This putative ancestor would have had fossorial habits and moderate digging specializations, an adaptive profile maintained in *Xenodontomys-Actenomys*. *Eucelophorus* and *Ctenomys* would have independently evolved subterranean habits at least since the Pliocene. Although the earliest history of the only living representative, *Ctenomys*, is known only fragmentarily, remains from Esquina Blanca (Uquía Formation), in north-western Argentina, suggest a minimum age of around 3.5 Ma (Early–Late Pliocene) for the differentiation of the genus. This date agrees with recent molecular estimates.

## Introduction

Ctenomyidae is a rodent family endemic to southern South America that differentiated in the Pampean region of central Argentina during the global expansion of open environments that occurred in the Late Miocene (Verzi, 1999). Among caviomorphs, ctenomyids are characterized by a peculiar and derived dental morphology, and adaptations to digging and life underground (Reig, 1970, 1989). It is one of the most extensively studied groups of South American caviomorphs, partly due to its appealing evolutionary pattern. The extensive cladogenesis of the extant subterranean genus *Ctenomys* (nearly 85 nominal living species; Woods & Kilpatrick, 2005) has inspired fruitful studies of speciation rates and comparisons with the diversity patterns of extinct ctenomyid genera (Reig, 1970, 1989; Cook & Lessa, 1998; Lessa & Cook, 1998; Cook, Lessa & Hadly, 2000; Castillo, Cortinas & Lessa, 2005). However, this knowledge has not received adequate paleontological support. Although considerable information on morphofunctional and adaptive traits for burrowing has been advanced for fossil ctenomyids (Reig & Quintana, 1992; Quintana, 1994; De Santis & Moreira, 2000; Fernández, Vassallo & Zárate, 2000; Verzi & Olivares, 2006), knowledge of both the phylogeny and the probable age of the lineages and clades (Reig, 1989: fig. 4) is still insufficient to support macroevolutionary proposals (e.g. Cook *et al*., 2000).

In this context, there is a need for a revision of the boundaries of ctenomyid lineages and genera in the fossil record. Reig & Quintana (1992) proposed that the differentiation of genera within Ctenomyidae would have been related to the development of varied adaptations to digging and life underground. Nevertheless, such adaptations, occurring in different lineages, have yet to be evaluated in a phylogenetic context. Although the recognition of *Ctenomys* in the living fauna is incontrovertible, the boundaries of the genus become less defined in the fossil record. This is also to be expected, and possibly to an even greater extent, in the case of species that belong to completely extinct clades and lineages.

Wood & Collard (1999), Cela-Conde & Altaba (2002) and Cela-Conde & Ayala (2003) asserted the need to apply an explicit adaptation-rooted criterion for delimiting genera in the fossil record of hominids. This criterion involves assessment of both the monophyly and the adaptive profiles of the recognized clades. In this work, I follow this criterion for the delimitation of ctenomyid lineages and genera. I analyze the phylogeny and adaptive diversity of the Late Miocene to Recent crown ctenomyids (i.e. euhypsodont representatives of the family). Extinct species, belonging to this crown group, are known through both cranial and mandibular remains, which are able to provide more accurate phylogenetic and morphofunctional information. Based on such evidence and available data on chronology of fossils, I assess the boundaries of lineages and genera of Ctenomyidae, and discuss their age and evolutionary patterns.

