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The oldest South American tuco-tuco (late Pliocene, northwestern Argentina) and the boundaries of the genus *Ctenomys* (Rodentia, Ctenomyidae)

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Abstract

A new species of Ctenomyidae from the late Pliocene of Uquía Formation (northwestern Argentina) is described. The new remains consist of a fragmentary rostrum, and a left mandible with partial lower dentition. Its phylogenetic affinity and morphological specializations for tooth-digging support its assignation to the South American rodent genus *Ctenomys*. In this context, we highlight the importance of unique morphological specializations for the delimitation of genera within an intrafamilial clade in which similar adaptive strategies could have evolved more than once. The new materials are the oldest fossils for the genus (ca. 3.5 Ma), and their finding in the central Andes agrees with previous hypotheses about the possible area of origin of *Ctenomys*. They precede by about one million years the presence of *Ctenomys chapalmalensis* in the Pliocene of the Pampean region of central Argentina, the oldest record previously known for the genus. Nevertheless, the new species does not contribute key information about ancestral character states for the genus beyond those already known through *C. chapalmalensis*. The phylogenetic, adaptive and even chronological information supplied by these new materials would be linked to the differentiation of the genus rather than to its origin.

Keywords: Rodentia; *Ctenomys*; Genus boundaries; Morphological specializations; Late Pliocene

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Introduction

The family Ctenomyidae is a clade of South American caviomorph rodents with fossorial to subterranean habits. The group is first recorded in the late Miocene, and its evolutionary history shows decreased disparity and markedly increased diversity after the Pliocene. Towards the end of the Pliocene most of genera went extinct whereas the only genus that has survived to the present, *Ctenomys*, underwent an extensive cladogenesis. This diversification of *Ctenomys* was even more profuse during the Pleistocene (e.g. Reig et al. 1990: Fig. 2; Verzi 2008: Table 1 and Fig. 5).

Ctenomys includes approximately 85 living species with subterranean habits (Woods and Kilpatrick 2005) and more than 10 extinct species (Verzi et al. 2004a),

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Abbreviations: LDIAST, diastema length; MH, mandibular height at m1; MW, mandibular width (measured at base of coronoid apophysis); L, length; W, width.

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whose alpha systematics is in a state of flux due to the difficulty of assigning taxonomic hierarchy to the interpopulational variability (see Lessa 2000). Aside from this, *Ctenomys* is considered to be a very cohesive genus both morphologically and adaptively (Reig et al. 1990; Lessa and Cook 1998). The results from morpho-functional and allometric analyses of craniomandibular features of living species have supported this notion of morphological identity (Lessa 1993; Mora et al. 2003; Schleich and Vassallo 2003; Verzi and Olivares 2006; Vassallo and Mora 2007). However, depending on the conceptual framework applied, the boundaries of the genus can be less evident in the fossil record, and this situation may hinder our understanding of its evolutionary history. Verzi (2008) revised the boundaries of the ctenomyid genera through the assessment of their monophyly and adaptive identity (Wood and Collard 1999; Cela-Conde and Ayala 2003), in keeping with the hypothesis that the differentiation of these genera would have been linked to the development of varied adaptations to digging and life underground (Reig and Quintana 1992). In that proposal, the remains of a ctenomyid found in the Pliocene of Uquía Formation, in northwestern Argentina (Walther et al. 1998), were mentioned as the oldest record of genus *Ctenomys*. In this work, we provide the first description of these remains and discuss their belonging to the genus, their significance for both the delimitation of *Ctenomys* in the fossil record and the interpretation of their evolutionary history.

Material and methods

The specimens of extinct and living ctenomyids and octodontids studied (including casts) belong to the Mammalogical and Paleontological collections of the following institutions: Cátedra de Geología Histórica, Universidad Nacional del Sur, Argentina; Instituto y Museo de Ciencias Naturales, San Juan, Argentina; Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; Museo de La Plata, Argentina; Museo Municipal de Mar del Plata, Argentina; Paleontología Vertebrados Instituto Miguel Lillo, Tucumán, Argentina; Universidad Nacional de La Pampa, Argentina; Laboratorio de Evolución, Facultad de Ciencias, Universidad de la República, Uruguay; Museo Nacional de Historia Natural, La Paz, Bolivia; Museo Nacional de Historia Natural de Montevideo, Uruguay. Mandibular remains and teeth, including the available type specimens, of the following extinct ctenomyids were studied: *Xenodontomys simpsoni*, *Xenodontomys ellipticus*, *Xenodontomys elongatus* (late Miocene), *Actenomys priscus*, *Eucelophorus cabrerai*, *Eucelophorus chapalmalensis*, *Praectenomys rhombidens* (Pliocene), *Ctenomys chapalmalensis* (late Pliocene), *Ctenomys bonariensis*, *Ctenomys dasseni*, *Ctenomys intermedius*, *Ctenomys kraglievichi*, *Ctenomys latidens*, *Ctenomys magnus*, *Ctenomys orthognathus*, and *Ctenomys subassentiens* (Pleistocene). *P. rhombidens* and the holotypes of *C. latidens* and *C. bonariensis* were studied through casts and unpublished illustrations; *C. subassentiens* was revised through the illustrations of Frailey et al. (1980: Figs. 2 and 3). In addition, specimens of 25 living species of *Ctenomys* from Argentina, Brazil, Bolivia, and Uruguay were studied. The list of taxa and specimens examined can be found in Verzi et al. (2004a, b) and Verzi (2008: Appendix S1). Nomenclature of osteological and dental characters follows Verzi (2001, 2008) and Verzi and Olivares (2006). 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. Search for the shortest tree was made using the 'mswap+' option for exact solutions of the program NONA 2.0. Branch support was assessed by relative Bremer support (Goloboff 1993). All characters were considered as equally weighted and multistate characters were coded as non-additive. Allometric analyses and tests for differences among regression lines were made with the software SMATR (Warton et al. 2006; Falster et al. 2006).