## Materials and methods

Specimens of extinct and living ctenomyids and octodontids studied (Supplementary Material Appendix S1) belong to the mammalogical and paleontological collections of the following institutions: Museo de La Plata, Argentina (MLP); Museo Municipal de Mar del Plata, Argentina (MMP); Instituto y Museo de Ciencias Naturales, San Juan, Argentina (IMCN CM); Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina (MACN); Universidad Nacional de La Pampa, Argentina (GHUNLPam); Laboratorio de Evolución, Facultad de Ciencias, Universidad de la República, Uruguay (CA, EV); and Museo Nacional de Historia Natural, La Paz, Bolivia (CBF). More than 500 cranial and mandibular remains of extinct ctenomyids from Argentina, including the available type specimens, as well as casts and unpublished illustrations of the Bolivian species *Praectenomys rhombidens*, were examined (Quintana, 1994). The terminal taxa in the phylogenetic analysis were nominal genera. In the case of taxonomically polytypic genera, character states were recorded mainly from the species or chronomorphs (*sensu* Martin, 1993) known through both cranial and mandibular remains. Thus, most of the characters selected for *Xenodontomys* and *Eucelophorus* corresponded to the youngest chronomorphs *Xenodontomys ellipticus* (type species), *Xenodontomys elongatus* and *Eucelophorus chapalmalensis* (type species), respectively (Table 1; see Verzi, 2002); likewise, the analysis of *Paractenomys* characters was essentially performed on *Paractenomys chapalmalensis* (type species). Even so, traits preserved in mandibles that represent the oldest chronomorphs *Xenodontomys simpsoni*, *Eucelophorus cabrerai* and *Paractenomys* from Esquina Blanca were also considered. The living genus *Ctenomys* was analyzed through skulls and mandibles of adult specimens belonging to 25 living species from Argentina (*Ctenomys argentinus*, *Ctenomys australis*, *Ctenomys azarae*, *Ctenomys* '*chasiquensis*', *Ctenomys dorbignyi*, *Ctenomys fulvus*, *Ctenomys latro*, *Ctenomys magellanicus*, *Ctenomys maulinus*, *Ctenomys mendocinus*, *Ctenomys opimus*, *Ctenomys perrensi*, *Ctenomys porteousi*, *Ctenomys roigi*, *Ctenomys sociabilis*, *Ctenomys talarum*, *Ctenomys tuconax*, *Ctenomys tucumanus*), Bolivia (*Ctenomys frater*, *Ctenomys leucodon*, *Ctenomys lewisi*, *Ctenomys steinbachi*), Brazil (*Ctenomys flamarioni*) and Uruguay (*Ctenomys pearsoni*, *Ctenomys rionegrensis*) (see Morgan & Verzi, 2006; Verzi & Olivares, 2006). The species *Octodontomys gliroides* and *Octomys mimax*, of the sister family Octodontidae (Honeycutt, Rowe & Gallardo, 2003), were included as outgroups. Trees were rooted on the basal Echimyidae, *Thrichomys* (Leite & Patton, 2002; Galewski *et al*., 2005), according to the assumption that Echimyidae is the sister taxon of Octodontidae + Ctenomyidae (e.g. Cook & Lessa, 1998; Verzi, 2001; Leite & Patton, 2002; Honeycutt *et al*., 2003). The phylogenetic analysis was performed using the program NONA 2.0 (Goloboff, 1993) to find the most parsimonious trees and to assess branch support in the cladogram. All characters were considered as equally weighted, and multistate characters were coded as non-additive. In searching for the shortest tree, the option for exact solutions 'mswap + ' of the program NONA 2.0 was used. Branch support was assessed by calculating relative

**Table 1** Nominal species of extinct Ctenomyidae analysed in this study

| Species | Geographic and chronological distribution | References |
|---|---|---|
| *Xenodontomys simpsoni* | Central Argentina; Late Miocene | Kraglievich (1961), Verzi, Montalvo & Vucetich (1991) |
| *Xenodontomys ellipticus* | Central-eastern Argentina; Late Miocene | Kraglievich (1940), Verzi, Montalvo & Tiranti (2003) |
| *Xenodontomys elongatus* | Central Argentina; Late Miocene | Verzi *et al.* (2003) |
| *Actenomys priscus* | Central-eastern Argentina; Early-Late Pliocene | Verzi (2002) |
| *Eucelophorus cabrerai* | Central-eastern Argentina; Early Pliocene | Kraglievich (1940), Reig & Quintana (1992) |
| *Eucelophorus chapalmalensis* | Central-eastern Argentina; Early Pliocene-Middle Pleistocene | Reig & Quintana (1992), Verzi & Quintana (2005) |
| *Praectenomys rhombidens* | Western Bolivia; Early Pliocene? | Villarroel (1975), Quintana (1994) |
| *Paractenomys chapalmalensis* | Central Argentina; Late Pliocene | Verzi & Quintana (2005) |
| *Paractenomys* sp. (from Esquina Blanca) | Northwestern Argentina; Late Pliocene | Walther *et al.* (1998), Reguero *et al.* (2007) |

Bremer support (RB) (Goloboff, 1993). The nomenclature of osteological and dental characters partially follows Verzi (2001, 2002) and Verzi & Olivares (2006).

# Results

## Phylogeny

Comparative analysis of ctenomyids resulted in a matrix of 35 craniomandibular and dental characters (Supplementary Material Appendix S2). A single cladogram was obtained (Fig. 1), 69 steps long and with consistency index = 0.93 and retention index = 0.91. In this cladogram, the monophyly of Ctenomyidae was supported by the maxillary extended anterodorsally with respect to the premaxillary septum (character state $8^2$). In addition, the dental traits $29^3$ and $33^2$ may be reliably accepted as synapomorphies of Ctenomyidae within the Caviomorpha, according to available information (e.g. Reig, 1970; Verzi, 1999), even though they were ambiguous in the context of this analysis. *Eucelophorus* was the sister genus of the clade [(*Actenomys*-X*enodontomys*)((*Praectenomys*(*Ctenomys*-*Paractenomys*))]. This latter clade was supported by six unambiguous synapomorphies of the incisive foramina, zygoma, glenoid fossa and masseteric fossa of the mandible (character states $4^1$, $5^1$, $10^1$, $11^1$, $21^1$ and $25^1$). The states of characters 10, 11 and 21 could not be ascertained for *Xenodontomys* and *Praectenomys*, because their zygoma are not preserved (Supplementary Material Appendix S2). The *Xenodontomys*-*Actenomys* clade was supported by two unambiguous synapomorphies in the ventral margin of the rostrum and alveolar sheath of the molars (character states $6^1$ and $15^1$); in addition, these taxa share dental traits that, although technically uninformative within this analysis, are clearly synapomorphies (character states $23^3$ and $34^3$). The clade [(*Praectenomys*(*Ctenomys*-*Paractenomys*)] was supported by synapomorphies in the bottom of m1 alveolus and the morphology of M3 and m3 (character states $28^1$, $32^2$ and $35^1$). The morphology of m3 was homoplastically shared by this clade and *Octodontomys*. Finally, *Ctenomys* clustered with *Paractenomys* based on the morphology of the rostral masseteric fossa, and the position of the bottom of the upper incisor alveolar sheath (character states $1^1$ and $3^1$). Both taxa also show similarities in the external auditory meatus and epitympanic sinus, zygomatic process of the squamosal, lateral palatine plate, auditory bulla and postcondyloid process (character states $16^2$, $17^1$, $18^1$, $20^1$ and $24^2$), but these similarities did not represent unambiguous synapomorphies in this analysis.

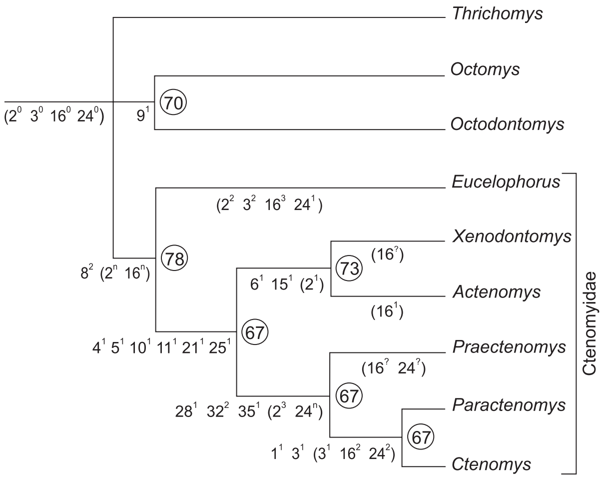

**Figure 1** Single most parsimonious tree of crown Ctenomyidae, showing unambiguous synapomorphies and ordering of character states, representing burrowing specializations (in brackets), below each node or branch; *n* indicates ambiguous character-states, and ? denotes unknown (missing) characters. Numbers within circles internal to each node indicate relative Bremer support values resulting from evaluation of 800 trees up to 31 steps longer than the optimum (see Supplementary Material Appendix S2).

RB for the [(*Xenodontomys*-*Actenomys*)((*Praectenomys* (*Paractenomys*-*Ctenomys*))] clade decreased from the maximum 100 to 67 when suboptimal trees, four steps longer than the optimum, were considered. Support for the clades [*Praectenomys*(*Ctenomys*-*Paractenomys*)] and (*Ctenomys*-*Paractenomys*) also decreased from 100 to 67 in trees up to six steps longer. When trees up to seven steps longer were considered, RB for Ctenomyidae diminished to 78. Finally, RB for *Xenodontomys*-*Actenomys* decreased from 100 to 75, and then to 73, for trees up to six and eight steps longer, respectively. All these RB values were maintained, even when 800 trees up to 31 steps longer were considered (Fig. 1).

The topology obtained here is mostly consistent with the phylogeny proposed by Reig and Quintana (in Reig, 1989: fig. 4), based on stratigraphic information and previous systematic data (Hoffstetter *et al.*, 1971; Villarroel, 1975). The relationship between *Octodontomys* and *Octomys* agrees with previous molecular analyses that place the former within the sister family Octodontidae (see Verzi, 2001; Honeycutt *et al.*, 2003).