Results and discussion

Systematics

Order Rodentia Bowdich, 1821
Suborder Hystricomorpha Brandt, 1855
Infraorder Hystricognathi Brandt, 1855
Family Ctenomyidae Lesson, 1842
Ctenomys Blainville, 1826
Ctenomys uquiensis new species

Type. – MLP 96-II-29-1, damaged left mandible with part of the condyloid and angular regions, an intra-alveolar portion of the incisor, and the dp4-m2.

Hypodigm. – The type and MLP 96-II-29-2, small rostral fragments, with fragments of the intra-alveolar portions of the incisors, and the left DP4; isolated right DP4 and left M1 or M2.

Etymology. – *uquiensis*, after Uquía Formation, which yielded the hypodigm of the new species.

Horizon and locality. – The remains were found in Uquía Formation (late Pliocene), at the type locality, Esquina Blanca (Jujuy Province, northwestern Argentina, Fig. 1). Information on fauna, stratigraphy and chronology of Uquía Formation may be found in Marshall et al. (1982), Orgeira (1993), Cione and Tonni (1995, 1999), Walther et al. (1996, 1998) and Reguero et al. (2007). MLP 96-II-29-1 and 2 were found in the basal

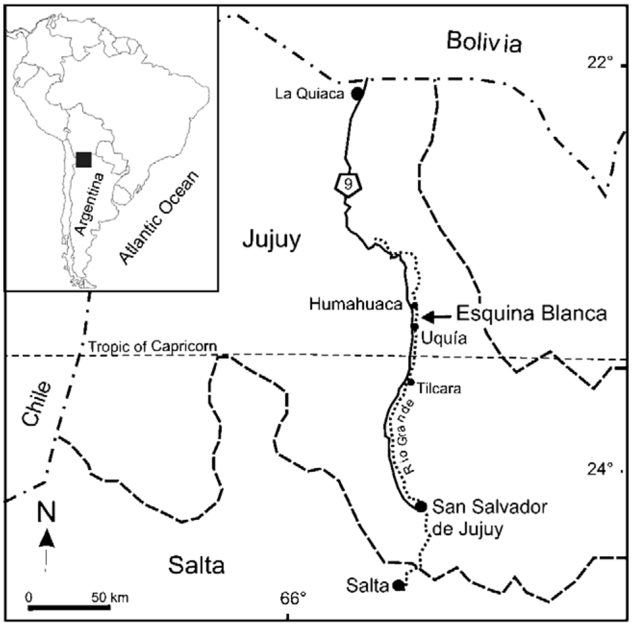

Fig. 1. Geographical location of the fossil bearing beds of Uquía Formation (Pliocene) at Esquina Blanca (Jujuy province, northwestern Argentina). Inset illustrates the location of the area within South America.

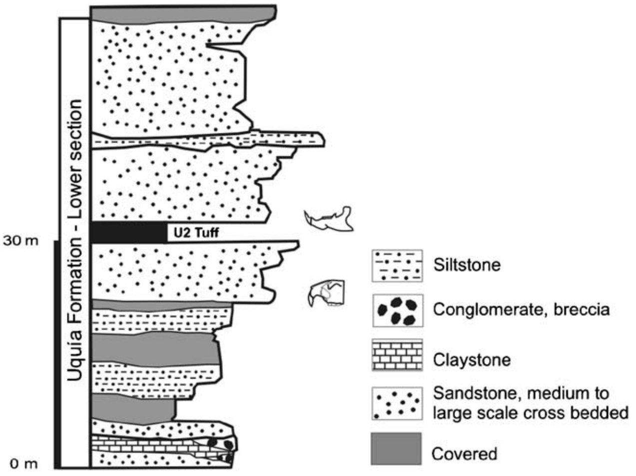

Fig. 2. Schematic stratigraphic profile of the lower section of Uquía Formation at the type locality, Esquina Blanca (modified from Reguero et al. 2007). The mandible and rostrum icons indicate the stratigraphic provenance of *Ctenomys uquiensis* sp. nov. MLP 96-II-29-1 (type) and MLP 96-II-29-2, respectively.

levels (lower section in Prado et al. 2000:134–135; Reguero et al. 2007). MLP 96-II-29-1 was found in the paleomagnetic unit 4 of Walther et al. (1998), approximately 30 m from the base, immediately adjacent to the U2 tuff of Walther et al. (1998, in Reguero et al. 2007), and MLP 96-II-29-2 was collected at slightly more than 20 m from the base (Fig. 2). Marshall et al. (1982) reported a 40K-40Ar dating for a dacite tuff near the base of the exposure (LGM 202), which yielded 3.54 ± 0.04 Ma (see also Reguero et al. 2007).

Measurements (in mm). – Type, LDIAST: 6.94; MH: 7.68; MW: 13.15; Ldp4-m2: 7.92; Ldp4: 2.56; Wdp4: 1.65; Lm1: 2.51; Wm1: 1.77; Lm2: 2.34; Wm2: 1.65; Wi1: 1.77. MLP 96-II-29-2, LDP4: 2.22; WDP4: 1.99.

Diagnosis. – A small and gracile *Ctenomys* species, with occlusal surface of dp4-m2 wider and shorter than in the remaining species. Anterior wall of dp4 alveolus low, without the marked step present in the Pleistocene to Recent (modern) *Ctenomys*. Lower diastema slightly longer than in *C. chapalmalensis*. Masseteric crest more expanded at its origin than in the latter species, and descending. Intra-alveolar portion of lower incisor proportionately narrow.

Description. – The remains from Esquina Blanca are especially similar to the extinct species *Ctenomys chapalmalensis* and *Praectenomys rhombidens*. MLP 96-II-29-1 is a gracile small-sized mandible (Fig. 3a). However, trabeculae are not evident on the surface of the bone (Montalvo 2002), which indicates it would correspond to an adult specimen. The diastema is scarcely concave, procumbent and long as in *P. rhombidens*. The anterior wall of the alveolus of dp4 is low as in *P. rhombidens* and *C. chapalmalensis*, unlike modern *Ctenomys* in which a marked step is formed at this level. The notch for the tendon of the M. *masseter medialis anterior* is level with m1, and almost at half the height of the mandibular body. A marked lateral crest (sensu Woods 1972) is present between the notch and the base of the coronoid process. The anterior margin of the coronoid process, although damaged, is level with the posterior part of the m2 as in *C. chapalmalensis* and modern *Ctenomys*; it is slightly more anterior, laterally covering the posterior end of the m2, in some modern *Ctenomys* (Verzi 2002: Table 3). In contrast, this margin is more posterior, at m3 level, in *P. rhombidens* and the remaining ctenomyids. The bottom of the dp4 alveolus is broken, exposing the base of the tooth. The bottom of the m1 alveolus forms a protuberance anteromedial to the origin of the masseteric crest. The anterior portion of this crest expands somewhat more markedly than in *C. chapalmalensis*. It is descending as in *P. rhombidens* and *C. chapalmalensis*, unlike modern *Ctenomys* in which it is subhorizontal or ascending. The masseteric fossa is subdivided into dorsal and ventral portions, both quite shallow. The articular surface of the condyle is narrow and proportionally long. The base of a wide ventrolateral apophysis of the postcondyloid process (Verzi and Olivares 2006) (Fig. 3a) is preserved; it is more posterior than in modern *Ctenomys*, as in *C. chapalmalensis*.

The i1 is proportionally narrow. The occlusal surfaces of the dp4-m2 are short and wide, as in *P. rhombidens*, and kidney-shaped, as in modern *Ctenomys* and *C. chapalmalensis*, with the lingual concavity more marked than in *Praectenomys* (cf. Fig. 3b and Quintana