## Adaptive and morphofunctional diversity

The disparity in craniomandibular and incisor morphology among ctenomyids reflects mainly different evolutionary pathways and degrees of adaptation to digging and underground life (Verzi, 2002; Verzi & Olivares, 2006). Moreover, as mentioned previously, the acquisition of different craniomandibular and dental adaptations to digging has been causally related to the differentiation of the genera (Reig & Quintana, 1992).

In accordance with an adaptation-rooted criterion, a genus represents a monophyletic unit that occupies a single adaptive zone (Wood & Collard, 1999; Cela-Conde & Ayala, 2003). In ctenomyids, as in other burrowing rodents, a major adaptive difference lies in the distinction between fossorial and subterranean strategies. According to Nevo (1999, p. 20), fossorial species spend a considerable time aboveground, while subterranean ones spend most of their lives underground, where they perform most of their biological functions (Genise, 1989; Stein, 2000; Vieytes, Morgan & Verzi, 2007). Relative orbit size in the skull is an indicator of subterranean habits (Pearson, 1984) *a priori* independent from digging ability (Verzi, 2002). According to their small relative orbit size, as indicated in the zygomatic arch (zygomatic index *sensu* Verzi, 2002), the extinct *Eucelophorus* and *Paractenomys* were essentially subterranean (Fig. 2; character state $17^1$). In contrast, *Actenomys* has a relatively large orbital region, similar to that of fossorial octodontids. Hence, although found to be associated with galleries (Genise, 1989; Fernández *et al*., 2000), this ctenomyid would have spent a significant part of its life above the surface (De Santis & Moreira, 2000; Verzi, 2002). Orbit size cannot be estimated in *Xenodontomys* and *Praectenomys*, because the zygomatic arch has not been preserved in these genera.

Nevertheless, fossorial and subterranean habits have been acquired independently more than once among ctenomyids. Moreover, the reliance on specializations linked to these habits to delimit ctenomyid lineages and genera is problematic, because parallelism and convergence (see Desutter-Grandcolas *et al*., 2005) are frequent, especially among species that occupy the subterranean adaptive zone (Nevo, 1999, p. 54). In this context, the search for exclusive morphofunctional specializations can assist in the delimitation of genera within clades in which subterranean habits have evolved more than once.

The masticatory morphology of fossil ctenomyids is consistent with the above-mentioned habits: *Eucelophorus* and the [*Praectenomys*(*Paractenomys*-*Ctenomys*)] clade have more noticeable specializations for digging (Reig & Quintana, 1992; Quintana, 1994; De Santis & Moreira, 2000; Fernández *et al*., 2000; Verzi, 2002; Verzi & Olivares, 2006). Some of these specializations, such as strong zygomatic arches and deeper mandibles for accommodating larger masseter muscles, and deeply inserted incisors, are universal among subterranean rodents, and have evolved independently in phylogenetically distant species (Hildebrand, 1985; Nevo, 1999; Stein, 2000). However, other traits associated with digging abilities are exclusive to these ctenomyids. According to a recent proposal about mandibular function during digging (Verzi & Olivares, 2006), particular specializations for the generation of bite forces at the incisors, and stabilization of the mandibular condyle, would have evolved in parallel in *Eucelophorus* and *Paractenomys*-*Ctenomys*. These specializations occur at the craniomandibular joint and the bottom of the upper incisor alveolar sheath; they are unique among caviomorphs and partially convergent with those of digging rodents of other continents (Figs 1, 3 and 4, and Supplementary Material Appendix S2).

Living *Ctenomys* species use both incisors and forelimbs in the construction of galleries (Vassallo, 1998). Upper incisor procumbency ranges from moderate to high in *Ctenomys*, whereas it is only moderate in its sister taxon *Paractenomys* (Verzi, 2002; Mora, Olivares & Vassallo, 2003: table 3). Notwithstanding this variability, in both *Ctenomys* and *Paractenomys*, the bottom of the incisor