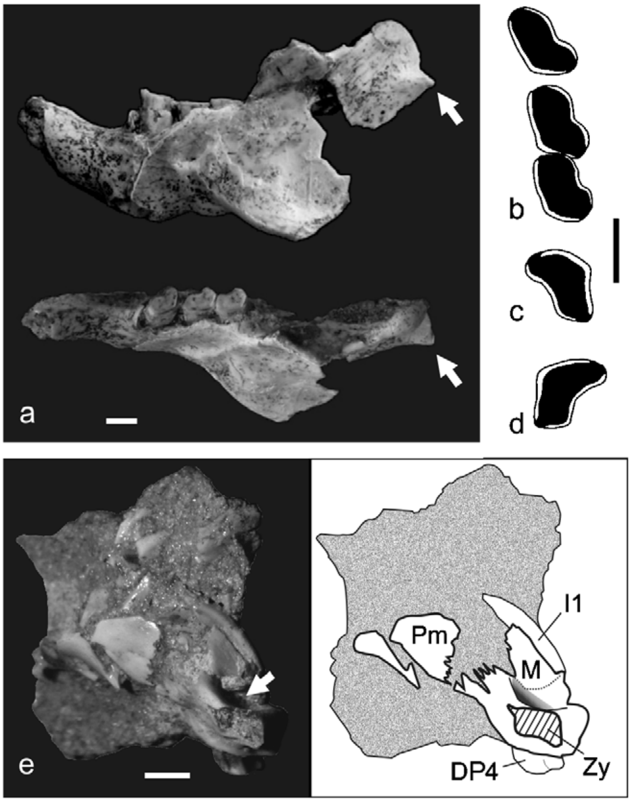

Fig. 3. *Ctenomys uquiensis* sp. nov., Esquina Blanca, Uquía Formation, Pliocene. Left hemimandible of the type MLP 96-II-29-1 (a) in external (top) and dorsal (bottom) views; arrow indicates the ventrolateral apophysis of the postcondyloid process. Occlusal view of the left dp4-m2 of the type (b). Right DP4 (c), and left M1 or M2 (d) of MLP 96-II-29-2. Fragment of rostrum MLP 96-II-29-2 in posterolateral view (e); schematic drawing shows preserved structures; arrow indicates the cavity in the maxillary that lodges the base of the alveolar sheath of I1. M, maxillary; Pm, premaxillary; Zy, anterior root of the zygomatic arch. Scales = 2 mm.

1994: Fig. 5). Wide dentine tracts are present on the anterolabial and posterolingual ends of each molar. A thin cement layer surrounds the dp4 and part of the labial side of the m1. The bottom of the m3 alveolus is oriented toward the rear, above the i1, as in *P. rhombidens*, *C. chapalmalensis* and modern *Ctenomys*.

MLP 96-II-29-2 is a fragmentary, much damaged, rostrum, with the left DP4 in situ, and the right DP4 and a left M1 or M2 as isolated pieces (Figs. 3c–e). According to the size of the upper molariforms, MLP 96-II-29-2 is similar to the type in size. The occlusal figure of the molariforms is similar to that of *C. chapalmalensis*, shorter and wider than in modern *Ctenomys*. The anterior lobe is more transverse than in *P. rhombidens*. The DP4 has a medial sharp edge as in *C. chapalmalensis* and modern *Ctenomys*. The rostrum fragment preserves the base of the zygomatic root, whose dorsal surface bears a cavity for the base of the incisor alveolar sheath as in *C. chapalmalensis* and modern *Ctenomys* (Fig. 3e). There is no lateral flange for the passage of the infraorbital nerve.

Phylogeny

A phylogenetic analysis was performed to assess the relationships of the species from Uquía, especially with respect to the other Pliocene *Ctenomys* species—*C. chapalmalensis*—the living species of the genus, and the sister species of *Ctenomys*, *P. rhombidens*. The primary homologies used to build the matrix (Tables 1 and 2) are mostly those used by Verzi (2008). The character 23 (“occlusal design of dp4-m2”, Table 1) is a simplified version of character 34 of Verzi (2008: Appendix S2). Twenty five living *Ctenomys* species are included in the tree as a single terminal, *Ctenomys*, because more thorough analyses of several more characters are necessary to assess the relationships among them (see e.g. Lessa and Cook 1998; Slamovits et al. 2001; Castillo et al. 2005). In this sense, the apomorphies of this terminal actually represent synapomorphies of the 25 living species analyzed. Trees were rooted on the echimyid *Thrichomys*; the genera *Octodontomys* and *Octomys*, from the sister family Octodontidae, were also included as outgroups (Verzi 2008).

A single cladogram was obtained (Fig. 4), 46 steps long, with consistency index = 0.94 and retention index = 0.94. *C. uquiensis* was clustered with the living *Ctenomys* and *C. chapalmalensis* by the position of the bottom of the upper incisor alveolar sheath (character state 3^1), morphology of the molariforms (character states 23^3 and 24^1) and morphology of the rostral fossa (character state 1^1, unknown in *C. uquiensis*). In addition, these taxa shared the morphology of the postcondyloid process (character state 17^2), but the lack of preservation of this character in *P. rhombidens* does not allow establishing at which level it could represent an unambiguous synapomorphy. The living *Ctenomys* shared with *C. chapalmalensis* the morphology of the external auditive meatus and epitympanic sinus, lateral palatine plate, and auditory bulla (character states 10^2, 12^1, and 13^1, respectively); however, these do not represent unambiguous synapomorphies because their states are not known for either *P. rhombidens* (as in Verzi 2008), or *C. uquiensis*.

Functionally significant morphological specializations of *C. uquiensis*

The masticatory strategy and molar morphology are essentially uniform in ctenomyids (Olivares et al. 2004; Verzi et al. 2004b). Accordingly, cranial morphological disparity of the group has been interpreted to reflect different pathways of adaptation to burrowing (Reig and Quintana 1992; Verzi and Olivares 2006).

Table 1. Description of characters used in the phylogenetic analysis.