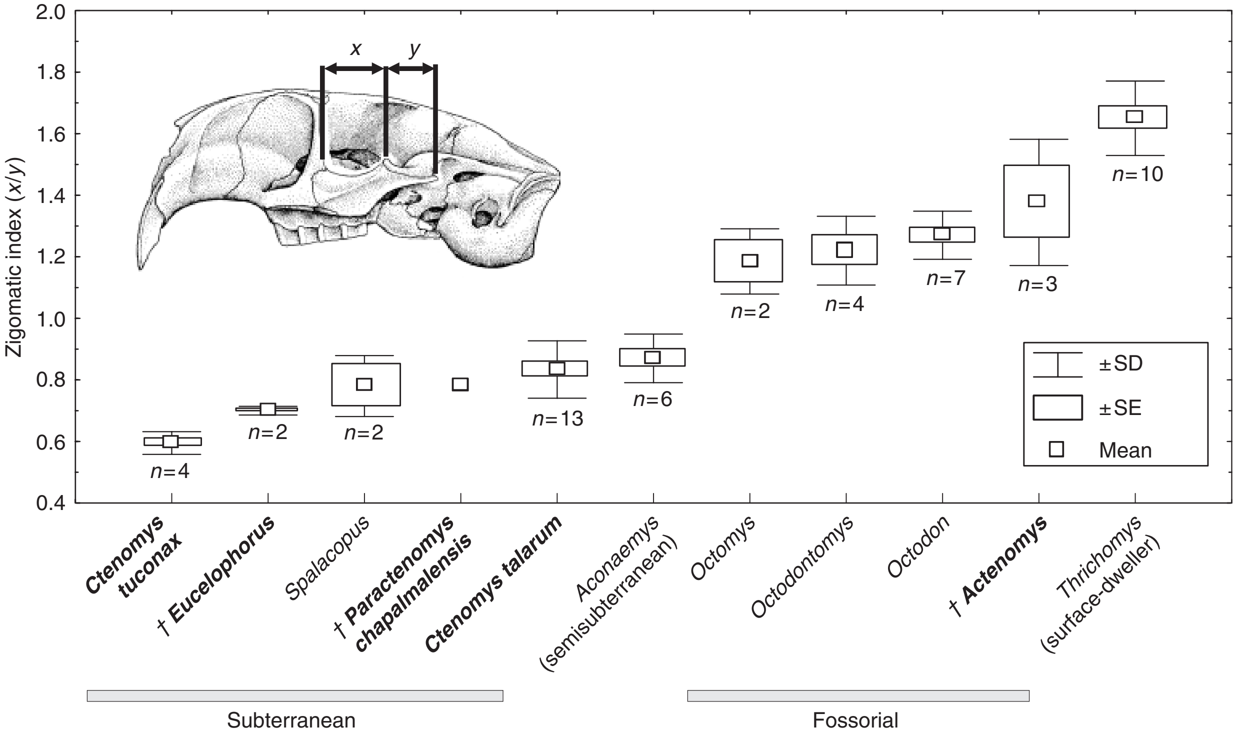

**Figure 2** Relative orbit size as indicated by zygomatic index for extinct and living ctenomyids (in bold), living octodontids and the echimyid *Thrichomys*.

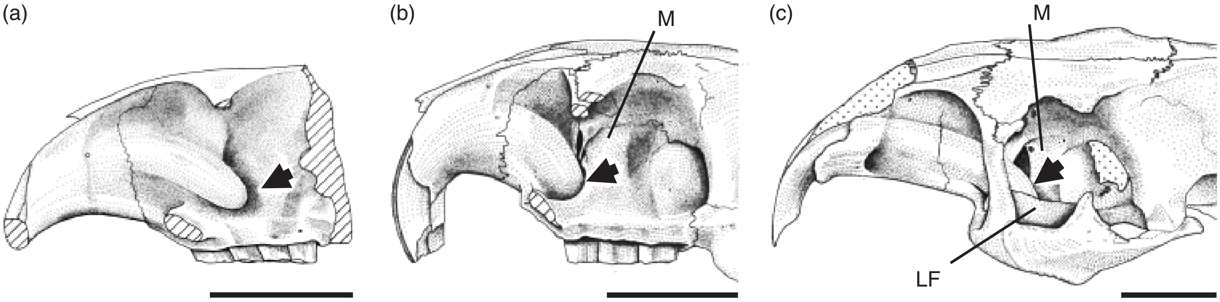

**Figure 3** Lateral view of the skull showing the position of the bottom of the upper incisor alveolar sheath (arrow) in: (a) *Praectenomys rhombidens* GB 248 (cast MMP 1237-M, Umala Formation, Pliocene, Aroma Province, La Paz Department, western Bolivia); (b) *Ctenomys australis* MLP 7.XI.95.3 (Recent, Buenos Aires province, central-eastern Argentina); (c) *Eucelophorus chapalmalensis* MMP 788-S (Vorohué Formation, Late Pliocene, coast of Buenos Aires province, central-eastern Argentina). The antorbital zygomatic ramus was missing in *P. rhombidens*, and it was removed in *C. australis*. Note that the bottom of the upper incisor alveolar sheath is free in *Praectenomys*, and it is housed in a maxillary cavity, anterior or lateral to the alveolar sheath of M1 (M), in *Ctenomys* and *Eucelophorus*, respectively; in addition, it is covered by the lateral flange of the canal for the infraorbital nerve (LF) in *Eucelophorus* (see character states in Supplementary Material Appendix S2 and Fig. 1). Scale bar = 10 mm. MLP, Museo de La Plata; MMP, Museo de Ciencias Naturales de Mar del Plata 'L. Scaglia'.

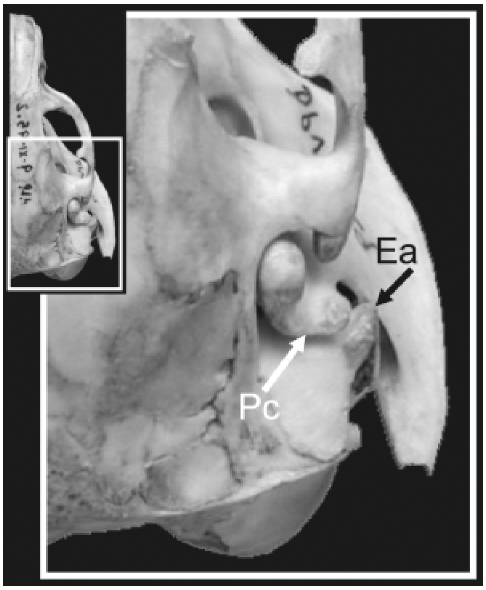

**Figure 4** Dorsal view of the right side (left side reversed) of the articulated skull and mandible, and detail of the jaw joint, in *Ctenomys fulvus* MLP 9.XI.95.2 (Recent, Catamarca province, north-western Argentina). Ea, external auditory meatus; Pc, postcondyloid process. MLP, Museo de La Plata.

alveolar sheath is not free, but housed in a cavity of the maxillary anterior to the alveolar sheath of M1 (character state $3^1$; Fig. 3). This condition protects the basal generative zone (cervical loop area, *sensu* Tummers & Thesleff, 2003) of the incisor, which can be damaged as a result of the great pressures exerted at the incisor tips in tooth-digging species (Zuri & Terkel, 2001). In the mandible, the postcondyloid process of *Ctenomys-Paractenomys* has a strong lateral apophysis (character state $24^2$) that is functionally linked to a tube-like external auditory meatus (character state $16^2$); both features are related to the presence of a postglenoid articular zone that stabilizes the jaw joint and prevents dislocation of the mandibular condyle when strong forces are exerted at the tip of the incisors during excavation (Fig. 4; Verzi & Olivares, 2006: figs 2 and 3). The lateral apophysis of the postcondyloid process is preserved in *Paractenomys* from Esquina Blanca.

*Eucelophorus* is the most specialized tooth digger among South American rodents (Verzi & Olivares, 2006; Vieytes *et al*., 2007). The upper incisors are highly procumbent and deeply inserted (Fig. 3; Verzi & Olivares, 2006: fig. 4d), and the bottoms of their alveolar sheaths are also protected, but differently than in *Paractenomys-Ctenomys*; they are housed in a cavity of the maxillary, lateral to the alveolar sheath of the M1 (character state $3^2$), and covered laterally and posteriorly by a wide lateral flange of the canal for the infraorbital nerve (character state $2^2$; Fig. 3). The postglenoid fossa is markedly broader than that of *Paractenomys-Ctenomys*, and the tube-like external auditory meatus is anteroposteriorly narrower (character state $16^3$; Verzi & Olivares, 2006: fig. 4). The mandibular condyle is surrounded, both dorsally and posteriorly, by this fossa and the auditory meatus; hence, a postcondyloid process is missing (character state $24^1$; Verzi & Olivares, 2006: fig. 5a).

*Xenodontomys-Actenomys* have short upper incisors, with their alveolar sheaths freely housed in the diastema (character state $3^0$) and surrounded by the dorsal margin of the lateral flange for the infraorbital nerve (character state $2^1$). *Actenomys* lacks a postglenoid articular region; this region is not preserved in *Xenodontomys*.