1. Rostral masseteric fossa: (0) dorsal to the alveolar sheath of I1, progressively narrow anteriad, shallow, and ending with a pointed outline level with the anterior end of the incisive foramina; (1) dorsal to the alveolar sheath of I1, deep and ending in a curved crest slightly anterior to or level with the premaxillary–maxillary suture; (2) with portions dorsal and ventral to the alveolar sheath of I1 present and shallow; the anterior end occupying almost the entire height of the rostrum and limited by a more straight crest located ventrally level with the anterior end of the incisive foramina or anterior to them; (3) with portions dorsal and ventral to the alveolar sheath of I1 present and very deep; portion ventral to I1 extending greatly anterior to the incisive foramina. This fossa provides attachment for the origin of M. *masseter medialis anterior*, and its depth indicates strong development of this muscle
2. Lateral flange of the canal for infraorbital nerve: (0) present, and with free dorsal margin; (1) present and with dorsal margin in contact with bottom of alveolar sheath of upper incisor; (2) very wide and covering bottom of alveolar sheath of upper incisor laterally and posteriorly; (3) very reduced or absent
3. Bottom of alveolar sheath of upper incisor: (0) free in the diastema, or in the orbital region; (1) lodged in a cavity of the maxillary, anterior to alveolar sheath of M1; (2) lodged in a cavity of the maxillary, lateral to alveolar sheath of M1
4. Incisive foramina: (0) with lateral walls concave and approximately symmetric anterior and posterior to the premaxillary–maxillary suture; suture located near middle of lateral wall of the foramen or more anteriorly; (1) foramina extended and progressively narrow anterior to the premaxillary–maxillary suture; suture nearer posterior part of the foramen
5. Premaxillary–maxillary suture at medial margin of incisive foramen: (0) level with its portion lateral to the foramen; (1) displaced forward
6. Ventral margin of rostrum: (0) not widened or only slightly widened but without protuberance at premaxillary–maxillary suture; (1) widened forming a marked protuberance level with premaxillary–maxillary suture
7. Incisive foramina: (0) wide, at least 1/4 of rostrum width (both measured at the premaxillary–maxillary suture); (1) narrow, less than 1/4 of rostrum width. Although this character is uninformative in the present analysis, state 1 is a synapomorphy of the 25 living *Ctenomys* species analyzed (see Phylogeny)
8. Anterior extension of the maxillary into posterior margin of incisive foramen: (0) scarcely developed or absent; (1) maxillary extended anteriad, on the same horizontal plane as premaxillary septum, constraining the incisive foramen posteriorly; (2) maxillary extended anterodorsally with respect to premaxillary septum, constraining the incisive foramen posteriad
9. Premaxillary septum: (0) with posterior ends of premaxillaries joined medially forming a pointed projection; (1) with posterodorsal ends of premaxillaries divergent, each one forming a lateral apophysis
10. External auditory meatus (EAM): (0) short, moderately protruding with respect to auditory bulla and epitympanic recess (ER); (1) forming a protruding tube with its anterior wall slightly to very concave; (2) forming a protruding tube very narrow anteroposteriorly and kidney-shaped in cross section due to marked concavity of its anterior wall; ER dorsal to the EAM, very narrow
11. Zygomatic portion of squamosal: (0) subhorizontal and forming at least the posterior half of paraorbitary process; (1) never reaching the end of paraorbitary process; this process formed mostly or exclusively by the jugal. State 1 is associated with a reduced orbital region, which is defined on the zygoma by a more anterior placement of the paraorbitary process
12. Maxillary and alisphenoid in basitemporal region: (0) contacting each other or separated by dorsal portion of the lateral palatine plate; (1) separated by dorsal portion of the lateral palatine plate, which is expanded over both the alveolar sheath of M3 and the alisphenoid; (2) strongly joined through a maxillary apophysis posterolateral to the M3 alveolar sheath
13. Auditory bulla: (0) ovoid; (1) pyriform, with anterior portion narrow and strongly oblique major axis; (2) pyriform, very narrow, with a pit ventrolateral to the EAM
14. Alveolar margin of the mandibular molar series: (0) descending ventromedially anterior to dp4; (1) not descending anterior to dp4
15. Origin of masseteric crest of the mandible: (0) incorporating the notch for the tendon of M. *masseter medialis*; (1) posterior to the notch. Although this character is uninformative in the present analysis, state 1 is a synapomorphy of Octodontidae-Ctenomyidae within the context of Caviomorpha (see Verzi, 1999)
16. Masseteric area of the mandible: (0) without protuberances corresponding to bottom portion of alveoli of molars; (1) with a rounded protuberance near origin of masseteric crest, corresponding to the bottom of alveolus of m2; (2) with a protuberance that lacks distinct margins, corresponding to the bottom of alveolus of m2, placed between dorsal and ventral divisions of the masseteric fossa; (3) with a marked ovoid protrusion corresponding to the bottom of alveolus of m3, between the dorsal and ventral divisions of the masseteric fossa; (4) with a scarcely visible protrusion corresponding to the bottom of alveolus of m3 in the dorsal division of the masseteric fossa. The states present in Octodontidae and Ctenomyidae are associated to the occurrence of hypsodonty
17. Postcondyloid process: (0) developed, with a weak protuberance on its ventral margin or without it; (1) very reduced or absent; (2) with a strong lateral apophysis on its ventral margin. The ventrolateral apophysis of *Ctenomys* adjusts to the EAM when the mandible is articulated in the postglenoid region (Fig 1; see Verzi and Olivares, 2006)
18. Mandibular diastema: (0) without a step anterior to dp4; (1) with a step anterior to dp4
19. Bottom of m1 alveolus: (0) slightly protruding in the mandible, and anterior to origin of masseteric crest; (1) forming a marked protrusion at origin of masseteric crest

Table 1. (*continued*)

20. Molars: (0) with flexi and flexids persistent in adults; (1) only with mesoflexus/id and hypoflexus/id persistent; (2) with flexi vestigial or absent, and reduced flexids; (3) with flexi/ids vestigial or absent. State 3 is a clear synapomorphy of Ctenomyidae (Verzi, 1999)
21. DP4-M2: (0) with transverse lophs; (1) eight shaped, with two transverse lobes separated by the hypoflexus and mesoflexus; (2) with posterior lobe not labially extended and without flexi
22. M3: (0) not reduced to moderately reduced, with morphology similar to remaining molars; (1) reduced, with occlusal outline subcircular and posterior lobe narrow; (2) reduced, with posterior or posterolingual face flat and anterior lobe protruding
23. Occlusal design of dp4-m2: (0) with transverse lophids; (1) figure eight-shaped; (2) subrhombic with weak labial and lingual folds (traces of flexids?), posterior lobe oriented posterolingually along greater axis of each molar; (3) crescent-shaped with a weak labial fold and a wider lingual concavity, posterior lobe of each molar more lingually oriented. The occlusal subrhombic morphology is ancestral to a more curved crescent-like shape in the *Xenodontomys* and *Eucelophorus* lineages (Verzi, 2002; Verzi et al., 2004b)
24. Posterolingual margin of anterior lobe of DP4: (0) not protruding or with a slightly rounded edge; (1) with a sharp edge
25. Implantation of m3: (0) dorsolateral to i1; (1) posterolateral or posterior, dorsal to i1

Table 2. Data matrix used in the phylogenetic analysis.

	1									2															
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5
Thrichomys	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	?	0
Octomys	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	1	0	0	0	1	1	0	1	?	0
Octodontomys	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	2	2	1	1	?	1
Xenodontomys	2	1	0	1	1	1	0	2	0	?	?	0	?	0	1	3	0	0	0	3	2	0	2	0	0
Eucelophorus	3	2	2	0	0	0	0	2	0	2	1	2	2	0	1	4	1	1	0	3	2	0	2	0	0
Praectenomys	2	3	0	1	?	0	0	2	0	?	?	?	?	1	1	2	?	0	1	3	2	2	2	0	1
Ctenomys (living)	1	3	1	1	1	0	1	2	0	1	1	1	1	1	1	2	2	1	1	3	2	2	3	1	1
C. uquiensis	?	3	1	?	?	?	?	?	?	?	?	?	?	1	1	2	2	0	1	3	2	?	3	1	1
C. chapalmalensis	1	3	1	1	1	0	0	2	0	1	1	1	1	1	1	2	2	0	1	3	2	2	3	1	1

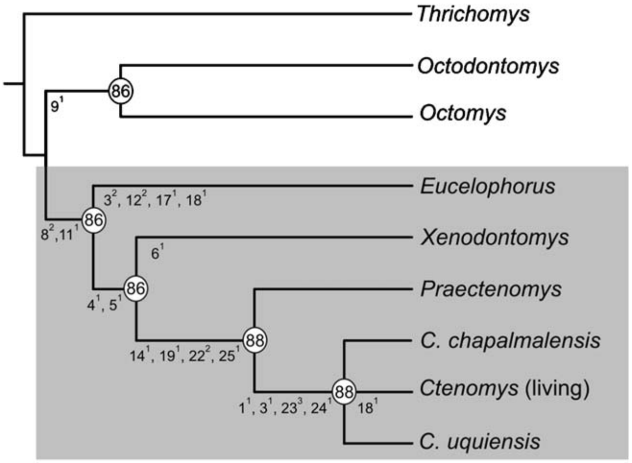

Fig. 4. Single most parsimonious tree of crown Ctenomyidae (shaded area) showing unambiguous synapomorphies. Numbers within circles internal to each node indicate relative Bremer support values resulting from evolution of 800 trees up to 31 steps longer than the optimum.

Moreover, Reig and Quintana (1992) proposed that the differentiation of the ctenomyid genera would have been linked to the acquisition of disparate adaptations to digging and life underground. In accordance with this hypothesis, Verzi (2008) applied an adaptation-rooted criterion, which involves an assessment of both the monophyly and the adaptive profiles of recognized clades (Wood and Collard 1999; Cela-Conde and Altaba 2002; Cela-Conde and Ayala 2003), to delimit lineages and genera in the fossil record of the family. According to this criterion, four cohesive lineages among crown ctenomyids (i.e. euhypsodont species of the Late Miocene to Recent) can be recognized: *Eucelophorus*, *Xenodontomys*-*Actenomys*, *Praectenomys*, and *Ctenomys* (Verzi 2008: Fig. 5). The *Xenodontomys*-*Actenomys* lineage would have had fossorial habits, while *Ctenomys* and *Eucelophorus* independently acquired craniodental specializations for subterranean life (definition of fossorial and subterranean habits follows Lessa et al. 2008); *Praectenomys* would have been at least fossorial