*Praectenomys* has procumbent upper incisors with their alveolar sheaths not enclosed (character state $3^0$) and deeply inserted behind the ventral zygomatic root and level with M1 (Fig. 3; Quintana, 1994; Verzi, 2002: table 3). The incisor morphology of *Praectenomys* resembles that of the subterranean octodontid *Spalacopus cyanus* (see Reig, 1970), but differs from that of other ctenomyids. Neither the craniomandibular joint nor the postcondylar portion of the mandible are preserved for this genus.

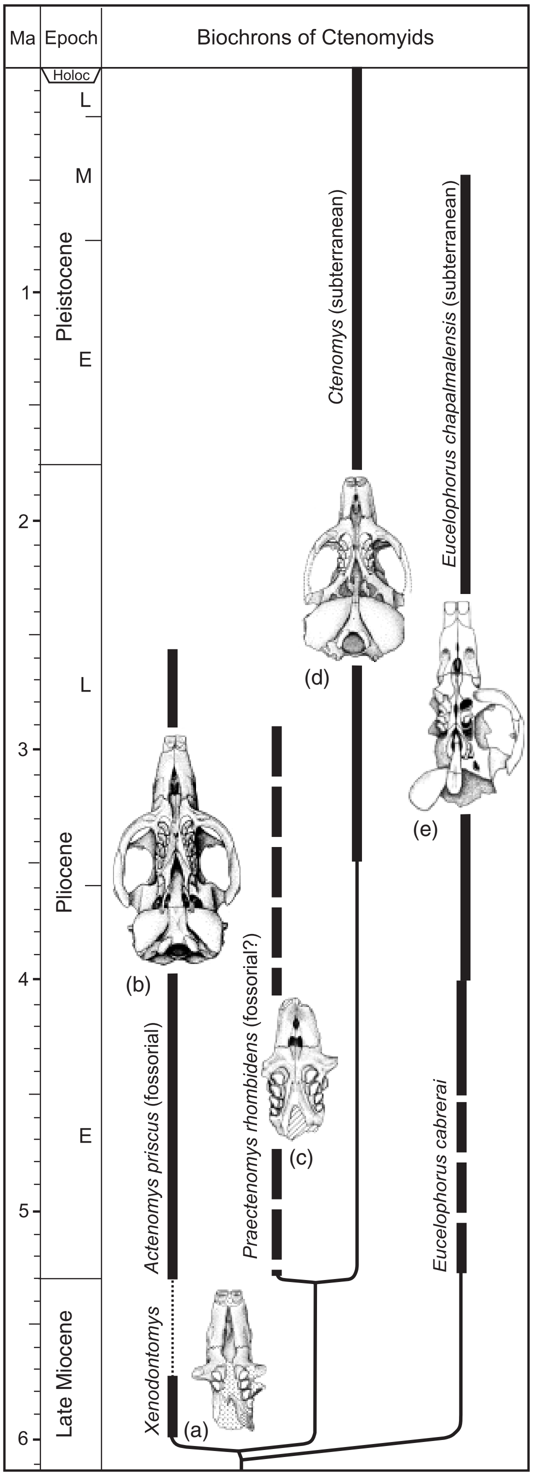

**Figure 5** Chronological distribution of crown ctenomyids. The chronological scale is according to Berggren *et al.* (1995). Ventral view of the skull of ctenomyids (not to scale): (a) *Xenodontomys ellipticus* MLP 63-VI-10-49 'Irene Formation', Late Miocene, Buenos Aires province, central-eastern Argentina; (b) MMP 1240-M, Chapadmalal Formation, Early–Late Pliocene, Buenos Aires province, central-eastern Argentina; (c) GB 248 (cast MMP 1237-M), Umala Formation, Pliocene, Aroma Province, La Paz Department, western Bolivia; (d) *Ctenomys chapalmalensis* MMP 481-S, San Andrés Formation, Late Pliocene, Buenos Aires province, central-eastern Argentina; (e) MMP 788-S, Vorohué Formation, Late Pliocene, Buenos Aires province, central-eastern Argentina. MLP, Museo de La Plata; MMP, Museo de Ciencias Naturales de Mar del Plata 'L. Scaglia'.