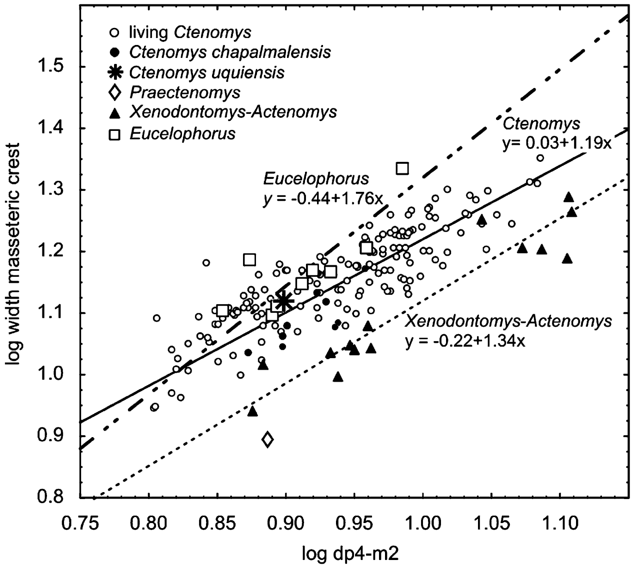

Fig. 5. Scatterplot of log-transformed width of masseteric crest at coronoid process vs dp4-m2 length in ctenomyids. Regression equations (Standard Major Axis) are shown next to each regression line.

(Fernández et al. 2000; Verzi and Olivares 2006; Vieytes et al. 2007; Lessa et al. 2008; Verzi 2008).

The species from Uquía has the same morphological specializations for tooth digging that occur in *C. chapalmalensis* and the modern *Ctenomys*. The presence of a ventrolateral apophysis of the postcondyloid process suggests the existence of a postglenoid articular region for stabilization of the mandibular condyle during digging (Verzi and Olivares 2006). Likewise, the morphology of the cavity for the base of the incisor alveolar sheath at the zygomatic root follows the same pattern as in other *Ctenomys*; this structure protects the basal generative zone of the incisor (cervical loop area, *sensu* Tummers and Thesleff 2003; see Verzi 2008: Fig. 3), which can be damaged as a result of the great pressures exerted at the incisor tips in tooth-digging species (Zuri and Terkel 2001).

Vassallo and Mora (2007: Fig. 1, Table 1) characterized the genus *Ctenomys* on the basis of an allometric trajectory in the width of the mandibular masseteric crest and the cross section of the incisors shared by living species. These authors indicated the existence of a bauplan in the mandible of living *Ctenomys*, when compared to the Pliocene ctenomyid *Actenomys* and living species of the sister family Octodontidae through analyses of static allometries. Both analyzed characters are linked to the generation of bite forces during digging, the first representing the relative development of masseter muscles (e.g. Hildebrand 1985; Stein 2000; Olivares et al. 2004).

Following the concept of this quantitative characterization of the genus, we assessed the relationship between the width of the masseteric crest and an estimator of body size in the species from Uquía compared to the remaining Ctenomyidae. Due to the limited preservation of the material, the width of the masseteric crest of the hemimandible was measured at the base of the coronoid apophysis. Although this measurement does not represent the maximum width of the masseteric crest, the landmark still fulfills a stricter homology criterion than the maximum mandibular width as classically measured. This feature was regressed onto dp4-m2 length; the latter is used here as estimator of body size because the variable 'mandibular height' previously used by Vassallo and Mora (2007) is strongly influenced by the degree of molar hypsodonty in ctenomyids. The dp4-m2 length showed good fit and isometry with respect to body mass for 43 specimens of 16 *Ctenomys* species (slope = 0.32, $r^2 = 0.7$, $p < 0.01$, Standard Major Axis).

For the genus *Ctenomys*, the width of the origin of the masseteric crest was positively allometric with respect to size (slope = 1.2, $r^2 = 0.73$, $p < 0.01$, Standard Major Axis), a result similar to the one Vassallo and Mora (2007) obtained for the maximum width of this crest. Despite the dispersion observed among the living *Ctenomys* ($n = 156$, 24 species), the existence of a characteristic *Ctenomys* pattern within the Ctenomyidae is still evident (Vassallo and Mora 2007). *Xenodontomys-Actenomys* and *P. rhombidens* were below the *Ctenomys* regression line (significantly different intercepts, $p < 0.001$; non-significantly different slopes, $p = 0.299$; statistical test not possible for *P. rhombidens*). Although the statistical tests showed significant differences between *Eucelophorus* and *Ctenomys* only in their intercepts ($p < 0.05$; non-significantly different slopes, $p = 0.136$), Fig. 5 shows a higher slope of the scaling of the masseteric crest width in *Eucelophorus*. The scatterplot shows that this feature does not by itself allow the unambiguous assignation of the new species to one of these two genera within the size interval that includes *C. uquiensis*.