## Boundaries and age of ctenomyid lineages and genera

Phylogenetic and adaptive-morphofunctional data support the assignment of *P. chapalmalensis* and the materials from Esquina Blanca to the genus *Ctenomys*, as partially proposed by Rovereto (1914) and Verzi & Quintana (2005). Likewise, results bear out the hypothesis that *Xenodontomys-Actenomys* represents a single lineage with an anagenetic evolutionary pattern (Verzi, Montalvo & Tiranti, 2003). The trends of morphological change in the mandible and molars of *Xenodontomys-Actenomys* do not imply a distinct adaptive change along the lineage; consequently, *Xenodontomys* is a paraphyletic genus and its older chronomorph, *X. simpsoni*, is the *species germinalis* of genus *Actenomys* (see Cela-Conde & Altaba, 2002). Nevertheless, the name *Xenodontomys* should be maintained to keep consistency with the literature and to facilitate systematics or biostratigraphic analyses.

Finally, even though the phylogenetic position of *Praectenomys* is consistent with its presumed ancestral condition with respect to *Ctenomys* (Villarroel, 1975; Reig, 1989), both the lack of information about its craniomandibular joint and its procumbency associated with a different insertion of incisors suggest that it be maintained as a distinct genus.

Figure 5 summarizes the phylogeny and age of ctenomyids. Crown Ctenomyidae are assumed to comprise four genera: the fossorial *Actenomys*, the subterranean *Ctenomys* and *Eucelophorus*, and *Praectenomys*, presumed to be at least fossorial. Of these, only *Ctenomys* is actually polytypic from an evolutionary standpoint, whereas the remaining genera are single lineages whose taxonomic 'species' (Table 1) represent chronomorphs. The nominal genus *Xenodontomys* includes the older chronomorphs of the *Actenomys* lineage.

The cladogenesis that gave rise to the crown group would have been synchronous with the phyletic evolution of *Xenodontomys*, and must have occurred immediately after the acquisition of euhypsodonty in an *X. simpsoni*-like ancestor during the Late Miocene (Verzi, 1999; Verzi, Vieytes & Montalvo, 2004). This putative ancestor would have had fossorial habits and moderate specializations for digging, an adaptive profile that would have persisted in the *Xenodontomys-Actenomys* lineage. *Eucelophorus* and *Ctenomys* would have evolved subterranean habits and tooth-digging specializations independently at least since the Pliocene. The Late Miocene history of both lineages is not known.

Information on the early history of *Praectenomys-Ctenomys* is fragmentary, partially owing to the diastrophic conditions of the Altiplano-Puna of Bolivia and north of Chile and Argentina (Marshall & Sempere, 1993), where the differentiation of this clade would have occurred (Spotorno *et al.*, 1995). *Praectenomys* has been referred to the Early Pliocene, but actually the available data hinder a temporal assignment more precise than the entire Pliocene (see review of the age of Umala Formation in Cione & Tonni, 1996). In the case of *Ctenomys*, the abundance of extinct species morphologically very close to living ones in Pleistocene deposits of Argentina, Bolivia and Uruguay has encouraged the notion that the oldest *Ctenomys* come from levels dating to *c.* 1.8 Ma (e.g. Reig, 1989: fig. 4; Cook *et al.*, 2000: fig. 9.8; Fernández *et al.*, 2000: fig. 8). However, the recognition of specimens from basal sections of the Uquía Formation in Esquina Blanca as a species of *Ctenomys* brings the minimum age for the differentiation of this genus to around 3.5 Ma (Fig. 5; see stratigraphy of Uquía Formation in Reguero, Candela & Alonso, 2007). This age is similar to the molecular estimate of 3.7 Ma proposed by Castillo *et al.* (2005).

In any case, the knowledge of the origin and early differentiation of ctenomyids, especially those of the ancestors of *Praectenomys*-*Ctenomys* and *Eucelophorus*, remains uncertain. Further understanding of these issues requires new findings in the Late Miocene–Pliocene of Bolivia and Argentina that may help to bridge the gaps in the fossil record of the family.

## Acknowledgements

I thank J. Vargas Mattos, J. Aparicio, E. Lessa, C. Montalvo, O. Scaglia, D. Romero, A. Dondas, A. Kramarz, E. Tonni, M. Reguero and S. Giannoni for granting access to materials under their care. I am grateful to E. Lessa for his valuable review of a first draft of the paper, I. Olivares for assistance with illustrations, C. Morgan and C. Deschamps for translation and C. Quintana for providing casts and unpublished drawings of *Praectenomys*. This paper was partially funded by grants CONICET PIP 5242 and UNLP 11/N442.

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## Supplementary material

The following material is available for this article online:

**Appendix S1.** Taxa and specimens examined.

**Appendix S2.** Description of characters and matrix used in the phylogenetic analysis.

This material is available as part of the online article from http://www.blackwell-synergy.com/doi/abs/10.1111/j.1469-7998.2007.00398.x

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