Delimiting the genus *Ctenomys*

Wood and Collard (1999), Cela-Conde and Altaba (2002), and Cela-Conde and Ayala (2003) asserted the need to apply explicit adaptation-rooted criteria, involving both an assessment of the monophyly and of the adaptive profiles, for delimiting genera in the fossil record of hominids. Collard and Wood (2007) revisited the available criteria and paid particular attention to the differences between the approaches followed by Wood and Collard (1999) and Cela-Conde and Altaba (2002). According to both proposals, a genus represents a monophylum that occupies a single adaptive zone; but Cela-Conde and Altaba accept the inclusion of the most primitive (ancestral) chronomorph of a lineage, i.e. the *species germinalis*, within the same genus as the rest of the lineage, even when it has a different adaptive strategy. This is not accepted by Wood and Collard, whose proposal gives equal weight to the adaptive and phylogenetic aspects; in other words, these authors do not accept the inclusion of the ancestor of a lineage in the same genus as its descendants if it is adaptively different. In addition, they accept the possibility of adaptive similarity between different monophyla (see Collard and Wood 2007: 1584–1585).

We agree with the proposal of Collard and Wood (2007), but consider that this conceptual framework should also take into account the possibility of independent acquisition of the same adaptive strategy within an intrafamilial clade. This could be frequent in closely related taxa subjected to similar selective pressures (Gould 2002: 1088–1089; Abouheif 2008 and literature cited therein). In this case, the search for exclusive functionally significant morphological specializations can assist in the delimitation of genera (Verzi 2008).

Adaptations to subterranean life have evolved independently in different rodent groups. Related cranial specializations such as small orbits, strong zygomatic arches and wider, deeper mandibles for accommodating larger masseter muscles, and procumbent and longer incisors, are widespread among subterranean rodents, especially in those species that primarily use the head and incisors for digging (Hildebrand 1985; Nevo 1999; Stein 2000). Among ctenomyids, the subterranean *Eucelophorus* and *Ctenomys* are quite similar in these features (Verzi 2008); for instance, although the relative expansion of the masseteric crest is somewhat greater in *Eucelophorus*, this feature does not allow the delimitation of either genus within a portion of their size range. However, these genera can be delimited because they belong to different clades, and because each of them has unique specializations of the jaw joint and bottom of the upper incisor alveolar sheath, related to a common tooth-digging strategy (Verzi and Olivares 2006; Verzi 2008).

Within the monophylum formed by *P. rhombidens*, *C. chapalmalensis*, the living *Ctenomys* and *C. uquiensis*, the functionally significant morphological specializations of the condylar region and the bottom of the alveolar sheath of the upper incisor support the inclusion of the species from Uquía within the genus *Ctenomys*, as previously suggested by Verzi (2008).

P. rhombidens is not nested within the *Ctenomys* clade; although this phylogenetic position does not reject its original status of independent genus, it does not allow rejection of its belonging to *Ctenomys* either. *Praectenomys* could have had subterranean habits (Quintana 1994) like the remaining members of its clade, or been at least fossorial (Verzi 2008); however, the morphology of the bottom of the upper incisor sheath and the lesser expansion of the masseteric crest in this species support its maintenance as an independent genus. Thus, its morphological specializations, rather than its phylogenetic position and adaptive strategy, assist in its delimitation within the monophylum.

The acceptance of the ctenomyid from Uquía as an early representative of *Ctenomys* supports a minimum age for the genus close to 3.5 Ma, which is consistent with molecular estimates (3.7 Ma, Castillo et al. 2005). Uncertainty on the age of *Praectenomys* (see review of the age of Umala Formation in Cione and Tonni 1996) prevents estimation of a maximum age for the *Ctenomys* clade (see Benton and Donoghue 2007). Beyond this, the new species precedes by about one million years the presence of *C. chapalmalensis* in the Pampean region of central Argentina, the oldest record previously known for the genus. In spite of its phylogenetic position, *C. chapalmalensis* has not been linked to the origin of the genus, but considered as part of an immigration event into the Pampasia triggered by climatic changes (Verzi and Quintana 2005). On the contrary, the phylogenetic position and geographical location of *C. uquiensis*, together with those of the sister genus *Praectenomys*, agree with previous hypotheses about a probable geographical origin of tuco-tucos in the central Andes (Reig et al. 1990; Spotorno et al. 1995). Nevertheless, the complex cladogenesis and the fragmentary knowledge of the early history of this genus preclude making generalized statements in this sense. Although the morphology of *C. uquiensis* does not hinder the acceptance of its ancestral condition with respect to the remaining *Ctenomys*, the characters supplied by this species do not contribute key information about ancestral character states for the genus beyond those already known through the other Pliocene species, *C. chapalmalensis*. Thus, we suggest that the phylogenetic, adaptive and even chronological information supplied by these materials is linked to the differentiation of the genus rather than to its origin. Further knowledge of character states at the basal node of *Ctenomys* and the *Praectenomys*-*Ctenomys* clade, acquired from a *Xenodontomys*-like ancestor (see Verzi 2008: Fig. 5), still depends on the finding of key materials that shed new light on these issues.

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